### PRODUCTIDINA

C. H. C. Brunton

[retired from The Natural History Museum, London]

Suborder PRODUCTIDINA Waagen, 1883 Superfamily PRODUCTOIDEA Gray, 1840 Family PRODUCTELLIDAE Schuchert, 1929 Subfamily PRODUCTININAE Muir-Wood & Cooper, 1960 Tribe PRODUCTININI Muir-Wood & Cooper, 1960

Caruthia LAZAREV & CARTER, 2000, p. 12 [\*C. borealis; OD]. Small, outline subrounded with welldifferentiated, subtriangular ears; lateral profile almost semicircular; corpus shallow; ribbing weak on both valves, originating on corpus; rugae weak dorsally; spines rare, scattered on venter and rows separating ears from flanks; lateral ridges in both valves, dorsally extending as weak marginal ridges. Upper Carboniferous (upper Bashkirian-lower Moscovian): USA (southeastern Alaska) .--—Fig. 1751, 1a-f. \*C. borealis, Prince of Wales Island; a-d, holotype, ventral, anterior, posterior, and lateral views, USNM 498809, ×2; e-f, dorsal valve interior, ventral and posterior views, ×2 (Lazarev & Carter, 2000).

### Tribe PARAMARGINIFERINI Lazarev, 1990

Tethysiella Kotlyar, Zakharov, & Polubotko, 2004, p. 521 [\*Productus (Productus) urushtensis LICH-AREW, 1936, p. 36; OD]. Small, transverse shells with prominent ears and well-developed trails that may be nasute, separated from the corpus by a cincture; ribbing is strong and rugae confined posterolaterally; spines appear to be in rows between ears and flanks plus some anterolaterally on ventral valve close to cincture. [A reason given for creating this genus was the near absence of spines, but the published photographs do not seem to support this. The genus was assigned to the Marginiferidae by its Russian authors (KOTLYAR, ZAKHAROV, & POLUBOTKO, 2004), but here it is thought to resemble Rugivestis (see BRUNTON & others, 2000, p. 431) belonging to the Paramarginiferini.] Upper Permian (Changhsingian): Russia (northwestern Caucasus mountains).-FIG. 1751,2a-e. \*T. urushtensis (LICHAREW), Urushten Formation; a, ventral valve exterior, ventral view,  $\times 2$ ; b, anterior view, ×1; c, incomplete ventral valve exterior, anterolateral view,  $\times 2$ ; *d*, ventral valve lateral view,  $\times 2$ ; e, dorsal valve exterior, ×2 (Kotlyar, Zakharov, & Polubotko, 2004).

### Subfamily OVERTONIINAE Muir-Wood & Cooper, 1960 Tribe AVONIINI Sarytcheva, 1960

Lazarevonia WATERHOUSE, 2001, p. 22 [\*Krotovia arcuata WATERHOUSE, 1978, p. 52; OD]. Small, somewhat resembling Quasiavonia in shape, having a moderately inflated umbo, but differing in its elongate and more frequent spine bases ventrally and small rounded bases with fine spines dorsally; weakly lamellose growth lines; lateral ridges may extend around visceral disc as slight shell thickening. Upper Permian (upper Capitanian-Changhsingian): Himalaya (western Nepal, Tibet).-FIG. 1752, 3a-f. \*L. arcuata (WATERHOUSE), West Dolpo, western Nepal; a, holotype, partially exfoliated ventral valve exterior, UQF 68815, ×2; b, partially exfoliated ventral valve exterior,  $\times 2$ ; c, mold of dorsal valve exterior,  $\times 2$ ; d, largely exfoliated dorsal valve exterior with remaining shell in areas of shell thickening, ×2 (Waterhouse, 1978); e, rubber replica of dorsal valve interior,  $\times 2$ ; *f*, internal mold of ventral valve, ×2 (Waterhouse, 2001).

#### Tribe COSTISPINIFERINI Muir-Wood & Cooper, 1960

- Callyconcha WATERHOUSE, 2001, p. 23 [\*Comuquia australis ARCHBOLD, 1984, p. 86; OD]. Resembles Comuquia in shape, but differs in having few strong ventral spines, mostly limited to flanks, and apparently no dorsal spines; lamellose growth lines present ventrally. Lower Permian (upper Sakmarian): Western Australia (Carnarvon Basin), ?southern Himalayas.—FIG. 1752, 1a-d. \*C. australis (ARCHBOLD), Callytharra Springs, Carnarvon Basin; a-c, holotype, ventral, dorsal, and posterior views, GSWA F11050, ×3.5; d, ventral valve exterior, ×3.2 (Archbold, 1984).
- **Dalinuria** L1 & GU, 1976, p. 245. Spelling correction for that listed in BRUNTON and others (2000, p. 434–435).

### Tribe KROTOVIINI Brunton, Lazarev, & Grant, 1995

Krotovia FREDERICKS, 1928, p. 779 [\*Productus spinosus J. SOWERBY, 1814 in 1812–1815, p. 155; OD] [=Guangia WATERHOUSE, 2002b, p. 46 (type, Krotovia inflata SHEN & others, 2000, p. 739, OD)] [Although it is tempting to reduce the stratigraphical range of Krotovia by the introduction of Guangia in the Upper Permian, justification based on morphological reasons has yet to be made. The original diagnosis of Guangia reads as



FIG. 1751. Productellidae (p. 2639).

if for the type species of Krotovia, but for "dorsal spines few." (WATERHOUSE, 2002b, p. 46). SHEN and others (2000, p. 739) describe their K. inflata as having numerous small dorsal spines, however, and their illustration supports this. The degree to which spine bases are swollen may increase in Permian species, but this small difference does not warrant a new genus. Guangia is a junior subjective synonym of Krotovia with description as in BRUNTON and others, 2000, p. 438.] Lower Carboniferous-Upper Permian: Eurasia, northern Africa.--FIG. 1752,2a-b. K. inflata (SHEN & others), Lopingian, southern Tibet; a, holotype, incomplete ventral valve exterior, NMVP148883, ×1.5; b, dorsal valve external mold, ×1.5 (Shen & others, 2000).

2640

#### Tribe LETHAMIINI Waterhouse, 2001

[Lethamiini WATERHOUSE, 2001, p. 17] [type genus, *Lethamia* WATER-HOUSE, 1973, p. 38]

Overtoniinae with shallow corpus cavity, fine dorsal and ventral spines, and weak concentric ornamentation. Upper Carboniferous (Kasimovian)–Lower Permian (Artinskian), ?Upper Permian (Changhsingian).

Lethamia WATERHOUSE, 1973, p. 38 [\*L. ligurritus; OD]. Resembles Stictozoster but larger with less distinctive spine bands; dorsal adult internal morphology more clearly defined, with median septum more prominent anteriorly and well-differentiated ears. [WATERHOUSE (2001) erected the tribe Lethamiini for this genus, which was not illustrated in BRUNTON and others (2000,

p. 436). Other genera probably within this tribe would be Amosia, Archboldina, Dyschrestia, Stictozoster, Tuberculatella, Tubersulculus, and Wooramella. Rugoclostus, mentioned by WATERHOUSE (2001) as possibly related, is felt to be distinctive because of its rugae, corpus depth, and strong hinge spines.] Lower Permian (Sakmarian)-Upper Permian (Changhsingian): New Zealand, eastern and Western Australia.-FIG. 1753, 1a-e. \*L. ligurritus, holotype, Roadian, mid-Permian, South Island, New Zealand, BR 957; a, internal mold, dorsal view; b, external mold of dorsal valve and ventral umbo; c, rubber replica of b; d, rubber replica of ventral valve exterior, ×1.5; e, rubber replica of posteromedian part of dorsal interior, ×1.5 (Waterhouse, 1982).

Amosia SIMANAUSKAS, 1996, p. 378 [\*A. sueroi; OD; =Productella aff. bifaria (STAINBROCK in AMOS, 1961, p. 91; 1979, p. 75)]. Small- to medium-sized concavoconvex shells with shallow corpus cavity, outline semicircular, and somewhat resembling Dyschrestia; ornament weakly lamellose, no ribbing; spines fine, but more robust at ears, close to hinge line, and anteriorly, dorsal spines sparse and fine; cardinal process sessile, quadrifid to trifid, not supported by short, narrow median septum, lateral ridges short; interiors endospinose. [SIMANAUSKAS (1996) placed his genus in the Overtoniidae and Overtoniinae of MUIR-WOOD and COOPER, 1960. The family Overtoniidae was not used in BRUNTON and others (2000), and the genus is here placed in the tribe Lethamiini.] Lower Permian (Sakmarian): Argentina (Tepuel-Genoa Basin, Chubut Province).-FIG. 1753,2a-f. \*A. sueroi, Chubut Province; a, ventral valve, anteroventral view,  $\times 2$ ; b, ventral valve viewed laterally,  $\times 2$ ; c,



FIG. 1752. Productellidae (p. 2639-2640).

incomplete ventral valve viewed obliquely showing spines,  $\times 2$ ; *d*, holotype, replica of incomplete dorsal valve interior, MLP 26003a,  $\times 3$ ; *e*, shell, dorsal view,  $\times 2$ ; *f*, replica from internal mold showing ventral interior,  $\times 2$  (Simanauskas, 1996).

- Archboldina WATERHOUSE, 2001, p. 22 [\*Pustula micracantha HOSKING, 1933, p. 49; OD]. Small, evenly spinose, concavoconvex shells resembling Wooramella, but with weakly rugose ears that lack spines, more strongly defined concentric ornament dorsally and somewhat swollen spine bases ventrally; dorsal interiors with anteriorly weak subperipheral rim and anteriorly elevated adductor muscle scars. [WATERHOUSE's (2001) suggestion that this genus might belong in his new tribe Lethamiini, is accepted here]. Lower Permian (upper Sakmarian): Western Australia.——FIG. 1754, 1a-f. \*A. micracantha (HOSKING), Callytharra Formation, Carnarvon Basin; a-b, lectotype, crushed dorsal valve, dorsal and ventral views, GSWA 1/4970b, ×2; c, crushed ventral valve exterior, ×1.8; d, dorsal valve exterior, ×1.6; e, interior showing subperipheral rim, prominent muscle scars, and brachial impressions,  $\times 1.8$ ; f, posterodorsal view showing cardinal process and high lateral ridges, ×2.2 (Archbold, 1984).
- **Tuberculatella** WATERHOUSE, 1982, p. 42 [\**T. tubertella*; OD]. Similar to *Lethamia*, but with pustulose ventral spine bases, a weak ventral median

sulcus, and narrow dorsal medium septum. [This genus was inadvertently omitted from BRUNTON and others (2000). The holotype is housed at Geological Survey of Thailand, Bangkok.] Upper Carboniferous (Kasimovian–Gzhelian): eastern Europe, Asia. ——FIG. 1754,3a–e. \*T. tubertella, Huai Bun Nak, Thailand; a–b, holotype, internal mold viewed ventrally and dorsally, TBR 579, ×2; c, dorsal valve external mold, ×2; d, latex replica of ventral valve exterior with swollen spine bases, ×2; e, ventral valve internal mold, posterior view showing muscle fields and median sulcus, ×2 (Waterhouse, 1982).

Wooramella Archbold in Hogeboom & Archbold, 1999, p. 260 [\*Pustula senticosta Hosking, 1933, p. 47; OD]. Medium sized, outline subrounded, concavoconvex profile, and shallow corpus cavity; spines on both valves arranged in concentric bands but absent from hinge lines; internal features poorly known, but cardinal process said to be bilobed and low, with short thin medium septum. [ARCHBOLD (in HOGEBOOM & ARCHBOLD, 1999) placed this genus in the Tubersulculinae BAMBER & WATER-HOUSE, 1971, but BRUNTON and others (2000, p. 434) placed it into the tribe Costispiniferini MUIR-WOOD & COOPER, 1960. If genera with relatively shallow corpus cavities were removed from the costispiniferins then Wooramella joins similar genera, such as Archboldina, Dyschrestia, Lethamia,



FIG. 1753. Productellidae (p. 2640-2641).

and Stictozoster, in the Lethamiini.] Lower Permian (upper Sakmarian): Western Australia.-—Fig. 1754,2a-g. \*W. senticosa (HOSKING), Callytharra Formation, Carnarvon Basin; a-c, lectotype, ventral, dorsal, and posterior views, GSWAFI/4970a1, ×1.8; d, crushed shell with ventral valve umbo missing and showing the dorsal cardinal process and medium septum, ×2 (Archbold, 1984); e-g, partially crushed shell, dorsal, ventral, and anterior views, ×1.5 (Archbold, 1999).

### Subfamily MARGINIFERINAE Stehli, 1954 Tribe PAUCISPINIFERINI Muir-Wood & Cooper, 1960

Jinomarginifera SHEN, SHI, & ARCHBOLD, 2003b, p. 231 [\*J. lhazeensis; OD]. Medium-sized marginiferine with deep corpus cavity, resembling Rectimarginifera, but with less coarse costae, weaker



FIG. 1754. Productellidae (p. 2641–2642).



FIG. 1755. Productellidae (p. 2642-2644).

median reticulation, and thin ventral spines on flanks, disc, and ears, lacking six major halteroid spines and with no dorsal internal anterior subperipheral ridge. *upper Upper Permian (upper Capitanian):* southern and western China, including southern Tibet.——FIG. 1755*a-e. \*J. lhazeensis; a-c*, holotype, posteroventrally exfoliated shell, ventral, anteroventral, and lateral views, NMV P308105, ×1.5; *d*, ventral valve exterior, ventral view, ×1.5; *e*, external mold of dorsal valve with fragment of ventral umbo in place, ×1.5 (Shen, Shi, & Archbold, 2003b).

### Subfamily PLICATIFERINAE Muir-Wood & Cooper, 1960 Tribe PLICATIFERINI Muir-Wood & Cooper, 1960

Labaella Kotlyar, Zakharov, & Polubotko, 2004, p. 517 [\*Productus (Productus) bajarunassi Licharew, 1937, p. 47 [111]; OD]. Medium to large Plicatiferini with widely extended ears; fine ribbing and delicate rugation forming reticulation over corpus with ribbing continued on trails; spine row at low angle from hinge line and grouped on anteroventral ear surface, rare elsewhere; dorsal interior resembles that of Plicatifera. [This genus somewhat resembles Lazarevia CARTER & POLETAEV, 1998, from the early Upper Carboniferous but differs in being smaller, with more prominent ears, and it has a clear median ventral sulcation. The authors placed the new genus in a new family, but this is unnecessary.] Upper Permian (upper Changhsingian): Russia (northwestern Caucasus mountains).-—Fig. 1756a-f. \*L. bajarunassi (LICHAREW), Nikitin Formation, Nikitin Ravine; a-c, anterior view, ventral view, and with corpus removed showing exfoliated dorsal valve exterior (the broken anterior edge shows as a crack line on a),  $\times 1$ ; d, internal mold of dorsal valve,  $\times 1$ ; *e*-*f*, shell viewed ventrally showing spine bases close to hinge line and on ears and anteriorly with anterior part of corpus and ventral trail missing, ×1 (Kotlyar, Zakharev, & Polubotko, 2004).

Lazarevia CARTER & POLETAEV, 1998, p. 125 [\*L. stepanowensis; OD]. Resembling Plicatifera in shape, but with more numerous, weaker, and less regular rugae on corpus; ribbing covering corpus and trails; spines fine, scattered sparsely over ventral valve, plus some near hinge line and row separating ears from flanks; corpus cavity shallow; ventral interior with variably developed submarginal rim. lower Upper Carboniferous (upper Bashkirian–lower Moscovian): Canadian Archipelago (Ellesmere Island).—FIG. 1757a–f. \*L. stepanowensis, Hare Fiord Formation; a–e, holotype, ventral, dorsal, anterior, posterior, and lateral views, GSC 115552, ×1; f. natural mold of ventral valve interior, ×1 (Carter & Poletaev, 1998).

### Family PRODUCTIDAE Gray, 1840 Subfamily PRODUCTINAE Gray, 1840 Tribe RETARIINI Muir-Wood & Cooper, 1960

Pitakpaivania WATERHOUSE, 2004, p. 69 [\*Kutorginella aprica GRANT, 1976, p. 143; OD]. Retariin lacking strong ventral sulcus, with weak reticulation on corpus only, but ribs becoming strong on trail; spines fine at hinge and on both corpus surfaces, strong halteroid on flanks and trail medianly, plus a pair anterodorsally; ventral interior with weak lateral ridges continuing across ears; dorsal interior with trifid cardinal process and lateral ridges continuing as weak submarginal ridges laterally. [Differentiation of this genus is not entirely clear, and in several characters it resembles Retaria MUIR-WOOD & COOPER, 1960 more closely than Kutorginella IVANOVA, 1951. The former typically comes from late Lower to early Upper Permian, while the latter is of late Upper Carboniferous age. GRANT (1976) commented on the similarity of his species to Retaria from Texas and further study may indicate that Retaria and Kutorginella are valid genera, with



FIG. 1756. Productellidae (p. 2644).



FIG. 1757. Productellidae (p. 2644).

*Pitakpaivania* being closely related to *Retaria*, or its junior synonym.] *Upper Permian (Guadalupian):* southern Thailand (Rat Buri Formation).——FIG. 1758, *Ia–g.* \**P. aprica* (GRANT), Ko Muk, Thailand peninsula; *a–d*, holotype, dorsal view of incomplete shell, lateral view, ventral view, and anterior view, USNM 212481, ×1.5; *e*, oblique dorsolateral view of shell showing a moderately deep corpus cavity, ×1; *f*, lateral view showing thick spines on flank and trail, ×1.5; *g*, incomplete ventral valve interior, ×1.5 (Grant, 1976).

### Subfamily DICTYOCLOSTINAE Stehli, 1954 Tribe DICTYOCLOSTINI Stehli, 1954

[nom. transl. BRUNTON, herein, ex Dictyoclostinae STEHLI, 1954, p. 316] [type genus, Dictyoclostus MUIR-WOOD, 1930, p. 103]

Medium to large; trails long, simple; ribbing complete with reticulation posteriorly; ventral spines commonly stout halteroid, dorsal spines absent; dorsal adductor scars positioned close to hinge line; marginal structures absent or weak. [The genera in this tribe are as in the Dictyoclostinae (BRUNTON & others, 2000, p. 488–496) other than for those in the Liraplectini, e.g., *Liraplecta* and *Tarimoplecta*.] *Lower Carboniferous (Viséan)–Upper Permian (Tatarian).* 

Callytharrella Archbold, 1985, p. 19 [\*Dictyoclostus callytharrensis PRENDERGAST, 1943, p. 13; OD]. [Since the publication of BRUNTON and others (2000, p. 489), ARCHBOLD has described (in HOGE-BOOM & ARCHBOLD, 1999) new topotypic material in which he demonstrated the presence of a curved row of spines on each flank, just anteroventral to the large reflexed ears, in addition to the large spines that grew near the posterior margins of the weakly rugose ears (BRUNTON & others, 2000, fig. 333,2a).] Lower Permian (Sakmarian): Western Australia, Himalayas.-FIG. 1758,3. \*C. callytharrensis (PRENDERGAST), Callytharra Formation, Carnarvon Basin, Western Australia; detail of ear and flank showing positions of spines on and close to ear, ×2 (Hogeboom & Archbold, 1999).

#### Tribe LIRAPLECTINI Chen & Shi, 2000

[Liraplectini CHEN & SHI, 2000, p. 329] [type genus, *Liraplecta* JIN & SUN, 1981, p. 137]

Dictyoclostinae with ribbed plus finely capillate dorsal valves. [The new tribe includes *Liraplecta* JIN & SUN, 1981, and *Tarimoplecta* CHEN & SHI, 2000; see below]. *Lower Permian* (Sakmarian–Kungurian).

Tarimoplecta CHEN & SHI, 2000, p. 336 [\* T. tarimensis; OD]. Medium-sized Liraplectini with planoconvex deep corpus cavity and long trail; ventral ribbing increasingly coarse anteriorly; rugae not extending onto venter; spines strong on ears and trail, sparse and finer on ventral corpus; cardinal process weakly trifid, supported by strong but short lateral ridges, and narrow median septum reaching anterior border of corpus. Lower Permian (Artinskian): northwestern China (Tarim Basin). -FIG. 1758,2a-d. \*T. tarimensis, Keziliqiman Formation, southern Xinjiang; a, holotype, ventral valve in anteroventral view, NMV P303392, ×1; b, ventral valve viewed ventrolaterally with dorsal valve internal mold viewed anteriorly to left, ×1; c, dorsal valve interior, ×1; d, incomplete ventral valve internal mold, ×1 (Chen & Shi, 2000).

### Subfamily YAKOVLEVIINAE Waterhouse, 1975

[Yakovleviinae WATERHOUSE, 1975, p. 11]

Productidae commonly with external reticulation on discs; spines widely scattered on ventral valve only; corpus cavity moderate



FIG. 1758. Productidae (p. 2644-2646).

to deep; lacking shagreen centrally in ventral umbo; commonly lacking dorsal internal marginal structures. [Following the joint revision of the Productellinae with BRUNTON in 1997 (in Brunton & Lazarev, 1997), LAZAREV has continued his revision of parts of the Productidae. Within this family LAZAREV (2000a and 2000b) has elevated the tribe Yakovleviini of BRUNTON and others (2000, p. 464) to a subfamily, removing it from the Productellidae where its position was somewhat insecure. The new subfamily contains four tribes, Yakovleviini WATERHOUSE, 1975, Latispiniferini LAZAREV, 2000b, Reticulatiini LAZAREV, 2000a, and Rigrantiini LAZAREV, 2000b. In addition, within these tribes, LAZAREV (2000b) described four new genera, which are presented below. LAZAREV based his revision largely on the distribution of a texture on the internal surfaces of the valves, especially in the ventral umbonal region; a texture of fine tubercles and pits that he called shagreen and interpreted as representing areas of mantle cavity.

The descriptions below are based on those by LAZAREV (2000a, 2000b, and 2000c) in translated versions of the Paleontological Journal, volume 34, numbers 4–6. Pages in square brackets indicate translations.] *Lower Carboniferous (upper Viséan)–Upper Permian (Kazanian).* 

### Tribe YAKOVLEVIINI Waterhouse, 1975

Ventral disc flattened and reticulate ornament commonly weak; spines few, thick, and placed symmetrically; corpus cavity may be only moderately deep. *Lower Carboniferous* (upper Viséan)–Upper Permian (Kazanian).

#### Tribe LATISPINIFERINI Lazarev, 2000

[Latispiniferini LAZAREV, 2000b, p. 26 [496]] [type genus, *Latispinifera* LAZAREV, 2000b, p. 27 [496]]

Discs strongly reticulate; spines in row around base of flanks, not arising from a ridge, becoming strong anterolaterally and of similar size to those anteriorly on ventral trail; dorsal disc with dimples representing positions of ventral spine bases. *Lower Carboniferous (upper Viséan)–Upper Permian (Kazanian).* 

In addition to the type genus, LAZAREV assigned *Sterochia* GRANT, 1976, and *Callytharrella* ARCHBOLD, 1985 (Dictyoclostinae of BRUNTON & others, 2000, p. 496 and p. 489 respectively) and *Costiferina* MUIR-WOOD & COOPER, 1960 (Paucispiniferini of the Productellidae of BRUNTON & others, 2000, p. 444) to the Latispiniferini. *Callytharrella* is here retained in the Dictyoclostinae.

Latispinifera LAZAREV, 2000b, p. 27 [496] [\*L. chaykensis; OD; =Reticulatia huecoensis SARYTCHEVA, 1977, p. 94, non KING, 1931, p. 68]. Valves thin shelled; in profile, border between corpus and trails indistinct; ribs on trail not coarse, six or more in 10 mm width; spines with thickest rows on flanks. Carboniferous (Viséan–Moscovian): Russia (Cape Chayka), northwestern Spain.—FIG. 1759a–e. \*L. chaykensis; a–b, holotype, ventral valve, anterior and posterior views, Moscovian, Cape Chayka, PIN 2833/26, ×1; c, ventral valve exterior, ventral view, ×1; d, dorsal exterior, ×1; e, internal mold of dorsal valve, ×1 (Sarycheva, 1977).

#### Tribe RETICULATIINI Lazarev, 2000

[Reticulatiini LAZAREV, 2000a, p. 40 [400]] [type genus, *Reticulatia* MUIR-WOOD & COOPER, 1960, p. 284]

Yakovleviinae of medium to large size and deep corpus cavity; both discs reticulate; ventral spines thick, halteroid, and numerous. [LAZAREV erected this tribe based on *Reticulatia* MUIR-WOOD & COOPER, 1960, which was assigned to the Dictyoclostinae of BRUNTON & others (2000, p. 496). LAZAREV's (2000a) action restricts *Reticulatia* to the Lower Permian of North America, while other Carboniferous species are assigned by LAZAREV (2000b) to his new genus Admoskovia.] Upper Carboniferous (Bashkirian)–Lower Permian (Artinskian).

Admoskovia LAZAREV, 2000b, p. 28 [499] [\*Dictyoclostus inflatiformis IVANOV, 1935, p. 64 [110]; OD]. Ears strongly defined, forming widest part of shell; reticulation on discs relatively weak; ribbing entire and may form weak plications on trail; spines on ears strongly developed, smaller spines in rows on flanks and scattered on venter; cardinal process



FIG. 1759. Productidae (p. 2648).

low, supported by strong lateral ridges extending to border of corpus posteriorly; median septum short. *Upper Carboniferous (Bashkirian–Kasimovian):* Eurasia and mid-Asia.——FIG. 1760*a–c. \*A. inflatiformis* (IVANOV), Kasimovian, River Medvedka of the Moscow river, Neverov Formation; *a*, ventral valve exterior showing ear spines, ×1; *b*, somewhat crushed ventral valve exterior showing hinge, ear, and flank spines, ×1; c, shell viewed ventrally with part of ventral valve missing to show dorsal interior, ×1 (Lazarev, 2000c).——FIG. 1760d. A. *ivanovorum* LAZAREV; incomplete dorsal valve inter ior, ×1 (Lazarev, 2000c).——FIG. 1760e. A. sp.; incomplete ventral valve interior, ×3 (new).



FIG. 1760. Productidae (p. 2648-2649).

#### Tribe RIGRANTIINI Lazarev, 2000

[Rigrantiini LAZAREV, 2000b, p. 28 [497]] [type genus, *Rigrantia* LAZAREV, 2000b, p. 28 [499]]

Reticulate ornament variably developed; spines at base of flanks thick and arising from prominent ridge; dorsal disc commonly dimpled; dorsal interior with narrow ridges separating ears. *?uppermost Lower Carboniferous, Upper Carboniferous (Serpukhovian)– Lower Permian (Artinskian).* 

- Bicarteria LAZAREV, 2000b, p. 28 [497] [\*Productus semireticulatus var. hermosanus GIRTY, 1903, p.

359; OD]. Spines at hinge thinner than larger (youngest) spines in rows at flanks; reticulate ornament commonly irregular and may not reach margin of venter; cardinal ridge weak, may diverge from hinge slightly. Upper Carboniferous (Serpukhovian–Kasimovian): North America, ?southeastern Urals.——Fig. 1761, 2a-f. \*B. hermosana (GIRTY), Bashkirian, Colorado, USA; a-c, ventral valve, ventral valve, ventral and lateral views,  $\times 1$ ; f, dorsal valve, lateral view,  $\times 1$  (Girty, 1903).

Superfamily ECHINOCONCHOIDEA Stehli, 1954 Family ECHINOCONCHIDAE Stehli, 1954 Subfamily JURESANIINAE Muir-Wood & Cooper, 1960 Tribe WAAGENOCONCHINI Muir-Wood & Cooper, 1960

**Contraspina** WATERHOUSE, 2002b, p. 46 [\**Productus purdoni* DAVIDSON, 1862, p. 31; OD]. Resembling *Waagenoconcha* (*Gruntoconcha*) but having more elongate outline and spine bases closely



FIG. 1761. Productidae (p. 2650).

spaced and fine posteriorly, becoming somewhat coarser anteriorly; well-developed median fold and sulcus from umbo to anterior margins; interiors unknown. *Upper Permian (Capitanian):* Pakistan (Salt Range).——FIG. 1762,2*a*–*f.* \**C. purdoni* (DAVIDSON); *a*–*c*, holotype, ventral, lateral, and dorsal views, BMNH B82367, ×1; *d*–*f*, juvenile specimen, ventral, lateral, and dorsal views, ×1 (new).

Fostericoncha WATERHOUSE, 2002b, p. 48 [\* Waagenoconcha? gigantea WATERHOUSE, 1983, p. 125; OD]. Large to gigantic transverse waagenoconchin with wide ears; ventral umbo low; sulcus and dorsal fold originating near umbos; spines fine on both valves, but thicker and lacking fine elongate bases toward ventral hinge and ears, dorsal spines from rounded pustules. [Preservation and quantity of available specimens are poor, so aspects of morphology remain unknown. In 1983 WATERHOUSE appeared to think his new species, ? W. gigantea, belonged to his new genus Wimanoconcha, placed in BRUNTON and others (2000, p. 516) within Waagenoconcha.] Upper Permian (upper Capitanian): Nepal. FIG. 1762, 1a-c. \*F. gigantea (WATERHOUSE), Pija Member, Manang; a-b, holotype, part of ventral valve external mold and its rubber replica, UQF73619, ×1; c, part of ventral valve internal mold, and at the margin, external mold, ×1 (Waterhouse, 1983).

### Superfamily LINOPRODUCTOIDEA Stehli, 1954 Family LINOPRODUCTIDAE Stehli, 1954 Subfamily LINOPRODUCTINAE Stehli, 1954

- Aurilinoproductus SHEN, SHI, & ARCHBOLD, 2003a, p. 79 [\*A. alatus; OD]. Median to large Linoproductinae with large triangular alae extending up to 20 mm beyond corpus width; spines not observed at hinge line, but on ears and common on venter with elongate spine bases. Upper Permian (Changhsingian): China (southern Tibet).——FIG. 1763,2a-e. \*A. alatus, Qubuerga Formation; a-d, holotype, viewed anteriorly, posteriorly, laterally, and ventrally, NMV P305973, ×1; e, incomplete ventral valve exterior, ×1 (Shen, Shi, & Archbold, 2003a).
- Cimmeriella ARCHBOLD & HOGEBOOM, 2000, p. 101 [\*Productus foordi ETHERIDGE, 1903, p. 19; OD]. Small to medium Linoproductinae with globose corpus shape and long trails; ventral profile strongly convex with weakly concave, geniculate dorsal valve; ribbing well defined, entire; rugae weak, on flanks only; spines confined to single rows close to hinge line, enlarging laterally; low cardinal process supported by short, wide medium septum and paired ridges partially enclosing adductor scars

posteriorly. Lower Permian (upper Sakmarian): Western Australia, Timor, Malaysia, Yunnan, Tibet, and Karakorum.——FIG. 1763, *Ia–f.* \**C. foordi* (ETHERIDGE), Callytharra Formation, Carnarvon Basin; *a–b*, ventral valve in ventral and posterior views, ×1; *c*, almost complete ventral valve in lateral view, ×1; *d*, ventral valve interior, ×1; *e–f*, incomplete dorsal valve viewed externally and internally, ×1.2 (Archbold, 1983).

### Subfamily ANIDANTHINAE Waterhouse, 1968

Anidanthus HILL, 1950, p. 9 [\*Linoproductus springsurensis BOOKER, 1932, p. 67; OD] [=Anidanthus WHITEHOUSE, 1928, p. 282, nom. nud.; ?Pseudomarginifera STEPANOV, 1934, p. 56 (type, Productus ussuricus FREDERICKS, 1924b, p. 8); Protoanidanthus WATERHOUSE, 1986, p. 60 (type, P. compactus; OD)]. [Protoanidanthus should have been included as a junior synonym of Anidanthus HILL, 1950 in the revised Treatise (BRUNTON & others, 2000, p. 531). WATERHOUSE (1986) diagnosed his genus as having smaller ears than Anidanthus. We believe this to be an intrageneric character. Protoanidanthus was described from the Lower Permian (Artinskian) of Australia (Queensland). The description of the genus Anidanthus in BRUNTON and others (2000, p. 531) remains unchanged, as do the entries for stratigraphy, distribution, and illustrations. This is only a note of emendation correcting an omission from the 2000 description of the genus Anidanthus.]

### Subfamily PAUCISPINAURIINAE Waterhouse, 1986

[Paucispinauriinae WATERHOUSE in WATERHOUSE & BRIGGS, 1986, p. 2]

Linoproductids with varied fine or strong spines commonly on both valves; those ventrally may have elongate spine bases. Lacking marginal structures or trails.

The subfamily name Grandaurispininae LAZAREV, 1986, used in the *Treatise* (BRUNTON & others, 2000, p. 533) has proved a junior synonym for Paucispinauriinae WATER-HOUSE in WATERHOUSE & BRIGGS, 1986. Some genera within the Grandaurispininae (BRUNTON & others, 2000) such as *Lyonia* have shallow corpus cavities and belong within the Auriculispininae below. *?Lower Permian, Upper Permian.* 

Pinegeria WATERHOUSE, 2001, p. 49 [\* Terrakea? pinegensis GRIGORIEVA in SARYTCHEVA, 1977, p. 144; OD]. Subcircular outline with relatively narrow hinge line and virtually no ears; semioval lateral profile with geniculate dorsal valve; prominent costellation and weak rugae dorsally; ventral



FIG. 1762. Echinoconchidae (p. 2650-2652).



FIG. 1763. Linoproductidae (p. 2652).

spines fine posteriorly, larger posterolaterally, laterally, and on trail, fine and erect on dorsal valve; cardinal process squat, trifid to quadrifid. [This species is readily distinguishable from the others described by GRIGORIEVA in 1977 as being a possible Russian *Terrakea* species.] *Upper Permian (Kazanian):* northern and western Russia.——FIG. 1764,2*a*–*e.* \**P. pinegensis* (GRIGORIEVA); *a*–*c.* holotype, shell viewed ventrally, dorsally, and laterally, PIN 1120/771, ×1; *d.*, detail of cardinal process viewed posteriorly, ×6; *e*, dorsal valve interior, ×1 (Sarytcheva, 1977).

Spargospinosa WATERHOUSE, 2001, p. 41 [\*Terrakea belokhini GANELIN in SARYTCHEVA, 1977, p. 141; OD]. Resembles Terrakea but said to be less strongly spinose at ventral hinge line; corpus quite deep and trail present; ventral spines erect, sparse at hinge and ears, scattered over corpus and trail, some may have swollen spine bases; ventral interior resembling Terrakea. [It appears that species attributed to Terrakea in the past and now divided into separate genera, whether from Australia or Russia, display continuous variation in their morphology (BRIGGS, 1998). A meaningful differentiation of nominal genera in this group is questionable, other than for the new genus Pinegeria.] Upper Permian (Wordian-Capitanian): Russian arctic (Siberia).-—Fig. 1764, 1a-f. \*S. belokhini (GANELIN); a-c, holotype, viewed anteroventrally with part of ventral trail missing, laterally and posteriorly showing part of ventral valve internal mold, PIN 28834/349,  $\times$ 1; *d*, another posterior view of partially exposed ventral internal mold and part of spinose hinge line on right, ×1; e-f, ventral valve exterior viewed ventrally and anteriorly, showing larger spine bases on trail, ×1 (Sarytcheva, 1977).



FIG. 1764. Linoproductidae (p. 2652-2654).

### Family MONTICULIFERIDAE Muir-Wood & Cooper, 1960 Subfamily AURICULISPININAE Waterhouse, 1986

Small- to medium-sized monticuliferids with transverse to elongate outlines, spines on ventral valve, but lacking or rare on dorsal valves; spine bases ventrally commonly elongate. Lower Carboniferous (Tournaisian)– Upper Permian (Changhsingian).

### Tribe AURICULISPININI Waterhouse, 1986

[nom. transl. WATERHOUSE, 2001, p. 30, ex Auriculispininae WATER-HOUSE in WATERHOUSE & BRIGGS, 1986, p. 57]

Auriculispinines with transverse outline viewed ventrally, but those with long trails became elongate in outline; spines may form clusters posteriorly and on ears. [Acceptance of the Lyoniini necessitates the use of the Auriculispinini for other genera in the subfamily. This is not the place to research the full redistribution of genera in this and other subfamilies, as does WATERHOUSE (2002b) with his five new tribes in this subfamily.] Lower Carboniferous (upper Tournaisian)–Upper Permian (Capitanian).

- Bocharella GANELIN & LAZAREV, 2000, p. 39 [41] [\*B. zyrjankensis; OD]. Small to medium sized with weakly concavoconvex corpus and geniculated trails of similar length; spines absent on ears, but short single rows at anterior margins of ears, elongate spine bases rare and mainly on trail; lateral ridges in both valves; cardinal process wide with paired supporting ridges from anterior ends of which a medium septum extends to three-quarters disc length. lower Upper Permian (Kazanian): northeastern Asia. FIG. 1765, 2a-d. \*B. zyrjankensis, Ufimian, lower Kazanian, Verkhnii Koargychan River; a, holotype, ventral valve viewed ventrally, PIN 2834/1562, ×1; b, ventral valve viewed anteroventrally, ×1; c, ventral valve viewed laterally,  $\times 1$ ; d, dorsal valve external mold showing lines of dimples representing spine positions on ventral valve, ×1 (Ganelin & Lazarev, 2000).
- **Costatamulus** WATERHOUSE in WATERHOUSE & BRIGGS, 1986, p. 58 [\*Auriculispina tumidus WATERHOUSE, BRIGGS, & PARFREY, 1983, p. 133; OD] [=Auritusinia WATERHOUSE, 2002b, p. 52 (type, Costatamulus tazawai SHEN & others, 2000, p. 743)]. [The only points of differentiation given by WATERHOUSE (2002b) for separating C. tazawai

from Costatamulus are more strongly developed rugae and more strongly developed ears on the new genus. Comparisons of the original descriptions and illustrations by WATERHOUSE (1986) and SHEN and others (2000) show similar ears and only some difference in the development of rugae, which tends to be a variable character. The type species of Costatamulus is Lower Permian in age, and that of Auritusinia is upper Upper Permian. The type species, C. tumidus, was illustrated in the genus entry of the Treatise (BRUNTON & others, 2000, p. 538). Here a second species from younger strata is illustrated.] Lower Permian (Artinskian)–Upper Permian (Changshingian): Australia, Tibet, central Himalayas.——FIG. 1765, 1a-c. C. tazawai SHEN & others, Lopingian, southern Tibet; a, holotype, ventral valve exterior, NMV P148917, ×1.5; b, ventral valve exterior with elongate spine bases, ×1.5; c, external mold of a dorsal valve showing one ear, ×1.5 (Shen & others, 2000).

- Kolymaella Ganelin & Lazarev, 2000, p. 40 [43] [\*Cancrinella ogonerensis ZAVODOWSKY, 1960, p. 65; OD]. Medium-sized, very weakly concavoconvex shells with geniculations and short trails; spines in single rows crossing each ear, with elongate spine bases on venter and tending to become arranged concentrically on trail; dorsal lateral ridges diverging from hinge line (40° to 45°); paired supporting ridges extending anteriorly from cardinal process base, no medium septum. lower Upper Permian (lower Kazanian): northeastern and Central Asia. FIG. 1765, 4a-e. \*K. ogonerensis (ZAVODOWSKY), Ufimian, Munugudzhak River; a, group of ventral valve exteriors,  $\times 1$ ; b, ventral valve exterior showing fine ribbing and swollen spine bases, ×1; c, dorsal valve interior, ×1; d, incomplete dorsal valve interior showing paired supporting ridges, ×1; e, dorsal valve external mold with cardinal process remaining, ×1 (Ganelin & Lazarev, 2000).
- Striapustula GANELIN & LAZAREV, 1999, p. 33 [246] [\*Productus koninckianus Keyserling, 1846, p. 203; OD]. Small, thin-shelled, concavoconvex specimens with long trails; ribbing fine on both valves, spines only ventrally, at hinge line and ears, scattered with swollen elongate bases on corpus and trail; rugae only posterolaterally; cardinal process bilobed, sessile, with shallow cardinal pit between paired weak ridges, cardinal ridges diverging slightly from hinge line toward ears, do not reach lateral margin, median septum reaches 0.8 disc length. Lower Permian (Artinskian-Kungurian): northeastern Asia (Verkhoyansk region, Pechora Basin), Spitsbergen.—FIG. 1765, 3a-d. \*S. koninckianus (KEYSERLING); *a*, ventral valve exterior, ×1; *b*, ventral valve anterior view,  $\times 1$ ; *c*, lateral view of shell,  $\times 1$ ; d, partially exfoliated dorsal valve interior, ×2 (Ganelin & Lazarev, 1999).-FIG. 1765, 3e. S. pectiniformis GANELIN & LAZAREV, Vokuta river; cast of natural external mold of ventral valve, ×2 (Ganelin & Lazarev, 1999).-FIG. 1765,3f. S. spitsbergiana (GOBBETT), Spitsbergen; ventral valve viewed laterally, ×1 (Ganelin & Lazarev, 1999).

### Tribe LYONIINI Waterhouse, 2001

[Lyoniini WATERHOUSE, 2001, p. 32] [type genus, *Lyonia* ArcHbold, 1983, p. 244]

Auriculispinines with wide hinges and one or two rows of ventral hinge spines; ribbing weakly developed and body spines with elongate bases; cardinal process sessile with low myophores. [This tribe contains a recognizable group of genera including Lyonia and Bandoproductus, now known to have shallow corpus cavities, and they should be removed from the Lindproductidae (BRUNTON & others, 2000, p. 529 and p. 533) and included in this tribe in the Monticuliferidae. Other genera assigned here are Nambdoania, Nambucculinus, and probably Nisalaria (described below). WATERHOUSE (2001) is probably correct in also assigning Cancrinelloides to this tribe.] Upper Carboniferous (upper Gzhelian)–Upper Permian (Changhsingian).

- Nambuccalinus WATERHOUSE, 2001, p. 33 [\*Lyonia bourkei BRIGGS, 1998, p. 147; OD]. Medium sized, somewhat transverse outline and with shallow corpus cavity; similar to Lyonia; spines on both valves, ventrally scattered, subprostrate from short spine bases plus two or three rows of larger spines along hinge margins, dorsally finer spines cover all but ears; rugae weak; dorsal cardinal ridges weak and median septum narrow, short. [WATERHOUSE (2001) placed this genus in his new tribe Lyoniini for its wide costellate shells with a shallow corpus and one or two rows of erect ventral hinge spines. The distinction, however, between the new genus and Lyonia can be made by the single row of hinge spines, perhaps fewer dorsal spines, and presence of dorsal dimples in the latter. The evidence from BRIGGS (1998) suggests that the dorsal interior of N. bourkei is closely similar to that of Lyonia, so the validity of Nambuccalinus remains questionable.] Upper Carboniferous (?upper Gzhelian), Lower Permian (Asselian): eastern Australia.---FIG. 1766, 1a-d. \*N. bourkei (BRIGGS), Giro Group, Asselian, Sydney-Bowen Basin; a, holotype, dorsal external mold of complete shell, UQF75314, ×2; b, rubber replica of posterior region of ventral valve exterior,  $\times 2$ ; *c*, external mold of dorsal valve showing on valve exterior that dimples represented ventral hinge spine positions, ×2; d, rubber replica of dorsal valve interior, ×2 (Briggs, 1998).
- Nambdoania WATERHOUSE, 2002b, p. 52 [\**Cancrinella papilionata* WATERHOUSE, 1978, p. 109; OD]. Resembles *Lyonia*, but lacks dorsal spines, and single rows of ventral hinge spines are less prominent; cardinal process less flattened than in *Lyonia* and supported by a short median septum and



FIG. 1765. Monticuliferidae (p. 2655–2656).



FIG. 1766. Monticuliferidae (p. 2656–2659).

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FIG. 1767. Monticuliferidae (p. 2656-2660).

weak cardinal ridges. Upper Permian (Changhsingian): Nepal.——FIG. 1767,2*a*–*e*. \*N. papilionata (WATERHOUSE), Nambdo Member, Dolpo, western Nepal; *a*, holotype, dorsal valve external mold, UQF 69029, ×1; *b*, ventral valve exterior, ×2; *c*, ventral valve external mold, ×2; *d*, dorsal valve external mold, ×1.5; *e*, dorsal valve interior, ×1.5 (Waterhouse, 1978).

Nikitinia KOTLYAR, ZAKHAREV, & POLUBOTKO, 2004, p. 521 [\*N. licharewi; OD; =Productus (Productus) cancriniformis LICHAREW, 1937, p. 38 [105], non CHERNYSCHEW, 1889]. Small with subcircular outline, small ears; concavoconvex profile and shallow corpus cavity; rugae dominate fine ribbing, especially ventrally over corpus; elongate spine bases accentuate ribs from which they arose, spine row close to ventral hinge extending to ears. [The authors only describe spines as being near the hinge and on the ears, but their illustrations and those of LICHAREW (1937) appear to show well-developed spine bases on the ventral corpus, similar to those of several linoproductoids. Their assignment to the Linoproductidae is not in accord with the current *Treatise* classification (BRUNTON & others, 2000, p. 526) largely because of the shallow corpus cavity.] *Upper Permian (Changhsingian):* Russia (north-western Caucasus mountains).——FIG. 1766,2*a*-*c*. \**N. licharewi*, Lower Urushten Formation, Urushten River; *a*, holotype, ventral view, CRMGE 268/2139, ×2; *b*, lateral view, ×1; *c*, partial internal mold of dorsal valve showing impressions from ventral valve spine row near hinge, ×2 (Kotlyar, Zakharev, & Polubotko, 2004).

Nisalaria WATERHOUSE, 2002b, p. 51 [\* Cancrinelloides (Bandoproductus) inflata WATERHOUSE, 1983, p. 130; OD] [= Cancrinella sp. WATERHOUSE, 1978, p. 76]. Weakly concavoconvex with low ventral umbo; spines in single row at hinge, on umbo, and scattered on venter, arising anteriorly from elongate spine ridges more prominent than costellation; no dorsal spines. [The three descriptions of the type species by WATERHOUSE (1978, 1983, and 2002b) differ slightly in terms of profile and umbonal inflation, so the above is based, to some extent, on the cited figures of 1978. WATERHOUSE (2002b) placed his genus in the Auriculispinini, but a lack of spine clustering at the hinge or ears seems more appropriate to the Lyoniini. The reference to *Cancrinella* sp. WATERHOUSE, 1978, was to his use of the name (no species mentioned) in 1978 for some specimens from the same locality as the type of *Nisalaria* and which would seem to be conspecific, although not named in 1978. It is not considered to belong to *Cancrinella* as now defined.] *Upper Permian (Changhsingian):* Nepal.——FIG. 1767, *1a–c.* \**C. inflata* (WATERHOUSE), Nisal member, Dolpo, western Nepal; *a*, holotype, ventral valve exterior, UQF 68909, ×1; *b*, ventral valve exterior, x2; *c*, incomplete dorsal valve exterior plus part of ventral trail external mold, ×2 (Waterhouse, 1978).

### Subfamily COMPRESSOPRODUCTINAE Jin & Hu, 1978

Regrantia WATERHOUSE, 2001, p. 28 [\*Striatifera linoproductiformis COOPER & GRANT, 1975, p. 1210; OD]. Moderately sized compressoproductines with variably narrow hinge resulting from attachment to hard substrates; lateral profile modest at ventral umbo, relatively flat corpus with weakly geniculate trail, dorsal valve concave and shallow corpus cavity; rugae irregular; posterolateral rhizoid spines with few scattered spines on ventral corpus; cardinal process weakly bilobed, from just posterior of hinge line, extending anteroventrally so as to lie ventrally on long narrow median septum. [The complete reclassification of the Linoproductoidea presented by WATERHOUSE (2001, p. 24) is based on keeping the superfamily "as a well-defined group, and separate from its ancestors," with the result that it differs from that adopted by BRUNTON and others (2000). WATERHOUSE placed his genus Regrantia in his tribe Compressoproductini, which was said to have a moderately high body corpus, and he described Regrantia as having a deep body corpus. However, inspection of the lavish original illustrations and full description (with measurements) of the type species by COOPER and GRANT (1975) shows it to have a shallow corpus depth, enabling it to fit well into the BRUNTON & others (2000) classification.] Lower Permian (Asselian): USA (Texas).-FIG. 1768, 1a-g. \*R. linoproductiformis (COOPER & GRANT), Neal Ranch Formation, Glass Mountains; a-c, holotype, viewed laterally, ventrally, and dorsally, USNM 153972b, ×1; d, posteroventral view of attached specimen showing rhizoid spines, ×2; e, posterior end of shell in dorsal view,  $\times 3$ ; f-g, dorsal valve interior and in lateral view showing disposition of cardinal process, ×2 (Cooper & Grant, 1975).

### Subfamily STRIATIFERINAE Muir-Wood & Cooper, 1960

[Striatiferinae MUIR-WOOD & COOPER, 1960, p. 328]

Shell large to medium; outline elongate or with tubiform trail, hinge narrow; spines commonly on ventral valve only.

### Tribe STRIATIFERINI Muir-Wood & Cooper, 1960

[nom. transl. Brunton, Lazarev, & Grant, 1995, p. 930, ex Striatiferinae Muir-Wood & Cooper, 1960, p. 328]

Large, with very shallow corpus; trails simple; spines fine, rarely also on dorsal valve; cardinal process of single ridge continuous with median septum.

Striatiferella LEGRAND-BLAIN in LEGRAND-BLAIN, DELVOLVÉ, & HANSOTTE, 1996, p. 195 [\*S. arizensis; OD]. Medium-sized, weakly concavoconvex shells with hinge line up to one-third maximum width and resembling Striatifera other than in its fine dorsal spines at ears and trail. Lower Carboniferous (upper Viséan-lower Serpukhovian): France (Pyrenees).—FIG. 1768,2a-e. \*S. arizensis; a-c, holotype, dorsal valve external mold, internal replica, MH5a1, ×1, and detail of external ornament at margin showing molds of spine bases, ×2; d-e, ventral valve external replica and internal mold, ×1 (Legrand-Blain, Delvolvé, & Hansotte, 1996).

#### Subfamily SCHRENKIELLINAE Lazarev, 1990

[Schrenkiellinae LAZAREV, 1990, p. 122]

LAZAREV (2004) argues for the elevation of this subfamily to full family status containing the Schrenkiellinae and his new subfamily the Coopericinae. Thus the Schrenkiellidae comes alongside the Linoproductidae and Monticuliferidae. An appraisal of this new classification is beyond the scope herein so the three new genera are here simply included within the Schrenkiellinae.

Coopericus Lazarev, 2004, p. 161 [\*Linoproductus angustus KING, 1931, p. 67; OD]. Schrenkiellin spine pattern of single hinge row of strong clasping spines with few or no other spines, together with an elongate outline; corpus convex, but with umbo and trails weakly convex in lateral profile; rugae prominent on ears and close to hinge line; cardinal process extending slightly posteriorly into small ventral umbo. [LAZAREV (2004) placed this genus in his new subfamily, the Coopericinae, separated from other schrenkiellids by its shell shape and stratigraphy.] Upper Carboniferous (Moscovian)-Lower Permian: Bone Spring Formation, North America (Texas), Russia (Moscow Basin).--Fig. 1769, 1a-h. \*L. angustus (KING), Skinner Ranch and Bone Spring Formations, Lower Permian, Glass Mountains, Texas; a-c, lectotype, ventral valve, ventral, lateral, and posterior views, YPM 11519a, ×1; d-e, ventral valve, lateral and posterior views, ×1; f-g, dorsal valve, external and internal views,  $\times 1$ ; h, posterior region of ventral valve with complete row of clasping spines viewed internally, ×1 (Cooper & Grant, 1975).



FIG. 1768. Monticuliferidae (p. 2660).

- Elalia LAZAREV, 2004, p. 159 [\**E. aljutovensis*; OD]. Size medium to large; ribs and interspaces approximately equal in width; rugae irregular, extending onto trail; spines in single row at hinge, relatively thick, with few or no other spines; cardinal process lobes medianly fused, and cardinal ridges weak. *Upper Carboniferous (Bashkirian–Gzhelian):* Russia, North America.—FIG. 1769,2*a–c.* \**E. aljutovensis*, early Moscovian, Moscow Basin, Russia; *a*, holotype, ventral valve viewed ventrally, PIN 3452/3161, ×1; *b*, dorsal valve exterior, ×1; *c*, dorsal valve interior, ×1 (Lazarev, 2004).—FIG. 1769,2*d. Elalia* sp.; ventral valve exterior, ×1 (Lazarev, 2004).
- Krekarpius Lazarev, 2004, p. 159 [\*Productus praelaevicostus Krestovnikov & Karpyshev, 1948,

p. 45; OD]. Medium sized with strongly convex ventral corpus profile, trail less convex; umbo projecting only weakly posterior to hinge line; rugae weakly developed, only at flanks; spines thin, most prominently in row close to hinge line, with thinner ones scattered on venter and flanks. Upper Devonian (upper Famennian)–Lower Carboniferous: Russia (southern Urals).—FIG. 1769, 3a-d. \*K. praelaevicostus (KRESTOVNIKOV & KARPYSHEV); *a-b*, ventral valve, ventral and posterior views, upper Famennian, southern Ural Mountains, ×1; c, ventral valve lateral view, upper Famennian, southern Ural Mountains, ×1 (Krestovnikov & Karpyshev, 1948); d, incomplete dorsal valve interior, Zelenetskii horizon, uppermost Famennian, Mid-Pechora region, Russia, ×1 (Lazarev, 2004).

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2662



FIG. 1769. Monticuliferidae (p. 2660-2661).

### Suborder STROPHALOSIIDINA Schuchert, 1913 Superfamily STROPHALOSIOIDEA Schuchert, 1913 Family STROPHALOSIIDAE Schuchert, 1913 Subfamily STROPHALOSIINAE Schuchert, 1913

- Biplatyconcha WATERHOUSE, 1983, p. 125, nom. nov. pro Platyconcha WATERHOUSE, 1975, p. 8, non LONGSTAFF, 1933, p. 41 (type, Platyconcha grandis WATERHOUSE, 1975, p. 8, OD)] [=Megalosia WATER-HOUSE, 1988, p. 44 (type, M. chuluensis, OD)]. Resembling Marginalosia, but large size and with no dorsal spines; narrow, but well-differentiated ventral interarea and strong teeth; dorsal valve thin shelled and elongate dimples representing ventral valve elongate spine bases; dorsal lateral ridges continue as subperipheral rim. [This genus was originally assigned to the Waagenoconchidae and in BRUNTON and others (2000, p. 516) to the Waagenoconchini. BRIGGS (1998) demonstrated that it is a strophalosiid, figuring the ventral interarea and teeth. It was BRIGGS who suggested that Megalosia was an objective synonym, and WATERHOUSE (2002b) acknowledges this. The same position was taken by SHEN, SHI, and ARCHBOLD (2003a), who figured examples of the type species from southern Tibet.] Upper Permian (Changhsingian): northwestern Nepal, southern Tibet.-FIG. 1770a-e. \*B. grandis (WATERHOUSE), Qubuerga Formation, north of Mount Qomolangma, Everest, southern Tibet; *a*, ventral valve exterior,  $\times 1$ ; *b*, dorsal valve exterior,  $\times 1$ ; c, ventral valve internal mold,  $\times 1$ ; d, dorsal valve internal mold, ×1 (Shen, Shi, & Archbold, 2003a); e, rubber cast of part of ventral valve showing teeth and interarea,  $\times 2$  (Briggs, 1998).
- Kufria WATERHOUSE, 2002b, p. 53 [\*Strophalosia blanfordi REED, 1944, p. 104; OD]. Medium sized, transversely subelliptical outline and low, convex ventral profile; dorsal disc flat with short trails; elongate ventral spine bases do not form strong ribs as in Licharewiella but are variable in length and strength, bearing fine spines anteriorly; interareas appear to be minute, but REED (1944) recorded an umbonal cicatrix. [Differentiation of this genus rests on its unusual external ornamentation of long, riblike spine bases, but REED's (1944) description and figures are of one specimen only. In 1944 REED attributed his previously described variety Productus (Waagenoconcha) abichi WAAGEN var. consors to his new species, but also, incorrectly, Strophalosia gerardi KING (1850, pl. 19,6–7), which illustrate the type specimen for the type species of Strophalosia, according to the ICZN (1962)]. Upper Permian (upper Capitanian): Pakistan (Salt Range).——FIG. 1771, 1a-b. \*K. blanfordi (REED), Chhidru Formation; holotype, by monotypy,

ventral and posterior views showing broken ventral umbo, GSI 16884, ×1.5 (Reed, 1944).——FIG. 1771,1*c*–*d. K. (Waagenoconcha) abichi* WAAGEN, var. *consors* (REED); internal cast of shell, ventral and posterior views with broken umbo exposing mold of cardinal process, ×1 (Reed, 1931).

Tupelosia ARCHBOLD & SIMANAUSKAS, 2001, p. 222 [\*T. paganzoensis; OD]. Circular to slightly elongate small shells with coarse, recumbent ventral spines, including a row close to hinge; cicatrix minute; teeth small; cardinal process squat, separated from short median septum by posteroventrally facing impressed adductor scars; shell substance thick. Lower Permian (Asselian): Argentina (Paganzo Basin).——FIG. 1771,2a-e. \*T. paganzoensis, Tupe Formation, upper Asselian; a-b, holotype, external and internal views of dorsal valve, DCG-MLP356f, ×3; c-e, ventral valve posterior, ventral, and internal views, ×3 (Archbold & Simanauskas, 2001).

### Subfamily DASYALOSIINAE Brunton, 1966

- Dasyalosia Muir-Wood & Cooper, 1960, p. 76 [\*Spondylus goldfussi von Münster, 1839, p. 44; OD] [=Bruntonaria WATERHOUSE, 2001, p. 85 (type, Dasyalosia panicula BRUNTON, 1966, p. 191, OD)]. Description as in BRUNTON and others, 2000, p. 569, including distributions. [WATER-HOUSE (2001) diagnosed his genus as being small with moderately to well-developed lamellae, and long, densely disposed ventral and dorsal spines of two series. This is acceptable. He described the ventral spines as mostly subprostrate, however, which is not true for either Dasyalosia goldfussi (see MUIR-WOOD & COOPER, 1960, p. 76) or for the two Irish species he assigned to his new genus (see BRUNTON, 1966, p. 191, pl. 2,9) in which there is a predominance of erect spines. In addition, WATERHOUSE (2001, p. 85) helped to differentiate his new genus from Dasyalosia by writing that the cardinal process of the latter is low when in fact the illustrations in MUIR-WOOD and COOPER (1960, pl. 6) are of a valve with a broken cardinal process (see BRUNTON, 1966, p. 190-191). Complete cardinal processes extend well posterior of the hinge line. As yet, insufficient clear distinction has been made to separate D. panicula BRUNTON from Dasyalosia, despite the stratigraphical interval, so Bruntonaria is placed into junior synonymy with Dasyalosia. The assertion that the Irish species of Dasyalosia are more similar to Acanthalosia than to Dasyalosia (WATERHOUSE, 2001, p. 85) is here rejected.] upper Lower Carboniferous-lower Upper Permian: Western Europe.-—FIG. 1772,*3a-b. \*D. goldfussi* (von MÜNSTER), lower Upper Permian, Gara, Germany; dorsal valve interior and posterior showing disposition of cardinal process, but with abraded terminal myophores, ×3 (new).
- Guadalupelosia ARCHBOLD & SIMANAUSKAS, 2001, p. 223 [\**Strophalosia inexpectans* COOPER & GRANT, 1975, p. 795; OD] [=*Muirwoodicia* WATER-HOUSE, 2002b, p. 54, obj.]. Medium-sized, weakly

2664



FIG. 1770. Strophalosiidae (p. 2663).

concavoconvex shells with short trails; hinge line about two-thirds maximum width, with low interareas and weakly convex narrow pseudodeltidium; cicatrix minute; delicate, fine recumbent spines on both valves; teeth small, but well formed; ventral adductor scars rounded with raised rims; inner socket ridges extending as cardinal then lateral ridges and continuing as subperipheral rim defining corpus area, which is fully bisected by narrow median septum. Upper Permian (Wordian): USA (western Texas). ——FIG. 1772, 2a-i. \* G. inexpectans (COOPER & GRANT), Cherry Canyon Formation; a-e, holotype, ventral valve anterior, posterior, lateral, ventral, and internal views, USNM 151229b, ×1; f, posterodorsal view showing interarea and teeth, ×3; g, dorsal valve exterior, ×1; b-i, interior and posteriorly, ×3 (Cooper & Grant, 1975).

2665



FIG. 1771. Strophalosiidae (p. 2663).

### Subfamily ECHINALOSIINAE Waterhouse, 2001

[Echinalosiinae WATERHOUSE, 2001, p. 57] [type genus, *Echinalosia* WATERHOUSE, 1967, p. 167]

[This subfamily, based on *Echinalosia* WATERHOUSE, 1967, separates those strophalosiids in BRUNTON and others (2000), mainly assigned to the Dasyalosiinae, but differentiated by having dorsal spines that are all erect. WATERHOUSE (2001) also included genera with lamellose or a fine radial ornamentation. The dorsal valve of *Echinalosia* is concave over the corpus, curving into a short trail, while those of *Dasyalosia* and *Crossalosia*, representing the remaining Dasyalosiinae, are flat over the corpus, and this feature should perhaps also be included in any discussion separating these strophalosiids.] *upper Lower Permian (Artinskian)– Upper Permian (Changhsingian).* 

Capillaria WATERHOUSE, 2001, p. 67 [\*Strophalosia preovalis var. warwicki MAXWELL, 1954, p.



FIG. 1772. Strophalosiidae (p. 2663-2667).

543; OD]. Small or medium-sized rounded shells resembling *Echinalosia*, but with fine capillae and few spines dorsally; ventral spines in two series, small unbonally and increasing in size to posterolateral margins and anteriorly. *Lower Permian* (*Sakmarian*)–*Upper Permian* (*Capitanian*): Eastern Australia and Tasmania.—FiG. 1773*a*-*e*. \**C. warwicki* (MAXWELL); *a*, holotype, ventral valve internal mold, UQF15626, ×2; *b*, cast of posterolateral region of ventral valve exterior, ×2; *c*, cast of shell exterior viewed posterodorsally, ×2; *d*, dorsal valve external mold showing fine capillae, ×3; *e*, cast of incomplete dorsal valve interior, ×2 (Briggs, 1998). Pseudostrophalosia CLARKE, 1970, p. 987 [\*Strophalosia brittoni MAXWELL, 1954, p. 543, partim.; OD]. Medium-sized ovate shells with geniculate dorsal valves and short trails; ventral spines semirecumbent, fine to coarse toward anterior and coarse at ears; dorsal spines fine, numerous and between weakly lamellose rugae; dorsal lateral ridges impersistent, but may continue as ear baffles and subperipheral rim. [BRIGGS (1998) published his study of the Strophalosiidina and Productidina of eastern Australia, which included the reinvestigation of this genus in which he recorded convincing evidence for its separation from *Wyndhamia*, where it was included in BRUNTON and others (2000, p.

![](_page_28_Picture_1.jpeg)

FIG. 1773. Strophalosiidae (p. 2665-2666).

574).] Lower Permian (Artinskian)–Upper Permian (Kazanian): East Australia.—FIG. 1774*a*-*e*. \**P*. *brittoni* (MAXWELL); *a*, replica of ventral valve exterior, ×2; *b*, mold of dorsal valve exterior, ×2; *c*-*d*, internal mold of ventral valve and replica of posterior region showing teeth, interarea, and muscle field, ×2; *e*, replica of dorsal valve interior, ×2 (Briggs, 1998).

### Subfamily MINGENEWIINAE Archbold, 1980

Melvillosia WATERHOUSE, 2001, p. 56 [\*M. canadensis; OD; nom. nov. pro Craspedalosia pulchella WATER-HOUSE, 1969, non DUNBAR, 1955, p. 81]. Small to medium size with oval to subtriangular outline; cicatrix minute to absent; interareas narrow but prominent ventrally; spines on ventral valve in two series, strong erect and fine semirecumbent with slightly swollen bases, dorsal valve with rare suberect spines; weakly to strongly lamellose with fine capillae, especially dorsally; interiors not known. [WATERHOUSE (2001) placed Melvillosia in the subfamily, altering its definition to include genera with capillate ornament, but he did not consider the presence of dorsal spines on his genus as significant. In view of MUIR-WOOD and COOPER's (1960) mention of rare capillae on dorsal valves of Craspedalosia, the distinction between it and Melvillosia is not entirely secure. If dorsal spines are considered important, then Orthothrix with its similar outline and lamellose plus spinose dorsal valve has to be compared.] Upper Permian (Wordian, ?Capitanian): Canadian Arctic.——FiG. 1772,1a–e. \*M. canadensis, Melville Island; a–b, holotype, viewed ventrally and dorsally, GSC 23828, ×1; c, detail of dorsal valve margin showing capillate lamellae and spine bases, ×4; d–e, specimen stripped of spines, ventral and dorsal views, ×1 (Waterhouse, 1969).

#### Family CHONOPECTIDAE Muir-Wood & Cooper, 1960

Eileenella RACHEBOEUF in WONGWANICH & others, 2004, p. 1081 [\**E. elegans;* OD]. Small leptaenidlike geniculate chonopectid shells with weak concentric, sublamellose growth lines, especially on short trail; ventral and dorsal valves almost flat; hinge spines not extending to ears; rounded peripheral ventral ridge bearing row of stubby, flattened spiny tubercles projecting anteriorly and anterolaterally; ventral valve interior with well-developed diductor muscle field divided by thin myophragm; dorsal interior with short and wide cardinal process supported by short inner socket ridges and median septum; thin, broadly lobate peripheral ridges bordering disc. *Upper Carboniferous (Namurian, Bashkirian):* southern

![](_page_29_Picture_1.jpeg)

FIG. 1774. Strophalosiidae (p. 2666–2667).

Thailand.——FIG. 1775, 1a-f. \**E. elegans*; *a*, holotype, rubber replica of ventral valve exterior showing anterior spinose tubercles, BMNH BD12524, ×5; *b–c*, rubber replica showing spine bases at hinge line and ventral valve internal mold,

 $\times$ 5; *d*, rubber replica of dorsal valve interior,  $\times$ 5; *e*, rubber replica of incomplete dorsal valve interior,  $\times$ 5; *f*, reconstruction drawing of articulated shell viewed laterally,  $\times$ 5 (Wongwanich & others, 2004).

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![](_page_30_Figure_1.jpeg)

FIG. 1775. Chonopectidae and Araksalosiidae (p. 2667-2669).

### Family ARAKSALOSIIDAE Lazarev, 1989 Subfamily RHYTIALOSIINAE Lazarev, 1989

Sinalosia MA & SUN in MA & others, 2002, p. 386 [\*S. rugosa; OD]. Small to medium weakly concavoconvex araksalosiids with short, wide interareas; cicatrix weak to absent; rugae fine and undulose, less prominent dorsally; spines thin, recumbent over ventral valve and rare erect thicker hinge spines; inner socket ridges short, well developed, median septum weak, reaching about midcorpus length. Upper Devonian (upper Frasnian): southern China (central Hunan).—Fig. 1775,2a-f. \*S. rugosa; a-c, holotype, ventral, dorsal, and lateral views, PUM 00017, ×2; d, posterodorsal view of shell showing interareas, pseudodeltidium, and chilidium, ×6; *e–f*, dorsal valve cardinalia, lateral and dorsal views, ×6 (Ma & others, 2002).

### Superfamily AULOSTEGOIDEA Muir-Wood & Cooper, 1960 Family AULOSTEGIDAE Muir-Wood & Cooper, 1960 Subfamily AULOSTEGINAE Muir-Wood & Cooper, 1960

Carilya ARCHBOLD in BRUNTON, COCKS, & LONG, 2001, p. 369 [\*Taeniothaerus miniliensis COLEMAN, 1957, p. 96; OD] [=Miniliconcha WATERHOUSE, 2004, p. 71, obj.]. Large subquadrate shell with weak ventral median sulcus, differing from Taeniothaerus in having finer and more densely arranged spines arising ventrally from small spine ridges, coarser clusters of spines directed posterolaterally from small ears and posterolateral margins; dorsal valve with dimples and fine spines; dorsal adductor scars enclosed posterolaterally by thickened shell. [The description of Carilya, based on species previously described as Taeniothaerus from Western Australia, narrows the definition of Taeniothaerus to species found in Tasmania and eastern Australia. WATER-HOUSE's junior objective synonym is based entirely on the specimens and holotype of COLEMAN, 1957.] Lower Permian (upper Artinskian–lower Kungurian): Western Australia.—FIG. 1776a-h. \*C. miniliensis (COLEMAN), Wandagee Formation, lower Kungurian, Minilya River, Čarnarvon Basin; *a–b,* holotype, viewed posteriorly and laterally, UWA 34445, ×1 (Coleman, 1957); c-d, lateral and part dorsal views (Muir-Wood & Cooper, 1960); e, dorsal valve interior, ×1 (Coleman, 1957); f-h, incomplete dorsal valve interior, exterior, and lateral view showing posteroventrally directed cardinal process, adductor scars, and incomplete long median septum, ×1 (Muir-Wood & Cooper, 1960).

- Saeptathaerus WATERHOUSE, 2002a, p. 230 [\*Aulosteges fairbridgei COLEMAN, 1957, p. 40; OD]. Medium to large aulostegine resembling Megasteges in shape and with bands of stronger, more erect spines on ventral trail, other ventral and thinner dorsal spines arising from anterior ends of spine ridges; ridges diverging narrowly from cardinal process base, enclosing dorsal adductor scars posterolaterally and almost equalling length of median septum. Upper Permian (Tatarian): Western Australia, Himalayas.-—Fig. 1777*a-f.* \*S. fairbridgei (COLEMAN), Herdman Formation, lower Tatarian, western Kimberly; a-d, holotype, internal cast of shell with little remaining shell material, posterior, dorsal (umbonal area), lateral, and ventral views, UWA 29438f, ×1; e-f, smaller internal cast, dorsal and ventral views, ×1 (Coleman, 1957).
- Taeniothaerus WHITEHOUSE, 1928, p. 281 [\*P. subquadratus MORRIS in STREZELECKI, 1845, p. 284; OD]. Large, relatively thick-shelled, sulcate ventral valve with irregular concentric bands of coarse, elongate spine bases and relatively thick spines interspersed with fewer finer spines anteriorly, plus stronger posterolateral spines; dorsal valve with concentric coarse dimples and few spines; dorsal adductor scars posteriorly bordered by ridges extending from cardinal process shaft. [The erection of Carilya results in the need for a redefinition of this genus.] Lower Permian (Artinskian): eastern Australia.-FIG. 1778a-d. \*T. subquadratus (MORRIS); a-b, lectotype, partly exfoliated ventral valve exterior viewed ventrally and laterally, near Hobart, Tasmania, BMNH B91171,  $\times 1$  (new); c, dorsal valve interior with exposed external mold anteriorly showing positions of spine bases, Berriedale Limestone, near Granton, Tasmania, ×0.8; d, incomplete dorsal valve inte-

rior, Counsel Creek Formation, Maria Island, Tasmania, ×1 (Parfrey, 1983).——FIG. 1779*a*–*b*. \**T. subquadratus* (MORRIS); *a*, ventral valve exterior showing finer spines anteriorly, Enstone Park Limestone, Elephant Pass, Tasmania, ×0.6 (Parfrey, 1983); *b*, replica of ventral valve exterior, Tiverton Formation, ×1 (Waterhouse, Briggs, & Parfrey, 1983).

#### Subfamily INSTITELLINAE Muir-Wood & Cooper, 1960

Licharewiconcha Kotlyar, Zakharev, & Polubotko, 2004, p. 517 [\*Productus (Sinuatella) subsinuatus LICHAREW, 1936, p. 116; OD]. Medium sized, subquadrate to transverse outline, strong triangular ears, probably with shallow corpus cavity and with well-differentiated trails; interarea wide, but short; ribbing well defined, but lacking on ears; rugae slightly more prominent than ribbing posteromedianly, not on anterior corpus, ears, or trails; median sulcus and dorsal fold start close to umbones; spines large (?), clasping clumps on lateral hinge line and ears, possibly finer spines on ventral corpus. [This genus was described in its own new family, but it fits well within the Institellinae. The genus authors do not mention a type specimen, but their figures 8.6-9 appear to match closely those of the named holotype by LICHAREW (1936) and figured by him as pl. 1,7a-c.] Upper Permian (upper Changhsingian): Russia (northwestern Caucasus mountains). -FIG. 1780,2a-f. \*L. subsinuatus (LICHAREW), Urushten Formation, near Kutan; a-d, possible holotype, almost complete shell, ventral, anterior, lateral, and dorsal views showing short interarea and impressions of ventral spine bases in a row between ears and flanks, CRMGE 890/2139, Severnaya Ravine,  $\times 1$ ; *e*, dorsal view of shell showing some ventral hinge spines projecting posteriorly,  $\times 1$ ; f, incomplete ventral valve exterior showing spine cluster at one ear and possible smaller spine bases on corpus, ×2 (Kotlyar, Zakharev, & Polubotko, 2004).

### Subfamily RHAMNARIINAE Muir-Wood & Cooper, 1960

Colemanosteges WATERHOUSE, 2002b, p. 49 [\* Taeniothaerus(?) fletcheri COLEMAN, 1957, p. 91; OD]. Small to medium-sized rhamnariine with a planoconvex profile and short trails; hinge line about one-half to three-quarters maximum width with narrow, short ventral interarea with open delthyrium; ventral spines coarse, recumbent with elongate bases and interspersed fine spines toward anterior margin, clusters on ears; spines fine dorsally; cardinal process buttress plates slightly divergent to posterior ends of weakly raised adductor scars. [The above follows COLEMAN's description and illustrations (1957).] Upper Permian (lower Tatarian): Western Australia, ?southern Tibet.— —Fig. 1780, 1a-e. \*C. fletcheri (COLEMAN), Liveringa

![](_page_32_Picture_1.jpeg)

FIG. 1776. Aulostegidae (p. 2669–2670).

![](_page_33_Picture_1.jpeg)

FIG. 1777. Aulostegidae (p. 2670).

Formation, western Kimberly, Australia; a-b, holotype, ventral valve, ventral and dorsal views, CPC 1950, ×0.67; c, holotype, ventral valve viewed laterally, CPC 1950, ×1; d, dorsal view of specimen with cluster of posteroventral spines, ×1; e, incomplete dorsal valve interior, ×1 (Coleman, 1957).

### Family TSCHERNYSCHEWIIDAE Muir-Wood & Copper, 1960

[nom. transl. BRUNTON, herein, ex Tschernyschewiinae MUIR-WOOD & COOPER, 1960, p. 126]

Description as in subfamily Tschernyschewiinae in BRUNTON and others (2000, p. 608).

Reedosepta WATERHOUSE, 2002b, p. 50 [\*Productus (Tschernyschewia) parilis REED, 1944, p. 86; OD]. Similar in size and shape to Tschernyschewia, but differing in its ventral ornamentation of pustulose spine bases of differing sizes, somewhat resembling the ornament of Juresania, clusters of erect spines lacking swollen bases on small ears and posterior flanks; dorsal spines with fewer and smaller spine bases. *Upper Permian (upper Capitanian):* Pakistan (Salt Range).——FIG. 1781, *Ia-f.* \**R. parilis* (REED), Middle *Productus* Limestone, Wargal Formation; *a-e*, lectotype, ventral, lateral, dorsal, and posterior views, GSI 16856 (selected by WATERHOUSE, 2002b), ×1.5, and detail of ventral valve spine base ornament, ×2; *f*, posterior view of broken ventral valve showing high median septum, ×1.5 (Reed, 1944).

Trigonoproductus WATERHOUSE, 2002b, p. 51 [\*Tschernyschewia inexpectans COOPER & GRANT, 1975, p. 915; OD]. Similar in size and outline to Tschernyschewia, but with well-formed ears, double row of strong rhizoid spines at ventral hinge line, and dorsal valve with well-developed anterior fold; dorsal valve median septum starting between adductor scars and reaching anterior border of disc. Lower Permian (Sakmarian): USA (western Texas). ——FIG. 1781,2a-f. \*T. inexpectans (COOPER & GRANT), Hess Formation, Glass Mountains; a-d, holotype, incomplete shell, dorsal, posterior, lateral, and anterolateral views showing part of shell interior, USNM 152681, ×1; e, ventral valve exterior in

![](_page_34_Picture_1.jpeg)

FIG. 1778. Aulostegidae (p. 2670).

![](_page_35_Picture_1.jpeg)

FIG. 1779. Aulostegidae (p. 2670).

anteroventral view,  $\times 1$ ; *f*, dorsal cardinalia, internal view,  $\times 2$  (Cooper & Grant, 1975).

### Order ORTHOTETIDA Waagen, 1884 Superfamily ORTHOTETOIDEA Waagen, 1884 Family SCHUCHERTELLIDAE Williams, 1953

Ventral valve variable in size and shape, deformed by attachment but normally with high ventral interarea; shell usually finely costellate rarely with secondary costation; discrete dental plates; cardinal process lobes low, discrete, becoming long and fused proximally into single shaft; socket ridges recurved to divergent, becoming fused with cardinal process base, brachiophore bases developing later, normally prolonged as brachiophores; shell extropunctate with oldest representatives retaining pseudopunctation. *Middle Devonian–Permian*.

#### Subfamily SCHUCHERTELLINAE Williams, 1953

Schuchertellopsis MAILLIEUX, 1939, p. 5 [\*S. durbutensis; OD]. Small (10 to 12 mm wide), irregularly shaped shells with ventral valve cemented almost completely to substrate; hinge line approximately widest part of shell, ventral profile irregular, dorsal profile plane to weakly convex; ventral interarea with arched pseudodeltidium, dorsal interarea weak; irregularly costellate; dental ridges unsupported; dorsal valve poorly known. [In WILLIAMS & BRUNTON (2000, p. 667), MAILLIEUX'S genus was questionably assigned to the Schuchertellinae of the Orthotetidina. In 1978 STRUVE divided the genus into two subgenera by the description of Schuchertellopsis (Krejcigrafella). Schuchertellopsis s.s. comes from the upper Frasnian of Belgium and Krejcigrafella from the lower Eifelian of Germany.

These subgenera are both closely and almost completely attached by their ventral valves, and at the time of preparation for the orthotetidines for the revised *Treatise* (Vol. 3, WILLIAMS & BRUNTON, 2000) it was not entirely clear as to whether they would best be classified with the orthotetidines or attached davidsonioids. The main feature differentiating these two taxa is shell structure; the former having laminar shell and the latter fibrous shell. Study of MAILLIEUX'S original collection shows the

2674

2675

![](_page_36_Figure_1.jpeg)

FIG. 1780. Aulostegidae (p. 2670-2672).

![](_page_37_Figure_1.jpeg)

FIG. 1781. Tschernyschewiidae (p. 2672-2674).

following orthotetidine features, not seen in davidsonioids: (1) wide ventral interarea with delthyrium covered completely by an arched pseudodeltidium, and (2) shell fabric laminar with pseudupunctae forming pustulose internal surfaces, and sparse extropunctae forming small depressions internally (Fig. 1782).

WILLIAMS and BRUNTON (2000) characterized the Schuchertellidae by, among other features, their unsupported teeth and extropunctate shell, the only family known to have such microstructures in the shell. The finding of extropunctae in *Schuchertellopsis*, together with its schuchertellid morphology, confirms its position in the Schuchertellidae, and its morphology is similar to the Schuchertellinae. The genus is, however, unique as yet in having both pseudopunctae and extropunctae; it is also the oldest known member of the family. We conclude, therefore, that the pseudopunctation is a holdover from ancestral stock that was pseudopunctate.

![](_page_38_Picture_1.jpeg)

Schuchertellopsis (Schuchertellopsis)

FIG. 1782. Schuchertellidae (p. 2677).

The extropunctation seen in *Schuchertellopsis* is less developed than in Carboniferous and Permian genera and would appear to be a new structure introduced to the family at about mid-Devonian time.] *Middle Devonian (Eifelian)–Upper Devonian (Frasnian):* western Europe, ?southern North America.

S. (Schuchertellopsis). Lacking ventral median septum; inner socket ridges extending at shallow angle from hinge, muscle fields indistinct; shell extropunctate and pseudopunctate. *Middle*  Devonian (Eifelian)–Upper Devonian (Frasnian): western Europe.—FIG. 1782*a–b.* \*S. (S.) *durbutensis*, Mailleux collection, Institut Royal des Sciences Naturelles de Belgique, Brussels; *a*, SEM of exfoliated internal surface of ventral valve showing cross-bladed laminae,  $\times 3000$ ; *b*, SEM of exfoliated ventral valve interior showing extropunctae, represented by pits, and pseudopunctae represented by tubercles,  $\times 300$  (new).

S. (Krejcigrafella) STRUVE, 1978.

### ORTHOTETIDA

DAVID A. T. HARPER

[University of Copenhagen]

Order ORTHOTETIDA Waagen, 1884 Suborder ORTHOTETIDINA Waagen, 1884 Superfamily CHILIDIOPSOIDEA Boucot, 1959 Family EOCRAMATIIDAE Williams, 1974 [Eocramatiidae WILLIAMS, 1974, p. 127; emend., HARPER, herein]

Subquadrate, costellate; apsacline ventral interarea with submesothyrid foramen and convex pseudodeltidium; narrow, hypercline dorsal interarea with small convex chilidium; teeth largely unsupported, ventral muscle scar more or less limited to delthyrial cavity; chilidial plates ankylosed to socket ridges or plates that are divergent or parallel with hinge line; dorsal adductor scars quadripartite about low myophragm; dorsal platforms variably developed; shell impunctate. [Identification of laminar secondary shell in the genus Neocramatia suggests assignment of this family to the Orthotetidina rather than the Plectambonitoidea. Moreover, cladistic analysis indicates a position for the family within the Chilidiopsoidea. This new assignment and the addition of Neocramatia to the family require some modification of the respective diagnoses for both the genera and the family]. Ordovician (Llanvirn-Ashgill).

- Eocramatia WILLIAMS, 1974, p. 128 [\*E. dissimulata; OD]. Planoconvex, gently uniplicate, finely costellate by branching and intercalation; socket ridges widely divergent, near parallel to hinge line. Ordovician (Llanvirn): England.-FIG. 1783, 1a-d. \*E. dissimulata, Hope Shale Formation, Brithdir Farm, Shropshire;  $a-\hat{b}$ , rubber replicas of dorsal exterior and interior, BMNH BB35489a,b, ×5.8; c-d, internal mold and rubber replica of ventral valve, BMNH BB35488a, ×3.5 (Williams, 1974).
- Neocramatia HARPER, 1989, p. 102 [\*N. diffidentia; OD]. Concavoconvex, costellate with branching and intercalated ribs; socket ridges divergent; bilobed dorsal platform present together with arcs of pustules in both ventral and dorsal valves near anterior margin. Ordovician (Caradoc): Scotland. FIG. 1783,2a-f. \*N. diffidentia, Myoch Formation, Girvan, southwestern Scotland; a-b, internal mold of ventral valve and rubber replica, HML 12412,  $\times 6$ ; *c*-*d*, internal mold of dorsal valve and rubber replica, HML 8910, ×9; e, rubber replica of dorsal exterior, HML 12148b, ×5; f, rubber replica of ventral exterior, HML 12148a, ×6.5 (Harper, 1989).

### TRIPLESIOIDEA

#### A. D. WRIGHT

[The University of Leicester]

# Suborder TRIPLESIIDINA Moore, 1952 Superfamily TRIPLESIOIDEA Schuchert, 1913 Family TRIPLESIIDAE Schuchert, 1913

Acaretyrricula JIN & CHATTERTON, 1997, p. 23 [\*A. tenuiguttae; OD]. Small, triradiate shell, waisted in front of narrow hinge line; both beaks elongate, ventral extremely so; pseudodeltidium monticulate; surface smooth apart from growth lines, anterior emargination formed by abrupt median deflection, giving tongue to dorsal valve, with corresponding ventral reflection of ventral valve; dental plates long, subparallel, cardinal process proximally grooved, distally unknown. Silurian (Llandovery): Canada (Northwest Territories).—FIG. 1783,3a-c. \*A. tenuiguttae, Telychian; a, holotype, view of ventral valve interior and interarea,  $\times 15$ ; b, ventral valve exterior, ×15; c, dorsal valve interior, ×20 (Jin & Chatterton, 1997).

![](_page_40_Figure_1.jpeg)

FIG. 1783. Eocramatiidae and Triplesiidae (p. 2678).

# CLITAMBONITIDINA

### MADIS RUBEL

[University of Tartu]

### Suborder CLITAMBONITIDINA Öpik, 1934 Superfamily CLITAMBONITOIDEA Schuchert & Cooper, 1931 Family ARCTOHEDRIDAE Williams & Harper, 2000

[Arctohedridae WILLIAMS & HARPER, 2000, p. 710; *emend.*, RUBEL, herein]

Costellate, unisulcate clitambonitoids with subpyramidal ventral valve; teeth simple, spondylium free; well-developed notothyrial platform with simple cardinal process; divergent rodlike brachiophores joined to hinge line by concave fulcral plates defining sockets and subtending narrow notothyrial plate flanking median elevation that extends anteriorly and divides subequally quadripartite adductor scars; ventral mantle

# canal system probably saccate with divergent *vascula media*. *Middle Cambrian*.

Arctohedra COOPER, 1936, p. 210 [\*A. minima; OD]. Transversely semioval with acute cardinal extremities, ventribiconvex to planoconvex, coarsely costellate to ramicostellate; well-developed notothyrial platform, simple cardinal process, and straight, divergent brachiophores. [The type species is illustrated in WILLIAMS and HARPER, 2000, p. 712, fig. 514, 1a-d. Description and illustration of silicified material from northeastern New South Wales (BROCK, 1998) has confirmed the presence of a cardinal process in this important genus; the diagnosis is emended accordingly and new illustrations provided. The new and more informative material from Australia provides more details of the cardinalia. Arctohedra is now regarded as more closely related to the clitambonitidines than the protorthides where it was provisionally placed, in the newly created Arctohedridae, by WILLIAMS and HARPER (2000, p. 710). That provisional assignment was based on the assumption that the free spondylium of Arctohedra, a basic protorthide character, is systematically more important than the cardinalia, both of which were considered to

![](_page_41_Picture_8.jpeg)

FIG. 1784. Arctohedridae (p. 2680-2681).

be orthide (WILLIAMS & HARPER, 2000, p. 710). A free spondylium, however, is now known to be characteristic of clitambonitidine juvenile shells (POPOV, VINN, & NIKITINA, 2001, p. 155). This discovery facilitates the transfer of the Arctohedridae (with Arctohedra but not Loperia WALCOTT; see p. 2682 herein) to the Clitambonitidina. The transfer greatly extends the stratigraphic range of the suborder.] Middle Cambrian: North America (Alaska), Australia (New South Wales), Central Asia (Turkestan, Tian Shan).-FIG. 1784a-e. A. austrina BROCK, Murrawong Creek Formation, northeastern New South Wales, Australia; a-b, external and internal views of dorsal valve, AMF97369, ×40; c-e, external, internal, and internal oblique views of ventral valve, AMF97373, ×21 (Brock, 1998).

### Superfamily POLYTOECHIOIDEA Öpik, 1934 Family POLYTOECHIIDAE Öpik, 1934

Tritoechia Ulrich & COOPER, 1936b, p. 624 [\*Deltatreta typica Schuchert & COOPER, 1932, p. 206; OD] [=Pinatotoechia BENEDETTO, 2001, p. 140 (type, P. acantha, OD)]. The so-called tubular

![](_page_42_Picture_4.jpeg)

FIG. 1785. Polytoechiidae (p. 2681).

spines that are diagnostic of *Pinatotoechia* (BENE-DETTO, 2001, fig. 3B) are identical with the aditicules characterizing the type species of *Tritoechia*.

Korinevskia POPOV, VINN, & NIKITINA, 2001, p. 149 [\*Billingsella akbulakensis ANDREEVA, 1960, p. 291; OD]. Similar to Protambonites, but complete chilidium, large ventral adductor scars, short dental plates; ventral mantle canal system saccate. Ordovician (upper Tremadoc-lower Arenig): southern Urals.—FIG. 1785a-e. \*K. akbulakensis (ANDREEVA); a-b, mold of ventral interior and rubber replica, ×2; c, rubber replica of dorsal interior, ×2; d, rubber replica of juvenile ventral exterior, ×2 (Popov, Vinn, & Nikitina, 2001).

# PROTORTHIDA

### DAVID A. T. HARPER

[University of Copenhagen]

Class RHYNCHONELLATA Williams & others, 1996 Order PROTORTHIDA Schuchert & Cooper, 1931 Superfamily PROTORTHOIDEA Schuchert & Cooper, 1931 Family PROTORTHIDAE Schuchert & Cooper, 1931

Loperia WALCOTT, 1905, p. 287 [\**Protorthis (Loperia) dougaldensis;* OD]. The genus *Loperia* WALCOTT is poorly known and is provisionally transferred from the Arctohedridae to the Protorthidae, where it was originally assigned in the first edition of the *Treatise* 

(MOORE, 1965). It does, however, possess distinctive cardinalia and resupination that may form the basis for an alternative taxonomic placement when the genus is revised in modern terms. *Middle Cambrian:* eastern Canada.

Saesorthis GEYER & MERGL, 1997, p. 796 [\*Israelaria simplicissima MERGL, 1983, p. 339; OD]. Medium sized, subequally biconvex, subrectangular, uniplicate, finely ramicostellate; apical plate small; brachiophore nubs small. Middle Cambrian: Morocco. ——FIG. 1786a-e. \*S. simplicissima (MERGL), Jbel Wawrmast Formation, lower Middle Cambrian; a, rubber replica of ventral interior, PIW 92IV137a, ×7; b, mold of dorsal interior, PIW 92IV118a, ×4; c, dorsal interior, PIW 92IV121, ×7; d, partially exfoliated dorsal valve, MM 189c, ×7 (Geyer & Mergl, 1997).

Protorthida

![](_page_44_Picture_1.jpeg)

FIG. 1786. Protorthidae (p. 2682).