ORTHIDA

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[with family descriptions composed jointly with Alwyn Williams, deceased, formerly of The University of Glasgow]

Order ORTHIDA Schuchert & Cooper, 1932
Suborder ORTHIDINA Schuchert & Cooper, 1932
Superfamily ORTHOIDEA Woodward, 1852
Family ORTHIDAE Woodward, 1852

Celsiorthis PATERSON & BROCK, 2003, p. 223 [**C. bulancis*; OD]. Medium sized, ventribiconvex, rectimarginate, ramicostellate; ventral interarea high, steeply apsacline to catacline; ventral muscle scar bilobed, dental plates large; brachiophores tusklike with thick bases; dental sockets wide and deep. *Lower Ordovician (Arenig):* Australia.——FIG. 1787,*2a–e*. **C. bulancis*, Tabita Formation, northwestern New South Wales; *a*, mold of ventral interior, AM F120716, ×4; *b*, rubber replica of ventral interior, AM F120714, ×7.5; *c*, rubber replica of ventral exterior, AM F120717, ×6; *d–e*, anterior and dorsal views of interior, AM F120710, ×7.5 (Paterson & Brock, 2003).

Leoniorthis EGERQUIST, 2003, p. 35 [**L. robusta*; OD]. Small, ventribiconvex, shallow sulcus, coarsely costellate; ventral muscle scar suboval; cardinal process forming high ridge. *Lower Ordovician (Arenig):* Estonia, western Russia.——FIG. 1787,*1a–c*. **L. robusta*, Volkhov Formation, Putilova, western Russia; *a*, ventral interior, PMU In 144, ×4; *b*, ventral exterior, PMU In 125, ×6; *c*, dorsal interior, PMU In 120, ×5 (Egerquist, 2003).

Suriorthis BENEDETTO, 2003, p. 225 [**S. depressus*; OD]. Small, dorsibiconvex, alate, sharply sulcate, costate or sparsely costellate; ventral muscle scar, short and triangular, *vascula media* strongly divergent; simple, bladelike cardinal process situated on small triangular notothyrial platform, continuous anteriorly with thick median ridge. *Lower Ordovician (Arenig):* Argentina.——FIG. 1788*a–f*. **S. depressus*, Suri Formation, northwestern Argentina; *a–b*, mold of ventral interior and rubber replica, CEGH-UNC 19801, ×5; *c–d*, mold of dorsal interior and rubber replica, CEGH-UNC 15762, ×5; *e*, rubber replica of ventral exterior, CEGH-UNC 15758, ×4; *f*, rubber replica of dorsal interior, CEGH-UNC 15920, ×5 (Benedetto, 2003).

Family ARCHAEORTHIDAE new family

[Archaeorthidae WILLIAMS & HARPER, herein, *nom. nov. pro* Nanorthidae HAVLÍČEK, 1977, p. 59] [type genus, *Archaeorthis* SCHUCHERT & COOPER, 1931, p. 243]

[ALWYN WILLIAMS and DAVID A. T. HARPER]

Generally small, ventribiconvex, costellate, commonly capillate orthoids with very short, curved interarea; teeth usually supported by short, recessive dental plates, suboval ventral muscle scar normally impressed on valve floor without median ridge; adductor track undifferentiated and relatively wide, normally not shorter than flanking diductor scars; pedicle callist well developed in some species; notothyrial platform normally present with variably developed, simple cardinal process; short, bladelike brachiophores variably disposed on either side of median ridge with posteromedian parts of anterior adductor scars inserted between posterior pair; ventral mantle canal system saccate with divergent *vascula media*, dorsal system more rarely impressed, digitate to pinnate. *Lower Ordovician (Tremadoc)–Upper Ordovician (Ashgill)*.

In 1931, SCHUCHERT and COOPER (p. 243) erected the subfamily Orthinae (within the Orthidae WOODWARD) for orthids with short, curved ventral interareas. In due course, the genera *Nanorthis* ULRICH and COOPER

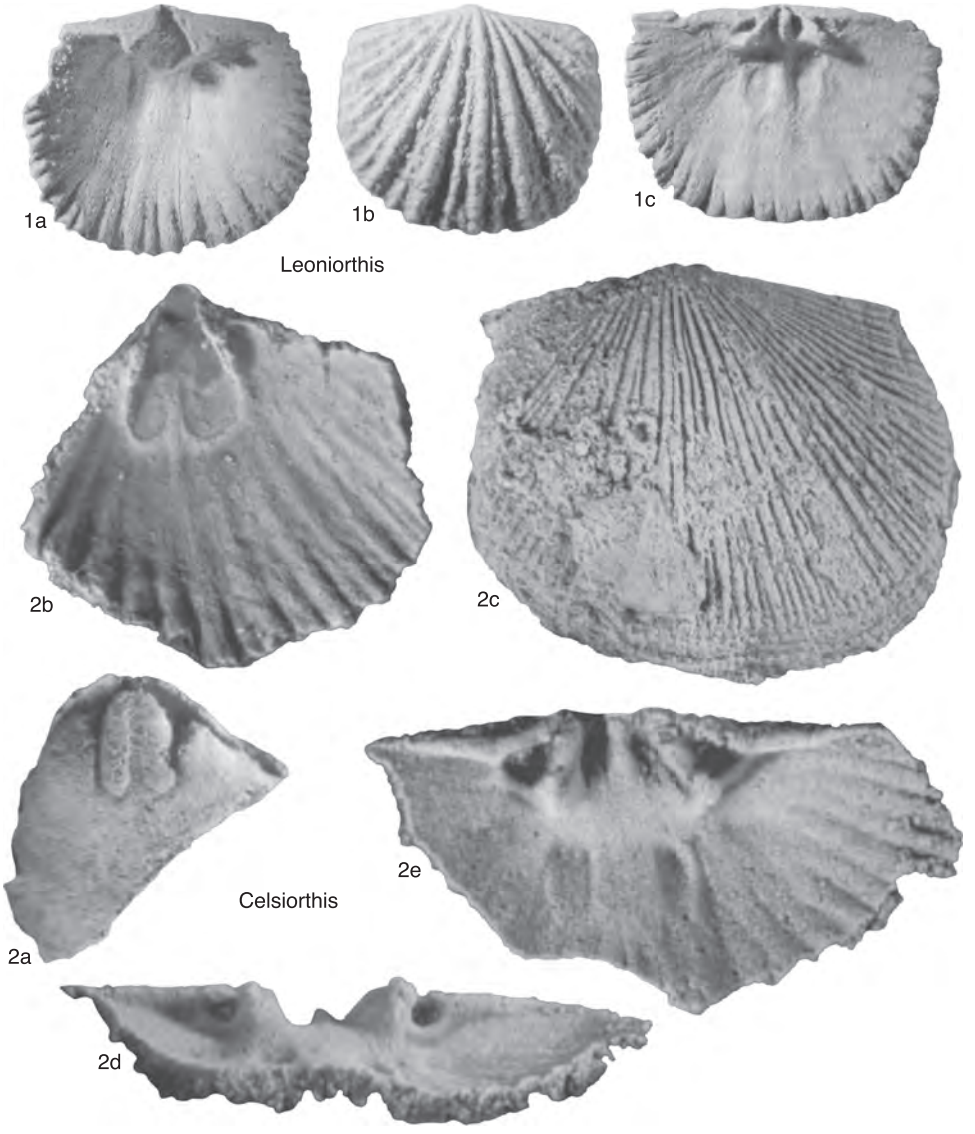

FIG. 1787. Orthidae (p. 2684).

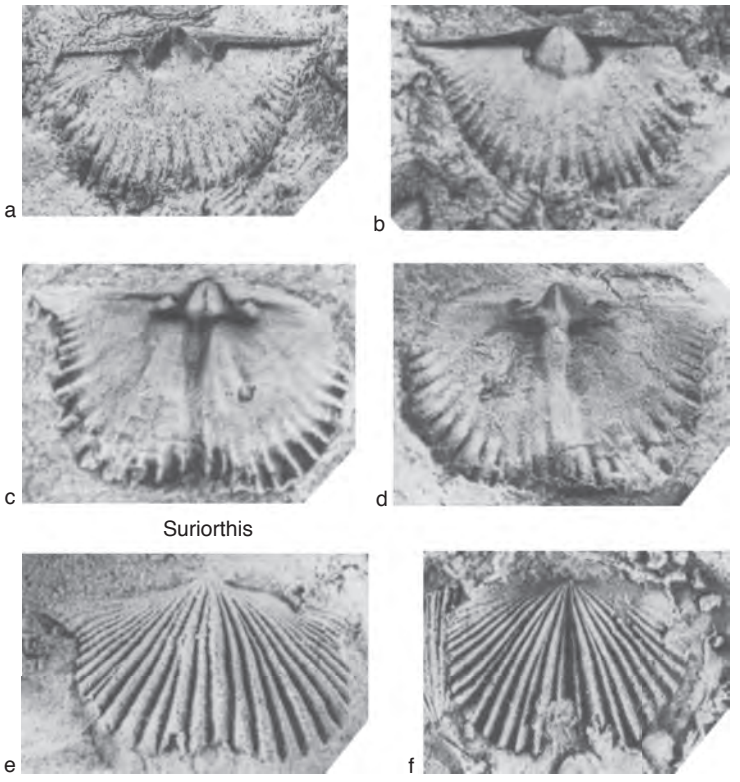

FIG. 1788. Orthidae (p. 2684).

(1936, p. 621) and *Nothorthis* ULRICH and COOPER (1938, p. 106) were assigned to the subfamily, a taxonomic practice continued by COOPER (1956a, p. 293) and adopted by WILLIAMS and WRIGHT (1965, p. 313).

In 1977, HAVLÍČEK proposed an extensive revision of the classification of the Orthida. It included the erection of the Nanorthidae (HAVLÍČEK, 1977, p. 59) for small orthids with a dalmanelloid appearance that are similar to the Ranorthidae but differ in their orthoid "dorsal muscle field, absence of fulcral plates and a fairly narrow notothyrial chamber." The new family embraced *Archaeorthis* SCHUCHERT and COOPER and *Trondorthis* NEUMAN [now reassigned to the Orthidae by WILLIAMS and HARPER (2000, p. 728)]. *Nothorthis* was reallocated to the Ranorthidae on the grounds that, contrary to previous opinion, it has fulcral plates (HAVLÍČEK, 1977a, p. 54).

WILLIAMS and HARPER (2000, p. 742–745) incorporated the Nanorthidae into their classification and assigned to the family eight more genera, including *Nothorthis*. Further phylogenetic analyses that credited *Nothorthis* with fulcral plates, as identified by HAVLÍČEK in illustrations of the type dorsal valve, supported its inclusion in the plectorthoid Ranorthidae (WILLIAMS & HARPER, 2000, p. 777). The assignments of *Nothorthis* to both the Nanorthidae and Ranorthidae were inadvertently published in WILLIAMS and HARPER (2000, p. 778), although the inclusion of *Nothorthis* within the Ranorthidae was expressedly preferred.

This confusing outcome prompted a reinvestigation of the cardinalia of *Nanorthis*

and *Nothorthis*, in the hope of determining their microstructures by SEM studies. Topotypes of the type species of both genera were obtained from the U.S. National Museum Collections, through the courtesy of Dr. J. Thomas Dutro. Unfortunately, the specimens, like the types themselves, are silicified. Even so, the valves had been finely enough replaced by silica to reveal features that were incompatible with any of the current taxonomic options. The brachiophores of *Nanorthis* are buttressed by supporting plates and subtend concave fulcral plates with the hinge line (see Fig. 1791,*2g–h*), while the brachiophores of *Nothorthis* are embedded in secondary shell that is built up as walls across the lateral margins of the sockets in simulation of fulcral plates (see Fig. 1789,*2g–h*). More surprisingly, the sharply crested ramicostellae of *Nanorthis* appear to have been indented by aditicules in the style of many plectorthoids (Fig. 1791,*2e–f*); and the more rounded costellae of *Nothorthis* bear silicified remnants of capillae (Fig. 1789,*2e–f*) that characterize the typical orthid.

These newly discovered features significantly change the position of the two genera within the orthide taxonomic hierarchy. The presence of supporting and fulcral plates in the cardinalia and probably of aditicules on the shell surface place *Nanorthis* within the Plectorthidae (SCHUCHERT & LEVENE, 1929) where it compares quite closely with *Desmorthis* ULRICH and COOPER. The assignment leads to the suppression of the Nanorthidae in favor of the earlier-founded Plectorthidae. This suppression deprives a group of dalmanellid-like orthoids of familial status. A new family has therefore been erected for them: the Archaeorthidae (based on their longest established genus), which can also accommodate *Nothorthis* with its simple cardinalia and capillate costellae.

The revision entails amended descriptions of both *Nanorthis* and *Nothorthis* as well as a diagnosis for the Archaeorthidae, which is little changed from that defining the suppressed Nanorthidae. The diagnoses of other archaeorthid genera are the same as those given by WILLIAMS and HARPER (2000, p. 742–745). Accordingly, this revision only lists such genera.

Alocorthis PATERSON & BROCK, 2003, p. 227 [**A. psygmatelos*; OD]. Medium sized, transverse, weakly ventribiconvex, rectimarginate, ramicostellate; ventral muscle scar subtriangular, slightly raised on secondary shell; cardinal process absent; brachiophores short and widely divergent, marked by furrows on dorsal surfaces and fanlike terminations. *Lower Ordovician (Arenig):* Australia.——FIG. 1789,*1a–c*. **A. psygmatelos*, Tabita Formation, northwestern New South Wales; *a–b*, rubber replica and internal mold of ventral valve, AM F120723, ×10; *c*, rubber replica of dorsal interior, AM F120719, ×16 (Paterson & Brock, 2003).

Archaeorthis SCHUCHERT & COOPER, 1931, p. 243 [**Orthis electra* BILLINGS, 1865–1865, p. 79; OD]. Described in WILLIAMS and HARPER (2000, p. 743).

Cyrtonotella SCHUCHERT & COOPER, 1931, p. 243 [**Orthis semicircularis* VON EICHWALD, 1829, p. 276; OD]. Described in WILLIAMS and HARPER (2000, p. 744).

Diplonorthis MITCHELL, 1977, p. 30 [**D. portlocki*; OD]. Described in WILLIAMS and HARPER (2000, p. 744).

Nicoloidea ZENG, 1987, p. 215 [**N. mina*; OD]. Described in WILLIAMS and HARPER (2000, p. 744).

Nothorthis ULRICH & COOPER, 1938, p. 106 [**N. delicatula*; OD]. Subquadrate with obtuse cardinal extremities, rounded, capillate ramicostellae; teeth deltidiodont (crural fossettes not recorded), suboval ventral muscle scar impressed on callosity; short, divergent brachiophores with secondary shell deposits forming lateral boundaries to sockets. *Lower Ordovician (Tremadoc–Llanvirn):* eastern North America, Baltic, Siberia, Scotland, Bohemia, China, Ireland, Central Asia (Altai Mountains).——FIG. 1789,*2a–d*. **N. delicatula*, Tremadoc, eastern North America; *a*, ventral exterior, ×3; *b*, dorsal exterior, ×3; *c*, ventral interior, ×4; *d*, dorsal interior, ×4 (Ulrich & Cooper, 1938).——FIG. 1789,*2e–h*. **N. delicatula*, Tremadoc, eastern North America, topotypes; *e–f*, ventral exterior and detail showing silicified capillae on costellae, ×7, ×95; *g–h,* ventral and tilted views of cardinalia, ×33 (new).

Pleurorthis COOPER, 1956a, p. 329 [**P. fascicostellata*; OD] [=*Ambardella* ANDREEVA, 1987, p. 37 (type, *A. anabarensis,* OD)]. Described in WILLIAMS and HARPER (2000, p. 744).

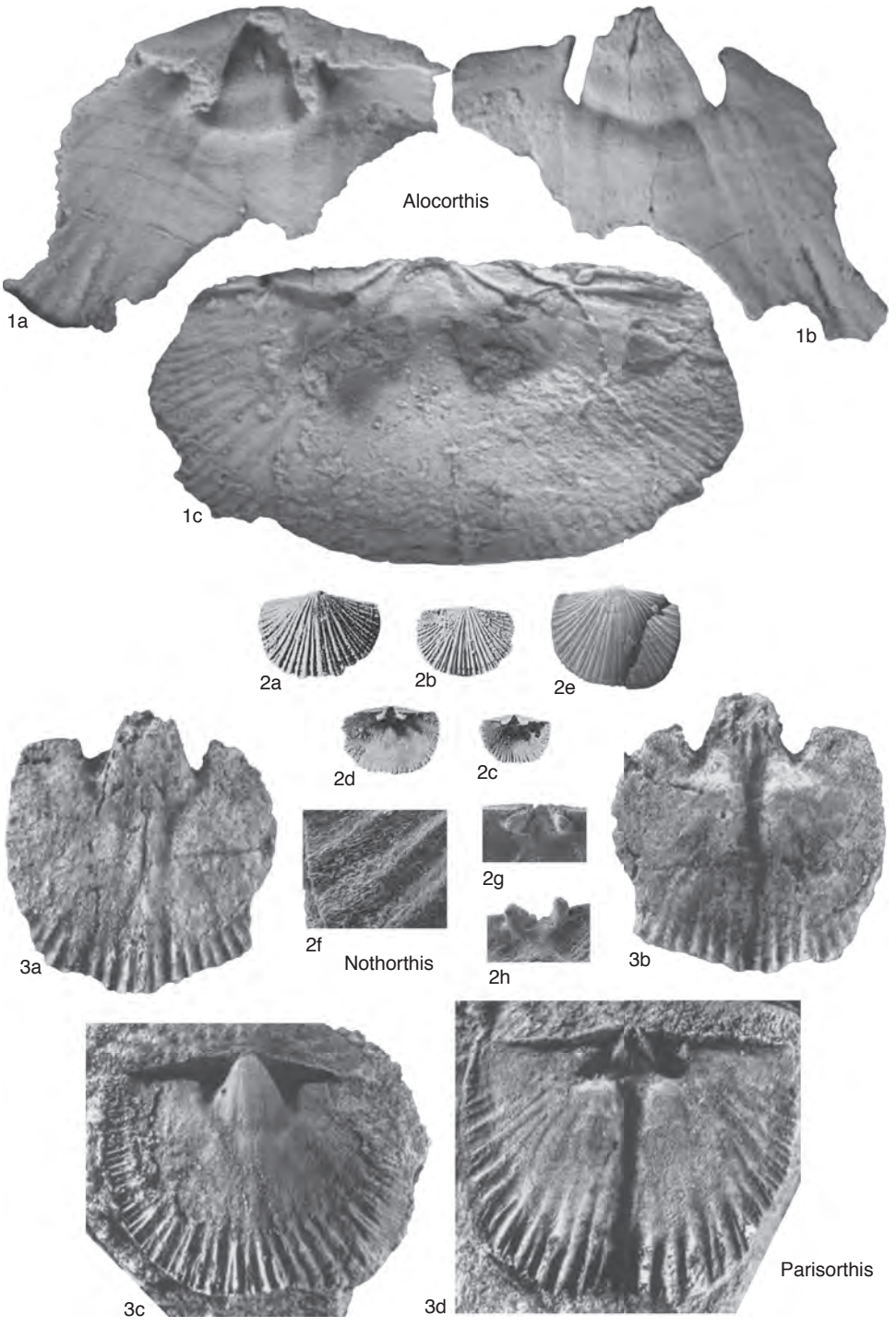

FIG. 1789. Archaeorthidae and Glyptorthidae (p. 2687–2690).

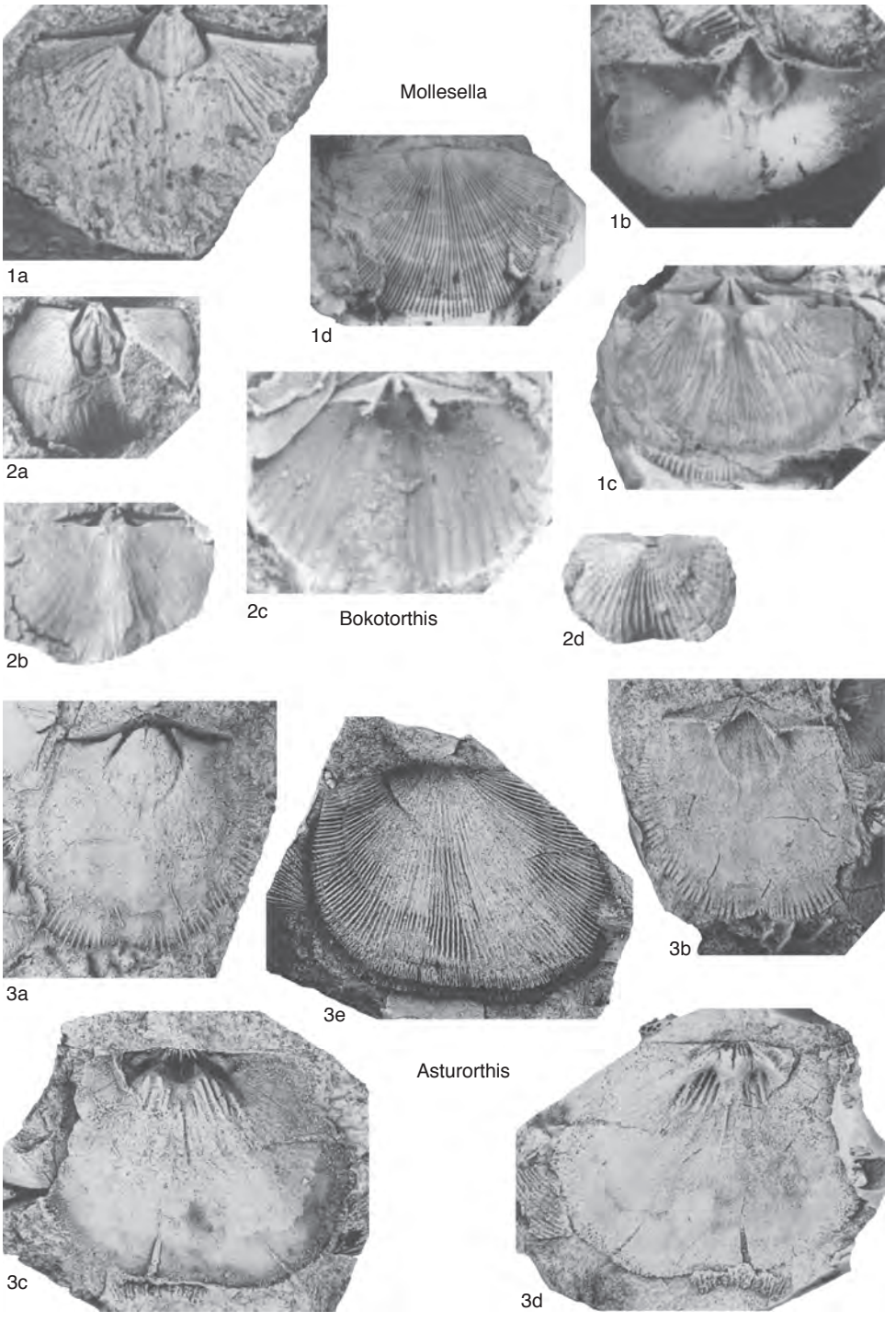

FIG. 1790. Hesperonomiidae, Hesperorthidae, and Plaesiomyiidae (p. 2690).

Riograndella Kobayashi, 1937, p. 422 [**R. subcircus*; OD]. Described in Williams and Harper (2000, p. 745).

Shoshonorthis Jaanusson & Bassett, 1993, p. 51 [**Orthis michaelis* Clark, 1935, p. 242; OD]. Described in Williams and Harper (2000, p. 745).

Xinanorthis Xu, Rong, & Liu, 1974, p. 145 [**X. striata*; OD]. Described in Williams and Harper (2000, p. 745).

Family GLYPTORTHIDAE Schuchert & Cooper, 1931

Parisorthis Zhan & Jin, 2005, p. 16 [**P. dischidanteris*; OD]. Medium sized, ventribiconvex, sulcate; shell surface multicostellate, imbricate, tuberculate; dental plates parallel, short; cardinal process with thick shaft and bilobed myophore on elevated notothyrial platform. *Middle Ordovician (Llanvirn):* China.——Fig. 1789,*3a–d*. **P. dischidanteris*, Dashaba Formation, Sichuan Province, southern China; *a–b,* ventral and dorsal interiors of conjoined valves, NIGP 134340, ×3; *c*, internal mold of ventral valve, NIGP 134345, ×2.5; *d*, internal mold of dorsal valve, NIGP 134347, ×4 (Zhan & Jin, 2005).

Family HESPERONOMIIDAE Ulrich & Cooper, 1936

Mollesella Benedetto, 2003, p. 231 [**M. planiventralis*; OD]. Large, convexiplane, semielliptical, sulcate, finely multicostellate; ventral muscle scar triangular; notothyrial platform raised with thickened, usually bulbous, cardinal process. *Lower Ordovician (Arenig):* Argentina.——Fig. 1790,*1a–d*. **M. planiventralis*, Molles Formation, northwestern Argentina; *a,* internal mold of ventral valve, CEGH-UNC 19649, ×1.5; *b,* rubber replica of ventral interior, CEGH-UNC 19673, ×1.5; *c*, internal mold of dorsal valve, CEGH-UNC 15895c, ×5; *d,* rubber replica of dorsal exterior, CEGH-UNC 19654, ×1.2 (Benedetto, 2003).

Family HESPERORTHIDAE Schuchert & Cooper, 1931

Asturorthis Villas & Cocks, 1996, p. 573 [**A. sarreoensis*; OD]. Large, dorsibiconvex, subquadrate, ramicostellate; delthyrium with apical plate; cardinal process bilobed with crenulated posterior surfaces. *lower Silurian (Llandovery):* Spain.——Fig. 1790,*3a–e*. **A. sarreoensis*, El Castro Formation, northern Spain; *a–b*, internal mold and rubber replica of ventral valve, DPO 29464, ×1.5; *c–e*, internal mold and rubber replicas of dorsal valve, interior and exterior, DPO 29467, ×1.5 (Villas & Cocks, 1996).

Family PLAESIOMYIIDAE Schuchert, 1913

Bokotorthis Popov, Nikitin, & Cocks, 2000, p. 848 [**Schizophorella kasachstanica* Rukavishnikova, 1956, p. 118; OD]. Medium sized, biconvex, uniplicate, coarsely costate. *Upper Ordovician (Caradoc):* Kazakhstan.——Fig. 1790,*2a–d*. **B. kasachstanica* (Rukavishnikova), Dulankara Formation, Chu-Ili Range; *a*, internal mold of ventral valve, CNIGR 38/12375, ×2; *b*, internal mold of dorsal valve, CNIGR 39/12375, ×3; *c*, rubber replica of dorsal interior, CNIGR 34/12375, ×4; *d*, rubber replica of ventral exterior, CNIGR 36/12375, ×2 (Popov, Nikitin, & Cocks, 2000).

Superfamily PLECTORTHOIDEA Schuchert & LeVene, 1929

Family PLECTORTHIDAE Schuchert & LeVene, 1929

[Alwyn Williams and David A. T. Harper]

Nanorthis Ulrich & Cooper, 1936, p. 621 [**Orthis hamburgensis* Walcott, 1884, p. 73; OD] [=*Evenkinorthis* Yadrenkina, 1977, p. 27 (type, *E. dualis,* OD)]. Subcircular with obtuse cardinal extremities, ramicostellae with sharp crests, apparently indented by aditicules; short, bladelike brachiophores with convergent supporting plates and fulcral plates, notothyrial platform rudimentary, lacking cardinal process. [*Evenkinorthis* has been erected for inadequately described and illustrated specimens from the Lower Ordovician of Siberia. With regard to such features as are unambiguously determinable, the genus is indistinguishable from *Nanorthis*. The reasons for amending the diagnosis of *Nanorthis* and transferring the genus from the Orthoidea (see Williams & Harper, 2000, p. 742) to the Plectorthoidea are given herein, p. 2684–2687.] *Lower Ordovician (Tremadoc):* cosmopolitan.——Fig. 1791,*2a–h*. **N. hamburgensis* (Walcott), western USA; *a*, dorsal exterior, ×4.5; *b*, ventral exterior, ×4.5; *c,* dorsal interior, ×6; *d*, ventral interior, ×6 (Ulrich & Cooper, 1938); *e–f,* topotypes, ventral exterior with detail showing siliceous nodules on costellae, interpreted as aditicules, ×12, ×35; *g–h*, topotypes, ventral and tilted views of dorsal cardinalia, ×27, ×24 (new).

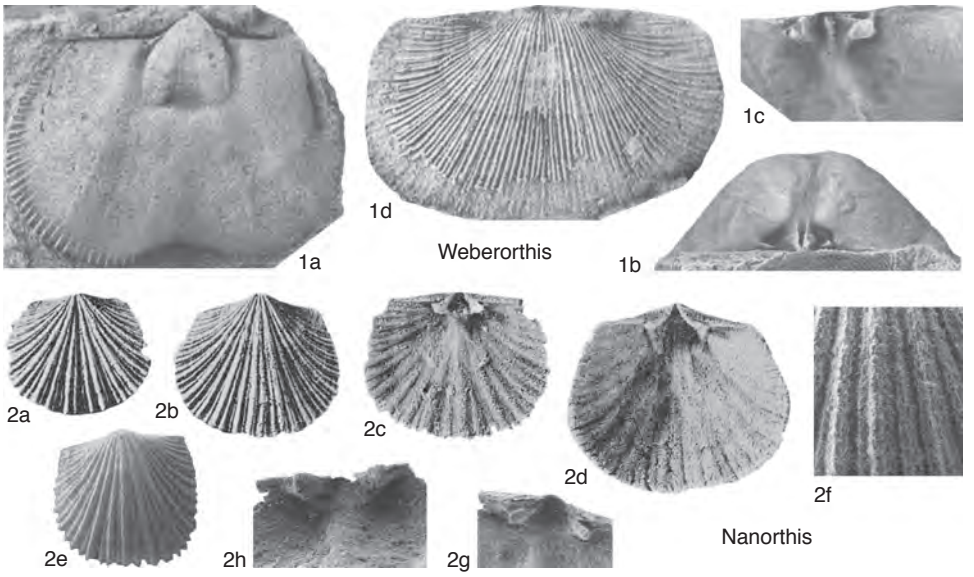

FIG. 1791. Plectorthidae (p. 2690–2691).

Weberorthis POPOV & COCKS, 2006, p. 277 [**Mimella brevis* RUKAVISHNIKOVA, 1956, p. 116; OD]. Medium sized, dorsibiconvex, subquadrate, uniplicate, finely multicostellate; short dental plates continuous anteriorly with muscle-bounding ridges completely confining ventral muscle field; high, narrow notothyrial platform with expanded, bulbous, cardinal process; ventrolaterally directed brachiophores with bases convergent onto median ridge. *Upper Ordovician (Caradoc):* Kazakhstan.——FIG. 1791,*1a–d*. **W. brevis* (RUKAVISHNIKOVA), Dulankara Formation, Chu-Ili Range; *a,* internal mold of ventral valve, BMNH BC 57749, ×2.5; *b–c*, posterior view of internal mold of dorsal valve and rubber replica of cardinalia, BMNH BC 57751, ×2, ×3; *d*, rubber replica of dorsal exterior, BMNM BC 57613, ×3 (Popov & Cocks, 2006).

Family EOORTHIDAE Walcott, 1908

Roanella BROCK & TALENT, 1999, p. 111 [**Orthis (Plectorthis) platystrophoides* CHAPMAN, 1911, p. 311; OD]. Small, semicircular to subquadrate, ventribiconvex, unequally costellate; deltidial plates fused to form symphytium; anterior margin of ventral muscle scar marked by raised median boss. [Although this genus has strong similarities with a number of billingselloids, its features, particularly those of the dorsal valve, are more typically orthoid; it is transferred pending data on shell structure.] *Upper Cambrian:* Australia.——FIG. 1792*a–i*. **R. platystrophoides* (CHAPMAN), Garvey Gully Formation, East Central Victoria; *a–e,* dorsal, ventral, anterior, lateral, and posterior views of conjoined valves, NMV P148697, ×3.5; *f–g*, external and internal views of ventral valve, NMV P148703, ×3.5; *h–i*, external and internal views of dorsal valve, NMV P148705, ×3.5 (Brock & Talent, 1999).

Family GIRALDIELLIDAE Williams & Harper, 2000

Kvania HAVLÍČEK, 1994, p. 298 [**Nothorthis kvanica* MERGL, 1984, p. 17; OD]. Small, ventribiconvex, subcircular, sulcate, fascicostellate; ventral muscle scar subpentagonal; notothyrial platform small, lacking cardinal process. *Lower Ordovician (Tremadoc):* Bohemia, Germany, Argentina.——FIG. 1793,*1a–c*. **K. kvanica* (MERGL), Milina Formation, Bohemia; *a*, internal mold of ventral valve, MM 076, ×14.5; *b*, internal mold of dorsal valve,

MM 075, ×6.6; *c*, internal mold of dorsal valve, MM 074, ×8.8 (Mergl, 1984).

Family PLATYSTROPHIIDAE Schuchert & LeVene, 1929

Gnamptorhynchos Jin, 1989, p. 75 [**P. regularis globata* Twenhofel, 1928, p. 177; OD]. Large, dorsibiconvex, globose, uniplicate, strong angular to subangular costae; well-developed dental plates; bladelike cardinal process, uni- or trilobate; elevated notothyrial platform supported by one or two ridges. [Jin & Zhan (2000) transferred Jin's aberrant genus from the rhynchonellids to the platystrophiids on the basis of its orthide ventral muscle field and dental plates.] *Upper Ordovician (Caradoc)–lower Silurian (Llandovery):* North America.——Fig. 1793,*2a–e*. **G. globatum* (Twenhofel), Ellis Bay Formation, Ashgill, Anticosti Island, Canada; dorsal, ventral, lateral, posterior, and anterior views of conjoined valves, YPM10420, ×2 (Jin & Zhan, 2000).

Siljanostrophia Zuykov & Egerquist, 2005, p. 2 [**S. jaanussoni*; OD]. Medium sized, biconvex, uniplicate, costate with shell surface additionally ornamented by thin hollow spines; ventral interior with pseudospondylium; cardinal process simple; elevated notothyrial platform supported by two ridges. *Upper Ordovician (Ashgill):* Sweden.——Fig. 1793,*3a–f*. **S. jaanussoni*, Boda Limestone, Dalarne; *a–d*, posterior, dorsal, ventral, and lateral views of conjoined valves, RM Br135287, ×3; *e*, ventral interior, RM Br 99630, ×4.5; *f*, dorsal interior, CNIGR 2/13121, ×3 (Zuykov & Egerquist, 2005).

Suborder DALMANELLIDINA Moore, 1952
Superfamily DALMANELLOIDEA Schuchert, 1913
Family DALMANELLIDAE Schuchert, 1913
Subfamily DALMANELLINAE Schuchert, 1913

Christiferina Cooper, 1956a, p. 961 [**C. cristata*; OD]. Small, ventribiconvex, subcircular, multicostellate; cordate ventral muscle scar; cardinal process with grooved shaft and expanded myophore capped by sharp crest; high median ridge bisecting dorsal muscle scar. *Middle Ordovician (Caradoc)*: Scotland, USA.——Fig. 1794,*1a–e*. **C. cristata,* Virginia; *a–c*, lateral, anterior, and dorsal views of conjoined valves, Edinburg Formation, Strasburg, USNM 117353, ×2; *d,* ventral interior, Chatham Hill Formation, Sharon Springs, USNM 111794c, ×2; *e,* dorsal interior, Chatham Hill Formation, Sharon Springs, USNM 111794d, ×2 (Cooper, 1956a).

?Minororthis Ivanov in Ivanov & Miagkova, 1950, p. 23 [**M. nalivkini;* OD]. Small, subquadrate with obtuse cardinal extremities, ventribiconvex, multicostellate; dorsal valve sulcate, ventral valve subcarinate; cardinal process flanked by high, divergent brachiophores. [The figured material is poorly preserved, lacks institution accession numbers, and is not well illustrated. The overall features suggest placement within the Dalmanellidae, possibly even the Dalmanellinae, but in the absence of critical information such as the nature of the shell substance, this assignment is tentative.] *Middle Ordovician (Caradoc):* Russia (central Ural Mountains).——Fig. 1794,*2a–d*. **M. nalivkini*; *a,* dorsal exterior, ×2; *b,* ventral valve, ×2; *c,* dorsal interior, ×2; *d,* internal mold of ventral valve, ×2 (Ivanov & Miagkova, 1955).

Subfamily ISORTHINAE Schuchert & Cooper, 1931

Pelecymya Mawson & Talent, 1999, p. 151 [**P. caperata*; OD]. Medium sized, biconvex to planoconvex, slightly sulcate, multicostellate; ventral muscle scar cordate to subpentagonal; dorsal adductor scars separated by strip of thickened shell bearing low, thin median septum. *Lower Devonian (Lochovian):* Australia.——Fig. 1794,*3a–d*. **P. caperata*, Windellama Limestone, southeastern Australia; *a–b*, ventral exterior and interior, AM F105137, ×5; *c–d*, dorsal exterior and interior, AM F105133, ×5 (Mawson & Talent, 1999).

Family HARKNESSELLIDAE Bancroft, 1928

Haymina Bogoyavlenskaya, 1991, p. 84 [**H. carinata*; OD]. Medium sized, subrectangular, dorsibiconvex, with ventral carina and narrow dorsal sulcus; ventral muscle field cordate, teeth small; notothyrium platform absent; cardinal process simple and bladelike; brachiophores short. *Middle Ordovician (Llanvirn):* Russia (Northern Urals).——Fig. 1795,*1a–c*. **H. carinata*, Khaiminskaya Formation; *a*, internal mold of ventral valve, 138/2087, ×1; *b*, internal mold of dorsal valve, 140/2087, ×1; *c*, detail of ornament, 136/2087, ×6 (Bogoyavlenskaya, 1991).

Family HETERORTHIDAE Schuchert & Cooper, 1931

Fehamaya Mergl, 1983, p. 340 [**F. circula*; OD]. Large, markedly ventribiconvex, rectimarginate

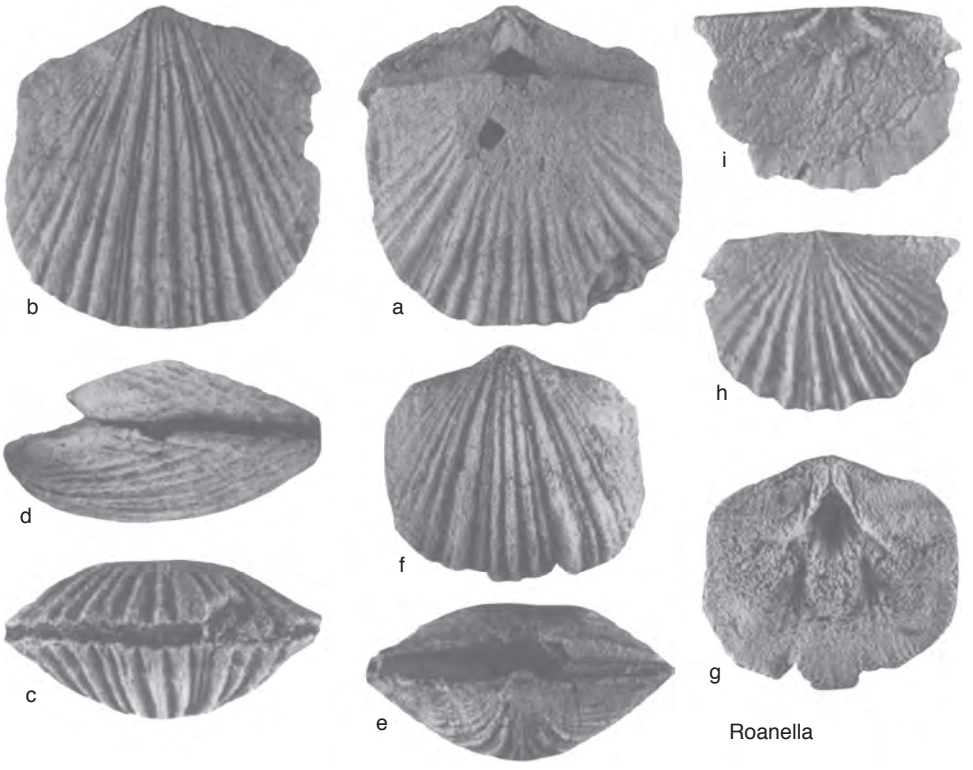

FIG. 1792. Eoorthidae (p. 2691).

valves, finely multicostellate; ventral muscle scar large and flabellate with diductors enclosing adductor scars; cardinal process large, posterior part of myophore bilobate; brachiophores short and divergent. *Upper Ordovician (Ashgill):* North Africa.——FIG. 1795,*2a–c.* **F. circula*, Hirnantian, upper Ashgill rocks, Foum el Fehamaya, Morocco; *a–b,* internal and external molds of ventral valve, VH 4015a,b, ×1.7; *c,* internal mold of dorsal valve, VH 4015d, ×1.3 (Mergl, 1983).

Family PAURORTHIDAE Öpik, 1933

Tenuiseptorthis MÉLOU in MÉLOU, OULEBSIR, & PARIS, 1999, p. 830 [**T. niliensis*; OD]. Small, planoconvex, rectimarginate, fascicostellate; widely divergent brachiophores, almost parallel to hinge line; ventral muscle scar short and wide; notothyrial platform reduced or absent, with small cardinal process and thin median septum. *Middle Ordovician (Llanvirn):* Algeria.——FIG. 1795,*3a–e.* **T. niliensis*, Argiles dOued Saret, Borj Nili; *a–b*, internal mold of ventral valve and rubber replica, LPB 17301, ×10; *c–d*, internal mold of dorsal valve and rubber replica, LPB 17302, ×10; *e*, rubber replica of ventral exterior, LPB 17306, ×2 (Mélou, Oulebsir, & Paris, 1999).

Superfamily ENTELETOIDEA Waagen, 1884

Family DRABOVIIDAE Havlíček, 1950

Draborthis MAREK & HAVLÍČEK, 1967, p. 280 [**D. caelebs*; OD]. Small, planoconvex, sulcate, multicostellate; ventral muscle scar large, oval; dorsal interior

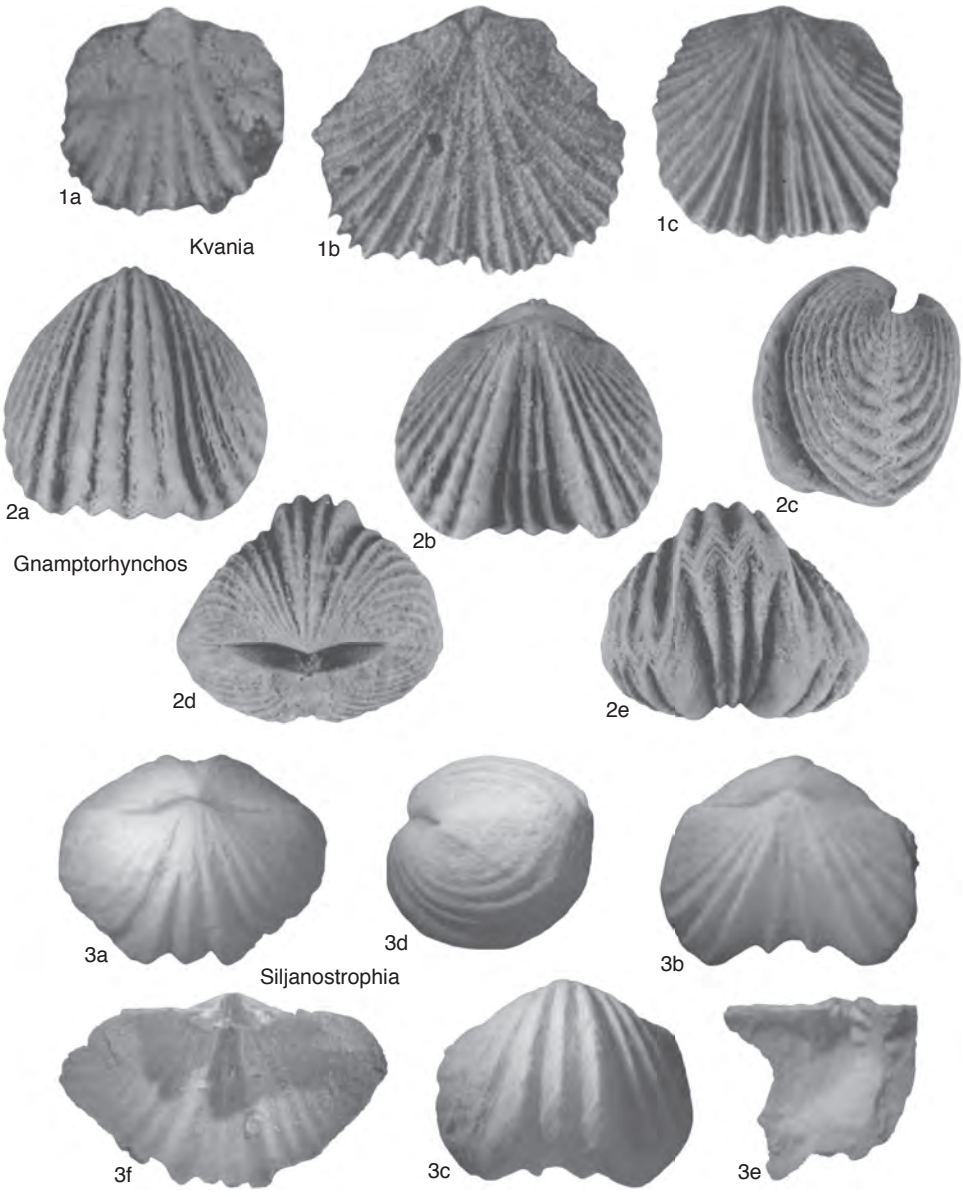

FIG. 1793. Giraldiellidae and Platystrophiidae (p. 2691–2692).

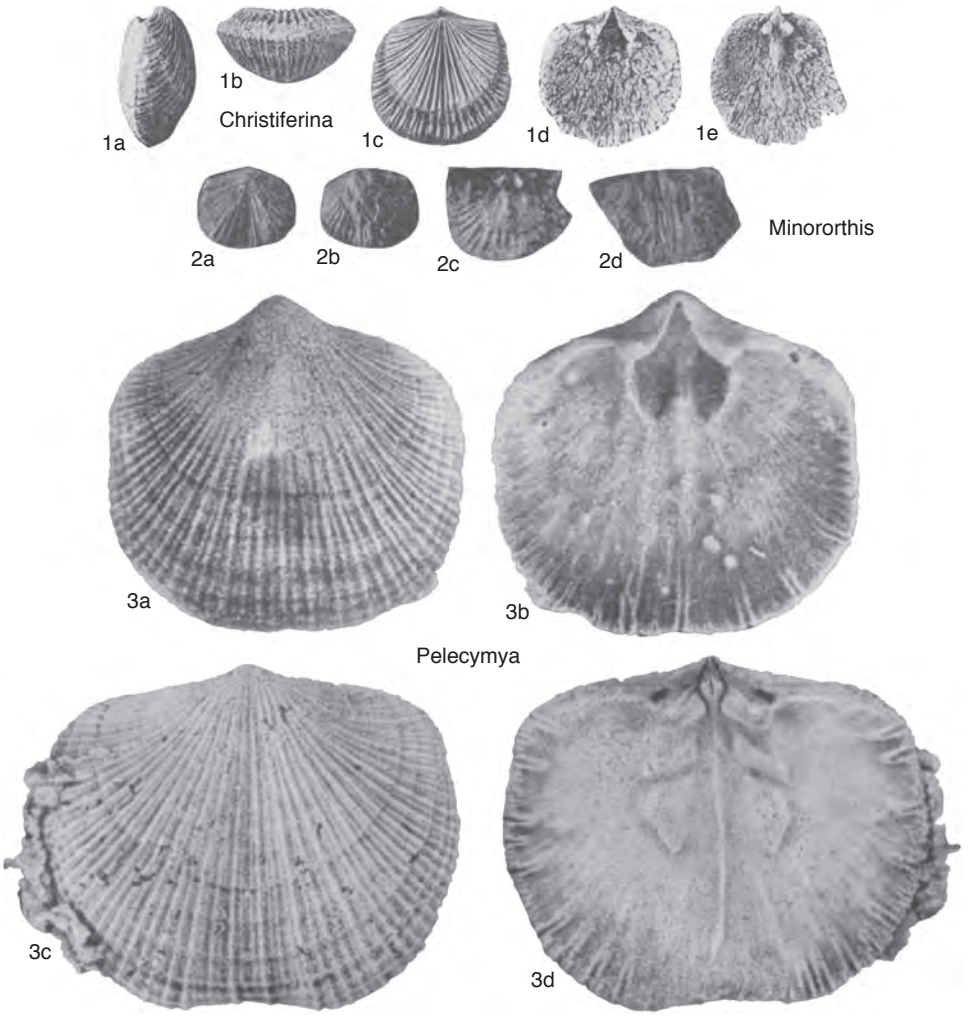

FIG. 1794. Dalmanellidae (p. 2692).

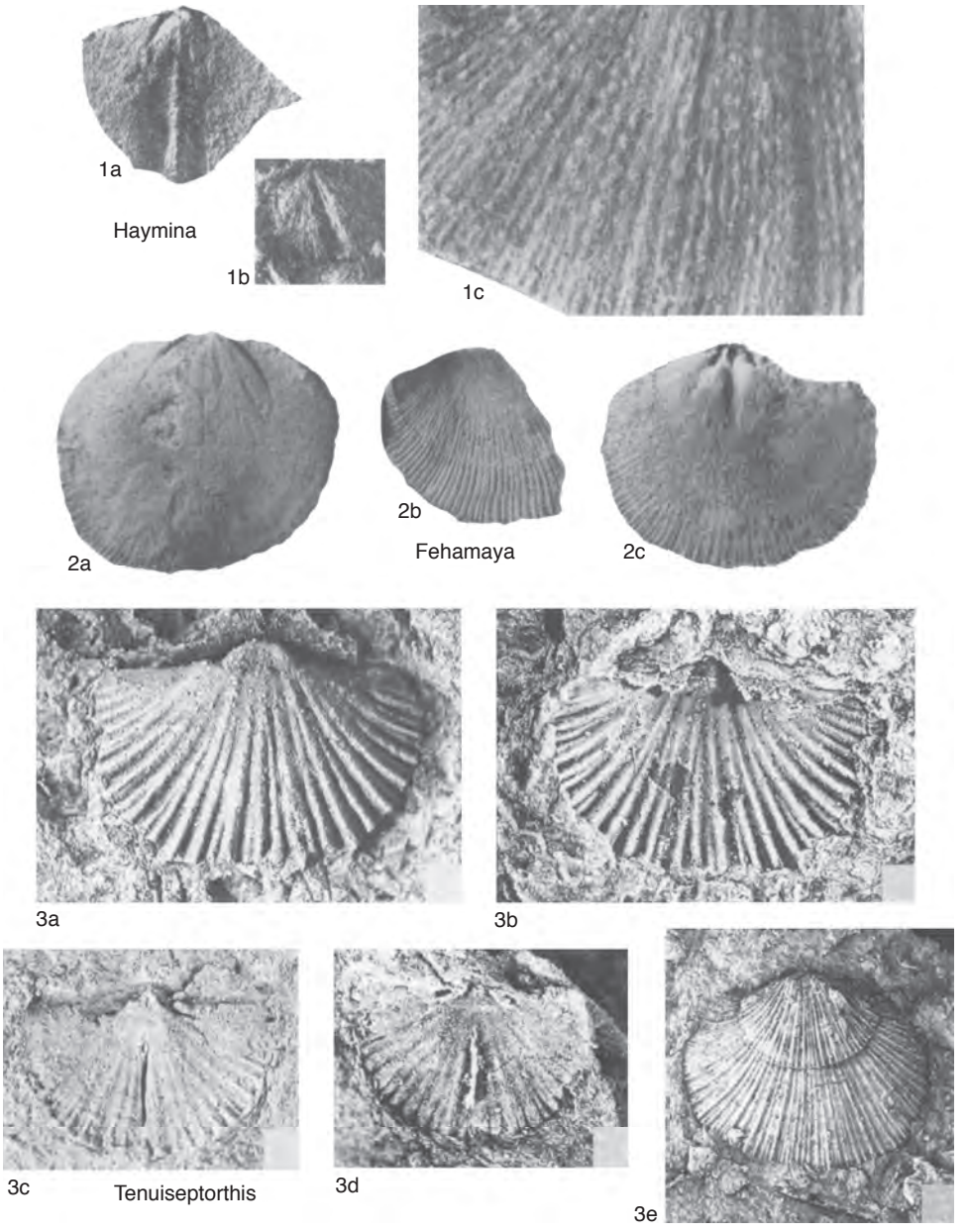

FIG. 1795. Harknessellidae, Heterorthidae, and Paurorthidae (p. 2692–2693).

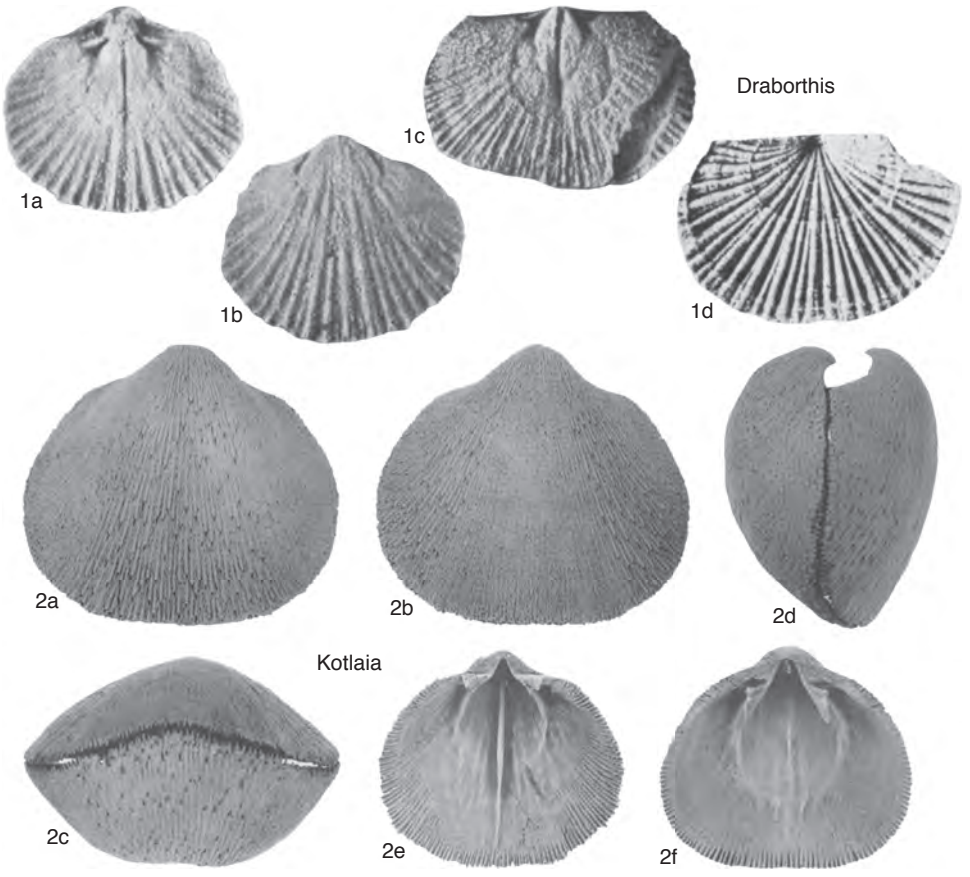

FIG. 1796. Draboviidae and Schizophoridae (p. 2693–2697).

with low septum and divergent brachiophore bases. *Upper Ordovician:* widespread.——FIG. 1796,*1a–d*. **D. caelebs,* Kosov Formation, Ashgill, Bohemia; *a–b*, dorsal and ventral views of conjoined internal molds, VH 1470, ×5; *c*, internal mold of dorsal valve, VH 1464a, ×5; *d*, external mold of dorsal valve, VH 531a, ×5 (Havlíček, 1977).

Family LINOPORELLIDAE Schuchert & Cooper, 1931

Lipanorthis BENEDETTO in BENEDETTO & CARRASCO, 2002, p. 656 [**L. andinus*; OD]. Medium sized, ventribiconvex, sulcate; ventral interarea curved, steeply apsacline to catacline; ventral muscle scar bilobed to cordate; cardinalia short with ridgelike cardinal process on low septalium. [Identification of endopunctae indicates this is a dalmanellidine (HARPER & others, 2004), and the genus is accordingly placed here rather than within the plectorthoids. The mold material illustrated here demonstrates clearly the presence of endopunctae, not immediately identifiable on the type species.] *Lower Ordovician:* Argentina.——FIG. 1797*a–d*. *L. santalaurae* BENEDETTO, Coquena Formation, Tremadoc; *a,* internal mold of ventral valve, CORD-PZ 30401-1, ×2.5; *b–c*, internal mold and rubber replica of dorsal interior, CORD-PZ 30434-1, ×5; *d*, rubber replica of dorsal exterior, CORD-PZ 30435.b-4, ×2.5 (Harper & others, 2004).

Family SCHIZOPHORIIDAE Schuchert & LeVene, 1929

Kotlaia GRANT, 1993, p. 4 [**K. capillosa*; OD]. Medium sized, subcircular, weakly sulcate, costellae fine and tubular; ventral interior with long, low median septum and short, divergent dental plates; brachiophores long and laterally compressed. *middle Permian–Upper Permian:* Greece, Pakistan.——FIG. 1796,*2a–f*. **K. capillosa*, Chhidru Formation, Upper Permian, Pakistan; *a–d*, ventral, dorsal, anterior, and lateral views of conjoined valves, USNM 402084, ×2; *e–f*, ventral and dorsal interiors, USNM 402085, ×2 (Grant, 1993).

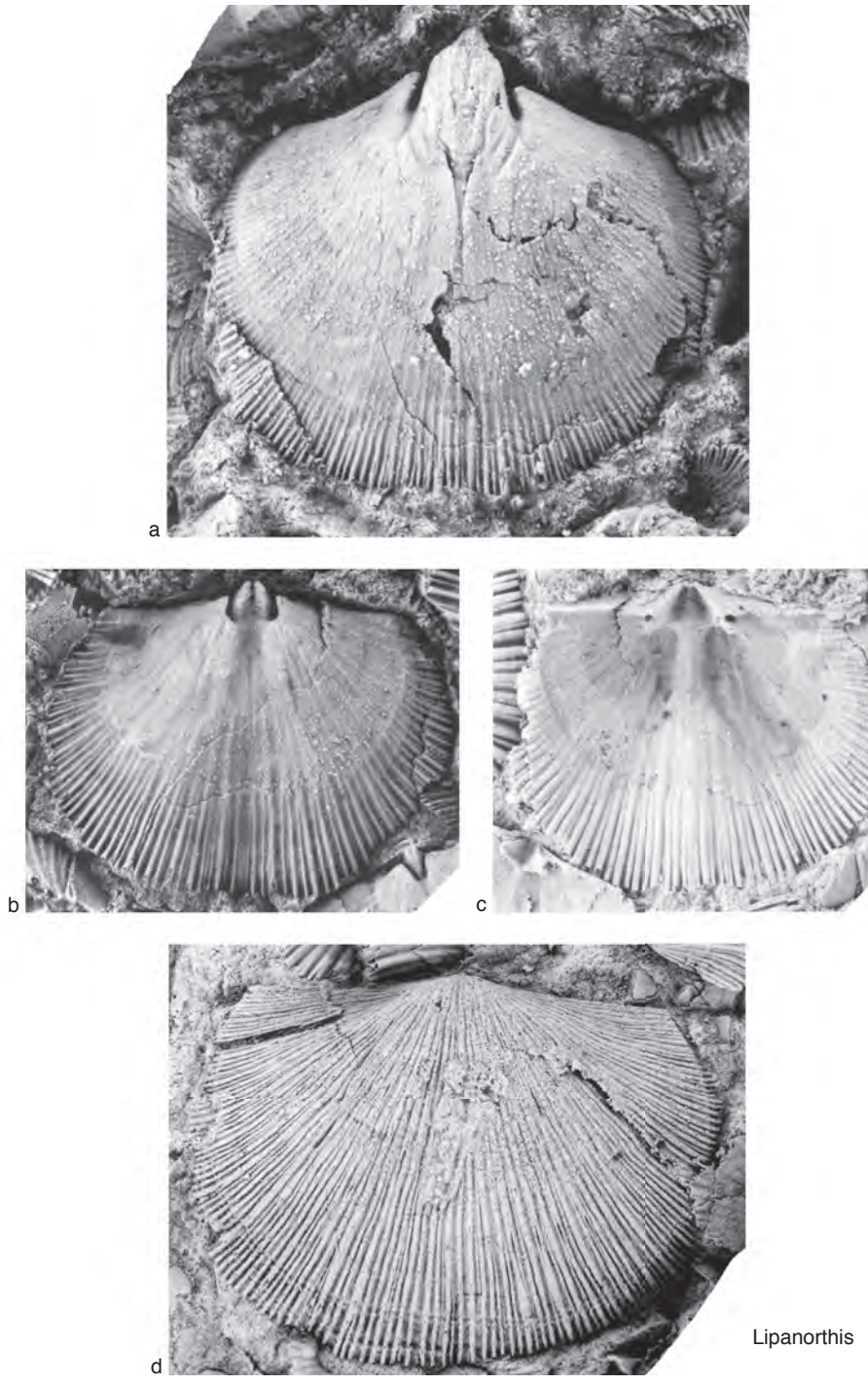

FIG. 1797. Linoporellidae (p. 2697).

PENTAMERIDA

SANDRA J. CARLSON
[University of California, Davis]

Order PENTAMERIDA Schuchert & Cooper, 1931
Suborder SYNTROPHIIDINA Ulrich & Cooper, 1936
Superfamily PORAMBONITOIDEA Davidson, 1853
Family HUENELLIDAE Schuchert & Cooper, 1931
Subfamily MESONOMIINAE Ulrich & Cooper, 1936

Radkeina LAURIE, 1997a, p. 185 [**R. taylori*; OD]. Small, strongly biconvex, fascicostellate shells; dental plates converging to form sessile spondylium supported anteriorly only by fairly high, wide median ridge, accessory septa present rarely; short, shallow recumbent socket plates; fulcral plates well developed, thick. Similar to *Glyptotrophia* with wide hinge line and distinct cardinal process, but biconvexity stronger, and dorsal adductor muscle field elevated on callosities. *Upper Cambrian (?Trempealeauan):* Australia (Queensland).——FIG. 1798,*1a–h.* **R. taylori*, Chatsworth Limestone, Georgina Basin; *a,* ventral valve exterior, ×4; *b,* ventral valve, lateral view, ×4; *c,* dorsal valve exterior, ×4; *d,* dorsal valve, posterior view, ×4; *e,* ventral valve interior, ×4; *f,* ventral valve interior, ×4; *g,* dorsal valve interior, ×4; *h,* dorsal valve interior, ×4 (Laurie, 1997a).

Subfamily RECTOTROPHIINAE Bates, 1968

Trigonostrophia BENEDETTO, 2003, p. 237 [**T. reversa*; OD]. Small to medium-sized triangular shells; exterior smooth with very fine radial striations; commissure gently lobate to parasulcate, with shallow sulcus in each valve, anterior margin of ventral valve strongly deflected dorsally; hinge line narrow with low, narrow interareas; teeth thin, short; parallel dental plates extending anteriorly and converging to form long, narrow pseudospondylium, extending to 40 percent of valve length, slightly raised above valve floor, supported anteriorly in some specimens by very low, short median septum; notothyrial platform short, slightly elevated anteriorly; cardinal process absent; dorsal mantle canal system digitate, with two pairs of straight trunks and several shorter, closely spaced minor trunks. Similar to *Rectotrophia*, but cardinal process absent, pseudospondylium longer and narrower. [BENEDETTO (2003) makes a case for separating *Rectotrophia* and *Trigonostrophia* from the huenellids and placing them into a revised family Rectotrophiidae BATES, 1968. The smooth exterior and narrower hinge line are the main characters upon which this reassignment is based; both of these characters can and do vary considerably among confamilial genera, even congeneric species. The presence of a pseudospondylium in *Rectotrophia*, *Trigonostrophia,* and the huenellids is considered here to represent a feature shared due to common ancestry. If Rectotrophiidae is recognized as a distinct family or as a distinct subfamily Rectotrophiinae within Huenellidae, it most likely shared more recent common ancestry with Huenellidae than any other family of syntrophiidines.] *Lower Ordovician (Arenig):* northwestern Argentina.——FIG. 1798,*2a–f.* **T. reversa*, Suri Formation, Famatina Range; *a,* ventral valve exterior, ×2.5; *b,* dorsal valve exterior, ×2; *c,* ventral valve interior mold, ×2.5; *d,* cast of ventral valve interior mold, ×2; *e,* posterior oblique view of dorsal valve interior mold, ×2; *f,* dorsal valve interior mold, ×2.5 (Benedetto, 2003).

Family CLARKELLIDAE Schuchert & Cooper, 1931

Parallelostrophia BENEDETTO, CECH, & ESBRY, 2003, p. 526 [**P. septata*; OD]. Medium-sized smooth shells; commissure apparently rectimarginate, lacking fold and sulcus; wide hinge line with well-developed ventral interareas; spondylium simplex supported by long, high median septum and two strong accessory septa; long, initially convergent, then subparallel socket plates, accessory septa may be present; adductor muscle field not discernible. Similar to *Calliglypha*, but lacking ornament, with rectimarginate commissure, strong ventral accessory septa and longer socket plates; similar to *Yangtzeella*, but rectimarginate and lacking septalium. *Lower Ordovician (lower Arenig):* Argentina (Precordilleran basin).——FIG. 1799,*1a–e.* **P. septata*, San Juan Formation, Cerro San Roque section; *a,* ventral valve exterior, ×2; *b,* ventral valve interior, ×2; *c,* ventral valve interior, anterior oblique view, ×2; *d,* dorsal valve interior, ×2; *e,* dorsal valve interior, ×2 (Benedetto, Cech, & Esbry, 2003).

Punastrophia BENEDETTO, 2001, p. 141 [**P. multiseptata*; OD]. Small- to medium-sized, smooth, subelliptical shells; hinge line narrow, with narrow interareas in each valve; spatulate spondylium simplex supported by a robust median septum extending anterior to spondylium, 3 or more pairs of thin, short accessory septa present; ventral mantle canals digitate; slightly elevated, concave,

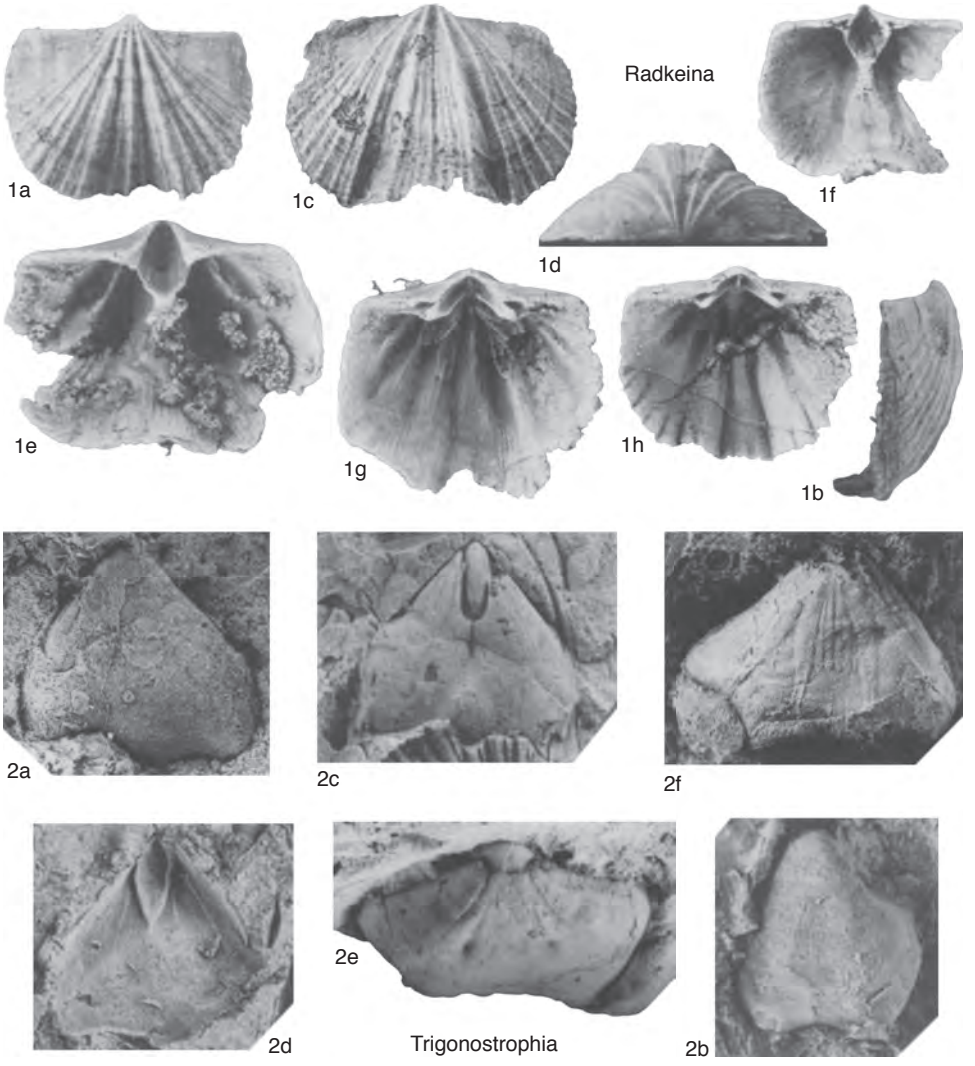

FIG. 1798. Huenellidae (p. 2699).

and somewhat triangular notothyrial platform present, cardinal process unknown; sockets delimited by distinct fulcral plates, socket plates with up to 3 pairs of long, shallow accessory septa; 2 or 3 distinct, shallow dorsal median septa present; dorsal mantle canal system digitate. Very similar to *Clarkella*, but *Punastrophia* has 2 or 3 shallow median dorsal septa and more pairs of accessory septae supporting ventral spondylium and dorsal socket plates. [The precise nature of the number and variation of the number of septa in each valve is somewhat unclear at this time; given the variation observed thus far, distinguishing a new genus apart from *Clarkella* appears warranted.] *Lower Ordovician (Arenig):* northwestern Argentina.

——FIG. 1799,*2a–e.* **P. multiseptata*, Vega Pinato, Puna region; *a,* ventral valve exterior mold, ×3; *b,* ventral valve interior mold, ×3; *c,* cast of ventral valve interior mold, ×4; *d,* dorsal valve interior mold, ×3; *e,* cast of dorsal valve interior mold, ×3 (Benedetto, 2001).

Superfamily CAMERELLOIDEA Hall & Clarke, 1895
Family PARASTROPHINIDAE Schuchert & LeVene, 1929

Eosotrophina ZHAN & RONG, 1995, p. 568 [**Camerella uniplicata* LIANG in LIU, XU, & LIANG, 1983,

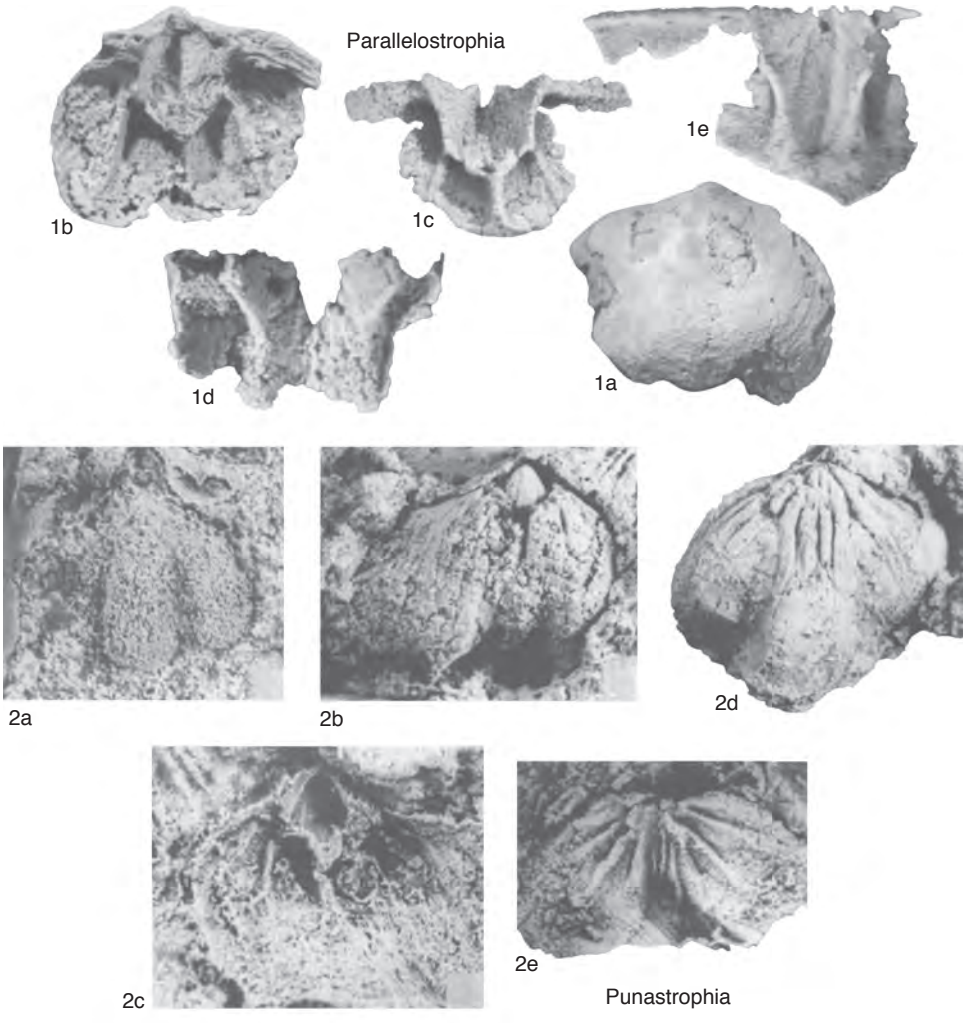

FIG. 1799. Clarkellidae (p. 2699–2700).

p. 282; OD]. Small- to medium-sized, smooth shells; outline rhombic to pentameral, wider than long; strongly uniplicate; teeth strong; spondylium duplex supported for entire length by low median septum extending anterior to spondylium; outer hinge plates well developed, widely divergent; long inner hinge plates that converge and unite with long median septum to form long septalium duplex, median septum increasing in height anteriorly; alate plates poorly developed, fine and very short. Similar to *Liostrophia* but smaller, with well-developed outer hinge plates and poorly developed alate plates. *Upper Ordovician (middle Ashgill):* East China (southwestern Zhejiang).——FIG. 1800,*1a–g.* **E. uniplicata* (LIANG), Xiazhen Formation, Dianbian-Shiyang, Jiangshan County; *a,* ventral valve exterior, ×2; *b,* articulated valves, posterior view, ventral below, ×2; *c,* articulated valves, anterior view, ventral below, ×2; *d,* dorsal valve exterior, ×2; *e,* articulated valves, lateral view, ventral on right, ×2; *f–g,* serial sections 1.6 and 2.6 mm from posterior end of specimen, ventral valve above, magnification not given (Zhan & Rong, 1995).

Ilistrophina POPOV, COCKS, & NIKITIN, 2002, p. 69 [**I. tesikensis;* OD]. Small, smooth shells; outline rounded pentameral, varies from wider than long to longer than wide; strongly uniplicate, fold and sulcus varies from rounded to broad and flat, originating anterior to midvalve; teeth small, strong; spondylium sessile posteriorly, raised and supported anteriorly by low median septum extending anterior

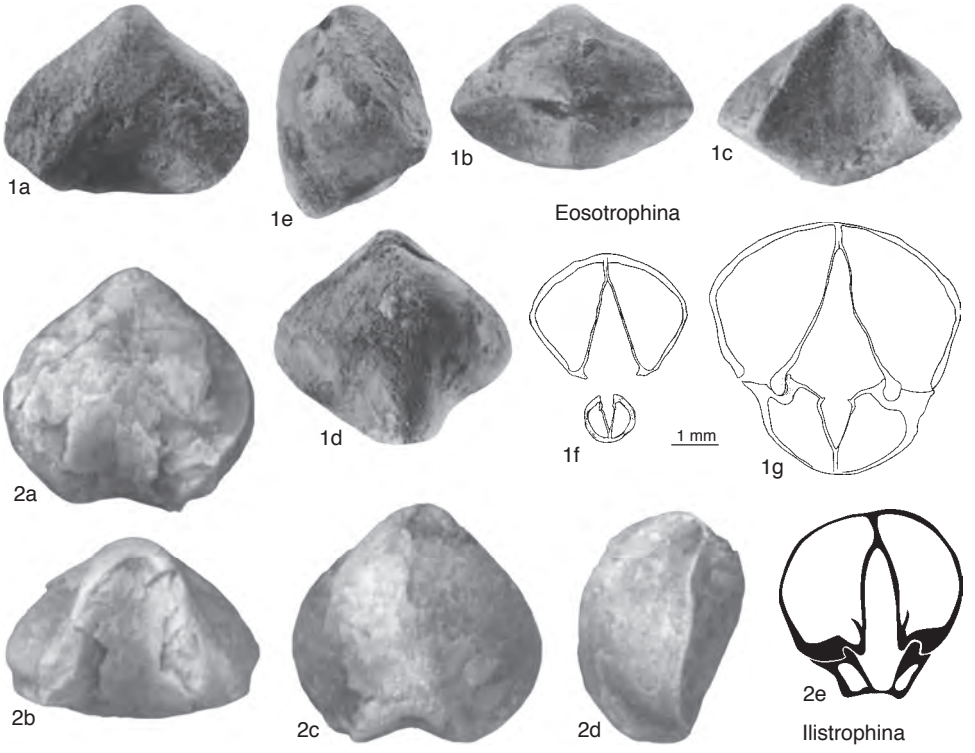

FIG. 1800. Parastrophinidae (p. 2700–2702).

to spondylium; outer hinge plates short, subparallel to convergent; inner hinge plates long, converging and uniting with long, high median septum to form long, deep septalium duplex; crura long; alate plates well developed. Similar to *Eosotrophina* but smaller and with sessile spondylium. *Upper Ordovician (lower Caradoc–middle Caradoc):* southeastern Kazakhstan (Chu-Ili Range).——FIG. 1800,*2a–e.* **I. tesikensis,* Anderken Formation, Tesik River; *a,* ventral valve exterior, ×4; *b,* articulated valves, anterior view, ventral below, ×4; *c,* dorsal valve exterior, ×4; *d,* articulated valves, lateral view, ventral on right, ×4; *e,* serial section 0.9 mm from posterior end of specimen, dorsal valve above, ×7 (Popov, Cocks, & Nikitin, 2002).

RHYNCHONELLIDA (part)

NORMAN SAVAGE

[University of Oregon]

Order RHYNCHONELLIDA Kuhn, 1949
Superfamily RHYNCHOTREMATOIDEA Schuchert, 1913
Family TRIGONIRHYNCHIIDAE Schmidt, 1965
Subfamily TRIGONIRHYNCHIINAE Schmidt, 1965

Tectogonotoechia GARCÍA-ALCALDE, 1998, p. 769 [**T. tectogonia*; OD]. Small with slightly elongate subpentagonal outline and dorsibiconvex profile. Beak suberect to erect; delthyrium with conjunct deltidial plates. Fold and sulcus narrow, arising at one-third shell length; anterior commissure uniplicate, rounded, dentate. Costae strong, angular, numerous, simple, extending from beaks. Dental plates short, thin, vertical; teeth short. Dorsal median septum low, short; septalium with cover plate; cardinal process lacking; crura unknown. *Lower Devonian (Lochkovian):* Spain.——FIG. 1801*a–l*. **T. tectogonia*, Felmin Formation, 1.3 km north of Barrios de Luna, Cantabrian Mountains, Dominio Palentino, northern Spain; *a–d*, holotype, dorsal, ventral, anterior, and lateral views, ×2; *e–l*, hypotype, serial sections 0.25, 0.35, 0.85, 1.1, 1.35, 1.5, 1.55, 1.6 mm from posterior, ×5 (García-Alcalde, 1998).

Subfamily RIPIDIORHYNCHINAE Savage, 1996

Hunanotoechia MA, 1993, p. 717 [**H. tieni*; OD]. Small; subcircular to subpentagonal outline; dorsibiconvex profile. Beak erect; small deltidial plates disjunct; foramen ovate, laterally flattened. Fold and sulcus arising at about midlength; anterior commissure uniplicate; tongue high, rounded, serrate. Costae numerous, angular with rounded tops, simple, from beaks, well developed over whole shell. Dental plates short, vertical or slightly divergent ventrally; teeth stout. Hinge plates short, horizontal, united at small septalium; dorsal median septum low, extending about one-third valve length; crural bases triangular in section; crura slender, laterally flattened distally. *Upper Devonian (upper Frasnian):* China.——FIG. 1802,*1a–j*. **H. tieni*, lower part of Changlungchieh Shale, Xikuangshan, central Hunan; *a–e*, holotype, dorsal, ventral, lateral, anterior, and posterior views, ×3; *f–j*, serial sections 0.4, 0.8, 1.0, 1.4, 1.8 mm from posterior, ×6 (Ma, 1993).

Orophomesorhynchus SARTENAER, 2001, p. 203 [**Terebratula huotina* DE VERNEUIL, 1845, p. 81; OD]. Medium size; subpentagonal outline; strongly dorsibiconvex profile. Ventral beak erect, projecting. Strong fold and sulcus arising at umbones; anterior commissure uniplicate; tongue high, trapezoid with rounded top, dentate. Costae strong, simple, regular, angular with rounded crests; starting near beaks; some parietal costae; lateral costae numerous,

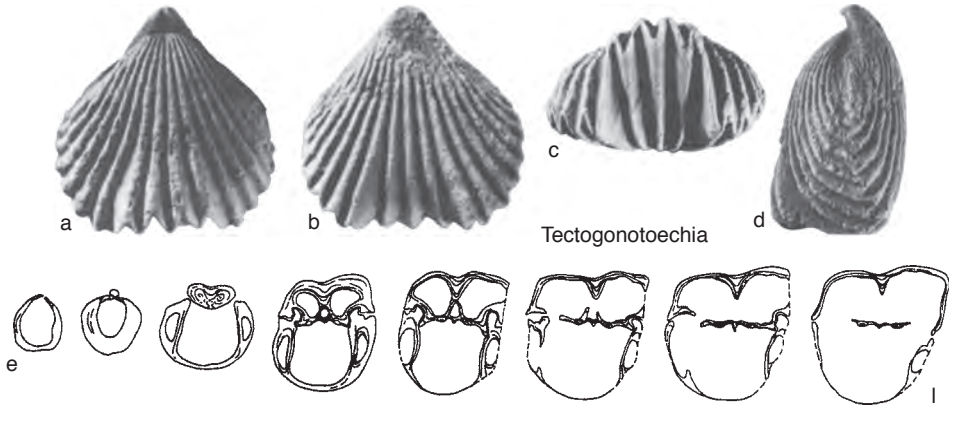

FIG. 1801. Trigonirhynchiidae (p. 2703).

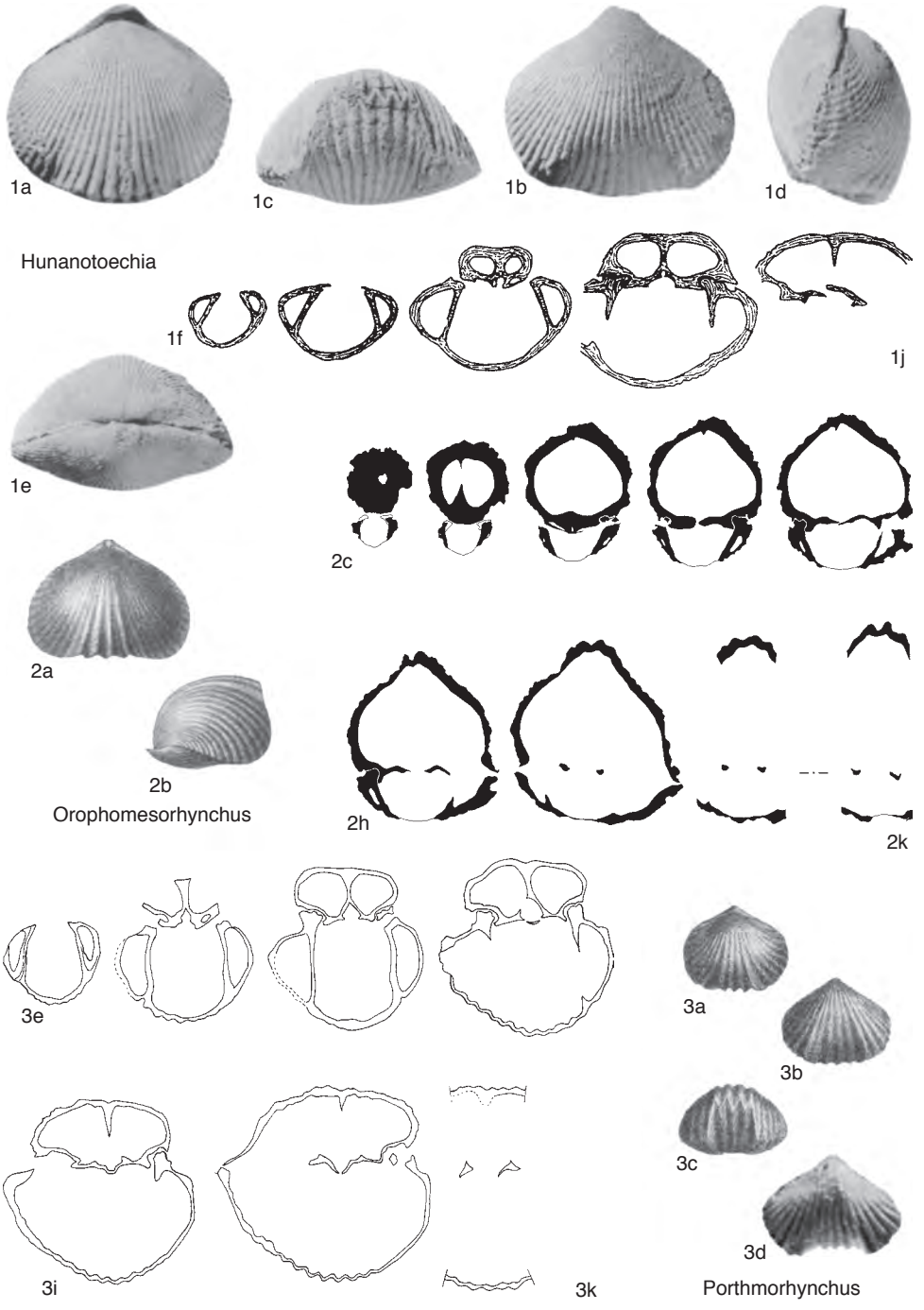

FIG. 1802. Trigonirhynchiidae (p. 2703–2705).

narrow, angular. Dental plates short, convergent ventrally; umbonal cavities narrow; teeth short, stout. Septalium and dorsal median septum lacking; hinge plates thick posteriorly, becoming thinner and almost meeting anteriorly; crural bases subtriangular in section; crura subtriangular in section proximally, becoming crescentic distally with convex surface dorsal. *Upper Devonian (lower Famennian):* European Russia.——Fig. 1802,*2a–k. *O. huotinus* (de Verneuil), Zadonsk beds, Horizon, Middle and Late *Palmatolepis triangularis* and *crepida* Zones, town of Zadonsk, left bank of River Don, Central Devonian Field; *a–b*, dorsal and lateral views, ×1 (de Verneuil, 1845); *c–k*, topotype, serial sections 1.15, 1.5, 2.2, 2.6, 3.1, 3.4, 4.05, 4.4, 5.25 mm from posterior, ×1.6 (Sartenaer, 2001).

Paropamisorhynchus Sartenaer, 2001, p. 201 [**Ripidiorhynchus* (?) *kotalensis* Brice, 1971, p. 38; OD]. Medium to large size; subcircular to subpentagonal outline; strongly dorsibiconvex profile. Ventral beak slightly incurved. Strong fold and sulcus arising close to beaks; anterior commissure uniplicate; tongue high, rounded, dentate. Costae strong, simple, angular with rounded crests, arising at beaks, some parietal costae present. Dental plates strong, convergent ventrally; teeth stout. Dorsal median septum high, extending well past hinge area; septalium short, with cover plate anteriorly; hinge plates united; crura subtriangular in section proximally, convex ventrolaterally in section distally. *Upper Devonian (middle Frasnian, ?lower Famennian):* Afghanistan.——Fig. 1803,*1a–p. *P. kotalensis* (Brice), Ghouk, bed 1 in Brice, 1971, west-central Afghanistan; *a–e,* holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1; *f–n*, topotype, serial sections 0.25, 0.65, 0.8, 0.9, 1.15, 1.4, 1.5, 1.75, 2.4 mm from posterior, ×3; *o–p*, paratype, serial sections 5.0, 6.1 mm from posterior, scale not given, copied at ×0.5 (Brice, 1971).

Piridiorhynchus Sartenaer, 2001, p. 192 [**P. confinium*; OD]. Medium size; subpentagonal outline; strongly biconvex to inflated profile. Beak erect to incurved; deltidial plates observed in sections. Fold and sulcus strong, narrow, extending from umbones; anterior commissure uniplicate; tongue high, rounded. Costae medium, angular with rounded top, simple, from beaks; parietal costae commonly present. Dental plates short, slightly convergent ventrally; teeth short, stout. Hinge plates short, divided, horizontally flattened; septalium small; dorsal median septum slender, high posteriorly, extending one-third valve length; crura rodlike proximally, convex ventrolaterally in section, slightly curved toward ventral valve distally. *Upper Devonian (lowermost Famennian):* Belgium, Russia.——Fig. 1803,*4a–o. *P. confinium*, Early *Palmatolepis triangularis* Zone, Sinsin, near Aye, Belgium; *a–e*, holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1; *f–o*, paratype, serial sections 1.05, 1.4, 1.7, 2.0, 2.45, 2.55, 2.85, 4.4, 4.8, 5.2 mm from posterior, ×1.6 (Sartenaer, 2001).

Poleomesorhynchus Sartenaer, 2001, p. 206 [**Camarotoechia gregeri* Branson, 1923, p. 91; OD]. Small to medium size with subtriangular to subpentagonal outline and dorsibiconvex profile. Ventral beak suberect to erect. Fold and sulcus strong, arising at umbones; anterior commissure uniplicate; tongue high, rounded, dentate. Costae distinct, simple, arising at beaks, angular with rounded crests; parietal costae present. Dental plates vertical, extending to hinge area; umbonal cavities large; teeth stout. Dorsal median septum low and thick, extending well past hinge area; hinge plates undivided; septalium deep, short, with cover plate; crura suboval proximally, convex ventrolaterally in section distally. *Upper Devonian (lower Frasnian)*: North America.——Fig. 1803,*3a–o. *P. gregeri* (Branson), Snyder Creek Shale, Cow Creek, Calloway County, central Missouri; *a–b*, topotype, dorsal and lateral views, ×1.1; *c,* second topotype, ventral view, ×1.1; *d–e*, third topotype, dorsal and lateral views, ×1.1 (Branson, 1923); *f–o*, topotype, serial sections 1.5, 1.75, 2.0, 2.25, 2.35, 2.55, 2.75, 2.9, 3.15, 3.3 mm from posterior, ×3.25 (Sartenaer, 2001).

Porthmorhynchus Sartenaer, 2001, p. 200 [**Rhynchonella ferquensis* Gosselet, 1887, p. 199; OD] [=*Hypselororhynchus* Sartenaer, 2001, p. 199 (type, *Ripidiorhynchus farsani* Brice in Brice & Farsan, 1977, p. 227, OD)]. Small to medium size with subpentagonal outline and dorsibiconvex profile. Ventral beak suberect to erect. Fold and sulcus strong, extending from near beaks; anterior commissure uniplicate; tongue high, trapezoidal, dentate. Costae strong, simple, angular with rounded crests, arising at beaks; parietal costae rarely present. Dental plates vertical, subparallel, short; umbonal cavities distinct; teeth stout. Dorsal median septum short, low; hinge plates separated by short, moderately deep septalium; cover plate present anteriorly; crura triangular in cross section proximally. *Upper Devonian (middle Frasnian–upper Frasnian):* Europe, Iran, Afghanistan.——Fig. 1802,*3a–k. *P. ferquensis* (Gosselet), middle Frasnian, Boulonnais, northern France; *a–c,* hypotype, dorsal, ventral, and anterior views, Massif d'Hestrud, Hestrud, ×1 (Gosselet, 1887); *d,* lectotype, ventral view, Calcaire de Ferques, Ferques, ×1; *e–k,* paratype, serial sections 0.65, 1.15, 1.4, 1.55, 1.75, 1.9, 2.1 mm from posterior, Calcaire de Ferques, Ferques, ×3 (Brice & Meats, 1972).

Saxulirostrum Sartenaer, 2001, p. 203 [**Rhynchonella (Stenocisma) contracta* var. *saxatilis* Hall, 1867, pl. 54A,*44–48;* OD] [=*Kedridorhynchus* Sartenaer, 2001, p. 199 (type, *Camarotoechia cedarensis* Stainbrook, 1942, p. 611, OD)]. Small with subpentagonal outline and dorsibiconvex profile. Ventral beak suberect to erect. Fold and sulcus strong, wide, arising at umbones; anterior commissure uniplicate, tongue high, dentate.

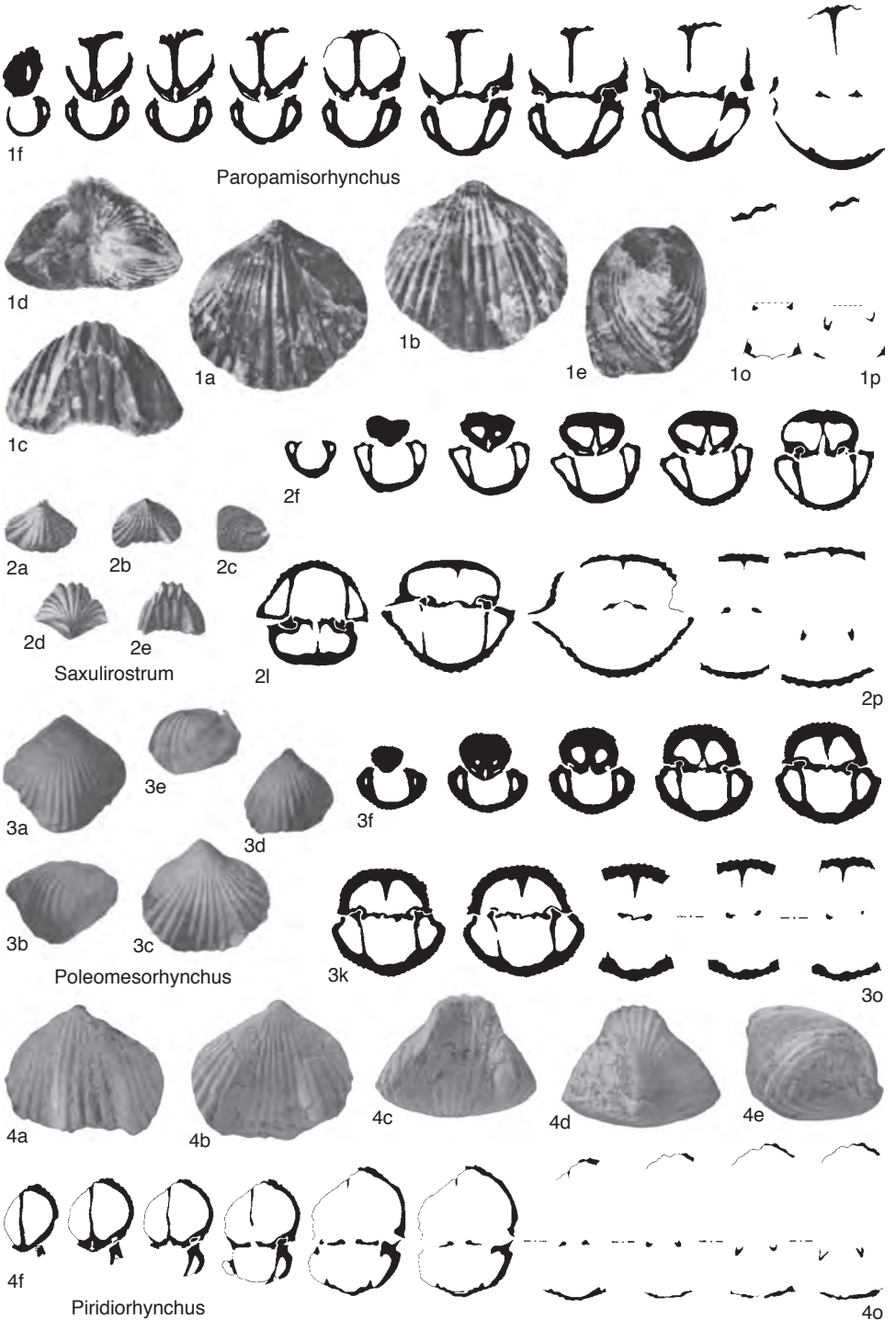

FIG. 1803. Trigonirhynchiidae (p. 2705–2707).

Costae strong, few, arising at beaks, angular with rounded crests, present on fold, sulcus, and flanks. Dental plates well developed, extend past hinge area, subvertical to slightly convergent ventrally; umbonal cavities large; teeth stout. Dorsal median septum short, low; septalium deep; hinge plates undivided; crura rodlike proximally in section, then V-shaped, then crescentic distally. *Upper Devonian (upper Frasnian)*: North America.——Fig. 1803,*2a–p. *S. saxatile* (Hall), Lime Creek Formation, Cerro Gordo Member, Rockford, Floyd County, Iowa; *a–e*, lectotype, dorsal, ventral, lateral, posterior, and anterior views, ×1 (Hall, 1867); *f–p*, topotype, serial sections 0.55, 1.0, 1.05, 1.15, 1.2, 1.4, 1.55, 1.75, 1.95, 2.0, 2.6 mm from posterior, ×4.4 (Sartenaer, 2001).

Superfamily UNCINULOIDEA Rzhonsnitskaia, 1956

Family HEBETOECHIIDAE Havlíček, 1960

Subfamily HEBETOECHIINAE Havlíček, 1960

Cerveratoechia García-Alcalde, 1998, p. 774 [**Hebetoechia cantabrica* Binnekamp, 1965, p. 25; OD]. Medium size; subpentagonal to subcircular outline with length slightly greater than width; equibiconvex to subglobular. Beak erect; foramen with disjunct deltidial plates. Dorsal fold and ventral sulcus arising at about one-third valve length; umbones smooth; tongue strong, rectangular; costae broad, angular, but with rounded crests, 3 or 4 on fold, 2 or 3 in sulcus, 4 or 5 on flanks; anterior commissure dentate with short marginal spines; squamae and glottae well developed. Dental plates short, slightly convergent ventrally; teeth small. Dorsal median septum high, septalium small, with short cover plate; calluslike cardinal process developed in more mature specimens; crural bases triangular in section; crura closely set, laterally flattened. Muscle fields well impressed. *Lower Devonian:* Spain, ?North Africa.——Fig. 1804,*2a–l. *C. cantabrica* (Binnekamp), Lochkovian, Lebanza Formation, Cantabrian Mountains, Dominio Palentino, northern Spain; *a–d*, holotype, dorsal, ventral, anterior, and lateral views, ×2; *e–l*, serial sections 0.5, 1.1, 1.45, 2.1, 2.45, 3.85, 4.1, 4.4 mm from posterior of young specimen, ×1.5 (García-Alcalde, 1998).

Lebanzuella García–Alcalde, 1999, p. 250 [**Uncinulus lebanzus* Binnekamp, 1965, p. 24; OD]. Medium size; subpentagonal outline; equibiconvex to subglobular; beak suberect; foramen with deltidial plates; dorsal fold and ventral sulcus arising at about one-third valve length; umbones smooth; tongue strong, rectangular; costae broad, angular but with rounded crests, 3 to 5 on fold, 2 to 4 in sulcus, 7 to 8 on flanks; anterior commissure dentate with short marginal spines; squamae and glottae well developed. Dental plates short, slightly convergent ventrally; teeth stout. Dorsal median septum moderately high, septalium small; multilobed cardinal process with about 6 thin lobes separated medially by groove; crural bases triangular in section; crura closely set, horizontally flattened proximally, laterally flattened distally. Muscle fields well impressed with low median myophragm in each valve. *Lower Devonian (Pragian):* Spain.——Fig. 1804,*1a–l. *L. lebanza* (Binnekamp), Lebanza Formation, Cantabrian Mountains, northern Spain; *a–d*, holotype, dorsal, ventral, lateral, and anterior views, top, Member E, of Lebanza Formation, Lebanza village, ×1 (Binnekamp, 1965); *e–l*, serial sections 0.9, 1.75, 2.05, 2.6, 2.95, 3.15, 4.1, 5.5 mm from posterior of hypotype from Member E of Lebanza Formation, Lebanza village; *e–h,* ×6, *i–l,* ×3 (García-Alcalde, 1999).

Family INNAECHIIDAE Baranov, 1980

[Innaechiidae Baranov, 1980, p. 78; *emend.,* Savage, herein]

Uncinuloidea lacking cardinal process, septalium absent or very small. *upper Silurian (Ludlow)–Middle Devonian (Eifelian).*

Subfamily INNAECHIINAE Baranov, 1980

[*nom. transl.* Savage, 1996, p. 253, *ex* Innaechiidae Baranov, 1980, p. 78]

Innaechiidae with median septum; dental plates very short. *Lower Devonian (Lochkovian–Pragian).*

Dubovikovia Baranov in Alekseeva & others, 1996, p. 82 [**Hebetoechia settedabanica* Rzhonsnitskaia in Alekseeva, 1967, p. 48; OD]. Small with transversely subpentagonal outline; dorsibiconvex profile, anteriorly inflated. Beak erect. Fold and sulcus developed anteriorly; tongue high, rectangular. Costae simple, developed from about midlength, flattened and grooved on *paries geniculatus;* marginal spines present. Dental plates short, slightly convergent ventrally; teeth very short. Dorsal median septum high, thin, extending about one-quarter valve length; hinge plates divided anterior of very short septalium; crural bases inclined mediodorsally; crura rodlike proximally, laterally flattened distally. *Lower Devonian (Lochkovian–Pragian):* eastern Siberia.——Fig. 1805,*1a–i. *D. settedabanica* (Rzhonsnitskaia), Lochkovian, lower part of Settedaban Formation, Sette-Daban Range, Tikhiy Creek; *a–d*, holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–i*, serial sections, intervals and distance from posterior not given, reoriented, ×3 (Alekseeva, 1967).

Family HYPOTHYRIDINIDAE Rzhonsnitskaia, 1956

Tullypothyridina Sartenaer, 2003, p. 31 [**Rhynchonella venustula* Hall, 1867, p. 346; OD]. Medium

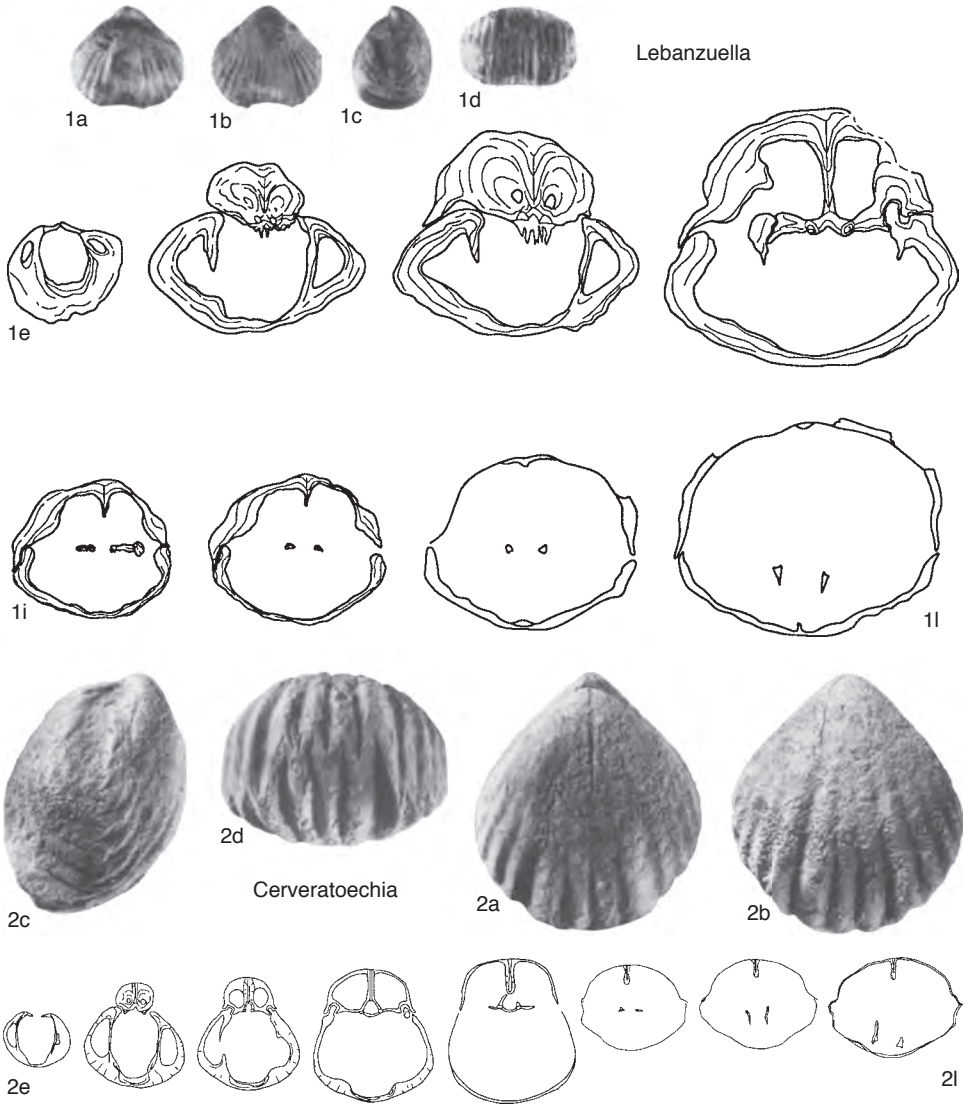

FIG. 1804. Hebetoechiidae (p. 2707).

to large; subcuboidal with subcircular outline and strongly dorsibiconvex profile; lateral and anterior margins steep to vertical. Ventral beak erect to incurved. Fold and sulcus weak, becoming most evident anteriorly; tongue very high, rectangular to rounded. Costae numerous, simple or rarely divided, arising at beaks, flattened and bearing median grooves from about midlength and especially on tongue; marginal spines developed. Dental plates short, slender, ventrally convergent; teeth small, short. Dorsal median septum and septalium absent; hinge plates divided, horizontal; cardinal process comprising distinct central ridge and several thin flanking growths; crura closely set, flattened horizontally, short, delicate. *Middle Devonian (upper Givetian)*: North America.——FIG. 1805,*2a–p*. **T. venustula* (HALL), Tully Limestone, Apulia Member, June's quarry, central New York; *a*, lectotype, anterior view, ×1 (Hall, 1867); *b–f*, topotype, dorsal, ventral, posterior, anterior, and lateral views, ×1; *g–p*, topotype, serial sections 0.95, 1.25, 1.325, 1.4, 1.55, 1.75, 1.95, 2.1, 2.25, 2.5 mm from posterior, ×2.3 but with enlargements (×4.6) of the cardinal process shown within sections *h–j* (Sartenaer, 2003).

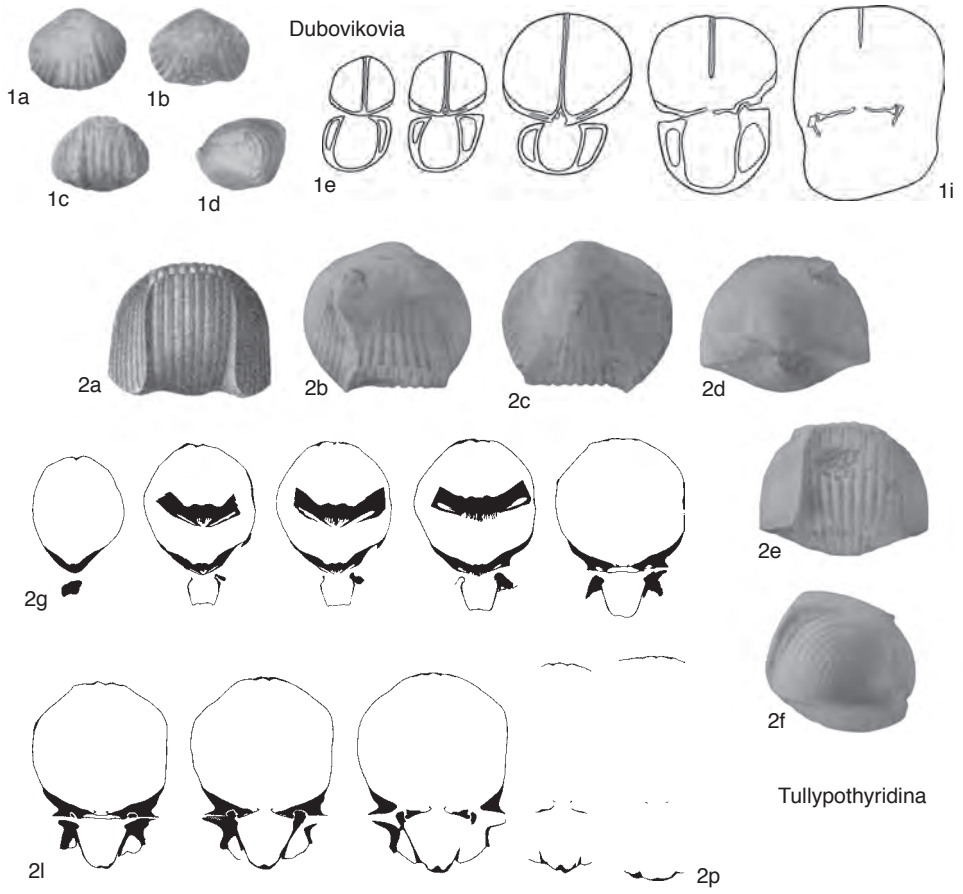

FIG. 1805. Innaechiidae and Hypothyridinidae (p. 2707–2708).

Superfamily CAMAROTOECHIOIDEA Schuchert, 1929
Family LEIORHYNCHIDAE Stainbrook, 1945
Subfamily LEIORHYNCHINAE Stainbrook, 1945

Azurduya CISTERNA & ISAACSON, 2003, p. 65 [**Camarotoechia chavelensis* AMOS, 1958, p. 839; OD]. Medium size, subtriangular to subpentagonal outline with width and length about equal; dorsibiconvex profile; lateral and anterior slopes gentle. Beak suberect. Dorsal fold and ventral sulcus developed only anteriorly. Simple subangular costae arising at umbones, 7–8 on fold and sulcus, up to 8 on flanks. Anterior commissure uniplicate. Dental plates anteriorly divergent, reaching up to one-fifth of valve length; teeth small, smooth, rounded. Dorsal median septum long, reaching one-third to half valve length; short septalium uniting hinge plates; dorsal muscle scars subrhomboidal in outline; crura unknown. *Lower Carboniferous (Tournaisian):* Argentina.——FIG. 1806,*1a–g*. **A. chavelensis* (AMOS), lower part of Malimán Formation, Cortaderas Creek, about 5 km northeast of Malimán, San Juan province; *a–e*, neotype, dorsal, ventral, lateral, posterior, and anterior views, ×2; *f–g*, topotypes, internal mold of ventral valve, and dorsal view of internal mold of articulated specimen, ×2 (Cisterna & Isaacson, 2003).

Sphaeridiorhynchus SARTENAER, PUSHKIN, & KOTLYAR, 1997, p. 39 [**S. kuzmichiensis*; OD]. Small to medium size; globular; subcircular outline and inflated, dorsibiconvex profile. Beak wide, slightly incurved, with small foramen; deltidial plates evident in sections. Fold and sulcus low, only visible anteriorly; anterior commissure uniplicate; tongue low. Median costae very weak; lateral costae absent. Dental plates lacking; teeth simple, short. Hinge plates short, divided; median septum and septalium absent; long crura closely set, oval to

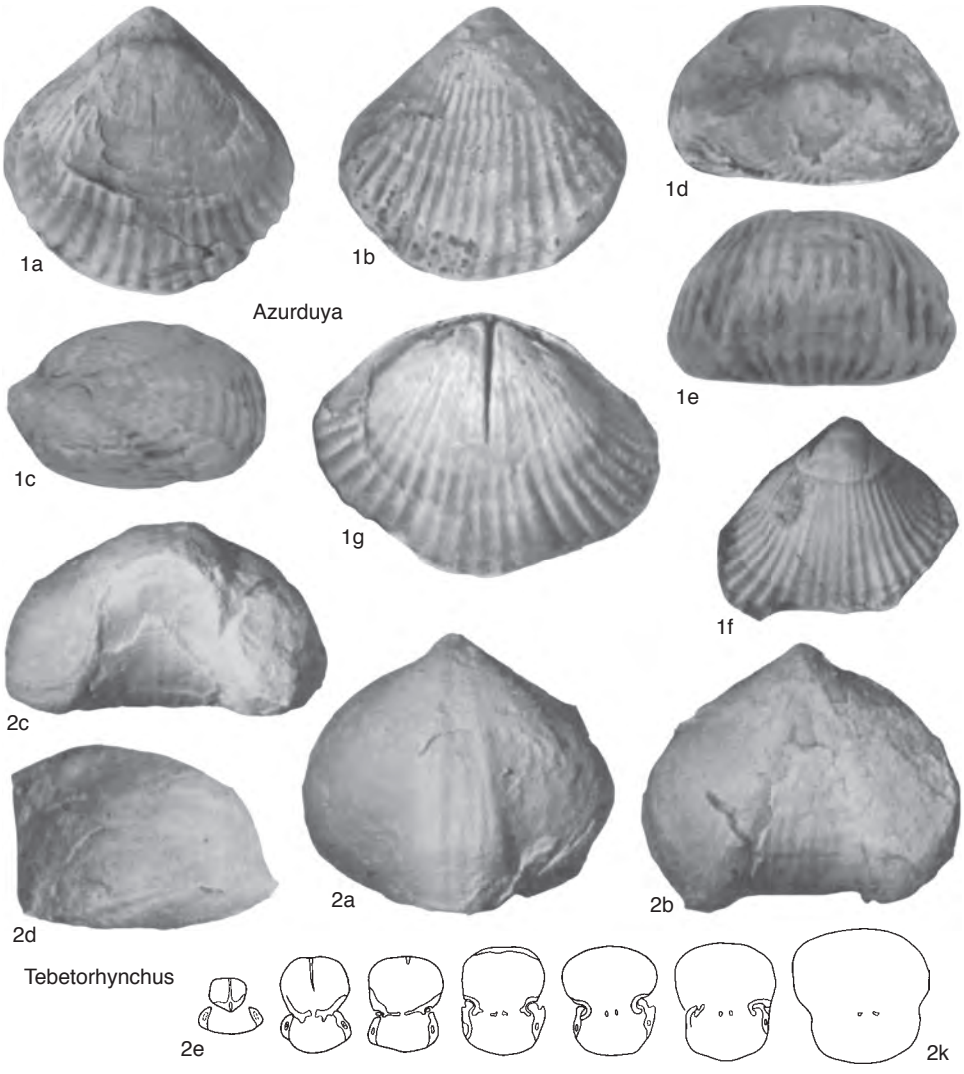

FIG. 1806. Leiorhynchidae (p. 2709–2710).

rounded in cross section. *Upper Devonian (lower Famennian):* Belarus, Ukraine.——FIG. 1807*a–n*. **S. kuzmichiensis*, Kuz'michi 1 borehole, Kuz'michi village, Pripyat Depression, near Minsk, Belarus; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, ×1; *f–n,* paratype, serial sections 1.15, 1.25, 1.45, 1.7, 1.9, 2.3, 2.5, 2.85, 4.3 mm from posterior, ×2.15 (Sartenaer, Pushkin, & Kotlyar, 1997).

Tebetorhynchus BARANOV in ALEKSEEVA & others, 1996, p. 74 [**T. abramovi*; OD]. Large; subcircular to transversely ovate outline; dorsibiconvex profile. Beak suberect. Fold and sulcus arising at umbones; anterior commissure uniplicate with high, rounded tongue. Costae very weak, restricted to fold and sulcus. Dental plates short; close to valve walls. Dorsal median septum short, low; septalium very short to absent; hinge plates divided; crura closely set, rodlike proximally, unknown distally. *Lower Devonian (Emsian):* northeastern Russia.——FIG. 1806,*2a–k*. **T. abramovi*, Khobochalinska Formation, *Ivdelinia ivdelensis* Zone, lower Emsian, right bank lower reaches of Tebeti River, Tas-Khayakhtakh; *a–d*, holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–k*, paratype, serial sections 0.5, 1.9, 2.9, 3.8, 4.1, 4.6, 5.7 mm from posterior, scale not given (Alekseeva & others, 1996).

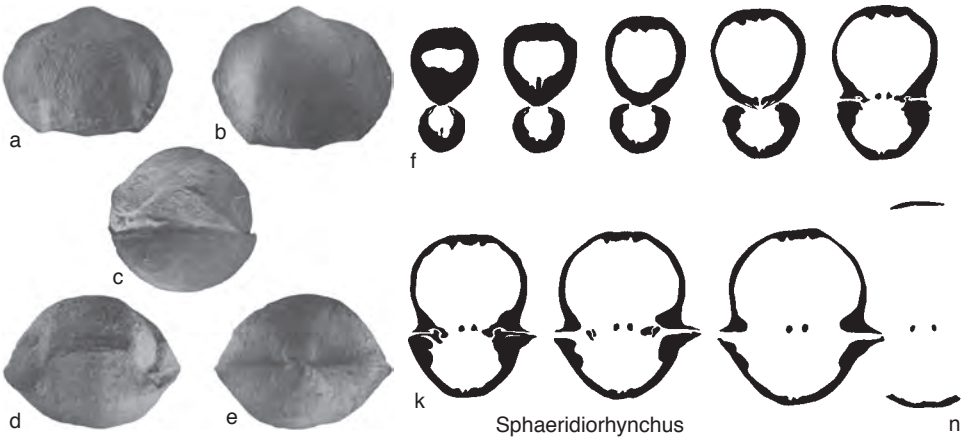

FIG. 1807. Leiorhynchidae (p. 2709–2710).

Subfamily CALVINARIINAE Sartenaer, 1994

Tchernarhynchia TCHERKESOVA, 1998, p. 44 [**T. dichotoma*; OD]. Medium to large size, with transversely ovate to subpentagonal outline and dorsibiconvex profile, anteriorly swollen; gentle lateral slopes. Ventral beak incurved, dorsal beak erect. Fold and sulcus strong, arising at umbones; anterior commissure uniplicate; tongue high, rounded, serrate. Costae fine, numerous, angular to rounded, arising at beaks, dichotomizing, strongly developed over whole shell surface. Dental plates short; teeth large. Dorsal median septum high, thin; septalium short, distinct; hinge plates divide just anterior of septalium; crura unknown. *Upper Devonian (middle Frasnian):* Russia.——FIG. 1808,*2a–k*. **T. dichotoma*, upper Zhandr Horizon, Lichutin, Gorbov Islands, Novaya Zemlya; *a–e*, holotype, dorsal, ventral, lateral, posterior, and anterior views, ×1; *f–k*, paratype, serial sections, intervals and scale not given (Tcherkesova, 1998).

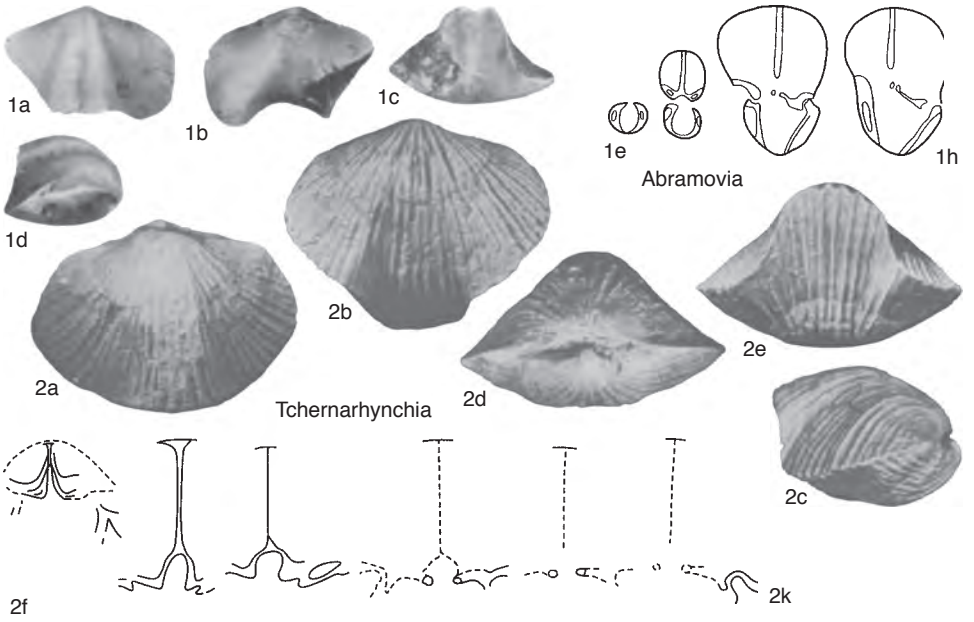

FIG. 1808. Leiorhynchidae (p. 2711–2712).

Subfamily BASILICORHYNCHINAE Savage, 1996

Leiorhynchidae with subcircular outline; high tongue; strong costae. Dental plates and dorsal median septum distinct. [Stratigraphic range emended herein.] *Lower Devonian–Upper Devonian*.

Abramovia Baranov in Alekseeva & others, 1996, p. 76 [**A. pteroidea*; OD]. Medium size; strongly transversely ovate outline with emarginate anterior margin; dorsibiconvex profile modified anteriorly by high fold. Ventral beak erect to incurved. Fold and sulcus arising at umbones and becoming strong anteriorly; fold with median broad groove, and sulcus with median rounded ridge; anterior commissure uniplicate to sulciplicate. Dental plates short, ventrally convergent. Dorsal median septum high, long; septalium short; hinge plates divided anterior of septalium; crura not described. *Devonian (Emsian–Famennian)*: Russia, Alaska.——Fig. 1808,*1a–h. *A. pteroidea*, Emsian, lower part of Krivoy Ruchey Formation, Selennyakh Ridge, right bank of Talyndzha River, upper reaches of Krivoy stream, northeastern Russia; *a–d*, holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–h*, paratype, serial sections, intervals not given, ×3.5 (Alekseeva & others, 1996).

Superfamily PUGNACOIDEA Rzhonsnitskaia, 1956

Family ROZMANARIIDAE Havlíček, 1982

[*nom. transl.* Havlíček, 1990, p. 214, *ex* Rozmanariinae Havlíček, 1982, p. 112; *emend.,* Savage, 1996]

Pugnacoidea with transversely ovate to subcircular outline; fold and sulcus sometimes low, generally fold in dorsal valve but may be in ventral valve; costae weak to absent; foramen with conjunct deltidial plates anteriorly. Dental plates short to absent. Dorsal median septum low or lacking; hinge plates divided; cardinal process absent. *Lower Devonian (Pragian)–Upper Devonian (Famennian)*.

Iphinerrhynx Havlíček & Vaněk, 1998, p. 72 [**I. iphinoe*; OD]. Small; subpentagonal to rounded outline; ventribiconvex profile. Beak incurved; ventral fold and dorsal sulcus wide, poorly differentiated; anterior commissure unisulcate; both valves smooth or with barely visible undulations. Dental plates short, thin, almost vertical or slightly divergent toward valve floor. Hinge plates divided; dorsal median septum lacking; crural bases and crura not recorded. *Lower Devonian (Pragian):* Czech Republic.——Fig. 1809,*1a–e. *I. iphinoe*, Slivenec Limestone, Kacak valley south of Hostim, Prague Basin, Bohemia; *a–c*, holotype, dorsal, ventral, and anterior views, ×5; *d–e*, serial sections 6.5, 6.0 mm from anterior, ×8 (Havlíček & Vaněk, 1998).

Leptoterorhynchus Sartenaer, 1998, p. 121 [**Rozmanaria magna* Biernat & Racki, 1986, p. 90; OD]. Transversely ovate outline and equibiconvex, lenticular profile. Beak wide, suberect to erect; may be resorbed by small foramen. Low ventral fold and shallow dorsal sulcus; anterior commissure unisulcate. Costae lacking. Dental plates short, rudimentary; teeth short and stout; ventral muscle field with distinct diductor scars enclosing elongate adductor scars. Hinge plates short, divided; septalium and dorsal median septum absent; crura laterally compressed with distal ends curved ventrally. *Upper Devonian (Famennian):* Poland, Germany.——Fig. 1809,*2a–l. *L. magnus* (Biernat & Racki), middle Famennian, Wola Quarry, Kowala, Holy Cross Mountains, Poland; *a–d*, holotype, dorsal, ventral, anterior, and lateral views, ×2 (Biernat, 1988); *e–l*, topotype, serial sections 0.4, 0.7, 0.9, 1.15, 1.25, 1.45, 1.8, 2.6 mm from posterior, ×2.2 (Sartenaer, 1998).

Novaplatirostrum Sartenaer, 1997, p. 27 [**N. sauerlandense*; OD]. Medium size shell. Subcircular outline and flattened, equibiconvex, lenticular profile. Beak erect to slightly incurved, in contact with dorsal posterior; foramen or delthyrium unknown. Low, wide dorsal fold and shallow ventral sulcus arising at about three-quarters shell length; anterior commissure uniplicate, undulate. Costae low, angular with rounded top, most evident anteriorly on fold and in sulcus; most of shell surface smooth. Dental plates rarely visible in thick shell walls; teeth small, wide, strong. Hinge plates divided, flat; dorsal median septum and septalium absent; crural bases stout, subtriangular in section; crura short, convex ventrolaterally, hooked distally. Muscle fields well impressed. *Upper Devonian (Famennian):* Germany.——Fig. 1810,*1a–o. *N. sauerlandense*, upper Famennian, Wocklum Limestone, Hasselbachtal, northwestern Saurerland; *a–e*, holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1 (Sartenaer, 1997); *f–o*, paratype, serial sections 1.0, 1.2, 1.4, 1.6, 1.7, 1.8, 2.25, 2.5, 2.8, 3.0 mm from posterior, ×2.2 (Sartenaer, 1997).

Phacoiderhynchus Sartenaer, 2000, p. 75 [**P. antiatlasicus*; OD]. Large; transversely elliptical outline; equibiconvex, lenticular profile. Beak erect to incurved. Low, wide, dorsal fold and shallow ventral sulcus arising at about two-thirds valve length; anterior commissure uniplicate, undulate. Costae low, angular, arising at about two-thirds shell length, well developed on fold, in sulcus, and also on flanks anterolaterally. Dental plates strong, convergent; teeth short, stout. Divided hinge plates wide, flattened; crural bases subtriangular in section; crura convex ventrolaterally in section, slightly curved distally toward ventral valve. Very short, delicate cardinal process. Dorsal median

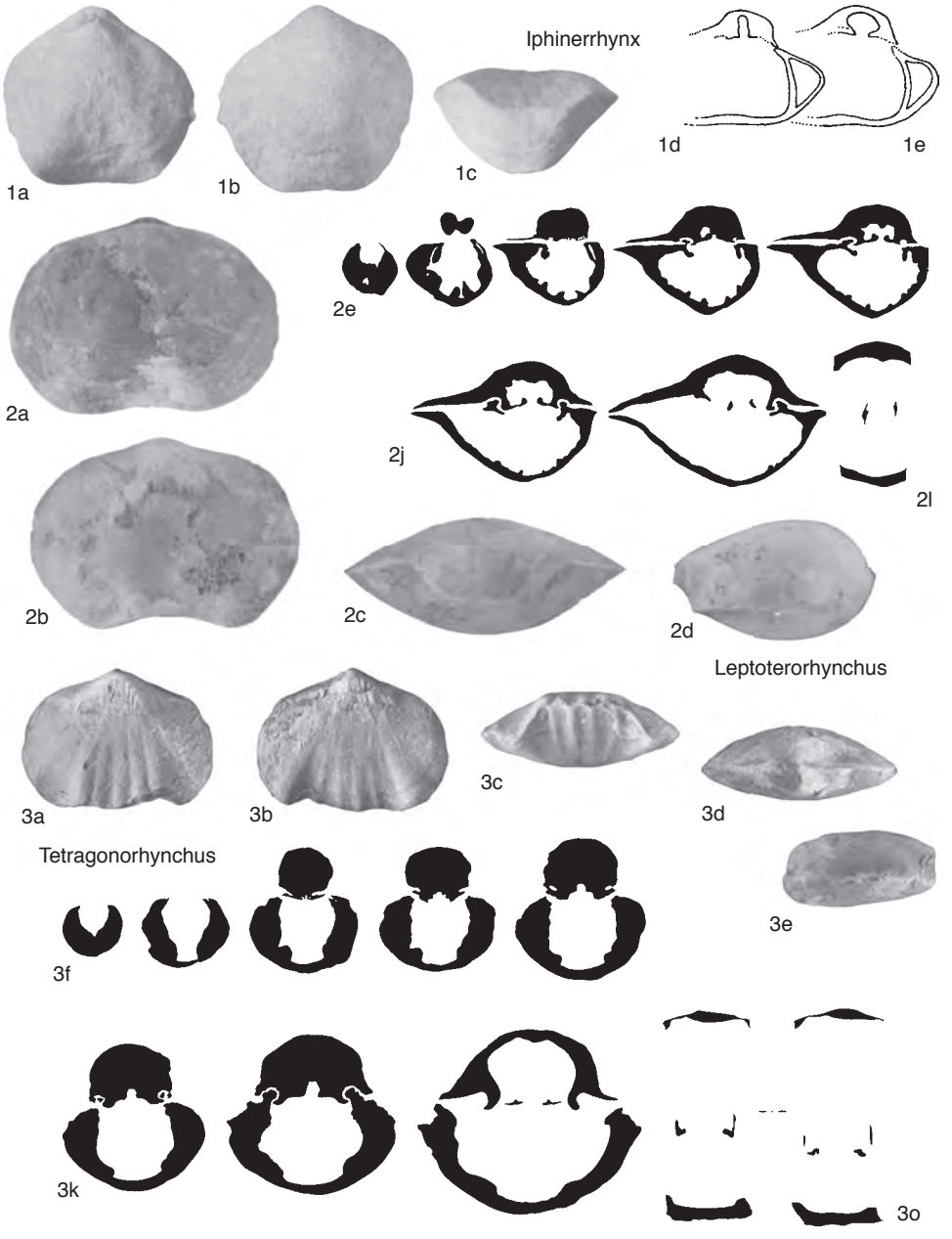

FIG. 1809. Rozmanariidae (p. 2712–2714).

septum absent. Muscle fields well impressed. *Upper Devonian (Famennian):* Morocco.——FIG. 1810,*2a–q*. **P. antiatlasicus*, middle Famennian, Maïder, southern Morocco; *a–e*, holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1; *f–k*, paratype, serial sections 0.75, 0.85, 0.925, 1.05, 1.25, 1.4 mm from posterior, ×2.4; *l–q*, paratype, serial sections 0.8, 1.0, 1.15, 1.55, 2.1, 3.1 mm from posterior, ×2.4 (Sartenaer, 2000).

Tetragonorhynchus SARTENAER, 1999a, p. 67 [**T. mrakibensis*; OD]. Medium size shell; subquadrangular to transversely ovate in outline with an

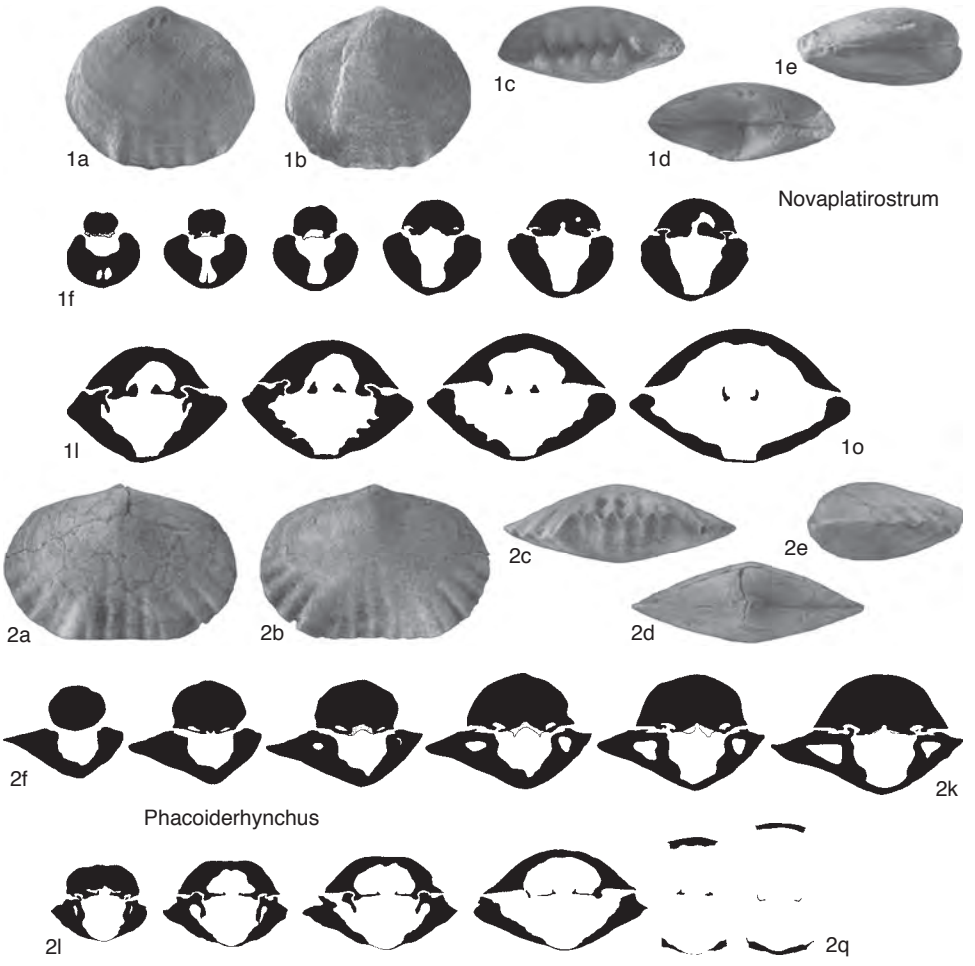

FIG. 1810. Rozmanariidae (p. 2712–2713).

equibiconvex, lenticular profile. Beak erect to incurved and resorbed by circular foramen. Low, wide dorsal fold and shallow ventral sulcus arising at about one-third valve length; faint median depression on fold and corresponding rise in sulcus; anterior commissure uniplicate, undulate. Costae low, rounded, from about midlength; most evident on fold and in sulcus, barely developed on flanks. Dental plates not visible in thick shell wall; teeth short. Divided hinge plates passing into short, flattened crural bases; crura short, ventrally curved at distal ends. Very short, delicate cardinal process visible in serial sections. Dorsal median septum absent. Muscle fields well impressed. *Upper Devonian (Famennian):* Morocco.——FIG. 1809,*3a–o.* **T. mrakibensis*, upper Famennian, upper Ibaoune Formation, Maïder, southern Morocco; *a–e,* holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1; *f–o,* paratype, serial sections 0.7, 1.05, 1.15, 1.31, 1.49, 1.55, 1.85, 2.45, 3.4, 3.9 mm from posterior, ×3.25 (Sartenaer, 1999a).

Family ASEPTIRHYNCHIIDAE Savage, 1996

Polyptychorhynchus SARTENAER, 1999b, p. 79 [**P. cavernosus*; OD]. Very large with transversely elliptical outline and biconvex profile. Ventral beak small, incurved; delthyrium with deltidial plates. Fold and sulcus wide, well marked, fold gently convex, sulcus strong anteriorly; anterior commissure uniplicate, tongue pronounced, trapezoidal. Flanks of both valves convex. Costae strong on fold and in sulcus, simple, arising at umbones, with rounded tops; costae on flanks arising at about midlength, wide, rounded. Shell thick, especially posteriorly. Dental plates short and mostly buried in shell wall; teeth stout, short,

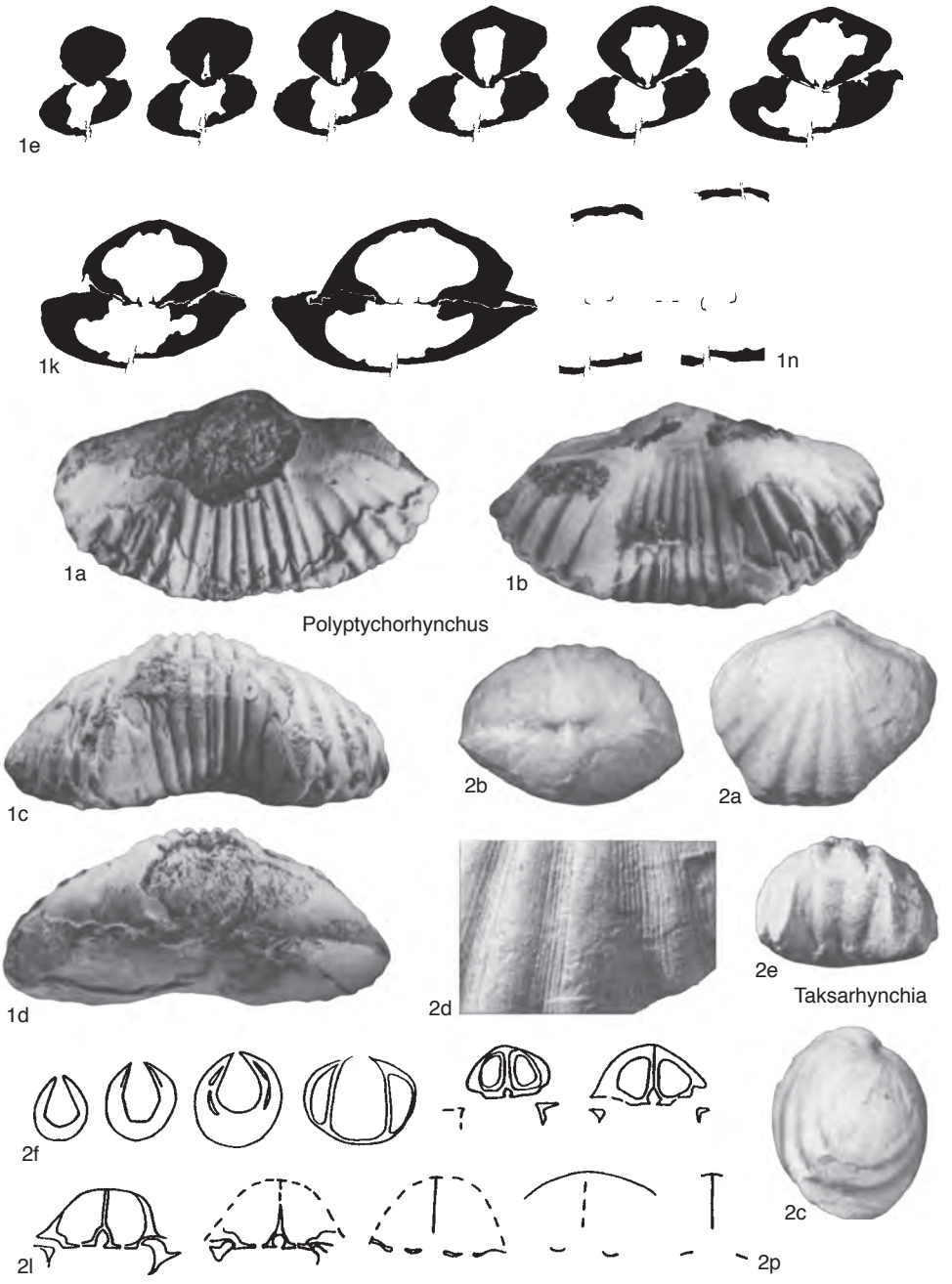

FIG. 1811. Aseptirhynchiidae and Yunnanellidae (p. 2714–2716).

wide; ventral muscle field well impressed. Dorsal median septum absent; hinge plates divided, subhorizontal, with short, wide sockets and low inner socket ridges; crural bases horizontal; crura subtriangular in cross section, distal parts curving ventrally, inner surfaces concave. *Upper Devonian (Famennian):* northwestern Australia.——FIG. 1811,*1a–n*. **P. cavernosus*, middle Famennian, Middle to Late *Marginifera* Zones, near Casey Falls, Virgin Hills Formation, Emanual Range,

Canning Basin, Western Australia; *a–d,* paratype, dorsal, ventral, anterior, and posterior views, ×1; *e–n,* serial sections 1.9, 2.2, 2.4, 2.7, 2.8, 3.0, 3.3, 3.9, 5.1, 6.4 mm from posterior, ×2 (Sartenaer, 1999b).

Family YUNNANELLIDAE Rzhonsnitskaia, 1959

Taksarhynchia TCHERKESOVA, 1997, p. 48 [**T. sobolevi*; OD]. Medium to large; subpentagonal outline with greatest width near hinge line; dorsibiconvex profile. Ventral beak incurved. Fold and sulcus strong, arising at umbones. Anterior commissure uniplicate, tongue high, typically tridentate. Costae coarse, angular with rounded crests, arising at umbones. Whole shell surface bearing fine radial striae. Dental plates short, subvertical. Dorsal median septum high, thin, extending anterior of hinge area. Septalium short; hinge plates horizontal, divided anterior of septalium; crural bases horizontal; crura horizontal proximally, unknown distally. *Upper Devonian (upper Famennian):* Russia.——FIG. 1811,*2a–p. *T. sobolevi*, Taksagerbei unit, Yurtaraga River, Taksa Range, central Taimyr, Russia; *a–c*, holotype, dorsal, posterior, and lateral views, ×1; *d*, holotype, striae, ×3; *e,* paratype, anterior view; *f–p*, same paratype, serial sections, intervals and distances from posterior and scale not given (Tcherkesova, 1997).

STENOSCISMATOIDEA

SANDRA J. CARLSON

[University of California, Davis]

Superfamily STENOSCISMATOIDEA Oehlert, 1887 (1883)
Family PSILOCAMARIDAE Grant, 1965
Subfamily PSILOCAMARINAE Grant, 1965

Bicamella WATERHOUSE, 2004, p. 88 [**Camarophoria timorensis* HAYASAKA & GAN, 1940, p. 129; OD]. Medium-sized shells, typically wider than long; outline subtriangular; weakly to strongly uniplicate; rounded to sharp costae, variable in number and intercalation style, commonly absent on valve flanks and near umbos, may be present on entire valve; beak prominent, incurved over delthyrium; delthyrium apparently open but constricted by dorsal valve; valve edges nonoverlapping; stolidium present; spondylium duplex supported by high median septum; hinge plate divided, very short but broad posteriorly, extending anterolaterally on each side of small, narrow, steep-sided camarophorium; intercamarophorial plate absent; cardinal process small; crura unknown. Similar to *Stenoscisma* externally and *Camarophorinella* internally but with stolidium. *Permian (?Artinskian):* Timor.——FIG. 1812,*1a–d. *B. timorensis* (HAYASAKA & GAN), Besleo Beds; *a,* ventral valve exterior, ×1; *b,* articulated valves, lateral view, ventral on left, ×1; *c,* dorsal valve exterior, ×1 (Hayasaka & Gan, 1940); *d,* section near posterior end of specimen, ventral valve below, ×1 (Broili, 1916).

Neopsilocamara SHEN & others, 2000, p. 747 [**N. laevis*; OD]. Medium-sized, smooth, thick shells; weakly to moderately dorsibiconvex; outline subcircular; commissure rectimarginate; beak prominent, incurved over delthyrium; delthyrium apparently open but constricted by dorsal valve; valve edges nonoverlapping; stolidium unknown; well-developed spondylium duplex supported by low median septum extending anterior to spondylium; intercamarophorial plate absent; cardinal process unknown; crura unknown. Similar to *Camarophorinella* but lacking costae and fold and sulcus; similar to *Psilocamara* but not uniplicate and not strongly dorsibiconvex. *Upper Permian (Wuchiapingian [lower Tatarian]):* China (Tibet).——FIG. 1812,*2a–e. *N. laevis*, Selong Group, Selong Xishan section; *a,* ventral valve exterior, ×1.5; *b,* posterior view, dorsal valve above, ×1.5; *c–e,* serial sections 0.54, 1.80, 2.29 mm from posterior end of specimen, dorsal valve above, ×2.5 (Shen & others, 2000).

Subfamily CYROLEXINAE Carlson, 2002

Careoseptum CARTER & POLETAEV, 1998, p. 139 [**C. septentrionalis*; OD]. Valves small, rounded pentameral in outline, strongly dorsibiconvex, smooth, strongly uniplicate, rarely weakly sulciplicate; valve edges nonoverlapping; beak short, erect to incurved; stolidium not apparent; delthyrium apparently open but constricted by dorsal valve; spondylium sessile posteriorly, elevated on low septum or more commonly free anteriorly; camarophorium supported by median septum only in extreme posterior, otherwise free; intercamarophorial plate absent; cardinal process unknown; crura unknown. *Upper Carboniferous (lower Moscovian):* Arctic Canada (northern Ellesmere Island).——FIG. 1812,*3a–k. *C. septentrionalis*, Hare Fiord Formation, Hare Fiord; *a,* ventral valve exterior, ×2; *b,* articulated valves, anterior view, ventral below, ×2; *c,* articulated valves, lateral view, ventral on right, ×2; *d,* dorsal valve exterior, ×2; *e–k,* serial sections 1.4, 1.7, 1.8, 2.0, 2.4, 2.6, 3.0 mm from posterior end of specimen, ventral valve above, ×4 (Carter & Poletaev, 1998).

Family STENOSCISMATIDAE Oehlert, 1887 (1883)
Subfamily STENOSCISMATINAE Oehlert, 1887 (1883)

Liufaia WATERHOUSE, 2004, p. 84 [**Stenoscisma tetricum* GRANT, 1976, p. 185; OD]. Medium-sized shells; elongated, narrow triangular outline, maximum shell width near anterior margin; numerous, subequal costae may be absent from umbo or straight lateral flanks or present on entire valve, commonly bifurcating or intercalating, may be simple; commissure rather weakly uniplicate; valve edges between beak and stolidium smooth, flattened, with dorsal valve strongly overlapping ventral; stolidium present on both valves but discontinuous between fold and flanks; nature of delthyrium unclear; deep spondylium sessile, supported anteriorly only by very low median septum; intercamarophorial plate extending beyond anterior edge of hinge plate, may be buried in gerontic shell material; hinge plate flat, broad, narrowing distally; crura present, similar to *Stenoscisma*; cardinal process wedge shaped, with apex pointing posteriorly. Similar to *Stenoscisma* overall, but with triangular valve outline, costae that branch and intercalate, and weak uniplication. *Lower Permian (upper Artinskian):* Thai-

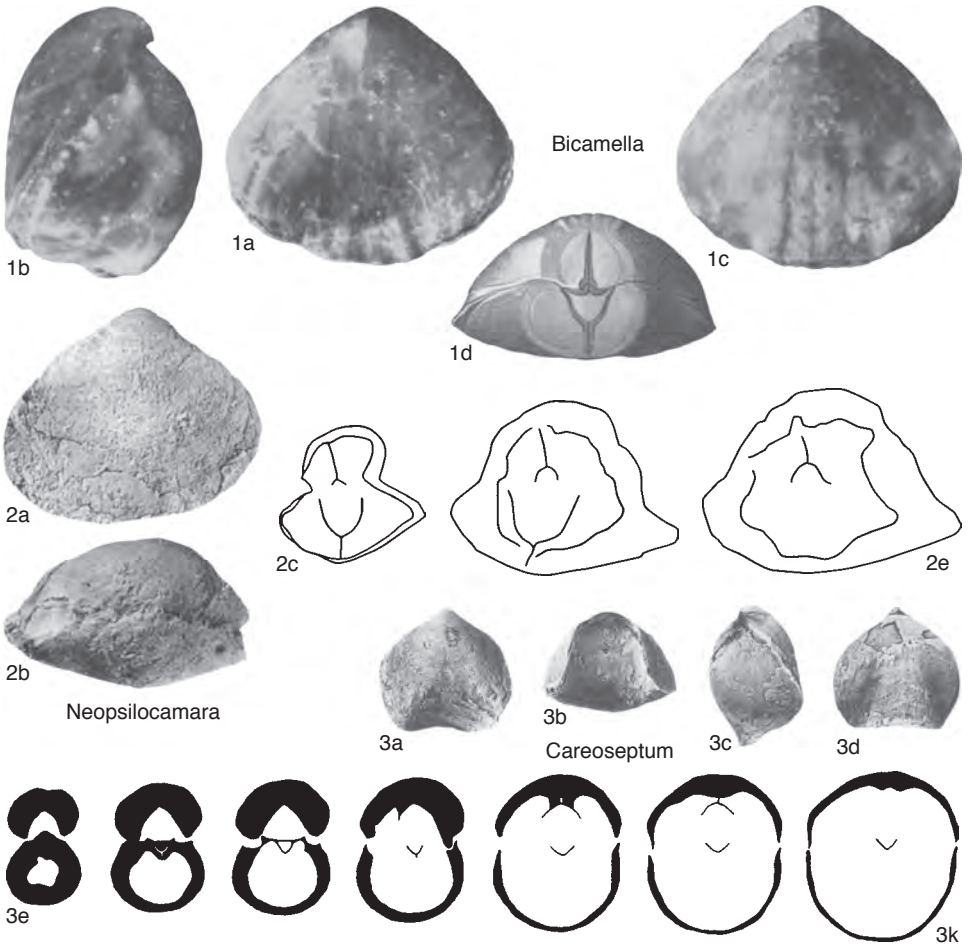

FIG. 1812. Psilocamaridae (p. 2717).

land, South Primoyre, Ussuriland, Japan, Inner Mongolia, northeastern China.——FIG. 1813,*1a–g.* **L. tetricum* (GRANT), Rat Buri Limestone, Ko Muk locality, southern Thailand; *a,* ventral valve exterior, ×1; *b,* articulated valves, lateral view, ventral on left, camarophorium and spondylium visible through broken exterior, ×1; *c,* articulated valves, anterior view, ventral below, stolidium visible, ×1; *d,* dorsal valve exterior, ×1; *e,* ventral valve interior, ×2; *f,* dorsal valve interior, ×1; *g,* detached camarophorium with crura and part of septum below, ×2 (Grant, 1976).

Sedecularia WATERHOUSE, 2004, p. 82 [**Stenoscisma glabra* WATERHOUSE in WATERHOUSE & BRIGGS, 1986, p. 67; OD]. Small- to medium-sized smooth shells; outline oval to subrounded; valves only weakly dorsibiconvex; commissure weakly uniplicate to rectimarginate; extent of valve edge overlap

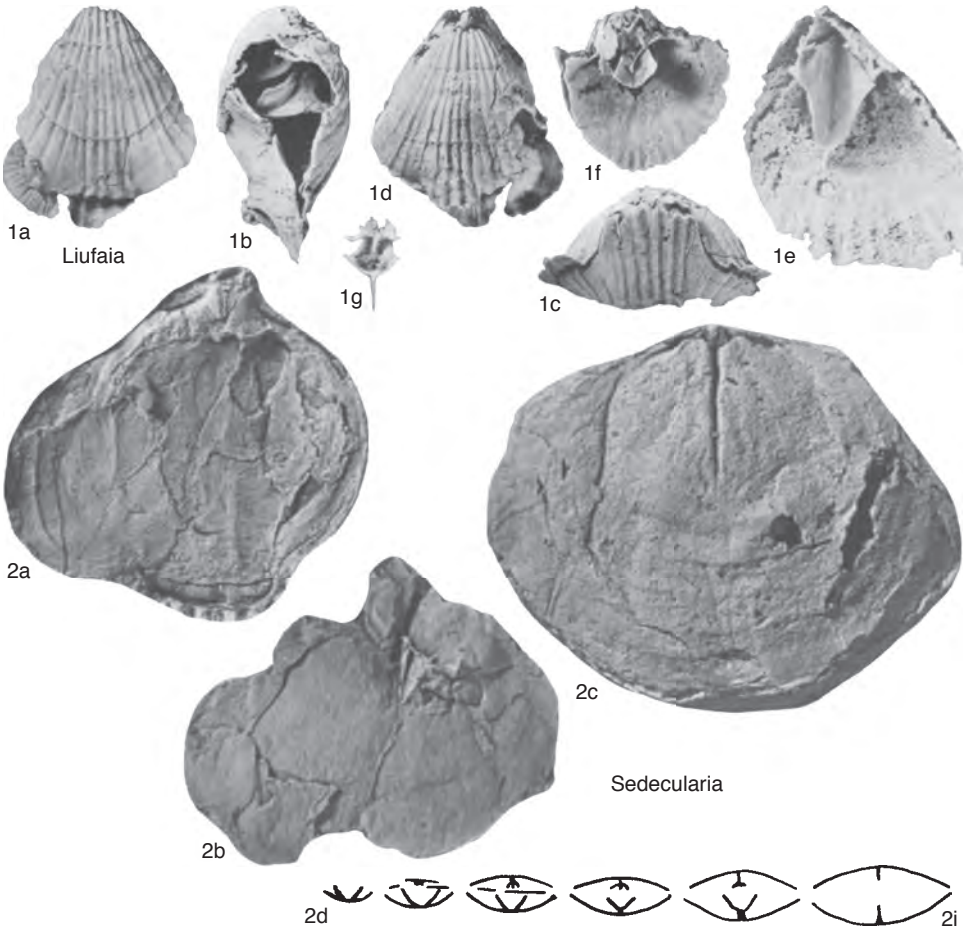

FIG. 1813. Stenoscismatidae (p. 2717–2719).

unknown; stolidium not apparent; beak straight; nature of delthyrium unclear; spondylium sessile, but supported anteriorly only by very low median septum extending a short distance anterior to spondylium; intercamarophorial plate high, short; cardinal process laminated; crura unknown. Similar to *Stenoscisma* but smooth, with subrounded and weakly dorsibiconvex valves. *Permian (Sakmarian–Kazanian):* Australia (Queensland).——FIG. 1813,*2a–i.* **S. glabra* (WATERHOUSE), Brae Formation, Bowen Basin; *a,* dorsal valve external mold with portion of ventral interior attached, ×3.2; *b,* ventral valve interior, partially crushed, ×2; *c,* dorsal valve internal mold, ×2; *d–i,* serial sections at 1 mm intervals from specimen posterior, ventral valve below, ×1 (Waterhouse, 2004).

DIMERELLOIDEA

NORMAN SAVAGE
[University of Oregon]

Superfamily DIMERELLOIDEA Buckman, 1918
Family PEREGRINELLIDAE Ager, 1965
Subfamily DZIEDUSZYCKIINAE Savage, 1996

[Dzieduszykckiinae SAVAGE, 1996, p. 257; *emend.,* SAVAGE, herein]

Large, transversly ovate Peregrinellidae with strong, simple, full costae; bisulcate or with dorsal sulcus and weak ventral fold; dental plates short, vertical; dorsal median septum short; crura long, thin, closely set. *Upper Devonian–Lower Carboniferous*.

Ibergirhynchia GISCHLER, SANDY, & PECKMANN, 2003, p. 293 [**Terebratula contraria* ROEMER, 1850, p. 31; OD]. Medium to large with transversely ovate to subpentagonal shell and biconvex profile. Biconvex profile with greater convexity in ventral valve; weakly sulcate dorsal valve with corresponding fold in ventral valve; fold may be flat topped. Anterior commissure weakly sulcate. Costae numerous, arising at beaks. Dental plates short, convex toward valve walls, convergent ventrally; teeth small; ventral muscle field weakly impressed. Dorsal median ridge short, low; wide, flat hinge plates; crura thin, rodlike. *Lower Carboniferous (upper Viséan):* Germany.——FIG. 1814,*2a–k.* **I. contraria* (ROEMER), Iberg Reef, Harz Mountains; *a–d,* neotype, dorsal, ventral, anterior, and posterior views, ×2.4; *e–k,* topotype, serial sections 0.3, 0.5, 0.9, 1.1, 1.2, 1.4, 1.5 mm from posterior, ×7 (Gischler, Sandy, & Peckmann, 2003).

Superfamily WELLERELLOIDEA Licharew, 1956
Family WELLERELLIDAE Licharew, 1956
Subfamily EXLAMINELLINAE new subfamily

[Exlaminellinae SAVAGE, herein] [type genus, *Exlaminella* CARTER & POLETAEV, 1998, p. 142]

Wellerellidae with strong plicae in anterior part of shell. Dental plates and dorsal median septum absent. Hinge plates divided. *Upper Carboniferous (upper or lower Moscovian)*.

Exlaminella CARTER & POLETAEV, 1998, p. 142 [**E. insolita*; OD]. Small; subtriangular to subpentagonal outline with dorsibiconvex profile, strongly inflated anteriorly. Ventral beak small, slightly incurved; foramen and delthyrium not observed. Fold and sulcus starting at midlength; anterior commissure uniplicate; tongue high, wide, typically tridentate. Plicae strong, simple, angular, arising at midlength. Dental plates and dorsal median septum absent. Hinge plates divided; crura falciform. Dorsal and ventral muscle scars well impressed. *Upper Carboniferous (upper Bashkirian or lower Moscovian):* Arctic Canada.——FIG. 1814,*1a–l.* **E. insolita*, lower Hare Fiord Formation, Ellesmere Island; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2; *e–l,* paratype, serial sections 0.6, 0.9, 1.0, 1.2, 1.5, 1.8, 2.2, 2.4 mm from posterior, ×4 (Carter & Poletaev, 1998).

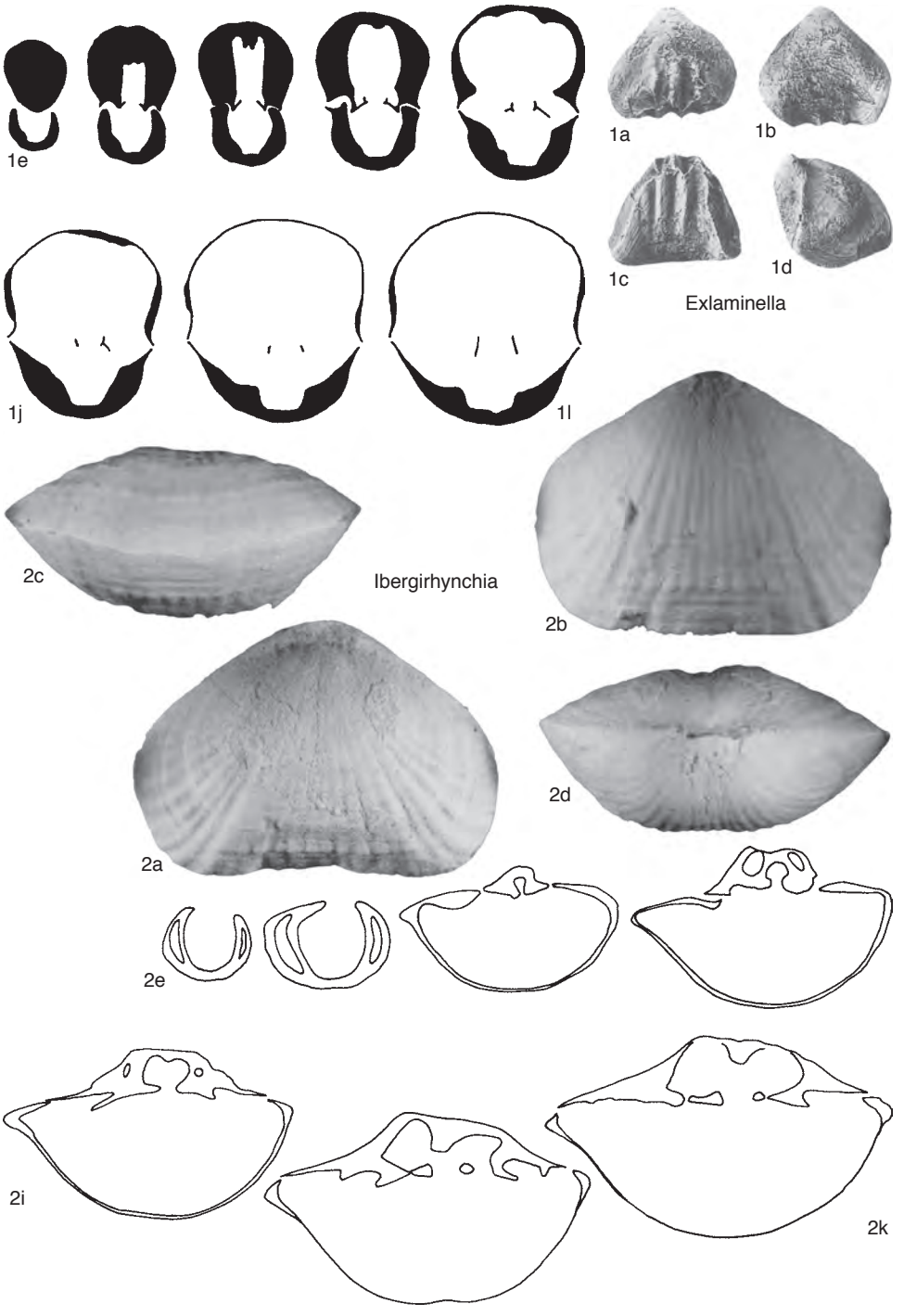

FIG. 1814. Peregrinellidae and Wellerellidae (p. 2720).

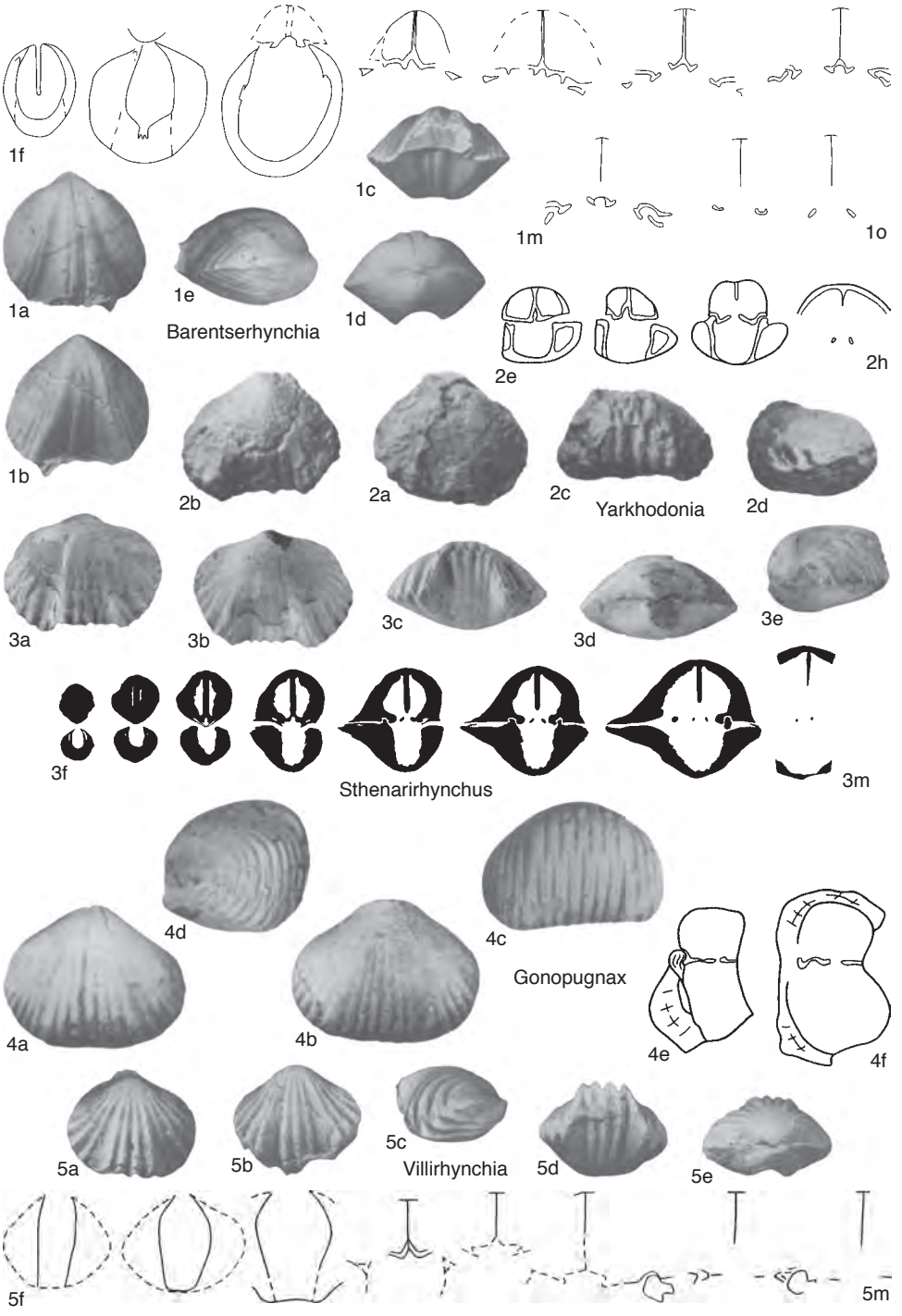

FIG. 1815. Synonyms (p. 2723).

SYNONYMS

Junior synonym of **Orbiculatisinurostrum** Sartenaer, 1984, p. 2. See also Savage in Savage & others, 2002, p. 1142.

Barentserhynchia Tcherkesova, 1999, p. 39 [**B. gorbovensis*; OD]. Medium size, subcircular to subpentagonal outline; biconvex profile; lateral and anterior slopes gentle. Beak erect to incurved. Fold and sulcus extending from umbones, progressively widening anteriorly; fold with medium groove that divides anteriorly, sulcus with low median ridge that divides anteriorly; anterior commissure uniplicate to sulciplicate. Costae low, weak, arising at umbones, increasing by bifurcation. Dental plates very short. Dorsal median septum thin, high, extending over one-fifth valve length; septalium short; hinge plates short, divided; crura closely set, slightly flattened rods, curving into ventral valve distally. *Upper Devonian (Frasnian):* Russia.——Fig. 1815,*1a–o*. **B. gorbovensis*, Vorononskaya Formation, lower part of Menshikov Horizon, southwestern William Island, northwestern Novaya Zemlya, northern Russia; *a–e*, holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1; *f–o*, topotype, serial sections 0.2, 0.3, 0.4, 0.7, 0.8, 0.9, 1.0, 1.1, 1.3, 1.7 mm from posterior, scale not given (Tcherkesova, 1999).

Junior synonym of **Plionoptycherhynchus** Sartenaer, 1979, p. 537. See also Savage in Savage & others, 2002, p. 1151.

Sthenarirhynchus Sartenaer, 1999c, p. 275 [**S. dionanti*; OD]. Medium to large, with transversely ovate outline and dorsibiconvex profile; gentle lateral slopes. Beak erect to incurved; foramen obscured by dorsal umbo. Fold and sulcus strong, arising at umbones; anterior commissure uniplicate; tongue high, trapezoid, serrate. Costae distinct, subangular, simple, extending from umbones, present on fold, sulcus, and flanks. Dental plates barely visible in serial sections at extreme posterior; ventral muscle field narrow, deeply impressed in thick shell material. Dorsal median septum long, high, thick; septalium short; hinge plates dividing immediately anterior of septalium; crura closely placed, fine, rodlike, straight. *Upper Devonian (middle Frasnian):* Belgium.——Fig. 1815,*3a–m*. **S. dionanti*, *Palmatolepis punctata* Zone, Marloie railway station, west of Dinant, southern Belgium; *a–e*, holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1; *f–m*, serial sections 0.65, 0.8, 1.15, 1.45, 1.65, 1.9, 2.2, 3.5 mm from posterior, ×3.25 (Sartenaer, 1999c).

Junior synonym of **Plionoptycherhynchus** Sartenaer, 1979, p. 537. See also Savage in Savage & others, 2002, p. 1151.

Villirhynchia Tcherkesova, 1999, p. 41 [**V. villiamensis*; OD]. Medium size; transversely ovate to subpentagonal outline and biconvex profile; gentle lateral slopes. Ventral beak erect to incurved. Fold and sulcus strong, arising at umbones; anterior commissure uniplicate; tongue high, dentate. Costae strong, angular, simple, extending from umbones; approximately 4 on fold, 3 in sulcus, several on flanks. Dental plates short, slightly convergent ventrally. Dorsal median septum long, high, thin; septalium short; hinge plates horizontal, divided anterior of septalium; crura closely set. *Upper Devonian (Frasnian):* Russia.——Fig. 1815,*5a–m*. **V. villiamensis*, Vorononskaya Formation, lower part of Menshikov Horizon, southeastern coast of William Island, northwestern Novaya Zemlya, northern Russia; *a–e*, holotype, dorsal, ventral, lateral, anterior, and posterior views, ×1; *f–m*, topotype, serial sections 0.2, 0.4, 0.6, 0.8, 0.9, 1.0, 1.1, 1.3 mm from posterior, scale not given (Tcherkesova, 1999).

Junior synonym of **Basilicorhynchus** Crickmay, 1952, p. 1. See also Savage in Savage & others, 2002, p. 1156.

Yarkhodonia Baranov in Alekseeva & others, 1996, p. 78 [**Y. recta;* OD]. Subcircular outline with dorsibiconvex profile. Beak erect to incurved. Fold and sulcus arising at about midlength. Anterior commissure uniplicate; tongue serrate. Costae few, coarse, subangular, restricted to anterior. Dental plates short, slightly convergent ventrally. Dorsal median septum short, low; septalium small, V-shaped; hinge plates divided anterior of septalium; crura closely set proximally, unknown distally. *Upper Devonian (lower Frasnian)*: northeastern Russia.——Fig. 1815,*2a–h*. **Y. recta*, Yarkhodonskaya Formation, *Mucrospirifer novosibiricus* Zone, upper reaches of Malii Yarkhodon River, Sredne Prikolimbyi, northeastern Asiatic Russia; *a–d*, holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–h*, paratype, serial sections 1.5, 1.7, 2.0, 2.7 mm from posterior, ×5 (Alekseeva & others, 1996).

Junior synonym of **Dogdoa** Baranov, 1982, p. 42. See also Savage in Savage & others, 2002, p. 1120.

Gonopugnax Baranov in Alekseeva & others, 1996, p. 94 [**G. galkini*; OD]. Medium size; transversely subpentagonal outline; dorsibiconvex profile. Beak erect. Fold and sulcus arising at umbones; strong anteriorly; anterior commissure uniplicate, tongue distinct, wide, rounded to trapezoid. Costae medium, simple, rounded, arising at umbones, flattened and grooved on *paries genicularis*; marginal spines present. Dental plates absent or mostly buried in callus. Hinge plates divided, horizontal; septalium, dorsal septum, and crura unknown. *Lower Devonian (lower Lochkovian):* eastern Siberia.——Fig. 1815,*4a–f*. **G. galkini*, Sagyr Formation, Selennyakh ridge; *a–d*, holotype, dorsal, ventral, anterior, and lateral views, right bank of Talyndzha River, Krivoy stream, ×1.1; *e–f*, paratype, two serial sections, intervals and distances from posterior, right bank of Talyndzha River, Gon stream, scale not given (Alekseeva & others, 1996).

Synonym of **Tchernarhynchia** Tcherkesova, 1998, p. 44, chosen herein by first revising author. See also Savage, herein, p. 2711.

Kumzharhynchia Tcherkesova, 1998, p. 41 [**K. bondarevi*; OD]. Shell large, transversely ovate

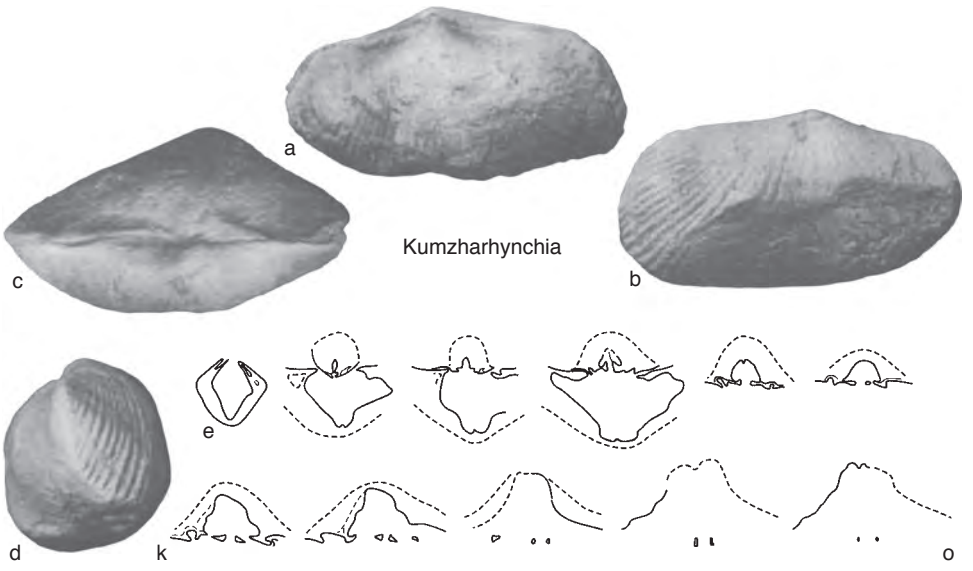

FIG. 1816. Synonyms (p. 2723–2724).

(holotype probably transversely deformed); dorsibiconvex profile, expanded anteriorly by fold. Ventral beak incurved. Fold and sulcus wide, arising at about one-third shell length; anterior commissure uniplicate. Costae fine, numerous, dichotomizing, developed over whole shell surface. Dental plates short; teeth poorly known. Dorsal median septum poorly known; septalium short, poorly known; hinge plates divided; crural bases triangular in section; crura rodlike, thin, closely set. *Upper Devonian (middle Frasnian):* Russia.——FIG. 1816*a–o*. **K. bondarevi*, upper Zhandr Horizon, upper reaches of Kumzha River, South Island of Novaya Zemlya; *a–d*, holotype, dorsal, ventral, posterior, and lateral views, ×1; *e–o*, paratype, serial sections, intervals and scale not given (Tcherkesova, 1998).

NOMINA DUBIA

The following genera are considered *nomina dubia,* in most instances because the type material is insufficiently well preserved or insufficiently well described to warrant generic status at this time.

Altaethyrella SEVERGINA, 1978, p. 38 [**A. megala*; OD]. Shell subpentagonal; fold and sulcus from umbones; anterior commissure uniplicate, tongue moderately high. Costae arising at beaks. Short dental plates. Short, ridgelike cardinal process; lacking septalium and dorsal median septum. [The figures of holotype mold specimen are poor, and the internal features are unclear. This genus is best considered as a *nomen dubium* until better topotype material is available. KULKOV and SEVERGINA (1989, p. 160–161) decided to make *Otarorhyncha* a junior subjective synonym of *Altaethyrella* and assign it to the Ancistorhynchoidea, a decision followed by POPOV, NIKITIN, and COCKS (2000), who assigned their subtriangular, more elongate material to *Otarorhyncha otarica* (RUKAVISHNIKOVA), the type species of *Otarorhyncha*. The type material of *Otarorhyncha* has a short median septum, however, and appears to belong to the Rhynchotrematoidea. The photographs of the calcareous topotype specimen provided for the revised *Treatise* (SAVAGE in SAVAGE & others, 2002, p. 1048, Fig. 707,*3a–d*) by NIKIFOROVA show a transversly subpentagonal specimen with distinctive ribbing different from that of the mold material of POPOV, NIKITIN, and COCKS (2000), which clearly lacks a median septum. Thus, assigning the material of POPOV, NIKITIN, and COCKS to *O. otarica* is unsound and does not help clarify the features of *Altaethyrella*.] *Upper Ordovician (Ashgill):* Altai, Siberia.——FIG. 1817,*4a–d*. **A. megala*, northwestern Altai, Kolmogorovo area, locality 12 of Severgina, Ordovsky suite; holotype, dorsal, ventral, anterior, and posterior views of internal mold, ×2 (Severgina, 1978).

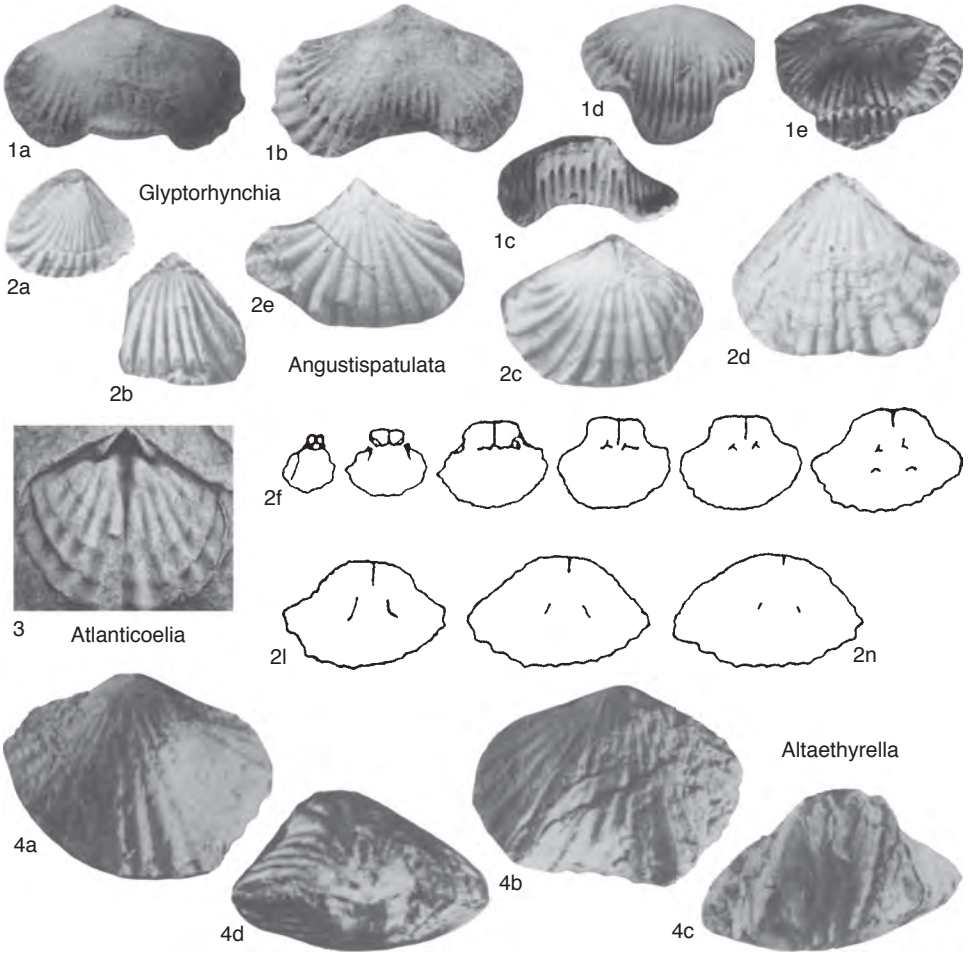

FIG. 1817. Nomina Dubia (p. 2724–2726).

Angustispatulata QIAN & ROBERTS, 1995, p. 265 [**A. campbelli*; OD]. Small with subpentagonal outline and biconvex profile; foramen small, deltidial plates conjunct. Fold and sulcus arising at umbones; anterior commissure uniplicate, tongue high, serrated; costae strong, simple, angular; arising at beaks, covering whole of shell. Dental plates short. Dorsal median septum long, slender; septalium short, without cover plate; hinge plates dividing immediately anterior of septalium; crura highly curved ventrally, laterally flattened. [Holotype (internal mold) is poorly illustrated, and features are uncertain. Other photographs of molds are inadequate. Serial sections are of specimen from a locality and formation different from that of the holotype. This genus should be considered a *nomen dubium* until it is reillustrated using better topotype specimens.] *Lower Carboniferous (upper Tournaisian)*: eastern Australia.——FIG. 1817,*2a–n*. **A. campbelli*, *Schellwienella burlingtonensis* brachiopod Zone, New England area of New South Wales; *a–b*, holotype, Ararat Formation, two views of internal mold, ×2; *c*, hypotype, mold of dorsal valve interior, ×2; *d*, mold of ventral valve exterior, ×2; *e*, mold

of ventral valve interior, ×2; *f–n*, hypotype, serial sections, Namoi Formation, intervals not given, ×1.5 (Qian & Roberts, 1995).

Atlanticoelia Koch, 1996, p. 1088 [**Atrypa acutiplicata* Conrad, 1841, p. 54; OD]. Small to medium, subcircular to subpentagonal outline, planoconvex to biconvex lateral profile; costae simple, strong, rounded crests, extending from beaks; broad dorsal sulcus. Interior poorly known. [This genus is best considered a *nomen dubium* until the type species is fully described and a lectotype designated. Conrad, 1841, p. 54, gave a brief description of material from the Onondaga Limestone near Waterville, New York, but without illustrations. Hall, 1867, pl. 57,*30–39,* and Hall & Clarke, 1895, pl. 53,*32–35,* described and illustrated the exterior of a specimen assigned to the species but from Jamesville, New York, 40 miles from Waterville, along with illustrations of interiors from Waterloo, New York, 50 miles west of Jamesville. Kindle, 1912, p. 84, described the species but used interiors from Pennsylvania, Virginia, and Maryland. Koch (1996, p. 1088, fig. 1), in proposing the new genus, illustrated a single dorsal internal mold from Rosendale, New York, many miles from all the above localities, and gave emphasis to the presence of a large, knob-like cardinal process, not noted by Conrad, Hall, or Kindle.] *Lower Devonian:* USA (New York).——Fig. 1817,*3. *A. acutiplicata* (Conrad); dorsal internal mold, ×1 (Koch, 1996).

Glyptorhynchia Shen & He, 1994, p. 449 [**G. lens*; OD]. Shell small, transversely ovate. Fold and sulcus from about midlength; anterior commissure uniplicate, tongue high. Costae numerous, simple, arising at umbones. Dental plates short. Hinge plates reported to be divided. [The interior of the genus is uncertain, therefore it is difficult to assign to a family or a genus. This genus is best considered as a *nomen dubium.*] *Upper Permian (Changhsingian)*: China.——Fig. 1817,*1a–e*. **G. lens*, Changhsing Formation, Guiding, Guizhou; *a–b*, holotype, dorsal and ventral views; *c–e*, paratype, anterior, ventral, and dorsal views, ×2 (Shen & He, 1994).

POST-PALEOZOIC RHYNCHONELLIDA

MIGUEL O. MANCEÑIDO,[1] E. F. OWEN,[2] and D.-L. SUN[3]

[[1]La Plata Natural Sciences Museum, Argentina; [2]retired from The Natural History Museum, London; and [3]Nanjing Institute of Geology and Palaeontology]

Since the manuscript for *Treatise* Part H, volume 4 (KAESLER, 2002) was submitted, not only were about a dozen new genera proposed, but a number of contributions addressing matters relevant for a better understanding of the order have appeared, some of which are summarized below.

The importance of crural types for classification and for unravelling major evolutionary lineages, when used in conjunction with other anatomical features, has been confirmed in an overview of the systematic relationships among the seven superfamilies presently recognized (MANCEÑIDO & OWEN, 2001). Individual crural types discussed and figured by SAVAGE and others (2002, p. 1036–1040, fig. 700–702) may be assembled according to structural and cross-sectional variation into four fundamental groups, as follows.

Arcual group, including arcuiform, spinuliform, plus distally expanded (=luniform) and spiculated variants, and possibly also clivuliform types.

Septifal group, comprising falciform, subfalciform, hamiform (=ex prefalciform), and septiform types, and certain structural or distal end modifications.

Raducal group, including raduliform, calcariform, and canaliform types (plus variations of their cross section and of their distal ends).

Ensimergal group, comprising mergiform, submergiform (=ex terebratuliform), ensiform, maniculiform, and perhaps also ciliform types (cf. MANCEÑIDO, 1998, 2000).

Certain features of the shell structure may prove helpful for the broad classification of basic stocks, although further work is needed, as noted by LEIDHOLD (1921) and AGER (1957, 1965), who called the attention to the potential value of the so-called shell mosaic (*Schalenmosaik* or *Schuppenpanzerstruktur*), occasionally observable on the inner surface of either valve and on internal molds of exceptionally well-preserved material. The mosaic results from regular stacking of calcitic fibers of the secondary layer of the shell wall, is very stable, and yields a characteristic geometrical pattern on the inside valve floor (WILLIAMS, 1997, Fig. 242.1, 242.3). Transverse sections of the valves may also show a characteristic fabric, particularly under SEM (WILLIAMS, 1997, Fig. 242.2, 242.4). Recent additional studies on Mesozoic and extant rhynchonellides (MOTCHUROVA-DEKOVA & TADDEI-RUGGIERO, 2000; MOTCHUROVA-DEKOVA, 2001; MOTCHUROVA-DEKOVA, SAITO, & ENDO, 2002) expanded earlier work (e.g., KAMYSHAN, 1977; SMIRNOVA, 1984) and report at least two distinct microstructural patterns. These are respectively made up of finer, isometric fibers, and less uniform, coarser, rhombic fibers, and have been claimed to have suprageneric significance. In fact, thus far the former, leptinoid type (fiber average size 5–30 µm) has been recorded in hemithiridoids and rhynchonelloids (Fig. 1818.1–1818.5), whereas the second, eurinoid type (fiber size range 40–140 µm wide) has been reported widely among pugnacoids and norelloids, seemingly even in a rhynchotetradoid (Fig. 1818.6–1818.12). Although little is known at present about the possible influence of ontogenetic stage and environmental factors upon mosaic coarseness and morphology, this is a line of research worth pursuing further.

Similarly, patterns of the mantle canal system represent fairly stable characters, yet apparently exhibit interesting variations between major stocks. Although illustrations of vascular markings in older literature often do not match the detail recorded in modern studies, certain broad indications

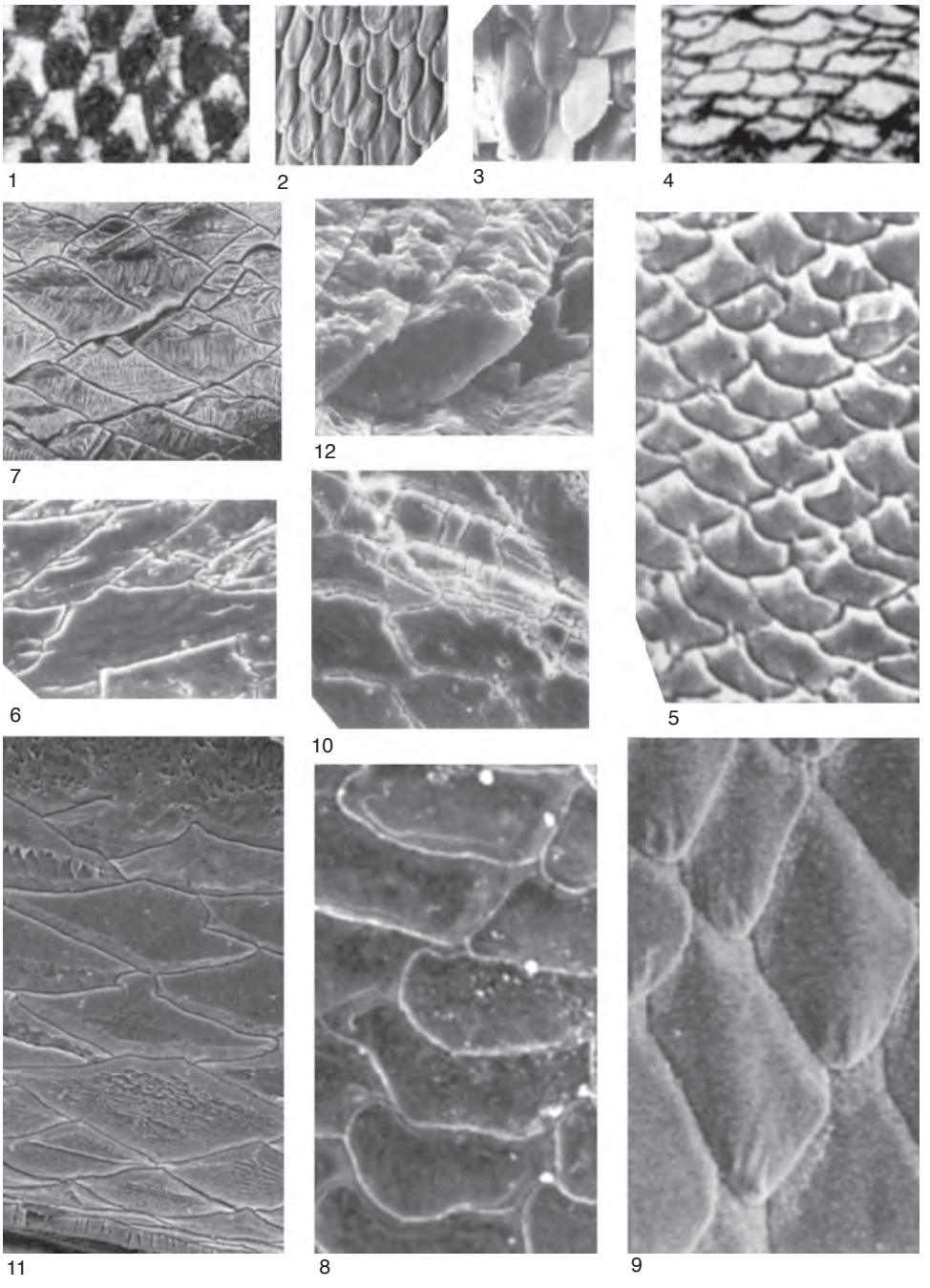

FIG. 1818. *For explanation, see facing page.*

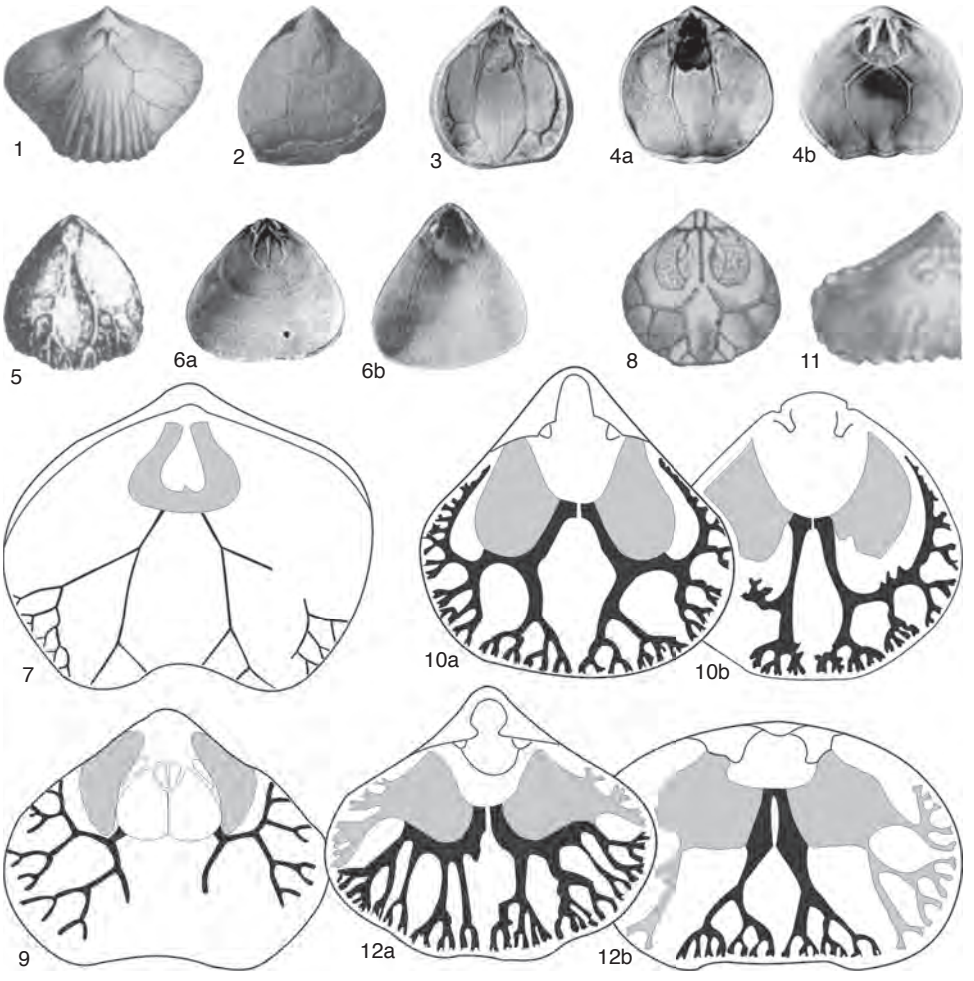

FIG. 1819. Mantle canal patterns, selected examples, both fossil (1, 2, 5, 7, 8, 9, 11) and extant (3, 4, 6, 10, 12); *1–4*, pugnacoids; *5–6*, norelloids; *7–8*, rhynchonelloids; *9–12*, hemithiridoids; *1*, Upper Jurassic *Lacunosella,* ×0.68 (Quenstedt, 1871 in 1868–1871); *2*, upper Oligocene *Aetheia*, ×1.26 (Cooper, 1959); *3*, Recent *Basiliola*, ×1.32 (Cooper, 1959); *4*, Recent *Rhytirhynchia,* ×1.32 (Cooper, 1959); *5*, Mid-Triassic *Norella,* ×1.2 (Bittner, 1890); *6*, Recent *Hispanirhynchia,* ×1.1 (Cooper, 1959); *7*, Upper Triassic *Superbirhyncha,* ×2 (Siblík, 2002); *8*, Lower Jurassic *Cuneirhynchia,* ×2 (Quenstedt, 1871 in 1868–1871); *9*, Upper Cretaceous *Bohemirhynchia,* approximately ×2.5 (Nekvasilová, 1973); *10*, Recent *Hemithiris,* approximately ×1.2 (Williams & Rowell, 1965b); *11*, Upper Jurassic *Torquirhynchia,* approximately ×0.5 (Quenstedt, 1871 in 1868–1871); *12*, Recent *Notosaria,* approximately ×1.5 (Williams & Rowell, 1965b).

FIG. 1818. Shell mosaic and secondary layer cross-sectional patterns, selected examples, both fossil (1, 3, 4, 5, 6, 7, 10, 12) and extant (2, 8, 9, 11) (all approximately ×500); *1*, rhynchonelloid; *2–5*, hemithiridoids; *6–7*, pugnacoids; *8–11*, norelloids; *12*, rhynchotetradoid; *1*, mosaic of Upper Jurassic *Rhynchonella* (Ager, 1957); *2*, mosaic of Recent *Notosaria* (Williams, 1990); *3*, mosaic of upper Aptian *Cyclothyris* (Smirnova, 1984); *4*, cross section of Upper Triassic *Fissirhynchia* (Radulović, Urošević, & Banjac, 1992); *5*, cross section of Mid-Jurassic *Isjuminella* (Taddei-Ruggiero & Ungaro, 1984); *6*, cross section of Lower Cretaceous *Lacunosella* (Smirnova, 1984); *7*, cross section of Upper Cretaceous *Costerymnaria* (Motchurova-Dekova & Taddei-Ruggiero, 2000); *8*, mosaic of Recent *Tethyrhynchia* (Logan & Zibrowius, 1994); *9*, mosaic of Recent *Frieleia* (Motchurova-Dekova, Saito, & Endo, 2002); *10*, cross section of Lower Cretaceous *Monticlarella* (Smirnova, 1984); *11*, cross section of Recent *Parasphenarina* (Motchurova-Dekova, Saito, & Endo, 2002); *12*, cross section of Upper Triassic *Austrirhynchia* (Michalík, 1993).

of kinship may be recognizable. Thus, a simplified, widely dichotomous, sparsely distributed pattern seems prevalent among Mesozoic and Recent pugnacoids (basilioline, acanthobasilioline, lacunoselline, and aetheine basiliolids; Fig. 1819.1–1819.4) and is similar to what is known in a few fossil and extant norelloids (norellid and frieleiid; Fig. 1819.5–1819.6). On the other hand, among Recent and fossil hemithiridoids, peripherally more densely branched patterns are known, sometimes inequidistributed saccate (e.g., hemithiridids and tetrarhynchiids) and sometimes apocopate lemniscate (notosariids and cyclothyridids; Fig. 1819.9–1819.12). The pattern in rhynchonelloids (Fig. 1819.7–1819.8) looks similar to that shown in hemithiridids and perhaps is somewhat intermediate between it and the pattern in basiliolids.

As pointed out by MANCEÑIDO and OWEN (2001), these interim results suggest a promising future and may stimulate the necessary additional research. It may be significant that molecular phylogenetic studies on living species result in hierarchical taxonomic relationships consistent with those achieved by morphological comparative studies, providing an assurance that classical paleontological methods remain a useful approach (see WILLIAMS, 2002, p. xxviii).

Superfamily PUGNACOIDEA Rzhonsnitskaia, 1959

Family BASILIOLIDAE Cooper, 1959

Subfamily PAMIRORHYNCHIINAE Ovcharenko, 1983

Orbirhynchopsis SUN & ZHANG, 1998, p. 227 [278] [**O. tianshuihaiensis*; OD]. Small, gently biconvex, roundly oval in outline; beak short, nearly straight; beak ridges angular; foramen circular, permesothyrid; deltidial plates triangular, barely touching; fold and sulcus scarcely developed; commissure rectimarginate to slightly and broadly uniplicate; ornamented with numerous low, round costae, occasionally bifurcating; umbonal region with fine costae or smooth. Dental plates conspicuous and slightly divergent ventrally; umbonal chambers narrow; hinge plates divided; crura falciform; pedicle collar present. [This genus is readily referable to Pamirorhynchiinae, being very similar to *Orbirhynchia* PETTIT and *Rahouiarhynchia* TCHOUMATCHENKO. Thus, in the previous entry for the latter (SAVAGE & others, 2002, p. 1208), the queried record from China may be deleted.] *Middle Jurassic (Callovian):* China (northern Karakorum, Tibet).——FIG. 1820,*1a–l.* **O. tianshuihaiensis*, Longshan Formation, Tianwendian and Tianshuihai; *a–d,* holotype, dorsal, lateral, anterior, ventral views, NIGP121059, ×1.5; *e–l,* transverse serial sections, distances in mm from ventral umbo, 0.4, 1.0, 1.5, 1.8, 2.0, 2.3, 2.5, 2.9, NIGP 121060, approximately ×4 (Sun & Zhang, 1998).

Family ERYMNARIIDAE Cooper, 1959

Subfamily ERYMNARIINAE Cooper, 1959

Costerymnaria MOTCHUROVA-DEKOVA & TADDEI-RUGGIERO, 2000, p. 182 [**C. italica*; OD]. Erymnariinae with numerous, well-developed costae, beginning from the umbonal region; shell elongate-subtriangular to subcircular, strongly subequibiconvex; anterior commissure asymmetrically twisted. Internal characters as in *Erymnaria*; dental plates convex in cross section; septiform crura, sometimes lyre shaped distally. *Upper Cretaceous (Cenomanian–upper Campanian):* Italy.——FIG. 1820,*2a–l.* **C. italica*, Cenomanian, Matese Group, Molise; *a–d,* holotype, dorsal, lateral, anterior, ventral views, PMNUF 6/M 16999, ×2; *e–l,* transverse serial sections, distances in mm from ventral umbo, 2.1, 2.8, 3.2, 3.8, 4.3, 4.7, 5.2, 5.4, PMNUF 7/M 16998-2, ×2.5 (Motchurova-Dekova & Taddei-Ruggiero, 2000).

Superfamily WELLERELLOIDEA Licharew, 1956

Family PONTISIIDAE Cooper & Grant, 1976

Subfamily PONTISIINAE Cooper & Grant, 1976

Saubachia SIBLÍK, 2000, p. 421 [**S. inflata;* OD]. Small, equibiconvex shells, globose, subtrigonal in outline; pronounced smooth stage, initial ribbing or a few rounded costae anteriorly; strong uniplication, fold slightly elevated; beak strong and low, suberect. Delthyrial cavity quadrate in cross section between thin, subparallel dental plates, lateral umbonal cavities semicircular; pedicle collar not observed; hinge teeth strongly crenulated, laterally expanded,

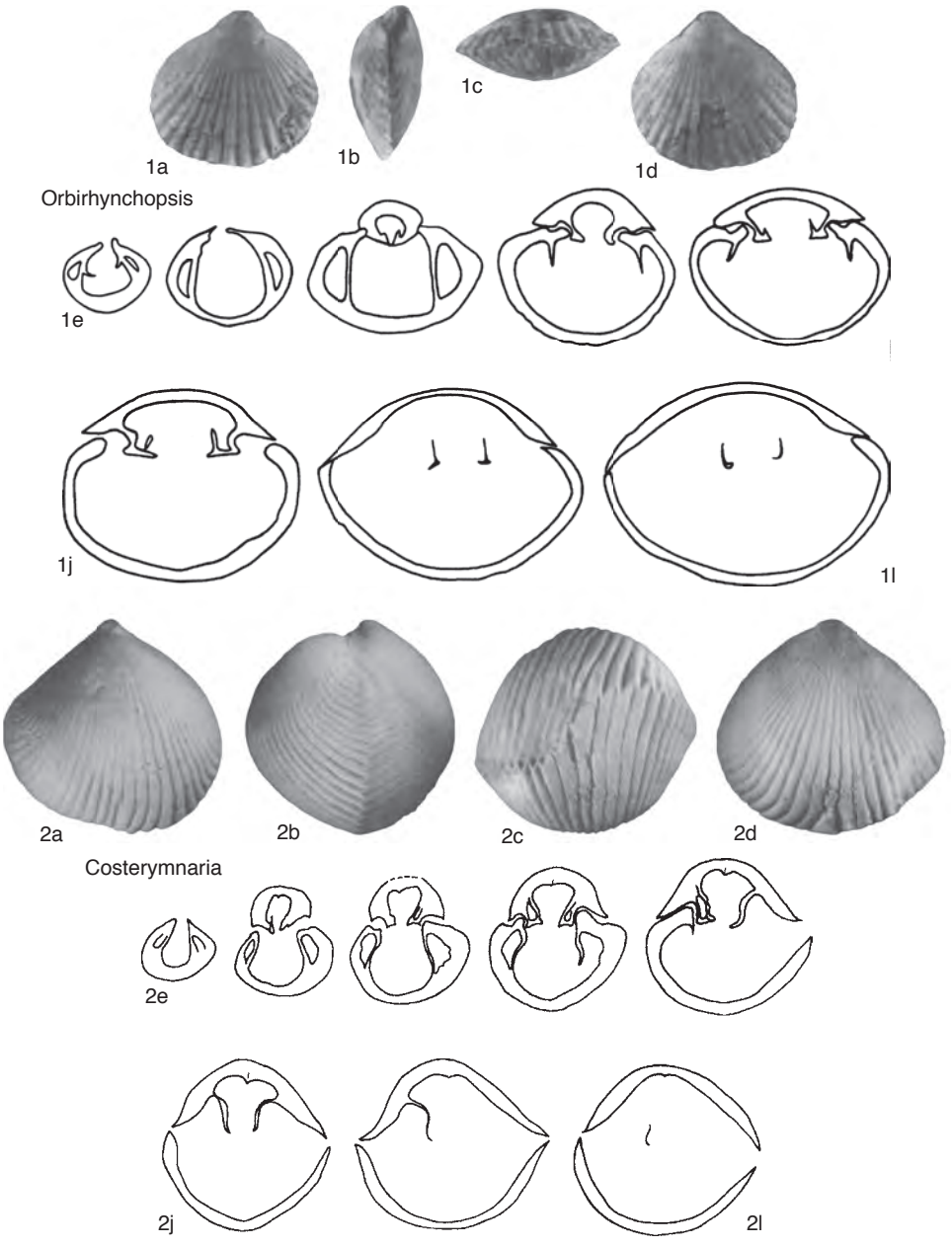

FIG. 1820. Basiliolidae and Erymnariidae (p. 2730).

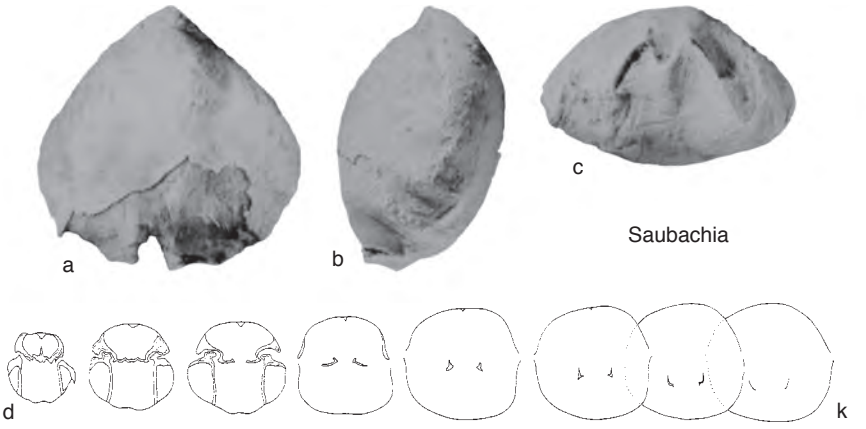

FIG. 1821. Pontisiidae (p. 2730–2732).

with hollows for reception of outer and inner socket ridges; septalium absent; hinge plates fused, their inner and outer parts characteristically delimited; dorsal median septum confined posteriorly only and reduced anteriorly to a low ridge; alleged raduliform crura, convex outward in cross section, fitting better into hamiform type. [This monotypic new genus was originally referred to Wellerellidae, which is consistent with hamiform (rather than raduliform) crura seen in sections, yet, it may likewise belong in Pontisiidae, as suggested by entire hinge plates and strong overall similarity to *Bodrakella* MOISEEV (it is probably ancestral to, if not synonymous with, the latter).] *Lower Jurassic (Hettangian):* Alps (Austria, Germany).—— FIG. 1821*a–k.* **S. inflata*, Kendlbach Beds, Saubachgraben, near Salzburg; *a–c,* holotype, dorsal, lateral, anterior views, coll. IPW, ×3; *d–k,* transverse serial sections, distances in mm from ventral umbo, 0.2, 0.5, 0.8, 1.1, 1.5, 1.7, 2.1, 2.25, ×2 (Siblík, 2000).

Superfamily RHYNCHONELLOIDEA d'Orbigny, 1847
Family RHYNCHONELLIDAE d'Orbigny, 1847
Subfamily RHYNCHONELLINAE d'Orbigny, 1847

Choffatirhynchia GARCÍA JORAL & GOY, 2004, p. 242 [**Rhynchonella Vasconcellosi* CHOFFAT in DUBAR, 1931, p. 122; OD]. Medium-sized, dorsibiconvex shells, subtetrahedral to globose, usually wider than long; well-marked subrectangular uniplication in anterior commissure, but rather ill-defined trilobation; with numerous, dense, simple, subangular costae (5 to 8 on fold) that extend full length (somewhat effaced near umbos, at most); suberect, narrow, prominent beak; foramen relatively large, cardinal area ill developed. Narrow, shallow septalium; dental plates thin, subparallel or slightly convergent ventrally, in section; crura raduliform. [Although this new genus was originally placed among Rhynchonellinae, certain affinities with Ivanoviellines may not be disregarded.] *Lower Jurassic (Toarcian):* Spain, Portugal, France, northern Africa.——FIG. 1822*a–k.* **C. vasconcellosi* (CHOFFAT), lower Toarcian, Turmiel Formation, Ariño, Teruel, Spain; *a–c,* dorsal, lateral, anterior views, DPUCM Ar.11.402, ×1.5; *d–k,* transverse serial sections, distances in mm from ventral umbo, 1.0, 1.9, 2.1, 2.5, 3.3, 4.0, 4.7, 5.0, DPUCM Ar.11.501, ×2.6 (García Joral & Goy, 2004).

Grestenella SIBLÍK, 2000, p. 435 [**Rhynchonella austriaca* SUESS, 1854, p. 53; OD]. Medium-sized shells, subtrigonal to subcircular in outline, dorsibiconvex; with strong uniplication in anterior commissure, and high fold well developed in anterior half of shell; multicostate, sharp, angular costae, rarely short, smooth area around umbones; beak usually high and strong, but shorter, slightly incurved in some globular specimens; beak ridges delimiting small impressed planareas. Delthyrial cavity subquadrate in cross section, lateral umbonal cavities subtrigonal; dental plates subparallel or slightly divergent ventrally; sometimes with pedicle collar and double deltidial plates; hinge teeth strong, straight, and crenulated; conspicuous, deep, v-shaped septalium between subhorizontal hinge plates; raduliform crura distally curving toward ventral valve, with strongly expanded ventral parts. [This monotypic new genus is referred to Rhynchonellidae, established mainly for subcynocephalous shells with unusual development of crural terminations; seems most closely related to *Rhynchonelloidea* BUCKMAN.] *Lower Jurassic:* Austria (Alps, pre-Alps).——FIG. 1823*a–m.* **G. austriaca* (SUESS), Sinemurian–Pliensbachian, Gresten Limestone, Pechgraben, near Weyer; *a–c,* lectotype, dorsal, lateral, anterior views, GBA 1854/6/13, ×1.5 (new,

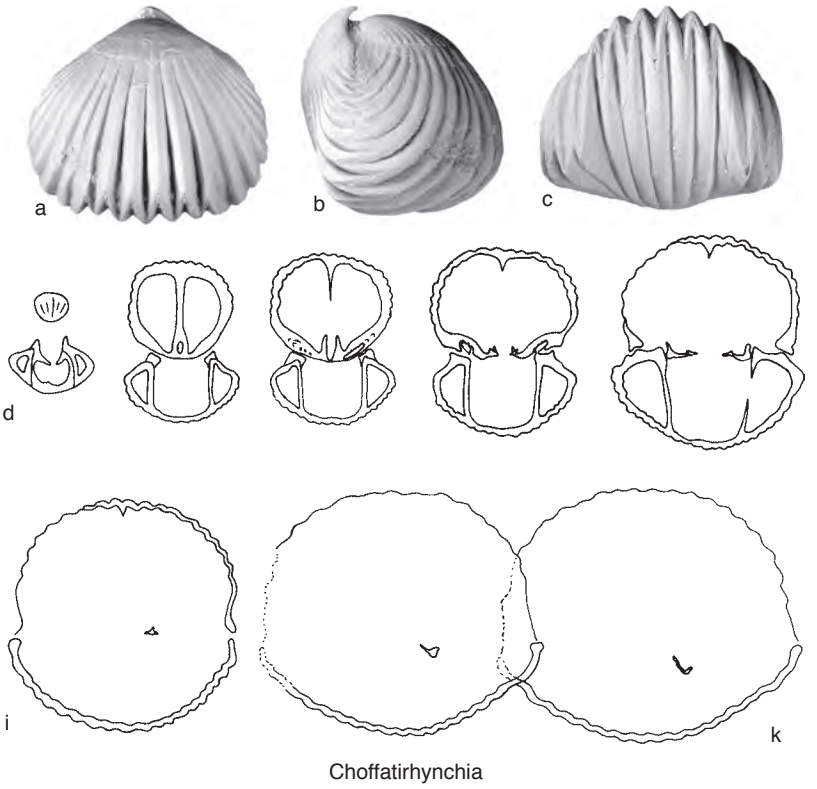

FIG. 1822. Rhynchonellidae (p. 2732).

courtesy of M. Siblík); *d–m,* topotype, transverse serial sections, distances in mm from ventral umbo, 1.0, 2.0, 2.4, 2.6, 3.1, 3.7, 4.6, 5.2, 5.4, 5.6, coll GBA, ×1.5 (Siblík, 2000).

Subfamily URALORHYNCHIINAE Manceñido & Owen, 2002

Superbirhyncha SIBLÍK, 2002, p. 101 [**Rhynchonella superba* BITTNER, 1890, p. 228; OD]. Medium to large, subtrigonal to rounded pentagonal in outline, width exceeding length in most cases; strongly dorsibiconvex in profile, ventral valve almost flat sometimes; fold and sulcus well developed anteriorly, but poorly detached from lateral slopes; anterior commissure with broad, strong uniplication; few, low, blunt costae on fold and sulcus, prominent anteriorly, but indistinct toward umbos; lateral and posterior parts nearly smooth or with poorly developed ribbing; slight posterior dorsal sulcation present; growth lines conspicuous along margins; ventral beak erect and slightly swollen, foramen small, submesothyrid. Shell walls very thick; lateral umbonal chambers filled largely with secondary callus, almost completely obscuring dorsally divergent dental plates; teeth strong, crenulated, inserted into large sockets; septalium short, narrow, but relatively deep and thickened; dorsal median septum strong, short, reduced to a ridge; inner socket ridges continuous with thick hinge plates; crura raduliform, proximally close to median septum; muscle scars usually strongly impressed. [This monotypic new genus was initially referred to Tetrarhynchiinae but in view of noticeable lack of squama and glotta, it may be better allocated among Rhynchonellidae, with affinities to Uralorhynchiinae most likely, on the basis of evident similarities to other Late Triassic genera such as *Sulcorhynchia* DAGYS and *Omolonella* MOISEEV (whereas resemblance to *Moisseievia* DAGYS seems superficial only). The species has been recorded from China, too, but such extension of the new genus range would require further substantiation.] *Upper Triassic (Norian):* Northern Alps (Austria).——FIG. 1824*a–o.* **S. superba* (BITTNER), Hallstatt Limestone, Hütteneckalpe; *a–c,* dorsal, anterior, lateral views, NHMW, ×1.5; *d–o,* transverse serial sections, distances in mm from ventral

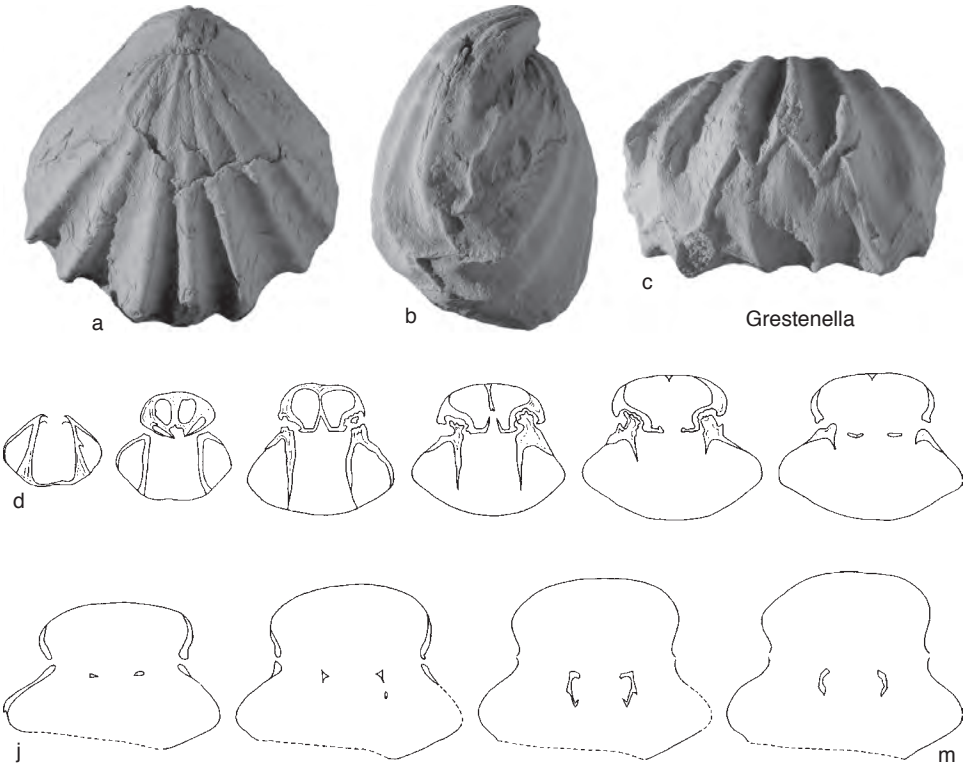

FIG. 1823. Rhynchonellidae (p. 2732–2733).

umbo, 0.7, 0.9, 1.3, 1.7, 2.3, 2.7, 3.4, 3.7, 3.9, 4.4, 4.6, 5.7, ×1.5 (Siblík, 2002).

Superfamily NORELLOIDEA Ager, 1959
Family NORELLIDAE Ager, 1959
Subfamily PARANORELLININAE Xu, 1990

Laevorhynchia SHEN & HE, 1994, p. 449 [453] [**L. tenuis*; OD]. Shell very small, ventribiconvex, transversely elliptical in outline; beak indistinct; dorsal valve nearly flat with anterior part slightly concave, forming wide and shallow sulcus; anterior commissure sulcate; surface smooth. Ventral interior with short dental plates; dorsal interior with an undivided hinge plate, but with shallow notch at anterior edge; crura "extending anteriorly" (SHEN & HE, 1994, p. 453; =possibly spinuliform). [This is an overlooked genus with evident affinities to Paranorellininae, yet discrimination from *Meishanorhynchia* CHEN & SHI in CHEN, SHI, & KAIHO, 2002, and *Paranorellina* DAGYS, 1974, not adequately solved, in part because serial sections (implicit in description of internal characters) were not published in original paper, and no comparisons with material from around Meishan-Changxing (Zhejiang) were given.] *Lower Triassic (lowest Scythian):* China (Guizhou).——FIG. 1825,*2a–d*. **L. tenuis*, lower Induan, Feihsienkuan Formation, Guiding; holotype, ventral, dorsal, lateral, anterior views, GD-8190, ×2 (Shen & He, 1994).

Meishanorhynchia CHEN & SHI in CHEN, SHI, & KAIHO, 2002, p. 154 [**M. meishanensis*; OD; =*Paranorellina*? *changxingensis* LIAO, 1984, p. 283, subj.]. Small and smooth shells with reversed fold and sulcus; subpentagonal to subcircular in outline; subequi- to dorsibiconvex in profile; anterior commissure rectimarginate to broadly sulcate; ventral median fold visible on umbonal region; shallow dorsal median sulcus beginning anterior to midlength; external surface with concentric growth lines and microscopic radial striae; few, short, round plicae, limited to anterior margins; lateral slopes smooth; beak and foramen small but distinct. Ventral valve with short, indistinct teeth; dental plates thin, short, fused to shell walls in early stage, then separate but laterally placed; dorsal inner hinge plate united posteriorly and divided

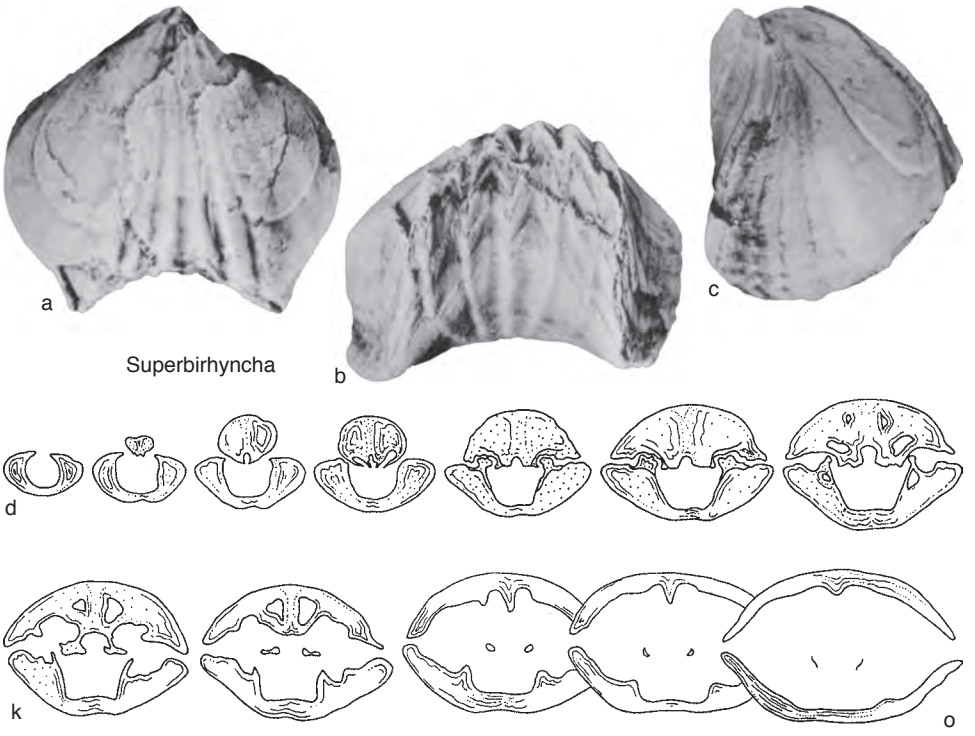

FIG. 1824. Rhynchonellidae (p. 2733–2734).

anteriorly; myophragm low, short; crura apparently spinuliform. [The claim that LIAO's species (which holds priority as a subjective synonym) is a *nomen nudum* is wrong; examination of well-preserved specimens held at Nanjing support a valid species with plainly smooth surface, thus alleged radial striae seem to be due to decortication of primary layer. In addition, spinuliform crura and overall shape are norellid features and may even be included within the scope of the genus *Paranorellina* DAGYS (like the previous genus).] *Lower Triassic (lowest Scythian=Griesbachian):* China (Zhejiang).——FIG. 1825,*1a–l.* **M. changxingensis* (LIAO), Griesbachian, Induan, upper Yinkeng Formation, Meishan; *a–d,* holotype, dorsal, anterior, ventral, posterior views, NMV P1456852, ×6; *e–l,* transverse serial sections, distances in mm from ventral umbo, 0.4, 0.6, 0.7, 1.0, 1.2, 1.3, 1.5, 1.9, NMV P1456856, ×4 (Chen, Shi, & Kaiho, 2002).

Family FRIELEIIDAE Cooper, 1959

Parasphenarina MOTCHUROVA-DEKOVA, SAITO, & ENDO, 2002, p. 301 [**P. cavernicola*; OD]. Micromorphic, teardrop-shaped, subcircular to suboval in outline, subequibiconvex in profile; shell thin, translucent to transparent, mostly smooth, but may bear radial striae on protegular nodes; anterior commissure rectimarginate; beak pointed, suberect; foramen hypothyrid, deltidial plates disjunct, auriculate. Dorsal valve lacking median ridge, but a shallow groove between two paired low ridges is often present instead. Crura spinuliform; cardinal process and septalium absent; hinge plates and inner socket ridges discrete posteriorly. [Living species are bathyal or from submarine caves. This further requires deletion of the Holocene record from Flores Sea in the previous entry for *Sphenarina* (MANCEÑIDO & others, 2002, p. 1325). In addition, the validity of distinguishing Frieleiinae from Hispanorhynchiinae on the basis of presence or absence of septalium has been questioned by MOTCHUROVA-DEKOVA, SAITO, & ENDO (2002).] *Holocene:* Japan and Flores Sea (off Bali).——FIG. 1826*a–l.* **P. cavernicola*, Miyako Island, Okinawa, Japan; *a–c,* holotype, dorsal, lateral, anterior views, UMUT RB 28220-MN01-a, ×15; *d,* detail of protegular nodes, UMUT RB 28220-R1-7; *e,* detail of ventral beak, UMUT RB 28219-R4-1; *f,* juvenile ventral interior, UMUT RB 28220-R5-11; *g–l,* transverse serial sections, distances in mm from ventral umbo, 0.5, 0.7, 0.8, 0.95, 1.05, 1.2, UMUT RB 28220-MN01-c, ×18 (Motchurova-Dekova, Saito, & Endo, 2002).——FIG. 1827*a–f.* **P. cavernicola*, Miyako Island, Okinawa, Japan; *a,* ventral interior, UMUT RB 28220-R2-9; *b,* dorsal

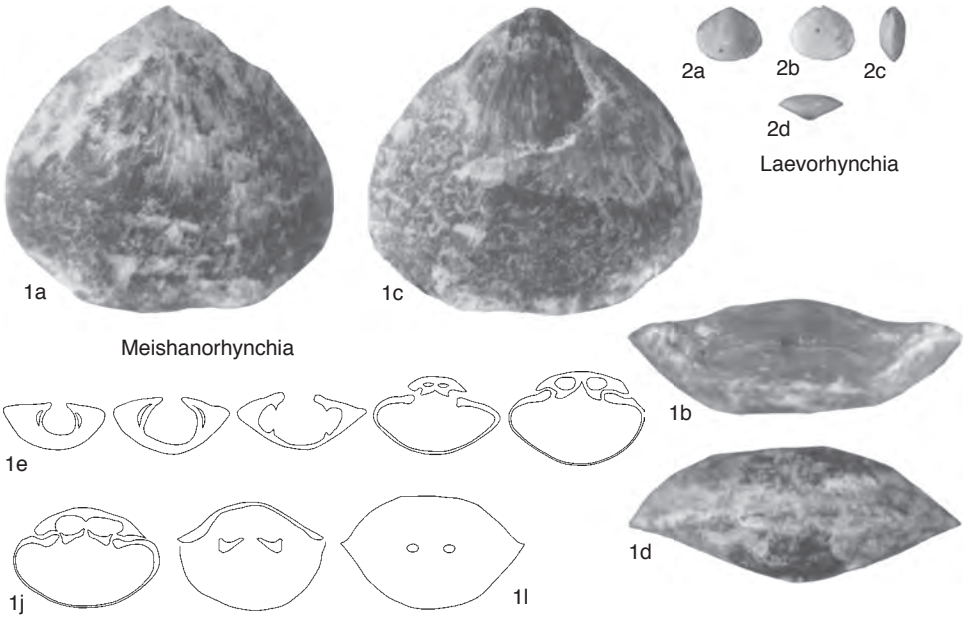

FIG. 1825. Norellidae (p. 2734–2735).

interior oblique view, UMUT RB 28220-R1-12; *c,* cardinalia, UMUT RB 28220-R1-3; *d,* detail of juvenile crus, UMUT RB 28220-R5-4; *e,* detail of crura, UMUT RB 28220-R1-10; *f,* schizolophe inside juvenile, UMUT RB 28214-MD03-a, ×32 (Motchurova-Dekova, Saito, & Endo, 2002).

Superfamily HEMITHIRIDOIDEA Rzhonsnitskaia, 1956

Family CYCLOTHYRIDIDAE Makridin, 1955

Subfamily CYCLOTHYRIDINAE Makridin, 1955

Woodwardirhynchia SIMON & OWEN, 2001, p. 57 [**Cretirhynchia cuneiformis* PETTITT, 1950, p. 6; OD]. Costate dorsibiconvex shells, slightly wider than long; costae dense, becoming subangular toward margins, with narrow intervening sulci; beak short and curved; beak ridges distinct, flanking conspicuous palintrope; hypothyridid, auriculate foramen. Pedicle collar well developed; dental plates divergent ventrally in their early stages and subparallel to slightly convergent anteriorly; forked hinge plates, generally short, triangular in outline with a ventral concave surface; crura diverging laterally, inwardly concave, and becoming straight in transverse section near distal end; thin median septum persistent on dorsal valve floor. [This genus was segregated from *Cretirhynchia* PETTITT and assigned to Cyclothyridinae.] *Upper Cretaceous (Turonian–Maastrichtian):* England, France, Belgium, ?Poland, ?India.——FIG. 1828*a–m.* **W. cuneiformis* (PETTITT), upper Turonian, Bardouville near Rouen, Seine Maritime, France; *a–e,* ventral, dorsal, lateral, anterior, posterior views, IRScNB IST 10832, ×1.74; *f–m,* transverse serial sections, distances in mm from ventral umbo, 2.35, 2.65, 3.15, 3.75, 4.2, 4.55, 4.8, 5.05, IRScNB IST 10832, approximately ×1.65 (Simon & Owen, 2001).

Family TETRARHYNCHIIDAE Ager, 1965

Subfamily CRETIRHYNCHIINAE Kats, 1974

?Harmignirhynchia SIMON & OWEN, 2001, p. 85 [**Cretirhynchia intermedia* PETTITT, 1950, p. 14; OD]. Multicostate, slightly biconvex, symmetrical shells, transversely oval in outline, always wider than long; lenticular in anterior view and lateral profile; numerous faint costae, sometimes reduced in number near commissure. Dental

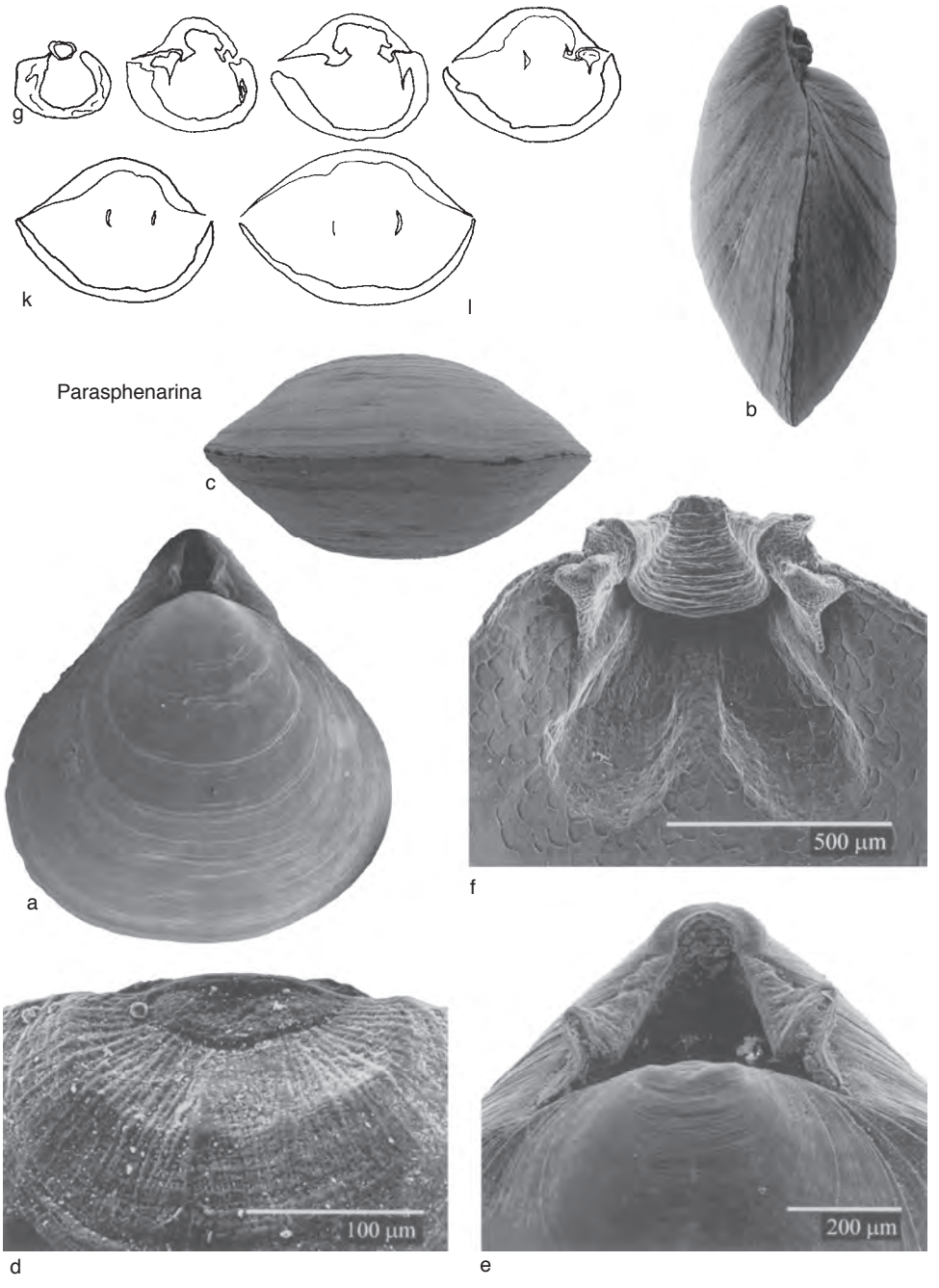

FIG. 1826. Frieleiidae (p. 2735–2736).

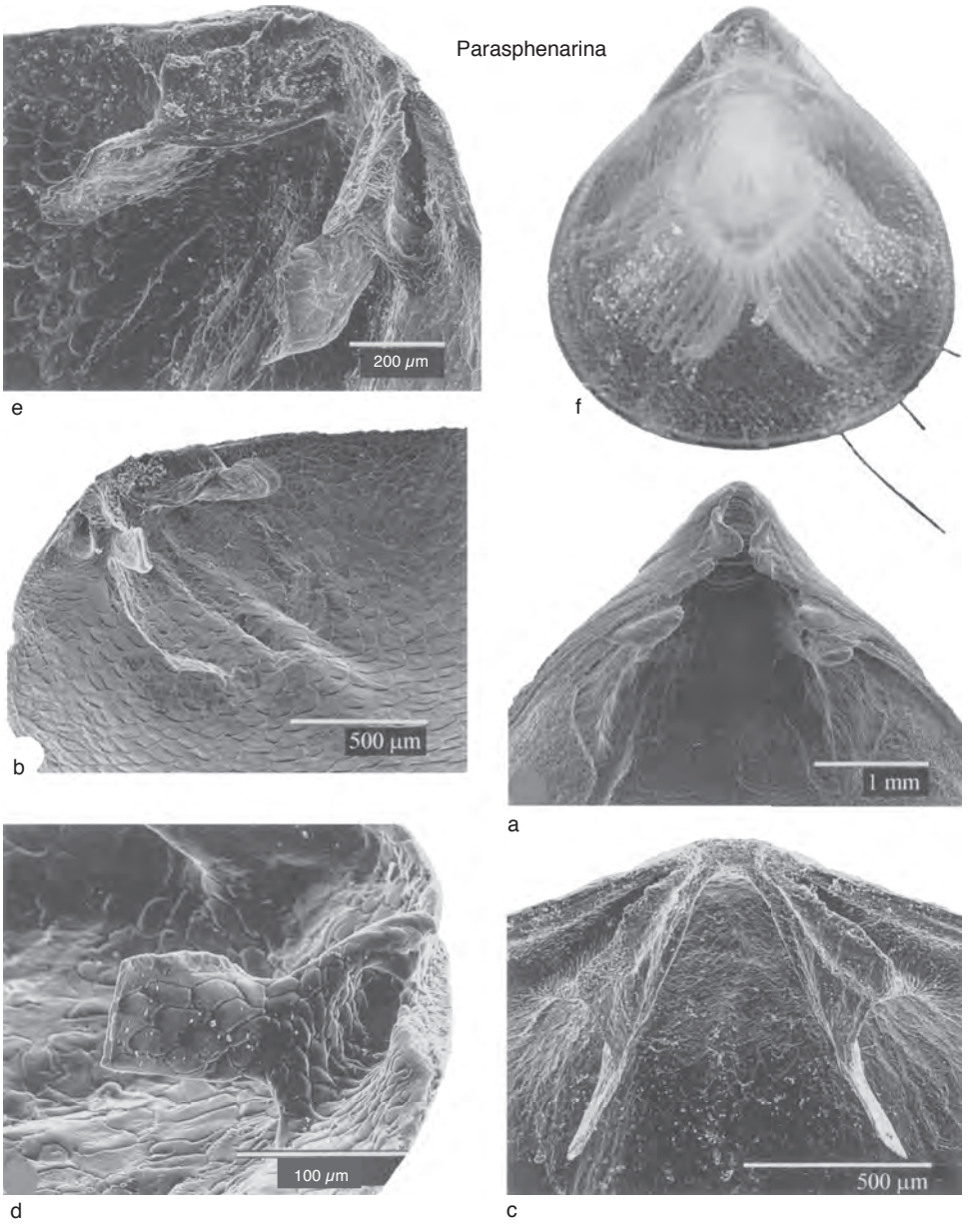

FIG. 1827. Frieleiidae (p. 2735–2736).

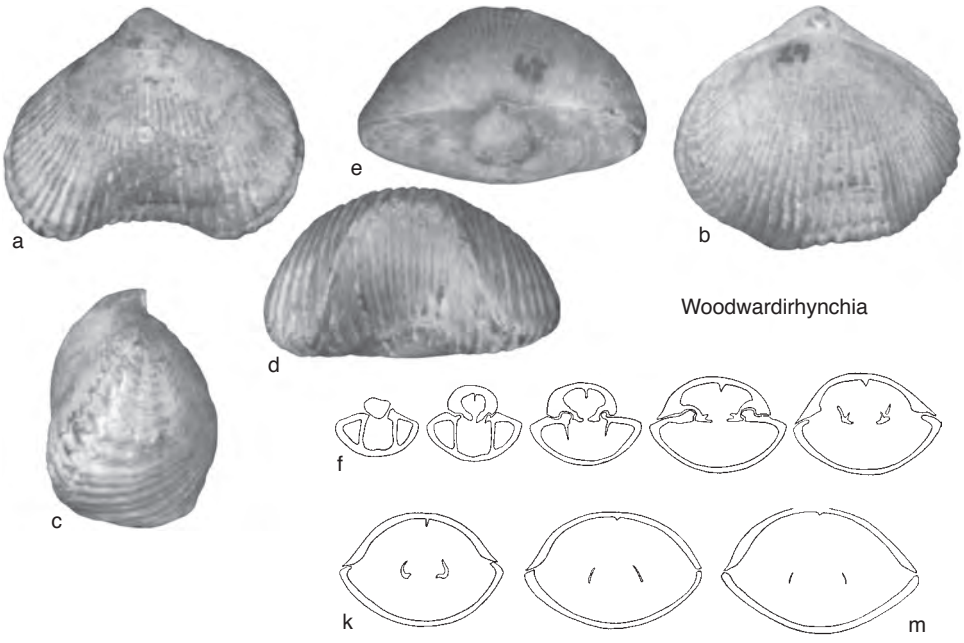

FIG. 1828. Cyclothyrididae (p. 2736).

plates convergent ventrally; dorsal myophragm low, short; hinge plates relatively wide and crural bases subquadrate but often inwardly concave; posterior part of crura strongly concave; crura steep, deflected ventrally, remaining close together or slightly diverging laterally; angle formed by distal parts of crura widely obtuse in transverse section. [Originally proposed as a subgenus of *Cretirhynchia* PETTITT, this genus is admittedly a close ally to *Homaletarhynchia* SIMON & OWEN; yet, both may be treated independently for having also such affinities to aphelesiines as inwardly concave crura, resembling subfalciform-hamiform in scope.] *Upper Cretaceous (lower Campanian–upper Campanian):* United Kingdom, Belgium.——FIG. 1829,*1a–m.* **H. intermedia* (PETTITT), lower Campanian, East Harnham, Wiltshire, England; *a–e,* topotype, ventral, dorsal, lateral, anterior, posterior views, BMNH B.92742-5, ×2.4; *f–m,* transverse serial sections, distances in mm from ventral umbo, 2.3, 3.0, 3.8, 4.15, 4.65, 4.85, 5.15, 5.55, BMNH B.92742-5, approximately ×1.46 (Simon & Owen, 2001).

?Homaletarhynchia SIMON & OWEN, 2001, p. 91 [**Terebratulites limbatus* VON SCHLOTHEIM, 1813, p. 113; OD]. Medium-sized, symmetrical, biconvex shells; ornamentation generally smooth or with very faint radial grooves; development of costae limited to anterolateral commissure; beak small, pointed, and generally curved; beak ridges well developed; hypothyridid foramen with conjunct, protruding deltidial plates. Dental plates ventrally convergent; pedicle collar rarely developed; dorsal myophragm stout, long; very strong hinge structure, with ventrally expanded inner socket ridges; crural bases subquadrate, crura slightly concave in their posterior part, remaining close together. [Originally proposed as a subgenus of *Cretirhynchia* PETTITT, this may be regarded as a full genus, perhaps ancestral to *Aphelesia* COOPER, due to inwardly concave crura, resembling hamiform-subfalciform in scope. Additional evidence in support of sound family reallocation is forthcoming from current detailed SEM studies of excavated crura and shell microstructure by MOTCHUROVA-DEKOVA and SIMON (2007).] *Upper Cretaceous (Santonian–*

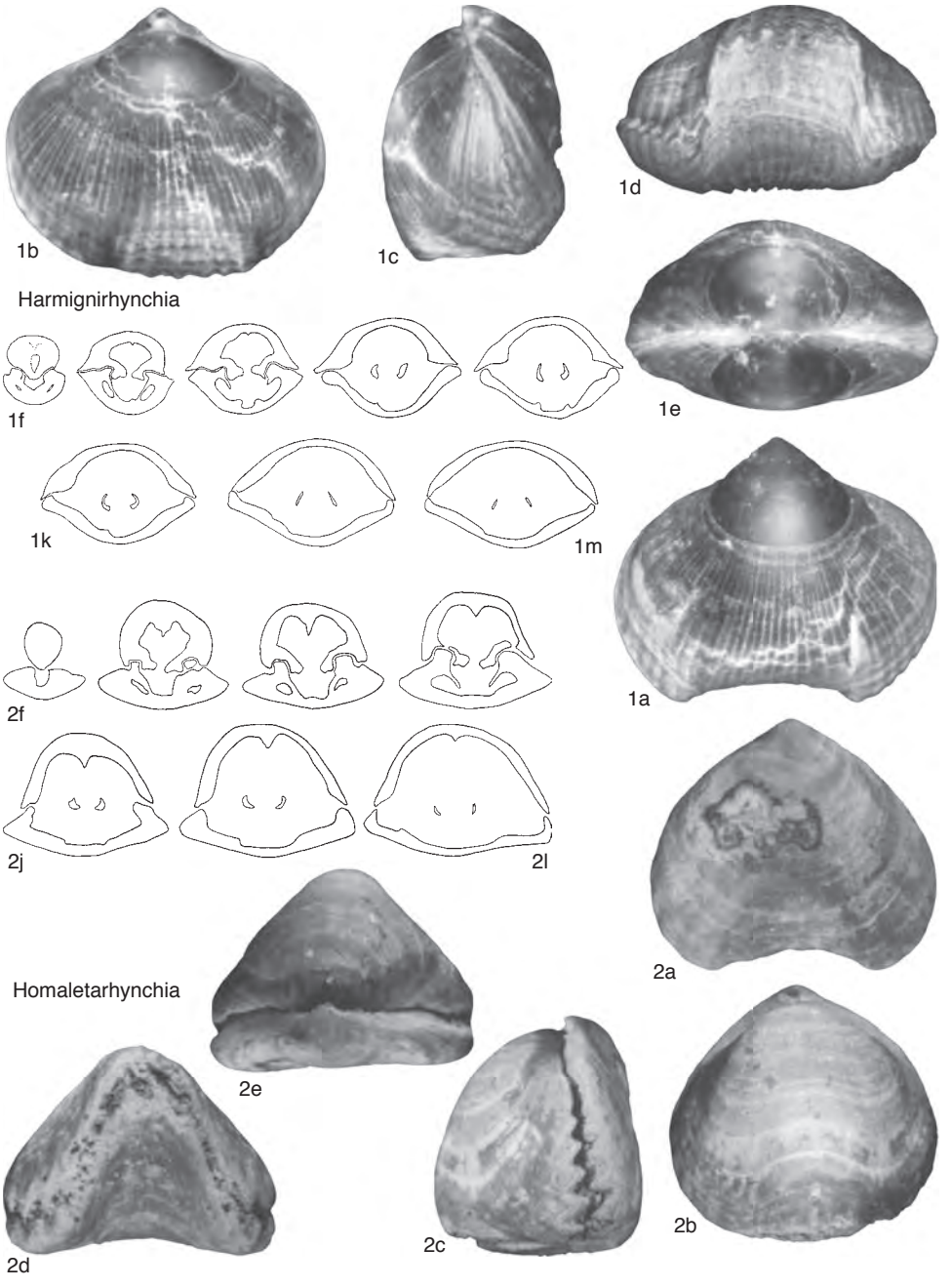

FIG. 1829. Tetrarhynchiidae (p. 2736–2741).

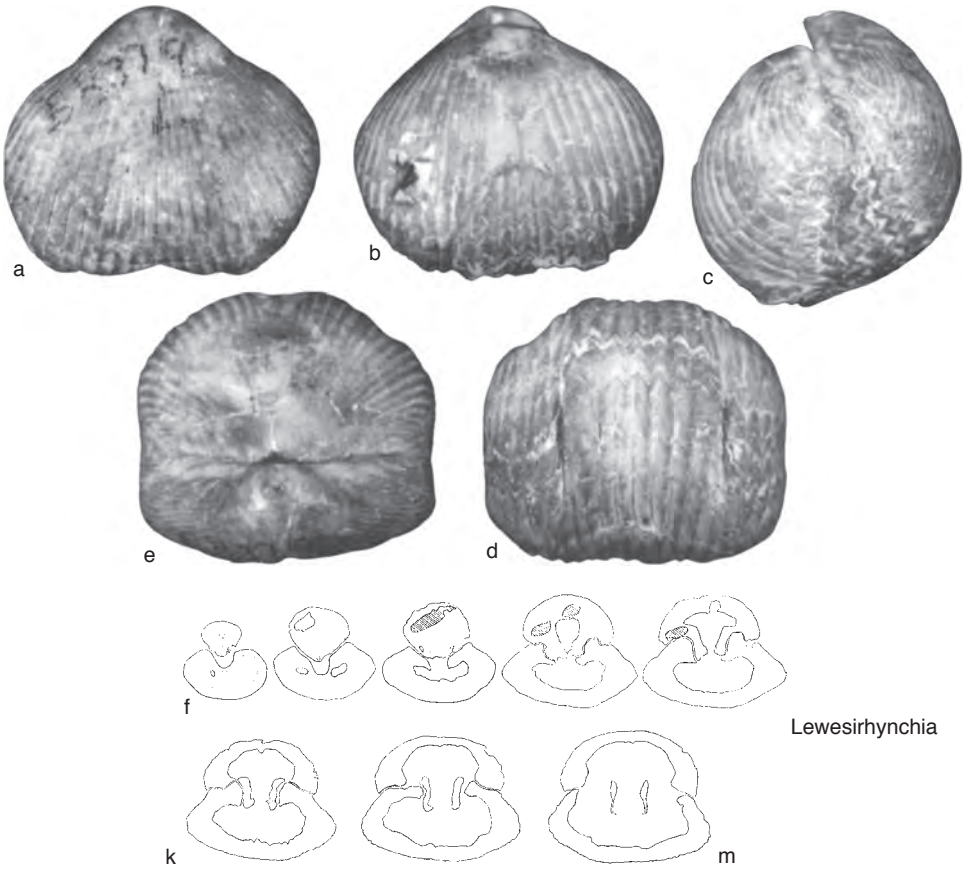

FIG. 1830. Tetrarhynchiidae (p. 2741).

Maastrichtian): England, Ireland, France, Belgium, Germany, Poland.—— FIG. 1829,*2a–l.* **H. limbata* (VON SCHLOTHEIM), upper Maastrichtian, Jandrain, Brabant, Belgium; *a–e,* hypotype, ventral, dorsal, lateral, anterior, posterior views, IRScNB IST 10838, ×1.87; *f–l,* transverse serial sections, distances in mm from ventral umbo, 0.8, 1.6, 2.0, 2.3, 2.55, 2.9, 3.2, IRScNB IST 10838, approximately ×1.65 (Simon & Owen, 2001).

Lewesirhynchia SIMON & OWEN, 2001, p. 77 [**Terebratula octoplicata* J. SOWERBY, 1816, in 1815–1818, p. 37; OD]. Multicostate, biconvex, symmetrical shells, with numerous costae generally faint near umbo, becoming elevated toward margins; near commissure, costae sometimes reduced in number, but incipient splitting of them is observed occasionally. Thick shelled, umbo filled with callus; pedicle collar absent; thick dental plates, convergent ventrally; dorsal myophragm variably developed; inner socket ridges extending anteriorly; hinge plates very small, triangular, becoming anteriorly indistinct; crural base inwardly concave, developing with hinge plate and anterior part of inner socket ridge, original hook structure visible in transverse section; crura raduliform, slightly diverging. [This genus was originally proposed as a subgenus of *Cretirhynchia* PETTITT, but both genera may be treated independently, pending further revision.] *Upper Cretaceous (Coniacian–lower Campanian, ?lower Maastrichtian):* United Kingdom, ?India. ——FIG. 1830*a–m.* **L. octoplicata* (SOWERBY), Coniacian, Chalk, Lewes, Sussex, England; *a–e,* topotype, ventral, dorsal, lateral, anterior, posterior views, BMNH B.8379-1, ×1.77; *f–m,* transverse serial sections, distances in mm from ventral umbo, 3.5, 4.35, 4.75, 5.65, 6.1, 6.65, 7.3, 8.05, BMNH B.8379-1, approximately ×1 (Simon & Owen, 2001).