SOME NEW SUBFAMILIES, GENERA

AND SPECIES OF

SUBORDER PRODUCTIDINA

(BRACHIOPODA)

By

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With 4 text-figures and 1 table

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Abstract

New brachiopod genera are proposed as *Quenstedtenia*, type species *Q. rugosa* n. sp. and *Villiconcha*, type species *Waagenoconcha magnifica* Cooper & Grant, 1975 (Echinoconchoidea), *Haereospina*, type species *Linoproductus undatus* Cooper & Grant, 1975, *Diadematia*, type species *Productus nodosus* Newberry, 1861, *Wardlawria*, type species *Productus missouriensis* Sayre, 1930, *Auriculatea*, type species *Linoproductus nasutus* King, 1931, *Xanthoserella*, type species *L. devargasi* Sutherland & Harlow, 1973, *Meniscuria*, type species *Linoproductus meniscus* Dunbar & Condra, 1932, and *Plicatomedium*, type species *L. oklahomae* Dunbar & Condra, 1932 (Linoproductoidea). A new Pennsylvanian subfamily Wardlawriinae based on *Wardlawria* is proposed within Linoproductidae, and new subfamily Plicoproductinae, based on *Plicoproductus* Ljaschenko, 1969, for a small mid-Devonian group within Kansuellidae, both significant for the history and development of the superfamily Linoproductoidea. New species *Quenstedtenia rugosa* is described from Timor, and *Asperulus yanagidai* is described from Thailand. Phylogenetic methodology, classification and relationships of some productidin subfamilies and families are discussed, involving Coopericinae Lazarev, Labaellidae Kotlyar et al., Licharewiconchidae Kotlyar et al., Marginovatiini Chen et al. and Schrenkiellidae Lazarev.

Key words: Brachiopoda, Productidina, new genera, classification.

New taxa: Subfamilies: Plicoproductinae, Wardlawriinae; new genera: *Auriculatea, Diadematia, Haereospina, Meniscuria, Plicatomedium, Quenstedtenia, Villiproductus, Wardlawria, Xanthoserella*; new species: *Asperulus yanagidai, Quenstedtenia rugosa*.

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INTRODUCTION

Some new subfamilies, genera and species are proposed for Late Paleozoic brachiopods belonging to the suborder Productidina. The classification largely follows that outlined by Waterhouse (2002), in which the development and interrelations are traced for each superfamily. As well, some Russian and other studies on new productidin families and groups of lesser rank are discussed in the framework of overall classification for the suborder. Particular attention is paid to recent studies on Linoproductoidea by Lazarev (2003, 2004). In 2003, he argued that further discrimination of genera was not necessary for phylogenetic interpretation, but in 2004 he added an important new genus, and in this study, special attention is paid to new genera which affect tribal and subfamilial boundaries and content. The repository for type material is mostly at the United States National Museum of Natural History, Smithsonian Institution, Washington DC, United States, where specimens are registered serially by number and with letter, prefixed by USNM. Other repositories are mentioned in the text.

THE DEVELOPMENT OF PRODUCTIDINA

Productidina are brachiopods distinguished at subordinal level as concavo-convex or planoconvex articulate shells as a rule attached by spines and for some by cicatrix, with diverse usually schizolophous or simple ptycholophous lophophore apparatus. Five separate superfamilies have been distinguished, commencing in the Devonian, and lasting mostly to the end of the Permian Period. These are recognised by a fusion of discriminants, centred on ornament which is diverse, elaborate, and variable, with several major kinds of spines and several types of radial ribs and concentric rugosities, as well as taking into account various kinds of internal features, and overall shape. Each of the superfamilies has a distinctive ornament, and although objections may be raised against what appears to be "superficial and external", it has been established that internal features are also consistently different, though to lesser degree. The exterior is more significant than in many brachiopod orders, because the spines evolved to make up a substantial proportion of individual biomass by Permian time, and involved attachment of the shell, in turn affecting or reflecting habitat, life position and feeding, mantle development and ontogeny. At family and generic level, differences in detail are substantial, and possible permutations are numerous; the history for Productidina is mostly one of sustained diversification virtually to the end of the Paleozoic Era, with few instances of convergence between superfamilies and rare even within subfamilies.

Nor did shell shape and architecture remain static. Size fluctuated, the dorsal valve changed between concave, convexo-concave, or planar, the ventral valve varied in convexity and sulcation or plication, and body thickness varied, in some cases to family or subfamily level as stressed by Brunton et al. (2000). Size of ears changed, repeatedly,

clearly affecting life position with attendant consequences, often concomitant with change in spine development. The trail as well varied from simple to complex, and consistently so within groups united by ornament. Genera united by type of ornament may be subdivided into smaller clusters often at tribal or subtribal level according to shape, or what G. A. Cooper used to call "build".

The interior of the shell was more conservative. The nature of muscle impressions, cardinal process and supports, and presence of additional septa varied, and was largely constant at what is deemed to be tribal, subfamilial or higher level; even aspects of the brachial shields, marginal ridges and internal pustulation and pitting may be consistent with type of ornament.

Adult morphology does not provide the only source for analysis. Shell structure is not widely known, and needs to be studied at a level summarized in Afanasieva (2002) rather than the generalist level offered in the revised brachiopod Treatise. The ontogeny for some of the genera provides indications of critical differences, at generic or no more than tribal level and also overall similarities at much higher levels (Waterhouse 1964). In addition, for adequate phylogenetic analysis, age must be under reasonable control, and paleoenvironment, paleogeography and biomal and community affiliation should at least be understood, as providing background that may or may not be significant, and therefore, in any objective study, essential for assessment. Many additional parameters available for living brachiopods are either not available, or have not been studied adequately, and cannot be weighed. But huge potential lies in the prospect of studies of the brachiopod genome, centring at least initially on the mitochondrial genome mtDNA.

Classification and phylogenesis have to be isometric and comprehensive. Any attempt to trace a phylogeny on the basis of only some of the genera is doomed to partiality and incompleteness, and to bias in selection of criteria. Any classification that ignores evolution through time is also ill-based. In modern times three all-embracing endeavours have been made. The first, by Muir-Wood & Cooper (1960), provided the initial and prime basis for substantial advance. Concentrating - as is reasonable - on type species of genera, Muir-Wood & Cooper (1960) provided fine illustrations and excellent but in places flawed descriptions, with an overall resultant classification. Building on that study, with much more data provided on early Productidina from McKellar (1970) and Lazarev (1987), Brunton et al. (2000)* adjusted the classification and gave short diagnoses and figures. Their work was of uneven value, because it included forced synonymies, omitted genera, provided inaccurate historical summaries, and sometimes disregarded rules of zoological nomenclature by incorrectly asserting priority for a study by Lazarev (1986). That study made proposals invalidated by the failure to provide definitions and comparisons (contrast ICZN 2000, article 13.1, p. 17).

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*See Appendix, p. 43

Nonetheless their work provided an excellent springboard for further refinement (Waterhouse 2001, 2002), by encouraging a fresh overview and giving references to a number of otherwise little known Chinese works. My own interest in the group commenced in the 1950's, and survey of literature seems to have been more extensive than in Brunton et al. (2000). The most obvious shortcoming in previous studies has been the inattention to Gondwana fossils, both in literature, and especially collections in museums, geological surveys and universities. Since 1954, I have been visiting and working in museums around the globe, failing however to cover adequately the collections of China, which were only briefly visited at Beijing and Nanjing. Literature provides an invaluable lead to brachiopod genera, but being able to examine specimens, figured and unfigured, is little short of indispensable, unless figures are of very high quality. On the basis of such studies, it was possible to foreshadow a classification in Waterhouse (1978) that is largely endorsed, not contradicted, by the data rather than the conclusions in Brunton et al. (2000). The classification is based on phylogenetic studies, and mutiple alternatives, as a paleontologically applicable version building on Hennigian principles, extended with time control. The summary provided by Waterhouse (2002) is readily useable and checkable through its index and diagnoses, by consulting the illustrations provided by Muir-Wood & Cooper (1960) and Brunton et al. (2000), or accessing substantial collections or library resources. At least the framework is established, and can be explored and tested. What needs to be avoided is the tendency for some systematists to offer excuses for failing to assess objectively what has been proposed.

The greatest need now is to present evolutionary charts and illustrations, a matter that requires time and resources. Some will urge the provision of cladistic analysis. These are discredited in some circles, but the exercise might be worth undertaking, if only to verify or falsify the claim that cladistics are necessary. Such a survey must be comprehensive, to assure objectivity, because the presentation of partial surveys may quicken the process, but distorts the analysis and cannot be free of the possibility of subjectivity. Complete cladistic analysis will be a formidable task. The revised brachiopod Treatise and Muir-Wood & Cooper (1960) are not always accurate enough for providing prime data. As well, initial proposals and diagnoses and figures need to be reinforced from subsequent studies - the tendency to rely on only the initial diagnosis and far too often, only the illustrations, with no attention even to the diagnosis or textual description, is one of the weaknesses in the revised brachiopod Treatise. The Treatise provides an overall survey of proposals in the literature, often with little if any revision of actual material , and too often on the basis of inadequate assessment. Thus the original material needs to be re-inspected, and the original and subsequent literature rechecked rather than rely on the revised brachiopod Treatise as sole guide.

SYSTEMATIC DESCRIPTIONS

Order Productida Sarytcheva & Sokolskaya, 1959
Suborder Productidina Waagen, 1883
Superfamily **PRODUCTOIDEA** Gray, 1840

[nom. transl. Mailleux 1941, p. 7 ex Productidae Gray, 1840, p. 151].

Diagnosis: Ventral spines few to numerous, halteroid and may be fine over ventral valve, may be clustered laterally, numerous over dorsal valve or absent. Radial ornament prominent, concentric ornament varied, shells small to large in size, simple to moderately elaborate trails. Corpus cavity shallow to deep, muscle scars generally dendritic, marginal ridges moderate to high.

Family **PRODUCTIDAE** Gray, 1840

[Productidae Gray, 1840, p. 151].

Diagnosis: Radial ornament predominant, dorsal marginal ridges or diaphragm high and slender.

Subfamily **PRODUCTINAE** Gray, 1840

[nom. transl. Brunton et al. 1995, p. 928 ex Productidae Gray, 1840, p. 151].

Diagnosis: Radial ornament, concentric ornament may be present, weak and over ventral valve posteriorly and laterally, ventral spines only, diaphragm and trails well developed.

Discussion: Related subfamilies Retariinae Muir-Wood & Cooper and Spyridiophorinae Muir-Wood & Cooper have somewhat stronger radials and differ in other aspects. Lazarev (2000) has pointed to evidence that, he considered, indicated Yakovleviinae Waterhouse, 1975 should be transferred from Linoproductidae to Productidae.

Tribe **DIAPHRAGMINI** Waterhouse, 2002

[Diaphragmini Waterhouse 2002, p. 20. Syn. Marginovatiini Chen, Tazawa & Shi, 2004, p. 447].

Diagnosis: Distinguished from Productini by having an open to dense cluster of spines on ventral ears or lateral umbonal slopes, other ventral spines numerous to rare. Weak concentric rugae may be developed, especially posteriorly.

Discussion: This tribe was recognised as closely allied to Productini, and including the genera *Diaphragmus* Girty, *Carlinia* Gordon, *Companteris* Lazarev, *Dowhatania* Waterhouse and *Lopasnia* Ilkhovsky. To this list should be added *Marginovatia* Gordon & Henry.

Marginovatiini is believed to be a synonym. It was proposed by Chen, Tazawa & Shi

in Chen et al. (2004, pp. 447, 448) for distinct genera cast as Linoproductinae that differed from genera placed in tribes Linoproductini and Stepanoviellini through possessing marginal ridges. No further analysis was provided. It seems that *Marginovatia* from which the tribe was named was assessed as linoproductoid simply by accepting previous work. The type species of *Marginovatia* is *Productus ovatus* var. *minor* Snider, 1915, p. 79 of mid-Visean to Bashkirian age. It has a high slender marginal ridge around the entire disc, an apomorphy unknown amongst Linoproductoidea, and particularly characteristic of Productidae. The radial ornament and spine details resemble those of Productidae, and show rather less approach in spine detail to members of Linoproductidae of similar age. Furthermore, *Marginovatia* has fine close-set concentric wrinkles over the posterior ventral valve, much as in genera within Productidae, and not particularly close to Carboniferous members of Linoproductidae. Assessing what is known of *Marginovatia*, as closely described by Gordon & Henry (1990, p. 533), the genus is judged to belong to Productinae, which is consistent with age range. From known characters, the genus belongs to Diaphragmini, as a rather small form, with high slender marginal ridges, and ventral spines in two rows with some additional spines over the ears. There may be found differences from Diaphragmini, but none appear to have been adduced so far.

Chen et al. (2004, p. 447) commented that "We consider that the subfamily and higher level classification is closer to the true phylogenetic relationships amongst various groups of linoproductids than the current classifications (Brunton et al. 2000, Waterhouse 2001). These schemes should be tested by phylogenetic analysis". The authors did not explain what they meant by phylogenetic analysis, or what was so wrong about the "current classification" in Brunton et al. or Waterhouse. Nor did they publish anything to show what they were pleased to call "true phylogenetic relationships", so how they knew about true phylogeny is less than clear. Moreover the assertion about any need to test classification by phylogenetic analysis, as if that had not already been done, must be queried. It is clear from a comprehensive reading of Brunton et al., and in particular the various studies by Dr C. H. C. Brunton with colleagues, and by Dr S. S. Lazarev (referred to later in this text), that those authors were careful to trace the beginnings and some developmental aspects of phylogenetic proliferation within Productidina, with time control and attention to morphological development and change. Similarly the Waterhouse studies (2001, 2002) were conducted in a framework of time control and close attention to chronological sequence, apomorphies, and noting of larger scale diversification and potential for reversification and Lazarusification. It would seem impossible for either of those two sets of authors to achieve wide-ranging classification without attention to phylogenetic analysis. Chen et al. (2004) referred to quantitative analysis, and such were certainly conducted. Possibly they meant to refer to the desirability of cladistic analysis. This approach is very simplistic, and it is not difficult to run a 10-20 character-based test for several genera, but I would not publish such a crude methology. The flaws in the procedure are obvious,

because no account can be taken of time control, homeomorphies, regressive and progressive evolution, bundling and parallelisms. Apomorphisms cannot be weighted, and gaps in analysis arise from incompletely known genera. Williams, Carlson & Brunton (1997) relied on cladistic analysis in brachiopod macro-classification, and were severely criticized by Afanasieva (2002), who briefly pointed out how the clade-based classification disagreed with various other lines of evidence. Most tellingly, interpretation of the cladistic analysis disagreed strongly with the brachiopod genome study by Cohen & Gawthrop (1997). Afanasieva (2002) concluded that cladistic analysis is "rejected as a method of systematics by most leading theorists of systematics and phylogeny".

Family **DICTYOCLOSTIDAE** Stehli, 1954

[nom. transl. Waterhouse 1978, p. 20 ex Dictyoclostinae Stehli, 1954, p. 316].

Diagnosis: Large shells with generally wide hinge and well formed ears, may have ginglymus, costae on both valves, as a rule reticulated by concentric growth rugae over disc, spines only on ventral valve, may be large and halteroid. Inner posterior hinge ridge well developed as a rule, marginal ridges low and broad, trails long, simple, may be mutiple.

Discussion: This family appears to have evolved from Productidae in the Early Carboniferous. Two subfamilies are recognized, Dictyoclostinae Muir-Wood & Cooper with a dense brush of posterior lateral ventral spines, and Callytharrellinae Waterhouse without the brush.

Subfamily **DICTYOCLOSTINAE** Stehli, 1954

[Subfamily Dictyoclostinae Stehli, 1954, p. 316].

Diagnosis: Dictyoclostid shells with posterior lateral cluster of spines, spines developed in row close to hinge or close to umbonal slopes of ventral valve, rare to numerous over rest of ventral valve.

Discussion: This subfamily is now subdivided into three tribes, Dictyoclostini Stehli and possibly Reticulariini Lazarev (2000), with an additional tribe, Labaellini.

Tribe **LABAELLINI** Kotlyar, Zakharov & Polubotko, 2004

[nom. transl. hic ex Labaellidae Kotlyar, Zakharov & Polubotko, 2004, p. 517].

Diagnosis: Large transverse shells with large ears and fine reticulate ornament. Hinge row of ventral spines, also ear spines and rare body spines.

Discussion: Labaellidae was proposed by Kotlyar et al. (2004) for a family with only one genus, *Labaella* Kotlyar, Zakharov & Polubotko, 2004, p. 517, for which the type species is *Productus (Productus) bajarunassi* Licharew (1936, p. 111, pl. 1, fig. 1-6) from Late Permian of the northwest Caucasus Mountains. It is of large size, with transverse shape, wide ears and finely reticulate ornament. Ventral spines are arrayed in a row close to the hinge and in groups over the ears and rare over the rest of the valve. There is a strong dorsal inner hinge ridge, low dorsal median septum, and dendritic muscle scars.

No comparisons with other families were provided by Kotlyar et al. 2004, and the superfamilial relationships not indicated. Such "failure to differentiate the taxon" does not conform with the requirements for valid zoological nomenclature (ICZN 2000, article 13.1, p. 17, article 13.2, p. 18). In my opinion, the genus *Labaella* is dictycloclostid, and it is distinguished primarily by the fineness of the concentric and radial ornament. It has large ears as especially exhibited by members of the dictyoclostid tribe Spinarellini Waterhouse, 2002, which are medium-sized to large shells with large ears and subdued or fine reticulate ornament. This tribe was recognized for several genera from the Permian of United States, involving *Spinarella* Cooper & Grant, *Nudauris* Stehli, *Rugatia* Muir-Wood & Cooper and *Xestosia* Cooper & Grant. Several of these genera were referred by Brunton et al. (2000) to Paucispiniferini but they lack the marginal ridges and strong strut spines found in members of this and allied tribes. Spinarellini are close to members of Callytharrellini Waterhouse, but have weaker or finer reticulate ornament, and slightly larger ears and weaker marginal ridge.

Although not fully clear from the description and figures provided by Kotlyar et al. (2004), there are several spines in front of the hinge row on the ears, which indicates an approach to Dictyoclostinae, and this subfamily includes shells with comparatively fine reticulate ornament, although most are less transverse, and have smaller ears.

Superfamily **ECHINOCONCHOIDEA** Stehli, 1954

[nom. transl. Lazarev 1990, p.109 ex Echinoconchidae Stehli, 1954, p. 326].

Diagnosis: Spines over both valves numerous and fine, uniform or varied in diameter, commonly in concentric bands, no strongly halteroid or strut spines, no radial ribbing. Maximum width generally in front of hinge, posterior dorsal septum may be cleft or paralleled by buttress plates, dendritic adductors, modest development of marginal ridges, dorsal internal pustules seldom very large, crowded anteriorly.

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

[nom. transl. Waterhouse 1978, p. 21 ex Waagenoconchinae Muir-Wood & Cooper, 1960, p. 252].

Diagnosis: Spines may vary in size, subuniform over different parts of shell, not associated in numerous repeated concentric bands of spines with differing diameters, dense and as a rule uniform on dorsal valve.

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

[Waagenoconchinae Muir-Wood & Cooper, 1960, p. 252].

Diagnosis: Spines fine, may change gradually or abruptly in diameter and nature of bases in few usually broad bands.

Discussion: Grant (1966, text-fig. 1) has shown that the ventral spines in

Waagenoconcha abichi (Waagen) bend sharply within the shell to enter the interior in front of the spine base. How widespread this phenomenon is remains unknown.

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

[nom. transl. Brunton et al. 1995, p. 929 ex Waagenoconchinae Muir-Wood & Cooper, 1960, p. 252].

Diagnosis: Interior without buttress supports.

Discussion: The allied tribe Balkasheconchini Waterhouse, 2002, p. 25 has buttress supports.

Genus *Wimanoconcha* Waterhouse, 1983a

Type species: *Productus (Ruthenia) wimani* Fredericks, 1934, p. 28.

Diagnosis: Large shells with convex sulcate ventral valve, high lateral ventral walls, may have anterior radial folds, dorsal valve with median fold, develops planiculate trail and heavily thickened disc late in ontogeny. Ventral spine bases somewhat variable, generally subelongate and often stout posteriorly, bases broad or widening forward and varied over mid-length, scattered erect spines over postero-lateral slopes, near mid-length along sulcus or in band or bands across shell, and over anterior shell, dorsal spines erect where known. Concentric growth steps and wrinkles subdued, anteriorly placed.

Discussion: Archbold (1993) stressed the presence of the radial folds in treating *Wimanoconcha* as a subgenus of *Waagenoconcha*, and referred to Kalashnikov (1986, pl. 121, fig. 7b) in observing that the dorsal valve may develop weak crenulations at the anterior margin, and become thickened anteriorly and internally in the region of the visceral disc. The acknowledgement of thickened dorsal valve conforms with and confirms the diagnosis for *Wimanoconcha* adduced by Waterhouse (1983a), notwithstanding the claim that the initial diagnosis had to be rejected. It needs to be restressed that the course of ontogenetic development in Productida may provide a valuable tool for assessing relationships, and that gerontic development often displays significant differences between genera which differ little from each other in their early growth phases (Waterhouse 1959, 1964, p. 40). The distinguishing features of *Wimanoconcha* as regards the dorsal valve when compared with that of *Waagenoconcha* are clearest at late stages of growth, an approach validated but not newly found in subsequent study. Brunton et al. (2000) referred to Archbold (1993) in claiming that *Wimanoconcha* was inseparable from *Waagenoconcha*, or, more accurately, their mis-spelled subgenus *Waagenoconcha* (*Waagenochocha*), but that view was not expressed by Archbold.

Archbold (1993) considered that *Waagenoconcha imperfecta* Prendergast, 1935, 1943 from the Wuchiapingian Hardman Member of the Canning Basin, Western Australia, belonged to *Wimanoconcha*. He did not accept the claim, as in Coleman (1957, p. 82), that the Basleo specimens referred to *Productus waageni* Rothpletz (1892) by Broili (1916,

pl. 118, fig. 1-5) were conspecific. Archbold (1993) also acceptably pointed out that specimens from New Zealand which had been tentatively deemed to be close to *imperfecta* by Waterhouse (1982) were not well enough preserved to secure identification. Specimens of *imperfecta* figured by Coleman (1957), Skwarko (1993) and Archbold (1993, text-fig. 11A-H, 12A-K, 13A-G) show spines as in type *Wimanoconcha*, with elongate and also rounded bases over the ventral valve, and erect spines over the dorsal valve. Concentric wrinkles and growth steps may appear anteriorly, and the gerontic dorsal valve shows distinct thickening.

Gruntoconcha Angiolini, 1995, text-fig. 16.6 from the Karakorum, type species *G. macrotuberculata* Angiolini, has not been extensively figured, but has characteristic strong and elongate ventral spine-bases, and so may be treated as a full genus, subject to the need for complete description of the ornament of mature ventral and dorsal valves: without that information, the taxon remains poorly circumscribed. Brunton et al. (2000, p. 517) followed Angiolini (1995) in classing the form as a subgenus of *Waagenoconcha*, together with "*Waagenochocha* Chao". This latter name appears to be a lapse, as no such name has ever been formally proposed for any brachiopod. And anyway, the subgeneric name should surely have been the same as the generic name. These authors included *abichi* Waagen as an ally of *Gruntoconcha.* The types, as figured by Waagen (1884, pl. 74, fig. 1-7) from the Cephalopod bed of the Chhidru Formation (or Wargal Formation?), Salt Range, Pakistan, show elongate spine bases over the first formed part of the ventral valve, surrounded by a broad band of erect spines, much like the ornament of small specimens of *Waagenoconcha humboldti* (D'Orbigny), the type species of *Waagenoconcha*. Similar ornament was also figured by Grant (1966, see pl. 131, fig. 2b, c, 3a) for well preserved *W. abichi* from the Salt Range.

<p style="text-align:center">Genus Quenstedtenia n. gen.</p>

Derivation: Named for F. A. Quenstedt.

Type species: *Quenstedtenia rugosa* n. sp., here designated.

Diagnosis: Medium-large shells with ventral sulcus and low dorsal fold, incurved ventral umbo, and obtuse cardinal extremities without ears. Both valves covered by low concentric wrinkles and growth steps or cinctures. Ventral spine bases over most of valve elongate and moderately dense to well spaced, erect spines limited to lateral posterior slopes, and to short anterior bands or single rows in mature specimens. Dorsal spine bases erect around posterior lateral margins, elongate over middle and anterior shell.

Resemblances: This genus is distinguished by the presence of close-set concentric rugae and steps over both valves, more regular and better defined than in other waagenoconchiform genera. In addition elongate spine bases are developed over most of the ventral valve, with erect spines limited to posterior lateral slopes and a few narrow anterior rows. Dorsal spine bases are elongate, except postero-laterally. The appearance

thus comes closest to *Wimanoconcha*, but the ventral valve in this form has more erect spines medially, and its dorsal valve is covered by erect spines, as far as known, whereas the present genus has mostly elongate dorsal spine bases. Of other genera, the closest is *Waagenoconcha* Chao, and this has bands of erect spines at mid-length and anteriorly, as well as broad bands with elongate spine bases, and erect dorsal spines, with few irregular concentric rugae or growth-steps. Ventral spine bases of *Quenstedtenia* are not as coarse as those of *Gruntoconcha* Angiolini, lack the strong erect lateral ventral spines and wide ears of *Fostericoncha* Waterhouse, and lack the many fine erect spines posteriorly in *Contraspina* Waterhouse. *Villiconcha* n. gen. has only erect spines over the entire ventral and dorsal valve. None of these genera shows comparable concentric ornament or elongate spine bases over the dorsal valve.

Quenstedtenia rugosa n. sp.

1892 *Productus abichi* not Waagen Rothpletz, p. 76, pl. 10, fig. 20.

1916 *P. waageni* not Rothpletz Broili, p. 14, pl. 118 (4), fig. 1-5.

1928 *P. purdoni* not Davidson Hamlet, p. 23, pl. 4, fig. 1, pl. 5, fig. 1.

1978 *"Productus" waageni*. Waterhouse, pl. 2, fig. 2, 3.

?1989 *Waagenoconcha waageni*. Archbold & Bird, p. 108, text-fig. 3.C-D.

Derivation: ruga - fold, Lat.

Holotype: Specimen figured by Broili (1916, pl. 118 (4), fig. 2) and refigured with dorsal view by Waterhouse (1978, pl. 2, fig. 2, 3), from Basleo, Timor, here designated. Kept at Geologisch-paläontologisches Institut und Museum, Bonn.

Diagnosis: Medium-large shells with comparatively wide hinge and deep ventral sulcus, anterior dorsal fold, close-set concentric rugae over both valves, most ventral and dorsal spines with elongate bases.

Description: Ventral spine bases are elongate and sessile over most of the valve, and vary in length from 3.7mm to 0.6 mm. They become fine and erect anteriorly in a very few rows, as in the holotype and the specimen figured by Hamlet (1928, pl. 4, fig. 1a). Fine erect spines are also developed postero-laterally. Elongate bases also cover much of the dorsal valve, but spines are erect postero-laterally, as is also illustrated by Hamlet (1928, pl. 5, fig. 1a) and possibly indicated at the anterior by Rothpletz (1892, pl. 10, fig. 20). Concentric wrinkles are close-set, even over the umbonal region, for both valves, at an estimated 7 in 5mm over the ventral umbo of the holotype, and 4 in the next 5mm, compared with 2 or so in 5mm near the anterior margin, and 3 in 5mm at the anterior margin.

Resemblances: Rothpletz (1892, pl. 10, fig. 20, a, b) figured a specimen from Ajer Mati, Timor, as *Productus abichi* that displays concentric rugae and close-set spines with mostly elongate bases and anterior sulcus: the presence of a dorsal fold is not clear. Hamlet (1928) referred large specimens from Basleo, Timor, to *Productus* (now *Contraspina*) *purdoni* Davidson, and there is some similarity to Davidson's species, but

unlike the Hamlet material, *purdoni* is more elongate with sharply defined dorsal fold and narrower hinge, and less prominent concentric rugae, and differs in its ventral spines. The Hamlet specimens are likely to be fully mature, and belong to *rugosa*. Moderately large ventral valves from the Maubisse Formation near Kasliu village, west Timor, were described as *waageni* by Archbold & Bird (1989). Ventral spine bases are elongate and moderately well spaced, and wrinkles are less conspicuous than in type *rugosa*.

Productus waageni Rothpletz (1892, pl. 10, fig. 19, a, b) from Ajer Mati, Timor, is close to this species in shape and size and has close-set elongate spine bases or sessile spines. But the Rothpletz species differs from the new species in having an inconspicuous if any ventral sulcus and low median fold, and in lacking concentric rugae, whereas *Quenstedtenia rugosa* has moderate to deep sulcus, and strong concentric rugae. The Basleo specimen figured by Hamlet (1928, pl. 4, fig. 3) as *Productus humboldti* not D'Orbigny was compared to *Waagenoconcha waageni* by Archbold & Bird (1989, p. 108). Hamlet's specimen has only shallow ventral sulcus, and was figured as showing a low ventral interarea of strophalosioid appearance: it is not waagenoconchid. This has been verified from examination of Hamlet's material at the Geologisch Instituut, Amsterdam and Mineralogisch-Geologisch Museum, Technische Hogeschool, Delft. There are some well preserved specimens, such as one labelled L8505, and the specimens are little inflated, with ventral sulcus, dorsal fold, umbonal cicatrix, small nepionic bulge, and many fine dense dorsal spines. In some but not all respects Hamlet's material approaches *Productus waageni* of Rothpletz, for which the hinge area is damaged and obscure.

Bathymyonia or allied genus is represented at Aitali, Timor, by a specimen figured as *Productus punctatus* not Martin by Hamlet (1928, pl. 4, fig. 2). It shows fine erect spines, followed by slightly thicker subsessile spines in bands. In the species *rugosa*, ventral spines are aligned along concentric rows, with elongate bases, and spines are in a strong quincunxial pattern, but they are of much the same thickness throughout, without regular well defined bands of narrow and thick spines.

<div align="center">Genus Villiconcha n. gen.</div>

Derivation: villus - tuft of wool, concha - bivalve, shell, Lat.

Type species: *Waagenoconcha magnifica* Cooper & Grant, 1975, p. 1044, here designated.

Diagnosis: Large shells characterized by fine dense spines on both valves, without prolonged bases, hinge at maximum width with obtuse cardinal extremities, ears not extended, shallow sulcus and low fold as a rule, dorsal hinge ridge well developed and median septum long.

Discussion: This genus is close to *Waagenoconcha* in most respects, and distinguished by its uniformly fine spines over the ventral valve, without the extended spine bases that are seen over the umbonal and parts of the anterior shell in

Waagenoconcha. Contraspina Waterhouse, type species *Productus purdoni* Davidson, is also close, but its fine spines over the umbonal portion are succeeded by spines with prolonged bases anteriorly. *Wimanoconcha* is larger with more elongate and stouter spine bases as well as fine erect spines and thick dorsal valve and anterior radial rugae, and *Fostericoncha* has sturdy erect ventral spines laterally, many spines with elongate bases, and large ears.

The type species of *Villiconcha*, *Waagenoconcha magnifica* Cooper & Grant (1975, p. 1044, pl. 354, fig. 1-15, pl. 355, fig. 18-24, pl. 356, fig. 7-16) comes from the China Tank, Willis Ranch and Appel Ranch Members, as well as an intervening lens in the Glass Mountains of Texas. The designated holotype is USNM 149676a (Cooper & Grant 1975, pl. 355, fig. 18-21) from the Willis Ranch Member, and its dorsal hinge shows well formed pits. Other species described from the Glass Mountains include *W. platys* Cooper & Grant and *W. convexa* Cooper & Grant from the Road Canyon Formation, so that the genus is found in faunas of Guadalupian age. *W. prophetica* Cooper & Grant from the much older Graham Formation is typical *Waagenoconcha*, and *W. sulcata* Cooper & Grant from the Hueco Formation needs closer examination of its ornament.

Superfamily **AULOSTEGOIDEA** Muir-Wood & Cooper, 1960

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

Discussion: This superfamily is regarded as belonging to Productidina, following Briggs (1998) and Waterhouse (1983b).

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

[nom. transl. Waterhouse 2002, p. 29 ex Echinosteginae Muir-Wood & Cooper, 1960, p. 101].

Diagnosis: Characterized by lack of dorsal spines, ventral spines may be rhizoid, marginal ridges may be high.

Discussion: This family includes a wide range of morphotypes.

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

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

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

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

[nom. transl. Waterhouse 2002, 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, as per Brunton et al. 2000, p. 599. Syn. Licharewiconchidae Kotlyar, Zakharov & Polubotko, 2004, p. 517].

Diagnosis: Ornament elaborate and varied, reticulate as a rule, interarea low. No skirt.

Discussion: Genera within this subfamily are of characteristic appearance, with reticulate ornament, low interareas, and ventral spines, generally including a row along the hinge. It was suggested by Waterhouse (2002, p. 30) that Institellini Muir-Wood & Cooper, 1960 could be distinguished from Sinuatellini Muir-Wood & Cooper, 1960 by the presence of a skirt in the former, and lack of skirt in the latter, but Brunton et al. (2000) made no such distinction.

Kotlyar et al. (2004, p. 517) proposed a new family Licharewiconchidae based on their new genus *Licharewiconcha*, named for *Productus (Sinuatella) subsinuatus* Licharew (1936, p. 116, pl. 1, fig. 7-15). The new family was said to involve "strongly geniculate productaceans (sic) having long curving rhizoid spines, ventral interarea with open delthyrium, closely spaced dictyoclostid reticulate sculpture" and costellae increasing by repeated branching. No comparisons were offered with *Sinuatella, Institella* or allies, and evidently the family was regarded as productoid rather than aulostegoid. But the ornament, which includes rhizoid spines, trail, interarea and other aspects, are aulostegoid. The nature of the ornament and the number of ventral ear spines suggest a close approach to several members within Institellini, but no skirt was reported, suggesting, if correct, that the genus may be placed within Sinuatellini Muir-Wood & Cooper (1960, p. 123).

The Middle Permian genus *Glyptosteges* Cooper & Grant was regarded by Waterhouse (2002) as youngest member of the tribe, but *Licharewiconcha* is latest Permian in age.

Superfamily **LINOPRODUCTOIDEA** Stehli, 1954 (Table 1, p. 26)
[nom. transl. Waterhouse 1978, p. 20 ex Linoproductinae Stehli, 1954, p. 319].

Diagnosis: Ribbing regular and generally fine over both valves. Spines over much of ventral valve, may be dense over ears, often evenly and well spaced over disc and trail, where of moderate and subequal diameter, dorsal spines restricted to some genera and groups, concentric rugae present to varying degree, trail simple. Adductor scars smooth, striate or dendritic, marginal ridges subdued, dorsal pustules varied but numerous.

Discussion: Linoproductoidea are characterized by fine radial ribbing on both valves, and spines that are neither as fine or as numerous as in some other superfamilies, or as a rule include massive strut spines. Brunton et al. (2000) assigned linoproductoid genera to two families, Linoproductidae and Monticuliferidae, whereas Lazarev (2003) recognized additional families as Schrenkiellidae and Fluctuariidae. Lazarev (1990, 2003, 2004) has provided provocative analyses of the evolution within the group, and his 2003 article assessed the Brunton et al. (2000) scheme as "phylogenetically unacceptable", an expression much more dismissive than the revision by Waterhouse (2001, 2002). Lazarev (2003) regarded the emphasis by Brunton et al. (2000) on depth of body cavity, presence

of dorsal spines, and features of dorsal interior, especially cardinal process, as misplaced, and limited more to genera rather than higher categories, which agrees to some extent with Waterhouse (2001, 2002).

The Lazarev classification

According to Lazarev (2003), four families could be recognized amongst Carboniferous Linoproductoidea. Linoproductidae were to be characterized by shells with ventral spines thicker anteriorly than posteriorly, and the presence of more ribs behind the ventral trail spines than in front. For Monticuliferidae, ribs were said to be the same in front of and behind the ventral trail spines. Schrenkiellidae was deemed to show similar spine-rib relations, and to have posterior ventral spines thicker than anterior spines. Fluctuariidae was characterized by strong concentric rugae. All families were described as "new" in the abstract, but all family groups had been previously named, Linoproductidae and Monticuliferidae having been treated as families since Muir-Wood & Cooper (1960). Monticuliferidae, Fluctuariidae and Schrenkiellidae were considered by Lazarev (2003) to be closely related, Monticuliferidae commencing in Devonian, and the other two, together with Linoproductidae, starting in Early Carboniferous. Development and variation in morphology were recognized, and no enumeration of constituent genera was undertaken. Although supposedly examining Carboniferous Linoproductoidea, the articles omitted any reference to Anidanthinae, Auriculispininae and Paucispinauriinae, which appeared no later than upper Pennsylvanian.

Two morphological aspects were emphasized as critical apomorphies. One matter concerned the number of ribs behind a ventral trail spine as compared with the number in front of the base. For three of the families, spine-rib relationships were conservative, with ribs not affected by ventral trail spines. This, according to Lazarev (2003), reflected the derivation from Devonian Linoproductoidea, specifically the Early Devonian genus *Eoproductella*, in which the spine bases are thicker than the radial ribs, but have no affect on the linearity or continuity of radial ribs. Another phylogenetic consideration was the development of spines in a row along the hinge, said to be reminiscent of Chonetidina, from which Productidina had evolved.

This classification, presented only in outline and with narrow focus on some Russian and North American genera, appears difficult to defend. No matter what the speculations were over phylogenetic significance of costae and spine relations and hinge spines, the morphological observations were not always accurate, or applicable to his recognized families; nor can family members be consistently distinguished by those particular features. In addition, the ranking of families seems to have been justified on the basis of apomorphies or morphological space between entities that were never assessed either in their entirety, or in relation to the other numerous - and neglected - groups within Linoproductoidea. The

considerations of the range of linoproductoid genera are in fact so narrow, that when the superfamily is looked at in comprehensive overview, some of the "families" shrink to being no more than tribes or subfamilies.

Monticuliferidae

Monticuliferidae, in spite of the Lazarev analysis, must remain based on the very unusual genus *Monticulifera*. Much of the ventral valve of *Monticulifera* has characteristic spinose monticules, and ribs may be of the same number fore and aft, or more numerous behind the monticule, or more numerous in front of the monticule. This is illustrated best by Muir-Wood & Cooper (1960, pl. 125, fig. 6-12, 14) for the type species, as in Brunton et al. (2000, text-fig. 374.2c). Anteriorly, in Muir-Wood & Cooper (1960, pl. 125, fig. 6), small spines without elongate bases lie athwart single ribs. Monticuliferidae should be treated as an unusual family for a few genera, just as in Waterhouse (2001, 2002), or possibly as an offshoot from Linoproductidae, although the ventral muscle field differs from that of Linoproductidae. *Monticulifera* itself was ignored by Lazarev (2003). He relied on analysis of much older shells misidentified as *Ovatia*, but there is little evidence to show phylogenetic connection.

Schrenkiellidae and Linoproductidae

 Genera of Linoproductidae were regarded as differing through their development on the ventral valve of one or two hinge spine rows, spines thicker anteriorly than along the hinge, and with ribs more numerous behind trail spines than in front. Schrenkiellidae was treated by Lazarev (2003) as a significant group, characterized by spines distinctly more developed along the ventral hinge than over the trail, by the flatter disc, maximum width at the hinge, and tendency toward a rounded-triangular outline. If these parameters were to be accepted as diagnostic for Schrenkiellidae, then few genera would belong, even fewer than the handful acknowleged by Brunton et al. (2000) and Waterhouse (2002). Moreover, *Schrenkiella* itself may not have spines over the visceral disc or ventral trail, which is hardly conducive to analysing hinge-disc-trail spine comparisons, or rib-spine relationships. Later Lazarev (2004) proffered an expanded list of possibly related genera, thereby changing the family parameters, though that was not admitted. He included, with a query, *Bandoproductus* Jin & Sun, *Cimmeriella* Archbold & Hogeboom, *Dictyoclostoidea* Jin & Hu, and *Permundaria* Nakamura, Kato & Choi, and expressed no doubt about the relationship with *Lyonia* Archbold and *Striatospica* Waterhouse. Some of these genera have wide flat disc and strong row of hinge spines, and *Cimmeriella* has a swollen disc. *Coopericus* was placed in an allied subfamily.

Considerable emphasis was placed on the row of hinge spines: these were supposed to reflect a reversion to chonetiform ancestry, and because of this assertion, Lazarev claimed that he was using truely phylogenetic procedure, unlike any other worker. The assertion is commendable for its lateral thinking, but less than proven, though there is obviously some similarity, probably at least as a matter of function for some genera. The

hinge row of spines in Linoproductoidea - and indeed widely through Productidina - generally emerges in front of the cardinal margin, and never exhibits a sharp angulation, whereas chonetid spines are generally angled within the shell, and emerge at the junction between interarea and outer shell. They are never found as a double row in chonetiform genera, and do not bend inwards to form a clasping ring. Lazarev regarded the ventral hinge row in Linoproductidae as being essentially different from that of Schrenkiellidae, because the spines were less thick than anterior spines, and because two rows rather than one row appeared in some species of *Linoproductus*. However a close ally of *Linoproductus*, described below as *Haereospina*, has thick posterior spines, and *Striatospica,* a supposed schrenkiellid, has slightly disarrayed ventral hinge spines, relict from two or three rows. This is also true of *Nambuccalinus*, a close ally of *Lyonia*.

Emphasis on thick posterior spines alone, and disregard for the other diagnostic criteria, would allow incorporation into Schrenkiellidae of various otherwise dissimilar linoproductoid genera, such as *Grandaurispina* Cooper & Grant, because this and other genera share the posterior row or rows of large ventral hinge spines which are broader than anterior spines. But such genera differ from *Schrenkiella* and *Striatospica* in shape and internal detail and various other aspects of ornament, including spines. Since various productidin genera developed at various times a hinge row of strong ventral spines, as for example in Horridoniini, Brunton et al. (2000) and Waterhouse (2002) treated the development as of no more than tribal, and often of only generic significance, and that treatment appears to be strongly defensible.

As well, the flatness of disc emphasized by Lazarev (2003) for Schrenkiellidae is repeated in other strands of Linoproductoidea. For example, genera within Lyoniini Waterhouse, 2001 have strong hinge spines and broad visceral disc, but differ substantially from *Schrenkiella* and allies in the nature of spine bases, and in tending to have more ribs behind the trail spines than in front, and in the ornament of ribs which swell and pinch, rather than remain simple, parallel-sided and linear. Lazarev (2004) included some of these lyoniin genera in his expanded Schrenkiellidae, and omitted others such as *Nambdoania* and *Nambuccalinus*. Genera within Lyoniini are very close in most respects, other than in width and thin disc, to members of Auriculispininae Waterhouse, 1986 and Paucispinauriinae Waterhouse, 1986 (syn. Grandaurispininae Lazarev, 1990), which have precedence over Schrenkiellidae Lazarev, 1990. *Lyonia* and *Bandoproductus*, like other members of the tribe, differ from *Schrenkiella* in shape, disc thickness, number of hinge rows and nature of costation (some have more ribs behind the body and trail spines), nature and definition of costae, spine bases and auriculation.

So what are true and restricted Schrenkiellidae? To judge from genera listed by Lazarev (2003, 2004), there seems to be only one close ally of *Schrenkiella*, and that is *Striatospica.* Yet *Striatospica* approaches Linoproductidae with its more numerous hinge spines that do not lie in a single chonetiform row. Another of his alleged allies,

Dictyoclostoidea, has different micro-ornament of numerous fine and varied ribs, and scattered swellings, reminiscent of Monticuliferidae, to which it should be transferred. There is no obvious spine pattern identical to that of *Schrenkiella. Permundaria,* although included by Lazarev (2004), remains a mystery genus. It has no obvious spines, but its ornament does include close-set regular concentric wrinkles, and such are weakly suggested in *Schrenkiella*, and more strongly developed in members of Kansuellidae and some Linoproductidae (eg. Striatiferinae and Proboscidellinae).

In view of these cautions, the difference in spine-rib relations between *Linoproductus* and *Schrenkiella* noted by Lazarev (2003) requires careful appraisal. No good reason has been provided to explain why the ornament of the ventral trail should be regarded as more significant than that of the visceral disc, given that ornament over the trail is often variable, having been formed at a stage of comparatively rapid growth, as judged from growth increments, and as well, the circumferential cross-section of the trail constricts in some species, and expands in others. There are four critical parts to the ornamented ventral valve in linoproductoides, involving the nepionic shell, the visceral disc, the trail, and the ears, with umbonal slopes also to be considered. The similarity-dissimilarity of each of these sections is regarded as potentially significant, as in Waterhouse (2001, 2002). By and large, the nature of spines and the rib-spine relationship seems overall much the same for both visceral disc and trail in Linoproductidae, unlike the arrangement in some Kansuellidae.

Strong emphasis on the spine-rib relations as family- significant must cope with the fact that *Linoproductus* itself appears to vary in numbers of ribs behind and in front of the trail spines. Indeed Lazarev stated that a majority of species in *Linoproductus* showed the spine-rib pattern, as if to imply that a minority of *Linoproductus* species did not show the feature, and that is what I have also found. If species within a genus can vary to such an extent, then the distinction would seem to be of less than generic value, let alone of familial standing, and while it is true that flexibility and change of morphology must be accommodated in any understanding of evolution, the possibilities of special pleading and artificiality increase overwhelmingly, especially when analysis of family group characters does not take special care to note the characters of even the type species of the name genus. This omission may be remedied herein for *Linoproductus*. The type species of *Linoproductus* Chao, 1928, *L. cora* (D'Orbigny, 1842), as well figured by Kozlowski (1914), does not consistently show that ribs are clearly more numerous behind the ventral trail spines than in front, but the species does have large spine bases over visceral disc and trail which substantially disrupt the rib pattern. Amongst specimens figured as *cora* from the same area (not necessarily the same stratigraphic level), Samtleben (1971, pl. 7, fig. 2a, b) figured a ventral valve that shows a few spines over the visceral disc with ribs more numerous behind rather than in front. The original specimen described by d'Orbigny (1847) was refigured by Tschernyschew (1902, text-fig. 69, p. 622) and Girty (1920, pl. 55, fig. 1, a). It shows one more rib behind a prominent anterior spine than in front.

If it is deemed that the distinctions emphasized for Schrenkiellidae by Lazarev (2003) carry family-group significance, then the family group based on *Stepanoviella*, initially proposed as Stepanoviellinae Waterhouse, 1975, is relevant. *Stepanoviella* Zavodowsky and its comparatively well known allied genera, such as *Globiella* Muir-Wood & Cooper, *Chianella* Waterhouse, *Cimmeriella* Archbold & Hogeboom and *Liraria* Cooper & Grant have a row of hinge spines, more feebly developed than in *Striatoplica* and possibly *Schrenkiella*, and narrow ventral disc and fine trail spines that do not disrupt through-going ribs. The ribs are like those of *Schrenkiella*, persistent, evenly spaced, and not varying irregularly throughout their length in width and height. Differences between *Stepanoviella* and *Schrenkiella* and their family groups involve chiefly shape and musculature. The spines along the ventral hinge are not large in *Schrenkiella* itself, and the shape for *Striatospica* is less extreme than in *Schrenkiella*, approaching that of *Stepanoviella* and allies. Ventral adductor impressions are comparatively smooth in *Stepanoviella*, and dendritic in *Schrenkiella*. Were the narrow range of principles enunciated by Lazarev (2003) to be followed, Stepanoviellidae would take precedence over Schrenkiellidae, and be co-ranked with Linoproductidae. Indeed Lazarev (2004) proposed that *Cimmeriella*, a member of Stepanoviellini, belongs to Schrenkiellidae - but evidently he preferred to use his family name, rather than accept the international rules of zoological nomenclature (ICZN 2000) regarding priority.

There are two other family groups to be considered. Anidanthinae Waterhouse, 1968 also has through-going ribs carrying ventral spines without change as a rule, though ribs do branch in front of spines in some specimens. Ventral hinge spines are usually stouter than trail spines, though again, rare exceptions may be found. Anidanthinae is a very distinctive group, with strong dorsal lamellae or concentric rugations. The family group name is senior to Schrenkiellidae, and most species and genera generally exemplify well the hinge row of spines which are stouter than body spines, and through-going body and ventral trail spines. Given that some ventral trail ribs increase in front of spines, anidanthins may have to be ranked as a discrete family, according to the Lazarev proposals.

Gigantoproductinae Muir-Wood & Cooper, 1960 also has a ventral hinge row of spines, and through-going ventral ribs not differing behind or in front of the trail spines. This is a more distinctive group. Lazarev (2003) has indicated significant distinctions for *Gigantoproductus* and allies, that he considered to be in need of further enquiry, involving the presence of papillae and pits to form "shagreen structure", which pointed to a mantle rather than the more usual coelomic cavity. Whilst this may be significant, and indeed worthy as ranking as a third apomorphy in the view of Lazarev (2003), there is no reason so far to justify assessment of the character as of higher than subfamily ranking. Even though its ranking may well outweigh the so-called apomorphies based on hinge row spine size and ribs before and behind ventral trail spines, its classificatory significance seems likely to be complex, because the phenomenon occurs in disparate groups, and

seems to develop late in ontogeny of some Productida, raising the possibility that it is the thickness and maturity of mantle that is involved, rather than presence or complete absence.

As shown below in a discussion of Linoproductinae, *Schrenkiella* is one genus amongst a plexus of genera centred on *Linoproductus*, and recognition of *Schrenkiella* as a family group seems contentious. The family groups based on *Gigantoproductus, Anidanthus, Schrenkiella* and *Stepanoviella* are here judged to be allies of Linoproductidae, much as in Waterhouse (2002). This is based on the observation that the size of hinge spines is not of family-level significance, and on the premise that the number of ventral trail spine-ribs for and aft is not consistent enough to demand priority for classifying *Linoproductus*, let alone for interpreting evolutionary development.

Fluctuariidae

Fluctuariinae Nalivkin, 1979 was discarded by Brunton et al. (2000) but elevated to a full family by Lazarev (2003). Yet only three genera could be mentioned as constituents by Lazarev (2003). One of these, *Helenaeproductus* Lazarev, was regarded as a synonym by Brunton et al. (2000), but on the other hand *Cancrinella* Fredericks and *Auritusinia* Waterhouse may be added. The genus *Fluctuaria* of Early Carboniferous age has ventral spines that are not clearly visible in the most accessible illustrations, as provided by Muir-Wood & Cooper (1960) and Brunton et al. (2000), but studies by Davidson (1861) and Sarytcheva (1963), as elaborated below, reinforce the view of Lazarev (2003) that the family group ranged from Early Carboniferous to Late Permian, and is distinct from Linoproductidae and Monticuliferidae. Fluctuariinae is best treated as a subfamily, because allied subfamily groups have similar but weaker concentric rugae (Kansuellinae, Auriculispininae, Paucispinauriinae) with similar spine bases. Undariini and Siphonosiini come especially close to Fluctariinae.

The suppositions by Lazarev (2003) that three families arose simultaneously from Monticuliferidae in the Early Carboniferous, and the claim that Schrenkiellidae reverted to aspects of its chonetiform ancestry, seem to amount at best to a dubious phylogeny. The plucking of a scattering of genera, ignoral of well established family groups and numerous genera, and unwillingness to analyse more complex schemes, are not sound phylogenetic procedure.

An alternative classification

Waterhouse (2001, 2002) subdivided most of the linoproductoids into Linoproductidae with short ventral spine bases, variable in width, entering or closed off from the interior (Text-fig. 1, 2) , and Kansuellidae (Text-fig. 3, 4), with ventral spine bases that are swollen and prolonged posteriorly within the shell over the entire visceral disc. Two minor families were discriminated as Monticuliferidae and Yakovleviidae. The nature of the spine bases was regarded as a highly significant apomorphy, and reflective of considerable difference

in mantle development. The feature stands out as a major difference between the two major suites of linoproductoids: it is further associated with a difference in the nature of ribbing, because ribs are well defined and comparatively even in Linoproductidae, and are less regular in Kansuellidae and associates. These distinctions may be readily observed, and there is little variation - unlike strength of spines along the hinge and certainly unlike the rib numbers before and behind trail spines. Whatever their significance, the nature of spine bases is consistent, widespread and useful. To my mind, classification and phylogeny have to be in harmony, and are best advanced through assessment of widely shared characters of taxa that palpably differ from other widely shared features in other taxa, as well as tracing antecedents and development within groups. Such a classification may well prove to be no more than a framework to be refined and modified, but it is objective, and offers a comprehensive start. To ignore widely occurring and consistent criteria, and to set aside numerous genera from consideration, risks exaggerating the importance of variable and sometimes obscure aspects of morphology, as assessed from a handful of genera, and force us to explain the shared nature of spine bases and ribs as due to repeated convergences. We would end up treating Productidina in the way that Triassic Ammonoidea were treated, when authorities ignored the significance and constancy of sutural detail (Waterhouse 1994, pp. 17-21), and developed a model of reiterative and simultaneous convergence in sutural morphology from unrelated stock, zone after zone.

Moreover, unlike the study by Lazarev (2003), all known genera were recast and itemized in the revised classification by Waterhouse (2002), in order to reduce ambiguities, although some genera remain uncertain, thanks to poor material or inadequate description. Although it may seem possible that an evolutionist would be free to pick on any one or two of a large range of morphological features to construct a phylogeny, there are constraints imposed by widely shared morphologies, and in particular, the Fluctuariinae (if interpreted correctly), Auriculispininae and Paucispinauriinae (syn. Grandaurispininae) are closely interrelated, sharing a number of morphological aspects, and differing strongly in a number of these aspects from both Linoproductidae and Monticuliferidae. The family groups based on *Fluctuaria* and *Schrenkiella* were named later than other proposed family groups, and involve few genera, which show limited morphological difference from other genera, and are therefore judged to be of less than familial rank. Whatever the preferable model, it appears clear that the Productidina were a rapidly evolving group that reiterated and diversified in morphology, with new family groups arising from time to time.

Family **LINOPRODUCTIDAE** Stehli, 1954

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

Diagnosis: Ribs distinct, well defined and close-set, ventral spines virtually all erect or suberect, without prolonged bases.

Subfamily **LINOPRODUCTINAE** Stehli, 1954

[Linoproductinae Stehli, 1954, p. 319].

Diagnosis: Ventral spines only in most genera, body cavity deep or shallow, both valves with fine close-set radial ornament, concentric ornament inconspicuous except laterally in some species.

Tribe **LINOPRODUCTINI** Stehli, 1954

[nom. transl. Waterhouse 2001, p. 25, ex Linoproductinae Stehli, 1954, p. 316].

Diagnosis: Row of hinge spines moderately to well developed, maximum shell width generally in front of hinge, or close to hinge. Ventral ribs may be more numerous behind rather than in front of trail spines, or of same number. No dorsal spines or pronounced rugae. Depth of body cavity variable, often thick.

Discussion: The genus *Linoproductus* Chao includes a number of species of Pennsylvanian to Late Permian age. The genus supposedly ranged as high as Kazanian according to Brunton et al. (2000, p. 527), which is Middle Permian, not Upper Permian as in Brunton et al. But *Linoproductus lineatus* (Waagen, 1884, p. 673, pl. 66, fig. 1, 2, pl. 67, fig. 3) is found in the Kalabagh Member, Wargal Formation, and Kufri Member, Chhidru Formation, of Wuchiapingian (Late Permian) age in the Salt Range, Pakistan. Species of the genus are characteristically large, with moderate to thick visceral disc, and closely covered by even costae. Spines are limited to the ventral valve, and form a single row along the hinge in a number of species, or a double row, rarely with additional spines on the ears: the spines are erect and generally diverge outwards, and are as a rule of moderate strength, neither very fine or very thick. Spines over the disc and trail are rare to moderately common, often varying from species to species, and are typically thick, and may span two or three costae (Text-fig 2A P. 34), and may be surrounded by an aureole. Over parts of the shell, including the trail, two up to four costae may converge on a spine, and resume in front fewer in number; but this is far from invariant, and examples can be found with more costae in front of the spine than behind, and for other parts of the shell, costae are through-going. No comprehensive study on a large population or succession of populations in a substantial collection has yet been made to test the variation, and although available evidence suggests that the variation is inconsistent and not reliable at generic or even specific level, the variation in itself suggests some difference from other allied genera. Internally, the ventral adductors are large and dendritic from comparatively early in ontogeny.

There are a number of genera which share the large size and dendritic adductor scars (where known), with moderate to thick body cavity and spines limited to the ventral valve, and development of at least one hinge row. *Balakhonia* Sarytcheva (Visean - Bashkirian) has a single row of moderately stout spines along the hinge (see Sarytcheva 1963, pl. 38, fig. 6), and fine body spines, with close-set costae slightly irregular in course, but not apparently disrupted by the spines. Ventral muscle scars are subdendritic. This

genus has so far been placed with *Linoproductus. Marginirugus* Sutton, of lower Visean age, although placed with Productidae by Brunton et al. (2000), has only a low broad dorsal marginal ridge, and is somewhat linoproductid, with hinge row of moderately strong spines, and very fine spines at the start of the ventral trail. The position requires evaluation. *Schrenkiella* Barchatova of Sakmarian and younger age has a wide hinge and gently convex disc, with a row of strong hinge spines. There appear to be fine body spines with through-going costae (see Brunton et al. 2000, text-fig. 396.1a), but the text stated no body spines were present. *Striatospica* Waterhouse of late Middle Permian age has very strong hinge spines staggered along two or three rows, and fine costellae, without additional spines, and with close-set low concentric rugae. *Ovatia* Muir-Wood & Cooper of Early Carboniferous age is small and highly convex, with thick body cavity and subdued concentric wrinkles becoming high laterally. Hinge spines lie in one or two rows, and additional spines lie at the junction with umbonal slopes. Body spines are rare to numerous and close in diameter to those along the hinge. In the type species, there may be more costae behind the body and trail spines than in front, but this is not without exception, and for some trail spines the reverse is true. Ventral adductor scars are strongly dendritic. *Ovatia* was classed as Monticuliferidae by Brunton et al. (2000). However, its spines and costation differ substantially from those of *Monticulifera* and allies, and are closer to the arrangement in *Linoproductus,* as in Waterhouse (2002). *Haereospina* n. gen., described below and of Early Permian age, is very close to *Linoproductus*, and has stout hinge spines, and spines anteriorly that lie across costae, and are so thick that it is not easy to tell the number of ribs before and aft: there is some suggestion of variation, with several more ribs in front for one example. Low dorsal wrinkles are present, but adductor scars are not exposed. *Plicatomedium* n. gen., described below, is large with linoproductid ribs, hinge row of prominent spines, and anterior ventral fold. The genus comes close to *Schrenkiella*, but has more convex visceral disc and obtuse rather than extended cardinal margin. It is of Pennsylvanian age. *Xanthoserella* n. gen., described below, is a little inflated genus with spines limited to a ventral hinge row. An exceptional genus *Diadematia* n. gen., as described below, lacks ventral hinge spines, but is shaped moderately like *Linoproductus* and more like *Ovatia*. Arguably *Linoprotonia* Ferguson of upper Tournaisian-early Visean age is allied, but it has a number of ear spines, and with its thin disc possibly approaches Auriculispininae. No body spines are present, hindering placement. Knowledge of the nature of the ventral adductors would help determine the subfamily or tribal position.

Coopericinae was proposed as a subfamily within Family Schrenkiellidae by Lazarev (2004, p. 157), to incorporate a single named genus *Coopericus* Lazarev. This genus bears a row of close-set comparatively fine hinge spines, finer body spines, and arched venter. Lazarev (2004) failed to compare the subfamily with any family group other than Schrenkiellinae. *Coopericus* is linoproductin, because there are two obscure rows of hinge spines in one of the species, *Linoproductus semisulcatus* Cooper & Grant (1975, pl. 431,

fig. 8), and the species are large. Ventral adductors have not been described for any of the constituent species recognized by Lazarev (2004).

Amongst these preceeding genera, the most distinctive is *Ovatia*, because of its oval outline, considerable convexity, short hinge and strongly incurved ventral umbo. Its shape and its comparatively numerous hinge spines indicate a life position different from that of *Linoproductus* and the other genera. Lazarev (2003) has indicated that a new genus, close to *Ovatia* in shape, differs in the relationship between ventral trail spines and ribs, and this despite shape seems to have been regarded as monticuliferid with restricted *Ovatia* as linoproductid, although this is not entirely clear. His family assignments were not clearly made, and anyway, the position is better assessed from the actual morphology. Possibly another form may be represented by species with more of a brush of spines on the ventral ears as described by Carter (1987) from the Banff Formation of Canada. The variations in spinosity and ribbing amongst these forms suggest that the hinge spine numbers and rib number fore and aft of ventral trail spines are of no more than generic significance. There would appear to be good reason for reviving the family group based on Ovatiinae Lazarev, 1990, p. 121, although abandoned by Brunton et al. (2000) and Lazarev (2003, 2004). The unit should be treated as a subtribe, within Linoproductini, and is herein so amended, to Subtribe Ovatiinai.

Notwithstanding the emphasis on Schrenkiellinae in Brunton et al. (2000) and Schrenkiellidae in Lazarev (2003, 2004), it seems difficult to justify the ranking at family level, because *Schrenkiella* is so close to *Linoproductus* and others deemed to be within the same ambit. Lazarev (2003) has claimed that the ventral ribs are through-going with regard to spines in schrenkiellids, but this is also true of various *Linoproductus* species; also the hinge spine row is always single in *Schrenkiella*, and may be double in *Linoproductus* - but not always. Spines are larger along the hinge than over the disc and trail in schrenkiellids, but a close relative of *Linoproductus*, *Haereospina,* has large spines along the hinge, and some specimens of type *Striatospica*, close to *Schrenkiella*, may display disarrayed hinge spines relict from two or three rows. Some of the variations enumerated previously seem to be of a significance limited to genera rather than higher categories. The interpretations of Lazarev take a different, arguably more philosophic approach, and are perhaps more concerned with principles and what are clearly rather simplistic evolutionary concepts - it is rather difficult to avoid stating the obvious - whereas I consider that characters which vary within species and within genera cannot be used to discriminate families to any high degree of reliability. It is therefore proposed to substantially downscale the family-group name based on *Schrenkiella*, insofar as the family limits advocated by Lazarev (2003) appear to incorporate only *Schrenkiella* itself. As a possibility, the family group may serve as a subtribe to incorporate linoproductiform genera with row of sturdy ventral hinge spines and fine if any anterior spines, and somewhat variable visceral disc, not like the Lazarev model, but defensible. The number of genera herein

Table 1. Classification of Superfamily Linoproductoidea.

Family Linoproductidae Stehli, 1954
    Subfamily Linoproductinae Stehli, 1954
        Tribe Linoproductini Stehli, 1954
            Subtribe Linoproductinai Stehli, 1954
            Subtribe Schrenkiellinai Lazarev, 1990
            Subtribe Coopericinai Lazarev, 2004
            Subtribe Ovatiinai Lazarev, 1990
        Tribe Stepanoviellini Waterhouse, 1975
            Subtribe Stepanoviellinai Waterhouse, 1975
            Subtribe Lamiproductinai Liang, 1990
    Subfamily Devonoproductinae Muir-Wood & Cooper, 1960
    Subfamily Eoproductellinae Lazarev, 1987
    Subfamily Anidanthinae Waterhouse, 1968
    Subfamily Gigantoproductinae Muir-Wood & Cooper, 1960
        Tribe Gigantoproductini Muir-Wood & Cooper, 1960
        Tribe Semiplanini Sarytcheva, 1960
    Subfamily Striatiferinae Muir-Wood & Cooper, 1960
        Tribe Striatiferini Muir-Wood & Cooper, 1960
        Tribe Compressoproductini Jin & Hu, 1978
    Subfamily Proboscidellinae Muir-Wood & Cooper, 1960
Family Kansuellidae Muir-Wood & Cooper, 1960
    Subfamily Kansuellinae Muir-Wood & Cooper, 1960
    Subfamily Plicoproductinae Waterhouse, new
    Subfamily Fluctuariinae Nalivkin, 1979
        Tribe Fluctuariini Nalivkin, 1979
        Tribe Siphonosiini Lazarev, 1990
        Tribe Undariini Waterhouse, 2001
    Subfamily Wardlawriinae Waterhouse new
    Subfamily Auriculospininae Waterhouse, 1986
        Tribe Auriculospinini Waterhouse, 1986
        Tribe Lyoniini Waterhouse, 2001
        Tribe Filiconchini Waterhouse, 2001
    Subfamily Paucispinauriinae Waterhouse, 1986
        Tribe Paucispinauriini Waterhouse, 1986
        Tribe Coolkilellini Waterhouse, 2001
Family Monticuliferidae Muir-Wood & Cooper, 1960
    Subfamily Monticuliferinae Muir-Wood & Cooper, 1960
    Subfamily Tongluellinae Liang, 1990
?Family Yakovleviidae Waterhouse, 1975 (or Productidae)
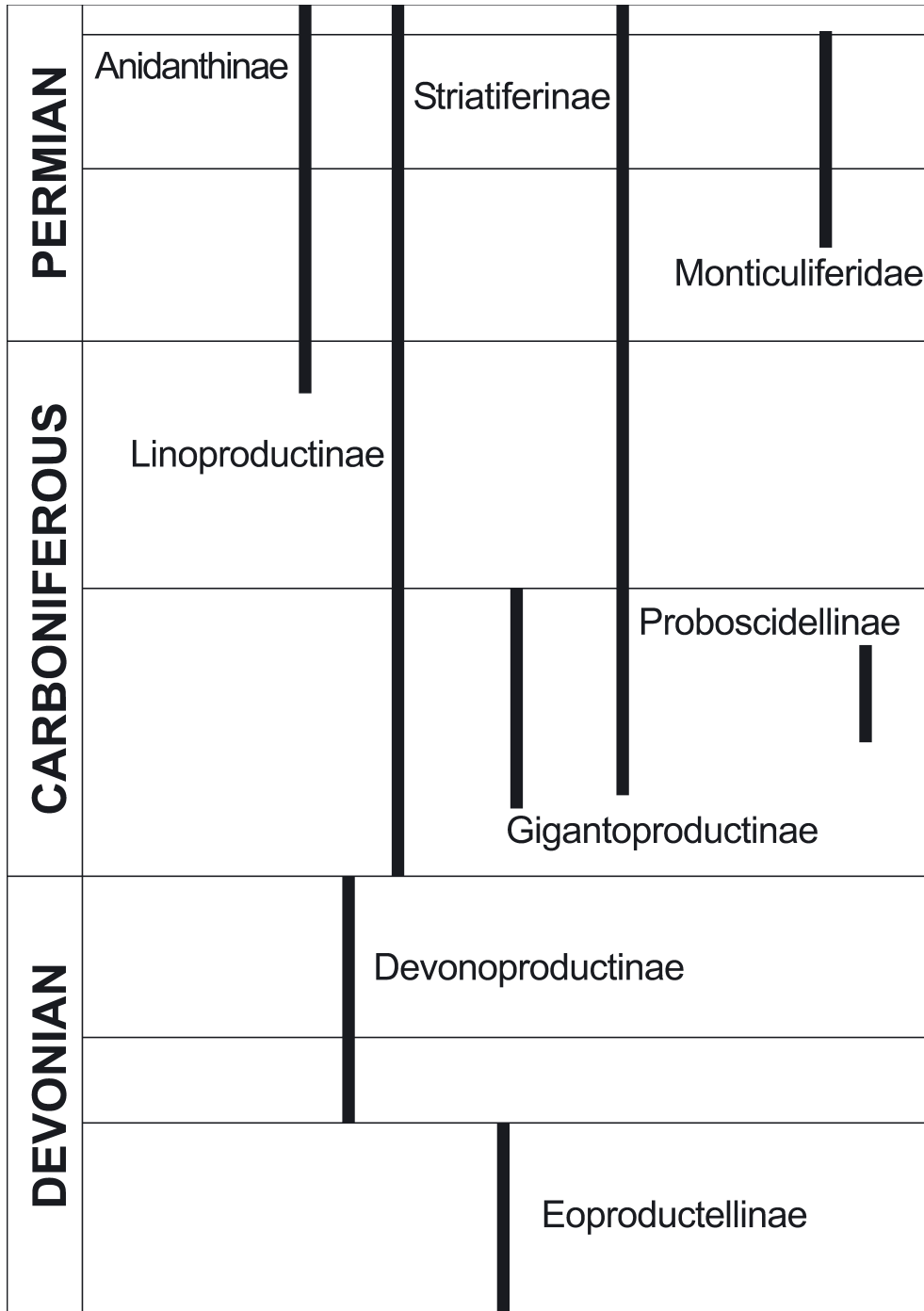
Text-fig. 1. Evolution of subfamilies within Family Linoproductidae, showing approximate known ranges of constituent subfamilies, and Monticuliferidae.

assigned to the group is more substantial and the genera are far less variable than the arrangement posited by Lazarev (2004). The overall lineage sequentially through the Carboniferous Period involved Ovatiinai, followed by Schrenkiellinai, and then Linoproductinai and Coopericinai.

Subtribe **LINOPRODUCTINAI** Stehli, 1954

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

Diagnosis: Ventral valve with sturdy spines over visceral disc.

Genus *Haereospina* n. gen.

Derivation: haereo - hold, cling, spina - thorn, Lat.

Type species: *Linoproductus undatus* Cooper & Grant, 1975, p. 1149, here designated.

Diagnosis: Of small size, characterized by strong halteroid clinging spines in row along hinge, hinge may be at maximum width with small ears, mid-length almost as wide, ventral valve swollen with few low concentric rugae laterally, dorsal valve concave with close-set concentric rugae. Body spines large, few over mid-disc and flanks, comparative number of ribs behind and in front of ventral trail spines obscure. No dorsal spines, both valves ornamented by close-set branching ribs.

Resemblances: This genus is distinguished by the row of ventral spines along the ventral hinge which are long and thick, and curved inwardly so as to form an attachment ring, to enclose an object such as a crinoid stem. A small cicatrix is present on the umbo. Cooper & Grant (1975, p. 1150) suggested that the specimens were probably free-living during adult-hood, but also observed (p. 1782) that the holotype would seem to have been attached throughout most of its life. Although the ventral spines were recorded by those authors as being few, they are moderately close-set and numerous on the lateral ventral slopes in one specimen figured by Cooper & Grant (1975, pl. 433, fig. 34). But this individual may need closer examination to determine its identification, because other figured specimens appear to have fewer lateral spines of a different nature. The numbers of ribs behind and in front of ventral spines are obscure, and possibly more numerous behind some spines, and in front of some of the others (see Cooper & Grant 1975, pl. 433, fig. 27), and ventral trail spines are not clearly illustrated. The species was described by Cooper & Grant (1975, p. 1149, pl. 433, fig. 27-43), with holotype USNM 149454d, figured in pl. 433, fig. 41-43, coming from the Taylor Ranch Member of the Hess Formation, Glass Mountains, Texas.

There is some approach in the nature of radial ribs and the clasping ring formed by a row of ventral hinge spines to *Coopericus* Lazarev, 2004 based on type species *Linoproductus angustus* King, 1931, from the Bone Spring and Skinner Ranch Formations of Texas, with associated species *C. semisulcatus* (Cooper & Grant, 1975) and *C. undatus* (Cooper & Grant, 1975), from the Neal Ranch and Hess Formations of the Glass Mountains,

Texas. These species have a ventral hinge row or rows of fine and close-set spines, curved into a ring. Anterior ventral spines are very fine, and do not disrupt the ribs.

Other linoproductinin species and genera are close in shape, but generally are larger, with fewer concentric rugae on the dorsal valve, and notably, less prominent hinge row of spines. The strength of the ventral hinge row of spines in *Haereospina* suggests a possible relationship to *Schrenkiella* Barchatova, 1973 and *Striatospica* Waterhouse, 1975, but these genera are more transverse with less inflated flatter disc and simple ribs with no spines.

Subtribe **SCHRENKIELLINAI** Lazarev, 1990

[nom. transl. Waterhouse 2001, p. 25 ex Schrenkiellinae Lazarev, 1990, p. 122].

Diagnosis: Ventral spines strong along hinge, spines if any slender over disc and trail. Body cavity moderate to thin.

Discussion: A variety of shells fall within this ambit, including *Balakhonia* Sarytcheva and *Striatospica* Waterhouse. All are close to *Linoproductus* in many aspects, including dendritic ventral adductor scars, and some *Linoproductus* have only one row of hinge spines, and ventral trail ribs passing through spines without increase or decrease. Some members of Schrenkiellinai have more than a single row of hinge spines. As herein interpreted, a number of the genera are of Early and Late Carboniferous age. *Schrenkiella* is based on a Sakmarian species, and evidently ranged through much of the Permian Period, notwithstanding the report by Brunton et al. (2000, p. 562) that the genus was to be found only in Sakmarian deposits. It is represented in the Late Permian of the Kufri Member, Chhidru Formation, Salt Range, Pakistan, by *Productus (Linoproductus) simensis* Tschernyschew *abrupta* Reed (1944, p. 56, pl. 16, fig. 4, 4a), and also reported from the *Lamnimargus himalayensis* Zone at Marbal Pass, northwest Himalaya, by Waterhouse & Gupta (1979, pl. 4, fig. 4, 5, 8). The species *abrupta* has a large gently inflated disc, concave anterior and long nasute trail, with hinge spines and no body spines.

Genus *Plicatomedium* n. gen.

Derivation; plico - fold, medium - middle, Lat.

Type species: *Linoproductus oklahomae* Dunbar & Condra, 1932, p. 251, here designated.

Diagnosis: Large with wide hinge at less than maximum width, swollen venter, anterior ventral fold and dorsal sulcus. Ornament of linoproductid radial ribs, converging anteriorly over ventral fold, prominent row of ventral hinge spines, and rare body spines sited inconspicuously on ribs.

Resemblances: This genus is distinguished by its prominent row of ventral hinge spines and anterior ventral fold. *Coopericus* Lazarev, 2004 comes close in many aspects with ventral hinge spines that converge medially to form a clasping ring, but the spines

are finer, more close-set and more numerous, and there is no ventral fold anteriorly. *Schrenkiella* Barchatova, 1973 is also moderately close, but has wide cardinal extremities, with ventral hinge spines comparably developed, though the development of a clasping ring is not apparent. The visceral disc is broader and ventral valve less convex, and is sulcate over the anterior visceral disc and start of the trail, and low narrow concentric rugae are developed. Body spines are absent. Anteriorly a ventral plication may develop in *Schrenkiella*, as in the species *S. triangulata* Barchatova. There is some approach to *Ovatia* sp. of Carter (1972, pl. 1, fig. 1-6) from the Kinderhookian Gilmore City Limestone, Iowa, noted to be schrenkiellid by Lazarev (2003). The Iowan material has more spines along the ventral hinge, fine costellae, and lacks anterior ventral fold.

Linoproductus oklahomae was initially described by Dunbar & Condra (1932, pl. 44, fig. 1, 2a, b) from the Stanton Formation of upper Pennsylvanian age in Oklahoma. The figured specimens were cited as cotypes, and here, the specimen figured in pl. 44, fig. 1 is designated lectotype, because it shows more of the ventral spines. Specimens are kept at the Peabody Museum, Yale University. Excellent figures of well preserved specimens were also provided by Muir-Wood & Cooper (1960, pl. 111, fig. 1, 2) from the Okesa Sandstone of Oklahoma, from material kept at the Smithsonian Institution. Another species was figured as *L. carinata* Dunbar & Condra (1932, pl. 30, fig. 1-3) and this has less tumid disc. This species also shows some approach to *Schrenkiella*, but maximum width lies in front of the hinge, and there is no median sulcus towards the anterior disc, and spines lie over the ventral valve as well as along the hinge. It is common in the Kanwaka shale of Kansas. There is some approach to *Linoproductus nasutus* King, 1931 from the Appel Ranch Member of the Word Formation in the Glass Mountains of Texas, but this form has large ears and few and coarse spines along the ventral hinge. A broad low ventral fold is present anteriorly.

<p style="text-align:center">Genus Xanthoserella n. gen.</p>

Derivation: Xantho, sea-nymph, daughter of Nereus - Lat.

Type species: *Linoproductus devargasi* Sutherland & Harlow, 1973, p. 57, here designated.

Diagnosis: Medium-sized, elongate, little inflated shell with small flat ears at less than maximum width, well developed ventral spines in row along hinge, no body or dorsal spines, low concentric rugae laterally on ventral valve, and covering dorsal valve.

Resemblances: This genus is named for a species noted by its authors as possibly representing a new genus. The closest similarities lie with *Balakhonia* Sarytcheva, 1963 and *Schrenkiella* Barchatova, 1973, of Early Carboniferous and Permian age respectively. These two genera share a well formed row of ventral hinge spines and come close in general appearance. *Balakhonia* is particularly close, and is distinguished by its more elongate outline, presence of some spines over the visceral disc, less regular low concentric

rugae on the dorsal valve, and larger cardinal process with lobes more divided. The median septum in front of the cardinal process is broad and conspicuous, whereas the median septum of the new genus is slender and low. *Schrenkiella* is of different shape, wider at the hinge, with large ears, and tendency for nasute anterior. In its simple dish-like shape, with few spines and even linear ribs, the new genus recalls aspects of Gigantoproductinae, but the genus is linoproductid, judged from the dorsal interior as figured by Sutherland & Harlow (1973, pl. 12, fig. 11), and hinge spines are very stout laterally, and there is no ginglymus.

Xanthoserella devargasi was described by Sutherland & Harlow (1973, pl. 12, fig. 7-11) from the lower part of the La Pasada Formation, New Mexico, and deemed to be of Morrowan age. The designated holotype is OU 7774, figured by Sutherland & Harlow (1973, pl. 12, fig. 7a-c), and kept at the University of Oklahoma. The gentle convexity, strong lateral hinge spines and fine costellae and other attributes characterize a very distinctive genus.

<p style="text-align:center">Genus Meniscuria n. gen.</p>

Derivation: from specific name, meniscus.

Type species: *Linoproductus meniscus* Dunbar & Condra, 1932, p. 255, here designated.

Diagnosis: Large little inflated transverse shells with wide cardinal extremities and large ears, very gentle if any sulcus or fold, trail not geniculate, narrow body cavity. Spines limited to ventral valve, in double row along hinge and scattered, rare, small and erect over remainder of valve. Low lateral wrinkles on ventral valve and dorsal valve traversed by more close-set low wrinkles.

Resemblances: Although Dunbar & Condra (1932) evaluated this species as very close to *Linoproductus cora*, it is readily distinguished by its low inflation, thin disc, fine spines and wide ears, with other differences. One of the closest of genera is *Xanthoserella*, described above, and this form has maximum width near mid-length, with smaller ears, single row of more prominent hinge spines and no body spines. Overall, the two genera appear to be closely allied. *Schrenkiella* Barchatova is also closely allied, especially in overall outline with large ears and maximum width at the cardinal extremities. This genus has a solitary row of spines along the hinge, and has an anterior ventral sulcus or flattening, and tendency to form anterior fold. It is of Permian age. *Plicatomedium* n. gen. is less close in shape, with smaller ears and anterior median fold, with other differences.

The type species was described from a number of stations, including the Kansas City and Lansing Groups and Plattsburg Limestone of Nebraska, Cherryvale shale and De Kalb Limestone, Missouri, and from Kansas. The cotypes were found in the Home Creek Limestone at the top of the Canyon Group in Texas, and the specimen figured by Dunbar & Condra (1932, pl. 30, fig. 4a, b) is here designated as lectotype. It is kept at the

Peabody Museum, Yale University. Cooper & Grant (1975, p. 1147) recorded large specimens from the Gray Limestone Member and *Uddenites*-bearing Shale Member in the Gaptank Formation and Neal Ranch Formation of the Glass Mountains, but they also noted a possible approach of their *meniscus* specimens to *L. inornatus* P. B. King (1938) from north-central Texas.

Subtribe COOPERICINAI Lazarev, 2004

[nom. transl. hic ex Coopericinae Lazarev, 2004, p. 160].

Diagnosis: Moderate-sized to large well inflated shells, bearing ventral hinge spines in single or double row, body spines slender or absent.

Discussion: Overall, members of this tribe are very close to Linoproductinai in shape, but have a spine pattern closer to that characteristic of Schrenkiellinai, which are little inflated shells. Lazarev (2004) preferred to interpret the group as closer to *Schrenkiella* and allies, and placed in a family separate from that of *Linoproductus*. My feeling is that further study of Carboniferous linoproductiform genera is required, to unravel the evolutionary trends. Thus far, study is revealing a number of Carboniferous genera, hitherto unnamed, that are close to *Schrenkiella*, and differ from *Linoproductus* and *Coopericus* in inflation.

Producta corrugata M'Coy (1844, p. 20, fig. 13) from Early Carboniferous of Ireland, and widely reported from western Europe, notably as *Productus cora* not d'Orbigny by Davidson (1861, pl. 36, fig. 4, pl. 42, fig. 9), shows considerable approach to *Coopericus*, as a large and inflated shell with small ears and concentric rugae. Hinge spines form a double row, and probably are not clasping. The assumption that a single row of hinge spines helped characterized schrenkielliform and coopericiform stock may thus be set aside, and it appears that in many linoproductoid genera and associations, the number of rows varied, usually between one or two rows.

Genus *Auriculatea* n. gen.

Derivation: auris - ear, late - broadly, Lat.

Type species: *Linoproductus nasutus* King, 1931, p. 76, here designated.

Diagnosis: Small inflated nasute shell with arched venter and anterior median fold, ears wide and at maximum width, row of sturdy ventral hinge spines, few other ventral spines, not disrupting the ribs.

Resemblances: Like *Schrenkiella* and *Striatospica,* this genus has a prominent row of ventral hinge spines, and few anterior spines with ribs passing through. It differs from these genera in having a swollen venter and short anterior ventral median fold, and so is of different appearance. As pointed out by Cooper & Grant (1975), the type species is

close to the Pennsylvanian species *Linoproductus oklahomae* Dunbar & Condra, now the type species of *Plicatomedium*. The present form differs in its smaller size, greater inflation, fewer spines along the hinge, more restricted ventral fold, and larger ears. The nature of the muscle scars is not known.

Linoproductus nasutus was described from what is now the Appel Ranch Member of the Word Formation, now lower Capitanian in age, by King (1931, pl. 17, fig. 8a-c, 9a, b), with holotype YPM 11523, figured in pl. 17, fig. 9a, b, and kept at the Peabody Museum, Yale University. The species was later revised by Cooper & Grant (1975, p. 1148, pl. 433, fig. 19-23). King (1931) commented on the approach to *Linoproductus schrenki* (Stuckenburg), and Lazarev (2004) noted similarities to and differences from *Coopericus*.

Subtribe **OVATIINAI** Lazarev, 1990

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

Diagnosis: Medium-sized subglobular shells with highly arched venter and incurved ventral umbo, comparatively short hinge, fine costae. Ventral spines moderately numerous along hinge or absent, scattered or rare over disc and trail, or radially aligned along mid-line.

Discussion: Ovatiinae was proposed by Lazarev (1990) for a number of genera now dispersed in several subfamilies, including Auriculispininae and Stepanovellinae. The list of genera included *Auriculispina* Waterhouse, 1975, which became name-bearer for Auriculispininae Waterhouse, 1986. The revised brachiopod Treatise included *Ovatia* within Auriculispininae, and made no mention of Ovatiinae. However *Auriculispina* is much less tumid than *Ovatia*, and has elongate spine-bases over the visceral disc, with other differences. Here *Ovatia* is judged to be much closer to Linoproductini, following Waterhouse (2002). It is distinguished from Linoproductini by its fine radial ribs and short hinge and swollen ventral valve, with moderately thick body cavity. As discussed previously, species referred to *Ovatia* display a range of ventral spines, and probably include one or more genera, yet to be named.

The newly proposed genus *Diadematia* as described below is very close to *Ovatia* in shape, as indicated by some of the original material figured by Newberry (1861, 1876). The ventral umbo is strongly incurved, the valve swollen and convex, the hinge short, and the trail flaring. Further specimens figured by Sutherland & Harlow (1973) have a shape closer to that of *Globiella* and *Cimmeriella*, and it is here assumed that they are either less mature, or less completely preserved. Both sets of specimens have comparable costae and comparable median row of ventral spines. The spines differ substantially from those of *Ovatia*, and from the arrangement in any other linoproductoid. The relationship of the genus to other linoproductoids is therefore not certain, and the assignment is based on shape and ribs.

Genus *Diadematia* n. gen.

Text-fig. 2B, C

Derivation: diadema - royal head-dress, Lat.

Type species: *Productus nodosus* Newberry, 1861, p. 124, here designated.
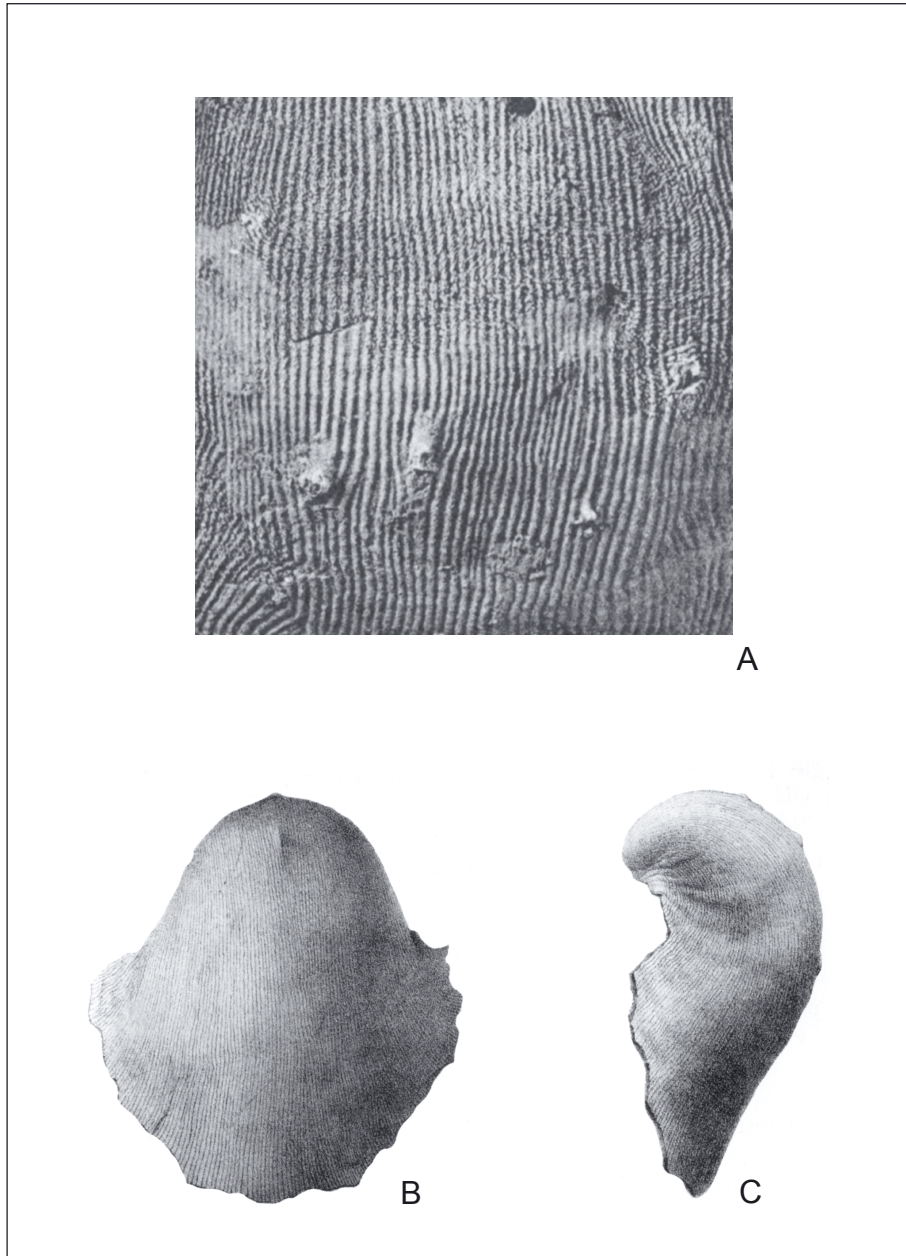
Text-fig. 2. A. Detail of ventral exterior towards trail of *Linoproductus*, enlargement of specimen figured as cf. *cora* (d''Orbigny) by Muir-Wood & Cooper (1960, pl. 111, fig. 6), x3.

B,C. *Diadematia nodosus* (Newberry). Newberry's (1876, pl. 3, fig. 3, a) drawings of specimen collected after the original description, x1. His figured specimens are now all lost.

Diagnosis: Distinguished by median longitudinal row of prominent ventral spines, no hinge row of spines, no dorsal spines.

Discussion: Even immature specimens of this genus may be readily distinguished from otherwise similar shells referred to *Globiella* Muir-Wood & Cooper and *Cimmeriella* Archbold & Hogeboom by the median row of ventral spines, and lack of other body spines or hinge row of spines from the ventral valve. In the latter regard, individuals amongst genera within Stepanoviellini may lack hinge spines, or have very small spines along the hinge. The species *nodosus* was originally described from rocks of Morrowan age in New Mexico by Newberry (1861, pl. 1, fig. 7, a, b) and thoroughly revised by Sutherland & Harlow (1973, p. 56), with synonymy and citation of a neotype OU 7770 (pl. 12, fig. 3), kept at the University of Oklahoma, New Mexico. In overall shape this specimen comes very close to *Globiella, Cimmeriella*, *Stepanoviella* and allies, and is distinguished by the distribution of its spines. But larger specimens were figured by Newberry (1861, 1876), and these show a shape much closer to that of *Ovatia*. It is therefore assumed that the *Diadematia* evolved from *Ovatia* stock, of Early Carboniferous age. Alternatively, *Diadematia* may have arisen from the loss of hinge and body spines except for a median row that developed perhaps along a median ventral fold as seen in linoproductin genera *Schrenkiella* and *Plicatomedium*. This view is not favoured, as it would also have involved change in shape and costation.

A median row of spines is very rare amongst genera of Productidina, and is found in *Leioproductus* Stainbrook, classed as belonging to Tribe Leioproductini Muir-Wood & Cooper, and in *Admodorugosus* Brunton & Mundy and *Acanthoplecta* Muir-Wood & Cooper of Tribe Levitusiini. Both fall within Subfamily Leioproductinae of the Horridonioidea Muir-Wood & Cooper (Waterhouse 2002, p. 17).

Tribe **STEPANOVIELLINI** Waterhouse, 1975

[nom. transl. Waterhouse 2001, p. 25 ex Stepanoviellinae Waterhouse, 1975, p. 12].

Diagnosis: Small to small-medium in size with moderate hinge width, body corpus slender, ventral spines may form weak hinge row not as prominent as in many Linoproductini, or not developed, rare and fine or absent over body of shell as a rule. Erect dorsal spines in some genera. Ventral adductor field smooth rather than dendritic.

Discussion: Treatment of this family group by Brunton, Lazarev et al. (2000, pp. 527, 533), is difficult to comprehend. The subfamily Stepanoviellinae Waterhouse, 1975 was regarded as a synonym of Linoproductinae (p. 527). But the genus *Stepanoviella* was placed as a member not of Linoproductinae but of Grandaurispininae Lazarev, 1990. How Linoproductinae can be senior synonym of Stepanoviellinae yet not include *Stepanoviella* is a mystery. And when the same authors also placed *Stepanoviella* as a member of Grandaurispininae Lazarev "1986" - correctly 1990 - readers should wonder why priority was not acknowledged for Stepanoviellinae Waterhouse, 1975. The implication is that the

author(s?) preferred his - or their - own names, regardless of international rules for zoological nomenclature.

Stepanoviellini embrace a group of largely Permian genera that are overall close to Linoproductini, but are smaller in size, with more variable spinosity, generally with hinge row of spines, but in some genera without hinge spines, and in some genera with dorsal spines. The ventral spines generally form a hinge row, coarser than over the visceral disc and trail, or of the same size, and ribs generally pass through ventral trail spines without change in number, and spines are erect without posteriorly prolonged bases. The ventral adductor scars are smooth or may be weakly striate until very late in ontogeny. Linoproductini are larger shells, and may have spines stronger or weaker anteriorly than along the hinge, and may have more ribs behind, or sometimes in front of ventral spines. The ventral muscle platform is markedly dendritic. Linoproductini are chiefly Carboniferous to Early Permian, and Stepanoviellini are mostly Permian.

The genus *Stepanoviella* was selected as name giver because it was understood that a better known genus *Globiella* Muir-Wood & Cooper was a junior synonym, as claimed by Grigorieva (1962), and noted by Waterhouse (1970) and Cooper & Grant (1975, p. 1156). *Globiella* was the preferred choice, but could not validly be used if the name was a synonym. *Stepanoviella* does have oval outline, fine radial ribs, hinge spines and erect anterior body spines of comparable diameter, and is unusual in having dorsal spines. It has somewhat smooth oval adductor impressions. A new genus to be described from New Zealand has more dorsal spines, stronger ribs, fewer hinge spines, and smooth ventral adductors. *Liraria* Cooper & Grant is close in shape, with large spines along the ventral hinge, and few small body spines. Cooper & Grant (1975) incorrectly stated the spines were dorsal ("brachial") - not so. Ventral adductor scars are small and not dendritic. *Globiella* has a row of hinge spines in many but not all specimens, and body spines are few and fine, or not developed. The ventral adductors are smooth, at least until late in ontogeny. *Cimmeriella* Archbold & Hogeboom is close, with coarser ribs. Ventral adductor scars are smooth, and there is generally a row of spines along the hinge, of moderate strength, and in one species from the Jungle Creek Formation of Arctic Canada, Shi & Waterhouse (1996, p. 99) recorded some specimens that showed two rows of hinge spines. Body spines may be missing, as from the type species *C. foordi* (Archbold), or are few and fine. Shi & Waterhouse (1996, pl. 15, fig. 13) noted one Canadian specimen that showed a thick ventral spine, but this is exceptional, and may be regarded as a sport or caused by shell damage, unless a different genus is involved. Generally the body spines have through-going ribs. *Chianella* Waterhouse has coarse ribs and hinge row of moderately strong spines, and tiny body spines.

Two other genera lack hinge spines, *Asperulus* Waterhouse & Piyasin, and *Lamiproductus* Liang.

Subtribe **STEPANOVIELLINAI** Waterhouse, 1975

[nom. transl. Waterhouse 2001, p. 25 ex Stepanoviellinae Waterhouse, 1975, p. 12].

Diagnosis: Radial ornament linear and simple.

Discussion: This family group was merged with Linoproductini by Brunton et al. (2000), whereas a different view was expressed by Waterhouse (2002). One reason for deciding to retain Stepanoviellini lay in the supposed absence of a ventral row of hinge spines, according to Waterhouse (2002), but this does not apply to several genera, including *Stepanoviella* (see Zavodowsky 1960, 1970, pl. 89, fig. 1b), and in the revised diagnosis, the presence of such spines is recognized, whilst noting that they vary from moderate in size to small and inconspicuous, to absent.

Members of this subtribe are readily distinguished from Lamiproductinai Liang, 1990 by their simpler radial ornament, whereas costellae in Lamiproductinai branch erratically (Waterhouse 2002, p. 33).

Members of Stepanoviellinai are Permian in age, but some Pennsylvanian species assigned to *Linoproductus* may require reassessment. For example, *Linoproductus pumilis* Sutherland & Harlow, 1973 from late Morrowan or early Atokan La Pasada Formation of New Mexico, and possibly Morrow Group of Oklahoma, is close to Stepanoviellinai in shape and ornament. There are hinge spines and a number of ear spines, and scattered body spines over the ventral valve, and no dorsal spines. Unfortunately the interior is not known: the nature of the ventral adductors might provide a critical indication of affinities.

Tribe **LAMIPRODUCTINAI** Liang, 1990

[nom. transl. Waterhouse 2001, p. 26 ex Lamiproductidae Liang, 1990, p. 466].

Diagnosis: Radial ornament branching, intercalated and erratic, no ventral hinge spines, body spines fine, erect. Dorsal accessory septa well developed.

Discussion: There is no clearly developed row of spines along the ventral hinge, although rare spines may occur on the inner ears. This suggests the genus *Diadematia*, described above, but that genus is treated as Ovatiinai because of its shape. The ventral spine bases in Lamiproductinai are not wide, and do not appear to be prolonged, and ventral adductor scars are smooth or striate, not dendritic.

Genus *Asperulus* Waterhouse & Piyasin, 1970

Type species: *Productus asperulus* Waagen, 1884.

Diagnosis: Diverging ribs and scattered erect spines over the ventral valve, rare or missing from ears. Concentric growth lines and cinctures dense.

Discussion: *Lamiproductus* Liang, 1990 is very close in costation, but the shells are more elongate and the ventral umbo more prominent, and body spines more scattered, compared with *Asperulus*. Its concentric growth lines and cinctures are less prominent than in *Asperulus*, but separation from *Asperulus* remains open to question.

Asperulus yanagidai n. sp.

1970 *Asperulus asperulus* not Waagen Waterhouse & Piyasin, p. 132, pl. 23, fig. 2-5.

Derivation: Named for J. Yanagida.

Holotype: Specimen figured by Waterhouse & Piyasin (1970, pl. 23, fig. 5), here designated. From lower Rat Buri Limestone (early Guadalupian - Middle Permian) at Khao Phrik, south Thailand, kept at Royal Ontario Museum, Toronto.

Diagnosis: Subelongate shells with moderately sturdy but few ventral body spines, rarely on inner ears, costae well formed and erratic with branching especially on dorsal valve, interspaces narrow, both valves crossed by fine growth increments, ventral ears marked by growth ridges.

Resemblances: This species is distinguished from *Asperulus asperulus* Waagen, 1884, pl. 79, fig. 3-6 from the Lopingian (Late Permian) Wargal Limestone and possibly lower Chhidru Formation (Kufri Member) of the Salt Range, Pakistan, by its more elongate outline and sturdy costae and fewer ventral spines over the disc. From the upper Guadalupian Lengwu Formation of China, *Lamiproductus typicalis* Liang (1990, pl. 35, fig. 1-12, 14-18, text-fig. 26) includes elongate shells with less deep and narrow interspaces, broader ribs, less marked concentric growth lines, and few spines. The ventral umbo is prominent with long posterior walls. *L. usualis* Liang (1990, pl. 35, fig. 13) is more transverse with more subdued ribs.

Family **KANSUELLIDAE** Muir-Wood & Cooper, 1960
Text-fig. 3

[nom. transl. Waterhouse 2001, p. 29 ex Kansuellinae Muir-Wood & Cooper, 1960, p. 336].

Diagnosis: Some to many ventral spines, emerging anteriorly over disc from a slight to considerable swelling, through which the hollow spine base is prolonged posteriorly. One, two or rarely three ribs may pass forward into the swollen spine base, and one or even no rib may continue forward from the swelling. Erect spines may be numerous close to hinge and over ears, and in some forms over trail. Concentric wrinkles often developed. Ventral muscle field set into shell, not raised anteriorly above the floor.

Discussion: Members of Kansuellinae are very large with thin disc, ginglymus and small brachiophores. In shape and size they are close to Gigantoproductinae, apart from spine bases, ribbing, and strong tendency to have narrow concentric rugae. In the present classification, the similarity is deemed to be due to convergence. The possibility remains that the two subfamilies developed as a separate family, and that the spine base peculiarities developed by convergence, and such may be argued from shape, some internal features, and presence of shagreen surface in *Kansuella* as well as *Gigantoproductus*. But shape and size seem likely to be related to the development of coelomic cavity in the umbonal region, and indeed shagreen surface appears to develop at late mature and gerontic stages of development amongst Strophalosiidina and various Productidina.

Subfamily **FLUCTUARIINAE** Nalivkin, 1979

[Fluctuariinae Nalivkin, 1979, p. 107. Syn. Magniplicatinini Waterhouse, 2001, p. 21].

Diagnosis: Shells with ornament dominated by concentric rugae.

Discussion: There are discrepancies in figures purporting to depict the type species of *Fluctuaria* Muir-Wood & Cooper, namely *Productus undatus* Defrance, 1826. Muir-Wood & Cooper (1960, pl. 115, fig. 11-20) and Brunton et al. (2000, text-fig. 366a-d) showed elongate shells with no clearly visible spines on the ventral valve, and well differentiated ribs. The Muir-Wood & Cooper text mentions spines as occurring in two rows along the hinge, clustered on the ears, and rare over the rest of the ventral valve, with no further detail: the figures imply that such spines were very small. De Koninck (1847, pl. 5, fig. 3, a-c) provided a figure of a similar though less elongate specimen, but wrote of two ribs joining to form a tubule, which implies the elongate hollow spine bases typical of Kansuellidae. Different figures were provided by Davidson (1861, pl. 34, fig. 7-13) in which elongate spine bases are prominent and close-set over the ventral valve (see Text-fig. 4A, B, p. 41), and Sarytcheva (1963, pl. 37, fig. 6-11) illustrated a ventral valve with erect spines crowded along the hinge in two or three rows, and elongate spine bases moderately numerous over the rest of the valve. All the figures show convex ventral valves with strong concentric wrinkles, but the Muir-Wood & Cooper and Brunton et al. suite of specimens is more elongate and swollen, and the costae more differentiated. That different species are involved seems likely, but whether the difference in spine detail is due to preservation or to different genera having been misidentified requires further investigation. If the type material is close to that figured by Muir-Wood & Cooper (1960), its affinities remain to be determined, and may well prove to be like those of Linoproductidae, as judged by Waterhouse (2002). In the meantime, it is assumed that Davidson and Sarytcheva have illustrated typical and well preserved specimens, and that they characterize the genus and subfamily.

That means that Magniplicatinini Waterhouse becomes a synonym, and that the subfamily ranged from Visean into Late Permian. Genera are few, and include *Fluctuaria*, *Magniplicatina* Waterhouse, *Auritusinia* Waterhouse, *Cancrinella* Fredericks, and possibly *Teleoproductus* Li Li and *Mistproductus* Yang De-Li. Ornament of the kind illustrated by Davidson (1861) and Sarytcheva (1963) is also well developed in the much less rugose subfamilies Auriculispininae and Paucispinauriinae, proposed after Fluctuariinae.

Subfamily **WARDLAWRIINAE** new

Name Genus: *Wardlawria* n. gen.

Diagnosis: Large shells with row of hinge spines, ribs subeven and close-set, bearing fine elongate bases on ventral valve, ribs continuing in front of spine.

Resemblances: This subfamily is based on a solitary genus which evidently belongs to a an intermediate phase of evolution. Its ribs show the relationship to spines that appear
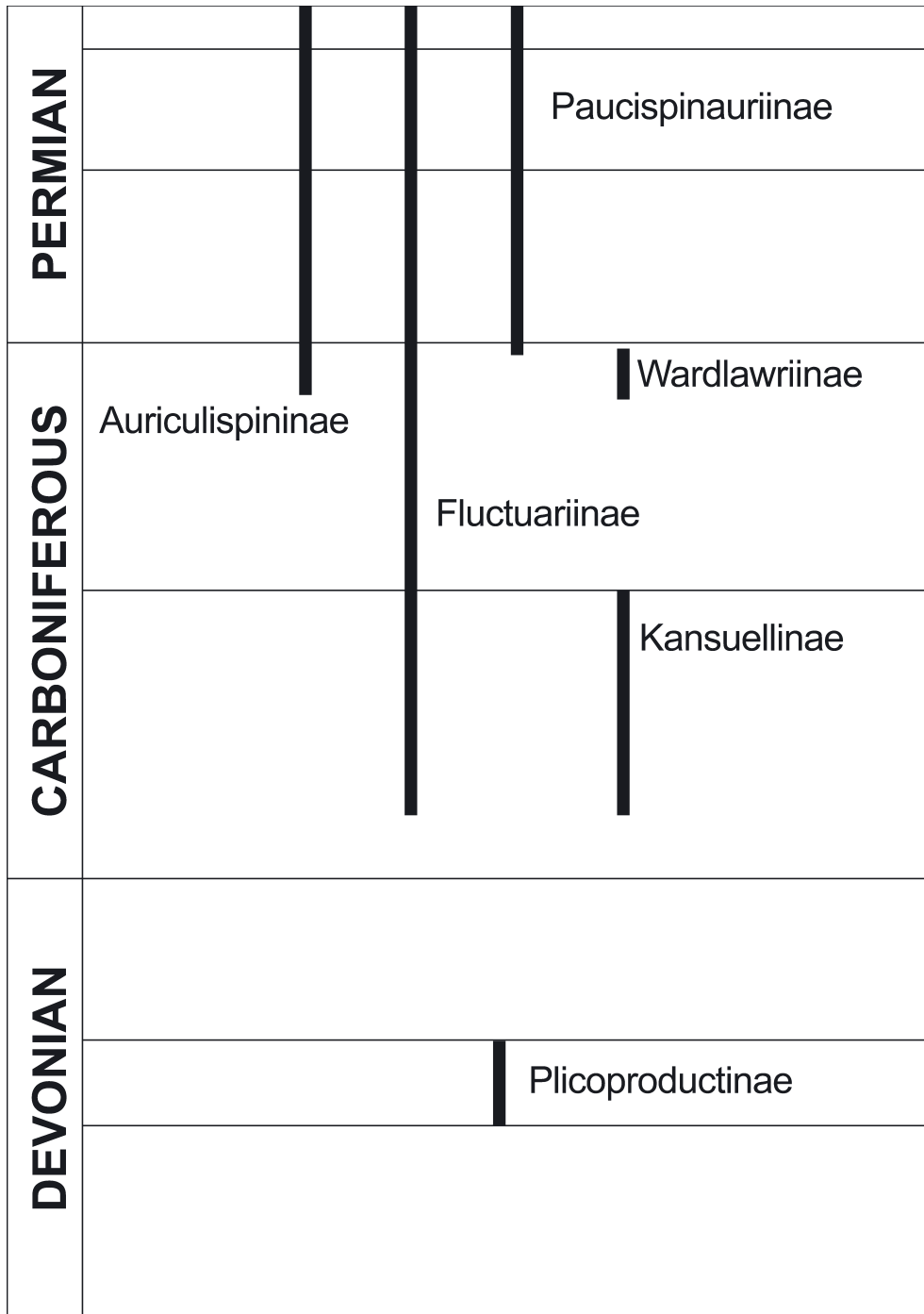
Text-fig. 3. Evolution of subfamilies within Family Kansuellidae, showing approximate known ranges of constituent subfamilies.

in Anidanthinae and Gigantoproductinae, and the ribs are only slightly less regular than in these subfamilies. Unlike genera of Auriculispininae and Paucispinauriinae, ventral spine bases are very elongate and slender. With a row of well developed spines along the hinge, of much the same diameter as body spines, the sole genus within the subfamily approaches various genera within Auriculispininae, especially Lyoniini Waterhouse, but appears to have a slightly thicker visceral disc, approaching that of Paucispinauriinae.

Genus **Wardlawria** n. gen.

Text-fig. 4C

Derivation: Named for B. R. Wardlaw.

Type species: *Productus missouriensis* Sayre, 1930, here designated.

Diagnosis: Large transverse shells with not very thick visceral disc, obtuse cardinal extremities and small non-protruding ears. Both valves covered by close-set subeven costae; spines limited to ventral valve, in row of erect close-set spines of moderate diameter along hinge, and subevenly in quincunx over ventral valve, of comparable or slightly greater diameter, with long weakly swollen bases, ribs as a rule continuing forward in front of spines, rarely splitting into two.

Resemblances: The type species has been referred to *Linoproductus* over recent years, but differs principally in the nature of the ventral body spines, which have long elongate bases (Text-fig. 4C). The genus is readily distinguished from Kansuellinae through size and shape, and lacks the concentric rugae so prominent in members of Fluctuariinae. Large often transverse members of Lyoniini have a comparable row of hinge spines, especially the late Permian genus *Nambdoania* Waterhouse, but *Nambdoania* is small, with more concentric wrinkles, less subeven ribs, and thinner visceral disc. *Paucispinauria* Waterhouse may have comparable hinge row, but its visceral disc may be thicker, and its ventral spines (Text-fig. 4D) are more prominent, the ribs less regular, and dorsal spines

A   B   C   D
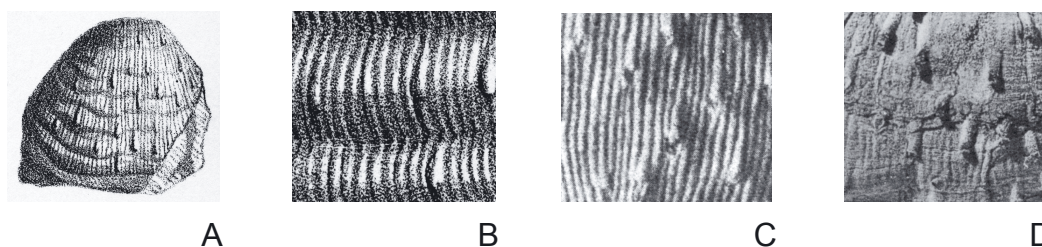
Text-fig. 4. A, B. *Fluctuaria undatus* (Defrance), as figured by Davidson (1861, pl. 34, fig. 7, 9a) from Derbyshire and Settle, Yorkshire, x1, x6 approx.

C, *Wardlawria missouriensis* (Sayre), detail of ventral ornament as figured by Dunbar & Condra (1932, pl. 28, fig. 2) from De Kalb Limestone, Missouri, x7.

D. *Paucispinauria concava* (Waterhouse), detail of ventral ornament, x2.

are present. *Coolkilella* Archbold and allies also may have hinge row, and show thick visceral disc with more concentric rugae, few disc spines and very different shape.

The type species is of Missourian age. It has been well described and figured from the De Kalb Limestone of Missouri by Dunbar & Condra (1932, p. 252, pl. 28, fig. 1-5, pl. 29, fig. 6, 7), with the ventral spine detail shown in pl. 28, fig. 2. Muir-Wood & Cooper (1960, pl. 114, fig. 13-16) also provided excellent figures of specimens from the Drum Limestone of Missouri. The species has a large convex ventral valve with few gentle concentric rugae, but the dorsal valve is more closely rugose. Ribs generally continue in front of the spine, and occasionally increase to two in front, or converge behind the spine and become one in front.

Other and allied species of Carboniferous age are to be expected. For instance a small ventral valve figured by Davidson (1861, p. 160, pl. 34, fig. 6, a, b) from Carboniferous limestone north of Glasow shows elongate slender spine bases behind spines. The specimen was identified, with caution, as *Productus carbonarius* de Koninck, but de Koninck's figures do not clearly show elongate spine bases.

Subfamily **PLICOPRODUCTINAE** n. subfam.

Name Genus: *Plicoproductus* Ljaschenko, 1969, p. 14.

Diagnosis: Small and "primitive" linoproductoids with ribs on both valves, tend to branch in front of ventral spines and dorsal pits, spines supported by elongate bases, and restricted to ventral valve. Low interareas and small teeth.

Resemblances: *Plicoproductus* is based on type species *Productella mosolovica* Ljaschenko, 1958, p. 93 and has well formed ribs on both valves, with intervening finer ribs, and some ribs appear to branch in front of spine bases over the middle and anterior valve. Spines are limited to the ventral valve, and have long broad bases, tapering posteriorly, and the dorsal valve shows long pits. *Striatoproductella* Krylova, 1962, type species *Striatoproductus tunguensis* Nalivkin, 1960, p. 319, has fine elongate ventral spine bases on the ventral valve, dorsal pits, and fine and coarse radial ribs on both valves. *Hanaeoproductus* Ficner & Havlicek, 1978, p. 65, type species *Productus rittbergensis* Quenstedt, 1871, p. 613 was judged to be synonymous by Brunton et al. (2000, p. 549). The genera are of Middle Devonian age, Eifelian and Givetian respectively, in Eurasia.

These genera differ from *Eoproductella* Rzhonsnitzkaya in ornament. This latter genus has fine well defined ribs very like those of Linoproductidae, and it is placed as Eoproductellinae Lazarev, 1987. Close-set coarse erect spines cross two or three ribs, which are through-going. Genera within Devonoproductinae Muir-Wood & Cooper, 1960, are even more distinctive, with or without fine ribs on the ventral valve, and often numerous and erect ventral spines, including a well defined hinge row in some genera. The dorsal valve bears strong concentric lamellae. The genera are of Early to Middle Devonian age, and look very like forebears of Anidanthinae, which lack teeth, sockets and interarea, but

have somewhat similar spines, ribs and concentric laminae, and even muscle scars, although they lack the weak lateral ridges of the dorsal interior. There is a long time gap between Devonoproductinae and Anidanthinae, but although Anidanthinae may have converged morphologically from different stock, the similarity is striking and may imply failure to find intervening taxa. *Eoproductella* on the other hand, as reported by Lazarev (2003), may well represent the forebear for Linoproductini, though there alternate possibilities. Plicoproductinae, with the earliest occurrences of elongate spine bases, was presumably ancestral to Visean and Serpukhovian Kansuellinae and upper Pennsylvanian Wardlawriinae. The diversity and morphological space between the comparatively sparse Devonian and Carboniferous linoproductoid groups indicate that much remains to be discovered, unless there was very rapid evolution.

Acknowledgements

APPENDIX

The contents of the article called "Productidina" by Brunton, Lazarev et al. (2000) in the revised brachiopod Treatise range beyond the purported title by including part of a different suborder, Strophalosiidina. This was apparently written by the same authors, although Lazarev (2003, p. 492) has repudiated a large section of the Strophalosiidina text, which he evidently regarded as less than acceptable. Lazarev stated that most of the strophalosiidin text had been prepared only by R. E. Grant, except for that on early members of the suborder. A further section on Strophalosiidina was presented by different authors, as Richthofenioidea by Wardlaw et al. (2000). The confusion over the limits of Productidina and Strophalosiidina, even in the titles, is possibly explicable in terms of differences in view between the associated authors, rather than to carelessness. The view of Lazarev (1987, p. 48; 1989, 1990, p. 77) was that Strophalosiidina excluded Richthofenioidea, and included Lyttonioidea (now Lyttoniidina). Thus it is perhaps significant that the Strophalosiidina under the heading of Productidina, to which Lazarev contributed, or rather as he now says, contributed little, did not include Richthofenioidea. Brunton et al. (2000, p. 565) in small print after the major heading for the suborder Strophalosiidina, pretended - that seems to be the most accurate verb, as is explained shortly - that the suborder was to be used as set out by Lazarev (1989), and explicitly denied the view offered in the original proposal and definition by Waterhouse (1975, 1978). Waterhouse included

Richthofenioidea, and excluded Lyttonioidea. Extraordinarily, and in contradiction of Brunton et al. (2000, p. 565), the lay-out in the revised brachiopod Treatise and descriptions by Brunton et al. (2000) and Wardlaw et al. (2000) did not follow the Lazarev view of Strophalosiidina, and did follow the Waterhouse interpretaion, by excluding lyttoniids, and including Richthofenioidea. The Waterhouse view was acknowledged in an article in the revised brachiopod Treatise, purporting to be by Brunton, Lazarev & Grant (2000, p. 351), but again, Lazarev (2003, p. 492) complained that he had not checked that particular text, only the figures, so it seems there were problems, and he evidently disagreed with parts of that text. There may have been substantial differences between the various authors over the Productidina and Strophalosiidina, perhaps to the stage where it became impossible to achieve even a semblance of unity and consistency, as noted herein on *Stepanoviella* and Stepanoviellinae (p. 35). Given that the evolution and classification of such a large and diverse suborder as Productida is not only complex but open to various interpretations, differences between the authors are to be expected. That is no different from the divergence in views and possibilities over many scientific problems. I see no reason for concealing the fact, and I find the authorship explanation by Lazarev (2003) to be commendable. It may asked whether it would have been preferable to have noted the different view-points in the revised brachiopod Treatise, and so clarified what appear to be inconsistencies, and oversights, and contradictions. Most if not all are explicable in terms of differing views by different authors. What a task it must have been for the editor and principal author to achieve the final presentation.

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