

RETZIIDINA

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All retziidines, as here considered, are endopunctate in contrast to the impunctate condition of athyridines and koninckinidines. A tertiary layer is absent in the retziidines, being present in the koninckinidines and in some athyridines. The ribbed or plicate (rarely smooth) shells of the retziidines and their cardinalia resemble those of the rhynchonellides from which they differ mainly in the calcification of a spiralium similar to those present in the athyridines. The primary whorls of each spiral cone grew near the midline of the shell, coiled approximately parallel with the plane of symmetry, and were united by a posteriorly situated jugum, commonly spiny, but without a saddle and stem (Fig. 1079–1080). Accessory jugal lamellae are known in some genera. In the Neoretziinae the accessory jugal lamellae are secondarily connected to the spiralia, and in the Hungarispirinae they are intercalated with spiralia loops to the apex (Fig. 1079). In the three retziidine superfamilies a pedicle collar is commonly present, but the dental plates are extremely short or absent. A cardinalia is present and is more like the cardinal plate of the athyridines than the septalium of meristelloids and retzielloids (Fig. 1081–1082). The outer hinge plates are well developed in contrast to the inner hinge plates, which are commonly short, without a dorsal foramen, or absent. Moderately to strongly developed cardinal flanges protrude posteroventrally (Fig. 1082), and a moderate to very high dorsal median septum is commonly present beneath the cardinal plate. Externally, *Parazyga* diverged from other ribbed rhynchospirinoids through the development of numerous, long, hollow spines anteriorly or anterolaterally directed and not known in any other athyridid taxa (see ALVAREZ,

1999b). The mongolospiroids differ from all other retziidines in the smoothness of the shell, a character sufficiently important in itself to warrant a different superfamilial grouping.

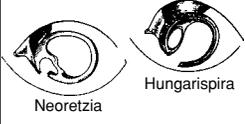
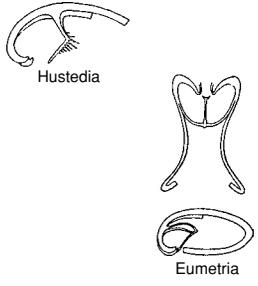
Triassic	 <p>Neoretzia Hungarispira</p>
Permian	
Carboniferous	 <p>Hustedia</p> <p>Eumetria</p>
Devonian	 <p>Trematospira Parazyga</p>
Silurian	 <p>Rhynchospirina</p>

FIG. 1079. Main types of retziidine brachidium (Alvarez, 1999).

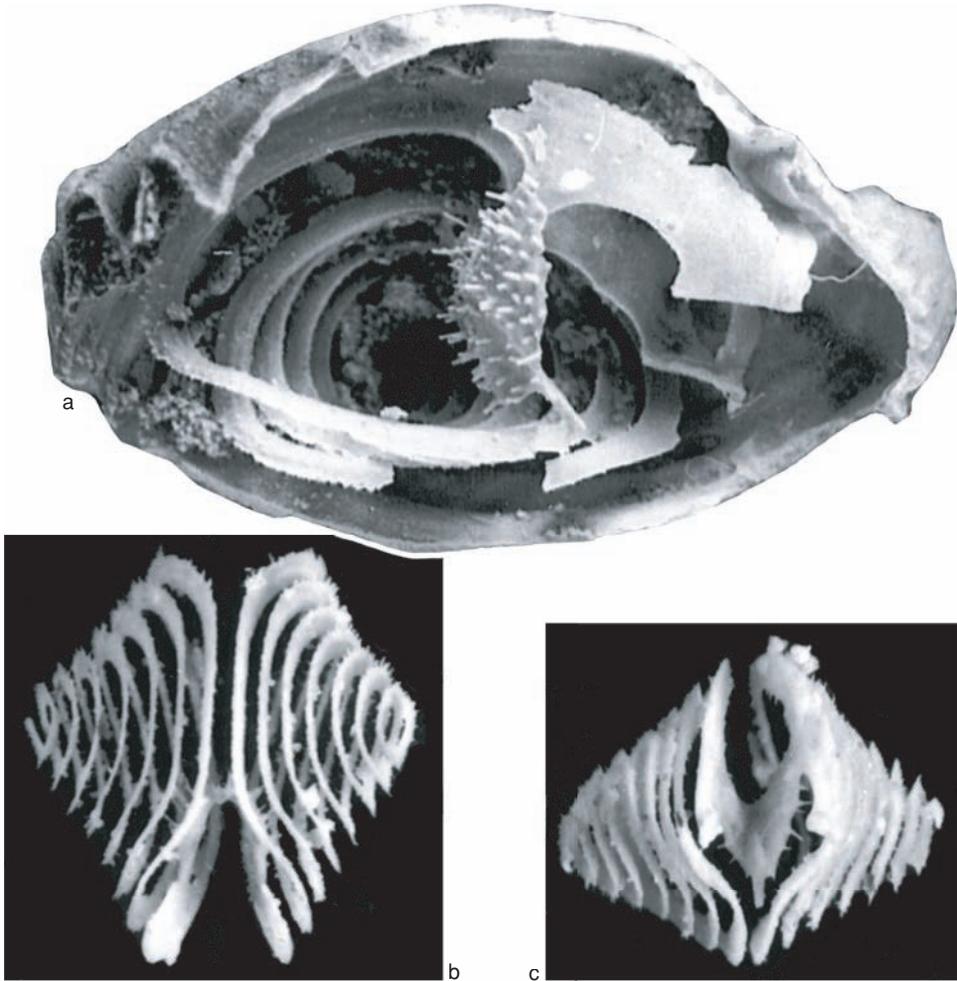


FIG. 1080. *a*, Side view of broken specimen of *Hustedia pugilla pugilla* COOPER & GRANT, showing large, spiny jugum, USNM 154482b, $\times 10$; *b-c*, ventral and posterior views of complete and spiny spiralium with jugum, USNM 154482a, $\times 8$ (Alvarez, 1999; photographs courtesy of the late G. A. Cooper & the late R. E. Grant).

Suborder RETZIIDINA Boucot, Johnson, & Staton, 1964

[*nom. correct.* BOUCOT, JOHNSON, & STATON, 1965, p. 649, *pro* suborder Retzioida BOUCOT, JOHNSON, & STATON, 1964, p. 813; *emend.*, ALVAREZ, RONG, & BOUCOT, 1998, p. 845]

Ribbed or plicate, rarely smooth, with or without spines, moderately to strongly rostrate, astrophic to almost strophic athyridides *sensu lato*; commonly with distinct

ventral area and umbo moderately to strongly curved; delthyrium commonly completely covered; pedicle collar commonly present; dental plates commonly absent; hinge plate without dorsal foramen, commonly short or absent; outer hinge plates well developed; cardinal flanges moderately to strongly developed; moderate to very high dorsal median septum commonly present; jugum commonly spiny and posteriorly

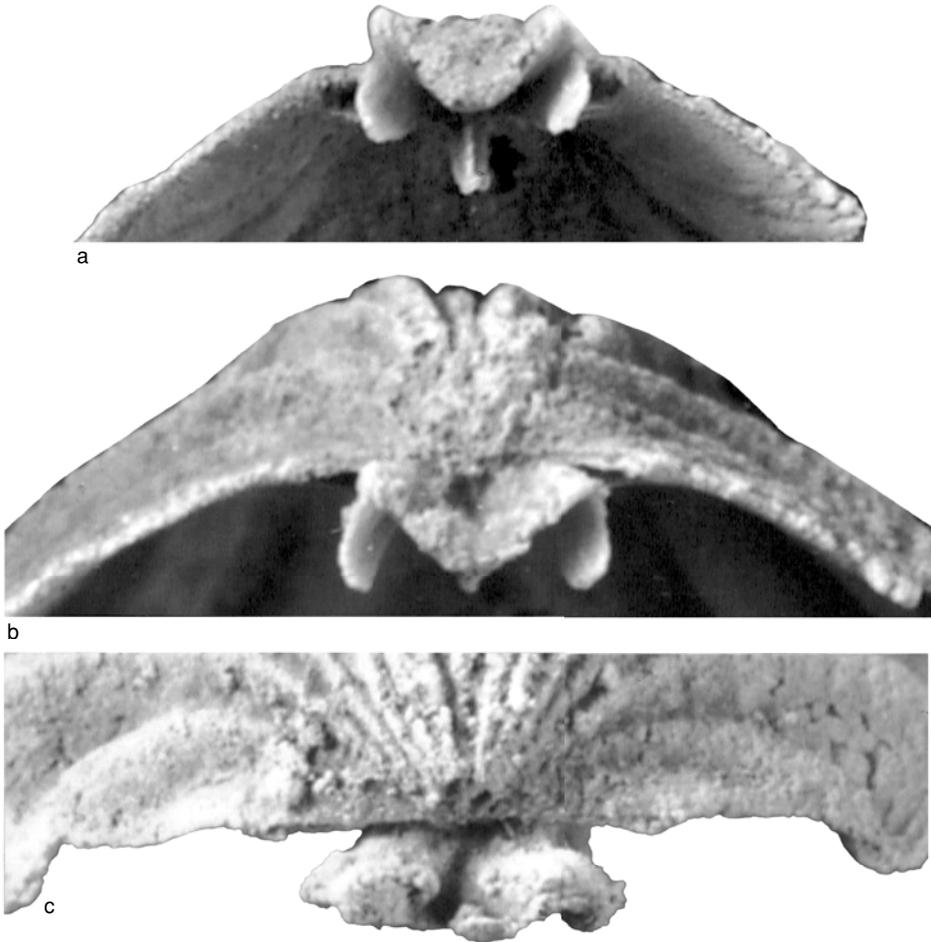


FIG. 1081. *a–c*, *Hustedia glomerosa* COOPER & GRANT, ventral, posteroventral, and posterior views of cardinalia, USNM 154455a, $\times 10$ (new; photographs courtesy of the late G. A. Cooper & the late R. E. Grant).

situated; jugal saddle absent; short, roof-shaped process directed posteriorly from jugum may be present; jugal stem may be present; accessory jugal lamellae commonly absent, rarely secondarily connecting with spiralia (Neoretziinae) or intercalating with spiralia loops to the apex (Hungarispirinae); shell substance punctate (punctae simple, nonbranching, in oldest taxa, branching intensively in the Triassic Neoretziinae and Hungarispirinae); tertiary layer absent. [WATERHOUSE (1981), considering that the suborder Retziidina (sensu BOUCOT, JOHNSON, & STATON, 1964) differs substantially from spiriferides, atrypides, and athyridides,

proposed placing it in a separate order, Retziida. WATERHOUSE provides as a diagnosis for the order the one given by BOUCOT, JOHNSON, & STATON (1964) for the suborder but did not discuss its contents. Most authors prefer to consider the retziidines as a suborder (the most derived within the athyridides; e.g., ALVAREZ, RONG, & BOUCOT, 1998) rather than as an independent order. Doing so reduces the number of paraphyletic groups named in the phylogenetic analysis of the spirebearers (see discussion by ALVAREZ & CARLSON, 1998).] *Silurian (lower Llandovery)–Upper Triassic (upper Norian)*.



FIG. 1082. 1a–b, Posterior (SEM, $\times 22$) and ventral (SEM, $\times 20$) views of *Homoeospira evax* (HALL), cardinalia, USNM 497429 (new); 2, ventral view of *Trematospira multistriata* (HALL), cardinalia, I2120, Hall collection, SEM, $\times 9$; 3, ventral view of *Rhynchospirina formosa* (HALL), cardinalia, I1859, Hall collection, SEM, $\times 20$ (Alvarez & Brime, 2000).

Superfamily RETZIOIDEA Waagen, 1883

[*nom. correct.* HARPER, 1993, p. 448, *pro* Retziacea BOUCOT, JOHNSON, & STATON, 1964, p. 813, *nom. transl. ex* Retziinae WAAGEN, 1883, p. 486; *emend.*, ALVAREZ, RONG, & BOUCOT, 1998, p. 845]

Retziidines clear astrophic to almost strophic in younger taxa, with strongly to very strongly rostrate shells, ribbed or costate in younger taxa; growth lines weak, closely spaced; frills not developed; alternate adult folding to opposite folding in younger taxa (neoretziidines); ventral cardinal area (palintrope) moderate to extensive in younger taxa, apsacline to orthocline; dental plates absent (except *Retzia*); cardinal plate nonperforate; cardinal flanges developed moderately to strongly, in younger taxa; dorsal median septum present, except in *Eumetria*, and very high in *Retzia* and Triassic taxa; jugal stem present and long; arms and differently developed accessory jugal lamellae may be present, especially in

younger taxa. *Silurian* (upper Ludlow)–*Upper Triassic* (upper Norian).

Family RETZIIDAE Waagen, 1883

[*nom. transl.* HALL & CLARKE, 1894, p. 840, *ex* Retziinae WAAGEN, 1883, p. 486; *emend.*, ALVAREZ, RONG, & BOUCOT, 1998, p. 845]

Astrophic shell commonly large; subequally biconvex, elongate-oval costate, commonly without fold and sulcus; median and flank costae same width; deltidial plates conjunct; foramen in permesothryridid position; ventral umbo strongly curved; pedicle collar commonly present; arms of jugum present but not developed into accessory jugal lamellae. *upper Silurian* (?Ludlow), *Lower Devonian*–*Lower Permian*.

Retzia KING, 1850, p. 137 [**Terebratula adrieni* DE VERNEUIL & D'ARCHIAC, 1845, p. 471; OD] [= *Trigeria* BAYLE, 1878, pl. 13, obj.]. Thin but high dental plates; pedicle collar well developed; cardinal flanges, thin and flat, projecting posteroventrally; hinge plate short, in comparison with long, flat outer hinge plates, supported by high, thin median septum; jugum projecting posteroventrally as long

stem that may give rise to short, pronglike bifurcations or become thick and spiny. *upper Silurian* (?Ludlow), *Lower Devonian–Lower Carboniferous* (Viséan): ?Fergana, ?Urals, ?Inner Mongolia, ?Ludlow; Spain, France, Germany, Kuznetsk, Altay, Novosibirsk area, southern China (Guangxi), *Lower Devonian–Middle Devonian*; Donetz, Kuznetsk, Kazakhstan, Siberia, northeastern China, *Upper Devonian–Lower Carboniferous* (Viséan).—FIG. 1083, 1a–aa. **R. adrieni* (DE VERNEUIL & D'ARCHIAC), upper Emsian, Asturias, Spain; a–e, lectotype, dorsal, ventral, lateral, anterior, and posterior views, D852, de Verneuil Collection, $\times 1$ (new; photographs courtesy of N. Podevigne); f–r, transverse serial sections showing umbonal regions 0.20, 0.60, 0.80, 1.10, 1.30, 1.50, 2.10, 2.30, 2.60, 2.70, 2.90, 3.30, 3.60 mm from ventral umbo, DPO/F24242; s–z, transverse serial sections showing cardinalia and brachidium 1.30, 1.60, 5.00, 5.60, 6.00, 6.30, 6.40, 6.60 mm from ventral umbo, DPO/F24243 (new); aa, lateral view of jugum (Hall & Clarke, 1893).

Acambona WHITE, 1865, p. 27 [**A. prima*; OD]. Externally similar to *Eumetria* but slightly longer and finely costate; pedicle collar present; cardinal flanges moderately developed, projecting posteriorly; spiralia and jugum unknown. [Although WHITE's contribution was presented to the Boston Society of Natural History on February 5, 1862, the papers presented to the Society during the years 1862 and 1863 were published in 1865 in volume IX of the Proceedings.] *Lower Carboniferous* (upper *Tournaisian–lower Viséan*): North America, ?Belgium, ?Kazakhstan, ?Mongolia.—FIG. 1083, 2a–b. **A. prima*, Iowa; dorsal and lateral views, $\times 1$ (Weller, 1914).

Eumetria HALL, 1863b, p. 59 [**Retzia vera* HALL, 1858a, p. 704; SD WAAGEN, 1883, p. 487]. Symphytium gently incurved; foramen in permesothyrigid position; dental plates absent; incipient pedicle collar poorly developed or absent; hinge plate raised high above dorsal valve floor by outer hinge plates; high cardinal flanges ventrally forked; median septum absent; lateral branches of jugum originating well posteriorly, projecting anteriorly at low angle; jugal arch projecting posteroventrally as long, straight stem bifurcating into short arms. [Fixation of type species is usually credited to HALL (1863b) or DALL (1877). HALL, however, did not explicitly designate a species as type species for *Eumetria* and included more than one, therefore it is not possible to apply the principle of monotypy, and DALL (1877, p. 28) gave two types for *Eumetria*: *Retzia vera* HALL and *R. serpentina* DE KONINCK. The first unequivocal designation of the type species seems to be that of WAAGEN (1883, p. 487), who properly considered *Retzia vera* HALL, as the type of the genus (Article 69.1; ICZN, 1999).] *Lower Carboniferous–Lower Permian*: North America, Belgium, Kazakhstan, Kuznetsk basin, Siberia, Verkhoyansk, northeastern and southern

China, ?Australia (New South Wales), *Lower Carboniferous*; Spitzbergen, Verkhoyansk, *Upper Carboniferous*; USA (Maryland), *Lower Permian*.—FIG. 1084a–e. **E. vera* (HALL), Viséan–lower Serpukhovian, Illinois, USA; dorsal, ventral, lateral, anterior, and posterior views, USNM 497426, $\times 1.5$ (new).—FIG. 1084f–r. *E. osagensis* (SWALLOW), Lower Carboniferous, Alberta, Canada; transverse serial sections 1.1, 2.1, 2.4, 2.8, 3.6, 4.2, 5.4, 7.0, 7.4, 8.6, 9.4, 10.0, 11.2 mm from ventral umbo, GSC 63347 (adapted from Carter, 1987).—FIG. 1084s–v. *E. verneuiliana* (HALL), Viséan–lower Serpukhovian, Indiana, USA; s, jugum, ventral view; t, jugum, lateral view (adapted from Hall & Clarke, 1893); u, interior view of articulated but incomplete shell showing cardinalia and large ventral pedicle opening, I 1392, $\times 9.7$; v, interior view of articulated shell (ventral up) showing articulation and cardinalia with ventrally projecting, widely forked cardinal flanges, I 1392, $\times 13.7$ (Brunton, Alvarez, & MacKinnon, 1996).

Family NEORETZIIDAE Dagsy, 1972

[*nom. transl.* GRUNT, 1986, p. 7, ex Neoretziidae DAGYS, 1972, p. 103; *emend.*, ALVAREZ, RONG, & BOUCOT, 1998, p. 845]

Shell commonly small, except in *Neoretzia*; almost strophic; anterior margin may be emarginate; ventral umbo moderately curved in old taxa but straight in several Triassic taxa; ventral cardinal area commonly orthocline; deltidial plates conjunct; pedicle collar may be present; arms of jugum only present in some Triassic taxa in which they continue into accessory jugal lamellae secondarily connected with spiralia (Neoretziinae) or intercalated with spiralia loops to apex (Hungarispirinae). *Silurian* (upper Ludlow)—*Upper Triassic* (upper Norian).

Subfamily NEORETZIINAE Dagsy, 1972

[Neoretziinae DAGYS, 1972, p. 103]

Shell small to large (*Neoretzia*); convexity moderate to strong; strongly to very strongly rostrate; ventral umbo straight or nearly so; costate; fold and sulcus absent or narrow sulcus from umbo present in both valves; moderate to extensive ventral cardinal area; dorsal median septum very high and long; accessory jugal lamellae connect secondarily with spiralia. *Middle Triassic* (Anisian)—*Upper Triassic* (upper Norian).

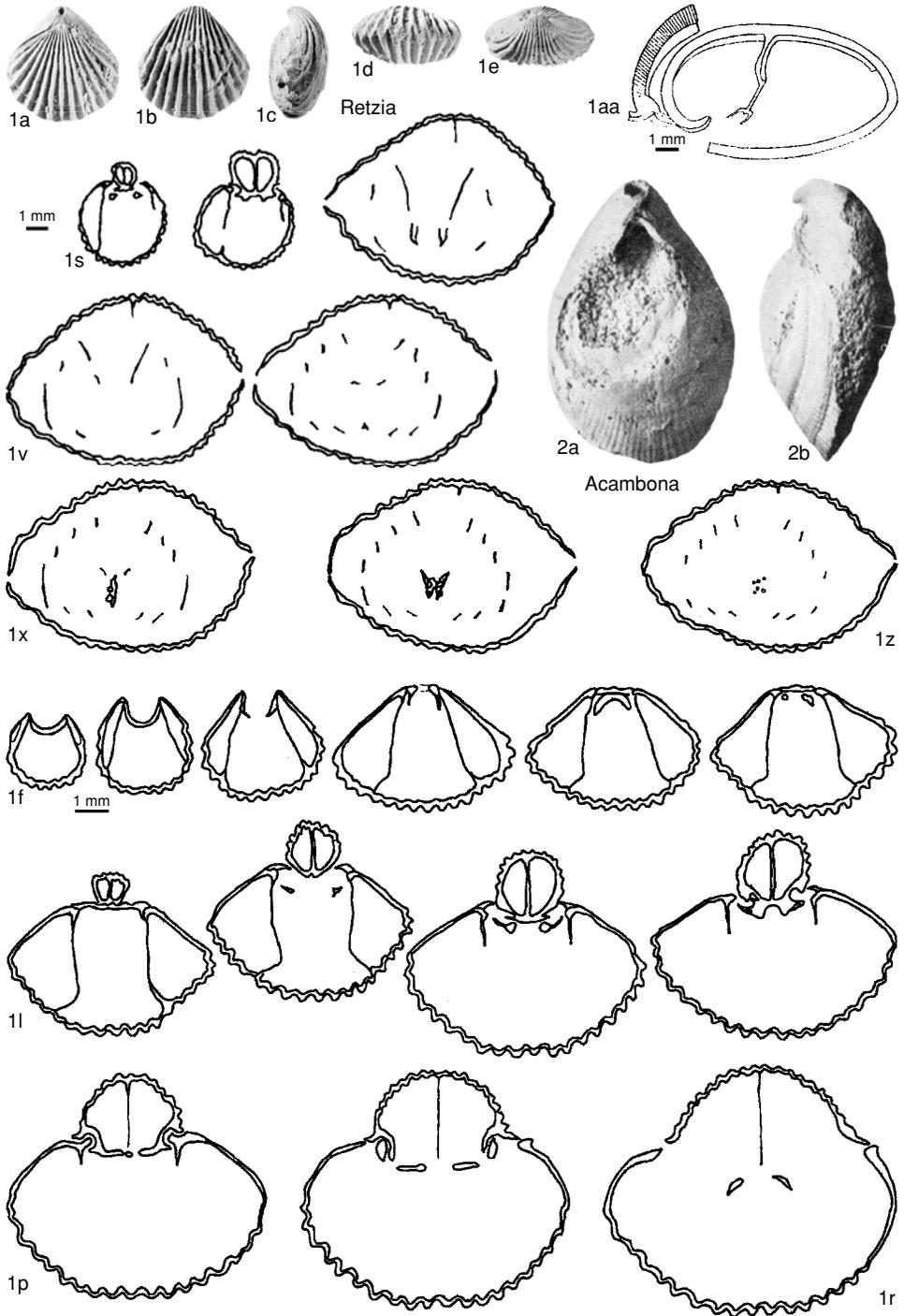


FIG. 1083. Retziidae (p. 1587–1588).

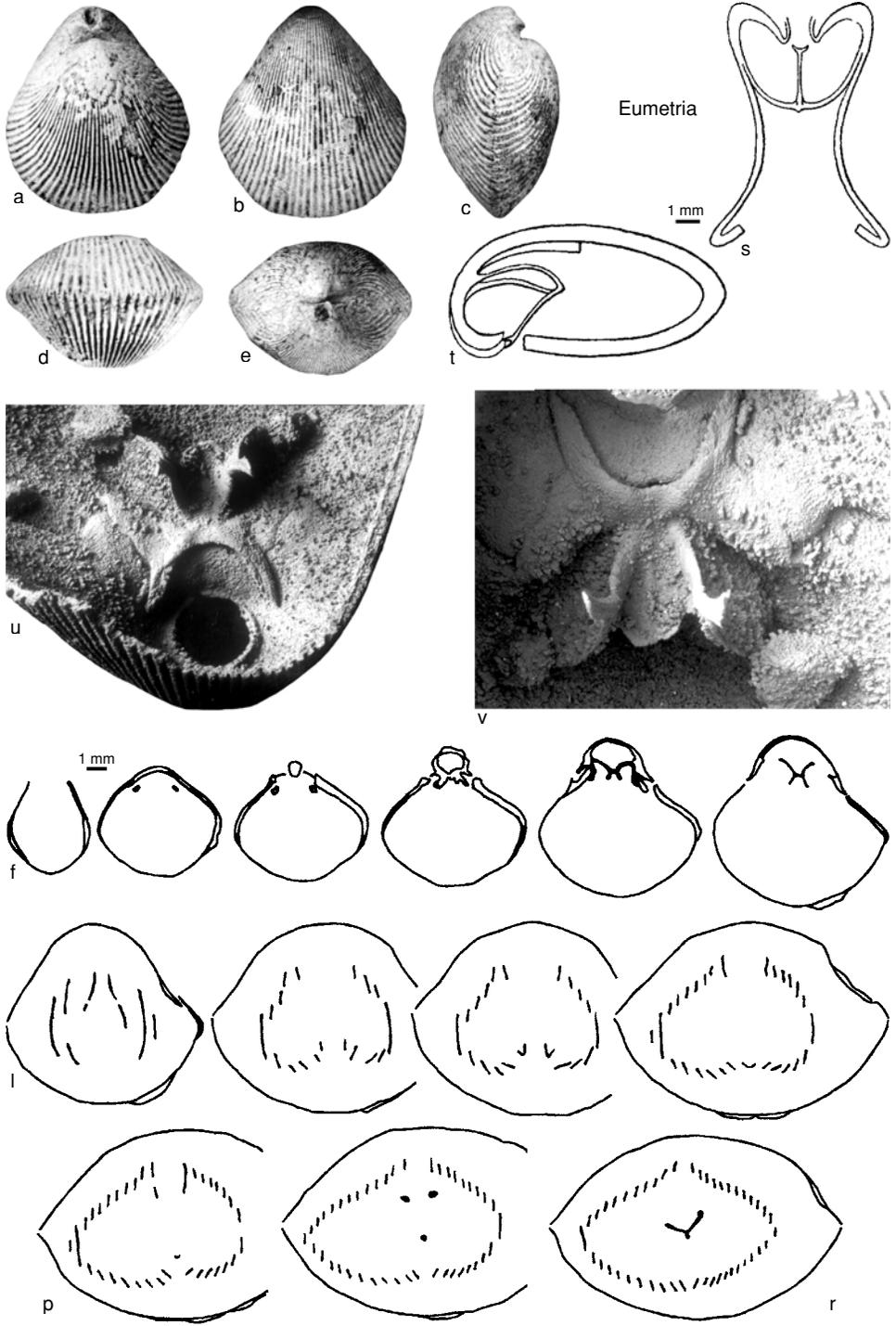


FIG. 1084. Retziidae (p. 1588).

Neoretzia DAGYS, 1963, p. 130 [**Retzia superbescens* BITTNER, 1890, p. 281; OD; = *Waldhemia superba* SUESS in DAVIDSON, 1856, p. 48]. Subequally biconvex, elongate oval shells with few subangular costae; ventral valve beak nearly straight, foramen in permesothyrnid position; internally similar to *Retzia* but without dental plates and with much thicker cardinal flanges and hinge plates; jugum very posteriorly situated, projecting anteroventrally as a complex stem that rejoins primary lamellae on ventral half. *Middle Triassic (Anisian)*—*Upper Triassic (upper Norian)*: Slovakia, *Anisian*; Austria, Hungary, Romania, Crimea, Iran, Caucasus, Himalayas, Pamir, southern and western China (Tibet), *Upper Triassic*.—FIG. 1085, 1a–s. **N. superba* (SUESS), Rhaetian; a, holotype, ventral view, Hirtenberg, Austria, MGBW 3828, $\times 1.3$ (Pearson, 1977); b–d, dorsal, ventral, and lateral views, northern Caucasus, IGiG 47/2443, $\times 1$ (Dagys, 1963; photographs courtesy of the late A. S. Dagys); e–r, transverse serial sections 0.3, 0.8, 1.8, 3.3, 3.7, 4.2, 4.5, 4.9, 6.1, 6.9, 7.6, 8.3, 8.6, 9.1 mm from ventral umbo, distance from ventral umbo to first section approximate, northern Caucasus (adapted from Dagys, 1963); s, jugum, lateral view, northern Caucasus, approximately $\times 1.8$ (Dagys, 1974).

Cassianospira DAGYS, 1972, p. 103 [**Retzia loczyi* BITTNER, 1900, p. 29; OD]. Very small, strongly inequivalve, elongate subpentagonal shells, with few subangular costae and narrow dorsal sulcus with fine median costa extending from umbo; ventral beak very high and straight; symphytium wide and high; foramen in submesothyrnid position; pedicle collar absent; cardinal flanges and hinge plate thick, supported by long septum; jugum not well known, stem essentially as in *Neoretzia*. *Upper Triassic (Carnian)*: southern Alps, Carpathians, Hungary.—FIG. 1085, 2a–m. **C. loczyi* (BITTNER), Hungary; a–d, dorsal, ventral, lateral, and anterior views, IGiG 394/287, $\times 3$ (Dagys, 1963; photographs courtesy of the late A. S. Dagys); e–m, transverse serial sections 0.6, 1.7, 1.8, 2.1, 2.65, 3.2, 3.4, 3.7, 3.9 mm from ventral umbo, distance from ventral umbo to first section approximate, IGiG 394/289 (adapted from Dagys, 1972).

Subfamily HUNGARISPIRINAE

Dagys, 1972

[Hungarispirinae DAGYS, 1972, p. 101]

Shell small; convexity of adult valves moderate; very strongly rostrate; ventral umbo straight; costate; narrow sulcus from umbo present in both valves; ventral cardinal area extensive; dorsal median septum very high and long; accessory jugal lamellae free and intercalated with spirallial loops to apex. *Upper Triassic (Carnian)*.

Hungarispira DAGYS, 1972, p. 102 [**Retzia aracanga* BITTNER, 1900, p. 30; OD]. Similar to *Cassianospira* but multicostate, foramen in permesothyrnid position, jugum projecting posteroventrally as long stem, accessory jugal lamellae continuing intercalated with spirallial loops to apex. *Upper Triassic (Carnian)*: Italy, Hungary.—FIG. 1086, 1a–t. **H. aracanga* (BITTNER), Hungary; a–d, dorsal, ventral, lateral, and anterior views, IGiG 394/284, $\times 3$ (Dagys, 1972; photographs courtesy of the late A. S. Dagys); e–s, transverse serial sections 0.8, 1.6, 1.8, 2.4, 2.6, 2.8, 3.0, 3.1, 3.2, 3.4, 3.5, 3.75, 3.9, 4.1, 4.7 mm from ventral umbo, distance from ventral umbo to first section approximate, IGiG 394/286 (adapted from Dagys, 1972); t, jugum, lateral view (Dagys, 1974).

Subfamily HUSTEDIINAE Grunt, 1986

[Hustedinae GRUNT, 1986, p. 7; emend., ALVAREZ, RONG, & BOUCOT, 1998, p. 847]

Small to medium shell; convexity strong in adult valves (except *Hustedtiella*); strongly rostrate; ventral umbo moderately curved; ribbed (adult shell with fewer than 15 ribs); fold and sulcus, if present, weak and restricted to anterior one-third valve length or narrow sulcus from umbo may develop in both valves; ventral cardinal area moderate; pedicle collar present; dorsal median septum moderately high and short; arms and accessory jugal lamellae absent. *Carboniferous (Tournaisian)*—*Upper Triassic (Carnian)*.

Hustedia HALL & CLARKE, 1893, p. 120 [**Terebratula mormoni* MARCOU, 1858, p. 51; OD]. Subequally biconvex, elongate-oval, costate shells; commissure strongly plicate and slightly uniplicate, rectimarginate, or sulcate; emarginate; costae simple with same width in median region as in flanks, slightly raised median costa on dorsal valve may be present; symphytium transversely flat, longitudinally gently concave; foramen in submeso- to permesothyrnid position; blunt hinge teeth elongate transversely along hinge; pedicle collar short; hinge plate thick, strongly recurved to extend posteriorly along inner face of symphytium, rather short; bladelike crura slightly divergent and directed almost ventrally; short, ligulate process extending forward from base of hinge plate; short median septum in apex beneath hinge plate, extending forward as low median ridge; lateral branches of jugum originating quite posteriorly, projecting anteroventrally as spiny lamellae that join medianly and project posteroventrally in long, sharp, spiny stem. *Carboniferous (Tournaisian)*—*Permian (Tatarian)*: cosmopolitan.—FIG. 1087, 1a–e. **H. mormoni* (MARCOU), Upper Carboniferous, Nebraska, USA; dorsal, ventral, lateral, anterior, and posterior views, USNM

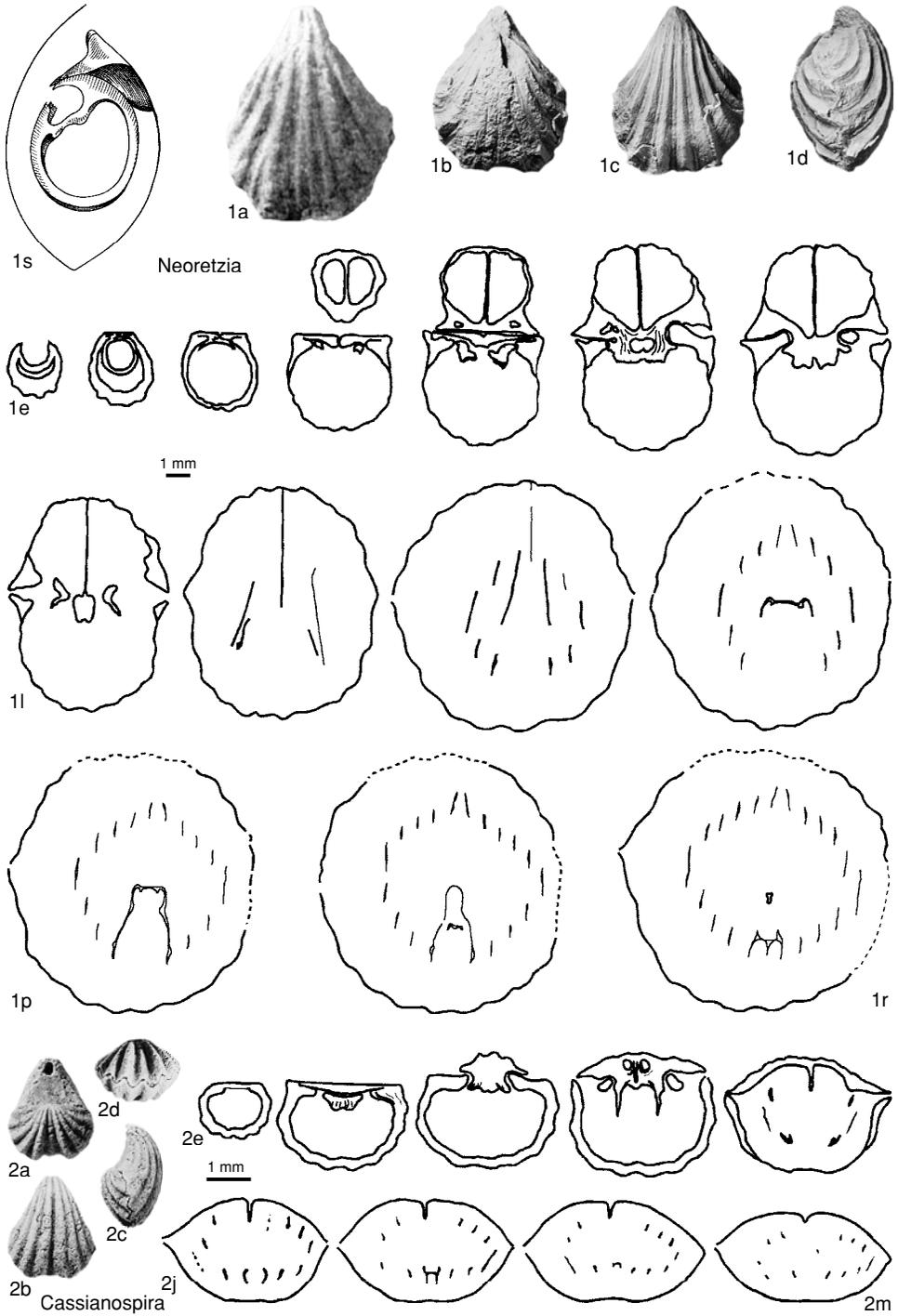


FIG. 1085. Neoretziidae (p. 1591).

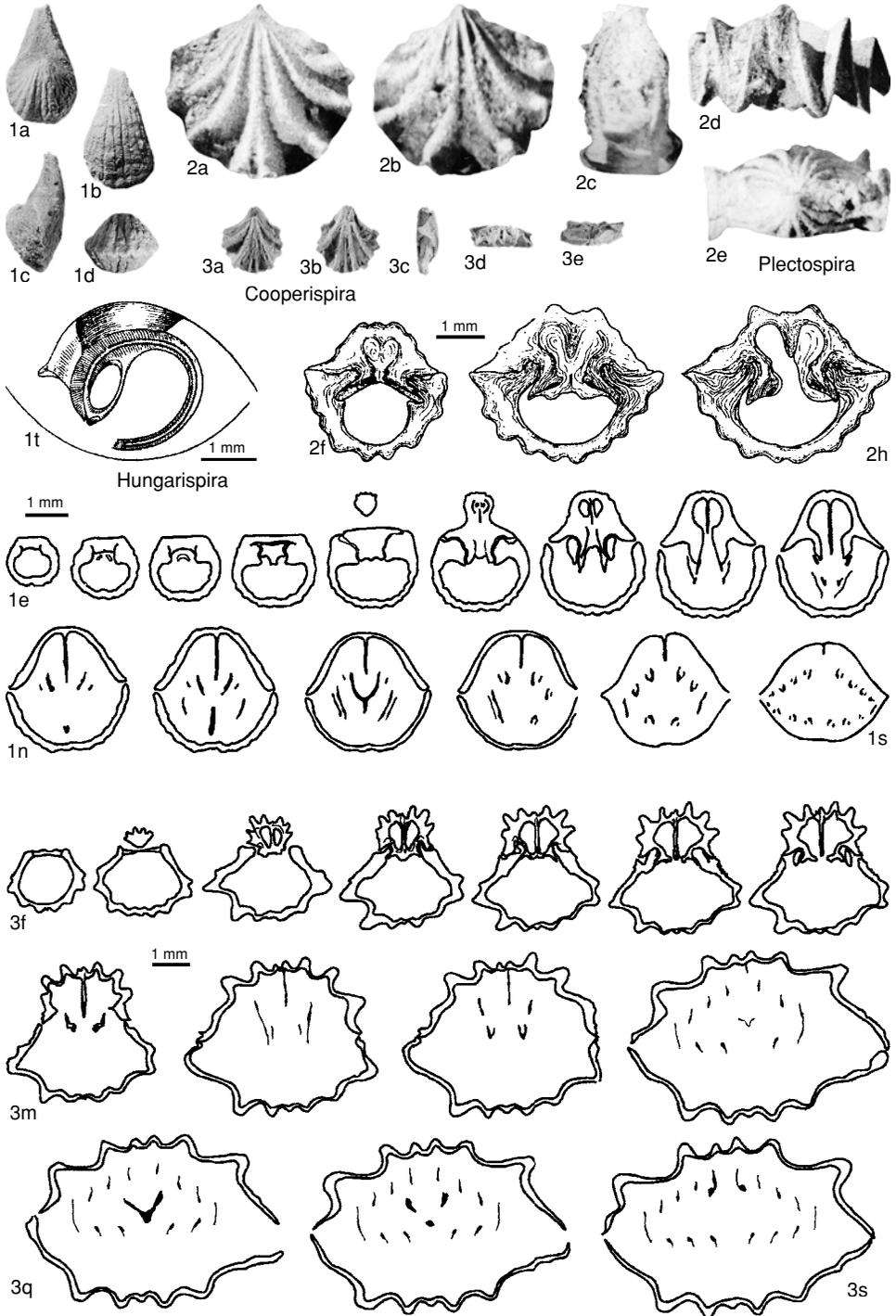


FIG. 1086. Neoretziidae (p. 1591–1596).

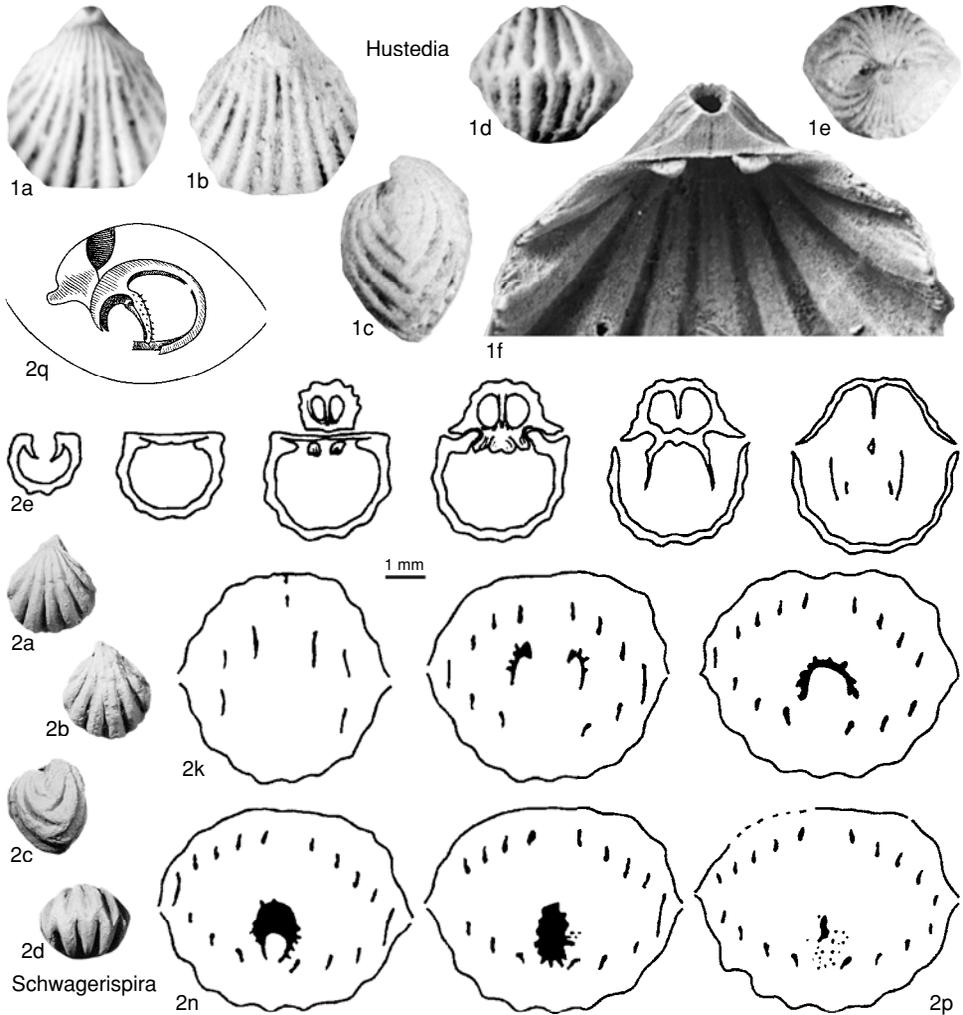


FIG. 1087. Retziidae (p. 1591–1595).

497428, $\times 3$ (new).—FIG. 1087, 1f. *H. glomerosa* COOPER & GRANT, Permian, Texas, USA; ventral umbo viewed dorsally, USNM 154456, $\times 4$ (Cooper & Grant, 1976b). [See also Fig. 1080–1081, p. 1585–1586, in introduction.]

Hustedtiella DAGYS, 1972, p. 100 [**H. planicosta*; OD] [= *Hustedtiella* DAGYS, 1974, p. 166, incorrect subsequent spelling]. Subequally biconvex, longitudinally oval shells with low, rounded costae. Ventral valve beak short, slightly incurved, foramen in mesothyridid position; cardinal plate essentially as in *Schwagerispira* but cardinal flanges less developed, septum shorter and thicker; jugum projecting posteroventrally as short, simple stem. *Lower Triassic*: Russia (Primorya), Romania.—FIG. 1088, 2a–

s. **H. planicosta*, upper Scythian, Primorya; a–d, holotype, dorsal, ventral, lateral, and anterior views, IGiG 380/1, $\times 2$ (Dagys, 1972; photographs courtesy of the late A. S. Dagys); e–r, transverse serial sections 0.3, 0.6, 0.8, 0.9, 1.3, 1.6, 1.9, 2.1, 2.8, 3.1, 3.7, 4.5, 5.0, 5.3 mm from ventral umbo, distance from ventral umbo to first section approximate, IGiG 380/3 (adapted from Dagys, 1972); s, jugum, lateral view, approximately $\times 4$ (Dagys, 1974).

Schwagerispira DAGYS, 1972, p. 101 [**Retzia schwageri* BITTNER, 1890, p. 21; OD]. Subequally biconvex, subcircular shells with coarse, angular costae; foramen in permesothyridid position; cardinal flanges and hinge plates thick, supported by high, thin,

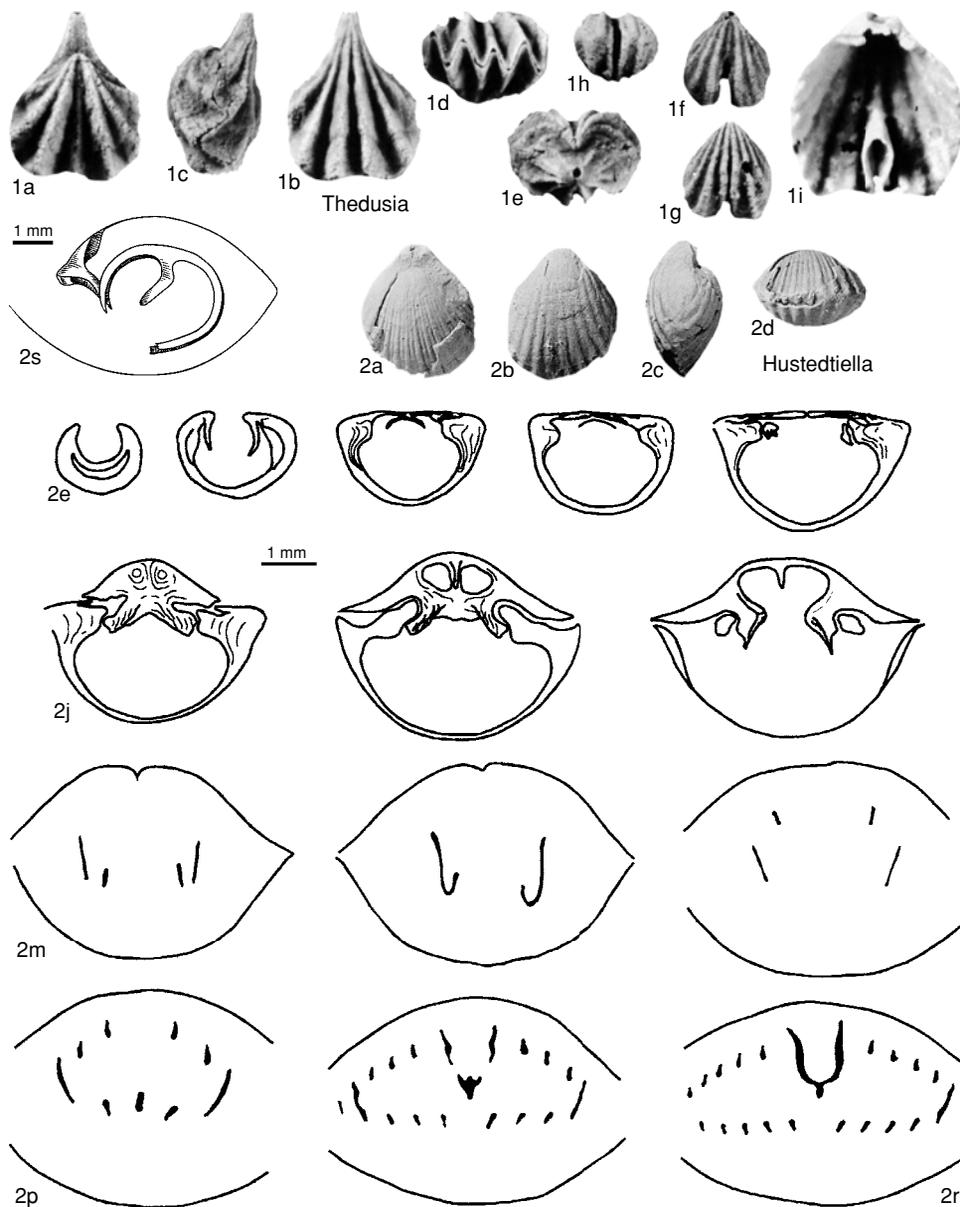


FIG. 1088. Retziidae (p. 1594–1596).

long septum; jugum essentially as in *Hustedtia*. *Middle Triassic (Anisian)–Upper Triassic (Carnian)*: Slovakia, Hungary, Bulgaria, Romania, Primorya, northwestern, southern, and central China, Qinghai.—FIG. 1087, 2a–q. **S. schwageri* (BITTNER), Anisian, Bulgaria; a–d, dorsal, ventral, lateral, and anterior views, IGiG 394/281, $\times 2$ (Dagys, 1972; photographs courtesy of the late A. S.

Dagys); e–p, transverse serial sections 0.3, 0.5, 0.8, 1.05, 1.25, 1.45, 2.1, 2.5, 2.8, 2.9, 3.0, 3.2 mm from ventral umbo, distance from ventral umbo to first section approximate, IGiG 394/283 (adapted from Dagys, 1972); q, jugum, lateral view, approximately $\times 5.5$ (Dagys, 1974).

Thedusia COOPER & GRANT, 1976b, p. 2806 [*Hustedtia meekana trigonalis* GIRTY, 1909, p. 396;

OD]. Similar to *Hustedia* but smaller, dorsibiconvex, having more elongate ventral beak, ligate stage of folding with deep dorsal valve sulcus, and emarginate anterior. *Upper Carboniferous–Upper Permian (Capitanian)*: southern China (Guangxi), *Upper Carboniferous*; USA (western Texas), *upper Sakmarian–Capitanian*.—FIG. 1088, 1a–e. **T. trigonalis* (GIRTY), Capitanian, western Texas; dorsal, ventral, lateral, anterior, and posterior views, USNM 154499d, $\times 3$ (Cooper & Grant, 1976b).—FIG. 1088, 1f–i. *T. discissa* COOPER & GRANT, upper Sakmarian–Artinskian, western Texas; f–h, dorsal, ventral, and anterior views, USNM 153264u, $\times 4$; i, interior of ventral valve, USNM 154497e, $\times 11$ (Cooper & Grant, 1976b).

Subfamily PLECTOSPIRINAE Alvarez, Rong, & Boucot, 1998

[Plectospirinae ALVAREZ, RONG, & BOUCOT, 1998, p. 847]

Shell small; convexity in adult valves strong; strongly rostrate; ventral umbo moderately curved; ribbed (adult shell having fewer than 15 ribs); fold and sulcus narrow and strong, present in entire valve, if costate, different from on flanks; dorsal median septum long and moderately high; arms and accessory jugal lamellae absent. *Silurian (upper Ludlow)–Middle Devonian (Givetian)*, ?*Lower Carboniferous*.

Plectospira COOPER, 1942, p. 228, *nom. nov. pro* *Ptychospira* HALL & CLARKE, 1893, p. 112, *non* SLAVIK, 1869 [**Terebratula ferita* VON BUCH, 1835, p. 76; OD]. Subequally biconvex, pauciplicate shells of lenticular outline, dorsal fold commonly consisting of elevated median plication frequently with median groove in anterior part, which has corresponding ridge in sinus of opposite valve; foramen in submeso- to permesothyrigid position; cardinal plate essentially as in *Homoespira*; jugum projecting posteroventrally as very long, simple stem. *Silurian (upper Ludlow)–Middle Devonian (Givetian)*, ?*Lower Carboniferous*: Europe, Altay, Kuznetsk, China, Australia (New South Wales), *upper Ludlow–Givetian*; North America, Verkhoyansk, Kuzbass, Kuznetsk, Mongolia, eastern Australia, ?*Lower Carboniferous*.—FIG. 1086, 2a–b. **P. ferita* (VON BUCH), Middle Devonian, Eifel, Germany; a–e, dorsal, ventral, lateral, anterior, and posterior views, USNM 497427, $\times 3$ (new); f–h, transverse serial sections 1.50, 1.95, 2.15 mm from ventral umbo, distance from ventral umbo to first section approximate, GIB Nr75 (Siehl, 1962).

Cooperispira ALVAREZ, RONG, & BOUCOT, 1998, p. 847 [**Terebratula subferita* DE VERNEUIL, 1850, p. 174; OD]. Externally resembling *Plectospira* but with subpentagonal outline, elongate ventral beak, narrow and shallow sulcus on ventral valve, with

fine median costa extending from umbo; dorsal valve with wider but also shallow sinus with fine median costa that bifurcates posteriorly, lateral plicae high, angular, sharp crested; foramen in permeso- to epithyrigid position; dental plates and pedicle collar absent; cardinal plate essentially as in *Retzia*; jugum projecting ventrally as very short, simple stem. *Lower Devonian (Emsian)*: northwestern Spain.—FIG. 1086, 3a–s. **C. subferita* (DE VERNEUIL); a–e, dorsal, ventral, lateral, anterior, and posterior views, D690, de Verneuil Collection, $\times 3$ (new; photographs courtesy of N. Podevigne); f–s, transverse serial sections 0.5, 1.2, 1.3, 1.5, 1.7, 1.8, 1.9, 2.0, 2.5, 2.7, 3.5, 3.6, 3.7, 3.9 mm from ventral umbo, DPO/F24239 (Alvarez, Rong, & Boucot, 1998).

Superfamily MONGOLOSPIROIDEA Alekseeva, 1981

[*nom. transl.* ALVAREZ, RONG, & BOUCOT, 1998, p. 847, *ex* Mongolospiridae ALEKSEEVA in ALEKSEEVA, MENDBAIAR, & ERLANGER, 1981, p. 108]

Clearly astrophic retziidines with moderately to strongly rostrate, completely smooth shells; ventral cardinal area (palintrope) moderately developed, almost orthocline; dental plates extremely short, supporting strong teeth; pedicle collar present; hinge plate supported by high, long median septum; jugum without stem. *Lower Devonian*.

Family MONGOLOSPIRIDAE Alekseeva, 1981

[*nom. correct.* GRUNT, 1986, p. 7, *pro* Mongolospiridae ALEKSEEVA in ALEKSEEVA, MENDBAIAR, & ERLANGER, 1981, p. 108, *nom. imperf.*]

Characters as for superfamily. *Lower Devonian*.

Mongolospira ALEKSEEVA, 1977, p. 63 [**M. turgensis*; OD] [=Mongolospira ALEKSEEVA, 1981, p. 108, incorrect subsequent spelling (Art. 33.3, ICZN, 1999)]. Subequally biconvex, elongate-oval, medium shells; dorsal fold and ventral sulcus absent; ventral valve beak high, incurved; deltidial plates conjunct; foramen in permesothyrigid position. *Lower Devonian*: northwestern Mongolia.—FIG. 1089a–l. **M. turgensis*; a–d, holotype, dorsal, ventral, lateral, and anterior views, PIN 3602/1, $\times 2$; e, dorsal view, PIN 3602/3, $\times 3.5$ (Alekseeva, 1977; photographs courtesy of R. E. Alekseeva); f–h, transverse serial sections 0.8, 3.0, 4.3 mm from ventral umbo, showing ventral umbonal region and cardinalia, PIN 3602/8; i–l, transverse serial sections 3.0, 4.0, 4.5, 5.0 mm from ventral umbo, showing spirillum and jugum, PIN 3602/9 (adapted from Alekseeva, 1977).

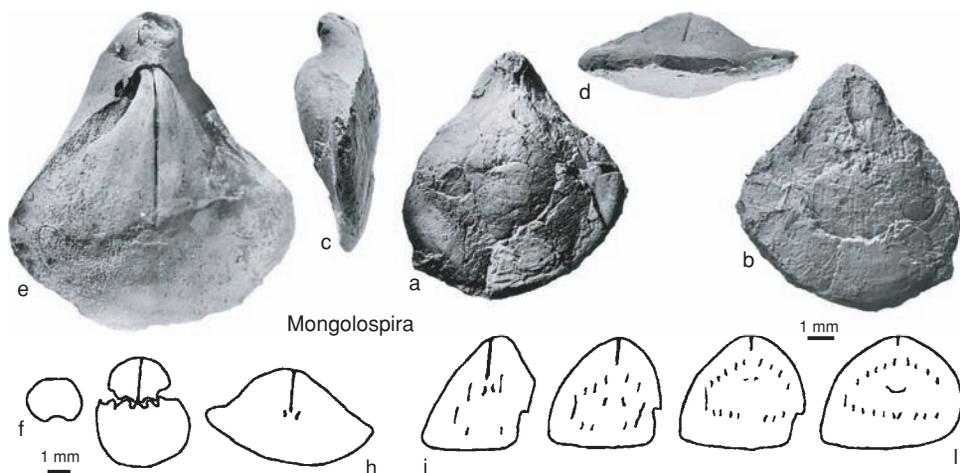


FIG. 1089. Mongolospiridae (p. 1596).

Superfamily RHYNCHOSPIRINOIDEA Schuchert, 1929

[*nom. transl.* ALVAREZ, RONG, & BOUCOT, 1998, p. 847, *ex* Rhynchospirinoidea SCHUCHERT, 1929, p. 22]

Clear astrophic retziidines with moderately rostrate, ribbed shells (adult shells with more than 15 ribs); growth lines weak to strong and commonly widely spaced, may develop into short frills; hollow spines may be present; weak, alternate adult folding; ventral cardinal area (palintrope) reduced, apsacline; short dental plates supporting strong teeth may be present; hinge plate short or absent; jugum projecting backward as broad, short, roof-shaped process, jugal stem absent. *Silurian (lower Llandovery)–Upper Devonian (Frasnian)*.

Family RHYNCHOSPIRINIDAE Schuchert, 1929

[Rhynchospirinoidea SCHUCHERT, 1929, p. 22; *emend.* ALVAREZ, RONG, & BOUCOT, 1998, p. 847] [=Rhynchospirinae SCHUCHERT, 1894, p. 105]

Shell commonly large; ventral umbo strongly curved; deltidial plates commonly conjunct; short, moderately high dorsal median septum present, except in *Homoeospirella*; lateral branches of jugum vertical. [The reference to Article 39 of the Code made by BOUCOT, JOHNSON, & STATON

(1965, p. 652) was based on the 1st Edition of the Code published in 1961. That article was modified in the 2nd Edition (1964) and had changed significantly by the 3rd Edition (1985) [see also 4th ed., 1999]. The new family-group name takes its own author and date, but does not take the priority of the name it has replaced, therefore the date 1894 should not be used. Similarly, the replacement generic name takes its own author and date but does not take the date of the name it replaced.] *Silurian (lower Llandovery)–Upper Devonian (Frasnian)*.

Rhynchospirina SCHUCHERT & LEVENE, 1929b, p. 121, *nom. nov. pro Rhynchospira* HALL, 1859a, p. 29, *non* EHRENBERG, 1845 [**Waldheimia formosa* HALL, 1857a, p. 88; OD] [=Rhynchospira HALL, 1859b, p. 213, *nom. nud.*]. Externally similar to *Homoeospira* but deltidial plates conjunct and foramen in meso- to permesothyridid position; short dental plates may be present; incipient pedicle collar variably developed or absent; cardinal plate trapezoidal with flat cardinal flanges, projecting posteroventrally; hinge plate short (in comparison with long, flat outer hinge plates), thick, extending as transverse process between cardinal flanges and supported by short median septum extending anteriorly as low ridge. *Silurian (Wenlock)–Upper Devonian (Frasnian)*: North America, Venezuela, Podolia, southwestern Urals, Mongolia, Gorno-Altay, western Qinling, Tibet, *Wenlock–Middle Devonian*; Gorno-Altay, *Upper Devonian*.—FIG. 1090, 1a–f. **R. formosa* (HALL), Lochkovian, Lower Helderberg Group, New York, USA; a–e, lectotype, dorsal, ventral, lateral, anterior, and posterior views,

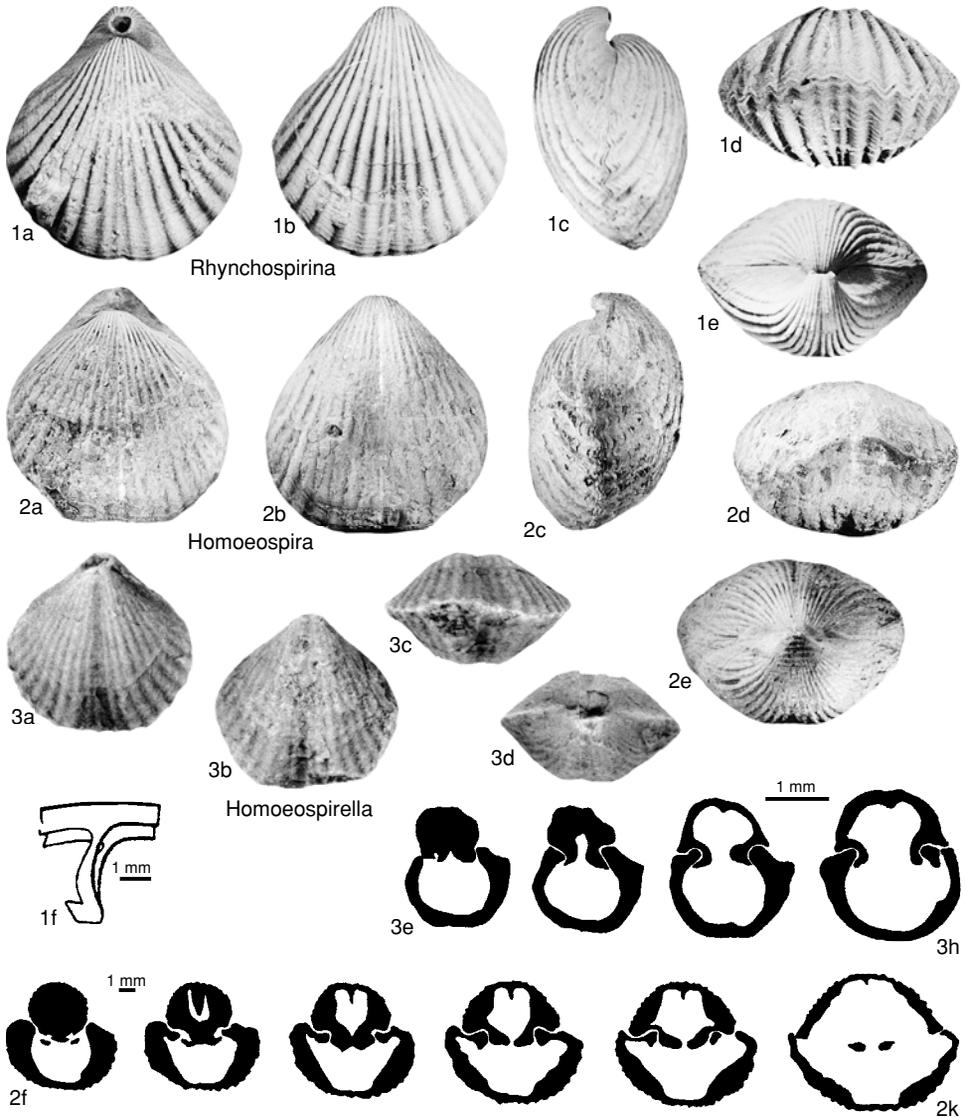


FIG. 1090. Rhynchospirinae (p. 1597–1600).

AMNH 33399, Hall collection, $\times 2$ (Alvarez & Brime, 2000); *f*, lateral view showing jugum (Hall & Clarke, 1893). [See also Fig. 1082.3, p. 1587, in introduction.]

Homoeospira HALL & CLARKE, 1893, p. 112 [**Rhynchospira evax* HALL, 1863a, p. 213; SD HALL & CLARKE, 1894, p. 986]. Subequally biconvex, elongate oval to subpentagonal costate shells, with or without poorly defined fold and sulcus, or shells may be faintly bisulcate; median costae narrower than costae on flanks; delthyrium may be open or restricted by disjunct or conjunct deltidial plates showing median fold; foramen in submeso- to

permesothyridid position; dental plates absent; cardinal flanges poorly developed or absent, hinge plate extremely short, supported by stout median septum extending anteriorly as ridge; long, flat, anteriorly divergent outer hinge plates; jugum essentially as in *Trematospira*. [Fixation of type species is usually credited to SCHUCHERT (1897, p. 231), although the first unequivocal designation of the type species seems to be that of HALL & CLARKE (1894, p. 986). *Homoeospira* is a frequent incorrect subsequent spelling of *Homoeospira*.] *Silurian (Wenlock)–Lower Devonian (Lochkovian)*: North America, ?Argentina, United Kingdom, Gotland,

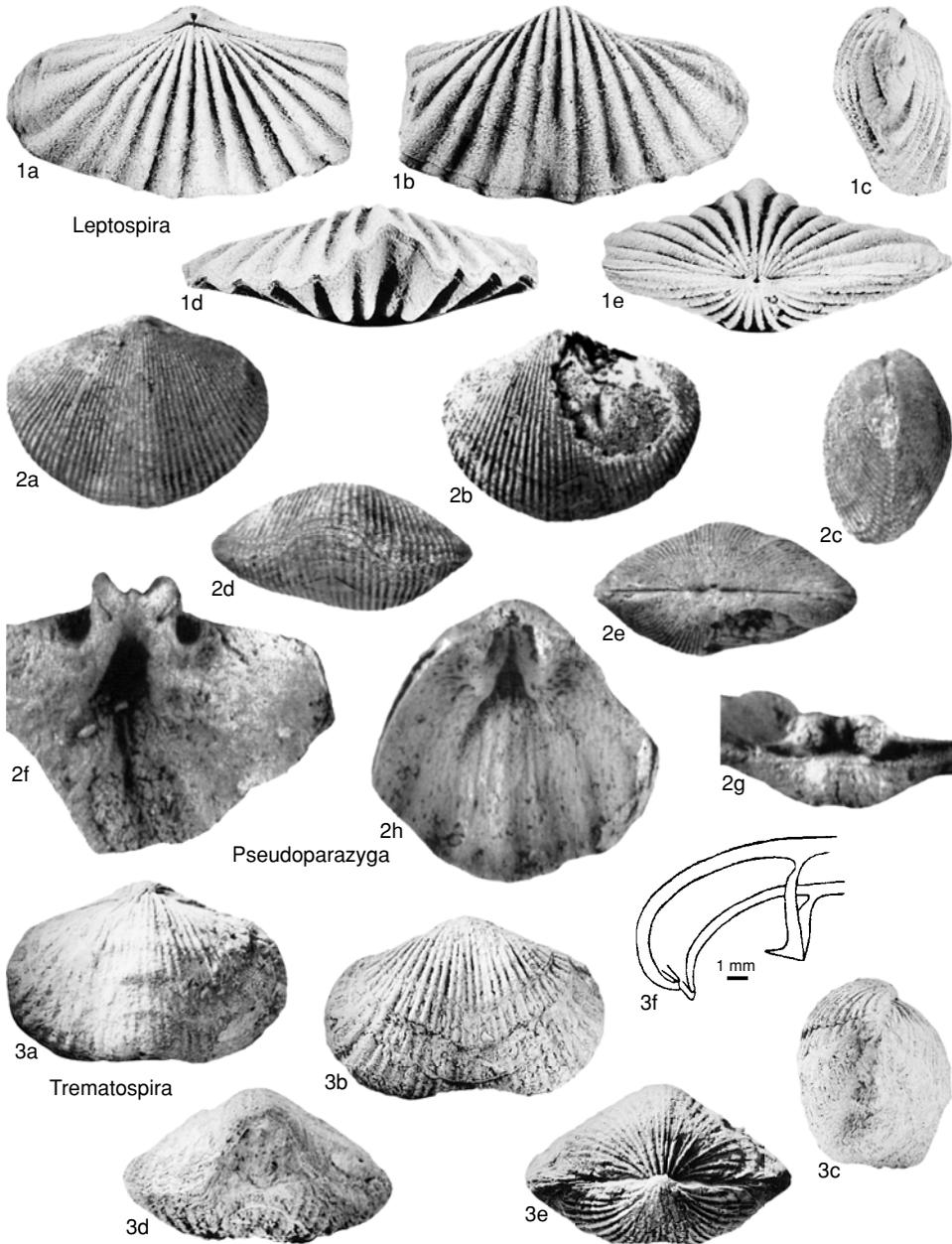


FIG. 1091. Rhynchospirinidae (p. 1600–1601).

Bohemia, Estonia, Ukraine, Vaigach, ?China, Wenlock–Ludlow; Poland, Belgium, Lochkovian. —FIG. 1090, 2a–k. **H. evax* (HALL); a–e, lectotype, dorsal, ventral, lateral, anterior, and posterior views, upper Wenlock, Waldron, Indiana, USA, AMNH 36619, Hall collection, $\times 1.5$ (Alvarez & Brime, 2000); f–k, transverse serial sections 3.8,

4.0, 4.1, 4.6, 4.7, 5.0 mm from ventral umbo, Wenlock, Newson Station, Tennessee, USA, OU 6289 (adapted from Amsden, 1968). [See also Fig. 1082.1, p. 1587, in introduction.]

Homoeospirella AMSDEN, 1968, p. 90 [**H. costatula costatula*; OD]. Resembling *Homoeospira* in external and internal configuration but hinge plate and

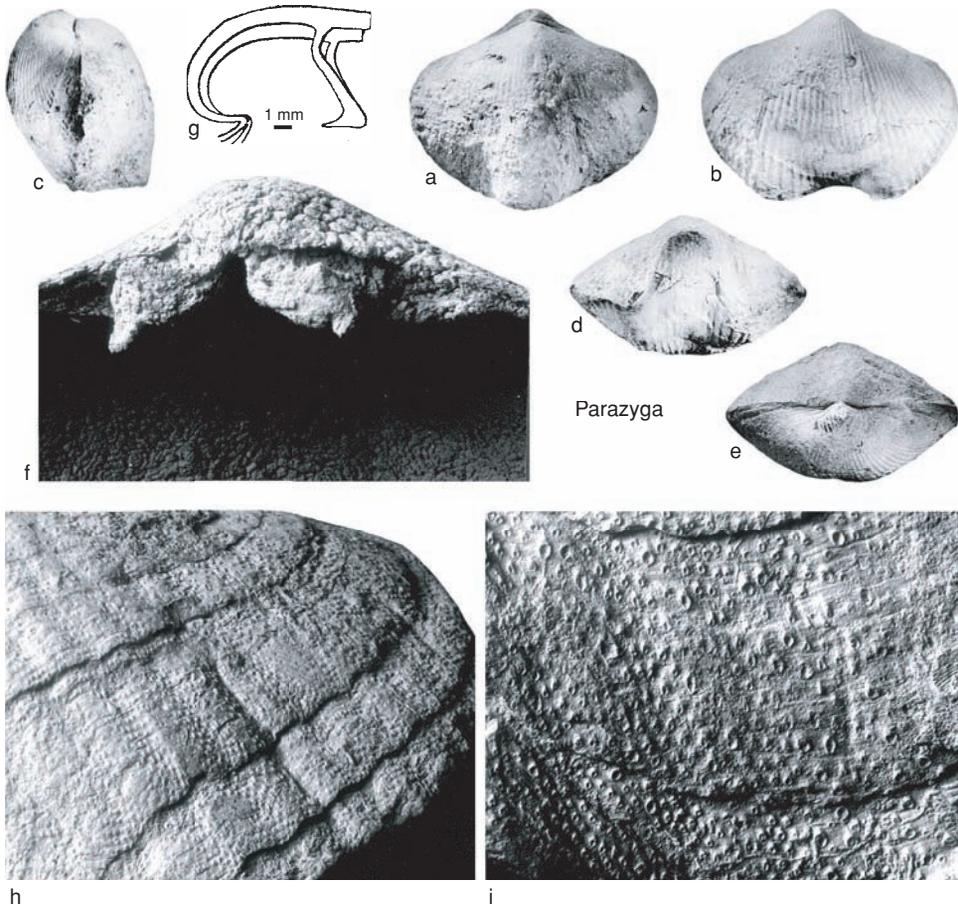


FIG. 1092. Parazygidae (p. 1601).

dorsal median septum absent; spiralia and jugum unknown. *Silurian* (lower Llandovery–Wenlock), *Lower Devonian* (?Pragian): Wales, lower Llandovery; USA (Oklahoma, Arkansas), *Wenlock*; USA (southern Oklahoma), ?Pragian.—FIG. 1090,3a–h. **H. costatula costatula*, Wenlock, Oklahoma, USA; a–d, holotype, dorsal, ventral, anterior, and posterior views, OU 6401, $\times 1$ (Amsden, 1968); e–h, transverse serial sections 0.4, 0.5, 0.7, 0.8 mm from ventral umbo, OU 8439 (adapted from Amsden, 1968).

Leptospira BOUCOT, JOHNSON, & STATON, 1964, p. 814 [**Trematospira costata* HALL, 1859a, p. 27; OD]. External shape as in *Trematospira*, but pauciplicate; cardinalia as in *Rhynchospirina*; spiralia and jugum unknown. [The name *Trematospira costata* is commonly attributed to HALL (1859b, p. 210) but this name was made available by HALL (1859a, p. 27) since in the latter paper the name was accompanied by an indication (Art. 12.2, ICZN, 1999).] *Lower Devonian* (Lochkovian)–

Upper Devonian (lower Frasnian): central and north-eastern USA.—FIG. 1091,1a–e. **L. costata* (HALL), Lochkovian, Lower Helderberg Group, New York, USA; lectotype, dorsal, ventral, lateral, anterior, and posterior views, AMNH 2461, Hall Collection, $\times 2$ (Alvarez & Brime, 2000).

Pseudoparazyga JOHNSON, 1970b, p. 181 [**Trematospira cooperi* MERRIAM, 1940, p. 82; OD]. Similar to *Trematospira* with pedicle collar present and dental plates absent; spiralia and jugum unknown. *Lower Devonian*: USA (Nevada).—FIG. 1091,2a–h. **P. cooperi* (MERRIAM); a–e, holotype, dorsal, ventral, lateral, anterior, and posterior views, USNM 96372, $\times 1$; f–g, interior and posterior views of dorsal valve, USNM 157161, $\times 3$; h, ventral valve interior, USNM 157163, $\times 1.5$ (Johnson, 1970b).

Trematospira HALL, 1859a, p. 27 [**Spirifer multi-striatus* HALL, 1857a, p. 59; SD HALL & CLARKE, 1893, p. 126; validated ICZN Opinion 1900, 1998b, p. 133]. Subequally biconvex, transverse oval, costate shells, commonly with dorsal fold and

ventral sulcus; costae subangular, approximately same width in medial regions as flanks, bifurcating anteriorly; deltidial plates conjunct; foramen in mesothyridid position; short dental plates may be present; greatly elevated cardinal plate deeply divided by median longitudinal groove, thick cardinal flanges projecting into pedicle cavity; small bilobate process may be developed between cardinal flanges, supported by short median septum extending anteriorly as low ridge, frequently obsolete; short, acute, and simple process extending horizontally backward from jugum. *Lower Devonian (Lochkovian–Pragian)*: North America.—FIG. 1091, 3*a–f*. **T. multistriata* (HALL), Lochkovian, Helderberg Group, New York, USA; *a–e*, lectotype, dorsal, ventral, lateral, anterior, and posterior views, AMNH 33375, Hall collection, $\times 1.5$ (Alvarez & Brime, 2000); *f*, lateral view of jugum (Hall & Clarke, 1893). [See also Fig. 1082.2, p. 1587, in introduction.]

Family PARAZYGIDAE
Alvarez, Rong, & Boucot, 1998

[Parazygidae ALVAREZ, RONG, & BOUCOT, 1998, p. 847]

Shell medium with numerous, long, hollow spines anteriorly or anterolaterally directed; ventral umbo moderately curved; moderately long and thick, medially concave dental plates; pedicle collar; triangular outer

hinge plates well developed, projecting posteriorly as thin, flat cardinal flanges; crural bases strongly divergent, inner hinge plates absent; dorsal myophragm present; lateral branches of jugum inclined anteriorly. *Middle Devonian (Givetian)*.

Parazyga HALL & CLARKE, 1893, p. 127 [**Atrypa hirsuta* HALL, 1857a, p. 168; SD HALL & CLARKE, 1894, p. 995]. Subequally biconvex, transversely oval, subcircular or elongate shells with sparse lamellose growth lines; dorsal fold and ventral sulcus commonly present; costae simple, numerous, fine, rounded at same width across shell; conjunct deltidial plates present or absent; foramen in permesothyridid position; dental plates stout; jugum as in *Trematospira* but with lateral branches slightly inclined anteriorly. [Fixation of type species is usually credited to SCHUCHERT (1897, p. 301), but the first unequivocal designation of the type species is that of HALL and CLARKE (1894, p. 995).] *Middle Devonian (Givetian)*: North America.—FIG. 1092*a–i*. **P. hirsuta* (HALL), Hamilton Group, New York, USA; *a–e*, lectotype, dorsal, ventral, lateral, anterior, and posterior views, I1714, Hall collection, Albany, $\times 1.5$; *f*, cardinalia, I1716, Hall collection, $\times 12$ (Alvarez & Brime, 2000); *g*, lateral view of jugum (Hall & Clarke, 1893); *h*, exterior with spines, USNM 497414, $\times 9.5$; *i*, exterior with spines, USNM 497414, $\times 19$ (Alvarez, 1999b).

KONINCKINIDINA

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Since the koninckinidines first came to the notice of paleontologists in the mid-nineteenth century, they have been a source of controversy, particularly with regard to their systematic position. Because of their highly distinctive concavoconvex outline and typically strophic shell, koninckinidines have in the past been regarded by various authors as somewhat unusual strophomenides (COWEN & RUDWICK, 1966; DAGYS, 1973), whereas others have regarded them as spiriferides *sensu lato* (DAVIDSON, 1884; BOUCOT, JOHNSON, & STATON, 1965; WILLIAMS, 1968; BRUNTON & MACKINNON, 1972;

HARPER & others, 1993). MUIR-WOOD (1965) included the Early Jurassic superfamily Cadomelloidea within the Chonetidina, but the subsequent discovery by COWEN and RUDWICK (1966) of a spiral brachidium within *Cadomella davidsoni*, which was included in the genus *Cadomella* by MUIR-WOOD (1965), was considered sufficient grounds for synonymizing the Cadomelloidea with the Koninckinoidea. The type species of *Cadomella*, *C. moorei* (DAVIDSON), however, is now considered to be morphologically and taxonomically quite distinct from *C. davidsoni* (which is herein placed in

Koninckodonta), thus prompting the dissociation of the cadomelloids from the koninckinidines. In this revision, the Cadomelloidea are placed in *incerta sedis* (see volume 5 of *Treatise* Part H, Brachiopoda, Revised, in preparation).

Suborder KONINCKINIDINA Harper, 1993

[Koninckinidina HARPER in HARPER & others, 1993, p. 450]

Smooth, strophic, concavoconvex shells with well-developed interareas in both valves; dental plates absent; spiralia directed ventrolaterally; jugum with accessory lamellae continuing between primary volutions of spiralia to their ends; shell impunctate; tertiary layer present. *Middle Triassic–Lower Jurassic*.

Superfamily KONINCKINOIDEA Davidson, 1853

[*nom. correct.* HARPER in HARPER & others, 1993, p. 450, *pro* Koninckinacea BOUCOT, JOHNSON, & STATON, 1964, p. 820, *nom. transl.* ex Koninckinidae DAVIDSON, 1853b, p. 92]

Quadrato to subtriangular, strongly concavoconvex, smooth shells with very narrow mantle cavity. Pedicle foramen generally very small and permesothyrid to epithyrid. Beak ridges well defined. Hinge line either wide with low, well-developed interareas, or narrow with interareas replaced largely by palintropes in both valves; triangular delthyrium occupied by smooth, convex symphytium arching over small, commonly trilobed, posteromedian callosity in dorsal valve. Cardinalia consisting of posteromedian myophore bounded by a pair of robust inner socket ridges from near distal extremities of which extend a pair of slender, anteroventrally directed, pronglike crura. Brachidium consisting of ventrolaterally directed, paired spiral lamellae; broader, dorsal, primary spiral lamellae diverging from crura at sharp angle and uniting medially in a jugum; narrower, ventral, accessory lamellae originating on jugum and intercoiled with dorsal, primary spiral lamellae to their ends. Secondary layer fibers large and rhomboidal in cross section; thick, prismatic, tertiary shell

layer present; impunctate. *Middle Triassic–Lower Jurassic*.

Family KONINCKINIDAE Davidson, 1853

[Koninckinidae DAVIDSON, 1853b, p. 92]

Characters as for superfamily. *Middle Triassic–Lower Jurassic*.

Koninckina SUESS in DAVIDSON, 1853b, p. 92 [**Producta leonhardi* WISSMANN, 1841, p. 68; OD] [= *Koninckia* SUESS in WOODWARD, 1854, p. 231, *nom. null.*]. Smooth, strongly concavoconvex shells, variably subquadrate in outline with low ventral umbo that is strongly incurved in adults; hinge line straight and well developed; posterolateral shell margins commonly alate; very small epithyrid pedicle foramen and very low interareas commonly obscured by excessive curvature in umbones in adults. [Location of type specimen unknown.] *Upper Triassic*: Italy (Dolomites), Dinaric Alps, Carpathians, Caucasus, Pamirs, Laos, China, Indonesia. —FIG. 1093, 1a–c. **K. leonhardi* (WISSMANN), Dolomites; dorsal, lateral, anterior views, $\times 5$ (new). —FIG. 1093, 1d. *K. leopoldi austriacae* BITTNER; dorsal interior showing spiral brachidium, $\times 2$ (Bittner, 1890).

Amphiclina LAUBE, 1866, p. 28 [**Producta dubia* MÜNSTER, 1841, p. 68; OD]. Subpentagonal to subtriangular in outline with prominent, acuminate umbo; small permesothyrid pedicle foramen; narrow, triangular interareas located medially between prominent dorsal and ventral palintropes; smooth, convex symphytium arching over small, commonly trilobed, posteromedian callosity in dorsal valve. [Location of type specimen unknown.] *Upper Triassic*: Dolomites, Carpathians, Dinaric Alps, Balkans, Caucasus, Pamirs, Himalayas, Primor'ye region. —FIG. 1093, 2a–d. *A. amoena* BITTNER, Dolomites, Italy; a, dorsal view, $\times 2.4$ (Brunton & MacKinnon, 1972); b–d, ventral, lateral, anterior view, $\times 1$ (Bittner, 1890).

Amphiclinodonta BITTNER, 1888, p. 288 [**A. liasina*; OD]. Smooth, gently concavoconvex shells, outline subtriangular, with strongly acuminate ventral umbo and very narrow hinge line; very small permesothyrid pedicle foramen; very small, narrow, triangular interareas; submarginal tubercles well developed on valve interiors. *Upper Triassic–Lower Jurassic*: Dolomites, Carpathians, Dinaric Alps, Austria, Pamirs, *Upper Triassic*; Dolomites, *Lower Jurassic*. —FIG. 1093, 3a–c. **A. liasina*, Liassic, Austria; dorsal, lateral, anterior views, $\times 2$ (Bittner, 1888). —FIG. 1093, 3d–e. *A. zugmayeri* BITTNER, Upper Triassic, Austria; ventral valve interior, oblique view of ventral valve interior, $\times 2$ (Bittner, 1890).

Carinokoninckina JIN & FANG, 1977, p. 59 [**Koninckina expansa* BITTNER, 1890, p. 132; OD] [= *Ctenokoninckina* XU, 1978, p. 283]. Externally similar to *Koninckina* but ventral interior bearing

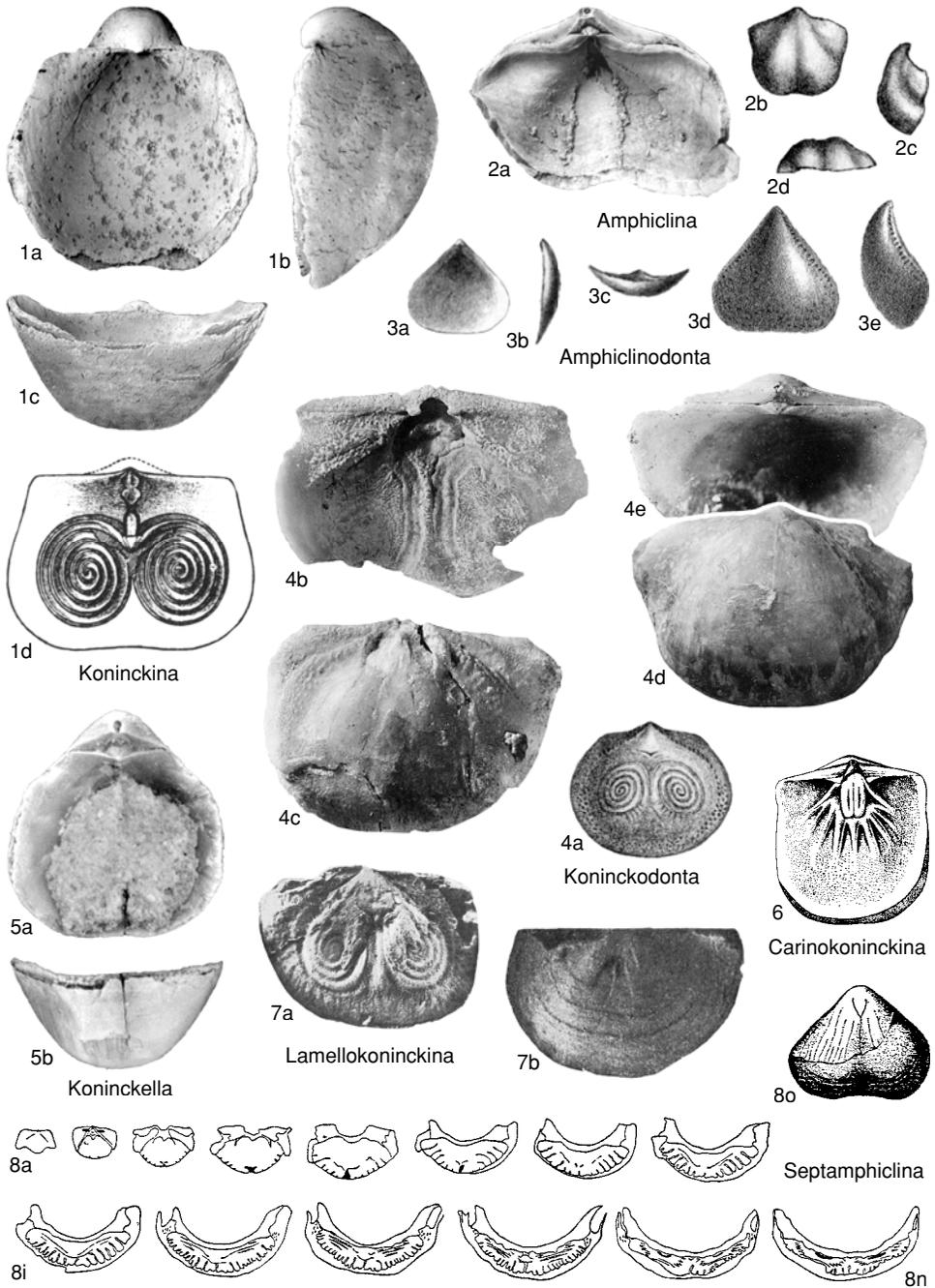


FIG. 1093. Koninckinidae (p. 1602–1604).

many (possibly pallial) ridges extending radially from ventral muscle scars. [May be synonymous with *Koninckina*. Location of type specimen unknown.] *Upper Triassic*: China.—FIG. 1093, 6. C.

jindingensis JIN & FANG; ventral valve interior, X3 (Jin & Fang, 1977).
Koninckella MUNIER-CHALMAS, 1880, p. 280 [**Leptaena liasiana* BOUCHARD in DAVIDSON &

- MORRIS, 1847, p. 250; OD]. Similar to *Koninckina* but rounded subtriangular in outline and with less curvature of ventral umbo; hinge line generally less than half maximum width; narrow, triangular interareas clearly visible in adults; small permesothyrud pedicle foramen; smooth, convex symphytium arching over small, commonly trilobed, posteromedian callosity in dorsal valve. [Location of type specimen unknown.] *Middle Triassic–Lower Jurassic*: France, Austria, Italy (Dolomites).—FIG. 1093, 5a–b. *K. triadica* BITTNER, Upper Triassic, Dolomites; dorsal, anterior view, $\times 8.5$ (new).
- Koninckodonta** BITTNER, 1893, p. 137 [**K. fuggeri*; OD]. Concaconvex, smooth, transversely subquadrate with rounded lateral margins, hinge line generally greater than half maximum width, ventral interarea low and wide, small permesothyrud pedicle foramen; smooth, convex symphytium; valve interiors strongly tuberculate around valve margins. *Lower Jurassic*: Austria, France.—FIG. 1093, 4a. **K. fuggeri*; dorsal interior, $\times 2$ (adapted from Bittner, 1893).—FIG. 1093, 4b–e. *K. davidsoni* (EUDES-DESLONGCHAMPS); b–c, ventral, dorsal interior; d–e, ventral, dorsal exterior, $\times 2$ (Davidson & Morris, 1847).
- Lamellokoninckina** JIN & FANG, 1977, p. 57 [**L. heqingensis*; OD]. Similar in external outline to *Koninckina* but bearing concentric growth lamellae, which are adorned with very fine radial striae. [May be synonymous with *Koninckina*.] *Upper Triassic*: China.—FIG. 1093, 7a–b. **L. heqingensis*, Yunnan; dorsal valve interior, dorsal exterior showing concentric growth lamellae, $\times 4$ (Jin & Fang, 1977).
- Septamphiclina** JIN & FANG, 1977, p. 57 [**S. qinzhaiensis*; OD]. Similar to *Carinokoninckina* but submarginal tubercles well developed on valve interiors. [May be synonymous with *Amphiclinodonta*.] *Upper Triassic*: China.—FIG. 1093, 8a–o. **S. qinzhaiensis*, Yunnan; a–n, transverse serial sections, $\times 3$ (adapted from Jin & Fang, 1977); o, part ventral exterior, part ventral internal mold showing multisepta (possibly pallial markings), $\times 3$ (Jin & Fang, 1977).

UNCERTAIN

FERNANDO ALVAREZ and PAUL COPPER

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The three spire-bearing families Dayiidae, Anoplotheceidae, and Kayseriidae, and the Leptocoeliidae, have commonly been classified in the superfamily Dayioidea (=Dayiaceae) alongside the Atrypoidea (e.g., SCHUCHERT, 1896; RZHONSNITSKAIA, 1960a; BOUCOT, JOHNSON, & STATON, 1964, 1965; JOHNSON, 1970b). Based on the orientation of the spiral cones and the type of jugum, COPPER (COPPER, 1973b, 1973c, 1986a; COPPER & GOURVENNEC, 1996) assigned the *Coelospira* (*Bifida* and *Kayseria* included) and *Dayia* groups to the Athyridida and assigned *Cyclospira* to the lissatrypids. Later, CAMPBELL and CHATTERTON (1979) considered that the Dayioidea, as defined by BOUCOT, JOHNSON, and STATON (1965), were not a natural group. They separated the ribbed from the smooth dayioids and placed *Kayseria* in the family Kayseriidae. More

recently HARPER and others (1993) considered the spiriferids and atrypids as different orders, placing the athyrids, retziids, dayiids, koninckinids, and spiriferidinids, all with subordinal rank, into the order Spiriferida. Other authors (e.g., DAGYS, 1996; ALVAREZ & CARLSON, 1998; ALVAREZ, RONG, & BOUCOT, 1998) did not include the dayioids (*sensu* BOUCOT, JOHNSON, & STATON, 1965) within the athyridides or considered their inclusion debatable (GRUNT, 1989).

The Leptocoeliidae, despite having some similarities with the Anoplotheceidae, were considered as rhynchonelloids by COCKS (1978) because of the absence of evidence for a spirial apparatus. This was accepted by HARPER and others (1993) and SAVAGE (1996); see also Leptocoeliidae (p. 1081 herein).

Based on the presence of ventrolaterally directed spiralia and a simple or complex jugum, the Dayiidae, Anoplothecidae, Kayseriidae, and Uncitidae (placed as uncertain in the previous *Treatise* (MOORE, 1965, p. 649) are here excluded from the Atrypida (COPPER, 1973b, 1973c, 1986a). ALVAREZ and CARLSON (1998) and ALVAREZ, RONG, and BOUCOT (1998) considered their accommodation within the Athyridida *sensu lato* as problematic. The principal reasons for uncertainty over their classification are their spiralian characteristics, including umbonal blades curving posterolaterally almost parallel with the commissural plane; an acute jugum resembling that of most meristelloids but placed below the spiral cones near the dorsal valve interior; grooved spiralian whorls or with double spiralian lamellae arising from the outer side of grooved whorls, or with accessory lamellae that intercalate with spiralian loops up to the apex, resembling that of some athyrididines and retziidines; the type of articulation with nearly vertical short, stubby, platelike teeth fixed directly to sides of valve; the unusual cardinalia; and the distinctive, long, narrow, strongly divergent ventral diductor scars, present in the so-called smooth dayioids. COPPER (herein) interprets both the Dayiidae (because of shell shape, dentition, and laterally directed spiralia), and the Anoplothecidae and Kayseriidae (because of similarities in their complex jugal structures, and possession of grooved or double spiralian whorls), as being Athyridida. These features are unknown in any Spiriferida.

Suborder UNCERTAIN Superfamily DAYIOIDEA Waagen, 1883

[*nom. correct.* HARPER, 1993, p. 449, *pro* Dayiacea RZHONSNITSKAIA, 1960a, p. 264, *nom. transl. ex* Dayiinae SCHUCHERT, 1913a, p. 409, *nom. correct. pro* Dayinae WAAGEN, 1883, p. 486; *emend.*, ALVAREZ & COPPER, herein]

Smooth, with or without fine growth lines, ventribiconvex to planoconvex or weakly concavoconvex, impunctate shells; distal ends of crura strongly divergent laterally; spiralia ventrolaterally directed; jugum simple, medially to anteriorly located. *Sil-*

urian (?Llandoverly, Wenlock–Přidoli), Lower Devonian (?Lochkovian).

Family DAYIIDAE Waagen, 1883

[*nom. transl.* RZHONSNITSKAIA, 1960a, p. 264, *ex* Dayiinae SCHUCHERT, 1913a, p. 409, *nom. correct. pro* Dayinae WAAGEN, 1883, p. 486; *emend.*, ALVAREZ & COPPER, herein] [=Protozeugidae TWENHOFEL, 1914, p. 29]

Characters as for superfamily. *Silurian* (?Llandoverly, Wenlock–Přidoli), Lower Devonian (?Lochkovian).

Dayia DAVIDSON, 1881c, p. 291 [**Terebratulula navicula* J. de C. SOWERBY, 1839, p. 611; OD] [=*Daya* KOKEN, 1896, p. 240, incorrect subsequent spelling (Art. 33.3, ICZN, 1999)]. Small, longitudinally ovate to subcircular or subpentagonal, ventri- to planoconvex, relatively thick shell, mainly posterior of ventral valve; small, hypercline beak; commissure weakly sulcate-rectimarginate; teeth small, short, solid, dental plates absent; narrow groove for small ventral adductors; ventral diductor scars wide, diverging anteriorly; dorsal valve with long, low septum to near midshell, flabellate adductor scars; spiralia with 3 to 7 whorls; jugum angular, situated anteriorly, may project posteriorly as a short stem. Distinct from *Protozeuga* in relatively flat dorsal valve, more complex spiranium. *Silurian* (Ludlow–Přidoli), Lower Devonian (?Lochkovian): Ireland, United Kingdom, Baltic Basin, Ukraine, ?western slopes Urals.—FIG. 1094, 2a–u. **D. navicula* (J. de C. SOWERBY), Ludlow, England; a–c, neotype, dorsal, anterior, and lateral views, Herefordshire, GSM 103291, ×2; d–o, transverse serial sections, 1.18, 1.95, 2.3, 2.51, 2.93, 3.98, 5.0, 5.91, 6.47, 7.03, 7.59, 7.8 mm from ventral umbo, distance from ventral umbo to first section approximate, Herefordshire, ×3 (Tucker, 1968); p–q, ventral and lateral views showing reconstructed spiranium and jugum, ×3 (new); r–t, dorsal, anterior, lateral views, Shropshire, ×2.3; u, view of specimen with most of its dorsal valve broken to show jugum and spiranium, Shropshire, ×3 (Glass in Davidson, 1882).

Protozeuga TWENHOFEL in SAVAGE, 1913a, p. 51 [**Waldheimia* ? *mawei* DAVIDSON, 1881b, p. 145; OD]. Very small shell (less than 3 to 4 mm wide), weakly ventribiconvex to planoconvex; sulcate commissure with small fold in sulcus to produce plicosulcate condition; teeth minute, solid; crura medial to slightly laterally directed; spiralia of fewer than 2 whorls; jugum simple, medial, apex slightly posteriorly directed. Distinguished from derived *Dayia* by its very small shell, weakly plicosulcate commissure, small spiralia with few whorls, smaller jugum. *Silurian* (?Llandoverly, Wenlock): United Kingdom, Baltic Basin.—FIG. 1094, 1a–g. **P. mawei* (DAVIDSON), Wenlock, Shropshire, United Kingdom; a–d, dorsal, ventral, lateral, and anterior views; e, anterior view showing plicosulcate anterior commissure, ×7.5 (Davidson, 1881b); f–g, ventral and lateral views of reconstructed spiranium and jugum, ×3 (new).

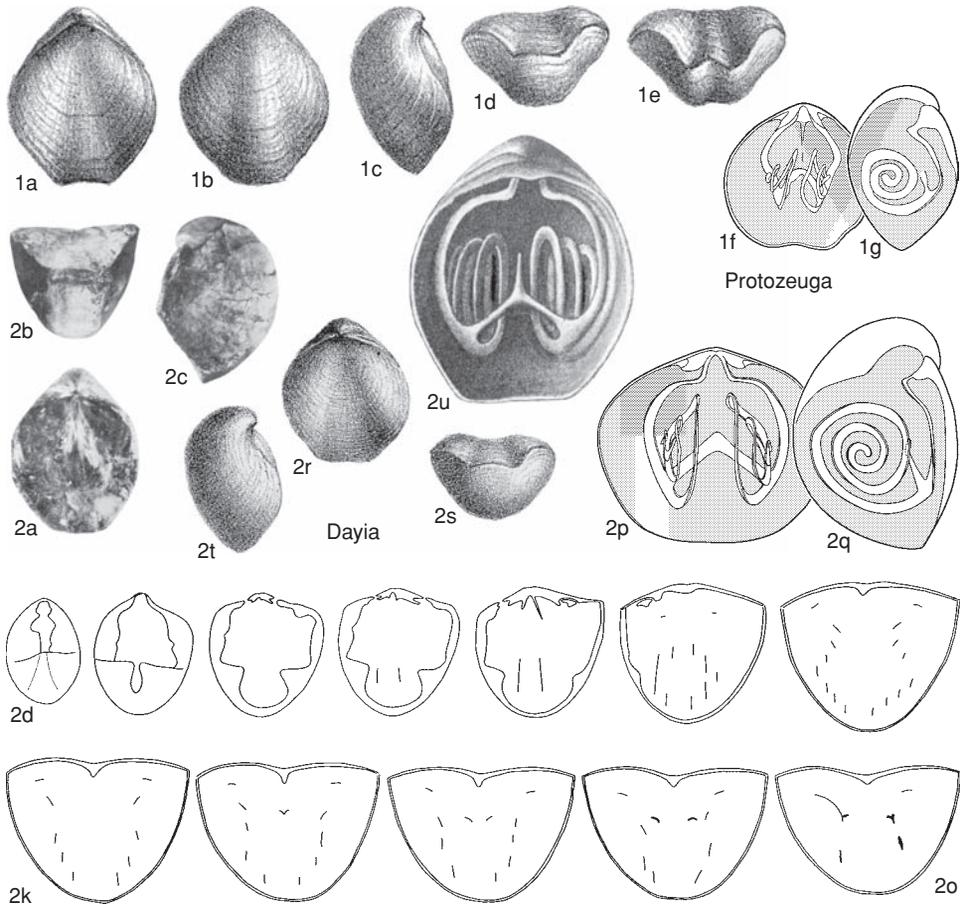


FIG. 1094. Dayiidae (p. 1605).

Superfamily
ANOLOTHECOIDEA
Schuchert, 1894

[*nom. transl.* ALVAREZ, RONG, & BOUCOT, 1998, p. 835, ex Anoplothecinae SCHUCHERT, 1894b, p. 103; *emend.*, ALVAREZ & COPPER, herein]

Minute to medium, commonly ventribiconvex to concavoconvex, elongate to transversely oval shells, slightly rostrate, ventral umbo commonly moderate to strongly curved; narrow and astrophic hinge line; ventral cardinal area reduced, foramen small or absent, delthyrium open; surface with ribs or low, rounded plications commonly crossed by numerous, fine, regularly developed growth lines that could be lamellose; anterior commissure rectimarginate, unisul-

cate or biplicate; pedicle support absent; ventral valve commonly with thick shell, teeth short, solid, nearly vertical, dental plates absent; long median septum commonly present in both valves; cardinal process variably developed, inner socket ridges slightly overhanging sockets; umbonal blades of spiralia sharply bent from tips of crura in lateral (*Coelospira*) or posterolateral direction (*Kayseria*); spiral cones ventral to ventrolaterally directed; elaborate jugum joining primary lamellae of each cone, commonly sitting over median dorsal septum; with jugal stem that may be thick (*Coelospira*), may bifurcate distally into 2 short jugal arms (*Bifida*), or that may extend

as long accessory jugal lamellae, continuing intercoiled with primary volutions of spiralia to ends (*Kayseria*); in some anoplothecids with grooved spiralia whorls, accessory lamellae derived from outer, ventral side of spiral whorl; frequently, the spiralia are spinose on their outer edges with jugum on its anterior edge; shell impunctate. *Silurian* (?Wenlock, lower Ludlow)—*Middle Devonian* (*Givetian*).

Family ANOLOTHECIDAE Schuchert, 1894

[*nom. transl.* BOUCOT, JOHNSON, & STATON, 1964, p. 807, *ex Anoplothecinae* SCHUCHERT, 1894b, p. 103; *emend.*, ALVAREZ & COPPER, herein] [=Coelospiridae HALL & CLARKE, 1894, p. 840]

Ventribiconvex to concavoconvex shells; frequently with general naviculate aspect; lamellose growth lines may be numerous and regularly developed (e.g., *Anoplotheca*, *Bifida*) or only anteriorly developed (e.g., *Coelospira*, *Navispira*); spiral whorls grooved, jugal blade may develop from dorsal base of jugum and be directed ventroposteriorly toward jugal arms that may be short (e.g., *Bifida*) or long and fused with main spiralia whorls to make a groove. *Silurian* (?Wenlock, lower Ludlow)—*Middle Devonian* (*Givetian*).

Subfamily ANOLOTHECINAE Schuchert, 1894

[Anoplothecinae SCHUCHERT, 1894b, p. 103]

Minute to medium, smooth or with ribs developed primarily toward umbones; growth lamellae commonly with fibrose or spinelike extensions; internally median septa well developed in both valves, often dividing posterior half of shell into 2 compartments; jugal arms short; laterally to ventrally directed spiralia of less than 7 whorls; spiralia whorls grooved. *Silurian* (*Přidolí*)—*Middle Devonian* (*Givetian*).

Anoplotheca SANDBERGER, 1855, p. 5 [**Terebratula venusta* SCHNUR, 1853, p. 180; OD; =*Productus lamellosus* SANDBERGER & SANDBERGER, 1856 in 1849–1856, p. 351] [=*Hoplotheca* BIGSBY, 1878, p. 36, obj.]. Medium, planoconvex to weakly ventribiconvex shells, with lenticular outline; ribs clearly present apically, shell commonly smooth anteriorly; about midventral valve a median rib starts, reaching anterior commissure; ventral valve with long thin

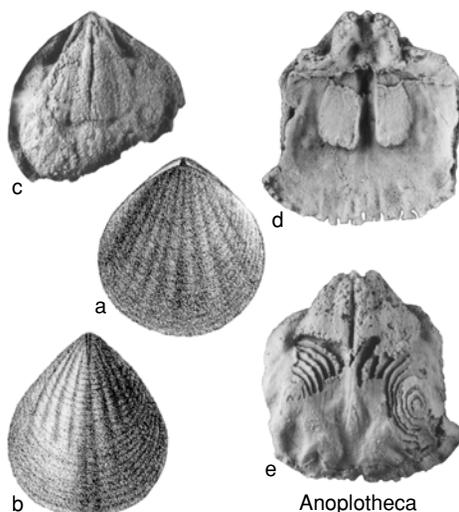


FIG. 1095. Anoplothecidae (p. 1607).

septum dividing muscle field; dorsal muscle field strongly impressed; cardinal process prominent, bilobed; spiralia ventrally slightly laterally directed, 6 to 8 whorls; structure of jugum unknown. Differs from *Bifida* in larger size, less carinate shell, with weaker ribs. [This genus requires revision.] *Lower Devonian* (*Emsian*): Germany (Eifel region), France.—FIG. 1095a–c. **A. venusta* (SCHNUR), Eifel; a–b, dorsal and ventral views, $\times 1.5$ (Hall & Clarke, 1895); c, mold of interior of ventral valve, USNM 140384, $\times 2$ (Boucot, Johnson, & Staton, 1964).—FIG. 1095d–e. *A. sp.*, upper Emsian, Germany; dorsal and ventral views of internal mold, USNM 140383, $\times 3$ (Boucot, Johnson, & Staton, 1964).

Bifida DAVIDSON, 1882, p. 27 [**Terebratula lepida* D'ARCHIAC & DE VERNEUIL, 1842, p. 368; OD] [=*Dablispira* HAVLÍČEK, 1998, p. 119 (type, *Anoplotheca* (*Bifida*) *dablia* HAVLÍČEK, 1956, p. 590)]. Small ventribiconvex shells, commonly with carinate ventral midrib pair; concentric growth lamellae, distinct, rhythmic, commonly developed as bushy, spinose external layer covering shell; commissure rectimarginate or weakly sulcate; short, small, solid teeth with inner notch for dorsal socket plates; strong ventral median septum; thick cardinal plate with weak cardinal process; crura medial, with high angles at junction with spiralia; spiralia grooved, with 3 to 7 whorls; jugal saddle resting on high dorsal septum, slightly projected as abortive accessory lamellae. Similarly grooved spiralia as in *Navispira* and *Coelospira*, but differing externally in small shell, very enlarged ventral midrib pair; differs from *Anoplotheca* mainly in smaller size, distinct concentric growth lamellae, and bushy spinose fibers. *Lower Devonian* (*Emsian*)—*Middle Devonian* (*lower Givetian*): Eurasia, North America.—FIG. 1096, 1a–p. **B. lepida* (D'ARCHIAC & DE VERNEUIL);

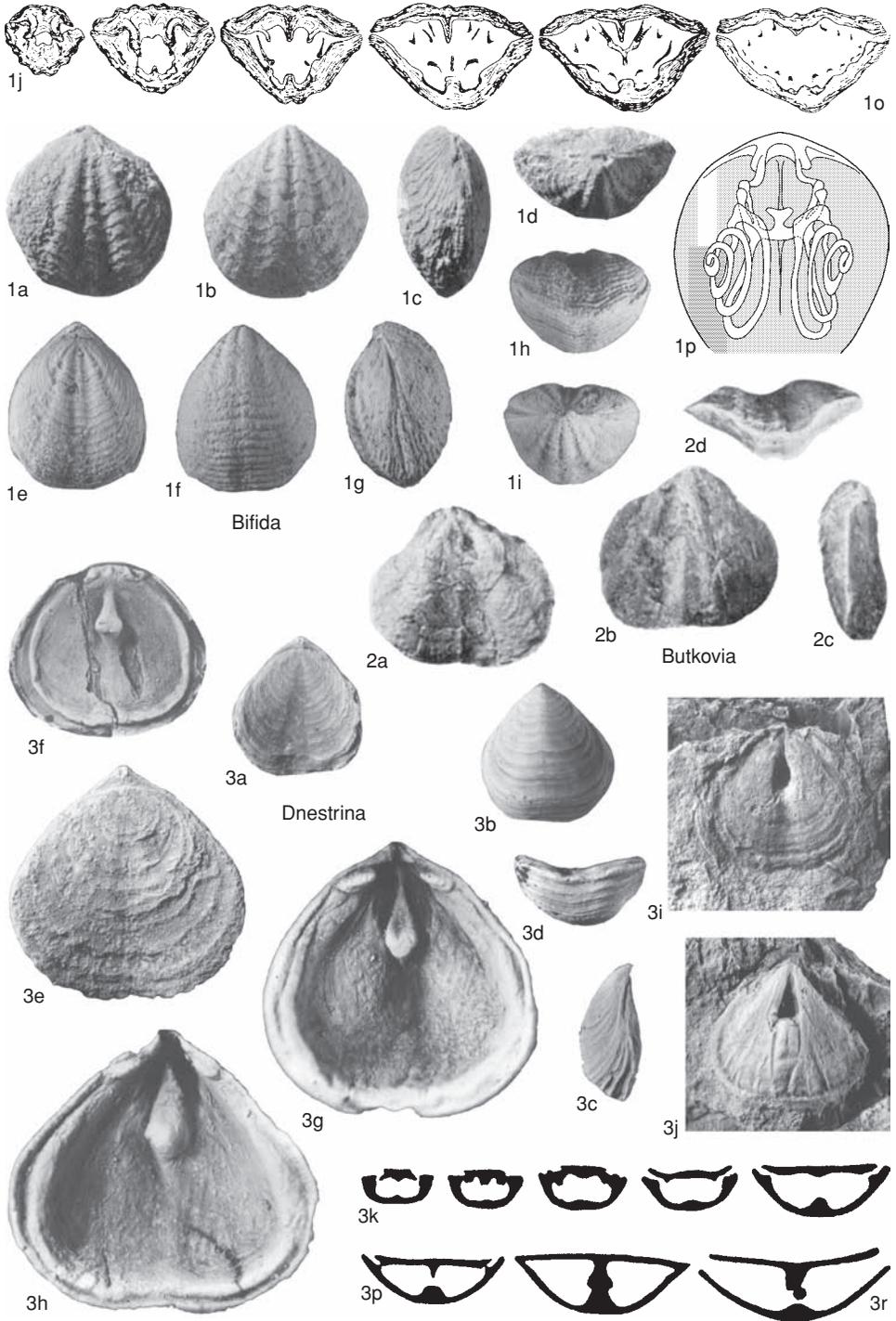


FIG. 1096. Anoplotheceidae (p. 1607–1609).

a-d, dorsal, ventral, lateral, and posterior views, BMNH BB 58557, $\times 4$ (Copper, 1973b); *e-i*, dorsal, ventral, lateral, anterior, and posterior views, USNM 140378, $\times 4$ (Boucot, Johnson, & Staton, 1964); *j-o*, transverse serial sections, 0.9, 1.5, 1.9, 3.1, 3.4, 4.2 mm from ventral umbo, BMNH BB 58564, $\times 4$ (adapted from Copper, 1973b); *p*, ventral view of dorsal interior showing reconstructed spirulum and jugum, BMNH BB 58564, $\times 5$ (Copper, 1973b).

?**Butkovia** BARANOV, 1987, p. 113 [**B. eximia*; OD]. Very small, ventribiconvex to planoconvex shells; smooth except for strong ventral midrib pair and small rib in sulcus; thick shelled; small, protruding umbo, possibly lacking deltidial plates; sulcate to plicosulcate commissure; cardinalium massive, high dorsal septum strong; brachidia unknown. Similar to *Bifida*, *Anoplotheca*, and *Coelospirina* but lateral ribs and concentric ornamentation weakly developed or absent. [Interior poorly known; spiralia and jugum unknown; requires revision.] *Lower Devonian (Pragian–Emsian)*: northeastern Siberia (Chilmaga Range, Kolyma).—FIG. 1096, 2*a-d*. **B. eximia*; holotype, dorsal, ventral, lateral, and anterior views, YaTGU 120/40, $\times 5$ (Baranov, 1987).

?**Dnestrina** NIKIFOROVA & MODZALEVSKAYA, 1968, p. 206 [**D. gutta*; OD]. Minute to small, concavoconvex to planoconvex, longitudinally ovate to subpentagonal shells covered by numerous, lamellose growth lines; ribs absent; dorsal sulcus shallow, originating in umbo, ventral median fold high but poorly defined laterally, anterior commissure rectimarginate to slightly sulcate; ventral interior relatively short, prominent, bulbous, widening anteriorly, ventral median septum dividing small muscle fields, pressed against similar median septum on dorsal valve that thickens medially, bifurcating slightly and sharply reduced anteriorly; cardinal process small; marginal borders present; spirulum and jugum unknown. Differs from *Anoplotheca* and *Bifida* in lacking ribs, and in prominent concentric growth lamellae. [Needs revision. When erected, this genus was included in the Atrypidae.] *upper Silurian (Přídolí)*: Podolia, Moldavia, western Europe.—FIG. 1096, 3*a-r*. **D. gutta*, Moldavia; *a-d*, holotype, dorsal, ventral, lateral, and anterior views, CNIGR 1/9543, $\times 3$ (Nikiforova & Modzalevskaya, 1968; photographs courtesy of T. L. Modzalevskaya); *e*, dorsal view showing pedicle foramen and lamellose growth lines, $\times 5.2$ (new; photographs courtesy of T. L. Modzalevskaya); *f*, dorsal interior, $\times 4$; *g*, ventral interior, $\times 6$; *h*, ventral interior showing median septum and well-developed marginal borders, $\times 6$; *i-j*, dorsal and ventral internal molds, $\times 4$ (Nikiforova & Modzalevskaya, 1968; photographs courtesy of T. L. Modzalevskaya); *k-r*, transverse serial sections, 1.5, 1.7, 1.8, 2.1, 2.4, 2.7, 3.1, 4.6 mm from ventral umbo, distance from ventral umbo to first section approximate, $\times 5$ (adapted from Nikiforova & Modzalevskaya, 1968).

Subfamily COELOSPIRINAE Hall & Clarke, 1895

[*nom. transl.* AMOS & BOUCOT, 1963, p. 441, ex Coelospiridae HALL & CLARKE, 1894, p. 840]

Coarsely ribbed, small shells lacking fibrous shell layer, distinct concentric growth lamellae; ventral midrib pair commonly clearly defined; weak ventral and dorsal median septa; complex jugum as in Anoplotheцинаe, but accessory lamellae fused into single spirulum with grooved spiral whorls. *Silurian (?Wenlock, lower Ludlow)–Middle Devonian (Givetian)*.

Coelospira HALL, 1863b, p. 60 [**Leptocoelia concava* HALL, 1857a, p. 107; OD]. Small, ventribiconvex to planoconvex, longitudinally to transversely ovate shells with evenly convex profile; surface with numerous, relatively fine ribs, commonly median ventral ribs tending to be smaller than laterals; poorly developed growth lines commonly occurring at irregular intervals, few growth lamellae may develop anteriorly; anterior commissure rectimarginate to weakly sulcate; ventral diductor scars long, large, elliptical, broadening anteriorly, commonly divided by thin, bladelike median septum; platform elevating ventral muscle attachment area poorly developed or absent, cavity anterior to adductor scars much shallower than in *Navispira*; short, solid teeth, dental sockets well developed, inner socket ridges broadly divergent, may extend anterolaterally parallel to internal dorsal valve margin; cardinal process commonly bilobate to trilobate; a broad and posteriorly thick crest commonly dividing small, posterior, adductor scars, quickly narrowing anteriorly, separating broad triangular anterior adductor scars. Differs from *Navispira* in lack of prominent, carinate ventral midrib pair. *Lower Devonian (Lochkovian)–Middle Devonian (Eifelian)*: North America, Venezuela, Argentina, Turkey, northern China, Australia.—FIG. 1097, 4*a-d*. **C. concava* (HALL), Lochkovian, Albany County, New York, USA; *a*, lectotype, ventral view, AMNH 28456; *b*, ventral view, AMNH 28461; *c*, dorsal view, AMNH 28457; *d*, ventral valve internal mold, Gaspé, Lochkovian, USNM 156281, $\times 3$ (Boucot & Johnson, 1967b).

?**Coelospirella** SU, 1976, p. 202 [**C. dongbeiensis*; OD]. Small, plano- to concavoconvex shells, resembling *Navispira* but with weak ribs that do not bifurcate; internally short dental plates were reported, but additional information (provided by Su Yangzheng, 2001) confirms that dental plates are absent and that spirulum and jugum are as in *Coelospira*. Said to differ from *Coelospira* by lacking bifurcating ribs, from *Bifida* in convexity, from *Anoplotheca* by its muscle area and vascular marking, from *Coelospirina* by convexity, type of cardinal process, and nature of ventral muscle field. [Poorly represented

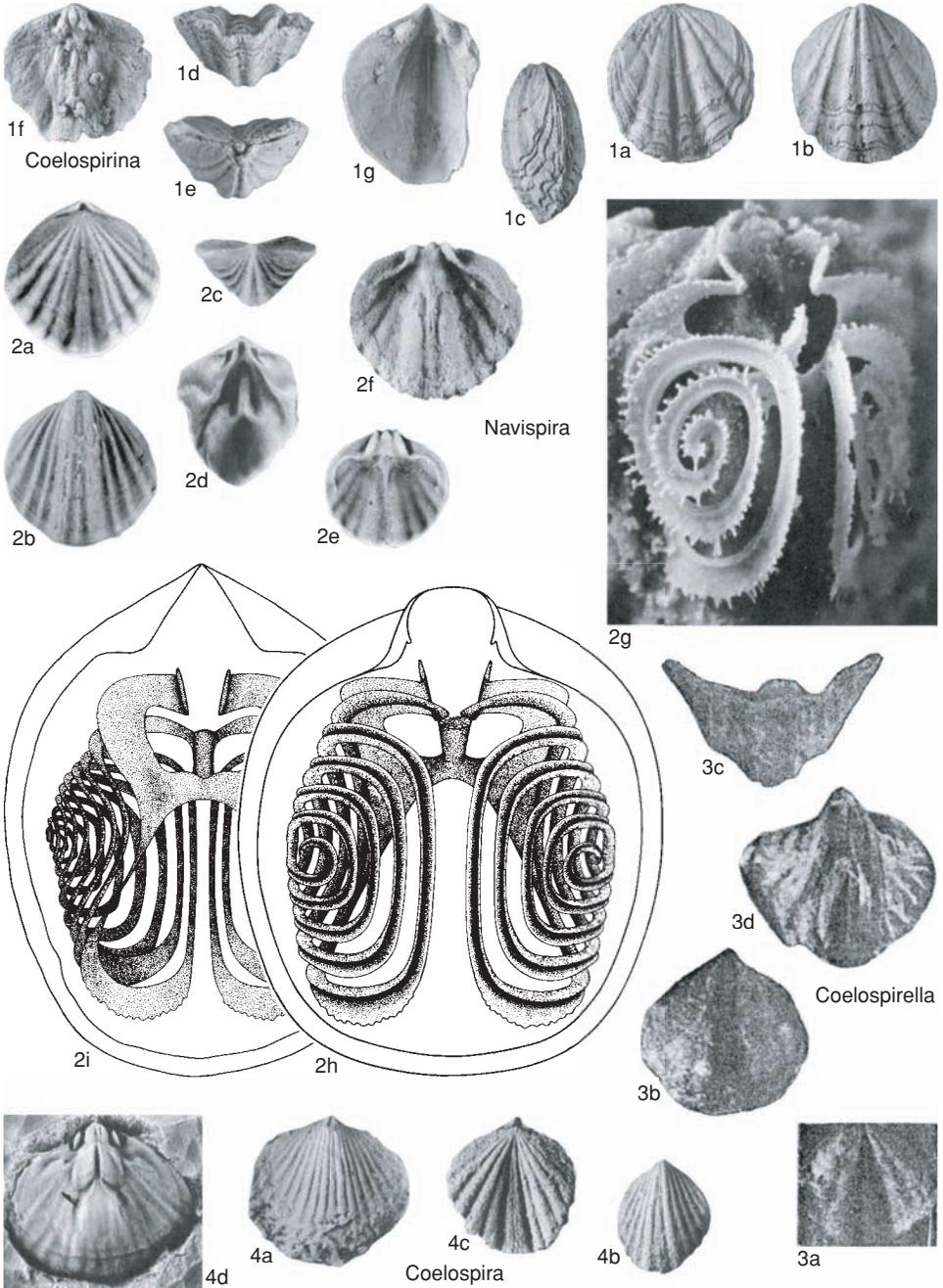


FIG. 1097. Anoplotheceidae (p. 1609–1612).

and known, requires revision.] *upper Silurian (Pridoli)—Lower Devonian (Emsian)*: Inner Mongolia, northern China, Kazakhstan, eastern Russia.—FIG. 1097, 3a–d. **C. dongbeiensis*, Emsian, Inner Mongolia, northern China; a, dorsal view, NS12014; b, ventral view, NS12003; c, posterior

view, NS12303; d, internal mold of ventral valve, NS12006, ×3 (Su, 1976). **Coelospirina** HAVLIČEK, 1956, p. 586 [*C. modica*; OD]. Shells resembling *Coelospira* with few irregularly spaced, anteriorly concentrated growth lamellae; stronger and sharply edged plications; cardinal

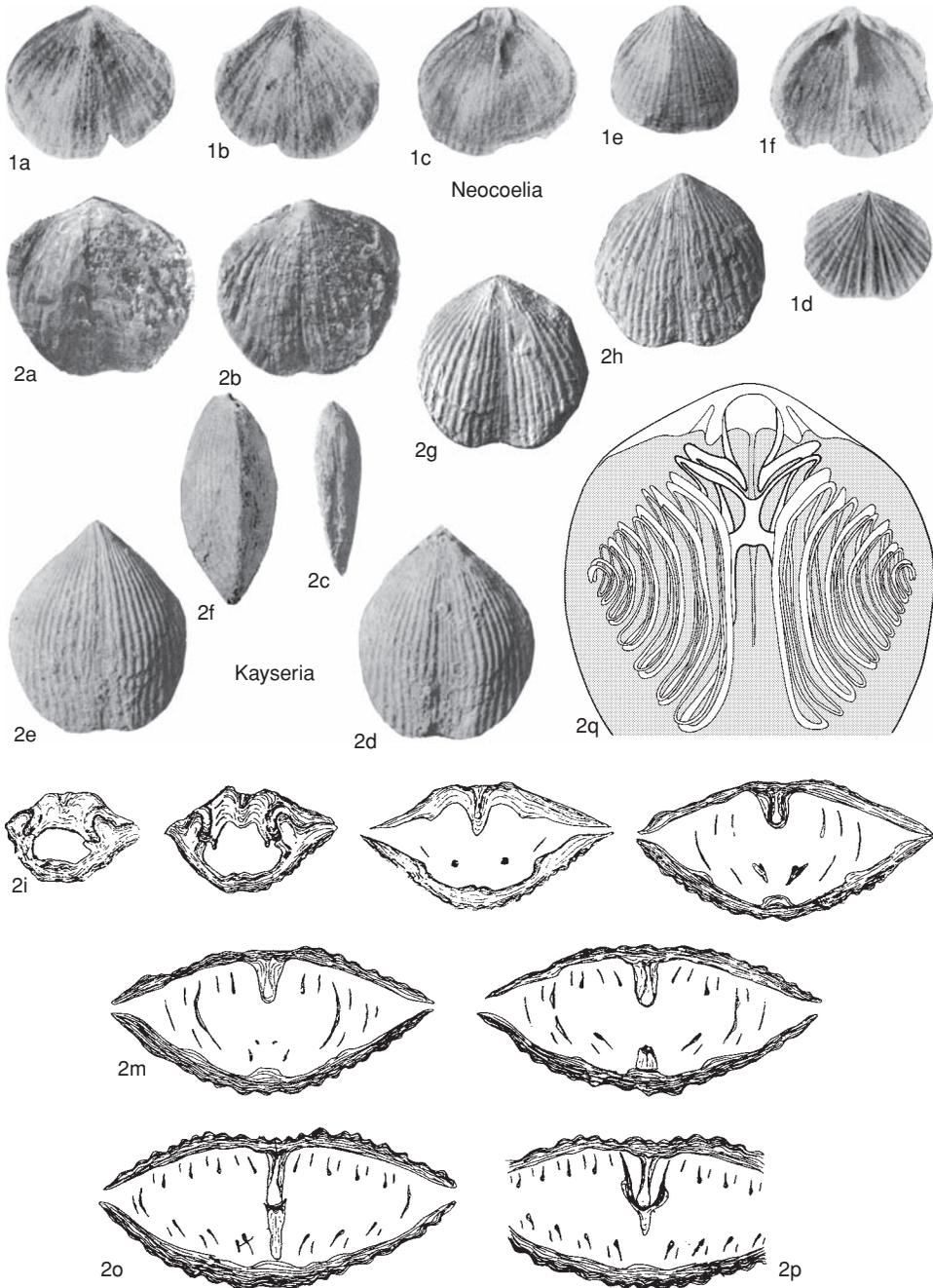


FIG. 1098. Kayseriidae (p. 1612).

process not bilobed; spiralia and jugum poorly known. [Requires revision. May be synonymous with *Coelospira*.] Lower Devonian (upper Emsian): Czech Republic, Germany, Gorno-Altay.—FIG. 1097, 1a–g. **C. modica*, Zlichov Limestone, Praha-Hlubocepy, Czech Republic; a–e, dorsal, ventral,

lateral, anterior, and posterior views, USNM 140379; f, dorsal valve interior, USNM 140380; g, ventral valve interior, USNM 140379, $\times 3$ (Boucot, Johnson, & Staton, 1964). *Navispira* AMSDEN, 1983b, p. 1253 [*Anoplotheca* (*Coelospira*) *saffordi* FOERSTE, 1903, p. 709; OD].

Similar to *Coelospira*, but smaller, longitudinally ovate, with strong ventral midrib pair, producing carination, separated by smaller central rib; ventral diductor scars relatively narrow and small, separated by short, stout median septum commonly thickening anteriorly; ventral muscle attachment area elevated on platform of thickened shell material, thinning abruptly at its anterior margin to produce conspicuous cavity; dorsal interior similar to *Coelospira*, but with cardinal process smaller and knoblike or absent. *Silurian* (?Wenlock, lower Ludlow)—Lower Devonian (Emsian): North America, Venezuela, Bolivia, Gotland, Kazakhstan, Ludlow; North America, Lochkovian; Australia, Emsian.—FIG. 1097, 2a–d. **N. saffordi* (FOERSTE), Ludlow, Perrysville Quadrangle, Tennessee; a–b, dorsal and ventral views, USNM 339088; c, posterior view, USNM 339091; d, interior of ventral valve, USNM 339090, $\times 4$ (Amsden, 1983b).—FIG. 1097, 2e. *N. virginia* (AMSDEN), Ludlow, Jeannette Quadrangle, Tennessee; interior of dorsal valve, USNM 339093, $\times 4$ (Amsden, 1983b).—FIG. 1097, 2f–g. *N. kennethensis* (BOUCOT & JOHNSON), Ludlow, Logansport, Indiana; f, dorsal valve interior, USNM 156318, $\times 4$; g, ventral, slightly lateral, view of brachiojugal structures, USNM 156320, $\times 10$ (Boucot & Johnson, 1967b).—FIG. 1097, 2h–i. *N. dayi* CHATTERTON, Emsian, New South Wales, Australia; ventral and dorsal views of reconstructed brachiojugal structures, approximately $\times 10$ (Campbell & Chatterton, 1979).

Family KAYSERIIDAE

Boucot, Johnson, & Staton, 1964

[Kayseriidae BOUCOT, JOHNSON, & STATON, 1964, p. 807; emend., ALVAREZ & COPPER, herein]

Weakly biconvex shells with median sulcus in both valves and opposite folding, anterior margin slightly emarginate; numerous, fine ribs, evenly sized on flanks, being finer in the sulci; few growth lines crossing ribs at irregular intervals; deltidial plates and pedicle supports absent; teeth short, massive, nearly vertical, with notches for cardinalium, dental plates absent; median septum present in both valves; short, thick, imperforate apically, subtrapezoidal cardinal plate (without dorsal cavity below) with weak cardinal process; umbonal blades of spiralia sharply bent from tips of crura in posterolateral direction; spiral cones ventrolaterally directed, accessory lamellae long, continuing intercoiled with primary volutions of spiralia to ends; jugum resting on prominent dorsal septum and produced ventrally up to broad,

flat, even concave, ventral median septum. *Middle Devonian* (Eifelian–Givetian).

Kayseria DAVIDSON, 1882, p. 21 [**Orthis lens* PHILLIPS, 1841, p. 65; OD]. Medium, rather flat, subcircular to subpentagonal or elongate oval shell, with tiny, slightly curved, ventral beak and minute foramen; 2 thick ribs may define sulcus laterally on both valves; rare growth lamellae projecting outwardly; ragged-edged cardinal process internally. *Middle Devonian* (Eifelian–Givetian): Eurasia.—FIG. 1098, 2a–c. **K. lens* (PHILLIPS), upper Eifelian, Devon, England; lectotype, dorsal, ventral, and lateral views, GSM 50872, $\times 2$ (Copper, 1973b).—FIG. 1098, 2d–f. *K. nobnensis* COPPER, lower Eifelian, Eifel, Germany; holotype, dorsal, ventral, and lateral views, BMNH BB 58563, $\times 2$ (Copper, 1973b).—FIG. 1098, 2g–q. *K. dividua* (SCHNUR), lower Eifelian, Eifel, Germany; g–h, dorsal and ventral views, BMNH BB 59010, $\times 2$ (Copper, 1973b); i–p, transverse serial sections, 0.9, 1.2, 1.9, 2.6, 3.1, 3.6, 4.2, 4.5 mm from ventral umbo, BMNH BB 59010, $\times 5$ (adapted from Copper, 1973b); q, ventral view of dorsal interior showing reconstructed spiranium and jugum, BMNH BB 59010, $\times 5$ (Copper, 1973b).

Family UNCERTAIN

?*Neocoelia* MCKELLAR, 1966, p. 2 [**N. boucoti*; OD]. Shell with very numerous, fine, low ribs, most of which bifurcate; ventral muscle field poorly defined with a short, low septum; teeth solid, lacking dental cavities; cardinal process small, bilobate; dorsal median septum high, extending to midline; spiranium and jugum unknown. [Poorly represented and known, requires revision. When erected, *Neocoelia* was regarded as a close relative to *Anoplotheca* and *Kayseria*, with its shape suggesting closer affinity to the former. In the absence of revision of this genus, ALVAREZ prefers to regard it tentatively as belonging to the Anoplotheceidae, while COPPER suggests a closer relationship with *Kayseria*, of which *Neocoelia* seems to be an early relative.] *Lower Devonian* (?Emsian), *Middle Devonian* (Eifelian): Australia (Queensland).—FIG. 1098, 1a–f. **N. boucoti*; a–b, holotype, external mold of dorsal valve and rubber mold, GSQ F3696; c, holotype, rubber mold of dorsal interior, GSQ F3696; d, rubber mold of dorsal valve exterior, GSQ F9537; e, rubber mold of incomplete ventral valve exterior, GSQ F3695; f, rubber mold of dorsal interior, GSQ F3689, $\times 2$ (McKellar, 1966).

Superfamily UNCITOIDEA d'Orbigny, 1847

[nom. transl. JUX & STRAUCH, 1966, p. 177, ex Uncitidae d'ORBIGNY, 1847, p. 268]

Diagnosis as for family. *Middle Devonian* (Givetian).

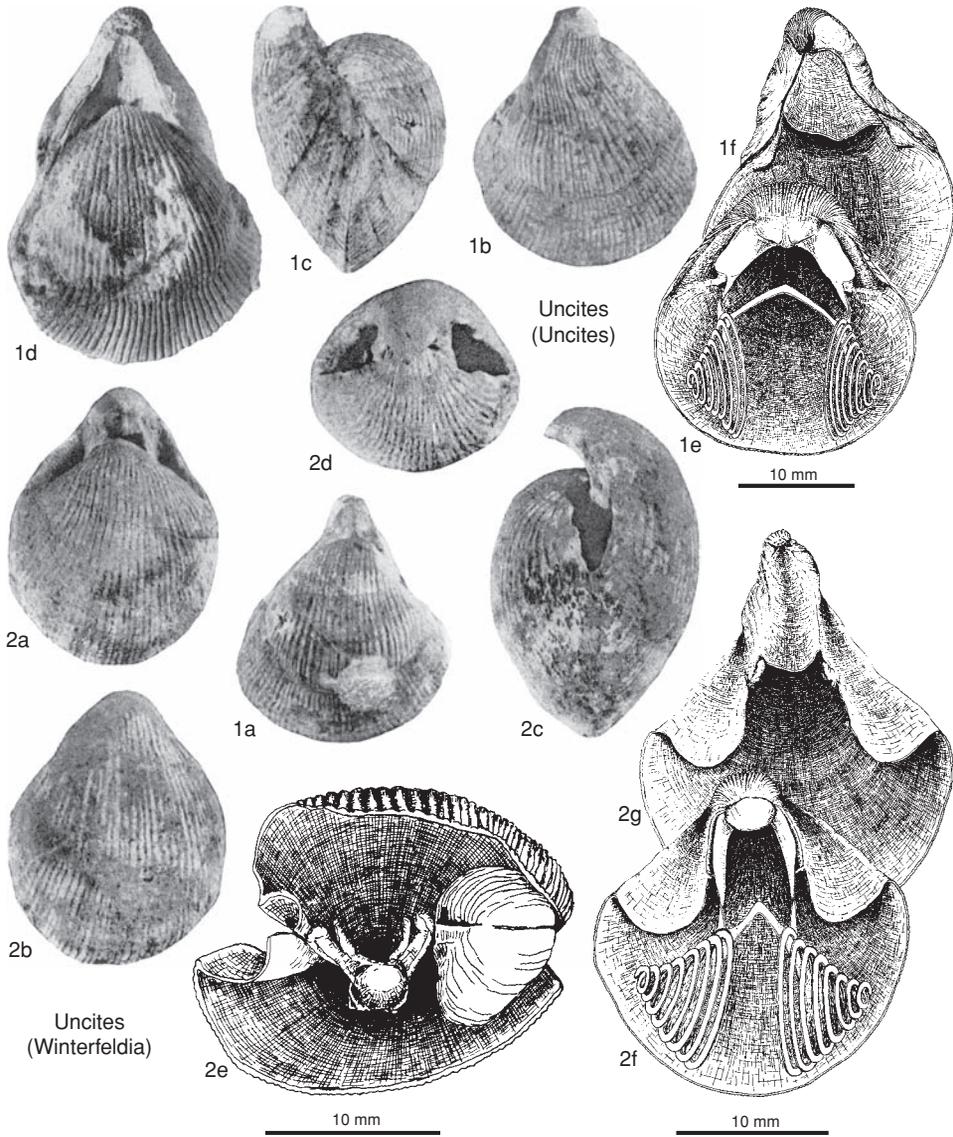


FIG. 1099. Uncitidae (p. 1614).

Family UNCITIDAE d'Orbigny, 1847

[Uncitidae d'ORBIGNY, 1847, p. 268]

Impunctate, ribbed, asymmetric, large-beaked shells with deltidium; ventrolaterally directed spiralia, simple, posteriorly located jugum. [Commonly, the family Uncitidae is

attributed to WAAGEN (1883, p. 487, 494) as a subfamily, later raised to family rank by SCHUCHERT (1929, p. 22). However, it had been made available already by D'ORBIGNY (1847, p. 268; see JUX & STRAUCH, 1966; MANCENIDO, OWEN, & MORRIS, 1993, p. 197).] *Middle Devonian (Givetian)*.

Uncites DEFRANCE in DE BLAINVILLE, 1825, p. 630 [**Terebratulites Gryphus* [sic] VON SCHLOTHEIM, 1820 in 1820–1823, p. 259; OD; =*Uncites gryphoides* DEFRANCE, 1827, p. 152]. Evenly ribbed, biconvex, generally elongate, highly variable, asymmetrical shells; shell wall thick, massive; very large, talonlike, protruding, pointed, ventral beak; concentric growth lines present, irregularly spaced; flanks lateral to delthyrium, smooth; foramen absent, but some shells possessing koskinoid perforations; large delthyrium occupied by single, concave deltidium, rarely with medial separation into separate plates; teeth solid, lacking dental plates or cavities; no clear median septa evident in either valve; muscle impressions weak; massive cardinalium; spiralia lateral to ventrolateral, with 6 or more whorls; simple, arched jugum pointed posteriorly. [For discussion of *Uncites* see JUX & STRAUCH, 1966.] *Middle Devonian (Givetian)*: Eurasia, western Europe, China, Vietnam.

U. (Uncites). Beak with narrow smooth flanks; large, triangular, concave deltidium; hinge plate short, in comparison with long, flat outer hinge plates, short, laterally divergent crura; 6 or more

lateroventral spiral whorls; simple wide jugum. Distinct from *Winterfeldia* in lacking brood pouches and possessing broad cardinal plate, widely diverging crura, wide jugum. *Middle Devonian (Givetian)*: Eurasia, China, ?North America.—FIG. 1099, 1a–f. **U. (U.) gryphus* (VON SCHLOTHEIM), Germany; a–c, lectotype, dorsal, ventral, and lateral views; d, dorsal view, $\times 1$; e–f, interiors of dorsal, ventral valves (Jux & Strauch, 1966).

U. (Winterfeldia) SPRIESTERSBACH, 1942, p. 197 [**U. paulinae* WINTERFELD, 1895, p. 658; OD]. Generally smaller than *Uncites*, and distinguished by presence of brood pouches (parathyridia), W-shaped cardinal margin; narrow cardinal plate with thick process on top, medial and subparallel crura, narrow jugum, widely spaced spiralia whorls. *Middle Devonian (Givetian)*: western Europe.—FIG. 1099, 2a–g. **U. (W.) paulinae* WINTERFELD, upper Givetian, Germany; a–d, lectotype, dorsal, ventral, lateral, and posterior views; e, interior view of brood pouches, $\times 1$; f–g, interiors of dorsal, ventral valves (Jux & Strauch, 1966).

UNCERTAIN

FERNANDO ALVAREZ and RONG JIA-YU

[The University of Oviedo; and Academia Sinica, Nanjing]

Order, Suborder, and Family UNCERTAIN

Weibeia FU, 1982, p. 171 [**W. spiriferoides*; OD]. Small shell, subequally biconvex, subpentagonal, with growth lines, dorsal fold and ventral sulcus slightly developed only anteriorly; interior poorly known, dental plates and crural plates high and

parallel; spiralia and jugum unknown. Poorly known, needs revision. [When erected, this genus was included in the Athyrididina, Meristellidae.] *Upper Ordovician (lower Caradoc)*: northern China (Dongzhuang, Liquan, Shaanxi Province).—FIG. 1100a–e. **W. spiriferoides*; holotype, dorsal, ventral, lateral, anterior, and posterior views, $\times 3$ (Fu, 1982; photographs courtesy of Fu Li-pu).

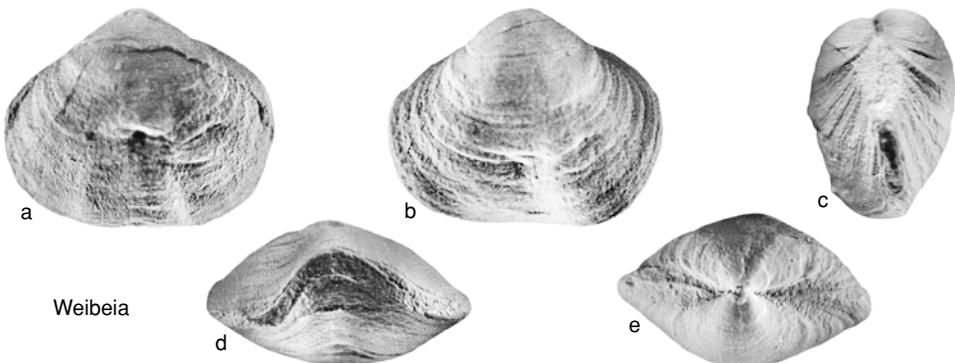


FIG. 1100. Uncertain (p. 1614).

NOMENCLATORIAL NOTE

NORMAN M. SAVAGE

[University of Oregon]

**KATUNIELLA, NEW NAME FOR THE
GENUS *KATUNIA*, KULKOV, 1963
(BRACHIOPODA, RHYNCHONELLIDA)
PREOCCUPIED BY
KATUNIA ROMANENKO, 1962
(ARTHROPODA, TRILOBITA)**

During preparation of the manuscript for volume 4 of the revised brachiopod *Treatise on Invertebrate Paleontology*, Jill Hardesty, Assistant Editor for the *Treatise*, Paleontological Institute, University of Kansas, kindly informed me that the rhynchonellid genus name *Katunia* KULKOV, 1963, p. 54, is preoccupied by a trilobite genus published by ROMANENKO and ROMANENKO, 1962, p. 25 (see p. 1139 herein). I communicated with Dr. Nikolay KULKOV suggesting he publish a replacement name and he responded asking that, as he has now retired, I publish the replacement name *Katuniella*. According to Article 60 of ICZN rules (1999) I here propose the name *Katuniella* KULKOV, with reference to his letter (personal communication, 24 October, 2000), as replacement name for *Katunia* KULKOV, 1963, not *Katunia* M. F. ROMANENKO (in M. F. Romanenko, & E. V. Romanenko, 1962). The type species for *Katuniella* is *Katunia subtrigonata* KULKOV, 1963, p. 54.

ACKNOWLEDGMENTS

I thank Jill Hardesty for bringing this matter to my attention, Tatiana L. Modzalevskaya and Yu. I. Tesakov for help in communicating with Nikolay Kulkov, and Alison (Pete) Palmer for providing information about the paper by ROMANENKO and ROMANENKO.

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NOMENCLATORIAL NOTE

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**BONDAREVIA, NEW NAME FOR THE
GENUS *TRISEPTATA* BONDAREV,
1965 (BRACHIOPODA,
PENTAMERIDA) PREOCCUPIED BY
TRISEPTATA HOSHIDE, 1958
(PROTOZOA, SPOROZOA)**

In 1965, BONDAREV (in BONDAREV & others, 1965) erected the genus *Triseptata* to distinguish an unusual porambonitoid brachiopod known from several dozen isolated dorsal and ventral valves, and one complete, articulated, but deformed specimen. The specimens were collected from the lower Arenig (Lower Ordovician) of Novaya Zemlya. These large costellate brachiopods with a rectimarginate commissure possess a pseudospondylium and cardinal process characteristic of Huenellidae, accessory septa, a notothyrial platform, and an elevated dorsal adductor muscle field characteristic of Clarkellidae, and a septalium characteristic of Syntrophiidae (CARLSON, herein, p. 935). This unusual combination of porambonitoid features prevented BONDAREV from referring this genus to an established family, thus it was relegated to Porambonitoidea Incertae familiae. In the process of revising the brachiopod volumes of the *Treatise on Invertebrate Paleontology*, it was discovered that the name *Triseptata* was preoccupied by a sporozoan *Triseptata* HOSHIDE, 1958 (see p. 931 herein). *Triseptata* BONDAREV, 1965 is thus an objective homonym requiring a replacement name, according to Article 60 of the International Code of Zoological Nomenclature (1999). I propose the name *Bondarevia nomen novum* as a replacement for *Triseptata* BONDAREV, 1965, not *Triseptata* HOSHIDE, 1958. *Bondarevia* derives from the surname of V. I. BONDAREV, the author of the brachiopod genus. The type species of *Bondarevia* is *B.*

nelidovi BONDAREV in BONDAREV & others, 1965, p. 34. *Bondarevia* is monospecific, with *B. nelidovi* the only species recognized thus far (see also BONDAREV, 1968; SAPELNIKOV, 1980, 1985).

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