ATHYRIDIDA

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Order ATHYRIDIDA Boucot, Johnson, & Staton, 1964 Suborder ATHYRIDIDINA Boucot, Johnson, & Staton, 1964 Superfamily ATHYRIDOIDEA Davidson, 1881 Family ATHYRIDIDAE Davidson, 1881 Subfamily ATHYRIDINAE Davidson, 1881

Ceresathyris Havlíček in Havlíček & Vaněk, 1998, p. 89 [* Terebratula ceres BARRANDE, 1847, p. 395; OD]. Small to medium, dorsibiconvex shells of subpentagonal to elongated elliptical outline; maximum width at midvalve; with numerous (up to 40 in a specimen 15 mm long), evenly spaced, short growth lamellae; with shallow ventral sulcus and low dorsal fold with or without shallow median groove; anterior commissure weakly uniplicate; ventral beak moderately to strongly incurved, with small, circular foramen in permesothyridid position; delthyrium open, obscured by dorsal beak; shell thick in umbonal region; dental plates obscured by callus, free only anteriorly, subparallel to slightly convergent ventrally; lateral apical cavities very short; ventral muscle field weakly impressed; cardinalia thick posteriorly, dental sockets poorly developed anteriorly, cardinal flanges absent, hinge plate short, apically perforated by large foramen, slightly convex ventrally; without dorsal septum or myophragm; spiral cones laterally directed, jugum unknown. [This genus resembles Athyris M'Coy externally, but the umbonal region is thick shelled in both valves, dental plates are subparallel to slightly convex ventrally, obscured by callus, free only anteriorly, and reportedly without ventral foramen, but it seems to be present in some of HAVLÍČEK's illustrations (e.g., HAVLÍČEK in HAVLÍČEK & VANĚK, 1998, pl. 8,12a). It differs from Leptathyris SIEHL in its hinge plate being slightly convex ventrally as in some Pachyplax ALVAREZ & BRUNTON, from which Ceresathyris differs in growth lamellae morphology and ventral interior. The lack of information on the brachiojugal system makes impossible its comparison with those developed by other athryridid genera. May be synonymous with Athyris.] Lower Devonian (Pragian): Europe (Bohemia).——FIG. 1831,2a-l. *C. ceres (BARRANDE), Koneprusy Limestone, Koněprusy, Prague Basin; a-c, dorsal, ventral, and anterior views, Havlíček collection, VH 12123a, ×2 (Havlíček & Vaněk, 1998; photographs courtesy of the late V. Havlíček); d-l, transverse serial

sections 13.7, 13.5, 13.0, 12.7, 12.6, 11.1, 11.6, 11.8, 12.2 mm from anterior margin of shell (adapted from Havlíček & Vaněk, 1998).

- Drovithyris JAFARIAN [1973, unpublished manuscript deposited in the Université Claude Bernard, Lyon, France (M. A. JAFARIAN, personal communication, 7 May, 2002)]. This genus was described as a subgenus of *Athyris* by JAFARIAN, 1973, and listed but not described or diagnosed, as both subgenus and genus by JAFARIAN, 2000, p. 223, tables 3–4 respectively. Only one species, *Athyris (Drovithyris)* genus nov. and sp. nov. [sic] was included in the genus-subgenus by JAFARIAN (2000, p. 229, pl. 3,10a-b, 11a-b). [This genus is in need of proper validation.] Upper Devonian (?middle Frasnian, upper Famennian): southeastern Anarak, north of Esfahan, Chah-Riceh, Iran.
- Grinnellathyris LI & JONES, 2002, p. 656 [*G. alvarezis; M]. Small, commonly elongate, subelliptical, rarely circular or slightly transverse, equally biconvex to slightly ventribiconvex shells; maximum width near midvalve; surface with numerous (up to 16 in a specimen 12 mm long) short growth lamellae; ventral beak prominent, recurved, foramen large, rounded, permesothyrid, delthyrium open; shallow sulcus originating at about midlength; anterior commissure weakly uniplicate to slightly parasulcate; dental plates short, dorsally convergent, lateral apical cavities narrow, teeth small; cardinal plate imperforate, subtriangular, flat to slightly concave ventrally, cardinal flanges absent, socket ridges low; no dorsal septum or myophragm; laterally directed spiralia of fewer than about 10 whorls; U-shaped jugum, lateral branches of jugum almost vertical, starting midway along length of dorsal valve; jugal saddle moderately developed, jugal stem and accessory lamellae absent. [This genus differs from externally similar Athyris M'Coy and Protathyris KOZLOWSKY mainly in its imperforate cardinal plate, which is not trilobed anteriorly (Protathyris), jugum without stem and accessory jugal lamellae, and jugal saddle only moderately developed; differs from Buchanathyris TALENT in shorter dental plates, not being concave medially, jugum with jugal saddle moderately developed and without short, posteriorly directed, stemlike process. Although similar in shell size and internal structures, Johnsonathyris SAVAGE, EBERLEIN, & CHURKIN differs in shell being strongly biconvex, subglobular, ventral foramen minute, commissure strongly uniplicate anteriorly, shell exterior with fine growth lamellae crossed by regularly developed fine costellae, cardinal plate medially crested, and jugum placed anterior of midlength, without any saddle. When erected, Grinnellathyris was tentatively included in the Athyridinae, although the



FIG. 1831. Athyrididae (p. 2742-2744).

authors considered it advisable to establish a new subfamily, Johnsonathyridinae, for athyridines, as Johnsonathyris and Grinnellathyris, with imperforate cardinal plate. In the athyridids, the dorsal foramen is generally small or even very small, and easy to be overlooked when dorsal interiors are studied from serial sections of few specimens that are commonly adults. This feature is not evident if only adult or gerontic specimens are studied as it may become partially or completely infilled by secondary shell thickening during ontogeny. Grinnellathyris is therefore kept here also within the Athyridinae.] Middle Devonian (Eifelian): Bathurtst Insland, Grinnell Peninsula, North Kent Island, Arctic Canada.——FIG. 1832a-s. *G. alvarezis, Bird Fiord Formation, Grinnell Peninsula, Devon Insland, Arctic Canada; a-e, holotype, dorsal, ventral, lateral, anterior, and posterior views, UA 12090, \times 5.5; *f*, ventral view showing growth lamellae, UA 12091, ×3 (Li & Jones, 2002); g-s, transverse serial sections 0.7, 1.3, 1.7, 1.9, 2.1, 2.3, 2.5, 2.7, 3.1, 4.5, 6.85, 7.1, 7.5 mm from ventral umbo (adapted from Li & Jones, 2002).

Pachyplaxoides GRUNT in GRUNT & RACKI, 1998, p. 369 [*P. postgyralea; M]. Small to medium, ventribiconvex to nearly equally biconvex shells of subpentagonal to subcircular outline; equidimensional to slightly wider than long, commonly widest near midlength, with maximum thickness at posterior third of shell; with numerous (up to 20 in a specimen 27 mm long), variably developed growth lamellae; shallow ventral sulcus and flat, or slightly depressed medianly, dorsal fold beginning in posterior third of shell; anterior commissure weakly uniplicate; ventral beak short, incurved, truncated by small, permesothyridid foramen; delthyrium open, obscured by dorsal beak; internally without dental plates; no dorsal septum or myophragm; cardinal flanges absent, cardinal plate thin, subtrapezoidal, apically perforated, ventrally concave anteriorly, crural bases poorly developed; spires seem to be present but their number, disposition, and jugum unknown. [This genus differs from closely related athyridids such as Protathyris KOZLOWSKI and Alvarezites STRUVE, with similar, delicate, and not very long growth lamellae, in its general morphology and internal characters. It differs from Lamellosathyris JIN & FANG and Pachyplax ALVAREZ & BRUNTON in its external ornamentation, type of cardinalia, and lack of dental plates. Lamellosathyris has long, radially corrugated shell flanges extending from rugae of both valves. In Pachyplax, the growth lamellae are thick and overlap strongly so that the combination of lamellae and the entrapped sediment between them gives a rough, rugose external appearance to the shells, which are rather different than those of Pachyplaxoides. Internally, in *Pachyplax* as in many other Devonian related genera, more or less developed cardinal flanges are confined posteriorly on the hinge plate, a myophragm divides the dorsal muscle scars, and more or less clear dental plates support the hinge teeth; all these structures are absent in Pachyplax-

oides. In Lamellosathyris the cardinal flanges project posteroventrally and the diductor myophores spread over most of ventral surface of the reduced but heavily thickened cardinal plate. The genus differs externally from Planalvus CARTER and Densalvus CARTER, also without dental plates; Planalvus is slightly uniplicate, dorsibiconvex with an almost flat ventral valve; while Densalvus is rectimarginate, with strongly inflated ventral valve and weakly convex dorsal valve. The lamellae of Pachyplaxoides are not finely striated and fringed with minute solid spines (Planalvus) or weakly and finely capillate (Densalvus). Lack of information on the brachiojugal system makes impossible its comparison with those developed by other athryridid genera.] Upper Devonian (upper Frasnian): central Poland (Holy Cross Mountains), Germany (Eifel).---FIG. 1831, 1a-s. *P. postgyralea; a-d, holotype, dorsal, ventral, lateral, and anterior views, Quarry Reichle, Prümer Mulde, Eifel, Germany, SFM 59509, ×1.2; e, enlargement of ornament of ventral valve, Łgawa Hill, Bolechowice, Holy Cross Mountains, central Poland, GIUS 4-1477/GL-102, ×7.5 (Grunt & Racki, 1998); f-s, transverse serial sections 1.4, 1.6, 1.7, 2.0, 2.2, 2.4, 2.7, 2.8, 2.9, 2.95, 3.0, 3.3, 3.7, 4.0 mm from ventral umbo, Łgawa Hill, Bolechowice, Holy Cross Mountains, central Poland, GIUS 4-1477/GL-140, (adapted from Grunt & Racki, 1998).

Subfamily ATHYRISININAE Grabau, 1931

[Athyrisininae GRABAU, 1931a, p. 509; emend., RONG & others, 2004, p. 824]

Shell small to large, moderately rostrate, commonly with very strong ventral umbo curvature; growth lamellae generally well developed, may be squamose; fold and sulcus well developed; dental plates commonly short (long in Bruntosina), converging dorsally, may become subparallel anteriorly; dorsal myophragm absent; cardinal plate and jugum essentially as in Athyris, but without cardinal flanges. [Recently, RONG and others (2004), in their revision of this subfamily, excluded from the Athyrisininae the following genera: Pseudohomeospira Nikiforova, Ikella Tyazheva, Squamathyris MODZALEVSKAYA, and Homeathyris MODZALEVSKAYA. They placed them in a new athyridid subfamily, Homeathyridinae (see below). In addition to the type genus, Athyrisina HAYASAKA (in YABE & HAYA-SAKA), RONG and others (2004) included in the subfamily Athyrisininae the following genera: Parathyrisina WANG in WANG, YU, & WU, Athyrisinoidea CHEN & WAN in WAN,



FIG. 1832. Athyrididae (p. 2742-2744).

Neoathyrisina CHEN, and *Bruntosina* RONG & others from South China (plus western Sichuan and Qinling regions) and northern Vietnam.] *Lower Devonian (Pragian)–Middle Devonian (Givetian).*

Athyrisina HAYASAKA in YABE & HAYASAKA, 1920, p. 176; emend., RONG & others, 2004, p. 827 [*A. squamosa; OD] [=Kwangsia GRABAU, 1931a, p. 204 (type, K. yohi, OD); Plectospirifer GRABAU, 1931a, p. 379 (type, P. heimi, OD); Kwangsialu GRABAU, 1932, p. 82 (type, K. yohi, OD); Pseudoathyrisina CHEN, 1979, p. 17 (type, P. fasciata, OD); Athyrisinopsis ZHANG, 1983, p. 354 (type, *A. uniplicata*, OD)]. Small to large shells with rounded subpentagonal to transversely elliptical dorsal outline, with short to relatively long hinge line, ventribiconvex lateral profile; ventral sulcus and dorsal fold usually well developed; pauciplicate to costellate, radial elements may bifurcate; growth lamellae numerous, commonly well developed and regularly spaced; dental plates thin, short, lateral apical cavities very narrow; cardinal plate perforated apically by minute foramen, spiralia with 10 to 18 whorls. [Distinguished from other Athyrisininae by having 3 or more ribs in the sulcus, of the same width as those on the flanks. Radial elements are more numerous in *Athyrisina* than in *Bruntosina* RONG & others and *Parathyrisina* WANG, and the



FIG. 1833. Athyrididae (p. 2745-2746).

ribs bounding the sulcus are similar to those on the flanks and sulcus.] Lower Devonian (upper Pragian)–Middle Devonian (Givetian): southern China (northern Sichuan, southeastern Guizhou, eastern Yunnan, Guangxi), Qinling region (western and eastern Shaanxi, southeastern Gansu, northernmost Sichuan), western Sichuan (Ganzi Block), northern Vietnam.— FIG. 1833a–e. *A. squamosa; neotype, dorsal, ventral, lateral, anterior, and posterior views, Yangmaba Formation, upper Emsian, Heitupo, Wenchuan County, northern Sichuan Province, NIGP 134224, ×1.5 (Rong & others, 2004).

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Bruntosina Rong & others, 2004, p. 837 [*Athyrisinopsis gansuensis ZHANG in ZHANG & FU, 1983, p. 355; OD; = Athyrisinopsis trapeziformis ZHANG, 1987, p. 126]. Medium to large, elongate oval, subcircular to transversely oval and nearly equally biconvex shells; ventral sulcus and dorsal fold well developed; pauciplicate on flanks, without bifurcation or intercalation, a single costa characteristically present in middle of sulcus, and shallow furrow on middle of fold; variably spaced growth lamellae, on any of which there are up to 80 growth lines; dental plates thin, long, and parallel, lateral apical cavities wider than for subfamily; cardinalia, spiralium and jugum essentially as in Athyrisina. [Bruntosina has a more restricted distribution than the other athyrisinins: it is only known from upper Emsian and Eifelian of the West Qinling Mountains. It resembles Athyrisina HAYASAKA, type genus of Athyrisininae, but has fewer plications (generally 2) on flanks, and ribs bounding the sulcus are stronger. Radial elements are more numerous in Athyrisina, being simple costae or less frequently costae and costellae. Bruntosina characteristically has a single, narrow costa in the middle of the sulcus, whereas Athyrisina has three or more ribs (of the same width as those on the flanks) in the sulcus, and Parathyrisina WANG has no radial elements on the sulcus or

fold. Growth lamellae are numerous and regularly spaced in Athyrisina, but in Bruntosina they are variably spaced (up to 5 on adult valves), with up to 80 fine growth lines on each lamellae. Internally, dental plates are long and parallel in Bruntosina, but very short, with very narrow lateral apical cavities in Athyrisina and Parathyrisina.] Lower Devonian (upper Emsian)–Middle Devonian (Eifelian): China (western and eastern Qinling, southeastern -FIG. 1834a-j. *B. gansuensis (ZHANG), Gansu).---Dangduo Formation, upper Emsian-lower Eifelian; a-e, holotype, dorsal, ventral, lateral, anterior, and posterior views, Pulaigou, Tewo County, southeastern Gansu, XB 239, ×1.5; f-h, dorsal, ventral, and anterior views, Xiawunagou, Tewo County, southeastern Gansu, XB 231, ×1.5; i-j, ventral view and enlargement showing characteristic single costa in middle of sulcus and concentric ornamentation, Dangduobeigou, Tewo County, southeastern Gansu, XB 230, ×1.5, ×8.5 (Rong & others, 2004).—FIG. 1835a-u. *B. gansuensis (ZHANG), Dangduo Formation, upper Emsian-lower Eifelian; transverse serial sections 1.2, 1.9, 2.6, 3.0, 4.0, 4.6, 5.0, 5.5, 5.9, 6.1, 6.7, 8.6, 9.7, 10.3, 10.6, 10.8, 11.4, 12.2, 12.5, 14.9, 15.2 mm from ventral umbo, distance from ventral umbo to first section approximate, Pulaigou, Tewo County, southeastern Gansu, ×1.5 (Rong & others, 2004).

Parathyrisina WANG in WANG, YU, & WU, 1974, p. 41; emend., RONG & others, 2004, p. 832 [*P. bella; OD; =Athyrisina tangnae HOU, 1963, p. 416] [=Athyrisinoides CHEN & WAN in XU, WAN, & CHEN, 1978, p. 351 (type, A. typica, OD); Athyrisinoidea CHEN & WAN in WAN, 1980, p. 105 (type, A. typica, OD), nom nov. pro Athyrisinoides CHEN & WAN in XU, WAN, & CHEN, 1978, p. 351; Neoathyrisina CHEN, 1988, p. 36, obj.]. Commonly small to medium, rarely large, transverse subelliptical to subcircular outline, equally to subequally biconvex shells; pedicle opening large, palintrope reduced; ventral sulcus and dorsal fold rounded, commonly well developed, without radial elements; lateral slopes bearing 3 or more costae, growth lamellae well developed; interior and jugum essentially as in *Athyrisina*. [This genus is distinguished from other Athyrisiniae in lacking radial elements on sulcus and fold; internally, the dental plates are long and parallel in *Bruntosina* but very short with very narrow lateral apical cavities, in both *Athyrisina* and *Parathyrisina*. For illustrations see ALVAREZ & RONG, 2002, fig. 1022*a*–*x* and revision in RONG & others, 2004.] *Lower Devonian (upper Pragian– upper Emsian):* southern China (Guangxi, Sichuan), southeastern Gansu, northwestern Sichuan, western Qinling.

Subfamily CLEIOTHYRIDININAE Alvarez, Rong, & Boucot, 1998

Bruntonathyris CHEN, SHI, & ZHAN, 2003, p. 853 [*B. amunikeensis; OD]. External shape, folding, and concentric ornamentation resembling those of transverse Actinoconchus M'COY; exfoliated surfaces displaying a delicate radial pattern. Interior similar to that of some cleiothyridinins; cardinalia with poorly developed cardinal flanges. Spiralium and jugum unknown. [This genus was assigned by its authors to the Cleiothyridininae notwithstanding the absence of flat, solid spinelike projections from growth lamellae, anteriorly and anterolaterally directed, which are diagnostic of that subfamily. In fact, these shells could be either athyridinins or cleiothyridinins dependent on their ornamentation, which is not well preserved in the material studied; internal structure of brachidia unknown.] Lower Carboniferous (upper Tournaisian-Viséan): northwestern China (Qaidam Basin), upper Tournaisian-Viséan; southern China, Japan (Akiyoshi), Russia (Urals, Moscow Basin, Donetsk Basin), England, Viséan.—FIG. 1836a-p. *B. amunikeensis, Tournaisian, Chuanshangou section, Qaidam Basin, northwestern China; a-e, holotype, dorsal, ventral, lateral, anterior, and posterior views, NMV P309563, ×1.5; f-h, dorsal and ventral views, and detail of ventral umbonal region, exfoliated, showing radial striae, NMV P309561, ×1.5, ×3; *i-o*, transverse serial sections 0.5, 1.5, 2.0, 2.5, 3.2, 3.7, 4.0 mm from ventral umbo, NMV P309564; p, dorsal interior reconstructed from serial sections, NMV P309564 (Chen, Shi, & Zhan, 2003).

Subfamily DIDYMOTHYRIDINAE Modzalevskaya, 1979

Fastigata BARANOV & AL'KHOVIK, 2001, p. 41 [**F. longa*; M]. Small-sized, elongate subelliptical to subpentagonal, subequally biconvex, rectimarginate to slightly uniplicate shells; widest and thickest near midlength; ventral beak slightly curved, delthyrium reportedly covered by deltidial plates; valve surface with spaced growth lamellae and fine tubular ribs similar to that of some atrypids; dental plates short, thin to more or less thick, converging slightly

dorsally; cardinal plate apically perforated, slightly ventrally concave posteriorly to slightly ventrally convex anteriorly; cardinal flanges absent; low and short dorsal myphragm may be present; spiralia with up to six laterally directed whorls, jugum with relatively short saddle and stem, accessory jugal lamellae very short or absent. [Fastigata is similar to Pseudoprotathyris in shape, but differs in its ornamentation, cardinalia, and jugum. It differs from Atrythyris in its hinge plate not being depressed medially, poorly developed cardinal flanges, and much shorter accessory jugal lamellae; it differs from Bruntonathyris by inner hinge plates situated in similar plane to the outer hinge plates. Exfoliated surfaces in Bruntonathyris display a delicate radial pattern; in Fastigata, although material is too poorly preserved, fine tubular ribs seem to be interrupted by regular growth lamellae.] Lower Devonian (lower Lochkovian): Tas-Khayakhtakh Ridge and southern Verkhoyansk region, eastern -FIG. 1837, 2a-t. *F. longa; a-d, holo-Yakutia.type, dorsal, ventral, lateral, and anterior views, lower Sette-Daban Formation, Sette-Daban Ridge, southern Verkhoyansk region, eastern Yakutia, IGN SO RAN 171/1, ×3; e-f, partly exfoliated ventral valve showing tubular ribs, basal Datna Formation, Tas-Khayakhtakh Ridge, IGN SO RAN 171/7, ×3, ×10 (Baranov & Al'khovik, 2001); g-s, transverse serial sections 0.5, 0.7, 0.8, 1.1, 1.85, 2.6, 2.7, 3.4, 3.6, 3.9, 4.1, 4.5, 4.6 mm from ventral umbo, distance from ventral umbo to first section approximate, lower Sette-Daban Formation, Sette-Daban Ridge, southern Verkhoyansk region, eastern Yakutia IGN SO RAN 171/8; t, transverse serial section at approximately 2.0 mm from ventral umbo, lower Sette-Daban Formation, Sette-Daban Ridge, southern Verkhoyansk region, eastern Yakutia, IGN SO RAN 171/9 (adapted from Baranov & Al'khovik, 2001).

Mica BARANOV & AL'KHOVIK, 2001, p. 44 [*M. borea; M] [=Micathyris BARANOV & AL'KHOVIK, 2001, p. 42, fig. 2, incorrect subsequent spelling]. Very small, subequally biconvex shells with outline elongate subelliptical; dorsal fold and ventral sulcus absent or poorly developed anteriorly; growth lines weak; ventral beak high, slightly curved, delthyrium reportedly covered by deltidial plates; dental plates thin, high, short, subparallel, teeth small; hinge plate ventrally concave, apically perforated, septum or dorsal myophragm absent; spiralia with up to four laterally directed whorls, jugum poorly preserved, seemingly without saddle, stem, or accessory jugal lamellae. [Mica resembles Fastigata, Glassina, Dogdathyiris, or Svetlania in outline and lateral profile, but differs internally by nature of cardinalia and brachidium; this genus requires revision.] Lower Devonian (Emsian): Ulakhan-Sis Ridge, eastern Yakutia.-FIG. 1837, 1a-l. *M. borea; a-d, holotype, dorsal, ventral, lateral, and anterior views, Krivoi Ruchei Formation, Ulakhan-Sis Ridge, eastern Yakutia, IGN SO RAN 171/16, ×3 (Baranov & Al'khovik, 2001); e-l, transverse serial sections 1.3, 1.5, 1.8, 2.2, 2.4, 2.7, 3.0, 3.3



FIG. 1834. Athyrididae (p. 2746).

Athyridida



FIG. 1835. Athyrididae (p. 2746).



FIG. 1836. Athyrididae (p. 2747).



FIG. 1837. Athyrididae (p. 2747-2752).

mm from ventral umbo, distance from ventral umbo to first section approximate, Krivoi Ruchei Formation, Ulakhan-Sis Ridge, eastern Yakutia, IGN SO RAN 171/22 (adapted from Baranov & Al'khovik, 2001).

Pygmis BALIŃSKI, 2002, p. 299 [*Nucleospira jablonensis BIERNAT, 1983, p. 142; M]. Small, smooth, slightly rostrate, ventribiconvex to nearly equally biconvex, weakly uniplicate; delthyrium open; subcircular to subpentagonal, commonly widest near midlength; internally with short, subparallel dental plates; cardinal plate apically perforated; spiralia with up to 5 laterally directed whorls and complete jugal arch. [This genus differs from externally similar Helenathyridinae in lacking a double spiralium with the accessory jugal lamellae intercalating with spiralial loops to apex; differs from Leptathyris in weakly uniplicate, not faintly bisulcate, anterior commissure and cardinal plate without a medial depression. Pygmis differs from Nucleospira, where the type species was placed originally, in having dental plates, very different cardinalia, and neither low median ridge on both valves nor the typical external ornamentation of fine, solid spines covering entire shell and projecting radially at different angles from valve surface of well-preserved Nucleospira. Most features are typically didymothyridine, but shell interiors are affected by recrystallization, and consequently the details of the cardinalia, spiralium, and jugum were missed on serial sections; better, nonrecrystallized specimens are needed to check its taxonomic position within the Athyrididae and its possible phylogenetic relationship with the Helenathyridinae.] Upper Devonian (Famennian): southern and central Poland (Kraków area, Holy Cross Mountains), ?Turkestan.--FIG. 1838a-y. *P. jablonensis (BIERNAT); a-e, holotype, dorsal, ventral, lateral, anterior, and posterior views, Jabłonna, Holy Cross Mountains, central Poland, ×3 (new; photographs courtesy of A. Baliński); f-h, ventral, lateral, and anterior views, Debnik, Kraków area, southern Poland ZPAL Bp 46/57b, ×1.5 (Baliński, 2002; photographs courtesy of A. Baliński); i-p, transverse serial sections 0.4, 0.6, 0.65, 0.7, 0.75, 0.9, 1.2, 1.3 mm from ventral umbo, ZPAL Bp 46/57e; q-v, transverse serial sections 0.6, 0.7, 2.2, 2.5, 2.6, 2.8 mm from ventral umbo, ZPAL Bp 46/58; w-y, transverse serial sections 3.25, 3.4, 3.7 mm from ventral umbo, ZPAL Bp 46/57f (adapted from Baliński, 2002).

Subfamily HOMEATHYRIDINAE Rong & others, 2004

[Homeathyridinae Rong & others, 2004, p. 842] [Type genus, *Homeathyris* MODZALEVSKAYA, 1997a, p. 7]

Shell small to medium, biconvex, moderately to strongly rostrate, costate, or costellate; growth lamellae commonly poorly developed, but may be squamose (*Squa*-

mathyris); fold and sulcus variably developed, variably developed furrow, commonly shallow, may divide medially the dorsal fold (Homeathyris); hypothyridid pedicle opening commonly partially closed by deltidial plates; dental plates commonly short, converging dorsally, may become subparallel anteriorly; large delthyrial chamber with pedicle support consisting of pedicle collar (Pseudohomeospira) or two variably developed curved plates, formed of secondary layer, medially and apically situated between dental plates and joined with them at their posterodorsal end (*Homeathyris* and *Squamathyris*); cardinal plate apically perforated posteriorly; hinge plate ventrally concave in early forms, flat in latest species; spiralium and jugum resembling that of typical athyridines but with very short accessory lamellae. Silurian (Ludlow-Přídolí).

Genera assigned. In addition to the type genus, Pseudohomeospira NIKIFOROVA and Squamathyris MODZALEVSKAYA were placed in this subfamily. [These three genera were removed by RONG and others (2004) from the Athyrisininae, where they were commonly placed (e.g., NIKIFOROVA, 1970; MODZALEVSKAYA, 1981, 1994, 1997a, 1997b; GRUNT, 1984, 1986; ALVAREZ, RONG, & BOUCOT, 1998; ALVAREZ & RONG, 2002). See RONG and others (2004) for comparison with other subfamilies of the Athyrididae.]

Homeathyris MODZALEVSKAYA, 1997a, p. 7; emend., RONG & others, 2004, p. 824 [*H. insularis; OD] [=Homeathyris MODZALEVSKAYA in MODZALEVSKAYA & others, 1994, p. 66, nom. nud.; Homeathyris MODZALEVSKAYA, 1994, p. 147, nom. nud.]. Small to medium, subequally to ventribiconvex shells of subpentagonal to longitudinally oval outline; hypothyridid pedicle opening partially covered by deltidial plates; variably developed furrow dividing the dorsal fold medially; ornament of costae or low plications, bifurcated costellae developed in sulcus and median furrow, growth lamellae poorly developed, commonly absent; dental plates short, lateral cavities narrow, delthyrial chamber with two variably developed curved plates medially, apically situated between dental plates, and joined with them at their posterodorsal end; hinge plate subtriangular, ventrally concave; spiralia with 7-10 whorls. [This genus differs externally from Pseudohomeospira NIKIFOROVA and Squamathyris MODZALEVSKAYA in having a variably developed



FIG. 1838. Athyrididae (p. 2752).

furrow dividing the dorsal fold medially. Growth lamellae are poorly developed in Homeathyris and Pseudohomeospira, but well developed (being squamosus) in Squamathyris. Internally, Homeathyris and Squamathyris have a subtriangular and ventrally concave hinge plate, while this is almost flat in Pseudohomeospira. Homeathyris and Squamathyris also differ from Pseudohomeospira in having medially and apically situated plates between the dental plates and joined with them at their posterodorsal ends, while Pseudohomeospira has a pedicle collar. These pedicle supports are commonly longer, in relation to the total length of the ventral valve, in Homeathyris than in the other two genera.] upper Silurian (Ludfordian): Russia (Arctic Russia, southern island of Novaya Zemlya, Dolgii Island, western slope of the Central Urals).--Fig. 1839a-s. H. plicatella (MODZALEVSKAYA), Zelenets Formation, Dolgii Island; a-k, transverse serial sections 10.7, 10.0, 9.9, 9.0, 8.3, 8.2, 7.4, 7.1, 6.8, 6.7, 6.6 mm from anterior margin of the shell, CNIGR N2/13099; I-s, tangential serial sections, parallel to commissural plane, 4.3, 4.2, 4.0, 3.7, 3.3, 2.8, 2.7, 1.9 mm from dorsal valve, CNIGR N3/13099 (Rong & others, 2004). [See also FIG. 1021,2a-b in ALVAREZ & RONG, 2002; and revision in RONG & others, 2004.]

- Pseudohomeospira Nikiforova, 1970, p. 139; emend., RONG & others, 2004, p. 846 [*P. polaris; OD]. Small, biconvex, elongate oval, costate shells; ventral sulcus and dorsal fold weakly developed anteriorly; costae subangular or rounded, each valve with 12-16 costae, bifurcating in fold and sulcus; hypothyridid pedicle opening may be partially closed by deltidial plates; pedicle collar present; short ventral ridge may be present apically; dental plates thin, of moderate length, dorsally convergent apically, with very narrow lateral apical cavities, subparallel posteriorly; minute dorsal foramen, very low dorsal myophragm may be present apically; spiralia directed laterally, jugum unknown. [Pseudohomeospira is more elongate than Homeathyris and Squamathyris, which are commonly almost equidimensional. Pseudohomeospira characteristically has a weakly developed dorsal fold and ventral sulcus displayed only anteriorly. Ventral beak relatively high, slightly curved, with a hypothyridid pedicle opening partially closed by deltidial plates and pedicle support resembling internal characteristics of didymothyridin Collarothyris MODZALEVSKAYA, 1970, from beds of Ludlow age in western Russia and adjacent areas. Better, nonrecrystallized specimens are needed, which will allow the study of jugal structures.] upper Silurian (Přídolí): Russia (Arctic Russia, southern island of Novaya Zemlya, Vaigach Island, western slope of Polar and Central Urals).——FIG. 1840, *1a-g. *P. polaris*, Tselebej Formation, western slope of Polar Urals; transverse serial sections 10.0, 9.4, 9.3, 8.5, 8.3, 7.9, 7.6 mm from anterior margin of shell, CNIGR N86/10629 (Rong & others, 2004). [See also FIG. 1021,1a-b in ALVAREZ & RONG, 2002; and revision in RONG & others, 2004.]
- Squamathyris MODZALEVSKAYA, 1981, p. 153; emend., RONG & others, 2004, p. 848 [*S. glacialis; OD]. Shell of medium size, biconvex, moderately to strongly rostrate, subpentagonal outline, with strong costae and numerous and squamose growth lamellae; ventral sulcus and dorsal fold moderately developed; hypothyridid pedicle opening restricted laterally by deltidial plates; dental plates short, delthyrial chamber with two variably developed curved plates medially and apically situated between dental plates and joined with them at their posterodorsal end; hinge plate subtriangular, ventrally concave; spiralia with up to ten whorls, jugum unknown. [This genus differs from Homeathyris and Pseudohomeospira in having stronger costae and numerous and squamose growth lamellae. Internally, the hinge plate is ventrally concave in Squamathyris but almost flat in Pseudohomeospira. Squamathyris also differs from Pseudohomeospira in having medially and apically situated plates between the dental plates and joined with them at their posterodorsal ends as in Didymothyris, while Pseudohomeospira has a pedicle collar; the internal jugal structure is unknown.] upper Silurian (Ludfordian): Russia (Arctic Russia, southern island of Novaya Zemlya, Vaigach and Dolgii islands). ——FIG. 1840,2a-n. *S. glacialis, Zapadno-Khatanzeya Formation, southern island of Novaya Zemlya; transverse serial sections 16.0, 15.6, 15.5, 14.5, 13.6, 13.2, 13.05, 13.0, 12.5, 12.4, 12.2, 12.0, 11.95, 11.9 mm from anterior margin of the shell, CNIGR N5/13099 (Rong & others, 2004). [See also fig. 1021,3a-d in ALVAREZ & RONG, 2002; and revision in RONG & others, 2004.]

Subfamily JANICEPSINAE Posenato, 2001

[Janicepsinae POSENATO, 2001, p. 204] [Type genus, *Janiceps* Frech, 1901, p. 551]

Commonly small to medium size, rarely larger, subtrigonal to transversely subrectangular, astrophic to almost strophic shells, moderately to strongly biconvex, with ventral sulcus and dorsal sulcate fold; lateral plications may be developed; smooth, with fine growth lines; ventral beak short, incurved, truncated by small, permesothyridid foramen; delthyrium open, obscured by dorsal beak; pedicle support absent; dental plates thin, relatively short, may be close to valve walls or obscured by callus but distinct in specimens sectioned, low dental flanges may support teeth anteriorly; cardinal plate subquadrangular and thick, serrated cardinal flanges moderately to strongly developed posteroventrally, carrying the myophores deeply into the ventral umbo; inner socket



FIG. 1839. Athyrididae (p. 2752-2754).

ridges high; dorsal foramen infilled; dorsal myophragm or septum absent; jugum as in *Athyris* with short accessory jugal lamellae. [There is a great external and internal morphologic variation within the species and genera traditionally included within the Spirigerellinae (e.g., GRUNT, 1986; ALVAREZ, RONG & BOUCOT, 1998; POSENATO, 1998, 2001; ALVAREZ & RONG, 2002). The variability displayed by the Comelicaniinae from the Southern Alps was studied in detail by POSENATO (1998) who recently suggested (POSENATO, 2001) that some Permian shells, included until now within the subfamily

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FIG. 1840. Athyrididae (p. 2754).



FIG. 1841. Athyrididae (p. 2757-2758).

Spirigerellinae, are paedomorphic derivatives of the Comelicaniinae. To avoid a polyphyletic origin to the spirigerellins, POSENATO (2001) erected the Janicepsinae for Janiceps and Comelicothyris. The shells of the Comelicaniinae are large to extremely large, while the Janicepsinae shells are small to moderately so, and it is likely that the failure to develop in the Janicepsinae some characters of the immediate ancestors was probably achieved by early sexual maturity, progenesis, than by delayed somatic development of certain parts, neoteny. As possibly paedomorphism was involved more frequently than described, a complete and detailed revision of the species included in the Spirigerellinae, and related groups, is needed to better understand their phylogenetic affinities.] Upper Permian (Changhsingian).

Genera assigned. When the subfamily was erected, two genera were included: Janiceps FRECH, 1901 and Comelicothyris POSENATO, 2001. According to Article 16.2 of the 4th edition of the Code (1999), any new family-group name published after 1999 must satisfy the provisions of Articles 13–15 and must be accompanied by citation of the name of the type genus (the name from which the family-group name is formed). Although POSENATO did not expressly cite *Janiceps* as the type genus for the subfamily, it is clear throughout the paper that the subfamily-group name was formed from that genus. Authorship, date, and bibliographic reference of the work in which *Janiceps* was established was provided by the author, thereby avoiding possible ambiguities.

Janiceps FRECH, 1901, p. 551; emend., POSENATO, 2001, p. 205 [*Spirigera peracuta STACHE, 1878, p. 152; SD Schuchert & LeVene, 1929, p. 70]. Small to medium sized, subtrigonal, biconvex, and astrophic shells with ventral sulcus and dorsal sulcate fold, lateral grooves may be developed; anterolateral extremities pointed or rounded; ventral umbo small, recurved, and pointed; only very fine growth lines; pedicle support absent; dental plates thin and short, mostly buried in secondary shell material; cardinal plate subquadrangular and thick; inner socket ridges high; dorsal foramen absent; cardinal flanges variably developed; dorsal myophragm or septum absent; jugum as in Athyris with short accessory jugal lamellae. Upper Permian (Changhsingian): Italy (southern Alps). [Extralpine, older occurrences from Transcaucasia (upper Djulfian to lower Dorashamian) and China (Wuchiapingian and Changhsingian) need revision (POSENATO, 2001).]--FIG. 1841a-g. *J. peracuta (STACHE), upper Changhsingian, southern Alps; a-e, dorsal, ventral, lateral, anterior, and posterior views, Monte Croce di Comelico, Stache collection, MGBW 1878/1/47a, ×1.5 (Posenato, 2001; photographs courtesy of R. Posenato); f-g, reconstruction of

internal characters of dorsal valve viewed ventrally and laterally, Val Brutta, MDTF 6 (Posenato, 2001). [See also Fig. 1045,*3a–t* in ALVAREZ & RONG, 2002; and revision in POSENATO, 2001.]

Comelicothyris POSENATO, 2001, p. 217 [*Athyris protea var. recticardinis MERLA, 1930, p. 67; OD]. Shell medium sized, strongly biconvex, rounded triangular to subpentagonal or transverse subrectangular, almost strophic; maximum width near midvalve; ventral sinus relatively deep and dorsal sulcus on slightly raised fold; dental plates very thin and short, not fused to thick lateral walls; cardinalia as in Comelicania, with well-developed cardinal flanges and myophores facing sagittal plane; spiralia and jugum poorly known. [The outline of Comelicothyris juveniles is rounded-subtriangular and Janiceps-like, while the outline of adults resembles that of late Comelicania species. This genus differs from Comelicania in its smaller size, maximum width near midvalve, not at hinge margin, lack of small winglike extensions at cardinal extremities, dental plates thin, short, and not fused to lateral walls. Juveniles and adult Janiceps have an astrophic, subtriangular to rhomboidal shell with maximum width at anterior third of shell, close to front. In Janiceps the thin and short dental plates may be buried in secondary shell material that is strongly developed in umbonal cavities, and low dental flanges may support teeth anteriorly (see POSENATO, 1998, 2001). Araxathyris differs from Comelicothyris in its parasulcate to bisulcate anterior commissure; growth laminae widely and irregularly spaced; medially concave dental plates forming narrow sessile spondylium; cardinal plate thinner, triangular, apically perforated, with lower cardinal flanges; short and low myophragm, tertiary layer present (e.g., GRUNT, 1965, 1986).] Upper Permian (upper Changhsingian): eastern southern Alps .---- FIG. 1842a-p. *C. recticardinis (MERLA); a, lectotype, ventral view, Monte Croce di Comelico, Merla collection, MDGP 24840, ×1; b, ventral view, Monte Croce di Comelico, Merla collection, MDGP 24834, ×1 (Posenato, 2001; photographs courtesy of R. Posenato); c-p, transverse serial sections 0.45, 1.5, 2.55, 2.7, 3.2, 4.05, 4.15, 4.3, 4.5, 4.85, 5.35, 6.15, 6.85, 7.1 mm from ventral umbo, Val Brutta, MDTF 15 (Posenato, 2001).—FIG. 1842q-t. C. laterosulcata POSENATO; holotype, dorsal, ventral, lateral, and posterior views, Sass de Putia, Bolzano, MDTF 54, ×0.8 (Posenato, 2001; photographs courtesy of R. Posenato).

Subfamily PLICATHYRIDINAE Alvarez, 1990

Anathyris VON PEETZ, 1901, p. 134 [*Spirifera phalaena PHILLIPS, 1841, p. 71; SD SCHUCHERT & LEVENE, 1929a, p. 29]. Small to very large transverse shells commonly with overall winged outline; almost opposite to more or less well-developed mixed folding; pedicle foramen in permesothyridid position; delthyrium wide, triangular, open or partially restricted laterally by narrow deltidial plates; internally similar to *Plicathyris. Lower Devonian (Emsian)–Upper Devonian (Frasnian), ?Lower Carboniferous:* northwestern Spain, France, Bohemia, Czech Republic, northern Africa, Saudi Arabia, *Emsian*; England, Timan, Kuznetsk Basin, North America, *Middle Devonian*; Timan, Urals, Kuznetsk basin, Afghanistan, *Frasnian*; ?Hunan, *?Lower Carboniferous.*

- A. (Anathyris). Medium to very large transverse Anathyris with overall winged outline; hinge line almost straight, equal to or slightly shorter than maximum width; folding almost opposite and anterior commissure straight in juveniles, passing during ontogeny to develop a clearer mixed folding; ventral cardinal area well defined, rather high, subtrapezoidal, concave, ranging from apsacline to almost catacline in lateral regions to strongly curved anacline centrally; area covered by numerous, close and horizontal, well-marked growth lines; internally teeth and dental plates thicker than in Plicathyris; in late growth stages of some specimens dorsal foramen filled. [For discussion of its type species and other species included, see ALVAREZ, 1990, p. 206-207. The inclusion of A. rhomboidalis from the Lower Carboniferous of Hunan, China, may extend the range from the Upper Devonian, Frasnian, but its assignment is uncertain.] Lower Devonian (Emsian)-Upper Devonian (Frasnian), ?Lower Carboniferous: northwestern Spain, France, northern Africa, Saudi Arabia, Emsian; England, Timan, Kuznetsk Basin, North America, Middle Devonian; Timan, Urals, Kuznetsk basin, Afghanistan, Frasnian; ?Hunan, ?Lower Carboniferous. [For illustrations, see ALVAREZ & RONG, 2002, fig. 1039.]
- A. (Ranathyris) HAVLÍČEK, 1998, p. 120 [*Anathyris inconsueta HAVLÍČEK, 1956, p. 620; M]. Small to medium, rounded subpentagonal Anathyris with strongly biconvex lateral profile; maximum width anterior to midlength, close to anterior margin; ventral beak thick, incurved, with large pedicle foramen; poorly developed mixed folding, folds round, poorly developed, or absent in ventral valve, ventral median sulcus shallow to moderately deep and subangular; dorsal valve with narrow median depression bounded by two rounded submedian folds; lateral folds gentle and rounded in both valves; teeth small, supported by short, thin, nearly parallel dental plates; spiralia and jugum unknown. [HAVLÍČEK (1998) established a new subgenus for this widespread and relatively common mid-Paleozoic genus; Ranathyris is based only on A. inconsueta HAVLIČEK. As many of the diagnostic features of this subgenus are manifest in the main Anathyris line, their use is restricted.] Lower Devonian (lowest Emsian): Prague Basin (Bohemia).--FIG. 1843, 1a-g. *A. (R.) inconsueta (HAVLÍČEK), Zlíchov Formation; a, holotype, ventral view, Havlíček collection, VH13268b, ×1 (Havlíček, 1956); b-c,



FIG. 1842. Athyrididae (p. 2758).

dorsal and ventral views, VH13268a, $\times 1$; *d–e*, ventral and anterior views, Havlíček collection, VH13190a, $\times 1.4$; *f*, dorsal interior, Havlíček collection, VH13274c, $\times 2.7$; *g*, drawing of ventral valve interior, Havlíček collection, VH13270a (Havlíček, 1998).

Subfamily SPIRIGERELLINAE Grunt, 1965

Gruntea SHI, SHEN, & ARCHBOLD, 1999, p. 347 [*Posicomta grunti SHI & SHEN, 1997, p. 46; M]. Small to medium, moderately subequally biconvex shells, subpentagonal or rounded subtriangular to subcircular, equidimensional to wider than long, commonly widest slightly anterior to midlength, with broadly spaced growth lamellae; ventral sulcus narrow, originating from beak as a prominent groove, slightly widening and deepening anteriorly; anterior commissure uniplicate; ventral beak strongly incurved, often closely appressed to dorsal umbo, foramen very small or absent, delthyrium completely filled by dorsal umbo without deltidial plates; dental plates thin, fused to thick shell walls or obscured by callus; cardinalia typically spirigerellin; spiralia and jugum unknown. [Gruntea is possibly synonymous with Posicomta GRUNT, but with a slightly more subtriangular 2760



FIG. 1843. Athyrididae (p. 2758-2760).

outline, dental plates being fused to thick shell walls, and having a deeper impressed ventral muscle field; internal structure of brachidia unknown.] *Upper Permian:* China (Xizang, southern Tibet), ?northwestern India.——FIG. 1843,2*a-i.* **G. grunti* (SHI & SHEN), ?Kazanian, Tatarian, Selong Group, Selong Xishan section, southen Tibet, China; *a-c*, holotype, dorsal, ventral, and anterior views, NMV P145689, ×2.8 (Shi & Shen, 1997); *d-i*, transverse serial sections 0.8, 1.2, 2.5, 3.0, 4.0, 7.0 mm from ventral umbo (adapted from Shi & Shen, 1997). Superfamily MERISTELLOIDEA Waagen, 1883 Family MERISTIDAE Hall & Clarke, 1895 Subfamily MERISTINAE Hall & Clarke, 1895

Cammerista HAVLIČEK in HAVLIČEK & VANĚK, 1998, p. 85 [**Terebratula calypso* BARRANDE, 1847, pl. 16,10; OD]. Small to medium size; elongate oval

Athyridida



FIG. 1844. Meristidae (p. 2760-2761).

in outline, longer than wide; subequally biconvex; smooth but for few growth lines and low, rounded costellae, present only on anterior half; rectimarginate to slightly uniplicate anterior commissure; ventral beak moderately incurved, pierced by minute foramen; small, conjunct deltidial plates reportedly present; dental plates high, long, converging ventrally, reinforced by mystrochial plates; thin, gently convex shoelifter developing between dental plates, starting anterior of plates; septalium supported by high and thin median septum; spiralium and jugum unknown. [Cammerista is similar to Dicamara but with mystrochial plates and lacking dorsal shoelifter. It differs from Dicamaropsis in its ventral shoelifter being relatively narrow, placed between ventrally converging dental plates, deeper septalium without middle knob, and lack of dorsal shoelifter. In Dicamaropsis the shoelifter supports ventrally parallel dental plates. Lack of information on the brachiojugal system makes impossible its comparison with those developed by other meristelloid genera.] Silurian (?Llandovery, ?Ludlow), Lower Devonian (Pragian): ?North America (Oklahoma), Ludlow; ?Russia (Gorny Altai), Llandovery; Europe (Bohemia), Pragian.--FIG. 1844a-k. *C. calypso (BARRANDE), Pragian, Koněprusy Limestone, Koněprusy, Prague Basin, Bohemia; a-c, holotype, dorsal, ventral, and anterior views, L 23898, ×3.4; d-e, ventral, and lateral views, Havlíček collection, VH 10798a, ×2.2 (Havlíček & Vaněk, 1998; photographs courtesy of the late V. Havlíček); f-k, transverse serial sections 12.8, 12.4, 12.0, 11.9, 11.4, 10.3 mm from anterior margin of shell (adapted from Havlíček & Vaněk, 1998).

Subfamily UNCERTAIN

2761

Muhuathyris SUN & others, 2004, p. 240 [*M. circularis; M]. Medium-sized meristids with subcircular to subpentagonal outline; dorsal fold and ventral sulcus commonly weak; well-developed dental plates, laterally buttressed by mystrochial plates, converging to form a spondylium sitting on long, low median septum; septalium rhombic, relatively broad, supported by low median septum and by a pair of plates laterally; spiralium and jugum unknown. [Articulated shells were not found; the diagnosis is presently based on isolated valves, 13 dorsal and 11 ventral, found in the same beds. Assigned by its authors to the Rowleyellinae, these medium-sized meristid shells resemble Camarophorella HALL & CLARKE externally and in their ventral interior, but clearly differ in the dorsal interior; in Muhuathyris the septalium is typically meristelloid but a pair of plates support laterally the septalium; Muhuathyris also lacks the dorsal shoe-lifter characteristic of Meristidae subfamilies and the long cruralium characteristic of Rowleyellinae, so its subfamily affinity is uncertain.] Lower Carboniferous (Tournaisian): southwestern China (Guizhou).-FIG. 1845a-s. *M. circularis, Muhua III section, Changshun County; a-d, holotype, dorsal, ventral, lateral, and posterior views of dorsal valve, PKUM02 0012, ×1.3; e, cardinalia viewed anteroventrally, PKUM02 0012, ×7.7; f, cardinalia viewed anteriorly, PKUM02 0014, ×8; g, paratype, dorsal interior viewed anterolaterally, PKUM02 0015, ×10.2; *h–j*, paratype, external, internal, and posterior views of ventral valve, PKUM02 0004, ×1.5; k, paratype, anterior



FIG. 1845. Meristidae (p. 2761-2762).

view of ventral valve, PKUM02 0005, ×1.8; *l-s*, transverse serial sections of broken dorsal valve, 0.16, 0.25, 0.34, 0.50, 0.65, 0.82, 0.91, 1.00 mm from dorsal umbo (Sun & others, 2004; photographs courtesy of Yualin Sun).

Family UNCERTAIN

Bimeristina GARCIA-ALCALDE, 2003, p. 107 [*B. binnekampi; M]. Small to medium, elongate to equidimensional, rounded-subpentagonal, moderately biconvex, faint sulcus on both valves, anterior commissure rectimarginate or almost rectimarginate; dorsal septum long; jugal arch projecting as long stem, moderately inclined posteriorly, bifurcating into accessory jugal lamellae that reunite with stem; a second pair of accessory jugal lamellae

joining laterally the jugal arch with second whorl of each spiralial cone. [This genus resembles externally the subfamily Whitfieldellinae; septalium and dental plates are as in Triathyridinae; the jugum is similar to that of Meristella HALL except that in Bimeristina, the jugum projects also laterally into two apophyses that connect the jugal arch with secondary lamellae of spiralium; this unusual jugal system was reconstructed from serial sections made parallel to commissural plane from one specimen; sections of more specimens, especially those perpendicular to the plane of symmetry, are important to confirm the morphology of this complex jugum. At present, although all other features are typically meristellide, the development of laterally directed apophyses on the jugal arch makes the family assignment uncertain.] Lower Devonian (Pragian): Spain (Palencia, Aragón, Guadalajara), ?Czech Republic.——FIG. 1846, *Ia–p. *B. binnekampi*, Lebanza Formation, Lebanza, Palencia, northern Spain; *a–d*, holotype, dorsal, ventral, lateral, and anterior views, DPO 30895, ×1; *e–i*, transverse serial sections 2.0, 2.5, 2.95, 3.5, 4.7 mm from ventral umbo, DPO 38570; *j–o*, tangential serial sections, parallel to commissural plane, 3.2, 3.7, 4.65, 5.1, 5.55, 5.7 mm to ventral valve, DPO 38572; *p*, ventral view of reconstructed jugum, ×3 (adapted from García-Alcalde, 2003).

- Fayettella WATKINS, 1999, p. 16 [*F. peninsulensis; M]. Small, thin, smooth, with few growth lines, subtrigonal to elongate oval in outline, greatest width anterior to midvalve, dorsi- to almost equibiconvex; rectimarginate; ventral beak prominent, narrow, slightly to moderately curved, delthyrium high, open, anteriorly obscured by strongly incurved dorsal beak, foramen small, permesothyrid; long, cyrtomatodont hinge teeth supported by short dental plates; dorsal interior without septum and septalium but with spoon-shaped cardinal plate supported by two crural plates connected to valve floor; median ridge or myophragm dividing long, elongate, but poorly impressed muscle scars; spiralium and jugum unknown. [When erected, this genus was included in the superfamily Meristelloidea, but no family assignment was attempted. Externally, this genus resembles young Whitfieldella, but its unusual cardinalia makes the assignment uncertain. Lack of information on the brachiojugal system makes impossible its comparison with those of other meristelloid genera.] lower Silurian (Aeronian): USA (Burnt Bluff Group, Great Lakes Region, Wisconsin, Michigan).----FIG. 1847a-i. *F. peninsulensis, Hendricks Formation, Fayette, Michigan; a-e, holotype, dorsal, ventral, lateral, anterior, and posterior views, MPM28522, ×12.6, ×13, ×6.25, ×11.7, ×6.5; f, ventral interior, MPM28525, ×4.5; g-h, dorsal interior viewed ventrally and anteroventrally, MPM28523, ×5; i, drawing of dorsal interior viewed anteroventrally (Watkins, 1999; drawing and photographs courtesy of R. Watkins & P. Mayer).
- Iuxtathyris Havlíček in Havlíček & Vaněk, 1998, p. 90 [* Terebratula vultur BARRANDE, 1847, p. 385, pl. 14,4; M]. Small to medium, equibiconvex, smooth shells with subquadrate to transversely elliptical outline, maximum width at midvalve; ventral beak short, incurved, closely appressed on dorsal umbo; weak dorsal fold and ventral sulcus starting near umbo, less commonly developed only anteriorly; anterior commissure weakly uniplicate; tongue low, wide, trapezoidal; dental plates short, medially concave; dorsal valve with short, shallow septalium supported by high, long, bladelike septum; spiralia with up to 5 laterally directed whorls and reportedly with angular jugal saddle, with a sharp crest anteroventrally, without jugal stem. [This rare genus has an unusual combination of dorsal internal characters including dorsal septalium, typically meristelloid; and jugum with jugal saddle, typically athyridoid. Jugal system

known from few serial sections taken in only one specimen; jugal morphology requires further investigation. Presence of supported septalium suggests affinity with Meristelloidea.] *Lower Devonian* (*Pragian*): Europe (Bohemia).——FIG. 1848*a-l.* **I. vultur* (BARRANDE), Koněprusy Limestone, Koněprusy, Prague Basin; *a-c*, dorsal, ventral, and anterior views, Havlíček collection, VH 12777a, ×2.3; *d-l*, transverse serial sections 13.9, 13.0, 12.0, 11.1, 10.6, 10.4, 10.1, 9.8, 9.7 mm from anterior margin of shell (adapted from Havlíček & Vaněk, 1998; photographs courtesy of the late V. Havlíček).

- Kellerella NIKITIN & POPOV in NIKITIN, POPOV, & HOLMER, 1996, p. 93 [*K. ditissima; M]. Smooth, ventribiconvex, elongate subtriangular to subpentagonal outline; anterior commissure more or less parasulcate; sulcus very shallow, occasionally with low median plication, fold very low, both originating in anterior third of shell, often near anterior margin, bounded laterally by two plications; ventral valve often subcarinate posteriorly; small, strongly curved beak, delthyrium narrow, deltidial plates absent; interior with small, delicate teeth supported by small dental plates, close to posterolateral valve margins; cardinalia small, without inner hinge plates, median septum or myophragm absent; spiralia with up to 4 laterally directed whorls and very short, discrete, posteroventrally directed jugal processes. [This genus is differentiated from Ordovician smooth Lissatrypidae in having the spiralial whorls laterally directed and short, disjunct jugal processes posteroventrally directed. It resembles Nikolaispira, from which it mainly differs in the type of cardinalia. For overall affinity, see comments in square brackets in Nikolaispira.] Upper Ordovician (lower Caradoc-lower Ashgill): southeastern Kazakhstan (Chu Ili Range), lower Caradoc-middle Caradoc; central Kazakhstan (Dulankara Regional Stage, northern Betpak-Dala Desert), upper Caradoc-lower Ashgill.-FIG. 1849a-q. *K. ditissima; a-e, holotype, dorsal, ventral, lateral, anterior, and posterior views, CNIGR 39/12888, ×3 (Nikitin, Popov, & Holmer, 1996; photographs courtesy of L. E. Popov); f-o, transverse serial sections 0.7, 1.2, 1.6, 2.6, 3.0, 3.2, 3.5, 3.9, 4.3, 6.0 mm from ventral umbo, distance approximate from ventral umbo to first section, and between sections (Nikitin, Popov, & Holmer, 1996); p-q, ventral and lateral views showing reconstructed spiralium and jugal processes (Popov, Nikitin, & Sokiran, 1999).--Fig. 1849r-dd. K. misiusi POPOV, NIKITIN, & SOKIRAN, Anderken Formation, lower Caradoc-middle Caradoc, eastern Kazakhstan; r-bb, transverse serial sections 0.1, 0.9, 1.2, 1.3, 1.8, 2.8, 3.8, 4.8, 5.8, 7.5, 8.8 mm from ventral umbo; cc-dd, ventral and lateral views showing reconstructed spiralium, short jugal processes, and approximate position of serial sections (adapted from Popov, Nikitin, & Sokiran, 1999).
- Nikolaispira NIKITIN & POPOV in NIKITIN, POPOV, & HOLMER, 1996, p. 95 [*N. rasilis; M]. Smooth,

2763



FIG. 1846. Uncertain (p. 2762-2768).



FIG. 1847. Uncertain (p. 2763).

ventribiconvex, elongate subpentagonal; parasulcate; shallow ventral sulcus and low dorsal fold originating anterior to midvalve, bounded laterally by two plications; small, incurved beak, delthyrium open; interior with small teeth supported by short, thin, laterally placed dental plates; deep, narrow septalium, also reported as cruralium, supported by low, thin median septum reportedly present; spiralia with up to 4 laterally directed whorls and small, discrete, posteroventrally directed jugal processes. [This genus is similar to such coeval smooth atrypids as Cyclospira or Rozmanospira, from which it differs in having more than one laterally directed spiral whorl. It has a less corrugated adult commissure than Manespira. It resembles the Silurian Dayia, from which it differs in having small, discrete jugal processes instead of the simple and medially to anteriorly located, jugum of Dayia.

Nikolaispira is possibly synonymous with Kellerella, but with different cardinalia. When erected, Nikolaispira and Kellerella were included in the Athyridoidea, Meristellidae, and considered as the earliest athyridides. The cardinalia of these two genera are distinctly different from those developed by early Athyridida as Hindella (=Cryptothyrella) or Whitfieldella. Only some Upper Ordovician (?Caradoc, Ashgill), strongly convex and rostrate Hyattidinidae developed a cardinalia with thin, flat, triangular, inner hinge plates separated by a narrow fissure, which could resemble the small cardinalia, without inner hinge plates, of Kellerella. Weibeia and Apheathyris, both from the lower Caradoc of northern China, are too poorly known to allow comparison. Nikolaispira and Kellerella have small, discrete, jugal processes (as Manespira and derived Atrypida) but lack the complete jugum



FIG. 1848. Uncertain (p. 2763).

of most primitive Atrypida and all Athyrididina and Retziidina. In both genera, the spiral whorls are, as in most primitive Atrypida and homeomorphic Dayioidea, placed ventrally, with the jugal processes dorsally or posterodorsally located. In the Athyridida, however, the spiral whorls tend to occupy the complete volume available in the shell interior, and the jugum is typically placed between the spiral cones, not below them (near the dorsal interior). This genus is assigned to Athyridida because it has more than one spiral whorl that is laterally directed, but its overall affinity is uncertain. To better evaluate affinities between closely related early spire bearers and envisage phyletic lineages, new discoveries of internally well-preserved Ordovician brachiopods are needed. Nikolaespira is an incorrect subsequent spelling of Nikolaispira.] Upper Ordovician (lower Caradoc-lower Ashgill): southeastern Kazakhstan (Chu Ili Range), lower Caradocmiddle Caradoc; central Kazakhstan (Dulankara Regional Stage, northern Betpak-Dala Desert), upper Caradoc-lower Ashgill.——FIG. 1846,2a-x. *N. rasilis; a-e, holotype, dorsal, ventral, lateral, anterior, and posterior views, CNIGR 44/12888, ×3; f-j, paratype, dorsal, ventral, lateral, anterior, and posterior views, CNIGR 45/12888, ×3 (Nikitin, Popov, & Holmer, 1996; photographs courtesy of L. E. Popov); k-v, transverse serial



FIG. 1849. Uncertain (p. 2763).

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FIG. 1850. Retziellidae (p. 2768-2769).

sections; *w*, lateral view of sectioned specimen showing approximate position of serial sections (adapted from Nikitin, Popov, & Holmer, 1996); *x*, ventral view showing reconstructed spiralium and jugal processes (adapted from Popov, Nikitin, & Sokiran, 1999).

Superfamily RETZIELLOIDEA Rzhonsnitskaya, 1974 Family RETZIELLIDAE Rzhonsnitskaya, 1974

Ikella TYAZHEVA, 1972, p. 205; emend., RONG & others, 2004, p. 849 [**I. numerosa*; OD]. Small, subequally to ventribiconvex shells of rounded subpentagonal to elongate subelliptical outline; costae rounded, faint, bifurcating or not, in corresponding position on each valve, growth lines faint, not lamellose; dorsal fold and ventral sulcus poorly developed anteriorly, commonly absent; delthyrium may be restricted laterally by narrow deltidial plates; dental plates and pedicle support absent; cardinal plate wide, flat, not perforated apically and

supported posteriorly by very short ridge; dental sockets deep, bordered by ventrolaterally directed prominent inner socket ridges, overhanging socket; spiralia with 7-12 whorls, apices laterally directed, jugum unknown. [The cardinalia of Ikella, as described by MODZALEVSKAYA in RONG & others, 2004, clearly differ from the hinge plates present in the athyrisinids and homeathyridins. It resembles the cardinalia of some retzielloids, although typically retzielloids have variably developed outer hinge plates, and the inner hinge plates are absent or form a short, shallow septalium partially covered by long, platelike crural bases, supported by a moderately high median septum (e.g., Retziella, Metathyrisina). The highly crystalline nature of the matrix has made examination of the internal structure very difficult, so the spiralium remains poorly known and the jugal structures are unknown; therefore, the superfamilial and familial assignments of this genus should be regarded as provisional.] Lower Devonian (upper Emsian)–Middle Devonian (lower Eifelian): Russia (Bashkorkostan, western slope of Southern Urals).--FIG. 1850*a-o.* *I. numerosa, below mouth of Karagailka River, Malyi



FIG. 1851. Neoretziidae (p. 2769-2771).

Ik River, western slope of Southern Urals; *a–d*, dorsal, ventral, lateral, and anterior views, Zhavoronkova collection, CNIGR N6/13099, ×1.4; *e–o*, transverse serial sections 9.0, 7.5, 7.2, 7.0, 6.8, 6.7, 6.6, 6.5, 6.3, 6.2, 5.7 mm from anterior margin of shell, Zhavoronkova collection, CNIGR N8/13099 (Rong & others, 2004).

Suborder RETZIIDINA Boucot, Johnson, & Staton, 1964 Superfamily RETZIOIDEA Waagen, 1883 Family NEORETZIIDAE Dagys, 1972 Subfamily HUSTEDIINAE Grunt, 1986

Coveenia Alvarez & Brunton, 2000, p. 821 [**Retzia ulothrix* DE KONINCK, 1843 in 1841–1844, p. 292; OD]. Medium-sized shells with subcircular to trans-

versely oval outline and biconvex to dorsibiconvex profile, 7 to 11 strong costae on ventral valves and a median dorsal costa, forming a highly zigzag anterior commissure; fine pustulose to spinose microornament, frequently present; internally dorsal median septum and pedicle collar weak to absent; cardinalia lacking ligulate process, jugum without spines, jugal stem poorly developed or absent. Lower Carboniferous (Tournaisian-Viséan): western Europe (including British Isles).----FIG. 1851a-e. *C. ulothrix (DE KONINCK), Ivorian, Tournaisian, Tournai, Belgium; a-d, neotype, dorsal, ventral, lateral, and anterior views, de Koninck collection, IRScNB a5507, ×3; e, ventral view showing rounded costae and typical microornament, de Koninck collection, IG4789(1), ×5 (Alvarez & Brunton, 2000).---FIG. 1852a-i. *C. ulothrix (DE KONINCK), Ivorian, Tournaisian, Tournai, Belgium; transverse serial sections 1.4, 3.1, 3.7, 3.9, 5.1, 6.4, 6.7, 6.8, 7.7 mm from ventral



FIG. 1852. Neoretziidae (p. 2769–2771).

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FIG. 1853. Neoretziidae (p. 2769-2771).

umbo, BMNH B20147 (Alvarez & Brunton, 2000).——FIG. 1852*j*–*z*. *C. tilsleia* ALVAREZ & BRUNTON; *j*–*x*, transverse serial sections 0.2, 0.7, 0.8, 2.2, 2.5, 2.9, 3.4, 3.5, 3.8, 4.3, 4.7, 5.2, 6.2, 6.4, 6.9 mm from ventral umbo, Asbian, Viséan, Treak Cliff, Derbyshire, England, BD 10479; *y*–*z*, ventral and lateral reconstruction of jugum (Alvarez & Brunton, 2000).——FIG. 1853*a*–*g. C. tilsleia* ALVAREZ & BRUNTON; *a*–*c*, holotype, dorsal, lateral, and anterior views, Asbian, Viséan, Treak Cliff, Derbyshire, England, Tilsley collection, BD9701, $\times 2.2$; *d*, detail of external microornamentation, Asbian, Viséan, Alstonfield, Staffordshire, England, Davidson collection, B5388, $\times 10$; *e*, interior of dorsal valve, Asbian, Viséan, Carrich Lough, County Fermanagh, Ireland, BB63417, $\times 5$; *f-g*, cardinalia on posteroventral and anteroventral views, Asbian, Viséan, Carrich Lough, County Fermanagh, Ireland, BB63417, $\times 43.5$, $\times 37.6$ (Alvarez & Brunton, 2000).

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SPIRIFERIDA AND SPIRIFERINIDA

Réмy Gourvennec and John L. Carter

[Université de Bretagne Occidentale; retired from Carnegie Museum of Natural History]

Order SPIRIFERIDA Waagen, 1883 Suborder SPIRIFERIDINA Waagen, 1883 Superfamily ADOLFIOIDEA Sartenaer, 1966 Family ADOLFIIDAE Sartenaer, 1966 Subfamily ADOLFIINAE Sartenaer, 1966

- Brevispinifera GARCÍA-ALCALDE, 2005, p. 81 [*Spirifer Cabanillas DE VERNEUIL & D'ARCHIAC, 1845, p. 475; OD]. Capillate with pustulose spine bases normal to surface; long dental plates and occasional delthyrial plate; short crural plates and ctenophoridium present; otherwise similar to Brevispirifer. Lower Devonian (upper Emsian): northern Spain.—FIG. 1854,3a-e. *B. cabanillas (DE VERNEUIL & D'ARCHIAC); a-d, ventral, dorsal, lateral, and anterior views, ×1; e, enlarged view of ventral valve showing spinose ornament, ×5 (García-Alcalde, 2005). [Rémy Gourvennec]
- Ferronia GARCÍA-ALCALDE, 2005, p. 75 [*Spirifer subspeciosus DE VERNEUIL, 1850, p. 179; OD]. Small, transverse; curved apsacline ventral interarea with open delthyrium; fold and sulcus smooth, somewhat flattened anteriorly; flanks plicate; surface capillate with marginal spines; long dental plates; delthyrial plate lacking; short crural plates; ctenophoridium present on secondary shell elevation. Lower Devonian (upper Emsian): northern Spain ——FiG. 1854,2a-d. *F. subspeciosa (DE VERNEUIL); a-c, holotype, ventral, dorsal, and lateral views, ×1 (Comte, 1938); d, dorsal interior, ×1 (García-Alcalde, 2005). [Rémy Gourvennec]
- Paillettia GARCÍA-ALCALDE, 2005, p. 83 [*Spirifer Paillettii DE VERNEUIL, 1850, p. 177; OD]. Small, transverse, with acute cardinal angles; ventral interarea high, slightly curved with open delthyrium; fold and strong median sulcus rib developing a typical long anterior protrusion of shell; flanks costate; surface capillate with marginal spines; dental plates thin and short; short crural plates and ctenophoridium present on a thick secondary shell platform. [The species name (a dedication to A. Paillette) was incorrectly spelled paillettii by DE VERNEUIL in place of *paillettei*. The latter, correct spelling was used by subsequent authors and is accepted here.] Lower Devonian (upper Emsian)-Middle Devonian (lower Eifelian): northern Spain, Algeria. FIG. 1854, 5a-e. *P. paillettei (DE VERNEUIL), upper Emsian, northern Spain; ventral,

dorsal, lateral, anterior, and posterior views, ×2 (García-Alcalde, 2005).——FIG. 1854,*5f. P.* sp. cf. *cancellata* GARCÍA-ALCALDE, upper Emsian, northern Spain; enlargement of ventral valve showing ornament, ×5 (García-Alcalde, 2005). [Rémy Gourvennec]

Subfamily PINGUISPIRIFERINAE Havlíček, 1971

Microttia GARCÍA-ALCALDE, 2005, p. 90 [**M. collensis;* OD]. Small, slightly transverse; ventral interarea apsacline to catacline, with narrow deltidium; fold and sulcus smooth, narrow, somewhat flattened; flanks with few strong costae; surface with capillae and microfila; long dental plates; crural plates lacking. *Lower Devonian (upper Emsian):* northern Spain.——FIG. 1854, *Ia–e.* **M. collensis;* holotype, ventral, dorsal, lateral, anterior, and posterior views, ×3 (García-Alcalde, 2005). [Rémy Gourvennec]

Superfamily CYRTOSPIRIFEROIDEA Termier & Termier, 1949 Family CYRTOSPIRIFERIDAE Termier & Termier, 1949 Subfamily CYRTOSPIRIFERINAE Termier & Termier, 1949

- Nikospirifer GRETCHISHNIKOVA, 1996, p. 34 [*N. praebisinus; OD]. Medium size; transverse with acute cardinal extremities; ventral interarea high, curved, apsacline to catacline; fold and sulcus well delimited, costate; flanks with numerous simple costae; surface with tubercles; dental plates thin, long, subparallel; delthyrial plate present; dorsal interior unknown. *Middle Devonian (Givetian):* Transcaucasus.—FIG. 1855, *Ia*–g. *N. praebisnus; *a*–e, holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1; f, microornament, ×4; g, transverse section, ×2 (Gretchishnikova, 1996). [Rémy Gourvennec]
- Pripyatispirifer PUSHKIN, 1996, p. 43 [*Cyrtospirifer belorussicus LIASHENKO, 1959, p. 207; OD]. Small to medium size; cardinal angles acute to slightly mucronate; ventral interarea low, curved, apsacline; delthyrium narrow, almost entirely covered by deltidium (or possibly stegidium) with central foramen; fold and sulcus well defined, costate; surface with fila and capillae; dental plates short; subparallel, thick crural bases without crural plates; multilobed cardinal process possibly lacking cteno-

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FIG. 1854. Adolfiidae and Ambocoeliidae (p. 2772-2776).

phoridium. Upper Devonian (lower Famennian): Belarus.——FIG. 1855,2*a*–*g*. **P. belorussicus* (LIASH-ENKO), Pripyat, Lyakhovichi 54 borehole; *a*–*e*, dorsal, ventral, anterior, posterior, and lateral views, $\times 1.5$; *f*–*g*, dorsal and ventral interiors, $\times 5$ (Pushkin, 1996). [Rémy Gourvennec]

Subfamily CYRTIOPSINAE Ivanova, 1972

Pseudocyrtiopsis Ma & Day, 1999, p. 618 [**Cyrtiopsis spiriferoides* GRABAU, 1931b, p. 486; OD]. Small to medium size; cardinal angles generally



FIG. 1855. Cyrtospiriferidae (p. 2772-2773).

mucronate; high, slightly curved, apsacline ventral interarea; delthyrium covered by pseudodeltidium apically pierced by foramen; fold and sulcus well delimited, costate; flanks costate; microornament capillate, becoming pustulate on adult stage; dental plates and delthyrial plate present; bilobed ctenophoridium located on cardinal platform. *Upper Devonian (lower Famennian):* southern and northwestern China, ?Belgium.——FIG. 1856, *Ia–g. *P. spiriferoides* (GRABAU), central Hunan, southern China; *a–e*, dorsal, ventral, anterior, posterior, and lateral views, ×1.5; *f*, transverse section of ventral valve, ×2.5 (Ma & Day, 1999). [Rémy Gourvennec]

Tiocyrspis SARTENAER, 1994b, p. 32 [*Spirifer (Cyrtiopsis) klähni PAECKELMANN, 1942, p. 163; OD]. Medium size; generally ventribiconvex with obtuse and blunt cardinal extremities; ventral interarea apsacline; delthyrium entirely covered by pseudodeltidium (stegidium); fold and sulcus costate, well delimited; median costae generally narrower and divided; flanks with numerous, flat-rounded, simple plications; surface with radial or subradial capillae and spines; dental plates thick, long, intrasinal; no delthyrial plate; crural bases and ctenophoridium present. *Upper Devonian (upper Frasnian):* Germany, Belgium.——FiG. 1856,2*a-g.* **T. klaehni* (PAECKELMANN), Germany; *a-e*, dorsal, ventral, anterior, posterior, and lateral views, ×1; *f*. microornament, ×7; *g*, transverse section, ×1.5 (Sartenaer, 1994b). [Rémy Gourvennec]

Family CONISPIRIFERIDAE Ma & Day, 2000

[Conispiriferidae Ma & Day, 2000, p. 456] [type genus, *Conispirifer* LIASHENKO, 1985, p. 16]

Entire shell plicate; fold and sulcus weak to obsolescent; delthyrial plate very short. Upper Devonian (middle Frasnian–upper Frasnian). [Rémy Gourvennec]

Conispirifer LIASHENKO, 1985, p. 16 [**C. rotundus;* OD]. Subrectangular cardinal extremities; fold and sulcus weak, obsolescent, variably developed anteriorly; delthyrial plate short; budlike ctenophoridium; otherwise similar to *Pyramidaspirifer*.



FIG. 1856. Cyrtospiriferidae (p. 2773-2774).

Upper Devonian (middle Frasnian–upper Frasnian): central and western North America, Germany, central Russian Platform.——FIG. 1857, *1a–e.* **C. rotundus*, Timan; *a–e*, holotype, dorsal, ventral, anterior, posterior, and lateral views, approximately ×1 (Liashenko, 1985). [Rémy Gourvennec]

Pyramidaspirifer MA & DAY, 2000, p. 459 [*Platyrachella alta FENTON & FENTON, 1924, p. 165; OD]. Small to medium size with wide hinge line and extended cardinal extremities; ventral interarea high, flat, catacline to slightly procline; narrow delthyrium with small apical pseudodeltidium; fold and sulcus costate, poorly defined, originating close to apex; flanks plicate; surface with fila and pustulose capillae; short, widely spaced dental plates and delthyrial plate present; ctenophoridium on septalium-like cardinal platform. Upper Devonian (upper Frasnian): North America.——FIG. 1857, *2a–f.* **P. alta* (FENTON & FENTON), Iowa, USA; *a–e*, holotype, dorsal, ventral, anterior, posterior, and lateral views, ×2; *f*, transverse section of dorsal valve, ×4 (Ma & Day, 2000). [Rémy Gourvennec]

Superfamily AMBOCOELIOIDEA George, 1931 Family AMBOCOELIIDAE George, 1931 Subfamily AMBOCOELIINAE George, 1931

Ogilviecoelia SHI & WATERHOUSE, 1996, p. 119 [*O. inflata; OD]. Very small, subrounded, length and



FIG. 1857. Conispiriferidae (p. 2774-2775).

width subequal; ventribiconvex but dorsal valve anteriorly flattened or slightly concave; sulcus narrow, deep; microornament of few short elongate grooves, spines absent; ventral muscle field large, elongate-oval, well differentiated; crural plates sessile. *Permian (upper Sakmarian):* Canada (Yukon Territory).——FIG. 1854,4*a*–*c.* **O. inflata;* holotype, ventral, dorsal, and lateral views, ×2 (Shi & Waterhouse, 1996).

Superfamily MARTINIOIDEA Waagen, 1883 Family ELYTHYNIDAE Gourvennec in Carter & others, 1994

Planispirifer BREIVEL & BREIVEL, 1999, p. 91 [*P. apertus; OD]. Large, slightly transverse; cardinal extremities angular to rounded; ventral interarea moderately high, curved, apsacline, with open delthyrium; fold and sulcus well delimited, wide anteriorly, smooth or with incipient ridge in sulcus anteriorly; surface with densely crowded elongate tubercles radially distributed in quincunx; dental plates present; well-developed crural bases not meeting valve floor; ctenophoridium present. [This genus was originally assigned to the Eospiriferinae, but its ornament is not compatible with such an assignment, the Elythynidae being a better placement.] Lower Devonian (Pragian): northeastern Urals.——FIG. 1858,5a-f. *P. apertus; a-d, holotype, dorsal, ventral, anterior, and lateral views, $\times 0.7$; e, ornament, $\times 3$; f, apical section of dorsal valve, ×3 (Breivel & Breivel, 1999). [Rémy Gourvennec]

Family MARTINIIDAE Waagen, 1883 Subfamily MARTINIINAE Waagen, 1883

- Chapursania ANGIOLINI, 1995, p. 210 [**C. tatianae;* OD]. With coarse sinuous vascular impressions connected by transverse channels; otherwise similar to *Tiramnia* GRUNT, 1977. *Permian (Guadalupian):* northern Pakistan.—FIG. 1858,4*a*-*b*. **C. tatianae; a,* holotype, mold of ventral interior, ×1; *b*, diagram of ventral vascular system, ×1.5 (Angiolini, 1995). [John Carter]
- Ladoplica XU & GRANT, 1996, p. 310 [*L. zigzagiformis; OD]. Medium size, moderately to strongly inflated, subequally biconvex; outline subpentagonal; beak strongly incurved; small interareas on both valves; sulcus shallow, flattened, producing large tongue anteriorly in type species. Permian (Changhsingian): China.—FIG. 1858, Ia-d. *L. zigzagiformis; holotype, dorsal, ventral, lateral, and anterior views, ×1 (Xu & Grant, 1996). [John Carter]

Subfamily ELIVELLINAE Carter, 1994

Chuiella CHEN & SHI, 1999, p. 266 [*Martiniella chinglungensis CHU, 1933, p. 48; OD]. Medium size, ventribiconvex, outline subovate to transversely subquadrate; ventral interarea well developed, delthyrium wide and open; sulcus variably developed; microornament of capillae and growth lines; interior with dental adminicula and short crural plates. [This genus is proposed as a replacement name for all the previously described species ascribed to the genus Martiniella GRABAU & TIEN, 1931. The authors restrict Martiniella to

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FIG. 1858. Elythynidae, Martiniidae, and Ingelarellidae (p. 2776–2779).


FIG. 1859. Ingelarellidae (p. 2778-2779).

its type species, *M. nasuta* GRABAU & TIEN, 1931, a nomen nudum.] Lower Carboniferous (Tournaisian): China.——FIG. 1858,2*a*-*c*. **C. chinglungensis* (CHU); syntype, ventral, posterior, and lateral views of ventral valve, ×1 (Chu, 1933). [John Carter]

Family INGELARELLIDAE Campbell, 1959 Subfamily INGELARELLINAE Campbell, 1959

Geothomasia WATERHOUSE, 1998, p. 23 [* Tomiopsis teicherti ARCHBOLD & THOMAS, 1986b, p. 593; OD]. Medium size, outline transversely subovate; fold and sulcus well developed; flanks with low plicae; shell substance thin; ventral adminicula thin, often subparallel, extending forward to near midlength; dorsal adminicula short to moderate in length, often widely diverging. [This taxon was originally proposed as a subgenus of *Tomiopsis* BENEDIK-TOVA, 1956.] *Permian (Cisuralian–Guadalupian):* Australia.——FIG. 1859,2*a–c.* **G. teicherti* (ARCH-BOLD & THOMAS), Artinskian; holotype, ventral, dorsal, and anterior views, ×1 (Archbold & Thomas, 1986b). [John Carter]

Johndearia WATERHOUSE, 1998, p. 18 [*Ingelarella isbelli CAMPBELL, 1961, p. 181; OD]. Large, with thickened valves; flanks smooth or weakly plicate; fold and sulcus weak; ventral and dorsal adminicula short, often buried in callus; ventral median ridge anterior to muscle field; otherwise similar to Ingelarella. [This taxon was originally proposed as a subgenus of the genus Tomiopsis BENEDIK-TOVA, 1956.] Permian (Cisuralian–Lopingian): Australia, New Zealand.—FIG. 1859,1*a–b. *J.* *isbelli* (CAMPBELL), Australia; holotype, ventral and dorsal internal molds, ×1 (Campbell, 1961). [John Carter]

Tigillumia WATERHOUSE, 1998, p. 26 [*Martiniopsis biparallela WATERHOUSE, 1987, p. 25; OD]. Flanks lacking plicae, sulcus absent or weak, fold generally lacking; ventral adminicula long, closely set, enclosing narrow muscle field bounded laterally by ridges that coalesce anteriorly; dorsal adminicula of moderate length; otherwise similar to Martiniopsis. Permian (Cisuralian–Guadalupian): Australia, New Zealand.——FIG. 1858,3a–b. *T. biparallela (WATERHOUSE), Artinskian, Australia; a, holotype, ventral internal mold, ×1; b, ventral internal mold, ×2 (Waterhouse, 1987). [John Carter]

Subfamily GLENDONIINAE

Clarke, 1992

- Mesopunctia WATERHOUSE, 1998, p. 41 [*Notospirifer macropustulosus WATERHOUSE, 1968, p. 76; OD]. Small, slightly transverse; fold and sulcus smooth, rounded; flanks with few rounded plicae; microornament of fine elongate grooves with small thick pustules posteriorly and short mesopunctae anteriorly. Permian (Cisuralian-Guadalupian): New Zealand, Australia.——FIG. 1860,3a-b. *M. macropustulosus (WATERHOUSE), Cisuralian, New Zealand; a, holotype, mold of ventral interior, ×3; b, mold of dorsal interior, ×3 (Waterhouse, 1968). [John Carter]
- Monklandia WATERHOUSE, 1998, p. 37 [*M. gympiensis; OD]. Large, slightly transverse, strongly plicate; sulcus wide, shallow, with two weak plicae; fold low, flattened, with median groove; microornament of C-spines with fine anterior grooves; ventral adminicula long; dorsal adminicula short but long for family. Permian (Cisuralian): Australia.——FIG. 1860,4a-b. *M. gympiensis; a, holotype, mold of dorsal interior; b, internal mold of ventral valve, ×1 (McClung, 1978). [John Carter]
- Wairakispirifer WATERHOUSE, 1998, p. 40
 [*Notospirifer microstriatus WATERHOUSE, 1964, p. 170; OD]. Small, transverse, weakly inflated; sulcus well developed, smooth; fold low, wide; flanks with well-developed plicae; ventral adminicula well developed; dorsal adminicula lacking; microornament of quincuntially arranged fine grooves with punctae anteriorly penetrating secondary layer. Permian (Cisuralian): New Zealand, Australia.
 —FIG. 1860,2a-b. *W. microstriatus (WATERHOUSE), New Zealand, holotype; a, ventral valve mold, ×2; b, latex cast showing exterior ornament, ×4 (Waterhouse, 1964). [John Carter]

Subfamily NOTOSPIRIFERINAE Archbold & Thomas, 1986

Papulinella WATERHOUSE, 1998, p. 34 [*Notospirifer hillae CAMPBELL, 1961, p. 185; OD]. Medium to large, transversely subovate outline; fold and sulcus moderately well developed; sulcus smooth, fold rarely with median groove; flanks with few broad low plicae; microornament of quincuntially and densely arranged spinules with narrow anterior grooves passing into globose cavities within primary layer; otherwise similar to *Notospirifer. Carboniferous (?Kasimovian), Permian (Cisuralian):* Australia, New Zealand.——FIG. 1860, *1a–c. *P. billae* (CAMP-BELL), Cisuralian, Australia; *a–b*, holotype, ventral valve mold and latex cast, ×1; *c*, enlarged latex cast of dorsal valve exterior, ×2 (Campbell, 1961). [John Carter]

Superfamily SPIRIFEROIDEA King, 1846

Recently WATERHOUSE (2004) proposed a complete revision of the classification of the Spiriferoidea with the erection of several new subfamilies and genera while other suprageneric taxa were drastically redistributed. Mostly based on the external morphology of ribbing, of fold-sulcus, and, to a lesser extent, on aspects of the cardinal extremities, this classification leads to a mixture of morphologically different genera in inconsistent (sub)families that are not retained here. Taking into account both internal and external features, most of the subfamilies erected by WATERHOUSE (2004) should be assigned elsewhere. For example, there are strong affinities between Neospiriferinae, Gypospiriferinae, and Kaninospiriferinae, and there is no reason for placing them in different families. The family Choristitidae (sensu CARTER & others, 1994) is a consistent entity, and we do not consider it necessary to remove the Angiospiriferinae and Tangshanellinae and replace them with the Prospirinae and Purdonellinae; the resulting family Choristitidae (sensu WATERHOUSE, 2004) is much less homogeneous (e.g., including genera with or without delthyrial plate).

Focusing on the lack of ventral adminicula and the presence of dorsal adminicula in *Alphaneospirifer* GATINAUD, 1949, WATERHOUSE (2004) erected the family Alphaneospiriferidae that was assigned to *Incertae Sedis*. Nevertheless, the presence of well-developed crural plates is not incompatible with an assignment of the genus to the Tangshanellinae: although the occurrence of crural plates is rare in the Spiriferoidea,



FIG. 1860. Ingelarellidae (p. 2779).

some exceptions are known in different families, and the erection of a new family is not regarded here as necessary.

Concerning the 16 new genera erected by WATERHOUSE (2004), their descriptions and figures are not sufficiently developed to allow a clear opinion about their status. Further work beyond the scope of this contribution is needed to test the classification by WATERHOUSE (2004), and the new genera are tentatively assigned to existing families.

[The author (RG) is most grateful to Dr. Lucia Angiolini (Università degli Studi di Milano) for her helpful comments on Permian spiriferids.]

Family SPIRIFERIDAE King, 1846 Subfamily PROSPIRINAE Carter, 1974

- Atylephorus Sartenaer & Plodowski, 1996, p. 57 [*Spirifer tornacensis DE KONINCK, 1883, p. 373; OD]. Large, transverse, ventribiconvex, mucronate; ventral interarea apsacline, weakly concave, with subparallel borders; sulcus narrow, shallow, costate, poorly defined; fold narrow, low, costate, rising above flanks only near anterior margin, well delimited by fold bounding grooves; flanks with numerous, slightly flattened costae with narrow interspaces; costae near fold and sulcus freely bifurcating; ventral interior with stout divergent adminicula and short delthyrial plate buried in callus. Carboniferous (Tournaisian): Belgium. FIG. 1861, 2a-e. *A. tornacensis (DE KONINCK); neotype, dorsal, ventral, anterior, posterior, and lateral views, ×1 (Sartenaer & Plodowski, 1996). [John Carter]
- Donispirifer POLETAEV, 2000, p. 279 [*Spirifer (Neospirifer?) baschkovensis ROTAI, 1951, p. 34; OD]. Medium size, subsemicircular to subquadrate in outline; moderately subequally biconvex; maximum width at hinge line, ears slightly mucronate; fold and sulcus moderately narrow, well defined; sulcus rounded to subangular; fold low, sharply delimited by deep bounding interspaces; ventral interarea low, sharply defined, almost parallel sided, truncated laterally; flanks with moderately numerous, simple, bifurcating, or more rarely, trifurcating costae near fold-sulcus; ventral interior with short divergent dental adminicula. Carboniferous (Bashkirian-Moscovian): Ukraine, Urals, USA (?New Mexico).-FIG. 1861, 1a-d. *D. baschkovensis (ROTAI), Moscovian, Ukraine; holotype, ventral, dorsal, lateral, and posterior views, ×1 (Rotai, 1951). [John Carter]

Subfamily SERGOSPIRIFERINAE Carter in Carter & others, 1994

Eobrachythyris BRICE, 1971, p. 182; emend., BRICE, 1997, p. 72; BRICE in BRICE & NICOLLIN, 2000, p. 57 [*E. provvalis; OD]. Small to medium size; length and width nearly equal; outline subovate to rounded subquadrate; fold and sulcus weakly developed but well differentiated; lateral slopes with few simple costae or divided costae near sulcus-fold in younger forms; sulcus smooth or with median costa and 1 or 2 obsolete lateral costae; delthyrial plate lacking or rudimentary, buried in apical callosity. Upper Devonian (Famenian)–Lower Carboniferous (Tournaisian): Afghanistan, Iran, Morocco. [See CARTER, 2006, p. 1779, fig. 1173.] [Rémy Gourvennec]

Family CHORISTITIDAE Waterhouse, 1968 Subfamily ANGIOSPIRIFERINAE Legrand-Blain, 1985

Unicostatina WATERHOUSE, 2004, p. 184 [*Sulciplica subglobosa CLARKE, 1990, p. 64; OD]. Medium size, with obtuse to rounded cardinal angles; delthyrium open; sulcus with single median costa; dental plates present; otherwise similar to Sulciplica. [This genus, as other genera in the subfamily Angiospiriferinae, was assigned to the Trigonotretidae by WATERHOUSE (2004) but is maintained here in the Choristitidae.] Permian (Asselian): Tasmania.—FIG. 1861,3a-c.
*U. subglobosa (CLARKE), Tasmania; a, ventral view, ×1; b, holotype, posterior view, ×1; c, ventral interior, ×1 (Clarke, 1990). [Rémy Gourvennec]

Family TRIGONOTRETIDAE Schuchert, 1893 Subfamily NEOSPIRIFERINAE Waterhouse, 1968

- Cracowspira WATERHOUSE, 2004, p. 151 [*Fusispirifer laminatus WATERHOUSE, 1987, p. 23; OD]. [Junior subjective synonym of Fusispirifer WATERHOUSE, 1966 (see CARTER, 2006, p. 1799).] [Rémy Gourvennec]
- Fasciculatia WATERHOUSE, 2004, p. 95 [*F. greenlandicus; OD]. [Junior subjective synonym of Kaninospirifer KULIKOV & STEFANOV in STEFANOV, KULIKOV, & SULTANAEV, 1975 (see CARTER, 2006, p. 1799).] [Rémy Gourvennec]
- Georginakingia WATERHOUSE, 2004, p. 184 [*Spirifera avicula MORRIS, 1845, p. 282, non SOWERBY, 1844, p. 160; OD]. [Junior subjective synonym of Fusispirifer WATERHOUSE, 1966 (see CARTER, 2006, p. 1799).] [Rémy Gourvennec]
- Gobettifera WATERHOUSE, 2004, p. 100 [**G. angulata;* OD]. [Junior subjective synonym of *Septospirifer*



FIG. 1861. Spiriferidae and Choristitidae (p. 2781).



FIG. 1862. Trigonotretidae (p. 2784).



FIG. 1863. Trigonotretidae (p. 2784).

WATERHOUSE in BAMBER & WATERHOUSE, 1971 (see CARTER, 2006, p. 1799).] [Rémy Gourvennec]

- Lutuginia POLETAEV, 1997, p. 309 [*Spirifer lutugini ROTAI, 1931, p. 73; OD]. Medium size, outline transversely subovate; cardinal extremities rounded, hinge line shorter than maximum width in adults; fold and sulcus well developed, almost V-shaped; sulcus flaring anteriorly, incorporating additional costae; fold rising moderately, almost carinate; ventral interarea low, acutely triangular; costae numerous, bifurcating 2 or 3 times to form distinct fascicles on lateral slopes, each fascicle composed of 3 to 6 costae; entire surface regularly imbricate; ventral interior with short, thin delthyrial plate and short, thin, subparallel adminicula; shell substance thin. Carboniferous (upper Viséan–lower Bashkirian): Ukraine, Russia, Kazakhstan.-FIG. 1862, 1a-d. *L. lutugini (ROTAI), upper Serpukhovian, Ukraine; holotype, ventral, dorsal, posterior, and anterior views, ×1 (Rotai, 1931). [John Carter]
- Occidalia ARCHBOLD, 1997, p. 216 [*O. shahi; OD]. Strongly transverse with alate cardinal extremities; lateral slopes with several moderate to strong plicae covered with fasciculate costae; fold and sulcus narrow, crudely V-shaped; sulcus anteriorly deflected to form tongue nearly perpendicular to lateral commissure; microornament of tegulate growth lamellae and weak capillae. *Permian* (*Cisuralian–Arkinskian*): Western Australia, India. ——FIG. 1862,2a–c. *O. shahi, Artinskian, Western Australia; holotype, dorsal, posterior, and anterior

views of latex cast, ×1 (Archbold, 1997). [John Carter]

- Ovispirifer WATERHOUSE, 2004, p. 99 [*Spirifer oldhamianus WAAGEN, 1883, p. 518; OD]. Hinge line short; widely rounded cardinal angles; plicae few with simple bifurcating costae; otherwise similar to Gypospirifer. Middle Permian (lower Guadalupian): Pakistan.——FIG. 1863a-b. *O. oldhamianus (WAAGEN), Salt Range; dorsal, ventral views, ×1 (Waagen, 1883). [Rémy Gourvennec]
- Quadrospira Archbold, 1997, p. 214 [*Neospirifer plicatus Archbold & Thomas, 1986a, p. 133; OD]. Large, outline subquadrate in type species; fold and sulcus well developed; flanks with few medium to strong plicae with fasciculate costae; ventral interarea wide, truncated by small mucronations; microornament tegulate and capillate. [This genus was proposed as a subgenus of Neospirifer. The latter cannot be firmly diagnosed until its microornament is elucidated, however. It seems prudent to consider Quadrospira a separate genus for the time being.] Permian (Cisuralian): Australia, Timor, and southeastern Asia.—FIG. 1862, 3a-d. *Q. plicata (ARCHBOLD & THOMAS), Artinskian, Western Australia; holotype, dorsal, posterior, anterior, and ventral views, ×1 (Archbold & Thomas, 1986a). [John Carter]
- Wadispirifer WATERHOUSE, 2004, p. 138 [*Neospirifer grandis ARCHBOLD & THOMAS, 1986a, p. 143; OD]. [Junior subjective synonym of *Betaneopirifer* GATI-NAUD, 1949 (see CARTER, 2006, p. 1789).] [Rémy Gourvennec]

Subfamily TRIGONOTRETINAE Schuchert, 1893

- Costuloplica WATERHOUSE, 2004, p. 188 [*Neospirifer campbelli senilis MAXWELL, 1964, p. 31; OD]. Small to large, transverse; 6–9 pairs of ribs separated by narrow interspaces; dental adminicula short; dental plates low; umbonal callosity present; crural plates low and strong; low to absent dorsal median septum. [This genus was originally assigned to the subfamily Costuloplicinae, which is not recognized here.] Carboniferous (Serpukhovian-Moscovian): Australia, Russia (Baikal region), Kazakhstan, Argentina.—FIG. 1864,2a–d. *C. senilis (MAXWELL), Australia; a–b, dorsal, ventral views, ×1; c, internal mold of dorsal valve, ×1; d, holotype, interior of ventral valve, ×1 (Maxwell, 1964). [Rémy Gourvennec]
- Koenigoria WATERHOUSE, 2004, p. 173 [*Trigonotreta neoaustralis ArcHBOLD & THOMAS, 1986a, p. 152; OD]. [Junior subjective synonym of Trigonotreta KOENIG, 1825 (see CARTER, 2006, p. 1801).] [Rémy Gourvennec]
- ?Maxwellispirifer WATERHOUSE, 2004, p. 127 [*Neospirifer campbelli exora MCKELLAR, 1965, p. 10; OD]. Small, transverse, with rounded cardinal angles; delthyrium open; costae coarse; dental plates and short adminicula present; delthyrial plate lacking; moderate apical shell thickening; cteno-



FIG. 1864. Trigonotretidae (p. 2784-2785).

phoridium, thick crural plates, and low median septum (possible myophragm) present. [This is a poorly defined genus, possibly a synonym of some neospiriferin.] *Lower Carboniferous (Serpukhovian):* Australia.— FIG. 1864,*3a–b. *M. campbelli exora* (MCKELLAR); *a*, dorsal view, ×1.5; *b*, holotype; ventral view, ×1.5 (McKellar, 1965). [Rémy Gourvennec]

Tegulispirifer POLETAEV, 2000, p. 282 [*Spirifer tegulatus TRAUTSCHOLD, 1876, p. 354; OD]. Medium to large; outline subrhomboidal in juveniles to transversely subovate in adults; maximum width attained at hinge line; cardinal extremities mucronate in juveniles, often subangular in adults; fold and sulcus well developed and defined, rounded to subangular; ventral interarea acutely triangular in juveniles, truncated in adults; delthyrium closed by stegidial plates fused with apical callosity; flanks with numerous freely bifurcating costae, forming fascicles of 7 to 9 ribs at anterior commissure; fascicles usually forming 1 or 2 weak plicae on each flank; microornament regularly imbricate; ventral interior obscured by callus. *Carboniferous (upper Serpukhovian–Kasimovian)*: Ukraine, Russia, Spain.—FIG. 1864, *1a–c. * T. tegulatus* (TRAUTSCHOL), Moscovian–Kasimovian, Moscow Basin; *a–b*, holotype, ventral and lateral views, X1; *c*, dorsal valve, X1 (Ivanov & Ivanova, 1937). [John Carter]

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Family SPIRIFERELLIDAE Waterhouse, 1968

Aequalicosta WATERHOUSE, 2004, p. 193 [*Eliva inflata COOPER & GRANT, 1976a, p. 2239; OD] [Junior subjective synonym of Elivina FREDERIKS, 1924 (see CARTER, 2006, p. 1805).] [Rémy Gourvennec]

- Bamberina WATERHOUSE, 2004, p. 218 [*Elivina? annectens COOPER & GRANT, 1976a, p. 2242; OD]. Small, hinge line short; sulcus shallow with median trough; flanks with broad, low, rarely bifurcate costae; microornament pustulose; short dental plates and adminicula; small, thick crural plates, ctenophoridium and low median septum (possible myophragm) present. Permian (Guadalupian–Lopingian): USA (Texas), Canada, Himalaya, Verkhoiansk Range, Western Timor.——FIG. 1865, 1a–g. *B. annectens (COOPER & GRANT), Lopingian, Texas, USA; a–e, holotype, dorsal, ventral, anterior, posterior, lateral views, ×1; f, ventral interior, ×2; g, dorsal interior, ×2 (Cooper & Grant, 1976a). [Rémy Gourvennec]
- Canalisella WATERHOUSE, 2004, p. 217 [**Spiriferella leviplica* WATERHOUSE & WADDINGTON, 1982, p. 26; OD]. [Junior subjective synonym of *Spiriferella* CHERNYSHEV, 1902 (see CARTER, 2006, p. 1805).] [Rémy Gourvennec]
- Darbandia ANGIOLINI, 2001b, p. 336 [*D. vagabunda; OD]. Medium to large, with extended ventral umbo and very high, weakly apsacline to nearly orthocline, ventral interarea; hinge line moderately narrow; flanks with bifurcating costae that produce poorly defined fascicles; microornament absent; ventral interior with apical callosity and divergent dental adminicula. Permian (Guadalupian-Wordian): Pakistan.——FiG. 1865,4a-c. *D. vagabunda, Wordian; holotype, ventral, dorsal, and lateral views, ×1 (Angiolini, 2001b). [John Carter]
- Dissimiliplica WATERHOUSE, 2004, p. 226 [*Spirifer mexicanus var. compactus GIRTY, 1909, p. 361; OD]. [Junior subjective synonym of *Elivina* FRED-ERIKS, 1924 (see CARTER, 2006, p. 1805).] [Rémy Gourvennec]
- Hunzina ANGIOLINI, 1995, p. 186 [*H. electa; OD]. Medium size, outline subovate to subtriangular; hinge line narrow, apsacline; delthyrium open; fold and sulcus moderately developed, slightly narrow; surface costate with bifurcations near fold-sulcus and sometimes forming few fascicles; ventral valve with thick callus obscuring adminicula; microornament of pustules and capillae. Permian (Cisuralian): Pakistan, China.—FIG. 1865,2a-c. *H. electa, Sakmarian, Pakistan; a-b, holotype, lateral and ventral views, ×1; c, dorsal valve, ×1 (Angiolini, 1995). [John Carter]
- Quispira WATERHOUSE, 2004, p. 225 [**Elivina detecta* COOPER & GRANT, 1976a, p. 2244; OD]. [Junior subjective synonym of *Elivina* FREDERIKS, 1924 (see CARTER, 2006, p. 1805).] [Rémy Gourvennec]
- Tintoriella ANGIOLINI, 1996, p. 195 [*Spirifera rajah SALTER in SALTER & BLANDFORD, 1865, p. 59; OD]. Large, strongly plicate; hinge line less than maximum width; delthyrium open; fold and sulcus narrow; flanks with strong fascicles of 3 to 6 costae; dental adminicula long and high; otherwise similar to Spiriferella. Permian (Lopingian): Himalayan Region.—FIG. 1865, 3a-b. *T. rajah

(SALTER), Wuchiapingian, Kashmir; holotype, dorsal and ventral views, ×1 (Davidson, 1866). [John Carter]

Superfamily PAECKELMANNELLOIDEA Ivanova, 1972

[nom. correct. WATERHOUSE, 2004, p. 227, pro Paeckelmanelloidea CARTER in CARTER & others, 1994, p. 347, nom. correct. pro Paeckelmanellacea IVANOVA, 1981, p. 22, nom. transil. ex Paeckelmanellidae IVANOVA, 1972, p. 40]

WATERHOUSE (2004), as suggested by REED (1944), proposed an emendation of the name *Paeckelmanella* LIKHAREV, 1934 to *Paeckelmannella*, since the intention of LIKHAREV was clearly a dedication of the genus to W. PAECKELMANN. The spelling of LIKHAREV's genus by subsequent authors shows no consistency. Such an emendation seems acceptable according to the *Code* (1999, Art. 33), and the names of suprageneric taxa are consequently corrected. [Rémy Gourvennec]

Family STROPHOPLEURIDAE Carter, 1974 Subfamily STROPHOPLEURINAE Carter, 1974

Triangularia POLETAEV, 2001, p. 492 [*T. tumida; OD]. Small to medium, subtriangular to subquadrate in outline; maximum width at hinge line; ears subangular to mucronate; sulcus narrow, with single subangular rib; fold moderately to well developed, with carinate median crest, forming anterior prolongation with ventral median rib; ventral interarea moderately high, concave, variable in inclination; delthyrium narrow; flanks with few rounded plications separated by interspaces of equal width; microornament of regularly spaced growth lamellae and fine capillae; ventral interior lacking septa or plates. Carboniferous (upper Serpukhovian): Ukraine.—FIG. 1866,2a-c. *T. tumida; holotype, ventral, lateral, and dorsal views, ×2 (Poletaev, 2001). [John Carter]

Subfamily BASHKIRIINAE Nalivkin, 1979

?Varuna WATERHOUSE, 2004, p. 186 [*Spirifer varuna DIENER, 1915, p. 43; OD]. Small, transverse; dental plates and short crural plates present; otherwise similar to Adminiculoria. [The genus was originally assigned to the Angiospiriferinae, but it is similar to Adminiculoria and is tentatively placed in the Strophopleuridae.] Carboniferous (Serpukhovian-Bashkirian): India.—FIG. 1866, 1a-b. *V. varuna (DIENER); a, lectotype, dorsal view, ×1; b, ventral interior, ×1 (Waterhouse, 2004). [Rémy Gourvennec]



FIG. 1865. Spiriferellidae (p. 2786).



FIG. 1866. Strophopleuridae and Brachythyrididae (p. 2786-2789).

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Subfamily PTEROSPIRIFERINAE Waterhouse, 1975

- Johncarteria WATERHOUSE, 2004, p. 230 [*Spiriferinaella scalpata COOPER & GRANT, 1976a, p. 2217, non Spirifernaella scalpata, lapsus calami; OD]. [Junior subjective synonym of Pteroplecta WATER-HOUSE, 1978 (see CARTER, 2006, p. 1818).] [Rémy Gourvennec]
- Yukonospirifer SHI & WATERHOUSE, 1996, p. 122 [*Y. yukonensis; OD]. Medium to large, transversely subtrigonal in outline, subpyramidal in profile; ventral umbo poorly produced; fold and sulcus rounded, not well defined; ventral interarea high, flattened, almost catacline, vertically grooved; hinge line denticulate; flanks and fold-sulcus covered with numerous, freely bifurcating, subfasciculate costae; ventral interior with delthyrial plate and high, long adminicula; dorsal interior and microornament unknown. Permian (Cisuralian–Sakmarian): Canada (Yukon Territory).——FIG. 1866,4a–e. *Y. yukonensis; holotype, lateral, anterior, ventral, dorsal, and posterior views, ×1 (Shi & Waterhouse, 1996). [John Carter]

Superfamily BRACHYTHYRIDOIDEA Fredericks, 1924

Remark: As in the superfamily Spiriferoidea (see above), WATERHOUSE (2004) proposed a revision of the superfamily Brachythyridoidea, in which he emphasized the absence of ventral adminicula and moved subfamilies from the Spiriferoidea to the Brachythyridoidea. WATERHOUSE (2004) also erected the family Brachythyrinidae (not the Brachythyridinidae as spelled on p. 236) and the subfamily Pustuloplicinae, which again leads to a mixture of taxa with different morphologies (e.g., delthyrial morphology, deltidial cover, ornament), and his classification is not followed here. [Rémy Gourvennec]

Family BRACHYTHYRIDIDAE Frederiks, 1924 Subfamily SKELIDORYGMIDAE Carter in Carter & others, 1994

Phragmobrachythyris POLETAEV, 1999, p. 260 [*P. stylaensis; OD]. Medium to large, outline transversely subquadrate, moderately to strongly inflated; hinge line narrow, cardinal extremities rounded; delthyrium covered by deltidium; fold and sulcus moderately developed, rounded, ribbed; lateral slopes costate; median sulcal costa weaker than lateral sulcal costae; costae on flanks broad, flattened, those nearest fold-sulcus may bifurcate at umbo; ventral interior with short distinct myophragm; otherwise similar to *Skelidorygma*. *Carboniferous (Tournaisian–Viséan)*: Ukraine, Russia, Mongolia, Australia, Britain, USA.——FiG. 1866,*3a–c.* **P. stylaensis*, Viséan, Donetz Basin; holotype, ventral, posterior, and lateral views of ventral valve, ×1 (Poletaev, 1999). [John Carter]

Suborder DELTHYRIDINA Ivanova, 1972 Superfamily DELTHYRIDOIDEA Phillips, 1841 Family HYSTEROLITIDAE Termier & Termier, 1949 Subfamily HYSTEROLITINAE Termier & Termier, 1949

Gaspespirifer Bizzarro & Lespérance, 1999, p. 1065 [*Spirifer gaspensis BILLINGS, 1874, p. 44; OD]. Medium to large, transverse; cardinal extremities acute to mucronate; ventral interarea curved, apsacline; fold and sulcus smooth with subtrapezoidal section anteriorly; flanks with simple plications; surface with growth lamellae and marginal spines; curved dental plates present; ventral muscle field variably impressed; short crural plates and ctenophoridium present. Lower Devonian (Pragian-Emsian): North and South America, France.—FIG. 1867, 1a-c. *G. gaspensis (BILL-INGS), Emsian, Gaspé Peninsula; a, lectotype, posterior view, $\times 1.1$; *b-c*, dorsal and ventral views of internal mold, ×1.2 and ×0.9 respectively (Bizzarro & Lespérance, 1999). [Rémy Gourvennec]

Subfamily FIMBRISPIRIFERINAE Pitrat, 1965

Bultynckia GARCÍA-ALCALDE, 2004, p. 22 [*Spirifer Rojasi DE VERNEUIL, 1850, p. 178; OD]. Medium to large, brachythyrid, entirely ribbed; ventral interarea curved, apsacline with deltidial plates joining apically in a short deltidial cover; ribs generally simple or 1 to 3 internal pairs bifurcating anteriorly; microornament capillate with marginal spines; long dental plates and short crural plates present. Lower Devonian (Pragian–Emsian): Spain, western France.——FIG. 1867,2a–f. *B. rojasi (DE VERNEUIL); a–e, dorsal, anterior, posterior, ventral, and lateral views, X1; f, transverse section, X7 (García-Alcalde, 2004). [Rémy Gourvennec]



FIG. 1867. Hysterolitidae, Acrospiriferidae, and Cyrtinopsidae (p. 2789–2791).

Family ACROSPIRIFERIDAE Termier & Termier, 1949

[nom. transl. JOHNSON & HOU in CARTER & others, 1994, p. 351, ex Acrospiriferinae TERMIER & TERMIER, 1949, p. 96] [type genus, Acrospirifer HELMBRECHT & WEDEKIND, 1923, p. 952]

Medium to large size, transverse, generally capillate with fila, occasionally with a tendency to develop marginal spines; crural plates variably present. [JANSEN (2001a) illustrated spines on some well-preserved specimens attributed to Acrospirifer primaevus from the regio typica (but not from the type locality). We cannot be sure that these specimens are conspecific with the type specimens of the genus Acrospirifer, which when illustrated by JAHNKE (1971) show no spines. If we retain the possibility of a spinose Acrospirifer, the genus may become restricted to its type species only. The genus Filispirifer erected by JANSEN (2001b) in order to gather most of the capillate species previously assigned to *Acrospirifer* also shows a slight tendency to develop rudimentary marginal spines, indicating that the two genera are very closely related.] Lower Devonian (upper Lochkovian)–Middle Devonian (Eifelian). [Rémy Gourvennec]

Filispirifer JANSEN, 2001b, p. 269 [*F. merzakhsaiensis; OD]. 5 to 15 ribs on each flank, those bordering sulcus often deflated; ornament capillate (with a low tendency to develop marginal spines); notothyrial platform poorly expressed; otherwise similar to Acrospirifer. Lower Devonian (upper lower Pragianlower lower Emsian): Europe, northern Africa, Turkey.—FIG. 1867,5a-c. *F. merzakhsaiensis, Dra-Ebene, Morocco, holotype; a-b, dorsal, posterior views, ×0.7; c, ornament, ×4.9 (Jansen, 2001b). [Rémy Gourvennec]

Family CYRTINOPSIDAE Wedekind, 1926 Subfamily CYRTINOPSINAE Wedekind, 1926

Jehlanaria HAVLIČEK in HAVLIČEK & VANĚK, 1998, p. 94 [*Cyrtina vlasta HAVLIČEK, 1956, p. 607; OD]. Small, cyrtiniform, with high catacline to procline ventral interarea; narrow deltidial plates fused apically; fold and sulcus well delimited, smooth; flanks with one obsolete plication; dental plates united to median septum to form narrow spondylium. Lower Devonian (Pragian): Czech Republic (Prague Basin).—FIG. 1867,4a-c. *J. *vlasta* (HAVLÍČEK), dorsal, ventral, and posterior views, ×7.1 (Havlíček & Vaněk, 1998). [Rémy Gourvennec]

Subfamily ARASPIRIFERINAE Johnson in Carter & others, 1994

Boucotiellina García-Alcalde, 2004, p. 27 [*Spirifer Ezquerra de Verneuil, 1850, p. 178; OD]. Small, transverse to slightly mucronate; high, apsacline ventral interarea with open delthyrium; fold and sulcus smooth; lateral plications strong, angular; microornament capillate and spinose; dental plates and low, short, poorly developed median septum; short crural plates and small, rudimentary ctenophoridium [The genus is assigned to the Araspiriferinae due to the presence of short crural plates. A median septum is a characteristic of the Cyrtinopsinae, but it is poorly developed here, and moreover the Cyrtinopsinae lack crural plates.] Lower Devonian (upper Emsian): northern Spain, northern China (?Nei Mongol).——FIG. 1867, 3a-e. *B. ezquerrai (DE VERNEUIL); a-d, ventral, posterior, dorsal, and anterior views, $\times 2$; *e*, transverse section, ×3 (García-Alcalde, 2004). [Rémy Gourvennec]

Superfamily RETICULARIOIDEA Waagen, 1883 Family RETICULARIIDAE Waagen, 1883 Subfamily RHENOTHYRIDINAE Gourvennec in Carter & others, 1994

- Lubricospirifer CHEN & YAO, 1999, p. 238 [*L. gumoensis; OD]. Medium size; rounded or slightly elongate with high, apsacline, curved ventral interarea; delthyrium open; fold and sulcus well defined; flanks smooth or with 1–2 weak plicae; surface with growth lamellae and marginal spines; dental plates thin, subparallel; faint delthyrial ridges; crural plates united in trough or septalium; ctenophoridium present. Lower Devonian (upper Emsian): southern China.—FiG. 1868a-f. *L. gumoensis, central Guangxi; a-c, lectotype, dorsal, ventral, and anterior views, ×1.5; d, lateral view, ×1; e, microornament, ×10; f, transverse section, ×2 (Chen & Yao, 1999). [Rémy Gourvennec]
- Plicambocoelia BOUCOT & BRUNTON in WONGWANICH & others, 2004, p. 1081 [*P. tansathieni; OD]. [Junior subjective synonym of Echinocoeliopsis HAMADA, 1968 (see CARTER & GOURVENNEC, 2006, p. 1857).] [Rémy Gourvennec]
- Quasiprosserella BOUCOT & COCKS in BOUCOT, COCKS, & RACHEBOEUF, 1999, p. 855 [*Q. samedensis; OD]. [Junior subjective synonym of Prosserella GRABAU in GRABAU & SHERZER, 1910 (see CARTER & GOURVENNEC, 2006, p. 1852).] [Rémy Gourvennec]



FIG. 1868. Reticulariidae (p. 2791).

Order SPIRIFERINIDA Ivanova, 1972 Suborder CYRTINIDINA Carter & Johnson in Carter & others, 1994 Superfamily CYRTINOIDEA Frederiks, 1911 Family CYRTINIDAE Frederiks, 1911

- Cyrtina DAVIDSON, 1859 in 1858-1863, p. 66. Cyrtina (Hystricocyrtina) Havlíček in Havlíček & VANĚK, 1998, р. 100 [**Cyrtina kazi kazi* Наvlíček, 1956, р. 606; OD]. Pseudodeltidium pierced by large foramen; ornament of relatively strong, erect, randomly distributed spines; otherwise similar to Cyrtina (Cyrtina). [Hystricocyrtina was erected as a new genus by HAVLÍČEK (1998), but it is so close to Cyrtina, except for its ornament, that we retain it here only at the subgeneric rank. Thus the genus Cyrtina now includes two subgenera: C. (Cyrtina), the diagnosis of which corresponds to that given in JOHNSON, 2006, p. 1881, and C. (Hystricocyrtina) here described.] Lower Devonian (Pragian): Czech Republic (Prague Basin).-FIG. 1869, 1a-d. *C. (H.) kazi (HAVLIČEK); a-c, dorsal, ventral, and posterior views, $\times 6.5$; d, dorsal interior, ×9.2 (Havlíček & Vaněk, 1998). [Rémy Gourvennec]
- Moniellocyrtina GARCIA-ALCALDE, 2001, p. 126 [*M. orthoclina; OD]. Large with orthocline to slightly anacline, strongly curved, high ventral interarea;

otherwise similar to *Cyrtina. Lower Devonian (upper Emsian):* northern Spain.——FiG. 1869,*2a–d. *M. orthoclina;* ventral, dorsal, lateral, and anterior views, ×3 (García-Alcalde, 2001). [Rémy Gourvennec]

Suborder SPIRIFERINIDINA Ivanova, 1972 Superfamily SYRINGOTHYRIDOIDEA Frederiks, 1926 Family SYRINGOTHYRIDIDAE Frederiks, 1926 Subfamily PERMASYRINXINAE Waterhouse, 1986

Remark: The assignment of the following genera to the family Syringothyrididae, subfamily Permasyrinxinae remains provisional until the presence of perideltidial areas or syrinx is elucidated.

Cundaria ARCHBOLD, 1996, p. 28 [**C. aquilaformis*; OD]. Outline transversely and acutely triangular with wide alate cardinal extremities; costae on ears may bifurcate; fold with shallow median groove; sulcus with pair of weak costae on sides; fold well delineated; delthyrium very wide; microornament of grooves with posterior papillae and anterior pits. *Permian (Cisuralian–Artinskian)*: Western Australia.—FIG. 1870, *Ia–e.* **C. aquilaformis*;

2792



FIG. 1869. Cyrtinidae (p. 2792).

holotype, internal mold in dorsal, ventral, and posterior views and incomplete latex cast of dorsal and posterior exteriors, ×1 (Archbold, 1996). [John Carter]

- **?Kyutepia** KLETS, 1998, p. 95 [*K. alata; OD]. Presence of perideltidial areas unknown; otherwise similar to Myodelthyrium. [If Kyutepia alata KLETS, 1998, lacks perideltidial areas then the genus is valid and should be assigned to the Licharewiidae.] Permian (Cisuralian): northeastern Siberia.——FIG. 1870,2a-c. *K. alata; a, holotype, partial internal mold of ventral interarea, ×1.5; b, internal mold of ventral interarea showing muscle impressions and median ridge on delthyrial plate, ×1; c, mold of dorsal valve interior, ×1 (Klets, 1998). [John Carter]
- Pachycyrtella ANGIOLINI, 2001a, p. 126 [*P. omanensis; OD]. Large, outline subtrigonal; ventral interarea high, concave, apsacline to orthocline; sulcus narrow, shallow, smooth; fold well delineated, low, with deep mesial furrow; flanks with moderately coarse costae; ventral interior with long thick delthyrial plate and long adminicula that surround much of muscle field; shell substance very thick; otherwise similar to Cyrtella. Permian (Cisuralian–Sakmarian): Oman, Afghanistan, India, ?Australia.—FIG. 1871,2a-b. *P. omanensis, Sakmarian, Oman; holotype, dorsal and ventral views, ×1 (Angiolini, 2001a). [John Carter]
- **?Syrella** ARCHBOLD, 1996, p. 32 [**S. occidenta*; OD]. Small to medium, transversely subovate in outline, ventribiconvex; flanks with up to 12



FIG. 1870. Syringothyrididae (p. 2792–2793).



FIG. 1871. Syringothyrididae (p. 2793–2796).



FIG. 1872. Licharewiidae (p. 2796).

pairs of rounded simple costae; ventral interarea of moderate height, concave, apsacline; fold and sulcus well delineated; fold with shallow depression or groove for entire length; ventral adminicula extending forward about one-third valve length; ventral muscle field with several myophragms that become stronger with age. [Assignment of this genus to the Permasyrinxinae is uncertain because perideltidial areas are unknown. It could well belong in the Licharewiidae.] *Permian (Cisuralian– Artinskian):* Western Australia.—FiG. 1871,*3a–e.* **S. occidenta*; *a–d*, holotype, internal mold in dorsal, posterior, and anterior views, latex cast of dorsal valve, ×1.25; *e*, ventral view showing muscle field, ×1 (Archbold, 1996). [John Carter]

Woolagia ARCHBOLD, 1997, p. 218 [* W. playfordi; OD]. Medium size, strongly transverse, with acutely subtrigonal outline; fold with broad mesial furrow and pair of low lateral costae; sulcus smooth or with weak pair of lateral costae; flanks with moderately numerous, simple, rounded costae; ventral interarea moderately low, concave, apsacline; ventral interior with short, thick dental adminicula and short, thick delthyrial plate; microornament of delicate radial grooves only. *Permian (Cisuralian– Artinskian*): Western Australia.——FIG. 1871, *1a–d. *W. playfordi;* holotype, posterior, anterior, dorsal, and ventral views of internal mold, ×1 (Archbold, 1997). [John Carter]

Family LICHAREWIIDAE Sliusareva, 1958

Nahoniella SHI, 1998, p. 935, nom. nov. pro Yukonella SHI & WATERHOUSE, 1996, p. 127, non Yukonella SENOWBARI-DARYAN & REID, 1986, p. 900 [*Yukonella plana; OD]. Delthyrial plate large, covering half or more of delthyrium; ovarian impressions poorly developed; otherwise similar to Permospirifer. Permian (Cisuralian-Artinskian): Canada (Yukon Territory).—FIG. 1872a-c. *N. plana (SHI & WATERHOUSE); a, holotype, ventral valve, ×1; b, ventral interior, latex cast, ×1; c, dorsal exterior, ×1 (Shi & Waterhouse, 1996). [John Carter]

Superfamily PENNOSPIRIFERINOIDEA Dagys, 1972 Family SPIROPUNCTIFERIDAE Carter in Carter & others, 1994

Spiropunctifera Ivanova, 1971, p. 120.

S. (Larbontella) LEGRAND-BLAIN, 1996, p. 201 [*Spiropunctifera (Larbontella) dubari; OD]. Costae freely bifurcating on flanks and foldsulcus; dorsal adminicula moderately long; otherwise similar to S. (Spiropunctifera). Carboniferous (upper Viséan or lower Serpukhovian): French Pyrenees.—FIG. 1873a-c. *S. (L.) dubari; holotype, exterior, interior, and posterior mold, ventral valve, ×1.5 (Legrand-Blain, 1996). [John Carter]



FIG. 1873. Spiropunctiferidae (p. 2796).

THECIDEIDA

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Order THECIDEIDA Elliott, 1958 Superfamily THECIDEOIDEA Gray 1840 Family THECIDELLINIDAE Elliott, 1958 Subfamily THECIDELLININAE Elliott, 1953

Kakanuiella LEE & ROBINSON, 2003, p. 344 [* Thecidellina hedleyi THOMSON, 1915, p. 463; OD]. Small, subtriangular, hinge line relatively short, ventral interarea flat with no trace of pseudodeltidium or delthyrial notch; ventral valve with sessile hemispondylium bounded laterally by slightly concave vertical plates, teeth subtriangular, relatively widely spaced, floor of valve ornamented by tiny, acicular crystallite calcite spines on either side of high bladelike median septum extending almost to anterior border; dorsal valve variable but usually subquadrate, relatively flattened away from convex umbonal region, cardinal process broad rectangular in outline, border narrow, outer surface of subperipheral rim ornamental by low ribs, brachial bridge with ventral groove (marsupial notch) and small, posteriorly directed spur, median septum typically tapering posteriorly, extending to edge of body cavity, ventral edge flanked by anteriorly divergent, serrated ridges to create appearance of small central depression, brachial lobes auriform with serrated margins but without intrabrachial depressions, probably not canopied; fibrous secondary shell completely suppressed, shell composed of acicular crystallite calcite intermixed with patches of interlocking granules of calcite, especially in teeth; groove and spur structure on brachial bridge possibly indicative of sexual dimorphism. [LÜTER (2005, p. 105) regarded the marsupial notch as a diagnostic lacazellin character and placed Kakanuiella in subfamily Uncertain. Because it is only present in females, however, and the presence or absence of a marsupial notch cannot be established in the majority of fossil thecideides, Kakanuiella currently remains assigned to the Thecidellininae.] Paleogene-Holocene: New Zealand (Oamaru District), lower Eocene (Ypresian)-lower Oligocene (Rupelian); New Zealand (Chatham Rise), Holocene. FIG. 1874a-e. *K. hedleyi (THOMSON); a, ventral valve interior, Priabonian, Cape Wanbrow, ×14; b, acicular crystallites on valve floor, Priabonian, Cape Wanbrow, University of Otago, OU43125a, ×1400; c, dorsal valve interior, Priabonian, Cape Wanbrow, OU43127, ×16; *d*, dorsal valve interior, Rupelian, Kakanui, ×18; *e*, dorsal valve marginal ornament, Rupelian, Kakanui, OU43122, ×75 (Lee & Robinson, 2003).

Family THECIDEIDAE Gray, 1840 Subfamily LACAZELLINAE Backhaus, 1959

- Ospreyella Lüter & Wörheide in Lüter, Wörheide, & REITNER, 2003, p. 1425 [*O. depressa LÜTER in LÜTER, WÖRHEIDE, & REITNER, 2003, p. 1425; OD]. Medium size, pyriform, unequally biconvex, dorsal valve almost lidlike, with low anterior uniplication, ventral valve cup-shaped with small cicatrix, ventral interarea flat, clearly developed with convex pseudodeltidium; ventral valve interior papillose with papillae more prominent near edge, hemispondylium projecting anteriorly with upraised edges and prominent median myophragm; outer rim of dorsal valve strongly papillose, cardinal process incipiently trilobed with bulbous median ridge, median septum with sinus replaced anteriorly by shallow sulcus breaching subperipheral rim to reach anterior margin, posteriorly median ridge upraised, free-standing, and folded backward with edges convoluted to form up to four short ramuli and terminating as a median concave channel (median ramus) connected to jugum, brachial lobes long, narrow, crescentic with serrated edges and small perforate reticulum connecting with jugum and posterior extensions interdigitating with ramuli; endopunctate; mantle spiculate; sexually dimorphic, brachial bridge of females with marsupial notch. [The organization of the brachial skeletal elements is reminiscent of the arrangement in Vermiculothecidea.] Holocene: Western Pacific (Coral Sea).—FIG. 1875a-g. *O. depressa, Coral Sea, Osprey Reef, off Cooktown, Australia; a, holotype, female ventral valve interior, QM G318534, ×5; b, paratype, female dorsal valve interior, ZMB 2000, \times 7; c, three-quarters profile view showing marsupial notch, $\times 30$; d, paratype, male dorsal valve anterior view showing sulcus, ZMB 2005, ×7; e, enlargement of ventral valve interior showing hemispondylium, ×27; f, paratype, male ventral valve showing jugum (arrow) and bridge (arrowhead), ZMB 2004, ×15, g, juvenile dorsal valve interior, ZMB 2001, ×30 (Lüter, Wörheide, & Reitner, 2003).
- **Protolacazella** BAKER, 2005, p. 1311 [**P. scripta* BAKER, 2005, p. 1312; OD]. Small, outline rounded to rounded and transversely oblong, large attachment scar and high free ventral wall usually with shallow anterior sulcus, hinge line only slightly less than maximum width of shell, ventral interarea



FIG. 1874. Thecidellinidae (p. 2797).

Thecideida



FIG. 1875. Thecideidae (p. 2797).

narrow, laterally attenuated with small, indistinct, shallowly convex pseudodeltidium; ventral valve with large sessile hemispondylium with characteristic W outline, inner surface of free ventral wall ornamented by low tubercles; dorsal valve with high subperipheral rim with outer surface ornamented by elongate tubercles, median septum with well-developed sinus and short ramuli, brachial cavities occupied typically by two brachial tubercles supporting perforate brachial lobes, posteriorly arching toward midline to form a reticulum united with jugal pillar; impunctate; probably possessed marsupium indicative of sexual dimorphism. The unobtrusive ventral interarea together with an angle of intersection between commissural plane and plane containing attachment scar typically about 60°, giving shell a characteristically triangular lateral profile. *Middle Jurassic (upper Aalenian)*: England (Cotswolds). ——FIG. 1876a-z. *P. scripta; a-c, sectioned paratype, dorsal, lateral, anterior views, BMNH BD9381, ×20; d, paratype, ventral valve interior, BMNH BD9380, ×20; e-f, holotype, dorsal valve interior, anterior view, BMNH BD9379, ×20; g, paratype, typically preserved dorsal valve interior, BMNH BD9382, ×20; h, early juvenile dorsal valve interior, BMNH BD9383, ×35; i-z, paratype, serial horizontal sections, ventral valve stippled, BMNH BD9381, ×10 (Baker, 2005).



FIG. 1876. Thecideidae (p. 2797-2799).

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TEREBRATULIDINA

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Order TEREBRATULIDA Waagen, 1883 Suborder TEREBRATULIDINA Waagen, 1883 Superfamily DIELASMATOIDEA Schuchert, 1913 Family DIELASMATIDAE Schuchert, 1913

- Campbellelasma SMIRNOVA, 2004b, p. 24 [*C. variiforme; OD]. Small to medium, smooth, biconvex, subpentagonal, may have slight sulcus in ventral valve; beak incurved, foramen labiate. Pedicle collar present; dental plates short, septalium resting on septum of variable height; outer hinge plates concave, crural processes wide, loop narrow. Permian (Kazanian): Russia (eastern Russian Platform).—FIG. 1877,4a-j. *C. variiforme; a-c, holotype, dorsal, lateral, and anterior views, PIN 4898/1710, a, ×2, b-c, ×1; d-j, serial transverse sections 1.0, 2.0, 3.0, 3.3, 3.65, 4.05, 5.05 mm from first section, ×1 (Smirnova, 2004b).
- Grigorjevaelasma SMIRNOVA in SMIRNOVA, MADISON, & ESAULOVA, 2004, p. 40 [*G. rossica; OD]. Small, smooth, ventribiconvex, elongate oval to subpentagonal. Pedicle collar present; dental plates long, inner hinge plates V-shaped, may be supported by septum, outer hinge plates slightly concave; crura long; crural bases oblique, loop 0.4 dorsal valve length, transverse band broadly arched. Permian (Kazanian): Russia (eastern Russian Platform).
 ——FIG. 1877, 1a-e. *G. rossica; a-c, holotype, dorsal, lateral, and anterior views, PIN 4898/45, ×1; d-e, reconstructions of loop, ×1 (Smirnova, Madison, & Esaulova, 2004).
- Gruntelasma SMIRNOVA in SMIRNOVA, MADISON, & ESAULOVA, 2004, p. 50 [*G. bajtuganensis; OD]. Small, smooth, ventribiconvex, elongate to subtrigonal, anterior commissure rectimarginate to uniplicate. Pedicle collar present; dental plates short, inner hinge plates widely arched, outer hinge plates and crural bases horizontal, crura long, loop 0.3 dorsal valve length, transverse band strongly arched. Permian (Kazanian): Russia (eastern Russian Platform).——FIG. 1877,2a-e. *G. bajtuganensis; a-c, holotype, dorsal, lateral, and anterior views, PIN 4898/1, ×1; d-e, reconstructions of loop, ×1 (Smirnova, Madison, & Esaulova, 2004).

Family BEECHERIIDAE Smirnova, 2004

Sokelasma SMIRNOVA, 2004a, p. 166 [*S. guttiformis; OD]. Small, smooth, biconvex, rounded, anterior commissure slightly uniplicate. Dental plates variable, narrow outer hinge plates discernible in apical region of beak; septalium supported by crural plates and distinct septum; crural plates attached to valve floor, close to or separated from inner socket ridges; loop narrow, 0.4 dorsal valve length, transverse band broadly arched. Differs from *Beecheria* in biconvex valves, distinct septum, narrow outer hinge plates and position of crural plates. *Permian (Kazanian):* Russia (eastern Russian Platform). ——FIG. 1877, *3a–k.* **S. guttiformis; a–c*, holotype, dorsal, lateral, and anterior views, PIN 4898/75, ×1; *d–k*, serial transverse sections 1.0, 1.4, 1.95, 2.2, 2.3, 2.9, 3.5, 3.9 mm from first section, ×1 (Smirnova, 2004a).

Family UNCERTAIN

- Adygellopsis SUN & SHI in JIN & others, 1985, p. 228 [*A. pentagonalis; OD]. Small, roundly pentagonal, biconvex, anterior commissure rectimarginate; beak massive, slightly incurved, beak ridges angular; foramen subcircular, mesothyrid to permesothyrid; deltidial plates covering delthyrium. Pedicle collar absent; dental plates inclined toward lateral wall; teeth thin, long; cardinal process obscure; hinge plates narrow; septalium shallow, small; inner socket ridges strongly developed; septum high, stout, extending to midvalve; crural process low, loop deltiform, more than 0.5 dorsal valve length, with low-arched transverse band. Differs from Adygella in lacking a septalium and in loop. Upper Triassic: China (Yunnan).-FIG. 1878, 1a-i. *A. pentagonalis; a-b, dorsal and lateral views, ×1; c-i, serial transverse sections 0.2, 3.9, 4.3, 4.5, 4.8, 6.9 mm from first section, ×1 (Jin & others, 1985).
- ?Athyrorhynchia Xu & Liu, 1983, p. 91 [*A. athyroformis; OD]. Small to medium, smooth or with fine costellae; subpentagonal, biconvex, ventral sulcus wide, shallow; anterior commissure uniplicate; beak short, strongly incurved, concealing delthyrium. Dental plates nearly parallel; hinge plates discrete, fused with socket ridges; no median septum; loop unknown. [The status of this genus is uncertain as the loop is unknown.] Middle Triassic: China (Qinghai).—FIG. 1878,2a-h. *A. athyroformis; a-c, dorsal, lateral, and anterior views, ×1; d-h, incomplete serial transverse sections 1.2, 1.6, 2.4, 3.1, 3.6 mm from ventral umbo, ×1 (Xu & Liu, 1983).
- ?Paradygella LIAO & SUN, 1974, p. 352 [*P. magna; OD]. Large, smooth, oval, biconvex; anterior commissure uniplicate; beak large, foramen large, permesothyrid. Pedicle collar thick, long; dental plates extending to valve floor; no cardinal process; hinge plates divided, septalium with median ridge;



FIG. 1877. Dielasmatidae and Beecheriidae (p. 2801).

median septum long and high, loop short, deltiform. [The status of this genus is uncertain as no serial sections are available for this species.] *Middle Triassic:* China (Sichuan).——FIG. 1878,6*a*–*c.* **P. magna;* dorsal, lateral, and anterior views, ×1 (Liao & Sun, 1974).

- ?Proanadyrella Xu & Liu, 1983, p. 106 [*P. circularia; OD]. Small to medium, subcircular to oval, smooth, ventribiconvex, anterior commissure sulciplicate; beak small, incurved. Pedicle collar present; dental plates divergent, reaching lateral walls; cardinal process bilobate, hinge plates discrete, inner socket ridges well developed, crural plates attached to floor of dorsal valve; median septum present, loop long, possibly lacking ascending branches (loop may be broken). Differs from Antezeilleria in having median septum and sulciplicate commissure. [The status of this genus is uncertain because loop of type specimen may be broken.] Lower Triassic: China (Qinghai).-FIG. 1878, 3a-h. *P. circularia; a-c, dorsal, lateral, and anterior views, $\times 2$; d-h, serial transverse sections 0.9, 1.8, 2.5, 3.3, 4.6 mm from ventral umbo, ×2 (Xu & Liu, 1983).
- **?Pseudopygoides** XU, 1978, p. 303 [**P. jueyongensis*; OD]. Medium, subpentagonal, ventribiconvex; shell margin geniculate; anterior commissure rectimarginate, may have resorbed so-called keyhole; beak low, erect; foramen circular, mesothyrid; beak ridges obtusely rounded. No pedicle collar or dental plates; cardinal process may be present; dorsal septum low, short; septalium V-shaped, wide, deep; loop moderately long, deltiform. [The status of this genus is uncertain because the internal structures are not fully known.] Upper Triasic: Tibet.——FIG. 1878,5*a*–*h*. **P. jueyongensis*; *a*–*c*, dorsal, lateral, and anterior views, ×1; *d*–*h*, incomplete serial transverse sections, no distances given, ×1 (Xu, 1978).
- ?Thyratryaria XU & LIU, 1983, p. 92 [*T. pinguis; OD]. Small to medium, elongate oval to pear shaped, rarely circular, strongly biconvex, smooth, inner layer of shell ornamented with irregular radial costellae, anterior commissure uniplicate or slightly sulciplicate; beak low, incurved, foramen large, incurved. Dental plates present; hinge plates narrow, divided; crural plates reaching floor of dorsal valve; loop short, not fully known. [The status of this genus is uncertain because the internal

Terebratulida



FIG. 1878. Uncertain (p. 2801-2803).

structures are not fully known]. *Middle Triassic:* China (Qinghai).——FIG. 1878,4*a–h.* * *T. pinguis;* a-c, dorsal, lateral, and anterior views, $\times 2$; d-h, serial transverse sections 0.9, 2.0, 3.1, 4.4, 5.1 mm from ventral umbo, $\times 2$ (Xu & Liu, 1983).

Superfamily TEREBRATULOIDEA Gray, 1840 Family UNCERTAIN

Almiralthyris CALZADA BADIA, 1994, p. 42 [*Terebratula sampelayoi BATALLER, 1943, p. 33; OD]. Very large, smooth, ventribiconvex, oval to subpentagonal in outline, strongly biplicate; foramen small, permesothyrid, loop narrow, short, triangular, without crural points. *Eocene (Bartonian*): Spain. ——FIG. 1879, *5a–d. *A. sampelayoi* (BATALLER); *a–c*, holotype, dorsal, lateral, and anterior views, MGSB 2704, ×0.6; *d*, reconstruction of loop, ×1 (Calzada Badia, 1994).

Eichwaldithyris SMIRNOVA, 2001, p. 602 [**R. rasilis*; OD]. Medium, oval to pear shaped, anterior commissure uniplicate or biplicate; plications in anterior third; beak high, curved, foramen submesothyrid. Pedicle collar present; cardinal process low; hinge plates wide, concave; crural 2804



FIG. 1879. Uncertain and Orthotomidae (p. 2803-2807).

bases high, ventrally sharp and dorsally keeled; crural processes wide; loop slender, 0.25 dorsal valve length; descending branches short, transverse band arched. *Lower Cretaceous:* Crimea, Ukraine. ——FIG. 1879,*3a–d.* **R. rasilis; a–c,* holotype, dorsal, lateral, and anterior views, MGSB, ×1; d, reconstruction of loop, ×2 (Smirnova, 2001).

Olencothyris COOPER, 1942, p. 233 [**Terebratula* harlani MORTON, 1828, p. 73; OD]. Large, smooth, elongate oval, ventribiconvex; anterior commissure uniplicate to sulciplicate; foramen large, submesothyrid, symphytium mostly concealed. Ventral valve thickened posteriorly; pedicle collar long, tubular; cardinal process large, semielliptical; crural processes large, triangular; crural bases forming ridge along inner edge of narrow, concave outer hinge plates; loop variable, 0.3 dorsal valve length, triangular, with strongly arched transverse band; some loops with long terminal points resembling those of some Jurassic loboidothyridoids. *Paleocene:* USA (New Jersey, North Carolina).——FIG. 1879,4*a*-*d.* **O. harlani* (MORTON), New Jersey; *a*-*c*, dorsal, lateral, and anterior views, ×0.5; *d*, interior of dorsal valve, ×1 (Cooper, 1983).

Superfamily LOBOIDOTHYRIDOIDEA Makridin, 1964 Family UNCERTAIN

- Aschuthyris OVTSHARENKO, 1993, p. 17 [*A. aschuensis; OD]. Medium, biconvex, anterior lateral commissures rectimarginate. Outer hinge plates slender, fused with inner socket ridges; crura wide, directed ventrally; loop approximately 0.5 dorsal valve length, flanges slender, subparallel, transverse band strongly arched with median fold. Upper Jurassic: southwestern Pamirs.—FIG. 1880,2a-c. *A. aschuensis; dorsal, lateral, and anterior views, ×1 (Ovtsharenko, 1993).
- Dhosathyris OVTSHARENKO, 1993, p. 16 [* Terebratula dhosaensis KITCHIN, 1900, p. 15; OD]. Medium size, biplicate, biconvex. Cardinal process well defined; outer hinge plates horizontal with subperpendicular crural bases; crura wide, directed ventrally; loop broad, less than 0.5 dorsal valve length, transverse band thin, flanges subparallel. Upper Jurassic: Pamirs, India.——FIG. 1880,3a–d. D. dhosaensis (KITCHIN); a–c, dorsal, lateral, and anterior views, ×1; d, reconstructions of loop, ×1 (Ovtsharenko, 1993).
- Neaguithyris GEORGESCU, 1991, p. 242 [*N. neagui; OD]. Medium, smooth, ventribiconvex, subpentagonal; anterior commissure sulciplicate. Cardinal process bilobate; hinge plates very thin; loop short (0.25 dorsal valve length); transverse band strongly bilobate. Middle Jurassic (upper Bajocian-lower Bathonian): Romania (eastern Carpathians).
 —FIG. 1880, 4a-i. *N. neagui; a-c, holotype, dorsal, lateral, and anterior views, LPB IIIb0196, ×1; d-i, serial transverse sections 1.2, 3.5, 5.0, 5.8, 7.5, 9.2 mm from ventral umbo, ×1 (Georgescu, 1991).
- Peristerothyris MANCENIDO, 1983, p. 349 [**P. columbiniformis*; OD]. Very large, smooth, subcircular to subpentagonal, biconvex, anterior commissure biplicate; beak massive, incurved; foramen large, permesothyrid. Cardinal process broad, flat, crenulated; hinge plates not keeled, with a distally cuneate, virgate core and a distally clubbed, concave sheath. *Lower Jurassic (?Sinemurian, Pliensbachian):* Argentina, USA (?California).—FIG. 1880,5*a*-*h*. **P. columbiniformis*, Argentina; *a-c*, dorsal, lateral, and anterior views, ×0.5; *d*-*h*, serial transverse sections 5.9, 8.3, 9.8, 12.2, 12.7 mm from ventral umbo, ×1 (Manceñido, 1983).
- Sogxianthyris SUN, 1981, p. 235 [*S. pentagonalis; OD]. Medium, subpentagonal, unequally biconvex to nearly planoconvex; anterior commissure sulciplicate; smooth or weakly capillate; beak large, protuberant, foramen large, epithyrid. Pedicle collar ringlike; no dental plates, cardinal process low, bilobate; hinge plates divided and slightly concave; crural bases attached to outer hinge plates ventrally; loop trigonal, 0.5 dorsal valve length; terminal points long. Middle Jurassic: Tibet.—FIG. 1880,6a-j.

**S. pentagonalis; a–c,* dorsal, lateral, and anterior views, ×1; *d–j,* serial transverse sections 4.9, 6.8, 8.1, 9.1, 11.8, 14.4, 16.7 mm from ventral umbo, ×1 (Sun, 1981).

Thadiqithyris ALMÉRAS, 1987, p. 189 [**T. thadiqiensis*; OD]. Medium size, biconvex, rectimarginate; lateral and anterior commissure finely multiplicate; foramen large, labiate, epithyrid; symphytium narrow; loop 0.5 dorsal valve length. *Middle Jurassic (Callovian):* Saudi Arabia, Syria.——FIG. 1880, *Ia-c.* **T. thadiqiensis*, Syria; dorsal, lateral, and anterior views, ×1 (Alméras, 1987).

Superfamily DYSCOLIOIDEA Fischer & Oehlert, 1891 Family UNCERTAIN

- Buckmanithyris TCHORSZHEWSKY, 1990, p. 33 [*B. dziruliensis; OD]. Medium size, subpentagonal, smooth, strongly unisulcate; cardinal process small, loop very short. Lower Jurassic: Carpathians, Caucasus.—FIG. 1879,6a–j. *B. dziruliensis, ?Carpathians; a–c, dorsal, lateral, and anterior views, ×1; d–j, serial transverse sections 1.3, 1.6, 1.85, 2.0, 2.3, 4.0, 4.8 mm from ventral umbo, ×1.5 (Tchorszhewsky, 1990).
- Carinatothyris TCHORSZHEWSKY, 1990, p. 33 [*Terebratula (Pygope) aspasia MENEGHINI [MGH], var. carinata HAAS, 1912, p. 258; OD]. Small, smooth, subtriangular to rhomboidal; median ridge in dorsal valve, anterior commissure strongly unisulcate; loop short, rounded. Lower Jurassic: Italy.——FIG. 1879, *Ia*-c. *C. carinata (HAAS); dorsal, lateral, and anterior views, ×1 (Tchorszhewsky, 1990).

Superfamily UNCERTAIN Family ORTHOTOMIDAE Muir-Wood, 1936

[Orthotomidae MUIR-WOOD, 1936, p. 224]

Small, smooth or rarely capillate, adult shells hypothyrid, with triangular delthyrium bordered by jugate deltidial plates below tapering, acute beak; no dental plates; loop short, deltiform. *Lower Jurassic*.

Orthotoma QUENSTEDT, 1869 in 1868–1871, p. 315 [*Terebratula heyseana QUENSTEDT, 1869, p. 315, non DUNKER, 1847; =Orthotoma spinati RAU, 1905, p. 54; SD BUCKMAN, 1918, p. 96] [=Orthoidea FRIREN, 1876, p. 1 (type, O. liasina, OD)]. Ventribiconvex, becoming sulcoconvex, anterior commissure rectimarginate to unisulcate, beak ridges angular. Cardinal process minute, projecting vertically as two small ears; hinge plates in transverse section ventrally convex, dorsally inclined, tapering, not differentiated from inner socket ridges; loop short (0.3 dorsal valve length) with low arched transverse band. Lower Jurassic: Europe, China, ?Saudi Arabia.—FIG. 1879,2a-d. 2806



FIG. 1880. Uncertain (p. 2805).



FIG. 1881. Uncertain (p. 2807-2808).

**O. spinati* (RAU), Germany; *a–c*, dorsal, lateral, and anterior views, ×2; *d*, reconstruction of loop, ×2 (Muir-Wood, 1965).——FIG. 1879,*2e–o. O. quenstedti*, Germany, serial transverse sections at 0.1 to 0.3 mm intervals, ×3 (Muir-Wood, 1965).

Superfamily UNCERTAIN Family UNCERTAIN

Falciferula TCHOUMATCHENCO, 1987, p. 56 [*F. stoytchevi; OD]. Medium, subtriangular, biconvex, anterior commissure broadly unisulcate or sulcipli-

cate; foramen large. Crural bases thin, falcifer; loop narrow, 0.3 dorsal valve length, may be spinose; transverse band strongly arched. *Jurassic:* Algeria. ——FIG. 1881, *Ia-d. *F. stoytchevi; a-c,* dorsal, lateral, and anterior views, ×1; *d,* ventral view of loop, ×1 (Tchoumatchenco, 1987).

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Lobothyroides XU, 1978, p. 307 [*L. striata; OD]. Large, oval, ventribiconvex, smooth or with obscure striae laterally and anteriorly, beak short; foramen large, mesothyrid, anterior commissure rectimarginate. Pedicle collar present; dental plates absent; cardinal process small; outer hinge plates narrow, tapering; loop narrow, short (less than 0.3 dorsal valve length), transverse band strongly arched. *Upper Triassic:* southwestern China (Sichuan).

FIG. 1881,2a-c. *L. striata; a-b, dorsal and lateral views, ×1; c, close up of ornament, ×2 (Xu, 1978).

- Mayaothyris Sun, 1987, p. 74 [*M. typica; OD]. Small to medium, oval, biconvex; shell ornamented with broad, sharply angular costae from umbo; foramen permesothyrid; delthyrium covered by symphytium, anterior commissure rectimarginate; no dental plates, cardinal process low; hinge plates separate, merged with inner socket ridges; crural plates united with floor of dorsal valve, slightly inclined toward midline; crural bases arising from ventral side of hinge plates; crura of *Dielasma* type; loop possibly short; other loop details unknown. [Description is based on one incomplete, now sectioned, individual.] Lower Cretaceous (Aptian): northern Tibet.——FIG. 1881,4a-m. *M. typica; a-d, dorsal, ventral, lateral, and anterior views, ×1; e-m, serial transverse sections of incomplete damaged specimen 1.6, 2.9, 3.6, 4.8, 5.5, 6.4, 6.9, 7.2, 7.4 mm from ventral umbo, ×1 (Sun, 1987).
- Pseudorhaetina SANDY in STANLEY & others, 1994, p. 19 [*P. antimoniensis; OD]. Medium to large, subpentagonal, biconvex, foramen permesothyrid, anterior commissure biplicate. Hinge plates narrow, crural bases well developed; crural processes high; no median septum; juvenile loop simple deltiform; adult loop 0.5 dorsal valve length, long flanged; transverse band high arched. [The loop develops in characteristic terebratuloid fashion from simple extensions of the crura, but the adult loop resembles that of loboidothyridoids.] Upper Triassic (Norian): Mexico. FIG. 1881, 6a-f. *P. antimoniensis; a-c, dorsal, lateral, and anterior views, ×2; *d*-*e*, reconstruction showing loop development, ×5; f, reconstruction showing loop development, ×2 (Sandy, 1998).
- Vex HOOVER, 1979, p. 9 [* Terebratula semisimplex WHITE, 1879, p. 108; OD]. Small to medium, subtriangular to subpentagonal, ventribiconvex, smooth posteriorly, variably multicostate anteriorly; anterior commissure rectimarginate to slightly uniplicate, beak erect to incurved, foramen small, deltidial plates disjunct. Distinct pedicle collar; no dental plates; cardinal process well developed, bilobate; outer hinge plates broad, planar; no inner hinge plates; no median septum; loop delicate, with large crural processes; descending lamellae slender; loop not fully known. Lower Triassic: USA (Idaho).——FIG. 1881,5a-e. *V. semisimplex (WHITE); *a*-*c*, lectotype, dorsal, lateral, and anterior views, USNM 8190a, ×2 (Hoover, 1979); d-e, ventral and lateral views of cardinalia and broken loop, ×2 (Cooper, 1983).
- Zenobiathyris CRAIG, 1999, p. 427 [*Z. mutabilis; OD]. Small to medium, subpentagonal, biconvex, capillate, rugose, anterior commissure rectimarginate to uniplicate; foramen large, mesothyrid, deltidial plates conjunct. Pedicle collar narrow, sessile; cardinal process delicate; no median septum;

crural base fused to inner socket ridge, no hinge plates discernible; loop short, thin; transverse band short, wide, with median fold. No illustration of loop available. *Upper Cretaceous (Santonian– Maastrichtian):* Western Australia (Perth Basin, Carnarvon Basin).——FIG. 1881, *3a–c. *Z. mutabilis*; holotype, dorsal, lateral, and anterior views, WAM83.3148a, ×2 (Craig, 1999).

Suborder TEREBRATELLIDINA Muir-Wood, 1955 Superfamily ZEILLERIOIDEA Allan, 1940 Family ZEILLERIIDAE Allan, 1940 Subfamily ZEILLERIINAE Allan, 1940

- Paraulacothyris SUN & ZHANG, 1998, p. 267 [*P. qipuqiapuensis]. Small, smooth, globose, rounded subpentagonal, smooth, strongly sulcate; beak low, erect, beak ridges rounded, palintrope small, foramen small, circular and permesothyrid; delthyrium covered by symphytium. Dental plates parallel; pedicle collar short. Hinge plates thick, septalium narrow and shallow, supported by stout and high median septum that extends almost to anterior margin; crural bases attaching to dorsal side of hinge plates; crura hamiform; crural processes not developed; cardinal process poorly developed; loop teloform, extending about 0.75 valve length, with narrow descending lamellae, broad ascending lamellae, and wide, saddle-shaped transverse band. [SUN & ZHANG (1998) assigned Paraulacothyris to the family Laqueidae, subfamily Aulacothyropsinae; however, similarities with Bakonyithyris VOROS, 1983, and Aulacothyris DOUVILLÉ, 1879, particularly in sulcation and teloform loop, suggest assignment to the subfamily Zeilleriinae is more appropriate.] Lower Jurassic: China (Karakorum -FIG. 1882, 3a-n. *P. qipuqiapuensis; region).*a*-*c*, dorsal, lateral, and anterior views, $\times 1$; *d*-*n*, serial transverse sections 1.0, 1.7, 2.7, 4.0, 4.4, 5.1, 5.7, 6.1, 8.0, 8.5, 9.0 mm from ventral umbo, ×1 (Sun & Zhang, 1998).
- Pictetella Radulović, Radulović, & Rabrenović 2002, p. 790 [*P. serbica; OD]. Small, 7 to 8 strong costae, moderately biconvex, elongate oval to subcircular, anterior commissure multiplicate. Beak suberect to erect, beak ridges sharp and short, defining narrow palintrope; foramen large, mesothyrid. Dental plates lamellar and gently curved. Cardinal process not developed; septalium well developed, concave posteriorly, broadening and shallowing anteriorly, supported by high median septum; outer hinge plates buttressing inner socket ridges, inner hinge plates thin and anteriorly subhorizontal. Loop teloform, thin and very long with narrow descending and wide ascending branches. [RADULOVIĆ, RADULOVIĆ, & RABRENOVIĆ (2002) assigned Pictetella to family Dallinidae, subfamily Gemmarculinae; on the basis of the revised diagnoses of both family Dallinidae and

Terebratulida



FIG. 1882. Zeilleriidae, Uncertain, Terebratellidae, and Dallinidae (p. 2808–2810).

subfamily Gemmarculinae (MACKINNON & LEE, 2006), *Pictetella* is now reassigned to the family Zeilleriidae.] *Lower Cretaceous (Barremian, ?Valang-inian):* Serbia, ?Switzerland.—FIG. 1882, *1a-m.* **P. serbica*; Barremian, eastern Serbia; *a-c*, dorsal,

lateral, and anterior views, Museum d'Histoire Naturelle, Geneva, VR76/1, \times 1; *d–m*, serial transverse sections 0.4, 1.7, 2.2, 2.5, 3.2, 3.6, 4.5, 5.0, 7.0, 9.0 mm from ventral umbo, \times 2 (Radulović, Radulović, & Rabrenović, 2002).

Superfamily KINGENOIDEA Elliott, 1948 Family UNCERTAIN

Trigonellina BUCKMAN, 1907, p. 342 [* Terebratulites pectunculus VON SCHLOTHEIM, 1820, p. 272; OD]. Small, transverse, shell thick, scaly, ornamented by several well-spaced, rounded, opposite carinae, foramen with conjunct deltidial plates; hinge line nearly strophic; small median septum in ventral umbo. Cardinalia with inner socket ridges prominent, cardinal process small, small cardinal platform buttressed by median septum extending to midvalve, loop small, diploform. Upper Jurassic: Europe.——FIG. 1882,2a-b. *T. pectunculus (VON SCHLOTHEIM), Germany; a, dorsal view; b, drawing of dorsal valve interior, ×4 (adapted from von Zittel, 1870).

Superfamily TEREBRATELLOIDEA King, 1850 Family TEREBRATELLIDAE King, 1850 Subfamily UNCERTAIN

Erihadrosia Hiller & MacKinnon, 2000, p. 76 [*Stethothyris epsilon Allan, 1940, p. 287; OD]. Very large, smooth, elongate oval; ventribiconvex, anterior commissure rectimarginate to slightly unisulcate; beak slender, strongly incurved; foramen small, mesothyrid; cardinal area wide, low to hidden, convex to concave; shell strongly thickened posteriorly, but thin anteriorly. Cardinal process very large, cuplike; socket ridges, crural bases, and hinge plates becoming fused to restrict hinge trough; median septum high, bifurcating posteriorly to join with cardinalia posterior of crura, becoming thicker. Neogene (lower Miocene-middle Miocene): New Zealand. FIG. 1882, 5a-c. *E. epsilon (ALLAN); *a*-*b*, dorsal and lateral views, ×0.5; c, interior view of broken conjoined valves, $\times 0.5$ (Hiller & MacKinnon, 2000).

Family DALLINIDAE Beecher, 1893 Subfamily DALLININAE Beecher, 1893

Pegmathyris HATAI, 1938, p. 225 [*Dallina miyatokoensis HATAI, 1936b, p. 315; OD]. Similar to Dallina but differing in thicker shell, rectimarginate folding, high symphytium, straighter and stronger beak, strong cardinal process, stronger median septum, inner hinge plate horizontal instead of inclined. Miocene: Japan.—FIG. 1882,4. *P. miyatokoensis (HATAI); dorsal view, ×1 (Elliott & Hatai, 1965).

Superfamily UNCERTAIN Family UNCERTAIN

Antigoniarcula Elliott, 1959, p. 146 [*Argiope perrieri Eudes-Deslongchamps, 1853, p. 5; OD].

Small, transverse, alate, hinge line strophic; test costate and scaly; foramen large; deltidial plates narrow. Pedicle collar present; cardinal process small, hinge plates small, delimited by inner socket ridges, supported anteriorly by very short, thin median septum, crura thin and delicate, loop angular, apparently teloform, anteriorly produced into sharp points [The loop reconstruction is uncertain in this genus.] *Lower Jurassic:* Western Europe.——FIG. 1883,*Ia-c.* **A. perrieri* (EUDES-DESLONGCHAMPS), France; *a–b*, dorsal and ventral valve views, ×2; *c*, dorsal valve interior showing loop, reconstructed, ×2 (Elliott, 1965).

- Eogryphus HERTLEIN & GRANT, 1944, p. 88 [*E. tolmani; OD]. Medium, smooth, subcircular to ovate, ventribiconvex; dorsal valve with shallow median sulcus, anterior commissure rectimarginate to unisulcate; beak short, slightly incurved, foramen very small, permesothyrid; deltidial plates conjunct; thick dorsal median septum present; other internal characters unknown. *Eocene:* USA (California). —FIG. 1883,5. *E. tolmani; holotype, dorsal view, UCLA 6203, ×1 (Hertlein & Grant, 1944).
- Gwyniella JOHANSEN, 1987, p. 26 [*G. persica; OD]. Minute, smooth, subcircular to subpentagonal in outline, resupinate to biconvex; beak very low, recessed; foramen hypothyrid. Hinge weak, brachidium poorly developed, consisting of short, delicate crura and short, high, pointed septal pillar; lophophore probably schizolophous. Paleocene (lower Danian): Denmark.——FIG. 1883,3a-c. *G. persica; a, holotype, dorsal view, MGUH 16953, ×10; b, interior of ventral valve, ×10, c, interior of dorsal valve, ×10 (Johansen, 1987).
- Hercothyris COOPER, 1979, p. 25 [*H. borroi; OD]. Medium, pentagonal to oval, ventribiconvex, smooth to faintly costellate in posterolateral regions, uniplicate; foramen large, mesothyrid, deltidial plates conjunct. No dental plates; ventral interior with strong median septum extending to midvalve. Cardinalia consisting of strong socket ridges fused to crural bases; no outer hinge plates; cardinal process small and transverse; dorsal median septum long, bladelike, triangular; loop probably long, possibly teloform. Eocene: Cuba.-FIG. 1883,2a-f. *H. borroi; a-c, holotype, dorsal, lateral, and anterior views, USNM 549396a, ×1; d, dorsal interior, $\times 1$; e, transverse section showing dorsal median septum extending to ventral valve, $\times 2$; f, transverse section 10 mm anterior to beak, showing dorsal septum tapering anteriorly, ×2 (Cooper, 1979).
- Holobrachia ZEZINA, 2001b, p. 66 [**H. vietnamica*; OD]. Medium, biconvex, smooth, subcircular to subpentagonal, anterior commisure unisulcate, deltidial plates conjunct; foramen small, submesothyrid, beak short, erect. Dental plates curved and partially obscured by shell thickening in gerontic specimens; cardinalia prominent, with small cardinal process located posteromedianly between stout inner hinge plates; cardinalia uniting anteriorly with median septum that extends for 0.33 valve length. Adult loop modified trabecular,



FIG. 1883. Uncertain (p. 2810-2812).

lacking crura. Holocene: off Vietnam .----—Fig. 1883,4a-c. *H. vietnamica; a-b, holotype, dorsal and anterior views, IO N XI-52-13/1, $\times 2$; c, drawing of loop, ×2 (Zezina, 2001b).

- Kingenella POPIEL-BARCZYK, 1968, p. 72 [*K. kongieli; OD]. Small to medium, subcircular to oval in outline, smooth or slightly capillate, strongly biconvex, rectimarginate; beak ridges weak, beak obtuse, generally truncated but may be recurved; deltidial plates disjunct, foramen hypothyrid. Ventral valve with short pedicle collar, hinge teeth small, thick; no dental plates; cardinal process vestigial, outer and inner hinge plates fused to produce a flat platform attached to very long median septum; crura short, loop trabecular, strongly spiculate. Upper Cretaceous: Poland, Belgium, Ukraine. -FIG. 1883,8a-d. *K. kongieli, Maastrichtian, Poland; *a-c*, holotype, dorsal, lateral, and anterior views, MZ VIII Bra. 411/7, ×2; d, dorsal valve interior, ×2 (Popiel-Barczyk, 1968).
- Kurakithyris HATAI, 1946, p. 98 [*K. quantoensis; OD]. Biconvex, rectimarginate to unisulcate, foramen possibly permesothyrid, deltidial plates conjunct, median ridge low; hinge teeth weak, with ventrally recessive dental plates, no median ridge in ventral valve; pedicle collar indistinct. Cardinalia weak, divided into inner and outer hinge plates by swollen bases of crural processes, inner hinge plate troughlike, supported by median septum, excavated beneath; descending branches attached to median septum by short connecting bands in young but becoming free in adult. [The status of this genus is doubtful. It is based on a single specimen that was said to have no loop preserved (HATAI, 1948).] Pliocene: Japan—FIG. 1883,6. *K. quantoensis; lateral view, ×1 (Hatai, 1965c).
- Leptothyrellopsis BITNER & PISERA, 1979, p. 82 [*L. polonicus; OD]. Minute, shell smooth, elongate oval, flatly biconvex, anterior commissure rectimarginate, beak erect, foramen large, subtriangular, hypothyrid, deltidial plates narrow. No pedicle collar; inner socket ridges high; high, platelike septal pillar in dorsal valve. Upper Cretaceous: Poland, Denmark.—FIG. 1883,7a-c. *L. polonicus, Poland; a-b, holotype, dorsal and lateral views, ×10; c, dorsal valve interior, ×10 (Bitner & Pisera, 1979)
- Luppovithyris LOBATSCHEVA, 1990, p. 100 [*L. ovalis; OD]. Medium, biconvex, elongate-oval or rounded-pentagonal, prominently costate around commissure, rectimarginate to commonly uniplicate with weakly developed fold and sulcus; beak short, erect, beak ridges rounded, foramen small, mesothyrid. Dental plates short, ventrally divergent; pedicle collar present. Inner socket ridges fused to massive hinge plates, inner hinge plates long, well developed; septalium broad, buttressed by high, wedgelike septum extending for about 0.33 length of dorsal valve; cardinal process present; crural bases prominent dorsally; loop teloform. [For discussion of problems associated with this genus, see LEE & SMIRNOVA, 2006, Glosseudesia, p.

2062.] Lower Cretaceous (Neocomian): Turkmeni--FIG. 1884, 4a-n. *L. ovalis; a-c, holotype, stan.dorsal, lateral, and ventral views, $\times 1$; d-n, serial transverse sections 0.6, 1.4, 2.0, 3.1, 3.9, 4.3, 4.6, 5.3, 6.15, 7.3, 11.7 mm from ventral umbo, ×1 (Lobatscheva, 1990).

- Lutetiarcula Elliott, 1954, p. 727 [*L. perplexa; OD]. Small, biconvex, solid, strong brachial cardinalia, cardinal process low, median septum well developed, extending nearly to anterior margin; curved lateral brachial ridges on valve floor. Eocene: France.—FIG. 1884,2a-b. *L. perplexa; a, dorsal valve interior, $\times 5$; b, posterior view of dorsal valve interior, ×5 (Elliott, 1954).
- Magas J. SOWERBY, 1816 in 1815-1818, p. 39 [*M. pumilus (illustrated in FAUJAS, 1798, pl. 26,6); OD; = Terebratulites chitoniformis VON SCHLOTHEIM, 1813, p. 113 (see WIND, 1954, p. 79)]. Small, smooth, planoconvex, unisulcate, beak strongly incurved, deltidial plates narrow, triangular, beak ridges sharp. Ventral interior with constricted beak area, hinge teeth with swollen bases, short, low median ridge tapering anteriorly and posteriorly with deep muscle scars. Cardinalia wide, inner socket ridges thick, sunken median cardinal platform with small cardinal process raised on this; septalium but tressing cardinalia and rising very high as anteriorly directed pillar, crura short, descending branches narrow, straight, broadly attached to septum beneath two posteriorly directed curved lamellae, loop annular; spiculate. Upper Cretaceous: Europe.—FIG. 1884, 1a-e. *M. chitoniformis (VON SCHLOTHEIM); a-b, dorsal and lateral views, $\times 2$; c-d, interior views of ventral and dorsal valve with reconstructed loop, ×4.2; e, lateral view of reconstructed loop, ×2 (Elliott & Hatai, 1965).
- Miogryphus Hertlein & Grant, 1944, p. 95 [*M. willetti; OD]. Medium, smooth or with few anterior radial plications; subpentagonal to ovate, biconvex with low dorsal median fold, anterior commissure rectimarginate to unisulcate; foramen large, possibly mesothyrid; symphytium present; dorsal median septum present; other internal characters unknown. Miocene: USA (California).-FIG. 1885, 3a-c. *M. willetti; holotype, dorsal, ventral, and anterior views, CAS 7361, ×1 (Hertlein & Grant, 1944)
- Praeneothyris KATZ, 1962, p. 143 [*P. darvaensis; OD]. Large, subcircular, smooth, rectimarginate, beak erect, strongly incurved, foramen minute, mesothyrid. Hinge teeth large, cardinal process and dorsal median septum thickened; ventral septum may be present; loop teloform. Upper Cretaceous: Tadzhikistan, Caucasus, Bulgaria, India, Madagascar.—FIG. 1885, 4a-d. *P. darvaensis, Tadzhikistan; a-c, dorsal, lateral, and anterior views, ×1; d, reconstruction of loop, ×1 (Katz, 1962).
- Rhynchora DALMAN, 1828, p. 135 [* Terebratula costata NILSSON, 1827, p. 37; OD; =Anomites costatus WAHLENBERG, 1821, p. 62; Anomia pectinata LINNAEUS, 1758, p. 701]. Large, thick shelled,



FIG. 1884. Uncertain (p. 2812-2816).

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FIG. 1885. Uncertain (p. 2812-2816).

ventribiconvex, coarsely costate, unisulcate; foramen very large, small deltidial plates; hinge teeth large, widely separated, short, low median ridge; cardinalia thick, rounded, socket ridges thick and fused with cardinal platform; cardinal process a large, slightly raised median surface area on platform, hollows under cardinal platform beneath crural processes, median septum thin, supporting cardinalia, high posteriorly and extending to midvalve; loop unknown. *Upper Cretaceous*: northwestern Europe.——FIG. 1885, *Ia–f.* **R. pectinata* (LINAEUS), Sweden; *a–d*, lectotype, exterior, interior, lateral, and anterior views of dorsal valve, Linnean Collection, Linnean Society of London, ×1 (Brunton, Cocks, & Dance, 1967); *e–f*, dorsal and lateral views, ×1 (Elliott & Hatai, 1965).



FIG. 1886. Uncertain (p. 2815-2816).

- Rhynchorina OEHLERT, 1887, p. 1326 [*Anomites spathulatus WAHLENBERG, 1821, p. 62; OD]. Similar to *Rhynchorina*, but differing in smooth exterior, cardinalia with very wide concave outer hinge plates, marked crural bases with convex inner hinge plates arching over septum and meeting in median ridge, which runs back to cardinal process, loop similar to that of *Magas. Upper Cretaceous:* northwestern Europe.——FIG. 1886,3. *R. spathulata (WAHLENBERG); interior of dorsal valve, ×5 (Elliott & Hatai, 1965).
- Simplicithyris ZEZINA, 1976b, p. 101 [*S. kurilensis; OD]. Small, smooth, slightly biconvex, rectimarginate to slightly unisulcate; foramen permesothyrid, deltidial plates narrow; pedicle collar broad, dental plates strong; median septum subrectangular; no cardinal process, crura, brachial loop, or spicules. Differs from Amphithyris in possession of dental plates and permesothyrid foramen and from Pumilus in possession of dental plates, smooth inner surface, and lack of spicules. Holocene: northwestern Pacific (Kurile-Kamchatka

region).——FIG. 1886, *1a–d. *S. kurilensis; a,* holotype, dorsal view, IO XI-52-1, ×4; *b*, interior of ventral valve, ×4; *c–d*, interior of dorsal valve, ×4 (Zezina, 1976b).

- Tiaretithyris TCHOUMATCHENCO, 1986, p. 113 [*T. tiaretensis; OD]. Small to medium, smooth, subcircular to subpentagonal, ventribiconvex, commissure broadly uniplicate; foramen small, circular, mesothyrid. Dental plates well developed; cardinal process present or absent; septum long, crural bases short, adult loop teloform. Differs from Kachathyris in lacking capillae. Upper Jurassic: Algeria.——FIG. 1885,2a-d. *T. tiaretensis; a-c, holotype, dorsal, lateral, and anterior views, ×1; d, reconstruction of loop, ×1 (Tchoumatchenco, 1986).
- Timacella RADULOVIĆ & RADULOVIĆ, 2002, p. 405 [*Waldheimia (Zeilleria) timacensis ANTHULA, 1903, p. 50; OD]. Medium size, biconvex, semi-ribbed, outline elongate oval to rarely subcircular; beak small, erect with mesothyrid circular foramen; fold and sulcus not developed; anterior commissure rectimarginate, crenulate; internal characters as in Psilothyris. Cretaceous (upper Barremian): Carpatho-Balkanides, eastern Serbia.——FIG. 1886,6a-c. *T. timacensis (ANTHULA); neotype, dorsal, lateral, and anterior views, RGF VR 25/15, ×1 (Radulović & Radulović, 2002).
- Xinjiangthyris SUN & WANG, 1984, p. 95 [*X. ovalis; OD]. Large, transversely oval, rectimarginate, smooth, planoconvex to biconvex; beak slightly incurved, foramen mesothyrid, delthyrium covered with henidium; beak ridges angular. Teeth large, with swollen bases; no dental plates; cardinalia strong, massive; cardinal process high, bulbous, with bilobate myophore; hinge plates thick, united with and supported by stout septum; septalium short; loop teloform. Upper Cretaceous: China (Xinjiang).——FIG. 1886,2a-b. *X. ovalis; holotype, dorsal and lateral views, ×1 (Sun & Wang, 1984).

- Yabeithyris HATAI, 1948, p. 498 [*Y. notoensis; OD]. Smooth, anterior commissure rectimarginate, symphytium short, with median ridge; pedicle collar indistinct. Dental plates ventrally recessive, cardinalia with deep divergent trough posteriorly, crural bases divergent, median septum well developed. *Miocene:* Japan.—FIG. 1884,3. *Y. notoensis; dorsal valve exterior, ×1 (Hatai, 1948).
- Yuezhuella JIN & YE in YE & YANG, 1979, p. 69 [*Y. minor; OD]. Small, roundly pentagonal, biconvex, smooth; anterior commissure rectimarginate to weakly uniplicate; foramen submesothyrid. Dental plates short, slightly divergent; hinge plates fused with inner socket ridges; septalium wide, shallow, supported by long, high septum; crura short; loop long (about 0.5 dorsal valve length); descending branches uniting with septum anteriorly. Lower Cretaceous-Upper Cretaceous: Tibet. ——FIG. 1886,4a-m. *Y. minor; a-c, dorsal, lateral, and anterior views, X2; d, anterior view of interior, X2; e-l, serial transverse sections 0.12, 1.0, 1.5, 1.9, 2.1, 2.6, 3.0, 3.3 mm from ventral umbo, X2; m, loop reconstruction, X2 (Ye & Yang, 1979).
- Zhidothyris JIN, SUN, & YE in JIN & others, 1979, p. 216 [*Z. carinata; OD]. Small to medium, elliptical, ventribiconvex, smooth; anterior commissure unisulcate; dorsal valve with wide, deep sulcus, ventral valve carinate posteriorly; beak strongly incurved, foramen small, mesothyrid; symphytium arched. Dental plates short, parallel; hinge plates narrow, separate; crural plates erect and attached to floor of valve; septum long, high; loop long. Upper Triassic: China.——FIG. 1886,5a-c. *Z. carinata; dorsal, lateral, and anterior views, ×1 (Jin & others, 1979).——FIG. 1886,5d-q. Z. yulongensis SUN; serial transverse sections 1.7, 2.6, 2.8, 3.3, 3.7, 4.1, 5.0, 6.4, 6.8, 7.0, 7.2, 7.5, 7.9, 9.7 mm from ventral umbo, ×1 (Sun, 1981).

UNCERTAIN

A. J. Boucot

[Oregon State University, Corvallis]

Order and Superfamily UNCERTAIN

Family UNCERTAIN

Microbilobata JIN & CHATTERTON, 1996, p. 47 [*M. avalanchensis; OD]. Very small, subpentagonal outline, smooth, dorsal sulcus, with low, rounded, medial costa, and corresponding ventral sulcus and medial costa, moderately biconvex, emarginated anterior commissure, no evident deltidial plates. Ventral internal features obscured, dorsal loop narrow, anteriorly pointed, relatively long. Punctae possibly present. [This enigmatic shell may represent an early centronelliform loop-bearer reminiscent of the terebratuloids; if so it is the earliest member of the taxon or a convergent development that possibly simulates that taxon. Alternatively, it may be a late representative of those Ordovician atrypaceans bearing a loop that is basically a jugum without accompanying spiralia. The questionable presence of punctae in Microbilobata is unhelpful in making any decision. The earliest Pridolian terebratuloids as well as subsequent earlier Devonian taxa in that group have an external form very different from Microbilobata. See also JIN & LEE, 2006, p. 2252.] Silurian (upper Wenlock): northwestern Canada.-FIG. 1887a-g. *M.

avalanchensis; a–c, dorsal, lateral, and anterior views, $\times 42$; *d–e,* ventral and side views, $\times 32$; *f,* dorsal view, $\times 30$; *g,* silicified shell with ventral valve removed to show acuminate loop, $\times 40$ (Jin & Chatterton, 1996).

Subfamily MUTATIONELLINAE Cloud, 1942

Aqqikkolia Sun & CHEN, 1998, p. 198 [*A. kalachukaensis; OD]. Small, ventribiconvex, coarsely costate, subcircular, triangular delthyrium. Strong hinge teeth, short dental lamellae. Cardinal plate unsupported by crural plates. Loop unknown. Punctae unrecognized. [The absence of fold or sulcus removes this taxon from placement in the Brachzyginae or Adreninae of the Meganteridae, but makes placement in the Mutationellinae reasonable. However, the nonrecognition of either a loop or punctae makes assignment to the terebratuloids somewhat uncertain.] Devonian (Emsian): China (Kunlun region, Xinjiang).-FIG. 1888a-w. *A. kalachukaensis; a-d, dorsal, ventral, lateral, and anterior views, $\times 5$; *e-w*, serial transverse sections 0.2, 0.5, 1.0, 1.3, 1.5, 1.7, 1.9, 2.0, 2.1, 2.3, 2.6, 2.7, 2.8, 2.9, 3.1, 3.2, 3.3, 3.4, 3.5 mm from ventral umbo (Sun & Chen, 1998).



FIG. 1887. Uncertain (p. 2817).

2819



FIG. 1888. Uncertain (p. 2817).

UNCERTAIN

NORMAN SAVAGE

[University of Oregon]

Order UNCERTAIN Family CARDIARINIDAE Cooper, 1956

[Cardiarinidae COOPER, 1956b, p. 527]

Very small, cordiform, emarginated, biconvex brachiopods with beak straight, projecting; foramen round, apical; symphytium flat elongate. Surface smooth, impunctate. Dorsal parathyridia. Dental plates supporting narrow, elongate teeth. Hinge plates undivided; crura possibly supporting loop. *Upper Carboniferous:* USA, Europe.

Although assigned to the Rhynchonellida by COOPER (1956b), he considered the ordinal affinities of Cardiarina to be uncertain. Richard HOARE (personal communication, 1995) examined Dickerson Shale brachiopods (Pennsylvanian, Desmoinesian, Texas) that included specimens he assigned to Cardiarina. He observed a partial loop during serial sectioning and concluded Cardiarina was possibly a terebratulid. HOARE and MAPES (1997) described the Texas material as ?Cardiarina cordata and illustrated sections and a reconstructed dorsal valve interior based on the sections. During preparation of the Rhynchonellida for Volume 4 of the revised Treatise (KAESLER, 2002), it was decided to transfer *Cardiarina* to the Terebratulida, although it was included in the Rhynchonellida in the 1965 *Treatise* (MOORE, 1965). The family Cardiarinidae is not in volumes 4 or 5 of the revised *Treatise*; to avoid the omission of this well-known genus from the *Treatise* it now seems appropriate to include *Cardinarina* in the *Treatise* Supplement herein under order Uncertain.

Cardiarina COOPER, 1956b, p. 527 [*C. cordata; OD]. Very small with cordiform, emarginated outline and biconvex profile. Beak straight, projecting; foramen round, apical; symphytium flat elongate. Bisulcate with strong dorsal sulcus and weak ventral sulcus; anterior commissure rectimarginate to sulcate. Surface smooth, impunctate. Dorsal parathyridia deep. Dental plates extending from foramen along margins of symphytium to support teeth and then laterally to valve margin; teeth narrow, elongate, with medially directed tips. Hinge plates undivided; notothyrial platform thick; sockets elongate, curved; outer socket ridges thin; inner socket ridges thick, high; crura possibly supporting loop; muscle fields poorly known. Upper Carboniferous (upper Pennsylvanian): USA, Europe.—FIG. 1889,1a-h. *C. cordata, upper Magdalena Formation, Sacramento Mountains, Grapevine Canyon, New Mexico, USA; a-b, dorsal and oblique dorsolateral views of holotype; c, ventral valve interior; d, dorsal valve interior, ×20; e-f, drawings of interior and lateral views of ventral valve showing symphytium, teeth, and long dental plates, $\times 20$; g-h, interior and lateral views of dorsal valve showing parathyridium and cardinalia, ×20 (Cooper, 1956b).

UNCERTAIN

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Order UNCERTAIN Superfamily UNCERTAIN Family TROPIDOLEPTIDAE Schuchert, 1896

[nom. transl. SCHUCHERT & COOPER, 1932, p. 152, ex Tropidoleptinae SCHUCHERT, 1896, p. 330]

Transverse, subquadrate, concavoconvex to planoconvex, costellate valves; massive cyrtomatodont teeth supported by strong dental plates; ventral muscle scar large and flabellate with large diductors flanking narrow adductors; high, complex cardinal process on thick notothyrial platform; pair of long crurae with apophyses; hinge plates subdued; thick median septum bisecting elongate diductor scars, expanded distally;



FIG. 1889. Cardiarinidae and Tropidoleptidae (p. 2820-2821).

shell endopunctate. [Placement of this common and distinctive group of brachiopods has proved difficult. *Tropidoleptus* has, for example, been related to orthides, strophomenides, and terebratulides. In the first edition of the *Treatise*, the genus was assigned to the Enteletoidea (WRIGHT, 1965, p. 328), largely on the basis of its general shape and the presence of punctation. The cyrtomatodont dentition, however, and complex cardinalia with crurae, apophyses, and a median septum are more typical of some of the more unusual rhynchonellides, for example, the Uncinuloidea, and more specifically the Eatoniidae. A punctate shell condition, nonetheless, has not been reported for that group.] *Devonian*.

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Tropidoleptus HALL, 1857, p. 151 [*Strophomena carinata CONRAD, 1839, p. 64; OD]. Concavoconvex, subquadrate with narrow ventral fold and dorsal sulcus, broad, rounded costae and costellae. Devonian: cosmopolitan.—FIG. 1889,2a-i. *T. carinatus (CONRAD); a-e, ventral, dorsal, lateral, anterior, and posterior views of conjoined valves, Hamilton Group, New York State, BMNH B 75889, ×1; f-g, internal mold and rubber replica of ventral valve, Hamilton Group, New York State, BMNH B 10549, ×1; h-i, internal mold and latex replica of dorsal interior, Stadtfeld Beds, Humerich, Oberstadtfeld, Germany, BMNH B 94629, ×1 (new).