

PENTAMERIDA

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Order PENTAMERIDA Schuchert & Cooper, 1931

[*nom. transl.* MOORE in MOORE, LALICKER, & FISCHER, 1952, p. 220, *ex* suborder Pentameroidea SCHUCHERT & COOPER, 1931, p. 247]

[Diagnosis prepared by S. J. CARLSON
and A. J. BOUCOT]

Small to very large articulated brachiopods, subquadrate to subpentamerid to elongate-oval in outline; commonly strongly biconvex; commissure uniplicate, less commonly rectimarginate or unisulcate; hinge line either strophic with well-developed interareas or astrophic; exterior smooth, costate, or costellate, rarely pitted, granulose, or rugose. Delthyrium open, rarely partly closed by deltidial plates; teeth deltidiodont, rarely cyrtomatodont; dental plates well developed, commonly forming spondylium, rarely pseudospondylium or remaining discrete and subparallel; spondylium commonly supported by median ridge or septum, rarely absent; ventral muscle field, when visible, commonly restricted to spondylium; ventral mantle canals, when visible, commonly digitate, rarely saccate. Notothyrium, when present, open; cardinal process commonly absent, rarely as low vertical ridge on floor of valve or on callosity or narrow shelf at valve posterior; inner socket ridges short and blunt; socket plates commonly convergent, may unite with low median septum to form septalium, or remain discrete, subparallel, and continue anteriorly into extensions of varying length, rarely forming cruralium, rarely divergent; crura absent in early taxa, occur as rodlike or bladlike processes in later taxa; lophophore configuration unknown; adductor muscle field commonly well developed, oval or petaloid, rarely elevated on low callosities; dorsal mantle canal systems commonly poorly developed, digitate. Secondary shell structure fibrous, becoming dominantly prismatic in many later groups, impunctate. [The first

stratigraphic occurrence of Pentamerida in the Toyonian is somewhat questionable. *Tcharella* (tentatively assigned to Syn-trophopsinae, see p. 941) occurs in the Toyonian, but is so poorly known that its assignment to Pentamerida is questionable. *Cambrotrophia* is the first unquestionable pentameride genus; it first appears in the Middle Cambrian (Amgaian).] *Lower Cambrian (Toyonian)*–*Upper Devonian (Frasnian)*.

Pentamerides comprise a relatively small but significant group (approximately 170 genera) of early and middle Paleozoic articulated brachiopods. The crown-group rhynchonellates—including the extant rhynchonellides, terebratulides, and thecideides, and the extinct atrypides, athyridides, spiriferides, and spiriferinides—together trace their closest common ancestry to the extinct pentamerides (see chapter on Brachiopod Classification, WILLIAMS, CARLSON, & BRUNTON, 2000, p. 1–27). For this reason, pentamerides play a particularly important role in our understanding of articulated brachiopod evolution and phylogeny.

Evolution in the Pentamerida is characterized primarily by changes in hinge line width and the degree and nature of development of dental plates in the ventral valve (commonly converging to form a spondylium) and socket plates in the dorsal valve, which may converge to form a septalium. Four stages of morphological innovation can be recognized: the origin of the pentameride clade itself and of the rhynchonellide clade, the camerelloid clade, and the pentameridine clade, three successively more derived subclades within Pentamerida (Fig. 617).

Pentamerides can be distinguished from their orthide ancestors by several distinctive features that necessarily also characterize the Porambonitoidea. Convexity of adult valves evolved from weak to moderate or quite

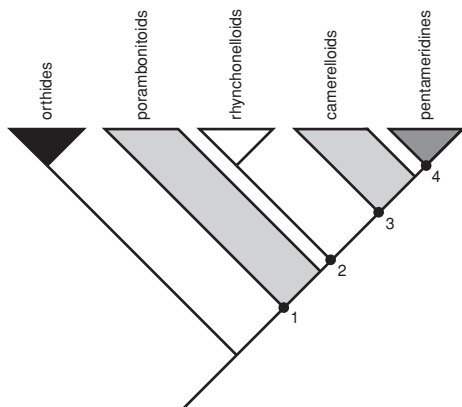


FIG. 617. Generalized cladogram adapted from CARLSON (1996, fig. 1), simplified to show the orthides (*black*) as a sister group to the pentameridines (*shaded*); the paraphyletic parambonitoids and camerelloids (*light shading*); and monophyletic rhynchonelloids (*white*) and pentameridines (*dark shading*). Numbered nodes mark four stages of morphological innovation within the order, as discussed in text (adapted from Carlson, 1996).

strong and from equibiconvex to pronounced dorsibiconvexity. The commissure changed from rectimarginate to strongly uniplicate as a deep dorsal fold and ventral sulcus developed. The hinge line commonly decreased from wide to medium width and the interareas were reduced, particularly in the dorsal valve. Dental plates became quite distinct and their orientation changed from divergent to convergent, most commonly forming a spondylium in the ventral valve. The cardinal process was generally lost, although a few primitive syntrophiidines retained a rudimentary process and a few pentameridines evolved a cardinal process secondarily. Adductor muscle attachment areas in the dorsal valve evolved from quadrilobate to elongate oval within the syntrophiidines. Muscle scars are seldom expressed on pentameridine valves.

Within the order Pentamerida, two suborders are recognized: the more primitive, paraphyletic Syntrophiidina, with highest diversity in the Ordovician, and the derived, monophyletic Pentameridina, with highest diversity in the Silurian (Fig. 617–618). Syn-

trophiidina includes two superfamilies—Porambonitoidea and Camerelloidea—that may be distinguished primarily by the presence or absence of a wide hinge line and interareas, the nature of the ventral spondylial structure, and presence or absence of crura and associated dorsal cardinalia. The more representative of these are illustrated in Figures 619–620. Pentameridina includes four superfamilies—Stricklandioidea, Pentameroidea, Clorindoidea, and Gypiduloidea—that may be distinguished primarily by variation in their dorsal interiors. In particular, the disposition of the hinge plates, relative to rodlike or bladlike crura, gave rise to a number of differently styled cardinalia. The more representative of these are illustrated in Figures 619–621. Stricklandioid shell structure is distinctly different from the other pentameridines, but syntrophiidine shell structure is too poorly known to allow generalizations about the evolution of shell structure across the entire order.

Differing opinions exist among the authors of this chapter regarding the ancestry of the Pentameridina. One of us (S. J. C.) holds that the pentameridines comprise a distinctive, derived group whose ancestry is shared with the camerelloids (Fig. 617), most likely the parastrophinids, despite the fact that they possess alate plates (a unique derived feature), or possibly the parallelasmatids, with which pentameridines share a spondylium duplex, lengthening of the cardinalia, and bladlike crura.

The other authors (A. J. B., R. J.-Y., and R. B. B.) share a somewhat different view, outlined below. In the pre-Ashgill, the Llanvirn and Caradoc in particular, there are a handful of relatively provincial genera with low abundance that may include the precursors of the undoubted pentameroids. Included here are the Parallelasmatidae and *Vaga*, from the uppermost Caradoc of Kazakhstan, that possess hinge plates similar to those of the Pentameridina rather than of the varied taxa within the Syntrophiidina. For none of these genera, however, may one be certain of the details of the hinge plates

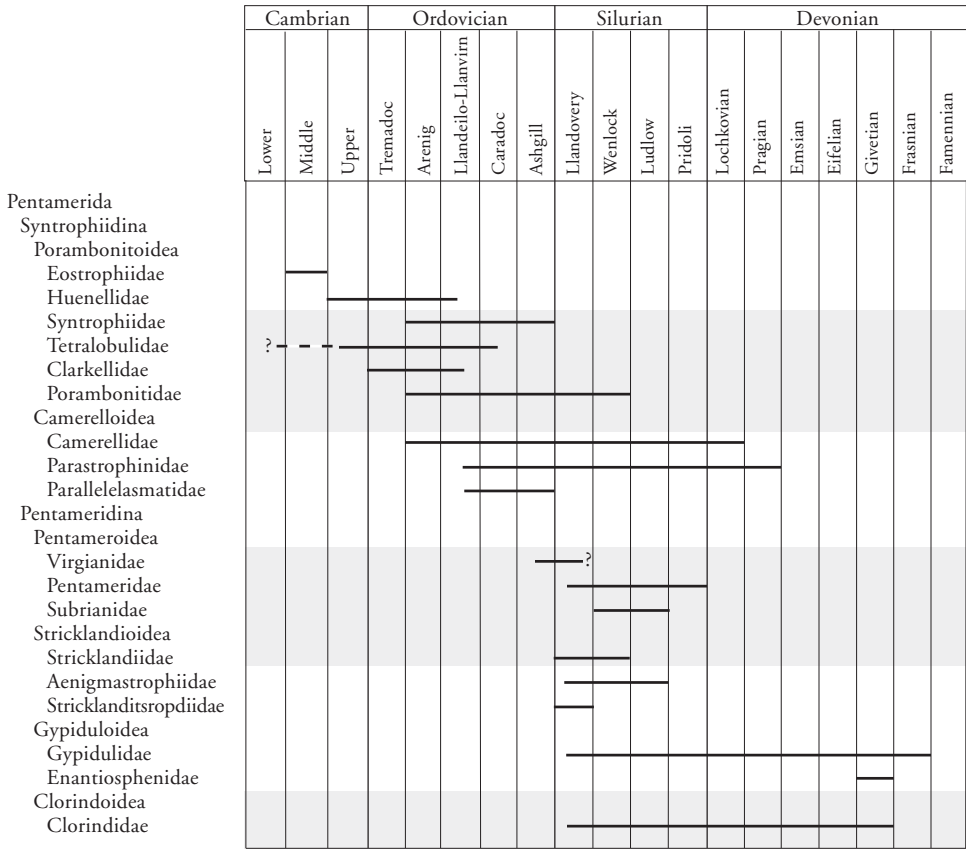


FIG. 618. Stratigraphic ranges of pentameride families; not to absolute time scale; all epochs or stages shown as equal in length (new).

(using traditional pentameroid terminology), and for none of them are there useful data about shell structure. In a general sort of way one is more inclined to see the origins of the Pentameridina within the pre-Ashgill or possibly pre-Caradoc Syntrophiidina owing to overall external and internal similarities. When the genera within the varied syntrophiidine families are considered, however, it is currently unclear just where such origins might be. The alate plates of the parastrophinids rule them out, while the relatively simple camerellid cardinalia similarly make them unlikely ancestors. The very specialized cardinalia of *Brevicamera* rule it out. The very specialized ventral interior of the Xenelasmatinae rules them out as potential ancestors, as does the spondylium simplex of

the Syntrophiidae. There are probably no better prospects in terms of potential ancestors for the other families.

PENTAMERIDE MORPHOLOGY Overall Size and Shape

Size varies considerably, but the largest pentamerides (*Zdimir*, *Supertrilobus*, and *Kirkidium*) are very large indeed (up to 20 cm long), are among the most derived in the order, and appear relatively late stratigraphically within their respective families. Biconvexity increased over time, expressed as dorsibiconvexity in the syntrophiidines and most commonly ventribiconvexity in the pentameridines (Fig. 622). Very generally, valve outline transformed from wider than long to longer than wide (although several

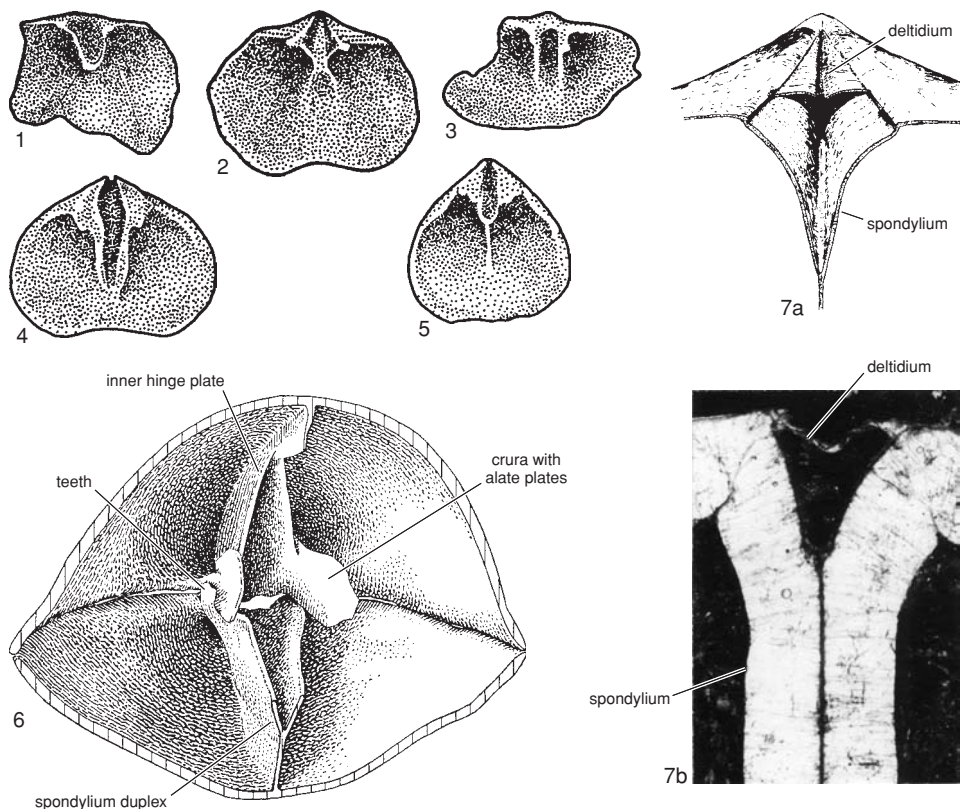


FIG. 619. Features of the ventral interior; 1, *Huenella texana*, pseudospondylium lacking a median ridge or septum; 2, *Tetralobula delicatula*, sessile spondylium supported anteriorly only by broad ridge; 3, *Xenelasma syntrophioides*, parallel dental plates; 4, *Porambonites schmidti*, long, parallel dental plates that converge anteriorly; 5, *Camerella bella*, spondylium simplex on high median septum (new); 6, *Parastrophina hemiplicata*, $\times 6$ (St. Joseph, 1941); 7, *Pentamerus* sp. cf. *P. oblongus* SOWERBY, Silurian, Reynales Formation, New York; 7a, drawing of silicified specimen ($\times 3$) showing deltidium and spondylium duplex; 7b, photomicrograph of part of section through ventral valve posterior showing deltidium and spondylium, $\times 10$ (Amsden, 1965).

exceptions exist, e.g., *Aliconchidium*); and from subquadrate in wide-hinged forms (*Glyptotrophia*); to subpentameral in narrow-hinged forms (*Syntrophopsis*); to subtriangular, round, or elongate oval in astrophic forms (*Idiostrophia*, *Liricamera*, *Virgiana*). Derived pentamerides (*Conchidium*) are much more rostrate than primitive pentamerides (*Huenella*).

Ornament

Ornament varies considerably among pentamerides. Every family exhibits nearly the full complement of ornament types, from smooth (*Palaeostrophia*) to various

types of radial ribs (*Anastrophia*, *Mesonomia*) to a range of more unusual kinds of ornament—concentric lamellae (*Imbricatia*), radial grooves (*Geniculogypa*), spines (*Acanthoglyphia*), nodules or granules (*Calliglyphia*, *Devonogypa*), or pits (*Punctolira*, *Porambonites*, *Wyella*).

Fold and Sulcus

Most of the earliest and more primitive pentamerides possess a strongly uniplicate commissure (*Plectotrophia*), which persisted through much of the evolutionary history of the group (including the clorindoids). Many pentameridines are rectimarginate

(*Rhipidium*); the unisulcate condition has evolved independently at least once, if not more (*Gypidula*).

Hinge and Dentition

A clear transformation from wide, strophic hinge lines (*Huenella*) to successively narrower strophic hinge lines (*Clarkella*) to astrophic hinge lines (*Pentamerus*) is apparent, although wide hinge lines reappeared in more derived pentamerides (most stricklandioids, *Aliconchidium*, *Gypidulella*). While width of the hinge line varies within species, it usually varies within a small, predictable range. Predominantly astrophic species may include individuals with very narrow, strophic hinge lines, but predominantly strophic species only rarely include astrophic individuals. Most pentamerides have deltidiodont dentitions; a few porambonitids (*Porambonites*) and camerelloids (*Camerella*, *Idiostrophia*) appear to have cyrtomatodont dentitions.

Ventral Interior

Dental plates extend from below the teeth to the floor of the valve and may diverge anteriorly, remain parallel, or converge. The dental plates were transformed during pentameride evolution from small, insignificant features (*Cambrotrophia*) to larger, convergent plates that may form a pseudospondylium or one of three different types of true spondylia. The transformation order predicted in a purely structural sense (successive enlarging, converging, and raising of the dental plates above the valve floor) is reflected in the phylogenetic pattern as well. A pseudospondylium lacks a median septum but possesses a low, curved ridge that connects the anterior ends of the dental plates and surrounds the thickened callus of the ventral muscle field (*Huenella*, *Mesonomia*; Fig. 619.1). A sessile spondylium is characterized by a low, median ridge or septum that supports and raises only the anterior portion of a spoon- or trough-shaped spondylium formed by the convergence of the dental plates (*Tetralobula*, *Stichotrophia*; Fig.

619.2). The posterior portion of a sessile spondylium remains confluent with the valve floor. A single, narrow median septum supports the entire length of a simplex spondylium (*Camerella*, *Clarkella*; Fig. 619.5), while a duplex spondylium is supported by a duplex septum, apparently most commonly formed from the extension and fusion of the anterior portion of the dental plates themselves (*Pentamerus*, *Liostrophia*; Fig. 619.6–619.7), although the septum itself, distinct from the dental plates, can appear to be divided in two by a thin layer of prismatic shell (*Parastrophinella*; see Fig. 619.7b). Although they are commonly assumed to be homologous, the homology of a simplex and duplex spondylium or even all duplex spondylia has not yet been clearly established. At least three different times in pentameride evolution, the median septum (and thus spondylium) was lost, and the dental plates returned to a subparallel orientation (*Xenelasma*, *Stenocamara*, *Rhabdostrophia*; Fig. 619.3–619.4). Accessory plates that appear to support the spondylium at approximately right angles to the dental plates may be present (*Yangtzeella*) but are not common.

Ventral muscle attachment sites are present but not particularly well developed in the spondylia of most pentamerides. Some pentameridines (some species of *Stricklandiella*, *Chiastodoca*, *Proconchidium*, *Pleurodium*, *Plicidium*, *Pentamerus*, and *Clorinda*), however, possess well-developed muscle-attachment areas on the anterior margin of the dorsal surface of the spondylium.

Dorsal Interior

Evolution in elements of the dorsal interior is perhaps the most complex and distinctive aspect of pentameride evolution. Confusion about terminology and homology of features of the pentameride dorsal interior is common in the literature; ontogenetic development of the pentameride cardinalia is very poorly known. Features that are likely homologues on the basis of positional similarity may have several different terms applied to

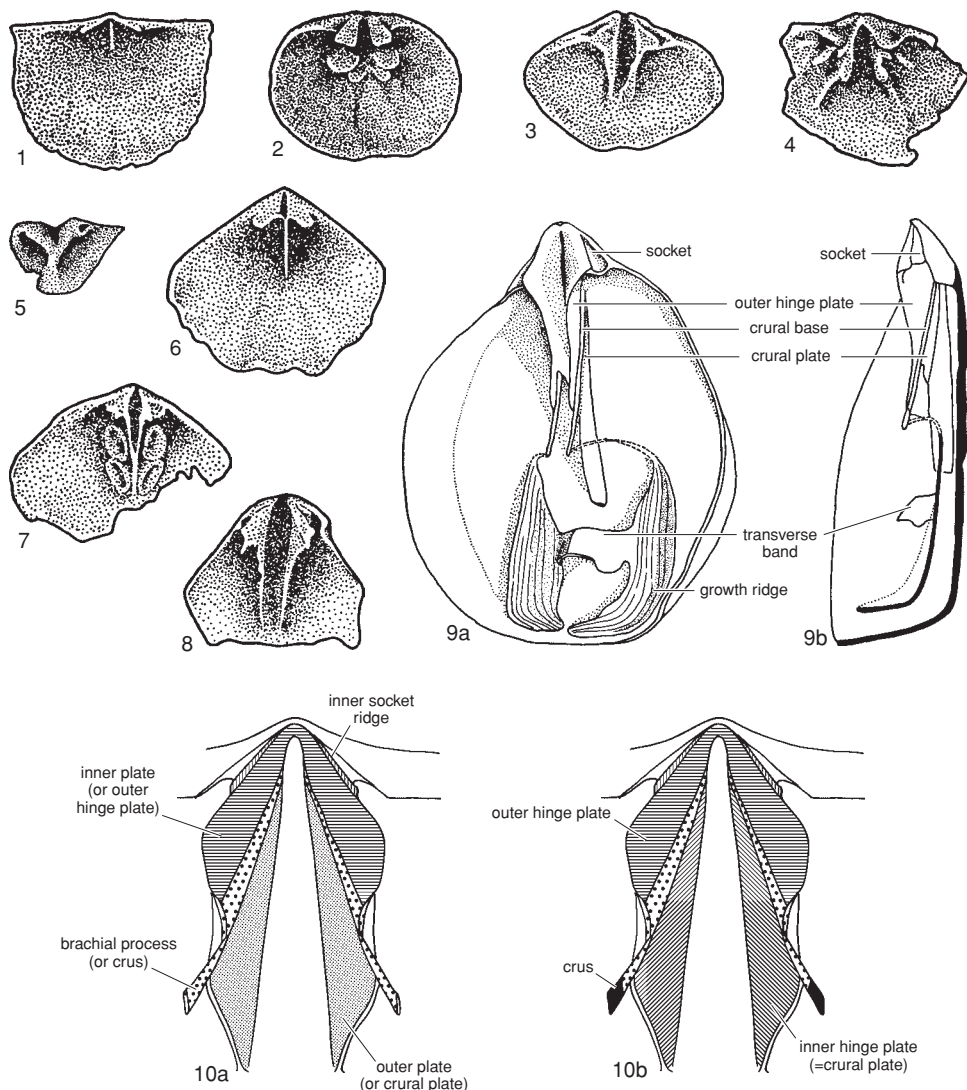


FIG. 620. Features of the dorsal interior; 1, *Mesonomia magna*, cardinal process, simple socket plates; 2, *Tetralobula delicatula*, petaloid socket plates, raised muscle platforms; 3, *Porambonites schmidti*, long socket plates with long extensions; 4, *Clarkella* sp., socket plates with short extensions and accessory septa; 5, *Xenelasma syntrophioides*, wide, short septalium; 6, *Camerella bella*, narrow septalium; 7, *Perimecocoeilia semicostata*, outer and inner hinge plates, septalium (not cruralium) with adductor muscle scars anterolateral; 8, *Metacamarella pentagonum*, crura, long parallel inner hinge plates (new); 9a–b, *Enantiosphen vicaryi* (DAVIDSON), dorsal valve in oblique ventral and lateral views, showing loop, Middle Devonian, England (adapted from Williams & Wright, 1961); 10, *Gypidula* sp., comparison of 10a, former terminology (now obsolete) of dorsal cardinalia (Williams & Rowell, 1965), and 10b, current terminology of dorsal cardinalia (Williams, Brunton, & MacKinnon, 1997).

them, while a single term may be applied to several features of questionable homology. For this reason, we explain below what terms we use, why we use them, and how they compare to previously used terms.

A separate terminology evolved with respect to pentameridine cardinalia (also referred to as the brachial apparatus or brachial plates). The terms used were inner plate (or inner lamellae), brachial process (or brachial

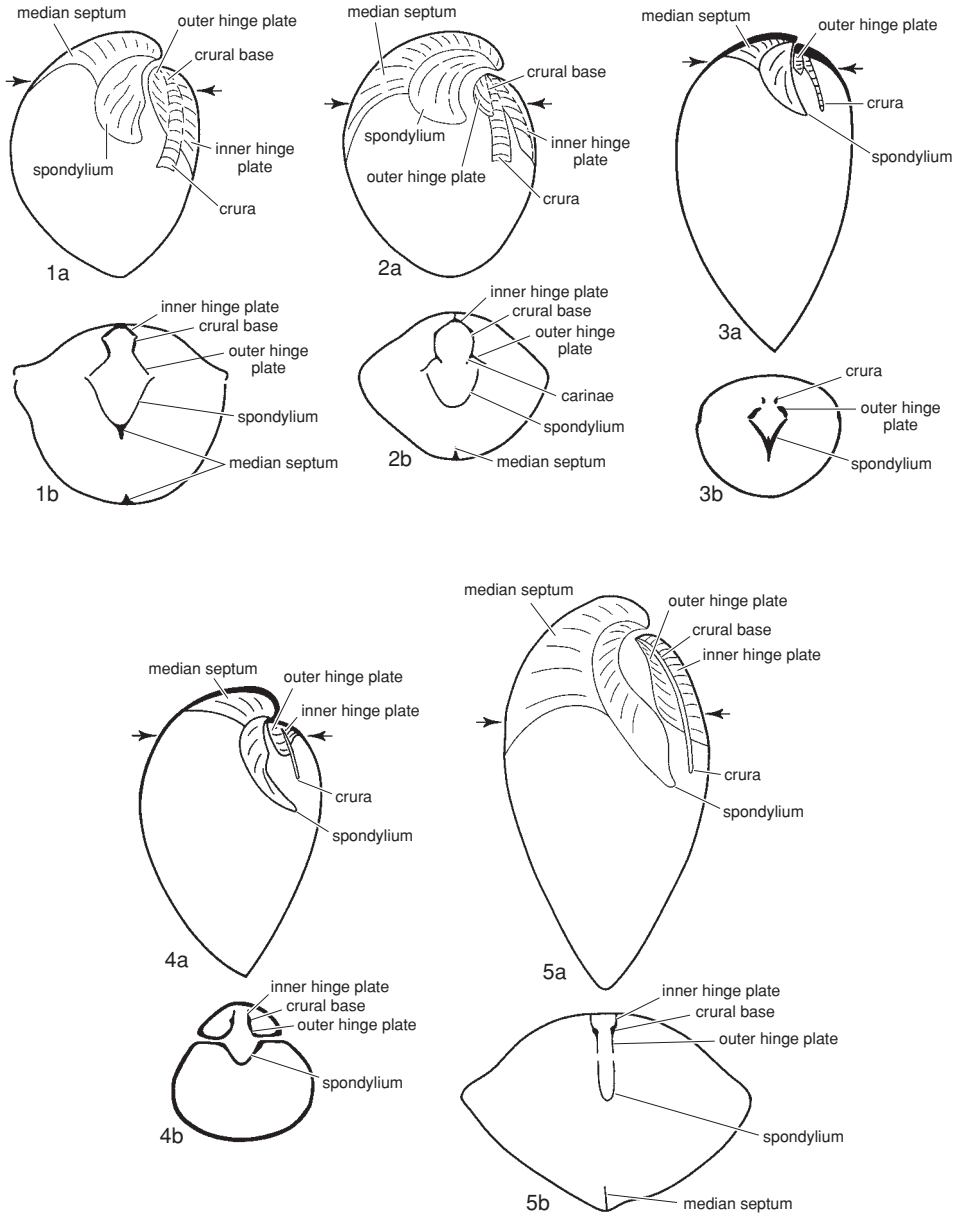


FIG. 621. 1a–b, *Amsdenina roemeri*, gypiduloid; 2a–b, *Clorindella areyi*, clorindoid; 3a–b, *Costistricklandia gaspeensis*, stricklandioid; 4a–b, *Virgiana barrandei*, virgianid; and 5a–b, *Pentamerus* sp. cf. *P. oblongus*, pentamerid; longitudinal sections (above, ventral valve at left) and transverse sections (below, ventral valve below) showing internal structure, arrows on longitudinal sections show position of transverse sections (adapted from Amsden, 1965).

lamellae), and outer plate (or outer lamellae) (Fig. 620.10a), largely following SCHUCHERT and COOPER (1932) and AMSDEN (1953, 1964). These features appear to be homologous with the outer hinge plate, crus (crura),

and inner hinge plate, respectively, of other rhychonellates (CARLSON, 1993). Although now entrenched in the literature, the unique pentameride terminology obscures these apparent homologies, and their use is no longer

recommended (BRUNTON, ALVAREZ, & MAC-KINNON, 1996). All four authors of this pentameride chapter accept, with varying reluctance, the new terminology. Until early ontogenies have been studied within at least a few pentameridines, however, there is still the possibility that outer and inner hinge plates are not homologues of inner and outer lamellae or crura of brachial processes (A. J. B.).

Plate terminology differs depending on the presence or absence of crura. Outer and inner hinge plates lie on the posterolateral and anteromedian sides of the crus respectively. In keeping with terminology applied to the ventral valve (e.g., dental plates), in taxa lacking crura we use the more generalized term socket plate for the plate that extends from the inner socket ridge to the floor of the valve. Socket plates can vary from short and subparallel to recumbent (*Mesonomia*; Fig. 620.1) to convergent (*Tetralobula*, *Syntrophopsis*; Fig. 620.2) or divergent (*Clarkella*, *Acanthoglyphia*; Fig. 620.4). Socket plates that remain discrete may possess long, anterior extensions that are narrower and longer than the plates themselves (*Porambonites*, *Clarkella*; Fig. 620.3–620.4) and may be homologous to inner hinge plates in taxa possessing crura. Elongate and subparallel inner hinge plates exist in *Metacamarella* (Fig. 620.8) and *Pentamerus* (Fig. 621.5).

Accessory plates that appear to support the socket plates at approximately right angles may be present; their terminology and homology (in, for example, Clarkellidae) are unclear and confusing in the literature (*Stichotrophia*). Alate plates, characteristic of

the Parastrophinidae, diverge anterolaterally from the outer side of the inner hinge plates and appear to be dorsal extensions of bladelike crura (Fig. 619.6). Boucot, Rong, and Blodgett employ herein the term carina for a small keel or ridge along the crural base to describe the form of the dorsal interiors of their genera, as has been customary for these taxa. This use of the term is additional to the definition used in Part H, Revised, Volume 1 (KAESLER, 1997), where the term carina is restricted to an external feature. There should be no confusion here since one usage is purely for an external feature and the other for an internal feature.

A true septalium, in which the socket plates (or inner and outer hinge plates) converge and unite to form a duplex septum that forms a raised triangular structure posteriorly, evolved at least twice in the pentamerides (in the Syntrophiiidae, *Xenelasma*, Fig. 620.5, and Camerellidae, *Camerella*, *Perimecocoelia*, Fig. 620.6–620.7). A sessile septalium is formed by socket plates that converge and meet on the valve floor, lacking a septal elevation (*Brevicamera*). A cruralium is defined as a structure that houses the adductor muscles, while the septalium houses only the diductor and pedicle adjustor muscles and specifically excludes the adductor muscles, which may be located more anteriorly (KAESLER, 1997, p. 437). The relationship between septalium and cruralium is commonly unclear, however, particularly in pentamerides for which muscle scars are indistinct. When direct evidence of adductor muscle scars is lacking, the term cruralium is avoided.

SYNTROPHIIDINA

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Suborder SYNTROPHIIDINA Ulrich & Cooper, 1936

[*nom. correct.* BIERNAT, 1965, p. 526, *pro* suborder Syntrophioidea ULRICH & COOPER, 1936, p. 627, *nom. transl. et emend. ex* superfamily Syntrophioacea SCHUCHERT & COOPER, 1931, p. 247]

Commonly small to medium size (less than 2 cm), rarely larger; most wider than long, outline varies from subquadrate to subelliptical to oval as hinge line width varies; strong dorsibiconvexity, not commonly rostrate; uniplicate, rarely rectimarginate; delthyrium open; inner hinge plates (or socket plate extensions), if present, never enclose adductor muscle field. *Lower Cambrian (Toyonian)–Lower Devonian (Pragian)*.

The Syntrophiidina is divided into the older, primitive Porambonitoidea and the younger, more derived Camerelloidea, both of which are paraphyletic (Fig. 617). Mosaic and iterative evolution among the porambonitoids make it somewhat difficult to define unambiguously the families within the group. Although most taxa in each family share common character states (presence or absence of a cardinal process; pseudospondylium, sessile or simplex spondylium, or parallel dental plates; septalium or discrete socket plates), different states are developed in at least a few taxa in each family. Families within the derived taxa—camerelloids and pentameridines—are more easily discerned, largely by features of the cardinalia.

In general, Syntrophiidina transformed from primitive orthidelike morphologies (for example, *Mesonomia* or *Glyptotrophia*) with wide hinge line and subquadrate outline, poorly developed fold and sulcus, small but distinct cardinal process, pseudospondylium or no spondylium at all, and no septalium, to derived, rhynchonellide-like morphologies (for example, *Camerella*, *Plectocamara*, or *Parastrophina*) with an astrophic hinge line, costate ornament, presence of crura, nature of the socket plates, and occasional presence

of a septalium (Fig. 619–622). Rhynchonellida (and descendants from the rhynchonellides; see chapter on Classification, KAESLER, 2000, p. 1) originated from within the Syntrophiidina, as a sister group to the clade of Camerelloidea plus Pentameridina (Fig. 617). Rhynchonellides share a number of primitive characters with the derived porambonitoids (dorsibiconvexity, uniplicate commissure, and some features of the dorsal interior) and share numerous derived characters (listed above) with the camerelloids.

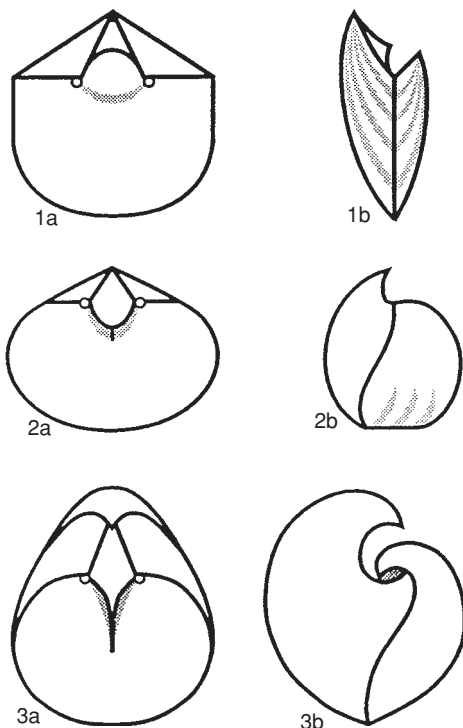


FIG. 622. Generalized drawings of overall shape; 1, orthide; 2, syntrophiidine; 3, pentameridine; on left, ventral valve interior; on right, lateral view of articulated valves, ventral valve on left (adapted from Carlson, 1993).

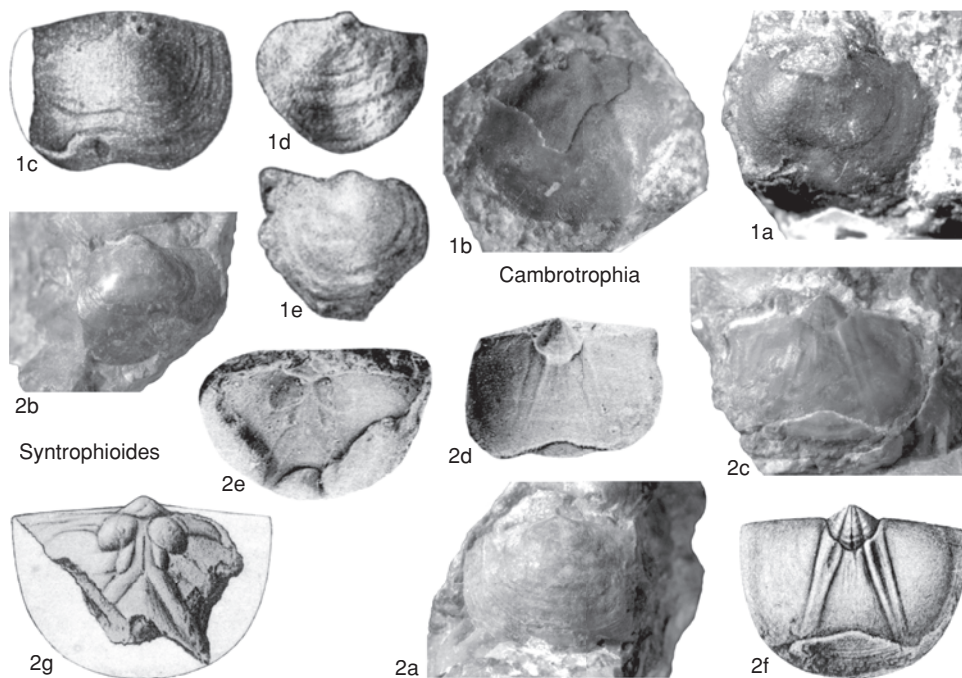


FIG. 623. Eostrophiidae (p. 930–931).

**Superfamily
PORAMBONITOIDEA
Davidson, 1853**

[*nom. correct.* CARLSON, herein, *pro* Porambonitacea BIERNAT, 1965, p. 526, *nom. transl. ex* Porambonitidae DAVIDSON, 1853b, p. 99]

Exterior smooth, costate, costellate, or with radial rows of subcircular pits; hinge line strophic, varying in width; interareas well developed to obsolete, ventral areas commonly wider than dorsal; dental plates converge to form sessile, rarely simplex, spondylium, less commonly form pseudo-spondylium or remain discrete and subparallel; cardinal process absent, rarely present as low vertical ridge on floor of valve or on callosity or narrow shelf at valve posterior; short socket plates commonly discrete and convergent, may unite with low median septum to form simplex septalium, or remain subparallel and rarely extend anteriorly, rarely divergent; crura absent. *Lower Cambrian (Toyonian)–lower Silurian (Wenlock).*

**Family EOSTROPHIIDAE
Ulrich & Cooper, 1936**

[Eostrophiidae ULRICH & COOPER, 1936, p. 627]

Smooth shells; outline commonly subquadrate; moderate biconvexity; weakly uniplicate; wide hinge line; spondylium commonly absent; ventral mantle canals digitate; cardinal process absent; socket plates poorly developed. *Middle Cambrian.*

Cambrotrophia ULRICH & COOPER, 1937, p. 78, *nom. nov. pro Eostrophia* ULRICH & COOPER, 1936, p. 627, *non* DALL, 1890 [**Syntrophia cambria* WALCOTT, 1908, p. 106; OD]. Small to medium in size, hinge line nearly as wide as widest part of shell, poorly developed interareas. *Middle Cambrian (Amgaian)*: USA (Utah), Canada (Quebec), Siberia, Kazakhstan, ?Australia.—FIG. 623, 1a–e. **C. cambria* (WALCOTT); a, ventral valve exterior, Ute Formation, Utah; b, hypotype, partly exfoliated ventral valve, Ute Formation, Utah, USNM 52477, ×3 (new); c, dorsal valve exterior, Ute Formation, Utah, ×3 (Walcott, 1908); d, ventral valve exterior, Kazakhstan; e, dorsal valve exterior, Kazakhstan, ×1 (Nikiforova, 1960d).

Syntrophioides SCHUCHERT & COOPER, 1931, p. 247 [**Billingsella harlanensis* WALCOTT, 1905, p. 236; OD]. Hinge line as wide or wider than widest part of shell, interareas relatively wide, pseudospondylium poorly developed; inner socket ridges short, supported by short, convergent but discrete socket plates; dorsal adductor muscle field well developed with weak callosities. *Middle Cambrian (Mayaian)*: Russia (Urals), southern USA.—FIG. 623, 2a–g. **S. harlanensis* (WALCOTT), Rogersville Shale, Tennessee, USA; *a*, ventral valve exterior; *b*, dorsal valve exterior; *c*, hypotype, ventral valve interior mold, USNM 52252, $\times 2$ (new); *d*, cast of ventral valve interior mold; *e*, cast of dorsal valve interior mold, $\times 2$ (Schuchert & Cooper, 1932); *f*, drawing of ventral valve interior mold; *g*, drawing of dorsal valve interior mold, $\times 2$ (Walcott, 1912).

Family HUENELLIDAE Schuchert & Cooper, 1931

[Huenellidae SCHUCHERT & COOPER, 1931, p. 247]

Costate or costellate, rarely smooth; subquadrate in outline; strongly uniplicate; wide hinge line, rarely narrow, with well-developed interareas; teeth strong; dental plates converge slightly to form pseudospondylium, rarely sessile spondylium, or remain parallel; cardinal process present as low vertical ridge, less commonly absent; socket plates short, small, discrete, commonly convergent, may be recumbent; dorsal adductor muscle field commonly well developed with weak callosities, elongate oval in outline. *Upper Cambrian (Dresbachian)*–*Lower Ordovician (lower Llanvirn)*.

Subfamily HUENELLINAE Schuchert & Cooper, 1931

[*nom. transl.* SHAW, 1953, p. 143, ex Huenellidae SCHUCHERT & COOPER, 1931, p. 247] [=Rectotrophiinae BATES, 1968, p. 176]

Costate, rarely smooth; pseudospondylium present, rarely with parallel dental plates; socket plates subparallel to convergent, rarely unite with median septum to form septalium. *Upper Cambrian (Dresbachian)*–*Lower Ordovician (lower Llanvirn)*.

Huenella WALCOTT, 1908, p. 109 [**Syntrophia texana* WALCOTT, 1905, p. 294; OD]. Type species costate; pseudospondylium tending toward sessile spondylium in some, with anterior edge supported by broad, low ridge that widens anteriorly; cardinal process present in type species, lacking in some others. *Upper Cambrian (Dresbachian)*–*Lower Ordovi-*

cian (Tremadoc): USA, Canada, Siberia, China.—FIG. 624, 1a–f. **H. texana* (WALCOTT), Upper Cambrian, USA; *a*, ventral valve exterior, Packsaddle Mountain, Texas; *b*, ventral valve exterior, Packsaddle Mountain, Texas; *c*, ventral sulcus, anterior view, Packsaddle Mountain, Texas; *d*, dorsal valve exterior, Packsaddle Mountain, Texas; *e*, hypotype, dorsal valve, lateral view, Packsaddle Mountain, Texas, USNM 52494, $\times 4$ (new; photographs courtesy of Michael Bassett); *f*, ventral valve interior, pseudospondylium, Gallatin Valley, Wyoming, $\times 3$ (Ulrich & Cooper, 1938).—FIG. 624, 1g. *H. abnormis* (WALCOTT), ?Upper Cambrian, Yellowstone National Park, Wyoming, USA; drawing of dorsal valve interior, $\times 2$ (Walcott, 1912).

Bondarevia CARLSON, herein, p. 1616, *nom. nov. pro Triseptata* BONDAREV in BONDAREV & others, 1965, p. 34, *non* HOSHIDE, 1958 [**Triseptata nelidovi* BONDAREV in BONDAREV & others, 1965, p. 34; M]. Large costellate shells, subelliptical in outline; commissure rectimarginate; pseudospondylium supported by two short accessory septa; cardinal process a relatively high ridge on narrow shelf at posterior of notothyrial cavity; short, narrow socket plates converge and unite with long median septum to form deep septalium, supported by 2 long accessory septa; dorsal adductor muscle field slightly elevated. [This genus, known from only 1 species, is highly distinctive in its morphology and, as it becomes better known, may warrant subfamily status within the Huenellidae, suggested tentatively by BONDAREV in BONDAREV & others (1965, p. 35). It has an unusual combination of characters including the pseudospondylium and cardinal process of Huenellidae, accessory septa, notothyrial platform, and elevated dorsal adductor muscle field of Clarkellidae, and septalium of Syntrophiidae, in addition to its large size and rectimarginate commissure.] *Lower Ordovician (lower Arenig)*: Novaya Zemlya.—FIG. 625, 3a–n. **B. nelidovi* (BONDAREV), Nelidovsk beds; *a*, ventral valve exterior; *b*, articulated valves, ventral valve on right, $\times 1$ (Bondarev, 1968); *c–e*, serial sections of ventral valve showing pseudospondylium and accessory septa, $\times 4$; *f–j*, serial sections of dorsal valve showing cardinal process and notothyrial platform, $\times 4$ (Bondarev & others, 1965); *k*, ventral valve interior, in section; *l*, dorsal valve mold, posterior view; *m*, dorsal valve interior mold; *n*, cast of *m*, $\times 1$ (Bondarev, 1968).

Eosyntrophopsis YADRENKINA, 1989, p. 77 [**E. njuicus*; OD]. Small smooth shells, rectimarginate; hinge line wide, but interareas reduced; low, wide median ridge extending anterior to pseudospondylium; cardinal process absent. *Lower Ordovician (Tremadoc)*: southeastern Siberia.—FIG. 624, 3a–d. **E. njuicus*, Loparsk beds, Njuya River; *a*, ventral valve exterior; *b*, ventral valve interior mold; *c*, ventral valve interior; *d*, dorsal valve interior mold, $\times 3$ (Yadrenkina, 1989).

Huenellina SCHUCHERT & COOPER, 1931, p. 247 [**Huenella triplicata* WALCOTT, 1924, p. 526; OD].

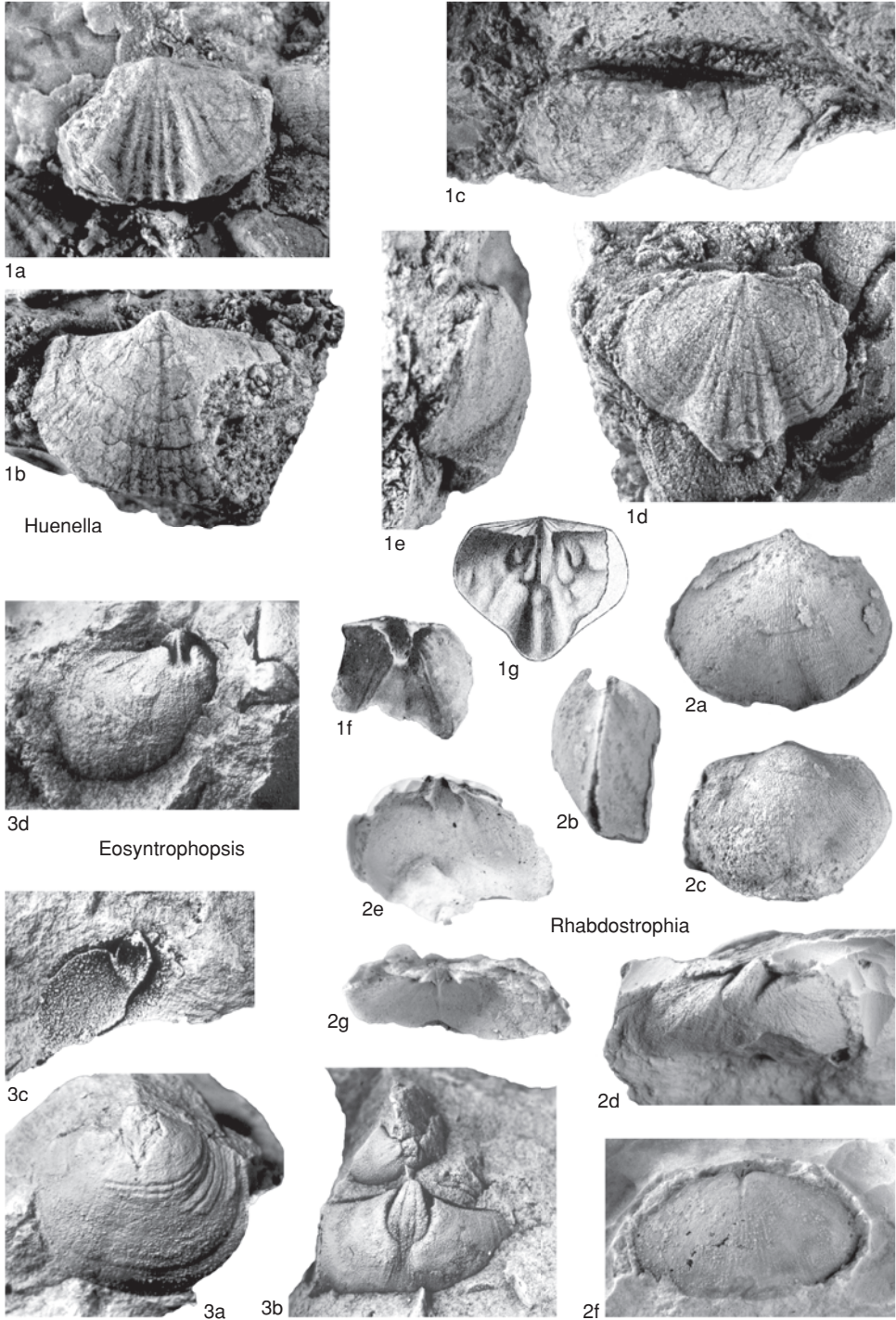


FIG. 624. Huenellidae (p. 931–934).

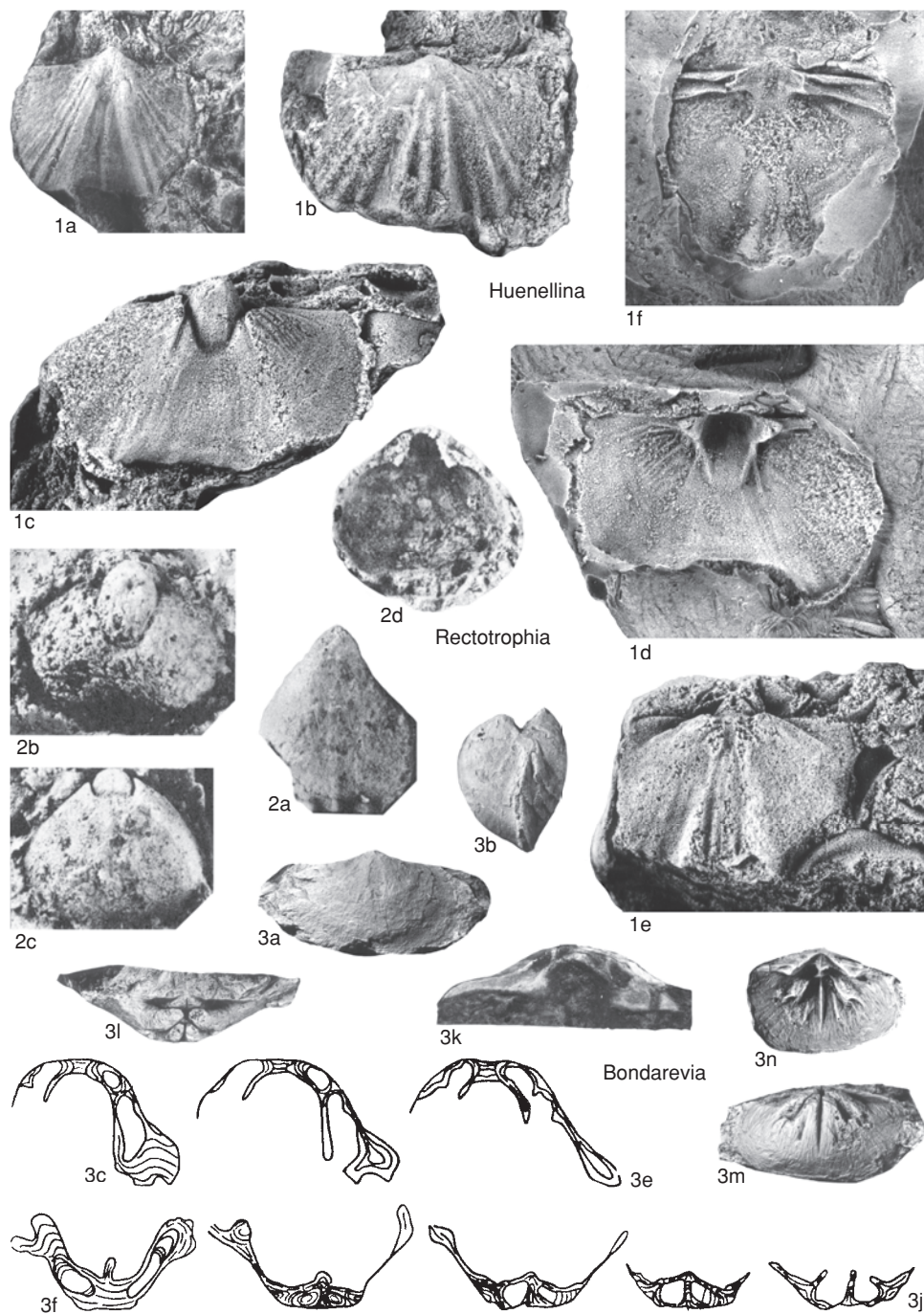


FIG. 625. Huenellidae (p. 931–934).

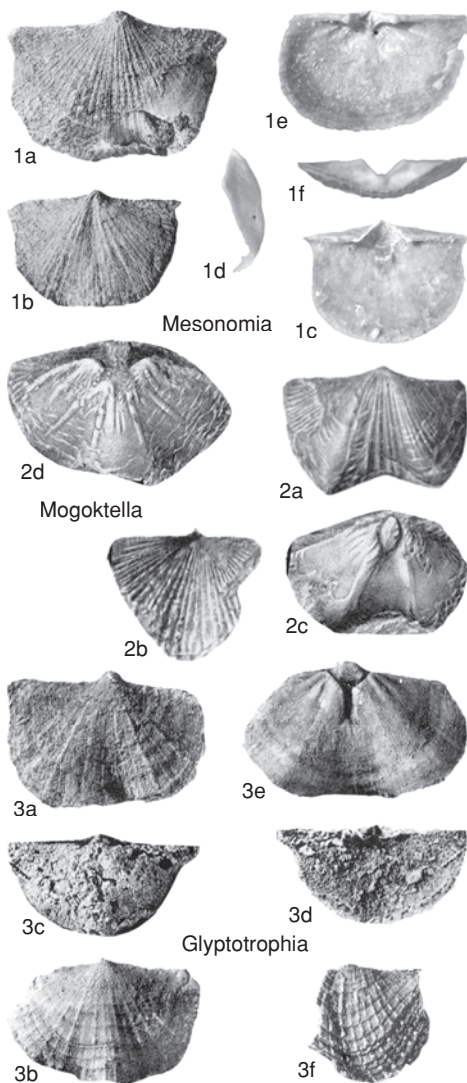


FIG. 626. Huenellidae (p. 934–935).

Similar to *Huenella*, but with 2 long lateral septa that emerge at low angle to hinge line and do not support the wide, short socket plates; cardinal process absent. *Upper Cambrian* (Franconian–Trempealeuan): Novaya Zemlya.—FIG. 625, 1a–f. **H. triplicata* (WALCOTT), hypotype; *a*, ventral valve exterior, PMO A3293; *b*, dorsal valve exterior, PMO A3350; *c*, ventral valve interior mold, PMO A3352; *d*, latex cast of *c*, $\times 3$; *e*, dorsal valve interior mold, PMO A3348; *f*, latex cast of *e*, $\times 4$ (new; photographs courtesy of Michael Bassett).

Rectotrophia BATES, 1968, p. 176 [**R. globularis*; OD]. Small smooth shells, weakly uniplicate; hinge line narrow, less than half widest part of shell, interareas reduced; pseudospondylium

long and wide; cardinal process on slightly thickened notothyrial platform. *Lower Ordovician* (Arenig): Wales, northeastern China.—FIG. 625, 2a–d. **R. globularis*, Treiorwerth Formation, Wales; *a*, ventral valve exterior; *b*, ventral valve interior mold; *c*, dorsal valve interior mold; *d*, cast of *c*, $\times 3$ (Neuman & Bates, 1978).

Rhabdostrophia NEUMAN, 1989, p. 68 [**R. striatisculpta*; OD]. Finely ramicostellate; biconvexity moderate; relatively weakly uniplicate; strong dental plates discrete, subparallel; cardinal process may be present on low, rhomboidal notothyrial platform formed by convergent socket plates. *Lower Ordovician* (Arenig–lower Llanvirn): Norway.—FIG. 624, 2a–g. **R. striatisculpta*, Holonda Limestone; *a*, ventral valve exterior; *b*, articulated valves, ventral on left; *c*, dorsal valve exterior; *d*, ventral valve interior mold; *e*, cast of ventral valve interior; *f*, dorsal valve interior mold; *g*, cast of dorsal valve interior, $\times 2$ (Neuman, 1989).

Subfamily MESONOMIINAE Ulrich & Cooper, 1936

[Mesonomiinae ULRICH & COOPER, 1936, p. 627]

Costellate; hinge line commonly widest part of shell; pseudospondylium, rarely sessile spondylium, present; cardinal process present; socket plates subparallel to recumbent. [Some genera in this subfamily are very orthidelike in their overall morphology and may be more appropriately classified in the Orthida.] *Upper Cambrian* (Dresbachian)–*Lower Ordovician* (Tremadoc).

Mesonomia ULRICH & COOPER, 1936, p. 627 [**Eorthis iophon* WALCOTT, 1924, p. 507; OD]. Fine but distinct costellae; biconvexity weak to moderate; weakly uniplicate, dorsal sulcus reverts to fold early in growth. *Upper Cambrian* (Dresbachian)–*Lower Ordovician* (Tremadoc): USA, Canada, ?Kazakhstan, ?eastern China.—FIG. 626, 1a–b. **M. iophon* (WALCOTT), Tremadoc, Mons Formation, Alberta, Canada; *a*, ventral valve exterior; *b*, dorsal valve exterior, $\times 2$ (Ulrich & Cooper, 1938).—FIG. 626, 1c–f. *M. magna* COOPER, Fort Sill Formation, Oklahoma, USA; *c*, ventral valve interior; *d*, ventral valve, lateral view; *e*, dorsal valve interior; *f*, dorsal valve, anterior view, USNM 116694, $\times 1.66$ (new).

Glyptotrophia ULRICH & COOPER, 1936, p. 627 [**G. imbricata*; OD]. Small shells with fine costellae and strong concentric lamellae; biconvexity moderate; shallow sessile spondylium supported anteriorly only by low, wide median ridge. *Upper Cambrian* (Trempealeuan)–*Lower Ordovician* (Tremadoc): USA, Canada, eastern China, ?Kazakhstan.—FIG. 626, 3a–d. **G. imbricata*, Tremadoc, Mons Formation, Alberta, Canada; *a*, ventral valve exterior; *b*, dorsal valve exterior; *c*, dorsal valve interior mold; *d*,

cast of *c*, $\times 3$ (Ulrich & Cooper, 1938).—FIG. 626, 3*e–f*. *G. jasperensis* (KINDLE), Tremadoc, Mons Formation, Alberta, Canada; *e*, ventral valve interior mold; *f*, ornament, dorsal valve, $\times 3$ (Ulrich & Cooper, 1938).

Mogoktella ANDREEVA, 1968, p. 82 [**M. islendica*; OD]. Parvicostellate; biconvexity strong; teeth weak; cardinal process a well-developed ridge on raised notothyrial platform; socket plates very rudimentary. *Upper Cambrian (Franconian)*: northwestern Siberia.—FIG. 626, 2*a–d*. **M. islendica*, Chopko River; *a*, ventral valve exterior; *b*, dorsal valve exterior; *c*, ventral valve interior; *d*, dorsal valve interior, $\times 2$ (Andreeva, 1968).

Family SYNTROPHIIDAE Schuchert, 1896

[Syntrophiidae SCHUCHERT, 1896, p. 320]

Costate or smooth shells; outline rounded quadrate to wide elliptical; weakly unipli- cate; narrow to medium hinge line, rarely wide; interareas reduced or obsolete, rarely wide and well developed; dental plates commonly discrete and subparallel, rarely converge to form spondylium simplex; cardinal process absent; narrow socket plates may converge and unite with long median septum to form septalium, or may remain discrete. *Lower Ordovician (Arenig)*–*Upper Ordovician (Ashgill)*.

Subfamily SYNTROPHIINAE Schuchert, 1896

[*nom. transl.* ULRICH & COOPER, 1936, p. 631, *ex* Syntrophiidae SCHUCHERT, 1896, p. 320]

Smooth shells with wide hinge line and well-developed interareas; spondylium simplex and septalium present. *Lower Ordovician (Arenig)*.

Syntrophia HALL & CLARKE, 1893, p. 216 [**Triplesia lateralis* WHITFIELD, 1886, p. 303; OD] [=*Syntrophia* HALL & CLARKE, 1892, p. 270, *nom. nud.*]. Type species relatively large; biconvexity moderate; uniplication developed only near commissure; spondylium simplex supported only in the posteriormost portion by high median septum, spondylium nearly free in some species; long, deep socket plates converge and unite with long median septum to form long, broad, shallow septalium. *Lower Ordovician (Arenig)*: USA, Canada, Europe, Greenland, Russia, Siberia, China.—FIG. 627, 1*a–b*. **S. lateralis* (WHITFIELD), Cassin Formation, Vermont, USA; *a*, dorsal valve exterior, $\times 1.5$; *b*, posterior view of complete but exfoliated specimen showing spondylium and septalium (as

molds), $\times 2$ (Ulrich & Cooper, 1938).—FIG. 627, 1*c–i*. *S. torynifera* (ULRICH & COOPER), Smithville Formation, Arkansas, USA; *c*, ventral valve exterior; *d*, articulated valves, ventral valve on right; *e*, dorsal valve exterior, open delthyrium and well-developed interareas; *f*, ventral valve interior, spondylium nearly free; *g*, ventral valve interior, anterior view; *h*, ventral valve interior, oblique lateral view; *i*, dorsal valve interior, septalium, $\times 2$ (Ulrich & Cooper, 1938).

Subfamily XENELASMATINAE Ulrich & Cooper, 1936

[*nom. correct.* BIERNAT, 1965, p. 534, *pro* Xenelasminae ULRICH & COOPER, 1936, p. 631]

Costate or costellate shells, rarely smooth, with narrow to medium hinge line; dental plates discrete and subparallel, spondylium absent. *Lower Ordovician (Arenig)*–*Upper Ordovician (Ashgill)*.

Xenelasma ULRICH & COOPER, 1936, p. 631 [**X. syntrophioides*; OD]. Small smooth shells; biconvexity moderate; relatively strong uniplication commencing anterior to umbo; narrow hinge line, less than half widest part of shell; dental plates long, nearly half valve length, and closely spaced; ventral adductor muscle field anterior to and commonly separated from diductors by very low ridge; narrow, very short septalium simplex supported by median septum commonly extending anterior to septalium, less commonly sessile septalium lacking median septum; elongate oval dorsal adductor muscle field well developed. *Lower Ordovician (Arenig)*: USA, Russia (Urals).—FIG. 627, 2*a–i*. **X. syntrophioides*, USA; *a*, ventral valve exterior, Gorman Formation, Texas; *b*, articulated valves, ventral on right, Gorman Formation, Texas; *c*, dorsal valve exterior, Gorman Formation, Texas; *d*, articulated valves, anterior view, ventral valve below, Gorman Formation, Texas; *e*, ventral valve interior, Gorman Formation, Texas; *f*, hypotype, dorsal valve interior, Gorman Formation, Texas, USNM 328688, $\times 3$ (new); *g*, ventral valve interior, Rockdale Run Formation, Maryland, $\times 4$; *h*, dorsal valve interior, Rockdale Run Formation, Maryland, $\times 6$ (Sando, 1957); *i*, cast of ventral valve interior mold, Longview Formation, Virginia, $\times 3$ (Ulrich & Cooper, 1938).

Rhyselasma YADRENKINA, 1972, p. 177 [**R. akittiense*; OD]. Small costate shells; hinge line narrow, less than half widest part of shell; socket plates discrete and subparallel, median septum and septalium absent. [Interiors generally poorly known.] *Lower Ordovician (Arenig)*: Siberia.—FIG. 627, 3*a–d*. **R. akittiense*; *a*, ventral valve exterior, Ugorian beds, Kulumba River; *b*, dorsal valve exterior, Ugorian beds, Kulumba River, $\times 4$ (Yadrenkina, 1982); *c*, ventral valve interior, drawing from etched exteriors, Chunkski stage, Khantaika River; *d*, dorsal

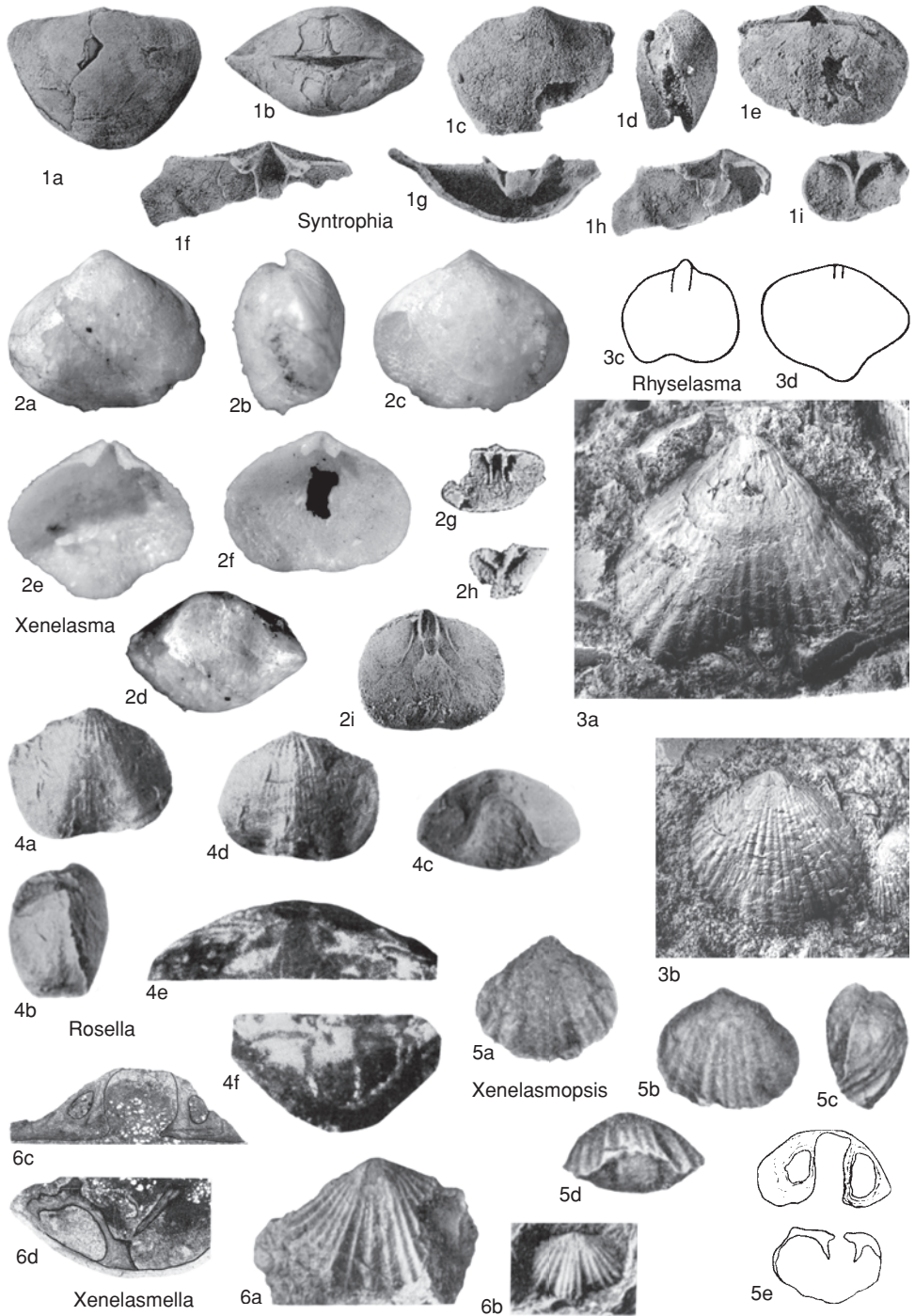


FIG. 627. Syntrophiidae (p. 935–937).

valve interior, drawing from etched exteriors, Chunski stage, Khantaika River, $\times 3$ (Yadrenkina, 1972).

Rosella ANDREEVA, 1972, p. 52 [**R. karakulensis*; OD].

Large, strongly parvicostellate shells with weak but distinct growth lines; biconvexity strong; hinge line wide but narrower than widest part of shell; teeth weak; dental plates long, subparallel, widely spaced; socket plates discrete and subparallel, median septum and septalium absent. *Lower Ordovician (Arenig)*: Russia (Urals).—FIG. 627, 4a–f. **R. karakulensis*, Kuragan Suite, southern Urals; *a*, ventral valve exterior; *b*, articulated valves, ventral on right; *c*, articulated valves, anterior view; *d*, dorsal valve exterior, $\times 1$; *e*, ventral valve, ground section near beak; *f*, dorsal valve, ground section near beak, $\times 2$ (Andreeva, 1972).

Xenelasmella ROZMAN, 1964b, p. 137 [**X. graciosa*; OD].

Costate shells; biconvexity strong; strong and angular uniplication; hinge line wide, but narrower than widest part of shell; teeth strong; septalium wider than in *Xenelasma*. [Interiors generally poorly known.] *Lower Ordovician (lower Llanvirn–upper Llanvirn)*: Siberia, northwestern China.—FIG. 627, 6a–d. **X. graciosa*, Sienskii beds, Kalychan stream, Siberia; *a*, ventral valve exterior; *b*, dorsal valve exterior, $\times 2$; *c*, ventral valve section, $\times 4$; *d*, dorsal valve section, $\times 6$ (Rozman, 1964b).

Xenelasmopsis ROZMAN, 1968, p. 56 [**X. selemnjahia*; OD].

Costae on anterior half of valve only; biconvexity strong; hinge line astrophic or extremely narrow; teeth weak; socket plates discrete and subparallel, median septum and septalium absent. *Upper Ordovician (Ashgill)*: Siberia.—FIG. 627, 5a–e. **X. selemnjahia*, Sakyndzhinskaya Suite, Selenniakhsk Range; *a*, ventral valve exterior; *b*, dorsal valve exterior; *c*, articulated valves, ventral valve on left; *d*, articulated valves, anterior view, $\times 2$ (Rozman, 1968); *e*, articulated valves, section, ventral valve above, $\times 4$ (Rozman, 1970).

Family TETRALOBULIDAE

Ulrich & Cooper, 1936

[Tetralobulidae ULRICH & COOPER, 1936, p. 627] [=Syntrophopsidae ULRICH & COOPER, 1936, p. 630]

Smooth to finely costellate, may also have strong concentric lamellae that may intersect to form radial rows of subcircular pits; outline rounded quadrate to wide elliptical; dental plates converge to form sessile spondylium supported anteriorly only by low, wide median ridge or septum, rarely as pseudospondylium or spondylium simplex or duplex; cardinal process absent, only rarely present; socket plates commonly long, robust, convergent but discrete, rarely forming sessile septalium. *Lower Cambrian*

(*Toyonian*), *Upper Cambrian (Franconian)*–*Upper Ordovician (lower Caradoc)*.

Subfamily TETRALOBULINAE

Ulrich & Cooper, 1936

[*nom. transl.* SAPELNIKOV, 1980, p. 10, ex Tetralobulidae ULRICH & COOPER, 1936, p. 627; *emend.*, CARLSON, herein]

Costellate, commonly with weak to strong concentric lamellae; moderately biconvex; weak uniplication commencing anterior to umbo; wide to medium hinge line with well-developed interareas; sessile spondylium present, rarely as pseudospondylium or spondylium simplex or duplex, 2 long accessory septa may be present; long, petaloid socket plates converge but remain discrete, rarely with accessory septa or forming sessile septalium; dorsal adductor muscle field commonly well developed, may be slightly elevated, with strong callosities. *Lower Ordovician (Tremadoc–Arenig)*.

Tetralobula ULRICH & COOPER, 1936, p. 628 [**T. delicatula*; OD].

Finely costellate, with weak but distinct concentric growth lines; teeth strong; sessile spondylium supported anteriorly by low, wide ridge that widens further as it extends slightly anterior to spondylium; 2 long accessory septa may be prolonged in front of spondylium; dorsal adductor muscle field elevated on callosities, petaloid in shape, posterior scars commonly larger than anterior. *Lower Ordovician (Tremadoc–Arenig)*: USA, Canada, Siberia, ?Kazakhstan, China.—FIG. 628, 1a–f. **T. delicatula*, Chepultepec Formation, Virginia, USA; *a*, ventral valve exterior; *b*, dorsal valve exterior; *c*, ventral valve interior; *d*, dorsal valve interior, $\times 3$ (Ulrich & Cooper, 1938); *e*, ventral valve, posterior view, teeth, sulcus; *f*, ventral valve, lateral view, USNM Biologic Collection, $\times 3$ (new).

Diseppta ZENG, 1987, p. 237 [**Tetralobula?* *yichangensis* ZENG, 1977, p. 50; OD] [=Diseppta ZENG, 1983, p. 48, *nom. nud.*].

Costellate without concentric lamellae; biconvexity strong; strongly uniplicate; teeth small; sessile spondylium supported anteriorly by relatively high duplex septum and 2 short accessory septa, not prolonged in front of spondylium; socket plates converge to form short, weak sessile septalium supported by 2 short accessory septa. *Lower Ordovician (Tremadoc)*: southern China.—FIG. 628, 2a–f. **D. yichangensis* (ZENG), lower Nantsinkuan Formation, Hubei; *a*, ventral valve exterior; *b*, dorsal valve exterior; *c*, dorsal valve, anterior view; *d*, ventral valve interior, $\times 2$; *e*, ventral valve interior, anterior view, $\times 3$; *f*, dorsal valve interior, $\times 2$ (Zeng, 1983).

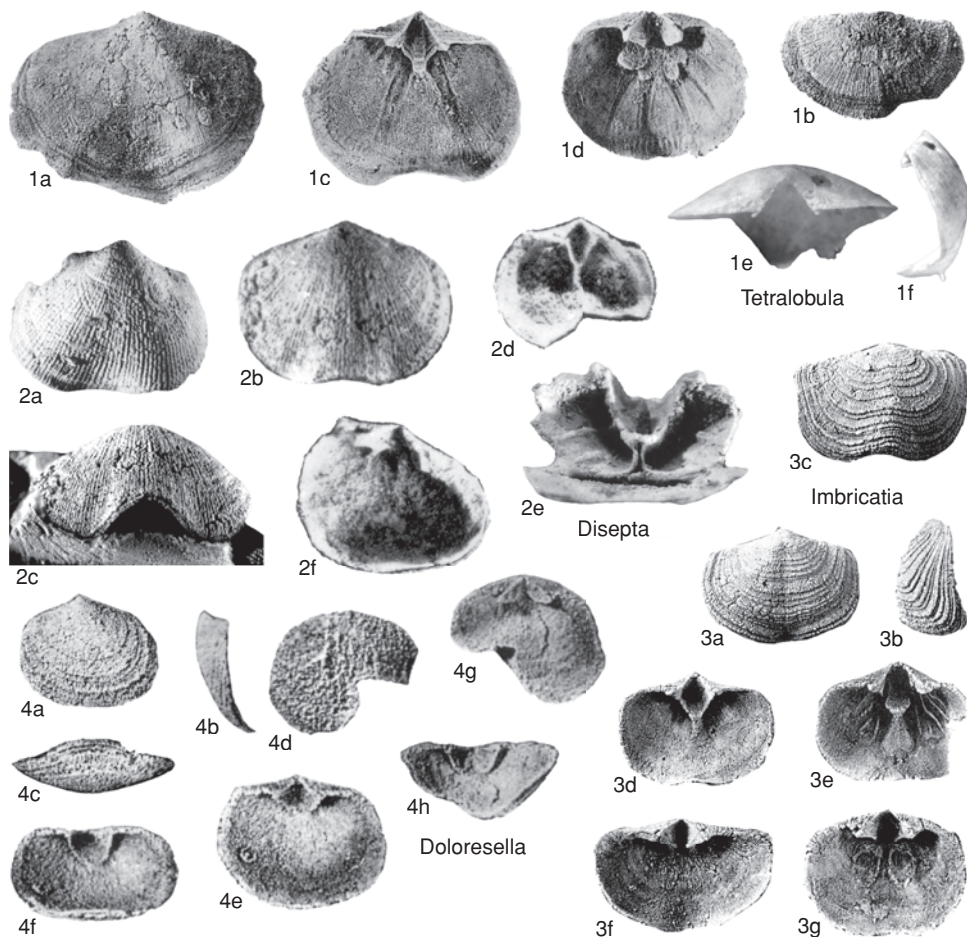


FIG. 628. Tetralobulidae (p. 937–938).

Doloresella SANDO, 1957, p. 122 [**D. concentrica*; OD]. Ornament similar to *Tetralobula*; uniplication near anterior margin only; teeth small; pseudospondylium present but poorly developed; median ridge absent; accessory septa absent; dorsal adductor muscle field poorly developed, not elevated on callosities. *Lower Ordovician (Arenig)*: USA (Maryland), Russia, China.—FIG. 628, 4a–h. **D. concentrica*, Rockdale Run Formation, Maryland, USA; a, ventral valve exterior; b, ventral valve lateral view; c, ventral valve anterior view; d, dorsal valve exterior; e, ventral valve interior; f, ventral valve interior, oblique; g, dorsal valve interior; h, dorsal valve interior, oblique, $\times 2$ (Sando, 1957).

Imbricatia COOPER, 1952, p. 21 [**I. lamellata*; OD] [= *Thaumatrophia* WANG, 1955, p. 342 (type, *T. sinensis*); *Thaumatrophia* BIERNAT, 1965, p. 531,

nom. null.]. Finely costellate with strong, sharp, concentric lamellae; teeth small; spondylium structure quite variable, type species with sessile spondylium supported anteriorly by low, wide ridge, others with spondylium simplex supported by high, wide median septum; accessory septa absent; dorsal adductor muscle field not elevated, but weak callosities are present. [*Thaumatrophia* has strong teeth and is strongly uniplicate but is otherwise very similar to *Imbricatia*.] *Lower Ordovician (Tremadoc)*: USA, Canada, Kazakhstan, Novaya Zemlya, China, ?Argentina.—FIG. 628, 3a–g. **I. lamellata*, Cool Creek Formation, Oklahoma, USA; a, ventral valve exterior; b, dorsal valve exterior; c, dorsal valve lateral view; d, ventral valve interior; e, ventral valve interior, gerontic individual; f, dorsal valve interior; g, dorsal valve interior, gerontic individual, $\times 2$ (Cooper, 1952).

Subfamily SYNTROPHOPSINAE

Ulrich & Cooper, 1936

[*nom. transl.* ANDREEVA, 1982, p. 58, ex *Syntrophopsidae* ULRICH & COOPER, 1936, p. 630; *emend.*, CARLSON, herein] [= *Palaeostrophinae* ULRICH & COOPER, 1936, p. 627; *Rhysostrophinae* SAPELNIKOV, 1980, p. 11]

Smooth or costellate, rarely costate; strongly biconvex; strongly uniplicate; narrow hinge line with well-developed to reduced interareas; sessile spondylium present, accessory septa rare; socket plates commonly long, convergent but discrete, rarely forming sessile septalium. *Lower Cambrian (Toyonian)*, *Upper Cambrian (Franconian)*—*Upper Ordovician (lower Caradoc)*.

Syntrophopsis ULRICH & COOPER, 1936, p. 630 [**S. magna*; OD]. Type species large, others commonly small to moderate in size; smooth; uniplication present only on anterior half; teeth relatively small; long, sessile spondylium supported at anterior only by low, wide ridge that widens to broad, slightly elevated triangular area anterior to spondylium between digitate mantle canals, median ridge absent in some species; long socket plates discrete and closely spaced; fulcral plates present under sockets; very weak callosities mark dorsal adductor muscle field. *Lower Ordovician (Tremadoc–Arenig)*: USA, Scotland, southern China, north-central Russia, Siberia, Tasmania, ?Argentina.—FIG. 629,1a–g. **S. magna*, Odenville Formation, Alabama, USA; *a*, ventral valve exterior; *b*, articulated valves, ventral valve on left; *c*, dorsal valve exterior; *d*, articulated valves, posterior view; *e*, articulated valves, anterior view; *f*, ventral valve interior; *g*, dorsal valve interior, $\times 1.5$ (Ulrich & Cooper, 1938).

Altunella LIU, ZHANG, & DI, 1984, p. 160 [**A. typica*; OD]. Costate shells, length and width nearly equal; very strongly biconvex; uniplication present on entire valve; interareas narrow; sessile spondylium supported by 2 accessory septa; weak, narrow sessile septalium supported by short median septum. [Interiors poorly known.] *Upper Ordovician (lower Caradoc)*: northwestern China.—FIG. 629,2a–d. **A. typica*, Maleziji Group, Xinjiang; *a*, ventral valve exterior; *b*, dorsal valve exterior; *c*, lateral view, ventral valve on left; *d*, anterior view, ventral valve below, $\times 1.5$ (Liu, Zhang, & Di, 1984).

Bobinella ANDREEVA, 1968, p. 80 [**B. kulumbensis*; OD]. Similar to *Syntrophopsis*, but parvicostellate; weakly uniplicate; interareas narrow to obsolete. *Upper Cambrian (Franconian)*: northwestern Siberia.—FIG. 629,4a–d. **B. kulumbensis*, Kulumba River; *a*, ventral valve exterior; *b*, dorsal valve exterior; *c*, ventral valve interior mold; *d*, dorsal valve interior mold, $\times 3$ (Andreeva, 1968).

Hesperotrophia ULRICH & COOPER, 1936, p. 630 [**H. obscura*; OD]. Similar to *Syntrophopsis*, but finely costellate; weak, narrow uniplication. [Interiors

poorly known.] *Lower Ordovician (Arenig)*: Canada (Alberta).—FIG. 629,3a–d. **H. obscura*, Sarbach Formation; *a*, ventral valve exterior; *b*, dorsal valve exterior, $\times 2$; *c*, fine costellae, $\times 4$; *d*, dorsal valve interior mold, $\times 2$ (Ulrich & Cooper, 1938).

Palaeostrophia ULRICH & COOPER, 1936, p. 627 [**Syntrophia orthia* WALCOTT, 1906, p. 11; OD]. Smooth, moderately biconvex shells; uniplication very deep and rounded, reverts from gentle unisulcation early in ontogeny in some individuals; type species with medium hinge line, others narrow to medium in width; teeth strong; sessile spondylium narrow, supported at anterior only by short, low, wide median ridge not prolonged anterior to spondylium; shallow notothyrial cavity; socket plates narrow, very short, delicate, may have thickened callus of shell in between; dorsal adductor muscle field elongate oval in outline. *Upper Cambrian (Franconian)*—*Lower Ordovician (lower Llanvirn)*: USA, Canada, Norway, Russia, Kazakhstan, China, South Korea.—FIG. 629,5a–b. **P. orthia* (WALCOTT), upper Franconian—lower Trempealeauan, Chaumitien Limestone, Tsinan, China; *a*, dorsal valve exterior, $\times 2$; *b*, dorsal valve interior, $\times 3$ (Ulrich & Cooper, 1938).—FIG. 629,5c–j. *P. sp.*, upper Franconian—lower Trempealeauan, Wilburns Formation, Texas, USA; *c*, ventral valve exterior; *d*, ventral valve exterior, lateral view; *e*, ventral valve, posterior view; *f*, dorsal valve exterior; *g*, dorsal valve exterior, lateral view; *h*, dorsal valve exterior, posterior view; *i*, ventral valve interior; *j*, dorsal valve interior, USNM Biologic Collection, $\times 2$ (new).

Plectotrophia ULRICH & COOPER, 1936, p. 627 [**P. bridgei*; OD]. Similar to *Palaeostrophia*, but with fine, widely spaced costellae, some nearly smooth; uniplication strong and angular; hinge line wide, may be widest part of shell; socket plates narrow, short, convergent but discrete, rarely unite to form short sessile septalium duplex; dorsal adductor muscle field not well developed. *Upper Cambrian (Franconian)*: USA, Canada (Alberta).—FIG. 630,1a–b. **P. bridgei*, Wilburns Formation, Texas, USA; *a*, ventral valve exterior; *b*, ventral valve exterior, lateral view; *c*, dorsal valve exterior; *d*, dorsal valve exterior, lateral view; *e*, ventral valve interior; *f*, dorsal valve interior, $\times 2$; *g*, dorsal valve interior, socket plates discrete; *h*, dorsal valve interior, socket plates nearly united, $\times 3$ (Ulrich & Cooper, 1938).

Rhysostrophia ULRICH & COOPER, 1936, p. 630 [**R. nevadensis*; OD]. Similar to *Syntrophopsis*, but with strong costae; moderately biconvex; hinge line width varies considerably, narrow in type species, with narrow interareas; teeth strong; short spondylium structure commonly sessile and supported at anterior only by short, wide median septum, but may be simplex and supported for entire length; socket plates discrete but approach a sessile septalium in some individuals. *Lower Ordovician (Arenig–lower Llanvirn)*: USA, Canada, Europe, Siberia, ?New Zealand.—FIG. 630,2a–f. **R. nevadensis*,

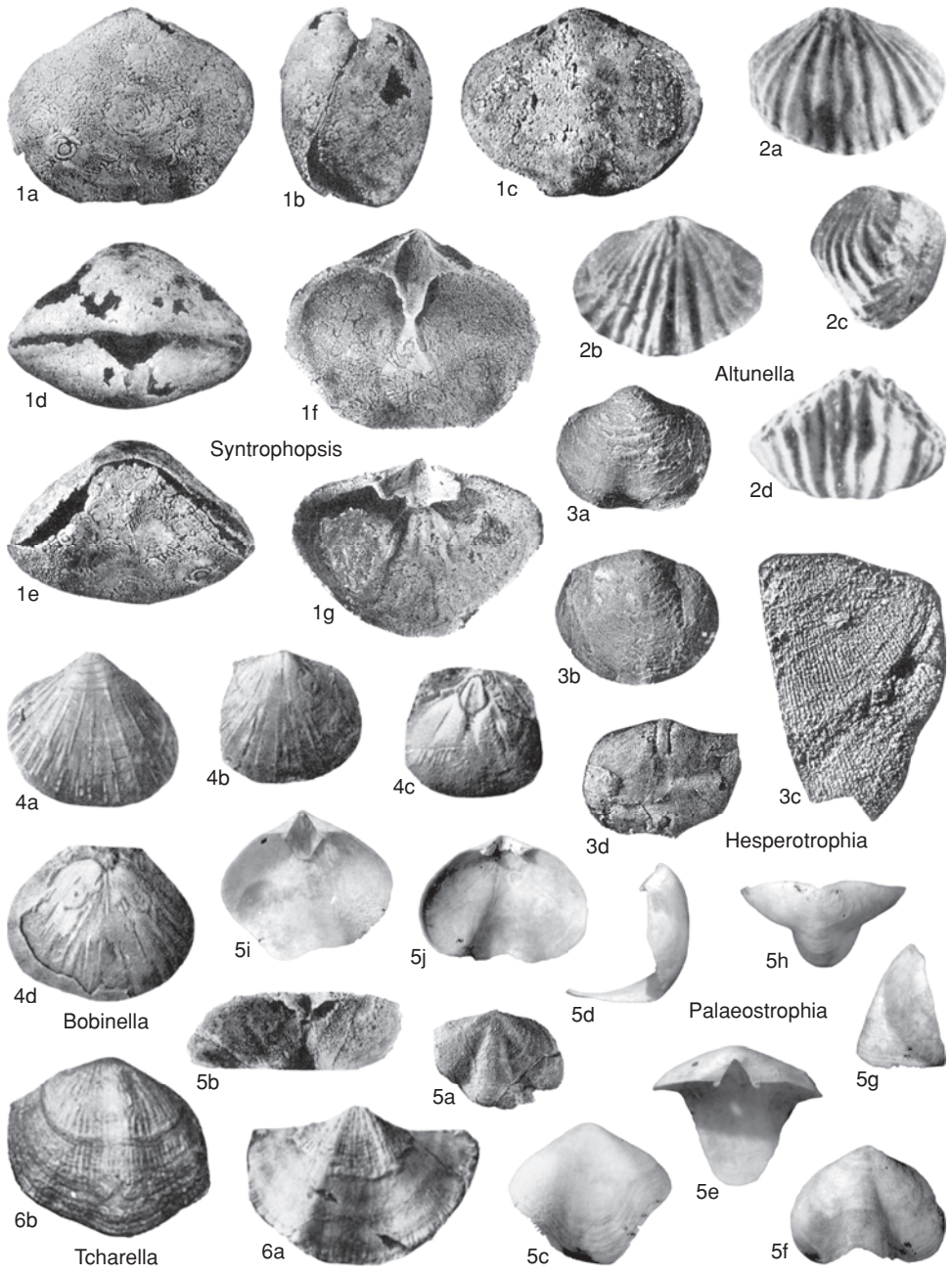


FIG. 629. Tetralobulidae (p. 939–941).

upper Pogonip Formation, Nevada, USA; *a*, ventral valve exterior; *b*, articulated valves, ventral valve on left; *c*, dorsal valve exterior, $\times 1$; *d*, articulated valves, anterior view; *e*, dorsal valve interior mold,

$\times 1.5$; *f*, dorsal valve interior, oblique mold, $\times 2$ (Ulrich & Cooper, 1938).—FIG. 630, 2*g*. *R. vagans* (REED), Hølanda Limestone, Norway; ventral valve interior, $\times 2$ (Neuman, 1989).

?*Tcharella* ANDREEVA, 1987, p. 38 [**T. amgensis*; OD]. Costellate; subquadrate in outline; moderately biconvex; uniplication narrow, present on entire valve; hinge line wide, as wide as widest part of shell; interareas very narrow; inner socket ridges short, socket plates appear to be absent. [Ventral interior unknown. *Tcharella* (tentatively assigned here to Syntrophopsinae) occurs unquestionably in the Toyonian; the genus is so poorly known that its assignment to Pentamerida is questionable.] *Lower Cambrian (Toyonian)*: Siberia.—FIG. 629,6a–b. **T. amgensis*, Kooteniella zone, Amga River; a, ventral valve exterior; b, dorsal valve exterior, $\times 1.5$ (Andreeva, 1987).

Subfamily PUNCTOLIRINAE
Andreeva, 1982

[Punctolirinae ANDREEVA, 1982, p. 58; *emend.*, CARLSON, herein]

Fine costellae and concentric lamellae intersect and merge to form distinctive radial rows of subcircular pits; wide to medium hinge line with well-developed interareas; teeth strong; sessile spondylium (rarely pseudospondylium) present, accessory septa uncommon; ventral mantle canal systems saccate; cardinal process only rarely present; socket plates convergent but discrete, septalium absent. *Lower Ordovician (Tremadoc–lower Llanvirn)*.

Punctolira ULRICH & COOPER, 1936, p. 628 [**P. punctolira*; OD]. Type species medium size, others may be quite large; strongly biconvex; uniplication strong and angular, reverts from gentle unisulcation early in ontogeny in some individuals; cardinal process very rarely present as low ridge; dorsal adductor muscle field well developed, petaloid, with strong callosities. *Lower Ordovician (Tremadoc–Arenig)*: USA, Canada, Argentina, China, Russia.—FIG. 631,1a–e. **P. punctolira*, Tremadoc; a, ventral valve exterior, Mons Formation, Alberta, Canada; b, ventral valve, anterior view, Mons Formation, Alberta, Canada (Ulrich & Cooper, 1938); c, dorsal valve exterior, Goodwin Formation, Nevada, USA; d, dorsal valve, anterior view, Goodwin Formation, Nevada, USA, $\times 2$; e, ornament, Goodwin Formation, Nevada, USA, $\times 10$ (Ulrich & Cooper, 1938).—FIG. 631,1f–g. *P. orientalis* WANG & XU, Arenig, Lunshan limestone, Tangshan, China; f, ventral valve interior; g, dorsal valve interior, $\times 2$ (Wang & Xu, 1966).

Cuparius ROSS, 1971, p. 125 [**C. cardilatus*; OD]. Moderate to large size; moderately biconvex; uniplication strong and broad, present only on anterior half; narrow median septum does not extend anterior to spondylium; notothyrial cavity shallow; socket plates long, deep, subparallel, and uniting with valve in short, slightly divergent, anterior extensions, not petaloid as in *Tetralobula*; fulcral

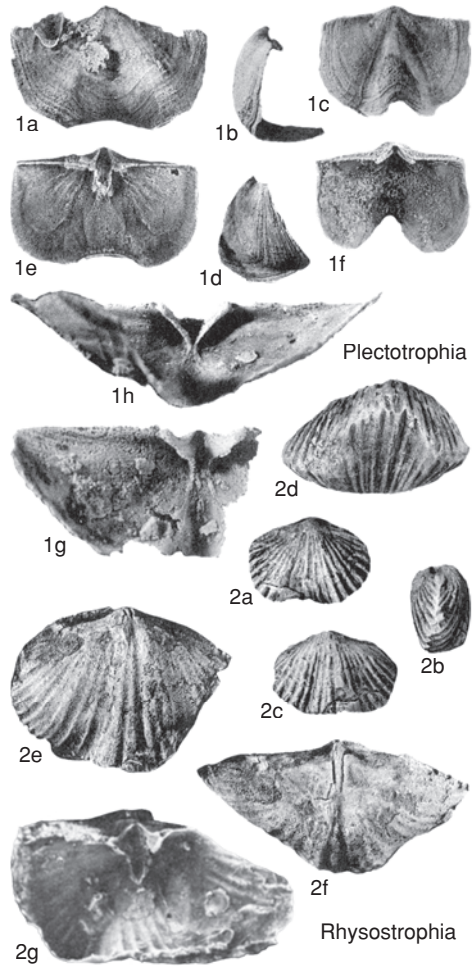


FIG. 630. Tetralbulidae (p. 939–940).

plates present under sockets; dorsal adductor muscle field poorly developed. [NEUMAN and BATES (1978) synonymized *Cuparius* with *Rugostrophia*, and XU and LIU (1984) synonymized *Cuparius* with *Punctolira*, but differences in ventral and dorsal interiors warrant recognition of all 3 genera.] *Lower Ordovician (lower Llanvirn)*: USA, Canada, Siberia.—FIG. 631,2a–f. **C. cardilatus*, Antelope Valley Limestone, Nevada, USA; a, ventral valve exterior; b, articulated valves, ventral on left; c, dorsal valve exterior; d, articulated valves, anterior view; e, ventral valve interior; f, dorsal valve interior, $\times 2$ (Ross, 1971).

Pseudoporambonites ZENG, 1977, p. 51 [**P. yichangensis*; OD] [=*Porambonitoidea* XU in XU, WAN, & CHEN, 1978, p. 315 (type, *P. hupeihensis*)]. Large to very large in size; length and width nearly equal; dorsal and ventral valve convexity nearly equal; weak uniplication present only on anterior half;

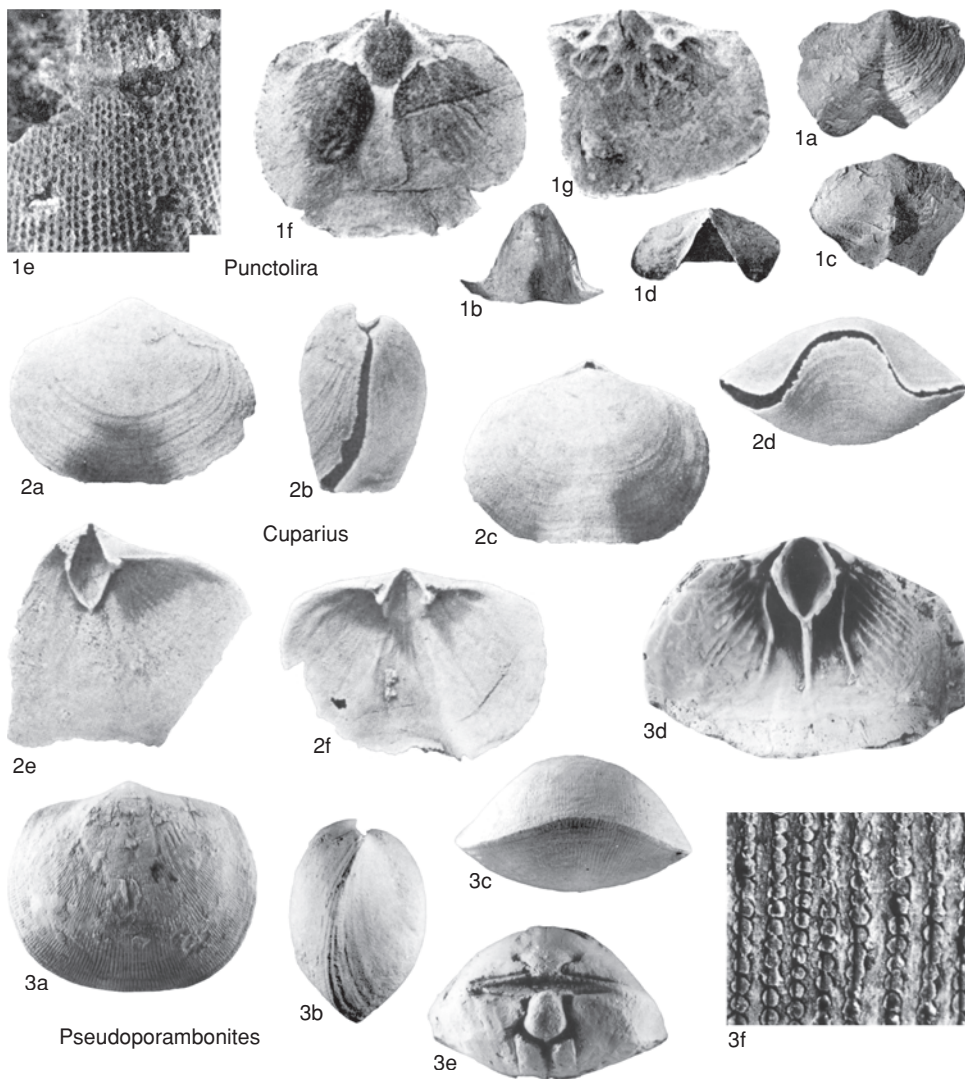


FIG. 631. Tetralobulidae (p. 941–942).

sessile spondylium supported by relatively high, narrow median septum; 2 long accessory septa present, prolonged in front of spondylium; dorsal adductor muscle field poorly developed. [*Porambonitoides* lacks uniplication and has smaller hinge teeth but appears to be well within the variability of *Pseudoporambonites*.] *Lower Ordovician (Arenig)*: southwestern China. —FIG. 631,3a–f. **P. yichangensis*, Dawan Formation, Hubei, China; *a*, ventral valve exterior; *b*, articulated valves, ventral on left; *c*, articulated valves, anterior view, ventral below; *d*, ventral valve interior; *e*, mold of articulated valves, posterior view, ventral below, $\times 1$; *f*, ornament, $\times 10$ (Zeng, 1977).

Rugostrophia NEUMAN, 1971, p. 118; *emend.*, NEUMAN, 1976, p. 40; NEUMAN & BATES, 1978, p. 607 [*R. silvestris*; OD]. Large shells; strongly biconvex; concentric lamellae distinct and strong; strong uniplication present on entire valve; long pseudo-spondylium present; socket plates short and narrow; fulcral plates present under sockets; dorsal adductor muscle field well developed, petaloid, with weak callosities. *Lower Ordovician (upper Arenig–lower Llanvirn)*: USA, Canada, Argentina. —FIG. 632,1a–d. **R. silvestris*, New Brunswick, Canada; *a*, ventral valve interior mold; *b*, cast of *a*; *c*, dorsal valve interior mold, post-depositional elongation in anterior-posterior direction; *d*, cast of dorsal valve

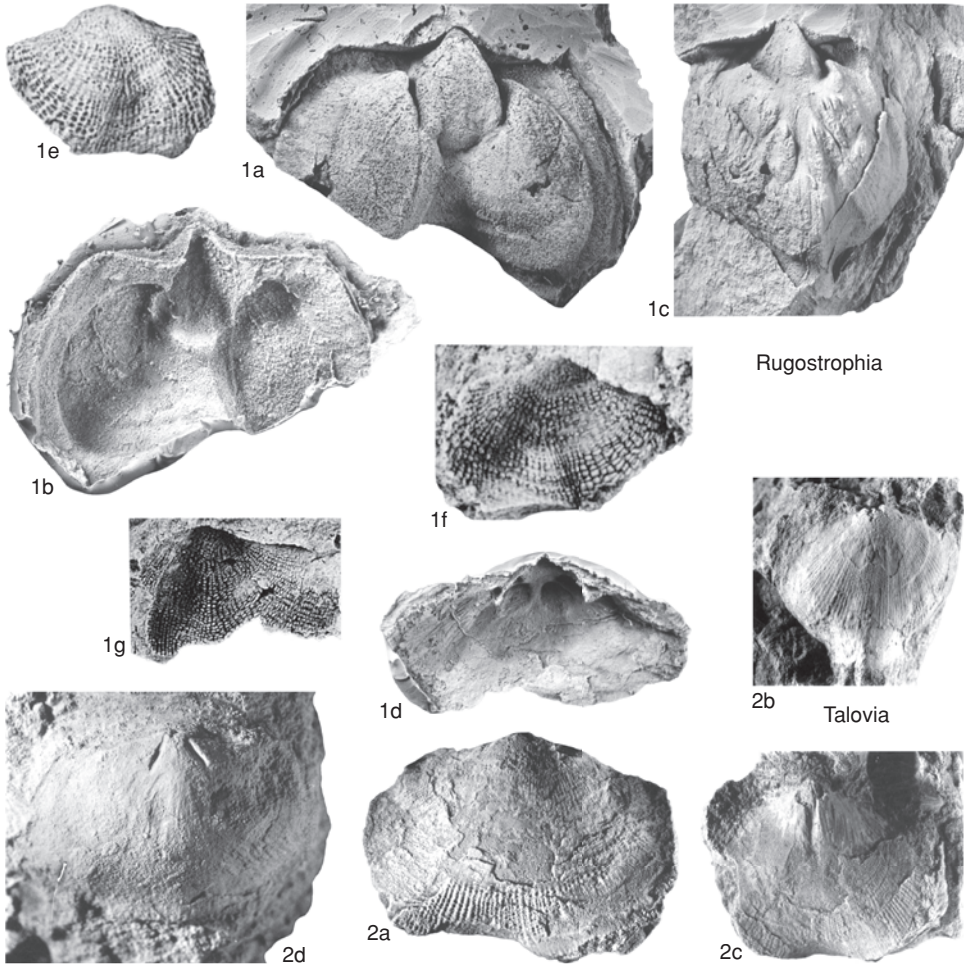


FIG. 632. Tetralobulidae (p. 942–943).

interior mold, $\times 1.5$ (Neuman, 1971).—FIG. 632, 1e–g. *R. latireticulata* NEUMAN, Newfoundland, Canada; e, ventral valve exterior mold; f, cast of e, $\times 1.5$; g, dorsal valve exterior mold, $\times 1$ (Neuman, 1976).

Talovia SEVERGINA, 1975, p. 62 [*T. reticulata*; OD]. Small shells; moderately biconvex; weak unipliication present near anterior margin only; sessile spondylium short, narrow, and shallow; 2 short accessory septa present; long inner socket ridges supported by wide, deep, slightly divergent socket plates; dorsal adductor muscle field poorly developed. Lower Ordovician (lower Llanvirn): Russia (Gorno-Altay).—FIG. 632, 2a–d. **T. reticulata*, Rudnikovo Formation; a, ventral valve exterior, $\times 3$; b, dorsal valve exterior, $\times 1.5$; c, ventral valve interior mold, $\times 2$; d, dorsal valve interior mold, $\times 3$ (Severgina, 1975).

Family CLARKELLIDAE
Schuchert & Cooper, 1931

[Clarkellidae SCHUCHERT & COOPER, 1931, p. 247] [=Yangtzeellidae ZENG, 1986, p. 79]

Commonly smooth, may be costellate or with strong concentric lamellae, rarely with spines or nodules; outline subpentamerale to subelliptical; strongly unipliicate; hinge line varies from wide to narrow with well-developed to reduced interareas; spondylium simplex, less commonly sessile spondylium, rarely duplex spondylium, or absent entirely; two short accessory septa may be present; cardinal process rare, diductor muscles

attach on callosity or narrow shelf at posterior of notothyrial cavity; socket plates subparallel to divergent, commonly continue anteriorly into short divergent extensions, rarely with 2 or 4 long accessory septa, or forming a kind of septalium simplex; adductor muscle field commonly well developed, rarely slightly elevated, with weak callosities. *Lower Ordovician (Tremadoc–lower Llanvirn).*

Clarkella WALCOTT, 1908, p. 110 [*Polytoechia? montanensis* WALCOTT, 1905, p. 295; OD]. Small to medium shells; smooth; strongly biconvex; uniplication strong and quite angular in some species, present on anterior half only; hinge line narrow, less than half widest part of shell; interareas narrow; teeth small; spondylium simplex supported along entire length by high median septum that extends anterior to spondylium; 2 or more short accessory septa present rarely in some species; socket plates fairly long, shallow; 4, less commonly 2, long accessory septa support socket plates. *Lower Ordovician (Tremadoc–Arenig)*: USA, Canada, southwestern China, Korea, Russia, Siberia, Kazakhstan.—FIG. 633, 1a–b. **C. montanensis* (WALCOTT), Montana, USA; *a*, ventral valve exterior; *b*, dorsal valve exterior, $\times 1.5$ (Ulrich & Cooper, 1938).—FIG. 633, 1c–d. *C. mcgerriglei* ULRICH & COOPER, Hastings Creek Formation, Quebec, Canada; *c*, paratype, ventral valve exterior; *d*, paratype, dorsal valve exterior, USNM 91477, $\times 2.5$ (new).—FIG. 633, 1e–g. *C. sp.*; *e*, ventral valve interior, Hastings Creek Formation, Quebec, Canada, $\times 3$ (Schuchert & Cooper, 1932); *f*, dorsal valve interior, Upper Cool Creek Formation, Oklahoma, USA; *g*, anterior view of *f*, Upper Cool Creek Formation, Oklahoma, USA, USNM 116750, $\times 2.5$ (new).

Acanthoglypha WILLIAMS & CURRY, 1985, p. 257 [*Streptis affinis* REED in GARDINER & REYNOLDS, 1909, p. 151; OD]. Parvicostellate with strong concentric lamellae bearing hollow, bifurcating spines; moderately ventribiconvex; subquadrate in outline; weakly uniplicate; hinge line wide, but narrower than widest part of shell; interareas reduced; teeth weak; sessile spondylium supported anteriorly only by low, wide median ridge that does not extend anterior to spondylium; accessory septa absent; socket plates widely divergent, lacking anterior extensions; dorsal adductor muscle field elongate oval, strongly elevated, and marked by strong callosities. [COCKS (1978) reexamined the lectotype of *Streptis affinis* and placed the species in *Calliglypha*; differences in ornament and dorsal muscle field warrant separate generic status for *Acanthoglypha* and *Calliglypha*.] *Lower Ordovician (Arenig)*: Ireland.—FIG. 633, 2a–g. **A. affinis* (REED), Tourmakeady Limestone; *a*, dorsal valve exterior mold, $\times 3$; *b*, bifurcating spines, $\times 14$; *c*, dorsal valve exte-

rior, anterior view, $\times 3$; *d*, ventral valve exterior, anterior view; *e*, ventral valve interior, $\times 5$; *f*, dorsal valve interior; *g*, dorsal valve interior, $\times 4$ (Williams & Curry, 1985).

Calliglypha CLOUD, 1948, p. 468 [**C. miseri*; OD]. Small shells; fine costellae and strong concentric lamellae intersect to form nodular ornament; strongly biconvex; subquadrate outline; weakly uniplicate; hinge line wide, often widest part of shell; interareas relatively wide; teeth strong; narrow spondylium simplex; accessory septa absent; socket plates short, shallow, divergent, lacking anterior extensions. *Lower Ordovician (Arenig)*: USA, Britain, Russia, ?Argentina.—FIG. 633, 4a–g. **C. miseri*, El Paso Formation, Texas, USA; *a*, ventral valve exterior; *b*, ventral valve exterior, anterior view, $\times 2$; *c*, dorsal valve exterior, $\times 3$; *d*, ventral valve interior, $\times 2$; *e*, ventral valve interior, oblique view; *f*, dorsal valve interior; *g*, dorsal valve interior, oblique view, $\times 3$ (Cloud, 1948).

Diaphelasma ULRICH & COOPER, 1936, p. 629 [**D. pennsylvanicum*; OD]. Smooth shells; very strongly biconvex; commonly broadly uniplicate, but width and depth varies; hinge line narrow; teeth strong; spondylium simplex supported along entire length by high median septum that extends anterior to spondylium for considerable distance, in some individuals most extreme posterior of spondylium may be sessile; accessory septa absent; minute cardinal process may be present as low ridge on callosity at valve posterior, rarely on short notothyrial platform; short, shallow, widely divergent socket plates, supported in some species by 2 short accessory septa; elongate oval dorsal adductor muscle field poorly developed. *Lower Ordovician (Arenig)*: USA, Canada, Argentina, Britain, Russia.—FIG. 633, 3a–i. **D. pennsylvanicum*, Longview Limestone, Pennsylvania, USA; *a*, ventral valve exterior; *b*, ventral valve exterior, lateral view; *c*, ventral valve exterior, anterior view; *d*, dorsal valve exterior; *e*, dorsal valve exterior, lateral view; *f*, dorsal valve exterior, anterior view, $\times 1.5$; *g*, ventral valve interior, $\times 3$; *h*, dorsal valve interior; *i*, dorsal valve interior, oblique view, $\times 1.5$ (Ulrich & Cooper, 1938).

Fenxiangella WANG, 1978, p. 224 [**F. deltooides*; OD]. Small smooth shells, length and width subequal; moderately biconvex; subtriangular outline; weakly uniplicate near anterior margin only; hinge line narrow; dental plates subparallel, spondylium, median septum, and accessory septa absent; deep, divergent socket plates, lacking anterior extensions; accessory septa absent; dorsal adductor muscle field poorly known. [Genus rather poorly known.] *Lower Ordovician (Arenig)*: southwestern China.—FIG. 634, 1a–d. **F. deltooides*, Dawan Formation, Hubei; *a*, dorsal valve exterior; *b*, articulated valves, ventral on left; *c*, anterior view, ventral below; *d*, posterior view, ventral below, $\times 4$ (Wang, 1978).

Stichotrophia COOPER, 1948, p. 473 [**S. lamellata*; OD]. Finely costellate with strong concentric lamellae; subquadrate to subelliptical in outline;

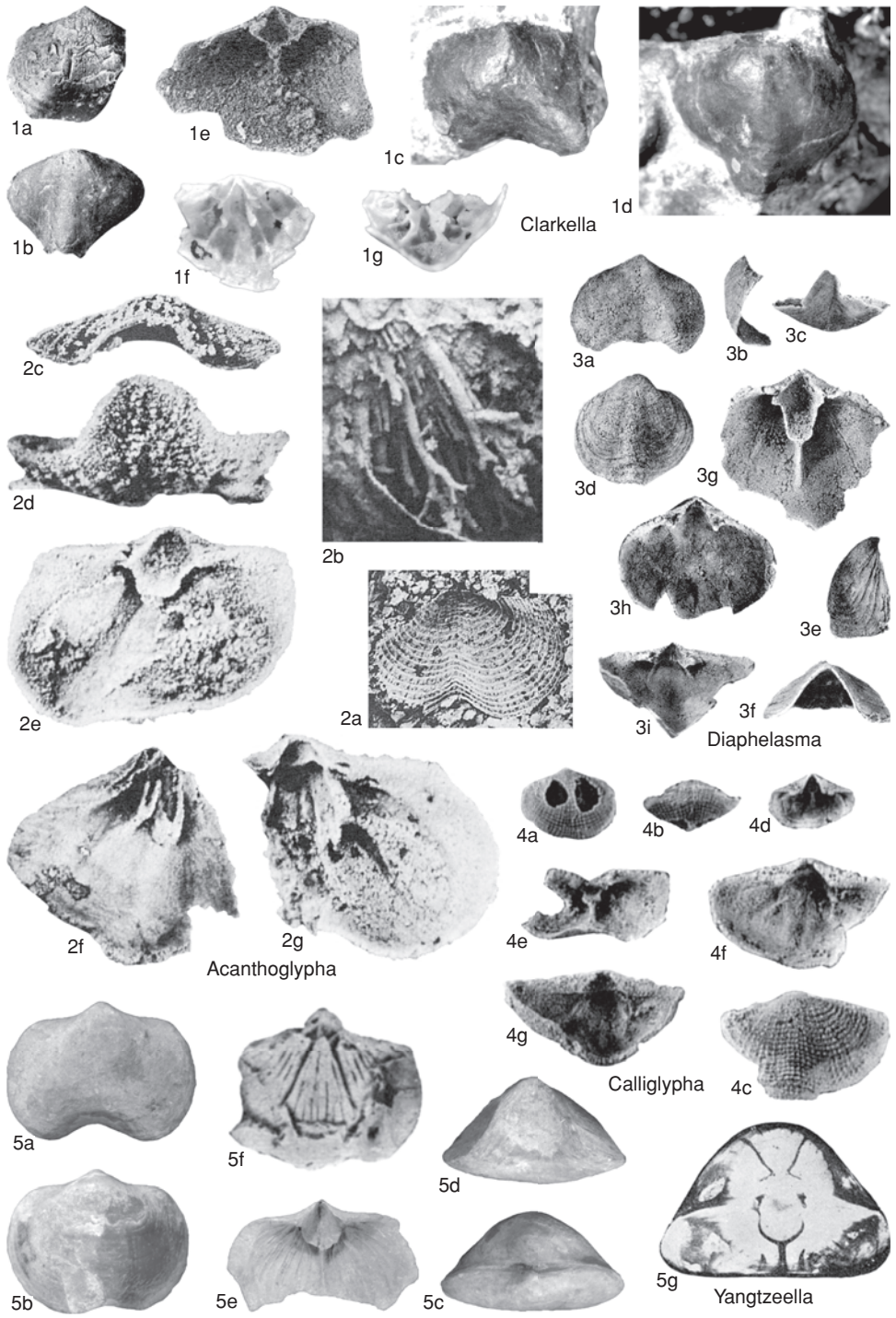


FIG. 633. Clarkellidae (p. 944–947).

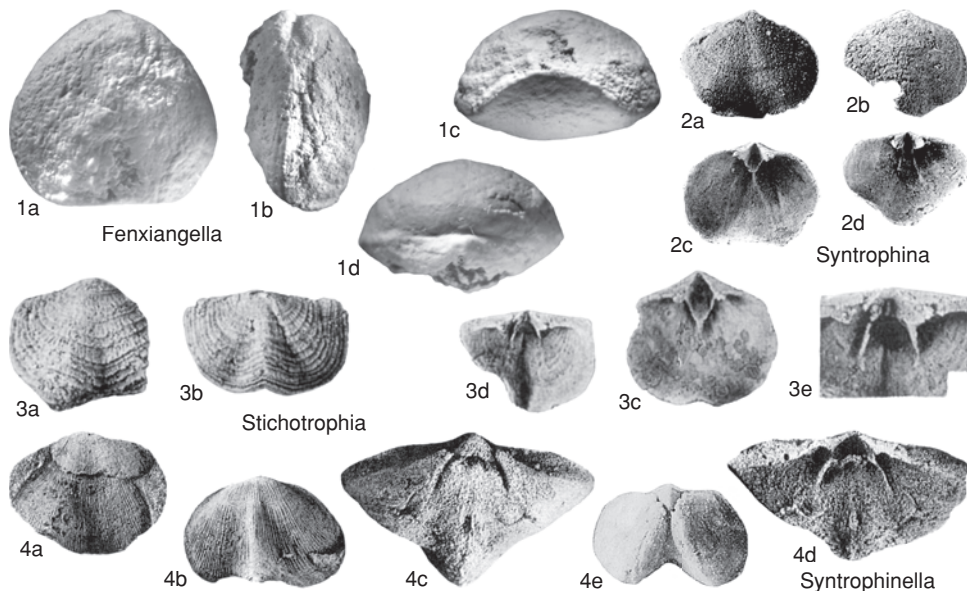


FIG. 634. Clarkellidae (p. 944–946).

hinge line wide, but narrower than widest part of shell; interareas relatively wide; teeth strong; sessile spondylium, supported at anterior only by low, narrow median septum that does not extend anterior to spondylium; accessory septa absent; cardinal process may be present as low ridge on callosity at valve posterior; subparallel socket plates continue anteriorly into short, receding, divergent extensions [these extensions have been referred to in the literature as accessory septa, but they are coplanar with the socket plates and do not support them]; dorsal adductor muscle field not well developed. *Lower Ordovician (Arenig)*: USA, southern China, ?Russia.—FIG. 634, 3a–e. **S. lamellata*, Longview Limestone, Virginia, USA; a, ventral valve exterior; b, dorsal valve exterior; c, ventral valve interior; d, dorsal valve interior, $\times 2$; e, close up of d, $\times 4$ (Cooper, 1948).

Syntrophina SCHUCHERT & COOPER, 1931, p. 247 [**Syntrophina campbelli* WALCOTT, 1908, p. 107; OD] [=*Syntrophina* ULRICH in WELLER & ST. CLAIR, 1928, p. 74, *nom. nud.*]. Smooth shells, with strong concentric lamellae in some species [not visible on type species]; uniplication variably developed; hinge line narrow; teeth strong; spondylium simplex relatively short and narrow, may be sessile at extreme posterior of valve; 2 short accessory septa present rarely in some species; deep petaloid socket plates continue anteriorly into short, divergent extensions, similar to *Stichotrophia*. *Lower Ordovician (Tremadoc)*: USA, Canada, Argentina, Ireland, Kazakhstan, Novaya Zemlya, China, India.—FIG. 634, 2a–d. **S. campbelli* (WALCOTT), McKenzie Hill Formation, Oklahoma, USA; a, ventral valve

exterior; b, dorsal valve exterior; c, ventral valve interior; d, dorsal valve interior, $\times 2$ (Cooper, 1952).

Syntrophinella ULRICH & COOPER in KOBAYASHI, 1934, p. 164 [**S. typica*; OD] [=*Syntrophinella* SCHUCHERT & COOPER, 1932, p. 224, *nom. nud.*]. Finely costellate; entire valve strongly uniplicate, may be quite angular; hinge line narrow; sessile spondylium, supported at anterior only by low, narrow median septum that extends anterior to spondylium; 2 very short accessory septa may be present near the spondylium posterior; subparallel socket plates continue anteriorly into short, widely divergent extensions, similar to *Stichotrophia*. *Lower Ordovician (Tremadoc)*: USA, Canada, China, North Korea, Kazakhstan.—FIG. 634, 4a–e. **S. typica*, Longview Limestone; a, ventral valve exterior, wax replica of mold, Virginia, USA; b, dorsal valve exterior, wax replica of mold, Virginia, USA, $\times 2$; c, dorsal valve interior mold, Virginia, USA, $\times 2$; d, wax replica of mold in c, Virginia, USA, $\times 3$ (Ulrich & Cooper, 1938); e, ventral valve interior mold, Alabama, USA, $\times 2$ (Kobayashi, 1934).

Yangtzeella KOLAROVA, 1925, p. 219 [**Schizophoria poloi* MARTELLI, 1901, p. 302; OD]. Large smooth shells; moderately biconvex; weakly uniplicate; hinge line wide, but narrower than widest part of shell; large, knoblike teeth and sockets may interlock in some individuals; wide spondylium appears to be supported along entire length by low, wide, long duplex median septum; from 2 to 6 short accessory septa commonly present, not prolonged in front of spondylium; socket plates converge to form short, deep septalium-like structure supported by 2 widely spaced, divergent septa that extend anteriorly

only of so-called septalium for some distance; from 2 to 4 short accessory septa present posteriorly; it is unclear whether short crura may be present; dorsal adductor muscle field poorly developed. [MARTELLI (1901) named the type specimens *Schizophoria poloi*. WELLER (1913) subsequently and erroneously referred these specimens to *Triplecia poloi*, as have many others including KOLAROVA (1925; while reassigning them to *Yangtzeella*), causing some confusion in the literature.] *Lower Ordovician (Tremadoc-lower Llanvirn)*: China, ?Kazakhstan.—FIG. 633,5a-f. **Y. poloi* (MARTELLI), Arenig, Dawan Formation; *a*, ventral valve exterior, Hubei; *b*, dorsal valve exterior, Hubei; *c*, articulated valves, posterior view, ventral valve below, Hubei; *d*, articulated valves, anterior view, ventral valve below, Hubei; *e*, ventral valve interior, USNM 339345, Hubei, ×1 (new); *f*, dorsal valve interior mold, Guizhou, ×1 (Xian & Jiang, 1978).—FIG. 633,5g. *Y. yichangensis* ZENG; section through articulated valves, ventral valve below, showing duplex spondylium and divergent dorsal septa, ×2 (Zeng, 1986).

Family PORAMBONITIDAE Davidson, 1853

[Porambonitidae DAVIDSON, 1853b, p. 99]

Large shells (greater than 2 cm) with fine costellae and concentric lamellae that intersect to form radial rows of subcircular pits; outline highly variable; strongly uniplicate; hinge line varies in width, interareas reduced; teeth strong and knoblike, possibly cyrtomatodont; very long dental plates vary in orientation from subparallel to convergent, forming long sessile spondylium supported at anteriormost edge by low, wide median ridge; cardinal process commonly absent, rarely present as low ridge on narrow shelf at posterior of notothyrial cavity; long, subparallel to convergent socket plates commonly continue anteriorly into long, subparallel extensions that may converge at anteriormost end, appearing to form long sessile septalium; adductor muscle field commonly well developed with weak callosities. *Lower Ordovician (Arenig)–lower Silurian (Wenlock)*.

Porambonites PANDER, 1830, p. 95 [**P. intermedia*; SD HALL & CLARKE, 1893, p. 225]. Biconvexity very strong; uniplication commences on anterior half; dental plates commonly remain parallel for most of their considerable length, converging only at their anteriormost ends to join with median ridge; ventral adductor muscle field anterior to and commonly separated from diductors by very low ridge;

very long socket plates and extensions commonly remain subparallel for entire length, may converge only at their anteriormost ends to join with median ridge; internal features in both valves commonly thicken and coalesce in older individuals. [Loss of the type specimens of *P. intermedia*, the legally established type species, has caused some systematists to recognize *P. reticulatus* informally instead, in agreement with more than a century of usage. See BIERNAT, 1965, p. 532 for further discussion on designation of type species of this genus.] *Lower Ordovician (Arenig)–lower Silurian (Wenlock)*: Canada, Argentina, Russia, Europe, Himalayas, India, China, Australia, South Africa.

P. (Porambonites). Subelliptical to circular in outline, valve proportions may be quite variable; hinge line distinct but narrow, less than half widest part of shell; cardinal process commonly absent, rarely present as low ridge. *Lower Ordovician (Arenig)–Upper Ordovician (Ashgill)*: Russia, Estonia, Europe, Britain, Himalayas, China, Australia, ?South Africa.—FIG. 635,1a-e. *P. (P.) planus* PANDER, Arenig, Glauconite limestone, Estonia; *a*, ventral valve exterior; *b*, articulated valves, lateral view, ventral valve on right; *c*, dorsal valve exterior; *d*, posterior view, ventral valve above; *e*, anterior view, ventral valve above, USNM 81599, ×1 (new).—FIG. 635,1f-g. *P. (P.) intercedens* PANDER, Upper Ordovician, Hohenholm, Estonia; *f*, dorsal valve exterior; *g*, posterior view, ventral valve above, beaks ground off showing dental and socket plates, USNM 26897, ×1 (new).—FIG. 635,1h-i. *P. (P.) schmidti* NOETLING, lower Llanvirn, Estonia; *h*, ventral valve interior; *i*, dorsal valve interior, ×1 (Schuchert & Cooper, 1932).

P. (Equirostra) COOPER & MUIR-WOOD, 1951, p. 195, *nom. nov. pro Isorhynchus* KING, 1850, p. 112, *non* SCHOENHERR, 1833 [**Terebratulites aequirostris* VON SCHLOTHEIM, 1820 in 1820–1823, p. 282; OD]. Subtriangular in outline, longer than wide; hinge line extremely narrow, astrophic in some individuals. *Lower Ordovician (lower Llanvirn)–Upper Ordovician (Caradoc)*: Russia, Estonia, Europe, Canada.—FIG. 635,3a-e. **P. (E.) aequirostris* (VON SCHLOTHEIM), Vaginaten Limestone, Russia; *a*, ventral valve exterior; *b*, articulated valves, lateral view, ventral valve on right; *c*, dorsal valve exterior; *d*, posterior view, ventral valve above; *e*, anterior view, ventral valve above, USNM 26898, ×1 (new).—FIG. 635,3f-g. *P. (E.) baueri* (NOETLING), middle Ordovician, Estonia; *f*, ventral valve interior; *g*, dorsal valve interior, USNM 85369A, ×1 (new).

P. (Noetlingia) HALL & CLARKE, 1893, p. 229 [**Spirifer tcheffkemi* DE VERNEUIL, 1845, p. 129; M]. Moderate to large size; subquadrate to subelliptical in outline; hinge line wide, but narrower than widest part of shell; cardinal process present as low ridge on narrow shelf in notothyrial cavity; long socket plates converge and

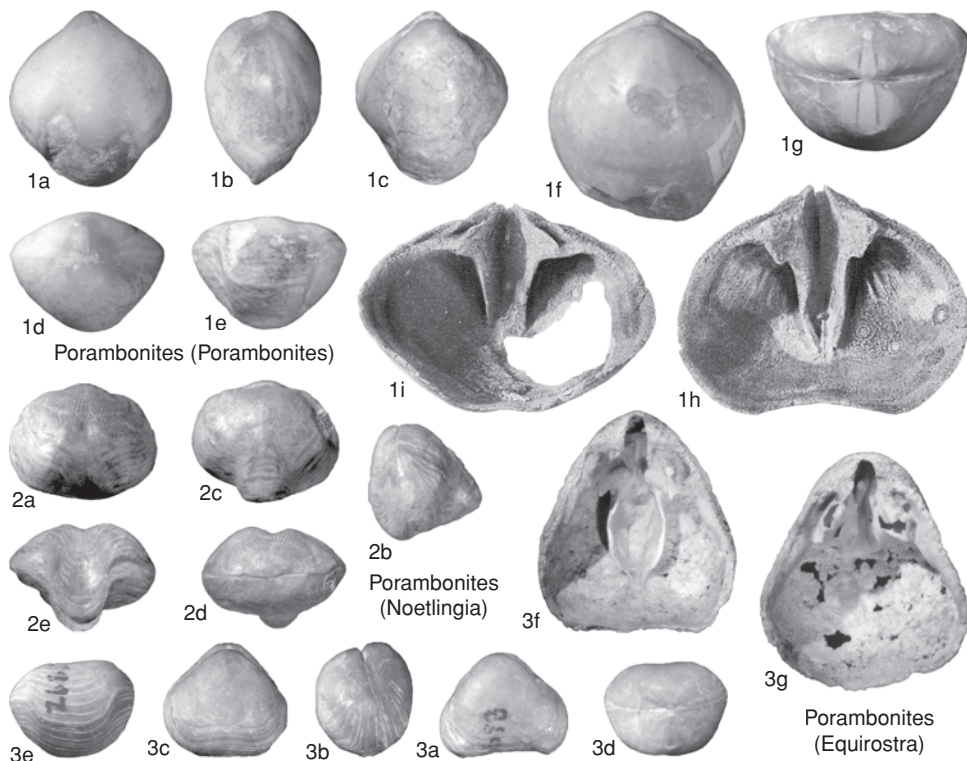


FIG. 635. Porambonitidae (p. 947–948).

unite anteriorly only with short median septum to form long sessile septalium. *lower Silurian (Llandovery–Wenlock)*: Russia.—FIG. 635, 2a–e. **P. (N.) tcheffkini* (DE VERNEUIL), Pulkovka River; a, ventral valve exterior; b, articulated valves, lateral view, ventral valve on left; c, dorsal valve exterior; d, posterior view, ventral valve above; e, anterior view, ventral valve above, USNM 346824, $\times 1$ (new).

Superfamily CAMERELLOIDEA Hall & Clarke, 1895

[*nom. correct. et emend.* CARLSON, herein, *pro* Camerellacea NIKIFOROVA, 1960d, p. 201, *nom. transl. et correct. ex* Camerellidae HALL & CLARKE, 1895, p. 355]

Commonly costate or paucicostate, rarely costellate or smooth; outline subtriangular to subcircular, less commonly subelliptical; hinge line astrophic, rarely narrow and strophic; interareas commonly obsolete; dental plates converge to form simplex or duplex spondylium, rarely sessile spondylium; accessory septa absent; ventral mantle canals unknown; cardinal process absent; outer hinge

plates converge and either remain discrete, subparallel and commonly continue anteriorly into long, subparallel inner hinge plates, or may converge to form simplex, duplex, or less commonly sessile, septalium; short, rod-like or bladelike crura present. *Lower Ordovician (Arenig)–Lower Devonian (Pragian)*.

Family CAMERELLIDAE Hall & Clarke, 1895

[*nom. correct.* SCHUCHERT & COOPER, 1931, p. 248, *pro* Camerellidae HALL & CLARKE, 1895, p. 355; *emend.*, ULRICH & COOPER, 1938, p. 248] [=Brevicameridae COOPER, 1956a, p. 560; Karakulinidae ANDREEVA, 1972, p. 55]

Small shells; paucicostate, costate, or smooth; commonly strongly uniplicate, may be rectimarginate; spondylium simplex supported by high median septum that commonly extends anterior to spondylium, rarely sessile or duplex spondylium, less commonly subparallel dental plates; narrow, relatively long hinge plates commonly converge on long median septum to form deep,

narrow septalium simplex or duplex, rarely sessile or absent; alate plates absent; crura, when present, rodlike. *Lower Ordovician (Arenig)–Lower Devonian (Lochkovian)*.

Subfamily CAMERELLINAE

Hall & Clarke, 1895

[*nom. transl. et correct.* BIERNAT, 1965, p. 535, ex Camarellidae HALL & CLARKE, 1895, p. 355]

Spondylium simplex supported by high, narrow median septum, rarely as sessile or duplex spondylium. *Lower Ordovician (Arenig)–Lower Devonian (Lochkovian)*.

Camerella BILLINGS, 1859b, p. 301 [**C. volborthi*; SD HALL & CLARKE, 1893, p. 219] [= *Camarella* DALL, 1877, p. 18, *nom. null.*; *Rhynchocamara* SCHUCHERT & COOPER, 1931, p. 248 (type, *R. plicata*)]. Most species small, some moderate in size; type species and most others paucicostate, some species with strong costae on entire valve, few species with tiny granules or bumps over surface; uniplication commonly present on anterior third of valve only; teeth small; relatively long spondylium simplex, rarely duplex; short, deep outer hinge plates, nearly horizontal in some species; long, narrow inner hinge plates converge and unite with long median septum to form short, deep, narrow septalium duplex; short, rodlike crura visible in some species, not type species; dorsal adductor muscle field weakly developed. [*Rhynchocamara* was named for rectimarginate forms; uniplication varies sufficiently to warrant synonymy.] *Lower Ordovician (upper Llanvirn)–Silurian (Wenlock)*: Canada, USA, Britain, northern Europe, Russia, Siberia, Kazakhstan, China, Mongolia, ?India, ?Bolivia.—FIG. 636, 1a–d. **C. volborthi*, upper Llanvirn, Rockland Formation, Ontario, Canada; *a*, ventral valve exterior; *b*, articulated valves, lateral view, ventral valve right; *c*, dorsal valve exterior; *d*, articulated valves, anterior view, ventral below, $\times 2$ (Cooper, 1956a).—FIG. 636, 1e–f. *C. bella* FENTON; upper Llanvirn, Macy Formation, Missouri, USA; *e*, ventral valve interior; *f*, dorsal valve interior, $\times 2$ (Cooper, 1956a).

Bleshidium HAVLIČEK, 1982b, p. 371 [**Atrypa patellina* BARRANDE, 1879b, pl. 147; OD] [= *Bleshidimerus* HAVLIČEK in HAVLIČEK & ŠTORCH, 1990, p. 101 (type, *Rhynchonella irregularis* BARRANDE, 1879b, pl. 4)]. Nearly circular outline; moderately biconvex; costae present on fold and sulcus only, concentric lamellae present as gentle rugae; uniplication highly variable, may be absent; hinge line narrow, less than half widest part of valve; spondylium simplex supported by very high, narrow median septum; socket plates short, deep, convergent; anterior extensions [comparable to inner hinge plates] absent; crura unknown; median septum may be absent or present and short; septalium absent. [*Bleshidimerus* is very strongly uniplicate

with angular, bifurcating costae; appears to be within variability of *Bleshidium*.] *Silurian (Wenlock–Přídolí)*: Czech Republic.—FIG. 636, 2a–e. **B. patellinum* (BARRANDE), lower Ludlow, upper Kopanina Formation, Prague basin, Bohemia; *a*, ventral valve exterior; *b*, dorsal valve exterior; *c*, articulated valves, anterior view, ventral above, $\times 6.2$ (Havliček & Štorch, 1990); *d–e*, transverse sections, ventral valve above, $\times 15$ (Havliček, 1982b).—FIG. 636, 2f. *B. sp. cf. B. papalae* HAVLIČEK & ŠTORCH, Motol Formation; ventral valve interior mold, $\times 3$ (Havliček & Štorch, 1990).

?**Branconia** GAGEL, 1890, p. 62 [**B. borussica*; M]. Large smooth shell; subelliptical outline, wider than long; very strongly ventribiconvex; strongly rostrate; strongly unisulcate; ventral and dorsal interiors unknown, except for long median septum present in both valves. [Only 1 poorly known specimen exists; it may not be a syntrophiid.] *Upper Ordovician (Caradoc)*: ?Poland (Prussia).—FIG. 637, 1a–d. **B. borussica*; *a*, drawings of ventral valve exterior; *b*, dorsal valve exterior; *c*, articulated valves, lateral view, ventral on left; *d*, articulated valves, posterior view, ventral above, $\times 1$ (Gagel, 1890).

Brevicamera COOPER, 1956a, p. 560 [**B. camerata*; OD]. Small, paucicostate shells; subelliptical outline, wider than long; biconvexity strong; uniplication broad and strong, present only on anterior half of valves; very short spondylium simplex supported posteriorly by narrow, commonly low, median septum; short, deep, convergent outer hinge plates; short, rodlike crura present; inner hinge plates converge slightly but join floor of valve in widely separated, subparallel lines to form a broad, long sessile septalium; long, low median septum extending anterior to, and does not support, septalium; dorsal adductor muscle field well developed with weak callosities. *Lower Ordovician (upper Llanvirn)*: southern USA.—FIG. 637, 3a–g. **B. camerata*, Pratt Ferry Formation, Alabama; *a*, ventral valve exterior; *b*, ventral valve, lateral view; *c*, ventral valve, anterior view; *d*, dorsal valve exterior; *e*, dorsal valve, lateral view; *f*, ventral valve interior, $\times 2$; *g*, dorsal valve interior, $\times 4$ (Cooper, 1956a).

Idiostrophia ULRICH & COOPER, 1936, p. 631 [**I. perfecta*; OD] [= *Trigonotrophia* ANDREEVA, 1972, p. 54 (type, *Idiostrophia paucicostata* COOPER, 1956a, p. 588)]. Type species small, others may be very small; distinctly triangular outline, sides of both valves do not taper gently to commissure, but flex sharply to meet in a plane perpendicular to commissural plane; paucicostate; rectimarginate, but single, narrow radial groove runs down center of each valve; socket plates short, deep, convergent; anterior extensions [comparable to inner hinge plates] absent; crura unknown; septalium rather long. [*Trigonotrophia* lacks the distinctive strangulate grooves and possesses only 3 to 4 costae on anterior margin; is otherwise indistinguishable from *Idiostrophia*.] *Lower Ordovician (Arenig–upper Llanvirn)*: Canada, USA, Argentina, Britain, Europe, northern Russia, Siberia.—FIG. 637, 6a–e.

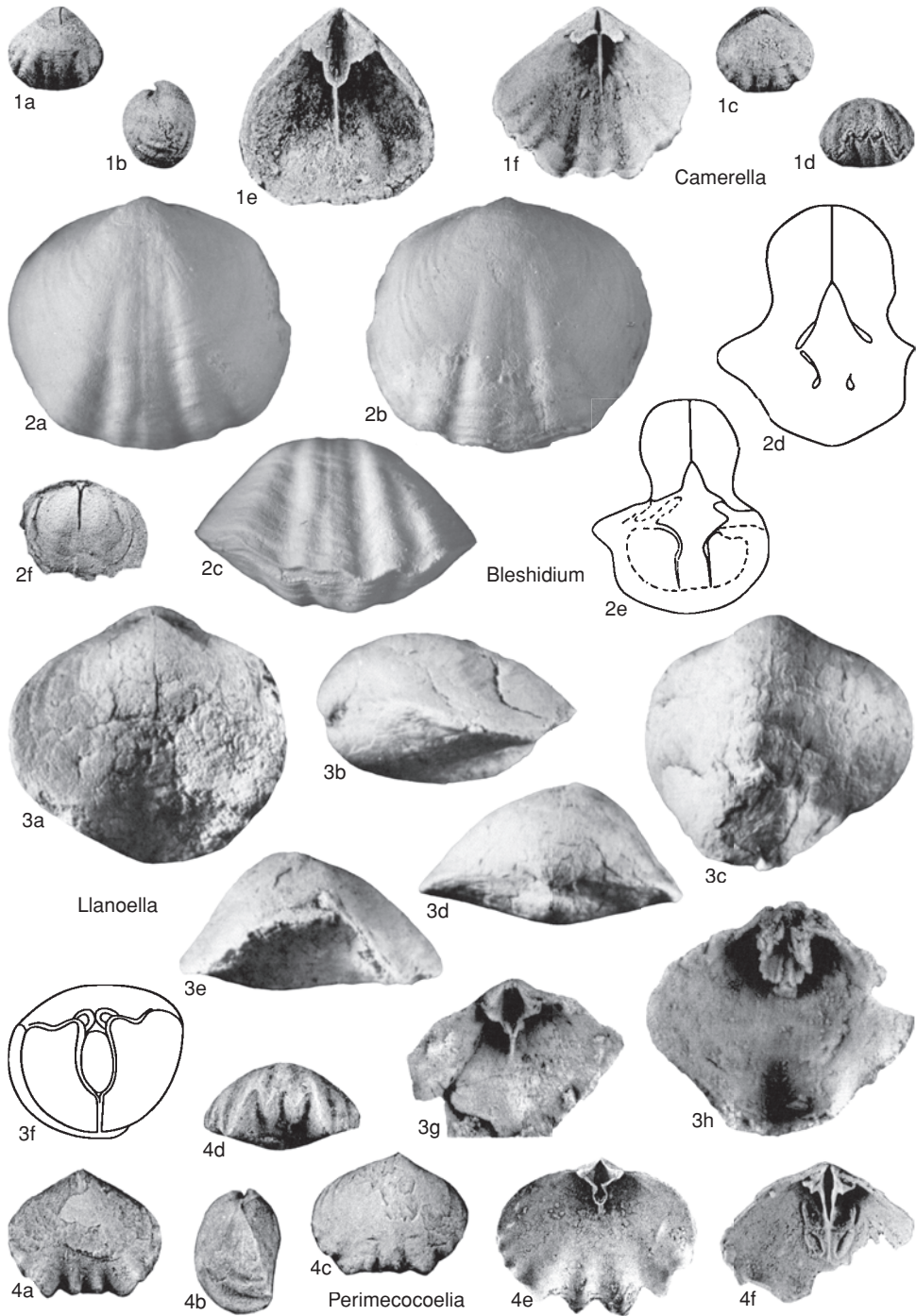


FIG. 636. Camerellidae (p. 949–952).

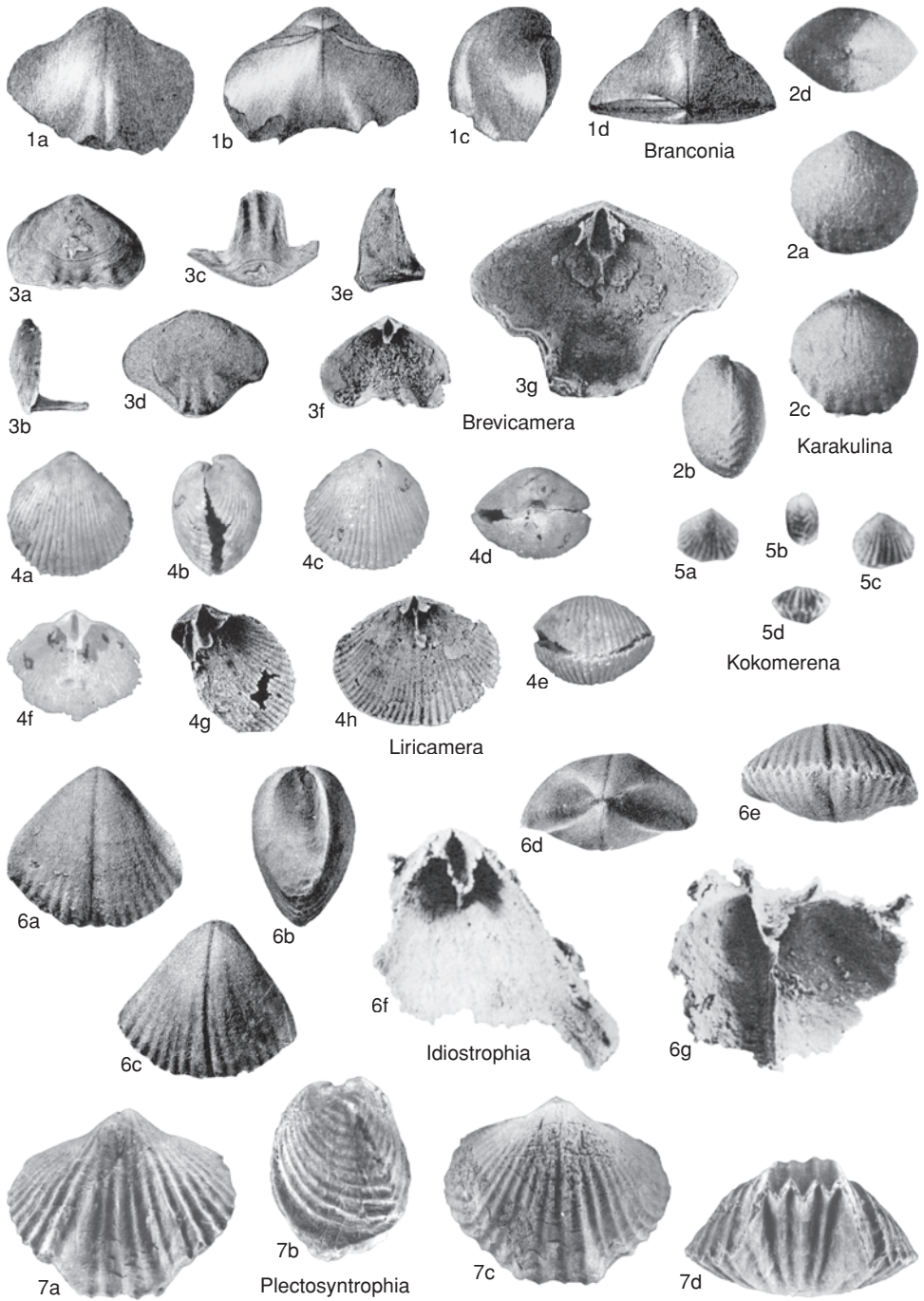


FIG. 637. Camerellidae (p. 949–953).

- **I. perfecta*, upper Llanvirn, Mystic conglomerate, Quebec, Canada; *a*, ventral valve exterior; *b*, articulated valves, lateral view, ventral on right; *c*, dorsal valve exterior; *d*, articulated valves, posterior view, ventral below; *e*, articulated valves, anterior view, ventral below, $\times 1.5$ (Ulrich & Cooper, 1938).—FIG. 637,6f–g. *I. costata* ULRICH & COOPER, upper Arenig, Tourmakeady Limestone, Ireland; *f*, ventral valve interior, $\times 5$; *g*, dorsal valve exterior, oblique anterior view, $\times 11$ (Williams & Curry, 1985).
- Karakulina** ANDREEVA, 1972, p. 55 [**K. nana*; OD]. Elongate oval in outline; paucicostate; rectimarginate; dorsal median septum and septalium absent. [Valve interiors rather poorly known.] *Lower Ordovician (Arenig)*: northern Russia (Urals).—FIG. 637,2a–d. **K. nana*, Kuragan Suite, Kinderlya River; *a*, ventral valve exterior; *b*, articulated valves, lateral view, ventral on left; *c*, dorsal valve exterior; *d*, articulated valves, posterior view, ventral above, $\times 4$ (Andreeva, 1972).
- Kokomerena** MISIUS, 1986, p. 182 [**K. prima*; OD]. Subtriangular to subelliptical in outline, wider than long; entire valve costate; moderately biconvex; weak uniplication, present near anterior margin only; teeth strong; sessile spondylium may be supported at anterior only by low, wide median ridge, which may be absent; fairly long, wide, sessile septalium present; dorsal median septum absent. *Upper Ordovician (lower Caradoc)*: Kirgizia.—FIG. 637,5a–d. **K. prima*, Tabylygat River; *a*, ventral valve exterior; *b*, articulated valves, lateral view, ventral on right; *c*, dorsal valve exterior; *d*, articulated valves, anterior view, ventral above, $\times 1$ (Misius, 1986).
- Liricamera** COOPER, 1956a, p. 592 [**L. nevadensis*; OD]. Nearly circular in outline; entire valve finely costellate; moderately biconvex; commonly rectimarginate, may be very weakly uniplicate; hinge line narrow, less than half widest part of shell; interareas narrow; teeth strong; deep spondylium simplex of medium length; crura very short, rod-like; dorsal interior otherwise similar to *Camerella*. *Lower Ordovician (lower Llanvirn–upper Llanvirn)*: western USA, northwestern Tibet.—FIG. 637,4a–b. **L. nevadensis*, lower Llanvirn, Pogonip Group, Nevada, USA; *a*, ventral valve exterior; *b*, articulated valves, lateral view, ventral on right; *c*, dorsal valve exterior; *d*, articulated valves, posterior view, ventral above; *e*, articulated valves, anterior view, ventral above; *f*, ventral valve interior, USNM 117174, $\times 1.6$ (new); *g*, ventral valve interior, oblique view; *h*, dorsal valve interior, $\times 2$ (Cooper, 1956a).
- Llanoella** BOUCOT, 1975a, p. 351 [**L. stephensi*; OD]. Medium to large shells; outline subelliptical, wider than long; commonly smooth, larger individuals with costae at anterior margin only; moderately biconvex; strong uniplication, present on entire valve; teeth relatively strong; spondylium simplex much like *Camerella*; outer hinge plates convergent; long inner hinge plates converge both dorsally and ventrally to form long cylindrical septalium with ventral edge of each plate terminating in an unusual tubular structure; cruralium housing dorsal adductor muscle field present anterior to septalium. *Lower Devonian (Lochkovian)*: southern and western USA.—FIG. 636,3a–f. **L. stephensi*, Pillar Bluff Limestone, Texas; *a*, ventral valve exterior; *b*, articulated valves, lateral view, ventral below; *c*, dorsal valve exterior; *d*, articulated valves, posterior view, ventral below; *e*, articulated valves, anterior view, ventral below, $\times 1.5$; *f*, drawing of transverse section, dorsal valve, $\times 3$ (Boucot, 1975a).—FIG. 636,3g–h. *L. sp.*, Rabbit Hill Limestone, Nevada; *g*, ventral valve interior, $\times 3$; *h*, dorsal valve interior, $\times 4$ (Johnson, 1970b).
- Neostrophia** ULRICH & COOPER, 1936, p. 631 [**N. subcostata*; OD]. Smooth with very short, weak costae near anterior margin only, present only on fold and sulcus; moderately biconvex; uniplication commonly broad and strong, may be weak, only on anterior third of valves; hinge line extremely narrow, but discernible; interiors similar to *Camerella*. *Lower Ordovician (upper Llanvirn)*: Canada, USA.—FIG. 638,2a–e. **N. subcostata*, Mystic conglomerate, Quebec, Canada; *a*, ventral valve exterior; *b*, articulated valves, lateral view, ventral left; *c*, dorsal valve exterior; *d*, articulated valves, anterior view, ventral below; *e*, posterior section through articulated valves, ventral below, $\times 2$ (Ulrich & Cooper, 1938).
- Perimecocoelia** COOPER, 1956a, p. 593 [**P. semicostata*; OD]. Most species moderate in size, some small; subelliptical in outline, wider than long; paucicostate, with short broad costae present only on anterior third of valves; moderately biconvex; spondylium simplex of variable length that narrows anteriorly, in some individuals nearly divided into anterior-posterior chambers by pinching inward of dental plates near midlength; supported by relatively low, wide median septum; outer hinge plates convergent, receding; long inner hinge plates converge to form long septalium supported by short median septum; crura unknown, but crural bases commonly visible on hinge plates; dorsal adductor muscle field well developed, marked by weak callosities. *Lower Ordovician (upper Llanvirn)*: USA, Kazakhstan.—FIG. 636,4a–f. **P. semicostata*, USA; *a*, ventral valve exterior, Effna Formation, Virginia; *b*, articulated valves, lateral view, ventral right, Effna Formation, Virginia; *c*, dorsal valve exterior, Effna Formation, Virginia; *d*, articulated valves, anterior view, ventral below, Effna Formation, Virginia; *e*, ventral valve interior, Pratt Ferry Formation, Alabama; *f*, dorsal valve interior, Pratt Ferry Formation, Alabama, $\times 2$ (Cooper, 1956a).
- Plectocamara** COOPER, 1956a, p. 596 [**P. costata*; OD]. Very small size; outline quite variable; strong, angular costae on entire valve; uniplication broad and strong, on entire valve; narrow sessile spondylium, commonly decreases in width on anterior half, supported at anterior only by short, low, narrow median septum; petaloid socket plates convergent, nearly horizontal, join floor of valve to form short,

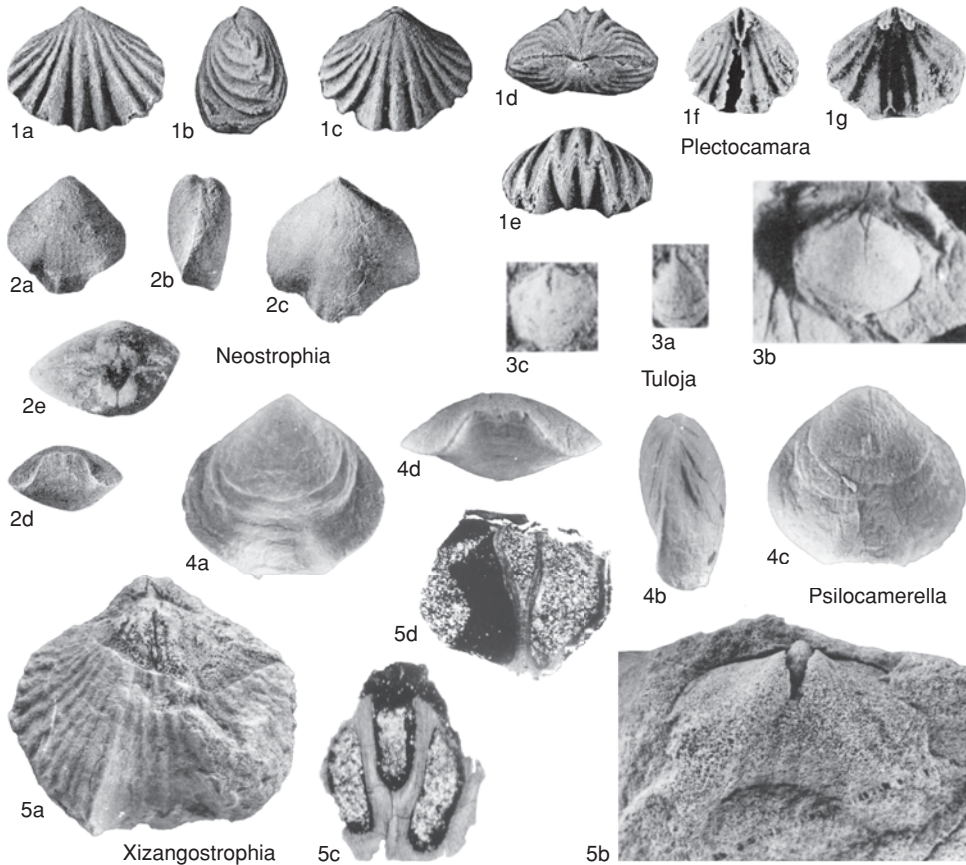


FIG. 638. Camerellidae (p. 952–954).

shallow, sessile septalium; dorsal median septum variable in length or absent; crura unknown, but crural bases visible. *Lower Ordovician (upper Llanvirn)–Upper Ordovician, ?Silurian*: USA, Alaska, Siberia, western China.—FIG. 638, 1a–g. **P. costata*, upper Llanvirn, Lincolnshire Formation, Tennessee, USA; *a*, ventral valve exterior; *b*, articulated valves, lateral view, ventral right; *c*, dorsal valve exterior; *d*, articulated valves, posterior view, ventral below; *e*, articulated valves, anterior view, ventral below; *f*, ventral valve interior; *g*, dorsal valve interior, $\times 3$ (Cooper, 1956a).

Plectosyntrophia FU, 1982, p. 129 [**P. qilianshanensis*; OD]. Shells medium in size; subpentagonal in outline, wider than long; strong costae on entire valve; teeth strong; sessile spondylium supported at anterior only by short, low, wide median ridge; septalium duplex long, wide, supported by high median septum; crura unknown. *Lower Ordovician (lower Llanvirn)*: northwestern China.—FIG. 637, 7a–d. **P. qilianshanensis*, Yingou Formation, Gansu; *a*, ventral valve exterior; *b*, articulated

valves, lateral view, ventral on right; *c*, dorsal valve exterior; *d*, articulated valves, anterior view, ventral below, $\times 2$ (Fu, 1982).

Psilocamerella FU, 1982, p. 128 [**P. planosulcata*; OD] [= *Psilocamerella* FU, 1980, p. 2, *nom. nud.*]. Shells small; subpentagonal in outline, wider than long; smooth, but gentle concentric rugae may be present; moderately biconvex; uniplication may be absent or broad and weak, near anterior margin only; spondylium simplex supported by low, narrow median septum; septalium supported by short median septum; dorsal adductor muscle field unknown. [Dorsal interior poorly known.] *Upper Ordovician (Caradoc)*: northwestern China.—FIG. 638, 4a–d. **P. planosulcata*, Jinghe Formation, Shaanxi; *a*, ventral valve exterior; *b*, articulated valves, lateral view, ventral on left; *c*, dorsal valve exterior; *d*, articulated valves, anterior view, ventral below, $\times 3$ (Fu, 1982).

Tuloja SEVERGINA in ROZMAN & SEVERGINA, 1983, p. 24 [**T. karasuensis*; OD]. Very small size; nearly circular outline; smooth, with weak concentric

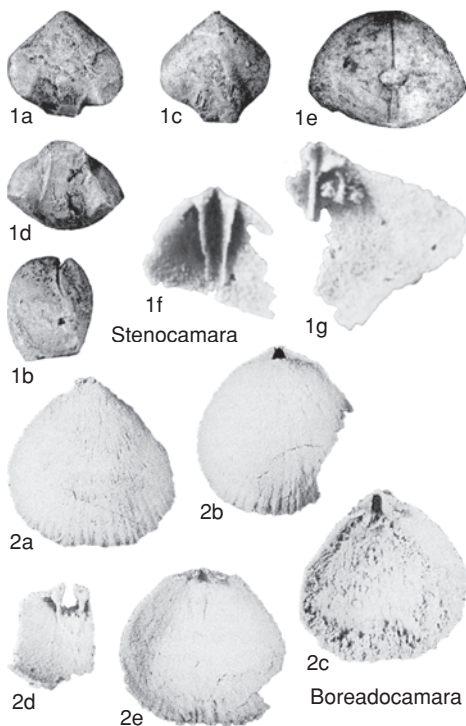


FIG. 639. Camerellidae (p. 954).

lamellae; moderately ventribiconvex; rectimarginate; spondylium simplex supported by long, narrow median septum. [Valve interiors poorly known; may be juvenile of another species.] *Lower Ordovician (upper Llanvirn)*: south-central Russia, Mongolia. —FIG. 638, 3a–c. **T. karasuensis*, Bugryshikhinsk beds, northeastern Gorno-Altay; *a*, ventral valve exterior; *b*, ventral valve interior mold, $\times 5$; *c*, dorsal valve interior mold, $\times 4$ (Rozman & Severgina, 1983).

Xizangostrophia RONG, 1976, p. 150 [**X. sinensis*; OD]. Subpentagonal outline, wider than long; costae on entire valve; moderately biconvex; uniplication broad, strong, on entire valve; spondylium duplex supported by low, wide median septum; cruralium duplex may be present anterior to narrow septalium. [Taxon very poorly known.] *Lower Ordovician (Arenig–lower Llanvirn)*: southern Tibet. —FIG. 638, 5a–d. **X. sinensis*, lower Llanvirn, lower Chiatsun Formation, Nyalam; *a*, dorsal valve exterior; *b*, ventral valve interior mold, $\times 2$; *c*, section through ventral valve showing spondylium duplex; *d*, section through dorsal valve showing septalium or cruralium, $\times 8$ (Rong, 1976).

Subfamily STENOCAMARINAE Cooper, 1956

[Stenocamarinae COOPER, 1956a, p. 602]

Discrete, subparallel dental plates, spondylium lacking. *Lower Ordovician (Arenig–upper Llanvirn)*, ?*Upper Ordovician (Ashgill)*.

Stenocamara COOPER, 1956a, p. 602 [**S. perplexa*; OD]. Small to medium in size; outline similar to *Camerella*; type species smooth, other species may be paucicostate, but only on fold and sulcus near anterior margin; uniplication broad, strong, angular, present only on anterior half of valves; teeth small; discrete dental plates long, very closely spaced; median septum absent; short, shallow socket plates converge and unite with very long, high median septum to form short, deep, wide septalium; crura unknown; dorsal adductor muscle field not well known. *Lower Ordovician (Arenig–upper Llanvirn)*, ?*Upper Ordovician (Ashgill)*: USA, Norway, Estonia, north-central Russia. —FIG. 639, 1a–e. **S. perplexa*, upper Llanvirn, Mosheim Formation, Tennessee, Alabama, USA; *a*, ventral valve exterior; *b*, articulated valves, lateral view, ventral on right; *c*, dorsal valve exterior; *d*, articulated valves, anterior view, ventral below, $\times 1$; *e*, articulated valves, posterior view, ventral below, $\times 2$ (Cooper, 1956a). —FIG. 639, 1f–g. *S.?* sp., lower Llanvirn, Antelope Valley Limestone, Nevada, USA; *f*, ventral valve interior; *g*, dorsal valve interior, $\times 5$ (Ross, 1967).

Boreadocamara CURRY & WILLIAMS, 1984, p. 308 [**B. fragilis*; OD]. Small size; nearly circular in outline; weak costae present on entire valve, stronger near anterior margin only; moderately biconvex; rectimarginate; hinge line narrow, less than half widest part of shell; discrete dental plates very short; short socket plates discrete, septalium absent; elongate dorsal adductor muscle field well developed. *Lower Ordovician (Arenig)*: Scotland. —FIG. 639, 2a–e. **B. fragilis*, Ben Suardal Limestone, Isle of Skye; *a*, ventral valve exterior; *b*, dorsal valve exterior; *c*, ventral valve interior; *d*, ventral valve interior, oblique view; *e*, dorsal valve interior, $\times 4$ (Curry & Williams, 1984).

Family PARASTROPHINIDAE Schuchert & LeVene, 1929

[*nom. trans.* ULRICH & COOPER, 1938, p. 248, ex Parastrophininae SCHUCHERT & LEVENE, 1929b, p. 121; *emend.*, ST. JOSEPH, 1941, p. 371] [=Anastrophiidae NIKIFOROVA, 1960d, p. 202]

Commonly costate, may be costellate, rarely smooth; weakly to strongly uniplicate; spondylium duplex supported by low median septum, less commonly as sessile duplex spondylium; outer hinge plates short, inner

hinge plates long and parallel or converge to form simplex or duplex septalium, rarely sessile septalium; 2 relatively large alate plates present, diverge anterolaterally from outer side of hinge plates, as dorsal extensions of bladeliike crura. *Lower Ordovician (upper Llanvirn)–Lower Devonian (Pragian)*.

Parastrophina SCHUCHERT & LEVENE, 1929b, p. 121, *nom. nov. pro Parastrophia* HALL & CLARKE, 1893, p. 221, *non* FOLIN, 1875 [**Atrypa bemiplicata* HALL, 1847, p. 144; OD]. Small to medium in size; subelliptical in outline, wider than long; strong, angular costae present near anterior margin only, valves otherwise smooth; dorsibiconvexity strong; dorsal umbo commonly more pronounced than ventral, may make valves appear falsely unisulcate; uniplication broad and strong, commences anterior to umbo; teeth strong; narrow spondylium duplex supported for entire length by low, narrow median septum that extends anterior to spondylium; short, shallow outer hinge plates, nearly horizontal in some species, extend into long inner hinge plates that converge and unite with long median septum to form long, narrow septalium duplex; long, bladeliike crura; dorsal adductor muscle field well developed, elongate oval in outline. *Lower Ordovician (upper Llanvirn)–Upper Ordovician (Ashgill)*: USA, eastern Canada, Britain, northern Europe, Ukraine, Russia, Kazakhstan, Siberia, China.—FIG. 640, 1a–e. **P. bemiplicata* (HALL), upper Llanvirn, Martinsburg Formation, USA; *a*, ventral valve exterior, Virginia; *b*, articulated valves, lateral view, ventral on right, Virginia, $\times 2$; *c*, dorsal valve exterior, Virginia; *d*, articulated valves, anterior view, ventral valve below, Virginia, $\times 1$; *e*, section through articulated valves 9.5 mm from posterior end, dorsal valve above, showing alate plates, New York, $\times 4$ (St. Joseph, 1941).—FIG. 640, 1f–g. *P. bilobata* COOPER, upper Llanvirn, Pratt Ferry Formation, Alabama, USA; *f*, ventral valve interior, $\times 3$; *g*, dorsal valve interior, $\times 4$ (Cooper, 1956a).—FIG. 640, 1h. *P. rotundiformis* (WILLARD), Caradoc, Prosser Formation, Iowa, USA; articulated valves, interior view of valve posteriors, ventral below, $\times 3$ (Cooper, 1956a).

Anastrophia HALL, 1867a, p. 162–163, *nom. nov. pro Brachymerus* SHALER, 1865, p. 69, *non* DE JEAN, 1834 [**Pentamerus verneuili* HALL, 1857a, p. 104; OD] [= *Savageina* BOUCOT, 1975a, p. 355 (type, *Terebratula deflexa* J. de C. SOWERBY in MURCHISON, 1839, p. 625)]. Strong costae cover entire valve surface, minimal bifurcation anteriorly; exaggerated dorsibiconvexity; uniplication broad and strong; hinge line astrophic, less commonly strophic, of variable width; teeth strong; wide, long sessile spondylium duplex supported anteriorly only by low, narrow median septum that extends anterior to

spondylium, less commonly supported along entire length by relatively high duplex median septum; short outer hinge plates, slightly splayed out, that extend into long, subparallel inner hinge plates anterior to long, bladeliike crura; median septum and septalium absent; internal features often thickened in older individuals, anterior ends of hinge plates may converge, simulating sessile septalium, not unlike *Porambonites*; alate plates vary in length; adductor muscle field quadrilobate, may have weak callosities. [*Savageina* was distinguished as being about one-half the size of *Anastrophia* and much wider than long, but appears to be within the variability of *Anastrophia*; synonymy follows HAVLIČEK & ŠTORCH, 1990.] *Silurian (Wenlock)–Lower Devonian (Pragian)*: USA, Canada, Britain, Europe, Ukraine, Russia, Kazakhstan, China, Mongolia, Indochina, Australia, Venezuela.

A. (Anastrophia). Medium to large size, less commonly small; subelliptical to subtriangular in outline; costae relatively fine; hinge line astrophic or less commonly narrow, strophic. *Silurian (Wenlock)–Lower Devonian (Pragian)*: USA, Canada, Britain, Europe, Ukraine, Russia, Kazakhstan, China, Mongolia, Indochina, Australia, Venezuela.—FIG. 640, 2a–f. **A. (A.) verneuili* (HALL), Lochkovian, lower Helderberg Group, New York, USA; *a*, ventral valve exterior; *b*, dorsal valve exterior, $\times 1$ (Shimer & Shrock, 1944); *c*, ventral valve interior; *d*, dorsal valve interior; *e*, articulated valves, interior view of valve posteriors, ventral below, $\times 1.5$ (Schuchert & Cooper, 1932); *f*, section through articulated valves, dorsal valve below, showing alate plates, $\times 2$ (St. Joseph, 1941).

A. (Grayina) BOUCOT, 1975a, p. 354 [**A. magnifica* KOZŁOWSKI, 1929, p. 140; OD]. Size variable; outline subquadrate; costae very coarse and angular, with pronounced bifurcation near margins of fold and sulcus; hinge line wide and strophic, may be as wide as widest part of valve; ventral interarea present, varies from reduced to extensive. *Silurian (Wenlock)–Lower Devonian (Pragian)*: USA, Canada, Europe, Russia, Kazakhstan, Australia.—FIG. 640, 3a–e. **A. (G.) magnifica* KOZŁOWSKI, Lochkovian, Roberts Mountain Formation, Nevada, USA; *a*, ventral valve exterior; *b*, articulated valves, lateral view, ventral on right; *c*, articulated valves, anterior view, ventral valve below; *d*, ventral valve interior, $\times 2.5$; *e*, dorsal valve interior, $\times 2$ (Johnson, Boucot, & Murphy, 1973).

Eoanastrophia NIKIFOROVA & SAPELNIKOV, 1973, p. 65 [**E. antiquata*; OD]. Similar to *Anastrophia* externally but uniplication broad and shallow, present on entire valve; teeth weak; deep, narrow spondylium duplex supported along entire length by low median septum that does not extend anterior to spondylium; socket plates converge to form deep, narrow septalium simplex supported on long, low

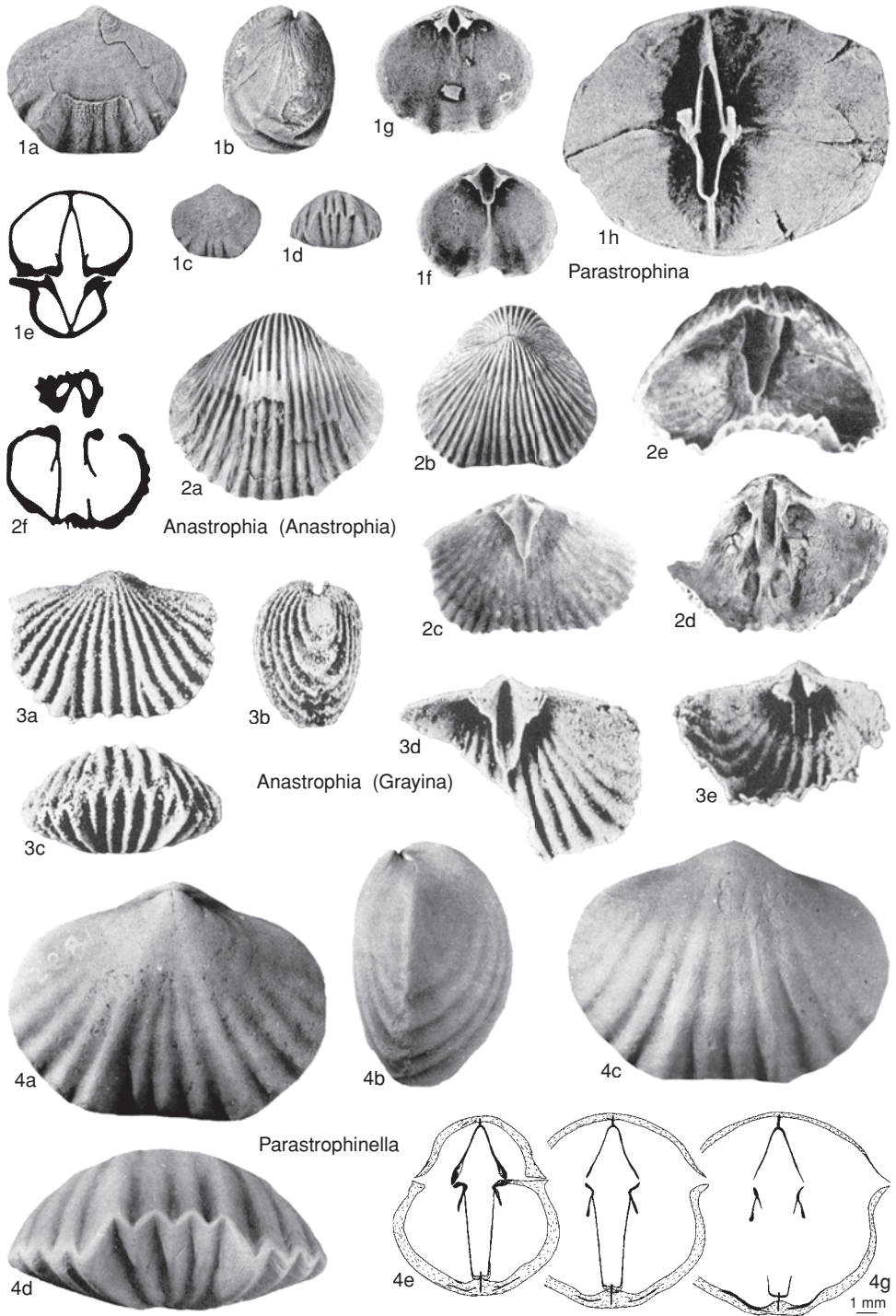


FIG. 640. Parastrophinidae (p. 955–958).

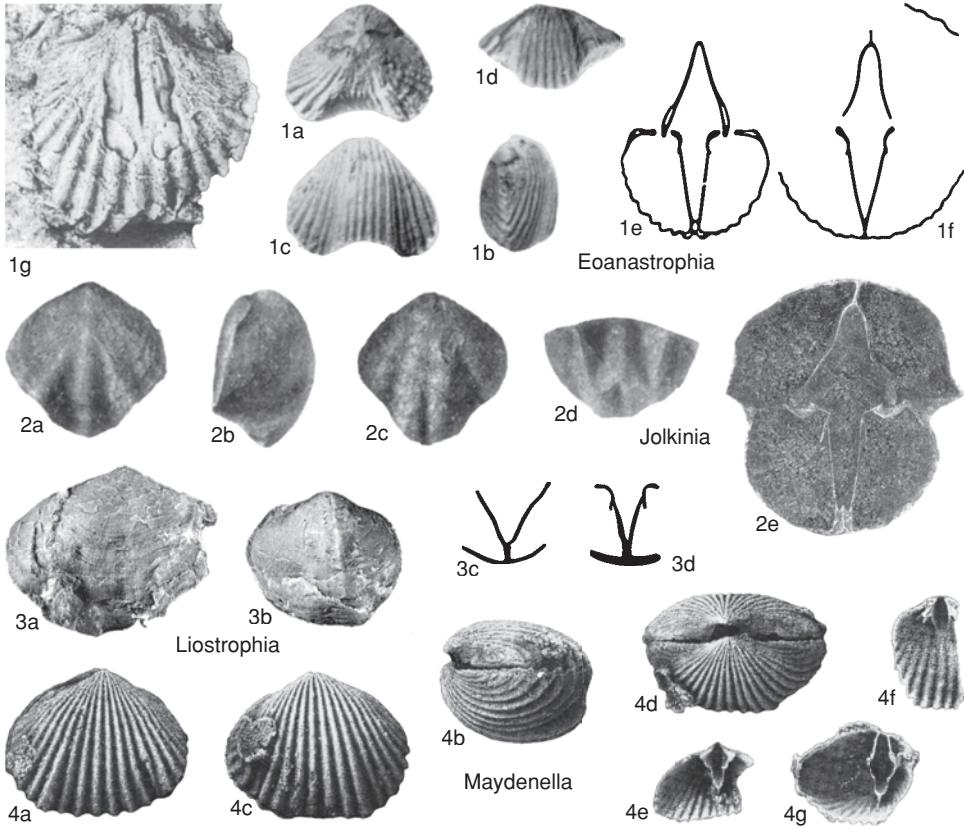


FIG. 641. Parastrophinidae (p. 955–958).

median septum; alate plates may be weakly developed or rarely absent. *Upper Ordovician* (*Caradoc–Ashgill*): Russia, Kirgizia, Kazakhstan, Europe.—FIG. 641, 1a–f. **E. antiquata*, Caradoc or Ashgill, Zeravshan Range, Tadzhikistan; *a*, ventral valve exterior; *b*, articulated valves, lateral view, ventral on left; *c*, dorsal valve exterior; *d*, articulated valves, anterior view, ventral valve above, $\times 1$; *e–f*, serial sections 0.6 and 0.9 mm from posterior end of specimen, ventral valve above, $\times 3.5$ (Nikiforova & Sapelnikov, 1973).—FIG. 641, 1g. *E. pentamera* (MENEHINI), Ashgill, Rosan Formation, Armorican Massif, France; dorsal valve interior mold, $\times 2$ (Melou, 1990).

Jolkinia BREIVEL & BREIVEL, 1988, p. 36 [**Camarella turjensis* KHODALEVICH, 1939, p. 8; OD]. Similar to *Parastrophina* but strongly plicate on anterior half only, with up to 3 plicae on fold and sulcus; hinge line narrow, less than half width of valves; spondylium wide. *Silurian* (*Wenlock*): Russia (Urals).—FIG. 641, 2a–e. **J. turjensis* (KHODALEVICH), Elkinsk beds, eastern Urals; *a*, ventral valve exterior; *b*, articulated valves, lateral view, ventral

on left; *c*, dorsal valve exterior; *d*, articulated valves, anterior view, ventral valve above, $\times 1$; *e*, section through articulated valves, ventral valve above, $\times 3.5$ (Breivel & Breivel, 1988).

Liostrophia COOPER & KINDLE, 1936, p. 355 [**L. glabra*; OD]. Similar to *Parastrophina*, but smooth, not costate; medium to large size; uniplication broad and shallow; spondylium wide; septalium relatively wide. [Genus rather poorly known.] *Upper Ordovician* (*Ashgill*): eastern Canada, ?Ireland, Kazakhstan, ?northwestern China.—FIG. 641, 3a–d. **L. glabra*, Whitehead Formation, Quebec; *a*, ventral valve exterior; *b*, dorsal valve exterior, $\times 1$; *c*, section through ventral valve beak; *d*, section through dorsal valve, 3 mm from beak, $\times 3$ (Cooper & Kindle, 1936).

Maidenella LAURIE, 1991, p. 85 [**M. asymmetrica*; OD]. Small to medium in size; strong costae present on entire valve; uniplication strong and deep; hinge line strophic, narrow, less than half width of valve; teeth strong; ventral interarea reduced, dorsal interarea obsolete; wide sessile spondylium supported anteriorly by short, low

median septum that may or may not extend anterior to spondylium; short, subparallel to convergent outer hinge plates that extend into long, subparallel inner hinge plates, anterior to short, bladelike crura, forming long, shallow, flat-bottomed, sessile septalium; alate plates short. *Lower Ordovician (upper Llanvirn)*: Tasmania.—FIG. 641,4a–g. **M. asymmetrica*, upper Cashions Creek Limestone; *a*, ventral valve exterior; *b*, articulated valves, lateral view, ventral above; *c*, dorsal valve exterior; *d*, articulated valves, posterior view, ventral valve above; *e*, ventral valve interior; *f*, dorsal valve interior; *g*, articulated valves, interior view of valve posteriors, ventral below, $\times 2$ (Laurie, 1991).

Parastrophinella SCHUCHERT & COOPER, 1931, p. 248 [*Pentamerus reversus* BILLINGS, 1857, p. 295; OD]. Medium to large size; strong costae present on anterior half of valves; exaggerated dorsibiconvexity; dorsal umbo more pronounced than ventral, making valves appear falsely unisulcate; uniplication broad and relatively shallow; teeth small; narrow spondylium duplex, sessile only at extreme posterior, supported in anterior by low, narrow median septum that extends anterior to spondylium; short, subparallel to convergent outer hinge plates that extend into long, closely spaced inner hinge plates, anterior to long, bladelike crura, that converge only near valve floor and unite with short, low median septum at anteriormost edge to form long, very narrow sessile septalium or very low septalium simplex. *Lower Ordovician (upper Llanvirn)*–*Silurian (Wenlock)*: USA, eastern Canada, Britain, northern Europe, Ukraine, Estonia, Russia, Siberia, China, Mongolia, India.—FIG. 640,4a–g. **P. reversa* (BILLINGS), Ashgill, Ellis Bay Formation, Anticosti Island, Canada; *a*, ventral valve exterior; *b*, articulated valves, lateral view, ventral on left; *c*, dorsal valve exterior; *d*, articulated valves, anterior view, ventral valve below, $\times 2.5$; *e–g*, serial sections 2.2, 2.8, and 3.2 mm from posterior end of specimen 20.5 mm long, ventral valve above (Jin & Copper, 1997).

Family PARALLELELASMATIDAE Cooper, 1956

[Parallelelasmatidae COOPER, 1956a, p. 611] [=Saloniidae SAPELNIKOV, 1972, p. 39; Vagidae SAPELNIKOV, 1973, p. 40]

Smooth or costate, may have strong concentric lamellae; weakly to strongly uniplicate; spondylium duplex or simplex supported by high median septum, rarely sessile; short outer hinge plates converge and remain discrete, subparallel, and continue anteriorly into long, subparallel inner hinge plates; median septum and septalium absent; alate plates absent; bladelike crura present. *Lower Ordovician (upper Llanvirn)*–*Upper Ordovician (Ashgill)*.

Metacamarella REED, 1917, p. 934; *emend.*, WILLIAMS, 1962, p. 231 [*Stricklandinia? balcletchiensis* DAVIDSON, 1883, p. 166; OD] [=*Metacamarella* SCHUCHERT & COOPER, 1931, p. 248, *nom. null.*; *Parallelelasma* COOPER, 1956a, p. 611 (type, *P. pentagonum*)]. Medium to large size; subtriangular in outline, longer than wide; costae wide, present only on anterior half, valves otherwise smooth; broad and shallow uniplication near anterior margin only, may be absent; teeth long and slender; very wide, short spondylium duplex commonly decreases in width on anterior half, supported for entire length by median septum of variable height that extends anterior to spondylium, some spondylia nearly free anteriorly; outer hinge plates very short, convergent to nearly horizontal, and extend into long, subparallel inner hinge plates that extend anteriorly well beyond long, recurved bladelike crura; adductor muscle field elongate oval. [*Parallelelasma* appears to differ from *Metacamarella* only in having a higher ventral median septum supporting the spondylium, and shorter and straighter crura, features that can vary widely among individuals.] *Lower Ordovician (upper Llanvirn)*–*Upper Ordovician (Caradoc)*: southeastern USA, Britain, Norway, Estonia.—FIG. 642,6a–b. **M. balcletchiensis* (DAVIDSON), Caradoc, Balclatchie Conglomerate, Scotland; *a*, dorsal valve exterior; *b*, dorsal valve interior, $\times 1$ (Williams, 1962).—FIG. 642,6c–f. *M. pentagonum* COOPER, upper Llanvirn, Pratt Ferry Formation, Alabama, USA; *a*, ventral valve exterior, $\times 2$; *d*, articulated valve fragments, lateral view, ventral valve on right, $\times 3$; *e*, ventral valve interior; *f*, dorsal valve interior, $\times 8$ (Cooper, 1956a).

Didymelasma COOPER, 1956a, p. 615 [**D. longicrurum*; OD]. Small to very small size; length and width approximately equal; appears elongate oval in outline; dorsal and ventral valves equal and moderate in convexity; valves smooth, but weak costae may be present anteriorly only in broad, shallow, distinct fold and sulcus; short, narrow spondylium simplex or duplex; dorsal interior appears similar to *Metacamarella* with long, subparallel inner hinge plates, but valve interiors rather poorly known; crura long and straight, not curved. *Upper Ordovician (Caradoc–Ashgill)*: USA, Canada, Australia, China, Russia, Kazakhstan, Siberia.—FIG. 642,2a–e. **D. longicrurum*, Ashgill, Lebanon Formation, Tennessee, USA; *a*, ventral valve exterior; *b*, articulated valves, lateral view, ventral valve on right; *c*, dorsal valve exterior; *d*, articulated valves, anterior view, ventral valve below; *e*, slab showing valve exteriors and dorsal and ventral valve interiors, $\times 3$ (Cooper, 1956a).

Limstrophina FU, 1982, p. 132 [**L. ptychorete*; OD] [=*Limstrophia* FU, 1980, p. 2, *nom. null.*]. Small size; wider than long; subelliptical to subpentagonal in outline; weak costae and concentric rugae present on entire valve; valves equally and strongly biconvex; uniplication broad and very shallow, covers entire valve; hinge line appears to be narrow, strophic; valve interiors poorly known but appear to

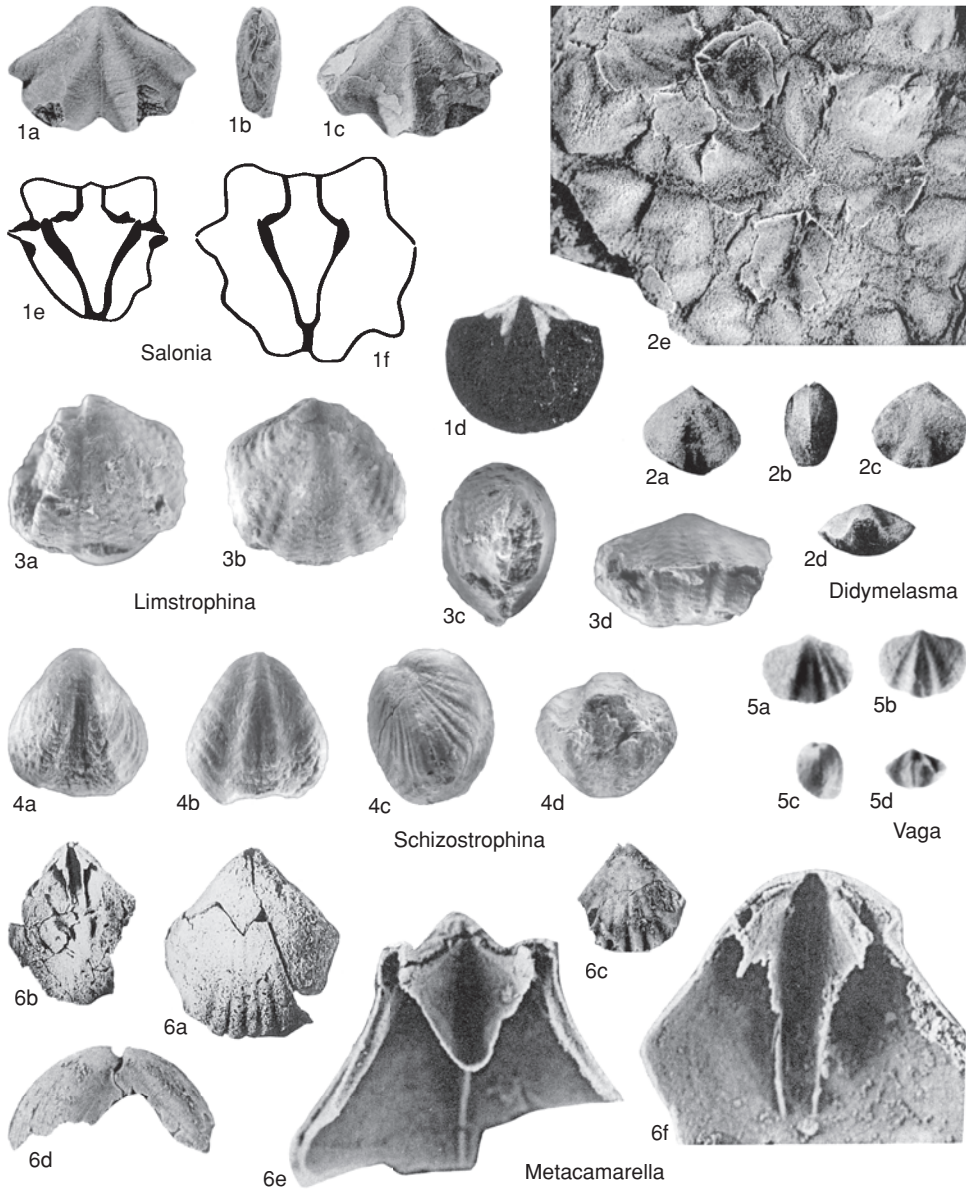


FIG. 642. Parallelelasmataidae (p. 958–960).

contain spondylium supported by median septum, and narrow, discrete, parallel socket plates. [*Limstrophina* known from only a single specimen.] Upper Ordovician (Caradoc): northwestern China.—FIG. 642,3a–d. **L. psychorete*, Jinhe Formation, Shaanxi Province, Liqan; a, ventral valve exterior; b, dorsal valve exterior; c, articulated valves, ventral

on left; d, articulated valves, anterior view, ventral below, $\times 3$ (Fu, 1982). **Salonia** COOPER & WHITCOMB, 1933, p. 500 [**S. magnaplicata*; OD]. Small to medium size; valve proportions vary; subtriangular, trilobate, or subelliptical in outline; valve form dominated by 3 to 4 smooth, angular costae or plicae present on

entire valve; ventribiconvexity moderate, umbo strongly rostrate; uniplication strong, angular; dorsal sulcus appears to revert to fold during growth; very short, sessile spondylium supported anteriorly by low, short median septum that does not extend anterior to spondylium; short, narrow outer hinge plates extend into relatively short inner hinge plates that converge but remain discrete anterior to very long, curved crura. *Upper Ordovician (lower Caradoc)*: northeastern USA.—FIG. 642, 1a–f. **S. magnaplicata*, Salona Formation, Pennsylvania; *a*, ventral valve exterior; *b*, articulated valves, lateral view, ventral valve on right; *c*, dorsal valve exterior, $\times 2$; *d*, close up of posterior of dorsal interior [semicircular lower outline is artificial and does not reflect shape of dorsal valve outline], $\times 6$ (Cooper, 1956a); *e–f*, sections through articulated specimen, ventral valve below, 0.5 and 0.8 mm from beak, $\times 5$ (Cooper & Whitcomb, 1933).

Schizostrophina FU, 1982, p. 132 [**S. margarita*; OD] [= *Schizostrophia* FU, 1980, p. 2, *nom. null.*]. Small size; valves smooth, rarely with few, coarse plicae; ventribiconvexity very strong; uniplication broad and strong, covers entire valve; valve interiors poorly known but appear to contain spondylium

supported by median septum, and narrow, divergent socket plates. *Upper Ordovician (Caradoc)*: northwestern China.—FIG. 642, 4a–d. **S. margarita*, Jinhe Formation, Shaanxi Province, Liquan; *a*, ventral valve exterior; *b*, dorsal valve exterior; *c*, articulated valves, ventral on right; *d*, articulated valves, anterior view, ventral below, $\times 3$ (Fu, 1982).

Vaga SAPELNIKOV & RUKAVISHNIKOVA, 1973, p. 33 [**V. sinualis*; OD]. Small size; wider than long, sub-elliptical in outline; angular plicae present primarily on fold and sulcus, valves otherwise smooth; valves equally and strongly biconvex; uniplication broad, strong, angular, covers entire valve; short, narrow, shallow spondylium simplex supported by high, short median septum; very short, narrow outer hinge plates extend into very short inner hinge plates that converge but remain discrete anterior to robust, bladeliike crura. *Upper Ordovician (upper Caradoc)*: Kazakhstan.—FIG. 642, 5a–d. **V. sinualis*, Chu-Ili Mountains; *a*, ventral valve exterior; *b*, dorsal valve exterior; *c*, articulated valves, ventral on left; *d*, articulated valves, ventral valve below, $\times 1$ (Sapelnikov & Rukavishnikova, 1973).

PENTAMERIDINA

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Suborder PENTAMERIDINA Schuchert & Cooper, 1931

[*nom. correct.* AMSDEN, 1965, p. 541, *pro* Pentameroidea SCHUCHERT & COOPER, 1931, p. 247]

Shells ranging from small to large, with very large examples known from the three superfamilies but few very small examples known. The key subordinal character a spondylium commonly, but not invariably supported by a median septum. Tripartite cardinalia involving inner and outer hinge plates separated by crura. Ornamentation and shell convexity highly variable. *Upper Ordovician (middle Ashgill)–Upper Devonian (Frasnian)*.

Although the origins of the pentameroid brachiopods are veiled in uncertainty, they first occurred with any certainty and in some taxonomic as well as numerical abundance in the mid-Ashgill with the appearance of the Virganiidae. The virganiids are typical thick-shelled pentameroids, many reaching a large size (10 cm in length) and commonly occurring in monospecific aggregations that can extend laterally for kilometers or more, as is typical of the younger Silurian and Devonian pentameroids as well. The pentameroids are typically a benthic assemblage 3, inner shelf, photic zone group (BOUCOT, 1975a).

In the pre-Ashgill, the Llanvirn and Caradoc in particular, there is a handful of

numerically uncommon, relatively provincial genera that may include the precursors of the undoubted pentameroids. Included here are COOPER's (1956a) Parallelelasmatidae and SAPELNIKOV and RUKAVISHNIKOVA's (1973) not too well understood *Vaga* from the upper Caradoc of Kazakhstan. The five parallelasmids plus *Vaga*, whose familial position is possibly virgianid, possess hinge plates like those of the Pentameridina rather than of the varied taxa within the Syntrophiidina. For none of the six genera involved here (five parallelasmids plus *Vaga*) may one be certain of the details of the hinge plates, however, and for none of them are there useful data about shell structure that could be compared with profit to that available for the Pentameridina. There is also lack of information on the shell structure of the Syntrophiidina. (Traditional pentameroid terminology for the inner and outer hinge plates, plus the crura, has been inner and outer brachial lamellae, plus the brachial processes. We defer to the decision made by the editors in replacing the older terminology (see Fig. 620.10). Until early ontogenies have been studied within at least a few pentameroids, however, there is still the possibility that hinge plates are not homologs of brachial lamellae or crura of brachial processes.)

In a general sort of way one is more inclined to see the origins of the Pentameridina within the pre-Ashgill or possibly pre-Caradoc Syntrophiidina owing to overall external and internal similarities. When the genera within the varied syntrophiid families are considered, however, it is currently unclear just where such origins might be. The alate plates of the parastrophinids rule them out, while the relatively simple camerellid cardinalia similarly make them unlikely ancestors. The very specialized cardinalia of *Brevicamera* rule it out. The very specialized ventral interior of the Xenelasmatinae makes it too specialized to serve as an ideal ancestor, as does the spondylium simplex of the Syntrophiidae. There are probably no better prospects for the other families.

The relationships within the Pentameridina are complicated by repeated instances of homeomorphy, convergence, and parallelism. It is almost as though the basic pentameroid genome held within itself the capacity for some permutations and combinations that were variably expressed time after time. For example, the relatively large, strongly costate, thick-shelled *Conchidium*-type shell has been repeated in the virgianids with *Pleurodium*, in the subrianids with *Conchidium*, in the Pentameridae with *Kirkidium*, and in the Gypiduloidea with *Zdimir* (= *Conchidiella*); no clorindid *Conchidium* type has yet been seen, but it would not be all that extraordinary if one were to be uncovered ultimately. A review of the fossil record is given below.

The Virgianidae of the mid-Ashgill to middle Llandovery include varied external morphologies. Mention has already been made about how similar *Pleurodium* is externally to the large, ribbed shells, all of which were formerly placed into *Conchidium*. The bulk of the virgianids were extinct well before the end of the Ashgill, however, with only the aspondylose, smooth form *Holorhynchus* and the clorindiform *Brevilamnula* bridging the Ordovician-Silurian boundary. Neither of these genera is morphologically gradational into the Llandovery virgianids. The well-defined Llandovery virgianids (*Virgiana* [Fig. 621.4], *Virgianella*, *Borealis*, *Pseudoconchidium*, *Mariannaella*, *Pleurodium*, *Plicidium*) include varied external forms. All of them, however, were gone by the end of the Aeronian (mid-Llandovery) or possibly Telychian (late Llandovery). *Borealis* can easily be thought of as a precursor to *Pentamerus* (Fig. 621.5) of the later Llandovery. *Pentamerus*, in turn, can easily serve as the precursor of the costate and smooth younger Silurian Pentameridae (BOUCOT & JOHNSON, 1979).

The Subrianidae, ranging from the later Wenlock to the Ludlow, pose problems since there are no truly transitional forms between them and their most logical precursors, the

Pentameridae. The Subrianidae, however, may have been neotenually derived from the Pentameridae by a process of reduction in length of the hinge plates, plus the addition of medially projecting crura.

The gypiduloids (see Fig. 621.1) seem likely to have evolved from the mid-Ashgillian *Galeatellina*, whereas the clorindoids (see Fig. 621.2) probably evolved from the mid-Llandovery *Brevilamnulella*.

We place the Pentamerellinae into the Clorindoidea owing to their clorindid external form. *Pentamerella*, however, lacks carinae in the dorsal valve, as do most gypidulinids. We place *Levigatella* (Levigatellinae) into the Gypidulidae despite the presence of carinae in the dorsal valve because of its gypidulid external form.

The Stricklandioidea clearly have a pre-Silurian origin relatively independent of the Virgianidae, as is shown both by their unique internal features in both valves, particularly the cardinalia (see Fig. 621.3), and by the presence of prismatic shell on the medial faces of the hinge plates rather than on the lateral faces as is true of the Virgianidae and their potential descendants discussed above. Despite the characteristic form of their cardinalia, however, the stricklandiids possess the long, rodlike crura so characteristic of the Ashgill and younger Virgianidae and Pentameridae that make it clear that the origins of the two groups cannot be too remote from each other. We divide the Stricklandiidae into two subfamilies, Stricklandiinae and a new subfamily Kulumbellinae. The earliest kulumbellid is probably *Microcardinalia mullochensis* (REED, 1917). The Aenigmastrophidiidae probably evolved from the Kulumbellinae, since their specialized morphologies are closer to that subfamily than that of the Stricklandiinae.

The affinities of the Aenigmastrophidiidae were previously considered to be very uncertain (BOUCOT & RONG, 1994). We now conclude that they have more in common with the stricklandiids than with any other group since the cardinalia and ventral interior of

aenigmastrophidiids are similar to those in *Kulumbella* s.l. *transversa* (GRABAU) (see RONG & YANG, 1981) and other stricklandiids lacking outer hinge plates. Notable is the distinctive, later diversification of the Aenigmastrophidiidae, with their unique cardinalia and external forms.

The affinities of the internally poorly known Stricklandistrophidiidae are also uncertain but fit most comfortably within the stricklandioids.

The Enantiosphenidae are most reasonably viewed as gypiduloids with unusual external form plus the presence of a loop (see Fig. 620.9), the latter being a convergently developed feature that has no relationship to the terebratuloid loop.

The suborder is divided into the superfamilies Pentameroidea, Stricklandioidea, Gypiduloidea, and Clorindoidea.

Superfamily PENTAMEROIDEA M'Coy, 1844

[*nom. transl.* SCHUCHERT, 1896, p. 320, ex Pentameridae M'COY, 1844, p. 103]

[Materials prepared by A. J. BOUCOT, RONG JIA-YU, & ROBERT B. BLODGETT]

Shells tend to be large; moderately to strongly ventribiconvex; exterior smooth, costellate, costate, or diagonally rugose; interareas absent except in some Subrianinae; ventral interior with well-developed spondylium formed from medially fused plates and commonly supported by a median septum formed from the basal and anterior continuation of those plates; hinge teeth well developed; inner hinge plates may be conjunct to form a cruralium; hinge plates may be laminar or curved in cross section, long or short, and may be tripartite; crura may protrude medially; ventral valve with outer lamellar layer and inner prismatic layer, dorsal valve with lamellar layer and with or without prismatic layer; prismatic layer on hinge plates of Virgianidae and Pentameridae invariably situated on lateral faces of plates. *Upper Ordovician (middle Ashgill)—Silurian (Přidolí)*.

Family VIRGIANIDAE
Boucot & Amsden, 1963

[Virgianiidae BOUCOT & AMSDEN, 1963, p. 296]

Median septum in ventral valve relatively short, less commonly long or absent; hinge plates relatively short, extending short distance anterior of inner socket ridges; outer hinge plates parallel to each other for only a short distance. *Upper Ordovician (middle Ashgill)–Silurian (lower Wenlock)*.

Subfamily VIRGIANINAE
Boucot & Amsden, 1963

[*nom transl.* BOUCOT, RONG, & BLODGETT, herein, ex Virgianiidae BOUCOT & AMSDEN, 1963, p. 296] [=Tcherskidiinae SAPELNIKOV, 1972, p. 35; Holorhynchinae SAPELNIKOV, 1973, p. 40; Holorhynchusinae SAPELNIKOV, 1985a, p. 19]

Small to large; smooth or costate; ventral median septum of variable length, present in some; hinge plates commonly short and crura short; prismatic and lamellar shell in investigated genera; commonly no fold or sulcus. *Upper Ordovician (middle Ashgill)–Silurian (lower Wenlock)*.

Virgiana TWENHOFEL, 1914, p. 27 [**Pentamerus barrandei* BILLINGS, 1857, p. 296; OD]. Small to medium; ventribiconvex, subcircular to elongate; weak to strong costae to sublattice; spondylium short with median septum short. *Silurian (lower Llandovery–middle Llandovery)*: North America, Asia.

V. (*Virgiana*). Medium; strongly ventribiconvex; prominent ventral beak; umbo may be smooth. *Silurian (lower Llandovery–middle Llandovery)*: North America, Asia.—FIG. 643, 1a–g. *V. (*V. barrandei*) (BILLINGS), Anticosti, Quebec, Canada; a–d, lateral, ventral, dorsal, and posterior views of articulated specimen, Becscie River Formation, $\times 1$ (Schuchert & Cooper, 1932); e, anterior view of articulated specimen, Becscie River Formation, $\times 1$ (Amsden, 1965); f–g, ventral and lateral of articulated specimen, Gun River Formation, $\times 1$ (Boucot, Johnson, & Rubel, 1971).—FIG. 643, 1h–j. V. (*V. mayvillensis*, Mayville Dolomite, Mayville, Wisconsin, USA; h–i, dorsal and posterior views of articulated specimens, $\times 1$; j, dorsal interior, $\times 2$ (Boucot, Johnson, & Rubel, 1971).

V. (*Platmyrella*) FOERSTE, 1909a, p. 70 [**P. manniensis*; OD]. Small to medium; ventral beak weak; gently biconvex with valves subequally sized. *Silurian (middle Llandovery)*: midcontinent North America.—FIG. 643, 2a–j. *V. (*P.*

manniensis, USA; a–c, dorsal, posterior, ventral, Tennessee, no formation given, $\times 1$ (Amsden, 1965); d–g, ventral, lateral, anterior, and posterior of articulated specimen, Brassfield Formation, Ohio, $\times 1.5$; b, posterior view of ventral interior, Brassfield Formation, Ohio, $\times 3$; i, posterior view of interior, Brassfield Formation, Ohio, $\times 2$; j, posterior view of dorsal interior, Brassfield Formation, Ohio, $\times 3$ (Boucot, Johnson, & Rubel, 1971).

Borealis BOUCOT, JOHNSON, & RUBEL, 1971, p. 274 [**Gypidia borealis* EICHWALD, 1843, p. 74; OD]. Medium; smooth; ventribiconvex; elongate; short, broad spondylium supported by well-developed median septum. *Silurian (lower Llandovery)*: Baltic region, South China, Russia (Kolyma, Siberia).—FIG. 644, 1a–g. *B. *borealis* (EICHWALD), Juuru Stage, Estonia; a–d, lateral, ventral, dorsal, and lateral views of articulated specimens, $\times 1.3$; e, dorsal view of interior mold, $\times 1.4$; f, interior of ventral valve, $\times 1.5$; g, dorsal view of dorsal interior mold, $\times 2$ (Boucot, Johnson, & Rubel, 1971).

Holorhynchus KIAER, 1902, p. 68 [**H. giganteus*; OD]. Smooth; strongly ventribiconvex; spondylium unsupported by median septum. *Upper Ordovician (middle Ashgill)–Silurian (middle Llandovery)*: Eurasia, North America (including Alaska).

H. (*Holorhynchus*). Large; subcircular to variable outline; short, low median ridge may be present in dorsal valve. *Upper Ordovician (middle Ashgill)*, *Silurian (?lower Llandovery)*: Eurasia, USA (Alaska).—FIG. 645a–g. *H. (*H. giganteus*, Sandvik, Oslo region, Stage 5; a–d, ventral, dorsal, lateral, posterior views of articulated specimen, $\times 1$; e–f, dorsal and posterior views of dorsal mold, $\times 1$; g, dorsal view of dorsal interior mold, $\times 1.5$ (Boucot, Johnson, & Rubel, 1971).

H. (*Nondia*) BOUCOT & CHIANG, 1974, p. 66 [**N. canadensis*; OD]. Medium; moderately biconvex; subrhomboidally shaped outline; median ridge in dorsal valve. *Silurian (lower Llandovery–middle Llandovery)*: western Canada.—FIG. 646a–e. *H. (*N. canadensis*, Nonda Formation, British Columbia; ventral, anterior, dorsal, posterior views of articulated specimen, lateral view, $\times 1.5$ (Boucot & Chiang, 1974).

Proconchidium SAPELNIKOV in NIKOLAEV & SAPELNIKOV, 1969, p. 15 [**Conchidium munsteri* St. JOSEPH, 1938, p. 301; OD] [=Norgium BREIVEL & BREIVEL in ANTSIGIN & others, 1970, p. 7, obj.]. Medium; subcircular to elongate; costellate; ventral median septum extending almost to anterior margin and longer than spondylium; long outer hinge plates; inner hinge plates shorter than outer; cardinal process may be present. *Upper Ordovician (middle Ashgill)*: Urals, Central Asia [Sredni Azii], Kazakhstan, Norway, Arctic Canada, northern Greenland.—FIG. 644, 3a–g. *P. *munsteri* (St. JOSEPH), Norway, Stage 5b; a–d, ventral of internal mold, ventral of internal mold, dorsal view of internal mold, dorsal view of internal mold, Skien

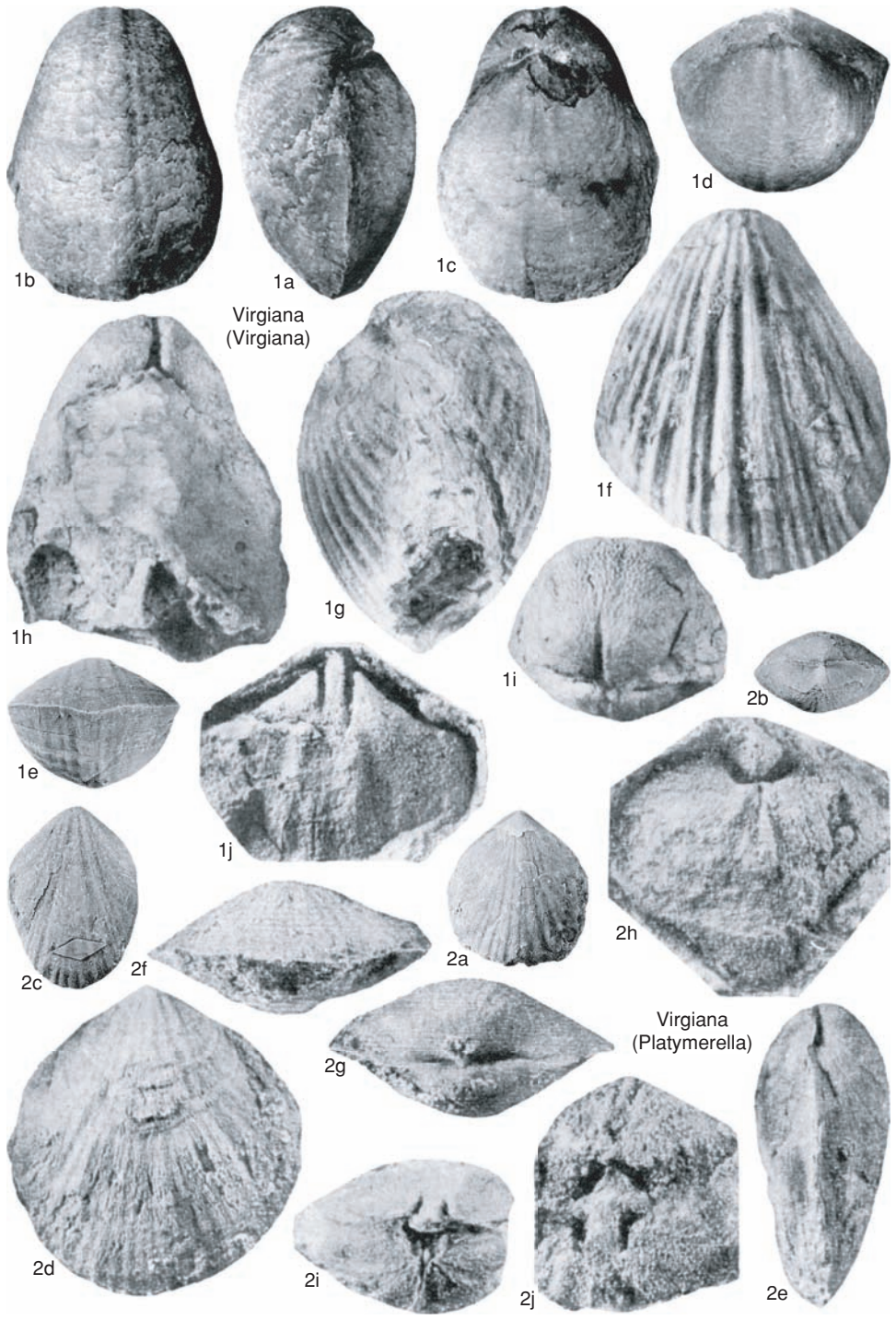


FIG. 643. Virganiidae (p. 963).

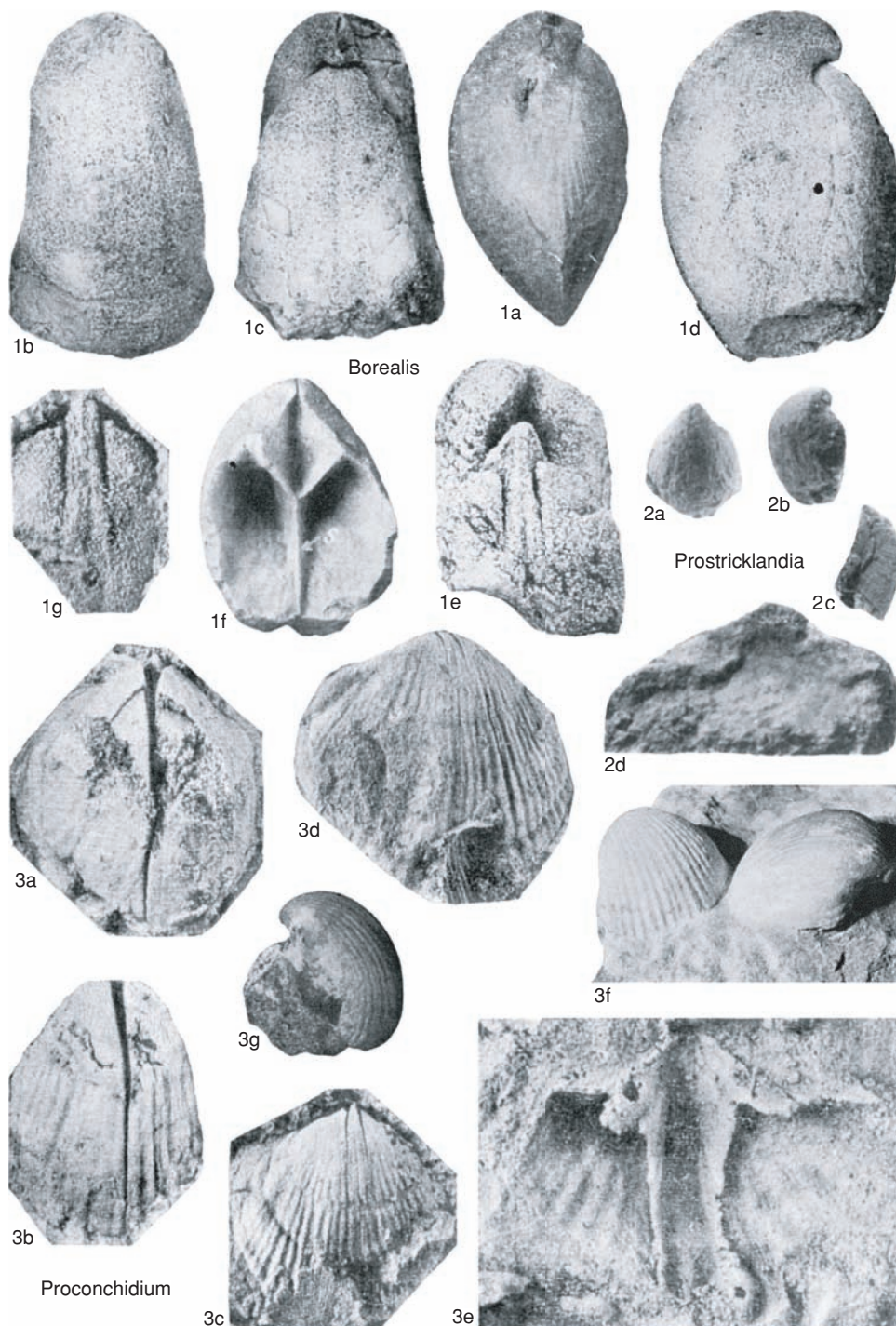
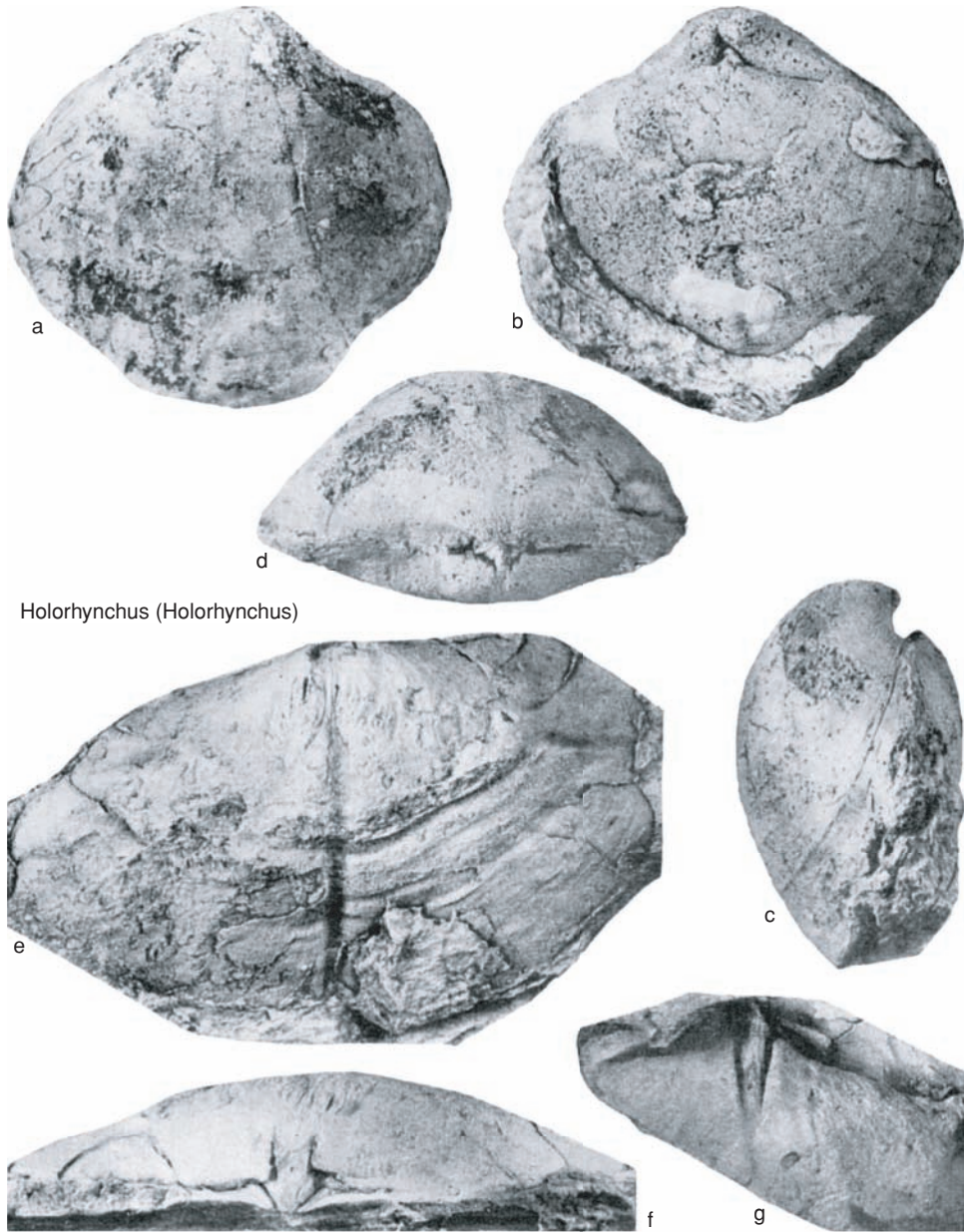


FIG. 644. Virgianidae (p. 963–966).



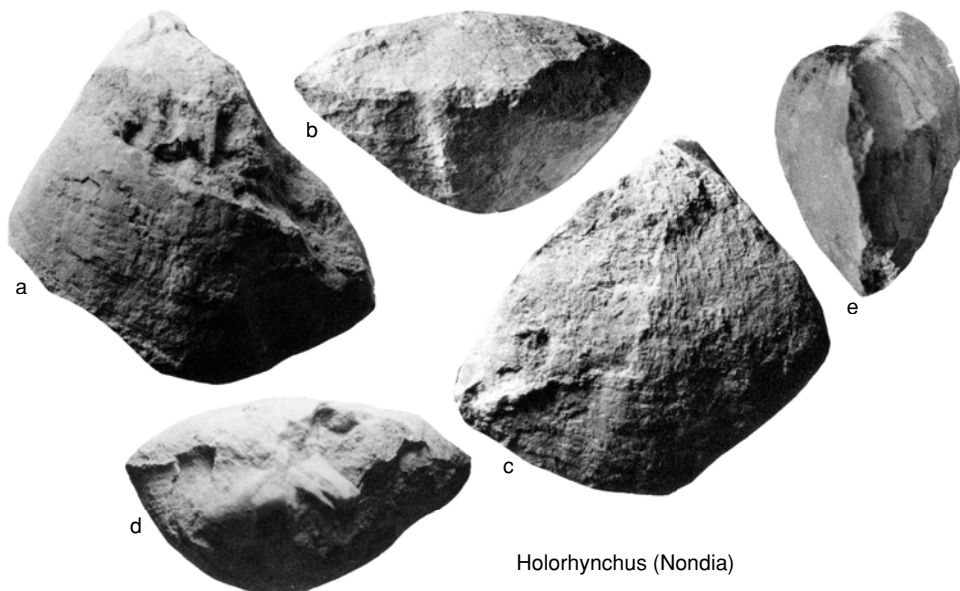
Holorhynchus (*Holorhynchus*)

FIG. 645. Virganiidae (p. 963).

region, Oslo, $\times 1.5$; *e*, rubber replica of dorsal interior, Ringerike area, Oslo region, $\times 4$ (Boucot, Johnson, & Rubel, 1971); *f-g*, ventral plus side, and lateral, $\times 1$ (St. Joseph, 1938).

Prostricklandia RUKAVISHNIKOVA & SAPELNIKOV, 1973, p. 106 [**P. prisca*; OD]. Small; smooth; moderately ventribiconvex; possibly with relatively straight hinge line and possibly well-developed interarea;

long ventral median septum supporting short spondylium; short hinge plates. *Upper Ordovician (middle Ashgill)*: Kazakhstan.—FIG. 644, 2*a-d*. **P. prisca*, Ulkuntass Stage [Gorizont], Chu'ilii Mountains, Pribalkhash, southeastern Kazakhstan; *a-b*, ventral and lateral views, $\times 1$; *c*, dorsal interarea, $\times 3$; *d*, lateral view showing median septum, $\times 1$ (Rukavishnikova & Sapelnikov, 1973).



Holorhynchus (Nondia)

FIG. 646. Virgianidae (p. 963).

Pseudoconchidium NIKIFOROVA & SAPELNIKOV, 1971, p. 52 [**P. kozhimbicum* NIKIFOROVA in NIKIFOROVA & SAPELNIKOV, 1971, p. 53; OD] [=Paraconchidium RONG & YANG in RONG, XU, & YANG, 1974, p. 198 (type, *P. shigianensis*, OD)]. Large; variably sized costae anteriorly, irregularly bifurcating to costellate; ventribiconvex; aseptate to variably developed ventral median septum; long spondylium; basally convergent inner hinge plates, outer hinge plates, and crura. *Silurian* (middle Aeronian, ?lower Telychian): USA (Alaska), South China, Arctic Urals, Russia (Kolyma, Vaygach).—FIG. 647, 2a–d. **P. kozhimbicum* (NIKIFOROVA), upper Llandovery–lower Wenlock, Pechora region, Russia; a, posterior view of internal impression, $\times 1$; b–d, ventral, lateral, and dorsal views, $\times 1$ (Nikiforova & Sapelnikov, 1971).

Tcherskidium NIKOLAEV & SAPELNIKOV, 1969, p. 12 [**Conchidium? unicum* NIKOLAEV, 1968, p. 47; OD]. Large; costellate; strongly ventribiconvex; elongate; spondylium supported by moderately long median septum; relatively short inner hinge plates; laterally inclined; outer hinge plates about twice as long as inner; crura well developed. *Upper Ordovician* (middle Ashgill): Russia (Kolyma, Taymyr), northern Greenland, USA (Alaska), South China, ?Kazakhstan.—FIG. 648a–d. **T. unicum* (NIKOLAEV), Iryudinsk Stage [Gorizont], Ina River, Omulevsk Mountains, Russia; ventral, dorsal, lateral, dorsal views, $\times 1$ (Nikolaev & Sapelnikov, 1969).

Virgianella NIKIFOROVA & SAPELNIKOV, 1971, p. 49 [**V. vaigatschensis* NIKIFOROVA in NIKIFOROVA & SAPELNIKOV, 1971, p. 49; OD]. Large; smooth; ventribiconvex; very short ventral median septum

supporting spondylium. *Silurian* (middle Llandovery–lower Wenlock): Arctic Urals, Central Asia [Sredni Azii], northern Greenland, South China, Russia (Kolyma, Vaygach).—FIG. 647, 1a–c. **V. vaigatschensis* (NIKIFOROVA), upper Llandovery–lower Wenlock, Pechora River, Arctic Urals, Russia; dorsal, ventral, lateral views, $\times 1$ (Nikiforova & Sapelnikov, 1971).

Subfamily MARIANNAELLINAE Sapelnikov & Rukavishnikova, 1975

[Mariannaellinae SAPELNIKOV & RUKAVISHNIKOVA, 1975a, p. 71]

Medium; transverse; smooth to plicate; fold and sulcus commonly well developed; very short median septum, if present, supporting spondylium; inner hinge plates absent or very short; prismatic shell commonly present. *Upper Ordovician* (middle Ashgill)–*Silurian* (Llandovery): Asia, Europe, North America.

Mariannaella SAPELNIKOV & RUKAVISHNIKOVA, 1975b, p. 7 [**M. koksengirensis*; OD]. Small to medium; costate; ventral fold and dorsal sulcus well developed; median septum absent or short, supporting short spondylium; short hinge plates, inner hinge plates very short or absent, outer hinge plates massive, short, free. *Silurian* (Llandovery): Kazakhstan.—FIG. 649, 1a–c. **M. koksengirensis*, Alpeisk Stage [Gorizont], Chingiz Range; ventral, ventral, dorsal views, $\times 1$ (Sapelnikov & Rukavishnikova, 1975a).—FIG. 649, 1d. *M. levisulcata*, Alpeisk

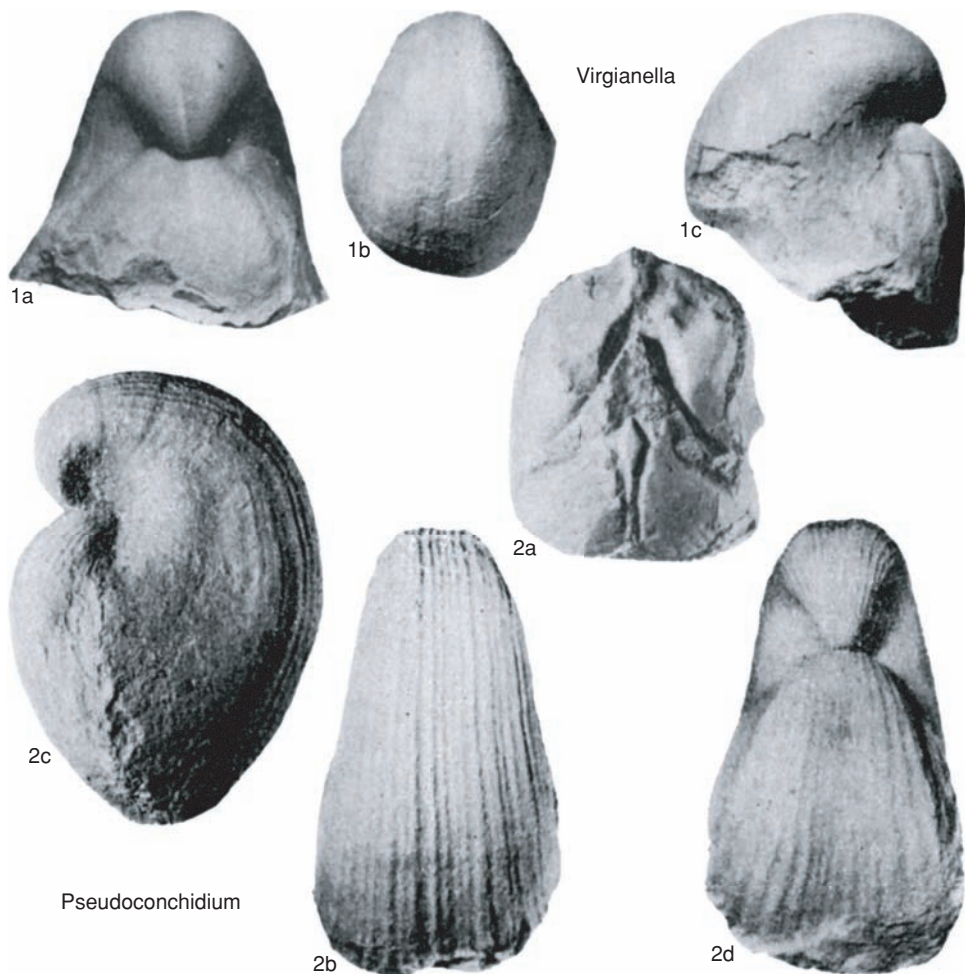


FIG. 647. Virgianidae (p. 967).

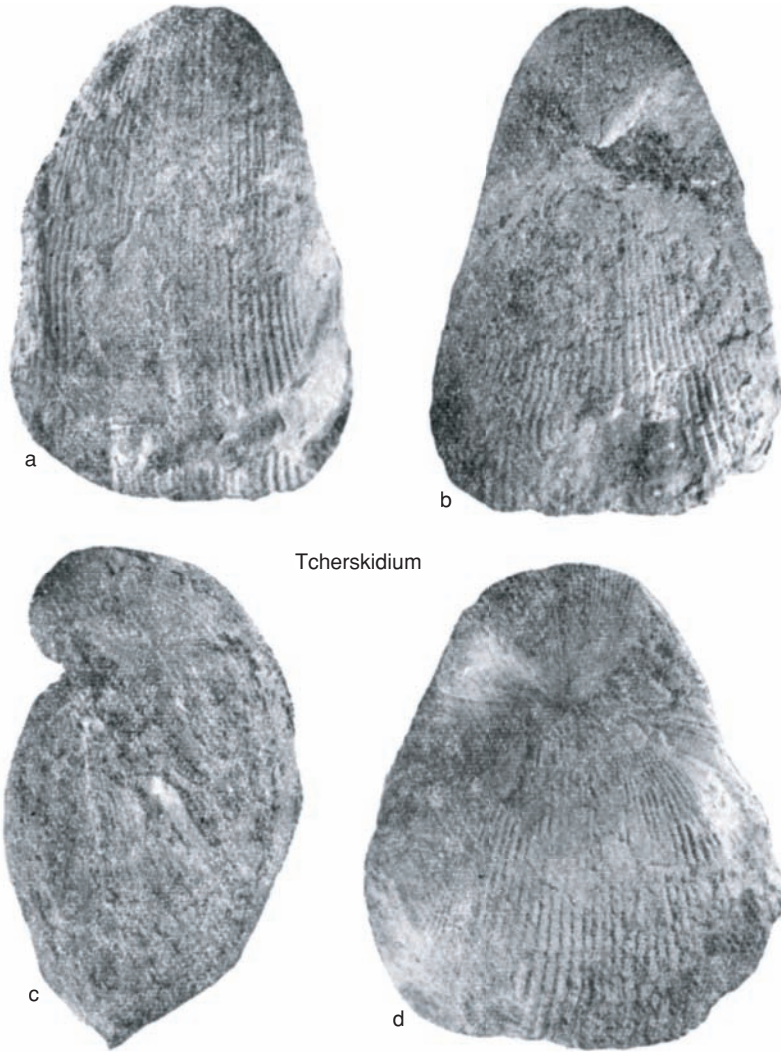
Stage [Gorizont], western Pribalkhash, southeastern Kazakhstan; lateral view, $\times 1$ (Sapelnikov & Rukavishnikova, 1975a).

Brevilamnulella AMSDEN, 1974, p. 62 [**Clorinda? thebesensis* SAVAGE, 1913a, p. 125; OD] [= *Antigaleatella* SAPELNIKOV & RUKAVISHNIKOVA, 1975a, p. 74 (type, *A. laevis*, OD); *Brevilamnula* BOUCOT & CHIANG, 1974, p. 72, *nom. null.*]. Small; smooth to weakly costate anteriorly; ventral sulcus and dorsal fold; uniplicate anterior commissure; small spondylium and short median septum; very short inner hinge plates, thicker outer hinge plates, with noncarinate crura. *Upper Ordovician (middle Ashgill)*—*Silurian (middle Llandovery)*: North America, Europe, Asia.—FIG. 649, 4a–i. **B. thebesensis* (SAVAGE), Leemon Formation, Cape Girardeau County, Missouri, USA; a–e, ventral, lateral view of ventral valve, dorsal view of exterior,

anterior view of ventral valve, lateral view of dorsal valve, $\times 2$; f–g, oblique view of dorsal cardinalia, dorsal interior; h, oblique posterior of ventral valve, $\times 5$; i, oblique view of ventral valve interior, $\times 3$ (Amsden, 1974).

Disulcatella FU, 1982, p. 134 [**D. didyma*; OD]. Small; smooth; subcircular to transverse; ventribiconvex; bisulcate; short median septum supporting short spondylium; short hinge plates. *Silurian (upper Rhuddanian–lower Aeronian)*: North China.—FIG. 649, 5a–e. **D. didyma*, Zhaohuajing Formation, Zhaohuajing, Tongxin County, Ningxia Province; ventral, dorsal, lateral, anterior, posterior of articulated specimen, $\times 3$ (Fu, 1982).

Eoconchidium ROZMAN, 1967, p. 62 [**E. indigiricum*; OD]. Small to medium; transverse; costate; ventribiconvex; short median septum, no more than one-



Tcherskidium

FIG. 648. Virganiidae (p. 967).

third shell length, supporting longer spondylium; short hinge plates. *Upper Ordovician (middle Ashgill)*: Russia (Kolyma), Kazakhstan, USA (Alaska).—FIG. 649,2a–d. **E. indigiricum*, Selenyakh Ridge, northeastern Russia; ventral, dorsal, lateral, anterior, $\times 2$ (Rozman, 1967).

Galeatellina SAPELNIKOV & RUKAVISHNIKOVA, 1976, p. 122 [**Galeatella kajnarensis* SAPELNIKOV & RUKAVISHNIKOVA, 1975a, p. 71; OD] [= *Galeatella* SAPELNIKOV & RUKAVISHNIKOVA, 1975a, p. 71, *non* MUIR-WOOD & COOPER, 1960, p. 173]. Small; biconvex; smooth; ventribiconvex; dorsal sulcus and ventral fold similar to *Gypidula*; short median septum supporting short spondylium; short hinge plates. *Upper Ordovician (middle Ashgill)*: Kazakhstan.—FIG. 649,3a–d. **G. kajnarensis* (SAPELNIKOV &

RUKAVISHNIKOVA), Tolensk superhorizon, Chingiz Range, southeastern Kazakhstan; ventral, dorsal, lateral, anterior views, $\times 1$ (Sapelnikov & Rukavishnikova, 1975a).

Subfamily PLEURODIINAE
Rong & Yang, 1977

[Pleurodiinae RONG & YANG, 1977, p. 75]

Medium to large; transverse; evenly costate to plicate; commonly no fold or sulcus; long spondylium supported by short median septum; outer and inner hinge plates short; long crura; prismatic layer absent. *Silurian*

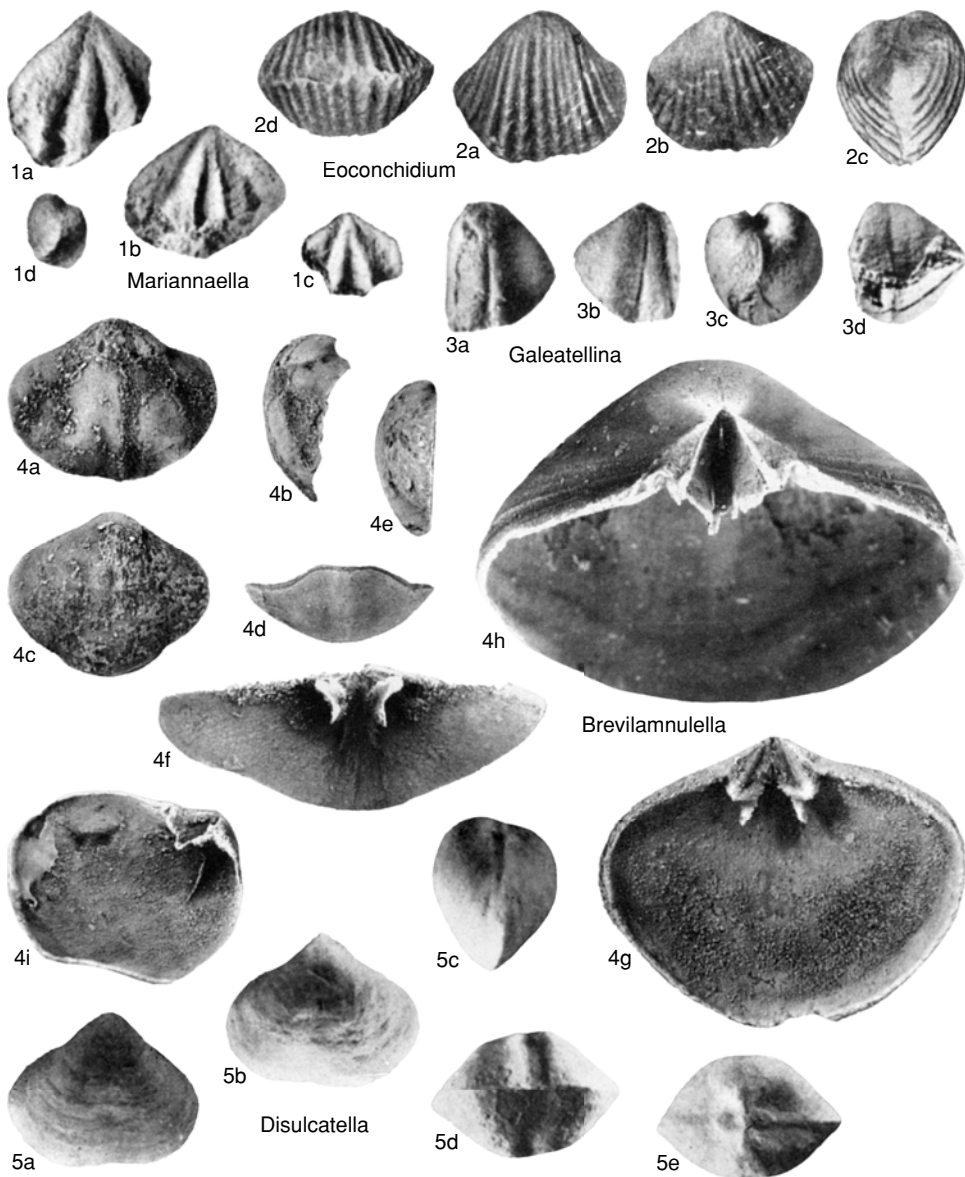


FIG. 649. Virgianidae (p. 967–969).

(middle Aeronian—upper Aeronian): South China.

Pleurodium WANG, 1955, p. 111 [**Conchidium tenuiplicatus* GRABAU, 1925, p. 80; OD]. Medium to large; transverse, evenly costate. *Silurian* (upper Aeronian): South China.—FIG. 650, 1a–f. **P. tenuiplicatus* (GRABAU), upper part of Lopoping Formation, Dazhongba, Fenxiang, western Hubei; a–e, ventral, dorsal, posterior, anterior, lateral views,

×1 (Wang, 1955); f, impression of dorsal interior, ×1 (Rong & Yang, 1981).

Plicidium RONG & YANG, 1981, p. 203 [**Virgiana? sinanensis* RONG & YANG in RONG, XU, & YANG, 1974, p. 197; OD]. Medium; subcircular; coarsely costate; anteriorly bifurcating costae; similar internally to *Pleurodium* but differs in its coarse ornamentation. *Silurian* (middle Aeronian): South China.—FIG. 650, 2a–e. **P. sinanensis* (RONG & YANG), Xiangshuyuan Formation, northeastern

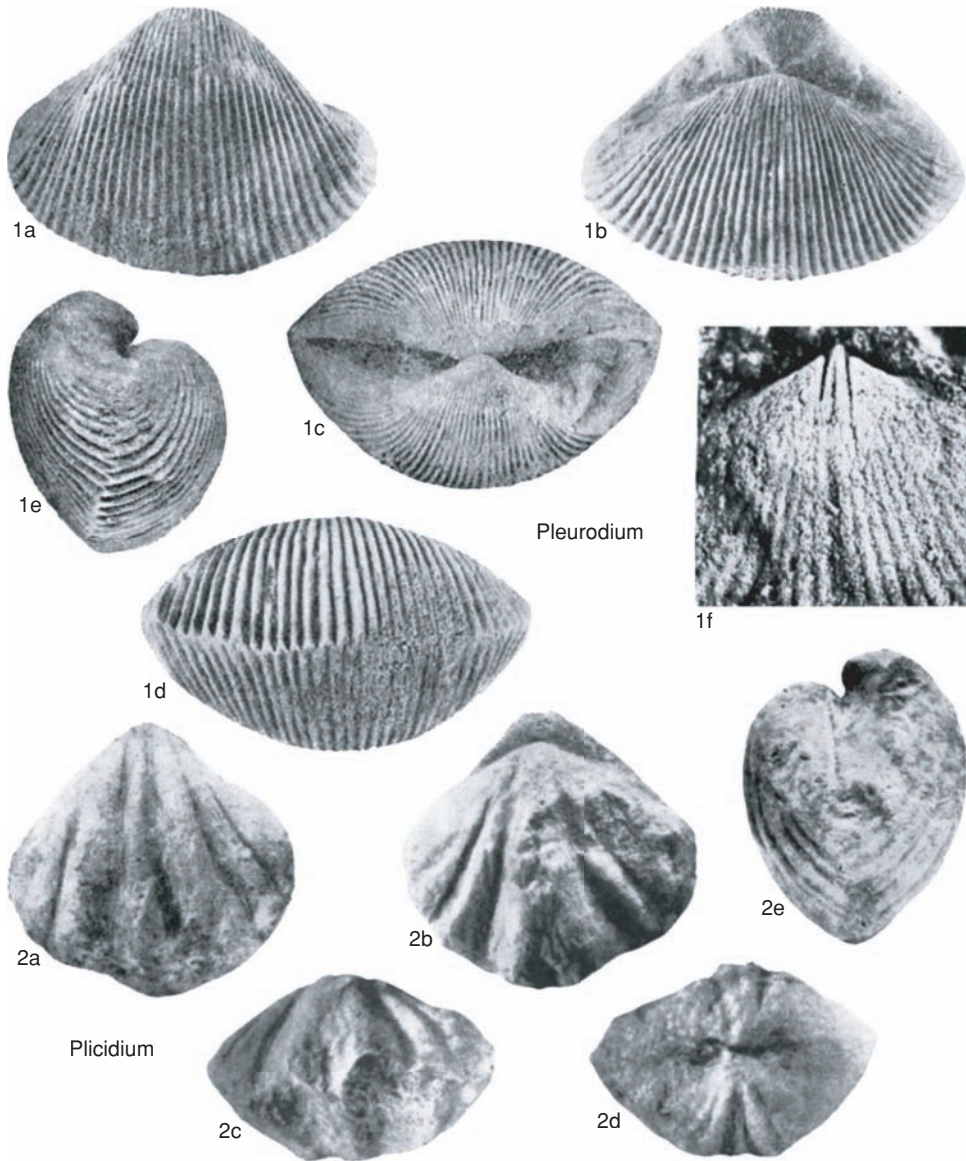


FIG. 650. Virgianidae (p. 970–971).

Guizhou; *a–d*, ventral, dorsal, anterior, posterior views, $\times 1$; *e*, lateral view, $\times 2$ (Rong & Yang, 1981).

Family PENTAMERIDAE M’Coy, 1844

[Pentameridae M’COY, 1844, p. 103] [=Pentameroidinae AMSDEN, 1953, p. 144; Brooksininae SAPELNIKOV, 1973, p. 40; Conchidiidae SAPELNIKOV, 1973, p. 40, *pars*]

Ventral valve median septum and spondylium variable in length; deltidium not al-

ways preserved; relatively long hinge plates commonly subparallel, and sometimes fused medially, laminar in cross section; cardinal process or striated area for diductor attachment may be present. [*Nanukidium* does possess carinae supporting the posterior extensions of the crura, a feature otherwise restricted to the Subrianinae but interpreted by

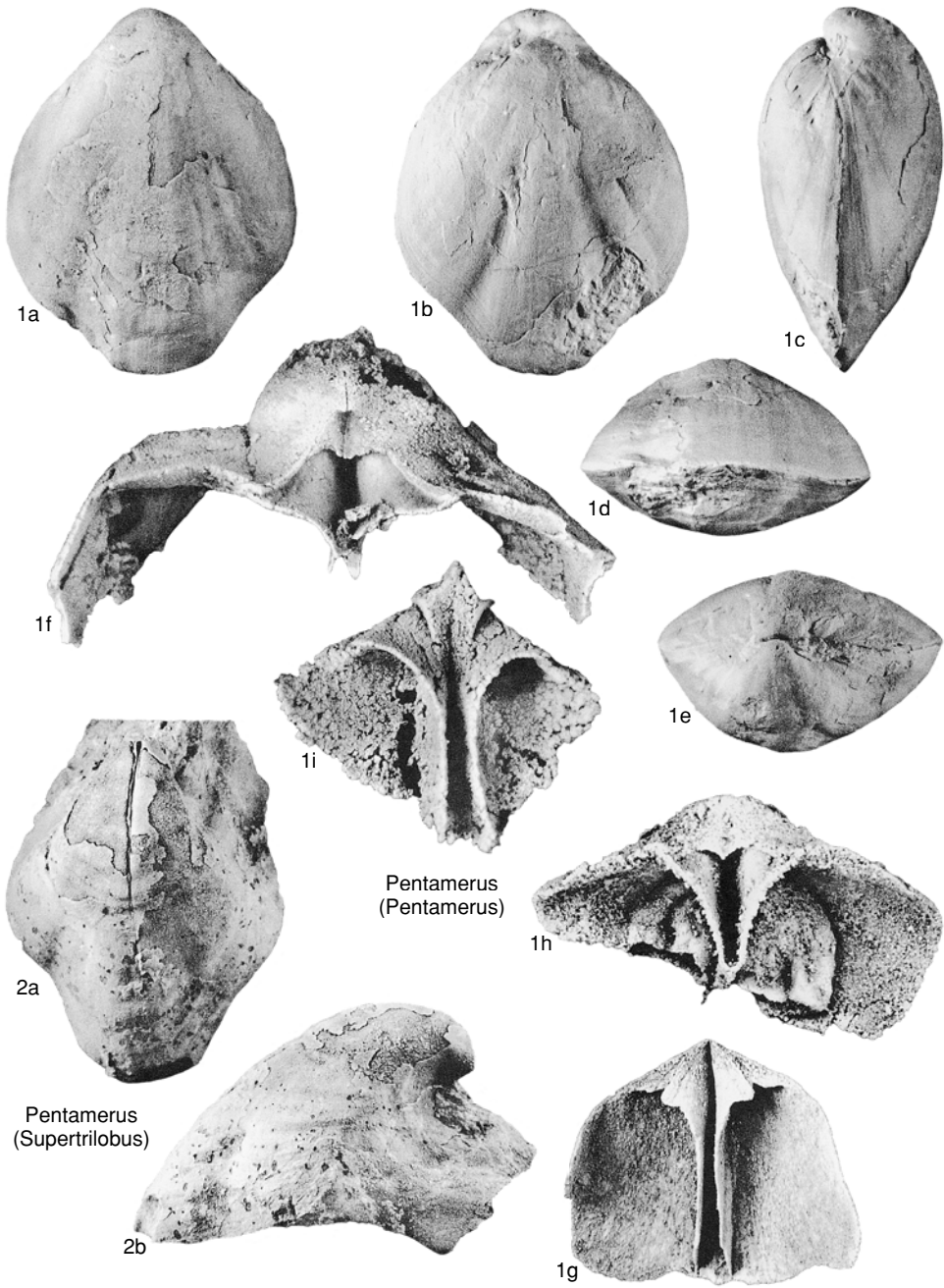
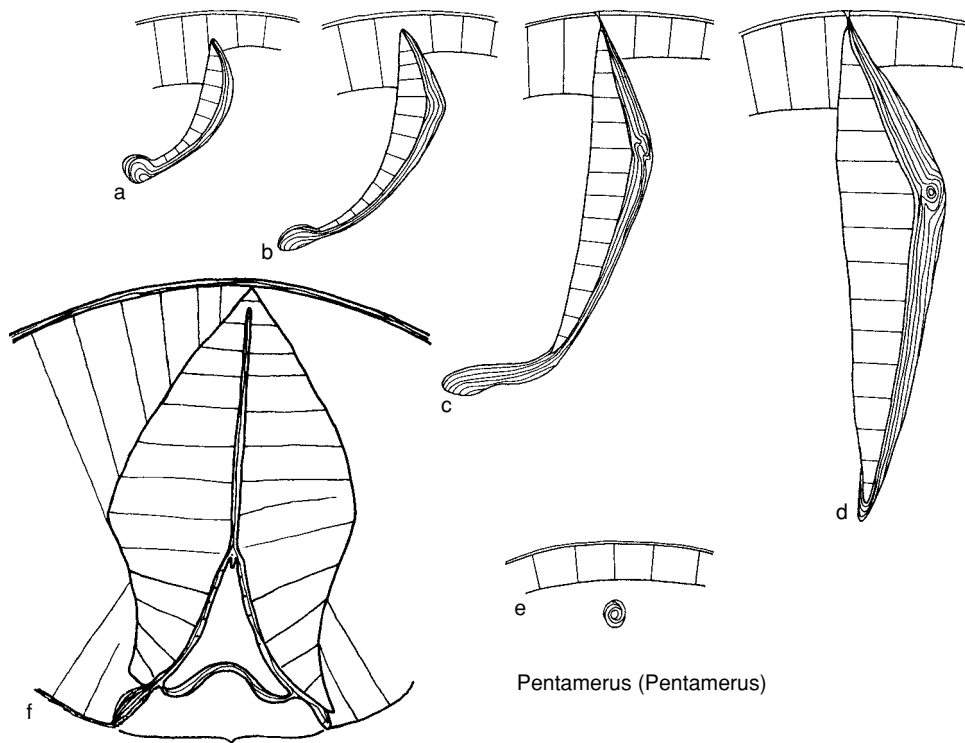


FIG. 651. Pentameridae (p. 973).

us as an example of convergence, since it is otherwise a homeomorph of *Kirkidium* in all regards; i.e., ours is the most parsimonious

explanation.] *Silurian* (middle Aeronian—Prídoli): North America, Europe, Asia, Australia.



Pentamerus (Pentamerus)

FIG. 652. Pentameridae (p. 973).

Pentamerus J. SOWERBY, 1813 in 1812–1815, p. 73 [**P. oblongus* J. de C. SOWERBY, 1839, p. 641; ICZN, 1954, Opinion 297; Opinion 297 placed *Pentamerus* J. SOWERBY, 1813 in 1812–1815, on the Official List of Generic Names in Zoology; *Pentamerus oblongus* J. de C. SOWERBY, 1839, was designated the type species and added to the Official List of Specific Names in Zoology. The following names were placed on the Official List of Rejected and Invalid Generic Names in Zoology: *Gypidia* DALMAN, 1828; *Trimurus* CALDWELL, 1934; *Miopentamerus* ALEXANDER (née CALDWELL), 1936; *Miopentamerus* WOODS, 1937. *Pentamerus laevis* J. SOWERBY, 1813 in 1812–1815, was placed in the Official Index of Rejected and Invalid Names in Zoology]. Medium to large; smooth; subequally biconvex; Ziegler's blisters present in small percentage; trilobate, with fold on each valve; ventral median septum about one-half valve length, hinge plates discrete, subparallel, and long. [Ziegler's blisters (see BOUCOT in BOUCOT & McCUTCHEON, 1986) are calcitic partitions present in the posterior portion of one or both umbonal chambers; they are anterior of a space that may be filled either with clear calcite or sediment, and are interpreted as a teratological condition; their presence in samples of both *Pentamerus* and *Pentameroides* is considered to have phylogenetic value.]

Silurian (upper Aeronian–Ludlow): North America, Europe, Asia, Australia.

P. (Pentamerus). Moderately biconvex. *Silurian (upper Aeronian–Wenlock)*: North America, Europe, Asia, Australia.—FIG. 651, 1a–e. **P. (P.) oblongus*; ventral, dorsal, lateral, anterior, posterior views, Jupiter Formation, Anticosti Island, Quebec, Canada, $\times 1$ (Boucot & Johnson, 1979).—FIG. 652a–f. **P. (P.) oblongus*; sections showing hinge plate and crural development and spondylium, Wallington Limestone, central New York, USA, $\times 2$ (Gauri & Boucot, 1968).—FIG. 651, 1f–i. *Pentamerus* sp., USA; f, interior of ventral, Wallington Limestone, central New York, $\times 2$; g, interior of dorsal, Wallington Limestone, central New York, $\times 1$; h, interior of ventral, Wallington Limestone, central New York, $\times 2$; i, interior of dorsal, Louisville Limestone, Louisville, Kentucky, $\times 3$ (Boucot & Johnson, 1979).

P. (Supertrilobus) BOUCOT & JOHNSON, 1979, p. 100 [**S. hawthornensis*; OD]. Large; ventral fold very large and prominent, strongly biconvex. *Silurian (upper Wenlock–Ludlow)*: central North America.—FIG. 651, 2a–b. **P. (S.) hawthornensis*, Racine Dolomite, Cook County, Illinois, USA; interior of ventral, side view, $\times 1$ (Boucot & Johnson, 1979).

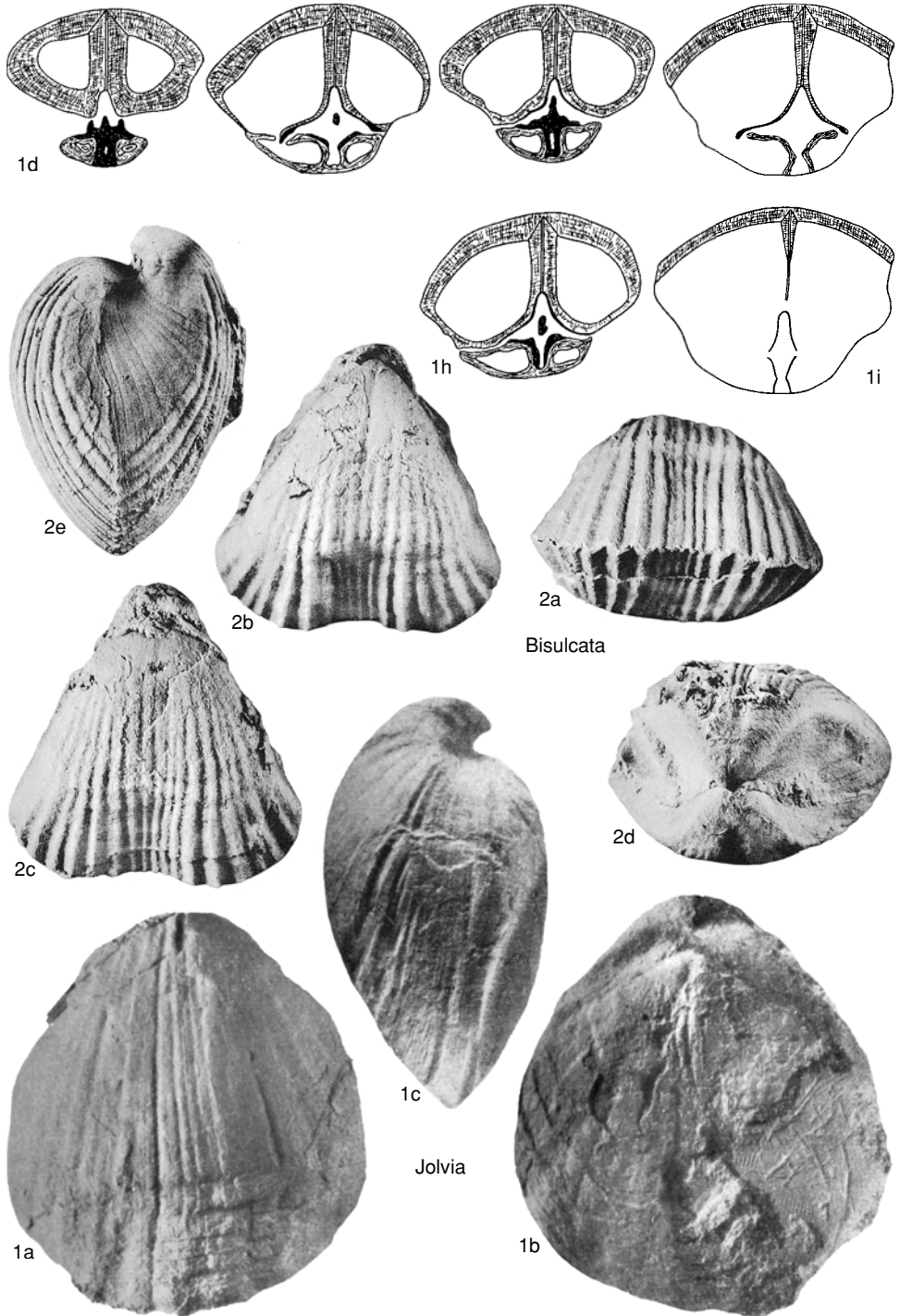


FIG. 653. Pentameridae (p. 975–976).

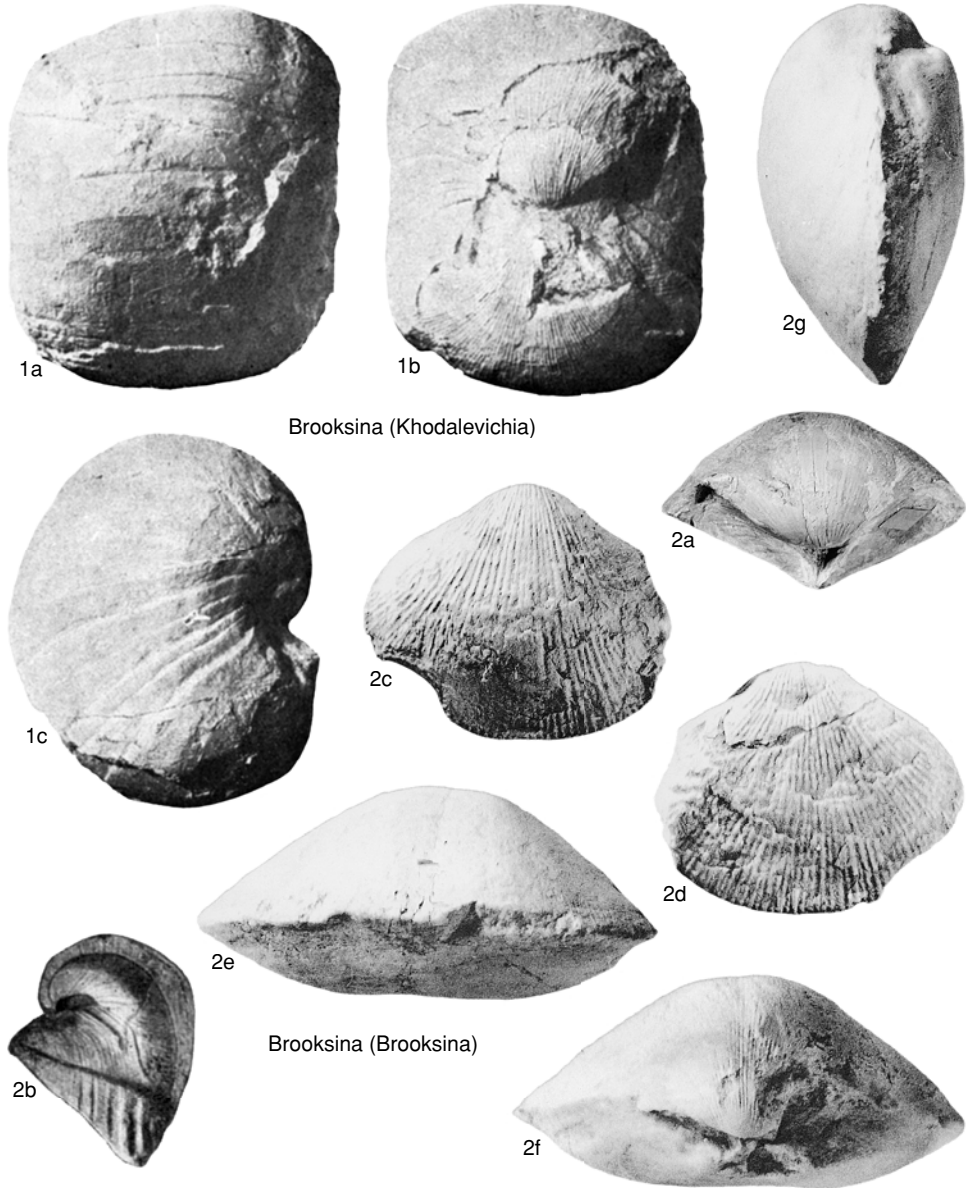


FIG. 654. Pentameridae (p. 975–976).

Bisulcata BOUCOT & JOHNSON, 1979, p. 117 [**B. indianensis*; OD]. Medium; moderately biconvex; costate; shallow sulcus on each valve, moderately long ventral median septum and longer spondylium, hinge plates as in *Kirkidium*. *Silurian* (upper Wenlock–Přídolí): midcontinent North America, Urals.—FIG. 653, 2a–e. **B. indianensis*, Kenneth Limestone, Logansport, Indiana, USA; a–c, anterior, ventral, dorsal views, $\times 2$; d–e, posterior, lateral views, $\times 1.25$ (Boucot & Johnson, 1979).

Brooksina KIRK, 1922, p. 2 [**B. alaskensis*; OD]. Medium; costate; dorsibiconvex with dorsal valve beak strongly curved, extending posteriorly beyond ventral beak, ventral median septum very long, discrete hinge plates. *Silurian* (upper Wenlock–Ludlow): western North America, Urals, Central Asia [Sredni Azii], Kazakhstan, Altai Mountains.
B. (Brooksina). Medium; moderately biconvex. *Silurian* (upper Wenlock–Ludlow): western North America, Urals, Central Asia [Sredni Azii],

- Kazakhstan, Altai Mountains.—FIG. 654, 2a–b. *B. (*B.*) *alaskensis*, Heceta Limestone, Prince of Wales Island, southeastern Alaska, USA; *a*, posterior view, $\times 1$ (Amsden, 1965); *b*, lateral view of interior, $\times 1$ (Kirk, 1922).—FIG. 654, 2c–g. *B. (*B.*) striata*, Striatum Stage [Gorizont], eastern slope of northern Urals, Russia; *c–d*, dorsal, ventral views, $\times 2$; *e–g*, anterior, posterior, lateral views, $\times 1.5$ (Boucot & Johnson, 1979).
- B. (*Khodalevichia*)** BOUCOT & JOHNSON, 1979, p. 116 [**Brooksina*(?) *crassa* KHODALEVICH, 1939, p. 35; OD]. Very inflated, almost hemispherical valves, ventribiconvex. *Silurian* (*Ludlow*): Urals.—FIG. 654, 1a–c. *B. (*K.*) *crassa* (KHODALEVICH), Striatum Stage [Gorizont], Isovsk Region, eastern Urals; anterior, posterior, lateral views, $\times 1$ (Khodalevich, 1939).
- Capelliniella** STRAND, 1928, p. 38, *nom. nov. pro Capellinia* HALL & CLARKE, 1893, p. 249, *non* TRICHESE, 1874 [**Capellinia mira* HALL & CLARKE, 1893, p. 249; OD]. Smooth; dorsibiconvex; not markedly trilobate; very long ventral median septum, hinge plates as in *Pentamerus*. *Silurian* (*upper Wenlock–Ludlow*): North America, Urals, Central Asia [Sredni Azii], Malaysia.—FIG. 655, 1a–d. *C. *mira* (HALL & CLARKE), Racine Formation, Racine, Wisconsin, USA; dorsal, ventral, posterior, lateral views, $\times 1$ (Boucot & Johnson, 1979).
- Eokirkidium** KHODALEVICH & SAPELNIKOV, 1970, p. 196 [**E. jachteljaensis*; OD]. Strongly biconvex; finely costate; no ventral median septum, dorsal interior as in *Kirkidium*. *Silurian* (*upper Wenlock–Ludlow*): Urals, Altai Mountains, Central Asia [Sredni Azii], Kazakhstan.—FIG. 655, 2a–e. *E. *jachteljaensis*, Striatum Stage [Gorizont], Ivdel region, eastern slope of northern Urals; ventral, ventral, lateral, anterior, dorsal views, $\times 1$ (Khodalevich & Sapelnikov, 1970).
- Harpidium** KIRK, 1925, p. 1 [**H. insignis*; OD]. Smooth; nontrilobate; strongly ventribiconvex; dorsal interior as in *Pentamerus*. *Silurian* (*middle Aeronian–Ludlow*): North America, Europe, Asia.
- H. (*Harpidium*)**. Ventral median septum very short; long spondylium. *Silurian* (*upper Aeronian–Ludlow*): North America, Urals, Asia.—FIG. 656, 1a–f. *H. (*H.*) *insignis*, Heceta Limestone, Prince of Wales Island, Alaska, USA; side view of interior, ventral, lateral, lateral, posterior, anterior views, $\times 1$ (Kirk, 1925).
- H. (*Isovelia*)** BREIVEL & BREIVEL in ANTSIGIN & others, 1970, p. 52 [**I. regina*; OD] [= *Carmanella* BOUCOT in BERRY & BOUCOT, 1970, p. 30, *nom. nud.*; *Apopentamerus* BOUCOT & JOHNSON, 1979, p. 104 (type, *A. racinensis*; OD)]. Large; marked umbonal thickenings in ventral posterior region; ventral median septum moderately long. *Silurian* (*upper Aeronian–Ludlow*): midcontinent North America, Urals, China.—FIG. 657a–d. *H. (*I.*) *regina*, Wenlock, Isovsk region, eastern slope of central Urals; ventral, posterior, lateral, ventral views, $\times 1$ (Antsigin & others, 1970).—FIG. 657e–g. *H. (*I.*) maquoketa*, Hopkinton Dolomite, Jones County, Iowa, USA; ventral view of interior, lateral view of internal mold, posterior view of internal mold, $\times 1$ (Boucot & Johnson, 1979).
- H. (*Sulcipientamerus*)** ZENG, 1987, p. 240 [**S. sulcus*; OD]. Large; elongate; unevenly biconvex with dorsal valve gently convex to weakly concave, sulcate anteriorly in some specimens, ventral valve deep; ventral fold; unisulcate anterior margin; short ventral median septum. *Silurian* (*middle Aeronian–upper Aeronian*): Yangtze Gorge region.—FIG. 656, 2a–d. *H. (*S.*) *sulcus*, central China; anterior, lateral, ventral, dorsal views, $\times 1$ (Zeng, 1987).
- Jolvía** SAPELNIKOV, 1960b, p. 56 [**J. multiplexa* SAPELNIKOV, 1960b, p. 58; OD]. Low, broad costae variably present; long median septum, ventribiconvex; variably developed ventral fold and dorsal sulcus, massive cardinal process commonly developed. *Silurian* (*upper Llandovery–lower Wenlock*): eastern slope Urals.—FIG. 653, 1a–i. *J. *multiplexa*, basal Wenlock, Novo-Lialinsk region; *a–c*, ventral, dorsal, lateral views, $\times 1$; *d–i*, serial sections, $\times 0.875$ (Sapelnikov, 1960b).
- Kirkidium** AMSDEN, BOUCOT, & JOHNSON, 1967, p. 865 [**Pentamerus knighti* J. SOWERBY, 1813 in 1812–1815, p. 73; OD] [= *Prækirkidium* BREIVEL & BREIVEL, 1988, p. 54 (type, *P. uncinus*, OD)]. Coarsely costate; unequally biconvex with ventral valve deeper; nontrilobate, long ventral median septum, hinge plates as in *Pentamerus*, crura very prominent. *Silurian* (*upper Wenlock–Pridoli*): North America, Europe, Asia, Australia.
- K. (*Kirkidium*)**. Strongly biconvex. *Silurian* (*upper Wenlock–Pridoli*): North America, Europe, Asia, Australia.—FIG. 658, 2a–c. *K. (*K.*) *knighti*, Aymestry Limestone, England; *a–b*, lateral, lateral view of interior, $\times 0.67$; *c*, posterior view, $\times 1$ (Murchison, 1839).
- K. (*Bateridium*)** SU, RONG, & LI, 1985, p. 84 [**B. bateroboensis*; OD]. Large; biconvex; nonlobate *Kirkidium* with fine costae; thin, long median septum reaching almost to anterior margin and supporting somewhat short, narrow spondylium; inner hinge plates parallel, extending anteriorly about two-thirds length of dorsal valve; median flangelike ridges on lateral faces of hinge plates. *Silurian* (*Wenlock–Ludlow*): North China, central Urals.—FIG. 659a–f. *K. (*B.*) *bateroboensis*, Bateaobao Formation, Bateaobao, Inner Mongolia; posterior view of internal mold, lateral view of interior, lateral view of interior, lateral, ventral view of internal mold, dorsal view of internal mold, $\times 1$ (Su, Rong, & Li, 1985).
- K. (*Pinguella*)** BOUCOT & JOHNSON, 1979, p. 114 [**Rhipidium pingue* AMSDEN, 1949a, p. 47; OD]. Medium to large; moderately biconvex. *Silurian* (*upper Wenlock–Pridoli*): North America, Europe, Asia, Australia.—FIG. 658, 1a–i. *K. (*P.*) *pingue* (AMSDEN), Brownsport Formation, western Tennessee, USA; *a–e*, ventral, dorsal, ventral,

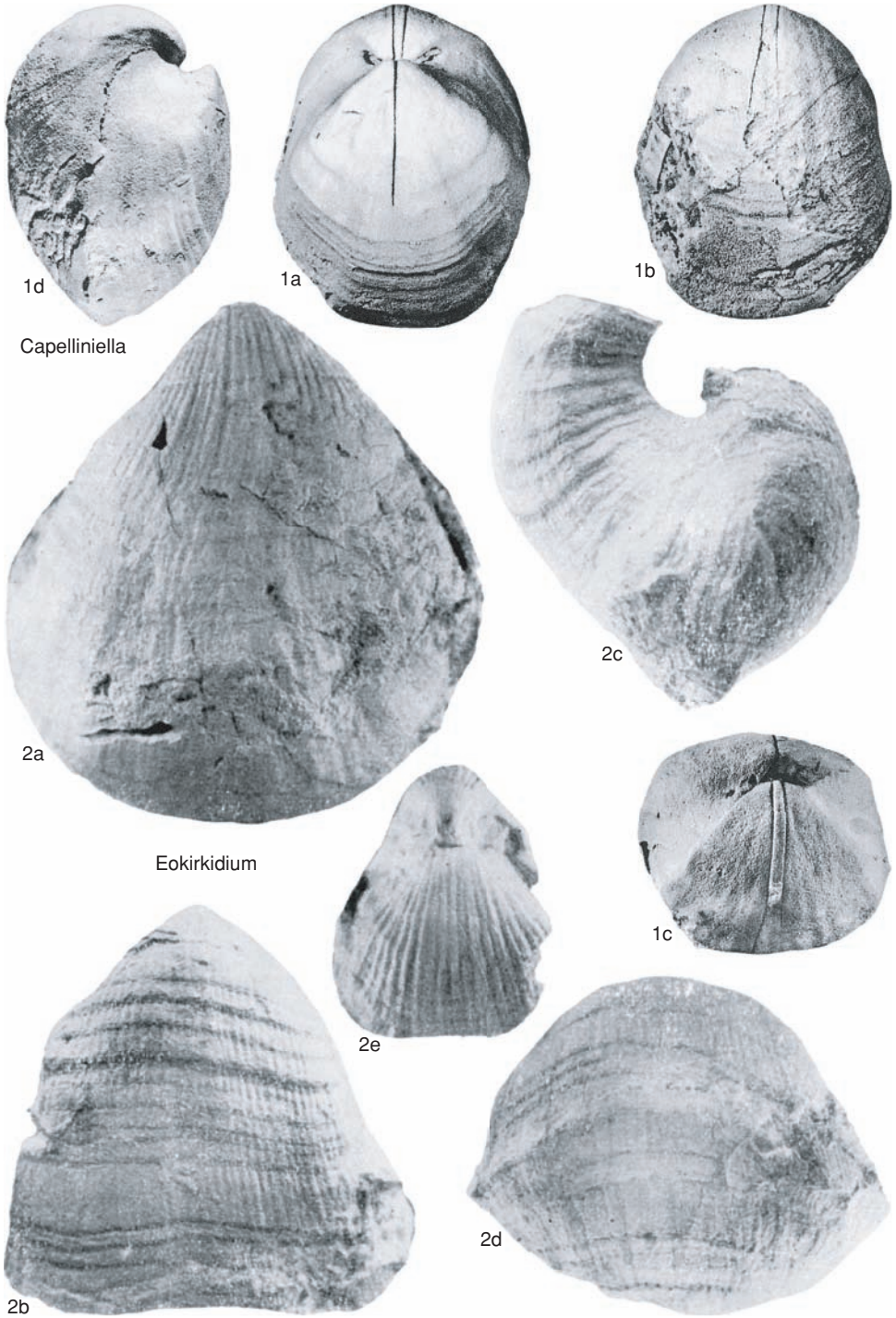


FIG. 655. Pentameridae (p. 976).

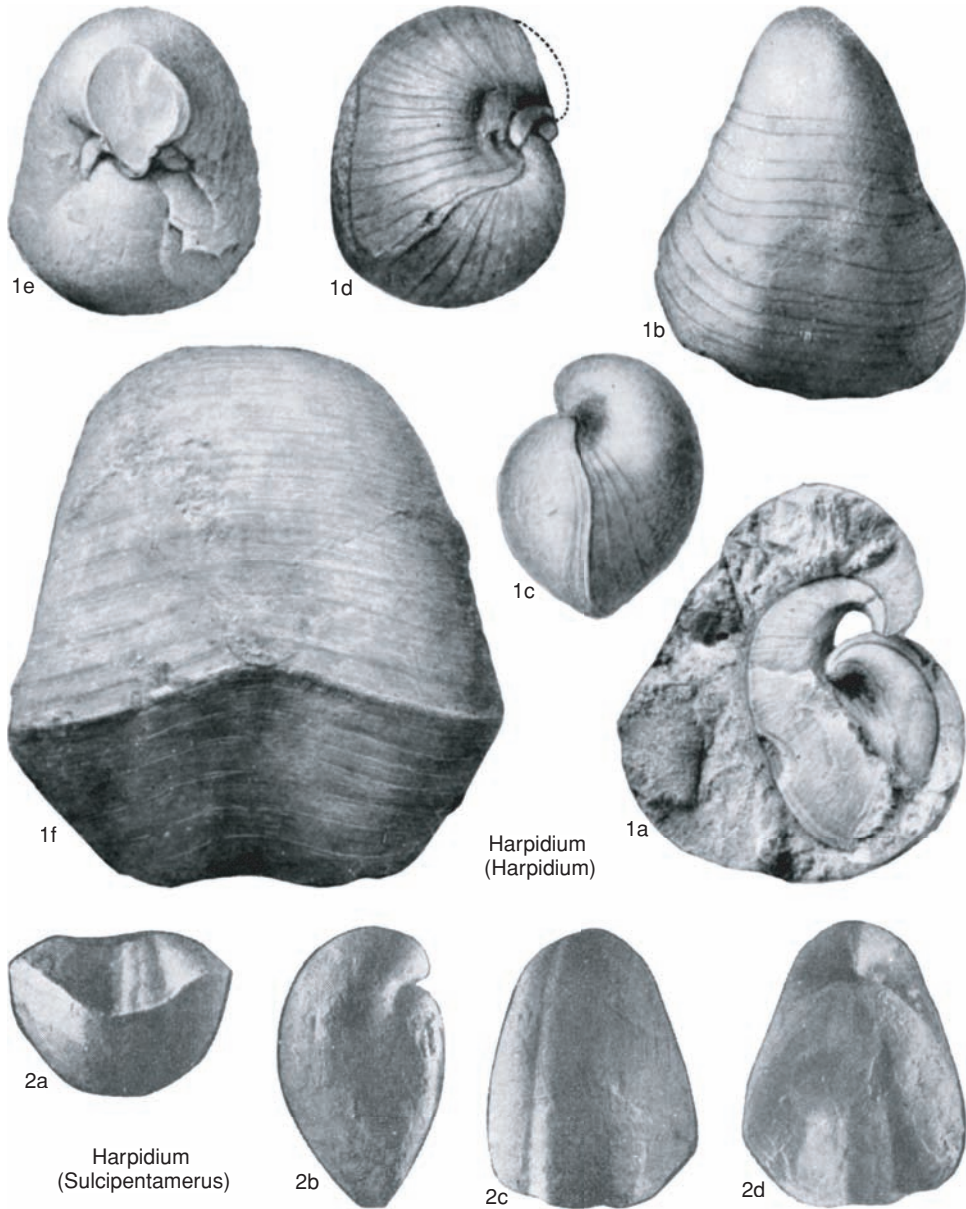


FIG. 656. Pentameridae (p. 976).

posterior, anterior views, $\times 2$; *f-g*, posterior, lateral views, $\times 1.5$; *b*, ventral view, $\times 1$; *i*, impression of dorsal interior, $\times 1$ (Boucot & Johnson, 1979).

Lissocoelina SCHUCHERT & COOPER, 1931, p. 248 [**Pentamerus pergibbosus* HALL & WHITFIELD, 1875, p. 139; OD]. Medium to large; very deep ventral

valve; radial costellae poorly developed anteriorly, very long ventral median septum. *Silurian* (*upper Wenlock-Ludlow*): midcontinent North America.

—FIG. 660*a-h*. **L. pergibbosa* (HALL & WHITFIELD), Racine Dolomite, Hawthorne, Illinois, USA; *a-e*, dorsal, ventral, anterior, lateral, lateral views, $\times 1$ (Boucot & Johnson, 1966*b*); *f-h*,

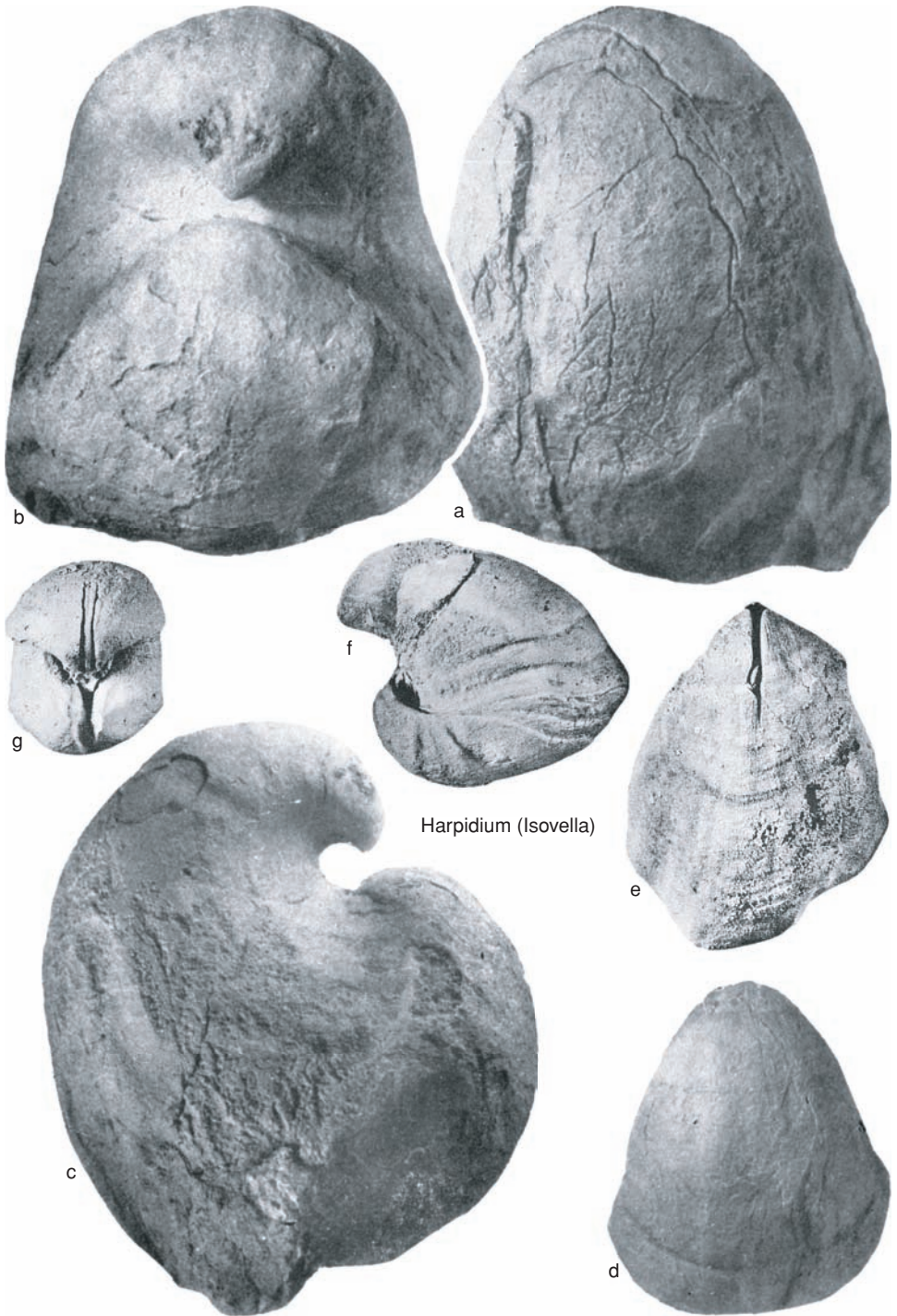


FIG. 657. Pentameridae (p. 976).

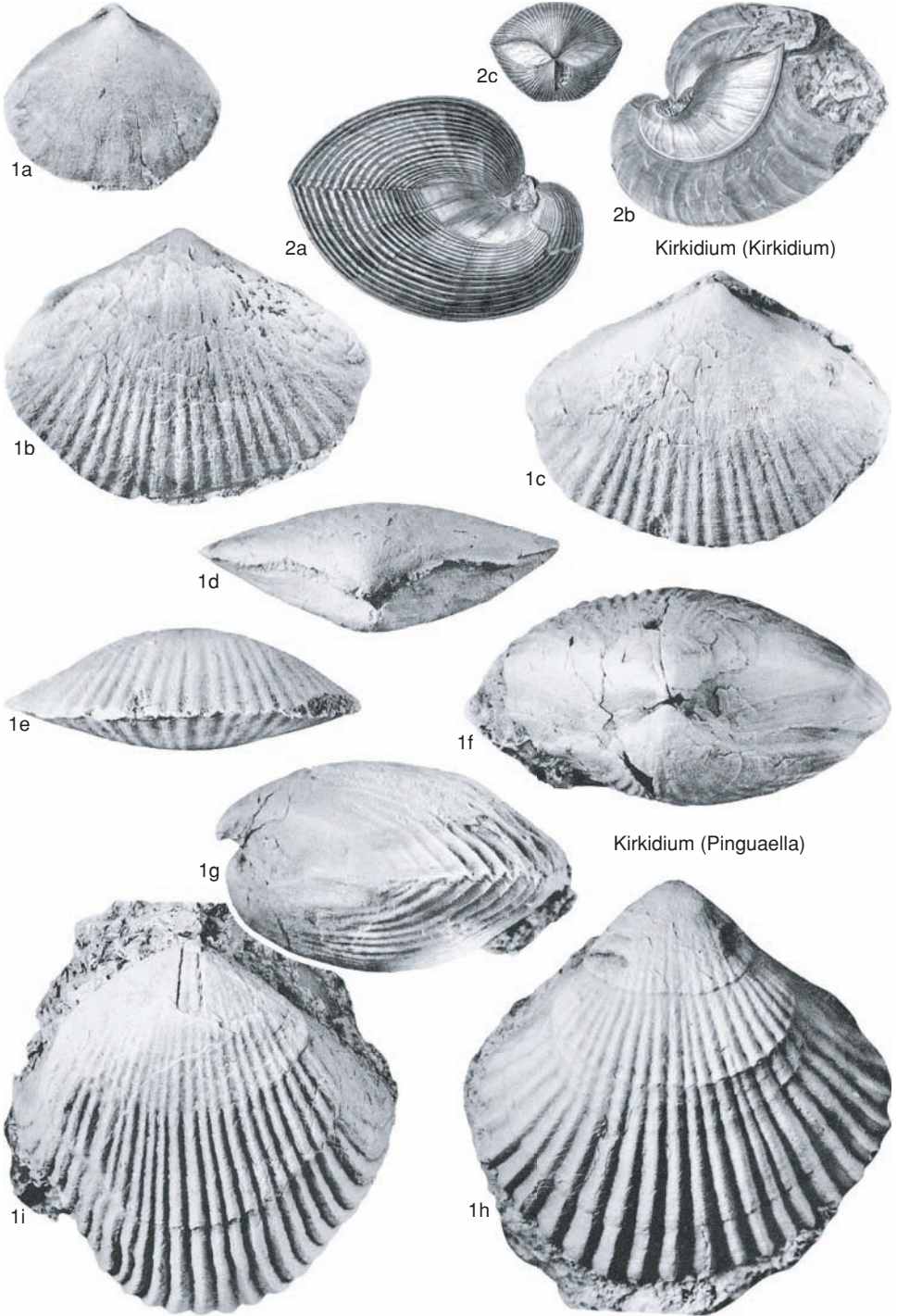
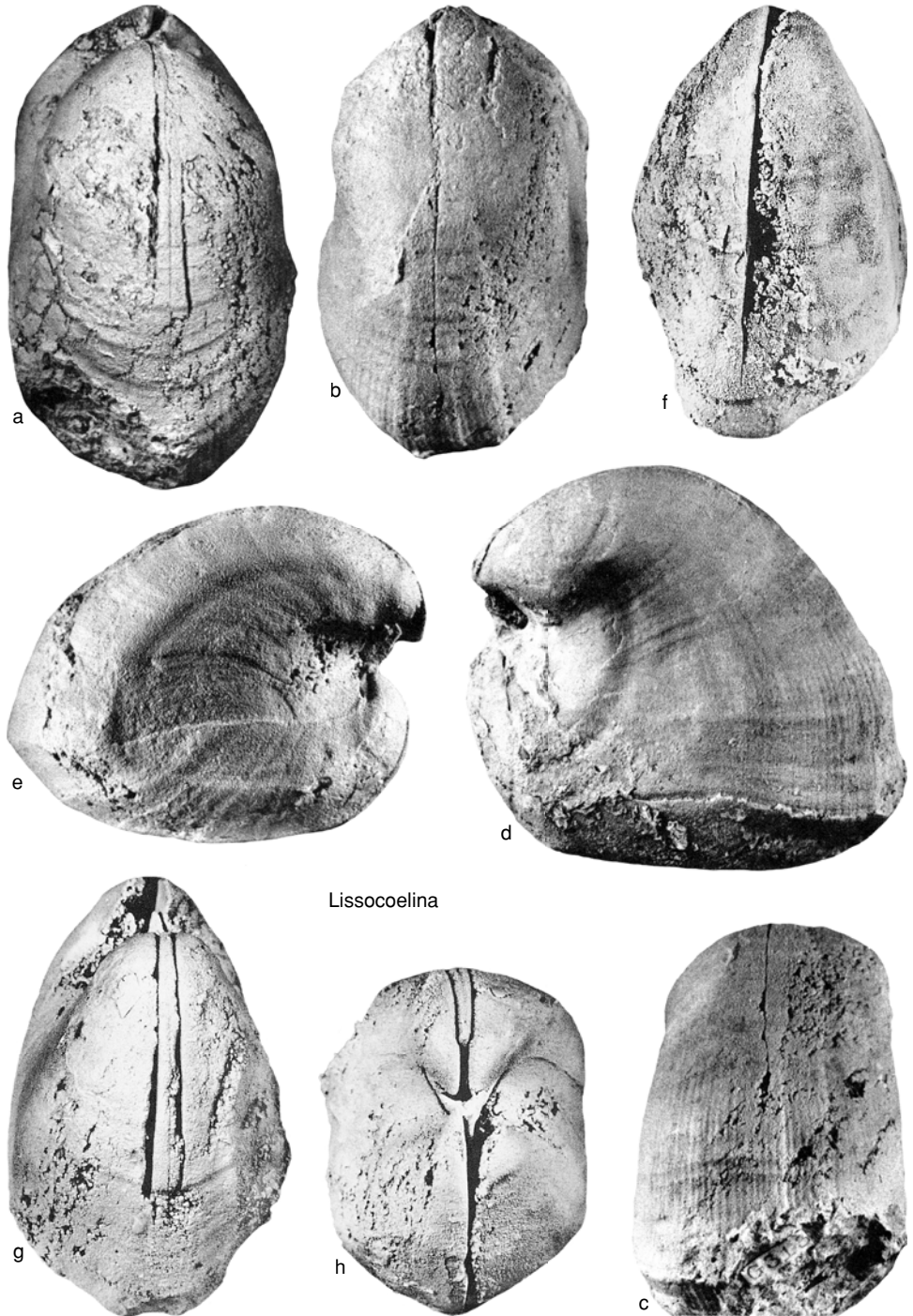


FIG. 658. Pentameridae (p. 976–979).



FIG. 659. Pentameridae (p. 976).



Lissocoelina

FIG. 660. Pentameridae (p. 978–983).

- impression of ventral interior, impression of dorsal interior, impression of posterior interior, $\times 1$ (Boucot & Johnson, 1979).
- Nanukidium** JONES, 1979, p. 1261 [*Rossella arctica* JONES, 1978, p. 547; OD; *non Rossella* CARTER, 1872]. Medially directed carinae support inner extensions of crura; otherwise similar to *Kirkidium*, ventral median septum very long. *Silurian* (*Ludlow-lower Pridoli*): Canadian Arctic, USA (southeastern Alaska).—FIG. 661,2a–d. **N. arctica* (JONES), Read Bay Formation, Somerset Island, Arctic Canada; a–c, ventral, dorsal, lateral views; d, serial section, $\times 1$ (Jones, 1978).
- Pentamerifera** KHODALEVICH, 1939, p. 22 [**Pentamerus taltiensis* CHERNYSHEV, 1893, p. 183; OD]. Smooth; ventral median septum very long, almost extending to anterior margin; nontrilobate, ventribiconvex, dorsal interior as in *Pentamerus*. *Silurian* (*Ludlow*): USA (Nevada), Urals, Central Asia [Sredni Azi], northwestern China.—FIG. 661,1a–d. **P. taltiensis* (CHERNYSHEV), Striatum Stage [Gorizont], Ivdel region, eastern slope Urals; ventral, dorsal, lateral, lateral of interior, $\times 1$ (Khodalevich, 1939).
- Pentameroides** SCHUCHERT & COOPER, 1931, p. 248 [**Pentamerus subrectus* HALL & CLARKE, 1893, p. 238; OD]. Smooth to chevronlike ornamentation, inner hinge plates fused to form a cruralium supported by a median septum. *Silurian* (*upper Llandovery–upper Wenlock*).
- P. (Pentameroides)**. Smooth; lenticular; trilobate; external homeomorph of *Pentamerus*. [Type material unsuitable for illustration.] *Silurian* (*upper Llandovery–upper Wenlock*): North America, Europe.—FIG. 662a–f. *P. (P.)* sp.; a–e, ventral, dorsal, lateral, posterior, anterior views of internal impression, Schoolcraft Dolomite?, Calumet County, Wisconsin, USA, $\times 1$ (Boucot & Johnson, 1979); f, serial section, Meritton Limestone, Thorold, Ontario, Canada (Gauri & Boucot, 1968).
- P. (Callipentamerus)** BOUCOT, 1964a, p. 887 [**Pentamerus corrugatus* WELLER & DAVIDSON, 1896, p. 173; OD]. Variably ornamented with chevronlike corrugations; otherwise similar to *Pentameroides*. *Silurian* (*upper Llandovery–lower Wenlock*): midcontinent North America.—FIG. 663,2a–f. **P. (C.) corrugatus* (WELLER & DAVIDSON), Hopkinton Dolomite, Monticello, Iowa, USA; dorsal, posterior, ventral, lateral, dorsal, ventral views, $\times 1$ (Boucot, 1964a).
- P. (Reveroides)** SAPELNIKOV, 1976, p. 32 [**P. jolvensis* SAPELNIKOV, 1961a, p. 103; OD] [= *Sapelnikovia* BOUCOT & JOHNSON, 1979, p. 118, homonym]. Smooth; bisulcate; anteriorly or posteriorly conjunct inner hinge plates, inner hinge plates separate posteriorly, becoming conjunct anteriorly; spondylium and median septum of equal length. *Silurian* (*upper Llandovery–Wenlock*): Ontario, northern Greenland, Urals, Altai Mountains, Canadian Arctic.—FIG. 663,1a–c. **P. (R.) jolvensis* SAPELNIKOV, basal Wenlock, Novo-Lialinsk region, eastern slope of central Urals; ventral internal mold, dorsal internal mold, lateral view, $\times 1$ (Sapelnikov, 1961a).
- Rhipidium** SCHUCHERT & COOPER, 1931, p. 249 [**Pentamerus knappi* HALL & WHITFIELD, 1872, p. 184; OD]. Finely to coarsely costate; faintly to very trilobate, discrete inner hinge plates, median septum about half valve length. *Silurian* (*Wenlock–Ludlow*): North America, Europe.
- R. (Rhipidium)**. Coarsely costate; moderately biconvex; faintly trilobate to nontrilobate. *Silurian* (*upper Wenlock*): midcontinent North America.—FIG. 664a–e. **R. (R.) knappi* (HALL & WHITFIELD), Louisville Formation, Kentucky, USA; ventral, dorsal, lateral, posterior, anterior views, $\times 1$ (Boucot & Johnson, 1979).
- R. (Ectorhipidium)** BOUCOT & JOHNSON, 1979, p. 102 [**Conchidium trilobatum* KINDLE & BREGER in KINDLE, 1904, p. 436; OD]. Very large, costate, anteriorly bifurcating; elongate, lenticular; very strongly trilobate. *Silurian* (*Ludlow*): midcontinent North America.—FIG. 665a–c. **R. (E.) trilobatum* (KINDLE & BREGER), Wabash Formation, Huntington, Indiana, USA; ventral, anterior, and lateral views of internal impressions, $\times 1$ (Boucot & Johnson, 1979).—FIG. 666a–c. **R. (E.) trilobatum* (KINDLE & BREGER), Wabash Formation, Huntington, Indiana, USA; posterior, posterior, and ventral views of internal impressions, $\times 1$ (Boucot & Johnson, 1979).
- R. (Pararhipidium)** BOUCOT & JOHNSON, 1979, p. 101 [**Pentamerus tenuistriatus* LINDSTRÖM in ANGELIN & LINDSTRÖM, 1880, p. 24; OD]. Finely costate; elongate-pyriform, lenticular; faintly trilobate to nontrilobate. *Silurian* (*upper Wenlock–Ludlow*): North America, Sweden, Urals, Kazakhstan, Malaysia.—FIG. 667a–d. **R. (P.) tenuistriatum* (LINDSTRÖM), Gotland, Sweden; a–c, lateral, dorsal, ventral views, Slite beds, Färo, $\times 1$ (Boucot & Johnson, 1979); d, serial section, Slite Group, Eskelhem, $\times 30$ (Gauri & Boucot, 1968).
- Stenopentamerus** BOUCOT & JOHNSON, 1979, p. 111 [**Pentamerus oblongus* var. *compressa* KINDLE & BREGER in KINDLE, 1904, p. 437; OD]. Smooth, strongly biconvex and very laterally compressed, very long ventral median septum. *Silurian* (*upper Wenlock–Ludlow*): midcontinent North America, Kazakhstan.—FIG. 668,1a–e. **S. compressa* (KINDLE & BREGER), Racine Dolomite, Cook County, Illinois, USA; lateral view of ventral, lateral, posterior, ventral posterior, dorsal interior view, $\times 1$ (Boucot & Johnson, 1979).
- Twenhofelia** BOUCOT & SMITH, 1978, p. 271 [**Stricklandia exploitensis* SHROCK & TWENHOFEL, 1939, p. 260, *pars*; OD]. Subcircular; costellate, with some costae anteriorly bifurcating; ventribiconvex; conjunct inner hinge plates form base of cruralium. *upper Silurian*: Canada (Newfoundland).—FIG. 668,2a–e. **T. exploitensis* (SHROCK & TWENHOFEL), Upper Black Island Marble, Bay of Exploits region, northern Newfoundland; a, ventral view, $\times 1.5$; b, ventral view, $\times 1$; c, dorsal view, $\times 1$; d, ventral



FIG. 661. Pentameridae (p. 983).

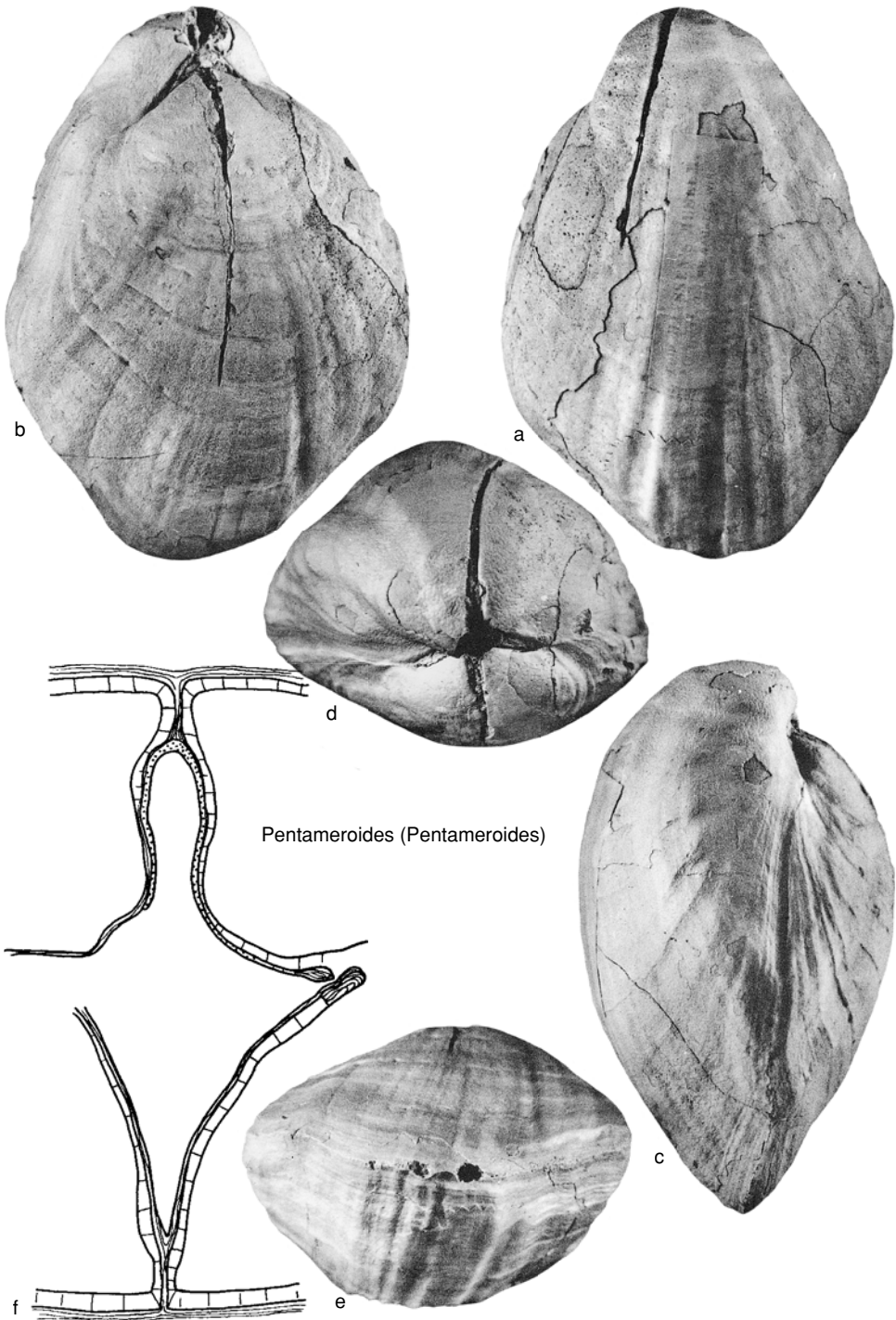


FIG. 662. Pentameridae (p. 983).

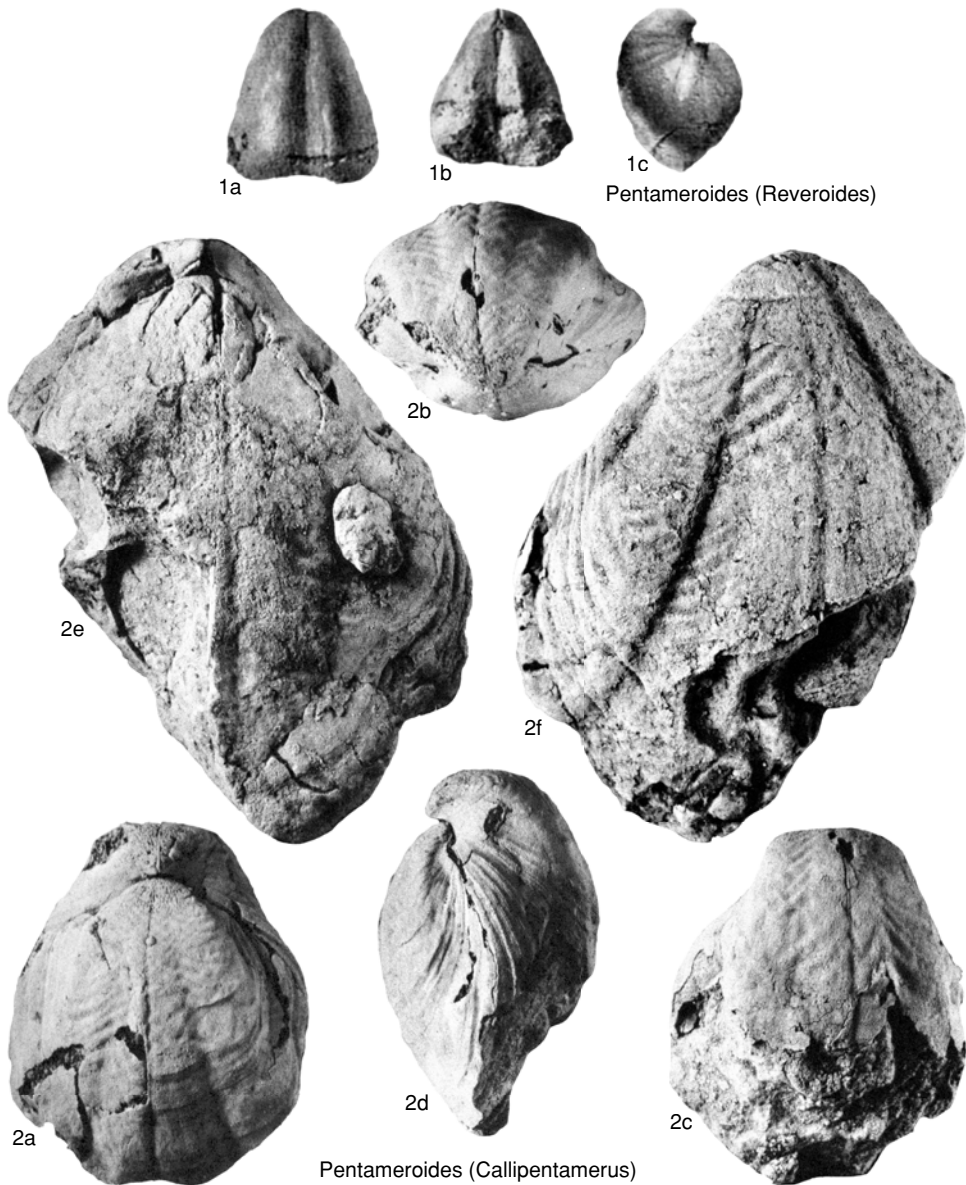


FIG. 663. Pentameridae (p. 983).

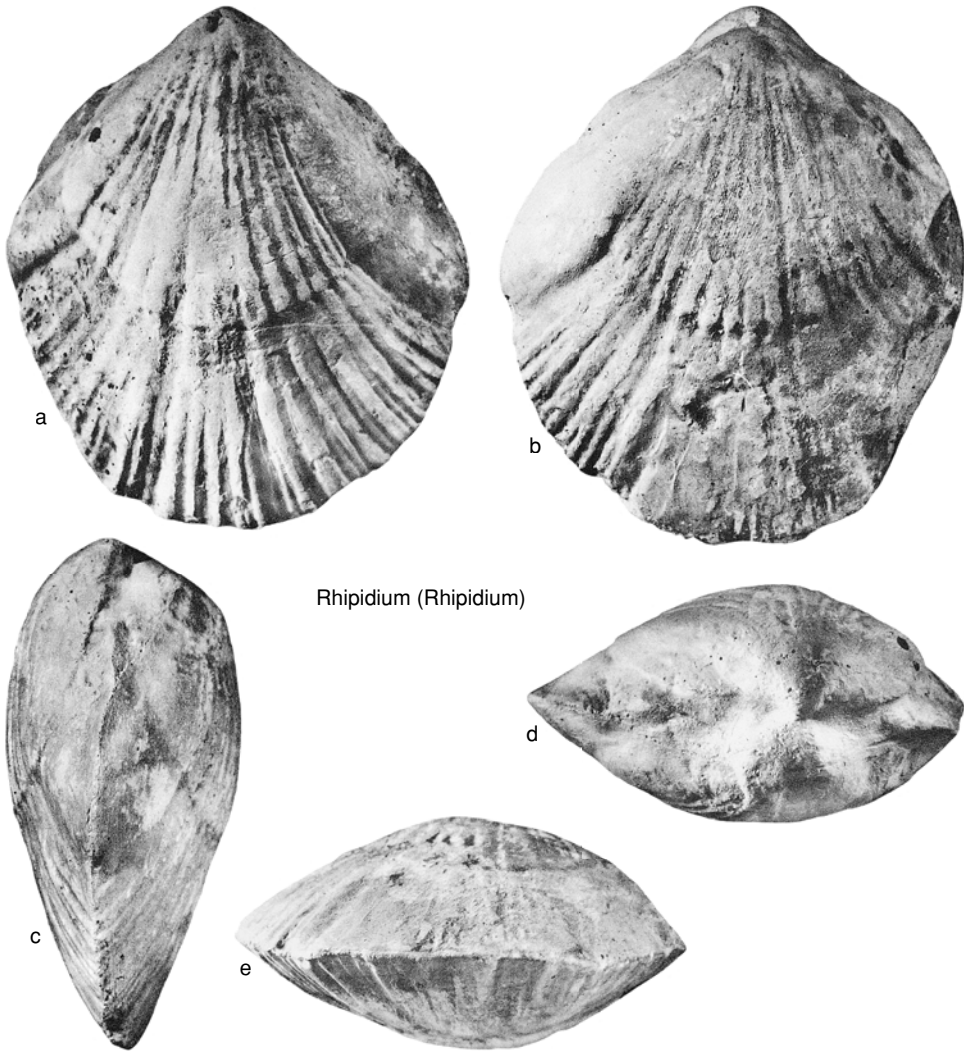
posterior, $\times 2$; *e*, dorsal view, $\times 1.1$ (Boucot & Smith, 1978).

Family SUBRIANIDAE Sapelnikov, 1963

[*nom. transl.* BOUCOT, RONG, & BLODGETT, herein, *ex* Subrianiinae SAPELNIKOV, 1963a, p. 65]

Hinge plates relatively short, usually one-third or much less than dorsal valve length;

prominent, medially projecting, subcylindrical, crural bases converge in dorsal direction toward plane of symmetry; inner hinge plates laterally inclined basally; outer hinge plates laterally inclined distally; deltidium and cardinal process may be present; ventral median septum. *Silurian* (*Wenlock–Ludlow*): Eurasia, North America, Australia.



Rhipidium (Rhipidium)

FIG. 664. Pentameridae (p. 983).

Subfamily SUBRIANINAE
Sapelnikov, 1963

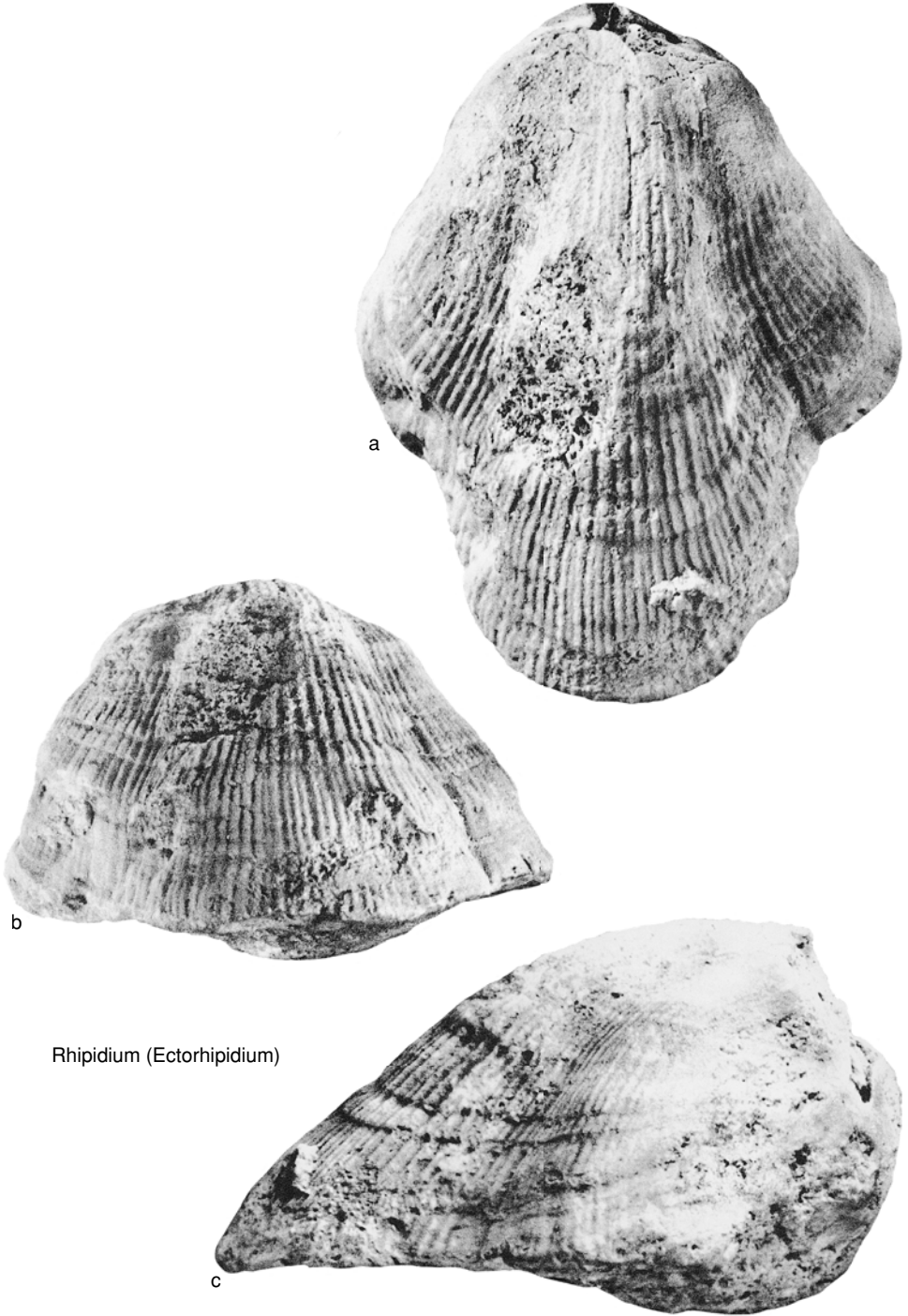
[Subrianinae SAPELNIKOV, 1963a, p. 65]

Cardinalia very short, inner hinge plates submerged in secondary shell material, outer hinge plates very short. *Silurian* (Wenlock–Ludlow): Urals.

Subriana SAPELNIKOV, 1960a, p. 111 [**S. subrini*; OD]. Medium, transverse; few, angular, coarse plicae; biconvex with ventral valve deeper; free spondylium; strongly unisulcate; outer hinge plates projecting

anteriorly beyond very short inner hinge plates submerged in secondary tissue; crura present. *Silurian* (lower Ludlow): Urals.—FIG. 669, 1a–d. **S. subrini*, upper Wenlock, Istok River, eastern Urals; ventral, dorsal, lateral, anterior views, $\times 1$ (Sapelnikov, 1960a).

Vagranella SAPELNIKOV, 1960a, p. 116 [**V. diversoplicata*; OD]. Small to medium; costate to costelate; short, free spondylium and no median septum; cardinalia and ventral interior similar to *Subriana*. *Silurian* (Wenlock–Ludlow): Urals.—FIG. 669, 2a–m. **V. diversoplicata*, Isovsk Stage [Gorizont], Istok River, eastern slope of Urals; a–c, ventral, dorsal views, $\times 1$ (Sapelnikov, 1972); d–m, serial sections (Sapelnikov, 1985a).



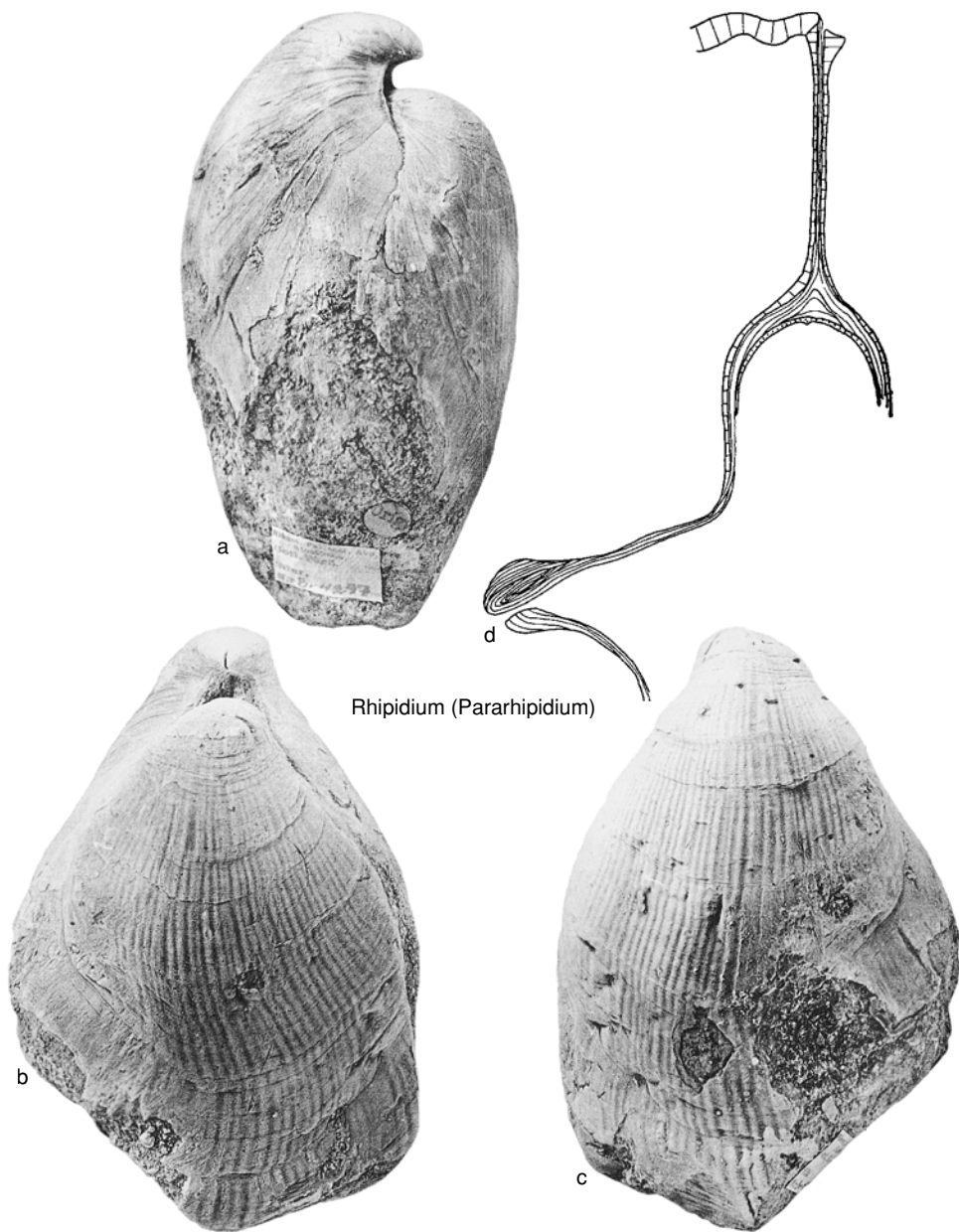
Rhipidium (Ectorhipidium)

FIG. 665. Pentameridae (p. 983).



Rhipidium (Ectorhipidium)

FIG. 666. Pentameridae (p. 983).



Rhipidium (Pararhipidium)

FIG. 667. Pentameridae (p. 983).

Subfamily CONCHIDIINAE
Sapelnikov, 1973

[Conchidiinae SAPELNIKOV, 1973, p. 40]

Relatively short, laterally concave hinge plates unsubmerged by secondary shell ma-

terial. *Silurian* (Wenlock–Ludlow): Eurasia, North America, Australia.

Conchidium OEHLERT, 1887a, p. 1311 [**Anomia bilocularis* HISINGER, 1799, p. 285; OD]. Medium; subcircular to elongate; costellate, commonly anteriorly bifurcating; unequally biconvex with ventral

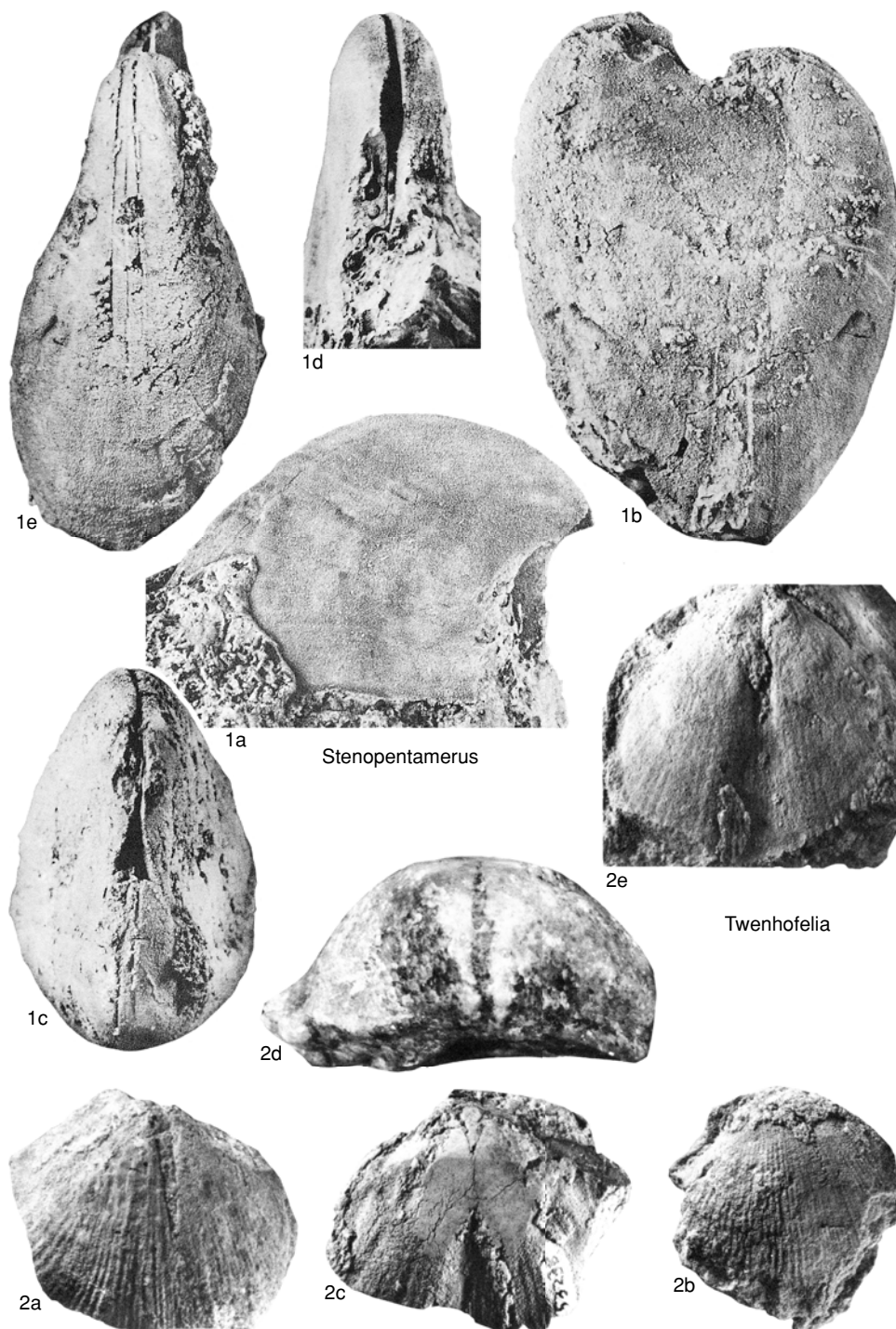


FIG. 668. Pentameridae (p. 983–986).

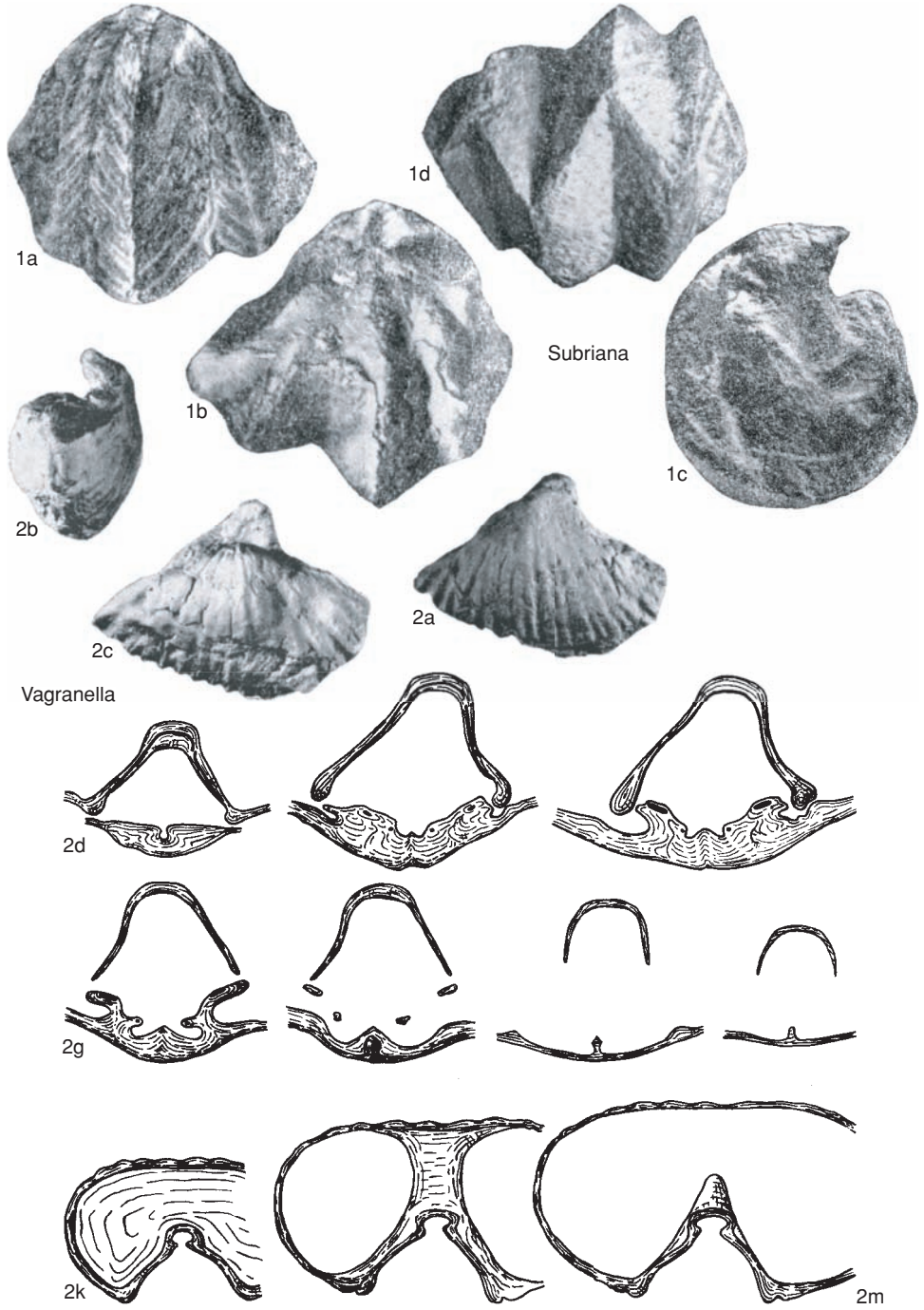


FIG. 669. Subrianiidae (p. 987).

- valve deeper; well-developed median septum and spondylium; outer hinge plates laterally inclined basally, inner hinge plates laterally inclined distally; crural bases variably projecting medially. *Silurian* (*upper Wenlock–Ludlow*): Eurasia, North America.—FIG. 670, 1a–g. **C. bilocularis* (HISINGER), Klinteberg Group, Klinteberget, Gotland, Sweden; a–b, dorsal, posterior views, $\times 1$; c, ventral interior, $\times 1.5$ (Schuchert & Cooper, 1932); d–e, lateral, ventral views, $\times 1$ (Amsden, 1965); f, dorsal interior, $\times 2$; g, cross section of dorsal shell, $\times 6$ (Amsden, Boucot, & Johnson, 1967).
- Aliconchidium** ST. JOSEPH, 1942, p. 247 [**A. yassi*; OD]. Medium to large; elongate to transverse; large, strongly developed ventral interarea; sulcate to nonsulcate ventral valve; costellate; very twisted beak common; hinge line long to short; internally as in *Conchidium*. *Silurian* (*Ludlow*): eastern Australia.—FIG. 671, 1a–f. **A. yassi*, Bowspring Limestone, Yass area, New South Wales; a–b, ventral, ventrolateral views; c–d, ventral interiors, $\times 1$; e, dorsal interior, $\times 2$; f, dorsal interior, $\times 1$ (Boucot, Johnson, & Link, 1969).
- Cymbidium** KIRK, 1926, p. 2 [**C. acutum*; OD]. Small; subcircular; plicate to costate ornament that may bifurcate; no median septum in ventral valve; unsupported spondylium; cardinalia shorter than in *Conchidium*, otherwise similar. [Type material unsuitable for illustration.] *Silurian* (*Wenlock–Ludlow*): USA (Alaska, Nevada), Arctic Canada.—FIG. 672, 1a–f. *C. imitor*, Roberts Mountains Formation, Birch Creek area, Eureka County, Nevada; a, ventral interior, $\times 3$; b–d, ventral exterior, ventral posterior, ventral anterior, $\times 1.5$; e, ventral interior, $\times 2$; f, dorsal interior, $\times 2$ (Johnson, Boucot, & Murphy, 1976).—FIG. 672, 1g. *C. sp.*, Cape Phillips Formation, Baillie Hamilton Island, Arctic Canada; dorsal interior, $\times 3.3$ (Zhang Ning, 1989a).
- Lamelliconchidium** KULKOV, 1968, p. 38 [**L. tchergense*; OD]. Medium; subcircular to elongate; concentric, lamellose ornamentation; fine costellae may bifurcate anteriorly; cardinalia as in *Conchidium*; medium septum almost reaching anterior margin, supporting spondylium. [Type material unsuitable for illustration.] *Silurian* (*Ludlow*): Altai Mountains (Russia), USA (Nevada).—FIG. 670, 2a–h. *L. micropleura*, Roberts Mountains Formation, Eureka County, Nevada; dorsal posterior, dorsal anterior, dorsal interior, ventral exterior, ventral interior, ventrolateral, anteroventral, dorsal interior, $\times 1.5$ (Johnson, Boucot, & Murphy, 1976).
- Lissidium** LENZ, 1989, p. 1223 [**L. erugatus*; OD]. Smooth; short spondylium free or supported by very short median septum; cardinalia as in *Conchidium*. *Silurian* (*Wenlock–Ludlow*): USA (Nevada), Canada (Northwest Territories).—FIG. 671, 2a–d. **L. erugatus*, Whittaker Formation, southern Mackenzie Mountains, Northwest Territories; ventral interior, ventral exterior, oblique ventral interior, dorsal interior, $\times 2.3$ (Lenz, 1989).—FIG. 671, 2e–g. *L. lissa*, Roberts Mountains Formation, Eureka County, Nevada; e–f, ventral interior, ventral exterior, $\times 3$; g, ventral interior, $\times 4$ (Johnson, Boucot, & Murphy, 1976).
- ?**Plicocoelina** BOUCOT & JOHNSON, 1966b, p. 1038 [**Pentamerus occidentalis* HALL, 1852, p. 341; OD]. Small to medium; posteriorly smooth, costellae bifurcating anteriorly; cap-shaped dorsal valve and very deep ventral valve; cardinalia similar to *Conchidium*; ventral median septum of variable length. *Silurian* (*Ludlow*): midcontinent North America.—FIG. 672, 3a–g. **P. occidentalis* (HALL), Greenfield Dolomite, Wood County, Ohio, USA; a–b, dorsal internal mold, rubber replica of dorsal interior, $\times 2$; c–e, lateral, ventral, posterior views, $\times 1$; f–g, ventral interiors, $\times 2$ (Boucot & Johnson, 1966b).
- Raridium** SAPELNIKOV & MIZENS in SAPELNIKOV, MIZENS, & SHATROV, 1987, p. 56 [**Eoconchidium? rarum* SAPELNIKOV & RUKAVISHNIKOVA, 1975a, p. 67; OD]. Small; subcircular; ventral sulcus and dorsal fold; ventribiconvex; costate; short median septum supporting short spondylium; short hinge plates, with medially directed carinae. *Silurian* (*Ludlow*): Pribalkhash, Kazakhstan.—FIG. 673, 1a–e. **R. rarum* (SAPELNIKOV & RUKAVISHNIKOVA), Akkansk Stage [Gorizont], southeastern Kazakhstan; ventral, dorsal, lateral, anterior, ventral views, $\times 1$ (Sapelnikov & Rukavishnikova, 1975a).
- Severella** SAPELNIKOV, 1963b, p. 15 [**Brooksina* (*S.*) *magnificaformis*; OD]. Small; coarsely costate to costellate; costellae may bifurcate anteriorly; fold or sulcus present alternatively on either valve in separate species; short spondylium and median septum shorter than spondylium; cardinalia as in *Conchidium*. [Type material unsuitable for illustration.] *Silurian* (*Wenlock–Ludlow*): Urals, USA (Nevada).—FIG. 673, 2a–f. *S. munda*, Roberts Mountains Formation, Eureka County, Nevada; a–c, ventral interior, ventral posterior, ventral exterior, $\times 2$; d, dorsal exterior, $\times 1.25$; e, dorsal interior, $\times 2$; f, dorsal interior, $\times 5$ (Johnson, Boucot, & Murphy, 1976).
- Spondylopyxis** JOHNSON, BOUCOT, & MURPHY, 1976, p. 47 [**S. ignotus*; OD]. Smooth; undulating, irregular, rugose concentric markings; subcircular; spondylium supported by median septum, short in small specimens, long in large specimens; lenticular lateral profile; cardinalia as in *Conchidium*. *Silurian* (*Ludlow*): USA (Nevada), Arctic Canada.—FIG. 672, 2a–f. **S. ignotus*, Roberts Mountains Formation, Eureka County, Nevada; a, ventral exterior, $\times 3$; b–d, posterior, ventral exterior, dorsal exterior, $\times 6$; e, dorsal interior, $\times 8$; f, ventral interior, $\times 4$ (Johnson, Boucot, & Murphy, 1976).
- Vosmiverstum** BREIVEL & BREIVEL in ANTSIGIN & others, 1970, p. 54 [**Conchidium triquetrum* SAPELNIKOV, 1961b, p. 47; OD]. Similar to *Conchidium* except for its relatively short spondylium and

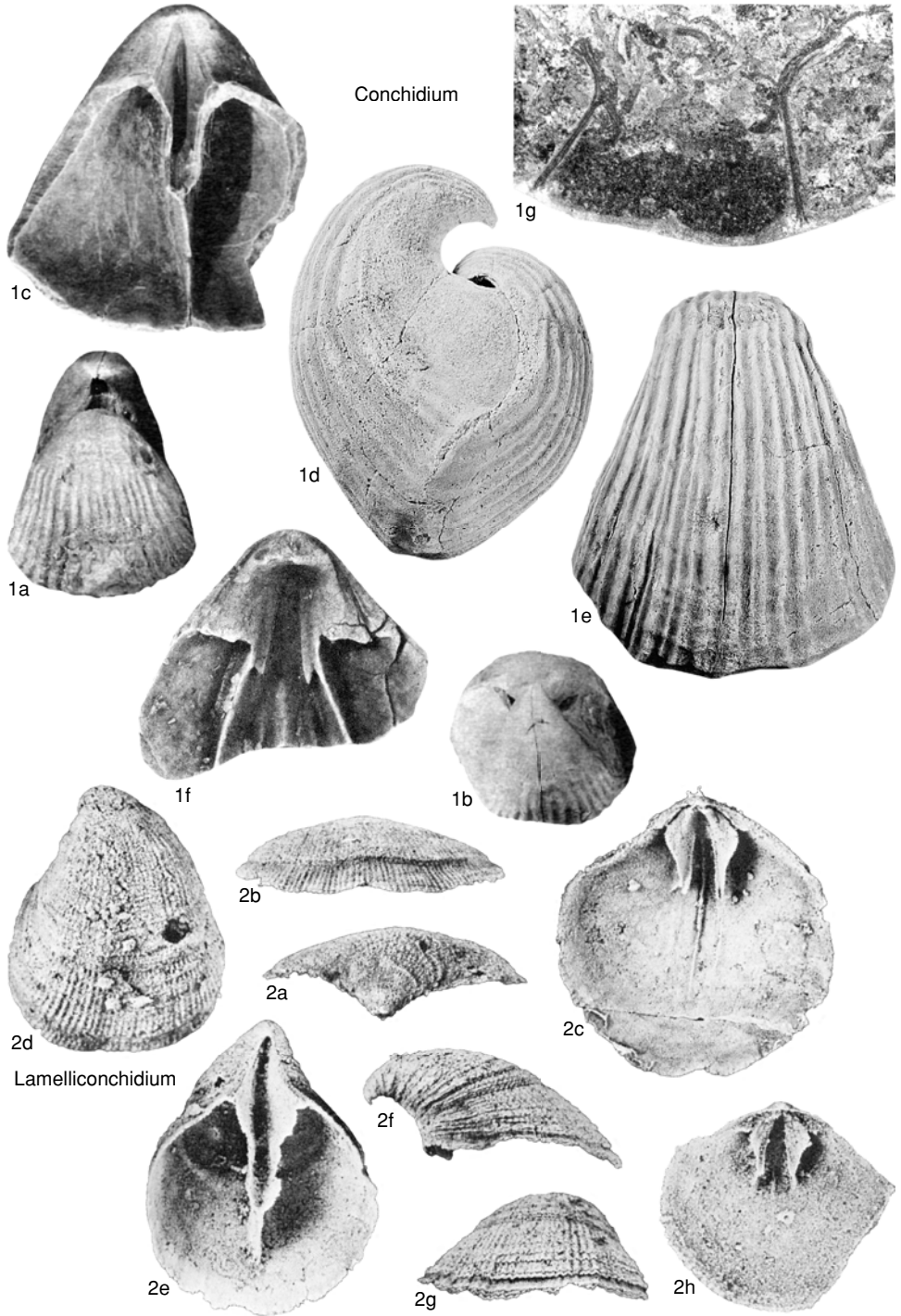


FIG. 670. Subrianidae (p. 990–993).

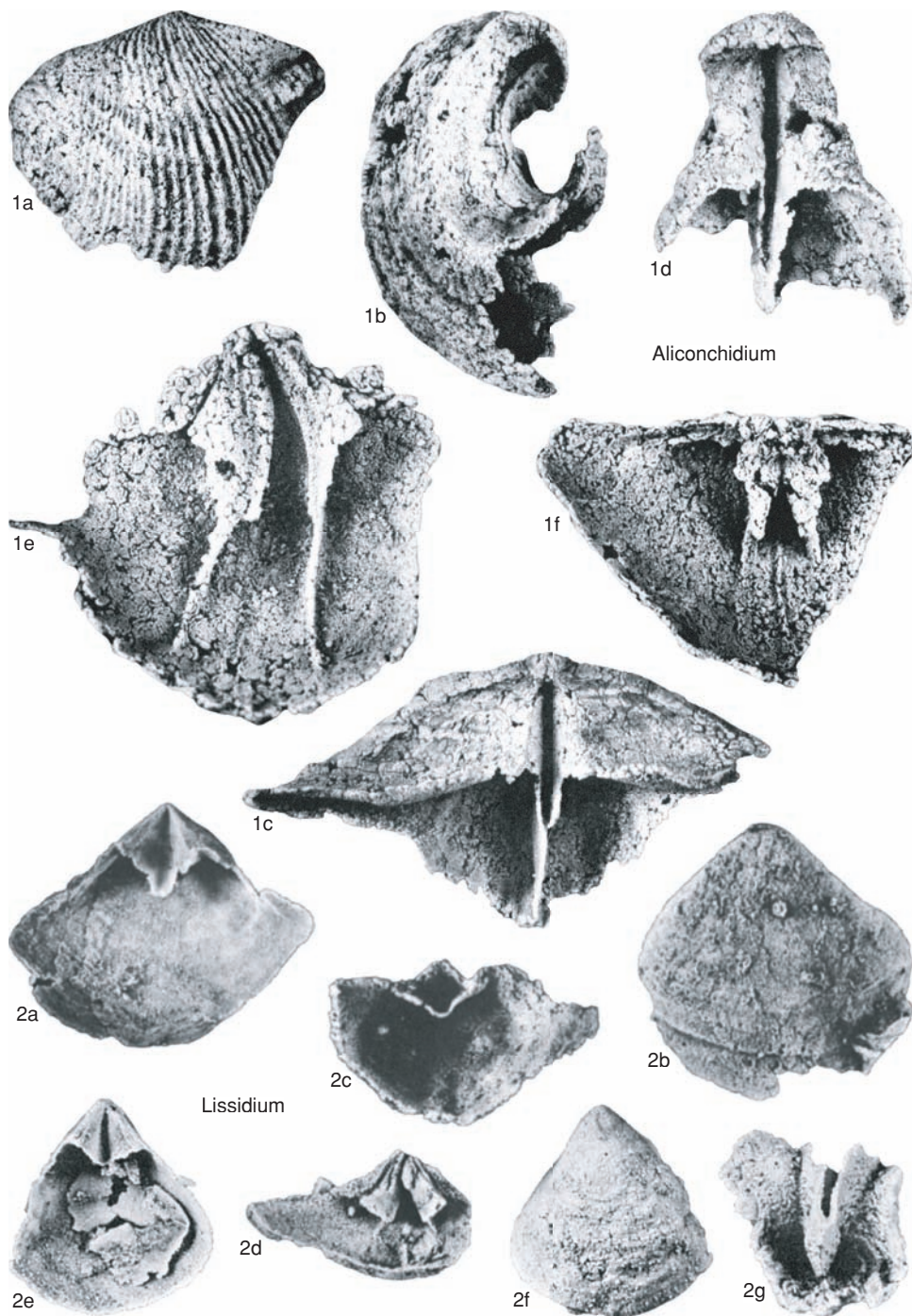


FIG. 671. Subrianidae (p. 993).

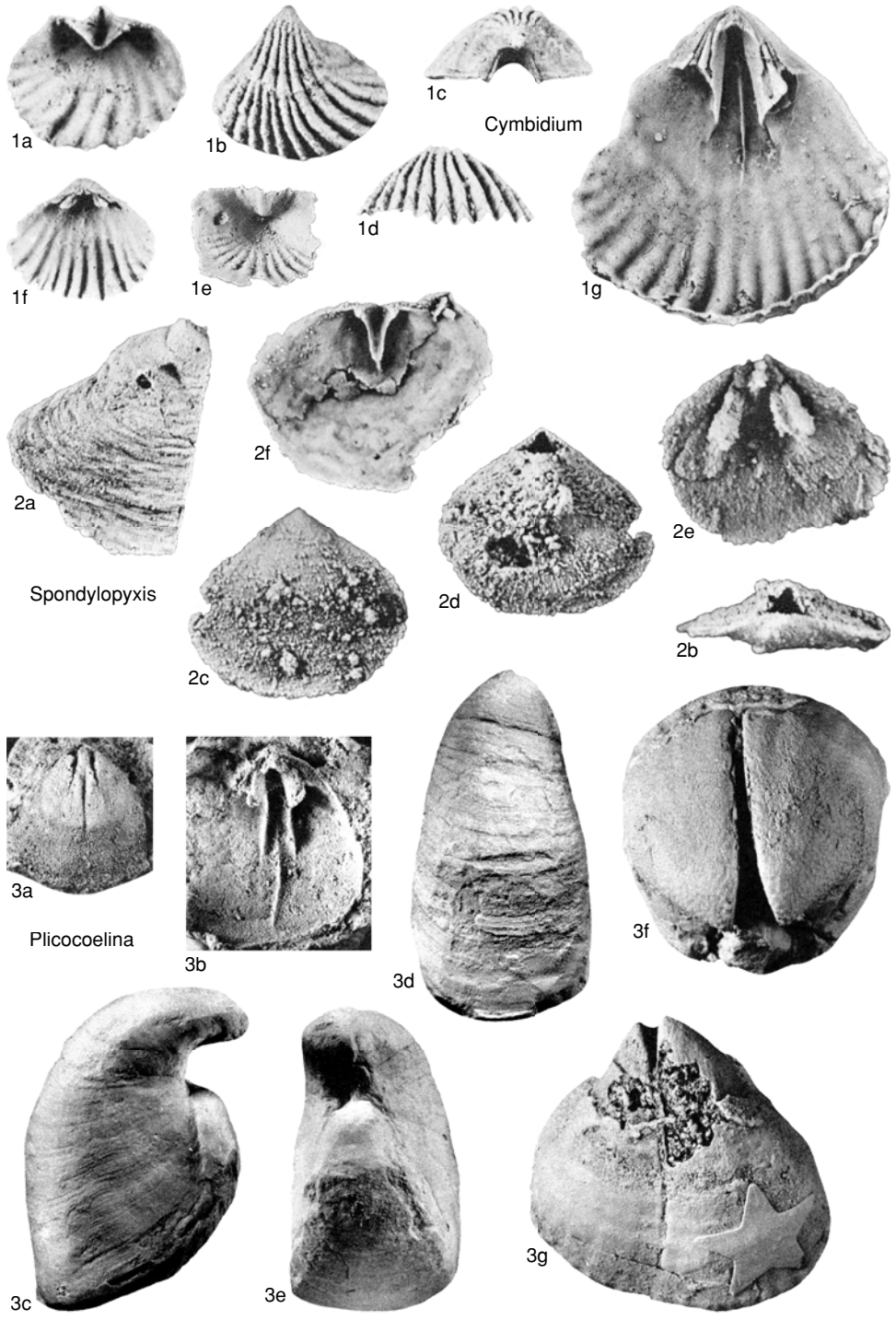


FIG. 672. Subrianiidae (p. 993).

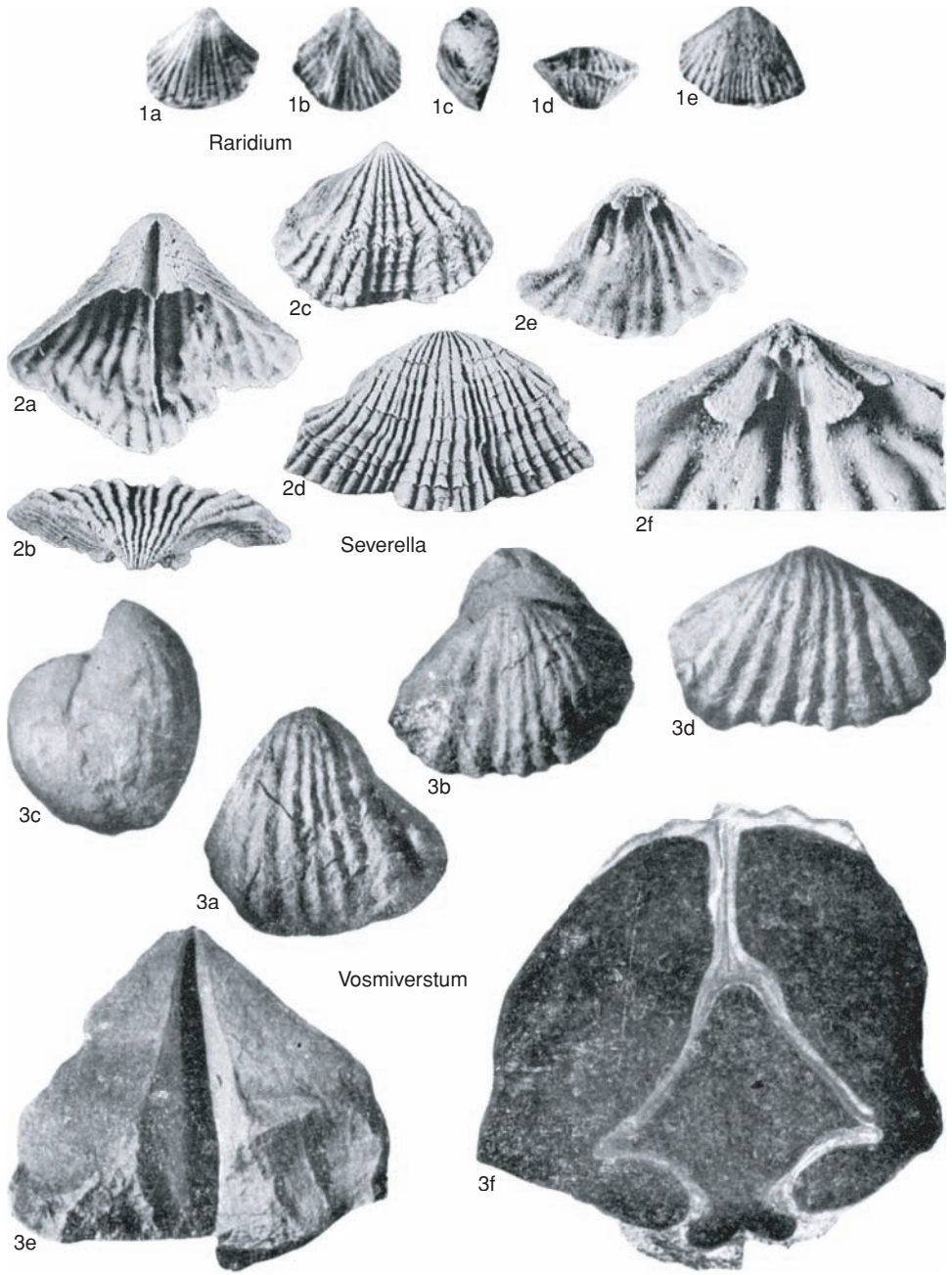


FIG. 673. Subrianidae (p. 993–997).

supporting median septum, which is much shorter than spondylium; cardinalia as in *Conchidium*. *Silurian* (upper Wenlock–Ludlow): Urals, USA (Nevada, California), Canadian Arctic.—FIG.

673.3a–f. **V. triquetrum* (SAPELNIKOV), Wenlock, Novo-Lialinsk region, eastern Urals; a–e, ventral, dorsal, lateral, dorsal, ventral interarea, ×1; f, serial section, ×3 (Antsigin & others, 1970).

Superfamily
STRICKLANDIOIDEA
Schuchert & Cooper, 1931

[*nom. transl.* BOUCOT, RONG, & BLODGETT, herein, *pro* Stricklandiidae SCHUCHERT & COOPER, 1931, p. 248]

[Materials prepared by A. J. BOUCOT, RONG JIA-YU, & ROBERT B. BLODGETT]

Small to very large; smooth, costate, or diagonally rugose; moderately biconvex to convexoconcave; long to short, well-developed interareas and hinge lines; ventral valve median septum short or absent; short spondylium; brachial apparatus relatively short; inner hinge plates in earlier forms of Stricklandiinae; rodlike crura present; outer hinge plates long or short. *Silurian* (*lower Llandovery–Ludlow*).

Family STRICKLANDIIDAE
Schuchert & Cooper, 1931

[Stricklandiidae SCHUCHERT & COOPER, 1931, p. 248] [=Stricklandiidae HALL & CLARKE, 1895, p. 355; Stricklandiidae AMSDEN, 1953, p. 146; Stricklandiacea SAPELNIKOV, 1973, p. 40, *pars*]

Ventral median septum well developed; dental sockets relatively short; inner hinge plates present in earlier forms, lost in younger forms; short spondylium supported by short median septum. *Silurian* (*lower Llandovery–upper Wenlock*).

Subfamily STRICKLANDIINAE
Schuchert & Cooper, 1931

[Stricklandiinae SCHUCHERT & COOPER, 1931, p. 248]

Prismatic layer present on medial faces of hinge plates of investigated genera. *Silurian* (*lower Llandovery–lower Wenlock*).

Stricklandia BILLINGS, 1859a, p. 132 [**Atrypa lens* J. SOWERBY in MURCHISON, 1839, p. 637; SD OEHLERT, 1887a, p. 1310] [=Stricklandinia BILLINGS, 1863a, p. 370, *obj.*]. Medium to large; smooth to anteriorly weakly plicate; subcircular to elongate; interareas relatively wide in older forms to narrower in younger forms; moderately ventribiconvex, rodlike crura; outer hinge plates enlarged in younger forms. *lower Silurian*: North America, Eurasia.—FIG. 674, 1a–e. **S. lens* (SOWERBY), 70.8 meters, Sulustvere borehole, Llandovery, Adavere Stage [Gorizont], Estonia; ventral, dorsal, posterior, anterior, lateral views, $\times 1.5$ (Rubel, 1970).—FIG. 674, 1f–g. *S. lens progressa*, C. beds, Sefin footbridge, Llandovery, Wales; mold of dorsal cardinalia, internal mold of posterior, $\times 1$ (Williams, 1951).

?**Aenigmastricklandia** ZIEGLER, 1966a, p. 347 [**A. contorta*; OD]. Small; subcircular; unequally ventribiconvex; coarse, irregularly branching costae; prominent growth lines; high dorsal fold and corresponding ventral sulcus; straight hinge line; small outer hinge plates. *Silurian* (*upper Aeronian*): Wales.—FIG. 674, 3a–d. **A. contorta*, south of Presteigne; internal dorsal mold, posterior view of rubber replica of exterior of ventral valve, internal mold of ventral valve, anterior view of internal mold of ventral valve, $\times 2$ (Ziegler, 1966a).

Costistricklandia AMSDEN, 1953, p. 143 [**Stricklandia gaspeensis* BILLINGS, 1859a, p. 134; OD]. Large to very large; subcircular to elongate; similar to youngest form of *Stricklandia* but with costae that bifurcate anteriorly; moderately ventribiconvex; relatively large outer hinge plates and crura. *Silurian* (*upper Telychian–lower Wenlock*): eastern North America, Europe, Novaya Zemlya.—FIG. 674, 2a–c. **C. gaspeensis* (BILLINGS), La Vieille Formation, Québec; a, dorsal interior showing brachial processes, La Vieille Cove, east of Gascons, $\times 2$; b, posterior of ventral valve exterior, Port Daniel, $\times 1$ (Schuchert & Cooper, 1932); c, dorsal valve exterior, $\times 1$ (Amsden, 1965).

Ehlersella BOUCOT & JOHNSON, 1966a, p. 569 [**Stricklandinia davidsoni* BILLINGS, 1868, p. 59; OD]. Medium to large; subcircular to elongate; crisscross concentric and chevronlike plications; unequally ventribiconvex; short hinge line; inner and outer hinge plates. *Silurian* (*upper Aeronian–lower Telychian*): Canada (Quebec), USA (Alabama).—FIG. 675a–e. **E. davidsoni* (BILLINGS), Jupiter Formation, Pavillion River, Anticosti Island, Quebec; dorsal, ventral, anterior, posterior, lateral exteriors, $\times 1$ (Boucot & Johnson, 1966a).—FIG. 675f–i. *E. norwoodi*, Red Mountain Formation, Tuscaloosa County, Alabama; f, dorsal internal mold, $\times 4$; g, rubber replica of dorsal interior, $\times 2$; h, ventral internal mold, $\times 1.5$; i, dorsal internal mold, $\times 1$ (Boucot & Johnson, 1966a).

Subfamily KULUMBELLINAE
new subfamily

[Kulumbellinae BOUCOT, RONG, & BLODGETT, herein]

Small to medium; smooth to costate, or crisscross ornament; subcircular to elongate; interarea relatively narrow to wide; gently biconvex to concavoconvex; inner hinge plates in earlier forms, lost in younger forms. *Silurian* (*lower Llandovery–upper Wenlock*).

Kulumbella NIKIFOROVA, 1960c, p. 61 [**K. kulumbensis*; OD]. Large; subcircular to transverse; gently concavoconvex with ventral valve slightly deeper; long, narrow interarea; crisscross ornamentation; short outer hinge plates and crura. *Silurian* (*middle Llandovery*): Siberia, eastern Canada (Anticosti Island).—FIG. 676, 1a–e. **K. kulumbensis*, Kulumb River, Siberia; ventral exterior, dorsal exterior, external lateral, internal ventroposterior, ventral exterior impression, $\times 1$ (Nikiforova, 1960c).

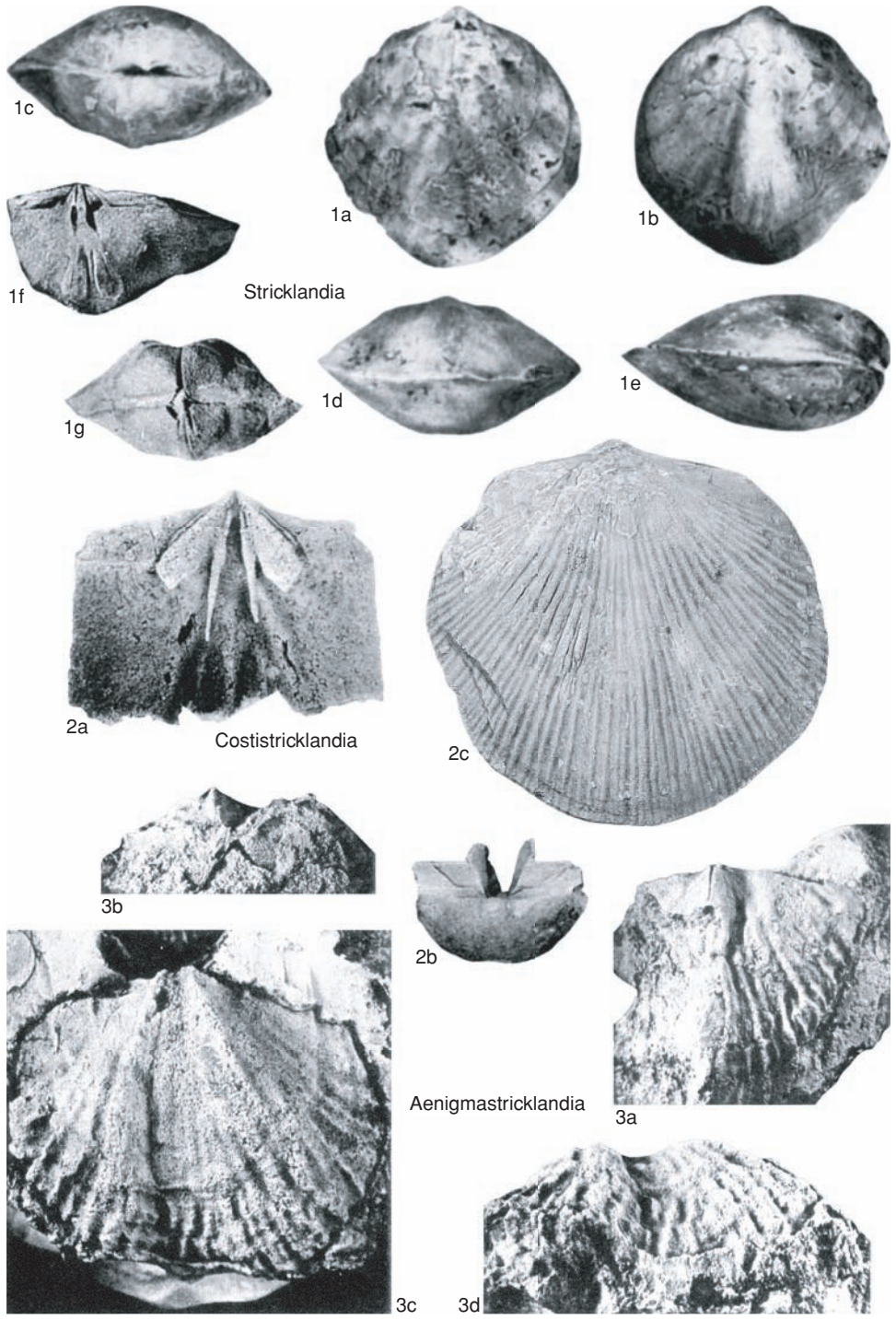


FIG. 674. Stricklandiidae (p. 998).

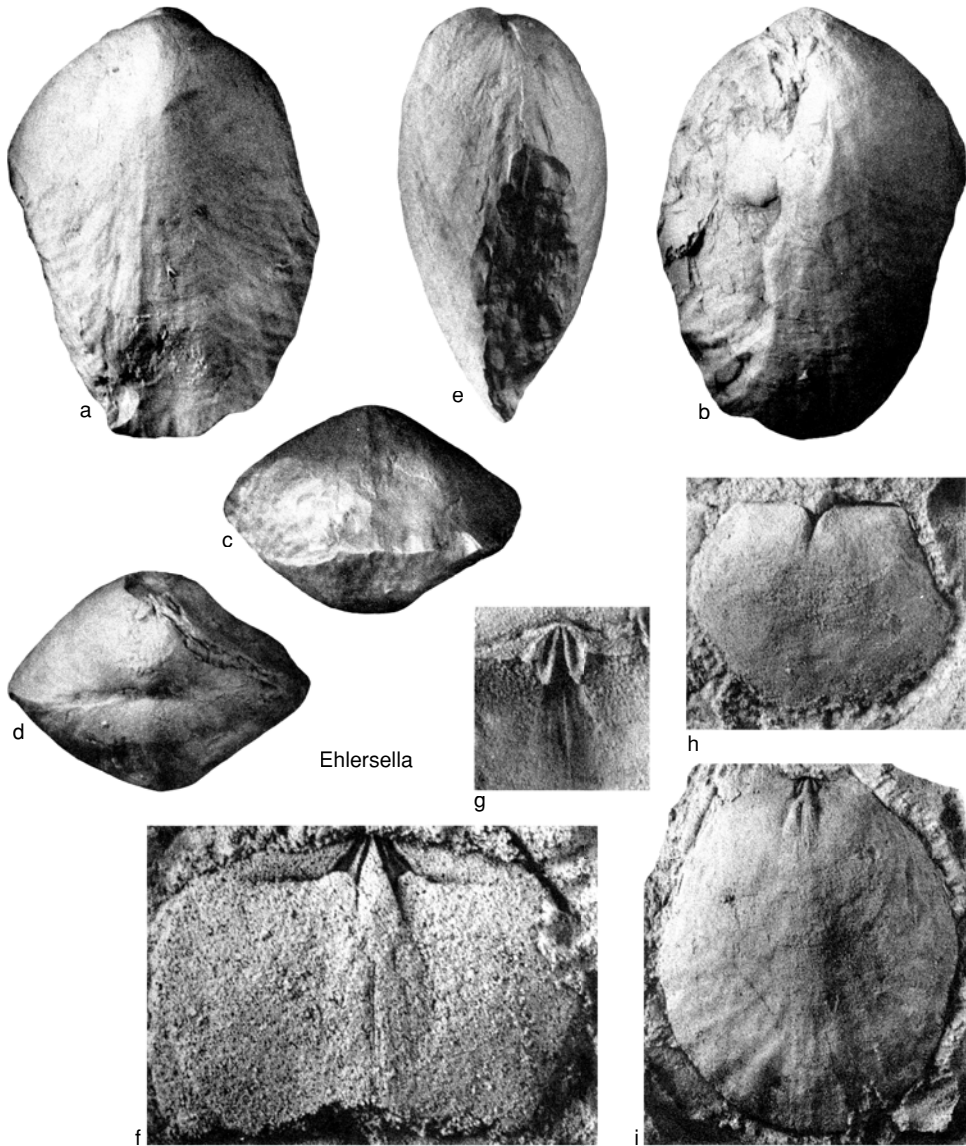


FIG. 675. Stricklandiidae (p. 998).

Chiastodoca JIN & COPPER, 1998, p. 451 [**Stricklandia salteri* BILLINGS, 1868, p. 61; OD]. Medium to large; subcircular to subelliptical, weakly biconvex, with long, straight hinge line, narrow ventral and dorsal interarea, divaricate ribs, short, low ventral median septum supporting broad, U-shaped spondylium, no inner hinge plates. *Silurian (upper Aeronian–lower Teleychian)*: eastern North America, South China, Kazakhstan, Estonia, Norway, Sibe-

ria, northern Greenland.—FIG. 676, 2a–b. **C. salteri* (BILLINGS), Ferrum Member, Jupiter Formation, Anticosti Island, Quebec; ventral exterior, dorsal exterior, $\times 2$ (Jin & Copper, 1998).

Microcardinalia BOUCOT & EHLERS, 1963, p. 51 [**Stricklandinia triplesiana* FOERSTE, 1890, p. 323; OD]. Medium; smooth to anteriorly weakly plicate; subcircular to very elongate; ventribiconvex; inner hinge plates in older forms, lost in younger forms;

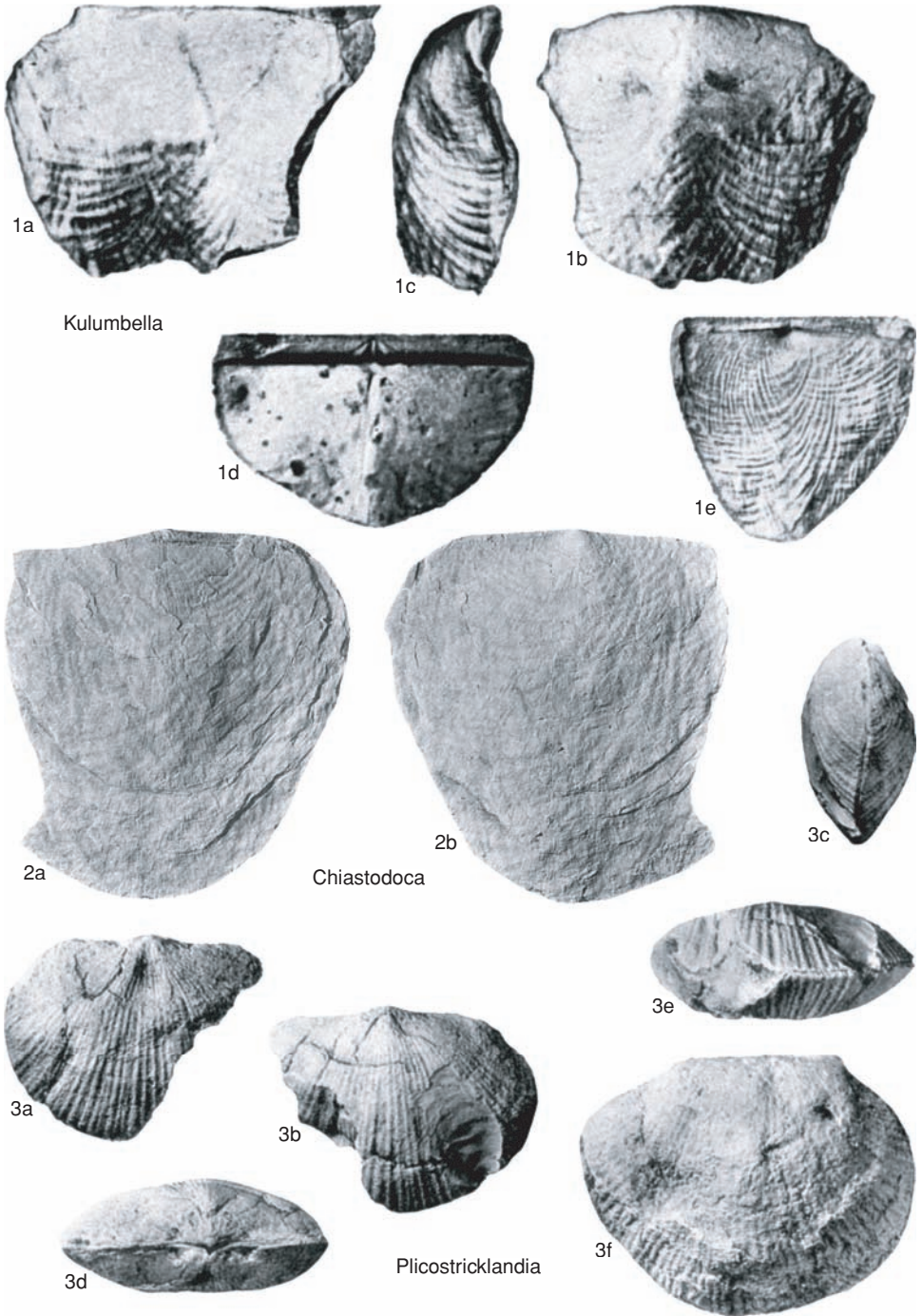


FIG. 676. Stricklandiidae (p. 998–1002).

small outer hinge plates. Equivalently aged forms similar to *Stricklandia* except smaller and possessing smaller outer hinge plates. *Silurian* (*middle Llandovery–upper Llandovery*): midcontinent North America, Scotland.—FIG. 677,2a–d. **M. triplesiana* (FOERSTE), Brassfield Limestone, Dayton, Ohio, USA; dorsal, ventral, lateral, and posterior exteriors, $\times 1$ (Amsden, 1966).—FIG. 677,2e–f. *M. raberensis*, basal Cordell Dolomite, Chippewa County, Michigan, USA; *e*, dorsal interior, $\times 2$; *f*, enlargement of preceding, $\times 4$ (Boucot & Ehlers, 1963).—FIG. 677,2g–j. *M. protriplesiana*, Black-gum Formation, Cherokee County, Oklahoma, USA; *g–h*, lateral and posterior views of spondylium, $\times 2$; *i*, dorsal interior from side, $\times 8$; *j*, dorsal interior from above, $\times 2$ (Amsden, 1966).

Plicostricklandia BOUCOT & EHLERS, 1963, p. 55 [**Stricklandia multilirata* WHITFIELD, 1878, p. 81; OD]. Medium; subcircular to transverse; costae bifurcating anteriorly; moderately ventribiconvex; straight hinge line; small outer hinge plates. Similar to *Costistricklandia* except for smaller size and smaller outer hinge plates. *Silurian* (*upper Telychian–Wenlock*): midcontinent North America.—FIG. 676,3a–f. **P. multilirata* (WHITFIELD); *a–e*, ventral, dorsal, lateral, posterior, anterior exteriors, Hopkinton Dolomite, Delhi, Iowa, USA, $\times 1$; *f*, dorsal exterior, Engadine Dolomite, Drummond Island, Michigan, USA, $\times 1$ (Boucot & Ehlers, 1963).

Stricklandiella SAPELNIKOV & RUKAVISHNIKOVA, 1973, p. 36 [**S. aseptata*; OD]. Smooth; large; laterally elongate; long hinge line; moderately ventribiconvex; narrow interareas; dorsal fold and ventral sulcus; uniplicate commissure; no median septum under short spondylium; short outer hinge plates, submerged in secondary material, laterally directed. *Silurian* (*Llandovery*): Kazakhstan.—FIG. 677,1a–d. **S. aseptata*, Salamatk Suite, Koizharilgan Mountains, southern Kazakhstan; dorsal internal mold, ventral internal mold, ventral posterior internal mold, mold of ventral exterior, $\times 1$ (Sapelnikov & Rukavishnikova, 1973).

Family AENIGMASTROPHIIDAE

Boucot & Rong, 1994

[Aenigmastrophidae BOUCOT & RONG, 1994, p. 405]

Small to medium; transverse; long, straight hinge line; long, well-defined, narrow interareas; profile weakly to moderately biconvex to weakly concavoconvex; spondylium short, wide, shallow, sessile or supported by low, short median septum; crura widely divergent, rodlike; short outer hinge plates only, bordered posteriorly by narrow, lengthy hinge grooves; ventral median septum short, posterior, low, septum possibly present in dorsal valve. Prismatic layer lack-

ing in some taxa, unrecognized overall. [If *Stricklandistrophia* belongs to this group, SAPELNIKOV and KULKOV's (1976) family name Stricklandistropiidae has precedence.] *Silurian* (*Wenlock–Ludlow*): USA (Nevada, California), Canada (Northwest Territories).

Aenigmastrophia BOUCOT, 1971, p. 156 [**A. cooperi*; OD]. Small to large; gently concavoconvex; ventral interarea long and narrow, apsacline; much narrower, anacline dorsal interarea; smooth; transverse; short, sessile spondylium; rodlike crura laterally directed at a very high angle, very short outer hinge plates. *Silurian* (*Ludlow*): USA (Nevada, California).—FIG. 678,1a–e. **A. cooperi*, Roberts Mountains Formation, Eureka County, Nevada; *a–c*, interior, posterior, lateral views of dorsal valve, $\times 4$; *d–e*, dorsal interior, exterior views, $\times 5$ (Johnson, Boucot, & Murphy, 1976).—FIG. 678,1f. *A. greggi*, Ludlow age sandstone, Siskiyou County, California; rubber replica of dorsal interior, $\times 1$ (Boucot, 1971).

Rugolepyros LENZ, 1989, p. 1224 [**R. latispondylus*; OD]. Medium; hemicircular outline; weakly biconvex; moderately strong, discontinuous, irregular, concentric rugae; apsacline, long ventral interarea and short, anacline dorsal interarea; large, wide, shallow, spatulate, posteriorly sessile spondylium; rodlike crura cemented to valve floor; short, laterally directed outer hinge plates. *Silurian* (*Wenlock*): Canada (Northwest Territories).—FIG. 678,2a–f. **R. latispondylus*, Whittaker Formation, southern Mackenzie Mountains; *a*, ventral exterior, $\times 2.4$; *b*, ventral interior; *c*, ventral interior; *d*, ventral exterior, $\times 4.4$; *e*, ventral interior, $\times 8$; *f*, dorsal interior, $\times 4.2$ (Lenz, 1989).

Vadimia BOUCOT & RONG, 1994, p. 407 [**V. nevadensis*; OD]. Dorsal valve gently sulcate; costae coarse; laterally elongate; spondylium short, wide, shallow, supported by short median septum; short rodlike crura cemented to valve floor; very short outer hinge plates. *Silurian* (*Ludlow*): USA (Nevada).—FIG. 679a–e. **V. nevadensis*, Roberts Mountains Formation, Eureka County; *a–b*, ventral interior and exterior; *c*, anterior view of ventral interior, $\times 3$; *d–e*, interior and exterior of dorsal valve, $\times 5$ (Johnson, Boucot, & Murphy, 1976).

?Family STRICKLANDISTROPHIIDAE Sapelnikov & Kulkov, 1976

[Stricklandistropiidae SAPELNIKOV & KULKOV, 1976, p. 113]

Internal structures not well known. Spondylium well developed, with or without median septum. Brachial interior with no inner hinge plates. Similar to the Aenigmastrophidae in having a very long, straight

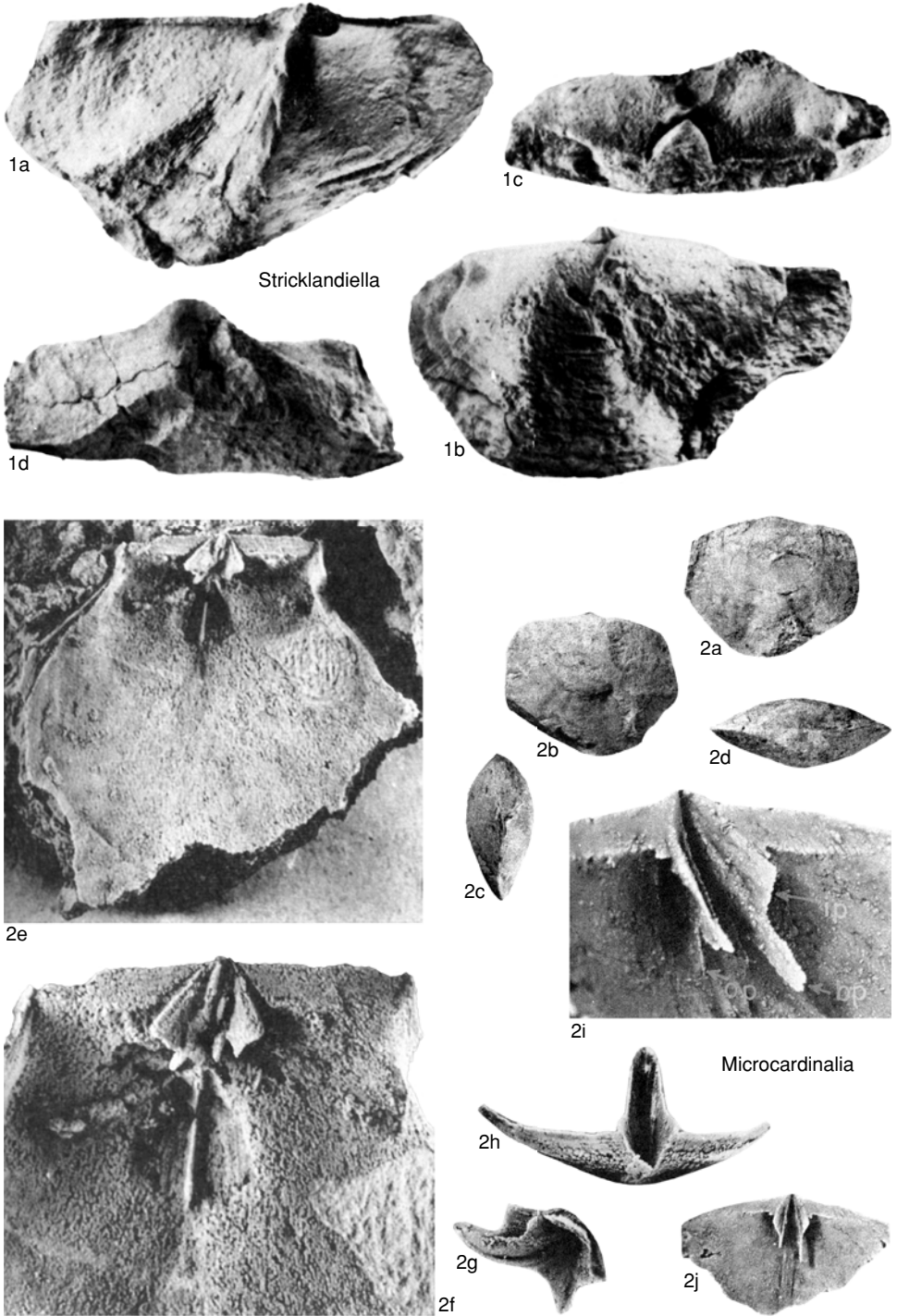


FIG. 677. Stricklandiidae (p. 1000–1002).

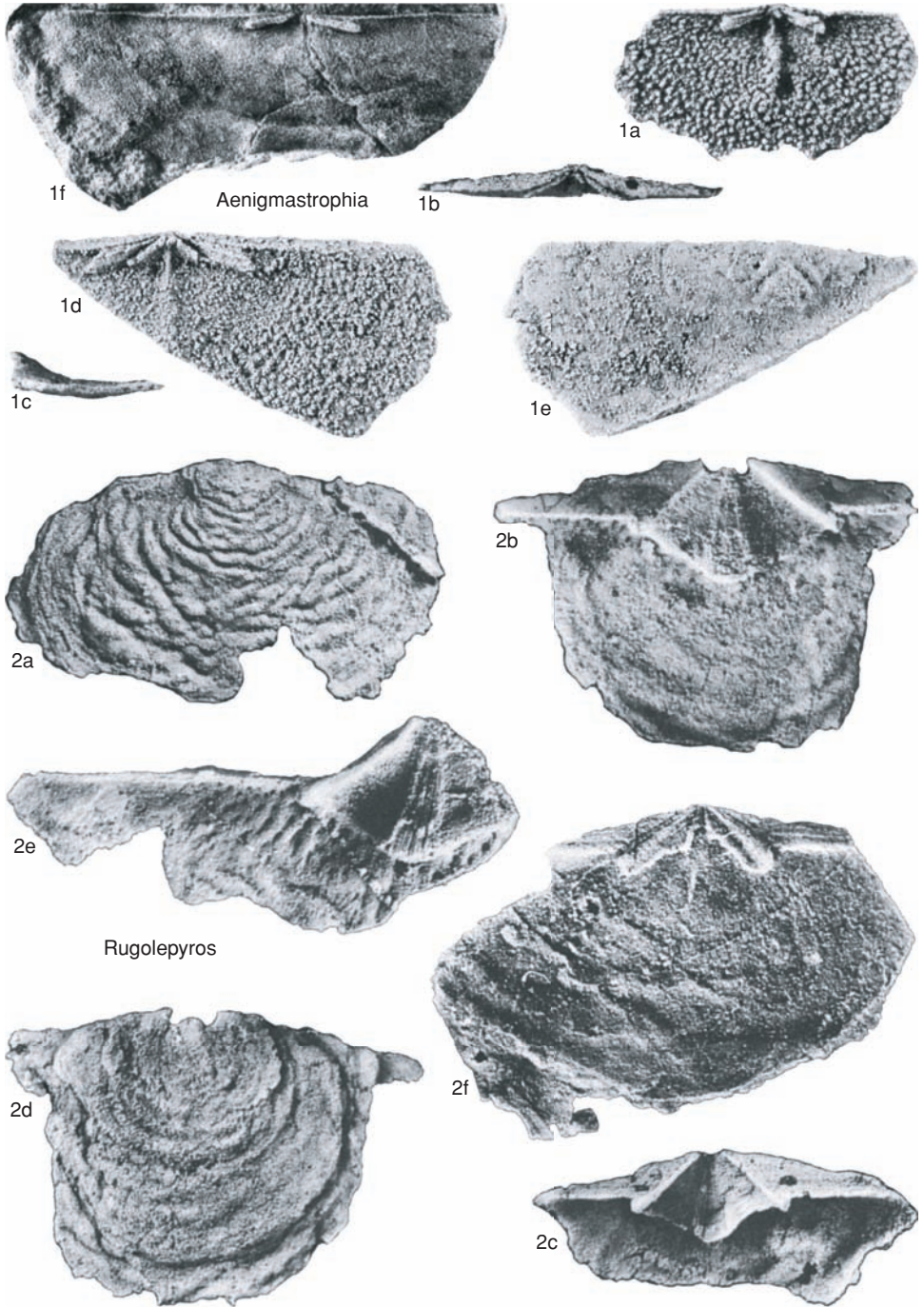


FIG. 678. Aenigmastrophiidae (p. 1002).

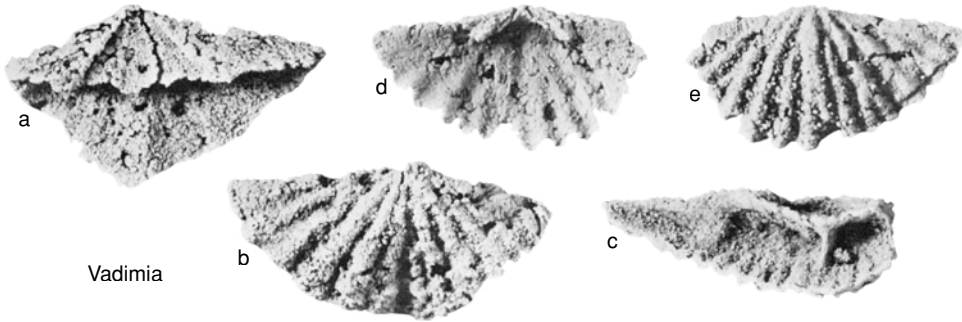


FIG. 679. Aenigmastrophiiidae (p. 1002).

hinge line and well-developed interareas. Moderately biconvex as contrasted with the flattish aenigmastrophiiids. Uniplicate commissure. [Whether the 2 genera within this family are stricklandids remains uncertain owing to ignorance of their internal structures adequate to confirm such an assignment.] *Silurian* (*Llandovery*): Altai Mountains, Kazakhstan.

Stricklandistrophia SAPELNIKOV & RUKAVISHNIKOVA, 1975a, p. 96 [**S. lata*; OD]. Small to medium; alate, suboval, ventral sulcus, dorsal fold, long hinge line; costellae that bifurcate anteriorly; dorsal interarea linear; central interarea, low, wide; short ventral median septum supporting short spondylium; massive, very short outer, laterally inclined hinge plates, crura. *Silurian* (*Llandovery*): Kazakhstan.—FIG. 680, 1a–f. **S. lata*, Alpeisk Stage [Gorizont], Dzhungar Alatai; ventral exterior, dorsal exterior, ventral exterior, dorsal exterior, lateral view, dorsal exterior, $\times 1$ (Sapelnikov & Rukavishnikova, 1975a).

Spondylostrophia KULKOV, 1967, p. 33 [**S. lata*; OD]. Small; alate; hinge line long, straight; interareas well developed; dorsal sulcus and ventral sulcus; costae that may bifurcate anteriorly; spondylium short, U-shaped; ventral median septum absent; outer hinge plates thin, relatively short, laterally directed. *Silurian* (*upper Llandovery*): Altai Mountains.—FIG. 680, 2a–e. **S. lata*, Chagirsk? Suite; ventral exterior, dorsal exterior, anterior external, ventral exterior, dorsal exterior, $\times 2$ (Kulkov, 1967).

Superfamily GYPIDULOIDEA Schuchert & LeVene, 1929

[*nom. transl.* SAPELNIKOV in SAPELNIKOV & RUKAVISHNIKOVA, 1975a, p. 127, ex Gypidulinae SCHUCHERT & LEVENE, 1929a, p. 15]

[Materials prepared by ROBERT B. BLODGETT,
A. J. BOUCOT, & RONG JIA-YU]

Pentameridines typically unisulcate, smooth or costate to costellate; hinge plates lyre shaped or laterally concave in cross section; inner hinge plates discrete or coalesced to form cruralium; crura bladelike. *Silurian*

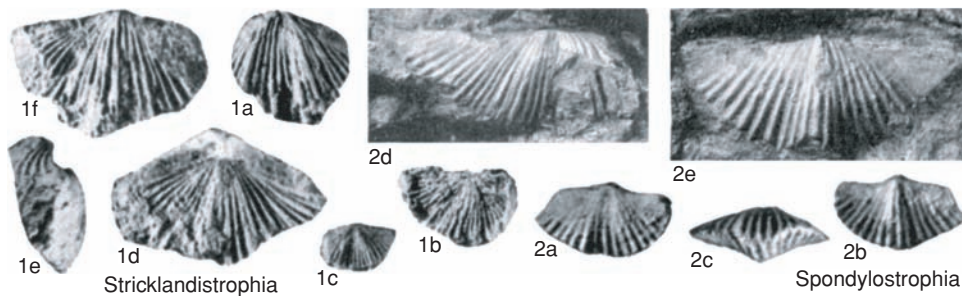


FIG. 680. Stricklandistrophiiidae (p. 1005).

(upper Llandovery)—Upper Devonian (Frasnian).

Family GYPIDULIDAE
Schuchert & LeVene, 1929

[nom. transl. RZHONSNITSKAIA, 1961, p. 47 ex Gypidulinae SCHUCHERT & LEVENE, 1929a, p. 15]

Gypiduloids usually with well-developed dorsal sulcus and ventral fold, rarely absent; shell surface costate, plicate, or smooth; hinge plates lyre shaped in cross section; some have inner hinge plates that diverge basolaterally. *Silurian (Telychian)—Upper Devonian (Frasnian)*.

Subfamily GYPIDULINAE
Schuchert & LeVene, 1929

[Gypidulinae SCHUCHERT & LEVENE, 1929a, p. 15] [=Sieberellinae SAPELNIKOV, 1973, p. 41]

Galeatiform gypidulids; shell surface smooth, costate, or plicate; costae or plicae when present not split at anterior commissure; microornament generally lacking, without tubercles, pits, or concentric lines; crura arched in cross section; inner hinge plates discrete or united into cruralium. *Silurian (Telychian)—Upper Devonian (Frasnian)*.

Gypidula HALL, 1867b, p. 163 [**Gypidula typicalis* AMSDEN, 1953, p. 140, nom. nov. pro *Pentamerus occidentalis* HALL, 1858a, p. 514, non HALL, 1852; OD HALL, 1867b, p. 380] [=*Metabolipa* GODEFROID, 1974, p. 5 (type, *Pentamerus greindli* MAILLIEUX, 1909, p. 230, OD); *Neometabolipa* GODEFROID, 1974, p. 23 (type, *N. duponti* GODEFROID, 1974, p. 24, OD)]. Size variable, shell oval to subcircular in outline; strongly ventribiconvex, ventral beak arched over dorsal; variably costate or plicate anteriorly; inner hinge plates discrete. [HALL (1867b, p. 380) designated *Pentamerus occidentalis* HALL, 1858a, as the type species of his new genus *Gypidula*. *Pentamerus occidentalis* HALL, 1858a, is a homonym of *Pentamerus occidentalis* HALL, 1852, the latter being a species of *Plicocoelina*. AMSDEN, 1953, p. 140, replaced *Pentamerus occidentalis* HALL, 1858a (not *Pentamerus occidentalis* HALL, 1852) with *Gypidula typicalis*.] *Silurian (Telychian)—Upper Devonian (Frasnian)*: widespread in Europe, Asia, North America, North Africa, Australia. —FIG. 681,2a–d. **G. typicalis* (AMSDEN), Cedar Valley Group, Iowa, USA; a–c, dorsal, anterior, lateral views, $\times 1$ (Amsden, 1965); d, serial section at 5.0 mm from tip of ventral umbo (Godefroid, 1979).

Amsdenina BOUCOT, 1975a, p. 357 [**Sieberella roemeri* HALL & CLARKE, 1892, p. 247; OD]. Similar to

Sieberella, but differs in having rounded costae separated by rounded interspaces; umbo smooth; short median septum and spondylium; inner hinge plates wedged into shell dorsally, almost conjunct posteriorly, becoming discrete anteriorly. *Silurian (Wenlock–Přídolí)*: Canadian Arctic Islands, Wenlock; midcontinent North America (Tennessee, Oklahoma), northern Appalachians (Maine, Quebec, New Brunswick), Ludlow–Přídolí. —FIG. 681,1a–d. **A. roemeri* (HALL & CLARKE), Brownport Formation, Tennessee; a–c, ventral, dorsal, lateral views, $\times 1$; d, polished section, $\times 2$ (Amsden, 1949a).

Ascanigypa HAVLIČEK in HAVLIČEK & ŠTORCH, 1990, p. 113 [**Pentamerus ascanius* BARRANDE, 1879b, pl. 80, fig. III; OD]. Smooth shells similar to *Gashao-miaoa*, but differs in having low ventral fold and dorsal sulcus; externally similar to *Gypidula*, but differs in lack of costae; fold low, well developed in anterior part of shell; sulcus shallow; anterior commissure rectimarginate in juveniles, becoming unisulcate in adults; microornament not observed; ventral median septum short; inner hinge plates converge medially, less commonly diverging anteriorly. *Silurian (upper Wenlock)*: Czech Republic. —FIG. 681,3a–d. **A. ascania* (BARRANDE), Motol Formation, Prague region; lateral, ventral, anterior, dorsal views, $\times 1.7$ (Havlíček & Štorch, 1990).

Brevisseptum SAPELNIKOV, 1960b, p. 109 [**Conchidium (Brevisseptum) oriens*; OD]. Medium-sized shells, suboval outline, usually more transverse; similar to *Sieberella*, but lacking well-developed fold and sulcus; ventribiconvex, evenly convex in width or with weak fold, coarsely costate, costae irregular, simple or dividing near anterior margin into 2 to 3 branches; anterior commissure convex dorsally; inner hinge plates short, discrete; thin, very short ventral median septum. *Silurian (lower Ludlow)*: Urals. —FIG. 681,4a–d. **B. oriens*, Isovsk Stage [Gorizont], Istok River, eastern Urals; ventral, dorsal, lateral, anterior views, $\times 1$ (Sapelnikov, 1985a).

Cadudium HAVLIČEK, 1985b, p. 296 [**Pentamerus caducus* BARRANDE, 1847, p. 469; OD]. Globose shells with unisulcate commissure; ventral fold low, commonly with pair of low, rounded plications anteriorly, sometimes obscure; dorsal sulcus shallow, flanked by rounded rib on either side, sulcus smooth or bearing median plication; lateral sides of both valves smooth or with short, weak plications; inner hinge plates short, discrete. *Silurian (Ludlow)—Lower Devonian (Lochkovian)*: Czech Republic, Urals, Ludlow–Přídolí; Urals, Tian Shan, Lochkovian. —FIG. 681,5a–c. **C. caducum* (BARRANDE), Přídolí Formation, Prague region; anterior, posterior, dorsal views, $\times 2.6$ (Havlíček & Štorch, 1990).

Carinagypa JOHNSON & LUDVIGSEN, 1972, p. 128 [**Gypidula loweryi* MERRIAM, 1940, p. 81; OD]. Large, smooth to faintly medioplicate; ventral fold and dorsal sulcus weakly developed; ventral median septum present or absent; hinge plates discrete,

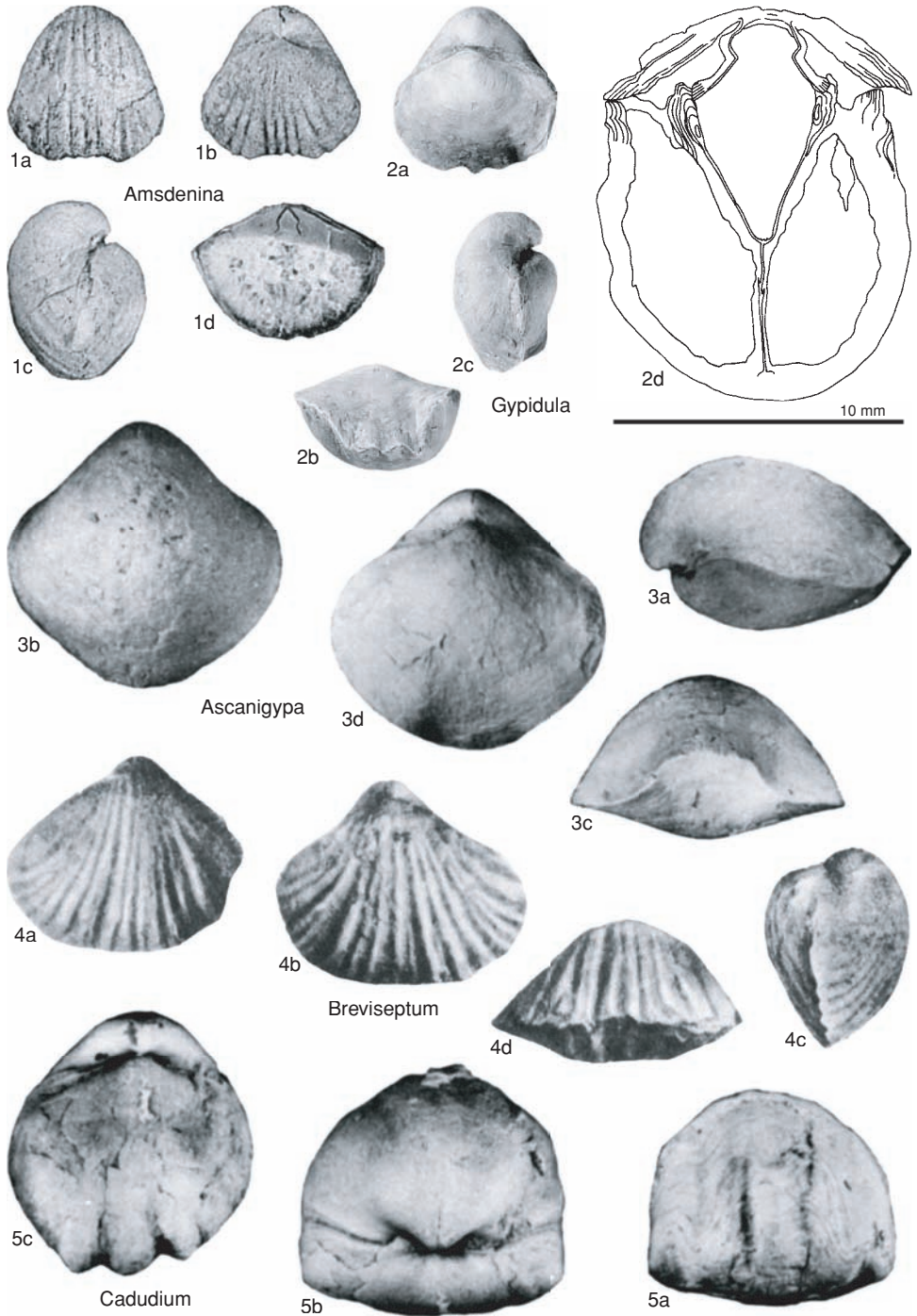


FIG. 681. Gypidulidae (p. 1006).

- with single pair of ventrally directed carinae. *Lower Devonian* (upper Lochkovian)—*Middle Devonian* (Eifelian): Czech Republic, Canadian Arctic, upper Lochkovian; USA (Nevada, Alaska), Yukon Territory, Arctic Canada, Emsian—Eifelian.
- C. (Carinagypa).** Ventral medium septum present. *Lower Devonian* (upper Lochkovian)—*Middle Devonian* (Eifelian): Canadian Arctic Islands, Czech Republic, upper Lochkovian; USA (Nevada, Alaska), Yukon Territory, Arctic Canada, Emsian—Eifelian.—FIG. 682,3a–b. *C. (*C.*) *loweryi* (MERRIAM); *a–e*, ventral, dorsal, lateral, posterior, anterior views, McColley Canyon Formation, Eureka County, Nevada, ×1 (Johnson, 1970b); *f–h*, dorsal serial sections, Michelle Formation, Yukon Territory, Canada, ×6 (Johnson & Ludvigsen, 1972).
- C. (Aseptagypa)** BRICE, 1982, p. 26 [*C. (*A.*) *maclareni*; OD]. Similar to *C. (Carinagypa)*, but differs in lacking ventral septum, resulting in completely free spondylium. *Lower Devonian* (Emsian)—*Middle Devonian* (Eifelian): Canadian Arctic Islands, USA (east-central Alaska, Nevada), Yukon Territory.—FIG. 682,2a–e. *C. (*A.*) *maclareni*, Blue Fiord Formation, Eifelian, Ellesmere Island, Canadian Arctic Islands; *a–d*, dorsal, ventral, anterior, lateral views of articulated specimen, ×1; *e*, serial section at 11.1 mm from ventral umbo, ×2.1 (Brice, 1982).
- Caryogyps** JOHNSON, BOUCOT, & MURPHY, 1976, p. 53 [*C. *plicata* JOHNSON, BOUCOT, & MURPHY, 1976, p. 54; OD]. Small; angularly plicate with short ventral beak; wide ventral fold and dorsal sulcus; inner hinge plates discrete. *Silurian* (*Ludlow*): USA (Nevada, Idaho).—FIG. 683,4a–e. *C. *plicata*, Roberts Mountains Formation, Eureka County, Nevada; anterior, dorsal, ventral, posterior, lateral views, ×5 (Johnson, Boucot, & Murphy, 1976).
- Galeatagypa** SAPELNIKOV, 1981, p. 11 [**Pentamerus pelagicus* BARRANDE, 1847, p. 469; OD]. Similar to *Gypidula* internally; relatively angular dorsal sulcus margins and correspondingly angular ventral fold margins; ranging from no costa in dorsal sulcus to a prominent dorsomedian costa, if present extending almost to beak region and having corresponding ventral groove. [This genus was established as a subgenus of *Gypidula* by SAPELNIKOV, 1981.] *upper Silurian*—*Middle Devonian* (Eifelian): Europe, Asia, western and Arctic North America.—FIG. 684,2a–e. *G. *pelagica* (BARRANDE), Lochkov Formation, Prague region, Czech Republic; ventral, lateral, dorsal, anterior, posterior views, ×1 (Barrande, 1879b).
- Gashaomiaioia** RONG, SU, & LI, 1985 (July), p. 34 [**Gypidula* (*Gashaomiaioia*) *glabera*; OD] [= *Lysidium* HAVLÍČEK, 1985b (October), p. 299 (type, *Pentamerus integer* BARRANDE, 1847, p. 464; *Rectigypidula* ZHANG Yan, 1987, p. 108 (type, *Gypidula parva* BIERNAT, 1966, p. 30)]. Similar to *Gypidula* internally but differs in being totally smooth and in lacking dorsal sulcus and ventral fold; anterior commissure rectimarginate or weakly curved ventrally. *Silurian* (*Přídolí*)—*Lower Devonian* (*Pragian*), *Middle Devonian*: Neimonggol, Czech Republic, Austria (Carnic Alps), *Přídolí*—*Pragian*; Poland, China, *Middle Devonian*.—FIG. 683,2a–d. *G. *glabera* (RONG, SU, & LI), Xibiehe Formation, Darhan Mumingan Joint Banner, Inner Mongolia, China; lateral, ventral, dorsal, anterior views, ×2 (Rong, Su, & Li, 1985).
- Gypidulina** RZHONSNITSKAIA, 1956b, p. 49 [**Pentamerus optatus* BARRANDE, 1847, p. 471; OD] [= *Sieberina* ANDRONOV, 1961, p. 88, obj.]. Essentially smooth shells with sharply defined ventral fold and dorsal sulcus, both of which may sometimes bear low, obscure costae; ventral median septum thin, short; inner hinge plates closely drawn together or united to form cruralium; internally similar to *Gypidula*. *Lower Devonian*: Novaya Zemlya, Urals, Tian Shan, Salair, Altai Mountains, Czech Republic, ?North America (Gaspé).—FIG. 684,4a–d. *G. *optata* (BARRANDE), Koneprusy Limestone, Prague region, Czech Republic; ventral, lateral, posterior, anterior views, ×1 (Barrande, 1879b).
- Gypiduloides** SAVAGE in SAVAGE & BAXTER, 1995, p. 1035 [*G. *craigensis*; OD]. Small, transversely pentagonal, ventribiconvex; nongaleatiform, pauciplicate; plications well developed, rounded, with pronounced low profile in posterior and anterior view; fold and sulcus wide; anterior commissure intraplicate. *Upper Devonian* (*Frasnian*): USA (southeastern Alaska).—FIG. 684,3a–e. *G. *craigensis*, Wadleigh Limestone; dorsal, ventral, anterior, posterior, lateral views, ×4.5 (Savage & Baxter, 1995).
- Levigypa** SAPELNIKOV, 1985b, p. 9 [**Gypidula substricta* MALYGINA & SAPELNIKOV, 1973, p. 75; OD]. Medium, smooth, fold and sulcus very weak to absent; longitudinally elongate with thin, elongate ventral beak; ventral fold weakly developed or absent; massive, short ventral median septum; inner hinge plates widely separated, subparallel, fused with inner shell layer. *Lower Devonian* (Emsian): southern Tian Shan, Kyrgyzstan.—FIG. 684,1a–c. *L. *substricta* (MALYGINA & SAPELNIKOV), Manaksk Stage [Gorizont], Isfara River region, Kyrgyzstan; *a–b*, ventral, lateral views, ×1; *c*, serial section of ventral valve, ×10 (Malygina & Sapelnikov, 1973).
- Lysigypa** HAVLÍČEK in HAVLÍČEK & KUKAL, 1990, p. 139 [*L. *morosoides*; OD]. Similar to *Gashaomiaioia*, but inner hinge plates converge basally to form cruralium. Smooth, unisulcate; anterior commissure rectimarginate or weakly curved ventrally or dorsally; large spondylium, supported by very short ventral median septum. *Lower Devonian* (*Pragian*—*Emsian*): Czech Republic.—FIG. 683,1a–c. *L. *morosoides*, Suchomasty Limestone, Prague region; ventral, dorsal, anterior views, ×2.1 (Havlíček & Kukul, 1990).
- Multicosta** KHODALEVICH & BREIVEL in BREIVEL & BREIVEL, 1977, p. 71 [**Gypidula osturalica* KHODALEVICH & BREIVEL, 1959, p. 22; OD]. Coarsely costate shells, costae generally simple, sharp, covering most of shell but not found near either beak; gently ventribiconvex; fold and sulcus absent or weakly

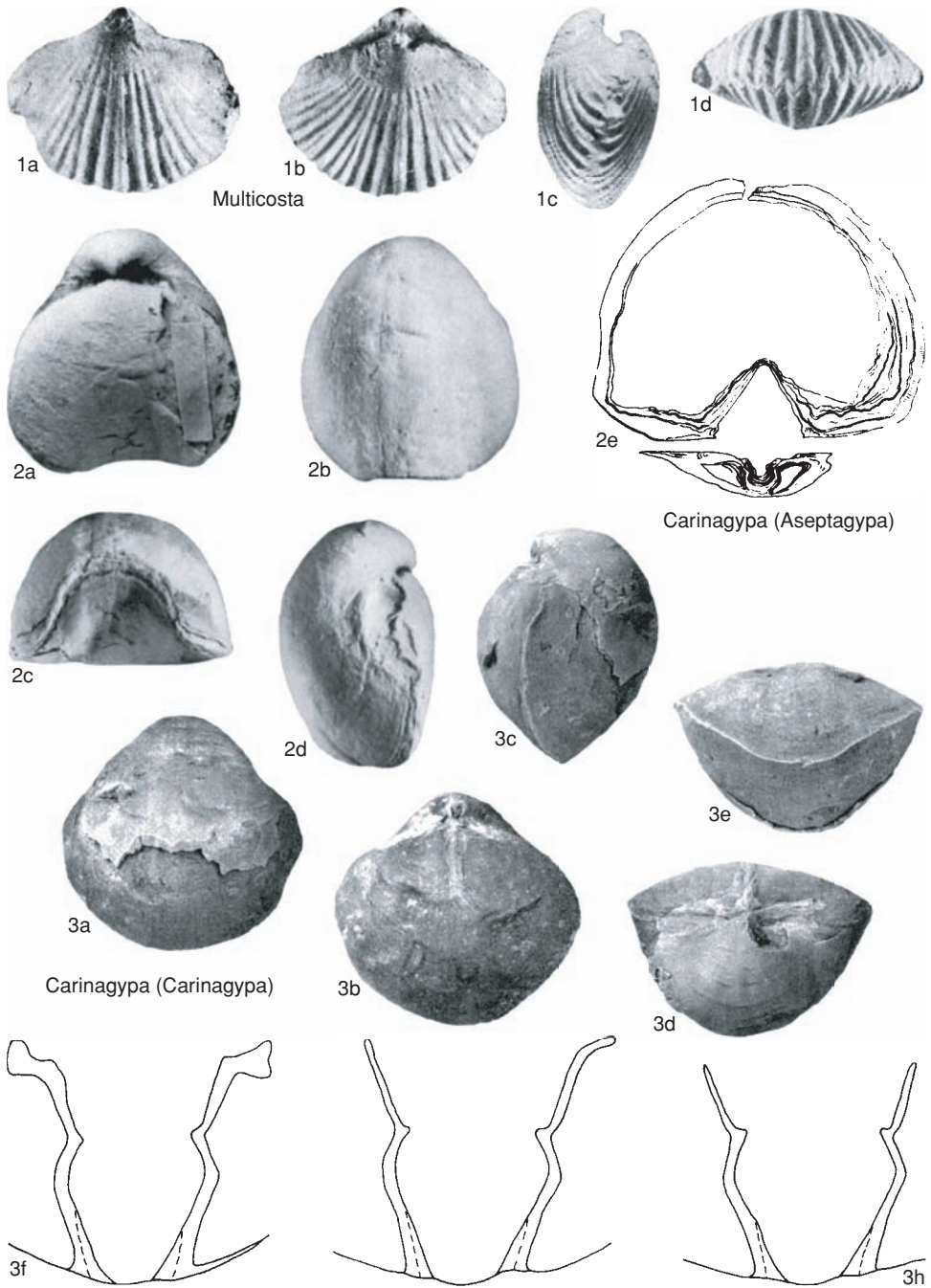


FIG. 682. Gypidulidae (p. 1006–1009).

developed anteriorly. Lower Devonian–Middle Devonian (lower Eifelian): Urals, ?Tian Shan.—FIG. 682, 1a–d. **M. osturalica* (KHODALEVICH &

BREIVEL), Emsian–earliest Eifel, Ivdel region, eastern slope of Urals; ventral, dorsal, lateral, anterior views, $\times 1$ (Khodalevich & Breivel, 1959).

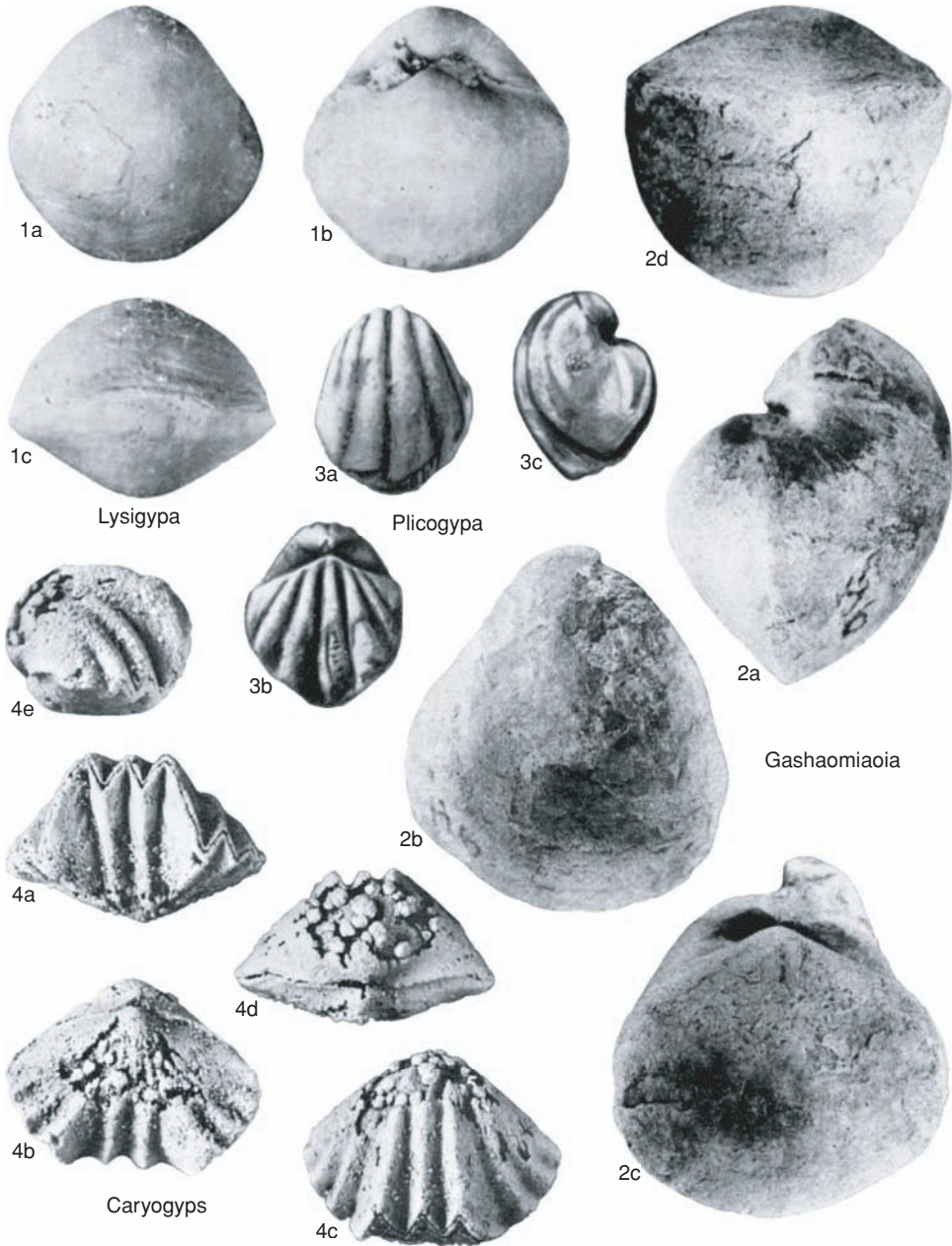


FIG. 683. Gypidulidae (p. 1008–1013).

Novozemelia CHERKESOVA, 1973, p. 28 [**N. olgae*; OD]. Medium; elongate-oval; weak anterior costae; weak fold and sulcus; short ventral median septum with long spondylium; ventral mantle canals well developed. [May be a synonym of *Carinagypa* if

carinae can be demonstrated.] *Lower Devonian (upper Emsian)–Middle Devonian (lower Eifelian)*: Novaya Zemlya.—FIG. 685, 2a–e. **N. olgae*, Kabinin Stage [Gorizont], South Island, Novaya Zemlya; a–c, ventral, dorsal, anterior views, $\times 1$; d,

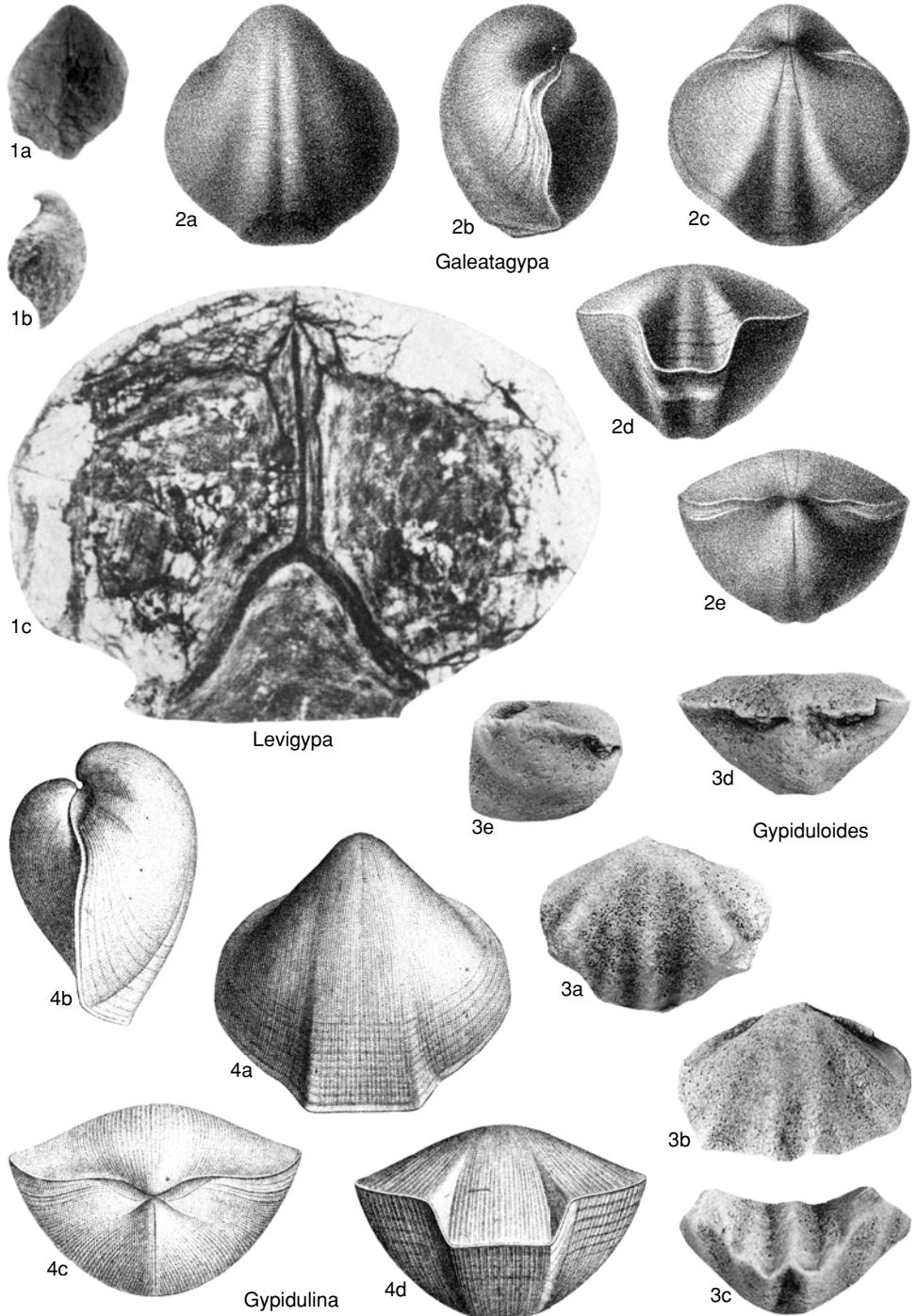


FIG. 684. Gypidulidae (p. 1008).

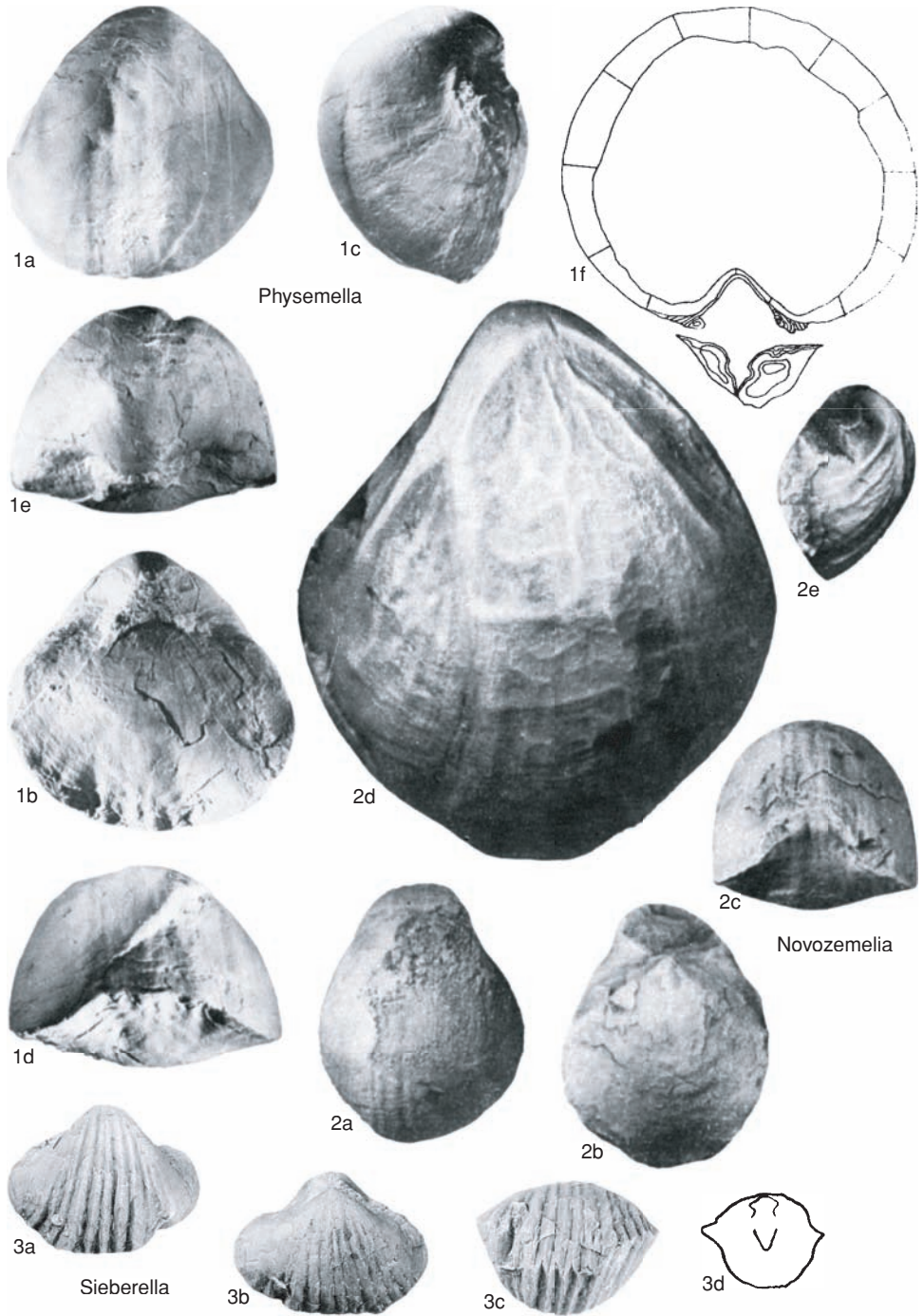


FIG. 685. Gypidulidae (p. 1010–1013).

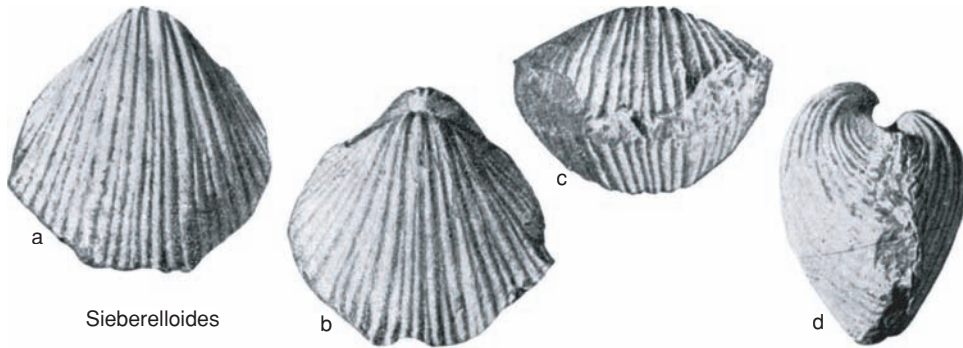


FIG. 686. Gypidulidae (p. 1013).

ventral view showing vascular marks, $\times 3$; *e*, side view showing vascular marks, $\times 1$ (Cherkesova, 1973).

Physemella GODEFROID, 1974, p. 49 [**P. maillieuxi* GODEFROID, 1974, p. 52; OD]. Similar to *Gypidula* externally, but ventral valve median septum absent or very short, hinge plates basally conjunct to form cruralium supported by median septum. *Upper Devonian (Frasnian)*: Belgium.—FIG. 685, 1*a–f*. **P. maillieuxi*, middle Frasnian, Couvin; *a–e*, ventral, dorsal, lateral, anterior, posterior views, $\times 1$; *f*, serial section at 6.0 mm from ventral umbo, $\times 3$ (Godefroid, 1974).

Plicogypa RZHONSNIKAIA, 1975, p. 27 [**Pentamerus kayseri* VON PEETZ, 1901, p. 165; OD]. Similar to *Gypidula* but more coarsely ribbed, plicae extending anteriorly from beak, simple to bifurcate; inner hinge plates relatively high, parallel to one another, intersecting dorsal valve floor at nearly right angle. *Lower Devonian (Lochkovian)–Middle Devonian (Eifelian)*: Russia (Kuznetsk basin, Taymyr), Altai Mountains, USA (southwestern Alaska), Canadian Arctic Islands, Germany (Harz Mountains).—FIG. 683, 3*a–c*. **P. kayseri* (VON PEETZ), Krekov Stage [Gorizont], Kuznetsk basin; ventral, dorsal, lateral views, $\times 1$ (Rzhonsnikaia, 1975).

Sieberella OEHLERT, 1887a, p. 1311 [**Pentamerus sieberi* VON BUCH in BARRANDE, 1847, p. 465; OD]. Medium size, ventribiconvex; costate shells; outline typically transverse, subellipsoidal, less commonly rounded; costae simple, strongly angular in cross section, covering entire shell or restricted to anterior half; V-shaped interspaces separating costae; inner hinge plates variably united to form cruralium or even low median septum; ventral median septum absent or low. *Lower Devonian (Lochkovian)–Middle Devonian (Givetian)*: widespread in Europe, North America, North Africa, Kazakhstan, Tian Shan, Salair, Urals, Vietnam.—FIG. 685, 3*a–d*. **S. sieberi* (VON BUCH), Koneprusy Limestone, Prague region, Czech Republic; *a–c*, ventral, dorsal, anterior views, $\times 1$; *d*, serial section at 7.9 mm from ventral valve beak, $\times 2$ (Amsden, 1965).

Sieberelloides SAPELNIKOV, 1985a, p. 107 [**Sieberella weberi* KHODALEVICH, 1951, p. 38; OD]. Finely costate, suboval shells; costae extending anteriorly from beak, increasing by bifurcation; ventral fold absent or weakly developed, dorsal sulcus indistinct, developed only anteriorly; hinge plates converge basally to form sessile cruralium; short ventral median septum. [The generic name *Sieberelloides* was used by RZHONSNIKAIA (1975, p. 20) as a text citation without diagnosis or comparison but with the designation of *Sieberella weberi* KHODALEVICH as the type species. The status of *nomen nudum* applies to her usage of the name; hence, SAPELNIKOV's 1985a description stands as the first legal usage, since it fulfills the ICZN rules for the establishment of a new generic name.] *Lower Devonian (Emsian)–Middle Devonian (lower Eifelian)*: Urals.—FIG. 686*a–d*. **S. weberi* (KHODALEVICH), Emsian–lower Eifelian horizon, Serov region, eastern Urals; ventral, dorsal, anterior, lateral views, $\times 1$ (Khodalevich, 1951).

Subfamily IVDELINIINAE Sapelnikov, 1985

[Ivdeliniinae SAPELNIKOV, 1985a, p. 118] [=Ivdeliniinae SAPELNIKOV, 1973, p. 41, original spelling]

Strongly ventribiconvex, costate to plicate, usually with median furrows on ribs at anterior margin; unisulcation well expressed; crura crescentic in cross section. *Lower Devonian (Lochkovian)–Middle Devonian (Eifelian)*.

Ivdelinia ANDRONOV, 1961, p. 45 [**Gypidula ivdelensis* KHODALEVICH, 1951, p. 22; OD] [= *Procerulina* ANDRONOV, 1961, p. 76 (type, *Pentamerus acutolobatus procerulus* BARRANDE, 1879b, p. 60)]. Medium to large sized, galeatiform; costate to plicate, costae distinctly bifurcating anteriorly, crossed by

fine concentric ridges; with or without ventral median septum; outer hinge plates discrete or rarely united into cruralium. *Lower Devonian (Lochkovian)*—*Middle Devonian (Eifelian)*: Europe, Urals, Central Asia [Sredni Azii], Siberia, USA (Alaska), *Lochkovian–Emsian*; Europe, Urals, Russia (Kolyma, Salair), Canadian Arctic Islands, *Eifelian*.

I. (*Ivdelinia*). With strongly raised costae or plicae, with median septum. *Lower Devonian (Lochkovian)*—*Middle Devonian (Eifelian)*: Europe, Urals, Central Asia [Sredni Azii], Siberia, USA (Alaska), *Lochkovian–Emsian*; Europe, Urals, Russia (Kolyma, Salair), Canadian Arctic Islands, *Eifelian*.—FIG. 687, 1*a–d*. **I. (I.) ivdelensis* (KHODALEVICH), upper Emsian–lower Eifelian, Ivdel region, eastern slope Urals; ventral, dorsal, anterior, lateral views, $\times 1$ (Khodalevich, 1951).—FIG. 687, 1*e–f*. *I. procerulus*, Koneprusy Limestone, Prague region, Czech Republic; dorsal, ventral views, $\times 1$ (Andronov, 1961).

I. (*Ivdelinella*) BRICE, 1982, p. 34 [**I. (I.) ellesmerensis* BRICE, 1982, p. 36; OD]. Similar to *I. (Ivdelinia)*, but differs in lacking a ventral median septum and having very low costae. *Lower Devonian (Emsian)*—*Middle Devonian (Eifelian)*: Canadian Arctic Islands.—FIG. 687, 2*a–e*. **I. (I.) ellesmerensis*, Blue Fiord Formation, Ellesmere Island; *a–c*, dorsal, ventral, posterior views of articulated specimen, $\times 1$; *d*, anterior view of another articulated specimen, $\times 1$; *e*, serial section at 5.25 mm from ventral beak, $\times 2.6$ (Brice, 1982).

Ivdelinella KIM, 1981, p. 36 [**I. trilobata* KIM, 1981, p. 37; OD]. Medium, outline subrhomboidal; high median fold and deep sulcus, lateral plications poorly developed, present only on large specimens; inner hinge plates united into low septum. *Lower Devonian (Lochkovian–Pragian)*: USA (southwestern Alaska), *Lochkovian*; Tian Shan, *Pragian*.—FIG. 687, 3*a–d*. **I. trilobata*, Manak Stage [Gorizont], Nuratau Range, southern Tian Shan; ventral, dorsal, lateral, anterior views, $\times 1$ (Kim, 1981).

Subfamily LEVIGATELLINAE

Rzhonsnitskaia, 1975

[Levigatellinae RZHONSNITSKAIA, 1975, p. 20]

Smooth with microsculpture of thin concentric growth lines; carinae well developed; inner hinge plates widely spaced and strongly inclined away from one another basally. *Silurian (upper Llandovery)*—*Lower Devonian (Lochkovian)*.

Levigatella ANDRONOV, 1961, p. 38 [**Gypidula olga* KHODALEVICH, 1939, p. 15; OD]. Small to medium sized, transverse, ventribiconvex; unisulcation well

developed and wide, short ventral median septum; inner hinge plates basolaterally directed, well-developed carinae. *Silurian (upper Llandovery)*—*Lower Devonian (Lochkovian)*: Altai Mountains, *upper Llandovery*; northeastern Siberia, *Wenlock*; Urals, Tian Shan, *Ludlow–Lochkovian*.—FIG. 687, 4*a–f*. **L. olga* (KHODALEVICH); *a–d*, ventral, dorsal, lateral, anterior views, Severouralsk Stage [Gorizont], eastern slope northern Urals, $\times 1$; *e*, external ornamentation, Severouralsk Stage [Gorizont], eastern slope northern Urals, $\times 6$; *f*, serial section of dorsal valve, Isovsk Stage [Gorizont], eastern slope central Urals, $\times 6$ (Sapelnikov, 1985a).

Subfamily DEVONOGYPINAE

Breivel & Breivel, 1977

[Devonogypinae BREIVEL & BREIVEL, 1977, p. 70]

Tuberculate microsculpture; weakly developed fold and sulcus; smooth umbonal region. *Silurian (Ludlow)*—*Middle Devonian (Givetian)*.

Devonogypa HAVLÍČEK, 1951, p. 5 [**Gypidula (Devonogypa) spinulosa*; OD] [= *Devonogypa (Glabrigalites)* STRUVE, 1992, p. 547 (type, *D. (G.) glabrigal* STRUVE, 1992, p. 548)]. Medium to large, smooth, strongly ventribiconvex with microsculpture of granules or fine spines arranged in oblique or horizontal rows; ventral fold absent or weakly developed, dorsal sulcus absent or shallow; inner hinge plates widely discrete. *Middle Devonian (Eifelian–Givetian)*: Czech Republic, Poland, Germany, Caucasus.—FIG. 688, 2*a–f*. **D. spinulosa*; *a*, dorsal view, Celechovice, Czech Republic, $\times 1$ (Havlíček, 1951); *b–e*, ventral, lateral, dorsal, anterior views, Skaly beds, Holy Cross Mountains, Poland, $\times 1$; *f*, external ornament, Skaly beds, Holy Cross Mountains, Poland, $\times 8$ (Biernat, 1966).

Gypidulella KHODALEVICH & BREIVEL, 1959, p. 26 [**G. pennatula*; OD]. Medium, wide, gently biconvex, finely costate; long, straight hinge line; dorsal sulcus and ventral fold wide and flat, developed anteriorly; exterior shell surface tuberculate; hinge plates adjoin each other basally. *Lower Devonian (upper Emsian)*—*Middle Devonian (lower Eifelian)*: Urals.—FIG. 688, 1*a–f*. **G. pennatula*, upper Emsian–lower Eifelian, Taltiisk Stage [Gorizont], eastern slope northern Urals; *a–d*, ventral, dorsal, lateral, anterior views, $\times 1$; *e*, external ornamentation, $\times 3$; *f*, serial section, $\times 4$ (Khodalevich & Breivel, 1959).

Pseudosieberella GODEFROID, 1972, p. 3 [**P. corrugata* GODEFROID, 1972, p. 6; OD]. Externally similar to *Sieberella* but differs in having small tubercles; discrete inner hinge plates. *Lower Devonian (Emsian)*—*Middle Devonian (Eifelian)*: Czech Republic, *Emsian*; Belgium, Germany, *Eifelian*.—FIG. 689, 1*a–f*. **P. corrugata*, Couvinian Stage

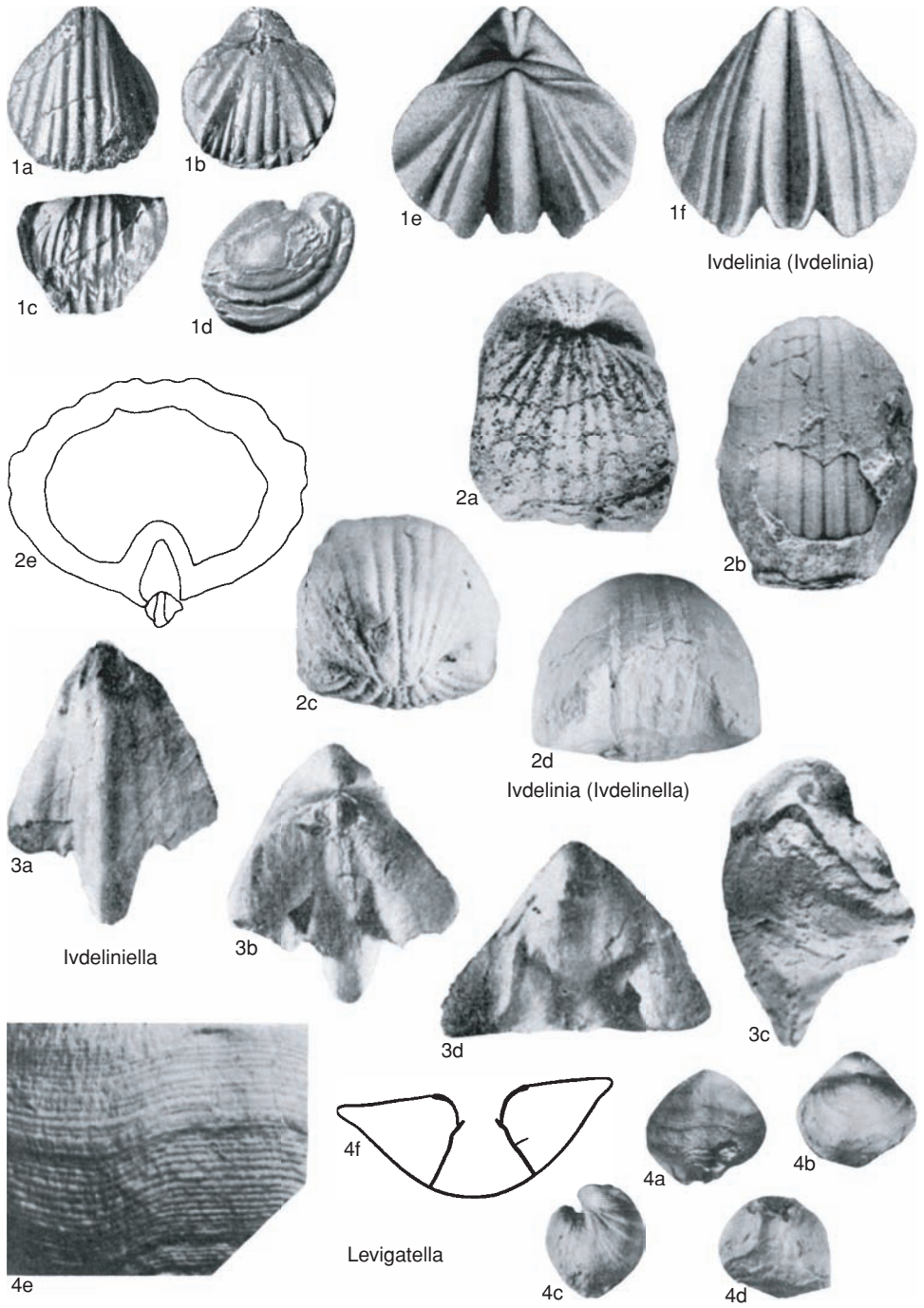


FIG. 687. Gypidulidae (p. 1013–1014).

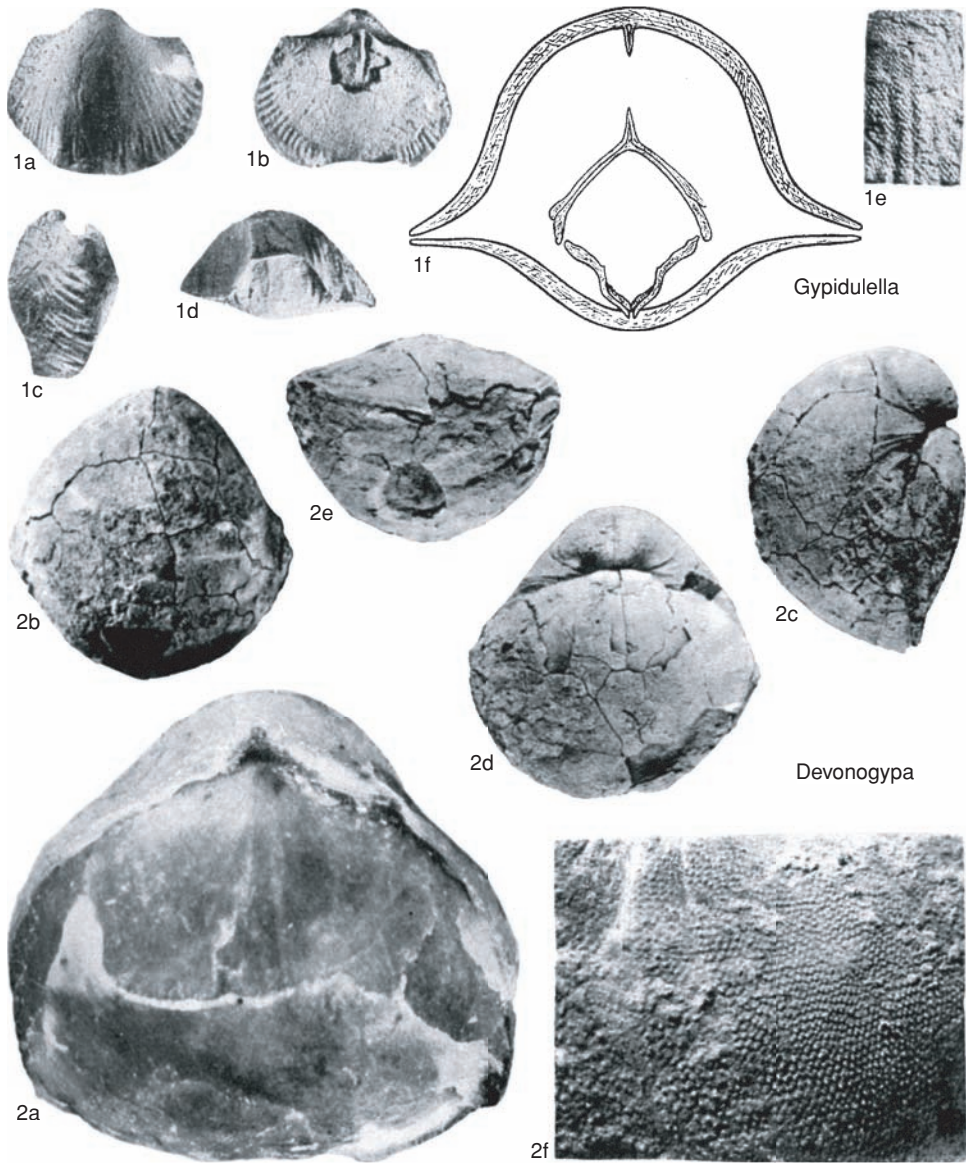


FIG. 688. Gypidulidae (p. 1014).

[Gorizont], Couvin, Belgium; *a–e*, ventral, dorsal, lateral, anterior, posterior views, $\times 1.5$; *f*, serial section at 8.0 mm from ventral umbo, $\times 2.5$ (Godefroid, 1972).

?*Wyella* KHODALEVICH, 1939, p. 21 [**Eichwaldia uralica* CHERNYSHEV, 1893, p. 179; OD]. Medium; smooth to plicate with honeycomb-like pitted exterior; fold and sulcus variably developed; inner hinge

plates discrete. *Silurian (Ludlow)–Middle Devonian (upper Eifelian)*: Urals, Central Asia [Sredni Azii], Kazakhstan, *Ludlow–Pridoli*; Urals, *Pragian–upper Eifelian*.—FIG. 689, *2a–e*. **W. uralica* (CHERNYSHEV), Isovsk Stage [Gorizont], Vagran River, eastern Urals; *a–d*, ventral, dorsal, lateral, anterior views, $\times 1$; *e*, external ornamentation, $\times 8$ (Sapelnikov, 1985a).

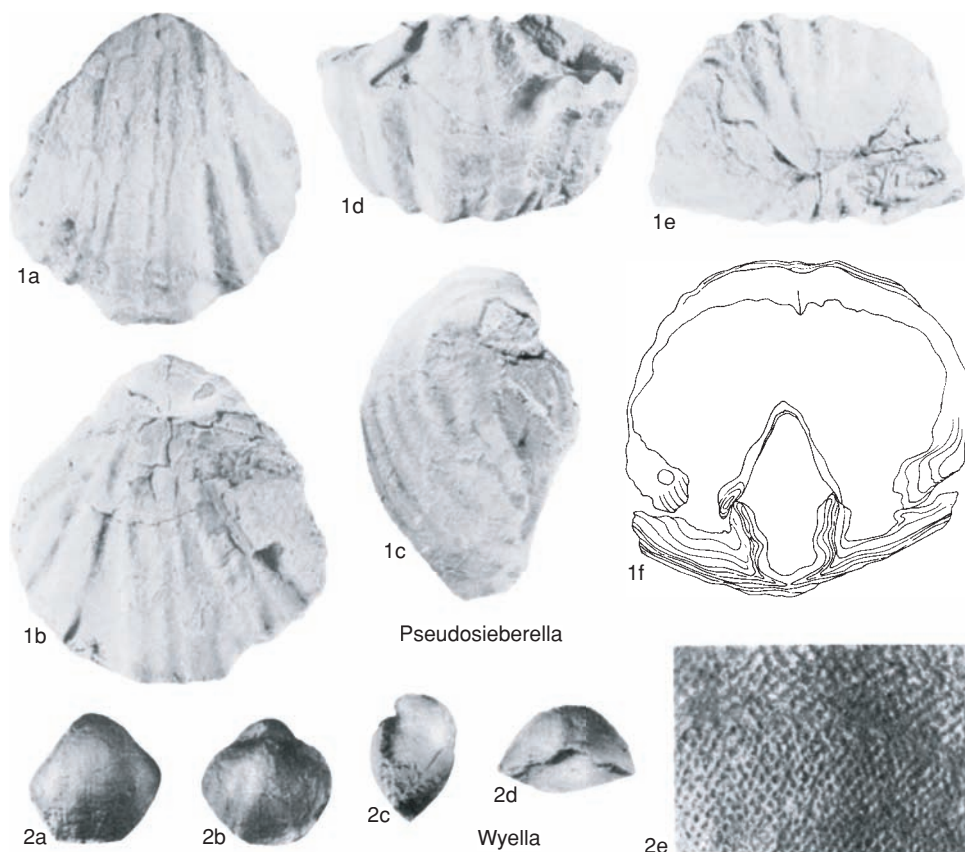


FIG. 689. Gypidulidae (p. 1014–1016).

Subfamily CONCHIDIPELLINAE
Rzhonsnitskaia, 1961

[Conchidiellinae RZHONSNITSKAIA, 1961, p. 47]

Medium to large sized, elongate, shells externally similar to *Kirkidium*, usually costate, rarely smooth; fold and sulcus absent or poorly developed. Lower Devonian (*Emsian*)–Middle Devonian (*Givetian*).

Zdimir BARRANDE, 1881, p. 171 [**Z. solus*; OD; =*Porambonites?* *robustus* BARRANDE, 1879b, p. 97] [= *Conchidiella* KHODALEVICH, 1939, p. 32 (type, *Pentamerus pseudobaschkiricus* CHERNYSHEV, 1885, p. 55)]. Shell large, inner hinge plates discrete, hinge plates lyre shaped. [Type material unsuitable for illustration.] Lower Devonian (*upper Emsian*)–Middle Devonian (*Givetian*): Czech Republic, Germany, Belgium, Carnic Alps, Urals, Russia (Novaya Zemlya, Salair, northeastern Siberia), Tian Shan,

Transcaucasus, South China, Japan.—FIG. 690, 1a–c. *Z. pseudobaschkiricus sibiricus*, Shandinsk Stage [Gorizont], Gurevsk region, Siberia; ventral, dorsal, lateral views, $\times 1$ (Rzhonsnitskaia, 1975).

Biseptum KHODALEVICH & BREIVEL, 1959, p. 39 [**B. rectecostatum*; OD]. Costate, costae commonly non-bifurcating; consists of fused inner hinge plates so that short median septum supports cruralium. Lower Devonian (*upper Emsian*)–Middle Devonian (*lower Eifelian*): Urals.—FIG. 691, 1a–d. **B. rectecostatum*, Taltiisk Stage [Gorizont], Ivdel region, eastern Urals; a–c, ventral, dorsal, lateral views, $\times 1$; d, serial section, $\times 2$ (Khodalevich & Breivel, 1959).

?**Glyptogypa** STRUVE, 1992, p. 549 [**Pentamerus galaeatus* var. *multiplicata* [C.] F. ROEMER, 1854 in 1852–1854, p. 352; OD]. Similar to *Zdimirella*, but differs in having costellae that commonly bifurcate and in having inner hinge plates that unite to form cruralium. Middle Devonian (*Eifelian*): Germany, France, Poland.—FIG. 690, 2a–e. **G. sp.* cf. *G. multiplicata* (ROEMER), Skaly beds, Holy

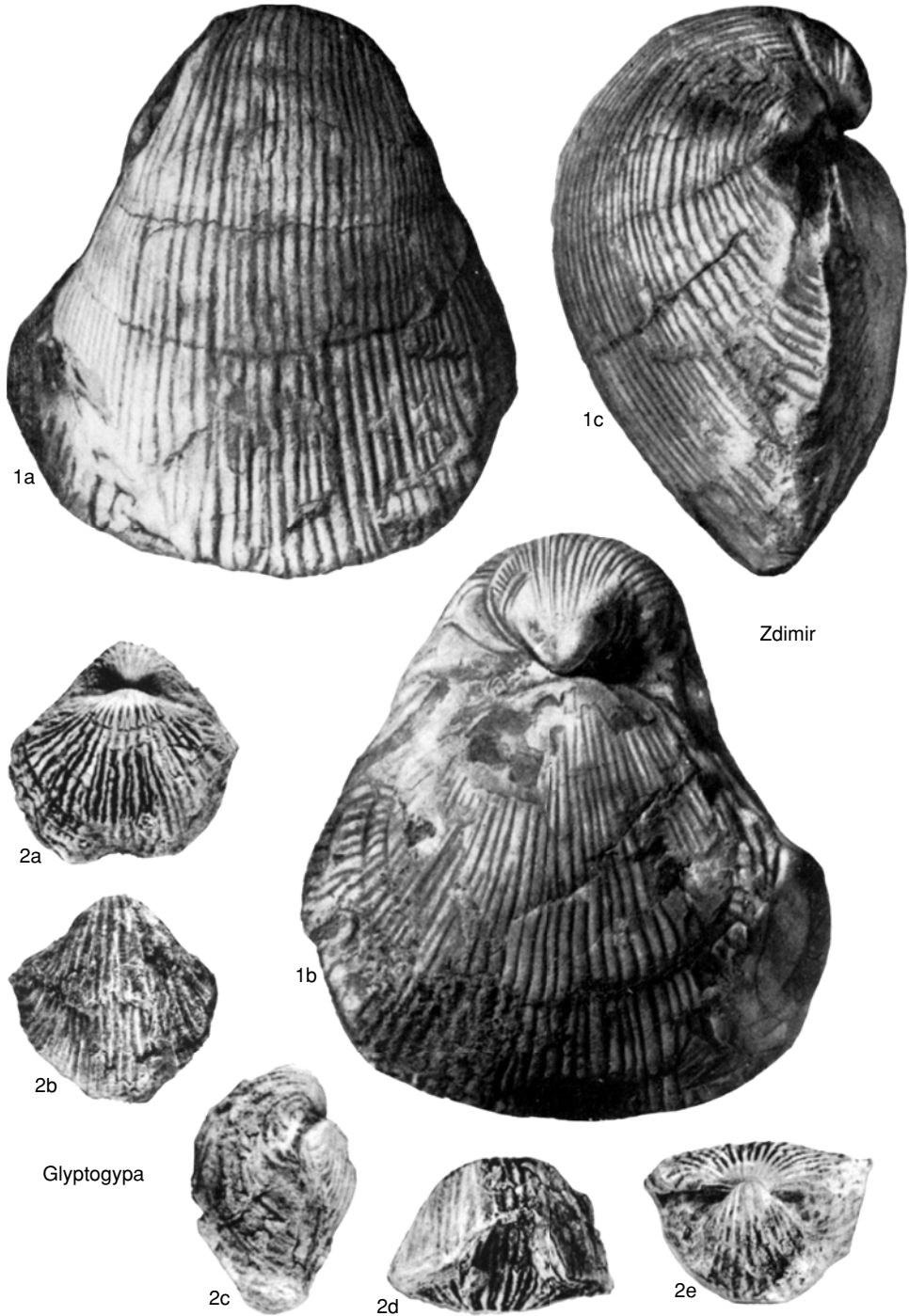


FIG. 690. Gypidulidae (p. 1017–1020).

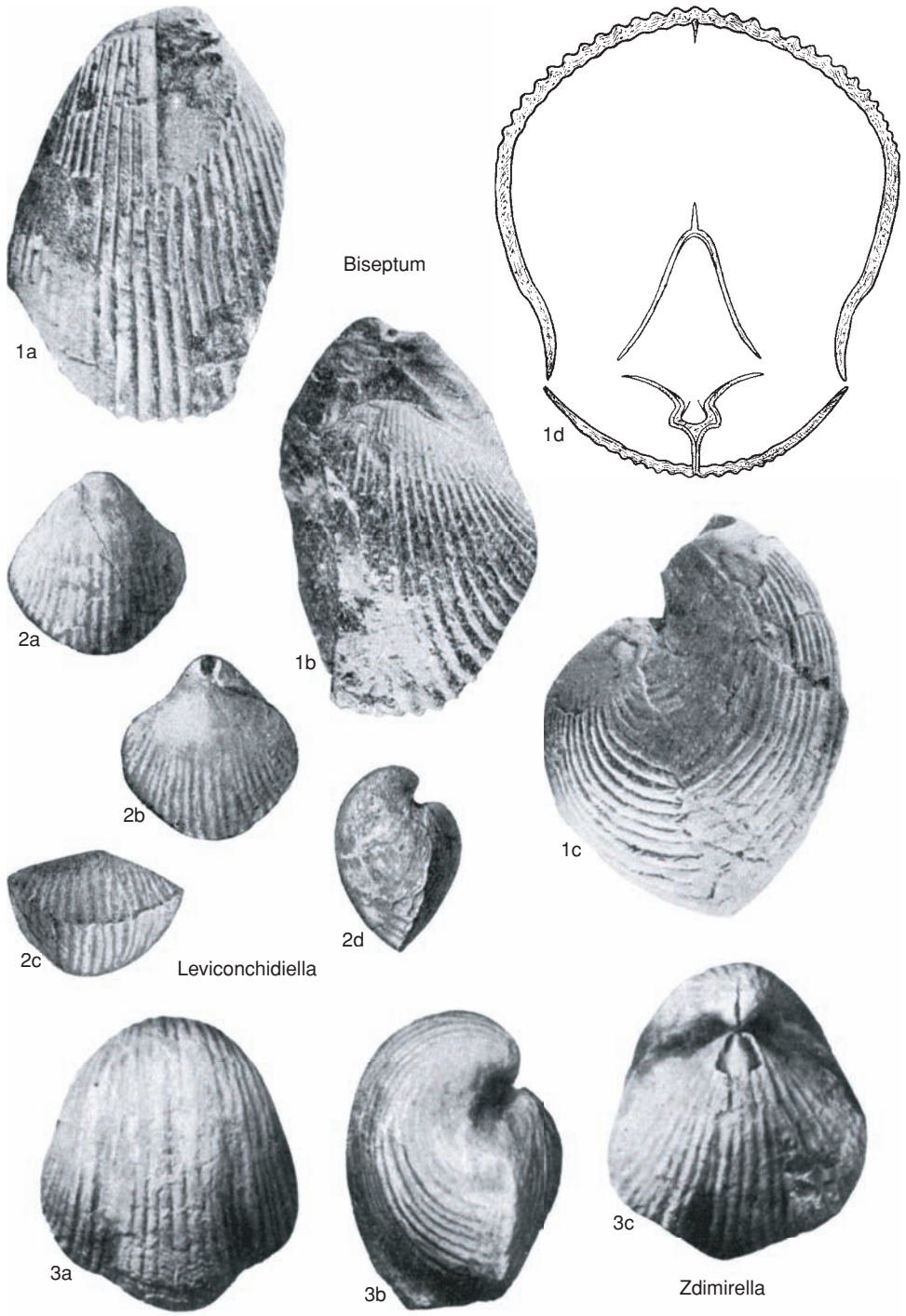


FIG. 691. Gypidulidae (p. 1017–1020).

Cross Mountains, Poland; dorsal, ventral, lateral, anterior, posterior views, $\times 1$ (Biernat, 1966).

Leviconchidiella RZHONSNIITSKAIA, 1960c, p. 301 [**Sieberella? vagranica* KHODALEVICH, 1951, p. 39; OD]. Subcircular to transverse, anteriorly costate, entirely lacking or with weakly developed ventral fold and dorsal sulcus; costae simple, flatly rounded; anterior commissure rectimarginate or weakly deflected ventrally; inner hinge plates discrete. *Lower Devonian (Emsian)–Middle Devonian (Eifelian)*: Urals, Tian Shan, Kuznetsk basin.—FIG. 691, 2a–d. **L. vagranica* (KHODALEVICH), Karpinsk Stage [Gorizont], Serov region, eastern Urals; ventral, dorsal, anterior, lateral views, $\times 1$ (Khodalevich, 1951).

?**Zdimirella** CHERKESOVA, 1973, p. 32 [**Z. kuzmini*; OD]. Large, strongly ventribiconvex; costellate, costellae extending from umbo; ventral fold and dorsal sulcus well expressed in anterior half of shell; inner hinge plates disjunct; ventral median septum high and long. *Middle Devonian (lower Givetian)*: Novaya Zemlya, western Canada.—FIG. 691, 3a–c. **Z. kuzmini*, basal Givetian, South Island, Novaya Zemlya; ventral, lateral, dorsal views, $\times 1$ (Cherkesova, 1973).

Subfamily GENICULIGYPINAE Blodgett & Boucot, 1998

[Geniculigypinae BLODGETT & BOUCOT, 1998, p. 454]

Prominent geniculation developed in both valves; microornament composed of fine radial grooves. *Middle Devonian (Givetian)*.

Geniculigypa BLODGETT & BOUCOT, 1998, p. 454 [**Sieberella newtonensis* IMBRIE, 1959, p. 369; OD]. Medium, ventribiconvex shells; anterior commissure nearly rectimarginate; smooth with microornament of fine radial grooves; inner hinge plates united to form cruralium supported by median septum. *Middle Devonian (Givetian)*: USA (Michigan).—FIG. 692a–f. **G. newtonensis* (IMBRIE), Newton Creek Limestone; a–e, posterior, anterior, ventral, dorsal, lateral views, $\times 3$; f, oblique ventral, $\times 6$ (Blodgett & Boucot, 1998).

NOMEN NUDUM

Schegultania ANDRONOV, 1961, p. 108 [no type species designated]. In same work ANDRONOV assigned to the genus three species: *S. karpinskii* ANDRONOV, 1961, *S. archangelskii* ANDRONOV, 1961, and *S. sp.* ANDRONOV, 1961. SAPELNIKOV (1985a, p. 134–135) redescribed the genus, and restricted to it only *S. karpinskii* [from the *Zdimir Zone* of northern Urals (upper Emsian–lower Eifelian)]. The other two species of ANDRONOV he indicated belong to unrelated, nonpentamerid brachiopods. SAPELNIKOV did not formally designate *S. karpinskii* as the type species of *Schegultania*.

GENERA REJECTED FROM THE GYPIDULIDAE

Levibiseptum XIAN, 1975, p. 31, placed in Rhynchospiriferinae by CARTER & others (1994, p. 337).

Family ENANTIOSPHENIDAE Torley, 1934

[Enantiosphenidae TORLEY, 1934, p. 93]

Specialized forms with crura terminating in loop; supporting plates consisting of outer hinge plate, crura, inner hinge plate; hinge plates unite to form median septum. *Middle Devonian (Givetian)*.

Enantiosphen WHIDBORNE, 1893, p. 97 [**Meganteris? vicaryi* DAVIDSON, 1882, p. 20; SD HOLZAPFEL, 1908, p. 123]. Large, smooth, biconvex, transversely elliptical to subtriangular shells; lateral and anterior margins of both valves strongly geniculate; spondylium supported on high median septum; crura extending forward and expanding to form broad plates connected to one another by transverse plate supported in center by median septum. *Middle Devonian (Givetian)*: England, Germany, Urals.—FIG. 693a–d. **E. vicaryi* (DAVIDSON), Massenkalk, Bilveringsen, Germany; a–b, dorsal, lateral views, $\times 1$ (Holzapfel, 1908); c–d, dorsal median septum and large part of loop, reconstruction of brachial loop and apparatus, $\times 1$ (Leidhold, 1928).—FIG. 694a–d. **E. vicaryi* (DAVIDSON); a, cross section, Massenkalk, Bilveringsen, Germany, $\times 1$ (Torley, 1934); b–d, dorsal, lateral views of brachial apparatus, ventral interior, no horizon or locality provided, $\times 1$ (Williams & Wright, 1961).—FIG. 693e. *E. torleyi*; posterior view, $\times 1$ (Holzapfel, 1908).

Enantiosphenella JOHNSON, 1974, p. 67 [**E. cybele* JOHNSON, 1974, p. 68; OD]. Similar to *Enantiosphen* but differs in its lack of median septa in both valves, resulting in discrete, long dental plates in ventral valve that enclose sessile spondylium, and in closely spaced, discrete, long, subparallel inner hinge plates in dorsal valve. *Middle Devonian (Givetian)*: USA (Nevada).—FIG. 695a–f. **E. cybele*, Denay Limestone, western Roberts Mountains; a–c, tilted view of ventral interior, ventral interior, posterior view of ventral exterior; d, ventral exterior; e–f, tilted view of dorsal interior, dorsal interior, $\times 2$ (Johnson, 1974).

Superfamily CLORINDOIDEA Rzhonsnitskaia, 1956

[*nom. transl.* BLODGETT, BOUCOT, & RONG, herein, ex Clorindinae RZHONSNIITSKAIA, 1956b, p. 49]

[Materials prepared by ROBERT B. BLODGETT,
A. J. BOUCOT, & RONG JIA-YU]

Small to medium-sized, galeatiform, uniplicate shells; smooth or costate; brachial

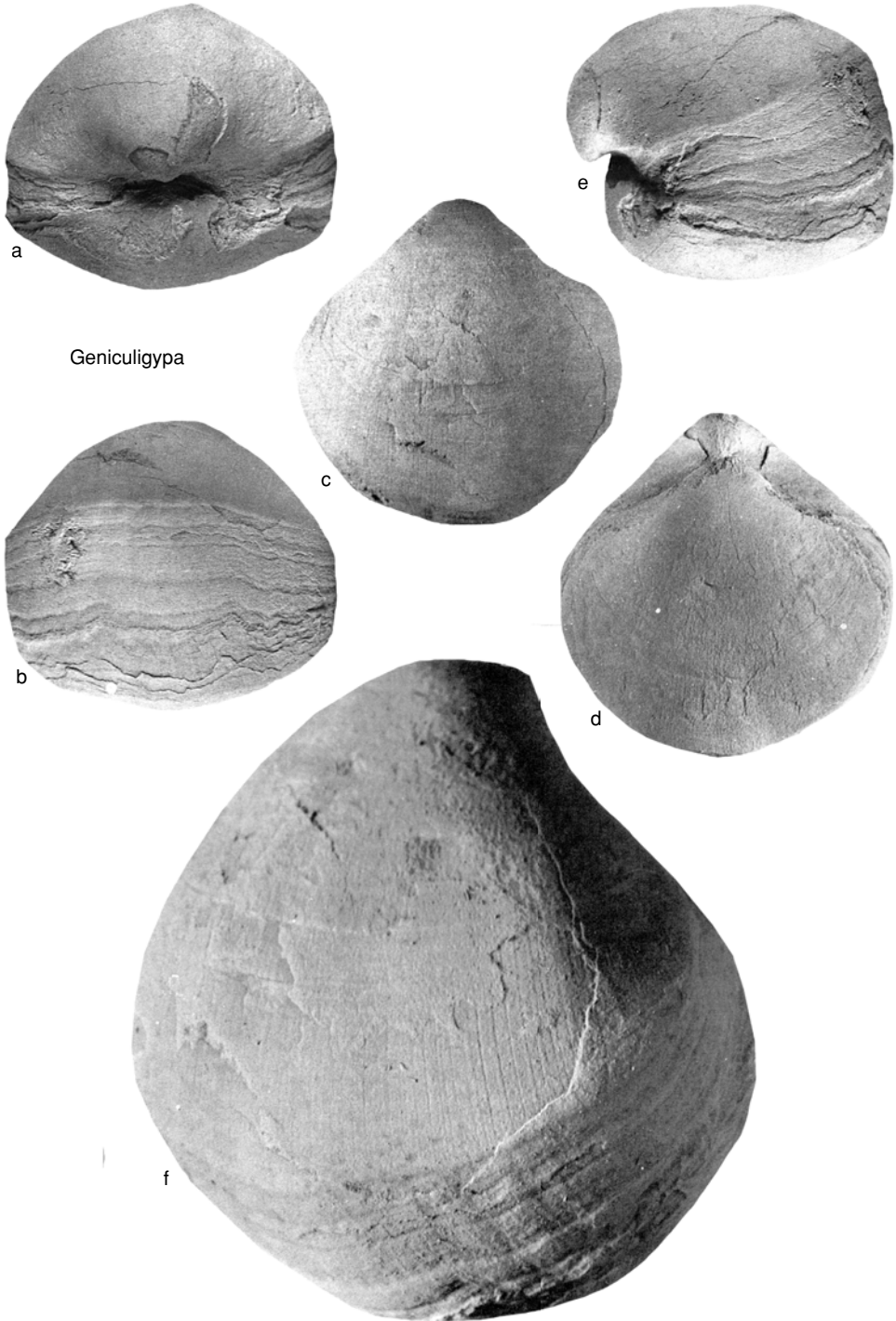
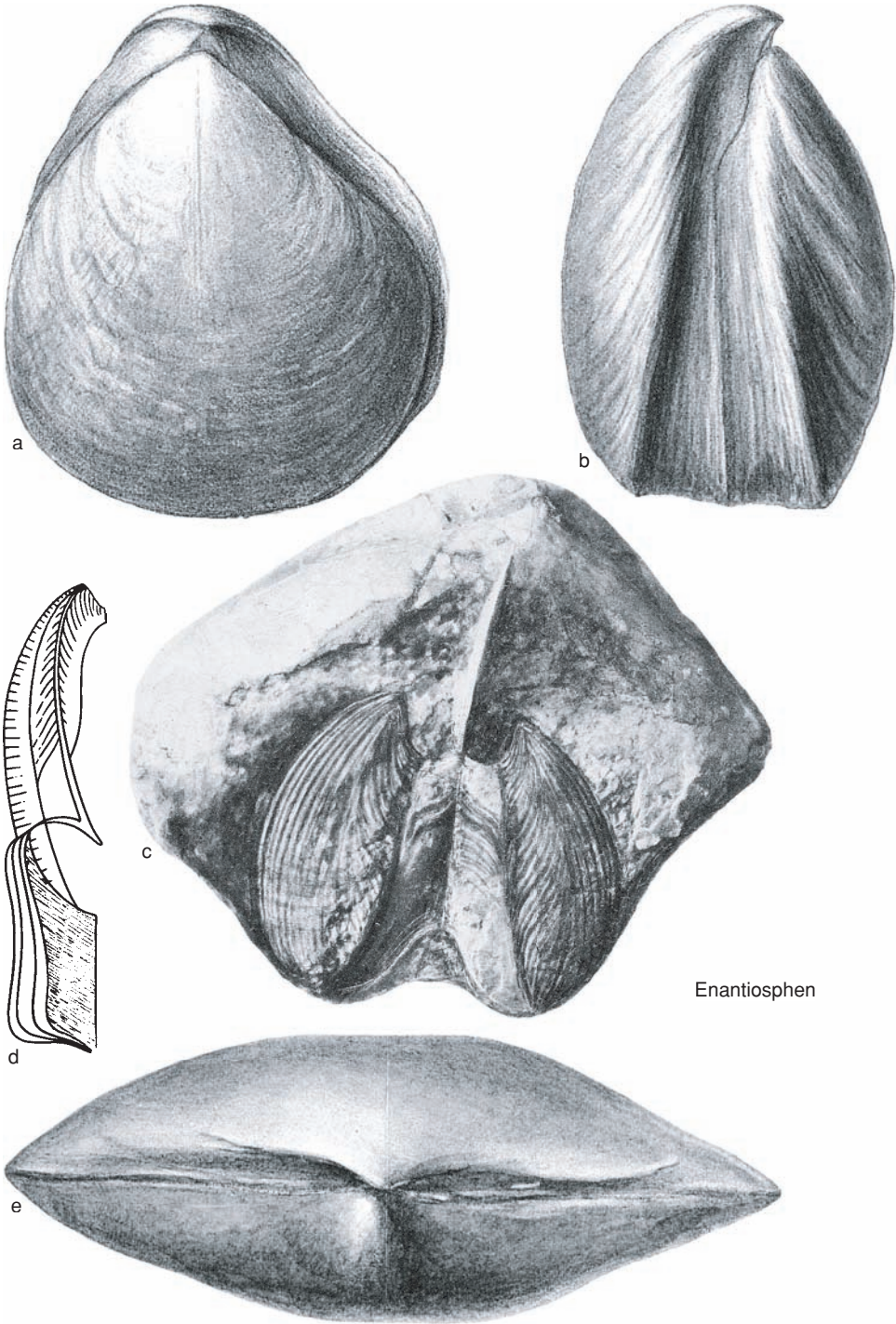


FIG. 692. Gypidulidae (p. 1020).



Enantiosphen

FIG. 693. Enantiosphenidae (p. 1020).

apparatus well developed with exceedingly short inner hinge plates that are discrete or united to form cruralium; hinge plates may be lyre shaped or straight in cross section; crura bladelike in cross section; carinae commonly developed. *lower Silurian (Rhuddanian)*–*Middle Devonian (Givetian)*.

Family CLORINDIDAE
Rzhonsnitskaia, 1956

[*nom. transl.* RZHONSNITSKAIA, 1961, p. 47, ex Clorindinae RZHONSNITSKAIA, 1956b, p. 49] [=Barrandellinae ANDRONOV, 1961, p. 34; Antirhynchonellidae NIKIFOROVA, 1960d, p. 205]

Description as for superfamily. *lower Silurian (Rhuddanian)*–*Middle Devonian (Givetian)*.

Subfamily CLORINDINAE
Rzhonsnitskaia, 1956

[Clorindinae RZHONSNITSKAIA, 1956b, p. 49]

Smooth. *Silurian (Rhuddanian)*–*Middle Devonian (Givetian)*.

Clorinda BARRANDE, 1879b, p. 109 [**C. armata*; OD]. Small to medium, smooth, ventribiconvex; dorsal fold and ventral sulcus well developed anteriorly, inner hinge plates discrete, widely spaced apart; hinge plates not lyre shaped in cross section; carinae present. *Silurian (Rhuddanian)*–*Middle Devonian (Givetian)*: widespread in Europe, Asia, North America, Greenland, Australia, North Africa.—FIG. 696, 1a–c. **C. armata*, Hlubocepy Limestone, Prague region, Czech Republic; lateral, dorsal, posterior views, ×1 (Barrande, 1879b).—FIG. 696, 1d–f. *C. tumidula*, Gun River Formation, Anticosti, Québec, Canada; ventral, anterior, dorsal views, ×1 (Schuchert & Cooper, 1932).

Antirhynchonella OEHLERT, 1887a, p. 1311 [**Atrypa linguifera* J. de C. SOWERBY in MURCHISON, 1839, p. 629; OD] [=*Barrandella* HALL & CLARKE, 1893, p. 241, obj.; in 1955, ICZN (Opinion 374) placed *Antirhynchonella* (type, *Atrypa linguifera* J. de C. SOWERBY in MURCHISON, 1839, p. 629) on The Official List of Generic Names; *Antirhynchonella* QUENSTEDT, 1871 in 1868–1871, *nom. nud.*, and *Barrandella* HALL & CLARKE, 1893, were added to The Index of Rejected and Invalid Generic Names in Zoology]. Medium, smooth, strongly ventribiconvex shell; dorsal fold rounded; inner hinge plates united to form cruralium that may or may not be supported by median septum; lyre-shaped cross section; carinae present. *Silurian (Aeronian)*–*Middle Devonian (Givetian)*: Europe, Siberia, Turkestan, South China, North America, Venezuela, *Aeronian*–*Přídolí*; Urals, Czech Republic, *Lochkovian*–*Emsian*; Poland, South China, *Givetian*.—FIG. 696, 3a–g. **A. linguifera* (J. de C.

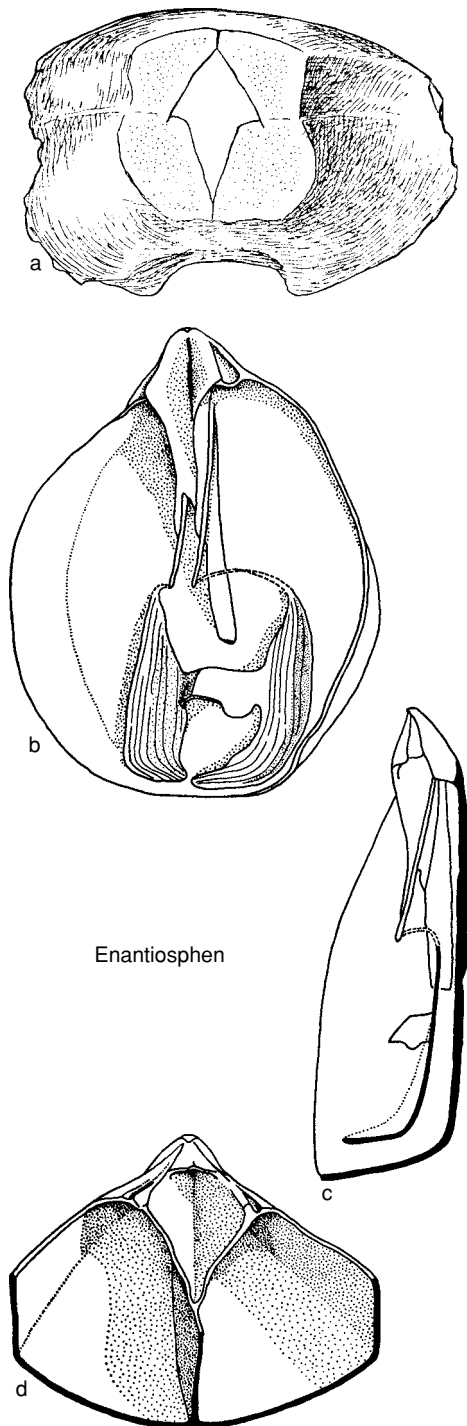


FIG. 694. Enantiosphenidae (p. 1020).

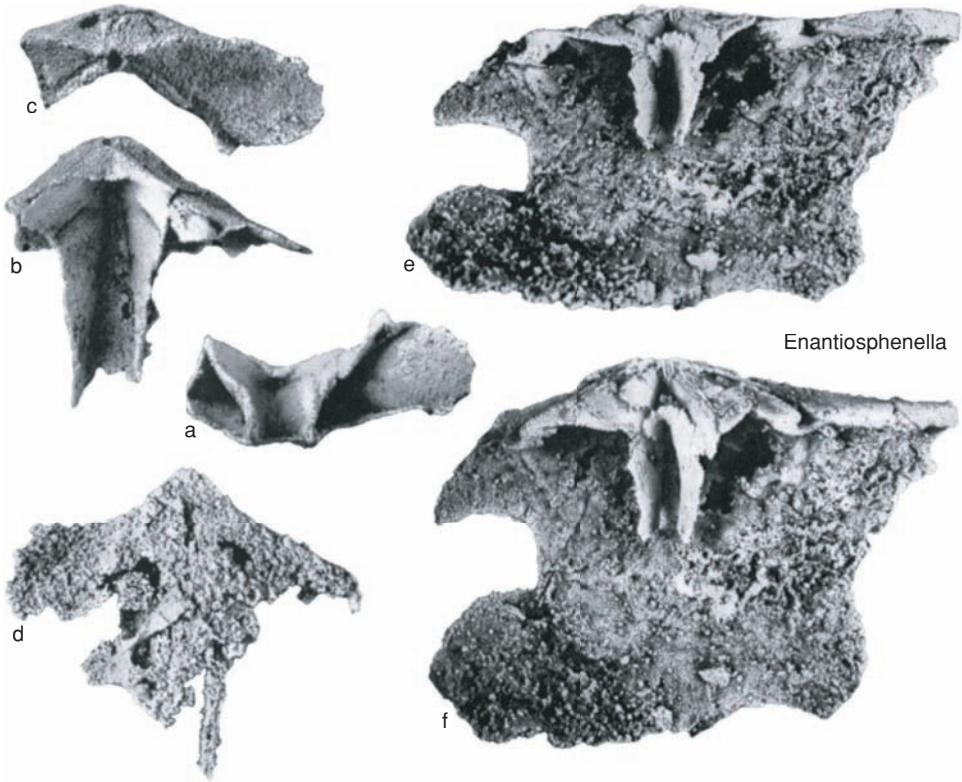


FIG. 695. Enantiosphenidae (p. 1020).

SOWERBY), Wenlock Limestone, Dudley, England; *a-c*, lateral, dorsal, anterior views, $\times 1$; *d-g*, serial sections, $\times 2$ (Amsden, 1965).

Barrandina BOOKER, 1926, p. 131 [**Pentamerus linguifera* var. *wilkinsoni* ETHERIDGE, 1892, p. 52; OD]. Medium, smooth, outline suboval, generally transverse; ventral umbo large, highly arched and strongly thickened; dorsal fold and ventral sulcus well developed; inner hinge plates discrete; hinge plates with lyre-shaped cross section; carinae small or absent. *upper Silurian*: Australia (New South Wales), Czech Republic, Urals.—FIG. 696,2*a-d*. **B. wilkinsoni* (ETHERIDGE), Barrandella Shales, Yass, New South Wales; dorsal, ventral, lateral, anterior views, $\times 1$ (Booker, 1926).

Boucotides AMSDEN, 1968, p. 44 [**B. barrandei* AMSDEN, 1968, p. 45; OD]. Medium, smooth clorindinid with inner hinge plates uniting to form cruralium or even low median septum; hinge plates with lyre-shaped cross section, lacking carinae; similar to *Antirhynchonella* but differs in having a deep V-shaped sulcus and corresponding ridgelike fold. *Silurian (Wenlock)*: USA (Arkansas), Czech Republic.—FIG. 696,5*a-d*. **B. barrandei*, St. Clair Limestone, Batesville district, Arkansas; *a*,

dorsal view, $\times 2$; *b-c*, ventral, anterior views, $\times 1$; *d*, ventral view, $\times 2$ (Amsden, 1968);

Indaclor HAVLÍČEK in HAVLÍČEK & ŠTORCH, 1990, p. 119 [**I. sellarius* HAVLÍČEK & ŠTORCH, 1990, p. 120; OD]. Small, externally similar to *Clorinda* with low, rounded fold on dorsal valve; anterior commissure uniplicate; ventral sulcus absent or weakly developed; inner hinge plates lacking; no carinae or lyre-shaped cross section. *Silurian (upper Wenlock-Ludlow)*: Czech Republic.—FIG. 696,4*a-d*. **I. sellarius* HAVLÍČEK & ŠTORCH, Motol Formation, Prague region; anterior, ventral, dorsal, lateral views, $\times 2.5$ (Havlíček & Storch, 1990).

Subfamily PENTAMERELLINAE Sapelnikov, 1973

[Pentamerellinae SAPELNIKOV, 1973, p. 40]

Exterior surface costate. *Silurian (Telychian)*—*Middle Devonian (Givetian)*.

Pentamerella HALL, 1867b, p. 373 [**Atrypa arata* CONRAD, 1841, p. 55; OD]. Variable size, ventribi-convex; inner hinge plates united to form

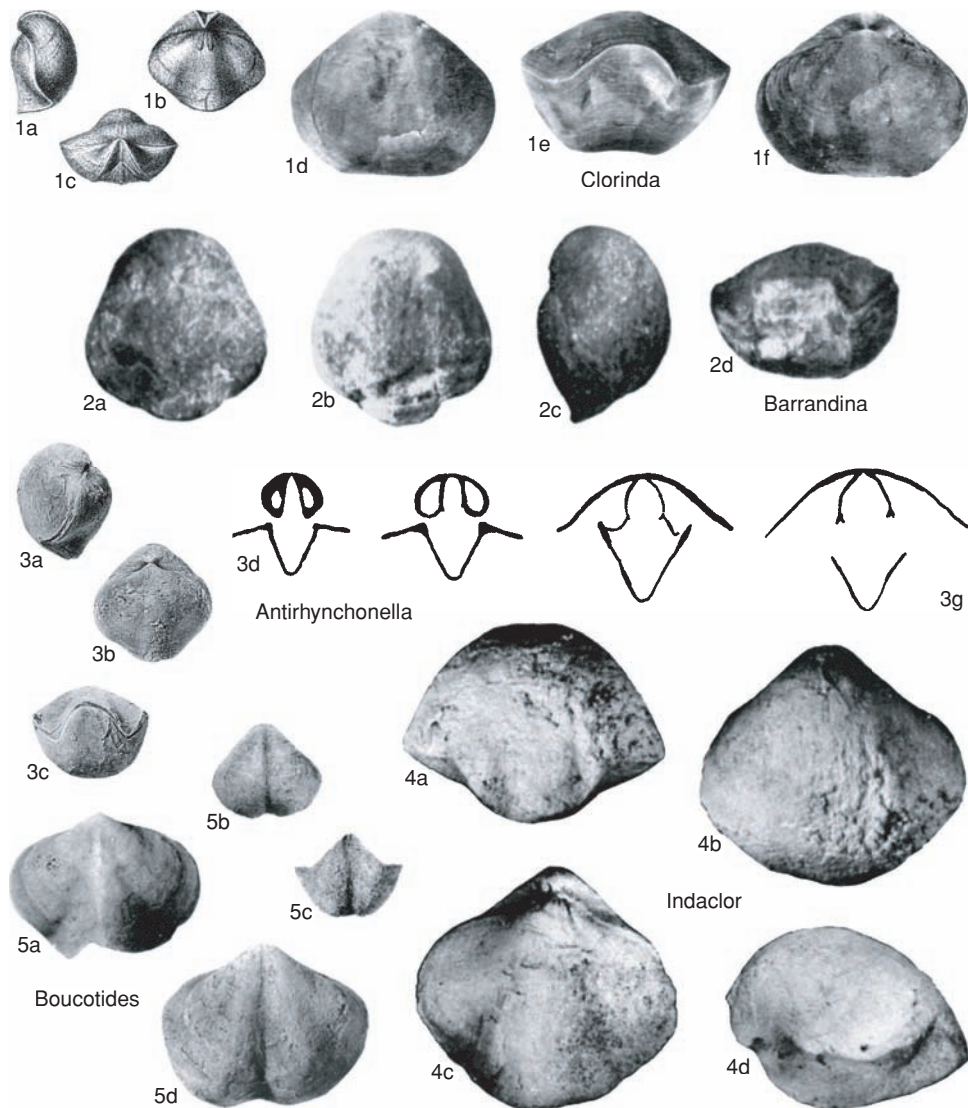


FIG. 696. Clorindidae (p. 1023–1024).

cruralium, sometimes supported by median septum; hinge plates with lyre-shaped cross section; noncarinate. *Lower Devonian (Emsian)–Middle Devonian (Givetian)*: North America, Europe, Siberia.—FIG. 697, 3a–c. **P. arata* (CONRAD), Schoharie Formation, Albany County, New York, USA; anterior, dorsal, lateral views, $\times 1$ (Schuchert & Cooper, 1932).

Clorindella AMSDEN, 1964, p. 236 [*Barrandella areyi* HALL & CLARKE, 1893, p. 368; OD]. Small, paucicostate shell; costae coarse, subangular, undivided

anteriorly; outer hinge plates and crura join with upper (ventral) edge of processes projecting as carinae; inner hinge plates unite above dorsal valve floor to form cruralium; hinge plates with lyre-shaped cross section; carinae present. *Silurian (Telychian)*: USA (New York).—FIG. 697, 4a–h. **C. areyi* (HALL & CLARKE), Clinton Group; a–e, posterior, ventral, anterior, lateral, dorsal views, Rochester, $\times 2$ (Amsden, 1964); f–h, transverse serial sections at 2.5, 3.1, and 4.0 mm from tip of ventral valve beak, $\times 3$ (Amsden, 1965).

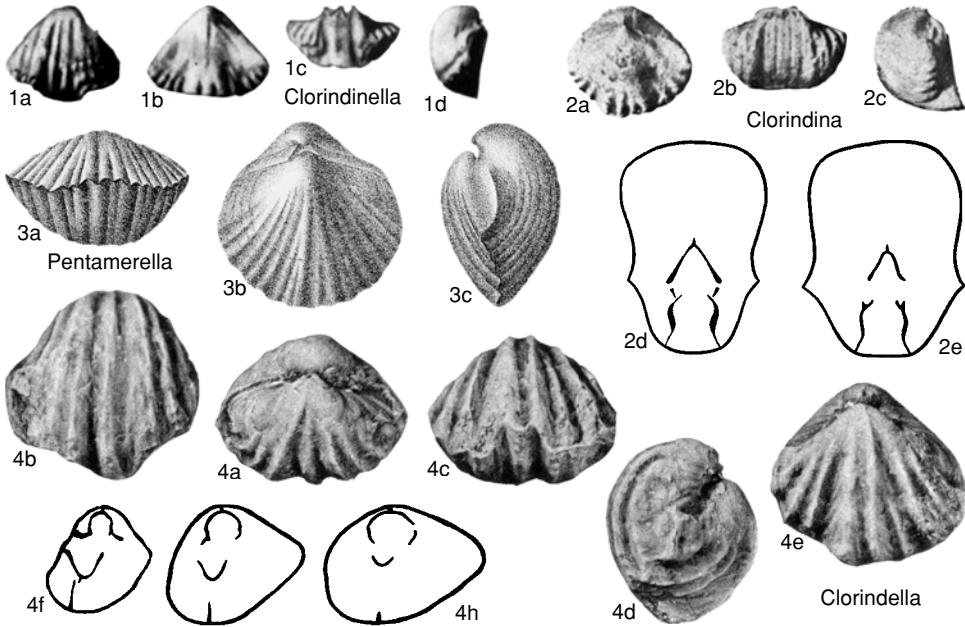


FIG. 697. Clorindidae (p. 1024–1026).

Clorindina KHODALEVICH, 1939, p. 11 [**C. uralica*; OD]. Medium, strongly to moderately inflated, ventribiconvex; uniplication developed anteriorly; costae divided by longitudinal furrows anteriorly; longitudinal furrows at anterior margin; inner hinge plates discrete; hinge plates weakly lyre shaped; carinae may or may not be present. *Lower Devonian–Middle Devonian (Eifelian)*: Russia (Novaya Zemlya, Kolyma), Altai Mountains, Urals, Salair, Tian Shan, *Lower Devonian*; Germany, *Eifelian*. —FIG. 697,2a–c. **C. uralica*, Saumsk Stage [Gorizont], Nadezhdin region, eastern Urals; dorsal, anterior, lateral views, $\times 2$ (Khodalevich, 1939). —FIG. 697,2d–e. *C. arataeformis*, Solovykhin beds, Altai Mountains; serial sections, $\times 3.7$ (Sapelnikov, 1985a).

Clorindinella RZHONSNIITSKAIA, 1975, p. 61 [**C. alaica*; OD; =*Clorindina alaica* NIKIFOROVA, 1960d, pl. 25, fig. 4a–d, *nom. nud.*]. Small, with sharp-edged lateral and anterior commissure; ventral sulcus wide

with trapezoidal or arched tongue; costae rounded, with longitudinal furrows at anterior margin; ventral septum and spondylium short; hinge plates discrete; lyre-shaped cross section; carinae may or may not be present. [The type species was given by RZHONSNIITSKAIA (1975, p. 61) as *Clorindina alaica* NIKIFOROVA, 1960d, which appeared only as an illustration (pl. 25, fig. 4a–d) in the brachiopod volume of the *Osnovy Paleontologii* (T. G. SARYCHEVA, ed., 1960). Because it lacks a written description or diagnosis, the usage by NIKIFOROVA in 1960d stands as a *nomen nudum*. RZHONSNIITSKAIA in 1975 gave a description of the species, and under ICZN rules this usage is accepted as the first legal usage of the species name.] *Lower Devonian (Emsian)–Middle Devonian (Eifelian)*: Urals, Kuznetsk Basin, Tian Shan, ?western Europe. —FIG. 697,1a–d. **C. alaica*, Baskuskan Limestone, Gurevsk, Siberia; ventral, dorsal, anterior, lateral views, $\times 1$ (Rzhonsniitskaia, 1975).