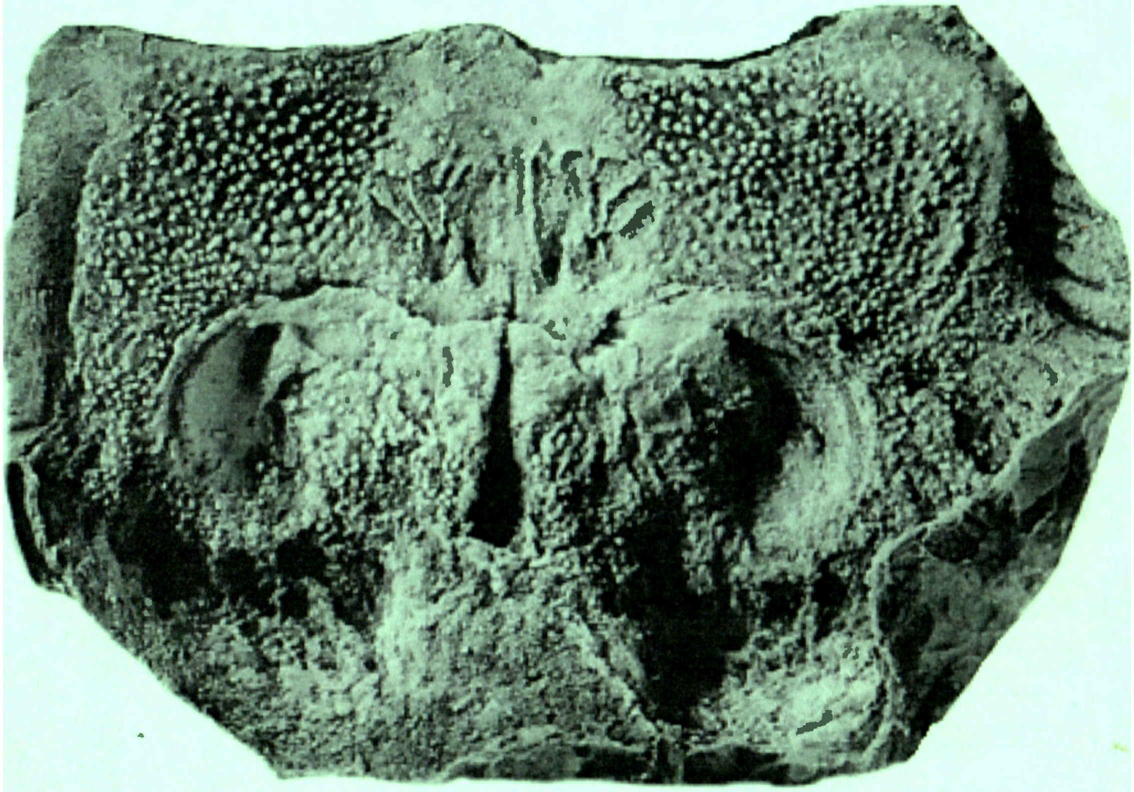
THE EVOLUTION AND CLASSIFICATION OF PRODUCTIDA (BRACHIOPODA)



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INFRASUBORDER AULOSTEGIMORPHI WATERHOUSE, 2010A

[Aulostegimorphi Waterhouse, 2010a, p. 10].

This infrasuborder includes Aulostegoidea and Richthofenoidea. These superfamilies evolved from Strophalosioidea. Aulostegoidea evolved directly from Rhytialosiinae, and not through the intermediacy of Productelloidea, and in turn gave rise to Richthofenioidea.

10. Superfamily AULOSTEGOIDEA Muir-Wood & Cooper, 1960

Fig. 10.1

[Nom. transl. Waterhouse, 1975, p. 6 ex Aulostegidae Muir-Wood & Cooper, 1960, p. 94].

Taxonomy: Cooper & Grant (1975, p. 822) in December, and Waterhouse (1975) in May, clearly upgraded Aulostegidae to superfamily rank, and were followed by Waterhouse (1978, p. 21). Brunton et al. (2000) preferred to attribute the recognition to themselves (Brunton et al. 1995, p. 932). Strangely enough, three of the same authors (or at least they were supposed to have authored it – see also p. 209) in a separate part of the *Revised Brachiopod Treatise* acknowledged that Cooper & Grant (1975) and Waterhouse (1978) had recognized the superfamily (Brunton, Lazarev & Grant 2000, p. 351). But Lazarev (2003, and in translated version Paleont. Zhurn. 37 (5), p. 492) disavowed participation in the authorship of this latter article, as if he preferred the far less accurate version in Brunton et al. (2000). Given the discrepancies of the two articles, and the disavowal of one version by S. S. Lazarev, it would appear that C. H. C. Brunton wrote the text for Brunton, Lazarev & Grant (2000), and apparently S. S. Lazarev was sole author of the relevant section on at least the introduction for Aulostegoidea.

There is an additional problem. Brunton et al. (2000) and Waterhouse (2002b) included Scacchinellidae Licharew, 1928a, b in Superfamily Aulostegoidea Muir-Wood & Cooper, 1960, but this is clearly in error, and was addressed in Rozanov (2003) by referring Family Aulostegidae to Superfamily Scacchinelloidea. Paleontologists may object to placing so many genera under the family-group name based on a highly exceptional and comparatively rare genus. That is the problem shared with the superfamily Proboscidelloidea, a widespread and diverse group named for a highly exceptional genus. One solution was proposed by Waterhouse (2010a, p. 14, table 1), in which the aulostegoids and scacchinelloids were divided into three superfamilies, Aulostegoidea, Institelloidea and Scacchinelloidea. In this summary, the first two superfamilies are merged, and Scacchinelloidea recognized as a highly exceptional group.

Diagnosis: Shells generally but not always attached by spines, often rhizoid, or attached by direct cementation, ventral interarea generally present, dorsal interarea small or often absent, no chilidium. Trails may be simple, geniculate, or elaborate. Shallow to deep body corpus, brachial ridges enclose small productiform shields, each side of anterior adductors. Cardinal process bilobate in early genera, high in later genera and may have anterior supporting blades as buttress plates but no lateral buttress plates.

Discussion: For many years, *Aulosteges* and allies have been associated with strophalosiids, principally on the bases of deformed ventral umbo and common presence of interarea, with insistence that strophalosiids and allies were primarily distinguished by being cemented at the ventral umbo. Researchers in Australia and New Zealand have not been satisfied with that interpretation (Coleman 1957). Waterhouse (1964, p. 55; 1978, p. 20; 1983b, p. 192) explained that in his view the productiform outline of the brachial ridges in particular, as well as aspects of ornament and cardinal process and hinge, demonstrated a closer relationship to Productidina rather than Strophalosiidina. These proposals were elaborated by Briggs (1998), and that view was accepted by Archbold (2001). The Briggs' study provides the best rationale published to date, and the nature of the brachial shields remains the most convincing of morphological ties. But the present analysis of evolution and source of the aulostegoids shows a more complicated relationship. It appears that the aulostegoids evolved independently of other productiform superfamilies, directly from Strophalosioidea, and not through an intermediate productelloid source. The aulostegoids like other superfamilies lost various attributes typical of Strophalosioidea, such as teeth and sockets and large brachial shields, but evolved into subproductiforms, not from Productelloidea, but from Strophalosioidea. In this course, they may be matched with the course of evolution shaped by Echinoconchoidea, and by Scacchinelloidea and by superfamilies in Linoproductidina. Furthermore, Aulostegoidea gave rise to a new superfamily, Richthofenioidea.

The strong and regular rogation of Institinini Muir-Wood & Cooper of Tournaisian age, amongst the oldest of Aulostegoidea, suggest that Rhytialosiinae (Strophalosioidea) offered a potential source for the superfamily.

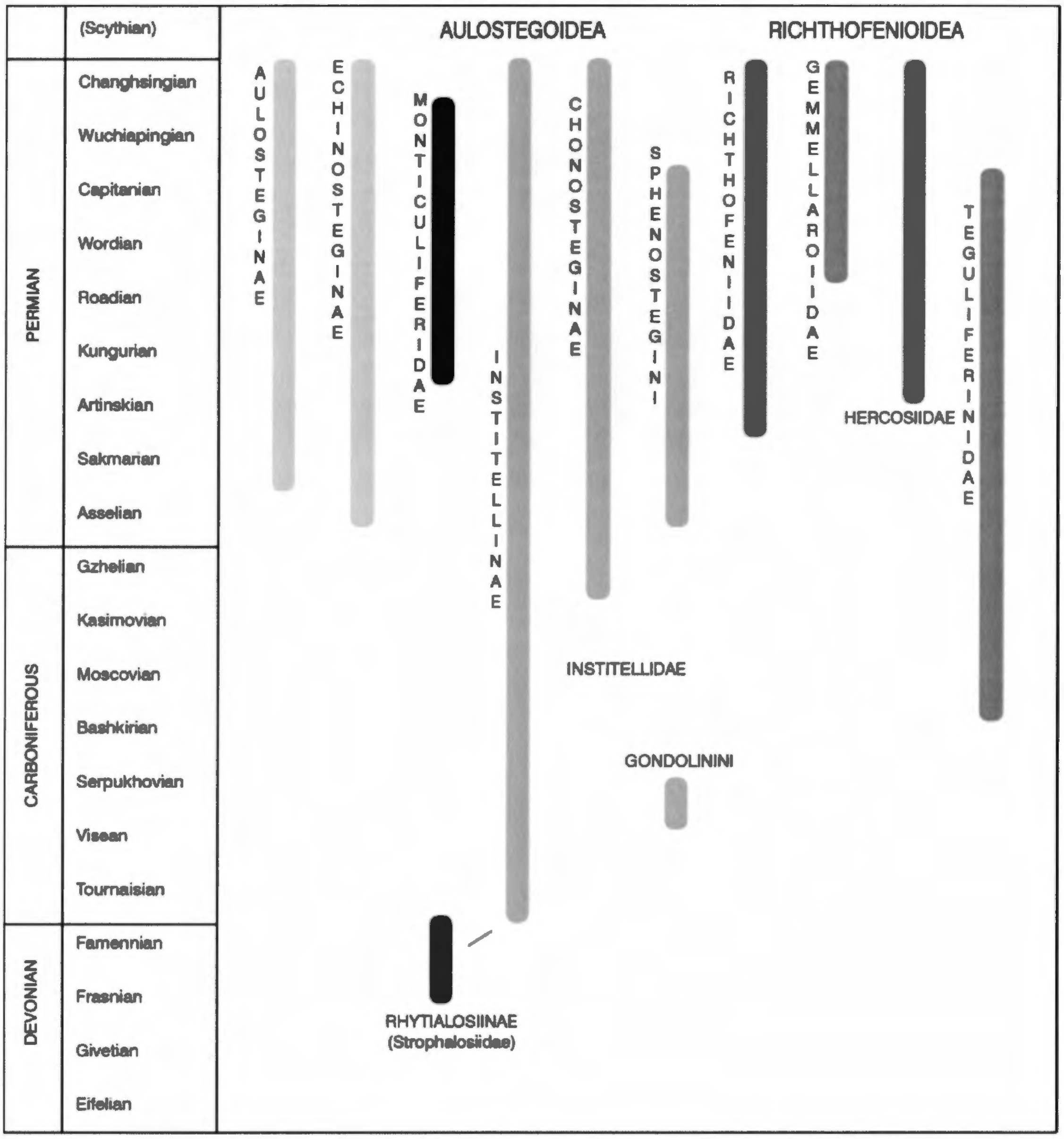


Fig. 10.1. Range chart for superfamilies Aulostegoidea and Richthofenioidea, which are associated as members of Aulostegimorphi, because Richthofenioidea arose from Aulostegoidea during the Late Carboniferous, as shown by Sutherland (1996), and Aulostegoidea arose in turn independently of other superfamilies from Rhytialosiinae, a subfamily within Chonopectidae Muir-Wood. The superfamily was highly diversified, and indeed two groups, Echinosteginae and Gondolininae may eventually be upgraded to family level. Aulosteginae encompases relatively large and simple genera, chiefly from cooling faunas of the Middle Permian in Russia as Aulosteginae, and the cool south temperate faunas of the southern paleohemisphere as Taeniothaerini and Megastegini. They are readily distinguished from the smaller and more elaborately spinose and commarginally ribbed members of paleotropical Echinosteginae. Even more elaborate ornament, with radial ribbing prominent, was developed in Institellinae, and companion group Chonosteginae developed elaborate margins, both limited to the paleotropical realm. But Gondolininae was simpler in ornament, with fine radial ribs, and little in the way of commarginal ornament, or prominent spination. And Monticuliferidae, although rare and confined to paleotropical faunas of east Asia, displayed a special monticular ornament of small surface swellings, often crossed by capillae. Richthofenioidea were more outstanding, often mimicking the shape of a solitary coral, with specialized internal structures in the ventral valve, as discussed on p. 294, a high median septum in some, and a very reduced dorsal valve.

Rhytialosiinae are completely strophalosiiform, whereas Institinini lack teeth and sockets, and are rarely cicatrixed, but do have interareas, again illustrating the overlap and duality of relationships within Productida.

Classification: Aulostegidae was depicted in major outline by Muir-Wood & Cooper (1960), and expanded by Cooper & Grant (1975) and Brunton et al. (2000, p. 587). The latter recognized three families, Aulostegidae, Cooperinidae and Scacchinellidae, the latter two with a small number of genera and highly distinctive, the Aulostegidae large with a diversity of morphotypes. Here the associations are re-examined, with recognition of two additional families, and transfer of Cooperinidae to Strophalosiidina, recognition of Scacchinelloidea as distinct from Aulostegoidea, and some revision of relationships and generic ties. To express the interrelationships and origins requires substantial elaboration of nomenclature, with the introduction of additional grades in classification, as discussed on p. 12. Within Aulostegoidea, the status for various groups is downgraded in order to squeeze all related genera and their groups into one superfamily. The superfamily is highly diversified, and indeed could be subdivided, as outlined by Waterhouse (2010a, Table 1, p. 14).

Family Aulostegidae Muir-Wood & Cooper, 1960

Ornament predominantly spinose.

- Subfamily Aulosteginae Muir-Wood & Cooper, 1960

Spines on both valves; thick and thin, erect and prostrate. Buttress plates often present.

  - Tribe Aulostegini Muir-Wood & Cooper, 1960
  - Tribe Taeniothaerini Waterhouse, 2002b
  - Tribe Megastegini new tribe

- Subfamily Echinosteginae Muir-Wood & Cooper, 1960

No dorsal spines as a rule, no buttress plates.

  - Tribe Echinostegini Muir-Wood & Cooper, 1960
  - Tribe Aglesiini Muir-Wood & Cooper, 1960

Family Institellidae Muir-Wood & Cooper, 1960

Ribbing usually prominent. Spines ventral and often sparse, no prolonged bases, no ear clusters as a rule, no buttress plates.

- Subfamily Institellinae Muir-Wood & Cooper, 1960

Strongly ribbed or reticulate.

  - Tribe Institellini Muir-Wood & Cooper, 1960
    - Subtribe Institellinai Muir-Wood & Cooper, 1960
    - Subtribe Sinuatellinai Muir-Wood & Cooper, 1960
  - Tribe Institinini Muir-Wood & Cooper, 1960

- Subfamily Chonosteginae Muir-Wood & Cooper, 1960

Strongly geniculate with complex valve margins.

- Subfamily Gondolininae Jin, Brunton & Lazarev, 1998

Homeomorph of *Striatifera*, with rhizoid umbonal spines.

  - Tribe Gondolinini Jin, Brunton & Lazarev, 1998
  - Tribe Sphenostegini Waterhouse, 2002b

Family Monticuliferidae Muir-Wood & Cooper

Fine ribs or smooth, monticules.

- Subfamily Monticuliferinae Muir-Wood & Cooper, 1960
- Subfamily Tongluellinae Liang, 1990

Table 12. Classification of the Aulostegoidea Muir-Wood & Cooper, 1960.

Family **AULOSTEGIDAE** Muir-Wood & Cooper, 1960

[Aulostegidae Muir-Wood & Cooper, 1960, p. 94].

Diagnosis: Spines on both valves, varied, erect and/or prostrate, often differing in diameter, no regular ribs. Interarea may be well developed on especially ventral valve. Shells often large, planoconvex as a rule, with dorsal valve planar or gently convex over visceral disc, trail simple. Cardinal process large, bifid to quadrifid, often at angle to commissure, may be supported by buttress plates, adductor scars dendritic, marginal ridge development generally low except in some groups.

Subfamily **AULOSTEGINAE** Muir-Wood & Cooper, 1960

[Aulosteginae Muir-Wood & Cooper, 1960, p. 95].

Diagnosis: Medium-sized shells with erect and often prostrate spines over both valves. Ventral interarea moderately high as a rule.

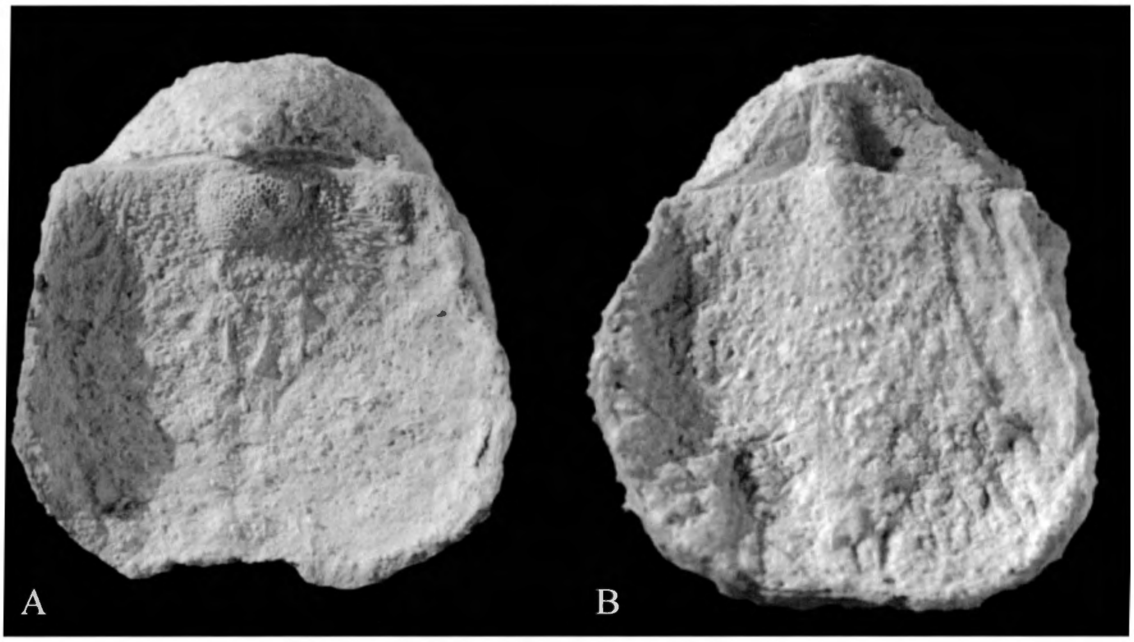


Fig. 10.2. *Aulosteges fragilis* (Netschajew). Dorsal aspects of specimens BR 3056, x2.5, and BR 3057, x2.8, from Kyibshevkar, Kazanian Stage, Russia. JBW photo.

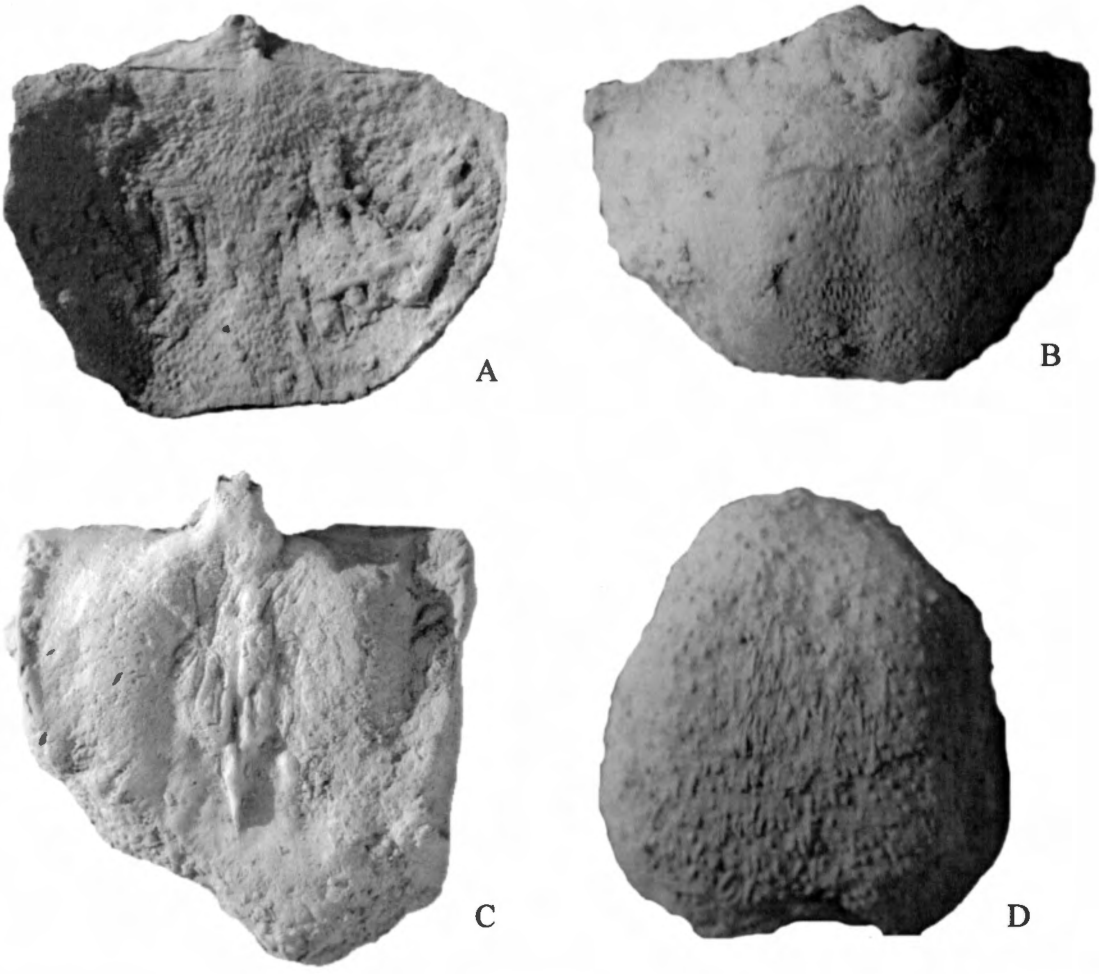


Fig. 10.3. A-C, *Wyatkina gigas* (Netschajew). A, B, ventral and dorsal aspects of specimen with valves conjoined, BR 3054, x1. C, dorsal interior, BR 3058, x1.1. D, *Aulosteges fragilis* (Netschajew), ventral aspect of BR 3056, x1.9. From Kyibshevkar, Kazanian Stage, Russia. JBW photo.

Discussion: Brunton et al. (2000, p. 587) reported that Aulosteginae had "elaborated trails" but this is not correct for any of the genera they included in the group.

Tribe **AULOSTEGINI** Muir-Wood & Cooper, 1960

Fig. 10.2, Fig. 10.3

[Nom. transl. hic ex Aulosteginae Muir-Wood & Cooper, 1960, p. 95].

Diagnosis: Medium-sized shells with erect and often prostrate spines over ventral valve, including pseudodeltidium, erect thin or thick spines which may be rhizoid over dorsal valve. Ventral interarea moderately high. Lower Permian (Sakmarian) to Middle Permian (Wordian).

Genus: *Aulosteges* von Helmerson, *Wyatkina* Fredericks.

Discussion: The cardinal process in *Wyatkina* bears two lateral sturdy supports sloping obliquely forward, but well behind the adductor scars. There appear to be no buttress plates, unlike the arrangement in *Aulosteges* (see Muir-Wood & Cooper 1960, pl. 10, fig. 18, 19). Muir-Wood & Cooper (1960, p. 99) erroneously referred to figures of *Wyatkina* in Netschajew (1911, pl. 3, fig. 1, 2) but these figures were labelled *Productus hemisphaeroidalis* and *P. cancrini* in the original text, and do not belong to *Wyatkina*. The correct reference is to Netschajew (1894). Netschajew (1911, pl. 7, fig. 7) did illustrate a dorsal valve as *Strophalosia* cf. *gigas*, and also figured some dorsal valves of the species, referring them to *Strophalosia* sp. indet. Brunton et al. (2000, p. 591) stated that dorsal spines were possibly absent from *Wyatkina*, but in fact they are numerous.

Tribe **TAENIOTHAERINI** Waterhouse 2002b

Fig. 10.4

[Nom. transl. hic ex Taeniothaerinae Waterhouse, 2002b, p. 27].

Diagnosis: Large shells with erect and/or prostrate spines on both valves, not rhizoid, spine bases usually elongate, and patterns variable. Buttress plates in dorsal valve. Lower and Middle Permian (Sakmarian – Wordian).

Genera: *Taeniothaerus* Whitehouse, *Taeniothaerus* (*Lakismatia*) Waterhouse, *Carilya* Archbold (syn. *Miniliconcha* Waterhouse), *Lipanteris* Briggs, *Reedoconcha* Kotlyar.

Discussion: This tribe embraces genera that lack rhizoid spines, and shells are consistently large with stronger and less crowded spine bases. It seems unlikely that these shells were closely attached other than through halteroid spines, and their stability may have depended substantially on their large size and thick corpus, as well as ear spines. The ventral umbo acted more as a resting platform than cemented attachment area.

Genus ***Taeniothaerus*** Whitehouse, 1928

Fig. 8, p. 16

Type species: *Productus subquadratus* Morris, 1845, p. 248 from Berriedale Limestone (Artinskian) of Tasmania, Australia.

Diagnosis: Large with thick body corpus, ventral interarea, spines on each valve of mostly one size, in quincunx over both valves and with elongate bases. Cardinal process large with buttress plates.

Discussion: This genus is characteristic of slightly warmer water faunas in east Australia and New Zealand, and is found also in Irian Jaya, Western Australia, Indian subcontinent, Tibet, Pamirs, and possibly Afghanistan and Oman.

Taeniothaerus farleyensis Briggs, 1998

Fig. 10.5 – Fig. 10.7

1909 *Productus subquadratus* [not Morris] – Etheridge & Dun, p. 9 (part).
1950 *Aulosteges* (*Taeniothaerus*) *subquadratus* [not Morris] – Hill, p. 6, pl. 6, fig. 4 (part, not pl. 1, fig. 1 = *subquadratus*; pl. 5, fig. 1, 2 = *homevalensis*).
1998 *Taeniothaerus farleyensis* Briggs, p. 136, Fig. 69A-F.
1998 *T. homevalensis* [not Briggs] – Briggs, p. 137 [referred the specimen of Hill 1950, pl. 6, fig. 4 to *homevalensis*].
1998 *Reedoconcha* sp. Briggs, p. 133, Fig. 68A-C.

Holotype: UQF 75291 from Farley Formation (?Artinskian), Sydney Basin, New South Wales, Australia, figured by Briggs (1998, Fig. 69A, B, D), OD.

Diagnosis: Large *Taeniothaerus* with shallow ventral sulcus and low fold, beak not distorted, interarea well formed, also developed in dorsal valve, ventral spine bases long and slender, dorsal ornament of elongate dimples and crowded fine spines with subdued bases.

Material: Two ventral valves, five dorsal valves and a number of broken and crushed fragments: most slightly crushed, registered as UQF 13534, 13535, 13540, 13543 and 26439, from Lakes Creek Group, Rockhampton, Queensland, Australia. (See Crouch & Parfrey 1998, p. 17).

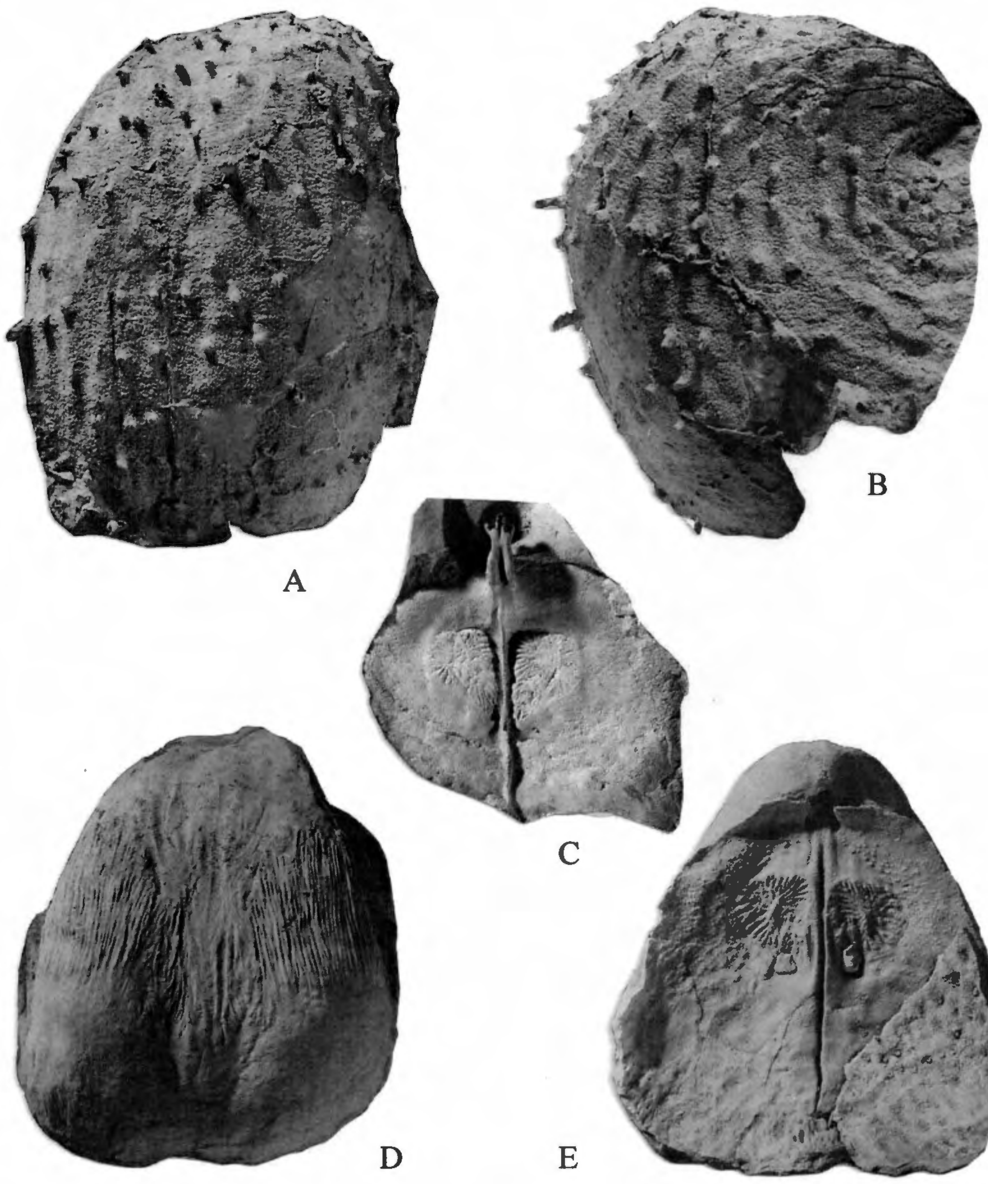


Fig. 10 4. *Lipanteris sparsispinosus* Briggs. A, B, ventral and lateral aspects of UQF 72797, holotype. C, latex cast of dorsal interior, UQF 72796. D, ventral aspect of internal mould, holotype, UQF 72797. E, dorsal aspect of internal mould, UQF 72801. Specimens from Fairyland Formation (Sakmarian), Queensland, Australia, x1. See Briggs in Waterhouse (1986a). D. J. C. Briggs, photo.

Dimensions in mm:

UQF	Width	Length	Height	Valve
26438	85	95	25	ventral
26439	95	88	14	dorsal
13545	76	80	19	dorsal
13535	96	85	13	dorsal

Fig. 10.5. *Taeniothaerus farleyensis* Briggs, external mould of dorsal valve and ventral beak UQF 13543 from Nerimberah Quarry, Lake's Creek Group (Sakmarian), Queensland, Australia, x0.8.
JBW photo.

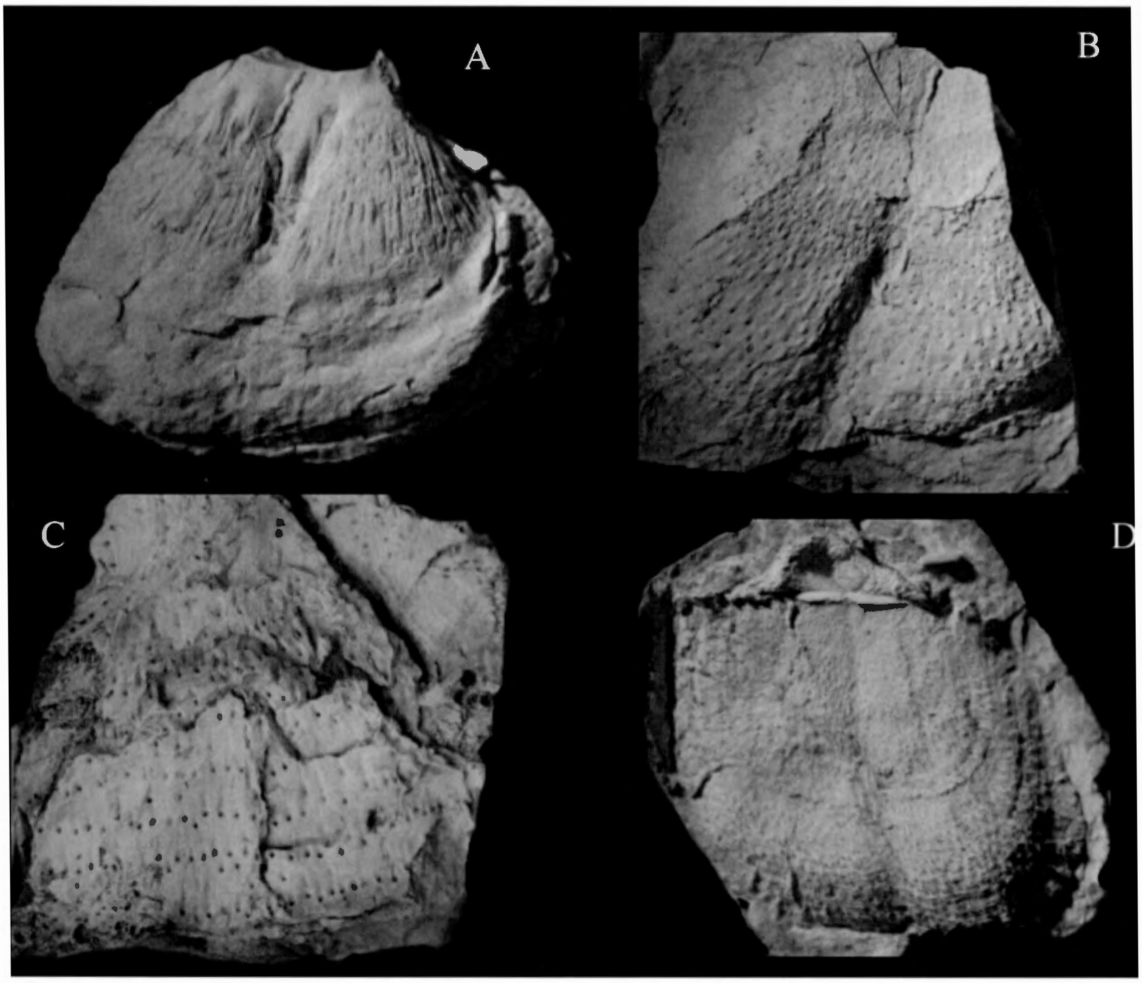


Fig. 10.6. *Taeniothaerus farleyensis* Briggs. A, ventral internal mould UQF 13540, x0.66. B, dorsal external mould UQF 26439, x0.66. C, external mould of ventral valve UQF 26439, x0.75. D, dorsal external mould with ventral umbo, UQF 13535, x0.6. From Lakes Creek Group (Sakmarian), east Queensland. JBW photo.

Description: Ventral valve large with incurved umbo, umbonal angle measures 100°, not deformed, low concave interarea strongly marked by horizontal growth lines and weak vertical striae, divided by pseudodeltidium under umbo, arched to leave a gap where the outer side of the cardinal process impacted (UQF 26440). The ventral valve is traversed by a moderately well formed shallow and narrow sulcus. Cardinal extremities are abruptly obtuse, with angle of 100-110°. The dorsal disc is gently concave and curves gradually into a low trail. A narrow fold commences close to the dorsal hinge, which carries a low flat interarea steeply inclined forward from the disc. Ventral ornament over the umbo consists of fine erect spines 0.4-0.5mm in diameter, and erect spines lie up to 2-3mm apart along concentric rows up to 7mm apart anteriorly, reaching a diameter of 0.8mm, but usually slightly less. Very low spine ridges extend posteriorly towards the preceeding spine row, 3mm up to 7mm long: they gradually increase forward in height and width to terminate anteriorly at the spine base. Some ridges are present without spines. Growth-increments are very fine, up to 35 in 5mm anteriorly, to suggest a life-span close a year or slightly more. Dorsal spines are fine over the entire valve, anteriorly becoming as coarse as those of the ventral valve, up to 2 to 2.5mm apart along rows 2-4mm apart. Spine-bases are less conspicuous than in the ventral valve, but intervening dimples are well formed and elongate. In most specimens the dorsal spines are erect, but anteriorly over the trail of a few specimens some (UQF 13535) to many spines (UQF 13542) are prostrate and the dimples are subrounded rather than elongate.

Ventral adductors sited on two broad ridges, between strongly grooved diductor impressions. The shell, not preserved, appears to have been thin in one specimen, as the external ornament is preserved on the interior, with no other internal markings, but is thicker in other specimens, which have smooth internal surface, and the anterior shell surface bears fine pustules. Cardinal process long and narrow, with deep trough in one specimen, bearing a median slender internal ridge in the other (UQF 13534). The median septum extends from in front of the process for up to 0.75 of the length of the valve. Adductor scars are large and dendritic, without obvious subdivision into pairs, and a low platform extends forward from the anterior shaft of the cardinal process. The posterior floor is smooth and the anterior floor in front of the adductor scars and especially over the anterior disc and trail bears deep pits which possibly extended into the spines.

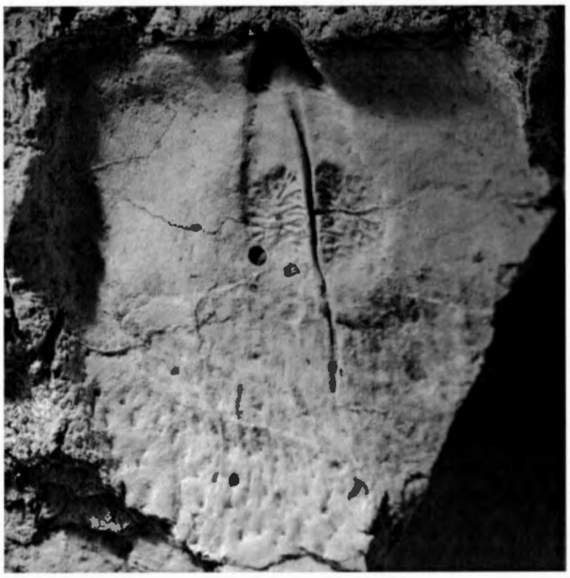


Fig. 10.7. *Taeniothaerus farleyensis* Briggs, dorsal internal mould UQF 13534 from Lakes Creek Group, (Sakmarian), Queensland, x1. JBW photo.

Resemblances: *Taeniothaerus farleyensis* Briggs is strongly arched, and although Briggs (1998) stressed that the hinge of *farleyensis* was short, this is not confirmed from the figure of the holotype UQF 75291 (Briggs 1998, Fig. 69B) as being very much shorter than in other species of *Taeniothaerus*. According to the Briggs' text, ventral spines in *farleyensis* are usually 0.6mm in diameter and dorsal spines are 0.3-0.4mm in diameter, compared with up to 0.8mm in the ventral valve and 0.4-0.5mm in the dorsal valve of *T. homevalensis* Briggs in Waterhouse et al. 1983, but spines are up to 1mm in diameter with bases 3-5mm long in the *farleyensis* topotype UQF 75290 (Briggs 1998, Fig. 69F). Over the ventral ears, spine bases are only 0.6mm thick in UQF 75289, and form rows of closely spaced spines in curtains, but another external mould has more numerous spines, and those of UQF 75292 have many fine spines in clumps. The spine-bases as figured for *farleyensis* are not as as coarse as those over the venter of *homevalensis*, but are just as numerous. On the other hand, dorsal spines are finer and spaced further apart in *farleyensis*, and the dorsal valve is less dimpled, and the ventral muscle field smaller. Adequate information on the stratigraphic position of type *farleyensis* is apparently not available.

Briggs (1998) referred a Yarrol specimen of Maxwell (1964, pl. 7, fig. 35) to the same species, but it has much finer and denser spines.

Genus ***Reedoconcha*** Kotlyar, 1964

The genus *Reedoconcha* Kotlyar, 1964, type species *Productus* (*Taeniothaerus*) *permixtus* Reed, 1932, p. 12 from Early Permian of Kashmir, was named for large shells with elongate crowded spine bases over the ventral valve, numerous postero-lateral spines and essentially no ventral interarea, and elongate spine bases on the dorsal valve. Aspects of the type species have been recently redescribed and refigured by Waterhouse & Chen (2007, pl. 3, fig. 3-5), based on examination of the type material at the Geological Survey of India, Kolkata (Calcutta). Although Briggs (1998, p. 133) distinguished the genus from *Taeniothaerus* by means of its very elongate closely crowded spine-ridges, slight secondary thickening, and smaller size, it is difficult to attribute any generic significance to such criteria. *Reedoconcha* shows long thin ventral spine bases which swell near the anterior terminus and bear a spine. The bases are shown by Reed (1932) as being up to 13-14mm long, whereas they are usually nearer 7-11mm long in Australian *Taeniothaerus*: this variation in length hardly constitutes a generic difference, and Waterhouse & Chen (2007) noted that the length of the ventral spine-bases had been exaggerated in some of Reed's figures. The amount of secondary thickening and size seem taxonomically insignificant, as a reflection of environmental conditions. In the dorsal valve the spine bases are also elongate, narrow and close-set (Waterhouse & Chen 2007, pl. 3, fig. 3). The dorsal interior (Waterhouse & Chen 2007, pl. 3, fig. 4) shows a low ridge on one side in front of the cardinal process, which may be interpreted as a distortion rather than a lateral buttress plate, but although there may remain some room for uncertainty, this specimen is now interpreted as belonging to *Ramaliconcha guryulensis*, as explained on pp. 264, 265. One clear difference from type *Taeniothaerus* lies in the lack of a ventral interarea, emphasized by Reed (1932) as the lack of a "hinge area", and confirmed in his pl. 3, fig. 4a. In studies of Australian species of *Taeniothaerus*, it has been assumed that the presence or absence of a ventral interarea is somewhat variable, but possibly this is in error. No lateral buttress plates are present in two dorsal interiors (Reed 1932, pl. 2, fig. 6, 7), the latter figure showing the interior well. Two well defined species *brenensis* and *permixtus* were recognized by Reed (1932). Reed (1944, pp. 75, 76) pointed out the approach of these forms to two additional species from the Lower Productus Limestone, or Amb Formation, of the Salt Range, Pakistan, described as *Productus* (*Taeniothaerus*) *notabilis* Reed and *P.* (*Taeniothaerus*) *cotteri* Reed, with a similar-looking ventral valve from the lower Agglomeratic Slate or Nagmarg beds of Kashmir, figured by Bion (1928, p. 32, pl. 3, fig. 8). These have finer more closely spaced ventral spines and short bases. The dorsal interior is not known.

The scope of *Reedoconcha* was reviewed by Angiolini in Angiolini et al. (1997, p. 389) in terms of species to be allocated to the genus. Specimens figured as *Taeniothaerus permixtus* by Termier et al. (1974, p. 96, pl. 11, fig. 1-8) from Afghanistan are only moderately close, specimens displaying finer ornament closer to that of another Agglomeratic species of Kashmir, *brenensis* Reed, 1932. They have a low and concave ventral interarea, unlike *permixtus* or *brenensis*. Internal detail is not clear. *Taeniothaerus rusticus* Grunt in Grunt & Dmitriev (1973, pl. 4, fig. 1-6) has finer but otherwise similar ornament, as noted by Angiolini in Angiolini et al. (1997, p. 389), but a ventral interarea is present, and the dorsal interior, although illustrated, is not entirely clear, but apparently without lateral buttress plates. *Taeniothaerus aifamensis* Archbold (1991, Fig. 3F-I) from the Early Permian Aifam Group of Irian Jaya clearly belongs to *Taeniothaerus*, though referred to *Reedoconcha* by Angiolini, and regarded as allied to *Reedoconcha* by Archbold & Gaetani (1993). On the other hand *T. iranicus* Sestini (1966, p. 19, pl. 2, fig. 3a-4) from the Geirud Formation, Member D, of Early Permian age, is echinoconchid, notwithstanding the reference to *Reedoconcha* by Angiolini in Angiolini et al. (1997, p. 389). There are fine numerous spines with short elongate bases over the ventral valve, and a strong single median septum extends in front of the cardinal process (Fantini Sestini 1966, pl. 2, fig. 4). So-called *T.* cf. *permixtus* from the same fauna is also an echinoconch. The material described from the Saiwan Formation of southeast Oman by Angiolini in Angiolini et al. (1997, Fig. 8.7-16), although referred to

Reedoconcha permixtus, has shorter spine bases over the ventral valve than displayed by the Kashmir material, and shows a low triangular ventral interarea, and well developed buttress plates, but apparently no lateral buttress plates. A reference missed by most authors is provided by Yang & Zhang (1982, pl. 2, fig. 1, 2), who recorded *Taeniothaerus permixtus* from the Lower Permian of Xizang (Tibet). The material is more rounded in outline than either *permixtus* or *kashmiricus*, shows no external ornament, and illustrates what appears to be a taeniothaerin internal dorsal valve.

Archbold & Gaetani (1993) suggested that *Productus* (*Buxtonia*) *kashmiricus* Reed (1932, p. 15, pl. 2, fig. 5-8, pl. 3, fig. 4-6, pl. 4, fig. 6-9, var. pl. 4, fig. 10) could represent juvenile and submature specimens of the larger *permixtus* and *brenensis*. This would appear unlikely, because *kashmiricus* is more transverse and is more strongly geniculate, and spine bases are less prolonged, only up to 3mm long and often shorter, with examples figured by Waterhouse & Chen (2007, pl. 3, fig. 6, 7), although the species apparently belongs to *Reedoconcha*. Angiolini in Angiolini et al. (1997) pointed out that the material figured by Archbold & Gaetani (1993) as *kashmiricus*, supposedly immature *permixtus*, had coarser ornament with more erect spines than shown by *permixtus*. The figures provided by Archbold & Gaetani (1993) indicate two different species, one (pl. 4, fig. 1) possibly close to *kashmiricus*, the other (pl. 4, fig. 2) much more elongate, with strong elongate spine bases, and likely to be an immature *permixtus*. Confusing the nature of internal detail for *permixtus*, an unlabelled but figured specimen in Reed (1932, pl. 4, fig. 11) and refigured in Waterhouse & Chen (2007, pl. 3, fig. 8) has lateral buttress plates. It presumably comes from the Agglomeratic Slate of Sakmarian-Artinskian age in Kashmir, and seems likely to belong to *Ramaliconcha guryulensis* new genus, new species (see p. 264). If the specimen belongs to *Reedoconcha*, then this genus is rhamnariid, but such is deemed uncertain at best, and probably unlikely.

Briggs (1998, p. 133) allocated a specimen from "the Lower Marine Series" at Cessnock, Hunter Valley, Sydney Basin, Australia, to *Reedoconcha*, noting that it had been recorded as *Productus subquadratus* by Etheridge & Dun (1909, p. 9). The specimen has moderately thick shell, and the ventral spine bases are slender, not very coarse, and are not visible on the interior shell. The interarea was not visible, so that any identification with *Reedoconcha* remains uncertain.

Tribe **MEGASTEGINI** new tribe

Name genus: *Megasteges* Waterhouse, 1975, p. 6 from Nisal Member (Changshingian), Senja Formation, Nepal.
Diagnosis: Spines suberect to subprostrate in both valves, without prolonged bases and without rhizoid spines. Long buttress plates. Permian (Sakmarian to Changhsingian).
Genera: *Megasteges* Waterhouse, *Austrothaerus* Waterhouse.
Discussion: These two genera are distinguished by the nature of the spines on both valves, which differ from those of Aulostegini with its thick or thin rhizoid spines and Taeniothaerini, with its prolonged spine bases. The dorsal valve of *Megasteges* is gently convex over much of the venter. *Austrothaerus* Waterhouse (2010a, p. 15) from the Sakmarian or early Artinskian Camila Formation of Queensland, Australia, has a moderately developed ear-brush, and the ventral spines are comparatively uniform in size and erect, apart from fine prostrate spines anteriorly. Dorsal spines are in two high-angled series, 0.1-0.2mm diameter and 0.4mm diameter. In *Megasteges*, the ear brush is less developed, and ventral spines are erect and of varying diameters, and dorsal spines are uniformly thin and of one series. This genus is found in Lopingian deposits of Nepal and Tibet, and is not of Capitanian age as claimed by Brunton et al. (2000), nor especially close to *Wyakina* Fredericks. The types of *Megasteges* and *Austrothaerus* are kept at the Queensland Museum, Hendra, Brisbane, rather than "repository unknown" as alleged by Brunton et al. (2000, p. 587) for *Megasteges*. (See Waterhouse 1978, p. 69).

Subfamily **ECHINOSTEGINAE** Muir-Wood & Cooper, 1960

[Echinosteginae Muir-Wood & Cooper, 1960, p. 101].
Diagnosis: Characterized by the usual absence of dorsal spines, ventral spines may be rhizoid. Marginal ridges may be high, no buttress plates.
Discussion: There is a wide range of morphotypes, opening the question of whether the group should be expanded to a full family, as proposed by Waterhouse (2010a). Members of the group lack radial ribbing apart from capillae in some forms, and usually lack dorsal spines. The trail is often very well developed, without being as elaborate as in Chonosteginae, and shells have a more slender disc than in Aulosteginae.

Tribe **ECHINOSTEGINI** Muir-Wood & Cooper, 1960

Fig. 10.8 - Fig. 10.10A - C

[Nom. transl. hic ex Echinosteginae Muir-Wood & Cooper, 1960, p. 101].

Diagnosis: Medium-sized to moderately large, often subquadrate genera with well developed and usually numerous postero-lateral ventral rhizoid spines, dorsal spines usually absent, light or no radial ornament, low to high interarea, with pseudodeltidium as a rule. Strong dorsal marginal ridge, adductor scars well developed in both valves. Lower Permian (Asselian) to Upper Permian (Changhsingian).

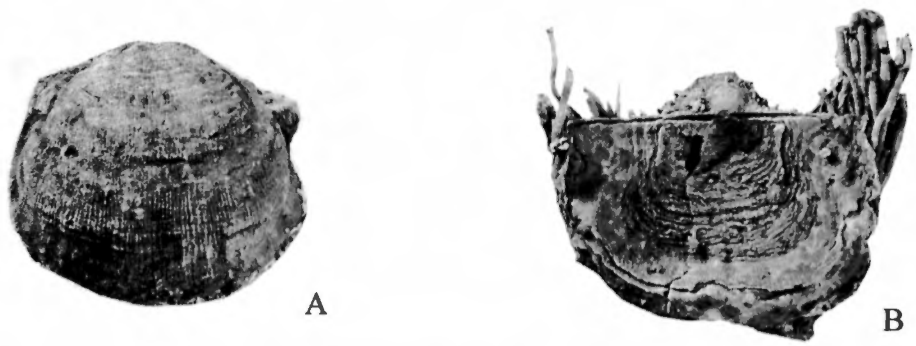


Fig. 10.8. A, *Limbella costellata* Cooper & Grant, ventral aspect of holotype USNM 149086a, from Gaptank Formation, x0.8. B, *L. wolfcampensis* (King). dorsal aspect of USNM 149049c from Neal Ranch Formation. Specimens from west Texas, United States, of late Carboniferous and Asselian age, x1. See Cooper & Grant (1975, pl. 214, 216).

Genera: *Echinosteges* Muir-Wood & Cooper, *Cactosteges* Cooper & Grant, *Edriosteges* Muir-Wood & Cooper, *Jinyugania* new genus, *Lercarella* Mascle & Termier, *Limbella* Stehli, ?*Mistproductus* Yang, *Neoedriosteges* Liang, *Spuriosia* Cooper & Grant.

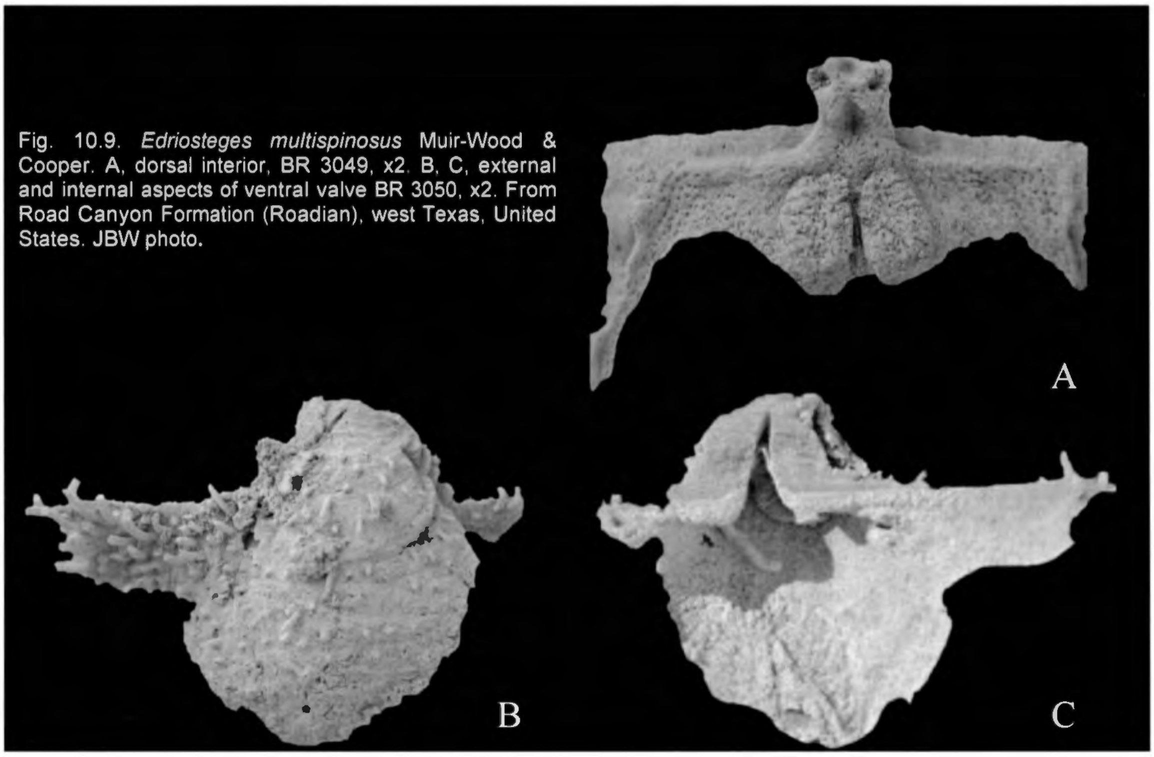


Fig. 10.9. *Edriosteges multispinosus* Muir-Wood & Cooper. A, dorsal interior, BR 3049, x2. B, C, external and internal aspects of ventral valve BR 3050, x2. From Road Canyon Formation (Roadian), west Texas, United States. JBW photo.

Discussion: This tribe is distinguished by the lack of strongly developed radial ornament, though fine radials are often present. *Limbella* Stehli differs in having an open delthyrium and distinctive cardinal process, as discussed by Cooper & Grant (1975, p. 832).

Cactosteges Cooper & Grant (1975) was assigned to Aulostegidae by its authors, and replaced in Rhamnariinae by Brunton et al. (2000). However *Cactosteges* lacks the lateral buttress plates which help typify Rhamnariinae, as shown by Waterhouse (2010a, p. 21), except arguably for one specimen (Cooper & Grant 1975, pl. 230, fig. 45), which is not the type and in that regard differs from other specimens (Cooper & Grant 1975, pl. 230, fig. 39, 40, 42, 44, 46, 47, 49, pl. 231, fig. 46, 47, 50). In this specimen, it appears that the posterior hinge ridge each side of the cardinal process trends more obliquely forward than usual. Unlike other genera *Cactosteges* may display numerous dorsal spines, which are rare in *Edriosteges* and usually lacking from other genera. *Spuriosia* Cooper & Grant, 1975, p. 898 was assigned to Rhamnariinae by its authors and by Brunton et al. (2000, p. 605), but lacks lateral buttress plates and belongs to Echinostegini.

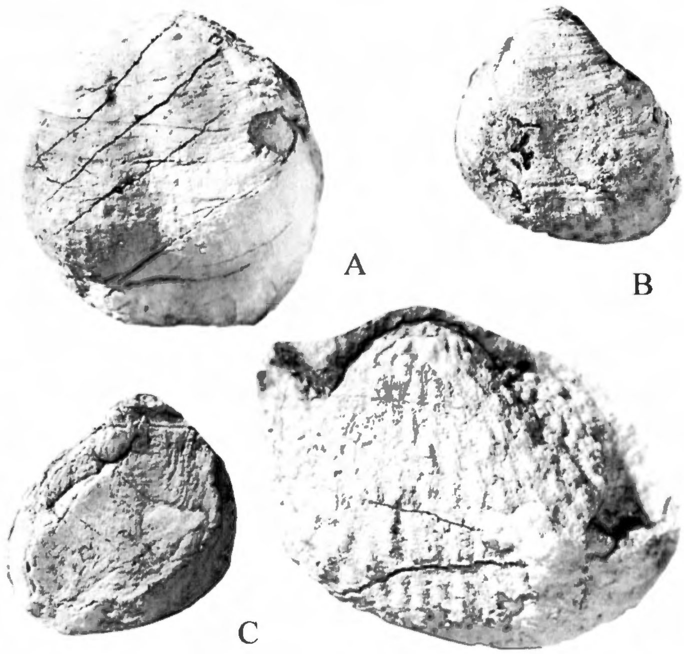


Fig. 10.10. A-C, *Edriosteges shyokensis* Waterhouse, x1.3. A, ventral valve. B, ventral aspect of holotype. C, dorsal aspect of specimen with valves conjoined. D, *Chonostegoides* cf. *baisalensis* Sarytcheva, ventral valve, x2.5. From upper Shyok Valley (Wuchiapingian), northwest India, x2. Specimens unregistered, kept at CASG, Chandigarh, India. J. Coker & JBW photo.

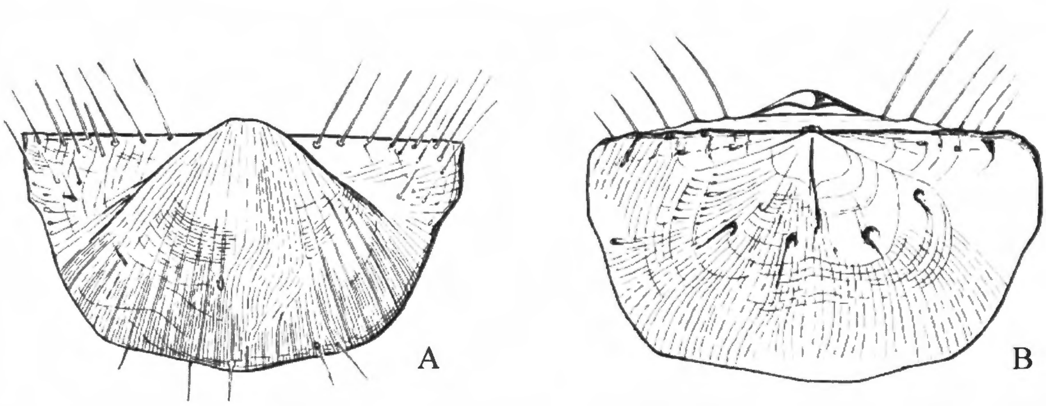


Fig. 10.11. *Lercarella sicana* Mascle & Termier, sketches of ventral and dorsal aspects provided in Mascle & Termier (1970, Fig. 1A, B), from Middle Permian of Sicily, x 1?. (Size not in caption).

Genus ***Lercarella*** Mascle & Termier, 1970

Fig. 10.11

Lercarella Mascle & Termier (1970, p. 188, pl. 17, pl. 18, Fig. 1, 2) comes from flysch in Sicily, and was regarded as a linoproductid by its authors, and treated as a member of Linoproductidae, subfamily uncertain, by Brunton et al. (2000, p. 563). The presence of a high and wide ventral interarea as well as a number of spines over the ears and scattered over the disc, suggests an aulostegoid. The nature of the spines is not clear, but the apparent absence of spines from the dorsal valve, and lack of prominent buttress plates would allow a position within Edriosteginae, and the fine ribs are like those of *Limbella* Stehli. The presence or absence of a pseudodeltidium has not been determined.

Genus ***Jinyugania*** new genus

Fig. 10.12

Derivation: Named for Jin Yugan.

Type species: *Strophalosia poyangensis* Kayser, 1883, p. 190 from Lopingian of southeast China, here designated.

Diagnosis: Moderately large with row of ventral hinge spines and few additional spines laterally, without numerous spines close to the hinge, body spines fine and roughly in quincunx, fine rugae. Dorsal valve without spines.

Discussion: The most distinctive aspect of this genus is provided by the fine closely-spaced narrow rugae that cover especially the dorsal valve: these may be frilled or wavy. An extensive synonymy is provided in Chen et al. (2005, p. pp. 358, 359). Other species that belong to the genus include *Edriosteges acuminatus* Liao (1980, pl. 4, fig. 12-14) and *Aulosteges subplicatilis* Frech (1911). Huang (1932, p. 66, pl. 4, fig. 7-13) has provided good figures for the type species, reinforcing Kayser (1883, pl. 28, fig. 8, 10), and the narrow rugae are shown in a study by Shen & Zhang (2008, Fig. 3.20, 3.21). *Edriosteges* Muir-Wood & Cooper, type species *E. multispinosus* Muir-Wood & Cooper, has more and stronger ventral spines postero-laterally, and the dorsal valve is smooth, apart from indistinct commarginal ornament. The ventral valve in *Jinyugania* often appears to be finely capillate, but possibly this is variable or reflects wear, because Huang (1932) wrote of false radiating striae, due clearly to a measure of decortication. Yet some figures by Liang (1990, pl. 17, fig. 4-15) show capillae. Some ventral valves show closely spaced very fine rugae. Internally the dorsal median septum extends approximately as far forward as the anterior limit of the brachial shields, whereas the septum extends further forward in some specimens of *E. multispinosus*, though this appears variable.

Fig. 10.12. Dorsal aspect of external mould with valves conjoined, BR 3163, possibly close to *Jinyugania poyangensis* (?) (Kayser), but with commarginal rugae more subdued, or worn. Specimen x2, from northern Thailand (Changhsingian). JBW photo.

Specimens ascribed to *Edriosteges poyangensis* by Sarytcheva (1965, pl. 32, fig. 4-6) from the Gnishik faunas of Armenia are capillate over both valves, and rugae are much less fine and regular. Numerous spines lie close to the hinge in three rows, and ventral spines are arranged in quincunx over most of the ventral valve, as in *Edriosteges*.

From the mid-Permian Sosio faunas, shells figured as *Institella salomonensis* (Gemmellaro, 1892) by Cooper & Grant (1975, pl. 246, fig. 1-4) show considerable approach in having fine commarginal rugae over the disc of both valves but the trail is capillate. There appear to be few posterior ventral spines. *Institella* normally has stronger ribs and more marked reticulation, and strong halteroid spines in two or three rows along the hinge.

Aulosteges medlicottianus Waagen (1884, p. 663, pl. 62, fig. 1-4) from the Amb Formation of the Salt Range, Pakistan, is somewhat similar to *Jinyugania poyangensis* in the nature of its ventral spines, but has fewer and better spaced dorsal commarginal rugae. Fine capillae are present on both valves, but appear to be subsurface, and the dorsal valve was explicitly stated to be smooth by Waagen (1884). One outstanding aspect is the nature of the brachial shields, which are small and lie well behind the anterior end of the dorsal median septum, approaching the shields shown in *poyangensis* by Huang (1932, pl. 4, fig. 9).

Genus ***Mistproductus*** Yang, 1991

Mistproductus from the lower Qixia (Chihsia) beds of the Yishan area in Guangxi, China, is moderately large with fine costellae and low closely spaced irregular rugae over both valves. Spines are limited to the ventral valve, in some three irregular rows along the hinge and include disc spines that are either prostrate or have posteriorly elongate bases – not shown in the figures provided by Brunton et al. (2000, Fig. 366.3a-c), but clearly displayed by Yang (1991, pl. 1, fig. 20), assuming all of the figured material is conspecific. Spines were also described as large and rhizoid on the ears. The ventral valve holotype is nasute anteriorly, and was reported to have a cicatrix, though this is not clear in figures. The cardinal process has broad diverging lateral supports, behind a long single dorsal septum, a high marginal ridge and weakly dendritic adductors. The dorsal marginal ridge is moderately developed. Brunton et al. (2000, p. 530) referred the genus to Linoproductinae, with a query, but aspects of the shape and ornament, figures and descriptions do not support this placement, and the relationship merits further enquiry. The shape, size, presence of cicatrix and rhizoid spines and the poor definition of the ears suggest an aulostegid position. This would not fully accord with the lack of an interarea, nor perhaps with the ornament displayed in Yang (1991, pl. 1, fig. 20) that seems to suggest a few elongate spine bases, though none are clearly shown in another figure (pl. 1, fig. 17a, b). *Neoedriosteges* Liang, 1990 shows some approach, with its fine radial capillae, and lack of a ventral interarea, and *Limbella* Stehli, as figured by Cooper & Grant (1975) from the Glass Mountains, west Texas, also has moderately similar ornament with some prostrate spines that look as if they have elongate spine bases (Cooper & Grant 1975, pl. 216, fig. 11). This genus has a ventral interarea.

Genus ***Neoedriosteges*** Liang, 1990

Neoedriosteges Liang, 1990, pp. 150, 460 from the Middle and Late Permian of China, mostly Longtan Formation, is based on *N. transversa* Liang, 1990, pl. 17, fig. 1-3, which includes one of the original figures of *poyangensis* in Kayser (1883, pl. 28, fig. 9). It was distinguished from *Edriosteges* and in particular *poyangensis* by the thin visceral cavity and lack of a ventral interarea, as well as plicated trail, related to spine bases, and irregular pseudopunctae, whereas *poyangensis* has aligned pseudopunctae. *Neoedriosteges* was synonymized with *Edriosteges* by Brunton et al. (2000, p. 594), but this is questionable.

Tribe **AGELESIINI** Cooper & Grant, 1975

[Nom. transl. hic ex Agelesiidae Cooper & Grant, 1975, p. 980].

Diagnosis: Triangular shells with large elongate ears, reduced ventral interarea, moderately strong concentric ornament, strong ear baffles, dorsal adductor scars may be raised. Lower to Middle Permian.

Genera: *Agelesia* Cooper & Grant, ?*Liolimbella* Li Li, ?*Rhytibulbus* Li Li, *Xenosteges* Muir-Wood & Cooper.

Discussion: *Xenosteges* Muir-Wood & Cooper was placed in Echinosteginae by Brunton et al. (2000, p. 599), but is much closer in shape and ornament to Agelesiini. It was pointed out by Brunton et al. (2000, p. 467) that the poorly known *Liolimbella* Li Li (in Ding Yung-jie et al., 1991) looks somewhat like *Rhytibulbus* Li Li, also found in beds of Lower Permian age in China, and this is adopted, though the material needs to be examined.

Family **INSTITELLIDAE** Muir-Wood & Cooper, 1960

[Nom. transl. Waterhouse 2010a, p. 15 ex Institellinae Muir-Wood & Cooper, 1960, p. 117].

Diagnosis: Corpus reticulate or lineate, no dorsal spines, prominent row or rows of posterior spines as a rule, interareas low, cardinal process low and broad.

Discussion: Institellidae is a family represented by a number of genera in tribes and subfamilies, and was treated as a superfamily by Waterhouse (2010a), an approach set aside herein, but arguably to be further considered. Were that to be the case, the family group ranks would need to be upgraded.

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

[Institellinae Muir-Wood & Cooper, 1960, p. 117].

Diagnosis: Trails ribbed, bordered or not by gutters, flanges or skirts.

Tribe **INSTITELLINI** Muir-Wood & Cooper, 1960

[Nom. transl. Waterhouse 2002b, p. 30 ex Institellinae Muir-Wood & Cooper, 1960, p. 117].

Diagnosis: As for subfamily.

Subtribe **INSTITELLINAI** Muir-Wood & Cooper, 1960

Diagnosis: Trails ribbed, bordering structures of gutters, flanges or skirts. Lower Carboniferous (upper Visean) to Middle Permian (Wordian).

Genera: *Institella* Muir-Wood & Cooper, *Craspedona* Cooper & Grant, *Limbifera* Brunton & Mundy, *Polymorpharia* Cooper & Grant, *Spinosteges* Liang.

Discussion: This group is restricted to forms with skirts. *Limbifera* is considered to belong with this group. It has rather linear posterior spines and regularly reticulate disc, very low ventral interarea, ventral skirt, and raised adductor platform. Initially Brunton & Mundy (1988b, p. 63) referred the genus to Sinuatellidae, which seems preferable to the claim that the genus belongs with the productelloid tribe Semicostellini, as proposed by Brunton et al. (2000, p. 463). The brachial loops lie well forward, and suggest an aulostegoid arrangement. *Spinosteges* Liang was rated as a member of Semicostellini by Brunton et al. (2000, p. 464), but *Spinosteges* is very close to *Limbifera*, and Liang (1990) considered the genus to be aulostegoid.

Subtribe **SINUATELLINAI** Muir-Wood & Cooper, 1960

Fig. 10.13

[Nom. transl. Waterhouse 2002b, p. 30 ex Sinuatellidae Muir-Wood & Cooper, 1960, p. 123. Syn. Costellariinae Muir-Wood & Cooper, 1960, p. 124, based on *Costellaria* Muir-Wood & Cooper, 1960 not Swainson 1840 (Treat. Malacol., p. 320), as per Brunton et al. 2000, p. 599; syn. Licharewiconchidae Kotlyar, Zakharov & Polubotko, 2004, p. 517].

Diagnosis: No bordering skirt. Ornament elaborate and varied, often reticulate, interarea low, cardinal process low, broad. Lower Carboniferous (Visean) to Upper Permian (Changhsingian).

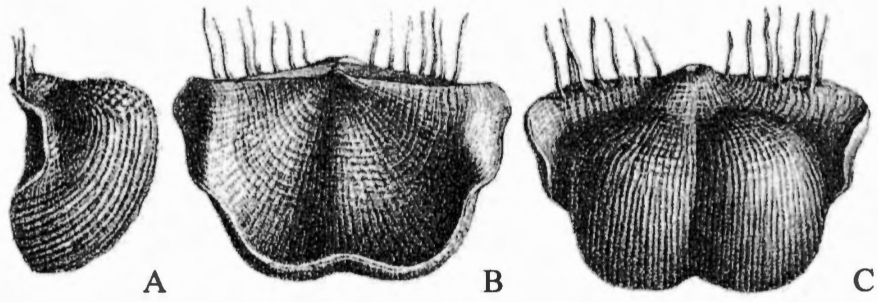


Fig. 10.13. *Sinuatella sinuatus* (Koninck), lateral, dorsal and ventral aspects of specimen from Lower Carboniferous of Derbyshire, England, figured by Davidson (1861, pl. 33, fig. 8a-c), x2 approx.

Genera: *Sinuatella* Muir-Wood, *Costellarina* Cooper & Muir-Wood, 1967 (nom. nov. pro *Costellaria* Muir-Wood & Cooper, 1960 non Swainson 1840, Treat. Malacol., p. 320), *Glyptosteges* Cooper & Grant, *Huaitakia* new genus, *Licharewiconcha* Kotlyar, Zakharov & Polubotko.

Discussion: These genera were included with Institellinae by Brunton et al. (2000, p. 604) but are here separated because they lack a skirt.

Genus ***Huaitakia*** new genus

Fig. 10.14

Derivation: Named from Huai Tak, settlement in north Thailand.

Type species: *Glyptosteges? percostatus* Waterhouse, 1983d, p. 120 from Huai Tak Formation (Changhsingian), north Thailand, here designated.

Diagnosis: Small, ears large, costae strong, interareas well formed. Spines few over visceral disc and trail of ventral valve, no strong posterior halteroid spines.

Discussion: This genus is very close in shape and ornament to *Glyptosteges* Cooper & Grant, 1975, p. 876, which is represented by five species in the Skinner Ranch and Bone Spring Formations of lower and upper Kungurian age in west Texas, United States. The Thai genus is younger, and differs in lacking the prominent and comparatively numerous halteroid spines developed close to the ventral hinge of *Glyptosteges*. Instead the ventral ears of the Thai type species are more or less smooth without strong spines. *Huaitakia* differs further in lacking the close-set growth laminae and low slender rugae of that genus. In that respect it marks a varion, a strong deviation from parental and coeval stock. No other genus comes close.


A B C

Fig. 10.14. *Huaitakia percostatus* (Waterhouse). A, C, latex cast and internal mould, x3, x2, of holotype, TBR 407. B, latex cast of ventral exterior, TBR 408, x3. From Huai Tak Formation (Changhsingian), northern Thailand. See Waterhouse (1983d). J. Coker & JBW photo.

Tribe **INSTITININI** Muir-Wood & Cooper, 1960

[Nom. transl. hic ex Institininae Muir-Wood & Cooper, 1960, p. 164].

Diagnosis: Concentric wrinkles prominent, spines and elevations sited along wrinkles, and posterior spines developed. Lower Carboniferous (Tournaisian – Visean).

Genera: *Institina* Muir-Wood & Cooper, *Archaiosteges* Carter, *Kwantovia* new genus, *Retroplexus* Brunton & Mundy, *Rugicostella* Muir-Wood & Cooper, *Stipulina* Muir-Wood & Cooper.

Discussion: Institinini associates several genera with allied ornament and of much the same age, some previously scattered in different groupings, and with reticulation less prominent than in Institellini. *Institina* was treated as a member of Institellinae by Brunton et al. (2000, p. 599), and the subfamily Institinini not even mentioned as a synonym. *Stipulina* Muir-Wood & Cooper, of upper Visean age, has an interarea (counter to Muir-Wood & Cooper 1960, p. 200), extending not far along the hinge but comparatively high, and heavy ridges lie inside the ventral ears. There are no teeth, and brachial shields are constricted. *Stipulina* is shaped like *Agelesia* from the Cathedral Mountain Formation of the Glass Mountains, Texas, but has coarse rugae and different spines, and is distinctly older than members of the Agelesiini, with which it was associated in the *Revised Brachiopod Treatise*. *Rugicostella* Muir-Wood & Cooper, put in Institellinae by Brunton et al. (2000, p. 603), displays productid brachial shields with possible scar of attachment of lophophore spirals according to Muir-Wood & Cooper (1960, p. 167, pl. 59, fig. 10-12), smooth adductors and clasping spines.

Genus ***Kwantovia*** new genus

Fig. 10.15

Derivation: Named from Kwanto Massif, Japan, source of type species.

Type species: *Rugicostella sakagamii* Yanagida, 1973, p. 104 from a Visean fauna at Mitsuzawa, Kwanto Massif, Japan, here designated.

Diagnosis: Inflated shells with close-set commarginal rugae, spines limited to ventral valve, spines prominent posteriorly, fine over disc, emerging from short prominent ribs or spine bases over long trail.

Discussion: *Kwantovia* is related to *Rugicostella* Muir-Wood & Cooper, 1960 and *Retroplexus* Brunton & Mundy, 1988b. All three are of similar shape, and have long posterior and postero-lateral ventral spines, those of *Kwantovia* being poorly preserved, and closely spaced commarginal rugae. The prime difference lies in the ornament over the ventral trail. The ventral trail of *Rugicostella* has coarse costae, well developed in the type species *R. nystianus* (Koninck), and seen in a Japanese occurrence reported by Yanagida (1965). The ventral trail of *Retroplexus* shows few anterior ribs, and fine radial ribs are developed: it is very close to *Rugicostella*. In *Kwantovia*, fine radial ribs are not developed, and the ventral trail is ornamented by well defined short ribs, each usually bearing a spine. *Kwantovia* has a rather irregular growth habit, with small cicatrix, often relatively high interarea, and cincture less developed than in *Rugicostella*. The dorsal adductor platform is narrow and high (Yanagida 1973, pl. 15, fig. 3a, Fig. 7). It is readily distinguished from the other two genera, which appear to be more closely related to each other.

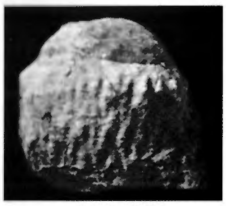


Fig. 10.15. *Kwantovia sakagamii* (Yanagida), anterior view of ventral valve GK-D 31168 from Visean of Kwanto Massif, Japan, x1, showing distinctive trail. See Yanagida (1973).

Subfamily **CHONOSTEGINAE** Muir-Wood & Cooper, 1960

Fig. 10.10D, Fig. 10.16, Fig. 10.17

[Subfamily Chonosteginae Muir-Wood & Cooper, 1960, p. 113].

Diagnosis: Small shells with complex spinose corpus margin, strong geniculation, short trails, strong anterior ribs, generally low to moderate interareas. Upper Carboniferous (?Gzhelian) to Upper Permian (Changhsingian).

Genera: *Chonosteges* Muir-Wood & Cooper, *Chonostegoides* Sarytcheva, *Costisteges* Liao, ?*Strophalosiina* Licharew, *Urushtenia* Licharew, *Urushtenoidea* Jin & Hu (?syn. *Uncisteges* Jin & Hu).

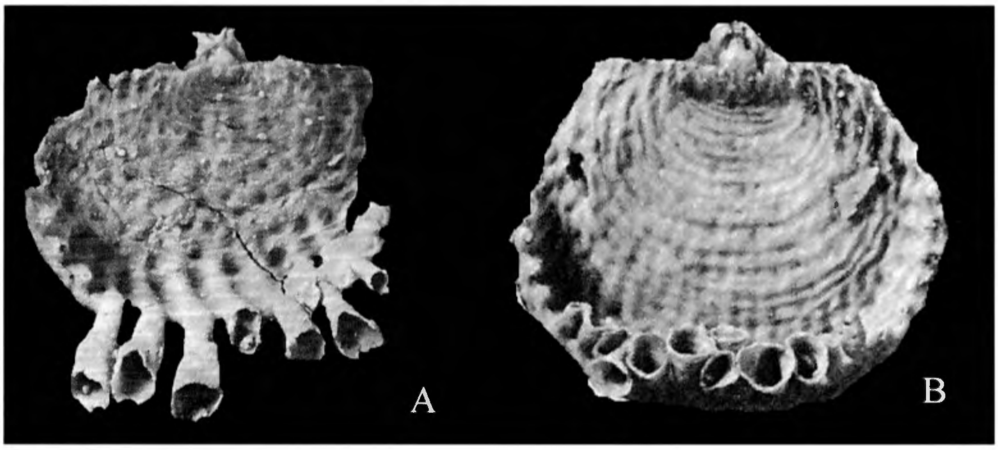


Fig. 10.16. A, *Chonosteges variabilis* Cooper & Grant, dorsal exterior USNM 154155, x4. B, *C. pulcher* Cooper & Grant, dorsal exterior USNM 154157f, x2. Specimens from Cathedral Mountain Formation (Kungurian), Texas, United States, showing intake funnels around anterior margin. See Cooper & Grant (1975, pl. 243, 244).

Discussion: *Strophalosiina* has moderately high ventral interarea, and anterior costae suggestive of Chonosteginae, but the anterior margin is simpler, or at least appears so, suggesting flexigenesis, unless the corpus margin is incompletely preserved. It was formerly placed in Echinosteginae by Brunton et al. (2000, p. 599). *Uncisteges* Jin & Hu, 1978, p. 117 is based on *Eomarginifera crenulata* Ting in Yang Tsun-yi et al. 1962. *Uncisteges maceus* Jin, 1965, p. 19 in Jin & Hu (1978, p. 117, pl. 2, fig. 7, 8) has less commarginal ornament than in *Urushtenoidea* Jin & Hu 1978, p. 116, but the genera were judged to be synonymous by Brunton et al. (2000, p. 592). A posterior platform formed by buttress plates, with small "antron", was described for *Urushtenia* by Jin, whereas the adductors were reported to be raised and an alveolus is developed, according to the original diagnosis of *Urushtenoidea,* based on *Urushtenia chaoi* Jin (1963, p. 15. pl. 2, fig. 7, 8, 13-17). Presumably one of the authors in Brunton et al. (2000) later came to judge the difference to be of no account, and good illustrations and redescription of the types are required to consolidate the re-assessment.

Fig. 10.17. *Urushtenia pseudomedusa* (Tschernyschew) . A, B, posterior and anterior views of ventral valve BR 3064, x1.5. C, dorsal aspect of specimen with valves conjoined, BR 3067, x2. D, decorticated dorsal interior of BR 3066, x2. Anterior margin may be broken. From Schwagerina beds (Sakmarian) near Sterlitamak, Russia. The anterior margins likely to be broken. JBW photo.

Subfamily **GONDOLININAE** Jin, Brunton & Lazarev, 1998

[Gondolininae Jin, Brunton & Lazarev, 1998, p. 8].

Diagnosis: Elongate trigonal shell with fine ribs. Commarginal ornament subdued or absent.

Tribe **GONDOLININI** Jin, Brunton & Lazarev, 1998

[Nom. transl. hic ex Gondolininae Jin, Brunton & Lazarev, 1998, p. 8].

Diagnosis: Elongate triagonal shells with fine ribs, long narrow ventral interarea, rhizoid spines on ventral umbonal margins. Lower Carboniferous (upper Visean – lower Serpukhovian).

Genus: *Gondolina* Jin & Liao.

Discussion: As pointed out by Jin, Brunton & Lazarev (1998), *Gondolina* Jin & Liao in Wang et al. 1966, p. 412 is a homeomorph of another exceptional genus *Striatifera*, and its origins are obscure.

Tribe **SPHENOSTEGINI** Waterhouse, 2002b

[Nom. transl. hic ex Sphenosteginae Waterhouse, 2002b, p. 29].

Diagnosis: Small often ovally subtriangular shells with relatively high ventral interarea and subtriangular shape, fine ventral spines as a rule, and lacking the burst of strong and generally rhizoid postero-lateral spines found in most Echinosteginae and most constituents of Institellidae. Both valves finely ribbed. Marginal ridges not strong. Lower Permian (Asselian?) to Middle Permian (Capitanian?).

Genera: *Sphenosteges* Muir-Wood & Cooper, *Baissalosteges* Kotlyar, *Spirisosium* de Gregorio, *Strophalosiella* Licharew.

Discussion: This tribe associates genera that were placed with Echinosteginae by Brunton et al. (2000, p. 595), but differ in shape, ventral ornament, and dorsal interior (Waterhouse 2010a, p. 14, table 1). The presence of fine ribs over both valves and often triangular shape in genera of the tribe suggest an association with Gondolinini, and the group is distinguished from Gondolinini by its more prominent spines. *Strophalosiella* Licharew, 1935, p. 375 is not well known, but has lower interarea, whereas the ornament is like that of *Sphenosteges*.

Family **MONTICULIFERIDAE** Muir-Wood & Cooper, 1960

[Nom. transl. Waterhouse 1978, p. 29 ex Monticuliferinae Muir-Wood & Cooper, 1960, p. 327].

Taxonomy: Liang (1990, p. 197) also used Monticuliferidae. Brunton et al. 2000, p. 536 cited their own article by Brunton et al. (1995, p. 929) as being first to treat Monticuliferidae as a full family. That is incorrect. This procedure seems to have been an almost default or reflex action: anything not named by Muir-Wood & Cooper (1960) and a few select authors was credited to themselves. That does not necessarily indicate self-glorification, and although it diminishes the reliability of the *Revised Brachiopod Treatise*, may be construed as a time-saving device to reduce the amount of back-ground research in order to meet critical dead-lines, and any view that it was relatively unimportant to resolve the authorship of rank change is surely reasonable. The focus in that work was primarily on the initial proposal of genera, and it may be speculated that dead-lines placed a considerable burden on authors who undertook massive commitment for several major chapters.

Diagnosis: Typified by small round tumulae or blisters called monticules over the exterior, or taxa derived from such stock. An erect spine may arise from the middle of each swelling. Ribs if present pass into and out of or over the monticules. Interareas well developed on each valve and seemingly but not definitely with a pseudodeltidium. Ventral muscle field raised anteriorly, cardinal process broad and trifid, brachial shields rather elongate.

Discussion: This family was conceived initially as a subfamily within Linoproductidae by Muir-Wood & Cooper (1960), a step that appears well justified by the fine radial capillae which appear on *Monticulifera* itself, although not on all of the few associated genera. After careful consideration, the group has been re-evaluated as a member of Aulostegoidea, for these reasons: 1, the group does not fit with any member of Linoproductoidea, in detail of ornament, shape, cardinal process, or muscle scars for the most part. 2, the type 6 construct of disc and trail (see p. 24) is like that of various aulostegoids such as *Institella* and *Sinuatella*. 3, capillae are present in some aulostegoids, such as *Limbifera*, *Lercarella*, *Gondolina* and *Edriosteges*. 4, the monticules show a moderate approach to the tubercles found in *Edriosteges tuberculatus* (King). 5, the ventral interarea is well developed (Liang 1990, pl. 37, fig. 5), whereas it is largely absent from Linoproductoidea. 6, the chordate ventral muscle field is very like that of *Sinuatella* Muir-Wood, 1928 (see Muir-Wood & Cooper, 1960, pl. 57, fig. 9, 11). 7, the cardinal process is broad rather than dominated by a central shaft, with weak suggestion of lateral supporting plates (Muir-Wood & Cooper 1960, p. 327).

Several of these indications are not finally conclusive. For instance *Compressoproductus* shows fine radial ornament and a chordate ventral muscle field, and *Fluctuaria* Muir-Wood & Cooper and *Sartenaeria* new genus have what may be loosely termed submonticules. But these genera relate to others within the linoproductoid spectrum, whereas Monticuliferidae does not conform as a whole, and appears to be better placed within Aulostegoidea, given its general shape and various attributes. At the same time, it forms a unique group within that superfamily, lacking prominent postero-lateral ventral spines, lacking a high dorsal marginal ridge, and showing unique ornament.

Brunton et al. (2000) expanded the scope of Monticuliferinae by adding Auriculispininae Waterhouse, Compressoproductinae Jin & Hu, Devonoproductinae Muir-Wood & Cooper, Eoproductellinae Lazarev, Gigantoproductinae Muir-Wood & Cooper, Striatiferinae Muir-Wood & Cooper and Schrenkiellinae Lazarev. Many of these subfamilies have very different ornament, and the prime reason for association, having a moderately shallow body corpus, as advocated by Brunton et al. (2000) and Brunton (2007), seems to have limited validity. Waterhouse (1986b) also allocated Auriculispininae to the family, but this view is now set aside. *Monticulifera* has unusual monticules, which are only moderately similar to the slightly swollen spine bases that lie posterior to the ventral spines in Auriculispininae. Instead, the auriculispinin ornament is much closer to that of Proboscidellinae Muir-Wood & Cooper.

Sartenaeria new genus (p. 409) shows blister-like swellings of shell over the ventral valve, traversed by fine ribs. The genus is of Visean age in northern Europe, and judged to belong to Proboscidelloidea, from its elongate spine bases, and its shape.

Subfamily **MONTICULIFERINAE** Muir-Wood & Cooper, 1960

Fig. 10.17, Fig. 10.18

[Monticuliferinae Muir-Wood & Cooper, 1960, p. 327].

Diagnosis: Capillae present. Lower Permian (Artinskian) to Upper Permian (Wuchiapingian?).

Fig. 10.17. *Monticulifera sinensis* (Frech), ventral view of USNM 123013, as figured by Muir-Wood & Cooper (1960, pl. 125, fig. 6), x 1.5 From Capitanian? of Kongshien, Szechuan, China.

Genera: *Monticulifera* Muir-Wood & Cooper (syn. *Choanoproductus* Termier & Termier, *Sinoproductus* Chan & Li), *Chilianshania* Yang & Ting (= *Capillifera* Jin & Ye, invalid; syn *Pseudomonticulifera* Zhao & Tan), *Zhenania* Ding.

Discussion: This subfamily is typified by a few genera, largely as itemized by Brunton et al. (2000, pp. 536, 537). There is a long single dorsal medium septum in *Monticulifera*, and the cardinal process is described as broad and trifid with low median shaft bearing a broad shallow cleft, and two distinct lateral lobes (Muir-Wood & Cooper 1960, p. 327). *Choanoproductus* Termier & Termier, 1970a was judged to be indeterminate by Brunton et al. (2000, p. 643) and considered likely to be a junior synonym of *Monticulifera* by Waterhouse (2002b, p. 53). (See p. 457).

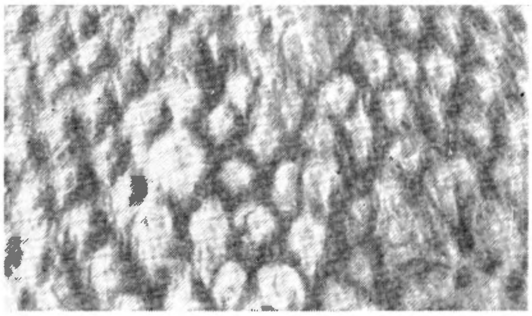


Fig. 10.18. *Monticulifera shizilingensis* Liang. Detail of ventral ornament, as shown by Liang (1990, pl. 37, fig. 7) from Lengwu Formation (Capitanian?), Zhejiang, China, x4.

Subfamily **TONGLUELLINAE** Liang, 1990

[Tongluellinae Liang, 1990, p. 202].

Diagnosis: Capillae or monticules may be lacking. Middle Permian (Guadalupian).

Genera: *Paramonticulifera* Tong (syn. *Tongluella* Liang), ?*Zhejiangoproductus* Liang.

Discussion: The obscure genus *Zhejiangoproductus* Liang, 1990, p. 196, pl. 30, fig. 5-11 is largely smooth, with few spines limited to hinge and ears. It is shaped like Monticuliferidae in size, outline, wide sulcus, large disc and geniculate trail, but Liang (1990) placed the genus in Horridoniidae. The lack of monticules implies a strong deviation from monticuliferid stock.

Brunton et al. (2000, p. 537) considered that *Paramonticulifera* Tong, 1978, p. 234 had priority over *Tongluella* Liang, 1990, p. 202 [p. 466].

11. Superfamily **RICHTHOFENIOIDEA** Waagen, 1885

Fig. 10.1

[Nom. correct. Brunton et al. 1995, p. 933 pro Richthofeniacea Muir-Wood, 1955, p. 69 nom. transl. ex Richthofeniidae Waagen, 1885, p. 729].

Diagnosis: Ventral valve conical or sphenoid, dorsal valve cap-like or sunk below ventral margin, ventral margin attached to substrate directly or by rhizoid spines or both; interarea absent.

Discussion: This fascinating superfamily is briefly and well discussed by Wardlaw et al. (2000). They drew attention to the uncertainty, indicated by ', surrounding the relationships of several of the genera. The group evolved from Aulostegoidea during Upper Carboniferous time (Sutherland 1996), and differences in morphology from Aulostegoidea warrant full superfamily status. Indeed the exceptional morphology amongst Productida might be better signified through designation at a higher rank. The classification is spaced out, with only one genus in some family groups. Exceptional morphology is exemplified by a subperipheral ring of endospines in the ventral valve which branched and amalgamated to form a net, called a coscinidium, over the opening. A myocoelidium is formed in the ventral valve of some genera as a chamber for attachment of muscles.

Family Richthofeniidae Waagen, 1885
Family Hercosiidae Cooper & Grant, 1975
Family Teguliferinidae Muir-Wood & Cooper, 1960
Subfamily Teguliferininae Muir-Wood & Cooper, 1960
Subfamily Cyclacanthariinae Cooper & Grant, 1975
Tribe Cyclacanthariini Cooper & Grant, 1975
Tribe Collumatini Waterhouse, 2002b
Subfamily Zalverinae Brunton, 1996
Family Gemmellaroiidae Williams, 1953

Table 13: Superfamily Richthofenioidea Waagen, 1885.

Family **RICHTHOFENIIDAE** Waagen, 1885

Fig. 11.1

[Richthofeniidae Waagen, 1885, p. 729].

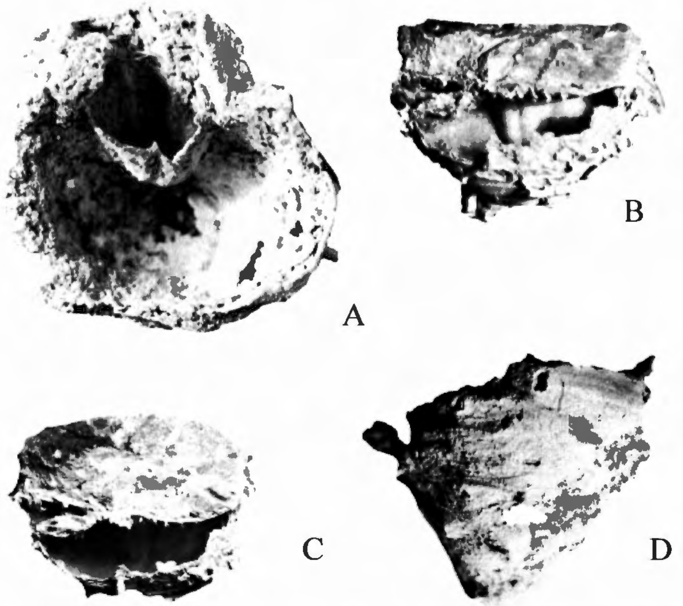


Fig. 11.1. A, D, Richthofeniid gen. & sp. indet. apertural and lateral views of ventral valve ROM 31976 (formerly B 338), x 3. B, C, *Globosobucina scopae* Waterhouse & Piyasin, internal views, showing internal face of myocoelidium through gap between ventral and dorsal valves, ROM 31974 (formerly B 538), x3 approx. From Rat Buri Formation (Roadian), Khao Phrik, southern Thailand. See Waterhouse & Piyasin (1970). B. O'Donovan & JBW photo.

Diagnosis: Conical, spines rhizoid, ventral myocoelidium. Lower Permian (?Artinskian) to Upper Permian (?Changhsingian).

Genera: *Richthofenia* Kayser, *Coscinarina* Muir-Wood & Cooper, *Globosobucina* Waterhouse & Piyasin, *Seseloidia* Grant, ‘*Striirichthofenia* Lu Tong-Chen.

Family **HERCOSIIDAE** Cooper & Grant, 1975

Fig. 11.2, Fig. 11.3

[Hercosiidae Cooper & Grant, 1975, p. 928].

Diagnosis: Conical, rhizoid spines and high blade-like ventral median septum. Lower Permian (Artinskian) to Upper Permian (Changhsingian).

Genera: *Hercosia* Cooper & Grant, *Hercosestria* Cooper & Grant, ‘*Neorichthofenia* Shen, He & Zhu, *Sicularia* Grant, ‘*Strophorichthofenia* Termier et al.

Discussion: Juvenile *Hercoestria* has a myocoelidium.

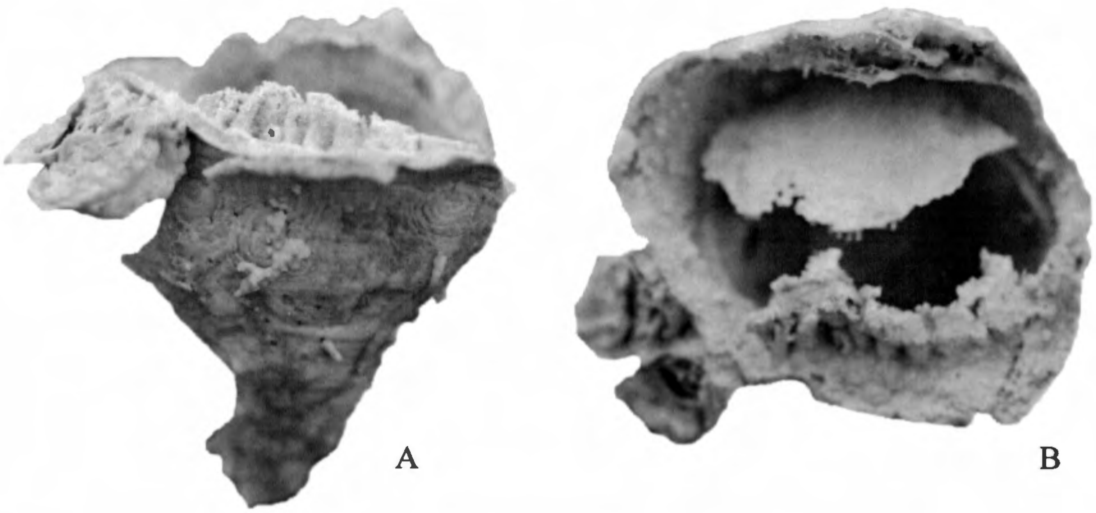


Fig. 11.2. *Hercosia uddeni* (Böse), lateral and dorsal-apertural views of BR 3059, silicified specimen, x3. From Cathedral Mountain Formation (Kungurian), west Texas, United States. JBW photo.

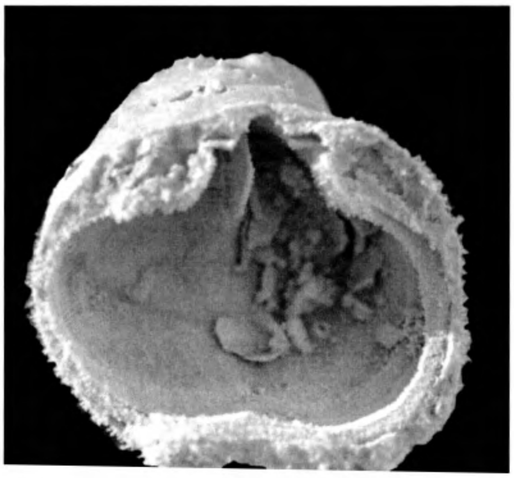


Fig. 11.3. *Hercosia uddeni* (Böse), apertural view of ventral valve showing median septum, BR 3069, silicified specimen, x4. From Cathedral Mountain Formation (Kungurian), west Texas, United States. JBW photo.

Family **TEGULIFERINIDAE** Muir-Wood & Cooper, 1960

[Teguliferinidae Muir-Wood & Cooper, 1960, p. 92].

Diagnosis: Conical, spines rhizoid or absent, coscinidium present or absent, ventral muscle callosity.

Discussion: Wardlaw et al. (2000) treated this group as a subfamily of Cyclacanthariidae Cooper & Grant. But the Cooper-Grant taxon was named later, and therefore was relegated to subfamily level by Waterhouse (2002b).

Subfamily **TEGULIFERININAE** Muir-Wood & Cooper, 1960

[Nom. transl. Brunton et al. 1995, p. 933 ex Teguliferinidae Muir-Wood & Cooper, 1960, p. 92].

Diagnosis: Obliquely conical or sphenoid, spines rhizoid, no coscinidium. Upper Carboniferous (Bashkirian) to Lower Permian, possibly younger Permian.

Genera: *Teguliferina* Schuchert & Le Vene (nom. nov. pro *Tegulifera* Schellwien, 1898 non Saalmüller, 1880), *Acritosia* Cooper & Grant, *Ardmosteges* Sutherland, *Planispina* Stehli, *Proteguliferina* Licharew.

Subfamily **CYCLACANTHARIINAE** Cooper & Grant, 1975

[Nom. transl. Brunton et al. 1995, p. 933 ex Cyclacanthariidae Cooper & Grant, 1975, p. 938].

Diagnosis: Conical with coscinidium or rim of protective spines.

Tribe **CYCLACANTHARIINI** Cooper & Grant, 1975

[Nom. transl. hic ex Cyclacanthariidae Cooper & Grant, 1975, p. 938].

Diagnosis: Rhizoid supporting spines. Middle Permian (Roadian – Capitanian).

Genera: *Cyclacantharia* Cooper & Grant, *Sestropoma* Cooper & Grant, *Taphrosestria* Cooper & Grant.

Tribe **COLLUMATINI** Waterhouse, 2002b

[Collumatini Waterhouse, 2002b, p. 45].

Diagnosis: No supporting rhizoid spines. Middle Permian (Roadian).

Genus: *Collumatus* Cooper & Grant.

Subfamily **ZALVERINAE** Brunton, 1996

[Nom. transl. Wardlaw et al. 2000, p. 617 ex Zalveridae Brunton, 1996, p. 53].

Diagnosis: Conical, no external or apertural spines, weakly attached. No coscinidium. Upper Carboniferous (Bashkirian – Moscovian).

Genus: *Zalvera* Brunton.

Family **GEMMELLAROIIDAE** Williams, 1953

[Gemmellaroiidae Williams, 1953, p. 10].

Diagnosis: Conical with long ventral interarea, spines few, on ventral valve only or absent. Dorsal valve cap-like, myocoelidium present. Middle Permian (? Wordian) to Upper Permian (Changhsingian).

Genera: *Gemmellaroia* Cossmann (nom. nov. pro *Megarhynchus* Gemmellaro, 1894 not de Laporte, 1832, mis-spelled *Megalorhynchus* de Gregorio, syn. *Gemmellaroiella* Mabuti), *Cyndalia* Grant.

12. SUBORDER OLDHAMINIDINA WILLIAMS, 1953 = SUBORDER LYTTONIIDINA WILLIAMS, HARPER & GRANT, 2000

Fig. 12.1

[Oldhaminidina Williams, 1965, p. 510, pro suborder Oldhaminoidea Williams, 1953, p. 286. Alt. Lyttoniidina Williams, Harper & Grant, 2000, p. 619].

Taxonomy: Williams (1953, p. 510) recognized Oldhaminidina, and this name was replaced by Lyttoniidina by Williams, Harper & Grant, 2000, p. 619, in what is no more than a name adjustment (Waterhouse 2010a). Oldhaminidina has clear priority, and the shift in name seems slightly unfortunate, in so far as *Lyttonia* does not feature as a genus within Lyttoniidina, because the name *Lyttonia* has proved to be a junior synonym of *Leptodus* Kayser, 1883. Evidently it was deemed necessary or at least highly desirable to project the family group name into ordinal categories, though this is nowhere mandated by the International Code for Zoological Nomenclature (1999). There are disadvantages in following such a rigorous but self-imposed and non-stipulated procedure, because it impels the conservation and application or misapplication of unsatisfactory names, either based on a highly exceptional and untypical genus hardly representative of the group as a whole, or even, as in this case, still-born, a junior synonym, a non-genus. It would surely be advantageous and benefit taxonomy as a whole to be allowed to characterize major groupings of taxa through use of ordinal names that embraced most of the taxa by selecting an appropriate rather than first-proposed family group, instead of strangling the descriptive power of ordinal nomenclature by insisting on priority imposed by family group rather than ordinal nomenclature, regardless of suitability. Oldhaminidina is much to be preferred over Lyttoniidina, and has priority. Furthermore, as argued by Waterhouse (2010a), Lyttoniidina reflects simply a name-shift, and the concept and authorship should remain attributed to Williams (1953).

Diagnosis: Dorsal valve consists mainly of lobate brachial plate, ventral valve much larger and deeper with variably developed posterior flap, but no interarea, articulation structures weakly developed, spines rarely present, secondary shell layer pseudopunctate.

Discussion: The anatomy and classification were well discussed by Williams, Harper & Grant, 2000. There are relatively few genera and not many groups for making up a full suborder, so that it may be wondered why the family group units are not downscaled into tribes, and superfamilies reduced to families. But the imperative, long realised by Williams, is to express the morphological distance from other Productida.

SUPERFAMILY LYTTONIOIDEA WAAGEN, 1883
Family Lyttoniidae Waagen, 1883
Subfamily Lyttoniinae Waagen, 1883
Subfamily Poikilosakinae Williams, 1953
Family Rigbyellidae Williams, Harper & Grant

SUPERFAMILY LOCZYELLOIDEA LICHAREW, 1937
Family Loczyellidae Licharew, 1937
Subfamily Loczyellinae Licharew, 1937
Subfamily Lithocothiinae new subfamily
Subfamily Caninellinae Liang, 1990

Family Permianellidae He & Zhu, 1979

Table 14. Classification of Suborder Oldhaminidina (=Lyttoniidina) Williams, 1953.

The overall evolution of the group is presented by Williams, Harper & Grant (2000, Fig. 454, p. 630). It pictures the group as arising from "an assumed ancestral strophalosioid group represented by *Falafer* Grant", which is very close to the present model, and stands at odds with the interpretation by Brunton et al. (2000) that *Falafer* was judged to be an aulostegoid. Although it may be conjectured that this was the view of Brunton and/or Lazarev rather than that of Grant, who had died in late 1994 (see Brunton, Lazarev & Grant 2000, p. 362), that would be unfair, because Grant (1976) strongly favoured an aulostegid relationship. *Falafer* may be classed in a very small superfamily Cooperinoidea, a group which arose from Strophalosioidea, not Aulostegoidea, and Oldhaminidina also arose from Strophalosioidea. The nature of the large lobate brachiophores in Oldhaminidina suggest derivation from Cooperinoidea, sourced in turn from within Strophalosiidae. But the fossil record of Cooperinoidea is largely limited to the Permian Period, with rare possible occurrences in the Pennsylvanian (see p. 271), and it remains uncertain whether Cooperinoidea represent hold-overs from ancestral stock, or, rather less likely, degenerates from Oldhaminidina that somehow redeveloped spination and other elaborations.

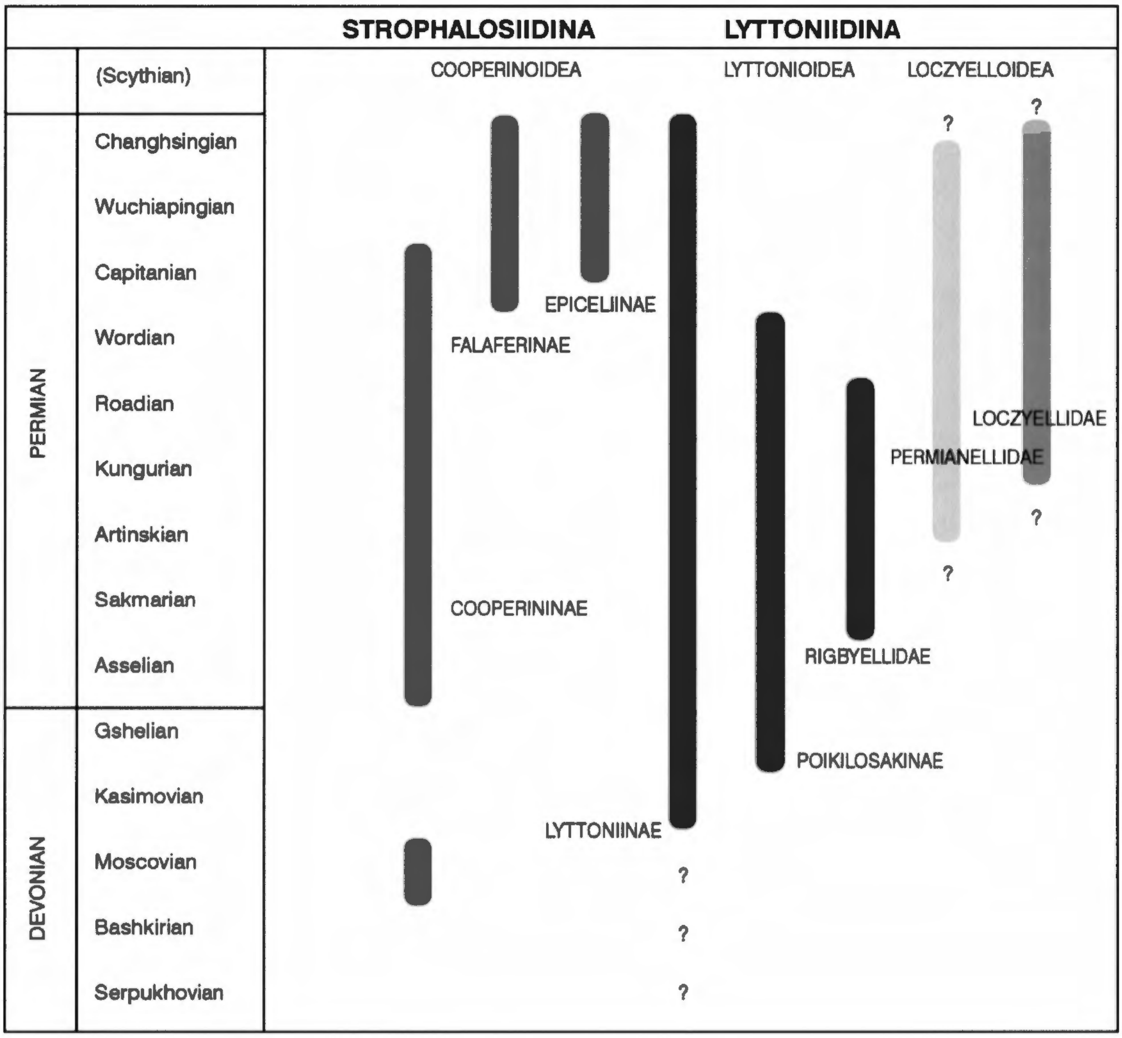


Fig. 12.1. Range chart for Lyttoniidina, shown with Cooperinoidea which has a complex lophophore, more elaborate than that of most Strophalosiidina, and approaching that of Lyttoniidina. Age control poor, especially for Loczyelloidea, but is addressed by Shen & Shi (1998).

12. Superfamily **LYTTONIOIDEA** Waagen, 1883

[Nom. transl. Licharew in Sarytcheva, Licharew & Sokolskaya 1960, p. 237 ex Lyttoniinae Waagen, 1883, p. 396].

Diagnosis: Ventral valve usually convex to varying degree, of somewhat irregular outline. The dorsal valve consists largely of a lobate brachial plate, and the ventral valve has a variably developed posterior flap of shell, and a vallum. The secondary shell is pseudopunctate.

Discussion: The vallum is named for an internal rib within the margin of the valve, surrounding the median internal shell. Cooperinidae also displays a ridge around the margin of the ventral valve. Lyttoniinae was first proposed by Waagen (1883) on the basis of his genus *Lyttonia*, which he proposed, improperly, as a substitute for *Leptodus* Kayser (1883), named for what Kayser believed were the remains of fish teeth. Williams (1965, pp. 517, 518) outlined some of the subsequent discussions and proposals and concluded that Lyttoniinae should stand, on the basis that it had been more widely employed that other proposed names, appealing to the Zoological Code 1961, art. 40, a. Priority and rules appear to offer more convincing reasons for assessing the name: it is a strange form of science – or is it pseudoscience, a discredit to taxonomy – to rely on repeated error to prove, or rather excuse, a case, and one can only deprecate the misplaced tolerance of error-acceptance, based on the non-scientific value accorded to "historical usage". It is enshrined in the Code – and perhaps the Code should be changed. Whilst a count based on a few decades of usage seems to outnumber a correction, one would hope that taxonomy will endure for many centuries, and so eventually correct procedure will come to overwhelm the errors of the past. Ill-usage, no matter how often enshrined by repetition, does not and should not sanctify.

Family **LYTTONIIDAE** Waagen, 1883

[Nom. transl. Noetling 1905, p. 129 ex Lyttoniinae Waagen, 1883, p. 396].

Diagnosis: Vallum lobate; dorsal valve consisting of median indentations with variable number of lobes and septa, directed laterally or antero-laterally. Ventral adductor scars flanked by variably developed smaller diductor scars.

Discussion: The classification is accepted from Williams, Harper & Grant (2000). There are a great many synonymies, yet to be tested.

Subfamily **LYTTONIINAE** Waagen, 1883

Fig. 8, Fig. 12.2 - Fig. 12.5

[Lyttoniinae Waagen, 1883, p. 396].

Diagnosis: Shells basically symmetrical, although irregular through growth habitat. ?Lower Carboniferous, Upper Carboniferous to Upper Permian (Changhsingian).

Fig. 12.2. *Leptodus* sp. indet. sp. A, external view of ventral valve ROM 31734 (formerly B 356), x3. B, exterior of dorsal valve B 360, x3. From Rat Buri Formation (Roadian), Khao Phrik, southern Thailand. See Waterhouse & Piyasin (1970). B. O'Donovan & JBW photo.

Fig. 12.3. *Leptodus* sp. internal view of ventral valve B 356, x3. From Rat Buri Formation (Roadian), Khao Phrik, southern Thailand. See Waterhouse & Piyasin (1970). Kept at Royal Ontario Museum, Toronto. B. O'Donovan & JBW photo.

Genera: *Leptodus* Kayser (syn. *Gubleria* Termier & Termier, *Spinolyttonia* Sarytcheva, *Lyttonia* Waagen, *Lyttonia* (*Digitia*) Gregorio, *L.* (*Irma*) Gregorio, *L.* (*Vincia*) Gregorio, *L.* (*Prisca*) Gregorio, *Juxoldhamina* Liang, *Semigublerina* Liang), *Cardinocrania* Waagen (syn. *Pseudokeyserlingina* Fredericks), *Collemataria* Cooper & Grant, *Coscinophora* Cooper & Stehli, *Eolyttonia* Fredericks (syn. *Uralina* Schuchert & LeVene, nom nov. pro *Uralia* Licharew, 1925 non Mulsant, Verreaux & Verreaux, 1866, *Paraleptodus* Li & Gu), *Keyserlingina* Tschernyschew (syn. *Parakeyserlingina* Fredericks, *Chaoella* Licharew), *Loxophragmus* Cooper & Grant (syn. *Palaeoldhaminia* Liang), *Matanoleptodus* Liao, *Oldhamina* Waagen (syn. *Waagenopora* Frech, *Oldhamella* Noetling, *Oldhamia* Zittel nom. null.), ?*Oldhaminella* Wanner, *Petasmaia* Cooper & Grant, *Pirgulia* Cooper & Muir-Wood (pro *Pirgula* Gregorio, 1930 non *Pirgula* Tessman, 1921).

Discussion: A cautious assessment of genera is provided by Williams, Harper & Grant (2000) with suggestions over a number of synonymies, and note made of some genera of contentious validity. *Keyserlingina*, based on a single ventral valve, is supposedly from Lower Carboniferous (age unspecified), and from Upper Carboniferous to Lower Permian. Most genera are limited to Permian, especially Roadian to Changhsingian.

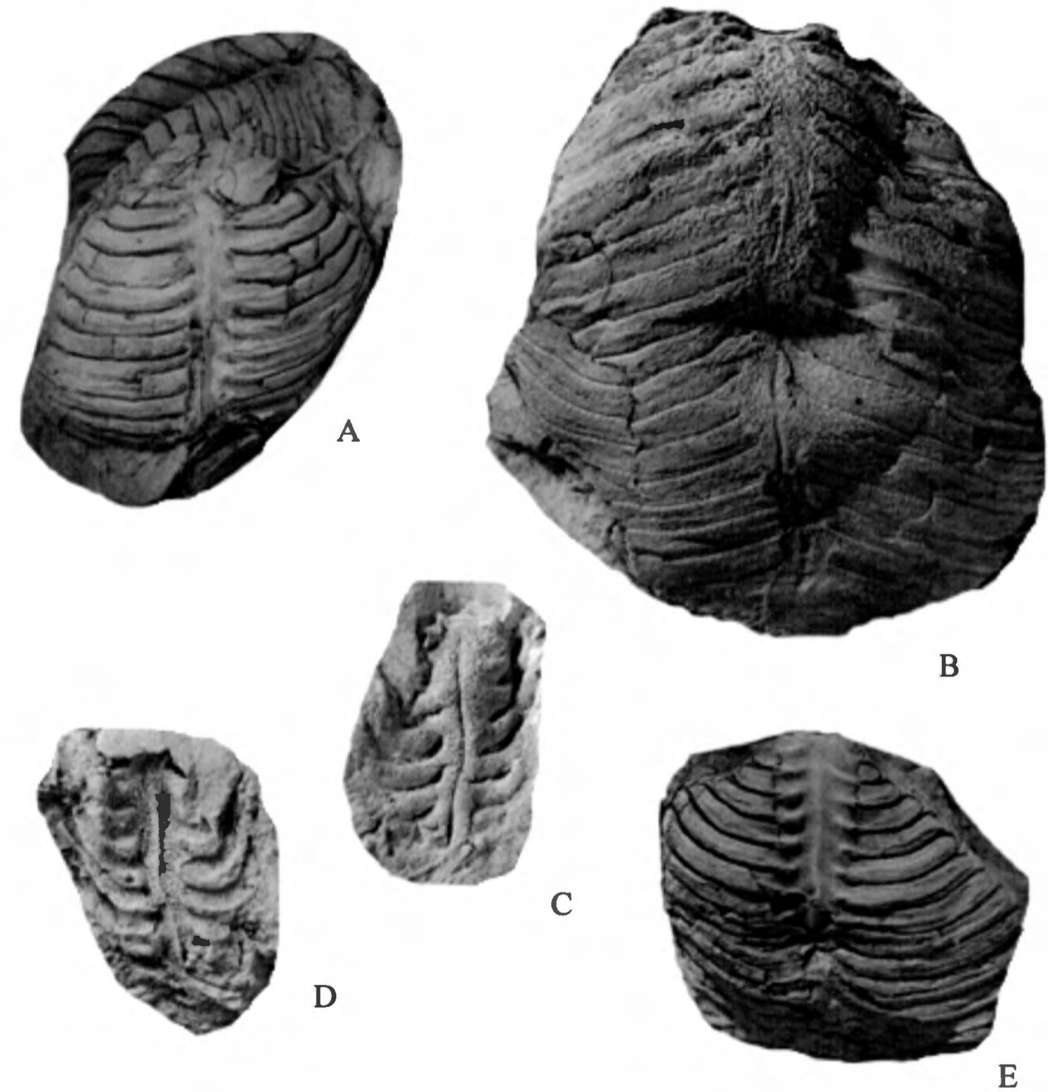


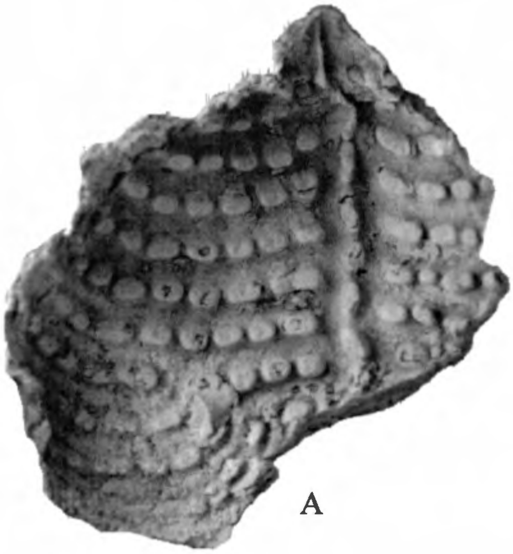
Fig. 12.4. *Oldhamina squamosa* Huang. A, internal mould of ventral valve, unregistered, x1. B, unregistered internal mould of ventral valve, x1. C, D, latex cast and dorsal external mould, TBR 441, x3. E, unregistered internal mould of ventral valve, x1. From Huai Tak Formation (Changhsingian), northern Thailand, kept at Geological Survey Division, Department of Mineral Resources, Bangkok, Thailand. JBW photo.

Subfamily **POIKILOSAKINAE** Williams, 1953

[Nom. transl. Williams, Harper & Grant 2000, p. 635 ex Poikilosakidae Williams, 1953, p. 287].

Diagnosis: Ventral diductor scar longer on right side, cardinal process deformed, dorsal valve deeply slit medianly. Upper Carboniferous to Upper Permian.

Genera: *Poikilosakos* Watson (syn. ?*Prokeyserlingina* Fredericks), *Adriana* de Gregorio (syn. *Stita* Gregorio), *Choanodus* Cooper & Grant, *Pseudoleptodus* Stehli, *Sceletonia* Cooper & Grant.



A

B

Fig. 12.5. *Coscinophora nodosa* Cooper & Stehli. A, internal view of ventral valve, BR 3074, x1.5. Unlike the numerous figures of *Coscinophora* in Cooper & Grant (1974), a low ridge passes over the posterior smooth area on to the median ventral ridge. B, external aspect of ventral valve BR 3075 , x1. From Cathedral Mountain Formation (Kungurian), west Texas, United States, x1. JBW photo.

Family **RIGBYELLIDAE** Williams, Harper & Grant, 2000

Fig. 12.6

[Family Rigbyellidae Williams, Harper & Grant, 2000, p. 638].

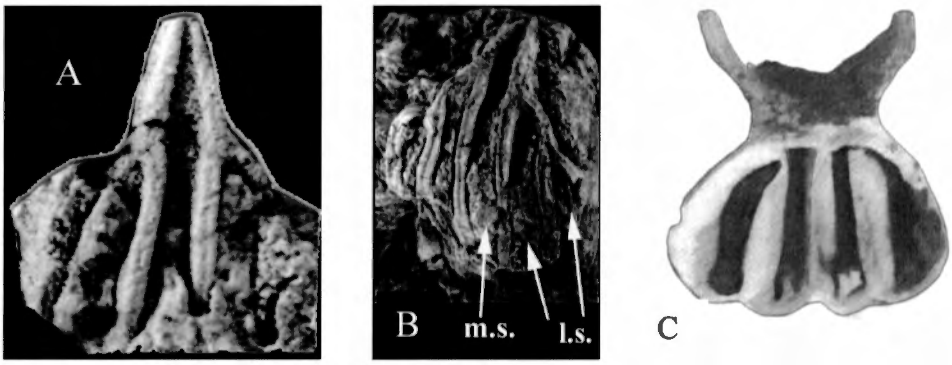


Fig. 12.6. A, B, *Pararigbyella quadrilobata* Shen & Zhang, internal moulds of two ventral valves NIGP130769, x4, and NIGPI30774, x2 approx., from south Hunan (Wuchiapingian), China. Photographs supplied by Shen Shuzhong. l.s. = lateral slit, m.s. = median slit. C, *Rigbyella girtyi* (Wanner & Sieverts), ventral interior USNM 147719b from Bell Canyon Formation (Capitanian), Texas, United States, x4. Redrawn from Cooper & Grant (1974, pl. 182, fig. 30). JBW del.

Diagnosis: Small transversely oval shells, ventral valve cup-like with longer medio-anterior section extending vertically from attachment area of beak and to lesser degree from everted posterior flap, up to six or seven septa subparallel to median axis, fitting in corresponding dorsal lobes, muscle scars symmetrical, cardinal process bilobed. Middle Permian (Roadian) to Upper Permian (Wuchiapingian). .

Genera: *Rigbyella* Stehli, *Paralyttonia* Wanner, *Pararigbyella* Shen & Zhang.

Discussion: The horn-like flaps (Fig. 12.6C) approach the structure seen in Permianellidae and in Lithocothinae. Williams, Harper & Grant (2000, p. 639) stated that the family was of Lower Permian age, but type *Rigbyella* is Capitanian (Grant 1976, pp. 169, 173) and Shen & Zhang (2008) recorded Wuchiapingian material.

13. Superfamily **LOCZYELLOIDEA** Licharew, 1937

[Nom. transl. hic ex Loczyellinae Licharew, 1937, p. 83. Syn. Paritistegacea Liang, 1990, p. 376 [487]].

Diagnosis: Oval to elongately bilobate to varying degree, ornament of growth lines or fine tubercles, large brachial shields of simple outline.

Discussion: The superfamily is best known from *Permianella* and allies, and these brachiopods are so similar externally to *Loczyella* and allies that all are regarded as belonging to the one superfamily. The shells are concavo-convex and may be bilobate, attached by projections of the everted posterior flap. The flange is variably developed and marginal to a low vallum. Age data summarized by Williams, Wardlaw & Grant (2000) is meagre.

Critics may well suggest that the handful of known genera amounts to no more than a tribe within lyttoniid brachiopods. But it is agreed with Williams et al. 2000 that morphological distinction is most clearly expressed by superfamilial standing. However reservations may be expressed over their preference for basing the superfamily group name on Permianellidae He & Zhu, 1979. Williams, Harper & Grant (2000) noted that at least one species ascribed to *Loczyella* Frech, 1911 showed attributes of their Permianelloidea, because Jin Yugan identified a Caucasus species as permianellid, and *Loczyella*, whilst not well known, is at least remotely like *Permianella*. It should be understood that the classification is premised on a considerable degree of uncertainty, but is here preferred as a tentative reconciliation of relationships, rather than a suspension of classification and relationships, pending fuller clarification. The uncertainties are clearly outlined by Williams, Harper & Grant (2000, p. 642).

Family **LOCZYELLIDAE** Licharew, 1937

[Nom. promoveo hic ex Loczyellinae Licharew, 1937, p. 83].

Diagnosis: Shovel-shaped to triangular with rounded anterior margin and sides diverging from umbo, ventral valve with prominent umbo, gently convex, medianly smooth or weakly sulcate, no median gap so that not bilobed. Ornament of growth lines only, no tubercles.

Discussion: This family is poorly known. Three genera as in Williams, Wardlaw & Grant (2000, p. 641) and rare additional forms are referred to the group. They agree overall in shape to some extent, the lack of any median slit, and the absence of surface tubercles, but differ in internal plates and presence or absence of vallum. Jin Yugan advised R. E. Grant that *Loczyella* (?) *parvula* Licharew resembled permianellids (as quoted by Williams, Wardlaw & Grant, 2000, p. 642), and the authors were surely correct in associating the group with permianellids, because of overall shape and the presence of a posterior flap and vallum, in the case of *Loczyella*, and in the case of *Litocothia*, the presence of teeth. Previously, Frech (1901), Muir-Wood & Cooper (1960), Williams (1964, p. 464) and Liang (1990) had all favoured a relationship with Richthofeniidae, and Mou & Liu (1989) with Terebratulida, whereas Licharew (1930) had more appositely preferred an alliance close to *Lyttonia*, in times when nothing was known of permianellids. This is not the only occasion when a senior paleontologist proves to have been in the right.

Subfamily **LOCZYELLINAE** Licharew, 1937

[Loczyellinae Licharew, 1937, p. 83].

Diagnosis: Ventral valve elongate, curved in outline, with apparently no auricles, ornament only of growth-lines. Ventral interior with vallum. Dorsal valve concave with low median fold. Permian.

Genus: *Loczyella* Frech, *Parvuliella* new genus.

Discussion: Williams, Harper & Grant (2000, p. 641) described shells of the subfamily as shovel-shaped to triangular with rounded anterior margin and sides diverging acutely from umbones. The ventral valve of *Loczyella* is gently convex and medianly sulcate with flanks at steep angle to the venter. The internal posterior valve is poorly known, and the dorsal valve concave with low median fold, and both valves ornamented by growth lines. There are apparently no auricles.

Not a single figure for these genera was provided by Williams, Harper & Grant (2000, p. 642), understandably because figures are poor, and obscure. Nonetheless, copies are provided herein from relevant publications, to try to convey something of the species and genera.

Genus ***Loczyella*** Frech, 1901

Fig. 13.1

Loczyella is based on *L. nankinensis* Frech (1901, p. 503, Fig. 15a-f, 1911, p. 166) from Late Permian near Nanjing, Kiangsu Province, China, and no further material for the species has been described. The lectotype, here designated, as figured in Fig. 13.1a-c, and here reproduced for apparently the first time, shows a large ventral valve without well defined sulcus, no apparent auricles, with long protruding umbo and small "holdfast" near or at the beak – as in many permianellids. The surface bears low growth lines, and shows no spines and apparently no tubercles, unlike permianellids. The inner view of the valve (see Fig. 13.1C) suggests a low vallum and wide flange. Two further figures in Frech (1901), not reproduced here, show additional aspects.

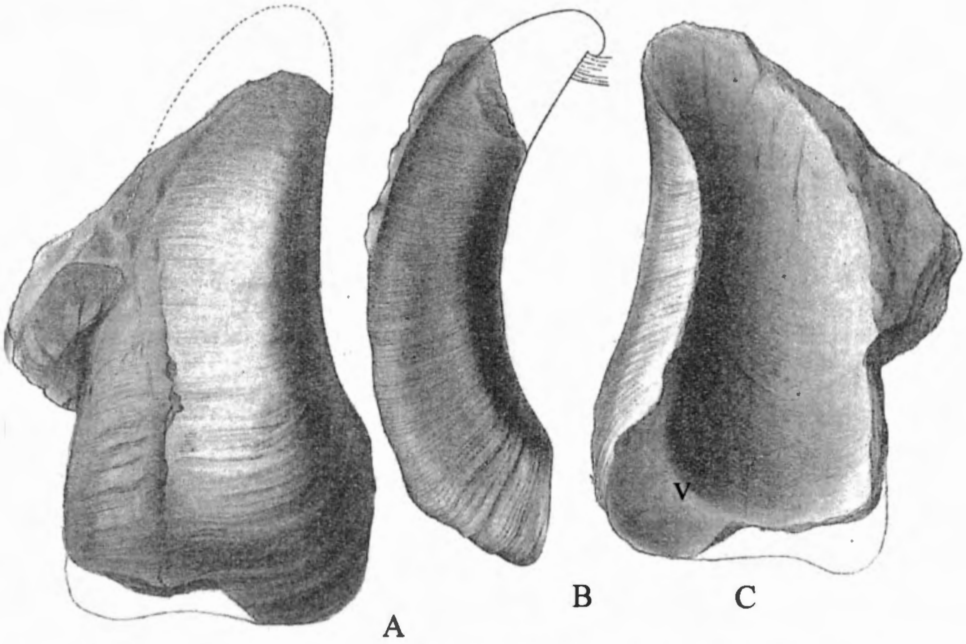


Fig. 13.1. *Loczyella nankinensis* Frech, as figured by Frech (1901, fig. 15a-c), x1 presumably. A and B are ventral and lateral aspects and C shows what Frech called the inner view, indicating a vallum (v). From Late Permian of Kiangsu Province, China.

Genus ***Parvuliella*** new genus

Fig. 13.2

Derivation: Based on species name, parvula.

Type species: *Loczyella* (?) *parvula* Licharew 1930, p.436 from Permian (Capitanian) of North Caucasus, here designated.

Diagnosis: Small, ventral sulcus and dorsal fold well defined.

Discussion: This species has helped play a leading role in the interpretation for *Loczyella* in Williams, Harper & Grant (2000), following the comment by Jin Yugan that the species looked permianellid. On the other hand, Licharew (1930) emphasized that the ornament consisted of only growth-lines, without the tubercles typical of Permianellidae. Unlike *Loczyella*, there is a well developed ventral sulcus and dorsal fold, and the sulcus shallows anteriorly. *Caninella* Liang, 1990 (see below) also has sulcus and fold, but the shell is less elongate and more bluntly triangular in shape, with better defined ventral sulcus, and high more developed dorsal fold. There are no auricles in *Parvuliella*. Shen & Shi (1998, Fig. 5) allocated a Capitanian age.

The holotype and paratype is kept at the Tschernyschew Museum in St Petersburg, Russia, and come from limestone in Severnaya Balka, a tributary of the Laba River in the Caucasus.

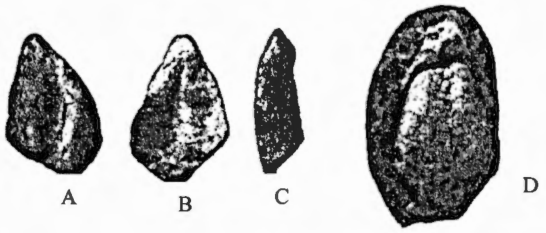


Fig. 13.2.*Parvuliella parvula* (Licharew), as figured by Licharew (1930, Fig. 1, 2) from the North Caucasus, Russia. A - C, holotype x1.5, showing for B the dorsal aspect, and C, lateral aspect. D, cast of ventral valve, x1.

Subfamily **CANINELLINAE** Liang, 1990

[Nom. transl. hic ex Caninellidae Liang, 1990, p. 216 (p. 468)].

Diagnosis: Triangular shells with ventral sulcus and low dorsal fold, small ears. Two low ventral septa, no median septum. Permian.

Fig. 13.3. *Caninella zhinanensis* Liang, ventral aspect of specimen from mid-Permian of South China, x1. The markings do not indicate ornament, but are more a matter of poor drafting and reproduction, and only the general shape with sulcus is reliable. See Liang (1990, pl. 39, fig. 1). JBW del.

Genera: *Caninella* Liang, ?*Cyrtalosia* Termier & Termier.

Discussion: This subfamily is distinguished by having a distinct hinge with well-formed ears. It is better known internally than *Loczyella*, for which there is no certainty at present over internal septation.

Genus ***Caninella*** Liang, 1990

Fig. 13.3

Genus *Caninella*, with type and only known species *Caninella zhinanensis* Liang (1990, pp. 216, 468, pl. 39, fig. 1-8) from the Middle to Late Permian of China, is extremely difficult to interpret from the figures, because of their poor reproduction. Liang (1990) described the shell as small and conical, like a canine tooth, conical in lateral aspect, concavo-convex in section, with straight hinge line, small ears and acute cardinal extremities, and truncated anterior. The ventral valve has a shallow median sulcus. The dorsal valve is described as deeply concave with linear interarea and weak median fold, and the shell surface is smooth, without ornament. Two lateral septa and no median septum are found in the ventral valve, and a low median septum and no cardinal process is present in the dorsal valve.

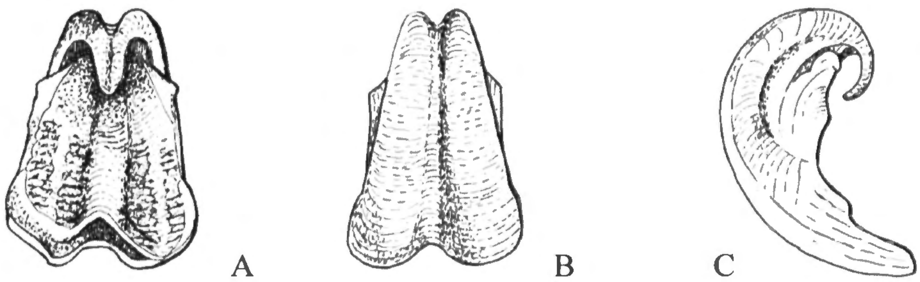


Fig. 13.4. *Cyrtalosia circinata* Termier & Termier. A – C, dorsal, ventral and lateral aspects of holotype, from Termier & Termier (1970a), holotype, x3. From Late Permian of Cambodia. This genus shows some approach towards Permianellidae (see below), and Liang (1990) has noted the similarity between Permianellidae and *Incisius* Grant of Cooperinoidea (see p. 269), but *Incisius* has conspicuous spines.

The genus *Cyrtalosia* Termier & Termier (1970a, p. 455) from Cambodia (see Fig. 13.4) is shaped somewhat like *Caninella*, though with wide hinge, and moderately like a simplified precursor to *Permianella,* and it is said to lack spines. However Grant (1976) considered that the material had been silicified and suggested that evidence for spines had been lost in the process of silicification, a matter demanding further enquiry.

Subfamily **LITOCOTHIINAE** new subfamily

Fig. 13.5

Name genus: *Litocothia* Grant, 1976, p. 166 from early Middle Permian Rat Buri Limestone (Roadian) of south Thailand, here designated.

Diagnosis: Small bilobate ventral valve without ears, ornamented by fine commarginal filae, posterior flap, large cicatrix, no internal septa. Teeth; vallum low and fine.

Discussion: *Litocothia* is a highly exceptional genus, well described by Grant (1976) on the basis of the ventral valve. The apical region is undoubtedly oldhaminidin, with a small everted posterior flap, and there are teeth. Unlike *Loczyella*, there is no vallum, unless represented by the very slender ridge which is lettered v in Fig. 13.5B. There is a broad shallow ventral sulcus, but as in *Loczyella* there are no pustules. The genus was classed as Loczyellinae by Williams, Harper & Grant (2000, p. 642), but the morphology differs to some extent. Unlike *Caninella*, the shape is more transverse with a posterior flap, and there are no ears and no ventral septa.

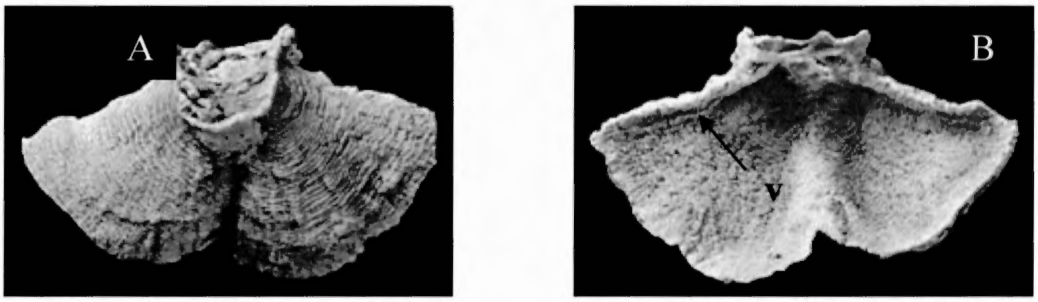


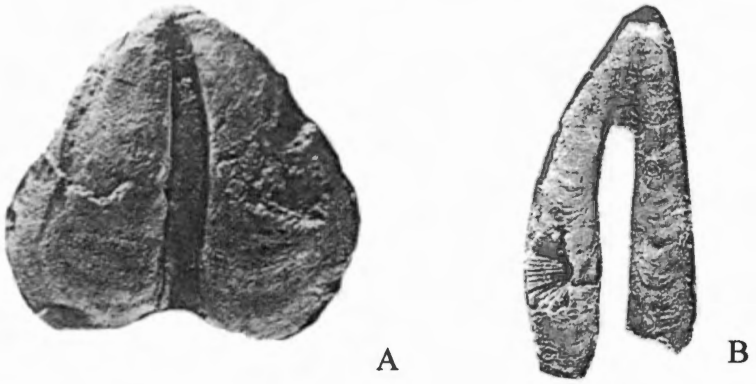
Fig. 13.5. *Litocothia cateora* Grant. A, B, external and internal aspects of ventral valve USNM 212579, holotype, x5. From Ko Muk, Rat Buri Limestone (Roadian), Thailand, showing posterior flap and possible vallum = v. From Grant (1976, pl. 30, fig. 19, 23).

Family **PERMIANELLIDAE** He & Zhu, 1979

Fig. 13.6 – Fig. 13.7

[Permianellidae He & Zhu, 1979. Syn. Tenerellidae Liang, 1990, pp. 374, 486; Paritistegidae Liang, 1990, pp. 376, 487].

Fig. 13.6. A. Specimen identified as *Dicystoconcha lapparenti* Termier et al. by Wang & He (1991), ventral valve F109146, x2. B, *Permianella typica* He & Zhu, ventral valve F109148a, x1.2. From Permian of China. See Wang & Jin 1991.



Diagnosis: Shells elongate and clearly bilobed, variably emarginated, attached by horn-like unreflexed everted posterior flap, ornament of small crowded tubercles. Raised ventral dental areas, well defined muscle platform, flange variably developed, with marginal to low vallum. Dorsal valve circumscribed by low marginal ridge, cardinal process bilobed and connected to low ridges enclosing sockets, adductor scars variably impressed each side of median ridge, pair of low ridges extend medianly along inner edge of valve lobes. Shell for some taxa punctate. Permian.

Genera (fide Williams et al. 2000): *Permianella* He & Zhu, *Dicystoconcha* Termier & Termier (syn. *Dipunctella* Liang, *Guangjiayanella* Yang De-Li, *Guangdongina* Mou & Liu, *Paritisteges* Liang, *Fabulasteges* Liang), *Laterispina* Wang & Jin, *Tenerella* Liang (syn. *Obliqunsteges* Liang, *Sicyusella* Liang). Much doubt still pertains, as noted on p. 306.

Discussion: The ventral interior of permianellids displays raised dental areas and well defined median muscle platform. The dorsal hinge is bounded by a ridge, extending laterally as ears, and a bilobed cardinal process adjoins diverging socket ridges. The adductor scars are variably impressed on the inner side of the exterior sulcus. A pair of low ridges lies along the valve lobes.

Synonymies and morphologies are discussed by Wang & Jin (1991) and Williams, Harper & Grant (2000), and the section is expanded, with attention focused in part on synonymies, and on the study by Liang which was largely set aside in the *Revised Brachiopod Treatise*. *Laterispina* Wang & Jin [Ching], 1991 has teeth and spinose projections (Shen et al. 1993). Shen & Shi (1998) provided detailed ages and occurrences.

The Liang Interpretation

A number of genera proposed by Liang (1990, p. 370) were assigned to a separate suborder Dipunctellidina, and subdivided amongst two superfamilies. Liang's Dipunctellidina was based in part on the presence of punctae in the shell, and in other respects the morphology is outlined above in the diagnosis for Permianellidae. There has been at least one instance where the punctae have been independently verified by Mou & Liu (1989, pl. 2, fig. 8) for their species *perforans*. The observations therefore seem likely to have been correct, but are here regarded as not altering relationships to potentially beyond subfamily level, but nonetheless demand elaboration of the brachiopod shell structure as summarized by Williams (1997). This fresh interpretation is based on the similarity to punctae in genera of the spiriferidin superfamily Ingelarelloidea Campbell, reported by Waterhouse (1964, 1998). Members of this superfamily are normally impunctate, although rare instances of taleolae have been reported by Campbell (1959) and Waterhouse (1964). However two genera with several species, in most respects very close to Notospiriferidae, have large and well developed punctae called mesopunctae in the thick median layer of shell (Waterhouse 1964, pl. 14, fig. 10, pl. 15, fig. 6, pl. 37, fig. 4, 6; Armstrong 1970, p. 293), equal to endopunctae in common parlance. The genera were interpreted as exceptional in shell structure, but otherwise fitting in well with Notospiriferidae, in turn a prominent member of Ingelarelloidea. This understanding is extended to the punctae and family interrelationships between Permianellidae and Dipunctellidina. Permianellidae has priority, and is therefore retained as name-giver.

Liang (1990) subdivided his permianelliform genera into several categories, depending on shape and symmetry. Two superfamilies and families and genera were proposed, but whether all genera have endopunctae (or mesopunctae) remains unclear, Shen & Shi (1998, p. 268) stating that Permianellidae were pseudopunctate.

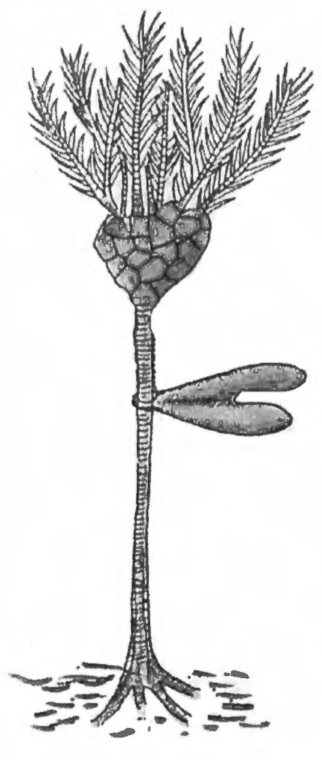


Fig 13.7. Reconstruction of habitat for permianellid, according to Wang & Jin (1991, Fig. 10), slightly altered.

Superfamily Dipunctelloidea Liang, bilaterally asymmetrical.

Family Dipunctellidae Liang, shells straight, not subdivided by a gap.

Genus *Dipunctella* Liang, sides parallel, shell not curved.

Genus *Obliqunsteges* Liang, shell arched transversely, "fixing foramen" or posterior ventral flap especially large.

Family Tenerellidae Liang, shells arched in longitudinal profile and split by a gap.

Genus *Tenerella* Liang, shells "strongly" coiled longitudinally.

Superfamily Paritistegoidea Liang, shells bilaterally symmetrical. Two ventral septa developed for shells with known interior.

Family Paritistegidae Liang, shell straight and not split.

Genus *Paritisteges* Liang, small to median size, ventral valve pustulose, dorsal valve smooth.

Genus *Fabulasteges* Liang, small, as wide as long.

Genus *Sicyusella* Liang, elongate, deep ventral sulcus, gently curved longitudinally, interior not known.

Liang (1990) added many further details. Of these genera, only *Tenerella* was accepted, provisionally, by Williams, Harper & Grant (2000, p. 641), and on the basis that the ventral flange, which is neither described nor revealed, is neglible as in *Dicystoconcha*. For their synonymy of *Dicystoconcha*, Williams, Harper & Grant explained that they regarded genera placed in synonymy had been erected "for shells with trivial variations in shape." How they knew the differences were trivial was not explained. If the permianellid shell was free-living, as illustrated by Wang & Jin (1991,fig. 10) and repeated as Fig. 13. 7, then shells were free to pursue a predetermined shape ungoverned by constraints from varying substrate. On the other hand, it would seem reasonable to posit that if two lobes were vertical one above the other in a life position, the lower one might grow further than the upper one – or vice versa, and the longitudinal curvature in some specimens might reflect tidal or current action through development. What is required is examination of a substantial collection of specimens from one locality, to determine if there was natural variation in symmetry and longitudinal curvature, and the specimens described by Mou & Liu (1982) seem to reflect such natural variation.

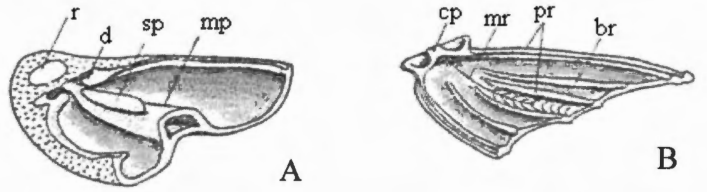


Fig. 13.8. The morphology of permianellids, slightly altered from Wang & Jin (1991, Fig. 3) and Shen et al. (1993, fig. 2). A, ventral interior. B, dorsal interior. br, longitudinal ridge; cp, cardinal process, between dental sockets; d, dental prominence; mp, central platform; mr, median ridge; pr, flange (marginal ridge); r, attachment ring; sp, median septum.

Genus ***Dicystoconcha*** Termier, Termier, Lapparent, & Marin, 1974

Fig. 13.9

The type species *Dicystoconcha lapparenti* Termier & Termier in Termier et al. (1974, p. 122, pl. 22, fig. 1, 2, Fig. 22) from "lower Murghabian"of Afghanistan has been reported as a widespread genus in southern, southeast and east Asia, and appears to have been substantially elaborated by Wang & Jin (1991) and Williams, Wardlaw & Grant (2000, p. 639). The type species is based on a single dorsal valve (Fig. 13.9), and is strongly bilobed, each lobe divided by a deep slit extending for much of the length of the specimen, and with a pustular external surface. Wang & Jin (1991, pl. 1, fig. 1-9, pl. 3, fig. 1-7) in describing what purported to be the same genus and species from the Lower Permian of southeast China, incorporated specimens that have a well defined ventral sulcus. But their figures show that this is largely infilled with shell ornamented by pustules: there is only one exception (pl. 1, fig. 7), which has a gap extending for only half of the length of the shell. *Dipunctella* Liang, 1982 was regarded as a synonym. The type species of this genus has two high ventral septa, and is long with two lobes separated by a very narrow groove and almost parallel flanks. One lobe is shorter than the other, judged significant by Liang (1990), but not by Wang & Jin (1991). Another synonymized taxon, *Guangjiayanella* Yang De-li (1984, p. 212, pl. 31, fig. 12-16 comes from the Lower Permian of the Lower Qixia (Chihsia) Limestone of Hubei, China. The third synonymized taxon, *Guangdongina* type species *G. xiamoensis* Mou & Liu (1989, pl. 1, fig. 1-9, pl. 2, fig. 1-7), and two further species *G. perforans* Mou & Liu (1989, pl. 3, fig. 1-3) and *G. leguminiformis* Mu & Liu (1989, pl. 3, fig. 4-8) appear to lack the interlobal gap, at least for the exterior of the ventral valve figured in pl. 1, fig. 7, but a number of ventral valves have a median strip of matrix, concealing the nature of the division. A dorsal exterior (pl. 2, fig. 6) has a gap that extends for only half of the length of the specimen. Possibly the gap is moderately long for the other two species (pl. 3, fig. 1 – half the length – and pl. 3, fig. 4). These specimens are slightly curved in longitudinal profile, and the lobes are of differing lengths in different specimens. The figure of Mou & Liu (1989, pl. 2, fig. 8) illustrates large punctae in the species *perforata*. The elaborate internal morphology illustrated for permianellids by Wang & Jin (1991, Fig. 3), as replicated in Fig. 13.8, has yet to be endorsed for various permianellid species, and further study might uncover some differences. After all, the interior of the ventral valve in type *Dicystoconcha* remains unknown.

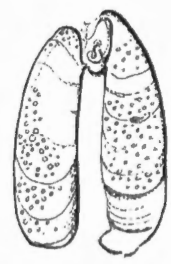


Fig. 13.9. *Dicystoconcha lapparenti* Termier & Termier, holotype dorsal valve as figured by Termier et al. (1974, Fig. 22) from Middle Permian of Afghanistan, x1.

Campi et al. (2000, p. 37) considered that *Permianella* differed in displaying only one septum on the central platform, and included all of the genera described by Liang (1982, 1990) in *Permianella*. Larger questions remain, over whether *Dicystoconcha* and *Permianella* are punctate likely other proposed taxa placed currently in synonymy, and what are the shell structures and septation in different members of Loczyellidae.

SUBORDER LINOPRODUCTIDINA, NEW SUBORDER

This group is proposed for three superfamilies Paucispiniferoidea Muir-Wood & Cooper, Linoproductoidea Stehli and Proboscidelloidea Muir-Wood & Cooper, symplesiomorphic superfamilies that arose from the strophalosiiform Family Devonoproductidae. They share predominantly radial ornament but differ in details of spination and interior. Origins appear, from the fossil record, to have stemmed from a costellate chonetid, at least generically different from the smooth anopliid ancestors of Productidina and Strophalosiidina.

Family **DEVONOPRODUCTIDAE** Muir-Wood & Cooper, 1960

[Nom. transl. Waterhouse 2010a, p. 31 ex Devonoproductinae Muir-Wood & Cooper, 1960, p. 177].

Diagnosis: Radial ribs as a rule on both valves, spines limited to ventral valve with hinge row and no specialized spines, dorsal valve with concentric lamellae in one subfamily. Interareas, teeth and dental sockets. Ventral adductors smooth or weakly striate longitudinally.

Discussion: Proposed as a subfamily and member of Linoproductidae Stehli and retained as such by Brunton et al. (2000), this group was elevated to family rank by Waterhouse (2010a, p. 31). Members are strophalosiiform, not productiform. The family is unusual in several respects. Its ventral adductor scars are unlike those of Linoproductidae in being smooth, and the dorsal valve in one subfamily carries prominent concentric lamellae. Internally, and unlike many but by no means all Linoproductidina, there may be a low but distinct marginal ridge, high posteriorly, in each valve. Members of the family are similar to members of Productellidae through their articulation and outline of feeding apparatus, when compared with other brachiopod stock, but had a separate ancestry, and subsequent developments in evolution transformed them from close allies or paramorphs to precursors of separate and diverse superfamilies.

Subfamily **DEVONOPRODUCTINAE** Muir-Wood & Cooper, 1960

Fig. 14.1

[Devonoproductinae Muir-Wood & Cooper, 1960, p. 177].

Diagnosis: Suberect spines over ventral valve and along hinge, spines may be wider than ribs which cover ventral valve, dorsal valve with commarginal lamellae as traces of trails, and weak radials. Ear baffles on ventral valve, weak dorsal lateral ridges and submarginal ridge. ?Middle Devonian (Givetian) to Upper Devonian (Frasnian).

Genus: *Devonoproductus* Stainbrook (syn. *Striatoproductus* Nalivkin), *Chonopectoides* Crickmay.

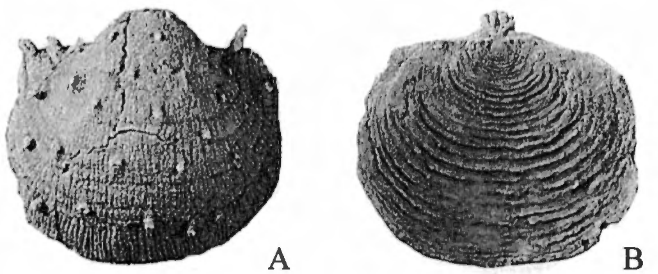


Fig. 14.1. *Devonoproductus walcotti* (Fenton & Fenton). A, ventral valve USNM 123923d, x3. B, dorsal valve USNM 123923e, x3. Hackberry Cerro Gordo Member (Upper Devonian), Iowa, United States. See Muir-Wood & Cooper (1960, pl. 45, fig. 6, 10).

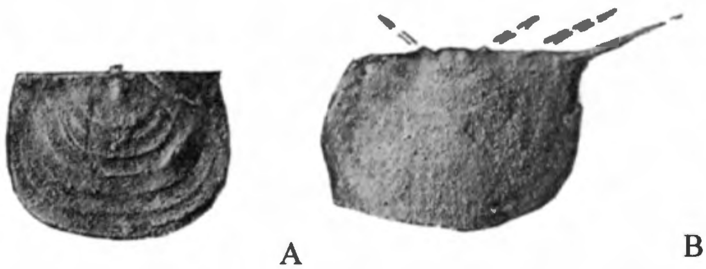
Discussion: *Devonoproductus* Stainbrook, 1943, p. 55 is of Upper Devonian age, and has a costellate ventral valve and laminate dorsal valve. A row of spines lies along the ventral hinge as in few genera of Productellidae, and spines occur in rough quincunx over the ventral valve. There is a low ventral interarea with narrow delthyrium, minute ventral teeth, obscure ventral muscle scars, bilobate or quadrilobate cardinal process and smooth dorsal adductors, the genus having been closely described by Muir-Wood & Cooper (1960, p. 178). The row of hinge spines and the presence of fine ventral valve costellae obviously approach features of Linoproductidae, encouraging placement in that family by Muir-Wood & Cooper (1960), whereas Brunton et al. (2000) referred the subfamily to Monticuliferidae, presumably on the assumption that the moderately shallow corpus cavity was of supreme significance. It is difficult to justify that position. One interesting facet is that Crickmay (1963, pp. 24, 25) recorded a cicatrix in some specimens of two of the species that he described.

A number of the characteristic features of *Devonoproductus* are found in Subfamily Anidanthinae Waterhouse, 1968a – strongly costate ventral valve, with hinge row of spines, laminate dorsal valve usually without spines, and smooth dorsal and ventral adductor impressions. The strongly strophalosiiform aspects of *Devonoproductus* were lost, and costation strengthened on the dorsal valve, and in several anidanthin genera, the ears of usually the dorsal valve became very large. The first known appearance of Anidanthinae is in Pennsylvanian faunas of Canada and northeast Russia, so that there is a considerable gap in the fossil record between Devonoproductinae and Anidanthidae.

Another family group that shows similar attributes is Paucispiniferidae Muir-Wood & Cooper, 1960. The earliest member of Paucispiniferidae, Productininae Muir-Wood & Cooper, 1960 of late Devonian age has ventral ribs and dorsal concentric lamellae, reminiscent of Devonoproductinae and Anidanthinae, with smooth adductor scars, and no teeth or interareas, but distinguished by the development of ventral strut spines. The group appears to given rise to Bibatiolinae and Paucispiniferinae.

The morphologies of the two groups imply that the subfamily Devonoproductinae gave rise to very different families, one classed as Paucispiniferidae through Productininae, the other classed as Anidanthidae. In providing a fork in the course of evolution, the subfamily has to remain distinct from both lineages.

Chonopectoides Crickmay, 1963, p. 23 of upper Middle Devonian age is similar to *Chonopectus* in shape and hinge spines (p. 230), and lack of spines over the disc and trail. There are low ventral ribs, bifid cardinal process, and teeth and sockets. Radial ribs are faint and only on the ventral valve, and a row of prominent ventral hinge spines is developed, but no disc spines. A view of the cardinal process in Brunton et al. (2000, Fig. 383.2d) suggests four posterior lobes, a marked improvement on the comparable figure in Crickmay (1963, pl. 15, fig. 3), and approaching those of *Devonoproductus* (Brunton et al. 2000, Fig. 383.1d), compared with the bilobed cardinal process of *Chonopectus* shown by Muir-Wood & Cooper (1960, pl. 36, fig. 14).



A B

Fig. 14.2. *Chonopectoides catamorphus* Crickmay, dorsal exterior and ventral valve holotype PRI 27124, x8. From Moberley Member (Givetian), western Canada. See Crickmay (1963, pl. 15).

Subfamily **EOPRODUCTELLINAE** Lazarev, 1987

[Eoproductellinae Lazarev, 1987, p. 49].

Diagnosis: Erect spines only on ventral valve, both valves ribbed. Early Devonian (Pragian) to Middle Devonian (Emsian).

Genus: *Eoproductella* Rzhonsnitzkaya.

Discussion: *Eoproductella* is strophalosiiform in attributes. It is regarded as the progenitor for Linoproductidae as supported by all available evidence. Further study shows that whereas the genus provided root-stock for Linoproductoidea, based on the nature of the spines and ribs, the other predominant linoproductidin groups arose from different genera classed in separate subfamilies.

Subfamily **PLICOPRODUCTINAE** Waterhouse, 2004b

Fig. 14.3

[Plicoproductinae Waterhouse, 2004b, p. 42].

Diagnosis: Spines only on ventral valve, with posteriorly prolonged bases, both valves ribbed. Low interareas, small teeth and sockets. Middle Devonian (Eifelian – middle Givetian).

Genera: *Plicoproductus* Ljaschenko, *Striatoproductella* Krylova (syn. *Hanaeproductus* Ficner & Havlíček).

Discussion: Ventral spines have elongate and prolonged bases in *Plicoproductus* and *Striatoproductella*, and the shells are well ribbed, especially in *Striatoproductella*. This subfamily provided the root stock for a major group of Linoproductidina, assigned to Superfamily Proboscidelloidea Muir-Wood & Cooper, 1960. This is characterized, like Plicoproductinae, by costate ornament and by ventral disc spines bases being prolonged over the valve surface, but without teeth or sockets and with productiform brachial shields.

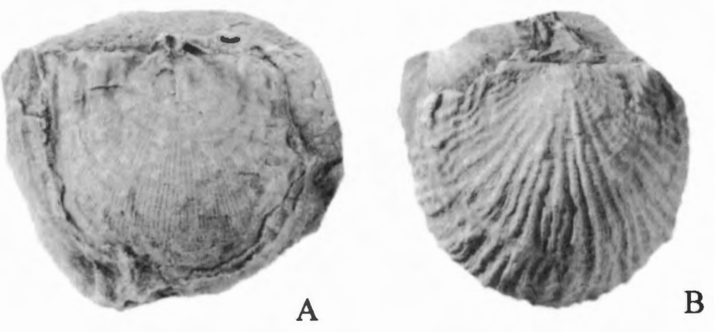


Fig. 14.3. A, *Striatoproductella tunguensis* (Nalivkin),dorsal valve from Middle Devonian (Givetian) of Siberia, x2. B,*Plicoproductus mosolovicus* (Ljaschenko), ventral valve from Middle Devonian (Eifelian) of Russia, x2. See Brunton et al. (2000, Fig. 384.2c, 3d).

15. Superfamily **PAUCISPINIFEROIDEA** Muir-Wood & Cooper, 1960

Fig. 15.1

[Nom. transl. hic ex Paucispiniferinae Muir-Wood & Cooper, 1960, p. 319].

Diagnosis: Characterized by ventral strut spines in a number of genera. Shells small to medium in size, radial ornament usually prominent, no dorsal spines as a rule, interior may be close to that of marginiferoids in usually displaying prominent marginal ridges. Dorsal trails simple or mutiple.

Discussion: This is a newly recognized group, united by ancestry and often the sharing of strut spines, which are long and sturdy erect spines, evenly distributed over the ventral valve in some groups, in pairs, or along the median line, and for early component members, by lamellate dorsal valve. Available evidence for two of the families points to a source from the strophalosiiform Devonoproductinae.

- **Family Paucispiniferidae Muir-Wood & Cooper, 1960**
    - Subfamily Paucispiniferinae Muir-Wood & Cooper, 1960
        - Tribe Paucispiniferini Muir-Wood & Cooper, 1960
        - Tribe Retimarginiferini Shi & Waterhouse, 1996
        - Tribe Probolioniini Muir-Wood & Cooper, 1960
            - Subtribe Probolioniinai Muir-Wood & Cooper, 1960
            - Subtribe Kozlowskiinai Brunton, Lazarev & Grant, 1995
    - Subfamily Productininae Muir-Wood & Cooper, 1960
    - Subfamily Bibatiolinae Waterhouse, 2002b
    - Subfamily Chonetellinae Licharew, 1960
        - Tribe Chonetellini Licharew, 1960
        - Tribe Odonovaniini new tribe
- **Family Anidanthidae Waterhouse, 1968a**
    - Subfamily Anidanthinae Waterhouse, 1968a
    - Subfamily Lirariinae new subfamily
    - Subfamily Lamiproductinae Liang, 1990
- **Family Yakovleviidae Waterhouse, 1975**
    - Subfamily Yakovleviinae Waterhouse, 1975
    - Subfamily Muirwoodiinae new subfamily
    - Subfamily Paramarginiferinae Lazarev, 1990

Table 15. Superfamily Paucispiniferoidea Muir-Wood & Cooper, 1960.

It is considered that the Upper Devonian to Lower Carboniferous Productininae, characterized in part by subpentagonal shape, lamellate dorsal valve and few specialized spines, evolved from Devonoproductinae, and gave rise to Lower Carboniferous members of Bibatiolinae of comparable shape and allied spine distribution, and loss of dorsal lamellae, with heavy posterior to postero-lateral marginal ridge development, and thence diverged into other groups with strut spines, grouped here under Paucispiniferidae. Probably Bibatiolinae within this family also gave rise to Yakovleviidae Waterhouse, with linoproductiform ribbing and paucispinaurian strut spines in some genera. Although internal detail is somewhat marginiferoid, the development of marginal ridges is very subdued as a rule. Anidanthidae also arose from Devonoproductinae, showing similar dorsal and ventral ornament, and similar muscle scars.

Family **PAUCISPINIFERIDAE** Muir-Wood & Cooper, 1960

[Nom. transl. hic ex Paucispiniferinae Muir-Wood & Cooper, 1960, p. 319].

Diagnosis: Genera with low number of strut spines on ventral valve, usually symmetrically disposed. No dorsal spines.

Discussion: The distinctive ventral ribbing and dorsal commarginals in early members strongly suggest derivation from Devonoproductinae, an earlier Devonian strophalosiiform family (p. 307). Strong deviation must have been involved, with the loss of teeth, sockets, interareas, and change to brachiophores. Devonoproductinae, as limited herein and in Waterhouse (2004b), has ventral ribs and erect spines, and dorsal laminae. Internally the subfamily displays smooth adductor scars, strophalosiiform brachial ridges, teeth and sockets and interareas, and low marginal ridges in each valve, high across the ventral ears. It appears that two groups, Productininae and Anidanthinae, each were sourced from Devonoproductinae, because they shared many features, especially the lamellate dorsal valve.

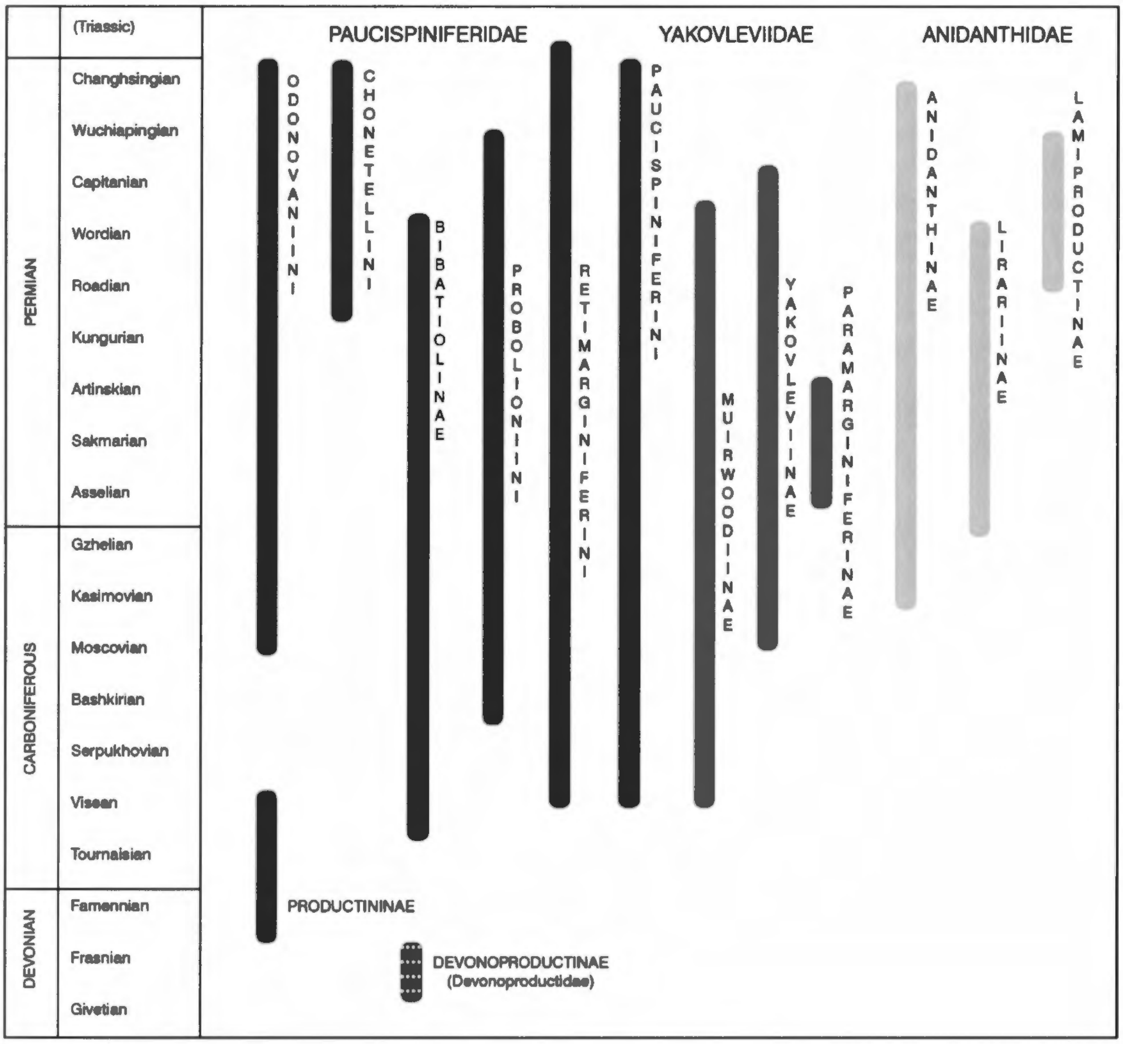


Fig. 15.1A. Range chart for Superfamily Paucispiniferoidea.

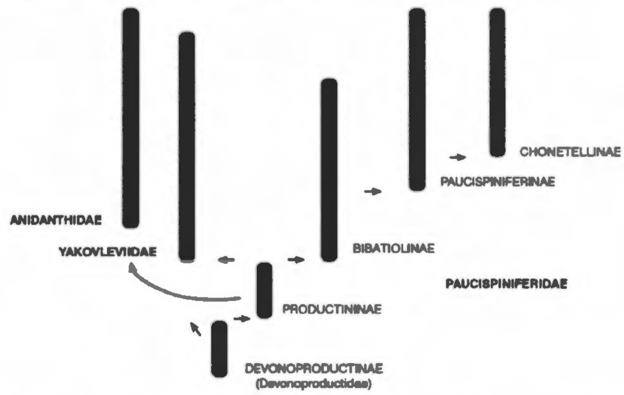


Fig. 15.1B. Simplified development of subfamilies within Paucispiniferidae and development of Yakovleviidae and Anidanthidae.

Both lost teeth, sockets, interareas and large brachial shields, and both retained the large comparatively smooth ventral adductor platform. One group developed strut spines to evolve into Productininae, followed by other subfamilies and tribes within Paucispiniferidae, with varied and often specialized spines and often high marginal ridges. The other group developed into Anidanthidae, much closer to the original stock, and retaining low marginal ridges and for most genera only ventral spines. This relationship between Anidanthidae and Paucispiniferidae was partly anticipated at a general level by Waterhouse (1966, 1967a). It shows how complex the interrelationships are between family groups, and suggests that any expression of interrelations by classification is no easy task, given the need for sequential study to unravel relationships.

Subfamily **PAUCISPINIFERINAE** Muir-Wood & Cooper, 1960

[Paucispiniferinae Muir-Wood & Cooper, 1960, p. 319].

Diagnosis: Shells with generally six or more large strut spines on ventral valve. Dorsal trail simple or mutiple.

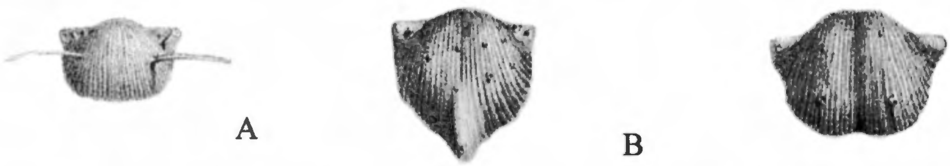
Tribe **PAUCISPINIFERINI** Muir-Wood & Cooper, 1960

Fig.15.2 - Fig. 15.4

[Nom. transl. Brunton et al. 1995, p. 927 ex Paucispiniferinae Muir-Wood & Cooper, 1960, p. 319].

Diagnosis: Transverse shells with varied radial and concentric ornament and three pair of large strut spines on ventral valve, large ears, transverse outline. Dorsal trail simple. Lower Carboniferous (Visean) to Upper Permian (Changhsingian).

Genera: *Paucispinifera* Muir-Wood & Cooper, ?*Anemonaria* Cooper & Grant, *Caruthia* Lazarev & Poletaev, *Cathaysia* Jin, *Eomarginia* new genus, *Eomarginifera* Muir-Wood (syn. *Lissomarginifera* Lane), *Glabauriella* new genus.



A B C

Fig.15.2. *Eomarginifera longispinus* (Sowerby). Ventral valves as figured by Davidson (1861, pl. 35, fig. 5, 16, and 7), from Lower Carboniferous of Yorkshire, England, x1.

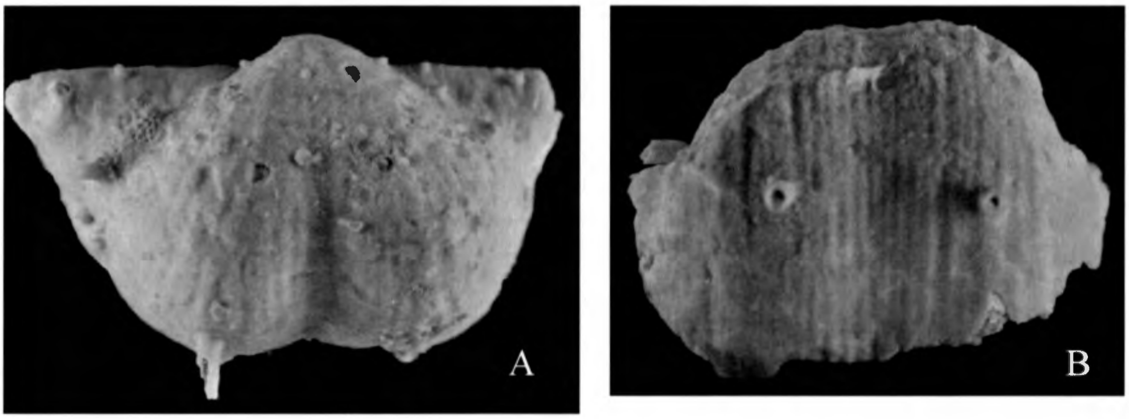


Fig.15.3. *Paucispinifera auriculata* Muir-Wood & Cooper. A, B, posterior and anterior views of ventral valve UQF 81927 from UQL 3911, x2 approx., Word Formation (Wordian), Glass Mountains, Texas, United States. Photographs supplied by A. Rozevelds, Queensland Museum, Brisbane, Australia.

Discussion: Several genera such as *Nudauris* Stehli and *Spinarella* Cooper & Grant that were placed in this group by Brunton et al. (2000, p. 447) are transferred to Dictyoclostidae, because they lack strut spines and heavy marginal ridges. *Eomarginifera* is placed in this tribe, because the trail is simple. *Anemonaria* Cooper & Grant, 1969, type species *A. sublaevis* (King, 1931 syn. *A. inflata* Cooper & Grant, 1969) causes some difficulty, because it is not clear whether or not strut spines are developed. The type species has a well developed umbonal slope row, and no hinge row, and the spines found in the position of strut spines in *Paucispinifera* are not particularly strong, nor even regularly in the same position. On the other hand Hoover (1981) considered that *Anemonaria sublaevis* might be closely related to two species of *Paucispinifera* described as *Paucispinifera sulcata* Cooper & Grant (1975, pl. 418, fig. 1-51, pl. 475, fig. 21, 22) and *P. costellata* Cooper & Grant (1975, pl. 426, fig. 23-26). These have finer spines than in type *Paucispinifera*. Both have a row of ventral hinge spines, not found in *Anemonaria*. Over recent years it has become common to refer the Arctic species *Productus pseudohorrida* Wiman, 1914 to *Anemonaria* (see Rozanov 2003, Angiolini & Long 2008), together with *auriculata* Shi & Waterhouse (1996, pl. 6, fig. 10-28, Fig. 24). Both these species have a well developed umbonal slope row of spines, no apparent hinge row of spines, and especially well developed anterior strut spines, so that their relationship to *Anemonaria* is not entirely certain, *Caruthia* Lazarev & Carter possibly offering an alternative, even though type *Caruthia* lacks a sulcus and is more elongate. Adding to the uncertainty is the morphology of two Canadian species of Gzhelian (Late Carboniferous) age, which are shaped like type *Caruthia*, bear strut spines, and have not only a row of umbonal slope spines like *Caruthia*, but display spines along the hinge that are said to be missing from type *Caruthia*. They belong to *Paucispinifera*, despite the differences in shape.

Fig. 15.4.*Paucispinifera intermedia* Cooper & Grant. A, ventral exterior BR 3078, x2.3. B, dorsal interior BR 3079, x2.5. From Willis Ranch Member (Wordian), west Texas, United States. JBW photo.

Genus ***Eomarginia*** new genus

Fig. 15.5

Derivation: eos – dawn; margino – with border, Lat.

Type species: *Eomarginifera megalotis* Roberts, 1976, p. 58 from unnamed formation (Visean) in northern New South Wales, Australia, here designated.

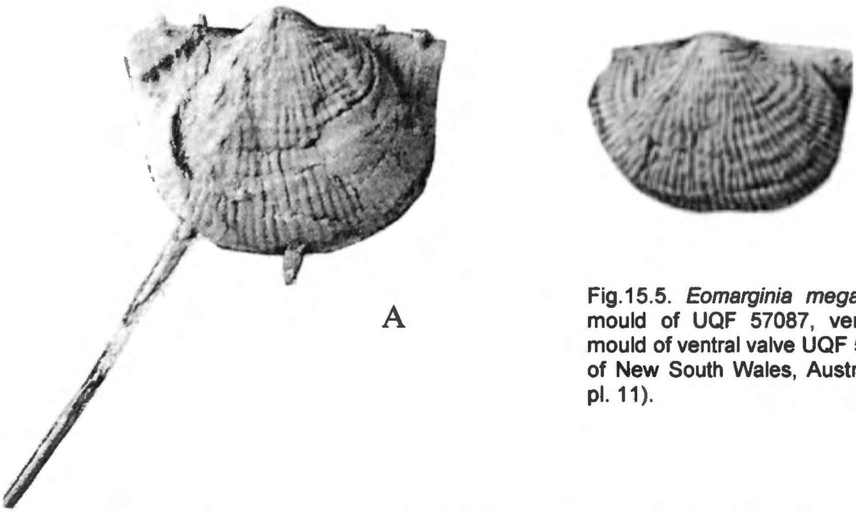


Fig.15.5. *Eomarginia megalotis* (Roberts). A, latex mould of UQF 57087, ventral valve, x2. B, latex mould of ventral valve UQF 57090, x1.5. From Visean of New South Wales, Australia. See Roberts (1976, pl. 11).

Diagnosis: Reticulate shells with strong internal ridge across dorsal ears, five strut spines on ventral valve anterior and two sturdy erect spines each side of umbo along hinge.

Discussion: The type species together with *Eomarginifera paradoxa* Cambell, 1957 are like *Eomarginifera* Muir-Wood, 1930, based on *Productus longispinus* Sowerby, 1814 from the lower Visean of Scotland, with many similar species in the northern hemisphere. *Eomarginifera* has six strut spines and no additional spines along the ventral hinge, more dendritic dorsal adductors, and higher dorsal marginal ridge. But in other respects, the two genera are close, and readily distinguished by shape, size and ornament from the younger genera within the tribe.

Genus ***Caruthia*** Lazarev & Carter, 2000

The genus *Caruthia* Lazarev & Carter, 2000, type species *Caruthia borealis* Lazarev & Carter, 2000, p. 13, is paucispiniferin, and comes from the Ladrones Limestone (Atokan), Prince of Wales Island, southeast Alaska. The type species differs from *Kozlowskia* in being more rounded in outline with lower umbonal walls and swollen disc, and slightly more ventral spines, and apparently lacking subdued concentric ornament over the venter, and has an umbonal slope row of spines, and no hinge row of spines. Whether there are ear spines is not clear, and the comparatively dark and small figures at a magnification of only x1 possibly suggest a spine on the inner ear, as in Lazarev & Carter (2000, Fig. 1D, K). Lazarev & Carter (2000) evaluated the genus as a member of Productinini Muir-Wood & Cooper, 1960, which they equated with Chonetellini Licharew, 1960, and provided a suggested interpretation of the evolution of the tribes. *Caruthia* as Productinini was accepted by Brunton (2007, p. 2639), but he rightly refused to merge Chonetellini with Productinini. *Caruthia* does share some attributes with Productinini, but the lack of conspicuous commarginal dorsal lamellae, coupled with presence of high marginal ridges, and the apparent presence of a pair of large anterior strut spines, one each side of the anterior sulcus (see Lazarev & Carter 2000, Fig. 1Q, R) is more consistent with a position in Paucispiniferinae. Indeed, as described by Lazarev & Carter, *Caruthia* is very close in some respects to *Anemonaria* Cooper & Grant, because both share an umbonal slope row of ventral spines. The type species of *Anemonaria* is moderately large and more transverse and less swollen than type *Caruthia,* and has fewer disc and trail spines, and lacks the row of dorsal pits found in type *Caruthia* that oppose the seat of ventral spines. It generally has a prominent spine on the outer ear, not present as far as can be discerned in *Caruthia*. The tribal to superfamilial position of *Caruthia* remains to be verified from particular attention to the presence or absence of the strut spines, confirmation that hinge spines are absent, clarification of the presence or absence of any ear spine, and the nature of internal pustulation. But clearly dorsal laminae are lacking, unlike members of Productininae. The emphasis placed by Lazarev & Carter (2000) on so-called shagreen structure in the ventral valve does not progress relationships very much, because posterior central papillation or "shagreen" texture is also found in some *Paucispinifera* (Muir-Wood & Cooper 1960, pl. 122, fig. 15) and various other genera, not mentioned by those authors.

Genus ***Anemonaria*** Cooper & Grant, 1969

Fig. 15.6A, B

Type species: *Anemonaria inflata* Cooper & Grant, 1969, p. 8, a junior synonym of *Marginifera sublaevis* King, 1931, p. 89 from Cathedral Mountain Formation (Kungurian), Texas, United States.

Diagnosis: Shell transverse and almost smooth as a rule, with ventral spines in prominent row along umbonal slopes, and scattered other spines, including some close to anterior sulcus, solitary spine present on outer ventral ear. Marginal ridges feebly developed.

Discussion: *Anemonaria* was treated as paucispiniferin by Brunton et al. (2000, p. 444), and this may be correct. But the type species shows rather weak development of what may be strut spines, and moreover the position of spine insertion is somewhat irregular, as confirmed by further material from Venezuela, described by Hoover (1981). That is interpreted herein as a pointer that strut spines could potentially weaken as a flexigenic possibility. *Productus pseudohorrida* Wiman, 1914 has also been referred to *Anemonaria*, initially suggested by Waterhouse (1971a), and followed by Sarytcheva (1977), Ustritsky (1979), Lazarev (2005a), Angiolini & Long (2008), Tazawa (2011) and others.The best preserved Arctic material is that described as *Anemonaria pinegensis* (Licharew) and *A. pseudohorrida* (Wiman) in Sarytcheva (1977, pl. 17, fig. 4, 5, pl. 18, fig. 1-14, Fig. 73, 74), and at least one Russian specimen so identified appears to show rare hinge spines (Sarytcheva 1977, pl. 18, fig. 10a), perhaps exceptional, misinterpreted, or indicative of a different genus. A dorsal marginal ridge is feebly developed, it would appear, as in type *Anemonaria* (Sarytcheva 1977, Fig. 72d, 73b). None of Sarytcheva's specimens show the outer ear spine found in the type species of *Anemonaria*. Possible mounds or pits are visible in one dorsal valve ascribed to *Anemonaria*, opposite the umbonal slope row of ventral spines (Sarytcheva 1977, pl. 18, fig. 1z), whereas type *Anemonaria* lacks such pits. The uncertainty underlines the need for reassessment of these various Arctic species. Canadian Arctic material of Guadalupian (mid-Permian) age differs from *Anemonaria sublaevis* (King) in having a much longer trail, and thicker shell, and the cardinal spine is missing from the outer ventral ear, although the ears on some specimens carry two or three finer spines. On the other hand the umbonal slope row of spines is well developed, and there is no hinge row of spines, and only feeble marginal ridges. Some specimens show anterior strut spines, others do not.

Fig. 15.6. A, B, *Anemonaria sublaevis* (King). A, posterior ventral aspect of ventral valve USNM 153883b, showing umbonal slope row of spines and cardinal spine, x1.5. B, ventral valve USNM 153883a, x1. From Cathedral Mountain Formation (Kungurian) of west Texas, United States. C, D, *Glabauriella quadrata* (Cooper & Grant), lateral and ventral aspects of USNM 153986b from Word Formation (Wordian), west Texas. See Cooper & Grant (1975, pl. 408, 423).

Genus ***Glabauriella*** new genus

Fig. 15.6C, D

Derivation: glaber – smooth; auris – ear, Lat.

Type species: *Paucispinifera quadrata* Cooper & Grant, 1975, p. 1132 from China Tank, Willis Ranch and Appel Ranch Members, and intervening levels (Roadian, Wordian), Glass Mountains, Texas, United States, here designated.

Diagnosis: Large lateral and anterior strut spines, umbonal slope row well developed, no row of spines along hinge, rare scattered other spines, low ribs. Shell large for tribe, transverse and sulcate; dorsal marginal ridge well developed.

Discussion: The genus has been closely described and well illustrated by Cooper & Grant (1975, pl. 417, fig. 1-5, pl. 423, fig. 1-23, pl. 424, fig. 1-39). The species *quadrata* is close to *Paucispinifera* in many respects, although the cardinal process tends to be wider with broad ventral lips, but lacks the distinctive spines close to the ventral hinge. In that respect it comes much closer to *Anemonaria* Cooper & Grant, but has stronger ribs, much stronger strut spines, stronger ribbing, deeper sulcus, larger adductor scars and better formed dorsal marginal ridge. *Anemonaria* as a rule carries a single spine on each outer ear, but this is generally missing from *Glabauriella*. Another genus, *Caruthia* Lazarev & Carter, 2000 has more vaulted ventral valve and so differs considerably in shape, and strut spines, if present, appear to be limited to the anterior ventral valve. The row of pits developed in the dorsal valve of *Caruthia* is absent from the new genus.

Tribe **RETIMARGINIFERINI** Shi & Waterhouse, 1996

Fig.15.7, Fig.15.8

[Nom. transl. hic ex Retimarginiferinae Shi & Waterhouse, 1996, p. 70].

Diagnosis: Visceral disc reticulate, hinge and umbonal slope rows of spines, strut spines symmetrically disposed, trail simple or mutiple. Lower Carboniferous (Visean) to Upper Permian (Changhsingian), Early Triassic?.

Genera: *Retimarginifera* Waterhouse (syn. *Uraloproductus* Ustritsky), *Alitaria* Muir-Wood & Cooper (= *Alifera* Muir-Wood & Cooper, 1960 non *Alifera* Pander, 1830), *Caricula* Grant, *Kurtomarginifera* Xu, *Paryphella* Liao (syn.*Spinoparyphella* Liang?), *Rugivestis* Muir-Wood & Cooper, *Tethysiella* Kotlyar, Zakharov & Polubotko.

Discussion: This tribe is very close to Paucispiniferini, but commarginal rugae are more strongly developed. *Retimarginifera* is treated as senior synonym of *Uraloproductus*, as discussed on p. 456. Immature specimens of *Rugivestis* are close in appearance to immature *Retimarginifera*, apart from being not as broad, and for example

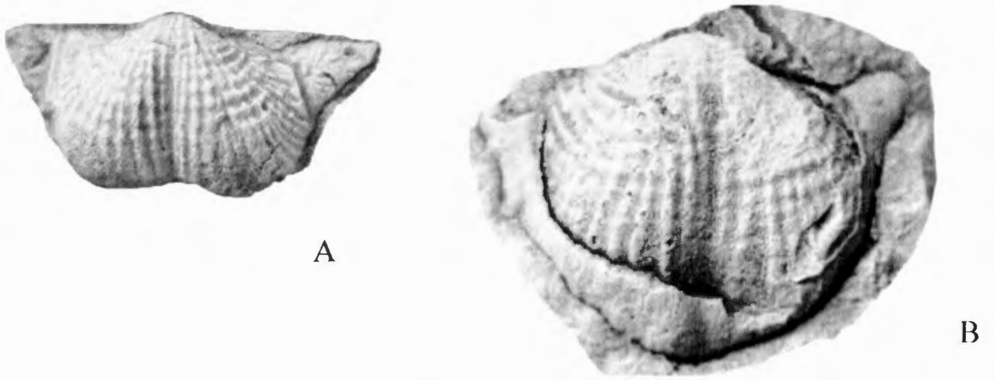


Fig.15.7. A, *Retimarginifera perforata* Waterhouse, topotype ventral valve BR 3080 from Byro Group (Artinskian), Western Australia, x2. See Waterhouse (1970). B, *Rugivestis arctica* Shi & Waterhouse, ventral valve GSC 133297 from GSC loc. 55249, Yukon Territory, Canada, x2. (See Shi & Waterhouse 1996). JBW photo.

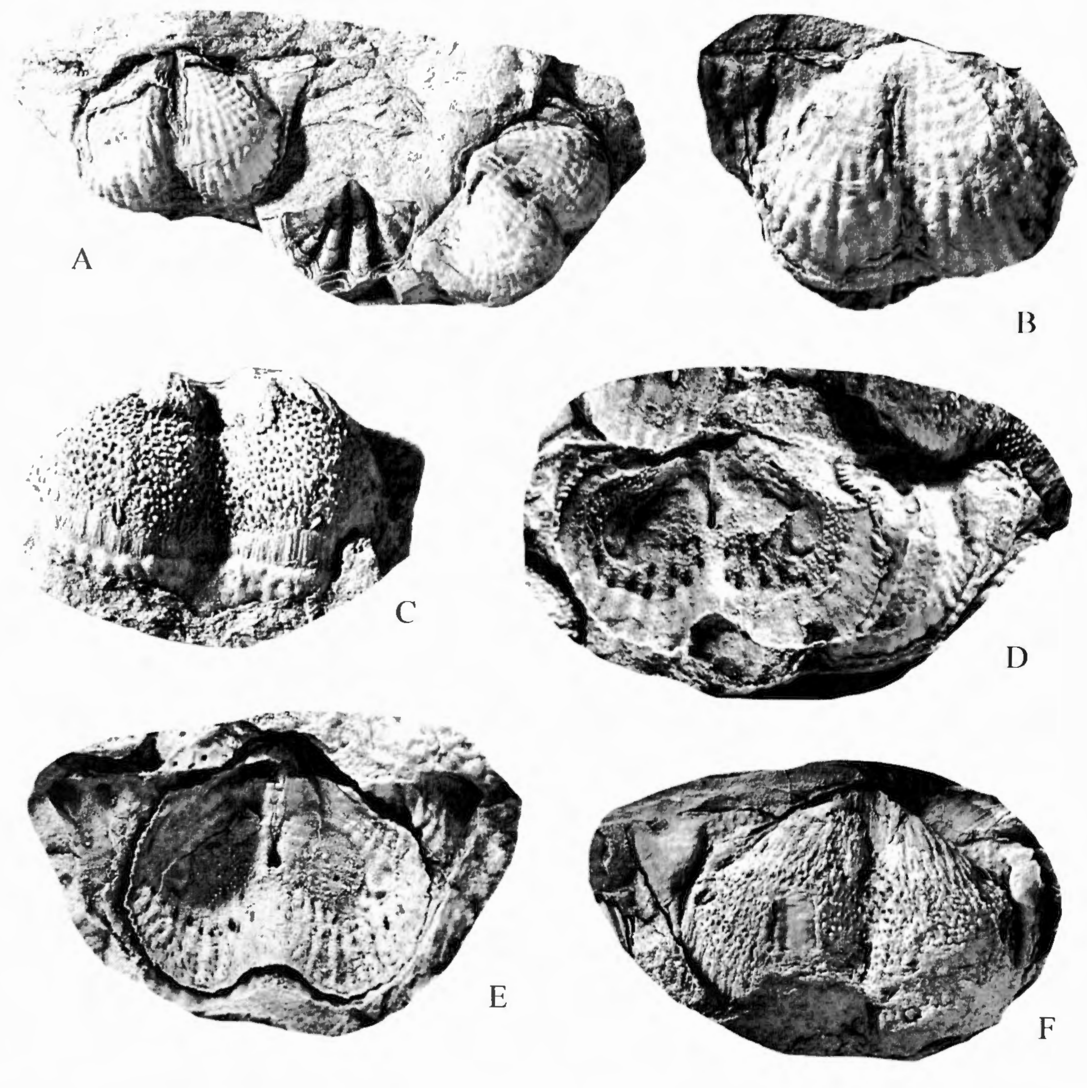


Fig. 15.8. *Retimarginifera alata* Waterhouse. A, ventral valves TBR 76 and 77 with external mould of ventral valve of ?*Spiriferellina* sp., x2. B, ventral valve TBR 86, x3. C, anterior view of ventral internal mould TBR 81, x3. D, dorsal internal mould TBR 85, x3. E, dorsal aspect of internal mould, TBR 82, x3. F, internal mould of ventral valve TBR 84, x3. Specimens from Ko Yao Noi Formation (Sakmarian), southern Thailand. See Waterhouse (1981b). J. Coker & JBW photo.

example, supposed *Uraloproductus* sp. A of Shi & Waterhouse (1996, p. 71, pl. 6, fig. 40-42, text-fig. 25A) appears to be immature *Rugivestis*. What distinguishes *Rugivestis* from *Retimarginifera* is the nasute nature of the mature ventral valve, a feature not shown by mature *Retimarginifera* or *Caricula*. Similar nasutation as well as disc ornament is shown by the early Carboniferous *Alitaria* Muir-Wood & Cooper and also *Paryphella* Liao and *Tethysiella* Kotlyar et al. of Permian age. *Spinoparyphella* Liang 1990, p. 11 was tabulated with type species in a stratigraphic column, but does not appear to have been described. *Rugivestis* was placed as Paramarginiferini by Brunton et al. (2000), and Brunton (2007) evaluated *Tethysiella* Kotlyar et al., 2004 as falling close to *Rugivestis*: indeed distinction proves difficult. *Kurtomarginifera* Xu, type species *K. spinatus* (= *spinata*) Xu (1987, p. 225, pl. 12, fig. 1, 2, 9) from the Upper Permian (lower Changhsingian) of South China has reticulate posterior, ventral sulcus, geniculate dorsal valve, halteroid spines near the posterior margin, and row of spines along the umbonal slopes, and large anterior strut spines (Xu 1987, pl. 12, fig. 9). The genus was placed as a synonym of *Transennatia* by Brunton et al. (2000, p. 447), but the arrangement and nature of spines rule this out. (See pp. 99, 100).

The distribution of the tribes is suggestive. Lower Carboniferous members were largely paleotropical in a broad sense, and Paucispiniferini and Probolioniini remained so and extended into northerly paleotemperate regions. But Retimarginiferini developed as well a strong presence in south paleotemperate latitudes.

Tribe **PROBOLIONIINI** Muir-Wood & Cooper, 1960

[Nom. transl. hic ex Probolioniinae Muir-Wood & Cooper, 1960, p. 237].

Diagnosis: Subquadrate or subelongate shells with commarginal and radial ornament, large ventral strut spines, ears small. Mutiple dorsal trails.

Subtribe **PROBOLIONIINAI** Muir-Wood & Cooper, 1960

[Nom. transl. hic ex Probolioniinae Muir-Wood & Cooper, 1960, p. 237].

Diagnosis: Subquadrate or subelongate shells with commarginal and radial ornament, large ventral strut spines, ears may be small. Lower Permian (Sakmarian) to Upper Permian (Wuchiapingian).

Genera: *Probolionia* Cooper, *Lamnimargus* Waterhouse.

Discussion: This group is very close to Paucispiniferini, and is distinguished by shape and possession of numerous dorsal trails. The distinctive features include ventral sulcus, ribbing and weak rugae, with up to six or so strut spines, and traces of former but no longer functional strut spines on the earlier formed shell, and well developed ventral marginal ridge. The type species of *Probolionia* Cooper comes from central Oregon, United States, and is of Sakmarian age, as shown by Shi & Waterhouse (1996) and Waterhouse (1976b, p. 72), not Kungurian as claimed by Cooper (1957) and Brunton et al. (2000, p. 469).

The type species of *Lamnimargus* Waterhouse, 1975, based on *Productus himalayensis* Diener, 1899, p. 39 is widely recognized in the Himalaya of Nepal and Kashmir, even extending to the Shyok Valley (Brookfield & Gupta 1984). it was diagnosed in part by the presence of several trails as in Probolioniini, but this causes difficulty where mainly ventral valves are preserved. The ventral ears are weakly ornamented to largely smooth, whereas the ventral ears of the otherwise somewhat similar genus *Retimarginifera* Waterhouse, 1970 bear stronger ribs and commarginal rugae, unless decorticated. Both genera have ventral strut spines, and a row of spines extends both along the hinge and along the umbonal slopes, as in *Paucispinifera* Muir-Wood & Cooper, 1960, a genus with less reticulate ornament. *Retimarginifera* is found over south Asia, Western Australia and Timor, whereas *Lamnimargus* has been reported from more paleotropical faunas, in the Permian of Japan, China, Inner Mongolia and South Primoyre (Tazawa 2006, 2008a, p. 3).

Subtribe **KOZLOWSKIINAI** Brunton, Lazarev & Grant, 1995

[Nom. transl. hic ex Kozlowskiini Brunton, Lazarev & Grant, 1995, p. 928].

Diagnosis: Subquadrate or subelongate shells with commarginal and radial ornament, large ventral strut spines, strong as a rule across anterior ventral valve. Upper Carboniferous (Atokan, ie. Bashkirian – lower Moscovian) to Middle Permian (Roadian).

Genera: *Kozlowskia* Fredericks, *Cornumukia* new genus, *Opiparia* new genus, *Sutherlandika* new genus.

Discussion: These genera have, basically, the mutiple dorsal trails shown by *Probolionia*, but strong strut spines lie anteriorly in a row across the ventral anterior, as well as at posterior lateral extremities. The group demonstrates flexigenic tendencies, with varying development and loss of key morphological features. *Kozlowskia* has mutiple trails, prominent strut spines and a row of hinge spines rather than an umbonal slope row. New genus *Cornumukia* has lost the hinge spines, whereas *Sutherlandika* new genus, the oldest known genus of the subtribe, has a row of spines along the umbonal slopes rather than hinge, and was widespread in Late Carboniferous and Early Permian of North America. Both genera have mutiple trails. *Opiparia* has increased the number of anterior ventral spines, but reverted to a single dorsal trail.

Genus ***Sutherlandika*** new genus

Fig. 15.9

Derivation: Named for P. K. Sutherland.

Type species: *Kozlowskia montgomeryi* Sutherland & Harlow, 1973, p. 35 from La Pasada Formation (Atokan) of New Mexico, United States, here designated.

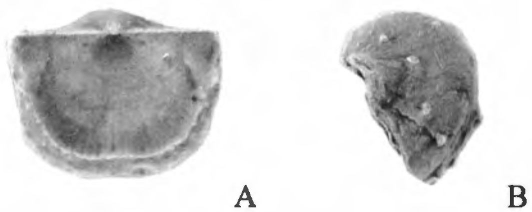


Fig. 15.9. *Sutherlandika montgomeryi* (Sutherland & Harlow). A, dorsal view of specimen OU 7651, holotype, with valves conjoined. B, lateral view of ventral valve showing umbonal slope row of spines. OU 7650 from La Prasada Formation (Atokan), New Mexico, United States, x2. See Sutherland & Harlow (1973, pl. 5, fig. 19d, e).

Diagnosis: Small shells with prominent ventral strut spines, two along venter in the plane of symmetry, two laterally on the anterior slope, and one on each flank near the cardinal extremities. Row of well spaced spines along umbonal slopes. Ribs low, many dorsal trails, marginal ridges high.

Discussion: Unlike *Kozlowskia*, *Sutherlandika* displays a row of well spaced spines along the ventral umbonal slopes, whereas *Kozlowskia* has a row of well spaced spines close to the hinge. *Productus splendens* Norwood & Pratten, 1855, widespread in the Pennsylvanian of United States, as described by Dunbar & Condra (1932) and Muir-Wood & Cooper (1960) is congeneric, the umbonal slope row of ventral spines being displayed for example by Muir-Wood & Cooper (1960, pl. 63, fig. 1). From the basal Skinner Ranch Formation, *Kozlowskia alata* Cooper & Grant (1975, pl. 312, fig. 1-20, pl. 453, fig. 34) has mutiple trails and an umbonal slope row of spines (see Cooper & Grant 1975, pl. 312, fig. 7) as in *Sutherlandika*. The presence of a nasute trail and cluster of thin spines in front and scattered over the trail point to some development from the Pennsylvanian species.

Genus ***Opiparia*** new genus

Fig. 15.10B, D

Derivation: From species name, opipara.

Type species: *Kozlowskia opipara* Grant (1976, p. 121) from Rat Buri Limestone (Roadian) at Phanynga, northwest Ko Muk, south Thailand, here designated.

Diagnosis: Ventral strut spines numerous anteriorly, hinge row of spines, trail simplified and not mutiple.

Discussion: This genus is interpreted as a derivative of *Kozlowskia*, which has lost its mutiple trails and increased the number of anterior ventral spines. The interior has remained much as in *Kozlowskia* and allies, with strong marginal ridges and zygidium. Interestingly, a companion genus *Cornumukia* has retained the mutiple trails but reduced the number of anterior spines, and developed much finer ribs.

Genus ***Cornumukia*** new genus

Fig. 15.10A, C

Derivation: Combination of species name cornuta and part name of locality Ko Muk, Thailand.

Type species: *Kozlowskia cornuta* Grant (1976, p. 118) from Rat Buri Limestone (Roadian) at northwest Ko Muk, south Thailand, here designated.

Diagnosis: Transverse with extended ears, fine ribs and few if any anterior spines, hinge row of spines developed. Mutiple dorsal trails and high marginal ridges.

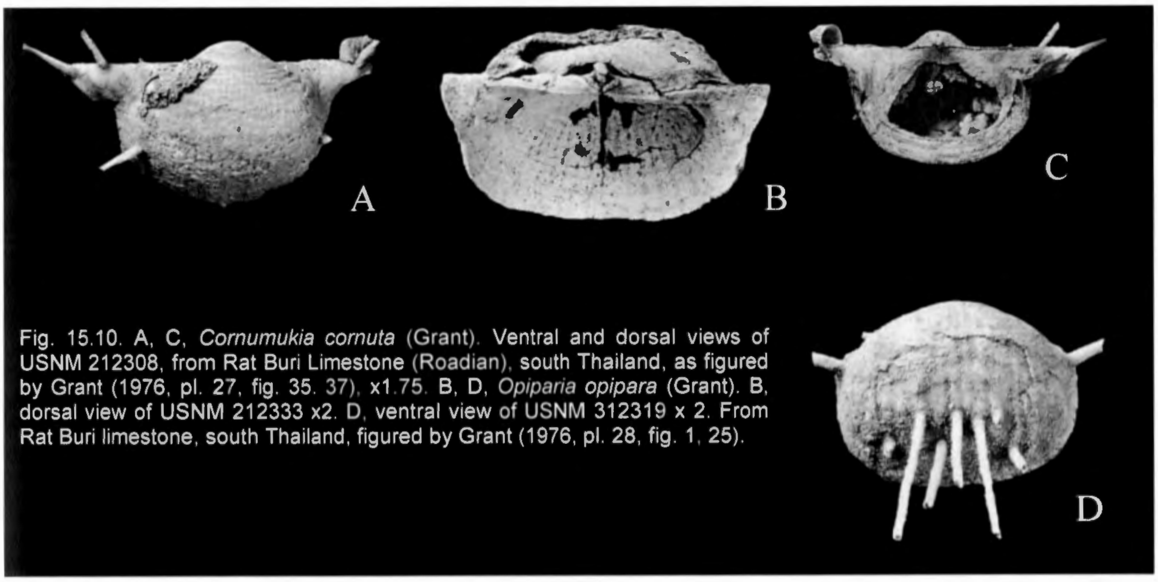


Fig. 15.10. A, C, *Cornumukia cornuta* (Grant). Ventral and dorsal views of USNM 212308, from Rat Buri Limestone (Roadian), south Thailand, as figured by Grant (1976, pl. 27, fig. 35. 37), x1.75. B, D, *Opiparia opipara* (Grant). B, dorsal view of USNM 212333 x2. D, ventral view of USNM 312319 x 2. From Rat Buri limestone, south Thailand, figured by Grant (1976, pl. 28, fig. 1, 25).

Discussion: This genus developed from *Kozlowskia*, retaining the mutiple trails and distinctive ventral and dorsal internal features, but developing large ears and fine ribs, and losing most or all of the anterior strut spines. A row of spines is present thinly along the hinge, with large pair of strut spines on extremities, and another pair on anterior lateral visceral slopes, and rare other spines, including an anterior spine developed on the trail medianly in some specimens. The species is well described by Grant (1976). The sister genus *Opiparia* is readily distinguished by the increase in number of ventral anterior spines, simplication of the trail and coarser costae.

Subfamily **PRODUCTININAE** Muir-Wood & Cooper, 1960

Fig. 15.11

[Productininae Muir-Wood & Cooper, 1960, p. 181].

Diagnosis: Ribbing on ventral valve and more faintly on dorsal valve, concentric lamellae prominent on dorsal valve, no ventral sulcus in most genera. Ventral spines few and moderately well developed, generally includes strut spines. Teeth, sockets and interareas absent, no buttress plates or cleft in posterior dorsal median septum, ridge usually high across ventral ears, dorsal anterior pustules small. Upper Devonian (Famennian) to Lower Carboniferous (Visean).

Genera: *Productina* Sutton, *Argentiproductus* Cooper & Muir-Wood (nom. nov. pro *Thomasella* Paul, 1942 non Fredericks, 1928 = *Thomasia* Fredericks, 1928; *Thomasiina* Paeckelmann, 1931 non Newstead & Carter, 1911), *Dorsirugatia* Lazarev, *Productellina* Reed, *Quospina* new genus.

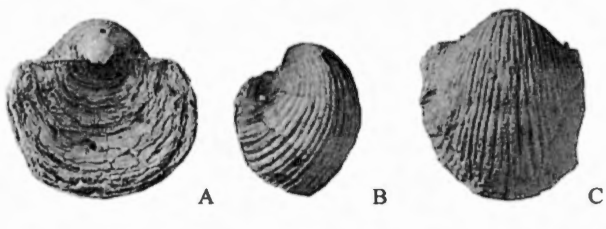


Fig. 15.11. *Productina sampsoni* (Weller). A, dorsal view of USNM 124169a, x3, B, dorsal oblique view of USNM 66857a, x3, and C, ventral aspect of USNM 123972a, x2. Mississippian specimens from New Mexico and Missouri, United States. See Muir-Wood & Cooper (1960, pl. 123, fig. 5, 8, 6).

Discussion: Shape, spinosity and interior suggest that this group provided a source for Bibatiolinae followed by Chonetellinae. The subfamily is descended from Devonoproductinae, with which it shares radially ribbed ventral valve and sublamellate dorsal valve, and is not closely related to Overtonioidea, which stemmed from Productellidae. Ventral spines are arrayed in an unusual pattern as three symmetrically disposed strut spines in *Argentiproductus*, and two in *Productellina*, and a short row of posterior ventral spines close to the umbonal flanks characterizes *Productina* and *Dorsirugatia*, the latter genus distinguished in part by exceptionally weak ventral ribbing. Muscle scars lack dendritic ridges (*Argentiproductus*). Brachial shields are large, elongate and directed forward in *Productina* (Muir-Wood & Cooper 1960, pl. 45, fig. 13, 15; Brunton et al. 2000, text-fig. 279.1e), and although marginal ridges are only low, but present in *Productina* Sutton, 1938, a strong internal ridge lies across the ventral ears in *Argentiproductus* (Brunton & Mundy 1993, text-fig. 6. 13b; Brunton et al. 2000, Fig. 279.2e), as well as *Dorsirugata* Lazarev in Lazarev & Suur'suren, 1992 and *Productellina* Reed. The dorsal concentric laminae of Productininae are usually well developed, stronger than in overtoniids and other groups, which are mostly younger than the oldest Productininae.

Caruthia Lazarev & Carter, 2000, p. 12 was evaluated as a member of Productinini by those authors, followed by Brunton (2007, p. 2639), but shape and ornament on both valves differs substantially, especially in the lack of dorsal lamellae and differently placed strut spines, and the genus is allocated to Paucispiniferinae, based on shape and spinose ornament.

The complex tangle regarding the generic name *Argentiproductus* is summarized in Brunton et al. (2000, p. 426) and Muir-Wood & Cooper (1960).

Genus ***Quospina*** new genus

Fig. 15.12A

Derivation: quo – where, place; spina – thorn, Lat.

Type species: *Productina morrisi* Roberts, 1976, p. 42 from unnamed formation in the *Rhipidomella fortimuscula* Zone (upper Visean), New South Wales, Australia, here designated.

Diagnosis: Large for subfamily and sulcate. Three postero-lateral strut spines each side of ventral umbo, no anterior coarse spine or spines. Dorsal valve lamellate, ribbing may be weak.

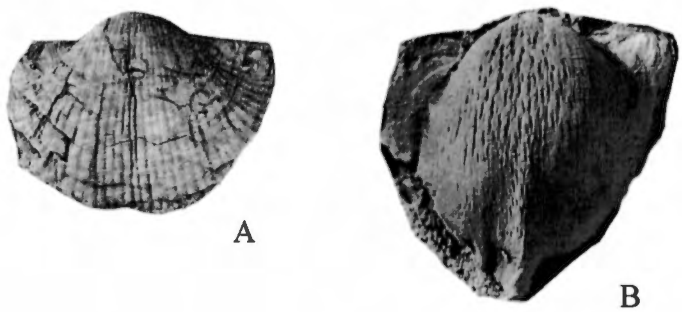


Fig. 15.12. A, *Quospina morrisi* (Roberts), ventral valve exterior from *Rhipidomella fortimuscula* Zone (Visean) of New South Wales, Australia, x1.5. See Roberts (1976, pl. 7, fig. 30). Now kept at Australian Museum, Sydney.
B, *Chonetella nasuta* (Waagen). Ventral internal mould CASGF 754, from *Lamnimargus himalayensis* Zone (Wuchiapingian), Marbal Pass, Himalayas, Northwest India, x2. See Waterhouse & Gupta (1979b). J. Coker & JBW photo.

Discussion: The type species is found in the upper Visean *Rhipidomella fortimuscula* Zone of New South Wales, and is characterized in part by its relatively large size for the subfamily, with coarse costae and ventral sulcus. Three spines are developed postero-laterally each side of the umbo at the base of the umbonal flanks, and there are no anterior ventral spines. The presence of a posterior dorsal internal ridge is not clear: possibly there is none. *Productina macdonaldi* Roberts, 1976, p. 41 from the same zone in New South Wales is moderately close but much smaller, and apparently not sulcate, although the ribs are, for the size, coarse. Roberts (1976) identified upper Kohlenkalk specimens of Germany assigned to *Productus* (*Thomasina*) *pectinoides* [non Phillips] by Paeckelmann (1931, p. 188, pl. 17, fig. 13-16) with the Australian species *morrisi*. The species *pectinoides* Phillips was assigned to *Argentiproductus* Cooper & Muir-Wood, 1951 by Muir-Wood & Cooper (1960), but Brunton & Mundy (1993, p. 106) placed *pectinoides* in *Productina*. They referred *macdonaldi* Roberts to *Argentiproductus* and kept *globosa* Roberts (1963), a small strongly concavo-convex species, in *Productina*. The species *morrisi* was left unmentioned. Brunton & Mundy (1993) emphasized shape, ribs, and lastly spines as significant for discriminating *Productina* and *Argentiproductus*. *Productina* was regarded as elongate and globose, with ribs comparatively more rounded in cross-section and not becoming noticeably wider anteriorly, and the median spine or spines tending to be absent. But the Australian species *macdonaldi, morrisi* and *striata* are more transverse than elongate and in that respect differ from

Productina. Even so, *Productina striata* Roberts displays median eccentrically placed strut spines, and so appears to belong to *Argentiproductus*, and *globosa* Roberts (1963), not well known, appears close to *Productina*, as in Brunton & Mundy (1993), with a row of concentrically arranged spines over the trail.

Dorsirugatia Lazarev in Lazarev & Suur'suren, 1992 is close to *Quospina* in terms of having three spines over each flank either side of the umbo, but the genus is small with highly swollen ventral valve, no sulcus and only subdued ribs, and strong internal dorsal ridge. It is of Upper Devonian (Upper Famennian) age in Mongolia.

Subfamily **BIBATIOLINAE** Waterhouse 2002b

[Bibatiolinae Waterhouse, 2002b, p. 15].

Diagnosis: Small transverse shells with wide hinge and well rounded anterior and lateral margins, nasute anterior, ventral sulcus absent or restricted to median disc, both valves costate, dorsal valve not lamellate, dorsal trail simple. Spines few, involve three or more strut spines. Ventral and dorsal marginal ridges well developed. Lower Carboniferous (Visean) to Middle Permian (Wordian).

Genera: *Bibatiola* Grant, *Bothrionia* Cooper & Grant, *Eomarginiferina* Brunton.

Discussion: In shape these shells are like *Chonetella* (see below), but have different spines and high marginal ridges, and differ from Paucispiniferinae in shape and in having three or more strut spines, one median, and one or more on each flank of the ventral valve. These genera are particularly close in shape and in strut spines to Productininae, but lack dorsal lamellae. As well as giving rise to Chonetellinae through loss of the strut spines, the subfamily or some close ally appears to have given rise to Yakovleviidae, members of which retained strut spines.

Subfamily **CHONETELLINAE** Licharew, 1960

[Nom. transl. hic ex Chonetellidae Licharew, 1960, p. 226. Syn. Haydenellinae Jin & Hu, 1978, p. 113].

Diagnosis: Transversely subtriangular with wide hinge and often nasute anterior, smooth or with low ribs, no strut spines, hinge may have low ginglymus, shallow body corpus, dorsal valve not lamellate, trail simple. Dorsal anterior pustules may be large, marginal ridge variable in development, often weak.

Discussion: This is a distinctive group of Permian genera, treated as a tribe by Brunton et al. (2000, p. 427), but well separated from Productininae in its different spine pattern, lack of dorsal commarginal lamellae, and appearance of large dorsal pustules anteriorly. It apparently developed as an offshoot from Bibatiolinae, judged from the fossil record, being especially close in shape, and having lost the strut spines.

Tribe **CHONETELLINI** Licharew, 1960

Fig. 15.12B

[Nom. transl. Brunton et al. 1995, p. 926 ex Chonetellidae Licharew, 1960, p. 226].

Diagnosis: No dorsal spines. Transversely subtriangular with wide hinge and nasute anterior, smooth or with low ribs, spines may be limited to row in front of ventral hinge, no strut spines, hinge may have low ginglymus, shallow body corpus, dorsal anterior pustules may be large, no thick or high marginal ridge. Middle Permian (Roadian) to Upper Permian (Changhsingian).

Genera: *Chonetella* Waagen, *Celebetes* Grant, *Chianella* Waterhouse, *Haydenella* Reed, ?*Haydenoides* Chan, *Huatangia* Liao & Meng, *Ogbinia* Sarytcheva, *Parachonetella* Liao, *Planihaydenella* Chang.

Discussion: As opposed to the report of minute teeth in *Chonetella* by Brunton et al. (2000), Grant (1976, p. 138) denied that teeth were present, on the basis of well preserved material from the Salt Range, Pakistan. As well, Grant (1976, p. 159) stated that *Haydenella* was linoproductoid from the nature of its cardinal process, but Brunton et al. (2000) more acceptably regarded the genus as chonetellin.

Huatangia Liao & Meng, 1986, p. 78 lacks strong spines, and is placed as Chonetellini, given the apparent lack of strut spines and lack of dorsal laminae, rather than in Probolioniini as favoured by Brunton et al. (2000). Admittedly it does have a strong marginal ridge, recalling that of Bibatiolinae, with the possibility that spines have been secondarily lost. The cardinal process is possibly unifid.

Haydenoides Chan in Yang De-li et al. (1977, p. 352), type species *H. orientalis* Chan, was synonymized with *Spinomarginifera* by Brunton et al. (2000, p. 439). It is not very close to *Spinomarginifera*, having moderately prominent radial ribs, at least over the ventral valve (Chan in Yang De-li et al. 1977, pl. 140, fig. 13a-c; Yang De-li

1984, p. 219, pl. 33, fig. 10a, b, 11a-c), and relatively few ventral spines. Chan compared the form to *Haydenella* Reed, which seems closer, at least externally, but the interiors differ, Chan suggesting that *Haydenella* lacked a broad marginal ridge and had a more evenly concave dorsal valve and thinner body corpus.

Genus ***Chianella*** Waterhouse, 1975

Fig. 15.13

Type species: *Avonia? chianensis* Chao, 1927, p. 126 from Hsiaokiang Limestone (uppermost Early Permian – late Artinskian to Roadian), Jiangxi, China.

Diagnosis: Hemispherical to ellipical shells with broad and occasionally branching ribs bearing scattered ventral spines.

Discussion: This genus was assessed as a member of Auriculispininae by Brunton et al. (2000, p. 538) and Chen & Shi (2006, pl. 14, fig. 1-24), but figures by Chen & Shi (2006, pl. 14, fig. 1-24) of the type species from the Tarim Basin, although not topotypic, show broad ribs with occasional branches, and scattered spines with slightly swollen bases over the disc and trail, and according to the text, a row along the hinge, even though such are not visible in most figures, apart from Chen & Shi (2006, pl. 14, fig. 2 (left side) and perhaps fig. 7. To judge from other figures there appear to be additional spines over the anterior ears or umbonal slopes, suggestive of two or three rows along the umbonal slopes (Chen & Shi 2006, pl. 14, fig. 1, 7, 8, 9, 19, 21). The ornament thus suggests a close relationship to Chonetellini, especially *Haydenella*, as indicated in several Chinese studies, including Jin & Hu (1978, p. 113) and Liang (1990, p. 171). *Haydenella* shows similar occasionally branching weaker costae, and has a row of spines diverging from and in front of the hinge, close to the base of the umbonal slope (Muir-Wood & Cooper 1960, pl. 65, fig. 14). Chen & Shi (2006) noted that *Haydenella* was distinguished from *Chianella* by its less regularly spaced costae, significantly larger size and a row of spines on each flank. Unlike *Auriculispina* and allies, the ventral spines in both genera lack elongate bases.

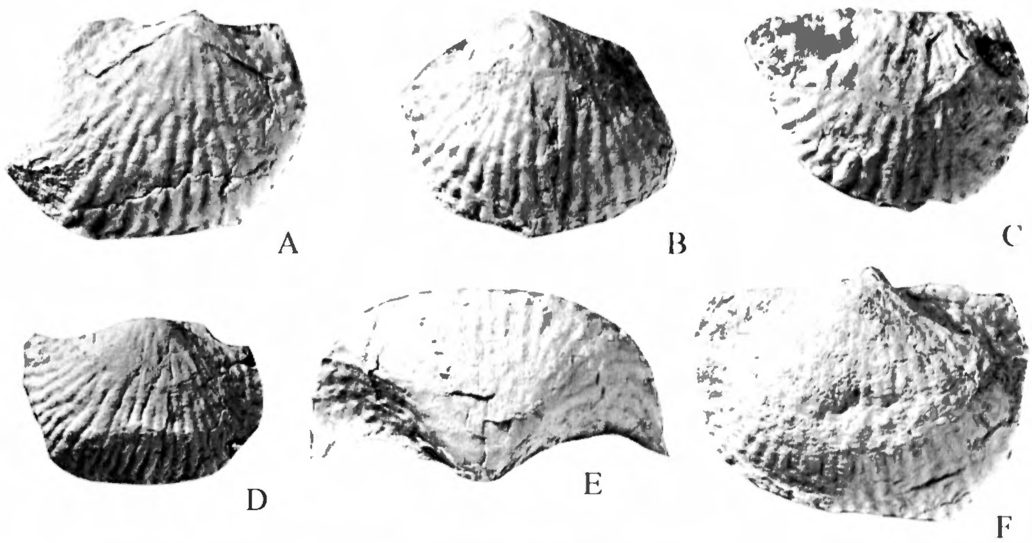


Fig. 15.13. *Chianella chianensis* (Chao). A, dorsal valve IGPS108899-900, x1. B, C, anterior and posterior views of ventral valve IGPS108901, x1. D, ventral valve IGPS108903, x1. E, posterior view of ventral valve IGPS108902, x1. F, dorsal view of dorsal external mould IGPS108904, x1.5. Specimens from middle Qipan Formation (Kungurian), China. Photographs courtesy of Chen Zhong-Qiang, Wuhan, China.

From the Maokou rocks (Middle Permian) of China, *Longyania* Zhu, 1990, p. 71 was assigned to synonymy of *Chianella* by Brunton et al. (2000, p. 538), as accepted uncritically by Waterhouse (2002b) and Chen & Shi (2006). The type species *L. magna* Zhu (1990, p. 72, pl. 14, fig. 33) is larger than *Chianella*, as noted by Brunton et al. (2000), and has very wide hinge and signs of fine ribs, fine pustules (or fine external spines?), low anterior radial ribs, and vague indications of a thick posterior lateral spine, and low rugae on one ear. The sole published figure is very obscure, but somewhat suggestive of a yakovleviid, but this is not certain.

Tribe **ODONOVANIINI** new tribe

Name genus: *Odonovania* new genus, here designated.

Diagnosis: Chonetellinae distinguished by presence of spines on dorsal valve. Marginal ridge may be high. Upper Carboniferous (Moscovian) to Upper Permian (Changhsingian).

Genera: *Odonovania* new genus, *Yanagidania* new genus, ?*Pseudohaydenella* Liang.

Discussion: Genera assigned to Chonetellini, as in Brunton et al. (1995, p. 995; 2000, p. 428), and most Paucispiniferidae have only ventral spines. *Pseudohaydenella* Liang, 1990 was said to have a ventral frill or fringe, but remains obscure. The dorsal valve was stated to be ornamented "like that of the ventral valve" (p. 464), which bears costae, rugae and spines, but the nature of the dorsal ornament cannot be verified from figures, and whether dorsal spines are really present remains uncertain. Its nasute ventral outline suggests likely kinship with Chonetellinae, and the possibility that it is a junior synonym of *Chianella* Waterhouse, 1975. *Odonovania* has been chosen as name giver to the tribe because its dorsal spines can be figured, whereas those of *Yanagidania* were reported, but not figured. The two genera spanned a lengthy time interval.

Genus ***Odonovania*** new genus

Name: Named for Brian O'Donovan, photographer.

Type species: *Odonovania dorsospinosa* new species from Braga Member, Marsyangdi Formation (Changhsingian), Nepal, here designated.

Diagnosis: Transverse shells with ventral fold and dorsal spines laterally.

Odonovania dorsospinosa new species

Fig. 15.14

Derivation: dorsum – back; spina – thorn, Lat.

Holotype: Specimen 2006.81.324 figured as Fig. 15.14A from PMm4, Mungji Member (Changhsingian), Nepal, here designated.

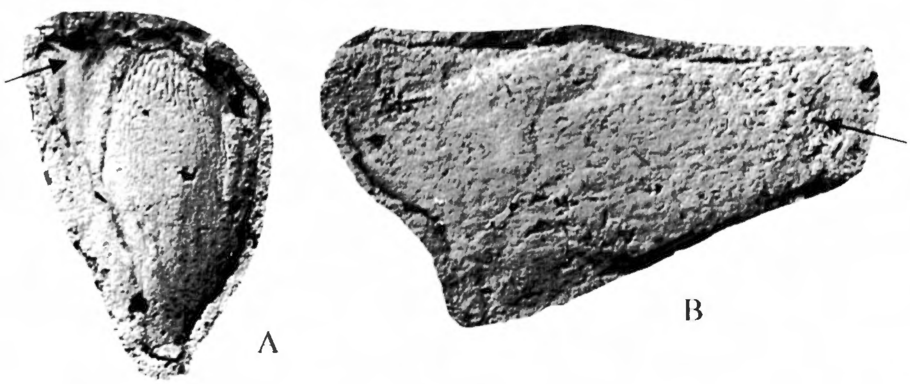


Fig. 15.14. *Odonovania dorsospinosa* new genus, new species. A, ventral internal mould from PMc1, Chho Member, hinge showing spine to left, as arrowed, x3. B, holotype, dorsal external mould, showing spine bases in lateral cluster as dark holes and arrowed, from PMm4, Mungji Member, x4. From Late Permian Senja Formation (Changhsingian), north-central Nepal. Material kept at Canterbury Museum, Christchurch, New Zealand. N. Hiller & JBW photo.

Material: Single ventral valve from PMc1, one ventral valve, one dorsal valve and a specimen with valves conjoined but little of ventral valve remaining from PMm4, Chho and Mungji Members, Marsyangdi Formation, Nepal. See Appendix A, part G, pp. 480, 481. Kept at Canterbury Museum, Christchurch.

Dimensions in mm, ventral valves from PMm4

Width	Length	Height
13	13.5	?3
18	12	6

Description: Ventral valve from PMc1 elongated by deformation, with large ears, median low fold, nasute anterior margin, shows one lateral hinge spine, others lost or concealed in matrix; ventral valve from PMm4 has several fine erect spine-bases preserved along hinge row. Interior has fine elongate ridges posteriorly, indicating part of muscle field, and very fine low pustules over much of valve. The ventral valve of the specimen with valves conjoined from PMm4 is less deformed, and comparatively smooth with no spines left after weathering. Its anterior is weakly nasute. The holotype is a very wide but probably stretched dorsal valve (width 22mm, length ?13.5mm, height ?4mm), with nasute anterior, but no fold. Ears are large and spine-bases subevenly spaced about 1mm apart over ears and outer margins, 0.2-0.4mm in diameter. Another specimen some 14mm wide and 8mm long has growth laminae medianly and is smooth laterally. Fine erect spines are present postero-laterally. The cardinal process is small.

Discussion: These specimens clearly belong to a genus distinct from any genus so far named in Chonetellinae. The ventral valves lack ribs and are more transverse than *Chonetella nasuta* Waagen (1884, pl. 81, fig. 3-8; Grant 1976, pl. 42, fig. 1-17) from the beds at Jabbi in the Chhidru Formation, Salt Range, Pakistan, and also described from the *Lamnimargus himalayensis* Zone at Marbal Pass, Kashmir, by Waterhouse & Gupta (1979b). *Chonetella semicostata* Waterhouse (2004a, p. 64) from bands 3, 4, 8, 9, 10, 11 of the Selong Group in the Selong Xishan section in south Tibet (Shi & Shen 1997; Shen et al. 2000, p. 739, text-fig. 9.23-28, table 6) has anterior ventral ribs, unlike the present specimens. Grant (1970, p. 136, pl. 1, fig. 20, 20b) figured a small ventral valve from the Khisor white sandstone of the Salt Range (see Waterhouse 2010b), which probably belongs to *semicostata*, as it lacks posterior ribs, and has fine anterior ribs.

Stratigraphy: The species is found in members of the Marsyangdi Formation, of late Permian age immediately below the Pangjang Member with *Otoceras woodwardi* Griesbach, in central Nepal (see Waterhouse 2010b). Further specimens are (temporarily) not available for illustration because of the Christchurch earthquake.

Genus ***Yanagidania*** new genus

Fig. 15.16

Derivation: Named for Juichi Yanagida.

Type species: *Desmoinesia prayongi* Yanagida, 1975, p. 21 from Khao Luak beds (Moscovian) near Loei, north Thailand, here designated.

Diagnosis: Transverse and may be nasute, ribs strong, umbonal part crossed by low rugae. Suberect spines scattered over ventral valve, including hinge and umbonal slopes, ears and trail, but not forming persistent rows; spines rare on dorsal valve, marginal ridges strong in both valves.

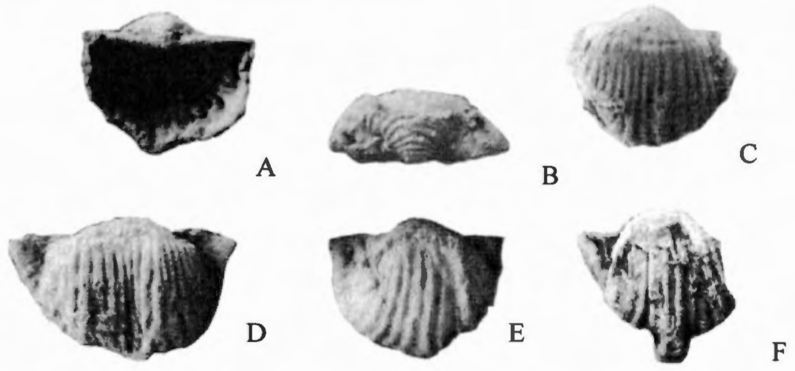


Fig. 15.16. *Yanagidania prayongi* (Yanagida). A, B, E, dorsal, posterior and ventral views of holotype, GK-D 31305. C, ventral valve GK-D 31498. D, anterior ventral valve GK-D 31499. F, ventral anterior view of GK-D 31501. Specimens from Huai Lang (Upper Carboniferous), Loei area, Thailand, x2. See Yanagida (1975).

Discussion: The type species was originally ascribed to *Desmoinesia* Hoare, 1960, because of the presence of spines on both valves and high marginal ridges, not to mention somewhat similar age, but the costae have a different pattern, persisting well and not fading or branching or appearing afresh by intercalation: moreover the shape differs considerably and is chonetellid in its wide hinge and in some specimens nasute anterior. In many respects the genus is close in appearance to *Bothrionia* Cooper & Grant (1975, p. 984), Subfamily Bibatiolinae, with several species known from the Guadalupian of Texas, United States, but *Bothrionia* has a prominent spine on each ear, and a pair in front near the sulcus, and no dorsal spines are present. Like the new form, marginal ridges are high in each valve, suggesting that genera of Odonovaniini were derived from Bibatiolinae. *Yanigidania* has low but definite commarginal rugae over the first formed part of the ventral shell, and there are no such rugae in the North American species. Ribs are stronger than in *Odonovania* from Nepal, and this genus is not known to show commarginal rugae.

Family **ANIDANTHIDAE** Waterhouse, 1968a

[Nom. transl. Sarytcheva 1977, p. 53 ex Subfamily Anidanthinae Waterhouse, 1968a, p. 1172].

Diagnosis: Costellate, with ventral row of hinge spines, erect ventral body spines, dorsal spines rarely present. Adductor scars comparatively smooth, brachial shields productiform but comparatively large for productiform families.

Discussion: Anidanthidae evolved from Family Devonoproductidae, Subfamily Devonoproductinae Muir-Wood & Cooper, 1960, which has ornament close to that of Anidanthinae, but is strophalosiiform, with teeth, sockets, interareas and large brachial shields. One intriguing aspect is that this same subfamily Devonoproductinae appears to given rise to Productininae, which in turn evolved into Paucispiniferinae. Years before, the approach of *Anidanthus* to such genera was noted by Waterhouse (1966, 1967a), and earlier, Muir-Wood & Cooper (1960) had considered that *Paucispinifera* and *Anidanthus* to be related in so far as both were treated as Linoproductidae. Those prospective relationships were ignored in the *Revised Brachiopod Treatise*.

Subfamily **ANIDANTHINAE** Waterhouse, 1968a

Fig. 15.17 - Fig. 15.19

[Subfamily Anidanthinae Waterhouse, 1968a, p. 1172].

Diagnosis: Well defined costellae, hinge spines moderately developed, visceral and trail spines inconspicuous as a rule, no dorsal spines, with rare exception. Dorsal valve lamellate to varying degree. Upper Carboniferous (?Moscovian or younger) to Upper Permian (Changhsingian).

Genera: *Anidanthus* Whitehouse (syn. *Nothokuvelousia* Waterhouse), *Akatchania* Klets, *Anidanthia* new genus, *Fusiproductus* Waterhouse, *Kuvelousia* Waterhouse, *Megousia* Muir-Wood & Cooper, *Mongousia* Manankov, *Protoanidanthus* Waterhouse, ?*Pseudomarginifera* Stepanov.

Discussion: Brunton et al. (2000, p. 531) also recognized *Protanidanthus* Liao, 1979 and *Zia* Sutherland & Harlow, 1973 as members of Anidanthinae, but *Zia* shows little similarity to the subfamily, belonging to Reticulatiinae (p. 130), and *Protanidanthus* Liao lacks dorsal lamellae and so is deemed to belong to Lirariinae (p. 332). As well, *Protoanidanthus* Waterhouse, 1986b was overlooked by Brunton et al. (2000), but appears to be a valid genus and is widespread in high paleolatitudes of both hemispheres (Briggs 1998), subject to the nature of *Pseudomarginifera* Stepanov, 1934, a genus which is which is so poorly known that its limits are yet to be circumscribed. Two Siberian species ascribed to *Anidanthus* by Klets (2005, pl. 9, fig. 1-11), *A. boikow* (Stepanov) and *A. megensis* Solomina, are of interest in that the high quality illustrations suggest that the dorsal valve was not thickened (eg. Klets 2005, pl. 9, fig. 1b), and indicate that the dorsal wings were not large and laterally twisted, as far as they are preserved (Klets 2005, pl. 9, fig. 4, 8, 9, 10). The ventral ears are relatively larger, it would appear, than those of other related genera. But whether these species are congeneric with the type species of *Pseudomarginifera* requires further consideration. The type species of *Pseudomarginifera*, *Productus ussuricus* Fredericks, 1924, p. 8, pl. 2, fig. 17', 17" from Ussuriland, east Russia, involves a ventral valve without large ears, but possibly broken, and a dorsal valve with moderately large ears, not as extended as those of *Anidanthus*, but possibly incomplete. It appears that the dorsal valve was not thickened anteriorly into a wedge. Specimens identified with *ussuricus* from South Primoyre were examined and figured in Sarytcheva (1977, pl. 5, fig. 1-5, Fig. 34). They come closest to *Protoanidanthus* Waterhouse, but have slightly larger ventral ears, and the anterior shell tends to be nasute, whereas nasutation is not often found in the three species so far ascribed to *Protoanidanthus* from east Australia (Briggs 1998). Thus *Pseudomarginifera* may well prove to be distinct from *Anidanthus*, and very close to *Protoanidanthus*, which may perhaps be better treated as a subgenus of *Pseudomarginifera*. But too many uncertainties remain for *Pseudomarginifera* to be adequately circumscribed. It seems quite possible that dorsal ears have been broken short, and that they originally were as large as those of *Megousia* Muir-Wood & Cooper, 1960, and potentially *Pseudomarginifera* could take priority over that genus. *Nothokuvelousia* Waterhouse, 1986b, based on material from the Rose's Pride Formation of the southeast Bowen Basin, Queensland, Australia, is now considered to be the same as *Anidanthus,* and the type species *aurifera* is synonymized with *springsurensis.* It was synonymized with *Kuvelousia* Waterhouse, 1968a by Brunton et al. (2000), but differs in the nature of its dorsal extended ears, which are smooth, not ribbed. The dorsal ears on *Anidanthus* are very large, not small as portrayed by Muir-Wood & Cooper (1960) or Brunton et al. (2000), nor variable as claimed by Brunton (2007) in asserting that *Protoanidanthus* had no validity, and it should be realized that assessments by these authors were made without recourse to field study or even perusal of extensive collections at Australian institutions: they relied on small collections of misidentified and non-topotypic material in northern institutions, as if type material and descriptions, especially from the southern hemisphere, were not important. The genus *Megousia* Muir-Wood & Cooper, 1960 has dorsal ears which typically curve and twist forward, whereas those of *Anidanthus* extend laterally. As well, *Megousia* has a non-thickened strongly geniculate dorsal trail, and denticulate ventral hinge. *Kuvelousia* Waterhouse, 1968a is close to *Megousia*, and differs in having a massively thickened dorsal valve and high ventral marginal ridge.

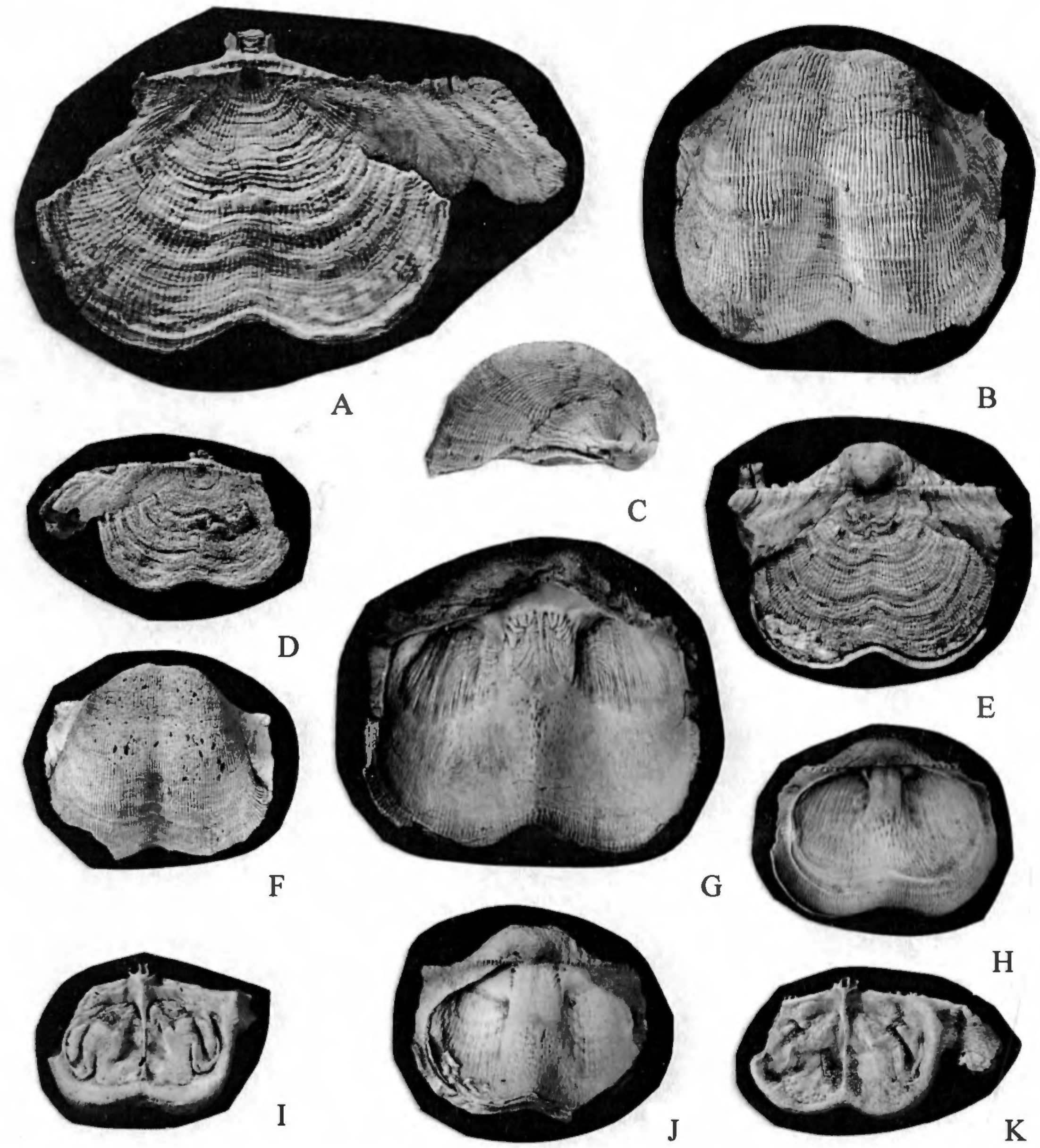


Fig. 15.17. *Kuvelousia sphiva* Waterhouse. A, dorsal valve, unregistered specimen at Geological Survey of Canada, x2. B, ventral valve USNM 153464c. C, lateral aspect of GSC 22912. D, K, dorsal valve exterior and internal aspects, USNM 154464i. E, dorsal aspect of specimen with valves conjoined, GSC 22912. F, J, ventral valve exterior and interior, GSC 22900. G, interior of ventral valve USNM 153464d. H, interior of ventral valve 153464c. I, dorsal interior, USNM 153464h. Specimens from GSC loc. 76029, Assistance Formation (Roadian), Cameron Island, Canada, x1. In Waterhouse (1968a), the material was considered to have come from above the Assistance Formation, and was called Degerbols Formation? by Brunton et al. 2000) , but is likely to be Trold Fiord Formation. B. O'Donovan & JBW photo.

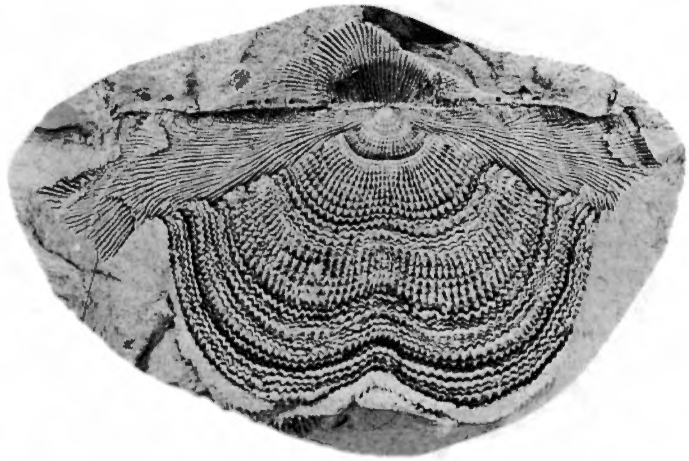


Fig.15.18. *Kuvelousia leptosa* Waterhouse., dorsal external mould and posterior part of ventral valve with row of hinge spines, left as holes. USNM 151591j, holotype, x2. From Canyon Butte Formation (Sakmarian), Oregon, United States. See Waterhouse (1968a). B. O'Donovan & JBW photo.

Anidanthus is similar in having thickened dorsal trail, and has laterally extended ears, but unlike *Kuvelousia*, lacks hinge denticulations. New genus *Anidanthia* is close in its non-denticulate hinge and laterally extended ears without a twist, but like *Megousia* has a long and slender geniculate trail which is not thickened or wedge-like. *Anidanthus* and *Anidanthia* belonged to the southern Permian paleohemisphere, whereas *Megousia* and *Kuvelousia* belonged to the northern Permian paleohemisphere. The transverse and fusiform genus *Fusiproductus* Waterhouse, 1966 is present in east Asia and possibly Texas, United States, and *Protoanidanthus* is present in high paleolatitudes of the southern and northern hemispheres (Shi & Waterhouse 1996, Briggs 1998, p. 199), depending of course on how the nature of *Pseudomarginifera* turns out. *Akatchania* Klets in Abramov & Grigorieva 1988, p. 135 of northeast Russia has well separated dorsal lamellae and ventral spines only near the hinge. The ventral adductor scars are smooth and elongate.

Fig.15.19. *Kuvelousia* sp. GSC 27030, x2, showing twisted dorsal ear, from GSC loc 53848, Permian sandstone unit, Yukon Territory, Canada, probably Middle Permian in age (see p. 479). Note the unusually large brachial shields. (See Bamber & Waterhouse 1971). B. O'Donovan & JBW photo.

Genus ***Anidanthus*** Whitehouse, 1928

Type species: *Linoproductus springsurensis* Booker, 1932, p. 67 from Cattle Creek Formation (Artinskian) of Bowen Basin, Queensland, Australia.

Diagnosis: Small shells, spines only on ventral valve, in hinge row and scattered over disc and trail, ribs over both valves, dorsal valve lamellate and wedge-shaped without discrete trail, and large laterally extended ears.

Discussion: Controversy over the authorship of *Anidanthus* has been discussed by Waterhouse & Chen (2007, p. 16). Those authors, together with Briggs (1998), preferred to ascribe the authorship to Whitehouse (1928), whereas Brunton et al. (2000) granted the authorship to Hill (1950), yet placed *Pseudomarginifera* Stepanov, 1934 in synonymy. Hill (1950) was first to describe the genus as *Anidanthus* according to the rules of the International Subcommission of Zoological Nomenclature (1999), but such rules did not apply when Whitehouse (1928) first proposed the genus, and certainly in practise, genera proposed before 1931 were deemed acceptable despite failure to use binomial nomenclature (see ICZN 1999, p. 67. article 67.2.2). "Although making no description or diagnosis, Whitehouse indicated specimens typical of his genus which had been previously described (and figured), and one of these at least was subsequently placed in a well defined species, which may therefore be taken as type species, following normal procedure with genus caelebs" (Waterhouse 1966, p. 20). Melville (1984) in scrutinising just a few aspects of *Anidanthus*, ignored that discussion. But Waterhouse & Chen (2007) argued that tolerance should be allowed for a genus proposed before the rules became established, and considered Whitehouse (1928) to be the author. Dorothy Hill would be the last person to have stooped to name-claiming.

Anidanthus perdosus new species

Fig. 15.20

1984 *Anidanthus* sp. Campbell et al., fig. 6. 11-13.
1993 *Megousia solita* [not Waterhouse] – Briggs & Campbell, p. 326, fig. 3.1-10.
1993 Anidanthid cf. *Megousia solita* – Briggs & Campbell, p. 32, fig. 3.11, 12.
1998 *M. solita* – Briggs, p. 207, Fig. 98F- I (part, not Fig. 97A-E = *solita* Waterhouse).
2001 Anidanthin gen. & sp. indet. Waterhouse, pp. 26, 44.
2002a Anidanthin gen. & sp. indet. Waterhouse, p. 27.

Derivation: perdo – dissipate, waste, Lat.

Holotype: UQF 75365 figured by Briggs (1998, Fig. 98F-H) and Fig. 15.20 herein from Branxton Subgroup (Kungurian), north Sydney Basin, Australia, here designated.

Diagnosis: Transverse shells, dorsal ears large and extend forward close to the visceral disc, dorsal valve wedge-shaped, without extended dorsal trail.

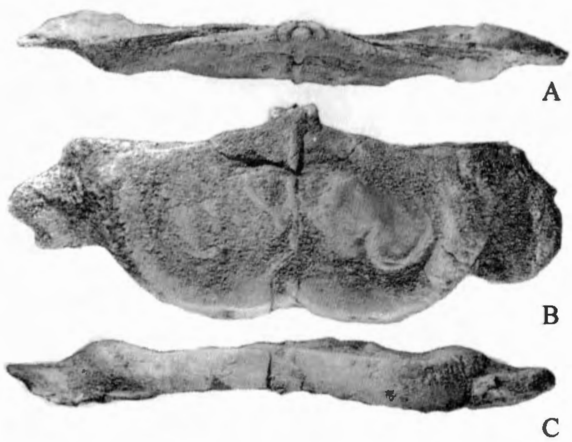


Fig. 15.20. *Anidanthus perdosus* new species, posterior, ventral and anterior aspects of dorsal valve holotype UQF 75365 from Branxton Subgroup (Kungurian), Sydney Basin, New South Wales, Australia, x1.5. From Briggs (1998).

Discussion: The material in the synonymy is characterized by a wedge-shaped dorsal valve, well figured in the various publications. As well, the lateral ears are moderately large and extend forward – they are not as extended nor as wide as in *Anidanthia paucicostatus* (Waterhouse). Both ventral and dorsal valves are wider than in *springsurensis* Booker (1932, pl. 3, fig. 1-6, pl. 4, fig. 1-7), as confirmed for specimens from Rose's Pride Formation (Waterhouse 1986b, pl. 14, fig. 3, 10-19), and shape provides the most ready distinction between the two species. Details are further described in the above synonymy.

The type material comes from the Branxton Subgroup in the Sydney Basin in New South Wales. From New Zealand, comparable material has been found in the Queens Beach Formation on Stephens Island, northern South Island, but the formation is of Triassic age, and the material reworked from older but unknown deposits (Waterhouse 2002a, p. 142). Elsewhere similar specimens are found in the Caravan Formation of Wairaki Downs, southern New Zealand, of early middle Kungurian (Filippovian) age (Briggs & Campbell 1993, Waterhouse 2002a, p. 27).

Genus *Anidanthia* new genus

Derivation: Variant spelling from *Anidanthus*, the name proposed by Whitehouse (1928) for allied genus.

Type species: *Anidanthus paucicostatus* Waterhouse, 1986b, p. 62 from Elvinia Formation (Sakmarian) of southeast Bowen Basin, north Queensland, here designated.

Diagnosis: Shells moderately large for the subfamily, with prominent radial ornament, spines limited to ventral valve, forming well defined hinge row, scattered and rare over disc and trail. Dorsal ears laterally extended, not twisted, trail long, geniculate, not thickened.

Discussion: Careful examination of anidanthin genera in east Australia shows that the group has been misrepresented to some extent. *Anidanthus springsurensis* (Booker, 1932, p. 67), the type species of *Anidanthus*, was interpreted substantially on the basis of material from Homevale, north Bowen Basin, Queensland, rather than the type locality in the Cattle Creek Formation of the southwest Bowen Basin, examples being provided by Hill (1950), Waterhouse (1968b), Briggs (1998), Brunton et al. (2000) and Brunton (2007). Muir-Wood & Cooper (1960) based their interpretation of *Anidanthus* partly on Homevale material, and treated anidanthids from Kimbriki, New South Wales, as typical for illustrating the genus. The Kimbriki shells have reduced dorsal ears, and are referable to *Protoanidanthus compactus* Waterhouse, 1986b. Waterhouse (1986b) established that Homevale and Elvinia material differed at least specifically from type *springsurensis*, and, as well, a separate genus *Nothokuvelousia* was discriminated in the Rose's Pride Formation of southeast Bowen Basin, distinguished from Homevale and Elvinia material by its wedge-like dorsal valve. Briggs (1998) synonymized *Nothokuvelousia* with *Anidanthus*, and was right to do so, because it is now realized that type *Anidanthus* also has a wedge-like dorsal valve. By contrast, the Elvinia and Tiverton anidanthids have a non-thickened dorsal valve with separate mutiple trails, just as in *Protoanidanthus*, but differ from *Protoanidanthus* in having extended dorsal ears.

Anidanthia is like *Megousia* Muir-Wood & Cooper, 1960 in having laterally extended dorsal ears and a moderately long slender trail. It differs from *Megousia* in the nature of the dorsal ears, which extend laterally, and rarely forwards in *Anidanthia*. An additional distinction for *Megousia*, pointed out by Brunton et al. (2000, p. 532), is that the dorsal ears bear ribs which curve antero-dorsally, whereas the external ears in what is now *Anidanthia* are smooth, or more accurately, smoother, for there is some variation. In *Megousia*, the ears show a forward twist, as displayed in the Glass Mountains species described by Cooper & Grant (1975) from Texas as *auriculata, definita, flexuosa*, and *mucronata*. The generic position of species *girtyi* (King) is uncertain due to incomplete preservation, unless it belongs to *Protoanidanthus*. The species *waagenianus* Girty from the Capitanian looks close to *Fusiproductus* Waterhouse.

Anidanthus is a very distinctive form, characterized by extended dorsal ears which are smooth externally, and by an anteriorly thickened dorsal valve in which mutiple trails are fused into a wedge, unlike the trail of other forms in which the trail is comprised of separate sheets of shell or a single thin structure. The wedge-shaped dorsal valve is clearly figured in the illustrations in Booker (1932, pl. 4, fig. 1, 2, 3), and also by Waterhouse (1986b, pl. 14, fig. 13, 16-18) for material described, wrongly, as a separate species and genus. Briggs (1998, Fig. 97I, J, K) figured few and uninformative specimens from the Cattle Creek Formation, and lumped in other material of uncertain age. None of the *Revised Brachiopod Treatise* studies, or the overview by Muir-Wood & Cooper (1960), provided any figures or analysis of genuine *Anidanthus*.

Anidanthus springsurensis (Booker) is typical of the Cattle Creek Formation and Rose's Pride Formation of the Bowen Basin, Queensland, in the *Ingelarella plica* Zone of east Australia and New Zealand (Waterhouse 2008). A slightly younger species, *Anidanthus perdosus*, is present in the Branxton Subgroup at Belford Dome, north Sydney Basin, figured by Briggs (1998, Fig. 98F-I) as *Megousia solita* not Waterhouse. This also has a wedge-shaped dorsal valve with thick trail, indicative of *Anidanthus* s.s. Type and other specimens of *M. solita* show mutiple separate trails that are not amalgamated into a wedge (eg. Briggs 1998, Fig. 98A, C, D) and are now deemed to belong to *Anidanthia*. The alternative, adopted by Briggs (1998), is to regard the nature of the dorsal trail as variable and of no taxonomic significance. So far, it has been found that collections from single stations are consistent in that aspect of their morphology, and it is judged advisable to treat generic and specific names as reflective of morphology, with the limits circumscribed through extensive observation. Whilst it may be deemed to be "only" an ecologic factor, this is not established for productid dorsal valves, and the feature is a significant morphological feature of various strophalosiid genera such as *Wyndhamia* and *Arcticalosia*, a yakovleviid called *Archboldevia*, and a waagenoconchid genus called *Wimanoconcha*: it is an objective morphological feature. The trail in species with wedge-like dorsal valve is short and often not externally geniculate or semi-geniculate. Not a single specimen of the anidanthid specimens from the lower and middle Tiverton Formation and partly correlative Elvinia Formation of the Bowen Basin in Queensland, shows a wedge-shaped dorsal valve, whereas dorsal valves from the upper Cattle Creek Formation and correlative Rose's Pride Formation at a younger level in the Bowen Basin are all wedge-shaped in section.

Anidanthia paucicostata (Waterhouse, 1986b)

Fig. 15.21, Fig. 15.22

1892 *Productus* sp. indet. Etheridge, pl. 12, fig. 17.
1932 *Linoproductus springsurensis* [not Booker] – Booker, p. 67, pl. 4, fig. 5-7? (part, not pl. 3, fig. 1-6, pl. 4, fig. 1-4 = *springsurensis*).
1950 *Anidanthus springsurensis* – Hill, pl. 7, fig. 1, 3, 4 (part, not fig. 2, 5, 6 = *springsurensis*).
1964 *A. springsurensis* – Maxwell, p. 44, pl. 7, fig. 13-16.
1964 *A. springsurensis* – Hill & Woods, pl. P6, fig. 8, 10, 11 (part, not fig. 9 = *springsurensis*).
1968a *Megousia* sp. Waterhouse, p. 1174, pl. 154, fig. 7, 12, 13.
1968b *A. springsurensis* – Waterhouse, p. 236, pl. 1, fig. 1, 4, 5, 6, text-fig. 2A, B, D (part, not pl. 1, fig. 2, 3, text-fig. 2C, 3 = *springsurensis*).
1972 *A. springsurensis* – Hill, Playford & Woods, pl. P6, fig. 8, 10, 11 (part, not fig. 9 = *springsurensis*).
1974 *A. springsurensis* – McCarthy et al., Fig. 4J.
1980 *A. springsurensis* – McClung, pl. 19.1, fig. 6.
1986b *A. paucicostatus* Waterhouse, p. 62, pl. 13, fig. 23-27, pl. 14, fig. 1, 2, 4-9.
1998 *A. springsurensis* – Briggs, p. 204, Fig. 97A-F, G?, H? (part, not Fig. 97I-K = *springsurensis*).
1998 *A. cessnockensis* Briggs, p. 201, Fig. 96A, C, G (part, not B, D, E, F, H, I = *Protoanidanthus compactus* Waterhouse).

Holotype: For *paucicostata*, UQF 74083 from Elvinia Formation, southeast Bowen Basin, figured by Waterhouse (1986a, pl. 13, fig. 25), OD. For *cessnockensis*, UQF 75357 from Farley Formation, figured by Briggs (1998, Fig. 96A, C), OD.

Diagnosis: Shells moderately elongate as a rule with arched venter, moderately coarse costae, often with fine intercalated costellae.

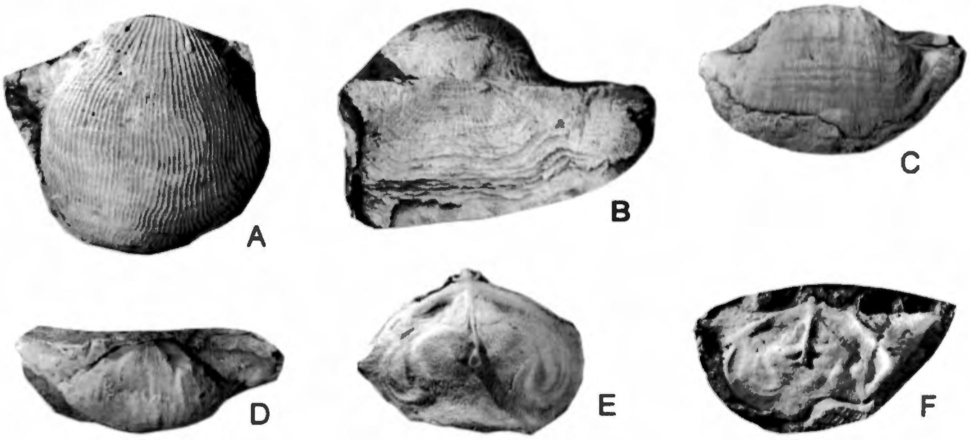


Fig. 15.21. *Anidanthia paucicostata* (Waterhouse). A, latex cast of ventral valve UQF 81206 from UQL 4511, x1.2. B, dorsal aspect of latex cast UQF 81207 from UQL 4511, x1.1. C, D, anterior ventral and posterior ventral aspect of ventral internal mould UQF 81208 from UQL 3127, x1. E, latex cast of dorsal interior UQF 81271 from UQL 4510, x1.5. F, latex cast of dorsal interior UQF 81210 from UQL 4509, x1.5. Tiverton Formation (Sakmarian), Queensland, Australia. JBW photo.

Material. Numerous specimens are available from the Elvinia and Tiverton Formations (Sakmarian) of the Bowen Basin, Queensland, and the Farley Formation of the Sydney Basin in New South Wales, Australia. *Paucispinauria geniculata* and *Taeniothaerus subquadratus* Zone.

Description: Descriptions are provided in the synonymies and will be elaborated in Waterhouse & Shi (in press).

Resemblances: This species is more elongate than *Anidanthus springsurensis* (Booker), and normally is not sulcate, and there are many intercalate ribs. It appears that the variation is mostly displayed by *paucicostata*: the ornament in *springsurensis* appears to be consistently fine; that of *paucicostata* is generally coarser, but includes specimens with more numerous and more differentiated costae, partly because of rib splitting and intercalation. The species *paucicostata* is slightly but distinctly older than *springsurensis*, and differs strongly in the nature of the dorsal valve and trail. Another difference lies in the nature of the visceral disc, which, in undistorted specimens, is larger and more transverse and sulcate in *springsurensis* than in *paucicostata*.

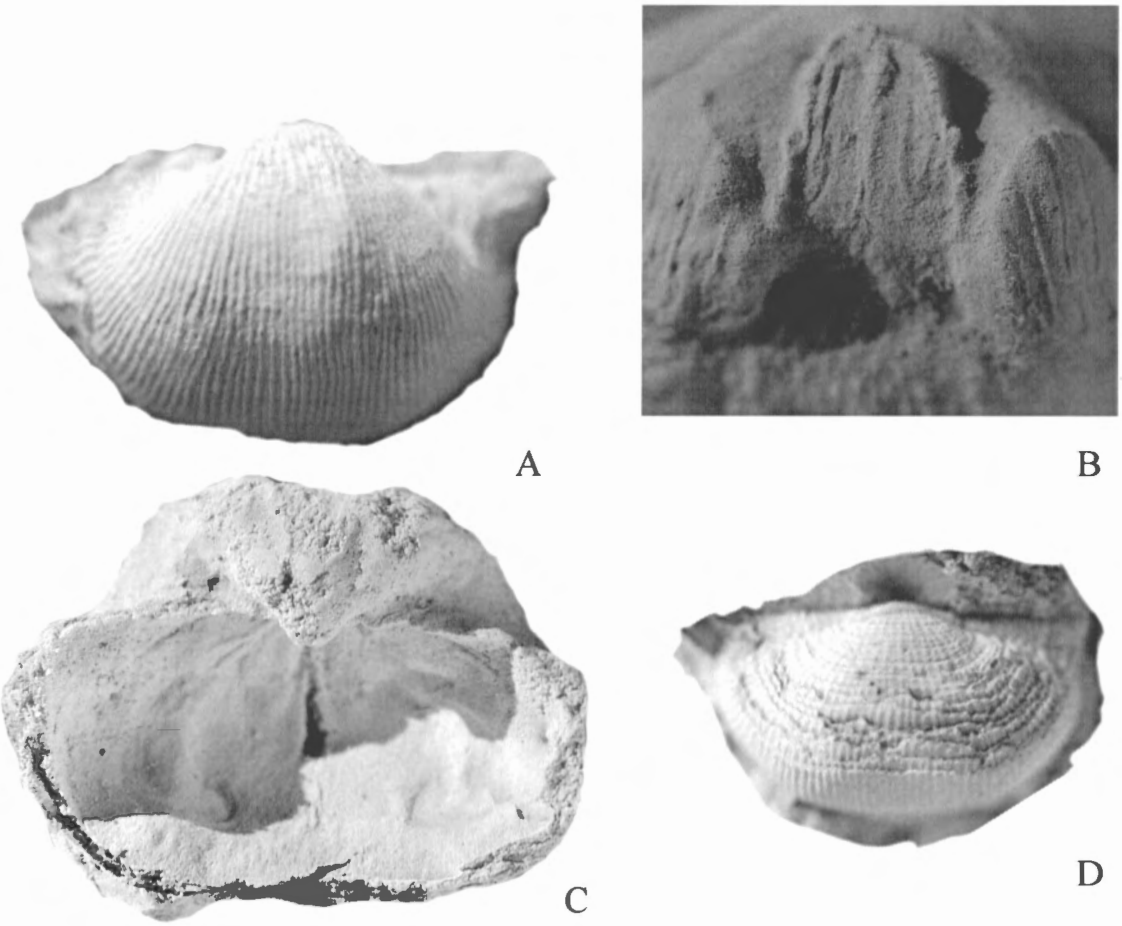


Fig.15.22. *Anidanthia paucicostata* (Waterhouse). A, latex cast of ventral exterior UQF 81212 from UQL 4509, x3. B, ventral aspect of internal mould UQF 81271 from UQL 4510, x6. C, dorsal aspect of internal mould of both valves UQF 81209 from UQL 2620, x3. D, dorsal valve exterior UQF 81270 from UQL 4510, x2. Dorsal ears are incomplete. Tiverton Formation (Sakmarian), Queensland, Australia. JBW photo.

Briggs (1998) recognized a separate Australian species *cessnockensis* from the Farley Formation of the northern Sydney Basin at Singleton, Hunter Valley, New South Wales. The species overlaps *paucicostata* in range. Two species were lumped in his description, and one suite of specimens is reallocated to *Protoanidanthus compactus* Waterhouse. Judged from published figures, costae number six to eight in 5mm on the ventral valve of type *cessnockensis*, and in the text were counted at eight to eleven in 5mm anteriorly. The species was said to be distinguished by its prominent sublamellate concentric wrinkles with higher wider crests, and flatter dorsal valve for which the anterior margin is placed well behind that of the ventral valve. But the strength and nature of the concentric dorsal wrinkles appears variable on populations, with no consistent stratigraphic record, and no explanation was provided why the synonymy for the species in Briggs (1998) includes occasional individuals referable to *springsurensis* and *paucicostata,* even under the criteria adduced by Briggs (1998). Close examination of the Tiverton suites shows no consistent pattern, and the dorsal lamellae of the Tiverton and Elvinia specimens are as slender as in the holotype of *cessnockensis* (Briggs 1998, Fig. 96C) from the Farley Formation at Singleton, Hunter Valley, and the dorsal anterior margin lies close to the ventral anterior margin, as far as they are preserved. Unfortunately it is not possible to adequately compare the nature and strength of dorsal concentric ornament on *springsurensis* types, for few examples have been illustrated, with only the interior so far figured, and it has not been possible to find the types: they do not appear to be kept at either the Australian Museum or Queensland Museum.

Genus ***Mongousia*** Manankov, 2008

Fig. 15.23

Type species: *Anidanthus spineus* Manankov, 1992, p. 74 from Tsagan-Temete horizon (Wordian), Mongolia.
Discussion: Figures provided by I. N. Manankov show the diagnostic presence of dorsal spines, and the twist in the dorsal ears and long slender trail that indicate a relationship to *Megousia* Muir-Wood & Cooper, 1960.

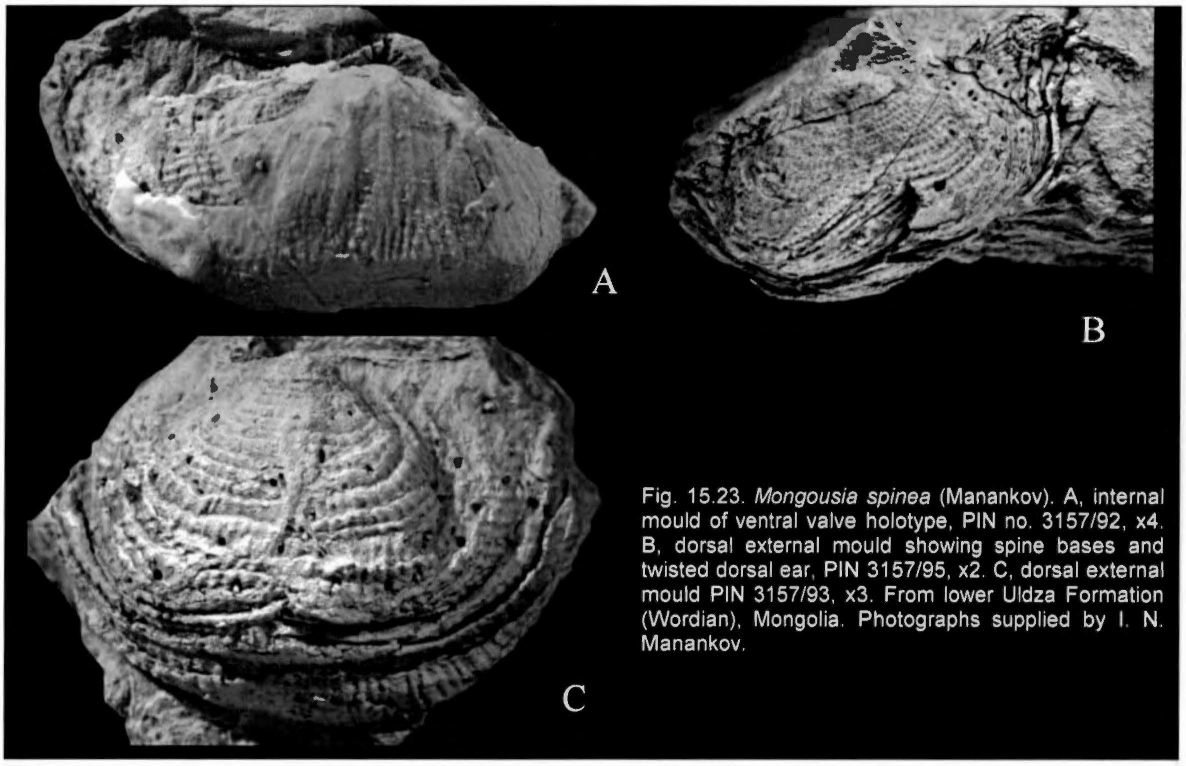


Fig. 15.23. *Mongousia spinea* (Manankov). A, internal mould of ventral valve holotype, PIN no. 3157/92, x4. B, dorsal external mould showing spine bases and twisted dorsal ear, PIN 3157/95, x2. C, dorsal external mould PIN 3157/93, x3. From lower Uldza Formation (Wordian), Mongolia. Photographs supplied by I. N. Manankov.

Subfamily **LIRARIINAE** new subfamily

Fig. 15.24

Name genus: *Liraria* Cooper & Grant, 1975, p. 1156 from Bone Spring Formation (Artinskian), Texas, United States, here designated.

Diagnosis: Both valves costellate, spines inconspicuous, limited to ventral valve, forming row along or close to hinge, may be scattered and erect over ventral valve. Dorsal valve not lamellate. Ventral adductors smooth or deeply scored by longtudinal grooves. Lower Permian (Asselian) to Middle Permian (Wordian).

Genera: *Liraria* Cooper & Grant, *Calandisa* new genus, *Cimmeriella* Archbold, *Globiella* Muir-Wood & Cooper, *Protanidanthus* Liao.

Discussion: *Liraria* Cooper & Grant, 1975 has fine ribs over both valves, a row of ventral hinge spines, and small erect spines over the ventral disc, much like those of *Anidanthus*. Unlike *Anidanthus*, the dorsal valve lacks commarginal laminae. No member of the subfamily displays very large dorsal ears, or wedge-like dorsal valve. In *Liraria*, the cardinal process is low with median shaft deeply divided in two, with a zygidium. Ventral adductor scars were described as small and located within a pit, and dorsal adductor scars are not strongly impressed, and neither smooth nor clearly dendritic. Cooper & Grant (1975, p. 1157, pl. 434, fig. 28, 30) drew attention to the presence of two dorsal ridges, one each side of the median septum, between the adductor scars. They erred in stating (1975, p. 1156) that spines lay only on the dorsal valve. *Cimmeriella* Archbold in Archbold & Hogeboom, 2000, p. 101, based on *Productus foordi* Etheridge, 1903, and best figured in Archbold (1983), is characterized by strong ribs. It has rather smooth ventral and dorsal adductor scars, and although two lateral ridges are not clearly developed in the dorsal valve, the medium septum shows two fine longitudinal slits between the adductors (Archbold 1983, Fig. 5S, T), and the adductors appear to be bordered laterally by a ridge. The ventral adductors in an allied species *C. flexuosa* (Waterhouse) are somewhat longer. *Protanidanthus* Liao, 1979, although referred to Anidanthinae by Brunton et al. (2000, p. 533), is said to lack dorsal laminae by Brunton et al. (2000), and may be placed in Lirariinae.

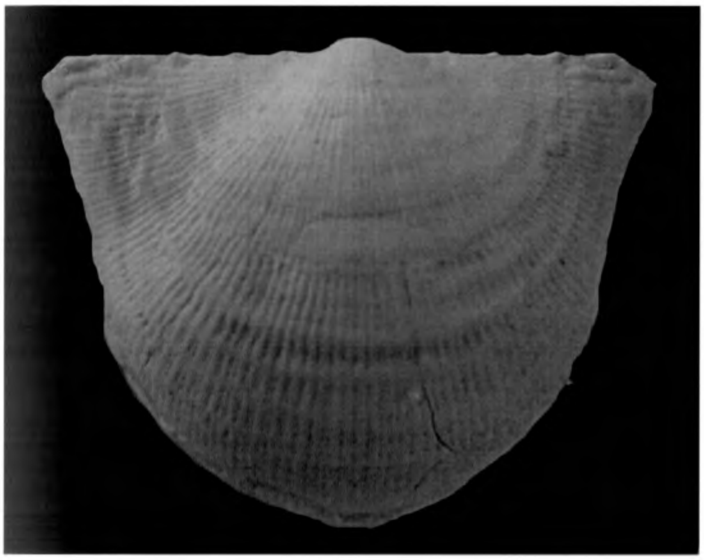


Fig. 15.24. *Globiella hemisphaerium* (Kutorga) ventral valve BR 3060, x4, from Kazanian of Russian Platform. JBW photo.

Genus ***Calandisa*** Waterhouse & Campbell new genus

Derivation: Named for C. A. Landis.

Type species: *Calandisa solitarius* new genus, new species from Takitimu Group (Artinskian), Dunton Range, New Zealand, here designated.

Diagnosis: Small highly arched shells with costellae over both valves, spines in hinge row, rare body spines, and one to five strong spines on each outer ear, additional to hinge row spines of other genera.

Discussion: This genus displays the shape and ribbed ornament characteristic of Lirariinae, and has a row of spines in front of the ventral hinge, and few spines over the disc or trail. The ventral adductor scars are comparatively smooth. What distinguishes the new genus is the presence of a few large spines on the outer ventral ear, about midway between the hinge and anterior border.

Calandisa solitarius Waterhouse & Campbell new species

Fig. 15.25

Derivation: solitarius – alone, Lat.

Holotype: BR 2400 from GS 12669, Takitimu Group (Artinskian), Dunton Range, New Zealand, figured as Fig. 15.25B, here designated. See Appendix A, part B, p. 477.

Diagnosis: Transverse to highly elongate shells with rare ventral spines, and large spine on outer ventral ear.

Material: Some ten ventral valves and scarce dorsal valves from Takitimu Group, Dunton Range, New Zealand.

Dimensions in mm: ventral valves

BR	Width	Length	Height
3091	26	14	
3065	22	17	8
2400	22+	24	12 rubber
2402	21.5	25	9.5
2407	24	19	10.5
2484	16	12.5	5

Description: Shells weakly transverse, the ventral valve highly convex, umbo incurved with angle of 95-100°, and wide with moderately large convex ears and obtuse cardinal extremities. Transverse convexity is reduced medianly, but there is no sulcus, and the anterior commissure varies from slightly receeded or produced. The dorsal valve is

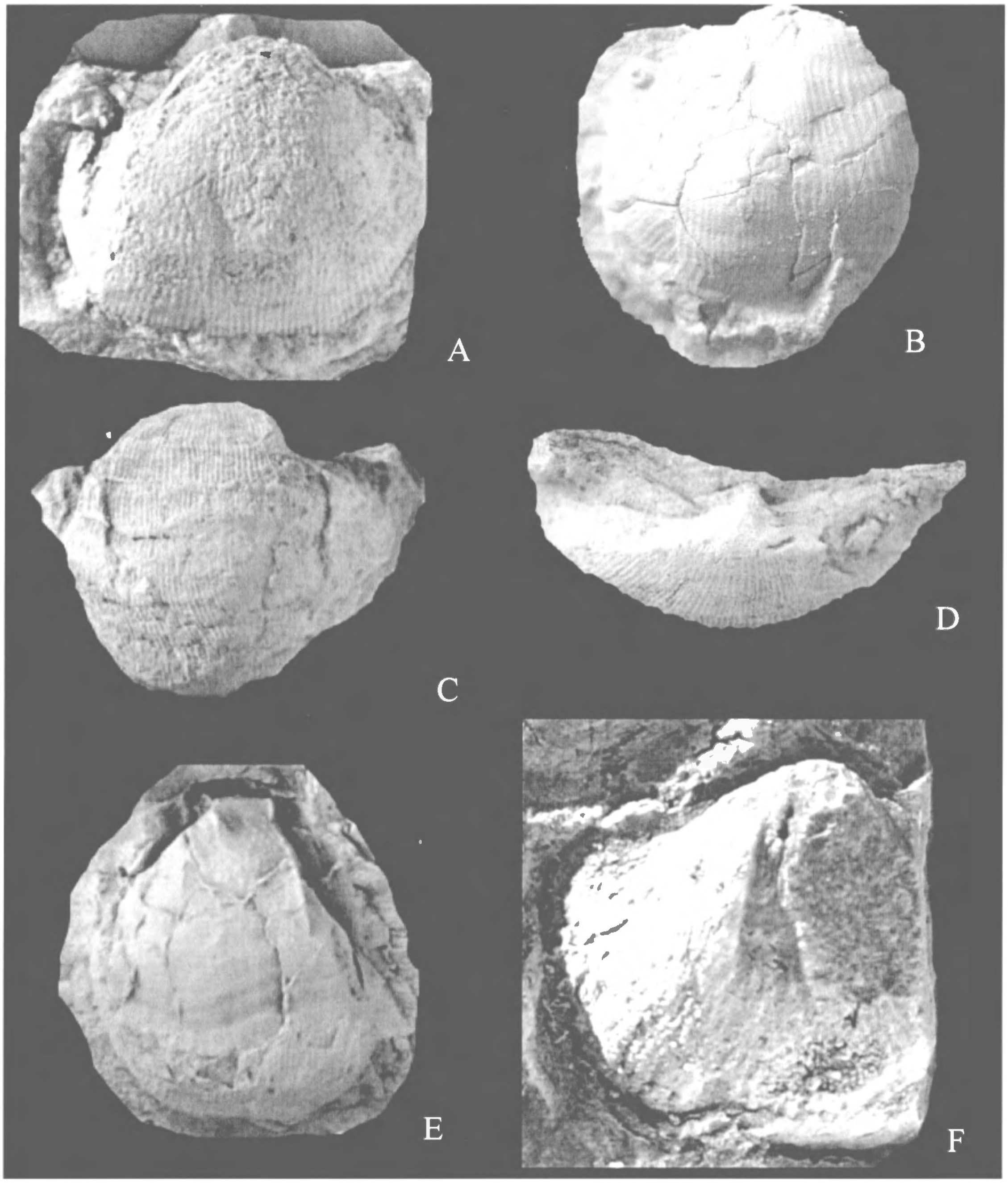


Fig. 15.25. *Calandisa solitarius* Waterhouse & Campbell. A, ventral internal mould BR 3065, x3. B, latex cast of ventral valve holotype, BR 2400, x3. C, D, ventral and posterior aspects of ventral valve BR 3091, x2. E, internal mould, ventral valve BR 2486, x2.5. F, internal mould of ventral valve BR 2402, x3.5. From GS 12669, Takitimu Group (Artinskian), Dunton Range, New Zealand. JBW photo.

concave over the disc, and the large ears are concave, and the trail subgeniculate and moderately long. Both valves are crossed by fine radial ribs, eight in 5mm at mid-length on the ventral valve, and covering the ears. The ventral valve is also covered over disc and trail by low to very low rugae, at least thirteen on the largest specimen, and marking the ears of some specimens, and there are fine closely spaced growth increments which arch hingewards over the ribs. The dorsal valve bears very low growth rugae and pauses, but no laminae. A single row of spines lies along the ventral hinge, the outermost spine 1mm wide, and strong erect spines varying between one and five lie on each outer ear; erect spines lie over the anterior disc and start of trail, each with a diameter between 0.2 and 0.3mm, arising from the crest of a costa, which passes through otherwise undisturbed.

Ventral adductor scars short and wide, smooth and raised; diductor scars oval, more anteriorly positioned and scarcely impressed, floor in front with large pits, remainder of floor finely pustuled. In another specimen the adductors are more elongate.

Resemblances: The distinctive feature of this species, as for the genus, lies in the presence of the large erect spine or spines on each ventral ear. Otherwise the genus and species is moderately close to *Liraria* Cooper & Grant, 1975 and *Cimmeriella* Archbold & Hogeboom, 2000.

Authorship, Repository: The material is deposited at GNS (Institute of Geological and Nuclear Sciences, Lower Hutt, New Zealand). Accompanying species which will be described separately indicate a likely Artinskian age. Co-author of the genus and species is Hamish Campbell, GNS Science, Lower Hutt, New Zealand.

Subfamily **LAMIPRODUCTINAE** Liang, 1990

Fig. 15.26, Fig. 15.27, Fig. 20.1, p. 457

[Nom. transl. hic ex Lamiproductidae Liang, 1990, p. 204 [p. 466].

Diagnosis: Characterized by branching and erratic costellae, crossed by fine growth cinctures, scattered fine erect body spines and few spines along hinge of ventral valve. Middle Permian (Roadian) to Upper Permian (Wuchiapingian).

Genus: *Asperlinus* Waterhouse & Piyasin (syn. *Lamiproductus* Liang), plus new genus yet to be named..

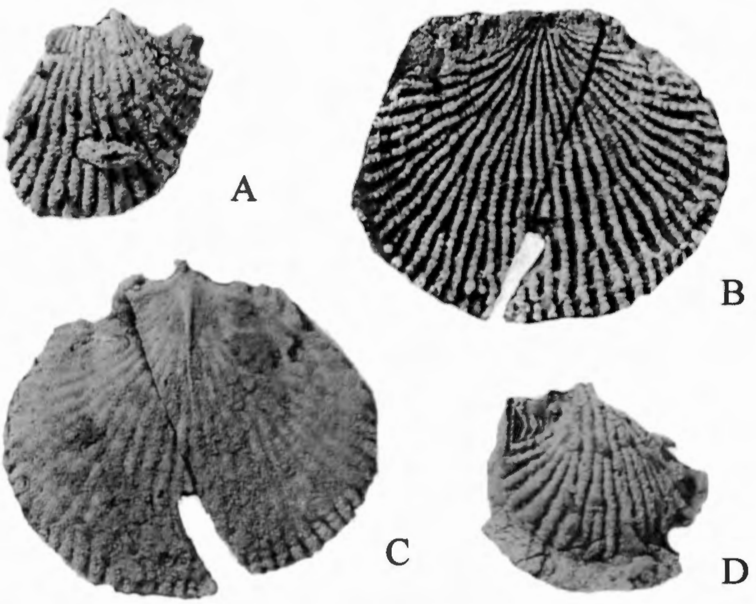


Fig. 15.26. *Asperlinus asperulus* (Waagen). A, ventral valve B 674. B, C, external and internal views of immature dorsal valve B 354, now ROM 32131. D, ventral valve B 349, now ROM 32127. Specimens from Rat Buri Limestone (Roadian), Khao Phrik, southern Thailand, x3, kept at Royal Ontario Museum, Toronto. See Waterhouse & Piyasin (1970).

Discussion: Liang (1990, pl. 35) proposed Lamiproductidae for a single genus *Lamiproductus* Liang from Zhejiang Province of China. He stressed the nature of the "dendritic" ribs. Unrealized by Liang (1990), genus *Asperlinus* Waterhouse & Piyasin, 1970, type species *Productus asperulus* Waagen, 1884, pl. 79, fig. 3-6 from the Kufri Member, Chhidru Formation, of the Salt Range, Pakistan, is closely related, and apparently senior synonym. The exteriors of both type species are very close at generic level, although costae on the Chinese ventral valves branch more and spines are fewer. Good figures of the ventral valve of the Thai species were provided by Yanagida (1970, p. 83, pl. 15, fig. 15a-d) under the heading *Cancrinella* sp. indet. The interior of the dorsal valve has comparable marginal ridges and septum, as may be assessed by comparing figures in Waagen (1884, reproduced in Brunton et al. 2000, text-fig. 376.4d) with figures in Liang (1990, pl. 35, fig. 11). The cardinal process has widely splayed lateral lobes, not fused externally, and the adductor scars are not clearly shown on either valve, being masked by the ribbing from the exterior.

A further genus is represented by *Terrakea japonica* Tazawa (2008b, Fig. 3) from the lower Kanokura Formation (Wordian), of the Kitakami Mountains in northeast Japan. This form has crowded spines over the ventral valve, including inner ears and umbonal slopes, but lacks the inner pair of posterior dorsal ridges. Unlike *Terrakea*, there are no dorsal spines, and no elongate bases to the ventral disc spines. The material shows in one specimen smooth adductor scars, though these as a rule are masked by the ribbing visible on the exterior.

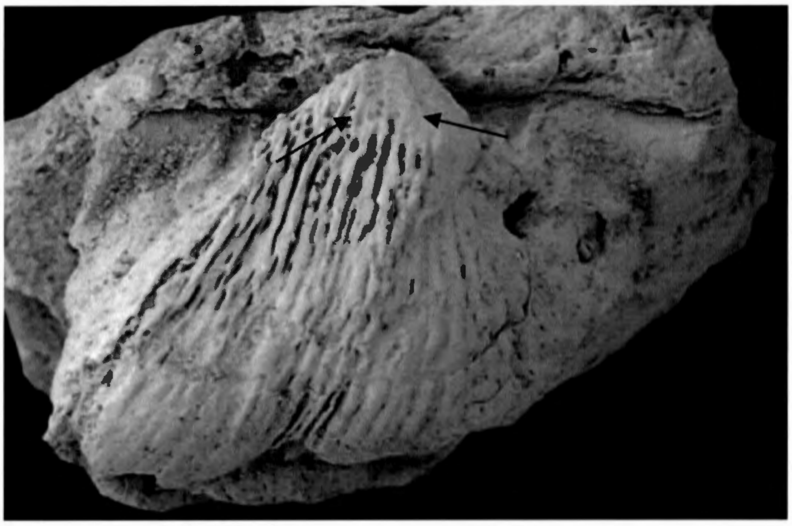


Fig. 15.27. Lamiproductin new genus, *japonica* Tazawa. Ventral internal mould NU-B708, x5 approx., from a small tributary of Imosawa, Imo, Iwate Prefecture, Japan, showing smooth adductor scars between arrows. Specimen kindly loaned by Jun-ichi Tazawa. JBW photo.

Asperlinus and the new genus from Japan display aspects unusual for Anidanthidae, in that spines over the ventral umbonal region show short elongate bases, especially well displayed in the illustrations of Yanagida (1970). Yet the spines in general appear to pass straight through the shell, without any posterior or forward prolongation, and the smooth adductors in the ventral valve of *japonica* Tazawa suggest an alliance with Anidanthidae. On the other hand the strong and branching ribs mark a most unusual aspect for Anidanthidae.

Brunton et al. (2000) made no mention of Lamiproductidae and synonymized *Lamiproductus* with *Pseudohaydenella* Liang, 1990. *Asperlinus* was recognized separately, as a member of Auriculispininae Waterhouse (Brunton et al. 2000, p. 537). Figures of *Pseudohaydenella* were poorly reproduced in Liang, and suggest that the genus is more convex than *Lamiproductus*, and has simpler ribbing. In turn Brunton et al. (2000) suggested that *Chianella* Waterhouse might prove to be senior synonym for *Pseudohaydenella,* which seems possible from general morphology, including the ribs, even though the anterior shell is weakly nasute, and appears from the text to have dorsal spines. The uncertainties require resolution through re-examination of type *Pseudohaydenella*.

Family **YAKOVLEVIIDAE** Waterhouse, 1975

[Nom. transl. Waterhouse 1978, p. 20 ex Yakovleviinae Waterhouse, 1975, p. 11; see Shi 1995, p. 54].

Diagnosis: Wide hinge and geniculate trail, fine radial ornament and weak if any concentric ornament, may display strut spines. Marginal ridges low to well formed, corpus thickness varies from thin to thick.

The affinities of *Yakovlevia* Fredericks, 1925

The genus *Yakovlevia* Fredericks, name giver of Yakovleviinae Waterhouse, 1975, has been assigned over a few years to various family groups, ranging from chonetid, paucispiniferid, linoproductid, productellin, plicatiferin, and productid. Fredericks (1925, p. 7) treated it as a subgenus of *Chonetes*, justified by the wide hinge, row of hinge spines, and fine costellae. Stepanov (1937, p. 112) transferred the taxon to a subgenus of *Productus*, and Muir-Wood & Cooper (1960, p. 323) allocated the genus to Paucispiniferinae Muir-Wood & Cooper, 1960, then regarded as a subfamily within Linoproductidae. Kotlyar (1961) synonymized *Muirwoodia* Licharew, 1947 with *Yakovlevia*. Yakovleviinae Waterhouse was considered by Waterhouse (1975) to be readily distinguished from Paucispiniferinae, which displays more numerous strong spines, a zygidium and cardinal process and dorsal marginal ridge, and the subfamily was deemed to be linoproductoid, because of the fine costellae, and distinguished by transverse shape with wide hinge, and the presence on at least the allied genus *Muirwoodia* of a few thick strut spines, otherwise unknown in linoproductids. This position was endorsed in a detailed study of the genus by Shi (1995), and Lazarev (1990) followed Waterhouse (1978) in elevating the subfamily to a full family. Further appraisal by Lazarev in Brunton & Lazarev (1997) transferred the genus and allies to Tribe Yakovleviini of Subfamily Productellinae. Brunton et al. (2000, pp. 464ff) shifted Yakovleviini to being a tribe in Subfamily Plicatiferinae, along with numerous other tribes and families in Family Productellidae, and were followed by Tazawa (2001) and Angiolini & Long (2008). Although that position has been elaborated at length by Lazarev (1996) on the basis of what was strongly advocated as a very superior technique called "meronomic analysis", his conclusions did not last any longer than Fredericks' initial claim that *Yakovlevia* was chonetid. In a further shift, the group was restored to subfamily status by Lazarus (2000a, 2000b, 2000c), and retained as belonging to Productellidae, as again endorsed by Brunton (2007, p. 2648). Three additional dictyoclostiform tribes were recognized within Yakovleviinae, namely Latispiniferini Lazarev, Reticulatiini Lazarev, and Rigrantiini Lazarev. All genera assigned to these three tribes tend to show large size and strong reticulation of radial and concentric ornament over the visceral disc, morphological features missing from *Yakovlevia* and *Muirwoodia*. In addition, *Muirwoodia* has massive strut spines, which are never developed in members of Latispiniferini, Reticulatiini, and Rigrantiini, nor Dictyoclostidae. Despite such differences, Lazarev argued for a strong approach to a number of dictyoclostiform genera, based on the presence of a posterior central smooth shell, or what may be termed a Lazarevian patch, due to lack of posterior central papillation or "shagreen" texture over the internal surfaces of the valves, especially in the ventral umbonal region (Lazarev 2000b, p. 25). This interpretation appears less than conclusive, because such a pattern is also found in some specimens of other groups and genera (such as *Umboanctus* Waterhouse in Buxtoniidae) and although it must be allowed that *Yakovlevia* and allies constitute an unusual group, their relationship to dictyoclostid-like genera appears remote. Observations on shagreen pattern are summarized and discussed on pp. 18-22. Discussion of Reticulatiinae is provided on p. 130. Lazarev (2011) again reassessed the position, now asserting a preference for placement in Productidae, and noting the less than usual profile (type 6 herein, p. 24) with its comparatively gently convex ventral valve and anterior disc thickening, and trail at high angle to the disc.

Of obscure derivation and relationships, *Yakovlevia* is transverse with flat disc, and its fine radial ornament and sharply geniculate trail suggest Linoproductoidea. Yet there are differences from Linoproductoidea, or at least, other families assigned to that superfamily. The hinge is unusually wide with acute cardinal extremities and muscle scars differ (Tazawa 2001). In the allied genus *Muirwoodia* Licharew, there are four very prominent strut spines, as well as few other body spines and poorly developed row of spines along the ventral hinge. A ginglymus may be developed, and internally the ventral muscle platform is broad and raised, the body cavity moderate to thick, and pustules dense, large and numerous anteriorly. Apart from the strut spines, aspects of the shell, including flat disc, geniculate trail, fine ribs, ginglymus, raised adductor platform, wide low cardinal process, long dorsal septum, and rather elongate brachial shields, suggest aspects of Monticuliferidae Muir-Wood & Cooper (see p. 288). The strut spines and arguably the fine ribs recall Paucispiniferoidea, but the marginal and ear baffle ridge development is low and the trail comparatively simple, in contrast to multiple trails common in Paucispiniferidae and Anidanthidae.

Lazarev (1996) considered that *Yakovlevia* and *Muirwoodia* were related to *Inflatia* Muir-Wood & Cooper, 1960, a Lower Carboniferous (upper Visean) genus of somewhat different appearance, with sulcus, reticulate ornament, prominent hinge row of ventral spines but no strut spines, and weak development of marginal ridging. Given the presence of thicker costae in *Inflatia*, reticulate disc, the different spine ornament, and the different nature of the adductor scars which are broad and strongly dendritic in the ventral valve (Gordon, Henry & Treworgy 1993), and different anterior pustulation, it is suggested that *Inflatia* is indeed dictyoclostid, and not closely related to *Yakovlevia* and allies. Possibly *Inflatia* has posterior central papillation, considered to be missing from *Yakovlevia* (see p. 157). In 2011, Lazarev dropped any reference to *Inflatia* as being part of the yakovlevinin scenario.

It was claimed by Lazarev (1996) that the Carboniferous genus *Sajakella* Nasikanova in Sarytcheva (1968, p. 141), of upper Visean to Bashkirian age, provided the link between *Yakovlevia* and *Inflatia*. Even though the relevance of *Inflatia* is deemed unlikely, *Sajakella* is close to *Yakovlevia* and *Muirwoodia* in the presence of fine radial ornament and overall shape. Two anterior strut spines are developed in *S.* (?) *martianovi* (Nasikanova), as shown by Sarytcheva (1968, pl. 19, fig. 7b), and though such are less apparent in the type species, strut spines were clearly figured for the type species by Klets (2005). The three species assigned to *Sajakella* in Sarytcheva (1968) have wide hinge, moderately high trail, rather gently convex ventral disc, and moderately well defined although low commarginal rugae over the visceral disc. There are slender non-dendritic adductors, although the anterior adductors are broader and narrow and posterior adductors are slender and dendritic in the ventral valve of *S. dzhinsetuensis* Lazarev (1992) as figured by Rozanov (2003, pl. 44, fig. 4). *Sajakella* does have coarser ribs than in *Yakovlevia*, and shows commarginal rugae, which are absent or weak in *Muirwoodia* or *Yakovlevia*. According to Lazarev (2011), so-called *Marginatia monachovae* (Litvinovich et al. 1969) from the Early Visean Ishim Horizon of Kazakhstan belongs to a new genus similar in appearance to *Sajakella*, with reticulate disc, rare large spines on the trail, and no dorsal spines, representing the earliest yakovleviid. This is close in age to the putative ancestral subfamily Bibatiolinae.

Other possible links

A number of possible ties with other genera and groups have been suggested for *Yakovlevia* and its immediate allies, and two further possibilities remain to be considered, noting that further genera fall in Type 6 category of body shape (see p. 24). Genera that display somewhat comparable shell build and profile include *Sinuatella* Muir-Wood, 1928, p. 37, based on the Early Carboniferous species *Leptaena sinuata* Koninck, 1851, p. 654, well figured in Muir-Wood & Cooper (1960, pl. 57, fig. 1-15). This genus is close in overall shape, flattish disc, steeply inclined moderately long trail and large ears. Spines are arranged along the ventral hinge and the ventral muscle field is chordate, and a low dorsal ridge may encircle the valve, best defined along the hinge. Differences from *Yakovlevia* lie in the firm ribbing and well developed reticulate pattern over the disc, and the presence of further ventral ear spines, with no strut spines. *Sinuatella* has well developed interarea and wide hinge. Another genus that is close in shape is *Institella* Muir-Wood & Cooper, 1960, p. 164, based on *Productus marginalis* Koninck, 1846, p. 238, with more ventral spines and finely reticulate pattern. Both of these genera lack strut spines, and in spite of the similarity in shape, appear to have belonged to different stock, undoubtedly aulostegoid, whereas *Yakovlevia* and allies display few aulostegoid attributes other than the presence of a ginglymus, fine costellae, and chordate ventral muscle field. In particular, the spine pattern is not like that of any known aulostegoid genus. Furthermore, the similarity in disc is often at only early growth stages, because mature yakovleviids often developed a very thick body corpus.

Were the *Yakovlevia* group to be regarded as non-linoproductoid, it would be allied to Paucispiniferidae, just as first evaluated by Muir-Wood & Cooper (1960), through sharing comparable ornament and spine detail, and somewhat similar Type 6 build and profile. There are some further indications: the dorsal pustules are large and limited to one or two rows in yakovleviid genera, notably *Muirwoodia* (*Grandaurea*) as described below, much as in *Paucispinifera* itself, and the dorsal adductors may be separated by suggestions of slender anderidia, again as indicated in some *Paucispinifera* (see Muir-Wood & Cooper 1960, pl. 122, fig. 7, 9). The inner adductors of *Paucispinifera* tend to be smooth until later ontogeny, just as in *Muirwoodia* (*Grandaurea*) as figured as *Muirwoodia* by Muir-Wood & Cooper (1960) and as *Yakovlevia* by Cooper & Grant (1975), and large and dendritic outer adductors are similarly disposed in both genera. The cardinal processes differ to some extent in each suite, but from an internal aspect may be somewhat similar in the way the two lateral lobes slope inwards with thickened lips along the posterior inner margins, parallel to the hinge, though more exaggerated in several *Paucispinifera* (cf. Cooper & Grant 1975, pl. 423, fig. 23, pl. 424, fig. 33 for *Paucispinifera* with pl. 471, fig. 22 for "*Yakovlevia*") . No adequate figures for the ventral muscle scars are provided for *Paucispinifera* by Cooper & Grant (1975), because of reliance on silicified material, and the valve is deeply convex, hindering photography. But the much greater convexity would probably have led to a different shape anyway, in comparison with the gentle convexity of *Yakovlevia* and allies. In dictyoclostiform genera, which offer the alliance preferred by Lazarev (2000a) and Brunton (2007), the internal and anterior pustules of the dorsal valve are much more numerous and less prominent, and cardinal process taller and with different lobes, often quadrifid. The posterior adductors are relatively larger and more posteriorly placed, without the ridges found in paucispiniferids or yakovleviids. These differences are reinforced by the differences in shape, ribs and spines. Figures in Cooper & Grant (1975) suggest that posterior central papillation is missing from mature dorsal valves of *Muirwoodia* (*Auriculatea*), whereas papillation appears to be present in some but not all *Paucispinifera*.

There are differences between Paucispiniferidae and Yakovleviidae. The yakovleviid shape is more transverse and trail shorter in some species and genera, matters that may be ascribed to familial constraints, but other species, including *Muirwoodia pseudoartiensis*, have long but simple trails. A substantial difference lies in the development of marginal ridges. Marginal ridges are high in the ventral valves and in virtually all dorsal valves of Paucispiniferidae, whereas ridges are not clearly developed in *Muirwoodia* or *Yakovlevia*. In the very well preserved material from the Permian of the Glass Mountains, Texas, United States, there is a very low marginal ridge in each valve (see Cooper & Grant 1975, pl. 472, fig. 27, 32). It may therefore be proposed that *Yakovlevia* and allies are a special group that virtually lost its marginal ridges, except for *Paramuirwoodia* Zhang in Zhang et al., 1983, *Paramarginifera* Fredericks, 1916, and *Archboldina* Angiolini & Long. This interpretation is favoured by details of ribs and spines and the shape is unusual but is reflected to some extent by a few other genera, notably *Paucispinifera* itself. The differences from other families are so great that a separate family appears to warranted, with evidence pointing to derivation from early Paucispiniferidae. The purported ties with *Inflatia* Muir-Wood & Cooper, 1960 are rejected: this is regarded as a dictyoclostid – together with *Tenaspinus* Brunton & Mundy, 1994, despite their inclusion in Yakovleviini by Brunton et al. (2000, pp. 466, 467). *Sajakella* is regarded as a likely yakovleviid, together with *Muirwoodia*.

Subfamily **YAKOVLEVIINAE** Waterhouse, 1975

Fig. 15.27A

[Yakovleviinae Waterhouse, 1975, p. 11].

Diagnosis: Yakovleviidae lacking strut spines. Slender body corpus. Upper Carboniferous (lower Moscovian) to Middle Permian (Guadalupian).

Genera: *Yakovlevia* Fredericks, *Archboldevia* Angiolini & Long, *Elucidatea* new genus.

Discussion: The lack of strut spines, to judge from the morphology and the age of constituent genera, suggests a secondary development from genera with strut spines. Lazarev (2011) conceived Yakovleviini (Yakovleviidae herein) as offering a simple trend through time in loss of body cavity, and for that reason regarded the group as a member of Productidae rather than Productellidae, based on what at least some would regard as precarious logic. His supposedly youngest genus, *Yakovlevia*, indeed has a low corpus cavity, as possibly the end member of Yakovleviinae as here understood, but the corpus is just as slender in the Moscovian genus *Elucidatea*, as here described. Members of Muirwoodinae as outlined below include a number of Pennsylvanian up to late Middle Permian (Capitanian) genera and species with comparatively thick visceral disc: the claim that the body corpus became more slender through time was achieved, in this instance, by selecting genera from two separate groups. Trends were not always unidirectional. For example *Muirwoodia* has a comparatively thick disc, whereas its close ally *Grandaurea* new subgenus has broader disc and apparently thinner corpus, implying a complex development of change in part controlled by geographic situations.

Fig. 15.27. A, *Yakovlevia kaluzinensis* Fredericks, ventral valve x1, internal mould. Original figure of Fredericks (1925). From upper Lower Permian, northeast Russia. B, *Archboldevia impressus* (Toula), dorsal interior as figured by Wiman (1914, pl. 19, fig. 27), x1, from Vøringen Member (Kungurian?), Spitzbergen.

Genus ***Elucidatea*** new genus

Derivation: eluceo – shine, Lat.

Type species: *Elucidatea peterormus* new species from Khao Luak Formation (Moscovian), north Thailand, here designated.

Diagnosis: Average size for family, transverse with inconspicuous ears, wide hinge, costae well defined, crossed by moderately emphasized commarginal rugae, spines limited to ventral valve, in row along hinge and row close to umbonal flanks, rare and irregular over remainder of valve. Ventral adductor scars small and subrounded, smooth even in late maturity. Single row of anterior dorsal pustules in front of brachial shields.

Discussion: A species from the Late Carboniferous of Thailand is like other members of Yakovleviinae in so far as there are no conspicuous strut spines on the ventral valve, but differs a little in shape, and has small pointed ears, and more emphasized commarginal rugae over the visceral disc, especially over the dorsal valve. There is a row of posterior ventral spines, arranged along the base of the umbonal slopes, as well as another row close to the hinge. In that regard, the new genus resembles *Duartea* Mendes, 1959, which possibly has two posterior rows of fine spines in the ventral valve, one along the hinge, the other along the umbonal flanks, but the original description of the type species of *Duartea, Productus batesianus*, may be interpreted as indicating the presence of six strut spines (as quoted shortly). The commarginal rugae of the new genus are markedly stronger than in *Duartea batesianus*, and the corpus is very thin, unlike the thick body cavity of *Duartea*, assuming that was correctly reported. Internal features are well displayed, whereas those for *Duartea* are not known. The Thai species is close to *Sajakella* in the strength of commarginal rugae, but lacks the large anterior strut spines and has an umbonal flank row of spines.

There is thus a remarkable distribution for the family in Late Carboniferous time, *Duartea* being found only in Brazil, and *Elucidatea* in far distant Thailand. In high northerly latitudes of Canada and northeast Russia, *Muirwoodia* is developed in place of *Duartea* (Klets 2005).

Elucidatea peterormus new species

Fig. 15.29 - Fig. 15.30

1975 *Chaoiella* aff. *C. grünewaldti* [not Krotow] – Yanagida, p. 25, pl. 3, fig. 8a, b.

Derivation: Named for Peter Orme.

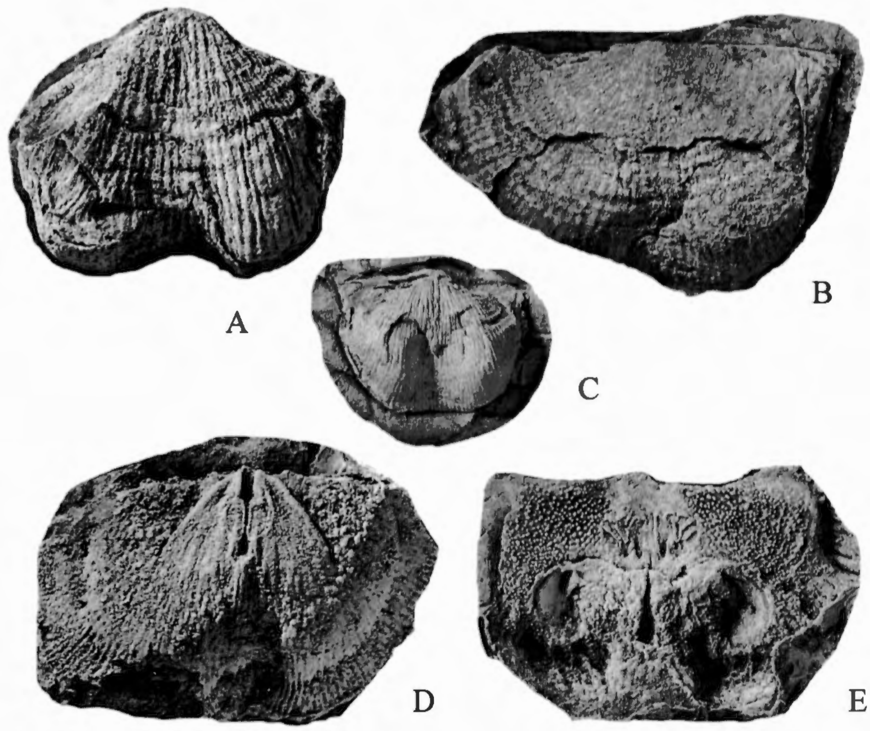


Fig. 15.29. *Elucidatea peterormus* new genus, new species. A, ventral valve, x2. B, dorsal valve with attached part of ventral valve showing row of hinge spines, x2. C, external mould of dorsal valve with part of visceral disc and ventral valve, x1. D, internal mould of ventral valve, x2. E, internal mould of dorsal valve, x2. From Upper Carboniferous at Huai Bun Nak, north Thailand, unregistered material kept at Geological Survey Division, Department of Mineral Resources, Bangkok, Thailand. JBW photo.

Holotype: BR 3043 from Khao Luak Formation (Moscovian) at Huai Bun Nak, near Loei, north central Thailand, figured as Fig. 15.30C, here designated.

Diagnosis: Average size for family, ventral spines form rows posteriorly, one row on umbonal slopes, another along the hinge, rare moderately strong spines anteriorly on some ventral valves, commarginal rugae moderately developed over disc of both valves, corpus slender.

Material: About nine ventral valves, two dorsal valves and two specimens with valves conjoined from soft dense mudstone at Huai Bun Nak, north central Thailand.

Dimensions in mm: (ventral valve, slightly deformed)

BR	Width	Length	Height	
3043	36	25	9.5	holotype
3045	28	23	8.5	
Dorsal valve:				
3045	29	20	10	

Description: Specimens transverse with small pointed ears at maximum width, low ginglymus developed along hinge of both valves, umbonal slopes very low, sulcus commences at umbo and persists to anterior margin at angle of 25-28°, with narrowly concave to subangular floor, trail subgeniculate. Rarely, the sulcus commences near the start of the trail. Dorsal valve subgeniculate, trail about half the length of the disc, fold commences variably near umbo or over the disc. Ribs cover both valves, some six to seven in 5mm over mid-disc, six to eight in 5mm anteriorly, well defined for entire length. Low commarginal rugae developed over disc, better defined over dorsal valve, numbering about 16, posterior ventral ears smooth. Fine erect spines developed in a row close to hinge and along an anterior row at base of umbonal slope. Some specimens suggest a weakly developed anterior erect spine on one side of the sulcus, whereas others indicate no anterior spines. The presence of such a spine in a few specimens possibly implies a degeneration from a former strut spine of an ancestral genus – or a potential development of a strut spine. Such possibilities imply that the classification will need to be amended to more flexibly reflect the changes in different lineages, when they are better understood.

Ventral adductor scars small and suboval, smooth. Diductor scars large, striate, but difficult to distinguish from external ribbed ornament until late maturity, extend posteriorly beyond adductors and well in front; muscle scars divided by myophragm in late maturity. At late maturity shell thickening obscures the external ribbing on the interior surface, and the posterior floor bears large pits.

In a moderately mature specimen, the cardinal process is low, with prominent median shaft from internal view and lateral lobes. A well developed hinge ridge is present. A broad linear rise commences in front, and divides into a low median ridge with lateral ridge each side, between subtriangular adductor scars, marked by one or two ridges, but not dendritic, and the anterior median septum is well formed but not thick. Brachial shields are small, and anterior pustule row moderately developed. Coarse pits lie over the lateral posterior floor, and finer pits and pustules lie between the brachial shields and over the trail. Posterior papillation is developed centrally in front of the cardinal process. In a more mature specimen a smooth area or Lazarevian patch lies in front of the hinge, with pitted and pustuled floor to each side. The adductor scars are comparatively large and dendritic, and the median septum starts just before the anterior end of the scars, and widens anteriorly, stopping before the start of the trail. The brachial shields are small and lie each side of the septum, and a row of large pustules is developed in front along the geniculated start of the trail.

Discussion: *Elucidatea* is characterized in part by two posterior rows of spines on the ventral valve, compared with only one row of hinge spines in *Yakovlevia* and *Archboldevia*. It is to be noted that a specimen displays posterior central papillation in a specimen towards maturity, whereas this "shagreen" is lacking from fully mature specimens. The internal detail provides some interesting comparisons. In *Sajakella* Nasikanova, the ventral adductors are elongate, whereas in the present species, the adductors are small and oval, and diductors very large and longer, even in late maturity. One late mature specimen of *Muirwoodia* (*Grandaurea*) *sulcata* (Cooper & Grant 1975, pl. 472, fig. 32) shows small somewhat smooth or less dendritic adductors, but in most species, well known thanks to studies by Muir-Wood & Cooper (1960) and Cooper & Grant (1975), the ventral adductors are elongate and dendritic, and the diductor scars smaller and laterally placed. In the dorsal valve of *Muirwoodia* (*Grandaurea*), the dorsal adductors are comparably large, and lie in two pair, including a small inner and narrow pair, with similar pattern in other species of the same subgenus. The median septum extends forward a varying amount, and the emphasis applied for lino-productids by Lazarev (2009, 2010) on the termination of the septum vis-à-vis the brachial shields must be deemed irrelevant and inapplicable as far as Yakovleviidae are concerned: that applies even to the few Thai specimens and is sustained by the various specimens figured as *Yakovlevia* by Cooper & Grant (1975). In *Muirwoodia* figured by Klets

(2005, pl. 11), the ventral adductor scars are slender and long, and dorsal adductors clearly differentiated between internal and external larger scars. There are several rows of large pustules in front of the brachial shields around the start of the trail. In *Archboldevia* Angiolini & Long, the dorsal median septum is strong posteriorly.

Stratigraphy: The specimens come from near Loei, collected by K. Pitakpaivan and J. B. Waterhouse in 1964. The beds were mapped as Khao Luak Formation by Javanaphet (1969), as expanded further in Bunopas (1981). Fusulines from beds above the brachiopods have been assigned to the *Fusulina pulchella* Zone of the upper Moscovian Myachkovian Horizon of the Russian Platform. The age of the present fauna is possibly Podolian. Further brachiopods from the fauna were described by Waterhouse (1982b). Yanagida (1975) figured a ventral valve from Upper Carboniferous beds at Huai Luang, near Wang Saphung, north Thailand.

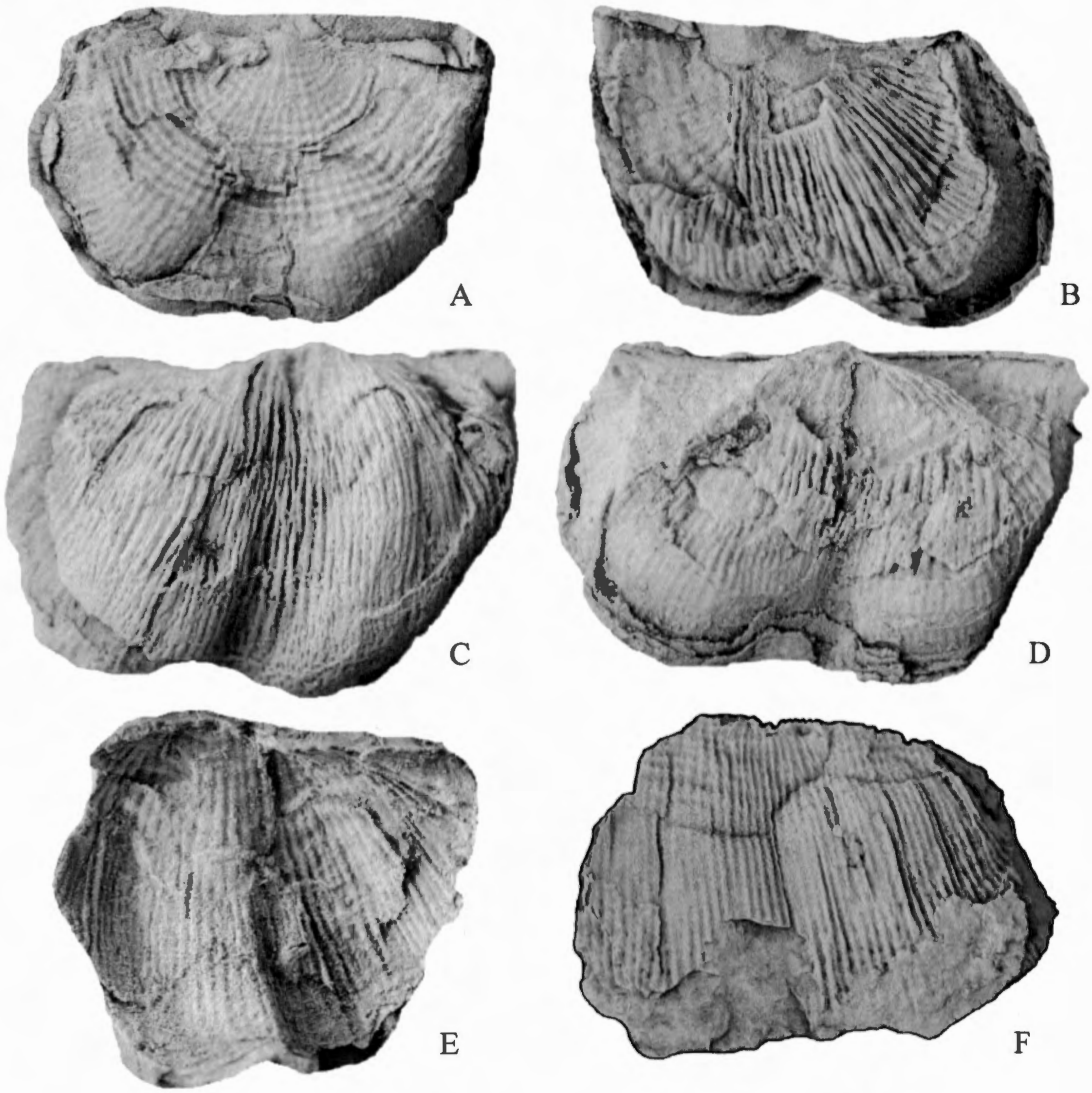
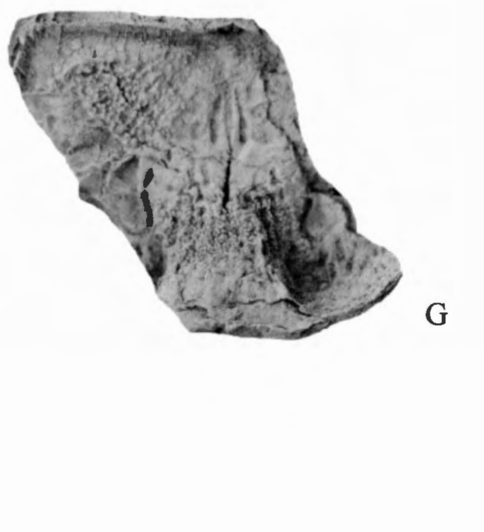


Fig. 15.30. *Elucidatea peterormus* new genus, new species. A, external mould of dorsal valve, BR 3046, x2. B, ventral aspect of internal mould BR 3093, x2. C, internal mould of specimen with valves conjoined, ventral view BR 3043, x2, holotype. D, internal mould of ventral valve BR 3045, x2. E, external mould of ventral valve BR 3042, x2. F, anterior internal mould of ventral valve BR 3044, x1.5. G, dorsal internal mould of BR 3047, x2. From Upper Carboniferous at Huai Bun Nak, Thailand. JBW photo.



Genus ***Archboldevia*** Angiolini & Long, 2008

Fig. 15.28B

Archboldevia Angiolini & Long, 2008, type species *Productus impressus* Toula, 1875, appears to be very close to type *Yakovlevia* (Fig. 8.27), and the published justification for the genus seems to have followed the less than reliable interpretation of *Yakovlevia* in Brunton et al. (2000) and been based on a comparison with *Muirwoodia* Licharew, rather than type *Yakovlevia*. However, as Angiolini & Long (2008) indicated, the dorsal valve is thickened, and the large size and nature of the dorsal valve, including high marginal ridge, as well shown by Wiman (1914, pl. 19, fig. 24-27), appears distinctive. The authors observed a ventral hinge row of spines, and although the spines on *Yakovlevia* are poorly known, with no clear indication of any spines on the figures provided by Fredericks (1925, pl. 3, fig. 64-66; see also Lazarev 1990, pl. 39, fig. 12, 13; Rozanov, 2003, p. 123, pl. 43, fig. 17-19), the text by Fredericks (1925) reported a row of hinge spines in type *Yakovlevia*. The other feature that is clearly shown by Fredericks is the ventral muscle field, and this was stated to be different in *Archboldevia*, and although no illustration or detailed analysis was provided by Angiolini & Long (2008), the diductors are raised anteriorly, as in some *Compressoproductus* and some aulostegoids. *Archboldevia* is of late Cisuralian age according to Angiolini & Long (2008). Those authors noted that some authorities have favoured a very late Permian age for the uppermost beds of the Vøringen Member of Spitsbergen. In particular, Nakamura et al. (1987) argued for a Late Permian age, later modified in Nakamura et al. (1992).

Subfamily **MUIRWOODIINAE** new subfamily

Name genus: *Muirwoodia* Licharew, 1947 from Pechora (Lower Permian), Russia, here designated.

Diagnosis: Strut spines well developed, usually two up to six. Ventral marginal ridge not conspicuous. Lower Carboniferous (Visean) to Middle Permian (Wordian).

Genera: *Muirwoodia* Licharew, *Muirwoodia* (*Grandaurea*) new subgenus, ?*Duartea* Mendes, *Dzhiremulia* new genus, *Harkeria* new genus, *Sajakella* Nasikanova.

Discussion: *Muirwoodia* is the most common of all yakovleviid genera, and the subfamily is readily distinguished by the presence of strut spines, and lack of strong marginal ridges.

Genus ***Muirwoodia*** Licharew, 1947

Type species: *Productus mammatus* Keyserling, 1846, p. 206 from Lower Permian of northern Russia.

Diagnosis: Subquadrate to subpentagonal shells with four strut spines.

Subgenus ***Grandaurea*** new subgenus

Fig. 15.31

Derivation: grand – large; aurea – ear, Lat.

Type species: *Yakovlevia hessorum* Cooper & Grant, 1975, p. 1181 from the China Tank and Willis Ranch Members (mostly Wordian) of the Word Formation, Glass Mountains, west Texas, here designated.

Diagnosis: Transverse shells with hinge at maximum width, distinguished by large ears, ventral strut spines well developed, usually numbering four, in one pair on the outer ears and another pair on the anterior flanks of the sulcus, with relict strut spines and on some specimens rare additional strut spines, a row of spines along ventral hinge and a few scattered over disc and anterior trail.

Discussion: This subgenus is close to *Muirwoodia* Licharew, 1947, and distinguished by the much larger ears, with lateral flanks converging forward, whereas *Muirwoodia* (*Muirwoodia*) has smaller ears, similar row of small ventral hinge spines, and subparallel lateral flanks. In addition, *Grandaurea* is apparently less inflated, though this is not certain. *Muirwoodia* (*Muirwoodia*) is found widely in Upper Pennsylvanian and Lower Permian Arctic deposits of Russia and Canada, extending into western United States, whereas *Muirwoodia* (*Grandaurea*) typifies the paleotropical faunas of west Texas, being represented by five species of Guadalupian age. *Yakovlevia* Fredericks and its ally *Archboldevia* Angiolini & Long are shaped just like *Grandaurea*, with large ears and anteriorly converging lateral flanks, but strut spines are lacking. *Archboldevia* has spines limited to the ventral hinge row, and the dorsal valve is thickened.

The type species of *Muirwoodia* (*Grandaurea*) is fully illustrated by Cooper & Grant (1975, pl. 434, fig. 1-8, pl. 452, fig. 29-34, pl. 473, fig. 1-17, pl. 474, fig. 1-24). Figures indicate the presence of slender anderidia in the dorsal valve, continuing posteriorly from the ends of the brachial ridges (Cooper & Grant, 1975, pl. 473, fig. 1) and with various other illustrated species show well the thickened hinge bearing internal pits, and the prominent pustules at the start of the dorsal trail.

Fig. 15.31. *Muirwoodia* (*Grandaurea*) *hessorum* (Cooper & Grant), ventral valve showing prominent strut spines, USNM 153980h, holotype, x1, from Willis Ranch Member (Wordian), Glass Mountains, Texas, United States. See Cooper & Grant (1975).

Genus ***Sajakella*** Nasikanova, 1968

Sajakella Nasikanova, based on type species *S. formosa* Naskanova in Sarytcheva, 1968, p. 141 from the Bashkirian Keregetass Suite of Kazakhstan, is yakovleviid in form, with very wide hinge and low rugae across the posterior disc, well defined sulcus over the ventral disc, and long trail. Ventral spines are of moderate strength only, and no clearly defined row lies along the hinge according to illustrations.

The material described as *Sajakella* (?) *martianovi* (Lapina, 1957, p. 86, pl. 15, fig. 14-19), Ustritsky & Chernyak (1963, p. 90, pl. 11, fig. 11-13), Nasikanova (in Sarytcheva 1968, p. 142, pl. 19, fig. 7-11) and Semenova in Ifanova & Semenova (1972, p. 36, pl. 1, fig. 18, 19) has slightly stronger commarginal ornament, shorter trail, and two prominent strut spines as compared with type *Sajakella*, and Lazarev (1990, pl. 39, fig. 1) compared a specimen from lower Bashkirian beds of the southern Urals. The species was named by Serapichsky in Lapina (1957) from the Carboniferous Vereian level, and originally assigned to *Muirwoodia*: the general shape is comparable, though commarginal rugae are slightly stronger over the visceral disc than in the type species *mammata*, and strut spines less than clear, whereas anterior strut spines are prominent in the material described in Ustritsky & Chernyak (1963) and Nasikanova (1968). There is no clear sign of two such strut spines in the figures of the original suite allocated to *Sajakella formosa*, or in *S. muromzevi* Grigorieva (in Sarytcheva 1968, p. 143, pl. 19, fig. 12-17, fig. 64) or *S. dzhinsetuensis* Lazarev in Lazarev & Suur'suren (1992; Rozanov 2003, pl. 44, fig. 1-4) from the upper Visean of Mongolia, but there are more slender but still stout spines over the anterior trail, especially in *formosa* (Nasikanova in Sarytcheva 1968, pl. 19, fig. 1a, 2a, 4a) and also on the lateral flank below the ear (pl. 19, fig. 2b). Is it possible that these species are recording a change from species with moderately firm anterior ventral spines, into a species with clearly developed strut spines, or as a more likely prospect, a weakening of strut spines into more slender less strut-like spines? Such a possibility may have been expressed by the recognition of *martianovi* as only questionably close to *Sajakella* by Nasikanova in Sarytcheva (1968) in recording well preserved material from the Koksyusk and

Chakellmess Complexes of west Kazakhstan. From Taimyr, specimens recorded in Ustritsky & Chernyak (1963, p. 90, pl. 11, fig. 11-13) from the Makarov Horizon and Even Suite have deeper sulcus and less defined costae, but show the two prominent anterior strut spines, partly explaining why they were referred by Ustritsky & Chernyak (1963, p. 90, pl. 11, fig. 11-13) to *Eomarginifera* Muir-Wood, a paucispiniferid genus that also has strut spines. Certainly the species *martianova* has to be considered a member of Yakovleviidae, whether or not the Taimyr material is conspecific. Modifications were introduced by Klets (2005, pl. 11, fig. 8, 9, 11, 12) in figuring material as *martianova* from the Tilask Suite of Upper Carboniferous age in south Verchoyan. Although the specimens show no clear strut spines, they were referred to *Muirwoodia*. Klets (2005, pl. 11, fig. 13, 14) showed that specimens supposed to belong to *Sajakella formosa* possessed two pair of strut spines, with anterior pair each side of the anterior ventral sulcus, and one at least on the outer side of a diductor scar. There clearly needs to be further appraisal of *Sajakella* and *martianova*, but provisionally, *Sajakella* is regarded as a member of Muirwoodiinae. Possibly it has pairs of anterior and lateral strut spines, though this needs to be verified from well preserved material.

Genus ***Duartea*** Mendes, 1959

Fig. 15.32

Type species: *Productus batesianus* Derby, 1874, p. 54 from the Itaituba Group (Bashkirian), Brazil.

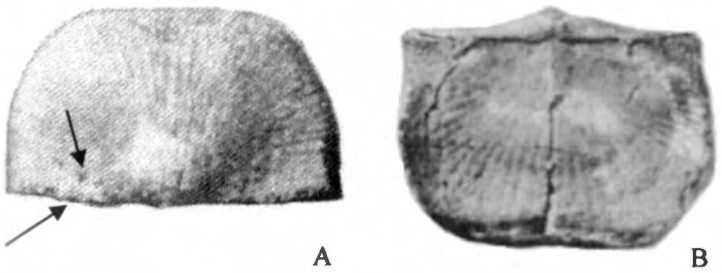


Fig. 15.32. *Duartea batesianus* Derby from Upper Carboniferous Itaituba Group, Brazil, x2. From Mendes (1959, p. 465). Arrows point to rows of spines along hinge and umbonal slopes.

Discussion: *Duartea* has intercalated ventral costae, and dorsal costae branch, judged by material from Itaituba and kept at the Smithsonian Institution, Washington D.C., United States. Diductor scars are feebly fringed, and there is no visible ventral marginal ridge, but a dorsal hinge ridge is moderately developed. Internally, there are many strong ventral pustules postero-laterally, and smaller but sharp and pointed pustules anteriorly. The dorsal adductors are small and not clearly dendritic. *Duartea* was diagnosed in Brunton et al. (2000, pp. 465, 466) as "resembling *Yakovlevia* externally, but moderately deep corpus; spines in weak row now separating ears, slight posterior reticulation, ribs become weak anteriorly". Just what the single row separating the ears is meant to signify is murky, not to say erroneous, but the figure (Brunton et al. 2000, Fig. 310.3a) suggests a row of fine spines along each umbonal flank: indeed the figure also arguably suggests a row along the hinge. Mendes (1959, p. 60) reported "Nao ha cardinal spines". Further confounding confusion is the proposed synonymy in Brunton et al. (2000), partially with *Muirwoodia* Licharew, detail not explained, and *Paramuirwoodia* Zhang. The nature of these two genera is clarified herein by analysis of their morphologies, and it is clear that the three genera are distinguishable. One important aspect of *Duartea* has been particularly obscured in the diagnosis presented by Brunton et al. (2000). According to the original description by Derby (1874), there are "large tubular spines distributed over the surface, one near each ear or sometimes two in or near the sinus, near the front, and one, on each side, about midway between the one on the ear and the one near the sinus. Occasionally one or more of these spines is duplicated, and on some specimens there are half cicatrixed spines to indicate that a second series of spines, similar to the one described, had been broken off in the growth of the shell". (Translated from Derby, 1874 and see Gonsalves 1952, pp. 75, 76). Derby's text clearly suggests that stout and possibly strut spines are developed, although omitted from the diagnosis in Brunton et al. (2000). There is no mention in the text of the posterior spine rows, but the umbonal slope row is visible in published figures, and several figures show the anterior pair of strut spines on each side of the sulcus. The reference to weak reticulation seems reasonable: the reticulation is weaker than in *Sajakella* and much stronger than in *Yakovlevia*. Although *Muirwoodia* was treated as a partial synonym of *Duartea* by Brunton et al. (2000), *Muirwoodia* does not show the row of spines developed along the base of the umbonal flanks.

Genus ***Dzhiremulia*** new genus

Derivation: From place-name, where genus is represented from Dzhirem-Ula section, southeast Mongolia.

Type species: *Yakovlevia conlustratus* new species from Assistance and Trold Fiord Formations (Roadian, Capitanian) of Arctic Canada, here designated.

Fig. 15.33. *Dzhiremulia conlustratus* new genus, new species, dorsal and ventral aspects of GSC 36549, x1.5 from C-4016, Assistance Formation (Roadian), Ellesmere Island, Canadian Arctic. JBW photo.

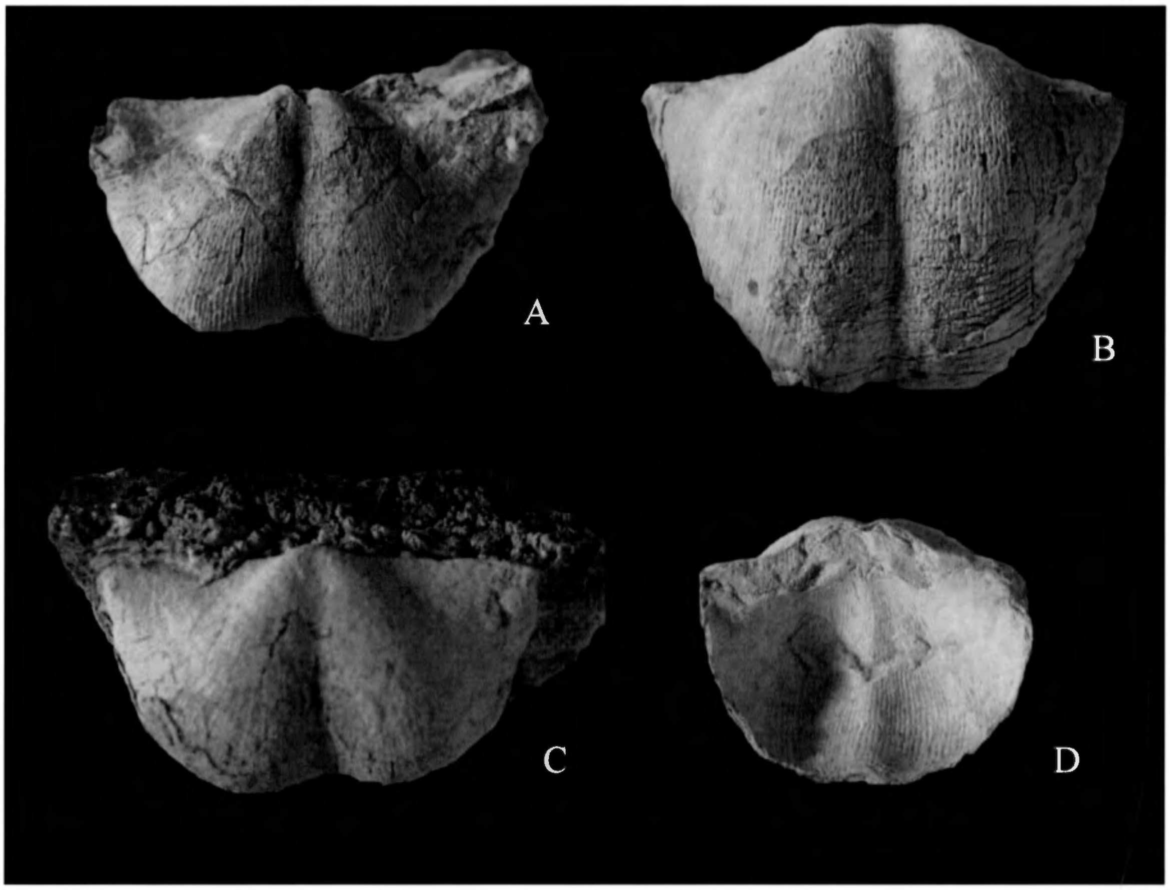


Fig. 15.34. *Dzherimulia conlustras* new genus, new species. A, ventral valve, posterior aspect, GSC 136070, from C-4019, holotype, x1. B, ventral view, GSC 136073 from C-4025, x1.3. C, ventral posterior view of GSC 136072 from C-4016, x1. D, dorsal view of GSC 52417 from. C-4019, x1. From Assistance Formation (Roadian), Ellesmere Island, Arctic Canada. JBW photo.

Diagnosis: Moderately large, Strut spines limited to a pair at cardinal extremities, small spines along hinge margin and in one or two rows along posterior trail. Corpus moderately thick.

Discussion: The genus is distinguished by the distribution of spines, with strut spines limited to one solitary pair. *Muirwoodia* (*Muirwoodia*) and *M.* (*Grandaurea*) have two pair of strut spines, and *Harkeria* new genus has three pair.

***Dzhiremulia conlustratus* new species**

Fig. 15.33 – Fig. 15.37

Derivation: conlustro – lighten, illuminate, Lat.

Holotype: GSC 136070 figured as Fig. 15.34A, Fig. 35A, B from C-4019, Assistance Formation, Ellesmere Island, Canada, here designated.

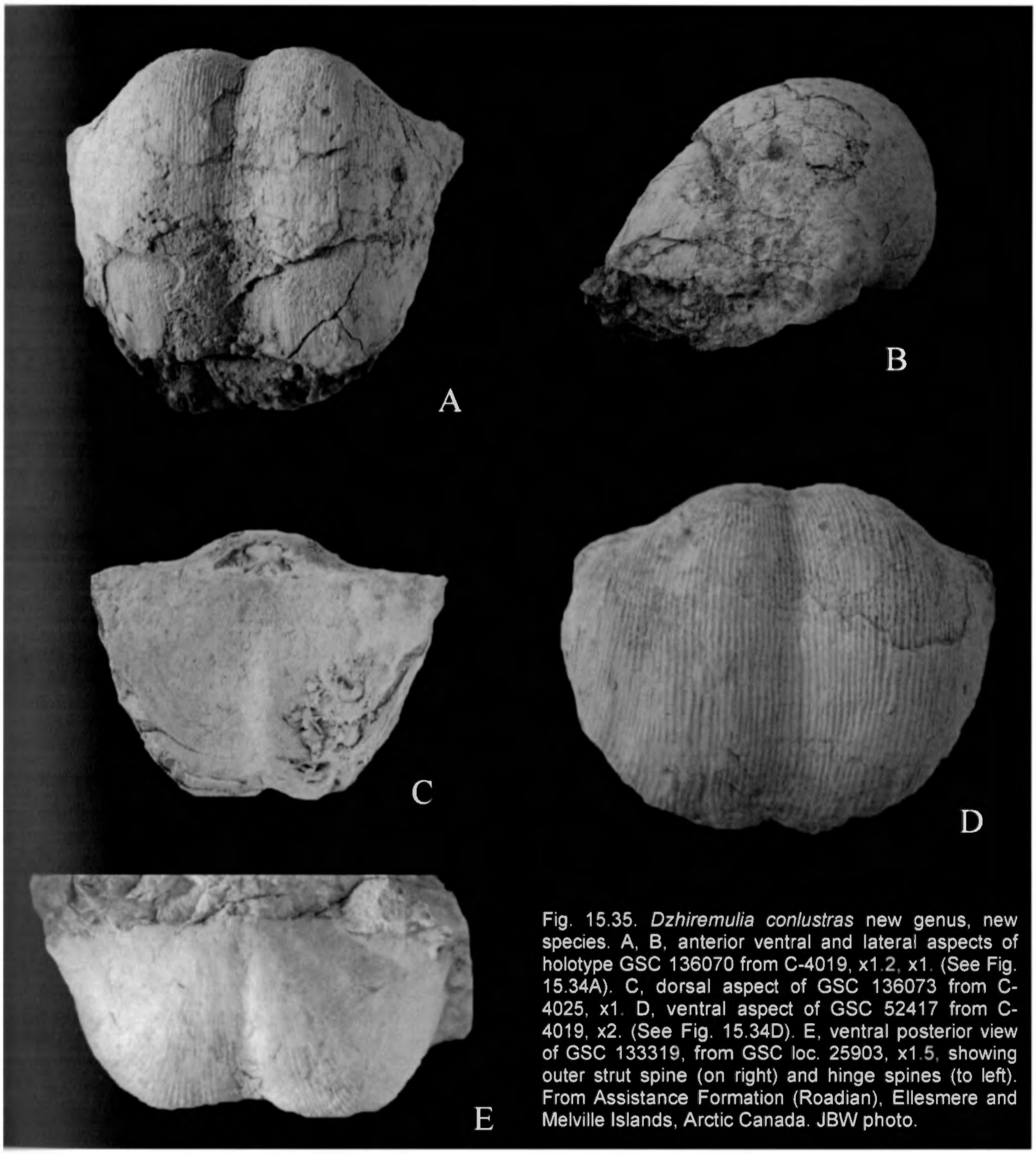


Fig. 15.35. *Dzhiremulia conlustras* new genus, new species. A, B, anterior ventral and lateral aspects of holotype GSC 136070 from C-4019, x1.2, x1. (See Fig. 15.34A). C, dorsal aspect of GSC 136073 from C-4025, x1. D, ventral aspect of GSC 52417 from C-4019, x2. (See Fig. 15.34D). E, ventral posterior view of GSC 133319, from GSC loc. 25903, x1.5, showing outer strut spine (on right) and hinge spines (to left). From Assistance Formation (Roadian), Ellesmere and Melville Islands, Arctic Canada. JBW photo.

Diagnosis: Moderately large with one pair of strut spines, one at each cardinal extremity, fine hinge spines and small number of anterior spines especially close to geniculation. Ears and sulcus moderately well defined. Ventral valve highly curved so that the trail very long and anterior lies almost parallel to first formed part of shell.

Material: Four specimens with valves conjoined and several dorsal valves from C-4019*, two ventral valves from C-4008**, two specimens with valves conjoined from C-4016*, two ventral valves from C-3996**, three specimens with valves conjoined and four ventral valves (possibly with dorsal valves masked) from C-4028 (Tanquary Formation), a ventral valve from C-4003* and specimen with valves conjoined from C-4025*. Two ventral valves and a specimen with valves conjoined from GSC loc. 58977, Degerbols Formation, Ellesmere Island. Chiefly Assistance* and Trold Fiord** Formations (Roadian, Capitanian), Devon Island, Arctic Canada. See Appendix, part C, p. 479.

Dimensions in mm:

GSC specimens	Width	Length	Height
133311 (C-4019)	46	28	24
133320 (C-4019)	40	35	20
136070 (C-4019)	52	43	27
136072 (C-4016)	52.5	32.5	26
136073 (C-4025)	49.5	37	22

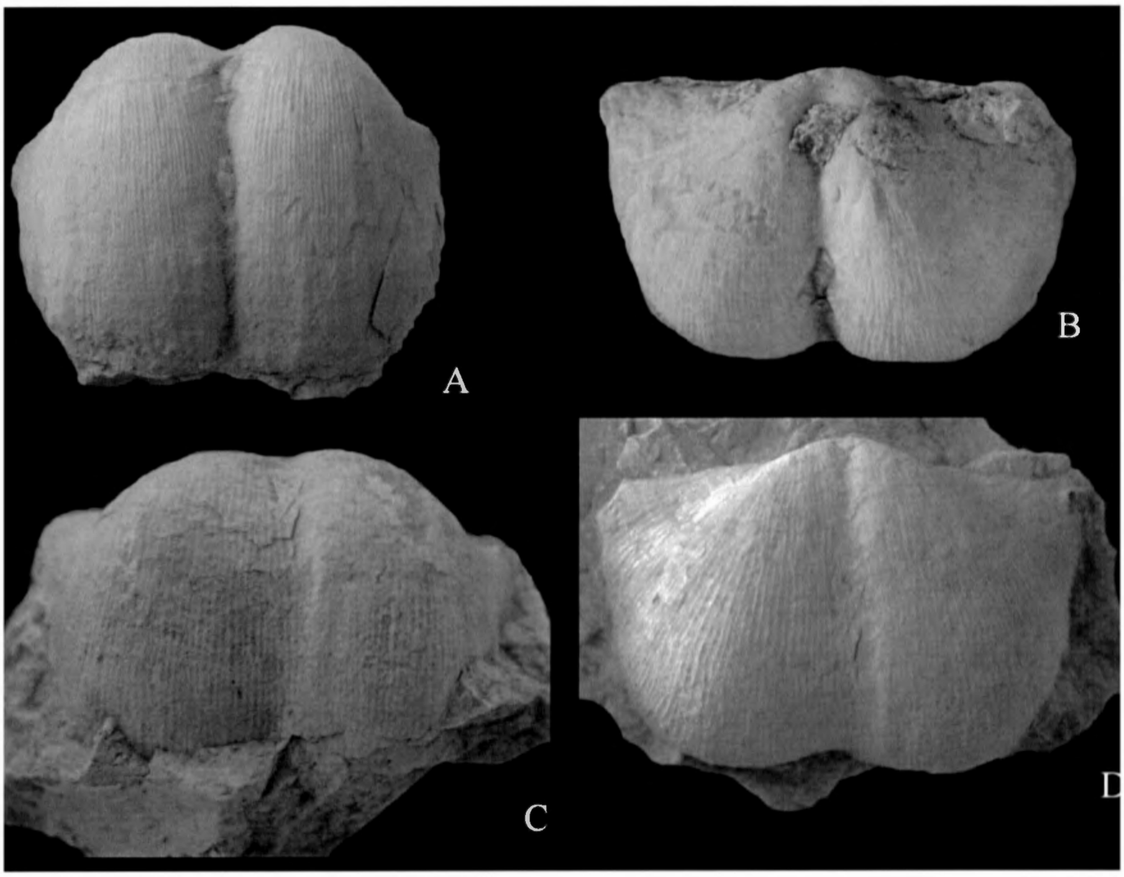


Fig. 15.36. *Dzhiremulia conlustratus* new genus, new species. A, B, ventral and anterior views of GSC 133320 from C-4019, Ellesmere Island. C, D, anterior and posterior ventral valve GSC 133319 from GSC loc. 25903, Melville Island. (See Fig. 15.35E). Specimens from Assistance Formation (Roadian), Arctic Canada, x1.5. JBW photo.

Description: Specimens moderately large, the largest specimen being 56mm wide. The ventral umbo is low and extends only slightly beyond the hinge and umbonal walls are low and diverge at 130°. Umbonal slopes as a rule are gently convex in section and grade gently into convex ears, and the median sulcus widens at 45° from the umbo, but the angle constricts anteriorly, to be reduced to 30°. Rarely the floor is channeled, but usually it is subangular to abruptly rounded: in one specimen the sulcus disappears anteriorly. The maximum width of the shell lies at the hinge, and the ears protrude only slightly. Ginglymus low, and median gap occupied by external face of cardinal process. For the dorsal valve, the fold commences a little in front of the hinge, and there is no nepionic area, and ears are poorly discriminated and weakly concave. Compared with the ventral valve the dorsal disc is only weakly concave, so that the body corpus is comparatively thick. The trail is subgeniculate and well extended, and often curves so much as to lie parallel to the first formed part of the ventral disc, having grown in the opposite direction, although this may have been affected by gentle post-burial distortion. The fold and sulcus continue over the trail. Both valves are ornamented by costellae, numbering about 16 in 10mm over mid-valve, and weakly converging into a trough-like anterior sulcus, or lying parallel in other specimens. Some specimens show erratic and impersistent traces of rugae or growth steps, not well marked. A strut spine lies close to each marginal extremity of the ventral valve, extending postero-laterally, and up to 1.5mm in diameter. A few well spaced fine spines lie close to the hinge, with a row of fine hinge spines preserved in a number of specimens (see Fig. 15.35E), more than nine in number each side of umbo, subevenly spaced, and up to 0.3mm in diameter. Other fine and erect spines lie over the ventral disc and trail, especially towards the anterior third of trail, where a short row of three to five spines may be discerned each side of the sulcus on some specimens, and less than 0.6mm in diameter (GSC 136074).

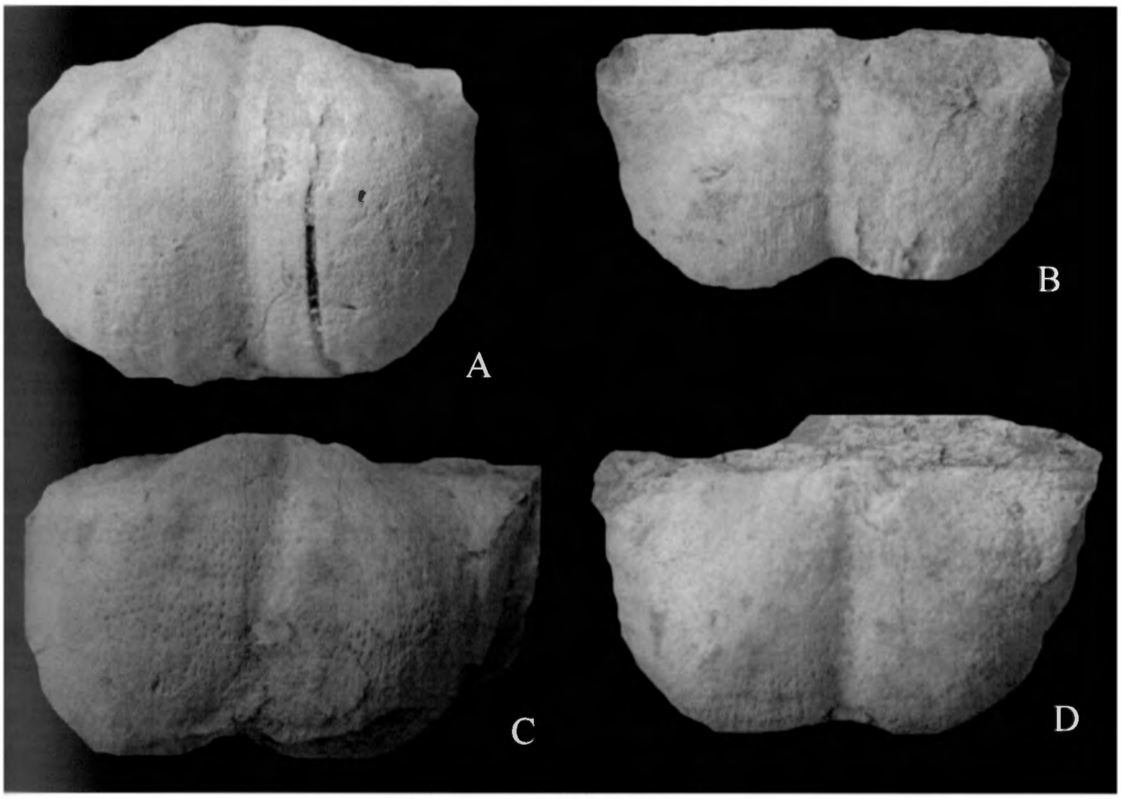


Fig. 15.37. *Dzhiremulia conlustras* new genus, new species. A, B, anterior and posterior ventral aspects of worn GSC 136068. C, D, anterior and posterior ventral aspects of worn GSC 133311. Specimens from C-4019, Assistance Formation (Roadian), Ellesmere island, Canada, x1.5. JBW photo.

Ventral adductors sited on a very narrow and elongate platform, with shallow diductor impressions each side. GSC 36819 from locality C-4016 has a very long median dorsal septum extending well towards the anterior edge of the disc, and in the other specimen from the same locality the posterior septum is very fine, and the muscle scars scarcely discernible. The brachial shields enclose a very small smooth area and large papillae cover the median floor.

Resemblances. *Yakovlevia dzhiremulensis* Manakov, 1998, p. 490, pl. 8, fig. 15-17 is allied, with similar spines. It comes from Mongolia (Outer Mongolia) in the *Alispiriferella lita – Kaninospirifer adpressum* Zone, considered to be of Kazanian (Wordian) age, and a few specimens from the overlying *Echinauris jisuensis* Zone, considered to be of "lower Tatarian" (late Guadalupian) age. The species is large with more pointed cardinal extremities and flanks converging more anteriorly, and sulcus deeper posteriorly in most specimens, compared with the Canadian form. Of Arctic species described, *Productus duplex* Wiman (1914, pl. 14, fig. 3-7) is moderately close in appearance. It comes from the Brachiopod Chert of Spitsbergen, and according to Gobbett (1964, p. 113) has anterior strut spines, so is not congeneric.

Genus ***Harkeria*** new genus

Derivation: Named for Peter Harker.

Type species: *Harkeria studiosus* new species from Assistance Formation (Roadian), Devon Island, Canada, here designated.

Diagnosis: Six strut spines on ventral valve, two at cardinal extremities and two pair on each flank in front of geniculation. Hinge row of fine spines. Corpus moderately thick.

Discussion: Apparently like *Duartea* Mendes and unlike most other members of Muirwoodiinae, this genus is characterized by having six strut spines. Unlike *Duartea*, the new genus lacks a row of spines along the umbonal flanks and commarginal rugae are not conspicuous. So far, the genus seems to be comparatively rare in the Canadian Arctic Archipelago, but it is represented by a number of species in Neimongol (Inner Mongolia), as described by Lee & Gu (1976), Liu & Waterhouse (1985) and others. The genus is close in appearance to *Muirwoodia* Licharew, 1947, but this genus has two strut spines at the cardinal extremities and only one pair anteriorly, as shown by Shi (1995), Shi & Waterhouse (1996, fig. 34A) and Klets (2005).

Harkeria studiosus new species

Fig. 15.38, Fig. 15.39

1960 *Muirwoodia mammata* [not Keyserling] – Harker, p. 58, pl. 16, fig. 1-5.
1964 *M. mammata* – Gobbett, p. 112, pl. 13, fig. 23 – 26 (not 28).

Derivation: studeo – eager, zealous, Lat.

Holotype: GSC 13531 from Assistance Formation (Roadian), Devon Island, Canada, figured by Harker in Harker & Thorsteinsson (1960, pl. 15, fig. 1-3), here designated.

Diagnosis: Relatively small and transverse with shallow anterior ventral sulcus, fine ribs and six prominent strut spines.

Material: A small collection of specimens with valves conjoined from GSC loc. 26406, Assistance Formation, Devon Island, and also C-3996, Trold Fiord Formation (Capitanian), Ellesmere Island, Canada. See p. 479. As well half a dozen similar specimens from silty shale, from unknown locality in northern Canada, possibly Van Hauen Formation (Wordian).

Fig. 15.38. *Harkeria studiosus* new genus, new species, ventral valve GSC 133313, x1.5, from C-3996, Trold Fiord Formation (Capitanian), Ellesmere island, Canada. Arrows point to bases of anterior strut spines. JBW photo.

Description: Specimens small, with the disc comparative flat and trail longer than disc and extending at high angle, the holotype measuring 27mm wide and 18mm long, the ventral umbo broad with angle of 150°, hinge at maximum width and acute cardinal extremities, and very low ventral ginglymus. The ventral sulcus is broad with angle of 40°, commencing close to the umbo and widening to the anterior commissure, with slightly angular or gently concave floor, and the dorsal fold commences a little in front of the hinge. The trail curves evenly on from the disc. Both valves covered by costellae, 14 in 10mm on the anterior slope. Spines limited to ventral valve. Six strut spines are developed, a pair at the cardinal extremities, and two pair on the flanks, in front of the start of the trail. Five or six finer spines lie along the hinge each side of the umbo, but no additional spines are developed over the umbonal slopes.

Four specimens with valves conjoined are allocated to this species from an uncertain Canadian Arctic locality (possibly Van Hauen Formation?), of mid-Permian age, judged from the associated fauna, and are used to demonstrate features of the interior. The largest measures 28mm wide and 17.5mm long, with 13-16 costellae in 10mm anteriorly. The sulcus is usually narrower than in the types, measuring 30° in three of the specimens and 40° in the other. Ventral adductor scars are elongate and smooth in one specimen, unlike those of *Elucidatea* (cf. Fig.

15.29D with Fig. 15.39C, D) and shorter in another: this has slight oblique markings laterally at the anterior end; the adductors in both specimens are divided by a low narrow myophragm. Diductors are well rounded and moderately impressed. The posterior floor is slightly thickened and bears numerous papillae. The four anterior strut spines are well marked internally. The dorsal interior is distinctive, but the cardinal process is not preserved. The adductor scars lie in a single oval to tear-shaped pair, comparatively smooth and outlined by a bordering groove. The floor of the valve between the scars and to each side is smooth, and a slender median septum commences near the anterior scars, and extends well forward, to a single row of large papillae. In one specimen the papillae are joined by two further somewhat irregular rows of papillae. Brachial shields are well outlined, and are small and project forward, enclosing comparatively smooth areas. The remainder of the floor bears sublinear pits and papillae. The posterior valve floor in front of the cardinal process is almost smooth, lacking the coarse pustules developed to each side, but shows extremely fine and scattered pits. Such fine pits would probably be not preserved in silicified material, or displayed by shells preserved in unfavourable matrix.

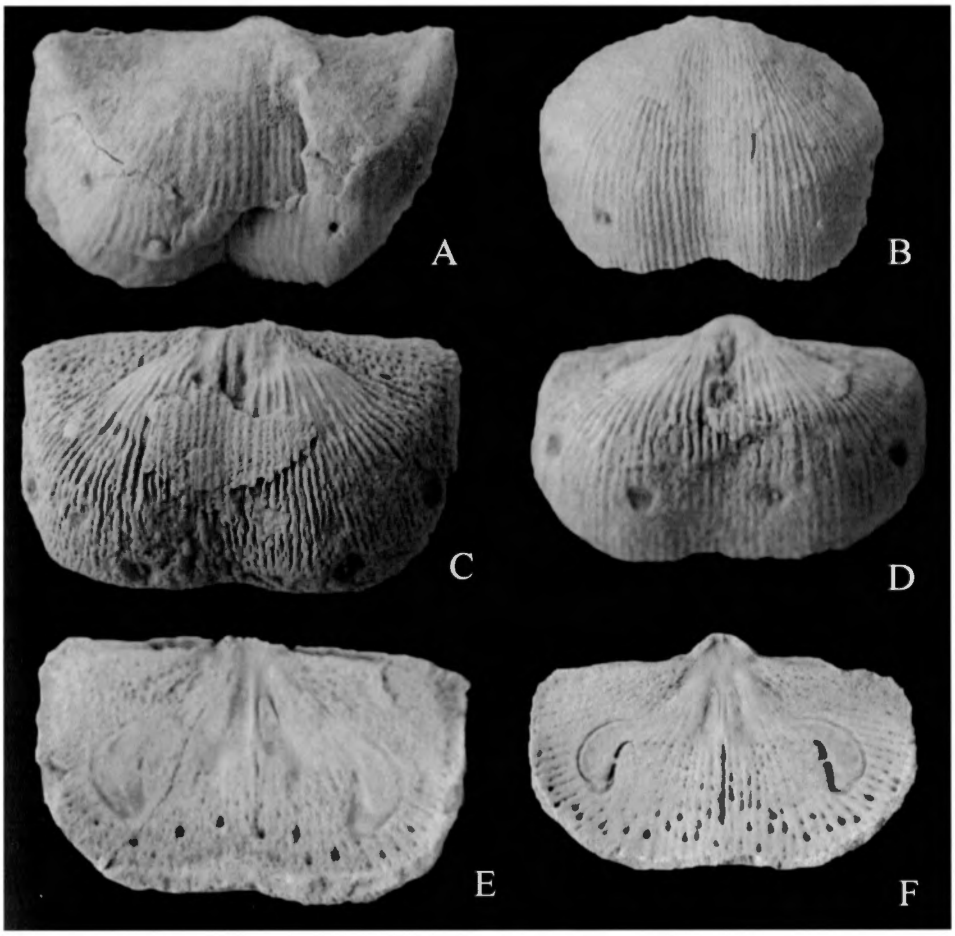


Fig. 15.39. *Harkeria studiosus* new genus, new species, x2. A, ventral aspect of GSC 133314 from GSC loc. 26406, Assistance Formation (Roadian), Devon Island. B, ventral valve GSC 133318. C, E, ventral and dorsal aspects of mostly internal mould of valves conjoined, GSC 133321. D, F, ventral and dorsal aspects of specimen with valves conjoined, GSC 133322. B – F from ?Van Hauen Formation (Wordian?), Canadian Arctic. JBW photo.

Resemblances: The type specimens were compared with *Muirwoodia mammatus* (Keyserling, 1846) by Harker in Harker & Thorsteinsson (1960), but although there is some similarity in shape, the presence of six rather than four strut spines marks a ready distinction. This difference distinguishes the species from various species discussed by Harker. Gobbett (1964) described somewhat similar material as *Muirwoodia mammatus* with somewhat similar strut spines from the Brachiopod Chert of Isfjorden in Spitsbergen.

A ventral valve from C-4067 (see p. 479), in the Nansen Formation of the Canadian Arctic, displays a number of strut spines, and has a comparatively flat disc and stronger rugae compared with the present species.

There is a close approach to a number of species with six strut spines that have been described from the Permian of Neimongol or Inner Mongolia. One of the closest species was recorded (like the present holotype) as *Muirwoodia mammata* by Liu & Waterhouse (1985, p. 17, pl. 4, fig. 4-6) from the Houtoumiao Formation in the *Dyoros lamellosa* – *Stenoscisma ovalia* assemblage, of Kungurian to Kazanian (Roadian-Wordian) age. The specimens are similar in shape and ornament, but have more protruding cardinal extremities, shallow sulcus and coarser ribs (eight to ten in 10mm). The species described as *Yakovlevia borealis* Liu & Waterhouse (1985, p. 19, pl. 3, fig. 4-6) from the lower Zhesi Formation of likely Middle Permian age in Neimongol is much larger, but shows the same distribution of six strut spines and row of spines close to the hinge. *Y. convexa* Liu & Waterhouse, 1985, p. 20, pl. 3, fig. 7, pl. 4, fig. 1-3 from the Zhesi Formation is large and convex with finer costellae and shallower more anterior sulcus, but the text and figures are not clear over the number of strut spines. A large number of Yakovleviidae have been described from Neimongol, including studies by Lee & Gu (1976), Lee & Gu in Lee et al. (1980) and Zhan & Lee (1977), but the spine detail is often obscure. However it is clear that six-spined species are more common in Inner Mongolia than in other regions.

Subfamily **PARAMARGINIFERINAE** Lazarev, 1990

Fig. 15.40

[Paramarginiferinae Lazarev, 1990, p. 82].

Taxonomy: The name was first proposed in a thesis by Lazarev (1986a, p. 23), as cited by Brunton et al. (2000), but the 1986a work was not a publication, and the cited date invalid.

Diagnosis: Shells with fine radial ribs, a few (two) ventral strut spines and prominent internal marginal ridge. Lower Permian.

Genera: *Paramarginifera* Fredericks, *Paramuirwoodia* Zhang.

Fig. 15.40. *Paramarginifera clarkei* (Tschernyschew). Ventral valves figured by Tschernyschew (1902, pl. 58, fig. 1, 2), from Schwagerina-kalk, Tastuba, Russia, x1. A fuller overview is provided by illustrations of the genus in Muir-Wood & Cooper (1960, pl. 60).

Discussion: One genus that shows many similarities to *Yakovlevia* and *Muirwoodia* is *Paramarginifera* Fredericks, 1916, pp. 61, 64, from the Early Permian Schwagerina Limestone of the Urals, Russia, based on *Marginifera clarkei* Tschernyschew (1902, pp. 328, 651, pl. 47, fig. 6, 7, pl. 58, fig. 1-3), further figured by Muir-Wood & Cooper (1960, pl. 60, fig. 11-14) – see Fig. 15.40 herein – and classed as Marginiferinae by Muir-Wood & Cooper (1960). This genus has a moderately planar type 6 ventral disc, long trail, fine costellae, with large anterior strut spines and row of spines along the hinge. Costellae tend to converge in the sulcus as may be seen especially in *Muirwoodia*. The special attributes of *Paramarginifera* are clear, for a cincture is developed in the ventral valve. Although the figures provided by Tschernyschew (1902) may not suggest yakovleviid affinities, the range of illustrations provided by Muir-Wood & Cooper (1960) show well the closeness to other members of the family. In its fine ribbing, *Paramarginifera* differs from that of any other probolioniin or paucispiniferin shell, and relates to *Paramuirwoodia* Zhang in Zhang et al., 1983, which has a lower dorsal marginal ridge.

Brunton et al. (2000, p. 429) allocated a large number of genera to Paramarginiferini, which display a diversity of morphologies, belonging to Yakovleviidae, Marginiferiidae, Paucispiniferoidea and Productidae.

Genus ***Paramuirwoodia*** Zhang, 1983

Paramuirwoodia as figured by Zhang in Zhang et al. (1983, p. 298, pl. 133, fig. 1a-d) is like *Muirwoodia* in shape, with wide disc and long trail, and appears to have a pair of anterior strut spines. There are subdued commarginal rugae over the disc, approaching those of *Duartea* and some species of *Muirwoodia*, but what is outstanding is the development of a sturdy internal ventral ridge across the ears, and a moderately developed marginal ridge in the dorsal valve. *Paramuirwoodia* was synonymized with *Duartea* by Brunton et al. (2000, p. 465), and it is close in shape and ornament, but although the nature of the interior is not clear in all details for *Duartea*, no dorsal marginal ridge has ever been reported. The dorsal marginal ridge in *Archboldevia* (Fig. 15.27B) differs, developed around the inner rim of a wedge-shaped valve.

16. Superfamily **LINOPRODUCTOIDEA** Stehli, 1954

Fig. 16.1, Table 15

[Nom. transl. Waterhouse, 1978, p. 20 ex Linoproductinae Stehli, 1954, p. 319. Syn. Striatoidea Nalivkin, 1979].

Diagnosis: Small to large shells usually with trail, often geniculate; ornament of well developed ribbing as a rule and on both valves, spines varied and often numerous, never forming strut spines, spines rarely present on dorsal valve. Muscle scars normally dendritic to some degree, or striate, cardinal process bilobed or trilobed, papillation may be distinctive in different groups.

Discussion: During the Late Carboniferous and Permian Periods, linoproductidin brachiopods flourished as major groups, one centred on linoproductoids, the other represented by auriculispinans and paucispinaurians. But this was not recognized by Muir-Wood & Cooper (1960), because they focused on Early Carboniferous faunas of United States and Europe, and Permian of United States and northern Europe, those regions at that time having supplied most of the first descriptions of genera. All of these areas were of paleotropical affinities during Late Paleozoic time, which encouraged a plethora of evolution with development of some peculiar deviations from the norm. In turn these exceptional forms somewhat distorted the classification, because auriculispinaurans and paucispinaurians were lumped with linoproductids. A few close relatives were discriminated as highly exceptional groups, such as Proboscidellinae, named for peculiar brachiopods with ventral valve which developed into a long tube. So when genera later discriminated as auriculispinids and paucispinauriids were eventually distinguished, they could only by the rules of seniority be classified as belonging to one of the very unusual and minor family groups, and the name genus of the superfamily does not reflect the general appearance of the majority of genera. Whilst this awkwardness could be bypassed to some extent by changing ranks, that would upset the overall balance of the group and impinge on the ranking of non-productid groups, so it is judged preferable to accept the status quo.

In the course of this overall study, it is shown that evolution proceeded to some extent in "sheets" or "waves", affecting different genera and species of different family groups as they evolved from a strophalosiiform to productiform morphology. But whether that occurred in the case of gigantiform Linoproductidina is not clear. It is possible that almost simultaneous evolution occurred in separate stocks during Carboniferous time to yield "gigantic" or exceptionally large linoproductidin brachiopods characterized in two of the groups by conical brachial supports, or by lateral buttress plates, or spines with elongate bases, or shells with closely spaced commarginal rugae. Most of these gigantoproductiform genera were associated in one subfamily by Brunton et al. (2000, p. 550), understandably because they share such outstandingly large size and shape. The ventral spines of *Gigantoproductus*, aligned along the hinge, and erect with small bases over the ventral valve as a rule, would appear to be linoproductiform, and indeed approaching schrenkiellin morphology: placement in Monticuliferidae by Brunton et al. (2000) is difficult to justify. Whatever the source, the unusual interior, involving an elaboration of muscle scars and the origination of brachial cones marks a development contingent on the large size (or vice versa). Yet *Semiplanus* and allies lack brachial cones, and spines tend to be more numerous, erect anteriorly, but with low ramps posteriorly. Like *Gigantoproductus*, the body cavity is slender, but the dorsal adductors are non-dendritic, and quite possibly the semiplanins arose from different stock entirely, convergent with rather than derived from gigantoproductids. Like *Gigantoproductus, Kansuella* has brachial cones, and differs in detail with regard to its muscle scars and its well-formed interareas with pseudodeltidium, and lack of lateral buttress plates. The outstanding difference lies in the nature of its ventral spines, with prolonged and well defined bases, seemingly suggestive of the spines found in Proboscidellidae, Auriculispinidae and Paucispinauriidae. On the other hand, members of Wardlawriinae show the large size and shape of gigantiform Linoproductidina, and have spines with elongate bases that differ in detail from those of Proboscidelloidea, because the hollow cores do not bend forward through the shell from the spine base. These imply that *Semiplanus, Kansuella* and allies, although having spines that have elongate bases, developed independently of the Proboscidelloidea, and with large size and other shared attributes involving lateral buttress plates and brachial cones, were related to Gigantoproductidae.

Family **LINOPRODUCTIDAE** Stehli, 1954

[Nom. transl. Muir-Wood & Cooper 1960, p. 296 ex Linoproductinae Stehli, 1954, p. 319].

Diagnosis: Shells oval in outline, transverse or elongate, usually symmetrical, free-living, umbo prominent, ears developed, venter arched. Ventral spines only, shell often large, body cavity deep or shallow, both valves with fine

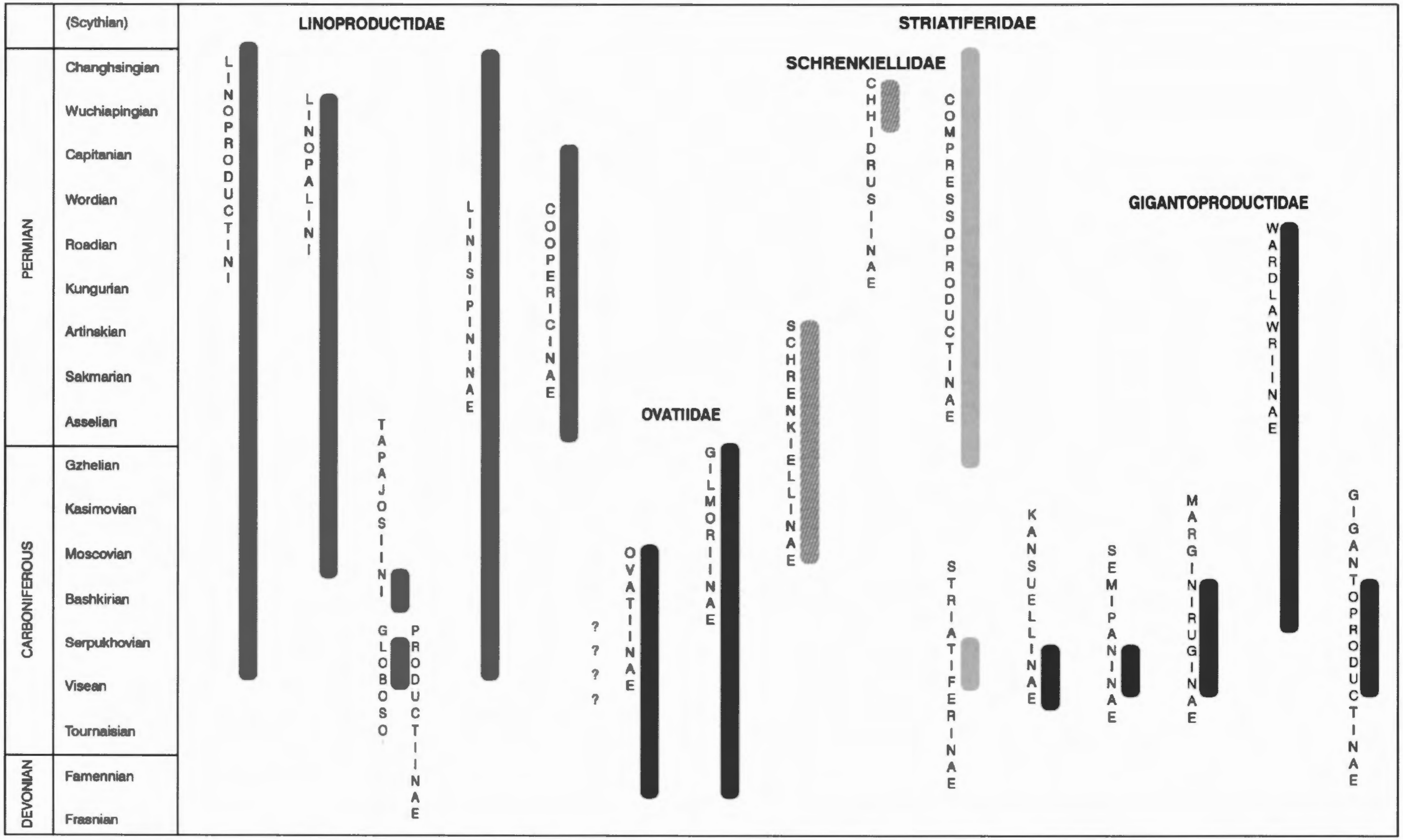


Fig. 16.1. Range chart for Superfamily Linoproductoidea.

close-set radial ornament, commarginal ornament inconspicuous. Cardinal process large, outer lobes not fused dorsally.

Discussion: The treatment of Linoproductinae is very different from that offered by Brunton al (2000, pp. 527-530). These authors provided a generalized diagnosis, as consisting of "linoproductids without marginal structures or dorsal spines", yet *Linoproductus* itself has a narrow marginal ridge, as illustrated by Brunton et al. (2000, Fig. 365.1f), and *Marginovatia*, incorporated in the subfamily by Brunton et al., is diagnosed in part by a high dorsal marginal ridge (Brunton et al. 2000, Fig. 365.3f). Many linoproductoids, not just Linoproductinae, lack dorsal spines. Eight genera were placed in the subfamily, and of these, only one, *Linoproductus* itself, remains in the subfamily. The improved understanding rests substantially on more careful study of the family by one of the Treatise authors, S. S. Lazarev, which swept away the claims of the *Revised Brachiopod Treatise*, rendering it thoroughly out of date.

The probable source of Linoproductidae is provided by *Eoproductella* Rzhonsnitzkaya, in Subfamily Eoproductellinae Lazarev, 1987, p. 49. This genus is ribbed on both valves and displays spines only on the ventral valve. It is strophalosiiform, with interareas, teeth and sockets, and is of Early and Middle Devonian (Pragian – upper Givetian) age. To judge from the fossil record, Eoproductellinae evolved into Ovatiidae, Subfamily Ovatiinae, represented by a few genera of Late Devonian and Early Carboniferous age, characterized by swollen ventral valve, a number of spines along the ventral hinge, and scattered few erect body spines. This developed into Linoproductidae, characterized by larger size, stronger spines and different cardinal process. Another subfamily descendent from Eoproductellinae, Gilmoriinae of Late Devonian and Early Carboniferous age, characterized by wider shells with more extended hinge, evolved into Schrenkiellidae, with wide hinge and fewer spines, and possibly into the very large Gigantoproductidae.

It is to be noted that the ranks of groupings recognized for the Linoproductidae in this study could arguably be reduced, ie. tribes instead of subfamilies, and subfamilies instead of families. But studies by Lazarev (2004-2010) allocated subfamily rank to Coopericinae etc, and would recognize Schrenkiellidae as a full family. His groupings have very few genera, even where reinforced where possible by further studies as in this thesis, and involve limited morphological differences.

Family Linoproductidae Stehli, 1954
- Subfamily Linoproductinae Stehli, 1954
  - Tribe Linoproductini Stehli, 1954
  - Tribe Linipalini Lazarev, 2010
  - Tribe Tapajosiini new tribe
- Subfamily Linispininae Lazarev, 2006
- Subfamily Coopericinae Lazarev, 2004
- Subfamily Globosoproductinae new subfamily

Family Ovatiidae Lazarev, 1990
- Subfamily Ovatiinae Lazarev, 1990
- Subfamily Gilmoriinae new subfamily

Family Schrenkiellidae Lazarev, 1990
- Subfamily Schrenkiellinae Lazarev, 1990
- Subfamily Chhidrusiinae new subfamily

Family Striatiferidae Muir-Wood & Cooper, 1960
- Subfamily Striatiferinae Muir-Wood & Cooper, 1960
- Subfamily Compressoproductinae Jin & Hu, 1978

Family Gigantoproductidae Muir-Wood & Cooper, 1960
- Subfamily Gigantoproductinae Muir-Wood & Cooper, 1960
- Subfamily Semiplaninae Sarytcheva, 1960
- Subfamily Marginiruginae new subfamily
- Subfamily Wardlawriinae Waterhouse, 2004b
- Subfamily Kansuellinae Muir-Wood & Cooper, 1960

Table 16. Superfamily Linoproductoidea Stehli, 1954.

Subfamily **LINOPRODUCTINAE** Stehli, 1954

[Linoproductinae Stehli, 1954, p. 319].

Diagnosis: Hinge spines in one to rarely three rows. Body spine bases moderately large.

Discussion: Coopericinae has a row of stout hinge spines and few if any other spines; Linispininae has a number of spine rows close to the ventral hinge, and Globosoproductinae has few hinge spines and swollen elongate shape.

Tribe **LINOPRODUCTINI** Stehli, 1954

Fig. 7, p. 12

[Nom. transl. Waterhouse 2001, p. 25 ex Linoproductinae Stehli, 1954, p. 319].

Diagnosis: Spines evenly distributed or rare over ventral valve, hinge spines in one to rarely three rows. Body spine bases moderately large. Upper Carboniferous (Moscovian) to Middle Permian (Roadian). Full range not certain, probably commencing in the Tournaisian or Visean.

Genera *Linoproductus* Chao (syn. *Euproductus* Whitehouse, *Cora* Fredericks), *Haereospina* Waterhouse, *Linoproductoides* Lazarev, *Liniunus* new genus, *Sublinoproductus* Lazarev.

Discussion: Linoproductini is qualified by the nature of the other tribes in the subfamily. Lazarev (2010) limited the family group based on *Linoproductus* to shells that had outer ear spines as thick as those on the trail, shared an unusual cardinal process, and possessed a dorsal median septum which overlapped in extent with the ends of the brachial ridges. That may be correct, but greater emphasis is here placed on details of spine distribution, with a degree of tolerance accepted for spine diameter, and with due attention to the dorsal interior. The outer ear spines of type *Linoproductus* are not always as broad as those of the trail, and the same appears to be true for *Sublinoproductus pentagonalis* Lazarev, 2010, pl. 3, fig. 6, 7.

Genus ***Liniunus*** new genus

Fig. 16.2

Derivation: linea – thread, line; unus – single, Lat.

Type species: *Linoproductus kaseti* Grant, 1976, p. 154 from Rat Buri Limestone (Roadian), southern Thailand, here designated.

Diagnosis: Single row of hinge spines, fine near umbo, strong laterally and thicker than most but not all ventral disc and trail spines. Cardinal process broad with wide central shaft bearing deep notch and often bent ventrally, lateral lobes lower and spaced well apart; median septum extends forward beyond ends of brachial ridges.

Fig. 16.2. *Liniunus kaseti* (Grant). Two fragmentary ventral valves illustrating the coarse lateral hinge spines in B and fine disc and trail spines in A, typical of the genus. A, BR 342, now ROM 32165, and B340, now ROM 32163. From Rat Buri Limestone (Roadian) at Khao Phrik, south Thailand. x 1.5. B. O'Donovan and JBW photo.

Discussion: This genus is moderately close to *Linoproductus* Chao, 1927, based on type species *Productus cora* d'Orbigny, 1842 from the Asselian Copacabana Group of Bolivia. Unlike the new genus, there are no fine single costal spines over the venter and trail in *L. cora*, and the thick spines disrupt two to four costellae. The dorsal septum and cardinal process are moderately close in both genera, and the cardinal process bends ventrally in *Liniunus*, especially in small specimens, the process apparently straightening later. A deep pit lies close to the posterior end of the process on the ventral face, and the lateral lobes are widely splayed, and lower than the central shaft. No alveolus is developed at the base of the process in *Liniunus*. In immature dorsal valves of *Liniunus*, the median septum arises some distance in front of the cardinal process and there is no buttress platform or mounds, but in more mature specimens, an anterior platform has developed in front of the cardinal process, between the cardinal hinge supports, with a rounded surface which may bear a shallow groove that with increased maturity becomes infilled. No such groove in the narrow platform of *Linoproductus cora* was illustrated by Samtleben (1971, pl. 7, fig. 4), but a broad shallow pit is figured in front of the cardinal process by Kozlowski (1914, Fig. 8). In both of these illustrations, there is the indication of a weakly defined anterior mound and even faint suggestions of subdued or incipient lateral buttress plates. Such plates are more clearly present in Bashkirian linoproductoids of Tribe Tapajosiini, found in the Amazon Basin (see p. 360). A mound is developed in some *Sublinoproductus* (Lazarev 2008, pl. 6, fig. 15, 16b) but is missing in *Linispinus* (Lazarev 2006, pl. 10). In mature specimens the dorsal septum extends nearly as far as the anterior terminations of the brachial shields.

The row of strong spines along the hinge might suggest a relationship to Coopericinae Lazarev, but the distribution of body spines is close to that of *Linoproductus.* Following the evaluations of linoproductid genera by Lazarev in his studies, the genus could arguably be cast as a member of a separate tribal or subfamily unit characterized by having hinge spines much thicker than most body spines, but only one genus is known, and there are rare ventral body spines as thick as those along the outer hinge.

Linipalus Lazarev, 2007, p. 421 from Podolian and younger beds of the Moscow Basin normally has two or even three rows of spines along the hinge, and even thicker spines on the anterior trail, whereas the ventral hinge spines form one row in *Liniunus kaseti*, and the outer hinge spines are 0.1 to 0.2mm thicker than spines nearer the umbo (Grant 1976, pl. 41, fig. 17 – 1mm cf. 0.9mm and fig. 28, 1.1mm cf. 0.8 or 0.9mm). As a rule, outer hinge spines in *Liniunus* are markedly thicker than most spines of the trail. This is clearly demonstrated in fragments from the same horizon figured in Waterhouse & Piyasin (1970, pl. 22, fig. 18, 19, pl. 23, fig. 1), which belong to the same species, and show similar ribs and low umbonal walls. This feature appears to be exceptional, for in most other linoproductid genera, spines over the disc and trail tend to be as thick or thicker than outer spines of the hinge row. In *Liniunus*, only a few ventral disc spines are as thick or almost as thick as outer hinge spines. For these, as many as four costellae pass into a spine base. But usually, a spine arises from a single rib. The cardinal process is moderately like that of *Linipalus* and *Sublinoproductus* Lazarev, with low lateral lobes spaced well apart from the central shaft, a high shaft bearing a deep but circumscribed notch, closer to that of *Sublinoproductus* than that of *Linipalus* (see Lazarev 2009, Fig. 1 and illustrations in various articles), but not exactly the same, the pit being distinctive, but tending to be infilled with increasing maturity. The dorsal septum and brachial shields bear much the same interrelationship as in *Sublinoproductus. Sublinoproductus* has trail spines as strong as those along the hinge, and the present genus may prove to be an offshoot of that genus.

Productus lineatus Waagen, 1884 from the Wuchiapingian faunas of the Salt Range, Pakistan is somewhat similar in internal detail, but has usually two rows of hinge spines and larger anterior ventral spines (Waagen 1884, pl. 66, fig. 1, 2, pl. 67, fig. 3, text-fig. 21). There are fine spines over the disc and trail which help distinguish a new taxon, called *Lineatina* (see below).

Tribe **LINIPALINI** Lazarev, 2010

[Nom. transl. hic ex Linipalinae Lazarev, 2010].

Diagnosis: One or two up to three rows of spines along hinge, thickest spines over anterior disc and trail. Dorsal septum long, extending as far as end of brachial ridges, cardinal process broad with lateral lobes well spaced. Middle Carboniferous (Moscovian – Podolian) to Upper Permian (Wuchiapingian).

Genera: *Linipalus* Lazarev, *Lineatina* new genus.

Discussion: No concise diagnosis for the tribe or subfamily has been offered by Lazarev at the time of writing, but he stressed that *Linipalus* and allies were to be distinguished from *Linoproductus*, with various aspects offered throughout his text. The lack of a formal and concise diagnosis goes against procedures required by the International Code for Zoological Nomenclature to validate a family group name, but intentions were clear, at least in the abstract, so the family group name is ascribed by courtesy to S. S. Lazarev. For *Linipalus*, Lazarev stressed that anterior ventral spines were much thicker than in *Linoproductus. Linoproductus* does have anterior spines thicker than those along the hinge, but the difference in thickness between hinge and anterior spines is not as great. The degree of similarity between the two suggests a moderately close relationship.

Genus ***Lineatina*** new genus

Derivation: Named from species name, based on linea – thread, line, Lat.

Type species: *Productus lineatus* Waagen, 1884, p. 673 from upper Wargal Formation (Wuchiapingian) of Salt Range, Pakistan, here designated.

Diagnosis: Large, hinge spines normally in two rows, thick laterally, a few scattered broader spines over anterior disc and trail, with a number of finer spines that may be moderately numerous anteriorly. Commarginal rugae high postero-laterally, faint but present over disc and trail. Cardinal process broad, lateral lobes well spaced from much higher median lobe, with wide median depression; median septum extends as far forward as terminal ends of brachial shields.

Discussion: The type species is outlined below. Lazarev (2007) drew attention to its similarity to *Linipalus* Lazarev, 2007, and later implied that it may not be exactly the same genus, without specifying why. One outstanding aspect of similarity is offered by the dorsal interior, as figured by Waagen (1884, Fig. 21) in showing comparable cardinal process, septum and brachial shields (Lazarev 2008), and the other is the nature of the anterior spines, which are much thicker than those along the hinge. In detail, there are a number of differences. The spine rows in the new genus lie closer to the hinge, but otherwise vary: as noted by Waagen (1884), there is a degree of uncertainty about how reliable the detail of spine extrusion is, because of the possibility that preservation is imperfect, and partly because there may have been variation from individual to individual, and partly because spines broken or rendered redundant may have their exit sealed off (see p. 24). Waagen (1884, Fig. 21) illustrated one specimen, to show one row along the bend of the shell at the hinge margin, and the second row as lying very close and just in front, commencing a little after the first row. From observation of a number of specimens kept at the Geological Survey of India, Kolkata, and in the field, the regularity of spines may have been idealized, and some specimens indicate only one row, not always at the hinge margin. Anterior spines include much broader spines, well described by Waagen (1884) as interrupting up to four costae. But an additional and significant aspect regards the spines over the disc and trail. There are a number of finer spines, arising from a single costa, such as never found in Russian species of Carboniferous age, according to the studies by Lazarev. A few might be represented anteriorly in the holotype of *lineatus* (Waagen 1884, pl. 66, fig. 1a), and in the photograph of *Productus (Linoproductus) lineatus* var. *sirrensis* Reed (1944, pl. 11, fig. 1). They are further illustrated herein, as Fig. 16.3.

Internally, the ventral muscle scars, especially the diductors, are huge and wide, but such detail for Russian *Linipalus* does not appear to have been provided. In the dorsal valve, the median cardinal process of *Lineatina* is much higher, with a broader but shallower ventral scoop, compared with the smaller deeper pit of *Linipalus*. The presence of subdued buttress mounds in *Linipalus* is indicated for *L. tschernyschewi* (Ivanov, 1935) by Lazarev (2008, pl. 7, fig. 10, and there are broad but ill-defined mounds indicated for *L. perkhurovensis* Lazarev (2008, pl. 7, fig. 15), but none for *L. sinuosus* Lazarev (2008, pl. 7, fig. 11b). Buttress mounds appear to be small at best in two specimens of *Linipalus fredericksi* Lazarev (2007, pl. 10, fig. 10, 13), though this is not the type species for the genus. There are no buttress mounds in *Lineatina* (Waagen 1883, fig. 21, p. 673), nor in the linoproductoid of Grant (1970, pl. 2, fig. 9) from the Khisor Member above the Kufri beds in the Chhidru Formation of the Salt Range, Pakistan. The dorsal adductor scars are distinctly larger than any figured in Russian *Linipalus*.

Lineatina lineatus (Waagen, 1884)

Fig. 16.3

1884 *Productus lineatus* Waagen, p. 673, pl. 66, fig. 1, 2, pl. 67, fig. 3, text-fig. 21.
1931 *Productus (Linoproductus) lineatus* – Reed, p. 12.
1944 *Productus (Linoproductus) lineatus* – Reed, p. 54.
1944 *P. (Linoproductus) lineatus sirrensis* Reed, p. 55, pl. 11, fig. 1, 1a.

Lectotype: Specimen figured by Waagen (1884, pl. 66, fig. 1, 1a) from Kalabagh Member, upper Wargal Formation (Wuchiapingian) of Musakheyl, Salt Range, Pakistan, here designated. Holotype by monotypy for *sirrensis*, sole specimen figured by Reed (1944), from Kufri Member, lower Chhidru Formation (Wuchiapingian) at Sirra, Salt Range, Pakistan. Kept at Geological Survey of India, Kolkata.

Diagnosis: Large specimens with median ventral flattening. Fine spines variable in number from few to moderately numerous, scattered over anterior disc and trail.

Discussion: The lectotype is selected for a specimen from the upper Wargal Formation, where specimens are most common. Reed (1944, p. 54) has summarized the views on the species by various authorities. Spine detail for the anterior shell is displayed on specimens collected by me in 1964 from the upper Wargal Formation at Zaluch Nala, Salt Range, and some detail was provided for the Waagen specimens in Waterhouse (1978, p. 74).

Linoproductus lineata (Waagen) has been widely reported in China, Inner Mongolia and to less extent Japan, as summarized in a synonymy by Shi & Shen (2001, p. 248), but detail provided for the various specimens does not suffice to endorse specific and often even generic identity.

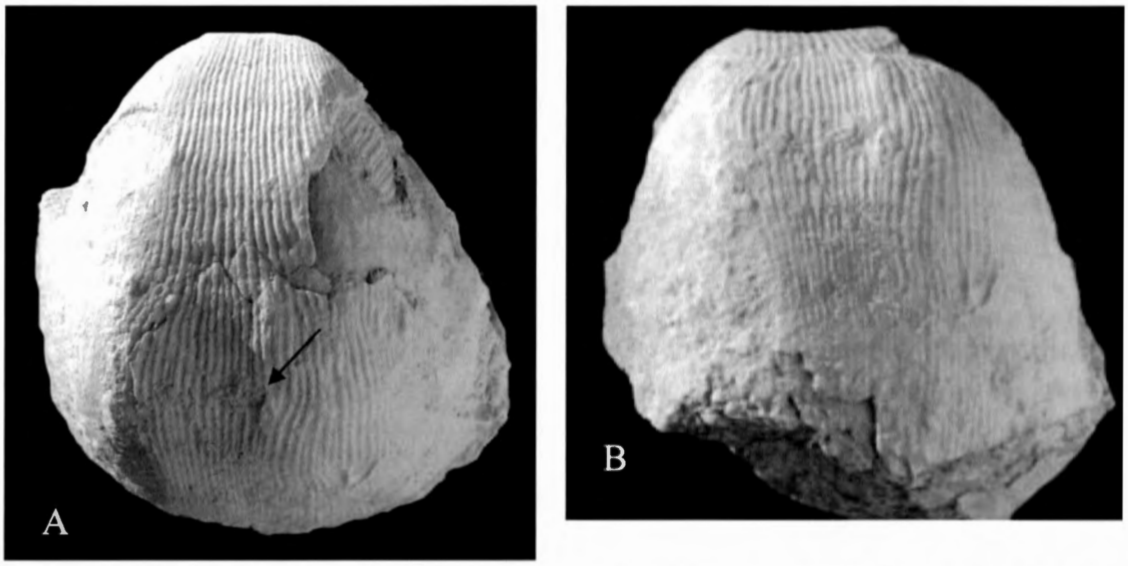


Fig. 16.3. *Lineatina lineatus* (Waagen). A, B, ventral and anterior ventral valve, showing fine spines in addition to coarse spines, the arrow pointing between an example of each kind. Lower Chhidru Formation, Kufri Member (Wuchiapingian), Chhidru Nala, Salt Range, Pakistan. BR 3063, x1.5. JBW photo.

Lineatina superba (Reed, 1944)

1884 *Productus cora* [not d'Orbigny] – Waagen, p. 677, pl. 56, fig. 3, pl. 67, fig. 1, 2.
1944 *Productus (Linoproductus) cora* var. *superba* Reed, p. 56, pl. 16, fig. 4, 4a.

Holotype: Sole specimen figured by Reed (1944) from top of Wargal or base of Chhidru Formation, near Mohra, Salt Range, by monotypy. See Waterhouse (1978, p. 75).

Diagnosis: Venter gently rounded rather than flattened to concave. Fine and very coarse spines developed over disc and trail.

Discussion: This species displays the same spine pattern of fine and coarse spines over the anterior ventral valve as in *lineatus* Waagen. The material recorded by Waterhouse (1978, pp. 74, 119, pl. 11, fig. 6-8, pl. 23, fig. 2-4) from the *Biplatyconcha grandis* Zone of the Nisal Member and *Spiriferella rajah* fauna of the Luri Member in the Senja Formation of west Nepal is now assigned to *Costatumulus crassicostata* Waterhouse, 1983c.

There is some similarity to *Linoproductus magnispina* Dunbar & Condra, 1932, p. 244, pl. 27, fig. 6-8 from the Hughes Creek Shale, Nebraska, United States, but this species is smaller, and no fine spines are known over the venter. The hinge row consists mostly of comparatively fine spines along a row, with a few out of line. Pending knowledge of the interior, the species appears close to *Linipalus* Lazarev, based on type *Linoproductus cora* var. *tschernyschewii* Ivanov (1935, p. 35, pl. 5, fig. 1, 2, 5, 7, pl. 7, fig. 8), but now restricted to pl. 5, fig. 1 as holotype, with further Kasimovian material figured by Lazarev (2008, pl. 7, fig. 6-10). In addition Lazarev included in the synonymy var. *tschernyschewi* of Ivanov (1935, pl. 6, fig. 3). But this specimen is labelled, incorrectly no doubt, as *Linoproductus lineatus* [non Waagen] in the captions by Ivanov.

Tribe **TAPAJOSIINI** new tribe

Fig. 16.4

Name genus: *Tapajosia* new genus from Itaituba Group (Bashkirian), Amazon Basin, Brazil, here designated.

Diagnosis: Dorsal valve with well developed lateral buttress plates. Otherwise like Linoproductinae, with differing rows of ventral hinge spines. Upper Carboniferous (Bashkirian).

Genera: *Tapajosia* new genus, *Amazonoproductus* Chen, Tazawa & Shi.

Discussion: This tribe is recognized for basically for two genera that in terms of shape, size, and ornament, including ribs and spines, conform with genera allocated to Subfamily Linoproductinae Stehli, 1954. Both genera have scattered and rare sturdy erect spines over the ventral valve, and *Amazonoproductus* has two rows of slender spines along the ventral hinge, whereas *Tapajosia* has a row of thicker spines along the hinge, close in diameter to those over the remainder of the valve. Internally, the dorsal valve of both genera has well developed lateral buttress plates. Whilst the difference in hinge spinosity might suggest different tribal allegiances for each of the two genera, the unusual dorsal interior indicates this was of secondary consideration, and the two genera developed together in the Itaituba Formation of Brazil. As an alternative, two different linoproductin lineages independently converged in the nature of the dorsal interior, but this is judged unlikely. Throughout the outlines of linoproductin genera and tribes provided in this study, attention is drawn to the development or absence of buttress mounds, changes throughout ontogenetic development and even the incipient development of lateral buttress plates, but none of the genera show such well developed plates as the two genera in this tribe. The dorsal interior of type *Linoproductus, L. cora* (d'Orbigny), shows moderately developed buttress mounds in front of the cardinal process, with three ridges leading forward from the anterior margin in Samtleben (1971, pl. 7, fig. 4), and two on one side, one on the other in a detailed figure provided by Kozlowski (1914, fig. 8a1, p. 14). *Sublinoproductus barchatovae* Lazarev (2010, pl. 4, fig. 4) of Artinskian age from the Sula River, Russia, shows somewhat comparable but simpler broad buttress mounds, as does *S. pentagonalis* Lazarev (2010, pl. 3, fig. 9, 10b) from the same general area, and also of Artinskian age. The upper Carboniferous Kasimovian species *coralineatus* Ivanov, 1935, the type species of the genus *Sublinoproductus* Lazarev (2008, pl. 6, fig. 15, 16b), has a very broad posterior dorsal septum, but less developed buttress mounds, whereas a dorsal interior figured as *S. ivanovi* Lazarev (2008, pl. 7, fig. 3) from Kasimovian faunas shows a long buttress mound. The type species of *Linoproductoides, L. aljutovensis* Lazarev (2006, pl. 9, fig. 6, 8) from the Vereian Substage has a deep pit on the internal face of the cardinal process, with small if any buttress mounds. Buttress mounds are seldom developed in Linispininae, to judge from material figured by Lazarev, nor, it would appear, in Schrenkiellidae. The recognition of a tribe based on this morphology, amounts to a shift from emphasis on spine detail, for classification needs to be flexible in order to cope with ever shifting and non-linear alliances and deviations in the course of evolution.

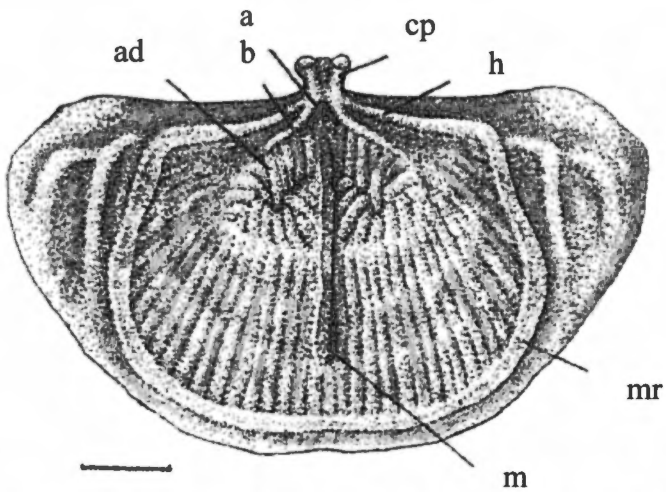


Fig. 16.4. *Amazonoproductus amazonensis* Chen, Tazawa & Shi, dorsal interior NU-B553 from lower Itaituba Formation (Bashkirian), Amazon Basin, Brazil, slightly altered from Chen et al. (2004, Fig. 6). Scale bar 15mm. a = alveolus, ad = adductor scar, b = lateral buttress ridge, cp = cardinal process, h = lateral or hinge ridge, m = median septum, mr = marginal ridge,.

The distinctive interior is close to that found in two other genera with linoproductoid ornament, *Marginirugus* Sutton and *Balakhonia* Sarytcheva, but these are not fully comparable in all aspects, as discussed below, so it is deemed likely that Tapajosiini evolved independently from Linoproductini, as a closely allied tribe sharing common ancestry, given that the overall shape and spination is so close to these genera. Members of Tapajosiini are known only from the Parana Basin in Brazil, where glacial sediment is known extensively (Holz et al. 2008), yet the faunas show little resemblance to those of Greater Gondwana over Australia and south Asia, and limited similarity to marine faunas of Argentina.

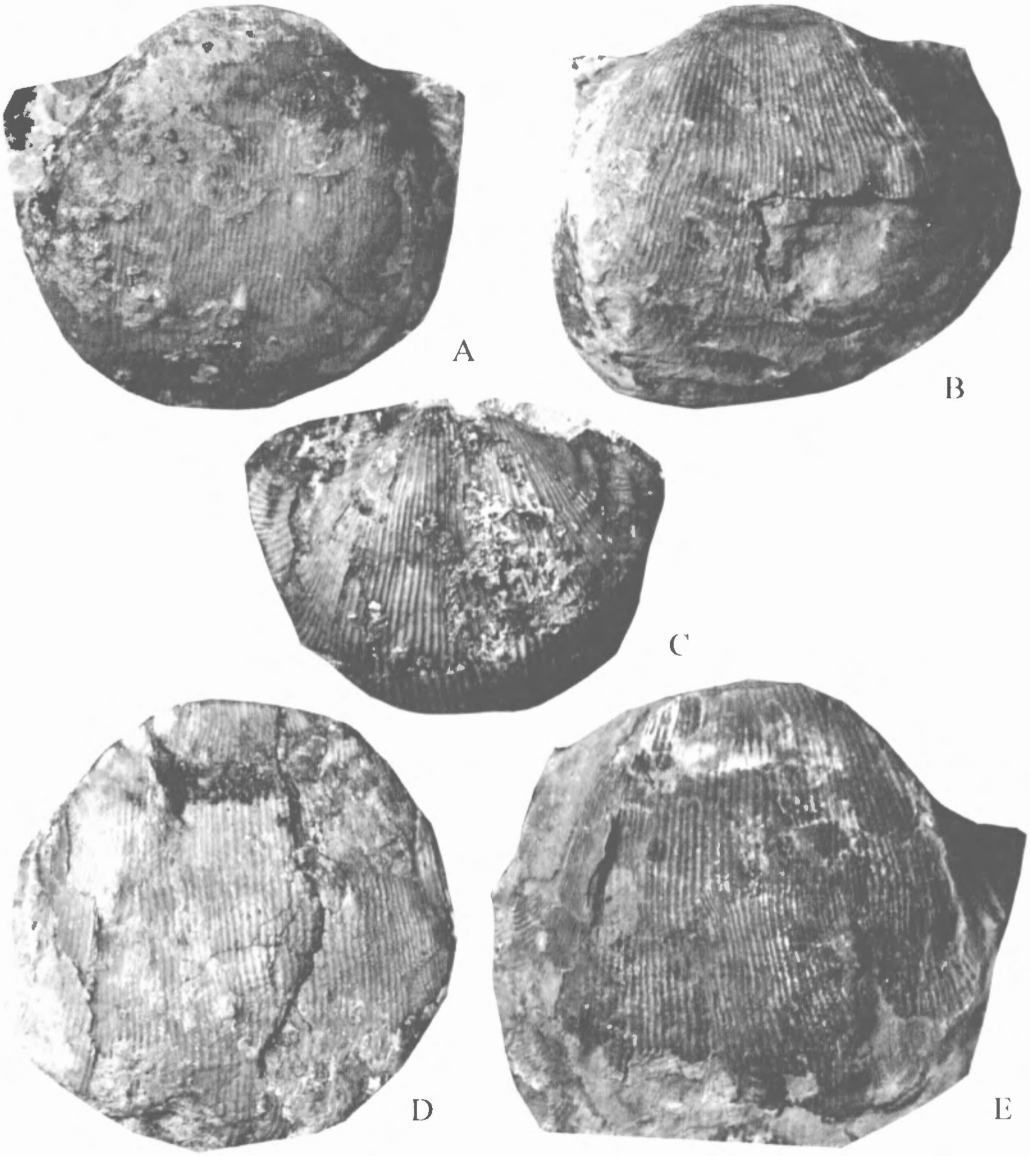


Fig. 16.5. *Tapajosia caima* (Chen, Tazawa & Shi), ventral valves from lower Itaituba Formation (Morrowan, Bashkirian) of Amazon Basin, Brazil. A, NU-B565-4. B, NU-B565-4.5. C, NU-B565-4.3. D, NU-B565-4.6. E, NU-B565-4.2. Photographs supplied by Chen Zhong-Qiang, x0.9.

Genus ***Tapajosia*** new genus

Fig. 16.5

Derivation: Named from the Tapajos River which flows through the Itaituba Formation.

Type species: *Linoproductus caima* Chen, Tazawa & Shi in Chen et al. 2004, p. 453 from the lower Itaituba Formation (Bashkirian), Amazon Basin, Brazil, here designated.

Diagnosis: Large with distinctive radial ribs, minor wrinkles, moderately stout spines in single row along ventral hinge, thick spines scattered over ventral valve, dorsal interior with well defined lateral buttress plates.

Discussion: *Linoproductus caima* Chen, Tazawa & Shi was well described from collections made by J. Tazawa, and the types are housed in the Department of Geology, Faculty of Science, Niigata University, Japan. Correlations for the lower Itaituba Formation are discussed in the same article, by Chen, Tazawa, Shi & Matsuda (2004). The species *caima* is distinguished from an allied species *Tapajosia derbyi* (Mendes, 1959, p. 54) in the same fauna, by its greater size, more regular ribbing with wider interspaces, and dorsal interior that lacks a deep alveolus, and a longer dorsal septum, with other differences. Both species are similar in their ventral spines, and differ in that regard from *Amazonoproductus* Chen, Tazawa & Shi, 2004, p. 449, which has two rows of fine spines along the hinge. Internally, the dorsal valve of *Amazonoproductus* shares lateral buttress plates, but also has well developed hinge ridges and high marginal ridge completely encircling the visceral disc.

The descriptions of *Linoproductus derbyi* and *L. caima* were made to fall under the heading of Tribe Marginovatiini Chen, Tazawa & Shi, but this was surely an inadvertent error, because Tribe Linoproductini has long priority, and the authors distinguished Marginovatiini from Linoproductini "by the presence of marginal ridges in both valves or the dorsal valve only". *Marginovatia* does have a high dorsal marginal ridge as in *Amazonoproductus,* but the dorsal valve of *Linoproductus* itself also can develop a marginal ridge, though not as high. Lateral buttress plates are developed only in *Amazonoproductus* and *Tapajosia*, and are missing from *Marginovatia*, and from the numerous dorsal interiors known for *Linoproductus* and allies.

Subfamily LINISPININAE Lazarev, 2006

[Linispininae Lazarev, 2006, p. 523].

Diagnosis: Ears of ventral valve bear three or more rows of spines or sometimes clusters of spines in poorly to clearly discernible rows. Lower Carboniferous (Visean) to Upper Permian (Changhsingian).

Genera: *Linispinus* Lazarev, *Aurilinoproductus* Shen, Shi & Archbold, *Levisapicus* Tong, *Lineacrassus* new genus, *Lineaproductus* new genus, *Linispinella* Lazarev.

Discussion: Lazarev (2006, 2007, 2009, 2010) expanded the scope of his analyses on linoproductid genera and included not only data on thickness of disc and distribution of spines and relationship to ribbing, but significant aspects of spine diameter distribution and cardinal process. Body spines in Linispininae are not substantially thicker than hinge spines, and are allowed some variation, from approximately similar diameter, to slightly thicker or thinner. The cardinal process is more erect than in Linoproductinae where well known, and there appears to be no posterior mound on the floor in front of the cardinal process. In *Linispinus longus* Lazarev (2006, pl. 10, fig. 11, 16) of Moscovian age (Kashirian Substage), there is a prominent alveolus and no buttress mounds, and in Lazarev (2006, pl. 10, fig. 14, 15), there appears to be a somewhat obscure swelling in front of the base of the cardinal process. *L. staricensis* (Ivanov, 1935) of similar age has no prominent buttress plates and also may not have an alveolus.

Genus ***Lineaproductus*** new genus

Derivation: linea – to make straight, Lat; productus - brachiopod name.

Type species: *Productus corrugatus* M'Coy, 1844, p. 107, from Lower Carboniferous (Visean) of Ireland, here designated.

Diagnosis: Large shells with double or rarely triple or even four rows of spines along the hinge, no large spines over the visceral disc, and moderately strong commarginal rugae over both valves.

Discussion: Externally, this genus is close to *Linoproductus* Chao, 1927, based on *Productus cora* d'Orbigny, 1842 from the Copacabana Group (Asselian) at Cochacabamba, Bolivia, in its shape and large size, and presence of strong regular radial ribs. One difference is the stronger development of lateral commarginal rugae in the new form, but the most marked difference from Linoproductinae lies in the absence of large erect spines over the visceral disc and trail, sometimes surrounded by an aureole of smooth shell, which help typify *Linoproductus* (see Muir-Wood & Cooper 1960, pl. 111, fig. 6). In the new taxon, spines over the ventral disc and trail are absent or few and fine, and along the hinge they are numerous, in two to rarely four rows, and fine. A large skirt is preserved in some specimens of *corrugatus*, and such is not normally observed in *Linoproductus.*

The species *corrugatus* has hinge spines approaching those of *Linoprotonia* Ferguson, and M'Coy (1844) compared the species with *hemisphaericus*, now the type species of *Linoprotonia*. In collections kept at the Natural History Museum, London, samples of *corrugatus* are often labelled as belonging to genus *Linoprotonia*. Ferguson (1971) commented that *Linoprotonia* was externally linoproductid and internally gigantoproductid. Spines are moderately close, but more numerous posteriorly and laterally, and *corrugatus* is distinguished by the elongate shape, steeper umbonal slopes, thick corpus, presence of more wrinkles, flaring trail, and lack of brachial cones. The overall shape of *Lineaproductus* is linoproductin, with maximum width usually in front of the hinge, and approaching the shape of two genera, *Globosoproductus* Litvinovich & Vorontsova, 1983 and *Xinjiangiproductus* Yao & Fu, 1987, though spine detail differs. That is interpreted as signifying a degree of commonality. Some detail for the genera remains uncertain, hindering closer comparison, but neither genus is so inflated and incurved as *corrugatus* (see below).

The cardinal process would seem unlikely to have the lateral lobes fused dorsally as in Ovatiidae, given the size of the species. But the cardinal process is not known to me, and until this can be determined, allocation to Linispininae may be deemed provisional.

The following notes are prepared from examination of collections in the Museum of Natural History, Ireland, in Dublin, and the Natural History Museum, London, and Sedgwick Museum, Cambridge, England. The registration and identification largely follows the attached labels, but greater and more extensive analysis is required to narrow down the specific limits, and the principal focus is on the detail of spines and costation.

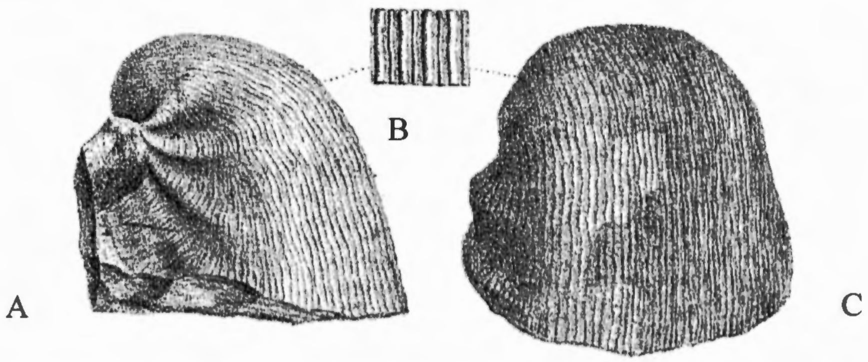


Fig. 16.6. *Lineaproductus corrugatus* (M"Coy). Original figures provided by M'Coy (1844, pl. 20, fig. 13), reduced as in his study from width of 80mm. A, C, lateral and anterior ventral aspects, and B, detail of ornament. From Lower Carboniferous of Ireland.

Lineaproductus corrugatus (M'Coy, 1844)

Fig. 16.6 - Fig. 16.8

1843 *Productus comoides* [not Sowerby] – Koninck, p. 172, pl. 11, fig. 2, a, b, fig. 5, a, b.
1844 *Producta corrugata* M'Coy, p. 107, pl. 20, fig. 13.
1846 *Productus cora* [not d'Orbigny] – Koninck, p. 148, pl. 4, fig. 4, a, b, pl. 5, fig. 2, a-d.
1847 *P. cora* – Koninck, p. 50, pl. 4, fig. 4, a, b, pl. 5, fig. 2, a-d.
1855 *P. corrugatus* – M'Coy, p. 459.
1861 *P. cora* – Davidson, p. 148, pl. 36, fig. 4, pl. 42, fig. 9.
See Paeckelmann (1931, pp. 210-211) for further early bibliography.

Holotype: F5804, Museum of Natural History, Ireland, in Dublin, from Salman, Man of War, Balbriggan, Co., figured by M'Coy (1844, pl. 26, fig. 13).

Diagnosis: Large with moderately well formed ventral hinge rows of fine spines, fine erect spines scattered over ventral disc and trail. Commarginal rugae cross dorsal disc, strong laterally on ventral valve, trail long and may flare as a skirt.

Description: The species has been widely reported from Visean faunas across northern Europe, including Ireland, Scotland, England, Wales, Germany and Belgium. The holotype F 5804 (Fig. 16.6) is about 80mm wide, and disc wrinkles may branch, and erect ventral spines are visible anteriorly. Amongst collections chiefly from outcrops in England and kept at the Natural History Museum, London, the specimen figured by Davidson (1861, pl. 36, fig. 4a, b, pl. 42, fig. 9), B 13886 from Settle, Yorkshire, measures 55.6mm wide, 55mm long and 31mm high. Wrinkles are strong and mostly lateral on the ventral valve but cross the posterior disc and lie weakly over the anterior shell, and are more close-set over the dorsal valve. Three rows of erect spines (rather than two as figured) lie along the ventral hinge, and possible fine spines arise from the crest of the costae, usually with no disruption, but occasionally, two ribs extend forward from the spine base, although certainty is hindered by the defoliated surface. Spine bases are not conspicuous and not elongate. B 53831-2 mentioned as *corrugatus* by Vaughan (1905, p. 239) from Wichwar near Bristol are more gigantoproductiform. There can be some deviation of costae, as in a specimen B 22712 from Visé, Belgium. The trails of B 55768 and B 23700 from the upper Grey Limestone at Axton and B 48591 from D2 Gratton Hill, Narrowdale, Staffordshire, may flare peripherally. The Axton specimen is 58mm wide, 64mm long and 30mm high, and the Gratton specimen is 80+mm wide, 75+mm long and 57mm high. From the Koninck collection of Visé, Belgium, B 64706 identified as *corrugata* shows the dorsal interior, with slender dorsal septum, short hinge ridge and dendritic adductors.

Fergusson (1971) regarded *corrugatus* as belonging to *Linoprotonia*. In commenting on the Davidson material (D1 – Visean), he stated *ashfellensis* Ferguson was tightly coiled and *corrugata* least tightly coiled. Body spines in being scattered and fine are closer to those of gigantoproductids rather than *Linoproductus*, but *corrugatus* has coarser wrinkles than usual for Gigantoproductinae, and is elongate. B 13883 from Co. Kildare, Ireland, measures 50mm wide, 41mm long and 30mm high. B 53807 from D2 Thorpe Cloud, Derbyshire, has fine close-set dorsal wrinkles over a gently concave disc, and the trail is geniculate, and visceral cavity 7.5mm high in the shell almost 50mm long.

At the Sedgwick Museum, Cambridge, specimen E 9605, labelled *Productus cora* from the Carboniferous Limestone at Settle, Yorkshire, has many ear spines in three or four rows, low regular rugae, fine differentiated ribs, and no clearly defined adductor scars. Preservation is such that no clearly defined spines lie over the disc and trail, but rare knobs are present. There is a large skirt with ribs and low commarginal rugae as over the disc around the lateral and anterior margin. By contrast, E 9488, identified as *Linoproductus cora* (d'Orb.) from Ronaldsway, Isle of Man, by M'Coy (1855, p. 463) has anterior *Linoproductus*-like large spine bases, with costae converging anteriorly into the spine. It appears close to *Linoproductus* Chao, but full detail is not available.

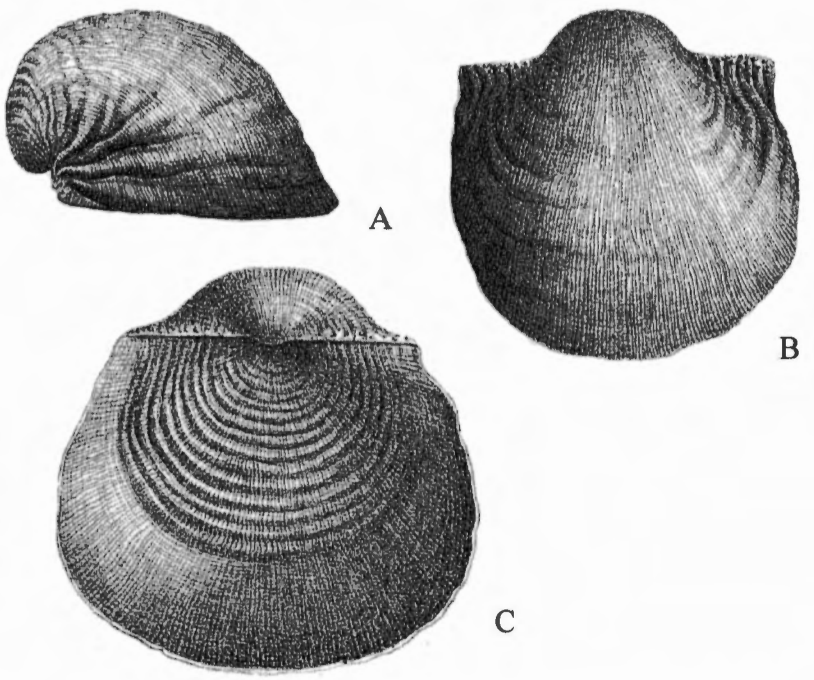


Fig. 16.7. *Lineaproductus corrugatus* (M'Coy). A, B, ventral and dorsal aspects of specimen B 13886 figured by Davidson (1861, pl. 36, fig. 4, pl. 42, fig. 9), figures reduced to x0.7 approx., originally 55mm wide, from Settle, Yorkshire. C, dorsal aspect of specimen, x0.8 approx. from ?Derbyshire. From Lower Carboniferous of England.

Liu Fa (1987, p. 125, pl. 1, fig. 30, pl. 2, fig. 1-8) recorded *Linoproductus* cf. *corrugatus* from mid-Carboniferous Benxi Formation of Liaoning Province, northeast China, but his specimens are smaller and more elongate and inflated, with hinge spine detail obscure. The upper Serpukhovian specimen from the Donetz Basin, Ukraine, figured as *corrugatus* by Aisenverg (1983, pl. 42, fig. 5a, b) is much closer. Reed (1943) noted reference to *corrugatus* in Delépine (1928, p. 26, pl. 4, fig. 45, 46, pl. 6, fig. 67-69) and Paeckelmann (1931, p. 210, pl. 19, fig. 1, 2). Paeckelmann judged that M'Coy's species was closely allied to *Productus ovatus* Hall (1858, p. 674, pl. 24, fig. 1), Weller (1914, p. 132, pl. 16, fig. 1-15) and Sutton (1938, p. 558, pl. 65, fig. 8-13) from the lower Mississippian Chester Group of Illinois, Missouri and Iowa etc. of United States. These specimens are similar in their commarginal rugae, and scarcely visible ventral body spines and long trail. Ventral hinge spines are not clearly illustrated in Weller or

Sutton, and body spines seem slightly more conspicuous. *Linispinus crassus* Lazarev, 2008 of Kasimovian age in Russia has two well formed rows of ventral spines close to the hinge and traces of a third row, with low buttress mounds (pl. 6, fig. 13) or none, and possible alveolus (pl. 6, fig. 4).

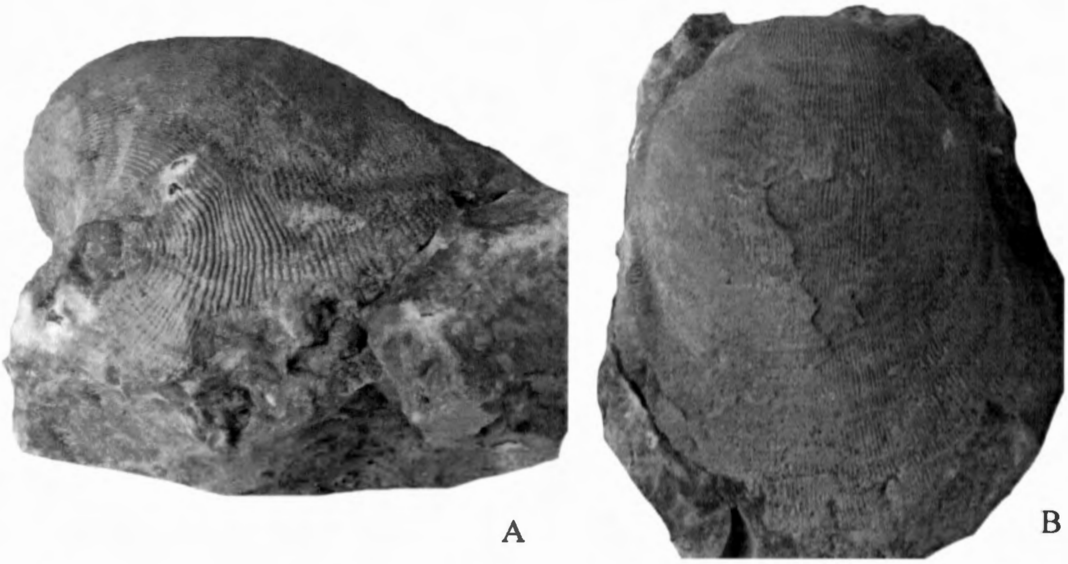


Fig. 16.8. *Lineaproductus corrugatus* (M'Coy). A, B, lateral and ventral aspects of E 9605 x1.3 from Carboniferous Limestone of Settle, Yorkshire, England. Photographs supplied by Matt Riley, Sedgwick Museum, Cambridge, England, x1.

Genus ***Lineacrassus*** new genus

Derivation: linea – thread, line; crassus – stout, Lat.

Type species: *Lineacrassus inflatus* new species from Member B (Asselian), Jungle Creek Formation, Yukon Territory, Canada, here designated.

Diagnosis: Large swollen shells with well developed costellae: spines of modest thickness in row along hinge, row of thin spines between or in front near the umbo, become as strong laterally, outer ears with additional spines. Body spines over single costae, usually slender but include thicker spines. Cardinal process largely in plane of posterior dorsal valve, median septum short.

Discussion: This genus is large and inflated, close to *Linoproductus*, but with few moderately thick spines over the ventral disc and trail, that intersect two to often four costae. The ears of *Linoproductus* lack any extra spines, and the type species is less elongate. Internally, the cardinal process of *Linoproductus* is bent ventrally and a well developed alveolus is developed, whereas the ventral face of the cardinal process in the new genus leans only a little dorsally from the plane of the dorsal interior, and a median notch is shallow. The dorsal median septum is shorter in *Lineacrassus*, and does not extend as far forward as the inner terminus of each brachial shield. Both *Linoproductoides* Lazarev, 2006 and *Sublinoproductus* Lazarev, 2008 have more strong spines over the ventral disc and trail, close in thickness to strongest spines along the hinge, whereas such spines are rare in the new genus, but present. *Linoproductoides* has usually two rows of hinge spines, and the median lobe of the cardinal process is little higher than the lateral lobes, and a deep alveolus is developed. The type species is of Moscovian age in Russia. *Sublinoproductus* from the late Carboniferous and early Permian of Russia has two cardinal rows of spines, the outer lobes of the cardinal process rather than the whole process inclined ventrally, and long median septum extending beyond the distal end of the brachial shields. *Liniunus* new genus has a single row of spines along the hinge, thick and thin spines over the visceral disc, and the cardinal process is bent ventrally, and the median septum long.

Linispinus Lazarev has a number of ventral hinge spines in two, three or more rows, and body spines are close in diameter to those of the outer hinge – there are no finer body spines. The cardinal process is moderately close, and buttress mounds are poorly developed or absent as a rule. There are many small points of difference between the two genera. *Linispinella* Lazarev, 2006 from Bashkirian faunas of the southern Urals has many fine spines, 0.6mm in diameter over the ears, and larger body spines, up to 1mm in diameter. *Lineaproductus* new genus has more rows of finer spines arranged along the ventral hinge, and body spines are similarly fine, without the additional coarser spines displayed by *Lineacrassus*.

Levisapicus Tong, (1990, p. 66, pl. 11, fig. 1a-e, Fig. 10), type species *giganteus* Tong from Yanbian, Sichuan, China, considered to be very Late Carboniferous, is close in many respects, although with more concave dorsal valve and stronger postero-lateral wrinkles, and possibly more splitting of ribs into '"sheaves". Ribbing is said to be missing posteriorly, a ventral interarea or ginglymus is well developed, and a dorsal hinge ridge is not developed, all constituting differences from the new genus. The cardinal process is more massive, and ear spines are more numerous, crowded and finer, and ears are finely rugose.

Lineacrassus inflatus new species

Fig. 16.9, Fig. 16.10

Derivation: inflatus – pompous, puffed up, Lat.

Holotype: GSC 133323, figured as Fig. 16.10A, C, F, G herein from Member B (Asselian), Jungle Creek Formation, Yukon Territory, Canada, here designated.

Diagnosis: Very large, a little variable in shape, typically with incurved ventral umbo and swollen venter, rarely somewhat less convex medianly, costellae fine, spines few and inconspicuous.

Material: Sixteen ventral valves, one dorsal valve and four specimens with valves conjoined from Member B, Jungle Creek Formation, Canada. See Appendix A, part C, p. 478.

Dimensions in mm:

Specimen GSC	Width	Length	Height	
133323	71.5	102	48	holotype
133325	72	66+	39	
133324	73	90est.	41	

Description: Shells large and elongate, ventral valve swollen with broad umbo, umbonal angle 100°, convex umbonal walls, and hinge either at maximum width or almost at maximum width; large gently convex ears, weakly set off from the umbonal walls, and bearing alate cardinal extremities with angle of 70°. The disc is high and vaulted, convex in most shells or with gentler convexity medianly and the trail extended, one specimen measuring 97mm long, 70mm wide and 58mm high. There is no sulcus or fold, but anteriorly the margin may be recessed, and in others extended as a tongue. The dorsal valve is gently concave with large concave ears, and the disc very thick, with a small gently convex nepionic portion, and anterior shell curving gently into an extended trail. Both valves are covered by fine ribs, twelve in 10mm posteriorly and ten in 10mm anteriorly, but the number varies slightly: crests are rounded and interspaces of similar width. Over the anterior trail the ribs may become erratic in course. Costal increase appears to be by intercalation of the ventral valve and by branching on the dorsal valve. A row of closely spaced spines about 0.5mm up to 1mm in diameter as a rule emerge postero-laterally from the ventral hinge, and the slightly swollen bases may measure 1.5 even up to 2.5mm across, without the spines themselves becoming very sturdy at the cardinal extremity. A second row of spines is visible in several specimens, only half the diameter or less, and gradually diverging, at 2mm from the hinge row at a distance of 25mm or more from the beak, where the spines are as thick or thicker than those of the hinge row. Two further and shorter rows lie on the anterior ear, the third row becoming sturdy, up to 1.5mm wide, and the fourth row nearest the umbonal slope comparable in thickness as far as can be seen. Other spines over the visceral disc and trail are rare, slender and erect, emerging from the crests of costellae without perturbation over the disc, and less than 1mm across. Very rare spines up to 1.5mm wide lie on the trail of very few specimens, where they lie athwart three ribs, which resume unaltered in front. The dorsal valve has no spines. Rugae may be limited to the ventral ears or faintly suggested on the trail of the ventral valve: other specimens have few or no rugae. Rugae tend to be somewhat stronger over the dorsal disc of at least some specimens.

Ventral adductor scars large and dendritic, diductor scars large and bearing longitudinal grooves. Cardinal process broad and trilobate, the ventral face lying in the plane of the posterior dorsal valve, with shallow median groove on the ventral face of the shaft and shallow posterior notch. It is supported by hinge ridges curving each side from anterior base, placed behind a very low and broad platform, without raised buttress mounds. Median septum may be slender or broad posteriorly, extending for almost half of the length of the disc. Adductor scars large and dendritic, but subdivision not clear: only part of the brachial loops is visible, and the inner termini lies in front of the end of the cardinal process. The posterior floor is smooth, and the shell thin, only 1mm thick.

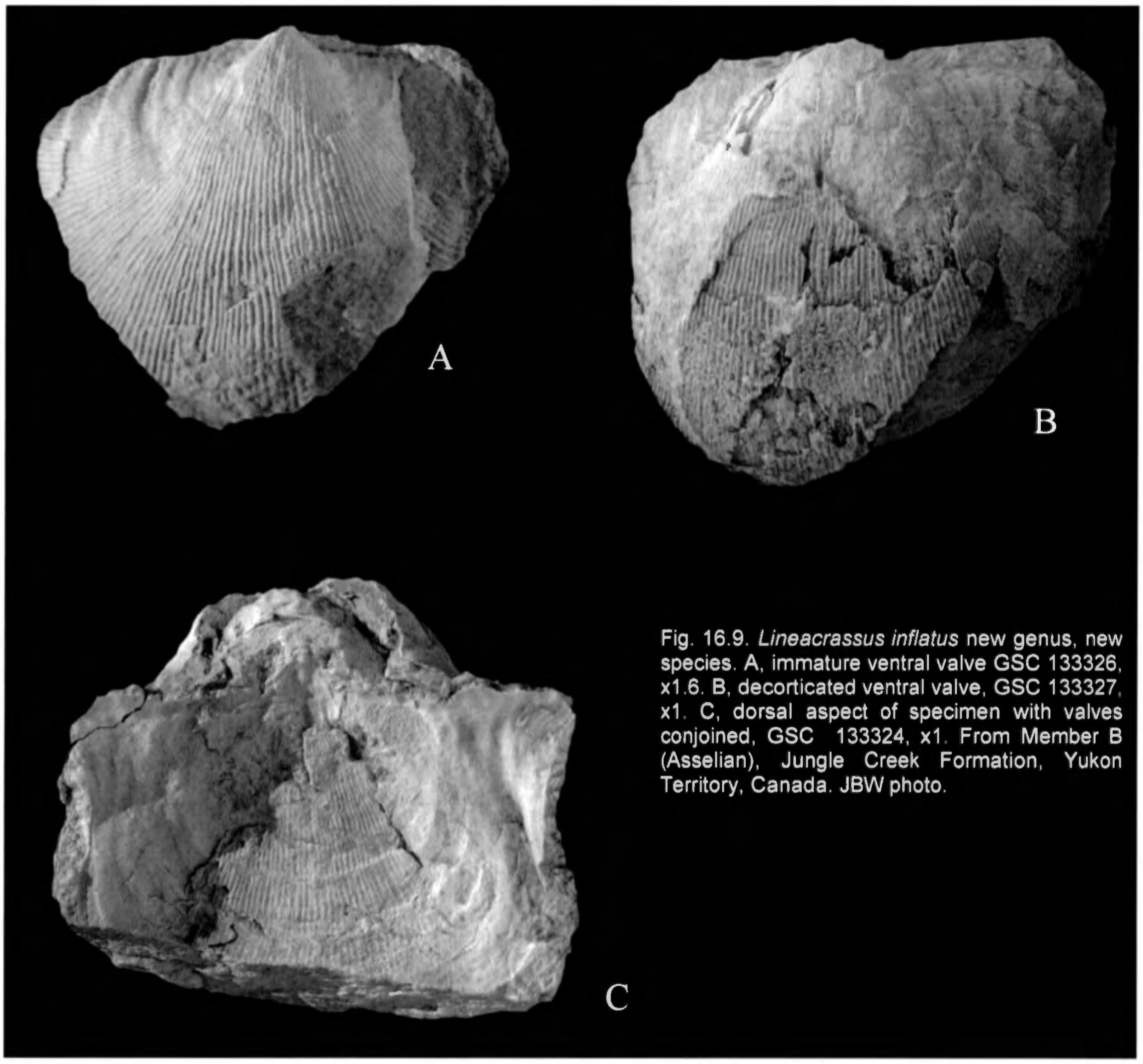


Fig. 16.9. *Lineacrassus inflatus* new genus, new species. A, immature ventral valve GSC 133326, x1.6. B, decorticated ventral valve, GSC 133327, x1. C, dorsal aspect of specimen with valves conjoined, GSC 133324, x1. From Member B (Asselian), Jungle Creek Formation, Yukon Territory, Canada. JBW photo.

Resemblances: This species is characterized by its large size, with highly vaulted ventral valve and large ears. The Canadian material is especially close in shape and size to the cited lectotype of the Russian species commonly called *Linoproductus dorotheevi* Fredericks, but differs over the number and distribution of ear spines, as far as can be ascertained. A number of the original suite of specimens figured by Tschernyschew (1902) include broader specimens with more gently convex median venter, and one specimen has a shallow ventral sulcus. The costellae appear to number ten to fifteen in 10mm anteriorly on the ventral valve of Tschernyschew's material, a degree of variation which renders it difficult to circumscribe the Tschernyschew species, but costae are usually close to twelve in 10mm, slighter finer than in the present suite. Material figured by Gobbett (1964, pl. 10, fig. 8, 9, pl. 11, fig. 1-5) from the Upper Wordiekammen Limestone of Bunsow Land, Spitsbergen, indicates moderately thick spines in the hinge spine row, and what seem to be comparable spines over the disc, but no additional spines over the ventral ears, at least in pl. 11, fig. 2. The material described as *Linoproductus dorotheevi* (Fredericks) from the *Muirwoodia transversa* and *Jakutoproductus verchoyanicus* Zones of the overlying Jungle Creek Formation in the Ogilvie Mountains in the Yukon Territory of Canada by Shi & Waterhouse (1996, pl. 15, fig. 25-28, pl. 16, fig. 1-9, 11; text-fig. 31) includes smaller specimens, none of which display the fully arched median venter, and the sole specimen figured by Cooper (1957, pl. 6D, fig. 27-29) as *L.* cf. *lutkewischi* (Stepanov) from Coyotte Butte Formation of Oregon has a broad gently convex venter, and slightly stronger ribbing. By contrast, the material from Spitsbergen (Wiman 1914, Gobbett 1964, Czarniecki 1969) resembles the lectotype of *dorotheevi.* It tends to be flatter medianly over the ventral

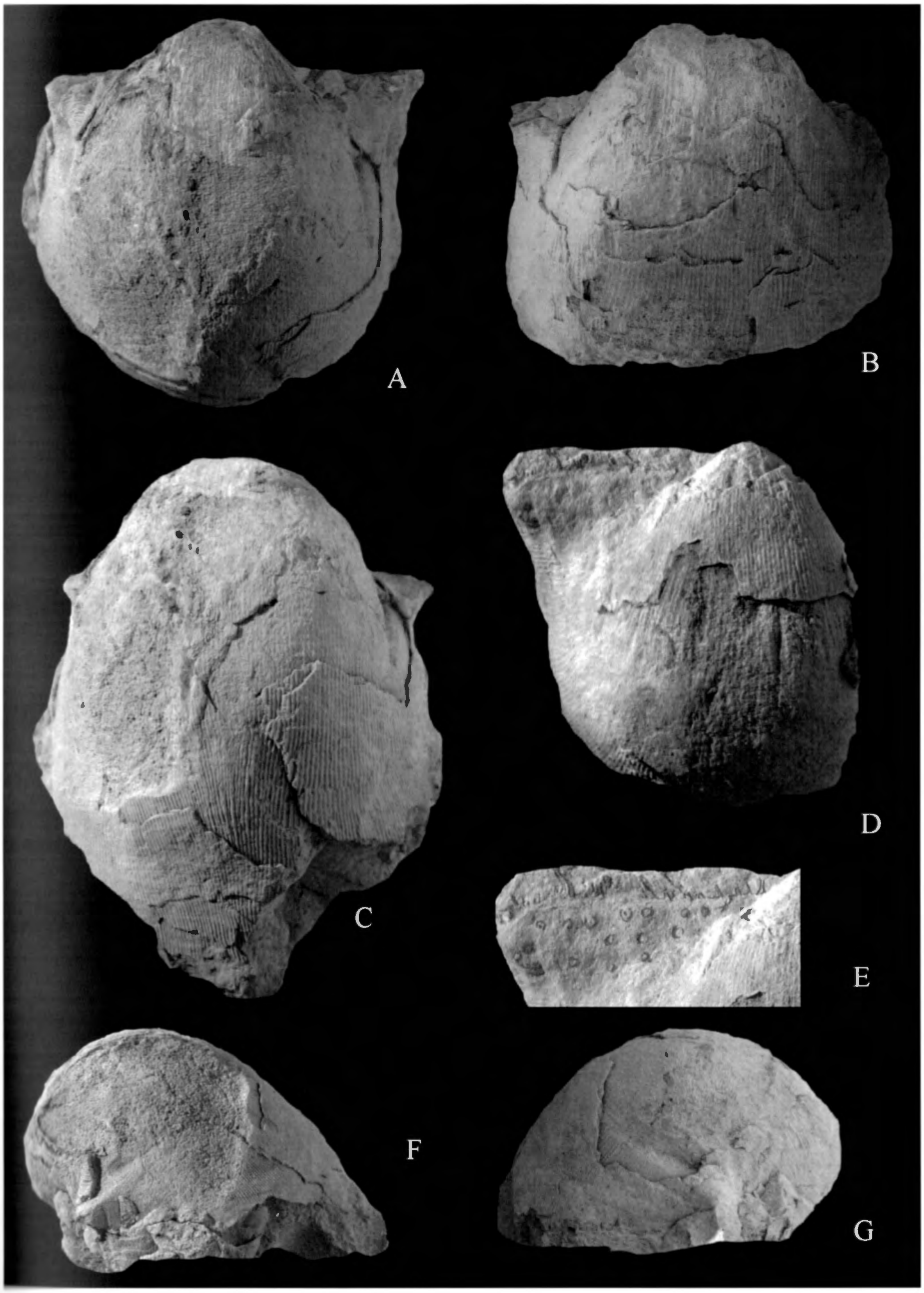


Fig. 16.10. *Lineacrassus inflatus* new species. A, C, F, G, ventral valve holotype, GSC 133323, ventral posterior, x0.8, ventral, x0.7, and two lateral views, x0.6. B, ventral view of GSC 133324, x0.9. (See Fig. 16.9C). D, E, ventral valve and retouched ear detail of spine position, GSC 133325, x1, x1.5. From Member B (Asselian), Jungle Creek Formation, Yukon Territory, Canada. JBW photo.

valve, and have more conspicuous coarse disc spines, although some very fine spines are also visible (Shi & Waterhouse 1996, pl. 16, fig. 1, 3), and no additional spines lie on the ventral ears. Some caution is required concerning aspects of the material. Shi & Waterhouse (1996) recorded ventral hinge spines as reaching 0.5mm in diameter, but figured none, and did not make it clear how far from the umbo such fine spines were sited. They also stated that coarser spines were developed over the ventral valve, but such are shown in only one heavily damaged, and therefore challengeable specimen (pl. 15, fig. 25). Their identification with *dorotheevi* must be deemed open to question, but when they published the description, little detail was available to them over Russian *Linoproductus*, for Lazarev had not commenced his revision of Russian linoproductoids, and they had to rely largely on similarities of shape. Major clarification of the ornament on *dorotheevi* was provided by Lazarev (2008) from material and a previously unavailable manuscript of B. K. Licharew, to show two thick spines 1.3mm to 1.5mm in diameter along the hinge, and spines as thick on the trail: whether the spines were arranged along the hinge in one or two rows was not made clear. The generic position for *dorotheevi* was left unresolved.

Linoproductus semisulcatus Cooper & Grant (1975, p. 1148, pl. 431, fig. 7-12) from the Neal Ranch and Lenox Hills Formations of Early Permian age in west Texas is judged to be congeneric. This species has a staggered double row of ventral hinge spines, and scattered rare moderately strong and also thinner spines over the disc and trail, and the dorsal trial is long. Cooper & Grant (1975) described a tuft of fine spines on the posterior margin and ears, and a sulcus that is confined to the median part of the ventral valve. The United States species is smaller and slightly less arched than the Canadian form, with stronger posterior lateral wrinkles.

Genus ***Levisapicus*** Tong, 1990

Levisapicus Tong, in Tong et al. 1990, pp. 66, 100, type species *L. giganteus* Tong (1990, pl. 11, fig. 1a-e, Fig. 10) from the Zhigou Formation (Asselian or Sakmarian) of Szechuan, China, has a group of spines on the ears, unlike *Linoproductus*, yet was synonymized with *Linoproductus* by Brunton et al. (2000, p. 527). The type species *Levisapicus giganteus* Tong is close to *Linispinus*, but the ear spines are particularly numerous, and are comparatively close in diameter to those over the visceral disc and trail, though spines overall are possibly slightly narrower relative to shell size, compared with *Linispinus*. No comparison with *Levisapicus* was offered in the various linoproductid studies by Lazarev (2006 etc.). Further detail is provided on p. 367.

Genus ***Aurilinoproductus*** Shen, Shi & Archbold, 2003

Aurilinoproductus Shen, Shi & Archbold (2003, p. 79) from Changhsingian faunas of south Tibet was distinguished primarily by its large and laterally extended ears. The ventral ears carry three rows of sturdy erect spines, with further anterior ear spines (Shen, Shi & Archbold (2003, pl. 10, fig. 5), indicating placement within Linispininae Lazarev. The spines are approximately as coarse as body spines (pl. 10, fig. 1, 5, 10), and any difference in diameter appears to be less than 0.2mm. *Aurilinoproductus* was ignored in the studies on Linoproductidae by Lazarev (2006 etc.).

It would seem that the authors included two genera in their figures: those of pl. 10, fig. 7, 14 have finer ribs, low subregular wrinkles, and fine spines with elongate bases, in contrast to specimens illustrated especially by Shen et al. (2003, pl. 10, fig. 1-3, 10, 11, 13). The fine-ribbed specimens (Shen et al. 2003, pl. 10, fig. 7, 14) might be the same as specimens described as *Costatumulus polliciformis* (Waterhouse, 1978) by Shen, Shi & Archbold (2003, p. 80, pl. 10, fig. 15-22), a species reassessed as belonging to *Coolkilella* Archbold by Waterhouse & Chen (2007, p. 22).

Subfamily **COOPERICINAE** Lazarev, 2004

[Coopericinae Lazarev, 2004, p. 160].

Diagnosis: Moderate to large-sized well inflated shells bearing ventral hinge spines of moderate strength in single row, ventral body spines rare or absent. Lower Permian (Asselian) to Middle Permian (Capitanian).

Genera: *Coopericus* Lazarev, *Auriculatea* Waterhouse, *Grantevia* new genus.

Discussion: This is a minor group, with a spine pattern close to that of Schrenkiellidae Lazarev, and inflated, swollen ventral valve like that of *Linoproductus*. Lazarev (2004) judged the group to be closer to *Schrenkiella* and at first treated it as a subfamily within Schrenkiellidae, clearly in error, because Coopericinae is much more inflated, but at the time of the proposal Lazarev (2004) was firmly convinced that schrenkiellid genera were distinguished by possessing only one row of hinge spines, compared with linoproductid shells which had two rows of hinge spines. Although Brunton (2007) considered the validity of the group to be "beyond the scope" of his update of Productida for the *Revised Brachiopod Treatise*, probably meaning he questioned it, but did not like to say so, Waterhouse (2004b, p. 32) accepted Lazarev's proposal as a family group, whilst modifying the rank, and relating the group to Linoproductidae. Lazarev (2004) and Brunton (2007) included *Elalia* Lazarev (2004) and *Krekarpius* Lazarev (2004) in Coopericinae. These two genera have vaulted ventral valves, and spines are best developed along the ventral hinge, with possible rare other spines on *Elalia*, and thin spines scattered over the venter and flanks of *Krekarpius*. They are closer to *Ovatia* in the thinness of ribs and the nature of the cardinal process as far as known, and are re-assigned to the Subfamily Gilmoriinae, Family Ovatiidae Lazarev. *Auriculatea* Waterhouse, 2004b, based on *Linoproductus nasutus* King, 1931, p. 76, is very similar to *Coopericus*, but has a nasute ventral valve and ears at maximum width, with prominent row of hinge spines and few other ventral spines. It is like *Coopericus* in its vaulted shape and thick visceral disc, but resembles *Schrenkiella* and allies in its prominent ears and anterior ventral fold.

Eventually, as summarized in 2010, Lazarev came to accept the obvious ties with Linoproductidae, and treated Coopericinae as a subfamily within Linoproductidae, as strongly argued by Waterhouse (2002b) and by Sone & Leman (2005).

Detail is well preserved and described for the type and only species of *Coopericus*, *Linoproductus angustus* King, 1931 from the Bone Spring and Skinner Ranch Formations of west Texas, United States. The internal dorsal valve is figured by Cooper & Grant (1975, pl. 432, fig. 13) to show a medium septum extending to the base of the cardinal process between two lateral hinge ridges, and no buttress mounds or platform. Such detail is not available for other genera in the subfamily.

Genus *Grantevia* new genus

Derivation: Named for Richard E. Grant.

Type species: *Linoproductus semisulcatus* Cooper & Grant, 1975, p. 1148 from Neal Ranch and Lenox Hills Formations (Asselian, Sakmarian), west Texas, United States, here designated.

Diagnosis: Large shells with highly vaulted and incurved ventral valve, dorsal valve somewhat flattened over disc, ventral hinge spines of moderate strength, arranged in row, and reinforced laterally over outer ears by a few further halteroid spines; body spines rare.

Discussion: This genus like *Coopericus* is not common, and the two are closely allied. *Grantevia* is the older of the two genera, similar in size and overall appearance, and distinguished by having a tuft of a few posterior lateral spines close to the hinge, and slightly more prominent but rare body spines. The older genus *Auriculatea* has slightly stronger hinge spines in a simple row, and few body spines, and the venter is swollen with short anterior median fold, so that *Coopericus* marks a reversion in some respects to that genus.

Subfamily **GLOBOSOPRODUCTINAE** new subfamily

Name genus: *Globosoproductus* Litvinovich & Vorontsova, 1983 from mid-Visean of Russia, here designated.

Diagnosis: Low rugae, no lateral buttress plates, no brachial cones. Lower Carboniferous (Visean, Lower Serpukhovian).

Genera: *Globosoproductus* Litvinovich & Vorontsova, *Datangia* Yang De-Li (syn. *Moderatoproductus* Litvinovich & Vorontsova).

Discussion: Genera in the group are discriminated by their moderately transverse shape. The two genera involved have always been allocated to Gigantoproductidae, but the particular attributes of that family, such as brachial cones and lateral buttress plates are missing, and the shells are not closely rugose, and body spines are erect. The difference from gigantoproductids is well illustrated by Litvinovich & Vorontstova (1983), with the provision of sketched internal detail for *Gigantoproductus* (Fig. 1.1-4) as reproduced in Fig. 16.29, in contrast to *Moderatoproductus*, which is a synonym of *Datangia* (Fig. 2.1,2) and *Globosoproductus* (Fig. 1.5). *Datangia* and *Globosoproductus* are both comparatively large, which apparently induced a favoured alliance with Gigantoproductidae, and the shells are somewhat swollen and elongate, without, as far as can be discerned, a thick body corpus. Ventral spines are scattered and erect, sometimes with slight aureoles, and rare dorsal spines are found in *Globosoproductus*. Thin spines lie in a row along the hinge in *Globosoproductus*, and apart from having fewer hinge spines or rugae, and thicker body spines, the genera are moderately close in shape to *Lineaproductus* new genus.

Family **OVATIIDAE** Lazarev, 1990

[Nom. transl. hic ex Ovatiinae Lazarev, 1990, p. 121].

Diagnosis: Medium to small subglobular shells with highly or gently arched venter and incurved ventral umbo, short hinge, fine costae. Ventral spines few to numerous along hinge, absent, scattered or rare over disc and trail, or radially aligned along mid-line. Outer lobes of cardinal process fused dorsally. Body corpus thin to thick. Development usually symmetrical.

Subfamily **OVATIINAE** Lazarev, 1990

[Ovatiinae Lazarev, 1990, p. 121. Syn. Marginovatiini Chen, Tazawa & Shi in Chen, Tazawa, Shi & Matsuda 2004, p. 447].

Diagnosis: Shells highly arched, body corpus thick or thin. Upper Devonian (Famennian) to Middle Carboniferous (Moscovian).

Genera: *Ovatia* Muir-Wood & Cooper, *Arcuatusia* new genus, *Diadematia* Waterhouse, *Igniculus* new genus, *Marginovatia* Gordon & Henry.

Discussion: Lazarev (1990, p. 121) proposed Subfamily Ovatiinae, recognized as a useful group by Waterhouse (2004b), with the addition of a Pennsylvanian genus *Diadematia* Waterhouse. Ovatiinae included according to Lazarev (1990) a number of genera now dispersed in several subfamilies, including Auriculispininae and Stepanoviellinae, two subfamilies that Lazarev persistently ignored for some years, although proposed well before Ovatiinae. He included in Ovatiinae the genus *Auriculispina* Waterhouse, which became name-bearer for Auriculispininae Waterhouse, 1986a (see p. 440): that would mean Ovatiinae was a junior synonym of Auriculispininae. Indeed Ganelin & Lazarev (1999) later came to believe that Auriculispininae was senior synonym of Ovatiinae, but the morphologies of the two groups, involving shape, ribbing, spines and other detail, are very different. Brunton et al. (2000, p. 544) ignored Ovatiinae, and classed the genus in Auriculispininae. But *Ovatia* is close to Linoproductinae in its ornament of firm ribbing and erect spines, whereas Auriculispininae has less regular ribbing and has ventral spines over the disc with elongate spine bases. There are further differences in the nature of the ventral adductor scars, which are dendritic in *Ovatia*, and striate and posteriorly impressed in *Auriculispina*. In most respects, *Ovatia* is close to Linoproductidae. Differences between *Linoproductus* and *Ovatia* can be assessed as no more than familial, involving smaller size, and fusion or separation of the outer lobes of the cardinal process. On the other hand there is a degree of similarity to Lirariinae new subfamily, involving such genera as *Globiella, Cimmeriella* and *Liraria*. These genera come close in size and general appearance to *Ovatia* to some extent, with rather similar ornament, but slightly different shape and different cardinal process. Ventral muscle scars tend to be more dendritic in *Ovatia*, so that convergence appears to have occurred between linoproductoid (Ovatiidae) and lirariin (Anidanthidae) genera. After a few years, Lazarev (2006) placed *Ovatia* in Linispininae. In 2010, Lazarev indicated that *Ovatia* belonged to a "new" subfamily, and ignored his own earlier work, which included proposal as a subfamily (Lazarev 1990), inclusion in Auriculispininae (Ganelin & Lazarev 1999), and placement in Linispininae (Lazarev 2006). These ongoing changes in interpretation seem to me to be understandable, because his views are responding to new information that he has uncovered, and perhaps any worker as productive as S. S. Lazarev may feel entitled to forget or adjust without acknowledging any correction aspects of his previous reports.

The type species of *Ovatia, O. elongata* Muir-Wood & Cooper, 1960, p. 311 from the lower Fayetteville Formation (Mississippian) of Oklahoma, United States, is well known and widespread in faunas of Tournaisian to lower Serpukhovian age. It differs from mid-Carboniferous linoproductids in its highly vaulted ventral valve, and the cardinal process is exceptional, with, as shown by Muir-Wood & Cooper (1960, p. 311), the lateral lobes uniting on the external face, and the median lobe inconspicuous from an internal view, and more prominent but still lower than the lateral lobes from an external view. The dorsal median septum extends just beyond the brachial terminations. Devonian occurrences in the former Soviet Union, reported by Bublichenko (1971) and Litvinovich et al. (1975) in Kazakhstan, Nalivkin (1979) in the Urals and in Timan-Pechora by Fotieva (1985), were endorsed by Carter (1988, p. 43). Grechishnikova (1966, pl. 8, fig. 6-10) described *Ovatia laevicosta* (Girty) from Rudny Altai, figuring only ventral valves, and Fotieva (1985, pl. 3, fig. 21 reported the same form in the Turneisk beds of Timan - Pechora. Whether these identifications are correct remains to be clarified. Thus Fotieva (1985) assigned specimens to *Ovatia praelaevicosta* (Krestovnikov & Karpyshev), now the type species of *Krekarpius* Lazarev, and other species treated as *Ovatia* in the literature require re-evaluation.

Specimens reliably classed as *Ovatia* are small to medium in size with incurved ventral umbo, short hinge and well defined ears, and the dorsal valve deeply concave and usually geniculate. Ribs are fine, increase especially on the dorsal valve by bifurcation, and are crossed by low wrinkles especially on the dorsal valve. Ventral spines form one or two rows along the hinge, a small group on the outer ears, and lie scattered over the ventral disc and trail (Muir-Wood & Cooper, 1960, p. 311), with aureoles conspicuous. Spines are rare or absent on the dorsal valve. Ventral adductor scars are deeply scored by sublinear grooves (Muir-Wood & Cooper 1960, pl. 114, fig. 12), and may bear posterior dendritic markings and the dorsal adductors are finely dendritic. Muir-Wood & Cooper (1960, p. 312) listed a number of species from the United States, and only one from Asia, and species are widespread in Europe. Muir-Wood & Cooper (1960) and Brunton (1966) denied that *Ovatia* was present in England. Yet *Linoproductus bioni* Muir-Wood (1931, pl. 9, fig. 4, 4a, text-fig. 6, 7) from the upper *Dictyoclostus teres* band, Gillalees Beck, Bewcastle, C2 subzone (B 56417) in northern Cumberland (Cumbria) and from the Cambeck beds, considered to have been derived from the *Linoproductus globosus* Zone, C1, is of comparable shape and size (23mm wide), and clarification of hinge spines would help determine affinities more precisely. Ribs are fine, two to three per mm, to 20-25 in 5mm, and as many as six or seven may converge on a spine base, with two to four continuing forward from the spine base. This material shows the interior well, and there are subdendritic muscle scars, with grooves erratically and obliquely crossing the adductors. Wrinkles are low over the ventral disc and higher on the trail.

Reed (1943, p. 96) erected a new variety *Productus* (*Striatifera*) *corrugatus* M'Coy *spinulifera* Reed for Upper Devonian shells from southeast England that were referred to *corrugatus* by Whidborne (1897, p. 173, pl. 21, fig. 4, 5), and distinguished by the presence of numerous fine ventral spinules over the fine ribs. The small size, fine ribs and numerous ventral spines imply a possibly new genus of Ovatiinae, but preservation of Whidborne's figured material is such that further material is required before establishing its nature and limits.

Marginovatia Gordon & Henry, 1990 of Visean to Bashkirian age in United States is similar in shape to *Ovatia*, with different spine pattern, involving fewer hinge spines. *Marginovatia* was nominated as name genus for Tribe Marginovatiini Chen, Tazawa & Shi in Chen, Tazawa, Shi & Matsuda (2007) on the basis of its well developed ventral and dorsal marginal ridges. The tribe was treated as a member of Linoproductinae Stehli. Two other genera were included. *Amazonoproductus* Chen, Tazawa & Shi from the Upper Carboniferous of Brazil was shown to have a well developed dorsal marginal ridge, but this genus is very close to members of Linoproductinae in shape, shape and ornament, and a dorsal marginal ridge is developed in the type species of *Linoproductus* Chao, *Productus cora* d'Orbigny, as figured by Brunton et al. (2000, Fig. 365.1f), and also in species described as *Sublinoproductus pentagonalis* Lazarev (2010, pl. 3, fig. 9) and *S. barchatovae* Lazarev (2010, pl. 4, fig. 4). The third genus placed in the tribe Marginovatiini by Chen et al. (2004) was *Mistoproductus* Yang De-li, 1991 from Artinskian – Kungurian of South China. It differs from the other two genera in having fine ribs, closely spaced commarginal rugae, spines clustered close to the hinge, and moderately sturdy semi-prostrate spines with elongate or prostrate bases over the ventral visceral disc. In conclusion, Marginovatiini as interpreted by Chen et al. (2004) appears to be polyphyletic, and the uniqueness of the marginal ridge overvalued.

Genus ***Arcuatusia*** new genus

Fig. 16.11 – Fig. 16.14

Derivation: arcuatus – curved, arched, Lat.

Type species: *Ovatia prolata* Carter (1987, p. 40) from the Banff Group (Tournaisian) of western Canada, here designated.

Diagnosis: Small highly arched shells with ventral spines crowded in well organized rows along hinge and over ears, fine over ventral disc and trail, moderately thick body corpus.

Discussion: The Tournaisian species *Ovatia prolata* Carter (1987, p. 40, pl. 5, fig. 1-17), holotype GSC 63281 figured by Carter (1987, pl. 5, fig. 11, 12, 16, 17) from the Banff Group of western Canada, has very fine ribs, 30-40 in 10mm at 25mm from the beak, and small spines over disc and trail. The ventral ears are convex, with the outer part steeply

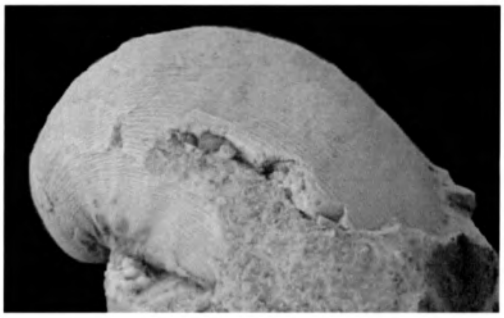


Fig. 16.11. *Arcuatusia prolata* (Carter), lateral aspect of ventral view of GSC 63280 from Banff Formation (Tournaisian), Canada, x2. JBW photo.

inclined, and one or two of the spine rows may form ridges parallel to the hinge. Along the ventral hinge spine rows increase in number from one near the beak to six on the outer ears, as well as additional spines between the rows, and rows continue forward around the outer or lateral margins. The diameter of the hinge spines increases from approximately 0.2mm near the umbo to 0.6mm laterally. This is obscurely confirmed in figures provided in the initial

Fig. 16.12. *Arcuatusia prolata* (Carter), oblique lateral-left view of GSC 63280 from Banff Formation (Tournaisian), Canada, x2.5. JBW photo.

study by Carter (1987, p. 40, pl. 5, fig. 1, 6, 10) which show very fine and crowded spines on the ears and opposing dimples on the dorsal ears (fig. 10). Over the disc and rarely, the trail, some three ribs converge and continue forward from a spine base, but many of the scattered disc spines are erect with bases little disturbing the costae from which they arise. Rugae are strong postero-laterally on the ventral valve and low over the dorsal valve.

Fig. 16.13. *Arcuatusia prolata* (Carter), ventral view of ears and spine bases, GSC 63280 from Banff Formation (Tournaisian), Canada, x4. Ear spines emerge from transverse ridges on one side, but less so on the other in this specimen. JBW photo.

The dorsal valve is only gently concave over the disc, and the trail geniculate or subgeniculate, and there are no dorsal spines. Ventral muscle scars are only lightly imprinted, and difficult to delineate. The dorsal cardinal process is small and bilobed, and lateral ridges are short, and diverge little from the hinge line. Further detail is provided by Carter (1987).

The genus is very close to *Ovatia* in many respects, including elongate shape, attenuated ventral umbo, and maximum width well forward. Costation is finer on the Canadian form. The ventral hinge spines of *Ovatia* differ, with one or two rows of spines reported by Muir-Wood & Cooper (1960, p. 311) near the hinge margin and a "group near cardinal angles on rugae" (Muir-Wood & Cooper 1960, p. 311, pl. 114, fig. 1-12), though little further detail is provided. Ventral spines over the disc and trail of type *Ovatia* are rendered conspicuous by being surrounded by an aureole. The body corpus is thick in *prolata*, whereas that of *Ovatia* is much thinner (Muir-Wood & Cooper 1960, p. 311).

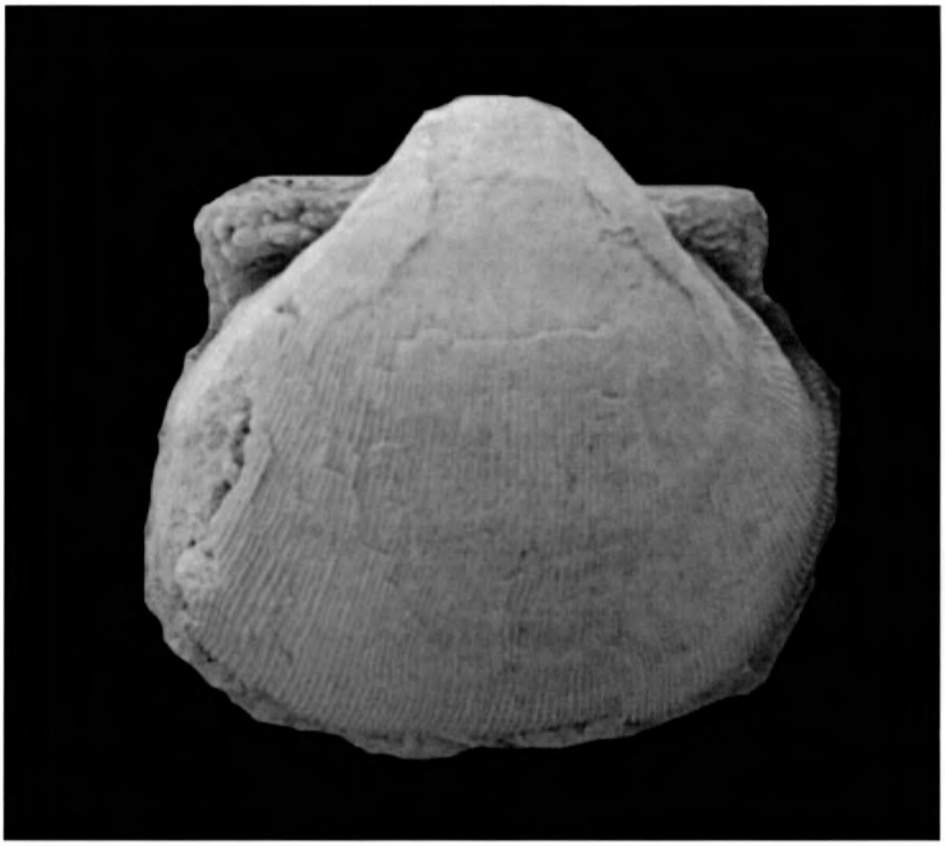


Fig. 16.14. *Arcuatusia prolata* (Carter), ventral view of GSC 63280 from Banff Formation (Tournaisian), Canada, x3.5. JBW photo.

Genus ***Igniculus*** new genus

Derivation: igniculus – small fire.

Type species: *Productus* (*Linoproductus*) *semicubiculus* Bell, 1929, p. 114 from the Windsor Group (Visean), Nova Scotia, Canada, here designated.

Diagnosis: Small shells with broad and not prolonged ventral umbo, wide hinge at maximum width, large ears especially on dorsal valve, numerous hinge spines and few other erect spines.

Discussion: Shells are small, and of unusual shape for Ovatiinae, in having maximum width at the hinge, wide ears, and ventral umbo that is little prolonged. By contrast, *Ovatia* has long incurved ventral umbo with extended posterior walls and maximum width placed well forward, much as in *Arcuatusia* new genus, *Marginovatia* Gordon & Henry and *Diadematia* Waterhouse, 2004b. Other than shape, the new form is close to *Ovatia* and allies in the nature of costation and in the hinge spines, which closely approach those of *Arcuatusia*, but are not arranged in rows. There is some similarity, especially in ventral ear spines, to *Comagunia* new genus (see p. 433), but ventral body spines are erect, without prolonged bases.

Igniculus semicubiculus (Bell, 1929)

Fig. 16.15, Fig. 16.16

Productus (*Linoproductus*) *semicubiculus* Bell (1929, p. 114, pl. 17, fig. 4, 5, 6, 6a), from the Windsor Group of Visean age in Nova Scotia, Canada, is a member of Ovatiinae, but is a little less tumid than *Ovatia*. The holotype was cited as ventral valve GSC 7951, as figured by Bell (1929, pl. 17, fig. 6, 6a). Some of the specimens are covered by faint irregular commarginal rugae or growth steps over both valves. Bell (1929) enumerated some 15 stout spine bases over the ears, compared with 25 to 50 fine spines on the ears in *Comagunia lyelli* (Verneuil) – see p. 433 – as well as rare body spines. These are fine and erect, arising from single costae, and lying in short rows on the anterior shell. There are corresponding pits on the dorsal ears. Two small ventral valves on the slab, cut out from Bell's figure, involve a tiny ventral valve 5mm wide with only one or two posterior spines, and an even smaller specimen 3mm wide with no visible spines. Costae increase by branching and by intercalation. The species differs from *Ovatia* in being less vaulted, and in lacking large spine bases, often with aureoles, from the ventral disc and trail.

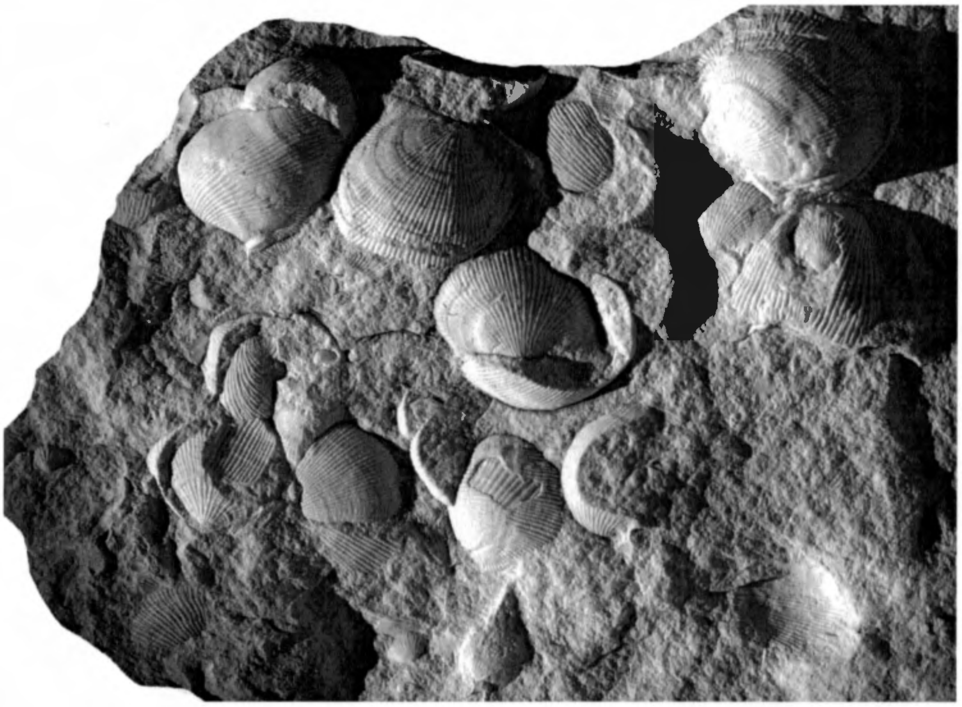


Fig. 16.15. Specimens of *Igniculus semicubiculus* (Bell) on block GSC 7947 from Windsor Group (Visean), Nova Scotia, Canada, x2. JBW photo.

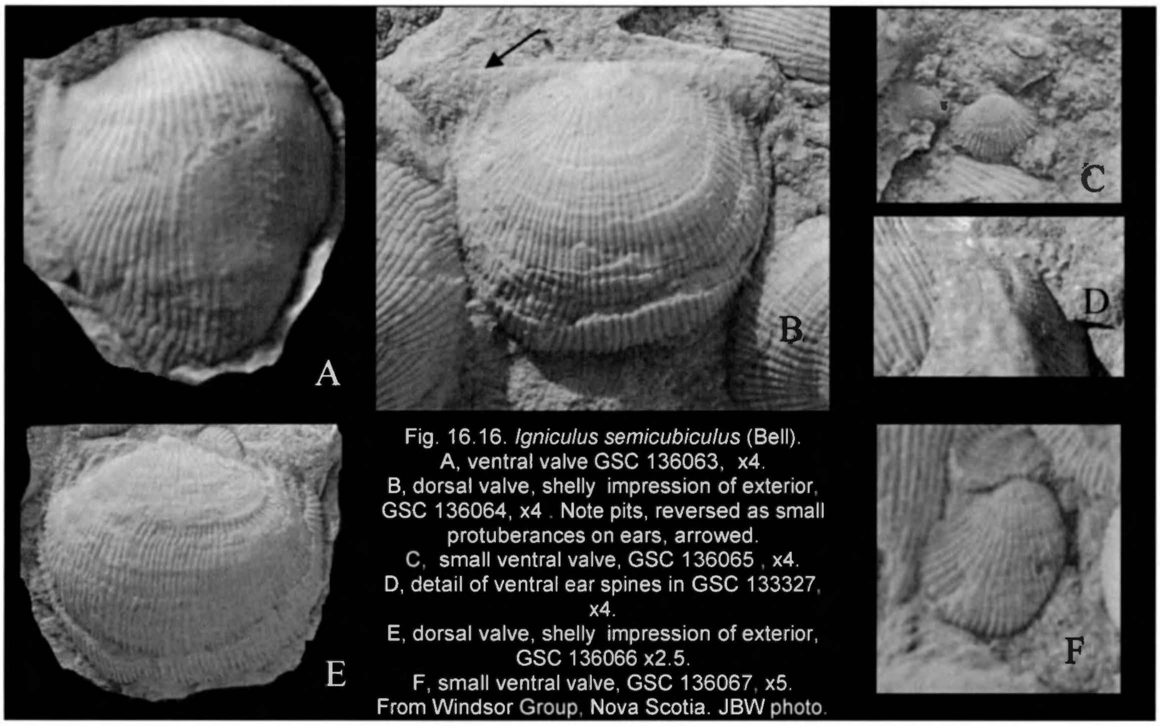


Fig. 16.16. *Igniculus semicubiculus* (Bell).
A, ventral valve GSC 136063, x4.
B, dorsal valve, shelly impression of exterior, GSC 136064, x4. Note pits, reversed as small protuberances on ears, arrowed.
C, small ventral valve, GSC 136065, x4.
D, detail of ventral ear spines in GSC 133327, x4.
E, dorsal valve, shelly impression of exterior, GSC 136066 x2.5.
F, small ventral valve, GSC 136067, x5.
From Windsor Group, Nova Scotia. JBW photo.

Subfamily **GILMORIINAE** new subfamily

Name genus: *Gilmoria* new genus from Gilmore Limestone (Early Carboniferous) of Iowa, United States, here designated.

Diagnosis: Small to medium in size, with subequilateral to weakly transverse shape, wide hinge, fine costellae, row or rows of hinge spines and few additional ventral spines, cardinal process lobes fused posteriorly. Upper Devonian (Famennian) to Upper Carboniferous (Gzhelian).

Genera: *Gilmoria* new genus, *Elalia* Lazarev, *Krekarpius* Lazarev.

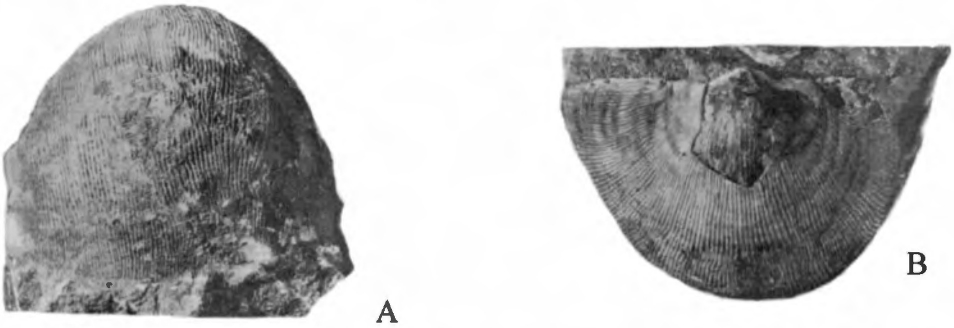


Fig. 16.17. *Elalia rhenanus* (Paeckelmann) x1, figured by Paeckelmann (1931, pl. 20, fig. 5-7, pl. 21, fig. 1) from upper Kohlenkalk (Upper Carboniferous) near Aachen, Germany.

Discussion: These genera are regarded as members of Ovatiidae, as indicated by the medium size, fine ribs, and the way the outer lobes of the cardinal process are fused medianly on the outer face, at least where known. *Elalia* and *Krekarpius* were referred to Coopericinae Lazarev by Lazarev (2004) and to Schrenkiellinae Lazarev by Brunton (2007, p. 2660), but ribs are strong and coarse in *Coopericus* Lazarev, like those of Linoproductidae, and its cardinal process is like that of other Linoproductidae in having the lateral lobes unfused externally. Coopericinae is here restricted to genera with a row of sturdy hinge spines and few other ventral spines, just as in *Coopericus*. By contrast, members of Gilmoriinae have thin scattered body spines, and may have more than one row of spines along the hinge. It will be noted that *Krekarpius* Lazarev is based on *Productus praelaevicostatus* Krestovnikov & Karpyshev, 1948, a species commonly referred to *Ovatia* in Russian literature until the revision by Lazarev (2004). Differences from Ovatiinae are not great, but *Ovatia* and allies tend to be more elongate, with narrower hinge and usually more incurved ventral umbo and more numerous hinge spines. *Krekarpius* is a transverse linoproductid developed ultimately from Eoproductellinae, with a time range of Upper Devonian (Famennian) to Lower Carboniferous.

Genus ***Gilmoria*** new genus

Derivation: Named from Gilmore Limestone, Iowa, United States.

Type species: *Gilmoria gilmorensis* new species from Gilmore Limestone (Early Carboniferous), Iowa, United States, here designated.

Diagnosis: Transverse, with wide hinge, slender corpus, ventral spines in prominent row along hinge, with a few further fine spines, fine spines scattered over disc and trail, but rare.

Discussion: This genus is transverse and much less vaulted than *Ovatia* Muir-Wood & Cooper, 1960, and lacks the cluster of spines on the outer ears, and has a very thin corpus. *Gilmoria* displays a hinge row of thick spines interspersed with a row of finer spines further from the hinge. There is no cluster on the ears or umbonal slopes, and scattered anterior spines are present on the ventral valve, and dimples on the dorsal valve. The genus belongs to Ovatiidae, and in its hinge development of spines and thin disc was conceivably a precursor of *Schrenkiella*.

Gilmoria gilmorensis new species

Fig. 16.18

1972 *Ovatia* sp. Carter, p. 480, pl. 1, fig. 1-6.

Derivation: Named for Gilmore Limestone.

Holotype: USNM 176807 from Gilmore Limestone (Early Carboniferous), Iowa, United States, figured by Carter (1972, pl. 1, fig. 2), here designated.

Diagnosis: Medium-sized, transverse to equidimensional, obtuse cardinal extremities, row of sturdy hinge spines with finer spines in irregular second row, and rare slender anterior ventral spines.

Description: Shells of medium size, ventral valve gently convex with broad umbo protruding a little beyond wide hinge, cardinal extremities obtuse, venter slightly produced. Dorsal valve gently concave with no obvious geniculation; visceral disc slender. Both valves ornamented by fine costellae, numbering 10-12 in 5mm on anterior ventral valve, commarginal rugae moderately developed on ventral valve near hinge and low but covering dorsal valve, which also displays a number of elongate pits. A row of sturdy spines extends along the ventral hinge, directed postero-laterally, and very fine spines arise amongst the sturdy spines, or just in front of them. Fine erect spines also arise from the ventral costellae, near the anterior margin. There is no cluster of spines postero-laterally, over ears or umbonal slopes, and no dorsal spines.

Fig. 16.18. *Gilmoria gilmorensis* new genus, new species. Ventral valve holotype USNM 176807. From Early Carboniferous Gilmore Limestone of Iowa, United States. See Carter (1972).

Ventral interior not known. The dorsal interior displays a row of pits close to the hinge, reflecting the ventral hinge row of spines, and a hinge ridge slopes outwards from the hinge margin. The cardinal process is bifid with two refolded lobes widely separated from an internal aspect, like that of *Ovatia*, the lobes joined externally, deeply divided internally. The median septum is slender and extends beyond mid-length, and adductors are weakly defined, and the posterior floor bears fine tubercles. The hinge ridges pass obliquely forward into lateral marginal ridges which extend for about half of the length of the valve.

Resemblances: The Gilmore Limestone species comes from a faunal interval judged to be post-Kinderhookian and pre-Osagean, according to Carter (1972). In identifying the material as *Ovatia*, Carter noted that the material was more transverse and had a wider hinge than usual for *Ovatia*. *Elalia* Lazarev (2004, p. 159) of Bashkirian – Gzhelian age in Russia and Europe has spines in a single row along the hinge with few or no other spines, and is more arched medianly. *Krekarpius* Lazarev, 2004, p. 159 is moderately transverse and less vaulted, and has thin spines in a row close to the hinge, and thinner spines over the venter and flanks. It is of upper Famennian and Lower Carboniferous age in the southern Urals of Russia.

Family **SCHRENKIELLIDAE** Lazarev, 1990

[Nom. transl. Lazarev 2000a ex Schrenkiellinae Lazarev, 1990, p. 122].

Taxonomy: The family group unit was proposed as a nomen nudum with no diagnosis, discussion or indication of name genus by Lazarev (1986a, p. 30). Brunton et al. (2000, p. 562) mistakenly indicated the date of the taxon as Lazarev, 1986a. That is incorrect, and the name was eventually published by Lazarev (1990, p. 122), as acknowledged by Brunton (2007, p. 2660).

Diagnosis: Medium-sized to large transverse and costate shells with long hinge, inconspicuous ventral umbo, medianly flattened ventral disc, spines in row near hinge margin, with or without further spines. Body corpus slender, outer cardinal process lobes not fused. Development usually symmetrical.

Subfamily **SCHRENKIELLINAE** Lazarev, 1990

Fig. 16.19

[Schrenkiellinae Lazarev, 1990, p. 122].

Diagnosis: Large shells with trail continuing in plane or disc and virtually imperceptible externally. Upper Carboniferous (Moscovian?) to Lower Permian (Sakmarian).

Genera: *Schrenkiella* Barchatova (syn. ?*Achunoproductus* Ustritsky, *Indigia* Barchatova), *Meniscuria* Waterhouse, *Plicatomedium* Waterhouse, *Praeschrenkiella* new genus, ?*Striatospica* Waterhouse, *Xanthoserella* Waterhouse.

Discussion: Schrenkiellinae are characteristically medium to large shells with shallow corpus cavity and wide hinge bearing usually a single row of moderately thick spines, and no or rare other erect spines, restricted to the ventral valve. The group is limited to comparatively few genera, that probably evolved from a genus such as *Gilmoria*. Upper Carboniferous members such as *Praeschrenkiella*, *Meniscuria* and *Plicatomedium* have a few body spines, lost by Permian time for the genera *Schrenkiella* and *Striatospica*. In *Xanthoserella devargasi* (Sutherland & Harlow, 1973, pl. 12, fig. 11), the median septum begins well in front of the cardinal process, without buttress platform or mounds. The trail, indicated by a fold, continues in the curved plane of the disc. The selection of *Schrenkiella* as name giver for the subfamily has proved to be well justified, even though the genus is understood mainly from the ventral valve only, with dorsal valves seldom preserved. Exceptionally, dorsal valves are preserved for a new Canadian genus, and for a new genus, *Chhidrusia*, assessed as belonging to a new subfamily.

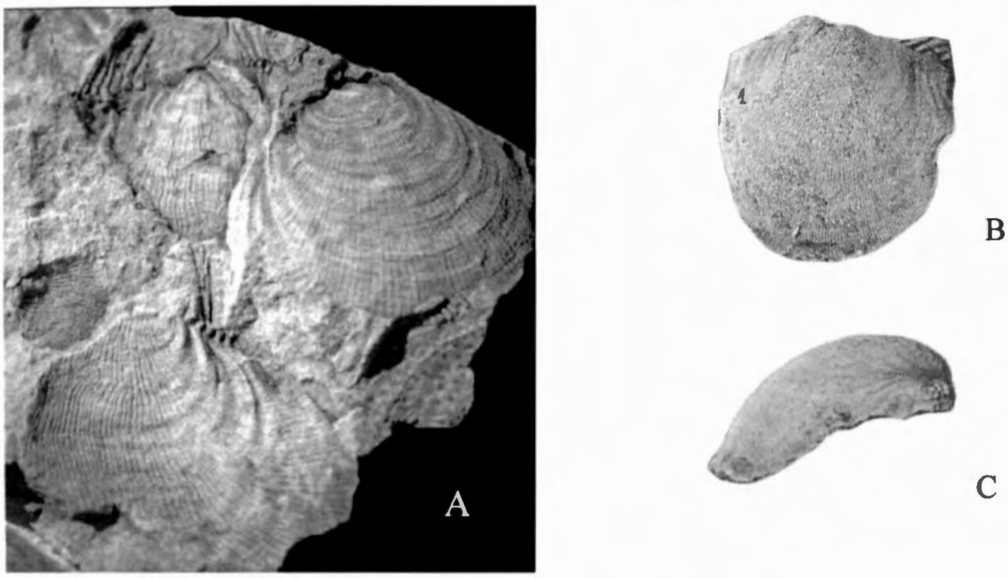


Fig. 16.19. A, *Xanthoserella campbelli* (Roberts), x2. AMF 109664 at upper left, AMF 109663 at lower left, AMF 79868 to upper right, from Visean at Greenhills, New South Wales, Australia. Photo Li Shenzhong and see Roberts (1964). B, C, *Xanthoserella devargasi* (Sutherland & Harlow), ventral and lateral aspects of holotype, OU 7774 from Atokan of New Mexico, United States, x1. See Sutherland & Harlow (1973, pl. 12, fig. 7a, b).

Lazarev (2004) claimed that Linoproductidae was characterized by two rows of spines along the ventral hinge, and Schrenkiellidae was characterized by having one row of spines along the hinge (Lazarev 2004). But Lazarev (2008) later admitted that some linoproductids displayed only one row of hinge spines, thereby overturning his earlier justifications, which were clearly too narrowly based. At least some specimens of the type species of *Linoproductus, L. cora* (d'Orbigny) from the Cochacabamba Group of Bolivia display a single row of spines (Kozlowski 1914, pl. 6, fig. 2; Chronic 1949, 1953, pl. 7, fig. 7-9; Muir-Wood & Cooper 1960, pl. 111, fig. 3, 6; Branisa 1965; Ahfeld & Branisa 1960; Samtleben 1971, pl. 7, fig. 3 and Brunton et al. 2000, Fig. 365.1b). Not all figures are clear, and some could be interpreted as displaying two uneven rows. But that would not establish that two rows are typical, but rather that there was some variation, so that the one or two row presence was variable within more or less type and topotype *Linoproductus*, and should not be used as an exclusive familial discriminant. Of course *Linoproductus* itself was not the oldest member, and may represent a later development of its group, and earliest members, of Lower Carboniferous (Visean) age, remain to be explored. Furthermore, genera associated with *Schrenkiella* by Lazarev in Brunton et al. 2000 have more lateral spines along the hinge, as in *Striatospica* Waterhouse (see for example the type species as figured by Brunton et al. 2000, Fig. 397.1a), so that the number of hinge rows does not appear to be a completely consistent basis for family distinction. To Waterhouse (2004a), *Linoproductus* and *Schrenkiella* were deemed to be closely related, by sharing the same style of costate ornament, lack of dorsal spines, presence of dendritic muscle scars, and concentration of spines along the hinge. *Schrenkiella* is much closer to *Linoproductus* than to Anidanthinae, Grandaurispininae and Siphonosiinae, and however the genera are arranged, *Schrenkiella* and allies fall closer to Linoproductidae than any other group.

In the course of paleontological and evolutionary study, it is necessary to avoid setting aside all but one major parameter. In assessing the value of a similar approach, Pitrat (1965, p. 699) considered it necessary to criticise a comparable "single-minded attention to the details of sulcal costae" in a study by Gatinaud (1949) of several spiriferoids. The prime emphasis on a row of hinge spines on the ventral valve of ribbed productids led Lazarev (2004) to add the genera *Bandoproductus* Jin & Sun, 1981 and *Lyonia* Archbold, 1983 to a purported Family Schrenkiellidae. These genera differ substantially from schrenkiellins in having a striate and posteriorly impressed rather than dendritic ventral muscle field, and anteriorly prolonged spine tunnels, pointing to a relationship with Auriculispinidae Waterhouse, and this is confirmed by the presence of numerous ventral spines over the visceral disc which have elongate bases posteriorly, and anteriorly prolonged spine tunnels, in contrast to linoproductid genera which have erect spines without anteriorly prolonged bases. Moreover *Lyonia* has dorsal spines, which are not known in *Schrenkiella* or in accepted or supposed allies such as *Striatospica* Waterhouse or in *Permundaria* Nakamura, Kato & Choi.

Sone & Leman (2005) claimed that Waterhouse (2001, p. 28) had transferred Schrenkiellinae to Linoproductidae on the basis that it had a conspicuous row of ventral hinge spines, but this is an unwarranted mis-representation, with the implication that Waterhouse was unaware that other linoproductoids had a row of ventral hinge spines. The implication is incorrect, and Waterhouse (2001, 2002b) clearly stated that *Schrenkiella* and alliesshared not only a hinge row of ventral spines, but particular form of radial costation, and dendritic muscle scars with *Linoproductus* and allies.

As a further matter for concern, Brunton et al. (2000) placed *Schrenkiella* and allies in Monticuliferidae, presumably because of the thinness of the disc, which is regarded as inconclusive in itself and needs to be qualified by considerations of ornament. In this case, the ornament differs considerably, and is much closer to that of Linoproductidae, as noted by Waterhouse (2001) and Sone & Leman (2005). Monticuliferidae is now assessed as aulostegoid, not linoproductoid (see p. 290).

Striatospica Waterhouse, 1975 was treated as a member close to *Schrenkiella* by Brunton et al. (2000, p. 563), as sustained in other studies by Lazarev. But the same genus was also regarded as a synonym of *Haydenella* Reed, regarded as a unit within Chonetellini by Brunton et al. (2000, p. 428). This synonymy seems highly unlikely, given the strong differences in ornament, involving spines and ribs. But the genus does display two irregular rows of long hinge spines, unlike the arrangement of Permian Schrenkiellinae, as if suggestive of an aulostegoid alliance, and the position may require further consideration.

Genus *Praeschrenkiella* new genus

Type species: *Praeschrenkiella waddingtonae* new genus, new species from Member A (Gzhelian), Jungle Creek Formation, north Canada, here designated

Diagnosis: Large transverse shells with ventral spines in row along hinge and in a few anterior rows.

Discussion: According to Brunton et al. (2000), *Schrenkiella* is found only in Sakmarian deposits of Russia and possibly Australia, the latter occurrence justified by an incomplete ventral valve figured from the Lyons Group (Asselian or Sakmarian) of Western Australia by Archbold (1983, Fig. 1A, B). *Schrenkiella* has only a row of hinge spines (Brunton et al. 2000, p. 562). ?*Achunoproductus* Ustritsky, 1971, p. 21 was referred to synonymy of *Schrenkiella* by Brunton et al. (2000), as was *Indigia* Barchatova, 1973, p. 100. All three taxa are of Sakmarian age, from the northern Urals. Of other genera referred to the subfamily by Brunton et al. (2000), *Striatospica* Waterhouse, 1975, p. 11 is moderately (but not unreservably) close to *Schrenkiella* as a small capillate form with hinge spines only, from the upper Capitanian of China, and *Dictyoclostoidea* Jin & Hu, 1978 is more closely allied to Liraplectini (p. 159), in displaying reticulate disc and fine capillate costae. *Permundaria* Nakamura, Kato & Choi, 1970 is difficult to decipher – it does have a wide hinge and poorly discriminated ears and fine costellae, with close-set well defined commarginal rugae. There are no spines and the genus is allocated to Compressoproductinae Jin et al. Further genera are to be added from the Pennsylvanian of United States, including *Plicatomedium* Waterhouse, 2004b, p. 29, based on *Linoproductus oklahomae* Dunbar & Condra, with well developed ventral hinge row and high anterior ventral fold, distinguished from *Schrenkiella* by its more vaulted ventral valve, and triangular shape with hinge at maximum width and lateral margins converging anteriorly to the narrow median fold, approaching that of *S. triangulata* (Barchatova, 1973) from Timan, of Sakmarian age. Commarginal rugae are few and strong.

Meniscuria Waterhouse, 2004b, p. 31, type *Linoproductus meniscus* Dunbar & Condra, 1932, p. 255, pl. 30, fig. 4, 5 of Pennsylvanian age from Texas, is a large little inflated transverse form with gentle if any sulcus and fold, slender visceral disc, non-geniculate trail, and spines in a double row along the hinge and scattered over the ventral valve: all spines are slender and without prominent bases. The genus is close in its arched yet thin disc to *Elalia* Lazarev, 2004, which was proposed earlier in the same year for a Bashkirian – Gzhelian genus in the Moscow Basin of Russia, but has larger ears, less conspicuous commarginal rugae, and more transverse less vaulted shape.

The type species of *Xanthoserella* Waterhouse, 2004b, p. 30, *Linoproductus devargasi* Sutherland & Harlow, 1973, from the Morrowan (Pennsylvanian) of United States has a row of hinge spines and no body spines, and there is no ventral anterior fold, but low concentric rugae are present (Fig. 16.19B, C). The visceral disc is thin and elongate. A Visean New South Wales species described as *Fluctaria campbelli* Roberts, 1964a (see Fig. 16.19A) is very close to type *Xanthoserella*, apart from better developed rugae and vertically directed rather than laterally directed hinge spines, as recorded by Waterhouse (2010a, p. 29, fig. 7). Such a difference in spine orientation implies that the spines developed, at maturity, a much larger loop, as indicated in the study by Grant (1963) on *Linoproductus magnispinus* Dunbar & Condra (1932), a species here deemed to belong to *Linipalus* Lazarev.

Praeschrenkiella waddingtonae new species

Fig. 16.20

1971 *Linoproductus schrenki* [not Stuckenberg] – Waterhouse in Waterhouse & Bamber, pl. 12, fig. 6.

Derivation: Named for Janet Waddington.

Holotype: GSC 136098 figured as Fig. 16.20A herein, from Member A, Jungle Creek Formation (Gzhelian), Yukon Territory, Canada, here designated.

Diagnosis: Large shells with low inflation, obtuse cardinal extremities not extended into ears, narrow anterior fold on ventral valve.

Material: Five ventral valves and three dorsal valves from Member A (Gzhelian), lower Jungle Creek Formation, Ogilvie Mountains, Yukon Territory, Canada. See Appendix, Part C, p. 478.

Dimensions in mm:

Specimen GSC	Width	Length	Height	
133328	66	54	13	
133331	65	45	13	
136098	43	27	4	holotype

Description: Specimens large, weakly transverse, wide hinge without extended extremities, cardinal angle obtuse, maximum width placed a little in front near posterior third of shell width. Ventral umbo subdued, broad with angle of 120°, little incurved, low ginglymus developed, ears weakly differentiated, especially in specimens not fully mature (see Fig. 16.20D) and gently convex, disc gently convex without sulcus, and a narrow fold arises over the trail which extends for the anterior third of the shell length. Dorsal valve gently concave with poorly differentiated but slightly dorsad ears, and a very low anterior fold arises behind mid-length: shallow anterior sulcus corresponds with the ventral fold. Both valves ornamented by costellae, seven to eight in 5mm at mid-valve and four to five in 5mm at lateral anterior margin, increase by intercalation, ribs with rounded crests. Dorsal costellae similar, numbering six in 5mm near anterior margin, arise by intercalation and have rounded crests. Fine growth increments number up to ten in 1mm, coarse often alternating with fine, and two to four minor growth steps. Very fine growth laminae are developed at least over the middle and anterior shell. Spines in a row along the ventral hinge, only 1-2mm apart along much of the length, but spaced further apart laterally, erect, and 1mm in diameter. Short ventral spines in six to ten irregular rows anteriorly. Internal detail not revealed, apart from a low median septum extending from near the hinge of the dorsal valve.

Resemblances: The genus is distinguished by the short scattered anterior spines. In the type species of *Schrenkiella* Barchatova, 1973, p. 97, *Productus schrenki* Stuckenberg (1875, p. 88), also figured by Tschernyschew (1902, pp. 290, 628, pl. 27, fig. 1), Brunton et al. (2000, Fig. 396.1a, b) and Lazarev (2004), from the Indiga River of Sakmarian age in the Urals, the ventral valve is more arched than the Canadian form and has a broader and lower anterior ventral fold, a row of fine ventral spines, and projecting cardinal extremities. Allied specimens, probably of a separate species, were figured as this form from the Turuzov Suite of Taimyr Peninsula by Ustritsky & Chernyak (1963, p. 82, pl. 12, fig. 4-7), with broader anterior fold and less extended cardinal extremities. *S. timanica* Barchatova (1973, pl.

29, fig. 1), also figured by Brunton et al. (2000, Fig. 396.1c, d) is also more inflated, and *S. triangulata* Barchatova (1973; Brunton et al. 2000, Fig. 396.1e) has subangular cardinal extremities at maximum width, and long narrow median ventral fold. *S. umboplanata* Barchatova (1973, pl. 30, fig. 2) has a broad anterior ventral fold and well rounded postero-lateral extremities. These Russian species are of Sakmarian age. The suggestion in Waterhouse (2004a) that *Linoproductus periovalis* Waterhouse, 1983b, p. 221 from the Khisor Sandstone Member (or White Sand of Waagen 1891) might belong to *Schrenkiella* remains conjectural, because no spines are preserved.

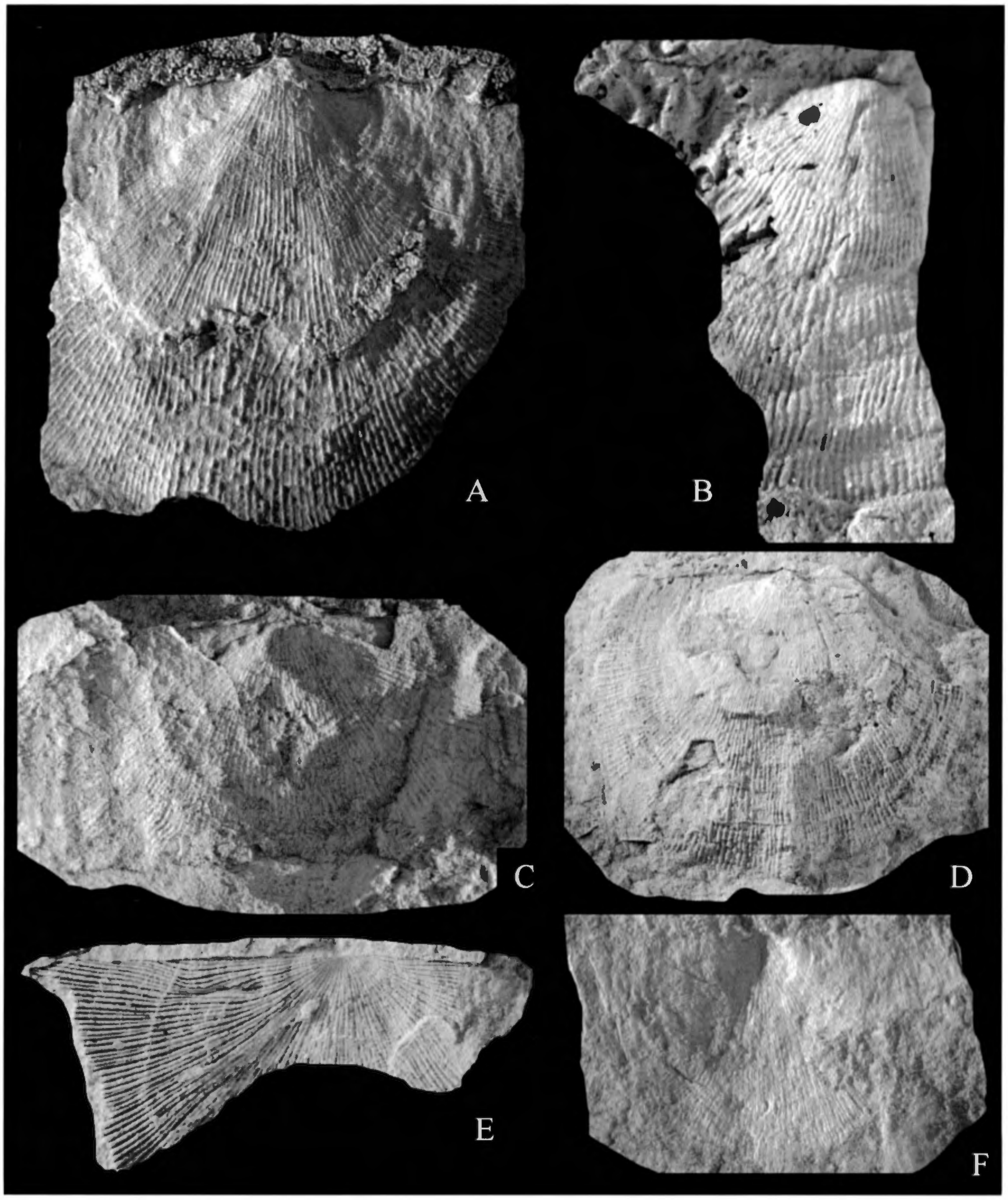


Fig. 16.20. *Praeschrenkiella waddingtonae* new genus, new species. A, ventral internal mould GSC 136098, holotype, showing hinge spines projecting posteriorly in plane of disc, x1. B, internal mould of ventral valve GSC 133329, x1.8. C, dorsal valve GSC 133330, x1, backlit from right. D, ventral valve GSC 133328, x0.9, showing narrow ears. E, posterior part of external mould of ventral valve GSC 133332, x1.7. F, exterior of dorsal valve GSC 133331, x1.5. From Member A (Gzhelian), basal Jungle Creek Formation, Ogilvie Mountains, Yukon Territory, Canada. x1. JBW photo.

Praeschrenkiella costata new species

Fig. 16.21

Derivation: costa – rib, Lat.

Holotype: GSC 133312, from Member A (Gzhelian), Jungle Creek Formation, Yukon Territory, Canada, figured in Fig. 16.21, here designated.

Diagnosis: Ribs comparatively coarse.

Material: A few fragmentary but otherwise well preserved specimens from Member A (JBW 578) of Jungle Creek Formation, Yukon Territory, Canada.

Description: Shells moderately large cardinal extremities obtuse, short anterior ventral sulcus fading anteriorly, ribs coarse, 3 to four in 5mm anteriorly, ventral ribs increase by intercalation, crossed by fine growth laminae, six to eight in 1mm anteriorly. Dorsal valve concave, with narrow anterior sulcus and low swelling each side. Row of fine ventral hinge spines, and distinct broader short anterior ventral spines in a few irregular rows. Dorsal median septum extends to mid-length, broad posteriorly, and continued anteriorly as very low fine ridge, divides two elongate adductor scars crossed by fine feathery dendritic ribs.

Resemblances: The species is characterized by the coarse costae.

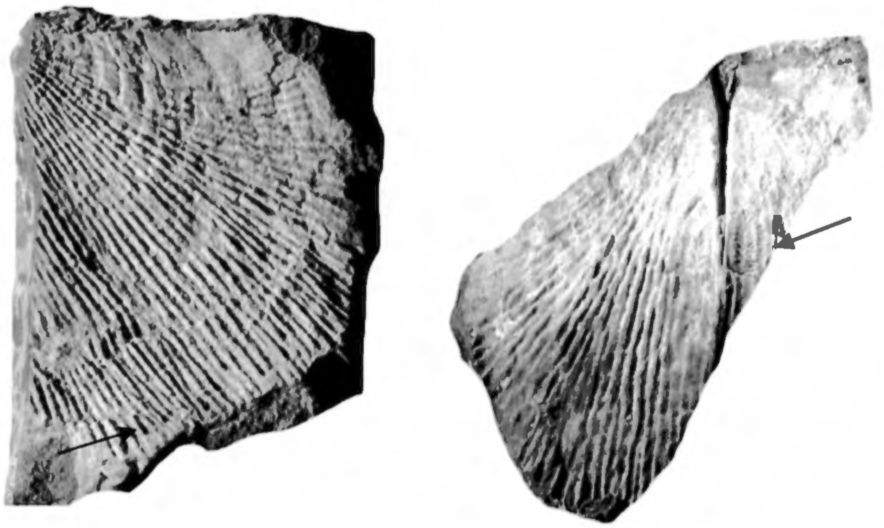


Fig. 16.21. *Praeschrenkiella costata* new genus, new species. A, external mould of ventral valve GSC 133312. B, internal mould of dorsal valve GSC133315. Specimens from Member A (Gzhelian), Yukon Terriory, Canada, x1. JBW photo. Arrows point to spine bases and adductor scars.

Subfamily **CHHIDRUSIINAE** new subfamily

Diagnosis: Single row of ventral hinge spines, no other spines. Trail long and distinct. Upper Permian (Wuchiapingian).

Genus: *Chhidrusia* new genus.

Discussion: The genera placed in Schrenkiellinae Lazarev all have virtually imperceptible trails, and so are dish-shaped, like members of Overtoniidae, Gigantoproductidae, and some other genera. By contrast, *Chhidrusia* has a long and geniculate trail, yet otherwise agrees in ornament of ribs and spines with *Schrenkiella*.

Genus ***Chhidrusia*** new genus

Fig. 16.22

Derivation: Named from Chhidru, village in Salt Range, Pakistan.

Type species: *Productus* (*Linoproductus*) *simensis abrupta* Reed, 1944, p. 57 from Kufri Member (late Wuchiapingian), Chhidru Formation, Pakistan, here designated.

Diagnosis: Moderately large, ventral disc almost flat over visceral disc, moderately long geniculate trail. Row of ventral hinge spines, no further spines.

Discussion: *Productus* (*Linoproductus*) *simensis abrupta* Reed (1944, p. 56, pl. 12 [not pl. 16 as in the text], fig. 1a, b) from the late Wuchiapingian Kufri Member, Chhidru Formation or so-called Upper Productus Limestone of the Salt Range, Pakistan, looks like *Schrenkiella*, as first noted by Waterhouse & Gupta (1979b, p. 26), through having a weakly alate hinge at maximum width, a broad sulcus over the anterior disc, and medianly arched ventral trail, and the species was referred to *Schrenkiella* by Waterhouse & Chen (2007, p. 15). The trail is exceptionally high and strongly geniculate, whereas the ventral trail curves imperceptibly on from the disc in the various species figured as *Schrenkiella* by Barchatova (1973) and Brunton et al. (2000), and the Canadian new species described above as *Praeschrenkiella waddingtonae* and *P. costata*. This is well demonstrated for ventral valves figured in lateral profile by Barchatova (1973, pl. 29, fig. 1e), repeated in Brunton et al. (2000, Fig. 396.1d) and additionally in Brunton (2000, Fig. 396.1b). The figure in Reed (1944) suggests anterior ventral spines, but such are not mentioned in the text (Reed (1944, p. 58). Material from the *Lamnimargus himalayensis* Zone at Marbal Pass, northwest India (Waterhouse & Gupta 1979b, pl. 4, fig. 4, 5, 8), also of Wuchiapingian age, is conspecific, and has a geniculate distinctive ventral trail, definitely without spines. Unlike most *Schrenkiella*, the Marbal Pass material shows aspects of the dorsal interior, with cardinal process, strong hinge ridge, long fine median septum and weakly impressed non-dendritic adductor scars.

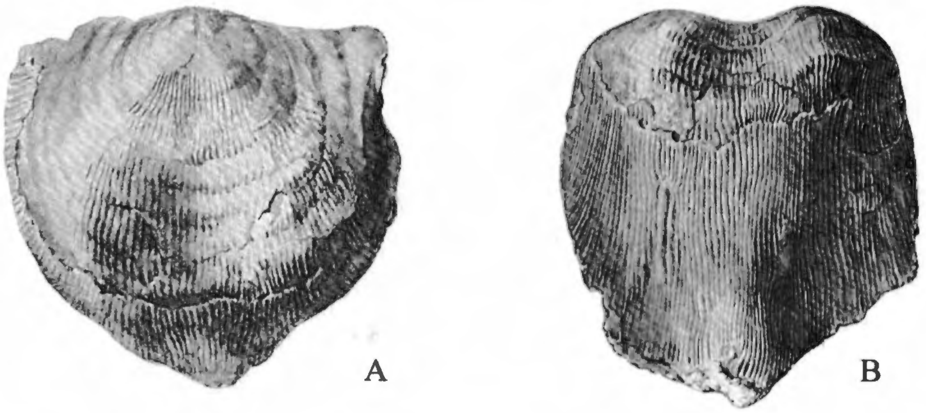


Fig. 16.22. *Chhidrusia abrupta* (Reed). Ventral and anterior views of holotype, showing long trail, from lower Chhidru Formation (Wuchiapingian), Salt Range, Pakistan, x1. From Reed (1944, pl. 12, fig. 1, 1a).

Family **STRIATIFERIDAE** Muir-Wood & Cooper, 1960

[Nom. transl. hic ex Striatiferinae Muir-Wood & Cooper, 1960, p. 328].

Diagnosis: Elongate and often asymmetric shells, not free living, narrow hinge, spines may be on dorsal valve, cardinal process with single myophore lobe.

Discussion: This minor but highly distinctive family group was placed in Monticuliferidae by Brunton et al. (2000), and shifted to Linoproductidae (Linoproductoidea) on account of the nature of the spines by Waterhouse (2002b). Brunton et al. (2000, p. 560) regarded Proboscidellini Muir-Wood & Cooper as a sister tribe, but proboscidellin spines are quite different, having elongate posterior bases and extended forward within the shell. Members of Striatiferinae adopted a nesting habit, crowded in clusters, or resting propped against other shells, whereas in the allied subfamily Compressoproductinae, *Compressoproductus* was more solitary in habit according to Cooper & Grant (1975), though individuals often rested against shells of varying description. The origins are difficult to judge, but the more open coiling and expansion of the shell in Gilmoriinae suggests a source more likely than Ovatiinae.

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

[Nom. transl. Brunton et al. 1995, p. 930 ex Striatiferinae Muir-Wood & Cooper, 1960, p. 328].

Diagnosis: Shallow body corpus, short hinge, elongate irregular subtriangular to subquadrate shape, simple trails, simple cardinal process passing into median septum. Spines may be inconspicuous, hinge may be wide. Lower Carboniferous (upper Visean – Serpukhovian).

Genera: *Striatifera* Chao, *Striatiferella* Legrand-Blain in Legrand-Blain, Delvolvé & Hansotte.

Discussion: *Striatiferella* Legrand-Blain in Legrand-Blain et al. (1996) has dorsal spines, and is one of the few members of Linoproductoidea to show this feature, apart from some Gigantoproductidae, such as *Titanaria* Muir-Wood & Cooper and *Semiplanus* Sarytcheva, and rarely in Globosoproductinae.

Genus ***Striatifera*** Chao, 1927

Fig. 16.23

Striatifera, based on type species *Productus striata* Fischer, 1837, p. 181, is of irregular shape, and may be transverse and gently convex or narrow, high and tubular. Many specimens form narrow cones – like clustered conulariids or the bivalve *Pinna*, but more inflated and irregular in shape, and ribs are often split or intercalated. Ears are weakly defined but may be large, with wide or narrow hinge bearing splayed spines, erect in some species, flat-lying in others, in three to five rows on the posterior shell. For recognition of species, the collections will need to be evaluated along the lines established for *Compressoproductus* by Cooper & Grant (1975), in which rather similar-looking species are carefully distinguished. Amongst English and Welsh specimens of Lower Carboniferous age that are kept at the Natural History Museum, London, England, B 48790 from D2 Park Hill, Longnor, has many ear spines, and other spines are erect or have slightly prolonged bases. B 48775 from D2 Narrowdale, Staffordshire, has small erect spines, narrower than the ribs from which they arise, and often at the crests of low small growth wrinkles. B 48786 from D2 Parkhouse Hill, Derbyshire, is similar. B 48795 from D2 at Narrowdale, Staffordshire, shows a row of possible spine bases as knobs close to the hinge, posterior to fine growth lines. Rib interspaces are narrower than the ribs. B 23941 from the Middle White Limestone of Graig-faunr in Wales has a number of small apparently erect spines, especially anteriorly. B 8945 in the Gilbertson Collection shows a few short spine bases protruding forward over the anterior margin. Specimens BB 54294-5 from Wetton, Staffordshire, display very fine growth increments and tiny spine rises on the costae. The bases appear to be aligned along low wrinkles.

Fig. 16.23. *Striatifera striata* (Fischer), ventral valve B 5779, x2. From Lower Carboniferous limestone of Settle, Yorkshire, England. JBW photo.

Specimens of *Striatifera* identified as *spinifera* (Paeckelmann), involving BB 8767 and 8761-2, from the Visean Okian Series, Alexin beds ($C1_{Ab}$), Ogarero, Moscow Basin, Russia, have many ventral hinge spines, and some body ventral spines show a slight ramping from rib to spine, but most are erect, and arise from a single rib, with two ribs continuing forward.

Subfamily **COMPRESSOPRODUCTINAE** Jin & Hu, 1978

Fig. 16.24

[Compressoproductinae Jin & Hu, 1978, p. 115].

Diagnosis: Characterized by fine radial ornament, few and erect ventral spines found especially near hinge, low body corpus. Shells often with well defined commarginal rugae, may become asymmetric from nestling in host. Upper Carboniferous (Gzhelian) to Upper Permian (Changhsingian).

Genera *Compressoproductus* Sarytcheva (?syn. *Substriatifera* Kotlyar), *Fallaxoproductus* Li, Gu & Li, ?*Permundaria* Nakazawa, Kato & Choi, *Regrantia* Waterhouse, *Sarytchevinella* Waterhouse.

Discussion: The subfamily is close to Linoproductidae, not Monticuliferidae as in Brunton et al. (2000, p. 546). The high and often narrow ventral valve and fine radial ornament are reminiscent of *Striatifera* Chao, of Carboniferous age, with narrow short spine bases. *Substriatifera* Kotlyar, 1964, p. 123, was based on *Productus mytiloides vladivostokensis* Fredericks, 1925, p. 17, pl. 2, fig. 80, 81 and is difficult to decipher. It was synonymized with *Compressoproductus* by Brunton et al. (2000), and there is no obvious difference between the two genera, judged from figures. Possible *Compressoproductus* is found in Gzhelian deposits of the Ogilvie Mountains in northwest Canada: otherwise the genus and associated forms are Permian in age.

The dates and articles for publication of *Productus djulfensis* Stoyanow (1910b [not 1910a], 1915), the type species for *Sarytchevinella* Waterhouse, have been clarified by Sone (2009). The publication date of 1916 has been challenged through Stoyanow's claim of a 1915 date for publication, as supported by Sone (2009). The outer cover for my copy of the monograph bears the date 1915. But the inner front page with title, author and publication detail bears the date 1916, to imply that the publication was not available for sale until 1916. These were war years after all, entailing difficulties over synchronizing of print runs and availability for sale. It would have been simple enough to print off copies of the outer cover with what proved to be an overoptimistic date, or on the other hand, print off the main text with what proved to be a pessimistic date. Normally, the date of publication is treated as no sooner than the latest date indicated in the publication, which is clearly 1916. The matter is academic, because no question has arisen of any threat of synonymy.

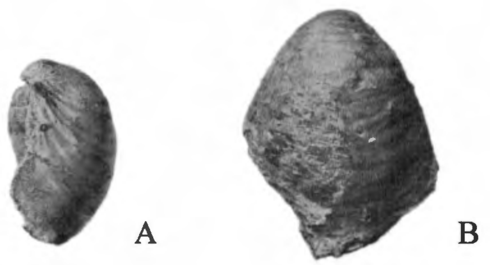


Fig. 16.24. *Sarytchevinella djulfensis* (Stoyanov). A, B, lateral and ventral aspects of ventral valve as figured by Stoyanov (1915, pl. 5), from Djulfian (Wuchiapingian) of Armenia, x1.

Genus ***Compressoproductus*** Sarytcheva, 1960

Type species: *Compressoproductus morahpressus* Waterhouse & Piyasin, 1970, p. 133, new name for *Productus compressus* Waagen, 1884, p. 710 not Say, 1823. In Case 3352 Sone (2000) asked the International Code for Zoological Nomenclature to suppress the proposed name *morahpressus* on the grounds that workers had ignored the change (eg. Brunton et al. 2000, p. 546). The ICZN opinion 2201 concluded that "An application for the proposed conservation of *Productus compressus* Waagen, 1884 is not approved". Of course *Productus compressus* Waagen not Say is the type species of *Compressoproductus*, and it would be reasonable to cite this, and indeed the matter was never in doubt. But the omission of "not Say" or even Waagen by various authors is in error, and the failure to cite the correctly named taxon does not reflect well on the understanding of the genus and its taxonomy. Nor should careless taxonomy be defended by suspension of the rules. Perhaps it is time to set aside permanently any endorsement of such egregious procedure. If an author knows the correct name, he should use it, and correct any error, not seek to protect the error. The problem lies in the present Code for Zoological Nomenclature, which undercuts the science of taxonomy by being open to sanctify carelessness or error, and being willing to endorse the claim that "customary usage" is of merit. Science should always strive to reflect reality, not human error.

Diagnosis: Medium-sized shells with radial ribs and closely spaced commarginal rugae, ventral ears large but often inclined in plane of lateral walls, bearing few to usually many spines, and fine erect spines may form nodes over the ribs. Ventral adductor scars scalloped. Cardinal process unifid.

Discussion: One outstanding attribute of at least some *Compressoproductus* lies in the scalloped diductor muscle field, with strong pustules just in front, as illustrated herein (Fig. 16.26). Some of the species described by Cooper & Grant (1975) show a similar ventral interior, including *C. curtus* Cooper & Grant (1975, pl. 460, fig. 16, 21, 32, 33) and *C. flabellatus* Cooper & Grant (1975, pl. 461, fig. 48, 50, 66), both species coming from the Cathedral Mountain Formation in the Glass Mountains, west Texas, United States. As stressed by Brunton (2007), the body cavity is slender, not thick as mistakenly asserted by Waterhouse (2002b).

Compressoproductus pentagonalis Waterhouse, 1983d

Fig. 16.25, Fig. 16.26

1980 *Stepanoviella djulfensis* [not Stoyanow] – Liao, p. 247, pl. 4, fig. 26-28.
1983d *Compressoproductus pentagonalis* Waterhouse, p. 128, pl. 3, fig. 11, 12.
1983d *Sarytchevinella tenuissima* Waterhouse, p. 126, pl. 3, fig. 13-15 (part, not pl. 4, fig. 1, 2 = *Globiella*).

Holotype: TBR 438 figured by Waterhouse (1983d, pl. 3, fig. 11). For *tenuissima,* TBR 431 figured by Waterhouse (1983d, pl. 3, fig. 14). Both from the Lopingian Huai Tak Formation of north Thailand.

Diagnosis: Small, very fine ribbing, diductor scars impressed in scallop shape.

Fig. 16.25. *Compressoproductus pentagonalis* Waterhouse, internal mould of ventral valve BR 3048, showing some of the bases of the row of hinge spines as arrowed, x2. From Huai Tak Formation (Changhsingian), north Thailand. JBW photo.

Discussion: This species was in part mistakenly assigned by Waterhouse (1983d) to *Sarytchevinella* Waterhouse, a compressoproductin form (see p. 386). A freshly prepared topotype specimen from the Huai Tak Formation shows part of a row of well developed spines near the ventral hinge, and a few more anteriorly placed spine bases.

Fig. 16.26. *Compressoproductus pentagonalis* Waterhouse. A, interior of ventral valve TBR 430, x1.7. B, internal mould, ventral valve TBR 431, x1.5. From Huai Tak Formation, north Thailand (Changhsingian). See Waterhouse (1983d).

Genus ***Permundaria*** Nakamura, Kato & Choi, 1970

Fig. 16.27, Fig. 16.28

Permundaria Nakamura, Kato & Choi, 1970, type species *P. asiatica* Nakamura et al. was described from the Middle Permian Kanokura Formation of the southern Kitakami Mountains in Japan, and paratype from limestone at Sisophon, Cambodia. The type material is characterized by wide hinge, thin corpus, and closely spaced and regular commarginal wrinkles. The type species and a close ally *P. tenuistriata* Tazawa have been closely examined by Tazawa (1974) to confirm that the ornament lacks spines, even though the figure in Tazawa (1974, pl. 43, fig. 3b) might suggest tiny spinules along the crest of rugae. Further specimens assigned to *asiatica* from Japan by Tazawa (2001, p. 296, Fig. 7.17a-7.19) show more varied fine wrinkles but agree in shape, with large slender and poorly defined ears and virtually imperceptible umbonal slopes.

Fig. 16.27. *Permundaria asiatica* Nakamura, Kato & Choi. A, C, internal and external mould of ventral valve UHR 19698. B, *P. tenuistriata* Tazawa, holotype UHR 19700. Specimens from Kitakami Mountains, Iwate Prefecture, Japan, of Guadalupian age, x0.7 approx. Photographs courtesy of J. Tazawa.

Somewhat similar material from middle Permian at Sisophon had already been assigned a different species level name, as *Cancrinella undata tenuistriata* Chi-Thuân (1961, p. 282, pl. 2, fig. 2, pl. 5, fig. 11a, b), which may also include *C. cancriniformis* (not Tschernyschew) of Chi-Thuân (1961, pl. 1, fig. 17). The Chi-Thuân material is poorly preserved, and virtually indeterminate generically from figures, and its whereabouts now not known. The specimen figured by Chi-Thuân (1961, pl. 5, fig. 11a, b) is here cited as lectotype for species *tenuistriata* (Chi-Thuân, 1961), and whilst the obscurity of its generic position threatens to compromise the authorship and specific name of *Permundaria tenuistriata* Tazawa, with an outside possibility that Chi-Thuân's species also belongs to *Permundaria*, it is believed that indistinct spine-bases may be discerned in Chi-Thuân (1961, pl. 5, fig. 11a).

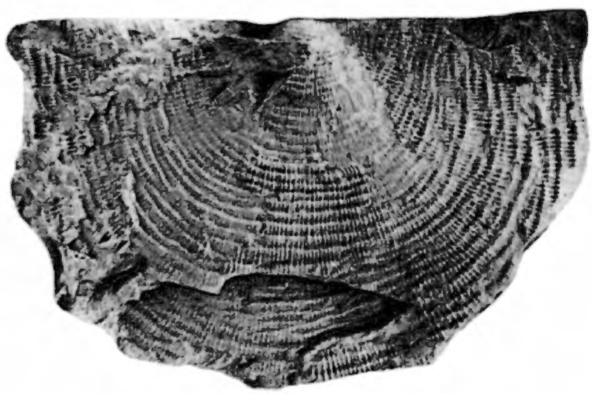


Fig. 16.28. *Permundaria shizipuensis* Jin & Liao, ventral valve NIGP22479 x1 from Maokou beds (Guadalupian), Guizhou, China. See Jin et al. (1974, pl. 162, fig. 18).

The slender disc and wide hinge of *Permundaria* encouraged placement within Schrenkiellinae Lazarev, as in Brunton et al. (2000), although the ornament of regular commarginal wrinkles would suggest different tribal allegiances. Waterhouse (2002b, p. 36) proposed that a position within Auriculispininae seemed likely. An alternative position is preferred, as Compressoproductini Jin & Hu. Members of the tribe show fine rugae and fine costellae, and body spines may be rare. *Permundaria* generally has small ears in the plane of the commissure, and lacks spines, whereas *Compressoproductus* has large and spinose ears which may be inclined at a high angle to the hinge.

Permundaria shizipuensis Jin & Liao in Jin, Liao & Feng (1974, p. 310, pl. 162, fig. 18) from the Maokou limestone of Guizhou, South China, is very similar in overall shape to *P. asiatica*, with slightly raised ventral umbo and large but poorly discriminated ears showing a weakly alar projection at the hinge. The commarginal rugae and narrow ribs are close to those of *Compressoproductus*. Its radial and commarginal ornament approaches that of *Labaella* Kotlyar et al. 2004, but *Labaella* has larger ears, more prominent sulcus and spines along the hinge.

Sone & Leman (2005) described spines on their *Compressoproductus perplexa* from the Bera Formation of Malaysia, but the species belongs to Lyoniini (see pp. 446-447).

Family **GIGANTOPRODUCTIDAE** Muir-Wood & Cooper, 1960

[Nom. transl. hic ex Gigantoproductinae Muir-Wood & Cooper, 1960, p. 330].

Diagnosis: Medium-sized to large, symmetrical, hinge at or near greatest width, shell fully covered by close-set ribs and narrow interspaces, commarginal rugae low and regular or absent, spines erect or posteriorly prolonged, usually limited to ventral valve, but dorsal spines may be present in some taxa, shallow corpus cavity, cardinal process trilobed or quadrilobed, pit present as a rule. Brachiophore cones commonly distinct.

Discussion: Brunton et al. (2000, p. 550) assembled all gigantiproductiform genera in one subfamily, with two tribes, Gigantoproductini and Semiplanini Sarytcheva. The subfamily was characterized by shells of large size with slender corpus and general absence of marginal structures, and common presence of a cardinal process pit. Spines were reported on dorsal valves of some Gigantoproductini, and in a number of Semiplanini, which lack brachial cones. Gigantoproductidae probably sourced from Gilmoriinae (p. 377), sharing wide hinge, rows of hinge spines, and fine erect body spines. The following account is provisional, and depends largely on acceptance of the *Revised Brachiopod Treatise* account which envisaged the gigantiform brachiopods as closely related, and setting aside the possibility that they were polyphyletic. Even so, several different streams may be recognized. Gigantoproductinae have erect spines, brachial cones and lateral buttress plates. *Semiplanus* and allies lack brachial cones, display lateral buttress plates, and also display ventral spines different from those of *Gigantoproductus*, in that spines have long posterior bases. *Kansuella* Chao, assigned to a separate subfamily by Muir-Wood & Cooper (1960), that was not recognized by Brunton et al. (2000), not only has somewhat similar spines, but lacks lateral buttress plates, and has brachial cones, and as well, the shell is closely and evenly rugose. The ventral spines of *Semiplanus* and *Kansuella* at least superficially approach in external appearance the spines of Proboscidelloidea (p. 404), which have posteriorly elongate bases. Yet Proboscidelloidea embrace shells of much smaller size, which never bear lateral buttress plates, so that gigantiform development within their stock would have been highly exceptional. Exceptional is not impossible, but given the views of Muir-Wood & Cooper (1960) and the *Revised Brachiopod Treatise*, these shells with long ventral spine bases are regarded as a gigantiform development. A small association of relatively large shells that are between gigantiform and linoproductiform in appearance also have elongate bases to the ventral spines, and the core of these spines, unlike those of Proboscidelloidea where known (ie. Paucispinauriidae and Auriculispinidae), does not pass forward as well as back from the spine base. These shells, belonging to Wardlawriinae, are regarded as a group within Gigantoproductidae, descendent from Semiplaninae.

Subfamily **GIGANTOPRODUCTINAE** Muir-Wood & Cooper, 1960

[Gigantoproductinae Muir-Wood & Cooper, 1960, p. 330].

Diagnosis: Medium-sized to very large shells, hinge at or close to greatest width, rugae low or absent, spines erect, may be rare, may be surrounded by aureole, usually limited to ventral valve, shallow corpus cavity, cardinal process pit present and lateral buttress plates usually well developed, branching from medium septum behind the posterior adductors. Brachiophore cones distinct. Lower Carboniferous (Visean – Serpukhovian).

Genera: *Gigantoproductus* Prentice (nom. nov. pro *Gigantella Sarytcheva*, 1928 non Ekman, 1905), *Beleutella* Litvinovich, *Linoprotonia* Ferguson, ? *Serbarinia* Morozov, ?*Titanaria* Muir-Wood & Cooper, ?*Vitiliproductus* Jin & Liao (syn. *Connectoproductus* Donakhova), *Xinjiangiproductus* Yao & Fu.

Discussion: Gigantoproductins are very large linoproductoids, characterized by small and highly raised brachial shields, and cones which are dome-shaped prominences related to lophophore spirals that leave an imprint on the inner ventral valve, and also between the brachial shields of the dorsal valve. A number of genera are poorly known – some indeed are based on only the ventral or dorsal valve – and such genera of uncertain nature are provisionally included in Gigantoproductinae. For instance *Serbarinia* Morozov, 1985, based on *Productus kalugensis* Sarytcheva, 1928, p. 61 from the lower upper Visean of the Moscow Basin, Russia, is not very well known, and it is not clear whether lateral buttress plates are present or not. There are very low rugae. *Vitiliproductus* is known only from ventral valves. *Beleutella* Litvinovich has brachial cones, but the dorsal interior remains relatively obscure. *Titanaria* Muir-Wood & Cooper, 1960, p. 334 from North America and Africa was said to have no dorsal cones, yet the dorsal interior as photographed seems to have some interfering shell or structure and could be suggestive of cones present but damaged (see Muir-Wood & Cooper 1960, pl. 130, fig. 4). *Xinjiangiproductus* Yao & Fu, 1987, p. 96 is shaped like *Datangia* Yang De-li, but has brachial cones, and the presence or absence of lateral buttress plates is not clear.

Beleutella Litvinovich and *Xinjiangiproductus* Yao & Fu range into lower Serpukhovian, and *Beleutella modesta* Legrand-Blain, 1973, text-fig. 8 preserves a pseudodeltidium, earlier thought to be a characteristic feature of *Kansuella* Chao (see p. 401).

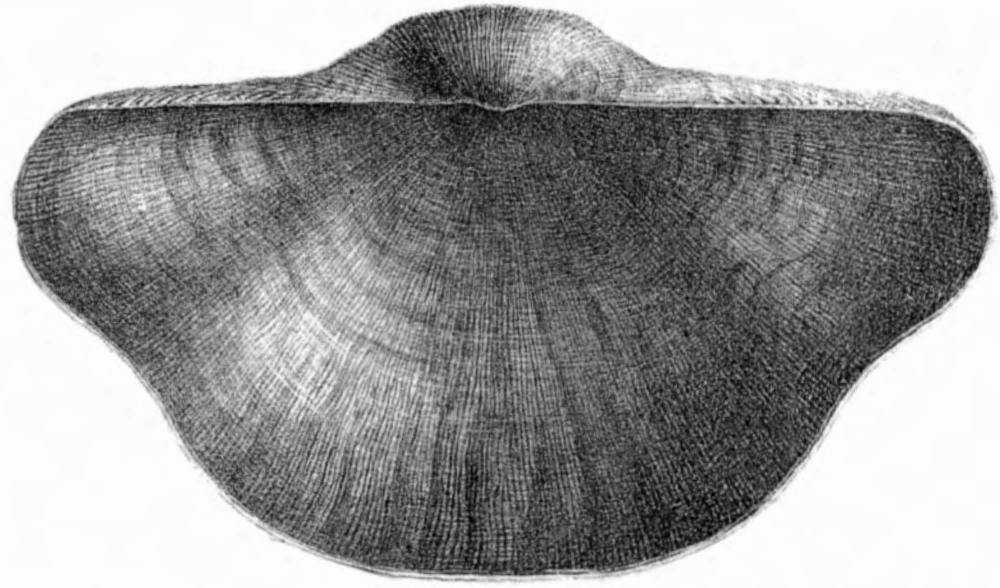


Fig. 16.29. *Gigantoproductus giganteus* (Martin), ventral aspect as figured by Davidson (1861, pl. 39, fig. 1) from Carboniferous limestone near Richmond, Yorkshire, England, x0.8.

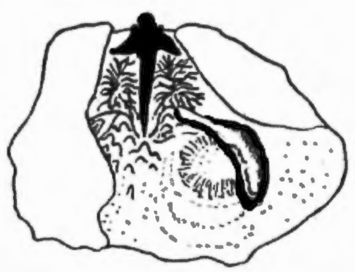


Fig. 16.30. *Gigantoproductus giganteus* (Martin), dorsal interior showing lateral buttress plates and brachial cones, altered slightly from Litvinovich & Vorontsova (1983, Fig. 1.4).

Genus ***Gigantoproductus*** Prentice, 1950

Fig. 16.29 - Fig. 16.31

Gigantoproductus Prentice, 1950 is very large and may have radial plicae, and the dorsal valve is gently concave, with no geniculation, and the trail may flare in some specimens. Spines form a row along the ventral hinge and are scattered or rare elsewhere: they may arise over the disc from a single rib which is undisturbed, or from a single rib that is replaced in front by two ribs, or from three ribs that are succeeded in front by two ribs. Ventral adductor scars (see Davidson 1861, pl. 37, fig. 1-3) are each divisible into two with separate detached smaller dendritic scars situated in front of the inner half of posterior scars: the posterior scars are crossed by fine almost feathery striae. Diductor scars are very large and flabellate, composed of a posterior triangular flattened portion with few transverse and radial ridges, and anterior broad finely striated surface (Fig. 16.31). The dorsal cardinal process is very large and trilobite or quadrilobate, as described in detail by Muir-Wood & Cooper (1960, p. 331). The median septum is broad, and the dorsal adductors divided into a dendritic posterior pair and smoother elevated portion. Two shallow rounded depressions lie in front, formed by lophophore spirals. The brachial scars are well defined and placed outside the low lophophore domes. Although not clearly shown in most published illustrations, lateral buttress plates are present, as figured by Litvinovich & Voronsteva (1983, Fig. 1.4). Papillation patterns are developed internally in both valves close to the hinge.

Gigantoproductus menchikoffi Legrand-Blain (1973, p. 125) from Algeria has posterior central papillation. The upper Visean species *G. meharezensis* Legrand-Blain, 1973 displays ventral hinge spines in two to four rows, and anterior spines are more or less erect. Very slight ramping of a few ventral spines is suggested in *Productus auritus* Phillips, 1836 (B 44311) from the Visean Lower Scar Limestone of Ulverston, Cumbria, England, but most ventral spines are erect and some have wide bases.

Muir-Wood & Cooper (1960) were unable to determine if dorsal spines were present in *Gigantoproductus*, but dorsal spines are numerous in *Titanaria* Muir-Wood & Cooper.

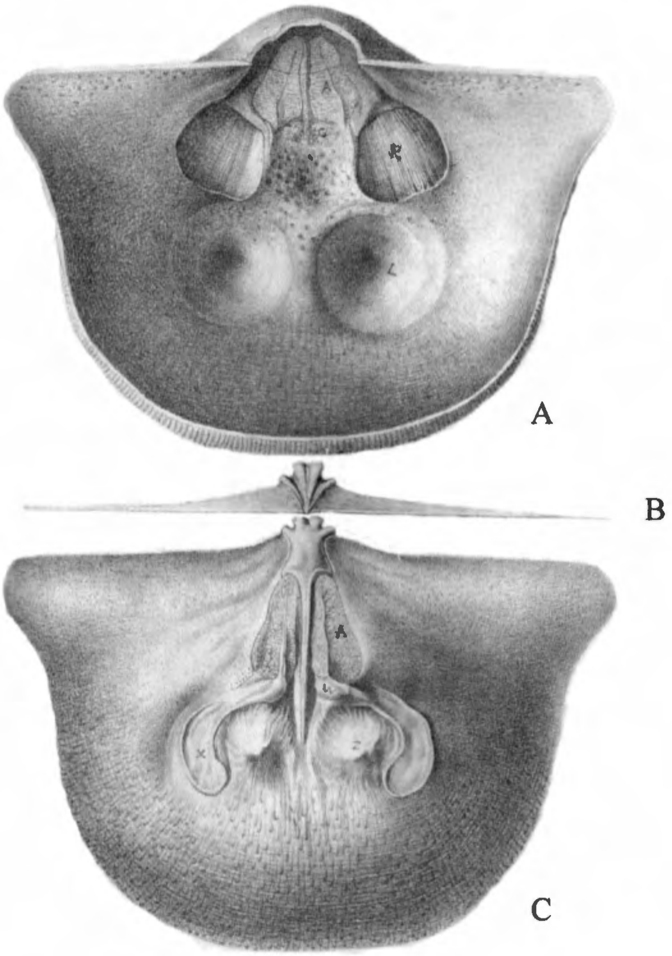


Fig. 16.31. *Gigantoproductus giganteus* (Martin). A, ventral valve interior, B, C, posterior and internal view of dorsal valve. Drawings provided by Davidson (1861, pl. 37, fig. 1-3). Specimen from Carboniferous limestone at Llangollen, Wales, x0.5. The cardinal process was supplemented from another specimen. A – adductor scars, C – adductor scar, R – diductor scars, X – "reniform impressions" or brachial shields, Z – "eminences corresponding to hollows L in the ventral valve", now called brachial cones.

Genus *Vitiliproductus* Jin & Liao, 1974

Vitiliproductus Jin & Liao in Jin et al., 1974, type species *Productus groeberi* Krenkel from the Visean of China, was judged to be linoproductin by Brunton & Mundy (1988a) and auriculispinin by Brunton et al. (2000, p. 546). Intersecting oblique rugae form tetrahedral elevations over the corpus, and marginal lateral rugae are well developed. Small ventral spines without posteriorly prolonged bases are developed near the hinge and scattered over the ventral valve, especially in *V. robertsi* Brunton & Mundy, 1988a, from northwest Australia. Roberts (1971, p. 129) regarded the form as gigantoproductid, as did Waterhouse (2002b, p. 34).

Genus ***Linoprotonia*** Ferguson, 1971

Fig. 16.32, Fig. 16.33

Linoprotonia Ferguson, 1971, p. 551, based on type species *Productus hemisphaericus* Sowerby, 1822, p. 31, pl. 328 of Asbian age (Lower Carboniferous) in south Wales, is also judged to be gigantoproductiform, even though classed as auriculispinin by Brunton et al. (2000, p. 539). Material has been examined in the Natural History. Museum, London, England. The holotype B 44114 of *hemisphaericus* as selected by Prentice (1949, p. 265) comes from D1 Carboniferous Limestone at Mgnydd-y-garez, near Kidwelly, south Wales, and has both valves intact, but too worn to show spine detail well. Topotypes include B 44115-6, and show low wrinkles and the shells are transverse like the specimens figured by Davidson (1861, pl. 40, fig. 4-8). Shells are finely costellate with somewhat differentiated ribbing, in which two ribs may lie behind a spine and one in front, or even three in front (BB 10679). There are numerous spines over the somewhat convex ventral ears, two to three rows only in the Davidson material, and scattered erect spines over the visceral disc, 3-6mm apart, although some specimens have few or no spines apparently over the ventral disc (BB 50989). Specimen B 408 is a well preserved large specimen, more transverse than material from Wales, with three or four rows of hinge spines and spines arising from a single costa, or from two costae that pass into one anteriorly. The dorsal valve lacks spines, and both valves carry low commarginal wrinkles. The cardinal process is low with a pit anteriorly as a rule, and brachial cones are developed, as in the specimen figured by Brunton et al. (2000, Fig. 376.1c), although the cones are not clear in their illustration, and lateral buttress plates are not clearly marked (Brunton et al. 2000, Fig. 378.1d), yet are present. Whilst there is some similarity to *Auriculispina* in costation and numerous ventral ear spines, the presence of brachial cones strongly indicates a relationship to *Gigantoproductus*, and the rare body spines lack posteriorly prolonged bases.

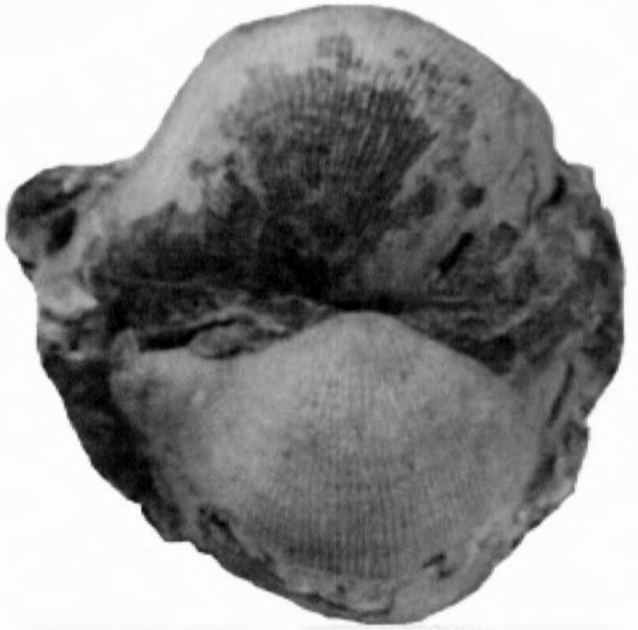


Fig. 16.32. *Linoprotonia hemisphaericus* (Sowerby), two ventral valves B 44314, x1.8 approx., figured by Davidson (1861, pl. 40, fig. 4) from Carboniferous limestone at Craven, Yorkshire, England, where the species is numerous. Davidson's figure showed numerous spines in a row along the hinge, now not clearly visible. JBW photo.

The numerous ear spines illustrated for *Linoprotonia* in Brunton et al. (2000, Fig. 378.1e) contrasts with those of the material assigned to *L. hikoroichiensis* Tazawa & Ibaraki (2009, Fig. 5.1-5 – see 5.5a,b) which has a single row of hinge spines only. It comes from the lower Hikoroichi Formation of Visean age in the southern Kitakami Mountains of Japan.

Brunton (1984) noted that the proportions of *Linoprotonia* were close to those of *Datangia* Yang De-Li, 1977, which has coarser ribs, similar arched ventral valve and convex ventral ears. He allowed that internally *Linoprotonia* was like *Gigantoproductus*, but considered that the fine ribs pointed to a linoproductid alliance. The observations need not be mutually exclusive, the ribs being linoproductoid and the cones gigantoproductin, though the ribs of Linoproductinae are not exactly the same as those of Gigantoproductinae, including *Linoprotonia*.

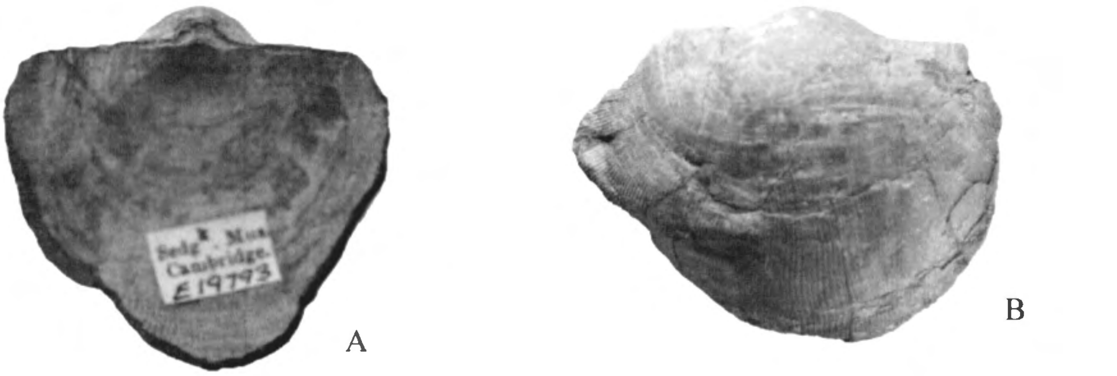


Fig. 16.33. A, *Linoprotonia corrugatohemisphaericus* (Vaughan), dorsal aspect of E 19793, x1.5, in boulder derived from *Cyrtina carbonaria* beds S2, Douk Gill Beck, Horton-in-Ribblesdale, west Yorkshire, England. B, *L. ashfeldensis* Ferguson, ventral valve BB 55750 from *Cyrtina carbonaria* beds, Westmorland (Cumbria), England, x0.9 approx. JBW photo.

Subfamily **SEMIPLANINAE** Sarytcheva, 1960

Fig. 16.34

[Nom. transl. hic ex Semiplanidae Sarytcheva, 1960, p. 231].

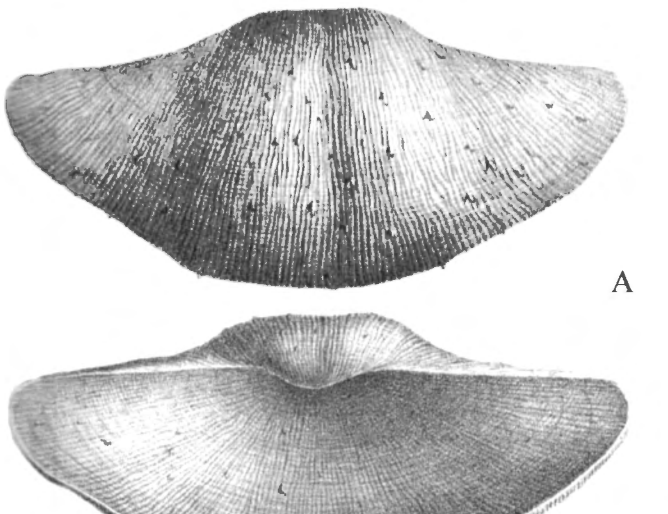


Fig. 16.34. *Semiplanus latissimus* (Sowerby). A. ventral view. B, dorsal aspect. From Lower Carboniferous of Ayrshire, Scotland, figured by Davidson (1861, pl. 35, fig. 1, 2), x1.

Diagnosis: Medium-size to large, ribs of varying width, spines on both valves or only ventral valve, dorsal septum broad but other dorsal ridges usually indistinct, no brachial cones. Lateral buttress plates present. Lower Carboniferous (middle Visean – lower Serpukhovian).

Genera: *Semiplanus* Sarytcheva, *Latiproductus* Sarytcheva & Legrand-Blain, *Semiplanella* Sarytcheva & Legrand-Blain, *Talasoproductus* Litvinovich & Vorontsova.

Discussion: Dorsal spines are developed in *Semiplanus* Sarytcheva, 1952, a fusiform genus with non-dendritic dorsal adductor scars, according to Muir-Wood & Cooper (1960, p. 333). The ribs increase on the ventral valve by intercalation and branching, and growth laminae and pauses are well developed. The spines may be numerous, and are erect on the trail, and although the nature of the spine bases is not entirely consistent over the disc, each costa often ramps up gradually to the spine, and the rib is finer in front. This is strongly suggested for Natural History Museum specimen B23533 from the Carboniferous Limestone in England, in which the ribs are slightly flatter and wider in front of the spine bases. Five or six rows of spines lie over the ventral ears. However *Semiplanus fragilis* Prentice (1956, pl. 22, fig. 3) shows round swellings on the ribs with central fine erect spines, and Prentice noted fine cardinal spines, at least five each side, and 5mm long. The dorsal adductor scars are striate. *Talassoproductus, Semiplanella* and possibly *Semiplanus* each appear to have low lateral buttress plates (Brunton et al. 2000, Fig. 392.1a, 392.1c, 2b). Given the lack of brachial cones, the source of the group may have differed from that of Gigantoproductinae, coming from a source allied to *Marginirugus* and allies, to suggest that the allegiances of Semiplaninae are uncertain. A relationship with Gigantoproductidae is indicated by the morphological congruence of shared lateral buttress plates and large size, and divergence suggested by the lack of brachial cones and the presence of posteriorly elongate spine bases.

Subfamily **MARGINIRUGINAE** new subfamily

Name genus: *Marginirugus* Sutton, 1938, p. 559 from the Keokuk Limestone of Missouri and Illinois (lower Visean), United States, here designated.

Diagnosis: Moderately large to medium-sized non-transverse costellate shells with well formed row of ventral hinge spines and other usually anterior fine ventral spines, no dorsal spines. Dorsal valve with hinge ridge, lateral buttress plates or mounds, and anderidia or lateral ridges, no brachial cones, moderate to thin body corpus, short trail, may be subgeniculate. Lower Carboniferous (Visean) to Upper Carboniferous (Bashkirian).

Genera: *Marginirugus* Sutton, *Balakhonia* Sarytcheva.

Discussion: At least some ventral spines over the visceral disc have slender elongate bases (see Brunton et al. 2000, Fig. 315a, f) and the interior is characterized by broad buttress mounds or ridges and slender anderidia. The dorsal interior is thus somewhat like that of Reticulumiini, a dictyoclostid tribe, and also Tapajosiini, a tribe within Linoproductidae, which is distinguished from the present tribe by having erect spines without prolonged bases. It is also close to Gigantoproductidae and Semiplaninae, and further inspection may confirm that the group displays spines like those of Wardlawriinae. Other than shape, many details within *Marginirugus* fall close to those of Semiplaninae, opening the possibility of tribal relationship.

Genus ***Marginirugus*** Sutton, 1938

Fig. 16.35

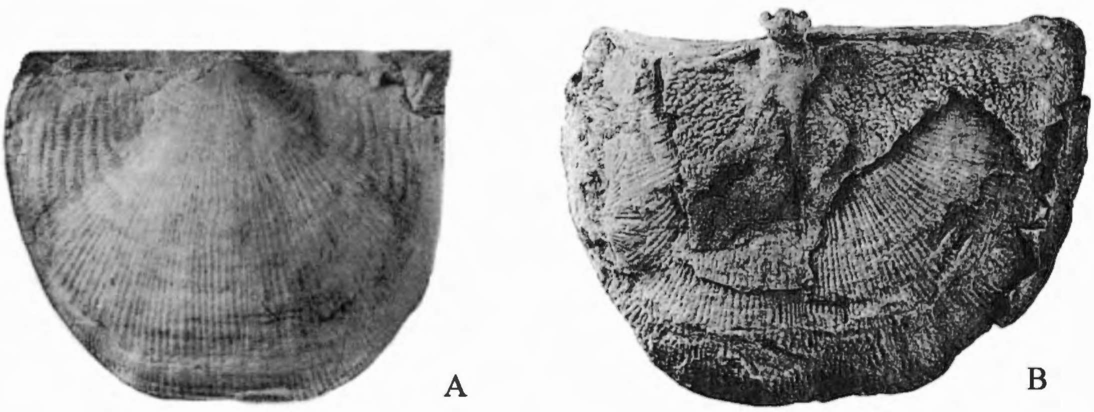


Fig. 16.35. *Marginirugus magnus* (Meek & Worthen). A, ventral exterior, USNM 124093. B, dorsal interior, USNM 119096, showing lateral buttress plates. From Keokuk Formation (Mississippian), Missouri, United States. See Muir-Wood & Cooper (1960, pl. 116, 117).

The genus *Marginirugus* Sutton, 1938 from the Mississippian of United States has linoproductoid ribbing, wide shallow-corpused disc and moderately developed trail, bearing a row of spines along the ventral hinge, and scattered ventral body spines that are generally erect although some do possess gently ramped bases; spines are erect anteriorly and over the trail. There are no dorsal spines. Adductor scars are strongly dendritic in both valves, and the cardinal process is trilobate in the type species *M. magnus* (Meek & Worthen, 1862, p. 142). A broad domal platform lies in front of the cardinal process, with pair of hinge ridges and short slender ridges like anderidia, and there is a thick but not high marginal ridge (Muir-Wood & Cooper 1960, pl. 116, fig. 4, 7). *Marginirugus* cf. *magnus* (Meek & Worthen) at the Natural History Museum, London, from 0.9mile south of My Judea, Arkansas, United States, shows small dendritic ventral adductors and weakly impressed almost smooth diductor scars in one specimen, and broad and striate diductor scars in another, in front of a small smooth non-pustuled floor each side of the dendritic adductors. Coarse pits also lie behind the diductors laterally, and fine pits lie in front over the floor of the valve, and seemingly over the posterior septum (Muir-Wood & Cooper 1960, pl. 116, fig. 4). Figures of *M. barringtonensis* (Dun, 1902, pl. 25, fig. 3, 5) from New South Wales, Australia, show distinct lateral buttress plates, as confirmed in Campbell (1956, pl. 50, fig.11).

Marginirugus Sutton was regarded as linoproductoid by Muir-Wood & Cooper (1960, p. 317), and as Productini by Brunton et al. (2000). Schrenkiellidae shows some approach but lacks lateral buttress mounds or anderidia in the dorsal valve, and its ventral spine bases are not prolonged.

Genus ***Balakhonia*** Sarytcheva, 1963

The genus *Balakhonia* Sarytcheva (Visean–?Bashkirian) is slender with body spines and moderately wide hinge, and Lazarev (2004) included the genus in Schrenkiellinae, and Brunton et al. (2000, p. 428) as Linoproductinae. The species illustrated as *B. kokdscharensis* (Groeber) from the Ostrogsk Suite by Sarytcheva (1963, pl. 38, fig. 4-8), and reported widely from Asia, has a very wide hinge with row of hinge spines. The type species, *B. ostrogensis* Sarytcheva (1963, p. 233, pl. 38, fig. 1-3) is less transverse and more vaulted. Body spines are not clear in these species, and some appear, uncertainly, to be erect – certainly there are no conspicuous elongate bases, although figures provided in Brunton et al. (2000, Fig. 365, 2a, b) of the holotype suggest slender posteriorly prolonged spine bases. Ventral adductor scars appear to be striate rather than dendritic, and the dorsal adductors carry strong grooves, suggestive of proboscidellid and especially auriculispinin rather than linoproductid links. The cardinal process is bilobed from a ventral perspective, broad and low, and the brachial shields are narrow and elongate. *B.silimica* (Semichatova, 1964, p. 192, pl. 3, fig. 2-5; Sarytcheva 1968, p. 149, pl. 21, fig. 2-7, pl. 22, fig. 1-3, Fig. 66) from the Bashkirian Stage of Bashkiria, north Russia, and reported from the Kokpectin Complex of Kazakhstan, has a row of strong spines at or in front of the ventral hinge and bilobed cardinal process and low dorsal hinge ridges, less widely divergent than in *Marginirugus*, which also differs in having a trilobed cardinal process. Two slender ridges support the cardinal process, although the relationship to adductor scars is not clear. In both *B. silimica* Semichatova and *B. insinuata*, as figured by Sarytcheva (1968, Fig. 65, 66), and in the type species *B. ostrogensis*, two broad ridges extend forward as lateral buttress plates from the cardinal process outside the adductor scars, and a slender pair of ridges extend as interadductorial ridges – or anderidia – and were interpreted as passing into the brachial shields (Sarytcheva 1963, Fig. 104a, pl. 28, fig. 3b). The anterior ventral valve of *Balakhonia similica* is swollen, differing in that regard from type *Balakhonia*, and having more acute and extended cardinal extremities and lower inflation and more anteriorly placed fold prolonged beyond the commissure, rather like *Schrenkiella* in many respects. Klets (2005, pl. 4, fig. 3-5) figured specimens from the Anomonan beds (Serpukhovian, Bashkirian) of northeast Russia. Somewhat similar material in Sarytcheva (1968, p. 147, pl. 20, fig. 1-7, Fig. 65) from the Keregetass Suite of west Kazakhstan was referred to *B. insinuata* (Girty 1911, 1915a, pl. 8, fig. 7, 8, pl. 9, fig. 1, 2a) from Wewoka Shale and Fort Scott Limestone of United States, and placed *Linoproductus oklahomae* Dunbar & Condra (1932, p. 251, pl. 44, fig. 1-2a) from the Stanton Formation of Oklahoma, in synonymy. Both American species are of Pennsylvanian age, and *oklahomae* has obtuse cardinal extremities, ovally transverse shape, less extended hinge, ventral hinge spines directed inwards, greater inflation and prominent ventral fold as in Schrenkiellinae (see p. 380).

Subfamily **WARDLAWRIINAE** Waterhouse, 2004b

[Wardlawriinae Waterhouse, 2004b, p. 39].

Diagnosis: Moderately large to medium-sized costellate shells with well formed row of ventral hinge spines and some to all ventral disc and trail spines with posteriorly prolonged bases, no dorsal spines, low commarginal rugae. Upper Carboniferous (Bashkirian) to Middle Permian (Roadian).

Genera: *Wardlawria* Waterhouse, *Lineabispina* new genus.

Discussion: *Wardlawria* is based on *Productus missouriensis* Sayre, 1930 from the Dekalb Limestone of Missouri, United States (Dunbar & Condra 1932, p. 252, pl. 28, fig. 1-5, pl. 29, fig. 6, 7; Muir-Wood & Cooper 1960, pl. 114, fig. 13-16; Waterhouse 2004b, text-fig. 4C). In size this genus approaches *Linoproductus*, but has very different spines over the ventral disc and trail: the spines are numerous over the disc and slender with elongate bases, unlike the large and rounded spines that emerge directly from the disc in Linoproductinae. Members of the tribe are even closer in shape to some Gigantoproductinae, being large, broad and with shallow disc, and the ventral spines with posteriorly prolonged bases resemble those of much more transverse *Semiplanus* Sarytcheva, 1952 of upper Visean age. This genus is older than *Wardlawria*, and it is deemed possible that Wardlawriinae are Upper Carboniferous survivors of gigantoproductid stock, which persisted as *Lineabispina* new genus into the Middle Permian Period.

Although the ventral spines over the body of the shell look externally like those of Auriculispininae, the much smaller size of genera in the latter subfamily points to a different lineage. Indeed, the elongate spines on the new genus *Lineabispina* appear to differ in so far as the core of the spine does not pass forward up into the spine, and then continue forward as a spine tunnel, as discussed and illustrated on p. 18 (see Fig. 11). The shell of this new genus is remarkably thin, allowing the course of the spine core to be analysed, and showing that no tunnels are present. Nor has any inner layer of shell been lost, as may be the case for Paucispiniferidae from the United States (see p. 418), because muscle scars are well preserved. Given these observations, coupled with the large size and the linoproductid nature of the ribbing, as opposed to the coarser and less regular ribbing typical of Proboscidelloidea, it is concluded that *Lineabispina* and its ancestral genus *Wardlawria* arose from Linoproductoidea, not Proboscidelloidea. The elongate spines are found over the trail, whereas in Proboscidelloidea, elongate spine bases occur over the ventral disc, and trail spines tend to be erect without prolonged bases.

Genus ***Lineabispina*** new genus

Derivation: linea – linen thread; bi – two; spina – thorn, Lat.

Type species: *Lineabispina ellesmerensis* new species from Assistance Formation (Roadian), Canadian Arctic, here designated.

Diagnosis: Medium large in size, ventral spines form row along hinge, scattered erect slender spines, and scattered or clustered larger spines with elongate bases over especially anterior disc and trail.

Discussion: The genus differs from *Wardlawria* in the presence of erect ventral spines over disc and trail without elongate bases, as well as spines with elongate bases: these are often larger than the erect spines.

Lineabispina ellesmerensis new species

Fig. 16.34 – Fig.16.40

Derivation: Named from Ellesmere island, Canadian Arctic, source of the material.

Holotype: GSC 136083 as figured in Fig. 16.34A, B, Fig. 16.40A from GSC loc. 26406, Assistance Formation, Canadan Arctic, here designated.

Diagnosis: Moderately large shells with broad ventral umbo, usually transverse and subcircular shape, and comparatively fine spines, a row close to the umbo and scattered disc and trail spines as strong as spines on the outer hinge, and distinguished by displaying posteriorly elongate bases, other disc and trail spines fine and erect.

Material: Fifteen ventral valves and three dorsal valves from GSC 26406, Assistance Formation, Devon Island, Canada. See Appendix A, part C, p. 479.

Dimensions in mm:

GSC specimen	Width	Length	Height
136078	42	44	21
136080	57	63	24
136081	47	47	20
136085	54	53	22

Description: Shells usually transverse, ventral umbo broad, as a rule 100-120°, and gently sloping and persistent

Fig. 16.34. *Lineabispina ellesmerensis* new genus, new species. A, B, ventral posterior and ventral aspects of ventral valve holotype GSC 136083, x1.4. The apparent spines to the right of the umbo in A are ribs from another shell fragment. From GSC loc. 26406, Assistance Formation (Roadian), Devon Island, Canadian Arctic. JBW photo.

umbonal slopes, ears may be large and convex and at maximum width, but poorly discriminated, the cardinal angle in some well rounded, in others bluntly angular at 75-80°. No sulcus, but some shells are flattened medianly, and a few specimens are more elongate with broad only gently convex venter and steep umbonal flanks. Dorsal valve gently concave, with large ears, and no fold and no nepionic area. A possible skirt is displayed by some specimens. The visceral disc of a specimen more than 70mm wide is only six mm thick, but is 9mm thick in a specimen GSC 136082 at least 46mm long and 42mm wide, a specimen that is exceptionally elongate. Ribbing is uniformly fine, six to seven in 5mm over much the ventral valve, rarely five in 5mm, and may form slightly irregular patterns. Ribbing covers the ears of both valves, and is slightly finer over the dorsal valve. Crests are narrow and interspaces U-shaped, and ribs arise by intercalation. Low rugae lie over the inner ears and over the outer umbonal slopes on some specimens, with very subdued rugae over the entire shell in a few specimens. Growth increments number between five and seven per mm. Spines lie in a moderately inconspicuous row close to the hinge, inner spines fine, the outer spines some 9mm from the umbo becoming more prominent at 0.6mm diameter and reaching 0.7mm diameter at 20mm from the umbo, and 1.3mm diameter at 25mm from the umbo in another specimen, but the diameter of outermost spines is not secure. Most spines over the disc and trail arise from the crest of a single rib, and measure less than 0.5mm in diameter, but on a number though not all specimens, larger spines are developed especially on the anterior disc and

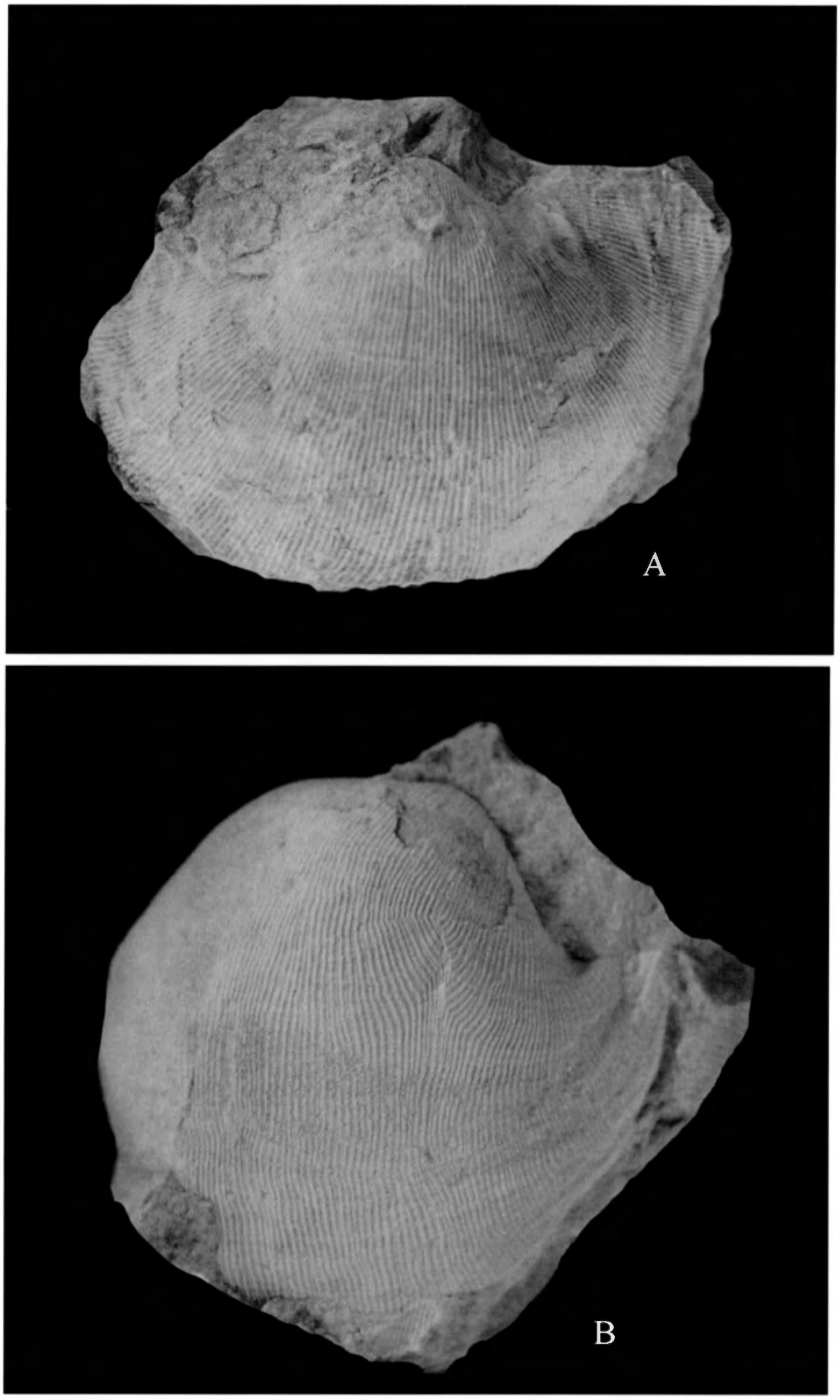


Fig. 16.35. *Lineabispina ellesmerensis* new genus, new species. A, ventral valve GSC 136077, x1.7. B, anterior view of ventral valve GSC 136085, x1.5, with few spines. From GSC loc. 26406, Assistance Formation (Roadian), Devon Island, Canadian Arctic. JBW photo.

trail, the largest 1.3mm in diameter, wider than any known hinge spine, and disrupting the costae, with five costae converging forwards into the spine, four passing forward from the base and then the inner pair merging into one. These spines have elongate bases often three or four mm long, and some spine bases are up to 7.5mm long. The ventral adductors are strongly dendritic, divided by a low myophragm, and impressed on very thin shell no more than 1mm thick. The diductors are very large, with radial grooves and ridges.

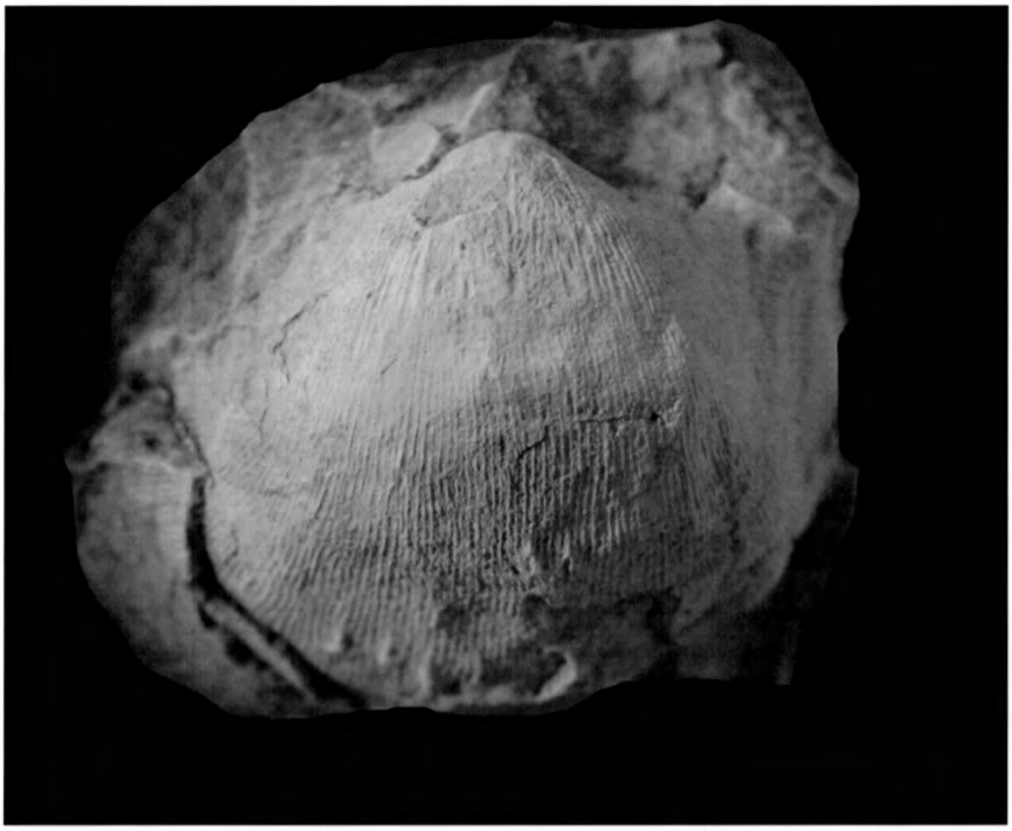
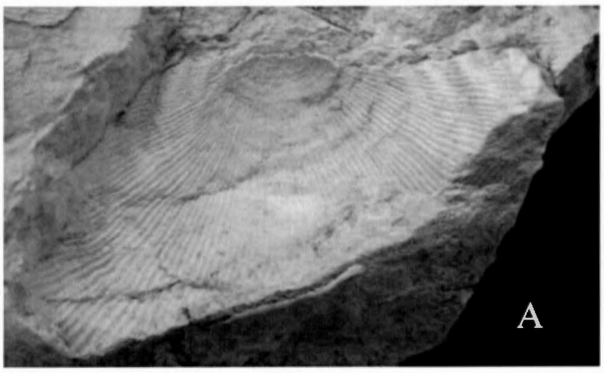


Fig. 16.36. *Lineabispina ellesmerensis* new genus, new species, ventral posterior aspects of ventral valve GSC 136080, x1.2. From GSC loc. 26406, Assistance Formation (Roadian), Devon Island, Canadian Arctic. JBW photo.

Fig. 16.37. *Lineabispina ellesmerensis* new genus, new species, ventral valve GSC 136081, x1.7. From GSC loc. 26406, Assistance Formation (Roadian), Devon Island, Canadian Arctic. Note similarity in shape, as with some other specimens, to the shape of *Linoprotonia* Ferguson (see Fig. 16.32). JBW photo.

Fig. 16.38. *Lineabispina ellesmerensis* new genus, new species, narrow ventral valve GSC 136078, x1.4. From GSC loc. 26406, Assistance Formation (Roadian), Devon Island Canadian Arctic. JBW photo.



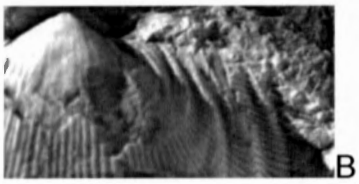
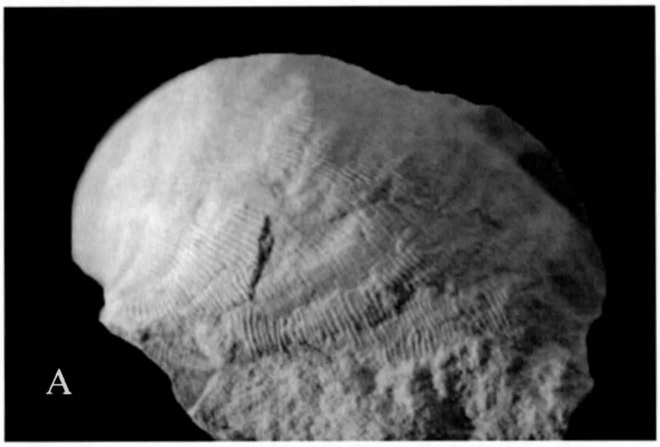


Fig. 16.39. *Lineabispina ellesmerensis* new genus, new species. A, dorsal valve GSC 136079, x2. B, detail showing ventral hinge spines, GSC 136084, x1.5. From GSC loc. 26406, Assistance Formation (Roadian), Canadian Arctic. JBW photo.



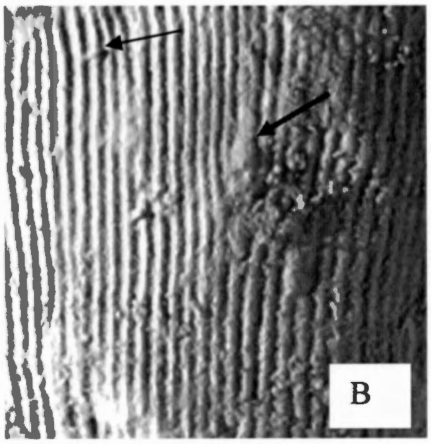


Fig. 16.40. *Lineabispina ellesmerensis* new genus, new species. A, lateral aspect of ventral valve holotype, GSC 136083, x1.5. B, detail of ornament showing coarse spines with elongate bases (thick arrow) and fine erect spines (fine arrow) on GSC 136078, x3. From GSC loc. 26406, Assistance Formation, Canadian Arctic. JBW photo.

Little of the dorsal interior is known. The dorsal median septum extends for two thirds of the length of the disc (GSC 136082), and the cardinal process lies largely in the plane of the visceral disc. In one very large but deformed specimen, small adductor scars are raised, and there is no sign of lateral buttress plates.

Resemblances: Unlike *Wardlawria missouriensis* (Say), the spines with elongate bases are not regularly arranged over the disc, and there are a number of additional spines with small bases. In general shape and ornament the two are close, but *missouriensis* has more commarginal rugae visible on the dorsal valve. The present species is moderately close to *Liniunus kaseti* (Grant, 1976), but has finer hinge spines. In other respects, the detail of body and trail spines comes close, but *kaseti* has no elongate ventral spine bases.

Subfamily **KANSUELLINAE** Muir-Wood & Cooper, 1960

Fig. 16.41 – Fig. 16.44

[Kansuellinae Muir-Wood & Cooper, 1960, p. 336].

Diagnosis: Large and transverse shells with prominent low commarginal rugae, ventral spines bearing elongate bases. Brachial cones developed internally, no lateral buttress plates, thin body corpus. Lower Carboniferous (Visean – Lower Serpukhovian).

Genera: *Kansuella* Chao, *Kueichowella* Yang Shi-pu, *Parakansuella* Tan Zhen-Xiu.

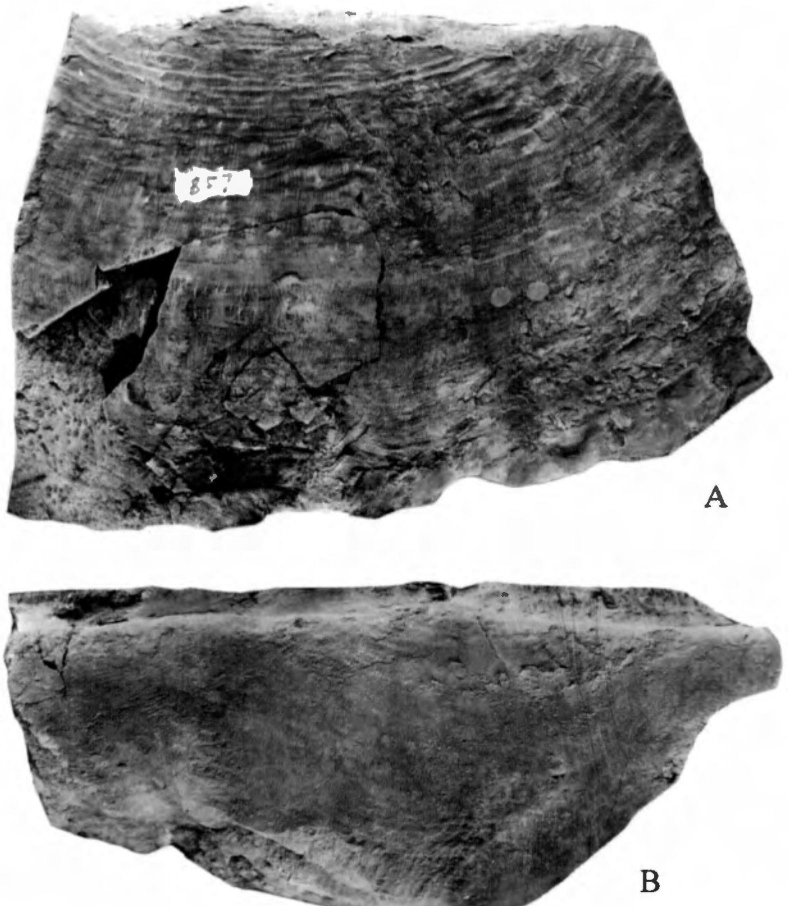


Fig. 16.41. *Kansuella kansuensis* Chao, x1, original specimens and topotypes, as described by Chao (1927), from Choniukou Formation (Visean), Cho-Nui-Kou, Wuwei City, Kansu, Gansu Province, China. A, ventral valve, cat. no. 857, figured by Chao (1927, p. 108, pl. 9, fig. 1). B, ventral view of a broken specimen figured by Chao (1927, pl. 10, fig. 1), paratype cat. no. 858. Specimens x0.9, photographs supplied by Chen Zhong-Qiang. Kept at Nanjing Institute of Geology & Palaeontology, Nanjing, P. R. China.

Discussion: The coarseness of the spine bases in *Kansuella* suggests a possible relationship to Permian Paucispinauriinae. *Kueichowella* Yang Shi-Pu in Feng & Jiang, 1978, p. 267 has closely spaced rugae and fine ribs like those of *Kansuella*. Unlike the apparently bilobed cardinal process of *Kansuella*, that of *Kueichowella* is simple and unifid, and there is no ginglymus. *Parakansuella* Tan Zhen-xiu, 1987, p. 123 appears to have a more inflated ventral umbo, and lacks such fine rugae. It is provisionally recognized but is poorly known internally. The type species of *Kansuella* has been reported in a number of studies, including Chen & Shi (2003, p. 157), but little has been added to the account in Muir-Wood & Cooper (1960), although these authors emphasized that the genus was not well understood. It is not clear from earlier studies whether or not lateral buttress plates are developed, and it appears from photographs provided by Dr Chen Zhong-Qiang, as confirmed in Chao (1927, pl. 9, fig. 2), that they are absent, differing in that respect from Semiplaninae or Gigantoproductinae, at least where known.

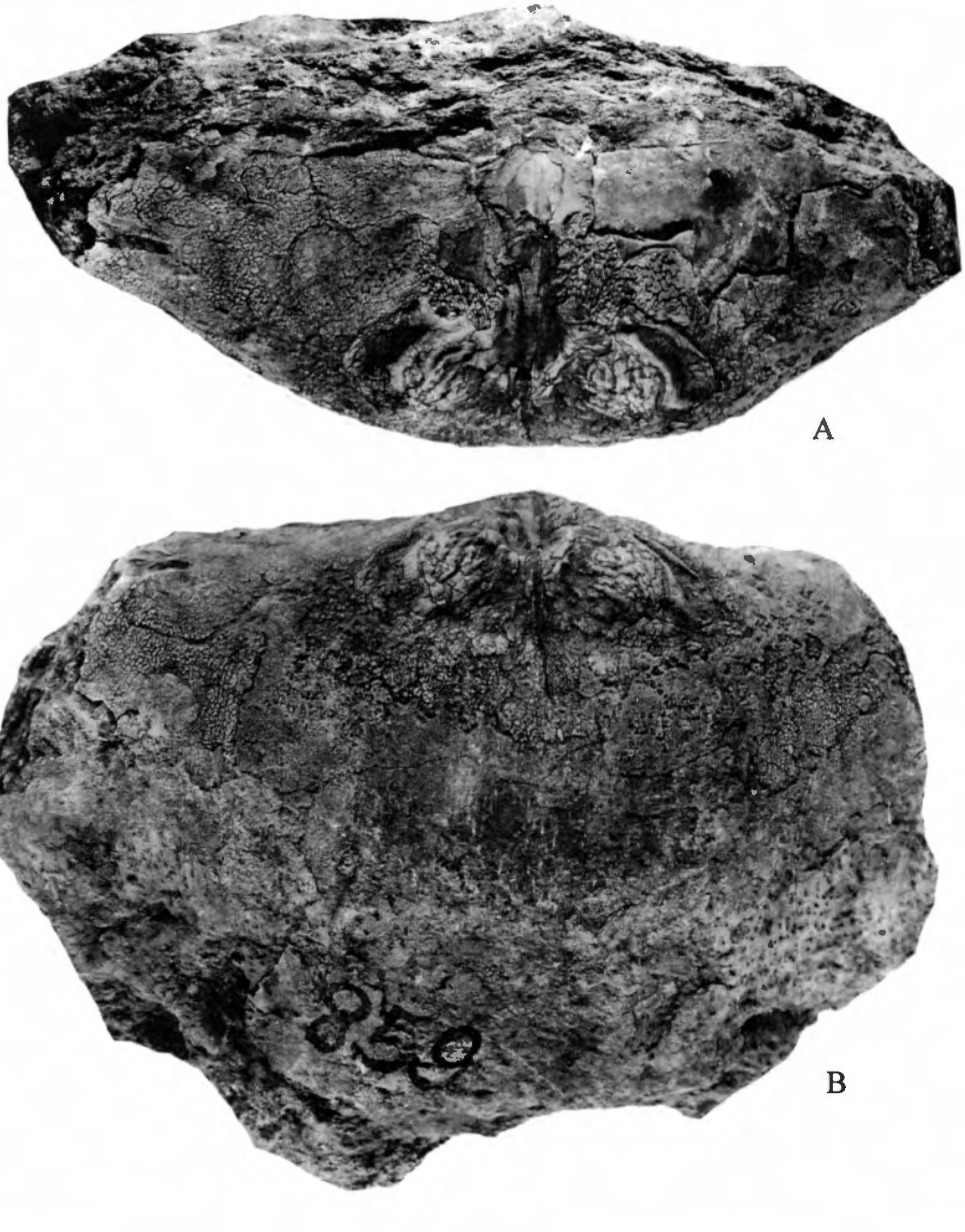


Fig. 16.42. *Kansuella kansuensis* Chao, from Choniukou Formation (Visean), Cho-Nui-Kou, Wuwei City, Kansu, Gansu Province, China. A, B, posterior and ventral views of topotype dorsal valve, cat. no. 859, figured by Chao (1927, pl. 9, fig. 2). Specimens x1, photographs supplied by Chen Zhong-Qiang. Kept at Nanjing Institute of Geology & Palaeontology, Nanjing, P. R. China.

Muir-Wood & Cooper (1960) treated Kansuellinae as a subfamily within Family Gigantoproductidae. Brunton et al. (2000) merged Kansuellinae with Gigantoproductinae, but spine detail, presence of low closely-spaced regular commarginal rugae, lack of lateral buttress plates, and muscle scars are very different, pointing to development from a separate source. However further study is required to consolidate the present classification.

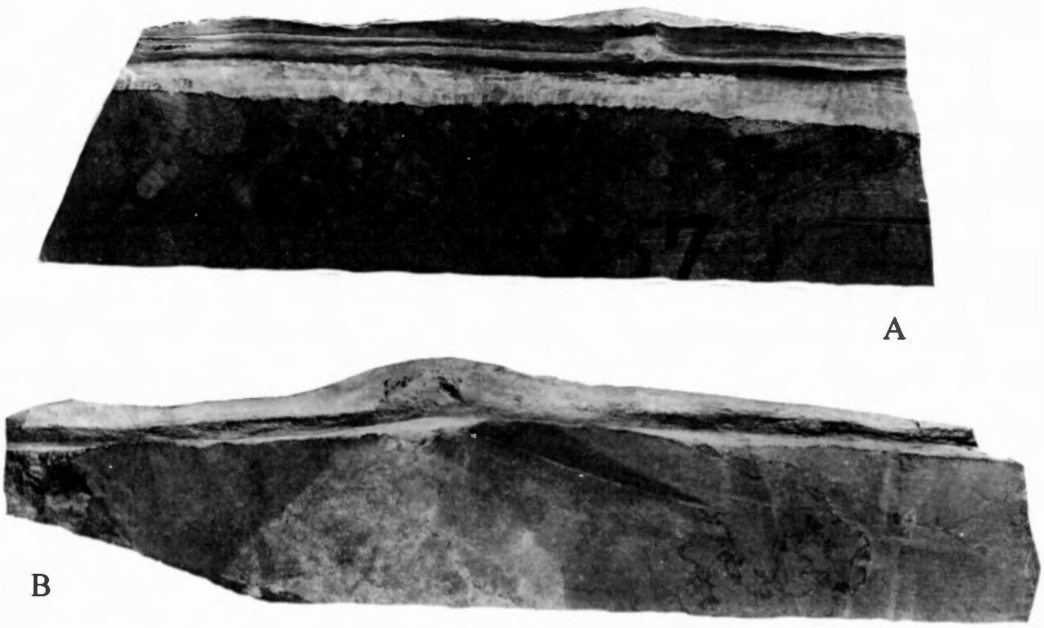


Fig. 16.43. *Kansuella kansuensis* Chao, from Choniukou Formation (Visean), Cho-Nui-Kou, Wuwei City, Kansu, Gansu Province, China. A, Dorsal valve interior, cat. no. 857, figured by Chao (1928, pl. 6, fig. 2). B, same specimen, more anterior view. Specimens x1, photographs supplied by Chen Zhong-Qiang. Kept at Nanjing Institute of Geology & Palaeontology, Nanjing, P. R. China.

Fig. 16.44. *Kansuella* sp.from Upper Visean of Scotland, also figured by Brunton et al. (2000, Fig. 389c), x1. Kept at Natural History Museum, London, England, B 5770. JBW photo.

17. Superfamily **PROBOSCIDELLOIDEA** Muir-Wood & Cooper, 1960

Fig. 17.1, Table 16

[Nom. transl. hic ex Proboscidellinae Muir-Wood & Cooper, 1960, p. 325].

Diagnosis: Both valves costate unless ribbing secondarily lost; ventral spines over disc with elongate bases.

Discussion: In Linoproductoidea the ventral disc spines are erect as a rule without posteriorly or anteriorly prolonged bases. In Proboscidelloidea spine-bases are prolonged posteriorly over the outer surface, and, in at least Permian and late Carboniferous members of the group, are prolonged forwards within the shell from the spine base (see Fig. 11, p. 18), as if keeping contact with the mantle edge (Waterhouse 2004a, 2010a). Possibly this explains the considerable degree of variability in the ribbing on the ventral valve, in contrast to the consistent pattern of ribs for members of Superfamily Linoproductoidea. Because ventral disc spines followed a tortuous course into and through the shell, they could never developed a substantial diameter, in contrast to spines which passed directly from the interior to exterior through the shell. In addition, commarginal rugae are widely present, and much more organized than in Linoproductoidea. The fossil record indicates that the two superfamilies arose each from within a different subfamily of Family Devonoproductidae, Superfamily Proboscidelloidea from Subfamily Plicoproductinae, and Superfamily Linoproductoidea from Subfamily Eoproductellinae.

Members of Proboscidelloidea are comparatively rare in Devonian and Early Carboniferous faunas world-wide. They seem to be scarce in China, where, as an example, Chen & Shi (2003, pl. 9, fig. 18, 19) were able to record only two specimens from Visean – Serpukhovian of the Tarim Basin, northwest China. Allies are also very rare in the Devonian and Early Carboniferous of Gondwana, and a number of studies on Australian Carboniferous faunas have found very few proboscidellans. But the family flourished during Permian time in high paleolatitudes as well as throughout the paleotropics.

Family Proboscidellidae Muir-Wood & Cooper, 1960

Subfamily Proboscidellinae Muir-Wood & Cooper, 1960
Subfamily Undariinae Waterhouse, 2001
Subfamily Fluctuariinae Nalivkin, 1979
Subfamily Dawesioniinae new subfamily

Family Paucispinauriidae Waterhouse, 1986a

Subfamily Paucispinauriinae Waterhouse, 1986a
Tribe Paucispinauriini Waterhouse, 1986a
Tribe Holotricharinini new subfamily
Subfamily Magniplicatininae Waterhouse, 2001
Tribe Magniplicatinini Waterhouse,2001
Subtribe Magniplicatininai Waterhouse, 2001
Subtribe Cancrinellinai new subtribe
Tribe Engellinini new tribe
Subfamily Coolkilellinae Waterhouse, 2001

Family Auriculispinidae Waterhouse, 1986b

Subfamily Auriculispininae Waterhouse, 1986b
Subfamily Filiconchinae Waterhouse, 2001
Subfamily Lyoniinae Waterhouse, 2001
Subfamily Siphonosiinae Lazarev, 1990

Family Stepanoviellidae Waterhouse, 1975

Table 17. Classification of Proboscidelloidea Muir-Wood & Cooper, 1960.

The source of the superfamily is believed to be Plicoproductinae Waterhouse, 2004b, p. 42, based on *Plicoproductus* Ljaschenko and *Striatoproductella* Krylova, of Early and Middle Devonian (Eifelian – middle Givetian) age. In these genera, spines are limited to the ventral valve, with posteriorly prolonged bases, and both valves bear ribs. The genera are strophalosiiform, with low interareas, small teeth and sockets (p. 308).

The classification contains several uncertainties. Two of the families, Paucispinauriidae and Auriculispinidae seem well established, and although diverse, classifiable in a number of subfamilies and tribes of principally Upper Carboniferous and Permian age, with some indications of Lower Carboniferous roots. But there is also an array of chiefly Lower Carboniferous groupings with few genera that are difficult to interrelate. They may each represent isolated developments, but their ancestry and successors remain obscure and to a degree conjectural, reflecting a failure of preservation or, as seems more than likely, the need for further study, and a problem that hopefully will be clarified from future work.

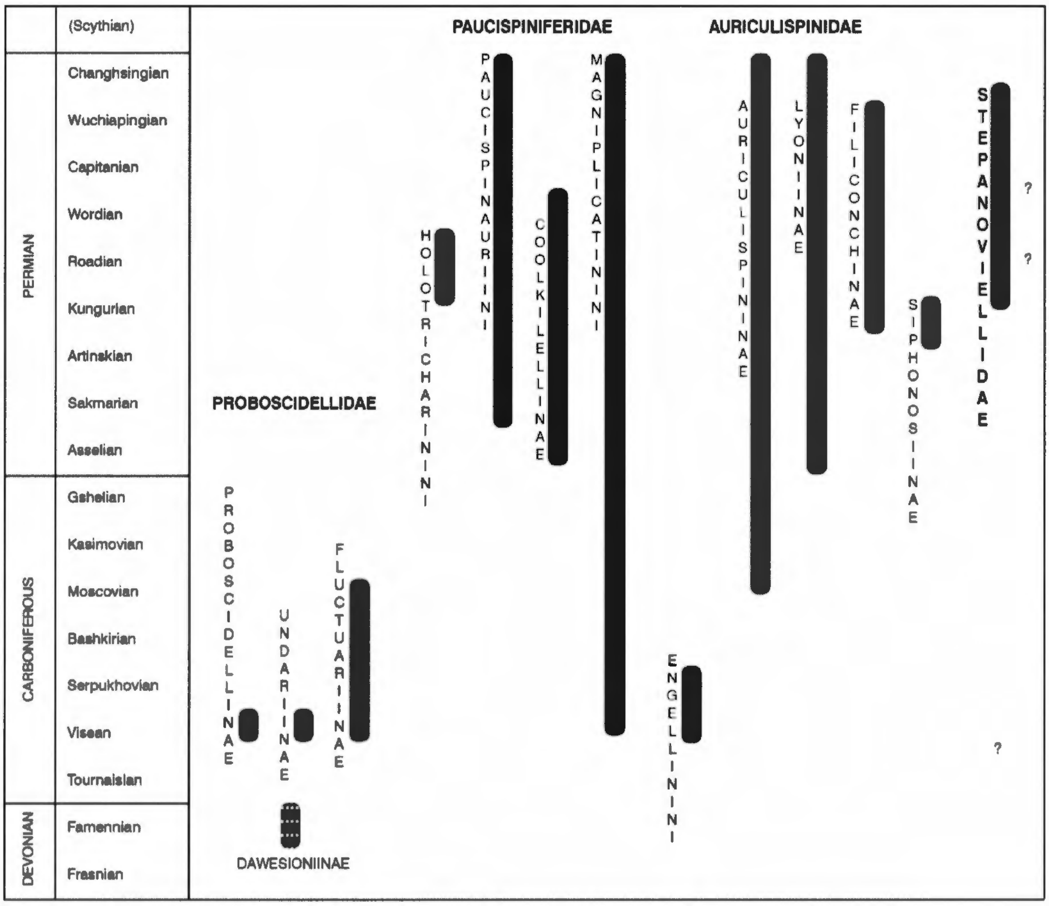


Fig. 17.1A. Range chart for Superfamily Proboscidelloidea.

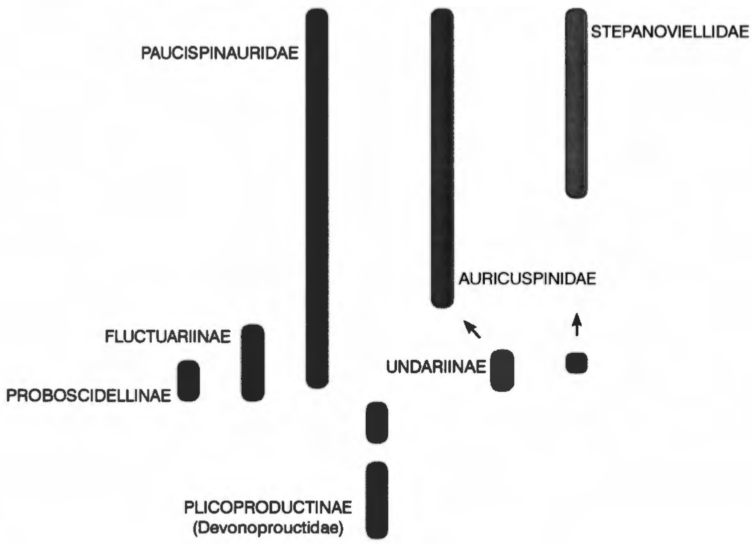


Fig. 17.1B. Simplified range chart for Proboscidelloidea Muir-Wood & Cooper, 1960 through Devonian to Permian. Fluctuariinae, and Proboscidellinae link with Paucispinauriidae, but Undariinae seem likely forebears of Auriculispinidae. Stepanoviellidae possibly has an early forebear, unnamed, in Ireland.

Family **PROBOSCIDELLIDAE** Muir-Wood & Cooper, 1960

[Nom. transl. Archbold 1983, p. 237 ex Proboscidellinae Muir-Wood & Cooper, 1960, p. 325].

Diagnosis: Spines over ventral disc have posteriorly prolonged bases, and often forward projecting spine tunnels. Regular commarginal rugae, no dorsal spines. Trail well developed. Cardinal process bifid.

Subfamily **PROBOSCIDELLINAE** Muir-Wood & Cooper, 1960

[Proboscidellinae Muir-Wood & Cooper, 1960, p. 325].

Diagnosis: Hinge narrow, trail long and tubular. Muscle field lightly impressed, dendritic. Lower Carboniferous (upper Visean).

Genus: *Proboscidella* Oehlert.

Discussion: *Proboscidella* Oehlert is an unusual genus with bifid cardinal process, unlike that of the unifid process in contemporaneous linoproductiform Striatiferinae. The nature of the spine bases is not clearly shown in the otherwise excellent figures provided by Muir-Wood & Cooper (1960, pl. 39, pl. 124), and the most conspicuous spines lie close to the hinge, and are erect without prolonged bases. Inspection of material from Visé, Belgium, kept at the Natural History Museum, London, shows that body spines have elongate bases.

Genus ***Proboscidella*** Oehlert, 1887

Type species: *Productus proboscideus* Verneuil, 1840, p. 259 from upper Visean of Belgium.

Diagnosis: Hinge narrow, ventral trail forms very long and irregular tube, with low rugae, elongate spine bases, no dorsal spines, cardinal process bilobed, dorsal marginal ridge.

Fig. 17.2. *Proboscidella proboscideus* (Oehlert). Ventral valve of B 18083, x4, from Settle, Carboniferous limestone, England. JBW photo.

Proboscidella proboscidea (Verneuil, 1840)

Fig. 17.2, Fig. 17.3

1840 *Productus proboscideus* Verneuil, p. 259, pl. 3, fig. 3a-d.
1960 *Proboscidella proboscidea* – Muir-Wood & Cooper, p. 325, pl. 39, fig. 14, 15, pl. 124, fig. 1-6.

Amongst specimens kept at the Natural History Museum, London, England, from the Lower Carboniferous of Visé, Belgium, B 45682 as figured by Muir-Wood (1928, pl. 12, fig. 16a, b) shows a few ventral spines with elongate bases,

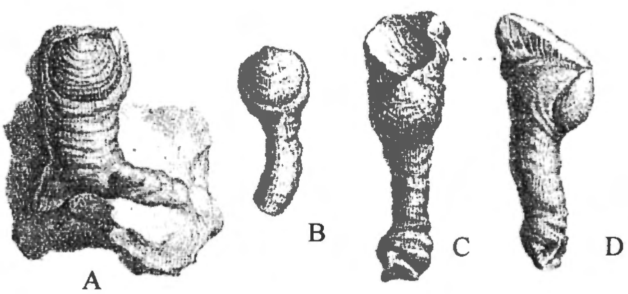


Fig. 17.3. *Proboscidella proboscideus* (Oehlert). Specimens figured by Davidson (1861, pl. 33, fig. 1-3) from Carboniferous limestone (Visean) near Settle, Yorkshire, England, x1.

better developed on B 13897. The dorsal median septum is long. In B 5814, from Visé, Belgium, ventral spine bases cross the interspace between wrinkles, or traverse one wrinkle and next interspace, or ramp up the posterior side of the wrinkle. B 18049 from Visé shows smaller spine bases three times wider than the ribs, and the rib may split into two in front of the spine. Specimen B 20011 (number obscured) from Lower Carboniferous, D_2, Castleton, Derbyshire, England, appears to have dendritic adductor scars on both valves.

Subfamily **UNDARIINAE** Waterhouse, 2001

[Nom. transl. hic ex Undariini Waterhouse, 2001, p. 34].

Diagnosis: Elongate oval shells, may be asymmetric, well formed long trail, fine diversified ribs, erect and prostrate ventral spines with prolonged and only slightly swollen bases, no dorsal spines, no well formed dorsal marginal ridge. Lower Carboniferous (upper Visean).

Genus: *Undaria* Muir-Wood & Cooper, ?*Donakovia* new genus.

Discussion: *Undaria* is another of those exceptional Early Carboniferous genera, of irregular shape, in some respects approaching *Proboscidella* Oehlert, but lacking the extravagantly long ventral tube and without any prominent dorsal marginal ridge. There is considerable approach to the Early Permian genus *Siphonosia* Cooper & Grant (1975, pl. 466), referred to Siphonosiinae Lazarev, 1990, and *Siphonosia* has elongate ventral spine bases over the ventral visceral disc, and elongate rhizoid spines posteriorly, short tubiform ventral trail, and marginal structures in both valves. Its double dorsal septum and different cardinal process show that the genus was derived from Auriculispininae. *Undaria* and *Siphonosia* were carefully compared and contrasted by Cooper & Grant (1975). Each genus appears to have arisen independently from different stock, and each represents an extreme and short-lived independent development.

Genus ***Undaria*** Muir-Wood & Cooper, 1960

Type species: *Undaria manxensis* Muir-Wood & Cooper, 1960, p. 317 from Isle of Man (upper Visean), England.

Diagnosis: Small with tubiform trail, low rugae and elongate spine-bases, cardinal process bilobed, dorsal median septum long and slender.

Undaria erminea (Koninck, 1842)

Fig. 17.4, Fig. 17.5

1842 *Productus ermineus* Koninck, p. 181, pl. 10, fig. 5.
1847 *P. ermineus* – Koninck, pl. 6, fig. 5, pl. 18, fig. 1.
1960 *Undaria erminea* – Muir-Wood & Cooper, p. 319, pl. 118, fig. 1, 2, 12, 13.

At the Natural History Museum, London, England, in the Koninck collection from Visé, Belgium, specimen B 44060 shows several sturdy spine bases on the ventral valve that are prolonged over the low wrinkles and into the preceeding wrinkle. There is a long dorsal median septum and heavy hinge ridge. Ventral spine base ridges also appear in B 64944. B 13897 from the Carboniferous Limestone of Gateham and Welton, Staffordshire, England, suggests that elongate hollows lie on the dorsal exterior, and that ventral hinge spines curve towards the umbo.

In the Davidson Collection from Lower Carboniferous at Settle, Yorkshire, England, BB 61537 shows dense ribs, four or five per mm, and a row of erect spines along the hinge, and spines over the anterior ear. There are short spine bases 0.6-0.7mm long, spines emerging two to four ribs apart from the crests of wrinkles, and the bases nearly twice as wide as the ribs. Specimens from Cork, Ireland, have more wrinkles and finer ribs (B 40210).

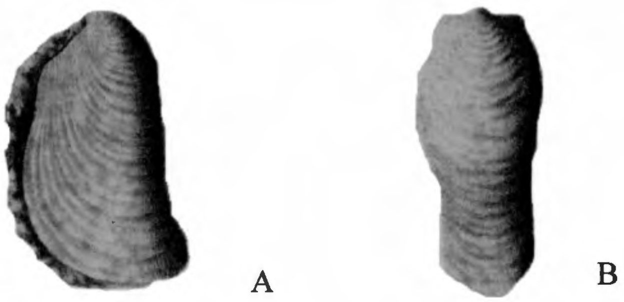


Fig. 17.4. *Undaria erminea* (Koninck), ventral aspects as figured in Koninck (1847, pl. 6, fig. 5), x1, from Visean of Belgium.

At the Sedgwick Museum, Cambridge, E 9519 from Lower Carboniferous at Settle has three or four rows of hinge spines and wrinkles somewhat like those of *Fluctuaria*.

Undaria manxensis Muir-Wood & Cooper, 1960 has a ventral valve which is less convex than that of *erminea*, and is evenly curved longitudinally, without a cincture or constriction at the start of the trail. The posterior dorsal septum in one specimen figured by Muir-Wood & Cooper (1960, pl. 118, fig. 7-9) shows a tiny double septum in front of the cardinal process, but only a broad septum lies in the same position in another shell (Muir-Wood & Cooper 1960, pl. 118, fig. 10, 11).

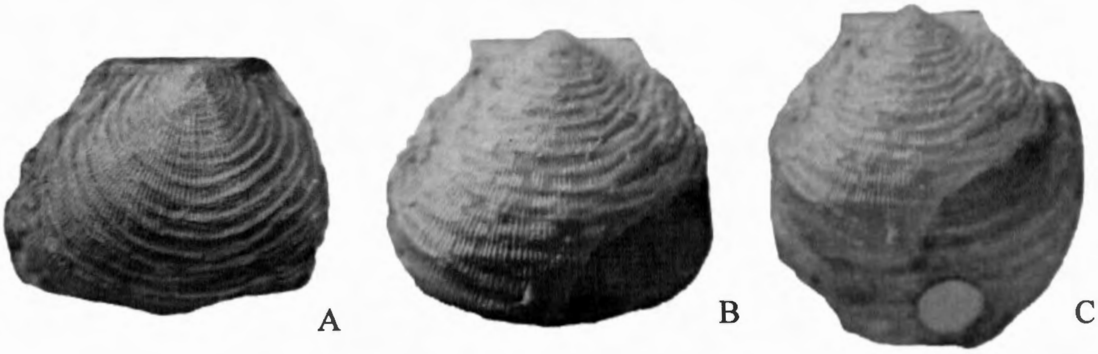


Fig. 17.5. *Undaria erminea* (Koninck). A, ventral valve E 10099, x2. B, C, ventral posterior and ventral anterior views of B 5749, x2, also figured by Davidson (1861, pl. 33, fig. 5). From Lower Carboniferous limestone at Settle, Yorkshire, England. JBW photo.

Genus ***Donakovia*** new genus

Fig. 17.6

Derivation: Named for L. M. Donakova.

Type species: *Ovatia markovskii* Donakova, 1975, p. 167 from Kipchask Horizon (lower Visean), southern Urals, Russia, here designated.

Diagnosis: Small, long ventral trail, subgeniculate dorsal valve, both valves ornamented by fine ribs and low closely spaced commarginal rugae, ventral valve with few hinge spines and elongate spine bases over venter. Cardinal process bifid, median septum apparently single. Ventral adductor platform raised posteriorly, striate.

Discussion: *Ovatia markovskii* as described by Donakova (1975, 1977) from Kipcak beds of lower Visean age in the southern Urals does not belong to *Ovatia*, because some ventral spines have elongate bases, and shells tend to be less vaulted, and hinge spines few, and closely spaced commarginal rugae cover both valves. The figures (Donakova 1975, p. 167, pl. 66, fig. 10, pl. 70, fig. 4; 1977, p. 120, pl. 28, fig. 1-5) suggest a proboscidellid form of moderately small size, both valves covered by costae, and no spines over the dorsal valve, which appears semi-geniculate. Of particular interest are the figures in Donakova (1975, pl. 66, fig. 10; 1977, pl. 28, fig. 2) which illustrate ventral valves with very long trail narrowing forward, and suggestive of the genus *Undaria* Muir-Wood & Cooper, 1960 from the Lower Carboniferous of Belgium and England. It is significant that both valves of *Undaria* bear even and closely spaced commarginal rugae, and somewhat similar rugation is developed in *markovskii*, and a bifid cardinal process is present in both genera. Unlike *Undaria, markovskii* has a less extended dorsal valve with subgeniculation, and lacks the dorsal pits that are well developed in *Undaria*. *Undaria* Muir-Wood & Cooper, 1960, p. 317, pl. 118 has a row of ventral spines along the hinge, and the ventral interior is not known according to Muir-Wood & Cooper (1960, p. 317) so that it cannot be confirmed if there was a large raised ventral adductor platform like that of *Donakovia*. In so far as *Proboscidella* has shallow dendritic adductor scars, the ventral adductor field of *Donakovia* indicates a different taxon and arguably different lineage. Present placement is provisional and reflects the number of proboscidelloid genera of early Carboniferous age yet to be fully sorted.

Commarginal rugae of *Donakovia* are not as coarse as those found in members of Fluctuariinae, nor *Globicorrugata* new genus, but are close to those of *Engellinus* new genus and *Proboscidella* Muir-Wood & Cooper. *Donakovia markovskii* differs from all of these genera in its ventral adductor field, which is raised and large, with a few longitudinal striae. It seems to lack conspicuous ventral hinge spines, with only two fine spines suggested at the hinge in the holotype (Donakova 1977, pl. 28, fig. 1). It differs from Auriculispininae in having a bifid cardinal process and inconspicuous hinge spines, but the species does suggest potential early stock which may have evolved into the subfamily, and appears to have been related to *Undaria* through shape, strength of costae and nature of ventral spines.

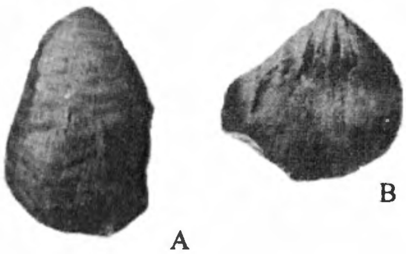


Fig. 17.6. *Donakovia markovskii* (Donakova). A, ventral valve showing fine rugae and elongate spine bases, No. 5/10848. B, interior of ventral valve, No. 7/10848. Kept at Tschernyschew Museum, St Petersburg, Russia. From Kipchask Horizon (lower Visean), Urals, x1. See Donakova (1977, pl. 28).

Ovatia markovskii was twice described as a new species by Donakova (1975, p. 167) and Donakova (1977, pp. 120, 121). The holotype is the same specimen in both studies, but the second published study adds more figured specimens.

Incerte sedis, aff Umariinae

Genus ***Sartenaeria*** new genus

Derivation: Named for Paul Sartenaer.

Type species: *Productus koninckianus* Verneuil, 1845, p. 273 from Visé (Visean), Belgium, figured by Koninck (1847, pl. 11, fig. 2a-e), here designated.

Diagnosis: Small, elongate and swollen shells with fine radial filae and very low wrinkles, disrupted by rounded or slightly elongate swellings bearing spines in quincunx.

Discussion: *Productus koninckianus* Verneuil, 1845, was named for Lower Carboniferous material from Belgium that Koninck (1842, pl. 9, fig. 3a, b) had called *P. cancrini* [not Verneuil], a name properly applied to a species largely characteristic of the Lower Permian Period and initially recorded from Russia. The Belgium material, confusingly changed in identification to *P. spinulosus* [non Sowerby] by Koninck (1847, p. 103, pl. 11, fig. 2a-e), has broadly rounded tumulae or monticules, lying athwart very fine costellae. From Koninck's figure, the specimen is approximately 15mm wide, 17.5mm long and 11.5mm high, the height being close to four fifths of the width. Davidson (1861, p. 230, pl. 53, fig. 7, a-c) illustrated a ventral valve of similar shape from Settle, northern England, with less swollen, slightly elongated, and more numerous spine bases, in nearly twice as many rows, and nearly twice as many spines across a row, so that his specimen, although congeneric, need not be conspecfic. Material like the original figures from Belgium is widespread, although not common, in the Early Carboniferous of England, and is represented at the Natural History Museum, London. B 53778 from D2 Thorpe Cloud, Derbyshire, has very low wrinkles, close-set ribs, and swollen spine bases that are not prolonged. The relationship to ribs is varied: one rib leads into the swelling, and two to four ribs continue forward from the base. B 48829 from Settle, Yorkshire, has low irregular wrinkles and small spines that are erect or have short elongate bases.

At the Sedgwick Museum, Cambridge, specimens E 9643 and E 9642 from Settle, renumbered E 50081 and 50092, have very fine radial lirae, 3-5 in 1mm, and tubercles in quincunx, and very low commarginal wrinkles about 1mm apart. The swellings do not change the number and nature of the ribs, and there are no clearly developed spines over the swellings. Spine bases slightly elongated, especially towards the side of E 50081, in which a few elongate spine bases are present, 2-3mm long and 1mm wide, and low wrinkles. This form thus differs from the Belgium species in the presence of a few elongate spines, yet otherwise is very close in the presence of the tumulae. Low concentric rugae are present, and the anterior is weakly nasute. One specimen measures 10mm wide, 14mm long and 8mm high, approximately. Another measures 10.5mm wide, 11.5mm long and 6.5mm high. No dorsal valves appear to be present, so that various details of this material remain to be determined, and the identity with *koninckianus* not fully secure. On the one hand, monticule-like swellings are present, on the other hand, spine bases may be slightly or substantially elongated, as if allied to Proboscidellinae, although specimens have only fine rugae, not as conspicuous as those of some other Lower Carboniferous genera within the subfamily.

These specimens differ from *Productus keyserlingianus* Koninck (1846, p. 239, pl. 14, fig. 6, a, b, c, d; 1847, p. 134, pl. 14, fig. 6, a, b, c, d), because *keyserlingianus* is transverse with swollen spine bases and apparently no radial lirae or commarginal rugae, but described as having light concentric growth striae by Koninck, to imply an avoniid relationship (Fig. 17.8). Specimens figured as *keyserlingianus* by Davidson (1861, p. 174, pl. 34, fig. 15, a-c, 16) are shown with very fine radial lirae but as these are not mentioned in the description, they might be simply a drawing device. Spines show swollen bases. The species *keyserlingianus* was not mentioned by Muir-Wood & Cooper (1960) under any generic heading.

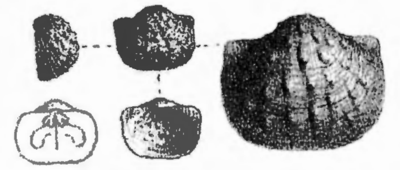


Fig. 17.8. *Productus keyserlingianus* Koninck as figured by Davidson (1861, pl. 34, fig. 15, a-c, 16) from Lower Carboniferous limestone at Settle, north England.

Sartenaeria koninckianus (Verneuil, 1845)

Fig. 17.9, Fig. 17.10

1842 *Productus cancrini* [not Verneuil] – Koninck, p. 179, pl. 9, fig. 3a, b.
1845 *P. koninckianus* Verneuil, pp. 253, 274.
1847 *P. spinulosus* [not Sowerby] – Koninck, p. 103, pl. 11, fig. 2a-e.

Lectotype: Specimen figured by Koninck (1842, pl. 9, fig. 3a ; 1847, pl. 11, fig. 2a-c), here designated. From Visean of Belgium, kept at Natural History Museum of Belgium, Brussels.

Fig. 17.9. *Sartenaeria koninckianus* (Verneuil). Original figures in Koninck (1847, pl. 11, fig. 2), x1, called *Productus spinulosus* not Sowerby. Visean of Belgium.

Taxonomy: Koninck (1842, p. 179) applied the name *cancrini* to Russian material sent to him by Verneuil, and to Early Carboniferous material from Visé, Belgium (1842, pl. 9, fig. 3a, b). In 1844, p. 475, Verneuil and Murchison included *Productus cancrini*, ascribed to Verneuil and Murchison, in a list of Permian fossils of Europe, and the list included Lower Carboniferous forms. Verneuil (1845, p. 273) mentioned the prior use of the name, which he attributed to Koninck and himself, and restricted *cancrini* to the Permian form from the River Solva in European Russia. The name *Productus koninckianus* was proposed by Verneuil (1845, p. 274) for the Belgium Lower Carboniferous material ascribed by Koninck to *cancrini*. In his later work, Koninck (1847, p. 105) confused *koninckianus* Verneuil with *P. spinulosus* Sowerby.

However the foregoing outline, reinforced by Muir-Wood & Cooper (1960, p. 301) and Gobbett (1964, p. 102), is contradicted by certain Russian studies, such as Netschajew (1911), Kashirtsev (1955, p. 77), Ifanova (1972, p. 110) and Ganelin & Lazarev (1999, p. 247). These authors regarded *koninckianus* as having been authored by Keyserling (1846, p. 203, pl. 4, fig. 4a-c), and considered that the species was based on Russian material of Permian age from south Timan, material which is extant and kept at the Mining Institute Museum, St Petersburg. Frebold (1937, p. 32) even indicated that the two taxa were one and the same, but this is not correct. Keyserling's species was distinguished from *cancrini* by its greater curvature and more inflated umbo of the ventral valve. The dorsal valve is deeply concave and spines arise from single lira. *P. cancrini* has a geniculate dorsal valve, and small distinct ears crowded with spines. Two lirae usually coalesce to form an elongated spine base. Netschajew (1911, p. 137, pl. 3, fig. 7-10, pl. 4, fig. 1) stated that *Productus koninckianus* was authored by Keyserling (without giving detailed synonymy), and figured specimens with fine ribs and numerous spines that lack noticeably swollen bases. There must be some caution about this Russian view, given that the publication by Keyserling (1846) work post-dated that by Verneuil (1845), and it is difficult to escape both the early history of nomenclature, and the more recent clear repetitions by Muir-Wood & Cooper (1960) and Gobbett (1964) which confirm the early work, as well as other studies that used the specific name in the sense of Verneuil, rather than Keyserling (eg. Toula 1873, p. 282; Renz 1940, p. 153, pl. 3, fig. 12a-d; Liao 1979, pl. 2, fig. 27, 28), although in fact different taxa were involved. Tschernyschew (1902) shortened the Keyserling name to *konincki*, and was more or less followed by Wiman (1914, p. 71), perhaps to avoid homonymy, but invalid as an emendation, in so far as the emendation was not formalized. The use of *koninckianus* sensu Keyserling (1846) seems to be in defiance of all but some Russian literature, and it would appear best to resolve the conflict by assigning a new name to Keyserling's material, for which the types are extant, and for which revision has been provided by Ganelin & Lazarev (1999). Here the Russian form is renamed *ganelini* new species (see p. 445), and ascribed to *Costatumulus*, an auriculispinid.

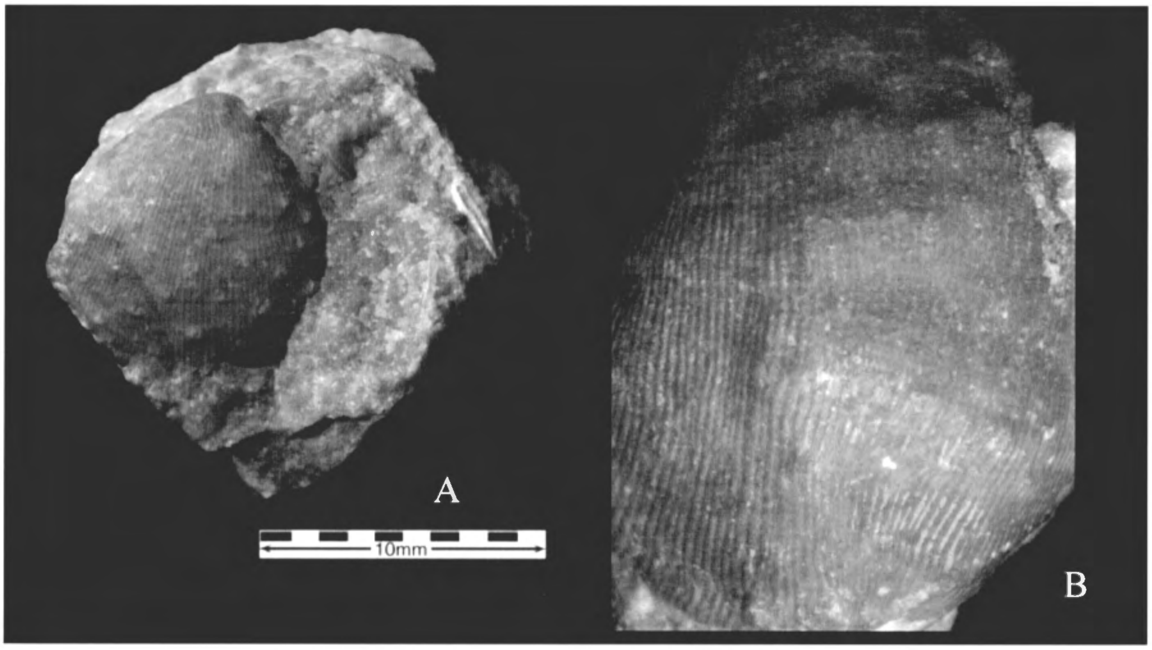


Fig. 17.10. *Sartenaeria koninckianus* (Verneuil)? Ventral valves at Sedgwick Museum. A, E 50081 with scale. B, anterior ventral valve, E 50092, 11mm wide. From Carboniferous Limestone at Settle, England. Photographs supplied by E. Harper & Matt Riley.

Subfamily **DAWESIONIINAE** new subfamily

Name genus: *Dawesionia* new genus from Milkman Member (Famennian) of Queensland, Australia, here designated.

Diagnosis: Costae strong, irregular posterior low fine rugae over both valves, ventral valves include anterior spines with elongate bases. No long trail or strong rugae.

Genus: *Dawesionia* new genus.

Discussion: This group stands apart from the other members of the family in lacking a long trail, and having finer and more posterior rugae. Spines are restricted to the ventral valve, and critically, include a few along the hinge and scattered anterior spines with elongate bases. There is a central rib with erect spines, and this is regarded as a generic feature, like that of *Diadematia* Waterhouse in the Ovatiinae. Unlike Ovatiinae, the ribbing is coarser and less regular, more like that of Proboscidelloidea, especially younger members in Paucispinauriidae and Auriculispinidae with more regularly disposed ventral spines. The spine bases are much less conspicuous, and narrower than in *Plicoproductus* Ljaschenko or *Striatoproductella* Krylova of the Devonoproductidae, and as well dorsal pits are developed in these genera, which are further distinguished by the presence of teeth, sockets, and interareas. The ribs are strong and occasionally branch, to recall *Asperlinus* of the Lamiproductinae, at present interpreted as a member of Anidanthidae. With such a meagre fossil record, it seems likely that *Dawesionia* represents a cryptic group, yet to be clarified.

Genus ***Dawesionia*** new genus

Derivation: Named from Dawes Range, source of the fossil.

Type species: *Dawesionia milkmani* new species from Milkman Member (Famennian), Cania, Queensland, Australia, here designated.

Diagnosis: Long umbonal slopes, and closely spaced fine ribs over both valves, bearing erect ventral spines along a median row, and a few spines, some with elongate bases, no dorsal spines. Fine commarginal growth lines or subrugae posteriorly on both valves.

Discussion: The genus is distinguished by its strong costae and spines with elongate bases, scattered over the ventral valve, with no hinge row, but forming a median row of erect spines and fine commarginal lineaments. *Diadematia* Waterhouse, 2004, p. 34, based on *Productus nodosus* Newberry, 1861, p. 124 from Morrowan faunas of New Mexico, United States, and further revised by Sutherland & Harlow (1973, p. 56) is also costate, with median row of ventral spines, fine and well formed regular ribs, and no other spines, and is judged to be ovatiid, because of the fine and even ribbing. *Igniculus* new genus is close to *Dawesionia* new genus in shape, but lacks a median spine row and has most spines aggregated over the ears (p. 375). *Eoproductella* Rzhonsnitzkaya, 1980 has fine ribs and erect ventral spines, but shows no median row, and no fine subrugae, and lateral spines are thicker. The hinge apparatus is well distinguished, with interarea, teeth and sockets in *Eoproductella*, but there is no such sign of these features in the Queensland form. The type species of *Dawesionia* was hesitantly referred to *Mesoplica* Reed, 1943 in earlier studies, but has finer although stronger ribs, unlike those of any horridonioid, although the median row of ventral spines does provide a degree of similarity.

The ribs are much less regular and subevenly spaced than those characteristic of *Ovatia* and allies.

Dawesionia milkmani new species

Fig. 17.7

1967 *Mesoplica* aff. *praelonga* [not Sowerby] – Hill, Playford & Woods, pl. D13, fig. 6, 7.
1968 *Mesoplica* aff. *praelonga* – Dear, p. 6, table 1.
1970 *Mesoplica?* sp. McKellar, p. 25, pl. 6, fig. 1-4.

Derivation: Named from Milkman Creek, Cania, Queensland.

Holotype: GSQ F 11404 (Fig. 17.7) from Milkman Creek Member (Famennian), Queensland, Australia, here designated.

Diagnosis: As for genus.

Material: Bulk collections are housed at the Queensland Museum storage centre from a number of localities, as recorded by Dear (1968). See Appendix A, part A, p. 477.

Fig. 17.7. *Dawesionia milkmani* new genus, new species, holotype GSQ F 11404, x1.5, from Milkman Member (Famennian), Cania, Queensland, Australia. See McKellar (1970, pl. 6, fig. 1b).

Description: The species was described by McKellar (1970). Outline subquadrate and anteriorly spreading, with the holotype measuring 25mm in width and 18mm in length, and maximum width near the anterior third of the shell length. There are prolonged ventral umbonal walls and no ventral sulcus or dorsal fold. Ribs are very fine, seven to nine in 5mm on the flanks, arise within three mm of the umbo and bifurcate often, even splitting into three ribs over the trail, with the median rib intercalated. A pair of low costae passes along the mid-line in many specimens, and anteriorly lateral ribs converge on this pair. Dorsal ribbing is somewhat similar, but may commence a little further from the hinge, and ribs converge on a median furrow. Ears lack ribs but are marked by the rugae. A row of coarse erect ventral spines lies along the mid-line, 2-3mm apart, and fine prostrate or suberect spines arise each side, a number with elongate bases gradually emerging from costal crests. Both valves bear fine closely spaced and low commarginal rugae, nine in 5mm on the ventral umbonal region, and about fourteen in 5mm on the dorsal valve. The dorsal interior displays fine and short hinge ridges, and a low and narrow median septum extending as far as mid-length.

Resemblances: The species shows little resemblance to other known forms and McKellar (1970) dismissed any similarity to *Mesoplica praelonga* (Sowerby). The strength of the costae and the way they branch recalls aspects of Lamiproductinae Liang (see p. 335), and further assessment may be required.

Subfamily **FLUCTUARIINAE** Nalivkin, 1979

[Fluctuariinae Nalivkin, 1979, p. 107].

Diagnosis: Small highly vaulted elongate shells with prominent commarginal rugae, spines numerous close to ventral hinge and varying over ventral valve, arising from crest of wrinkles. Body corpus thin to moderately thick, cardinal process bifid. Lower Carboniferous (upper Visean) to Upper Carboniferous (Bashkirian or Moscovian).

Genus: *Fluctuaria* Muir-Wood & Cooper, *Barringtonia* Waterhouse, *Tortilisia* new genus.

Discussion: The proposal of Subfamily Fluctuariinae was ignored by Brunton et al. (2000), who referred *Fluctuaria* to Linoproductinae, although differences from that subfamily are substantial. The presence of strong commarginal wrinkles and the generally bifid cardinal process suggest a closer approach to *Proboscidella* Muir-Wood & Cooper and other Early Carboniferous genera that display commarginal rugae and bifid cardinal process, rather than to Linoproductidae. *Fluctuaria* is not easy to interpret because the wrinkles are so strong that much internal detail is masked. The excellent illustrations provided for *Fluctuaria* by Muir-Wood & Cooper (1960, pl. 115) are not fully representative, in that many specimens identified with the type species show a pronounced swelling of costae (not swellings of the shell with several ribs as in *Sartenaeria*) as they cross the crest of the wrinkles, and the illustrations in Muir-Wood & Cooper (1960) show this for only parts of some specimens, as weakly suggested in Muir-Wood & Cooper (1960, pl. 115, fig. 14). The swellings on *Fluctuaria* to some extent recall the monticules of Monticuliferidae Muir-Wood & Cooper, 1960, but in detail are not very similar. The overall aspect of the swellings, the strongly defined costae and wrinkles, the numerous spines along the hinge, and bifid cardinal process in *Fluctuaria* suggest that other genera with commarginal rugae and fewer hinge spines and more body spines bearing conspicuously elongated bases, and trifid or quadrifid cardinal process need not be closely related, and whilst they could have been allied to Fluctuariinae, they at least equally might have been derived independently. Thus genera such as *Cancrinella, Magniplicatina* and *Auritusinia* with strong plications were classed by Waterhouse (2002b) in Magniplicatini Waterhouse, 2001, of Paucispinaurinae. These have a cardinal process that is trilobed rather than bilobed, but sometimes display a narrowly separated double septum posteriorly in the dorsal valve, possibly approaching what appears to be a double septum of the dorsal interior figured for *Fluctuaria* by Muir-Wood & Cooper (1960, pl. 115, fig. 13; Brunton et al. 2000, Fig. 366.2b). Although most genera of Paucispinauriidae lack strong wrinkles, they possibly arose from stock that included *Dawesionia* (see opposite), and involved genera contemporaneous with *Fluctuaria* and allies, such as Engellinini (p. 431) and *Globicorrugata* (p. 424). *Ovatia* Muir-Wood & Cooper is close in overall shape, with lateral wrinkles, but disc and trail wrinkles are absent or subdued and wrinkles do not carry small protuberances. Spines are low and moderately in quincunx, without prolonged bases.

Genus ***Fluctuaria*** Muir-Wood & Cooper, 1960

Type species: *Productus undatus* Defrance, 1826, p. 354 from Visean of Belgium.

Diagnosis: Highly vaulted small shells with varied ribs and strong wrinkles, spines restricted to ventral valve, in a few well defined rows along the hinge, and rare over disc and trail, costae often swollen over crests of wrinkles.

Fluctuaria undatus (Defrance, 1826)

Fig. 17.11

1826 *Productus ondé* Defrance, p. 354.
1843 *P. undatus* - Koninck, p. 156, pl. 12, fig. 2.
1847 *P. undatus* – Koninck, p. 59, pl. 5, fig. 3a, b, c.
1960 *Fluctuaria undata* – Muir-Wood & Cooper, p. 303, pl. 115, fig. 11-20.

Description: Lower Carboniferous material identified as this species has been examined in the Natural History Museum, London, and Sedgwick Museum, Cambridge, England. Notes are offered on material as labelled, though not all identifications need be specifically accurate, because the variation in ornament suggests the presence of more than one species. On the other hand, such species could have been more variable in their hinge ornament – a matter requiring closer study. In the Dr A. Lewis collection at the Natural History Museum, London, specimens B 18043-4 from Visé, Belgium, show very fine erect ear spines in three or four rows, and another specimen has only two rows. There are possible spines arising from the crests of the wrinkles and anteriorly, a few swollen, not elongate, swellings are developed. The swellings make the row of knobs at the crest seem to be linked by a low transverse rib. One of these specimens measures 26mm wide, 21.5mm long and 11.5mm high. Further Visé specimens from the Koninck collection at the Natural History Museum, London, include B 64738 with only one row of hinge spines on the ventral valve, and two or three prominent swollen not prolonged anterior spine bases. A specimen with the same registration number is unusual with low wrinkles and a few ribs that swell behind the spines, and bifurcate in front. One of these specimens measures 35.5 wide, 29 mm long and 17mm high with hinge 21.5mm wide, and another 35.5mm wide, 33mm long, 25.5mm high and hinge width at 27.5mm. The latter measured specimen has a weak ventral sulcus with nasute anterior, the wrinkles are moderately developed, and there are two rows of hinge spines with one or two spines anteriorly, with swollen rather than elongate bases. B 97485 in the Paul Mohr collection measures 26.5mm wide, 26.5mm long and 10.7mm high with thick visceral disc. There is a hinge row of tiny spines, which may be pointing to a separate species. Wrinkles are close-set and interspaces are subangular or trench-like and the crests are raised as nodes in concentric bands along the rugae, but disc spines are not clearly shown. The dorsal valve has low wrinkles and no nodes or spines. Spines at the broken anterior edge of a ventral valve in the collection B 97485 have a raised and thick ramp, and emerge from the crest of a growth wrinkle. B 422 from Bolland, England, also has one hinge row, as does B 97485. In B 23101 from near Castleton, Isle of Man, some spines are posteriorly prolonged with broad bases. There are two ribs per mm and one intervening slender rib, and rare anterior spine bases twice as thick as the ribs and nearly 2mm long, in a specimen 17mm long. Ribs bifurcate in front of the spine. Another specimen B 13844 has large scattered anterior spine bases that are not prolonged. On specimens from Redesdale, commarginal wrinkles tend to be subrounded, and spine bases are more elongate. B 337 from Craven, Yorkshire, is undulatiform and some spines arise from the crests of the wrinkles, with not very swollen or prolonged bases. Muir-Wood & Cooper (1960, p. 303) reported two hinge rows of spines on ears.

Rare spines on B 5788 from Campsie, Stirlingshire, Scotland, show a little ramping to crests, with one hinge row on another specimen and no dorsal spines. On one of six specimens the spine base passes over the posterior back-tread of the wrinkles into the anterior face or to the crest of the next wrinkle. Other specimens have slightly raised posterior ramps or swellings.

Fig. 17.11. *Fluctuaria undata* (Defrance), ventral valve BB 18952, x3. From Lower Carboniferous of Belgium. JBW photo.

At the Sedgwick Museum, Cambridge, E 10099 from Settle, Yorkshire, is of typical shape and wrinkling, with very fine and erect spines arising from crests of wrinkles, rarely thicker than the ribs. E 10100-16 from Settle are mostly 10-15mm long and the crests of wrinkles are more rounded than angular. A number of specimens lack strongly differentiated ribs, such as E 40197 and E 95493 from Little Island, Cork, and wrinkles are more angular in section than in specimens from Redesdale. Ribs are weakly differentiated in specimens E 58754-5 from Park Hill, D2, Derbyshire.

The species has been reported widely, though not reliably, but some reports indicate material that appears to belong to the genus, such as *Fluctuaria* cf. *undata* of Carter & Poletaev (1998, p. 136, Fig. 7.19 – 7.22) from Hare Fiord Formation of Atokan (Late Bashkirian or early Moscovian) age on Ellesmere Island, Canada. The ventral valve is less vaulted than in *undatus*, and the obscurity of hinge spines, at least from descriptions and figures, prevents secure specific identification.

Genus ***Tortilisia*** new genus

Fig. 17.12, Fig. 17.13

Derivation: Named from species, as applied by M'Coy, 1844.

Type species: *Producta tortilis* M'Coy, 1844, p. 116 from Lower Carboniferous of Ireland, here designated.

Diagnosis: Small with numerous strong and regular commarginal rugae and fine radial costellae, ventral spines close to hinge and rare over disc and trail.

Discussion: This species has been variously treated as a possible synonym of *Fluctuaria undata* (Defrance), or ignored, as by Muir-Wood & Cooper (1960). Like *Fluctuaria undata* it has strong wrinkles, but they are much lower and more numerous, with the difference between *Tortilisia* and *Fluctuaria* much greater than in better known genera represented by numerous species, such as *Cancrinella* Fredericks or *Magniplicatina* Waterhouse. In addition the ventral valve is much less vaulted and none of the fine ribs show swellings across the crests of rugae.

Fig. 17.12. *Tortilisia tortilis* (M'Coy), original figure presented by M'Coy (1844, pl. 20, fig. 14) from Carboniferous of Ireland, x1.

The holotype of *tortilis*, B 5799 (M'Coy 1844, p. 116, pl. 20, fig. 14), inspected at the Museum of Natural History, Dublin, Ireland, is supposed to lack spines, but a few are present with elongated bases, not thick, and the wrinkles are lower and more numerous than those of *Fluctuaria undatus*. Davidson (1861, p. 162, pl. 34, fig. 13) figured a similar specimen from Tullynagaigy, Fermanagh, Ireland. Amongst specimens from England that are kept at the Sedgwick Museum, Cambridge, E 10097 from shale in the Carboniferous limestone of Derbyshire, identified as *tortilis* M'Coy 1855, p. 474, is gently convex and has some 19 irregular wrinkles and deep interspaces, all of subequal size, whereas the wrinkles and interspaces of *Fluctuaria undata* are fine posteriorly and very strong, deep and high anteriorly. Spines have elongate slender bases less than 1mm wide and some 2.5mm long, and two rows of erect spines lie along the hinge with one or two more on the ears. In specimen E 11004 from Reef Knoll, Cracoe, west Yorkshire, a number of spiky nodes indicate spine bases over the ears: it is probably *Tortilisia*.

Fig. 17.13. *Tortilisia tortilis* (M'Coy), ventral valve BD 9966, from Lower Carboniferous at Thorpe Cloud, Derbyshire, England, x3. Note row of hinge spines. JBW photo.

Genus ***Barringtonia*** Waterhouse, 2010a

Fig. 17.14

The nature of the interior and the ventral disc and trail spines are facets obscure for *Fluctuaria* and *Tortilisia*. But these aspects are better preserved on a related genus from the southern Carboniferous paleohemisphere, *Barringtonia* Waterhouse, 2010a, p. 32, that does much to clarify affinities, because it shows spines that are better preserved, and a little more of the internal morphology. The type species was initially described as *Fluctuaria magnificans* Campbell & McKelvey, 1972, p. 32 from the Copeland Road Formation of Visean age in northern New South Wales, Australia. It is like *Fluctuaria* in overall shape, fine ribbing and strong rugation, and has close-set costae which are not differentiated. Spines, which are limited to the ventral valve, are erect and crowded over the posterior ventral valve near the hinge and over large ears, but are arranged in a cluster, not in rows as in *Fluctuaria*. Unlike

Fluctuaria, apart from some exceptions, nodes are not usually developed at the crest of the rugae, but the rugae bear crowded fine spines which may be hooked, and the costa behind each spine is slightly broader, suggestive of but not the same as the prolonged spine bases of *Proboscidella* and allies. The spines are arranged along the crest of the wrinkles: they thus lie in commarginal rows, not in quincunx like those of *Proboscidella* and especially members of Auriculispininae and Paucispinauriinae. The cardinal process is broad and bifid internally, with a deep alveolus, but the two lobes are less discrete than in *Fluctuaria*, and the dorsal median septum is single. Detail of the muscle field is obscured by the ribs from the exterior.

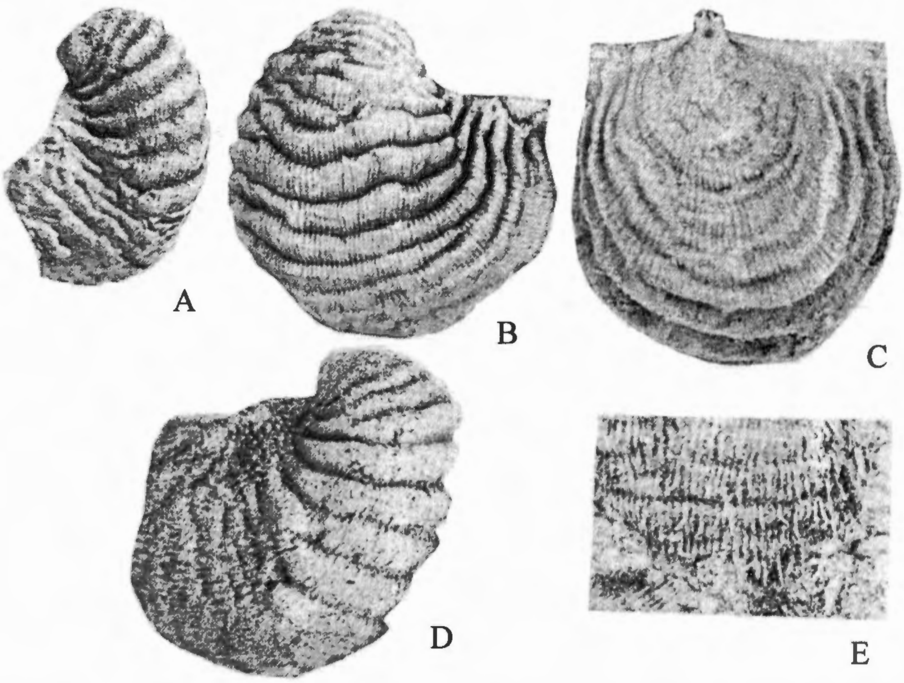


Fig. 17.14. *Barringtonia magnificans* (Campbell & McKelvey). A, lateral view of ventral valve, holotype, ANU 21511, x2.2. B, ventral lateral aspect of internal mould ANU 21870, x2. C, latex cast of dorsal interior, ANU 21512, x3. D, ventral lateral aspect of latex cast, ANU 21508a, x 3. E, detail of ornament, ANU 21507b, x3. From Copeland Road Formation (Visean), Barrington, New South Wales, Australia, as figured by Campbell & McKelvey (1972, pl. 1).

Family **PAUCISPINAURIIDAE** Waterhouse, 1986a

[Nom. transl. hic ex Paucispinauriinae Waterhouse, 1986a, p. 2. Syn. Grandaurispininae Lazarev, 1990, p. 130].

Taxonomy: Paucispinauriinae was proposed by Waterhouse (1986a, June, p. 2) at the same time as Grandaurispininae Lazarev (1986a, June, p. 32) was listed, but not proposed or discussed. Brunton et al. (2000, p. 533) claimed that Paucispinauriinae had not been proposed until September, 1986 (Waterhouse 1986b, p. 37), and did not acknowledge that the Lazarev proposal was in a list, with no diagnosis or explanation. Lazarev (1986a) did not provide a description or definition that stated in words characters which purported to differentiate the taxon (cs. International Commission for Zoological Nomenclature 1999, article 13.1, p. 17). Waterhouse (1986a) did provide a brief explanation, and indicated both the name genus and allied genera. The proposal was reinforced shortly afterwards by Waterhouse (1986b). Not until 1990 did Lazarev (1990, p. 130) provide validation, and its validity dates from 1990. Prior mentions, even though promoted by Brunton et al. (2000), carry no standing, according to the rules of zoological nomenclature. This was accepted without acknowledging any correction by Brunton (2007, p. 2652).

Diagnosis: Shells small to medium in size, ventral spines generally with elongate bases in regular quincunx over disc, crowded or rare over ears and in row or rows along hinge, dorsal spines usually present, crowded, erect, sometimes differentiated and unusually large for Productida. Radial ribs and weak to strong concentric rugae. Body corpus usually moderately thick and trail extended, often geniculate. Cardinal process trilobed, dorsal medium septum single or with shallow slit near the adductors, forming double ridge in some genera, but less markedly than in many Auriculispinidae.

Family relationships: Paucispinauriidae differs from Linoproductidae in having less well defined radial ribs that may be spaced further apart, and in ventral disc spines having prolonged bases. Various paucispinauriid genera have a thick body cavity as in Linoproductidae, but this is regarded as of lesser importance, because ontogenetic studies show that species and genera which are thin-disced at maturity could become thick-disced at a gerontic stage of development. A number of paucispinaurian genera carry thin and even thick spines also on the dorsal valve, and several otherwise similar genera differ only in the presence or absence of dorsal spines. Auriculispinidae have thin body corpus, less regular ventral spines, more transverse shape as a rule, and generally shorter and thinner ventral spine bases, and often no dorsal spines, which are thin if present. The ventral adductor scars of Auriculispinidae are striate until late maturity, and generally sited on a platform which is raised anteriorly and inset into the posterior wall posteriorly, whereas the ventral adductor scars of Paucispinauriidae are dendritic, and less impressed into the shell.

The origins for the family are not entirely clear. The oldest member appears to be Magniplicatininae represented by at least one genus *Globicorrugata* new genus in Visean faunas, and by genera of Engellini. It may be noteworthy that *Proboscidella* Muir-Wood & Cooper of comparable age and with bifid rather than trifid cardinal process may display somewhat paucispinaurian dendritic adductor scars, not to mention a very long trail.

Subfamily **PAUCISPINAURIINAE** Waterhouse, 1986a

[Paucispinauriinae Waterhouse, 1986a, p. 2].

Diagnosis: Ventral spines with spines crowded over both valves. Dendritic adductor scars, body corpus often thick.

Tribe PAUCISPINAURIINI Waterhouse, 1986a

Figs. 11, 13, 16, Fig. 17.15, Fig. 21.2 – Fig. 21.5

[Nom. transl. Waterhouse 2001, p. 35 ex Paucispinauriinae Waterhouse, 1986a, p. 2].

Diagnosis: Spines with elongate bases over visceral disc, dorsal spines present and may be differentiated. Permian (Sakmarian – Changhsingian).

Genera: *Paucispinauria* Waterhouse, *Appelinaria* new genus, *Bellaspinosina* new genus, *Grandaurispina* Muir-Wood & Cooper, *Pinegeria* Waterhouse, *Saetosina* Waterhouse, *Spargospinosa* Waterhouse, *Terrakea* Booker, ?*Vagarea* new genus.

Discussion: The evolution is summarized on pp. 459-464 as offering an example of development within a tribe. Genera are distinguished by spine pattern, including the distribution of thick and thin spines over both valves, as shown by Waterhouse (1986a, b).

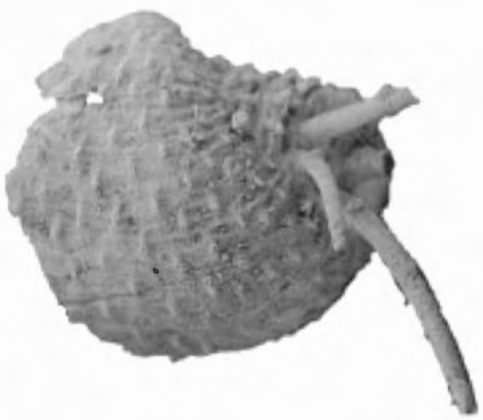


Fig. 17.15. *Grandaurispina kingorum* Muir-Wood & Cooper, oblique view of silicified ventral valve and ear, showing radial ornament and spines which are very large in the concavity between ears and umbonal slopes, and may show fine projections, BR 3052, x2. Silicified specimen from Appel Ranch Member (Capitanian), west Texas, United States. JBW photo.

Terrakea Booker was first described from the Permian of east Australia, and is represented there by a number of species. It was claimed by Waterhouse (1971b) that closely allied forms had been allocated to a different genus *Grandaurispina* Muir-Wood & Cooper, recognized in the late Early Permian and Middle Permian of United States. Cooper & Grant (1975, p. 1162) tried to refute the alliance, and in turn, Briggs (1998, p. 163) was dismissive of their objections. Some of their analyses relied on an inadequate understanding of the morphology and variation displayed by *Terrakea* and east Australian allies, concerning the cardinal process and dorsal median septum. But Cooper & Grant (1975) raised two aspects which require further consideration. According to Cooper & Grant (1975), *Grandaurispina* differed from *Terrakea* in displaying dimples in front of ventral and dorsal spines. But none of their numerous figures of ventral valves for *Grandaurispina* show such dimples, and dimples are not visible in the few specimens available for immediate study, nor are dimples present over the ventral valve of *Terrakea*. That objection is therefore set aside. There are dorsal dimples over Australasian *Terrakea* and United States *Grandaurispina*. A second difference lay in the nature of spine bases within the ventral shell, and this objection carries more weight. The spine bases form long spine tunnels in *Terrakea*, which were said to be absent from *Grandaurispina*. This would surely constitute a highly significant difference. As far as I can see, the observation by Cooper & Grant (1975) was correct: ventral spines in *Grandaurispina* appear to pass directly into the lumen of the visceral disc. Moreover the ventral disc spines have slightly elongate and rather swollen bases on some specimens, somewhat overtonioid in appearance. Yet the cardinal process and various internal details involving dorsal septum and papillation are comparable between suites of United States *Grandaurispina* and Australian *Terrakea*, and external appearance is close. What cannot be adequately compared is the nature of muscle scars, very poorly known for the American species. At present, the two suites are regarded as cotribal, as also concluded by Briggs (1998) and Brunton et al. (2000). But that admittedly downplays the significance of the ventral spine bases. Whether that reflects an evolutionary difference or an ecological one requires further study. Should the difference prove valid in an evolutionary sense, Grandaurispininae Lazarev, 1990 would embrace the genera from United States, as distinct from the Australian genera, and familial position would require further consideration. It is noteworthy that a Canadian species assigned to *Terrakea* by Waterhouse (1971b, pl. 1) clearly has spine tunnels, as in east Australian forms, and it may in turn reflect on the danger of relying on silicified material, in place of shells and moulds. It was allowed by Muir-Wood & Cooper (1960) and Cooper & Grant (1975) that ventral muscle scars were poorly preserved, often the adductors being faint and seldom dendritic, and virtually nothing being ascertainable of diductor scars: the same is true of material from west Texas that is available to me. This either is signifying a significant difference from Australian paucispinaurians, or alternatively implies that the inner shell of the ventral valve has been lost from specimens of Texas, and not replaced properly by silica. In that case, spine tunnels would be also lost, together with much of the muscle scars and papillation. Provisionally, this explanation is adopted. The matter might be most easily resolved by preparing Glass Mountains material that has come from clastic sediment, and has not been silicified.

Genus ***Appelinaria*** new genus

Fig. 17.16

Derivation: Named from source beds found just below Appel Ranch Member, Glass Mountains, west Texas, United States.

Type species: *Grandaurispina crassa* Cooper & Grant, 1975, p. 1164 from Appel Ranch Member (lower Capitanian), Word Formation, west Texas, here designated.

Diagnosis: Highly vaulted shells with only moderate ventral ear brush of comparatively thin spines, sturdy ventral disc and trail spines, dorsal spines of two different diameters, thick posteriorly, costae comparatively strong.

Discussion: The designated type species differs from *Grandaurispina* Muir-Wood & Cooper, 1960 in many respects. The ventral ear brush of spines is less developed, with thinner and fewer spines, and ventral body spines are comparatively thick. In the dorsal valve, the posterior lateral spines are much thicker than the fine spines over the rest of the valve, and approach in thickness those of the ventral ears and ventral lateral slopes, whereas dorsal spines in *Grandaurispina* are all slender. The shell is highly vaulted, with steep ventral lateral walls, ribbing is well defined, and the cardinal process very sturdy. *G. rudis* Cooper & Grant (1975, p. 1170) from the Getaway Member of the Cherry Canyon Formation, west Texas, is congeneric. Both species are Capitanian in the international scale, because the Appel Ranch Member of the upper Word Formation in west Texas is now treated as possibly Capitanian, but the type species is also found in a lens below the Appel Ranch Member, possibly of the same age, or perhaps Wordian.

No Australian genus is exactly comparable, and all species lack the sturdy postero-lateral spines of the dorsal valve. *Terrakea* Booker, 1929 has a strong burst of spines over the ventral ears and lateral slopes, and dorsal spines are stronger over the anterior trail, whereas they are only moderately thick over the trail in the American species. *Paucispinauria* Waterhouse, 1986a differs in the same way, but its postero-lateral ventral spines are thick but few in number, approaching those of *Appelinaria*. Ventral body spines are thick and ribs strong in *Paucispinauria*, but shells are more transverse with thinner visceral disc and the cardinal process less sturdy. The dorsal interior of

Appelinaria is like that of *Grandaurispina* in having posterior ridges slope forward from the hinge, whereas the comparable ridges in Australian and New Zealand species and genera lie closer to the hinge as a rule.

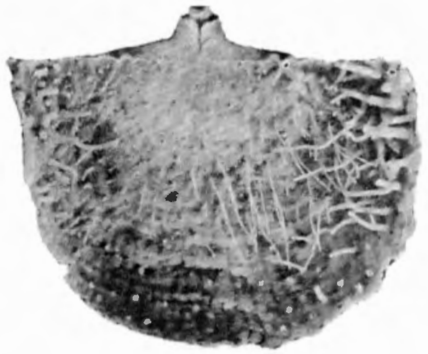


Fig. 17.16. *Appelinaria crassa* (Muir-Wood & Cooper), USNM 150018p, dorsal exterior showing coarse postero-lateral spines and thin anterior and central disc spines. From Appel Ranch Member (Capitanian), west Texas, United States, x2.5. See Cooper & Grant (1975, pl. 438).

Genus ***Bellaspinosina*** new genus

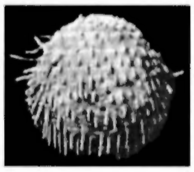
Fig. 17.17

Derivation: belle – neat; spina – thorn, Lat.

Type species: *Grandaurispina bella* Cooper & Grant, 1975, p. 1162 from Willis Ranch and Appel Ranch Members (Wordian, Capitanian), Word Formation, west Texas, United States, here designated.

Diagnosis: Vaulted and elongate shells with small ears, spines fine on both valves, erect over umbonal slopes, with short elongate bases over most of ventral valve, may be finer over the anterior disc and trail than over much of the ventral disc, spines fine, dense and erect over dorsal valve, dorsal dimples and pustules prominent.

Fig. 17.17. *Bellaspinosina bella* (Cooper & Grant), ventral valve USNM 149988b. From Willis Ranch Member (Wordian), Glass Mountains, Texas, United States, x1. See Cooper & Grant (1975, pl. 442, fig. 8).



Discussion: *Bellaspinosina* is characterized by its almost uniformly fine spines over both valves. It is thus readily distinguished from *Grandaurispina* Cooper & Grant, 1975, which has prominent and thick halteroid spines along the umbonal slopes of the ventral valve, and differs from *Appelinaria* new genus which has thicker ventral spines, stronger radial ribs and spines of two different diameters over the dorsal valve. In the nature of the spines, the new genus comes closest to *Saetosina* Waterhouse, 1986b, based on *Terrakea multispinosa* Dear, 1971 from the Flat Top Formation of the southern Bowen Basin, Queensland, Australia, of upper Wordian age. *Saetosina* shows similarly fine and dense spines over both valves, and although the ventral spines tend to be slightly more prostrate over the ventral disc, and the body shape is more transverse with larger ears and thinner visceral disc, such differences need not be of generic significance, allowing the possibility that either both arose from common stock, or the American species perhaps evolved from the Australian form. But there are further, if slight, differences. The spines on the American form are more regularly disposed over disc and trail, whereas those of the Australian species *multispinosa* tend to show banding, with slight differences in diameter and even bands with few or no spines (see Dear 1971, pl. 7, fig. 2b; Waterhouse 1986b, pl. 13, fig. 9), as figured herein (Fig. 21.6, p. 462), and the dorsal valve of *Saetosina* bears less conspicuous dimples and pustules. In addition the dorsal interior of *Bellaspinosina* is close in some aspects to that of North American *Grandaurispina*, suggesting that the genus may have arisen from that genus, rather than by migration. It displays slightly more emphasized posterior dorsal hinge ridges and postero-lateral ridge, more elongate tubercles over the dorsal anterior and less emphasized adductor scars (perhaps affected by incomplete silicification), compared with *Saetosina*.

Grandaurispina rara Cooper & Grant, 1975, p. 1169 from the Appel Ranch Member is congeneric.

Genus *Vagarea* new genus

Derivation: Taken from species name.

Type species: *Grandaurispina? vaga* Cooper & Grant, 1975, p. 1172 from Cathedral Mountain Formation (Kungurian), west Texas, United States, here designated.

Diagnosis: Large roundly subquadrate shells without radial ornament. Ventral spines form dense tuft on lateral slopes, body spines suberect and arise from elongate bases, arranged in approximately quincunxial pattern, dorsal spines fine, erect, arise between dimples. Internal ridge high across ventral ears, dorsal hinge ridge well formed but marginal ridge not clearly developed, long septum, numerous moderately spaced anterior papillae near start of trail.

Discussion: *Vagarea* is known from a single species, typified by its lack of radial ornament, but otherwise close to Paucispinauriini in most detail, including shape and cardinal process, and distribution and nature of spines as far as they can be discerned from photographs, although detail of the bases is not clear. The cardinal process appears to be much like that of other paucispinaurians, with widely splayed lateral lobes and high central shaft bearing a moderately deep but narrow median cleft, as seen from a ventral aspect. Anterior dorsal papillae are moderately like those of *Grandaurispina* and allied genera. The internal ridge which crosses inside the ears (Cooper & Grant 1975, pl. 435, fig. 31, 32) in at least one ventral valve is much higher than usual for paucispinaurians, including other west Texas species, but the dorsal interior is much the same as in west Texan species assigned to *Grandaurispina*, apart from a tendency for the posterior ridge to lie closer to the hinge. Cooper & Grant (1975) compared the species with the marginiferid *Echinauris* Muir-Wood & Cooper, 1960, whilst noting differences in spinosity and the cardinal process. The genus is moderately close to *Bellaspinosina*, with slightly coarser ventral spines and few dorsal spines.

Genus *Saetosina* Waterhouse, 1986b

Fig. 21.6

Type species: *Terrakea multispinosa* Dear, 1971, p. 18 from Flat Top Formation (Wordian) of Queensland, Australia.

Diagnosis: Both valves covered by costellae and very fine and numerous spines arranged in quincunx, ventral spines provided with elongate bases over much of disc and part of trail, spines numerous and erect over umbonal slopes and anterior ears, no thick spines; dorsal valve with dimples.

Discussion: Although *Saetosina* was relegated to synonymy of *Terrakea* Booker by Briggs (1998) and Brunton et al. (2000, p. 534), the type species and the slightly older species *S. dawsonensis* Waterhouse differ from all members of that genus in the lack of thick spines close to the ventral hinge and often over the dorsal trail: instead all spines are fine and subuniform, rather than differentiated. Posteriorly the ventral ears have few spines near the hinge, but erect spines are numerous over the anterior ears and umbonal slopes. In addition, as tends to be common amongst species with spines that are fine, there is some tendency for spines on both valves of *multispinosa* to be aggregated in bands, an aspect never seen in *Terrakea* or *Paucispinauria*. Extensive figures of the two species are provided by Dear (1971, pl. 7, fig. 1-11), Parfrey (1988, pl. 2, fig. 22, pl. 3, fig. 6-10), Briggs (1998, Fig. 88A-E) and Waterhouse (1986b, pl. 13, fig. 6-12).

A species from the Snapper Point Formation, New South Wales, Australia, called *Terrakea rhylstonensis* Briggs (1998, p. 168, Fig. 83A-H), not very well known, might prove to have been a precursor species. It might have been expected that a genus with uniform and fine spines would have been first to appear, to be followed later by genera with more differentiated spines, but that does not accord with the actual fossil record.

Genus *Spargospinosa* Waterhouse, 2001

Type species: *Terrakea belokhini* Ganelin in Sarytcheva, 1977, p. 141, from Omolon Suite (Capitanian), Kolyma-Omolon Basin, northeast Russia.

Diagnosis: Medium size, weakly transverse and vaulted, trail moderately long. Ventral spines form row along ventral hinge, scattered over ventral valve, rare over ears. Dorsal spines especially over lateral and anterior shell, moderately sturdy over trail, varied in number over ears.

Discussion: This genus is like *Terrakea* in having both valves costellate, and moderately thick visceral disc, with gently concave dorsal valve and high trail. The dorsal spines are close to those of *Paucispinauria* Waterhouse in New Zealand and Australia, including a number of sturdy erect spines over the trail. The ventral spines are outstanding, in forming a row along the ventral hinge, with comparatively few or none otherwise on the ears and the umbonal slopes.

Other paucispinaurian genera have more posterior spines, that vary according to genus in width and distribution, as outlined previously.

There is some similarity to *Muirwoodia* (?) *korkodonensis* Licharew in Kashirtsev 1959, pl. 19, fig. 3 and conspecific *Cancrinella* (?) *obrutschewi* Kashirtsev, 1959, p. 42, pl. 16, fig. 5 from the Kolyma-Omolon Basin, northeast Russia, also figured by Zavodowsky (1970, pl. 65, fig. 13-16) and especially Ganelin in Sarytcheva (1977, pl. 20, fig. 10-16, Fig. 79). Valves are costellate, and ventral spines over the anterior have long spine bases, and the dorsal trail displays a few erect sturdy spines. No hinge or ear spines appear to be indicated in the figures, and the internal dorsal posterior ridges slope forward at a high angle from the hinge.

Taxonomy: The species was spelled *belochini* in the caption by Ganelin in Saytcheva (1977, Fig. 80), and this is regarded as a lapse. Figures of the type species were provided in Sarytcheva (1977, pl. 20, fig. 17, 18, pl. 21, fig. 1-3), but only the latter plate was mentioned in the description.

Tribe **HOLOTRICHARININI** new tribe

Name genus: *Holotricharina* Cooper & Grant, 1975, p. 1173 from Cathedral Mountain and Road Canyon Formations (Kungurian, Roadian), west Texas, here designated.

Diagnosis: Spines of two sizes over ventral disc, strong but not dense postero-laterally, halteroid spines clustered over the ears and umbonal slopes, and in parallel rows over disc and trail; dorsal spines mostly fine. Ventral valve with low commarginal rugae, without ribs, dorsal valve with fine ribs and close-set commarginal rugae.

Discussion: Only one genus is known for this tribe, represented by the type species and two more (one unnamed) from Texas, and an additional unnamed form from the Palmarito Formation of Venezuela (Hoover 1981). It is outstanding in that the dorsal valve is rugose and capillate, and the ventral disc bears coarse and fine spines, and somewhat finer commarginal rugae, with no ribs. The ornament is unusual for paucispinaurians or auriculispinans, in which ventral disc spines are comparatively homogeneous as a rule, and arranged in quincunx. However it is true that ventral disc spines are not entirely uniform in *Paucispinauria* and allies, with a few fine spines appearing for instance in the type species of *Paucispinauria, P. concava* (see Waterhouse 1964, pl. 10, fig. 7), or *Terrakea brachythaera* (see Waterhouse 1964, pl. 13, fig. 11), but the very scarcity and apparent randomness of distribution suggest that their appearance is not part of a regular pattern. The loss of ventral ribs is exemplified by *Vagarea* new genus in the Cathedral Mountain Formation of west Texas, and possibly this provided source stock, although the ventral spines in *Vagarea* are comparatively uniform and far less crowded. This latter genus shows regular ventral disc spines, and the dorsal valve carries low closely spaced rugae. Ear and umbonal slope spines appear to be slightly more numerous. A further distinction from Texan species of *Grandaurispina* and allies lies in the presence of fine closely spaced commarginal rugae, especially well developed in *Holotricharina sparsa* Cooper & Grant and also in the Venezuelan specimens assigned to *H. hirsuta*. It is not certain that ventral disc spine bases are prolonged either over the shell surface, or within the shell.

The ventral muscle field of *Holotricharina* seems poorly preserved, occupied by long ridges possibly reflective of spine bases. The dorsal adductor scars were not described, but figured as having an irregular but not strongly dendritic surface. Further details of the interior of *Holotricharina*, including a slightly unusual cardinal process, are provided by Cooper & Grant (1975, pp. 1174, 1175), and the cardinal process was called linoproductid, or, under present understanding, linoproductidin. But it should be recalled that Cooper & Grant (1975) tended to put forward a rather broad view of what constituted a linoproductid cardinal process, which in turn governed their overall classification, for they also argued that *Undellaria*, almost undoubtedly an overtonoid, was linoproductid, as discussed on p. 192. Nonetheless in this instance, there is better justification. *H. sparsa* Cooper & Grant (1975, pl. 445, fig. 28) has a broad cardinal process, with narrow median shaft and wide lateral clefts between the median divided shaft and lateral lobes. Several rows of well developed pustules lie in a band in front of the end of the dorsal median septum, better developed than in Paucispinauriini. In the Venezuelan material, the cardinal process has only a "minute median lobe", and Cooper & Grant (1975, p. 1174) described the median lobe as generally small, somewhat elevated, with deep median cleft. By contrast, the median lobe is prominent in *Grandaurispina kingorum* Muir-Wood & Cooper – see Cooper & Grant (1975, pl. 437, fig. 18, 22, 28); *G. elongata* Cooper & Grant (1975, pl. 441, fig. 22) and *G. gibbosa* Cooper & Grant (1975, pl. 440, fig. 33, 35); *Appelinaria crassa* (Cooper & Grant 1975, pl. 438, fig. 24, 28) and *A. rudis* (Cooper & Grant 1975, pl. 439, fig. 22); *Bellaspinosina bella* (Cooper & Grant 1975, pl.

442, fig. 37) and *B. rara* (Cooper & Grant 1975, pl. 443, fig. 15, 21), and *Vagarea vaga* (Cooper & Grant 1975, pl. 435, fig. 21, 24). The cardinal process of *Holotricharina* is not quite the same as that of *Grandaurispina* and accompanying genera, but the significance is hard to ascertain. The cardinal process of New Zealand *Terrakea brachythaera*, as figured by Waterhouse (1964, text-fig. 31) does vary in the height of the median shaft and relative width of the lateral lobes, but the *Holotricharina* cardinal process is distinct, possibly but not necessarily modified from a paucispinaurian process. There is a deep anterior pit in young specimens that is later infilled, and a single septum is developed, apart from indications of a possible cleft in a few specimens that are somewhat obscure in the photographs. No ear baffles are present, but well formed posterior dorsal ridges slope forward from the hinge as in paucispinaurian genera of Texas, and continue forward at least a little around the posterior disc.

Grant (1976, p. 102) pointed out that there were some similarities between *Holotricharina* and *Dyschrestia* Grant, especially in the ventral spines of two distinct sizes. He noted the difference in the dorsal septum, high in *Holotricharina*, low in *Dyschrestia*. The dorsal papillae were stated to differ, but in fact seem somewhat similar anteriorly, though in more rows in *Holotricharina* (compare the specimen figured by Grant 1976, pl. 22, fig. 17 with that in Cooper & Grant 1975, pl. 444, fig. 44). The difference that must be rated as most significant lies in the cardinal process. In *Dyschrestia*, it is bilobed and overtoniid, with only a low median ridge, replaced by a groove in some specimens. (See Grant 1976, pl. 22, fig. 17, 32). Figures of the cardinal process in *Holotricharina* suggest a somewhat bilobed appearance, because of the deep broad median cleft, but each lateral division has a broad inner lobe and narrow outer lobe, as if modified from a paucispinaurian cardinal process.

The view suggested by Waterhouse (2002b), that the genus belonged to Costispiniferinae, would fit with the spine pattern and otherwise largely smooth ventral valve, and possibly accommodate the aspects of the cardinal process. *Echinauris* Muir-Wood & Cooper, 1960 as illustrated by Cooper & Grant (1975, pl. 326 to 341) is moderately close in many respects, some specimens even showing dorsal fine rugae, but none are known that display dorsal ribs. In addition, dorsal anterior pustules are much more numerous, in four or five rows in *Holotricharina*, better defined but moderately close to the arrangement in Paucispinauriini, compared with fewer rows and coarser pustules in Marginiferidae and Costispiniferidae.

Subfamily **MAGNIPLICATININAE** Waterhouse, 2001

[Nom. transl. hic ex Magniplicatinini Waterhouse, 2001, p. 49].

Diagnosis: Commarginal rugae moderately to strongly developed, otherwise close to Paucispinauriini in costation. Spines not differentiated to same extent. Interior much as in Paucispinauriini.

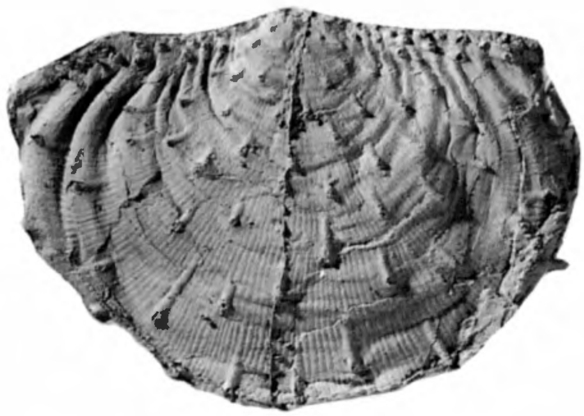


Fig. 17.18. *Magniplicatina superba* Waterhouse, latex cast of ventral valve UQF 70093, x3, from Brae Formation (Kungurian), Queensland, Australia, showing disc, with little displayed of trail. Disc spines have posteriorly prolonged bases. J. Coker & JBW photo.

Discussion: Compared with Auriculispinidae Waterhouse, 1986b, disc spine bases are generally more elongate and wrinkles are stronger. Ventral adductors are striate and especially dendritic throughout ontogeny (Shi & Waterhouse 1996, p. 96), at least in Permian members, and are not posteriorly impressed into the posterior wall, whereas ventral adductor scars are striate and subelongate rather than dendritic at early into full maturity in several Auriculispinidae, and are impressed into the posterior wall. In a number of instances, that results in the adductor scars being scarcely if at all perceptible in paucispinaurians, especially in Tribe Magniplicatini, because they tend to be masked by costae and rugae from the exterior, whereas auriculispinids developed a palpably visible adductor platform. Brunton et al. (2000, pp. 533, 543) assigned *Cancrinella* to Grandaurispininae (ie. Paucispinauriinae) and *Magniplicatina* to Auriculispininae, but the two genera are so close that the difference in dorsal spinosity would seem to be of generic importance only. *Magniplicatina* is now known to be widespread in the northern hemisphere, including Glass Mountains, Texas, United States. Such species were assigned to *Cancrinella* by Cooper & Grant (1975), until corrected by Brunton et al. (2000, p. 544). To judge from the fossil record, *Magniplicatina*, which includes various species previously referred to *Cancrinella*, is more widespread and more numerous than other genera of Paucispinauriinae during Permian time. ?*Teleoproductus* Li Li, in Li Li, Yang Deli, & Feng Ru-lin (1986, p. 230) from the Longyin Formation (Sakmarian – Wordian) of Guangxi, China, has strong rugae and nasute trail, but spine detail and interior are poorly known.

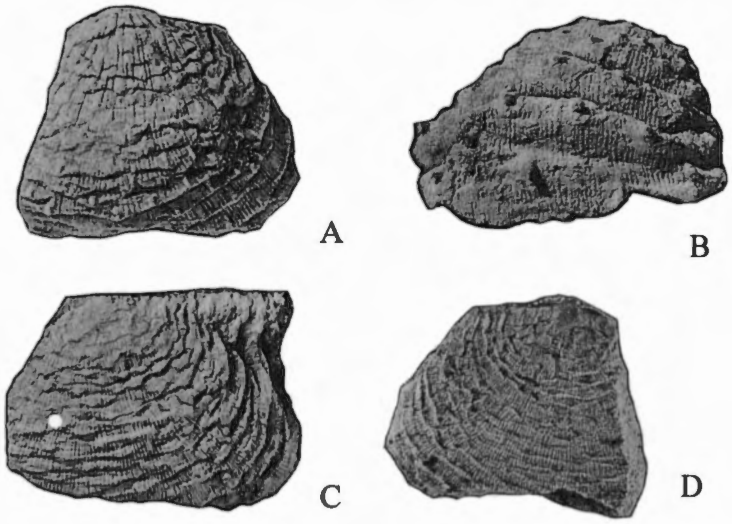


Fig. 17.19. *Magniplicatina magniplica* (Campbell). A, D, ventral and dorsal aspects of internal mould, BR 848. B, anterior view of ventral PVC cast, BR 737. C, dorsal external mould of BR 848, as figured in A, C. From Letham Formation (Kungurian), Wairaki Downs, New Zealand, x2. S. N. Beatus & JBW photo.

Tribe **MAGNIPLICATININI** Waterhouse, 2001

[Magniplicatinini Waterhouse, 2001, p. 49].

Diagnosis: Concentric wrinkles regular and strongly developed. Body corpus thin to rarely moderately thick. Otherwise close to Paucispinauriini in costation, ventral spines in hinge row or several rows, Dorsal spines present in at least one genus. Ventral adductors dendritic, cardinal process trilobed.

Fig. 17.20. *Magniplicatina superba* Waterhouse, latex cast of trail, showing ornament of ribs and large forward-inclined spines without posteriorly prolonged bases. Unregistered specimen from Brae Formation (Kungurian), Queensland, kept in UQF collection at Queensland Museum, Hendra, Brisbane, Queensland, Australia, x3.

Subtribe **MAGNIPLICATININAI** Waterhouse, 2001

Fig. 17.18 – Fig. 17.20

[Nom. transl. hic ex Magniplicatinini Waterhouse, 2001, p. 49].

Diagnosis: Commarginal wrinkles equally developed on both valves. Lower Carboniferous (Visean) to Upper Permian (Changhsingian).

Genera: *Magniplicatina* Waterhouse (syn. *Helenaeproductus* Lazarev), *Auritusinia* Waterhouse, *Commarginalia* new genus, *Globicorrugata* new genus, *Rugania* new genus, ?*Teleoproductus* Li Li.

Genus ***Globicorrugata*** new genus

Derivation: globosus – sphaerical; corrugo – to wrinkle, Lat.

Type species: *Globicorrugatus settlensis* new species from Lower Carboniferous (Visean) of England, here designated.

Diagnosis: Medium small in size, well inflated, closely costate with moderately strong wrinkles, spine rows along hinge and in quincunx over ventral valve only, bases elongate; dorsal dimples, single median septum, trilobed cardinal process, adductor scars not strongly dendritic.

Discussion: Some Early Carboniferous proboscidelloid species with strong wrinkles show limited resemblance to *Fluctuaria* Muir-Wood & Cooper. They have rows of hinge spines, and elongate ventral disc spines arranged in quincunx, with elongate but not swollen bases and no dorsal spines. They display what appears to be only a moderately thick visceral disc. The cardinal process varies somewhat, and in *Globicorrugata inflata* new species is shown to have a high median shaft with two low lateral lobes from a ventral aspect, so that it differs from the bifid cardinal process of contemporaneous genera such as *Proboscidella, Undaria*, or *Fluctuaria*. The median septum is single and long. These features suggest that the species are closer to Paucispinauriidae than to Proboscidellidae. Paucispinauriini itself may be readily excluded: genera have a thick disc and strong spines and dorsal spines, without regular and often strong wrinkles, whereas Magniplicatinini includes genera with strong dorsal wrinkles, dorsal spines present or absent, but comparatively slender to only moderately thick disc as a rule. *Auritusinia* Waterhouse has very large ears (Fig. 17.25), strong wrinkles and thin disc, and *Cancrinella* Fredericks has strong dorsal wrinkles and spines. Coolkilellinae Waterhouse, based on *Coolkilella* Archbold has thick disc as a rule, ventral but no dorsal spines, a geniculate dorsal valve that is often pitted, moderate, often low wrinkles, and is typified by subquadrate shape, different from that of the species under consideration. Of these three choices, Auriculispinini is close apart from the stronger rugae, Magniplicatinini is close apart from the thicker disc, and Coolkilellinae is close apart from different shape and low wrinkles. In the Early Carboniferous it is to be expected that morphologies converge back in time. A prime guide for classification has been found in the nature of the ventral adductors, which are shallow and dendritic in Paucispinauriidae, and striate and recessed into the posterior wall in Auriculispinidae. The English material under consideration seems to provide no indication of the scars, which might imply that the scars were lightly impressed. The Russian material as figured indicates lightly impressed possibly striate scars. The species are assigned to Paucispinauriidae, which is consistent with most aspects of the morphology, but the lack of clearly defined dendritic muscle scars and a degree of uncertainty over the thickness of the body corpus mean that the placement remains provisional.

Cancrinella Fredericks is distinguished by its dorsal spines. It has a non-rugose ventral disc, double dorsal septum as a rule (Brunton et al. 2000, Fig. 370.2d), deeper cardinal process notch, dendritic adductor scars, and dorsal hinge ridge in front of the hinge. *Magniplicatina* Waterhouse is closer in that the ventral disc is rugose, and dorsal spines are lacking. There is a single dorsal septum as a rule, and moderate if any alveolus, and a ridge lies along the dorsal hinge. The visceral disc is thinner, and the cardinal process broader with wider median shaft, and better defined adductor scars in both valves. The shape of *Magniplicatina* is more transverse as a rule, and dorsal pits are less elongate.

Globicorrugata settlensis new species

Fig. 17.21, Fig. 17.22

1861 *Productus undatus* [not Defrance] – Davidson, p. 161, pl. 34, fig. 7-12 (part, not fig. 13 = *Tortilisia tortilis* (M'Coy)).

Derivation: Named from Settle, Yorkshire, England.

Holotype: B13986 from Carboniferous Limestone (Visean), Yorkshire, figured by Davidson (1861, pl. 34, fig. 9), here designated.

Diagnosis: Medium in size, moderately inflated, with low to moderately defined commarginal rugae and ventral spines with moderately swollen bases, arranged in quincunx.

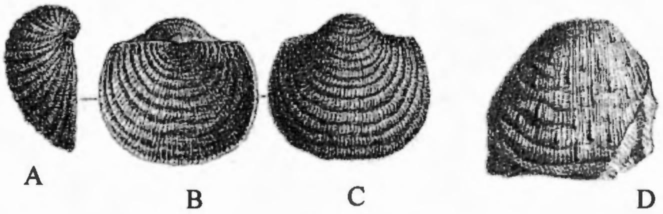


Fig. 17.21. *Globicorrugata settlensis* new species, x1. A – C, specimen with valves conjoined, now possibly lost, figured by Davidson (1861, pl. 34, fig. 10) from Lower Carboniferous of Campsie, Stirlingshire, Scotland. D, ventral valve figured by Davidson (1861, pl. 34, fig. 7) from Lower Carboniferous of Derbyshire, England.

Description: The holotype is a ventral valve some 18mm wide, 18.8mm long and 12mm high, with well-arched visceral disc, no sulcus, and obtuse cardinal extremities, on ears that are of moderate size only. The shell is crossed by angular-crested wrinkles about 2.5mm apart, and close-set costellae, 12-14 ribs in 5mm anteriorly. Spines are arranged in some three rows in front of the ventral hinge, and emerge in quincunx over the visceral disc, and bases are over 2mm long anteriorly, less than 1mm wide, and some 2.5mm apart, moderately prominent and may extend across the interspace to the rear to commence at the anterior slope of the preceeding wrinkle. Muscle scars cannot be discerned. Spine bases swell anteriorly, and the ribs may be through-going, or two ribs join to form one spine base, or more commonly, two ribs commence in front of the spine base. Further specimens come from various Lower Carboniferous localities in England. Specimen B 23069 from Redesdale shows four rows of erect spines on the ears, and strong anterior spines, emerging from a single rib, or with two ribs merging into one. The dorsal valve was figured

Fig. 17.22. *Globicorrugata settlensis* new genus, new species, ventral valve E 10097, x4, from Lower Carboniferous of Derbyshire, England. This specimen was identified as *Productus tortilis* [non M'Coy] by M'Coy (1855, p. 474). JBW photo.

by Davidson (1861, pl. 34, fig. 10) and cannot be found in the collections, but some dorsal valves are available from Redesdale, and show low wrinkles with no spines, such as B 54019-24 from the Redesdale Ironstone Shales UrB2. One specimen B 54024 measures 16mm wide, 16.5mm long and 10.1mm high, and a dorsal valve shows a median dorsal septum. Specimens numbered BD 9739-40 shows undifferentiated ribs, low wrinkles, elongate ventral spine bases more or less in quincunx, and a row of hinge spines with a few in front. B 9740 measures 23.5mm wide, 19mm long and 7mm high, and a ventral valve is 18.5mm wide, 17mm long and 12mm high. The ventral umbonal angle is 95°, and ears lie at maximum width with recession in front, and there are four or five ribs in 5mm from the umbo. From Thorpe Cloud, Dove Dale, west of Ilam, Derbyshire, BD 11294 has moderately weak wrinkles and only weakly differentiated costae: it comes from the Visean, of Asbian upper B2 age. Specimen BD 9967 from Thorpe Cloud displays varying relations of ribs to spine bases, with three ribs behind and two ribs in front of a spine base, or two ribs behind and three ribs in front.

At the Sedgwick Museum, Cambridge, E 14864 from Treak Cliff, Castleton, Derbyshire, has ventral spines in regular quincunx, with elongate bases and two ribs behind, one rib in front, or two behind, and two in front. There are three to four rows of erect spines on the ears. Another specimen is figured in Fig. 17.22.

Resemblances: The species has lower wrinkles than developed in *Fluctuaria undata* (Defrance) and has ventral spines arranged in a different and quincunxial pattern, and the spines have elongate bases tapering posteriorly, and not subrectangular and swollen. The present species is less elongate and less inflated than *Globicorrugata inflata* new species, described below, from the Kuznetz Basin of Kazakhstan, and elongate dimples are less conspicuous over the dorsal valve.

Globicorrugata inflata new species

1963 *Fluctuaria undata* [not Defrance] –Sarytcheva, p. 229, pl. 37, fig. 6-11, text-fig. 101, 102.

Derivation: inflatus – swollen, Lat.

Holotype: PIN No. 143/141, Ostrogsk Suite (Visean-Namurian) of Kuznetz Basin, Kazakhstan, figured by Sarytcheva (1963, pl. 37, fig. 6a-e), here designated.

Diagnosis: Medium small in size, elongate and arched, with moderately well defined commarginal rugae crossed by fine ribs. Erect spines lie in two or three rows along the ventral hinge, and spines over the ventral valve are arranged in quincunx with elongate bases. Dorsal valve without spines, elongate hollows conspicuous. Cardinal process trifid with shallow alveolus, dorsal septum slender, extending for less than half the length of the valve. Dorsal hinge ridge prominent.

Description: This species was described by Sarytcheva (1963) as *Fluctuaria undata* (Defrance), and an extensive synonymy provided, most authors assigning the form to *undatus*, although Yanishevsky (1935, p. 56, pl. 1, fig. 1-11) referred specimens to *Productus* (*Linoproductus*) aff. *cancriniformis*. His was a more accurate assessment, because of the nature of the ventral body spines which have elongate spine bases, arranged in quincunx. The visceral disc is moderately thick and the trail long, without being geniculate. The cardinal process from an internal aspect is trifid, with high median lobe divided into two by a median trough, and shallow alveolus below, and two splayed lower outer lobes, unlike the bifid cardinal process of Fluctuarinae. The nature of the ventral adductors is not entirely clear: they are not obviously dendritic, and could be striate: they are definitely not impressed as in Auriculispinidae. Dorsal adductors are not impressed, and the medium dorsal septum is long with no median cleft.

Resemblances: In contrast to *Fluctuaria undata* (Defrance), this new species has ventral spines arranged over the disc in quincunx, not arising from submonticules along the crest of the concentric rugae, and the rugae are much lower, and the costellae less differentiated. Of the taxa mentioned in the synonymy by Sarytcheva (1963), few if any conform with the present species, and other material referred to *undatus*, such as that by Ivanov (1935, pl. 9, fig. 2, 8) belong neither to *undatus* nor the present form. But various specimens figured by Sarytcheva (1937, pl. 7) are somewhat similar, although *Cancrinella venevi* Sarytcheva (1937, pp. 90, 111, pl. 7, fig. 8a-h, 9, 10, text-fig. 21) from Serpukhovian faunas of Russia is more vaulted with narrow body corpus and spines forming a row along the hinge, and cluster on the ears, and scattered ventral body spines. Specimens so labelled from the Okian Series, Venev beds, labelled C_1^v, from Sukhoi, Osetrik River, Moscow Basin, BB 8759 and 8766 at the Natural History Museum, London, show few if any hinge spines on the ventral valve, and three ribs may converge on a spine base, with two continuing forward, or others arise from a single costa, or two ribs may continue forward, with only one rib posteriorly. Some spines are erect, others ramped, and wrinkles develop laterally. The material from the Upa beds that is referred to *Cancrinella panderi* Auerbach is not so well known (Sarytcheva 1937, pl. 7, fig. 11a-d) and so difficult to compare fully, but has few well defined commarginal rugae. By contrast, the Serpukhovian specimens referred to *C. undata* [not Defrance] by Sarytcheva (1937, pl. 7, fig. 1-6) and *undatus* var. *irregularis* (pl. 7, fig. 7) have stronger and more regular rugae.

Genus ***Commarginalia*** Waterhouse & Nazer new genus

Derivation: co – with, parallel; margino – border, Lat.

Type species: *Commarginalia yukonensis* Nazer & Waterhouse new species from Ettrain Formation (Kasimovian), Yukon Territory, Canada, here designated.

Diagnosis: Small, both valves ornamented by radial ribs and moderately well formed commarginal rugae, ventral spines numerous over comparatively large ears and arranged in quincunx over ventral disc and trail, with elongate bases; no dorsal spines. Adductor scars dendritic or striate.

Discussion: This genus is close to several genera, but has numerous ventral ear spines, more as in members of the Tribe Engellinini (see p. 431) rather than the one to three rows of hinge spines typical of Magniplicatininai. In other respects, the genus comes close to typical Magniplicatinini. *Magniplicatina* Waterhouse has stronger commarginal rugae, and spines form one to three well formed rows along the hinge, rather than a moderately dense cluster. *Cancrinella* is readily distinguished by the presence of fine dorsal spines. *Calytrixia* Waterhouse, 2020a and *Platycancrinella* Waterhouse, 1983a have numerous ear spines, with *Platycancrinella* sharing large ventral ears, but these two genera like *Cancrinella* have virtually no rugae over the ventral valve, and *Costatumulus* Waterhouse displays hinge spines in well formed rows, and commarginal rugae are more subdued or missing.

A scattering of species of mostly Permian age with well developed rugae and numerous ventral ear spines appears to belong to this genus. *Platycancrinella kletsi* Waterhouse is congeneric, based on *Cancrinella grandis* [non Solomina] Abramov & Grigorieva, 1988, p. 123 from the Sakmarian Kigiltass Group of northeast Russia, together with *Magniplicatina transversa* [non Briggs] of Briggs (1998, Fig. 91A) from the Sakmarian – Artinskian Lakes Creek Group of east Queensland, and other species include *Costatumulus sidorkini* Manankov from the lower Sakmarian to lower Artinskian Adaatsag faunal assemblage of central Mongolia (see Manankov 2012). These species all share low commarginal rugae, numerous ventral ear spines, spines in quincunx with elongate bases over the ventral disc and trail, with no dorsal spines, as well as fine radial ribbing.

Commarginalia yukonensis Nazer & Waterhouse new species

Fig. 17.23

Derivation: Named for Yukon Territory, Canada.

Holotype: GSC 37249 figured herein as Fig. 17.23A-E from GSC loc. 57062, Ettrain Formation (Kasimovian), Ogilvie Mountains, Yukon Territory, Canada, here designated.

Diagnosis: Moderately arched with thin visceral disc and sturdy costellae, wrinkles low and spines stout with elongate bases.

Material: Some fifty specimens from localities in the Ettrain Formation (Kasimovian), Ogilvie Mountains, Yukon Territory, Canada, including GSC 53699, 53793, 56924, 57062, 57071, and 57247. Half the specimens come from a JBW locality halfway between GSC loc. 53725 and loc. 53730, section 116H – 1B. See Appendix A, part C, p. 477.

Dimensions in mm:

Specimen GSC	Width	Length
37249	12	11
37250	21	16
37251	18	18
37256	23	24

Description: Shell of small to medium size for the genus, ventral valve moderately arched with umbo extended slightly beyond hinge, ears small and flat and clearly separated from umbonal slopes, no ventral sulcus. Dorsal valve gently concave, the disc abruptly separated from the geniculate trail which is as long as the disc. Costellae cover both valves, numbering 11-14 in 5mm, interspaces narrow. Moderately strong irregular rugae cross the ventral disc, approximately 2mm apart, and coalesce in part to form six rugae across ears, interspaces may be U-shaped or trough-like. Erect spines lie in two rows along the ventral hinge and more erect spines crowded over the anterior ears. Prostrate spines lie in quincunx over the remainder of the valve, with prominent bases nearly 3mm long and 0.6mm wide, occasionally crossing two wrinkles. The dorsal valve has quincunxially arranged elongate depressions over the disc, rounded hollows on the ears, and closely spaced commarginal rugae crossing the disc. Ventral muscle scars little impressed, possibly striate, and without clear dendritic markings. Shell thin and interior reflective of spine bases and tunnels. The cardinal process is small, with high median lobe and widely spaced more prominent lateral lobes, and lateral ridges extend along the hinge line.

Resemblances: *Platycancrinella kletsi* Waterhouse, 2010a, p. 42, Fig. 12, originally figured as *Cancrinella grandis* [not Solomina] by Abramov & Grigorieva (1988, p. 123, pl. 10, fig. 19, pl. 11, fig. 1-4) from the Sakmarian Kigiltass Group of Verchoyan, northeast Russia, has subdued wrinkles and the specimens are very transverse, and dorsal pits are conspicuous. The present specimens are less transverse and have slightly stronger ribbing and slightly more conspicuous ventral spines over the disc. An allied Permian species is found in the Early Permian Lakes Creek

Group of Queensland, not yet formally named (Briggs 1998, Fig. 91A [not 91B-J = *M. transversa* Briggs, a junior synonym of *Magniplicatina undulata* Waterhouse]; and discussed by Waterhouse (2010a, p. 43, Fig. 13), with slightly stronger wrinkles and apparently fewer disc spines. In general appearance, and with moderately numerous ear spines, this Canadian species is close to *Magniplicatina boonensis* (Swallow, 1860, p. 217), also described as *Productus pertenuis* Meek (1872, p. 164, pl. 1, fig. 14a-c, not pl. 8, fig. 9a-d), and further figured by Dunbar & Condra (1932, p. 258, pl. 32, fig. 1-5), Muir-Wood & Cooper (1960, p. 301, pl. 112, fig. 8-13) and Sutherland & Harlow (1967, pl. 136, fig. 3-6). The original material probably came from the Oread division of the Douglas Group at the mouth of the Platt River, Nebraska, and the species is reported to range through much of the Pennsylvanian in United

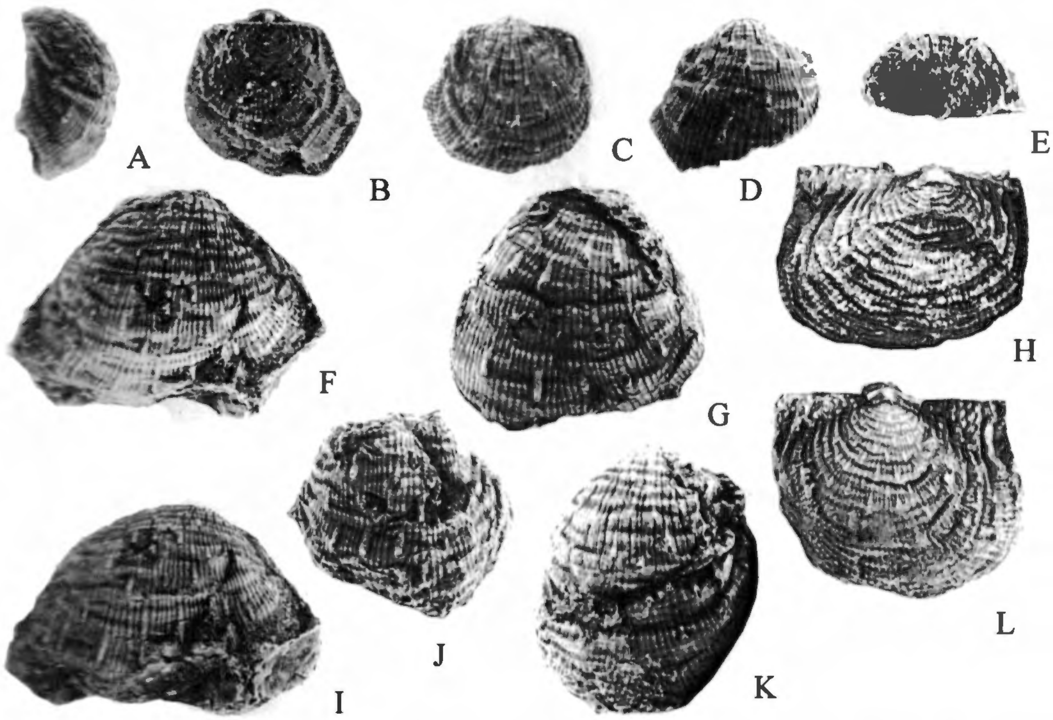


Fig. 17.23. *Commarginalia yukonensis* Nazer & Waterhouse. A-E, holotype, lateral, dorsal, ventral, antero-ventral and posterior views of GSC 37249, from GSC loc. 57062. F, I, ventral and antero-ventral views of ventral valve GSC 37250 from near GSC loc. 53727. G, ventral view of ventral valve GSC 37251 from GSC loc. 53727. H, natural broken internal mould of dorsal valve GSC 37252 from GSC loc. 57247. J, anterior ventral valve GSC 37252 from GSC loc. 53727. K, ventral view of ventral valve GSC 37254 from GSC loc. 53727. L, natural mould of dorsal valve GSC 37255 from GSC loc. 53727. Numerous pits over the dorsal ears oppose spines on the ears of the ventral valve. Specimens from Ettrain Formation, Ogilvie Mountains, Yukon Territory, Canada, x2 except Fig. 17.23H, x1. R. E. Nazer photo.

States. Muir-Wood & Cooper (1960) illustrated material from the Finis Shale of Texas. Inflation and shape are close, but ears are larger on the Canadian form, and spines more numerous on the ears and spines slightly more prominent over the ventral disc, and dorsal pits more elongate on the ventral valve. For *Cancrinella parva* Cooper & Grant (1975, pl. 428, fig. 19-40) from the Neal Ranch Formation and Poplar Tank Member of the Skinner Ranch Formation in west Texas, the shape is more elongate and wrinkles are more numerous. It is difficult to determine the distribution of ear spines from figures, because the spines are well preserved and long, masking the bases. Dorsal spines were not described, but appear to be present in a specimen figured by Cooper & Grant (1975, pl. 428, fig. 38). No dorsal spines are visible in some figured specimens (Cooper & Grant, 1975, pl. 428, fig. 33, 35), but that is only assessed from figures. *Cancrinella planumbona* Cooper & Grant (1975, p. 1153, pl. 429, fig. 1-7) appears to belong to *Commarginalia*, and comes from the Wordian China Tank Member of west Texas.

Nazer (1977, p. 126) referred the Canadian material to *Cancrinella cancriniformis* (Tschernyschew 1889, pl. 7, fig. 32, 33, a), a Russian species of chiefly Asselian age (eg. Tschernyschew 1902, pl. 2, fig. 5, 6; Einor 1946, pl. 5, fig. 1; Sarytcheva & Sokolskaya 1952, pl. 20; Solomina 1960, pl. 8, fig. 3-7; 1970, pl. 5, fig. 9; Mironova 1960, pl. 1, fig. 16 and Ustritsky & Chernyak 1963, pl. 13, fig. 6-8, pl. 14, fig. 1-5), and widely if unreliably reported from upper Carboniferous and early Permian faunas of Europe, Asia and Arctic. The species has a more arched and transverse ventral valve, as indicated by Sarytcheva 1977, pl. 20, fig. 1, which refigures the Asselian (Lower Permian) specimen shown in Tschernyschew (1889, pl. 7, fig. 32), and shows few ear spines.

Genus ***Rugania*** new genus

Fig. 17.24

Derivation: ruga – wrinkle, Lat.

Type species: *Cancrinella subquadrata* Cooper & Grant, 1975, p. 1155 from Word Formation (Willis Ranch and Appel Ranch Members, Wordian, Capitanian) of west Texas, United States, here designated.

Diagnosis: Medium-small, both valves rugose, and both valves spinose, ventral hinge spines in two rows.

Discussion: This genus is close to *Magniplicatina*, but is distinguished by having numerous spines over the dorsal valve (not just limited to the anterior as claimed in the text by Cooper & Grant, 1975). None of the other genera have dorsal spines, and *Teleoproductus* Li Li has an extended ventral tongue, with comparatively few ventral disc or trail spines. *Cancrinella* Fredericks is similar in having dorsal spines, but has crowded spines over the ventral ears and lower umbonal flanks, and the ventral valve is much less rugose. The interior of *subquadrata* displays a trilobed cardinal process, with median lobe bearing deep groove on the ventral face and lateral lobes widely splayed, a strong hinge ridge sloping forward laterally, and well formed median septum, bearing a median slit in some specimens.

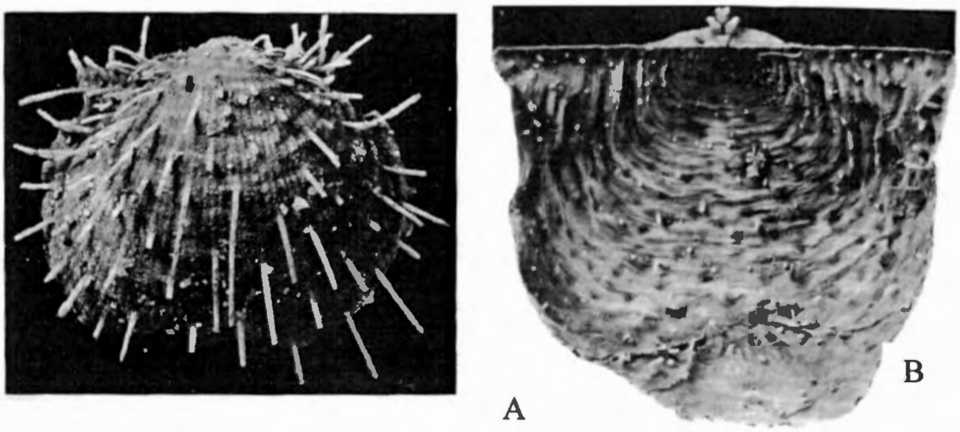


Fig. 17.24. *Rugania subquadrata* (Cooper & Grant). A, ventral valve 152777, holotype. B, dorsal exterior, USNM 153858a. From Willis Ranch Member (Wordian), west Texas, United States, x3. See Cooper & Grant (1975, pl. 429).

Genus ***Auritusinia*** Waterhouse, 2002b

Fig. 17.25

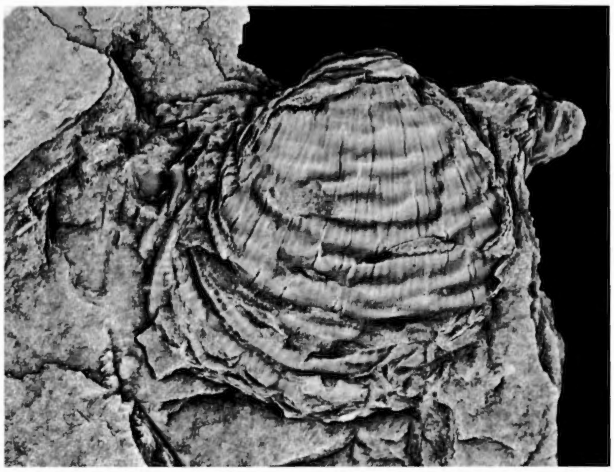


Fig. 17.25. *Auritusinia tazawai* (Shen, Archbold, Shi & Chen), ventral valve holotype NMV 148917, x2, showing large ears, which were cropped out from the previously published figure (Shen et al. 2000, pl. 12, fig. 7). From Selong Group (Changhsingian), south Tibet. Photo supplied by David Holloway, National Museum of Victoria, Melbourne, Australia.

Auritusinia Waterhouse from the Late Permian of south Tibet has moderately strong wrinkles and very large ears. This genus was referred to synonymy of *Costatumulus* Waterhouse by Brunton (2007, p. 2655), but *Auritusinia* has much larger ears and much stronger wrinkles than known for *Costatumulus,* and the ventral adductor platform is dendritic (Shen et al. 2000, Fig. 12.14), not striate and deeply impressed into the posterior wall. The large ears were cropped out of the figure in Shen et al. (2000, Fig. 12.7), but left in Shen et al. (2000, Fig. 12.12). The dorsal cardinal process is very large, as confirmed by inspection of the material at the Museum of Victoria, Melbourne, Australia.

Subtribe **CANCRINELLINAI** new tribe

Name genus: *Cancrinella* Fredericks, 1928, pp. 784, 791 from Kazanian (Wordian) of Orenburg, Russia, here designated.

Diagnosis: Ventral valve not rugose over disc and trail, ventral ear spines crowded. Lower Permian (Asselian) to Upper Permian (Changhsingian).

Genera: *Cancrinella* Fredericks, *Calytrixia* Waterhouse, *Platycancrinella* Waterhouse.

Discussion: These genera are close to Magniplicatininai in internal detail, and in being finely costate with dorsal rugae, but differ in that the rugae are inconspicuous or absent from the ventral disc and trail. In addition the ventral hinge spines do not form rows, but are crowded over the ears and lower umbonal slopes. Grigorieva, Ganelin & Kotlyar in Sarytcheva (1977, p. 127) mentioned a new subfamily Cancrinellinae, but did not discuss or define the subfamily, so that it appear that the proposal was merely conjectural. Muir-Wood & Cooper (1960, p. 302) noted that their *Cancrinella* involved two groups, species with no rugae or rugae developed only on the ears and flanks, and a group with rugae crossing the venter (They did not note that the dorsal valves in both groups were rugose).

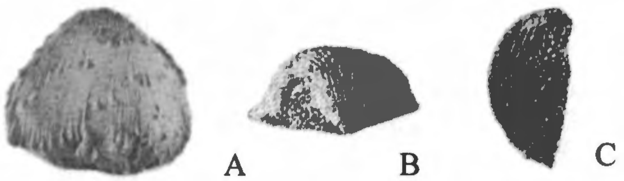


Fig. 17.26 *Cancrinella cancrini* (Verneuil). A, ventral aspect of PIN no. 1119/2131. B, C, posterior and lateral aspects of ventral valve, PIN no. 1511/957. From Middle Permian of Russia, x1. See Sarytcheva (1977).

Genus ***Platycancrinella*** Waterhouse, 1983a

Fig. 17.27, Fig. 17.28

Type species: *Platycancrinella grandauris* Waterhouse, 1983a from Pija Shale (Changhsingian) of Nepal.

Diagnosis: Thin body cavity, ventral valve weakly rugose, dorsal valve more strongly rugose, ribs coarse, spine tunnels prominent, ventral hinge spines in dense cluster over ears, body spines semi-recumbent with elongate spine bases, no dorsal spines. Ventral adductors strongly striate, reflecting external ribs, or dendritic, not incised.

Discussion: This genus looks very like *Cancrinella* Fredericks, 1928, but lacks dorsal spines. Brunton et al. (2000, p. 533) confused the two genera, but the difference is readily ascertained. *Magniplicatina* Waterhouse, 1983c is moderately close, lacking dorsal spines, with commarginal wrinkles stronger, especially on the ventral valve, and the hinge bearing one to three well organized rows of spines, whereas ear spines are more crowded and less organized in *Platycancrinella*. *Calytrixia* Waterhouse, 2010a, p. 39 from the Lower Permian (Asselian) Calytrix Formation of the Canning Basin, Western Australia, is similar in most respects, as a small transverse shell, with strong ribs and coarse postero-lateral spines, and likely to have been ancestral to the other two genera.

In having numerous spines over the ventral ears, *Platycancrinella* closely resembles *Auriculispina* Waterhouse, 1975, based on *Cancrinella levis* Maxwell, 1964 from Late Carboniferous of Queensland, Australia. In *Auriculispina* the ventral adductors are subrectangular in shape, striate or smooth, with well defined borders and deeply impressed posteriorly. The dorsal septum is double or split. In *Platycancrinella* as in *Magniplicatina* and allies the ventral adductors are less impressed and less deeply striate, and usually dendritic, and the dorsal median septum is often simple, though there is a shallow median cleft at mid-length in some specimens.

The type species was described from the Pija Shale Member of the Senja Formation in north-central Nepal, of Changhsingian age, and somewhat similar specimens are figured from the slightly older (Wuchiapingian) Zewan Formation of Kashmir (Fig. 17.28). Species very close to *Platycancrinella* in general shape, size and ornament differ in having finer ribs with regular and stronger commarginal rugae over the ventral valve, and are therefore distinguished as *Commarginalia* new genus (see p. 426), allied to *Magniplicatina* Waterhouse, but with ear spines like those of *Platycancrinella*.

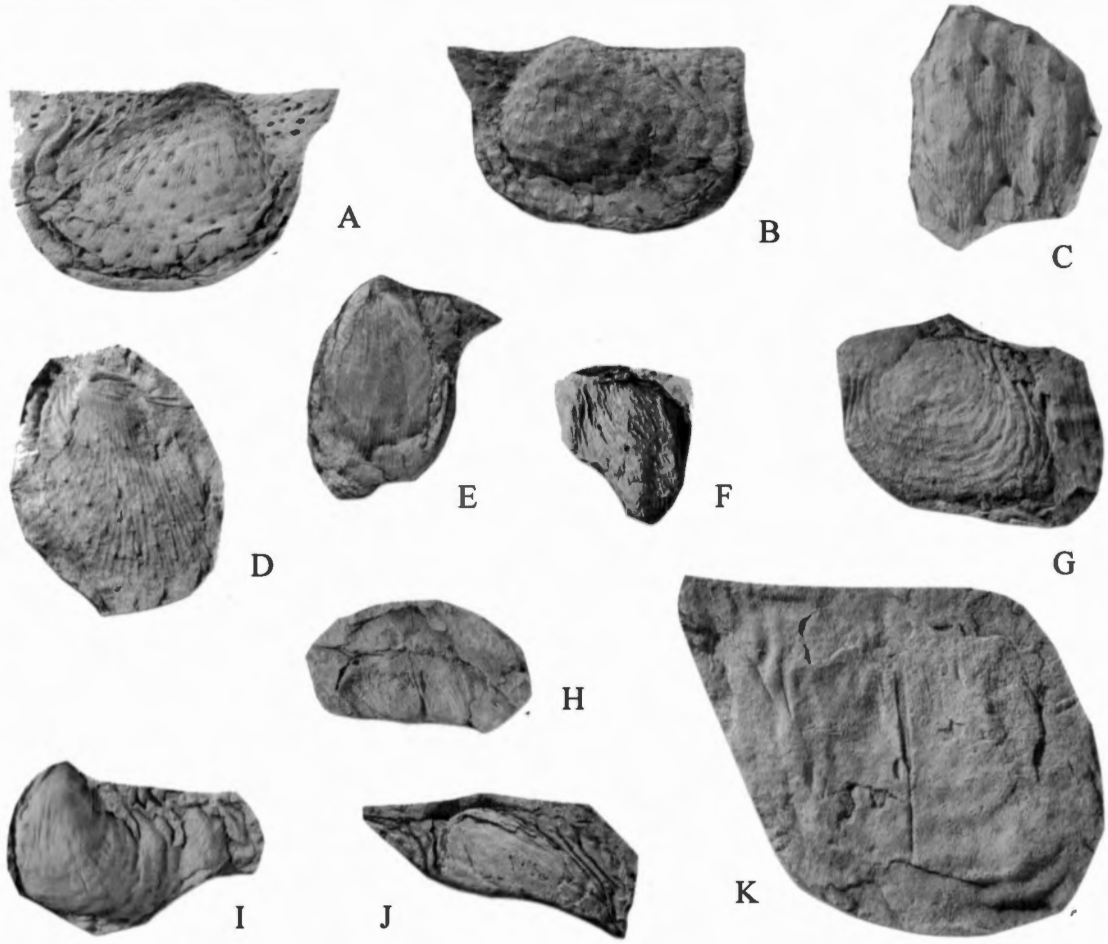


Fig. 17.27. *Platycancrinella grandauris* Waterhouse. A, B, external mould and latex cast of holotype, ventral valve UQF 73620. C, latex cast of ventral valve, unregistered specimen. D, worn ventral valve, unregistered specimen. E, worn internal mould of ventral valve, unregistered specimen. F, worn external mould of dorsal valve, unregistered specimen. G, dorsal external mould UQF 73621. H, internal mould of both valves, dorsal aspect with part of ventral external mould to right, UQF 73624.1, ventral internal mould UQF 73622. J, worn ventral valve UQF 73623. K, dorsal internal mould UQF 73625, x 2. Specimens from Pija Shale Member (Changhsingian), Manang, Nepal. These include the original figures of the species, poorly reproduced in Waterhouse (1983a). Specimens x 1, except K, x 2.

Tribe **ENGELLININI** new tribe

Name genus: *Engellinus* new genus from Faulkland Formation (Visean or early Serpukhovian) of New South Wales, Australia, here designated.

Diagnosis: Small to moderately large shells with slender body corpus, fine ribs over both valves, spines fine, usually crowded over ventral ears, scattered over ventral disc with slender prolonged bases, erect over trail. Spines present or absent from dorsal valve. Commarginal rugae may be developed regularly over both valves, subdued to moderate in strength. Adductor scars weakly to moderately dendritic. Lower Carboniferous (Visean, ?lower Serpukhovian).

Genera: *Engellinus* new genus, *Comagunia* new genus, ? *Minisculinella* new genus, *Papiliolinus* Waterhouse & Gupta.

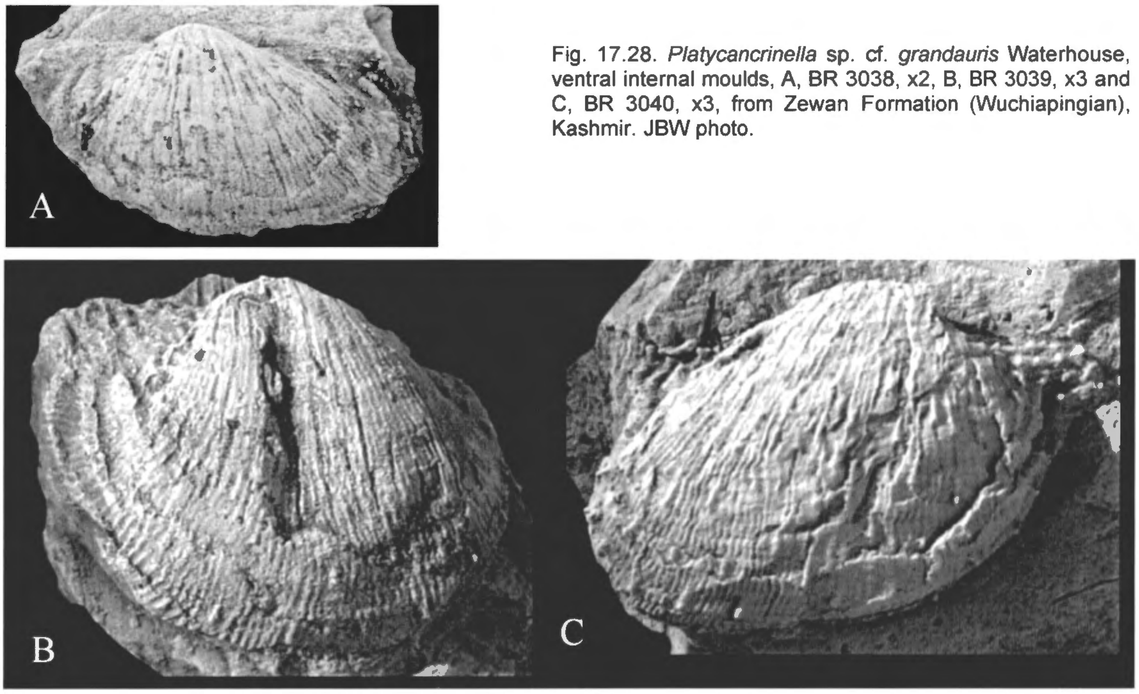


Fig. 17.28. *Platycancrinella* sp. cf. *grandauris* Waterhouse, ventral internal moulds, A, BR 3038, x2, B, BR 3039, x3 and C, BR 3040, x3, from Zewan Formation (Wuchiapingian), Kashmir. JBW photo.

Discussion: Two genera are known from Lower Carboniferous faunas of India and east Australia which have fine radial ornament and low commarginal rugae and slender spines with elongate bases over the ventral disc. The ventral adductors may be smooth posteriorly and have ridges in front, and the dorsal cardinal process is bifid in the type species of *Engellinus* (Peou & Engel, 1979, Fig. 7A9), but trifid in an associated species (Peou & Engel 1979, Fig. 7.B3, 4), and the dorsal median septum is long and simple. The dorsal adductors are flabellate or weakly dendritic, not strongly dendritic as in Permian Paucispinaurini, nor incised and striate as in Auriculispininae. *Engellinus* and *Papiliolinus* are characterized by numerous fine erect spines over the ventral ears, low subdued commarginal rugae, and fine radials. *Engellinus* is paucispinaurian in so far as the dorsal median septum is long and simple, less like that of *Auriculispina*, and the cardinal process may be bifid or trifid, showing a development beyond the bifid cardinal process of Proboscidellinae or Fluctuariinae and towards that typical of Paucispinauriidae and Auriculispinidae. The tribe is regarded as companion to Magniplicatinini, represented in correlative Visean faunas, but is less paucispinaurian in its attributes.

Genus ***Engellinus*** new genus

Fig. 17.29, Fig. 17.30

Derivation: Combination of surname of Brian A. Engel; linus – rib, Lat.

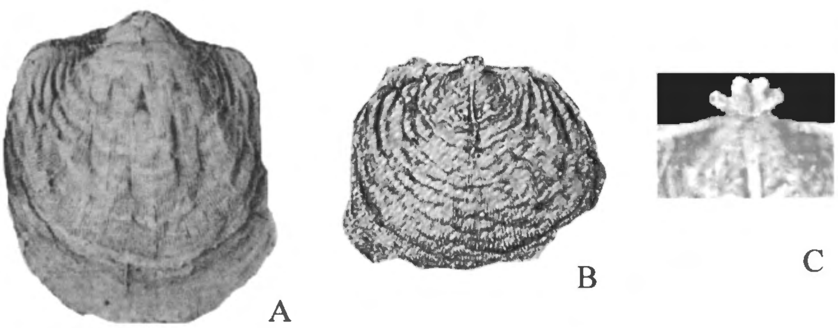


Fig. 17.29. *Engellinus rawdonvalensis* (Peou & Engel). A, latex cast of ventral external mould AMF 121171, x1. B, C, *Engellinus kerripitensis* (Peou & Engel). B, latex cast of dorsal external mould with part of disc, holotype AMF 109665, x1. C, cardinal process x3 for same specimen. From Faulkland Formation (Visean, lower Serpukhovian?), New South Wales, Australia. See Peou & Engel (1979)

Type species: *Linoproductus* (*Balakhonia*) *rawdonvalensis* Peou & Engel, 1979, p. 147 from Faulkland Formation (late Visean or early Namurian), New South Wales, Australia, here designated.

Diagnosis: Moderately large with slender visceral disc, both valves ornamented by fine ribs, outer hinge spines numerous, other spines scattered over ventral visceral disc and trail, with slender elongate bases. No dorsal spines.

Discussion: The species named *rawdonvalensis* is a very distinctive form, with slender disc and very fine ribs. *Linoproductus* (*Linoproductus*) *kerripitensis* Peou & Engel (1979, p. 147) from the same beds is congeneric. There are fine spines with elongate bases, more or less in quincunx, over the ventral disc. Both species were re-examined in Waterhouse (2010a, p. 37, Fig. 10). The specimens are very close in general appearance to *Papiliolinus* Waterhouse & Gupta, 1977, p. 160 from the Fenestella Shales of northwest India, which also has slender visceral disc, fine ribbing, slender distinct rugae and numerous spines near the ventral hinge. The difference is that *Papiliolinus eishmakami* Waterhouse & Gupta has small erect spines over the dorsal valve.

Cancrinella (?) *makhinini* Klets (2005, pl. 4, fig. 6-8) from the Amonoman Suite (Serpukhovian, Bashkirian) of northeast Russia appears to moderately close, with very weak rugae, but does not appear to have been formally described – and Klets died before he could clarify the species. The nature of dorsal ornament and internal muscle impressions are not clear.

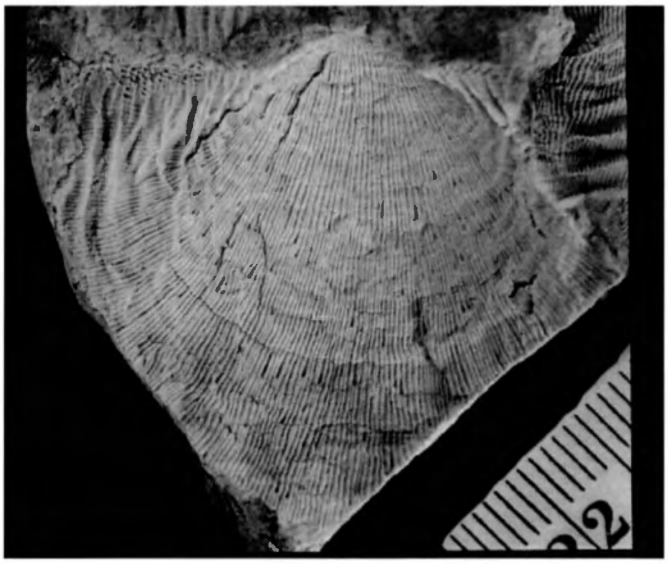


Fig. 17.30. *Engellinus rawdonvalensis* (Peou & Engel, ventral external mould AMF 121171 (formerly NUF 3608), showing numerous ear spines and fine elongate body spines. Scale in mm. Li Wengzhong photo.

Genus ***Comagunia*** new genus

Derivation: Named from Comagun River, tributary of Avon River, Windsor, Nova Scotia, Canada.

Type species: *Productus lyelli* Verneuil in Lyell, 1845, table, from Windsor Group (Visean), Canada, here designated.

Diagnosis: Small highly arched shells with fine erect spines crowded near the hinge, rare disc spines with short elongate bases, moderate to negligible commarginal rugae.

Discussion: This genus is close to *Engellinus* from Australia and *Papiliolinus* from India, in having fine ribbing and dense array of posterior ventral spines, but species are much more vaulted. There are fine spines with elongate bases, more or less in quincunx, over the ventral disc, somewhat like the body spines in *E. rawdonvalensis*.

Comagunia lyelli (Verneuil, 1845)

Fig. 17.31, Fig. 17.32A,

1845 *Productus lyelli* Verneuil in Lyell, table.
1855 *P. lyelli* – Dawson, p. 219, fig. 27g.
1929 *P.* (*Linoproductus*) *lyelli* – Bell, p. 112, pl. 16, fig. 4, 4a, ?6, ?9, 11.

Neotype: GSC 7952a figured by Bell (1929, pl. 16, fig. 4, 4a), from Windsor Group (upper Visean), east Canada, and figured as Fig. 17.31, Fig. 17.32A, here designated. This nomination protects *dawsoni* Beede (see below).

Diagnosis: Subequilateral with fine costellae, numerous ear spines, slightly prolonged bases for spines over ventral disc and rugae restricted to posterior lateral margins.

Discussion: *Productus lyelli* Verneuil is distinguished primarily by the numerous fine erect spines along the hinge and over the ventral ears (see Bell 1929, pl. 16, fig. 4, 9). One outstanding specimen GSC 7684 allocated by Bell (1929, p. 114, pl. 16, fig. 6) to *Productus lyelli* var. b displays regularly spaced spines with short elongate bases over the venter. It is otherwise like *lyelli*. Some specimens called *lyelli* var. a by Bell (1929, p. 113, pl. 16, fig. 9?, 11) also lack prominent or regular commarginal rugae, and may well be allied. But one specimen GSC 7949 (Bell 1929, pl. 16, fig. 10), found in what dark bituminous calcareous shale (like the preceeding two specimens), has shorter hinge line. (See Fig. 17.33).

Unlike *Comagunia dawsoni* (Beede) from the same beds, commarginal rugae are only clearly developed on the posterior lateral shell, but faint commarginal rugae cover the valves. Costellae are fine, and other ventral spines few and with comparatively narrow subelongate bases. This species was listed in a table by Lyell (1845) as *Productus Lyelli* de Verneuil, and mentioned in a very general way with a figure in Dawson (1855, p. 219, fig. 27g). The original figure for *lyelli* shows a specimen that lacks commarginal rugae, and although the drawing falls far short of a good rendition, the standard of other sketched fossils strongly indicates that strong commarginal rugae would have been represented had they been present. It was believed by Bell (1929) that the species was further described as *Productus cora* [non d'Orbigny] by Davidson (1863, pp. 174, 175, pl. 9, fig. 22, 23), but this specimen displays commarginal rugae. Ornament along the hinge is not preserved.

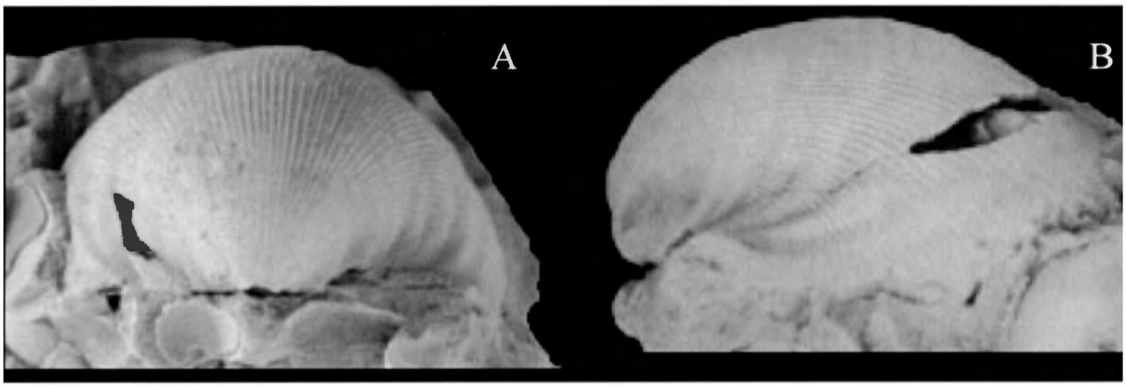


Fig. 17.31. A, *Comagunia lyelli* (Verneuil). Posterior and lateral aspects of ventral valve neotype GSC 7952a, x2.5, x3. From Windsor Group (Visean). JBW photo.

Comagunia dawsoni (Beede, 1911)

Fig. 17.32B

1863 *Productus cora* [non d'Orbigny] – Davidson, pp. 174, 175, pl. 9, fig. 22, 23.
1911 *P. dawsoni* Beede, p. 162, fig.
1911 *P dawsoni acadicus* Beede, p. 162, fig.
1929 *Productus* (*Linoproductus*) *lyelli* [non Verneuil] – Bell, p. 112, pl. 16, fig. 1, 2, 2a, 3, 5, 7, 8.

Holotype: Sole specimen NYSM 8448 figured by Beede (1911) from Windsor Group, Cape Le trou, Grindstone Island, Anticosti Island, Canada. Holotype for *dawsoni acadicus*, NYSM 8449, sole figured specimen in Beede (1911).

Diagnosis: Both valves marked by closely spaced costellae and low commarginal rugae, ventral ear spines numerous, other ventral spines few.

Description: A specimen measures 20mm long and wide according to Beede (1911), with a hinge width of 15mm and height of 4mm, though the figure suggests a width of 24mm and length of 27mm. A well preserved specimen GSC 7952b, figured by Bell (1929, pl. 16, fig. 7), measures 24mm wide, 22.5mm long and 10.5mm high. Amongst material figured by Bell, a complete ventral valve measures 28mm wide and 32mm long, and a dorsal valve is 27mm wide, 25mm long and 16mm high. The thickness of the disc is not entirely clear, but a figured specimen about 32mm long suggests a disc close to 6mm in thickness. The ventral umbo is broad and incurved, and the ears well formed with a dense array of spines, counted at 25 to 50 by Bell (1929). There are few body spines, and anterior spines are fine and seemingly erect. No dorsal spines are present. Costellae range from 10-12 in 5mm anteriorly, somewhat differentiated, and both valves are covered by fine commarginal rugae, two or usually three in 5mm anteriorly, even over the ventral valve, but stronger postero-laterally on the dorsal valve, where they tend to to be less symmetrical with partial growth stops. The cardinal process has two large lobes ventrally, but whether there is a median lobe is not clear. The dorsal septum is single and sturdy.

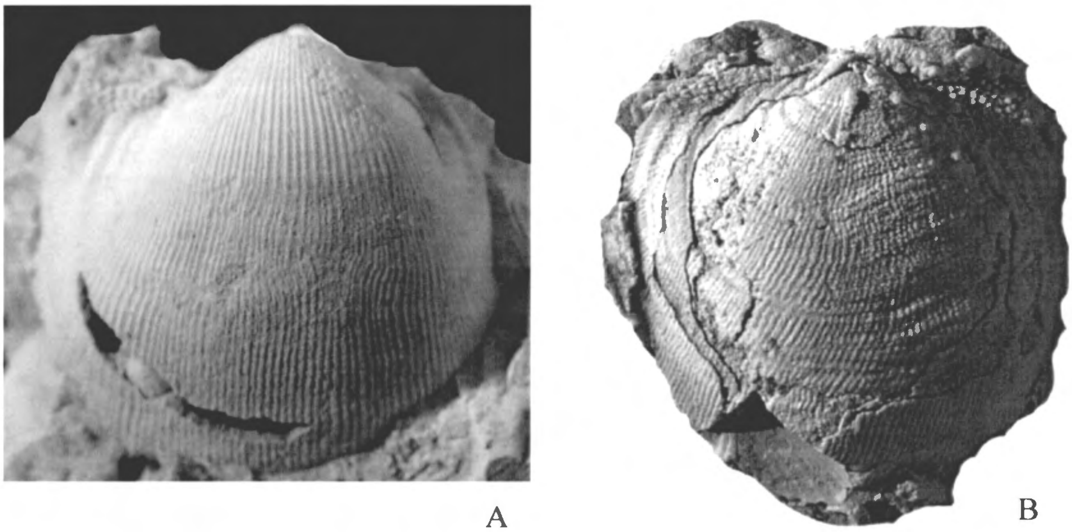


Fig. 17.32. A, *Comagunia lyelli* (Verneuil), neotype, ventral valve GSC 7952a, x3. B, *Comagunia dawsoni* (Beede). GSC 7952b, x2.5, dorsal valve interior with part of ventral valve posteriorly. Specimens from Windsor Group (Visean), Nova Scotia, Canada. JBW photo.

Discussion: In many respects, the species is close to *Engellinus rawdonvalensis* (Peou & Engel, 1979) from Australia, showing fine ribbing, regular commarginal wrinkles, and dense spines over the ventral ears, but the Australian species also displays fine spines with elongate bases over the venter. The species *dawsoni* is distinctly more arched than *Engellinus* from Australia, in that respect approaching *Comagunia lyelli* (Verneuil) from the same faunas in Nova Scotia.

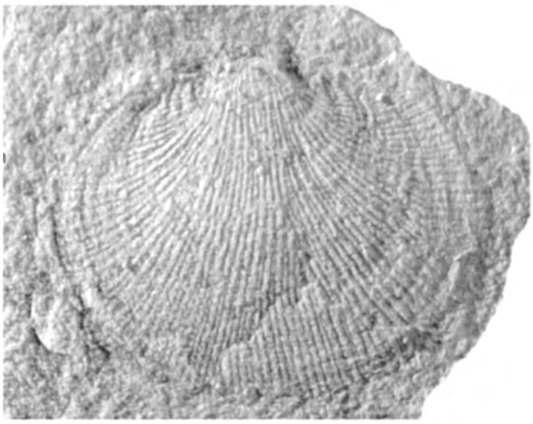


Fig. 17.33. *Comagunia* sp. GSC 7945, x4.5, from bituminous beds of lower Windsor Group (Visean), Nova Scotia, Canada. JBW photo.

A number of these specimens were regarded by Bell (1929) as belonging to *Productus lyelli* Verneuil in Lyell, 1845, p. 221, but unlike the original material, and subsequent figures, the specimens have more prominent regular commarginal rugae over both valves, and they are therefore discriminated. Bell (1929) nominated one of the rugose specimens as neotype for *lyelli*, but the specimen differs in its ornament, so the nomination was inappropriate, because his nominated specimen belongs to *dawsoni* Beede, 1911.

Comagunia auriculispinus (Beede, 1911, p. 116 and figure), and including *Productus* (*Linoproductus*) *dawsoni* [non Beede] of Bell (1929, p. 114, pl. 17, fig. 1) from the Windsor Group of Nova Scotia is weakly transverse in shape, with crowded posterior spines, drawn as somewhat broader in the figure by Beede (1911).

Genus ***Papiliolinus*** Waterhouse 1977

Fig. 17.34

The type species *Papiliolinus eishmakami* comes from India (Waterhouse & Gupta, 1977, p. 160; 1979a, p. 130), and is based on specimens described as *Productus undatus* not Defrance by Diener (1899) from the Fenestella Shales of Kashmir. It has slender body corpus, fine costellae and numerous ear spines and slender ventral body spines and fine erect dorsal spines anteriorly. The ventral muscle field is not visible, and the dorsal valve displays a cardinal process with deep ventral cleft, small pit, simple dorsal medium septum, and no accessory septa: adductor scars are obscured by the external ribs (Waterhouse 2004a, p. 219, pl. 2, fig. 14).

Fig. 17.34. *Papiliolinus eishmakami* Waterhouse & Gupta, latex cast of dorsal valve with anterior dorsal spines, holotype GSI 6226, x2. From Fenestella Shales (Visean – Serpukhovian), Kashmir. JBW photo.

Paeckelmann (1931, p. 223, pl. 21, fig. 2-4) considered that his *Productus* (*Linoproductus*) "*striatus* (Fischer)" nov. var. *spinifera* from the Carboniferous of Germany somewhat resembled *Productus lyelli* Verneuil of Bell (1929), but in its large size and low inflation, his taxon approaches *Papiliolinus.*

Two dorsal valves figured as *Cancrinella* sp. by Chen & Shi (2003, p. 154, pl. 9, fig. 18, 19) from Visean-Serpukhovian of the Tarim Basin, northwest China, display low commarginal rugae, fine ribs and scattered spines. The ears indicate what are either fine pits or fine spine bases, numerous and close-set, that recall the ventral ears of *Engellinus* and *Papiliolinus*, and if pits, presumably opposed numerous spines on the ventral valve. The comparatively numerous dorsal disc spines signal an ally of *Papiliolinus.*

Genus ***Minisculinella*** new genus

Fig. 17.36, Fig. 17.37

Derivation: minime – very little, Lat.

Type species: *Productus undiferus* Koninck, 1846, p. 153 from Tournai and Visé, Belgium, here designated.

Diagnosis: Small elongate shells with slender disc, fine ribs, subdued and low rugae, ventral spines along the hinge and scattered over ventral valve, dorsal spines.

Discussion: This is a small genus, characterized by fine ribs and small ventral spines, and low growth wrinkles or growth lines. It has escaped attention over recent years, and has been left unmentioned in recent overviews by Muir-Wood & Cooper (1960) and Brunton et al. (2000) or Licharew (1960). Lower Carboniferous specimens were figured from Visé and Tournai, and that from Tournai (Koninck 1846, 1847, pl. 11, fig. 5a-e) is selected as lectotype.

Fig. 17.36. *Minisculinella undiferus* (Koninck), specimen figured from Tournai, Belgium, by Koninck (1847, pl. 11, fig. 5a-c), x1.

Radial ribs and low concentric rugae are present, and the slopes were said to be "most spinose", with reference by Koninck to "hollow tubes", presumably meaning spine bases. It is not clear from the text whether spines were on both valves or only the ventral valve, but are drawn as present on the dorsal valve. Rare Lower Carboniferous material was described from Settle, Yorkshire, England, by Davidson (1861, p. 230, pl. 53, fig. 5, 6), and illustrated as highly concavo-convex, with ribs and inconspicuous spines. The shell margins in Davidson (1861, pl. 53, fig. 6) are reflected. Delicate spines were said to arise from the surface of the valves (note plural), and are more numerous on the ears close to the cardinal edge (Davidson 1861, p. 231).

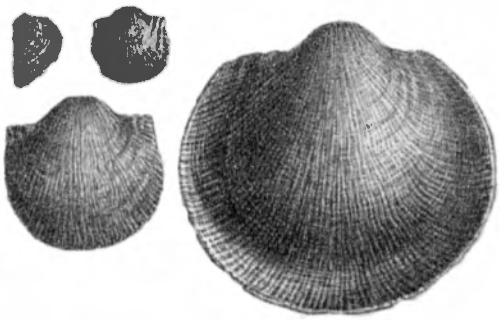


Fig. 17.37. *Minisculinella undiferus* (Koninck). Lateral and ventral aspects of ventral valves figured by Davidson (1861, pl. 53, fig. 5, 6) from Lower Scar limestone (Visean) near Settle, Yorkshire, England. The smaller two specimens at natural size.

The descriptions may be amplified from examination of small collections kept at the Natural History Museum, London. Ventral valves labelled *undiferus* Koninck from Little Island, Cork, Ireland, such as B 40199, only 6.5mm wide, show a row of spines along the hinge, with anterior ventral spines swelling from the crest of wrinkles, and a second specimen has high knobs on the wrinkles but no clear spines. From the same locality, B 40210 has three hinge rows, low indefinite wrinkles except laterally, and spine bases that are short but clearly defined and prolonged over the ventral disc, erect on the trail, and three ribs per mm.

The ornament suggests an early form of Paucispiniferidae, related to members of Engellini, and the size is small, the wrinkles very low, and the spines not prominent, unlike for example Visean species such as *Globicorrugata* (see p. 424). The shell is smaller and more concavo-convex than *Engellinus* and scarcely rugose, with fewer posterior spines, but shares fine radials. *Ovatia* has different spines with less elongate bases and no dorsal spines and longer umbonal slopes.

Subfamily **COOLKILELLINAE** Waterhouse, 2001

Fig. 17.38, Fig. 17.39

[Coolkilellini Waterhouse, 2001, p. 49].

Diagnosis: Small compact shells with moderately thin to thick body cavity and steep high umbonal slopes, long ventral body spine bases, few or weak hinge spines, no dorsal spines, closely costellate, weak or scarcely any commarginal wrinkles. Dorsal valve geniculate, ornament may be pitted. Lower Permian (Asselian) to Middle Permian (Wordian).

Genera: *Coolkilella* Archbold, *Kasetia* Waterhouse, *Liaozhuotingia* new genus, *Magadania* Ganelin, *Nisalaria* Waterhouse.

Discussion: These genera are similar to each other in shape and ornament, and are very close to *Paucispinauria* and

Fig. 17.38. *Coolkilella khangsarensis* Waterhouse & Chen, dorsal aspect of specimen with valves conjoined, from Nambdo Member, (Changhsingian), north-central Nepal, x2. Kept at Canterbury Museum, Christchurch, New Zealand.

allies, but more subrectangular to quadrate in outline and less convex ventral valve. The genera share elongate ventral spine bases, and unlike Paucispinauriinae, lack dorsal spines. Ventral adductors are weakly dendritic or weakly striate. The dorsal septum may be short, and there is no double dorsal septum. Possibly the tribe needs to be subdivided, because the body corpus is thin in *Liaozhuotingia* new genus *and Nisalaria* but thicker in *Coolkilella* and *Kasetia*. The ventral valve is weakly rugose in *Nisalaria*, *Liaozhuotingia*, and *Coolkilyella*, more strongly rugose in *Kasetia* and and very feebly rugose in *Magadania*.

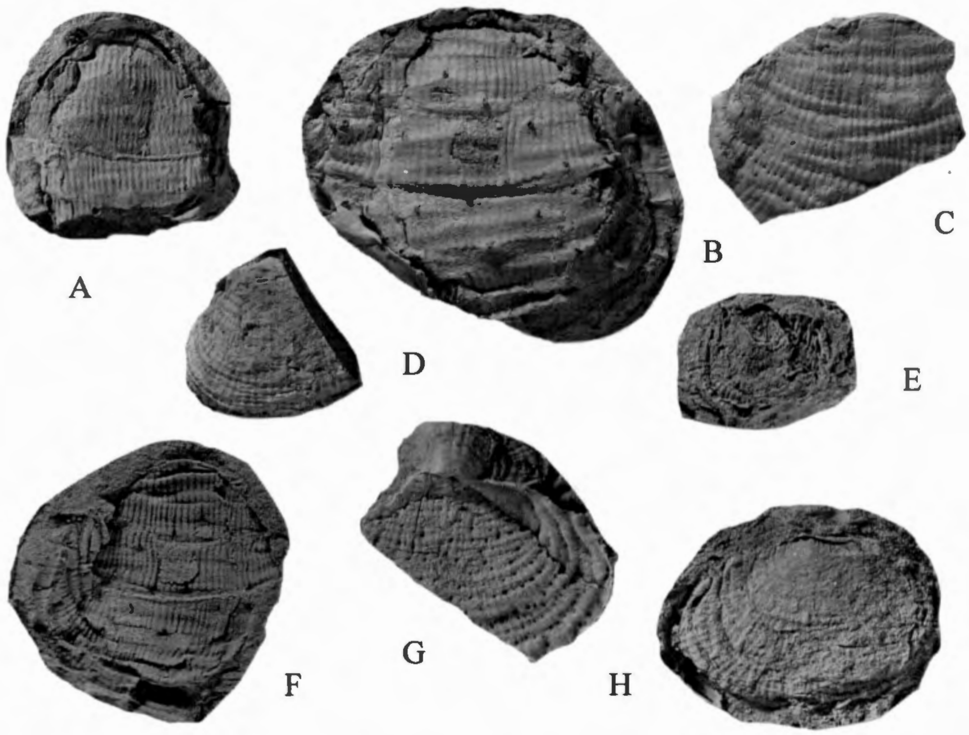


Fig. 17.39. *Kasetia kaseti* Waterhouse. A, F, latex cast and external mould of ventral anterior, unregistered specimen (kept with TBR specimens), x2.5. B, latex cast of ventral anterior, unregistered specimen, x3. C, G, holotype, latex cast of ventral exterior and dorsal view of internal mould with both valves conjoined, TBR 287, x2.5. D, ventral internal mould TBR 375, x1.5. E, ventral external mould TBR 97, x2. H, worn dorsal valve interior, TBR 285, x2.5. From Ko Yao Formation (Sakmarian), south Thailand. See Waterhouse (1981b). All specimens kept at Geological Survey Division, Department of Mineral Resources, Bangkok, Thailand. J. Coker & JBW photo.

Genus ***Liaozhuotingia*** new genus

Fig. 17.40A-D

Derivation: Named for Liao Zhuo-ting.

Type species: *Cancrinella pseudotruncata* Ustritsky, 1960 from upper Early Permian of Tarim Basin, northwest China, here designated.

Diagnosis: Highly arched shells with long ears and slender body corpus, ventral spines closely spaced and fine with elongate bases over ventral valve, and erect in a dense array over inner ears and adjoining umbonal slopes, hinge row or rows not well known. No dorsal spines, but dimples opposite ventral ear spines, and closely spaced elongate dimples over disc. Rugae low and closely spaced over both valves. Ventral muscle field little impressed.

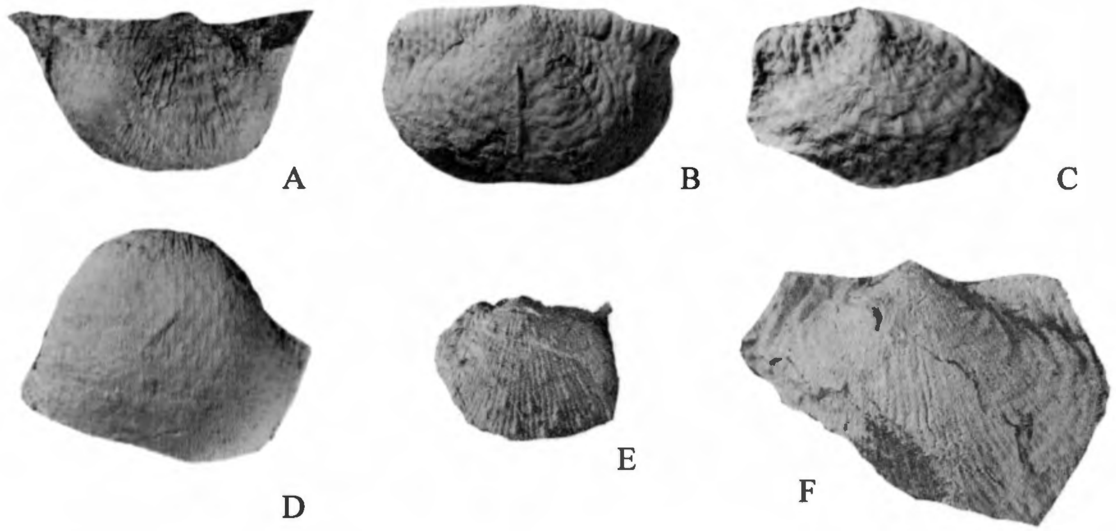


Fig. 17.40. A-D, *Liaozhuotingia pseudotruncata* (Ustritsky). A, D, posterior and anterior aspects of ventral internal mould IGPS108885. B, dorsal valve, interior view, IGPS108884. C, external mould of dorsal valve IGPS108886. Specimens from Qipan Formation (Artinskian), northwest China, x1.5. Photographs courtesy of G. R. Shi. See Chen & Shi (2006). E, F, *Nisalaria inflata* (Waterhouse). E, holotype, ventral valve UQF 68909, holotype, x1. F, ventral valve UQF 68910, x2. From Nisal Member (Changhsingian), west Nepal. J. Coker & JBW photo.

Discussion: The species has been described as *Cancrinella pseudotruncata* by Ustritsky (1960, p. 36, pl. 6, fig. 10-13, pl. 7, fig. 1-3) and Zhang et al. (1983, p. 296, pl. 130, fig. 13-16), to be later revised as *Costatumulus* by Chen (2004, p. 24, pl. 4, fig. 9) and Chen & Shi (2006, p. 159, pl. 12, fig. 13, 17-19, pl. 15, fig. 4). *Cancrinella* has spines on both valves, and *Costatumulus* has well developed hinge spines and few spines along the inner ears and outer umbonal slopes, and the ventral muscle field is deeply impressed and striate, so that both generic assignments are inappropriate. *Nisalaria* Waterhouse, 2002b (see Fig. 17.40E, F) differs in having better spaced and coarser ventral disc spines, but is comparable in having long large ears and relatively close-spaced ventral spines and dorsal dimples. Unlike *Liaozhuotingia*, it lacks the numerous spines along the inner ears and outer umbonal slopes, and has a single row of spines along the hinge. *Coolkilella* Archbold and *Kasetia* Waterhouse are moderately similar in overall shape, spinosity, dimples and ribs, but have thicker visceral disc and lack the numerous inner ear spines. *Calytrixia* Waterhouse is closer, insofar as the visceral disc is comparatively thin, and spines are numerous over the inner ear and outer umbonal slopes. This genus, as figured by Foster & Waterhouse (1988, fig. 8d-h) and Archbold (1995, Fig. 6A-L), is found in early Permian deposits of the Calytrix Formation, Canning Basin, Western Australia, and differs from the new genus in having a less arched ventral valve with coarser ribs and spines, and less conspicuous dimples over the dorsal valve, and is treated as an early member of Cancrinellinai.

The synonymy proposed by authors for *pseudotruncata* Ustritsky has included material figured by Merla (1934, p. 261, pl. 25, fig. 24-26, pl. 26, fig. 5-10), but these specimens appear to be narrower and more vaulted. Though referred to *pseudotruncata*, *Cancrinella* sp. of Grant (1976, pl. 33, fig. 17, 18, pl. 44, fig. 36) from the early Middle Permian of Thailand has few inner ear spines.

Genus ***Nisalaria*** Waterhouse, 2002b

Fig. 17.40E, F

Type species: *Cancrinelloides (Bandoproductus) inflata* Waterhouse, 1983a, p. 130 from Nisal Member (early Changhsingian) of Nepal.

Diagnosis: Small, subequidimensional, ears long and large, body corpus slender, ventral spines arranged in close quincunx, with short prominent elongate bases, erect spines in a row along hinge, dorsal dimples elongate and prominent, low close-set ventral rugae.

Discussion: The ventral muscle field is not large and deeply inset: it is paucispinaurian rather than auriculispinan. Brunton (2007) referred the genus to Lyoniini, but there are substantial differences, Lyoniini being more transverse and larger, with different ventral muscle field. The comments with regard to *Nisalaria* by Brunton (2007, pp. 2659, 2660) are mystifying, and underline the need to check statements concerning the original references. Brunton stated that the three descriptions of the type species by Waterhouse (1978, pp. 76, 77; 1983a, p. 130; 2002b, p. 51) "differ slightly in terms of profile and umbonal inflation", but any such differences are remarkably hard to find, and were not specified. Brunton stated that he therefore relied on the figures cited in Waterhouse (1978, pl. 11, fig. 13-18), which he alleged "would seem to be conspecific". Of course they were conspecific – these, and only these, were the cited types in Waterhouse (1983a, 2002b). There is no "seem" about it, nor possibility of confusion, except from the uncertainty conjured by Brunton. He then pronounced that the specimens of Waterhouse (1978) were " not considered to belong to *Cancrinella*"....., which was what was established by Waterhouse (1983a, 2002b). The mystification and uncertainties conjured up by Brunton (2007) are somewhat contradicted by his captions for the illustrations of the genus, which figured the holotype and correctly allowed that it is holotype, as illustrated by Waterhouse in 1978 and cited by Waterhouse (1983a).

Family **AURICULISPINIDAE** Waterhouse, 1986b

[Nom. transl. hic ex Auriculispininae Waterhouse, 1986b, p. 57].

Diagnosis: Both valves ornamented by slightly irregular ribs, ventral spines arranged along hinge in one to four rows, and lie in quincunx over the visceral disc, with slender to thick elongate bases: spines further prolonged anteriorly within the shell. Spines erect over ventral trail, and if present, erect and undifferentiated over dorsal valve, usually absent. Shell also crossed by very subdued to moderately well formed commarginal rugae. Ventral interior characterized by rectangular and striate adductor scars, often impressed into the posterior wall; dorsal valve may have low hinge ridge and low to broad median septum, often doubled posteriorly, without conspicuous marginal ridge. Visceral disc normally slender.

Discussion: Costellae are not as linear as in Linoproductidae, and the shells are smaller and often more transverse and less coiled. Proboscidellinae and Undariinae are similar, except for their much more extended ventral valve. The elongate spine bases in Auriculispinidae recall those of the larger shells *Wardlawria* and *Lineabispina*, but the core of the spine bends forward into the shell from the spine base (Fig. 11, p. 18), unlike the ventral spines in Wardlawriinae. The cardinal process has a high median shaft, and is not bilobed from a ventral view. Evolution of the family is summarized on p. 464.

The family is close to Paucispinauriidae Waterhouse, which is distinguished by its dendritic adductor scars in both valves, and tendency to have thicker visceral disc and dorsal spines. The assignment of genera to Auriculispininae by Brunton et al. (2000, p. 537) seems disorganized, and the stress in their diagnosis of the subfamily on the absence of sockets is completely unwarranted, for sockets and teeth are absent as well from other groups within Linoproductoidea and Proboscidelloidea, and the statement that Auriculispinini was characterized by a cluster of hinge or ear spines is not true of several Permian members.

In Rozanov (2003), Ovatiinae Lazarev was treated as a synonym of Auriculispininae, but the ventral spines in the two subfamilies are quite different, as are the muscle scars, commarginal rugation, nature of ribs and other features, explained elsewhere in the text (see p. 372) and Waterhouse (2004b).

Source of the subfamily is open to further study. It may be correct that Paucispinauriinae have a long history in being represented by the newly named genera *Globicorrugata* and *Engellinus*, with low wrinkles and slender posteriorly prolonged ventral spines in Visean faunas. On the other hand, *Donakovia*, based on *Ovatia markovskii* as described by Donakova (1977, p. 120, pl. 28, fig. 3) from Kipcak beds of lower Visean age in the southern Urals shows the auriculispinin ventral adductor field. This genus does not appear to belong to *Ovatia*, because some ventral spines have elongate bases, and shells tend to be less vaulted, and hinge spines few. The figures (Donakova 1975, p. 167, pl. 66, fig. 10, pl. 70, fig. 4; 1977, pl. 28, fig. 1-5) suggest a proboscidelloid form of moderately small size, both valves covered by costae, and no spines over the dorsal valve, which appears semi-geniculate. In its ventral adductor field, which is raised and large, with a few longitudinal striae, *Donakovia* differs from all these genera. It displays a bifid cardinal process, and seems to lack conspicuous ventral hinge spines, with only two fine spines suggested at the hinge in the holotype (Donakova 1977, pl. 28, fig. 1). Thus it differs from Auriculispininae in having a bifid cardinal process and inconspicuous hinge spines, but given its distinctive ventral muscle field, *markovskii* does suggest potential early stock that may have evolved into the subfamily, and may have been related to *Undaria* through shape, strength of costae and nature of ventral spines. *Undaria* Muir-Wood & Cooper, 1960, p. 317, pl. 118 has a row of ventral spines along the hinge, and is like *Donakovia* in its regular fine rugae. Although the ventral interior is not known according to Muir-Wood & Cooper (1960, p. 317, the type specimens, because of their mode of preservation, do not show any sign of a large raised ventral adductor platform.

Subfamily **AURICULISPININAE** Waterhouse, 1986b

Fig. 17.41, Fig. 17.42

[Auriculispininae Waterhouse, 1986b, p. 57].

Diagnosis: Normally transverse genera with variable number of spines near hinge, usually in well formed rows, may be crowded on ears, none on dorsal valve, low wrinkles. Upper Carboniferous (Kasimovian) to Upper Permian (Changhsingian).

Genera: *Auriculispina* Waterhouse, *Cancrinelloides* Ustritsky, *Costatumulus* Waterhouse (syn. *Striapustula* Ganelin & Lazarev), *Umaria* new genus.

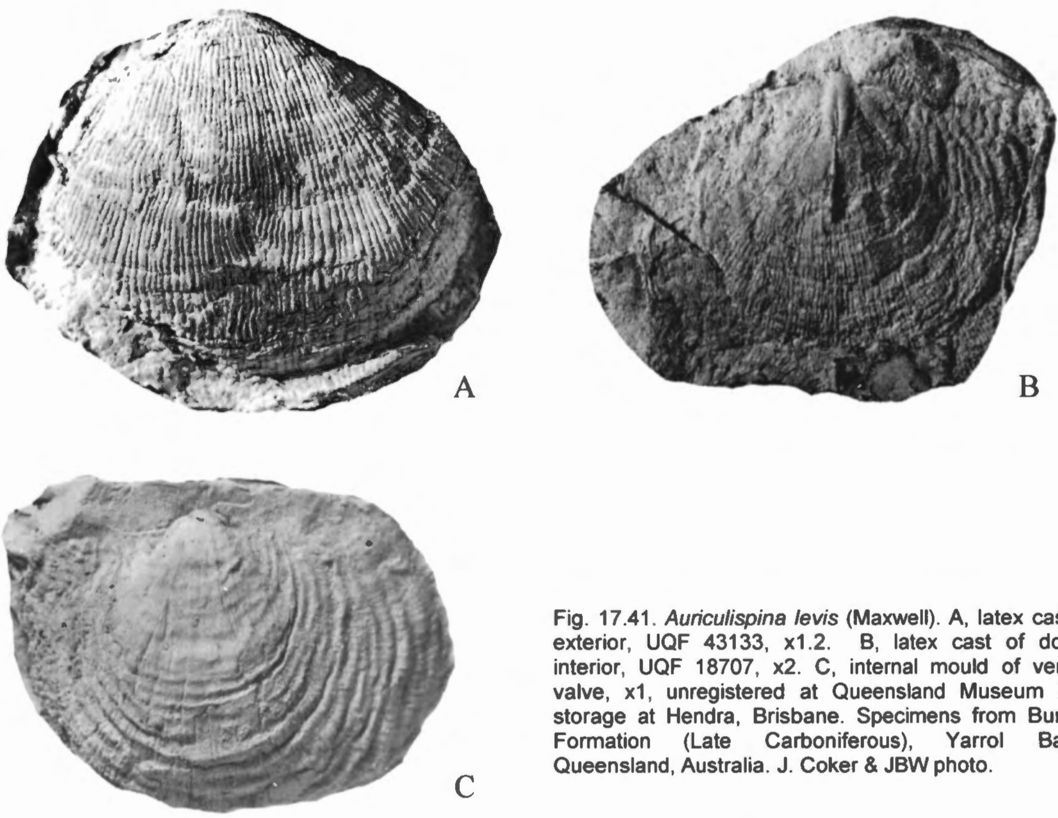


Fig. 17.41. *Auriculispina levis* (Maxwell). A, latex cast of exterior, UQF 43133, x1.2. B, latex cast of dorsal interior, UQF 18707, x2. C, internal mould of ventral valve, x1, unregistered at Queensland Museum bulk storage at Hendra, Brisbane. Specimens from Burnett Formation (Late Carboniferous), Yarrol Basin, Queensland, Australia. J. Coker & JBW photo.

Discussion: This tribe was especially numerous in Permian time, in higher paleolatitudes of both hemispheres. *Linoprotonia* Ferguson, 1971 was put in the subfamily by Brunton et al. (2000, p. 539) and has a number of spines on the ventral ears, with a row of hinge spines (Brunton et al. 2000, Fig. 378.1e), but it is re-assigned to Gigantoproductidae, because of the presence of brachial cones and lack of elongate ventral spine bases.

It may well be contended that the numerous ear spines on *Auriculispina* reinforce the age difference of this genus from the other tribal constituents, but *Cancrinelloides* Ustritsky also has a number of ear spines (see Sarytcheva 1977). The other genera centre more on *Costatumulus*, close in turn to *Umaria*: these have fewer hinge spines, and in many respects they are close to Filiconchinae, which embraces a small group of genera similar to each other in shape and trail, and two groups could arranged as subtribes: permutations will become increasing refined as alliances and differences are more closely understood.

Fig. 17.42. *Auriculispina levis* (Maxwell). A, ventral external mould UQF 18704. B, holotype ventral internal mould, UQF 18705. Specimens from Burnett Formation (Upper Carboniferous), Yarrol Basin, Queensland, Australia, x2. J. Coker & JBW photo.

Genus ***Umaria*** new genus

Fig. 17.43, Fig. 17.44

Derivation: Named from Umaria, name of region in central India.

Type species: *Productus umariensis* Reed, 1928, p. 371 from Umaria Coal Measures (Sakmarian), central India, here designated.

Diagnosis: Concavo-convex shells with narrow body corpus, fine ribs cover both valves, one or two rows of ventral hinge spines, body spines few or moderately numerous in quincunx, may have elongate spine bases, or be erect, no dorsal spines, no dorsal dimples, low commarginal rugae or growth steps. Ventral adductors elongate, weakly striate, impressed posteriorly.

Discussion: Representatives of this genus were described from Umaria, central India, with the geology explained by Gee (1928), as two species and two subspecies by Reed (1928), and these were subsequently aggregated as one species by Mitra & Chakraborty (1965), Sastry (1977) and Archbold (1983). There is considerable variation, and arguably, two species should be distinguished, one centred on *umariensis*, with few to many ventral spines, and one centred on *rewahensis* Reed, 1928, with no spines other than along the ventral hinge. Archbold (1983, Fig. 4H) illustrated a median septum that is not doubled, although Reed (1928, pl. 28, fig. 6) showed four diverging dorsal septa in a drawing, difficult to reconcile with actual specimens. The species have been referred variously to *Globiella, Stepanoviella*, *Costatumulus* and *Bandoproductus. Globiella* Muir-Wood & Cooper differs in lacking spines over the disc that have elongate spine bases, and its ventral adductors are not impressed posteriorly. *Stepanoviella* Zavodowsky has a ventral row of umbonal slope spines and dorsal spines, absent from the present form. *Bandoproductus* has regular ventral spines in quincunx with elongate bases, and usually a single row of hinge spines, and prominent dorsal dimples.

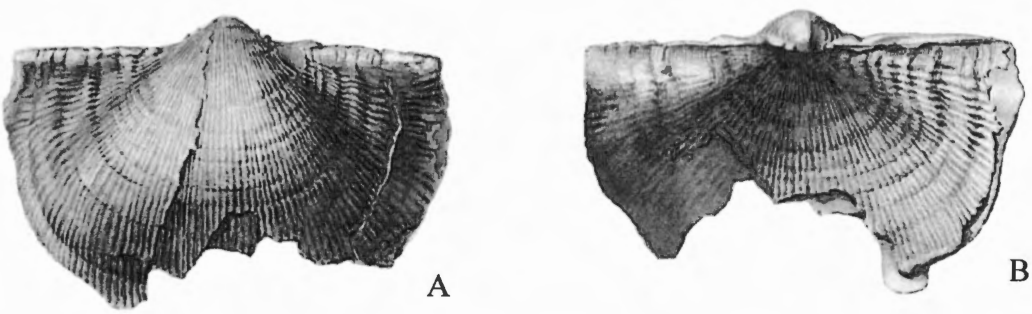


Fig. 17.43. *Umaria umariensis* (Reed). Ventral and dorsal aspects of a specimen from Umaria Coalfield (Sakmarian), central India. Kept at Geological Survey of India, Kolkata. See Reed (1928, pl. 31, fig. 1, 1a), x1.5.

There are limited differences between *Costatumulus tumida* and *Umaria umariensis*, which is slightly older, of early Sakmarian age. Ears are larger and more pointed in the Queensland species, and many species are more convex. The hinge spines usually form two rows in *tumida*, whereas a single row of spines is developed in many specimens of *umariensis,* but a few specimens show parts of two rows (Reed 1928, pl. 31, fig. 2, pl. 32, fig. 7, pl. 33, fig. 5). This latter specimen shows two rows, one along the hinge, one angling forward from the hinge, and in various specimens, one or other row, or parts of the row, may fail to develop or not be preserved. On *C. tumida*, ventral spines cover much of the visceral disc and trail, in regular quincunx. Virtually all of the Umaria shells have much less spinose ornament, except for one variety, *P. umariensis spinifera* Reed, and in this form, body spines are only slightly swollen, according to Archbold (1983, p. 248) in describing the species as *Globiella*, and the spines in his photographs are more slender than illustrated in the drawings provided by Reed (1928). An even more consistent difference is exhibited by the dorsal valve in *Costatumulus*, which has evenly developed slightly elongate pits, whereas pits are completely lacking from the Umaria species. There are other less significant differences: the Indian specimens tend to show low growth steps, replaced by rugae in the Queensland specimens, and costae tend to increase more in front of spines. The muscle field of the Indian material is rarely well preserved and so difficult to compare adequately, but Archbold (1983, Fig. 4D, E) has figured long and weakly striate ventral adductors.

Fig. 17.44. *Umaria umariensis* (Reed) from Umaria Coalfield (Sakmarian), central India. Scale in mm. Kept at Queensland Museum, bulk storage, Hendra, Brisbane, Australia. J. Coker & JBW photo.

Archbold (1983, p. 248) considered that *Globiella gracilis* Jin, Liang & Wen, 1977 from Early Permian of south Tibet was the closest of other species to the Indian form, and this may well be correct. But no dorsal valves were figured by these authors. *Globiella rossiae* Fantini Sestini (1966, p. 284, pl. 4, fig. 1-6) from the Geirud D Formation of northern Iran is congeneric. It has a row of hinge spines, and either no spines or only very fine other ventral spines, and the dorsal valve lacks spines and pits, and has a single dorsal septum (Fantini Sestini 1966, pl. 4, fig. 1a). The ventral adductors are subrectangular and comparatively smooth. Sestini (1966) noted the closeness to *umariensis*, and indeed recorded unfigured material as cf. *umariensis*. Angiolini (1995, p. 174) recorded cf. *rossiae* from the Sakmarian of the Karakorum Range in Pakistan, but *Globiella*? *rossiae* in Grunt & Dmitriev (1973, p. 107, pl. 7, fig. 6-8) from Bolorian of the southeast Pamirs is larger with stronger commarginal and radial ornament.

Genus ***Striapustula*** Ganelin & Lazarev, 1999

Younger members of Auriculispininae have been widely and closely studied, especially from Australian faunas. An interesting development in Russia is provided by *Striapustula* Ganelin & Lazarev, 1999, represented by a succession of species that in shape strongly mimic mid-Permian members of the southern genus *Terrakea* Booker of east Australia (see Waterhouse 1982a, 1986b, Waterhouse & Shi 2010), in having a highly arched ventral valve with rather small ears, and apparently with moderately thick body corpus, although this was not specified in the description. But unlike *Terrakea*, spines are missing from the dorsal valve of *Striapustula*, and possibly, the ventral and dorsal adductors are not dendritic, although it appears that these are not very well preserved, for they have not been adequately described. No dorsal pits were described, and no external dorsal valves figured, but dorsal interiors indicate what appears to be the inside of large dorsal external pits. In fact the morphology of *Striapustula* so far as it has been recorded strongly suggests a close approach to *Costatumulus* Waterhouse, 1986b, p. 58, a genus widely represented in Australia and known to extend into Asia, including parts of India (Singh & Archbold 1993) and New Zealand (Waterhouse 2001). Waterhouse (2001, p. 32) speculated that the genus would be found in Canada, based on specimens figured as *Cancrinella singletoni* Gobbett by Shi & Waterhouse (1996, pl. 17, fig. 16, 17). In the dorsal valve of *Striapustula*, the median septum is broad posteriorly and usually divided by a median slit, and there is a strong posterior ridge some distance in front of the hinge, and the ridge continues as a sturdy structure across the lateral shell in front of the dorsal ears. Much the same structures are developed in type *Costatumulus*. The Russian species tend to be smaller with smaller ears and more vaulted ventral valve than in some Australian forms, but such differences are hardly of generic significance, because there are a number of Australian species which are well preserved and agree in all details with type *Costatumulus*, except for the thickness of the body cavity and the steepness and height of the ventral posterior walls, just as is true of *Striapustula*. Possible differences in the detail of the muscle scars and internal ridges need to be treated with caution, given the poorer preservation of the Russian material compared with that of the type species *C. tumida* (Waterhouse), and the likelihood that geographic distance and younger age and smaller size would naturally lead to developmental differences. Even over the short interval of time represented by species in Russia, Ganelin & Lazarev (1999) were able to trace significant changes through the lineage in Russia. It appears that the genus *Costatumulus*, with *Striapustula* as a synonym, is widespread, but has not yet been found in paleotropical faunas.

Genus ***Costatumulus*** Waterhouse, 1986b

Fig. 17.45, Fig. 17.46

Type species: *Auriculispina tumidus* Waterhouse in Waterhouse, Briggs & Parfrey, 1983, p. 133 from Tiverton Formation (Sakmarian), Queensland, Australia.

Fig. 17.45. *Costatumulus tumida* (Waterhouse), ventral valve UQF 81428 from UQL 4509, Tiverton Formation, (Sakmarian), Queensland, Australia, x2. JBW photo.

Diagnosis: Medium-sized shells covered by ribs, spines limited to ventral valve, in row or few rows along the hinge and in quincunx over the disc and trail, dorsal valve with pits in quincunx. Rugae low and usually limited to posterior lateral flanks. Ventral adductors striate until late ontogeny, dorsal septum usually single, may have median slit or show double septum.

Discussion: Evolution and distribution of the genus is summarized on pp. 458-459.

Costatumulus ganelini new species

1846 *Productus koninckianus* [not Verneuil] – Keyserling, p. 203, pl. 4, fig. 4.
1955 *P. (Cancrinella) koninckianus* – Kashirtsev, p. 77, pl. 1, fig. 15.
1972 *Cancrinella koninckiana* – Ifanova, p. 110, pl. 4, fig. 6 (not fig. 7, 8).
1999 *Striapustula koninckianus* – Ganelin & Lazarev, p. 247, pl. 7, fig. 1-10.

Derivation: Named for Victor G. Ganelin.

Holotype: Sole specimen figured by Keyserling (1846, pl. 4, fig. 4), kept at Mining Institute Museum, St Petersburg, from the Soiva River, south Timan, Russia.

Diagnosis: Narrow moderately vaulted shells with steep umbonal flanks, ventral spines in two or three rows along the hinge, and staggered rows over disc, and arranged in somewhat concentric rows over the trail, associated with two or three low rugae, rugae otherwise only near the ears. No dorsal spines.

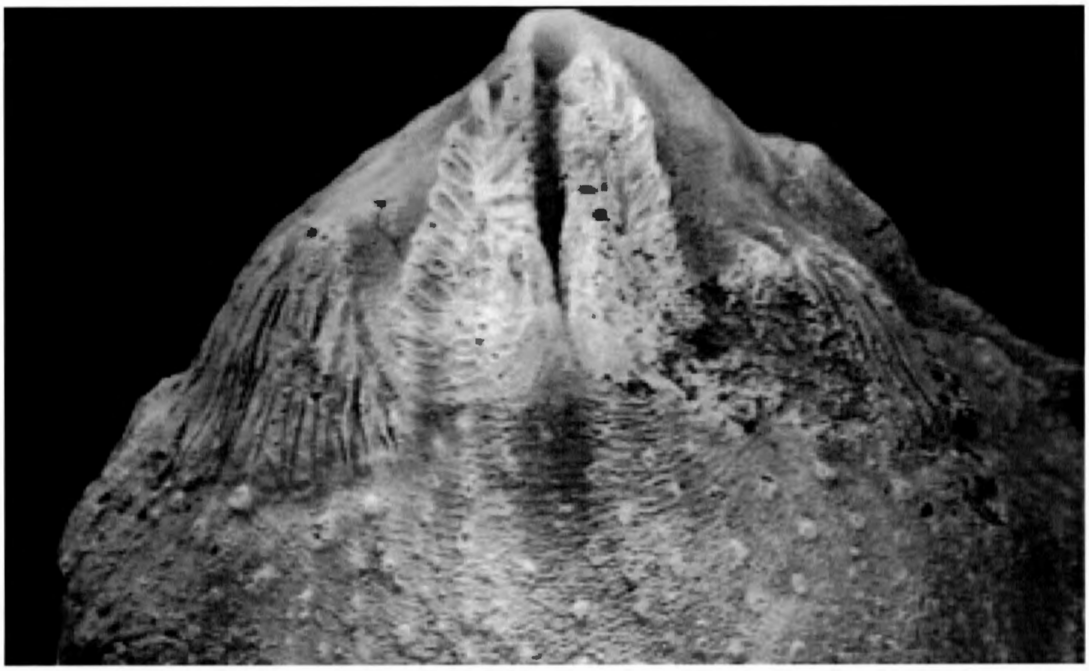


Fig. 17.46. *Costatumulus tumida* (Waterhouse), late mature internal mould, in which the striate and prominent adductor platform, deeply recessed into the posterior wall, has developed dendritic markings, UQF 44027, Tiverton Formation (Sakmarian), Queensland, Australia, x3.5. JBW photo.

Discussion: Ganelin & Lazarev (1999) illustrated and described the species mainly from Kungurian deposits of the Pechora coalfield of northwest Russia, and compared the form with other Russian occurrences. Their synonymy is presented here. Tschernyschew (1902, pp. 291, 621) applied the name *konincki* to *koninckianus* Keyserling, but did not explain that he was substituting this as a replacement, and his name has been ignored in later literature, or dismissed as an error.

As summarized herein (see pp. 409-410), and also concluded by Muir-Wood & Cooper (1960) and Gobbett (1964), *Productus koninckianus* was first named by Verneuil (1845, p. 274) for a Lower Carboniferous species from Belgium, as distinct from *Productus cancrini* Verneuil (1845, p. 273, pl. 16, fig. 8, a-c, pl. 18, fig. 7). The name *koninckianus* Keyserling cannot be applied to the present species, because when proposed, it was still-born as a junior homonym of *koninckianus* Verneuil, 1845 which belongs to a different species and genus. Therefore the Permian species of Soiva River, Russia, is named after V. G. Ganelin, who has contributed much to the clarification of the species.

Subfamily **LYONIINAE** Waterhouse, 2001

Fig. 17.47, Fig. 17.48

[Nom. transl. hic ex Lyoniini Waterhouse, 2001, p. 32].

Diagnosis: Transverse shells with wide hinge and broad visceral disc with gently convex ventral valve, slender body corpus, both valves costellate. Spines usually only on ventral valve, forming well defined row close to the hinge, and arranged in quincunx with elongate bases over the visceral disc. Some genera have more numerous spines over the ventral ears, and have dorsal spines. Ventral adductor scars lightly to moderately defined, lightly striate and not strongly dendritic. Lower Permian (Asselian) to Upper Permian (Changhsingian).

Genera: *Lyonia* Archbold, *Ainimia* new genus, *Bandoproductus* Jin & Sun (mis-spelled *Pondoproductus* Jin, 1985, pl.

1, fig. 19, 20), *Masitoshia* new genus, *Nambuccalinus* Waterhouse, *Nambdoania* Waterhouse, *Nikitinia* Kotlyar, Zakharov & Polubotko.

Discussion: This tribe was recognized as valid by Brunton (2007), and includes the genera *Lyonia* Archbold and *Nambuccalinus* Waterhouse, both with dorsal spines, whereas other genera have only ventral spines. *Lyonia* is particularly close in shape to *Bandoproductus*, which lacks dorsal spines, helping to demonstrate that presence or absence of dorsal spines in some stock may not be significant to other than generic, subtribal, or tribal level.

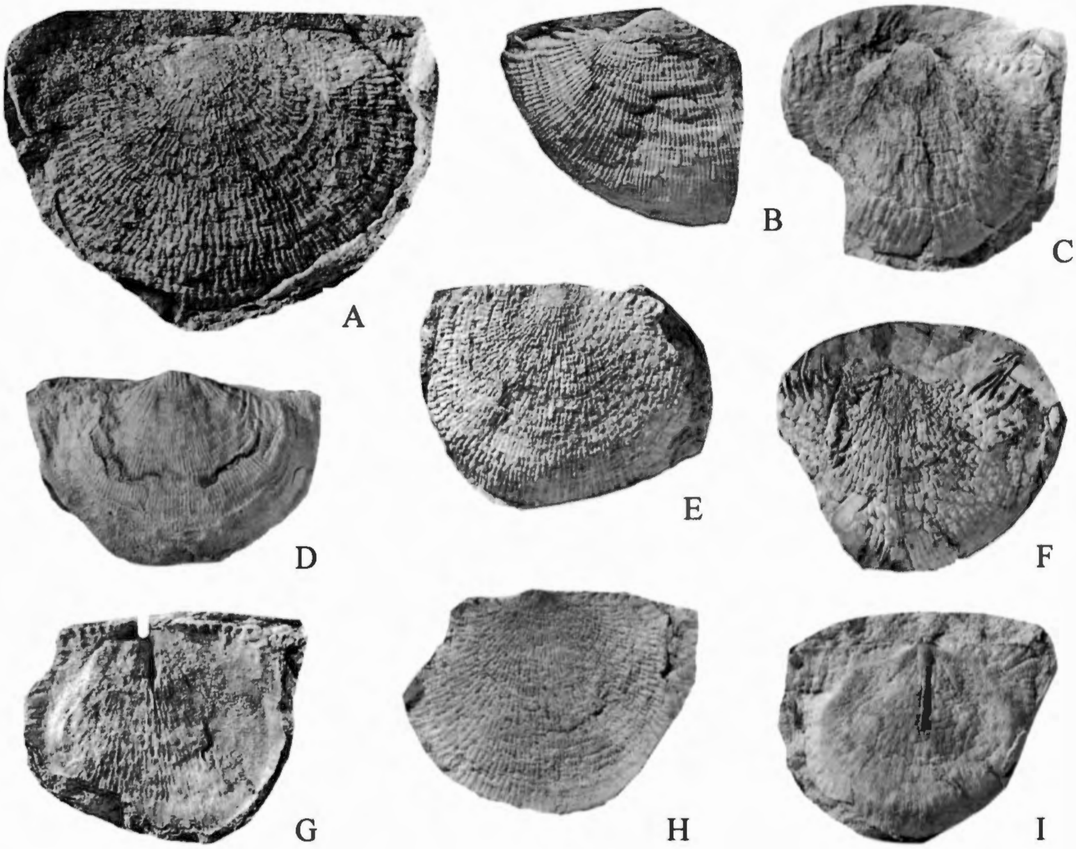


Fig. 17.46. *Bandoproductus monticulus* (Waterhouse). A, external cast of dorsal external mould, TBR 493. B, latex cast of exterior, TBR 494. C, F, internal mould and latex cast of exterior, ventral valve holotype TBR 495. D, internal mould, ventral valve TBR 496. E, G, H, external latex cast and internal and external mould of dorsal valve TBR 499. I, latex cast of dorsal interior, TBR 500. Specimens x 0.9, from Pebbly Mudstones (Asselian) of Phuket Group, Ko Muk, except Fig. 17.46 D from Ko Phi Phi, southern Thailand. See Waterhouse (1982c). J. Coker & JBW photo.

The lower age range for this tribe is not certain. Older genera such as *Lyonia* are found with the palynomorph *Converrucosporites confluens*, which commenced in the late Carboniferous, with radiometric evidence for an age of 305 Ma (Stephenson 2009). *Nambuccalinus* could prove to be pre-Permian or very early Permian.

Genus ***Masitoshia*** new genus

Fig. 17.47

Derivation: Named for Masitoshia Sone.

Type species: *Permundaria perplexa* Sone & Leman, 2005, p. 604 from Bera Formation (Wordian), Malaysia, here designated.

Diagnosis: Medium-large transverse with regular commarginal rugae and row of ventral hinge spines, and fine scattered body spines, ventral valve subgeniculate.

Discussion: So-called *Permundaria perplexa* Sone & Leman, 2005 from the Bera Formation of Pahang, Peninsular Malaysia, of Wordian age, has a hinge row of spines, and scattered spines over the ventral disc, including a number of erect spines over the posterior lateral shell. Although the authors stated that body spines were erect with no distinct hollow bases, spines with prolonged bases are strongly suggested in some figures, such as Sone & Leman (2005, Fig. 3.5) and subfusc spines indicated in Sone & Leman (2005, Fig. 3.14 and Fig. 3.16 and Fig. 3.20). The species therefore apparently belongs to Lyoniinae. Certainly the body spines appear only on some specimens, to judge from figures. In the presence of ribs, row of hinge spines, and lack of dorsal spines, the form clearly is close to *Bandoproductus* Jin & Sun. There appears to have been a degree of evolution from type *Bandoproductus*, in the change of ventral body spines to being small and scattered and possibly more erect, and development of regular and well developed commarginal rugae, and subgeniculate ventral valve with what Sone & Leman termed a subperipheral rim.

Sone & Leman (2005) considered that Afghanistan specimens of lower Murghabian age which had been identified as *Permundaria sisophonensis* by Termier et al. (1974, p. 131, pl. 27, fig. 1-3) were close to *P. perplexa*. There are numerous fine wrinkles and the figures suggest a few spines on the distinct ventral ears, and strong spines were described along the cardinal margin. Two further specimens, figured in Termier et al. (1974, pl. 27, fig. 7, 8) were excluded by Sone & Leman (2005): they possibly belong to *Nisalaria* Waterhouse (see p. 432).

Nikitinia Kotlyar, Zakharov & Polubotko, 2004, p. 521 from the lower Urushten Formation of the Caucasus, interpreted as lyoniin by Brunton (2007, p. 2659), appears to be a late development, retaining the well developed commarginal rugae, and displaying exaggerated ventral spine bases and long dorsal dimples.

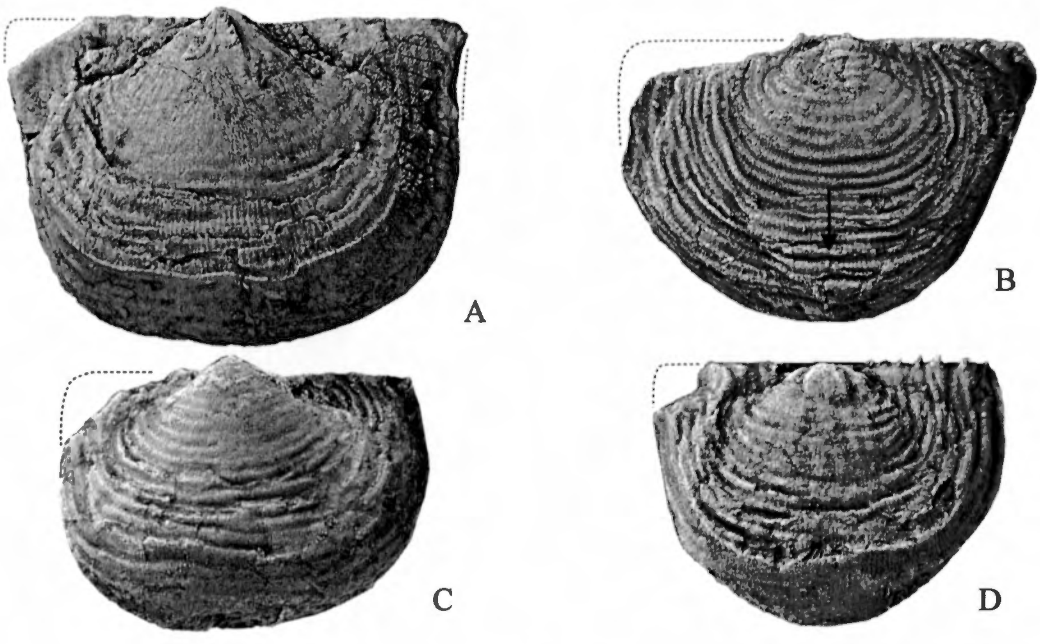


Fig. 17.47. *Masitoshia perplexa* (Sone & Leman) from Bera Formation (Wordian), Malaysia. A, ventral view of UKM-F567, x1.6. B, ventral view of holotype UKM-F564. with rare disc spines (arrowed). C, ventral view UKM-F563. D, ventral view UKM-F562. Note the subperipheral rim in Fig. 17.47A and D. (See Sone & Leman 2005). Photos provided by Masitoshe Sone.

Genus ***Ainimia*** new genus

Fig. 17.48

Derivation: Named from Ainim River, west Irian Jaya, site of fossil.

Type species: *Linoproductus pigrami* Archbold, 1981, p. 12, from Aifat Formation (early Guadalupian), Aifam Group, west Irian Jaya. Kept at Indonesian Macropaleontological Collection (IMC), Paleontology Laboratory, Geological Research and Development Centre, Bandung, Indonesia.

Diagnosis: Shells with very wide hinge, large ears and very low ventral umbonal walls, small ventral umbo, ornament of fine costellae, subdued commarginal growth steps and wrinkles, row of tubercles along hinge and spines with elongate bases in quincunx over ventral valve, no dorsal spines, visceral disc thin and muscle scars not impressed.

Discussion: This genus is distinctive. The type species was assigned to *Linoproductus* by Archbold (1981), and the close ribbing is suggestive of that superfamily, but the thin visceral disc and the elongate ventral spine bases rule out an alliance with that genus or other Linoproductidae. Sone & Leman (2005) compared the species with *Permundaria* Nakamura, Kato & Choi, 1970, and indeed the hinge is wide and the visceral disc thin. But concentric wrinkles are less regularly developed, and spines with elongate bases cover the ventral valve, whereas such spines are lacking from *Permundaria*. Certainly the spines are closer to those developed on *Permundaria perplexa* Sone & Leman, 2005, but that species differs considerably from *Permundaria*, having narrower hinge, higher ventral umbonal walls, and spinose ornament, approaching features of *Bandoproductus* Jin & Hu, although body spines are well spaced and fine compared with those typical of that genus. The thin disc and lack of dorsal spines in *Ainimia* are characteristic, although not exclusively so, of Auriculispinidae Waterhouse, and the wide hinge with ventral spines points to Lyoniinae Waterhouse. Compared with *Bandoproductus* Jin & Hu, *Ainimia* has a wider hinge and lower convexity, and no conspicuous dorsal dimples. *Nambdoania* Waterhouse is more inflated and does not have such a wide hinge, and *Masitoshia* new genus has regular commarginal rugae.

Genera allocated to Auriculispininae may be readily distinguished from the present genus. *Auriculispina* has numerous erect spines over the ventral ears and stronger commarginal rugae. *Costatumulus* has a more vaulted visceral disc and narrow hinge, with usually two or three spine rows along the ventral hinge. In addition to thin disc and no dorsal spines, these genera have subrectangular and striate ventral adductor scars, but such cannot be determined for the new genus, probably because the visceral disc is so thin. *Mistproductus* Yang De-li, 1991 from south China has moderately defined commarginal rugae and fine costellae, and spines are numerous along the hinge. The corpus cavity is thicker, and the hinge wide and anterior venter tumid: whatever its subfamilial position, it is readily distinguished from the new genus.

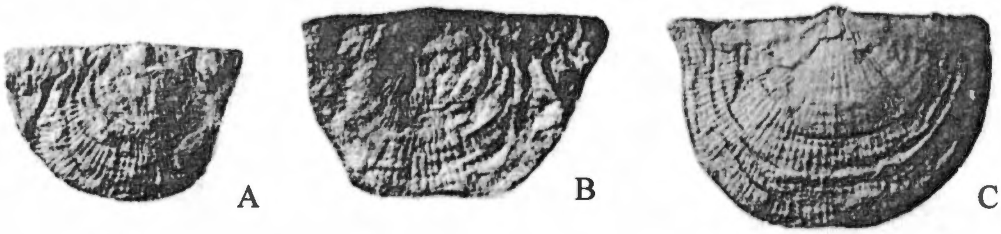


Fig. 17.48. *Ainimia pigrami* (Archbold). A, ventral valve IMC 21, x1.5. B, ventral valve external mould IMC 20 x1.75. C, holotype dorsal valve interior, IMC 19, x2. From Aifat Formation (?Roadian), West Papua (Irian Jaya). See Archbold (1981).

Subfamily **FILICONCHINAE** Waterhouse, 2001

[Nom. transl. hic ex Filiconchini Waterhouse, 2001, p. 33].

Diagnosis: Shell weakly transverse as a rule, with ventral disc usually of low convexity, subrectangular outline and geniculate trail. Ventral body spines numerous with elongate bases, spines few and organized in row or rows close to hinge. Dorsal valve with or without spines, trail subgeniculate, interior distinguished by development of a double ridge posteriorly, may replace the dorsal median septum. Lower Permian (Kungurian) to Upper Permian (lower Changhsingian).

Genera: *Filiconcha* Dear, *Cameronovia* new genus, *Kolymaella* Ganelin & Lazarev, *Spitzbergenia* Kotlyar.

Discussion: Although this tribe was ignored by Brunton (2007), it is very distinctive, with its roundly subquadrate shape, and shell build of Type 6 (see p. 24), the visceral disc shallow and becoming higher anteriorly. There are regular ventral spines with elongate bases in quincunx, fine costellae, and double dorsal septa. Members tend to have posterior dorsal ridges which slope obliquely forward laterally, and in some specimens, what appears to be lateral buttress plates are developed, as in *Spitzbergenia loveni* (Wiman 1914, pl. 17, fig. 18; Kotlyar in Sarytcheva 1977, Fig. 87). Apart from shape, most detail is close to that of Auriculispininae, and the dorsal interior is particularly close to that of *Auriculispina* and *Costatulumus*. There are some similarities to members of Levipustulini Lazarev, involving such genera as *Levipustula* Maxwell and *Jakutoproductus* Kashirtsev (see pp. 58ff), which have regular ventral spines with elongate bases, and show somewhat similar cardinal process and double dorsal septa, but lack radial ribs. The similarity is believed to be by morphological congruence, Levipustulini being related to the Overtonioidea, Filiconchini to Proboscidelloidea.

A possible ally, yet to be fully understood, is *Cancrinella snjatkovi* Zavodowsky (1960, p. 65, pl. 1, fig. 13, 14; 1970, pl. 63, fig. 2-6) from the Omolon fauna of northeast Russia, occurring with the ammonoid *Sverdrupites* of Roadian (lower Guadalupian) age. Although initially described as *Cancrinella*, the brachial shields in the dorsal valve seem to be very large, as in strophalosiids, according to a figure in Zavodowsky (1970, pl. 63, fig. 3a), but no interareas are visible in the figures, and the specimen with large brachial shields is not the holotype, so that the species is almost surely not strophalosiiform. The spines are fine, numerous, erect and uniform, and seemingly erect. Very fine ribs are possibly visible, and the trail is short, and the dorsal valve possibly thickened, or with a short and geniculate trail, very like that of *Cameronovia* new genus and other members of Filiconchinae, and distinguished by having a highly arched ventral valve. Chen & Shi, 2006, pl. 1, fig. 23, 24, pl. 13, fig. 15 figured somewhat similar ventral valves from the Tarim Basin, China, of late Early Permian age. The species *snjatkovi* was referred to *Spitzbergiana* Kotlyar in Sarytcheva (1977, p. 159, pl. 26, fig. 15-17, pl. 27, fig. 1-4), and made the type species of what was considered to be a linoproductid genus *Omolonia* Ganelin, in Kashik 1990, and this was repeated by Biakov (2010, Fig. 1.5, pp. 24, 26). The name *Omolonia* was not available, having been already applied to a middle Devonian stringocephaloid *Omolonia* by Alekseeva in Alekseeva & Nuzhdina, 1967, p. 138. Chen & Shi (2006, p. 159) stated that Ganelin & Lazarev (2000) had "formally re-described *Omolonia*", but it is now agreed that this was not correct. Dr V. Ganelin intends to rename *Omolonia* Ganelin not Alekseeva.

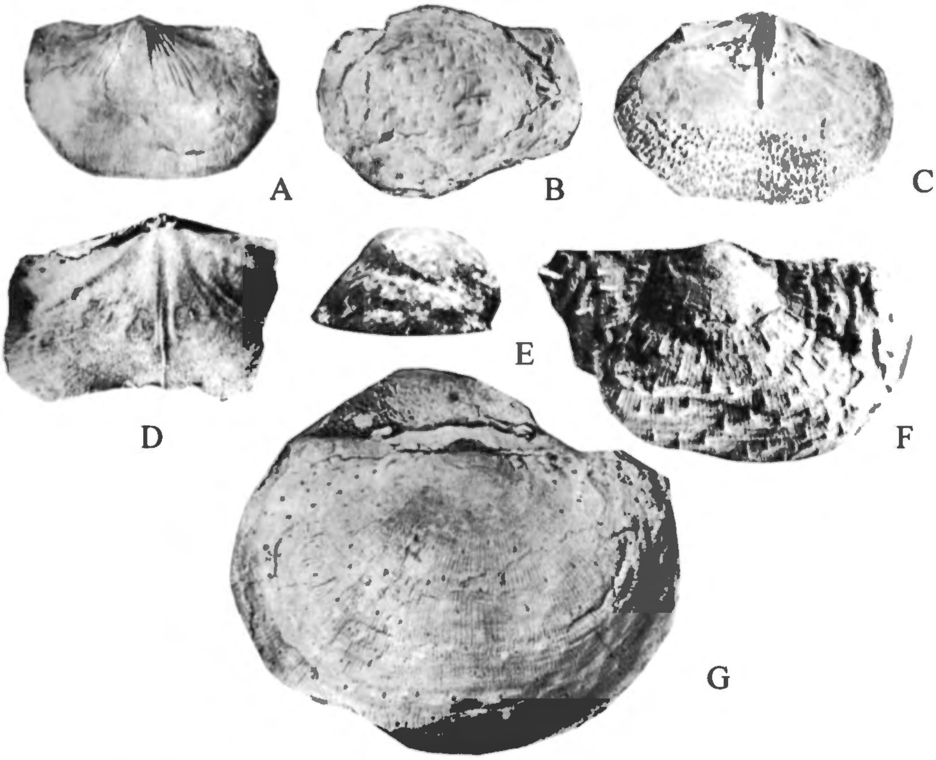


Fig. 17.49. *Filiconcha hillae* Dear. A, internal mould of ventral valve GSQ F 9832, x1. B, latex cast of ventral exterior, GSQ F 9472a, x1. C, dorsal internal mould GSQ F 9870, x1. D, latex cast of dorsal interior, GSQ F 10883, x3. E, lateral aspect of ventral internal mould, GSQ F 9843, x1. F, latex cast of ventral exterior, GSQ F 10922a, x2. G, external mould of dorsal valve, GSQ F 9829, x2. From Flat Top Formation (Wordian), Queensland, Australia. See Dear (1971).

Genus ***Filiconcha*** Dear, 1969

Fig. 17.49, Fig.17.50

Genus *Filiconcha* Dear, 1969, p. 299 is roundly subrectangular in outline with wide hinge, moderately developed row of hinge spines (see Dear 1971, pl. 21, fig. 10) and numerous spines with elongate bases over the visceral disc, and fine erect dorsal spines. The ventral adductor scars are impressed and posteriorly placed, with subrectangular outline, bearing striae until late in ontogeny, when oblique grooves develop. The dorsal adductors include a small rounded and smooth anterior pair. The cardinal process is trilobate from an inner or ventral aspect, with small alveolus, and two median ridges pass forward from a broad median ridge: in some specimens a median septum resumes in front. As well, there are support ridges that angle laterally from in front of the cardinal process. In short, the shape and interior of the dorsal valve are very distinctive. The type species of *Filiconcha* is found in the Wordian faunas of the Flat Top Formation in the Bowen Basin, Queensland, and another species is found in the Changhsingian Trig B Formation of New Zealand (Waterhouse 1976a, p. 238; 2002a, p. 33).

Fig. 17.50. *Filiconcha auricula* Waterhouse, showing double posterior median septum in latex cast of dorsal valve, BR 1709, x3. From boulder derived from Trig D Formation (Changhsingian), near Arthurton, Southland, New Zealand. JBW photo. See Waterhouse (1976a, 2002a).

Genus ***Spitzbergenia*** Kotlyar, 1977

From Kazanian (Wordian) faunas of northeast Russia, genus *Spitzbergenia* Kotlyar in Sarytcheva (1977, p. 155), type species *Productus loveni* Wiman (1914, pl. 17, fig. 12-18) from Spitzbergen, is very close to *Filiconcha*, and has elongate spines over the visceral disc, at least one but possibly two or three hinge rows of spines, and more spines in front, mirrored by dimples along the dorsal hinge, no dorsal spines, similar ventral adductors with oblique fine ridges late in maturity, and a dorsal valve with double submedian posterior ridges, and widely splayed lateral ridges. Posterior dorsal adductors become dendritic. *Filiconcha* and *Spitzbergenia* are very close in shape and other detail, with the unusual internal features of the dorsal valve found in both, even though *Spitzbergiana* lacks the dorsal spines found in *Filiconcha*. There seems to be a single row of hinge spines in the ventral valve as figured in Sarytcheva (1977, pl. 25, fig. 7b), but two rows are suggested by pits along the dorsal hinge (pl. 25, fig. 8b, 9). A slender median septum is present anteriorly in one figured dorsal valve (pl. 25, fig. 9). These Russian-figured specimens are not topotypes, coming from Novaya Zemlya, but they provide more detail that the original types or the additional material figured from the "Brachiopod Chert" of Spitzbergen by Gobbett (1964, pl. 14, fig. 7-9). Several other species were assigned to *Spitzbergenia* in Sarytcheva, but hinge spines are poorly displayed, so that generic affinities require further elucidation, but the various species are each relatively close in shape and size and what is visible of the ornament. A very slender anterior median septum is shown in *S. gracilis* Kotlyar in Sarytcheva (1977, pl. 26, fig. 4a, b).

Genus ***Kolymaella*** Ganelin & Lazarev, 2000

Ganelin & Lazarev (2000) ignored the attributes of these two genera, in erecting a new genus *Kolymaella* Ganelin & Lazarev, 2000. Like *Filiconcha*, it displays a well defined row of spines set in front of the wide hinge, and the shape, including wide disc, and elongate ventral spines, and ventral adductor platform (Ganelin & Lazarev 2000, pl. 6, fig. 16, 18) are filiconchin, and even more tellingly, the dorsal valve has a double ridge, with two lateral oblique ridges: the peculiar features of the tribe are replicated in *Kolymaella*, and questions remain over the validity of distinctions of *Kolymaella,* a question not addressed by Ganelin & Lazarev (2000). Whilst the lack of a dorsal septum from *Kolymaella* may point to a significant difference between *Kolymaella* and *Spitzbergenia*, it should be noted that the figures of *Kolymaella* possibly suggest a slight degree of decortication of shell, that has removed a thin topmost layer, to leave a pustular undershell. In that regard, internal moulds preserved in fine and non-calcareous matrix would be useful in helping to confirm the absence of an anterior median septum. A Late Permian species of *Filiconcha* from New Zealand has a very low median dorsal septum, as if reduction towards loss of septum were a general trend in the subfamily. *Kolymaella* is distinguished from *Filiconcha* by the lack of dorsal spines, and reduction of the dorsal median septum. The type species of *Kolymaella*, *ogonerensis* Zavodowsky, 1960 had been referred to

Cancrinelloides in Sarytcheva (1977, p. 151, pl. 24, fig. 4-8) but this placement received no attention from Ganelin & Lazarev (2000). *Cancrinelloides* differs in several ways – as a larger form, with a single median septum and modest array of ear spines. *K. ogonerensis* is shown as upper Solikamian by Ganelin & Lazarev (2000), slightly older than *Filiconcha* in Australia, and apparently *Spitzbergenia* in northeast Russia, Spitsbergen and Canada. The changes to internal morphology, especially in the dorsal valve, may be readily traced from the various species described in Dear (1969), Waterhouse (1976a, 2001), Sarytcheva (1977) and Ganelin & Lazarev (2000), accompanied by changes in the ventral hinge spines and in the adductor scars.

An older genus that was believed to have given rise to *Kolymaella*, and therefore the entire lineage, was described as *Bocharella* Ganelin & Lazarev, 2000, another genus in the Permian of Russia. These authors evaluated evolution as proceeding only from within an exclusive and geographically limited segment of the planet's linoproductidin populations. The type species *B. zyrjankensis* Ganelin & Lazarev came from the lower Solikamian faunas, and much older specimens have been reported, but not yet described. A few spines are present in a row over the anterior ventral ears, and some elongate spine bases lie over the visceral disc and especially trail. The authors were in some disagreement over the nature of their genus and its distinction from "*Striapustula*" (which is deemed to be a junior synonym of *Costatumulus* Waterhouse), and pointed to a flatter ventral disc and shorter trail as generic traits. But although such criteria, together with the hinge spines do offer distinctions, the apparent absence of a dorsal double ridge and lateral ridges affords some doubt about its ancestral position for *Kolymaella*, and the presence of a row of ventral spines along the base of the umbonal slopes indicates a position within Stepanoviellidae (see p. 454). All genera of Filiconchinae are much more likely to have arisen from *Costatumulus*, known from Sakmarian faunas of east Australia, or close ally.

Genus ***Cameronovia*** new genus

Derivation: Named from Cameron Island, Canadian Arctic Archipelago.

Type species: *Cameronovia milleri* new species from Assistance Formation (Roadian), Cameron Island, Canada, here designated.

Diagnosis: Small slender gently concavo-convex disc, geniculate trail. Capillae well developed on both valves. Spines in three or more rows along ventral hinge, dorsal spines well developed, erect over disc, may have swollen or prolonged bases, crowded on trail.

Discussion: This genus is like *Filiconcha* Dear, 1969 in having dorsal spines, thereby differing from the other Arctic genera, *Spitzbergenia* Kotlyar and *Kolymaella* Ganelin & Lazarev, and as far as known, the mystery species *snjatkovi* Zavodowsky, as discussed in the introduction to the subfamily. The spines are fewer over the disc compared with those of *Filiconcha*, and moderately numerous over the trail. On the ventral valve, one hinge row appears to be developed in *Filiconcha hillae* Dear, whereas three rows lie along the hinge, especially over the outer ears in the new genus, and continue around the outer margins. Internally the ventral adductor platform is more pronounced in *Filiconcha*, perhaps because of greater individual maturity. The dorsal interior is much the same in both genera, with the dorsal median septum a little longer in the Canadian genus.

Cameronovia milleri new species

Fig. 17.51

1971 *Cancrinelloides* aff. *loveni* [not Wiman] – Waterhouse in Bamber & Waterhouse, pl. 22, fig. 8, 10.

Derivation: Named for Alan K. Miller.

Holotype: GSC 36839 figured herein as Fig. 17.51B-E, from GSC loc. 76029, Trold Fiord Formation (Capitanian), Cameron Island, Arctic Canada, here designated.

Diagnosis: Small, comparatively flat disc, geniculate trail, ventral spines in rows close to hinge and prominent postero-laterally, elongate bases over disc and erect over trail. Dorsal spines occasionally with swollen or prolonged bases over disc, crowded and erect over trail.

Material: Single ventral valve from GSC loc. 35316, Melville island, and two specimens with valves conjoined from GSC loc. 76029, Trold Fiord Formation, Cameron Island; two specimens from GSC loc. 67255, ?Assistance Formation, Melville Island; and two ventral valves from GSC loc. 53821, Fish Creek, Permian sandstone unit, Yukon Territory, Canada. See Bamber & Waterhouse 1971, p. 182 and Appendix A, part C, p. 479.

Dimensions in mm:

GSC	Width	Length ventral	Length dorsal	Height	
36839	27.3	26.0	22.0	13.6	(GSC 76029, holotype)
36837	32.3	+32.5		9	(GSC 35316)
36838	+22.9	+23.9		13.6	(GSC 67255)

Description: Shell small, transverse, with umbo of 80-85° protruding only slightly beyond the broad hinge, cardinal angle close to 100°, subangular, with small slightly upturned or convex ears, poorly differentiated from broad umbonal slopes. Visceral disc gently rounded, with short anterior sulcus in some specimens, curving abruptly into short trail, the sulcus persisting to anterior margin, but weakly defined. Dorsal disc shallowly concave, especially over posterior

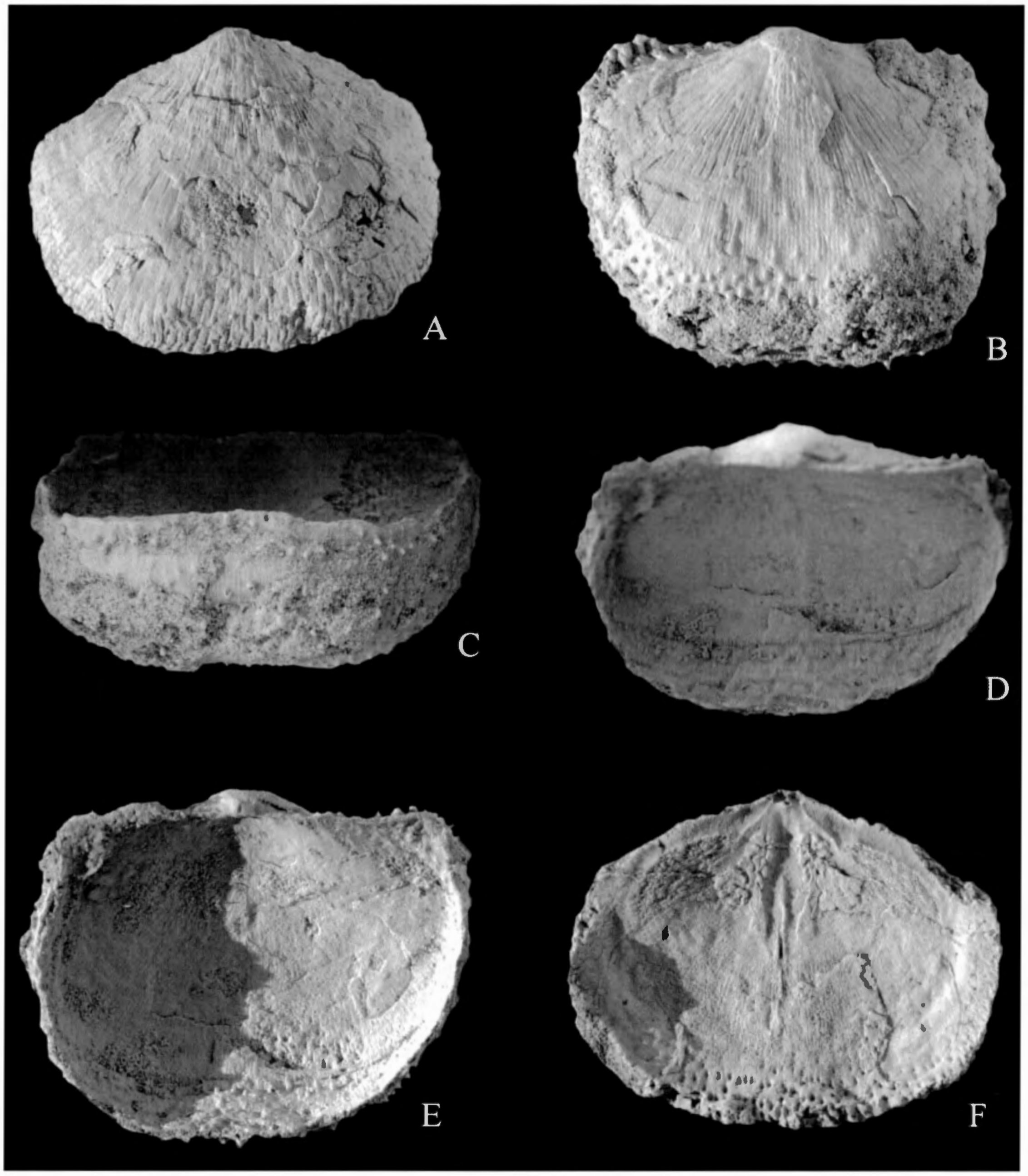


Fig. 17.51. *Cameronovia milleri* new genus, new species. A, F, ventral (x1.6) and dorsal (x1.7) views of GSC 36837, from GSC loc. 35316, Melville Island. The dorsal view shows the internal mould. B - E, ventral and dorsal views of holotype GSC 36839, from GSC loc. 76029, Cameron Island, x2.2, the dorsal views at various degrees of tilt. Trold Fiord Formation (Capitanian), Canadian Arctic. JBW photo.

third of length, tiny ears weakly reflected ventrally, and geniculate trail. Both valves covered by fine capillae, measuring three per mm over anterior median ventral disc, increase by branching and by intercalation, especially in front of spines over ventral valve; increase mostly by intercalation over dorsal valve; absent over posterior trail on holotype but appear over anterior ventral trail and over dorsal trail. A row of erect spines lies close to the ventral hinge, fine near the umbo, stronger laterally over the ears. Two or three further rows appear beyond the umbonal slopes, with an anterior row of rare slightly inclined spines, and these rows extend laterally, becoming moderately strong, and curving further around the lateral margin, where spines become finer. Body spines with elongate bases up to 4mm long cover the disc, in subregular quincunx, with shorter bases laterally, and bases only 2mm long near the start of the trail. Often two or three fine ribs extend forward from the spine base. Erect spines in some twelve rows cover the trail, crowded and not completely regular in distribution. A few fine erect spines lie over the tiny dorsal ears, and are well separated over the disc, and crowded in some six or so erratic commarginal rows over the dorsal trail.

The ventral adductor platform is elongate and striate, impressed anteriorly into the shell, and diductor scars are striate and large. Spine bases leave short tunnels over the posterior trail in two specimens. Cardinal process incompletely preserved, bearing deep median groove from ventral aspect, broad elongate mound in front with median slit, passing forward into two lateral septa extending almost to mid-length, very short median septum in front. To each side are dendritic posterior adductor scars, enclosing small less marked anterior adductor scars. There are faint traces of comparatively large brachial shields, and behind the posterior adductors lie suggestions of a low ridge, and low longer hinge ridge. Fine pustules cover much of the floor and larger endospines lie in three or four rows over the anterior disc.

Resemblances: The species is distinguished from *Filiconcha hillae* Dear, 1966 from the Flat Top Formation (Wordian) of the south Bowen Basin in Queensland, Australia, by the flatter disc, less concave dorsal valve, more geniculate trail, and by more rows of spines along the ventral hinge, shorter ventral disc spine bases, few dorsal disc spines, and more numerous spines over the ventral and dorsal trail (see Dear 1966, pl. 22, fig. 1-22; Waterhouse 1986a, pl. 11, fig. 10-18). There are various internal differences as well, including a longer dorsal septum in the Queensland species. *Filiconcha auricula* Waterhouse (1976, Fig. 4.3-14) from the *Plekonella multicostata* and especially the *Spinomartinia spinosa* Zones (Changhsingian) of New Zealand has lower capillae and very short bases for ventral disc spines, as well as larger ears, and scarcely perceptible dorsal median septum. Most allied species from the Arctic Permian have been ascribed to *Spitzbergenia* Kotlyar, and are characterized in part by the absence of dorsal spines. No figures for this genus show hinge spines very well, and the trail appears worn, and dorsal exteriors seldom well preserved. The best preserved species is *S. gracilis* Kotlyar (in Sarytcheva 1977, pl. 25, fig. 10, 26, fig. 1-5, Fig. 88) from the Selander Suite of Spitsbergen, with moderately flat disc, less elongate ventral spine bases, and stronger lateral oblique dorsal hinge ridges. Trail and ear spines are poorly preserved.

Subfamily **SIPHONOSIINAE** Lazarev, 1990

[Siphonosiinae Lazarev, 1990, p. 130. The name was proposed as a nomen nudum by Lazarev 1986a, p. 32].

Diagnosis: Elongate shells with short tubiform ventral trail, narrow hinge and rhizoid spines on ventral valve, marginal structures on both valves. Lower Permian (Kungurian).

Genus: *Siphonosia* Cooper & Grant, 1975.

Discussion: Figures of *Siphonosia* in Cooper & Grant (1975, pl. 466, fig. 5, 12, 14, 15, 24, 21, 24) indicate suberect to subprostrate body spines and scattered erect body spines over the ventral valve, suggestive of an alliance with Auriculispininae. This is strengthened by the development of a dense array of erect sturdy ear spines on the ventral valve, and presence of double posterior ridges in the dorsal valve, and a single shafted cardinal process with deep median cleft from a ventral perspective.

Siphonosia is like *Undaria* and *Proboscidella* in representing a specialized adaptation for inhabiting bioherms, often coralline. The granting of subfamilial status is justified on the basis of morphological distinction and space, and the subfamily is represented by one genus and few species.

Family **STEPANOVIELLIDAE** Waterhouse, 1975

[Nom. transl. hic ex Stepanoviellinae Waterhouse, 1975, p. 12].

Diagnosis: Radial ornament linear and simple, ears small. Prominent row of spines along anterior edge of ventral ears at base of umbonal slopes, other spines few if any, may include dorsal spines. Middle Permian (?Wordian) to Upper Permian (Changhsingian).

Genera: Stepanoviella Zavodowsky, *Bocharella* Ganelin & Lazarev, *Repinia* new genus.

Discussion: This family embraces a small group of genera from the upper Middle Permian and Late Permian faunas of northeast Russia. Commencement may have been pre-Wordian, because Ganelin & Lazarev (2000) reported older species of *Bocharella*, yet to be described. The family is characterized by having a row of ventral spines along the anterior and inner margin of the ventral ears. The spine pattern thus differs considerably from that of Auriculispinidae or Paucispinauriidae. The type species of *Stepanoviella, paracurvata* Zavodowsky, 1960, p. 336 from the Hivatch Suite (Lopingian), Gijigin Basin, northeast Russia, is based on small moderately to highly arched shells with costellae over both valves, spines in hinge row and umbonal slope row (Grigorieva in Sarytcheva 1977, pl. 27, fig. 6a), and scattered over ventral valve, with short to slightly elongate bases. Dorsal spines are rare to moderately numerous over the dorsal trail. Weak fine commarginal rugae lie over the ventral valve, and the dorsal valve has stronger, but weak and closely spaced dorsal laminae or rugae, best figured by Grigorieva in Sarytcheva (1977, pl. 27, fig. 7). The rather low quality figures provided in Zavodowsky (1970) and Grigorieva in Sarytcheva (1977) suggest somewhat decorticated specimens, with only traces of costellae, but authors involved with descriptions have treated the genus as costellate. The critical umbonal slope row of ventral spines is illustrated in Zavodowsky (1970, pl. 89, fig. 2a), and obscurely in the holotype (Zakharov, 1970, pl. 89, fig. 1b) and by Grigorieva in Sarytcheva (1977, pl. 27, fig. 6a, and 5b, the holotype). The ventral adductors lie on a platform projecting into the posterior wall, and almost planar but bearing weak striae or weakly dendritic markings (Zavodowsky 1970, pl. 89, fig. 4a, b; Grigorieva in Sarytcheva 1977, pl. 27, fig. 8). The dorsal interior is poorly preserved, and suggests a short broad dorsal septum, apparently subdivided (Zavodowsky 1970, pl. 89, fig. 5a).

So what are the affinities of *Stepanoviella*? The genus is readily distinguished from Linoproductinae, in its size, ornament, muscle scars and dorsal interior. It was proposed as name giver for Stepanoviellinae Waterhouse, 1975, at a time when the genus was believed to be senior synonym for the linoproductoid genus *Globiella*, and the subfamily was in fact interpreted largely if not entirely on the basis of the morphology of *Globiella*. The present analysis shows there are some differences between *Stepanoviella,* Family Stepanoviellidae, and *Globiella*, Subfamily Larariinae, Family Anidanthidae, particularly in the distribution of spines, the nature of the ventral adductor scars, and the presence of two additional ridges in the dorsal valve found in *Globiella* and *Liraria* is modified in *Stepanoviella*, towards the arrangement more typical of Auriculispinidae.

A small ribbed ventral valve extracted as a silicified specimen from the Lower Carboniferous of Ireland appears to have a row of spines along the umbonal slopes, and disc spines that have elongate bases. It was described as *Ovatia* sp. by Brunton (1966, pl. 19, fig. 9, 10), but differs from another small valve described by Brunton from much the same region, for this specimen lacks ventral disc spines with elongate bases (Brunton 1966, pl. 19, fig. 5-8). The lengthy time interval between the specimen with an umbonal slope row of spines from Ireland and members of Stepanoviellidae constrains any supposition that the specimen was necessarily ancestral, although its morphology is highly suggestive.

Although Brunton et al. (2000, p. 527) synonymized Stepanoviellinae with Linoproductinae Stehli, Brunton et al. (2000, p. 533) placed *Stepanoviella* itself in a different subfamily, a step difficult to justify, and understandable in so far as there are so many productid genera in such a complex array of family groupings that it is not difficult to overlook inconsistencies.

Genus ***Bocharella*** Ganelin & Lazarev, 2000

Genus *Bocharella* Ganelin & Lazarev, 2000 p. 39 from the Bochara River in northeast Russia was interpreted by its authors as an "initial evolutionary stage of a new phylogenetic lineage", limited in distribution as far as known to Arctic Russia and south Mongolia. The ventral ears have lost the spines, except for one row arranged on the "anterior side of the ear" or what might be called base of the anterior slope. The genus has been badly misrepresented in captions illustrating the type species by Brunton (2007, p. 2657, Fig. 1765.2). Fig. 2b shows a lateral view of the ventral valve, not an antero-ventral view fide Brunton (2007, p. 2655); Fig. 1765.2c is not a ventral valve viewed laterally, but a dorsal external mould and Fig. 1765.2d is not a dorsal valve, but a ventral valve. These corrections are obvious in the figures, and agree with the descriptions in Ganelin & Lazarev (2000), though it may be noted that the translation of their article persistently uses the incorrect term "pedicle valve" instead of ventral valve, and "brachial valve" instead of dorsal valve. The figures in the *Revised Brachiopod Treatise* are dark, but are much clearer in the original publication and English translation.

The genus was thought to have been derived from *Striapustula* by Ganelin & Lazarev (2000), and the hypothesis appears possible if *Costatumulus* is substituted as conjectural ancestor. But *Costatumulus* and its allies lack spines along the base of the ventral umbonal slopes, to signify a radical difference between *Bocharella* and Auriculispininae. Moreover the Irish specimen alluded to above may indicate much earlier roots, independent of Auriculispinidae. The adductor scars, not that well preserved it would appear, demonstrate possible auriculispinin affinities, or morphological congruence. The dorsal median septum appears to be single.

Genus ***Repinia*** new genus

Fig. 17.52

Derivation: Named from specific name repini.

Type species: *Cancrinella* (?) *repini* Zavodowsky, 1960, 1970, p. 105, from Omolon fauna (late Capitanian) of northeast Russia, here designated.

Diagnosis: Firm radial ribs over both valves, spines limited to row along base of ventral umbonal slopes, no further spines, no dimples over dorsal valve.

Fig. 17.52. *Repinia repini* (Zavodowsky). Ventral valve holotype No. 2/9081, from Omolon horizon (Capitanian), northeast Russia. Retouched from Zavodowsky (1970, pl. 64, fig. 1-3), x2.

Discussion: The type species is well figured by Zavodowsky (1970, pl. 64, fig. 1-3), and unambiguously shows the characteristic row of spines along the base of the ventral umbonal slopes, or anterior margin of the ventral ears. The ears are relatively large ears on both valves. Unlike the type species of *Bocharella*, the species *repini* appears to have no ventral disc spines and no pits in the dorsal valve. It was not mentioned by Ganelin & Lazarev (2000). *Stepanoviella* Zavodowsky has weaker radial ribbing and the umbonal slope row of spines is finer. The ventral valve is more arched, and ventral disc spines are suberect or subprostrate, and dorsal spines lie over the dorsal trail.

CLASSIFICATION UNCERTAIN OR DEBATED

18. SUBORDER UNCERTAIN

Brunton et al. (2000a, p. 642) drew attention to several more or less productiform genera for which the suborder was deemed uncertain. Three genera were involved.

The Upper Permian genus *Chonopectella* Sarytcheva, 1966 (nom. nov. pro *Chonopectoides* Sarytcheva, 1965, p. 232 non Crickmay 1963) is of subrounded shape and almost smooth thin shell with teeth. It has intersecting fine oblique rugae, single submedian rib, and rare spines at the hinge. The presence of teeth might suggest Strophalosiidina, accepting that the presence of the reported spines indicates a brachiopod rather than bivalve. There are no commarginal rugae or radials other than the median rib.

Ploughsharella Liang Wen-ping (1982, p. 227) and *Punctoproductus* Liang Wen-ping (1990, p. 368 [p. 481]) need to be examined at first hand – their position as Productidina seems open to question. Brunton et al. (2000a) dismissed the concept of Punctoproductida Liang, 1990 in which these two genera were placed. (See p. 36).

19. "NOMINA NUDA"

Several proposed genera within Productidina were regarded as nomina nuda by Brunton et al. (2000a, pp. 642, 643). Some may be retrieved; others remain in need of further study. Whereas the genera mentioned in "Suborder Uncertain" by Brunton et al. (2000a) are very difficult to interpret even generically, most of the so-called nomina nuda are fully open to interpretation and clarification, the position clarified by various studies beyond those considered by the *Revised Brachiopod Treatise*.

Genus ***Achunoproductus*** Ustritsky, 1971

Achunoproductus Ustritsky, 1971, p. 21 was not accompanied by formal description or illustrations. Brunton et al. (2000a) suggested the form was related to *Schrenkiella*. S. S. Lazarev has issued important articles on *Schrenkiella* and its allies, and has been well placed to examine the matter, but he has not offered any resolution or clarification of *Achunoproductus*.

Genus ***Uraloproductus*** Ustritsky, 1971

Uraloproductus Ustritsky, 1971, p. 21 was not described in terms of diagnostic characters, and was treated as a nomen nudum by Brunton et al. (2000a). But the genus was diagnosed and described by Abramov & Grigorieva (1983, p. 83) and Shi & Waterhouse (1996, p. 71), and illustrated also by Ifanova in Ifanova & Semenova (1972, pl. 6, fig. 10-14) and Solomina (1970, pl. 6, fig. 10; 1978, pl. 9, fig. 17, 18). Those studies were ignored by Brunton et al. (2000a). The genus is apparently a synonym of *Retimarginifera* Waterhouse, 1970, Tribe Retimarginiferini, showing similar reticulate ornament and shape (Ustritsky 1974). Whilst it may be noted that costae are coarser, the outline less transverse and the dorsal valve less concave for the type species of *Uraloproductus*, the differences are not great, and seem no more than specific in value. It thus seems likely that *Retimarginifera* is of sub-bipolar or bitemperate distribution in Western Australia and southeast Asia, and in Canada and Russia in the Urals and northeast, a pattern of distribution first recognized by Waterhouse (1969), followed by Ustritsky (1974). The spine pattern for *Uraloproductus* is not entirely clear, but the distribution of spines indicated by Shi & Waterhouse (1996, text-fig. 25B) seems likely, with strut spines and rare other spines, as shown for "*Uraloproductus* sp. B" from the Yukon Territory. (The other so-called *Uraloproductus* sp. A is deemed to be small *Rugivestis*). The spine pattern is best shown for *stuckenbergianus* by Ifanova (1972, pl. 6, fig. 12-14) and for *bilobatus* by Abramov & Grigorieva (1983, pl. 6, fig. 1), and there is no strong hinge or umbonal slope row apparent, but a few spines may occur along the umbonal slopes. A roughly similar pattern is indicated for *Retimarginifera celeteria* Grant (1976) from Thailand and *R. perforata* Waterhouse (1970) and *R. waterhousei* Archbold (1984) from Western Australia. The interior of the Russian species is poorly displayed, but is better known for other species. It should be noted that whereas Grant (1976) denied the presence of a dorsal marginal ridge, that is contradicted by figures in Waterhouse (1970) and

Archbold (1984, p. 118, Fig. 2Y, Z) and one is indicated in the type species by Coleman (1957, pl. 9, fig. 4, 6), and in the Thai species by Grant (1976, pl. 29, fig. 34).

Genus ***Chaoina*** Jin, 1974

Chaoina Jin in Jin, Liao & Hou (1974, p. 308) is very small and appears to be dictyoclostid. Knowledge of the form is comparable to that of *Tenaspina* Brunton & Mundy, and reservations may remain over the degree of maturity. But the genus shows a trail, despite its small size, and so is treated as Reticulatiinae (p. 130). There does not appear to be any diaphragm around the disc, discouraging the link with Productinae favoured by Brunton et al. (2000a).

Genus ***Choanoproductus*** Termier & Termier, 1970

Although *Choanoproductus* Termier & Termier (1970a, p. 459) was treated as a nomen nudum by Brunton et al. (2000a), the figures in Termier & Termier (1970a), with reference to a figure provided in Mansuy (1914, p. 18, pl. 2, fig. 12), appear to favour a relationship with *Monticulifera* Muir-Wood & Cooper, 1960, according to Waterhouse (2002b, p. 53). Monticules are figured by Mansuy (1914), and were described by Termier & Termier (1970a). By contrast, Brunton et al. (2000a) considered that the genus was likely to be strophalosiidine, but gave no reasons.

Genus ***Parapulchratia*** Chan, 1979

Parapulchratia Chan in Hou, Zhan & Chen (1979, p. 87) was based on *Productus pustulosus palliatus* Kayser, 1883, p. 186 and has no diagnosis. It should not be so difficult for this genus and species to be further clarified.

19. OBSCURE GENERA

A few genera are particularly obscure. *Longyania* Zhu, 1990, p. 71 was regarded as a synonym of *Chianella* by Brunton et al. 2000, p. 538), but this does not accord very well with the text or sole figure (see p. 322). *Pseudohaydenella* Liang, 1990, p. 174 is another genus in need of clarification (see p. 323). *Selloproductus* Termier et al. (1974, p. 143, pl. 28, fig. 1-3) is also very inadequately known, and seemingly linoproductoid as suggested by Brunton et al. (2000, p. 536). Available evidence for *Septoconcha* Termier et al. 1974, p. 125 , pl. 23, fig. 4-6) from Murgabian of Afghanistan points to a juresaniin alliance, as concluded by Brunton et al. (2000, p. 526).

20. UNCERTAIN FAMILY AFFILIATIONS

In any extensive classification, there are likely to be groups of uncertain affiliation, and it is considered that at least some gigantoproductiform brachiopods fall in this category, involving Semiplaninae and Kansuellinae, and associated Marginiruginae and Globosoproductinae. Further study of the ventral spine detail seems to be required. The small Permian group Lamiproductinae, centred on *Asperulus* Waterhouse & Piyasin, is deemed to belong to Anidanthidae, yet the spines over the ventral umbo might be interpreted as having elongate bases (see Fig. 20.1), although internal moulds appear to indicate that the spine bases pass straight through the shell into the lumen. The strong and branching ribs recall features of a Late Devonian genus *Dawesionia* new genus, an apparently early linoproductidin with no obvious descendents. Yet another linoproductidin, *Sartenaueria* new genus also requires consolidation. Cooperinoidea and its relationship to Oldhaminidina remains an open question. But of all genera and groups, greatest uncertainty surrounds the genus *Loczyella* Frech and the question of its nature and affinities (see pp. 301ff). It is clear from the substantial number of synonymies proposed by Williams, Harper & Grant (2000), that the suborder Oldhaminidina has proven a difficult group, and therefore calling for much closer study.

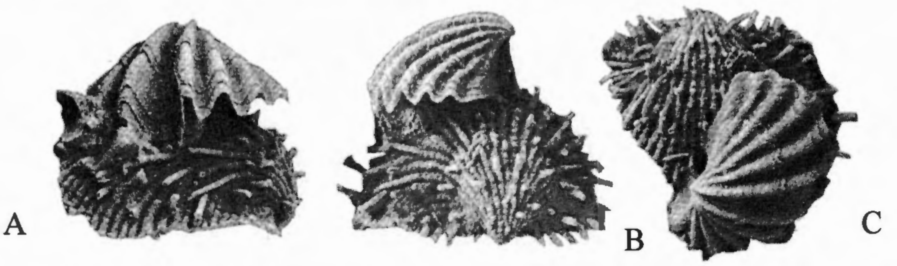


Fig. 20.1. *Asperlinus asperulus* (Waagen), lateral, posterior and ventral aspects of ventral valve as figured by Yanagida (1970, pl. 15, fig. 15b-c). From Rat Buri Limestone (Roadian), south Thailand, x2.

21. EXAMPLES OF EVOLUTION

1. At generic level. The morphology and distribution of *Costatumulus*. Fig. 21.1

As an example of variation within a genus, a brief example may be offered by *Costatumulus* Waterhouse (1986b), based on *Auriculispina tumida* Waterhouse in Waterhouse, Briggs & Parfrey (1983, p. 133) from the middle Tiverton Formation of upper Sakmarian and lower Artinskian age in the Bowen Basin, Queensland. Topotype material of the type species is figured herein (Fig. 17.45, Fig. 17.46, pp. 444, 445), and the genus is widespread.

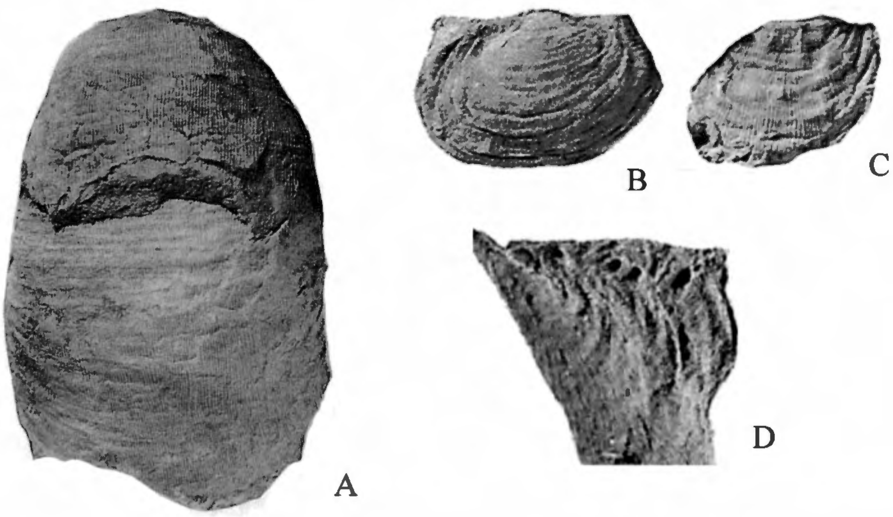


Fig. 21.1. A, *Costatumulus meritus* Waterhouse, ventral aspect of UQL 74009, holotype, from Cattle Creek Formation (upper Artinskian), Queensland, x1. B - D, *C. randsi* Balfe & Waterhouse. B, ventral valve UQF 69214, x1.3. C, fragmentary ventral valve UQF 69215, x1.5. D, ventral fragment showing hinge spines, UQF 69161, x3. From base of South Curra Limestone (?Lopingian), Gympie, Queensland. See Waterhouse (1986a, 2010a). Photo P. Balfe, J. Coker & JBW.

A species slightly older than the type species, *Costatumulus prolongata* Waterhouse, 1986b, p. 58 from the Fairyland Formation and elsewhere in the Bowen Basin, is small, narrow and more vaulted than *tumida*, with fine costellae but otherwise close. In New South Wales, Australia, *Costatumulus farleyensis* (Etheridge & Dun, 1909, p. 302) from the Farley Formation (upper Sakmarian) is similar in most aspects to the Queensland species *C. tumida*, but is often sulcate and has more numerous and finer ribs. A younger (Artinskian) species from Queensland, *C. meritus* Waterhouse, 1986b, p. 59, is highly arched with fine ribs and strong cardinal spines in two rows, and narrow dorsal dimples, whereas the late Permian species *C. randsi* Balfe & Waterhouse in Waterhouse (2010a, p. 34) is small and transverse with thin non-tumid disc: it may be no older than Lopingian. Hinge spines form a single row, joined by two more rows laterally: disc spines are in quincunx, but dorsal hollows are rare. The dorsal septum is strong.

Costatumulus irwinensis (Archbold, 1983, p. 238), originally ascribed to *Cancrinella* and coming from the lower Artinskian Fossil Cliff Formation of the Perth Basin and Callytharra Formation of the Carnarvon Basin in Western Australia, has well defined commarginal rugae, with dorsal dimples and strong hinge spines in mostly two rows. It is a highly vaulted shell with small but distinct ears, close to *C. prolongata* and *C. meritus* in shape. However a slightly younger species, *C. occidentalis* Archbold (1993, p. 14, 1997) from the *Sommeriella magnus* Zone of Artinksian age in the High Cliff Sandstone of the Perth Basin, Western Australia, is even more vaulted and narrow in outline. From the upper Sakmarian Garu Formation of the eastern Himalaya, *Costatumulus sahnii* Singh & Archbold (1993, p. 62) is close to *C. tumida*, and has two rows of hinge spines and well developed dorsal pits, and numerous ventral spines in quincunx. From the lower Qubuerga Formation (Lopingian) of south Tibet, China, *C. shengmiensis* Shen, Archbold & Shi (2001, p. 281) is also like *C. tumida*. *C. crassicostatina* Waterhouse (1983b, p. 222 – see Waterhouse & Chen 2007, p. 18) from beds of the same region and age is also close to the *tumida* template, but the dorsal valve is not known. The species is based on comparatively large ventral valves from the Nisal Member in west Nepal (Waterhouse 1978, p. 74, pl. 11, fig. 6-8) and younger specimens from the Luri Member (Waterhouse 1978, p. 119, pl. 23, fig. 2-4) are of comparable size and shape.

The late Carboniferous form from Argentina, *Costatumulus amosii* Taboada, 1998 has numerous ventral ear spines and low rugae across the disc, and belongs to *Auriculispina* Waterhouse, and the Lower Permian *C. sidorkini* Manankov from Mongolia is *Commarginalia*. The upper Lower Permian species *Cancrinella pseudotruncata* Ustritsky, 1960, reallocated to *Costatumulus* by Chen & Shi (2006, p. 159), belongs to *Liaozhuotingia* new genus (see p. 438), in Coolkilellinae, a paucispinaurian subfamily. But a substantial number of species from the high Arctic belong to *Costatumulus*, as far as can be discerned. These include species described as *Cancrinella singletoni* Gobbett (1964, p. 102) from the Upper Wordiekammen Limestone of Bünsow Land and *C. crassa* Gobbett (1964, p. 105) from Spitsbergen, of Upper Carboniferous age. Both of these species belong to the highly vaulted subgroup, and have strong posterior spine bases, and marked dorsal dimples: *singletoni* might also occur in the Yukon Territory of Canada.

Very similar species have been described as a distinct genus *Striapustula* by Ganelin & Lazarev (1999), involving *Productus koninckiana* Keyserling, 1846 not Verneuil, 1845, here renamed *ganelini* new species (see p. 444) from Kungurian of Verchoyan, *S. elongata* Ganelin & Lazarev and *S. magna* Ganelin & Lazarev from Djigdalin beds, and *S. pectiniformis* Ganelin & Lazarev from ?Lower Permian near Vorkut, all in northeast Russia. Ganelin & Lazarev (1999) enumerated developmental differences from species to species, noting the closeness of *pectiniformis* to *singletoni* Gobbett. They pointed to a gradual loss of the dorsal median septum, which culminated in *Striapustula*? sp. in the Kozhimrudnitskaya Formation of the Pechora Basin, to indicate a separate genus. All of these species basically are close in shape to the species of *Costatumulus* from Western Australia and *C. prolongata* and *C. meritus* from Queensland. Where adequately known, they agree with *Costatumulus* in detail of spines and dimples, with the major reservation centering on muscle scars, poorly known for some species, and especially obscure for the Spitsbergen material.

In summary, four major groupings may be recognized within *Costatumulus* and close allies:

A. Moderately arched: *tumida, farleyensis* (Queensland, New South Wales), *crassicostatina, sahnii, shengmiensis* (Himalaya).

B. Highly arched ventral valve: *prolongata, meritus* (Queensland), *irwinensis, occidentalis* (Western Australia), *singletoni, crassa* (Spitsbergen), *ganelini, magna, elongata* and *pectiniformis* (northeast Russia), with subgroupings.

C. slender, broad: *randsi* (Queensland).

D. No dorsal septum ("*Striapustula*" sp. (Pechora Basin) = new genus?

2. Evolution within a tribe: Paucispinauriini Fig. 21.2 – 21.6, Fig. 5.

Paucispinauriini began in Sakmarian time, and continued to almost the end of the Permian Period. It would appear that genera sourced from Magniplicatininae, which are found widely. Recent reviews of the genus *Terrakea* and related forms have been offered by Weldon & Shi (2003) and Tazawa (2008b), and the time ranges and relationships are adjusted to mesh with more detailed research. The oldest Paucispinauriini have fine ribs and spine bases, and muscle field and internal detail close to features in *Magniplicatina*, but have more subdued commarginal rugae, more developed longer and thicker spines over the ventral ears and especially umbonal slopes, and fine erect dorsal spines. In east Australia, the oldest known species has been described as *Terrakea pollex* Hill, 1950, a species with comparatively robust and numerous ventral ear spines, strong ventral disc spines with prolonged spine bases, and numerous fine erect spines over the dorsal valve. The species comes from the Sakmarian (Lower Permian) Fairyland Formation of the southeast Bowen Basin of Queensland, and Farley Formation of the Sydney Basin (Briggs 1998), with detailed stratigraphy and correlation provided in Waterhouse (1986b, 2008). The species *pollex* differs from *Terrakea* in so far as dorsal spines are all slender, whereas the type species of *Terrakea*, *T. brachythaera* (Morris) as revised by Waterhouse (1964) and Briggs (1998), includes anterior dorsal trail spines almost as thick as those on the ventral ears and umbonal slopes (see Fig. 21.3). In this regard, *pollex* is very like *Grandaurispina* Muir-Wood & Cooper, 1960 from the United States, as discussed shortly. Slightly younger beds in the lower middle Tiverton Formation of the north Bowen Basin have two species, one very close to *pollex*, as a new taxon, the other with small ventral ears and few large posterior spines, described as *geniculata* Waterhouse, also found in the Elvinia Formation

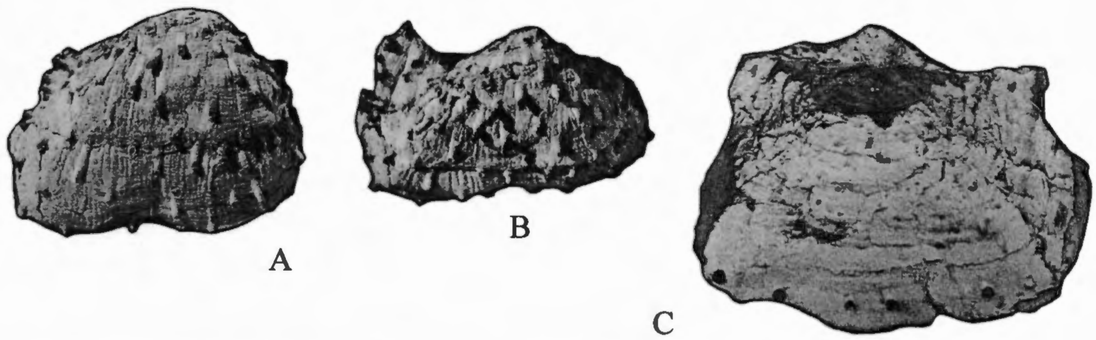


Fig. 21.2. *Paucispinauria concava* (Waterhouse). A, B, ventral and posterior views of PVC cast, BR 207. C, dorsal aspect of PVC cast, BR 200, holotype. Specimens from Letham Burn Member (Roadian), Wairaki Downs, New Zealand, x1.8. See Waterhouse (1964). S. N. Beatus & JBW photo.

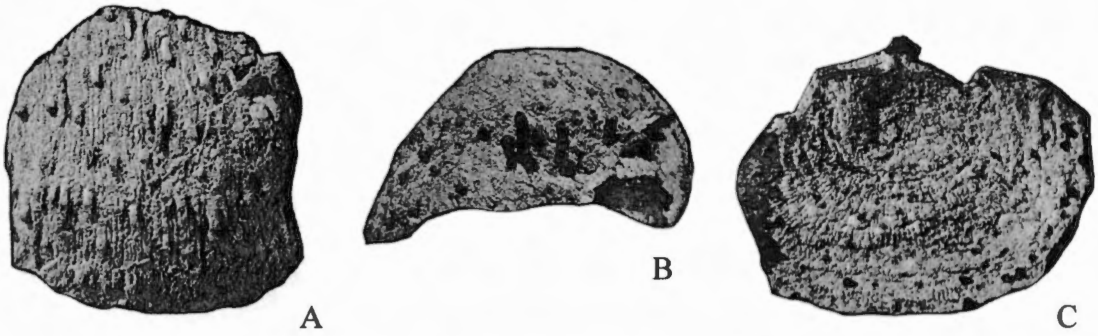


Fig. 21.3. *Terrakea brachythaera* (Morris). A, PVC cast, anterior ventral valve BR 932. B, lateral aspect of ventral PVC cast, BR 66. C, PVC dorsal cast, BR 146. Specimens from upper Mangarewa Formation (Capitanian), Wairaki Downs, New Zealand, x1.8. See Waterhouse (1964). S. N. Beatus & JBW photo.

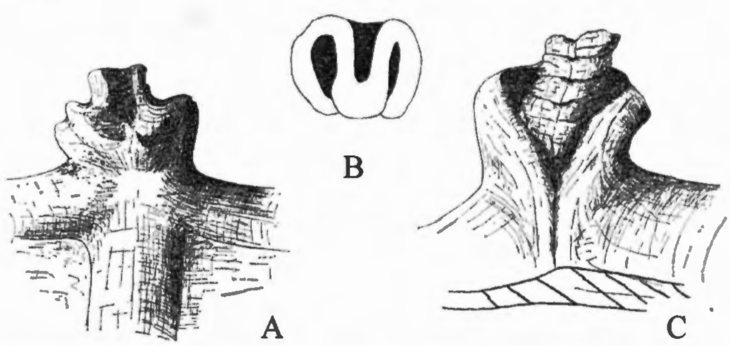


Fig. 21.4. *Paucispinauria concava* (Waterhouse), cardinal process. A, anterior view. B, top view from posterior aspect. C, posterior view. BR 788 from Letham Burn Member (Roadian), New Zealand, x7.5 approx. See Waterhouse (1964). JBW del.

of the southeast Bowen Basin. These mark a divergence in the group. Both display the spine pattern of *Grandaurispina* Muir-Wood & Cooper, one form close to *pollex*, with numerous and thick posterior ventral spines, the other with few posterior spines, called *geniculata* Waterhouse, the earliest species within the genus *Paucispinauria*, which has few strong ear spines and tends to develop very strong spines over the dorsal trail (Fig. 21.2C). The genus is found widely in east Australia and New Zealand. By Artinskian time, the species *dickinsi* Dear had evolved from *pollex* to develop large spines over the anterior dorsal valve, as in typical *Terrakea*, and retained the *pollex*-burst of posterior large ventral spines, as in *Grandaurispina*. Higher in the succession (Kungurian, Roadian), species have evolved from *geniculata* that display the *geniculata*-like paucity of posterior ventral spines, but continue to develop large anterior dorsal spines, typical of the genus *Paucispinauria*. Through Middle Permian into Lopingian faunas, species of *Paucispinauria* (*paucispinosa, concava, solida, verecunda*) alternate with species of *Terrakea* (*exmoorensis, etheridgei, brachythaera, quadrata, elongata*), and appeared to have been independent of substrate. A further genus appeared, *Saetosina* Waterhouse, represented by *S. dawsonensis* Waterhouse, 2001 and *S. multispinosa* (Dear, 1971), of Wordian age and typified by large size, and fine spines over both valves, tending to occur in bands in *multispinosa* (Fig. 21.6). There are no thick spines, either along the hinge or umbonal slopes, or anterior trail. A possible fore-bear may be represented in the somewhat obscure *Terrakea rhylstonensis* Briggs, 1998 from the poorly dated (possibly late Early Permian, possibly older) Snapper Point Formation of south Sydney Basin: this species has many posterior ventral spines, suggesting derivation from *pollex*-like stock, but all spines are subequal on both valves and comparatively fine. The youngest known paucispinaurian in high southerly paleolatitudes of east Australia and New Zealand is *Terrakea*? sp. from an upper Changhsingian fauna of the Pig Valley Limestone in Nelson, New Zealand (Waterhouse 1967b, Fig. 5), but the material is poorly preserved and identified provisionally from shape, with no spines preserved. The overall progression and diversification in east Australia and New Zealand is summarized by Waterhouse & Shi (2010, Fig. 4).

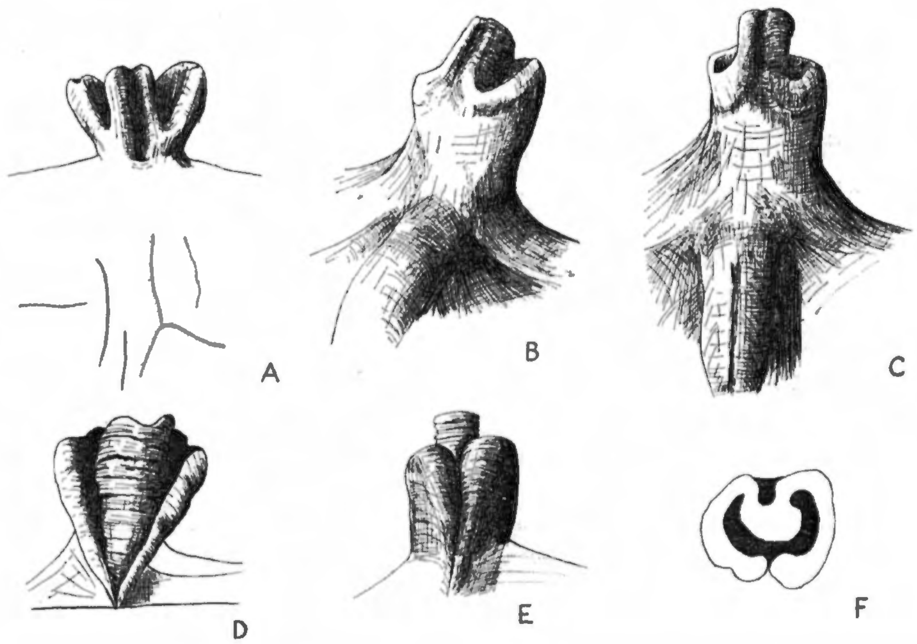


Fig. 21.5. *Terrakea brachythaera* (Morris), cardinal process. A, D, ventral and posterior views of specimen BR 65, with widely splayed lateral lobes. B, anterior lateral, C, ventral, E, posterior and F, top views of more usual process, in BR 344. From upper Mangarewa Formation (Capitanian), New Zealand, x5. See Waterhouse (1964). JBW del.

Subject to the cautions raised by Cooper & Grant (1975), as discussed on pp. 417-418, Paucispinauriini showed an abrupt entry in the paleotropical faunas of the very late Early Permian and mostly Middle Permian age in west Texas, United States (Waterhouse 2010c, 2011). They are distinctly younger than the Early Permian members of east Australia, and are judged to have been derived from those faunas. Although all have been referred to *Grandaurispina* Muir-Wood & Cooper, 1960 (Fig. 15.4), several strands can be discerned. Most do belong to *Grandaurispina*, including species *kingorum* Muir-Wood & Cooper, and *gibbosa, elongata*, and possibly *undulata*, named by Cooper & Grant (1975), from the China Tank, Willis Ranch and Appel Ranch Members of the Word Formation, of Wordian and early Capitanian age. These are close in many respects to *pollex* Hill from the Fairyland Formation of Queensland, with coarser posterior ventral spines and only fine dorsal spines. The posterior ventral spines are distributed over the umbonal flanks rather than ventral ears, and shells have strengthened posterior dorsal internal ridge, but are close to *pollex*, and conceivably descended from the Queensland *pollex*.

Two further genera appear to evolved from *Grandaurispina* stock. In new genus *Appelinaria*, the Capitanian species *crassa* and *rudis* named by Cooper & Grant (1975) developed high vaulted ventral valves with unusually strong ribs and spines over the disc, reduced number of posterior lateral spines, and thick as well as fine spines on the dorsal valve. In the presence of thick dorsal spines there is some approach to *Terrakea* and *Paucispinauria* in east Australia and New Zealand. But whereas the coarse spines are found mostly over the anterior dorsal trail in the Australasian species, the coarse spines are found postero-laterally in the American species. A further genus *Bellaspinosina* developed as *rara* (Cooper & Grant) and *bella* (Cooper & Grant) in the Appel Ranch and Willis Ranch Members, with no coarse spines and small ears, somewhat like *Saetosina* of east Australia, but of different shape and minor internal differences, to suggest possible local derivation rather than immigration.

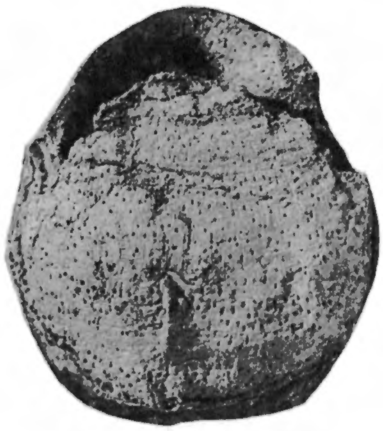


Fig. 21.6. *Saetosina multispinosa* (Dear). Dorsal view of UQF 74071, x2, dorsal external mould and ventral umbo, from Flat Top Formation (Wordian), Queensland. (See Waterouse 1986a). J. Coker & JBW photo.

This reconstruction seems logical, with time control and pointing to an independent flourishing of paucispinaurian stock in a region remote from source, during Middle Permian time. But there is an anomaly – not unexpectedly given the complexity of evolution. The earliest apparent paucispinaurian in west Texas is *Vagarea vaga* (Cooper & Grant) from the Cathedral Mountain Formation of Kungurian age. This lacks radial ribs. Simplistically it was an early migrant from east Australia that had arrived before the stock derived from *pollex* Hill gave rise to species of *Grandaurispina*, and perhaps older *Grandaurispina* may yet be found in United States or North America. But the possibility remains that it was this genus that gave rise to American *Grandaurispina*, having altered during the course of migration from Australia to United States (cf. Krassilov 1974, 1975, Waterhouse 1976c), followed by reversion to more normal paucispinaurian ornament. Of course there are other possibilities as well, including one that *Vagarea* is not paucispinaurian.

An unusual genus *Holotricharina* Cooper & Grant, 1975 is associated with the Texan species, reported from the Kungurian Cathedral Mountain Formation and found especially in the Road Canyon Formation (Roadian, lower Guadalupian), and also represented in Venezuela (Hoover 1981). It possibly evolved from *Vagarea*, having coarse and fine spines rather than homogeneous spines over the ventral visceral disc, and differs further in lacking ventral ribs, and displaying dorsal capillae and close-set rugae on both valves. The genus is distinct, and classed as a separate tribe, but was associated by Cooper & Grant (1975) and Hoover (1981) with *Grandaurispina*. It remains possible that these largely Middle Permian brachiopods of west Texas arose independently of Paucispinauriini, with mimicry heavily involved. Perhaps material from clastic deposits associated with the limestone that provided the material for the Cooper & Grant (1975) study will provide answers.

There is a scattering of more northerly occurrences of species unambiguously belonging to Paucispinauriini. *Terrakea arctica* Waterhouse, 1971b of Wordian age from Arctic Canada, Melville Island, appears to belong to *Grandaurispina*, although the dorsal valve has unusually elongate pustules. Weldon & Shi (2007) suggested that the "bilobed" cardinal process pointed to different affinities, but the deep median cleft of the median lobe is common in *Terrakea* and allies, and the lateral lobes are broad and well developed (Waterhouse 1971b, Fig. 4, cf. Waterhouse 1964, Fig. 24, 25). *T. echinata* Manankov (1992, p. 72, pl. 16, fig. 9-13) from the Middle Permian Uldzinsk Suite of northwest Mongolia has a number of ventral ear spines, not very coarse, and comparatively fine spines over both valves, with no coarse dorsal spines: it is closest to *Grandaurispina*. The other species assigned by Manankov to *Terrakea* are more difficult to identify. So-called *Terrakea vernacular* Manankov (1992, p. 71, pl. 17, fig. 10-15) from the same beds shows fine even commarginal rugae over both valves and large non-dendritic ventral adductor scars. Little in the pattern of spines and their distribution suggests identity with *Terrakea* Booker. Another species called *T. arguata* Manankov (1992, p. 73, pl. 17, fig. 6-9) also has a large non-dendritic ventral adductor platform (Manankov, 1992, pl. 17, fig. 6, 8), and very fine erect spines cover the venter (fig. 9). The likely generic position will be in Auriculispininae, but figures are obscure. *T. nalivkini* Grunt in Grunt & Dmitriev (1973, pl. 7, fig. 2-5) from the Kubergandian Suite (Darvas Stage) is not paucispinaurian and may be anidanthid.

Terrakea japonica Tazawa, 2008b has exceptionally strong costae and close-set ventral body spines without conspicuously elongate spine bases, according to figures in Tazawa (2008b, Fig. 3K, L), and the dorsal valve lacks spines, facets which firmly point to a non-paucispinaurian genus, because the ventral spines of *Terrakea* have elongate bases, and its dorsal spines are numerous. The ornament of *japonica* points strongly to a lamiproductin alliance (see p. 336 and Fig. 15.27). *T. nabekoshiyamensis* Tazawa (2012, p. 26, Fig. 4.13, 4.14) from the Changhsingian Toyoma Formation of Japan has ventral spines with elongate bases, and numerous fine erect dorsal spines; costellae are not clearly visible on illustrations but are reported in the text. There is some approach to *Grandaurispina*, but the generic position requires further assessment. *T. yanagidai* Tazawa (2008d, p. 336, fig. 3) from the Lopingian of Mizukoshi, central Kyushu, southwest Japan has fine and distinct costellae and ventral spines with elongate bases and spine tunnels, and erect dorsal spines, and well developed ventral ribs. The species is an undoubted member of Paucispinauriini, and lacks differentiated dorsal spines. Tazawa (2008c, p. 149) reported that erect spines were numerous over the ears, but they are not clearly shown in illustrations, which might imply that the spines were fine and suggestive of a distinctive new genus.

The tribe flourished in Arctic Russia, and includes genera characterized by a lack of sturdy ventral spines over the ears and umbonal slopes. *Pinegeria* Waterhouse, 2001, p. 49, type species *Terrakea pinegensis* Grunt in Sarytcheva 1977, p. 144, pl. 21, fig. 10, pl. 22, fig. 1-4 of Wordian (Kazanian) age has narrow hinge, with very small ears, strong distinctive ribs, few if any hinge spines, small spines with prolonged bases over the visceral disc and moderately strong erect spines around the lateral margins and trail of the ventral valve. Dorsal spines are fine and erect. *Productus hemisphaeroidalis* Netschajew (1894, pl. 4, fig. 1; 1911, pl. 3, fig. 1) from Kazanian faunas of Russia appears to belong to the same genus (Grigorieva in Sarytcheva 1977, p. 145, pl. 22, fig. 5-9, Fig. 82). The species as figured by Grigorieva is highly distinctive, with unique spinal and rib development.

Spargospinosa Waterhouse, 2001, p. 41, based on *Terrakea belokhini* Ganelin in Sarytcheva, 1977, p. 141, pl. 21, fig. 1-3, Fig. 80 is also distinctive, with a hinge row of ventral spines but otherwise few posterior and postero-lateral ventral spines, unlike any of the preceeding genera. The coarseness of dorsal spines over the trail points to a relationship, or at least morphological congruence with *Paucispinauria*. It comes from the Omolon Suite, of late Guadalupian age in northeast Russia. Various other species from the Omolon Suite were ascribed to *Terrakea* in Sarytcheva (1977). *T. korkodonensis* Licharew in Kashirtsev, 1959 belongs to or is close to *Spargospinosa*, as an interesting species, with apparently no ear spines, at least as figured, and dorsal spines limited to an anterior row of comparatively sturdy erect spines. *T. borealis* Ganelin in Sarytcheva (1977, pl. 21, fig. 4-8, Fig. 81) has somewhat different and finer spines, and its affinities are not fully clear: perhaps close to *Spargospinosa*, to judge from shape, but figures are too dark to be readily open for interpretation. *T. grandis* Ganelin in Sarytcheva (1977, pl. 21, fig. 9) is based on a solitary ventral valve, with somewhat rectangular and striate ventral adductors, and identification best deferred.

Brunton (2007, p. 2654) claimed that terrakiform genera display continuous variation, and so do not justify separation. He quoted Briggs (1998), who did not recognise *Saetosina* or *Paucispinauria*. But on the other hand the thirteen species described as "*Terrakea*" by Briggs (1998) were each emphasized by Briggs (1998) as being separate and consistent in morphology: the point of difference from Waterhouse (1986a) was that Briggs considered that these consistent differences (including shape and number, kind and placement of spines) did not justify generic separation, but weakened that opinion by admitting that subgenera could be recognized (Briggs 1998, p. 161). Using the same approach, he regarded various species of *Grandaurispina* as belonging to *Terrakea*, and considered that *Grandaurispina* could be justified by having long ventral spines on the flanks for some of the species. Whilst unwilling to underline the difficulties in Briggs' analyses, it should be noted that Briggs (1998) ignored the nature of the dorsal spines in the various species, and nowhere was able to point to any individuals or any species that showed a number of ventral ear spines and posterior-lateral slope spines intermediate between those of type *Terrakea* and type

Paucispinauria. His approach, like that of Brunton (2007), was much less analytical than that pursued by S. S. Lazarev in discrimination of linoproductid genera. Brunton (2007) not only ignored the overgeneralized nature of the Briggs analysis, but inconsistently recognized *Paucispinauria* (Brunton et al. 2000, p. 533) and *Pinegeria* (Brunton 2007, p. 2653). However it would be only fair to point out that he has never described or studied any form of Paucispinauriinae, so that his judgements were hypothetical, based on extrapolation from his first hand experience of some Lower Carboniferous brachiopods of Ireland and England.

3. Evolution within a subfamily: Echinalosiinae.

Echinalosiinae was a small but diversified subfamily, especially characteristic of high to moderate paleolatitudes during Permian time. Members are characterized by an umbonal cicatrix, interareas, teeth and sockets and large strophalosiiform brachial shields. The tribe that typifies the group and is based on *Echinalosia* Waterhouse has diverse spines of mostly two diameters over the ventral valve, and a single series of erect slender spines over the dorsal valve. The genera and species are thus close to members of Daysyalosiinae, which differed in having spines of two diameters over the dorsal valve. Genera and subgenera within Echinalosiini differ in the prominence of posterior hinge spines, surface ornament of capillae, or smooth ears without spines. During the late Middle Permian, or Guadalupian Series, a further group evolved as Marginalosiinai, treated as a subtribe, in which the ventral spines became reduced to one fine series, and *Marginalosia* flourished in the Late Permian of Nepal and New Zealand. Another tribe Wyndhamiini developed a thick and wedge-shaped dorsal valve during younger Early Permian (Cisuralian) time in the high paleolatitudes of eastern Australia and New Zealand, extending into Western Australia, and retaining ventral spines of two diameters, but proved to be short-lived. There was a close and parental relationship to another subfamily, Arcticalosiinae, with wedge-shaped dorsal valve and closely spaced subuniform ventral spines, found in the Middle Permian of the northerly temperate paleolatitudes. A related tribe Biplatyconchini evolved from Arcticalosiini during Late Permian time in moderate Permian paleolatitudes of the southern paleohemisphere, as a tribe that lost its dorsal spines and retained the close-set ventral spines. Individuals of this tribe became particularly large for Strophalosiidina.

4. Evolution within a family: Auriculispinidae.

Auriculispinidae embrace small-sized genera ornamented by fine ribs, and ventral spines arranged in different patterns close to the hinge, many spines posteriorly elongate and slender bases over the ventral disc, and the lumen of each spine continuing forward from the base within the shell. Dorsal spines are often not developed. Internally, the ventral adductors form prominent scars that are striate until late in ontogeny, and impressed into the posterior wall posteriorly, and the body corpus is normally slender.

Unlike most known Lower Carboniferous linoproductiform genera, the posterior dorsal septum of Auriculispininae is usually double and short. The unusual ventral adductor platform of Auriculispininae points to derivation from stock of which *Donakovia markovskii* (Donakova, 1975) from the lower Visean of the Urals represents a early Carboniferous example, as discussed on pp. 408-409. *Auriculispina* is found in the late Carboniferous of east Australia, and the subfamily became particularly abundant during Permian time, especially in temperate and high paleolatitudes of both hemispheres.

Other subfamilies are largely restricted to the Permian Period. Lyoniinae is a particularly distinctive association of mostly early Permian high to intermediate southern paleolatitudes, found in and immediately above glacial diamictites in Gondwana. It is characterized by a row of strong ventral hinge spines, and has other spines, including dorsal spines in two genera, and wide hinge. Members of Filiconchinae belong to a small group of shells sharing a distinctive subquadrate outline and Type 6 build of shell shape; the shape and double septum in the dorsal valve is characteristic, and genera are restricted to east Australia, New Zealand in the south and Canada, northeast Russia and Spitsbergen in the north, in all close to Auriculispininae, but with dorsal spines in two genera. Siphonosiinae on the other hand is found only in the paleotropical faunas of Texas, adapting to a biohermal habitat with specialized short tubiform trail, reminiscent of the specialized Lower Carboniferous genus *Proboscidella*.

In summary, this particular subfamily tended to characterize cold and temperate faunas of both hemispheres during Permian time, but is represented in the paleotropics, and indeed appears to have arisen from paleotropical stock of Lower Carboniferous age. The subfamilies are recognized principally on the basis of shape, with ornament and interior conforming to a consistent basic pattern, but showing second order adjustments and typicalities, consistent with shape, and often consistent with geographic distribution.

5. Evolution of a superfamily: Scacchinelloidea.

Until the present overview, Scacchinellidae has been regarded as a side-branch of Aulostegoidea (see Brunton et al. 2000, p. 607), supported by the presence of a high ventral interarea, and indeed the very unusual morphology as a whole, because aulostegoids were also highly plastic in their morphology. The most natural alliance lies with Tschernyschewiidae, because they also have a high medium ventral septum. Both have ornament on both valves of fine and closely spaced spines, looking especially like the patterns found in Waagenoconchidae, rather than the usually well separated and often erect spines typical of Aulostegoidea, and moreover, there is little sign of ribbing which often features in aulostegoids, but seldom in echinoconchoids. Scacchinelloids are thus, even from ornament and septal interior, a somewhat stand-alone group, and according to the present analysis, they are not aulostegoid at all, but arose independently from strophalosiiform stock.

Both Scacchinellidae and Tschernyschewiidae are mostly of Permian age, and seem to have undergone substantial internal morphological change from any known echinoconchoid or aulostegoid. One unusual feature of the dorsal interior of Scacchinellidae and Tschernyschewiidae is provided by the presence of lateral buttress plates. Balkhasheconchinae notably have such plates, unlike any echinoconchid amongst which *Balkhasheconcha* was originally placed. Moreover the spinose ornament of Balkhasheconchinae is moderately like that of Tschernyschewiidae, and there is no radial ornament and very short if any trail. Members of Balkhasheconchinae are found as two widely dispersed genera in east Australia and northeast Russia, as *Campbelliconcha* and *Buxtoniella* in faunas of upper Visean age, with genera *Balkhasheconcha* and *Ramaliconcha* distributed through Late Carboniferous and *Balkhasheconcha* persisting in Early Permian faunas of northern paleolatitudes, followed by *Ramaliconcha guryulensis* new species of Late Permian age in Kashmir. The interior and the ornament of *Buxtoniella* and *Campbelliconcha* are very like that of the strophalosiiform Araksalosiidae Lazarev, especially *Hamlingella* Reed, of upper Devonian age. It appears that descendents of araksalosiid stock abandoned the accoutrements of Strophalosiidina in evolving independently towards a productidin morphology, losing the teeth and sockets and enlarged brachial shields, to morph into Balkhasheconchinae.

Yet one more group helps to fill out the evolutionary record, called Rhamnariinae Muir-Wood & Cooper, 1960. Wrongly regarded by these authors and by Brunton et al. (2000, p. 604) as aulostegoid, these shells have similar ornament to Tschernyschewiidae, a low interarea, and well formed lateral buttress plates. One genus *Minisaeptosa* new genus even developed a short high median ventral septum. This subfamily demonstrates pleonasm, a partial retrodaption, or return, amongst some genera to strophalosiiform attributes, regaining interarea and cicatrix that are missing from Balkhasheconchinae, and in *Rhamnaria* the ventral hinge spines are strong, recalling those of some Araksalosiidae. Septasteginae have two long high dorsal septa, which may represent modified lateral buttress plates. A cicatrix may be well developed, as well as a high marginal ridge, and spines are echinoconchid or even juresaniin in appearance.

The superfamily Scacchinelloidea demonstrates well the potential for paraphyletic development: separate from Echinoconchoidea and Aulostegoidea, but displays in various genera attributes of both superfamilies, even though they arose from different sources within Strophalosiidina.

6. Evolution with an Infrasuborder: Productimorphi.

Productimorphi incorporate the productidan descendents from a single Devonian family Productellidae of Superfamily Productelloidea, the earliest member of Productidina, and completely strophalosiform in all attributes. The family and superfamily had evolved from chonetiform (anopliinan) stock into a strophalosiiform subfamily Chattertoniinae, that split through time into further subfamilies of Productellidae, and each of these subfamilies provided the source for superfamilies of Productidina, which emerged in the Late Devonian or Early Carboniferous, and flourished until the end of the Permian Period. Subfamily Productellinae with its characteristic alveolus, and a Tribe Margaritiproductini evolved into Lomatiphoridae, which may be regarded as the earliest member of Productoidea. Productoidea was a highly diverse group, subdivided into major families, Productidae, Retariidae, Buxtoniidae and Dictyoclostidae, characterized by strong ribs and usually well defined fine and posterior rugae. A second productellid subfamily, Helaspinae, provided source stock for Horridonioidea, a relatively minor group with comparatively few and often large spines, and little other ornament, and comparatively large individuals. A different and minor group of smaller individuals, with often organized spines and often strong ribs and rugae, Marginiferoidea, arose, it is proposed, from Orbinariinae. Both of these superfamilies, and especially Horridonioidea, were distributed mostly through the paleotropics and northern paleohemisphere, whereas Overtonioidea are found widely over both paleohemispheres. These are small shells with rugae often prominent, and no specialized spines, and evolved from the productellid tribe Dotswoodiinae, which commenced with representatives in both northern and southern paleohemipheres.

Productimorphi make up most constituents of Productidina. The remaining superfamily, Echinoconchoidea arose from a separate family member of Productelloidea, called Caucasiproductidae, characterized by numerous fine spines over both valves. Descendent echinoconchs are also characterized by numerous fine spines over both valves.

7. Evolution within suborders Strophalosiidina, Productidina and Linoproductidina.

The entire thesis of this study has been the way in which productiform superfamilies arose independently, at different times, from different strophalosiiform stock, exemplifying reiterative "sheet evolution" rather than "point source" evolution. It is as though there was a major and basic instability in most strophalosiiform stock, that impelled the loss of articulatory structures and change to feeding apparatus, along similar lines, and expanded the strategies of spine adhesion and shell strengthening through ornament. That might suggest the possible emergence of large gigantiform genera from different stocks, and the subparallel production of paucispinaurian genera in east Australia, New Zealand and in west Texas. Perhaps the same instability allowed the sort of evolution predicated by Taboada & Shi (2011) amongst Overtonioidea in which genera evolved separately from each other in Argentina and northeast Russia, separately, but along almost parallel lines.

OVERVIEW OF SUPERFAMILIES

RELATIVE SUCCESS OF THE SUPERFAMILIES

Table 18

Brachiopods, although very successful in terms of overall diversity and biomass throughout late Middle and Upper Paleozoic times, were limited in terms of their evolutionary capacity. They were and are restricted to marine conditions (but see Hiller 2011), and were immobile after an earliest growth stage, unless attached to and passively moved by a larger shell-fish, or sea-weed. Food had to come them. They did not swim or burrow into the sea-floor, for the great majority dwelled over the sea-bottom, sometimes on top of living or amongst dead shells, and more rarely were incorporated into bioherms. They were heavily impacted by the life-crisis at the end of the Permian Period, and so evidently lacked a certain degree of survivability. But within the limits of the phylum, and of all brachiopod orders, Productida showed, during the time they lived, the greatest diversity, and the widest range of morphologies. Compared with other brachiopods, no other group managed to so simplify the dorsal valve, or so elongate the ventral valve to mimic a coral-shape. Few so dominated short-lived faunal zones or sea-floors to develop virtually monospecific communities, apart from some strophomenids (s. l.), orthotetids (s. l.) and chonetids (s.l.). Few attained such large size, apart from some strophomenids, chonetids and spiriferids. The colonization of the shallow sea-floor and marine shelves by brachiopods often left little room for other biota, hard-shelled or soft, during Paleozoic time.

The success or otherwise of each superfamily may be broadly indicated through several simple parameters (Table 18). Simplest is the number of constituent genera: these may be readily counted. Of course, the number will be probably incomplete, but such applies to all superfamilies, and it is to be noted that most regions have had their Upper Paleozoic faunas studied, although some obviously need further work more than others. Secondly, the successful expansion of stock into a further superfamily must mark a degree of achievement. The size range provides additional information, not that it need be directly related to biomass of individuals, for small size may be coupled with high numbers. Lastly the geographic range is broadly assessed. The adaptation to specialized niches is readily assessed, but is not quantified, because most genera in the superfamilies dwelled much as other genera over the sea-floor. Variation from a basic sea-bottom habit, cohabiting with other species and phyla, became modified in several ways. Some adjusted to a coralline habit, building or participating in biohermal build-ups, through which biota were crowded into small reefs. Others were able to establish dense colonies of shell accumulation, often entirely or nearly monospecific. Yet others developed a very large size, "gigantic" in terms of brachiopods, and so achieve significant biomass at an individual level. The following summarizes the "success" of each superfamily.

Productelloidea

Productelloidea involved rather small strophalosiiform shells distinguished by the lack of ventral umbonal cicatrix and otherwise of somewhat generalized morphology: they never developed specialized structures or adapted to specialized habitats, and lived little beyond the Devonian Period. Having evolved from Chonetida, one of the families, Productellidae, became widely distributed and diversified in subtle ways. The ventral row of hinge spines so prominent in Chonetida lost importance, and subequal spines covered the ventral valve at least. They evolved into other longer-lived and more successful superfamilies, involving Overtonioidea, Horridonioidea, Marginiferoidea, and source for Productoidea, most of which were also moderately well distributed, but also limited in morphological range and niche adaptation. The minor group Caucasiproductidae, discriminated because of the presence of numerous dorsal spines, gave rise to Echinoconchoidea, characterized by its numerous spines.

Overtonioidea

Overtonioidea involved rather small productiform shells of somewhat generalized morphology, simplified from that of Productellidae: they never developed specialized structures or adapted to specialized habitats. But they were widely distributed and long-lived, appearing in late Devonian or Lower Carboniferous and lasting until the end of the Permian Period, with some occurrences in early Triassic. They were thus more than a transition group, and were successful in terms of distribution and diversity.

Horridonioidea

This is a small group of modest diversity, a number of the genera reaching comparatively large size, especially in the Lower Carboniferous, as well as some large individuals in the Arctic Permian. Otherwise the only exceptional morphology or adaptation was achieved in the nature of spines which often became very strong, usually close to the hinge and rarely over the dorsal valve. The superfamily does not appear to be found reliably in the southern paleohemisphere, and in the Permian was more characteristic of northern temperate paleolatitudes.

Marginiferoidea

Marginiferoidea developed for some forms elaborate trails and diverse patterns of spines and other ornament, with distinctive interior. Size remained small, and diversity moderate, with a degree of internal specialization regarding muscle supports and cardinal process and extended or multiple trails. Species are seldom found in overwhelming abundance, although prominent in many Upper Paleozoic faunas. Nor were the habitats other than the normal sea-floor distribution, but the superfamily was widely distributed, and even, rarely, penetrated high southerly paleolatitudes during warm-water invasion.

Productoidea

Like Productelloidea, Overtonioidea, Horridonioidea and Marginiferoidea, this superfamily on the whole remained conservative in morphology and habitat. Many genera increased in size, so that biomass and diversification was considerable at intervals. Spine patterns were of limited diversity, ribs and rib-like commarginals became prominent, and some interior specialization occurred in a few genera, involving muscle supports. Distribution was widespread, other than in high paleolatitudes under cold conditions, where occurrences are known, but not common.

Echinoconchoidea

The preceeding superfamilies, from Overtonioidea to Linoproductoidea, arose from within Productellidae, whereas Echinoconchoidea stemmed from sister family Caucasiproductidae. Echinoconchoidea are marked by slender and dense spines as a rule, which could form dense mats and made up a significant part of the biomass for each individual, and some achieved comparatively large size, such as *Echinaria* Muir-Wood & Cooper or *Patellamia* new genus. Diversity was moderate, and distribution widespread, with only rare occurrences in the high paleolatitudes of east Australia, but no specialized shape was developed.

Strophalosioidea

Strophalosioidea were an active and ongoing source of other superfamilies, and arguably might be deemed to have been the most successful of superfamilies, if measured in terms of progeny. They gave rise to Cooperinoidea, Aulostegoidea followed by Richthofenioidea, Scacchinelloidea and Lyttoniidina. They also displayed moderately high diversity and wide distribution, but of course their morphological variations were so great that separate superfamilies and even a separate suborder need to be recognized. Rarely, large size was achieved (*Biplatyconcha, Subtaeniothaerus*), and in the high Permian paleolatitudes of east Australia and New Zealand, strophalosiids such as *Echinalosia* and *Pseudostrophalosia* densely colonized sea-floors to form bands over 10m thick with what must be millions of individual shells. The superfamily displayed considerable diversity in ribbing and density and nature of spination, without achieving the specialization reached by some of the other superfamilies.

Scacchinelloidea

Scacchinelloidea were a moderately diverse group morphologically, but not numerous in terms of genera or species, and they were comparatively widespread, Rhamnariinae achieving a substantial record in southerly paleotemperate latitudes. Balkhasheconchinae appeared in moderate latitudes of both hemispheres, and is unknown in paleotropics. Paleotropical Tschernyschewiidae developed a high ventral septum and subconical ventral valve. But the most striking morphology is demonstrated by the paleotropical Scacchinellidae, with extended and in some cases comparatively large ventral valve that may contain infilling, and high ventral septum, and reduced dorsal valve, convergent with some richthofenoids as external mimicry of the coral shape.

Cooperinoidea

Cooperinoidea were an offshoot from Strophalosioidea, as small shells with specialized lophophores, whilst retaining a strophalosioid form of spines. They were predominantly of the Permian Period in paleotropical seas, and are of low diversity. They may be regarded either as a deviant short-lived stock, or relict transition from Strophalosioidea to Oldhaminidina.

Aulostegoidea

By contrast, Aulostegoidea developed a range of different spine and rib patterns, and some formed elaborate trails and diversified muscle supports and cardinal process. Large shells with substantial biomass were represented in high southerly paleolatitudes of Permian age as Taeniothaerini, and diversity was high. Notably, one offshoot is treated as a separate superfamily Richthofenioidea.

Richthofenioidea

This is a highly specialized superfamily, the dorsal valve acting as a lid on an extended ventral valve, approaching *Proboscidella* in shape, but more like a small solitary coral, and found in paleotropical bioherms, usually amongst an array of other species and genera, and supported by modest development of spines. The group was of moderate to low generic diversity, and seldom was found outside of the paleotropics.

Lyttonioidea

Lyttonioidea to my mind marks the acme of evolutionary achievement for virtually any brachiopod, in so far as radical change to morphology is concerned. Virtually only the feeding apparatus survived, with loss of most of the dorsal valve, whilst the ventral valve formed an irregular subconical dish. Like some strophalosioids, the lyttoniids were able to build up substantial virtually monospecific shell-banks. Generic diversity was modest, the time range especially Permian, though there has been unreliable reports of a Lower Carboniferous genus, and distribution was largely restricted to paleotropics, with rare occurrences in temperate zones. The group arose from Strophalosioidea, possibly through Cooperinoidea.

Superfamily	No. of genera	No. offshoot	Size range			Geographic range			
			S	M	L	N	P	S	A
Productelloidea	25	5	x			x	x	x	
Overtonioidea	45	1	x			x	x	x	x
Horridonioidea	30	0	x	x	?	x	x	x	
Marginiferoidea	45	0	x			x	x	x	x
Productoidea	103	0	x	x		x	x	x	x
Echinoconchoidea	56	0	x	x		x	x	x	
Strophalosioidea	81	3 + 2*	x	x	x	x	x	x	x
Scacchinelloidea	26	0	x	x	x	x	x	x	
Cooperinoidea	7	0-1^	x				x		
Aulostegoidea	54	1	x	x	x	x	x	x	x
Richthofenioidea	22	0	x	x			x		
Lyttonioidea	20	0-1~	x	x	?		x		
Loczyelloidea	8	0-1~	x	x			x		
Devonoproductidae	5	3							
Paucispiniferoidea	64	0	x			x	x	x	x
Linoproductoidea	59	0	x	x	x	x	x	x	
Proboscidelloidea	56	0	x	x	x	x	x	x	x

Table 18. Relative success of superfamilies.

N – northern hemisphere north of paleotropics, P – paleotropics, S – southern paleotemperate regions, A – southern high and cold paleolatitudes. Indeterminates are excluded.
S – small, M – median size; L – large or moderately large. * Two superfamilies descended from superfamilies derived from Strophalosioidea .^ covers Cooperinoidea as possible source for Lyttonioidea: ~ did Lyttonioidea provide the source for Loczyelloidea, or vice versa?

Loczyelloidea

Lozyelloidea are a very small and geographically restricted group, chiefly paleotropical and low temperate paleolatitudes, close to Lyttonioidea, with the shell a simple ovoid shape or divided into two, often forming two long wings. The time range is less, yet where known, more of the dorsal valve is retained, as if precursor to Lyttonioidea. Overall biomass was much less than for Lyttonioidea.

Family Devonoproductidae

Devonoproductidae arose independently from other early Productida as a strophalosiiform descendent from ribbed chonetid stock, and belonged to three subfamilies, each of which gave rise to linoproductidin superfamilies. Although limited in time range and distribution, the family evolved into Paucispiniferoidea, Linoproductoidea and Proboscidelloidea, which achieved greater diversity and variation in morphology.

Paucispiniferoidea

Paucispiniferoidea approached Marginiferoidea in the development of specialized spines in some lineages, and remained small shells without specialized habitats. Paucispiniferidae and Yakovleviidae were best represented in paleotropical and northerly paleolatitudes during Upper Carboniferous and Permian time, and Anidanthidae were in both hemispheres, tending to higher paleolatitudes. Although comparatively diverse in morphology, the generic diversity and species numbers were not substantial, whereas the geographic range matched that of Strophalosioidea.

Linoproductoidea

Linoproductoidea were amongst the most successful of Productida. They were highly diverse, and unlike Paucispiniferoidea with which they shared a devonoproductid ancestry, did not develop specialized strut or rhizoid spines, but did include a range of sizes, shapes and habitats. From one of the major groups arose the "gigantic" Gigantoproductidae, very large for brachiopods, although as usual occupying space on the sea-floor. Striatiferidae also developed large size, with a variably shaped subtriangular shell, and could be crowded in clusters. Many other Linoproductidae achieved a large size comparable to that of Productoidea and Horridonioidea, and were widespread, apart from high paleolatitudes of the southern hemisphere.

Proboscidelloidea

Genera within Proboscidelloidea were smaller than genera of Linoproductoidea, with somewhat different spine arrangement, that achieved even higher morphological diversity and greater biomass during Permian time, and were often numerous at individual level, as well being very widespread, suggesting an ability to speciate and diversify generically in the absence of some of the other brachiopod groups in high paleolatitudes, which meant they could tolerate cold conditions and long intervals of low light, and possibly different food sources. Within this group, paleotropical *Proboscidella* and *Undaria* in the Lower Carboniferous and *Siphonosia* in the Permian grew long high ventral valves, with the dorsal valve becoming like a cap or lid, and growing in clusters.

EVOLUTION AND PLACE

Table 19

As shown in Table 18, most Productida evolved first in paleotropical and low paleolatitudes, and all members of Cooperinoidea, Richthofenioidea, Loczyelloidea and most members of Lyttonioidea evolved solely in paleotropical waters: one exception being *Paralyttonia* Wanner in Timor (warm southerly paleolatitude). Virtually all of these superfamilies commenced in paleotropical waters: exceptions might be Productoidea, in which Buxtoniidae arose from south paleotemperate as well as paleotropical genera, and Scacchinelloidea, Balkhasheconchinae starting with genera from New South Wales and northeast Russia, probably at temperate to subtropical paleolatitudes during early Carboniferous time, and gave rise to Rhamnariinae (at first south temperate paleolatitude), followed by paleotropical Scacchinellidae and Tschernyschewiidae. The source probably lay in paleotropical and southern paleotemperate Araksalosiidae. Not that it is easy to determine paleolatitudes. Distinctions for Permian faunas were outlined some time ago, from world-wide and all-embracing cluster analyses (eg. Waterhouse & Bonham-Carter, 1975), where paleotropical waters are indicated by the presence of proxies and paleotropical dependents in the form of coral reef build-ups, warm-water fusulines, and high diversity faunas, and cold-water faunas are indicated by glacial deposits and chemical signatures, and low-diversity faunas. The methodology did not rely on mere diversity counts, but delineation for each family of climatic and distribution attributes summed from the whole, and seems more reliable than paleomagnetic interpretations. Recognition of faunal provinces is very complex (Waterhouse 2011), and the distinction for example of a Malvinocaffric Province and varying degrees of cosmopolitanism in Boucot & Blodgett (2001) may be noted for the Devonian Period. Devonian reconstructions are shown in Scotese & McKerrow (1990) and Scotese (1992), with a possible reconstruction for Gedinnian time showing oceanic gyres in Grunt & Zezina (2000, Fig. 3). During this period, much of the continental mass lay in the southern hemisphere, and the disposition of brachiopod faunas has been outlined by Boucot & Blodgett (2001). (Faunas in "arid belts" are counted as paleotropical, for sea is not arid). Problems remain, for even the delineation of "provinces" for the Permian should take care not to favour geographic rather than paleobiogeographic entities, and needs to be conducted zone by zone, certainly not stage by stage or even larger entities (Waterhouse 2010b, 2011). For the Permian faunas of east Australia, it is possible to recognize some 20 provinces, with additional gaps: yet these were reduced to a single "province" in Shi & Archbold (1993) and Shi (2006). In any one region, it is demonstrated that faunas change in affinities and composition repeatedly (Waterhouse & Shi 2010).

Thus full analysis lies beyond the scope of this study: instead the first appearances of new genera are assigned to paleogeographic regions, of paleotropical, northern temperate, southern temperate, and high latitude mostly cold-water east Australia and New Zealand. The application is very broad-brush, because some genera spanned several climatic zones, and as a rule, are allocated to the paleotropical belt. The paleotropical belt itself was subject to unexpected temperature range, as urged by Shi (2001) for southeast China. Compounding the difficulty is way paleofaunas expanded and contracted with climatic change and shift of continents. Such change can be unravelled, but the scope is too complex for this brief survey. A special area of Verchoyan-Kolyma in northeast Russia is distinguished for the Permian, but was not nearly as cold as Tasmania, New South Wales and Queensland in east Australia and northwest Nelson and the Brook Street Volcanic arc and fringing apron in New Zealand (the remainder of New Zealand to the east and north being of warmer temperate paleolatitudes with scattered warm-water fusulines). Attention is focused on the comparatively few genera that evolved in temperate and high latitude regions, because these were clearly exceptional, and connected to special events or special morphological and physiological traits.

Productelloidea

Amongst Productellidae, a few genera evolved in Canada and in Australia during Devonian time, when faunas were said to have been "cosmopolitan". According to reconstructions, Queensland lay in low Devonian paleolatitudes, as is reinforced by a number of what appear to have been paleotropical genera (see McKellar 1970), apparently close to the paleotemperate and paleotropical interface. Much of United States verged on south temperate paleolatitudes, along with parts of Europe during Devonian time. There is a minor component counted as northern temperate, including *Grandiproductella* and *Kavesia* (Ardviscini), which gave rise to Horridonioidea.

Overtonioidea, Horridonioidea

In contrast to many other groups, Overtonioidea show a remarkably "normal" and symmetrical distribution, with Kolyma-Verchoyan of northeast Russia playing a role in contributing new genera during the Late Carboniferous and Permian. Compared with other groups, the output in paleotemperate latitudes was considerable. Perhaps the most outstanding group was the largely Upper Carboniferous Levipustulinae Lazarev, especially notable for its prominence in paleotemperate latitudes, including northeast Russia, and intermediate to high paleolatitudes in the southern hemisphere of Argentine and east Australia. As a counterbalance, there were several tribes restricted to paleotropical latitudes.

On the other hand, Horridonioidea were skewed towards the northern hemisphere, with a high number of northerly first appearances, and other appearances limited to northern and eastern Australia, which was close to paleotropical in the Late Devonian. The position of north Australia during Tournaisian time is not secure, but it is deemed likely to have commenced its southerly drive. The superfamily is not otherwise represented in any Carboniferous or Permian fauna in Australia, and arose from Ardviscini, represented by genera of somewhat northerly habitats.

Marginiferoidea, Productoidea, Echinoconchoidea

Marginiferoidea were very strongly paleotropical. There were a few and distinctive first appearances amongst temperate faunas, and one unique marginiferid *Azygidium* in the late Sakmarian Fairyland Formation of Queensland (Hill 1950, Waterhouse 1986b). The Fairyland faunule which contains *Azygidium* is exceptional, illustrating a brief episode of warm waters in Queensland. Apart from this occurrence there were no known Permian marginiferoids in east Australia or New Zealand, indicating the predilection of this superfamily for warm waters.

Productoidea were also heavily weighted towards paleotropical origins, although a number were shared with the northern paleotemperate zone. Retariidae shared paleotropical and northerly affinities, but largely avoided southerly waters, until warm waters came to prevail in southeast Asia after early Permian time. There were only rare buxtoniid and dictyoclostid genera in southerly paleolatitudes, some arising as the Permian climate was becoming warmer, and some Carboniferous genera in east Australia and India which were moving from comparatively low paleolatitudes towards the south pole.

Although Echinoconchoidea were mostly paleotropical, Waagenoconchidae produced some southern paleotemperate genera. The diverse Devonian faunas of north Queensland, Australia, indicate very warm conditions, close to the paleotropics, although narrowly within southern temperate paleolatitudes. Lethamiini were minor, and restricted to southerly paleolatitudes.

Strophalosioidea

Strophalosioidea includes a few subfamilies and families dominated by first appearances in high latitude and temperate faunas. The Lower to Upper Devonian Donalosiinae is widespread in first appearances, counting the Queensland genera as low paleolatitudal, nearly paleotropical, but gave way to Strophalosiinae dominated by southerly first appearances, the group evidently responding well to the onset of cold conditions in the Pennsylvanian and Early Permian (Cisuralian). The highly diverse Dasyalosiidae included many paleotropical and paleotemperate components, and also incorporated Echinalosiinae which evolved most prolifically in temperate and even high paleolatitudes. By contrast Chonopectidae were largely restricted to tropical and more rarely temperate paleolatitudes. Araksalosiidae inhabited sea-floor that was moving northwards into the paleotropics from paleotemperate latitudes, involving *Araksalosia* and *Kahlella*, and *Rangaria* originated in New South Wales, moving southwards into colder paleolatitudes. Ctenalosiidae involved Ctenalosiinae of mostly paleotropical extent, Mingenewiinae with connotations of southern paleotemperate latitudes, and Craspedalosiinae in northern paleolatitudes.

Aulostegoidea, Scacchinelloidea

Aulostegoidea were somewhat similar. Aulostegini typified north temperate paleolatidues, and Taenothaerini and Megatsegini was well represented in southern paleolatitudes, especially east Australia. But many aulostegoids developed highly specialized adaptations to paleotropical conditions. Whilst Scacchinellidae and Tschernyschewiidae within Scacchinelloidea were exclusively paleotropical, Balkhasheconchinae is known in northerly paleolatitudes of the Lower Carboniferous and Lower Permian, and also represented in southern paleolatitudes of east Australia, whereas the source stock Araksalosiidae is found in faunas on crust that had earlier occupied especially southern and (less) northern temperate and tropical paleolatitudes of Late Devonian to Lower Carboniferous age. The oldest Rhamnariinae are found in southern temperate to high paleolatitudes, and like Paucispinauriini, appear to have penetrated the paleotropics of United States in Kungurian (latest Cisuralian) time, and generated further genera. Septasteginae were chiefly in southerly temperate or subtropical paleolatitudes, although *Enigmalosia* Czarniecki is of early Permian age in high northern paleolatitudes, but this seems an exceptional genus. Yet if truly rhamnariid and representative of the earliest members of the family, it points to a northerly origin that later spread successfully into the southern hemisphere.

Paucispiniferoidea

Paucispiniferoidea are a diverse group, with rather different families diversifying from one Devonian subfamily, Devonoproductinae. Paucispiniferidae are mostly tropical and north temperate, and south temperate paleolatitudes. But Anidanthidae have northern and southen paleotemperate connotations, as well as paleotropical, and played a significant role in high southerly paleolatitudes – indeed the paleotropical components may have owed much to incursions of cold-water faunas into the paleotropics. Yakovleviidae constituted a northerly counterpart, and largely split between northerly and paleotropical components.

Linoproductoidea

Linoproductoidea has a distribution close to that of Yakovleviidae. Overwhelmingly the group is of paleotropical origin, and showed only a few first entries in northerly and southerly temperate paleolatitudes.

Proboscidelloidea

Early Carboniferous proboscidellids were large paleotropical, but included paleotemperate southern latitude *Engellinus* and *Papiliolinus*, as well as paleotropical to subtropical *Minisculinella* and *Comagunia*. The ancestral subfamily Plicoproductinae included *Striatoproductella* Krylova from northeast Asia, which helped give rise to Proboscidelloidea, and as for Paucispiniferoidea, descendents also showed a propensity for dwelling in high or intermediate paleolatitudes in later times, to imply that some genera did not migrate under changed conditions of climatic change and continental displacement, but stayed put, and adapted as persistants. Auriculispinidae and Paucispinauriidae have a substantial component in high southerly paleolatitudes, and were thus like Strophalosioidea and Paucispiniferoidea (Anidanthidae) in being able to cope with low temperatures and considerable change in annual light regimes. Ultimately they arose from genera like or equivalent to *Plicoproductus* from northeast Asia, at moderate northerly paleolatitudes in Devonian time. They also contributed, by a lesser degree, to faunas of the northern paleotemperate realm. One of the more striking groups, Lyoniinae, was found mostly in southerly and often cold-water or recovery faunas, until penetrating or tolerating warm conditions in the late Permian as *Nikitinia*, but still in the southern paleohemisphere, and Filiconchinae managed to achieve bipolar or subpolar to high paleotemperate distribution, with no known paleotropical representation. Interestingly, Paucispinauriini displayed additional flexibility by commencing in high southerly paleolatitudes, and managing to penetrate the paleotropics in the very late Early Permian and later northern paleotemperate latitudes, to proliferate as several new genera.

Summary

In summary, most groups proliferated under paleotropical conditions, but there was active evolution, to a much lesser degree, in temperate paleolatitudes, and some special groups showed the ability to proliferate even under very cold conditions. The interplay between these groups and their dispersion, speciation and extinction or out-migration, not to mention changing climate and slow continental displacement, allowed for a variety of faunal association and changing exclusivity that produced virtually everywhere a very complex yet rational succession of faunizones and biogeographic provinces. The complexity was such that unravelling changes requires detailed systematics and detailed biozonation. The attempts at broad-brush generalizations, often marred by improperly excluding data and improperly lumping biozones into stages may yield results, but those results bear little relation to reality.

Superfamily	northeast Russia	north temperate	paleotropical	south temperate	east Australia
Productelloidea		4	16	?6	
Overtonioidea	3	14	22	5	1
Horridonioidea	1	14	12	3	
Marginiferoidea		4	35	5	1
Productoidea		9	78	15	
Echinoconchoidea		4	40	11	1
Strophalosioidea		10	37	24	10
Scacchinelloidea		4	13	9	
Cooperinoidea			7		
Aulostegoidea		1	47	2	4
Richthofenioidea			22		
Lyttonioidea			19	1	
Loczyelloidea			7	1	
Paucispiniferoidea	2	11	38	10	3
Devonoproductidae			3	2	
Linoproductoidea		7	46	6	
Proboscidelloidea	10	2	21	16	7

Table 19. Paleolatitudinal distribution of first appearances of genera and subgenera in superfamilies.

CONCLUSIONS AND RESERVATIONS
CHRONOMORPHIC ANALYSIS

The classification proposed in this study adds to the emphasis on morphology the additional parameter of derivation, so that superfamilies are sequentially compiled on the basis of both morphology and ancestry, and the difference between families within each superfamily summarizes the evolution of the superfamily.

The foregoing survey owes, as should be clear, a great deal to the *Revised Brachiopod Treatise*, which appeared under the guidance and drive of Alwyn Williams. Brunton et al. (2000) and Brunton (2007) provided an outstanding summary for Productida as used herein, particularly useful because of the provision of references and illustrations. Nonetheless it must be underlined that any student of Productida must, let me emphasize **MUST** - check both original sources and an expanded literature well beyond that containing the proposal and first species description. Desirably, original collections ought to be examined as well. That has been done only partially for this extensive review, with focus on Carboniferous and Permian. For Devonian, reliance has been placed on the *Revised Brachiopod Treatise* and original references, and there has been limited resort to first hand examination of collections, and only limited reference to non-type references. In so far as one of the prime emphases in this study is concerned with origins of superfamilies, that opens a field for further study. On the other hand, it may be stressed that there are many fine studies in the literature on Devonian Productida, especially well advantaged by the use of silicified material and preparation of moulds, notably for material from Australia, Canada and United States. It is noticeable in the *Revised Brachiopod Treatise* on Productida that the weakest coverage and least reliability is for the Permian Period, as in Curry & Brunton 2007, particularly with regard to faunas outside the paleotropical realm of the United States. On the one hand, synonymies and diagnoses indicated for Chinese and Australasian genera are often contentious, to say the least, and may be contradicted by the original documentation and morphology. As well, allocated ages may be wrong, or inconsistent. For example, in Brunton et al. (2000), the Rat Buri Limestone, with its rich faunas including a number of Productidina, is rated as late Early Permian (Artinskian), following Grant (1976), and elsewhere in the same *Revised Brachiopod Treatise* the very same faunas are treated as early Middle Permian, following Waterhouse & Piyasin (1970) and Waterhouse (1981a). The latter is correct, as established by fusulines and conodonts, and the age was quietly conceded without retraction in Brunton (2007). The Magnesian Limestone of north England may be called lower Middle Permian in Brunton et al. (2000), whereas it is Wuchiapingian (lower Upper Permian), as established by conodonts. Ages allocated to Permian brachiopods throughout the *Revised Brachiopod Treatise* are full of error (Waterhouse 2000a). Throughout the text there is an inconsistency in the use of Permian stages, and instead of referring to the international standard Guadalupian and Lopingian Series, Brunton et al. (2000) preferred the outdated scheme based on Russian outcrops, which has been superseded for many years by new and fully justified emphasis on faunas and outcrops in United States and China, as first proposed by Waterhouse (1983b), and ratified internationally (Jin 1996; Jin, Wardlaw et al. 1997). The "Kazanian" is often miscorrelated world-wide, time and again by Brunton et al. (2000) and by S. S. Lazarev in his various articles, and the old Tatarian Stage of Russia is next to useless, apart from patriotic, sentimental and historic value, being based on non-marine outcrops. Readers should be further aware that in the discussion of the stratigraphic distribution of Permian faunas, Curry & Brunton (2007, Fig. 1927, Fig. 1928) left out the entire Wuchiapingian Stage, a major unit of the period, long lasting and with more conodont zones than any other Permian stage. That, with other aspects, vitiates their discussion on the Permian Period. Such errors may seem inexcusable, but the truth is that accurate, or at least fully up-to-date age determinations and correlations require considerable familiarity with local and regional geology, or access to excellent and recent overviews, goals difficult to attain when reviewing world-wide faunas with hundreds of genera and thousands of species. It seems wise to acknowledge that age control is less than perfect, and can always be improved.

Reservations are often expressed by "experts" in geological articles about faunas that have been monographed as if this were a fault. That may be dismissed: it is the "understudied" faunas, or unstudied faunas, or faunas looked at piecemeal in short articles with limited context which provide the problem, compounded by the way in which sequential short articles repeat and even contradict themselves as study progresses. The ideal is surely provided by Cooper and Grant in their remarkable study of Glass Mountains brachiopods from Texas. The one reservation concerns the lack of revision by those same authors, and in that regard, authors of briefer articles, such as N. W. Archbold or S. S. Lazarev, or lengthy monographs authored or co-authored by authorities such as T. G. Sarytcheva and J. L. Carter, have often revisited studies and achieved greater depth of understanding.

From the point of view of systematics and classification, a number of the groups recognized many years ago (eg. Williams 1953, 1965, Muir-Wood 1965, Waterhouse 1978, Lazarev 1990) have been endorsed in Brunton et al. (2000) (Linoproductoidea, Echinoconchoidea, Aulostegoidea, Strophalosioidea, Richthofenioidea and Lyttoniidina), or at worst downscaled without discussion or adequate analysis, or even abrogated to themselves from earlier proposers. Productoidea in the *Revised Brachiopod Treatise* included a number of families, subfamilies and tribes in no clearly discernible pattern, and a major change has been the subdivision of Productoidea into four superfamilies, as first recognized in Waterhouse (1978), based on extensive scrutiny of material at the Smithsonian Institution, Washington, D. C. Such subdivision, together with analysis of first members and Devonian genera, strongly endorses and expands the recognition by Lazarev (1987, 1989, 1990) of a number of separate origins for productiform superfamilies from strophalosiiform stock. The present study further depicts reiterative and parallel evolution of productiform superfamilies, independently from other productiforms, notably in the case of Aulostegoidea and Echinoconchoidea, and consolidates the sourcing of Richthofenioidea from Aulostegoidea, and Oldhaminidina from Strophalosioidea.

The complexity of the evolutionary paths, and the associations of superfamilies, largely proven according to available evidence, underlines the potential for a classification more elaborate than that constructed in the *Revised Brachiopod Treatise*. One author S. S. Lazarev in a few years has hugely expanded knowledge of linoproductin brachiopods, with recognition of new genera and new subfamilies, overturning the *Treatise* classification for that group. The arrangement in the *Treatise* failed to recognize associations of superfamilies below those at subordinal standing, whereas such are strongly suggested within Productida. Moreover it is possible within classification to indicate relationships and morphological space to a degree greater than in the *Revised Brachiopod Treatise*, following the lead initiated by Williams (1953) in his treatment of lyttoniids. Lyttoniids are a small group of mostly if not entirely Upper Carboniferous and Permian age, that arose from Strophalosioidea. Because of their distinct construct – that is morphological distance from other Productida – they were assigned not just to a superfamily, but to a distinct Suborder Oldhaminidina, later changed to Lyttoniidina. The recognition of morphological space provides an additional tool, and may be signified by classificatory procedure. Within the suborder, a handful of exceptional genera were allocated superfamilial status as Permianelloidea (= Loczyelloidea), correctly in my view, because of morphological difference from any other lyttoniid. That approach provides a template for expressing interrelationships and degrees of closeness. There is scope for further elucidation in classification along these lines.

More fundamental aspects arise from consideration of the evolutionary development of Productida. Simplistically, procedures are constrained for phylogenetic or evolutionary analysis, because in all practicality, involving unsuitability of material, expense, time, availability of material and availability of practitioners, prospects of extensive DNA study seem no more than a dream. Even so, the results of enormous DNA researches into evolution remains unsettled, given the claim by K. Peterson (2012, Nature 28 June) that micro-RNA which are a group of small non-coding RNAs that regulate the expression of genes in a sequence-specific manner for the timed regulation of developmental events "tears apart traditional ideas about the animal family tree".

Williams, Harper & Grant (2000, Fig. 453) prepared a cladogram for 20 genera of Lyttoniidina, based on heuristic (stepwise random addition of taxa in 10 replicates) search of matrix, and 30 characters: the cladogram looks acceptable, and is based on a very small sample. Use of a "key" classification would have achieved much the same result. That is the only example of cladistics used for Productida, and those who claim to rely only on cladistics may choose to regard such an omission as a serious failure, with the travails represented by the *Revised Brachiopod Treatise* inadequate for analysis of evolution and classification.

However cladistics does entail several problems (eg. Campbell 1975, Lazarev 1993), despite the enthusiam for the methodology, and despite the relunctance to admit that manipulation can skew results away from objective assessment. Manipulation aside, by disregarding or being unable to handle data on time and place, cladistics may become theoretical rather than actual, and at best reductionist. Partly for that reason, cladistic terms of high descriptive and analytical value have been seldom applied in the current study, until an overall synthesis can be achieved in future work. The methodogy involved in this report is like that embraced by Lazarev (1989), and involves a careful tracking of genera and their species back through brief and successive intervals of time, in actuality rather than in theory, by step-wise sequencing of species and genera through well delineated biozones. There is considerable allowance for morphological change, which may yield confusing signals to cladistic analysis, yet are realistic and hopefully more easily reconciled with DNA analysis which can be sequence specific, and at the same time, glib assumptions about linear progression can be readily rejected: if development occurred along single tracks, it was no more than one of many possibilities. One of the dangers of cladistics and biological clock theory is that the "medium becomes the message", with too facile a ruling out of complexities, and inherent difficulty in coping with saltations. So how is morphological association, differentiation, and descent to be calibrated? By using tight control over time, and thereby incorporating highly significant data absolutely basic to evolution. "Change" and "succession" are critical, and require the ability to monitor ongoing change, through time and sequence. By having information on time-controlled successive changes, it is possible to track biotic associations and growth through even radical change in morphology, relying on select major characterics shared between family groups that seem at first sight to display considerably different morphological attributes. Thus, because linoproductids share unique characteristics of ornament with certain strophalosiiforms, it is possible to track lineages which lose such character-states as teeth and sockets, and interareas, and large brachial shields. Evolutionary lineages can continue through the loss of characters, just like a stick that appears to bend at the interface between air and water.

"Place" remains to be further explored and calibrated. Yet already signals are being provided within a number of tribes and subfamilies of hitherto unsuspected linkages and successions, awaiting further analysis, and to be incorporated with climate and climatic change, and possibly enforced migration, as discussed by Krassilov (1974, 1975) and Waterhouse (eg. 1976c).

The foregoing study has pushed much further than the *Revised Brachiopod Treatise* in establishing a proximate model of evolutionary lineages comprised of superfamilies which bundle genera, tribes, subfamilies and families that arose each from separate older productidin, strophalosiidin, or devonoproductid groups, and ultimately different chonetid ancestors. The analyses have underlined the reality of a number of alliances not indicated in the *Revised Brachiopod Treatise*, and delineated and smoothed out instances of polyphyly and paraphyly. Much remains to be done. There are as indicated a number of genera which remain obscure in various attributes, and the time ranges for many genera require consolidation. The most promising fields for further study would appear to lie in the Devonian of several parts of the globe, and the Upper Carboniferous may be expected to yield much that is new. Even so, thanks to the labours of many paleontologists, most especially Muir-Wood & Cooper (1960), the Productida are a closely studied and at least moderately well understood group, with a rather surprising history of evolutionary development.

APPENDIX A. STRATIGRAPHIC INFORMATION

Part A. AUSTRALIA

Devonian

McKellar (1970) described his brachiopods as coming mostly from the Myrtlevale and Star Formations in the Dotswood Group of what he called the Star Basin west of Collinsville, northern Queensland. The Star Basin is generally merged with the Burdekin Basin, and the Star Formation seems to be generally categorized as the Star Beds, which are lateral equivalents in part of the Myrtlevale Formation. Overall accounts with many references are provided by Wyatt & Jell (1980) and Brime et al. (2003, p. 752, Fig. 1).

Permian

The type species of the new genus *Anidanthia* is described from the Elvinia Formation of the southeast Bowen Basin (Waterhouse 1986b, 1987), and the Tiverton Formation of Homevale in the northern Bowen Basin (Waterhouse & Shi in press). Material is also found in the Farley Formation of the north Sydney Basin in the Hunter Valley (Briggs 1998). The Permian biozones based on brachiopods and molluscs are described for east Australia by Waterhouse (2008).

Specific localities mentioned in the text refer to collections from the Tiverton Formation (Sakmarian – Artinskian), exposed over low ridges near Homevale Station, north Bowen Basin, Queensland, as elaborated by Waterhouse & Shi (in press). The UQL collections, made for the Department of Geology & Mineralogy, University of Queensland, are kept at the Queensland Museum (bulk storage), Hendra, Brisbane.

Collected by K. S. W. Campbell & G. W. Tweedale, ca. mid 1950's:

UQL 2620. Tiverton Formation, Homevale Station, upper part of middle of three ridges, extending down on its southwest flank to the benched track at the molasses tank.

Collected by J. D. Armstrong, B. Runnegar, 10/1966:

UQL 3127. General collections near Homevale Station, through middle Tiverton Formation.

Collected by J. B. Waterhouse with P. Balfe and D. J. C. Briggs, 1/7/1979 and 2/7/1979. Grid reference MCKAY Sheet 584 281:

UQL 4509. NE flank to hill NE of molasses tank.

UQL 4510. Hill crest, calcareous band beyond gulch and molasses tank, further from the track.

UQL 4511. Band 4m thick up hillside NE of molasses tank and gulch.

Part B. NEW ZEALAND

Calandisa solitarius Waterhouse & Campbell is described from the Dunton Range, northern Southland, in beds mapped as Takitimu Group by Turnbull (2000). The fossils are accompanied by brachiopods such as *Echinalosia* and *Paucispinauria* of likely Artinskian age.

GS 12669, D42f0070, is described as exposed in the bed of the first major tributary on true right of Upukerora River, 300-400m upstream of forks in stream in main branch and upstream of Snowdon Slip. Grid ref. 45.23657°S, 168.03224°E. Collected by H. J. Campbell, C. A. Landis, I. M. Turnbull.

Part C. CANADA

1. Yukon Territory

The JBW localities are numerous and are located principally over a number of measured sections that are mapped in detail. The map and details of localities and distribution of these specimens will be provided separately in a forthcoming study of late Carboniferous and early Permian brachiopods from the Ogilvie Mountains. The collections on behalf of the Geological Survey of Canada come from the same region (Bamber & Waterhouse 1971). All type specimens are kept at the Geological Survey of Canada, Ottawa.

Hart River Formation

The Hart River Formation as proposed by Bamber in Bamber & Waterhouse (1971, p. 45) is described as recessive light and dark silty limestone, with type section on the northern bank of the Peel River, Yukon Territory. Typical faunas dominated by the brachiopod *Quadralosia* are of late Visean or early Serpukhovian (Chesterian) age.

Three GSC localities are listed below.

GSC 53743. Section 116H-1B, north bank of Peel River (65°53'N, 136°05.5'W), Yukon Territory. Collected by E. W. Bamber & D. Mayes. See Bamber & Waterhouse (1971, p. 226).

GSC 53745. Section 116H-1B, north bank of Peel River, Yukon Territory. Collected by E. W. Bamber & D. Mayes. See Bamber & Waterhouse (1971, p. 226).

GSC 53749. Section 116H-1B, north bank of Peel River, talus at 70 feet, Yukon Territory. Collected by E. W. Bamber.

Ettrain Formation

The Ettrain Formation is a resistant cliff-forming unit of sparry or micritic skeletal limestone containing lenses of chert, with type section near the Alaska-Canada border, at section 116F-9 (Bamber & Waterhouse, 1971, p. 53). A lower member 392m thick of light grey skeletal limestone with dark chert lenses is followed by yellow-brown weathering skeletal micritic limestone. Brachiopod faunas from the upper and middle Ettrain Formation were monographed by Nazer (1977), and shown to be of Kasimovian age.

GSC localities. These are recorded for Yukon Territory in Bamber & Waterhouse (1971, pp. 241-246), in measured sections as follows: GSC 53690, section 116H-1A; GSC 53693, section 116H-1A; GSC 53699, section 116H-1A; GSC 53725, section 116H-1B; GSC 53727 and GSC 53728, section 116H-1B; GSC 53730, section 116H-1B; GSC 53793, section 116G-9; GSC 53811, section 116G-98; GSC 53984, section 116F-9; GSC 56924, section 116J-4A; GSC 56931, section 116C-2; GSC 57062, section 116C-2; GSC 57069, GSC 57071 and GSC 57247, section 116C-2. For section detail see Bamber & Waterhouse (1971, pp. 241ff) and Bamber (1972).

Jungle Creek Formation

The Jungle Creek Formation, source of several of the fossils described herein, was named and described by Bamber in Bamber & Waterhouse (1971) as a medium to dark brownish grey-weathering sequence of variable lithology, including skeletal, partly conglomeratic limestone, micritic skeletal and spicular limestone, calcareous shale, siliceous mudstone and siltstone. As Bamber noted, it forms a relatively recessive interval between the light grey-weathering and cliff-forming Ettrain Formation below, and Tahkandit Formation above. The area providing fossils lies 15 km to the north of the Tatonduk River, in the headwaters of the Jungle and Ettrain Creeks, some 14km east of the Alaska border, in the same area that provides the type section for the underlying Ettrain Formation. Four members are recognized by the present writer in the lower Jungle Creek Formation, below the biozones and faunas described by Shi & Waterhouse (1996). Member A is dated as Gzhelian, Upper Carboniferous, and members B to D dated as Asselian, or basal Permian. Brunton et al. (2000) inaccurately treated the Jungle Creek Formation as Tahkandit Formation.

Member A

Member A lies immediately above the Ettrain Formation or its equivalents, as mapped by E. W. Bamber. It corresponds with unit a and especially b in the geological map of Shi & Waterhouse (1996, Fig. 4), and is approximately 230m thick in section 116F-9. There are a number of cyclothems, commencing with shale, and capped by limestone, with increasing quartz conglomerate to the north at section 116F-9. Detailed lithology and petrography of measured sections is provided by Bamber (1972, pp. 33-40) for the Jungle Creek East section 116F-9, which is also the type section for the Ettrain Formation, from unit 127 to unit 72 (p. 40). The lithologies for the Ettrain Creek East section 116F-16 start at unit 14 (Bamber 1972, p. 64) and continue to unit 67 (Bamber 1972, p. 58). Member A is only feebly represented in the type section of the Jungle Creek Formation as thin shaly beds marked as "Dos" in Bamber & Waterhouse (1971, Fig. 7) and Shi & Waterhouse (1996, Fig. 5).

Fauna: The faunas are rich and varied, and are classed as the *Septospirifer tatondukensis* Zone.

Member B

Member B is a thin unit, best represented in section 54 of Bamber (1972) by coarsely granular and shelly limestone 20m thick, lying above shale and sandstone. Units 68-70 are segregated with unit 67 as Member B. The member is represented by the lower part of unit c in Shi & Waterhouse (1996, Fig. 4), and is not widespread.

Member C

Member C is a distinctive unit, dominated by dolomite and up to 300m thick near the standard section 116F-16. It was mapped as the middle part of unit c by Shi & Waterhouse (1996, Fig. 4). The beds involve those itemized as units 72 to 96 in Bamber (1972, pp. 56-58) and consist of dolomitic sandstone, with occasional chert and shale.

Member D

Member D is a very distinctive unit, recessive, and exposed between the sandstone-dominated scarp of the overlying

"*Yakovlevia*" (= *Muirwoodia*) *transversa* Zone, and the underlying carbonate-dominated members A to C of the Jungle Creek Formation. At the standard section near section 116F-16, the unit is close to 80m in thickness, dominated by shelly siltstone, with intervals of fine sandstone, and measured as units 97-103 by Bamber (1972, p. 56). It is mapped as the uppermost part of unit c in Shi & Waterhouse (1996, Fig. 4). The member is developed above the equivalents of Member A in the type section of the Jungle Creek Formation in the Tatonduk River.

Further Yukon localities:

GSC 53821. Fish Creek section, 116P-6, 45 feet below top of Paleozoic. Yukon Territory. See Bamber (1977). Likely to be equivalent of Tahkandit Formation.

GSC 53848. Permian sandstone unit, section 116P-11. Collected by E. W. Bamber. Likely to be equivalent of Tahkandit Formation.

GSC 55249. Northern Yukon Territory, 65°28'N, 135°33'W. No stratigraphic placement, but fossils equivalent to those of the upper Jungle Creek Formation. Collected by Ray Price.

C-6167. Isolated outcrop in north Yukon, 65°20'N, 140°48'W. Mid Jungle Creek Formation. Collected by D. K. Norris.

2. Canadian Arctic localities

GSC 26406. Assistance Formation, Grinnell Peninsula, Devon Island, mapped and described by Harker & Thorsteinsson (1960, pp. 10-12).

GSC 25903. Disintegrated outcrop on top of cuesta ridge facing south, 3 miles north of lake on west side of Weatherall Bay, Melville Island. Likely to match Assistance Formation. Collected by E. T. Tozer, 1955.

GSC 35316. Melville Island, Sabine Peninsula, talus from Trold Fiord Formation. Collected by R. Thorsteinsson.

GSC 35317. Talus, Sabine Peninsula, Melville Island. ?Trold Fiord Formation. Collected by R. Thorsteinsson.

GSC 47846. Van Hauen Pass, Ellesmere Island. ?Degerbols Formation. Collected by R. Thorsteinsson.

GSC 52417. West wall Trold Fiord, Ellesmere Island, 4 miles from head of fiord. Canyon Fiord Formation. Collected by R. Thorsteinsson.

GSC 57687. Trold Fiord Formation, 18m above base, 11 km east of Easy Cape, Canyon Fiord, Ellesmere Island. Collected by R. Thorsteinsson.

GSC 58951. Canyon Fiord, North Camp, Ellesmere Island. ?Assistance Formation. Collected by P. Harker.

GSC 58959. Lower Canyon Fiord Formation, Bjorne Peninsula, Ellesmere Island. Collected by P. Harker. The formation is developed as a marginal facies belt on the south and east sides of the Sverdrup Basin (Douglas 1970, p. 571).

GSC 58977. Great Bear Cape, Ellesmere Island. Degerbols Formation, talus. Collected by P. Harker. See Waterhouse & Waddington (1982).

GSC 67255. Eastern Sabine Peninsula, Melville Island. ?Assistance Fomation. Collected by W. W. Nassichuk.

GSC 76029. Four miles northwest of Cape Fortune, Cameron Island, Trold Fiord Formation, Collected by A. R. Ormiston & A. H. McNair.

C-3996. Ellesmere Island, creek on southwest side of Mt Bridgman. Trold Fiord Formation. Collected by W. W. Nassichuk. See Waterhouse & Waddington (1982).

C-4003. Isolated outcrop north of Gap Lake, Ellesmere Island. 80°05'00"N, 83°25'00"W. Assistance Formation. Collected by W. W. Nassichuk.

C-4006. North side of Gap Lake, Ellesmere Island, 79°30'N, 83°25W. Trold Fiord Formation. Collected by W. W. Nassichuk.

C-4008. Ellesmere Island, stream NW of major drainage 2.5 miles north of head of Vesle Fiord. Trold Fiord Formation. Collected by W. W. Nassichuk.

C-4016. Ellesmere Island, 25 miles SE of Cape Lockwood, East Cape. 80°5'0" N, 81°5'0" W. Assistance Formation. Collected by W. W. Nassichuk. See Waterhouse & Waddington (1982).

C-4017. 25miles southeast of Cape Lockwood, east cape, Ellesmere island. Trold Fiord Formation. Collected by W. W. Nassichuk.

C-4019. 25 miles SE of Cape Lockwood, East Cape. Ellesmere Island, 80°5'00"N, 81°45'00"W. Assistance Formation. Collected by W. W. Nassichuk. See Waterhouse & Waddington (1982).

C-4025. Ellesmere Island, 80°05'N, 81°45'W, Assistance Formation. Collected by W. W. Nassichuk. See Waterhouse

& Waddington (1982).

C-4026. Ellesmere Island, 80°05'N, 81°45'W. Trold Fiord Formation. Collected by W. W. Nassichuk.

C-4028. Isolated outcrop, East Cape, 25 miles southeast of Cape Lockwood, Ellesmere Island. 80°05'00N, 81°45'00W. Tanquary Formation. Collected by W. W. Nassichuk, 1964.

C-4067. Creek 2 miles N of head of Blind Fiord on west side of major drainage, Raanes Peninsula, Ellesmere Island. Nansen Formation. Collected by W. W. Nassichuk.

C-4095. Section between Mt Schuchert and Mt. Barrel, Krieger Mts, Ellesmere Island. Degerbols Formation. Collected by W. W. Nassichuk. See Waterhouse & Waddington (1982).

C-13356. West side of Hecla Bay, Melville Island. Trold Fiord Formation. Collected by Atlantic Richfield.

Part D. UNITED STATES

Huge productid faunas come from the Glass Mountains and nearby ranges chiefly in Texas and have been described by Cooper & Grant (1974, 1975), with stratigraphic and faunal summaries presented in Cooper & Grant (1972, 1977): the material is kept mostly at the Smithsonian Institution, Washington D.C. I was priviledged to collect material on several expeditions, usually under the guidance of G. A. Cooper and R. E. Grant, and the bulk of the collected material was processed at the University of Toronto and is now kept at the Queensland Museum bulk storage, Hendra, Brisbane, Australia. Some small collections that were retained are used in this study for illustrating species and genera, and figured specimens have been passed on to GNS Science, Lower Hutt, New Zealand. Some Carboniferous specimens were supplied commercially.

UQL 3911. East side of small arroyo 0.55 mile N 15°W of hill 5611, 4.13 miles N 34°E of Hess Ranch, Hess Canyon, Glass Mts, west Texas.

Part E. THAILAND

Collections in Thailand were made over a number of years (1964 to 1994), under the guidance of Kaset Pitakpaivan, Department of Mineral Resources, Bangkok (Waterhouse 1981,1982b, 1982c, 1983d, Waterhouse & Piyasin 1970).

Part F. CHINA

In addition to an extensive field-collecting trip to China in 1980, material from the Maokou and Changhsing limestones was presented to me by Jin Yugan when he stayed with me in Brisbane, Australia, and by Liao Zhuo-ting when he stayed with me in Nelson, New Zealand.

Part G. NEPAL

Brachiopods have been collected by the writer from the Marsyangdi Formation of north-central Nepal, in the headwaters of the Marsyangdi River. Underlying and overlying faunas have been monographed (Waterhouse & Chen 2006, 2007; Waterhouse 2000b, 2002c, 2010b) and shown to be Changhsingian (Upper Permian), and Gangetian or upper "Griesbachian" (basal Triassic). The age of the Marsyangdi Formation is late Changhsingian.

The Marsyangdi Formation was named by Waterhouse & Shi (1991) as elaborated by Waterhouse (1994, 2004a, p. 42) for the youngest of Permian formations in the region. It lies immediately above the Senja Formation. Detailed geological maps of the formation and setting are provided by Waterhouse & Chen (2006, text-fig. 4, 5). The members may be summarized as follows:

(base) **Cho Member**: impersistent black or green-dark grey shale with surficial sulphur efflorescence, member up to 2m thick near the type section on the east side of ridge A (see below).

Hongde Member: dense and often dark sandy bioclastic limestone, 0.7m thick.

Mungji Member: metamorphosed carbonaceous mudstone 0.3 to 2m thick, with 25-30% graphite derived from carbonaceous material, minor muscovite, haematite staining, and considerable alteration. May be foetid, deposited under dysoxic conditions.

Braga Member: prominent red- or orange-patinaed limestone and intervening thin shale, 0.3 to 3m thick, especially rich in fossils, often with current bedding, or large fucoidal structures up to 20cm long inclined to the bedding.

Tengi Member: thin dark grey fossiliferous often foetid shale, 0.2 to 1m thick.

(top) **Gungsang Member**: dark red-, orange- or gold-patinaed limestone, 0.25 to 1m thick.

Amongst conodonts, *Mesogondolella sheni* (Mei) is a significant late Changhsingian form. The Marsyangdi Formation is overlain paraconformably by the Early Triassic Pengba Member of the Pangjang Formation, which lies on a surface that is apparently conformable, or may show very slight relief of 1-2cm. The key ammonoid *Otoceras* *woodwardi* Griesbach and bivalve *Claraia dieneri* Nakazawa are widespread in the region (Waterhouse 1994, 2000b). These latter forms are guides to the Gangetian Stage of Mojsisovics et al. (1895), placed at the base of the Triassic Period, and equivalent to the upper Griesbachian Stage of Canada (Waterhouse 2002a, p. 96).

Detail of localities:

PMc1. Chho Member, ridge A, east face south of small fault and prayer flag on crest, type section for the Marsyangdi Formation.

PMm4. Mungji Member, crest and especially east side of ridge B.

PMb5. Braga Member, crest and over some 20m to east of ridge B.

PM1. Peak 17315ft, 1m carbonate equivalent to upper Marsyangdi Formation, west of ridges A and B.

PM5. Kali Gandaki river valley, near Thini village and north of track between Tilicho and Jomson, level A of Waterhouse (2004a, p. 47).

Ridges A and B are mapped and figured in Waterhouse (2004a, Text-fig. 11, 15) and Waterhouse & Chen (2006, text-fig. 4).

Part H. INDIA, PAKISTAN

Upper Permian stratigraphy is summarized for this critical region in Waterhouse (2010b). The Geological Survey of India at Calcutta is an important repository of type material, and further material has been made available to me by S. C. Shah from Calcutta, A. S. Tewari From Dehra Dun, and Sangad Rao of Oil and Gas Commission, Dehra Dun, India. Salt Range outcrops in Pakistan were collected by me in 1964, when with J. M. Dickins and N. D. Newell, guided by A. Fatmi, Geological Survey of Pakistan. Other material has been provided by V. J. Gupta, Centre of Advanced Studies in Geology at Chandigarh, India. Although Gupta's macro- fossil material has been alleged to have come from other regions, but not the Himalayas, these allegations have not been substantiated as far as Carboniferous and Permian Productida covered in this monograph are concerned. His material has been carefully compared with the huge collections studied by Diener and Waagen at the Geological Survey of India, Calcutta, and with my own collections, and are fully verified as to source, often by independent researchers. For example, the faunal assemblage from the Bijni Tectonic Unit in the Garwhal Himalaya as described by Waterhouse & Gupta (1978), from material collected by Gupta, is clearly the same as that collected by John Talent, Macquarrie University, Sydney, Australia, and other collections described by Archbold & Singh (1993).

Part I. RUSSIA, ARMENIA

Apart from visits and collecting trips in the Urals and Moscow Basin in 1975 and Armenia in 1967, Tatiana Sarytcheva presented me with labelled material when visiting me at the University of Toronto. Figured material has been passed on to GNS, Lower Hutt, New Zealand.

J. ENGLAND, WALES, SCOTLAND, IRELAND, BELGIUM

These countries are important sources of classic brachiopod fossils of Lower Carboniferous age. Despite extensive study by Muir-Wood & Cooper (1960), and several articles by C. H. C. Brunton and D. J. C. Mundy and a few other authors, a number have been scarcely updated and in some cases completely ignored since the overview by Davidson in the mid-nineteenth century. There are extensive and well-labelled collections in a number of institutions, with source and species names reasonably reliable, but in need of revision. Some specimens have been supplied commercially.

APPENDIX B. SUMMARY OF NEWLY NAMED TAXA

Newly proposed genera within Suborder Productidina are *Spinellicosta*, type species *Spinulicosta dotswoodae* McKellar, 1970, *Proteusiella*, type species *Avonia proteus* Veevers, 1959, *Nalivkininius*, type species *Nigerinoplica nalivkini* Pushkin in Lazarev & Pushkin, 1986, *Costatonia*, type species *Chattertonia mackenzia* Perry, 1984 and *Nahannilusia*, type species *Spinulicosta prima* Chatterton & Perry, 1978 (Family Productellidae Schuchert), plus *Stainbrookia*, type species *Strophalosia butlerensis* Stainbrook, 1950 in Caucasiproductidae Lazarev. Further genera include *Fimbrininia*, type species *F. spinosa* new species, *Fimbrinusia*, type species *Fimbrinia borealis* Carter & Poletaev, 1998, *Taboadaia*, type species *Absenticosta bruntoneileenia* Taboada & Shi, 2011 and *Austroboreas*, type species *Lanipustula kletsi* Taboada & Shi, 2011 (Family Overtoniidae Muir-Wood & Cooper), *Costavonia*, type species *Productus minnewankensis* Shimer, 1926, and *Waggononia*, type species *Protoniella? waggonensis* Roberts, 1971 (Family Avoniidae Sarytcheva), *Engasia*, type species *Magnumbonella prolata* Roberts, 1971 and *Costadonia*, type species *Mesoplica? hillae* McKellar, 1970 (Family Leioproductidae Muir-Wood & Cooper), *Sangredonia*, type species *Horridonia? daltonensis* Sutherland & Harlow, 1973, *Inflatusia*, type species *I. ogilviensis* new species and *Calvadonia*, type species *Productus calva* Sowerby, 1829 (Family Horridoniidae Muir-Wood & Cooper), *Disparatia*, type species *D. nassichuki* new species and *Gadikao*, type species *Spinomarginifera concentrica* He & Shi, 2008 (Family Marginiferidae Stehli), *Nempemarginifera*, type species *Marginifera spinosocostata* Abich, 1900, *Piyasinia*, type species *Spinomarginifera plana* Waterhouse, 1983d and *Ciliciumia*, type species *Ciliciumia cilicia* new species (Family Costispiniferidae Muir-Wood & Cooper), *Nasutusia*, type species *Productus semireticulatus capitanensis* Girty, 1909, *Costacondraia*, type species *Dictyoclostus portlockianus crassicostatus* Dunbar & Condra, 1932 and *Nazeriproductus*, type species *Nazeriproductus nazeri* new species (Family Retariidae Muir-Wood & Cooper), *Anamarginatia*, type species *Marginatia mimica* Roberts, 1971, *Coronatonia*, type species *Kochiproductus coronus* Shiells, 1968 and *Kochiproductus* (*Dunbarovia*) new subgenus, type species *Kochiproductus plexicostatus* Dunbar, 1955, *Agirovia*, type species *Tolmatchoffia demaneti* Böger & Fiebig, 1963 (Family Buxtoniidae Muir-Wood & Cooper), and *Retiarisia*, type species *Dictyoclostus simplex* Campbell, 1957, *Robertsina*, type species *Marginatia patersonensis* Roberts, 1976, *Costaglobus*, type species *Inflatia engeli* Roberts, 1976, *Reticulumia*, type species *Reticulatia cinctifera* Roberts, 1976, *Boggabria*, type species *Antiquatonia spinulicosta* Roberts, 1976, *Bilinospina*, type species *Nudauris linospina* Cooper & Grant, 1975 and *Yacotania*, type species *R. globosa* Samtleben, 1971 (Family Dictyoclostidae Stehli). Further new genera are *Praelaminatia*, type species *Laminatia jacki* McKellar, 1970 and *Septumusia*, type species *Productus* (*Tschernyschewia*) *vicinalis* Reed, 1944 (Family Echinoconchidae Stehli), *Parasentosia*, type species *Sentosia? ignota* Carter, 1988, *Spinauricula*, type species *Sentosia profunda* McKellar, 1970, and *Plicosentosia*, type species *Sentosia plicata* McKellar, 1970 (Family Sentosiidae McKellar), *Glabrispinus*, type species *Kochiproductus elongatus* Cooper & Grant, 1975, *Patellamia*, type species *P. confinis* new species, *Putusia*, type species *Pustula oklahomae* Carter, 1999 and *Putapustula*, type species *Pustula multispinata* Roberts, 1963 (Family Waagenoconchidae Muir-Wood & Cooper), all in Echinoconchoidea.

Newly proposed genera for Strophalosiidina are *Fortispinalosia*, type species *Strophalosia fortispinosa* Hinchey & Ray, 1935, *Fimbrinialosia*, type species *Strophalosia perfecta* Waterhouse & Rao, 1983, *Crassispinosella*, type species *Strophalosia subcircularis* Clarke, 1969, *Strophalosiaria*, type species *Strophalosia concentrica* Clarke, 1990 and *Baikuralia*, type species *Strophalosia? bajkurica* Ustritsky, 1963 (Family Strophalosiidae Schuchert), *Maxwellosia*, type species *Strophalosia jukesi concava* Maxwell, 1954 and *Myrtlevalia*, type species *Acanthatia fragilis* McKellar, 1970 (Family Dasyalosiidae Brunton), *Rangaria*, type species *Acanthatia* (?) *rangariensis* Campbell & Engel, 1963 (Family Araksalosiidae Lazarev), *Mckellarosia*, type species *Strophoproductus rugosus* McKellar, 1970 and *Quadralosia*, type species *Q. delicata* new species (Family Chonopectidae Muir-Wood & Cooper), and *Quasimingenewia*, type species *P. imperator* new species (Family Ctenalosiidae Muir-Wood & Cooper), all within Strophalosioidea. Genera within Scacchinelloidea, Aulostegoidea and Cooperinoidea are *Titanisia*, type species *Scacchinella titan* Cooper & Grant, 1975 (Family Scacchinellidae Licharew), *Koyaonoia*, based on type species *Juresania? dissimilis* Waterhouse, 1981, *Minisaeptosa*, named for type species *Rhamnaria tenuispinosa* Cooper & Grant, 1975, *Shumardoria*, type species *Productus guadalupensis* Shumard, 1860, *Geniculatusia*, type species *Productus gangeticus* Diener, 1897, *Ramaliconcha*, type species *R. bitteri* new species, and *Campbelliconcha*, type species *Waagenoconcha delicatula* Campbell, 1956 (Family Rhamnariidae Muir-Wood & Cooper), and *Sierradiabloa*, type species *Tschernyschewia americana* Cooper & Grant, 1975 (Family Tschernyschewiidae Muir-Wood & Cooper), *Jinyugania*, type species *Strophalosia poyangensis* Kayser, 1883 (Family Aulostegidae Muir-Wood & Cooper), *Huaitakia*, type species *Glyptosteges percostatus* Waterhouse, 1983d and *Kwantovia*, type species *Rugicostella sakagamii* Yanagida, 1973 (Family Institellidae Muir-Wood & Cooper) and *Cooperinoides*, type species *Cooperina triangulata* Cooper & Grant, 1975 (Family Cooperinidae Pajaud). Within Oldhaminidina (= Lyttoniidina) the genus *Parvuliella* is proposed for *Loczyella* (?) *parvula* Licharew, 1930, in Family Loczyellidae Licharew, 1937.

Making up constituents of Suborder Linoproductidina are *Glabauriella*, type species *Paucispinifera quadrata* Cooper & Grant, 1975, *Quospina*, type species *Productina morrisi* Roberts, 1976, *Sutherlandika*, type species *Kozlowskia montgomeryi* Sutherland & Harlow, 1973, *Opiparia*, type species *Kozlowskia opipara* Grant, 1976, *Cornumukia*, type species *K. cornuta* Grant, 1976, *Odonovania*, type species *O. dorsospinosa* new species and *Yanagidania*, type species *Desmoinesia prayongi* Yanagida, 1975 (Family Paucispiniferidae Muir-Wood & Cooper), *Anidanthia*, type species *Anidanthus paucispinosa* Waterhouse, 1968b and *Calandisa* Waterhouse & Campbell, type species *C. solitarius* Waterhouse & Campbell new species (Family Anidanthidae Waterhouse), *Elucidatia*, type species *Elucidatia peterormus* new species, *Muirwoodia* (*Grandaurea*), type species *Yakovlevia hessorum* Cooper & Grant, 1975, *Dzhiremulia*, type species *D. conlustratus* new species, and *Harkeria*, type species *H. studiosus* new species (Family Yakovleviidae Waterhouse), *Lineaproductus*, type species *Productus corrugatus* M'Coy, 1844, *Lineacrassus*, type species *Lineacrassus inflatus* new species, *Liniunius*, type species *Linoproductus kaseti* Grant, 1976, *Lineatina*, type species *Productus lineatus* Waagen, 1884, *Grantevia*, type species *Linoproductus semisulcatus* Cooper & Grant, 1975, and *Tapajosia*, type species *Linoproductus caima* Chen, Tazawa & Shi in Chen et al. 2004 (Family Linoproductidae Stehli), *Lineabispina*, type species *L. ellesmerensis* new species (Family Gigantoproductidae Muir-Wood & Cooper), *Gilmoria*, type species *G. gilmorensis* new species, *Igniculus*, type species *Productus* (*Linoproductus*) *semicubiculus* Bell, 1929 and *Arcuatusia*, type species *Ovatia prolata* Carter, 1987 (Family Ovatiidae Lazarev), *Praeschrenkiella*, type species *P. waddingtonae* new species and *Chhidrusia*, type species *Productus* (*Linoproductus*) *simensis abrupta* Reed, 1944 (Family Schrenkiellidae Lazarev), *Donakovia*, type species *Ovatia markovskii* Donakova, 1975, *Tortilisia*, type species *Producta tortilis* M'Coy, 1844 (Family Proboscidellidae Muir-Wood & Cooper), with *Dawesionia*, type species *D. milkmani* new species, and *Sartenaeria*, type species *Productus koninckianus* Verneuil, 1845 questionably allied. *Engellinus*, type species *Linoproductus* (*Balakhonia*) *rawdonvalensis* Peou & Engel, 1979, *Comagunia*, type species *Productus lyelli* Verneuil in Lyell, 1845, *Commarginalia* Waterhouse & Nazer, type species *C. yukonensis* Nazer & Waterhouse new species, *Minisculinella*, type species *Productus undiferus* Koninck, 1846, *Globicorrugata*, type species *G. settlensis* new species, *Liaozhuotingia*, type species *Cancrinella pseudotruncata* Ustritsky, 1962, *Appelinaria*, type species *Grandaurispina crassa* Cooper & Grant, 1975, *Bellaspinosina*, type species *Grandaurispina bella* Cooper & Grant, 1975, *Vagarea*, type species *Grandaurispina? vaga* Cooper & Grant, 1975 and *Rugania*, type species *Cancrinella subquadratus* Cooper & Grant, 1975 are placed in Family Paucispinauriidae Waterhouse, *Umaria*, type species *Productus umariensis* Reed, 1928, *Masitoshia*, type species *Permundaria perplexa* Sone & Leman, 2005, *Animinia*, type species *Linoproductus aifamensis* Archbold, 1981 and *Cameronovia*, type species *C. milleri* new species in Family Auriculispinidae Waterhouse, and *Repinia*, type species *Cancrinella ? repini* Zavodowsky, 1960 in Family Stepanoviellidae Waterhouse.

Newly named species are *Fimbrianalosia ettrainensis* Nazer & Waterhouse, *Horridonia grandis*, *Tubersulculus reidi*, *Tityrophoria zimmermani*, *Kochiproductus imperiosus*, *Reticulatia oldershawi*, *Patellamia sulcata*, *Ramaliconcha guryulensis*, *Anidanthus perdosus*, *Praeschrenkiella costata*, *Costatumulus ganelini*, *Globicorrugata inflata*, *Calliprotonia mclareni*, *Glabrispina kingi*, and *Balkhasheconcha bamberi*. *Thuleproductus arcticus* (Whitfield), *Taeniothaerus farleyensis* Briggs, *Comagunia dawsoni* (Beede) and *C. auriculispinus* (Beede) are revised.

Newly named family groups in Productidina are Subfamily Chattertoniinae, based on *Chattertonia* Johnson, 1976, Subfamily Helaspinae and Tribe Helaspini, based on *Helaspis* Imbrie, 1959, Tribe Ardviscini, based on *Ardviscus* Lazarev, 1986b, Tribe Margaritiproductini, based on *Margaritiproductus* Lazarev, 1986b, Subfamily Orbinariinae, based on *Orbinaria* Muir-Wood & Cooper, 1960 and Subfamily Dotswoodiinae, based on *Dotswoodia* McKellar, 1970 (Family Productellidae Muir-Wood & Cooper), Crossacanthiini, based on *Crossacanthia* Gordon, 1966 and Tribe Lanipustulini, based on *Lanipustula* Klets, 1983 (Family Overtoniidae Muir-Wood & Cooper), Subtribe Costadoniinai, based on *Costadonia* new genus (Family Leioproductidae Muir-Wood & Cooper), Subfamily Baillieninae based on *Bailliena* Nelson & Johnson, 1968 and Tribe Karnelliini, based on *Karnellia* Lazarev, 2005b (Family Horridoniidae Muir-Wood & Cooper), Tribe Pseudoavoniini, based on *Pseudoavonia* Wang, 1983 (Family Marginiferidae Stehli), and Tribe Onopordumariini, based on *Onopordumaria* Waterhouse, 1971 (Family Costispiniferidae Muir-Wood & Cooper), Tribe Protoniellini, based on *Protoniella* Bell, 1929, and Subtribe Antiquatoniinai, based on *Antiquatonia* Miloradovich, 1945 (Family Retariidae Muir-Wood & Cooper), Dowhataniini, based on *Dowhatania* Waterhouse, 1979 (Family Buxtoniidae Muir-Wood & Cooper), and Subfamily Reticulumiinae, based on *Reticulumia* new genus (Family Dictyoclostidae Stehli), Subfamily Septariniinae and Tribe Septariniini, based on *Septarinia* Muir-Wood & Cooper, 1960 and Tribe Alatoproductini, based on *Alatoproductus* Jin & Hu, 1978 (Family Echinoconchidae Stehli), and Tribe Wimanoconchini, type species *Wimanoconcha* Waterhouse, 1983d

(Family Waagenoconchidae Muir-Wood & Cooper). Within Strophalosiidina, Subfamily Eostrophalosiinae, based on *Eostrophalosia* Stainbrook, 1943, Tribe Biplatyconchini, based on *Biplatyconcha* Waterhouse, 1978 and Subtribe Marginalosinai, based on *Marginalosia* Waterhouse, 1978 (Family Dasyalosiidae Brunton), Subfamily Whidbornellinae, based on *Whidbornella* Reed, 1943 and Subfamily Acanthatiinae, based on *Acanthatia* Muir-Wood & Cooper, 1960 (Family Araksalosiidae Lazarev), and Subfamily Bruntonariinae, based on *Bruntonaria* Waterhouse, 2001 (Family Ctenalosiidae Muir-Wood & Cooper), and Tribe Megastegini, based on genus *Megasteges* Waterhouse, 1975 (Family Aulostegidae Muir-Wood & Cooper). Within Oldhaminidina, Subfamily Litocothiinae is based on *Litocothia* Grant, 1976 (Family Loczyellidae Licharew). Within Linoproductidina, Tribe Odonovaniini is based on *Odonovania* new genus (Family Paucispiniferidae Muir-Wood & Cooper), Subfamily Lirariinae, based on *Liraria* Cooper & Grant, 1975 (Family Anidanthidae Waterhouse), Subfamily Muirwoodiinae, based on *Muirwoodia* (*Muirwoodia*) Licharew, 1947 (Family Yakovleviidae Waterhouse), Tribe Tapajosiini, based on *Tapajosia* new genus and Subfamily Globosoproductinae, based on *Globosoproductus* Litvinovich & Vorontsova, 1983 (Family Linoproductidae Stehli), Subfamily Gilmoriinae, based on *Gilmoria* new genus (Family Ovatiidae Lazarev), Subfamily Chhidrusiinae, based on *Chhidrusia* new genus (Family Schrenkiellidae Lazarev), Subfamily Marginiruginae, based on *Marginirugus* Sutton, 1938 (Family Gigantoproductidae Muir-Wood & Cooper), Subfamily Dawesioniinae new subfamily, based on *Dawesionia* new genus (?Family Proboscidellidae Muir-Wood & Cooper), Tribe Engellinini, based on *Engellinus* new genus, Subtribe Cancrinellinai, based on *Cancrinella* Fredericks, 1928 and Tribe Holotricharinini, based on *Holotricharina* Cooper & Grant, 1975 (Family Paucispinauriidae Waterhouse).

Superfamilies Productelloidea, Marginiferoidea, Horridonioidea and Productoidea are associated in Infrasuborder Productimorphi Gray. Family Devonoproductidae, Paucispiniferoidea, Linoproductoidea and Paucispiniferoidea are treated as Linoproductidina new suborder, and Aulostegoidea and Richthofenioidea grouped as Infrasuborder Aulostegimorphi Waterhouse, to express both origins and morphologies. Cooperinidae is elevated in standing to superfamily, and grouped with Strophalosioidea, Aulostegoidea and Scacchinelloidea in Suborder Strophalosiidina Waterhouse.

SOURCE OF NEW GENERA, SUBGENERA AND SPECIES, BY COUNTRY AND AGE

For page reference, see the index starting on p. 526.

Argentina

Permian: *Austroboreas, Taboadaia.*

Armenia

Permian: *Ciliciumia, Nempemarginifera.*

Australia

Devonian: *Costadonia, Dawesionia, Mckellarosia, Myrtlevalia, Plicosentosia, Praelaminatia, Proteusiella, Spinauricula, Spinellicosta.* Carboniferous: *Boggabria, Campbelliconcha, Costaglobus, Engasia, Eomarginia, Putapustula, Quospina, Rangaria, Retiarisia, Reticulumia, Robertsina, Waggononia.* Permian: *Anidanthia, Crassispinosella, Maxwellosia, Strophalosiaria.* New species: *Anidanthus perdosus.*

Belgium

Carboniferous: *Minisculinella, Sartenaeria.*

Bolivia

Permian: *Yacotania.*

Brazil

Permian: *Tapajosia.*

Canada

Devonian: *Costatonia, Nahannilusia.* Carboniferous: *Arcuatusia, Comagunia, Commarginalia, Costavonia, Disparatia, Fimbrinusia, Igniculus, Inflatusia, Nazeriproductus, Quadralosia, Ramaliconcha.* Permian: *Cameronovia, Dzhiremulia, Fimbrininia, Harkeria, Lineabispina, Lineacrassus, Patellamia, Praeschrenkiella.* New species are *Fimbrianalosia ettrainensis* Nazer & Waterhouse, *Horridonia grandis, Tubersulculus reidi, Tityrophoria zimmermani, Kochiproductus imperiosus, Reticulatia oldershawi, Patellamia sulcata, Praeschrenkiella costata, Calliprotonia mclareni,* and

Balkhasheconcha bamberi.

China

Permian: *Gadikao, Jinyugania, Liaozhuotingia.*

England

Carboniferous: *Globicorrugata.* Permian: *Calvadonia.*

Germany

Carboniferous: *Agirovia.*

Greenland

Permian: *Kochiproductus (Dunbarovia).*

India

Permian: *Fimbrinialosia, Geniculatusia.*

Ireland and Northern Ireland

Carboniferous: *Lineaproductus, Tortilisia.*

Irian Jaya, Indonesia

Permian: *Animia.*

Japan

Carboniferous: *Kwantovia, Yanagidania.*

Malaysia

Permian: *Masitoshia.*

Nepal

Permian: *Odonovania, Quasimingenewia.*

New Zealand

Permian: *Calandisa.*

Pakistan

Permian: *Chhidrusia, Lineatina, Septumusia.*

Russia

Devonian: *Nalivkininius.* Carboniferous: *Donakovia.* Permian: *Baikuralia, Repinia.* New species: *Costatumulus ganelini, Globicorrugata inflata.*

Scotland

Carboniferous: *Coronatonia.*

Thailand

Carboniferous: *Elucidatia, Yanagidania.* Permian: *Comumukia, Huiatakia, Koyaonoia, Opiparia, Piyasinia.*

United States

Carboniferous: *Fortispinalosia, Gilmoria, Parasentosia, Putusia, Sangredonia, Stainbrookia, Sutherlandika.* Permian: *Appelinaria, Bellaspinosina, Bilinospina, Cooperinoides, Glabauriella, Glabrispinus, Muirwoodia* (*Grandaurea*), *Grantevia, Minisaeptosa, Nasutusia, Rugania, Shumardoria, Sierradiabloa, Titanisia.* New species: *Glabrispina kingi.*

GENERA OF CHINA RETRIEVED FROM SYNONYMY

Various genera placed in synonymy by Brunton et al. (2000) appear to be valid. Most come from China, and include *Asioproductus* Zhan [Chan], *Calliomarginatia* Jin, *Chonostegoidella* Lin Yang, *Haydenoides* Chan, ?*Hubeiproductus* Yang De-li, *Kurtomarginifera* Xu, *Levisapicus* Tong, *Magniderbyia* Ting, *Neoedriosteges* Liang, *Neopugilis* Li, *Parabuxtonia* Yang & Zhang, *Paramuirwoodia* Zhang and *Truncatenia* Liao. These are discussed in the text and may be found by consulting the index.

APPENDIX C. GROUP IDENTIFICATION OF PRODUCTIDA THROUGH MORPHOLOGICAL ATTRIBUTES AND DERIVATION

Composite Key involving age, morphology and origins

SUPERORDER PRODUCTIFORMI

SHELLS CONCAVO-CONVEX OR PLANO-CONVEX AS A RULE. SPINOSE NORMALLY AT LEAST ALONG VENTRAL HINGE. SHELL PSEUDOPUNCTATE WITH TALEOLAE. NO VENTRAL PLATES. BRACHIA PTYCHOLOPHOUS OR SCHIZOLOPHOUS.

ORDER PRODUCTIDA

SHELLS SPINOSE NORMALLY AT LEAST OVER VENTRAL VALVE.

SUBORDER PRODUCTIDINA

INTERAREAS, TEETH AND SOCKETS LOST EARLY, BRACHIAL SHIELDS USUALLY REDUCED IN SIZE. EARLY STOCK WITHOUT UMBONAL CICATRIX. MEMBER SUPERFAMILIES INCLUDE OR DERIVED FROM PRODUCTELLOIDEA.

1. TRAIL INCONSPICUOUS. CARDINAL PROCESS BILOBED. DERIVED FROM SMOOTH CHONETID, AND THE ONLY SUPERFAMILY OF THE SUBORDER TO BE STROPHALOSIIFORM. AGE DEVONIAN................SUPERFAMILY PRODUCTELLOIDEA.

1A. Ornament principally of uniform spines over ventral valve only, without fine linear ribs over entire shell.............Family Productellidae.

1Aa. Ventral spines simple, may have dorsal spines, alveolus well developed......................Subfamily Productellinae.

1Aa1. Elongate spine bases or commarginal ridges, no ribs.............Tribe Productellini.

1Aa2. Ribs largely limited to trail of both valves, relict teeth and sockets...................Tribe Margaritiproductini. [Transition tribe to Lomatiphoridae].

1Ab. Ventral spine bases or ribs. Ventral myophragm as a rule, anderidia...................Subfamily Chattertoniinae.

1Ac. Well spaced ventral spines, no alveolus or anderidia........ Subfamily Helaspinae.

1Ac1. Ventral spines with or without prominent bases, dorsal valve with or without dorsal pits. Simple dorsal median septum ....Tribe Helaspini.

1Ac2. Comparatively smooth shells with fine erect spines, no dorsal pits, low lateral buttress plates.......... Tribe Ardviscini. [Transitional to Leioproductidae].

1Ad. Ventral spines, low ribs, low regular commarginal rugae..........Subfamily Dotswoodiinae.

1Ae. Ventral spines sturdy, low commarginal lamellae or rugae. Thick dorsal marginal ridge...............Subfamily Orbinariinae.

1B. Numerous and uniform fine spines over both valves................Family Caucasiproductidae.

.

INFRASUBORDER PRODUCTIMORPHI

NO INTERAREAS, NO TEETH, AS A RULE SMALL BRACHIAL SHIELDS. DERIVED FROM PRODUCTELLOIDEA.

2. SHELLS SMALL WITHOUT SPECIALIZED SPINES OR INTERNAL MARGINAL RIDGES. SPINES MAY HAVE ELONGATE BASES, RIBBING SUBDUED OR ABSENT, RUGATION FINE, FIRM OR ABSENT. TRAILS INCONSPICUOUS. CARDINAL PROCESS BIFID. DESCENDED FROM DOTSWOODINAE.. .... SUPERFAMILY OVERTONIOIDEA.

2A. Commarginal ornament may be well developed on both valves, radial ornament subdued or lacking. Spines on ventral or both valves, not specialized, subuniform, usually in quincunx.............Family Overtoniidae.

2Aa. Commarginal rows of strong ventral and usually dorsal spines, deep corpus cavity........Subfamily Overtoniinae.

2Ab. Commarginal ornament predominant..................Subfamily Plicatiferinae.

2Ab1. Hinge spines may be strong, no dorsal spines, ear baffles in dorsal valve.........Tribe Plicatiferini.

2Ab2. Low close-set commarginal rugae, dorsal spines............Tribe Absenticostini.

2Ab2. Deep corpus cavity, well spaced ventral spines, trail reflected as gutter..........Tribe Institiferini.

2Ab3. Low rugae and growth steps. Double dorsal septum, thick lateral buttress plates, marginal ridge ....Tribe Crossacanthiini.

2Ac. Long ventral spine bases over disc, fine commarginal wrinkles...........Subfamily Semiproductinae.

2Ac1. Deep corpus cavity, long trail, cleft posterior dorsal septum...........Tribe Semiproductini.

2Ac2. Shallow corpus cavity, short trail, no cleft in dorsal septum...........Tribe Rugaurini.

2Ad. Ventral spines prominent with elongate bases, dorsal spines often present. Subdued commarginal lamellae and subrugae. Dorsal septum may be subdivided into two............Subfamily Levipustulinae.

2Ad1. Lateral buttress plates ....Tribe Levipustulini.

2Ad2. No lateral buttress plates................Tribe Lanipustulini.

2B. Ornament dominated by spines and ribs. Body cavity moderate to deep ....Family Avoniidae.

2Ba. Ventral spines in weak commarginal rows, weak to moderately elongate bases or ribs, dorsal valve usually spinose, weak lamellae, alveolus..............Subfamily Avoniinae.

2Bb. Fine commarginal lamellae or rugae, costae on long trails, both valves spinose. No alveolus.............Subfamily Semicostellinae.

3. SMALL TO LARGE SHELLS, ERECT WELL SPACED AND OFTEN THICK SPINES IN YOUNGER GROUPS, LIMITED RADIAL ORNAMENT AND MODERATE IF ANY COMMARGINAL RUGAE. TRAIL MAY BE WELL DEVELOPED. DESCENDED FROM HELASPINAE...............SUPERFAMILY HORRIDONIOIDEA.

3A. Shells small to large, well spaced ventral spines, often including hinge and median row, dorsal spines few or absent. Cardinal process sessile, bilobed, each lobe notched on posterior face, adductors may become dendritic..............................Family Leioproductidae.

3Aa. Commarginal wrinkles low or absent. Shells small............Subfamily Leioproductinae.

3Aa1. Median ventral ridge with row of spines, no dorsal spines...........Tribe Leioproductini.

3Aa1a. Split dorsal median septum, lateral buttress plates............Subtribe Leioproductinai.

3Aa1b. Simple dorsal median septum, no lateral buttress plates.............Subtribe Costadoniinai.

3Aa2. No median ventral fold, dorsal spines rarely present. Lateral buttress plates where known.............Tribe Hunanoproductini.

3Ab. Commarginal wrinkles prominent, shells medium to large. Trail may be well developed. No lateral buttress plates. No dorsal spines..........Subfamily Levitusiinae.

3Ab1. Large shells, spine row on median ventral ridge............Tribe Levitusiini

3Ab2. Small, no median ventral ridge, spines few and well distributed...........Tribe Geniculiferini.

3Ab3. Medium to large, no ventral median ridge, spines numerous..................Tribe Araxilevini.

3B. Spines strong as a rule close to hinge, dorsal spines widely present, no prominent commarginal rugae or median ventral ridge. Trail may be well formed. Cardinal process large, trifid, median lobe deeply divided.........Family Horridoniidae.

3Ba. Spines strong along hinge of ventral and often dorsal valve, other spines well spaced, valve surface may be pustular and finely ribbed........ Subfamily Horridoniinae.

3Bb. Ventral and dorsal spines numerous, costae..........Subfamily Baillieninae.

3Bc. Dorsal spines strong along hinge and especially outer ears, no ventral hinge spines...........Subfamily Sowerbininae.

3Bc1. Second row of dorsal ear spines close in diameter to those of first row........ Tribe Sowerbinini.

3Bc2. Second row of dorsal ear spines much stronger than in first row.........Tribe Karnelliini.

4. SHELLS UP TO MEDIUM SIZE, SPINES AND TRAIL WELL DEVELOPED, MUSCLE SCARS USUALLY SMOOTH, INTERIOR WITH DORSAL AND OFTEN VENTRAL MARGINAL RIDGE AND "MARGINIFERIFORM" CARDINAL PROCESS. ZYGIDIUM COMMON. [DESCENDED FROM ORBINARIINAE?]...............SUPERFAMILY MARGINIFEROIDEA.

4A. Spines usually restricted to ventral valve. Ribs and commarginal rugae variably developed...............Family Marginiferidae.

4Aa. Shells variously ornamented, posterior ventral spine rows along hinge and / or umbonal slopes well formed............Subfamily Marginiferinae.

4Aa1. Shell smooth or with low to moderate radial and commarginal ornament..........Tribe Marginiferini.

4Aa2. Radial ribs strong on both valves.........Tribe Pseudoavoniini.

4Aa3. Closely spaced ribs and disc rugae prominent............Tribe Caucasoproductini.

4Ab. Ribs and commarginal rugae moderately developed, posterior rows of ventral spines, dorsal spines may be developed .... Subfamily Desmoinesiinae. [Note deviation].

4Ac. Ventral spines few, halteroid, umbonal slope or hinge row of spines not always well formed, shell may widen forwards...........Subfamily Scapharininae. [No well developed posterior ventral spine rows as a rule, so could be derived from Costispiniferidae or a separate family].

4B. Spines numerous on both valves, not forming prominent hinge or umbonal slope rows......Family Costispiniferidae.

4Ba. Spines crowded over both valves. Dorsal adductors normal, without bordering plates........Subfamily Costispiniferinae.

4Ba1. Strong spines. Ribs may be present.................Tribe Costispiniferini.

4Ba2. Spines very fine and numerous.....................Tribe Onopordumariini.

4Bb. Fine closely spaced spines and rugae over both valves. Marginal ridges especially well developed in dorsal valve, dorsal adductor scars bordered or divided by platelets..........Subfamily Spinomarginiferinae.

5. MEDIUM TO LARGE, TRAIL WELL DEVELOPED, SPINES FEW TO NUMEROUS AND MAY BE HALTEROID AND PROMINENT, RADIAL ORNAMENT WELL DEVELOPED, COMMARGINAL COSTATE ORNAMENT OF VARIABLE EXTENT, ADDUCTOR SCARS DENDRITIC. DESCENDED FROM PRODUCTELLINAE THROUGH LOMATIPHORIDAE...................SUPERFAMILY PRODUCTOIDEA.

Ventral spines may be in hinge row, well spaced over disc and trail, fine ribs, no dorsal spines. Alveolus or lateral buttress plates...................Family Lomatiphoridae.

5A. Radial ornament predominant, ventral spines only, diaphragm high..........Family Productidae.

5Aa. Spine rows near hinge, rare to moderate over disc..................Subfamily Productinae.

5Ab. Cluster of ventral spines on ears or lateral umbonal slopes, other ventral spines numerous to rare..................Subfamily Diaphragminae.

5B. Reticulate disc, spines in ventral hinge and umbonal slope rows as a rule, may have thick lateral or anterior spines, external dorsal pits common, no diaphragm........................Family Retariidae.

5Ba. Dorsal spines in many genera, marginal ridge usually high............Subfamily Retariinae.

5Ba1. Ears large, dorsal adductor platform not high and cup-like..........Tribe Retariini.

5Ba2. Shells and ears small, spines reduced, internal dorsal ridges not high across inner ears............ Tribe Protoniellini.

5Ba3. Spines in hinge row and comparable strength over disc, external ridge near base of ventral umbonal slopes, may have ear baffles...............Tribe Rigrantiini.

5Ba3a. Dorsal ears bordered anteriorly by groove. Dorsal pits............Subtribe Rigrantiinai.

5Ba3b. No bordering dorsal ear groove. Pits in some forms............Subtribe Antiquatoniinai.

5Ba4. Ears large. High dorsal internal ridges posteriorly, dorsal adductor platform may form elevated cup................Tribe Spyridophorini.

5Bb. Large as a rule, ears relatively small. Possibly no posterior central papillation [at maturity?]........................Subfamily Reticulatiinae.

5C. Often large, deep body corpus, costae prominent and may swell at base of each ventral disc spines. No internal posterior central papillation [at maturity?] as a rule ....Family Buxtoniidae.

5Ca. Spines on both valves as a rule, external dorsal pits ....Subfamily Buxtoniinae.

5Ca1. Ventral spines crowded on lateral umbonal slopes and inner to outer ears, swollen and/or weakly prolonged spine bases over ventral disc, numerous dorsal spines as a rule. Weak rugae............Tribe Buxtoniini.

5Ca2. Costae crossed by commarginal ribs, costae may anastomose anteriorly...........Tribe Spinifronsiini.

5Ca3. Numerous ventral spines, no dorsal spines, dorsal costae capillate............Tribe Dowhataniini.

5Cb. Ventral spines thin, bases little swollen or extended, may be crowded on ears or posteriorly, commarginal rugae may be weakly developed, dorsal spines may be present..............Subfamily Tolmatchoffiinae.

5Cc. No cluster of ventral ear spines, dorsal spines absent or rare...........Subfamily Marginatiinae.

5Cd. Spines in hinge and umbonal ear channel rows, dorsal valve without spines, dorsal costae capillate. Lateral buttress plates..............Subfamily Tyloplectinae.

5D. Often large, visceral disc reticulate, no umbonal slope row of ventral spines, spines without swollen bases, rare or missing from dorsal valve...............Family Dictyoclostidae.

5Da. Medium to large, reticulate ornament, dorsal pits variably present................Subfamily Dictyoclostinae.

5Da1. Spines as a rule clustered postero-laterally in small brush...........Tribe Dictyoclostini.

5Da2. Small, ornament moderately reticulate, hinge row of spines as a rule, few other spines...........Tribe Inflatiini.

5Da3. Dorsal ribs capillate...............Tribe Liraplectini.

5Da4. Hinge spines. Lateral buttress mounds or accessory plates in dorsal valve.................Tribe Reticulumiini.

5Db. Medium size, transverse, subdued reticulate ornament. Hinge row of ventral spines, other scattered spines..................Subfamily Spinarellinae.

5Cb1. Transverse, large ears. Hinge row and often additional outer ventral spines, no dorsal spines, visceral disc often thin, cardinal process often low.....................Tribe Spinarellini.

5Cb2 Well formed ventral hinge spines, may have dorsal spines, spines may be thick on trail.................Tribe Chaoiellini.

6. SPINES NUMEROUS, FINE, COVER BOTH VALVES, NEVER RHIZOID, STRUT OR STRONGLY HALTEROID, SPINE BASES LITTLE PROLONGED AS A RULE. NO RIBS. MARGINAL RIDGES USUALLY LOW. DESCENDED FROM CAUCASIPRODUCTIDAE (PRODUCTELLOIDEA)..........SUPERFAMILY ECHINOCONCHIOIDEA.

6A. Spines slender, recumbent, differing diameters in commarginal bands (= commargons), corpus cavity generally deep, adductor scars dendritic as a rule...........Family Echinoconchidae.

6Aa. Medium to large with commargons, spines usually differentiated in diameter over each commargon.........Subfamily Echinoconchinae.

6Aa1. Medium to large with step-like commargons ....Tribe Echinoconchini.

6Aa2. High relief commargon bands, symmetrical in profile, separated by wide smooth bands.............Tribe Karavankinini.

6Ab. Commarginal bands confined to anterior shell of both valves, ventral spine bases weakly prolonged. Dorsal septum often split...............Subfamily Juresaniinae.

6Ab1. Quincunxial elongate pustules and spine bases posteriorly, anterior commarginal bands poorly differentiated...............Tribe Juresaniini.

6Ab2. Anterior commarginal bands well differentiated.................Tribe Bathymyoniini.

6Ac. Commargons limited to anterior ventral valve, dorsal ornament of uniform spines........Subfamily Septariniinae.

6Ac1. Long median ventral septum............Tribe Septariniini.

6Ac2. No ventral septum........... Tribe Alatoproductini.

6B. Spines typically fine and numerous, largely uniform on both valves, corpus cavity slender, adductor scars usually not dendritic, cardinal process bifid............Family Sentosiidae.

6Ba. Spines thin, typically numerous, may have weakly elongate bases. ....Subfamily Sentosiinae.

6Bb. Elongate crowded spine bases like ribs on both valves................Subfamily Bagrasiinae.

6Bc. Spines uniformly fine and in quincunx over ventral valve, bases short to slightly elongate, dorsal spines numerous. Entire dorsal septum............... Subfamily Tubersulculinae.

6Bc1. Spines fine and crowded, high posterior lateral ridge..............Tribe Tubersulculini.

6Bc2. Spines moderately strong over both valves..............Tribe Lethamiini.

6Bd. Spines fine, separated by smooth commarginal bands, thin corpus cavity..........Subfamily Stictozosterinae.

6C. Spines subuniform over shell or in wide bands, dense and uniform on dorsal valve. Adductor scars normally dendritic............Family Waagenoconchidae.

6Ca. Spines closely spaced and uniform in extensive bands.............Subfamily Waagenoconchinae.

6Ca1. Dorsal disc weakly concave and trail geniculate...............Tribe Waagenoconchini.

6Ca2. Dorsal valve flat or gently concave, no distinct dorsal trail..............Tribe Wimanoconchini.

6Db. Spines subuniform and arranged in weakly commarginal rows..............Subfamily Pustulinae.

SUBORDER STROPHALOSIIDINA

MAJOR SUPERFAMILY STROPHALOSIOIDEA WITH CICATRIX AND INTERAREAS, TEETH, SOCKETS, LARGE BRACHIAL SHIELDS, DESCENDENT GROUPS LOSING AT LEAST SOME STROPHALOSIIFORM ACOUTREMENTS. NOT DESCENDED FROM PRODUCTELLOIDEA.

7. CICATRIX NORMALLY PRESENT. INTERAREAS, TEETH & SOCKETS, LARGE BRACHIAL SHIELDS. TRAIL MAY BE WELL DEVELOPED, OR DORSAL VALVE WEDGE-SHAPED, SPINES OFTEN MODERATELY DIFFERENTIATED. PSEUDODELTIDIUM. .... SUPERFAMILY STROPHALOSIOIDEA.

7A. Dorsal valve without spines as a rule..........................Family Strophalosiidae.

7Aa. Ventral spines only as a rule. Cardinal process usually trilobed..............Subfamily Strophalosiinae.

7Aa1. Ventral spines uniform or of two orders, or rarely, not developed. Dorsal valve smooth or capillate and/or dimpled..............Tribe Strophalosiini.

7Aa2. Strong radial ribs on both valves. Dorsal spines exceptionally developed...........Tribe Truncateniini.

7Ab. Ventral spines moderately stout and subuniform, usually includes sturdy hinge row. Cardinal process bilobed...........Subfamily Donalosiinae.

7B. Dorsal spines usually developed.................Family Dasyalosiidae.

7Ba. Crowded spines of two orders on each valve. Dorsal valve usually flat. Cardinal process trilobed as a rule............Subfamily Dasyalosiinae.

7Bb. Subuniform numerous spines over both valves. Bifid cardinal process.............Subfamily Eostrophalosiinae.

7Bc. Spines usually of one or two series on ventral valve, one series on dorsal valve. Cardinal process trilobed................Subfamily Echinalosiinae. [Several descendent variations].

7Bc1. Dorsal valve thin and with trail. Spines in two series over ventral valve ....Tribe Echinalosiini.

7Bc2. Ventral spines fine, numerous. Dorsal valve somewhat thickened, fine spines........................... Tribe Marginalosiini. [Derived from Echinalosiini with change to prime attributes].

7Bc3. Dorsal valve thickened in wedge. Coarse and rare fine ventral spines, fine dorsal spines..........................Tribe Wyndhamiini.

7Bd. Ventral spines subuniform, dense, dorsal valve flat-disced, usually wedge-shaped.....................Subfamily Arcticalosiinae.

7Bd1. Ventral spines uniform or subuniform in density. Dorsal spines..........Tribe Arcticalosiini.

7Bd2. No dorsal spines..........Tribe Biplatyconchini. [Note deviation from family definition, evolution proceeding erratically, but the tribe derived from echinalosiin stock].

7C. Fine radial and/or fine to strong commarginal ornament. Bifid cardinal process................Family Chonopectidae.

7Ca. Fine radial ornament. Prominent ventral hinge spine row..............Subfamily Chonopectinae.

7Ca2. No strong commarginal rugae.....................Tribe Chonopectini.

7Ca2. Strong commarginal rugae.............Tribe Semenewiini.

7Cb. Spines well ordered especially on ventral valve, may be rare or missing from dorsal valve. Hinge spines not strong. Fine commarginal rugae ....Subfamily Quadratiinae.

7Cc. Spines fine, fewer or missing from dorsal valve. Both valves finely rugose...........Subfamily Rhytialosiinae.

7D. Short to long lateral buttress plates. Cardinal process bilobed..............Family Araksalosiidae.

7Da. Dense spines on ventral or both valves, weak or strong ventral hinge spines, elongate ventral spine bases............Subfamily Araksalosiinae.

7Db. Dense spines on ventral or both valves, strong hinge spines, ventral spine bases long or valves ribbed..............Subfamily Whidbornellinae.

7Dc. Strong ventral hinge spines, further ventral spines erect and in quincunx, dorsal spines rare or absent, no radial ornament............Subfamily Acanthatiinae.

7E. Dorsal ornament predominantly lamellate, often capillate. Cardinal process trilobed.........Family Ctenalosiidae.

7Ea. Ventral spines, no dorsal spines.................Subfamily Ctenalosiinae.

7Eb. Spines on both valves, usually diverse ....Subfamily Bruntonariinae.

7Ec. No spines on either valve..............Subfamily Mingenewiinae.

7Ed. Ventral spines rhizoid, dorsal spines present or absent..............Subfamily Craspedalosiinae.

8. LATERAL BUTTRESS PLATES IN DORSAL VALVE. OTHERWISE SHELL VARIABLE IN SHAPE, VENTRAL VALVE MAY BE HIGH AND CONICAL, AND DORSAL VALVE CAP-LIKE, OR SHELL CONCAVO-CONVEX OR PLANO-CONVEX. VENTRAL SPINES MAY HAVE SHORT ELONGATE BASES, DORSAL SPINES USUALLY PRESENT. NO TEETH. VENTRAL MEDIUM SEPTUM MAY BE VERY HIGH. DESCENDED FROM ARAKSALOSIIDAE........................SUPERFAMILY SCACCHINELLOIDEA.

8A. Ventral valve may be high and conical, dorsal valve cap-like. High ventral medium septum, bilobed cardinal process.............Family Scacchinellidae.

8B. Medium size, concavo-convex. Cardinal process bifid or quadrilobed, median ventral septum rarely well formed.............Family Rhamnariidae.

8Ba. Size medium, often with cicatrix and with trail, ventral interarea as a rule, spines erect or suberect, less commonly elongate bases.............Subfamily Rhamnariinae.

8Bb. Moderately large, spines erect or often with elongate bases. No cicatrix, no interarea as a rule, low or no trail................Subfamily Balkhasheconchinae.

8Bc. Small shells, cicatrix usually present, low trail, elongate spine bases or ribs, closely spaced dorsal septa like modified lateral buttress plates...................Subfamily Septasteginae.

8C. Concavo-convex shells with or without ventral interarea, cicatrix common with supporting spines. Low if any dorsal trail. High ventral medium septum. High bilobed cardinal process.............Family Tschernyschewiidae.

9. VENTRAL VALVE ATTACHED AND COMPARATIVELY HIGH. NO HINGE TEETH. BRACHIAL APPARATUS SPECIALIZED. DESCENDED FROM DASYALOSIIDAE................SUPERFAMILY COOPERINOIDEA.

9A. Large umbonal cicatrix, both valves may be spinose, elongate to bilobed outline, ptycholophous or schizolophous brachidia..............Family Cooperinidae.

9Aa. Cicatrix surrounded by rhizoid spines, both valves may be spinose, brachidia as simple large schizolophes................Subfamily Cooperininae.

9Ab. Few ventral spines, no dorsal spines. Multilobed ptycholophous brachidia...............Subfamily Falaferinae.

9Ac. Spines only around cicatrix, present or absent from dorsal valve. Narrow with small interarea. Longitudinally oblique multilobed brachidia..............Subfamily Epiceliinae.

INFRASUBORDER AULOSTEGIMORPHI

VARIED ORNAMENT, MAY RETAIN CICATRIX AND INTERAREAS. DERIVED FROM STROPHALOSIOIDEA.

10. SHELLS HIGHLY VARIED IN ORNAMENT, TRAILS AND SHAPE, OFTEN WITH INTERAREAS AND IN SOME, A SCAR OF ATTACHMENT. NO TEETH. CARDINAL PROCESS BILOBATE IN EARLY GENERA, LARGE, TRIFID OR QUADRILOBED AS A RULE. BRACHIAL SHIELDS SMALL. DESCENDED FROM RHYTIALOSIINAE ....SUPERFAMILY AULOSTEGOIDEA.

10A. Spines varied on both valves, may be rhizoid, erect or prostrate, moderately high ventral interarea...............Family Aulostegidae.

10Aa. Medium-sized to large shells, dense spines on both valves. Buttress plates developed as a rule......Subfamily Aulosteginae.

10Aa1. Medium-sized shells with dense often rhizoid spines on both valves...........Tribe Aulostegini.

10Aa2. Large shells, spines subprostrate with elongate bases over both valves.........Tribe Taeniothaerini.

10Aa3. Medium to large shells with erect spines over both valves.........Tribe Megastegini.

10Ab. Ventral spines varied, may be rhizoid, dorsal spines often absent, marginal ridges may be high, no buttress plates...............Subfamily Echinosteginae.

10Ab1. Medium to large subquadrate genera, well developed postero-lateral rhizoid spines as a rule, light or no radials, strong dorsal marginal ridge..............Tribe Echinostegini.

10Ab2. Triangular shells, large ears, commarginal ornament, ear baffles.............Tribe Agelesiini.

10B. Corpus ornamented by ribs and/or commarginal rugae, ventral posterior spines usually prominent, no dorsal spines...................Family Institellidae.

10Ba. Trails ribbed, may have bordering gutters or flanges.................Subfamily Institellinae.

10Ba1. Corpus reticulate, bordering structures present or absent.............Tribe Institellini.

10Ba1a. Bordering structure.............Subtribe Institellinai.

10Ba1b. No bordering structure...........Subtribe Sinuatellinai.

10Ba2. Commarginal wrinkles prominent, hinge spines usually well developed.........................Tribe Institinini.

10Bb. Small, ribbed, complex spinose corpus margins, strong geniculation. May have buttress plates.................Subfamily Chonosteginae.

10Bc. Elongate trigonal shells with fine ribs, limited commarginal ornament, no burst of postero-lateral spines ....Subfamily Gondolininae.

10Bc1. Narrow interarea, rhizoid spines on ventral umbonal margins...........Tribe Gondolinini.

10Bc2. Ovally triangular shells with high interareas, fine ventral spines.........Tribe Sphenostegini.

10C. Transverse with thin corpus, distinctive ornament of monticules, ventral spines only.........Family Monticuliferidae.

10Ca. Capillae developed on both valves.........Subfamily Monticuliferinae.

10Cb. Capillae lacking, monticules present or possibly absent.............Subfamily Tongluellinae.

11. VENTRAL VALVE CONICAL OR SPHEROIDAL, ATTACHED TO SUBSTRATE BY CEMENTATION OR SPINES, DORSAL VALVE CAP-LIKE. DESCENDED FROM AULOSTEGOIDEA.............SUPERFAMILY RICHTHOFENIOIDEA.

11A. Ventral myocoelidium...........Family Richthofeniidae.

11B. High blade-like ventral septum............Family Hercosiidae.

11C. Spines rhizoid or may be absent. Ventral muscle callosity..........Family Teguliferinidae.

11Ca. Shells obliquely conical or sphenoid, spines rhizoid, no coscinidium...........Subfamily Teguliferininae.

11Cb. Shells conical with coscinidium or rim of protective spines............Subfamily Cyclacanthariinae.

11Cb1. Rhizoid supporting spines...........Tribe Cyclacanthariini.

11Cb2. No supporting rhizoid spines..............Tribe Collumatini.

11Cc. Conical shells with no external or apertural spines, no coscinidium...........Subfamily Zalverinae.

11D. Conical with high ventral interarea, spines few or absent, ventral myocoelidium.............Family Gemmellaroiidae.

SUBORDER OLDHAMINIDINA (= LYTTONIIDINA)

ENLARGED FEEDING APPARATUS, SPINES LOST AS A RULE. DESCENDED FROM STROPHALOSIIDINA.

12. DORSAL VALVE REDUCED TO A LOBATE BRACHIAL PLATE, LARGE AND ELABORATE FEEDING APPARATUS. VENTRAL VALVE CONVEX WITH POSTERIOR FLAP OF SHELL AND VALLUM. NO SPINES. NO TEETH................SUPERFAMILY LYTTONIOIDEA.

12A. Vallum lobate, dorsal brachial plate with variable number of lobes and septa................Family Lyttoniidae.

12Aa. Shells basically symmetrical, though individually irregular through growth habit......................Subfamily Lyttoniinae.

12Ab. Asymmetry indicated by diductor scar persistently longer on right side, cardinal process deformed, dorsal valve deeply slit medianly................Subfamily Poikilosakinae.

12B. Transversely oval small shells, cup-like ventral valve with longer medio-anterior section, basically symmetrical, flap-like holdfast. Brachial arms extend obliquely forward..............Family Rigbyellidae.

13. ELONGATELY OVAL OR BILOBATE SHELLS, SIMPLE LARGE FEEDING APPARATUS..................SUPERFAMILY LOCZYELLOIDEA.

13A. Shovel-shaped to triangular, may have ventral sulcus, dorsal fold, ornament of growth-lines, no tubercles.............Family Loczyellidae.

15Aa. Ventral valve with vallum. No ears................Subfamily Loczyellinae.

15Ab. Ventral valve with septa. Ears................Subfamily Caninellinae.

15Ac. Ventral valve with reduced vallum, no ears, teeth, no ventral septa............Subfamily Litocothiinae.

13B. Elongately bilobate, two lateral and medium septa in at least some genera, ornament of tubercles, teeth, vallum present. Shell pseudopunctate or perforate............Family Permianellidae.

SUBORDER LINOPRODUCTIDINA

SHELL CLOSELY RIBBED, MINOR OR NO UMBONAL CICATRIX. INCLUDES OR DERIVED FROM STROPHALOSIIFORM DEVONOPRODUCTIDAE, DESCENDED IN TURN FROM RIBBED CHONETID AND NOT THROUGH PRODUCTELLOIDEA OR STROPHALOSIOIDEA.

14. Strophalosiiform, normally without cicatrix. Ornament of ribs as well as spines...............Family Devonoproductidae.

14a. Ventral spines erect. Dorsal valve with commarginal laminae...................... Subfamily Devonoproductinae.

14b. Ventral spines erect, both valves ribbed.....................Subfamily Eoproductellinae.

14c. Ventral disc spines with elongate bases, both valves ribbed.................. Subfamily Plicoproductinae.

15. VARIOUSLY CHARACTERIZED, SOME SHELLS WITH STRUT SPINES AND DISTINCTIVE ORNAMENT, WELL DEVELOPED TRAIL. ADDUCTOR SCARS TEND TO BE SMOOTH. UNITED BY DEVELOPMENT AND DIVERSIFICATION FROM COMMON ANCESTOR DEVONOPRODUCTINAE.........................SUPERFAMILY PAUCISPINIFEROIDEA.

15A. Usually with a few ventral strut spines, no dorsal spines...........Family Paucispiniferidae.

15Aa. Shells with six or more ventral strut spines..........Subfamily Paucispiniferinae.

> 15Aa1. Transverse, varied radial and commarginal ornament, six strut spines, simple trail.........Tribe Paucispiniferini.
>
> 15Aa2. Subquadrate, small ears, mutiple dorsal trails as a rule..............Tribe Probolioniini.
>
> > 15Aa2a. Strut spines symmetrically distributed..................Subtribe Probolioniinai.
> >
> > 15Aa2b. Strut spines across anterior ventral valve............Subtribe Kozlowskiinai.
>
> 15Aa3. Visceral disc strongly reticulate............... Tribe Retimarginiferini.

15Ab. Ribs on ventral valve and more faintly on dorsal valve, which bears prominent lamellae. Spines few, may include three or more strut spines............ Subfamily Productininae.

15Ac. Transverse with nasute anterior, dorsal valve not lamellate, three or more ventral strut spines......... Subfamily Bibatiolinae.

15Ad. Transverse and often nasute anterior, dorsal valve not lamellate, spines may be limited to hinge, no strut spines.................Subfamily Chonetellinae.

> 15Ad1. No dorsal spines............Tribe Chonetellini.
>
> 15Ad2. Dorsal spines............Tribe Odonovaniini.

15B. Costellate, ventral spines not specialized, dorsal spines rarely present, adductors smooth.....Family Anidanthidae.

15.Ba. Both valves ribbed, dorsal valve lamellate, usually without spines, ventral spines along hinge and over disc and trail ....Subfamily Anidanthinae.

15Bb. Both valves ribbed, no dorsal lamellae................Subfamily Larariinae.

15Bc. Costae strong and branching................Subfamily Lamiproductinae.

15C. Transverse with wide hinge, finely ribbed, strut spines in a number of genera, no multiple trails, low to well formed marginal ridges................Family Yakovleviidae.

15Ca. No strut spines...................Subfamily Yakovleviinae.

15Cb. A few strut spines, thick internal marginal ridge...............Subfamily Paramarginiferinae.

15Cc. Regularly arranged strut spines, no high marginal ridge..............Subfamily Muirwoodiinae.

16. RIBS OVER BOTH VALVES, SPINES NORMALLY LIMITED TO VENTRAL VALVE, FINE TO HALTEROID, ERECT OR WITH PROLONGED BASES, NEVER STRUT-LIKE, NEVER EXTENDED FORWARD IN SHELL FROM BASE. TRAIL OFTEN GENICULATE. ADDUCTOR SCARS DENDRITIC OR STRIATE. DESCENDED FROM EOPRODUCTELLINAE.................SUPERFAMILY LINOPRODUCTOIDEA.

16A. Ribs distinct, spines with erect bases. Moderate to thick body corpus. Cardinal process normally trilobed, outer lobes not fused externally..................Family Linoproductidae.

16Aa. Spines in one or two rows along hinge, at least some body spines of comparable and often greater diameter .... Subfamily Linoproductinae.

16Aa1. Cardinal process often bent ventrally..............Tribe Linoproductini.

16Aa2. One to three rows of hinge spines, body spines much thicker...........Tribe Linipalini.

16Aa3. Hinge with one or two rows of thin or moderately thick spines. Dorsal interior with lateral buttress plates..............................Tribe Tapajosiini.

16Ab. Fine ventral hinge spines, coarse erect body spines. No lateral buttress plates, no brachial cones...............Subfamily Globosoproductinae. [Relationship requires further study].

16Ac. Ventral ears bear two or three or more rows of spines or clusters. Body spines close in diameter..........Subfamily Linispininae.

16Ad. Ventral hinge spines in one or few rows, body spines rare or absent, corpus moderate in thickness..............Subfamily Coopericinae.

16B. Medium to small shells with fine ribs; spines ventral, numerous to few along hinge, rare over rest of valve. Cardinal process with outer lobes fused externally..............Family Ovatiidae.

16Ba. Narrow high vaulted shells, incurved ventral umbo, spines often numerous along hinge, may form ventral median row............Subfamily Ovatiinae.

16Bb. Transverse, wide hinge, few spines along hinge................Subfamily Gilmoriinae.

16C. Large, disc thin, ventral spines often limited to row or rows along hinge.............Family Schrenkiellinae.

16Ca. Trail curves in plane of disc, not perceptible externally.................Subfamily Schrenkiellinae.

16Cb. Trail long and geniculate......................Subfamily Chhidrusiinae.

16D. Elongate shells with narrow to wide hinge, may be asymmetric in shape from nestling habit, cardinal process with single myophore lobe................Family Striatiferidae.

16Da. Large and irregular in shape, dorsal spines in one genus............Subfamily Striatiferinae.

16Db. Small shells with well developed commarginal wrinkles.............Subfamily Compressoproductinae.

16E. Large with wide hinge and often brachial cones. Dorsal spines in some genera..............Family Gigantoproductidae.

16Ea. Lateral buttress plates usually well developed, brachial cones normally present..........Subfamily Gigantoproductinae.

16Eb. Large, posteriorly prolonged ventral spine bases, cardinal process bifid or trifid, lateral buttress plates, no brachial cones.............Subfamily Semiplaniinae [Relationship requires further study].

16Ec. Shells productiform, some posteriorly elongate ventral spine bases, lateral buttress plates and anderidia, no brachial cones...................Subfamily Marginiruginae. [Relationship requires further study; aff. Semiplaninae?].

16Ed. Medium size, slender posteriorly elongate ventral spine bases, no tunnels. No lateral buttress plates or brachial cones......................Subfamily Wardlawriinae.[aff. Semiplaninae?].

16Ee Elongate ventral spine bases, bilobed cardinal process, no lateral buttress plates, brachial cones..................Subfamily Kansuellinae. [Relationship requires further study].

17. VENTRAL SPINES HAVE POSTERIORLY PROLONGED BASES, AND OFTEN FORWARD PROLONGED TUNNELS. USUALLY SMALL OR MEDIUM IN SIZE. DESCENDED FROM PLICOPRODUCTINAE.............SUPERFAMILY PROBOSCIDELLOIDEA.

17A. Low regular rugae. Cardinal process bifid..................Family Proboscidellidae.

17Aa. Long ventral trail, reduced dorsal valve, dorsal adductor scars dendritic..........Subfamily Proboscidellinae.

167Ab. Regular fine commarginal rugae, moderately long ventral trail...............Subfamily Undariinae. [Possibly related *Donakovia* has impressed striate ventral adductor platform].

17Ac. Strong commarginal rugae.......... Subfamily Fluctuariinae.

17Ad. Fine weak rugae or growth-lines, strong branching costae, inconspicuous trail..............Subfamily Dawesioniinae. [Relationships require further evaluation].

17B. Small to medium in size, dorsal spines often present, may be differentiated, body corpus usually thick, cardinal process trifid or modified, muscle scars dendritic..............Family Paucispinauriidae.

17Ba. Commarginal rugae subdued or absent. Dorsal spines common.............Subfamily Paucispinauriinae.

17Ca1. Spines subuniform over ventral disc, costate as a rule.............Tribe Paucispinauriini.

17Ca2. Spines of two series over ventral disc, no ventral ribs, fine rugae, cardinal process trifid, median lobe narrow and high..............Tribe Holotricharinini. [Affinities uncertain].

17Bb. Commarginal rugae strong. Dorsal spines present or absent, body corpus usually slender...............Subfamily Magniplicatininae.

17Bb1. Spines along hinge, numerous over ventral disc..........Tribe Magniplicatinini.

17Bb1a. Spines in ventral hinge rows. Disc and trail rugose.............Subtribe Magniplicatininai.

17Bb1b. Spines clustered over ventral ears, medium ventral disc without rugae................ Subtribe Cancrinellinai.

17Bb2. Slender body corpus, fine ribs, fine ventral spines usually numerous near hinge, dorsal spines rarely present, low regular or no rugae, cardinal process bifid or trifid.............Tribe Engellinini.

17Bc. Small compact shells without dorsal spines, weak wrinkles, cardinal process trifid............Subfamily Coolkilellinae.

17C. Body corpus usually thin, dorsal spines rarely present, ventral muscle field striate until late in ontogeny and set into in posterior wall, cardinal process trifid..............Family Auriculispinidae.

17Ca. Ventral spines only, spines in row or rows or crowded close to hinge, low commarginal rugae, dorsal septum normally double................Subfamily Auriculispininae.

17Cb. Medium in size and transverse as a rule, prominent row of ventral hinge spines, some genera with dorsal spines, body corpus thin...............Subfamily Lyoniinae.

17Cc. Flat disc, geniculate trail, subrectangular in shape with hinge spines, may have dorsal spines, double dorsal septum.............Subfamily Filiconchinae.

17Cd. Elongate shells with narrow hinge, rhizoid ventral spines, marginal structures in both valves............Subfamily Siphonosiinae.

17D. Row of spines along base of umbonal slopes. No outer ear spines, may have dorsal spines............Family Stepanoviellidae.

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