Norsk. geol. tidsskr., v. 17, p. 225-336, pl. 1-18.

Sohn, I. G.

(16) 1961, *Techniques for preparation and study of fossil Ostracoda:* Treatise on Invertebrate Paleontology, R. C. Moore, ed., Arthropoda 3, Pt. Q, p. 64-70, Geol. Soc. America & Univ. Kansas Press.

Ulrich, E. O., & Cooper, G. A.

(17) 1938, *Ozarkian and Canadian Brachiopoda:* Geol. Soc. America, Spec. Paper 13, 323 p., 58 pl.

Whittard, W. F., & Sisson, J. E.

(18) 1940, *Phenol formaldehyde resin as a casting material:* Geol. Mag., v. 77, p. 478-481.

Williams, Alwyn

(19) 1956, *The calcareous shell of the Brachiopoda and its importance to their classification:* Biol. Reviews, v. 31, p. 243-287.

———, & Wright, A. D.

(20) 1961, *The origin of the loop in articulate brachiopods:* Palaeontology, v. 4, p. 149-176.

Wiman, Carl

(21) 1907, *Über die fauna des westbaltischen Leptaenkalks:* Arkiv. Zool., v. 3(24), p. 1-20, 2 pl.

SOURCE OF ILLUSTRATIONS

(22) **Williams, Alwyn,** new

SYSTEMATIC DESCRIPTIONS

By D. V. Ager, T. W. Amsden, Gertruda Biernat, A. J. Boucot, G. F. Elliott, R. E. Grant, Kotora Hatai, J. G. Johnson, D. J. McLaren, H. M. Muir-Wood, Charles W. Pitrat, A. J. Rowell, Herta Schmidt, R. D. Staton, F. G. Stehli, Alwyn Williams, and A. D. Wright

CONTENTS

BRACHIOPODA

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] [Diagnosis prepared by Alwyn Williams, The Queen's University, Belfast]

Solitary, marine, bivalved, coelomate invertebrates bilaterally symmetrical about median plane normal to surface of separation between valves; shell chitinophosphatic or calcareous, attached to substratum by muscular stalk (pedicle) or secondarily cemented or free and composed of commonly larger pedicle (ventral) valve and brachial (dorsal) valve lined by mantle extensions of body wall; epistome possibly represented by brachial fold in front of mouth, feeding organ (lophophore) filamentar, 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; circulatory system open, commonly with dorsal contractile vescicle; coelom schizocoelic or enterocoelic; mostly dioecious. *L.Cam.-Rec.*

The term "Brachiopodes" was first used by Cuvier in 1805 (208a) for the "acephalous molluscs" *Lingula, Orbicula,* and *Terebratula,* but was not formalized until 1806 when Duméril (267a) proposed Brachiopoda as an order of Mollusca. Since then it has been customary to recognize the group either as a class of the Molluscoidea or Tentaculata, having equal status with the Ectoprocta and Phoronida, or latterly as a distinct phylum. From a palaeontological viewpoint, the promotion of the Brachiopoda to a phylum is taxonomically more realistic because the group, which includes some of the oldest known fossils, has always been decisively different from other invertebrates. Admittedly, embryological studies of living forms give some indication of the relationships between brachiopods and other phyla; but these supposed affinities are much more remote than those existing between inarticulate and articulate brachiopods. Moreover, comparative morphological studies of extinct brachiopods suggest that many distinguishing features of articulate groups were gradually derived from an archetypal stock that had much in common with some living inarticulates. These characteristics probably included an organic ectodermal skeleton consisting of two unarticulated valves; a pedicle that arose simply as an extension of the ventral body wall; a recurved gut with the anus located outside a ringlike lophophore containing the mouth; one pair of metanephridia; an open circulatory system; a nervous center including a subenteric ganglion located in the mesosome, and a triple regionated body with a poorly developed protosome undergoing atrophy. It is also likely that the development of the archetypal embryo involved radial cleavage, formation of the mouth at the blastopore and the differentation of a mantle rudiment which did not undergo reversal. No confident assertion can be made about the origin of the archetypal coelom because it is schizocoelic in at least one inarticulate species and enterocoelic in articulates: but in view of the homogeneity of the phylum, it is possible that the latter condition evolved from the former.

Such an assemblage of characters underlines both the individuality of the Brachiopoda and their affinity with the other lophophorates, the Ectoprocta and Phoronida. The larvae of all three phyla are best described as modified trochophores in which the mouth arises directly from the blastopore, although in respect of the brachiopod larva, the apical tuft is the only other point of resemblance with the trochophore. The presence of a lophophore, the lack of a well-defined protosome and the location of the main nerve centers in the mesosome are also typical of the three phyla. HYMAN (441a) assumed that the "horseshoe" shape of the phoronid and phylactolaematous lophophore represents the primitive lophophorate disposition. This is unlikely, since, as in the schizolophe, which is the nearest counterpart to the "horseshoe" arrangement among the brachiopods, a double arc of filaments containing the mouth can only arise by a growth distortion of an originally circular structure like that characteristic of young brachiopods and gymnactolaematous ectoprocts; and this must have been the generalized disposition.

Despite these similarities, the Brachiopoda are unique in a number of fundamental characteristics. From both Ectoprocta and Phoronida, they differ in having an ectodermal skeleton of two valves arranged ventrodorsally, chitinous setae (not always present and possibly matched by ectoproct vibracula), a principal ganglion that is subenteric (an auxiliary supraenteric ganglion occurs in articulates), an enterocoelic coelom (in articulates only), and an imperfect separation of the "mesocoel" and "metacoel" (except in *Crania* where a dividing septum is well developed). The phylum further differs from the Ectoprocta in the possession of metanephridia and a circulatory system, and from the Phoronida in the radial cleavage of the embryo and the open nature of the circulatory system.

These comparisons illustrate the dangers of categorizing the end products of evolution without allowing for the process itself. The brachiopods are certainly more likely to have been related to the ectoprocts and phoronids than to members of any other phylum. Yet so removed are they, through time and subsequent change, from a common ancestral design that whereas the phoronids fit reasonably well into the Protostomia, the brachiopods have many features that are more characteristic of the Deuterostomia. Many authors (e.g., 441a) have described the lophophorates as intermediaries between the protostomatous and deuterostomatous invertebrates. Even among living forms, such a relationship can only be demonstrated by a selective arrangement of data; whereas phylogenetic evidence suggests that the "deuterostomatous" characteristics of the brachiopods are more likely to have evolved independently of similar traits in other phyla. Indeed, in view of the long geological record of at least the brachiopods, there is some attraction in the speculation that certain of the more problematic invertebrate phyla, like the lophophorates, were derived independently from the Protozoa.

INARTICULATA

By A. J. Rowell
[Nottingham University]

Class INARTICULATA Huxley, 1869

[Inarticulata Huxley, 1869, p. 116] [=Lyopomata Owen, 1858, p. 339; Ecardines Bronn, 1862, p. 301; Pleuropygia Bronn, 1862, p. 301; Tretenterata King, 1873, p. 15; Gastrocaulia Thomson, 1927, p. 114]

Brachiopoda with chitinophosphatic or calcareous valves, punctate or impunctate, secondary layer never completely fibrous, periostracum chitinous in living species with phosphatic shells, of protein in calcareous-shelled forms; valves commonly held together only by muscles and body wall, rarely articulated and never by hinge teeth and dental sockets; lophophore never supported by shelly outgrowths from dorsal posterior margin; muscle system for opening and closing valves consisting of adductors and obliques (latter not demonstrable in acrotretaceans and neither pair identifiable in paterinaceans) with bases commonly located peripherally in body cavity. Pedicle of living species developing from ventral mantle and inferred to have originated in same manner in extinct groups. Coelom described as schizocoelic; shell, alimentary canal, and lophophore with median tentacle developing in larval stages of growth; settling without mantle reversal. Alimentary canal with functional anus, trocholophous stage of lophophore development with single (adlabial) or double (adlabial and ablabial) row of filaments. *L.Cam.-Rec.*

The major classification of the inarticulate brachiopods and the inferred evolution both within the class and between the classes have been discussed previously, but the possibility that two of the features which are typical of inarticulate brachiopods—origin of the pedicle from the ventral mantle and absence of mantle reversal—may also have occurred in some of the earlier articulate groups is worthy of reiteration. This possibility helps to emphasize the basic unity of the phylum and suggests that the two classes arose from a common ancestor whose early stages of development were probably similar in many respects to those of a living inarticulate. The two classes have seemingly diverged from this archetypal brachiopod, the inarticulates retaining many of its features which gradually were lost in the early phases of evolution of the Articulata.

There is a complete absence of articulation between the valves of all living inarticulate brachiopods and the majority of fossil forms. The shape of the dorsal pseudointerarea of many acrotretids, however, suggests that relative rotary and sliding movements between the valves was commonly inhibited, and in at least one genus (*Linnarssonella*), these movements were eliminated by the development of deep grooves which received the dorsal edge of the posterior margin of the pedicle valve. Interlocking structures along the posterior margin of both valves also arose independently in two other lower Paleozoic stocks, the obolid *Dicellomus* and the trimerellid *Dinobolus*. The form of articulation in the latter genus is very unusual, since a ventral median socket receives a single toothlike projection from the brachial valve; but all these hinge structures are only analogous, not homologous, with those commonly developed in the articulates. The peripheral position of the muscle bases within the body cavity is probably associated with the absence of articulation and the relatively high degree of freedom of movement between the valves. A lateral position of the attachment base would, from the mechanical viewpoint, be particularly advantageous for those oblique muscles controlling relative rotary movements between the valves.

In all living inarticulate brachiopods the two mantle margins are entire and discrete; they are neither interrupted medially by the pedicle nor fused along the posterior margin, but invariably are separated from each other by inner epithelium of the body wall. This relationship is inferred to have characterized the entire class. The gross form of the shell is of course controlled by the secretory behavior of the entire margin of both mantles, although the shape of the immediate substratum or host may considerably modify the form of species attached by cementation. However, the important modifications of the pedicle valve, peripheral to the pedicle opening, are determined entirely by the secretory ability of a narrow posteromedian sector of the ventral mantle. This narrow sector is variably disposed relative to the pedicle; in *Lingula* it is but a slender fold enclosed between the valves and taking no part in their secretion, whereas in *Discina* it is well developed, lying entirely posterior of the pedicle and its shell secretion fully integrated with that of the remainder of the mantle lateral to it. The secretory ability of this narrow strip of epithelium may vary not only in different stocks but also during the ontogeny of any individual. In many genera which had the adult pedicle restricted to a foramen in the pedicle valve, it was not so constrained in younger stages of development, when the pedicle opening breached the posterior margin of the valve and the posteromedian sector of the mantle was not involved in shell secretion (e.g., *Acrothele*). The pattern of secretory behavior of this strip of epithelium is commonly constant within the larger taxa; in the lingulaceans, for example, this sector of the mantle is never associated with shell secretion, although considerable variations in some closely related stocks are observed. Thus, in trematids the pedicle opening intersects the shell margin at all stages of growth, whereas in the contemporaneous discinids, although the pedicle opening in the young stages is similar to that of the trematids, it becomes progressively isolated from the posterior margin of the shell by the secretory activity of the posteromedian sector of the mantle, and in the adult condition the posterior margin of the pedicle valve is entire. A similar variation is seen between the Recent genera *Discinisca* and *Discina* and this variation in secretory ability gives rise to one of the principal differences between the genera of the Cambrian obolellids.

The inarticulate brachiopod lophophore is never supported by a shelly outgrowth from the posterior margin of the brachial valve, but it may be inferred that the variably modified posteroventral surface of the median septum of some acrotretids may have afforded a degree of support for the mouth segment. The complex saddle-shaped plate of *Ephippelasma*, arising near the center of the brachial valve, may likewise be interpreted as a lophophore support, probably the most ambitious attempt among members of the class, but in the majority of genera the lophophore must have been unsupported by a solid skeleton and suspended freely in the mantle cavity. Spicular support, of the type developed in some terebratellaceans, is unknown in living inarticulates and there is no evidence for its existence in fossil forms. If the lophophore of extant genera provides a reliable guide, any rigidity the organ may have possessed must have been afforded by the high proportion of connective tissue and muscle, possibly aided by the hydrostatic "skeleton" of the lophophore canal system. During the ontogeny of modern inarticulates, the lophophore passes from the initial trocholophe through the schizolophous condition to culminate in a spirolophe. The only known exception is *Pelagodiscus*, whose lophophore does not advance beyond the schizolophous stage. The apices of the spires have various attitudes, and the form of the shell does not provide a very reliable guide to their disposition; thus in *Crania* the apices of the spires are dorsally directed, but those of *Discina* and *Discinisca* are inclined ventrally, although the gross form of their shell is not unlike that of *Crania*. Consideration of the relationship between size of the shell and form of the lophophore during the growth of living inarticulates (WILLIAMS & WRIGHT, 1961, 879) suggests that in the smaller fossil genera, even when adult, the organ may have been only a schizolophe, or possibly a trocholophe.

Some variation may be noted of attachment of the inarticulate brachiopods to the substratum, which is reflected in the form or even absence of the pedicle. The modern lingulids are all burrowing animals attached to the bottom of the burrow by the distal end of a long contractile pedicle; a similar habit appears to have characterized their spatula-shaped ancestors at least as far back as the Ordovician. This mode of life is seemingly a very successful adaptation for an animal which lives in shallow water or even intertidally on a soft bottom. The ability to escape from a burrow blanketed by sediment and to form a new one if the previous burrow is disturbed in any way are obvious advantages when living in an environment in which the rate of sedimentation may locally be high. Withdrawal into the burrow will moreover assist in escaping predation and reduce the hazards of desiccation if intermittently exposed between tides. Living discinids are permanently attached by a much shorter pedicle and this method of attachment probably characterized the majority of inarticulate brachiopods. Loss of the pedicle, however, was a common trend in several stocks. The craniaceans probably never possessed a pedicle at any stage of their development and there is no evidence for its existence in either the craniopsids or trimerellids; in these genera growth of the pedicle was apparently suppressed, at least during postlarval stages. In the siphonotretacean *Helmersenia*, on the other hand, a pedicle was characteristic of the younger stages of growth but atrophied during later life when the pedicle foramen was progressively plugged and ultimately closed. Many genera which lack a pedicle lay free on the sea floor, but a cemented habit was adopted to varying degree in different stocks. Some of the early craniaceans were apparently unattached, but the majority were cemented by all or part of their pedicle valve to the substratum and although this valve is unknown in the acrotretid *Undiferina*, the irregular shape of the brachial valve suggests that this also was a cemented form. Attachment by cementation was developed independently in at least one craniopsid genus *(Craniops)*, which bears a clearly defined cicatrix on the pedicle valve, but the majority of genera in the stock seemingly lay free on the sea floor, as did all the trimerellids.

Order LINGULIDA Waagen, 1885

[*nom. transl.* Kuhn, 1949, p. 99 (*ex* suborder Lingulacea Waagen, 1885, p. 754), *nom. correct.* Goryansky, 1960, p. 173 (*pro* order Lingulacea Kuhn, 1949, p. 99)] [*emend.* Rowell, herein] [=Mesokaulia Waagen, 1885, p. 754 *(partim)*; Atremata Beecher, 1891, p. 354 *(partim)*; Mesocaulia Hall & Clarke, 1894, p. 322 *(partim)*]

Shell of calcium phosphate with some layers of organic material, more rarely calcareous (Craniopsidae, Trimerellacea), very finely punctate or impunctate, biconvex, beak terminal in both valves (except in some Craniopsidae); pedicle emerging posteriorly between valves (pedicle apparently absent in Craniopsidae and Trimerellacea). [Habitat marine, but some lingulids tolerant of reduced salinity.] *L.Cam.-Rec.*

The order contains the two superfamilies Trimerellacea and Lingulacea. Many authors have recognized the superfamily Obolacea, proposed by Schuchert in 1896 for forms which are here included within the Lingulacea. There seems little justification for giving separate superfamilial status to this group (178), which differs only in relative details from the lingulids in the posterior margin of the valves, musculature, thickness of shell, and inferred length of pedicle. The superfamily name, Lingulacea, is determined by priority of the available family-group names.

Superfamily LINGULACEA Menke, 1828

[*nom. transl.* Schuchert, 1896, p. 306 (*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 phosphatic (except in Craniopsidae), usually with some layers of organic material; valves subequal, pedicle valve in many forms slightly larger, bearing pedicle groove commonly separating orthocline, striated propareas (pedicle apparently absent in Craniopsidae); posterior margin of brachial valve may be merely thickened or possess pseudointerarea extending variable distance anteriorly as concave apical plate. *L.Cam.-Rec.*

Family LINGULIDAE Menke, 1828

[*nom. correct.* Gray, 1840, p. 155 (*pro* Lingulaceae Menke, 1828, p. 56, *nom. imperf.*)] [=fam. Lingulacea Menke, 1830, p. 95]

Elongate oval to spatulate in outline, more rarely subtriangular, gently biconvex; beak of pedicle valve with broadly triangular ventral depression or groove for passage of pedicle, posterolateral margins of valve thickened, striated, lacking flexure lines, but rarely forming well-defined triangular propareas. Beak of brachial valve with small, uninterrupted pseudointerarea, not extending as a plate into the valve. Principal musculature consisting of umbonal muscle, paired centrals, transmedians, anterior, outside and middle laterals. One pair of principal mantle canals *(vascula lateralia)* in each valve. Recent species with long, flexible pedicle, lophophore spirolophous, apices of spires medianly directed. *?Ord., Sil.-Rec.*

The lower stratigraphical range of the family is not precisely known. Many Ordovician species have been loosely referred to *Lingula*, but the internal structure of the valves is unknown and in these circumstances even the family assignment is doubtful.

All Recent lingulids live in burrows and this was probably a common mode of life in the family.

Lingula Bruguière, 1797, pl. 250 [**L. anatina* Lamarck, 1801, p. 141; ICZN pend.] [=*Pharetra* Bolton, 1798, p. 159 (type, *P. monoculoides*); *Ligula* Cuvier, 1798, p. 435 *(nom. null.)*; *Ligularius* Duméril, 1806, p. 170 *(nom. van.)*; *Lingularius* Schuchert & LeVene, 1929, p. 76 *(nom. null.)*]. Elongate, lateral margins gently convex to subparallel, ornament only of concentric growth lines; shell thin, slightly thickened in areas of muscle attachment. Internally without septa, low median ridge in brachial valve may be present extending from central scars to anterior lateral scars. *?Ord., Sil.-Rec.*, cosmop.——Fig. 158,*1*. **L. anatina* Lamarck, Rec., Andaman Is.; *1a,b*, ped. v. ext., int., ×1; *1c,d*, brach. v. ext., int., ×1 (Rowell, n).

Barroisella Hall & Clarke, 1892, p. 62 [**B. campbelli* Cooper, 1942, p. 228 (*nom. subst. pro Lingula subspatulata* Meek & Worthen, 1868, p. 437, *non* Hall & Meek, 1856; OD] [=*Barroisella* Hall & Clarke, 1889, p. 43 *(nom. nud.)*]. Elongate oval in outline, ornament of concentric growth lines; in pedicle valve propareas well developed for family, small but prominent, solid; large, median, elongate triangular scar extending forward half length of valve; brachial valve with low broad median ridge, bifurcating near middle of valve, between bifurcation second low ridge intercalated, probably bearing anterior lateral scars. *U.Dev.-Miss.*, N.Am.——Fig. 158,*2*. **B. campbelli* Cooper, U.Dev., USA(Ohio, *2a*; Ind., *2b,c*); *2a*, ped.v. int., ×4; *2b,c*, brach.v. int., int. impression, ×4, ×6 (*2a,b*, Rowell, n; *2c*, 555a).

Dignomia Hall, 1871, p. 2 [**Lingula alveata* Hall, 1863, p. 23; SM Hall, 1872, pl. 13]. Relatively large, wide, thin-shelled forms, long, conspicuous median ridge in both valves, with 2 low, broadly diverging ridges that extend anterolaterally from beak. *Dev.*, N.Am.——Fig. 158,*4*. **D. alveata* (Hall), M.Dev., USA(N.Y.); brach. v. int. impression, ×1 (Rowell, n).

Glottidia Dall, 1870, p. 157 [**Lingula albida* Hinds, 1845, p. 71; OD]. Externally similar to *Lingula*, but internally with 2 low septa in pedicle valve, diverging from beak extending forward about 0.3 length of shell; brachial valve with low median septum of similar length. *Eoc.-Rec.*, N. Am.-S.Am.-Eu.——Fig. 158,*3*. *G. palmeri* Dall, Rec., USA(Calif.); *3a*, ped.v. int., ×1; *3b*, brach. v. int., ×1 (Rowell, n).

Langella Mendes, 1961, p. 1 [**Lingula imbituvensis* Oliveira, 1930, p. 18; OD]. Similar to *Barroisella*, but having much shorter dorsal median ridge and lacking anterior intercalated ridge. *Permo-Carb.*, S.Am.——Fig. 158,*5*. **L. imbituvensis* (Oliveira), Tubarâo Ser., Brazil; *5a,b*, ped. v. and brach. v. int. impressions, ×6 (555a).

Lingulipora Girty, 1898, p. 387 [**Lingula (Lingulipora) williamsana*; OD]. Elongate oval in outline, shell relatively coarsely punctate, ornament of concentric growth lines and closely spaced, fine pustules with their long axis parallel to growth lines. Internal structure unknown. *M.Dev.-U.Carb.*, N.Am.-?W.USSR.——Fig. 158,*7*. **L. williamsana* (Girty), U.Dev., USA(Va.); brach. v. ext., ×3 (Rowell, n).

Trigonoglossa Dunbar & Condra, 1932, p. 35 [**Lingula nebrascensis* Meek, 1872, p. 158; OD]. Subtrigonal in outline, valves gently convex, ornament of strongly raised concentric lines separated by broad, flat interspaces. Posterior margin of pedicle valve internally like *Lingula*. *?Dev.-Carb.*, N.Am.-Eu.——Fig. 158,*6*. **T. nebrascensis* (Meek), Penn., USA(Tex.); ped. v. ext., ×1.5 (Rowell, n).

Family OBOLIDAE King, 1846

[Obolidae King, 1846, p. 28]

Rounded, suboval or elongate in outline, ornamented by growth lines rarely becoming lamellose or spiny; propareas of pedicle valve well developed. Principal musculature consisting of umbonal muscle that may be partly or completely divided into 2 separate muscles, paired centrals, transmedians, anterior, middle and outside laterals. *Vascula lateralia* of both valves baculate, converging slightly forward; *vascula media* of brachial valve commonly diverging from anterior projection of visceral area but adequately known only in Obolinae. *L.Cam.-U.Ord.*

Subfamily OBOLINAE King, 1846

[*nom. transl.* Dall, 1870, p. 154 (*ex* Obolidae King, 1846, p. 28)]

Rounded to suboval, flexure lines on ventral propareas; dorsal pseudointerarea well developed as striated, triangular plate divided into 2 propareas by poorly defined, broadly triangular, concave median depression (848). *L.Cam.-M.Ord.*

Obolus Eichwald, 1829, p. 274 [**O. apollinis*; SD Davidson, 1853, p. 135] [=*Ungula* Pander, 1830, p. 163 (type, *U. convexa*); *Ungulites* Bronn, 1848, p. 1342 *(nom. null.)*; *Obulus* Quenstedt, 1868, p. 732 *(nom. null.)*; *Euobolus* Mickwitz, 1896, p. 129 (obj.); *Eoobolus* Matthew, 1902, p. 94 (type, *Obolus (E.) triparilis* Matthew, 1902, p. 94; SD Rowell, herein)]. Subequivalve, circular to subtriangular in outline, gently convex;

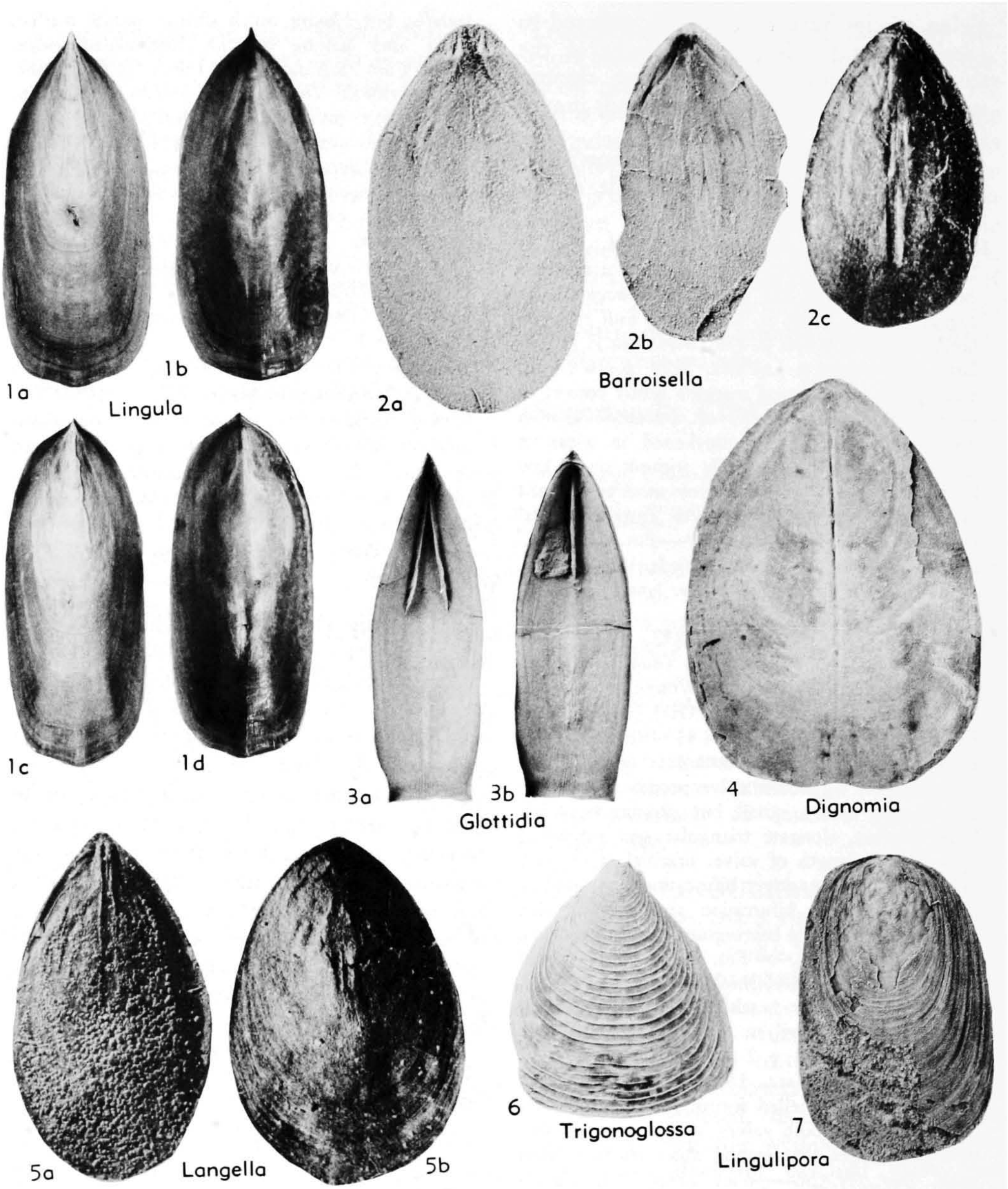

Fig. 158. Lingulidae (p. *H263*).

ornament of fine, concentric growth lines, fine radial ornament may be present; narrow, strongly defined pedicle groove; posterior half of pedicle valve thickened, indented by heart-shaped depression. Central, middle, and outside lateral muscles forming 2 composite scars anterolateral of depression, transmedians and anterior laterals forming 2 composite scars posterolateral of depression; posterior half of brachial valve thickened, anterior margin of thickening concave anteriorly; transmedians forming scars separate from combined middle and outside lateral scars, anterior lateral scars very anteriorly placed. *?L.Cam., M.Cam.-L. Ord., ?M.Ord.*, cosmop.——Fig. 159,2. **O. apollinis, L.Ord.*, Est.; *2a,b*, incompl. ped. v. ext., int., ×1.5; *2c,d*, incompl. brach. v. ext., int., ×2 (Rowell, n).

Aulonotreta Kutorga, 1848, p. 260 [**A. sculpta* (=**Obolus antiquissimus* Eichwald, 1843, p. 143); SD Hall & Clarke, 1894, p. 244] [=*Acri-*

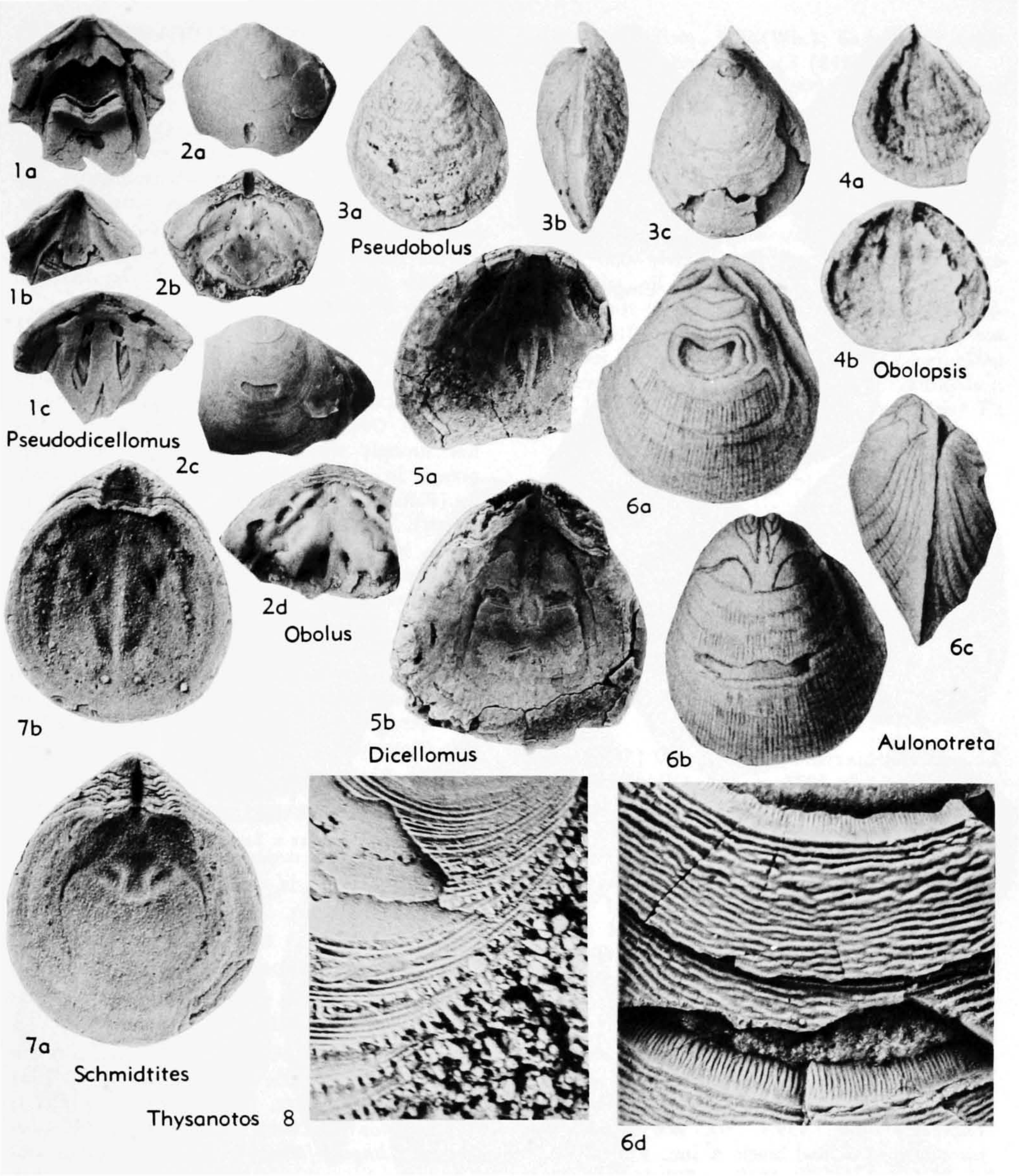

FIG. 159. Obolidae (Obolinae) (p. *H*263-*H*266).

tis VOLBORTH, 1869, p. 212 (obj.)]. Similar to *Obolus*, but concentric ornament of discontinuous, rounded, raised lines. More strongly biconvex than *Obolus* and visceral area more posteriorly placed. *L.Ord.*, Eu.(E.Baltic).——FIG. 159,6. **A. antiquissima* (EICHWALD), Est.; *6a,b*, ped. v. and brach.v. int. impressions, ×1.5; *6c*, both valves, int. impression lat., ×1.5; *6d*, detail of ornament, ×6 (*6a-c*, 848; *6d*, Rowell, n).

Dicellomus HALL, 1871, p. 3 [**Lingula polita* HALL, 1861, p. 24, proposed ROWELL, 1962, Z.N.(S.) 1504, ICZN pend.]. Small, biconvex, thick shell in 3 layers, middle layer punctate; pair of elongate, narrow grooves occupying position of propareas in brachial valve; visceral area of pedicle valve thickened; musculature similar to *Obolus*, usually well impressed. *U.Cam.(Cedaria-Crepicephalus Zones)*, N.Am.——FIG. 159,5. *D. occidentalis* BELL, USA(Mont.); *5a*, brach.v. int., ×5; *5b*, ped.v. int., incompl., ×5 (66).

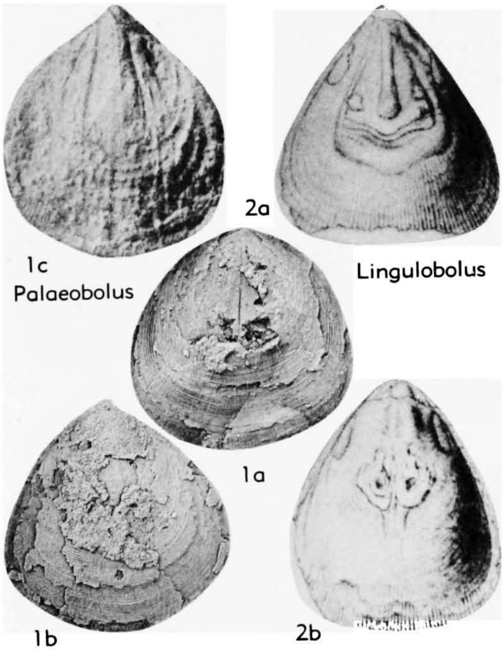

Fig. 160. Obolidae (Obolinae) (p. *H*266).

Lingulobolus Matthew, 1895, p. 260 [**Lingulella? affinis* Billings, 1872, p. 468; OD] [=*Sphaerobolus* Matthew, 1895, p. 263 (type, *Lingulella? spissa* Billings, 1872, p. 468)]. Large, oval to subtriangular in outline, strongly biconvex. Shell thick, ornament of concentric growth lines and fine radiating striae, thickened over visceral area of pedicle valve to form low platform of lamellar tissue. *L.Ord.,* N.Am.-?Eu.——Fig. 160,*2*. **L. affinis* (Billings), Newf.; *2a,b,* ped. v. and brach. v. int. impressions, ×2 (848).

?**Obolopsis** Saito, 1936, p. 349 [**O. margaritae*; OD]. Early obolids differing from *Obolus* in absence of striated pseudointerareas; posterior margins of both valves thickened. *L.Cam.,* Asia (Korea).——Fig. 159,*4*. **O. margaritae*; *4a,b,* incompl. ped. v. and brach. v. int., ×3 (703a).

Palaeobolus Matthew, 1899, p. 201 [**P. bretonensis;* OD] [=*Palaebolus* Goryansky, 1960, p. 173 *(nom. null.)*]. Suboval in outline, ventral *vascula lateralia* close together, only slightly diverging; externally similar to *Aulonotreta,* but less strongly convex and ornament more continuous. *M.Cam.,* N.Am.(N.Scotia).——Fig. 160,*1*. **P. bretonensis*; *1a,* brach. v. ext. exfoliated, ×2; *1b,c,* ped.v. ext., int. impression, both ×2 (*1c,* 848; *1a,b,* Rowell, n).

Pseudobolus Cooper, 1956, p. 194 [**Palaeoglossa gibbosa* Willard, 1928, p. 256; OD]. Slightly dorsibiconvex; similar to *Lingulobolus* externally, but lacking visceral platform in pedicle valve and musculature very poorly impressed. *M.Ord.,* N.Am.——Fig. 159,*3*. **P. gibbosus* (Willard), Murat F., USA(Va.); *3a-c,* ped. v. ext., both valves lat., brach. v. ext., all ×2 (189).

Pseudodicellomus Bell, 1962, p. 407 [**Dicellomus mosaicus* Bell, 1941, p. 216; OD]. Similar to *Dicellomus,* shell of 3 layers, middle one impunctate; pedicle groove widely triangular, external surface of valves minutely pitted. *U.Cam. (Conaspis Z.-Ptychaspis-Prosaukia Z.),* N.Am.——Fig. 159,*1*. **P. mosaicus* (Bell), USA(Tex.); *1a,b,* incompl. ped. v. int., both ×3.5; *1c,* incompl. brach. v. int., ×3.5 (67).

Schmidtites Schuchert & LeVene, 1929, p. 121 [*nom. subst. pro Schmidtia* Volborth, 1869, p. 208 (*non* Balsamo-Crivelli, 1863)] [**Schmidtia celata* Volborth, 1869, p. 209; OD]. Very similar to small *Obolus,* but posterior region of valves less strongly thickened and low median ridge present in central part of brachial valve. *L.Ord.,* Eu.(Baltic).——Fig. 159,*7*. **S. celatus* (Volborth), Tremadoc., Est.; *7a,b,* ped. v. and brach. v. int., ×6 (Rowell, n).

Thysanotos Mickwitz, 1896, p. 130 [**Obolus siluricus* Eichwald, 1843, p. 7; OD] [=*Mickwitzella* Walcott, 1908, p. 70 (obj.); *Thysanotus* Koliha, 1926, p. 317 *(nom. null.)*]. Similar to thin-shelled *Obolus* but ornament of narrow, raised concentric lines which at fairly regular intervals bear row of fine spines. *L.Ord.,* Eu.——Fig. 159,*8*. **T. siluricus* (Eichwald), Est.; detail of ornament, ×5 (Rowell, n).

Subfamily LINGULELLINAE Schuchert, 1893

[*nom. transl.* Schuchert & LeVene, 1929, p. 12 (*ex* Lingulellidae Schuchert, 1893, p. 149)]

Elongate obolids, strong flexure lines on ventral propareas, dorsal pseudointerarea well developed as striated triangular plate divided into 2 propareas by poorly defined, broadly triangular, concave median depression. *L.Cam.-U.Ord.*

Lingulella Salter, 1866, p. 333 [**Lingula davisii* M'Coy, 1851, p. 405; SD Dall, 1870, p. 159] [=*Lingulella* Salter, 1861, p. 98 *(nom. nud.)*; *Leptembolon* Mickwitz, 1896, p. 130 (type, *Obolus (L.) lingulaeformis*)]. Elongate oval to subtriangular in outline, subacuminate; thin-shelled, external ornament of concentric growth lines, inner layers of shell with fine radial striae, visceral area may be pustulose. Musculature apparently like *Obolus. L.Cam.-M.Ord., ?U.Ord.,* cosmop.——Fig. 161,*3*. **L. davisii* (M'Coy), U. Cam., Wales; *3a,* ped. v. int. impression, ×2; *3b,* brach. v. ext., ×2; *3c,d,* flattened int. impressions showing posterior margins, ped.v., brach.v., ×2 (Rowell, n).

Fordinia Walcott, 1908, p. 64 [**Obolus (Fordinia) perfectus*; OD]. Suboval outline; ornament of concentric growth lines; pedicle groove narrow, may continue as groove across thickened visceral region of pedicle valve, anterior margin of thickened area strongly concave, lateral margins bearing *vascula lateralia*; brachial valve with thickened area, posteriorly bearing broad, short median ridge, anterior of thickening low median ridge present in middle of valve. *M.Cam.-U.Cam.*, N. Am.——Fig. 161,*1*. *F. perfecta (Walcott), M. Cam., USA(Utah); *1a*, incompl. ped. v. int., ×4; *1b*, brach. v. int., ×4 (Rowell, n).

?Lingulepis Hall, 1863, p. 129 [*Lingula pinnaformis Owen, 1852, p. 583; SD Dall, 1870, p. 161]. Strongly acuminate, ventral beak elongated, valves moderately convex; ornament of concentric growth lines; shell fairly thick, inner layers punctate, radially striated. [Genus inadequately known.] *?L.Cam., U.Cam., ?L.Ord.*, N.Am.-?Greenl.-?Asia.——Fig. 161,*6*. *L. pinnaformis (Owen), U.Cam., USA(Wis.); *6a,b*, partly exfoliated ped. v., brach. v., ×3 (848).

Pseudolingula Mickwitz, 1909, p. 771 [*Crania quadrata Eichwald, 1829, p. 273; OD]. Broad, subrectangular outline, ornament of concentric growth lines. Umbonal muscle divided, producing pair of scars in both valves, remainder of musculature similar to *Obolus*. *Ord.*, N.Am.-Eu.——Fig. 161,*4*. *P. quadrata (Eichwald), U.Ord., Est.; *4a,b*, ped. v. and brach. v. ext., *4c*, both valves lat., all ×1 (Rowell, n).

Spinilingula Cooper, 1956, p. 210 [*S. intralamellata; OD]. Internally similar to *Lingulella*, but exterior lamellose, with short prone spines along anterior edge of lamellae. *M.Ord.*, N.Am.(Ala.).——Fig. 161,*2*. *S. intralamellata, Pratt Ferry F.;

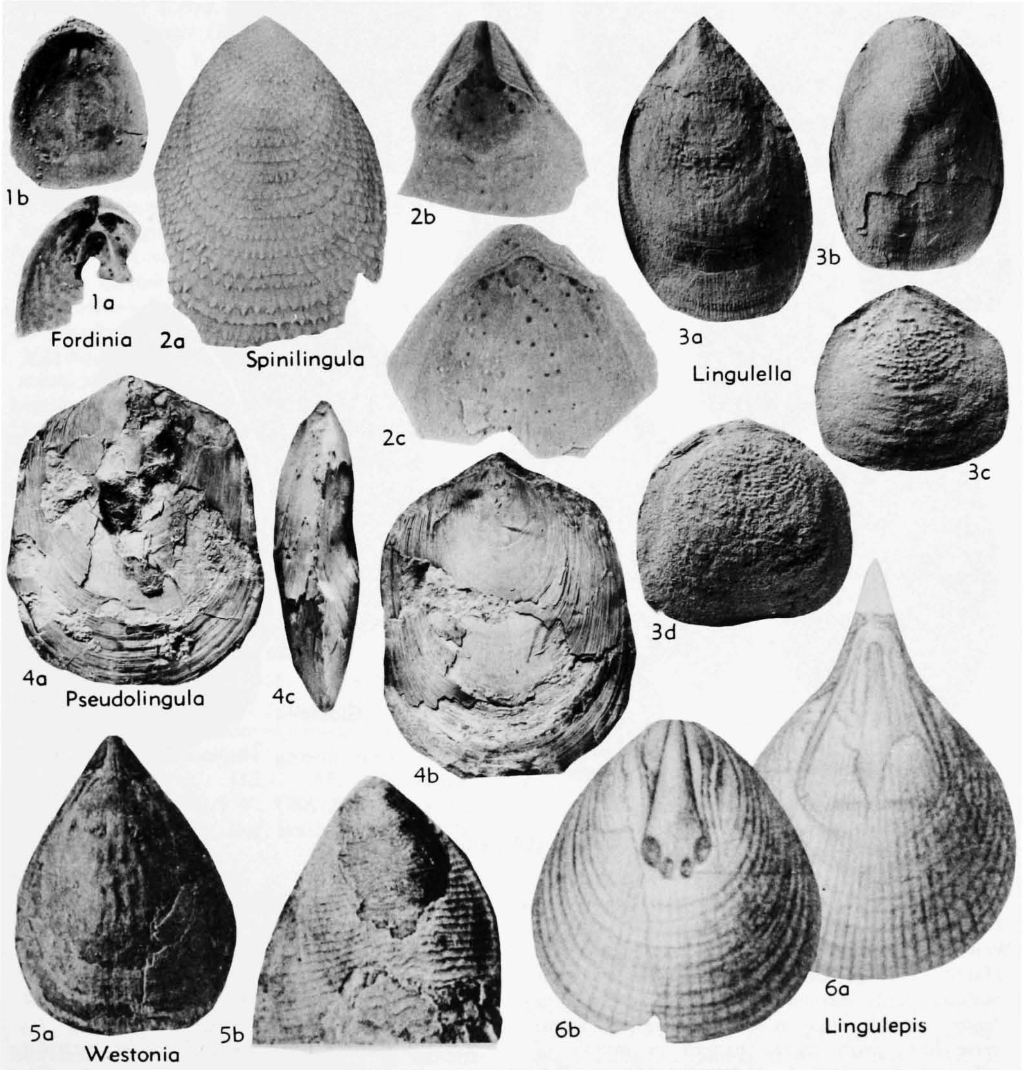

Fig. 161. Obolidae (Lingulellinae) (p. *H*266-*H*268).

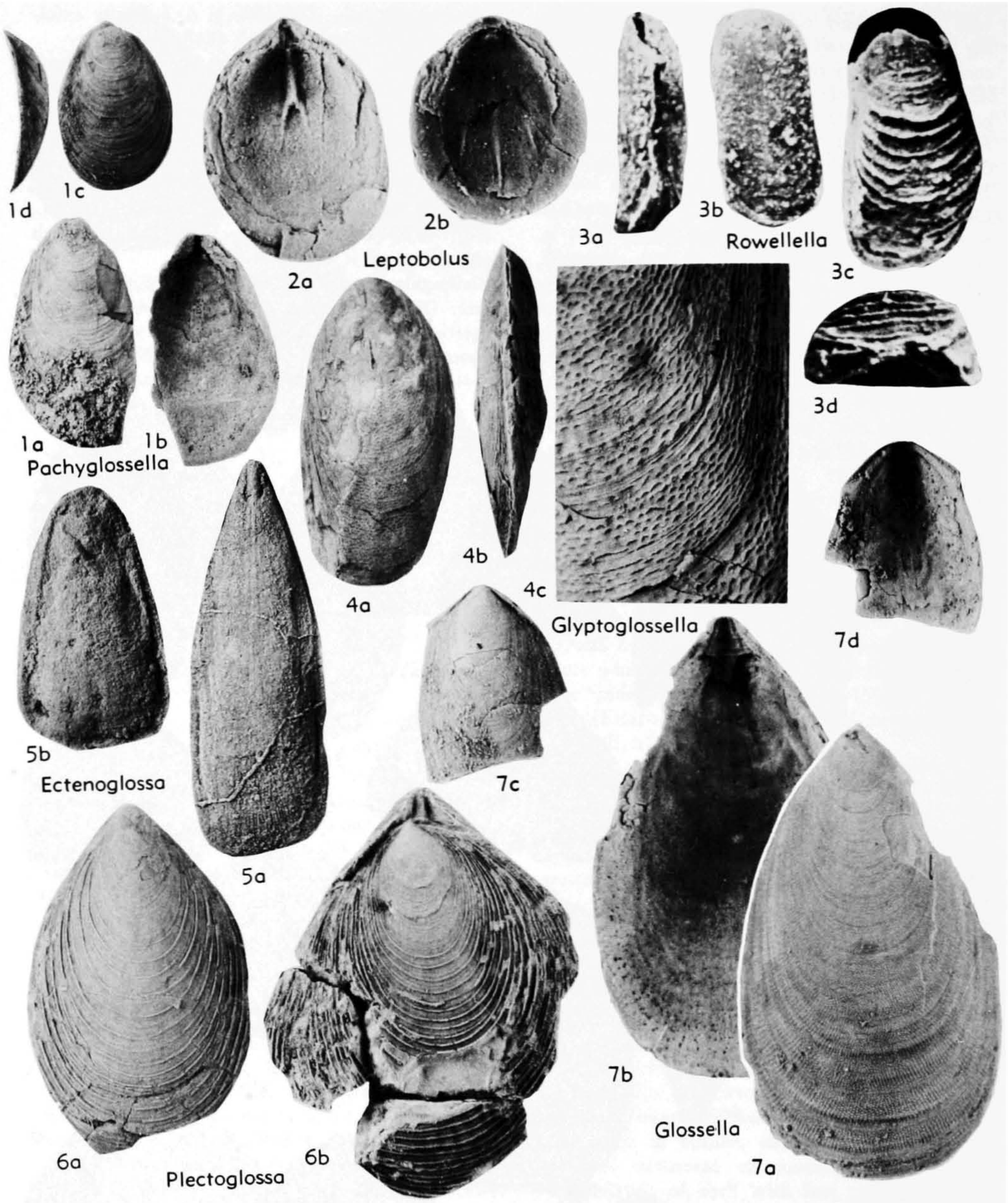

Fig. 162. Obolidae (Glossellinae) (p. *H*269).

2a, brach. v. ext., ×10; *2b,c,* incompl. ped. v. and brach.v. int., ×10 (189).

Westonia Walcott, 1901, p. 683 [**Lingula aurora* Hall, 1861, p. 24; OD]. Ovate-subtriangular outline, gently biconvex, ornament of fine concentric growth lines crossed by irregular, transverse lines, with zigzag pattern in middle of valves. *M.Cam.-M.Ord.,* N.Am.-Eu.-Asia.——Fig. 161,5. *W. linguloides* (Kobayashi), L.Ord., Alaska; *5a,* exfoliated ped. v., ×4; *5b,* detail of ornament, ×6 (825).

Subfamily GLOSSELLINAE Cooper, 1956

[Glossellinae Cooper, 1956, p. 213]

Elongate obolids, brachial valve lacking concave platelike pseudointerarea, posterior margin more or less thickened (189). *L. Ord.-U.Ord.*

Glossella Cooper, 1956, p. 228 [**G. papillosa*; OD]. Elongate oval outline, lateral margins subparallel to gently convex; ornament of concentric growth lines and radial rows of small granules similar to *Lingulasma,* but internally lacking septa or platforms; posterior margin of brachial valve sharply flexed, simulating propareas. *M.Ord.,* N.Am.-Eu. ——Fig. 162,*7*. **G. papillosa,* Pratt Ferry F., USA (Ala.); *7a,b,* ped. v. ext., int., ×5; *7c,d,* brach. v. ext., int., ×4 (189).

Ectenoglossa Sinclair, 1945, p. 63 [**Lingula lesueuri* Rouault, 1850, p. 727; OD]. Relatively long, narrow shells, lateral margins subparallel; ornament of concentric growth lines; 2 short subparallel ridges extending anteriorly from beak of pedicle valve. *L.Ord.-M.Ord.,* N.Am.-Eu.——Fig. 162,*5*. **E. lesueuri* (Rouault), L.Ord., Eu.; *5a,b,* impression ped. v. and brach. v. int., ×1.5 (Rowell, n).

Glyptoglossella Cooper, 1960, p. 601 [*nom. subst. pro Glyptoglossa* Cooper, 1956, p. 226 (*non* Brenske, 1895)] [**Glyptoglossa cavellosa* Cooper, 1956, p. 227; OD]. Elongate oval outline; ornament of concentric lamellae scalloped along their anterior margins. Muscles attached to thickened area in both valves; brachial valve with median septum extending to middle of valve. *M.Ord.,* N.Am.-Eu.——Fig. 162,*4*. **G. cavellosa* (Cooper), Shippensburg F., USA(Pa.); *4a,* brach. v. ext., ×2; *4b,* both valves lat., ×2; *4c,* brach. v. ornament, ×6 (189).

Leptobolus Hall, 1871, p. 2 [**L. lepis*; SD Dall, 1877, p. 42] [=*Leptobulus* Hall, 1871 *(nom. neg.)*]. Relatively small, suboval in outline; median ridge in pedicle valve interior extending to center of valve and forking; brachial valve interior with 1 to 3 low ridges, lateral ridges variably developed. *M.Ord.-U.Ord.,* N.Am.——Fig. 162,*2*. **L. lepis,* Trenton F., USA(Ky.); *2a,b,* ped. v. and brach. v. int., ×12 (189).

Pachyglossella Cooper, 1960, p. 601 [*nom. subst. pro Pachyglossa* Cooper, 1956, p. 223 (*non* Hodgson, 1843; *nec* Fauvel, 1868)] [**Pachyglossa dorsiconvexa* Cooper, 1956, p. 225; OD]. Elongate elliptical, strongly biconvex, thick-shelled; ornament only of concentric growth lines. *M.Ord.,* N.Am.-Eu.——Fig. 162,*1*. **P. dorsiconvexa* (Cooper), Pratt Ferry F., USA(Ala.); *1a,b,* ped. v. ext. and int., ×5; *1c,d,* brach. v. ext. and lat., ×3 (189).

Plectoglossa Cooper, 1956, p. 222 [**P. oklahomensis*; OD]. Pseudointerarea of pedicle valve divided medianly by low fold; shell suboval in outline, valves ornamented by strong, elevated concentric lines. *M.Ord.,* N.Am.——Fig. 162,*6*. **P. oklahomensis,* USA(Okla.); *6a,b,* ped. v. and brach. v. ext., ×4 (189).

Rowellella Wright, 1963, p. 233 [**R. minuta*; OD]. Small, dorsibiconvex, elongate, subrectangular shells; lateral, and to lesser extent, anterior margins of brachial valve geniculate ventrally; ornament of fairly strong concentric lamellae. Internally, dorsal muscle field limited anteriorly by low W-shaped ridge. *U.Ord.,* Eu. (Ire.).——Fig. 162,*3*. **R. minuta*; *3a,* both valves lat.; *3b,* ped. v. ext.; *3c,* brach. v. oblique ext.; *3d,* brach. v. ant.; all ×30 (895a).

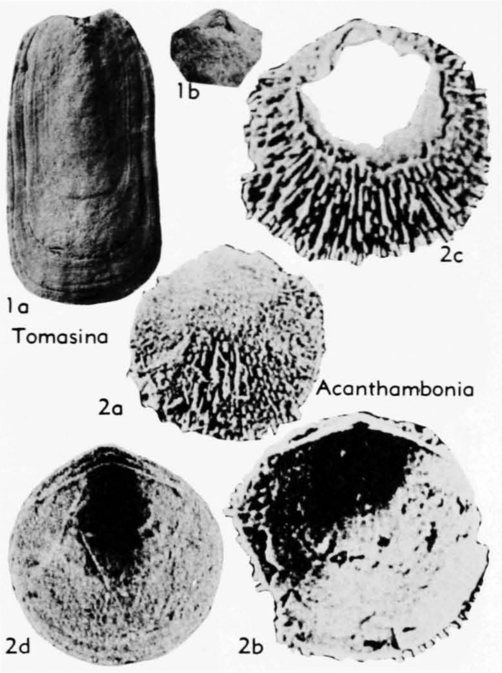

Fig. 163. Obolidae (Acanthamboniinae) *(2)*; (Subfamily Uncertain) *(1)* (p. *H*269-*H*270).

Subfamily ACANTHAMBONIINAE Cooper, 1956

[Acanthamboniinae Cooper, 1956, p. 211]

Small obolids, externally covered by abundant, minute, hairlike spines. Pedicle valve interior with narrowly triangular propareas separated by poorly developed pedicle groove, brachial pseudointerarea typical of family (189). *M.Ord.-U.Ord.*

Acanthambonia Cooper, 1956, p. 211 [**A. minutissima*; OD]. Suboval to subcircular in outline, biconvex. Muscle scars indistinguishable. *M.Ord.-U.Ord.,* N.Am.-Eu.(Ire.).——Fig. 163,*2*. *A. virginiensis* Cooper, Botetourt F., USA(Va.); *2a,b,* ped. v. ext. and int.; *2c,d,* brach. v. ext. and int., all ×15 (189).

Subfamily UNCERTAIN

Bistramia Hoek, 1912, p. 247 [**B. elegans*; OD] [=?*Pizarroa* Hoek, 1912, p. 246 (type, *P. quichuana*); *Tunarites* Cooper & Muir-Wood, 1951, p. 196 (*nom. subst. pro Tunaria* Hoek, 1912, p. 247

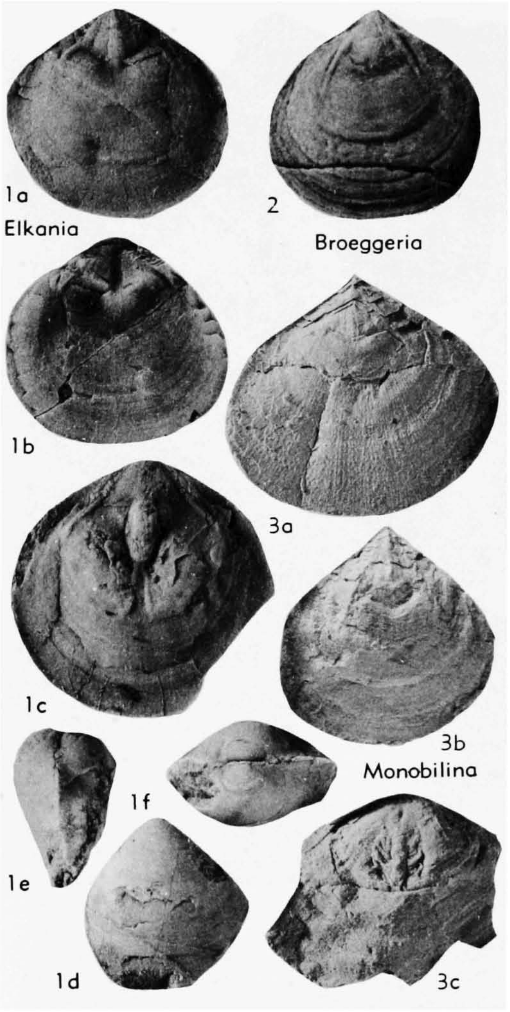

FIG. 164. Elkaniidae (p. *H*270).

(type, *Tunaria cochambina*), *non* LINK, 1807)]. Transversely oval, ornament of concentric growth lines, beak marginal; shell finely punctate. [Details of posterior margin and internal structure unknown (488).] *Ord.*, S.Am.(Bol.).

Palaeoglossa COCKERELL, 1911, p. 96 [*nom. subst. pro Glossina* PHILLIPS, 1848, p. 370 (*non* WIEDEMANN, 1830)] [**Lingula attenuata* SOWERBY, 1839, p. 641; OD] [=*Palaeoglossina* DUNBAR & CONDRA, 1932, p. 35 *(nom. null.)*]. Pedicle valve acuminate, brachial valve suboval; ornament of fine growth lines. Internal structure of genus unknown. *Ord.*, *?Sil.*, Eu.-N.Am.

Tomasina HALL & CLARKE, 1892, p. 65 [**Lingula criei* DAVIDSON, 1881, p. 372; OD] [=*Tomasina* HALL & CLARKE, 1891, p. 15 *(nom. nud.)*; *Thomasina* BIGOT, 1927, p. 721 *(nom. null.)* (*non* PAECKELMAN, 1931)]. Elongate subrectangular in outline, valves gently convex, ornament of fine concentric growth lines. Beak of pedicle valve distinctly elevated above plane of commissure, triangular opening beneath beak into which posterolateral margins of valves are strongly reflected. *L.Ord.*, Eu.——FIG. 163,*1*. **T. criei* (DAVIDSON), Sarthe; *1a*, latex impression, ped. v. int., ×1.5; *1b*, post. view latex impression ped. v. int., ×1.5 (Rowell, n).

Family ELKANIIDAE Walcott & Schuchert, 1908

[*nom. transl.* SCHUCHERT & LEVENE, 1929, p. 12 (*ex* Elkaniinae WALCOTT & SCHUCHERT, 1908, p. 144)]

Subtriangular to subcircular in outline, propareas in pedicle valve well developed, posterior region of both valves thickened by number of platelike lamellae oblique to shell surface, dorsal muscle scars commonly impressed deeply in thickened area. Ventral *vascula lateralia* diverging anterolaterally from lateral margins of thickened area, dorsal *vascula lateralia* disposed similarly to those of pedicle valve, *vascula media* diverging slightly from mid-line in front of thickened area (825). *U.Cam.-L.Ord.*

Elkania FORD, 1886, p. 325 [*nom. subst. pro Billingsia* FORD, 1886, p. 466 (*non* DE KONINCK, 1876)] [**Obolella desiderata* BILLINGS, 1862, p. 69; OD]. Ornament of concentric growth lines, moderate to strongly biconvex, beaks strongly incurved, thickened area in pedicle valve strongly developed, propareas inclined toward pedicle groove. *U.Cam.-L.Ord.*, N.Am.-?N.Afr.——FIG. 164,*1a-c*. **E. desiderata* (BILLINGS), L.Ord.(Levis Sh.), Que.; *1a,b*, ped. v. int. impression, ped. v. int., ×4; *1c*, brach. v. int. impression, ×4 (825). ——FIG. 164,*1d-f*. *E. hamburgensis* (WALCOTT), *U.Cam.*, USA(Nev.); *1d*, brach. v. ext., ×3; *1e,f*, both valves lat., post., ×4 (825).

Broeggeria WALCOTT, 1902, p. 605 [*nom. correct.* ULRICH & COOPER, 1936, p. 618 (*pro Bröggeria* WALCOTT, 1902, p. 605, *nom. imperf.*)] [**Obolella salteri* HOLL, 1865, p. 102; OD]. Similar to *Monobilina* but external shell without radial ornament. *U.Cam.-L.Ord.(Tremadoc.)*, N.Am.-Eu.-Asia(China)-?S.Am.(Arg.).——FIG. 164,*2*. **B. salteri* (HOLL), U.Cam., Eng.; ped. v. int. impression, ×6 (Rowell, n).

Monobilina SALTER, 1866, p. 334 [**Lingula plumbea* SALTER, 1859, p. 50; OD]. Similar to *Elkania* but all shell layers with fine costellate ornament, valves less convex, beak of pedicle valve more pointed, less incurved; thickened area in pedicle valve less strongly developed. *L.Ord.*, Eu.——FIG. 164,*3*. **M. plumbea* (SALTER), Wales; *3a,b*, ped. v. int. impressions, ×2: *3c*, brach. v. int. impression, ×1.5 (Rowell, n).

Family LINGULASMATIDAE Winchell & Schuchert, 1893

[Lingulasmatidae WINCHELL & SCHUCHERT, 1893, p. 149]

Medium to large lingulaceans, suboval to subrectangular in outline. Musculature of both valves borne on elevated platforms in posterior half of valve; platform of brachial valve supported anteriorly by high median septum (396). *M.Ord.-U.Ord.*

Lingulasma ULRICH, 1889, p. 383 [**L. schucherti*; OD] [=*Lingulelasma* MILLER, 1889, p. 351 (*nom. null.*)]. Ornament of growth lines and fine granules. *M.Ord.-U.Ord.*, N.Am.-Eu.——FIG. 165,*1a,b*. **L. schucherti*, Richmond F., USA(Ill.); *1a,b*, wax casts of ped. v. and brach. v. int., ×1 (Rowell, n).——FIG. 165,*1c*. *L. compactum* COOPER, Oranda F., USA(Va.); detail of ornament, ×8 (189).

Family ANDOBOLIDAE Kozlowski, 1930

[Andobolidae KOZLOWSKI, 1930, p. 301]

Medium-sized lingulaceans with very high, strongly bifid platform in brachial valve extending forward about 0.25 length of valve from beak, platform free for short distance anteriorly; lateral margins of both valves strongly thickened. *Ord.*

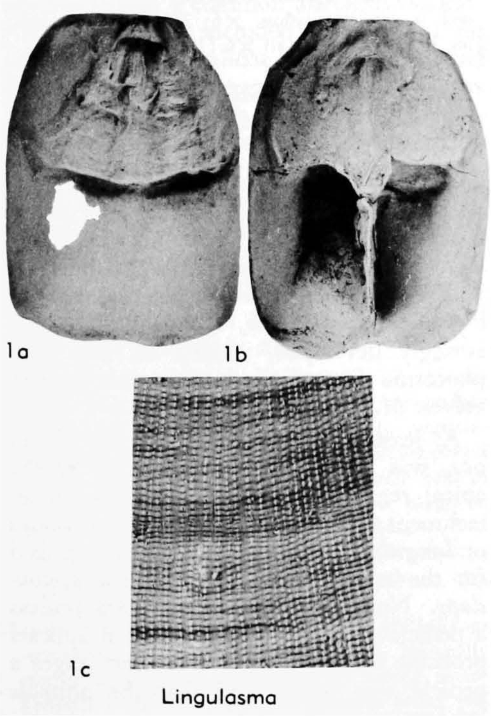

FIG. 165. Lingulasmatidae (p. *H*271).

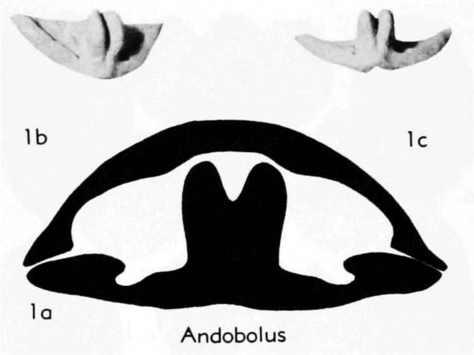

FIG. 166. Andobolidae (p. *H*271).

The systematic position of this family is somewhat doubtful, but the phosphatic shell, pedicle groove and gross form suggest that it is best regarded as an offshoot from the main obolid stock. The high platform is vaguely suggestive of the Trimerellidae, but several factors make it appear unlikely that the two families are closely related. The trimerellids are all essentially calcareous-shelled forms with platforms that differ considerably in details of morphology from those of *Andobolus*. Moreover, the contemporary Ordovician trimerellids have only very low, poorly developed platforms.

Andobolus KOZLOWSKI, 1930, p. 295 [**A. jackowskii*; OD]. Oval in outline, ventribiconvex, brachial valve almost flat posteriorly, convex in anterior third, low sulcus near beak. Pedicle valve with triangular pedicle groove and internally with broad, low, flattened median ridge. *Ord.*, S.Am. (Bol.).——FIG. 166,*1*. **A. jackowskii*; *1a*, diagram. transv. sec. through both valves, brach. v. below, ×3; *1b,c*, oblique and post. views of wax reconstruction of post. part of brach. v. based on ser. secs., ×1 (*1a*, 488; *1b,c*, Rowell, n, based on sections by Kozlowski, 488).

Family PATERULIDAE Cooper, 1956

[Paterulidae COOPER, 1956, p. 236]

Relatively small phosphatic-shelled forms; subelliptical, linguloid to subcircular in outline, gently biconvex; limbus in both valves, low pedicle groove or notch in pedicle valve (189). *Ord.-Sil.*

The musculature of the 3 genera referred to the family is imperfectly known; it appears to be basically linguloid, particularly in *Lingulops* and *Elliptoglossa*, but that of *Paterula* is farther removed from this pattern. A similar situation appears to exist

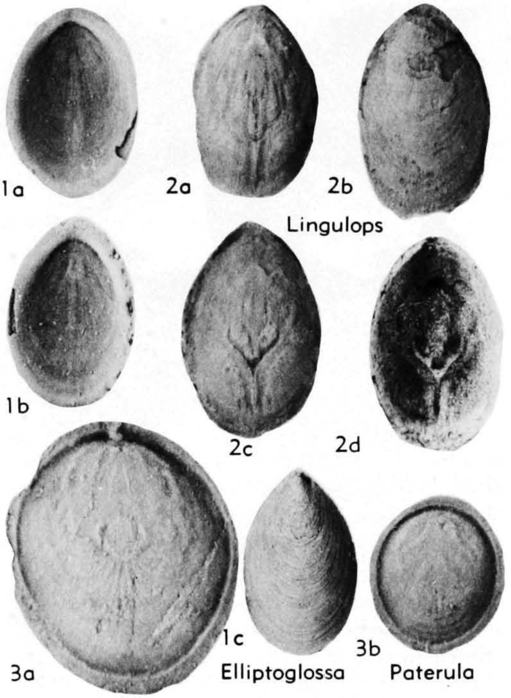

Fig. 167. Paterulidae (p. *H*272).

with the mantle canal system, although this is very poorly known. In *Lingulops* it is linguloid as far as it has been recognized, but the arrangement of the numerous fine canals in the pedicle valve of *Paterula* is unlike that of *Lingula*. It seems that *Paterula* has diverged farther than *Elliptoglossa* and *Lingulops* from the main linguloid stock, from which the family arose.

Lingulops has previously been placed with *Lingulasma* in the Lingulasmatidae. In their linguloid form, phosphatic shell, and the presence of some form of muscle platform, the two genera show some similarity. But *Lingulasma* has a very much larger shell, with characteristic beaded ornament and very high, strongly excavated platforms, the valves lacking a limbus. The presence of the latter in *Lingulops,* together with the low pedicle notch, size, and ornament, all suggest that the genus is better placed in the Paterulidae.

Paterula Barrande, 1879, p. 110 [**P. bohemica*; OD]. Shell thin, subcircular outline, brachial valve more convex than pedicle; pedicle valve with distinct pedicle notch, internally with 2 impressed lines, diverging slightly, extending to center of valve lateral of large central scar, numerous fine mantle canals radiating anteriorly and anterolaterally from central muscle scar, other muscle scars faintly impressed (189). *M.Ord.-U. Ord.,* N.Am.-Eu.——Fig. 167,*3*. *P. perfecta* Cooper, M.Ord., USA(Ala.) *(3a),* USA(Va.) *(3b)*; *3a,* ped. v. int. impression, ×15; *3b,* brach. v. int. impression, ×12 (189).

[Examinations of records indicates that *Paterula* Barrande, 1879, should be classed as a *nom. subst. pro Cyclus* Barrande, 1879, p. 110 (*non* deKoninck, 1841, p. 13) with type-species *Cyclus Bohemicus* Barrande, 1879, p. 110.]

Elliptoglossa Cooper, 1956, p. 241 [**Leptobolus? ovalis* Bassler, 1919, p. 230; OD]. Subelliptical to linguloid in outline, subequally biconvex; pedicle groove low, inconspicuous. Muscle pattern basically linguloid, but imperfectly known and faintly impressed. *L.Ord.-U.Ord.,* N.Am.-Eu.——Fig. 167,*1*. **E. ovalis* (Bassler), M.Ord., USA (Va.); *1a,* ped. v. int., ×8; *1b,c,* brach. v. int., ext., ×8 (189).

Lingulops Hall, 1872, p. 245 [**L. whitfieldi*; OD] [=*Ligulops* Hall, 1871, p. 2 *(nom. oblitum)*]. Externally like *Elliptoglossa.* In both valves anterior end of musculature borne on low platforms, that of brachial valve more strongly developed and may be slightly excavated anteriorly. Muscle pattern apparently basically linguloid, but except for anterior laterals and centrals of brachial valve poorly impressed. *Ord.-Sil.,* N.Am.——Fig. 167,*2*. *L. norwoodi* (James), M.Ord., USA(Ky.); *2a,* ped. v. int. impression, ×6; *2b-d,* brach. v. ext., int. impression, int., all ×6 (189).

Family CRANIOPSIDAE Williams, 1963

[Craniopsidae Williams, 1963, p. 346] [=Pholidopsidae Goryansky, 1960, p. 177 (*nom. nud.,* not based on valid generic name)]

Shell calcareous, impunctate, biconvex, elliptical to linguloid in outline, with strong concentric ornament, which may be lamellose, growth holoperipheral or mixoperipheral. Apparently lacking a pedicle, attached by cementation or free. Central muscle scars strongly developed, usually on low solid platform. Smooth limbus present in both valves. *M.Ord.-L.Carb.*

At least one genus in the family, *Craniops,* was attached by cementation of the apical region of the pedicle valve. An attachment scar does not occur in *Paracraniops* or *Lingulapholis* and has not been described for the rather poorly known *Pseudopholidops.* None of these three genera possess a pedicle groove or foramen and it appears probable that at least in the adult stages a pedicle was absent and that the animals lay free on the sea floor.

The taxonomic position of the family is

debatable. The genera referred to it usually have been included in the Craniacea. They agree with members of that superfamily in possessing a calcareous shell and they show a resemblance to some of them in having a limbus. Possibly, however, these characters developed independently in the two stocks. Several differences between the Craniopsidae and the Craniidae support this point of view. In the former family the shell is impunctate, lacking the arborescent punctae of the Craniidae, and the characteristic muscle and mantle-canal patterns of the craniids, which are usually well preserved, cannot be recognized in the Craniopsidae. In the latter family, moreover, the lateral margins of the body cavity are commonly well marked by narrow, very elongated scars, probably the site of attachment of dermal muscles. Among Recent genera, dermal muscles are well developed only in the lingulids and, as Huene (439) has noted, *Craniops* is internally more like *Lingula* than *Crania*. At the present time, one cannot be dogmatic, but it seems unlikely that the Craniopsidae developed from early craniaceans or that they and the craniaceans diverged from a common ancestral stock.

Cooper (189) included *Craniops* in his new family Paterulidae, which he placed in the Trimerellacea. The genus shows some similarities with the Paterulidae, particularly with *Lingulops,* which is here included in that family. However, the differences in shell composition and to a lesser extent in growth form seem to preclude *Craniops* being included in the Paterulidae and merit the retention of a separate family, of uncertain origin, but possibly derived from some *Lingulops* stock.

Craniops Hall, 1859, p. 84 [**Orbicula? squamiformis* Hall, 1843, p. 108; OD] [=*Pholidops* Hall, 1859, p. 489 (obj.)]. Attached by cementation of apical region of pedicle valve, holoperipheral growth, apices posterior of center, muscle field in both valves bounded anteriorly by low platform. *M.Ord.-L.Carb.,* N. Am.-S. Am.-Eu.-Asia.——Fig. 168,*1*. *C. implicata* (Sowerby), U.Sil.(Wenlock.); *1a,b,* ped. v. ext., int., ×6; *1c,d,* brach. v. int., ext., ×6 (Rowell, n).

Lingulapholis Schuchert, 1913, p. 295 [**Pholidops terminalis* Hall, 1859, p. 490; OD]. Internally similar to *Craniops,* but differs in having mixoperipheral growth, producing terminal beaks and well-developed pseudointerareas in both valves. No cementation attachment scar. *M.Ord.-Dev.,* N. Am.-Eu.——Fig. 168,*3*. *L. calceola* (Hall & Clarke), Dev., USA(Tenn.); *3a,* ped. v. int., ×5; *3b,c,* brach. v. ext., int., ×5 (Rowell, n).

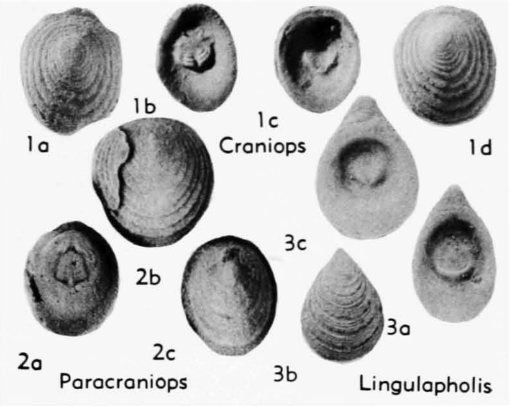

Fig. 168. Craniopsidae (p. *H*273).

Paracraniops Williams, 1963, p. 346 [**Craniops? pararia* Williams, 1962, p. 88; OD]. Outline and ornament similar to *Craniops,* differing in absence of attachment scar, of well-formed platform in brachial valve, and in presence of 2 low ridges in this valve diverging anterolaterally from apex. *M.Ord.,* Eu.-N.Am.——Fig. 168,*2*. **P. pararia* (Williams), Scot.; *2a,* ped. v. int. impression, ×4; *2b,c,* brach. v. ext., int. impression, ×4 (877).

Pseudopholidops Bekker, 1921, p. 64 [**P. scutellata*; OD]. Genus inadequately known; apparently similar to *Lingulapholis* but muscle platforms absent. *M.Ord.,* Eu.

Superfamily TRIMERELLACEA Davidson & King, 1872

[*nom. transl.* Schuchert & LeVene, 1929, p. 12 (*ex* Trimerellidae Davidson & King, 1872, p. 442)]

Large forms with thick calcareous shells, biconvex, inequivalved, elongate oval to transversely oval in outline, shell smooth except for growth lines; beak of pedicle valve prominent, pseudointerarea well developed, generally apsacline, divided into 2 propareas by triangular homeodeltidium. Internally, ventral umbo may be solid or divided into 2 umbonal chambers by cardinal buttress; muscle platforms present in both valves, solid or excavated, when excavated, cavity divided into 2 vaults by median partition that may extend anterior to platform. *M.Ord.-U.Sil.*

The musculature of this group is not well known. Both platforms appear to bear 2 or possibly 3 pairs of poorly defined scars, and additional pairs of scars occur in both valves lateral to the platform on the floor of the valve.

In *Dinobolus,* the valves possess a rudimentary form of articulation (606). A transverse plate on the posterior margin of the brachial valve fits into a corresponding depression, the cardinal socket, in the pedicle valve. No apical foramen is known and since the form of articulation prohibits the pedicle emerging between the valves the genus must have lain free on the sea floor. Other genera referred to the superfamily have not been found as well preserved as NORFORD's *Dinobolus* material, but the structure of their posterior margin, as far as known, is consistent with their having similar articulation.

Family TRIMERELLIDAE
Davidson & King, 1872

[Trimerellidae DAVIDSON & KING, 1872, p. 442]

Characters of superfamily (245). *M.Ord.-U.Sil.*

Trimerella BILLINGS, 1862, p. 166 [**T. grandis*; SD DALL, 1870, p. 160] [=*Gotlandia* DALL, 1870, p. 160 (type, *G. lindstroemi*)]. Large for family, elongate oval in outline, pseudointerarea of pedicle valve high, cardinal buttress broad, not extending onto ventral platform, umbonal cavities small or absent; platforms in both valves well developed, deeply vaulted, vaults separated by median partition that extends anterior to platform. *Sil.,* N.Am.-Eu.(Gotl.).——FIG. 169,*2a-d.* **T. grandis,* M.Sil., Ont.; *2a,b,* ped. v. int., int. impression, ×0.7; *2c,d,* brach. v. int., int. impression, ×0.7 (245).——FIG. 169,*2e. T. ohioensis* MEEK, M.Sil., USA(Ohio); ext. (restored), ×0.7 (396).

Dinobolus HALL, 1871, p. 4 [**Obolus conradi* HALL, 1868, p. 368; OD] [=*Conradia* HALL, 1872, p. 107 (obj.)]. Pseudointerarea of pedicle valve relatively low, umbo solid or small umbonal cavities separated by cardinal buttress; ventral platform hollow anteriorly, vaults small, supporting median partition broadly triangular posteriorly, narrowing anteriorly; dorsal platform vaulted anteriorly, supported by short median ridge. *L.Sil.-U.Sil.,* Eu.-N.Am.——FIG. 169,*5.* **D. conradi* (HALL), M.Sil., Wis. *(5a,b),* Iowa *(5c)*; *5a,b,* ped. v. int., int. impression, ×1; *5c,* brach. v. int. impression, ×1 (396).

Eodinobolus ROWELL, 1963, p. 37 [**Obolellina magnifica* BILLINGS, 1872, p. 329; OD]. Early trimerellids, externally like *Dinobolus* but platforms not vaulted, dorsal platform very low, median ridges poorly developed or absent, umbo of pedicle valve solid. *M.Ord.-U.Ord.,* N.Am.-Eu.——FIG. 169,*3.* **E. magnificus* (BILLINGS), M. Ord. (Rockland F.), Ont.; *3a,* ped. v. ext., ×1; *3b,c,* brach. v. ext., int., ×1 (189).

Monomerella BILLINGS, 1871, p. 220 [**M. prisca*; SD DAVIDSON & KING, 1874, p. 155]. Cardinal buttress well developed, extending forward nearly to front of platform, umbonal cavities deep, tubular. Ventral platform solid, widest anteriorly where it is slightly excavated, median ridge short or absent. Dorsal platform similar to *Dinobolus. Sil.,* N.Am.-NW.Eu.-?Asia(Kazakhstan).——FIG. 169,*4.* **M. prisca,* M.Sil., USA(Ill.); *4a,b,* ped.v. int., int. impression, ×1; *4c,* brach. v. int. impression, ×1 (396).

Rhynobolus HALL, 1871, p. 5 [**Obolus galtensis* BILLINGS, 1862, p. 168; SD DALL, 1877, p. 61] [=*Obolellina* BILLINGS, 1871, p. 222 (obj.); *Rhinobolus* HALL & CLARKE, 1892, p. 44 *(nom. van.)*]. Elongate oval in outline, pseudointerarea of pedicle valve high, platform inconspicuous posteriorly, anteriorly V-shaped in outline, steeply inclined posteriorly, umbo solid; dorsal platform low, not excavated, low median ridge may be present anterior to platform. *M.Sil.,* N.Am.-?Asia (Kazakhstan).——FIG. 169,*1.* **R. galtensis* (BILLINGS), Ont.; *1a,b,* ped. v. int., brach. v. int., ×1 (396).

Order ACROTRETIDA
Kuhn, 1949

[*nom. correct.* GORYANSKY, 1960, p. 178 (*pro* order Acrotretacea KUHN, 1949, p. 101)] [emend. ROWELL, herein] [=Daikaulia WAAGEN, 1885, p. 748 *(partim)*+Gasteropegmata WAAGEN, 1885, p. 744 *(partim)*; Neotremata BEECHER, 1891, p. 354 *(partim)*]

Usually circular or subcircular in outline, shell phosphatic or punctate calcareous; pedicle opening, when present, confined to pedicle valve, growth of pedicle valve holoperipheral or mixoperipheral; shell secretion of brachial valve more variable, beak marginal to subcentral. *L.Cam.-Rec.*

The original concept of the order has been extended to include the craniaceans and the phosphatic-shelled genera which ROWELL (680) grouped in the Siphonotretacea.

Suborder ACROTRETIDINA
Kuhn, 1949

[*nom. transl.* ROWELL, herein (*ex* order Acrotretida KUHN, 1949, p. 101)] [=Daikaulia WAAGEN, 1885, p. 748 *(partim)*; Discinacea WAAGEN, 1885, p. 748 *(partim)*; Diacaulia HALL & CLARKE, 1894, p. 323 *(partim)*]

Shell phosphatic, usually attached by pedicle throughout life. *L.Cam.-Rec.*

Superfamily ACROTRETACEA
Schuchert, 1893

[*nom. transl.* SCHUCHERT, 1896, p. 308 (*ex* Acrotretidae SCHUCHERT, 1893, p. 150)]

Pedicle valve commonly conical to subconical, more rarely convex, pseudointerarea

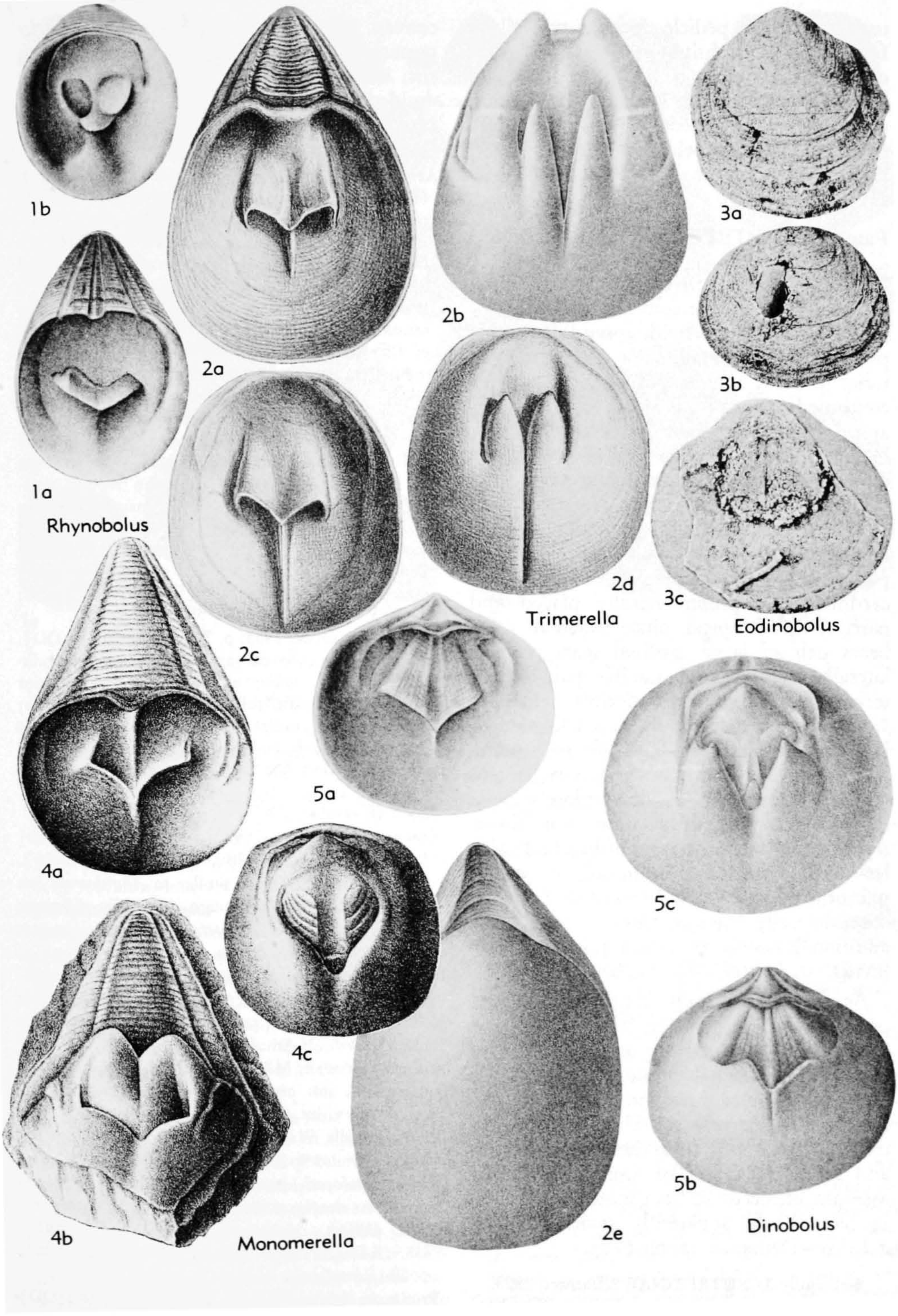

FIG. 169. Trimerellidae (p. *H*274).

usually present; pedicle opening typically a foramen at or slightly posterior to beak, less commonly an open triangular delthyrium; brachial valve usually with marginal beak, more rarely low cone (Conodiscinae); propareas variably developed; dorsal median ridge or septum usually present (189, 848). *L.Cam.-Dev.*

Family ACROTRETIDAE Schuchert, 1893

[Acrotretidae SCHUCHERT, 1893, p. 150]

Generally small to minute; pseudointerarea of pedicle valve commonly divided by intertrough or deltoid pseudointerarea; pedicle foramen small, at or somewhat posterior to beak, may be simple perforation or continued internally as some form of tube, apical process present in many species; brachial valve gently convex to gently concave, marginal beak, pseudointerarea well developed to obsolescent, anacline to orthocline, median septum usually present, may be merely a ridge or absent. Muscle scars of pedicle valve include pair of relatively large cardinal scars posterolaterally placed and pair of small apical pits. Brachial valve bears pair of large cardinal scars posterolaterally situated and smaller pair of anterior scars close together, near center of valve; another more doubtful scar is medially placed immediately in front of pseudointerarea. Ventral mantle canal system typically consists of pair of baculate *vascula lateralia* (more rarely pinnate as in *Conotreta*); mantle canal system of brachial valve less well known but commonly comprises pair of baculate *vascula lateralia* that diverge anterolaterally from in front of beak, with additional, poorly impressed pair of *vascula media*. *L.Cam.-U.Sil., ?L.Dev.*

Acrotretids definitely range into the Upper Silurian (Chimney Hill Limestone, Oklahoma) in North America and Upper Silurian (Wenlock Limestone) in England, but the upper stratigraphic limit is not satisfactorily determined. Undoubted acrotretids, known only from their pedicle valves and as yet incapable of more than family assignment, occur in float material collected in New York, apparently associated with a Lower Devonian fauna (70).

Subfamily ACROTRETINAE Schuchert, 1893

[*nom. transl.* MATTHEW, 1903, p. 74 (*ex* Acrotretidae SCHUCHERT, 1893, p. 150)]

Pedicle valve usually conical, more rarely convex, foramen circular at or immediately posterior to beak, apical process usually present; dorsal pseudointerarea well developed, divided into 2 propareas by triangular, concave median groove. *?L.Cam., M.Cam.-U.Ord.*

Acrotreta KUTORGA, 1848, p. 260 [**A. subconica*; SD DAVIDSON, 1853, p. 133]. Pedicle valve high, procline to catacline, with well-marked intertrough, internal structure unknown (848). [Genus inadequately known. Type material destroyed during World War II and satisfactory topotype material not yet found (GORYANSKY, personal communication, 1961). May be a senior synonym of *Conotreta.*] *?U.Cam., Ord.,* Eu.-?N.Am.-?Asia.

Angulotreta PALMER, 1955, p. 769 [**A. triangularis*; OD]. Pedicle valve moderately high, procline to catacline, narrow deltoid pseudointerarea present, internal pedicle opening at apex, apical process well developed, long, mainly on anterior slope of valve; in brachial valve median septum variably developed, strong to weak, may be digitate, posteriorly buttressing median groove. *U.Cam.,* N. Am.——FIG. 170,*1*. **A. triangularis, Aphelaspis* Zone, USA(Tex.); *1a-d,* ped. v. ext., lat., post., int., all ×10; *1e,* brach. v. int., ×10 (*1a-c,e,* 635a; *1d,* 67).

Apsotreta PALMER, 1955, p. 770 [**A. expansa*; OD]. Pedicle valve convex, apsacline, deltoid pseudointerarea low, wide; apical process on anterior slope, long, parallel-sided or expanding anteriorly; brachial valve similar to *Angulotreta,* septum not digitate. *U.Cam.,* N.Am.——FIG. 170,*2*. **A. expansa, Dunderbergia* Z. (USA(Tex.); *2a-d,* ped. v. ext., lat., post., int., all ×15; *2e,* brach. v. int., ×15 (Rowell, n).

Conotreta WALCOTT, 1889, p. 365 [**C. rusti*; OD] [=*Geinitzia* HALL, 1889, p. 43 *(nom. nud.)*]. Pedicle valve externally similar to *Angulotreta* but usually with fine intertrough, internally different, having pinnate *vascula lateralia* and apical process a large boss on anterior slope of valve which bounds internal pedicle opening anteriorly; brachial valve similar to *Angulotreta,* but propareas less well developed and cardinal scars more medianly placed. *Ord.,* N.Am.-Eu.——FIG. 170,*4*. *C. multisinuata* COOPER, M.Ord., USA(Va.); *4a-d,* ped. v. post., lat., int. cast, int. apical region, all ×6; *4e,* brach. v. int., ×10 (189).

Linnarssonella WALCOTT, 1902, p. 601 [**L. girtyi*; OD]. Similar to *Apsotreta* but apical process less well developed, posterolateral margins of dorsal propareas deeply grooved and median septum absent. *U.Cam.,* N.Am.——FIG. 170,*5*. **L. girtyi,* USA(S.Dak.); *5a,b,* ped. v. and brach. v. int., ×10 (Rowell, n).

Prototreta BELL, 1938, p. 405 [**P. trapeza*; OD] [=*Homotreta* BELL, 1941, p. 230 (type, *H. interrupta* BELL, 1941, p. 230)]. Similar to *Angulo-*

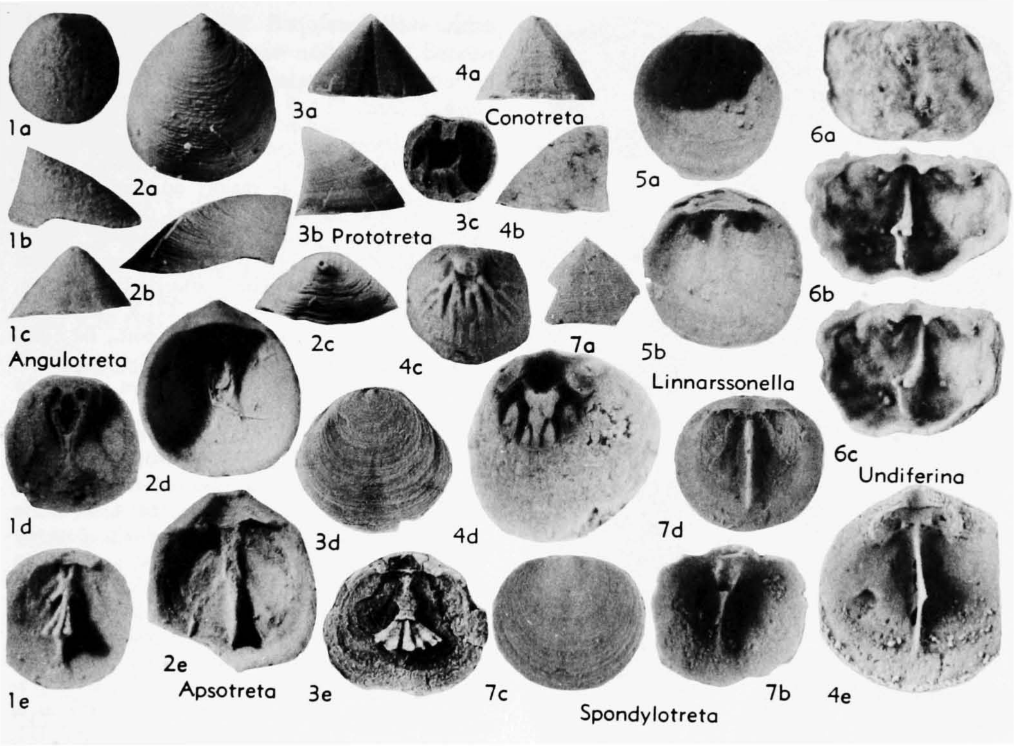

FIG. 170. Acrotretidae (Acrotretinae) (p. *H276-H277*).

treta, but pseudointerarea of pedicle valve divided by well-marked intertrough, internal pedicle foramen opening through apical process on posterior slope of valve. *?L.Cam., M.Cam.,* N.Am.-Eu.-Asia.——FIG. 170,*3*. **P. trapeza, M.Cam.,* USA(Mont.); *3a-c,* ped. v. post., lat., int. apical region, ×6, ×6, ×8; *3d,e,* brach. v. ext., int., ×6 (65).

Spondylotreta COOPER, 1956, p. 255 [**S. concentrica*; OD]. Ornament of fine, elevated concentric lines, pedicle valve procline; pedicle tube on inner posterior surface of valve, continued as forked ridge, supported apically by median septum; brachial valve gently concave, internally similar to *Angulotreta* but septum not digitate nor buttressing median groove. *M.Ord.-U.Ord.,* N. Am.-Eu.(Ire.).——FIG. 170,*7*. **S. concentrica,* Pratt Ferry F., USA(Ala.); *7a,b,* ped. v. post., int., ×6, ×10; *7c,d,* brach. v. ext., int., ×6 (189).

Undiferina COOPER, 1956, p. 262 [**U. rugosa*; OD]. Pedicle valve unknown, possibly cemented form; brachial valve convex, subrectangular outline, ornament of irregular wrinkles, concave median groove, not buttressed by septum, separating short, well-developed propareas, septum strong, highest anteriorly, ventral edge may bear slightly digitate plate. *M.Ord.,* N.Am.(Ala.).——FIG. 170,*6*. **U. rugosa*; *6a-c,* brach. v. ext., int., int., ×8 (189).

Subfamily LINNARSSONIINAE Rowell, n. subfam.

Pedicle valve depressed conical to convex, foramen circular at or immediately posterior to beak, apical process anterior of internal pedicle opening; median groove in brachial valve small, propareas obsolescent. *L.Cam.-U.Cam.*

Linnarssonia WALCOTT, 1885, p. 115 [**Obolella transversa* HARTT, 1868, p. 644; OD] [=*Pegmatreta* BELL, 1941, p. 231 (type, *P. perplexa*)]. Pedicle valve a relatively low cone, procline rarely apsacline, apex thickened by callosity anterior to internal pedicle foramen, subcircular in outline, extending slightly on to anterior slope of valve; brachial valve with small median groove, propareas minute or absent, low median ridge. *L.Cam.-M. Cam., ?U.Cam.,* N.Am.-Eu.——FIG. 171,*2*. *L. sagittalis* (DAVIDSON), M.Cam., Wales; *2a,b,* ped. v. and brach. v. int. impressions, ×4 (Rowell, n).

Acrothyra MATTHEW, 1901, p. 303 [**Acrotreta proavia* MATTHEW, 1899, p. 203; SD WALCOTT, 1912, p. 716]. Elongate, strongly apsacline, pseudointerarea long, divided by intertrough; apical process on anterior slope of valve, elongate, expanding anteriorly, depressed in center, bounded by raised rim; brachial valve with median ridge. *M.Cam.,* N.Am.

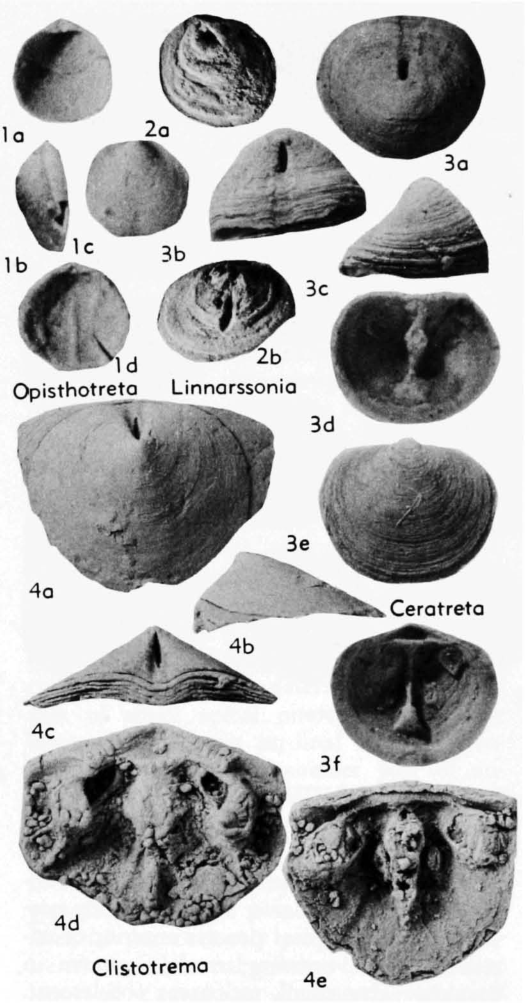

FIG. 171. Acrotretidae (Linnarssoniinae) *(1-2)*, (Ceratretinae) *(3-4)* (p. *H277-H278*).

Opisthotreta PALMER, 1955, p. 771 [**O. depressa*; OD]. Subcircular, pedicle valve low, apsacline, pseudointerarea small, concave; apical process very low, anteriorly expanding on anterior slope of valve; brachial valve with pitlike median groove, minute propareas and low median ridge. *U.Cam.*, N.Am.——FIG. 171,*1*. **O. depressa*, USA(Tex.); *1a*, ped. v. int.; *1b*, both valves lat.; *1c,d*, brach. v. ext., int., all ×15 (635a).

Subfamily CERATRETINAE Rowell, n. subfam.

Thick-shelled, pedicle valve conical, obtuse or rounded apex, intertrough well developed, external pedicle foramen elongated, apical process a ridge or buttress connecting anterior and posterior slopes of valve, bearing internal pedicle opening; brachial valve with well-developed median groove buttressed by median septum, propareas moderately well developed to obsolescent. *U. Cam.-L.Ord.*

Ceratreta BELL, 1941, p. 233 [**C. hebes*; OD]. Pedicle valve bluntly conical, procline; apical process a strong ridge mainly on posterior slope of valve, internal pedicle opening on ridge about halfway down posterior slope, median groove in brachial valve large, propareas absent, median septum abruptly pointed anteriorly. *U.Cam.* (*Conaspis* Z.), N.Am.——FIG. 171,*3*. **C. hebes*, USA(Mont.); *3a-d*, ped. v. ext., post., lat., int., ×12; *3e,f*, brach. v. ext., int., ×12 (Rowell, n).

Clistotrema ROWELL, 1963, p. 35 [*nom. subst. pro Orbicella* D'ORBIGNY, 1847, p. 269 (*non* DANA, 1846)] [**Orbicula buchii* DE VERNEUIL, 1845, p. 288; OD]. Large, very thick-shelled; pedicle valve obtusely conical, procline, pseudointerarea poorly defined, intertrough deep, external foramen in intertrough, one third distance down posterior slope; internal pedicle opening dorsally placed on extremely massive apical process which fills apical part of valve, extending as broad buttress across valve, widest anterior of internal pedicle opening, projecting into brachial valve. Muscle scars elevated on lamellar shell. Brachial valve with anacline propareas, cardinal muscle scars elevated as in pedicle valve. *L.Ord.*, USSR(N.W.).——FIG. 171, *4*. **C. buchii* (DE VERNEUIL), Tremadoc., Est.; *4a-c, e*, ped. v. ext. lat., post., int., ×5; *4d*, brach. v. int. ×5 (Rowell, n).

Subfamily SCAPHELASMATINAE Rowell, n. subfam.

Obtusely conical or conical with rounded apex. Intertrough usually well developed, foramen immediately posterior to apex; apical process a very low swelling, mainly anterior to foramen or absent. Brachial valve with median groove not buttressed by septum. Propareas variable, never large. [Possibly derived from the Ceratretinae.] *M.Ord.-U.Sil.*

Scaphelasma COOPER, 1956, p. 259 [**S. septatum*; OD]. Ornament lamellose peripherally; pedicle valve obtusely conical, foramen a short slit, apical process a low swelling nearly surrounding foramen; triangular median septum arising near center of valve. *M.Ord., ?U.Ord.*, N.Am.(Ala.)-?Eu.(Ire.).——FIG. 172,*1*. **S. septatum*, Pratt Ferry F., USA(Ala.); *1a-d*, ped. v. ext., post., lat., int., ×10; *1e,f*, brach. v. ext., int., ×10 (189).

Artiotreta IRELAND, 1961, p. 1138 [**A. parva*; OD]. Minute, thin-shelled; pedicle valve obtusely conical, foramen circular, internally pedicle apex slightly thickened anterior of foramen; brachial valve similar to *Scaphelasma* but median groove minute and propareas absent. *U.Sil.*, N.Am.

(Okla.).——Fig. 172,*2*. **A. parva,* Chimneyhill; *2a-c,* ped.v. ext., post., lat., ×40; *2d,e,* brach.v. int., ext., ×40 (Rowell, n).

?Rhysotreta Cooper, 1956, p. 258 [**R. corrugata*; OD]. Ornament of strong concentric rings; pedicle valve high, procline to catacline, foramen slightly posterior to apex, tear-shaped, no apical process; brachial valve concave, large pseudointerarea seemingly undivided, high median septum arising in front of beak. *M.Ord.,* N.Am.(Ala.).——Fig. 172,*3*. **R. corrugata,* Pratt Ferry F.; *3a,b,* ped.v. post., lat., ×10; *3c-e,* brach. v. int., int. oblique, lat., ×10 (189).

Subfamily TORYNELASMATINAE Rowell, n. subfam.

Pedicle valve conical with apical foramen minute, lacking apical process; brachial valve with undivided pseudointerarea, median septum arising slightly anterior to beak bearing shallow concave plate on its posteroventral edge. *M.Ord., ?U.Sil.*

Torynelasma Cooper, 1956, p. 257 [**T. toryniferum*; OD]. Pedicle valve acutely conical, apsacline, similar to *Acrothyra* but lacking apical process and well-defined pseudointerarea. Concave plate on median septum well developed. *M.Ord.,* N.Am. (Ala.).——Fig. 172,*5*. **T. toryniferum,* Pratt Ferry F.; *5a,b,* ped. v. post., lat., ×8; *5c-e,* brach. v. ext., int., lat., ×10 (189).

?Acrotretella Ireland, 1961, p. 1139 [**A. siluriana*; OD]. Pedicle valve procline, pseudointerarea undivided; brachial valve with small pseudointerarea and delicate concave-plate on septum. *U.Sil.,* N. Am.(Okla.)-?Eu.(Eng.).——Fig. 172,*4*. **A. siluriana,* Chimneyhill, USA(Okla.); *4a,b,* ped.v. ext., lat., ×25; *4c,d,* brach.v. ext., int., ×25 (445a).

Subfamily EPHIPPELASMATINAE Rowell, n. subfam.

Pedicle valve conical, lacking apical process, foramen circular, apical; brachial valve with pitlike median groove, minute proareas, and complex saddle-like plate arising in front of beak and attached only at its posterior end. *M.Ord., ?U.Ord.*

Ephippelasma Cooper, 1956, p. 261 [**E. minutum*; OD]. Minute, pedicle valve high, catacline to apsacline, beak prominent, intertrough indistinct; brachial valve concave. *M.Ord., ?U.Ord.,* N.Am. (Ala.)-?Eu.(Ire.).——Fig. 172,*6*. **E. minutum,* Pratt Ferry F., USA(Ala.); *6a,* ped. v. post., ×20; *6b-d,* brach. v. ext., int., int. lat., ×20, ×15, ×15; *6e,* int. ped. v. and brach. v. lat., ×20 (189).

Subfamily UNCERTAIN

Hisingerella Henningsmoen, 1948, p. 388 [**Atrypa? nitens* Hisinger, 1838, p. 77; OD]. Fine concentric ornament; pedicle valve a low cone, procline, narrow deltoid pseudointerarea, internal structure unknown except for long median ridge in brachial valve extending forward from beak. [Genus inadequately known.] *U.Ord.,* Scand.

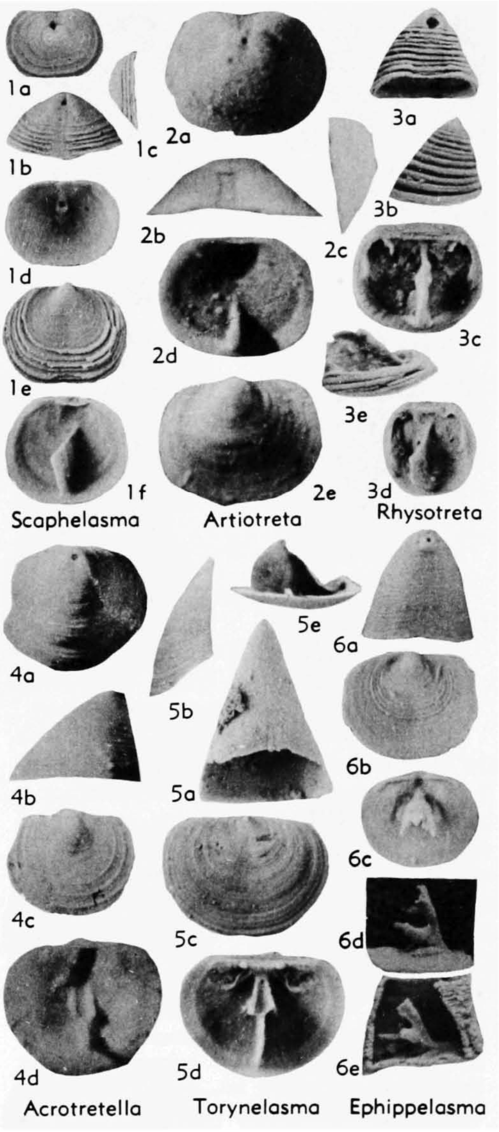

Fig. 172. Acrotretidae (Scaphelasmatinae) *(1-3)*, (Torynelasmatinae) *(4-5)*, (Ephippelasmatinae) *(6)* (p. *H278-H279*).

Keyserlingia Pander, 1861, col. 46 [**Orbicula reversa* de Verneuil, 1845, p. 289; SD Dall, 1871, p. 75] [=*Kayserlingia* Beecher, 1891, p. 354 *(nom. null.)*]. Small acrotretid, genus virtually unknown; pedicle valve subconical, with centrally placed apex. *L.Ord.,* Eu.(NW.USSR).

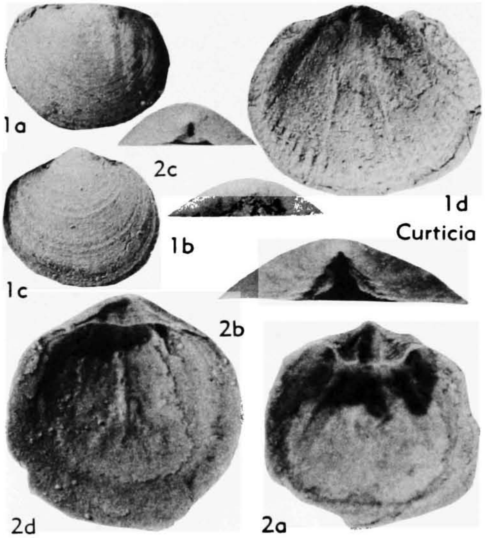

Fig. 173. Curticiidae (p. *H*280).

Family CURTICIIDAE Walcott & Schuchert, 1908

[Curticiidae Walcott & Schuchert, 1908, p. 143]

Ventribiconvex acrotretaceans in which the early pedicle foramen is enlarged dorsally by subsequent resorption to produce a triangular pedicle opening that separates 2 discrete propareas; brachial valve similar to Acrotretinae (682). [The family is thought to be derived from the Acrotretinae.] *U.Cam.*

Curticia Walcott, 1905, p. 319 [**C. elegantula*; OD]. Characters of family. *U.Cam.*, N.Am.——Fig. 173,*1*. **C. elegantula,* USA(Minn.); *1a,b,* ped. v. ext., post., ×4; *1c,d,* brach. v. ext., int., ×4 (682).——Fig. 173,*2*. *C. minuta* Bell, USA (Mont.); *2a-c,* ped. v. int., post., post. young specimen, ×16; *2d,* brach. v. int., ×16 (682).

Family ACROTHELIDAE Walcott & Schuchert, 1908

[*nom. transl.* Rowell, herein (*ex* Acrothelinae Walcott & Schuchert, 1908, p. 146) (*incl.* Schizopholidacea Schindewolf, 1955, p. 556)]

Pedicle valve depressed conical, with excentric apex usually in posterior third of valve, pseudointerarea triangular, commonly not well defined, may be absent; foramen circular, apical, or elongate ellipsoidal slightly posterior to apex; mantle canal pattern not well known in all genera referred to family, but typically consists of baculate *vascula lateralia* in pedicle valve arising behind foramen, running short distance laterally before bending abruptly forward to run subparallel with lateral margins of valve. Brachial valve with pair of *vascula lateralia* arising near beak and diverging laterally, *vascula media* seemingly originating near center of valve and passing anterolaterally. Pedicle valve with pair of posterolaterally placed cardinal scars and second smaller pair of scars near apex of valve. Cardinal scars of brachial valve similarly placed, with second smaller pair of scars near center of valve, close to median ridge. *L.Cam.-L.Ord.*

It is probable that the acrothelids provided the ancestral stock for the discinacean Orbiculoideinae. In the possession of a pedicle tube the genus *Orbithele* shows some similarity with members of that subfamily.

Subfamily ACROTHELINAE Walcott & Schuchert, 1908

[Acrothelinae Walcott & Schuchert, 1908, p. 146]

Brachial valve flat to gently convex, with marginal beak, internally with low median ridge extending forward from beak, never developed as septum; beaks of both valves commonly bearing short spines or tubercles. *L.Cam.-L.Ord.*

Acrothele Linnarsson, 1876, p. 20 [**A. coriacea*; SD Oehlert, 1887, p. 1270] [=*Dearbonia* Walcott, 1908, p. 78 (type, *D. clarki*); *Aerothele* Czarnocki, 1927, p. 742 (*nom. null.*)]. Ornament of fine concentric growth lines, usually with additional irregular wavy ridges bearing minute granules, producing fine granular ornament; 2 short spines on apex of pedicle valve immediately in front of elliptical foramen, 4 short spines arranged roughly in rectangle on beak of brachial valve; dorsal pseudointerarea an obtusely triangular plate adnate to inner surface of valve. *?L.Cam., M.Cam.,* Eu.-Asia-N.Am.-Australia-?N. Afr.——Fig. 174,*2*. **A. coriacea,* M.Cam., Sweden; *2a-c,* ped. v. ext., detail of apex, int., ×10, ×15, ×10; *2d-f,* brach. v. ext., detail of beak, post. int. (incomplete), ×10, ×15, ×10 (Rowell, n).

Orbithele Sdzuy, 1955, p. 9 [**Discina contraria* Barrande, 1868, p. 104; OD]. External form similar to *Acrothele* but differing from it and other members of subfamily in having pedicle opening continued internally as posteriorly directed pedicle tube, pedicle valve with 2 pairs of muscle scars posterolateral to foramen, not coalescing to form pair of cardinal scars. *L.Ord.(Tremadoc.),* Eu.——Fig. 174,*4*. **O. contraria* (Barrande); ped. v. int. impression, ×5 (734a).

Redlichella Walcott, 1908, p. 89 [**Acrotreta granulata* Linnarsson, 1876, p. 24; OD]. Externally similar to *Acrothele* with granular ornament; differs in larger, more deeply impressed dorsal cardinal muscle scars. *M.Cam.*, Eu. [Possibly best classed as subgenus of *Acrothele.*]

Schizopholis WAAGEN, 1885, p. 752 [**S. rugosa*; OD] [=*Discinolepis* WAAGEN, 1885, p. 749 (type, *D. granulata*)]. Pedicle opening long, narrow slit, originating just behind apex, not extending to posterior margin; without clearly defined pseudointerarea, apex of pedicle valve very excentric, near posterior margin, both valves ornamented by concentric growth lines. *L.Cam.*, Asia(Pak.).——FIG. 174,*1*. **S. rugosa*; *1a,b*, ped.v. ext., post., ×6; *1c,d*, brach. v. int. impression, ext. (partly exfoliated), ×6 (Rowell, n).

Subfamily CONODISCINAE Rowell, n. subfam.

Brachial valve depressed conical, beak subcentral. *?M.Cam., U.Cam., ?L.Ord.*

Conodiscus ULRICH & COOPER, 1936, p. 619 [**Acrothele burlingi* KOBAYASHI, 1935, p. 45; OD]. Ornament of concentric fila; pedicle valve similar to *Acrothele,* without pseudointerarea; brachial valve interior with low median ridge extending posteriorly from apex. *U.Cam., ?L.Ord.*, N.Am.——FIG. 174,*3*. **C. burlingi* (KOBAYASHI), USA (Alaska); *3a,b,* ped. v. ext. (partly exfoliated), int. impression, ×3, ×4; *3c,* brach.v. int. impression, ×3 (825).

?Discinopsis MATTHEW, 1892, p. 105 [**Acrotreta? gulielmi* MATTHEW, 1886, p. 37; OD] [=*Discinopsis* MATTHEW, 1889, p. 43 *(nom. nud.)*]. Genus poorly understood, known only from crushed material; possibly a synonym of *Acrothele,* described initially as having brachial valve with excentric apex. *M.Cam.*, N.Am.(N.B.).

Family BOTSFORDIIDAE Schindewolf, 1955

[*nom. transl.* ROWELL, herein (*ex* superfamily Botsfordiacea SCHINDEWOLF, 1955, p. 545)]

Pedicle valve convex, beak posteriorly placed, growth mixoperipheral, pseudointerarea clearly defined, apsacline, rarely catacline, divided into 2 propareas by open triangular delthyrium; *vascula lateralia* diverging anterolaterally from in front of beak, with 2 pairs of poorly defined subequal muscle scars, one pair posterolateral to mantle canal trunks, second pair posteriorly placed between trunks; brachial valve gently convex, marginal beak may bear 2 small tubercles; internally pseudointerarea, musculature, and mantle canal system similar to those of Acrothelidae (714). *L.Cam., ?M.Cam.*

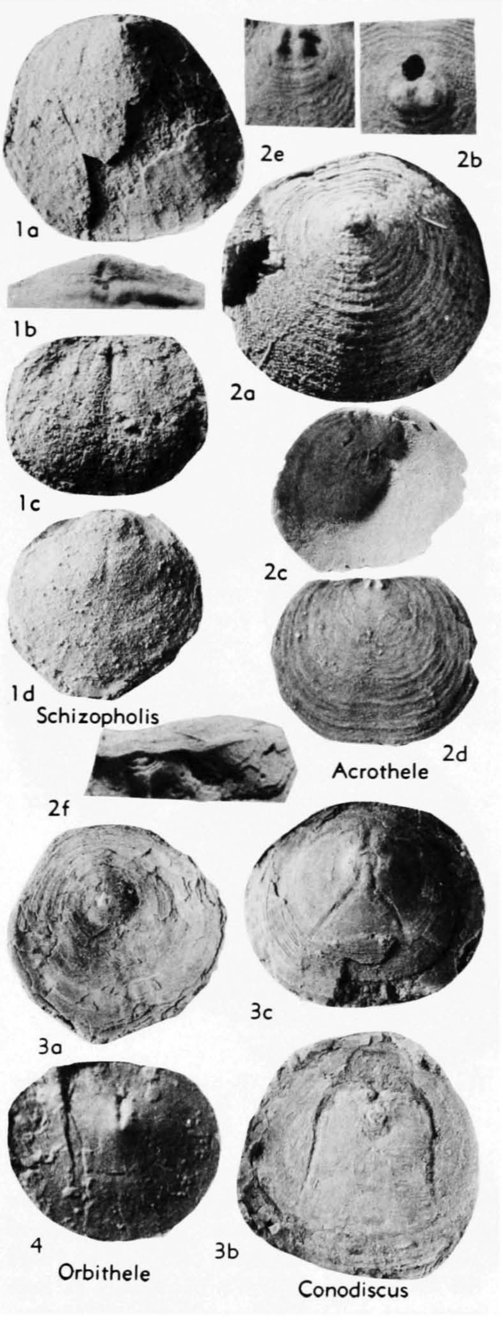

FIG. 174. Acrothelidae (Acrothelinae) *(1-2, 4)*, (Conodiscinae) *(3)* (p. *H*280-*H*281).

The genera here included in the family have been classified variously in the past. *Botsfordia* and *Glyptias* have usually been included in the Obolellidae and *Neobolus* placed in a family of its own in the Trimerellacea. The pedicle opening and pseudointerareas of *Botsfordia* and *Neobolus* are

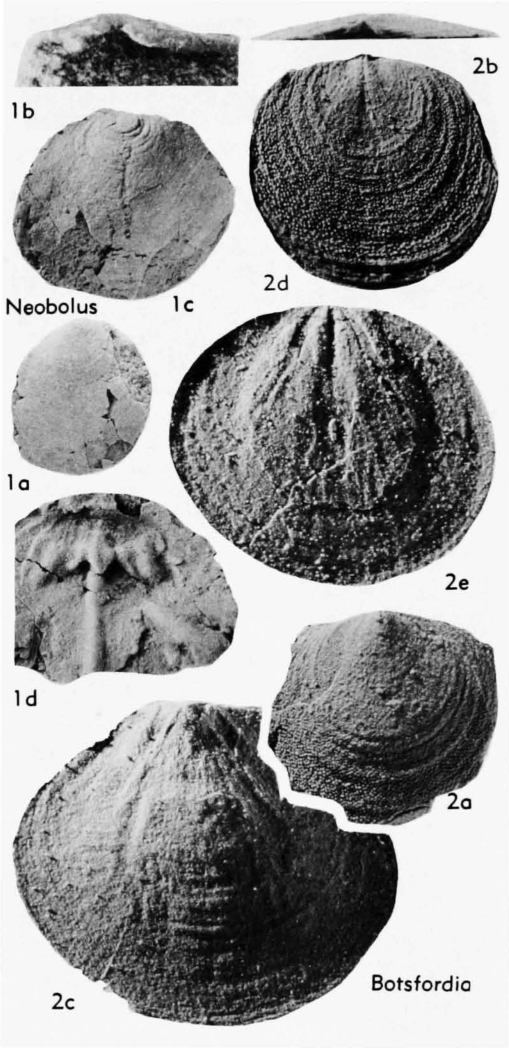

FIG. 175. Botsfordiidae (Botsfordiinae) *(2)*, (Neobolinae) *(1)* (p. *H*282).

similar and not characteristic of the superfamilies to which they have previously been referred (714). Problems are encountered also in respect to shell composition, both the Obolellidae and Trimerellidae, as here restricted, having calcareous shells, whereas the genera under consideration have phosphatic ones. The relation of the genera of the Botsfordiidae with other stocks is not very clear, but the external and internal structures, particularly of the brachial valve of *Botsfordia,* suggest that they are probably related to the Acrothelidae.

Subfamily BOTSFORDIINAE Schindewolf, 1955

[*nom. transl.* ROWELL, herein (*ex* Botsfordiidae SCHINDEWOLF, 1955, p. 545)]

Median ridge of brachial valve short, lacking dorsal platform. *L.Cam., ?M.Cam.*

Botsfordia MATTHEW, 1891, p. 148 [**Obolus pulcher* MATTHEW, 1889, p. 306; OD] [=*Mobergia* REDLICH, 1899, p. 5 (type, *M. granulata*)]. Ornament of concentric growth lines and minute granules, latter may cover entire shell or only apical regions. *L.Cam., ?M.Cam.,* N.Am.-Asia-Greenl.——FIG. 175,*2*. *B. granulata* (REDLICH), L.Cam., Pak.; *2a-c,* ped.v. ext., post., int. impression, ×8; *2d,e,* brach. v. ext., int. impression, ×8 (Rowell, n).

?Glyptias WALCOTT, 1901, p. 675 [**Lingula? favosa* LINNARSSON, 1869, p. 356; OD]. Pedicle opening apparently as in family; ornament of concentric growth lines crossed locally by irregular raised lines producing pitted appearance (848). *L.Cam.,* Eu.(Scand.).

Subfamily NEOBOLINAE Walcott & Schuchert, 1908

[Neobolinae WALCOTT & SCHUCHERT, 1908, p. 144]

Solid platform well developed internally in posterior part of brachial valve, bearing high process immediately in front of dorsal beak (714). *L.Cam.*

Neobolus WAAGEN, 1885, p. 756 [**N. warthi*; SD OEHLERT, 1887, p. 1263] [=*Lakhmina* OEHLERT, 1887, p. 1265 *(nom. subst. pro Davidsonella* WAAGEN, 1885, p. 762 (type, *D. linguloides*), *non* MUNIER-CHALMAS, 1880; *nec* FREDERIKS, 1926)]. Ornament of fine concentric growth lines. *L.Cam.,* Asia(Pak.).——FIG. 175,*1*. **N. warthi*; *1a,b,* ped.v. ext. (incompl.), post., ×3, ×4; *1c,d,* brach. v. ext. (incompl.), int. (incompl.), ×4 (Rowell, n).

Family UNCERTAIN

Discotreta ULRICH & COOPER, 1936, p. 619 [**Acrothele levisensis* WALCOTT, 1908, p. 85; OD]. Both valves depressed subconical, ornament of fine growth lines, apices smooth, situated behind center; small foramen in pedicle valve immediately behind apex, bounded laterally by 2 short folds; internally, foramen surrounded by low rim, low median ridge extending to center of valve, central area of valve smooth, peripherally strongly pitted. Musculature unknown. Brachial valve lacking median ridge, anterior part of apex with 2 diverging subrectangular ?muscle scars extending to center of valve. *L.Ord.,* N.Am.——FIG. 176, *1*. **D. levisensis* (WALCOTT), Que.; *1a,b,* ped. v. ext., int., ×4, ×3; *1c,* brach. v. int., ×3 (825).

Superfamily DISCINACEA Gray, 1840

[*nom. transl.* SCHUCHERT, 1896, p. 309 (*ex* Discinidae GRAY, 1840, p. 155)]

Growth of pedicle valve holoperipheral,

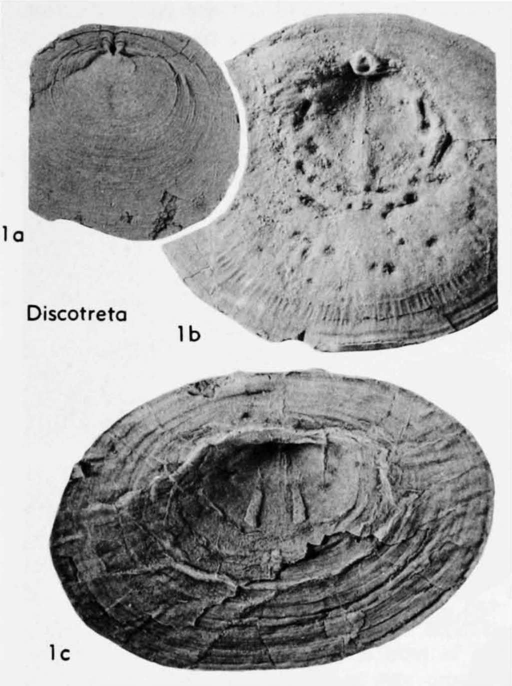

Fig. 176. Family Uncertain (p. *H*282).

that of brachial valve more variable, beak marginal to central; pedicle opening in young forms a triangular notch in posterior margin of pedicle valve, adult pedicle opening may be closed posteriorly or extend to margin of shell, anterior end of track of pedicle opening partially closed by listrium; pedicle valve without pseudointerarea (396). *Ord.-Rec.*

The shell structure of fossil discinaceans is unknown in detail. In Recent *Discinisca* the shell is homogeneous, minutely punctate, and not in alternate organic and phosphate layers.

Recent species belonging to the superfamily are all shallow-water forms, with exception of *Pelagodiscus atlanticus,* which has a large bathymetric range, but is typically abyssal.

Family TREMATIDAE Schuchert, 1893

[Trematidae Schuchert, 1893, p. 149]

Beak of brachial valve marginal, protruding beyond pedicle valve; pedicle opening extending to posterior margin of pedicle valve in all growth stages. *M.Ord.-Dev.*

Trematis Sharpe, 1848, p. 66 [**Orbicula terminalis* Emmons, 1842, p. 395; SD Davidson, 1853, p. 130]. Circular to suboval in outline, biconvex; surface of both valves ornamented by small superficial pits variably arranged, commonly in rough quincunx or in lines radiating from beak; pedicle valve with subcentral beak, convex, but depressed posteriorly, open pedicle notch in depression, margins of notch straight or concave toward mid-line; pseudointerarea of brachial valve adnate to inner surface of valve, low median ridge variably developed separating 2 bean-shaped composite muscle scars. *M.Ord.-U.Ord.,* N.Am.-Eu.——Fig. 177,*1. T. millipunctata* Hall, U.Ord., N.Am.; *1a,* ped. v. ext., exfoliated, ×2; *1b,c,* brach. v. ext., int., ×2, ×1.5; *1d,* both valves lat., ×2 (396).

Schizocrania Hall & Whitfield, 1875, p. 71 [**Orbicula? filosa* Hall, 1847, p. 99; OD]. Subcircular to subtriangular in outline, convexiplane to convexiconcave; brachial valve ornamented by fine costellae, pedicle valve by concentric fila, costellae may also occur. Pedicle valve circular in outline, pedicle opening broadly triangular, margins straight, listrium small; posterior margin of brachial valve slightly thickened, pair of elongate subtriangular muscle scars in posterior third of valve, second pair of poorly defined scars near center of valve. *Ord.-L.Dev.,* N.Am.-Eu.——Fig. 177,*2.* **S. filosa* (Hall), U.Ord., USA(Ohio, *2a,b*; N.Y., *2c*); *2a,* cluster of shells on strophomenoid, ×1; *2b,* ped. v. ext., ×2; *2c,* brach. v. int. impression, ×1.5 (*2a,* Rowell, n; *2b,c,* 396).

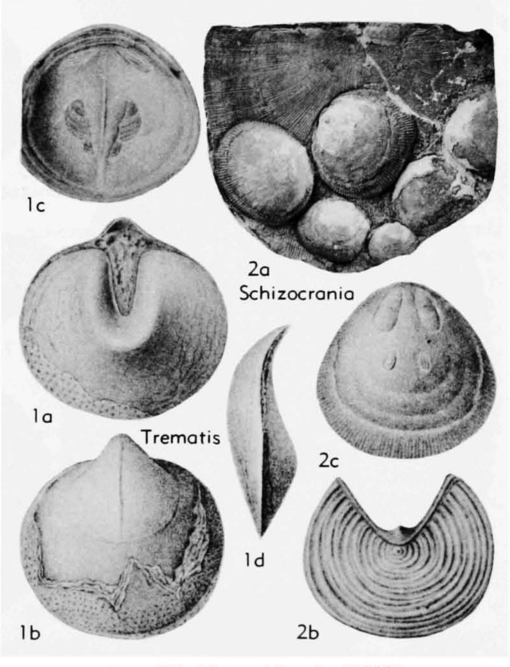

Fig. 177. Trematidae (p. *H*283).

Family DISCINIDAE Gray, 1840

[Discinidae Gray, 1840, p. 155] [=Orbiculidae M'Coy, 1844, p. 103]

Holoperipheral growth in brachial valve, which is usually conical to subconical; musculature consisting of 2 major pairs, anterior and posterior adductors, plus several pairs of oblique muscles, latter only adequately known in Recent species, which also possess

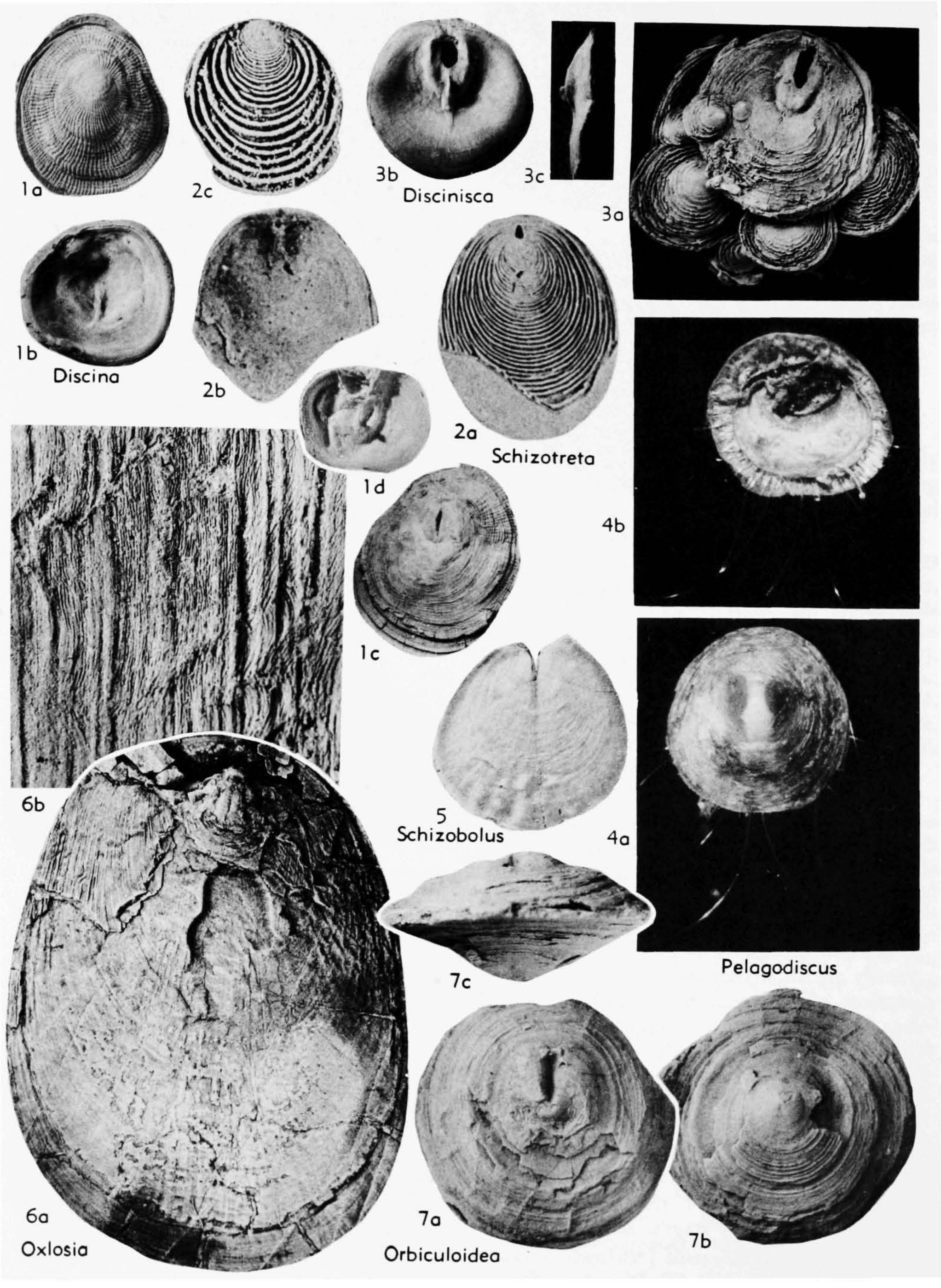

Fig. 178. Discinidae (Orbiculoideinae) *(2,7)*, (Disciniscinae) *(3-4)*, (Discininae) *(1)*; Family Uncertain *(5-6)* (p. *H*285-*H*287).

spirolophe or schizolophe, and have well-developed marginal setae (396). *Ord.-Rec.*

Subfamily ORBICULOIDEINAE Schuchert & LeVene, 1929

[Orbiculoideinae Schuchert & LeVene, 1929, p. 13] [incl. Acrosaccidae Willard, 1928]

Adult pedicle notch not open at posterior margin, track of pedicle opening relatively narrow, extending variable distance from apex along posterior slope of valve; listrium may almost close pedicle track leaving only small foramen which is continued obliquely backward through shell as pedicle tube. *Ord.-Perm.*

Orbiculoidea d'Orbigny, 1847, p. 269 [**Orbicula forbesi* Davidson, 1848, p. 334; ICZN plenary powers proposed Rowell, 1962, Z.N.(S.)1506, ICZN pend.]. Concentric ornament of both valves varying from fine growth lines to well-developed fila; brachial valve conical to subconical, apex not depressed and submarginal, as in *Schizotreta*; pedicle valve subconical to gently concave, pedicle track narrow, closed anteriorly by listrium, foramen at posterior end of slit continued obliquely through shell to open internally in front of posterior margin; low median ridge may occur in brachial valve extending anteriorly from apex. *Ord.-Perm.*, cosmop.——Fig. 178,*7*. **O. forbesi* (Davidson), Sil.(Wenlock), Eng.; *7a*, ped. v. ext., partly exfoliated, ×4; *7b*, brach. v. ext., part exfoliated, ×4; *7c*, both valves, post., ×4 (Rowell, n).

Lindstroemella Hall & Clarke, 1890, p. 16 [**L. aspidium*; OD] [=*Lindstromella* Hall & Clarke, 1889, p. 43 *(nom. nud.)*; *Lindstoemelia* Dunbar & Condra, 1932, p. 49 *(nom. null.)*]. Large, dorsibiconvex. Ornament of both valves strong concentric fila. Apex of brachial valve subcentral, internally with low median ridge anterior of apex, 2 ridges lateral of apex converging on median ridge, bounding anterior adductor scars; apex of pedicle valve central, pedicle opening long, narrow, sides in contact posteriorly, but not fused. *M.Dev.-Penn.*, N.Am.——Fig. 179,*1*. **L. aspidium*, M.Dev., USA(N.Y.); *1a*, ped. v. ext. impression, ×1; *1b*, brach. v. int., ×1 (396).

Lingulodiscina Whitfield, 1890, p. 122 [**Lingula exilis* Hall, 1860, p. 77; OD]. Genus poorly known, may be synonym of *Orbiculoidea*; apparently differs from that genus in having brachial valve elongate oval, almost linguloid in outline with beak submarginal. *Dev.*, N.Am.

Roemerella Hall & Clarke, 1890, p. 19 [**Orbicula grandis* Vanuxem, 1842, p. 152; OD] [=*Roemerella* Hall & Clarke, 1889, p. 43 *(nom. nud.)*]. Like large *Orbiculoidea* but having strongly concave pedicle valve with central apex and pedicle track on broadly elevated area within concave valve; brachial valve high cone with subcentral apex. *Dev.*, N.Am.-?Eu.

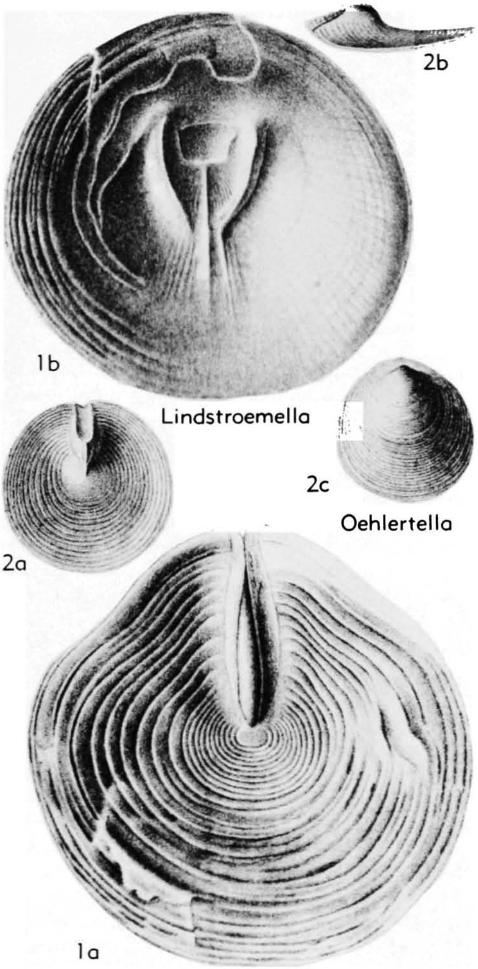

Fig. 179. Discinidae (Orbiculoideinae) *(1)*, (Disciniscinae) *(2)* (p. *H*285-*H*286).

Schizotreta Kutorga, 1848, p. 272 [**Orbicula elliptica* Kutorga, 1846, p. 123; OD] [=*Acrosaccus* Willard, 1928, p. 258 (type, *A. shuleri*)]. Both valves ornamented by well-developed concentric fila; brachial valve gently convex to flat in profile, beak submarginal; pedicle valve subconical, pedicle track and opening similar to *Orbiculoidea*, passage of pedicle through shell may produce low ridge on internal surface of posterior slope. *M.Ord.-Sil.*, N.Am.-Eu.-Asia.——Fig. 178,*2*. *S. corrugata* Cooper, Pratt Ferry F., USA(Ala.); *2a,b*, incompl. ped. v. ext., int., ×4; *2c*, brach. v. ext., ×6 (189).

Subfamily DISCINISCINAE Schuchert & LeVene, 1929

[Disciniscinae Schuchert & LeVene, 1929, p. 13]

Discinids with track of pedicle opening in broad depression of pedicle valve, track partially closed anteriorly by listrium, but pedicle tube not developed; pedicle opening lanceolate to suboval, separated from posterior margin of valve only by narrow band of periostracum. Ventral and dorsal *vascula lateralia* bifurcate, dorsal *vascula media* present. *?Carb., ?Trias., L.Jur.-Rec.*

In Recent species the pedicle is narrow where it emerges through the shell, but expands externally to fill the depressed area and is attached to its outer surface.

Discinisca Dall, 1871, p. 37 [**Orbicula lamellosa* Broderip, 1833, p. 124; OD]. Ornament variable, fine growth lines which may become lamellose, with or without fine ribs. Brachial valve convex to subconical, pedicle valve concave to slightly convex, with large depressed area around pedicle track, internally with small triangular median septum extending posteriorly from apex on to listrium. Lophophore spirolophous. *?Trias., L.Jur.-Rec.,* cosmop.——Fig. 178,*3*. **D. lamellosa* (Broderip), Rec., S.Am.; *3a,* cluster of valves, ped. v. and brach. v. ext., ×1; *3b,c,* ped. v. int., lat., ×1 (Rowell, n).

?**Oehlertella** Hall & Clarke, 1890, p. 15 [**Discina pleurites* Meek, 1875, p. 278; OD] [=*Oehlertella* Hall & Clarke, 1889, p. 43 *(nom. nud.)*]. Ornament of fine growth lines; dorsibiconvex, apex of brachial valve submarginal; pedicle valve similar to *Discinisca,* but pedicle opening more parallel-sided and lacking internal median septum. *Carb.(Miss.-Penn.),* N.Am.-?Eu.——Fig. 179,*2*. **O. pleurites* (Meek), USA(Ohio); *2a,b,* ped. v. int., lat., ×1; *2c,* brach. v. ext., ×1 (396).

Pelagodiscus Dall, 1908, p. 440 [**Discina atlantica* King, 1868, p. 170; OD]. Similar to *Discinisca,* but smaller, very thin-shelled, lophophore schizolophous. *?Mio., Rec.,* cosmop.——Fig. 178,*4*. **P. atlanticus* (King), Rec., N.Pac.; *4a,* brach. v. ext.; *4b,* ped. v. ext., both under water at ×6 (Rowell, n).

Subfamily DISCININAE Gray, 1840

[*nom. transl.* Rowell, herein (*ex* Discinidae Gray, 1840, p. 155)]

Rather thick-shelled discinids, track of pedicle opening a very narrow slit not extending to margin of valve, not situated in conspicuous depression of valve. Pedicle opening partially closed anteriorly by grooved listrium that forms outer surface of irregular median septum projecting above pedicle opening. Pedicle tube absent. Mantle canal system similar to that of Disciniscinae. *Rec.*

Externally the only genus in the subfamily is similar to a thick-shelled *Orbiculoidea.* Contrary to Hall & Clarke (396), the pedicle emerged through the valve with a similar inclination to that of *Orbiculoidea,* i.e., with the pedicle inclined posteriorly from outside to inside of the valve. *Discina* differs from *Orbiculoidea* in its very narrow pedicle opening, complete absence of a pedicle tube, presence of ventral median septum and to a lesser extent, in ornament. Although a conspicuous depression of the ventral valve around the pedicle opening is absent, the pedicle has a similar form to that of *Discinisca;* it expands abruptly after passing through the valve and is attached to the outer surface of the shell.

Discina Lamarck, 1819, p. 236 [**D. ostreoides* (=**Crania striata* Schumacher, 1817, p. 102); OD]. Irregularly subcircular, biconvex to convexi-concave, apices subcentral, ornament of concentric growth lines and fine costellae. Interior of pedicle valve with subtriangular median septum extending short distance posterior of apex, partially closing pedicle opening. Lophophore spirolophous. *Rec.,* W.Afr.——Fig. 178,*1*. **D. striata* (Schumacher); *1a,b,* brach. v. ext., brach. v. int., both ×1.5; *1c,d,* ped. v. ext., int., ×1.5 (Rowell, n).

Superfamily and Family UNCERTAIN

The following 2 genera previously have been included in the Discinacea, but it is doubtful that they are closely related to any of the genera assigned to it.

Oxlosia Ulrich & Cooper, 1936, p. 619 [*nom. subst. pro Eunoa* Clarke, 1902, p. 606 (*non* Malmgren, 1867)] [**Eunoa accola* Clarke, 1902, p. 607; OD]. Large, thin-shelled, ornament of concentric growth lines modified by obscure radial lines; outline subcircular to elongate oval. Brachial valve a depressed cone, apex between center and posterior margin; pedicle valve inadequately known, apparently flat, apex in similar position to that of brachial valve, pedicle opening triangular, extending from close behind apex to posterior margin. Internal structures unknown (825). *L. Ord.,* N.Am.——Fig. 178,*6*. *O. perplexa* Ulrich & Cooper, Que.; *6a,b,* brach. v. ext., detail of ornament, ×1, ×10 (825).

Schizobolus Ulrich, 1886, p. 25 [**Discina truncata* Hall, 1863, p. 28 (=**Lingula concentrica* Vanuxem, 1842, p. 168); OD]. Elongate oval in outline, biconvex, shell thin, ornamented by fine growth lines. Pedicle valve with beak posteriorly placed, not marginal, pedicle opening a triangular notch extending from beak to posterior margin, no listrium; internally low ridge may extend forward from beak to center of valve. Brachial valve with short, straight posterior margin, beak position similar to pedicle valve, internally low

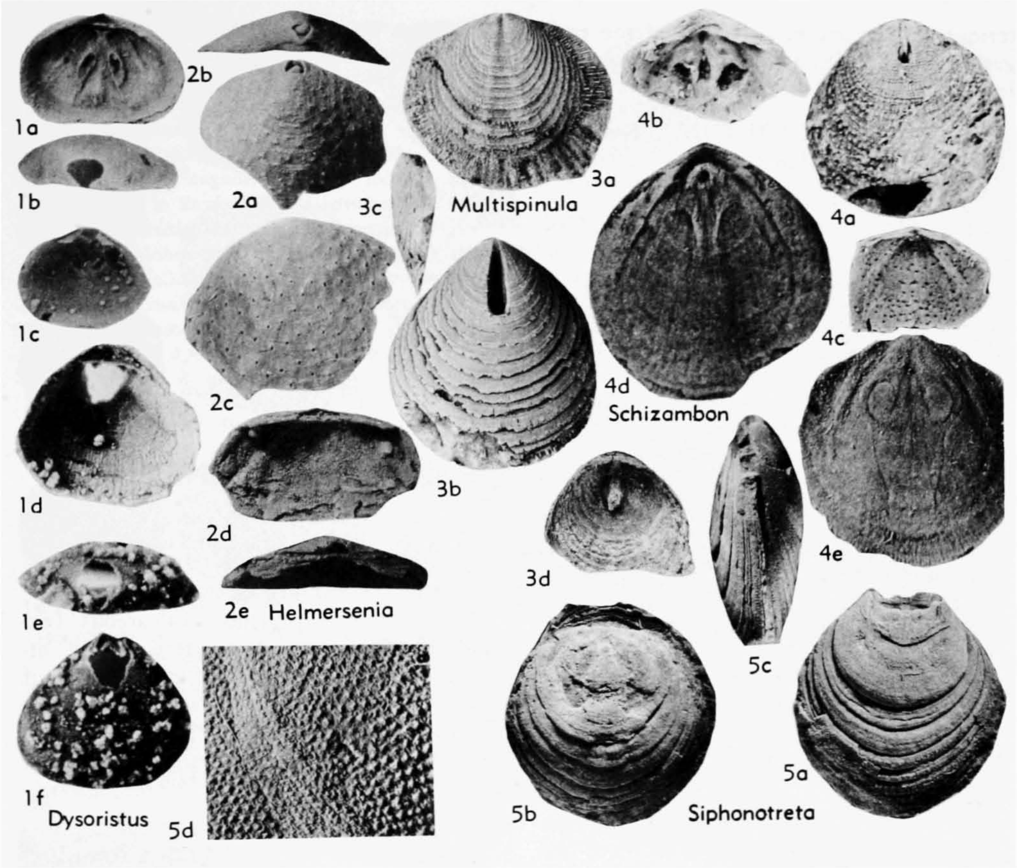

FIG. 180. Siphonotretidae (p. *H*288).

median ridge separates 2 faint subtriangular muscle scars in front of beak, pair of mantle canal trunks arising behind beak, passing forward, diverging slightly (396). *Dev.*, N.Am.-S.Am.——FIG. 178,*5*. **S. concentricus* (VANUXEM); ped. v. int. impression, ×5 (Rowell, n).

Superfamily SIPHONOTRETACEA Kutorga, 1848

[*emend.* ROWELL, 1962, p. 146; *nom. transl.* WALCOTT & SCHUCHERT, 1908, p. 145 (*ex* Siphonotretidae DALL, 1877, p. 62, *nom. correct. pro* fam. Siphonotretaeae KUTORGA, 1848, p. 253, *nom. imperf.*)]

Biconvex, usually ornamented by hollow spines; pedicle foramen circular and apical or may extend anteriorly, through resorption producing elongate triangular pedicle track; when elongate, posterior part of opening may be closed by plate which may be continued to form distinct anterodorsally directed pedicle tube; pseudointerarea of pedicle valve small or absent. Brachial beak marginal, pseudointerarea may be divided into 2 propareas by small pit (680). *U.Cam.-Ord.*

Musculature and mantle canal markings are inadequately known in the superfamily. A pair of large muscle scars in each valve, usually in the posterior third of the valve, other small impressions are occasionally seen that may be muscle scars. In both valves a pair of major mantle canals *(vascula lateralia)* arise near the beak and run forward roughly parallel with the margin of the shell. In well-preserved specimens of the brachial valve of *Schizambon* a second pair of trunks *(vascula media)* are seen that arise outside the muscle scars and converge toward the mid-line. It is not confidently known whether this second pair of mantle canal trunks is characteristic of the superfamily.

The origin of the superfamily is still uncertain, but the structure of the dorsal posterior margin, particularly that of the early genera, suggests that the acrotretaceans may have provided the ancestral stock.

Family SIPHONOTRETIDAE Kutorga, 1848

[*nom. correct.* DALL, 1877, p. 62 (*pro* Siphonotretaeae KUTORGA, 1848, p. 253, *nom. imperf.*)]

Characters of superfamily. *U.Cam.-Ord.*

Siphonotreta DE VERNEUIL, 1845, p. 286 [**Crania unguiculata* EICHWALD, 1829, p. 274; SD DAVIDSON, 1853, p. 131]. Suboval outline, ornament of fine concentric growth lines and scattered spine bases; foramen circular, apical, continued through thick beak as tube; pseudointerarea of pedicle valve large for family, strongly apsacline, its dorsal surface internally forming concave plate parallel to plane of commissure; pseudointerarea of brachial valve a flat plate overhanging interior of valve. *L.Ord.-M.Ord.*, Eu.-N.Am.-Asia-?Australia.——FIG. 180,*5*. **S. unguiculata* (EICHWALD), USSR; *5a*, ped. v. ext., beak damaged; *5b*, brach. v. ext.; *5c*, both valves lat., all ×1.5; *5d*, detail of ornament, ×6 (Rowell, n).

Dysoristus BELL, 1944, p. 146 [**D. lochmanae*; OD] [=*Dysozistus* GORYANSKY, 1960, p. 182 (*nom. null.*)]. Without spines, foramen circular to tear-shaped, may be partly closed by plate posteriorly. Beak of pedicle valve marginal, internally with posterior plate like *Schizambon*, but not adnate; propareas of brachial valve extremely narrow, separated by depressed concave plate (680). *U.Cam.*, N.Am.——FIG. 180,*1a-c*. **D. lochmanae*, USA(Mont.); *1a*, brach. v. int., ×6; *1b,c*, ped. v. post., int., both ×10 (680).——FIG. 180, *1d-f*. *D. transversa* (WALCOTT), USA(Nev.); *1d-f*, ped. v. int., post., ext., all ×16 (680).

Helmersenia PANDER, 1861, column 48 (no page numbers) [**Siphonotreta ladogensis* ZHEREMEZHEV, 1856, p. 73; SD WALCOTT, 1912, p. 367]. Externally similar to small *Siphonotreta*, but pseudointerarea of pedicle valve relatively smaller and extreme posterior tip of beak curved dorsally to form lip of foramen; pedicle opening sealed internally in adults. Brachial pseudointerarea divided into 2 triangular anacline propareas by median pit. *L.Ord.*, Eu.(Baltic).——FIG. 180,*2*. **H. ladogensis* (ZHEREMEZHEV), USSR; *2a,b*, incomplete ped. v. ext., post., both ×8; *2c-e*, incomplete brach. v. ext., int., post., all ×8 (680).

Multispinula ROWELL, 1962, p. 147 [**Schizambon macrothyris* COOPER, 1956, p. 267; OD]. Like *Schizambon* but larger and thicker-shelled, differs in having small pseudointerarea in pedicle valve and submarginal beak, with anterior part of shell lamellose, bearing row of spines on front edge of lamellae; pedicle opening externally like *Schizambon*, but pedicle confined to tube. *M.Ord.-U.Ord.*, Eu.-N.Am.——FIG. 180,*3*. *M. subradiata* (COOPER), Arline F., USA(Tenn.); *3a*, brach. v. ext., ×3; *3b-d*, ped. v. ext., lat., incompl., int., ×3, ×2, ×2 (*3a-c*, 189; *3d*, 680).

Schizambon WALCOTT, 1884, p. 69 [**S. typicalis*; SD OEHLERT, 1887, p. 1266] [=*Schizambonia* OEHLERT, 1887, p. 1266 (*nom. null.*)]. Relatively thin-shelled, ornament of concentric growth lines, commonly with short discontinuous costellae, surface usually covered with fine spines. Pedicle track anterior to beak, elongate triangular, posterior part covered by plate; beak of pedicle valve marginal, internally with plate adnate to posterior surface of valve. Brachial pseudointerarea like *Siphonotreta* but very narrow. *U.Cam.-L.Ord.*, N. Am.-S.Am.-Greenl.——FIG. 180,*4a-c*. **S. typicalis*, USA(Nev.); *4a,b*, ped.v. ext., incompl. int., both ×6; *4c*, incompl. brach.v. int., ×6 (680).——FIG. 180,*4d,e*. *S. australis* ULRICH & COOPER, Arg.; *4d*, ped. v. int., ×6; *4e*, brach. v. int. impression, ×6 (825).

Suborder CRANIIDINA Waagen, 1885

[*nom. correct.* ROWELL, herein (*pro* suborder Craniacea WAAGEN, 1885, p. 744] [=Gasteropegmata WAAGEN, 1885, p. 744 (*partim*); Gastropegmata HALL & CLARKE, 1894, p. 326 (*partim*); Craniida GORYANSKY, 1960, p. 176 (*partim*)]

Shell strongly punctate, calcareous (except Eoconulidae); some free, many attached by cementation of all or part of pedicle valve to some other object, no forms known to have possessed pedicle; growth usually holoperipheral in both valves, more rarely mixoperipheral. *?M.Cam., L.Ord.-Rec.*

Superfamily CRANIACEA Menke, 1828

[*nom. transl.* SCHUCHERT, 1896, p. 310 (*ex* Craniidae KING, 1846, p. 28, *nom. correct. pro* Craniaceae MENKE, 1828, p. 56, *nom. imperf.*)]

Characters of the suborder. *?M.Cam., L. Ord.-Rec.*

The Craniacea occur in the Lower Ordovician and are well developed by the Middle Ordovician when the superfamily was already represented by several genera. The extension of its time range into the Middle Cambrian is doubtful and is based on the occurrence of the poorly known *"Philhedra" columbiana* (WALCOTT) from British Columbia.

The systematic position of the genus *Eoconulus* is rather problematic. The low irregular cone suggests that it is the brachial valve of an animal which was attached by cementation of its pedicle valve, but the latter valve, however, is unknown. Internally, the relatively large posteriorly placed adductors recall the Craniidae, but no anterior adductors are known and the genus differs fundamentally from members of that

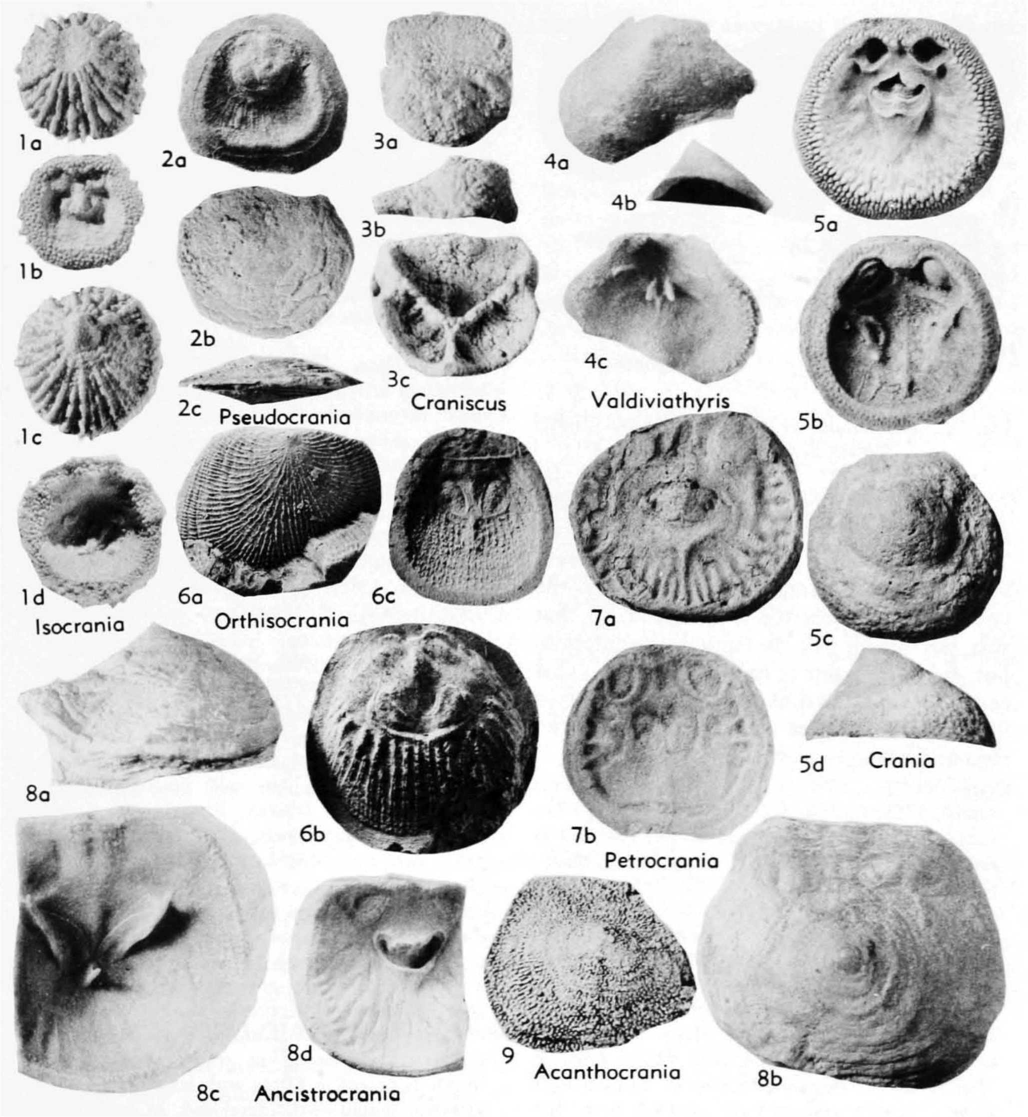

FIG. 181. Craniidae (p. *H*290-*H*291).

family in having a phosphatic shell. For these reasons the family Eoconulidae is introduced, since *Eoconulus* would not appear to be closely related to any other known craniacean. As COOPER, 1956 (189) has pointed out, the genus occurs with typical craniaceans and from what is known of its range cannot have been ancestral to them.

Family CRANIIDAE Menke, 1828

[*nom. correct.* KING, 1846, p. 28 (*pro* Craniaceae MENKE, 1828, p. 56, *nom. imperf.*)] [=fam. Craniacea MENKE, 1830, p. 96; Craniadae FORBES, 1838, p. 38; incl. Valdiviathyrididae, *nom. correct.* ROWELL, herein (*pro* Valdiviathyridae HELMKE, 1940, p. 235, *nom. imperf.*)]

Shell calcareous, punctate, punctae in brachial valve branching arborescently toward distal end; brachial valve usually conical, pedicle valve subconical or convex when free, conforming to shape of surface of attachment when fixed. Principal muscles consist of two pairs of adductors traversing shell dorsoventrally and two pairs of oblique muscles. *Vascula lateralia* of both valves pinnate, *vascula media* seemingly absent. Recent species with anus posteriorly placed on mid-line of shell, no marginal setae (439). *?M.Cam., L.Ord.-Rec.*

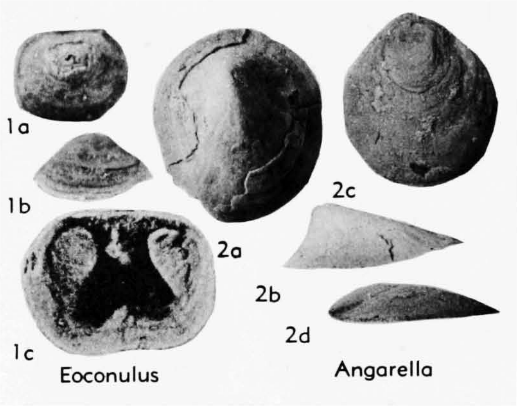

FIG. 182. Eoconulidae *(1)*; Superfamily and Family Uncertain *(2)* (p. *H*291).

Some Paleozoic species that belong to the family apparently lack a pedicle valve. These all appear to be forms that were attached by cementation. Presumably the ventral mantle secreted a periostracum that was responsible for the actual cementation, but did not secrete a calcareous shell. This condition is known as a transitory phase in the very early stages of development of the Recent *Crania anomala.*

Crania RETZIUS, 1781, p. 72 [**Anomia craniolaris* LINNÉ, 1758, p. 700; SD SCHMIDT, 1818, p. 71] [=*?Criopus* POLI, 1791, p. 34 (type, *Anomia imperforata* POLI, 1791, p. 34) (*non* GRAY, 1821); *Criopoderma* POLI, 1795, p. 255 (type, *Anomia turbinata* POLI, 1795, p. 189); *Orbicula* CUVIER, 1797, p. 435 (type, *Patella anomala* MÜLLER, 1776, p. 237); *Orbicularius* DUMÉRIL, 1806, p. 170 *(nom. van.)*; *Criopododerma* AGASSIZ, 1836, p. 104 *(nom. van.)*; *?Cryopus* DESHAYES, 1836, p. 314 *(nom. null.)*; *?Crania (Lissocrania)* WILLIAMS, 1943, p. 71 (type, *Crania dodgei* ROWLEY, 1908, p. 73)]. Attached by part or all of pedicle valve; ornament of concentric growth lines, low discontinuous radial lines present or absent; margins of both valves thickened, pustulose, may form limbus, anterior adductor scars close together; brachial valve conical to subconical. *?Carb., Cret.-Rec.,* cosmop.——FIG. 181,5. **C. craniolaris* (LINNÉ), U.Cret., Sweden; *5a,* ped. v. int., ×2; *5b-d,* brach. v. int., ext., lat., all ×2 (Rowell, n).

Acanthocrania WILLIAMS, 1943, p. 71 [**Crania spiculata* ROWLEY, 1908, p. 74; OD] [=*?Choniopora* SCHAUROTH, 1854, p. 546 (type, *C. radiata*)]. Attached, brachial valve conical, ornament of fine papillae or spines; anterior adductors usually larger than posterior adductors, margin of valve not thickened. Pedicle valve unknown, presumed thin or not calcified. *Ord.-Carb.,* N.Am.-Eu.——FIG. 181,9. *A. grandis* COOPER, Benbolt F., USA (Va.); brach. v. ext., ×1.5 (189).

Ancistrocrania DALL, 1877, p. 13 [*nom. subst. pro Cranopsis* DALL, 1871, p. 27 (*non* ADAMS, 1860)] [**Crania parisiensis* DEFRANCE, 1819, p. 313; OD]. Similar to *Crania* but brachial valve interior bearing 2 slender, posterolaterally directed processes originating near apex, in part bearing anterior adductor scars; low short median septum may be present; valve margin not thickened; attached by entire surface of pedicle valve, margin of valve thickened. *Cret., ?Rec.,* Eu.——FIG. 181,*8*. **A. parisiensis* (DEFRANCE), U.Cret., Eng.; *8a,* both valves lat. ext., ×2; *8b,c,* brach. v. ext., int., ×2; *8d,* ped.v. int., ×1 (*8a,d,* Rowell, n; *8b,c,* 681).

Craniscus DALL, 1871, p. 27 [**Crania tripartita* MÜNSTER, 1837, p. 297; OD]. Anterior adductor scars of brachial valve on 2 strong ridges extending posterolaterally from apex, united with median septum or ridge, structures dividing valve into 3 chambers; margins of valve not thickened. Pedicle valve of type-species unknown; in other species flat, attached by entire surface. *Jur.-Rec.,* Eu.-N.Am.-Australia-Japan-IndoPac.-Aleutian Is.——FIG. 181,*3*. **C. tripartitus* (MÜNSTER), Jur., Ger.(Thurnau); *3a-c,* brach. v. ext., lat., int., all ×4 (Rowell, n).

Isocrania JAEKEL, 1902, p. 1062 [**Crania egnaburgensis* RETZIUS, 1781, p. 75; SD SCHUCHERT & LEVENE, 1929, p. 69]. Both valves conical to subconical, brachial valve usually higher than pedicle, strongly costellate, attached only by apical region of pedicle valve, limbus well developed in both valves, pustulose. *U.Cret.,* Eu.-Afr.-Asia.——FIG. 181,*1*. **I. egnaburgensis* (RETZIUS), Eng.; *1a,b,* ped.v. ext., int., ×4; *1c,d,* brach.v. ext., int., ×4 (Rowell, n).

Orthisocrania ROWELL, 1963, p. 39 [**Pseudocrania divaricata* M'COY, 1851, p. 388; OD]. Free, costellate ornament; both valves convex, with beak initially marginal and growth mixoperipheral, may later become holoperipheral, catacline to apsacline, ventral pseudointerarea and anacline dorsal pseudointerarea developed in young stages, retained in adults except in forms with later holoperipheral growth; limbus well developed in both valves, not pustulose. Anterior adductor scars conspicuous, usually larger than posterior pair; branches of mantle canal system numerous (10-30), scarcely interrupted medianly. *M.Ord.-U.Ord.,* Eu.——FIG. 181,6. **O. divaricata* (M'COY); *6a,b,* ped. v. ext., int. impression, ×1.5; *6c,* brach. v. int., ×1.5 (Rowell, n).

Petrocrania RAYMOND, 1911, p. 229 [*nom. subst. pro Craniella* OEHLERT, 1888, p. 101 (*non* VON SCHLOTHEIM, 1820)] [**Craniella meduanensis* OEHLERT, 1888, p. 102; OD] [=*Punctopatella* GRUBBS, 1939, p. 559 (type, *P. corallifera*)]. Attached, pedicle valve thin; brachial valve conical, ornament of concentric growth lines, in some simulating ornament of host; characterized by pair of sigmoidal dorsal *vascula lateralia,* secondary canals branching off laterally; posterior adductors larger than anterior, margin of valves not thickened. *M.Ord.-Dev., ?Perm.,* Eu.-N.Am.-Asia.——FIG. 181,*7*. *P. hamiltoniae* (HALL), Ludlowville F., USA(N.Y.); *7a,* plasticene cast of ped.v. int., ×1.5; *7b,* plasticene cast of brach. v. int., ×1.5 (189).

Philhedra KOKEN, 1889, p. 465 [**P. baltica*; OD] [*non Philhedra* SCHMIDT, 1939] [=*Philedra* BEKKER, 1921, p. 34 *(nom. null.)*; *Propatella* GRUBBS, 1939, p. 558 (type, *P. magnacostata*)]. Similar to *Acanthocrania* but fine continuous or discontinuous costellate ornament; pedicle valve thin, commonly not calcified. *?M.Cam., L.Ord.-Carb.* N.Am.-Eu.-Asia.

Philhedrella KOZLOWSKI, 1929, p. 28 [**Philhedra (Philhedrella) mimetica*; OD]. Genus inadequately understood, interior of valves unknown; erected for species similar to *Philhedra* but smooth, lacking costellae; pedicle valve thin or not calcified. *?Ord., U.Sil.,* Eu.

Pseudocrania M'COY, 1851, p. 387 [**Orbicula antiquissima* EICHWALD, 1840, p. 169 (=**Crania petropolitana* PANDER, 1830, p. 100); SD DAVIDSON, 1853, expl. Pl. 9] [=*Palaeocrania* EICHWALD, 1854, p. 20 (obj.)]. Free, brachial valve conical, pedicle valve conical to flat, growth holoperipheral in both valves; ornament of growth lines and minute scattered papillae. Internally similar to *Orthisocrania. L.Ord.-M.Ord.,* Eu.(Balt.-Sweden-N.Ger.).——FIG. 181,*2*. **P. petropolitana* (PANDER); *2a,* ped. v. int., ×1.5; *2b,* incompl. brach. v. ext., ×1; *2c,* both valves lat., ×1 (Rowell, n).

Valdiviathyris HELMCKE, 1940, p. 237 [**V. quenstedti*; OD]. Pedicle valve unknown. Brachial valve similar to *Ancistrocrania*, but much smaller, thinner-shelled, processes more ventrally directed (681). *Rec.,* S.Ind.O.——FIG. 181,*4*. **V. quenstedti*; *4a-c,* brach. v. ext., lat., int., all ×6 (681).

Family EOCONULIDAE Rowell, n. fam.

Shell impunctate, phosphatic; brachial valve a low misshapen cone with pair of large adductor scars near posterolateral margins. *M.Ord.-U.Ord.*

Eoconulus COOPER, 1956, p. 282 [**E. rectangulatus*; OD]. Small to minute, probably attached by cementation of pedicle valve, latter unknown. *M.Ord.-U.Ord.,* N.Am.(Ala.-Va.)-Eu.(Ire.).——FIG. 182,*1*. **E. rectangulatus,* M.Ord., USA(Ala.); *1a-c,* brach. v. ext., lat., int., all ×15 (189).

GENERA DOUBTFULLY REFERRED TO CRANIACEA

Angarella, Pseudometoptoma, and *Eleutherocrania* are three rather similar genera which previously have been referred to the Craniidae (356), but their systematic position is debatable. Although their calcareous shells and some aspects of their gross shape recall this family, the microstructure of their impunctate shells differs markedly from that of the craniids. Moreover, although the musculature of these forms is not very well known, in *Angarella* the brachial valve shows a suggestion of 4 or 5 pairs of submarginally placed and bilaterally symmetrical muscles. Such a muscle pattern is unknown in the craniaceans, or indeed in any other brachiopod superfamily, but is similar to that of some monoplacophorans (Mollusca). Since the animals have been described as having 2 valves, however, a close relationship with the monoplacophorans is unlikely; much more must be known of the morphology of the 2 valves and their relationship to each other before the systematic position of these genera can be regarded as reasonably well established.

Angarella ASATKIN, 1932, p. 486 [**A. jaworowskii*; OD]. Large forms with relatively high, conical brachial valve, flat to gently convex pedicle valve, both valves without limbus. Attached by cementation of apical region of pedicle valve, possibly becoming secondarily free. Shell calcareous, impunctate, in 2 layers. Musculature inadequately known. *Ord.,* Asia(E.Sib.-Urals-Kazakhstan).——FIG. 182,*2*. **A. jaworowskii,* Sib.; *2a,b,* brach. v. ext. exfoliated, lat., ×1; *2c,d,* ped. v. ext., lat., ×1 (Rowell, n).

Eleutherocrania VON HUENE, 1899, p. 294 [**E. gibberosa*; OD]. Similar to *Pseudometoptoma,* but pedicle valve strongly convex to subconical. *U.Ord.-L.Sil.,* Eu.(Est.).

Pseudometoptoma VON HUENE, 1899, p. 282 [**Metoptoma siluricum* EICHWALD, 1842, p. 77; OD]. Free, externally like *Angarella,* but lacking attachment scar. *Ord.-L.Sil.,* Eu.(Baltic).

Order OBOLELLIDA Rowell, n. order

Shell essentially calcareous, biconvex, subcircular to elongate oval in outline. Pedicle valve with well-defined pseudointerarea; position of pedicle opening very variable, may emerge between valves, at apex of pedicle valve, or by subsequent resorption open anterior to apex of pedicle valve. Beak of brachial valve marginal. *L.Cam.-M.Cam.*

Superfamily OBOLELLACEA Walcott & Schuchert, 1908

[emend. ROWELL, 1962, p. 137] [*nom. transl.* GORYANSKY, 1960, p. 180 (*ex* Obolellidae WALCOTT & SCHUCHERT, 1908, p. 145)]

Ornament of concentric growth lines and

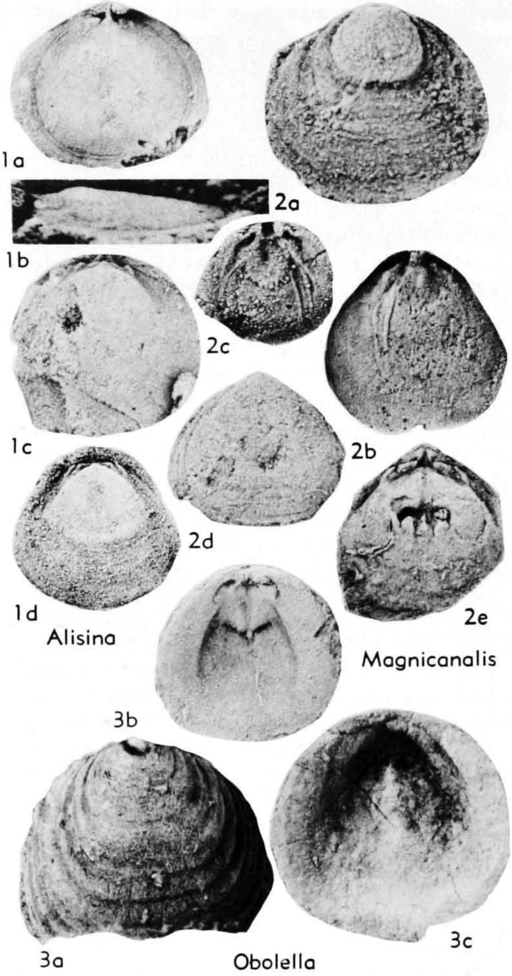

FIG. 183. Obolellidae (p. *H*292-*H*293).

fine radial striae. One pair of principal mantle canals *(vascula lateralia)* in pedicle valve diverging anterolaterally from in front of beak, posterior third of valve commonly thickened to produce very low, solid platform. Brachial valve with orthocline pseudointerarea, low median ridge variably developed, 2 pairs of principal mantle canals, one pair *(vascula lateralia)* diverging anterolaterally from in front of beak, second pair *(vascula media)* arising near center of valve, diverging slightly anteriorly; musculature in superfamily inadequately known but apparently a pair of cardinal scars in pedicle valve in front of propareas with second smaller pair of scars near mid-line, in front of ventral platform. Brachial valve with 2 pairs of cardinal scars, commonly united to form two scars immediately in front of propareas, third pair of muscle scars near center of valve. *L.Cam.-M.Cam.*

Family OBOLELLIDAE Walcott & Schuchert, 1908

[Obolellidae WALCOTT & SCHUCHERT, 1908, p. 145; emend. ROWELL, 1962, p. 138]

Characters of superfamily. *L.Cam.-M. Cam.*

The genera included in the family form a compact group, but one which displays remarkable variation in the nature of the pedicle opening. Superficially, some of the genera show a resemblance to the kutorginaceans, but they differ fundamentally from them in musculature, mantle canal pattern, and nature of the posterior margin of the brachial valve. The muscle scars of the obolellids are not concentrated medianly or elongated as in the kutorginaceans or articulates, and their distribution, with one or more pairs posterolaterally placed, agrees with the typical inarticulate pattern. It is unlikely that these posterolateral muscles are associated with the pedicle, since they are relatively deeply impressed and their position is more or less constant, irrespective of the position of the pedicle foramen, and it seems probable that they are the homologues of the posterior adductors of other inarticulates. The relationship of the family to remainder of the class is very obscure, however, since in shell composition and nature of the posterior margin of the pedicle valve they differ greatly from any other Cambrian stock and in spite of the small number of genera involved, the differences merit assignment of ordinal rank to the group.

The Obolellida form the oldest group of calcareous-shelled inarticulates, and its members are among the earliest elements that are known of brachiopod faunas. They were widely distributed and locally numerically abundant in the Early Cambrian, but the initial success of the stock was short-lived and it was extinct by the Middle Cambrian.

Obolella BILLINGS, 1861, p. 6 [**O. chromatica*; SD DALL, 1870, p. 163]. Variably developed pseudointerarea, apsacline to catacline; pedicle emerging through low groove which divides pseudointerarea medianly (680). *L.Cam., ?M.Cam.,* N.Am.-Greenl. - ?Asia - ?Australia.——FIG. 183,*3*. **O. chromatica,* L.Cam., Labrador; *3a,b,* incompl. ped.

v. ext., int., ×5, ×4; *3c,* brach. v. int. ×4 (*3a,* Bell, n; *3b,c,* 680).

Alisina Rowell, 1962, p. 141 [**Obolella atlantica* Walcott, 1890, p. 36; OD]. Pseudointerarea of pedicle valve apsacline to catacline, divided medianly by triangular elevation into 2 propareas; pedicle confined to narrowly conical pedicle tube sloping obliquely posteroventrally through thickened umbonal part of shell, foramen apical. *L.Cam.,* Eu.(Eng.)-N.Am.(Mex.).——Fig. 183,*1*. **A. atlantica* (Walcott), Newf.; *1a,b,* ped. v. int. impression; int. impression lat., ×4, ×5; *1c,d,* brach. v. int. impression showing pseudointerarea, int. impression, ×4 (680).

Bicia Walcott, 1901, p. 676 [**Obolella gemma* Billings, 1871, p. 218; OD]. Subtrigonal outline, beak of pedicle valve subacuminate, pseudointerarea orthocline to slightly apsacline, divided medianly by almost parallel-sided pedicle groove. Platform in pedicle valve well developed for family, posterolateral muscle scars deeply impressed. *L.Cam.,* N.Am.——Fig. 184,*1*. **B. gemma* (Billings), USA(N.Y.); *1a,b,* ped.v. ext., lat., ×5.3; *1c,* ped.v. int., ×7.5; *1d,* brach.v. int., ×4.4 (848).

Magnicanalis Rowell, 1962, p. 140 [**Obolella mobergi* Walcott, 1901, p. 673; OD]. Similar to *Obolella,* but with well-developed pseudointerarea in pedicle valve ornamented by strong growth lines crossed by deep hemiconical pedicle groove. *L.Cam.,* Eu.(Scand.).——Fig. 183,*2*. **M. mobergi* (Walcott), Sweden; *2a-c,* ped. v. ext., int. impression, incompl. int. (latex cast), all ×3; *2d,e,* brach. v. ext., incompl. int. impression, ×3 (680).

Trematobolus Matthew, 1893, p. 276 [**T. insignis;* OD] [=*Protosiphon* Matthew, 1897; p. 70 (type, *P. kempanum*); *Protosyphon* Goryansky, 1960, p. 181 *(nom. null.)*; *Trematobolos* Eastman, 1960, p. 288 *(nom. null.)*]. Large for family. Pseudointerarea of pedicle valve apsacline, divided medianly by groove. Pedicle track triangular, foramen at anterior end, about quarter length of valve in front of beak. Homeomorphic with *Schizambon. L.Cam.-M.Cam.,* N.Am.-Eu.-Asia(E. Sib.).——Fig. 184,*2*. *T. kempanum* (Matthew), L.Cam., N.B.; *2a-c,* ped. v. int. impression, incompl. int. impression showing pedicle opening, latex cast ext., ×1.6 *(2a,b)*, ×2 *(2c)*; *2d,e,* brach. v. int. impression, incompl. int. impression showing musculature, both ×1.6 (*2a,b,d,e,* 680; *2c,* Bell, n).

Order PATERINIDA Rowell, n. order

Shell phosphatic, rounded or elliptical in outline, growth usually holoperipheral in both valves. Pedicle valve convex to hemiconical, pseudointerarea divided by triangular delthyrium closed to variable extent by homeodeltidium. Brachial valve similar in external form, notothyrium partially closed by homeochilidium. *L.Cam.-M.Ord.*

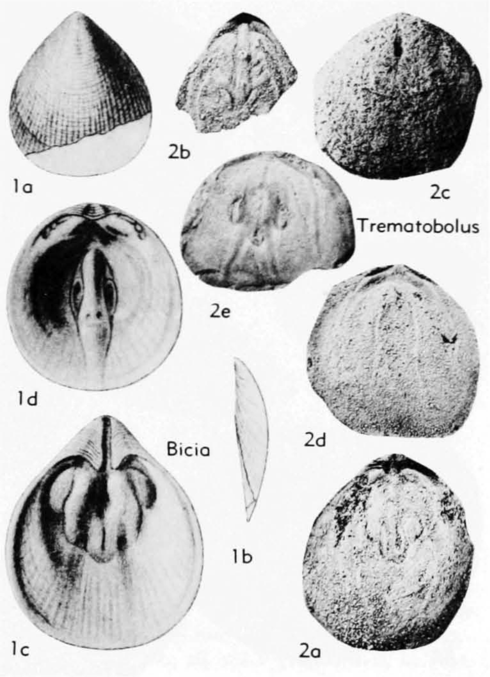

Fig. 184. Obolellidae (p. *H*293).

Superfamily PATERINACEA Schuchert, 1893

[*nom. transl.* Schuchert & LeVene, 1929, p. 11 (*ex* Paterinidae Schuchert, 1893, p. 148) incl. Dictyoninacea Cooper, 1956, p. 187]

Ventral pseudointerarea usually well developed, procline to apsacline, homeodeltidium convex. Brachial valve lower than pedicle valve, homeochilidium convex (65, 189). *L.Cam.-M.Ord.*

The paterinaceans are one of the earliest brachiopod stocks and originally were thought to be restricted to the Cambrian but are now known to range into the Middle Ordovician (189). The internal structure of many species referred to the superfamily is unknown and as Bell (65) has suggested, it is possible that some genera included in it are polyphyletic. The paterinaceans always have been difficult to place taxonomically; Schuchert (1893, 1897) included them in the Atremata, as did Walcott (1912) and while Thomson (1927) and Muir-Wood (1955) referred them to the Neotremata, Schuchert & LeVene

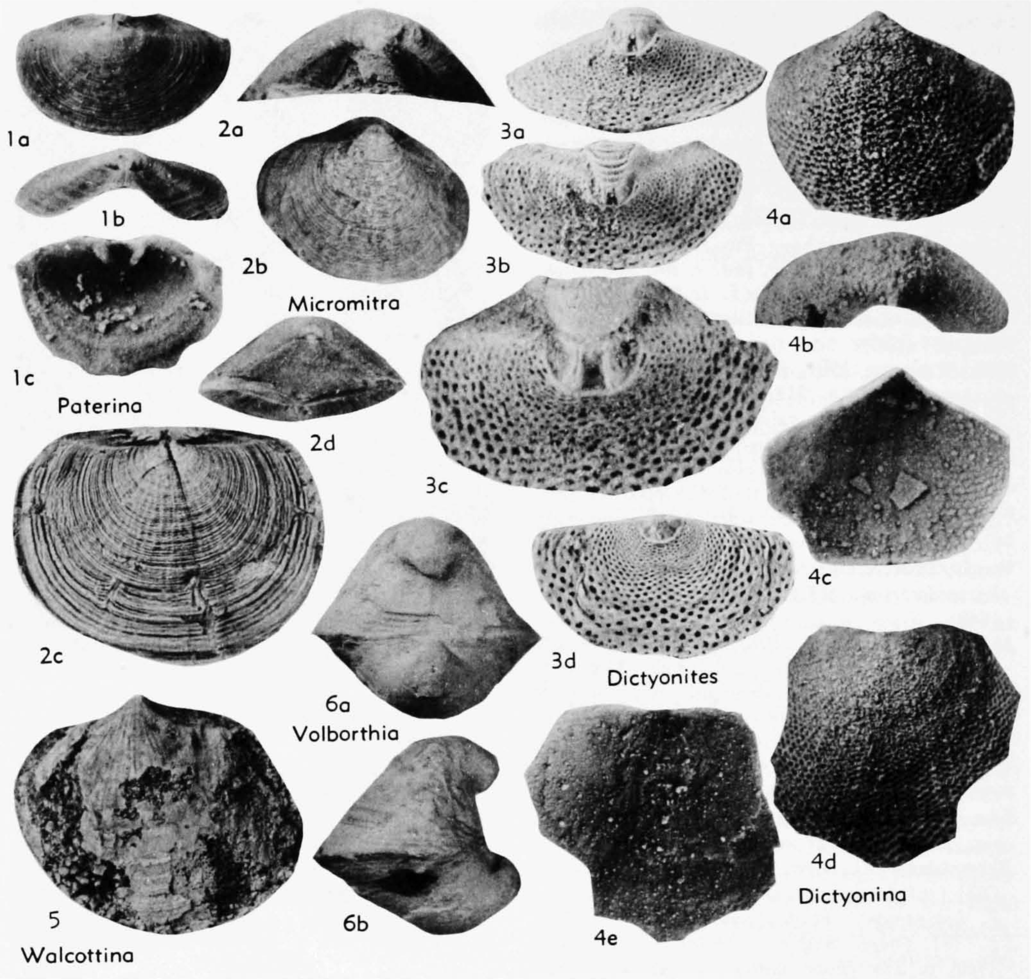

FIG. 185. Paterinidae *(1-4)*; ?Paterinida *(5-6)* (p. *H*295).

(1929) split the group, placing the Paterinidae in the Palaeotremata and the Micromitridae in the Atremata.

Superficially, the pedicle valve of the paterinaceans is somewhat similar to that of the acrotretaceans, but there are major differences. Characteristic of the superfamily is the absence of an apical pedicle foramen. It is usually assumed that the pedicle emerged between the valves and although this may well have occurred, the animals possibly may have lacked a pedicle (p. *H*89). In addition to the external differences between the paterinaceans and other inarticulate stocks, there are internal differences which together seem to be of sufficient magnitude to merit regarding the paterinaceans as a separate order. The lateral margins of the delthyrium are strengthened by broad diverging ridges in several genera and what are apparently muscle scars, although imperfectly known, all seemingly forming narrow triangular muscle tracks extending posteriorly to the beak. It is probable that we still do not know the position of all of the muscles, but in the pedicle valve there are two narrow tracks, diverging slightly forward and extending from the beak to near the mid-length of the valve. In the brachial valve two pairs of tracks occur, the larger pair extending forward from the beak to near the mid-length of the valve and forming a single median depression, with a much shorter pair, more externally placed, diverging anterolaterally. This pattern is quite unlike the muscle scar distribution of any other inarticulate brachiopod stock.

Family PATERINIDAE Schuchert, 1893

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

Characters of superfamily. *L.Cam.-M.Ord.*

Paterina BEECHER, 1891, p. 345 [**Obolus labradoricus* BILLINGS, 1861, p. 6; OD] [=*Iphidella* WALCOTT, 1905, p. 304 (*nom. subst. pro. Iphidea* BILLINGS, 1872, p. 477, *non* BAYLEY, 1865) (type, *Iphidea bella* BILLINGS, 1872, p. 477)]. Shell thin, seemingly single-layered, ornament of regular concentric fila. Homeodeltidium variably developed, usually large, lateral margins of delthyrium with 2 strong ridges on internal face uniting at apex of valve. *Cam.,* N.Am.-Eu.-Asia-Australia.——FIG. 185,*1*. **P. labradorica* (BILLINGS), L. Cam., Labrador; *1a-c,* ped. v. ext., post., int., all ×10 (Rowell, n).

Dictyonina COOPER, 1942, p. 228 [*nom. subst. pro Iphidella* WALCOTT, 1912, p. 359 (*non* WALCOTT, 1905)] [**Trematis pannulus* WHITE, 1874, p. 6; OD]. Ornament of small, superficial pits commonly formed by intersection of oblique raised lines. Homeodeltidium relatively small. *L.Cam.-M.Cam., ?U.Cam.,* N.Am.-Eu.-Asia.——FIG. 185, *4*. **D. pannula* (WHITE), L.Cam., USA(Nev.); *4a-c,* ped. v. ext., post., int., all ×15; *4d,e,* incompl. brach. v. ext., int., both ×15 (Rowell, n).

Dictyonites COOPER, 1956, p. 187 [**D. perforata*; OD]. Umbonal region of both valves imperforate, bearing 2 short ridges in pedicle valve and single median ridge in brachial. Ventral pseudointerarea well developed, homeodeltidium large, dorsal pseudointerarea and homeochilidium relatively small, remainder of shell perforated by large pores, possibly covered by thin outer shell layer in life. Interior of pedicle valve with short apical median ridge; musculature unknown. *M.Ord.,* N. Am.(Ala.).——FIG. 185,*3*. **D. perforata,* Pratt Ferry F.; *3a-c,* ped. v. ext., oblique post., detail of umbo, ×10, ×10, ×15; *3d,* brach.v. ext., ×10 (189).

Micromitra MEEK, 1873, p. 479 [**Iphidea? sculptilis*; OD] [=*?Icodonta* BELL, 1941, p. 212 (type, *I. typica*)]. Relatively thick shell of several layers, ornament basically reticulate, but variable, fine concentric fila crossed by costellae. Homeodeltidium and homeochilidium usually large, lateral margins of delthyrium apparently buttressed by ridges, as in *Paterina. Cam.,* N.Am.-Eu.-Asia-Australia.——FIG. 185,*2*. **M. sculptilis* (MEEK), M.Cam., USA(Mont.); *2a,b,* ped. v. post., ext., ×6; *2c,* brach. v. ext., ×6; *2d,* both valves post. incompl., ×6 (65).

GENERA DOUBTFULLY REFERRED TO PATERINIDA

Mickwitzia SCHMIDT, 1888, p. 24 [**Lingula? monilifera* LINNARSSON, 1869, p. 344; OD] [=*Causea* WIMAN, 1902, p. 53 (type, *C. formosa*)]. Relatively large, oval to subcircular in outline, ventribiconvex. Shell of 3 layers, outer pustulose, middle with fine reticulate ornament, inner coarsely punctate. Pedicle valve with elevated apex submarginal or recurved over posterior margin of valve, pseudointerarea poorly defined, apparently without pedicle opening. Brachial valve with low submarginal apex. Internal structure unknown. *L. Cam.,* Eu.-?N.Am.——FIG. 186,*1*. **M. monilifera* (LINNARSSON), Sweden; *1a-c,* ped. v. ext. exfoliated, lat., post., all ×1.5 (*1a,* Rowell, n; *1b,c,* 848).

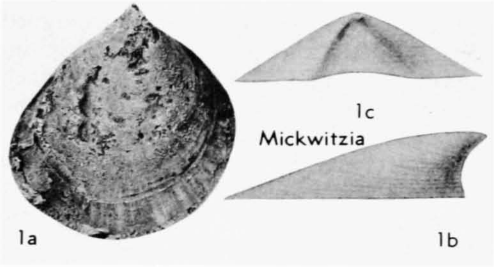

FIG. 186. ?Paterinida (p. *H*295).

Volborthia VON MÖLLER, 1870, p. 409 [**Acrotreta recurva* KUTORGA, 1848, p. 277; OD]. Fairly large, transversely ovate in outline, posterior margin straight; pedicle valve conical, beak inflated, recurved over well-defined catacline pseudointerarea which is divided into propareas by narrow ridge, pedicle opening apparently absent in adults. Brachial valve strongly convex, beak similar to pedicle valve, small anacline pseudointerarea. Valves ornamented by concentric growth lines. Internal structure unknown. *L.Ord.,* Eu.(NW. USSR).——FIG. 185,*6*. **V. recurva* (KUTORGA); *6a,b,* plaster cast of both valves post., lat., ×1.5 (Rowell, n).

Walcottina COBBOLD, 1921, p. 334 [**W. lapworthi*; OD]. Pedicle valve transversely oval, convex, beak recurved above or behind straight posterior margin; pseudointerarea poorly defined, pedicle opening probably triangular delthyrium beneath beak. Brachial valve unknown. Shell apparently phosphatic, in 3 layers, outer layer with fine concentric fila, middle layer with radial striae, inner layer apparently smooth. *L.Cam.,* Eu.(Eng.).——FIG. 185,*5*. **W. lapworthi*; partly exfoliated ped. v., ×5 (Rowell, n).

CLASS INARTICULATA—ADDENDUM

The genus *Ptychopeltis* PERNER was regarded as a monoplacophoran by KNIGHT & YOCHELSON, who in the *Treatise* provisionally assigned it to the Archinacellidae (p. *I*81).

Horný (433a, 433b) has recently argued that the gross form of the shell and its internal markings are inconsistent with such a taxonomic position and based on the genus he has erected a new family (Ptychopeltidae) which he considers is best referred to the inarticulate brachiopods. As Horný noted, several features of *Ptychopeltis* are reminiscent of characters found in some Inarticulata, and if he is correct in considering the shell phosphatic, then, superficially at least, the genus shows a degree of resemblance to the discinaceans. Some characteristics of the shell, however, notably such features as the strong ?dorsally directed commissure deflection, are unknown in any undoubted inarticulate brachiopod, and until the second (?pedicle) valve is discovered or the musculature discerned, the affinity of the family with brachiopods can at best be regarded as only tentatively established. It has not yet been possible for me to examine material of the genus and Horný's (433b, p. 62) diagnosis therefore is reproduced in full.

Family PTYCHOPELTIDAE Horný, 1961

[Ptychopeltidae Horný, 1961, p. 299]

"Subovate arched, saddle-shaped shells with small blunt apex near or at the apical margin; aperture semicircular, not in a plane; lateral sides rounded, curved deeply downwards, the abapical (anterior) margin curved strongly upwards to form a distinct saddle which is not too well expressed in young stages; outer surface with faint, crowded radial striation, striae not bifurcated; shell lamellar, probably carbonatic-phosphatic; inner structure without visible scars except the median groove and series of numerous small marginal scars bordering the apical and lateral sides of the shell, corresponding probably to the pallial sinuses." *M.Ord.*

Ptychopeltis Perner, 1903, p. 42 [**P. incola*; OD]. Characters of family. *M.Ord.*, Eu.

Class UNCERTAIN

By A. J. Rowell

[Nottingham University]

Order KUTORGINIDA Kuhn, 1949

[*nom. correct.* Goryansky, 1960, p. 181 (*pro* order Kutorginacea Kuhn, 1949, p. 99)] [*emend.* Rowell, herein] [=Palaeotremata Thomson, 1927, p. 118; ?incl. order Rustellacea Kuhn, 1949, p. 99]

Shell calcareous, biconvex; cardinal area present in pedicle valve but not clearly demarcated in all specimens from remainder of valve, small apical foramen, delthyrium widely triangular, partially closed by pseudodeltidium; teeth seemingly absent. Brachial valve with variably developed cardinal area, notothyrium may be restricted apically by chilidium, cardinal process absent. Two principal mantle canals in both valves, with numerous radially arranged grooves, probably vascular in origin; muscle field in each valve narrow, elongate, near mid-line of valve. *L.Cam., ?M.Cam.*

Superfamily KUTORGINACEA Schuchert, 1893

[*nom. transl.* Walcott & Schuchert, 1908, p. 144 (*ex* Kutorginidae Schuchert, 1893, p. 151)] [?incl. Rustellacea Walcott, 1908, p. 143 (*partim*)]

Characters of order. *L.Cam., ?M.Cam.*

The superfamily is here considered to include the Kutorginidae and Yorkiidae. Previously, *Yorkia* has always been regarded as a calcareous-shelled inarticulate brachiopod, related in some way to *Obolella* (680), but the systematic position indicated for *Kutorgina* has been more varied. The latter genus has been placed in the Inarticulata by some workers (e.g., 356) and regarded as an early articulate brachiopod by other students (e.g., Muir-Wood, 1955). Recent work on the internal structure of *Kutorgina* and *Yorkia* strongly suggests that they are closely related to each other and only distantly to any other stock. The mantle canal system of both genera, particularly of the brachial valve, which is better known, is basically the same, with two, characteristic, crescentic, principal canals; the musculature of the two genera is also seemingly similar and the gross structure of the pedicle valves is comparable.

Although a separate order (Rustellida Kuhn) has been erected for *Rustella,* this poorly known genus is provisionally included in the Kutorginacea. A distinct possibility exists that the type-species of *Rustella*

(R. edsoni) is a *Kutorgina,* but the preservation of the material does not allow this relationship to be established beyond doubt (739b).

The problematic affinities of the kutorginaceans are discussed elsewhere (p. *H*196, *H*227).

Family KUTORGINIDAE Schuchert, 1893

[Kutorginidae SCHUCHERT, 1893, p. 151; incl. Rustellidae WALCOTT, 1908, p. 143, and Schuchertinidae WALCOTT, 1908, p. 145]

Posterior margin of brachial valve unmodified, delthyrium widely triangular, pseudodeltidium relatively small. *L.Cam., ?M.Cam.*

Kutorgina BILLINGS, 1861, p. 8 [**Obolella cingulata*; OD] [=*Koturgina* BILLINGS, 1861, p. 8 *(nom. imperf.)*; *?Rustella* WALCOTT, 1905, p. 311 (type, *R. edsoni*)]. Cardinal area of pedicle valve orthocline, becoming anacline in old individuals which develop strongly convex valve; beak of brachial valve flexed abruptly above remainder of valve, notothyrium closed apically by small chilidium. Ornament of growth lines, lamellose peripherally, granular micro-ornament. *L.Cam.,* N.Am.-Eu.-Asia.——FIG. 187,*1a-c.* **K. cingulata* (BILLINGS), USA(Vt.); *1a,* ped.v. ext.; *1b,* brach. v. ext.; *1c,* both valves lat., all ×1.5 (Rowell, n).——FIG. 187,*1d,e. K. reticulata* POULSON, E. Greenl.; *1d,e,* ped. v. int. impression, brach. v. int. impression, both ×1.5 (Rowell, n).

?Schuchertina WALCOTT, 1905, p. 323 [**S. cambria*; OD]. Genus poorly known, apparently similar to *Kutorgina,* but subequally biconvex. *M.Cam.,* N.Am.

Family YORKIIDAE Rowell, 1962

[Yorkiidae ROWELL, 1962, p. 144]

Posterior margin of brachial valve bearing 2 narrowly triangular plates ornamented by lines parallel to their narrow base. *L. Cam.*

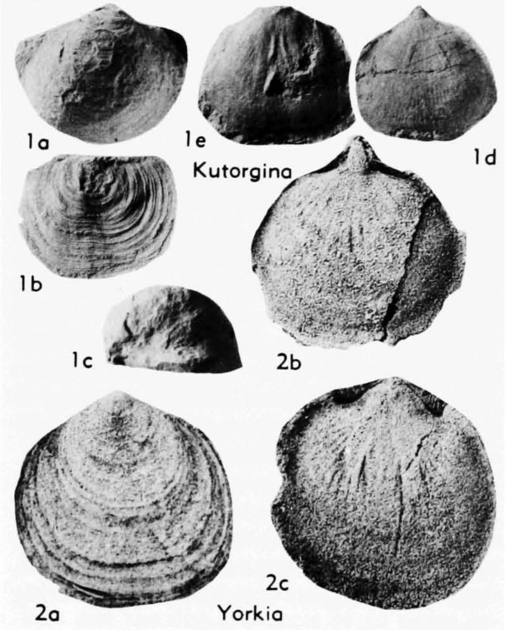

FIG. 187. Kutorginidae *(1)*; Yorkiidae *(2)* (p. *H*297).

Yorkia WALCOTT, 1897, p. 714 [**Y. wanneri*; OD] [=*Quebecia* WALCOTT, 1905, p. 320 (type, *Obolella circe* BILLINGS, 1872, p. 219)]. Pedicle valve with small pointed beak abruptly flexed above remainder of valve, cardinal area apsacline to catacline, pseudodeltidium well developed. *L. Cam.,* N.Am.——FIG. 187,*2.* **Y. wanneri,* USA (Pa.); *2a,b,* ped. v. ext. (wax cast), int. impression, both ×2; *2c,* brach.v. int. impression, ×2 (680).

ARTICULATA

By D. V. AGER, T. W. AMSDEN, GERTRUDA BIERNAT, A. J. BOUCOT, G. F. ELLIOTT, R. E. GRANT, KOTORA HATAI, J. G. JOHNSON, D. J. MCLAREN, H. M. MUIR-WOOD, CHARLES W. PITRAT, A. J. ROWELL, HERTA SCHMIDT, R. D. STATON, F. G. STEHLI, ALWYN WILLIAMS, and A. D. WRIGHT

Class ARTICULATA Huxley, 1869

[Articulata HUXLEY, 1869, p. 116] [=Arthropomata OWEN, 1858, p. 336; Testicardines BRONN, 1862, p.301; Clistenterata KING, 1873, p. 15; Pygocaulia THOMSON, 1927, p. 116] [Diagnosis prepared by ALWYN WILLIAMS, Queen's University of Belfast]

Valves calcareous and impunctate, punctate or pseudopunctate, with fibrous or variably prismatic secondary layer and nonfibrous primary layer commonly well differentiated, periostracum of protein in living species; hinge teeth and dental sockets composed of secondary shell, well developed or rarely lost or replaced; socket ridges commonly modified as crura (or homologues) associated with rarer loops or spires to provide support for lophophore; musculature for opening and closing valves about hinge axis consisting of diductor and adductor sets with bases commonly grouped posteromedially. Pedicle of living species developing from larval rudiment and controlled by dorsal as well as ventral adjustor muscles, inferred to have originated in same way in many extinct groups or to have arisen as extension of ventral body wall in others. Larval development involving differentiation of anterior lobe and mantle and pedicle rudiments, coelom enterocoelic; shell, alimentary canal, and lophophore without median tentacle, appearing after settling with mantle reversal occurring in living species but inferred not to have taken place in some extinct stocks. Alimentary canal ending blindly, row of ablabial filaments arising in addition to adlabial set only in post-trocholophous stages of lophophore development. *L.Cam.-Rec.*

The division of the Brachiopoda into two distinct classes is undeniably validated, as has been recognized for more than a century, by basic morphological, anatomical, and embryological differences among living species.

The exoskeletons of Recent articulates are immediately distinguishable from those of living inarticulates in being invariably calcareous with well-defined primary and secondary layers and in possessing a tooth-and-socket system of valve articulation and secondary shell outgrowths of variably developed crura or loops which support the lophophore, or both. Within articulate shells, the absence of an anus, presence of a relatively complex pedicle that developed independently of the rest of the body from an embryonic rudiment, fusion of outer lobes of the mantles along the posterior margin, and the distinctive grouping of a simplified musculature are further indications of a fundamental divergence within the phylum. The embryological differences are equally significant. In contrast to living inarticulates, a reversal of the mantle rudiment, an enterocoelic derivation of the coelom and an absence of a median tentacle throughout the development of the lophophore are all characteristic of the articulates. Indeed, Percival (1944), admittedly in support of a mistaken belief that there was also a difference in body orientation, contended that the similarity between the articulates and inarticulates was an expression of convergence rather than common ancestry and advocated their separation into two phyla.

An interpretive study of brachiopod history, like that outlined in the chapter on "Phylogeny and Evolution," does not, however, support such radical taxonomic reform. On the contrary it suggests that all brachiopods were descended from the same ancestral stock and that the articulates diverged at a relatively faster rate by a series of basic modifications which were introduced at different times during phylogeny and only cumulatively represent the distinctiveness of the class. Certainly the differences between the oldest Articulata and Inarticulata are not always as decisive as those between Recent representatives; while the Lower Cambrian Kutorginida cannot be assigned confidently to either class and may have evolved independently.

The only tangible evidence for these conclusions is, of course, based on changes in morphology of the shell. In this respect articulation seems to have been the most persistent feature of the class, because primitive teeth and sockets are found even in billingsellaceans, whereas their absence, as in members of the Productidina, was invariably due to degeneration. The structure of the shell and the presence of calcareous supports for the lophophore are much less diagnostic. The primary layer is poorly differentiated in most species of the Orthida and Strophomenida, and the nonfibrous test of the Dictyonellidina is really like that of the calcareous-shelled inarticulates. Skeletal outgrowths that undoubtedly gave support to the lophophore are also relatively late features of articulate history and in their most typical forms as crura, loops, and spires are characteristic only of the later Pentamerida, Rhynchonellida, Terebratulida, and Spiriferida.

There are, moreover, certain morphological features of extinct articulate groups that may be taken to indicate equally profound embryological and anatomical changes. The absence of a well-defined chamber for reception of the pedicle base among the Orthida, Strophomenida, and Pentamerida suggests that mantle reversal first took place during emergence of the Rhynchonellida and became a feature of articulate development only in members of that order and the related Spiriferida and Terebratulida. The gap between the pseudodeltidium and chilidium of the billingsellaceans and early Strophomenida was more likely sealed by a posterior body wall of inner epithelium than by extensions of outer epithelium. This arrangement, together with the restriction of the pedicle-outer epithelial junction to the ventral apical regions by growth of pseudodeltidium in members of the Billingsellacea, Clitambonitidina, Triplesiidina and Strophomenida, suggests that in such species, the pedicle, like that of the inarticulates, was an extension of the ventral body wall. Hence, it is feasible to assume that the articulates were originally closely related to the inarticulates and that, although taxonomic segregation into two classes is warranted, differences become less important as both groups are traced back in time.

For reasons outlined in the chapter on "Classification," the Articulata are here divided into six orders embracing 37 superfamilies. Two additional suborders, the Dictyonellidina and the Thecideidina, each comprising a small number of genera but undeniably related to the Articulata, have not as yet been assigned to an ordinal group. The former may ultimately prove to have arisen independently of the remaining articulates, thereby meriting ordinal rank in the manner of the Kutorginida, Paterinida, and Obolellida. The ancestry of the Thecideidina is at present debatable, with the Spiriferida, Terebratulida, and the Strophomenida each qualifying, to a variable degree, for the role.

The distinctions drawn between the six orders are decisively diagnostic only in respect of their modal morphology. It is, for example, convenient and indeed desirable in gross comparison, to visualize typical Orthida as impunctate or endopunctate shells with an open delthyrium and brachiophores, Strophomenida as pseudopunctate with a pseudodeltidium and socket ridges, Pentamerida as impunctate with a spondylium and homologues of crura, Rhynchonellida as impunctate with deltidial plates and crura, Spiriferida as impunctate or endopunctate with a variable delthyrial cover and spiralia, and Terebratulida as endopunctate forms with deltidial plates and a loop. Yet so recurrent were the processes of evolution that no one character is either exclusive to an order or invariably exhibited by all its members and the distinctiveness of an order depends solely on its unique combination of all characters. Consequently, ordinal diagnoses are variably repetitive and indications of changes in character combinations are commonly more important guides to the individuality of the taxa than the prevalence of a single feature.

ORTHIDA

By Alwyn Williams and A. D. Wright
[Queen's University of Belfast and Nottingham University]

Order ORTHIDA Schuchert & Cooper, 1932

[*nom. transl. et correct.* Moore in Moore, Lalicker, & Fischer, 1952, p. 220 (*ex* suborder Orthoidea Schuchert & Cooper, 1932, p. 43)] [*emend.* Williams & Wright, herein] [Materials for this order prepared by Alwyn Williams except Enteletacea and Triplesiidina by A. D. Wright]

Articulate brachiopods normally with unequally biconvex strophic shells and well-developed interareas and hinge lines; delthyrium and notothyrium open or less commonly closed by pseudodeltidium and chilidium, deltidial constrictions to delthyrium very rare. Ventral muscle field commonly not extending much beyond umbonal cavity, rarely elevated on spondylial or other structures of secondary shell. Cardinal process normally as median partition or differentiated into variably lobate myophore and shaft, rarely absent or forked; socket ridges commonly replaced by brachiophores with or without fulcral plates and convergent to divergent bases, less commonly bearing long processes which may have supported lophophore; lophophore inferred to have varied from schizolophous to spirolophous condition. Shell substance normally impunctate but also endopunctate and rarely pseudopunctate. *L.Cam.-U.Perm.*

The assignment of the Orthidina, Clitambonitidina, and Triplesiidina to the same ordinal group seems the best way to express the strong morphological affinities that exist between these primitive articulate brachiopods. All three suborders were mainly characterized by a strophic shell which lacked calcareous supports for the lophophore as well as a pedicle chamber. Indeed, only the forked cardinal process of the Triplesiidina and the spondylium of the Clitambonitidina

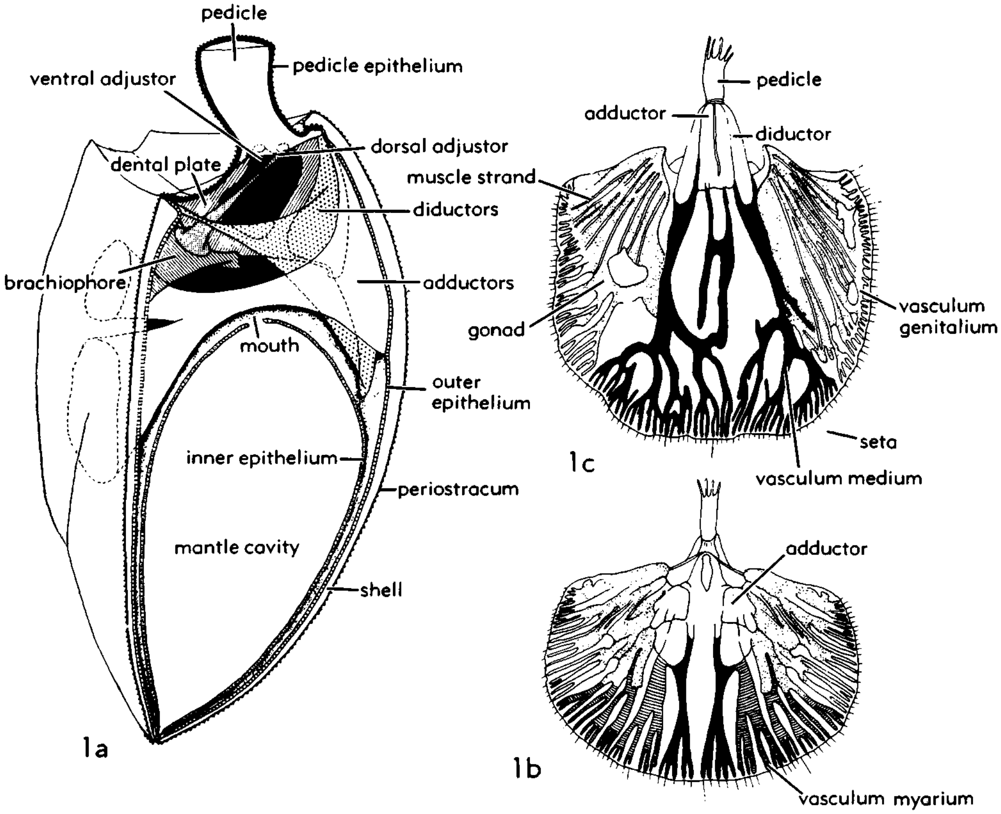

FIG. 188. *Howellites antiquior* (M'COY); *1a,* stylized reconstruction of musculature; *1b,c,* inferred morphology of soft parts viewed from dorsal and ventral exteriors (880).

may be regarded as the pre-eminent requisites for distinction at the subordinal level, because the pseudodeltidium, which is the other principal feature of these two groups, is also present in the billingsellaceans. Admittedly, the possession of a pseudodeltidium may be sufficiently important in itself to warrant an entirely different grouping. Yet the billingsellaceans have a great deal more in common with early orthaceans than the Triplesiidina, for example, and the failure of the pseudodeltidium to develop in some Clitambonitidina indicates that the open delthyrium was not unique to the orthaceans and enteletaceans.

Suborder ORTHIDINA Schuchert & Cooper, 1932

[*nom. correct.* WILLIAMS & WRIGHT, herein (*pro* Orthoidea SCHUCHERT & COOPER, 1932, p. 43)] [*emend.* WILLIAMS & WRIGHT, herein]

Plano-convex to convexo-concave, costate to finely costellate or parvicostellate with superimposed costae, ventral interarea commonly curved, apsacline, delthyrium rarely closed by apically perforate pseudodeltidium or deltidium, chilidium rarely developed; teeth simple, ventral muscle field almost invariably impressed on valve floor and dental plates; cardinal process absent, simple, or differentiated into variably lobate myophore and shaft; sockets defined by ridges or outer surfaces or brachiophores with or without fulcral plates, brachiophores as short plates or rods, less commonly with processes and variably disposed supporting bases; dorsal adductor field quadripartite, normally divided by median ridgelike extension of notothyrial platform; mantle canal systems saccate to lemniscate; shell substance impunctate or punctate. *L.Cam.-Perm.*

The Orthidina, as here constituted, are an assemblage of extinct Paleozoic stocks that include the oldest known articulate brachiopods. They were especially prolific during Cambro-Ordovician times and became so diversified as to anticipate most of the morphological characteristics of other groups. Many of these stocks, however, were short-lived deviations from a small number of persistent lineages and have little effect on the modal design of the three superfamilies making up the suborder. Moreover, the differences between *Eosotrematorthis, Orthambonites,* and *Howellites,* which display the modal characteristics of the Billingsellacea, Orthacea, and Enteletacea, respectively, although important, actually include a minority of skeletal features, so that a representative orthoid can be satisfactorily defined.

The exterior of a typical member of the Orthidina is quite distinctive. It is that of a biconvex strophic shell, subquadrate in outline, with a maximum width anterior of a well-developed hinge line and a curved apsacline ventral interarea which is longer than an anacline dorsal interarea. A strong, median dorsal sulcus is normally present and the shell surface is usually costellate. Variations include the convexo-concave profile of many plaesiomyids, the bilobed outline of *Dicoelosia*, the reduced or mucronate hinge lines of *Angusticardinia* and *Skenidioides* respectively, the obsolescent interareas of *Productorthis,* the dorsal median fold of *Platystrophia* and of *Enteletes* with its additional superimposed radial plications; and the absence of radial ornamentation in *Kotujella* or the common occurrence of hollow ribs among enteletaceans and plectorthids. The most important external difference, however, is the persistence of a chilidium and pseudodeltidium among billingsellaceans and their absence in the orthaceans and enteletaceans. Chilidial-like structures are known in some hesperonomiids, productorthinids, and plaesiomyids, and deltidial plates were variably developed in a few independent stocks like *Trematorthis, Barbarorthis*, and *Phragmophora*; but the latter structures, at least, are not homologous with the billingsellacean pseudodeltidium, and, in general, the notothyria and delthyria of the orthaceans and enteletaceans remained uncovered.

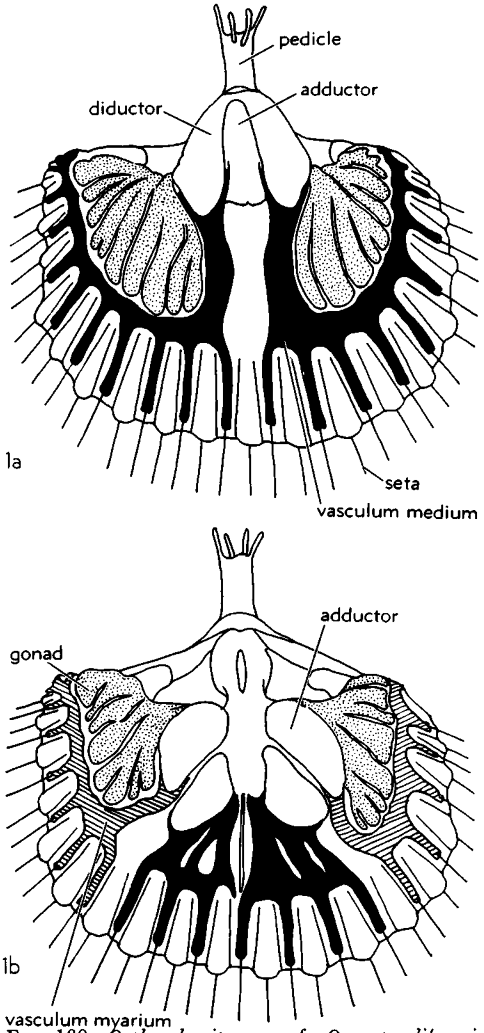

FIG. 189. *Orthambonites* sp. cf. *O. rotundiformis* COOPER; *1a,b,* stylized reconstruction of inferred morphology of soft parts viewed from the ventral and dorsal exteriors (Williams, n).

Basic similarities are also evident internally, because only shell structure is as important as the presence of the pseudodeltidium in the superfamilial classification of the Orthidina. Thus, all enteletaceans are endopunctate, in contrast to the impunctate condition of billingsellaceans and orthaceans, although other morphological features suggest that the earliest known enteletaceans, the paurorthids, dalmanellids, and angusticardiniids, became endopunctate independently of one another.

The ventral muscle impressions of the Orthidina are normally subtriangular or bilobed in outline and confined to the posterior half of the pedicle valve (Fig. 188, 189). The umbonal chamber was never differentiated to receive the base of the pedicle as in other orders. It was occupied,

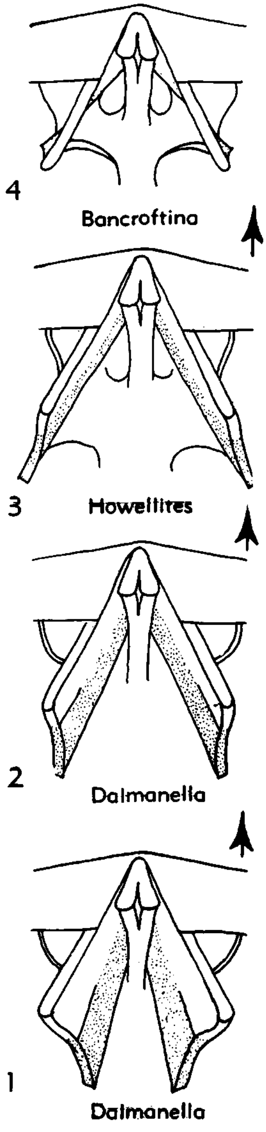

FIG. 190. Possible orthogenetic evolution of dalmanellid cardinalia involving lateral migration of brachiophore bases (shaded) from subtending an angle significantly less than that between tops of the brachiophores *(1)* to a not significantly smaller angle *(2)*, to a not significantly greater angle *(3)*, and to a significantly greater angle *(4)* (880).

solely by the muscle bases up to a variably developed pedicle callist, with the median adductor scars normally not enclosed anteriorly and the adjustors and lateral diductor lobes, at least in the orthaceans and enteletaceans, inserted on the inner surfaces of the dental plates (Fig. 188). In some stocks, like the plaesiomyids and heterorthids, the ventral muscle field was greatly splayed over the valve floor. In others, it was elevated on a spondylium (e.g., *Skenidioides*) or, as in *Parenteletes* and *Elasmothyris*, respectively, inserted on a shoe-lifter process or transverse plate. Yet such modifications as these were rare; indeed, the most important changes affecting the internal morphology were those that led to the diversification of the cardinalia.

The most commonly occurring cardinalia among the billingsellaceans, orthaceans, and enteletaceans are basically different from one another morphologically and, by inference, functionally. In all three groups, the notothyrial platform is normally well developed, as are the sockets for reception of the ventral teeth. In the billingsellaceans, the notothyrium is flanked by a pair of flat-lying plates or rods, more or less parallel with the hinge line, which acted principally as inner boundaries to the sockets, although they might also have received any dorsal adjustors that had developed. In the orthaceans and enteletaceans, on the other hand, the homologues of these socket ridges (brachiophores) are not only better developed rods or blades, which may be prolonged distally as processes, but subtend much greater angles with the hinge line. In this attitude they are more likely to have been elaborated into supports for the mouth segment of the lophophore. Moreover, the brachiophores of most enteletaceans and some orthaceans like the plectorthids are commonly supported by expanded bases and, together with fulcral plates, define sockets that are distally elevated above the floor of the brachial valve. The disposition of the brachiophore bases can vary greatly even within a series of closely related genera like those assigned to the Dalmanellidae. Using members of this family, it is possible to demonstrate a continuous gradient of change between arrangements in which the angle subtended by the brachiophore bases is significantly less or greater than that subtended by the tops of the brachiophores. Hence, although *Bancroftina, Dalmanella,* and *Howellites* are each characterized by a distinctive attitude, the last two genera together include species showing every conceivable variation in the disposition of the bases relative to the top of the brachiophores (Fig. 190). Generally, however, their attitude tends to be consistent in different stocks, so that they may converge onto a median septum to form a septalium, as in *Linoporella* and *Skenidioides,* or be widely divergent, as in *Enteletes.*

There are important differences in the origin and function of the diverse structures, collectively referred to as the cardinal process, that project posteriorly from the notothyrial platform. The lack of such outgrowths is relatively rare and represents the most primitive condition, although it is characteristic of species of the Ordovician enteletacean *Paurorthis,* while well-developed processes are found in such Cambrian stocks as *Billingsella* and the orthacean *Arctohedra.* In the majority of billingsellaceans and orthaceans, the commonest type of cardinal process consists of a median partition that effectively divides the posterior surface of the notothyrial platform into two halves, each of which received the dorsal ends of the diductor muscles. In a few stocks (e.g., *Dolerorthis, Hesperonomia*), the notothyrial areas flanking the median partitions were elaborated into ridges for reception of the diductor bases, and in the orthidiellids, these grew high and became fused with the median partition to form a trilobed process. In most orthaceans, however, further modification involved the migration of the diductor bases onto the posterolateral surfaces of the median partition, which, in consequence, is either indented by muscle impressions, as in some plectorthids or, more commonly, is differentiated into a bulbous crenulated myophore surmounting a thickened shaft, as in many plaesiomyids. This latter arrangement is prevalent among enteletaceans with the myophore mostly fashioned in a bilobed or trilobed manner, thereby separating the diductor bases from each other.

The dorsal ends of the adductor muscles were implanted posteromedially within the brachial valve of the Orthidina and normally left a pair of posterior and anterior scars on the valve floor on either side of a median ridge (Figs. 188, 189). The ridge was built up as a low anterior extension of the notothyrial platform and only rarely did it culminate in a high median septum, as in the cremnorthids, skenidiids, and kayserellids. In such stocks as these, the median septum effectively divided the mantle cavity into two compartments, each of which presumably contained a variably developed brachium; and in *Hyposmyonia* it also affords support for an elevated platform of secondary shell which accommodated the dorsal adductor bases. The most unusual modification is undoubtedly that found in *Tropidoleptus,* in which posteriorly directed outgrowths from a median septum became contiguous with greatly extended brachiophore processes to complete a loop, presumably for support of the lophophore.

Despite the variation that is known to have occurred in the mantle canal systems of the Orthidina, one of the least specialized patterns, comprising saccate and digitate distributions in the pedicle and brachial valves, respectively, is easily the most common among the billingsellaceans and orthaceans (Fig. 189). A lemniscate arrangement in both valves, on the other hand, is prevalent among the enteletaceans (Fig. 188). Yet these differences between superfamilies is not mutually exclusive. The ventral and dorsal patterns of the enteletacean paurorthids, for example, are saccate and digitate like most orthaceans, while those of the finkelnburgiids (digitate and digitate) and some plectorthids (saccate and digitate but with the gonads pervading the entire mantles) approach the enteletacean condition.

The dominance of the modal morphological assemblages outlined above is, of course, a reflection of the trends that characterized orthoid evolution. The billingsellaceans were really important only in their rôle as probable ancestors of the more advanced orthaceans, because they comprise an insignificant group, with only the more specialized members, equipped with a relatively well-developed articulation and a strong notothyrial platform, surviving into the Ordovician. In contrast, contemporary orthaceans not only underwent a remarkable radiation but also gave rise to four groups which persisted into the Silurian and did not become entirely extinct until the end of Devonian times. Two of these groups, the orthids and dolerorthids, epitomize the survival of a more primitive organization, whereas the plectorthids and skenidiids display a number of relatively advanced features.

The conservative nature of orthid and dolerorthid morphogeny is illustrated by the persistence of unsupported brachiophores, a simple cardinal process consisting of a median partition, rarely with ancillary notothyrial ridges, and a relatively small, compact ventral muscle field, largely confined to the umbonal chamber. Indeed, the dolerorthids seem to have diverged from their presumed ancestors, the orthids, only through the development of an advanced digitate to apocopate dorsal mantle canal system and a long ventral interarea, because other changes were duplicated in the orthids. Thus, the acquisition or suppression of costellae in related costate and costellate stocks is found in both families, while the strongly lamellose ornamentation of the glyptorthinids was repeated in the productorthinids, which also represented the climax of the trend that led to obsolescence of the short orthid interareas.

It is likely that the plectorthids, and even the skenidiids, arose from the older finkelnburgiids in late Cambrian times, because the brachiophores of all three groups are supported by expanded bases and the cardinal process was normally differentiated into myophore and shaft. Nonetheless, the most distinctive features of both the plectorthids and skenidiids were already established by early Ordovician times, including the high ventral interarea, spondylium, and high dorsal median septum of the latter family. Apart from a conspicuous lengthening of the ventral interarea in some species of *Mimella,* these features were not developed in the plectorthids, although a considerable diversification in other morphological aspects took place. Hollow ribs are a common characteristic of the plectorthinids and rhactorthinids, which also show an incipient development of a lamellose ornamentation. But the most divergent trends affecting external form were those that led to the emergence of mucronate and strongly plicate platystrophiinids and the contemporary rostrate cyclocoelinids. Internally, the most conspicuous changes affected the disposition of the brachiophore bases. Those of most plectorthids are convergent to subparallel and are associated with well-developed fulcral plates, but those of the mid-Ordovician *Rhactorthis* were so widely divergent as to define the sockets without the ancillary growth of fulcral plates.

The changes within the skenidiids were relatively minor, because, once established, the main characters, like the spondylium and brachiophore bases convergent onto a high median dorsal septum, remained more or less stable throughout stock history. In the course of time, however, a migration of the brachiophores toward the median plane probably occurred, because each fulcral plate of the Devonian stock *Skenidium* was sufficiently large to carry a subsidiary ridge as an inner boundary to the socket. This development is reminiscent of the definition of the inner socket ridges that took place during the evolution of the rhynchonellids, and it is probably also significant that in many skenidiids, the brachiophores were equipped with processes long enough to have given support to the mouth segment of the lophophore.

Three stocks of punctate enteletaceans appeared in the Lower Ordovician and include the earliest representatives of one of the three most successful enteletacean groups, the dalmanellids. The accompanying stocks, the primitive orthid-like paurorthids and the aberrant rhynchonelliform angusticardiniids, became extinct before the end of Ordovician times, and although the former achieved wide distribution during its relatively brief history, the latter was apparently restricted to Europe. The dalmanellids, on the other hand, were not only ubiquitous and persistent into the Lower Carboniferous but were also ancestral to the two other major groups, the enteletids and the rhipidomellids, both of which survived to the end of the Permian. Other divergences from the dalmanellids include the widespread *Dicoelosia,* with its distinctive bilobed outline, and less successful Devonian forms which were characterized by the presence of a strong dorsal median septum. Both these structural modifications were directed toward the longitudinal division of the mantle cavity, possibly as an aid to the feeding mechanism.

The dalmanellids differ from their presumed finkelnburgiid ancestors in the endopunctate condition of the shell and, ultimately, in their advanced cardinalia. The cardinalia of the early forms varied greatly, particularly in the attitude of the bases of the brachiophores relative to their tops. This variability, however, was reduced in time because divergent bases became standard in the later forms. The converse was true of the cardinal process, which initially progressed rapidly from the simple orthacean ridge to an undifferentiated bilobed type but became dominantly trilobed in the later forms, although still variable even within a single species. In such characters as these, together with the relatively small, compact ventral muscle field, which extends little beyond the umbonal chamber, and the rare development of hollow costellae, the dalmanellids constitute the least specialized enteletacean stocks.

The enteletids are represented in the Middle Ordovician by the drabovinids, which differ from contemporary dalmanellids in their very fine, hollow costellae, anteriorly extended ventral muscle field, and distinctive cardinalia. The cardinalia include a slender cardinal process with a crenulated, rather than distinctly lobate myophore, delicate, commonly tusklike brachiophores supported laterally by well-developed fulcral plates and dorsally by bases which may converge toward the median ridge, but with ridgelike anterior extensions on the valve floor directed medially toward the center of the adductor field. In late Ordovician times, this group was replaced by the schizophoriinids, in which the anterior extensions of the brachiophore bases diverge to contain the adductor field laterally. An accompanying trend was the relative deepening of the brachial valve to produce a dorsibiconvex profile, instead of the ventribiconvex to subequally biconvex profile of the Middle Ordovician forms. In the Carboniferous, the enteletinids evolved from a schizophoriinid stock. These new forms are morphologically very distinct, with their strongly globose form, abundant radial plications superimposed on the fine radial ornament, the internal strengthening of the dental plates and the high ventral median septum. These aberrant forms persisted alongside the standard *Schizophoria* until the end of the Permian.

The rhipidomellids are not known in pre-Silurian rocks, and although the heterorthids do show many similarities which suggest close affinities (or parallel development) it is difficult to envisage *Rhipidomella* as being a direct descendant of the rather specialized heterorthid genera at present known. Like the enteletids, the rhipidomellids possess a fine ornament of hollow costellae. Externally they differ in their subcircular outline, the shortness of their hinge lines and the shallowness of their valves, and show little tendency to develop fold or sulcus. A marked difference from the other two major groups is seen in the very large ventral muscle field in which the adductors are enclosed by the large diductor scars, the latter condition appearing only rarely in the dalmanellids. The cardinalia, too, are quite distinct from those of contemporary enteletids, especially in the swollen and lobate nature of the cardinal process and the strength of the brachiophores which bound the sockets without fulcral plates.

Like the contemporary *Schizophoria, Rhipidomella* was another successful, stable stock, persisting with little modification from early Silurian to late Permian times, and although it gave rise to several genera, none of these enjoyed the same degree of success as their progenitor.

Superfamily BILLINGSELLACEA Schuchert, 1893

[*nom. transl.* Williams, herein (*ex* Billingsellidae Schuchert, 1893, p. 152)]

Delthyrium covered by arched pseudodeltidium perforated by apical foramen, chilidium present but variably developed. Teeth primitive, with or without dental plates; ventral muscle field impressed on floor of pedicle valve; cardinal process absent or as simple ridge; sockets simple, socket ridges bladelike, unsupported; ventral mantle canal system saccate, dorsal probably digitate. Shell substance impunctate. *L.Cam.-L.Ord.*

Family BILLINGSELLIDAE Schuchert, 1893

[Billingsellidae Schuchert, 1893, p. 152]

Interareas and hinge lines well developed, pseudodeltidium strong, perforate apically, chilidium present; teeth large, dental plates variably developed, ventral muscle field with widely divergent diductor scars and large subtriangular adductor track commonly extending well anterior of umbonal cavity; cardinal process simple ridgelike, socket ridges as widely divergent short, unsupported blades, sockets cuplike; ventral canal system saccate, with proximal parts of *vascula media* divergent, dorsal digitate. *M.Cam.-L.Ord.*

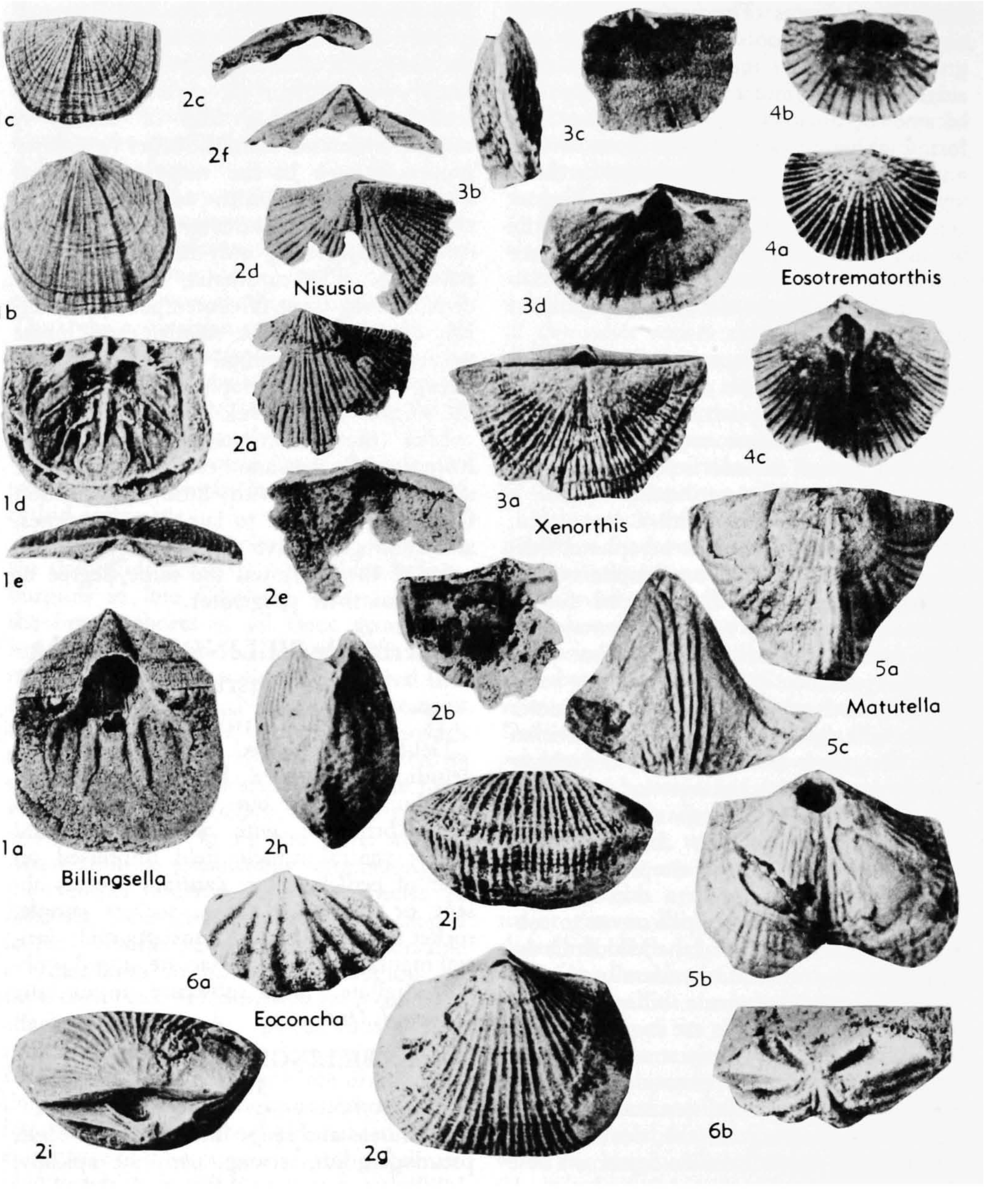

FIG. 191. Billingsellidae *(1, 3-4)*; Nisusiidae *(2, 5-6)* (p. *H*306-*H*307).

Billingsella HALL & CLARKE, 1892, p. 230 [**Orthis pepina* HALL, 1863, p. 134; OD]. Subquadrate in outline, unequally biconvex, with long orthocline to apsacline interarea in deeper pedicle valve, subdued multicostellate to unequally parvicostellate. *M.Cam.-L.Ord.*, cosmop.——FIG. 191,*1*. *B. perfecta* ULRICH & COOPER, U.Cam.(Dry Creek), USA (Idaho-Wyo.); *1a*, ped. v. int., ×3; *1b*, ped. v. ext., ×2; *1c*, brach. v. ext., ×2; *1d,e*, brach. v. int., post., ×3 (825).

Cymbithyris COOPER, 1952, p. 5 [**C. hami*; OD]. Like *Billingsella* but concavo-convex and lacking dental plates. *L.Ord.*, W.USA.

Eosotrematorthis WANG, 1955, p. 336 [**E. sinensis*; OD]. Like *Billingsella* but strongly costellate. *L. Ord.*, China.——FIG. 191,*4*. **E. sinensis*; *4a,b*, brach. v. ext., int., ×3; *4c*, ped. v., int., ×3 (852).

Xenorthis Ulrich & Cooper, 1936, p. 620 [**Strophomena stosei* Bassler, 1919, p. 250; OD]. Semioval in outline, subequally biconvex but with median fold in brachial valve; costellate and variably lamellose; interiors like those of *Billingsella* but dental plates rudimentary or absent; socket ridges rodlike, *?U.Cam.-L.Ord.*, E.USA-Ire.——Fig. 191,*3*. **X. stosei* (Bassler), U.Cam., USA (Md.); *3a*, brach. v. view of conjoined valves, ×2; *3b*, lat., ×2; *3c*, brach.v. int., ×4; *3d*, ped.v. int., ×3 (825).

Family NISUSIIDAE Walcott & Schuchert, 1908

[*nom. transl.* Schuchert & Cooper, 1931, p. 242 (*ex* Nisusiinae Walcott & Schuchert, 1908, p. 147)]

Interareas and hinge lines well developed, pseudodeltidium strong, foramen apical or anterior to apex through pedicle valve, chilidium variable; teeth rudimentary, dental plates absent, ventral muscle field rarely preserved but apparently with short adductor scar, and long divergent diductor scars; cardinal process absent or rudimentary; notothyrial platform rudimentary, socket ridges bladelike making acute angle with hinge line to define sockets; dorsal adductor scars, when present, as elongate impressions on either side of indistinct median ridge. *L.Cam.-M.Cam.*

Nisusia Walcott, 1905, p. 247 [**Orthisina festinata* Billings, 1861, p. 10; OD]. Subquadrate, subequally biconvex, with variable developed median sulcus in both valves, costellate, with beaded tuberculation along costellae at their intersections with strong concentric growth lines. *L.Cam.-M.Cam.*, N.Hemis.——Fig. 191,*2a-f*. **N. festinata* (Billings), L.Cam., USA(Va.); *2a-c*, brach. v. ext., int., post., ×2; *2d-f*, ped. v. ext., int., post., ×2 (176).——Fig. 191,*2g-j*. *N. deissi* Bell, M.Cam., USA(Mont.); *2g-j*, brach. v., ext., lat., ant. views of conjoined valves, ×2 (65).

Eoconcha Cooper, 1951, p. 4 [**E. austini*; OD]. Like *Nisusia* but coarsely costellate and with persistent median sulcus in brachial valve and fold in pedicle valve. *L.Cam.*, E.USA.——Fig. 191,*6*. **E. austini*, USA(Va.); *6a*, brach. v. ext., ×1.5; *6b*, post. view of ped. v. int. mold, ×2 (179).

Kotujella Andreeva, 1962, p. 87 [**K. calva*; OD]. Like *Matutella* but without radial ornamentation. *L.Cam.*, USSR.

Matutella Cooper, 1951, p. 6 [**M. clarki*; OD]. Subquadrate, with high narrow fold in brachial valve, costellate and sporadically imbricate; foramen large, excavated in floor of pedicle valve. *L.Cam.*, E.USA-USSR.——Fig. 191,*5*. **M. clarki*, USA(Va.); *5a,b*, brach. v. ext., ped. v. ext., ×2; *5c*, ant. view of ped. v., ×2 (179).

Superfamily ORTHACEA Woodward, 1852

[*nom. transl.* Walcott & Schuchert, 1908, p. 147 (*ex* Orthidae Woodward, 1852, p. 229)]

Delthyrium open, rarely constricted by deltidial plates or deltidium, chilidium rare; teeth simple, commonly with deep crural fossettes and supported by dental plates; ventral muscle field rarely supported by spondylium; cardinal process simple or differentiated, rarely absent; sockets simple or defined by fulcral plates, brachiophores commonly rodlike, less commonly with supporting bases convergent or divergent on floor of brachial valve; ventral mantle canal system commonly saccate, with proximal parts of *vascula media* convergent or divergent on to median plane, dorsal mantle canal system commonly digitate, rarely apocopate. Shell substance impunctate. *L.Cam.-U.Dev.*

Family EOORTHIDAE Walcott, 1908

[*nom. transl.* Schuchert & Cooper, 1931, p. 242 (*ex* Eoorthinae Walcott, 1908, p. 148)]

Interareas well developed, hinge lines wide, delthyrium and notothyrium open; teeth strong, commonly supported by receding dental plates, ventral muscle scar variably impressed on valve floor or pseudospondylium; cardinal process and notothyrial platform rudimentary, socket ridges widely divergent, bladelike, making acute angles with hinge line to define sockets; ventral mantle canal system saccate with proximal parts of *vascula media* divergent. *L. Cam.-L.Ord.*

Eoorthis Walcott, 1908, p. 102 [**Orthis remnicha* Winchell, 1886, p. 317; OD]. Subquadrate in outline; subequally biconvex, finely costellate, with variably superimposed secondary costation; ventral muscle field impressed on valve floor, subtriangular, with wide adductor track extending beyond diductor scars; cardinal process rudimentary, notothyrial platform scarcely raised off floor of brachial valve but supporting socket ridges, median ridge low. *U.Cam.*, USA-USSR.——Fig. 192,*4*. **E. remnicha* (Winchell), USA(Mont.); *4a,b*, brach. v. ext., int., ×2; *4c*, ped. v. int., ×3; *4d*, post. portion of brach. v., ×3 (65).

Apheorthis Ulrich & Cooper, 1936, p. 620 [**Eoorthis lineocostata* Walcott, 1924, p. 508; OD] [=*Apheoorthina* Havlíček, 1949, p. 99 (type, *A. ferrigena*)]. Like *Eoorthis* but with fascicostellate radial ornamentation and pseudospondylium in pedicle valve; cardinal process generally strong. *U.Cam.-L.Ord.*, N.Hemis.-S.Am.——Fig. 192,*1*. **A. lineocostata* (Walcott), U.Cam.(Manitou), USA(Colo.); *1a*, *1b*, ped. v. ext., int., ×2; *1c,d*,

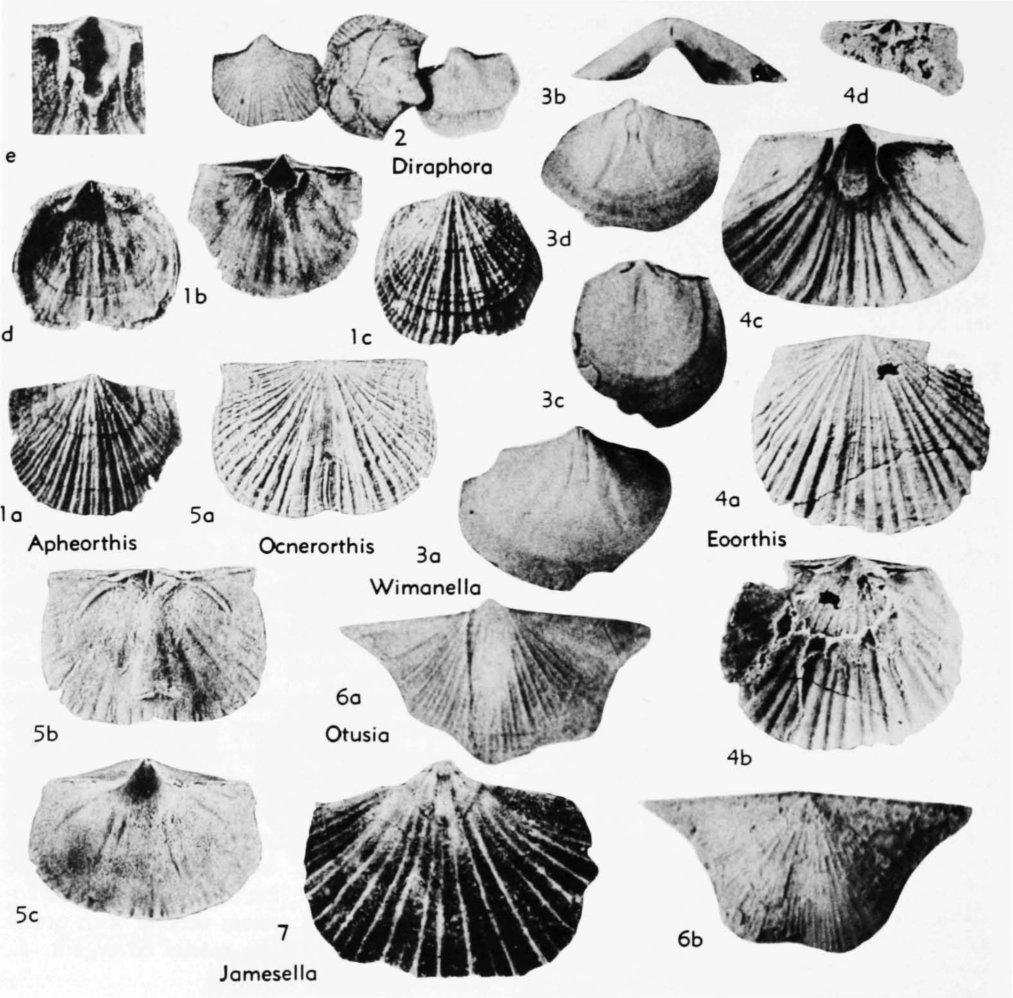

FIG. 192. Eorthidae (p. *H*307-*H*309).

brach. v. ext., int., ×2; *1e,* post. portion of ped. v. enlarged to show pseudospondylium, ×4 (825).

Diraphora BELL, 1941, p. 243 [**Eoorthis bellicostata* WALCOTT, 1924, p. 505; OD]. Like *Wimanella* but costellate. *M.Cam.,* W.N.Am.——FIG. 192,*2.* **D. bellicostata* (WALCOTT), USA(Mont.); 2 ped. v. exts., 1 ped. v. int. mold, ×1.5 (65).

Jamesella WALCOTT, 1905, p. 252 [**Orthis perpasta* POMPECKJ, 1896, p. 515; OD]. Like *Eoorthis* but coarsely costellate. *?M.Cam.-U.Cam.,* Eu. [The systematic position of this genus is uncertain. The type-species is reported as having an open delthyrium, but WALCOTT (1912, p. 733) described a pseudodeltidium in the species *Jamesella kuthani* POMPECKJ.]——FIG. 192,*7. J.* sp. cf. *J. perpasta* (POMPECKJ), U.Cam., Boh.; ped. v. int., ×2 (729).

Ocnerorthis BELL, 1941, p. 251 [**O. cooperi*; OD]. Subquadrate in outline, unequally biconvex to plano-convex, costellate; interiors like those of *Eoorthis* but without dental plates and with strong notothyrial platform and cardinal process. *U.Cam.-L.Ord.,* N. Am.(W. USA)-Eu.(Czech.). —— FIG. 192,*5.* **O. cooperi,* U.Cam., USA(Wyo.); *5a,b,* brach. v. ext., int., ×3; *5c,* ped. v. int., ×3 (65).

Otusia WALCOTT, 1905, p. 246 [**Orthis sandbergi* WINCHELL, 1886, p. 318; OD]. Transversely semioval and mucronate in outline, subequally biconvex, with strong median sulcus in brachial valve, costellate; interiors like those of *Eoorthis. U.Cam.,* N.Am.(USA).——FIG. 192,*6.* **O. sandbergi* (WINCHELL), Mont.; *6a,* ped. v. ext., ×4; *6b,* brach. v. ext., ×3 (65).

Wimanella WALCOTT, 1908, p. 98 [**W. simplex*; OD]. Subquadrate in outline, unequally biconvex, with pedicle valve more convex, shell surface without radial ornamentation; dental plates variably developed; delthyrial cavity with low short median ridge, adductor scars small, subcircular, flanked but not enclosed by divergent diductors; notothyrial platform absent, cardinal process absent or obscure. *?L.Cam., M.Cam.,* N.Am.——Fig. 192,*3*. *W. rossensis* Resser, M.Cam., Can.(B.C.); *3a,b,* normal, post. views of ped. v. int. mold, ×3; *3c,d,* brach. v. int., ped. v. int., molds, ×2 (65).

Family PROTORTHIDAE
Schuchert & Cooper, 1931

[Protorthidae Schuchert & Cooper, 1931, p. 242]

Interareas well developed, hinge lines wide, delthyrium and notothyrium open; teeth small, ventral muscle field supported by free spondylium; cardinal process and notothyrial platform variably developed, brachiophores bladelike and variably disposed; ventral mantle canal system saccate with proximal parts of *vascula media* divergent. *M.Cam.*

Protorthis Hall & Clarke, 1892, p. 231 [**Orthis billingsi* Hartt in Dawson, 1868, p. 644; OD]. Transversely subquadrate in outline, subequally biconvex, costellate; notothyrial platform shallow, median ridge absent, cardinal process absent, brachiophores short, widely divergent. *M.Cam.,* E.N.Am. ——Fig. 193,*7*. **P. billingsi* (Hartt), Can.(N. B.); ped. v. int., ×2.5 (729).

Arctohedra Cooper, 1936, p. 210 [**A. minima*; OD]. Like *Protorthis* but with subpyramidal pedicle valve and with well-developed cardinal process, notothyrial platform, and median ridge; brachiophores long and less divergent. *M.Cam.,* N. Am.——Fig. 193,*3a,b*. **A. minima,* USA(Alaska); *3a,* ped. v. ext., ×6; *3b,* brach. v. int., ×10 (176). ——Fig. 193,*3c,d*. *A. mertiei* Cooper, USA(Alaska); *3c,d,* ped. v. int., post., ×6 (176).

Loperia Walcott, 1905, p. 287 [**Protorthis (Loperia) dougaldensis*; OD]. Like *Protorthis* but convexo-concave and with low thick cardinal process. *M.Cam.,* E.Can.

Family HESPERONOMIIDAE
Ulrich & Cooper, 1936

[Hesperonomiidae Ulrich & Cooper, 1936, p. 621]

Interareas variable in length, hinge lines wide, delthyrium open, chilidium poorly developed; ventral muscle field subquadrate, extending beyond umbonal region; cardinal process as simple ridge, not ankylosed to variably developed notothyrial ridges, brachiophores short, rodlike; ventral mantle canal system saccate, dorsal digitate. *L.Ord.*

Hesperonomia Ulrich & Cooper, 1936, p. 621 [**H. planidorsalis*; OD]. Pedicle valve gently convex, brachial valve plane to concave, with feeble median sulcus, finely or rarely coarsely multicostellate; dental plates short, receding, diductor scars extending beyond but not enclosing adductor. *L.Ord.,* N.Am.——Fig. 193,*4*. **H. planidorsalis,* Sarbach, Can.(Alta.); *4a,b,* brach.v. ext., int., ×2; *4c,* ped. v. int., ×2 (825).

Hesperonomiella Ulrich & Cooper, 1936, p. 622 [**Protorthis porcias* Walcott, 1924, p. 504; OD]. Like *Hesperonomia* but unequally biconvex and with gentle median sulcus in shallower brachial valve. *L.Ord.,* N.Am.——Fig. 193,*8*. *H. minor* Walcott, Pogonip, USA(Utah); *8a,* ped. v. int., ×3; *8b,* brach. v. int., ×2 (189).

Jivinella Havlíček, 1949, p. 94 [**Orthis incola* Barrande, 1879, p. 94; OD]. Like *Hesperonomiella* but more coarsely costellate and with pseudospondylium in pedicle valve; notothyrial ridges strong. *L.Ord.,* Eu.(Czech.).

Family ORTHIDIELLIDAE
Ulrich & Cooper, 1936

[Orthidiellidae Ulrich & Cooper, 1936, p. 621]

Interareas and hinge lines of variable length, deltidium sporadically developed; ventral muscle field subtriangular, commonly extending in front of umbonal region, cardinal process developed as high ridge ankylosed to pair of notothyrial ridges simulating trilobed structure cemented to simple rod- or bladelike brachiophores by secondary shell; ventral mantle canal sytem saccate, with proximal parts of *vascula media* divergent, dorsal digitate. *L.Ord.-U.Ord.*

Orthidiella Ulrich & Cooper, 1936, p. 621 [**O. longwelli*; OD]. Unequally biconvex and wide-hinged, with deeper, commonly carinate pedicle valve and sulcate brachial valve costellate; delthyrium commonly restricted by apical plate simulating imperforate deltidium, teeth massive, with deep fossettes, dental plates short; diductor scars usually extending well beyond but not enclosing broad median adductor scar, brachiophores rodlike, variable in length, mainly encased in secondary shell. *L.Ord.,* N.Am.(W.USA).——Fig. 193,*5*. **C. longwelli,* Pogonip, Nev.; *5a,* brach. v. of conjoined valves, ×4; *5b,* ped. v. int., ×2; *5c,* ped. v. ext., ×3; *5d,* brach. v. int., ×4 (825).

Eostrophomena Walcott, 1905, p. 256 [**Strophomena (Eostrophomena) elegantula*; OD]. Concavo-convex, unequally parvicostellate with widely spaced costae and finely imbricate, delthyrium open, notothyrium with convex chilidium; teeth strong, dental plates short, ventral muscle field short and wide, slightly cordate, with diductor lobes extending slightly beyond anterior edge of wide adductor impressions, subperipheral rims strong in both valves; cardinal process simple, flanked by high chilidial plates which also support widely divergent rodlike brachiophores; dorsal adductor scars quadripartite, impressed on

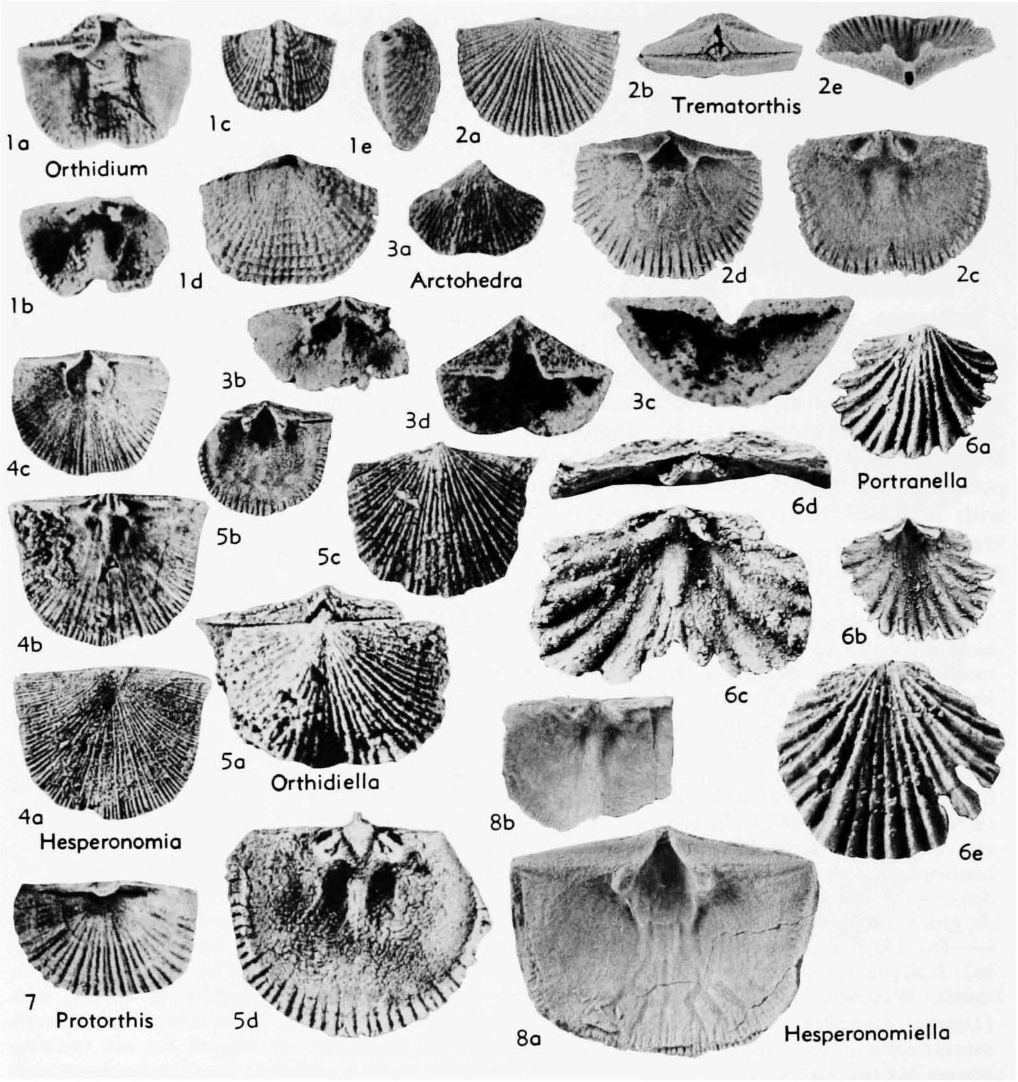

FIG. 193. Protorthidae *(3,7)*; Hesperonomiidae *(4,8)*; Orthidiellidae *(1-2, 5-6)* (p.*H*309-*H*311).

either side of median septum extending to subperipheral rim. [Good specimens recently collected by Dr. T. E. TJERNVIK show that this genus, which was previously known only as a ventral exterior and a poorly preserved dorsal interior, is an orthidiellid and differs from other members of that family in its parvicostellate ornamentation and concavo-convex profile.] *L.Ord.*, Sweden.——FIG. 193A,*1*. **E. elegantula* (WALCOTT), Tremadoc. (*Apatokephalus serratus* Zone), Västergötland *(1a,b)*, Biludden *(1c)*; *1a,b,* brach.v. int., ped.v. int., ×2; *1c,* exfoliated ped.v. ext., ×2 (Williams, n).

Orthidium HALL & CLARKE, 1892, p. 244 [**Orthis gemmicula* BILLINGS, 1862, p. 75; OD]. Strongly biconvex, commonly with high ventral umbo and like *Orthidiella* but with strongly imbricate concentric ornamentation and without apical plate in delthyrium. *L.Ord.,* N.Am.——FIG. 193,*1a-c*. **O. gemmicula* (BILLINGS), Can.(Que.); *1a,b,* ped. v. int., brach. v. int., ×6; *1c,* ped. v. ext., ×4 (825). ——FIG. 193,*1d-e*. *O. bellulum* (ULRICH & COOPER), Pogonip, USA(Nev.); *1d,e,* brach. v. ext., lat. view of conjoined valves, ×4 (189).

Portranella WRIGHT, 1964, p. 167 [**P. angulocostellata*; OD]. Like *Orthidiella* but with short hinge line, coarsely costellate ornamentation and without apical plate in delthyrium. *U.Ord.,* Ire.

——Fig. 193,*6*. **P. angulocostellata*; *6a,b,* ped. v. ext., int., ×2.5; *6c,d,* brach. v. int., post. views, ×3; *6e,* brach.v. ext., ×2 (895b).

Trematorthis Ulrich & Cooper, 1938, p. 112 [**T. masoni*; OD]. Like *Orthidiella* but with perforate deltidium, bladelike brachiophores and lower cardinal process. *L.Ord.,* N.Am.——Fig. 193,*2*. **T. masoni*, Pogonip, USA(Nev.); *2a,b,* brach. v., post. views of conjoined valves, ×3; *2c,* brach. v. int., ×4; *2d,e,* normal, post. views of ped. v. int., ×3 (189).

Family ORTHIDAE Woodward, 1852

[Orthidae Woodward, 1852, p. 229]

Interareas and hinge lines of variable length, delthyrium open, notothyrium rarely covered by chilidium; teeth with crural fossettes, dental plates variably disposed, ventral muscle field short, not extending much beyond umbonal cavity, commonly suboval, median adductor scars not enclosed by diductors; cardinal process simple, ridgelike, brachiophores rodlike, unsupported; ventral mantle canal system saccate, dorsal mantle canal system saccate to digitate. *M.Cam.-L. Dev.*

Subfamily ORTHINAE Woodward, 1852

[*nom. transl.* Schuchert & Cooper, 1931, p. 243 (*ex* Orthidae Woodward, 1852, p. 229)]

Interareas short incurved, hinge lines wide; notothyrium not covered by chilidium; dental plates short, receding, divergent. *M.Cam.-L.Dev.*

Orthis Dalman, 1827, p. 93 [**O. callactis* Dalman, 1828, p. 93, 96; SD Davidson, 1853, p. 101]. Subquadrate to semioval in outline, plano-convex, dorsal sulcus subdued; costate, with costae and interspaces bearing fine parvicostellae; ventral muscle field suboval, with long adductor scars; cardinal process as thin ridge within notothyrial cavity, brachiophores divergent, dorsal adductor quadripartite, proximal parts of ventral *vascula media* adjacent to each other along median plane. *L.Ord., ?M.Ord.,* cosmop.——Fig. 194,*7*. **O. callactis* Dalman, L.Ord., USSR; *7a-c,* ped. v. brach. v., post. views of conjoined valves, ×2; *7d,* brach. v. int., ×2 (729).

Archaeorthis Schuchert & Cooper, 1931, p. 243 [**Orthis electra* Billings, 1865, p. 79; OD]. Subcircular in outline, with narrow hinge line, unequally biconvex, pedicle valve commonly subcarinate, dorsal sulcus variably developed, costellate; ventral interior like that of *Orthis* but with large teeth and elongate callosity extending in front of muscle field; brachiophores short, divergent, cardinal process absent. *L.Ord., ?M.Ord.,* N.Am.-Eu.——Fig. 194,*2*. *A. biconvexa* Cooper, Womble Sh., USA(Okla.); *2a,b,* ped. v. ext., int., ×3; *2c,* brach. v. int., ×3 (189).

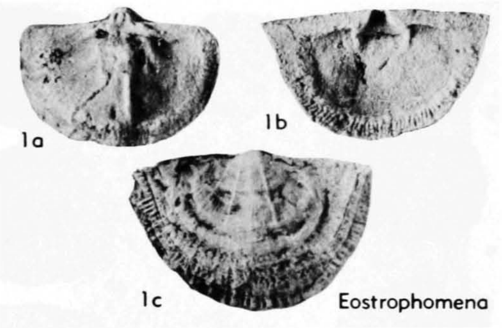

Fig. 193A. Orthidiellidae (p. *H*309).

Bohemiella Schuchert & Cooper, 1931, p. 242 [**Orthis romingeri* Barrande, 1879, p. 203; OD] [=*Shiragia* Kobayashi, 1935, p. 70 (type, *S. biloba*)]. Transversely suboval in outline, plano- to concavo-convex with broad shallow sulcus; costellate; teeth small, dental plates rudimentary, ventral muscle field small, subtriangular; cardinal process simple widening anteriorly, brachiophores long, triangular in section, proximal parts of ventral *vascula media* divergent. *M.Cam.,* Eu.(Czech.).——Fig. 194,*1*. **B. romingeri* (Barrande); *1a,* brach.v. view of conjoined valves, ×2; *1b,* ped.v. int., mold, ×2; *1c,* brach.v. int., ×2 (729).

Cyrtonotella Schuchert & Cooper, 1931, p. 243 [**Orthis semicircularis* Eichwald, 1829, p. 276; OD] [=*Planidorsa* Schuchert & Cooper, 1931, p. 244 (type, *P. bella*)]. Semioval in outline, concavo-convex, costellate; teeth small, dental plates widely divergent, ventral muscle scar subrhomboidal; cardinal process thick, high, brachiophores short, subparallel with hinge line to define slitlike sockets; proximal parts of ventral *vascula media* adjacent to each other at median plane. *M.Ord.,* N.Hemis.——Fig. 194,*10a,b*. **C. semicircularis* (Eichwald), USSR; *10a,b,* brach.v., post. views of conjoined valves, ×1 (729).——Fig. 194,*10c,d*; 195,*1*. *C. kukersiana* (Wysogorski), CII, USSR; *10c,* brach.v. int., ×1; *10d,* ped.v. int. mold, ×1 (710); 195,*1,* brach.v. int., ×2.25 (621).

Glossorthis Öpik, 1930, p. 82 [**G. tacens*; OD]. Subquadrate in outline, unequally biconvex, with variable median sulcus in shallower brachial valve, costate to coarsely costellate; ventral muscle field impressed on tonguelike pseudospondylium between slightly divergent dental plates and supported anteriorly by low ridge; cardinal process ridgelike, flanked by low notothyrial ridges. *M.Ord.,* Eu.——Fig. 194,*8*. **G. tacens,* CII, Est.; *8a,b,* brach.v. ext., int., ×1.5; *8c,* ped.v. int., ×1.5 (729).

Lenorthis Andreeva, 1955, p. 69 [**L. girardi*; OD]. Like *Orthis* but unequally biconvex, with costate to coarsely costellate radial ornamentation and divergent proximal parts of ventral *vascula media*. *L.Ord.-M.Ord.,* cosmop.——Fig. 194,*9*. *L. mostellerensis* (Cooper), M.Ord.(Porterfield), USA (Ala.); *9a,b,* brach.v., lat., views of conjoined

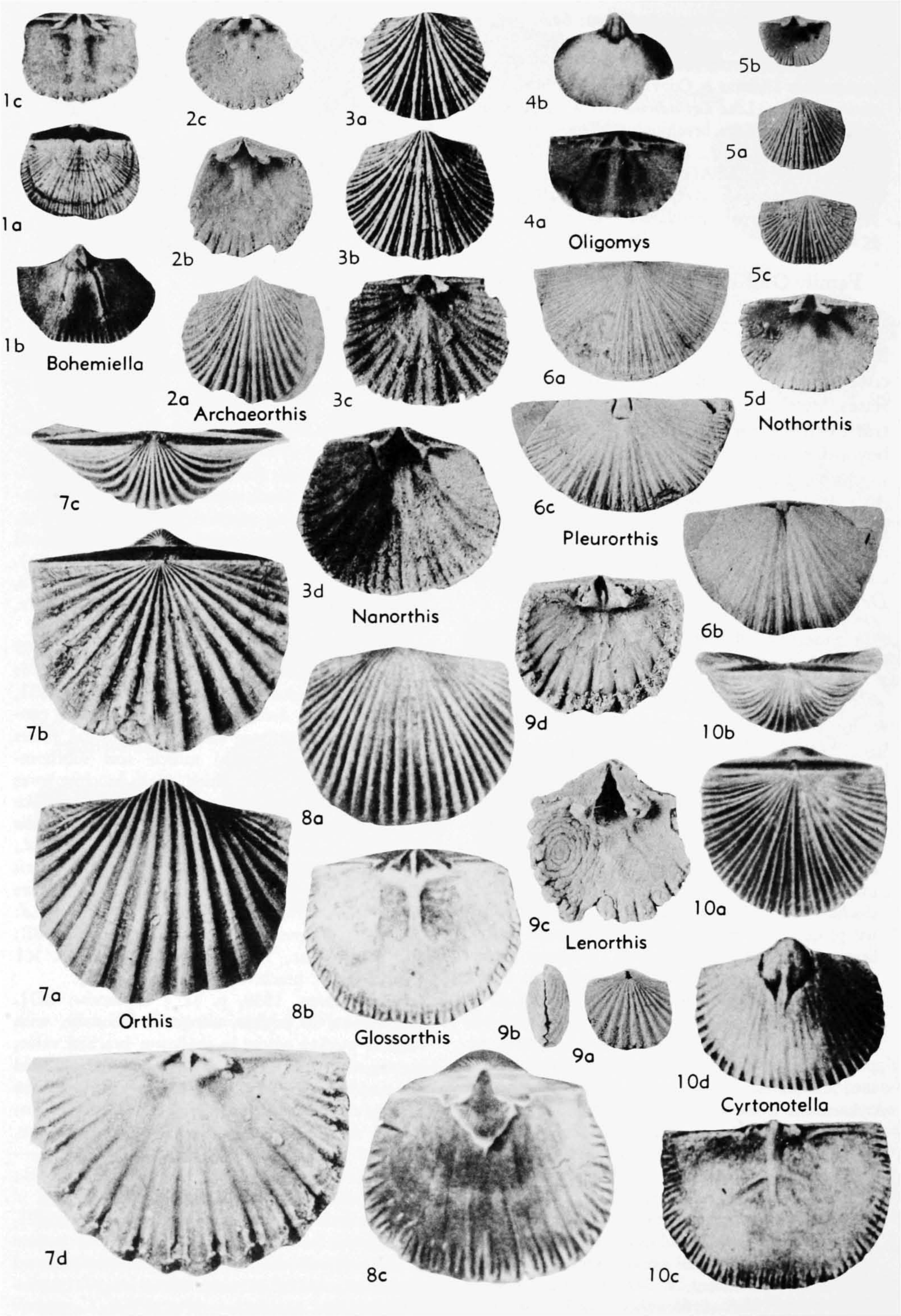

Fig. 194. Orthidae (Orthinae) (p. *H*311, *H*313).

valves, ×1; *9c,d,* ped.v. int., brach.v. int., ×2 (189).

Nanorthis Ulrich & Cooper, 1936, p. 621 [**Orthis hamburgensis* Walcott, p. 73; OD]. Like *Archaeorthis* but with small teeth, rudimentary cardinal process and notothyrial platform built up mainly around brachiophores to simulate supports; ventral muscle field with subtriangular adductor scars and narrow subcrescentic diductors; proximal parts of ventral *vascula media* divergent. *L.Ord.*, cosmop. ——Fig. 194,*3*. **N. hamburgensis* (Walcott), Canad., USA(Nev.-Colo.); *3a,b,* brach.v. ext., ped.v. ext., ×3; *3c,* brach.v. int., ×6; *3d,* ped.v. int., ×4 (825).

Nothorthis Ulrich & Cooper, 1938, p. 106 [**N. delicatula*; OD] [=*Althorthis* Andreeva, 1960, p. 288 (type, *A. kinderlensis*)]. Like *Nanorthis* but more transverse in outline and with well-developed notothyrial platform. *L.Ord.-M.Ord.*, N.Am.-Scot. ——Fig. 194,*5*. **N. delicatula,* L.Ord.(Canad.-Whiterock.), Can.(Que.); *5a-c,* ped.v. ext., ped.v. int., brach.v. ext., ×3; *5d,* brach.v. int., ×4.5 (189).

Oligomys Schuchert & Cooper, 1931, p. 243 [**Orthis exporrecta* Linnarsson, 1876, p. 12; OD]. Transversely oval in outline, unequally biconvex to plano-convex, finely parvicostellate with superimposed secondary costellation; teeth small, dental plates obsolete, ventral muscle field suboval, small, with adductor track widening anteriorly and extending beyond diductors; brachiophores short, widely divergent, cardinal process thickened anteriorly; proximal parts of ventral *vascula media* divergent, dorsal mantle canal system digitate. *M.Cam.*, NW.Eu.——Fig. 194,*4*. **O. exporrectus* (Linnarsson), Sweden; *4a,* brach.v. int., ×2.5; *4b,* ped.v. int. mold, ×2.5 (729).

Orthambonites Pander, 1830, p. 80 [**O. transversa;* SD Dall, 1877, p. 51]. Like *Orthis* but biconvex and with costate to coarsely costellate radial ornamentation. *L.Ord.-M.Ord.*, cosmop.——Fig. 196,*4*. *O. calligramma* Dalman, M.Ord., USSR; *4a-c,* brach.v., lat., post. views of conjoined valves, ×2 (729); *4d,* ped.v. int., ×1; *4e,* brach.v. int., ×2 (710).

Orthostrophia Hall, 1883, pl. 36, figs. 32-34 [**Orthis strophomenoides* Hall, 1857, p. 46; OD]. Subquadrate, subequally biconvex to resupinate, with median dorsal sulcus, costellate; ventral muscle field short, subtriangular, with wide adductor track; cardinal process expanded anteriorly, commonly flanked by discrete notothyrial ridges; mantle canal systems saccate but ventral *vascula media* short, divergent, with arcs limited to posterior half of valve and giving rise to branches anteriorly. *M.Sil.-L.Dev.*, N.Am.-Eu.——Fig. 196, *2*. *O. strophomenoides parva* Amsden, L.Dev. (Haragan), USA(Okla.); *2a,b,* ped.v., ant. views of conjoined valves, ×1; *2c,* lat. view of conjoined valves, ×1; *2d,e,* ped.v. int., portion of brach.v. int., ×2 (106).

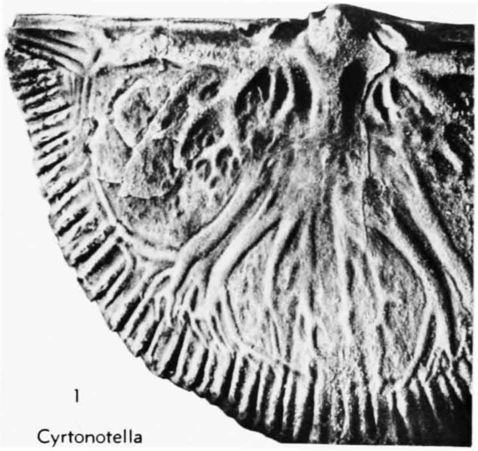

Fig. 195. Orthidae (Orthinae) (p. *H*311).

Pleurorthis Cooper, 1956, p. 329 [**P. fascicostellata*; OD]. Transversely subquadrate in outline, subequally biconvex, brachial valve commonly deeper, with median sulcus passing into broad median fold in adult shells; multicostellate to fasciocostellate; interiors like those of *Orthis*. *L.Ord.*, E.N.Am. ——Fig. 194,*6*. **P. fascicostellata,* Whiterock, Can.(Que.); *6a,* brach.v. ext., ×1; *6b,c,* brach.v. int., ped.v. int. molds, ×2 (189).

Prantlina Havlíček, 1949, p. 250 [*Orthis desiderata* Barrande, 1848, p. 59; OD]. Like *Taphrorthis* but with very gently convex to plane, vaguely sulcate brachial valve; cardinal process ridgelike, strong. *L.Ord.*, Eu.(Czech.).

Ranorthis Öpik, 1939, p. 119 [**R. norvegica*; OD]. Like *Nanorthis* but elongately semioval in outline with carinate pedicle valve, and gently convex to plane brachial valve with sharp, narrow median sulcus. *L.Ord.*, Eu.——Fig. 196,*5*. **R. norvegica,* Expansusschiefer, Nor.; *5a,* brach.v. ext., ×4; *5b,* brach.v. int. mold, ×4; *5c,* ped.v. int. mold, ×8 (622).

Riograndella Kobayashi, 1937, p. 422 [**R. subcircus*; OD]. Like *Taphrorthis* but with subparallel dental plates and without median ridge in elongately oval ventral muscle field. Age unknown, Bol.

Sinorthis Wang, 1955, p. 327 [**S. typica*; OD]. Like *Prantlina* but with elongately oval ventral muscle field and proximal parts of ventral *vascula media* divergent. *L.Ord.*, China.——Fig. 196,*3*. **S. typica,* Fenhsiang; *3a,* brach.v. view of conjoined valves, ×3; *3b,c,* ped.v. int., brach.v. int., ×3 (852).

Taphrorthis Cooper, 1956, p. 326 [**T. emarginata*; OD]. Subquadrate in outline, unequally biconvex with less deep, medianly sulcate brachial valve, costellate; teeth small, dental plates, short, divergent, ventral muscle field subcordate, divided

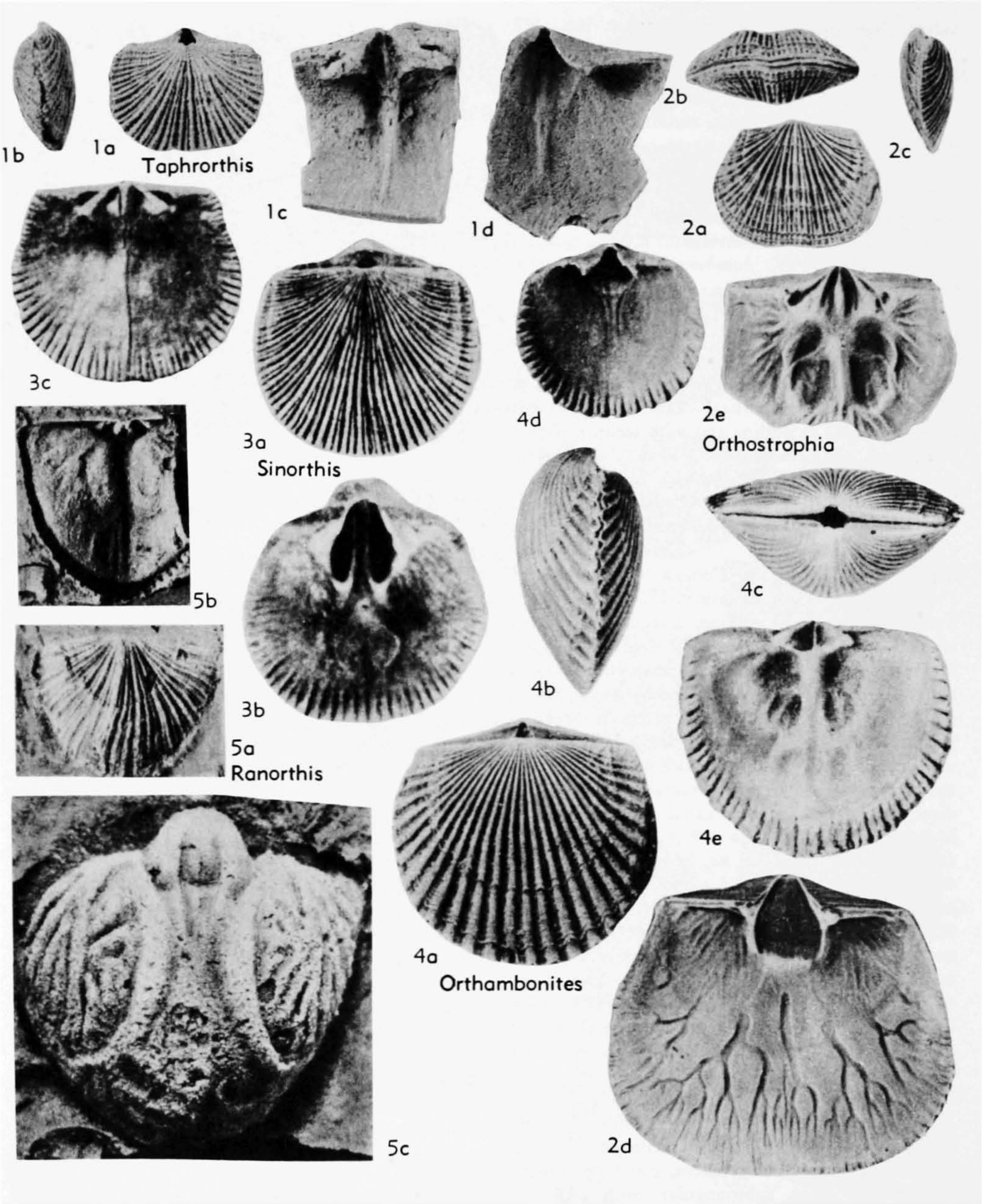

FIG. 196. Orthidae (Orthinae) (p. *H*313-*H*314).

by low median ridge prolonged anteriorly; cardinalia like those of *Orthis* with poorly developed cardinal process; proximal parts of ventral *vascula media* adjacent to each other at median plane. *M.Ord.,* N.Am.-Scot.-Ire.——FIG. 196,*1*. **T. emarginata,* Porterfield, USA(Tenn.-Ala.); *1a,b,* brach. v., lat. views of conjoined valves, ×2; *1c,* fragment of brach.v. int., ×3; *1d,* fragment of ped.v. int., ×2 (189).

Subfamily PRODUCTORTHINAE Schuchert & Cooper, 1931

[Productorthinae SCHUCHERT & COOPER, 1931, p. 243]

Imbricate to strongly lamellose, interareas very short to vestigial, hinge lines wide; notothyrium commonly covered with variably developed chilidium; dental plates short, receding, divergent. *Ord.*

Productorthis Kozlowski, 1927, p. 9 [**Productus obtusus* Pander, 1830, p. 87; OD]. Subquadrate, concavo-convex to unequally biconvex, pedicle valve deep, with swollen umbo, interareas vestigial, costate to costellate, with greatly extended and crowded concentric lamellose frills; teeth small, dental plates subparallel, short, bounding high callus impressed by wide adductor scars and narrow diductors that also encroach on to dental plates; cardinal process high, thick, bearing di-

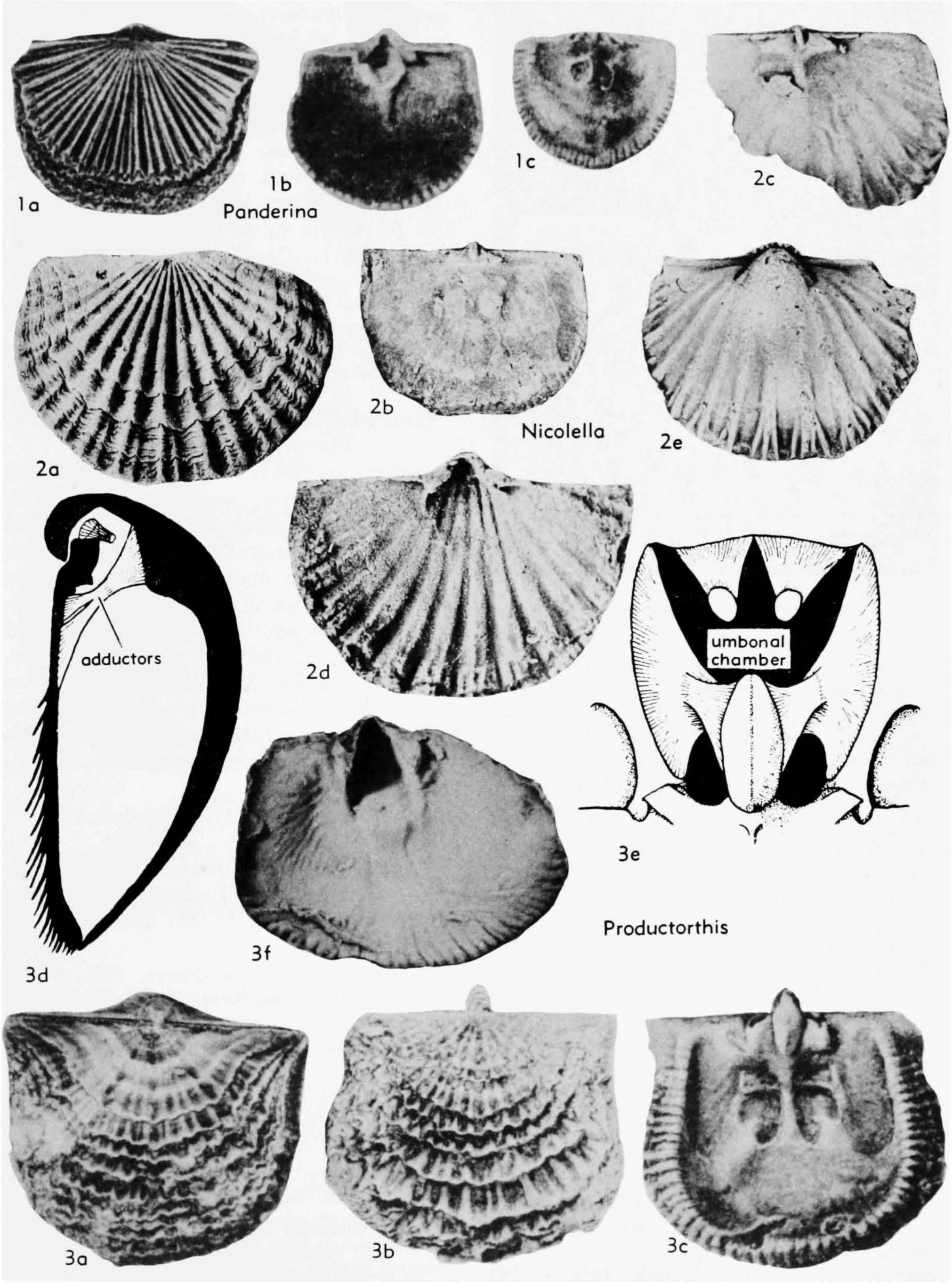

Fig. 197. Orthidae (Productorthinae) (p. *H*315-*H*316).

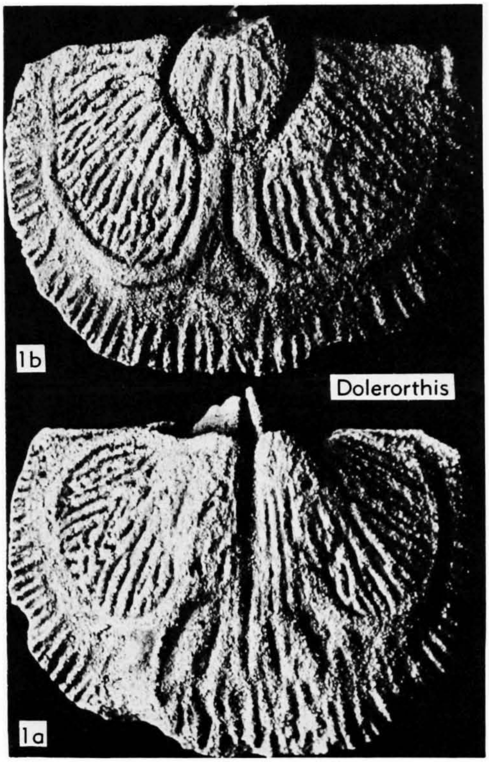

FIG. 198. Dolerorthidae (Dolerorthinae) (p. *H*316).

ductor scars posterolaterally, chilidium vestigial, brachiophores short, encased in secondary shell to define cup-shaped sockets; dorsal adductors scars quadripartite, with lobate anterior pair; ventral mantle canal system saccate, with *vascula media* greatly divided medianly. *L.Ord.-M.Ord.,* cosmop. ——FIG. 197,*3a-c. P. parallela* PANDER, L.Ord., USSR; *3a,* brach.v. view of conjoined valves, ×3; *3b,c,* brach.v. ext., int., ×3 (729).——FIG. 197, *3d-f. P. mitchelli* WILLIAMS, M.Ord., Eire; *3d,* reconstructions showing inferred disposition of muscles in median-lat. view, ×3; *3e,* ant. view of umbonal chamber, ×6; *3f,* vent. int., ×2.5 (876).

Nicolella REED, 1917, p. 860 [**Orthis actoniae* SOWERBY, 1839, p. 639; OD]. Externally like *Productorthis* but with less convex pedicle valve and relatively well-developed interareas, chilidium strong; dental plates divergent, ventral muscle field subcordate, diductor scars not enclosing narrow adductors; cardinal process high, brachiophores widely divergent, anterior adductor scars not bilobed. *M.Ord.-U.Ord.,* Eu.-N.Am.——FIG. 197,*2.* **N. actoniae* (SOWERBY), U.Ord.(Acton.), Eng.; *2a,* brach.v. ext., ×1.5; *2b,c,* brach.v. int., ×1.5; *2d,e,* ped.v. int., ped.v. int. mold, ×1.5 (Williams, n).

Panderina SCHUCHERT & COOPER, 1931, p. 243 [**Productus abscissus* PANDER, 1830, p. 86; OD]. Like *Productorthis* but with very short incurved ventral interarea and narrow plane dorsal interarea; cardinal process low, not united with short brachiophores. *L.Ord.,* Eu.-USSR.——FIG. 197,*1a.* **P. abscissa* (PANDER), USSR; *1a,* brach.v. view of conjoined valves, ×2 (729).——FIG. 197,*1b,c. P. tetragonum* (PANDER), B_1, USSR; *1b,c,* ped.v. int., brach.v. int., ×1.5 (729).

Subfamily PORAMBORTHINAE Havlíček, 1950

[*nom. transl.* WILLIAMS, herein (*ex* Poramborthidae HAVLÍČEK, 1950, p. 58)]

Interareas short, incurved, hinge lines wide; notothyrium not covered by chilidium; dental plates long, convergent on to floor of pedicle valve. *L.Ord.*

Poramborthis HAVLÍČEK, 1949, p. 107 [**P. kloucek̡i*; OD]. Semicircular in outline, subequally biconvex, finely multicostellate; ventral muscle field long, with narrow adductor scar; cardinal process and notothyrial platform rudimentary; proximal parts of *vascula media* divergent. *L.Ord.,* Eu.(Czech.).

Family DOLERORTHIDAE Öpik, 1934

[Dolerothidae ÖPIK, 1934, p. 180]

Ventral interareas long; hinge lines wide; teeth with oblique fossettes, supported by receding dental plates, ventral muscle field elongately subtriangular to subcordate with rounded anterior margins of diductor scars commonly extending beyond but not enclosing lanceolate adductors usually contained by low ridges; cardinal process ridgelike, rarely absent, brachiophores commonly as pair of long blades, triangular in section; ventral mantle canal system saccate with *vascula media* converging medianly. *L.Ord.-U.Sil.*

Subfamily DOLERORTHINAE Öpik, 1934

[Dolerorthinae ÖPIK, 1934, p. 180]

Strong concentric imbrication not developed, delthyrium and notothyrium open; dorsal mantle canal system apocopate. *M.Ord.-U.Sil.*

Dolerorthis SCHUCHERT & COOPER, 1931, p. 244 [**Orthis interplicata*; OD]. Unequally biconvex to convexo-concave, costate to costellate; cardinal process flanked by variably developed notothyrial ridges. *M.Ord.-U.Sil.,* N.Hemis.——FIG. 199,*5. D. duftonensis* (REED) *prolixa* WILLIAMS, Caradoc, Wales; *5a,b,* ped.v., brach.v. exts., ×1.5; *5c,* brach. v. int., ×2 (Williams, n).——FIG. 198,*1. D. rustica osiliensis* (SCHRENK), U.Sil.(Jaani Stage), Balt.; *1a,b,* dors., vent. int. molds, ×3 (621).

Subfamily HESPERORTHINAE Schuchert & Cooper, 1931

[Hesperorthinae SCHUCHERT & COOPER, 1931, p. 243]

Strong concentric imbrication not devel-

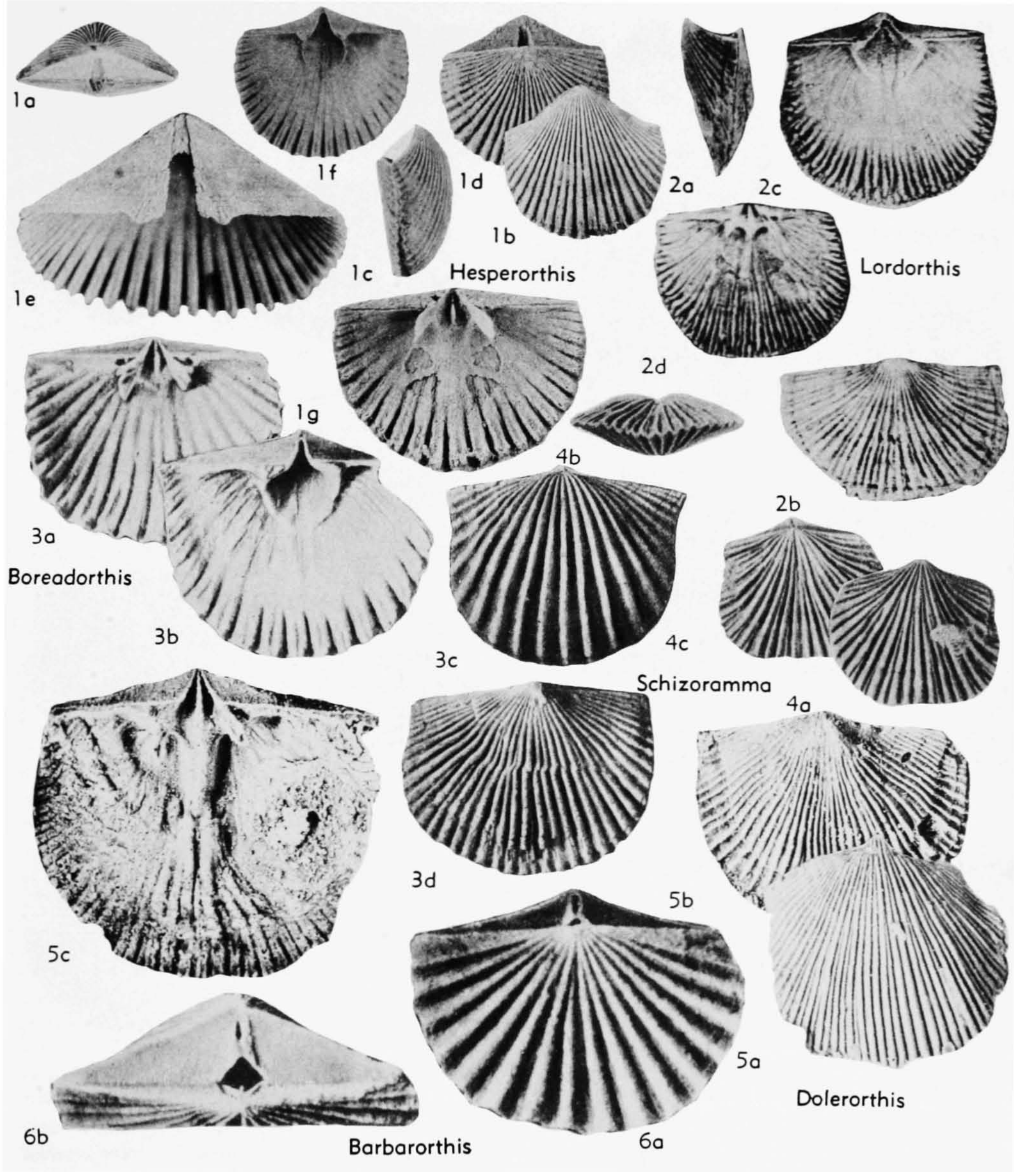

FIG. 199. Dolerorthidae (Dolerorthinae) *(5)*, (Hesperorthinae) *(1-4, 6)* (p. *H*316-*H*318).

oped, apical plate or deltidium and antigydium sporadically developed; dorsal mantle canal system digitate. *L.Ord.-U.Sil.*

Hesperorthis SCHUCHERT & COOPER, 1931, p. 244 [**Orthis tricenaria* CONRAD, 1843, p. 333; OD]. Plano- to gently concavo-convex, with high pedicle valve, costate, with very fine parvicostellae in the interspaces; apical plate and antigydium commonly developed especially in later species; median parts of ventral *vascula media* long, arcuate branches subperipheral. *L.Ord.-U.Sil.*, N.Hemis.——FIG. 199,*1a-e*. **H. tricenaria* (CONRAD), L.Ord., USA; *1a-d*, post., ped.v., lat., brach.v. views of conjoined valves, ×1; *1e*, post. view of ped.v., ×2 (189).——FIG. 199,*1f,g*. *H. australis* COOPER, L. Ord., USA (Tenn.); *1f*, ped.v. int., ×1; *1g*, brach. v. int., ×2 (189).

Barbarorthis ÖPIK, 1934, p. 183 [**B. foramenifera*; OD]. Like *Hesperorthis* but with perforate deltidium covering delthyrium. *U.Ord.*, Eu.——FIG. 199,*6*. **B. foramenifera*, F₁, Est.; *6a,b*, brach.v., post. views of conjoined valves, ×5 (621).

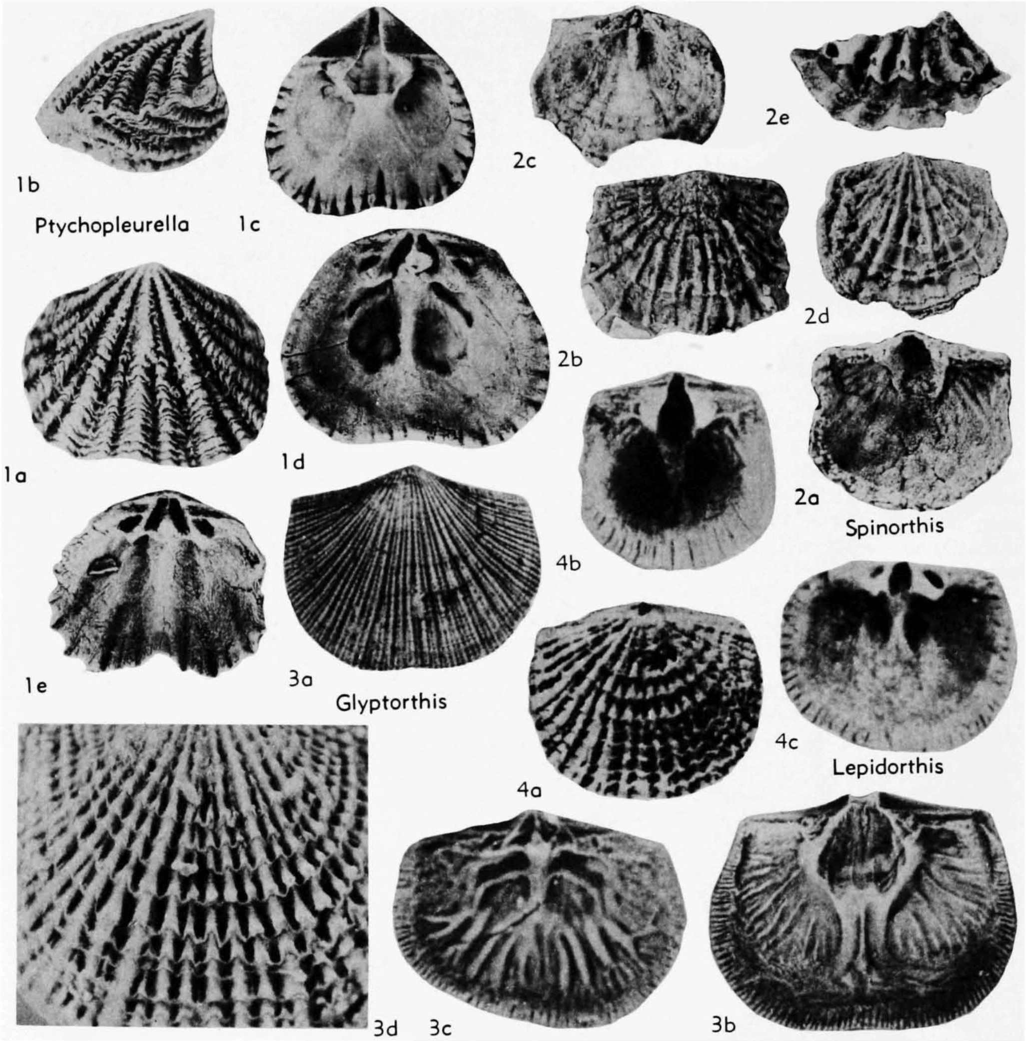

FIG. 200. Dolerorthidae (Glyptorthinae) (p. *H*319).

Boreadorthis ÖPIK, 1934, p. 184 [**B. crassa*; OD]. Like *Hesperorthis* but with strongly and uniformly convex brachial valve. *U.Ord.*, Eu.——FIG. 199,*3*. **B. crassa*, F1, Est.; *3a,b*, brach.v. int., ped. v. int., ×2; *3c*, brach.v. ext., ×1.5 (621).——FIG. 199,*3d*. *B. recula aequivalvata* ÖPIK, F1, Est.; ped. v. ext., ×1.5 (621).

Lordorthis ROSS, 1959, p. 446 [**L. variabilis*; OD]. Like *Hesperorthis* but with plane brachial valve of young shells becoming convex in adult shells and costellate radial ornamentation. *U.Ord.*, N.Am. (W.USA).——FIG. 199,*2*. **L. variabilis*; *2a*, lat. view of conjoined valves, ×1; *2b*, ped.v. ext., ×1; *2c,d*, ped.v. int., brach.v. int., ×1 (678).

Schizoramma FOERSTE, 1909, p. 77 [**Hebertella (Schizonema) fissistriata*; OD] [=*Schizonema* FOERSTE, 1909, p. 77 (type, *H. (Schizonema) fissistriata*)]. Like *Lordorthis* but with plane to uniformly convex and impersistently sulcate brachial valve and variably developed notothyrial ridges flanking cardinal process; median parts of ventral *vascula media* variable in length. *Sil.*, N.Hemis. ——FIG. 199,*4*. *S. hami* AMSDEN, U.Sil.(Henryhouse), USA(Okla.); *4a-c*, ped.v., ant., brach.v. views of conjoined valves, ×1 (30).

Subfamily GLYPTORTHINAE
Schuchert & Cooper, 1931

[Glyptorthinae SCHUCHERT & COOPER, 1931, p. 243]

Costate to costellate, with strong concentric imbrication disposed as frills or even drawn out as spines; delthyrium and notothyrium open, dorsal mantle canal system digitate. *L.Ord.-U.Sil.*

Glyptorthis Foerste, 1914, p. 257 [**Orthis insculpta* Hall, 1847, p. 125; OD]. Unequally biconvex, with deeper brachial valve bearing strong median sulcus, delthyrium open, triangular, ornamentation variably costellate, with strong imbrication commonly produced into frills; ventral adductor scars broad, rarely longer than diductor scars and commonly raised on median elevation of secondary shell extending forward into anterior half of valve; cardinal process ridgelike. *M.Ord.-L.Sil.,* N.Hemis.——Fig. 200,*3a-c*. **G. insculpta* (Hall), U.Ord.(Richmond.), USA(Ohio); *3a-c,* ped.v. ext., ped.v. int., brach.v. int., ×1.5 (729).——Fig. 200,*3d*. *G. costellata* Cooper, M.Ord. (Bromide), USA(Okla.); portion of brach. surface, ×4 (189).

Eridorthis Foerste, 1909, p. 223 [**Plectorthis (Eridorthis) nicklesi* Foerste, 1909; SD Schuchert & Le Vene, 1929, p. 58]. Like *Glyptorthis* but with dorsal median sulcus replaced by fold in adult shells. *M.Ord.-L.Sil.,* N.Am.-Eu.

Lepidorthis Wang, 1955, p. 330 [**L. typicalis*; OD]. Like *Glyptorthis* but without cardinal process. *L. Ord.,* China.——Fig. 200,*4*. **L. typicalis*, Fenhsiang; *4a,* brach.v. view of conjoined valves, ×3.5; *4b,c,* ped.v. int., brach.v. int., ×2.5 (852).

Ptychopleurella Schuchert & Cooper, 1931, p. 244 [**Orthis bouchardi* Davidson, 1847, p. 64; OD]. Like *Glyptorthis* but with subpyramidal pedicle valve and narrowly triangular delthyrium commonly restricted by lateral plates; radial ornamentation commonly costate or coarsely costellate, with raised costae bounding dorsal sulcus. *M.Ord.-U.Sil.,* cosmop.——Fig. 200,*1*. **P. bouchardi* (Davidson), Wenlock, Eng.; *1a,b,* ped.v., lat. views of conjoined valves, ×3.5; *1c,* ped.v. int., ×3; *1d,e,* brach.v. ints., ×2.5, ×3.5 (Williams, n).

Spinorthis Wright, 1964, p. 184 [**S. geniculata*; OD]. Like *Glyptorthis* but with adult shell geniculated dorsally and lamellae prolonged into suberect spines; dorsal interarea reduced. *U.Ord.,* Eire.——Fig. 200,*2*. **S. geniculata*; *2a,b,* ped.v. int., ext., ×2; *2c,d,* brach.v. int., ext., ×2; *2e,* fragment of shell, ×3.5 (895b).

Family PLAESIOMYIDAE Schuchert, 1913

[*nom. transl. et correct.* Williams, herein (*ex* Plaesiomiinae Schuchert, 1913, p. 382] [=Dinorthidae Schuchert & Cooper, 1931, p. 244]

Ventral interareas variably disposed, hinge lines wide; delthyrium and notothyrium rarely covered by deltidium and chilidium; ventral muscle field subquadrate, extending well beyond umbonal region; mantle canal system saccate, with proximal parts of *vascula media* short, divergent. *Ord.*

Subfamily PLAESIOMYINAE Schuchert, 1913

[*nom. correct.* Williams, herein (*pro* Plaesiomiinae Schuchert, 1913, p. 382)]

Mostly convexo-concave, with short rodlike brachiophores and cardinal process well differentiated into crenulated myophore and shaft. *Ord.*

Plaesiomys Hall & Clarke, 1892, p. 196 [**Orthis subquadrata* Hall, 1847, p. 126; OD]. Convexo-concave to unequally biconvex, pedicle valve commonly shallowly sulcate, costate to costellate, deltidium absent; teeth with oblique fossettes, dental plates short; ventral muscle field bilobed anteriorly, with diductor scars enclosing central oval adductors; adjustors prominent. *M.Ord.-U.Ord.,* cosmop.

P. (Plaesiomys). Variably convexo-concave, ventral interarea apsacline; radial ornamentation costellate. *M.Ord.-U.Ord.,* N.Hemis.——Fig. 201,*5*. **P. (P.) subquadrata* (Hall), U.Ord.(Richmond.), USA(Ohio); *5a,b,* ped.v., lat. views of conjoined valves, ×1; *5c,d,* brach.v. ext., int., ×1; *5e,* ped.v. int., ×1 (740).

P. (Dinorthis) Hall & Clarke, 1892, p. 195 [**Orthis pectinella* Conrad & Emmons, 1842, p. 394; OD] [=*Diorthis* Kobayashi, 1937, p. 12 *(nom. nud.)*]. Resembling *P. (Plaesiomys)* but radial ornamentation costate, exceptionally with incipient costellae. *M.Ord.,* N.Hemis.——Fig. 201, *3a,b*. **P. (D.) pectinella* (Conrad), Trenton., E.USA.; *3a,* ped.v. view of conjoined valves, ×1; *3b,* brach.v. ext., ×1 (740).——Fig. 201,*3c-e*. *P. (D.) holdeni* (Willard), Elway, USA (Tenn.); *3c,* lat. view of conjoined valves, ×1; *3d,e,* ped. v. int., brach.v. int., ×2 (189).

P. (Pionorthis) Schuchert & Cooper, 1931, p. 244 [**Orthis sola* Billings, 1866, p. 12; OD]. Like *P. (Plaesiomys)* but subequally biconvex. U.Ord., N.Am.——Fig. 201,*4*. *P. (P.) sola* (Billings), Richmond., USA(Ind.); lat. view of conjoined valves, ×1.5 (729).

P. (Retrorsirostra) Schuchert & Cooper, 1931, p. 244 [**Orthis carleyi* Hall, 1847, p. 120; OD]. Like *P. (Plaesiomys)* but with procline ventral interarea. *U.Ord.,* N.Hemis.——Fig. 201,*6*. **P. (R.) carleyi* (Hall), Richmond., USA(Ohio); *6a,b,* ped.v. lat. views of conjoined valves, ×1; *6c,* ped.v. int., ×1 (740).

Austinella Foerste, 1909, p. 224 [**Orthis kankakensis* McChesney, 1861, p. 77; SD Bassler, 1915, p. 1002]. Like *Plaesiomys (Pionorthis)* but with linear adductor track in pedicle valve broadening anteriorly and not enclosed by diductor scars. *U. Ord.,* N.Am.-Eu.

Campylorthis Ulrich & Cooper, 1942, p. 621 [**Strophomena deflecta* Conrad, 1843, p. 332; OD]. Like *Plaesiomys* and convexo-concave to unequally biconvex but finely costellate and with well-developed, apically perforate deltidium and chilidium. *M.Ord.,* USA-Scot.——Fig. 201,*1*. **C. deflecta* (Conrad), Platteville, USA(Wis.); *1a-d,* post., brach.v., lat., ped.v. views of conjoined valves, ×1 (189).

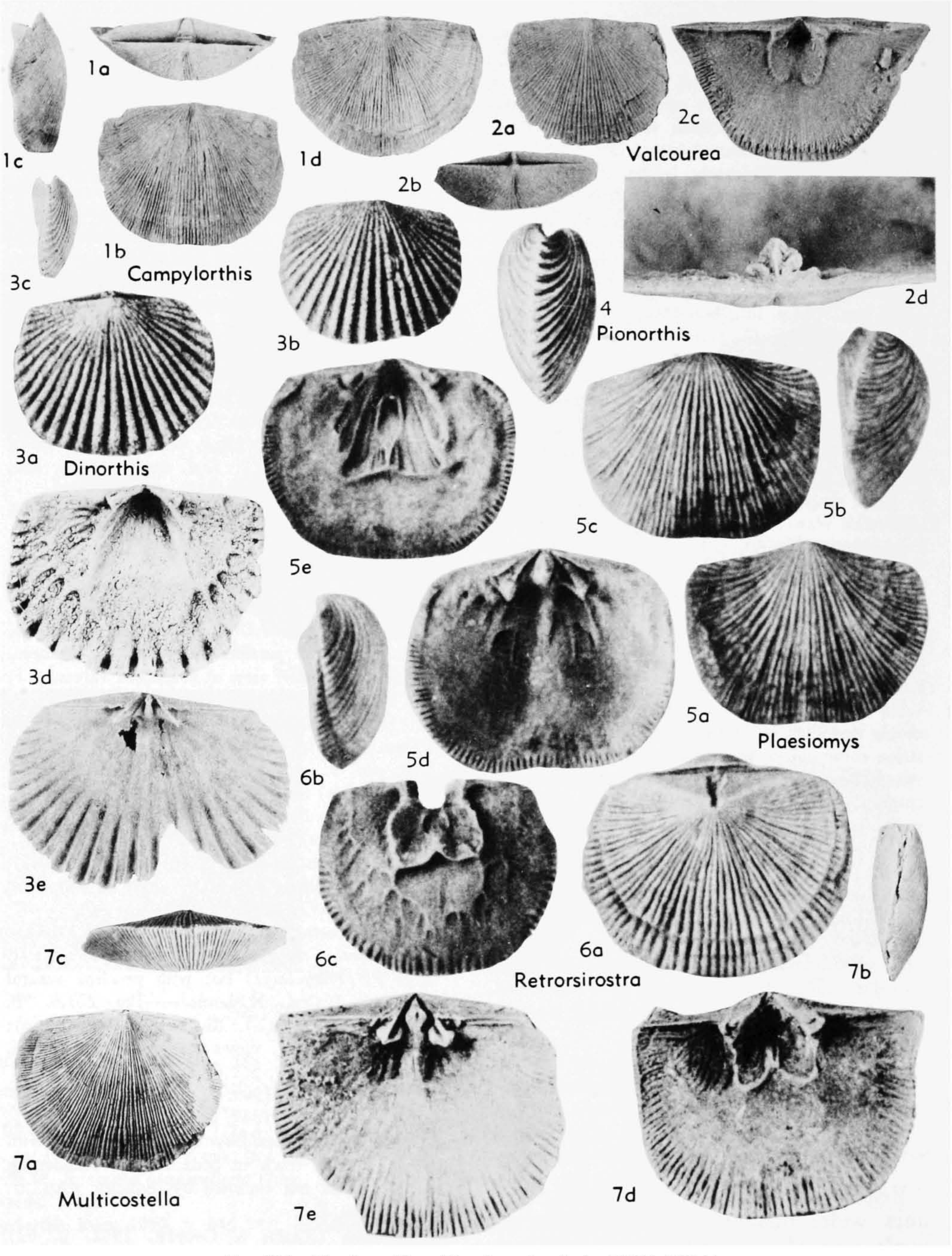

FIG. 201. Plaesiomyidae (Plaesiomyinae) (p. *H*319-*H*321).

Multicostella SCHUCHERT & COOPER, 1931, p. 244 [**Orthis? saffordi* HALL & CLARKE, 1892, p. 217; (OD]. Like *Campylorthis* but lacking deltidium and chilidium. *M.Ord.,* N.Hemis.

M. (Multicostella). Subequally biconvex, commonly with narrow median fold in pedicle valve and median sulcus in brachial valve dying away anteriorly. *M.Ord.,* N.Hemis.——FIG. 201,*7. M. (M.) semisulcata* COOPER, Lincolnshire, USA (Tenn.); *7a-c,* ped.v., lat., ant. views of conjoined valves, ×1; *7d,e,* ped.v. int., brach.v. int., ×2 (189).

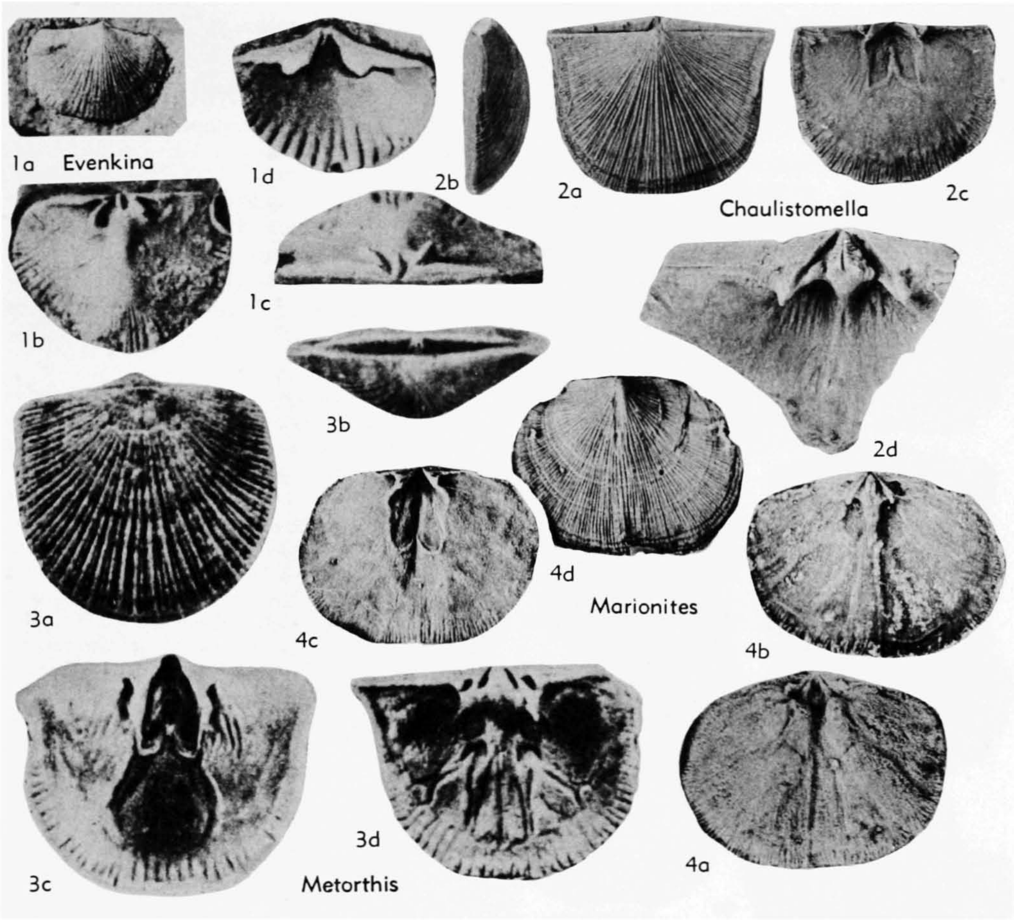

FIG. 202. Plaesiomyidae (Plaesiomyinae) *(2,4)*, (Evenkininae) *(1)*, Metorthinae *(3)* (p. *H*321-*H*322).

M. (Chaulistomella) Cooper, 1956, p. 432 [**C. inequistriata*; OD]. Resupinate in profile, with pedicle valve concave anteriorly and brachial valve uniformly convex; ventral median fold obscure. *M.Ord.*, E.N.Am.-Scot.——Fig. 202,*2*. **M. (C.) inequistriata,* Wardell, USA(Va.); *2a,b,* ped.v., lat. views of conjoined valves, ×1; *2c,* ped.v. int., ×1; *2d,* brach.v. int., ×2 (189).

M. (Marionites) Cooper & Muir-Wood, 1951, p. 195 [*pro Marionella* Bancroft, 1928, p. 181 (*non* Cobb, 1922)] [**Marionella typa* Banbroft, 1928, p. 181; OD]. Resupinate in profile and with median fold, commonly sharp and narrow, in pedicle valve. [The differences between *M. (Marionites)* and *M. (Chaulistomella)* are too finely drawn to be worth even subgeneric recognition. Nonetheless there is a distinct possibility that they typify European and American species groups that evolved independently of each other.] *M.Ord.*, G.Brit.——Fig. 202,*4*. **M. (M.) typa* (Bancroft), Caradoc, Eng.; *4a,b,* brach.v. int. and int. mold, ×1; *4c,d,* ped.v. int. and ext., ×1 (Williams, n).

Valcourea Raymond, 1911, p. 239 [**Plaesiomys strophomenoides* Raymond, 1905, p. 370; OD]. Convexo-concave with wide hinge line and well-developed deltidium and chilidium, narrow carinate median fold common in pedicle valve, radial ornamentation finely costellate; interiors like those of *Dinorthis* but with subperipheral rim in pedicle valve and median crest to myophore of cardinal process. *L.Ord.-M.Ord.*, N.Am.-Scot.——Fig. 201, *2a-c.* **V. strophomenoides* (Raymond), M.Ord. (Crown Point), USA(N.Y.); *2a,b,* ped.v., post. views of conjoined valves, ×2; *2c,* ped.v. int., ×3 (189).——Fig. 201,*2d. V. deckeri* Cooper, M.Ord.(Tulip Creek), USA(Okla.); *2d,* brach.v. post. view, ×3 (189).

Subfamily EVENKININAE Williams, n. subfam.

Unequally biconvex to plano-convex, with long bladelike divergent brachiophores rest-

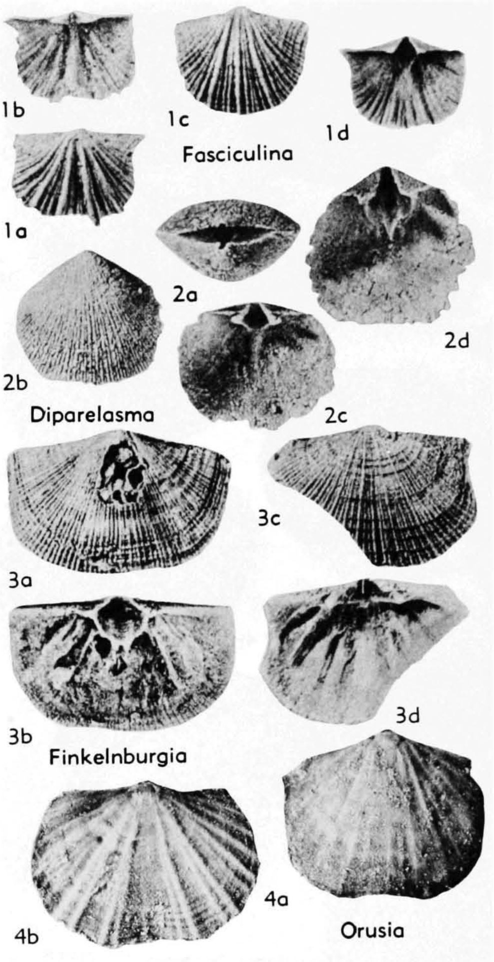

FIG. 203. Finkelnburgiidae (p. *H*322).

ing on floor of brachial valve throughout their entire length and poorly differentiated cardinal process. *M.Ord.*

Evenkina ANDREEVA, 1961, p. 96 [**E. anarbensis*; OD]. Subquadrate in outline, dorsal median sulcus present, costellate. *M.Ord.*, Sib.——FIG. 202,*1*. **E. anarbensis*; *1a*, ped.v. ext., ×2; *1b*, brach.v. int., ×3; *1c*, post. view of brach.v., ×3; *1d*, ped. v. int., ×4 (602).

Subfamily METORTHINAE Williams, n. subfam.

Plano-convex, with bladelike brachiophores raised above floor of brachial valve and undifferentiated cardinal process. *L. Ord.*

Metorthis WANG, 1955, p. 333 [**M. alata*; OD]. Subquadrate in outline, costellate; notothyrial edges elevated as chilidial plates. *L.Ord.*, China. ——FIG. 202,*3*. **M. alata*; *3a,b*, brach.v., post. views of conjoined valves, ×2.5; *3c,d*, ped.v. int., brach.v. int., ×2.5 (852).

Family FINKELNBURGIIDAE

Schuchert & Cooper, 1931

[*nom. transl.* SCHUCHERT & COOPER, 1932, p. 54 (*ex* Finkelnburgiinae SCHUCHERT & COOPER, 1931, p. 243)]

Interareas and hinge lines well developed, delthyrium and notothyrium open; teeth small, dental plates divergent, ventral muscle field variable; brachiophores with subparallel to convergent bases, fulcral plates small; mantle canal systems of both valves digitate. *U.Cam.-L.Ord.*

Finkelnburgia WALCOTT, 1905, p. 277 [**F. finkelnburgi*; OD]. Semioval in outline, subequally biconvex with variable developed dorsal median sulcus, costellate to unequally parvicostellate, rarely with hollow costellae; ventral muscle field of adductor and divergent diductor scars expanding anteriorly, impressed on raised callus of secondary shell between dental plates; cardinal process, simple, ridgelike, brachiophore bases convergent onto floor of brachial valve. *U.Cam.-L.Ord.*, N.Hemis. ——FIG. 203,*3*. *F. buttsi* ULRICH & COOPER, U. Cam., USA(Va.); *3a,b*, ped.v. ext., int., ×2; *3c,d*, brach.v. ext., int., ×2 (825).

Diparelasma ULRICH & COOPER, 1936, p. 623 [**D. typicum*; OD]. Like *Finkelnburgia* but subcircular in outline, with relatively short hinge line; radial ornamentation evenly multicostellate; cardinal process absent to simple; brachiophore bases convergent onto median ridge in brachial valve. *L. Ord.*, N.Am.——FIG. 203,*2*. **D. typicum*, U. Canad., USA(Ala.); *2a*, post. view of conjoined valves, ×2; *2b-d*, ped.v. ext., brach.v. int., ped.v. int., ×2 (825).

Fasciculina COOPER, 1952, p. 7 [**Orthis desmopleura* MEEK in HAYDEN, 1872, p. 295; OD]. Like *Finkelnburgia* but coarsely fascicostellate. *L.Ord.*, N. Am. (W.USA).——FIG. 203,*1*. *F. fasciculata* COOPER, Okla.; *1a,b*, brach.v. ext., int., ×2; *1c,d*, ped.v. ext., int., ×2 (181).

Orusia WALCOTT, 1905, p. 273 [**Anomites lenticularis* WAHLENBERG, 1821, p. 66; OD]. Like *Diparelasma* but without pseudospondylium in pedicle valve and cardinal process in brachial valve; brachiophore bases subparallel, united with floor of valve. *U.Cam., ?L.Ord.*, N.Hemis.——FIG. 203,*4*. **O. lenticularis* (WAHLENBERG), U.Cam., Sweden; *4a,b*, ped.v., brach.v. int. molds, ×5 (Williams, n).

Family PLECTORTHIDAE

Schuchert & Le Vene, 1929

[*nom. transl.* SCHUCHERT & COOPER, 1931, p. 243 (*ex* Plectorthinae SCHUCHERT & LEVENE, 1929, p. 14)]

Interareas and hinge lines of variable length, delthyrium and notothyrium open; teeth with oblique fossettes, supported by strong dental plates extending anteriorly, ventral muscle field variable but commonly elongately cordate; cardinal process almost invariably present and differentiated into crenulated myophore and shaft in adult shells; brachiophore bases either convergent

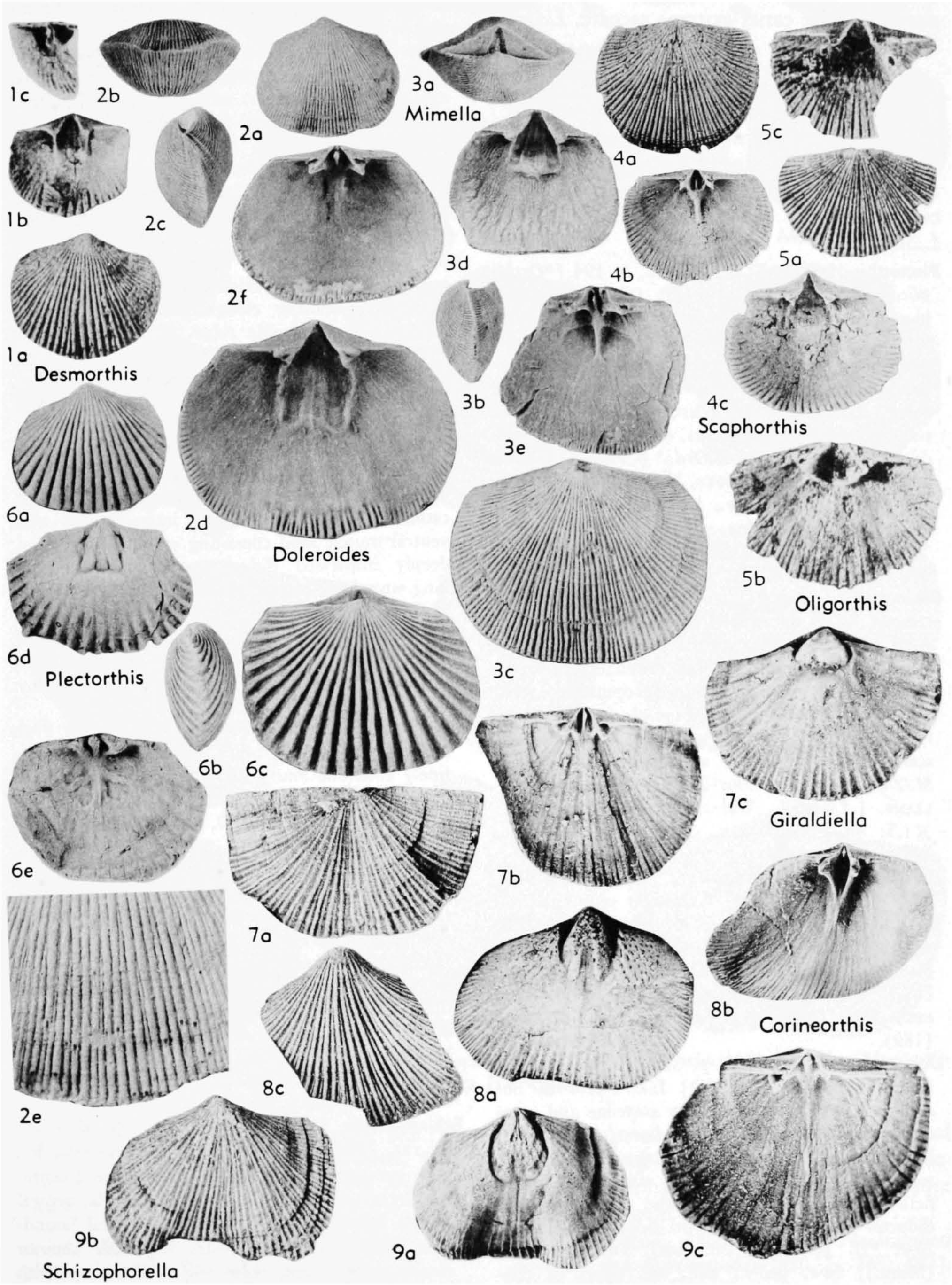

FIG. 204. Plectorthidae (Plectorthinae) (p. *H*324)

onto floor of brachial valve near junction of cardinal process and median ridge dividing quadripartite adductor scars and ankylosed to concave fulcral plates, or rarely divergent and replacing fulcral plates; ventral and dorsal mantle canal systems saccate. *L.Ord.-U.Sil.*

Subfamily PLECTORTHINAE Schuchert & Le Vene, 1929

[Plectorthinae Schuchert & LeVene, 1929, p. 14]

Costellate, with well-developed interareas and wide hinge lines, dorsal median fold absent or subdued; brachiophore bases either convergent or rarely subparallel. *L.Ord.-L.Sil.*

Plectorthis Hall & Clarke, 1892, p. 194 [**Orthis plicatella* Hall, 1847, p. 122; OD]. Subequally biconvex, with short, curved apsacline ventral interarea, coarsely costellate, commonly with one generation branching near umbones so as to simulate costate radial ornamentation, dorsal median sulcus shallow; ventral muscle scar cordate with subcrescentic diductor scars enclosing linear adductor track. *M.Ord.-U.Ord.*, N.Hemis.——Fig. 204,*6*. *P. ponderosa* Cooper, M.Ord.(Martinsburg), USA(Va.); *6a,b*, ped.v., lat. views of conjoined valves, ×1; *6c*, brach.v. view of conjoined valves, ×1.5; *6d*, ped.v. int. mold, ×1; *6e*, brach.v. int., ×1.5 (189).

Corineorthis Stubblefield, 1939, p. 67 [**C. decipiens*; OD]. Unequally biconvex to resupinate, with strongly convex, medianly sulcate brachial valve, costellate, with hollow costellae and strong regular imbrication simulating exopunctae in intercostellate grooves; ventral muscle field elongately cordate, diductors not enclosing long adductor scars which commonly are divided by groove. *M.Ord.*, G.Brit.——Fig. 204,*8*. *C. pustula* Williams, L.Llandeil., Wales; *8a*, ped.v. int. mold, ×1.5; *8b*, brach.v. int., ×1.5; *8c*, ped.v. ext., ×2 (Williams, n).

Desmorthis Ulrich & Cooper, 1936, p. 624 [**D. nevadensis*; OD]. Like *Plectorthis* but with hollow costellae, apical plate in delthyrium, simple ridgelike cardinal process and subparallel brachiophore bases. *L.Ord.*, N.Am.(W.USA).——Fig. 204,*1*. **D. nevadensis*, Pogonip, Nev.; *1a*, ped.v. ext., ×2; *1b,c*, ped.v. int., brach.v. int., ×3 (189).

Doleroides Cooper, 1930, p. 375 [**Orthis gibbosa* Billings, 1857, p. 296; OD] Like *Plectorthis* but costellate, with swollen hollow costellae and commonly with dorsal broad median fold indented by faint impersistent median sulcus; ventral muscle scar elongatedly cordate, with elliptical adductor field divided by single ridge and not enclosed by diductor scars. *M.Ord.*, N.Am.-Scot.——Fig. 204, *2a-e*. **D. gibbosus* (Billings), Decorah, USA (Minn.); *2a-c*, ped.v., ant., lat. views of conjoined valves, ×1; *2d*, ped.v. int., ×2; *2e*, portion of shell enlarged showing hollow costellae, ×2 (189).——Fig. 204,*2f*. *D. tennesseensis* Cooper, Lebanon, USA(Tenn.); *2f*, brach.v. int., ×2 (189).

Giraldiella Bancroft, 1949, p. 5 [**Orthis protensa* Sowerby, 1839, p. 638; OD]. Subequally biconvex or resupinate, with medianly sulcate brachial valve more convex, costellate; ventral muscle field short, subtriangular, with wide adductor scars; cardinal process linear, socket plates well developed, subparallel with dorsal hinge line. *L.Sil.*, G.Brit.——Fig. 204,*7*. **G. protensa* (Sowerby), U.Llandover., Wales; *7a,b*, brach.v. ext., int., ×2; *7c*, ped.v. int. mold, ×2 (Williams, n).

Hebertella Hall & Clarke, 1892, p. 198 [**Orthis sinuata* Hall, 1847, p. 128; OD]. Like *Doleroides* but convexo-concave or unequally biconvex, with wide fold in brachial valve and with wide diductor scars not enclosing elongately suboval adductor scars borne on double ridge. *M.Ord.-U.Ord.*, N. Am.-Ire.——Fig. 205,*5*. **H. sinuata* (Hall), U. Ord.(Maysvill.-Richmond.), USA; *5a-c*, ped.v., brach.v., lat. views of conjoined valves, ×1; *5d,e*, brach.v. int., ped.v. int., ×1 (740).

Mimella Cooper, 1930, p. 375 [**Pionodema globosa* Willard, 1928, p. 274; OD]. Like *Hebertella* but unequally biconvex, with long, slightly curved, catacline to apsacline ventral interarea and with ventral muscle field consisting of long subparallel, deeply impressed diductor scars not enclosing long, anteriorly expanding elevated adductor track. *M.Ord.*, N.Hemis.——Fig. 204,*3*. **M. globosa* (Willard), Porterfield, USA (*3a-c,e*, Va., *3d*, Tenn.); *3a,b*, post., lat views of conjoined valves, ×1; *3c*, ped.v. ext., ×2; *3d,e*, ped.v. int., brach.v. int., ×1 (189).

Oligorthis Ulrich & Cooper, 1936. p. 624 [**O. arbucklensis*; OD]. Like *Desmorthis* but more finely costellate and without cardinal process and apical plate in delthyrium. *L.Ord.*, N.Am.(W. USA).——Fig. 204,*5*. **O. arbucklensis*, Canad., Okla., *5a*, brach.v. ext., ×3; *5b*, brach.v. int., ×4; *5c*, ped.v. int., ×3 (825).

Scaphorthis Cooper, 1956, p. 502 [**S. virginiensis*; OD]. Subcircular in outline with short hinge line, unequally biconvex, with short, curved apsacline interarea in deeper pedicle valve, costellate; ventral muscle scar short, subcordate, with wide median adductor scar; cardinal process with thin bladelike myophore. *M.Ord.-U.Ord.*, N.Am.(E. USA)-Scot.-Ire.——Fig. 204,*4*. **S. virginiensis*, M.Ord.(Porterfield), USA(Va.); *4a-c*, brach.v. ext., brach.v. int., ped.v. int., ×2 (189).

Schizophorella Reed, 1917, p. 858 [**Orthis fallax* Salter, 1846, p. 72; OD]. Like *Corineorthis* but with greater convexity of brachial valve accentuated by strong median fold in adult shells; ventral muscle field long, with subparallel lateral boundaries formed of dental plates and their anterior extensions, adductor scar long and narrow with faint double ridges like *Hebertella*. *U.Ord.*, G.Brit.-

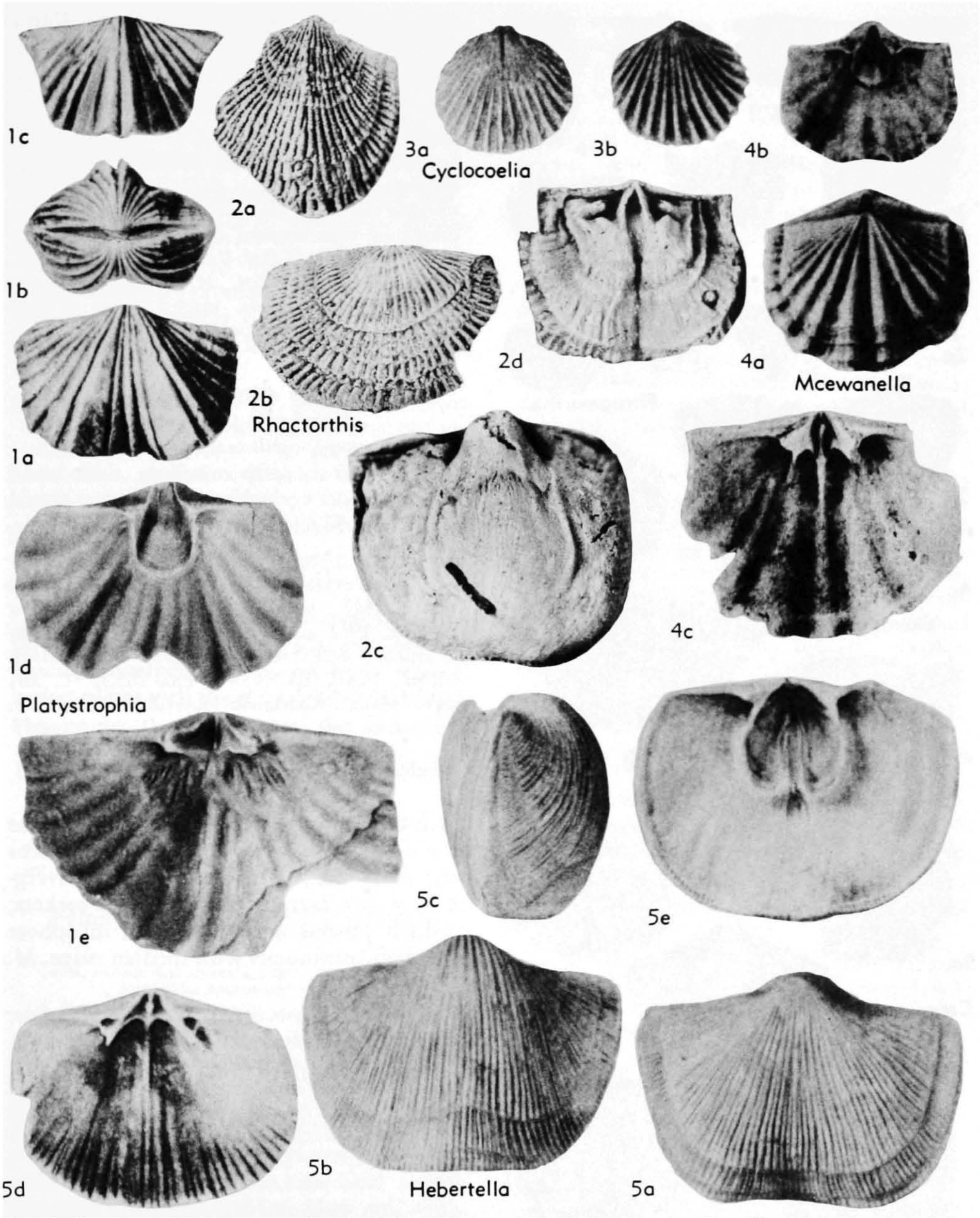

FIG. 205. Plectorthidae (Plectorthinae) *(5)*, (Platystrophiinae) *(1, 4)*, (Cyclocoeliinae) *(3)*, (Rhactorthinae) *(2)* (p. *H324-H326*).

Ire.——FIG. 204,*9. S. fallax* (SALTER), Scot.; *9a,* ped.v. view of int. mold of conjoined valves, ×1.5; *9b,* ped.v. ext., ×1.5; *9c,* brach.v. int., ×2 (Williams, n).

Subfamily PLATYSTROPHIINAE
Schuchert & Le Vene, 1929

[Platystrophiinae SCHUCHERT & LEVENE, 1929, p. 14]

Costate to costellate, with large subequal interareas and wide hinge lines, dorsal median fold strongly developed; brachiophore bases convergent. *M.Ord.-U.Sil.*

Platystrophia KING, 1850, p. 105 [**Terebratulites biforatus* VON SCHLOTHEIM, 1820, p. 265; OD]. Spiriferoid in outline, hinge line commonly mu-

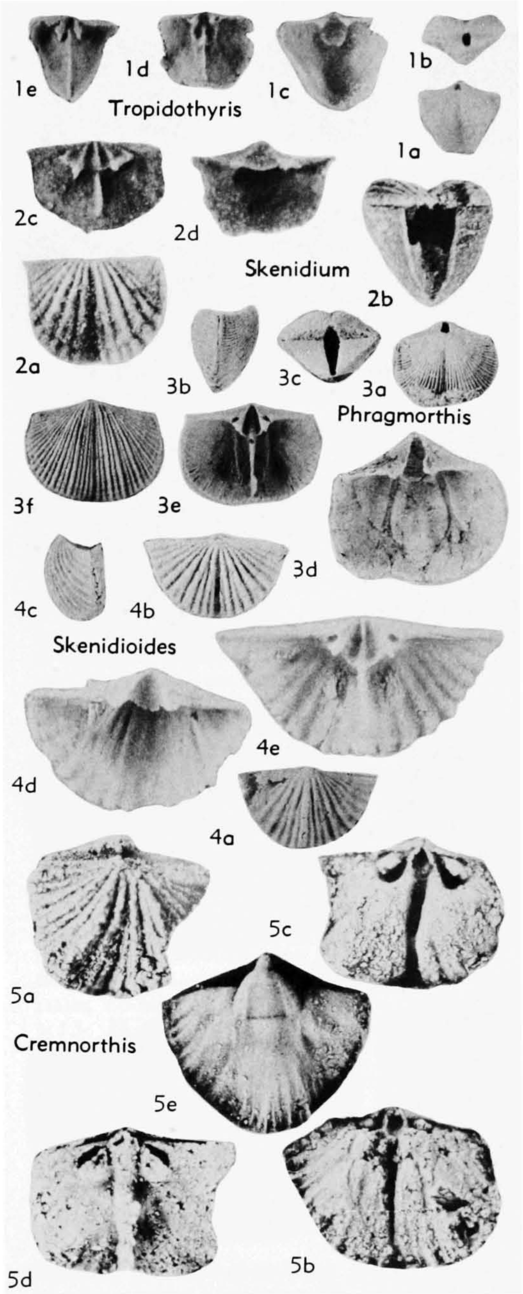

Fig. 206. Cremnorthidae (Cremnorthinae) *(5)*, (Phragmorthinae) *(3)*; Skenidiidae *(1-2, 4)* (p. *H*326-*H*327).

cronate, strongly biconvex, costate and finely pustulose; ventral muscle field elongate, with broad adductor scars and commonly elevated on platform of secondary shell in adult valves; cardinal process low, ridgelike. *M.Ord.-U.Sil.(Wenlock.),* cosmop.——Fig. 205,*1. P. laticosta* Meek, U.Ord. (Maysvill.), S.USA; *1a,b,* ped.v., post. views of conjoined valves, ×1 (740); *1c,* brach.v. ext., ×1 (740); *1d,e,* ped.v. int., brach.v. int., ×1.5 (729).

Mcewanella Foerste, 1920, p. 197 [**Platystrophia fernvalensis* McEwan, 1919, p. 428 (=**Hebertella lineolata* Savage, 1918, p. 267); OD]. Like *Platystrophia* but with costellate radial ornamentation commonly superimposed on costate arrangement of *Platystrophia. M.Ord.-U.Ord.,* N.Am.(USA)-G. Brit.-Eire.——Fig. 205,*4. M. raymondi* Foerste, U.Ord., USA(Mo.); *4a,* brach.v. view of conjoined valves, ×2; *4b,* ped. v. int., ×1; *4c,* brach. v. int., ×2 (740).

Subfamily CYCLOCOELIINAE
Schuchert & Cooper, 1931

[Cyclocoeliinae Schuchert & Cooper, 1931, p. 243]

Costate to coarsely costellate, with small interareas and very short hinge lines, dorsal fold faint; brachiophore bases convergent. *U.Ord.*

Cyclocoelia Foerste, 1909, p. 227 [**Atrypa sordida* Hall, 1847, p. 148; OD] [=*Encuclodema* Foerste, 1912, p. 227 (obj.)]. Rhynchonelliform in outline; shell thin, muscle scars not impressed. *U.Ord.,* N.Am.(E.USA).——Fig. 205,*3.* **C. sordida* (Hall), Cincinnati(Maysvill.), Ohio; *3a,b,* brach.v. int., ext., ×2 (729).

Subfamily RHACTORTHINAE Williams, 1963

[Rhactorthinae Williams, 1963, p. 371]

Costellate, with well-developed interareas and wide hinge lines, dorsal median sulcus well developed; brachiophore bases divergent, curving laterally so as to define sockets; cardinal process with crenulated myophore and shaft continuous with median ridge. *M. Ord.-U.Ord.*

Rhactorthis Williams, 1963, p. 371 [**R. crassa*; OD]. Unequally biconvex, with deep pedicle valve, multicostellate, with hollow costellae; dental plates short, receding, ventral muscle field subpentagonal, with wide aductor scars not enclosed by narrow divergent diductors. *M.Ord.-U.Ord.,* G.Brit.-Eire. ——Fig. 205,*2.* **R. crassa,* M.Ord.(Longvill.), Wales; *2a,b,* ped.v. ext., brach.v. ext., ×3; *2c,* ped.v. int. mold, ×3.5; *2d,* brach.v. int. mold, ×6.5 (Williams, n).

Family CREMNORTHIDAE
Williams, 1963

[Cremnorthidae Williams, 1963, p. 377]

Strongly biconvex, with deep narrow dorsal sulcus, delythrium and chilidium open; ventral muscle field short, subtriangular, dental plates short, stout, receding; cardinal process simple or differentiated, continuous with high dorsal median septum, subtriangular in outline, extending almost to anterior margin and dividing elongately oval dorsal adductor field; ventral mantle canal system saccate, with divergent *vascula media,* dorsal system unknown. *M.Ord.*

Subfamily CREMNORTHINAE Williams, 1963

[*nom. transl.* Williams, herein (*ex* Cremnorthidae Williams, 1963, p. 377)]

Adductor scar in ventral muscle field wide; cardinal process trilobed; brachiophores short, widely divergent, with bases curved laterally to define semioval sockets. *M.Ord.*

Cremnorthis Williams, 1963, p. 378 [**C. parva*; OD]. Fascicostellate, with angular costae and costellae. *M.Ord.,* Wales.——Fig. 206,*5*. **C. parva*; *5a,* brach.v. view of conjoined valves, ×6; *5b,c,* brach.v. mold, int., ×7, ×8.5; *5d,* brach.v. int., ×9.5; *5e,* ped.v. int. mold, ×6.5 (Williams, n).

Subfamily PHRAGMORTHINAE Williams, n. subfam.

Ventral muscle field undifferentiated; cardinal process ridgelike; brachiophores long, bases convergent onto median septum, socket plates well developed. *M.Ord.-U.Ord.*

Phragmorthis Cooper, 1956, p. 508 [**P. buttsi*; OD]. Multicostellate, with some costellae swollen. *M.Ord.-U.Ord.,* N.Am.-Scot.——Fig. 206,*3*. **P. buttsi,* M.Ord.(Porterfield), USA (*3a-c,* Va., *3d-f,* Tenn.); *3a-c,* brach. v., lat., post. views of conjoined valves, ×2; *3d,e,* ped.v. int., brach.v. int., ×4; *3f,* brach.v. ext., ×4.5 (189).

Family SKENIDIIDAE Kozlowski, 1929

[*nom. correct.* Schuchert & Cooper, 1931, p. 243 (pro Scenidiidae Kozlowski, 1929, p. 46]

Subpyramidal, with open delthyrium and chilidium; ventral muscle field contained in free or supported spondylium; brachiophores long, slender, commonly with bases convergent on high median septum and united laterally to socket plates or to hinge plates containing sockets; cardinal process simple or differentiated into shaft and crenulated myophore; dorsal adductor field shield-shaped, impressed on either side of septum; mantle canal systems rarely preserved. *L. Ord.-U.Dev.*

Skenidium Hall, 1860, p. 70 [**Orthis insignis* Hall, 1859, p. 173; SD Hall & Clarke, 1892, p. 241]. Pedicle valve high, with procline to apsacline interarea, brachial valve plane to gently convex, with median sulcus, costate to coarsely costellate; spondylium free anteriorly, supported apically by small septum; cardinal process linear, not continuous with median septum; large slightly concave plates lateral to brachiophores sharply indented near junction with hinge line to form sockets. *L.Dev.-U.Dev.,* cosmop.——Fig. 206,*2*. **S. insigne* (Hall), L.Dev., USA(N.Y.); *2a,b,* brach.v., post. view of conjoined valves, ×4; *2c,d,* brach.v. int., ped.v. int., ×4 (729).

Skenidioides Schuchert & Cooper, 1931, p. 243 [**S. billingsei*; OD]. Like *Skenidium* but with cardinal process commonly differentiated into shaft and compressed myophore and continuous with median septum; plates lateral to brachiophores, narrow, entirely and deeply concave to form sockets. *L.Ord.-U.Sil.,* cosmop.——Fig. 206,*4*. *S. costatus* Cooper, M.Ord.(Porterfield), USA(Va.-Tenn.); *4a-c,* ped.v., brach.v., lat. views of conjoined valves, ×4; *4d,e,* ped.v. int., brach.v. int., ×6 (189).

Tropidothyris Cooper, 1956, p. 507 [**T. pentagona*; OD]. Like *Skenidioides* but subpentagonal in outline, with smooth or faintly plicate external surface and with subparallel brachiophore bases attached to floor of brachial valve. *M.Ord.,* N.Am. (E.USA).——Fig. 206,*1*. **T. pentagona,* Porterfield, Ala.; *1a,b,* brach.v., post. views of conjoined valves, ×5; *1c,* ped.v. int., ×8; *1d,e,* brach.v. ints., ×8 (189).

Family TUVAELLIDAE Alichova, 1960

[Tuvaellidae Alichova, 1960, p. 190]

Interareas well developed, hinge line wide, deltidium and chilidium present, teeth strong, supported by receding dental plates, ventral muscle field elliptical; cardinal process short and thick, notothyrial platform wide. *L.Sil.*

Tuvaella Chernyshev, 1937, p. 11 [**T. rackovskii*; OD]. Costate, plano-convex to unequally biconvex, with deep median sulcus in brachial valve. *L.Sil.,* E.USSR.——Fig. 207,*1*. **T. rackovskii*; *1a-c,* ped.v., brach.v., post. views of conjoined valves, ×2 (710).

Family SAUKRODICTYIDAE Wright, 1964

[Saukrodictyidae Wright, 1964, p. 218]

Interareas short, hinge line wide, delthyrium and notothyrium open; costae and costellae developed within honeycomb network ornamenting shell surface; teeth supported by short strong dental plates; cardinal process simple, brachiophores short, divergent, with bases convergent onto notothyrial platform, fulcral plates absent. *U.Ord.*

Saukrodictya Wright, 1964, p. 218 [**S. hibernica*; OD]. Unequally biconvex, with strong median fold in deeper pedicle valve; ventral muscle field

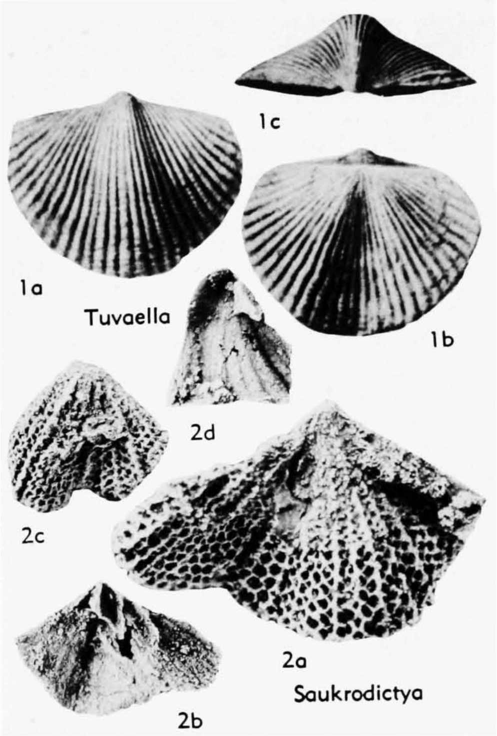

FIG. 207. Tuvaellidae *(1)*; Saukrodictyidae *(2)* (p. *H*327-*H*328).

poorly preserved, dorsal adductor field elongately subquadrate. *U.Ord.(Ashgill.)*; Eire.——FIG. 207, 2. **S. hibernica*; *2a,* incomplete brach.v. ext., ×9; *2b,* incomplete brach.v. int., ×5; *2c,d,* incomplete ped.v. ext., int., ×5 (895b).

Superfamily ENTELETACEA Waagen, 1884

[*nom. transl.* ALICHOVA, 1960, p. 193 (*ex* Enteletinae WAAGEN, 1884, p. 548); *emend.* WRIGHT, herein]
[Materials for this superfamily prepared by A. D. WRIGHT]
[Appreciation and thanks are expressed to the Trustees of the British Museum (Natural History) for permission to reproduce several illustrations from WILLIAMS, 1963 (ref. 878)]

Delthyrium and notothyrium open, rarely constricted by plate or plates; teeth supported by variably developed dental plates, ventral muscle field impressed on floor of pedicle valve, exceptionally raised above valve floor; cardinal process of lobate myophore and shaft, rarely simple or absent; sockets simple or defined by fulcral plates, brachiophores with bases convergent or divergent on floor of brachial valve, rarely extended to produce calcareous support to lophophore. Ventral mantle canal system commonly lemniscate, rarely saccate, dorsal lemniscate to digitate and pinnate. Shell substance punctate. *L.Ord.-U.Perm.*

Recent investigations show that the name applied to the superfamily of punctate orthoid-like brachiopods, Dalmanellacea, is incorrect according to present taxonomic procedure.

The Dalmanellacea were first given superfamilial status by SCHUCHERT & COOPER (1931, p. 245), the principal character used to separate this superfamily from the Orthacea being the punctate nature of the shell (p. 242). Since 1931, the name has been generally accepted in the literature concerned with brachiopod classification (e.g., COOPER, 1944, p. 351; MOORE, 1952, p. 220; MUIR-WOOD, 1955, p. 87; WILLIAMS, 1956, p. 284).

In the latest classificatory work, the Russian "Treatise" (Osnovy), ALICHOVA divides the punctate orthoid stocks into two superfamilies Rhipidomellacea and Enteletacea (1960, p. 183). Here the Rhipidomellacea include the family Dalmanellidae, the name Dalmanellacea being replaced on grounds of priority, ALICHOVA attributing the Dalmanellidae to SCHUCHERT, 1929, and the Rhipidomellidae to SCHUCHERT, 1913. However, as all categories in the family group are of co-ordinate status in nomenclature, and as a change in rank of a taxon within the family group does not affect authorship, there is no justification for the use of Rhipidomellacea instead of Dalmanellacea, as both superfamilies are ascribable to SCHUCHERT, 1913, the diagnosis of the Dalmanellinae being given before Rhipidomellidae (p. 382 of that work).

With respect to the Enteletacea, the subfamily Enteletinae was erected by WAAGEN (1884, p. 548) as a subfamily of the Orthidae, and accordingly it antedates any other family taxon within the punctate orthoid stocks. The division of these forms by ALICHOVA into two distinct groups at superfamilial level seems entirely unjustified on morphological considerations; thus, on the grounds of priority, the name Enteletacea has been adopted for the entire superfamily.

The change of superfamilial name may initially be inconvenient. Although both *Dalmanella* and *Enteletes* are equally widespread and well-known stocks, the former, appearing early in the evolution of the group (Middle Ordovician), is relatively unspecialized and is generally considered to be close to the basic stock from which the other members of the superfamily evolved. *Enteletes,* on the other hand, is an aberrant and specialized form, only appearing in Carboniferous and Permian times; from these considerations *Dalmanella* would appear to provide the better type-genus.

These grounds, however, in no way justify an appeal for the retention of the Dalmanellacea, which is accordingly suppressed in favor of Enteletacea.

Family ENTELETIDAE Waagen, 1884

[*nom. transl.* Alichova, 1960, p. 194 (*ex* Enteletinae Waagen, 1884, p. 548); *emend.* Wright, herein] [=Schizophoriidae Schuchert & LeVene, 1929, p. 15]

Variably biconvex, ventral interarea curved, apsacline, dorsal interarea shorter, commonly curved, anacline to strongly apsacline, delthyrium and notothyrium open, costellae fine, hollow, rarely with strong superimposed radial plications, fold and sulcus variably developed; ventral muscle field with prominent diductor scars, extending beyond but not enclosing adductor scars, which may be situated on median septum; extravagant development of dental plates and ventral median septum in later genera. Cardinal process with lobate myophore and shaft; stout, commonly tusklike brachiophores with bases varying in attitude, fulcral plates present; median septum absent or low, dividing subquadrate adductor field; ventral mantle canal system probably lemniscate, dorsal pinnate. *M.Ord.-U.Perm.*

Subfamily ENTELETINAE Waagen, 1884

[Enteletinae Waagen, 1884, p. 548]

Strongly biconvex or globose, with abundant strong radial plications anteriorly; dental plates and ventral median septum invariably well developed, pedicle callist very small or absent; brachiophore bases containing adductor field posterolaterally. *M.Carb.-U.Perm.*

Enteletes Fischer de Waldheim, 1825, p. 6 [**E. glabra* Fischer de Waldheim, 1830, pl. 26, figs. 6, 7; SM] [=*Anteletes* d'Orbigny, 1850 *(nom. null.)*; *Enteles* Schellwein, 1892 *(nom. null.)*; *Syntrilasma* Meek & Worthen, 1865, p. 277 (type, *Spirifer hemiplicatus* Hall, 1852); *Syntrielasma* Meek & Worthen, 1866, p. 321 *(nom. van.)*]. Small to medium-sized, globose, dorsibiconvex, strongly plicate anteriorly, with dorsal fold and ventral sulcus; dental plates strong,

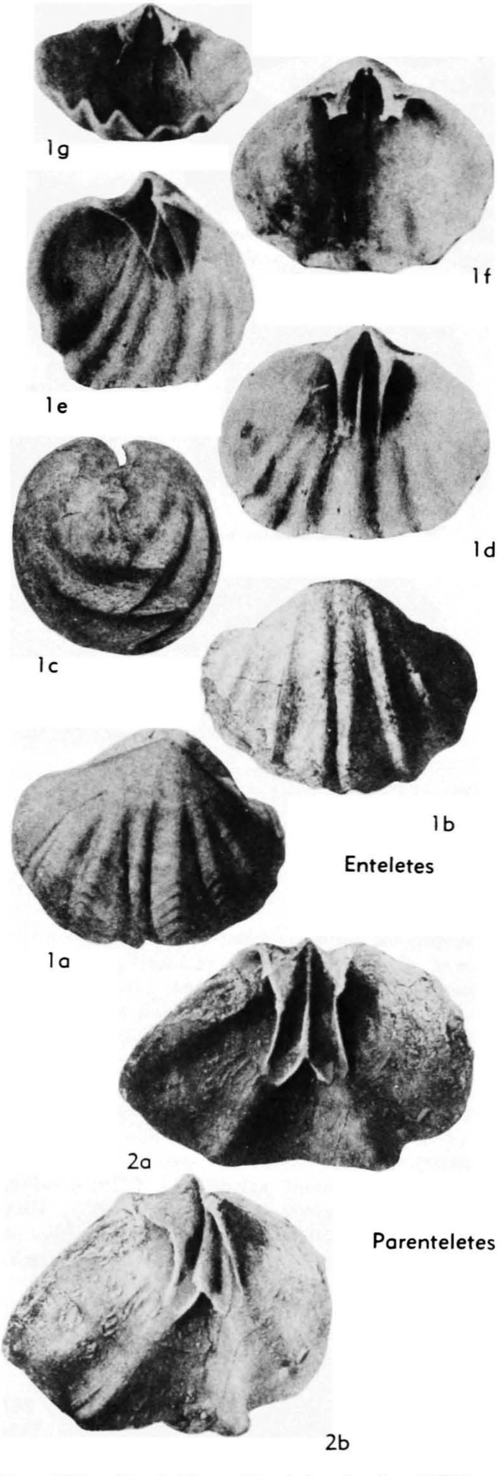

Fig. 208. Enteletidae (Enteletinae) (p. *H*329-*H*330).

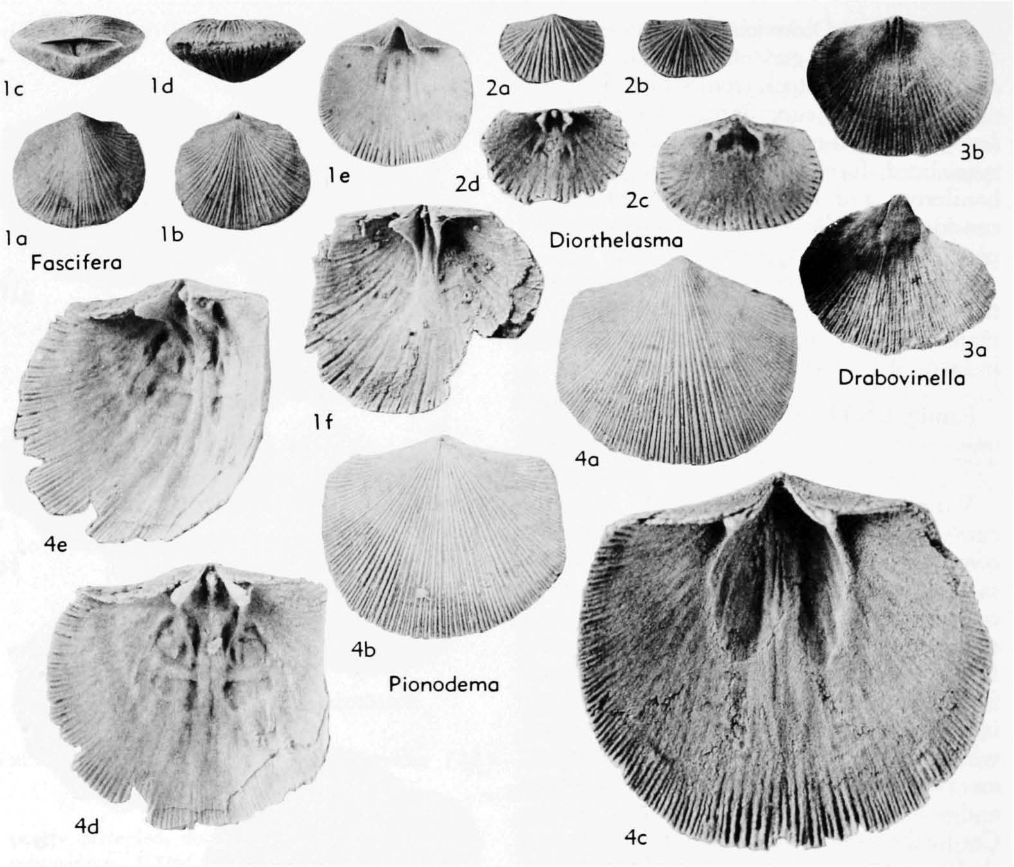

FIG. 209. Enteletidae (Draboviinae) (p. *H*331-*H*332).

subparallel, median septum strong, rising to crest near abruptly truncated anterior end, ventral muscle field narrowly restricted; cardinal process small, crenulated, on shallow notothyrial platform, brachiophores stout, tusklike, with strong, divergent bases; low, narrow median septum commonly developed, small posterior adductor scars lateral to larger anterior pair. *U.Carb.-U.Perm.,* widespread. ——FIG. 208,*1a-c. E. lamarcki* (FISCHER DE WALDHEIM), U.Carb., USSR; *1a-c,* ped.v., brach.v., lat. views of conjoined valves, ×1 (729).——FIG. 208,*1d-g. Enteletes* sp., Perm.(WordF.), USA (Tex.,Glass Mts.); *1d,e,* normal, oblique views of ped.v. int., ×2; *1f,g,* normal, ant. views of brach. v. int., ×2 (178).

Enteletella LIKHAREV, 1925, p. 719 [**E. nikschitchi*; OD]. Like *Enteletes,* but distinguished by convergence of dental plates to form spondylium. *U. Perm.,* USSR(Caucasus).

Enteletina SCHUCHERT & COOPER, 1931, p. 247 [**Enteletes latesinuatus* WAAGEN, 1884, p. 559; OD]. Like *Enteletes* but with dorsal sulcus and ventral fold. *U.Carb.-U.Perm.,* Asia-?N.Am.

Parenteletes KING, 1930, p. 48 [**P. cooperi*; OD]. Like *Enteletina* externally, but distinguished by presence of cella under anterior of ventral median septum. *U.Carb.-L.Perm.,* Eu.-Asia-N.Am.——FIG. 208,*2. *P. cooperi,* L.Perm.(Wolfcamp.), USA (Tex.); *2a,b,* normal, oblique views of ped.v. int., ×2 (729).

Subfamily DRABOVIINAE Havlíček, 1950

[Draboviinae HAVLÍČEK, 1950, p. 45; *emend.* WRIGHT, herein]

Profile lenticular, with pedicle valve commonly deeper than brachial valve, strong radial plications lacking; ventral median septum not strongly developed, pedicle callist usually present; anterior continuation of brachiophore bases converging on to median ridge and not containing adductor field posteriorly; brachiophore bases may converge directly on to median ridge. *M.Ord.-U.Ord.*

Drabovia HAVLÍČEK, 1950, p. 45 [**Orthis redux* BARRANDE, 1848, p. 49; OD]. Like *Fascifera,* but completely lacking median thickening to ventral muscle field. *M.Ord.,* Eu.-N.Afr.

?Comatopoma HAVLÍČEK, 1950, p. 54 [**C. bar-*

randei; OD]. Transversely subcircular, subequally biconvex, finely costellate, sulcate; ventral muscle field short, broad, commonly bilobate; cardinal process simple ridge, convergent brachiophore bases short, thin. _U.Ord._, Boh.

Diorthelasma Cooper, 1956, p. 997 [*_D. parvum_; OD]. Minute, transverse, ventribiconvex, with marked sulcus in shallow brachial valve; cordate ventral muscle field wide, short, pedicle callist not known, _vascula media_ strongly divergent; cardinalia like _Fascifera,_ dorsal adductor scars small, elongate, posterior pair situated lateral to anterior pair, median ridge lacking. _M.Ord.,_ SE.USA-Scot. ——Fig. 209,_2_. *_D. parvum,_ Porterfield, USA (Ala.); _2a,b,_ ped.v., brach.v. views of conjoined valves, ×4; _2c,d,_ ped.v. int., brach.v. int., ×6 (189).

Drabovinella Havlíček, 1950, p. 50 [*_Orthis drabovensis_ Barrande, 1879, pl. 61, fig. 5; OD]. Transverse, commonly large, subequally biconvex, apparently without fold or sulcus; ventral muscle field narrowly triangular, thickening to adductor field completely lacking; cardinal process shaft and convergent brachiophore bases very closely apposed, continued anteriorly as long, low, subparallel ridges. _M.Ord.,_ Boh.——Fig. 209,_3_. *_D. drabovensis_ (Barrande), Llandeil.; _3a,b,_ ped.v. int., brach.v. int., ×1 (Wright, n).

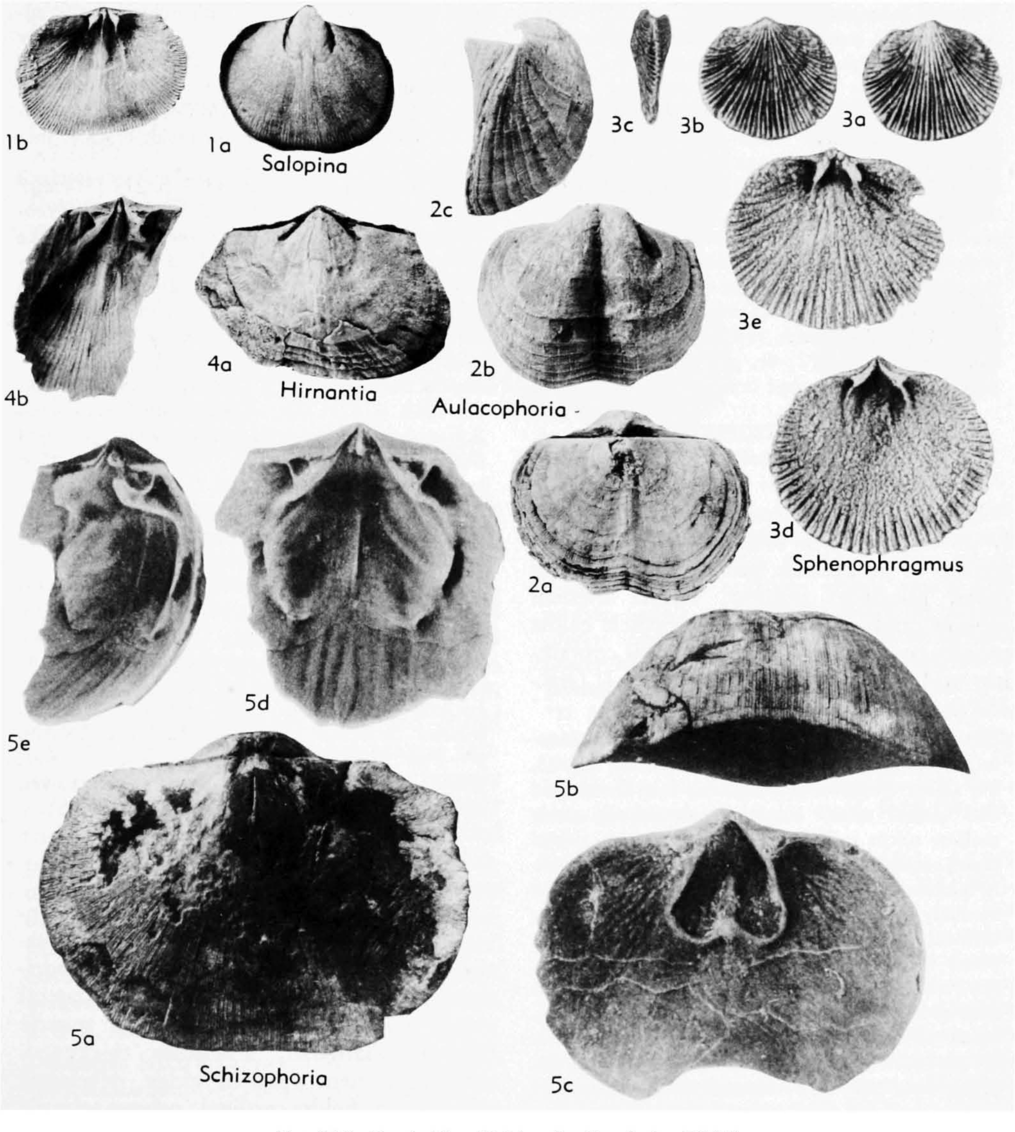

Fig. 210. Enteletidae (Schizophoriinae) (p. _H_332).

Fascifera Ulrich & Cooper, 1942, p. 620 [**F. subcarinata*; OD]. Distinguished from *Pionodema* by generally fascicostellate ornament, commonly persistent dorsal sulcus, poorly developed ventral median ridge, and narrower notothyrial platform with brachiophore bases variably convergent toward median ridge. *M.Ord.*, N.Am.-?Eu.(Scot.).——Fig. 209,*1a-e*. **F. subcarinata,* Wilderness, USA (Tenn.); *1a-d,* ped.v., brach.v., post., ant. views of conjoined valves, ×2; *1e,* ped.v. int., ×2 (189).——Fig. 209,*1f*. *F. stonensis* (Safford), Wilderness; USA(Tenn.); *1f,* oblique brach.v. int., ×3 (189).

Pionodema Foerste, 1912, p. 139 [*pro Bathycoelia* Foerste, 1909 (*non* Amyot & Serville, 1843)] [**Orthis subaequata* Conrad, 1843, p. 333; OD]. Subcircular to transversely elliptical, ventribiconvex to subequally biconvex with narrow dorsal sulcus of young stages usually lost or reverting to low fold in adult; ventral muscle field with commonly subflabellate diductor scars and elongate semielliptical adductor scars on median thickening; cardinal process with small, crenulated, bilobate myophore and slender shaft, brachiophore bases suberect, bounding broad notothyrial platform, with anterior extensions convergent on to median ridge. *M.Ord.-U.Ord.*, N.Am.-Scot-?Asia.——Fig. 209,*4*. **P. subaequata* (Conrad), M.Ord.(Barnhart), USA(Mo.); *4a,b,* ped.v., brach.v. views of conjoined valves, ×2; *4c,* ped.v. int., ×2; *4d,e,* normal, oblique views of brach.v. int., ×2 (189).

Subfamily SCHIZOPHORIINAE Schuchert & LeVene, 1929

[Schizophoriinae Schuchert & LeVene, 1929, p. 15]

Biconvex young growth stages commonly developing deep brachial valve and less convex or resupinate pedicle valve, strong radial plications lacking; ventral median septum rarely well developed, pedicle callist usually present; brachiophore bases containing adductor field posterolaterally. *U.Ord.-U.Perm.*

Schizophoria King, p. 106 [**Conchyliolithus (Anomites) resupinatus* Martin, 1809, pl. 49, fig. 13, 14; OD]. Transversely elliptical, low dorsal fold and ventral sulcus commonly developed, rarely shallow sulcus in both valves; teeth strong, dental plates extending as low ridges bounding elongatedly bilobate to broadly cordate muscle field, divided medially by anteriorly elevated adductor ridge; cardinal process typically with large lobate myophore in young stages, less prominent in adult. *Sil.-Perm.*, cosmop.——Fig. 210,*5a,b*. **S. resupinata* (Martin), L.Carb., Eng.; *5a,b,* ped.v., ant. views of neotype, ×0.7 (87).——Fig. 210,*5c-e*. *S. iowensis* (Hall), U.Dev., USA(Iowa); *5c,* ped.v. int., ×2; *5d,e,* normal, oblique views of brach.v. int., ×2 (729).

Aulacophoria Schuchert & Cooper, 1931, p. 247 [**Orthis keyserlingiana* de Koninck, 1843, p. 230; OD]. Like *Schizophoria* but with deep dorsal sulcus and narrow ventral fold; ventral interarea commonly flat, catacline. *L.Carb.*, Eu.——Fig. 210,*2*. **A. keyserlingiana* (de Koninck), Eng.; *2a-c,* ped.v., brach.v., lat. views of conjoined valves, ×1 (Wright, n).

Enteletoides Stuckenberg, 1905, p. 59 [**E. rossicus*; OD]. Like *Schizophoria* but with dental plates and ventral median septum extravagantly developed as in *Enteletes*. *U.Carb.*, C.Asia.

Hirnantia Lamont, 1935, p. 313 [**Orthis sagittifera* M'Coy, 1851, p. 398; OD]. Dorsibiconvex, commonly with shallow dorsal sulcus, distinguished from more finely costellate *Schizophoria* by suboval ventral muscle field with subtriangular adductor scars impressed, with no median ridge or thickening; cardinal process with small myophore and long shaft. *U.Ord.-L.Sil.*, Eu.(G.Brit.).——Fig. 210,*4*. **H. sagittifera* (M'Coy), U.Ord.(Ashgill.), Wales; *4a,b,* ped.v. int. mold, brach.v. int., ×1.5 (Wright, n).

Orthotichia Hall & Clarke, 1892, p. 213 [**Orthis? morganiana* Derby, 1874, p. 29; OD] [=*Orthotichina* Chernyshev, 1914 *(nom. null.)*]. Like *Schizophoria,* but with strong dental plates extending to front of ventral muscle field as high ridges and strong median septum, intermediate in development between *Schizophoria* and *Enteletoides*. *U.Carb.-U.Perm.*, widespread.

Salopina Boucot, 1960, p. 3 [**Orthis lunata* Sowerby, 1839, p. 611; OD]. Distinguished from small *Schizophoria* by ventribiconvex profile, persistent dorsal sulcus and cordate ventral muscle field lacking median ridge. *U.Sil.-L.Dev.*, W.Eu.-E.N.Am.——Fig. 210,*1*. **S. lunata* (Sowerby), U.Sil. (Ludlov.), Eng.; *1a,* ped.v. int. mold, ×1.5; *1b,* brach.v. int., ×2 (Wright, n).

Sphenophragmus Imbrie, 1959, p. 365 [**S. nanus*; OD]. Small, subcircular shells, initially ventribiconvex with brachial valve becoming resupinate in adult stages; ventral muscle field cordate, impressed, no median ridge or thickening; cardinal process with high, posteriorly directed, trilobed myophore. *M.Dev.*, E.N.Am.-C.N.Am.——Fig. 210,*3*. **S. nanus,* USA(Mich.); *3a-c,* ped.v., brach.v., lat. views of conjoined valves, ×2; *3d,e,* ped.v. int., brach.v. int., ×4 (445).

Family PAURORTHIDAE Öpik, 1933

[Paurorthidae Öpik, 1933, p. 11]

Small, subequally convex to ventribiconvex, ventral interarea typically curved, apsacline, dorsal interarea shorter, anacline, delthyrium open, rarely restricted by lateral plates, notothyrium open; ventral muscle field subtriangular, anteriorly thickened, with prominent median ridge developed anterior to field; cardinal process simple ridge or absent, brachiophores simple; ventral mantle canal system saccate, dorsal lemniscate to digitate. *L.Ord.-M.Ord.*

Paurorthis Schuchert & Cooper, 1931, p. 243 [**Orthambonites parva* Pander, 1830, p. 83; OD] [=*Nereidella* Wang, 1955, p. 338 (type, *N. typa*); *Paurorthina* Rubel, 1961, p. 187 (type, *P. resima*)]. Subcircular to subquadrate, sulcus in brachial valve, fascicostellate; ventral muscle field with adductor and median diductor lobes of variable size, median ridge commonly narrow, *vascula media* subparallel; brachiophores with bases greatly divergent relative to their tops, dorsal muscle field with small posterior and large anterior adductor scars, separated by strong median ridge. *L.Ord.-M.Ord.*, N.Eu.-N.Am.-Asia.——Fig. 211, *2a-d*. **P. parva* (Pander), L.Ord., USSR; *2a,b*, ped.v., brach.v. views of conjoined valves, ×2; *2c,d*, ped.v. int., brach.v. int., ×2 (729).——Fig. 211,*2e,f*. *Paurorthis sp.*, M.Ord.(Porterfield), USA (Tenn.); *2e,f*, ped.v. and brach.v. int. molds, ×2 (189).

Cyclomyonia Cooper, 1956, p. 974 [**C. peculiaris*]. Distinguished from *Paurorthis* by fine costellate ornament, initially subparallel ventral *vascula media* becoming widely divergent at front of broad median ridge, and dorsal posterior adductor scars arranged posterolateral to anterior pair. *M.Ord.*, E. USA.——Fig. 211,*1*. **C. peculiaris*, Porterfield, USA(Ala.); *1a,b*, ped.v. ext., int., ×2, ×3; *1c*, brach.v. int., ×4; *1d*, imperfect brach.v. int., ×3 (189).

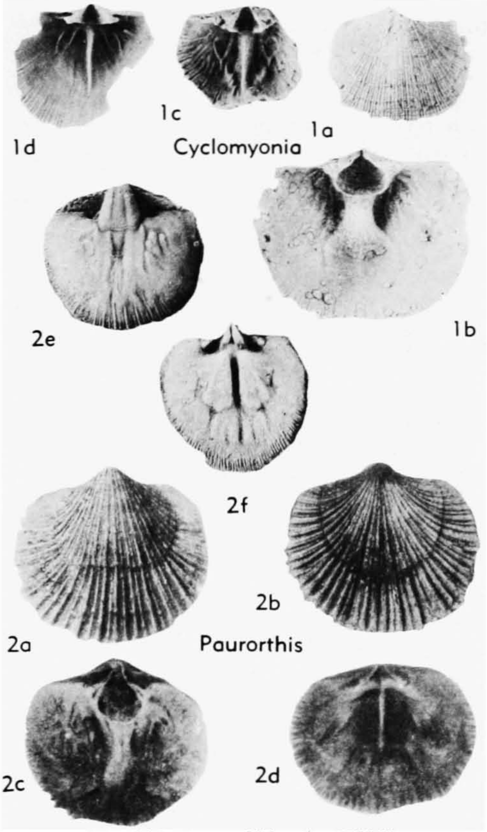

Fig. 211. Paurorthidae (p. *H*333).

Family DALMANELLIDAE Schuchert, 1913

[*nom. transl.* Schuchert & LeVene, 1929, p. 15 (*ex* Dalmanellinae Schuchert, 1913, p. 382)] [=Wattsellidae Schuchert & Cooper, 1931, p. 246; Isorthinae Schuchert & Cooper, 1931, p. 247; Onniellidae Öpik, 1933, p. 14]

Convexo-concave to plano-convex profile, ventral interarea curved, apsacline, dorsal interarea shorter, anacline, delthyrium and notothyrium open, coarsely fascicostellate to finely costellate ornament very rarely with hollow costellae, variably developed dorsal sulcus at least in young growth stages; ventral muscle field usually umbonal, broadly cordate to bilobed, with adductor scar rarely enclosed by median diductor lobes; cardinal process varying from simple ridge to elaborate trilobed myophore with shaft, bases of simple brachiophores variably disposed, fulcral plates commonly developed; dorsal adductor scar quadripartite, mantle canal system commonly lemniscate in both valves. *L.Ord.-L.Carb.*

Dalmanella Hall & Clarke, 1892, p. 205 [**Orthis testudinaria* Dalman, 1828, p. 115; OD] [=*Wattsella* Bancroft, 1928, p. 55 (type, *W. wattsi*); *Idiorthis* McLearn, 1924, p. 56 (type, *I. matura*); *Nocturnellia* Havlíček, 1950, p. 53 (type, *Orthis nocturna* Barrande, 1879)]. Subcircular, ventribiconvex, with variably developed dorsal sulcus, coarsely to finely costellate; ventral muscle field cordate, *vascula media* slightly divergent; cardinal process undifferentiated bilobed, brachiophore bases convergent onto median ridge, fulcral plates usually present. *L.Ord.-L.Sil.*, N.Hemis.——Fig. 212,*3a-e*. **D. testudinaria* (Dalman), U.Ord., Sweden; *3a-e*, ped.v., brach.v., lat., post., ant. views of conjoined valves, ×2 (880).——Fig. 212,*3f,g*. *D. wattsi* (Bancroft), M.Ord.(Marshbrook.), Eng.; *3f,g*, brach.v. int., ped.v. int. mold, ×1.5 (Wright, n).

Aulacella Schuchert & Cooper, 1931, p. 246 [**Orthis eifeliensis* Schnur, 1853, p. 213; OD]. Subequally biconvex, with low ventral fold and shallow dorsal sulcus, rarely reversed in adult shells; costellae hollow, ventral muscle scar elongatedly bilobate, *vascula media* slightly divergent; cardinal process usually trilobed, brachiophore bases greatly divergent relative to their tops. *M.Dev.-L.Carb.*, N.Hemis.——Fig. 212,*1*. **A. eifelensis* (de Verneuil), M.Dev.(Couvin.), Ger.-Pol.; *1a,b*, ped.v. ext., brach.v. ext., ×1.5; *1c*, brach.v. int., ×1.5 (729); *1d*, ped.v. int., ×2.5 (71).

Bancroftina Sinclair, 1946, p. 295 [_pro Raymondella_ Whittington, 1938 (_non_ Reed, 1935)] [_*Raymondella typa_ Whittington, 1938, p. 249, =_R. typa_ Bancroft, 1933, p. 3 (_nom. nud._); OD]. Ventral muscle field narrowly bilobate, initially subjacent _vascula media_ becoming divergent anteriorly; cardinal process undifferentiated trilobed, brachiophore bases subparallel to hinge line, ancillary struts present, fulcral plates rare. _M.Ord.-U.Ord.,_ G.Brit.-Ire.——Fig. 212,_4_. _*B. typa_ (Whittington), M.Ord.(Caradoc.), Eng.; _4a,_ ped.v. int. mold, ×1.5; _4b,c,_ brach.v. int. mold, cast, ×1.5 (Wright, n).

Cariniferella Schuchert & Cooper, 1931, p. 246 [_*Orthis carinata_ Hall, 1843, p. 267; OD]. Like _Aulacella_ but typically convexo-concave profile with persistent narrow dorsal sulcus and sharp ventral fold; myophore trilobate. _U.Dev.,_ N.Am.-W. Eu.-N. Afr.-C. Asia-Australia.——Fig. 212,_10_. _*C. carinata_ (Hall), USA(N.Y.); _10a,b,_ ped.v. ext., brach.v. ext., ×1.5; _10c,d,_ ped.v. and brach. v. int. molds, ×1.5 (729).

Cryptothyris Bancroft, 1945, p. 223 [_*Resserella paracyclica_ Bancroft, 1928, p. 56; OD] [=_Crassiorina_ Havlíček, 1950, p. 36 (type, _Orthis notata_ var. _crassior_ Barrande, 1879)]. Ventribiconvex profile, with brachial valve feebly sulcate in early growth stages only; ventral muscle field cordate, diductor lobes not extending much beyond broad adductor, _vascula media_ initially divergent; cardinal process undifferentiated bilobed, brachiophore bases slightly divergent relative to their tops, fulcral plates rare. _M.Ord.,_ Eng.-Boh.——Fig. 212, _7_. _*C. paracyclica_ (Bancroft), Caradoc, Eng.; _7a,b,_ ped.v. and brach.v. int. molds, ×3 (880).

Dedzetina Havlíček, 1950, p. 33 [_*Parmorthis (Dedzetina) macrostomoides_; OD]. Like _Resserella,_ but with convex brachial valve and divergent ventral _vascula media. U.Ord.(Ashgill.),_ Boh.

Diceromyonia Wang, 1949, p. 35 [_*Orthis tersa_ Sardeson, 1892, p. 331; OD]. Like _Paucicrura_ but with ventral muscle field composed of adductor scar enclosed by greatly elongated diductor scars. _U.Ord.,_ N.Am.——Fig. 212,_5_. _*D. tersa_ (Sardeson), USA(Iowa); ped.v. int., ×1.3 (851).

Eodalmanella Havlíček, 1950, p. 24 [_*Orthis socialis_ Barrande, 1879, pl. 63, fig. III, 1-7; OD]. Finely costellate, ventribiconvex, with wide hinge line, subcarinate pedicle valve and gently convex medially sulcate brachial valve; ventral muscle field broadly triangular, _vascula media_ divergent; cardinal process simple, ridgelike, brachiophore bases greatly divergent relative to their tops. _L. Ord.(Llanvirn.),_ Boh.——Fig. 212,_2_. _*E. socialis_ (Barrande); _2a,b,_ ped.v. int. mold and brach.v. int., ×2 (Wright, n).

Eremotrema Cooper, 1956, p. 959 [_*E. biconvexum_; OD]. Like _Howellites,_ but with fissured, trilobed cardinal process and ventral _vascula media_ initially adjacent. _M.Ord.,_ E.USA-Scot.——Fig. 212,_9_. _*E. biconvexum,_ Benbolt, USA(Va.); _9a-c,_ brach.v., post., lat. views of complete shell, ×2; _9d,_ ped.v. int., ×2; _9e,_ brach.v. int., ×3 (189).

Fascicostella Schuchert & Cooper, 1931, p. 246 [_*Strophomenes gervilii_ Defrance, 1827, p. 152; OD]. Like _Resserella_ but coarsely fascicostellate. _U.Sil._ (Pol.)-_L.Dev.,_ Eu.-N.Afr.-C. Asia-Australia-N.Z.——Fig. 212,_6_. _*F. gervilii_ (Defrance), L. Dev., Boh.; _6a,b,_ ped.v. ext., brach.v. ext., ×1.5 (729).

Heterorthina Bancroft, 1928, p. 59 [_*H. praeculta;_ OD] [=_Elsaella_ Alichova, 1960, p. 192 (_pro Bekkerella_ Rosenstein, 1943, _non_ Reed, 1936) (type, _Bekkerella bekkeri_ Rosenstein, 1943)]. Like _Onniella_ but with convex pedicle valve, subplanar brachial valve and large splayed ventral diductor scars, bounded by ridges uniting anteromedially to enclose small adductor scar, and widely divergent ventral _vascula media. M.Ord.-U.Ord.,_ Eu. (Eng.-Boh.-Est.)-?USA(Ohio).——Fig. 212,_8_. _*H. praeculta,_ M.Ord.(Caradoc.), Eng.; _8a,b,_ ped.v. int. mold, and brach.v. int., ×1.5 (Wright, n).

Howellites Bancroft, 1945, p. 203 [_*Resserella (Howellites) striata_; OD] [=_Mesodalmanella_ Havlíček, 1950, p. 26 (type, _M. flava_)]. Ventribiconvex, finely costellate with high ventral umbo and gently convex sulcate brachial valve; ventral muscle field bilobate, _vascula media_ slightly divergent and greatly divided; cardinal process undifferentiated bilobed, brachiophore bases slightly to greatly divergent relative to their tops, fulcral plates differentiated in some. _M.Ord.,_ G.Brit.-Boh. ——Fig. 212,_11_. _*H. striata_ (Bancroft), Caradoc., Wales; _11a,b,_ ped.v. ext., brach.v. ext., ×2.5; _11c,_ ped.v. int. mold, ×2.5; _11d,_ brach.v. int. mold, ×2.5; _11e,_ brach.v. int., ×3.5 (878).

Isorthis Kozlowski, 1929, p. 29 [_*Dalmanella (Isorthis) szajnochai_; OD]. Subequally biconvex profile, with shallow sulcus in brachial valve; ventral muscle field strongly bilobed, with long narrow diductor scars extending beyond thickened adductor ridge, _vascula media_ divergent; cardinal process small, variably lobate, brachiophore bases divergent relative to tops, fulcral plates commonly developed. _Sil.-M.Dev.,_ widespread.——Fig. 213, _3_. _*I. szajnochai_ (Kozlowski), U.Sil., Pol.; _3a-d,_ ped.v., brach.v., lat., ant. views of conjoined valves, ×1; _3e,_ brach.v. int., ×1.5 (Wright, n); _3f,_ post. part of ped.v. int., ×1.5 (729).

Levenea Schuchert & Cooper, 1931, p. 246 [_*Orthis subcarinata_ Hall, 1857, p. 43; OD] [=_Dalmanellopsis_ Khalfin, 1948, p. 208 (type, _D. septiger_)]. Like _Isorthis,_ but profile ventribiconvex, with trilobed cardinal process and pentagonal ventral muscle field. _Sil.-M.Dev.,_ N.Hemis. ——Fig. 213,_5_. _*L. subcarinata_ (Hall), L.Dev. (Birdsong), USA(Tenn.); _5a,b,_ ped.v. int., brach. v. int., ×1.5 (729).

Mendacella Cooper, 1930, p. 377 [_*Orthis uberis_ Billings, 1866, p. 42; OD] [=_Dalejina_ Havlíček, 1953, p. 5 (type, _D. hanusi_)]. Subequally biconvex profile; initial shallow sulcus of brachial

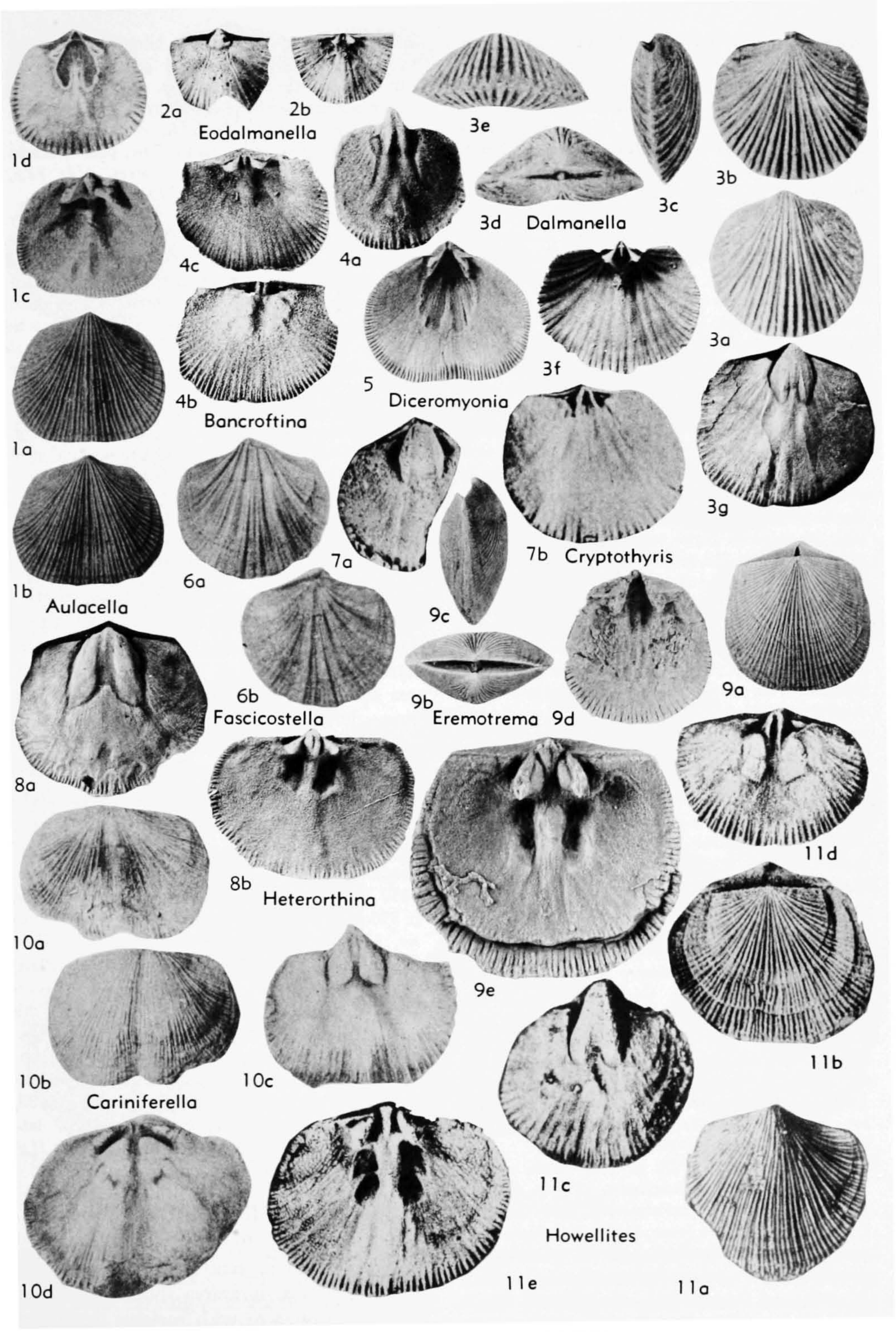

FIG. 212. Dalmanellidae (p. *H*333-*H*334).

valve replaced by fold in adult stages, with corresponding sulcus on adult pedicle valve, costellae hollow. Ventral muscle field bilobate, submedian diductor lobes extending beyond adductors; dental plates very short, commonly united with hinge line by secondary shell, *vascula media* slightly divergent. Cardinal process differentially bilobed to trilobed by fusion, brachiophore bases greatly divergent relative to tops, fulcral plates commonly developed. *U.Ord.-M.Dev.,* N.Am.-Eu.-C.Asia.——Fig. 213,*6*. **M. uberis* (Billings), U.Ord.(Richmond.), Anticosti; *6a-c,* ped.v., brach.v., ant. views of complete shell, ×2 (Wright, n); *6d,e,* brach.v. int., ped.v. int., ×2 (729).

Onniella Bancroft, 1928, p. 55 [**O. bröggeri*; OD] [=*Soudleyella* Bancroft, 1945, p. 209 (type, *S. soudleyensis*)]. Gently ventribiconvex with wide hinge line, small ventral umbo and shallow, sulcate, brachial valve; ventral muscle scar widely cordate, mantle canal systems lemniscate with ventral *vascula media* slightly divergent and greatly divided; cardinal process undifferentiated bilobed, brachiophore bases greatly divergent relative to their tops, fulcral plates rare. *M.Ord.-U.Ord.,* Eu.-N.Am.——Fig. 213,*4*. *O. grandis* Bancroft, M. Ord.(Acton.), Eng.; *4a,* ped.v. int. mold, ×2; *4b,* brach.v. int., ×1.5 (Wright, n).

Paucicrura Cooper, 1956, p. 956 [**Orthis rogata* Sardeson, 1892, p. 331; OD] [=*Cristiferina* Cooper, 1956, p. 961 (type, *C. cristata*)]. Ventribiconvex with gently convex sulcate brachial valve; ventral muscle field bilobate, *vascula media* divergent; cardinal process trilobed with median lobe forming variably developed crest, brachiophore bases divergent relative to their tops. *M. Ord.-U.Ord.,* N.Am.-Eu.——Fig. 213,*1*. **P. rogata* (Sardeson), M.Ord.(Trenton.), USA(Minn.); *1a-c,* ped.v., brach.v., post. views of complete shell, ×2; *1d,* brach.v. int., ×2 (189).

Proschizophoria Mallieux, 1912, p. 177 [**Orthis personata* Zeiler, 1857, p. 48; OD]. Large, convexo-concave, costellate, externally like *Schizophoria*; ventral muscle field broadly triangular; cardinal process with massive trilobed myophore continuous with long, thick, bladelike shaft; brachiophore bases divergent relative to their tops, continuous with ridge containing broadly suboval quadripartite adductor field. *Dev.,* W.Eu.-N.Afr.-C. Asia-E.N.Am.——Fig. 213,*8*. **P. personata* (Zeiler), L.Dev., Ger.; *8a,b,* brach.v. and ped.v. int. molds, ×0.7 (Wright, n), ×1.5 (729); *8c,* brach.v. cardinalia, ×1 (880).

Resserella Bancroft, 1928, p. 54 [**Orthis canalis* J. de C. Sowerby in Murchison, 1839, p. 630, pl. 13, fig. 12a; OD] [=*Parmorthis* Schuchert & Cooper, 1931, p. 246 (type, *Orthis elegantula* Dalman, 1828)]. Ventribiconvex to plano-convex costellate shells with plane to gently convex brachial valve and deep pedicle valve; ventral muscle field small, cordate, *vascula media* adjacent for much of their length; teeth and sockets crenulated; cardinal process differentially bilobed to trilobed by fusion, brachiophore bases greatly divergent, commonly with fulcral plates, elongatedly oval dorsal adductor field bounded by low ridges. *Sil.,* widespread.——Fig. 213,*7*. *R. elegantula* (Dalman), U.Sil.(Gotland.), Gotl.; *7a-c,* ped.v., brach. v., post. views of conjoined valves, ×2; *7d,e,* ped.v. int., brach.v. int., ×2 (729).

?**Teichertina** Veevers, 1959, p. 37 [**T. fitzroyensis*; OD]. Fascicostellate, ventribiconvex, transverse, with greatest width at hinge line; pedicle valve pyramidal, sulcus present in each valve, anterior margin emarginate; ventral muscle field possibly subapical; cardinal process bilobed, brachiophore bases subparallel to hinge line, fulcral plates present; brachial valve with quadripartite adductor field almost as long as valve; dorsal mantle canal system saccate-inequidistributate. *U.Dev.,* W.Australia.——Fig. 213,*2*. **T. fitzroyensis*; *2a-d,* ped.v., brach.v., lat., post. views of conjoined valves, ×3.5; *2e,* brach.v. int., ×3.5 (838).

Family DICOELOSIIDAE Cloud, 1948

[*nom. correct.* Roger, 1952, p. 82 (*ex* Dicaelosiidae Cloud, 1948, p. 374)] [=Bilobitidae Schuchert & Cooper, 1931, p. 246]

Outline bilobed with emarginate anterior margin resulting from sulcus in each valve. Hinge line of variable width, but shorter than maximum valve width; ventral interarea apsacline, dorsal interarea shorter, anacline, delthyrium and notothyrium open. Ventral muscle field with adductor scars not enclosed by diductor scars; cardinal process with short, bilobed myophore and shaft, brachiophores long, bladelike plates. *U.-Ord.-M.Dev.*

Dicoelosia King, 1850, p. 106 [=*Dicaelosia* King, 1850 *(nom. null.)*; =*Bilobites* Quenstedt, 1869, p. 550 *(obj.)* (*non* Rafinesque, 1831; *nec* d'Orbigny, 1839; *nec* Bronn, 1848)] [**Anomia biloba* Linné, 1767, p. 1154; OD]. Small, costellate, pedicle valve strongly convex, brachial valve varying from less convex to gently concave, with variably developed flattening of cardinal extremities; quadripartite dorsal adductor field rarely impressed. *U.Ord.-M.Dev.,* N.Am.-Eu.-C.Asia-Australia.——Fig. 214,*1*. **D. biloba* (Linné), U.Sil. (Wenlock.), Gotl.; *1a-e,* ped.v., brach.v., lat., post., ant. views of conjoined valves, ×3; *1f,g,* ped.v. int., brach.v. int., ×5 (Wright, n).

Family KAYSERELLIDAE Wright, n. fam.

Ventribiconvex, ventral interarea curved, apsacline, dorsal interarea shorter, anacline, delthyrium open or with variably developed apical plate or notodeltidium, ornament cos-

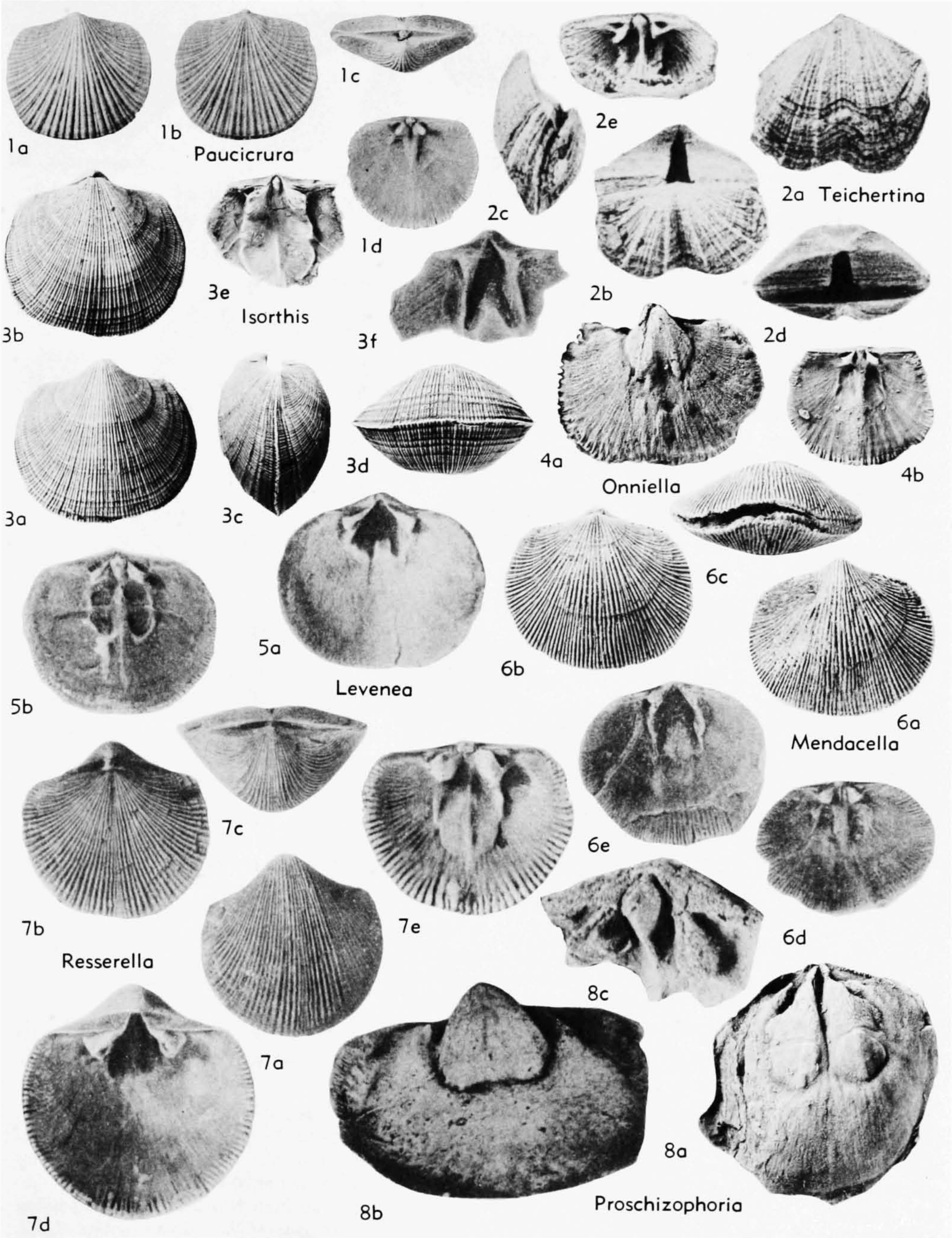

FIG. 213. Dalmanellidae (p. *H*334, *H*336).

tellate, sulcus in brachial valve; dental plates short, stout, receding; brachiophores short, stout, bases varying in attitude, fulcral plates commonly developed; shell space divided longitudinally by high dorsal septum of subtriangular outline, commonly extending ventrally to reach pedicle valve, and anteriorly almost to valve margin; ventral mantle canal system lemniscate, dorsal also probably lemniscate. *M.Dev.-U.Dev.*

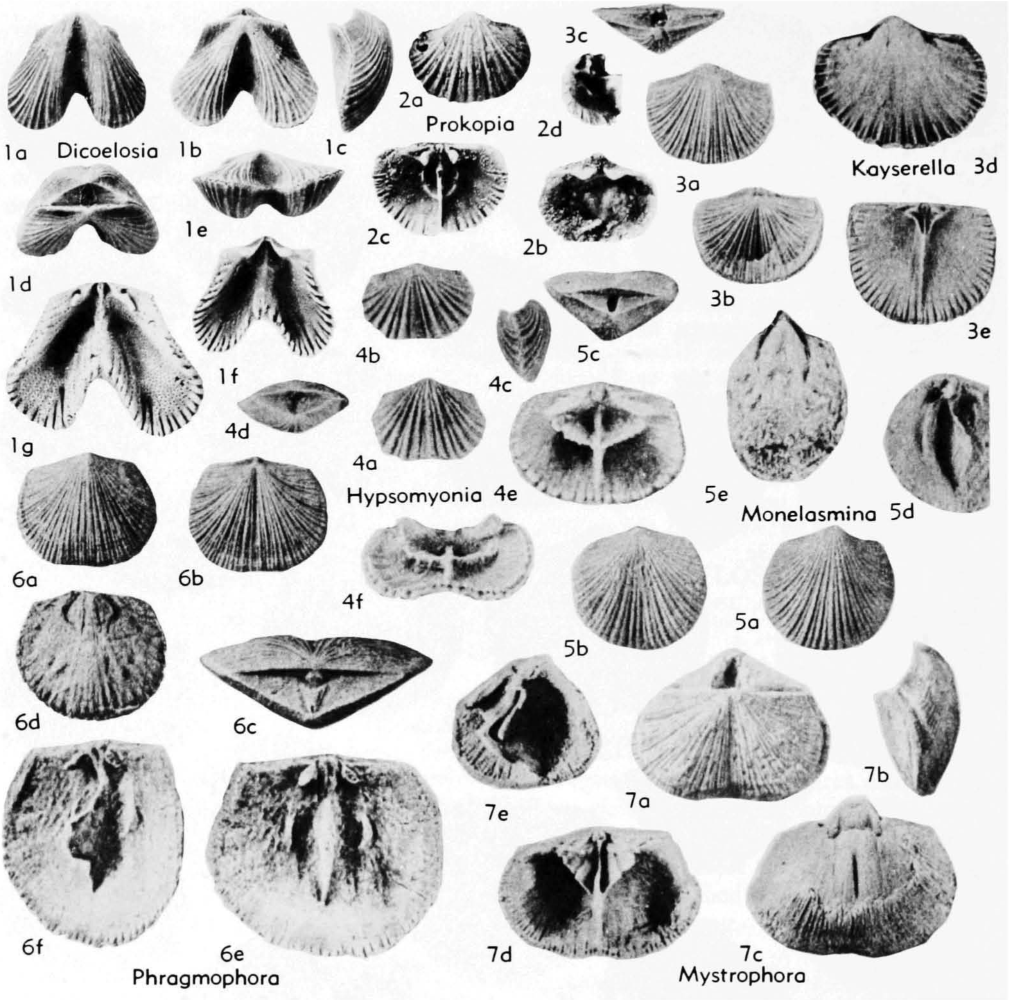

FIG. 214. Dicoelosiidae *(1)*; Kayserellidae (Kayserellinae) *(3)*, (Prokopiinae) *(2, 5-6)*; Mystrophoridae *(7)*; Hypsomyoniidae *(4)* (p. *H*336-*H*339).

Subfamily KAYSERELLINAE Wright, n. subfam.

Cardinal process with bilobate myophore and slender shaft, brachiophore bases convergent on to median septum to form septalium. *M.Dev.*

Kayserella HALL & CLARKE, 1892, p. 259 [**Orthis lepida* SCHNUR, 1853, p. 218; OD]. Subcircular to transverse, delthyrium open; ventral muscle field short, wide, adductor scars wide; fulcral plates present, dorsal adductor field not impressed, presumably situated on valve floor. *M.Dev.*, Eu.-E.N. Am.——FIG. 214,*3a-c*. **K. lepida* (SCHNUR), Ger.; *3a-c*, ped.v., brach.v., post. views of conjoined valves, ×2 (185).——FIG. 214,*3d,e*. *K. americana* COOPER, USA(N.Y.); *3d,e*, ped.v. int. mold, brach. v. int., ×3 (185).

Subfamily PROKOPIINAE Wright, n. subfam.

Cardinal process with myophore and shaft bilobate, brachiophore bases suberect, anteriorly divergent, adductor field clearly defined by thickened margin. *M.Dev.-U.-Dev.*

Prokopia HAVLÍČEK, 1953, p. 5 [**P. bouškai*; OD]. Small, subcircular to transverse, delthyrium containing flat apical plate; ventral muscle field indistinct; fulcral plates absent, adductor field suboval, divided by high median septum extending to anterior margin. *M.Dev.*, Boh.——FIG. 214,*2*. **P. bouskai*; *2a,b*, ped.v. ext., int., ×5; *2c,d*, brach.v. int., brach.v. int. (oblique), ×5 (Wright, n).

Monelasmina COOPER, 1955, p. 53 [**Orthis deshayesi* RIGAUX, 1873, p. 50; OD]. Like *Prokopia* but with small fulcral plates, subrectangular dorsal adductor field, apical plate apparently lacking; ventral muscle field subtriangular to elongatedly oval, adductor scars moderately wide, separating slender diductor scars, *vascula media* slightly divergent, greatly divided. *U.Dev.*, W.Eu.-W.Can.

——FIG. 214,*5*. **M. deshayesi,* Fr.; *5a-c,* ped.v., brach.v., post. views of conjoined valves, ×3; *5d,* brach.v. int. (oblique), ×4; *5e,* ped.v. int. mold, ×3 (185).

Phragmophora COOPER, 1955, p. 50 [**P. schnuri*; OD]. Subcircular, delthyrium closed by variably developed convex notodeltidium; ventral muscle field broadly triangular, adductor field wide, flanked by diductor scars of similar width, *vascula media* moderately divergent, greatly divided; fulcral plates commonly developed in larger shells, dorsal adductor field subquadrate, with median septum rarely reaching anterior margin. *M.Dev.,* Ger.-Pol.——FIG. 214,*6*. **P. schnuri,* Ger.; *6a,b,* ped.v., brach.v. views of conjoined valves, ×1; *6c,* post. view of conjoined valves, ×2; *6d,* ped.v. int. mold, ×1; *6e,f,* normal, oblique views of brach.v. int., ×2 (185).

Family MYSTROPHORIDAE Schuchert & Cooper, 1931

[Mystrophoridae SCHUCHERT & COOPER, 1931, p. 246]

Ventribiconvex, with high apsacline ventral interarea, dorsal interarea shorter, anacline, delthyrium and notothyrium open; ventral muscle field with adductor scars not enclosed by slightly longer diductor scars; cardinal process with bilobate myophore and shaft united with very high median septum which supports well-developed cruralium, brachiophores long, ventrally directed, fulcral plates present. *M.Dev.*

Mystrophora KAYSER, 1871, p. 612 [**Orthis areola* QUENSTEDT, 1871, p. 589; SD WILLIAMS & BREGER, 1916, p. 61]. Transverse, pedicle valve of subpentagonal outline, costellate, sulcus in brachial valve; ventral adductor field broad, ?short median septum anteriorly at mid-valve, *vascula media* subparallel; dorsal median septum very high, cruralium divisible into 4 plates. *M.Dev.,* W.Eu.——FIG. 214,*7*. **M. areola* (QUENSTEDT), Ger.; *7a,b,* brach.v., lat. views of conjoined valves, ×1.5; *7c,* ped.v. int. mold, ×1.5; *7d,e,* normal, oblique views of brach.v. int., ×2 (185).

Family HYPSOMYONIIDAE Wright, n. fam.

Ventribiconvex, interareas well developed, delthyrium and notothyrium open; dental plates short, receding, ventral muscle field not well known; cardinal process with bilobate myophore and shaft, brachiophore bases subparallel to hinge line, fulcral plates absent, adductor scars situated on platform rising from valve floor in front of brachiophores, supported medianly by strong septum. *M.Dev.-U.Dev.*

Hypsomyonia COOPER, 1955, p. 52 [**H. stainbrooki*; OD]. Small, transverse, costellate, with sulcus in brachial valve. *M.Dev.-U.Dev.,* N.Am.-C. Eu.-W. Australia.——FIG. 214,*4*. **H. stainbrooki,* U.Dev., USA(Iowa); *4a-d,* ped.v., brach.v., lat., post. views of conjoined valves, ×5; *4e,f,* normal, ant. views of brach.v. int., ×7.5 (185).

Family HARKNESSELLIDAE Bancroft, 1928

[*nom. transl.* ALICHOVA, 1960, p. 192 (*ex* Harknessellinae BANCROFT, 1928, p. 173); *emend.* WRIGHT, herein]

Transversely subquadrate, hinge line commonly mucronate, subequally biconvex to dorsibiconvex, ventral interarea apsacline, dorsal interarea commonly anacline to orthocline, delthyrium and notothyrium open, fascicostellate, prominent, commonly sharply angular, ventral fold and dorsal sulcus; ventral muscle field suboval to subpentagonal, diductor scars commonly extending only slightly anterior to narrowly rectangular adductor scars; cardinal process with lobate myophore and shaft, brachiophores variably disposed, notothyrial platform with deep adductor pits; mantle canal systems saccate to lemniscate. *M.Ord.-U.Ord.*

Harknessella REED, 1917, p. 862 [**Orthis vespertilio* SOWERBY, 1839, p. 640; OD]. Ventral muscle field subpentagonal, bilobed; brachiophores long, bladelike, bases convergent, fused or not fused to fulcral plates. *M.Ord.,* Eu.——FIG. 215,*4*. **H. vespertilio* (SOWERBY), Caradoc., Eng.; *4a,* ped.v. ext., ×1; *4b,c,* ped.v. int. molds, ×1; *4d,e,* brach. v. int. mold, cast, ×1 (Wright, n).

Horderleyella BANCROFT, 1928, p. 178 [**H. plicata*; OD]. Commonly small for family, coarsely fascicostellate; ventral muscle field small, suboval to rhomboidal; cardinalia small, crural pits and fulcral plates well differentiated. *M.Ord.,* Eng.-Wales. ——FIG. 215,*1*. **H. plicata,* Caradoc., Eng.; *1a,b,* ped.v. ext., brach.v. ext., ×1; *1c,* ped.v. int. mold, ×1; *1d,e,* brach.v. int. mold, cast, ×1 (Wright, n).

Reuschella BANCROFT, 1928, p. 180 [**R. semiglobata*; OD] [=*Reushella* ALICHOVA, 1960 *(nom. null.)*]. Like *Harknessella* but commonly larger with deep dorsal valve, coarser ornament, and shorter, more widely splayed brachiophores. *M. Ord.-U.Ord.,* Eu.-N.Am.——FIG. 215,*3a-d*. **R. semiglobata,* M.Ord.(Caradoc.), Eng.; *3a,* brach.v. ext., ×1; *3b,c,* brach.v. int. mold, cast, ×1; *3d,* cardinalia, ×2.5 (Wright, n).——FIG. 215,*3e*. *R.* sp. cf. *R. horderleyensis* BANCROFT, M.Ord. (Caradoc.), Wales; ped.v. int. mold, ×1.0 (878).

Smeathenella BANCROFT, 1928, p. 177 [**S. harnagensis*; OD]. Large, flatly dorsibiconvex, of strophomenoid appearance; ventral muscle field small, rhomboidal or anteriorly truncated; cardi-

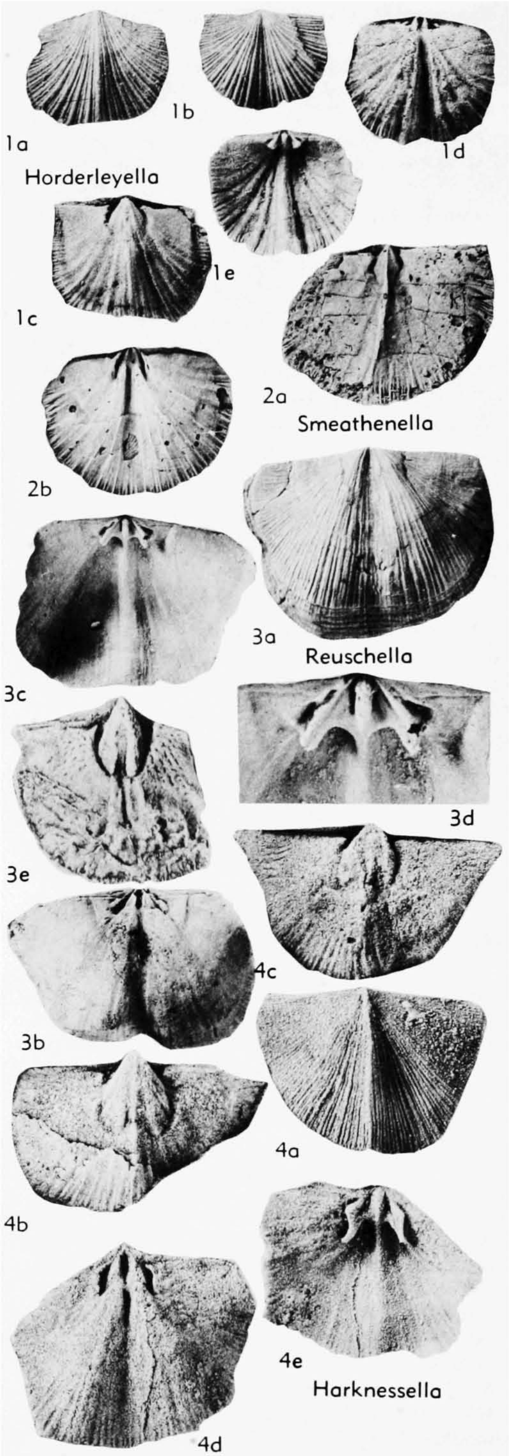

FIG. 215. Harknessellidae (p. *H*339-*H*340).

nal process small, brachiophores narrowly divergent, crural pits and fulcral plates not developed. *M.Ord.,* Eng.——FIG. 215,*2.* **S. harnagensis*; *2a,b,* ped.v. and brach.v. int. molds, ×1 (Wright, n).

Family HETERORTHIDAE Schuchert & Cooper, 1931

[Heterorthidae SCHUCHERT & COOPER, 1931, p. 246, *emend.* WRIGHT, herein]

Transversely subcircular to subquadrate with hinge line less than maximum shell width, concavo-convex to biconvex, ventral interarea apsacline, dorsal interarea anacline, delthyrium open, notothyrium open or with chilidium, typically finely costellate, rarely with ventral fold and dorsal sulcus; ventral muscle field large with long divergent, semicircular, commonly flabellate and scalloped, diductor scars with anterior ends widely separated, extending far beyond and not enclosing adductor scars; cardinal process narrow or semioval with commonly trilobate posteroventral surface, brachiophores ridgelike, fused to valve floor throughout their length, dorsal adductor field quadripartite, subcircular; dorsal mantle canal system lemniscate, ventral probably also lemniscate. *M.Ord.-U.Ord.*

Heterorthis HALL & CLARKE, 1892, p. 202 [**Orthis clytie* HALL, 1861, p. 90; OD]. Concavo-convex to plano-convex, chilidium well developed; ventral adductor scars small, commonly cordate; fulcral plates not differentiated; subperipheral ridge developed in adult valves. *M.Ord.-U.Ord.,* Eu.-E.N.Am.——FIG. 216,*1a,b.* **H. clytie* (HALL), M.Ord.(Trenton.), USA(Ky.); *1a,b,* ped.v. int., brach.v. int., ×1.5 (729).——FIG. 216,*1c-e. H. alternata* (SOWERBY), M.Ord.(Caradoc.), Eng.; *1c,* brach.v. ext., ×1.5; *1d,e,* ped.v. and brach.v. int. molds, ×1.5 (878).

Planoharknessella HAVLÍČEK, 1950, p. 42 [**P. planidorsa*; OD]. Plano-convex, with feeble fold and sulcus, chilidium lacking; ventral adductor scars poorly defined; crural pits small, fulcral plates feebly differentiated; subperipheral ridge lacking. *M.Ord.(Caradoc.),* Boh.——FIG. 216,*2.* **P. planidorsa*; *2a,* brach.v. ext., ×2; *2b,c,* ped.v. and brach.v. int. molds, ×2 (403).

Svobodaina HAVLÍČEK, 1950, p. 38 [**Orthis inclyta* BARRANDE, 1879, pl. 67, fig. 1; OD] [=*Svobodiana* ALICHOVA, 1960 *(nom. null)*]. Subequally biconvex to dorsibiconvex, chilidium lacking; ventral adductor scars small, poorly defined anteriorly; fulcral plates rarely defined; subperipheral ridge lacking. *M.Ord.-U.Ord.,* Eu.——FIG. 216,*3.* **S. inclyta* (BARRANDE), M.Ord.(Caradoc.), Boh.; *3a,b,* ped.v. and brach.v. int. molds, ×1.5 (403).

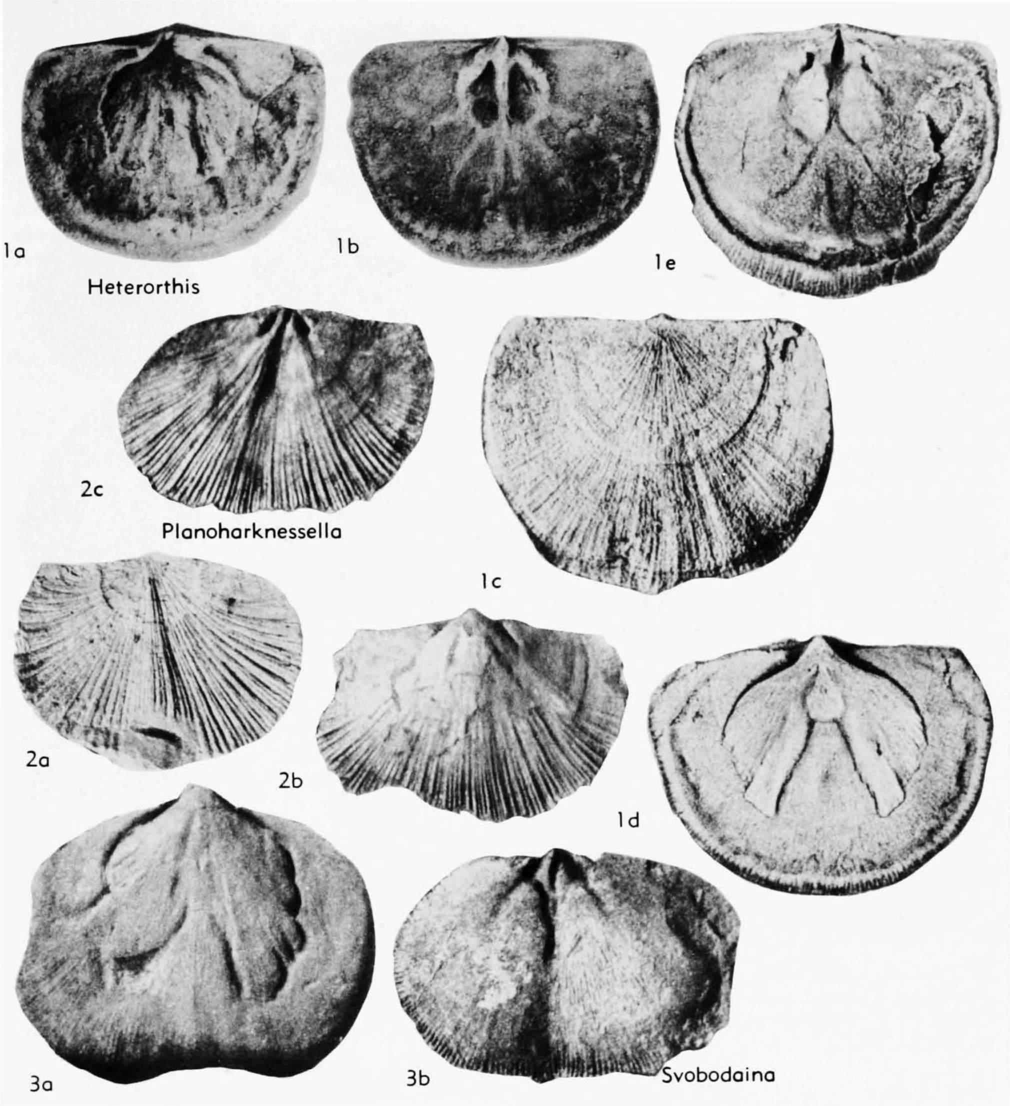

Fig. 216. Heterorthidae (p. *H*340).

Family RHIPIDOMELLIDAE Schuchert, 1913

[Rhipidomellidae Schuchert, 1913, p. 382]

Dorsibiconvex to plano-convex, ventral interarea apsacline to orthocline, dorsal interarea commonly orthocline, both becoming much reduced; delthyrium open, notothyrium with chilidial plates developed rarely, costellae hollow, fold and sulcus commonly not well developed; ventral muscle field large, oval to cordate, adductor scars elliptical, completely enclosed by diductors commonly with scalloped margins; cardinal process with lobate myophore and short shaft, brachiophores commonly short, blunt, with suberect bases, fulcral plates absent; ventral and dorsal mantle canal systems lemniscate. *L.Sil.-U.Perm.*

Rhipidomella Oehlert, 1890, p. 372 [*pro Rhipidomys* Oehlert, 1887 (*non* Wagner, 1844)] [**Terebratula michelini* Léveillé, 1835, p. 39; OD] [=*Blairella* Miller & Gurley, 1896 (*nom. nud.*); *Pseudodicoelosia* Boucot & Amsden, 1958, p. 162 (type, *Rhipidomella oklahomensis* Amsden, 1951, p. 76); *Loganella* Boucot & Amsden, 1958, p. 164 (type, *Rhipidomella lehuquetiana* Clarke, 1906, p. 202); *Rhipidomelloides* Boucot & Ams-

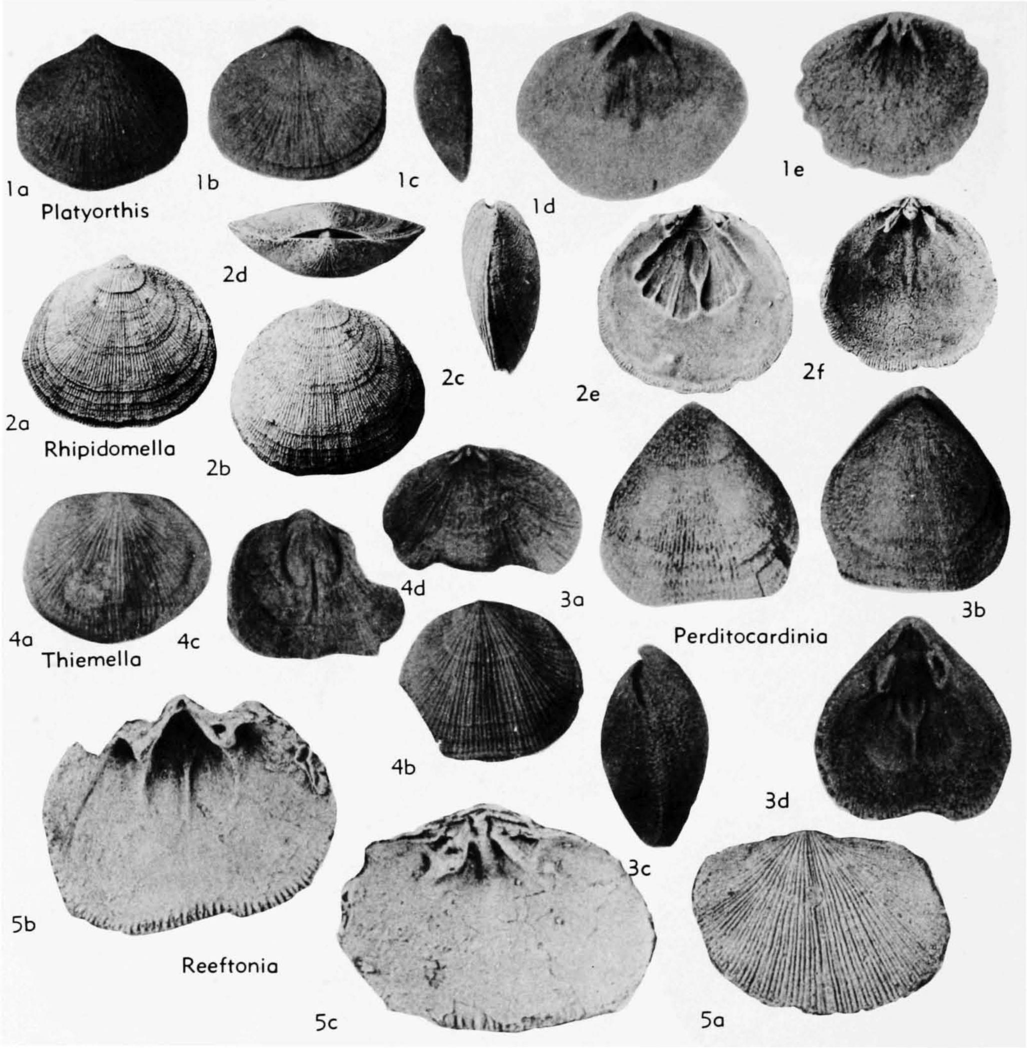

Fig. 217. Rhipidomellidae (p. *H*341-*H*343).

den, 1958, p. 165 (type, *Rhipidomella henryhousensis* Amsden, 1951, p. 74); *Strixella* Boucot & Amsden, 1958,. p. 170 (type, *Rhipidomella acutisulcata* Amsden, 1951, p. 75)]. Subcircular to subtriangular, dorsibiconvex, chilidial plates common in later forms; ventral muscle field suboval, diductor scars broad, with strongly scalloped margins, separated in front of adductor scars by ridge which rarely continues beyond muscle field. *L.Sil.-U.Perm.*, cosmop.——Fig. 217,2. **R. michelini* (Léveillé), L.Carb., Belg.; *2a-d,* ped.v., brach.v., lat., post. views of conjoined valves, ×1; *2e,f,* ped.v. int., brach.v. int., ×1 (Wright, n). [The four nominal genera erected by Boucot & Amsden in 1958 (106) differ from *Rhipidomella* and from one another only in features that normally are variable even within the limits of species. Thus, *Pseudodicoelosia* presumably is distinguished by a pronounced dorsal sulcus, short hinge line, and emarginate front edge; *Loganella* by abbreviation of the interarea and fusion of the cardinalia; *Rhipidomelloides* by the presence of flat marginal crenulations internally, rather than rounded ones; and *Strixella* by having an angular dorsal sulcus. A relatively short hinge line, which characterizes the whole group, is not strongly pronounced in *Pseudodicoelosia* (as in *Perditocardinia* or *Dicoelosia*) and its anterior emargination, a feature developed to some extent in many species of *Rhipidomella,* is not always evident in the type-species (30, pl. 15, fig. 37). The conspicuous dorsal sulcus of *Pseudodicoelosia* and *Strixella* seems not to be a diagnostic character differing from the dorsal sulcus commonly present, although tending to be shallow or impersistent, in *Rhipidomella.* The association of *Pseudodicoelosia, Rhipidomelloides,* and *Strixella* in the same strata (U.Sil., Henryhouse F., Okla.) suggests that they may be simply "form species."]

Perditocardinia Schuchert & Cooper, 1931, p. 246 [**Orthis dubia* Hall, 1858, p. 12; OD]. Like *Rhipidomella* but of rostrate form, with interareas obsolete and hinge line very narrow. *L.Carb.-M. Perm.*; N.Am.-S.Asia.——Fig. 217,*3*. **P. dubia* (Hall), Miss., USA(Ind.); *3a-c,* ped.v., brach.v., lat. views of conjoined valves, ×1; *3d,* ped.v. int., ×2 (729).

Platyorthis Schuchert & Cooper, 1931, p. 246 [**Orthis planoconvexa* Hall, 1859, p. 168; OD]. Subcircular to subelliptical, plano-convex; ventral muscle field broad, suboval to slightly cordate, diductor scars rarely with scalloped margins; cardinal process with large bilobed or trilobed myophore and medianly cleft shaft. *U.Sil.-M.Dev.,* widespread.——Fig. 217,*1*. **P. planoconvexa* (Hall), L.Dev.(Deerpark.), USA(Md.); *1a-c,* ped.v., brach.v., lat. views of conjoined valves, ×1; *1d,e,* ped.v. int., brach.v. int., ×1.5 (729).

Reeftonia Allan, 1947, p. 436 [**R. marwicki*; OD]. Transversely elliptical, plano-convex, sulcus in brachial valve; ventral muscle field cordate, diductor scars without scalloped margins; cardinal process with small undivided myophore and short shaft. *L.Dev.,* N.Z.——Fig. 217,*5*. **R. marwicki*; *5a,* brach.v. ext., ×2; *5b,c,* ped.v. int., brach.v. int., ×2 (27).

Thiemella Williams, 1908, p. 59 [**T. villenovia*; OD]. Like *Rhipidomella* but with prominent dorsal sulcus and ventral fold, and elliptical to subcordate ventral muscle field with median ridge extending well beyond muscle field. *U.Dev.-L.Carb.,* E.USA-Ger.——Fig. 217,*4*. **T. villenovia,* U.Dev. (Chemung.), USA(N.Y.); *4a,b,* ped.v. ext., brach. v. ext., ×1.5; *4c,d,* ped.v. int. mold, brach.v. int., ×1.5 (729).

Family LINOPORELLIDAE
Schuchert & Cooper, 1931

[Linoporellidae Schuchert & Cooper, 1931, p. 247]

Subequally biconvex to ventribiconvex, ventral interarea long, curved, apsacline, dorsal interarea shorter, curved, anacline, delthyrium and notothyrium open, fold and sulcus rarely well developed; ventral muscle field variable, dental plates strong; cardinal process simple ridge, continuous anteriorly with median septum, brachiophores long, bladelike, with bases convergent on to strong median septum to form septalium, fulcral plates present; ventral mantle canal system possibly saccate, dorsal probably lemniscate. *M.Ord.-U.Sil.*

Linoporella Schuchert & Cooper, 1931, p. 247 [**Orthis punctata* de Verneuil, 1848, p. 343; OD]. Subcircular to transverse, ornament costellate with radial rows of pits in interspaces; ventral muscle field elongate, clearly defined by anterior continuation of dental plates, adductor scars on median ridge which becomes more pronounced on valve floor in front of muscle field; cardinal process with expanded myophore and thin shaft, dorsal adductor field elongatedly oval. *L.Sil.-U.Sil.,* N.W. Eu.-E.N.Am.——Fig. 218,*5*. **L. punctata* (de Verneuil), U.Sil.(Gotland.), Sweden; *5a,b,* brach. v., lat. views of conjoined valves, ×2 (Wright, n); *5c,d,* ped.v. ext., int., ×1.5; *5e,* cardinalia, ×2 (729).

Elasmothyris Cooper, 1956, p. 983 [**E. concinnula*; OD]. Minute, transverse, ventribiconvex with sulcus in brachial valve, costellate; ventral muscle field on horizontal plate extending across delthyrial cavity between base of dental plates; cardinal process wtih expanded myophore. *M.Ord.,* E.USA.——Fig. 218,*2*. **E. concinnula,* Porterfield, Ala.; *2a-c,* ped.v., post., ant. views of conjoined valves, ×5; *2d,e,* ped.v. int., brach.v. int., ×8 (189).

Laticrura Cooper, 1956, p. 979 [**L. pionodema*; OD]. Subcircular, ventribiconvex, costellate with hollow costellae developed rarely; ventral muscle field subtriangular, adductor scars and median diductor lobes of similar size, apical plate variably developed; cardinal process without expanded myophore, brachiophores large, S-shaped in section, dorsal adductor field narrow, elongate. *M. Ord.-U.Ord.,* E.USA-Scot.-Ire.——Fig. 218,*7*. **L. pionodema,* M.Ord.(Porterfield.), USA(Va.); *7a-c,* ped.v., brach.v., lat. views of conjoined valves, ×2; *7d,e,* ped.v. int., brach.v. int., ×2, ×4; *7f,* ant. view of cardinalia, ×6 (189).

Orthotropia Hall & Clarke, 1894, expl. pl. 84 [**O. dolomitica*; OD(M)]. Ventribiconvex, interior very close to *Linoporella* but probably without expanded myophore; ornament unknown. *U.Sil.(Wenlock.),* USA(Wis.).

Salopia Williams, 1955, p. 409 [**Orthis salteri* Davidson, 1871, p. 255; OD]. Distinguished from *Laticrura* by very high, almost catacline ventral interarea, suboval ventral muscle field, simple bladelike brachiophores and commonly broader dorsal adductor field. *M.Ord.,* Eng.——Fig. 218,*1*. **S. salteri* (Davidson), Caradoc.; *1a-c,* vent., post., lat. views of ped.v. int. mold, ×2; *1d,* brach.v. int., ×2 (Wright, n).

Family ANGUSTICARDINIIDAE
Schuchert & Cooper, 1931

[*nom. transl.* Wright, herein (*ex* Augusticardiniinae Schuchert & Cooper, 1931, p. 243)] [=Apatorthidae Öpik, 1933, p. 5]

Biconvex with short hinge line, interareas short, curved, ventral apsacline, dorsal anacline, delthyrium and notothyrium open,

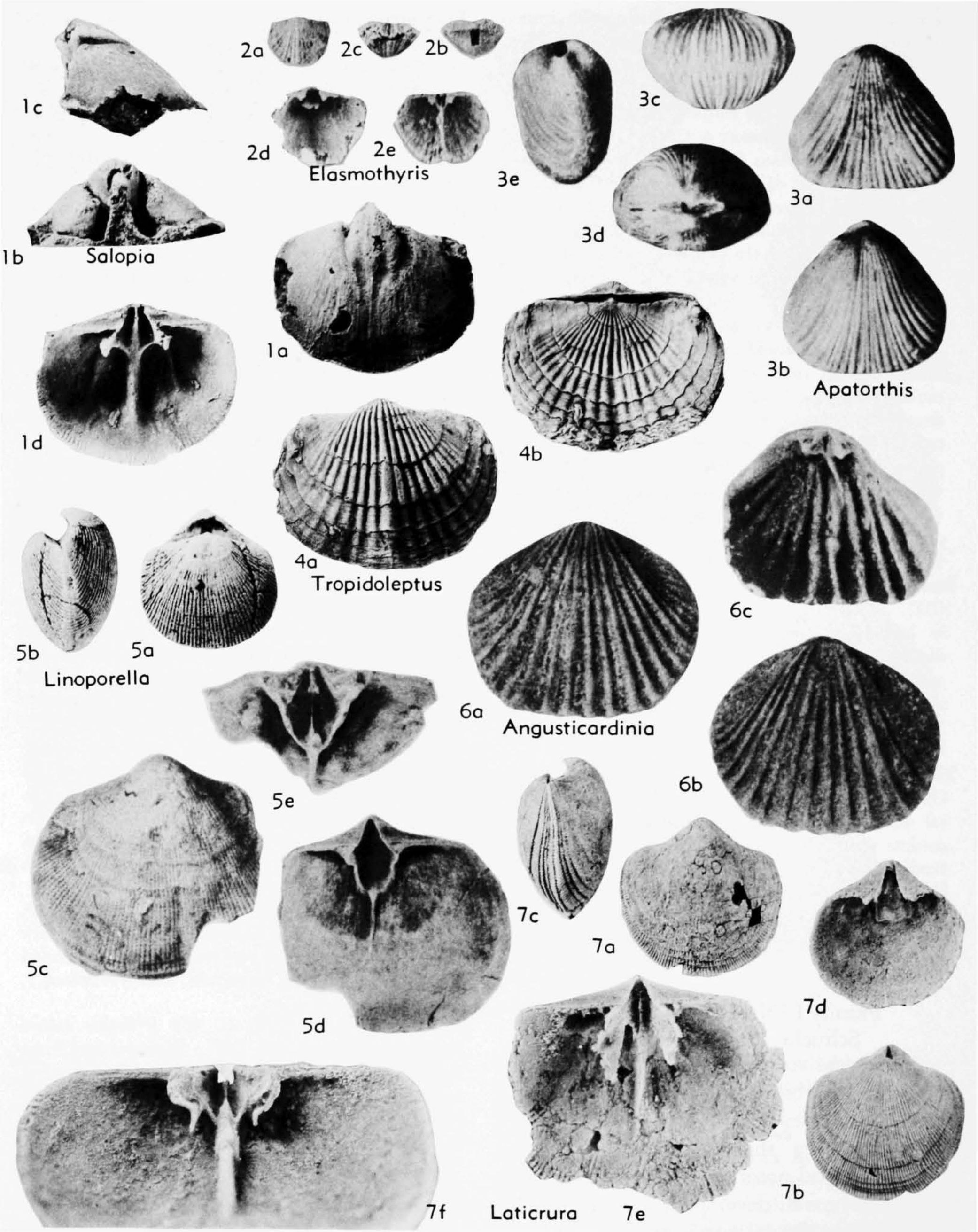

FIG. 218. Linoporellidae *(1-2, 5, 7)*; Angusticardiniidae *(3, 6)*; Tropidoleptidae *(4)* (p. H343-H346).

ornament of coarse subangular costae and costellae, dorsal fold and ventral sulcus variably developed; pedicle valve with small teeth supported by strong dental plates; cardinal process simple ridge or absent, brachiophores with bases convergent on to median septum; mantle canal systems unknown. *L.Ord.-U.Ord.*

The subfamily Angusticardiniinae, with the single genus *Angusticardinia*, was originally established as a subfamily of the Orthidae. ÖPIK (1933, p. 5-6) has indicated that

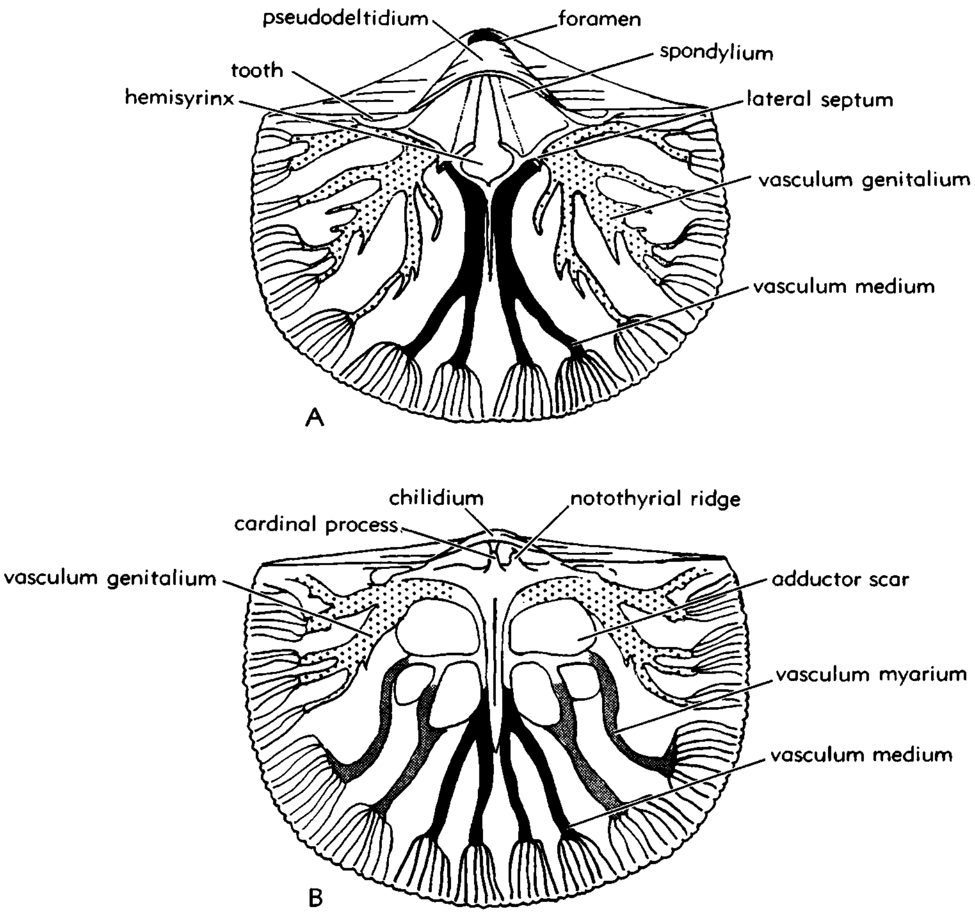

FIG. 219. Generalized illustrations of clitambonitidine pedicle valve *(A)* and brachial valve *(B)*, showing mantle canal systems of *Clitambonites* (after Öpik, 621).

the shell substance of *Angusticardinia* is probably punctate, although this is somewhat uncertain, as the examined shells have undergone recrystallization. The placing of the genus here with the punctate orthoid stocks is thus provisional; this necessitates suppression of the family Apatorthidae in favor of the Angusticardiniidae on grounds of priority.

Angusticardinia SCHUCHERT & COOPER, 1931, p. 244 [**Porambonites recta* PANDER, 1830, p. 97; OD]. Subcircular, small ears developed rarely, fold and sulcus feeble; cardinal process linear, brachiophores short, median septum prominent, dividing small quadripartite adductor scars. *L.Ord.,* E.Baltic-Boh. ——FIG. 218,*6*. **A. recta* (PANDER), USSR; *6a,b,* ped.v., brach.v. views of conjoined valves, ×3; *6c,* brach.v. int., ×3 (729).

Apatorthis ÖPIK, 1933, p. 5 [**A. punctata*; OD]. Subtriangular, ears small but pronounced, fold and sulcus well developed, surface finely granulated; cardinal process absent? *M.Ord.-U.Ord.,* Est. ——FIG. 218,*3*. **A. punctata,* M.Ord.; *3a-e,* ped.v., brach.v., ant., post., lat. views of conjoined valves, ×1.3 (620).

Family TROPIDOLEPTIDAE
Schuchert, 1896

[*nom. transl.* SCHUCHERT & COOPER, 1932, p. 152 (*ex* Tropidoleptinae SCHUCHERT, 1896, p. 330)]

Hinge line wide, ventral interarea well developed, orthocline, delthyrium open; dorsal interarea shorter, anacline, notothyrium covered by antigydium. Teeth massive, outer sides strongly crenulated, separate from hinge line, supported by stout dental plates. High cardinal process with deep double diductor pit on ventral surface at posterior of thick notothyrial platform; anteriorly, pair of long crura develop apophyses which possibly form loop with posteriorly directed outgrowths from high anterior part of median septum. *L.Dev.-U.Dev.*

Tropidoleptus HALL, 1857, p. 151 [**Strophomena carinata* CONRAD, 1839, p. 64; OD]. Concavo-convex, subquadrate with narrow ventral fold and dorsal sulcus, ornamented by broad, rounded costae. *L.Dev.-U.Dev.,* Eu.-N.Afr.-N.Am.-S.Am.——FIG. 218,*4*. **T. carinatus* (CONRAD), M.Dev. (Hamilton), USA(N.Y.), *4a,b,* ped.v. ext., brach. v. ext., ×1 (Wright, n).

Suborder CLITAMBONITIDINA Öpik, 1934

[*nom. correct.* WILLIAMS, herein (*pro* Clitambonitoidea ÖPIK, 1934, p. 75)]

Concavo-convex to convexo-concave, coarsely costellate to unequally parvicostellate, wide-hinged articulate brachiopods, commonly with long procline to apsacline ventral interarea and arched pseudodeltidium perforated by an apical foramen; shell substance impunctate or pseudopunctate. Teeth simple, rarely supplemented by denticles; ventral muscle field impressed exceptionally on floor of valve and on bounding dental plates, mostly on modified spondylium triplex or spondylium simplex; cardinal process usually a simple ridge fused posteriorly with strong, convex chilidium, rarely with ancillary ridges; socket ridges widely divergent, commonly ankylosed to strong, transverse notothyrial platform; dorsal adductor field quadripartite, normally divided by strong median ridge; mantle canal system in both valves pinnate with *vascula media*, *myaria*, and *genitalia* variably divided near nodes of origin. *Ord.*

DISCUSSION

The brachiopods classified as members of the Clitambonitidina constitute a fairly natural, but minor, group possessing a unique assemblage of morphological features, which, considered individually, are really more typical of other suborders within the phylum. This peculiarity is understandable in that Clitambonitidina have been recorded so far only from rocks of Ordovician age, a period when the definitive characters of many longer ranging groups were still being derived. Consequently, although they can be easily separated from other brachiopods, their "hybrid" qualities and the morphological instability of their contemporaries make it difficult to be certain about their origin.

With few exceptions, the Clitambonitidina are at first sight more like the Orthidina than any other group and the modal features of the 23 genera comprising the suborder confirm this impression (Fig. 219). Such characters include, for example, a biconvex, wide-hinged, costellate shell with a high ventral interarea and a simple ridgelike cardinal process, all of which are typically orthoid; and a pseudodeltidium pierced by a large apical foramen, a convex chilidium, and widely divergent socket ridges, which, together with the first set of characters, are so reminiscent of the billingsellid brachiopods that common ancestry seems the only acceptable explanation. Noteworthy variations of this basic pattern did occur and include the development of strong imbrication (e.g., *Clitambonites*), hollow costellae (e.g., *Tritoechia*), subsidiary notothyrial ridges flanking the cardinal process (e.g., *Clinambon*), and even the differentiation of the latter structure into a primitive myophore and shaft (e.g., *Eremotoechia*). Moreover, the pseudodeltidium (and to a lesser extent, the chilidium) is unknown among the Atelelasmatinae and Anomalorthinae so that the delthyrium of these stocks was open in the manner of the majority of the Orthidina. This loss of the pseudodeltidium does not seem to have arisen by resorption after its deposition. More probably it failed to develop during the differentiation of the young shell, which would account for the growth of low lateral plates flanking the delthyrium of *Atelelasma.* In any event, the pedicle must have remained functional throughout the life of most Clitambonitidina and was even additionally protected by an irregular, collar-like extension beyond the foramen of *Kullervo,* although ÖPIK (621, pl. 34, fig. 2b) has figured a remarkable seal of secondary shell plugging the foramen of *Antigonambonites planus* (PANDER).

The most conspicuous feature of the clitambonitoid shell is the spondylium, which, related as it is in its forward extension to

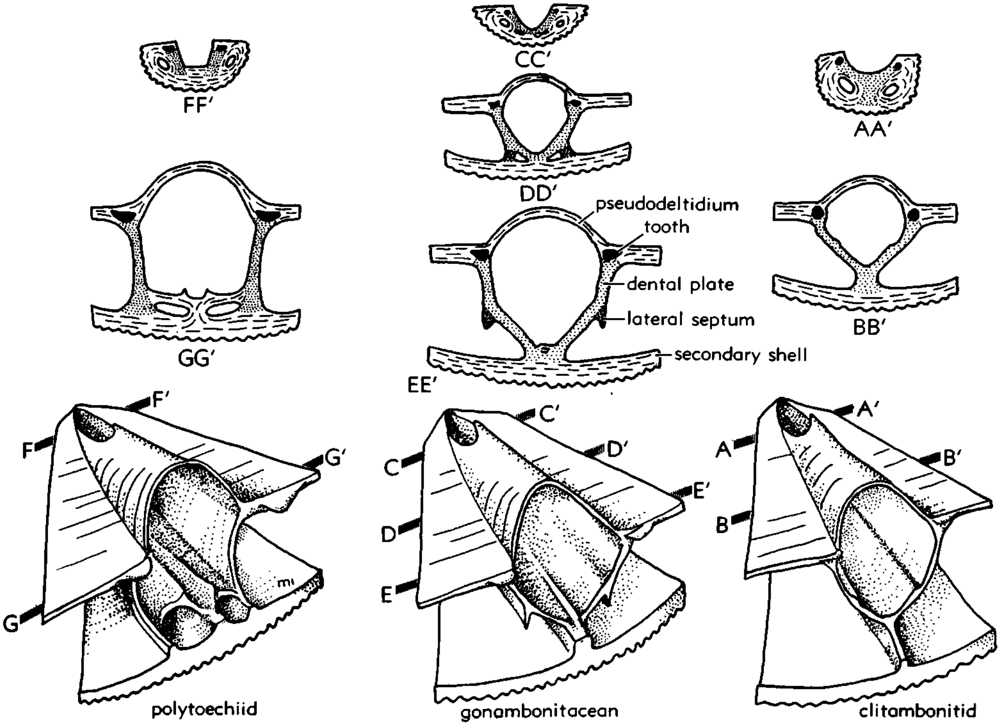

FIG. 220. Parts of three different clitambonitidine pedicle valves illustrating spondylia, with sections showing attitudes of the dental plates (Williams, n).

the exaggerated growth of the ventral interarea, commonly dominates the ventral interior (Fig. 220). Two greatly different types of support to the ventral muscle field were developed, dependent on whether the dental plates were subparallel to each other or convergent toward the floor of the pedicle valve, but a variety of arrangements were derived and are worthy of a brief note.

Among the polytoechiids the dental plates are disposed more or less parallel to each other and probably they gave support to at least the ventral adjustors, so that the ventral ends of both diductors and adductors were mainly inserted on the floor of the valve between the plates. This strip of floor, however, was built up as a raised solid platform by excessive deposition of secondary shell (pseudospondylium) and was commonly deeply undercut along its anterior margin on either side of a strong median ridge (Fig. 220). The resultant structure simulates a spondylium triplex in that it consists of a low platform accommodating the anterior part of the ventral muscle field and is supported by the bases of the containing dental plates and the median ridge.

The spondylium triplex of the gonambonitaceans was formed in an entirely different manner. Judging from sections through the spondylia of *Estlandia*, *Antigonambonites*, and *Progonambonites*, the structure in juvenile pedicle valves consisted essentially of a sessile spondylium formed by the convergence of the dental plates on to the floor of the valve (Fig. 220). The junction between the spondylium and the valve floor, however, was broken by a pair of conical hollows (presumably occupied by evaginations of shell-secreting outer epithelium) to form a triple septate base. In some genera (e.g., *Antigonambonites*) the spondylium continued to grow close to the floor of the valve and the lateral and median septa persisted as low supports. Yet in adult shells of other genera little or no trace of lateral septa are found in either high or sessile spondylia (*Oslogonites* and *Lacuna-*

rites, respectively), which therefore look very like the simple spondylia of the clitambonitids. Indeed, the gross morphology of the adult ventral interior can be misleading because in certain clitambonitids (e.g., *Atelelasma*) a pair of thin partitions that separated the *vascula media* and *genitalia* are commonly preserved on the under surface of the spondylium in a position occupied by the lateral septa of the Gonambonitacea.

The clitambonitid spondylium simplex is also formed by convergence of the dental plates but in this structure they become confluent above the valve floor (Fig. 220). Öpik (621, p. 22) reconstructed a morphogeny of the spondylium simplex from sections of an adult valve of *Clitambonites adscendens* Pander. He concluded that the arrangement in juvenile valves consisted of a pair of discrete dental plates flanking a median septum which became united into a single structure by secondary shell secretion during subsequent growth. Unfortunately, no young clitambonitid shells were available to test this interpretation, but prepared serial sections of *Clitambonites* sp. suggest that at any stage during growth the median septum extended in front of the convergent portions of the dental plates. Hence, during further enlargement of the spondylium, the septum was buried between later-deposited parts of the dental plates and now appears as an independent structure in thin sections.

The impressions of the ventral muscle field found on the surfaces of spondylia show that the arrangement was typically orthoid, with a broad undifferentiated adductor scar occupying the median zone and the diductors and ventral adjustors inserted on the sides, the latter just in front of the junctions with the teeth. Independently in both *Clinambon* and *Kullervo*, a pair of ridges grew toward each other partially to enclose a subconical chamber (hemisyrinx) for the reception of the ventral ends of the adductor muscles.

The Clitambonitidina, probably more than any other group of brachiopods, display in wonderful detail the impressions of the mantle canals on the internal surfaces of the shell (Fig. 219). Variation in pattern has been discussed in detail by Öpik (621) but essentially all genera show an abbreviation of the peripheral ramification of the *vascula media*, with a concomitant expansion in branching of the *vascula myaria* and *genitalia* (the pinnate condition of Williams, 875).

In the following systematic account of the Clitambonitidina, it is proposed to recognize two superfamilies, viz., the Clitambonitacea and the Gonambonitacea. The most important classificatory difference between these two groups, as at present constituted, is that the shell of the clitambonitaceans is impunctate, whereas that of the gonambonitaceans is pseudopunctate. Whether this contrast is a reflection of a strophomenoid rather than an orthoid ancestry for the gonambonitaceans cannot be profitably debated at present; but it may be significant that such typical strophomenoid features as unequally accentuated parvicostellae with interrupted rugation and denticular hinge lines are also known in the gonambonitaceans *Raunites* and *Anchigonites*, respectively. Either way, the Gonambonitacea present some remarkable examples of homeomorphy.

Superfamily CLITAMBONITACEA Winchell & Schuchert, 1893

[*nom. correct.* Cooper, 1956, p. 511 (*pro* Clitambonacea Schuchert & LeVene, 1929, p. 15, *nom. transl. ex* Clitambonitidae Winchell & Schuchert, 1893, p. 377)]

Plano-convex to biconvex multicostellate, with ventral muscle field impressed on floor and dental plates of pedicle valve on rudimentary spondylium triplex or on spondylium simplex; shell substance impunctate. *Ord.*

Family POLYTOECHIIDAE Öpik, 1934

[*nom. transl.* Williams, herein (*ex* Polytoechiinae Öpik, 1934, p. 76)] [=Tritoechiidae Ulrich & Cooper, 1936, p. 624]

Ventral interarea apsacline; strong, convex pseudodeltidium perforated apically. Ventral muscle field impressed either on valve floor between and along subparallel dental plates or on callus of secondary shell elevated anteriorly from valve floor and supported medially by ridge as rudimentary spondylium; notothyrial edges high, continuous with curved socket ridges, chilidium poorly developed. *L.Ord.-M.Ord.*

Polytoechia Hall & Clarke, 1892, p. 239 [**Hemipronites apicalis* Whitfield, 1886, p. 300; OD] [=*Deltatreta* Ulrich in Butts, 1926, p. 100

(type, *D. fillistriata* BUTTS, 1926; SD SCHUCHERT & COOPER, 1932, p. 108); *Deltorthis* ULRICH in POULSEN, 1927, p. 297 (*pro Waagenia* HALL, 1889, *non* KRIECHBAUMER, 1874) (obj.); *Martellia* WIRTH, 1936, p. 300 (type, *Orthisina giraldii* MARTELLI, 1901)]. Unequally biconvex, multicostellate. Ventral muscle field slightly elevated as spondylium triplex with median groove formed by convergence of 2 plates on to median septum; socket ridges supported by low, oblique plates uniting with valve floor as anterior boundary to notothyrial cavity; cardinal process simple. *L.Ord.*, N.Am.——FIG. 221,*2*. *P. subcircularis* (COOPER), USA(Okla.); *2a,b,* brach.v. int. and ext., ×3; *2c,* tilted view of ped.v. int., ×3 (181).

Eremotoechia COOPER, 1956, p. 513 [**E. cloudi*; OD]. Like *Tritoechia* but without hollow costellae, with more swollen dorsal umbo, and with cardinal process differentiated into short shaft and lobate myophore. *M.Ord.*, E.USA-Scot.——FIG. 221,*4*. **E. cloudi,* Porterfield, USA(Tenn.); *4a,b,* ped.v. and lat. views of conjoined valves, ×1; *4c,* ped.v. int., ×1; *4d,* brach.v. int., ×2 (189).

Pomatotrema ULRICH & COOPER in SCHUCHERT & COOPER, 1932, p. 109 [**P. muralis*; OD]. Like *Tritoechia* but plano-convex and without swollen hollow costellae within multicostellate ornamentation. *L.Ord.*, N.Am.——FIG. 221,*3*. **P. murale,* U.Canad., USA(Okla.); *3a,b,* brach.v. int. and ext., ×2; *3c,* ped.v. int., ×2 (825).

Tritoechia ULRICH & COOPER, 1936, p. 624 [**Deltatreta typica* SCHUCHERT & COOPER, 1932, p. 206; OD]. Unequally biconvex, multicostellate with scattered hollow costellae. Ventral muscle field inserted on floor of valve and along inner surfaces of long, slightly divergent dental plates with median ridge extending in front of slightly raised anterior margin to muscle field; cardinal process simple. *L.Ord.*, N.Am.-Eu.——FIG. 221,*1*. **T. typica* (SCHUCHERT & COOPER), M.Canad., USA (Okla.); *1a,b,* tilted views of ped.v. int., ×1; *1c,* ped.v. ext., ×1; *1d,e,* brach.v. int. and ext., ×2 (189).

Family CLITAMBONITIDAE Winchell & Schuchert, 1893

[Clitambonitidae WINCHELL & SCHUCHERT, 1893, p. 377]

Ventral interarea variably inclined; pseudodeltidium and chilidium variably developed. Ventral muscle field impressed on spondylium simplex. *Ord.*

Subfamily CLITAMBONITINAE Winchell & Schuchert, 1893

[*nom. transl.* SCHUCHERT & COOPER, 1931, p. 245 (*ex* Clitambonitidae WINCHELL & SCHUCHERT, 1893, p. 377)]

Pseudodeltidium arched; perforated by apical foramen; chilidium strong, continuous with widely divergent socket ridges. *Ord.*

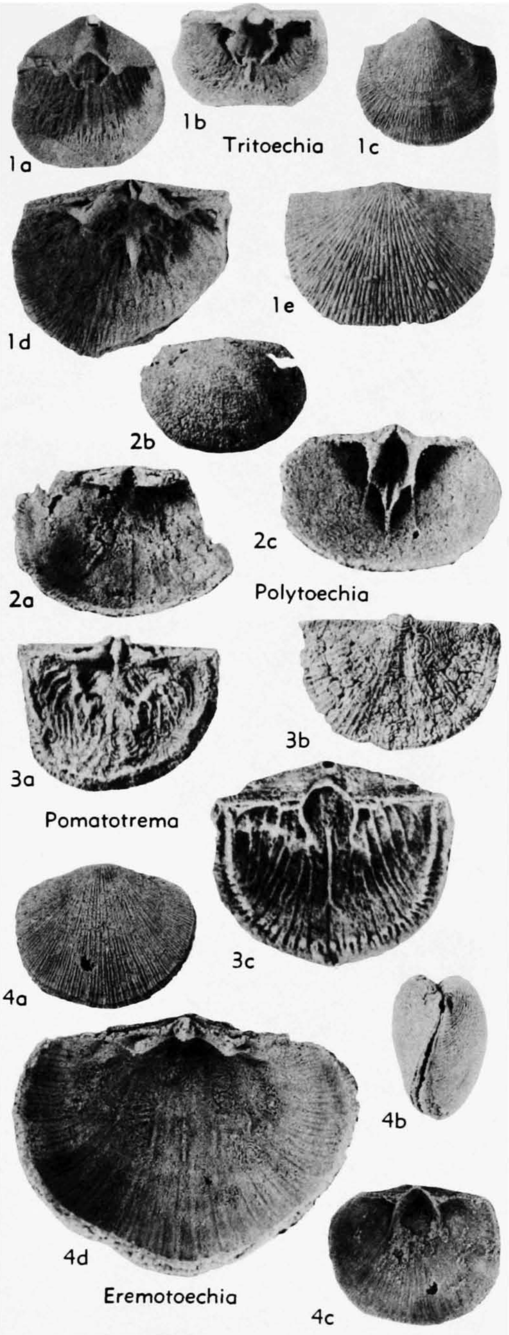

FIG. 221. Polytoechiidae (p. *H*348-*H*349).

Clitambonites AGASSIZ, 1846, p. 90 [**Pronites adscendens* PANDER, 1830, p. 71; SD HALL & CLARKE, 1892, p. 234] [=*Pronites* PANDER, 1830, p. 71 (obj.); *Orthisina* D'ORBIGNY, 1847, p. 267 (obj.)]. Pedicle valve with procline to apsacline

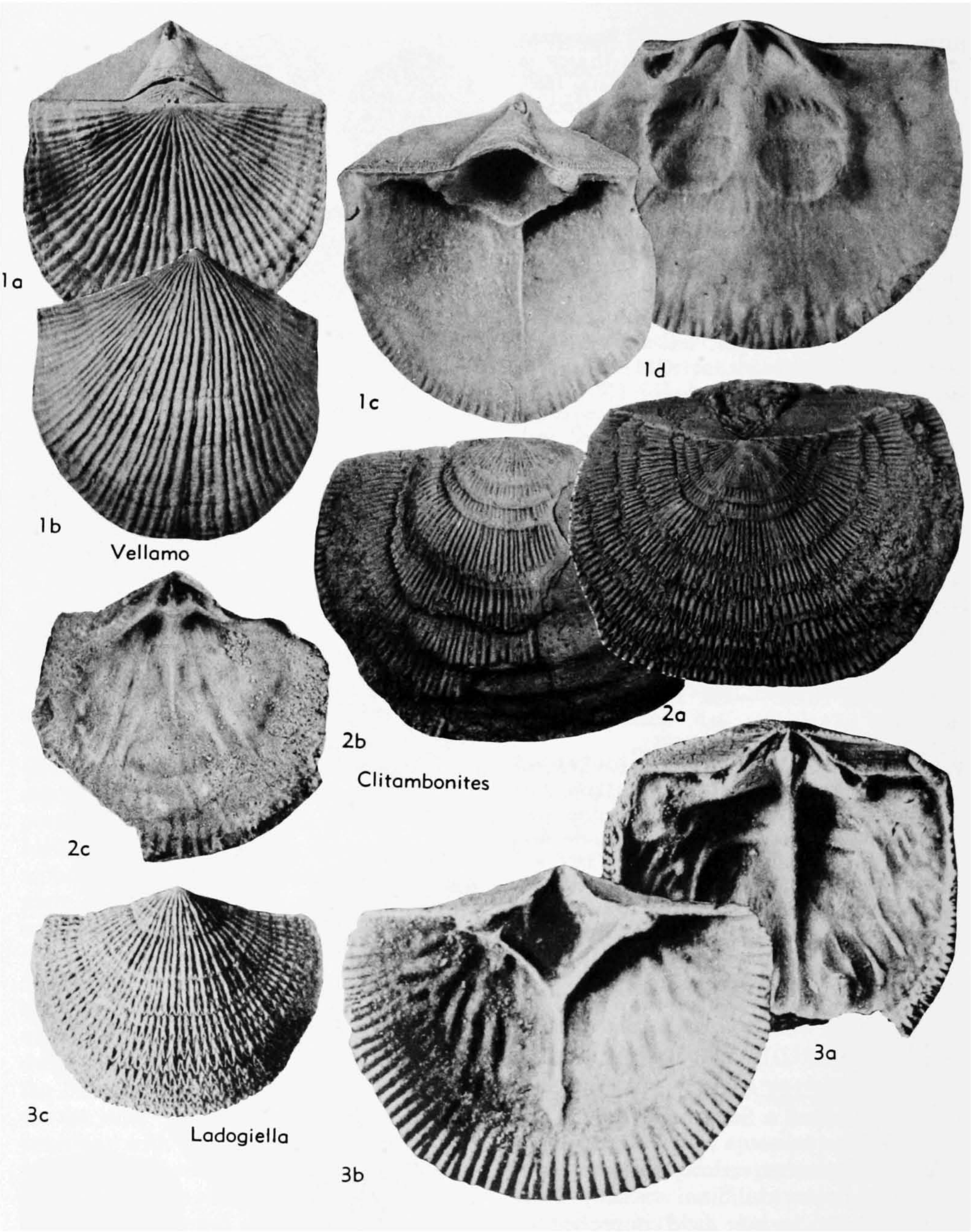

FIG. 222. Clitambonitidae (Clitambonitinae) (p. *H*349-*H*352).

interarea, brachial valve convex, multicostellate and imbricate; chilidium small, cardinal process simple. *L.Ord.-M.Ord.,* Eurasia. [*See* note, p. *H*904.]

C. (Clitambonites). Coarsely costellate and grossly, irregularly imbricate, with subpyramidal pedicle valve and gently convex brachial valve. *L.Ord.-M.Ord.,* Eurasia.——FIG. 222,2. **C. (C.) adscendens* (PANDER), L.Ord.(B_{III}), USSR; *2a,b,* ped.v. and brach.v. views of conjoined valves, ×1.5; *2c,* brach.v. int., ×2 (Rõõmusoks, n).

C. (Hemipronites) PANDER, 1830, p. 74 [**Hemipronites tumida* PANDER, 1830; SD DALL, 1877, p. 31]. Strongly biconvex with finely costellate

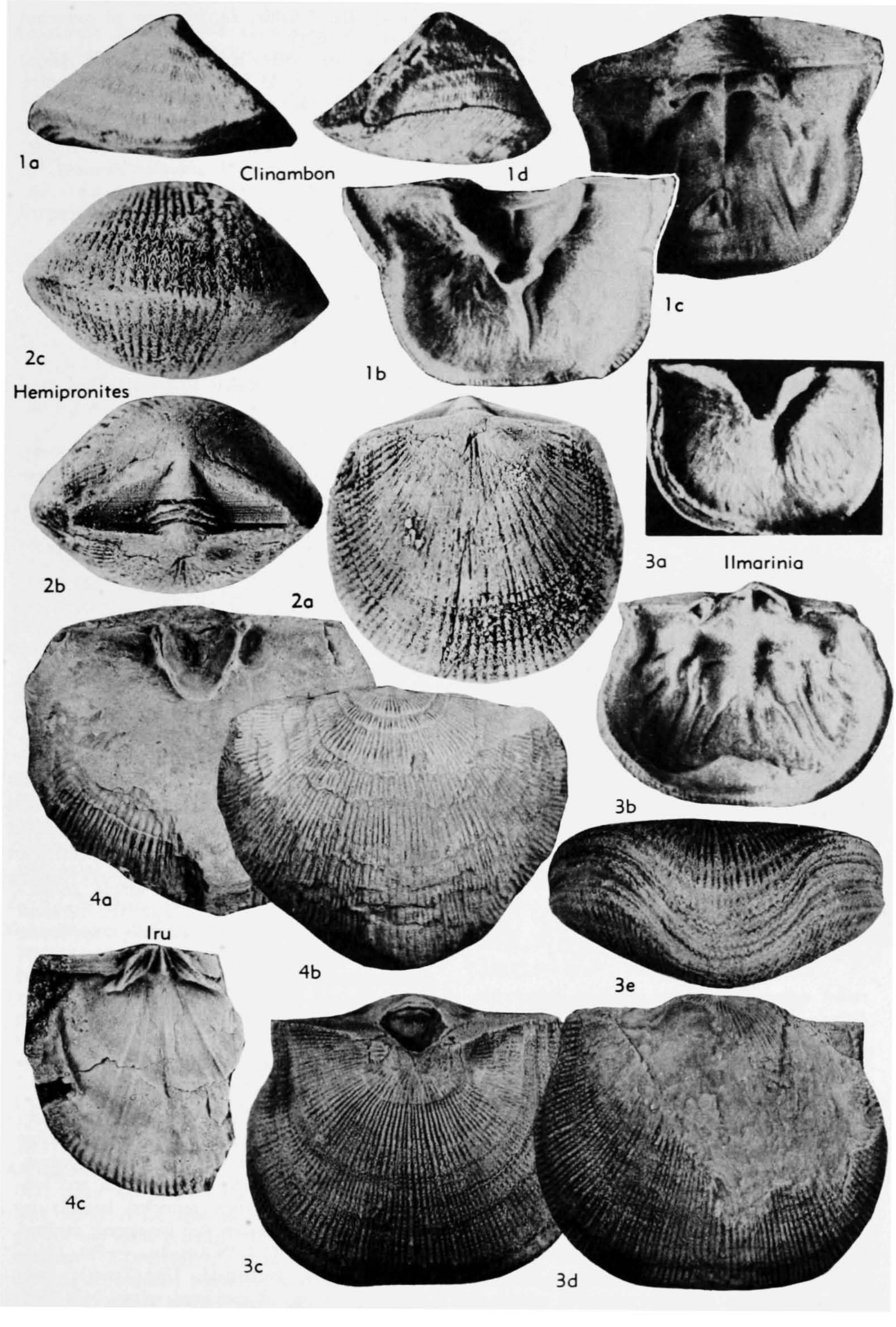

FIG. 223. Clitambonitidae (Clitambonitinae) (p. *H*350, *H*352).

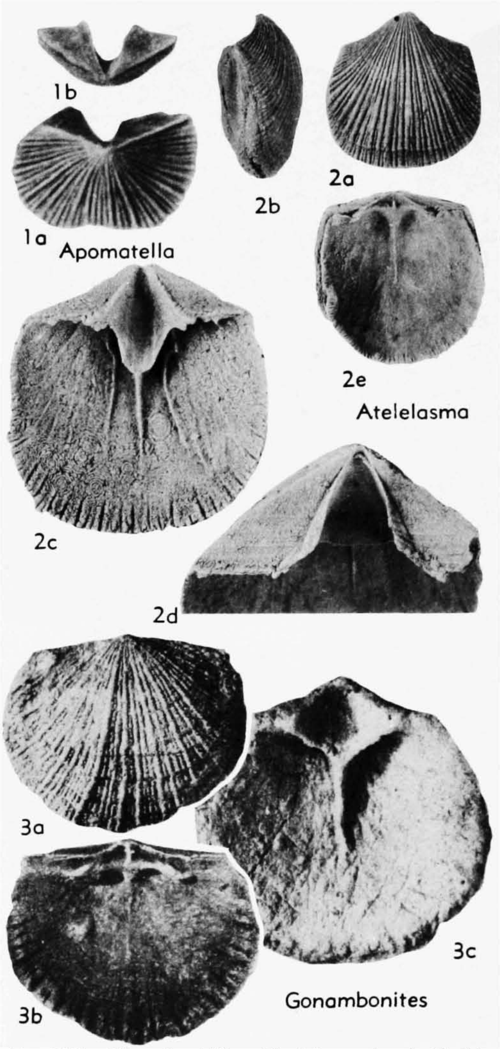

FIG. 224. Clitambonitidae (Atelelasmatinae) *(1,2)*; Gonambonitidae (Gonambonitinae) *(3)* (p. *H*352-*H*353).

radial ornamentation and subdued imbrication. *L.Ord.*, E.Eu.-China.——FIG. 223,*2*. **C. (H.) tumida* (Pander), L.Ord., E.Baltic; *2a-c*, brach. v., post., ant. views of conjoined valves, ×4.5 (Williams, n).

Clinambon Schuchert & Cooper, 1932, p. 115 [**Anomites anomala* von Schlotheim, 1822, p. 65; OD]. Like *Clitambonites* but not imbricate and with strongly procline ventral interarea; spondylium constricted by pair of inwardly directed ridges forming hemiconical chamber anteriorly; chilidium large, cardinal process flanked by subsidiary ridges. *M.Ord.*, USSR.——FIG. 223, *1a-c*. **C. anomalus anomalus* (Schlotheim), D_{I}-D_{III}; E.Baltic; *1a*, ant. view of conjoined valves, ×1; *1b,c*, ped.v. and brach.v. int., ×1 (621).——FIG. 223,*1d*. *C. anomalus praecedens* (Öpik), D_{I}, E.Baltic; *1a*, lat. view of conjoined valves, ×1 (621).

Ilmarinia Öpik, 1934, p. 125 [**Orthisina sinuata* Pahlen, 1877, p. 44; OD]. Unique in possessing dorsal fold and ventral sulcus, otherwise like *Clinambon* but without constricted spondylium and with large, open foramen. *M.Ord.-U.Ord.*, Baltic.——FIG. 223,*3*. **I. sinuata* (Pahlen), U. Ord.(F_{Ic}), E.Baltic; *3a,b*, ped.v. and brach.v. int., ×1 (621); *3c-e*, ped.v., brach.v. ant. views of conjoined valves, ×1.5 (Rõõmusoks, n).

Iru Öpik, 1934, p. 89 [*Orthisina concava* Pahlen, 1877, p. 17; OD]. Strongly convexo-concave costellate and imbricate. Spondylium sessile; cardinal process flanked by subsidiary ridges; socket ridges hatchet-shaped; dorsal median ridge absent; notothyrial platform weak. *L.Ord.*, USSR.——FIG. 223, *4*. **I. concava* (Pahlen), B_{III}, W.Russian Platform; *4a,b*, ped.v. int., brach.v. ext., ×1.5; *4c*, brach.v. int., ×2 (Rõõmusoks, n).

Ladogiella Öpik, 1934, p. 93 [**L. imbricata*; OD]. Externally like *Clitambonites* but with more strongly convex brachial valve, shorter ventral interarea and finer ornamentation. Spondylium sessile; chilidium vestigial; cardinal process massive, lanceolate and flanked by well-developed subsidiary ridges. *L.Ord.*, USSR.——FIG. 222,*3*. **L. imbricata*, E.Baltic; *3a*, brach.v. int., ×3; *3b*, ped.v. int., ×5; *3c*, ped.v. ext., ×3 (621).

Pahlenella Schuchert & Cooper, 1931, p. 245 [**Orthis trigonula* Eichwald, 1840, p. 148; OD]. Like *Vellamo* but concavo-convex, with prominent ventral fold and dorsal sulcus and with quadripartite dorsal adductors impressed on sessile shield-shaped plate of secondary shell. *L.Ord.*, USSR.

Vellamo Öpik, 1930, p. 212 [**Orthis verneuili* Eichwald, 1841, p. 51; OD]. Like *Clitambonites* but not imbricate and with flat or gently convex brachial valve and high subpyramidal, commonly asymmetrical, pedicle valve; foramen large and invariably open; cardinal process simple. *M.Ord.-U.Ord.*, N.Hemis.——FIG. 222,*1*. **V. verneuili* (Eichwald), U.Ord.(F_{Iab}), E.Baltic; *1a,b*, brach. v. and ped.v. views of conjoined valves, ×1.5; *1c,d*, ped.v. and brach.v. int., ×2 (Rõõmusoks, n).

Subfamily ATELELASMATINAE Cooper, 1956

[Atelasmatinae Cooper, 1956, p. 516]

Pseudodeltidium lacking, chilidium variably developed. *L.Ord.-M.Ord.*

Atelelasma Cooper, 1956, p. 517 [**A. perfectum*; OD]. Pedicle valve subpyramidal, with procline to apsacline interarea, brachial valve gently convex, multicostellate, commonly with swollen and hollow costellae; delthyrium restricted laterally by elevated plates; chilidium well developed; cardinal process simple. *M.Ord.*, N.Am.-Eu.——FIG. 224,*2*. **A. perfectum*, Porterfield, USA(Tenn.); *2a,b*, ped.v., lat. views of conjoined valves, ×1; *2c,d*, ped.v. int. and post. views, ×2; *2e*, brach.v. int., ×1 (189).

Apomatella Schuchert & Cooper, 1931, p. 245 [*_Orthisina ingrica_ Pahlen, 1877, p. 48; OD]. Like _Atelelasma_ but lacking hollow costellae, lateral plates to delthyrium and chilidium. _L.Ord._, Eu.——Fig. 224,_1_. *_A. ingrica_ (Pahlen), BII, Baltic; _1a,b_, ped.v. ext. and post. views, ×1 (729).

Superfamily GONAMBONITACEA Schuchert & Cooper, 1931

[_nom. transl._ Williams, herein (_ex_ Gonambonitinae Schuchert & Cooper, 1931, p. 245)]

Concavo-convex to convexo-concave, costellate to unequally parvicostellate, with ventral muscle field impressed on spondylium triplex; shell substance pseudopunctate. _Ord._

Family GONAMBONITIDAE Schuchert & Cooper, 1931

[_nom. transl._ Rubel, 1963, p. 92 (_ex_ Gonambonitinae Schuchert & Cooper, 1931, p. 245)] [=Estlandiidae Öpik, 1934, p. 129]

Ventral interarea variably inclined, pseudodeltidium and chilidium variably developed; spondylium triplex sessile to elevated; anterior impressions of dorsal adductors commonly smaller than posterior. _Ord._

Subfamily GONAMBONITINAE Schuchert & Cooper, 1931

[Gonambonitinae Schuchert & Cooper, 1931, p. 245]

Pseudodeltidium well developed, perforated by an apical foramen which may be closed in adult shells; chilidium strong, continuous with widely divergent and well-differentiated socket ridges supported by strong extensions of notothyrial platform. _L.Ord.-M.Ord._

Gonambonites Pander, 1830, p. 77 [*_G. latus_; SD Schuchert & LeVene, 1929, p. 63]. Unequally biconvex to convexo-concave with high, apsacline ventral interarea; finely costellate to unequally parvicostellate; spondylium triplex elevated, notothyrial platform and median ridge strongly developed, cardinal process flanked by subsidiary ridges. _L.Ord._(BIII), E.Baltic.——Fig. 224,_3_. *_G. latus_, USSR(Leningrad); _3a,b_, brach.v. ext., int., ×2 (684a).——Fig. 224,_3c_. _G._ sp., USSR (Leningrad); ped.v. int., ×1.5 (684a).

Anchigonites Öpik, 1939, p. 136 [*_A. conulus_; OD]. Like _Antigonambonites_ but not resupinate, high pedicle valve remaining convex throughout growth and plane brachial valve becoming slightly concave. _L.Ord._(BIII), Scand.-USSR.——Fig. 225,_2_. *_A. conulus_, Norway; _2a-c_, brach.v. and ped.v. int. molds, brach.v. ext. cast, ×4 (622).

Antigonambonites Öpik, 1934, p. 147 [*_Gonambonites plana_ Pander, 1830, p. 78; OD]. Resupinate and costellate. Spondylium mostly sessile, with rudimentary median septum; hinge line denticulate; dorsal adductor scars, subquadrate, widely spaced with posterior pair larger. _L.Ord._, Eu.——Fig. 225,_4_. *_A. planus_ (Pander) (BIIβ), Estonia; _4a,b_, brach.v. and ped.v. int., ×1.5; _4c_, ped.v. ext., ×2; _4d_, ped. view of foramen with seal of secondary shell, ×12 (621).

Estlandia Schuchert & Cooper, 1931, p. 245 [*_Orthisina marginata_ Pahlen, 1877, p. 33; OD]. Unequally biconvex with high, apsacline ventral interarea; multicostellate, costellae arising by intercalation and traversed by undercut lamellae to give interrupted tubular appearance. Spondylium triplex elevated; cardinal process flanked by subsidiary ridges; notothyrial platform and median ridge strongly developed; posterior dorsal adductor scars quadrate and larger than subtriangular anterior pair; subperipheral rims strong in both valves. _M.Ord._, Eu.——Fig. 225,_5a,b_. *_E. marginata marginata_ (Pahlen), (CII), Estonia; _5a_, brach.v. ext., ×1.5; _5b_, ped.v. ext., ×2 (Rõõmusoks, n).——Fig. 225,_5c,d_. *_E. marginata aspera_ (Pahlen), (CII), Estonia; _5c,d_, ped.v. and brach. v. int., ×2 (621).

Lacunarites Öpik, 1934, p. 175 [*_L. ilmatar_; OD]. Strongly concavo-convex, coarsely costellate, with strong, widely spaced imbrication forming radial series of lacunae in interspaces. Spondylium sessile, traces of lateral septa absent. _L.Ord._, USSR.——Fig. 225,_6_. *_L. ilmatar_, (BIII), Estonia; ped.v. ext., ×3 (Rõõmusoks, n).

Raunites Öpik, 1939, p. 135 [_pro Rauna_ Öpik, 1932, _non_ Münster, 1839] [*_Orthisina janischewskyi_ Lessnikov, 1924, p. 153; OD]. Resupinate, unequally parvicostellate, and finely imbricate, exceptionally with impersistent posterolateral rugae; cardinal process without flanking subsidiary ridges, teeth and socket ridges obsolescent, dorsal median ridge absent. _L.Ord._, USSR.——Fig. 225,_3a,b_. *_R. janischewskyi_ (Lessnikov), (BIIβ-γ), Estonia; _3a_, brach.v. int., ×1.5; _3b_, ped.v. int., ×1 (621).——Fig. 225,_3c_. _R. wolchowiana_ (Öpik), (BII), USSR(Leningrad); brach.v. ext., ×2 (621).

Subfamily ANOMALORTHINAE Ulrich & Cooper, 1936

[_nom. transl._ Williams, herein (_ex_ Anomalorthidae Ulrich & Cooper, 1936, p. 622)] [=Progambonitinae Rubel, 1963, p. 92]

Ventral interarea apsacline to anacline, delthyrium open, chilidium vestigal or lacking; spondylium triplex sessile to elevated. _L.Ord._

The systematic position of _Anomalorthis_ is uncertain. Ulrich & Cooper (825, p. 126) reported a sessile spondylium with traces of a median septum lying between the dental plates and also "scattered pseudopunctae like those occurring in the Strophomenacea." Nonetheless they concluded

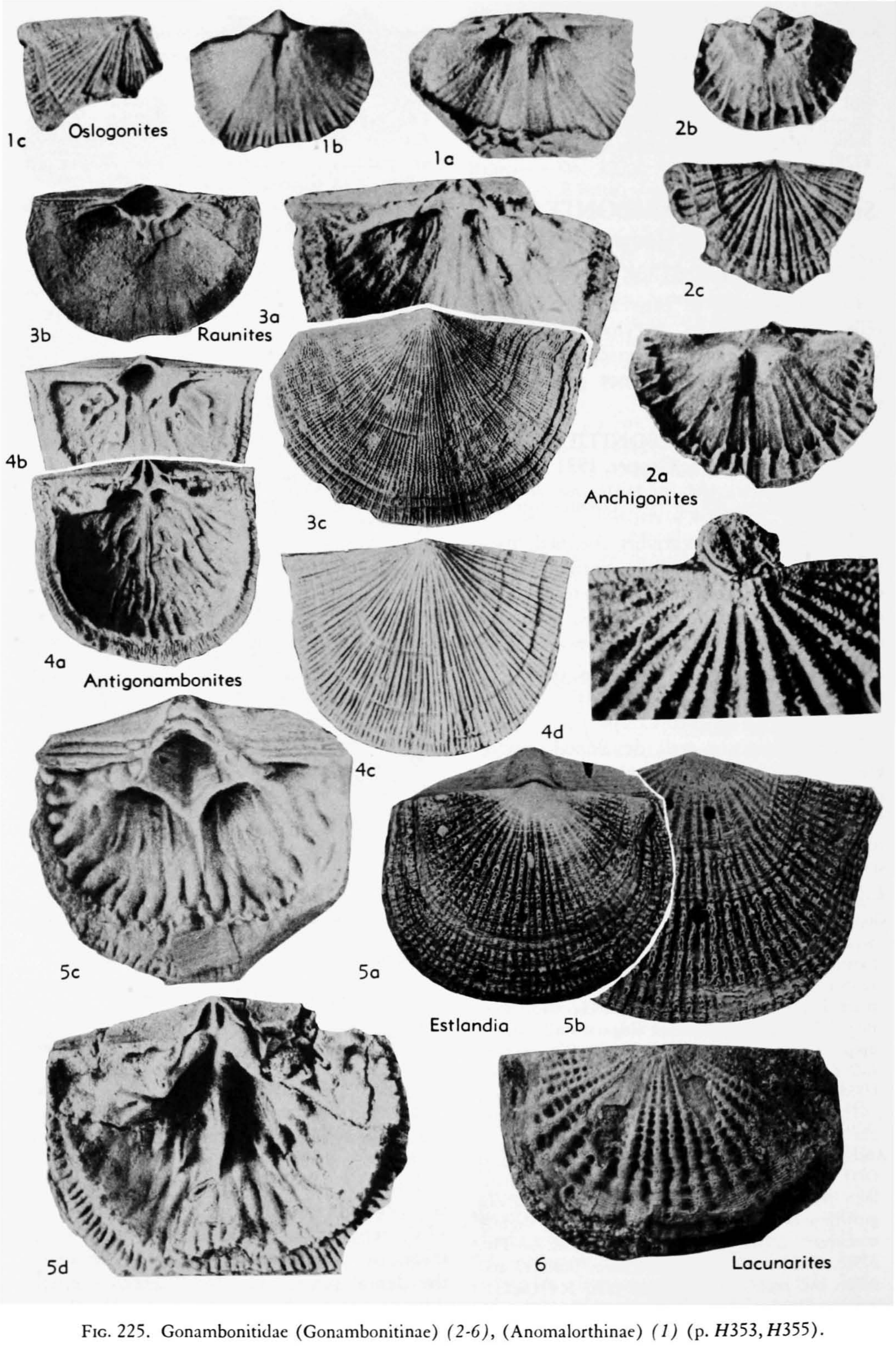

FIG. 225. Gonambonitidae (Gonambonitinae) *(2-6)*, (Anomalorthinae) *(1)* (p. *H*353, *H*355).

that the genus was more orthoid than clitambonitoid, especially in possessing "a flat imperforate deltidium." This structure is much more likely to be a raised pedicle callist or apical plate and despite the orthoid features of the genus it seems best to assign it to the Gonambonitacea.

Anomalorthis Ulrich & Cooper, 1936, p. 622 [**A. utahensis*; OD]. Unequally biconvex to convexiconcave, with long ventral interarea, finely multicostellate. Spondylium sessile; cardinal process simple, ridgelike. *L.Ord.*, W.USA.——Fig. 226,*1*. **A. utahensis*, Canad.-USA(Utah); *1a,b*, ped.v. int., lat. views, ×1; *1c*, brach.v. int., ×2; *1d*, ped.v. ext., ×2 (825).

Oslogonites Öpik, 1939, p. 133 [**O. costellatus*; OD]. Finely costellate, with flat to moderately convex brachial valve and high pedicle valve. Spondylium high with rudimentary lateral septa; notothyrial platform, concave, thin and bladelike, cardinal process absent, socket ridges weak. *L.Ord.*, Scand.——Fig. 225,*1*. **O. costellatus*, Expansusschiefer, Nor.; *1a-c*, brach.v. int., ped.v. int. mold, brach.v. ext., ×4 (622).

Progonambonites Öpik, 1934, p. 138 [**P. estonus*; OD]. Biconvex, finely imbricate to give costellate radial ornament beaded appearance; interior like that of *Oslogonites* except for presence of cardinal process. *L.Ord.*, Eu.——Fig. 226,*2*. **P. estonus*, (B$_{III}$), Estonia; *2a*, brach.v. ext., ×2.5; *2b,c*, post., ped.v. ext., ×1.5; *2d*, brach.v. int., ×2 (Rõõmusoks, n).

Family KULLERVOIDAE Öpik, 1934

[Kullervoidae Öpik, 1934, p. 70]

Coarsely costellate and imbricate, with well-developed pseudodeltidium and chilidium. Spondylium triplex constricted anteromedially by pair of inwardly directed plates forming semiconical chamber (hemisyrinx), lateral septa rudimentary. *M.Ord.-U.Ord.*

Kullervo Öpik, 1932, p. 70 [**Gonambonites panderi* Öpik, 1930, p. 234; OD]. Brachial valve flat to gently convex, pedicle valve subpyramidal, costellae commonly no more conspicuous than imbrication posterolaterally; foramen commonly large, with high irregular lip. Cardinal process flanked by subsidiary ridges, dorsal adductor scars widely spaced, subpetaloid. *M.Ord.-U.Ord.*, N. Hemis.——Fig. 227,*1*. *K. complectens* (Wiman) *albida* (Reed), U.Ord.(Ashgill.), Eire; *1a-e*, int., tilted int. ext., post., posterolat. views of ped.v., ×3; *1f,g*, brach.v. int., ext., ×5 (Wright, n).

Suborder TRIPLESIIDINA Moore, 1952

[*nom. correct.* Wright, herein (*pro* suborder Triplesioidea Muir-Wood, 1955, p. 89, *nom. transl. ex* order Triplesiida Moore, 1952, p. 221)]

[Materials for this suborder prepared by A. D. Wright]

[Appreciation is expressed to the Trustees of the British Museum (Natural History) for permission to reproduce several illustrations from Wright, 1964 (ref. 895b)]

The Triplesiidina form a very distinctive

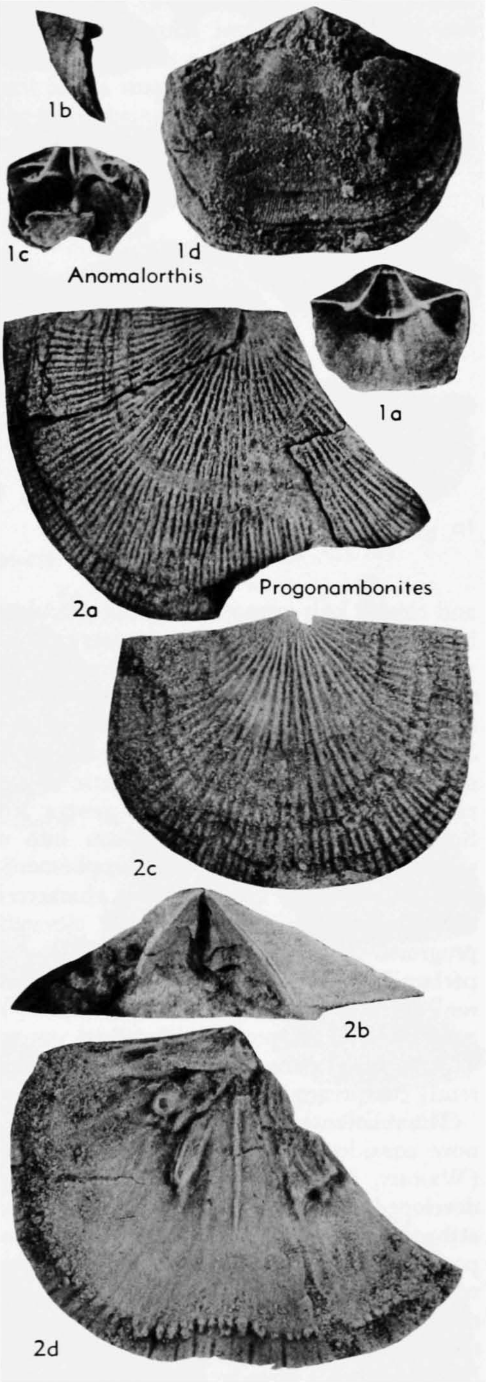

Fig. 226. Gonambonitidae (Anomalorthinae) (p. H355).

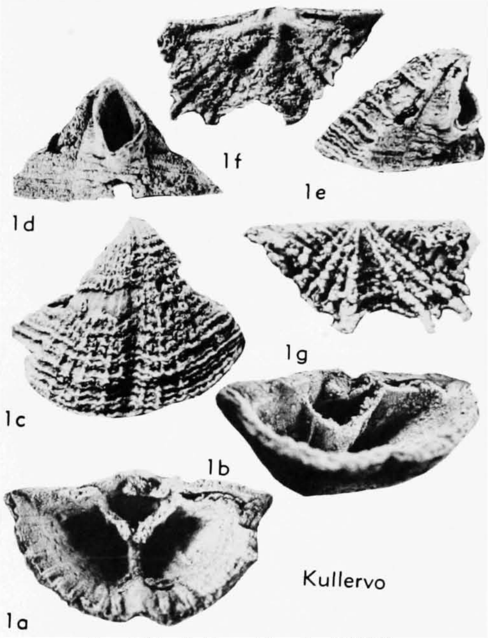

FIG. 227. Kullervoidae (p. *H*355).

and closely knit group among the articulate brachiopods. The external appearance is very variable, and before the internal structures were fully known, the various species and genera were assigned to such stocks as *Spirifer*, *Atrypa*, and *Orthis*. The discovery of the unusual and consistent nature of the cardinalia in the then known genera led SCHUCHERT (1913) to unite them into a single subfamily within the Strophomenidae. Subsequently the distinctive characters of the subfamily caused it to be elevated progressively to familial (ÖPIK, 1932), superfamilial (COOPER, 1944), and ordinal rank (MOORE, 1952); MUIR-WOOD (1955) reduced it to the present subordinal status. This suborder contains a single family, currently comprising ten genera.

The relationships of the Triplesiidina are now considered to lie with the Orthacea (WRIGHT, 1963), and they appear to have developed from a stock of small biconvex orthaceans in early Ordovician times. No possible transitional forms between the two stocks are yet known, and the earliest recorded genus, *Onychoplecia*, appearing in the Lower Ordovician Table Head Series of Newfoundland, already possessed the typical triplesiid characteristics. The group continued throughout the Ordovician and into the Silurian, being fairly widespread but rarely abundant. Although four genera were still present in the Wenlockian, representatives of the group are not known from the Ludlovian or later strata.

Biconvex, impunctate shells; ventral interarea with flat, medianly arched pseudodeltidium and apical foramen; dorsal interarea obsolete, cardinal process long, forked. *L.Ord.-U.Sil. (Wenlock.).*

The triplesioid shell varies greatly in outline from transversely elliptical (e.g., *Bicuspina*) to rounded (e.g., *Plectotreta*), tear-shaped (e.g., *Onychoplecia*) and elongate (e.g., *Onychotreta*). In profile the shell varies from biconvex to markedly dorsi-biconvex. A fold and sulcus are usually strongly developed, and are reflected in the presence of a uniplicate or, less commonly, sulcate anterior commissure. Asymmetrical shell development is typical of some genera (e.g., *Streptis*). Surface ornament is lacking, for example, in the smooth *Triplesia*; other forms show concentric growth lines, frills, and lamellae, commonly in combination with radial costae, costellae, or plications. It is these features of shell shape and ornament which provide the basis for generic distinction (823).

The pedicle valve interarea is normally curved, apsacline, and exceptionally is developed to great size (e.g., *Onychotreta*). The small foramen is restricted to the extreme apex of the delthyrium, and may resorb part of the ventral umbo, thus becoming situated anterior to the beak. The remainder of the delthyrium is filled by a flat pseudodeltidium, which lies flush with the interarea and which has a narrow fold running medianly from the foramen to the hinge line.

Internally, the pedicle valve may develop a more or less tubular passage for the pedicle between the foramen and valve interior. The teeth are normally supported by small dental plates. The muscle scars are only known for a few genera, where they consist of flabellate diductor scars surrounding, and all but enclosing, the cordate or lanceolate adductor scars. The meager evidence on the mantle canals indicates that they have a lemniscate pattern.

The brachial valve lacks an interarea, and the strongly convex dorsal umbo is tucked inside the pedicle valve. Internally, the valve possesses a long, forked cardinal process, which curves backward from its base at the posterior end of the brachial valve so as to extend into the ventral umbo. The myophores are located at the distal extremity of each prong, usually as deep grooves on the dorsal surface. On the posterior side of the shaft near its base is a calcareous hood, and lateral to it on either side is a short calcareous process which serves as the inner margin to the socket. The adult lophophore apparently is a dorsally directed spirolophe. In specimens showing muscle and mantle canal impressions, the dorsal muscle field has a larger anterior adductor pair and a smaller subcentral posterior pair, the latter being bounded laterally by a pair of gonocoels. The mantle canal patern is saccate (895).

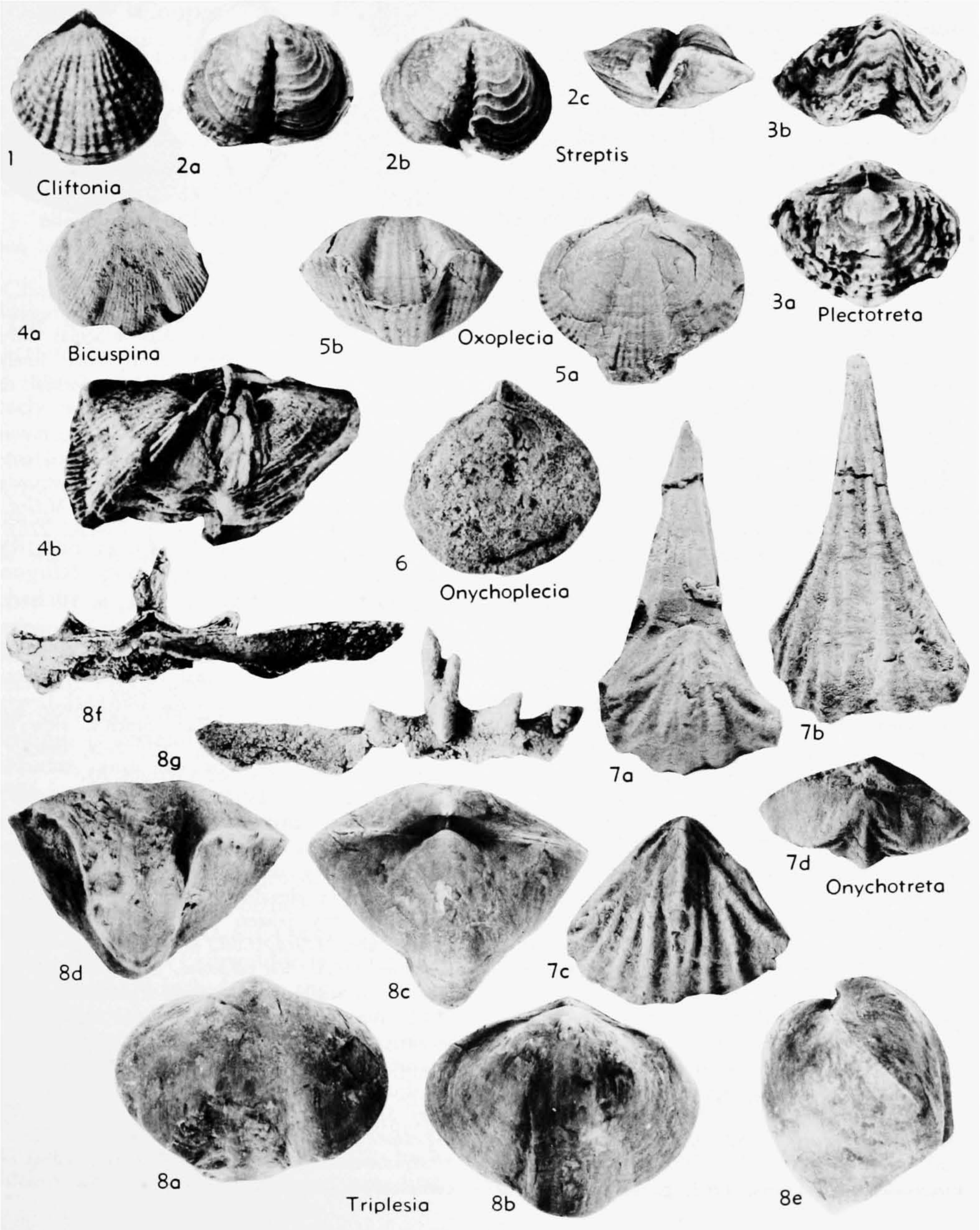

FIG. 228. Triplesiidae (p. *H*358-*H*359).

Superfamily TRIPLESIACEA Schuchert, 1913

[*nom. transl.* Cooper, 1944, p. 307 (*ex* Triplesiinae Schuchert, *nom. correct.* Schuchert & LeVene, 1929, p. 16, *pro* Tripleciinae Schuchert, 1913, p. 387)]

Characters of the family. *L.Ord.-U.Sil. (Wenlock.).*

Family TRIPLESIIDAE Schuchert, 1913

[*nom. transl.* Muir-Wood, 1955, p. 89 (*ex* Triplesiinae Schuchert, *nom. correct.* Schuchert & LeVene, 1929, p. 16, *pro* Tripleciinae Schuchert, 1913)]

Biconvex to markedly dorsi-biconvex, impunctate shells, normally with prominent undulation in anterior commissure. Pedicle-valve interarea with delthyrium closed by flat pseudodeltidium with narrow median fold extending anteriorly from small apical foramen. Brachial-valve interarea obsolete. Cardinal process long, forked, and directed backward, with hood commonly developed on posterior side of its base, and with short divergent processes on either side forming inner boundaries of sockets. *L.Ord.-U.Sil. (Wenlock.).*

Triplesia Hall, 1859, p. 44 [**Atrypa extans* Emmons, 1842; SD Hall & Clarke, 1892, p. 270] [=*Triplecia* Hall & Clarke, 1892 (obj.) *(nom. van.)*; *Dicraniscus* Meek, 1872, p. 279 (type, *D. ortoni*)]. Strongly trilobate, with pronounced dorsal fold and ventral sulcus; surface smooth, with only faint growth lines. *M.Ord.-U.Sil.(Wenlock.),* widespread.——Fig. 228,*8a-e*. **T. extans,* M.Ord.(Trenton.), USA(N.Y.); *8a-e,* ped.v. brach. v. post., ant., lat. views of complete shell, ×1.5 (895; Wright, n).——Fig. 228,*8f,g*. *T.* sp. cf. *T. insularis* (Eichwald), U.Ord.(Ashgill.), Ire.; dorsal and ventral views of cardinalia, ×5 (895b).

Bicuspina Havlíček, 1950, p. 18 [**Orthis cava* Barrande, 1848, p. 209; OD]. Transverse shells of spiriferoid outline; uniplicate, multicostellate, with well-developed pedicle tube. *M.Ord.-U.Ord.,* Eu.(Br.I.-Boh.-Est.).——Fig. 228,*4a*. **B. cava,* Llandeil., Boh.; ped.v. ext., ×1 (Havlíček, n).——Fig. 228,*4b*. *B. spiriferoides,* Caradoc., Br.I.; ped.v. int. mold, ×1.3 (895).

Brachymimulus Cockerell, 1929, p. 105 [*pro Mimulus* Barrande, 1879 (*non* Stimpson, 1860)] [**Mimulus perversus* Barrande, 1879, p. 109; OD]. Smooth form, close to *Triplesia* but with ventral fold and dorsal sulcus. *U.Ord.-L.Sil.,* Eu.-N.Am.

Cliftonia Foerste, 1909, p. 82 [**C. striata*; OD]. Externally like "small *Atrypa*" with subcircular outline and ornament of strong distant lamellae which undulate over costellae. *U.Ord.,* Ire.-Swed.; *L.Sil.,* EC.USA-Wales.——Fig. 228,*1*. *C. bellula* Ulrich & Cooper, L.Sil., USA(Okla.); brach.v., ext., ×2 (823).

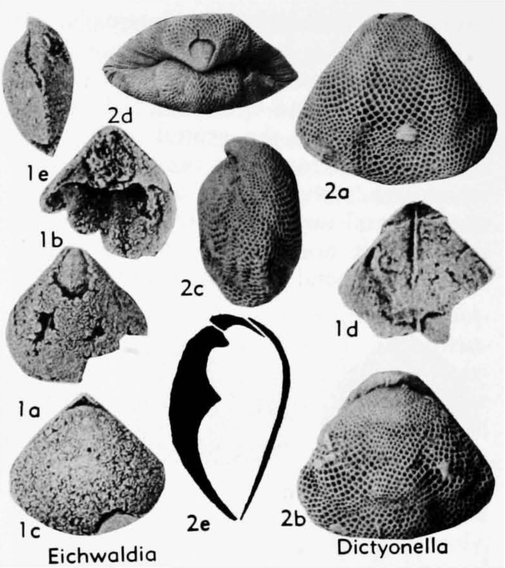

Fig. 229. Eichwaldiidae (p. *H*360).

Epacroplecia Williams, 1962, p. 155 [**Triplesia grayiae* Davidson, 1870, p. 198; OD]. Trigonal shell, with highly convex trilobate brachial valve and shallow pedicle valve; hinge short; finely costellate. Brachiophores subparallel, normal to hinge line, bladelike. *M.Ord.,* Scot.-?China.

Onychoplecia Cooper, 1956, p. 529 [**O. brevirostris*; OD]. Small form with tear-shaped outline, elongate beak and narrow hinge; narrowly lenticular in profile, smooth and uniplicate. *M.Ord.,* N. Am.(Newf.-N. Y.-Okla.-Tenn.).——Fig. 228,*6*. **O. brevirostris,* USA(Tenn.); brach.v. view of complete shell, ×2.5 (Wright, n).

Onychotreta Ulrich & Cooper, 1936, p. 339 [**O. mesleri*; OD]. Outline clawlike; pedicle valve greatly elongated, with very long interarea; dental plates long, parallel; brachial valve short; ornament coarsely costellate. *L.Sil.,* USA(Ark.).——Fig. 228,*7*. **O. mesleri*; *7a,b,* brach.v. view of complete shell, ped.v. ext., ×2; *7c,d,* brach.v. dorsal and post. views, ×2 (Wright, n).

Oxoplecia Wilson, 1913, p. 81 [**O. calhouni*; OD] [=*California* Bassler, 1915 *(nom. null.)*]. Roundly elliptical to transverse shells, uniplicate, characterized by well-developed costellate ornament and fine elevated concentric growth lines. Internally, may possess pedicle collar, but not pedicle tube. *M.Ord.-U.Sil.(Wenlock.),* Eu.-N.Am.——Fig. 228,*5*. **O. calhouni,* M.Ord.(Trenton.), Ont.; *5a,b,* brach.v., ant., views of complete shell, ×1.5 (Wright, n).

Plectotreta Ulrich & Cooper, 1936, p. 339 [**P. lindströmi*; OD]. Subcircular form characterized by strong concentric lamellae, and differentiated from *Streptis* by strong radial plications. *U.Sil. (Wenlock.),* NW.Eu.(Gotl.-Eng.).——Fig. 228,*3*. **P. lindströmi,* Gotl.; *3a,b,* brach.v., ant. views of complete shell, ×2 (Wright, n).

Streptis DAVIDSON, 1881, p. 150 [**Terebratula grayi* DAVIDSON, 1848, p. 331; OD]. Exterior with ornament of strong concentric lamellae, commonly developed into frills, and superimposed radial ribs. Uniplicate; usually showing marked asymmetry. *U.Ord.-U.Sil.*, N.Am.-Greenl.-Eu.——FIG. 228,2. **S. grayi*, U.Sil.(Wenlock.), Eng.; *2a-c*, ped.v., brach.v., ant. views of complete shell, ×3 (Wright, n).

ORDER UNCERTAIN—DICTYONELLIDINA

By A. J. ROWELL

[Nottingham University]

Suborder DICTYONELLIDINA Cooper, 1956

[*nom. correct.* ROWELL, herein (*pro* suborder Dictyonelloidea COOPER, 1956, p. 947)]

Shell calcareous, punctate; umbo of pedicle valve with inset, smooth, triangular umbonal plate. *M.Ord.-Perm.*

Superfamily EICHWALDIACEA Schuchert, 1893

[*nom. transl.* ROWELL, herein (*ex* Eichwaldiidae SCHUCHERT, 1893, p. 155)]

Characters of suborder. *M.Ord.-Perm.*

The most characteristic feature of the superfamily is the unusual modification of the umbo of the pedicle valve, nothing closely comparable to it being known in any other brachiopod stock. Extending anteriorly from the apex of the valve is a narrowly triangular smooth area, inset slightly below the level of the adjacent shell; this is the umbonal plate. It fills a triangular opening in the umbo and is attached by its lateral margins to the valve. Anteriorly, the umbonal plate is free and a broad, slitlike passage communicates between the inside and outside of the valve. This opening, although readily masked by crushing, is certainly present in the Eichwaldiidae and is recorded by DITTMAR (260) in the Isogrammidae. As in all extinct groups, the interpretation of the functional anatomical significance of shell structures is difficult, but it is probable that this passage functioned as a pedicle opening, as was suggested by HALL & CLARKE (1894).

Two families (Eichwaldiidae, Isogrammidae) are here included in the superfamily, differentiated from each other primarily by characters of the brachial valve. From what is known of their stratigraphical range, the two are separated from each other by a distinct time gap. The youngest Eichwaldiidae are recorded from the high Silurian and the Isogrammidae are first known from the Lower Carboniferous. Two alternative explanations of this hiatus are possible. The gap may be real, in which case the two families are not closely related, the resemblance between them indicating convergence rather than affinity, and the superfamily is polyphyletic. Alternatively, the absence of Devonian representatives may be explained in terms of failure of the fossil record. This negative approach is not very satisfactory, but in view of the rarity of the Isogrammidae and the close resemblance of the unusual modified ventral umbo of both families, it seems to be the most reasonable explanation.

The origin of this group of brachiopods is still unknown and there is even disagreement as to whether they should be referred to the Inarticulata or to the Articulata. GORYANSKY (1960, 356), for example, placed the Eichwaldiidae in the Inarticulata and the Isogrammidae in the Articulata. MUIR-WOOD (1955), taking a somewhat different view, referred both families to a suborder Incertae Sedis and assigned them to the articulates. The evidence on which to base a decision on this question is not very conclusive, but if the two families are regarded as related, then it appears on balance to favor the view that they are articulates. The calcareous shell suggests affinities with the Articulata, but, on the other hand, it is known that a calcareous shell has been developed independently in at least three and probably four separate inarticulate stocks. Similarly, the nature of articulation does not provide indisputable evidence of affinity, although that of *Isogramma* is reminiscent of the Articulata. It is the presence of a well-developed cardinal process in the Isogrammidae that suggests that they are articulates, for this structure, commonly developed in the Articulata, is unknown in any inarticulate stock.

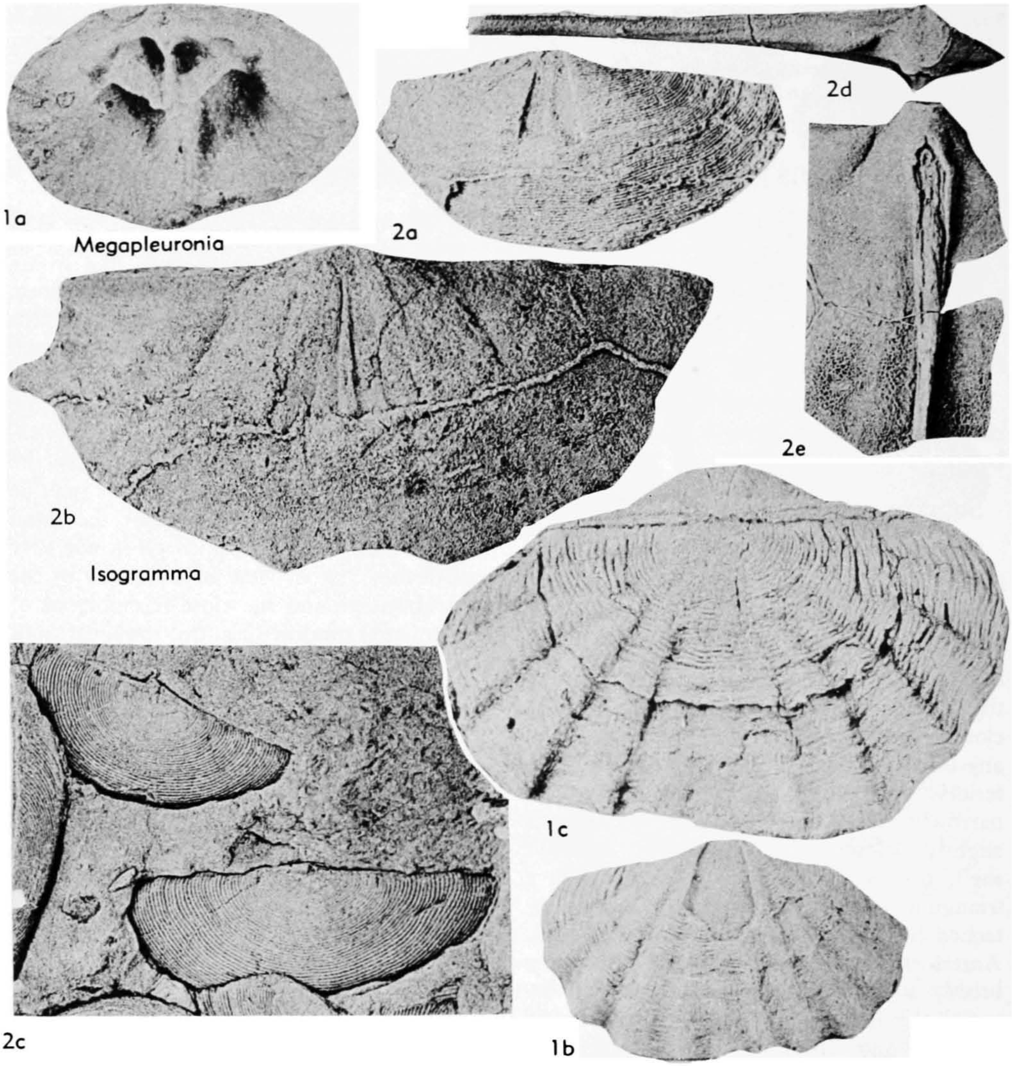

FIG. 230. Isogrammidae (p. *H*361).

Family EICHWALDIIDAE Schuchert, 1893

[Eichwaldiidae SCHUCHERT, 1893, p. 155]

Biconvex, triangular outline; long dental sockets in posterolateral margins of brachial valve, articulating with teeth in pedicle valve. *M.Ord.-U.Sil.*

Eichwaldia BILLINGS, 1858, p. 190 [**E. subtrigonalis*; OD]. External ornament only of fine concentric growth lines. Interior of brachial valve with prominent median septum extending nearly to anterior margin, small boss at posterior end of septum possibly functioning as cardinal process; musculature unknown. *M.Ord.*, Can.——FIG. 229, *1*. **E. subtrigonalis*, Rockland F., Ont.; *1a,b*, incompl. ped.v. ext., int., both ×2; *1c,d*, brach.v. ext., incompl. int., ×1, ×2; *1e*, both valves lat., ×1 (189).

Dictyonella HALL, 1868, p. 274 [**Atrypa coralifera* HALL, 1852, p. 281; OD] [=*Dyctionella* OEHLERT, 1887, p. 1267 (*nom. null.*)]. Very similar to *Eichwaldia*, differing in its ornament of rather coarse pits defined by intersecting, narrow, elevated lines. *Sil.*, N.Am.-Eu.-Asia.——FIG. 229,*2*. *D. capewelli* (DAVIDSON), Wenlock, Eng.; *2a*, ped. v. ext.; *2b*, brach.v. ext.; *2c*, both valves lat., *2d*, post.; *2e*, median long. sec., all ×3 (Rowell, n).

Family ISOGRAMMIDAE Schuchert & LeVene, 1929

[Isogrammidae Schuchert & LeVene, 1929, p. 18]

Shells transversely suboval in outline. Cardinal process with well-developed shaft, dental sockets relatively small, lateral to cardinal process (180). *Carb.-Perm.*

Isogramma Meek & Worthen, 1870, p. 36 [**Chonetes? millipunctatus* Meek & Worthen, 1870, p. 35; OD] [=*Aulacorhynchus* Dittmar, 1872, p. 2 (*non* Gould, 1834); *Aulacorhyna* Strand, 1928, p. 37 (*nom. subst. pro Aulacorhynchus* Dittmar, 1872 (*non* Gould, 1834) (type, *Aulacorhynchus pachti* Dittmar, 1872, p. 2)]. Large, concavo-convex; strong concentric ornament of elevated fila. Myophore strong, shaft bifurcating around dorsal median ridge; musculature of brachial valve obscure, in pedicle valve adductor scars on inner surface of umbonal plate, subflabellate diductor scars lateral to plate (5). *Carb.-Perm.*, N.Am.-Eu.-Asia.——Fig. 230,*2a-c. I. texanum* Cooper, Penn.(Gaptank F.), USA(Tex.); *2a,* latex replica ped.v. ext., ×1; *2b,* ped.v. int. impression, ×2; *2c,* brach.v. ext. mold, ×1 (180).——Fig. 230,*2d,e, I. renfrarum* Cooper, Penn.(Gonzales Sh.); USA(Tex.); *2d,e,* detail of cardinal process, post., dors., both ×2 (180).

Megapleuronia Cooper, 1952, p. 117 [**Productus fabianii* Greco, 1947, p. 1; OD]. Biconvex or concavo-convex; costate, with concentric ornament of discontinuous, raised lines. Ventral interior unknown, dorsal interior with muscle platform supported by median septum. *Perm.*, Eu.——Fig. 230, *1a.* **M. fabianii* (Greco), Italy; brach.v. int., ×1 (180).——Fig. 230,*1b,c. M. grecoi* Cooper, Italy; *1b,* ped.v. ext., ×2; *1c,* brach.v. ext., ×3 (180).

STROPHOMENIDA

By Helen Muir-Wood and Alwyn Williams

[British Museum (Natural History) and Queen's University of Belfast]

Order STROPHOMENIDA Öpik, 1934

[*nom. transl.* Moore *in* Moore, Lalicker & Fischer, 1952, p. 221 (*ex* suborder Strophomenoidea Öpik, 1934, p. 75); emended H. M. Muir-Wood & Alwyn Williams, herein] [Diagnosis prepared by Alwyn Williams]

Articulate brachiopods with plano- to concavo-convex, less commonly biconvex, resupinate or geniculated, shells; interareas lacking or vestigial to extravagantly developed, hinge lines rarely reduced; pseudodeltidium rarely absent, mostly strongly developed or continuous with ventral interarea, chilidium variably developed or indistinguishable from dorsal interarea; pedicle foramen, with sheath, supra-apical probably in all brephic shells but rarely open in adult shells, or attachment effected by cementation of pedicle valve with or without aid of open, tubular spines; spines may be present on brachial as well as pedicle valve, less commonly limited to margin of ventral interarea. Cardinal process rarely absent, elaborated from median partition or more commonly from pair of discrete lobes; socket ridges rarely strongly developed, commonly vestigial or absent; lophophore inferred to vary from schizolophous to spirolophous and attached plectolophous dispositions, less commonly supported by dorsal platforms or ridges, very rarely by calcareous spires. Ventral muscle field commonly expanded well beyond umbonal cavity, rarely borne on elevated structures; dorsal adductor field normally quadripartite rarely elevated. Shell substance pseudopunctate, very rarely impunctate. *L.Ord.-L.Jur.*

The Strophomenida constitute the largest ordinal group within the Brachiopoda, for the order embraces nearly 400 genera (including the largest and thickest shells known) distributed among nine superfamilies and four suborders. A taxonomic assemblage of this size inevitably includes a great variety of forms, but the morphological diversity displayed by members of the order is unprecedented, mainly because of the widespread adoption of an attached mode of life by cementation or spinous anchorage following the loss of a functional adult pedicle early in the evolutionary history of the group. Chonetidina and Productidina, for example, independently acquired spines or perforations containing outer epithelial strands by means of which support, through attachment to, or ramification within the substratum, was effected. A minority of strophomenaceans, most davidsoniaceans and all lyttoniaceans, on the other hand, remained attached for varying parts of their lives solely by cementation of the pedicle valves. Inflexible anchorage of this nature was probably the principal cause for repeated bizarre modifications in shell shape. Thus, conical shells were typical of late