cal, small, no spines recorded; teeth peglike and with myocoelidium; cardinal process lobes separated medianly, but continuous with sockets, prominent median septum and strong marginal crenulations; valve walls thick. *Upper Permian (?Capitanian, Changhsingian):* Greece.——FIG. 443,*4a–d*. **C. rudistiformis,* Capitanian, Episcopi Limestone, Hydra; *a,* ventral interior showing teeth, ×4; *b,* dorsal valve interior, ×6; *c,* holotype, anterior view of complete shell, USNM 460380, ×4; *d,* posterior view of complete shell, ×4 (Grant, 1993a).

Tectarea LICHAREW, 1928, p. 268 [**T. robinsoni;* OD]. Probably attached by umbo; exterior usually decorticated, probably capillate with intervening radially arranged pits; myocoelidium long, without septum or anterior groove, may be filled with secondary deposit; each valve with toothlike process and socket articulating with similar structures on other valve. *Lower Permian:* Europe (Caucasus).——FIG. 443,*6a–c*. **T. robinsoni; a,b,* ventral, dorsal views of specimen, ×3; *c,* transverse section showing cardinal process and myocoelidium, ×3 (Licharew, 1928).

LYTTONIIDINA

ALWYN WILLIAMS,[1] DAVID A. T. HARPER,[2] and R. E. GRANT[3]

[[1]The University of Glasgow; [2]University of Copenhagen; and [3]deceased]

Suborder LYTTONIIDINA new suborder

[Lyttoniidina WILLIAMS, HARPER, & GRANT, herein] [=Oldhaminidina WILLIAMS, 1965f, p. 510, *nom. nov. pro* suborder Oldhaminoidea WILLIAMS, 1953c, p. 286]

Grossly inequivalve productide brachiopods with the smaller dorsal valve consisting mainly of lobate brachidial plate; lacking rhizoid spines but rarely with spinose projections at ventral margin; ventral valve lacking interarea but with variably developed and disposed posterior flap of shell; hinge line normally covered by ventral shell, articulatory structures ill defined; secondary shell layer pseudopunctate. *?Lower Carboniferous, Upper Carboniferous–Upper Permian.*

The morphology and classification of the lyttonioid brachiopods warrant a full discussion. Although vaguely suggestive of a strophalosiidine ancestry, the morphology is so bizarre as to continue to defy any confident interpretation of its details. This is true not only of certain morphological features of both valves but also of the shell structure and growth of the valves themselves. Consequently, the interpretation of shell morphology and the classification presented here, although benefitting from much new data since publication of the last *Treatise* account of the group (WILLIAMS, 1965f, p. 511–521), may yet undergo fundamental revision.

The shells are functionally bivalved, with the inner surface of the ventral valve everywhere extending well beyond the edge of the dorsal valve so that some of the ventral mantle margin, despite evidence for retractability, must have been permanently exposed during life. Moreover, the significantly smaller dorsal valve generally has a highly lobate outline resembling that of a ptycholophous lophophore, which led TERMIER and TERMIER (1949b) to postulate that the exposed part of the valve is a brachidium.

There is another line of evidence that supports this interpretation. The shell structure of the ventral valve is pseudopunctate, with a thin primary layer orthodoxly forming the entire outer surface of the valve (Fig. 444), which is characteristically ornamented by growth banding, growth disturbances, and evidence of shell repair.

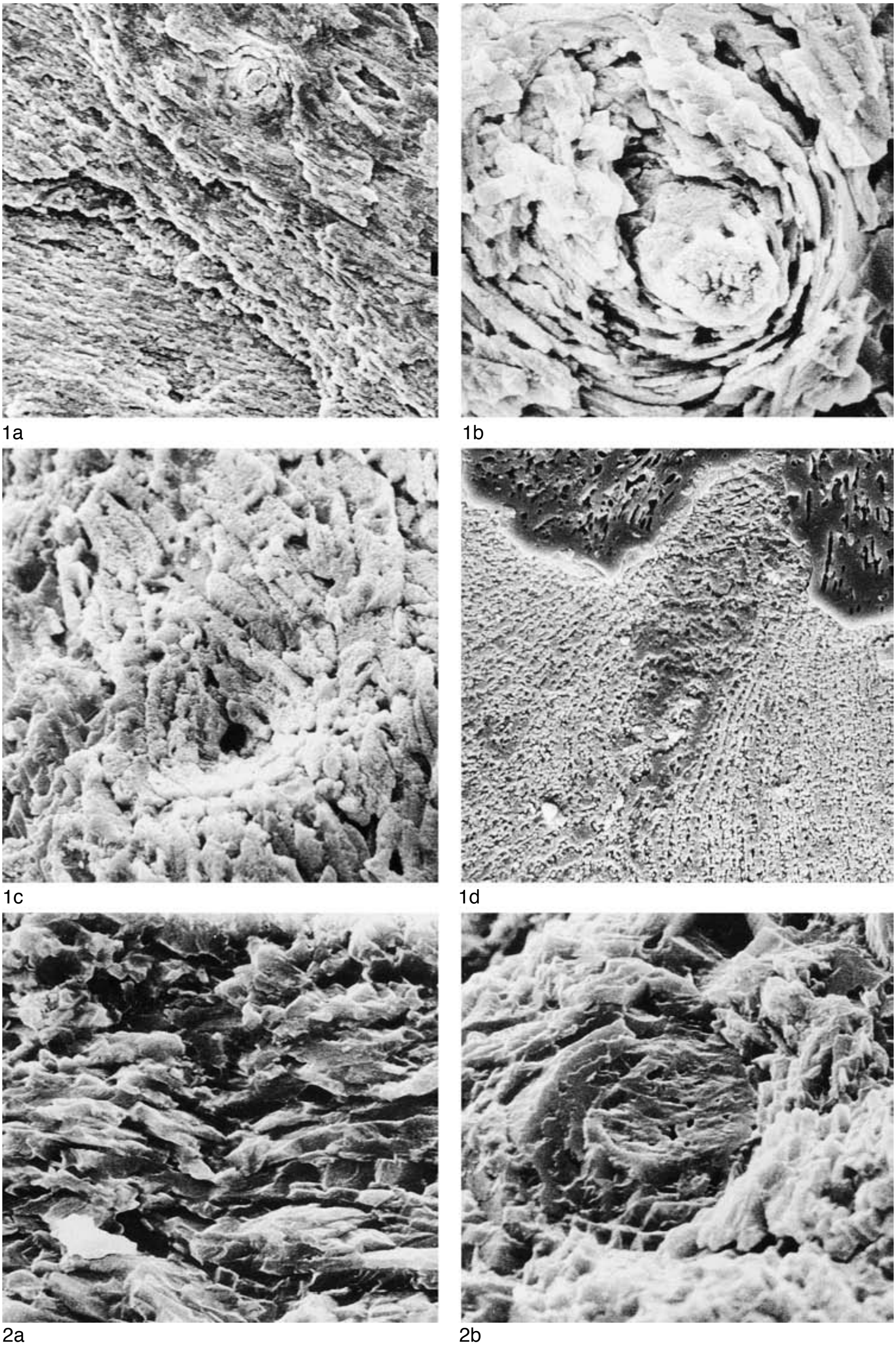

FIG. 444. *See explanation on facing page.*

In the structure generally identified as the dorsal valve, however, the primary layer is absent except for a small, posteriorly located, triangular area (Fig. 445) termed the false interarea by RUDWICK and COWEN (1968). The rest of the valve is made up exclusively of secondary pseudopunctate calcite (Fig. 444.1a–c) so that *both* external and internal surfaces are pierced by taleolae to give a finely tuberculate appearance identical with that of the ventral internal surface (WILLIAMS, 1953c, 1973). It can be demonstrated in other articulated brachiopods that structures like lophophore supports that are composed only of secondary shell were secreted within invaginations of outer epithelium independent of the mantle edge. Consequently it was assumed that the part of the lyttonioid dorsal valve that is also composed only of secondary shell was not an exoskeletal cover but an internal skeletal support (internal plate) to a highly lobate mantle infold (WILLIAMS, 1953c). The assumption is confirmed by sections of internal plates. They show distinct pseudopunctate layers characterized by taleolae pointing ventrally and dorsally and separated by a thin brachiotest (Fig. 446.1). According to this interpretation, the true dorsal valve is vestigial, being represented by the false interarea composed of both outer primary shell and the inner secondary layer forming the cardinal process lobes and the posteromedian part of the articulatory device.

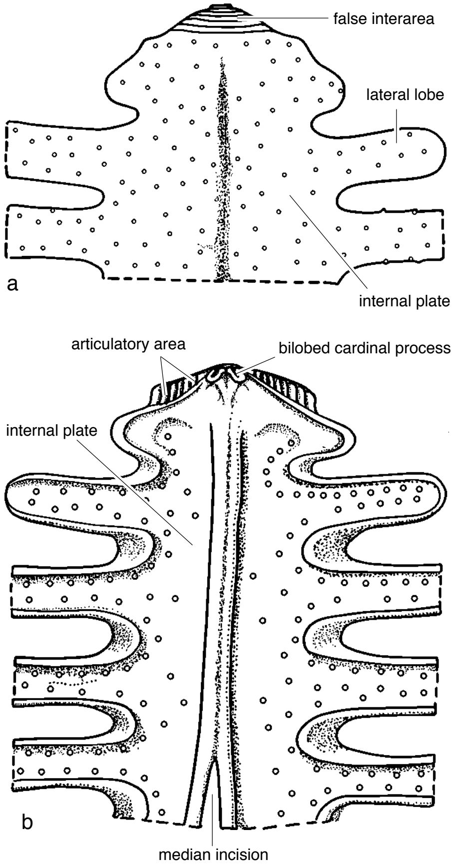

FIG. 445. Dorsal valve with internal plate of *Eolyttonia* sp., Permian, Texas; *a,* external and *b,* internal views (adapted from Williams, 1953).

The subsequent discovery by GRANT (1972) of a calcified ptycholophous brachidium, arising from the floor of the dorsal valve of the strophalosioid *Falafer* and resembling the lobate dorsal valves of early stocks as well as immature lyttonioids, appears to confirm the interpretation of TERMIER and TERMIER (1949b) and WILLIAMS (1953c). By imparting rigidity to an investing infold of the mantle, the inferred internal plate could have given support to the lophophore. Immature specimens of the earliest-known lyttonioid, *Poikilosakos,* possess a subcircular internal

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FIG. 444. Microstructure of lyttonioid shell; *1a–d, Oldhamina decipiens* (DE KONINCK), Permian, Salt Range, Pakistan; *1a,* general internal view (×300) of exfoliated lobe of dorsal valve showing pseudopunctae facing internally in upper right hand sector of micrograph and internal base of pseudopuncta facing externally in midregion along bottom with *1b,* another pseudopuncta, ×1400, *1c,* base of pseudopuncta, ×1300, and *1d,* etched resin-mounted section of pseudopuncta, ×3000; *2a,b,* fracture sections of ventral valve of *Poikilosakos petaloides* (WATSON), upper Pennsylvanian, Kansas; *2a,* section showing thin primary layer along top, succeeded inwardly by laminae of secondary layer, ×1800; *2b,* core of pseudopuncta, ×2300 (new).

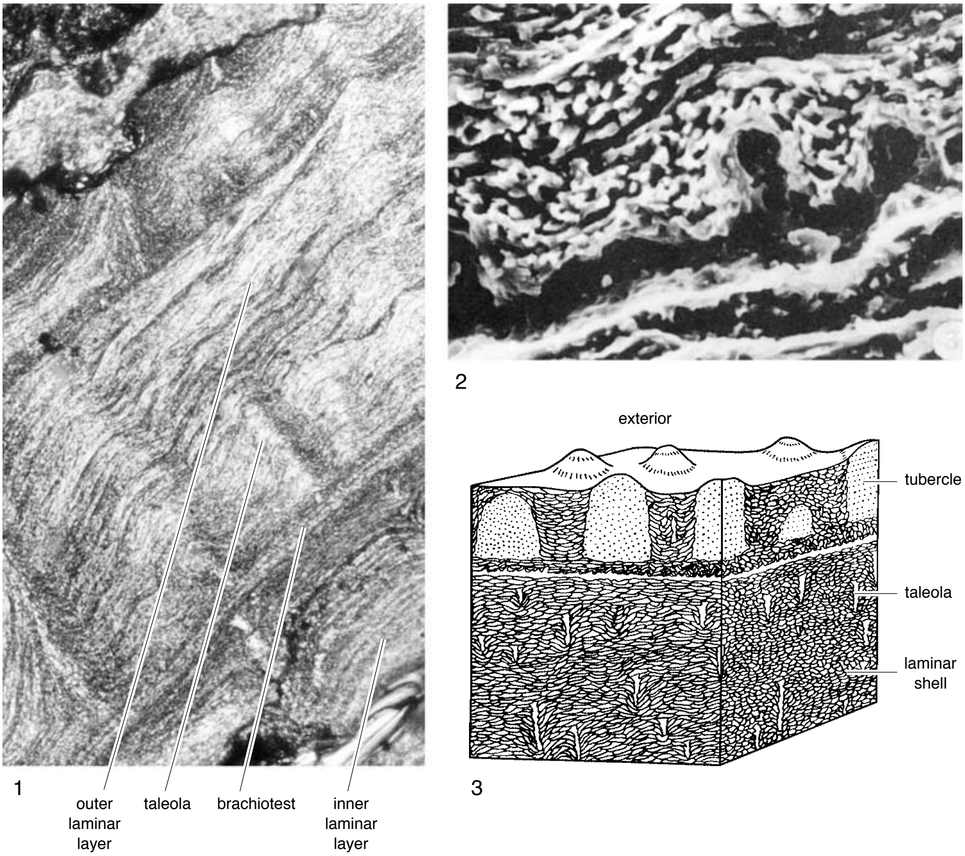

FIG. 446. *1,* Cellulose acetate peel of etched, resin-mounted section of dorsal valve of *Oldhamina decipiens* (DE KONINCK), Permian, Salt Range, Pakistan, showing brachiotest separating outer and inner laminar layers with taleolae, ×100 (new); *2,* SEM of section showing crenulated surfaces delineating interperiostracal gap (see FIG. 451) within ventral valve of *Dicystoconcha lapparenti* TERMIER & others, ×2300, Lower Permian, China; *3,* block diagram illustrating shell structure of permianellid (Wang & Jin, 1991).

plate with a median incision. Assuming the lophophore to have arisen from the mantle infold just within the edge of such a plate, it would have resembled the schizolophe; and with the development of lateral lobes to the internal plate, the feeding apparatus would have been transformed into a ptycholophe (Fig. 447).

The assumption that lyttonioid shells are virtually univalves in skeletal structure is by no means universally accepted. STEHLI (1956), for example, preferred to ascribe the anomalous distribution of primary shell to a physiological malfunction in an otherwise normally growing valve. The mantle lobes that are ultimately responsible for the growth of the shell are, however, differentiated from the same rudimentary mantle ring in living larvae; and, if this were also true for lyttonioid brachiopods, a fundamental difference in the shell structure of normally growing valves could hardly have arisen. Others, like G. A. COOPER (COOPER & GRANT, 1974, p. 384), have also continued to use dorsal or brachial valve for the entire dorsal structure purely on morphological grounds. The false interarea, although reminiscent of an obsolescent interarea and chilidium, however, is not homologous with them because growth was in an anterodorsal

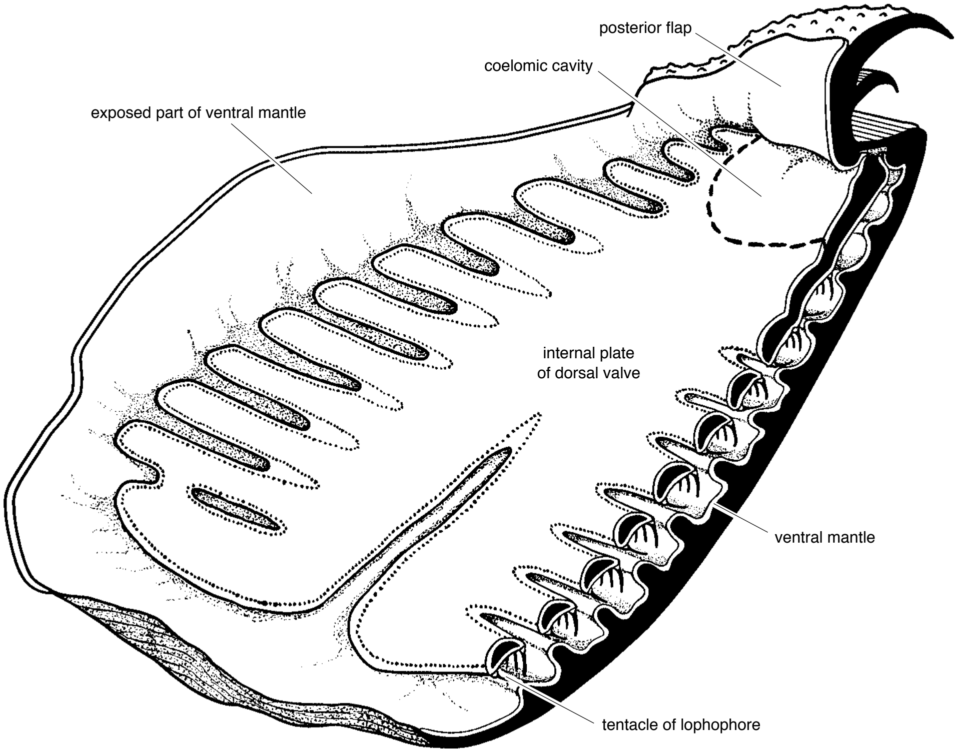

FIG. 447. Submedian view of *Eolyttonia* sp., Permian, Texas, reconstructed to show relationship between mantle lobes and shell (*solid black*) (Williams, 1953).

direction away from the cardinal process in a manner suggesting that expansion was controlled by a mantle edge coincident with the base of the triangle (WILLIAMS, 1953c).

The external and internal surfaces of the dorsal valve of permianellids are also tuberculate in a manner indicating that the valve is structurally homologous with that of lyttonioids and is likewise interpreted as an internal plate.

The morphology of the posterior part of the lyttonioid ventral valve is, in some respects, as anomalous as the structure of the dorsal valve. There is no interarea, but the posterior part of the ventral valve is extended anterodorsally as a flap (posterior flap) to overlie the dorsal valve, which is accommodated by a triangular impression (Fig. 448). This impression is also ornamented by growth lines parallel with the base and probably represents a zone of the posterior flap where secondary shell deposition was inhibited by the pressure of the heavily rutted periostracal cover to the dorsal valve. The flap is almost invariably sharply reflexed (reflexed zone) just anterior of the base of the impression and its attitude and shape can vary considerably. Specimens attached to a regular surface possess a flap that resembles a pair of ears extending laterally from the median reflexed area; in those that lay free on the sea floor throughout most of their lives the flap is greatly extroverted, so that the distal edge is usually in contact with the external surface of the ventral valve (Fig. 449); in those attached to irregular surfaces or crinoid stems the flap is closely adherent and molded to the substrate (Fig. 448); and, in at least two distinct stocks, *Keyserlingina* and *Pirgulia,* the flap grew forward with the rest of the ventral valve to form a deep cone (Fig. 450).

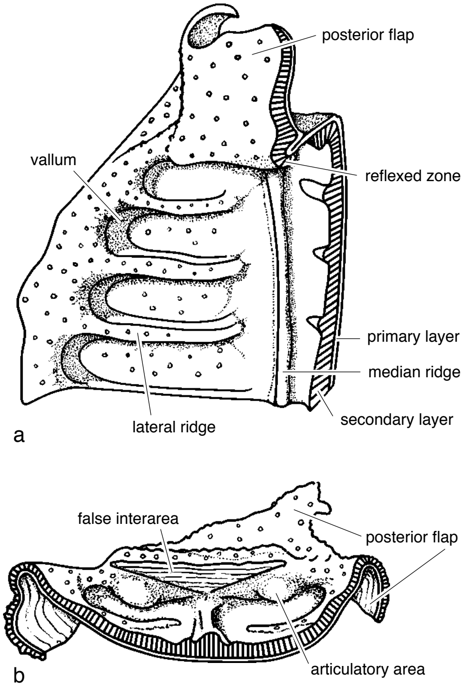

FIG. 448. Apical part of ventral valve of *Eolyttonia* sp., Permian, Texas, showing main morphological and structure features in *a,* submedian and *b,* anterior views (Williams, 1953).

Subsequent to the settling of spats, presumably by cementation of the apex of the ventral valve, the posterior flap assisted in fixation, as is well seen in lyttonioids attached to crinoid stems. It is envisaged as having been deposited by a posterior extension of the outer mantle lobe, capable of a rapid deposition of periostracum containing adhesive polymers and a thin film of shell. Evidently secretion by an extensible flap of the outer mantle lobe could be quickly terminated and the lobe then retracted along a rapidly exuded membrane in the manner of living species (WILLIAMS, 1971). Such retractions in quick succession would account for posterior flaps composed of paper-thin layers of shell consisting of both primary and secondary calcite that were commonly plastered one on top of another (Fig. 449).

The morphology of the permianellid ventral valve is not yet well known, but an everted posterior flap that assisted in attachment but without a strongly developed reflexed zone appears to have been characteristic of this group. The shell structure, however, appears to be identical with that of the dorsal valve. In effect the exteriors of both valves of permianellids are tuberculate and the entire shell has been interpreted as consisting of an outer tuberculate and an inner pseudopunctate zone with constituent tubercles and taleolae emerging at the external and internal surfaces respectively (WANG & JIN, 1991, p. 488) (Fig. 446.3). The tubercles are deeply embedded in laminar shell, which is disposed around them in the same way as laminae are around taleolae. The tubercles and taleolae appear to differ only in size and characterize two layers of laminar shell that were secreted by epithelial sheets facing each other. Yet the valve need not have been secreted within an epithelial fold in the manner inferred for the internal plate of the dorsal valve. WANG and JIN (1991, pl. III, fig. 1, 3) have illustrated the boundary between the outer and inner pseudopunctate layers as a space about 3 µm wide, bounded by crenulated surfaces. The crenulations appear to be sections of concentric, rounded folds with a wavelength of about 4 µm; and the surfaces bearing them are believed to have been the sites of the ventral periostracum (Fig. 446.2). On this assumption, the outer pseudopunctate tuberculate layer is homologous with the posterior flap of lyttonioids, folded back to become closely adherent to the exterior of the inner pseudopunctate layer representing the ventral valve in the othodox sense (Fig. 451).

Apart from the cardinal process, which, although highly variable, is essentially bilobed in the strophomenid fashion, lyttonioid internal features also show noteworthy departures from arrangements typical of other articulated brachiopods. The ventral valve has no teeth, but a pair of striated, convex surfaces (dental areas of WATSON, 1917) occur in the apical region; and these articulate with a pair of similarly striated, oval concave surfaces (sockets) lying anterolaterally to the cardinal process lobes and extending down to the first pair of lateral lobes in the dorsal valve. Cooper and Grant (1974, p. 390) disputed this interpretation. Instead they regarded the complementary grooves and ridges found in the hinge regions as having functioned as *dorsal* teeth and *ventral* sockets. In the absence of annotated illustrations, their description of this device is confusing. In any event, it is academic to attempt to interpret lyttoniidine articulation in terms of an orthodox tooth-and-socket arrangement except, however, for the permianelloid arrangement. According to Wang and Jin (1991, p. 485), a bilobed cardinal process in the dorsal valve is flanked by well-defined sockets that received convex dental areas developed in the ventral valve.

Cooper and Grant (1974, p. 386) noted that the "hinge generally is fairly uniform throughout the Lyttoniidae" (except for *Choanodus*), and the generic descriptions given here are based on the assumption that there is a significant difference between the articulatory devices of lyttonioids and permianelloids.

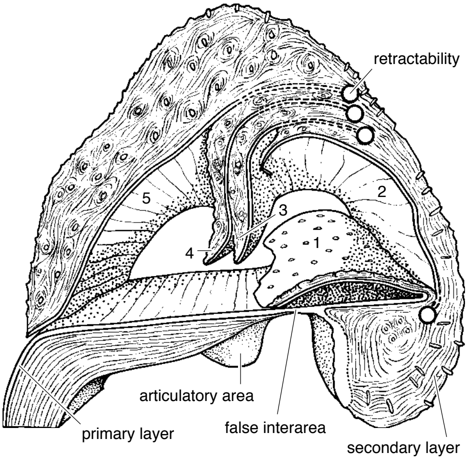

Fig. 449. Submedian portion of posterior flap of *Oldhamina decipiens* (de Koninck), Salt Range, Pakistan; numbers *1* to *5* denote successive layers of shell deposited by posterior flap; *circles* represent locations of minimum retractability of mantle flap necessary for deposition of each succeeding layer (Williams, 1953).

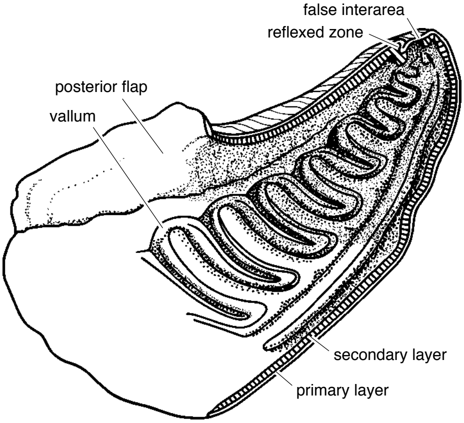

Fig. 450. Submedian view of interior of ventral valve of *Pirgulia* sp., Permian, Texas (Williams, 1953).

Muscle scars are preserved only sporadically throughout the entire suborder but include a pair of variably defined dorsal adductor scars on either side of the median ridge. The ventral impressions, on the other hand, can be asymmetrical in the lyttonioids, and the disposition of the ventral scars is indicative of two important groups (Stehli, 1956; Williams, 1965f; Cooper & Grant, 1974). In the first group (e.g., *Coscinophora*), a pair of large elongate adductor scars located submedianly are flanked by a pair of smaller, elongate diductors; this symmetrical field is commonly associated with median and submedian ridges. In the second group, which includes such forms as *Poikilosakos,* the right diductor is always larger than the left and is contained within an elongately semiconical sheath, while the adductor scars are obscure or represented by inconspicuous asymmetrical hollows located posteromedianly. This asymmetry is reflected in the uneven growth of the lobes of the cardinal process; that of *Poikilosakos,* for example, is unequally developed with the right lobe usually being the larger. Such asymmetry of scars may have been linked to a degeneracy of the muscle system. In any event, the dorsal valve was commonly so confined by the lateral walls of the ventral valve that it could not have slewed in the plane of articulation as believed by

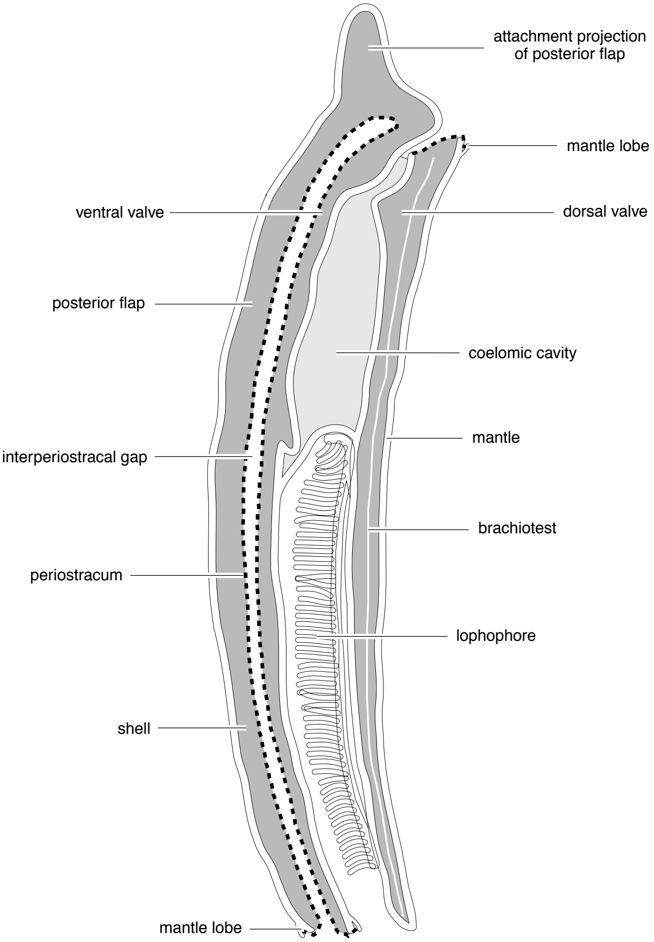

FIG. 451. Stylized submedian section of young permianellid shell showing inferred distribution of integument and soft parts *in vivo* (new).

WATSON (1917). Furthermore, the close proximity of the cardinal process lobes to the floor of the ventral valve and the physical constraint of the posterior flap immediately dorsal of the dorsal valve precludes any considerable movement normal to the plane of articulation (WILLIAMS, 1953c; RUDWICK & COWEN, 1968).

The permianelloid muscle system seems always to have been symmetrical (HE & ZHU, 1979; WANG & JIN, 1991), with the ventral scars impressed on and laterally to a narrow, hollow median platform.

In the earliest lyttonioid, *Poikilosakos,* a low bounding ridge lying well within the margin of the ventral valve completely surrounds the median area of the interior. The ridge was termed a flange by WATSON (1917) but was later renamed a vallum by COOPER and GRANT (1974, p. 385). There is little point to changing a well-established term in this way, although an additional term, like vallum, can serve a useful purpose. It is important, especially with regard to the permianelloids, to distinguish between the ridge and the marginal shell beyond; and it is here proposed to restrict the use of vallum for the ridge and flange for shell beyond.

During lyttonioid ontogeny and phylogeny, the vallum became increasingly looped

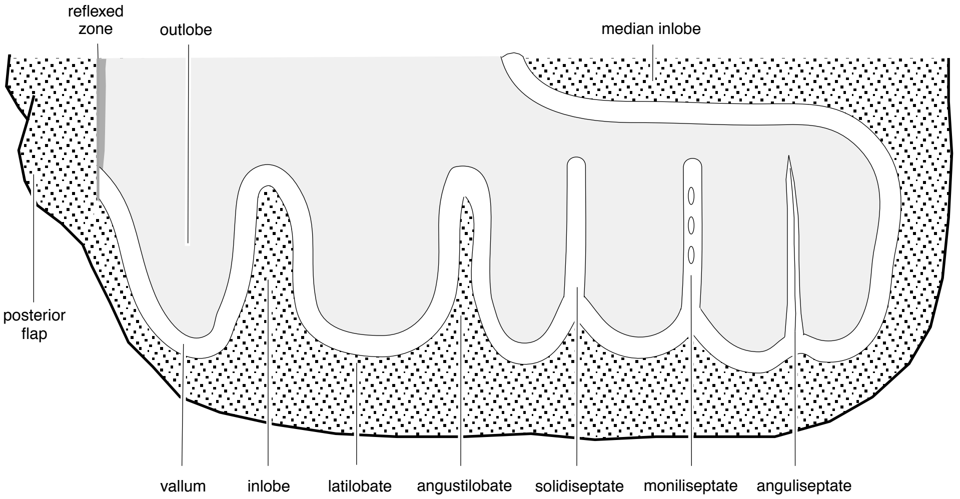

FIG. 452. Terminology used by COOPER and GRANT (1974, p. 385) to describe various stages in the compression of loops of vallum in ventral interior of lyttonioids (new).

with a complementary increase in the lobation of the dorsal valve. COOPER and GRANT (1974, p. 385) devised a complicated terminology to identify prescribed stages in the progressive compression of the loops of the vallum and their transformation into ridges and septa. Some of these terms are illustrated in Figure 452 but have not been used in any systematic way in the following descriptions of genera.

In young lyttonioid shells, the vallum was roughly subcircular in outline and was indented to form a median loop only; but during further growth involving resorption the vallum increased in size and became disposed as a small number of lateral loops in addition to the median one. Each loop was sufficiently open to include medianly a narrow strip of the valve floor bounded by an indented segment of the vallum (latilobate condition). The internal plate of the dorsal valve corresponded in outline to the disposition of the bounding ridge so that it was lobate and lay so close to the ventral valve that each lobe was seemingly isolated distally from its neighbor by a loop of the bounding vallum.

In later Lyttonioidea (e.g., *Keyserlingina, Paralyttonia*), the loops began to close by an increase in the size of adjacent segments of the vallum and their encroachment onto the intervening median strip of the valve floor (angustilobate condition) until, in extreme forms like *Oldhamina* and *Leptodus,* the ridge boundaries of each loop were completely united into one solid septal structure (solidiseptate condition) that may even develop a series of small crests (moniliseptate condition). In this manner the looped vallum of the earlier and more generalized Lyttonioidea was transformed into solid septa, the dorsal surfaces of which may be concave, bluntly convex, or sharp; and a pair of notches extending the length of the septa commonly developed to accommodate the edges of lobes to the internal plate.

Other modifications associated with evolution of the septal apparatus included an increase in the number of septa disposed symmetrically or asymmetrically about the median line, the progressive closure of the median incision of the dorsal valve, and the partial fusion of the lateral lobes by the growth of dissepiments.

The identification of the flange and vallum in the permianelloids is provisional. The valve margins of the permianelloid shell are more nearly coincident than those of the lyttonioids. But WANG and JIN (1991)

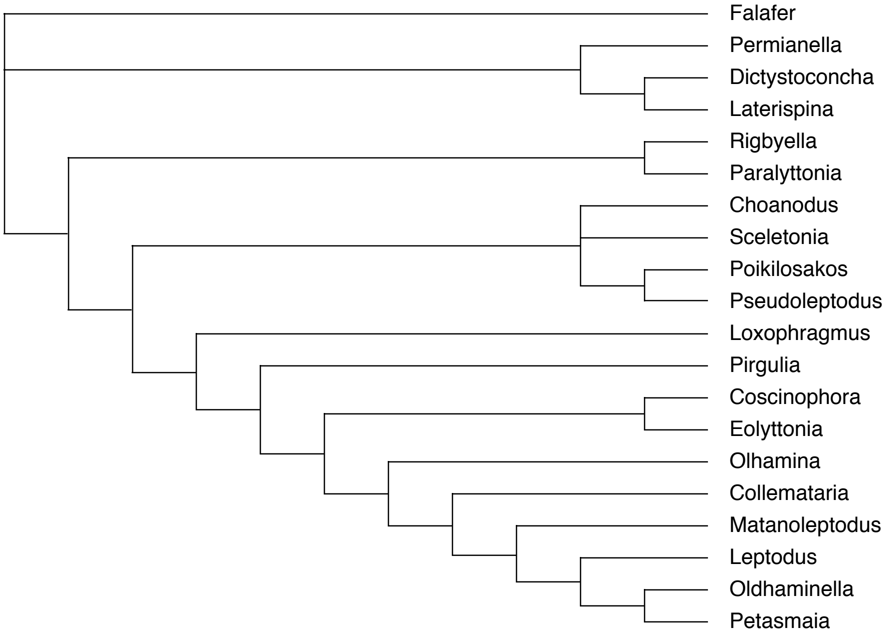

FIG. 453. Cladogram showing strict majority consensus of 39 trees derived by heuristic (stepwise random addition of taxa in 10 replicates) search of matrix composed of 20 genera, named in cladogram, and 30 characters, listed in Table 16 (new).

illustrate in diagrams and photographs a circumferential ridge in the permianellid ventral valve that has been identified as a vallum and a narrow surrounding flange that is extended as lateral spines in *Laterispina.* In this interpretation, the permianelloids and lyttonioids could have shared an ancestor with a distinctive bilobate shell.

The classification of the Lyttoniidina is still in a state of improvisation. All the lyttonioid genera described below are clearly related to one another but display degrees of morphological differences that normally call for some kind of convenient familial grouping. Thus, two families have long been recognized, the Poikilosakidae and the Oldhaminidae, based upon the symmetry of lobation (WILLIAMS, 1953c) or changes in the symmetry of the ventral muscle scars (STEHLI, 1956; COOPER & GRANT, 1974).

The permianelloids were initially recognized as a new order (HE & ZHU, 1979) but were subsequently reduced to familial rank (WANG & JIN, 1991) once their affinities with the lyttonioids had been established. Nonetheless, the permianelloids are quite distinctive and may yet be shown to be related to such aberrant genera as *Loczyella* and *Litocothia.* The phylogeny of the lyttonioids and permianelloids has been analyzed (SWOFFORD & BEGLE, 1993). The analysis, which excluded genera inadequately diagnosed or of doubtful affinities, was based on the characters defined in Table 16 and used the strophalosioid *Falafer* as an outgroup. The resultant majority consensus cladogram (Fig. 453) and the derived genealogy (Fig. 454) show that the lyttonioids consist of a group (the Rigbyellidae) with dorsal lobes parallel to the median plane of the valve rooted to a clade (the Lyttoniidae) that is composed of genera with laterally or radially disposed lobes, the Poikilosakinae and Lyttoniinae respectively. It also shows that *Falafer* and the permianelloids form a dichotomous stem group to the lyttonioids. When all the morphological characteristics of the excluded genera are known, a new group-

Table 16. States of 30 characters used in phylogenetic analysis of 19 genera in suborder Lyttoniidina, with strophalosioid *Falafer* as sister group, as shown in Figure 453 (new).

SHELL STRUCTURE

1. primary layer: present in both valves (0); reduced in dorsal valve (1); reduced in both valves (2).

SHELL SHAPE

2. size: small (<10 mm) (0); medium (1); large (>50 mm) (2).
3. outline: conforming to substrate (0); subcircular (1); transversely oval (2); elongately oval (3); fan shaped (4).
4. ventral valve: flat (0); cup shaped (1); conical (2); scooplike (3); convex (4).
5. ventral sulcus: present (0); absent (1).
6. posterior flap: absent (0); present (1).
7. growth of flap: absent (0); everted (1); forming cowl (2); forming long hood (3); rolled posteriorly (4); forming ringlike clasp (5).
8. attachment: beak (0); beak and spines (1); beak and posterior flap (2); entire ventral valve (3).
9. spines: present (0); absent (1); along lateral margin (2).
10. rhizoid spines: present (0); absent (1).
11. valve margins: coincident (0); dorsal within ventral (1).

VENTRAL INTERIOR

12. vallum: absent (0); open lobes (1); compressed lobes (2).
13. compressed lobes: absent (0); as grooved ridges (1); as septa (2); as sharp septa (3).
14. septal inclination: not applicable (0); vertical (1); inclined anteriorly (2).
15. septal segmentation: not applicable (0); continuous (1); beaded (2).

DORSAL VALVE

16. outline: unindented (0); bilobate (1); multilobate (2).
17. multilobation: undeveloped (0); elongately bilobate (1); laterally lobate (2); radially lobate (3); parallel lobate (4); laterally lobate, becoming radially lobate anteriorly (5); lateral lobes convex anteriorly (6).
18. number of lateral lobes: undeveloped (0); <10 (1); >10 (2).
19. lobe structure: not applicable (0); open (1); contiguous (2); punctured (3).
20. median slit: not applicable (0); open (1); virtually closed (2); punctured (3); open deep (4).

MUSCULATURE

21. ventral muscle platform: present (0); absent (1); hollow (2).
22. ventral diductor scars: symmetrical (0); asymmetrical (1).
23. diductor ridges: not developed (0); as sheath (1); discrete (2); as thickened boss (3).

ARTICULATION AND CARDINALIA

24. (bilobed) cardinal process: absent (0); single lobed (1); asymmetric bilobed (2); bilobed (3); quadrilobed (4).
25. articulatory processes: teeth and sockets (0); lyttonioid type (1); no dorsal articulating process (2); dental areas and sockets (3).
26. ventral interarea: present (0); absent (1).
27. dorsal valve: present (0); vestigial (1).
28. septal crenulation: absent (0); present (1); no septa (2).
29. cardinal process: essentially bilobed (0); fused, v-shaped (1).
30. reflexed zone: absent or vestigial (0); present (1).

ing is likely to emerge without necessarily compromising the suprageneric taxonomic hierarchy based on the data presently available (Fig. 454).

A great deal of nomenclatorial confusion has also arisen through an unwarranted action of Waagen (1883). The first described genus of the group was named *Leptodus* by Kayser (1883) in the belief that the incomplete specimen he examined represented the remains of fish teeth. Shortly afterward, Waagen ascertained their true nature and, because the name *Leptodus* perpetuated a serious misidentification, suppressed it in favor of *Lyttonia* Waagen, the type species of which was subsequently designated by Hall and Clarke (1894a). In the same publication, Waagen erected another genus (*Oldhamina*) and a new subfamily, the Lyttoniinae. Since then most European paleontologists (Noetling, 1905; Wanner & Sieverts, 1935; Licharew, 1932; etc.) have used the familial name Lyttoniidae, whereas Schuchert (1913a), presumably in order to

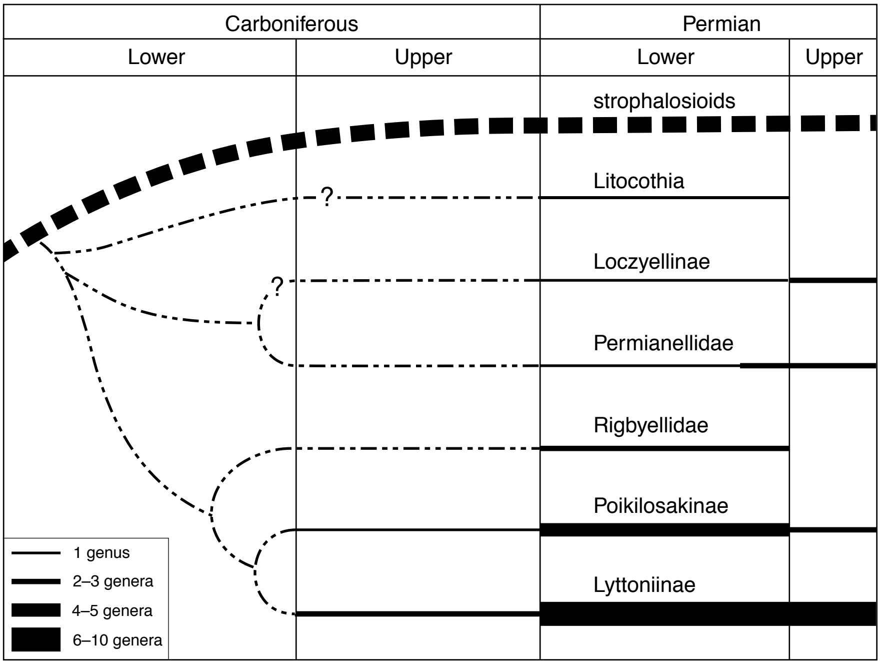

FIG. 454. Classification of Lyttoniidina, superimposed on an Upper Paleozoic chronostratigraphic chart, showing inferred relationship of taxa with one another and with assumed ancestral strophalosioid group represented by *Falafer* (new).

emphasize the invalid procedure adopted by WAAGEN, proposed Leptodinae as a suprageneric taxon in 1913, and (with LEVENE) established Oldhaminidae in 1929. In general, there is no doubt that the familial designation Lyttoniidae has been more widely used by paleontologists than either Oldhaminidae or Leptodinae (International Code of Zoological Nomenclature, STOLL & others, 1961, art. 40a) and was, therefore, adopted by WILLIAMS in 1965 (WILLIAMS, 1965f).

WILLIAMS (1953c, p. 286) had previously erected a new suborder for the group, the Oldhaminoidea, that was later corrected to Oldhaminidina (WILLIAMS, 1965f, p. 511). In effect, the superfamilial nomenclature of the Lyttoniidae remains confusingly hybrid. No rules of zoological nomenclature presently preclude the replacement of an ordinal (or subordinal) name by another deemed more suitable. In our opinion, it is now opportune to discard the name Oldhaminidina and replace it with Lyttoniidina, thereby bringing the suprageneric nomenclature of this group of brachiopods into a comprehensible progression through the taxonomic ranks.

Superfamily LYTTONIOIDEA Waagen, 1883

[*nom. transl.* LICHAREW in SARYTCHEVA, LICHAREW, & SOKOLSKAYA, 1960, p. 237, *ex* Lyttoniinae WAAGEN, 1883, p. 396]

Shape of shell irregular, exterior of ventral valve ornamented by growth lamellae and disturbances, that of dorsal valve by fine tubercles; posterior flap variably disposed but forming a narrow reflexed zone immediately dorsal of hinge of dorsal valve; ventral interior with circumferential ridge (vallum), intramarginal to wide flange, vallum initially disposed as open loops becoming compressed into septa, surrounding and interdigitating with lobate dorsal valve; lightly impressed muscle scars not supported by platforms; cardinal process essentially bilobed but commonly deformed. *?Lower Carboniferous, Upper Carboniferous–Upper Permian.*

Family LYTTONIIDAE Waagen, 1883

[*nom. transl.* NOETLING, 1905, p. 129, *ex* Lyttoniinae WAAGEN, 1883, p. 396] [=Oldhaminidae SCHUCHERT & LEVENE, 1929, p. 18]

Lobation of ventral vallum and dorsal valve consisting of median indentation with variable number of lobes (and septa) on either side, directed laterally or anterolaterally; ventral muscle field including large, submedian adductor scars flanked by pair of variably developed, smaller diductor impressions. *?Lower Carboniferous, Upper Carboniferous–Upper Permian.*

Subfamily LYTTONIINAE Waagen, 1883

[Lyttoniinae WAAGEN, 1883, p. 396] [=Leptodinae SCHUCHERT, 1913a, p. 387]

Commonly large lyttoniids with vallum of ventral valve compressed into more or less symmetrically arranged lateral, arcuate septa, inclined anteriorly with crenulated posterior sides; when present ventral diductor muscle scars and variably developed cardinal process symmetrical. *?Lower Carboniferous, Upper Carboniferous–Upper Permian.*

Leptodus KAYSER, 1883, p. 161 [**L. richthofeni;* OD] [=*Lyttonia* WAAGEN, 1883, p. 396 (type, *L. nobilis*); *Gubleria* TERMIER & TERMIER, 1960, p. 241 (type, *G. disjuncta*); *Spinolyttonia* SARYTCHEVA, 1964, p. 69 (type, *S. arakeljani*); *Lyttonia (Digitia)* DE GREGORIO, 1930, p. 32 (type, *L. (I.) princeps* var. *glomerata*); *Lyttonia (Irma)* DE GREGORIO, 1930, p. 32 (type, *L. (I.) bilobata*); *Lyttonia (Vincia)* DE GREGORIO, 1930, p. 31 (type, *L. (V.) asymmetrica*); ?*Lyttonia (Prisca)* DE GREGORIO, 1930, p. 31 (type, ?*L. (P.) fasciculata*); *Juxoldhamina* LIANG, 1990, p. 470 (type *L. imparilisa;* OD); *Semigublerina* LIANG, 1990, p. 469 (type *S. flabelata;* OD)]. Ventral valve scoop shaped, normally transversely oval, attached by beak and everted posterior flap; septa in ventral interior arcuate, normally sharp, tending to vertical disposition; muscle scars large, bounded laterally by high, medianly concave ridges; dorsal adductor scars elongate and impressed well anterior of hinge region; bilobed cardinal process elongate narrow. [The poor preservation of the type material of *L. richthofeni* and the almost simultaneous publication in 1883 of *Leptodus* and *Lyttonia* by KAYSER and WAAGEN respectively for congeneric species have played no small part in the subsequent proliferation of subjective synonyms. The genera and subgenera erected by DE GREGORIO, however, are poorly founded and inadequately described by any standard. Indeed, COOPER and GRANT (1974, p. 410) asserted that *Irma* and *Imperia* are algal forms. The subjective synonymy of *Spinolyttonia,* on the other hand, has been prompted by the rejection of COOPER and GRANT (1974, p. 387) of the family Spinolyttoniidae, erected by WILLIAMS (1965f, p. 521) for a lyttoniid with posterolateral spines. At the time, COOPER and GRANT, having never seen spinose oldhaminidines in the vast collections of mainly American material at their disposal, suggested that the Russian specimen had been misinterpreted. Subsequently the types of *Spinolyttonia arakeliani* SARYTCHEVA were examined at the Palaeontological Institute in Moscow by R. E. GRANT, who did not see any spines on the specimens (reported in correspondence 10 May, 1991). *Juxoldhamina* is intended for shells as in *Leptodus* with sharp septa as in *Oldhamina.* In view of the changes that ventral septa undergo during shell growth, we consider that the genus is not secure. In a like vein, the distinguishing feature of *Semigublerina,* sporadic culminations along the crest of the median septum, can occur in *Leptodus.*] *Permian:* Eurasia, USA (Texas), Australia.——FIG. 455,*3a,b.* **L. richthofeni,* Upper Permian, Lo-Ping, China; *a,* ventral view of partly exfoliated ventral valve, ×1; *b,* tilted view of partly exfoliated ventral valve, ×2 (Cooper & Grant, 1974).——FIG. 455,*3c,d. L. nobilis* WAAGEN, Upper Permian, Pakistan; *c,* ventral valve with attachment flap, ×1; *d,* partly conjoined valves attached to species of *Enteletes,* ×1 (Grant, 1976).

Cardinocrania WAAGEN, 1885, p. 745 [**C. indica;* OD] [=?*Pseudokeyserlingina* FREDERICKS, 1916, p. 64, hypothetical genus (FREDERICKS established a number of genera related to stages in the phylogeny of the group that had not actually been discovered as fossils.)]. Small subcircular ventral valve with raised, medianly indented anterior margin and everted posterior flap; raised submedian muscle scars developed posteriorly; dorsal valve unknown. [The validity of this genus is in dispute and cannot be confirmed until more topotypic material, including dorsal valves, has been collected. The *Cardinocrania* figured by WANNER and SIEVERTS (1935, pl. 6, fig. 1–2), which has an asymmetrical ventral muscle scar, has been identified as young *Pseudoleptodus* by COOPER and GRANT (1974, p. 410), who believed that the type ventral valves of *Cardinocrania* are young specimens of *Leptodus*]. *Permian:* Pakistan, Timor.

Collemataria COOPER & GRANT, 1974, p. 433 [**C. elongata;* OD]. Similar to *Leptodus* but normally subtriangular in outline with transverse, regularly arranged septa in ventral valve and more open lobes in dorsal valve; dorsal hinge region without articulatory processes, bilobed cardinal process with four myophore surfaces. *Permian:* USA (Texas), Venezuela, China.——FIG. 456,*1a–e.* **C. elongata,* Upper Permian, Word Formation, Texas; *a–c,* dorsal, lateral, ventral views of conjoined valves, ×1; *d,* dorsal view of partly conjoined valves, ×1; *e,*

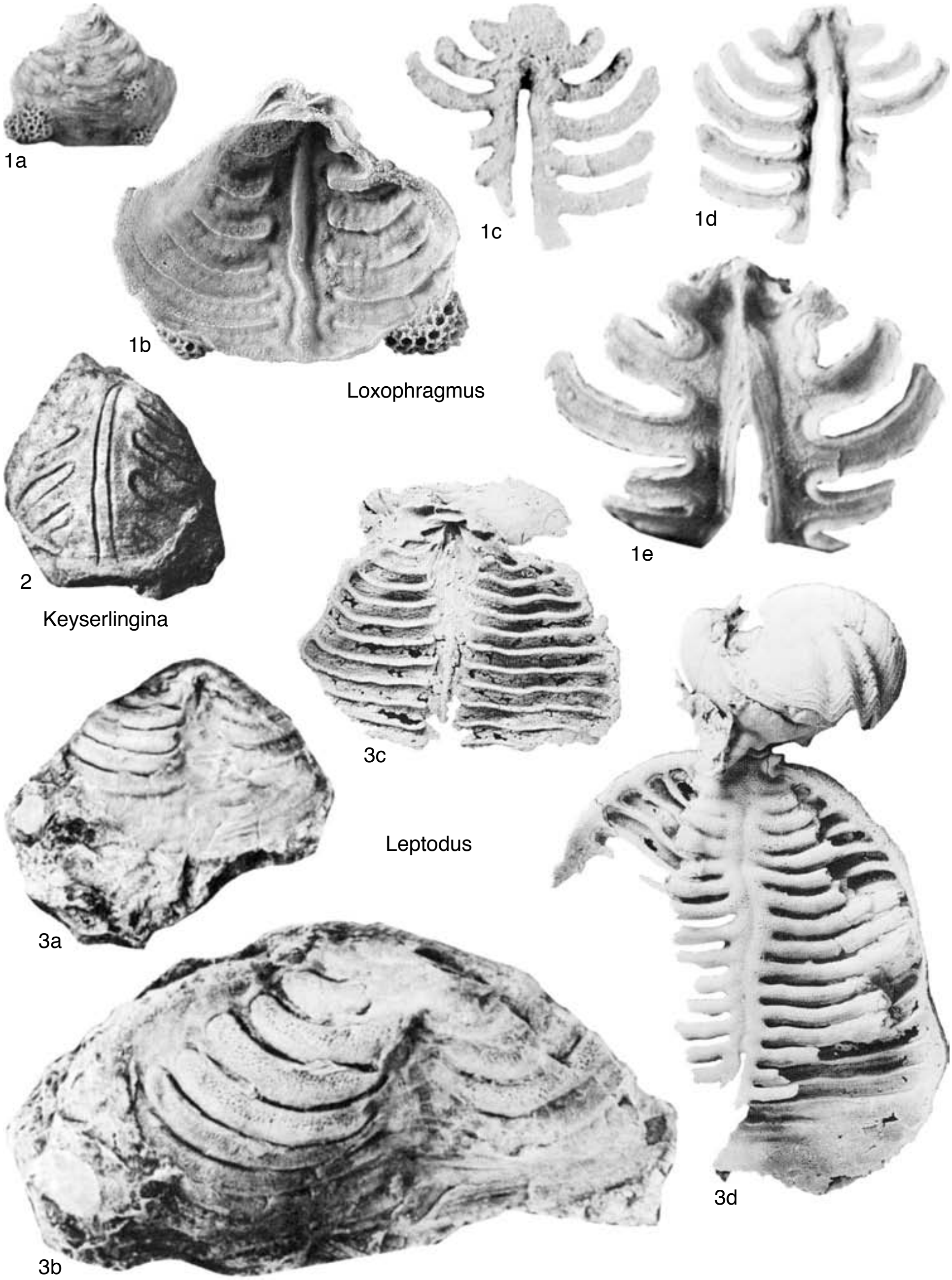

FIG. 455. Lyttoniidae (p. 631–634).

enlargement of posterior half of dorsal interior, ×3 (Cooper & Grant, 1974).

Coscinophora COOPER & STEHLI, 1955, p. 469 [**C. nodosa;* OD]. Similar to *Leptodus* but with numerous septa in ventral valve broken into discrete beads, more or less symmetrically disposed but commonly becoming radially aligned anteriorly; lobes of dorsal valve united by dissepiments to define a series of

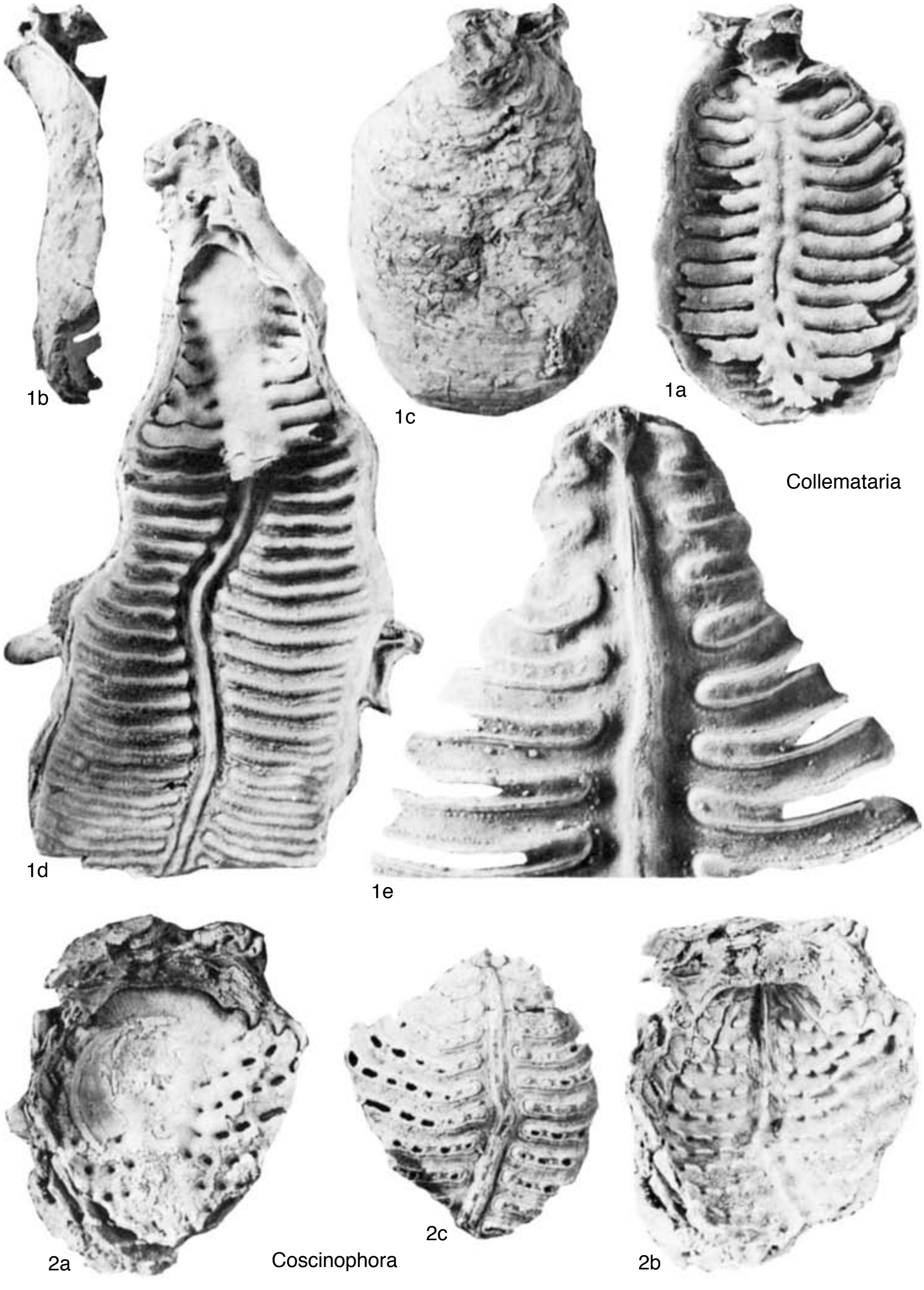

FIG. 456. Lyttoniidae (p. 631–633).

holes complementary to ventral beads. *Lower Permian:* USA (Texas).——FIG. 456,*2a–c.* **C. nodosa,* Lower Permian, Cathedral Mountain Formation, Texas; *a,* dorsal view of conjoined valves, ×1; *b,* ventral interior of same specimen, ×1; *c,* dorsal interior of same specimen, ×1 (Cooper & Grant, 1974).

Eolyttonia FREDERICKS, 1924, p. 25 [**Oldhamina (Lyttonia) mira* FREDERICKS, 1916, p. 74; OD] [=*Uralina* SCHUCHERT & LEVENE, 1929, p. 122 (type, *U. tastubaensis* LIKHAREV, 1925), *nom. nov. pro Uralia* LIKHAREV, 1925, p. 4, *non* MULSANT, VERREAUX, & VERREAUX, 1866; *Paraleptodus* LI & GU in LI, GU, & SU, 1980, p. 390 (type, *P. wuchangensis;* OD)]. Large with subconical ventral valve subcircular in outline, attached in part by everted posterior flap; numerous more or less symmetrically disposed lateral septa arcuate, thick with concave flat crests, median incision of dorsal valve slitlike and limited to anterior half; cardinal process having single shaft and bifid myophore. *Upper Carboniferous–Lower Permian:* Austria, Yugoslavia, *Upper Carboniferous;* northeastern China, Japan, Siberia, USA (Texas), Thailand, Timor, *Lower Permian.*——FIG. 457,*1a–c. E. chaotica* COOPER & GRANT, Upper Permian, Road Canyon Formation, Texas; *a,b,* dorsal exterior, interior of posterior part of same valve, ×1; *c,* enlargement of posterior part of same valve, ×3 (Cooper & Grant, 1974).——FIG. 457,*1d,e. E. circularis* COOPER & GRANT, Lower Permian, Cathedral Mountain Formation, Texas; interior, exterior of ventral valve, ×1 (Cooper & Grant, 1974).

Keyserlingina CHERNYSCHEV, 1902, p. 55 [**K. schellwieni;* OD] [=*Parakeyserlingina* FREDERICKS, 1916, p. 14 (type, *Keyserlingina darvasica* CHERNYSCHEV, 1914); *Chaoella* LIKHAREV, 1931, p. 161 (type, *C. caucasica*)]. Small, subconical by forward growth of posterior flap, attached broadly along posterior surface; vallum of ventral valve folded into narrow loops forming up to 7 pairs of lateral ridges and low median ridge split at anterior end; dorsal valve unknown. [This genus is poorly known by only a ventral valve. COOPER and GRANT (1974, p. 411) compared it with the poikilosakin *Pseudoleptodus* but, in the absence of any evidence of an asymmetrical ventral muscle field, left it among the lyttoniids as was done in the first edition of the Brachiopoda *Treatise* (WILLIAMS, 1965f, p. 518).] *?Lower Carboniferous, Upper Carboniferous–Lower Permian:* China (Guangdong, Guizhou), *?Lower Carboniferous;* Austria, *Upper Carboniferous;* China, ?Thailand, Russia (Urals, Caucasus), *Lower Permian.*——FIG. 455,*2. K. filicis* (KEYSERLING), Lower Permian, western Urals; internal mold of ventral valve, ×1 (Sarytcheva, Licharew, & Sokolskaya, 1960).

Loxophragmus COOPER & GRANT, 1974, p. 432 [**L. ellipticus;* OD] [=*Palaeoldhamina* LIANG in WANG & others, 1982, p. 230 (type, *P. kuzishanensis*)]. Subconical ventral valve with up to 10 or so pairs of crenulated, arcuate septa and deeply incised median slit; cardinal process slightly excentric. *Lower Permian:* USA, eastern China.——FIG. 455,*1a–e. *L. ellipticus,* Lower Permian, Cathedral Mountain Formation, Texas; *a,* exterior of ventral valve, ×1; *b,* interior of ventral valve, ×2; *c,d,* exterior, interior of dorsal valve, ×2; *e,* dorsal interior, ×4 (Cooper & Grant, 1974).

Matanoleptodus LIAO, 1983, p. 641 [**M. punctatus;* OD]. Ventral valve, suboval in outline, attached by much of external surface and everted posterior flap associated near its right anterior junction with valves, with few broken hollow spines; median septum strong, flanked by 5 or 6 pairs of arcuate, widely grooved lateral septa. [It is not clear from the illustrations whether the broken spines arise from the posterior flap. If they project inwardly from the *inner* surface of the posterior flap, they cannot be homologous with productide spines.] *Upper Permian:* China (Guangxi).——FIG. 457,*3a–c. *M. punctatus,* Upper Permian, Guangxi Province; *a,* ventral interior, ×2; *b,* enlargement of posterolateral part of ventral valve showing spine arrangement, ×5; *c,* ventral interior attached to bryozoan, ×1 (new).

Oldhamina WAAGEN, 1883, p. 403 [**Bellerophon decipiens* DE KONINCK, 1863, p. 8; OD] [=*Waagenopora* FRECH, 1902, p. 647 (type, *Oldhamina decipiens* DE KONINCK, 1863); *Oldhamella* NOETLING, 1905, p. 129 (type, *Bellerophon decipiens* DE KONINCK); *Oldhamia* VON ZITTEL, 1910, p. 280, *nom. null.*]. Ventral valve strongly convex, surface nearly smooth with fine growth banding; posterior flap recurved and rolled back in successive layers; internal septa medianly high, tapering laterally, sharp, inclined anteriorly, and strongly arcuate toward anterior to accommodate deep concavity of shell interior; dorsal valve with broad flattened hinge region and straight hinge line, cardinal process bilobed; median septum long, sharp, extending to anterior bifurcation of valve; lobes evenly spaced and more or less symmetrical, cambered with trailing edges anterior; external surface finely tuberculate. *Upper Permian:* Asia.——FIG. 458,*2a–c. *O. decipiens* (DE KONINCK), Upper Permian, Pakistan; *a,b,* posterior, dorsal views of dorsal valve, ×3; *c,* ventral interior, ×3 (Waagen, 1883).

Oldhaminella WANNER in WANNER & SIEVERTS, 1935, p. 232 [**O. philocrina;* OD]. Transversely oval ventral valve strongly convex with everted posterior flap; median septum extending almost to apex of valve, flanked by 3 or 4 pairs of arcuate lateral ridges formed by fusion of compressed loops, with anterior sides strongly developed as fine ridges; ventral muscle scars bounded by lateral ridges. [This genus is based on 2 ventral valves only. COOPER and GRANT (1974, p. 412) believed them to be immature *Leptodus.*] *Permian:* Timor.

Petasmaia COOPER & GRANT, 1969, p. 10 [**P. expansa;* OD]. Large, flat, subcircular ventral valve with numerous, symmetrically disposed, transverse or gently arcuate, sharp septa; strong bilobed cardinal process with 4 myophore surfaces. *Permian:* USA (Texas).——FIG. 458,*1a–d. *P. expansa,* Lower Permian, Cathedral Mountain Formation, Texas; *a,b,* exterior, interior of partly conjoined valves, ×0.66; *c,* dorsal interior, ×2; *d,* enlargement of posterior part of same valve, ×3 (Cooper & Grant, 1974).

Pirgulia COOPER & MUIR-WOOD, 1951, p. 195, *nom. nov. pro Pirgula* DE GREGORIO, 1930, *non Pirgula*

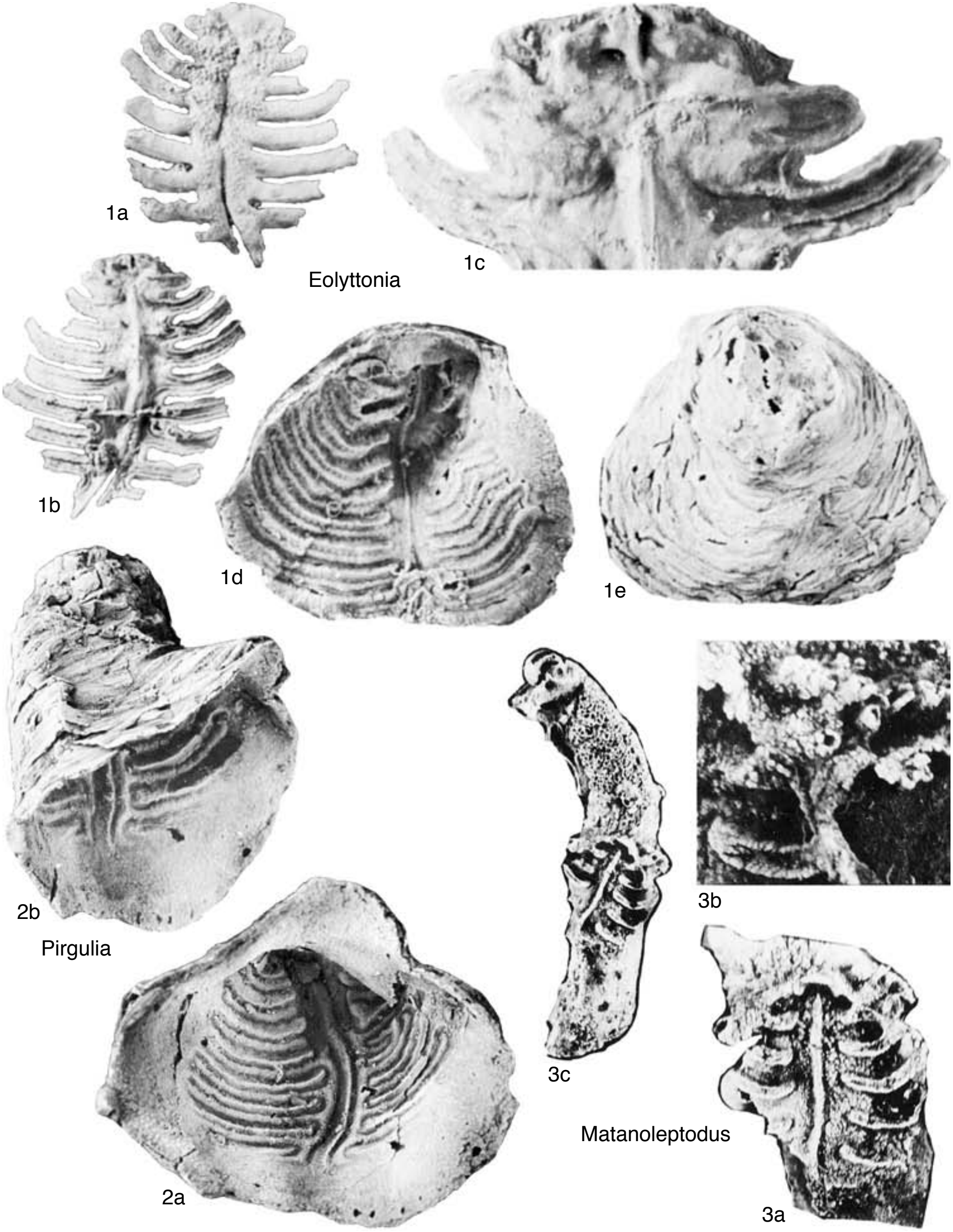

FIG. 457. Lyttoniidae (p. 634–635).

TESSMANN, 1921 [*?*Lyttonia (Pirgula) pediculata* DE GREGORIO, 1930, p. 30; OD]. Similar to *Leptodus* but with conical ventral valve attached apically and with blunt septa. *Permian:* Italy, USA (Texas).——FIG. 457,*2a,b. Pirgulia* sp., Lower Permian, Texas; dorsal, anterolateral views of ventral valve, ×1.5 (Williams, 1965f).

Subfamily POIKILOSAKINAE Williams, 1953

[*nom. transl.* WILLIAMS, HARPER, & GRANT, herein, *ex* family Poikilosakidae WILLIAMS, 1953c, p. 287]

Ventral diductor scar asymmetric with longer impression on right side; cardinal

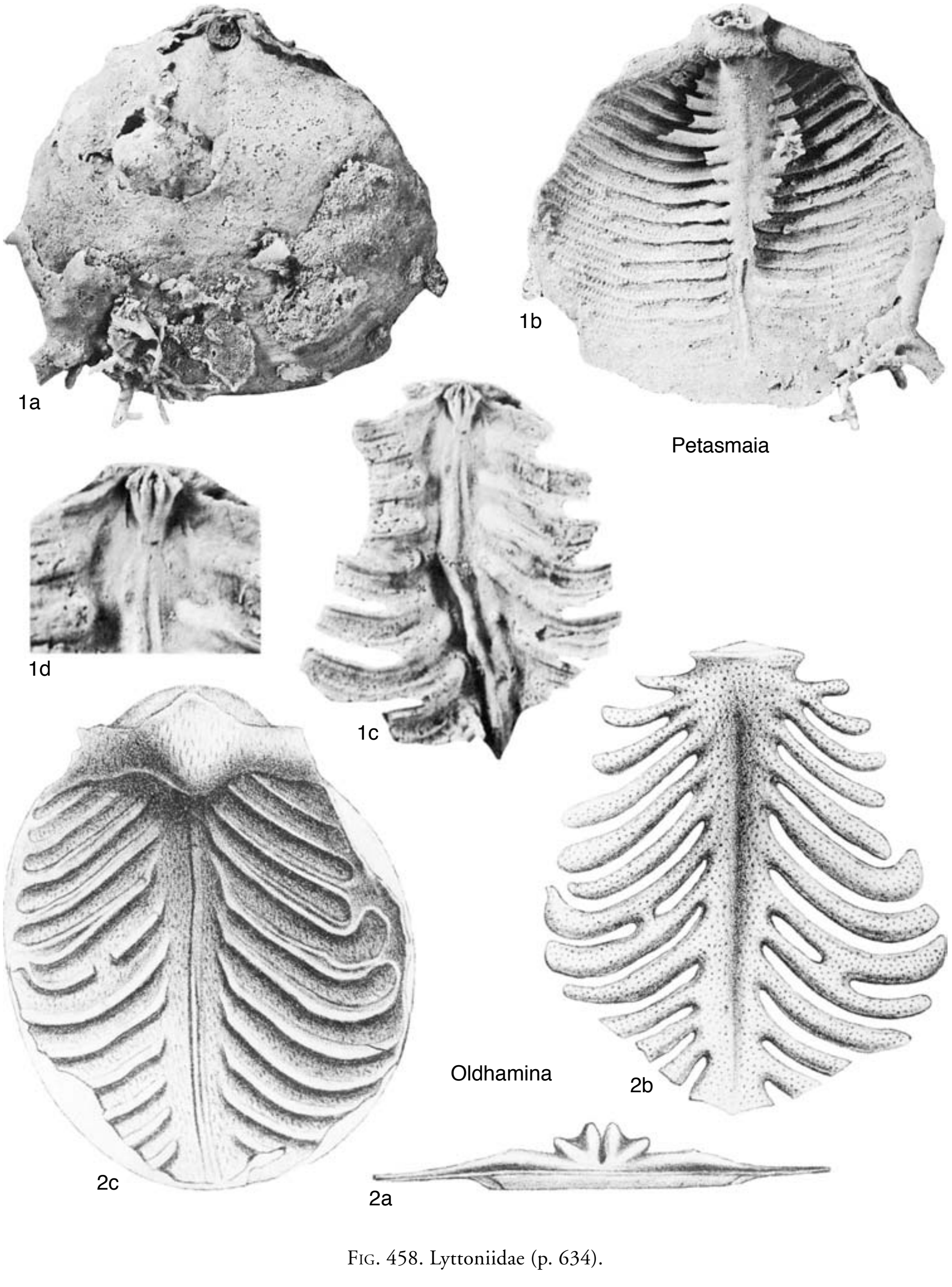

FIG. 458. Lyttoniidae (p. 634).

process deformed; dorsal valve deeply slit medianly. *Upper Carboniferous–Upper Permian.*

Poikilosakos WATSON, 1917, p. 212 [**P. petaloides;* OD] [=?*Prokeyserlingina* FREDERICKS, 1916, p. 64, hypothetical genus (FREDERICKS established a number of genera related to stages in the phylogeny of the group that had not actually been discovered as fossils.)]. Small, ventral valve attached by entire surface and everted posterior flap; vallum disposed in small number of lobes pointing anteriorly and laterally, irregular and distorted; ventral muscle marks asymmetric, with left diductor weak and divergent from midline, with right being stronger and

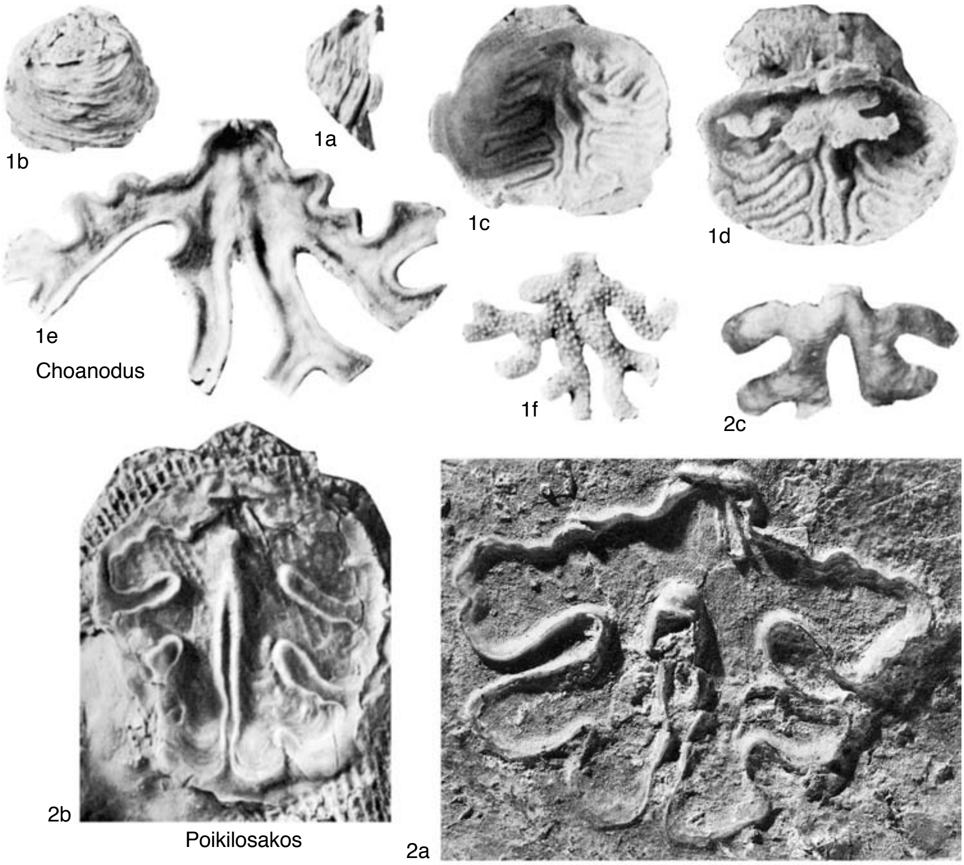

FIG. 459. Lyttoniidae (p. 636–637).

bounded by narrow sheath of shell. *Upper Carboniferous–middle Permian:* cosmopolitan, *Upper Carboniferous;* USA (Texas, New Mexico), *Lower Permian–middle Permian.*——FIG. 459,*2a–c*. **P. petaloides,* Upper Carboniferous; *a,* ventral interior, Graham Formation, Texas, ×3 (Williams, 1965f); *b,* elongate ventral interior, valve attached to fenestellid bryozoan colony, Graham Formation, Texas, ×2 (Cooper & Grant, 1974); *c,* dorsal exterior, Plattsmouth Limestone, Kansas, ×2 (Cooper & Grant, 1974).

Adriana DE GREGORIO, 1930, p. 32 [**A. osiensis;* OD] [=*Stita* DE GREGORIO, 1930, p. 32 (type, *Lyttonia (Stita) paupera;* OD)]. Ventral valve cone shaped; lobes and septa of ridge resembling vallum, on left side possibly single diductor scar. [The status of this genus, even as a brachiopod, has been challenged by RUDWICK and COWEN (1968, p. 153) and COOPER and GRANT (1974, p. 389), who were inclined to LIKHAREV's view (1964) that the vallum is an algal filament. More recently, however, the late R. E. GRANT tentatively identified an *Adriana*-like lyttonioid from the *Permian* of southern Thailand (1976, p. 161) and of Texas (written communication, May, 1991)]. *Permian:* Sicily, USA (?Texas), ?Thailand.

Choanodus COOPER & GRANT, 1974, p. 401 [**C. irregularis;* OD]. Subconical ventral valve with excessively wrinkled exterior, and internally with many, more or less paired, broad, lateral ridges; asymmetric bilobed cardinal process strongly developed. *Permian:* USA (Texas).——FIG. 459,*1a–f*. **C. irregularis,* Lower Permian, Cathedral Mountain Formation, Texas; *a,b,* lateral, ventral views of ventral exterior, ×1; *c,* interior of same valve, ×1.5; *d,* dorsal view of mature ventral valve with dorsal valve partly in place, ×2; *e,* interior dorsal valve, ×3; *f,* exterior of dorsal valve, ×2 (Cooper & Grant, 1974).

Pseudoleptodus STEHLI, 1956, p. 311 [**P. getawayensis;* OD]. Ventral valve subconical through forward growth of posterior flap, attached apically; lobes of vallum roughly symmetrical, compressed into 5 or more pairs of wide ridges; otherwise like *Poikilosakos. Lower Permian–Upper Permian:* USA, southern Thailand.——FIG. 460,*1a–e*. **P.*

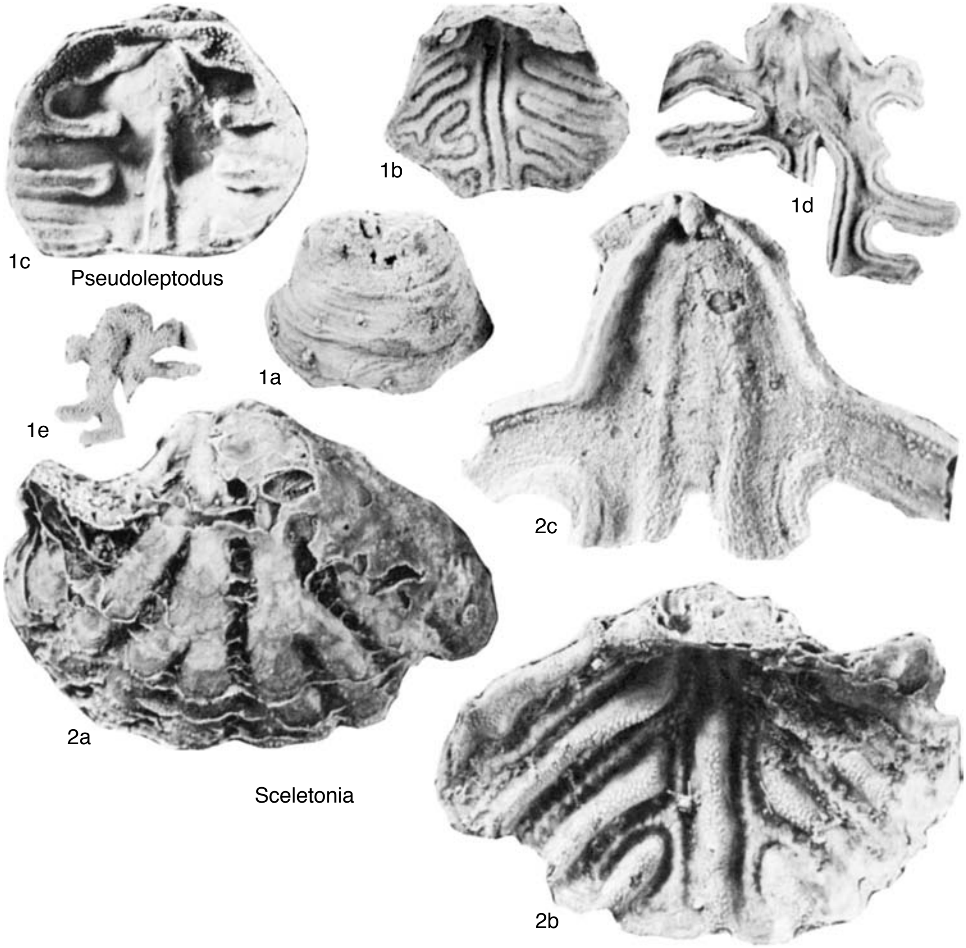

FIG. 460. Lyttoniidae (p. 637–638).

getawayensis, Lower Permian, Cherry Canyon Formation, Texas; *a,b,* external, internal views of ventral valve, ×1; *c,* ventral interior, ×2; *d,* interior of dorsal valve, ×2; *e,* exterior of dorsal valve, ×1 (Cooper & Grant, 1974).

Sceletonia COOPER & GRANT, 1974, p. 405 [**S. crassa;* OD]. Ventral valve cup shaped and deeply grooved externally corresponding to radially disposed, wide ridges internally; cardinal process asymmetrically bilobed. *Lower Permian:* USA (Texas), China (Guangxi Province).——FIG. 460,*2a–c.* **S. crassa,* Lower Permian, Skinner Ranch Formation, Texas; *a,b,* exterior and interior of ventral valve, ×2; *c,* dorsal interior, ×4 (Cooper & Grant, 1974).

Family RIGBYELLIDAE new family

[Rigbyellidae WILLIAMS, HARPER, & GRANT, herein]

Small, transversely oval shells, ventral valve cuplike with longer medioanterior sector (trail) arising more or less vertically from attachment area of beak and, to a lesser extent, from an everted posterior flap; up to 6 or 7 septa subparallel to median axis of shell with correspondingly disposed lobes of dorsal valve; ventral muscle scars symmetrical; cardinal process bilobed. *Lower Permian.*

Rigbyella STEHLI, 1956, p. 310 [**Paralyttonia girtyi* WANNER & SIEVERTS, 1935, p. 209; OD]. Ventral valve thick, margin scalloped and exterior coarsely costal in reflection of internal septa; septa normally uneven in number with median septum slightly higher than others, crests of septa rounded or sharp; ventral muscle scars small, impressed on low pad, bisected and bounded by low myophragms; dorsal valve lobate, smooth inside and outside except for weak growth bands. *Lower Permian:* USA (Texas), southern Thailand.——FIG. 461,*1a–d.* **R. girtyi,* Lower Permian, Bell Canyon Formation, Texas; *a–c,* ventral, lateral, dorsal views of ventral valve, ×3 (Cooper & Grant, 1974); *d,* dorsal view of partly conjoined valves, ×3 (Stehli, 1956).

Paralyttonia Wanner in Wanner & Sieverts, 1935, p. 207 [**P. permica;* OD]. Shell thin with conspicuous trail; ventral septa irregular in number and occasionally branching or bent, crests flat or concave; muscle scars large, distinctly impressed on pads; exterior of dorsal valve reported as smooth and finely tuberculate; cardinal process minute, dorsal adductor scars on low pads. *Lower Permian:* Austria, Japan, Thailand, Timor.——Fig. 461,*2a,b. P. tenax* Grant, Lower Permian, Thailand; *a,* interior of ventral valve attached to small linoproductidine, ×3; *b,* posterior view of ventral interior, ×3 (Grant, 1976).

Superfamily
PERMIANELLOIDEA
He & Zhu, 1979

[*nom. transl.* Williams, Harper, & Grant, herein, *ex* Permianellida He & Zhu, 1979, p. 136]

Concavoconvex, elongately bilobate, variably emarginate lyttoniidines with finely tuberculate exteriors; ventral valve attached to substrate mainly by hornlike projections of unreflexed, everted posterior flap; flange variably developed, marginal to low vallum; ventral interior with raised dental areas and well-defined median muscle platform; dorsal valve bounded by marginal ridge hinge line, narrow extending laterally as ears; dorsal interior with fused bilobed cardinal process ankylosed to divergent ridges defining sockets, adductor scars variably impressed on either side of median ridge corresponding to external sulcus; pair of low ridges also disposed medianly along valve lobes. *Permian.*

Family PERMIANELLIDAE
He & Zhu, 1979

[Permianellidae He & Zhu, 1979, p. 132]

Characters as for superfamily. *Permian.*

Permianella He & Zhu, 1979, p. 137 [**P. typica;* OD]. Gently concavoconvex, with a deep median incision in emarginate margin separating 2 elongate, subparallel lobes of shell; ventral flange developed as narrow fringe. *Upper Permian:* southern China.——Fig. 462,*1a–c.* **P. typica,* Upper Permian, southern China; *a,* internal mold of dorsal valve with adherent shell, ×2.75; *b,* external mold of dorsal valve, ×2.75; *c,* ventral valve, ×1.5 (He & Zhu, 1979).

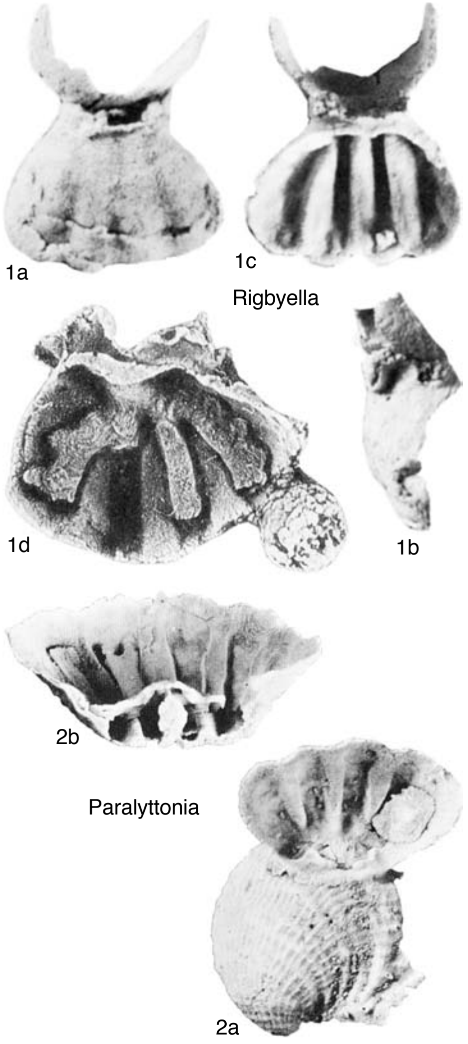

Fig. 461. Rigbyellidae (p. 638–639).

Dicystoconcha Termier & Termier in Termier & others, 1974, p. 122 [**D. lapparenti;* OD] [=*Dipunctella* Liang in Wang & others, 1982, p. 228 (type, *D. stenosulcata*); *Guangjiayanella* Yang De-li, 1984, p. 212[333] (type, *G. guangjiayanensis*); *Guangdongina* Mou & Liu, 1989, p. 458 (type, *G. xiamaoensis*); *Paritisteges* Liang, 1990, p. 488 (type, *P. latesculcata*); *Fabulasteges* Liang, 1990, p. 489 (type, *F. planata;* OD)]. Small shells with only shallow indentation in anterior zone of emarginate margin and with negligible ventral flange. [The genus was founded on a poorly preserved dorsal valve and is better understood through the review of permianellids by Wang and Jin (1991), which is the source of illustrations featuring specimens identified as conspecific with the type species. The genera placed in synonymy were erected for shells with trivial variations in shape]. *Lower Permian:*

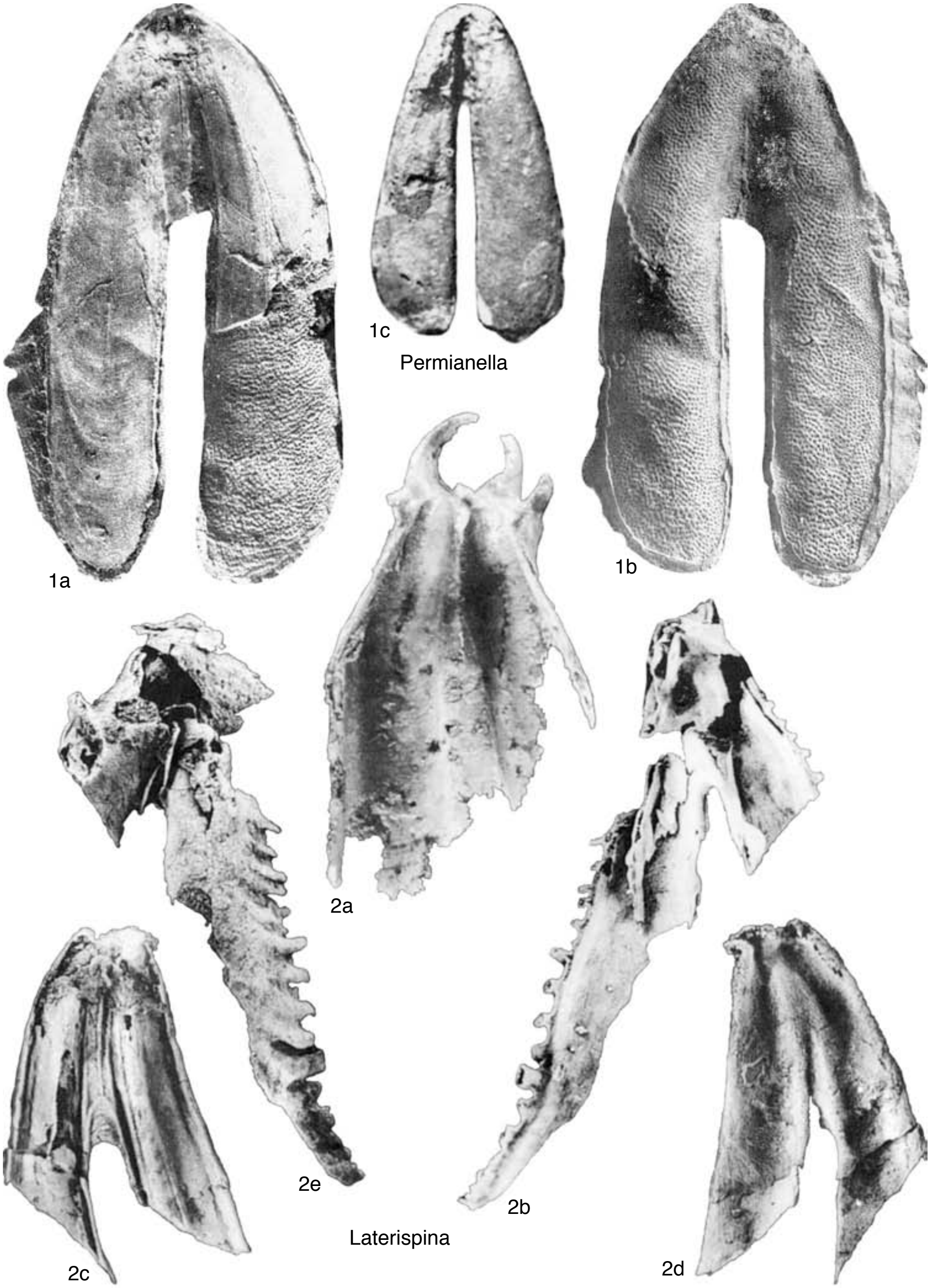

FIG. 462. Permianellidae (p. 639–641).

Afghanistan, southern China, Thailand.——FIG. 463,*3a,b.* **D. lapparenti,* Lower Permian, southern China; *a,* external mold of ventral valve, ×3; *b,* cluster ventral valves, ×2 (Wang & Jin, 1991).

Laterispina WANG & JIN, 1991, p. 496[500] [**L. liaoi;* OD]. Similar to *Permianella* but with more divergent lobes and with ventral flange prolonged laterally into spines. *Upper Permian:* southern China.

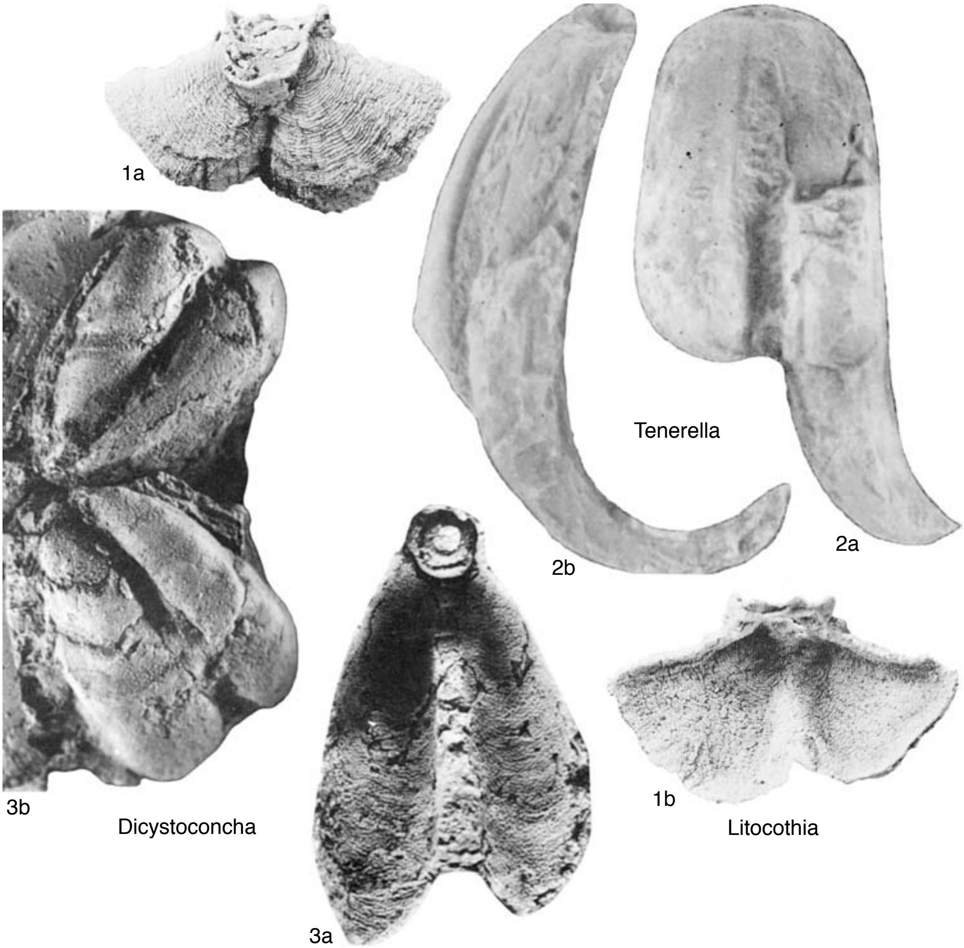

FIG. 463. Permianellidae and Uncertain (p. 639–642).

——FIG. 462,*2a–e.* **L. liaoi,* Upper Permian, southern China; *a,* ventral interior with attachment ring, ×3; *b,* ventral interior showing spines, ×1.5; *c,* dorsal interior, ×1.5; *d,* dorsal exterior, ×1.5; *e,* ventral exterior showing spines, ×1.5 (Wang & Jin, 1991).

Tenerella LIANG, 1990, p. 511 [**T. usualisa;* OD] [=*Obliqunsteges* LIANG, 1990, p. 511 (type, *O. distortus*); *Sicyusella* LIANG, 1990, p. 512 (type, *S. regularis*)]. Similar to *Permianella* but strongly concavoconvex and with curved, divergent lobes; nature of ventral flange unknown. [One of several generic names given to these concavoconvex shells has been provisionally accepted on the assumption that the ventral flange, which is neither described nor revealed in the illustration of the type species, is negligible as in *Dicystoconcha.* Two genera erected at the same time as *Tenerella* have been distinguished in minor changes in shell shape that are likely to reflect nothing more than specific variability.] *Middle Permian–Upper Permian:* southern China.——FIG. 463,*2a,b.* **T. usualisa,* Upper Permian, southern China; ventral, lateral views of ventral valve, ×2 (Liang, 1990).

Family UNCERTAIN

Subfamily LOCZYELLINAE Licharew, 1937

[Loczyellinae LICHAREW, 1937, p. 83]

Shells ornamented by growth lines, shovel shaped to triangular with rounded anterior margin and sides converging acutely to umbones; ventral valve gently convex, medianly sulcate with flanks almost at right angles to venter; dorsal valve correspondingly concave with low median fold; internal features unknown. [The uncertain taxonomic position of this group is opportunely discussed in the description of *Caninella* Liang.] *Permian.*

Loczyella Frech, 1901, p. 503 [**L. nankingensis;* OD]. Characters of the subfamily; no ears developed at hinge line of dorsal valve. *Permian:* China, Caucasus.

Caninella Liang, 1990, p. 216 [**C. zhinanensis;* OD]. Concavoconvex, uniplicate shells, trigonal in outline, anterior margin truncated, with small ears at narrow hinge line; ventral interior with pair of long lateral septa; dorsal interior with thin median septum and small cardinal process. [*Loczyella* and *Caninella* have been provisionally assigned to the same subfamily as they are evidently strophomenates, probably related to each other and possibly permianelloid in affinity. The genera, however, have been founded on poorly preserved specimens and study of better topotypic material may lead to changes in their taxonomic status.

The type material of *Loczyella* is so poorly preserved that descriptions of the genus have been based on the comments by Likharev (1930) on two specimens from the Permian of northern Caucasus, described as ?*Loczyella parvula* Likharev. Jin Yu-Gan (personal communication to R. E. Grant, 1991) has examined these specimens in the Institute of Geology, St. Petersburg, and identified them as permianellids as they are bilobate in outline and attached to a crinoid stem by the umbo. It remains to be seen whether topotypic *Loczyella* is congeneric with the specimens from Caucasus.

Caninella is not much better served, as it has been founded on three poorly preserved specimens, one of which, the holotype, is a subconical ventral valve with the umbo broken off and no dorsal valve attached. The relationship between *Caninella* and *Loczyella* is, therefore, not securely established nor is their taxonomic position within the Strophomenata.] *Upper Permian:* China (Zhejian).

Litocothia Grant, 1976, p. 166 [**L. cateora;* OD]. Small, transverse, bilobate ventral valve with deep, long median sulcus, ornamented by closely spaced fila, attached by beak; small everted posterior flap forming reflexed region dorsal of hinge; ventral interior featureless except for median raised zone corresponding to sulcus. [This ventral valve has a lyttonioid apical region and even its bilobation is reminiscent of juvenile lyttonioids. There is, however, no sign of a vallum within the valve, while the concentric ornamentation and the reflexed, posterior flap are presently unknown among the permianellids. For the time being the genus remains unattributed among the lyttoniidines.] *Lower Permian:* Thailand.——Fig. 463,*1a,b.* **L. cateora,* Lower Permian, Thailand; exterior, interior of ventral valve, ×4 (Grant, 1976).

UNCERTAIN

C. H. C. Brunton,[1] S. S. Lazarev,[2] R. E. Grant,[3] and Jin Yu-gan[4]

[[1]formerly of the Natural History Museum, London; [2]Palaeontological Institute, Moscow; [3]deceased; [4]Nanjing Institute of Geology and Palaeontology]

Suborder UNCERTAIN

?Chonopectella Sarytcheva, 1966, p. 135, *nom. nov. pro Chonopectoides, non* Crickmay, 1963 [**Chonopectoides permicus* Sarytcheva in Sarytcheva & Sokolskaya, 1965, p. 232; OD]. Poorly represented and known; small with weakly convex ventral valve, teeth; spines at hinge; intersecting fine, oblique rugae and single submedian rib. *Upper Permian (Capitanian):* Transcaucasia.——Fig. 464,*2a,b.* **C. permica* (Sarytcheva), Dzhulfinsky Formation, Ogbin; holotype, PIN 2071/52; *a,* ventral valve exterior, ×1; *b,* detail of ornamentation, ×5 (Sarytcheva & Sokolskaya, 1965).

Ploughsharella Liang Wen-ping in Wang & others, 1982, p. 227 [**P. putaoshanensis;* OD]. Poorly known; medium width, outline subtrigonal with extended ventral umbo and trigonal interarea; profile strongly ventribiconvex; seemingly lacking ribbing and spines, but with prominent growth lines; anterior commissure widely unisulcate; interiors unknown. [Liang placed as an unknown family in the Productidina, but even a productide assignment is in question.] *Upper Permian:* eastern China.z——Fig. 464,*1a–d.* **P. putaoshanensis,* Upper Permian, eastern China; shell viewed posteriorly, anteroventrally, anteriorly, laterally, ×1.3 (Wang & others, 1982).

?Punctoproductus Liang Wen-ping, 1990, p. 368[481] [**P. eximus;* OD]. Liang placed in his new order, the Punctoproductida, with endopunctae but no pseudopunctae, along with the Dipunctellidina [=*Dicystoconcha* (Permianellidae)]. Further defined as lacking spines, concavoconvex, and coarsely ribbed. [The claim for endopunctation in the Productida has not been supported, and the genus may not belong here]. *upper Upper Permian:* China.——Fig. 464,*3a–c.* **P. eximus,* upper Upper Permian, Lengwu Formation, Zhejiang; anterior, lateral, posterior views of shell, ×2 (Liang, 1990).

NOMINA NUDA

Achunoproductus Ustritsky, 1971, p. 21. No diagnosis provided, but possibly related to *Shrenkiella* in the Monticuliferidae. *Upper Carboniferous, ?Lower Permian:* Russia (Urals).

Chaoina Ching Yu-gan in Ching Yu-gan, Liao Zhao-ting, & Hou Hong-fei, 1974, p. 308 [**C. reticulatia;* OD]. Small, subquadrate, widest at hinge; dorsal valve sharply geniculate, but with shallow corpus cavity; ribbing strong, almost entirely costate; rugae on disks; spines in rows separating ears and scattered on ventral valve; cardinal process small, sessile; cardinal ridge thin; adductor scars elevated anteriorly; brachial ridges obscure. [Genus and species not defined, possibly

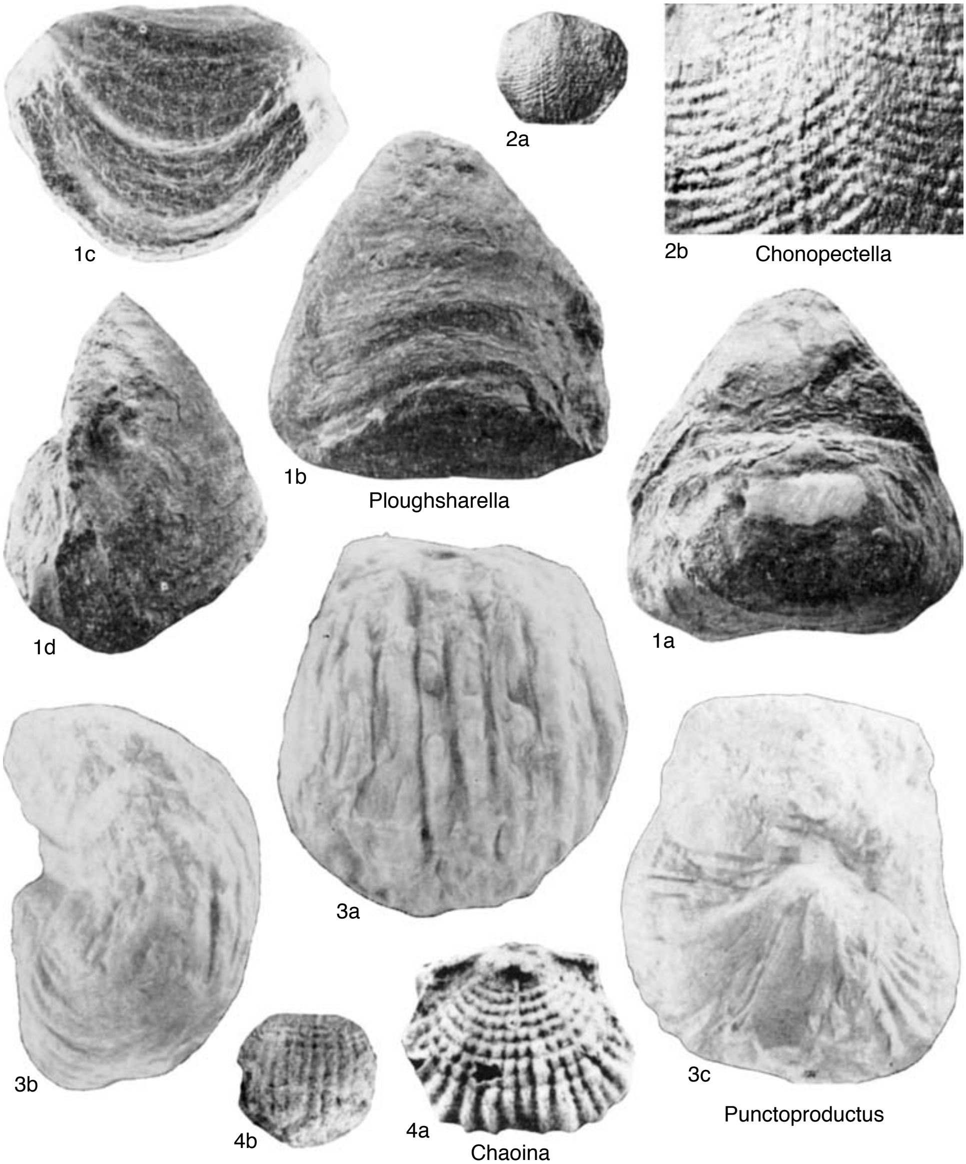

FIG. 464. Uncertain (p. 642–643).

belonging to the Productinae.] *Lower Permian (Kungurian):* southwestern China.——FIG. 464,*4a,b.* **C. reticulata,* Chihsian Formation, Sichuan; *a,* dorsal valve interior with much of shell missing, ×2; *b,* ventral valve viewed anteroventrally, ×1 (new).

Choanoproductus TERMIER & TERMIER, 1970, p. 459 [**C. guberi;* OD] [=*Choanoproductus* TERMIER & TERMIER, 1966, p. 609, *nom. nud.*]. No diagnostic descriptions for genus or species, or relationship provided. Illustrations of muscle scars only, possibly representing a strophalosiidine. *Upper Permian (Capitanian):* Cambodia.

Parapulchratia CHAN in HOU HONG-FEI, ZHAN LI-PEI, & CHEN BIN-WEI, 1979, p. 87 [**Productus pustulosus palliatus* KAYSER, 1883, p. 186; OD]. No diagnosis provided for genus or type specimen. KAYSER's specimens possibly representing several genera. *Upper Permian (?Changhsingian):* China.

Uraloproductus USTRITSKY, 1971, p. 21 [**Productus stuckenbergensis* KROTOW, 1885, p. 72; OD]. No description or diagnosis of genus provided. *Lower Permian:* Asian Arctic.

ORTHOTETIDA

Alwyn Williams,[1] C. Howard C. Brunton,[2] and A. D. Wright[3]

[[1]The University of Glasgow; [2]formerly of the Natural History Museum, London; and [3]The Queen's University, Belfast]

Order ORTHOTETIDA Waagen, 1884

[*nom. transl.* Williams & Brunton, herein, *ex* Orthotetinae Waagen, 1884, p. 576]

Strophic, commonly biconvex strophomenates; ventral interarea well developed, with pseudodeltidium; dorsal interarea short to obsolete, chilidium variably present; teeth deltidiodont, commonly supported by dental plates; cardinal process bilobed to forked; laminar shell pseudopunctate, less commonly impunctate or extropunctate. *Lower Ordovician (Llanvirn)–Upper Permian.*

Both suborders recognized as comprising the order Orthotetida were first associated by Schuchert (1913a, p. 387) as subfamilies of the family Strophomenidae. The triplesioids with their impunctate shell and biconvex profile did not, however, sit comfortably with the pseudopunctate concavoconvex strophomenides and were cited by Williams (1956, p. 284) as a superfamily, which did not easily fall into place in his six groupings; he suggested that they may belong to either his *Orthis* or *Pentamerus* groups. The triplesioids were regarded as an aberrant group of orthoids by Wright (1963a, 1965b). Through electron microscopy, Williams (1968a) was able to demonstrate that, along with other stocks, the triplesioids and orthotetoids possess a laminar secondary shell. He later suggested (Williams, 1970) that the two groups were closely related, having diverged from the billingselloid stock, probably in Late Cambrian times. The rare occurrence of pseudopunctae in triplesioids (Wright, 1970) supports this interpretation, as does the morphology of the pseudodeltidia and chilidia of the two groups (Wright, 1971, p. 350).

ORTHOTETIDINA

Alwyn Williams and C. Howard C. Brunton

[The University of Glasgow; and formerly of the Natural History Museum, London]

Suborder ORTHOTETIDINA Waagen, 1884

[*nom. transl.* Cooper & Grant, 1974, p. 256, *ex* Orthotetinae Waagen, 1884, p. 576]

Shells of variable size, strophic but commonly semicircular to subrounded in outline, profile variable, weakly concavoconvex to biconvex and ventrally subconical; functional pedicle present only in earliest known species; ventral valve usually cemented by umbo or greater part of shell surface to substrate, dorsal valve invariably convex in young growth stages; radial ornamentation normally well developed, essentially finely costellate by branching or intercalation; ventral interarea commonly with well-defined perideltidium; pseudodeltidium commonly forming complete cover to delthyrium; dorsal interarea becoming short but wide, chilidium well developed to obsolescent; teeth commonly supported by dental plates occasionally converging to form spondylium supporting entire ventral muscle field or septal chamber for adductor scars only; cardinal process bilobed, in many forms greatly extended ventrally with single proximal shaft, ankylosed with variably disposed socket ridges, socket plates, and variably developed brachiophores; shell typically pseudopunctate or, less commonly, extropunctate, impunctate in older stocks. *Upper Ordovician–Upper Permian.*

The orthotetidine brachiopods have always been the subject of taxonomic confusion. The distinctiveness shared by long-established genera, like *Orthotetes* FISCHER DE WALDHEIM, 1850, *Hipparionix* VANUXEM, 1842, and *Stroptorhynchus* KING, 1850, has never been in doubt; but their precise affinities with other brachiopod groups have repeatedly given free rein to broadly divergent taxonomic practices, well documented by MANANKOV (1979).

The first authoritative grouping of the orthotetoids within the Brachiopoda as a whole was that presented by SCHUCHERT (in SCHUCHERT & LEVENE, 1929, p. 16), who accepted the Orthotetinae of WAAGEN (1884) as a strophomenoid subfamilial repository, not only for all orthotetoid genera then known but also for an orthoid (*Orthidium*) with a vaguely orthotetoid cardinal process, as well as all resupinate strophomenides.

In the 1950s, when the superfamily Orthotetacea was first proposed (WILLIAMS, 1953b, p. 9), a number of families were erected by various students of the group so that, by the end of the decade, seven such taxa were recognized (WILLIAMS, 1953b; STEHLI, 1954; G. A. THOMAS, 1958; BOUCOT, 1959). These new taxa largely clarified the definitive orthotetoid character states although further complications arose with the assignment to the superfamily by WILLIAMS (1953b) of the Davidsoniidae, Gemmellaroiidae, Scacchinellidae, and the Thecospiridae for no better reason than that they were cemented strophic stocks allegedly without spines but with pseudopunctate shells.

By 1965, when the first edition of the brachiopod volumes of the *Treatise on Invertebrate Paleontology* was published (MOORE, 1965), the superfamily had acquired the name of Davidsoniacea in place of Orthotetacea in accordance with nomenclatorial rules of priority. Both the Gemmellaroiidae and Scacchinellidae had been found to be spinose and had been removed to the Productidina (MUIR-WOOD & COOPER, 1960, p. 66); and, although the Triassic spire-bearing Thecospiridae had been retained in the superfamily, the orthotetoids formed a reasonably well-defined group.

Since the 1965 *Treatise* study of the davidsoniaceans (WILLIAMS, 1965e, p. 405–412) the number of genera assigned to the group has more than doubled to 104. Only COOPER and GRANT (1974), who at the time were dealing mainly with Permian taxa, and MANANKOV (1979), however, have offered a comprehensive revision of the classification to cope with this generic proliferation. The most important steps taken by COOPER and GRANT were to transfer to the Strophomenidina all impunctate genera that were assembled within an amended Davidsoniacea into two families, the Davidsoniidae and Fardeniidae (a junior synonym of the Chilidiopsidae); and to erect a new suborder, Orthotetidina, for all pseudopunctate genera that were grouped into two superfamilies, the Orthotetacea and Derbyiacea, containing seven families and seven subfamilies. MANANKOV (1979), on the other hand, retained both impunctate and pseudopunctate taxa within an amended Davidsoniacea that embraced four families and ten subfamilies after the removal of the Thecospiridae and its promotion to the rank of superfamily with the Strophomenida. Previously, however, BRUNTON (1972) and BRUNTON and MACKINNON (1972) had transferred *Thecospira* to the Koninckinidae within the Spiriferida on the evidence of shell structure, pedicle foramen characteristics, and spiralium.

These two classifications differed fundamentally. MANANKOV's (1979) approach was essentially phylogenetic and prompted him to identify several recurrent trends, especially changes in shell shape and in the elaboration of dental plates and cardinalia. In contrast, COOPER and GRANT (1974) paid less attention to taxonomic complications that could have arisen from the recurrence of parallel trends, particularly in the development of the cardinalia; their approach was largely monothetic, leading, for example, to their transfer of all impunctate species from their Orthotetidina (COOPER & GRANT, 1974, p. 256) to the Strophomenidina despite the fact that the latter suborder is essentially pseudopunctate. Prior to the study by WILLIAMS and BRUNTON (1993) three very different, flawed

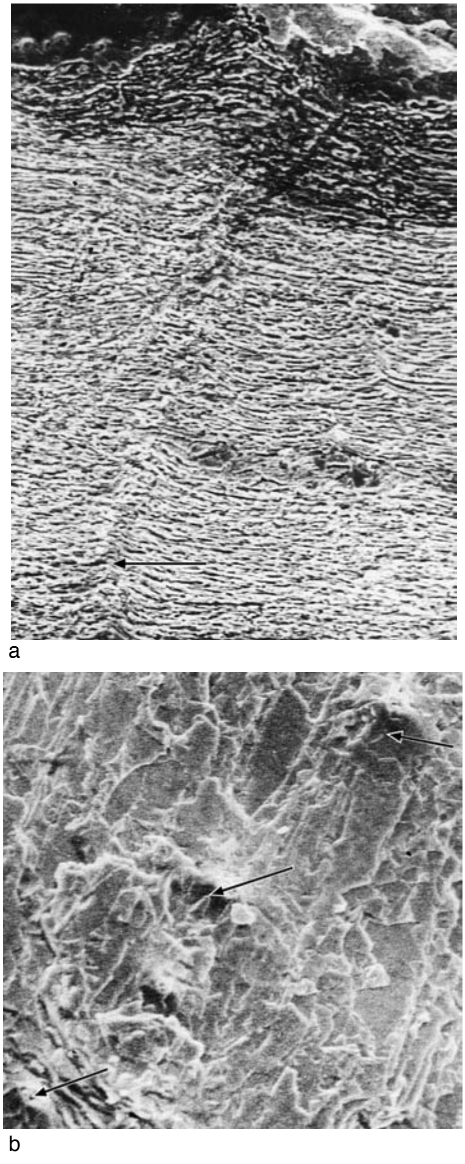

FIG. 465. Extropunctae of *Schuchertella lens* (WHITE) from uppermost Famennian, Louisiana Limestone, Missouri; *a,* polished and etched section with costellate exterior to top, SEM, ×130; *b,* external view of exfoliated surface within cross-bladed laminar succession, SEM, ×440; *arrows* point to extropunctae (new).

classifications were being used in systematic studies of orthotetidines and davidsoniaceans, as the case may be. Their deficiencies were brought into sharp focus during the updating of the taxonomy of the revision of the orthotetoids. Thus the oldest classification currently in use drawn up for the first edition of the *Treatise* is not only incapable of accommodating all valid genera erected since 1965 but also flawed in the way it used shell structure for taxonomic purposes. In particular, the classification did not take into account the discovery by G. A. THOMAS (1958, p. 36) that in *Streptorhynchus* and allied genera, microscopic conical flexuring of the laminar shell points outwardly (extropunctae of WILLIAMS & BRUNTON, 1993, p. 946), not inwardly as in the true pseudopunctate condition. In addition the studies of shell structure and morphology by WILLIAMS and BRUNTON (1993) and their use of phylogenetic analysis to assess the merits of the two other commonly used classifications by COOPER and GRANT (1974) and MANANKOV (1979) revealed that they are also deficient in one way or another.

A feature considered significant in the recognition of all orthotetoids by GRANT (1980) is the condition in which koskinoid perforations are concentrated around ventral umbos. WILLIAMS and BRUNTON (1993) investigated these perforations and concluded that they could not have developed as part of the brachiopod's growth and in consequence have no taxonomic value. Partly because *Gemmellaroia* and allied genera have koskinoid perforations, GRANT (1993a) transferred the Gemmellaroiidae from the Productida to the Orthotetidina. The recognition, however, that *Gemmellaroia* is spinose places it, as well as one other genus, within the richthofenioids. *Loczyella* is probably a permianellid, leaving *Cydalia* questionably placed within the Richthofenioidea.

The orthotetidines constitute one of the few suborders of the Brachiopoda characterized by several basic differences in the ultrastructure of their shells. All true orthotetids have a secondary shell of cross-bladed laminae bearing closely distributed pseudopunctae composed of microscopic conical deflections of the laminae that are directed inwardly. They evolved from the laminar-shelled chilidiopsoids that are impunctate except for a few specimens of Upper Ordovician *Fardenia,* which bear sporadically occurring, impersistent pseudopunctae. The pseudopunctate orthotetoids were in turn ancestral to the laminar-shelled schuchertellids (including the Streptorhynchinae), which are extropunctate with radially distributed microscopic conical deflections of the laminae pointing outwardly, tending to leave dimpled inner surfaces (Fig. 465).

The typical orthotetoid shell is ultrastructurally indistinguishable from that of the strophomenids although the pseudopunctate condition (Fig. 466) arose earlier in the latter group. So far as is known, the extropunctate condition is unique to the orthotetidines, while pseudopunctae with taleolae, so characteristic of the leptaenids, stropheodontids, chonetidines, productidines, and related aberrant Permian forms, have yet to be positively identified in orthotetidines.

The orthotetidines were also closely related to the other strophomenides in many basic morphological features (Fig. 467.2, 467.3). The presence, in Ordovician and lower Silurian species of both groups, of a pseudodeltidium with a supra-apical foramen is indicative of the existence of a ventral body wall in the living state (WILLIAMS, 1956, p. 258), which was absent from other articulated brachiopods except for some orthides. The sealing of the foramen in all later Paleozoic strophomenidines and orthotetidines confirms that atrophy of the pedicle had taken place throughout these groups by Carboniferous times. Subsequently, many strophomenides (including the orthotetidines) acquired a cementing habit; and, since the davidsoniids were also cemented to the substrate and appeared to have a pseudodeltidium, they were widely accepted as orthotetidines and, indeed, gave their name to the suborder. Yet, as JOHNSON illustrated (1982, pl. 1, fig. 11, 14), the so-called pseudodeltidium is a deltidium and, with the discovery (WILLIAMS & BRUNTON, 1993) that the shell is fibrous not laminar, *Davidsonia* and other related, cementing, middle-Paleozoic brachiopods with calcareous spiralia have been transferred to the atrypides.

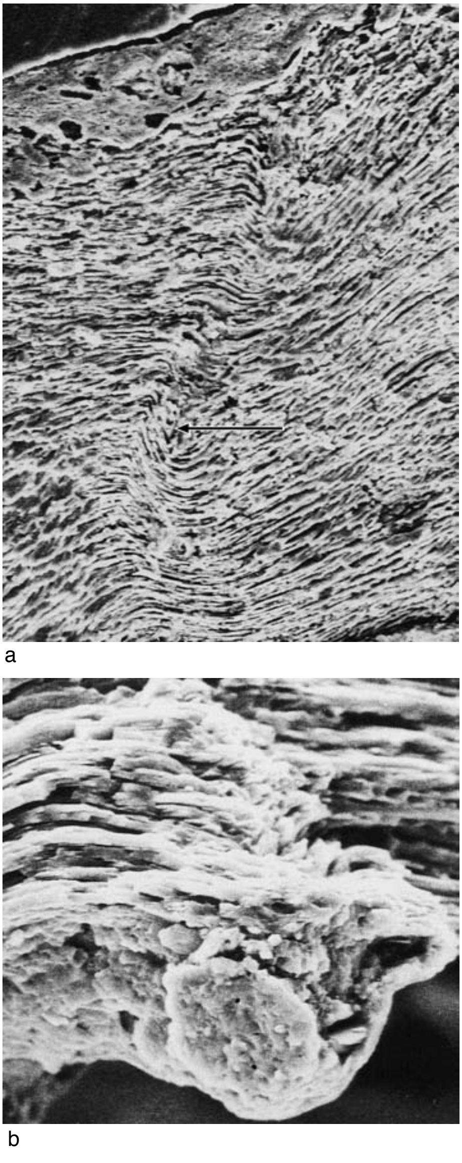

FIG. 466. Pseudopunctae of *Apsocalymma shiellsi* MCINTOSH from Lower Carboniferous, Lower Limestone Group, Scotland; *a,* polished and etched section with weathered exterior to top and *arrow* pointing to trace of pseudopuncta, SEM, ×210; *b,* fractured section of interior showing flexured laminae in relation to tubercle at internal surface, SEM, ×860 (new).

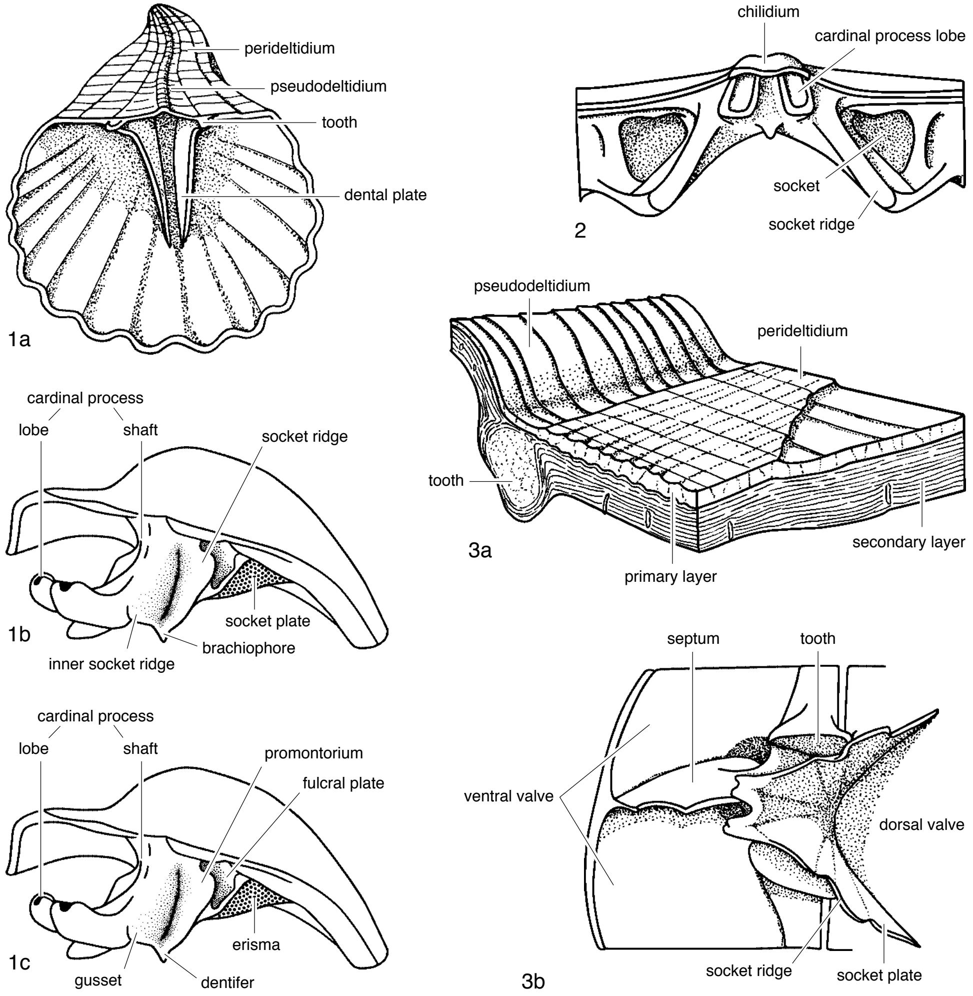

Fig. 467. Morphological features of orthotetidines; *1a–c, Meekella; 1a,* ventral valve interior (Williams, 1965d); *1b,c,* oblique lateral views showing structures in cardinalia, *1b,* terms used herein and *1c,* terms used by Cooper and Grant, 1974; *2, Schuchertella,* chilidium and adjacent structures of dorsal valve; *3a,b, Derbyia; 3a,* oblique three-dimensional diagram showing structure of part of interarea; *3b,* view of inside of shell looking posteriorly (Williams, 1965d).

The widespread acquisition by many orthotetidines of a cementing habit led repeatedly to the elevation of their shells above the substrate by excessive conical deepening of the attached ventral valves. This conical deepening was accompanied by complementary extensions of skeletal articulatory devices. The morphological effects were quite dramatic, especially with regard to variations in the proportional development of various ridges and plates supporting the teeth, the bilobed cardinal process accommodating the dorsal diductor bases, and other associated parts of the cardinalia defining the dental sockets. These exaggerated structures, exemplified by *Meekella* (Fig. 467.1), were given specific terms by Cooper and Grant (1974) in order to draw attention to their development within a few subfamilies. Many of these terms, however, are synonyms of others that were already widely used throughout the phylum for homologous structures (Fig.

467.1b–467.1c) and have not been used herein in taxonomic descriptions (see the chapter on morphology, p. 371 in Kaesler, 1997). Not surprisingly, these repeated trends gave rise to similar spectacular structures in several independent stocks. In Late Devonian to Early Carboniferous times elongate cardinal processes, taking with them other elements of the cardinalia, developed in the Adectorhynchinae, Streptorhynchinae, Derbyiinae, and Meekellinae and became very elongated with the conical deepening of ventral valves in Permian species of the last two subfamilies. The trends were broadly synchronous within a readily identifiable phylogeny that was evidently compatible with the stratigraphic ranges of constituent taxa (Fig. 468). As a result, previous classifications were dominated by the preferential weighting of one kind of feature, for example dental plates or socket plates, at the expense of others. In effect, homoplasy has played a more important role than homology in determining the structure of previous orthotetidine classifications.

These homoplastic trends can be disentangled by paying due regard to morphology as a whole through phylogenetic analysis and especially to the more stable changes attending the evolution of shell structure. The present classification attempts to meet these conditions. Even so, it is provisional on getting further information not only on the many poorly described genera currently in circulation but also on such taxa as *Diplanus* and *Hypopsia,* whose exquisitely silicified morphology could well be at variance with their original shell structure, which remains unknown.

Superfamily ORTHOTETOIDEA Waagen, 1884

[*nom. transl.* Williams, 1953b, p. 9, *ex* Orthotetinae Waagen, 1884, p. 576]

Ventral valve lacking supra-apical foramen, cemented or secondarily free with deformed conical shape characteristic of later groups; almost invariably finely costellate with secondary costation and impersistent rugation rarely developing later; pseudodeltidium well developed, normally convex or becoming flat with monticulus in later taxa, chilidium variably developed; dental ridges unsupported in some stocks, discrete or tending to converge to form apical chamber; dental plates, when present, converging to form spondylia or narrow medial chambers; myophragm variably developed in both valves; socket ridges recurved, becoming large, divergent, and ankylosed but with proximal single shaft of cardinal process lobes and with exaggerated brachiophores in independently derived later groups; shell structure pseudopunctate or more rarely extropunctate. *Middle Devonian–Upper Permian.*

Family ORTHOTETIDAE Waagen, 1884

[*nom. transl.* McEwan, 1939, p. 619, *ex* Orthotetinae Waagen, 1884, p. 576] [=Derbyoidinae Thomas, 1958, p. 21]

Large, subquadrate, ventribiconvex to resupinate, normally rectimarginate, finely costellate; ventral beak typically symmetrical, interarea apsacline with well-developed perideltidium and convex pseudodeltidium, dorsal interarea usually short, anacline with small chilidium occasionally grooved; dental ridges normally convergent on median ridge or septum, unsupported by dental plates; socket ridges commonly recurved, not ankylosed to low, discrete cardinal process lobes; ventral muscle scar flabellate, usually impressed; dorsal adductor scars rarely impressed, dorsal myophragm variably developed. *Lower Carboniferous–middle Permian.*

Orthotetes Fischer de Waldheim, 1829, p. 375 [**O. radiata* Fischer de Waldheim, 1850, p. 491; SD Girty, 1909, p. 192] [=*Pseudoorthotetes* Sokolskaya in Sarytcheva & others, 1963, p. 96 (type, *P. borodencovensis*); *Orthotetoides* Lazarev, 1984, p. 65 (type, *Orthotetes socialis* Fischer de Waldheim, 1850)]. Biconvex, rectimarginate, finely costellate by branching; usually with symmetrical ventral beak, convex pseudodeltidium, dorsal interarea linear to vestigial, chilidium small, grooved, dental ridges strong, convergent on high ventral median septum to define small delthyrial chamber commonly filled with secondary shell, less commonly extending anteromedianly for entire length of ventral interarea; socket ridges recurved; ventral muscle scar impressed, large, flabellate, dorsal myophragm

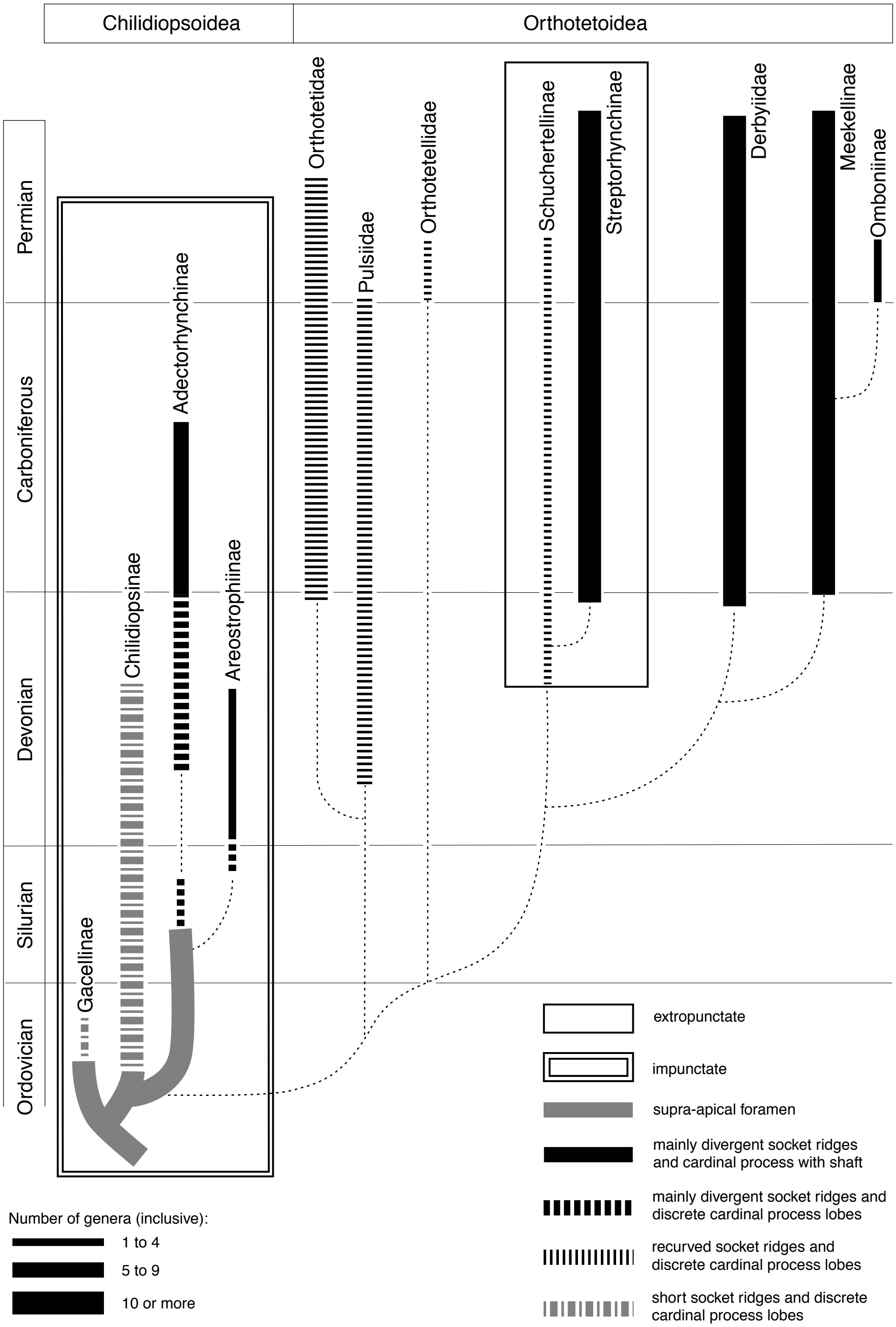

FIG. 468. Chronostratigraphy of orthotetidine phylogeny showing main trends in evolution of pedicle foramen, shell structure, and cardinalia; all taxa outside two designated boxes are pseudopunctate (new).

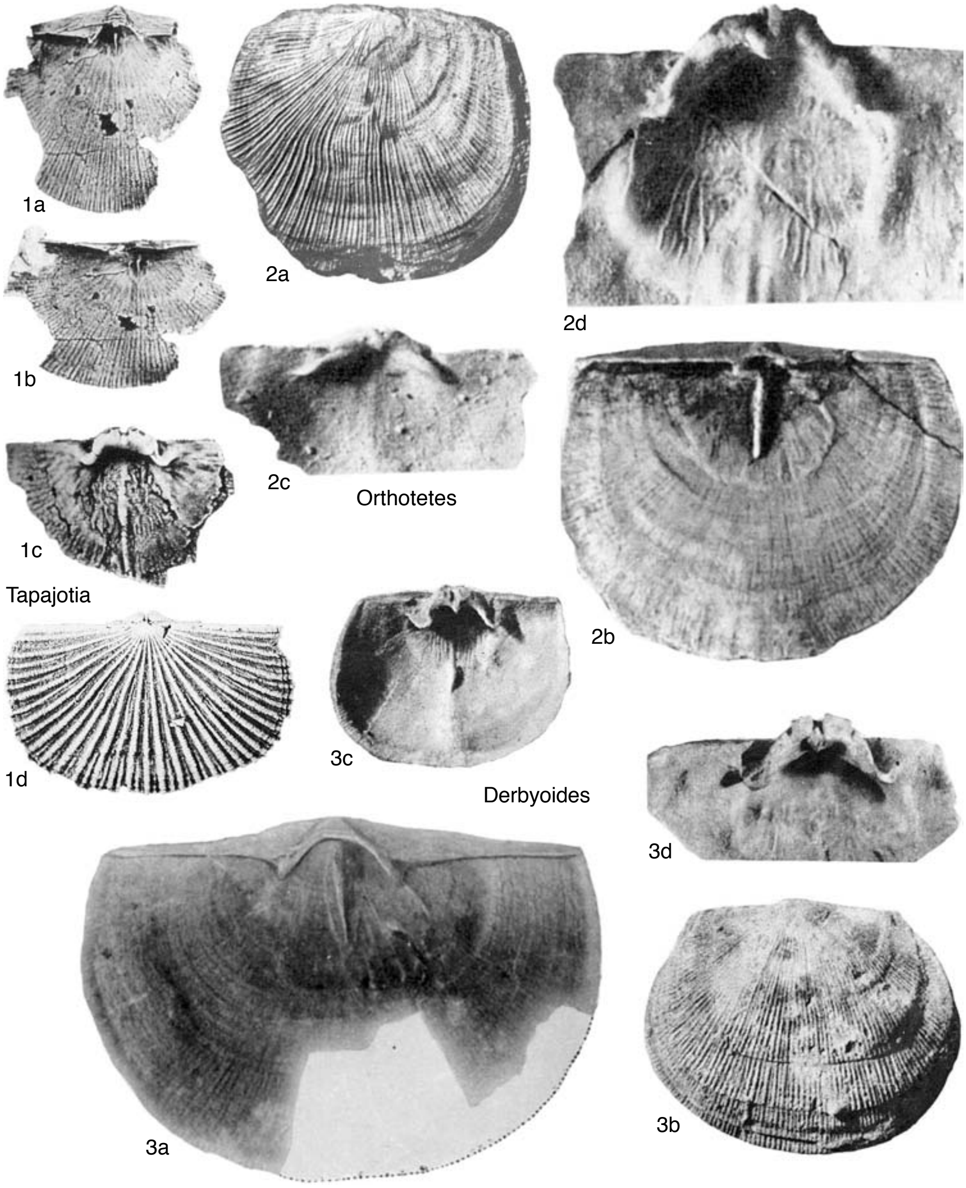

FIG. 469. Orthotetidae (p. 649–652).

broad, low. [*Pseudoorthotetes* was erected for species with longer delthyrial chambers and cardinal processes, *Orthotetoides* for species with medianly grooved chilidium and without dorsal myophragm. Until these differences are shown to be specifically constant, these genera are best treated as junior synonyms of *Orthotetes.*] *Lower Carboniferous–Lower Permian:* Eurasia.——FIG. 469,*2a–d.* **O. radiata* FISCHER DE WALDHEIM, Moscovian, Russia; *a,* ventral valve exterior, ×1 (Sokolskaya, 1954); *b,c,* ventral valve interior, dorsal valve interior, ×1; *d,* dorsal valve interior, ×2 (Manankov, 1973).

Apsocalymma McIntosh, 1974, p. 213 [**A. shiellsi;* OD]. Similar to *Brochocarina* but with vestigial pseudodeltidium complementing large, medianly grooved chilidium and strong, dorsal myophragm continuous with base of cardinal process. *Lower Carboniferous (upper Viséan):* Scotland.——Fig. 470,*2a–d.* **A. shiellsi,* Lower Limestone Group, Ayrshire; *a,b,* ventral valve, dorsal valve interiors, ×1; *c,* posterior view of dorsal cardinalia and chilidium, ×4; *d,* dorsal valve exterior, ×0.66 (McIntosh, 1974).

Brochocarina Brunton, 1968, p. 31 [**Schuchertella wexfordensis* Smyth, 1930, p. 555; OD]. Similar to *Orthotetes* but essentially planoconvex, finely parvicostellate by intercalation, intersected by fine concentric fila, with anacline dorsal interarea and arched chilidium; dental ridges convergent posteriorly on trifid ridge forming posterior boundary of faintly impressed ventral muscle scar with low myophragm. *Lower Carboniferous:* Ireland, ?Australia.——Fig. 470,*1a–e.* **B. wexfordensis* (Smyth), Asbian, County Fermanagh, Ireland; *a,* posterodorsal view of incomplete shell, ×1.5; *b,c,* ventral valve interior, exterior, ×0.8; *d,* detail of external ornamentation, ×3; *e,* dorsal valve interior, ×0.8 (Brunton, 1968).

Derbyoides Dunbar & Condra, 1932, p. 114 [**D. nebrascensis;* OD]. Similar to *Orthotetes* but more variable in shape with anterior commissure occasionally undulating; pseudodeltidium convex with median groove; dental ridges not cemented to low ventral myophragm; median node at base of cardinal process; dorsal adductor scars impressed, bilobate about low myophragm. *Upper Carboniferous–Lower Permian:* North America.——Fig. 469,*3a–d.* **D. nebrascensis,* Kasimovian, Nebraska; *a,* ventral valve interior, ×1 (Dunbar & Condra, 1932); *b,c,* exterior, interior views of dorsal valve, ×1; *d,* dorsal cardinalia, part of adductor scars, ×1.5 (Dunbar & Condra, 1932).

Liberella Liang, 1990, p. 104[456] [**L. cassidula;* OD]. Small to medium, commonly strongly uniplicate, finely costellate by branching, finely lamellose; pseudodeltidium and chilidium undescribed; dental ridges discrete of strong ventral myophragm ankylosed to internal surface of pseudodeltidium and bisecting faint, flabellate ventral muscle scar; short cardinal process with lobes fused medially into trifid structure; socket ridges recurved. *middle Permian:* China (Zhejiang Province).——Fig. 470,*3a–c.* **L. cassidula,* middle Permian, Zhejiang; *a,b,* dorsal valve, ventral valve exteriors, ×2; *c,* posterior view of internal mold, ×2 (Liang, 1990).

Tapajotia Dresser, 1954, p. 33 [**Streptorhynchus tapajotensis* Derby, 1874, p. 37; OD]. Similar to *Derbyoides* but with weak myophragm in ventral valve and nearly planar dorsal valve with more delicate cardinalia and without impressed dorsal adductor scars or myophragm. *Upper Carboniferous–Lower Permian:* Brazil.——Fig. 469,*1a–d.* **T. tapajotensis* (Derby), Itaituba, Bashkirian, Rio Tapajos; *a,b,* dorsal, anterodorsal views of incomplete ventral valve interiors, ×1; *c,* interior view of dorsal valve, ×1.5; *d,* exterior view of dorsal valve, ×2.1 (Brunton, 1968).

Tethorotes Manankov, 1979, p. 50 [**Ombonia grandis* Sokolskaya, 1968, p. 60; OD]. Similar to *Orthotetes* but more dorsibiconvex to resupinate and broadly unisulcate with impersistent concentric rugae; dorsal interarea anacline, chilidium with median groove; delthyrial chamber asymmetrical; median septal node at base of cardinal process; muscle scars faint. *Lower Carboniferous–Lower Permian:* Kazakhstan.——Fig. 471,*1a–c.* **T. grandis* (Sokolskaya), Serpukhovian, northern Pribalkhash; ventral valve internal mold, dorsal valve internal mold, latex replica of previous specimen showing cardinalia, ×1 (Manankov, 1979).

Werriea Campbell, 1957, p. 44 [**W. australis;* OD] [=*Permorthotetes* G. A. Thomas, 1958, p. 82 (type, *P. callytharensis*)]. Similar to *Orthotetes* but more variable in shape, mainly resupinate with some asymmetry to ventral beak, finely parvicostellate by intercalation, impersistently rugate; dorsal interarea short, anacline, cardinal process with median groove, as in *Permorthotetes;* small median node at base of cardinal process; brachiophores present as sharp, distal edges of recurved socket ridges. *Lower Carboniferous–Lower Permian:* Australia, North America.——Fig. 471,*2a–c.* **W. australis,* lower Viséan, New South Wales; *a,* holotype, internal mold of ventral valve, ×1; *b,* external mold of ventral valve, ×1; *c,* imperfect cast of cardinal process, ×1 (Campbell, 1957).——Fig. 471,*2d. W. callytherrensis* (Thomas), Permian, Australia; ventral valve interior, ×1 (Thomas, 1958).

Family PULSIIDAE
Cooper & Grant, 1974

[*nom. transl.* Williams & Brunton, herein, *ex* Pulsiinae Cooper & Grant, 1974, p. 256]

Mostly large, subquadrate, dorsibiconvex, mainly finely parvicostellate by intercalation, intersected by concentric fila; ventral interarea short, apsacline, perideltidium present, beak usually symmetrical; dorsal interarea short, anacline; pseudodeltidium and small chilidium convex; dental plates variable in disposition, strong but not reaching into anterior half of valve; socket ridges recurved; cardinal process lobes discrete, low, usually with grooved myophores; ventral muscle scars variable in size and in insertion on valve floor, myophragm rarely developed; dorsal myophragm present, but low. *Middle Devonian–Upper Carboniferous.*

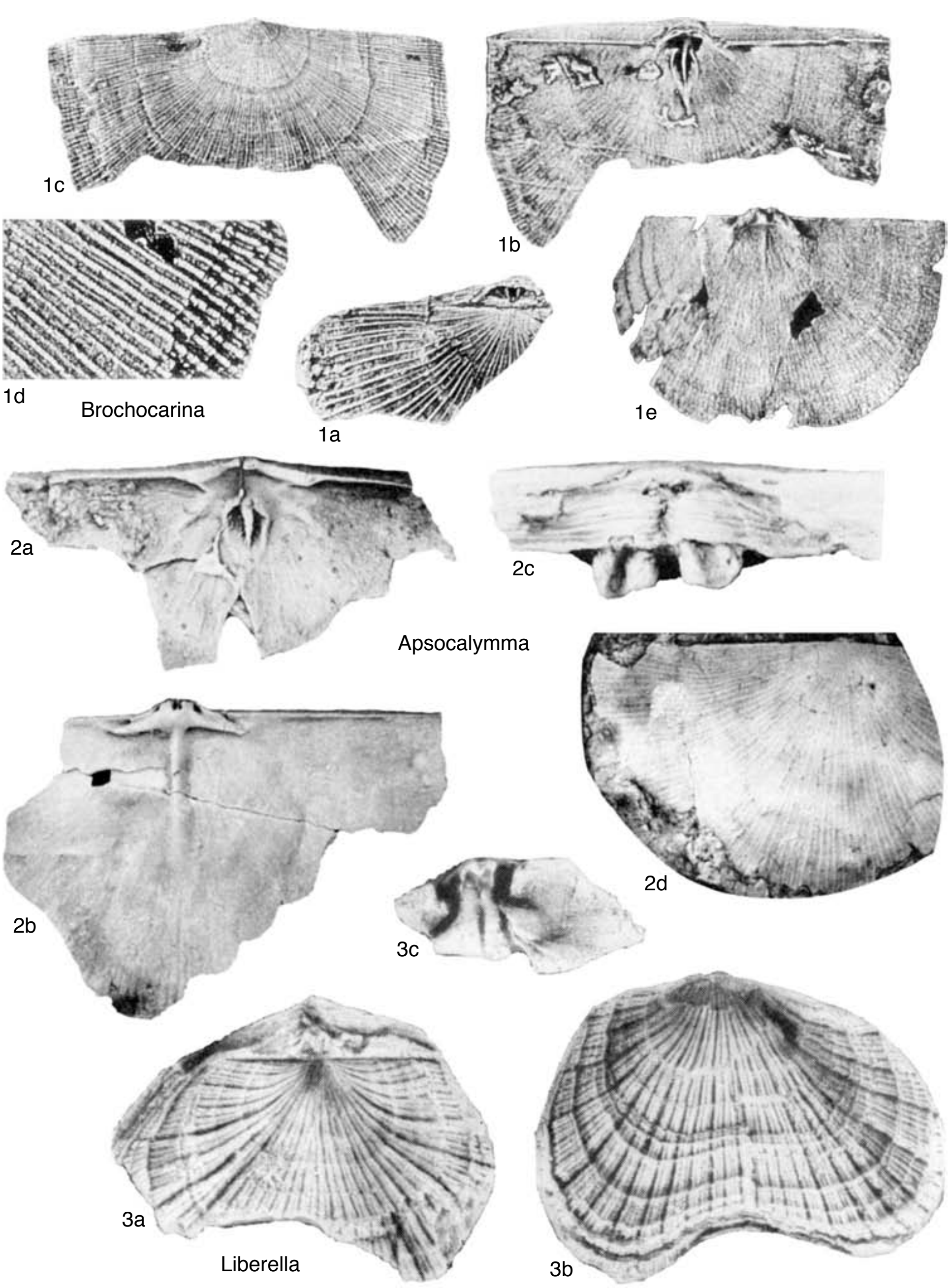

FIG. 470. Orthotetidae (p. 652).

Pulsia Ivanov, 1925, p. 113 [**P. mosquensis;* OD]. Commissure rectimarginate, concentric fila not reported within interspaces or on crests of parvicostellae; dental plates parallel, enclosing callus of secondary shell like pseudospondylium but ventral muscle scars indistinctly impressed; socket ridges well developed, recurved. *Carboniferous:* Russia. ——FIG. 472,*1a–c.* **P. mosquensis,* Kasimovian,

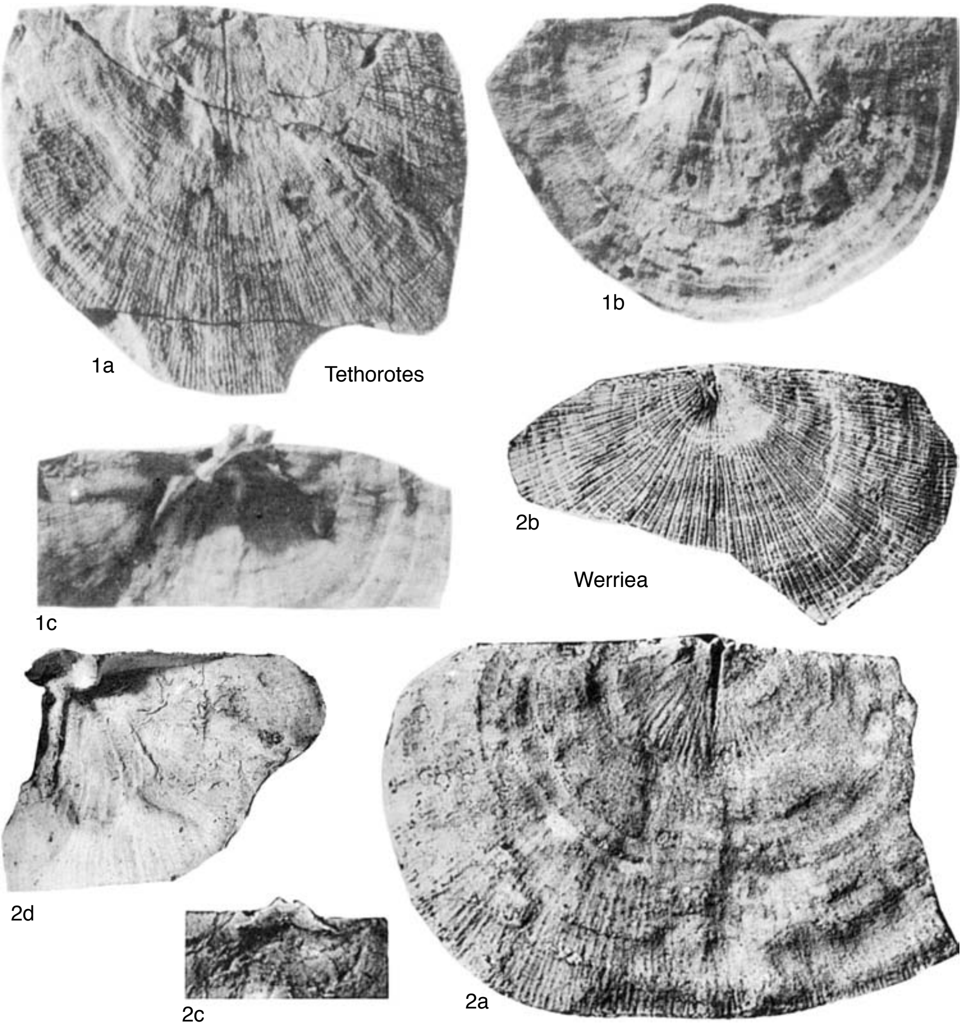

FIG. 471. Orthotetidae (p. 652).

Moscow District; *a,* ventral valve interior, ×0.5 (Sokolskaya, 1954); *b,c,* dorsal valve exterior, ventral valve exterior, ×1 (Orlov, 1960).

Schellwienella I. THOMAS, 1910, p. 92 [**Spirifera crenistria* PHILLIPS, 1836, pl. 216; OD] [=*Carlopsina* REED, 1954, p. 183 (type, *Spirifera radialis* PHILLIPS, 1836)]. Similar to *Pulsia* but commonly gently uniplicate with concentric fila forming serrations along crests of parvicostellae; dental plates short, divergent posteriorly, containing impressed, flabellate ventral muscle scars divided by low myophragm; socket ridges short, recurved. [*Carlopsina* was erected for those species with a short dorsal interarea. Dorsal valves of the type species that are better preserved than the crushed specimen figured by REED have linear or obsolescent interareas similar to those of *Schellwienella s.s.*] *Middle Devonian–Lower Carboniferous:* cosmopolitan.——FIG. 472,*2a–c.* **S. crenistria* (PHILLIPS), Viséan, Lancashire, England, lectotype, BMNH B19675; dorsal, ventral, posterior views of shell, ×1 (new).——FIG. 472,*2d,e. S. radialis* (PHILLIPS), Asbian, Fermanagh, Ireland; dorsal valve posterior, dorsal valve interior, ×1.3 (Brunton, 1968).

Family ORTHOTETELLIDAE Cooper & Grant, 1974

[Orthotetellidae COOPER & GRANT, 1974, p. 285] [=Hypopsiinae COOPER & GRANT, 1974, p. 256]

Variable profile but asymmetrical ventral valve frequently conical, with apsacline to

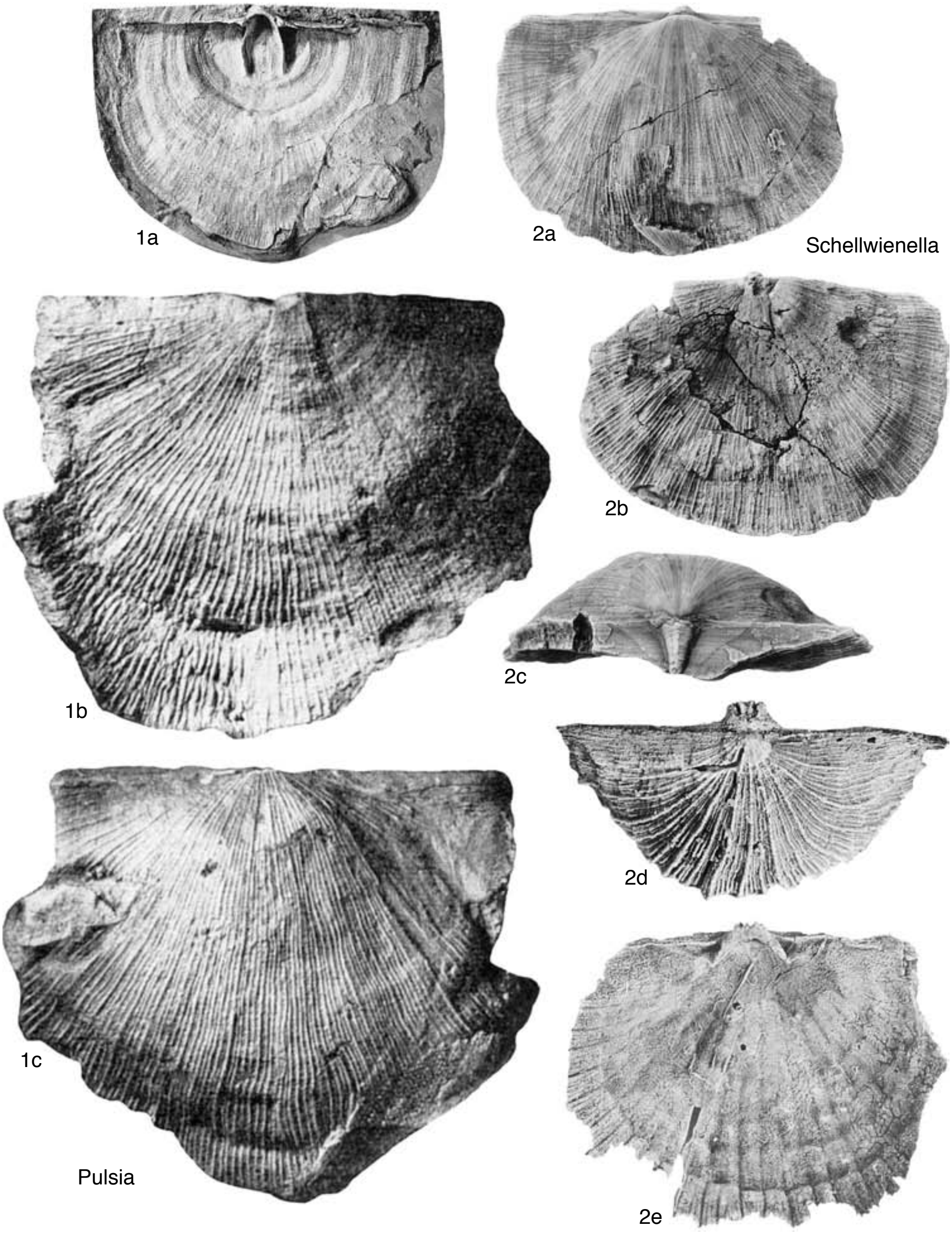

FIG. 472. Pulsiidae (p. 653–654).

procline interarea of variable length, finely costellate by branching or intercalation crossed by concentric fila; dental plates convergent to form spondylium supported by median septum or free, containing ill-defined ventral muscle scar; cardinal process with basal median node, lobes low, discrete; socket ridges recurved or divergent, brachiophores blunt, divergent. *Lower Permian.*

Orthotetella R. E. KING, 1931, p. 51 [**O. wolfcampensis;* OD]. Large, finely parvicostellate by branching; spondylium supported by median

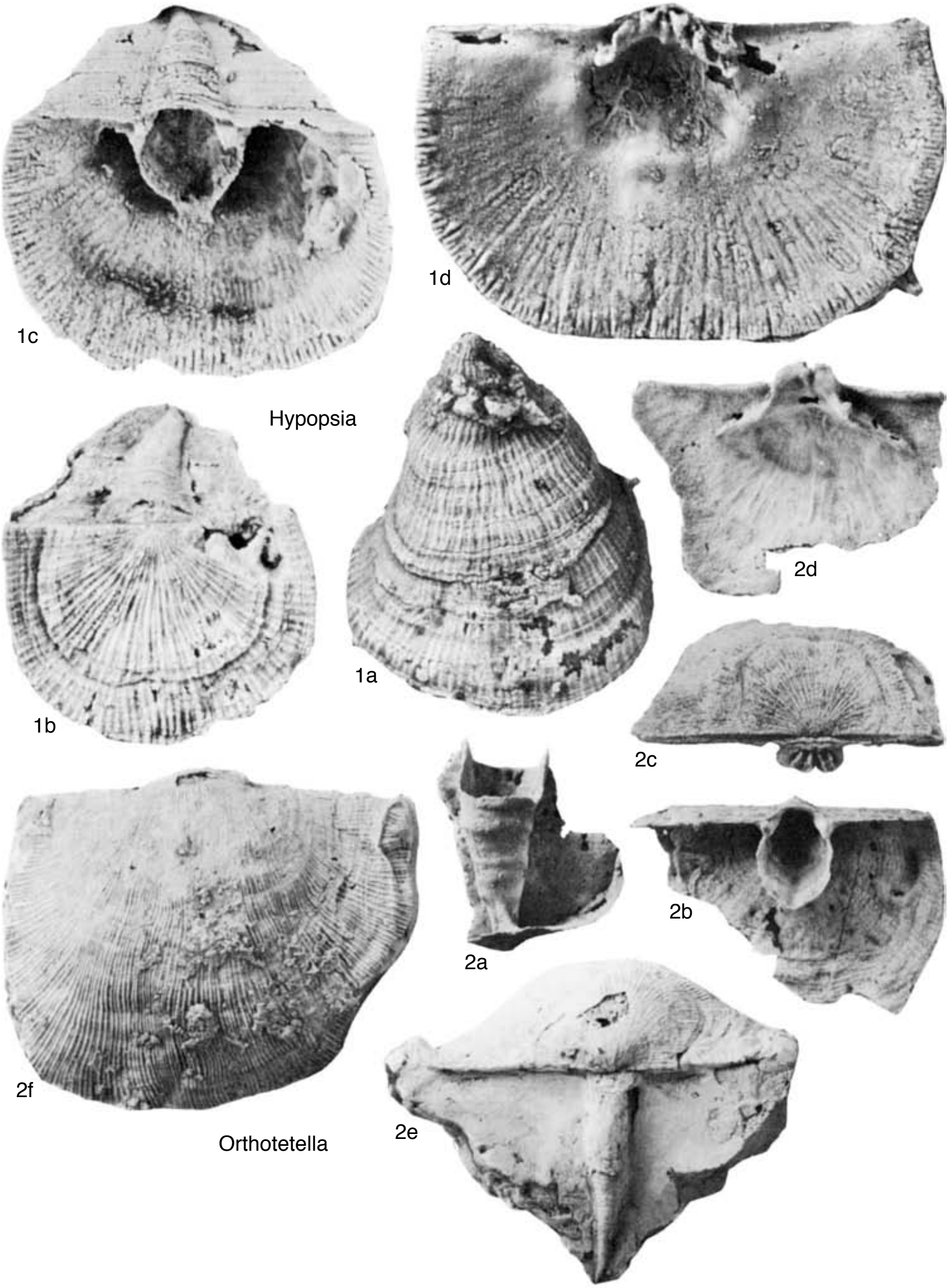

FIG. 473. Orthotetellidae (p. 655–657).

septum in young valves, becoming free in adult valves to form cone with convex pseudodeltidium, containing striate ventral muscle scars; socket ridges ankylosed to cardinal process lobes with slits on posteriorly directed myophores; dorsal adductor scars bilobed, lightly impressed about low myophragm. *Lower Permian:* western USA.——FIG. 473,*2a–f.* **O. wolfcampensis,* Wolfcampian, Texas; *a,* internal view of ventral valve showing tubular spondylium, ×1; *b,* ventral valve interior, ×1; *c,d,* posterior, interior views of dorsal valve, ×1; *e,f,* posterior, dorsal views of shell, ×1 (Cooper & Grant, 1974).

Hypopsia Cooper & Grant, 1974, p. 272 [**H. versuta;* OD]. Medium sized, finely parvicostellate by intercalation; spondylium initially supported by median septum but adnate on floor of adult valves; socket ridges not ankylosed to cardinal process, brachiophores long, divergent, dorsal adductor scars impressed, bilobed about low myophragm. *Lower Permian:* western USA.——Fig. 473,*1a–d.* **H. versuta,* Leonardian, Texas; *a,b,* holotype, ventral, dorsal views of shell, ×3; *c,d,* paratype, ventral valve interior, dorsal valve interior, ×2 (Cooper & Grant, 1974).

Family DERBYIIDAE Stehli, 1954

[*nom. transl.* Cooper & Grant, 1974, p. 256, *ex* Derbyiinae Stehli, 1954, p. 303] [=Diplaninae Cooper & Grant, 1974, p. 256; Dorsoscyphinae Roberts, 1971, p. 49]

Variable in size, outline, and disposition of anterior commissure, normally ventribiconvex, cemented with asymmetrical, high ventral beak, costellation variable in texture, crossed by concentric fila; ventral interarea variably disposed, perideltidium usually well developed, pseudodeltidium broadly convex or flat with narrow monticulus; dorsal interarea linear, chilidium complete, convex, or vestigial; dental ridges discrete, median septum normally strong, ankylosed to internal surface of pseudodeltidium; cardinal process lobes fused proximally, normally high with myophore slits, divergent socket ridges fused with cardinal process, brachiophores normally developed, ventral muscle scars large, flabellate, dorsal muscle scar impressed about myophragm. *Lower Carboniferous–Upper Permian.*

Derbyia Waagen, 1884, p. 576 [**D. regularis;* SD Hall & Clarke, 1892, p. 262] [=*Derbyaeconcha* Licharew, 1934b, p. 507 (type, *Derbya anomata* Licharew, 1932, p. 20); *Grabauellina* Licharew, 1934b, p. 507 (type, *Derbya (?Derbyina) mongolica* Grabau, 1931, p. 259), *nom. nov. pro Derbyina* Grabau, 1931, p. 259, *non* Clarke, 1913; *Magniderbyia* Ting, 1965, p. 265 (type, *Derbya magnifica* Licharew, 1939, p. 80), *nom. nov. pro Licharewiella* Sokolskaya, 1960, p. 219, *non* Ustritsky, 1960; *Pseudoderbyia* Licharew, 1934a, p. 211 (type, *P. netschajewi*); *Plicatoderbya* H. D. Thomas, 1937, p. 14 (type, *Orthotetes magnus* Branson, 1930, p. 26); *Wardakia* Termier & others, 1974, p. 94 (type, *Derbyia grandis* Waagen, 1884, p. 597); *Paraderbyia* Sun, 1983, p. 120 (type, *P. duomaensis*)]. Large, normally distorted in shape and uniplicate, finely costellate by branching and intercalation; pseudodeltidium flat with monticulus, chilidium small, occasionally with median groove, vestigial in later, larger species; dental ridges frequently convergent apically on high ventral median septum ankylosed to internal surface of pseudodeltidium; flabellate ventral muscle scar usually deeply impressed, occasionally with raised boundary; ridgelike brachiophores arising from massive socket plates and ridges fused with cardinal process of variable length; subcircular dorsal adductor scars variably impressed about low myophragm; commonly with interrupted rugation like low plication. [Genera cited as junior synonyms of the cosmopolitan, long-ranging *Derbyia* have been erected on morphological differences that were subject to specific variation in large samples of well-preserved specimens similar to those described by Cooper and Grant (1974, p. 292–318). Thus, such variation affected the persistence of rugation, the development of a raised anterior boundary to the ventral muscle scar, and the strength of the dorsal myophragm, the diagnostic features of *Plicatoderbyia, Magniderbyia,* and *Paraderbyia* respectively, and the relative strength of the dorsal and ventral myophragms and the development of a pseudodeltidial monticulus, which characterize *Wardakia.*] *Upper Carboniferous–Upper Permian:* cosmopolitan.——Fig. 474,*2a–c.* **D. regularis,* Amb Formation, Lower Permian, Salt Range, Pakistan; dorsal, ventral, posterior views of shell, ×1 (new).——Fig. 474,*2d,e. D. profunda* Cooper & Grant, Wolfcampian, Texas; *d,* paratype, broken specimen showing cardinalia and dental ridges, ×1; *e,* paratype, posterior view of dorsal valve, ×1 (Cooper & Grant, 1974).——Fig. 474,*2f. D. filosa* Cooper & Grant, Wordian, Texas; holotype, posteriorly tilted ventral valve interior, ×1 (Cooper & Grant, 1974).

Diplanus Stehli, 1954, p. 299 [**Streptorhynchus lamellatum* R. E. King, 1931, p. 49; OD]. Small, subconical, variable anterior commissure, costellate by branching, strongly lamellose; ventral interarea of variable length, pseudodeltidium convex; dorsal interarea abnormally anacline, chilidium with median groove; dental ridges discrete with large teeth, ventral muscle scar obscure; cardinal process of medium height with slitlike myophores; dorsal adductor scars impressed, bilobed frequently with raised margin, bisected by low myophragm. [Cooper & Grant (1974, p. 256) assigned this genus to the Schuchertellidae; but until the shell structure of unsilicified specimens has been determined, *Diplanus* is, on balance, provisionally identified as a derbyiid despite the absence of a median septum ankylosed to the pseudodeltidium.] *Lower Permian:* western USA.——Fig. 475,*1a–d.* **D. lamellatus* (King), Leonardian, Texas; *a,* ventral valve interior, ×2; *b,c,* posterior, interior views of dorsal valve showing cardinal process and sockets, ×4; *d,* holotype, posterior view of complete specimen, ×2 (Cooper & Grant, 1974).

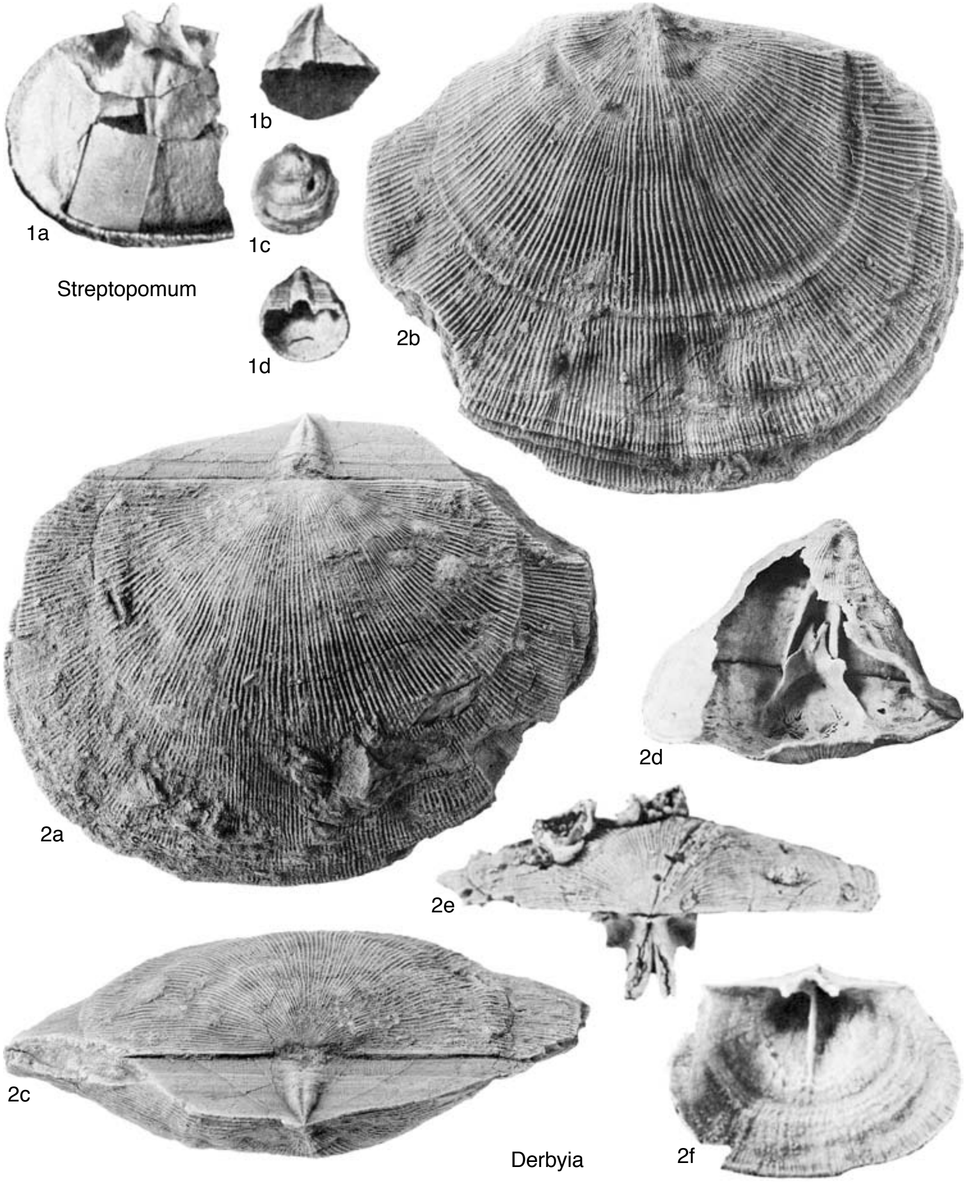

FIG. 474. Derbyiidae (p. 657–660).

Dorsoscyphus ROBERTS, 1971, p. 50 [**D. spinulosus;* OD]. Similar to *Derbyia* but small, ventribiconvex with subconical ventral valve, gently unisulcate, costellate by intercalation, lamellose; ventral interarea high, pseudodeltidium convex, chilidium reduced; cardinal process relatively low with basal median node and grooved myophores; socket ridges divergent, continuous with cuplike platform containing deeply impressed adductor scars about a strong dorsal myophragm; shell free of rugation. *Lower Carboniferous:* Western Australia.——FIG. 475,*3a–d.* **D. spinulosus,* Viséan, Bonaparte Gulf Basin; *a,b,* holotype, interior, exterior views of dorsal valve, CPC 10821, ×6; *c,d,* interior, exterior views of ventral valve, ×6 (Roberts, 1971).

Nothopindax COOPER & GRANT, 1974, p. 318 [**N. egregius;* OD]. Similar to *Derbyia* but normally ventribiconvex with subconical ventral valve,

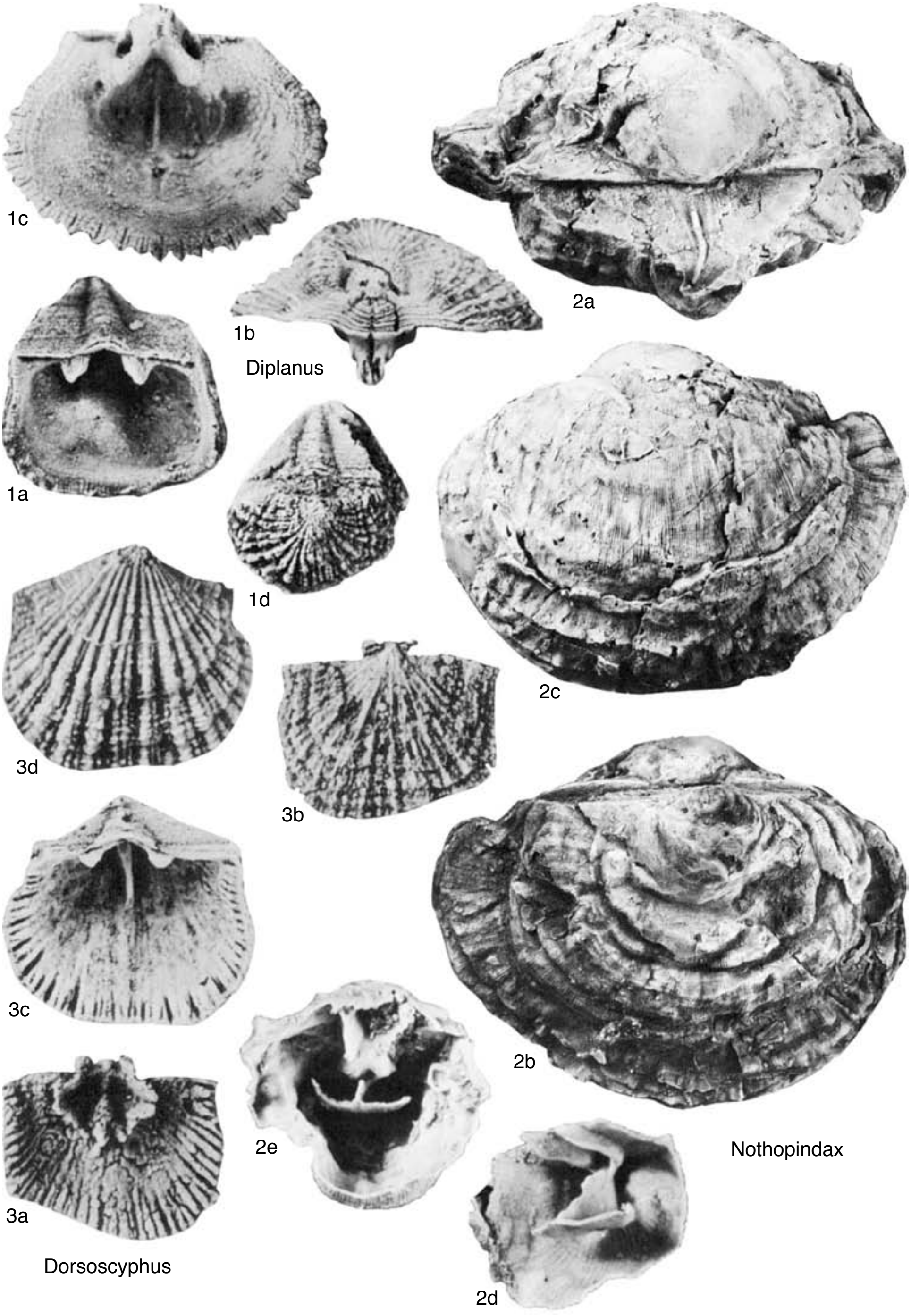

FIG. 475. Derbyiidae (p. 657–660).

rectimarginate, finely costellate by branching; ventral median septum anteriorly ankylosed to transverse, spatulate platform representing raised anterior boundary of ventral muscle scar; dorsal adductor scars ill defined, myophragm not developed. *Lower Permian:* western USA.——FIG. 475,*2a–e.*N. egregius,* Leonardian, Texas; *a–c,* paratype, posterior, dorsal, ventral views of shell, ×0.75; *d,* paratype, lateral view of ventral valve showing elevated muscle platform, ×2; *e,* holotype, posterior view of incomplete shell with cardinal process and median septum, USNM 151225c, ×1 (Cooper & Grant, 1974).

Streptopomum HAVLÍČEK, 1967, p. 207 [**Streptorhynchus mjatschkowensis* SOKOLSKAYA in SARYTCHEVA & SOKOLSKAYA, 1952, p. 54; OD] [=*Miniplanus* WATERHOUSE & PIYASIN, 1970, p. 101 (type, *M. minuta*)]. Similar to *Diplanus* but lacking concentric lamellae and dorsal interarea. [*Streptopomum* is morphologically close to *Diplanus* but its assignment to the Derbyiidae is also provisional on ascertaining its shell structure, which is presently unknown. *Miniplanus* from the middle Permian of Thailand is considered to be a junior synonym of *Streptopomum* despite the fact that it was mistakenly described by its authors as having a deltidium, crural plates, and a cardinal process with "4 to 6 low tubercles along the upper edge."] *Upper Carboniferous:* Russia.——FIG. 474,*1a–d. *S. mjatschkowensis* (SOKOLSKAYA), Moscovian, Moscow basin; dorsal valve interior, ventral valve posterior, exterior, dorsoposterior views of ventral valve, ×1 (Sarytcheva & Sokolskaya, 1954).

Family MEEKELLIDAE Stehli, 1954

[*nom. transl.* WILLIAMS, 1965e, p. 405, *ex* Meekellinae STEHLI, 1954, p. 303]

Medium to large, mostly rectimarginate, finely costellate mainly by branching, commonly secondarily costate or costellate; ventribiconvex; beak of subconical ventral valve generally not greatly distorted, interarea variable in height, procline to apsacline, perideltidium well developed, pseudodeltidium usually flat with monticulus, dorsal interarea linear, chilidium commonly reduced to boss; dental ridges discrete, supported by dental plates converging on median septum or on valve floor, flanked by flabellate diductor scars when muscle bases impressed, presumably with adductor attachment between dental plates; cardinal process lobes fused proximally into single shaft and bearing slitlike myophores distally; inner socket ridges divergent, ankylosed to cardinal process, brachiophores well developed, bladelike; dorsal adductor scars and myophragm variably developed. *Lower Carboniferous–Upper Permian.*

Subfamily MEEKELLINAE Stehli, 1954

[Meekellinae STEHLI, 1954, p. 303]

Rectimarginate, secondary costae and branching costellae normally fully developed in mature shell; ventral interarea high with flat pseudodeltidium and monticulus accommodating chilidium reduced to boss on posterior surface of shaft of long cardinal process curving posteroventrally; sockets delineated laterally by fulcral plates, brachiophores becoming pointed. *Lower Carboniferous–Upper Permian.*

Meekella WHITE & ST. JOHN, 1867, p. 120 [**Plicatula striatocostata* COX, 1857, p. 568; OD] [=*Gegenella* LI & GU, 1976, p. 236 (type, *G. gegenensis*)]. Medium sized, finely costellate by branching, ventral interarea high, procline to mainly apsacline; dental plates convergent onto floor of ventral valve and medial of rarely impressed, flabellate diductor scars; cardinal process usually moderately long; dorsal adductor scars variably impressed within distal ends of socket ridges, bilobed about low myophragm. [*Gegenella* from the Lower Permian of Inner Mongolia was erected for species that differed from *Meekella* in having dental plates well separated by a broad median septum. In fact, the degree of convergence of the dental plates of *Meekella* is quite variable and they frequently ankylose on the floor of the ventral valve with a callus of secondary shell that is comparable with the median septum of *Gegenella.*] *Carboniferous–Upper Permian:* cosmopolitan.——FIG. 476,*2a–e. *M. striatocostata* (COX), Moscovian, Iowa; *a–c,* dorsal, ventral, lateral views of shell, ×1; *d,* detail of shell ornament, ×5; *e,* posterior view of ventral valve, ×2 (new).——FIG. 476,*2f,g. M. attenuata* (GIRTY), Leonardian, Texas; *f,* oblique lateral view of cardinalia, ×4; *g,* ventral valve interior, ×1.5 (Cooper & Grant, 1974).

Alatorthotetina HE XI-LIN & ZHU MEI-LI, 1985, p. 200[203] [**A. sichuanensis;* OD]. Similar to *Orthothetina* but usually planoconvex with mucronate hinge line, finely costellate by branching, ventral diductor scars impressed lateral of short, parallel dental plates. *Upper Permian:* southwestern China.——FIG. 476,*1a–c. *A. sichuanensis,* Upper Permian, Sichuan; *a,* dorsal valve exterior, ×1; *b,* paratype, ventral valve exterior, ×1; *c,* paratype, ventral valve internal mold, ×1 (He & Zhu, 1985).

Asiomeekella LIANG, 1990, p. 120[458] [**A. isoconvexa;* OD]. Similar to *Meekella* in general appearance but with catacline ventral interarea, convex pseudodeltidium, less convergent dental plates bounding a pair of low submedial septa, and short cardinal process. [The assignment of this genus to the Meekellidae is provisional on a more compre-

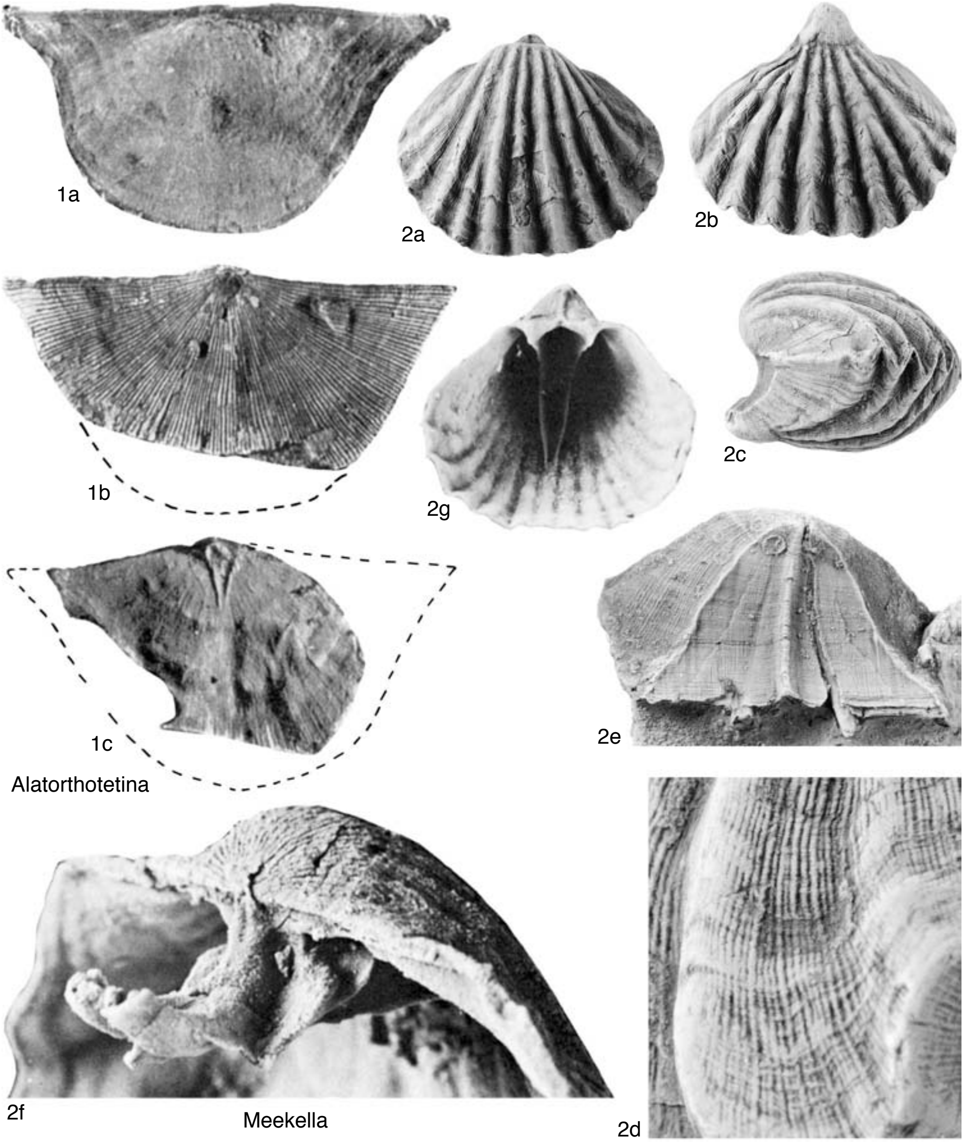

FIG. 476. Meekellidae (p. 660).

hensive description of the type species, based on better material. The submedial ridges between the dental plates on the floor of the ventral valve may be nothing more than radial striations that are commonly associated with muscle scars, while nothing is known about the cardinalia other than the fact that the cardinal process is large, stout but short.] *Carboniferous–Permian:* China.

Geyerella SCHELLWIEN, 1900, p. 12 [**G. gemmellaroi;* OD] [=*Turriculum* DE GREGORIO, 1930, p. 26 (type, *T. imperans*)]. Similar to *Meekella* but variable in size, finely costellate mainly by intercalation, secondary costation variable in amplitude and disposition, occasionally complicated by impersistent rugation; dental plates convering on high median septum, dorsal myophragm variably developed. *Upper Carboniferous–Permian:* cosmopolitan.——FIG. 477,*4a,b.* **G. gemmellaroi,* ?Kazanian, Valle de Sosio, Sicily; *a,* posterior view of shell, ×1; *b,* detail of shell, ×2 (new).——FIG. 477,*4c,d. G. hessi* COOPER & GRANT, Wolfcampian, Texas; paratype, interior of ventral valve showing spondylium, posteriorly tilted view of dorsal valve, ×1 (Cooper & Grant, 1974).

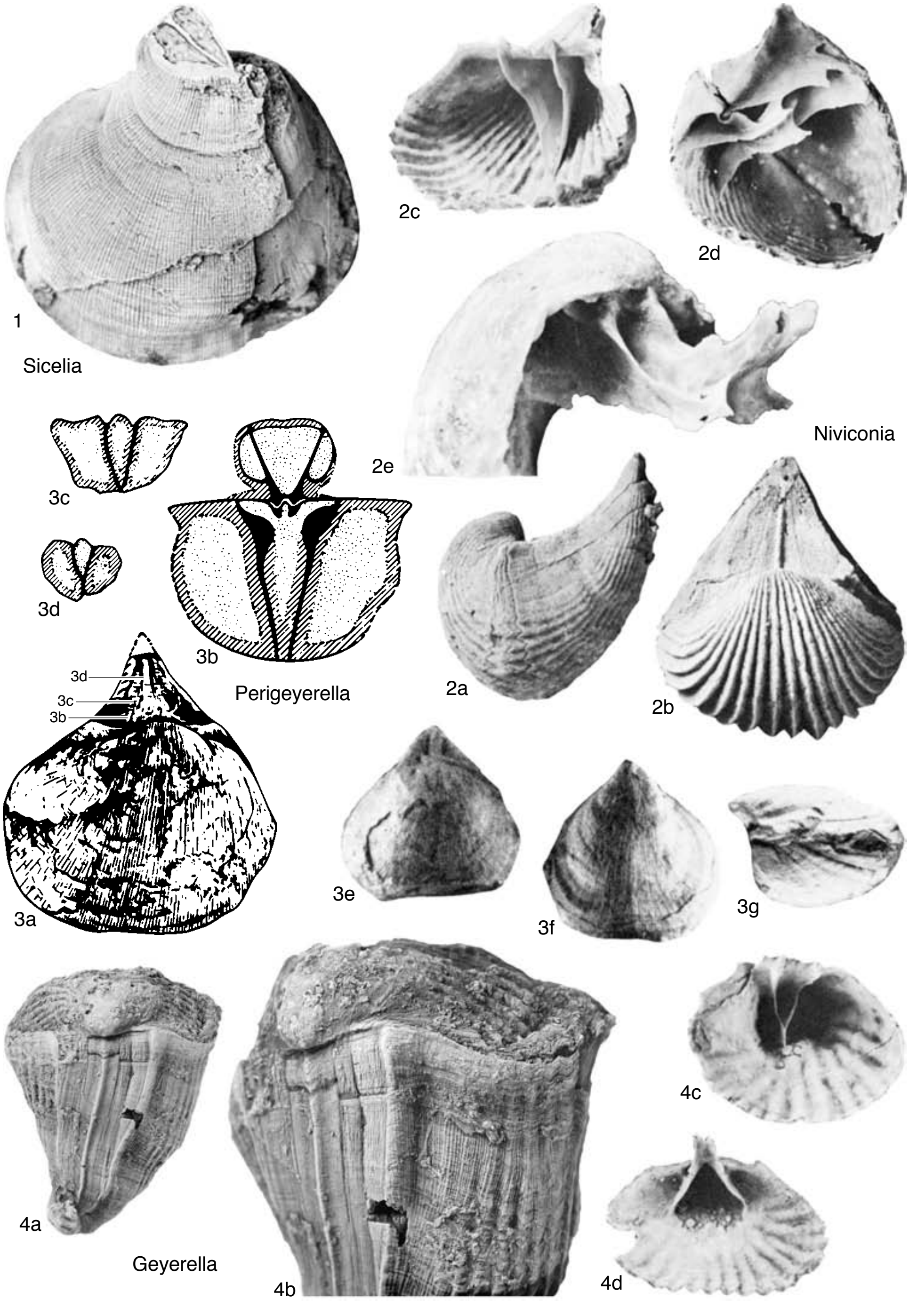

FIG. 477. Meekellidae (p. 661–664).

Niviconia COOPER & GRANT, 1974, p. 373 [**Meekella globosa* R. E. KING, 1931, p. 54; OD]. Similar to *Meekella* but generally large, strongly ventribiconvex with high conical ventral valve; low, even secondary costae; cardinal process high. *Permian (Artinskian–Kungurian):* western USA.——FIG. 477,*2a–e*. **N.*

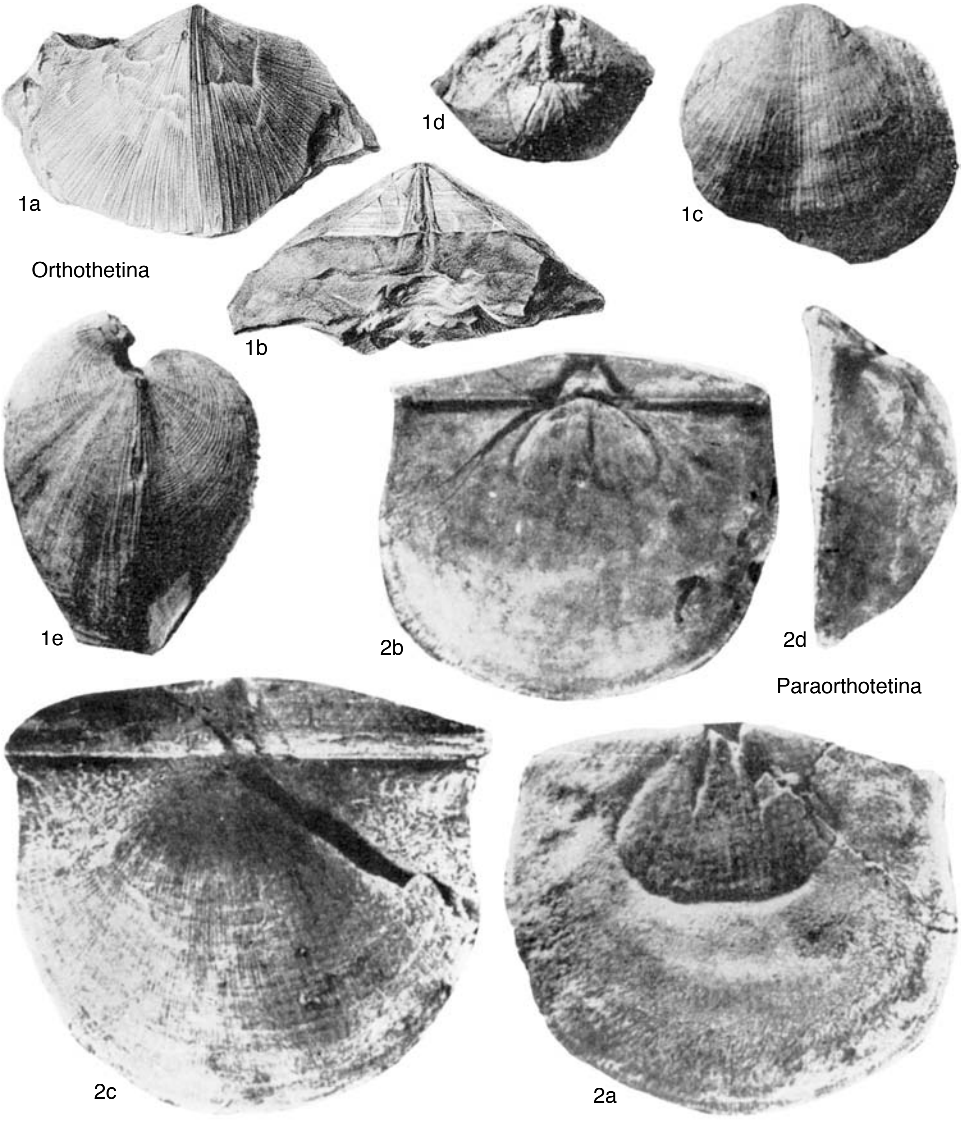

FIG. 478. Meekellidae (p. 663–664).

globosa (KING), Leonardian, Texas; *a,b,* lateral, dorsal views of shell, ×1; *c,* oblique view of ventral valve interior, ×1; *d,* posterolateral internal view of articulated valves, ×1; *e,* lateral view of cardinalia, ×2 (Cooper & Grant, 1974).

Orthothetina SCHELLWIEN, 1900, p. 8 [**Orthothetes persicus;* SD SCHUCHERT in SCHUCHERT & LEVENE, 1929, p. 91] [=*Lopingia* CHAN, 1979, p. 64 (type, *Orthotetes ruber* FRECH, 1911, p. 124)]. Similar to *Meekella* including strong monticulus in flat pseudodeltidium, dental plates converging separately onto floor of ventral valve, and fine costellation mainly by branching but without radial plicae of secondary costation. [*Lopingia* from the Permian of southern China appears to differ from *Orthothetina* only in the less convex to resupinate ventral valve.] *Carboniferous–Permian:* cosmopolitan.——FIG. 478,*1a–c.* **O. persicus* (SCHELLWIEN); *a,b,* exterior, posterior views of ventral valve, Kazanian, Persia, Iran, ×1 (Schellwien, 1900); *c,* dorsal valve exterior, Dzulfian, Transcaucasia, ×1 (Sarytcheva & Sokolskaya, 1965).——FIG. 478,*1d. O. iljinae* (SOKOLSKAYA), Guadalupian, Transcaucasia; holotype, posterior view of dorsal valve, ×1 (Sarytcheva & Sokolskaya, 1965).——FIG. 478,*1e. O. peregrina* (ABICH), Dzhulfian, Transcaucasia; lateral view, ×1 (Sarytcheva & Sokolskaya, 1965).

Paraorthotetina He Xi-lin & Zhu Mei-li, 1985, p. 198[203] [**Orthotetina provecta* Liao, 1980, p. 254; OD] [=*Parameekella* He & Zhu, 1985, p. 198[203] (type, *P. hauyinshanensis*)]. Similar to *Orthothetina* but with greatest width at hinge line and deeply impressed ventral muscle scars, including flabellate diductor insertions on either side of parallel dental plates containing impressions of elongate adductor bases; dorsal adductor scars also deeply impressed about strong median septum. [*Parameekella* was erected for contemporaneous orthotetoids which differed from species assigned to *Paraorthotetina* only in being ornamented by impersistent wrinkles which may be radially arranged. This is an infraspecific feature in other Permian orthotetoids, similar to many *Derbyia* species of Texas (Cooper & Grant, 1974); and there is no evidence as yet that rugation in the Chinese forms was any less variable.] *Upper Permian:* southwestern China.——Fig. 478,*2a–d.* **P. provecta* (Liao), Upper Permian, western Guizhou; ventral valve internal mold, dorsal valve internal mold, dorsal exterior, lateral view of internal mold, ×1 (He & Zhu, 1985).

Perigeyerella Wang, 1955a, p. 101[1955b, p. 346] [**P. costellata;* OD]. Similar to *Geyerella* but without secondary costation and rounded in outline, usually with less conical ventral valve with sharply pointed beak, broadly unisulcate, finely costellate mainly by branching cancellated by strong, concentric fila; dental plates becoming less convergent with growth so that narrow chamber with supporting median septum is characteristic of young ventral valve and sessile septal chamber or discrete dental plates typical of adult valve. *Upper Permian:* China.——Fig. 477,*3a–g.* **P. costellata,* Upper Permian, northern Guizhou; *a,* dorsal view of complete shell, ×1; *b–d,* serial sections at intervals shown on *a,* ×2 (Wang, 1955); *e–g,* dorsal, ventral, lateral views of shell, ×1 (Yang & others, 1977).

Sicelia Gortani & Merla, 1934, p. 284, *nom. nov. pro Canavaria* Merla, 1928, p. 70, *non* Oppenheim, 1899, *nec* Gemmellaro, 1886 [**Canavaria acropedion* Merla, 1928, p. 70; OD] [=*Gemmellaria* Fabiani & Ruiz, 1933, p. 7 (footnote), *non* Munier-Chalmas, 1873; *Parageyerella* He & Zhu, 1985, p. 203 (type, *P. daijiagouensis*); *Hamletella* Hayasaka, 1953, p. 92 (type, ?*Streptorhynchus altus* Hamlet, 1928)]. Similar to *Meekella* but without secondary costation, finely parvicostellate mainly by intercalation. [*Hamletella,* from the Permian of Timor, with its parvicostellate and impersistently rugate exterior, flat pseudodeltidium with monticulus, convergent, subparallel dental plates and divergent socket ridges, was summarized by its author as a *Meekella* without secondary costation or plication and with a more elongate ventral valve. These are the features distinguishing *Sicelia* from *Meekella.*] *Permian:* Eurasia. ——Fig. 477,*1.* **S. acropedion* (Merla), Upper Permian, Valle de Sosio, Sicily; ventral valve exterior, broken umbonal section, ×2 (Williams, 1965e).

Subfamily OMBONIINAE Sokolskaya, 1960

[Omboniinae Sokolskaya, 1960, p. 218]

Finely costellate by branching without secondary radial ornamentation; ventral beak distorted, interarea high with convex pseudodeltidium, dorsal interarea linear, chilidium usually small with median groove; cardinal process relatively low, socket ridges reduced, socket plates delicate, divergent containing lightly impressed bilobed dorsal adductor scars. *Permian.*

Ombonia Caneva, 1906, p. 54 [**O. canevai* Merla, 1931, p. 80; SD Merla, 1931, p. 80]. Medium sized, broadly uniplicate, lacking regularly developed concentric ornamentation; ventral interarea commonly apsacline; dental plates converging on strong, high median septum; ventral muscle scars obscure, dorsal myophragm variably developed. *Permian:* Eurasia, North America.——Fig. 479*a,b.* **O. canevai* Merla, Upper Permian, Dolomites, Italy; *a,* ventral valve internal mold; *b,* schematic diagram of dorsal valve interior, ×1 (Merla, 1931).——Fig. 479*c,d. O. dieneri* Licharew, Lower Permian, North Caucasus; *c,d,* dorsal, lateral views of shell, ×1 (Orlov, 1960).——Fig. 479*e–g. O. guadalupensis* (Girty), Guadalupian, Texas; ventral valve interior, exterior, dorsal valve interior, ×2 (Cooper & Grant, 1974).

Family SCHUCHERTELLIDAE Williams, 1953

[*nom. transl.* Stehli, 1954, p. 298, *ex* Schuchertellinae Williams, 1953b, p. 9]

Ventral valve variable in size and shape, deformed by attachment but normally with high ventral interarea; shell usually finely costellate rarely with secondary costation; discrete dental ridges and teeth unsupported by dental plates; cardinal process lobes low, discrete becoming long and fused proximally into single shaft; socket ridges recurved to divergent, becoming fused with cardinal process base, brachiophore bases developing later, normally prolonged as brachiopores; shell extropunctate. *Middle Devonian–Permian.*

Subfamily SCHUCHERTELLINAE Williams, 1953

[Schuchertellinae Williams, 1953b, p. 9]

Normally subconical, rectimarginate, costellate with concentric ornamentation; ventral interarea variably disposed, pseudo-

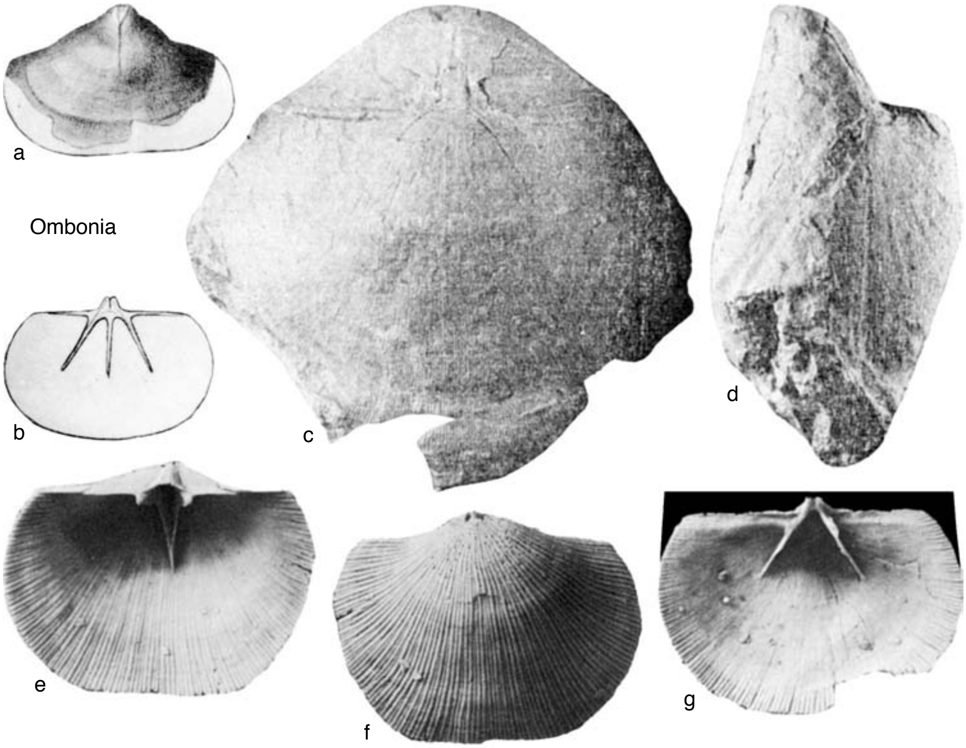

FIG. 479. Meekellidae (p. 664).

deltidium convex, dorsal interarea linear, chilidium normally present; ventral muscle scars usually faintly impressed without myophragm; low, discrete cardinal process lobes with myophore grooves, not ankylosed to recurved socket ridges, brachiophore bases usually prolonged as processes, dorsal muscle scars usually impressed about variably developed myophragm. *Middle Devonian–Lower Permian.*

Schuchertella GIRTY, 1904, p. 734 [**Streptorhynchus lens* WHITE, 1862, p. 28; OD]. Variable in size and in texture of costellae; ventral interarea usually anacline, chilidium convex; flabellate ventral muscle scars and impressed dorsal adductor scars, each set divided by low myophragm; extropunctae better developed in the dorsal valve. [Many middle and Upper Paleozoic schuchertelloid species, morphologically resembling *S. lens* (WHITE) from the Louisiana Limestone of Missouri, have been identified as *Schuchertella.* Some of these are now known to be impunctate; others of those that have been described as pseudopunctate are extropunctate like the type species. Until the shell structure of all such assigned species has been checked, the true stratigraphic and geographic range of *Schuchertella* is in doubt.] *Upper Devonian–Upper Carboniferous, ?Lower Permian:* ?cosmopolitan.——FIG. 480,*1a–f.* **S. lens* (WHITE), upper Famennian, Missouri; *a,b,* dorsal, ventral views of shell, ×1.5; *c,* posterior view of shell, ×2; *d,e,* ventral valve, dorsal valve interiors, ×1.5; *f,* close up of previous specimen showing cardinalia, ×4 (new).

Goniarina COOPER & GRANT, 1969, p. 2 [**G. pyelodes;* OD]. Similar to *Schuchertella* but small, more strongly subconical, secondarily free, relatively coarsely costellate; faintly impressed ventral muscle scar lacking myophragm and strongly impressed dorsal adductor scars on incipient, tuberculate platform with myophragm attaining maximum height anteriorly. *Lower Permian:* USA (Texas).——FIG. 480,*3a–f.* **G. pyelodes,* Wolfcampian, Texas; *a–d,* holotype, dorsal, lateral, ventral, posterior views of shell, USNM 150411g; *e–f,* paratypes, dorsal valve interior, ventral valve interior, ×4 (Cooper & Grant, 1974).

Serratocrista BRUNTON, 1968, p. 39 [**S. fistulosa;* OD]. Similar to *Schuchertella,* small and with more evenly developed costellae bearing arrays of short, pointed spines along crests; ventral interarea variably

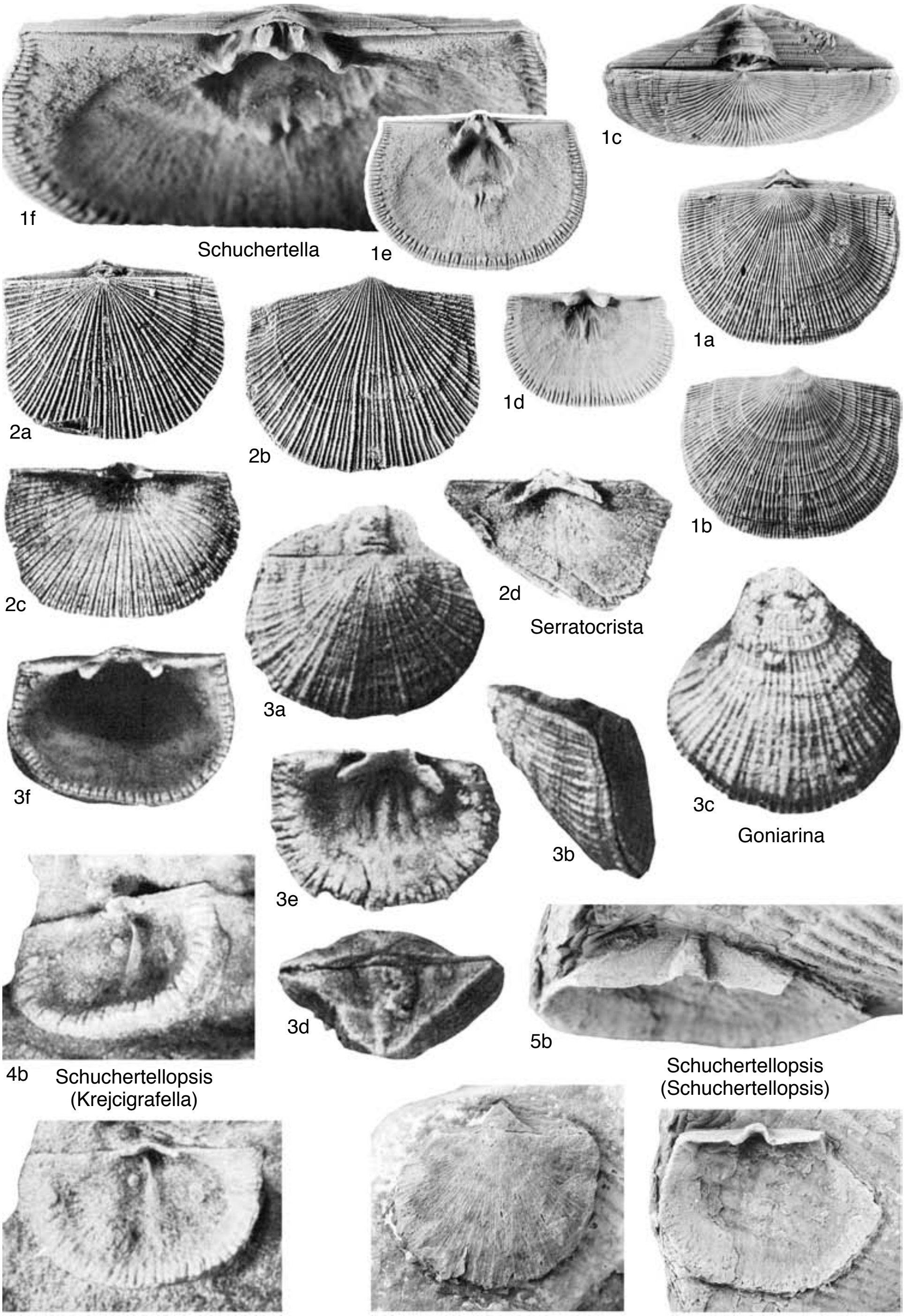

FIG. 480. Schuchertellidae (p. 665–667).

disposed, dorsal interarea and chilidium vestigial; muscle scars faint, lacking myophragms; socket ridges weak. *Lower Carboniferous (upper Viséan):* Ireland, northwestern Australia, ?North America.——Fig. 480,*2a–d.* **S. fistulosa,* Asbian, Fermanagh, Ireland; *a,b,* holotype, dorsal, ventral views of shell, ×1.8; *c,* ventral valve interior, ×1.6; *d,* incomplete dorsal valve interiors, ×1.7 (Brunton, 1968).

Schuchertellopsis Maillieux, 1939, p. 5 [**S. durbutensis;* OD]. Small (10 to 12 mm wide), irregularly shaped shells with ventral valves cemented almost completely to substrate; hinge line approximately widest part of shell, ventral profile irregular, dorsal profile plane to weakly convex; ventral interarea with arched pseudodeltidium, dorsal interarea weak; irregularly costellate; dental ridges unsupported; dorsal valves poorly known. [The assignment of this genus and its subgenera is uncertain, but it probably belongs here. It will be fully described and figured in the appendix of Volume 5 of this *Treatise* revision of the Brachiopoda following evaluation of its shell structure.] *Middle Devonian (Eifelian)–Upper Devonian (Frasnian):* western Europe, ?southern North America.

S. (**Schuchertellopsis**). *Schuchertellopsis* lacking ventral median septum; inner socket ridges extend at shallow angle from hinge, muscle fields indistinct. *Upper Devonian (upper Frasnian):* Belgium, ?southern North America (New Mexico).——Fig. 480,*5a–c.* **S. (S.) durbutensis,* attached to cyrtospiriferid shells, upper Frasnian, Belgium; *a,* syntype, ventral valve viewed dorsally, IRScNB a 1140, ×2; *b,* syntype, ventral valve viewed posteriorly, IRScNB a 1140, ×3; *c,* syntype, complete shell viewed dorsally, IRScNB a 1142, ×2 (new).

S. (**Krejcigrafella**) Struve, 1978, p. 97 [**S. (K.) krejcigrafi;* OD]. Resembles *S. (Schuchertellopsis),* but with ventral median septum from below pseudodeltidium to ridged marginal thickening. [Known only from ventral valves attached to stromatoporoids.] *Middle Devonian (lower Eifelian):* Germany (Eifel region).——Fig. 480,*4a,b.* **S. (K.) krejcigrafi,* lower Eifelian, Germany; holotype, ventral valve interior viewed dorsally and obliquely, SMF 31801, ×3 (Struve, 1978).

Subfamily STREPTORHYNCHINAE Stehli, 1954

[Streptorhynchinae Stehli, 1954, p. 299] [=Tropidelasminae Waterhouse, 1983a, p. 117]

Normally medium sized with variably disposed commissure and fine, branched costellae, secondary costation rare, concentric ornamentation variable; ventral interarea high, usually apsacline with convex pseudodeltidium rarely folded into monticulus, perideltidium rarely absent, dorsal interarea usually linear with chilidium; ventral muscle scars normally flabellate without myophragm; cardinal process lobes long, with myophore slots, fused proximally into single shaft, ankylosed to enlarged socket ridges (erismata), socket ridges usually well developed and prolonged as processes; dorsal muscle scars usually impressed, with low myophragm. *Carboniferous–Permian.*

Streptorhynchus King, 1850, p. 107 [**Terebratulites pelargonatus* von Schlotheim, 1816, p. 28; OD] [=*Lespius* de Gregorio, 1930, p. 24 (type, *L. favoritus*); *Mammosum* de Gregorio, 1930, p. 24 (type, *M. ipsium*)]. Small to medium sized, subconical, ventribiconvex, relatively coarsely costellate with concentric fila; ventral interarea apsacline, pseudodeltidium with monticulus, chilidium small, grooved medianly; ventral muscle scar flabellate, dorsal muscle scar faintly impressed; cardinal process high, occasionally with short median ridge or node at base. *Carboniferous–Permian:* cosmopolitan.——Fig. 481,*4a–f.* **S. pelargonatus* (von Schlotheim), Kazanian, Gera, Germany; *a–c,* ventral, anterior, lateral views of shell, ×1.5; *d,* posterodorsal view of shell, ×3; *e,* dorsal valve interior showing cardinalia; *f,* latex mold of dorsal valve interior showing articulation, ×2 (new).

Arctitreta Whitfield, 1908, p. 57 [**A. pearyi;* OD] [=*Grumantia* Ustritsky in Ustritsky & Tschernjak, 1963, p. 70 (type, *Streptorhynchus kempei* (Andersson) in Wiman, 1914)]. Medium to large sized, subpentagonal, ventribiconvex, rectimarginate, finely costellate, concentric ornamentation unknown; apsacline ventral interarea with convex pseudodeltidium and monticulus, vestigial dorsal interarea and chilidium; ventral muscle scar flabellate, dorsal scars faintly impressed about low myophragm; cardinal process high. *Permian:* Arctic North America, Greenland, Spitzbergen, Arctic Russia.——Fig. 481,*2a–d. A. kempei* (Andersson), Seladersk series, Upper Permian, Spitzbergen; *a,* ventral valve exterior, ×0.7; *b,* dorsal valve internal mold, ×1; *c,* ventral valve internal mold, ×0.67; *d,* juvenile dorsal valve interior, ×1 (Manankov, 1979).

Bothrostegium Cooper & Grant, 1974, p. 330 [**B. derbyoideum;* OD]. Similar to *Streptorhynchus* but small and more finely costellate, with variably disposed high interarea, grooved pseudodeltidium, conspicuous perideltidium, grooved chilidium; relatively low cardinal process; ventral muscle scar faint, dorsal muscle scar subcircular with low myophragm. *Lower Permian:* USA (Texas).——Fig. 481,*1a–f.* **B. derbyoideum,* Roadian, Texas; *a–d,* anterior, dorsal, posterior, lateral views of shell, ×3; *e,* paratype, dorsal valve interior, ×4; *f,* paratype, posterior view of cardinalia, ×3 (Cooper & Grant, 1974).

Chelononia Cooper & Grant, 1974, p. 327 [**C. neali;* OD]. Similar to *Streptorhynchus* but elongately pyramidal, variably biconvex, unisulcate and

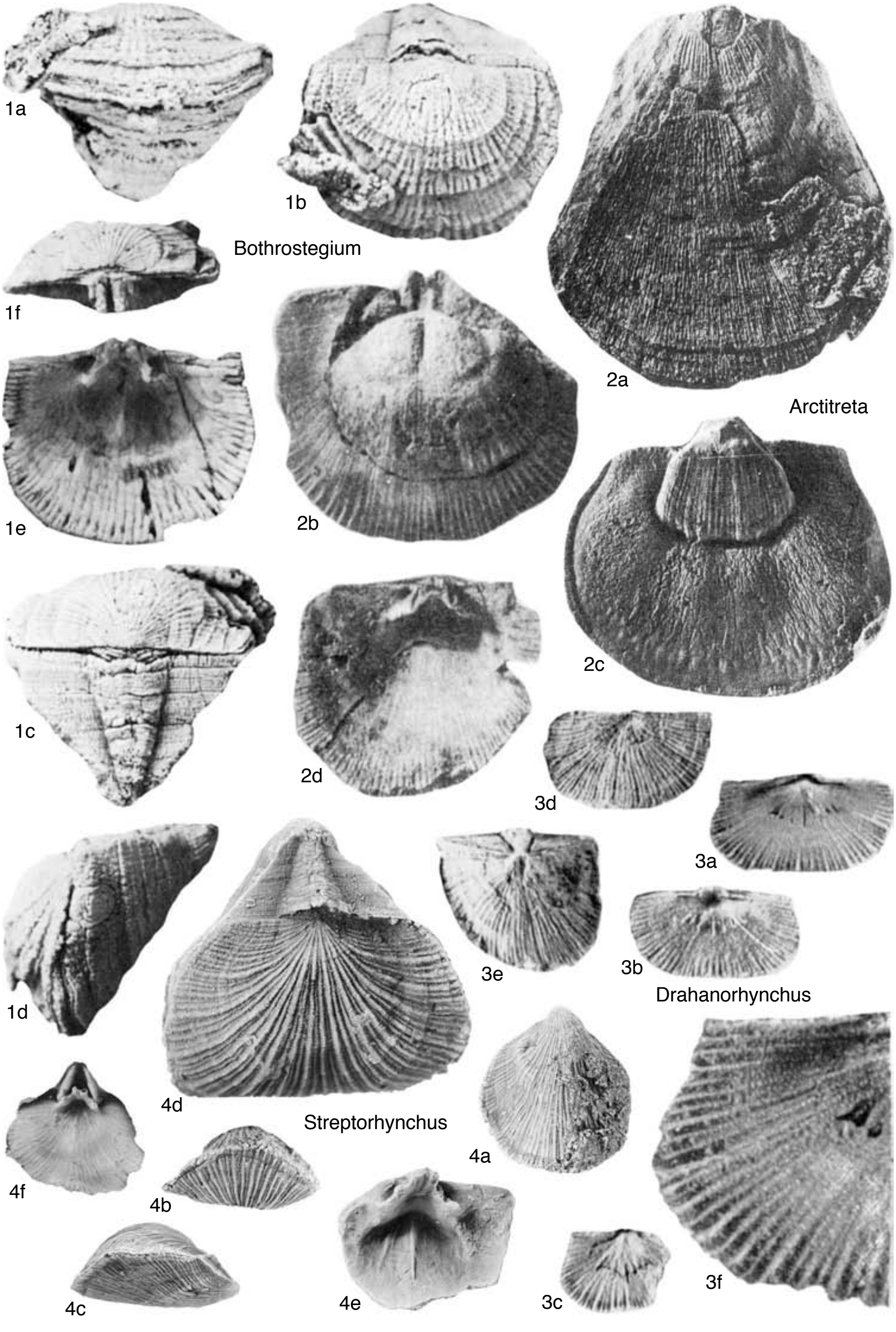

FIG. 481. Schuchertellidae (p. 667–670).

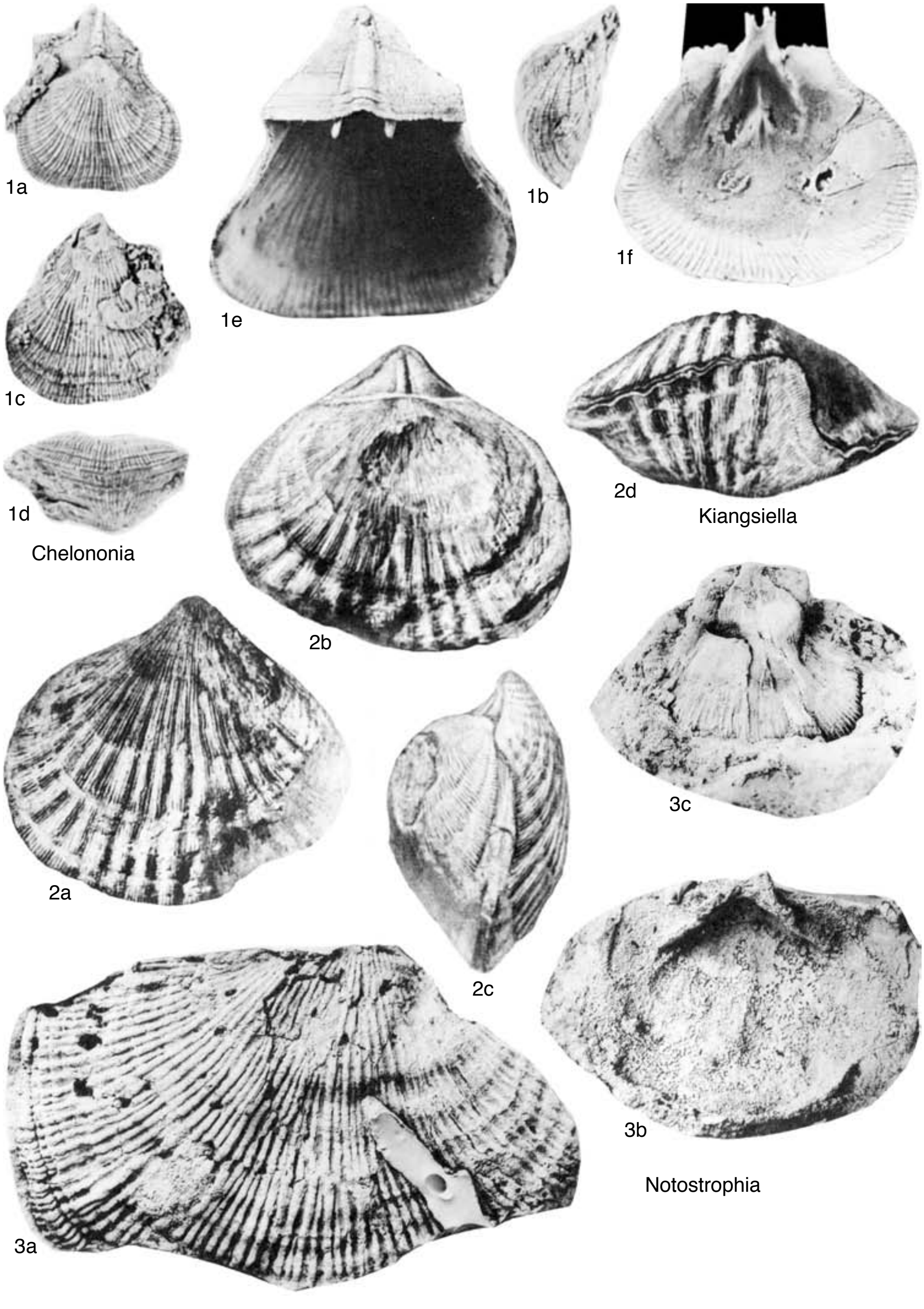

FIG. 482. Schuchertellidae (p. 667–670).

more finely costellate with concentric fila, evenly convex pseudodeltidium; impressed dorsal adductor scar and thick, low myophragm. *Lower Permian:* USA (Texas).——FIG. 482,*1a–f.* **C. neali,* Wolfcampian, Texas; *a–d,* holotype, dorsal, lateral, ventral, anterior views of shell, USNM 152646f,

×1; *e,f,* ventral valve of paratype, dorsal valve interior, ×2 (Cooper & Grant, 1974).

Drahanorhynchus HAVLÍČEK, 1967, p. 203 [**D. drahanicus;* OD]. Small, semioval, semiconical ventral valve, concave to plane dorsal valve, finely costellate with microscopic spines along crests; ventral interarea catacline to procline, pseudodeltidium convex, dorsal interarea and chilidium vestigial; dental plates and ventral median septum absent; socket ridges parallel with hinge line, fused with low cardinal process lobes with median process at base, dorsal adductor scar associated with myophragm flanked by 2 or 4 pairs of small radiating septa; shell extropunctate. [This genus is provisionally placed in the Schuchertellidae on the basis of its overall orthotetoid morphology, its lack of dental plates, and especially evidence from well-preserved molds that internal surfaces were indented by "closely crowded pits" (HAVLÍČEK, 1967, p. 204). The septal arrangement on the floor of a dorsal valve that is plane to concave in profile is anomalous, however, and the species requires further confirmatory investigation.] *Lower Carboniferous:* Czech Republic.——FIG. 481,*3a–f.* **D. drahanicus,* lower Viséan, Moravia; *a,b,* holotype, internal mold of dorsal valve, latex replica of same specimen, ×3; *c,d,* internal mold of incomplete dorsal valve, external mold of dorsal valve, ×3; *e,* internal mold of ventral valve, ×3; *f,* internal mold of dorsal valve showing small pits in radial arrangement, ×9 (Havlíček, 1967).

Kiangsiella GRABAU in CHAO, 1927a, p. 103 [**Orthotetes tingi* GRABAU, 1924, p. 359; OD]. Similar to *Streptorhynchus* but with strong, secondary costation and with well-developed median ridge at base of cardinal process; dorsal adductor scar impressed about low myophragm. *Upper Carboniferous–Permian:* Asia, Australia.——FIG. 482,*2a–d.* **K. tingi* (GRABAU), Lower Permian, southern Kiangsi, China; holotype, ventral, dorsal, lateral, anterior views of shell, ×1 (Chao, 1927a).

Notostrophia WATERHOUSE, 1973, p. 35 [**N. homeri;* OD]. Large, ventribiconvex with recurved margin to dorsal valve; ventral valve and recurved margin of dorsal valve finely costellate, rest of dorsal valve coarsely costate, rarely rugate; pseudodeltidium undescribed, chilidium platelike; teeth with low dental ridges (also referred to as plates), ventral muscle scar flabellate about low myophragm; cardinal process lobes low, grooved, with median node at base; socket ridges recurved; dorsal adductor scars impressed about short myophragm. [This genus has been assigned by its author to the Schuchertellidae and has been closely compared with the streptorhynchids *Arctitreta, Grumantia,* and an Australian species of *Streptorhynchus.* The author, however, who is given to an idiosyncratic usage of terminology in his systematic descriptions, has also reported the genus as being "pseudopunctate, 2 per mm." Until this and other features of the shell can be checked, no familial assignment of the genus can presently be made with any confidence.] *Lower Permian:* New Zealand.——FIG. 482,*3a–c.* **N. homeri,* Artinskian, Lower Permian, Southland; *a,* external latex cast of dorsal valve; *b,* latex cast of dorsal interior; *c,* internal mold of ventral valve, ×2 (Waterhouse, 1982c).

Taimyropsis USTRITSKY in USTRITSKY & TSCHERNJAK, 1963, p. 69 [**T. monstrosus;* OD]. This genus was erected for one incomplete asymmetrical, gently convex, rounded ventral valve ornamented by fine costellae and impersistent concentric rugae and with 2 subparallel, shallow grooves traced from the beak for about one-third the length of the valve. These grooves have been interpreted as incipient dental ridges and have been cited as distinguishing the specimen from *Orthothetina* and *Streptorhynchus.* In fact, the grooves could also represent striations associated with muscle scars; more specimens of both valves will have to be examined and described to assess the merits of this genus. *Permian:* Taimyr, Turuzovks Series.

Tropidelasma COOPER & GRANT, 1969, p. 3 [**T. culmenatum;* OD] [=*Erismatina* WATERHOUSE, 1983a, p. 117 (type, *E. cooperi*)]. Similar to *Streptorhynchus* but more finely costellate with flattish pseudodeltidium folded into narrow monticulus, short dorsal interarea, vestigial chilidium; fulcral plates confining sockets, faintly impressed ventral muscle scar, dorsal adductor scars impressed about slender myophragm. *Lower Permian:* USA (Texas), Thailand, ?Western Australia.——FIG. 483*a–e.* **T. culmenatum,* Wolfcampian, Lower Permian, Texas; *a,* holotype, posterior view of shell, USNM 147829b, ×1; *b,* paratype, lateral view of shell, ×1; *c,d,* paratypes, posterior view of ventral valve, posterior view of dorsal valve, ×1; *e,* paratype, internal view of cardinalia, ×3 (Cooper & Grant, 1974).

Superfamily CHILIDIOPSOIDEA Boucot, 1959

[*nom. transl.* WILLIAMS & BRUNTON, herein, *ex* Chilidiopsidae BOUCOT, 1959, p. 25] [=Fardeniacea JOHNSON, 1982, p. 973, *nom. transl. ex* Fardeniinae WILLIAMS, 1965e, p. 407]

Normally uncemented, rarely with functional pedicle in adult shell; commonly bilaterally symmetrical, rectimarginate; interareas commonly low, pseudodeltidium variable very rarely with monticulus, chilidium usually developed; dental ridges discrete, unsupported by dental plates in some younger stocks; socket ridges commonly short, recurved, rarely fused with cardinal process lobes, commonly low, discrete; brachiophores usually undeveloped; shell impunctate. *Upper Ordovician–Lower Carboniferous (lower Serpukhovian).*

Family CHILIDIOPSIDAE Boucot, 1959

[Chilidiopsidae BOUCOT, 1959, p. 25]

Uncemented with supra-apical foramen in ventral larval or adult valve; variably sized, symmetrical, semioval to subrounded, normally finely costellate with concentric fila; perideltidium present, occasionally obscure; dental plates short, mostly divergent; ventral muscle scar normally impressed occasionally about myophragm; socket ridges short and low, recurved laterally, not incorporating bases of discrete cardinal process lobes; dorsal muscle scar variably impressed, dorsal myophragm occasionally developed. *Upper Ordovician–Middle Devonian.*

Subfamily GACELLINAE new subfamily

[Gacellinae WILLIAMS & BRUNTON, herein]

Biconvex, uniplicate, supra-apical foramen present in adult ventral valve; interareas well developed, ventral apsacline to procline, dorsal anacline, perideltidium weakly defined, pseudodeltidium and chilidium well developed, convex; dental plates long, subparallel, flanking ventral muscle scar of elongated diductors and median, lanceolate adductors; socket ridges parallel with hinge line, dorsal adductor scars quadripartite about pair of divergent septa flanking low median ridge. *Upper Ordovician (Caradoc).*

Gacella WILLIAMS, 1962, p. 222 [**G. insolita;* OD]. Small, semioval, parvicostellate by intercalation, concentric fila well developed. *Upper Ordovician (Caradoc):* Scotland, southeastern USA.——FIG. 484*a–d.* **G. insolita,* Caradoc, Girvan, Scotland; *a,b,* dorsal, ventral views of shell; *c,d,* internal mold of ventral valve, dorsal valve interior, ×2.25 (Williams, 1965e).

Subfamily CHILIDIOPSINAE Boucot, 1959

[*nom. transl.* WILLIAMS & BRUNTON, herein, *ex* Chilidiopsidae BOUCOT, 1959, p. 25]

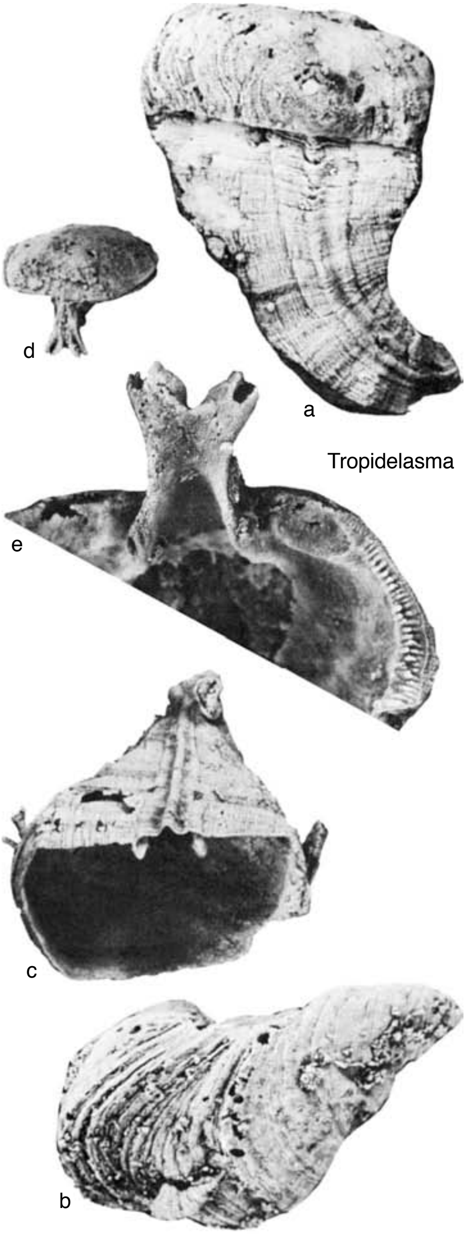

FIG. 483. Schuchertellidae (p. 670).

Mainly subquadrate, resupinate and rectimarginate with well-defined perideltidium, pseudodeltidium convex or occasionally vestigial; dental plates short, apical to divergent; short socket ridges mainly recurved, small, blunt brachiophores usually developed, ventral muscle scar usually large, flabellate. *Upper Ordovician–Middle Devonian.*

Coolinia BANCROFT, 1949, p. 7 [*?*Orthis applanata* SALTER, 1846, p. 72; OD] [=*Chilidiopsis* BOUCOT,

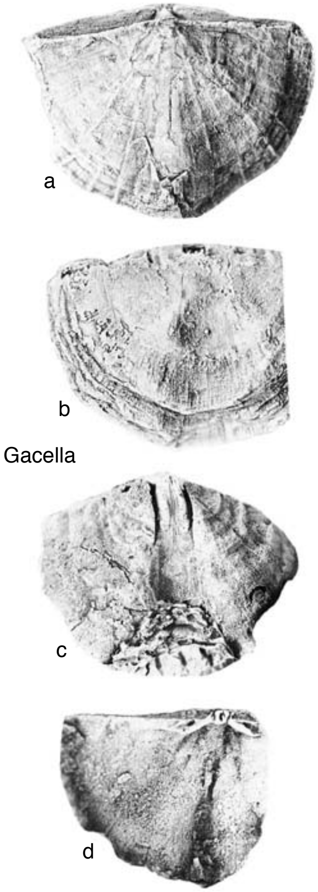

FIG. 484. Chilidiopsidae (p. 671).

1959, p. 25 (type, *Fardenia reedsi* Amsden, 1951, p. 84); *Krizistrophia* Havlíček, 1992, p. 176 (type, *K. micropoma*)]. Semioval to mucronate, biconvex, parvicostellate mainly by intercalation, fine concentric fila in interspaces, sporadically rugate; pedicle foramen not persisting in adult shell; pseudodeltidium apical; chilidium large; median basal node commonly developed between low cardinal process lobes, socket ridges recurved; ventral muscle scar flabellate, dorsal muscle scar divided by low myophore. [*Krizistrophia* Havlíček from middle Silurian limestones of Czech Republic is described as minute and as having strongly reduced cardinal process lobes. It is evidently a juvenile form of *Coolinia.*] *Silurian:* cosmopolitan.——Fig. 485,*2a–f.* **C. applanata* (Salter), upper Llandovery, Mayo, Ireland; *a,b,* ventral valve internal mold, latex replica of ventral interior, ×2; *c,* dorsal valve internal mold, ×2; *d,* latex replica of dorsal interior, ×4; *e,* ventral valve external mold; *f,* latex replica of ventral exterior, ×2 (new).

Fardenia Lamont, 1935, p. 310 [**F. scotica;* OD] [=*Saughina* Bancroft, 1949, p. 7 (type, *Strophomena pertinax* Reed, 1917, p. 907)]. Subquadrate, biconvex, relatively coarsely costellate mainly by branching, pedicle foramen usually persisting in adult shell, pseudodeltidium short, chilidium small, varying from pair of plates to complete cover; socket ridges recurved; muscle scars faint. *Upper Ordovician (Caradoc)–lower Silurian (Llandovery):* Europe.——Fig. 486*a–f.* **F. scotica,* Ashgill, Girvan, Scotland; *a,b,* exterior mold of dorsal valve, latex replica of same specimen, ×3.5; *c,* interior mold of dorsal valve; *d,* latex replica of same specimen, ×3.75; *e,f,* interior mold of ventral valve, latex replica of same specimen, ×3.5 (new).

Hipparionix Vanuxem, 1842, p. 124 [**H. proximus;* SD Hall & Clarke, 1892, p. 258] [=*Hipparionyx* King, 1846, p. 37]. Large, semioval, resupinate, rectimarginate, finely costellate (concentric ornamentation not preserved); pseudodeltidium large, convex; chilidium vestigial, dorsal interarea linear; dental plates divergent, posteriorly enclosing large, impressed, flabellate ventral muscle scar divided by low myophragm; cardinal process with high, discrete lobes, socket ridges recurved, dorsal muscle scars faint, divided by low myophragm. [*Iridistrophia* is presently distinguishable from *Hipparionix* by its parvicostellation arising by intercalation, interspacial concentric fila, and the median node between the cardinal process lobes. These differences, however, may be refuted when comparisons can be made between well-preserved specimens of both type species.] *Lower Devonian:* North America.——Fig. 485,*1a,b.* **H. proximus,* Lower Devonian, New York; dorsal valve interior, ventral valve interior mold, ×1 (Shimer & Shrock, 1944).

Iridistrophia Havlíček, 1965b, p. 292 [**Orthis umbella* Barrande, 1848, p. 206; OD] [=*Hinganella* Su, 1980, p. 285 (type, *Aesopomum chinensis* Hamada, 1971); *Magicostrophia* Zhu, 1985, p. 51 (type, *M. hingganensis;* OD)]. Large, semioval, resupinate, parvicostellate with fila in interspaces; pseudodeltidium convex, chilidium reduced or vestigal, dorsal interarea rudimentary; dental plates, long, divergent; basal median node between well-developed cardinal process lobes, concave socket ridges parallel with hinge line; muscle scars indistinct. [*Hinganella* Su from the Lower Devonian of northeastern China is now known to be impunctate and appears to differ from *Iridistrophia* only in the weak development of fila that could be ascribed to the state of preservation of the type specimens and in being sporadically unisulcate. *Magicostrophia* Zhu is inadequately described and poorly illustrated. According to known characters, including the disposition of socket ridges, it is a subjective synonym of *Iridistrophia,* but the pseudodeltidium and chilidium have still to be studied.] *Upper Ordovician, upper Silurian (Ludlow)–Lower Devonian (Emsian):* Europe, China, Argentina, *upper Silurian (Ludlow)–Lower Devonian (Emsian);* China, *Upper Ordovician.*——Fig. 485,*3a–d.* **I. umbella* (Barrande), Emsian, Bohemia; *a,* ventral valve exterior,

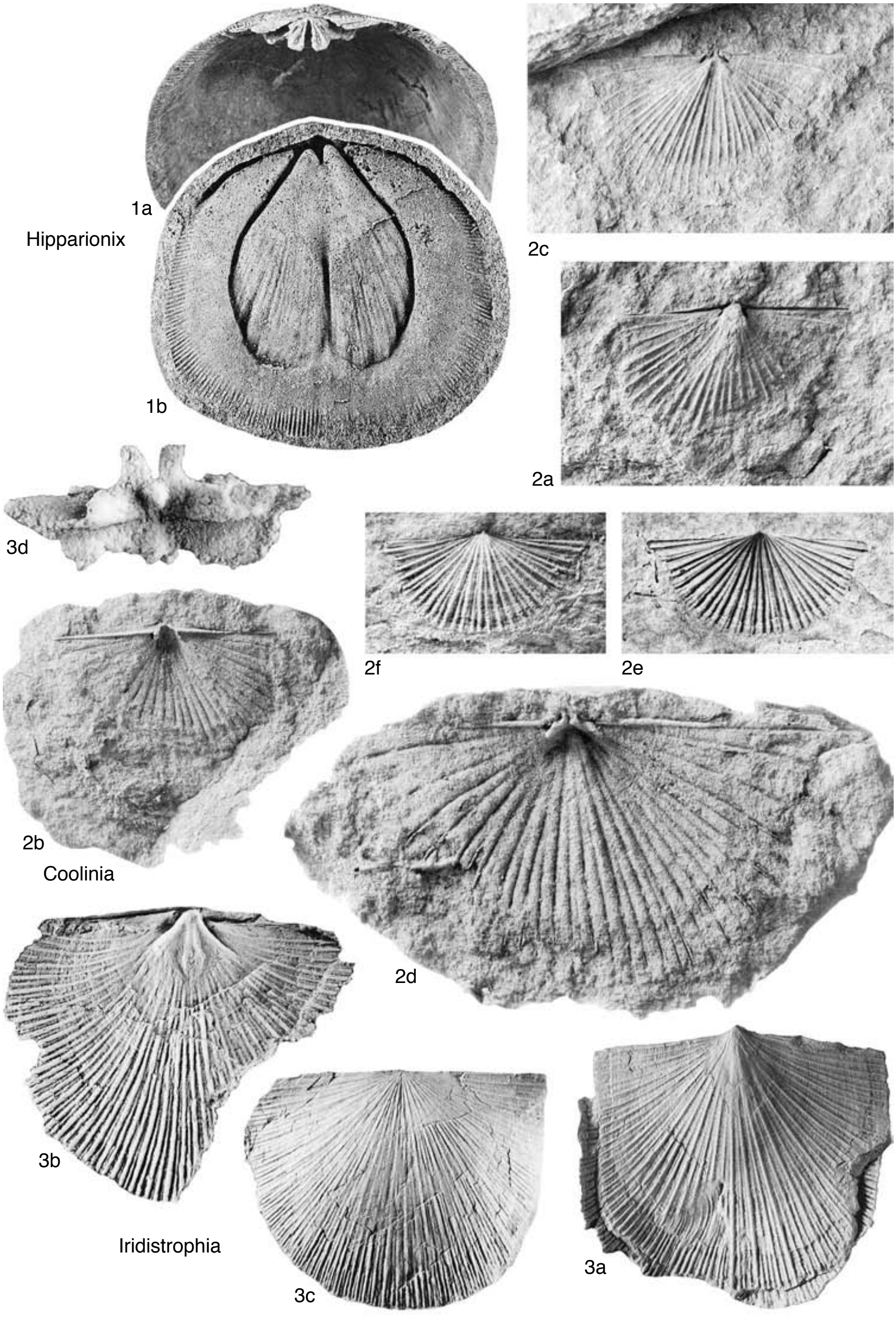

FIG. 485. Chilidiopsidae (p. 671–674).

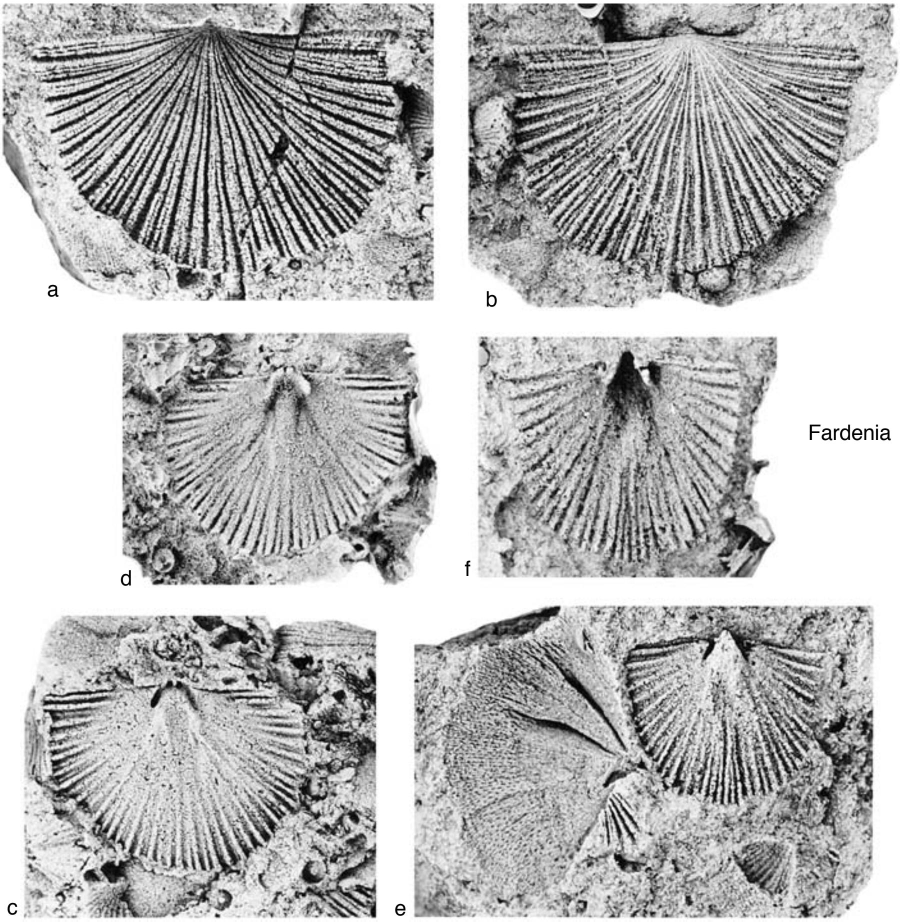

FIG. 486. Chilidiopsidae (p. 672).

×1.8; *b,c,* internal mold of ventral valve, dorsal valve exterior, ×1.5; *d,* internal view of cardinalia, ×4 (Havlíček, 1967).

Morinorhynchus HAVLÍČEK, 1965b, p. 291 [**M. dalmanelliformis;* OD]. Similar to *Fardenia* but subcircular and variably unisulcate; radial ornament tending to be finely fascicostellate, pseudodeltidium convex, chilidium of discrete plates; short socket ridges recurved parallel with hinge line; muscle scars faint with rhombic ventral impressions and lemniscate dorsal mantle canals. *upper Silurian (Ludlow):* Europe.——FIG. 487,*1a–c.* **M. dalmanelliformis,* Ludlow, Bohemia; holotype, ventral valve exterior, internal mold of ventral valve, internal mold of dorsal valve, ×2 (Havlíček, 1967).——FIG. 487,*1d–f. M. crispus* (LINDSTROM), Ludlow, Gotland, Sweden; *d,* syntype, ventral valve interior; *e,f,* lectotype, interior, exterior of dorsal valve, ×3 (Bassett & Cocks, 1974).

Pseudostrophomena RÕÕMUSOKS, 1963, p. 237 [* *P. reclinis;* OD]. Similar to *Coolinia* but small, subquadrate, and resupinate; median basal node between cardinal process lobes unknown; myophragm dividing ventral muscle scar, dorsal adductor scars faint. *Upper Ordovician:* Baltic region.——FIG. 488,*1a–f.* **P. reclinis,* upper Caradoc, Estonia; *a–c,* holotype, dorsal, ventral, lateral views of shell, ×1.7; *d,* holotype, posterior view of shell, ×2.4 (Rõõmusoks, 1963); *e,f,* dorsal interior, ventral interior, ×2 (new). [Note added in proof: but pseudopunctate, see p. 224.]

Valdaria BASSETT & COCKS, 1974, p. 18 [**V. testudo;* OD]. Similar to *Iridistrophia* but subcircular, gently resupinate, and uniplicate; parvicostellate interspaces without fila; chilidium small but entire; dental plates short, teeth weak; flabellate ventral muscle scar faintly impressed, dorsal muscle scar unknown. *lower Silurian–middle Silurian (Wenlock):* Sweden.

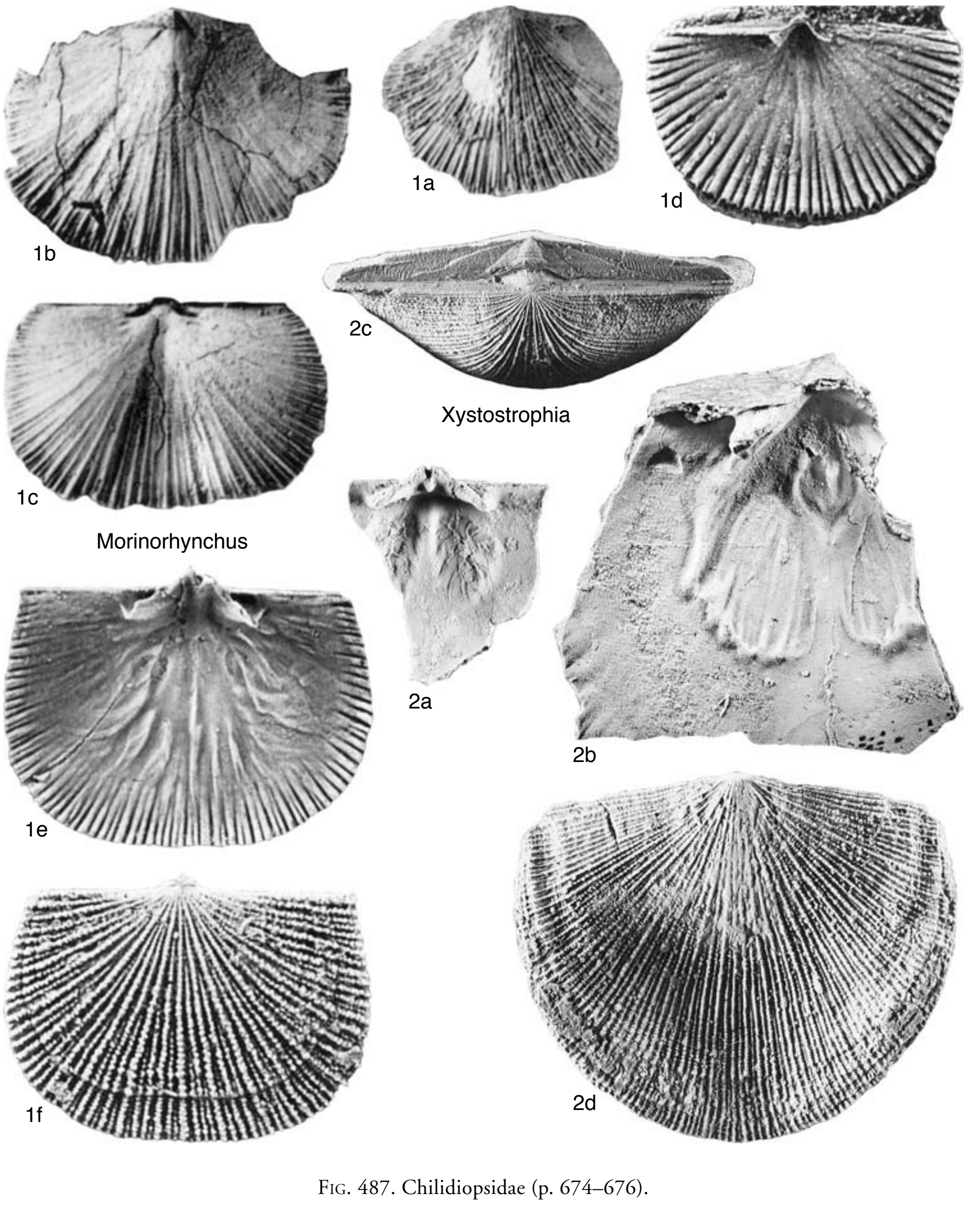

FIG. 487. Chilidiopsidae (p. 674–676).

——FIG. 488,*2a–c.* **V. testudo,* lower Wenlock, Gotland, Sweden; *a,* holotype, enlargement of interarea, ×2.25; *b,c,* ventral valve interior, ventral valve external mold, ×1.25 (Bassett & Cocks, 1974).

Xystostrophia HAVLÍČEK, 1965b, p. 292 [**Terebratulites umbraculum* SCHLOTHEIM, 1820, p. 256; OD] [=*Apicilirella* SU, 1976, p. 179 (type, *A. vulgaris*)]. Similar to *Coolinia* but larger, subquadrate, more resupinate with high convex pseudodeltidium and low chilidium; fila commonly extending as short spines along fine costellae; dorsal muscle scar divided by myophragm. [*Apicilirella* SU has been described by its author as unique among chilidiopsids in having a median ridge developed within the ventral muscle scar, which is not so. In other characteristics a close affinity with *Xystostrophia* was noted except for a stronger median elevation between the bases of the cardinal process lobes.] *Middle*

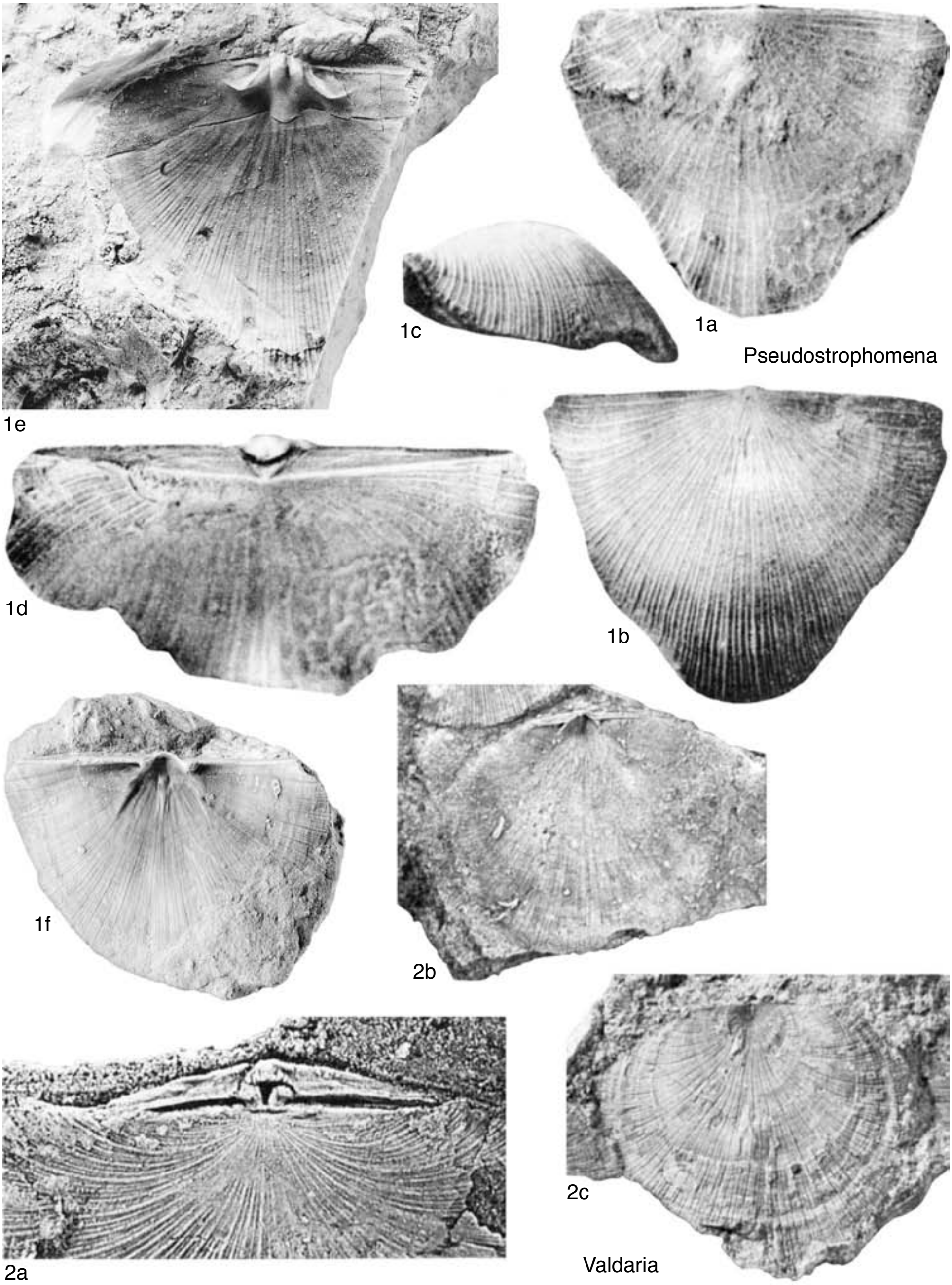

FIG. 488. Chilidiopsidae (p. 674–675).

Devonian: Europe.——FIG. 487,*2a–d.* **X. umbraculum* (SCHLOTHEIM), Givetian; *a,* incomplete dorsal valve, Holy Cross Mountains, Poland, ×1.5; *b,* ventral valve interior, Holy Cross Mountains, Poland, ×2; *c,d,* posterior, ventral views of shell, Rhineland, Germany, ×1.1 (Havlíček, 1967).

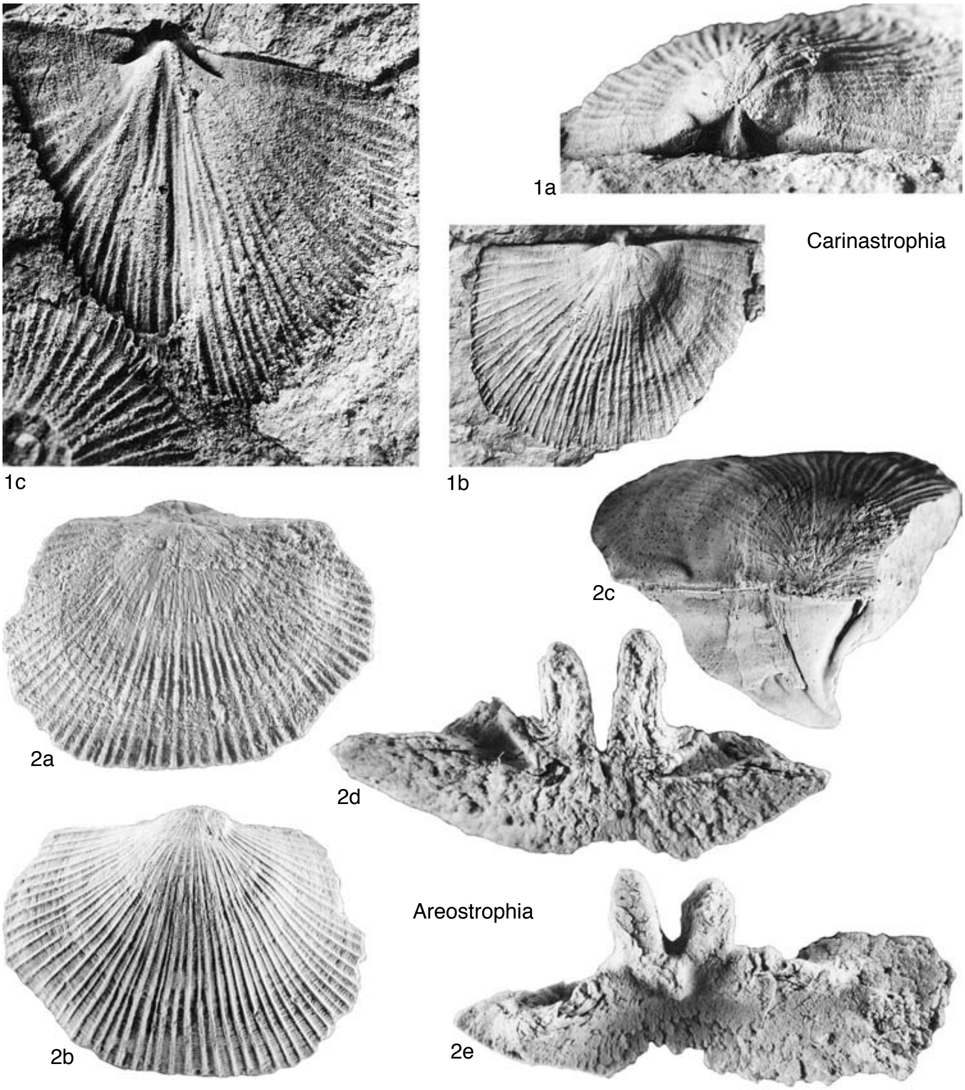

FIG. 489. Areostrophiidae (p. 678–679).

Family AREOSTROPHIIDAE Manankov, 1979

[*nom. transl.* WILLIAMS & BRUNTON, herein, *ex* Areostrophinae MANANKOV, 1979, p. 59]

Usually cemented by deformed ventral valve without trace of supra-apical foramen; variably sized, semioval to subconical, rectimarginate, variably costellate and concentrically ornamented; perideltidium present, occasionally obscure; dental ridges discrete, unsupported by dental plates, ventral muscle scar mostly faint, rarely associated with myophragm. *middle Silurian (Wenlock)–Lower Carboniferous (lower Serpukhovian).*

Subfamily AREOSTROPHIINAE Manankov, 1979

[Areostrophiinae MANANKOV, 1979, p. 59]

Medium to large, biconvex to resupinate; ventral interarea usually high but variable disposition, pseudodeltidium large, convex,

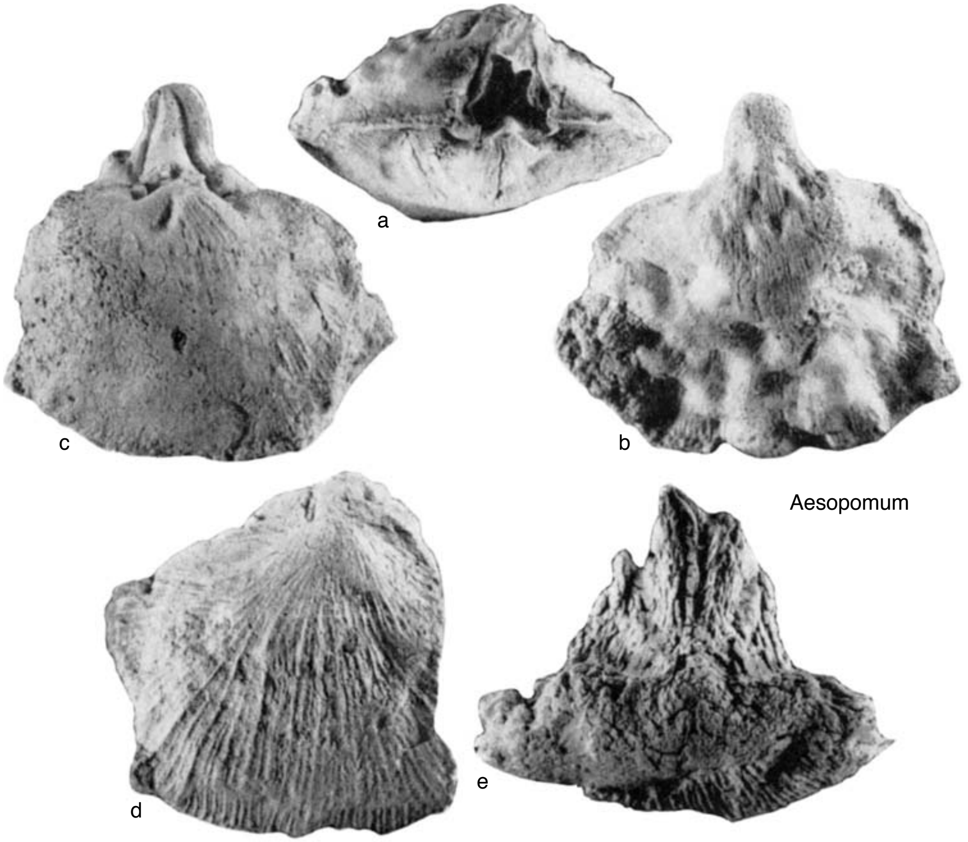

Fig. 490. Areostrophiidae (p. 678).

dorsal interarea lacking or short, anacline, chilidium not developed in adult valves; cardinal process lobes elongated, discrete or fused into proximal shaft, flanked by variably divergent socket ridges; dorsal adductor scars faint without myophragm. *upper Silurian–Middle Devonian (lower Eifelian).*

Areostrophia Havlíček, 1965b, p. 293 [*?*Orthis distorta* Barrande, 1879, p. 163; OD]. Large, biconvex, subrounded, parvicostellate by intercalation with fila in interspaces; ventral interarea commonly high, apsacline, dorsal interarea lacking; cardinal process lobes discrete, with myophore slits directed posteroventrally and united with strong inner socket ridges by divergent concave socket ridges. *upper Silurian–Lower Devonian:* Czech Republic, Siberia. ——Fig. 489,*2a–e*. **A. distorta* (Barrande), Pragian, Bohemia; *a,b,* dorsal, ventral valve exteriors, ×1.5; *c,* posterodorsal view of internal mold, ×1.5; *d,e,* external, internal views of cardinalia, ×3.5 (Havlíček, 1967).

Aesopomum Havlíček, 1965b, p. 293 [**Strophomena aesopea* Barrande, 1879, pl. 92, fig. 4, pl. 133, fig. 2; OD]. Similar to *Areostrophia* but subconical and irregular in shape with very high ventral interarea, dorsal interarea short, anacline; cardinal process lobes fused into single shaft, with myophore slits on posterior faces, ankylosed with divergent brachiophore bases and conspicuous, flanking socket ridges to form thick, concave socket plates (erismata); ventral muscle scar small, lightly impressed, without myophragm. *upper Silurian–Lower Devonian (Emsian):* Czech Republic, southern China.——Fig. 490*a–e*. **A. aesopeum* (Barrande), Bohemia; *a–c,* posterior, ventral, dorsal views of internal molds, Pragian, ×1.5; *d,* dorsal valve exterior, Pragian, ×1.5; *e,* posterior view of cardinalia, Emsian, ×2 (Havlíček, 1967).

Carinastrophia Gratsianova, 1975, p. 64 [**Areostrophia elinovi;* OD] [=*Xenizostrophia* Su, 1976, p. 181 (type, *X. spinosa*)]. Similar to *Areostrophia* but smaller with fine costellae slightly spinose at intersections with concentric fila; inwardly thickened dental ridges; median node between bases of cardinal process lobes. [*Xenizostrophia* Su from

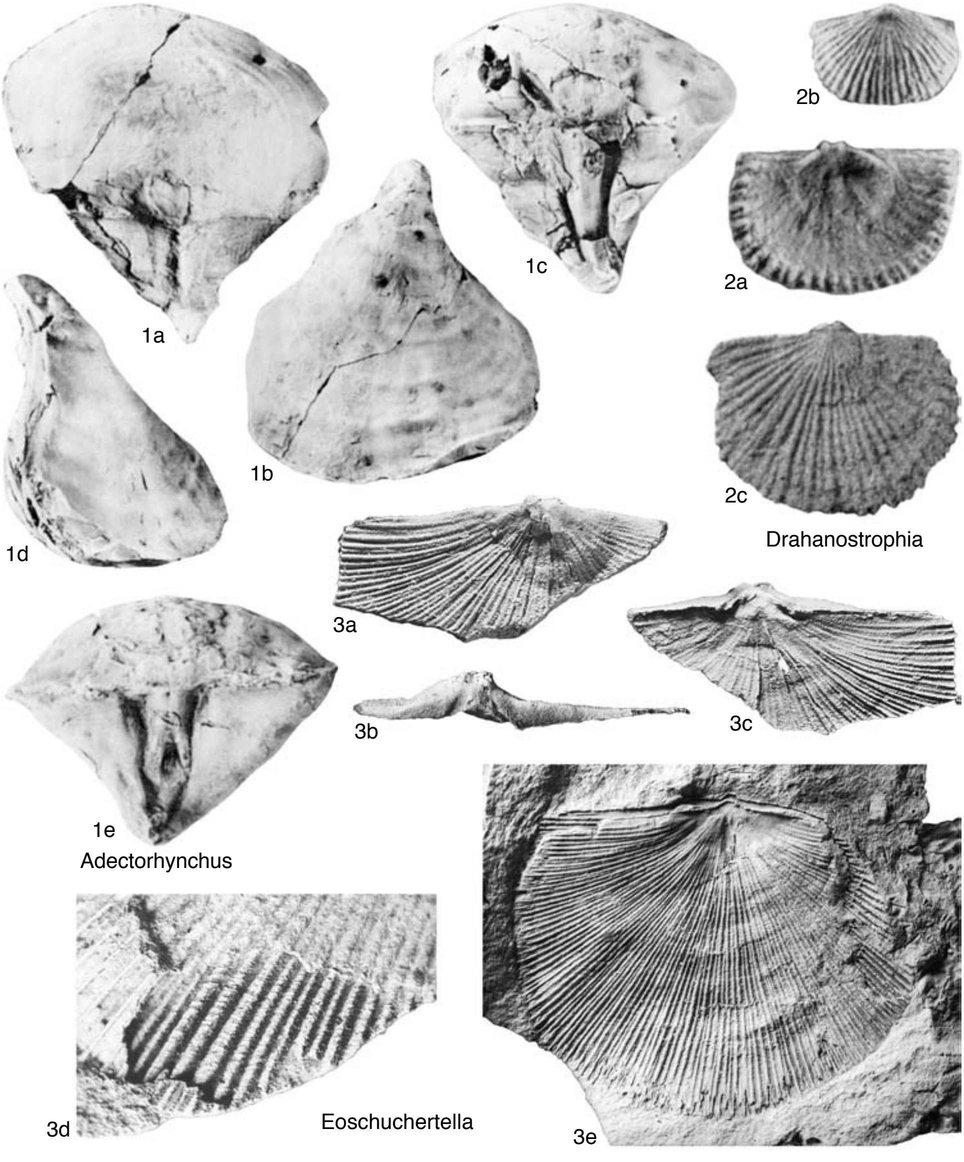

Fig. 491. Areostrophiidae (p. 680–681).

the Lower Devonian of Inner Mongolia is indistinguishable from *Carinastrophia* except for the more variable profile of the shell that, in the type species of the former, varies from planoconvex to ventribiconvex.] *Lower Devonian (upper Emsian)–Middle Devonian (lower Eifelian):* Russia (Gorno-Altai).——Fig. 489,*1a–c.* **C. elinovi* (Gratsianova), upper Emsian, Gorno-Altai, southwestern Siberia; *a,* posterior view of ventral valve internal mold, ×3; *b,* holotype, ventral valve internal mold, ×2; *c,* dorsal valve internal mold, ×3 (Gratsianova, 1975).

Subfamily ADECTORHYNCHINAE Henry & Gordon, 1985

[Adectorhynchinae Henry & Gordon, 1985, p. 36]

Small to medium sized, mostly subrounded, ventribiconvex to resupinate, coarsely to finely costellate; ventral interarea variable in height and disposition, pseudodeltidium normally convex, dorsal interarea short, mainly anacline, chilidium present,

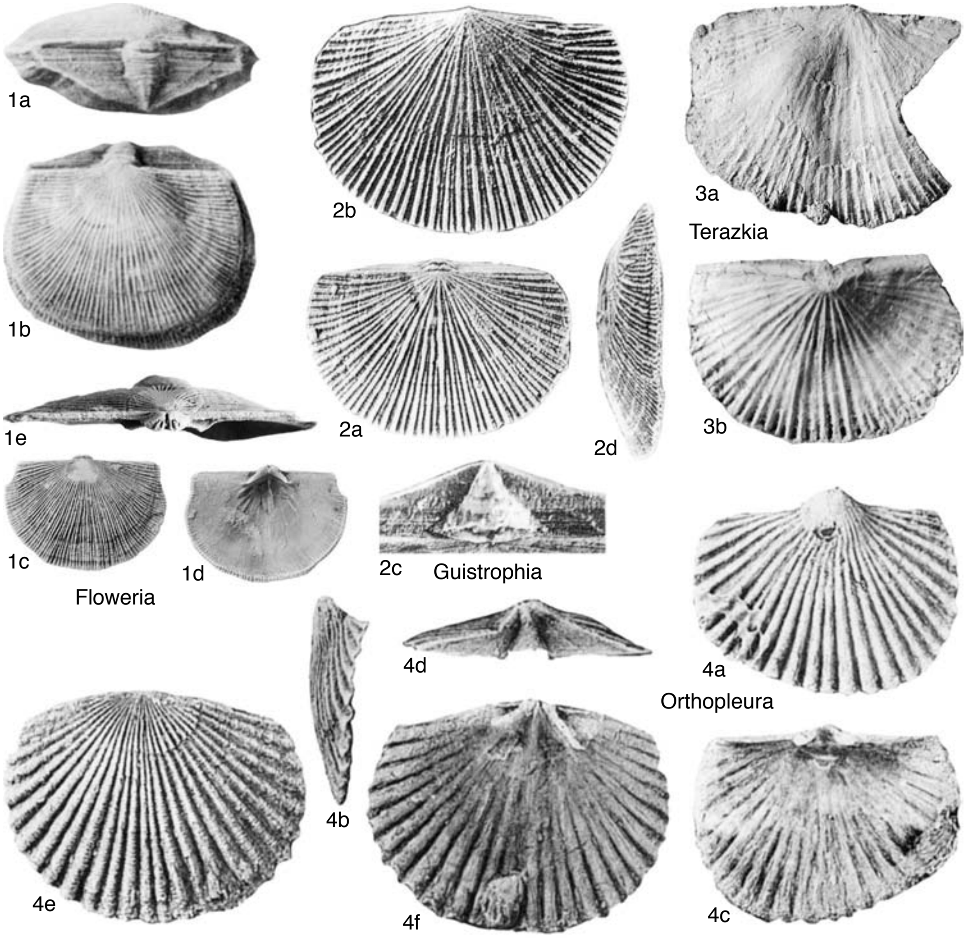

FIG. 492. Areostrophiidae (p. 681).

normally grooved medianly; socket ridges recurved to divergent, cardinal process lobes discrete or fused, rarely high with myophore slits. *middle Silurian (Wenlock)–Lower Carboniferous (lower Serpukhovian).*

Adectorhynchus HENRY & GORDON, 1985, p. 36 [**Streptorhynchus suspectum* GIRTY, 1929, p. 136; OD]. Ventribiconvex, normally subconical with high ventral interarea, flat to slightly convex pseudodeltidium with monticulus and linear dorsal interarea with short, medianly notched chilidium; finely parvicostellate with concentric fila; cardinal process lobes long with myophore slits, fused proximally into single shaft, united with socket ridges into thick socket plates (erisma) extending laterally; ventral muscle scar ill defined, myophragm low, dorsal muscle scar impressed about low myophragm. *Lower Carboniferous (lower Serpukhovian):* North America.——FIG. 491,*1a–e.* **A. suspectum* (GIRTY), upper Chesterian, Arkansas; *a,* posterodorsal view of shell, ×1; *b–d,* ventral, posterior, lateral views of internal mold, ×1; *e,* paralectotype, posterior face of cardinal process, ×3 (Henry & Gordon, 1985).

Drahanostrophia HAVLÍČEK, 1967, p. 202 [**D. ficneri;* OD]. Small, subquadrate, strongly ventribiconvex, costellate by branching; ventral interarea apsacline to catacline with convex pseudodeltidium, dorsal interarea linear with small chilidium either as single piece or pair of plates; cardinal process lobes small, bases ankylosed to widely divergent socket ridges extended laterally as small processes; ventral muscle scar indistinct, dorsal muscle scar broadly oval with low myophragm. [This genus is assigned to the Adectorhynchinae on a balance of features including the presence of a chilidium. It is, however, a rare chilidiopsoid and further study of some of the obscure characters may confirm a closer affinity with the Areostrophiinae, to which it is also cladistically linked.] *Middle Devonian (Givetian):* Czech Republic.——Fig. 491,*2a–c.* **D. ficneri,* Givetian, Moravia; *a,* dorsal valve interior, ×3.5; *b,* ventral valve exterior, ×2.8; *c,* dorsal valve exterior, ×3.8 (Havlíček, 1967).

Eoschuchertella Gratsianova, 1974, p. 83 [**E. popovi;* OD]. Similar to *Floweria* but strongly ventribiconvex, finely costellate by bifurcation with concentric fila in interspaces; socket ridges divergent at about 100°, tips extending ventrolaterally; muscle scars ill defined with occasional weak dorsal myophragm. *upper Lower Devonian–Middle Devonian (Eifelian):* Russia (Gorno-Altai).——Fig. 491,*3a–e.* **E. popovi,* upper Emsian, Gorno-Altai, southwestern Siberia; *a–c,* holotype, cast of ventral valve, interarea, dorsal valve, ×2; *d,* mold of concentric growth lines in intercostal spaces, ×5; *e,* internal mold of dorsal valve, ×1.5 (Gratsianova, 1974).

Floweria Cooper & Dutro, 1982, p. 53 [**Orthis prava* Hall in Hall & Whitney, 1858, p. 490; OD]. Planoconvex to unequally biconvex, subquadrate; finely costellate by intercalation; pseudodeltidium convex; discrete cardinal process lobes low, grooved, with median node at base; socket ridges recurved; muscle scars normally impressed, dorsal adductor scars usually divided by low myophragm. *Upper Devonian:* North America.——Fig. 492,*1a–e.* **F. prava* (Hall), Frasnian, Iowa; *a,b,* posterior, dorsal views of shell, ×2 (Cooper & Dutro, 1982); *c,d,* exterior, interior views of dorsal valve, ×1; *e,* posterior view of dorsal valve, ×2 (new).

Guistrophia Wang & Rong, 1986, p. 110[261] [**G. modesta;* OD]. Similar to *Floweria* but resupinate, parvicostellate, with short, weakly developed socket ridges; muscle scars unknown. *Lower Devonian (Emsian):* Guangxi, southern China.——Fig. 492,*2a–d.* **G. modesta,* lower Emsian, southern Guangxi, paratype; *a,* dorsal view of shell, ×2.5; *b,* ventral view of shell, ×3; *c,* posterior view of shell, ×8; *d,* lateral view of shell, ×1.5 (Wang & Rong, 1986).

Orthopleura Imbrie, 1959, p. 391 [**O. rhipis;* OD]. Small, subcircular, gently biconvex to planoconvex, costate to coarsely costellate with fine concentric fila; pseudodeltidium large, chilidium short, convex, perideltidium well developed; cardinal process lobes low, myophores directed posteriorly, socket ridges short, divergent; ventral muscle scar unknown, dorsal adductor scar lightly impressed about short myophragm. [This genus was described as being pseudopunctate, but no such structures were found in a recent SEM examination of a shell fragment.] *Middle Devonian:* North America.——Fig. 492,*4a–f.* **O. rhipis,* Traverse Group, Middle Devonian, Michigan; *a–d,* holotype, ventral valve exterior, lateral, interior, posterior views, ×3; *e,f,* dorsal exterior, interior, ×3 (Imbrie, 1959).

Terazkia Havlíček in Havlíček & Štorch, 1990, p. 94 [**Orthis expandens* Barrande, 1879, pl. 68, case VIII]. Subquadrate, convexiconcave, coarsely costellate by branching and intercalation, with concentric fila; ventral interarea low, catacline, with open delthyrium, dorsal interarea linear, chilidium not established because of poor preservation; cardinal process lobes discrete, low, socket ridges short, divergent, extending laterally. [This genus is poorly known and, pending further information on the nature of its chilidium and its internal morphology, is assigned to the Areostrophiidae solely on the judgment of its authors.] *middle Silurian (Wenlock):* Czech Republic.——Fig. 492,*3a,b.* **T. expandens* (Barrande), Wenlock, Bohemia; dorsal valve, ventral valve exteriors, ×2.2 (Havlíček & Štorch, 1990).

TRIPLESIIDINA

A. D. Wright
[Queen's University, Belfast]

Suborder TRIPLESIIDINA Moore, 1952

[*nom. correct.* Wright, 1965b, p. 355, *pro* suborder Triplesioidea Muir-Wood, 1955, p. 89, *nom. transl. ex* order Triplesiida Moore, 1952, p. 221]

Biconvex to markedly dorsibiconvex strophic and deltidiodont shells. Ventral valve with pseudodeltidium flush with interarea, typically arched medianly into monticulus; foramen apical. Dorsal valve interarea obsolete; internally with long, forked, posteroventrally recurved cardinal process and strong brachiophores. Secondary shell laminar, rarely with pseudopunctae. *Lower Ordovician (Llanvirn)–upper Silurian (lower Ludlow).*

The Triplesiidina form a distinctive and closely knit group among the articulated brachiopods. The external appearance is quite variable and, before the internal structures were fully known, the various species and genera were assigned to such stocks as *Atrypa, Orthis, Productus,* and *Spirifer.* The discovery of the unusual and consistent cardinalia in the then known genera led Schuchert (1913a) 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 subordinal status. The suborder contains but a single family; attempts to divide this into subfamilies (Amsden, 1968) or to establish additional family groups under the superfamily (Havlíček in Havlíček & Štorch, 1990) have not so far been acceptable due to the plasticity of the morphological characters within the plexus (Wright, 1971, 1993b). The variability is accentuated by asymmetrical growth, which affects shape, ribbing, and the anterior commissure widely within the group, and not simply a few well-known species of *Streptis.*

The discovery of the laminar nature of the secondary shell, coupled with morphology, enabled Williams (1968a, 1970) to identify a close relationship between the triplesioids and the davidsonioids (orthotetidines) and to suggest that both diverged from the billingselloid stock probably in Late Cambrian times. As yet the earliest known triplesioid is *Onychoplecia* from the lower Llanvirn Table Point Formation of Newfoundland (Ross & James, 1987), with *Triplesia* and *Oxoplecia* present in Wales by the later Llanvirn (Lockley & Williams, 1981). The group continued throughout the Ordovician and into the Silurian, being fairly widespread but rarely abundant. Although seven and possibly even nine genera were still present in the Wenlock, only one (*Plectotreta*) has so far been recorded from the Ludlow (Bassett & Cocks, 1974).

The triplesiidine shell varies greatly in outline from the wide-hinged, transverse *Bicuspina* to rounded *Cliftonia,* tear-shaped *Onychoplecia,* and elongate, clawlike *Onychotreta;* in profile the shell is less variable, from biconvex to markedly dorsibiconvex. A strong dorsal fold and ventral sulcus producing a uniplicate anterior commissure is typical; the reverse situation, with ventral fold and dorsal sulcus and a unisulcate commissure, is taken as a diagnostic generic character for the genera *Brachymimulus* and *Paraonychoplecia.* Variations of these basic commissural types are seen in some species of noncostate genera, sulciplicate in *Triplesia* and *Grammoplecia,* and plicosulcate and paraplicate in *Paraonychoplecia.* A sinusoidal anterior commissure produced by a relative twisting of either half of the shell characterizes *Amphiplecia,* many species of *Streptis,* and occasional specimens in populations of other genera. Surface ornament is lacking, for example, in the smooth *Triplesia;* other forms show fine concentric filae (*Caeroplecia*), elevated growth lines (*Oxoplecia*), stronger lamellae (*Cliftonia*), or frills (*Plectotreta*), commonly in combination with radial capillae, costellae, costae, or plications.

The ventral valve has a small apical or supra-apical foramen and a well-developed interarea that reaches exceptional lengths in *Onychotreta.* The delthyrium is closed by a pseudodeltidium flush with the interarea, characteristically with a narrow median fold (monticulus). The development of this structure may vary within a species, but in some later forms its absence is consistent enough to be useful as a generic character, as in *Brachymimulus, Placotriplesia,* and *Placocliftonia.* From the foramen, the pedicle may pass to the interior through thick umbonal calcite (pedicle passage) or may extend to the valve floor through a more or less tubular calcareous sheath (pedicle tube). The teeth are normally supported by dental plates. Muscle scars are known for only a few genera, where they consist of flabellate diductor scars surrounding and all but enclosing cordate or lanceolate adductor scars (see Fig. 495,*2d*). The meager evidence of the mantle canals indicates a saccate or lemniscate pattern.

Although the dorsal valve typically lacks an interarea, with the strongly convex umbo abutting on to the hinge line, a short yet distinct anacline area is known from some species of *Triplesia* including *T. ortoni* (Wright, 1971). In these cases the notothyrium is closed by a chilidium with a marked median fold. Internally the valve possesses a long, forked cardinal process that curves backward from its base on the hinge line to extend

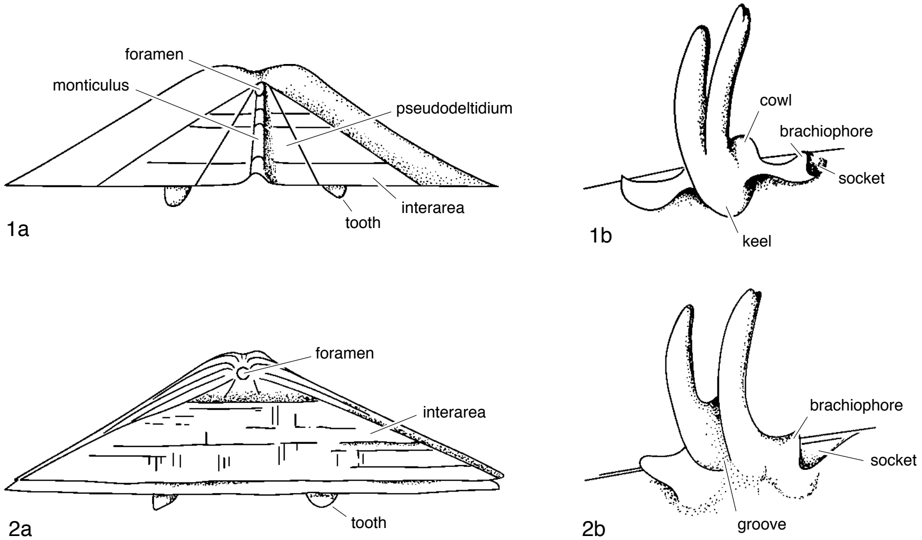

Fig. 493. Commonly associated triplesiid structures; *1a,* ventral valve with monticulate pseudodeltidium and *1b,* dorsal valve cardinalia with keeled cardinal process, cowl, and discrete brachiophores, as in *Triplesia; 2a,* pseudodeltidium lacking monticulus and *2b,* cardinalia with grooved process, each lobe closely fused to adjacent brachiophore, lacking cowl, as in *Ogmoplecia* (new).

posteriorly into the umbo of the ventral valve (see Fig. 494,*1f*). The myophores are located at the distal extremity of each prong, usually as deep grooves in the dorsal surface. At the proximal end, the process is covered by the chilidium if present; in some genera (e.g., *Triplesia,* Fig. 494,*1g*) a proximally directed cowl (hood of Wright, 1963a) arches over the shaft, closing any gap at the front of the pseudodeltidium when the valves are closed; these structures tend to be associated with a well-formed monticulus (Fig. 493). The forked cardinal process ranges from being cleaved from its proximal end, with each prong fused more to its adjacent brachiophore and forming a grooved process as in *Ogmoplecia* (see Fig. 496,*4d*), to the two prongs being fused proximally to form a keeled process as in *Triplesia* (see Fig. 494,*1f*). The pair of calcareous processes that define the anteromedian margins of the sockets differ from typical orthoid brachiophores in having their distal points directed posterolaterally. The adult lophophore is interpreted as being a dorsally directed spirolophe. Where specimens show muscle scars and mantle canal impressions, the dorsal muscle field has a subcentral anterior adductor pair and a broader posterior pair, which are flanked by saccate gonocoels (Wright & Jaanusson, 1993).

Superfamily TRIPLESIOIDEA Schuchert, 1913

[*nom. transl.* Wright, herein, *ex* superfamily Triplesiacea Cooper, 1944, p. 307, *nom. transl. ex* Triplesiinae Schuchert, 1929, p. 16, *nom. correct. pro* Tripleciinae Schuchert, 1913a, p. 387]

Characters as for suborder. *Lower Ordovician (Llanvirn)–upper Silurian (lower Ludlow).*

Family TRIPLESIIDAE Schuchert, 1913

[*nom. transl.* Öpik, 1932, p. 69, *ex* Triplesiinae Schuchert, 1929, p. 16, *nom. correct. pro* Tripleciinae Schuchert, 1913a, p. 387] [=Placotriplesiinae Amsden, 1968, p. 39, *partim;* Oxopleciidae Havlíček in Havlíček & Štorch, 1990, p. 60, *partim;* Onychotretidae Havlíček in Havlíček & Štorch, 1990, p. 62, *partim*]

Smooth to strongly ornamented shells of transverse to elongate outline, with fold and sulcus normally producing prominent undulation in anterior commissure; long forked cardinal process with cowl commonly developed on posterior side of base, anterior side keeled or grooved; inner boundaries of sockets defined by posterolaterally directed brachiophores. *Lower Ordovician (Llanvirn)–upper Silurian (lower Ludlow).*

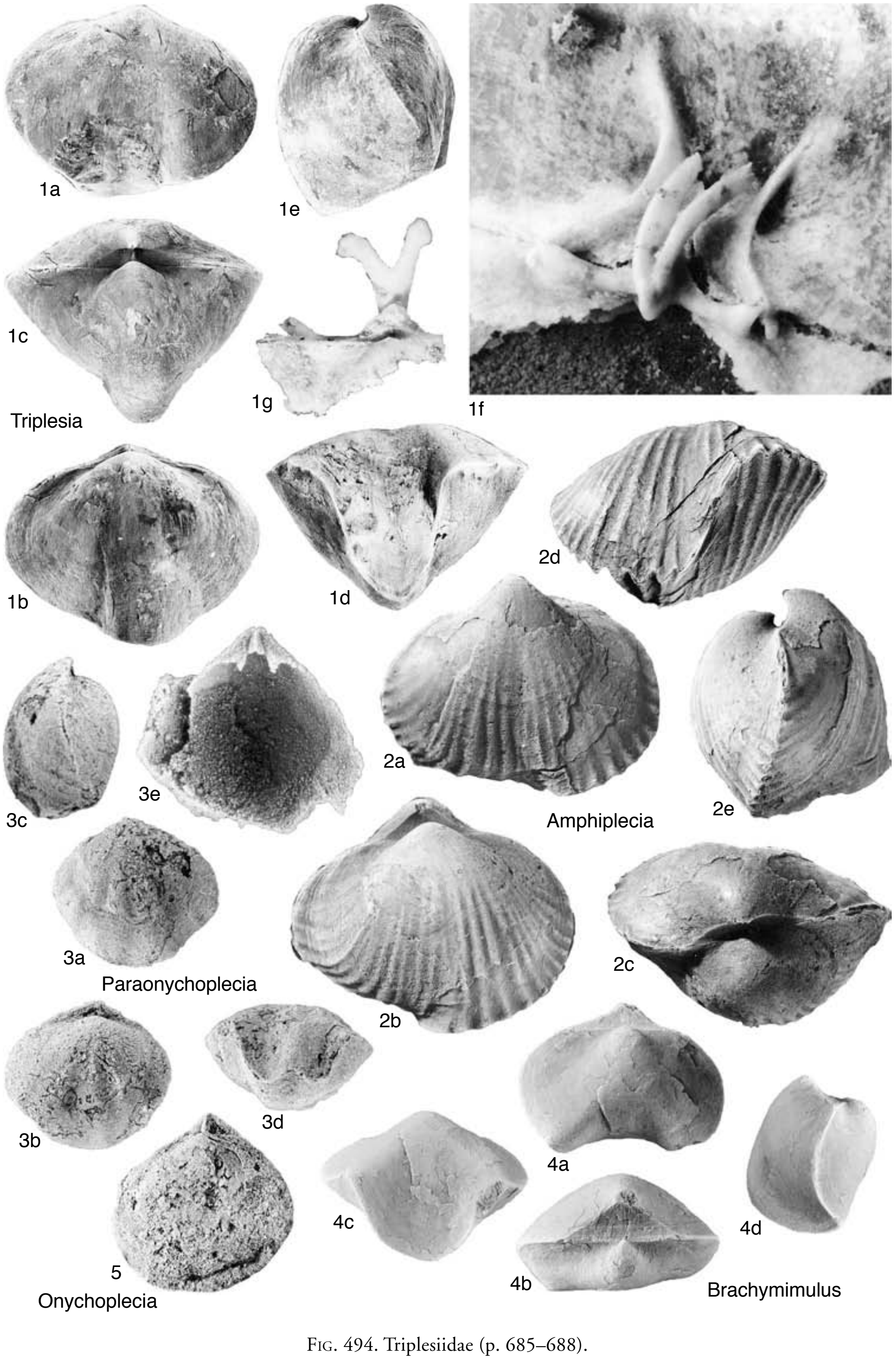

FIG. 494. Triplesiidae (p. 685–688).

Triplesia HALL, 1859b, p. 44 [**Atrypa extans* EMMONS, 1842, p. 395; SD HALL & CLARKE, 1892, p. 270] [=*Triplecia* HALL & CLARKE, 1892, obj.; *Dicraniscus* MEEK, 1872b, p. 279 (type, *D. ortoni*)]. Strongly trilobate with pronounced dorsal fold and ventral sulcus; surface smooth, with only faint growth lines; cardinal process keeled, cowl present. *Lower Ordovician (upper Llanvirn)–lower Silurian (upper Llandovery):* widespread in North America, Eurasia; Morocco.——FIG. 494,*1a–e.* **T. extans* (EMMONS), Caradoc, Trenton, New York; ventral, dorsal, posterior, anterior, lateral views of complete shell, ×1.5 (Wright, 1965b).——FIG. 494,*1f,g. T.* sp., Ashgill, Norway; anterolateral, posterodorsal views of silicified hinge regions, ×8 (new).

Amphiplecia WRIGHT & JAANUSSON, 1993, p. 99 [**A. tardicostata;* OD]. Transverse shells twisted about midline, commissure sinusoidal; umbonally smooth, developing coarse ribs with fine growth lamellae; monticulus commonly developed; cardinal process grooved, lacking cowl. *Upper Ordovician (Caradoc–Ashgill):* Sweden, Norway, Siberia.——FIG. 494,*2a–e.* **A. tardicostata,* Ashgill, Sweden; holotype, ventral, dorsal, posterior, anterior, lateral views, ×2 (Wright & Jaanusson, 1993).

Bicuspina HAVLÍČEK, 1950, p. 18 [**Orthis cava* BARRANDE, 1848, p. 209; OD]. Transverse shells with wide hinge, multicostellate, uniplicate; monticulate with long pedicle tube; low keeled cardinal process commonly cowled, brachiophores ponderous. *Ordovician (Llandeilo–Caradoc):* Europe, Morocco, Kazakhstan, China, Argentina.——FIG. 495,*2a–c.* **B. cava* (BARRANDE), Caradoc, Harnagian, Bohemia; *a,* ventral valve internal mold; *b,c,* dorsal, posterior views of dorsal valve internal mold, ×1.5 (Turek & Horný, new).——FIG. 495,*2d. B. spiriferoides* (M'COY), Caradoc, Soudleyan, Wales; ventral valve internal mold, ×1.3 (Wright, 1963a).

Brachymimulus COCKERELL, 1929, p. 105, *nom. nov. pro Mimulus* BARRANDE, 1879, p. 109, *non* STIMPSON, 1860 [**Mimulus perversus* BARRANDE, 1879, p. 109; OD]. Smooth with strong ventral fold and dorsal sulcus; hinge moderately wide, outline transverse; monticulus absent. *Silurian (Wenlock):* Bohemia.——FIG. 494,*4a–d.* **B. perversus* (BARRANDE); holotype, dorsal, posterior, anterior, lateral views, ×3 (Turek & Horný, new).

Caeroplecia WILLIAMS, 1974, p. 121 [**C. plicata;* OD]. Similar to *Oxoplecia* but with concentric ornament of fila, not lamellae, delayed rib development and short pedicle tube; cardinalia small, delicate, cardinal process keeled. *Ordovician (Caradoc):* England, Wales, Northern Ireland, USA (Tennessee, Virginia, Alabama).——FIG. 495,*3a–c.* **C. plicata,* Caradoc, Soudleyan, England; *a,* cast of ventral exterior, ×3; *b,* detail of ornament, ×15; *c,* cast of dorsal interior, ×3 (new).

Cliftonia FOERSTE, 1909a, p. 81 [**C. striata;* OD]. Strongly lamellose and costellate, subcircular, uniplicate shells; monticulate, but cowl lacking on keeled cardinal process; pedicle tube present. *Ordovician (upper Caradoc)–Silurian (Llandovery, ?Wenlock):* Morocco, France, *upper Caradoc;* widespread North America, Eurasia, Argentina, *Ashgill (Hirnantian);* North America, *Llandovery–?Wenlock.*——FIG. 495,*1a.* **C. striata,* Telychian, Tennessee; posteroventral view of asymmetrical ventral internal mold, ×2.5 (new).——FIG. 495,*1b. C. tubulistriata* (SAVAGE), Ashgill, Missouri; dorsal valve exterior, ×2 (Ulrich & Cooper, 1936a).

Craigella REED, 1935, p. 354 [**Triplesia grayiae* DAVIDSON, 1869, p. 198; OD] [=*Epacroplecia* WILLIAMS, 1962, obj.; *Nucleorhynchia* LIANG in LIU, XU, & LIANG, 1983, p. 272 (type, *N. hengtangensis*)]. Trigonal form with narrow hinge; dorsal valve highly convex, trilobate, ventral valve shallow with geniculate median tongue; ornament capillate or smooth; cardinal process low keeled, brachiophores bladelike, bases subparallel. *Upper Ordovician (Caradoc–Ashgill):* Scotland, Mongolia, eastern China.——FIG. 496,*1a–e.* **C. grayiae* (DAVIDSON), upper Caradoc, Scotland; *a–c,* lectotype, dorsal, anterior, lateral views, ×2.5; *d,* dorsal valve exterior, ×2.5; *e,* interior of dorsal valve, ×2.5 (new).

Grammoplecia WRIGHT & JAANUSSON, 1993, p. 104 [**G. triplesioides;* OD]. Trilobate to transverse shells, strongly uniplicate to sulciplicate, with capillate radial ornament; monticulus present or absent; keeled cardinal process. *Lower Ordovician (Llandeilo)–Upper Ordovician (Ashgill):* Sweden, Urals, Siberia, Kazakhstan, China, ?Scotland, ?USA (Alabama).——FIG. 495,*4a–f.* **G. triplesioides,* Ashgill, Sweden; *a–e,* holotype, ventral, dorsal, posterior, anterior, lateral views, ×2; *f,* detail of shell surface, ×15 (Wright & Jaanusson, 1993).

Ogmoplecia WRIGHT & JAANUSSON, 1993, p. 94 [**Triplecia plicata* WIMAN, 1907, p. 12; OD]. Coarsely ribbed uniplicate triplesiid with pseudodeltidium typically smooth, without monticulus; cardinal process grooved, lacking cowl. *Upper Ordovician (?Caradoc, Ashgill):* Baltic, British Isles, Belgium, Quebec, Siberia, ?British Columbia (Trenton), *?Caradoc.*——FIG. 496,*4a–e.* **O. plicata* (WIMAN), Ashgill, Öland; *a–c,* lectotype, ventral, posterodorsal, anterior views, ×1.3; *d,* latex cast of cardinalia, ×4; *e,* interarea of fragmentary ventral valve, ×8 (Wright & Jaanusson, 1993).

Onychoplecia COOPER, 1956, p. 529 [**O. brevirostris;* OD]. Small shells with tear-shaped outline, elongate beak, and narrow hinge; profile narrowly lenticular, uniplicate, smooth or rarely with costellae; monticulate; cowl on keeled cardinal process. *Ordovician (lower Llanvirn, ?upper Ashgill):* eastern North America, *lower Llanvirn–lower Caradoc;* ?England, ?China, *?upper Ashgill.*——FIG. 494,*5.* **O. brevirostris,* Tennessee; dorsal view of complete shell, ×2.5 (Wright, 1965b).

Onychotreta ULRICH & COOPER, 1936a, p. 339 [**O. mesleri;* OD] [=*Eilotreta* AMSDEN, 1968, p. 36 (type, *Rhynchotreta lenta* THOMAS, 1926); =*Lissotreta* AMSDEN, 1968, p. 37 (type, *Onychotreta plicata* ULRICH & COOPER, 1936a)]. Outline clawlike, with

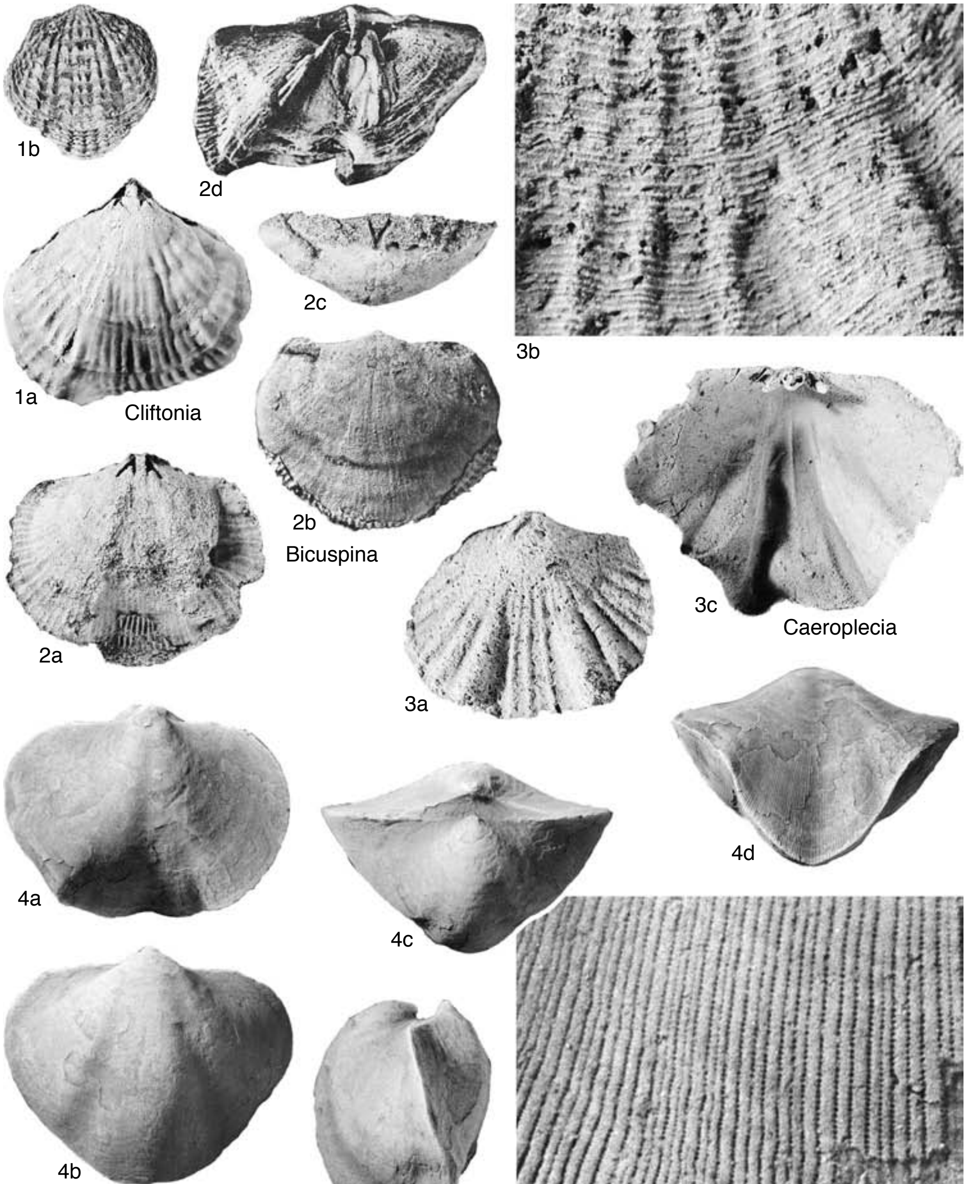

FIG. 495. Triplesiidae (p. 685).

ventral beak and monticulate pseudodeltidium extremely elongate; dorsal valve short; form and ornament variable, costellate to paucicostate or smooth, with asymmetry; fold and sulcus variably defined. *Silurian (Wenlock):* USA (Arkansas, Oklahoma), Bohemia.——FIG. 496,*2a–d.* **O. mesleri,* Wenlock, Arkansas; *a,b,* dorsal view of complete shell, ventral valve exterior, ×2; *c,d,* dorsal valve, exterior, posterior views, ×2 (Wright, 1965b).

Oxoplecia WILSON, 1913, p. 81 [**O. calhouni;* OD] [=*California* BASSLER, 1915, p. 1294]. Roundedly elliptical to transverse shells, costellate with distinc-

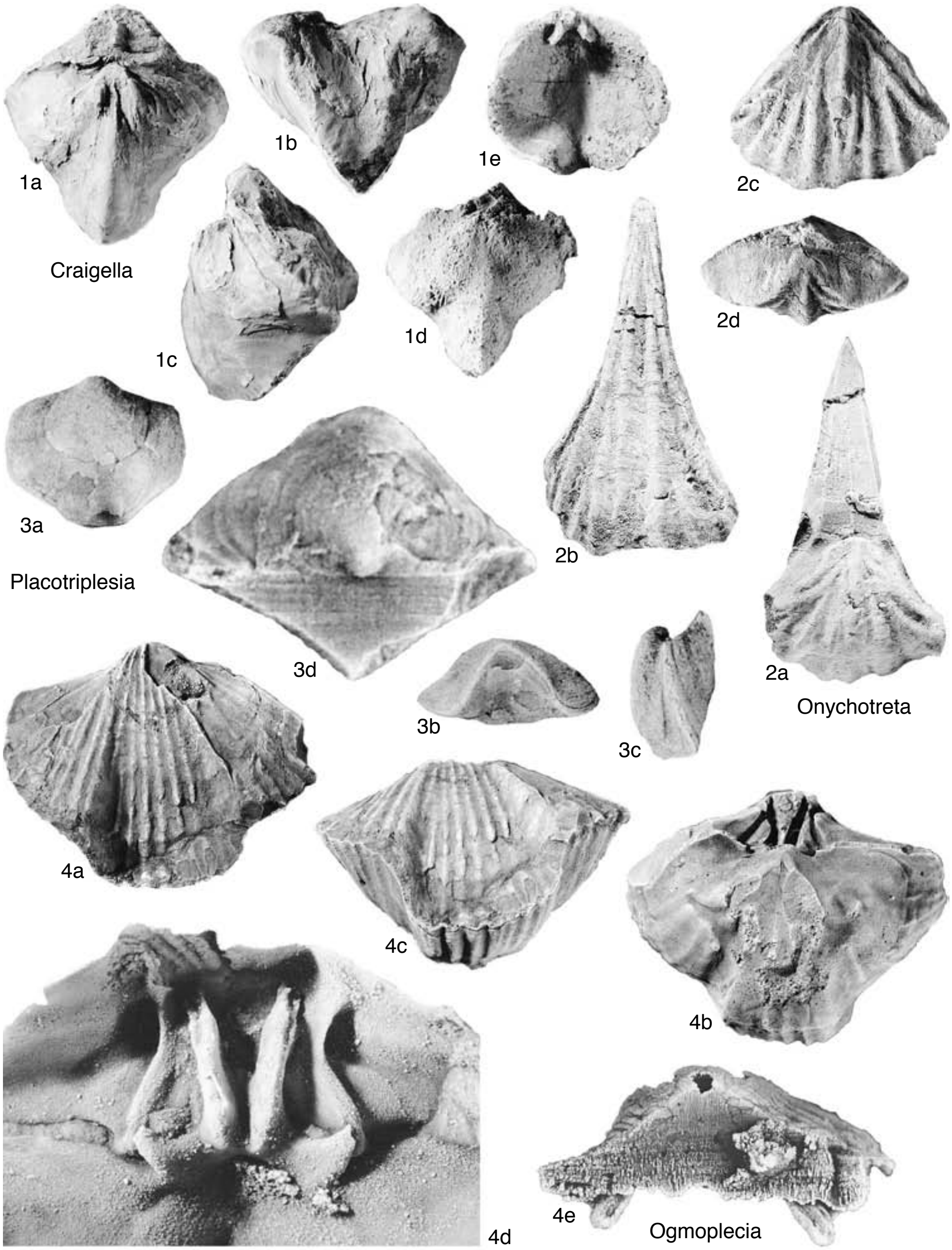

Fig. 496. Triplesiidae (p. 685–689).

tive fine, elevated, concentric growth lines; uniplicate. Monticulus may be lost anteriorly; pedicle tube not developed; cardinal process keeled, cowl lacking. *Ordovician (upper Llanvirn–Caradoc; ?Ashgill), Silurian (?Wenlock):* widespread North America, Eurasia.——Fig. 497,*4a,b.* **O. calhouni,* Caradoc, Ontario; holotype, dorsal, anterior views, ×1.5 (Wright, 1965b).——Fig. 497,*4c. O. gouldi* Ulrich & Cooper, Caradoc, Oklahoma; detail of ornament on dorsal valve, ×15 (new).

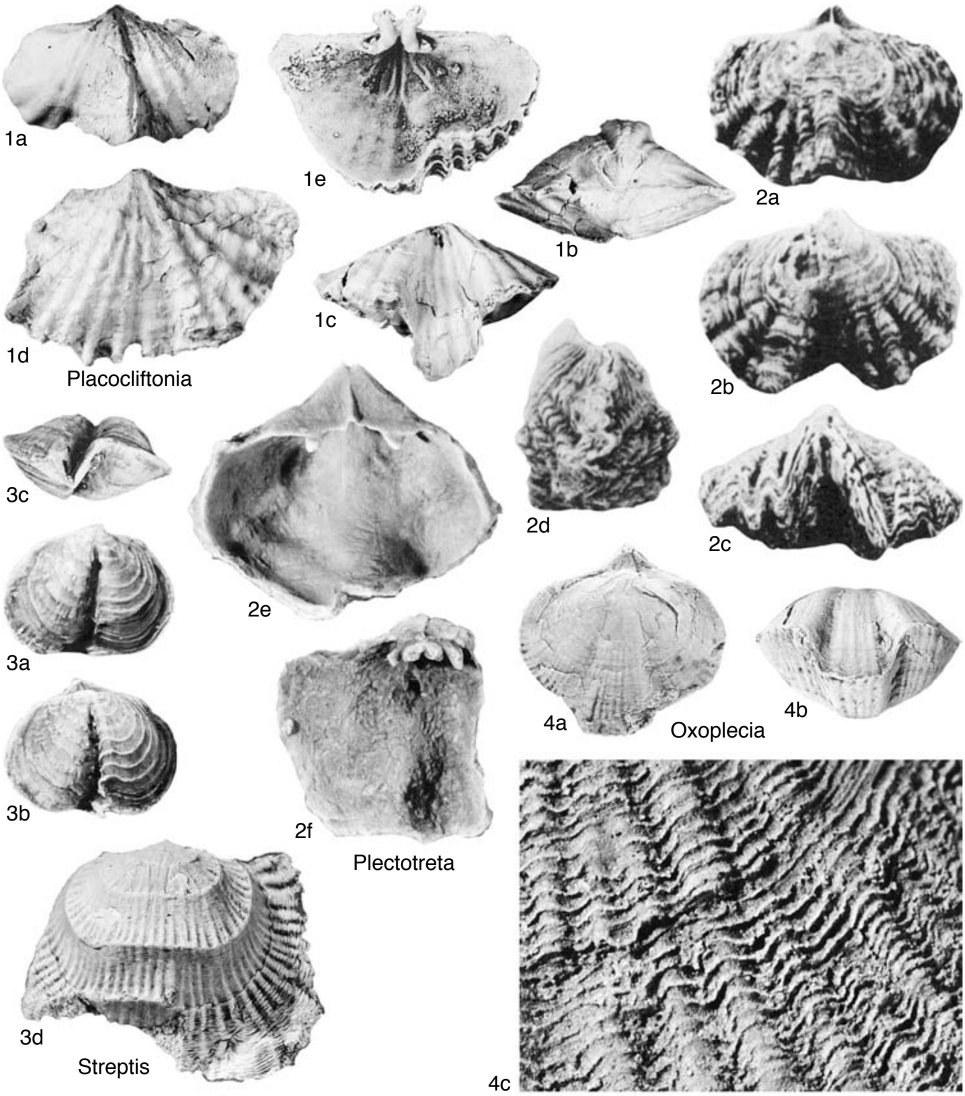

FIG. 497. Triplesiidae (p. 686–689).

Paraonychoplecia PERCIVAL, 1991, p. 133 [**P. inversa;* OD]. Smooth triplesiid with ventral fold and dorsal sulcus; hinge narrow, outline roundedly subtriangular to elongate, developing long, pointed ventral beak; monticulus present; cardinal process keeled. *Upper Ordovician (Caradoc)–Silurian (Wenlock):* Australia, Quebec, British Isles, USA (Arkansas, Oklahoma).——FIG. 494,*3a–e.***P. inversa,* Caradoc, New South Wales; *a–d,* ventral, dorsal, lateral, anterior views of complete shell, ×3; *e,* ventral valve interior and hinge region, ×12 (Percival, 1991).

Placocliftonia HAVLÍČEK in HAVLÍČEK & ŠTORCH, 1990, p. 60 [**Spirifer colibri* BARRANDE, 1848, p. 173; OD]. Transverse, variably asymmetrical shells, commissure uniplicate or sinusoidal; ribbing accentuated by strong concentric lamellae. Short pedicle tube, but monticulus obsolete; cardinal process grooved, lacking cowl. *Silurian (Wenlock):* Bohemia, USA (Wisconsin), Arctic Canada.——FIG. 497,*1a–d.* **P. colibri* (BARRANDE), Wenlock, Bohemia; *a–c,* holotype, dorsal, posterior, anterior views, ×2.1; *d,* ventral valve exterior, ×3.3 (Havlíček & Štorch, 1990).——FIG. 497,*1e. P. contorta* (ZHANG), Wenlock, Arctic Canada; dorsal valve interior, ×3.3 (Zhang, 1989b).

Placotriplesia Amsden, 1968, p. 40 [**Triplesia praecipta* Ulrich & Cooper, 1936a, p. 346; OD]. Smooth uniplicate shells resembling *Triplesia* but lacking monticulus and cowl on grooved cardinal process. *Silurian (Wenlock):* USA (Arkansas, Oklahoma, Tennessee), Bohemia, England, Estonia.——Fig. 496,*3a–d.* **P. praecipta* (Ulrich & Cooper), Wenlock, Arkansas, Oklahoma; *a–c,* ventral, anterior, lateral views of complete shell, ×4 (Amsden, 1968); *d,* posterior view of shell showing ventral interarea, ×7 (Amsden, 1973).

Plectotreta Ulrich & Cooper, 1936a, p. 339 [**P. lindstroemi;* OD]. Outline subcircular, becoming transversely elliptical, lamellose with strong radial plications; monticulate; cardinal process grooved with small cowl. *Silurian (lower Wenlock–lower Ludlow):* northwestern Europe (Gotland, England).——Fig. 497,*2a–f.* **P. lindstroemi,* Wenlock; *a–d,* dorsal, ventral, anterior, lateral views of complete shell, England, ×3.5 (Bassett, 1972); *e,* ventral valve, Gotland, ×4; *f,* damaged dorsal valve, Gotland, ×5 (Wright, 1993b).

Streptis Davidson, 1881, p. 150 [**Terebratula grayii* Davidson, 1848, p. 331; OD]. Small, commonly twisted shells, commissure uniplicate or sinusoidal; strong concentric lamellae, developing into frills; radial ribbing variable; monticulus present; cardinal process with cowl, keeled, becoming grooved by Wenlock. *Upper Ordovician (Cautleyan)–Silurian (Homerian):* Europe, Kazakhstan, North America, Greenland.——Fig. 497,*3a–c.* **S. grayii* (Davidson), Wenlock, England; *a–c,* ventral, dorsal, anterior views of complete shell, ×3 (Wright, 1965b).——Fig. 497,*3d. S. undifera* (Schmidt), Ashgill, Estonia; dorsal valve with incomplete fourth frill, ×3.3 (Hints, 1986).

BILLINGSELLIDA

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Order BILLINGSELLIDA Schuchert, 1893

[*nom. transl.* Williams & Harper, herein, *ex* Billingsellidae Schuchert, 1893, p. 152]

Concavoconvex to biconvex strophomenates with a long ventral interarea and a convex pseudodeltidium complementary to a chilidium, foramen apical; teeth transverse to deltidiodont, supported by variably disposed dental plates; muscle scars normally well defined but without evidence of adjustor bases; inner socket ridges more or less parallel with the hinge line; notothyrial platform well developed, normally with a ridgelike cardinal process; mantle canal systems saccate to pinnate; secondary layer of shell laminar or fibrous, impunctate, rarely pseudopunctate. *Middle Cambrian–Upper Ordovician (upper Ashgill).*

The grouping of the billingselloids and clitambonitidines into a new order is prompted by the phylogenetic analyses of Williams and others (1996) but is provisional on further studies of shell structure and the closure of the delthyrium. The secondary shell of clitambonitidines and billingselloids are respectively fibrous and laminar, which difference is also characteristic of the plectambonitoids and strophomenoids. The laths of billingselloid laminae, however, are not cross bladed but subparallel (Williams, 1970, p. 312) and may have evolved from flattened fibers. As for the delthyrial covers, Wright and Rubel (1996) have concluded that those of clitambonitidines are essentially deltidia rather than pseudodeltidia. The cover of the billingselloid delthyrium has always been described as a pseudodeltidium, although this has never been confirmed by an explicit study of young shells.

Notwithstanding these contradictions, the presence of mantle canal imprints along the ventral interareas of clitambonitidines (Wright, 1994b) suggests that this group, at least, had a posterior body wall as postulated for strophomenates as a whole, while the muscle systems of both the billingselloids and clitambonitidines appear not to have included pedicle adjustors.