1715*a–c*. **H. orienta*, Chengjiang Lagerstätte, Yu'anshan Formation; *a,* apex of dorsal valve exterior, showing delineated juvenile shell, with rows of pustules, ×40; *b,* detail of anterolateral margin, showing parallel thick tubes, with pyritized spinelike setae, NIGP11, ×30; *c,* detail of punctate shell structure with thick orthogonal canals exposed on exfoliated surface of ventral valve exterior, ×40 (new).——FIG. 1716*a–c*. **H. orienta*, Chengjiang Lagerstätte, Yu'anshan Formation; *a,* detail of anterior margin showing punctate shell structure with openings of thick canals and preserved thick spinelike setae, as well as thinner (=possible marginal) setae, NIGP33, ×7; *b,* detail of one canal showing wall and central canal, width may have been enlarged during taphonomy, ×150; *c,* detail of pustulose ornamentation, with openings (and pyritized matter inside, which may represent setae) of orthogonal canals close to umbo, NIGP9, ×200 (new).

CRANIATA

LEONID E. POPOV,[1] MICHAEL G. BASSETT,[1] and LARS E. HOLMER[2]

[[1]National Museum of Wales; and [2]University of Uppsala]

Subphylum CRANIIFORMEA Popov & others, 1993 Class CRANIATA Williams & others, 1996

POPOV, BASSETT, and HOLMER (2000) reviewed the problems surrounding the classification of the groups included currently within the Craniata. In most previous phylogenetic models it was assumed that the three main groups of craniates, the Craniidae, Craniopsidae, and Trimerellidae, had originated from separate organophosphatic-shelled ancestors around the Ordovician, approximately (e.g., WILLIAMS & ROWELL, 1965c, fig. 141). The craniates form a monophyletic group in the analyses by HOLMER and others (1995), POPOV, HOLMER, and BASSETT (1996), and POPOV, HOLMER, and BASSETT (2000, fig. 1), whereas several cladograms in the studies by WILLIAMS and others (1996) and WILLIAMS, CARLSON, and BRUNTON (2000) were inconclusive, in particular regarding the phylogenetic position of the craniates relative to the class Chileata. This problem clearly needs further study, and the phylogenetic relationships between the three orders of craniates are still unresolved. The enigmatic *Heliomedusa* SUN & HOU from the Early Cambrian Chengjiang Lagerstätte (Yu'anshan Formation), Yunnan, was most recently assigned provisionally to the order Craniopsida within the Craniata (POPOV & HOLMER, 2000a; ZHANG, HOU, & EMIG, 2003). It can now be shown (reference to section above) to belong within the stem-group brachiopods, however, together with *Mickwitzia*. Thus, there is no longer any member of the class Craniata recorded from the Lower Cambrian, with only a potential Middle Cambrian representative (POPOV & HOLMER, 2000a), and the Cambrian origin of the craniiforms remains a problem.

Potential synapomorphies of the Craniata include possession of a nonfibrous carbonate shell and the lack of a pedicle. The mode of attachment of modern craniids may be important for understanding the origin and evolution of the brachiopod holdfast, however; WILLIAMS, BRUNTON, and MACKINNON (1997, p. 353) proposed that the attachment of modern *Novocrania* (NIELSEN, 1991), which consists of a thin patch of epithelium that is central to a shell secreted holoperipherally during postlarval growth, probably had as its plesiomorphy an atrophied holdfast acting as a pedicle. It is possible that this type of attachment may possibly be close to the primitive type of craniiform-rhynchonelliform pedicle. No craniate preserves any clear trace of a larval shell (CHUANG, 1977; but see FREEMAN & LUNDELIUS, 1999 for a contrasting view), indicating that their ontogeny was like that of Recent *Novocrania* (NIELSEN, 1991), where the first shell is secreted only after

settlement. The mantle lobes remain separated throughout ontogeny (ROWELL, 1960), but NIELSEN (1991) showed that both valves are secreted initially within a single epithelial area on the dorsal side of the early postlarval stage. This may suggest that the adult separation of the mantle lobes represents a derived feature for the craniiforms, while fused mantle lobes may be the plesiomorphic state (and also in the paterinates and chileates). *?Middle Cambrian, Ordovician–Holocene.*

CRANIOPSIDA

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[National Museum of Wales; and University of Uppsala]

Order CRANIOPSIDA Gorjansky & Popov, 1985

Only four genera can still be referred unquestionably to this group, all of which are Ordovician to Carboniferous in age. Craniopsides are characterized by extremely simple craniiform morphology and an impunctate calcareous shell; the cladistic analysis by POPOV, BASSETT, and HOLMER (2000) indicated that they might represent a paraphyletic stem group from which the Craniida and Trimerellida were derived. The only possible Cambrian craniopside is now the problematic Middle Cambrian *Discinopsis* (POPOV, HOLMER, & BASSETT, 1996; POPOV, BASSETT, & HOLMER, 2000). *?Middle Cambrian, Ordovician–Lower Carboniferous (Tournaisian).*

CRANIIDA

MICHAEL G. BASSETT

[National Museum of Wales]

Since the earlier compilation of the craniide section in Volume 2 of the revised brachiopod *Treatise* (BASSETT, 2000), only two new craniid genera have been published, as detailed below. Molecular phylogenetic analyses (COHEN, GAWTHROP, & CAVALIER-SMITH, 1998; COHEN, 2000) have confirmed the evolutionary stability of the group and its relationships with other brachiopod clades, including phoronids. Such stability is also reflected in the evolution of the chemicostructure and fabric of the craniid shell, which has been virtually unchanged since the first appearance of the stock in the Early Ordovician (Arenig) (CUSACK & WILLIAMS, 2001a; WILLIAMS, CUSACK, & BROWN, 1999; PEREZ-HUERTA, CUSACK, & ENGLAND, 2007); especially important in these studies has been a greater understanding of ventral valve structure, not least because this valve is generally weakly developed and differentially mineralized by comparison with the dorsal valve.

The order Craniida continues to consist of a single family (Craniidae) within a single superfamily (Cranioidea).

Order CRANIIDA Waagen, 1885
Superfamily CRANIOIDEA Menke, 1828
Family CRANIIDAE Menke, 1828

Celidocrania LIU, ZHU, & XUE, 1985, p. 9 [40] [**C. luohensis*; OD]. [This genus was earlier synonymized with *Acanthocrania* (see BASSETT, 2000, p. 171).

They are certainly very close in dorsal morphology, in particular with a common ornamentation of coarse spines and papillae and with distinctively large anterior adductor muscle scars divided by a weak myophragm, although in *Celidocrania* this latter feature becomes a distinct longitudinal ridge anteriorly. Closer comparison was originally not possible based only on the original illustrations of the Chinese material from Hinggan Ling in Heilongjiant Province. Recently, however, it has been possible to examine type specimens of *Celidocrania,* which confirms their general similarity to *Acanthocrania,* with the possible exception of the distinct anterior ridge.

One factor to bear in mind when comparing the two genera is their differences in age. Known specimens of *Acanthocrania* first appear in the lower Upper Ordovician (Caradoc, Sandbian). The type specimens of *Celidocrania* are from the Dazhi-Xiqiue lithological interval of somewhat earlier, mid-Ordovician age (upper Arenig–lower Llanvirn; Liu, Zhu, & Xue, 1985).]

Deliella Halamski, 2004, p. 182 [**D. deliae*; OD]. Small, dorsal valve subconical, beak posteriorly subcentral, anterior face convex, posterior face subplanar; ornament of fine costae, branching costellae, and capillae; fine concentric growth lines forming a netlike granular pattern at intersection with radial ornament; encrusting; ventral valve not known. *Lower Devonian (Emsian)–Middle Devonian (Givetian)*: Poland, Germany, Ukraine, North America.

Mesocrania Smirnova, 1997, p. 998 [**Craniscus barskovi* Smirnova, 1972, p. 20; OD]. Dorsal valve low and undulose or weakly subconical with subcentral to posterocentral beak; shell outline subsquare through subrectangular to slightly rounded; weakly preserved growth lines and occasional short, irregular riblets; dorsal posterior adductor scars large, separated, close under posterior margin; anterior adductors large, rounded to kidney shaped, raised on flaring platform and separated by a slender ridge; limbus–marginal rim slender; shell structure with some branching punctate canals; encrusting; ventral valve not known. *Upper Jurassic (Oxfordian)–Lower Cretaceous (Berriasian)*: Ukraine.

Novocrania Lee & Brunton, 2001, p.5 [**Patella anomala* Müller, 1776, p. 237; OD]. [*Novocrania* is a *nomen novum* proposed as a replacement generic name for *Neocrania* Lee & Brunton, 1986, p. 150, which is preoccupied by an insect genus (Lepidoptera) published by Davis, 1978, p. 92 (type species, *Neocrania bifasciata*). Diagnostic characters, stratigraphic range, and geographic distribution of *Novocrania* are as set out by Bassett, 2000, p. 180, fig. 100,*2a–h* (under *Neocrania*); one amendment is to note that in fact the thin, encrusting ventral valve of Recent species, including the type species, is not uncommonly weakly calcified, confirming the disposition of large, submarginal, rounded, and separated posterior muscle scars, with large, posterocentral, medially united anterior scars within a heart-shaped pit bounded by a strong rim; ventral limbus broad, pustulose; vascular system pinnate.]

TRIMERELLIDA

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[National Museum of Wales; and University of Uppsala]

Order TRIMERELLIDA Gorjansky & Popov, 1985

The Trimerellida constitute a small but well-defined clade of quite large articulated organocarbonatic-shelled brachiopods. The analyses by Popov, Holmer, and Bassett (1996) and Popov, Bassett, and Holmer (2000) gave support for the view that they constitute a monophyletic group within the Craniata. The earliest known trimerellides, the Ussuniidae from the Llandeilo, show affinities with the craniopsides in their muscle system and other characters, as noted by Gorjansky and Popov (1986). *Ordovician (Llandeilo)–Silurian (Ludlow).*

Superfamily TRIMERELLOIDEA Davidson & King, 1872

Family TRIMERELLIDAE Davidson & King, 1872

[incl. Zhuzhaiidae Xu & Li, 2002, p. 419]

Belubula Percival, 1995, p. 48 [**B. spectacula*; OD] [?=*Zhuzhaiia* Xu & Li, 2002, p. 419 (type, *Z. transitense*)]. Shell large, globose, strongly biconvex; ventral valve with prominent, incurved beak; ventral interarea triangular, concave, divided by broad, concave homeodeltidium; ventral interior with deep umbonal cavities; muscle platform low, solid; cardinal buttress stout, wall-like; dorsal interior with low visceral platform, slightly vaulted anteriorly. *Ordovician (Caradoc, ?Ashgill):* Australia (New South Wales), ?China.——Fig. 1717,*4a–d*. **B. spectacula*, Belubula Limestone, Caradoc, New South Wales, Australia; *a*, dorsal valve interior, SUP73473, ×1.6;

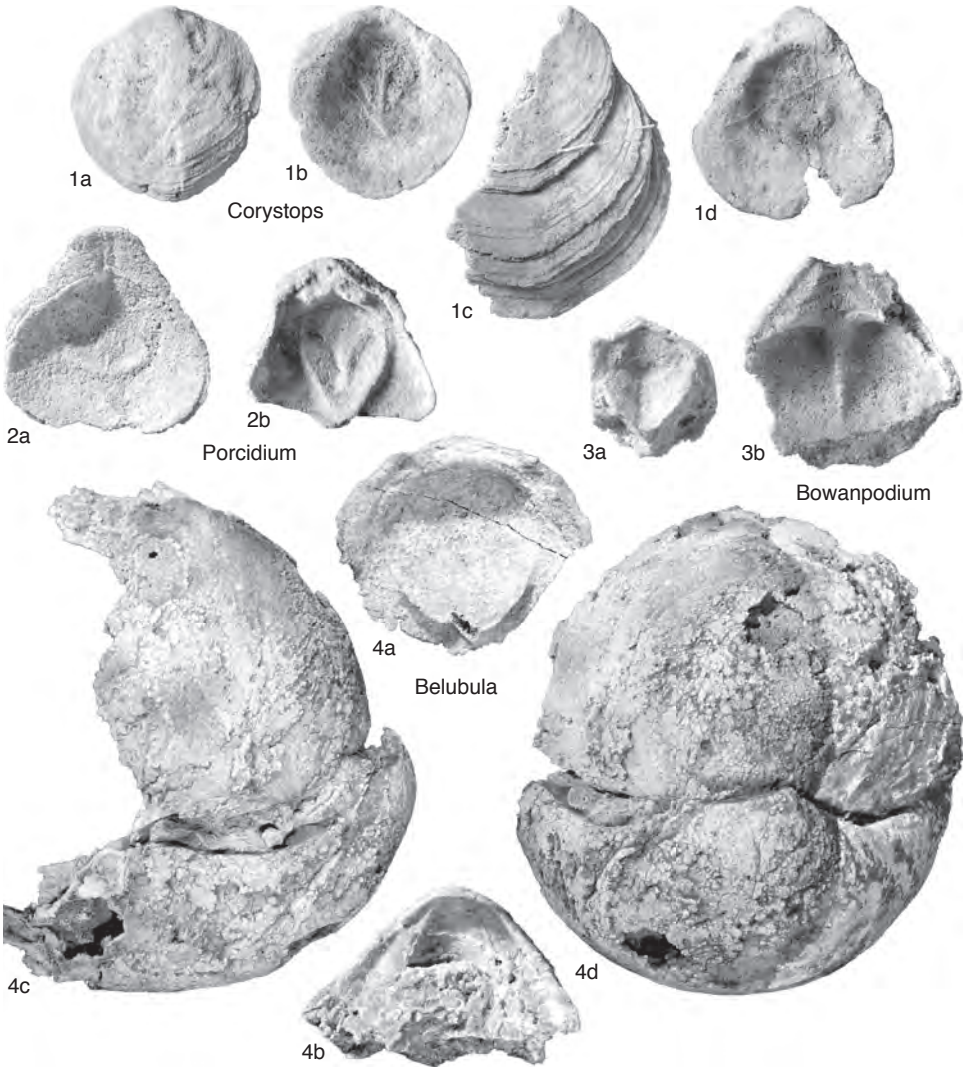

FIG. 1717. Trimerellidae (p. 2592–2594).

b, ventral valve, interarea, SUP73476, ×1; *c–d*, holotype, conjoined valves, lateral view, posterior view, SUP73470, ×1 (Percival, 1995).

Bowanpodium PERCIVAL, 1995, p. 55 [**B. solidum*; OD]. Shell biconvex; ventral valve with high interarea, divided by broad homeodeltidium; umbonal cavities vestigial, ventral muscle platform low, solid; cardinal buttress prominent, supported anteriorly by ridge; dorsal muscle platform solid, strongly thickened, elevated anteriorly and excavated anterolaterally, and with weak anterior median ridge. *Ordovician (Caradoc):* Australia (New South Wales).——FIG. 1717,*3a–b*. **B. solidum*, Quondong Limestone; *a*, holotype, dorsal valve interior, AMF60700, ×3; *b*, ventral valve interior, AMF60757, ×1.5 (Percival, 1995).

Corystops PERCIVAL, 1995, p. 55 [**C. lamellatus*; OD]. Shell dorsibiconvex to convexiplanar, lamellose; ventral interarea undivided, planar, and strongly apsacline; ventral interior with low, solid visceral platform; dorsal interior with low, solid visceral platform, divided anteriorly by median ridge. *Ordovician (Caradoc):* Australia (New South Wales).——FIG. 1717,*1a–d*. **C. lamellatus*, Quondong Limestone; *a–b*, holotype, dorsal valve exterior, interior of holotype, SUP63498, ×2; *c*, ventral valve exterior, SUP63502, ×2; *d*, ventral valve interior, SUP63503, ×2 (Percival, 1995).

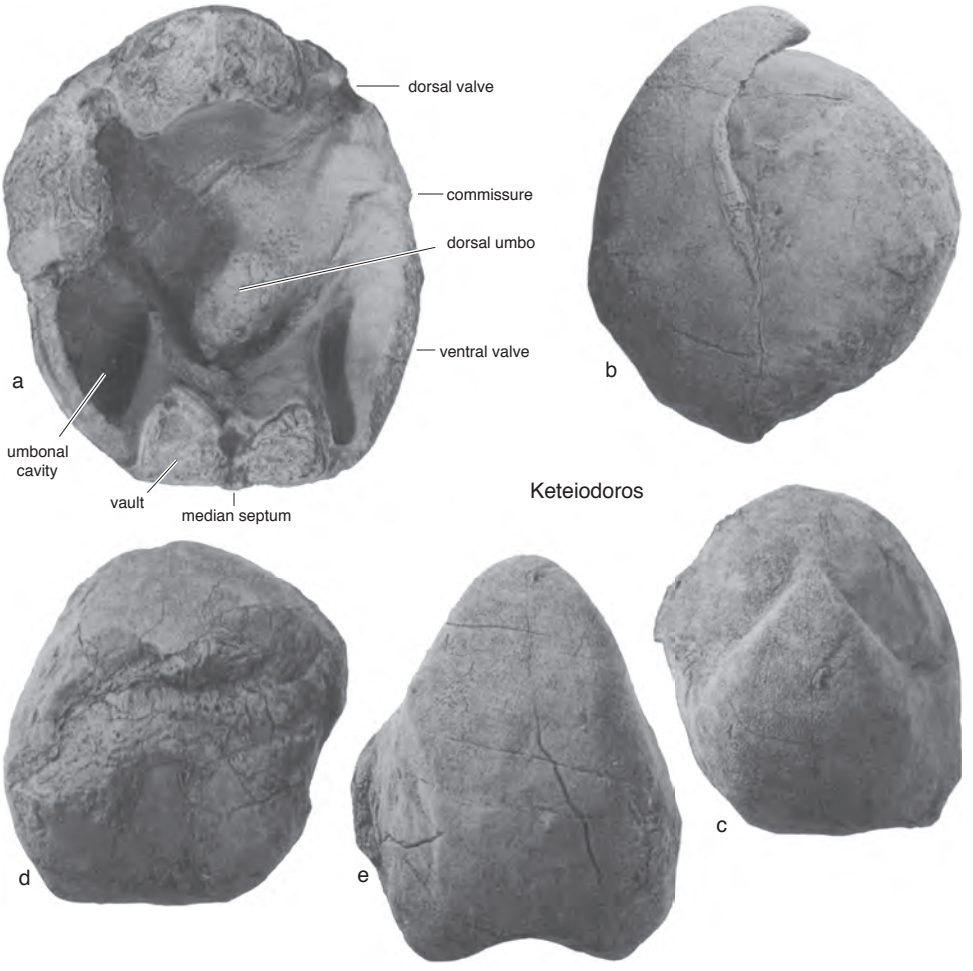

FIG. 1718. Trimerellidae (p. 2594).

Keteiodoros STRUSZ & others, 1998, p. 176 [**K. bellense*; OD]. Shell very large and strongly equibiconvex; ventral umbo long, incurved; dorsal umbo strongly incurved, bulbous, fitting against posterior end of ventral platform; long, thick longitudinally and transversely curved articulating plate, more or less concentric with umbo, extending from dorsal beak almost to surface of ventral platform; valve margins slightly overlapping dorsoventrally in front of flattened zones, serving as articulatory structure; both valves with deeply excavated, steep-sided platform supported by long median septum; ventral valve with deep umbonal cavities. *Silurian (Wenlock):* Australia (New South Wales).——FIG. 1718*a–e*. **K. bellense*, Dripstone Formation, southeast of Wellington, central New South Wales; *a*, holotype, anterior view of inside of complete articulated shell, AMF101116, ×0.4; *b–e*, lateral, posterior, anterior, and ventral views of complete articulated shell, AMF101117, ×0.4 (Strusz & others, 1998).

Porcidium PERCIVAL, 1995, p. 53 [**P. dorsilobum*; OD]. Shell dorsibiconvex; ventral interarea orthocline, planar to weakly concave, bisected by narrow ridgelike homeodeltidium, flanked by deep grooves; ventral interior with low, solid visceral platform, slightly elevated anteriorly; cardinal buttress rudimentary to absent; dorsal visceral platform low, solid, surrounded by raised peripheral rim, with anterior adductors bisected by low median ridge; hinge plate forming prominent curved transverse bar, with strongly impressed, paired internal oblique muscle scars. *Ordovician (Caradoc):* Australia (New South Wales).——FIG. 1717,*2a–b*. **P. dorsilobum*, Quondong Limestone; *a,* holotype, ventral valve interior, SUP63482, ×3; *b*, dorsal valve interior, SUP63493, ×3 (Percival, 1995).

CHILEATA

LEONID E. POPOV and LARS E. HOLMER

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Subphylum RHYNCHONELLIFORMEA Williams & others, 1996
Class CHILEATA Williams & others, 1996

The chileates include the two orders Chileida and Dictyonellida. The systematic position of the latter group has long been problematic (ROWELL, 1965; WRIGHT, 1981). The chileides were first discovered by POPOV and TIKHONOV (1990) from the Botomian of Kyrgyzstan, and they became extinct by the Middle Cambrian (POPOV & HOLMER, 2000b). The chileides are the earliest known organocarbonatic-shelled brachiopod with a strophic hinge line; however, there are no articulatory structures associated with the posterior margin, and POPOV and TIKHONOV (1990; see also POPOV, 1992) proposed that fused mantle lobes fixed the axis of rotation. The cladistic analysis by POPOV, BASSETT, and HOLMER (2000) indicated that the Cambrian Chileida and the Ordovician-Permian Dictyonellida form a monophyletic group defined mainly by the development of a large umbonal perforation, which is enlarged by resorption and can be covered by a posterior plate, termed the colleplax (WRIGHT, 1981). WRIGHT (1981) proposed that this structure (in the dictyonellides) served as a holdfast by means of an organic pad, and this interpretation is also likely for the chileides. POPOV, HOLMER, and BASSETT (1996) suggested that many of the characters of the chileides might be primitive, and thus they were used to polarize the character transformation in the cladistic analysis of the organocarbonatic-shelled forms. *Lower Cambrian (Botomian)–Permian*.

Class OBOLELLATA Williams & others, 1996
Order NAUKATIDA Popov & Tikhonov, 1990
Superfamily NAUKATOIDEA Popov & Tikhonov, 1990
Family PELMANELLIDAE Popov & others, 1997

[Pelmanellidae POPOV & others, 1997, p. 343]

Shell with rudimentary dorsal interarea; notothytrial platform lacking; ventral interior lacking denticles on anteris; posterior adductor scars on separate paired cardinal muscle platforms in both valves. *Lower Cambrian (Botomian–Toyonian)*.

Pelmanella POPOV & others, 1997, p. 343 [**P. borealis*; OD]. Shell ventribiconvex, elongate to subcircular, with straight anterior commissure; delthyrium open, narrow, triangular, with distal margins joined by anteris; ventral interior with central muscle platform separated from cardinal muscle platforms by deep oblique grooves; dorsal interior with medianly located anterior adductor scars divided by median ridge. *Lower Cambrian (Toyonian):* Greenland.——FIG. 1719*a–b*. **P. borealis*, Paralleldal Formation, Peary Land, central North Greenland; *a*, holotype, ventral valve interior, MGUH23743, ×5.4; *b*, dorsal valve interior, MGUH23747, ×5.4 (Popov & others, 1997).

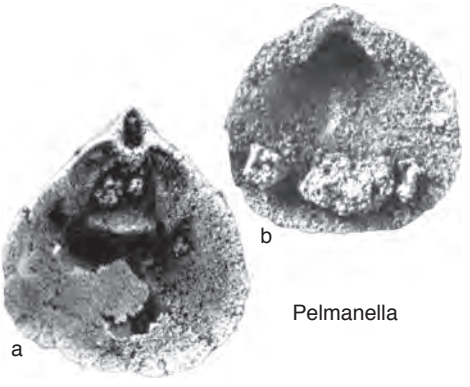

FIG. 1719. Pelmanellidae (p. 2595).

KUTORGINATA

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[National Museum of Wales, Cardiff; deceased, formerly of the University of Glasgow]

Class KUTORGINATA Williams & others, 1996

The Cambrian genus *Anomalocalyx* cannot be assigned with confidence to any existing class or lower-ranked suprageneric taxon. The genus has a well-developed convex pseudodeltidium, broad open notothyrium, and possibly a perforated ventral umbo, which features are characteristic only of kutorginides among Early to Mid-Cambrian rhynchonelliform brachiopods. *Anomalocalyx* also possesses dorsal sockets and socket ridges, which are otherwise present in the Nisusioidea. The taxonomic position of the genus is therefore most likely to be within the Kutorginida. The presence of paired denticles along the posterior margin and a long tubelike structure, which according to BROCK (1999) shows remarkable similarity to the elongate, tapering, tube-shaped structure of the Permian richthofenioid *Cyndalia*, are anomalous. These features are otherwise unknown among Cambrian rhynchonelliforms.

Order KUTORGINIDA Kuhn, 1949

Superfamily and Family UNCERTAIN

Anomalocalyx BROCK, 1999, p. 182 [**A. cawoodi*; OD]. Shell with deeply coniform ventral valve; ventral interarea catacline to weakly procline with narrow delthyrium, covered completely by evenly convex pseudodeltidium; dorsal valve with incurved umbo, wide, poorly defined, open notothyrium and broad median sulcus; ornament of low, broad costellae becoming fluted at commissural margin and regular concentric growth lamellae; ventral interior with a pair of rounded, dorsally directed, nublike denticles situated on either side of delthyrium, and elongate, tapering, tubelike structure extending toward posterior shell margin directly under pseudodeltidium; dorsal interior with small, divergent socket ridges bordering anteriorly shallow sockets excavated into posterior valve wall. *Middle Cambrian (Floran–Undillan):* Australia (New South Wales).——FIG. 1720*a–g*. * *A. cawoodi*, Murrawong Creek Formation, Murrawong Creek; *a*, holotype, ventral valve oblique posterior, ×45; *b–c*, posterior and side views, AM F97383, ×43; *d–e*, oblique lateral views of incomplete ventral valve showing tubelike structure, AM F107867, ×35; *f*, dorsal valve interior showing socket ridges, AM F107869, ×51; *g*, dorsal valve exterior, AM F107870, ×38 (Brock, 1999).

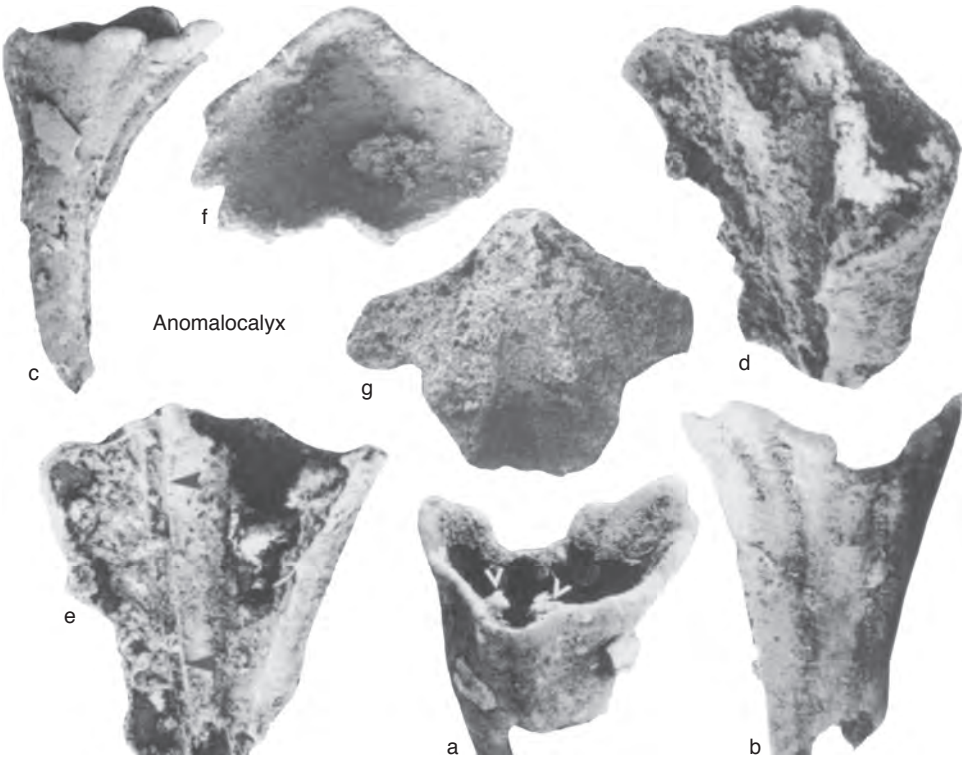

FIG. 1720. Uncertain (p. 2596).

STROPHOMENIDA

L. R. M. Cocks and Rong Jia-Yu

[The Natural History Museum, London; and Academia Sinica, Nanjing]

Class STROPHOMENATA Williams & others, 1996
Order STROPHOMENIDA Öpik, 1934

Since the publication of *Treatise Part H, revised,* volume 2 (Cocks & Rong, 2000, p. 216), an analysis of Ordovician brachiopods (Harper & others, 2004) has been published that includes not only the origins of the Strophomenoidea and Plectambonitoidea within the early Ordovician but also the differing distribution patterns within the two superfamilies (Fig. 1721), with the Plectambonitoidea peaking in the mid-Caradoc and the nondenticulate Strophomenoidea reaching their acme in the mid-Ashgill. The overall classification of the order remains unchanged from 2000.

Superfamily STROPHOMENOIDEA King, 1846

In the main treatment of the Strophomenoidea (Cocks & Rong, 2000, p. 217), the classification within the superfamily was based primarily on the different forms of the cardinal process, together with the presence or absence of denticles along the hinge line, which differentiated the various families following the analysis of Rong and Cocks (1994). This treatment has met with general acceptance and is unchanged here, apart from the addition of the subfamily Ungulomeninae within the Glyptomenidae.

Family STROPHOMENIDAE King, 1846
Subfamily STROPHOMENINAE King, 1846

Gunnarella Spjeldnæs, 1957, p. 149 [**Strophomena (G.) delta;* OD]. Outline semicircular; profile gently convex posteromedianly but anteriorly evenly resupinate, with concavity of up to 50°; distinctive ornament of costellae interrupting small rugellae over nearly all the valve surface; weak teeth but short dental plates extending anterolaterally to subparallel muscle-bounding ridges; ventral muscle field suboval and without bounding ridges anteromedianly; dorsal interior with short socket plates diverging at about 100°; dorsal side septa absent. [This genus is listed, and the type species figured, in Cocks & Rong, 2000, p. 302, fig. 194.*2a–b,* within Strophomenoidea family Uncertain. New understanding of the valve interiors (Cocks, 2005) enables firm positioning of the genus within the Strophomeninae.] *Ordovician (Caradoc–Ashgill):* Baltica and Avalonia.——Fig. 1722,*1a–c. G. magnifica* Cocks, Boda Limestone, middle Ashgill, Dalarna, Sweden; *a,* dorsal exterior, Kallholn Quarry, RMS Br 6988, ×2; *b*, holotype, dorsal exterior of conjoined valves showing interarea, Kallholn Quarry, RMS Br 6989, ×2.5; *c,* ventral interior, Osmundsberget Quarry, BMNH BC 58024, ×2 (Cocks, 2005).

Leigerina Rõõmusoks, 2004, p. 19 [**L. hiiuensis;* OD]. Semicircular outline; profile mainly gently biconvex, with dorsal valve slightly concave posteromedianly only. Ornament evenly parvicostellate; no rugae known. Relatively large apsacline ventral interarea with large pseudodeltidium; small anacline dorsal interarea with low chilidium. Ventral interior with relatively small flaring teeth merging anterolaterally with muscle-bounding ridges bordering subcircular muscle field; very thin and relatively inconspicuous ventral median septum. Dorsal interior with prominent erect cardinal process between prominent curved socket plates. Low myophragm and dorsal muscle field very weakly impressed. *Ordovician (Caradoc–Ashgill):* Baltica.——Fig. 1722,*2a–d. *L. hiiuensis,* Kõrgessare formation, Vormsi Stage, lower Ashgill, Estonia; *a,* holotype, dorsal exterior, Kõrgessare, TUG 1003-109, ×1.5; *b,* ventral interior, Kärdla, TUG 42-61, ×1.5; *c,* interarea of conjoined valves, Kõrgessare, TUG 50-30, ×2; *d,* dorsal interior, Kohila, TUG 106-20, ×1.5 (Rõõmusoks, 2004).

Nasutimena Jin & Zhan, 2001, p. 30 [**Strophomena fluctuosa* Billings, 1860, p. 57; OD]. Outline subtriangular to subpentagonal; smoothly geniculate profile; ornament unequally parvicostellate, with small concentric to crisscross rugae interrupted by the major costellae variably developed over all or part of shell. Ventral and dorsal interiors as in *Strophomena,* apart from shorter and weaker dorsal transmuscle septa. *Ordovician (Ashgill):* North America.——Fig. 1723*a–e. *N. fluctuosa; a–c,* holotype, dorsal, anterior, and ventral views of dorsal exterior, Vaureal Formation, middle Ashgill, Anticosti Island, Canada, GSC 2017, ×2; *d*, ventral

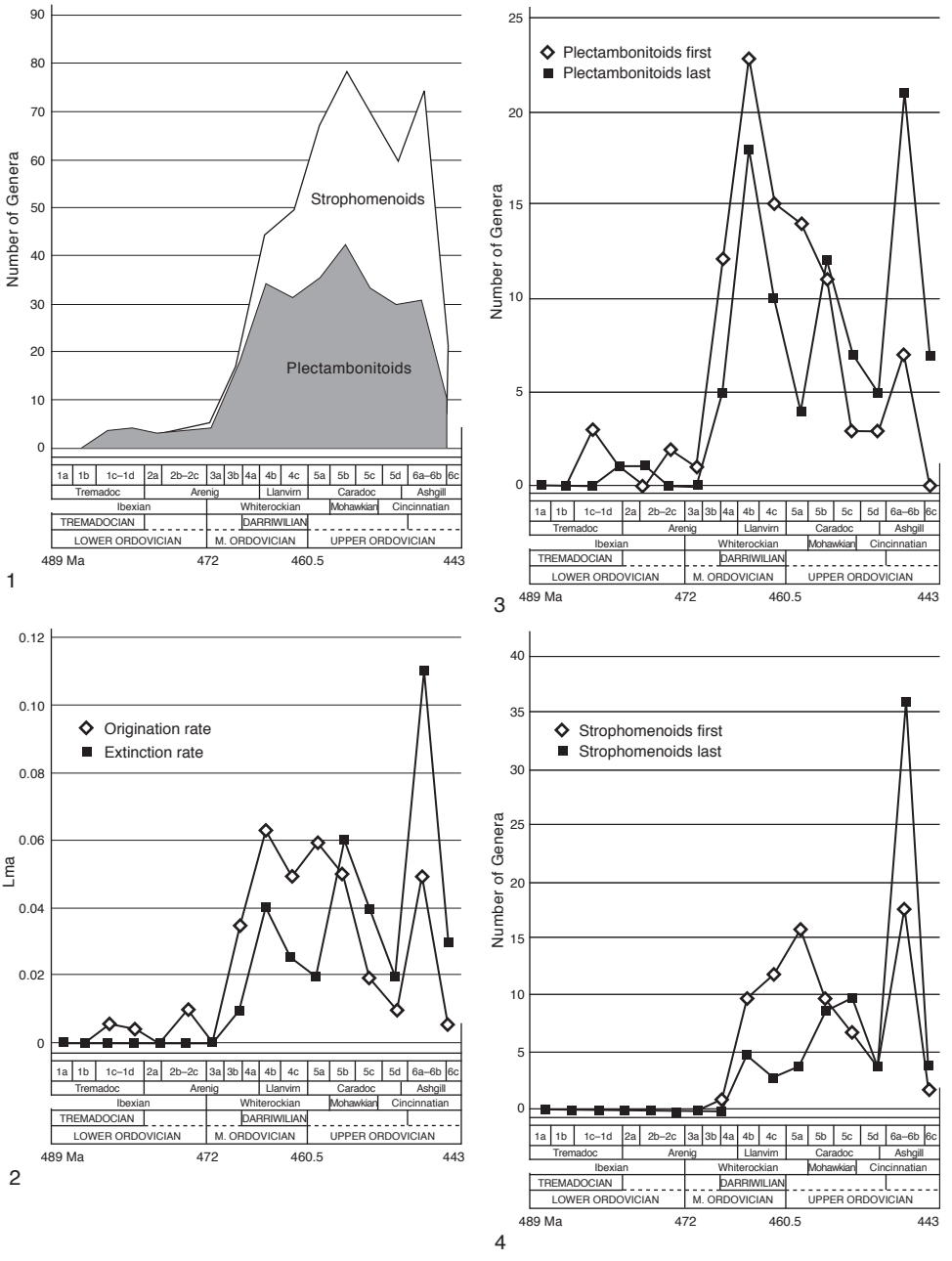

FIG. 1721. Strophomenide Ordovician diversity; *1,* absolute abundances of two superfamilies of strophomenide brachiopods; *2,* extinction and origination rates across strophomenoids; *3,* first and last appearances of plectambonitoideans; *4,* first and last appearances of strophomenoideans; *Lma,* lineage million years (adapted from Cocks in Harper & others, 2004).

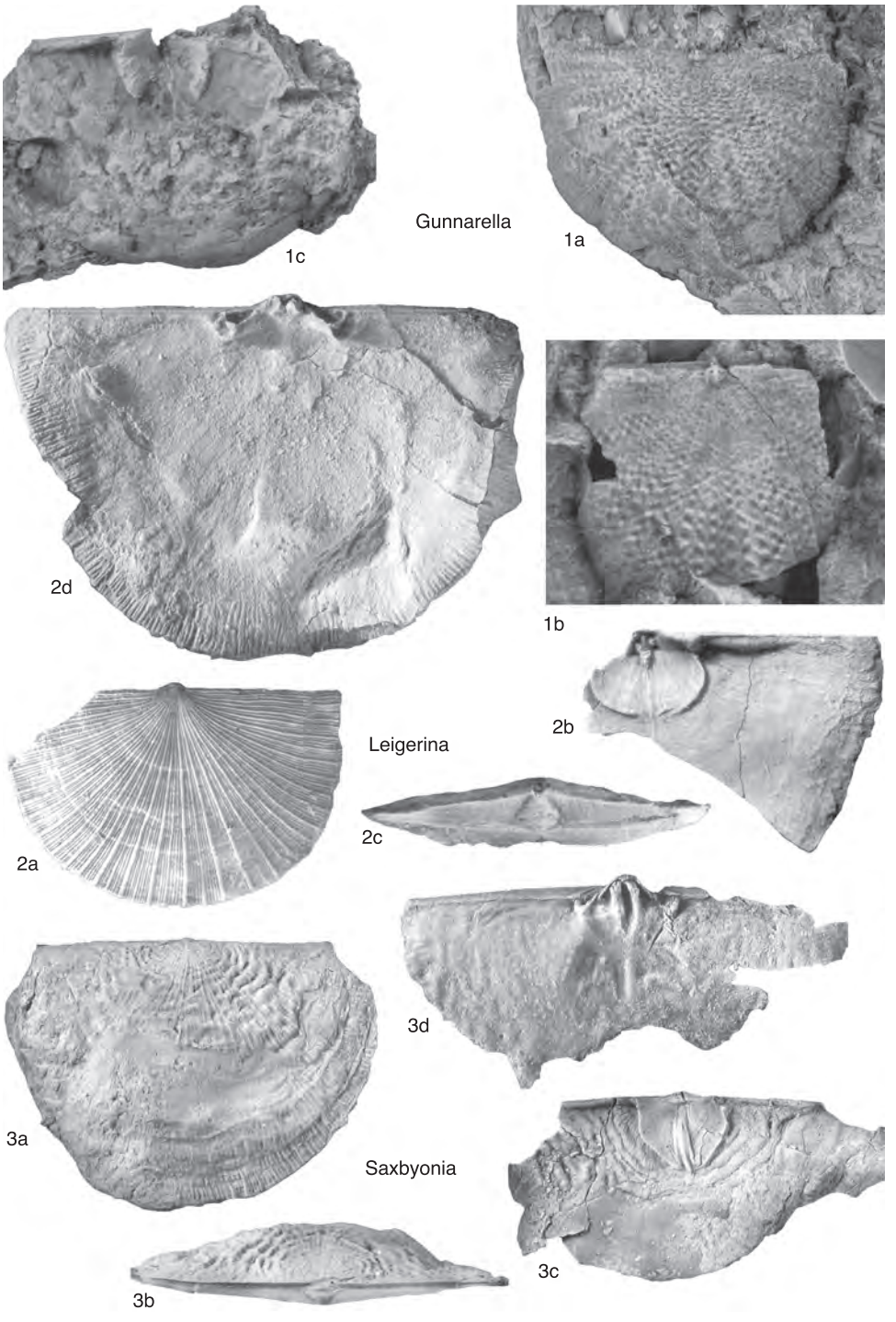

FIG. 1722. Strophomenidae (p. 2598–2602).

FIG. 1723. Strophomenidae (p. 2598–2602).

interior, Caution Creek Formation, middle Ashgill, Hudson Bay Lowlands, Canada, GSC 109020, ×2.5; *e,* dorsal interior, Stony Mountain Formation, Ashgill, southern Manitoba, Canada, GSC 109021, ×2.5 (new).

Pseudostrophomena Rõõmusoks, 1963, p. 237 [**P. reclinis;* OD]. [This genus has two entries: in Cocks & Rong, 2000, p. 224 within the Strophomenoidea, and in Williams and Brunton, 2000, p. 674 within the Chilidiopsoidea. Further work on and redescription of the type material from Estonia by Rõõmusoks (2004) has firmly established the presence of pseudopunctae and confirmed its position within the Strophomenoidea.] *Ordovician (Caradoc–Ashgill):* Baltic.

Saxbyonia Rõõmusoks, 2004, p. 20 [**S. fluctuosa;* OD]. Semicircular to trapezoidal outline. Profile initially biconvex; resupinate anteriorly. Ornament irregularly parvicostellate with distinctive small irregular rugae over much of the valve surface, particularly posteromedianly. Apsacline ventral interarea with pseudodeltidium; dorsal anacline interarea with chilidium of subequal size to pseudodeltidium, together filling delthyrium. Ventral interior with low teeth merging anterolaterally with subpentagonal muscle area, which is slightly raised and undercut. Dorsal interior with prominent cardinal process projecting posteriorly and extending for some distance anteriorly, uniting anteriorly onto low myophragm. Short but prominent curved socket plates. Dorsal muscle field poorly impressed. *Ordovician (Ashgill):* Baltica.——Fig. 1722,*3a–d. *S. fluctuosa,* Kõrgessare Formation, Vormsi Stage, lower Ashgill, Estonia; *a–b,* holotype, dorsal and posterior views of conjoined valves, Vormsi Island, TUG 80-132, ×1; *c,* ventral interior, Kõrgessare, Hiiuma Island, TUG 50-24, ×1.5; *d,* dorsal interior, Kohila, GMUT Br 1546, ×1.5 (Rõõmusoks, 2004).

Subfamily FURCITELLINAE Williams, 1965

Bekkerina Rõõmusoks, 1993, p. 50 [**Rafinesquina dorsata* Bekker, 1921, p. 73; OD] [=*Haljalanites* Rõõmusoks, 2004, p. 29 (type, *Rafinesquina anijana* Öpik, 1930, p. 197, OD]. [*Haljalanites* is identical in all significant external and internal generic characters to *Bekkerina,* whose type species, *B. dorsata*, was illustrated by Cocks & Rong, 2000, fig. 138,*3a–d*, and the two nominal genera also overlap in distribution.] *Ordovician (Darriwilian–lower Caradoc):* Baltica.——Fig. 1724,*1a–c. B. assatkini* (Alichova), Kahula Formation, Hajala Stage, lower Caradoc, Aluvere Quarry, Estonia; *a,* ventral exterior, TUG 77-161, ×2; *b,* ventral interior, TUG 1003-41, ×2.5; *c,* dorsal interior, TUG 72-73, ×2.5 (Rõõmusoks, 2004).

?Djindella Menakova , 1991, p. 25 [**D. plana;* OD]. Semicircular to subquadrate outline; profile gently planoconvex to biconvex with low ventral fold and dorsal sulcus; low apsacline ventral interarea with pseudodeltidium covering delthyrium; strong teeth supported by dental plates extending anterolaterally into well-developed muscle-bounding ridges that converge anteriorly and form a high muscle platform supported by a median septum; dorsal interior with bifid cardinal process and notothyrial platform, otherwise poorly known. [This genus was originally described as an orthoidean; its dorsal interior is still poorly known, and it may be congeneric with *Dzhebaglina* (Cocks & Rong, 2000, p. 237).] *Ordovician (Ashgill):* central Asia. ——Fig. 1724,*2a–c. *D. plana,* upper reaches of Dzhindy-Dariya River, Zerafshan Range, Tajikistan; holotype, dorsal, ventral, and lateral views of conjoined valves, Geological Museum of Tajikistan 1430/1, ×2 (Menakova, 1991).

Fenomena Zhan & Cocks, 1998, p. 45 [**F. distincta;* OD]. Profile planoconvex to slightly biconvex; rectangular to subsemicircular outline; large pseudodeltidium; small chilidium; dental plates short and weak with no ventral muscle-bounding ridges; strong bilobed cardinal process continuous with socket ridges laterally; short sockets with strong curved socket ridges; subperipheral rim in adults; elevated dissected dorsal muscle field; dorsal median septum. *Ordovician (Ashgill):* South China.——Fig. 1725,*2a–e. *F. distincta*, Changwu Formation, middle Ashgill, Dianbian, Zhejiang Province; *a*, latex of dorsal exterior, NIGP 128077, ×4; *b–c,* internal mold and latex cast of ventral valve, NIGP 128073, ×2; *d–e,* internal mold and latex cast of dorsal valve, NIGP 128076, ×4 (Zhan & Cocks, 1998).

Karomena Popov, Nikitin, & Cocks, 2000, p. 855 [**K. squalida*; OD]. Profile dorsibiconvex to convexoplane, with slightly uniplicate anterior margin; ventral interarea planar, apsacline, with convex pseudodeltidium; dorsal interarea anacline, with entire convex chilidium; unequally parvicostellate ornament; ventral interior long, straight, divergent dental plates; poorly defined subrhomboidal muscle field with no bounding ridges; adductor scars completely separating diductor scars; dorsal interior with bilobed, posteriorly facing cardinal process on high notothyrial platform; strong socket ridges curved backward toward hinge line and fused with cardinal process; small adductor muscle field bisected by fine but prominent short median septum and two pairs of short, variable side septa, the subparallel inner pair being stronger. *Ordovician (Caradoc):* Kazakhstan.——Fig. 1724,*3a–e. *K. squalida*, Otar Member, Dulankara Formation, upper Caradoc, Dulankara Mountain, Chu-Ili Range; *a–b,* ventral and lateral views of conjoined valves, CNIGR 63/12375, ×2; *c,* ventral internal mold, CNIGR 62/12375, ×2; *d–e,* dorsal internal mold, ×2, and latex cast, holotype, 61/12375, ×5 (Popov, Nikitin, & Cocks, 2000).

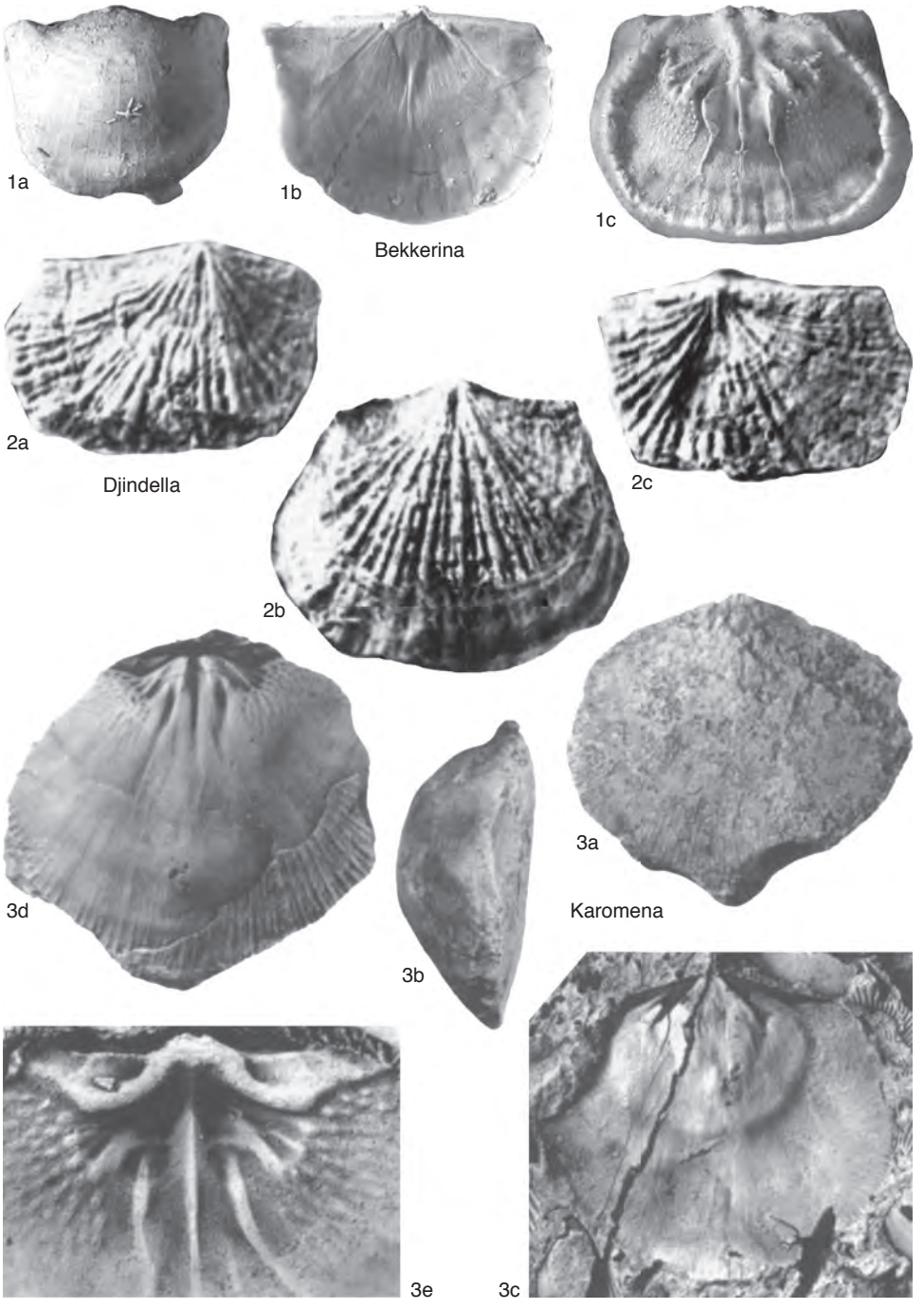

FIG. 1724. Strophomenidae (p. 2602).

Oepikoides Benedetto, 1995, p. 252 [**O. notus;* OD]. Dorsally gently geniculate profile; parvicostellate ornament; apsacline area with pseudodeltidium; suboval ventral muscle field without bounding ridges; similar to *Oepikina* in shape, but different internally in the lack of dorsal median septum, lateral septa, or subperipheral rim; internal papillae elongate, particularly posterolaterally; short flaring socket ridges; short erect cardinal process lobes directed posteriorly; mantle canals unknown. *Ordovician (Caradoc):* South America.——Fig. 1726,*1a–c. *O. notus*, Las Plantas Formation, lower Caradoc, Gualcamayo, northern Precordillera, Argentina; *a,* ventral exterior, CEGH-UNC 13501, ×1.5; *b,* ventral interior, CEGH-UNC 13717, ×1.5; *c,* holotype, dorsal interior, CEGH-UNC 13716, ×2 (Benedetto, 1995).

Oxostrophomena Nikitina & others, 2006, p. 173 [**Strophomena dubia* Rukavishnikova, 1956, p. 143; OD]. Subquadrangular outline; profile strongly convexoconcave with very weak rounded geniculation. Ventral interarea apasacline with pseudodeltidium, dorsal interarea anacline to orthocline with discrete chilidial plates. Ornament parvicostellate with irregular small rugellae posterocentrally. Ventral interarea with large striated teeth supported by divergent dental plates extending anteriorly into muscle-bounding ridges at sides only of the suboval muscle field. Dorsal interior with cardinal process of narrow triangular notothyrial platform; short straight socket ridges striated posteriorly and divergent anteriorly; relatively small muscle field poorly developed; very short thin dorsal median septum in valve center only; mantle canals saccate. *Ordovician (Darriwilian):* Kazakhstan.——Fig. 1725,*3a–f. *O. dubia*, Uzunbulak Formation, Kopalysai, Chu-Ili Range; *a–b,* dorsal and lateral views of dorsal exterior, USNM 485166, ×1.5; *c–d,* ventral interior mold and latex, USNM 485167, ×2; *e,* dorsal interior mold, ×2.2; *f,* latex mold, USNM 489169, ×3 (Nikitina & others, 2006).

Sakunites Rõõmusoks, 2004, p. 31 [**Leptaena luhi* Sokolskaya, 1954, p. 57; OD]. Outline semicircular with maximum width at hinge line or just anterior to it. Ventral valve profile gently convex, with minor and gradual geniculation near the anterolateral margins; dorsal valve relatively flat apart from gentle concavity at anterolateral margins. Umbo scarcely developed. Parvicostellate ornament with weak irregular rugae. Apsacline ventral interarea; smaller anacline dorsal interarea. Ventral interior with bilobed and slightly elevated muscle field surrounded by prominent muscle-bounding ridges. Dorsal interior with strong but short socket plates; narrow notothyrial platform; prominent muscle field with irregular margins that are elevated laterally. Short, fine dorsal median septum in valve center only. *Ordovician (Caradoc):* Baltica.——Fig. 1726,*2a–d. *S. luhi* (Sokolskaya), Vasalemma Formation, Oandu Stage, upper Caradoc, Estonia; *a,* ventral exterior, Tuula, TUG 72-237, ×2; *b,* ventral interior, Jõgisoo, TUG 72-175, ×1.5; *c–d,* exterior and interior of dorsal valve, Saku, TUG 72-173, ×2.7 (Rõõmusoks, 2004).

Tallinnites Rõõmusoks, 1993, p. 50 [**Oepikina? imbrexoidea* Sokolskaya, 1954, p. 51; OD] [=*Kukrusena* Rõõmusoks, 2004, p. 28 (type, *K. peetriensis,* OD)]. [See Cocks & Rong, 2000, p. 236. The nominal genus *Kukrusena* has all the generic characters of *Tallinnites,* whose type species, *T. imbrexoidea*, was illustrated by Cocks & Rong, 2000, fig. 144,*3a–c*.] *Ordovician (Darriwilian–lower Caradoc):* Baltica.——Fig. 1725,*1a–d. T. peetriensis* (Rõõmusoks), Viivikonna Formation, Kukruse Stage, lower Caradoc, Estonia; *a–b,* holotype, ventral and lateral views of ventral exterior, Peetri, TUG 1054-181, ×2; *c,* ventral interior, Peetri, TUG 72-201, ×1.8; *d,* dorsal interior, Humala, TUG 1003-345, ×2 (Rõõmusoks, 2004).

Trigrammaria Wilson, 1945, p. 140 [**T. trigonalis;* OD] [=*Microtrypa* Wilson, 1945, p. 144 (type, *M. altilis,* OD); *Crassoseptaria* Rõõmusoks, 2004, p. 37 (type, *Trigrammaria virve* Rõõmusoks, 1985, p. 134, OD)]. [The nominal genus *Crassoseptaria* has all the generic characters of *Trigrammaria,* whose type species, *T. trigonalis*, was illustrated by Cocks & Rong, 2000, fig. 145,*2a–c,* into which its type species was originally placed. See Cocks & Rong, 2000, p. 237.] *Ordovician (Darriwilian–Caradoc):* Laurentia, Baltica.——Fig. 1726,*3a–c. T. virve* Rõõmusoks, Paekna Formation, Nabala Stage, upper Caradoc, Estonia; *a*, holotype, conjoined valves, Laitse, TUG Br 1190, ×1.5; *b*, ventral interior, Nõmmeküla, TUG Br 1194, ×1.4; *c,* dorsal interior, Nõmmeküla, TUG Br 1193, ×4 (Rõõmusoks, 2004).

Family RAFINESQUINIDAE Schuchert, 1893
Subfamily RAFINESQUININAE Schuchert, 1893

Dirafinesquina Cocks & Zhan, 1998, p. 125 [**D. globosa*; OD]. Strongly convex ventral profile, gently concave and geniculate dorsal profile; semicircular outline; ventral bounding ridges surrounding a suboval and bilobed muscle field; cardinal process lobes variably developed from ponderous to weak but erect rather than anteriorly directed; low, short, straight, but variably thick socket ridges flaring laterally and separate from cardinal process; circular dorsal muscle field; low wide myophragm starting from notothyrial platform and narrowing anteriorly; mantle canals unknown. *Ordovician (Darriwilian–Caradoc):* Southeast Asia.——Fig. 1727,*3a–d. *D globosa*; Naungkangyi Group, lower Caradoc, Linwe, Shan States, Myamnar, Burma; *a,* lateral view of ventral internal mold, BMNH BB37607, ×1.5; *b–c,* dorsal and posterior views of ventral internal mold, BMNH BB37619, ×2; *d,* holotype, latex cast of dorsal interior, BMNH BB37593, ×5 (Cocks & Zhan, 1998).

Hedstroemina Bancroft, 1929, p. 58 [**H. fragilis;* OD] [=*Virunites* Rõõmusoks, 2004, p. 41 (type, *Rafinesquina orvikui* Oraspõld, 1956, p. 49, OD)]. [*Virunites* has the same generic external and internal characters as *Hedstroemina,* whose

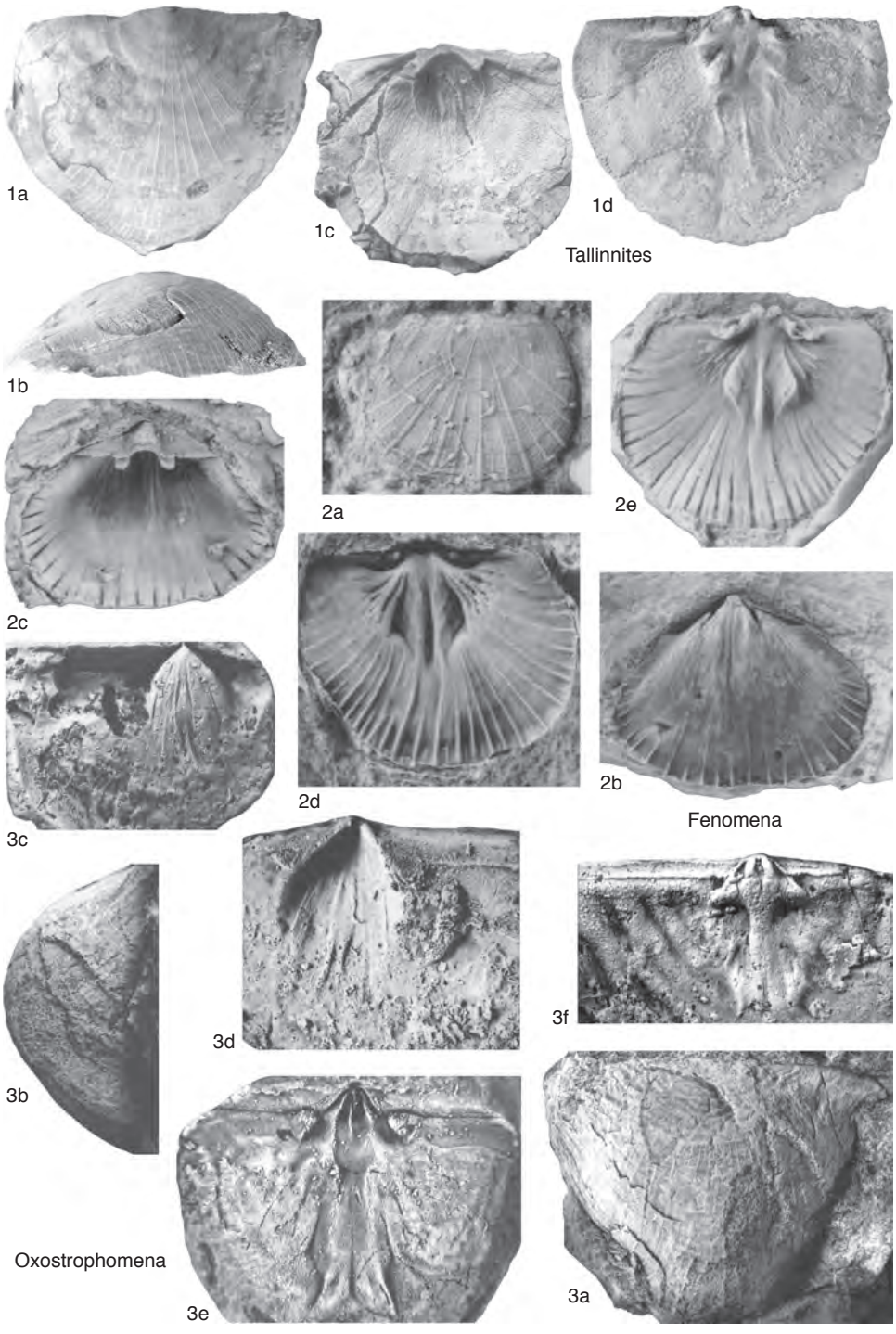

FIG. 1725. Strophomenidae (p. 2602–2604).

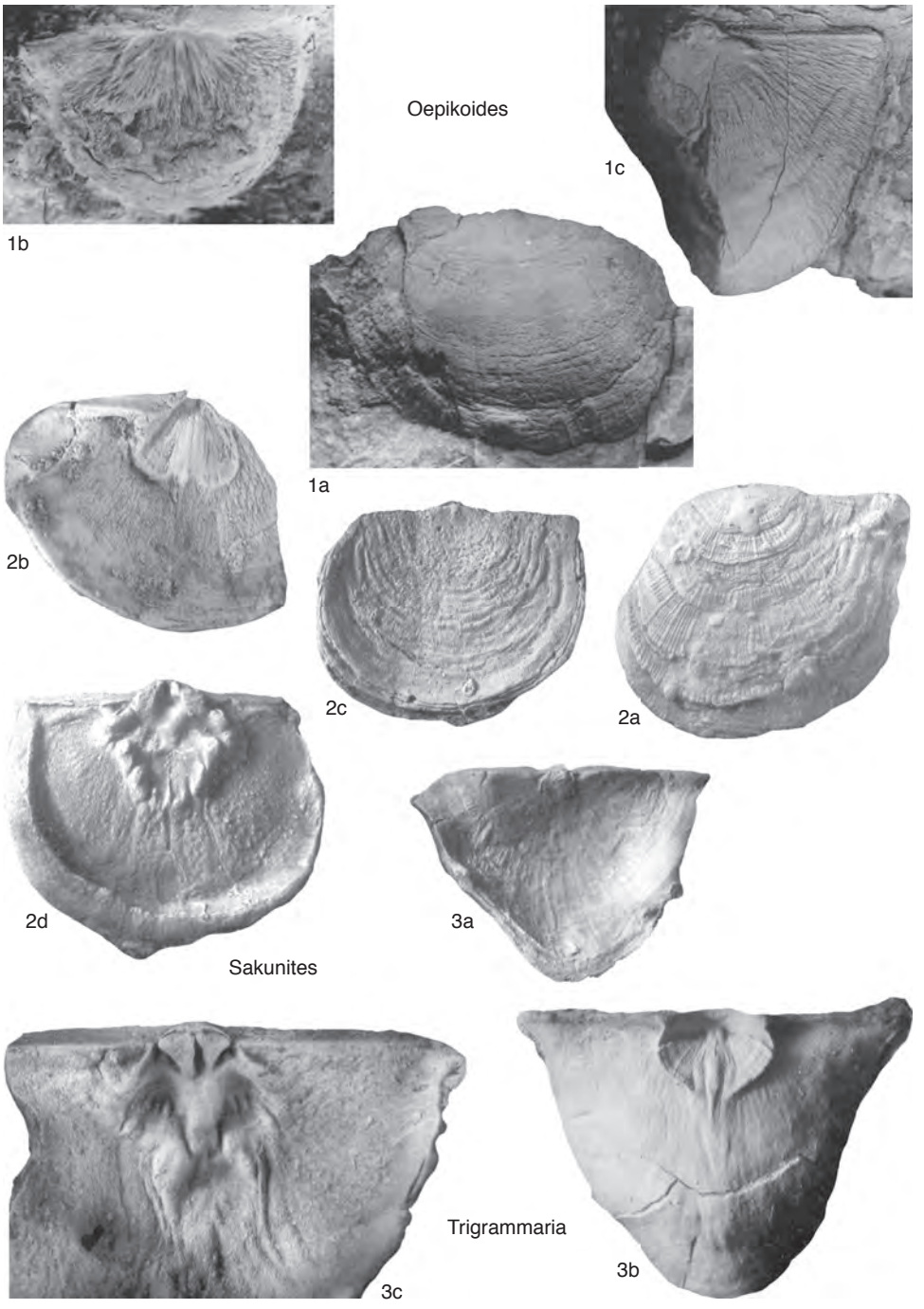

FIG. 1726. Strophomenidae (p. 2604).

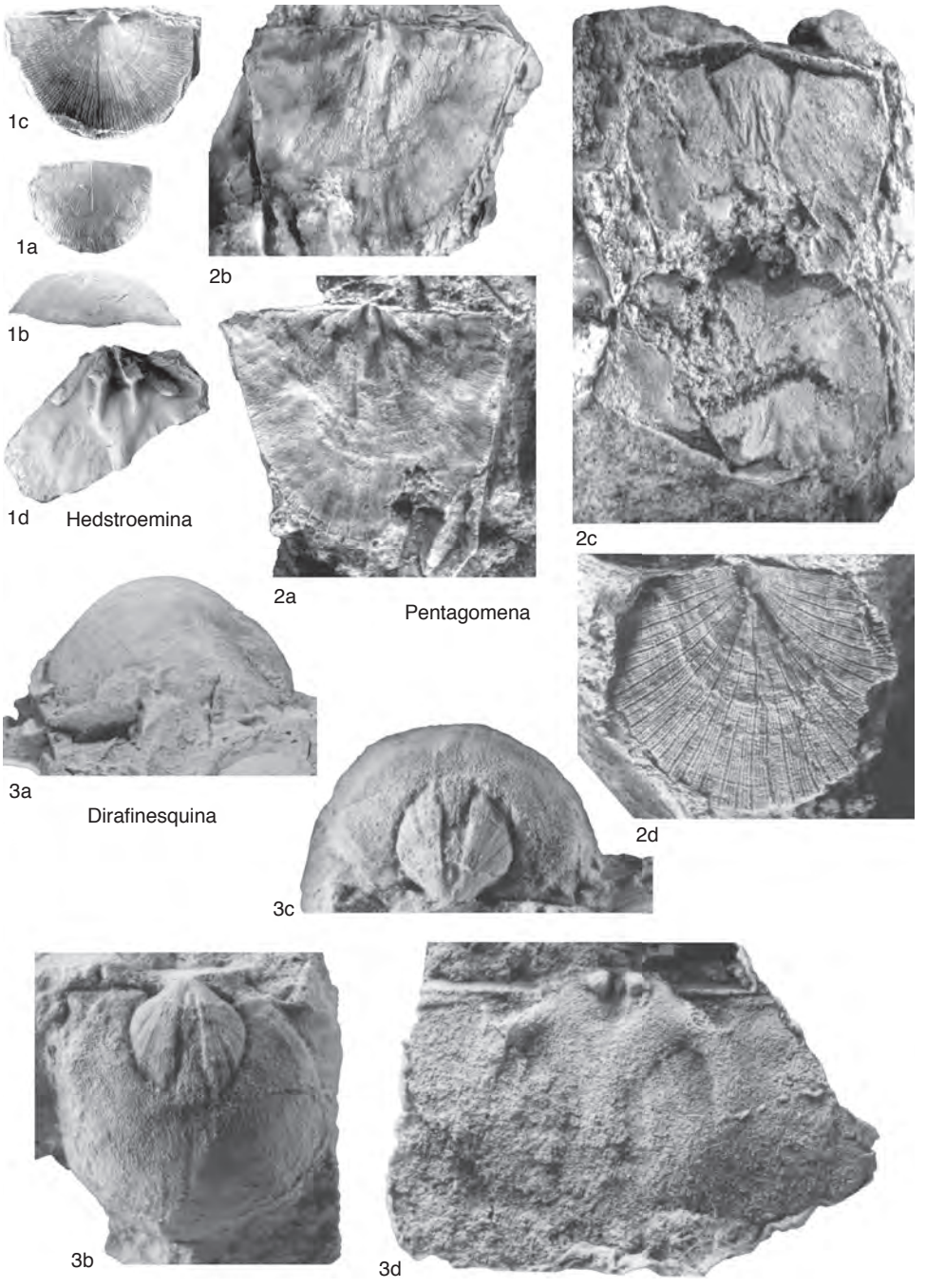

FIG. 1727. Rafinesquinidae (p. 2604–2608).

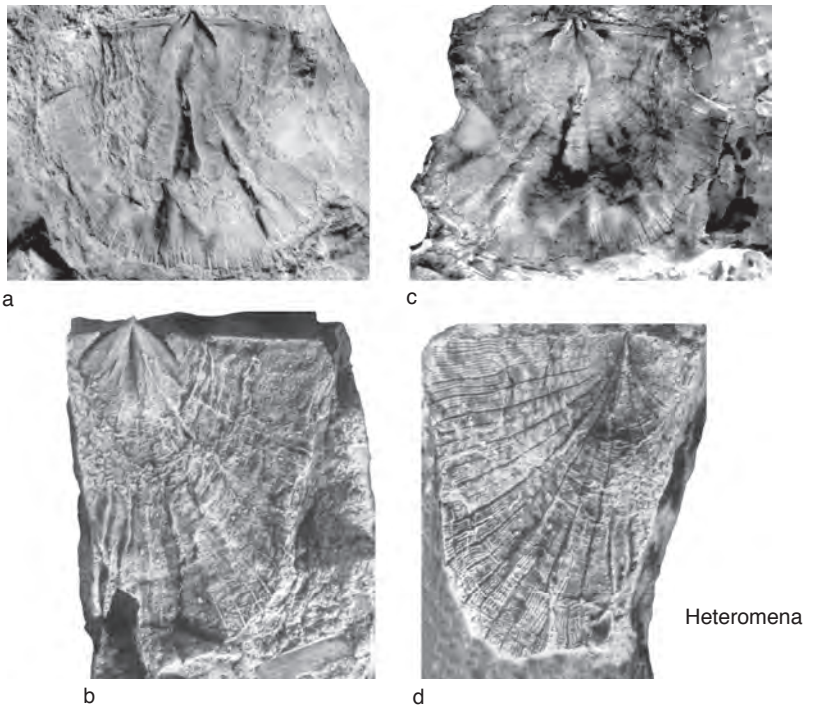

FIG. 1728. Rafinesquinidae (p. 2608).

type species, *H. fragilis*, was illustrated by COCKS & RONG, 2000, fig. 148,*2a–c*.] *Ordovician (Caradoc):* Avalonia, Baltica.——FIG. 1727,*1a–d. H. orvikui* (ORASPÕLD), Hirmuse Formation, Oandu Stage, middle Caradoc, Estonia; *a–b,* holotype, ventral and lateral views of ventral exterior, Oandu, TUG 1009-1, ×1; *c,* ventral interior, Tõrremägi, TUG 102-14, ×1.5; *d,* dorsal interior, Tõrremägi, TUG 102-13, ×3 (Rõõmusoks, 2004).

Heteromena ZHAN & JIN, 2005, p. 42 [**H. dorsiconversa;* OD]. Profile weakly concavoconvex. Ornament regular parvicostellae with irregular rugae in posteromedian area only. Small pseudodeltidium and chilidium. Ventral interior with short dental plates, diverging anteriorly; ventral muscle field subcircular in outline, with weak muscle-bounding ridges. Dorsal interior with cardinal process lobes strong but thin, platelike, with much of cardinal process posterior to hinge line; myophragm also thin but well developed; strong but short socket ridges diverging at about 120°; notothyrial platform absent; weakly impressed dorsal muscle field with no transmuscle septa. *Ordovician (Arenig–Llanvirn):* South China.——FIG. 1728*a–d. *H. dorsiconversa,* Dashaba Formation, upper Arenig–Llanvirn, Shuanghe, Changning County, Sichuan Province, southwestern China; *a–b,* internal and external molds of ventral valve, NIGP 134442, ×2; *c–d,* holotype, mold and latex cast of dorsal interior, NIGP 134441, ×2 (Zhan & Jin, 2005).

Pentagomena ZHAN & JIN, 2005, p. 40 [**P. parvicostellata;* OD]. Profile gently concavoconvex to weakly biconvex; vestigial pseudodeltidium; small chilidium; ornament of regular parvicostellae, rugae absent. Ventral interior with thin, widely diverging dental plates; ventral muscle field elongately subpentagonal with variably developed muscle-bounding ridges; thin notothyrial platform. Dorsal interior with cardinal process mostly anterior to hinge line; socket ridges relatively weak; subpentagonal dorsal muscle field weakly impressed; transmuscle septa weakly developed. *Ordovican (Arenig–Llanvirn):* South China.——FIG. 1727,*2a–d. *P. parvicostellata,* Dashaba Formation, upper Arenig–Llanvirn, Shuanghe, Changning County, Sichuan Province, southwestern China; *a,* mold of ventral exterior, NIGP 134437, ×2; *b,* ventral interior mold, NIGP 134435, ×2; *c–d,* holotype, dorsal internal mold and latex cast, NIGP 134421, ×2 (Zhan & Jin, 2005).

Subfamily LEPTAENINAE Hall & Clarke, 1895

Leptaena DALMAN, 1828, p. 94 [**L. rugosa;* SD KING, 1846, p. 28]. [See COCKS & RONG, 2000, p. 241, in which, in addition to *Leptaena (Leptaena),* there are also a large number of generic synonyms and the subgenus *Leptaena (Septomena)*. The distinctive ornament of *Leptaena (Ygdrasilomena)* is quite

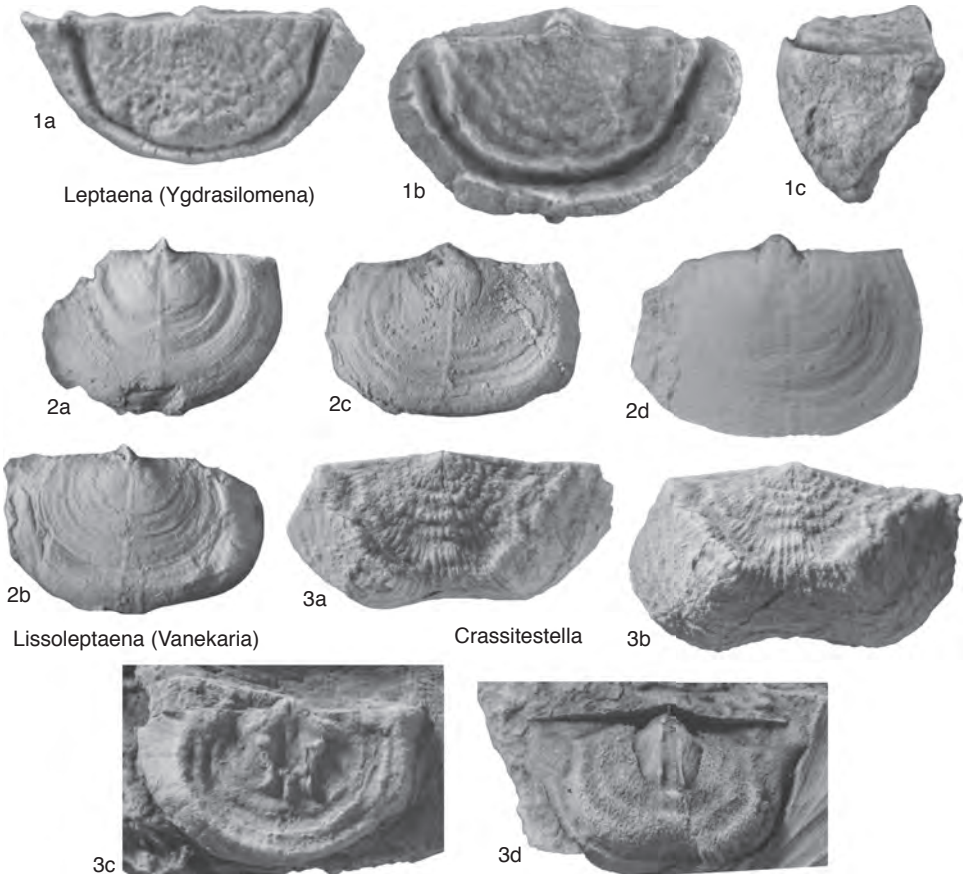

FIG. 1729. Rafinesquinidae (p. 2609–2610).

different from the regular rugae of the other two subgenera recognized within *Leptaena*.] *Ordovician (Llanvirn)–Devonian (Pragian, ?Emsian):* cosmopolitan.

Leptaena (Ygdrasilomena) COCKS, 2005, p. 260 [**L. (Y.) roomusoksi;* OD]. Profile, outline, and interior similar to *L. (Leptaena)* but with distinctive ornament of diagonal rugae forming an interference pattern on disc, in contrast to simple pattern of laterally extensive rugae in *L. (Leptaena)*. *Ordovician (Ashgill):* Sweden, Iran.——FIG. 1729,*1a–c. *L. (Y.) roomusoksi,* Boda Limestone, middle Ashgill, Osmundsberget Quarry, Dalarna, Sweden; holotype, ventral, dorsal, and lateral views of conjoined valves, RMS Br 102778a, ×4 (Cocks, 2005).

Crassitestella BAARLI, 1995, p. 39 [**Leptaena reedi* COCKS, 1968, p. 310; OD]. Ventral profile convex to rounded and geniculate, sharply geniculate dorsal profile; outline relatively transverse for family; parvicostellate ornament with continuous rugae except on trail; gently concave and apsacline ventral interarea with wide delthyrium; dorsal interarea short and anacline with small, convex chilidial plates extending laterally across hinge line as raised plates with flanking grooves; blunt teeth; dental plates short and stout, continuing as strong, curved muscle-bounding ridges not meeting anteriorly; strong cardinal process; sockets deep, subparallel to hinge line, sometimes crenulated; notothyrial platform high; strong socket ridges; short median ridge variably developed and may be grooved to form a double ridge; paired outwardly concave transmuscle septa strongest at midvalve length; occasional extra septa developed laterally; saccate mantle canal system. *Silurian (Llandovery):* Europe.——FIG. 1729,*3a–d. *C. reedi* (COCKS), Woodland Formation, Rhuddanian, Woodland Point, Girvan, Scotland; *a–b,* ventral exterior, BMNH B73341, ×3; *c,* ventral internal mold, BMNH BB31458, ×3; *d,* dorsal interior, BMNH B73342, ×3 (Cocks, 1968).

Lissoleptaena HAVLÍČEK, 1992, p. 171 [**L. lissodermis;* OD]. See COCKS and RONG, 2000, p. 250. *Lower Devonian*: Europe.

L. (Lissoleptaena). Similar to *Leptaena* but with no radial ornament laterally, although present near median plane; rugae faint. *Devonian (Lochkovian)*: Europe.

?L. (Vanekaria) Havlíček in Havlíček & Vaněk, 1998, p. 60 [**Lissoleptaena vicaria* Havlíček, 1992, p. 173; OD]. [This was designated as a separate genus even though its type species was orginally assigned to *Lissoleptaena*. There is a single prominent median costellae as the only radial ornament. The dental plates are shorter than *Lissoleptaena,* but the specimens are small. Although the ventral muscle field is stated to be subcircular and nonbilobate, their diagram and plate clearly shows a bilobate field as in *Lissoleptaena*. No dorsal interiors are known, but the name is provisionally retained here as a possible subgenus of *Lissoleptaena*.] *Lower Devonian*: Czech Republic.——Fig. 1729,*2a–d.* **L? (V.) vicaria,* Pragian, Bohemia; *a,* holotype, ventral valve, Slivenec Limestone, Srbsko, VH 5194, ×4.3; *b,* ventral valve, Dvorce-Prokop Limestone, Konváčka, Smíchov, VH 5196, ×4; *c,* ventral valve, Dvorce-Prokop Limestone, Konváčka, Smíchov, VH 8212, ×3.8; *d,* ventral valve, Dvorce-Prokop Limestone, Konváčka, Smíchov, VH 100902a, ×6 (Havlíček & Vaněk, 1998).

Family GLYPTOMENIDAE Williams, 1965

[*nom. transl.* Rong & Cocks, 1994, p. 664, *ex* Glyptomeninae Williams, 1965c, p. 388] [=Yushanomenidae Zeng & Hu, 1997, p. 8]

Cocks (2005) reviewed the appropriate subfamilial classification within the Glyptomenidae and concluded that the family is best divided into three subfamilies. The unifying familial character is the distinctive Type C cardinal process of Rong and Cocks (1994). In addition, to differentiate between the subfamilies, the nominal subfamily, the Glyptomeninae, has no side septa or dorsal median septum, the Teratelasminae has both side septa and a dorsal median septum, and the Ungulomeninae differs from the other two in the possession of a prominent dorsal diaphragm. A separate family, the Yushanomenidae, was erected by Zeng and Hu (1997), but this is placed in synonymy with the Teratelasminae (see below).

Subfamily GLYPTOMENINAE Williams, 1965

Glyptomenoides Popov & Cocks, 2006, p. 259 [**Rafinesquina girvanensis* Salmon, 1942, p. 571; OD]. Outline semicircular to subrectangular with maximum width at hinge line; profile with pedicle valve convex and gently geniculate, and dorsal valve relatively flat with dorsal geniculation; ventral interarea apsacline with small deltidial plates; dorsal interarea narrower, anacline with chilidium. Ornament unequally parvicostellate and irregularly rugate. Ventral interior with short stout teeth and short dental plates; muscle field bilobed, flabellate anteriorly and with short curved muscle-bounding ridges developed laterally only. Dorsal interior with small divided cardinal process lobes fused with prominent strong socket plates; short stout myophragm with bilobed muscle scars; pair of very small septa inside muscle area and a larger pair anterior to it and curved toward valve center; subperipheral diaphragm variably developed at geniculation point. Similar to *Glyptomena* but geniculate and rugate. *Ordovician (Caradoc):* Laurentia, ?Kazakhstan.——Fig. 1730,*1a–d.* **G. girvanensis* (Salmon), Balclatchie Formation, lower Caradoc, Girvan, Scotland; *a,* ventral internal mold, BMNH B 73288, ×2; *b–c,* mold and latex cast of dorsal interior, BMNH B 73290, ×3; *d,* latex cast of dorsal interior, BMNH B15213, ×4 (new).

Paromalomena Rong, 1984, p. 150 [**Platymena polonica* Temple, 1965, p. 407; OD]. See Cocks and Rong, 2000, p. 254. *Ordovician (Ashgill):* cosmopolitan.

P. (Paromalomena). Similar to *P. (Shanomena)* but with incipient anterior fold and corresponding sulcus and ornamentation of irregular and sporadic rugae and costellae of variable strength; ventral muscle field flabellate anteriorly; dorsal transmuscle septa absent. *Ordovician (Ashgill):* cosmopolitan.

P. (Shanomena) Cocks & Fortey, 2002, p. 68 [**Stropheodonta mcmahoni* Reed, 1915, p. 76; OD]. Similar to *P. (Paromalomena)* but with no anterior fold or sulcus; ornamentation of small irregular rugae, more pronounced anteriorly; fine subequal parvicostellae; ventral muscle field bilobed; weekly developed dorsal transmuscle septa. *Ordovician (Ashgill):* Burma (Myanmawr).——Fig. 1730,*2a–e.* **P. (S.) mcmahoni* (Reed), Panghsa-pye Formation, Hirnantian, Panghsa-pye, Northern Shan States; *a–b,* ventral internal mold and latex cast, BMNH BC 56785, ×2; *c–d,* lectotype, dorsal internal mold and latex cast, GSI 11611 (BMNH BC 56789), ×2; *e,* latex cast of dorsal valve, BMNH BC 56786, ×2 (Cocks & Fortey, 2002).

Subfamily TERATELASMINAE Pope, 1976

Tashanomena Zhan & Rong, 1994, p. 418 [**T. variabilis*; OD] [=*Yushanomena* Zeng & Hu, 1997, p. 9 (type, *Y. elegans,* OD)]. [*Yushanomena,* from the early Llandovery, Wangjiaba, Yushan county, Jiangxi Province, China, has all the generic characters of *Tashanomena* (Cocks & Rong, 2000, p. 256), but extends its stratigraphic range.] *Ordovician (Ashgill)–Silurian (Llandovery):* southeastern Asia.

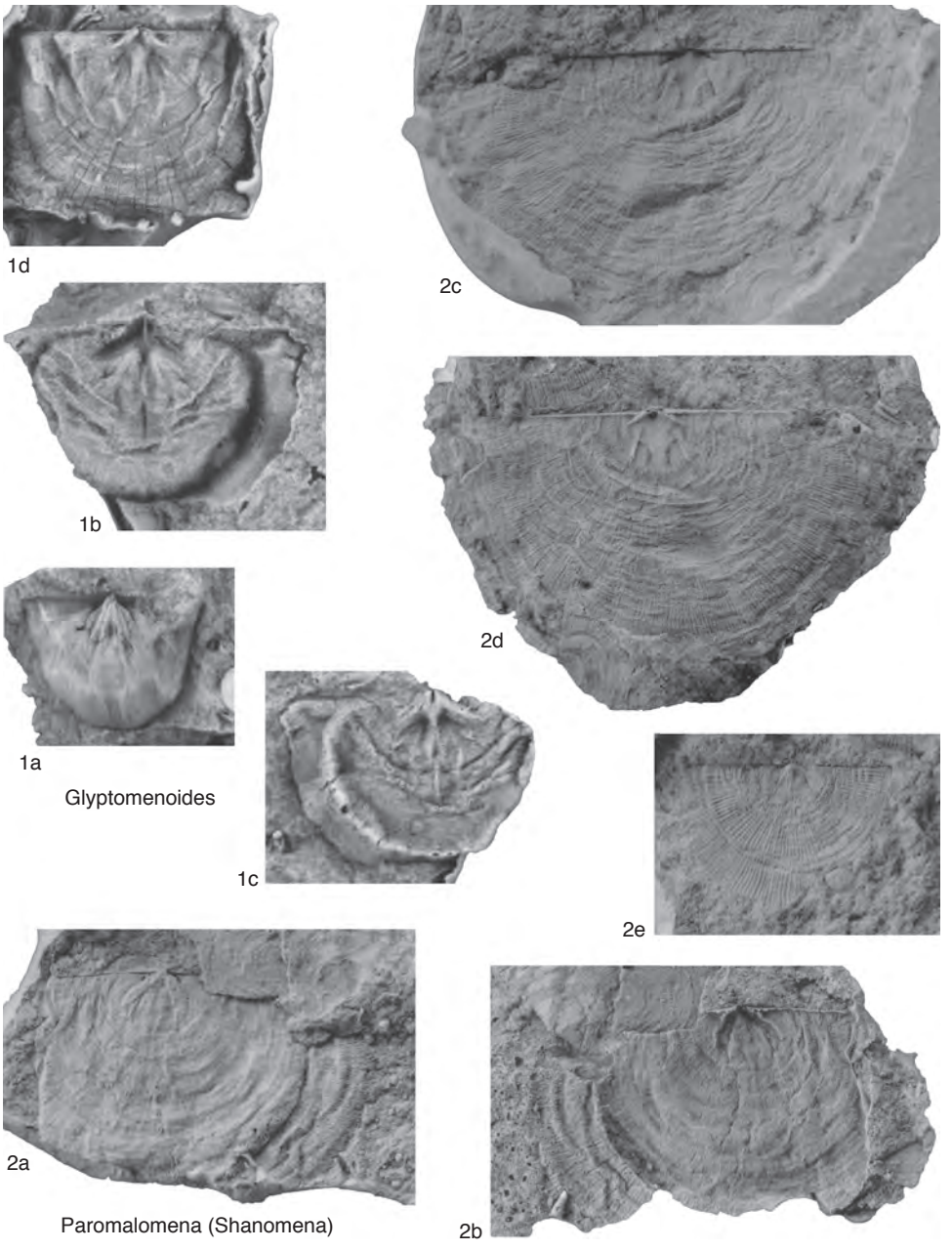

FIG. 1730. Glyptomenidae (p. 2610).

Trondomena COCKS, 2005, p. 264 [**T. bella;* OD]. Glyptomenid with gentle but normal convexity and elongately semicircular outline; robust flaring teeth; flaring crenulated dorsal socket plates, initially straight, but curving round anterolaterally, and supported by short dental plates; prominent dorsal socket plates curved and extending laterally up to half hinge width; weak subparallel dorsal side septa; dorsal median septum absent. *Ordovician (Ashgill):* Baltica.——FIG. 1731*a–e*. **T. bella*, Boda Limestone, middle Ashgill, Osmundsberget Quarry, Dalarna, Sweden; *a–b,* ventral and lateral views

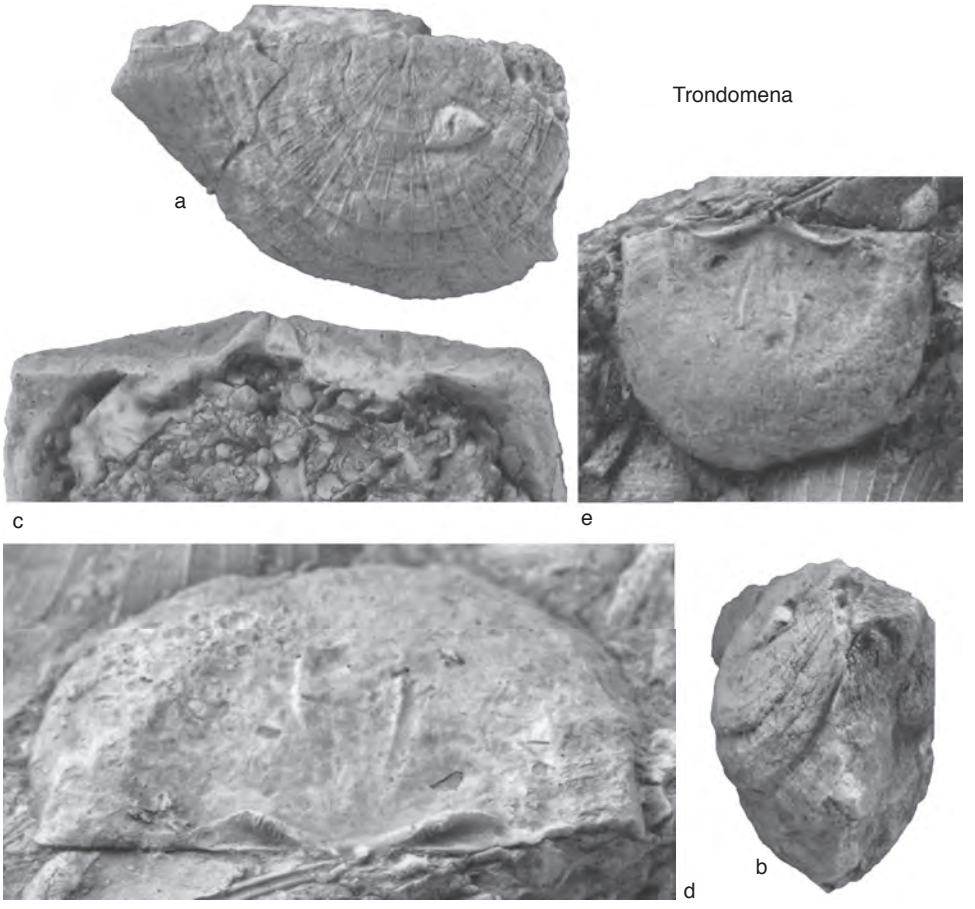

FIG. 1731. Glyptomenidae (p. 2611–2612).

of ventral valve, LO 9582, ×2; *c*, ventral interior showing interarea and teeth, BMNH BC 58018, ×1.5; *d–e,* holotype, posterior, ×3, and dorsal, ×1.5, views of dorsal interior, RMS Br 138091 (Cocks, 2005).

Subfamily UNGULOMENINAE Cocks, 2005

[Ungulomeninae COCKS, 2005, p. 265]

Glyptomenids with side septa, small dorsal median septum and substantial diaphragm. *Ordovician (Ashgill).*

Ungulomena COCKS, 2005, p. 265 [**U. lindstroemi;* OD]. Subquadrangular transverse outline; gently convex ventral valve with marked but evenly rounded geniculation at about two-thirds valve length; flat dorsal valve until geniculation, which matches ventral valve. Central ventral sulcus and dorsal fold on trail. Large apsacline interarea with large pseudodeltidium; smaller anacline dorsal interarea with chilidium smaller than pseudodeltidium. Ventral interior with large triangular teeth that flare sharply but diminish quickly laterally; dental plates initially diverging at about 90°. Dorsal interior with upright cardinal process; well-developed socket plates flaring laterally and curving posteriorly; weak myophragm extending anteriorly to a short weak median septum at about two-thirds disc length; pair of slightly curved to straight dorsal side septa only in disc center; variable but usually prominent dorsal diaphragm corresponding to the crest of geniculation, diaphragm undercut by up to 2 mm. *Ordovician (Ashgill):* Baltica.——FIG. 1732*a–g.* **U. lindstroemi,* Boda Limestone, Middle Ashgill, Osmundsberget Quarry, Dalarna, Sweden; *a–c,* ventral, dorsal, and lateral views of conjoined valves, ×2.5; *d,* posterior view of interarea of conjoined valves, LO 9583, ×3; *e*, ventral interior mold, BMNH BC 58233, ×2.5; *f–g,* dorsal view, ×2.5, and posterior view of dorsal valve, holotype, BMNH BC 57970, ×5 (Cocks, 2005).

FIG. 1732. Glyptomenidae (p. 2612).

Family AMPHISTROPHIIDAE Harper, 1973
Subfamily AMPHISTROPHIINAE Harper, 1973

Amphistrophia HALL & CLARKE, 1892, p. 292.

Amphistrophia (Amphistrophia) HALL & CLARKE, 1892, p. 292 [**Strophomena striata* HALL, 1843, p. 104; OD]. See COCKS and RONG, 2000, p. 260.

Amphistrophia (Sulcatastrophiella) BOUCOT & BLODGETT in BOUCOT, BLODGETT, & STEWART, 1997, p. 282 [**Amphistrophiella (Sulcatastrophia) stinnesbecki;* OD]. Similar to *A. (Amphistrophia)* but with relatively narrow but pronounced dorsal valve sulcus and corresponding ventral valve fold. *Silurian (Wenlock–Ludlow):* North and South America.——FIG. 1733,*2a–c. *A. (S.) stinnesbecki*, Canon de Caballeros Formation, Wenlock, Ciudad Victoria, northeastern Mexico; *a–b,* holotype, exterior and interior molds of ventral valve, USNM 220896, ×2; *c,* interior mold of ventral valve, IGM 6894a, ×2 (Boucot, Blodgett, & Stewart, 1997).

Family DOUVILLINIDAE Caster, 1939
Subfamily PROTODOUVILLININAE Harper & Boucot, 1978

Arcticastrophia LI & JONES, 2002, p. 653 [**A. costellata*; OD]. Similar to *Borealistrophia* LI & JONES, but with gently convex ventral valve lacking sulcus and ventral muscle-bounding ridges high and prominent, in order to support elevated muscle field in ventral valve. *Devonian (Eifelian):* North America.——FIG. 1733,*4a–d. *A. costellata*,

Baad Fiord Member of Bird Fiord Formation, Ensorcellement River, Grinnell Peninsula, Devon Island, Arctic Canada; *a–b,* holotype, dorsal view and dorsal interior, UA12086, ×2.3; *c*, paratype, ventral interior, UA12082, ×2.7; *d,* paratype, dorsal view, UA12081, ×2.5 (Li & Jones, 2002).

Borealistrophia Li & Jones, 2002, p. 650 [**B. rongi*; OD]. Similar to *Nadiastrophia*, but with much shorter, cordate ventral muscle scars, more prominent and thicker socket plates, and much shorter side septa in dorsal valve. *Lower Devonian (uppermost Emsian)–Middle Devonian (Eifelian):* North America.——Fig. 1733,*1a–c. *B. rongi*, Baad Fiord, Blubber Point, and Norwegian Bay members of Bird Fiord Formation, Eifelian, southwestern Ellesmere Island, North Kent Island, Devonian Island, Grinnell Peninsula and Bathurst Island, Arctic Canada; *a–b,* holotype, dorsal exterior and interior, UA12075, ×3.7; *c,* paratype, ventral interior, UA12078, ×3 (Li & Jones, 2002).

Cymostrophia Caster, 1939, p. 39 [**Leptaena stephani* Barrande, 1848, p. 230; OD]. See Cocks and Rong, 2000, p. 268. *Silurian (Ludlow)–Devonian (Givetian):* cosmopolitan.

C. (Cymostrophia). Transverse outline; strongly convex profile; ornament of very pronounced rugae interrupted by radial costellae. *Devonian (Lochkovian–Givetian):* cosmopolitan.

C. (Cymostrophiella) Havlíček in Havlíček & Vaněk, 1998, p. 63 [**Leptaena convoluta* Barrande, 1848, pl. 20,*8;* OD]. Although erected as an independent genus, differs from *Cymostrophia* only in ornament and is thus relegated to a subgenus here. Radial costellae absent on dorsal valve, where they are replaced by grooves; concentric rugellae absent or confined to ventral umbonal region to form very weak undulations. *Devonian (Pragian):* Czech Republic.——Fig. 1733,*3a–c. *C. (C.) convoluta* (Barrande); *a,* ventral exterior, Vinařice Limestone, west of Měňany, Bohemia, VH 10693g, ×1.5; *b,* dorsal exterior, Vinařice Limestone, west of Měňany, Bohemia, VH 10695i, ×2; *c,* ventral interior, Koněprusy Limestone, Koněprusy, Bohemia, VH 9491c, ×2 (Havlíček & Vaněk, 1998).

C. (Protocymostrophia) Harper & Boucot, 1978, p. 127 [**Strophomena ivanensis* Barrande, 1879, pl. 52,*IV 1-4, 9-12;* OD]. Similar to *C. (Cymostrophia),* but with suboval rather than transverse outline; gently concavoconvex profile; less pronounced interrupted rugae in ornament. *Silurian (Ludlow)–Devonian (Eifelian):* cosmopolitan.

Family LEPTOSTROPHIIDAE Caster, 1939

Eocymostrophia Baarli, 1995, p. 48 [**E. balderi*; OD]. Profile gently concavoconvex; outline transverse to semicircular; ornament regular but very fine parvicostellae with fine rugae broken by parvicostellae. Denticles on short denticular plates; dental plates absent; triangular ventral muscle field well impressed posterolaterally with short straight muscle-bounding ridges posterolaterally only; variable cardinal process lobes, but usually erect and ponderous; deep alveolar pit; very thin, poorly developed dorsal median septum and thin, straight, subparallel to slightly divergent dorsal transmuscle ridges. *Silurian (Llandovery):* Baltic. ——Fig. 1734,*1a–c. *E. balderi,* Vik Formation, Telychian, Sandvika, Norway; *a,* dorsal external mold, PMO 135.935, ×2; *b,* ventral internal mold, PMO 135.945, ×1.5; *c,* holotype, dorsal internal mold, PMO 135.968, ×1.5 (Baarli, 1995).

Mesoleptostrophia Harper & Boucot, 1978, p. 68 [**M. kartalensis;* OD]. [See Cocks & Rong, 2000, p. 286. There are already two subgenera, *Mesoleptostrophia* and *Paraleptostrophia,* within *Mesoleptostrophia.* It is uncertain whether or not *Rhytirugea* should be included within the genus, and, if so, what its relationships with the other subgenera are. It was erected as a subgenus of *Leptostrophiella*, which was synonymized within *Mesoleptostrophia* in Cocks & Rong, 2000, p. 286; however, it may be a synonym of *Paraleptostrophia*, but the characteristic cardinal process lobes of that subgenus are not described for *Rhytirugea.* The type species was previously assigned to *Rhytistrophia* by Havlíček, 1967.] *Silurian (Telychian)–Devonian (Eifelian):* cosmopolitan.

Mesoleptostrophia (Rhytirugea) Havlíček & Vaněk, 1998, p. 61 [**Leptaena sowerbyi* Barrande, 1848, p. 239; OD]. Outline semicircular and alate; shell thin; profile biconvex posteriorly but ventral valve subplanar anteriorly; ventral interarea low, apsacline, with small pseudodeltidium; dorsal interarea small and thin. Ornament costellate and often slightly undulose, with some intervening parvicostellae; irregular rugae variably developed over entire valve. Ventral interior with small ventral process; triangular muscle field, flabellate and weakly impressed anteriorly; small, lanceolate adductor scars. Dorsal interior with denticulate hinge line to over half valve width; massive cardinal process lobes; muscle field bounded posterolaterally by short substantial ridges. Mantle canals not impressed. *Devonian (Pragian):* Czech Republic. ——Fig. 1734,*2a–d. *M? (R.) sowerbyi* (Barrande); *a,* ventral exterior, Koněprusy Limestone, Koněprusy, NM L6673, ×1.5; *b–c,* holotype, dorsal view of conjoined valves, Koněprusy Limestone, Koněprusy, NM L6457, ×1.5 and ×3; *d,* dorsal internal mold, Zlíchov Limestone, Hlubočepy, VH 438, ×4 (Havlíček & Vaněk, 1998).

Nervostrophia Caster, 1939, p. 79 [**Strophomena nervosa* Hall, 1843, p. 266; OD]. See Cocks and Rong, 2000, p. 286. *Devonian (?Givetian, Frasnian):* cosmopolitan.

Nervostrophia (Nervostrophia). Description as for genus. *Devonian (?Givetian, Frasnian):* cosmopolitan.

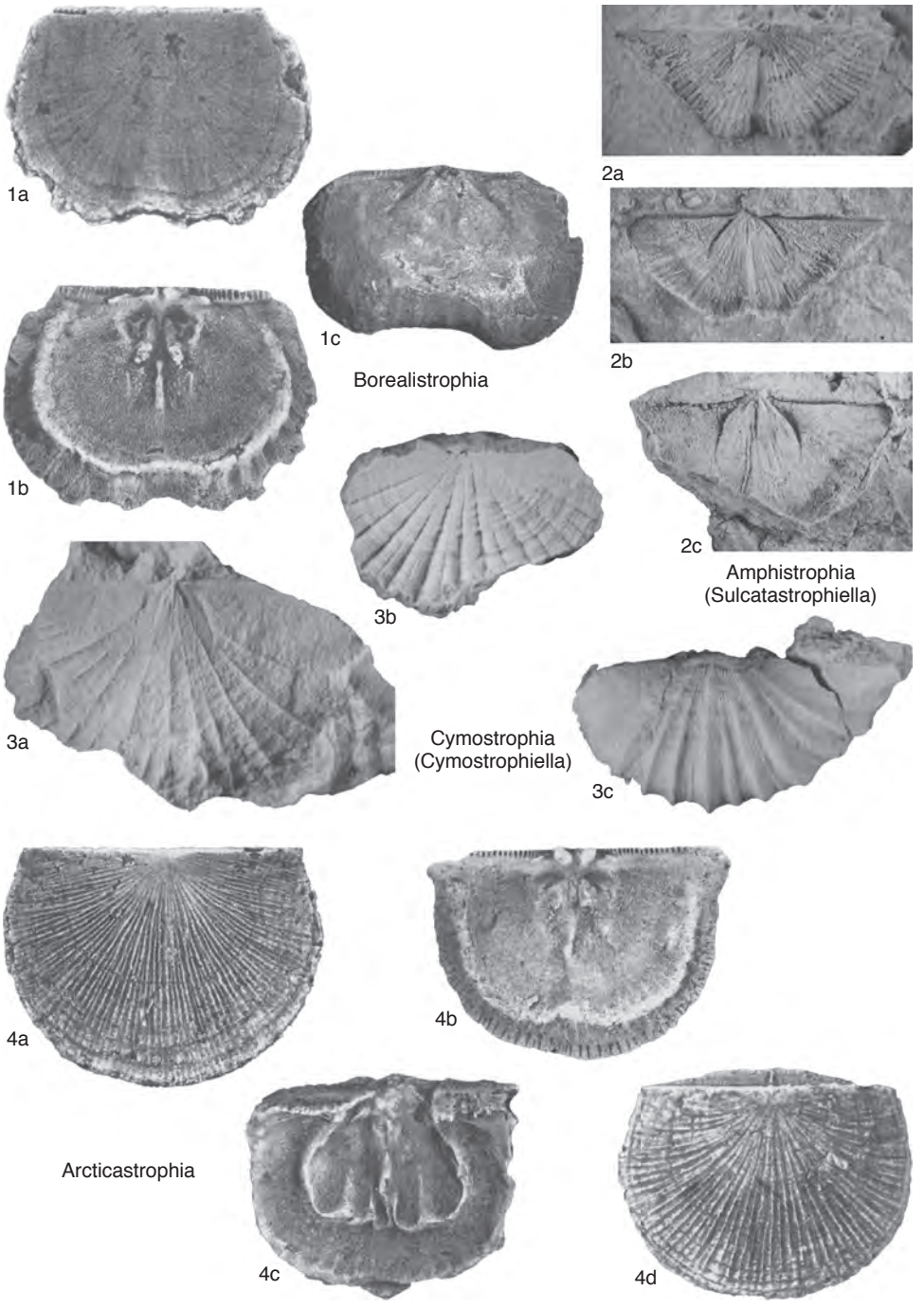

FIG. 1733. Amphistrophiidae and Douvillinidae (p. 2613–2614).

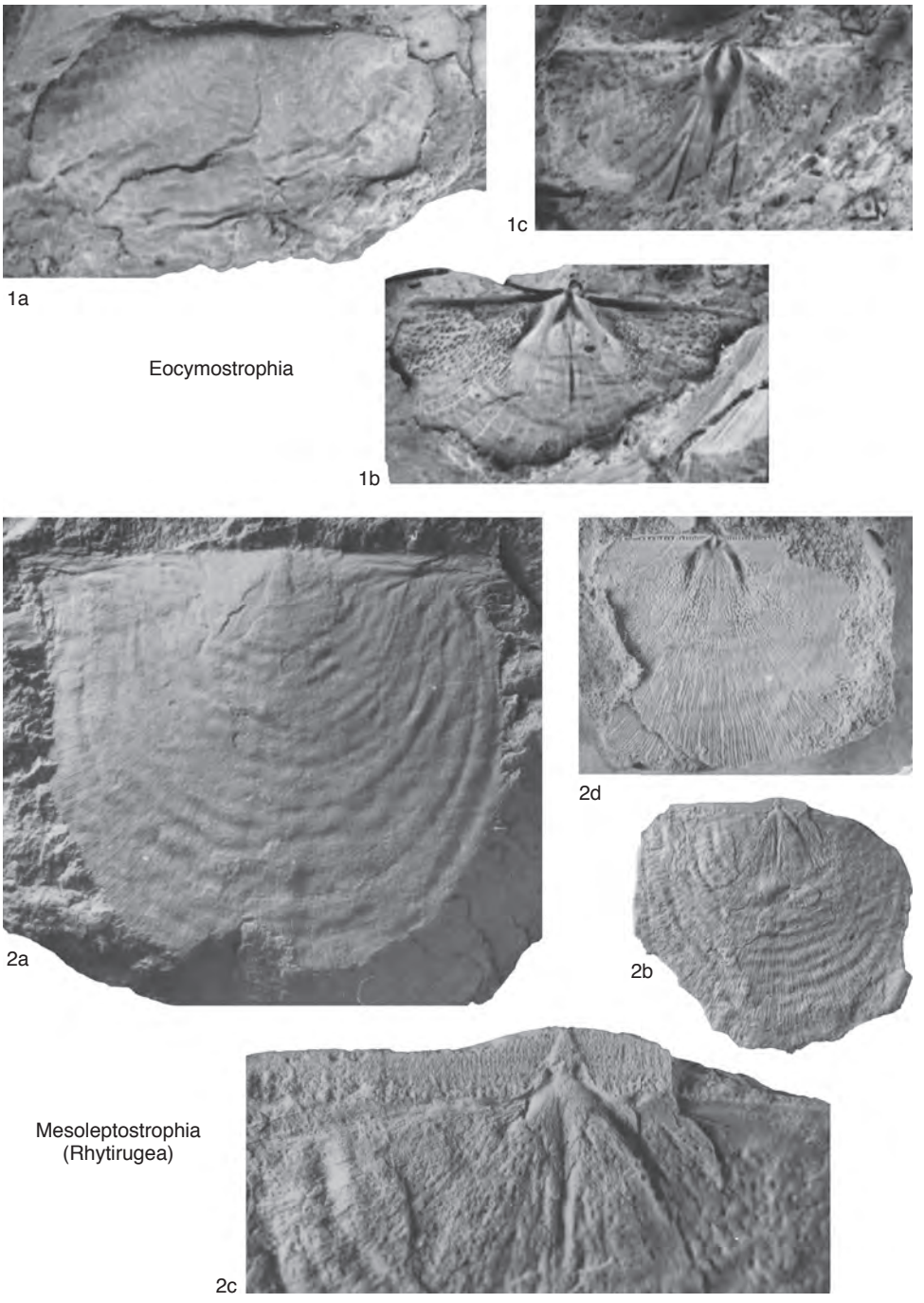

FIG. 1734. Leptostrophiidae (p. 2614).

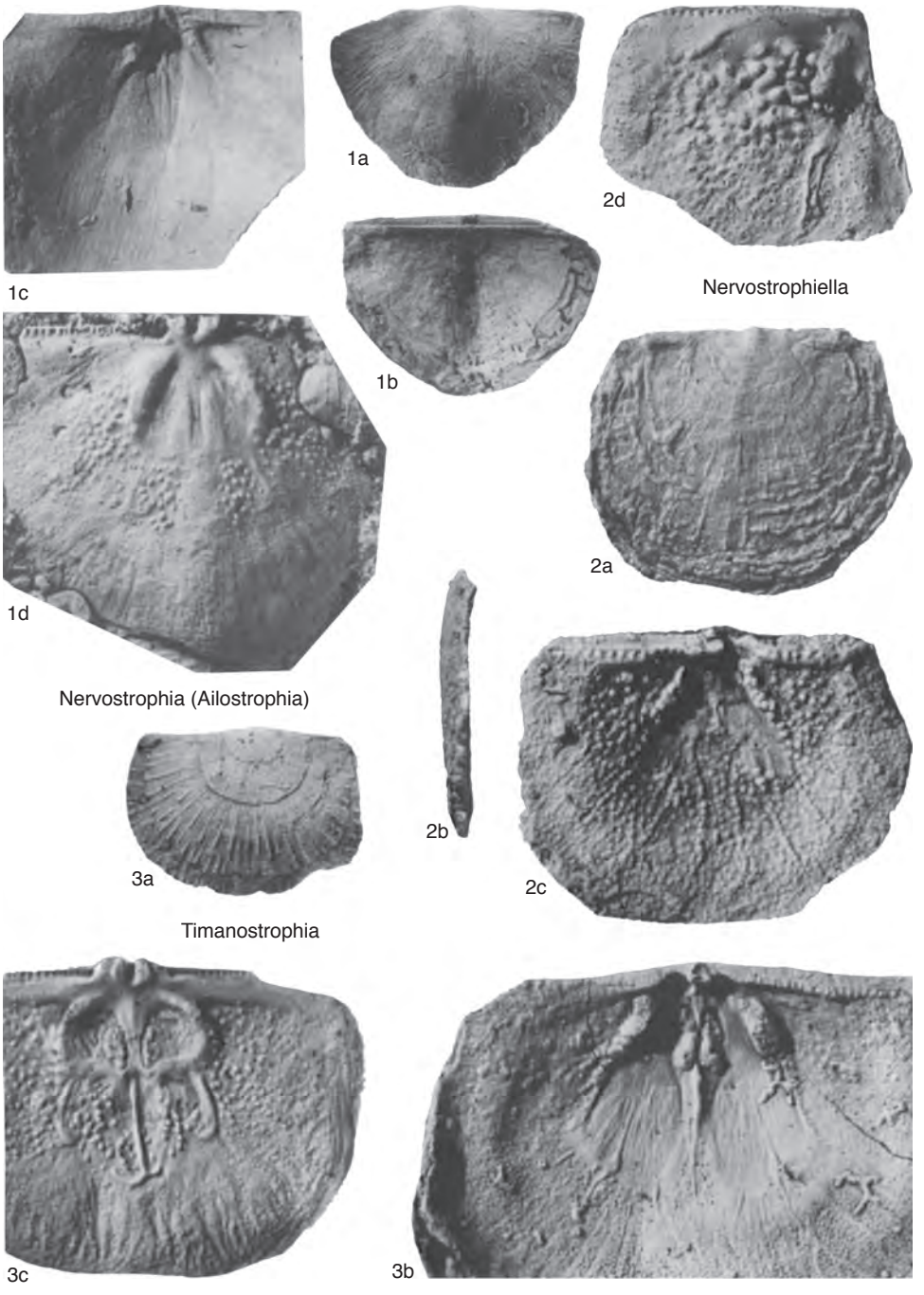

FIG. 1735. Leptostrophiidae (p. 2618).

FIG. 1736. Leptostrophiidae (p. 2618).

Nervostrophia (Ailostrophia) ALEKSEEVA, 2003, p. 25 [**Leptaena asella* DE VERNEUIL, 1845, p. 224]. [Although erected as a separate genus, this subgenus is very similar to *Nervostrophia,* in particular with the very distinctive ornament, in which the primary costellae are differentially and irregularly enhanced along their lengths. *Ailostrophia* only differs from *Nervostrophia* in having a carinate ventral valve that is more strongly convex than that of *Nervostrophia.*] *Devonian (Frasnian):* Russian Platform.——FIG. 1735,*1a–d. *N. (A.) asella* (VERNEUIL), Semilukskii Horizon, right bank of Don River, Pentino, central part of Russian Platform; *a–b,* ventral and dorsal views of conjoined shell, VNIGNI 141, ×3; *c,* ventral interior, VNIGNI 5367, ×3; *d,* dorsal interior, VNIGNI 5365, ×3 (Alekseeva, 2003).

Nervostrophiella ALEKSEEVA, 2003, p. 31 [**N. plana*; OD]. Similar to *Nervostrophia* in shape, outline, and interior features but with much smaller shell size, very fine and weak costellae sporadically enhanced near valve margin, and flat pseudodeltidium and chilidium. *Devonian (Frasnian):* Russia (southern Timan).——FIG. 1735,*2a–d. *N. plana*, Lyaiolskaya Formation, right bank of Lyaiol River; *a–b,* holotype, ventral and dorsal views of conjoined valves, VNIGNI 5495, ×4; *c,* ventral interior, VNIGNI 5496, ×4; *d,* dorsal interior, VNIGNI 5497, ×4 (Alekseeva, 2003).

Pseudoleptostrophia GAD, 1997, p. 192 [**Leptostrophia dahmeri* RÖSLER, 1954, p. 36; OD]. Outline semicircular; profile gently resupinate; ventral interarea apsacline and entire; dorsal interarea unknown. Ornament of fine multicostellae. Ventral interior similar to *Leptostrophia*, with prominent myophragm posteriorly, but with muscle-bounding ridges variable from straight to slightly incurved anteriorly. Dorsal interior with denticulate hinge line to over three-quarters of valve width; robust, erect cardinal process lobes, posterolaterally and parallel to which run very short socket plates no longer than cardinal process lobes. Short myophram within muscle field extending anteriorly into a very weak median septum up to one-third valve length. Mantle canals not impressed. *Devonian (Emsian):* Germany.——FIG. 1736. **P. dahmeri* (RÖSLER), Dillenberger Formation, lower Emsian, Dörsbachtal; mold of ventral exterior, GLR-P 5611/5, ×1.5 (new).——FIG. 1737*a–c. *P. dahmeri* (RÖSLER), Dillenberger Formation, lower Emsian, Dörsbachtal; *a,* lectotype, mold of ventral interior, GLR-P Mbg 2031, ×1.5; *b,* mold of ventral interior, GLR-P 5611/6, ×1.5; *c,* mold of dorsal interior, GLR-P Sch 194/18, ×1.5 (new).

Timanostrophia ALEKSEEVA, 2003, p. 29 [**T. ukhtensis*; OD]. Similar to *Nervostrophia* in shape, outline, and distinctive ornament but with thick and strong brachial ridges and brevisepta in dorsal valve. *Devonian (Frasnian):* Russia (Timan).——FIG. 1735,*3a–c. *T. ukhtensis*, Sirachoiskii Horizon, right bank of Ukhty River, Sirachoi, southern Timan; *a,* holotype, ventral and dorsal views of a conjoined shell, VNIGNI 5385, ×2; *b,* ventral interior, VNIGNI 5391, ×3; *c,* dorsal interior, VNIGNI 5394, ×3 (Alekseeva, 2003).

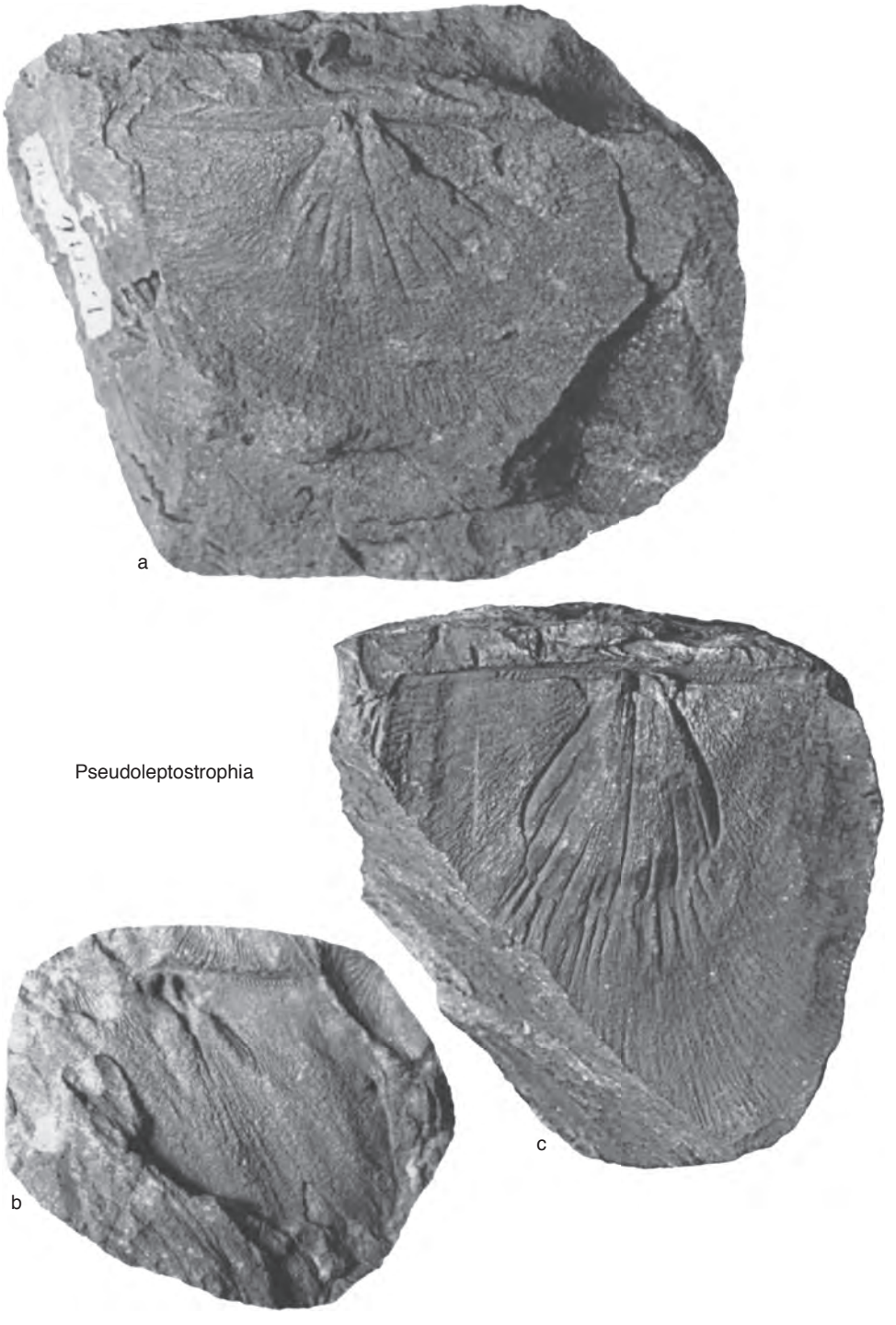

FIG. 1737. Leptostrophiidae (p. 2618).

Superfamily PLECTAMBONITOIDEA Jones, 1928

The familial and subfamilial taxonomy of the Plectambonitoidea has remained unchanged since the treatment in COCKS and RONG (2000, p. 304). More has been published on the Plectambonitoidean mode of life, however, which we did not discuss earlier. For example, DATTILO (2004) has described many specimens of the abundant *Sowerbyella rugosa*, from the Late Ordovician of Kentucky, United States. In these the brachiopods are in apparent life positions in which the shells have their hinge lines facing downward into the sediment and where sedimentary structures surrounding the individuals suggest that they may have been partially immersed in the sediment through burrowing. Whether these burrows were merely escape structures or whether *Sowerbyella* occupied them for longer periods is unclear. DATTILO (2004) surmised that the valves flapped both to escape from predators or other threats and also to burrow. COCKS (1970) had also envisaged that the valves flapped, certainly so that the plectambonitoids could return to an upright position if they had been overturned and possibly also so that water could be pumped between the valves to enhance the brachiopods' feeding, which would explain the substantial septa and bema in the dorsal valve. HURST (1976), however, while endorsing the concept of valve flapping for valve position recovery, presented a convincing reconstruction of the ontogeny of both soft and hard parts within the dorsal valve of the sowerbyellid *Eoplectodonta.* This showed the lophophore developing from a juvenile trocholophe into an adult schizolophe that would have enabled feeding through the ciliary action common to all living brachiopods and did not need to invoke any flapping to enhance food capture by the lophophore.

Family PLECTAMBONITIDAE Jones, 1928
Subfamily TAPHRODONTINAE Cooper, 1956

Bandaleta NIKITIN & POPOV, 1996, p. 5 [**B. plana*; OD]. Profile planoconvex to slightly concavoconvex; transverse outline; parvicostellate ornament; ventral pseudointerarea apsacline with pseudodeltidium; dorsal bilobed ventral muscle field with long divergent diductor scars; strong teeth; dental plates vestigial to absent; simple, small, knoblike cardinal process; high dorsal double septum continuing to subperipheral rim; subrectangular dorsal muscle field with bounding ridges; ventral mantle canals saccate and dorsal mantle canals lemniscate. *Ordovician (Darriwilian–Caradoc):* Kazakhstan.——FIG. 1738,*4a–d. *B. plana,* Dulankara Regional Stage, upper Caradoc, Betpak-Dala Desert; *a*, exterior of conjoined valves, CNIGR 3/12877, ×3; *b,* ventral internal mold, CNIGR 4/12877, ×3; *c–d,* latex cast and internal mold of dorsal valve, CNIGR 5/12877, ×2 (Nikitin & Popov, 1996).

Uzunbulakia NIKITINA & others, 2006, p. 178 [**U. rugosa;* OD]. Transverse outline; concavoconvex profile; small interarea with ventral pseudodeltidium; ornament finely multicostellate with rugellae posteriorly. Ventral interior with widely divergent short teeth; no dental plates; small bilobed muscle field; prominent subperipheral rim. Dorsal interior with small, simple, bulbous cardinal process; median ridge low and broad, proceeding from low notothyrial platform that becomes double-crested anteriorly and does not extend anteriorly beyond entire diaphragm. *Ordovician (Darriwilian):* Kazakhstan.——FIG. 1738,*1a–d. *U. rugosa,* Uzunbulak Formation, Uzunbulak, Chu-Ili Range; *a,* dorsal exterior, USNM 485144, ×3; *b,* holotype, ventral interior, USNM 485142, ×3; *c–d,* internal mold and latex cast of dorsal interior, USNM 485143, ×3 (Nikitina & others, 2006).

Family TAFFIIDAE Schuchert & Cooper, 1931
Subfamily TAFFIINAE Schuchert & Cooper, 1931

Tinopena LAURIE, 1997b, p. 712 [**T. shergoldi;* OD]. Profile concavoconvex; outline subcircular to transversely ovate; parvicostellate ornament; ventral interarea orthocline to apsacline; dorsal interarea catacline; chilidium completely covering notothyrium; subcordate ventral muscle field; teeth with shelflike fossettes; small dental plates; subperipheral rim in both valves; bladelike to subcircular cardinal process; short socket ridges; ovate posterior dorsal adductor muscle scars larger than subcircular

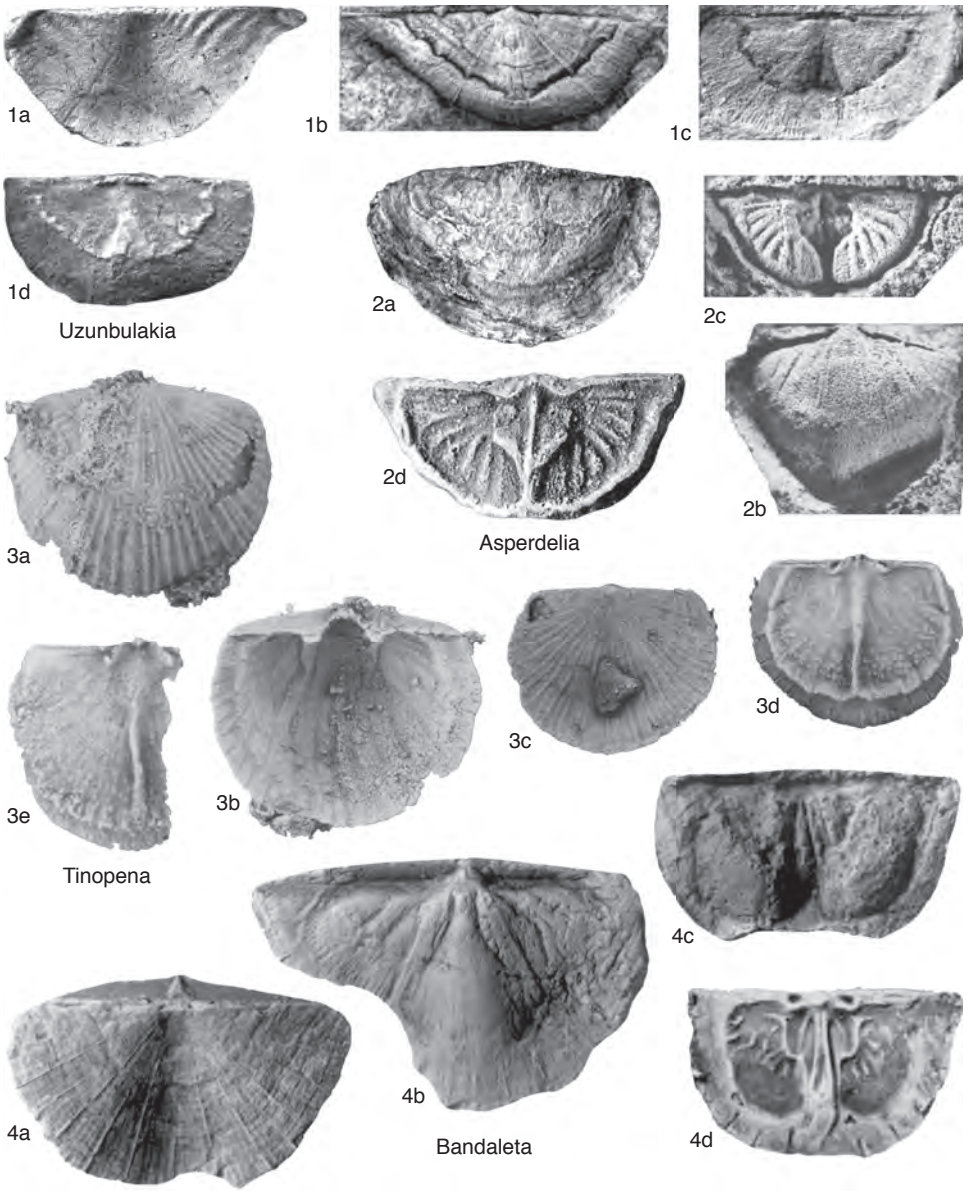

FIG. 1738. Plectambonitidae, Taffiidae, and Bimuriidae (p. 2620–2622).

anterior pair; narrow dorsal median septum to subperipheral rim; similar to *Spanodonta* but with dorsal median septum. *Ordovician (Darriwilian):* Australia.——FIG. 1738,*3a–e. *T. shergoldi,* Gap Creek Formation, Kunian Gap, Emanuel Range, Western Australia; *a–b,* exterior and interior views of ventral valve, CPC 33269, ×4; *c–d,* exterior and interior views of dorsal valve, CPC 33270, ×4; *e,* holotype, dorsal interior, CPC 33273, ×4 (Laurie, 1997b).

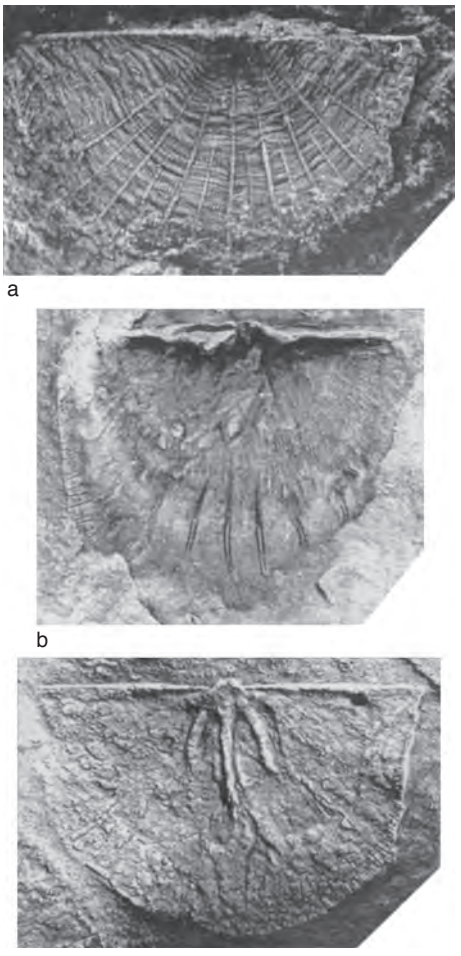

FIG. 1739. Leptellinidae (p. 2622).

Family BIMURIIDAE Cooper, 1956

Asperdelia NIKITINA & others, 2006, p. 176 [**A. villosa;* OD]. Outline transverse with alate cardinal extremities; profile concavoconvex with gently sulcate anterior commissure and short trail anterolaterally; ventral interarea apsacline; dorsal interarea ancline with prominent chilidium. Fine parvicostellate ornament; comae common. Ventral interior with short divergent teeth; muscle field weakly impressed. Dorsal interior with simple undercut cardinal process fused with socket plates; dorsal median septum present, crossing spearhead-shaped bema and extending anteriorly to strong subperipheral rim. Mantle canals saccate and strongly impressed in dorsal valve. *Ordovician (Darriwilian):* Kazakhstan.——FIG. 1738,*2a–d. *A. villosa,* Uzunbulak Formation, Kurzhaksai, Chu-Ili Range; *a,* ventral exterior, USNM 485161, ×2; *b,* ventral interior, USNM 485159, ×2.5; *c–d,* mold and latex of dorsal interior, USNM 489158, ×3 (Nikitina & others, 2006).

Family LEPTELLINIDAE Ulrich & Cooper, 1936
Subfamily PALAEOSTROPHOMENINAE Cocks & Rong, 1989

Anchoramena BENEDETTO, 1995, p. 251 [**A. cristata;* OD]. Outline semicircular to transverse; profile resupinate; unequally parvicostellate ornament with small posterolateral rugae; ventral interarea apsacline; vestigial pseudodeltidium; dorsal interarea anacline; no chilidium known; dental plates absent; differs from *Palaeostrophomena* in lacking bounding ridges to weakly developed ventral muscle field; relatively small trifid cardinal process; small socket plates flaring anterolaterally; dorsal median septum originating from anterior end of small notothyrial platform; well-impressed dorsal muscle field bounded posteriorly and laterally with prominent bounding ridges; well-impressed saccate mantle canals. *Ordovician (Caradoc):* South America.——FIG. 1739*a–c. *A. cristata*, Las Plantas Formation, lower Caradoc, River Gualcamayo, northern Precordilleras, Argentina; *a,* dorsal exterior, CEGH-UNC 13695, ×4; *b,* ventral interior, CEGH-UNC 13686b, ×2; *c,* holotype, dorsal interior, CEGH-UNC 13686a, ×2.5 (Benedetto, 1995).

Leptastichidia ZHAN & JIN, 2005, p. 34 [**L. catatonosis;* OD]. Convexoconcave, dorsal geniculation short; pseudodeltidium small. Ornament of unequal parvicostellae with accentuated major costellae; posterolateral rugae common. Ventral interior lacking dental plates; ventral muscle field small, trilobed, with straight anterior margin. Dorsal interior with ridgelike or sometimes bulbous cardinal process; socket ridges thin, high, raised laterally from valve floor; myophragm large, merging anteriorly with weak dorsal median septum; platform absent in both valves. *Ordovician (Arenig–Llanvirn):* South China.——FIG. 1740,*3a–d. *L. catatonosis,* Dashaba Formation, upper Arenig–Llanvirn, Shuanghe, Changning County, Sichuan province, southwestern China; *a–b,* ventral internal mold and latex cast, NIGP 134409, ×3; *c–d,* holotype, dorsal internal mold and latex cast, NIGP 134411, ×4 (Zhan & Jin, 2005).

Nikitinamena POPOV & COCKS, 2006, p. 266 [**N. bicostata;* OD]. Outline rhomboidal; profile concavoconvex; evenly geniculate; anterior commisure weakly uniplicate; ventral valve with widely diverging pair of low angular plications enclosing very shallow sulcus; ventral interarea apsacline with small apical pseudodeltidium; dorsal interarea hypercline with small separate chilidial plates. Ornament of fine unequal parvicostellae. Ventral interior with small teeth and small bilobed muscle

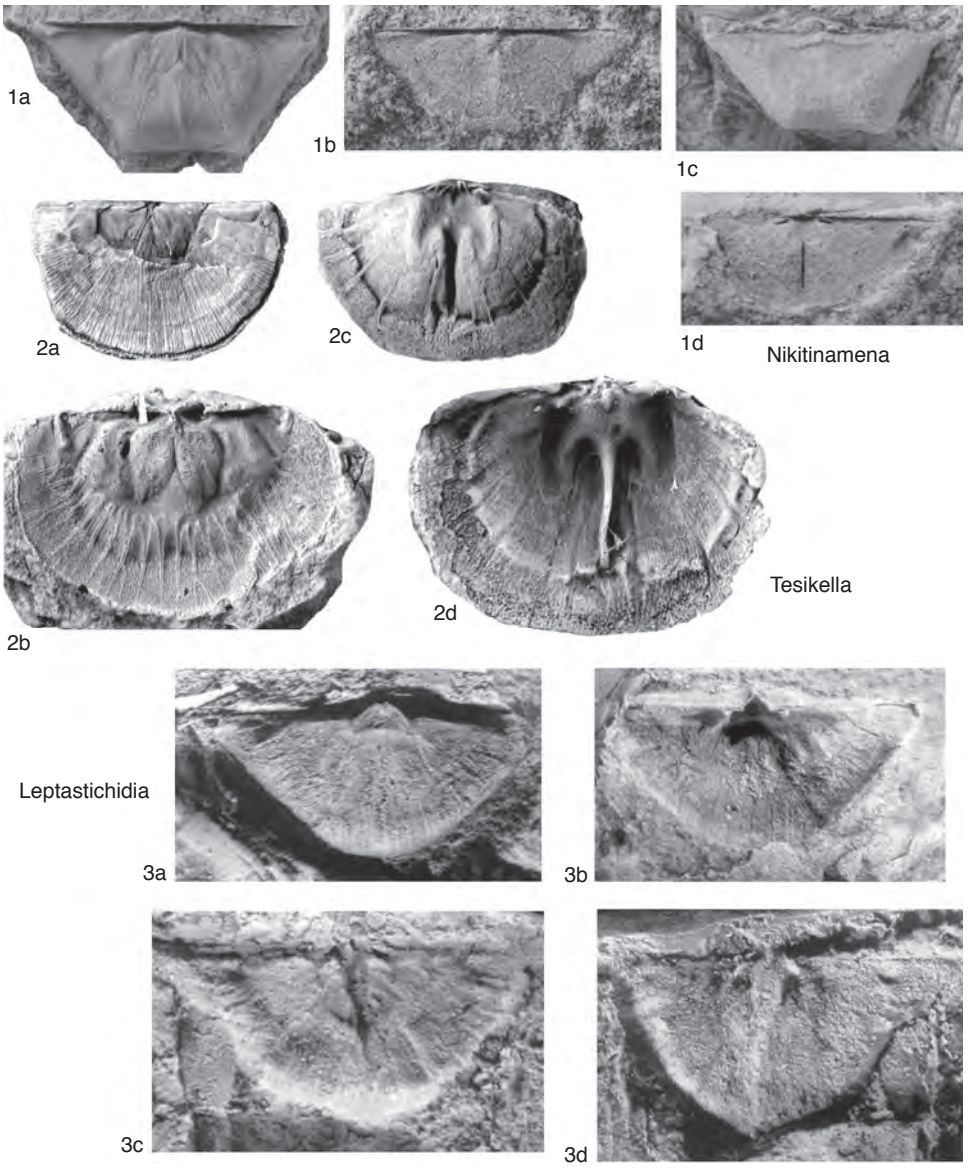

FIG. 1740. Leptellinidae (p. 2622–2624).

field with short adductor scars separating larger diductor scars; ventral mantle canals saccate with short, diverging vascular media. Dorsal interior with simple, bulbous cardinal process on low notothyrial platform; small, curved socket plates; fine median septum extending to midlength. *Ordovician (Caradoc):* Kazakhstan.——FIG. 1740,*1a–d. *N. bicostata,* Degeres Member, Dulankara Formation, upper Caradoc, Dulankara Mountains, Chu-Ili Range; *a,* holotype, ventral internal mold, BMNH BC 57716, ×4; *b*, internal mold of juvenile ventral valve, BMNH BC 57718, ×4; *c,* dorsal interior, BMNH BC 57717, ×3; *d,* dorsal internal mold, BMNH BC 57720, ×4 (Popov & Cocks, 2006).

Tesikella POPOV, COCKS, & NIKITIN, 2002, p. 44 [**Palaeostrophomena necopina* POPOV, 1980, p. 145; OD]. Outline semicircular to transversely subrectangular, maximum width just anterior to hinge line; profile gently resupinate; ventral interarea low, catacline with strong but narrow

pseudodeltidium; dorsal interarea low, anacline, with separate chilidial plates. Ornament parvicostellate. Ventral interior with double teeth; no dental plates; bilobed muscle field with low but entire muscle-bounding ridges; subperipheral rim variably developed. Dorsal interior with trifid cardinal process on low notothyrial platfom; low, widely divergent socket ridges. Strong narrow median septum over three-quarters of valve length joined anteriorly to subperipheral diaphragm. Mantle canals well impressed and saccate. *Ordovician (Caradoc):* Kazakhstan.——FIG. 1740,*2a–d. *P. necopina* (POPOV), Anderken Formation, lower to middle Caradoc, Anderkenyn-Akchoku, Chu-Ili Range; *a,* ventral exterior, BMNH BC 57434, ×2; *b,* mold of ventral interior, BMNH BC 57432, ×2; *c–d,* mold, ×2, and latex cast, ×3, of dorsal interior, BMNH BC 57604 (Popov, Cocks, & Nikitin, 2002).

Family LEPTESTIIDAE Öpik, 1933

Bekella NIKITINA & others, 2006, p. 185 [**B. paula;* OD]. Outline semicircular; profile concavoconvex; ventral interarea apsacline. Ornament finely parvicostellate. Ventral interior with small teeth; dental plates absent; small, poorly defined muscle field, anterolaterally to which are a pair of subquadrangular structures rising from valve floor. Dorsal interior with trifid cardinal process; small but distinctive bema bisected by a median septum that forks for a short distance anteriorly; small rod-shaped process rising from valve floor anterolateral to muscle field. Strong subperipheral diaphragm developed. Similar to *Leangella* except distinctive rodlike structures in interiors of both valves. *Ordovician (Darriwilian):* Kazakhstan.——FIG. 1741,*2a–e. *B. paula,* Uzunbulak Formation, Kurzhaksai, Chu-Ili Range; *a,* ventral exterior, USNM 485150, ×9; *b,d,* internal mold, ×5, and latex cast, ×8.5, USNM 485148: *c,e,* latex cast of dorsal interior oblique, ×10, and straight views, ×12, holotype, USNM 485155 (Nikitina & others, 2006).

Sortanella NIKITIN & POPOV, 1996, p. 9 [**S. quinquecostata;* OD]. Profile weakly resupinate with anterior margin sulcate in juveniles and uniplicate in adults; transverse outline; pseudodeltidium and chilidium well developed, unequal parvicostellate ornament; simple teeth; dental plates absent; cordate ventral muscle field with weak median ridge; two distinctive peripheral rims, the inner merging with hinge line at midwidth; trifid not undercut cardinal process; broad, short, strongly elevated dorsal median septum uniting anteriorly with diaphragm bounding small bema; dorsal subperipheral rim. *Ordovician (Caradoc):* Kazakhstan.——FIG. 1741,*3a–c. *S. quinquecostata,* Dulankara Regional Stage, upper Caradoc, Sortan-Manai Salt Marsh, Betpak-Dala Desert; *a,* ventral view of conjoined valves, CNIGR 11/12877, ×3; *b,* ventral internal mold, CNIGR 14/12877, ×3; *c,* dorsal internal mold, CNIGR 13/12877, ×3 (Nikitin & Popov, 1996).

Family XENAMBONITIDAE Cooper, 1956
Subfamily AEGIROMENINAE Havlíček, 1961

Cathrynia CANDELA, 1999, p. 91 [**C. puteus*; OD]. Outline semicircular to subrectangular; maximum width at hinge line; profile planoconvex; ventral interarea narrow, apsacline; dorsal interarea narrower and hypercline. Ornament finely parvicostellate with concentric filae. Ventral interior with short flaring teeth; small bilobed muscle field; very short median septum in posterior only; radial rows of papillae near anterolateral margins; weak peripheral rim often developed. Dorsal interior with simple undercut cardinal process fused with widely flaring, straight to slightly curved socket ridges; prominent median septum less than half valve length ending anteriorly and fused with pair of lateral septules; irregular bilobed bema bordered by coarse papillae. Mantle canals not impressed. *Ordovician (Caradoc):* Ireland.——FIG. 1742,*1a–d. *C. puteus,* Bardahessiagh Formation, middle Caradoc, Pomeroy, County Tyrone, Northern Ireland; *a,* latex cast of ventral exterior, K27230, ×10.5; *b,* ventral internal mold, K27340(7), ×10.5; *c–d,* holotype, mold and latex cast of dorsal interior, K27239, ×10.5 (Candela, 1999).

Tenuimena NIKITINA & others, 2006, p. 188 [**T. planissima;* OD]. Outline semicircular, maximum width just anterior to hinge line; profile planoconvex to weakly resupinate; small interarea with pseudodeltidium and chilidium. Ornament finely parvicostellate. Ventral interior with small flaring teeth; dental plates absent; suboval muscle field flanked posterolaterally by short, relatively straight muscle-bounding ridges. Dorsal interior with simple undercut cardinal process; short, flaring socket plates; fine median septum to half valve length. Mantle canals not impressed. Differs from other Aegiromeninae in lacking papillae and from *Chonetoidea* in lacking obvious bema and dental plates. *Ordovician (Darriwilian):* Kazakhstan.——FIG. 1742,*3a–c. *T. planissima,* Uzunbulak Formation, Kurzhakai, Chu-Ili Range; *a,* latex of ventral exterior, USNM 485108, ×2; *b,* ventral internal mold, USNM 485105, ×5; *c,* holotype, latex of dorsal interior, USNM 485105a, ×5 (Nikitina & others, 2006).

Family HESPEROMENIDAE Cooper, 1956

Rongambonites ZHAN & COCKS, 1998, p. 33 [**R. bella;* OD]. Outline semielliptical to semicircular;

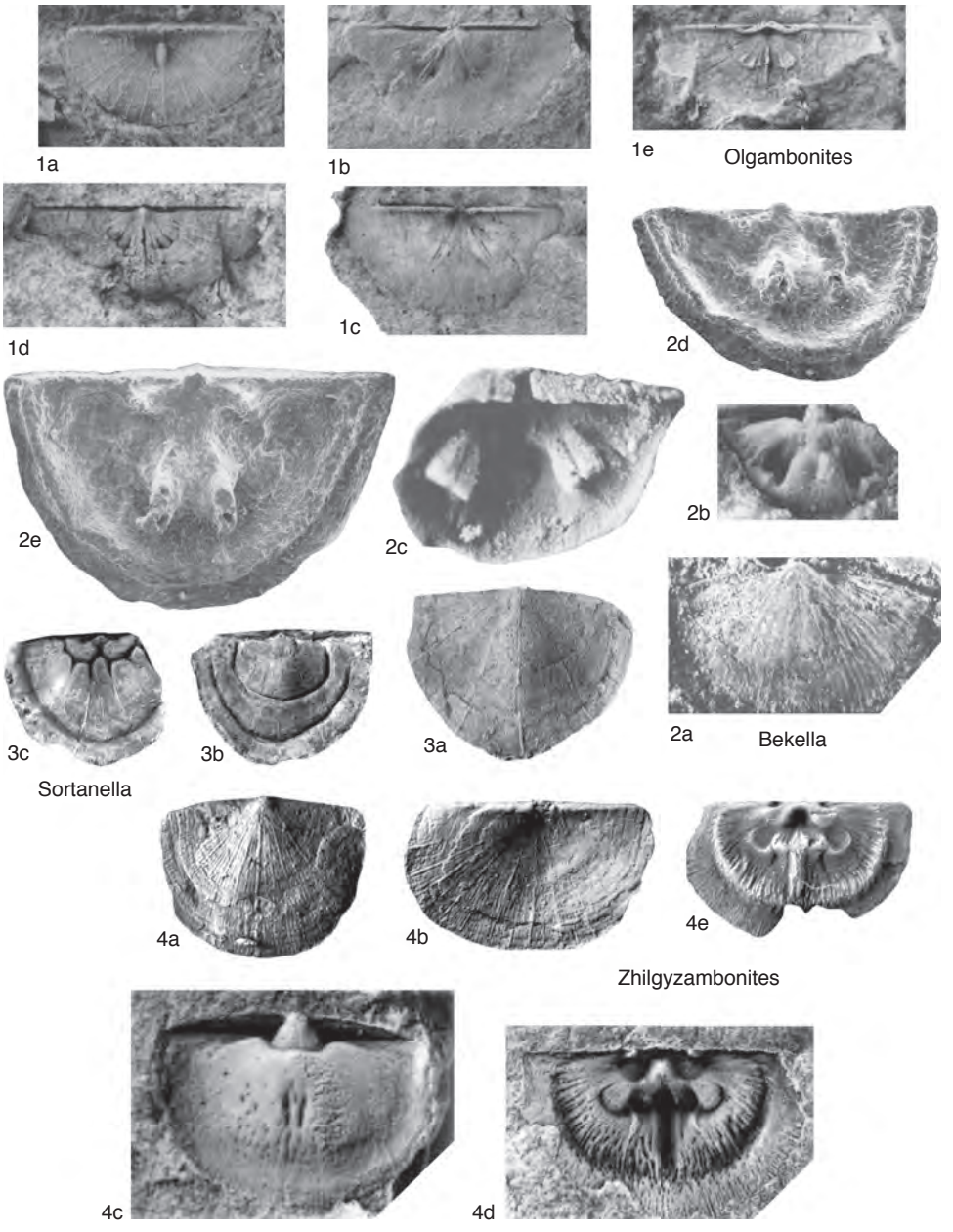

FIG. 1741. Leptestiidae and Sowerbyellidae (p. 2624–2627).

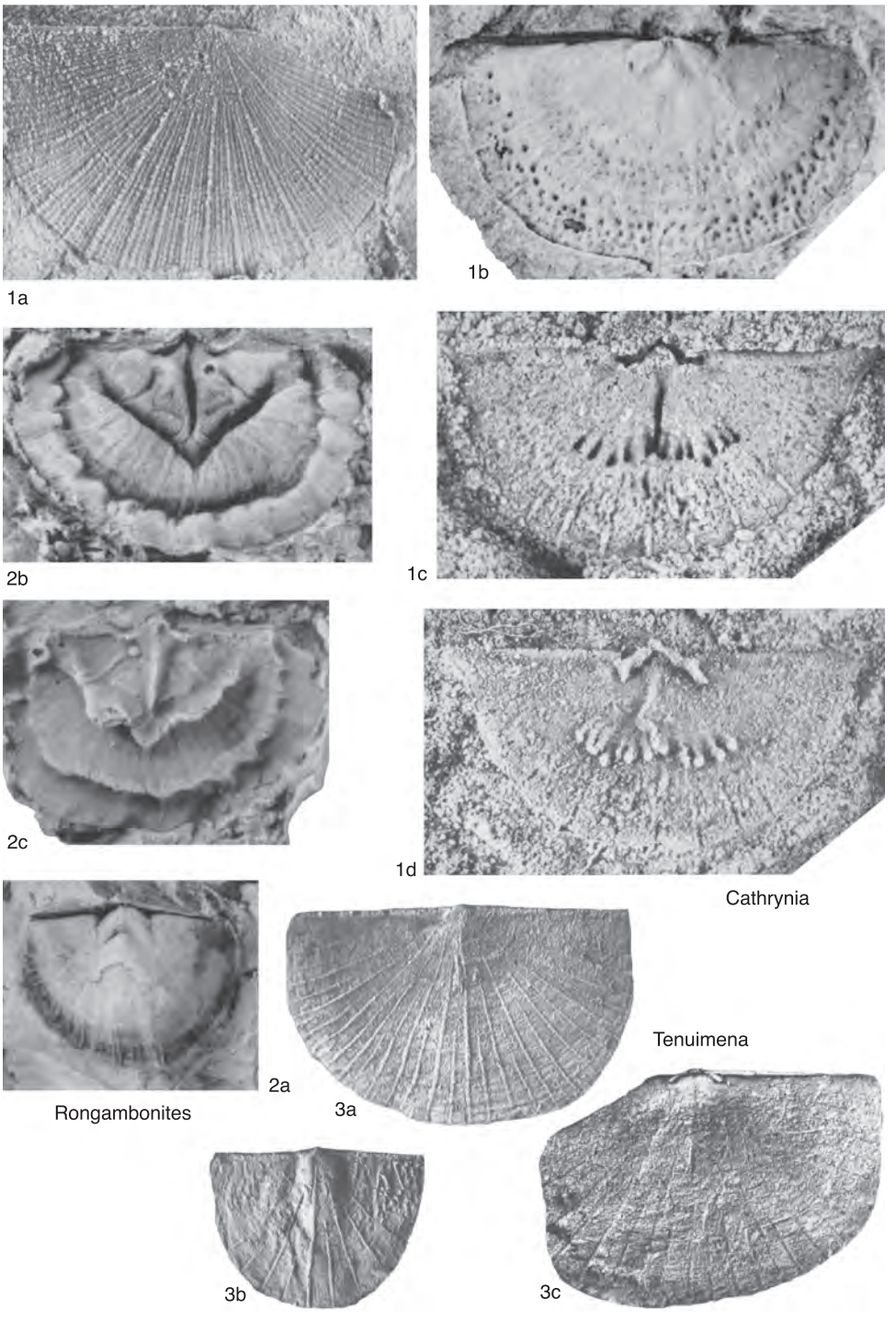

FIG. 1742. Xenambonitidae and Hesperomenidae (p. 2624–2627).

profile concavoconvex with strongly convex ventral valve and dorsal concavity variable; parvicostellate ornament; ventral interarea apsacline; dorsal interarea anacline; strong teeth; variable dental plates fusing anterolaterally with bounding ridges of relatively small bilobed ventral muscle field; undercut cardinal process strongly striated posteriorly and connecting laterally with curved socket plates; triangular platform with strong, straight, anterolateral bounding ridges joined anteriorly by a curved and raised section; high dorsal median septum not reaching platform anteriorly; muscle field variably impressed with weak, anterolaterally directed side septa. *Ordovician (Ashgill):* South China.——Fig. 1742,*2a–c. *R. bella,* Changwu Formation, middle Ashgill, Dianbian of Daqiao, Zhejiang Province; *a,* ventral internal mold, NIGP 128051, ×3; *b–c,* dorsal internal mold and latex cast, NIGP 128053, ×3 (Zhan & Cocks, 1998).

Family SOWERBYELLIDAE Jones, 1928
Subfamily SOWERBYELLINAE Jones, 1928

Olgambonites Popov, Cocks, & Nikitin, 2002, p. 50 [**O. insolita;* OD]. Outline transverse; profile gently resupinate; ventral interarea procline to slightly apsacline with apical pseudodeltidium; dorsal interarea anacline with separate chilidial plates. Ornament unequally parvicostellate. Ventral interior with small teeth; dental plates absent; small bilobed muscle field with short adductor scars completely separating larger diductor scars; ventral mantle canals lemniscate. Dorsal interior with simple undercut cardinal process fused with narrow socket ridges; fine median septum and bilobed bema bordered by rim and bearing up to 8 small side septa. *Ordovician (Caradoc):* Kazakhstan.——Fig. 1741,*1a–e. *O. insolita,* Anderken Formation, lower to middle Caradoc, Anderkenyn-Akchoku, Chu-Ili Range; *a,* latex cast of ventral exterior, BMNH BC 57592, ×4; *b–c,* mold and latex cast of ventral interior, BMNH BC 56664, ×4; *d–e,* holotype, mold and latex cast of dorsal interior, BMNH BC 56663, ×4 (Popov, Cocks, & Nikitin, 2002).

Zhilgyzambonites Popov, Cocks, & Nikitin, 2002, p. 52 [**Z. extenuata;* OD]. Outline rectimarginate; profile concavoconvex; ventral interarea apsacline with delthyrium completely covered by pseudodeltidium; dorsal interarea anacline with chilidium. Ornament of fine unequal parvicostellae. Ventral interior with small teeth; dental plates absent; muscle field small but raised high anteriorly; variably developed broad subperipheral rim. Dorsal interior with undercut cardinal process fused with flaring, curved socket ridges; deep alveolus and strongly elevated entire bema; prominent median septum originating anterior to bema and not extending anteriorly of prominent subperipheral rim. *Ordovician (Caradoc):* Kazakhstan.——Fig. 1741,*4a–e. *Z. extenuata,* Anderken Formation, lower to middle Caradoc, Anderken-Akchoku, Chu-Ili Range; *a,* latex cast of ventral exterior, BMNH BC 57490, ×6; *b,* latex cast of dorsal exterior, BMNH BC 57491, ×6; *c,* ventral internal mold, BMNH BC 57493, ×6; *d–e,* internal mold and latex cast of dorsal interior, BMNH BC 57492, ×5 (Popov, Cocks, & Nikitin, 2002).

CHONETIDINA

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INTRODUCTION

Since the publication of *Treatise, Part H, Brachiopoda (revised),* volume 2 (KAESLER, 2000), 28 new names have been published for brachiopods belonging to the suborder Chonetidina: 1 subfamily in the Rugosochonetidae (Riosanetinae), 23 genera (5 strophochonetids; 2 chonostrophiids; 8 anopliids, and 8 rugosochonetids), and 4 subgenera of *Neochonetes*. Stratigraphically speaking, these 27 generic and subgeneric names are distributed as follows: Silurian (2), Devonian (7), Carboniferous (7), and Permian (11). A twenty-fourth generic name, the Silurian genus *Zephyronetes* HAVLÍČEK, 1995, was unfortunately forgotten during the preparation of volume 2 and is included here.

Such a complementary list of recently described new taxa calls for some comments. When reading diagnoses and discussions (and comparisons between closely allied genera and type species) of several of the new taxa, it becomes clear that variations in the relative development of both external and internal morphological characters, which were recently considered to be of intrageneric value, are now used to distinguish new genera, while species-level characters are used to define subgenera. Such a splitting tendency inevitably leads to new genera (and subgenera) being defined upon increasingly discrete characters. Ultimately this leads to the monotypy of most genera (while subgenera will be elevated to the genus rank), followed by subfamilies and families. The Permian genus *Neochonetes,* which now includes six subgenera, is undoubtedly in need of further investigation. The same is true for the subfamily Anopliinae and the family Anopliidae in general.

The illustration of decalcified specimens, where only external and internal molds are preserved, provides inadequate information for the detailed comparisons required today if rubber positives (casts) are not also illustrated. This is especially important in the description of new taxa and their comparison with existing genera and species, so as far as is possible, both natural molds and replica figures are provided here.

Order PRODUCTIDA Sarytcheva & Sokolskaya, 1959
Suborder CHONETIDINA Muir-Wood, 1955
Superfamily CHONETOIDEA Bronn, 1862
Family STROPHOCHONETIDAE Muir-Wood 1962
Subfamily STROPHOCHONETINAE Muir-Wood 1962

Bacbonetes RACHEBOEUF & TONG-DZUY, 2000, p. 1052 [**B. janvieri*; OD]. Shell medium, transversely subrectangular, with faintly differentiated median enlarged costa in ventral valve; spines cyrtomorph extraverse, with two proximal spines lacking on left side; distal spines implantation alternating on both sides; dorsal interior with weakly elevated cardinal process; inner socket ridges poorly developed, low and short. *Lower Devonian:* Vietnam.——FIG. 1743,*2a–d*. **B. janvieri*; ventral exterior, dorsal exterior, ventral interior, dorsal interior, ×3 (Racheboeuf & Tong-Dzuy, 2000).

Cyrtochonetes RACHEBOEUF & TONG-DZUY, 2000, p. 1059 [**Chonetes indosinensis* MANSUY, 1916, p. 47; OD]. Shell medium, transversely subrectangular, with cyrtomorph intraverse, symmetrically arranged spines; weak ventral median enlarged costa in juveniles, becoming obscure with growth; dorsal interior with internally subglobose, deeply bilobed cardinal process. *Lower Devonian*: Vietnam.——FIG. 1743,*3a–c*. **C. indosinensis* (MANSUY); ventral exteriors, dorsal interior, ×3 (Racheboeuf & Tong-Dzuy, 2000).

Leptochonetina HAVLÍČEK, 1998, p. 117 [**L. vulgaris;* OD]. Shell small, thin, semicircular in outline with markedly convex ventral valve and moderately concave dorsal valve; surface smooth, rarely with median costa; orthomorph oblique spines, asymmetrically arranged, spines on right side appearing before left ones; cardinal process small, U-shaped; cardinal process pit elongate, extending anteriorly

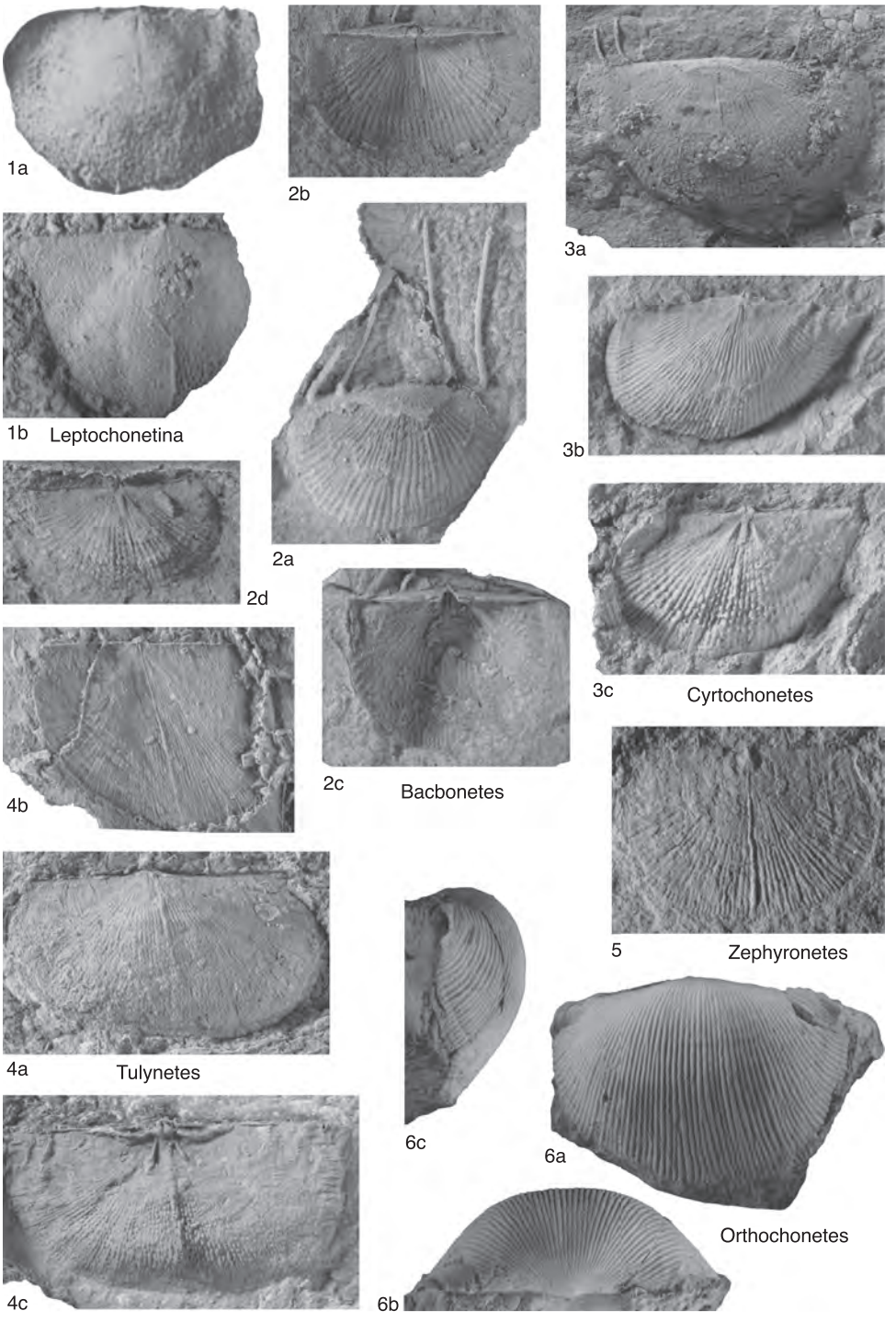

FIG. 1743. Strophochonetidae (p. 2628–2630).

to about one-quarter valve length; inner socket ridges long, straight, rather strong, widely divergent, almost parallel to hinge line; anderidia absent; low and short, breviseptum-like ridge, flanked by pair of weak lateral septa, may be developed. *Lower Devonian (Zlichovian):* Czech Republic (Bohemia).——Fig. 1743,*1a–b*. **L. vulgaris; a,* ventral valve internal mold, ×3.4; *b,* ventral internal mold with enlaged median costa, ×5.5 (Havlíček, 1998).

Tulynetes Racheboeuf & Tong-Dzuy, 2000, p. 1048 [**Chonetes hoabinhensis* Mansuy, 1914, p. 58; OD]. Shell medium, costellate with median enlarged costa variably developed, in ventral valve only or in both valves; spines orthomorph perpendicular, with two proximal spines lacking on left side; ventral interior with relatively short, laterally elongated, subrectangular hinge teeth; dorsal interior with strongly bilobed and dorsally geniculated cardinal process, elevated above valve floor; breviseptum-like, often spinose median ridge, and medially well-developed endospines; long, narrow, posteriorly bent inner socket ridges. *Lower Devonian:* Vietnam.——Fig. 1743,*4a–c*. **T. hoabinhensis* (Mansuy); ventral exterior, dorsal exterior, dorsal interior, ×3 (Racheboeuf & Tong-Dzuy, 2000).

Zephyronetes Havlíček, 1995, p. 56 [**Chonetes zephyrus* Barrande, 1879, pl. 46, IV, 1–3; OD; =*Strophochonetes (Zephyronetes)* Havlíček, 1995, p. 56]. Shell small and thin walled, almost biplanar in lateral profile; spines symmetrically arranged, orthomorph perpendicular to intraverse; dorsal interior with slender and long socket ridges; anderidia extremely reduced to undiscernible. *Silurian (Wenlock):* Czech Republic (Bohemia).——Fig. 1743,*5*. **Z. zephyrus* (Barrande); ventral exterior, ×5 (Havlíček, 1995).

Subfamily PARACHONETINAE Johnson, 1970

Orthochonetes Racheboeuf & Tong-Dzuy, 2000, p. 1065 [**Chonetes verneuili* Barrande, 1848, p. 248; OD]. Parachonetinae with transverse, markedly arched shell; spines numerous, orthomorph perpendicular, and symmetrically displayed; radial costellae relatively narrow, elevated, with vertical flanks. *Lower Devonian (Pragian):* Czech Republic (Bohemia).——Fig. 1743,*6a–c*. **O. verneuili* (Barrande); ventral valve, ventral, posterior, and lateral views, ×1.2 (Racheboeuf & Tong-Dzuy, 2000).

Family CHONOSTROPHIIDAE Muir-Wood, 1962

Balikunochonetes Chen & Archbold, 2002, p. 235 [**B. liaoi*; OD]. Shell medium, semicircular in outline; shell costellate; ventral valve exterior rugose forward; spines orthomorph, high angled, at 75° to 90°; myophragm long and elevated, extending anteriorly beyond midlength; dorsal median septum thin, extending to midlength; pentalobed myophore; anderidia at about 80°; accessory septa broad, thick, extending anteriorly almost to anterior margin, anteriorly divergent at 15° to 35°, with two pairs of subparallel, adventitious septa. [It appears that in the original diagnoses and descriptions, anderidia, accessory septa, and even socket ridges have been misinterpretated.] *Upper Devonian (Famennian):* northwestern China (Xinjiang).——Fig. 1744,*1a–b*. **B. liaoi; a,* ventral interior, ×2; *b,* dorsal interior, ×4 (Chen & Archbold, 2002).

Santanghuia Chen & Archbold, 2002, p. 233 [**S. santanghuensis*; OD]. Shell medium, semicircular in outline, with catacline interarea; shell finely costellate; spines orthomorph oblique, low angled, less than 45°; myophragm thick, high, extending anteriorly to midlength; strong cardinal process with pentalobed myophore; no dorsal median septum; anderidia faintly developed; accessory septa thick, broad, long, reaching anterior margin, anteriorly divergent at 10° to 20°. [The same misinterpretations for *Balikunochonetes* apply to this genus.] *Upper Devonian (Famennian):* northwestern China (Xinjiang).——Fig. 1744,*2a–c*. **S. santanghuensis;* ventral interior, dorsal interiors, ×4 (Chen & Archbold, 2002).

Family ANOPLIIDAE Muir-Wood, 1962 Subfamily ANOPLIINAE Muir-Wood, 1962

Adatsagochonetes Afanasjeva, 2004b, p. 164 [**A. mongolicus*; OD]. Shell medium, semicircular in outline; longitudinal profile concavoconvex, moderately arched; five pairs of oblique orthomorph spines at about 50°; ventral interior with myophragm extending anteriorly to midlength; dorsal interior with elevated cardinal process anteriorly bounded by cardinal process pit; no median septum or radial ridges; numerous irregularly displayed endospines on dorsal valve interior. [According to the author, *Adatsagochonetes* is similar to *Kaninochonetes,* from which it differs in the elevated cardinal process (instead of flattened) and by the absence of radially arranged endospines in the dorsal interior only. These variations in characters can be considered to be of intrageneric value.] *Lower Permian (Artinskian):* central Mongolia.——Fig. 1745,*1a–b*. **A. mongolicus;* ventral internal mold, dorsal internal mold, ×3 (Afanasjeva, 2004b).

Kaninochonetes Afanasjeva, 2004a, p. 35 [**K. kaninensis*; OD]. Shell medium, semicircular in outline, weakly concavoconvex; four or five pairs of oblique orthomorph spines at about 50°–60°; ventral interior with myophragm extending anteriorly to midlength; dorsal interior with flattened cardinal process anteriorly bounded by cardinal process pit; no median septum nor radial ridges; small endospines arranged in numerous radial rows.

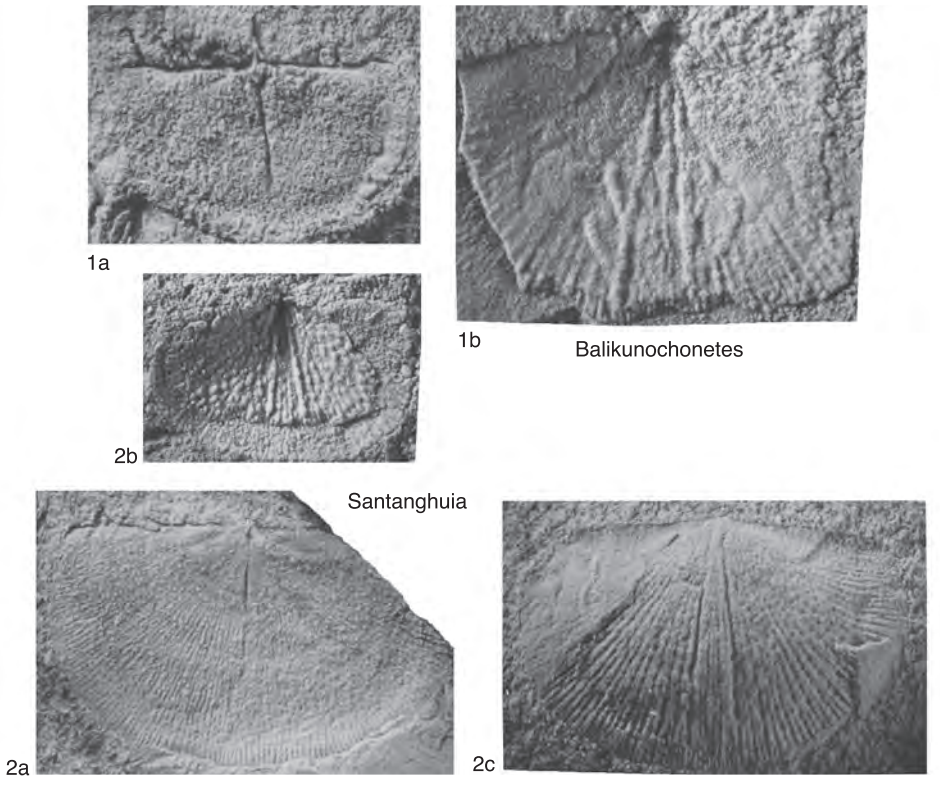

FIG. 1744. Chonostrophiidae (p. 2630).

Middle Permian (lower Guadalupian, Ufimian): northern part of Russian Platform.——FIG 1745,*2a–c*. **K. kaninensis*, Kanin Peninsula; ventral exterior, ventral interior, dorsal interior, ×3 (Afanasjeva, 2004a).

Palaeoanopliopsis AFANASJEVA, 2002, p. 627 [**P. glabra;* OD] [Junior subjective synonym of *Anopliopsis* GIRTY, 1938, p. 281; see RACHEBOEUF, 2000, p. 382]. [According to the author, *Palaeoanopliopsis* differs from *Anopliopsis* in its lack of flattened ears and by a longer dorsal median septum only. Variations in these characters are of intrageneric value; *Anopliopsis* is North American and Viséan to Namurian in age; *Palaeoanopliopsis* is from the Tournaisian, *Gattendorfia* Zone, of Germany.] (Afanasjeva, 2002).

Subfamily CAENANOPLIINAE Archbold, 1980

Chilenochonetes ISAACSON & DUTRO, 1999, p. 627 [**C. anna*; OD]. Shell medium, markedly concavoconvex, with maximum width anterior to hinge line; shell surface capillate with interspaces twice their width; ventral interior with short myophragm; hinge teeth small, laterally elongate; dorsal interior with large cardinal process pit, short median septum, not extending anteriorly beyond midline, with a pair of long and narrow accessory septa, short anderidia, and short, prominent, socket ridges. *Carboniferous (lower Tournaisian):* northern Chile.——FIG. 1746,*1a–d*. **C. anna; a,* ventral interior, ×2; *b,* dorsal interior, latex, ×2.5; *c–d,* ventral exterior and dorsal interior, latex, ×2 (Isaacson & Dutro, 1999).

Gibberochonetes AFANASJEVA, 2002, p. 59 [**G. gibber;* OD]. Shell small, semicircular; ventral sulcus distinct in largest shells; no dorsal fold; spines almost vertical or weakly cyrtomorph intraverse; ornament of rounded, thin, radial costae anteriorly bifurcating, crossed by very fine concentric growth lines; myophragm about one-fourth valve length; dorsal interior with low, knoblike cardinal process with cardinal process pit; no median septum or brachial ridges; strong endospines forming two weakly divergent radial rows near midline. [This genus was originally described within the subfamily Anopliinae, but according to its radial ornament, it is better placed within the subfamily Caenanopliinae, together with the genus *Caenanoplia,* from

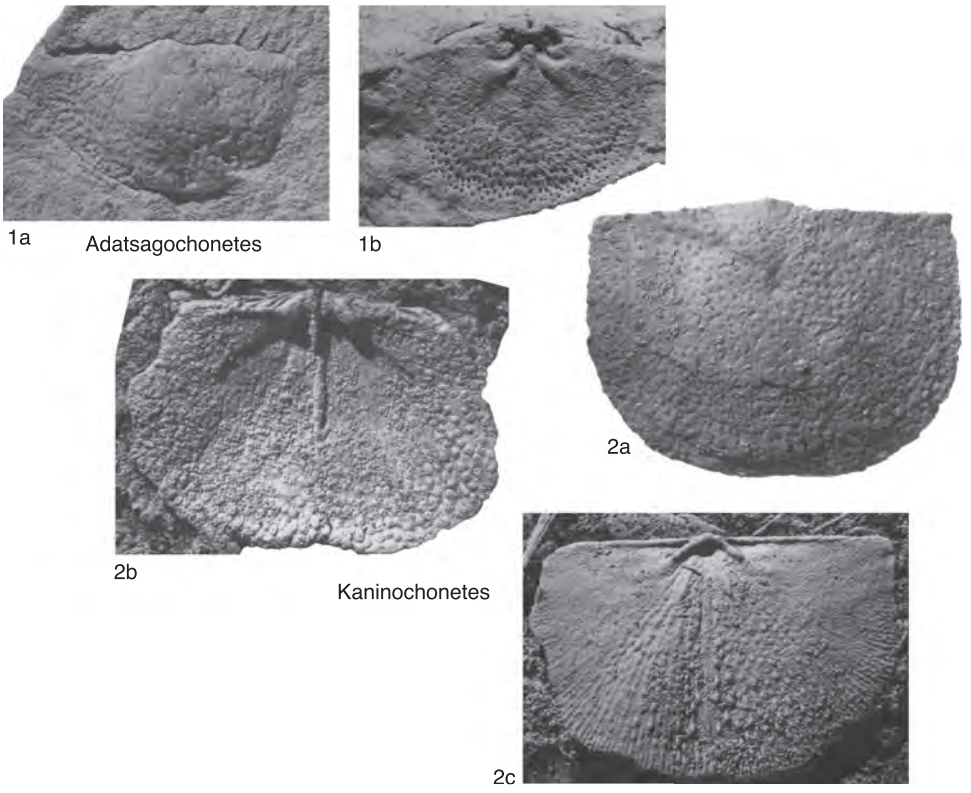

FIG. 1745. Anopliidae (p. 2630–2631).

which it differs in the development of a weak ventral sulcus and stronger radial external ornament. No suitable illustrations are available.] *Upper Devonian* (*Famennian*).

Gonzalezius TABOADA, 2004, p. 413 [**G. naranjoensis*; OD]. Shell weakly concavoconvex, subcircular in outline; shell surface capillate, with well-marked concentric growth lines; spines orthomorph oblique and symmetrically arranged; ventral interior with long and narrow myophragm and parallel hinge teeth; dorsal interior with cardinal process pit and two or more thin, weakly divergent accessory septa; short and narrow breviseptum; anderidia very thin, long, bladelike. *Carboniferous (Namurian):* Argentina.——FIG. 1746,*3a–c.* **G. naranjoensis,* San Juan Province; ventral external mold, ventral internal mold, dorsal internal mold, ×4 (Taboada, 2004)

Ogorella RACHEBOEUF, 2001, p. 579 [**O. janickae*; OD]. Shell small, with orthomorph oblique, symmetrical spines; radial ornamentation of costae originating anterior of beaks, widening up to commissures; ventral and dorsal interareas flat, lying in same plane; large pseudodeltidium and chilidium; stout, laterally elongated and horizontal hinge teeth; short myophragm dividing relatively small muscle field; dorsal interior with short septum supporting cardinal process, with low and wide myophore; anderidia long and narrow, strongly divergent; accessory septa markedly divergent, narrow, and spinose; periphery of both valves smooth, flat. *Middle Devonian (Givetian):* western Europe.——FIG. 1746,*4a–d.* **O. janickae*, Massif Armoricain; ventral exterior, dorsal exterior, ventral interior, dorsal interior, ×4 (Racheboeuf, 2001).

Pinegochonetes AFANASJEVA, 2000, p. 287 [**Chonetes pinegensis* KULIKOV, 1974, p. 144; OD]. Shell medium sized, semicircular in outline, concavoconvex to almost planoconvex, with distinct sulcus and fold; radial ornament of bifurcating and intercalating costae and costellae; spines oblique orthomorph at about 35°–40°, symmetrically arranged; ventral interior with stout myophragm extending about two-thirds valve length; dorsal interior with cardinal process elevated above valve floor, anteriorly bounded by cardinal process pit; inner socket ridges parallel to hinge line; no median septum or brachial ridges; inner surface covered with radially displayed endospines; two rows of

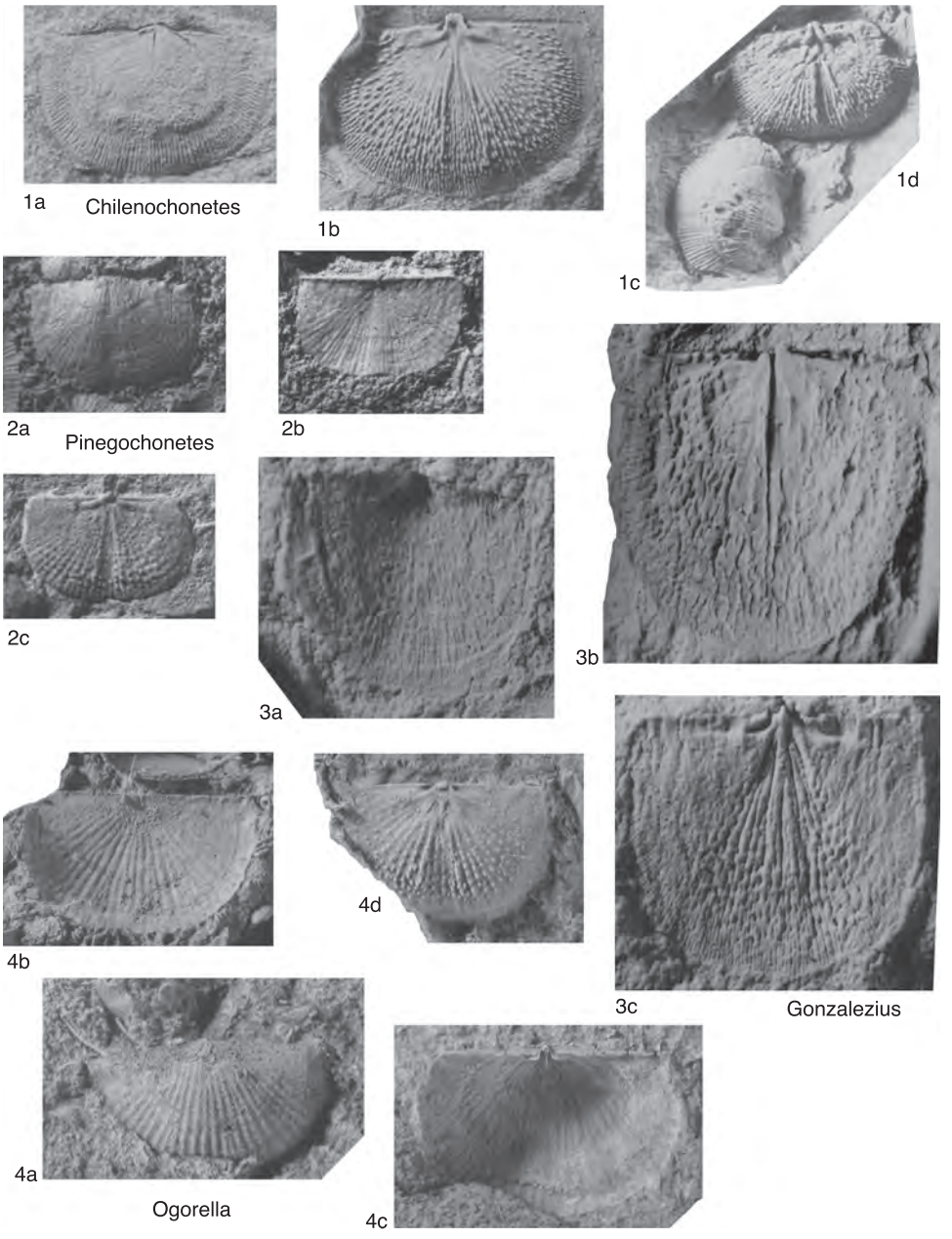

FIG. 1746. Anopliidae (p. 2631–2633).

stronger endospines forming accessory septa similar to feature near midline. [This genus was originally described within the subfamily Anopliinae, but according to its radial ornament, it is better placed within the subfamily Caenanopliinae.]

Upper Permian (lower Kazanian): north of Russian Platform (Arkhangelsk Region).——FIG. 1746,*2a–c*. **P. pinegensis* (KULIKOV), Pinega River; ventral exterior, dorsal exterior, dorsal interior, ×1.5 (Afanasjeva, 2000).

Family RUGOSOCHONETIDAE Muir-Wood, 1962
Subfamily RUGOSOCHONETINAE Muir-Wood, 1962

Neochonetes Muir-Wood, 1962, p. 87.

Neochonetes (Huangichonetes) Shen & Archbold, 2002, p. 335 [**Chonetes substrophomenoides* Huang, 1932, p. 3; OD]. Small, reverse, trapezoidal *Neochonetes* shell with small but prominent and acute ears, and conspicuous and moderately wide sulcus; strongly convex visceral disc; hinge spines projecting posterolaterally at 30°–40° to hinge line; radial costellae fine, numbering 30–50 near margin; ventral interior with very short myophragm. *Upper Permian (Lopingian):* South China.——Fig. 1747,*1a–d.* **N. (H.) substrophomenoides* (Huang); ventral internal mold, dorsal external mold, juvenile dorsal interior, adult dorsal interior, ×3 (Shuzhong Shen & Archbold, 2002).

Neochonetes (Nongtaia) Archbold, 1999, p. 75 [**N. (N.) taoni*; OD]. Similar to *Neochonetes (Neochonetes),* but shell small, subquadrate, with relatively narrow, distinct sulcus, distinct dorsal fold, distinct ornament of coarse capillae increasing in number by bifurcation. *middle Permian (lower Guadalupian (Ufimian = Roadian):* southeastern Asia.——Fig. 1748,*2a–d.* **N. (N.) taoni,* Ufimian, Thailand; ventral exterior, dorsal exterior, ventral interior, dorsal interior, ×4.5 (Archbold, 1999).

Neochonetes (Zechiella) Archbold, 1999, p. 78 [**Chonetes davidsoni* von Schauroth, 1856, p. 222; OD]. Small, thin-shelled *Neochonetes* with obsolescent radial capillae, sulcus absent, internal structures poorly developed. *middle Permian (lower Guadalupian (Ufimian = Roadian):* southeastern Asia, Germany, England.——Fig. 1748,*1a–b.* **N. (Z.) davidsoni* (von Schauroth), Germany; ventral valve with spines, dorsal side of articulated shell, ×4 (Archbold, 1999).

Neochonetes (Zhongyingia) Shen & Archbold, 2002, p. 333 [**Neochonetes zhongyingensis* Liao, 1980, p. 257; OD]. Reverse, trapezoidal outline with acute ears, greatest width at hinge line, with cardinal extremities extended; spines less than 45°; ventral valve slightly convex with shallow and broad sulcus; shell surface finely costellate; dorsal interior with long lateral ridges parallel to hinge line. *Upper Permian (Lopingian):* South China.——Fig. 1747,*2a–f.* **N. (Z.) zhongyingensis* (Liao); ventral and dorsal exteriors, latex, ventral internal mold and latex, dorsal interior, latex and internal mold, ×3 (Shen & Archbold, 2002).

Robertsella Chen & Shi, 2003, p. 135 [**Rugosochonetes macgregori* Roberts, 1971, p. 62; OD]. Shell medium, subrectangular in outline; valve exteriors densely costate and irregularly lamellose; cardinal extremities angular to subrounded; hinge spines orthomorph oblique; ventral interior with short myophragm; dorsal interior with high and thick inner socket ridges, bilobed cardinal process, large and deep cardinal process pit; short median septum not extending anteriorly beyond midlength, slightly elevated anteriorly. [There are no suitable illustrations available of the type species.] *Lower Carboniferous (Viséan):* northwestern China, Australia (New South Wales).——Fig. 1749,*2a–c. R. tarimensis* Chen & Shi, northwestern China; ventral exterior, ventral internal mold, dorsal interior, ×2 (Chen & Shi, 2003).

Tethyochonetes Chen & others, 2000, p. 5 [**Waagenites soochowensis quadrata* Zhan, 1979, p. 70; OD]. Shell small, transversely rectangular, strongly concavoconvex; cardinal extremities varying from acute to slightly semielliptical; ears smooth, broad, flattened, or slightly swollen; sulcus varying from deep, broad, and distinct to shallow, narrow, and indistinct; sulcal bounding flanks distinct to depressed; fold slightly raised to flattened; external ornament with robust and rounded costae, sometimes bifurcating; ventral myophragm thin and high, extending anteriorly to half valve length; cardinal process rounded and blunt, bilobed internally, trilobed externally; dorsal median septum stout, raised at its middle to anterior part, originating anterior to cardinal process pit, continuing forward for half valve length; lateral septa stout, short, and distinct; brachial scars strongly swollen and semicircular in outline. *Upper Permian (Wuchiapingian–uppermost Changhsingian):* eastern and southwestern China.——Fig. 1749,*1a–b.* **T. quadrata* (Zhan), uppermost Changhsingian; ventral valve, dorsal interior, ×3 (Chen & others, 2000).

Thuringochonetes Afanasjeva, 2002, p. 630 [**T. thuringicus;* OD]. Shell small, semicircular in outline, without sulcus and fold, and weakly concavoconvex; external ornament with very thin radial costellae, sometimes bifurcating, and alternating with some stronger radial costae; spines symmetrically arranged, oblique orthomorph to weakly cyrtomorph, low angled, becoming almost parallel toward cardinal angles; ventral myophragm restricted to umbonal region, dividing a markedly bilobate diductor muscle field; adductor scars adjacent, smooth, and semiellipical in outline; cardinal process knob shaped, anteriorly bounded by large cardinal process pit; dorsal median septum low and narrow, not extending beyond midlength of valve; anderidia relatively long. [The genus was originally placed within the family Strophochonetidae owing to the presence of enlarged capillae and to the strongly bilobed nature of the ventral muscle field. These characters do not support such a family assignment in comparison with features such as spines and the morphology of the dorsal interior.] *Lower Carboniferous (Tournaisian):* Thuringia and Rhenish Slate Mountains (Germany).

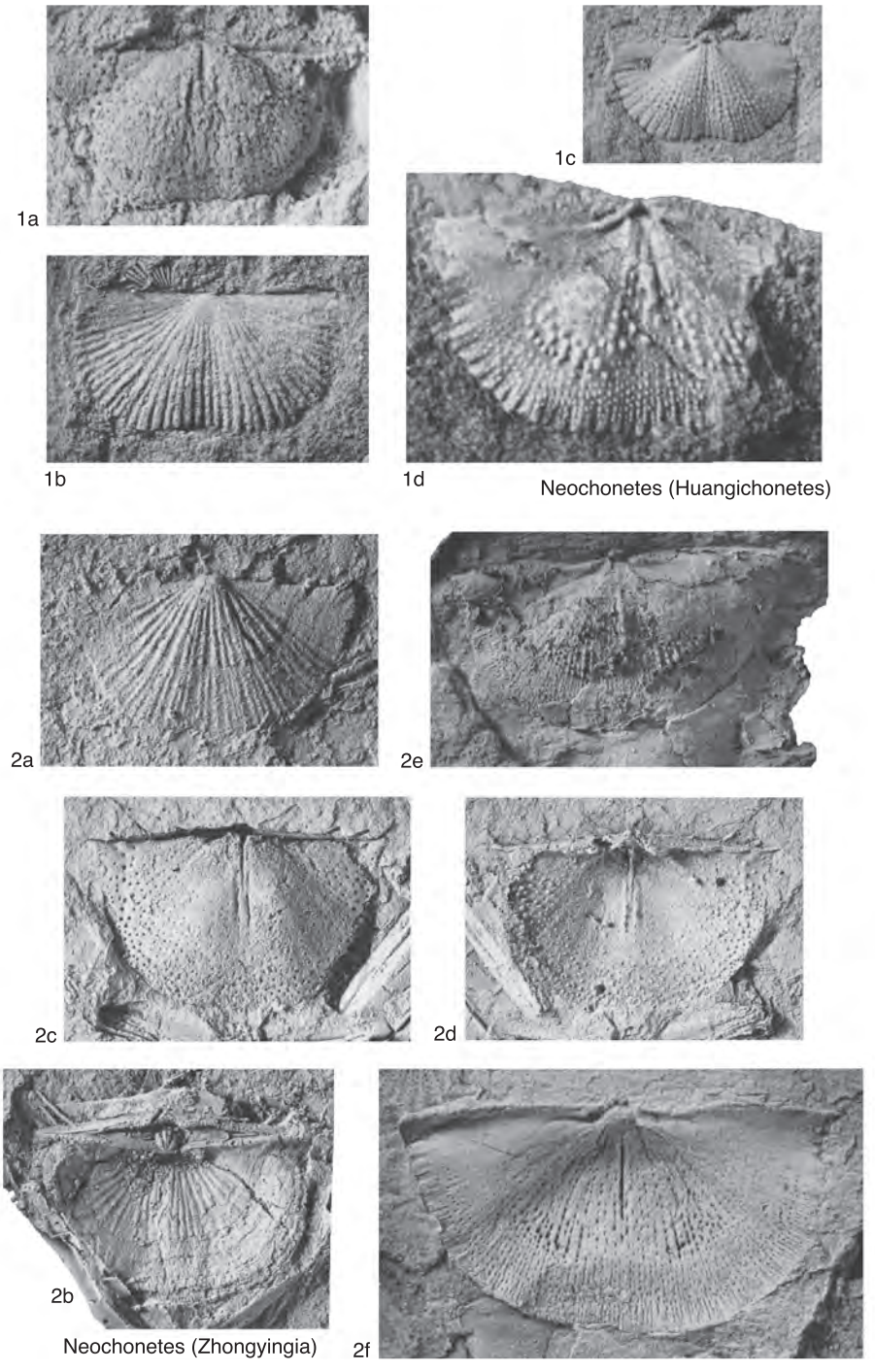

FIG. 1747. Rugosochonetidae (p. 2634).

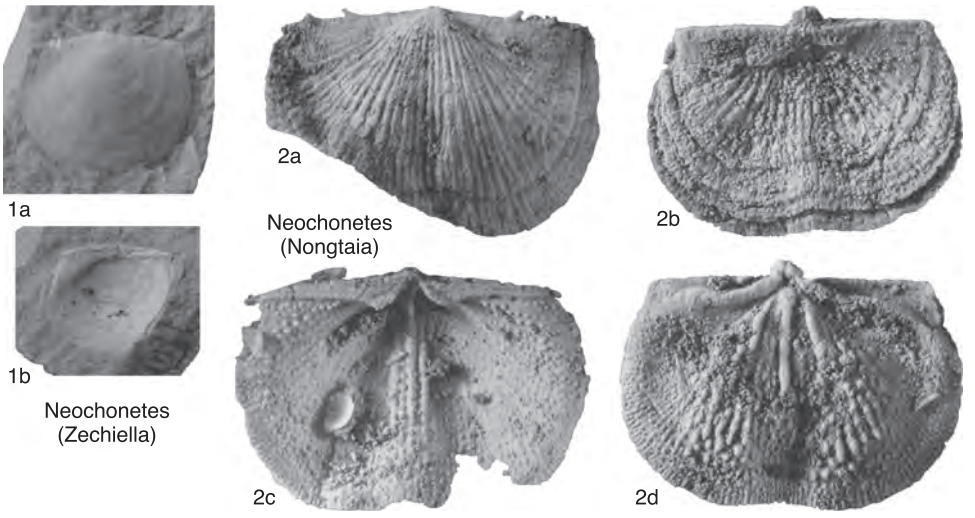

FIG. 1748. Rugosochonetidae (p. 2634).

——FIG. 1749,*3a–e*. **T. thuringicus;* ventral exterior, damaged ventral valve with spines, dorsal exterior, dorsal interior, ventral internal mold, ×4 (Afanasjeva, 2002).

Subfamily PLICOCHONETINAE Sokolskaya, 1960

Nisalarinia WATERHOUSE, 2004, p. 58 [**Rugaria nisalensis* WATERHOUSE, 1978, p. 60; OD] [Junior subjective synonym of *Rugaria* COOPER & GRANT, 1969; see RACHEBOEUF, 2000, p. 411]. [As stated by its author, the new genus mainly differs from *Rugaria* by longer anderidia, finer radial ribbing, smooth ears and posteriorly thicker myophragm (=ventral septum). These characters are considered to be within the limits of intrageneric variation.] (WATERHOUSE, 2004).

Subfamily RIOSANETINAE Martínez Chacón & Winkler Prins, 2000

[Riosanetinae MARTÍNEZ CHACÓN & WINKLER PRINS, 2000, p. 226] [Type genus, *Riosanetes* MARTÍNEZ CHACÓN & WINKLER PRINS, 2000, p. 226]

Small to medium rugosochonetids with costellate ornamentation; oblique orthomorph spines. Dorsal interior without median septum. *Lower Carboniferous (Tournaisian).*

Riosanetes MARTÍNEZ CHACÓN & WINKLER PRINS, 2000, p. 226 [**R. fernandezi*; OD]. Shell small with thin valves, planoconvex to slightly concavoconvex, subrectangular; cardinal extremities rounded; costellate ornamentation with fine costae and costellae, apart from smooth ears; external ornamentation especially prominent internally, indicating very thin valves; ventral interior with short myophragm, posteriorly elevated; without vascular ridges; dorsal interior with very thin anderidia, high and strong inner socket ridges, without median septum; tubercles placed in rows along the intercostal sulci, occasionally tubercles of central rows are more marked but never form septa; brachial ridges not developed. *Lower Carboniferous (lower Tournaisian).* northern Spain (Cantabrian Mountains).——FIG. 1750,*2a–c*. **R. fernandezi;* ventral internal mold, dorsal external mold, dorsal internal mold, ×5 (Martínez Chacón & Winkler Prins, 2000).

Aitegounetes CHEN & SHI, 2003, p. 138 [**A. aitegouensis*; OD] [=*Aitegouchonetes* CHEN & SHI, 2003, p. 138, lines 8 and 14, *nom. null.*; *Aitegouensis* CHEN & SHI, 2003, p. 138, line 17, *nom. null.*]. Shell small to medium, markedly concavoconvex, and subrectangular; cardinal extremities angular

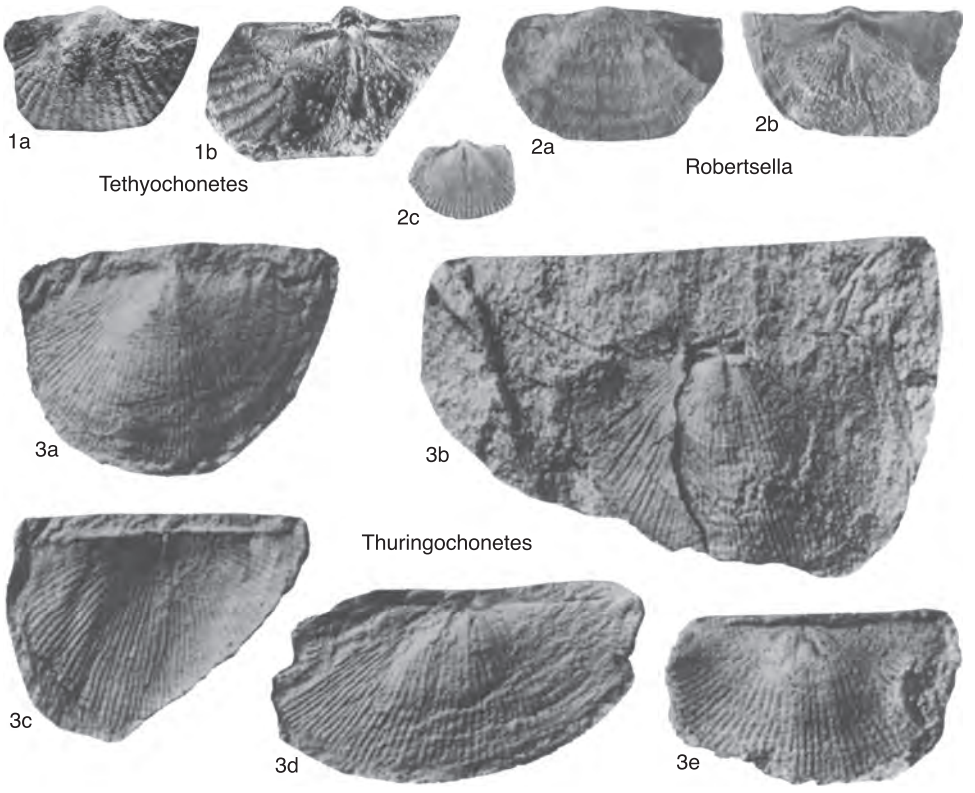

FIG. 1749. Rugosochonetidae (p. 2634).

to subrounded; valve exteriors strongly costellate except for weakly ribbed ears; oblique orthomorph, low-angled spines; ventral interior with thin myophragm about half valve length; dorsal interior with pair of short, thin anderidia, stout inner socket ridges, but without median septum; valve covered with radial rows of endospines, never fused; no brachial ridges. *Lower Carboniferous* (*Viséan*): northwestern China.——FIG. 1750,*3a–c*. **A. aitegouensis;* ventral exterior, dorsal exterior, dorsal interior, ×3 (Chen & Shi, 2003).

Linshuichonetes CAMPI & SHI, 2002, p. 110 [**L. elfinis*; OD]. Small, subquadrate to semicircular rugosochonetid, characterized externally by fine capillation, a weak or absent median sulcus and fold, internally by a lack of median, lateral, and accessory septa in dorsal interior; absence of vascular mantle canals in ventral interior and presence of distinct radiating rows of papillae in interiors of both valves, except on either side of midline in posterior part of dorsal valve, where only raised clusters of papillae occur. *Lower Permian (upper Artinskian)–middle Permian (Wordian):* southwestern China (Sichuan), Thailand.——FIG. 1750,*1a–c*. **L. elfinis*, Wordian, Sichuan, southwestern China; *a,* ventral exterior, ×7; *b–c,* dorsal exteriors, ×12, ×10 (Campi & Shi, 2002).

Subfamily STRIOCHONETINAE Waterhouse & Piyasin, 1970

Binderochonetes AFANASJEVA, 2004b, p. 162 [**B. manankovi*; OD] [Junior subjective synonym of *Striochonetes* WATERHOUSE & PIYASIN, 1970; see

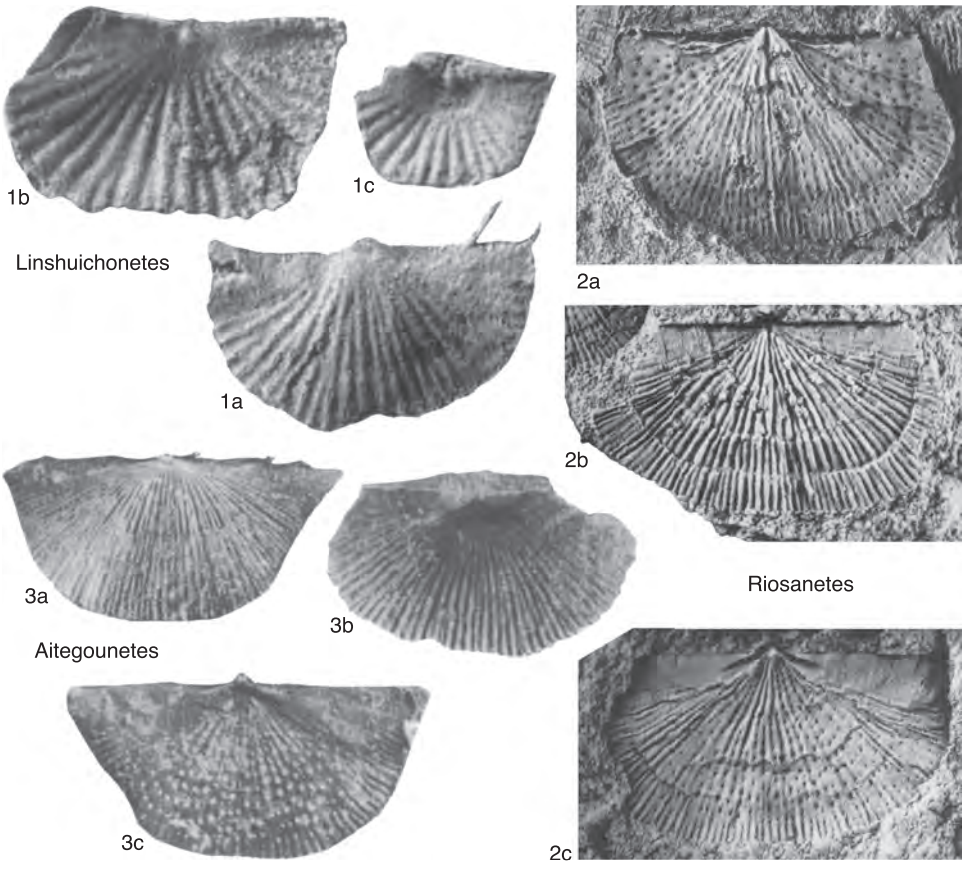

FIG. 1750. Rugosochonetidae (p. 2634–2636).

RACHEBOEUF, 2000, p. 415]. [The distinguishing characters given by the author in the diagnosis of the new genus, as well as in the comparison between the two type species (p. 164), are considered to be no more than intrageneric variations possibly resulting from evolutionary changes. Both type species are Upper Permian, that of *Striochonetes* (southern Thailand) being Kazanian in age, while that of *Binderochonetes* (northeastern Mongolia) is Tatarian in age.] (AFANASJEVA, 2004b).