CLASSIFICATION WITHIN PRODUCTIDINA AND STROPHALOSIIDINA

(BRACHIOPODA)

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With 9 tables

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Abstract

The classification of the Productidina and Strophalosiidina is discussed, and genera are organized in family groups to subtribal level, according to their evolutionary relationships. Seven superfamilies are recognized within Productidina, involving Productelloidea, Horridonioidea, Productoidea, Margiferoidea, Echinoconchoidea, Linoproductoidea and Aulostegoidea. Aulostegoidea are provisionally transferred from Strophalosiidina, and some small groups, including Caucasiproductinae and Cooperinidae are shifted to Strophalosiidina. Newly named productidin genera are *Guangia*, type species *Krotovia inflata* Shen et al., 2000 (Family Overtoniidae), *Contraspina*, type species *Productus purdoni* Davidson, 1862 and *Fostericoncha*, type species *Waagenoconcha? gigantea* Waterhouse, 1983a (Family Waagenoconchidae), *Colemanosteges*, type species *Taeniothaerus? fletcheri* Coleman, 1957 (Family Aulostegidae), *Reedosepta*, type species *Productus (Tschernyschewia) parilis* Reed, 1944 and *Trigonoproductus*, type species *Tschernyschewia inexpectans* Cooper & Grant, 1975 (Family Tschernyschewiidae), *Nisalaria*, type species *Cancrinelloides (Bandoproductus) inflata* Waterhouse, 1978, *Nambdoania*, type species *Cancrinella papilionata* Waterhouse, 1983a, and *Auritusinia*, type species *Costatumulus tazawai* Shen et al. 2000 (Family Kansuellidae), *Kufria*, type species *Strophalosia (Heteralosia) blanfordi* Reed, 1944 and *Muirwoodicia*, type species *Strophalosia inexpectans* Cooper & Grant, 1975 (Family Strophalosiidae).

Key words: Productidina, Strophalosiidina, Brachiopoda, classification.

New taxa: **Family group**: Orbinariini, Stictozosterini, Absenticostini, Bibatiolinae, Desmoinesiinae, Spinomarginiferinae, Geniculiferini, Araxilevini, Diaphragmini, Callytharrellinae, Spinarellini, Marginatiinae, Taeniothaerinae, Septasteginae, Sphenosteginae, Balkhasheconchini, Craspedalosiinae, Falaferinae, Collumatini; **genera**: *Auritusinia, Colmanosteges, Contraspina, Fostericoncha, Guangia, Kufria, Muirwoodicia, Nambdoania, Nisalaria, Reedosepta, Trigonoproductus*; **species**: *Balkhasheconcha grandis* (nom. nov.), *Septasteges praeclarus*.

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A. INTRODUCTION

Suborders Productidina Waagen, 1883 and Strophalosiidina Waterhouse, 1975 are diverse groups involving about 500 genera, ranging from Devonian to Permian or earliest Triassic age. Muir-Wood & Cooper (1960) treated the two as superfamilies, with nineteen families and a number of subfamilies, and virtually the same overview was presented by Muir-Wood (1965). Ongoing studies, particularly by Lazarev (1990), culminated in a wide-ranging and almost comprehensive overview by Brunton et al. (2000). Productidina were acknowledged as a suborder, and three superfamilies were recognized, Productoidea, Echinoconchoidea and Linoproductoidea. S. S. Lazarev in particular sought to include within the superfamilies the root stock, and also persuaded colleagues that recognition of tribes would allow downscaling of relationships. This has proved to be an eminently sensible procedure, applicable not only to brachiopods, but other diverse groups (Waterhouse 2001).

This study summarizes relationships between the tribes and subfamilies within Productidina and Strophalosiidina, building on the second brachiopod treatise (Brunton et al. 2000, Wardlaw et al. 2000). Ornament is emphasized, but there is no one golden key to relationships, which must be interpreted from an overall evaluation of time range and the complex and varied array of external and internal features. Any one feature, it seems, whether or not of prime value, may itself vary within a group sharing a number of other characteristics. Occasionally, there is a marked and outstanding feature that points towards an otherwise varied group being allied: yet even so, caution must remain over the possibility of independent convergence. Not surprisingly, uncertainties remain. Devonian productids and strophalosiids belong to a diversity of small tribes, as recognized in Brunton et al. (2000), which do not always fit readily into the superfamilies, and in some instances, options remain open.

Seven rather than three major groups are recognized with Productidina, subject to these cautions. They are traced where possible back in time into Devonian roots, with emphasis on the relatively objective "morphological space or distance" from other superfamilies, and on the timing of separation. This latter approach was skilfully employed by Lazarev (eg. 1990), and it is here applied to members within the Productoidea of Brunton et al. (2000).

Summary of productidin classification

Superfamily Productelloidea Schuchert, 1929

Spines as a rule not specialized, generally distributed evenly or arranged concentrically, concentric wrinkles prominent in several lineages, radial ornament generally subdued. Early genera may have teeth, sockets, interareas, non-dendritic adductor scars, and brachial ridges close to those of strophalosiids. Corpus cavity narrow, marginal ridges generally but not always low or absent.

This superfamily, separated from Productoidea of Brunton et al. (2000), embraces many of the less specialized genera, a number of which share attributes with members of Strophalosiidina. Other superfamilies developed more specialized spines, ornament, and internal detail. Various productelloid genera may have been ancestral to the other superfamilies. Productininae might be postulated as source stock for marginiferids, just as Devonoproductinae and Eoproductellinae appear to have been source for linoproductids (cf. Brunton et al. 2000, p. 546). Yet the Productininae and Devonoproductinae share ribbed ventral valve, lamellate dorsal valve and somewhat strophalosiiform brachial ridges, and are of upper Devonian age. The two are similar, yet gave rise to different superfamilies, and whether they be associated, or separated remains a moot point.

Superfamily Margiferoidea Stehli, 1954

Spines specialized, of varied diameter especially on ventral valve, and arranged in quincunx, or in rows close to or angled from hinge, or as large strut spines. Shell otherwise may be smooth, or moderately ribbed, with well developed and somewhat diverse or elaborate trails. Corpus cavity variable, cardinal process often high and may have a zygidium, adductor scars tend to be non-dendritic, brachial ridges productiform, marginal ridges moderate to high, anterior dorsal pustules may be large.

Likely forebears are regarded as stemming from within Productininae Muir-Wood & Cooper, of Upper Devonian age. These have a few specialized spines on the ventral valve, and tend to be lightly ribbed, with

concentrically ornamented dorsal valve. Earliest genera of typical marginiferids such as *Eomarginiferina* Brunton are close in shape and in having ribs and specialized spines (Subfamily Bibatiolinae new). Aspects of Productelloidea are retained in the smooth or plane nature of the adductor scars. Costispiniferidae, the youngest of the families, reverted to a generalized productelliform ornament, but the ventral spines remain differentiated.

Superfamily Horridonioidea Muir-Wood & Cooper, 1960

Spines moderately well developed, seldom numerous, scattered over ventral valve in early forms, later developing in row close to hinge on either dorsal or ventral valve or both, with few other spines, also in regular quincunx in another association, spines in early forms aligned along a median ventral fold. Surface otherwise largely smooth or displays low concentric wrinkles. Body corpus becomes deep, and size moderately large. Interior displays large cardinal process, dendritic adductors, no heavy marginal ridges, and typical dense pustulation.

The ancestral group for Upper Paleozoic horridonioids stemmed from within leioproductids of upper Devonian age. The superfamily is small and distinct.

Superfamily Productoidea Gray, 1840

Members of this superfamily often relatively large, radial ornament commonly prominent, with concentrics also developed over the disc in some groups to form a reticulate pattern. Spines not normally as large and specialized as marginiferid strut spines, but developed in rows close to hinge or along umbonal slopes: they may form a cluster of long brush spines over ventral ears or anterior umbonal slopes. Corpus cavity deep, cardinal process large, sometimes supported by buttress plates, adductor scars heavily dendritic, marginal ridge high in only one group, otherwise only moderately well formed, trail geniculate or mutiple, but simpler than in marginiferids.

Many of the larger productidins belong to this superfamily. No clear ancestral stock is apparent. The oldest group, Buxtoniidae, involves Tournaisian genera such as *Labriproductus* Cooper & Muir-Wood and *Setigerites* Girty which are closely costate, lack marginal ridges, and have a slit in the posterior median septum. Allied buxtoniids have buttress plates. Some genera such as *Lomatiphora* Roberts and *Spinocarinifera* Roberts within the Devonian to Lower Carboniferous Semiproductinae McKellar have buttress plates and moderately well formed costae, and others have cleft posterior dorsal median septum. Semiproductinae lack any sign of the ventral brush of spines that typify most buxtoniids, and in that respect approach the buxtoniid subfamily Marginatiinae, which also lack the spine brush. Another line of speculation might centre on the supposition that Retariinae could have arisen from *Plicatifera* (Plicatiferinae) by developing stronger radials and weaker concentric rugae. Both *Plicatifera* and Retariinae have high hinge ridges and ear baffles.

Superfamily Echinoconchoidea Stehli, 1954

Spines arise generally in concentric bands over one or both valves, always fine, though they may be differentiated in size, relatively regular in disposition, may be dense. Little or no radial ornament. Body corpus deep, adductor scars dendritic, trail short and simple, posterior hinge ridge but little development of marginal ridges.

This distinctive superfamily was recognized in Brunton et al. (2000). Ancestral genera are grouped as Sentosiidae McKellar, with upper Devonian *Laminatia* Muir-Wood & Cooper displaying many of the attributes of younger forms.

Superfamily Aulostegoidea Muir-Wood & Cooper, 1960

Characterized by irregular shape and generally attached habit, with various and sometimes specialized spines, deformed ventral umbo and scar of attachment, variously costate or smooth, generally high ventral interarea. Marginal ridges commonly low, but some genera feature complex interiors with high marginal ridges, elaborate muscle supports, and buttress plates. Brachial ridges productiform in outline.

Aulosteges and allies have long been regarded as allies of *Strophalosia*, and the superfamily placed within Strophalosiidina as recently as Brunton et al. (2000). However it appears that the attachment mode was a secondary development that developed in productidin stock in Early Carboniferous times, presumably from an ancestral Devonian productelloid that had already acquired productiform brachial ridges, lost the teeth and retained or possibly redeveloped the ventral interarea, and tended towards dendritic adductor scars. Productellinae have ventral interarea, cardinal process pit, and prostrate and halteroid spines, and

were possibly suited as a source. Lower Carboniferous aulostegids were diverse, including the finely ribbed *Gondolina* with long interarea, Institininae with concentric rugae and spines, and Institellinae with reticulate ornament and prominent rhizoid spines, overall suggesting a polyphyletic origin, or one of rapid diversification.

Superfamily Linoproductoidea Stehli, 1954

Typified by fine radial ornament on both valves, reinforced by low to strong concentric wrinkles or dorsal laminae on many genera; ventral spines fine and erect, or may arise from swollen or elongate spine bases emerging from shell along costae; spines may be numerous and large on ventral ears, and may be developed in one or several rows along hinge; dorsal spines erect, can include some of wide diameter, dorsal dimples may be prominent. Internally adductors may be dendritic, striate or plane, marginal ridge development modest, dorsal pustules generally inconspicuous, and trail long but simple.

Devonoproductus Stainbrook of Frasnian age is one apparent forebear, with costellae and suberect hinge spines and dorsal lamellae (Devonoproductinae Muir-Wood & Cooper), interpreted as ancestral to Linoproductinidae. *Eoproductella* Rhzonsnitzkaya is older at Pragian (Early Devonian), with costellae and ventral spines, of which the bases appear to be swollen and elongate, as better developed in middle Devonian allies. These are suggested as forebears for Family Kansuellidae. Teeth and sockets are present, and the dorsal valve carries dimples.

SUMMARY OF SUPERFAMILY ORIGINS

The superfamilies are demanded by the large number of tribes and subtribes in some of the larger groups, by their separation from each other since Devonian as a rule, and by the discreteness of smaller groups from the larger superfamilies, such that they cannot be regarded as closely linked. The sources may be summarized as follows:

Devonian source	Superfamily
Productellinae	Productelloidea
Productininae	Marginiferoidea
Leioproductinae	Horridonioidea
?Semiproductinae	Productoidea
Sentosiinae, Echinoconchinae	Echinoconchoidea
Productellinae	Aulostegoidea
Devonoproductinae, Eoproductellinae	Linoproductoidea

The source for Productoidea is open for further study, but Semiproductinae would suffice for Buxtoniidae. Alternatively, the group have arisen from within Linoproductoidea.

B. MORPHOLOGY, TAXONOMY AND AGE

MORPHOLOGY:

Strut spines are very thick and non-rhizoid holding spines on the ventral valve that served as struts, for balancing and anchoring (Waterhouse, 1981, p. 58, 2001).

Externally, dorsal valves in Productidina and Strophalosiidina are commonly concave or gently convex, and in many genera, curve gradually or abruptly into a trail at a steep angle to the visceral disc. Where the angle is considerable, they are termed **geniculate**. In a minority of genera, the anterior dorsal valve is greatly thickened, and the exterior is level with the commissure, so that the valve may be described as **planiculate** (new term, planus - flat [Lat.]). In shells with internal soft parts that are geniculate, the exterior dorsal shell may be geniculate, or planiculate.

Internally, dorsal valves have brachial ridges that vary somewhat in outline. They enclose **brachial**

shields, which are large and oriented longitudinally (**strophalosiiform**) in *Strophalosia* and allies, and are small, more laterally placed, with extended lateral ridge connecting to the muscle areas (**productiform**), in *Productus* and allies. There are intermediate and other variations.

TAXONOMY:

Family-group names proposed for Productidina by Lazarev (1986) are nomen nuda. They were not accompanied by published explanations - and one family group was named from a genus not by then described. The International Commission for Zoological Nomenclature (2000, article 13.1, p. 17) insists that proposals of new taxa must be accompanied by a description or definition that stated in words characters that purported to differentiate the taxon. Lazarev (1986) only listed names, that were not validated mostly until Lazarev (1990), and his names date from that publication.

It should also be noted that Brunton et al. (2000) proposed to elevate various family group rankings, and ascribed the changes to their study of Brunton et al. (1995), which made few formal declarations. Several of their proposals had been pre-empted in other studies, including for instance Cooper & Grant (1975) and Waterhouse (1975, 1978). Authorships of some family groups were wrongly attributed by Brunton et al. (1995) (ie. Rugaurini and Levipustulini): and downscaling of these groups were attributed afresh to Brunton et al. 2000. The series of wrong attributions and incorrect summaries concerning Strophalosiiidina are summarized on p. 39. This study does its best to be accurate and acknowledge priority, and also endeavours to follow the Code of Zoological Nomenclature.

AGE:

In the following discussion, age is generalized to major divisions of the periods. The revised brachiopod treatise, at least in the section on Productidina, provides ages for Permian genera that are extremely inaccurate (Waterhouse 2000), and probably the ages need to be reassessed by a panel of experts with wide-ranging experience. Possibly the Devonian and Carboniferous ages are much more accurate, but it seems preferable to harmonise the ages, and here they are simplified to the major subdivisions of each period.

SYSTEMATIC SEQUENCE:

Ultimately, it would appear to be preferable to order the family groups by age and parental relationships. Following an arrangement that depends on age of recognition would be more objective, but only in terms of research history. Here a compromise is followed, and in some instances family groups that are minor are relegated to the rear. Horridonioidea has been ordered according to age. The most convenient guide for illustrations and generic diagnosis is provided by Brunton et al. (2000) and Wardlaw et al. (2000), which may be accessed through their extensive index. Most of their Carboniferous and Devonian and a number of Permian synonymies have been accepted, but there is scope for more study, because not all Permian proposed synonymies in the revised brachiopod treatise withstand close examination.

C. CLASSIFICATION

*Asterisked genera are described or elaborated in Section D (p. 46).

Suborder **PRODUCTIDINA** Waagen, 1883

[nom. corr. Muir-Wood 1965, p. 448 pro suborder Productacea Waagen, 1883, p. 447].

1. Superfamily PRODUCTELLOIDEA Schuchert, 1929 (Table 1)

[nom. transl. Waterhouse 1978, p. 20 ex Productellidae Schuchert in Schuchert & Le Vene, 1929, p. 17. See Waterhouse 2001, p. 16].

Diagnosis: Genera include a number close to Strophalosiidina, with teeth and sockets, and reduced interareas evolved during and after Devonian into genera without teeth and interareas, and distinguished from Strophalosiidina by lack of attachment scar as a rule. Spines lack postero-lateral brushes or well organized rows or strut spines, other ornament concentric rather than radial. Adductor scars commonly not dendritic, brachial ridges productiform or strophalosiiform, or variations, lateral ridges appearing in lower Tournaisian; cardinal process broad or slender, bifid or trifid, in plane of commissure. Corpus cavity shallow, or rarely deep in Carboniferous and Permian.

1.1 Family **PRODUCTELLIDAE** Schuchert, 1929

[nom. transl. Muir-Wood & Cooper 1960, p. 145 ex Productellinae Schuchert, 1929, p. 17].

Diagnosis: Small shells with little radial ornament except anteriorly, spines usually restricted to ventral valve, arranged subevenly in quincunx.

Table 1. Superfamily Productelloidea Schuchert, 1929.

1.1 Family Productellidae Schuchert, 1929
1.1A Subfamily Productellinae Schuchert, 1929
1.1Aa Tribe Productellini Schuchert, 1929
1.1Ab Tribe Orbinariini Waterhouse, new
1.1B Subfamily Semiproductinae McKellar, 1970
1.1Ba Tribe Semiproductini McKellar, 1970
1.1Bb Tribe Lomatiphorini Roberts, 1971
1.2 Family Avoniidae Sarytcheva, 1960
1.2A Subfamily Avoniinae Sarytcheva, 1960
1.2Aa Tribe Avoniini Sarytcheva, 1960
1.2Ab Tribe Semicostellini Nalivkin, 1979
1.2B Subfamily Tubersulculinae Waterhouse, 1971
1.2Ba Tribe Tubersulculini Waterhouse, 1971
1.2Bb Tribe Levipustulini Lazarev, 1985
1.2Bc Tribe Rugaurini Lazarev, 1990
1.3 Family Overtoniidae Muir-Wood & Cooper, 1960
1.3A Subfamily Overtoniinae Muir-Wood & Cooper, 1960
1.3Aa Tribe Overtoniini Muir-Wood & Cooper, 1960
1.3Ab Tribe Stictozosterini Waterhouse, new
1.3B Subfamily Plicatiferinae Muir-Wood & Cooper, 1960
1.3Ba Tribe Plicatiferini Muir-Wood & Cooper, 1960
1.3Bb Tribe Absenticostini Waterhouse, new
1.3Bc Tribe Institiferini Muir-Wood & Cooper, 1960
1.4 Family Productinidae Muir-Wood & Cooper, 1960
1.4A Subfamily Productininae Muir-Wood & Cooper, 1960
1.4B Subfamily Chonetellinae Licharew, 1960

1.1A Subfamily **PRODUCTELLINAE** Schuchert, 1929

[Productellinae Schuchert, 1929, p. 17].

Diagnosis: Shells small with simple spines and little other ornament. Teeth and sockets present in a number of genera, no ear baffles, cardinal process lobes divergent, V-shaped dorsally, may have pit. Muscle scars not dendritic. Corpus cavity shallow.

1.1Aa Tribe **PRODUCTELLINI** Schuchert, 1929

[nom. transl. hic ex Productellinae Schuchert, 1929, p. 17].

Diagnosis: Spines usually limited to ventral valve, lateral ridges each side of cardinal process, no anterior slit or buttress plates, may have pit. Lower to Upper Devonian.

Genera: *Productella* Hall, *Chattertonia* Johnston, *Helaspis* Imbrie, *Productellana* Stainbrook, *Sinoproductella* Wang, *Spinulicosta* Nalivkin.

Discussion: Spines are erect or arise from swollen or extended bases, and no concentric ornament other than growth-lines is developed. Low ribs or spine bases are present in *Spinulicosta* and *Helaspis,* and dorsal spines are present in *Productellana* and rarely in *Productella* (Muir-Wood & Cooper 1960, p. 151). *Chattertonia* Johnson has "anderidia" between the dorsal posterior and anterior adductor scars. Brachial shields in *Helaspis* (Brunton et al. 2000, text-fig. 278.3c) and *Productella* (Muir-Wood & Cooper 1960, pl. 32, fig.15) are more obliquely directed than in strophalosiids, but larger than in productids. There are no ear baffles or heavy marginal ridging, and the cardinal process tends to be high with divergent lobes and anterior pit.

Stelckia Crickmay was included in Productellini by Brunton et al. (2000). It has a row of spines along the ventral mid-line, a feature that is found in a limited range of mostly early productidins, and the genus is here tentatively transferred to Leioproductinae.

1.1Ab Tribe **ORBINARIINI** new

Name genus: *Orbinaria* Muir-Wood & Cooper, 1960, p. 149.

Diagnosis: Attachment spines on ventral umbo, spines scattered over ventral valve, some with slightly swollen or posteriorly prolonged bases, weak concentric ornament. Very narrow interareas, teeth, heavy dorsal marginal ridge, somewhat strophalosiiform brachial ridges. Upper Devonian to Lower Carboniferous.

Genus: *Orbinaria* Muir-Wood & Cooper.

Discussion: *Orbinaria* is regarded as productellid, as in Muir-Wood & Cooper (1960, p. 149), although treated as a member of Rugauriini by Brunton et al. (2000, p. 461). It was attached in early growth by a ventral umbonal spine ring. There are no dorsal spines according to Muir-Wood & Cooper (1960), yet rare spines were recorded by Brunton et al. (2000). *Orbinaria* has attributes of productellids and strophalosiids, with its teeth, interareas, and brachial ridges, but lacks cicatrix.

1.1B Subfamily **SEMIPRODUCTINAE** McKellar, 1970

[Semiproductinae McKellar, 1970, p. 26].

Diagnosis: Medium size with deep corpus cavity and relatively long trails. Spines along hinge, spine bases long on ventral disc, quincunxial, ribs originate on disc and always on trail. Dorsal spines not usually present. Lateral hinge ridges short, no marginal ridges, teeth in early genera of questionable affinity. Upper Devonian and Lower Carboniferous.

Discussion: This group may have provided ancestral material for the Productoidea, insofar as some are ribbed with spines arising from the ribs, and lack strong concentric ornament. There is no brush of spines, and marginal ridges are inconspicuous, except along the hinge. The cardinal process is supported in some genera by buttress plates or cleft median dorsal septum, and thus the group could possibly have included forebears of Buxtoniidae, which involved forms with buttress plates and lacking heavy marginal ridges.

1.1Ba Tribe **SEMIPRODUCTINI** McKellar, 1970

[nom. transl. Brunton et al. 1995, p. 927 ex Semiproductinae McKellar, 1970, p. 26].

Diagnosis: Ventral spines close-set over disc and with prolonged bases, dorsal spines present or absent, fine concentric wrinkles, posterior dorsal septum cleft. Upper Devonian to Lower Carboniferous.

Genera: *Semiproductus* Bublichenko. *Acanthoproductus* Martynova, *Rhytiophora* Muir-Wood & Cooper.

Discussion: *Acanthoproductus* may suggest Leioproductinae, with fine concentrics and median spinose fold on ventral valve, but its close-set spines are like those of *Semiproductus. Rhytiophora* has close-set ventral spines with slightly prolonged bases and dorsal spines, close-set low wrinkles on both valves, and cleft posterior dorsal median septum. Ribs vary in definition on different species (Muir-Wood & Cooper 1960, Roberts 1971).

1.1Bb Tribe **LOMATIPHORINI** Roberts, 1971

[nom. transl. hic ex Lomatiphorinae Roberts, 1971, p. 84].

Diagnosis: Spines near hinge may lie in well formed row, ventral spines well spaced and arise from ribs with prolonged bases, or erect, no dorsal spines, both valves covered by ribs, dorsal valve usually with hinge ridges, buttress plates and/or alveolus or pit. Upper Devonian to Lower Carboniferous.

Genera: *Lomatiphora* Roberts, *Margaritiproductus* Lazarev, *Nigerinoplica* Lazarev, *Seminucella* Carter, *Spinocarinifera* Roberts (syn. *Nigeroplica* Nalivkin), ?*Yanguania* Yang Shi-Pu.

Discussion: This tribe was merged with Semiproductini by Brunton et al. (2000). *Lomatiphora* has large substrophalosiid brachial ridges inclined obliquely forward. The ventral valve ornament of *Nigerinoplica* and *Margaritiproductus* is poorly known, hindering understanding of their relationship to the early Devonian genus *Chattertonia*, which like these also has teeth, though not apparently a dorsal pit at the base of the

cardinal process. *Chattertonia* lacks ribs, and its spines appear to lack prolonged bases. The poorly known *Yanguania* also has spines without prolonged bases.

1.2 Family **AVONIIDAE** Sarytcheva, 1960

[Avoniidae Sarytcheva, 1960, p. 226].

Diagnosis: Productelliform shells, ornament dominated by spines, well spaced to close-set especially on ventral valve, with swollen or prolonged bases, weakly aligned concentrically, low concentric lamellae or wrinkles and low or anterior ribs only. No teeth, sockets or interareas, adductor scars not dendritic, brachial ridges productiform.

Discussion: Ornament is more noticeably concentric than in Productellidae, but less markedly than in Overtoniidae. Unlike genera of Productellidae, members are fully productiform.

1.2A Subfamily **AVONIINAE** Sarytcheva, 1960

[nom. transl. hic ex Avoniidae Sarytcheva, 1960, p. 226].

Diagnosis: Ventral spines arranged in weakly concentric rows, low radial ribs discontinuous or limited to anterior shell.

1.2Aa Tribe **AVONIINI** Sarytcheva, 1960

[nom. transl. Brunton et al. 1995, p. 926, ex Avoniidae Sarytcheva, 1960, p. 226. Syn. Breileeniini Brunton in Brunton & Lazarev, 1997, p. 389].

Diagnosis: Well spaced subconcentric spines on ventral valve, may arise from low ribs or swellings, dorsal valve also spinose, broad irregular lamellose bands, subdued radial ridges, may be discontinuous, on one or both valves, corpus cavity shallow to moderate in depth. Lower Carboniferous to Upper Permian.

Genera: *Avonia* Thomas, *Breileenia* Brunton, *Lazarevonia* Waterhouse, *Onavia* Lazarev, *Quasiavonia* Brunton, *Tuberculatella* Waterhouse.

Discussion: Genera come close to members of Productellidae, other than in the lack of interareas, teeth and strophalosiiform brachial ridges. Although *Avonia* was associated as a tribe within Overtoniinae by Brunton et al. (2000) there is considerable morphological space between the two, with *Avonia* and allies displaying much less concentric ornament.

Genus *Breileenia* Brunton, of upper Tournaisian to upper Serpukhovian age, was separated as Tribe Breileeniini by Brunton in Brunton & Lazarev, 1997. Ribs arise over corpus, and spines lie on both valves, and ventrally have elongate bases posteriorly. Spines lie along the ventral hinge and low concentric growth pauses or lamellae are present. *Breileenia* was linked with marginiferids *Desmoinesia* and *Sandia* in Brunton et al. (2000), and with *Desmoinesia* in Brunton & Lazarev (1997), but given the lack of data on the interior, the link is speculative, and it was acknowledged that *Breileenia* was like "ribbed Avoniini".

1.2Ab Tribe **SEMICOSTELLINI** Nalivkin, 1979

[nom. transl. Brunton et al. 1995, p. 927 ex Semicostellinae Nalivkin, 1979, p. 67].

Diagnosis: Concentric rugae moderately prominent, costae on long trails, often geniculate. Spines of moderate number, on both valves in several genera, bases may be extended in ventral valve. Marginal ridges may be moderately developed. Lower Carboniferous to Permian.

Genera: *Semicostella* Muir-Wood & Cooper, *Cinctifera* Muir-Wood & Cooper, *Maemia* Lazarev, *Overtoniina* Grunt, *Pharcidodiscus* Roberts, *Spinosteges* Liang.

Discussion: Several genera, including *Semicostella and Maemia*, show swollen extended spine bases as in *Avonia*. Although Brunton et al. (2000, p. 463) included *Limbifera* Brunton & Mundy in Semicostellini, presumably because it has ribbed geniculate gutter and ear baffles, the posterior disc is reticulate, and spines few, with a well developed row along the ventral hinge. The ventral muscle field is elevated and the genus is tentatively transferred to Institellini (6.2Ea).

1.2B Subfamily **TUBERSULCULINAE** Waterhouse, 1971

[Tubersulculinae Waterhouse, 1971, p. 205].

Diagnosis: Spines uniformly fine and arranged in quincunx on the ventral valve, bases short to

elongate, dorsal spines erect and numerous or absent. Radial ornament not developed, trail short. Corpus slender. Dorsal marginal ridges subdued to moderately developed, posterior dorsal septum almost always entire, dorsal pustules fine or moderately large, crowded in front of dorsal septum, brachial ridges productiform.

1.2Ba Tribe **TUBERSULCULINI** Waterhouse, 1971

[nom. transl. hic ex Tubersulculinae Waterhouse, 1971, p. 205. Syn. Krotoviini Brunton et al. 1995, p. 926].

Diagnosis: Ventral spines subuniform and evenly arranged and usually closely spaced over ventral valve in quincunx or concentric rows, dorsal spines fine, crowded. Lower Carboniferous to Lower Permian.

Genera: *Tubersulculus* Waterhouse, *Archboldina* Waterhouse, *Krotovia* Fredericks, *Scoloconcha* Gordon, *Undellaria* Cooper & Grant.

Discussion: As pointed out by Waterhouse (2001), the genus *Tubersulculus* lacks specialized and varied ventral spines, and lacks heavy marginal ridge development, high cardinal process with zygidium, and large few anterior dorsal pustules. These and other attributes indicate that *Tubersulculus* does not belong to Costispiniferini, counter to Brunton et al. (1995, 2000).

Undellaria Cooper & Grant shows some approach to *Tubersulculus*, but has more posterior lateral ventral spines, a tendency also displayed by *Krotovia*. There are no radial ribs in *Undellaria*, unlike linoproductids to which the genus has been previously referred, and the dorsal adductors are not dendritic, and the cardinal process small and bifid, being deeply subdivided.

1.2Bb Tribe **LEVIPUSTULINI** Lazarev, 1985

[nom. transl. Brunton et al. 2000, p. 452 ex Levipustulinae Lazarev, 1985, p. 72].

Taxonomy: Levipustulini was listed as a tribe and ascribed to Muir-Wood & Cooper (1960) by Brunton et al. (1995, p. 927).

Diagnosis: Spines in quincunx with elongate or swollen bases, absent dorsally in some Devonian and Permian genera. Concentric ornament subdued, mostly lamellate or in growth steps. Median septum may be broad in front of cardinal process, low posterior hinge ridge, marginal ridges low or absent. Lower Carboniferous to Lower Permian.

Genera: *Levipustula* Maxwell, *Barunkhuraya* Lazarev, *Bulahdelia* Roberts, *Impiacus* Lazarev & Suur'suren (syn. *Nudymia* Lazarev), *Jakutoproductus* Kashirtsev, *Lanipustula* Kletz, *Piatnitzkaya* Taboada, *Verchojania* Abramov.

Discussion: This group was placed with Plicatiferinae by Brunton et al. (2000, p. 452), but has much more subdued concentric ornament, without the well organized rugae seen in Overtoniidae. The well developed and uniform ventral spines are close to those of Tubersulculini, but bases tend to be elongate or slightly swollen, and spaced further apart, and several genera lack dorsal spines. Internal detail in both is close. A summary of the varying interpretations of Levipustulini by Lazarev (1986, 1987, 1990) and Brunton et al. 1995, 2000) is provided by Waterhouse (2001, p. 18). The dorsal median septum of *Piatnitzkaya*, unlike that of other genera, is cleft posteriorly, and the genus is discussed briefly by Waterhouse (2001, p. 22). *Barunkhuraya* is transferred from Avoniini (Brunton et al. 2000) because its ventral spines are levipustulin. It lacks dorsal spines, unlike avoniins.

1.2Bc Tribe **RUGAURINI** Lazarev, 1990

[nom. transl. Brunton et al. 2000, p. 459, ex Rugaurinae Lazarev, 1990, p. 88].

Taxonomy: Rugaurini was listed as a tribe and ascribed to Muir-Wood & Cooper (1960) by Brunton et al. (1995, p. 927).

Diagnosis: Concentric ornament subdued as growth lines, steps and lamellae on dorsal valve and low rugae on ventral valve, ventral spines fine with slender elongate bases, generally aligned concentrically. Ventral and dorsal spines in *Rugauris*, and only ventral spines in the other genera. No teeth or ear baffles or submarginal ridges, or cleft posterior dorsal median septum, posterior hinge ridge well developed. Upper Devonian to Lower Carboniferous.

Genera: *Rugauris* Muir-Wood & Cooper, *Carringtonia* Brunton & Mundy, *Iniproductus* Lazarev, *Planoproductus* Stainbrook.

Discussion: This tribe is distinguished by its fine numerous often somewhat concentrically aligned ventral spines and very low close-set concentric wrinkles. *Orbinaria* Muir-Wood & Cooper, placed in the

group by Brunton et al. (2000), differs in having less regular concentric wrinkles and fewer coarser spines, and also teeth and large marginal ridge (see Orbinariini 1.1Ab).

1.3 Family **OVERTONIIDAE** Muir-Wood & Cooper, 1960

[nom. transl. hic ex Overtoniinae Muir-Wood & Cooper, 1960, p. 183].

Diagnosis: Concentric ornament well developed on both valves, radial ornament subdued or generally lacking. Spines on both valves, or only the ventral valve, tend to be subuniform in size, except for a few distinctive genera, and arranged in quincunx, with short or no swollen bases. No teeth, no interareas, no buttress supports or cleft posterior dorsal median septum, adductor scars smooth, brachial shields tend to be productiform, low to moderate marginal ridges, dorsal pustules fine and numerous.

1.3A Subfamily **OVERTONIINAE** Muir-Wood & Cooper, 1960

[Overtoniinae Muir-Wood & Cooper, 1960, p. 183].

Diagnosis: Concentric rows of ventral and dorsal spines.

1.3Aa Tribe **OVERTONIINI** Muir-Wood & Cooper, 1960

[nom. transl. Brunton et al. 1995, p. 926 ex Overtoniinae Muir-Wood & Cooper, 1960, p. 183].

Diagnosis: Moderately strong spines arranged in concentric rows on both valves. Corpus cavity deep, prominent dorsal adductor scars, low to moderately well formed marginal ridges especially in dorsal valve, dorsal internal pustules small. Lower Carboniferous to Lower Permian.

Genera: *Overtonia* Thomas, *Fimbrinia* Cooper (nom. nov. pro *Fimbriaria* Muir-Wood & Cooper, 1960 non Froelich, 1802).

Discussion: *Fimbrinia* has parallel septa in front of the cardinal process, between the adductor scars.

1.3Ab Tribe **STICTOZOSTERINI** new

Name genus: *Stictozoster* Grant, 1976.

Diagnosis: Small, spines of even size on on ventral or usually both valves, arising from swollen or slightly elongate bases which tend to be arranged as one or more rows in concentric bands, especially on ventral valve, and separated by smooth concentric bands in front of small growth intervals. Slender corpus cavity, marginal ridges lightly if at all developed. Middle to Upper Permian.

Genera: *Stictozoster* Grant, *Darlinuria* Li & Gu, *Dorashamia* Sarytcheva, *Guangia* Waterhouse*.

Discussion: Grant (1976) in erecting the distinctive genus *Stictozoster* and assigning it to Productellidae, pointed out that the genus showed some attributes of Echinoconchidae in its concentric banding, although internal features differed from echinochonchiform genera and approached those of Productellidae. *Stictozoster* is characterized by numerous fine spines, arranged generally in concentric bands, and separated by short smooth bands.

Compared with *Stictozoster*, *Darlinuria* from Inner Mongolia has coarser, fewer spines, and concentric ridges. *Dorashamia* has concentric ridges over the ventral valve at least, but spines are few. The new genus here described as *Guangia* (see section D) has both valves covered by spines with swollen bases arranged in concentric rows and separated by narrow concentric bands.

Genera of Costispiniferini (Costispiniferinae) Muir-Wood & Cooper, to which *Stictozoster* and others were referred by Brunton et al. (2000), lack concentric banding and have internal marginal ridges to varying degree.

1.3B Subfamily **PLICATIFERINAE** Muir-Wood & Cooper, 1960

[Plicatiferinae Muir-Wood & Cooper, 1960, p. 201].

Diagnosis: Concentric ornament predominant, dorsal spines tend to be rare or absent as a rule. Corpus cavity shallow to moderate in depth.

1.3Ba Tribe **PLICATIFERINI** Muir-Wood & Cooper, 1960

[nom. transl. Brunton et al. 1995, p. 927 ex Plicatiferinae Muir-Wood & Cooper, 1960, p. 201].

Diagnosis: Spines over ventral valve involve a few stout well spaced halteroid spines near hinge,

flanks and anterior, may include additional fine spines, not numerous or dense; dorsal spines rare. Gently convex ventral disc and geniculate trail, ribbing anterior only or usually not developed but disrupted swellings along concentric crests may be radially aligned, concentric rugae strong as a rule. Ear baffles and posterior hinge ridges well developed on dorsal valve, dorsal anterior pustules inconspicuous. Carboniferous.

Genera: *Plicatifera* Chao, *Aseptella* Martinez Chacon & Winkler Prins, *Rugoconcha* Jin & Sun.

1.3Bb Tribe **ABSENTICOSTINI** new

Name genus: *Absenticosta* Lazarev, 1991, p. 58.

Diagnosis: Close to *Plicatifera* with concentric or strong concentric laminae or fine rugae, spines even in size, numerous and close-set over ventral valve, may be present more sparsely on dorsal valve. Lower to Upper Carboniferous.

Genera: *Absenticosta* Lazarev, *Crossacantha* Gordon, *Ferganoproductus* Galitskaya, ?*Platyselma* Gordon.

Discussion: The mid-Visean *Platyselma* Gordon, included in Plicatiferini by Brunton et al. (2000, p. 452), has erect ventral spines, no or possible dorsal spines, and subdued dorsal concentric lamellae, but no teeth or interarea. Like *Aseptella* Martinez & Chacon, and also *Jakutoproductus* Abramov, it carries a low double ridge in front of the dorsal adductor scars, not seen in *Plicatifera*, and its ventral spines somewhat approach those of *Ferganoproductus,* and the dorsal valve resembles that of *Crossacantha.*

1.3Bc Tribe **INSTITIFERINI** Muir-Wood & Cooper, 1960

[nom. transl. Brunton et al. 1995, p. 927 ex Institiferinae Muir-Wood & Cooper 1960, p. 203].

Diagnosis: Small shells with relatively deep corpus cavity, concentric rugae, ventral spines moderately well spaced, prostrate, no dorsal spines as far as known, ribs on trails, deflected as flanges or gutters. Lower Carboniferous.

Genera: *Institifera* Muir-Wood & Cooper, ?*Thomasella* Fredericks.

1.4 Family **PRODUCTINIDAE** Muir-Wood & Cooper, 1960

[nom. transl. hic ex Productininae Muir-Wood & Cooper, 1960, p. 181].

Diagnosis: Wide-hinged commonly ribbed shells with few spines limited to ventral valve, shallow corpus cavity, venter arched, dorsal valve commonly deeply concave.

1.4A Subfamily **PRODUCTININAE** Muir-Wood & Cooper, 1960

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

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

Genera: *Productina* Sutton, *Argentiproductus* Cooper & Muir-Wood, *Dorsirugatia* Lazarev, *Productellina* Reed.

Discussion: There is considerable morphological space between this family and Productellidae. Shape, spinosity and interior suggest that this group provided a source for both Chonetellinae and for Margiferoidea. Its classificatory position thus becomes a matter for contention, as to whether it is primarily productellid or margiferid. The present scheme suggests it was productelloid, and sourced margiferoids.

Ventral spines are arrayed in an unusual pattern in *Productina, Argentiproductus*, and *Productellina*. Muscle scars lack dendritic ridges (*Argentiproductus*). Brachial shields are large, elongate and forward directed (Muir-Wood & Cooper 1960, pl. 45, fig. 13, 15, Brunton et al. 2000, text-fig. 279.1e), and although marginal ridges are scarcely if at all developed, a strong internal ridge lies across the ventral ears (Brunton & Mundy 1993, text-fig. 6. 13b).

1.4B Subfamily **CHONETELLINAE** Licharew, 1960

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

Diagnosis: Transversely subtriangular with wide hinge and nasute anterior, smooth or with low ribs,

spines generally limited to row in front of ventral hinge, hinge may have low ginglymus, shallow body corpus, dorsal anterior pustules may be large, no thick or high marginal ridge. Middle and Upper Permian.

Genera: *Chonetella* Waagen, *Celebetes* Grant, *Haydenella* Reed, *Ogbinia* Sarytcheva, *Parachonetella* Liao, *Planihaydenella* Chang, *Pseudohaydenella* Liang.

Discussion: This is a distinctive group of Permian genera, treated as a tribe by Brunton et al. (2000, p. 427), but well separated from Productininae in its different spine pattern, lack of concentrics, and appearance of large dorsal pustules anteriorly. Grant (1976, p. 138) denied that teeth were present in *Chonetella*, and this is accepted, as opposed to the report of minute teeth in Brunton et al. (2000). As well, Grant (1976, p. 159) stated that *Haydenella* was linoproductoid from the nature of its cardinal process, but Brunton et al. (2000) regarded the genus as chonetellin. *Pseudohaydenella* Liang was said to have a ventral frill or fringe, and, ambiguously, dorsal spines, but remains very obscure. Its nasute ventral outline suggests likely kinship with Chonetellinae.

2. Superfamily MARGINIFEROIDEA Stehli, 1954 (Table 2)

[nom. transl. hic ex Marginiferidae Stehli, 1954, p. 321].

Diagnosis: Genera with specialized and varied spines, especially on ventral valve, often elaborate trails, well developed marginal ridges and ear-baffles.

Discussion: Members of this superfamily are distinguished by their variously distinctive spine patterns: spines occur on both valves and either varied or fine and dense in Costispiniferidae, ventral only and arranged in a ventral posterior row or rows in Marginiferidae, and involving specialized strut spines in Paucispiniferidae. As well, dorsal marginal ridges and ear baffles are well developed, both across the ears and anteriorly where associated with dorsal trails to varying degree. The cardinal process is marginiferid (Muir-Wood & Cooper 1960), often with zygidium, and dorsal anterior pustules often well developed and comparatively few in number. Dorsal adductors generally not dendritic, and brachial shields productiform.

The superfamily arose from within Productelloidea. One unlikely source may be suggested as Tubersulculinae, which has spine pattern and lack of concentric ornament approaching that of Costispiniferinae, and low marginal ridges. Brunton et al. (2000) grouped the two, but there are various morphological differences, and *Costispinifera* and allies appear to have sourced from Marginiferidae. Under the constraints of the fossil record and time parameters, it appears more likely that the Upper Devonian to Lower Carboniferous Productininae, with subpentagonal shape and few specialized spines, gave rise to Lower Carboniferous members of Bibatiolinae of comparable shape and allied spine distribution, with heavy marginal ridge development, and thence diverged into other groups with strut spines, grouped here under Paucispiniferidae. From that grouping, it appears, came Marginiferidae and Costispiniferidae.

A small group associated as Breileeniini Brunton in Brunton et al. (2000) possibly provides a complicating factor: *Breileenia* is of upper Tournaisian-Serpukhovian age and has weak ribs and elongate ventral spine bases. It externally approaches *Desmoinesia* Hoare of Upper Carboniferous age. *Desmoinesia* is clearly marginiferid, bearing hinge and umbonal slope row of ventral spines (see Muir-Wood & Cooper

Table 2. Superfamily Margniferoidea Stehli, 1954

2.1 Family Marginiferidae Stehli, 1954
2.1A Subfamily Marginiferinae Stehli, 1954
2.1B Subfamily Scaphariininae Cooper & Grant, 1975
2.2 Family Paucispiniferidae Muir-Wood & Cooper, 1960
2.2A Subfamily Paucispiniferinae Muir-Wood & Cooper, 1960
2.2Aa Tribe Paucispiniferini Muir-Wood & Cooper, 1960
2.2Ab Tribe Probolioniini Muir-Wood & Cooper, 1960
2.2B Subfamily Bibatiolinae Waterhouse, new
2.3 Family Costispiniferidae Muir-Wood & Cooper, 1960
2.3A Subfamily Costispiniferinae Muir-Wood & Cooper, 1960
2.3B Subfamily Desmoinesiinae Waterhouse, new
2.3C Subfamily Spinomarginiferinae Waterhouse, new

1960, p. 229 re *Rudinia*, an objective synonym), yet has dorsal spines as in Costispiniferidae. Unfortunately the interior of *Breileenia* appears not to be known, so that its nature is speculative, and may not have been like that of *Desmoinesia.* Even if *Breileenia* was internally like *Desmoinesia*, its spine pattern differs and is not marginiferid.

2.1 Family **MARGINIFERIDAE** Stehli, 1954

[nom. transl. Waterhouse 1978, p. 20 ex Marginiferinae Stehli, 1954, p. 321, see Waterhouse 2001, p. 23].

Diagnosis: Spines only on ventral valve, of modest number, many halteroid, radial and concentric ornament may be present. Corpus cavity shallow to deep. Heavy marginal ridges, dorsal trails simple or mutiple.

2.1A Subfamily **MARGINIFERINAE** Stehli, 1954

[Marginiferinae Stehli, 1954, p. 321. Syn. Hystriculininae Lazarev, 1990, p. 81, Caucasoproductinae Kotlyar, 1989, p. 121, Jiguloconchinae Lazarev, 1990, p. 81, Asioproductidae Liang, 1990, p. 161].

Taxonomy: Lazarev (1986) listed his names with no description or clarification. *Jiguloconcha*, name genus for Jiguloconchinae was not even described until Lazarev (1990): in 1986 the family unit was based on an undescribed genus. Although this procedure was endorsed by Brunton et al. (2000, p. 443), it contravenes the rules of zoological nomenclature.

Diagnosis: Spines on ventral valve well formed, may include row along umbonal flanks, and generally along hinge. Shells with moderately subdued, well defined, or no radial ornament, subdued to moderate concentric ornament forming reticulate pattern in some genera. Corpus cavity shallow to deep. Upper Carboniferous to Permian.

Genera: *Marginifera* Waagen (syn. *Strigospina* Liao), *Azygidium* Waterhouse, *Caucasoproductus* Kotlyar, *Cymoproductus* Xu, *Elliotella* Muir-Wood & Cooper, *Entacanthadus* Grant, *Hystriculina* Muir-Wood & Cooper, *Jiguliconcha* Lazarev, ?*Jipuproductus* Sun, *Lampangella* Waterhouse, *Liosotella* Cooper, *Minispina* Waterhouse, *Oncosarina* Cooper & Grant, *Otariella* Waterhouse, *Protoniella* Bell, *Shanxiproductus* Duan & Li, *Transennatia* Waterhouse (syn. *Gratiosina* Grant, *Asioproductus* Zhan, *Kurtomarginifera* Xu).

Discussion: *Minispina* was included by Brunton et al. (2000, p. 469) in Kozlowskiini: it shows the strong cancellate ornament of *Kozlowskia* and *Eomarginifera*, but is transverse and has a hinge row of spines.

2.1B Subfamily **SCAPHARININAE** Cooper & Grant, 1975

[nom. transl. hic ex Scapharinidae Cooper & Grant, 1975, p. 895. Syn. Incisiidae Grant, 1976, p. 103].

Diagnosis: Small shells, ventral spines few, strong and halteroid, without well formed umbonal slope or hinge row, little concentric or radial ornament. Some genera subtriangular in shape and sulcate, marginal ridges well developed in both valves. Permian.

Genera: *Scapharina* Cooper & Grant, *Callyconcha* Waterhouse, *Comuquia* Grant, *Cyrtalosia* Termier & Termier, *Incisius* Grant (possibly synonymous with *Cyrtalosia*), *Rhytisia* Cooper & Grant, *Simplicarina* Cooper & Grant.

Discussion: Brunton et al. (2000, p. 441) amalgamated most of the genera as Incisiini, and included *Scapharina* without realizing the family group implications.

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

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

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

2.2A Subfamily **PAUCISPINIFERINAE** Muir-Wood & Cooper, 1960

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

Diagnosis: Shells with generally 6 or more large strut spines on ventral valve.

2.2Aa Tribe **PAUCISPINIFERINI** Muir-Wood & Cooper, 1960

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

Diagnosis: Transverse shells with varied radial and concentric ornament and three pair of large strut spines on ventral valve, large ears, transverse outline. Permian.

Genera: *Paucispinifera* Muir-Wood & Cooper, *Anemonaria* Cooper & Grant, *Caricula* Grant, *Lamnimargus* Waterhouse, *Retimarginifera* Waterhouse.

Discussion: Several genera placed in this group by Brunton et al. (2000, p. 447) are transferred to Dictyoclostidae, because they lack strut spines and heavy marginal ridges.

2.2Ab Tribe **PROBOLIONIINI** Muir-Wood & Cooper, 1960

[nom . transl. hic ex Probolioniinae Muir-Wood & Cooper, 1960, p. 237. Syn. Paramarginiferinae Lazarev, 1990, p. 82; Kozlowskiini Brunton et al. 1995, p. 928].

Diagnosis: Subquadrate or subelongate shells with concentric and radial ornament, large ventral strut spines, ears small. Lower Carboniferous to Upper Permian.

Genera: *Probolionia* Cooper, *Alitaria* Cooper & Muir-Wood, *Cathaysia* Jin, *Eomarginifera* Muir-Wood, ?*Huatangia* Liao & Meng, *Kozlowskia* Fredericks, *Paramarginifera* Fredericks, ?*Paramuirwoodia* Zhang, *Paryphella* Liao (syn. *Spinoparyphella* Liang), *Rugivestis* Muir-Wood & Cooper.

Discussion: This group is very close to Paucispiniferini, and is distinguished by shape. The distinctive features include ventral sulcus, anterior nasutation in two genera, ribbing and weak rugae, with up to six or so functional strut spines, and well developed ventral marginal ridge. *Kozlowskia* and *Eomarginifera* have fewer dorsal trails than in *Probolionia*, but overall are close. Brunton et al. (2000, p. 429) included as Paramarginiferini Lazarev, 1986 an array of genera, some like *Paramarginifera* very close to *Probolionia*, others not necessarily marginiferid. As well a distinct association of transverse nasute shells was included, here separated. *Huatangia* lacks strong spines, and its position is not certain. *Paramuirwoodia* is tentatively placed here from the assessment by Shi (1995, p. 64).

2.2B Subfamily **BIBATIOLINAE** new

Name genus: *Bibatiola* Grant, 1976, p. 136.

Diagnosis: Small transverse shells with wide hinge and well rounded anterior and lateral margins, nasute anterior, ventral sulcus absent or restricted to median disc, both valves costate. Spines few, number 3 or more strut spines. Ventral and dorsal marginal ridges well developed. Carboniferous and Permian.

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

Discussion: In shape these shells are like *Chonetella*, but have different spines and high marginal ridges, and differ from Paucispiniferinae in shape, and three strut spine arrangement.

2.3 Family **COSTISPINIFERIDAE** Muir-Wood & Cooper, 1960

[nom. transl. hic ex Costispiniferinae Muir-Wood & Cooper, 1960, p. 217].

Diagnosis: Spines numerous and on both valves.

2.3A. Subfamily **COSTISPINIFERINAE** Muir-Wood & Cooper, 1960

[Costispiniferinae Muir-Wood & Cooper, 1960, p. 217].

Diagnosis: Subquadrate to suboval shells with spines on both valves, ventral spines differentiated, many coarse and halteroid, not arrayed along rows posteriorly, or developed into strut spines; ribs may be present, concentric laminae irregular. Corpus cavity shallow to generally deep. Cardinal process marginiferid, large pustules in one or two anterior rows on dorsal interior, marginal ridges moderately to very well developed, shells not geniculate and trails not conspicuous. Permian.

Genera: *Costispinifera* Muir-Wood & Cooper, *Dyschrestia* Grant, *Echinauris* Muir-Wood & Cooper, *Holotricharina* Cooper & Grant, *Paraplicatifera* Zhao & Tan, *Pseudoavonia* Wang.

Discussion: Poorly known *Paraplicatifera* and *Pseudavonia* have strong ribs and were included by Brunton et al. (2000, p. 436).

2.3B Subfamily **DESMOINESIINAE** new

Name genus: *Desmoinesia* Hoare, 1960, p. 226.

Diagnosis: Spines on ventral valve somewhat like those of marginiferids with umbonal slope or hinge

rows, tending to be mutiple, and rare to moderate number of dorsal spines. Ribs and concentric rugae moderately developed. Upper Carboniferous.

Genera: *Desmoinesia* Hoare (syn. *Rudinia* Muir-Wood & Cooper), *Sandia* Sutherland & Harlow.

Discussion: *Desmoinesia* is close to margniferids externally and internally, but the single spine rows have become slightly diffused by the presence of more spines, and dorsal spines are present. It is marginiferid internally. *Sandia* is not so close and has less developed dorsal marginal ridge (Sutherland & Harlow 1973). The group would appear to have been source material for younger and more spinose Costispiniferidae, and evolved from Margniferidae, as represented by *Protoniella* Bell, of upper Visean and lower Serpukhovian age. *Protoniella* bears scattered ventral spines, and a row of spines along the hinge and another from the umbo down the flanks (Bell 1929, Muir-Wood & Cooper, 1960, p. 265).

2.3C Subfamily **SPINOMARGINIFERINAE** new

Name genus: *Spinomarginifera* Huang, 1932, p. 16.

Diagnosis: Suboval to subquadrate shells with dorsal geniculation as a rule, characterized by very fine and closely spaced spines on both valves, ventral ornament may include some slightly stronger spines, dorsal valves with dimples and pits, and suggestion of concentric rugae, rugae may develop over ventral valve. Marginal ridges well developed, especially on dorsal valve. Upper Carboniferous to Upper Permian.

Genera: *Spinomarginifera* Huang, *Echinauriella* Lazarev, *Neoplicatifera* Jin, Liao & Hou, *Onopordumaria* Waterhouse, *Zhuaconcha* Liang.

Discussion: *Echinauriella* is particularly close to *Onopordumaria*, but is Upper Permian rather than Upper Carboniferous.

3. Superfamily HORRIDONIOIDEA Muir-Wood & Cooper, 1960 (Table 3)

[nom. transl. hic ex Horridoniinae Muir-Wood & Cooper, 1960, p. 292].

Diagnosis: Ornament characteristic, with minor radial and concentric ornament, few to moderately numerous and well spaced spines, may be specialized and very stout along the hinge. Corpus cavity generally but not always thick. Fine numerous pustules internally, no heavy marginal ridges.

Discussion: Of minor significance numerically, this group appears to form an independent lineage that commenced in Devonian with primitive genera bearing teeth, and lasted until Upper Permian.

Subfamily Horridoniinae Muir-Wood & Cooper was published at the same time as Leioproductinae. It does not enjoy page precedence, but is selected for the principal family group name because *Horridonia* was named and described long before *Leioproductus*.

Table 3. Superfamily Horridonioidea Muir-Wood & Cooper, 1960

3.1 Family Leioproductidae Muir-Wood & Cooper, 1960
3.1A Subfamily Leioproductinae Muir-Wood & Cooper, 1960
3.1Aa Tribe Leioproductini Muir-Wood & Cooper, 1960
3.1Ab Tribe Hunanoproductini Liang, 1990
3.1B Subfamily Levitusiinae Muir-Wood & Cooper, 1960
3.1Ba Tribe Levitusiini Muir-Wood & Cooper, 1960
3.1Bb Tribe Geniculiferini Waterhouse, new
3.1Bc Tribe Araxilevini Waterhouse, new
3.2 Family Horridoniidae Muir-Wood & Cooper, 1960
3.2A Subfamily Horridoniinae Muir-Wood & Cooper, 1960
3.2B Subfamily Lethamiinae Waterhouse, 2001

3.1 Family **LEIOPRODUCTIDAE** Muir-Wood & Cooper, 1960

[nom. transl. Waterhouse 1978, p. 20 ex Leioproductinae Muir-Wood & Cooper, 1960, p. 168].

Diagnosis: Shell small to large, ribbing normally absent or weak, never at beak, scattered ventral

spines, posterior spines may be in row along or inclined from hinge but often absent, dorsal spines as a rule absent. Cardinal process with pit or groove in front in various genera.

3.1A Subfamily **LEIOPRODUCTINAE** Muir-Wood & Cooper, 1960

[Leioproductinae Muir-Wood & Cooper, 1960, p. 168].

Diagnosis: Concentric wrinkles weak or absent, shells small.

3.1Aa Tribe **LEIOPRODUCTINI** Muir-Wood & Cooper, 1960

[nom. transl. Brunton, Lazarev & Grant in Brunton et al. 2000, p. 476 ex Leioproductinae Muir-Wood & Cooper, 1960, p. 168].

Diagnosis: Small shells with median ventral fold bearing row of spines, concentric rugae weak or absent, scattered spines, teeth in early genera. Dorsal median septum may be posteriorly cleft. Middle to Upper Devonian.

Genera: *Leioproductus* Stainbrook, *Ardviscus* Lazarev, *Bispinoproductus* Stainbrook, *Mesoplica* Reed, ?*Stelckia* Crickmay.

Discussion: The ventral median fold with line of spines on the ventral valve is an unusual feature for Productidina. It developed in several of the genera that were incorporated within Leioproductini by Brunton et al. (2000). *Stelckia* Crickmay of Middle Devonian (Givetian) age has teeth and sockets like *Ardviscus*, and light radial ribs or spine bases, concentric ornament and median ventral row of spines. It was classed in Productellinae by Brunton et al. (2000, p. 424), and unlike most but not all horridonioids and productelloids, has radials. The remaining genera are of upper Devonian (Famennian) age.

3.1Ab Tribe **HUNANOPRODUCTINI** Liang, 1990

[nom. transl. hic ex Hunanoproductinae Liang, 1990, p. 197 (465)].

Diagnosis: Shells smooth, or with gentle sulcus, no median ventral fold, lacking regular or pronounced concentric wrinkles, ventral spines variously in row along hinge or scattered and well spaced, no median row, dorsal spines rarely present. Teeth in some genera. Upper Devonian to Lower Carboniferous.

. Genus: *Hunanoproductus* Hou Hong-Fei, *Galeatella* Muir-Wood & Cooper, *Grandiproductella* Lazarev, *Kavesia* Lazarev, *Productelloides* Kotlyar.

Discussion: This a small assembly of diverse but simple genera, allied to *Leioproductus*, but lacking the median ventral fold and spine row. Dorsal spines seem to be figured for *Kavesia* by Kotlyar (1985), and *Hunanoproductus* and *Grandiproductella* have ventral spines at the hinge. Teeth are present in the latter genus and in *Productelloides*.

3.1B Subfamily **LEVITUSIINAE** Muir-Wood & Cooper, 1960

[Levitusiinae Muir-Wood & Cooper, 1960, p. 295].

Diagnosis: Medium to large shells, ventral spines scattered or in quincunx, row of spines along the hinge in some forms, concentric wrinkles prominent.

Discussion: Close to Leioproductinae, but shells larger and more typically productiform, and with regular concentric rugae.

3.1Ba Tribe **LEVITUSIINI** Muir-Wood & Cooper, 1960

[nom. transl. Brunton, Lazarev & Grant in Brunton et al. 2000, p. 453 ex Levitusiinae Muir-Wood & Cooper, 1960, p. 295. Syn. Acanthoplectinae Nalivkin, 1979].

Taxonomy: According to Brunton et al. (1995, p. 927), Levitusiini had been proposed by Lazarev (1985).

Diagnosis: Genera of relatively large size with regular concentric wrinkles at least over disc, moderate to deep body corpus, no radial ribs or striae, spines sparse, usually thin, spine row on median ridge, also spine row in front of ears, and suggested along or inclined from hinge, dorsal spines absent or rare. Weak cardinal ridges. Lower Carboniferous.

Genera: *Levitusia* Muir-Wood & Cooper, *Acanthoplecta* Muir-Wood & Cooper, *Admodorugosus* Brunton & Mundy, *Kadraliproductus* Galitskaya.

Discussion: *Admodorugosus* and *Kadraliproductus* have well defined concentric wrinkles, median ventral ridge, and scattered ventral spines as in *Levitusia*. The ventral median fold and/or median row of spines are shared with *Leioproductus*, which is regarded as closely allied. The ventral fold and spine row are somewhat evanescent features in populations and in allied species (Lazarev 1992), but even so are unusual enough to constitute a significant feature. Internal pustules are fine and numerous. Most genera lack dorsal spines, but such occur rarely in *Acanthoplecta*.

3.1Bb Tribe **GENICULIFERINI** new

Name: *Geniculifera* Muir-Wood & Cooper, 1960, p. 187.

Diagnosis: Small arched shells, wide hinge, low regular concentric wrinkles and lamellae, spines well scattered over ventral valve, no median ventral fold or sulcus, no median row of spines or hinge spines but some spines may appear at cardinal extremities, no teeth, no marginal ridges, low hinge ridges. Lower Carboniferous.

Genera: *Geniculifera* Muir-Wood & Cooper, *Magnumbonella* Carter, *Spinorugifera* Roberts.

Discussion: *Geniculifera* and *Spinorugifera* were included by Brunton et al. (2000, pp. 456ff) in Levitusiini, and have somewhat comparable spines and internal dense pustules, but show less emphasized concentric ornament, and no sign of the central row of spines and low fold medianly in the ventral valve. The spines are close to those of Avoniini, but have less swollen elongate bases, and concentric ornament is a little more prominent. The brachial shields are modified productiform in *Geniculifera* (Muir-Wood & Cooper 1960, pl. 47, fig. 15; Brunton et al. 2000, text-fig. 304.1d, 1e), extending forward rather than laterally. Genera are similar to each other in shape and ornament and interior, and differ from the somewhat disparate association grouped as Hunanoproductini.

3.1Bc Tribe **ARAXILEVINI** new

Name genus: *Araxilevis* Sarytcheva, 1965, p. 222.

Diagnosis: Large shells with subdued or no radial ornament and subdued but distinct concentric wrinkles, ventral spines rather regularly disposed over disc, form row diverging from hinge, scattered on trail, clustered on ears, no dorsal spines. Short numerous trails. Fine dense pustules internally. Upper Permian.

Discussion: The appearance of this distinctive genus is close to Horridonioidea, with referral to Levitusiinae by Sarytcheva (1965), and the genus is distinguished by the presence of the cluster of ear spines. Concentric wrinkles are low but regular, and decorticated shell indicates radial striae. This led Brunton et al. (2000) to suggest a position with Tyloplectinae, but this genus has no ear spines other than in a row along the hinge. Other Buxtoniidae have dorsal spines, and less developed concentric ornament.

?3.-Tribe indet.

The Upper Permian genus *Chonopectella* Sarytcheva, 1966 (nom. nov. pro *Chonopectoides* Sarytcheva, 1965 non Crickmay 1963) might speculatively be allied to Leioproductidae because of its shape and almost smooth shell. It has a small thin shell with intersecting fine oblique rugae, single submedian rib, and rare spines at the hinge. There are no concentric rugae or radials other than the median rib.

3.2. Family **HORRIDONIIDAE** Muir-Wood & Cooper, 1960

[nom. transl. Waterhouse 1978, p. 20 corr. hic ex Horridoniinae Muir-Wood & Cooper, 1960, p. 292].

Diagnosis: Medium to large shells as a rule, with spines in distinct pattern, varying in different genera, often on both valves and along hinge. Little radial or concentric ornament, minor internal thickening, dense pustulation in both valves.

3.2A Subfamily **HORRIDONIINAE** Muir-Wood & Cooper, 1960

[Horridoniinae Muir-Wood & Cooper, 1960, p. 292].

Diagnosis: Row of strong spines close to hinge along ventral and/or dorsal valve, scattered other spines, rare to moderately numerous over dorsal valve. Upper Carboniferous and Permian.

Genera: *Horridonia* Chao (syn. *Pleurohorridonia* Dunbar), *Baillenia* Nelson & Johnson, *Burovia*

Ustritsky, *Praehorridonia* Ustritsky, *Sowerbina* Fredericks, *Tityrophoria* Waterhouse.

Discussion: *Sowerbina* is regarded as valid (Bamber & Waterhouse 1971). *Praehorridonia* has a row of ventral spines along the hinge (Nelson & Johnson, 1968).

3.2B Subfamily **LETHAMIINAE** Waterhouse, 2001

[nom. transl. hic ex Lethamiini Waterhouse, 2001, p. 17].

Diagnosis: Spines numerous and evenly spaced over both valves, no special hinge row. Upper Carboniferous and Permian.

Genera: *Lethamia* Waterhouse, *Rugoclostus* Eaton, *Wooramella* Archbold.

Discussion: These genera are linked with *Horridonia* and *Leioproductus* through the dense internal pustulation and reduced ornament other than spines. Shells are moderately close to *Galeatella*, but dorsal spines are numerous. *Rugoclostus* has light radial and concentric ornament and moderately numerous dorsal and ventral spines.

4. Superfamily PRODUCTOIDEA Gray, 1840 (Table 4)

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

Diagnosis: Spines few to numerous, halteroid and fine over ventral valve, may be clustered laterally, rarely strong, may be numerous over dorsal valve. Radial ornament prominent, concentric ornament varied, shells small to large in size, simple to moderately elaborate trails. Corpus cavity shallow to deep, muscle adductor scars generally dendritic, marginal ridges moderate to high in only one of the constituent families.

Table 4. Superfamily Productoidea Gray, 1840

4.1 Family Productidae Gray, 1840
4.1A Subfamily Productinae Gray, 1840
4.1Aa Tribe Productini Gray, 1840
4.1Ab Tribe Diaphragmini Waterhouse, new
4.1B Subfamily Retariinae Muir-Wood & Cooper, 1960
4.1C Subfamily Spyridiophorinae Muir-Wood & Cooper, 1960
4.2 Family Dictyoclostidae Stehli, 1954
4.2A Subfamily Dictyoclostinae Stehli, 1954
4.2B Subfamily Callytharrellinae Waterhouse, new
4.2Ba Tribe Callytharrellini Waterhouse, new
4.2Bb Tribe Spinarellini Waterhouse, new
4.2C Subfamily Inflatiinae Sarytcheva, 1977
4.3 Family Buxtoniidae Muir-Wood & Cooper, 1960
4.3A Subfamily Buxtoniinae Muir-Wood & Cooper, 1960
4.3Aa Tribe Buxtoniini Muir-Wood & Cooper, 1960
4.3Ab Tribe Tolmachoffiini Sarytcheva, 1963
4.3Ac Tribe Spinifronsini Waterhouse, 1981
4.3B Subfamily Marginatiinae Waterhouse, new
4.3C Subfamily Tyloplectinae Termier & Termier, 1970

4.1 Family **PRODUCTIDAE** Gray, 1840

[Productidae Gray, 1840, p. 151].

Diagnosis: Radial ornament predominent, dorsal marginal ridge or diaphragm high and slender.

4.1A Subfamily **PRODUCTINAE** Gray, 1840

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

Diagnosis: Radial ornament, ventral spines only, concentric ornament weak, diaphragm and trails well developed.

4.1Aa Tribe **PRODUCTINI** Gray, 1840

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

Diagnosis: Closely ribbed on both valves, spines rare other than along hinge. Carboniferous.

Genus: *Productus* Sowerby (syn. *Protonia* Link, *Hubeiproductus* Yang De-Li, *Pyxis* Von Chemnitz).

4.1Ab Tribe **DIAPHRAGMINI** new

Name genus: *Diaphragmus* Girty, 1910, p. 217.

Diagnosis: Distinguished from Productini by cluster of erect spines on ears or lateral umbonal slopes, other ventral spines numerous to rare. Carboniferous.

Genera: *Diaphragmus* Girty, *Carlinia* Gordon, *Companteris* Lazarev, *Dowhatania* Waterhouse, *Lopasnia* Ilkhovsky.

Discussion: Most genera referred to Productini by Brunton et al. (2000, pp. 467, 469) differ from *Productus* in the details of spinose ornament.

4.1B Subfamily **RETARIINAE** Muir-Wood & Cooper, 1960

[Retariinae Muir-Wood & Cooper, 1960, p. 230].

Diagnosis: Generally somewhat transverse shells with reticulate disc, may have thick spines at base of ventral umbonal flanks or anterior, dorsal spines commonly present. Dorsal median septum long, marginal ridge and ear baffles high in dorsal valve. Lower Carboniferous to Upper Permian.

Genera: *Retaria* Muir-Wood & Cooper, *Antiquatonia* Miloradovich, *Calliomarginatia* Jin (syn. *Aspinosella* Waterhouse), *Kutorginella* Ivanova, *Promarginifera* Shiells, *Svalbardoproductus* Ustritsky, *Tesuquea* Sutherland & Harlow, *Thamnosia* Cooper & Grant (syn. *Neopugilis* Li?), *Thuleproductus* Sarytcheva & Waterhouse (syn. of *Svalbardoproductus*?), *Tubaria* Muir-Wood & Cooper.

Discussion: *Retaria* is regarded as distinct from *Kutorginella*, because it has a few irregularly disposed very large halteroid spines on the type and other species, more prominent than any spines in *Kutorginella*. *Calliomarginatia*, *Tesuquea* and *Tubaria* are distinguished by the absence of dorsal spines, and *Svalbardoproductus* by its very large size and fewer posterior spines than in *Thamnosia*. *Promarginifera* has thicker ribs than usual, but reticulate posterior disc, high hinge ridge, dendritic adductors and long dorsal septum suggest retariin affinities, as in Brunton et al. (2000, p. 475).

4.1C Subfamily **SPYRIDIOPHORINAE** Muir-Wood & Cooper, 1960

[nom. transl. hic ex Spyridiophoridae Muir-Wood & Cooper, 1960, p. 230].

Diagnosis: Coarse ribs with spine row on each arched ear, high internal ridge posteriorly in both valves, but no diaphragm or series of dorsal trails. Dorsal adductor platform forms elevated cup or spyridium. Upper Carboniferous and Lower Permian.

Genera: *Spyridiophora* Cooper & Stehli (mis-spelled *Spiridiophora* in Sarytcheva 1960), *Alexenia* Ivanova.

Discussion: These exceptional genera are upgraded from tribal status preferred by Brunton et al. (2000, p. 475).

4.2 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, ornament of costae over both valves, as a rule strongly reticulated by concentric growth rugae over disc, spines limited to ventral valve, may be large and halteroid. Internal posterior hinge ridge generally well formed, marginal ridges low, may be broad, trails long, simple and may be mutiple. The family appears to have evolved in Early Carboniferous from Productidae.

4.2A Subfamily **DICTYOCLOSTINAE** Stehli, 1954

[Dictyoclostinae Stehli, 1954, p. 316].

Diagnosis: Large reticulate shells with spines clustered laterally in brush or dense array on slope between ears and umbonal slope, or outer ears, may be numerous over trail. Lower Carboniferous to Lower Permian.

Genera: *Dictyoclostus* Muir-Wood, *Dasysaria* Cooper & Grant, *Kunlunia* Wang Zhi, ?*Liraplecta* Jin & Sun, *Pugilis* Sarytcheva, *Reticulatia* Muir-Wood & Cooper.

4.2B Subfamily **CALLYTHARRELLINAE** new

Name genus: *Callytharrella* Archbold, 1985, p. 19.

Diagnosis: Shells without a lateral cluster of spines, spines developed in row close to hinge or close to umbonal slopes of ventral valve.

4.2Ba Tribe **CALLYTHARRELLINI** new

Name genus: *Callytharrella* Archbold, 1985, p. 19.

Diagnosis: Shells large as a rule, moderately to weakly transverse, reticulate ornament well developed over posterior disc. Lower Carboniferous to Middle Permian.

Genera: *Callytharrella* Archbold, *Auloprotonia* Muir-Wood & Cooper, *Chaoiella* Fredericks, *Costiferina* Muir-Wood & Cooper, *Ozora* Carter, *Stereochia* Grant, *Zia* Sutherland & Harlow (syn. *Semilunataproductus* Han).

Discussion: *Costiferina* has a moderately broad marginal ridge in the type species, and was classed as Paucispiniferini by Brunton et al. (2000). Its reticulate ornament, large size and spines suggest a closer relationship to *Callytharrella* and allies. The broad ribs and wide ears also indicate an approach to *Rugatia* Muir-Wood & Cooper, placed within Spinarellini (see below). *Zia* was placed in Anidanthinae by Brunton et al. (2000).

4.2Bb Tribe **SPINARELLINI** new

Name genus: *Spinarella* Cooper & Grant, 1975, p. 1058.

Diagnosis: Medium-sized transverse shells with large ears and subdued reticulate ornament. Hinge ridge well developed, marginal ridges low or not developed, long dorsal median septum, anterior dorsal pustules moderately numerous. Cardinal process short. Permian.

Genera: *Spinarella* Cooper & Grant, *Nudauris* Stehli, *Rugatia* Muir-Wood & Cooper, *Xestosia* Cooper & Grant.

Discussion: This embraces a subset of genera from United States. *Spinarella, Xestosia* and *Nudauris* were referred to Paucispiniferini by Brunton et al. (2000) but lack strut spines and have low marginal ridges. Lazarev (1990, p. 81) referred *Nudauris, Spinarella* and *Xestosia* to Jiguliconchinae Lazarev, 1990. *Jiguliconcha* Lazarev, 1990 is poorly known, with no figured dorsal exterior or ventral interior, but appears marginiferid, and has small ears and marginiferid spine distribution and a few large anterior dorsal pustules.

4.2C Subfamily **INFLATIINAE** Sarytcheva, 1977

[nom. transl. hic ex Inflatiidae Sarytcheva, 1977, p. 102].

Diagnosis: Somewhat elongate to subequidimensional shells with subdued to moderate reticulate ornament, few spines on ventral valve only, form hinge row that may be well developed. Deep corpus cavity, hinge ridge, well developed cardinal process. Carboniferous.

Genera: *Inflatia* Muir-Wood & Cooper (syn. *Adairia* Gordon, Henry & Treworthy), *Kelamelia* Zhang Zi-Lin, *Keokukia* Carter, *Marginoproductus* Tan Zhen-Xiu, *Tenaspinus* Brunton & Mundy.

Discussion: Lazarev (1996), followed by Brunton et al. (2000), lumped Inflatiidae with Yakovleviidae, but *Inflatia* and *Yakovlevia* differ considerably in spine distribution and ornament, as analysed by Shi (1995). The relationship is further elaborated under Yakovleviidae (7.4).

Externally *Keokukia* approaches *Kutorginella*, and it together with *Kelamelia* and *Marginoproductus* was referred to Tribe Retariini by Brunton et al. (2000, p. 474). Internally *Keokukia* differs considerably from *Kutorginella* and *Retaria*, and is more dictyoctostid, with a high posterior hinge ridge in the dorsal valve, subdued marginal ridge and only moderately developed anterior dorsal pustules. *Kelamelia* and *Marginoproductus* are less well known, but seem close.

Limbifera show considerable approach. It has reticulate ornament and hinge row of spines quite unlike Semicostellini Nalivkin to which the genus was referred by Brunton et al. (2000, p. 463). It is distinguished by a ventrally geniculated skirt, and has raised ventral muscle field approaching that of

Yakovlevia. Overall, relationships seem closest with aulostegoids, especially Institellinae, close to the original relationship assessed by Brunton & Mundy (1988b).

4.3 Family **BUXTONIIDAE** Muir-Wood & Cooper, 1960

[nom. transl. Waterhouse 1978, p. 20 ex Buxtoniinae Muir-Wood & Cooper, 1960, p. 255].

Diagnosis: Large shells usually with deep body corpus, ribs over both valves somewhat irregular, because costae tend to swell where giving rise to especially ventral spines, dorsal spines widely present, no specialized strut or large halteroid spines. Concentric ornament usually weak or subdued. Narrow elongate pit generally in front of cardinal process, buttress plates may be present, adductor scars strongly dendritic, dorsal pustules large across broad anterior field, marginal ridges generally subdued, but hinge ridge or lateral cincture developed in some forms.

Discussion: Members of the upper Devonian - Lower Carboniferous Semiproductinae involving such genera as *Semiproductus*, *Lomatiphora* and *Spinocarinifera* have buttress plates or median slit in the posterior dorsal median septum, and spines in *Spinocarinifera* are erect and arise from ribs, though without the swelling typical of Buxtoniidae. Semiproductinae lack dorsal spines and ear clusters, and so approach members of Marginatiinae (Buxtoniidae).

4.3A Subfamily **BUXTONIINAE** Muir-Wood & Cooper, 1960

[Buxtoniinae Muir-Wood & Cooper, 1960, p. 255].

Diagnosis: Spines on both valves.

4.3Aa Tribe **BUXTONIINI** Muir-Wood & Cooper, 1960

[nom. transl. Brunton et al. 1995, p. 928 ex Buxtoniinae Muir-Wood & Cooper, 1960, p. 255. Syn. Kochiproductini Lazarev, 1985, p. 67].

Diagnosis: Ventral spines crowded on lateral umbonal slopes and inner to outer ears. Carboniferous to Lower Permian.

Genera: *Buxtonia* Thomas, ?*Bellaclathrus* Winters, *Flexaria* Muir-Wood & Cooper, *Gemmulicosta* Waterhouse, *Kochiproductus* Dunbar (syn. *Buxtonioides* Mendes), *Labriproductus* Cooper & Muir-Wood (nom. nov. pro *Worthenella* Girty 1938 not Walcott 1901), *Marginicinctus* Sutton, *Setigerites* Girty.

Discussion: *Gemmulicosta* was synonymized with *Buxtonioides* by Brunton et al. (2000, p. 407), but has longer swellings behind spine bases. *Buxtonioides* has ornament identical with that of *Kochiproductus*. Brunton et al. (2000) speculated that it lacked the bordering flange of *Kochiproductus*, but this is unproven, and the flange is not always shown in *Kochiproductus*. They also emphasized that *Buxtonioides* lacks adult buttress plates. So does *Kochiproductus*.

4.3Ab Tribe **TOLMACHOFFIINI** Sarytcheva, 1963

[nom. transl. Brunton et al. 1995, p. 928 ex Tolmachoffiidae Sarytcheva, 1963, p. 82].

Diagnosis: Spines on ventral valve not uniformly distributed, may be crowded on ears or postero-laterally, dorsal spines present. Lower Carboniferous to Lower Permian.

Genera: *Tolmachoffia* Fredericks, *Libys* Massa, Termier & Termier, *Niutoushania* Liao, *Piloricilla* Carter, *Scissicosta* Lazarev, *Squamaria* Muir-Wood & Cooper, *Tomiproductus* Sarytcheva, *Xinshaoproductus* Tan Zhen-Xiu.

Discussion: *Niutoushania* is transferred from Dictyoclostiini (Brunton et al. 2000, p. 494), and the presence of dorsal spines requires clarification. If none it is tyloplectin.

4.3Ac Tribe **SPINIFRONSINI** Waterhouse , 1981

[nom. transl. hic ex Spinifronsinae Waterhouse, 1981, p. 82].

Diagnosis: Costae erratic in course, increasing frequently by branching and intercalation, and may even rejoin anteriorly on ventral valve, crossed by low sharply defined concentric ridges. Spines scattered over disc and trail of both valves, crowded over ventral ears. Lower and early Middle Permian.

Genera: *Spinifrons* Stehli, *Peniculauris* Muir-Wood & Cooper.

Discussion: This is a distinctive group characterized by varied and complex ribbing.

4.3B Subfamily **MARGINATIINAE** new

Name genus: *Marginatia* Muir-Wood & Cooper, 1960, p. 262.

Diagnosis: Distinguished by lack of postero-lateral cluster of spines, spines in row close to ventral hinge. Other spines, ribs and interior as in *Buxtonia*, dorsal spines may be rare. Carboniferous.

Genera: *Marginatia* Muir-Wood & Cooper (syn. *Paramarginatia* Yang Shi-Pu), *Acanthocosta* Roberts, *Brasilioproductus* Mendes, *Tomilia* Sarytcheva, *Umboanctus* Waterhouse.

Discussion: The subfamily is close to Tolmachoffiini in the distribution of ventral and dorsal spines over the disc and trail, but is distinguished by the lack of a ventral cluster of spines.

4.3C Subfamily **TYLOPLECTINAE** Termier & Termier, 1970

[nom. transl. hic ex Tyloplectidae Termier & Termier, 1970, p. 457].

Diagnosis: Ribbed shells with erect spines emerging from slight swellings along ventral ribs. Spines also in hinge and umbonal-ear channel rows, not clustered. Dorsal valve without spines, ribs striate. Lower and ?Middle Permian.

Genera: *Tyloplecta* Muir-Wood & Cooper, *Pseudoantiquatonia* Zhan & Wu.

Discussion: Previously the relationship to Buxtoniidae was not realized, but the spine-rib interrelationship is the same. *Araxilevis* Sarytcheva, referred to the group in Brunton et al. (2000), has different ornament.

5. Superfamily ECHINOCONCHOIDEA Stehli, 1954 (Table 5)

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

Taxonomy: Lazarev (1990) was first as far as I am aware to recognize the superfamily ranking of echinoconchs. Brunton et al. (2000) attributed the elevation to Brunton et al. (1995, p. 928).

Diagnosis: Spines over both valves numerous and fine, commonly in concentric bands, spines may be varied in diameter, but not strongly halteroid or strut, no radial ribbing. Maximum width in front of hinge, posterior dorsal septum cleft or buttress ridges present, dendritic adductors, modest development of marginal ridges, dorsal internal pustules seldom very large, but crowded anteriorly.

Table 5. Superfamily Echinoconchoidea Stehli, 1954

5.1 Family Echinoconchidae Stehli, 1954
5.1A Subfamily Echinoconchinae Stehli, 1954
5.1Aa Tribe Echinoconchini Stehli, 1954
5.1Ab Tribe Karavankinini Ramovs, 1969
5.1B Subfamily Juresaniinae Muir-Wood & Cooper, 1960
5.1Ba Tribe Juresaniini Muir-Wood & Cooper, 1960
5.1Bb Tribe Bathymyoniini Lazarev, 1990
5.2 Family Waagenoconchidae Muir-Wood & Cooper, 1960
5.2A Subfamily Waagenoconchinae Muir-Wood & Cooper, 1960
5.2Aa Tribe Waagenoconchini Muir-Wood & Cooper, 1960
5.2Ab Tribe Balkasheconchini Waterhouse, new
5.2B Subfamily Pustulinae Waterhouse, 1981
5.3 Family Sentosiidae McKellar, 1970
5.3A Subfamily Sentosiinae McKellar, 1970
5.3Aa Tribe Sentosiini McKellar, 1970
5.3Ab Tribe Bagrasiini Nalivkin, 1979

5.1 Family **ECHINOCONCHIDAE** Stehli, 1954

[Echinoconchidae Stehli, 1954, p. 326].

Diagnosis: Planoconvex profile, short dorsal trail, spines recumbent, in concentric bands. Corpus cavity generally deep.

5.1A Subfamily **ECHINOCONCHINAE** Stehli, 1954

[nom. transl. Muir-Wood & Cooper, p. 243, ex Echinoconchidae Stehli, 1954, p. 326].

Diagnosis: Spines differentiated in size, no buttress plates or cardinal pit.

5.1Aa Tribe **ECHINOCONCHINI** Stehli, 1954

[nom. transl. Brunton et al. 1995, p. 929 ex Echinoconchidae Stehli, 1954, p. 326. Syn. Calliprotoniinae Lazarev, 1985, p. 71].

Diagnosis: Medium to large shells with cuesta- or step-like concentric bands, smooth posteriorly, spines differentiated in size along concentric bands, thick in one or two spine rows posteriorly, thin in rows anteriorly on each band, often subprostrate. Middle Carboniferous to Lower Permian, with Upper Devonian forebear (*Laminatia*).

Genera: *Echinoconchus* Weller, *Alatoproductus* Jin & Zhu (syn. *Chenxianoproductus* Liao & Meng, *Chonostegoidella* Li & Yang), *Calliprotonia* Muir-Wood & Cooper, *Echinaria* Muir-Wood & Cooper, *Laminatia* Muir-Wood & Cooper, *Stepanoconchus* Lazarev.

Discussion: Subfamily Calliprotoniinae Lazarev, 1985, sole member *Calliprotonia*, was distinguished only by its smaller size, higher marginal ridges, and slight differences in ornament involving more lamellose concentric bands. *Alatoproductus* was placed in Sentosiini by Brunton et al. (2000, p. 522), but is judged to be closer to echinoconchids.

Laminatia is included on the basis of its similar ornament, though of Upper Devonian age. Unlike the other genera it has non-dendritic adductor scars.

5.1Ab Tribe **KARAVANKININI** Ramovs, 1969

[nom. transl. Brunton et al. 1995, p. 929 ex Karavankininae Ramovs, 1969, p. 261].

Diagnosis: High relief concentric bands symmetrical in profile, tops bearing concentric rows of spines, distributed by size, separated by wider smooth bands. Lower Carboniferous to Middle Permian.

Genera: *Karavankina* Ramovs, *Echinoconchella* Lazarev.

5.1B Subfamily **JURESANIINAE** Muir-Wood & Cooper, 1960

[Juresaniinae Muir-Wood & Cooper, 1960, p. 266].

Diagnosis: Concentric bands generally confined to anterior, spines may be differentiated by size anteriorly, cardinal process with elongate pit, or two ridges passing forward in parallel one each side of the dorsal median septum, reminiscent of the ridges in *Fimbrinia*, buttress plates may be present in Carboniferous juveniles.

5.1Ba Tribe **JURESANIINI** Muir-Wood & Cooper

[nom. transl. Brunton et al. 1995, p. 929 ex Juresaniinae Muir-Wood & Cooper, 1960, p. 266].

Diagnosis: Quincunxial elongate pustules and spine bases posteriorly, concentric bands limited to anterior and poorly differentiated. Upper Carboniferous to Middle Permian.

Genera: *Juresania* Fredericks, *Ametoria* Cooper & Grant, *Densepustula* Lazarev, *Parajuresania* Lazarev, *Pulchratia* Muir-Wood & Cooper.

5.1Bb Tribe **BATHYMYONIINI** Lazarev, 1990

[nom. transl. hic ex Bathymyoniinae Lazarev, 1990, p. 117].

Diagnosis: *Juresania*-like ornament posteriorly and subechinoconchiform ornament anteriorly. Lower Carboniferous to Middle Permian.

Genera: *Bathymyonia* Muir-Wood & Cooper, *Buntoxia* Lazarev, *Cubacola* Lazarev, ?*Septarinia* Muir-Wood & Cooper, *Septiconcha* Termier et al., *Vediproductus* Sarytcheva.

Discussion: This group, proposed as a nomen nudum by Lazarev (1986, p. 29), was synonymized with Juresaniini by Brunton et al. (2000). *Septarinia* was classed with a question by Brunton et al. (2000) within Pustulinae, but has different posterior spines, spines in concentric bands anteriorly, a prominent dorsal fold, and ventral median septum.

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

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

Diagnosis: Spines may vary in size, but are subuniform over different parts of the shell, not associated in repeated patterns of concentric bands. Dense and uniform on dorsal valve.

Discussion: The family group was downgraded to a tribe by Brunton et al., but its ornament differs considerably from Echinoconchidae in lacking bands with differentiated spines.

5.2A Subfamily **WAAGENOCONCHINAE** Muir-Wood & Cooper, 1960

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

Diagnosis: Spines fine, suberect to erect over ventral valve, may change gradually or abruptly in diameter over portions of shell.

5.2Aa 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. Lower Carboniferous to Upper Permian.

Genera: *Waagenoconcha* Chao (mis-spelled *Waagenochocha* by Brunton et al. 2000, p. 517, syn. *Ruthenia* Fredericks), *Contraspina* Waterhouse*, *Fostericoncha* Waterhouse*, *Gruntoconcha* Angiolini, *Spinauris* Roberts, *Wimanoconcha* Waterhouse*.

Discussion: Frech (1911, pp. 57, 132), intending to name shells now called *Tschernyschewia*, made *Productus abichi* Waagen the type species of his new genus *Septoproductus,* as elaborated by Muir-Wood & Cooper (1960, pp. 126-127). A case has been prepared for suppression of the name (Brunton ICZN Case 3034). The species *abichi* is here considered to belong to *Waagenoconcha* Chao, 1927, not *Gruntoconcha* as supposed by Angiolini (1995) and Brunton et al. (2000, p. 517). Thus *Waagenoconcha* stands under threat of synonymy, unless the prior proposal of *Septoproductus* is set aside. My personal view is that in this instance the rules of zoological nomenclature may be obeyed, and not set aside: every suspension compromises and damages the principles. There will be little difference, and in my experience, the type collections (including *abichi*) at the Geological Survey of India, Calcutta, are in fine shape. (But see Waterhouse 2002, p. 155).

5.2Ab Tribe **BALKASHECONCHINI** new

Name genus: *Balkasheconcha* Lazarev, 1985.

Diagnosis: Waagenoconchiform shells with buttress supports in the dorsal valve.

Genera: *Balkasheconcha* Lazarev, *Buxtoniella* Abramov & Grigorieva.

5.2B Subfamily **PUSTULINAE** Waterhouse, 1981

[Pustulinae Waterhouse, 1981, p. 71].

Diagnosis: Medium to large shells with low rugae, spines arranged in weakly defined rows, no cardinal pit or buttress plates. Lower Carboniferous.

Genera: *Pustula* Thomas, ?*Etheridgina* Oehlert, *Scutepustula* Sarytcheva.

5.3 Family **SENTOSIIDAE** McKellar, 1970

[Sentosiidae McKellar, 1970, p. 27].

Diagnosis: Shallow corpus cavity, concentric bands of spines on ventral valve, spines little differentiated as a rule, dorsal spines crowded.

5.3A Subfamily **SENTOSIINAE** McKellar, 1970

[nom. transl. Brunton et al. 1995, p. 928 ex Sentosiidae McKellar, 1970, p. 27].

Diagnosis: No teeth, spines thin and numerous, may have elongate bases.

5.3Aa Tribe **SENTOSIINI** McKellar, 1970

[nom. transl. Brunton et al. 1995, p. 929 ex Sentosiidae McKellar, 1970, p. 27].

Diagnosis: Concentric rugae or lamellae may be in bands anteriorly. Upper Devonian to Upper Permian.

Genera: *Sentosia* Muir-Wood & Cooper, *Jakutella* Abramov, *Malloproductus* Tachibana, *Markamia* Jin & Shi (syn. *Tuberella* Li, *Uraloconchus* Lazarev), *Sentosioides* Lazarev, *Stegacanthia* Muir-Wood & Cooper.

Discussion: *Laminatia* Muir-Wood & Cooper has bands with diversified spines, as in Echinoconchini. It is of Famenian age, differs from Carboniferous Echinoconchini in having non-dendritic adductor scars, and was classed in Sentosiini by Brunton et al. (2000, p. 522). In terms of critical ornament, it is echinoconchid, whereas in musculature and age, it is sentosiid. *Productellana* Stainbrook, classed in Sentosiini by Brunton et al. (2000, p. 522), appears to be productellid, having interareas but no teeth, and well spaced large ventral spines and scattered thin dorsal spines. *Jakutella* is somewhat exceptional, and *Sentosioides* shows no concentric banding, although growth lines are prominent, suggestive of Rhytialosiinae (8.3A), which are however strophalosiid. Overall the amount of variation is very considerable, and different streams could be recognized.

The only Permian member allocated by Brunton et al. (2000, p. 522) was *Alatoproductus* Jin & Zhu, a remarkable form with dense subequal dorsal spines, and ventral ornament of concentric bands with fine possibly differentiated spines. It is herein transferred to Echinoconchidae.

5.3Ab Tribe **BAGRASIINI** Nalivkin, 1979

[nom. transl. Brunton et al. 1995, p. 929 ex Bagrasiinae Nalivkin, 1979, p. 109].

Diagnosis: Elongate spine bases, simulating ribs, on both valves. Short low buttress plates. Lower Carboniferous.

Genus: *Ericiatia* Muir-Wood & Cooper (syn. *Bagrasia* Nalivkin).

Discussion: This genus is moderately close to *Stegacanthia* Muir-Wood & Cooper.

6. Superfamily AULOSTEGOIDEA Muir-Wood & Cooper, 1960 (Table 6)

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

Taxonomy: Cooper & Grant (1975, p. 822) in December, and Waterhouse (1975) in May, clearly upgraded Aulostegidae to superfamily rank, and were followed by Waterhouse (1978, p. 21). Brunton et al. (2000) preferred to attribute the recognition to themselves (Brunton et al. 1995, p. 932). Strangely enough, three of the same authors elsewhere acknowledged that Cooper & Grant (1975) and Waterhouse (1978) had recognized the superfamily (Brunton, Lazarev & Grant 2000, p. 351).

Diagnosis: Shells generally attached by spines, often rhizoid, or by direct cementation, but with exceptions, ventral interarea generally present, dorsal interarea small or generally absent, no chilidium. Trails may be simple, geniculate, or elaborate, shallow to deep body corpus, brachial ridges enclose small productinid shields, each side of anterior adductors. Cardinal process high with anterior blades, may be supported by buttress plates.

Discussion: For many years post-World War 11, *Aulosteges* and allies have been associated with strophalosiids, principally on the bases of deformed ventral umbo and common presence of interarea, with insistence that strophalosiids and allies were primarily distinguished by being cemented by the ventral umbo. Researchers in Australia and New Zealand have not been satisfied with that interpretation. Waterhouse (1964, p. 55, 1978, p. 20, 1983c, p. 192) explained that in his view the productiform outline of the brachial ridges in particular, as well as aspects of ornament and cardinal process and hinge, demonstrated a closer relationship to Productidina rather than Strophalosiidina. These proposals were elaborated by former student D. J. C. Briggs, but his first attempts at publishing were blocked by referees. Eventually, he succeeded in publishing a thoughtful overview of the relationships (Briggs 1998), and this view was accepted by Archbold (2001). The Briggs' study provides the best rationale published to date, and the observation on the brachial shields remains the most convincing of morphological ties.

Classification: Aulostegidae was depicted in major outline by Muir-Wood & Cooper (1960), and expanded by Cooper & Grant (1975) and Brunton et al. (2000, p. 587). The latter recognized three families, Aulostegidae, Cooperinidae and Scacchinellidae, the latter two with a small number of genera, and highly distinctive, the Aulostegidae large with a diversity of morphotypes. Here the associations are re-examined, with recognition of an additional family, and transfer of Cooperinidae to Strophalosiidina, and some revision of relationships and generic ties.

Table 6. Superfamily Aulostegoidea Muir-Wood & Cooper, 1960

6.1 Family Aulostegidae Muir-Wood & Cooper, 1960
6.1A Subfamily Aulosteginae Muir-Wood & Cooper, 1960
6.1B Subfamily Taeniothaerinae Waterhouse, new
6.1C Subfamily Rhamnariinae Muir-Wood & Cooper, 1960
6.1D Subfamily Septasteginae Waterhouse, new
6.2 Family Echinostegidae Muir-Wood & Cooper, 1960
6.2A Subfamily Echinosteginae Muir-Wood & Cooper, 1960
6.2B Subfamily Sphenosteginae Waterhouse, new
6.2C Subfamily Chonosteginae Muir-Wood & Cooper, 1960
6.2D Subfamily Agelesiinae Cooper & Grant, 1975
6.2E Subfamily Institellinae Muir-Wood & Cooper, 1960
6.2Ea Tribe Institellini Muir-Wood & Cooper, 1960
6.2Eb Tribe Sinuatellini Muir-Wood & Cooper, 1960
6.2F Subfamily Institininae Muir-Wood & Cooper, 1960
6.2G Subfamily Gondolininae Jin et al. 1998
6.3 Family Sacchinellidae Licharew, 1928
6.4 Family Tschernyschewiidae Muir-Wood & Cooper, 1960

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

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

Diagnosis: Spines varied, erect and/or prostrate, often differing in diameter, on both valves, no ribs. Interarea well developed on especially ventral valve. Shells often large, planoconvex as a rule, with dorsal valve planar or gently convex over visceral disc, trail simple. Cardinal process large, bifid to quadrifid, often at angle to commissure, supported or not by buttress plates, adductor scars dendritic, marginal ridge development generally low.

6.1A Subfamily **AULOSTEGINAE** Muir-Wood & Cooper, 1960

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

Diagnosis: Medium-sized shells with prostrate and thick erect spines over ventral valve, erect and thick rhizoid spines over dorsal valve. Ventral interarea moderately high. Middle Permian.

Genus: *Aulosteges* von Helmerson.

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

6.1B Subfamily **TAENIOTHAERINAE** new

Name genus: *Taeniothaerus* Whitehouse, 1928, p. 281.

Diagnosis: Large shells with erect and/or prostrate spines on both valves, not rhizoid on dorsal valve, spine bases variable, spine patterns vary. Lower and Middle Permian.

Genera: *Taeniothaerus* Whitehouse, *Carilya* Archbold, *Lipanteris* Briggs, *Reedoconcha* Kotlyar, *Wyatkina* Fredericks.

Discussion: This subfamily embraces genera that are close to Aulosteginae, but differ in the lack of rhizoid spines. It seems unlikely that these shells were closely attached other than through halteroid spines, and their stability may have depended substantially on their large size and thick corpus. The ventral umbo may be deformed, but acted more as a resting platform than cemented attachment area.

6.1C Subfamily **RHAMNARIINAE** Muir-Wood & Cooper, 1960

[Rhamnariinae Muir-Wood & Cooper, 1960, p. 119. Possible syn. Ramovsininae Sremac, 1986, p. 14].

Diagnosis: Variable spine development on both valves, with or without elongate spine bases, interarea may be low, cardinal process supported by long buttress plates. Permian.

Genera: *Rhamnaria* Muir-Wood & Cooper, ?*Cactosteges* Cooper & Grant, *Colemanosteges*

Waterhouse*, *Megasteges* Waterhouse*, *Ramavectus* Stehli, ?*Ramovsina* Sremac, *Saeptathaerus* Waterhouse*, *Spuriosa* Cooper & Grant.

Discussion: Some genera previously associated with Aulosteginae are transferred to this subfamily. The buttress plates extend either side of the dorsal adductor scars, not like the extended anterior sides of the cardinal process which lie behind the adductor platform on *Taeniothaerus* and were termed buttress plates by Briggs (1998, text-fig. 67). *Rhamnaria* has a cicatrix on the ventral umbo. One peculiar feature of *Saeptathaerus* and *Megasteges* is that no specimens appear to show outlines of the brachial ridges. The one specimen so far figured as *Megasteges nepalensis* that indicated brachial ridges (Waterhouse 1978, pl. 9, fig. 12) was wrongly identified, because it lacks cardinal buttress plates; the specimen might be *Waagenoconcha*. However *Rhamnaria* has brachial ridges. Figures of *Cactosteges* in Cooper & Grant (1975, pl. 230, 231) suggest low buttress plates in only some specimens, and the genus also approaches *Edriosteges* and *Echinosteges*, but has dorsal spines. *Ramovsina* is poorly known.

6.1D Subfamily **SEPTASTEGINAE** new

Name genus: *Septasteges* Waterhouse & Piyasin*, 1970, p. 120.

Diagnosis: Small shells, numerous ventral spines rising from elongate bases in front of umbo, may be joined into continuous ribs, spines moderately crowded on ears. Dorsal spines thin, no prominent bases. Dorsal marginal ridge high and dorsal muscle scars on elevated septa. Middle Permian.

Genera: *Septasteges* Waterhouse & Piyasin, *Bilotina* Reed.

Discussion: A low to moderate interarea and small to large umbonal cicatrix are present. *Bilotina* was included in Juresaniinae by Brunton et al. (2000, p. 513), following Grant (1976) and Waterhouse & Piyasin (1970), but there is no sign of concentric banding. Rather its interarea, spines and costae and internal marginal ridge approach features of Aulostegoidea. The group is distinguished by the development of elongate spine bases joined up (*Septasteges*) or en echelon (*Bilotina*) over the ventral valve, with numerous spines, and by the unusual interior with high marginal ridge and adductoral septa.

Septasteges was described from well preserved material from the early Middle Permian of Thailand. Grant (1976) pointed out that the genus showed approaches to a Salt Range (Pakistan) species and genus, *Strophalosia (Bilotina) subtecta* Reed from the Amb Formation. He was able to prepare some Amb Formation material, which he called topotypes from the Khisor Range. The dorsal valve indicates possible dorsal adductor plates and possible high marginal ridge. Unlike the Thai specimens, no dorsal median septum was preserved. Unfortunately the evidence is not conclusive, and uncertainty remains over the nature of Grant's material, and over its identity with Reed's taxon.

Reed (1944, p. 109, pl. 8, fig. 1-8) described and illustrated his species well. Ventral valves are elongate, laterally compressed, parallel-sided, with steep lateral walls, inflated, shallow sulcus for the full length, not very close to the Thai form. The ventral umbo is strongly enrolled, with cicatrix and low interarea. There are small elongate pustules over the ventral umbo and posterior ventral valve, whereas the Thai material has spines arising directly from the umbonal shell. Anteriorly, spine bases in *subtecta* are very crowded and only moderately prolonged, and arranged in dense quincunx. The ornament of Thai ventral valves is best exemplified in material described by Grant (1976). In this form over most of the shell except posteriorly and laterally, the spines are aligned and rare along ribs, interpreted as spine bases. The ribs pass from the posterior shell to the anterior margin, with occasional introduction of a rare new rib by intercalation. Unlike the arrangement in *Bilotina subtecta*, the rises are not in quincunx, and are much longer, and less crowded. On the flanks, spine bases are long, but shorter than on the median shell. In the dorsal valve of Thai *Septasteges*, the spines arise from either an almost smooth shell (*S. acanthus*), or from small pustules (*S. praeclarus**). In *Bilotina*, the dorsal valve is heavily pitted and pustuled, and larger tubercles are developed laterally.

Reed (1944) recorded both a ventral and dorsal medium septum: the Thai species has no ventral septum. But Grant (1976) suggested that the ventral valve of type *Bilotina* did lack a septum, and the absence of the dorsal septum from Grant's dorsal valve of *subtecta* is probably due to preservation. In the meantime, pending clarification of the species involved, and the generic limits, *Septasteges* is treated as a valid taxon, distinguished, apparently, from *Bilotina* by less crowded and longer spine bases on the ventral valve and less pustular and pitted dorsal valve, with uncertainities remaining over how it compares with the

interior of *Bilotina*. It therefore lies under possible threat of synonymy, but, given the poor knowledge of *Bilotina subtecta*, is used as name bearer for the subfamily.

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

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

Diagnosis: Characterized by the absence of dorsal spines, ventral spines may be rhizoid. Marginal ridges may be high.

Discussion: There is a wide range of morphotypes.

6.2A Subfamily **ECHINOSTEGINAE** Muir-Wood & Cooper, 1960

[Echinosteginae Muir-Wood & Cooper, 1960, p. 101].

Diagnosis: Medium-sized to moderately large, often subquadrate genera with well developed postero-lateral ventral rhizoid spines, some to little or no radial ornament, low to high interarea, with pseudodeltidium. Strong dorsal marginal ridge, adductor scars well developed in both valves. Upper Carboniferous to Permian.

Genera: *Echinosteges* Muir-Wood & Cooper, *Edriosteges* Muir-Wood & Cooper, *Howseia* Logan, ?*Lercarella* Mascle & Termier, *Limbella* Stehli, *Neoedriosteges* Liang.

Discussion: *Limbella* is distinguished by fine radials. *Lercarella* is a poorly known genus, regarded as having an uncertain position in Brunton et al. (2000, p. 563). Its high and wide interarea, large size and posteriorly directed spines suggest Echinosteginae. The validity of *Neoedriosteges* requires assessment, and it was synonymized with *Edriosteges* by Brunton et al. (2000).

6.2B Subfamily **SPHENOSTEGINAE** new

Name genus: *Sphenosteges* Muir-Wood & Cooper, 1960.

Diagnosis: Small often ovally subtriangular shells with fine ventral spines as a rule, and lacking the burst of strong and generally rhizoid postero-lateral spines found in Echinosteginae. Marginal ridges not strong. Middle and ?Upper Permian.

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

Discussion: This subfamily associates genera that were placed with Echinosteginae by Brunton et al. (2000), but differ in shape, ventral ornament, and dorsal interior. Arguably *Strophalosiella* Licharew is allied: it is covered by fine ribs (cf. *Baissalosteges*), and has ventral spines, but the genus needs to be assessed.

6.2C Subfamily **CHONOSTEGINAE** Muir-Wood & Cooper, 1960

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

Diagnosis: Small shells with complex spinose corpus margin, strong geniculation, short trails, strong anterior ribs, generally low interareas. Permian.

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

Discussion: *Strophalosiina* has high ventral interarea, and anterior costae suggestive of Chonosteginae, but the anterior margin is simpler. It was formerly placed in Echinosteginae.

6.2D Subfamily **AGELESIINAE** Cooper & Grant, 1975

[nom. transl. Brunton et al. 1995, p. 932 ex Agelesiidae Cooper & Grant, 1975, p. 980].

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

Genera: *Agelesia* Cooper & Grant, ?*Liolimbella* Li Li, ?*Rhytibulbus* Li Li (mis-spelled *Rhytibulus* by Brunton et al. 2000, p. 467), *Xenosteges* Muir-Wood & Cooper.

Discussion: *Xenosteges* Muir-Wood & Cooper was placed in Echinosteginae by Brunton et al. (2000). It was pointed out by Brunton et al. (2000, p. 467) that the poorly known *Liolimbella* Li Li looked somewhat like *Rhytibulbus* (misspelled *Rhytibulus*), also found in beds of Lower Permian age in China, and this is adopted, though the material needs to be examined, or the description amplified.

6.2E Subfamily **INSTITELLINAE** Muir-Wood & Cooper, 1960

[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.

6.2Ea Tribe **INSTITELLINI** Muir-Wood & Cooper, 1960

[nom. transl. hic ex Institellinae Muir-Wood & Cooper, 1960, p. 117].

Diagnosis: Trails ribbed by bordering structures of gutters, flanges or skirts. Lower Carboniferous to Middle Permian.

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

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

6.2Eb Tribe **SINUATELLINI** Muir-Wood & Cooper, 1960

[nom. transl. hic 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].

Diagnosis: Ornament elaborate and varied, often reticulate, interarea low, cardinal process low, broad. Lower Carboniferous to Middle Permian.

Genera: *Sinuatella* Muir-Wood, *Costellarina* Cooper & Muir-Wood, 1967 (nom. nov. pro *Costellaria* Muir-Wood & Cooper, 1960 non Swainson), *Glyptosteges* Cooper & Grant.

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

6.2F Subfamily **INSTITININAE** Muir-Wood & Cooper, 1960

[Institininae Muir-Wood & Cooper, 1960, p. 164].

Diagnosis: Concentric wrinkles prominent, spines and elevations sited along wrinkles, and posterior spines developed. Lower Carboniferous.

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

Discussion: The subfamily associates several genera with allied ornament and of much the same age, previously scattered in different groupings. *Institina* was treated as a member of Institellinae by Brunton et al. (2000, p. 599), and the subfamily not even mentioned as a synonym. *Stipulina* is shaped like *Agelesia*, but has coarse rugae and different spines, and is distinctly older than members of the Agelesiinae, with which it was associated in the revised brachiopod treatise.

6.2G Subfamily **GONDOLININAE** Jin, Brunton & Lazarev, 1998

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

Diagnosis: Elongate triagonal shell with long narrow ventral interarea, rhizoid spines on ventral umbonal margins. Lower Carboniferous.

Genus: *Gondolina* Jin & Liao.

6.3 Family **SCACCHINELLIDAE** Licharew, 1928

[nom. transl. Williams 1953, p. 12 ex Scacchinellinae Licharew 1928, p. 265].

Diagnosis: Conical ventral valve with transverse partitions apically, lid-like dorsal valve and deep corpus cavity. Dorsal and ventral spines, including rhizoid spines. Prominent ventral median septum, widely bilobed cardinal process. Lower to Middle Permian.

Genera: *Scacchinella* Gemmellaro, *Derbyella* Grabau.

6.4 Family **TSCHERNYSCHEWIIDAE** Muir-Wood & Cooper, 1960

[Tschernyschewiidae Muir-Wood & Cooper, 1960, p. 126].

Diagnosis: Ornament somewhat waagenoconchid, varying to pustular, no to high interarea, concavo-convex profile, cicatrix common with support spines. Middle and Upper Permian.

Genera: *Tschernyschewia* Stoyanow, *Megatschernyschewia* Sremac, *Reedosepta* Waterhouse*, *Trigonoproductus* Waterhouse*.

Discussion: Muir-Wood & Cooper (1960) and Cooper & Grant (1975) evaluated Tschernyschewiidae as a full family, whereas Brunton et al. (2000, p. 608) relegated it to subfamily level within Scacchinellidae. The substantial differences in ornament and nature of the dorsal valve in the two groups support Muir-Wood & Cooper (1960).

The similarities between Tschernyschewiinae and Waagenoconchinae must raise questions about relationships and classification, as expressed, albeit fleetingly and inaccurately, by Waterhouse (1978, pp. 20, 21).

7. Superfamily LINOPRODUCTOIDEA Stehli, 1954 (Table 7)

[nom. transl. Waterhouse 1978, p. 20 ex Linoproductinae Stehli, 1954, p. 319. Syn. Striatoidea Nalivkin, 1979, p. 105].

Taxonomy: Brunton et al. (2000, p. 526) claimed that Brunton et al. (1995, p. 928) were first to recognize the superfamily. They did change the ending from -acea to -oidea.

Diagnosis: Ribbing regular and generally fine over both valves. Spines over much of ventral valve, may be dense over ears, generally evenly spaced over disc and trail, and of moderate and subequal diameter, dorsal spines restricted to some genera and groups, strut spines rarely present, concentric rugae present to varying degree, trails simple. Internally, adductor scars plane, striate or dendritic, marginal structures subdued, dorsal pustules varied but numerous.

7.1 Family **LINOPRODUCTIDAE** Stehli, 1954

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

Diagnosis: Ribs distinct, well defined and close-set, with moderately numerous ventral spines, few if any thick, and virtually all erect or suberect, without prolonged bases, may have aureole around spines over ventral corpus or trail. Few genera have dorsal spines or pronounced rugae. Depth of body cavity variable.

7.1A Subfamily **LINOPRODUCTINAE** Stehli, 1954

[Linoproductinae Stehli, 1954, p. 319. Syn. Ovatiinae Lazarev, 1990, p.121].

Diagnosis: Ventral spines only in most genera, shell often large, body cavity deep or shallow, both valves with fine close-set radial ornament, concentric ornament inconspicuous.

7.1Aa Tribe **LINOPRODUCTINI** Stehli, 1954

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

Diagnosis: Ventral spines, well developed row along hinge.

Subtribe **LINOPRODUCTINAI** Stehli, 1954

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

Diagnosis: Shells oval in outline, transverse or elongate, umbo prominent, ears developed, venter arched. Spines evenly distributed or rare over ventral valve and forming hinge row, development symmetrical and shell free-living. Lower Carboniferous to Upper Permian.

Genera *Linoproductus* Chao (syn. *Euproductus* Whitehouse, *Cora* Fredericks, *Levisapicus* Tong), *Balakhonia* Sarytcheva, *Linoprotonia* Ferguson (syn. *Connectoproductus* Donakova), *Marginirugus* Sutton, *Marginovatia* Gordon & Henry, *Ovatia* Muir-Wood & Cooper.

Discussion: *Marginirugus* Sutton is regarded as linoproductoid, not productoid, though included by Brunton et al. (2000) in Productini. Spines form a ventral hinge row, and others lie close to the start of the ventral trail; costellae are fine and close-set. The dorsal marginal ridge is low. Muir-Wood & Cooper (1960, p. 317) also placed the genus in Linoproductidae.

Table 7. Superfamily Linoproductoidea Stehli, 1954

7.1 Family Linoproductidae Stehli, 1954
7.1A Subfamily Linoproductinae Stehli, 1954
7.1Aa Tribe Linoproductini Stehli, 1954
Subtribe Linoproductinai Stehli, 1954
Subtribe Schrenkiellinai Lazarev, 1990
7.1Ab Tribe Stepanoviellini Waterhouse, 1975
Subtribe Stepanoviellinai Waterhouse, 1975
Subtribe Lamiproductinai Liang, 1990
7.1Ac Tribe Fluctuariini Nalivkin, 1979
7.1B Subfamily Devonoproductinae Muir-Wood & Cooper, 1960
7.1C Subfamily Anidanthinae Waterhouse, 1968
7.1D Subfamily Gigantoproductinae Muir-Wood & Cooper, 1960
7.1Da Tribe Gigantoproductini Muir-Wood & Cooper, 1960
7.1Db Tribe Semiplanini Sarytcheva, 1960
7.1E Subfamily Striatiferinae Muir-Wood & Cooper, 1960
7.1Ea Tribe Striatiferini Muir-Wood & Cooper, 1960
7.1Eb Tribe Compressoproductini Jin & Hu, 1978
7.1F Subfamily Proboscidellinae Muir-Wood & Cooper, 1960
7.2 Family Kansuellidae Muir-Wood & Cooper, 1960
7.2A Subfamily Kansuellinae Muir-Wood & Cooper, 1960
7.2B Subfamily Eoproductellinae Lazarev, 1987
7.2C Subfamily Auriculispininae Waterhouse, 1986
7.2Ca Tribe Auriculispinini Waterhouse, 1986
7.2Cb Tribe Lyoniini Waterhouse, 2001
7.2Cc Tribe Filiconchini Waterhouse, 2001
7.2Cd Tribe Siphonosiini Lazarev, 1990
7.2Ce Tribe Undariini Waterhouse, 2001
7.2D Subfamily Paucispinauriinae Waterhouse, 1986
7.2Da Tribe Paucispinauriini Waterhouse, 1986
7.2Db Tribe Coolkilellini Waterhouse, 2001
7.2Dc Tribe Magniplicatinini Waterhouse, 2001
7.3 Family Monticuliferidae Muir-Wood & Cooper, 1960
7.3A Subfamily Monticuliferinae Muir-Wood & Cooper, 1960
7.3B Subfamily Tongluellinae Liang, 1990
7.4 Family Yakovleviidae Waterhouse, 1975

Subtribe **SCHRENKIELLINAI** Lazarev, 1990

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

Taxonomy: The family group unit was proposed as a nomen nudum with no diagnosis, discussion or indication of name genus by Lazarev (1986, p. 30). Brunton et al. (2000) mistakenly indicated the date of the taxon as Lazarev 1986.

Diagnosis: Medium-sized to large transverse shells with long hinge, inconspicuous ventral umbo, medianly flattened ventral disc, spines in row near hinge margin only. Lower and Middle Permian.

Genera: *Schrenkiella* Barchatova (mis-spelled *Shrenkiella* by Brunton et al. 2000, p. 642, syn. ?*Achunoproductus* Ustritsky, *Indigia* Barchatova), *Dictyoclostoidea* Jin & Hu (syn. *Hypolinoproductus* Liang?), *Striatospica* Waterhouse.

Discussion: The row of conspicuous hinge spines is also found in *Linoproductus*, as well illustrated by Cooper & Grant (1975), so that the group is very close to Linoproductinai in spine pattern, and close to Stepanoviellini in shape.

7.1Ab Tribe **STEPANOVIELLINI** Waterhouse, 1975

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

Diagnosis: Small to medium in size, extended hinge in many genera, inconspicuous ventral umbo, transverse outline, and few, generally only ventral spines, not forming prominent hinge row. In several genera the body corpus is shallow.

Discussion: This group is characterized by small size, few and small ventral spines as a rule, rarely with dorsal spines (*Stepanoviella*), hinge may be wide. Costellae well and often closely developed, may be differentiated, on both valves. Linoproductini are less transverse with more prominent umbones, higher posterior walls and often better developed ears and prominent row of hinge spines.

Subtribe **STEPANOVIELLINAI** Waterhouse, 1975

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

Diagnosis: Radial ornament linear and simple. Permian.

Genera: *Stepanoviella* Zavodowsky, *Chianella* Waterhouse (syn. *Longyania* Zhu), *Cimmeriella* Archbold & Hogeboom, *Globiella* Muir-Wood & Cooper, *Liraria* Cooper & Grant.

Discussion: Brunton et al. (2000, p. 544) suggested that *Pseudohaydenella* Liang was possibly a synonym of *Chianella*, but it is nasute and possibly close to *Haydenella* (Chonetellinae 1.4B).

Subtribe **LAMIPRODUCTINAI** Liang, 1990

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

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

Genera: *Asperlinus* Waterhouse & Piyasin (syn. *Lamiproductus* Liang).

Discussion: Liang (1990) proposed Lamiproductidae for a single genus *Lamiproductus* Liang from Zhejiang Province of China. He stressed the "dendritic" ribs. Unrealized by Liang (1990), genus *Asperlinus* Waterhouse & Piyasin, 1970, type species *Productus asperulus* Waagen, 1884 from the Kufri Member, Chhidru Formation, of the Salt Range, Pakistan, is closely related, and possibly senior synonym. The exterior is very close at generic level, and the interior of the dorsal valve has comparable marginal ridges and septum (cf. Waagen 1884, reproduced in Brunton et al. 2000, text-fig. 376.4d with Liang 1990, pl. 35, fig. 11).

Brunton et al. (2000) made no mention of Lamiproductidae and synonymized *Lamiproductus* with *Pseudohaydenella* Liang, 1990. *Asperlinus* was recognized separately. *Pseudohaydenella* was very poorly figured in Liang, and seems to be more convex than *Lamiproductus*, and has simple ribbing. In turn Brunton et al. (2000) suggested that *Chianella* Waterhouse might prove to be senior synonym for *Pseudohaydenella,* which seems possible from the ribs, but is denied by the nasute nature of the anterior.

7.1Ac Tribe **FLUCTUARIINI** Nalivkin, 1979

[nom. transl. hic and cf. Waterhouse 2001, p. 25 ex Fluctuariinae Nalivkin, 1979, p. 107].

Diagnosis: Elongate shells close to Linoproductini, with differentiated ribs, concentric wrinkles, apparently no row of hinge spines. Carboniferous to Middle Permian.

Genus: *Fluctuaria* Muir-Wood & Cooper, ?*Teleoproductus* Li Li.

7.1B Subfamily **DEVONOPRODUCTINAE** Muir-Wood & Cooper, 1960

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

Diagnosis: Suberect spines over ventral valve and along hinge, spines may be wider than ribs which cover ventral valve, dorsal valve with concentric lamellae as traces of trails, and weak radials. Ear baffles on ventral valve, weak dorsal lateral ridges and submarginal ridge. Teeth and interareas in two of three genera. Middle and Upper Devonian.

Genera: *Devonoproductus* Stainbrook (syn. *Striatoproductus* Nalivkin), *Chonopectoides* Crickmay, *Poloniproductus* Biernat & Lazarev.

Discussion: *Poloniproductus* was well figured by Biernat & Lazarev (1988). *Devonoproductus* is more productiform than the other genera, as a convincing forebear of Linoproductidae.

7.1C Subfamily **ANIDANTHINAE** Waterhouse, 1968

[Anidanthinae Waterhouse, 1968, p. 1172].

Diagnosis: Well defined costellae, inconspicuous spines limited to the ventral valve. Dorsal valve lamellate to varying degree. Upper Carboniferous to Upper Permian.

Genera: *Anidanthus* Booker (syn. *Pseudomarginifera* Stepanov), *Akatchania* Kletz, *Fusiproductus* Waterhouse, *Kuvelousia* Waterhouse, *Megousia* Muir-Wood & Cooper, *Nothokuvelousia* Waterhouse, *Protanidanthus* Liao (possibly a synonym of *Fusiproductus*), *Protoanidanthus* Waterhouse.

Discussion: Members of the subfamily approach *Devonoproductus* Stainbrook in the presence of dorsal lamellae, and radials and spines on the ventral valve.

Zia Sutherland & Harlow, 1973 is regarded as Dictyoclostidae, counter to Brunton et al. (2000) and the linoproductid position assigned by its authors: it lacks dorsal lamellae and differs in many other respects.

7.1D Subfamily **GIGANTOPRODUCTINAE** Muir-Wood & Cooper, 1960

[Gigantoproductinae Muir-Wood & Cooper, 1960, p. 330].

Diagnosis: Gigantic, large, or medium-sized shells, hinge at greatest width, shallow corpus cavity, fully covered with close-set ribs, generally narrow interspaces, spines rare, erect, may be surrounded by aureole, cardinal process pit present as a rule.

7.1Da Tribe **GIGANTOPRODUCTINI** Muir-Wood & Cooper, 1960

[nom. transl. Brunton et al. 1995, p. 930 ex Gigantoproductinae Muir-Wood & Cooper, 1960, p. 330].

Diagnosis: Relatively large, thick-walled ventral valve, ventral umbo not strongly incurved, spines on ventral valve as a rule, cardinal process trifid with median ridge well developed or sole element, brachial cones commonly distinct. Carboniferous.

Genera: *Gigantoproductus* Prentice, *Beleutella* Litvinovich, *Datangia* Yang De-Li (syn. *Moderatoproductus* Litvinovich & Vorontsova), *Globosoproductus* Litvinovich & Vorontsova, *Serbarinia* Morozov, *Titanaria* Muir-Wood & Cooper, *Vitiliproductus* Jin & Liao, *Xinjiangiproductus* Yao & Fu.

Discussion: *Vitiliproductus* is a Lower Carboniferous genus with oblique rugae intersecting to form tetrahedral elevations over the corpus, and fine close-set radials are also present. Small ventral spines are developed near the hinge and scattered over the valve, especially in *V. robertsi* Brunton & Mundy, 1988a. These appear to lack posteriorly prolonged bases (Roberts 1971, pl. 31, fig. 3-6, 9-11). The genus was referred to Linoproductinae by Brunton & Mundy (1988a), and to Auriculispininae by Brunton et al. (2000, p. 546), whereas Roberts (1971, p. 129) recorded his material as a gigantoproductid.

7.1Db Tribe **SEMIPLANINI** Sarytcheva, 1960

[nom. transl. Brunton et al. 1995, p. 930 ex Semiplanidae Sarytcheva, 1960, p. 231].

Diagnosis: Medium to large in size, thin shell, incurved ventral umbo, spines either on ventral or both valves, cardinal process bifid or trifid with median ridges commonly developed, no brachial cones. Lower Carboniferous.

Genera: *Semiplanus* Sarytcheva, *Latiproductus* Sarytcheva & Legrand-Blain, *Semiplanella* Sarytcheva & Legrand-Blain, *Talasoproductus* Litvinovich & Vorontsova.

7.1E Subfamily **STRIATIFERINAE** Muir-Wood & Cooper, 1960

[Striatiferinae Muir-Wood & Cooper, 1960, p. 328].

Diagnosis: Elongate shells, narrow hinge, spines on ventral valve only, cardinal process with single myophore lobe.

7.1Ea Tribe **STRIATIFERINI** Muir-Wood & Cooper, 1960

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

Diagnosis: Large, shallow body corpus, short hinge, elongate subtriangular shape, simple trails, cardinal process of single ridge passing into median septum. Spines are inconspicuous, hinge wide, and body corpus shallow. Lower Carboniferous.

Genus *Striatifera* Chao.

7.1Eb Tribe **COMPRESSOPRODUCTINI** Jin & Hu, 1978

[nom. transl. Waterhouse 2001, p. 28 ex Compressoproductinae Jin & Hu, 1978, p. 115].

Diagnosis: Characterized by fine radial ornament, few and erect ventral spines found especially near hinge and moderately high body corpus. Shells may become asymmetric from nestling in host. Permian.

Genera *Compressoproductus* Sarytcheva (syn. *Substriatifera* Kotlyar), *Fallaxoproductus* Li, Gu & Li, *Regrantia* Waterhouse, *Sarytchevinella* Waterhouse.

Discussion: The tribe is close to Linoproductidae, not Monticuliferidae as in Brunton et al. (2000, p. 546). The high and often narrow ventral valve and fine radial ornament are reminiscent of other linoproductids, such as *Proboscidella* Oehlert and *Striatifera* Chao, of Carboniferous age, with narrow short spine bases as in Linoproductidae.

7.1F Subfamily **PROBOSCIDELLINAE** Muir-Wood & Cooper, 1960

[Proboscidellinae Muir-Wood & Cooper, 1960, p. 325].

Diagnosis: Cardinal process bifid. Hinge narrow, trail long and tubular. Lower Carboniferous.

Genus: *Proboscidella* Oehlert.

Discussion: Genus *Proboscidella* Oehlert is an unusual genus with bifid cardinal process, unlike that of Striatiferinae. The nature of the spine bases is poorly known, so that placement of the subfamily is provisional. There is some approach, apparently through convergence, with *Siphonosia* Cooper & Grant and *Undaria* Muir-Wood & Cooper, but these have posteriorly prolonged spine bases and are classed in Kansuellidae.

7.2 Family **KANSUELLIDAE** Muir-Wood & Cooper, 1960

[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 costae or ribs may pass forward into the swollen spine base, and none to one rib may continue forward from the swelling. Erect spines may be numerous on ventral ears. Concentric wrinkles often developed. Ventral muscle field set into shell, not raised anteriorly above floor.

Discussion: Members of this family are characterized by swollen and posteriorly prolonged spine bases over much of the ventral disc: the presence of dorsal spines varies. Costellae or capillae cover both valves, and tend to be less close-spaced than in Linoproductidae. Concentric wrinkling is subdued to well developed on both valves as a rule. The body cavity is generally but not always shallow, and may be deep.

7.2A Subfamily **KANSUELLINAE** Muir-Wood & Cooper, 1960

[Subfamily Kansuellinae Muir-Wood & Cooper, 1960, p. 336].

Diagnosis: Large and transverse, very close to Gigantoproductinae in size and shape. Bilobed cardinal process. Lower Carboniferous.

Genera: *Kansuella* Chao, *Kueichowella* Yang Shi-pu (syn. *Guizhouella* Yang Shi-pu), *Parakansuella* Tan Zhen-Xiu.

Discussion: Spine bases, nature of ribbing and development of concentric ornament help distinguish *Kansuella* from *Gigantoproductus* and allies.

7.2B Subfamily **EOPRODUCTELLINAE** Lazarev, 1987

[Eoproductellinae Lazarev, 1987, p. 49].

Diagnosis: Spines only on ventral valve, with posteriorly prolonged bases, valves also ribbed. Teeth and sockets. Early and Middle Devonian.

Genera: *Eoproductella* Rzhonsnitzkaya, *Plicoproductus* Ljaschenko, *Striatoproductella* Krylova (syn. *Hanaeproductus* Ficner & Havlicek).

Discussion: Spines have especially elongate and prolonged bases in *Plicoproductus* and *Striatoproductella*, of Middle Devonian age, and are well ribbed, especially in *Striatoproductella*.

7.2C Subfamily **AURICULISPININAE** Waterhouse, 1986

[Auriculispininae Waterhouse, 1986b, p. 57].

Diagnosis: Medium-sized with ovally transverse outline, ventral spines may be crowded on ears, scattered over rest of valve, where characterized over disc by elongate gently swollen bases with spine bases directed posteriorly within shell. Dorsal spines rare or absent. Costellae well developed, concentric wrinkles weak to well developed. Body corpus usually narrow.

Discussion: Costellae are not as linear, broad-crested or crowded as in Linoproductidae.

7.2Ca Tribe **AURICULISPININI** Waterhouse, 1986

[nom. transl. Waterhouse 2001, p. 30 ex Auriculispininae Waterhouse, 1986b, p. 57]

Diagnosis: Normally transverse genera with variable number of spines near hinge, often crowded on ears, none on dorsal valve, low wrinkles. Lower Carboniferous to Upper Permian.

Genera: *Auriculispina* Waterhouse, *Costatumulus* Waterhouse, ?*Mistproductus* Yang De-Li, *Nisalaria* Waterhouse*, *Papiliolinus* Waterhouse & Gupta*, ?*Permundaria* Nakazawa, Kato & Choi, *Platycancrinella* Waterhouse.

Discussion: *Platycancrinella* was synonymized with *Cancrinella* Fredericks by Brunton et al. (2000, p. 533) but it lacks dorsal spines and has different more transverse less inflated shape, more gently concave dorsal valve and large ears with many postero-lateral spines. *Cancrinella* differs in shape, has different ventral hinge spines, and many dorsal spines. The two are not synonymous, and belong to different subfamilies.

There is uncertainty about some genera allocated to the subfamily in the revised brachiopod treatise. *Teleoproductus* Li Li was assigned to the subfamily in Brunton et al. (2000, p. 544) but might be linoproductid, possibly allied to the somewhat older *Fluctuaria*. *Linoprotonia* appears to have a number of spines on the ventral ears, with a row of hinge spines, but whether it has prolonged spine bases is not clear: it is provisionally assigned to Linoproductinai.

Brunton et al. (2000, pp. 562, 563) included *Permundaria* Nakamura, Kato & Choi with *Schrenkiella*. *Permundaria* has fine radials, close-set concentric wrinkles and reportedly no spines, and so is difficult to interpret: it possibly has a thin body corpus to suggest Auriculispininae.

7.2Cb Tribe **LYONIINI** Waterhouse, 2001

[Lyoniini Waterhouse, 2001, p. 32].

Diagnosis: Transverse shells with wide hinge and single to double row of erect ventral spines along hinge, scattered body spines with weakly to moderately prolonged slightly swollen bases, dorsal valve may be pitted. Body cavity shallow, both valves with well defined costellae. Permian.

Genera: *Lyonia* Archbold, *Bandoproductus* Jin & Sun, *Cancrinelloides* Ustritsky, *Nambdoania* Waterhouse*.

Discussion: *Lyonia* is particularly close in shape to *Bandoproductus*, but has dorsal spines. This helps demonstrate that presence or absence of dorsal spines in some stock may not be significant to other than generic level.

7.2Cc Tribe **FILICONCHINI** Waterhouse, 2001

[Filiconchini Waterhouse, 2001, p. 33]

Diagnosis: Weakly transverse shells with flat ventral disc, subrectangular outline. Ventral body spines numerous with elongate bases, spines few and not organized in row close to hinge. Middle and Upper Permian.

Genera: *Filiconcha* Dear, *Spitzbergenia* Kotlyar.

Discussion: *Filiconcha* with dorsal spines and *Spitzbergenia* without dorsal spines are close but not identical in shape to *Lyonia* and allies. The difference lies chiefly in the development of hinge spines.

7.2Cd Tribe **SIPHONOSIINI** Lazarev, 1990

[nom. transl. Waterhouse 2001, p. 34 ex Siphonosiinae Lazarev, 1990, p. 130. The name was proposed as a nomen nudum by Lazarev 1986, p. 32].

Diagnosis: Elongate shells with short tubiform ventral trail, narrow hinge and rhizoid spines on ventral valve, marginal structures on both valves. Lower Permian.

Genus: *Siphonosia* Cooper & Grant, 1975.

Discussion: Figures of *Siphonosia* in Cooper & Grant (1975, pl. 466, fig. 5, 12, 14, 15, 24, 21, 24) indicate suberect to subprostrate body spines and scattered erect body spines over the ventral valve, suggestive of an alliance with Auriculispininae. This is strengthened by the development of a dense array of erect sturdy ear spines on the ventral valve.

7.2Ce Tribe **UNDARIINI** Waterhouse, 2001

[Undariini Waterhouse, 2001, p. 34].

Diagnosis: Asymmetric shells with moderately developed irregular hinge, fine diversified ribs, and erect and prostrate ventral spines with prolonged slightly swollen bases, no dorsal spines. No long tubiform trail or heavy dorsal marginal ridge. Lower Carboniferous.

Genus: *Undaria* Muir-Wood & Cooper.

Discussion: The genus *Undaria* Muir-Wood & Cooper looks somewhat similar to *Siphonosia* Cooper & Grant but is much less extreme in its development. The ventral valve, especially as shown in original figures by Muir-Wood & Cooper (1960, pl. 118, fig. 3-11, note fig. 5) appears to have elongate spine bases, indicating a relationship to Auriculispininae. The genus lacks dense ear spines, but variation in number of ear-spines is common in the subfamily. The genus was carefully compared with *Siphonosia* by Cooper & Grant (1975) and appears to have arisen independently from Auriculispinini. The two tribes appear to represent extreme, independent, and presumably "dead-end" developments.

7.2D Subfamily **PAUCISPINAURIINAE** Waterhouse, 1986

[Paucispinauriinae Waterhouse, 1986a, p. 2. Syn. Grandaurispininae Lazarev, 1990, p. 130].

Taxonomy: Paucispinauriinae was proposed by Waterhouse (1986a, June, p. 2) at the same time as Grandaurispininae Lazarev (1986, June, p. 32) was listed, but not proposed or discussed. Brunton et al. (2000, p. 533) claimed that Paucispinauriinae had not been proposed until September, 1986 (Waterhouse 1986b, p. 37), and did not acknowledge that the Lazarev proposal was in a list, with no diagnosis or explanation. Lazarev (1986) did not provide a description or definition that stated in words characters that purported to differentiate the taxon (cf. International Commission for Zoological Nomenclature 2000, article 13.1, p. 17). Waterhouse (1986a) did provide a brief explanation, and indicated both the name genus and allied genera. The proposal was reinforced shortly afterwards by Waterhouse (1986b) and Shi & Waterhouse (1996, p. 100). Not until 1990 did Lazarev (1990, p. 130) provide validation, and its validity dates from 1990. Prior mentions carry no standing, according to the rules of zoological nomenclature.

Diagnosis: Ventral spines generally with elongate bases in regular quincunx over disc, crowded or rare over ears and in row or rows along hinge, dorsal spines if present may be crowded, erect, sometimes unusually large for Productidina. Radial ribs and weak to strong concentric rugae. Body corpus usually moderately thick.

Family relationships: Paucispinauriinae differs from Linoproductidae in having less well defined radial ribs spaced further apart, and in ventral body spines having prolonged bases. Various paucispinauriin genera have a thick body cavity as in Linoproductinae, but this is regarded as of lesser importance. A number of genera carry thin spines also on the dorsal corpus, and several otherwise similar genera differ only in the presence or absence of dorsal spines. Auriculispininae have thin body corpus, less regular ventral spines, more transverse shape as a rule, and generally shorter ventral spine bases.

7.2Da Tribe **PAUCISPINAURIINI** Waterhouse, 1986

[nom. transl. Waterhouse 2001, p. 35 ex Paucispinauriinae Waterhouse, 1986a, p. 2].

Diagnosis: Shells with thick visceral cavity and ventral and dorsal spines, ventral spines numerous or rare over ears. Shape weakly transverse to subelongate, with well inflated ventral valve and high posterior shoulders. Concentric wrinkles weakly developed. Upper Carboniferous and Permian.

Genera: *Paucispinauria* Waterhouse, *Grandaurispina* Cooper & Grant, *Pinegeria* Waterhouse, *Saetosina* Waterhouse, *Spargospinosa* Waterhouse, *Terrakea* Booker.

7.2Db Tribe **COOLKILELLINI** Waterhouse, 2001

[Coolkilellini Waterhouse, 2001, p. 49].

Diagnosis: Small compact shells with moderately thick body cavity, long ventral body spine bases, few or weak hinge spines, no dorsal spines, closely costellate, weak concentric wrinkles. Dorsal valve geniculate, may be pitted. Permian.

Genera: *Coolkilella* Archbold, *Kasetia* Waterhouse, *Magadania* Ganelin.

Discussion: These genera are similar to each other in shape and ornament, and very close to *Paucispinauria* and allies, but distinguished by the absence of dorsal spines. The genera share elongate ventral spine bases.

7.2Dc Tribe **MAGNIPLICATININI** Waterhouse, 2001

[Magniplicatinini Waterhouse, 2001, p. 49].

Diagnosis: Body corpus moderately thick, concentric wrinkles strongly developed. Otherwise close to Paucispinauriini in costation, ventral spines in hinge row or rows, fine, body spines may have prolonged hollow bases, dorsal spines either absent or numerous and erect. Interior somewhat as in Paucispinauriini. Upper Carboniferous to Upper Permian.

Genera: *Magniplicatina* Waterhouse (syn. *Helenaeproductus* Lazarev), *Cancrinella* Fredericks, *Auritusinia* Waterhouse*.

Discussion: Compared with Auriculispininae Waterhouse, 1986, spine bases are generally more elongate and wrinkles are stronger. Ventral adductors are dendritic throughout ontogeny (Shi & Waterhouse 1996, p. 96), whereas ventral adductor scars are striate and subelongate rather than dendritic at early into full maturity in several Auriculispininae.

Brunton et al. (2000, pp. 533, 543) assigned *Cancrinella* to Grandaurispininae (ie. Paucispinauriinae) and *Magniplicatina* to Auriculispininae, but the two genera are so close that the difference in dorsal spinosity would seem to be of generic importance only. *Magniplicatina* is now known to be widespread in the northern hemisphere, including Glass Mountains, Texas. Such species were assigned to *Cancrinella* by Cooper & Grant (1975), until corrected by Brunton et al. (2000).

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

[nom. transl. Waterhouse 1978, p. 20 ex Monticuliferinae Muir-Wood & Cooper, 1960, p. 327].

Taxonomy: Brunton et al. (2000, p. 536) cited their own article (Brunton et al. 1995, p. 929) as being first to treat Monticuliferinae as a full family. See Liang 1990, p. 197.

Diagnosis: Typified by small round blister-like swellings called monticules over the ventral exterior. Erect spines may arise from the middle of the swelling, and the ribs continue forward into the monticule and persist in front. Ventral muscle field raised anteriorly, cardinal process broad and bifid, ginglymus may be developed, brachial shields somewhat elongate in outline. Permian.

Discussion: The family, recognized at this rank by Waterhouse (1978) as independently endorsed by Brunton et al. (1995, p. 929), was treated as an unusual member of Linoproductoidea by Waterhouse (2001). Members of Monticuliferidae may lack radial ornament, and have an unusual ventral muscle field, elevated anteriorly, and exceptional outline for the brachial ridges. The ginglymus on both ventral and dorsal valves and muscle field are well illustrated by Liang (1990, pl. 37, fig. 3, 5).

7.3A Subfamily **MONTICULIFERINAE** Muir-Wood & Cooper, 1960

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

Diagnosis: Capillae present.

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

7.3B Subfamily **TONGLUELLINAE** Liang, 1990

[Tongluellinae Liang, 1990, p. 202].

Diagnosis: Capillae lacking.

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

Discussion: The obscure *Zhejiangoproductus* is largely smooth, with few spines limited to hinge and ears. It is shaped like Monticuliferidae in size, outline, wide sulcus, large disc and geniculate trail.

7.4 Family **YAKOVLEVIIDAE** Waterhouse, 1975

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

Diagnosis: Somewhat transverse shells with geniculate trail, radial ornament and weak if any concentric ornament, strut spines. Lower Carboniferous to Middle Permian.

Genera: *Yakovlevia* Fredericks (syn. *Muirwoodia* Licharew), *Duartea* Mendes, *Sajakella* Nasikanova.

Discussion: Of obscure derivation and relationships, *Yakovlevia* is transverse with flat disc, and its fine radial ornament and sharply geniculate trail suggest Linoproductoidea. Four very prominent strut spines are present, as well as few other body spines and poorly developed row of spines along the ventral hinge. A ginglymus may be developed, and internally the ventral muscle platform is broad and raised, the body cavity moderate to thick, and pustules dense, large and numerous anteriorly. Apart from the strut spines, aspects of the shell, including flat disc, geniculate trail, fine ribs, ginglymus, raised adductor platform, wide low cardinal process, long dorsal septum, and rather elongate brachial shields suggest Monticuliferidae.

The strut spines and arguably the fine ribs recall Marginiferoidea, but the marginal and ear baffle ridge development is low and the trail comparatively simple. Lazarev (1996) considered that the genus is related to *Inflatia* Muir-Wood & Cooper, 1960, a Lower Carboniferous (upper Visean) genus of somewhat different appearance, with sulcus, reticulate ornament, prominent hinge row of ventral spines but no strut spines, and weak development of marginal ridging. It was claimed that the Carboniferous genus *Sajakella* provided the link. *Sajakella* does have coarser ribs than in *Yakovlevia*, but has four strut spines, like *Yakovlevia*, not *Inflatia*. Many of Lazarev's comparisons do not withstand close examination. Shi (1995) provided a critical analysis of affinities and morphologies and concluded that *Yakovlevia* was linoproductoid. Further, there may have been some confusion over the nature of *Sajakella*, which supposedly provided the critical link between *Yakovlevia* and *Inflatia*. *Sajakella barunkhurensis* Lazarev is not yakovleviid, but probolioniin, from its shape and distribution of strut spines, and umbonal slope row of spines.

Suborder STROPHALOSIIDINA Waterhouse, 1975 (Table 8)

Taxonomy: The taxonomy of this suborder has been discussed by Waterhouse (2001). Brunton et al. (1995) erroneously ascribed the suborder to Waagen (1883), although Waagen had not even proposed a family group unit for the genus. Without explicitly correcting the statement, Brunton et al. (2000, p. 565) shifted ground and ascribed the suborder to Schuchert (1913, p. 389), claiming that was done by Brunton et al. 1995: not so. Brunton, Lazarev & Grant (2000, p. 351) acknowledged that Cooper & Grant (1975) had "retained the Productidina with four superfamilies (Strophalosiacea, Aulostegacea, Richthofeniacea, and Productacea)"... whereas Waterhouse (1978) had recognized.... "Strophalosiidina (divided into Strophalosiacea, Richthofeniacea, and Aulostegacea..)". The three subdivisions of Strophalosiidina used by Waterhouse (1975, 1978) are the same as those recognized by Brunton et al. (2000). They claimed that they preferred to follow Lazarev. Lazarev (1987, p. 48) in fact had excluded Richthofenioidea from the suborder - as did Schuchert (1913). Indeed Lazarev (1987, p. 48, 1990, p. 77) included Lyttoniacea [Lyttoniidina], which is excluded from Strophalosiidina by Brunton et al. (2000), as in Waterhouse (1978). In Strophalosiidina "sensu Lazarev 1989", specifically noted by Brunton et al. (2000) as containing the revised brachiopod treatise understanding of Strophalosiidina, the article referred only to what are regarded as Strophalosioidea, with no mention of Richthofenioidea. Thus the original understandings of the *Strophalosia* group in Schuchert (1913) and Lazarev (1987, 1990) were far removed from Strophalosiidina as understood by both Brunton et al. (2000) and by Waterhouse (1975, 1978). The revised brachiopod treatise disregarded and misrepresented the prior proposals by Waterhouse, ascribed the suborder to Schuchert long after the suborder had already been proposed, stated that Lazarev had given the "correct" version, and claimed that the Lazarev version had been followed by Brunton et al. (2000). None of these claims withstand examination.

Table 8. Suborder Strophalosiidina Waterhouse, 1975

Superfamily Strophalosioidea Schuchert, 1913

8.1 Family Strophalosiidae Schuchert, 1913
8.1A Subfamily Strophalosiinae Schuchert, 1913
8.1Aa Tribe Strophalosiini Schuchert, 1913
8.1Ab Tribe Truncateniini Liao, 1982
8.1B Subfamily Echinalosiinae Waterhouse, 2001
8.1Ba Tribe Echinalosiini Waterhouse, 2001
8.1Bb Tribe Arcticalosiini Waterhouse, 2001
8.1C Subfamily Dasyalosiinae Brunton, 1966
8.2 Family Chonopectidae Muir-Wood & Cooper, 1960
8.2A Subfamily Chonopectinae Muir-Wood & Cooper, 1960
8.2B Subfamily Semenewiinae Muir-Wood, 1960
8.3 Family Araksalosiidae Lazarev, 1989
8.3A Subfamily Araksalosiinae Lazarev, 1989
8.3B Subfamily Donalosiinae Lazarev, 1989
8.3C Subfamily Caucasiproductinae Lazarev, 1987
8.3D Subfamily Quadratiinae Lazarev, 1989
8.3E Subfamily Rhytialosiinae Lazarev, 1989
8.4 Family Ctenalosiidae Muir-Wood & Cooper, 1960
8.4A Subfamily Ctenalosiinae Muir-Wood & Cooper, 1960
8.4B Subfamily Mingenewiinae Archbold, 1980
8.4C Subfamily Craspedalosiinae Waterhouse, new

Superfamily Cooperinoidea Pajaud, 1968

9.1 Family Cooperinidae Pajaud, 1968
9.1A Subfamily Cooperininae Pajaud, 1968
9.1B Subfamily Falaferinae Waterhouse, new
9.1C Subfamily Epiceliinae Grant, 1972

Superfamily Richthofenioidea Waagen, 1885

10.1 Family Richthofeniidae Waagen, 1885
10.2 Family Hercosiidae Cooper & Grant, 1975
10.3 Family Teguliferinidae Muir-Wood & Cooper, 1960
10.3A Subfamily Teguliferininae Muir-Wood & Cooper, 1960
10.3B Subfamily Cyclacanthariinae Cooper & Grant, 1975
10.3Ba Tribe Cyclacanthariini Cooper & Grant, 1975
10.3Bb Tribe Collumatini Waterhouse, new
10.3C Subfamily Zalverinae Brunton, 1996
10.4 Family Gemmellaroiidae Williams, 1953

8. Superfamily **STROPHALOSIOIDEA** Schuchert, 1913

[nom. corr. Brunton et al. 1995, p. 931 pro Strophalosiacea Muir-Wood & Cooper, 1960, p. 71 nom. trans ex Strophalosiinae Schuchert, 1913, p. 391].

Diagnosis: Teeth and sockets, large brachial shields outlined by low ridges, extending close to dis margins. Disc concavo- or plano-convex, body corpus mostly slender.

8.1 Family **STROPHALOSIIDAE** Schuchert, 1913

[nom. transl. Stehli 1954, p. 328 ex Strophalosiinae Schuchert, 1913, p. 391].

Diagnosis: Concavo- or plano-convex shells, attached by cicatrix and ventral spines, short trails.

8.1A Subfamily **STROPHALOSIINAE** Schuchert, 1913

[Strophalosiinae Schuchert, 1913, p. 391. Syn. Heteralosiinae Muir-Wood & Cooper, 1960, p. 80].

Diagnosis: Ventral spines only as a rule.

8.1Aa Tribe **STROPHALOSIINI** Schuchert, 1913

[nom. transl. hic ex Strophalosiinae Schuchert, 1913, p. 391].

Diagnosis: Shells without strong radials. Carboniferous to Upper Permian.

Genera: *Strophalosia* King (syn. *Leptaenalosia* King, *Heteralosia* King), *Biplatyconcha* Waterhouse (nom. nov. pro *Platyconcha* Waterhouse 1975 not Longstaff, 1933; syn. *Subtaeniothaerus* Solomina, *Megalosia* Waterhouse), *Coronalosia* Waterhouse & Gupta, *Etherilosia* Archbold, *Leptalosia* Dunbar & Condra, *Lialosia* Muir-Wood & Cooper, *Liveringia* Archbold, *Sphenalosia* Muir-Wood & Cooper.

Discussion: The type species of *Heteralosia* King still awaits adequate understanding. Briggs (1998) pointed out that species assigned to *Heteralosia* by Cooper & Grant (1975) from the Glass Mountains, Texas, belonged to *Etherilosia* Archbold.

8.1Ab Tribe **TRUNCATENIINI** Liao, 1982

[nom. transl. hic ex Truncateniinae Liao, 1982, p. 539. Syn. Licharewiellinae Archbold, 1986b, p. 98].

Diagnosis: Strong radial ornament. Permian.

Genera: *Truncatenia* Liao, *Costalosiella* Waterhouse, ?*Enigmalosia* Czarniecki, *Kufria* Waterhouse*, *Licharewiella* Ustritsky (syn. *Costalosia* Waterhouse & Shah, *Magniderbyia* Ting).

Discussion: This group is distinguished by its strong costae or long spine bases. *Truncatenia* is provisionally regarded as valid, contra Brunton et al. (2000), because it lacks the cluster of posterior ventral spines characteristic of *Licharewiella*. It has well developed marginal ridges, not so far confirmed for *Licharewiella*, which is based on externals only. Provisionally the genus *Costalosiella* is included in the tribe, because it shares the distinctive ribs with *Truncatenia* and *Licharewiella*, yet has strong dorsal spines.

The poorly known genus *Enigmalosia* of Upper Carboniferous age *might* be allied. It has ribs bearing spines, large umbonal cicatrix, indistinct interareas, capillate dorsal valve and costate trail, divided cardinal process, and no teeth. There are converging plates in front of the cardinal process, an indistinct breviseptum, lateral ridge along the hinge, and a cincture separating the trail from the disc (Czarniecki 1969). The genus was classed as Donalosiinae by Brunton et al. (2000, p. 582), but shows little similarity. As one alternative, the genus might prove to be aulostegoid, perhaps close to Institellinae, of which some genera develop ribs. The lack of teeth and unusual dorsal interior and disparate ornament on the two valves of *Enigmalosia* find no ready match, and perhaps the genus is member of an otherwise unknown possibly echinostegid tribe.

8.1B Subfamily **ECHINALOSIINAE** Waterhouse, 2001

[Echinalosiinae Waterhouse, 2001, p. 57].

Diagnosis: Shells distinguished from other members of family by possessing erect spines of one series over dorsal valve. Concentric lamellae developed to varying degree, radial filae generally weak or absent.

8.1Ba Tribe **ECHINALOSIINI** Waterhouse, 2001

[nom. transl. hic ex Echinalosiinae Waterhouse, 2001, p. 57].

Diagnosis: Ventral valve generally with two series of spines. Lower Carboniferous to Upper Permian.

Genera: *Echinalosia* Waterhouse (nom. nov. pro *Multispinula* Waterhouse 1966 not Rowell 1962), *Crossalosia* Muir-Wood & Cooper, *Hontorialosia* Martinez Chacon, *Marginalosia* Waterhouse, *Muirwoodicia* Waterhouse*, *Notolosia* Archbold, *Pseudostrophalosia* Clarke, *Wyndhamia* Booker.

8.1Bb Tribe **ARCTICALOSIINI** Waterhouse, 2001

[Arcticalosiini Waterhouse, 2001, p. 82].

Diagnosis: Ventral and dorsal spines of one order. Permian.

Genera: *Arcticalosia* Waterhouse, *Orthothrix* Geinitz.

Discussion: Members of Araksalosiidae Lazarev also have spines of one order, and these differ in

detail, along with various internal features.

8.1C Subfamily **DASYALOSIINAE** Brunton, 1966

[Dasyalosiinae Brunton, 1966, p. 192].

Diagnosis: Crowded spines of at least two orders on both dorsal and ventral valves. Lower Carboniferous to Upper Permian.

Genera: *Dasyalosia* Muir-Wood & Cooper, *Acanthalosia* Waterhouse, *Bruntonaria* Waterhouse.

8.2 Family **CHONOPECTIDAE** Muir-Wood & Cooper, 1960

[nom. transl. Brunton et al. 1995, p. 931 ex Chonopectinae Muir-Wood & Cooper, 1960, p. 157].

Diagnosis: Prominent row of hinge spines and sparse ventral corpus spines, fine radial and/or concentric ornament, cicatrix varied, hinge long and shell semicircular in outline, low corpus cavity.

8.2A Subfamily **CHONOPECTINAE** Muir-Wood & Cooper, 1960

[Chonopectininae Muir-Wood & Cooper, 1960, p. 157].

Diagnosis: Fine radial ornament, rugae subdued, cicatrix varied. Upper Devonian and Lower Carboniferous.

Genera: *Chonopectus* Hall & Clarke, *Dengalosia* Manankov & Pavlova.

8.2B Subfamily **SEMENEWIINAE** Muir-Wood, 1962

[Semenewiinae Muir-Wood, 1962, p. 33].

Diagnosis: Ornament of concentric wrinkles, may have fine radials, spines ventral only, along hinge and small over rugae. Lower Carboniferous.

Genera: *Semenewia* Paeckelmann (syn. *Palmerhytis* Brunton & Mundy), *Chonetipustula* Paeckelmann, *Parmephrix* Brunton & Mundy, *Plicaea* Aisenberg, ?*Plicatiferina* Kalashnikov.

Discussion: The membership of *Plicaea* Aisenberg and *Plicatiferina* Kalashnikov of Lower and Upper Carboniferous age respectively requires better knowledge of their spine distribution and interior. Both show concentric wrinkles as in Semenewiinae, coupled with slightly narrower hinge. The hinge is also at less than maximum width in growth-lines of *Semenewia* and *Parmephrix*, and *Plicaea* is only 5mm wide. *Plicatiferina* passes through growth stages with hinge at maximum width, but at maturity has more developed ears: it is younger than the other genera. Both were classed in Quadratiinae by Brunton et al. (2000, p. 584), and differ considerably from *Quadratia*.

8.3 Family **ARAKSALOSIIDAE** Lazarev, 1989

[Araksalosiidae Lazarev, 1989, p. 34].

Diagnosis: Radial ornament generally absent, short interareas, shallow corpus cavity, cardinal process pit, marginal ridges commonly absent.

Discussion: This family has been outlined through the studies of Lazarev (eg. 1989), as summarized by Brunton et al. (2000, pp. 576 ff.), and involves an array of forms inviting further study.

8.3A Subfamily **ARAKSALOSIINAE** Lazarev, 1989

[Araksalosiinae Lazarev, 1989, p.35].

Diagnosis: Mat of spines on ventral or both valves, elongate spine bases may form incipient ribs anteriorly, pseudodeltidium, chilidium, reduced cicatrix, no marginal structures, but may have buttress plates or prominent inner socket ridges. Upper Devonian to basal Carboniferous.

Genera: *Araksalosia* Lazarev, *Acanthatia* Muir-Wood & Cooper, *Hamlingella* Reed, *Kahlella* Legrand-Blain, *Ruthiphiala* Carter, *Whidbornella* Reed.

Discussion: Hinge spines are notably finer along the hinge in *Araksalosia* and *Hamlingella* than in the other genera.

[Donalosiinae Lazarev, 1989, p. 35].

Diagnosis: Spines relatively stout, usually only on ventral valve, may include hinge row and postero-lateral cluster, concentric ornament may be lamellose, radial ornament rare on trails. Pseudodeltidium and chilidium present, commonly with large cicatrix. Lower to Upper Devonian.

Genera: *Donalosia* Lazarev, ?*Auchmerella* Struve, *Australosia* McKellar, *Devonalosia* Muir-Wood & Cooper, *Dichacaenia* Cooper & Dutro, ?*Dotswoodia* McKellar, ?*Irboskites* Bekker, *Morganella* McKellar, *Oligorachis* Imbrie, *Ralia* Lazarev, *Truncalosia* Imbrie.

Discussion: Some of the genera listed from Brunton et al. (2000) are uncertain. *Auchmerella* is a mid-Devonian genus only known as a cemented ventral valve; *Dotswoodia* looks like *Semicostella* in some respects, *Irboskites* lacks spines, and *Enigmalosia* Czarniecki was included but might be truncateniin or echinostegid.

8.3C Subfamily **CAUCASIPRODUCTINAE** Lazarev, 1987

[Caucasiproductinae Lazarev, 1987, p. 49].

Diagnosis: Ventral spines thick, of even size and regular spacing, close-set dorsal spines. Middle and Upper Devonian.

Genera: *Caucasiproductus* Lazarev, *Eostrophalosia* Stainbrook, *Praewaagenoconcha* Sokolskaya, *Strophoproductus* Nalivkin.

Discussion: These genera lack cicatrix and so were assigned to Productidina, within Sentosiidae by Brunton et al. (2000, p. 516). Yet they have teeth and sockets and low interareas. Brachial ridges are poorly known but appear strophalosioid in *Caucasiproductus*. There are aspects which recall Echinalosiinae, but members of this subfamily have well developed attachment scar, more differentiated spines and other features that do not mandate direct descent from Caucasiproductinae. *Eostrophalosia* has dorsal spines, and well spaced ventral spines and symmetrical shape, and so is transferred to this subfamily from Donalosiinae.

8.3D Subfamily **QUADRATIINAE** Lazarev, 1989

[Quadratiinae Lazarev, 1989, p. 38 (34).

Diagnosis: Spines at low angle, rare on dorsal valve, concentric ornament well developed. Pseudodeltidium and chilidium commonly absent; marginal ridges present. Lower to ?Upper Carboniferous.

Genera: *Quadratia* Muir-Wood & Cooper, *Cyphotalosia* Carter.

Discussion: *Quadratia* is widespread and well preserved, and fails to show any umbonal cicatrix.

8.3E Subfamily **RHYTIALOSIINAE** Lazarev, 1989

[Rhytialosiinae Lazarev, 1989, p. 38 (35)].

Diagnosis: Undulose rugae, prominent and discontinuous; spines dense on ventral valve, fewer on dorsal valve. Upper Devonian.

Genera: *Rhytialosia* Lazarev, *Agramatia* Sokolskaya, *Steinhagella* Goldring, *Veeversalosia* Lazarev.

8.4 Family **CTENALOSIIDAE** Muir-Wood & Cooper, 1960

[nom. transl. hic ex Ctenalosiinae Muir-Wood & Cooper, 1960, p. 91].

Diagnosis: Dorsal ornament predominantly lamellate, may have fine radials, spines rare or absent. Ventral valve may be ribbed, and lack spines, or have rhizoid spines, cemented. Interior varied, may be septate, or bear hinge teeth.

Discussion: This group differs strongly from Strophalosiidae and Araksalosiidae in its ornament, with spines less prominent.

8.4A Subfamily **CTENALOSIINAE** Muir-Wood & Cooper, 1960

[Ctenalosiinae Muir-Wood & Cooper, 1960, p. 91].

Diagnosis: Short interarea, no dorsal spines, hinge lines denticulate. Middle Permian.

Genus: *Ctenalosia* Cooper & Stehli, *Girlasia* de Gregorio, ?*Mongolosia* Manankov & Pavlov.

Discussion: Brunton et al. (2000, p. 593) treated this subfamily as a member of Aulostegidae, but *Ctenalosia* has the brachial shields of strophalosioids (Brunton et al. 2000, text-fig. 423.1e). *Girlasia* is placed here because of its reportedly denticulate hinge. It looks strophalosioid in morphology, but was classed in Aulostegoidea by Brunton et al. (2000, p. 595).

8.4B Subfamily **MINGENEWIINAE** Archbold, 1980

[Mingenewiinae Archbold, 1980, p. 255].

Diagnosis: No cicatrix, dorsal valve has radial threads and lamellae. Ventral valve without spines. Lower to Upper Permian.

Genus: *Mingenewia* Archbold.

Discussion: *Mingenewia* has low ribs on the ventral valve, and ventral median septum. A new genus from Upper Permian of Nepal has no ventral ornament, nor ventral septum (see Waterhouse & Shi 1991).

8.4C Subfamily **CRASPEDALOSIINAE** new

Name genus: *Craspedalosia* Muir-Wood & Cooper, 1960, p. 82.

Diagnosis: Ventral valve with rhizoid spines, dorsal spines present or absent, dorsal valve lamellate with radials present, faint, or absent. Middle and Upper Permian.

Genera: *Craspedalosia* Muir-Wood & Cooper, *Melvillosia* Waterhouse.

Discussion: *Mongolosia* Manankov & Pavlova shows considerable approach in its dorsal valve, and has ventral spines along the hinge.

9. Superfamily **COOPERINOIDEA** Pajaud, 1968

[nom. transl. hic ex Cooperininae Pajaud, 1968, p. 158].

Diagnosis: Ventral valve attached and comparatively high, brachial ridges and brachidia specialized.

Discussion: Family Cooperinidae was classed as Aulostegoidea by Brunton et al. (2000, p. 605), but brachial shields appear to be modified from strophalosioid stock, and are unusual, so that they are separated as a distinct superfamily.

9.1 Family **COOPERINIDAE** Pajaud, 1968

[nom. transl. Cooper & Grant 1975, p. 822 ex Cooperininae Pajaud, 1968, p. 158].

Diagnosis: Small shells of elongate to bilobate outline, cemented by large cicatrix, ventral and commonly dorsal spines, hinge teeth, no pseudodeltidium, brachial ridges prominent.

9.1A Subfamily **COOPERININAE** Pajaud, 1968

[Cooperininae Pajaud, 1968, p. 158].

Diagnosis: Small shells with cicatrix surrounded by rhizoid spines, dorsal muscle platform short, brachidia as simple schizolophes. Permian.

Genera: *Cooperina* Termier, Termier & Pajaud, *Ansehia* Termier & Termier, *Atelestegastus* Cooper & Grant.

9.1B Subfamily **FALAFERINAE** new

Name genus: *Falafer* Grant, 1972, p. 216.

Diagnosis: Ventral muscle platform with median notch, multilobed ptycholophous brachidia, arching posteriorly. Few spines, limited to ventral valve.?Middle and Upper Permian.

Genus: *Falafer* Grant.

Discussion: The genus is very distinctive, given its ventral muscle platform and nature of brachidia. Ventral spines are few and are arrayed posteriorly around the cicatrix.

9.1C Subfamily **EPICELIINAE** Grant, 1972

[Epicelinae Grant, 1972, p. 223].

Diagnosis: Large for family, narrow with small interarea, ventral spines restricted around cicatrix, brachial ridges multilobed. Upper Middle and Upper Permian.

Genera: *Epicelia* Grant, *Ceocypea* Grant.

10. Superfamily **RICHTHOFENIOIDEA** Waagen, 1885

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

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

Discussion: This fascinating superfamily is briefly and well discussed by Wardlaw et al. (2000), and their classification is accepted herein. They drew attention to the uncertainty, here indicated by ', surrounding the relationships of several of the genera.

10. 1 Family **RICHTHOFENIIDAE** Waagen, 1885

[Richthofeniidae Waagen, 1885, p. 729].

Diagnosis: Conical, spines rhizoid, ventral myocoelidium. Permian.

Genera: *Richthofenia* Kayser, *Coscinarina* Muir-Wood & Cooper, *Globosobucina* Waterhouse & Plyasin, *Sesloidia* Grant, '*Striirichthofenia* Lu Tong-Chen.

10.2 Family **HERCOSIIDAE** Cooper & Grant, 1975

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

Diagnosis: Conical, rhizoid spines and ventral median septum. Permian.

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

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

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

Diagnosis: Conical, spines rhizoid or absent, ventral muscle callosity. Upper Carboniferous to Upper Permian.

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

10.3A Subfamily **TEGULIFERININAE** Muir-Wood & Cooper, 1960

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

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

Genera: *Teguliferina* Schuchert & Le Vene, *Acritosia* Cooper & Grant, *Ardmosteges* Sutherland, *Planispina* Stehli, *Proteguliferina* Licharew.

10.3B Subfamily **CYCLACANTHARIINAE** Cooper & Grant, 1975

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

Diagnosis: Conical with coscinidium or rim of protective spines.

10.3Ba Tribe **CYCLACANTHARIINI** Cooper & Grant, 1975

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

Diagnosis: Rhizoid supporting spines. Middle Permian.

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

10.3Bb Tribe **COLLUMATINI** new

Name genus: *Collumatus* Cooper & Grant, 1969, p. 6.

Diagnosis: No supporting rhizoid spines. Middle Permian.

Genus: *Collumatus* Cooper & Grant.

10.3C Subfamily **ZALVERINAE** Brunton, 1996

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

Diagnosis: Conical, no external or apertural spines, weakly attached. No coscinidium. Upper Carboniferous.

Genus: *Zalvera* Brunton.

10.4 Family **GEMMELLAROIIDAE** Williams, 1953

[Gemmellaroidae Williams, 1953, p. 10].

Diagnosis: Conical with long ventral interarea, spines few, on ventral valve only or absent. Dorsal valve cap-like, ventral myocoelidium present. Middle and Upper Permian.

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

D. DISCUSSION OF INDIVIDUAL GENERA

Repositories are indicated by the lettercode in front of registered type specimens provided for each species. B - Museum of Natural History, London; GSI - Geological Survey of India, Calcutta; NVM - National Museum of Victoria, Melbourne; PIN - Paleontological Institute, Moscow; UQ - University of Queensland (transferred to Queensland Museum), Brisbane; USNM - Smithsonian Institution, Washington DC; UWA - University of Western Australia, Perth.

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

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

Tribe **STICTOZOSTERINI** Waterhouse, new

Genus ***Guangia*** new

Derivation: Named for Guang R. Shi.

Type species: *Krotovia inflata* Shen et al. 2000, p. 739.

Diagnosis: Small convexo-concave shells distinguished by ornament of small spines and swollen bases, arranged in concentric rows over ventral valve, separated by smooth concentric bands reflecting growth steps and pauses. Dorsal spines few, arising between pits aligned singly along concentric bands. Hinge wide, ears large, trail non-geniculate, marginal ridge low to absent.

Discussion: This genus is represented by specimens from the Himalayan Upper Permian of Tibet and Nepal. The holotype by original designation is NVM 148883 from Bed 11, Selong Group, Selong Xishan section, south Tibet. It is distinguished from allied genera by its small moderately well spaced spines and swollen tubercles or dorsal pits arranged in single rows along concentric bands. Spines are larger without bases in *Darlinuria*, and are more numerous and finer with mutiple spine-rows in bands in *Stictozoster. Dorashamia* has only ventral bands, with few spines.

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

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

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

Genus ***Contraspina*** new

Derivation: contra - against, opposite, spina - spine, Lat.

Type species: *Productus purdoni* Davidson, 1862, here designated.

Diagnosis: Characterized by very fine close-set spines and small spine bases especially over posterior ventral valve, bases becoming more elongate anteriorly, and in front on large specimens the bases become small.

Discussion: The ventral ornament of this genus is to some extent the reverse of that displayed on *Waagenoconcha*, in which slender spines with elongate bases lie over the posterior ventral valve, and spine bases become short and rounded anteriorly. In the present genus, the spine bases are small and rounded posteriorly for 20-30mm, and then become elongate. The holotype, B 82367, by monotypy, of the type species *Productus purdoni* is figured by Davidson (1862, pl. 2, fig. 5a-b, Waterhouse 1978, pl. 1, fig. 24, pl. 2, fig. 1) from the Salt Range, Pakistan. It is accompanied by an unfigured specimen B 82369. The ventral

valve is decorticated over the middle and anterior third. I have two specimens which I collected from the Salt Range in the Chhidru Formation (Kufri Member), and Waagen (1884, pl. 73, fig. 1-3) figured well preserved material from the same member. Some Salt Range specimens figured by Reed (1944) also belong to the genus, including several named as varieties of *purdoni.* The shape of the type species displays moderately steep posterior walls, rather short hinge, dorsal valve with low median anterior fold and short geniculate trail, and dense fine spine bases. Anteriorly, radial folds may be developed. A number of other specimens have been referred to the species, but some should be reassigned.

The type species *purdoni* approaches *Waagenoconcha (Gruntoconcha) macrotuberculata* Angiolini but this is poorly preserved, and cannot be adequately compared for shape and dorsal valve. Reports of anterior rugae and steep posterior walls in *macrotuberculata* are not supported by the available figure, and perhaps the observations apply more to *Waagenoconcha abichi* (Waagen), deemed to be an ally by Angiolini (1995). The ventral spine pattern involves coarse often slightly elongate posterior spine bases and short coarse anterior spine bases for *macrotuberculata,* unlike the arrangement in *purdoni.*

Ruthenia Fredericks, 1928, p. 789, proposed for *Productus irginae* Stuckenberg, has numerous close-set fine spines with slender elongate bases over the posterior ventral valve, and in front bases become short (Chernyshev 1902, pl. 30, fig. 3, 4, pl. 52, fig. 1-4, Muir-Wood & Cooper 1960, pl. 89, fig. 15, 16). Ornament is like that of *Waagenoconcha.*

Termier et al. (1974, p. 125) claimed that Davidson's species *purdoni* belonged to *Septiconcha* Termier et al., type species *S. taeniosa* from Afghanistan. Their type species *taeniosa* has echinoconchid ornament with bands of diversified spines, not found in *Productus purdoni.*

Genus ***Wimanoconcha*** Waterhouse, 1983b

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

Diagnosis: Large shells with inflated ventral valve, high lateral ventral walls, anterior radial folds, distinguished by thickened dorsal valve with planiculate rather than geniculate trail (See Part B herein). Ventral spines close-set, somewhat variable in the nature of spine bases and diameter, bases elongate and slender posteriorly, broad or widening forward and varied over midlength, scattered erect spines, varied anteriorly; dorsal spines close-spaced, erect, bases small.

Discussion: *Wimanoconcha* is based on *Ruthenia wimani* Fredericks, 1934, p. 28, as cited by Waterhouse (1983b, p. 125). This species was proposed for *Productus purdoni* not Davidson of Wiman (1914, pl. 14, fig. 8, 9, pl. 15, fig. 1, 2, pl. 16, fig. 1-4). The lectotype selected by Gobbett (1964, p. 75) is the specimen figured by Wiman (1914, pl. 15, fig. 1, pl. 16, fig. 1, 2), from the Spirifer Limestone of Bjørnøya, and kept in the Rijksmuseum, Stockholm. Notwithstanding comments by Archbold (1993) and Brunton et al. (2000), *Wimanoconcha* is readily and objectively distinguished by its thickened dorsal valve, which is flat externally and lacks external geniculation and trail. Ventral spines are posteriorly fine with slender elongate close-set bases, as illustrated in the specimen figured by Wiman (1914, pl. 16, fig. 3), and bases become short and broad over anterior midlength of the lectotype, approaching those of *Gruntoconcha.* The ventral valve is elongate and swollen far more than in *Waagenoconcha.*

Dunbar (1955) assessed Frederick's species as a junior synonym of *Productus payeri* Toula, 1874, also figured by Frebold (1937). From examination of Toula's type material at the Natural History Museum, Vienna, Gobbett (1964, p. 76) concluded that Toula's specimens belonged to possible *Kochiproductus* (Toula 1874, pl. 4, fig. 1a-b, 3), *Horridonia timanica* (=*Sowerbina*), and *Waagenoconcha irginae.* Dunbar's Greenland specimens are well preserved (pl. 9, pl. 10), and clearly belong to *Wimanoconcha*, illustrating in fine detail the variation of ventral spines. Over the middle of the valve, the spine bases are elongate and expand forward to the base of the spine, but some spine bases are more cylindrical, and some spines emerge directly from the shell. Spines are less regular than in type *Waagenoconcha* or Himalayan-Salt Range examples. Laterally, the spine bases are narrow and spines generally emerge directly from the shell. The shells differ substantially from *Waagenoconcha* in their elongate shape, high vaulted ventral valve, flat dorsal valve, details of ventral spine pattern and rugation.

Several Russian authorities have illustrated *wimani* (eg. Ganelin 1984, pl. 22, fig. 1-5, pl. 23, fig. 1; Lazarev 1990, pl. 34, fig. 4, 5), but their specimens are not quite the same in shape or ornament, and seem to have been misidentified, thereby compromising an understanding of *wimani* and *Wimanoconcha.*

Genus ***Fostericoncha*** new

Derivation: Named for C. B. Foster; concha - shell, Lat.

Type species: *Waagenoconcha? gigantea* Waterhouse, 1983a, p. 125.

Diagnosis: Large shells with wide ears at maximum width of shell, ventral sulcus, dorsal fold extends for full length of shell, extended hinge and wide ears, dorsal valve concave, geniculate, slightly thickened over trail. Ventral spines mostly fine and erect posteriorly, but vary over shell a little in length of bases, with much stronger spines over ventral shoulder, extending well forward; dorsal spines fine, erect, numerous, arising from small pustules over disc.

Discussion: This genus is characterized by shape and spine details. The shell displays unusually large ears, with maximum width at the hinge (see Waterhouse 1983a, pl. 3, fig. 1), and well formed ventral sulcus and dorsal fold. *Waagenoconcha* Chao, 1927, type species *Productus humboldti* d'Orbigny, has maximum width at mid-length, and various species have a gentle shallow sulcus and low anterior fold. The spines of *Waagenoconcha* are numerous with elongate slender bases, and anteriorly, become fine and erect, without elongate bases. Body spines of the ventral valve of *Fostericoncha* are essentially similar. *W. (Gruntoconcha)* Angiolini, 1995 was distinguished for *Waagenoconcha* with "coarse elongate spine bases" and other discriminants of more doubtful value. Brunton et al. (2000, p. 517) allocated *Biplatyconcha* Waterhouse to synonymy of *Waagenoconcha*, but this genus differs considerably, having no dorsal spines, and having strophalosiid interior.

Fostericoncha gigantea (Waterhouse, 1983a)

1983a *Waagenoconcha? gigantea* Waterhouse, p. 125, pl. 3, fig. 1-4.

Holotype: UQF 73619 figured by Waterhouse (1983, pl. 3, fig. 3, 4) from Pija Member, Manang, Nepal, by original designation.

Diagnosis: Very large shells with wide ears and geniculate trail, ventral sulcus and dorsal fold, spines fine with short bases over most of valve, larger postero-laterally on ventral valve.

Material: A large specimen with valves conjoined, but broken, and a large dorsal valve enables the scope of the species to be broadened. The material comes from the Pija Member, of early Changhsingian age, in north-central Nepal.

Dimensions in mm: approximate, shells deformed, dorsal valve

Width	Length	Height
91	59	23
112	61	29

Description: Dorsal valves transverse with large subalate ears at maximum width, and well defined dorsal median fold. Entire surface densely covered by small erect spines, arising from small rounded pustules, dense over disc, and varying in spacing laterally and posteriorly. Growth increments are fine and subdued. Growth lines become more prominent over the trail, and spines are often aligned in a row for 10-20 spines. Shell 2mm thick over start of trail, compared with just over 1mm for the ventral valve. The other dorsal valve is similar but lacks growth laminae from the trail.

Tribe **BALKASHECONCHINI** Waterhouse, new

Genus ***Balkasheconcha*** Lazarev, 1985

Balkasheconcha grandis new name

1984 *Waagenoconcha gigantea* (not Waterhouse 1983a) Ganelin , p. 128, pl. 18, fig. 4, 5, pl. 19, fig. 1-4, pl. 20, fig. 1-7, pl. 21, fig. 1-5.

1990 *Balkasheconcha gigantea* (not Waterhouse) Lazarev, pl. 35, fig. 1-4.

Taxonomy: Two different species of waagenoconchiform genera were named *Waagenoconcha gigantea* by Ganelin (1984) and Waterhouse (1983a). The junior homonym is here renamed *grandis*. The holotype is the specimen PIN no. 2833/242 figured as *gigantea* by Ganelin (1984, pl. 19, fig. 1) by original designation.

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

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

Genus ***Megasteges*** Waterhouse, 1975

Type species: *Megasteges nepalensis* Waterhouse, 1975, by original designation.

Diagnosis: Large shells, ventral umbo deformed, interarea high, ornament of erect spines without swollen bases, in 2-3 orders. Dorsal valve with fine spines, cardinal process supported by short well formed buttress plates.

Discussion: *Megasteges* is well represented in Australia, and includes *Aulosteges randsi* Hill (Briggs 1998) from Queensland, together with *A. reclinis* Coleman and *Aulosteges baracoodensis* var. *septentrionalis* Etheridge, as also noted by Archbold (1986a), and also *Taeniothaerus coolkilyensis* Coleman from Western Australia. Possible occurrences have also been noted by Waterhouse (2001, p. 85) from the Khisor Member at the top of the Chhidru Formation of the Salt Range, Pakistan, and in the Hilton Limestone of Wairaki Downs, New Zealand. A dorsal valve from the Stephens Subgroup, New Zealand, figured as Aulostegidae genus indet. in Campbell et al. (1984, text-fig. 6.14) has the buttress plates typical of *Megasteges.*

Megasteges nepalensis Waterhouse, 1975

1975 *Megasteges nepalensis* Waterhouse, p. 6, pl. 1, fig. 8-10.

1978 *M. nepalensis* Waterhouse, Waterhouse, pp. 69, 109, pl. 8, fig. 15, pl. 9, fig. 1-11, 13, pl. 10, fig. 1, 3-5, pl. 21, fig. 9, 10.

Holotype: UQF 68878 figured by Waterhouse (1975, pl. 1, fig. 10, 1978, pl. 9, fig. 8, 9) from Nisal Member, Dolpo, by original designation.

Diagnosis: Elongate shells with ventral umbo often deformed, ventral valve usually sulcate, dorsal valve concave, trail low and geniculate; ventral spines erect and diverse, dorsal spines fine and erect.

Discussion: Brunton et al. (2000, p. 587) claimed that the repository for types of this genus was not known. Waterhouse (1978, p. 19) clearly stated (under a bold heading) that the types were kept at the University of Queensland, Brisbane. They have subsequently been moved into the care of the Queensland Museum, Brisbane.

Genus ***Saeptathaerus*** Waterhouse, 2002

Type species: *Aulosteges fairbridgei* Coleman, 1957, by original designation.

Diagnosis: Aulostegid shells with slightly distorted ventral umbo, high ventral interarea, ventral ornament of spines in quincunx arising from swollen elongate bases, dorsal valve concave, geniculate, fine erect spines. Ventral interior with no teeth, large muscle field, dorsal valve with high cardinal process supported by long diverging buttress plates.

Discussion: This genus is closely allied to *Megasteges*, but has somewhat longer and more widely diverging buttress plates in the dorsal valve. In *Saeptathaerus*, ventral spines arise from elongate swollen bases, whereas spines lack such bases and are varied in diameter on the type species of *Megasteges* (see Waterhouse 1978, pl. 9, fig. 5). The type species of *Saeptathaerus*, *Aulosteges fairbridgei* Coleman, 1957, comes from the Hardman Member and Port Keats Group of Western Australia, of Wuchiapingian age. The holotype is registered as UWA 29438f.

Genus ***Colemanosteges*** new

Derivation: Named for Patrick C. Coleman.

Type species: *Taeniothaerus? fletcheri* Coleman, 1957, p. 91, here designated.

Diagnosis: Medium-large shells with wide hinge and high wide ventral interarea, gently convex dorsal valve. Distinguished by ventral spines which are subprostrate and slender with inconspicuous bases either locally placed in patches or interspersed amongst spines with swollen elongate bases. Two close-set buttress plates and long median septum in dorsal valve.

Discussion: This genus is distinguished by a mix of spines with slender erect bases and spines with elongate swollen bases on the ventral valve. The type species was figured in Coleman (1957, p. 91, pl. 9, fig. 15-19, pl. 10, fig. 1-7) from the Hardman Member, Liveringa Formation, West Kimberley district. The holotype is registered as UWA 29427b.

Aulosteges transversa Jin in Zhang & Jin (1976, pl. 3, fig. 9-15) from Fd1V-5 and Jspf22, Selong Group, south Tibet, is apparently congeneric. It has slender spines with inconspicuous bases over the posterior ventral valve, and swollen elongate bases anteriorly. The hinge is wide, the ventral interarea high, and buttress plates well formed and subparallel.

Subfamily **SEPTASTEGINAE** Waterhouse, new

Genus ***Septasteges*** Waterhouse & Piyasin, 1970

Septasteges praeclarus new species

1976 *Bilotina acantha* (not Waterhouse & Piyasin) Grant, p. 148, pl. 36, fig. 24-30, 32-34, pl. 37, fig. 1-28, not pl. 36, fig. 31, 35, 36.

Derivation: prae-claerus - brilliant, excellent, Lat.

Holotype: USNM 212504 figured by Grant (1976, pl. 37, fig. 13-15), here designated.

Diagnosis: Moderately inflated for genus, wide hinge and ears with acute cardinal extremities, ventral interarea low, ventral spine bases aligned along rows, with low ridges connecting spines over median and anterior ventral valve, spines erect and crowded laterally. Dorsal anterior costate over trail, pitted over ears. Dorsal septum long, dorsal interior with coarse few pustules.

Discussion: This material comes from USNM locality 9270 in the early Guadalupian Rat Buri limestone at Phangna, south Thailand. It is distinguished from *Septasteges acanthus* by its wider hinge with small ears as opposed to the shorter hinge with obtuse margins of *acanthus*, and by the anterior costae prominent in the dorsal valve. The interarea is lower and broader, and posterior ventral valve a little more irregular compared with *acanthus*. Dorsal postero-lateral margins or ears are pitted, whereas they are smooth in *acanthus*. The dorsal interior has a longer dorsal septum, and coarse internal pustules lie in 2-3 rows between the marginal ridge and adductor plates, whereas there are some 6 rows in a similar part of the valve floor in *acanthus*. There are various other differences. The description in Grant (1976) elaborates detail: the one point to note is that the ventral valve has an interarea, as described by Waterhouse & Piyasin (1970), not a ginglymus as claimed by Grant (1976).

Grant (1976) also figured poorly preserved material from Khao Tok Nam (pl. 36, fig. 1) with distinctly shorter spine bases on the ventral valve, and two worn ventral valves from Ko Muk NE (pl. 36, fig. 35, 36), also with short spine bases.

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

Genus ***Reedosepta*** new

Derivation: Named for F. R. C. Reed; saepta - fence, Lat.

Type species: *Productus (Tschernyschewia) parilis* Reed, 1944, p. 86, here designated.

Diagnosis: Tschernyschewiiform shells characterized by coarse pustules at base of spines, both valves spinose, ventral median septum high. Ventral interarea low or absent.

Discussion: *Tschernyschewia typica* Stoyanov, 1910, 1915 of Djulfa, Armenia, is also characterized by its median septum, but has a low ventral interarea. The two genera are distinguished by their different external ornament. That of *Tschernyschewia* is almost an exact homeomorph of *Waagenoconcha*. The suberect spines have slender elongate bases, and anteriorly the bases become much shorter. In the new genus, the bases are much larger, and swollen, looking like the ornament typical of the posterior shell of *Juresania*. Postero-laterally, the spines in the new form are sturdy, and erect. Dorsal ornament of the new genus consists of spines and low round to elongate pits and pustules, coarser than in *Tschernyschewia*. *Megatschernyschewia* Sremac also has finer ornament, and high ventral interarea.

Other Salt Range species belong to this genus (Reed 1944).

Reedosepta parilis (Reed, 1944)

1944 *Productus (Tschernyschewia) parilis* Reed, p. 86, pl. 17, fig. 2, 2, a-d, 3, pl. 18, fig. 7, 7a.

Lectotype: GSI 16856 figured by Reed (1944, pl. 17, fig. 2, a-d), here designated.

Discussion: The species is figured by Reed (1944), with detail of the ventral ornament, showing spines emerging from the middle of some of the tubercles. The species comes from the Kalabagh Member of the Wargal Formation, Salt Range, Pakistan, of Wuchiapingian age (late Permian).

Genus ***Trigonoproductus*** new

Derivation: tri - three, Lat., productus - brachiopod genus.

Type species: *Tschernyschewia inexpectans* Cooper & Grant, 1975, p. 915, here designated.

Diagnosis: Transverse uniplicate shells with large obliquely truncated ears, large elongated spine bases with short stout spines on ventral valve, and strong stout rhizoid spines along the posterior margin, dorsal valve with thinner spines on bases, and dimples. Interarea very low.

Discussion: This form is like no other so far known amongst Tschernyschewiidae, in having a trigonal shape, with median third bordered each side by flaring antero-lateral margins, imparting a uniplicate anterior and lateral margin with comparately strong dorsal fold. As well an irregular double row of sturdy rhizoid spines lies along the ventral margin. Over the median ventral valve there are elongate slender ridges, bearing swollen spine bases at mid-length, or gradually widening anteriorly to bear a spine of varying width, and continuing anteriorly as a slender ridge. In addition there are scattered slender spine bases. Overall the ventral ornament differs considerably from that typical of either *Tschernyschewia, Megatschernyschewia* or *Reedosepta*. (Holotype USNM 152681).

There are various other differences, some specific, and well described and illustrated by Cooper & Grant (1975).The species comes from the Taylor Ranch Member of the Hess Formation, Glass Mountains, Texas, of Early Permian or Cisuralian age, older than most *Tschernyschewia* or *Reedosepta*.

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

Subfamily **AURICULISPININAE** Waterhouse, 1986

Tribe **AURICULISPININI** Waterhouse, 1986

Genus ***Papiliolinus*** Waterhouse & Gupta, 1977

Type species: *Papiliolinus eishmakami* Waterhouse & Gupta, 1977, by original designation.

Diagnosis: Moderately large shells with wide hinge and slender corpus, both valves covered by very fine radials, low irregular concentric wrinkles, spines restricted to ventral valve, small and mostly close to hinge, with short bases up to 1mm long, spines dense over inner ears. Lower Carboniferous (Visean - Serpukhovian).

Discussion: The genus was based on material described as *Productus undatus* (not De France) by Diener (1899) from the "Fenestella Shales" of Kashmir, with additional material. The holotype as designated by Waterhouse & Gupta (1977, p. 162) is GSI 6226, figured by Diener (1899, pl. 1, fig. 9). Diener misinterpreted specimens as dorsal valves, but this was corrected by Waterhouse & Gupta (1977, p. 162), though ignored by Brunton et al. (2000, p. 544).

Genus ***Nisalaria*** new

Derivation: Named from Nisal, settlement in Dolpo, west Nepal.

Type species: *Cancrinelloides (Bandoproductus) inflata* Waterhouse 1983a, here designated.

Diagnosis: Ears moderately large, maximum width well forward of hinge, both valves closely costate, single row of spines along hinge with rare additional spines on outer ears, body spines moderately numerous over ventral valve, with short elongate bases, wrinkles low and mostly over lateral slopes; dorsal valve with low concentric growth lines and subdued incomplete wrinkles, no spines.

Discussion: *Costatumulus* Waterhouse, 1986b has usually two rows of hinge spines, and smaller ventral ears, but is otherwise close in shape and general appearance. *Bandoproductus* Jin & Sun, 1981 also has a somewhat subrectangular outline with small ears and row of strong ventral hinge spines. The present form differs in overall shape from that genus, although close in several respects. Both *Costatumulus* and *Bandoproductus* are mostly Early Permian in age, whereas *Nisalaria* is Upper Permian. *Cancrinelloides* Ustritsky in Ustritsky & Chernyak (1963) of Middle and possibly Late Permian age has numerous ear spines and more swollen postero-lateral ventral valve with subrectangular outline.

Nisalaria inflata (Waterhouse, 1983a)

1978 *Cancrinella*? sp. Waterhouse, p. 76, pl. 11, fig. 13-18.

1983a *Cancrinelloides (Bandoproductus) inflata* Waterhouse, p. 130.

Holotype: UQF 68909 figured by Waterhouse (1978, pl. 11, fig. 13, 15) from Nisal Member, Dolpo, Nepal, by original designation.

Diagnosis: Transverse shells with moderately arched venter and short hinge with large ears. Single row of spines along hinge, and scattered rare body spines, more numerous near beak, with short prolonged bases, wrinkles postero-laterally.

Tribe **LYONIINI** Waterhouse, 2001

Genus ***Nambdoania*** new

Derivation: Nambdo, village in Dolpo, west Nepal.

Type species: *Cancrinella papilionata* Waterhouse, 1978, p. 109, here designated.

Diagnosis: Shells of moderate size with transverse outline, hinge much less than maximum width of shell, small ears, ventral valve gently convex, without sulcus, dorsal valve almost flat over disc and with low geniculate trail. Fine ventral spines in single row along hinge, fine spines arranged with short prolonged bases on costellae over ventral valve; dorsal valve has long dimples, no spines, hinge pits or hinge dimples; both valves have low wrinkles. Muscle field lightly impressed, dorsal median septum long.

Discussion: This genus is shaped moderately like *Bandoproductus* Jin & Sun, 1981, and has a row of hinge spines and comparable ventral spines which arise from costellae, flat dorsal disc with geniculate trail, and long dorsal septum, as pointed out by Waterhouse (1983a). *Bandoproductus* is characteristic of Early Permian faunas in Gondwana (see Briggs 1998), especially lower Tastubian deposits (Waterhouse 2002). The present species is very much younger, coming from the Changhsingian Nambdo Member of Nepal. It differs from Early Permian species in its smaller size, narrower hinge, much less conspicuous and finer hinge spines and finer radial ornament. Ventral muscle scars are much more faintly impressed than in *Bandoproductus*. Slightly elongate moderate to crowded pits cover the dorsal valve of *papilionata,* as found in some species of *Bandoproductus*.

Nambdonia papilionata (Waterhouse, 1978)

1978 *Cancrinella papilionata* Waterhouse, p. 109, pl. 21, fig. 11-21, pl. 22, fig. 1-3.

1983a *Cancrinelloides (Bandoproductus) papilionata* (Waterhouse) Waterhouse, p. 130.

Holotype: UQF 69029 figured by Waterhouse (1978, pl. 21, fig. 16) from Nambdo Member, west Dolpo, Nepal, by original designation.

Diagnosis: Small shells with row of comparatively fine spines along short hinge, body spines with short prolonged bases, costellae fine and regular, dimples prominent over dorsal valve.

Subfamily **PAUCISPINAURIINAE** Waterhouse, 1986

Tribe **MAGNIPLICATININI** Waterhouse, 2001

Genus ***Auritusinia*** new

Derivation: auritus - large ear, Lat.

Type species: *Costatumulus tazawai* Shen et al. 2000, p. 743, here designated.

Diagnosis: Characterized in part by large ears and extended hinge line at maximum width of shell. Both valves costellate and bearing moderately strong concentric rugae, ventral spines weakly developed along hinge, arranged over venter with comparatively short bases, long spine bases within shell, no dorsal spines.

Discussion: The type species of this genus was assigned to *Costatumulus* Waterhouse by its authors, but rugae are stronger on both valves, especially the ventral valve. The new genus is closer in the strength of its rugae to *Magniplicatina*, but differs from both this genus and *Costatumulus* in its extended ears, whereas ears are only moderately well developed in *Costatumulus* and less in *Magniplicatina*, and in both the maximum width generally lies at mid-length. Spines lie in one or two rows along the hinge in both Australian genera, and there are faint signs of small spines along parts of the hinge in the illustrated material of *tazawai,* without any textual clarification. Spines over the venter in *tazawai* have short bases, as in examples

of *Magniplicatina* species in the Permian of Texas, described as *Cancrinella* not Fredericks by Cooper & Grant (1975), and in *Costatumulus*. The ventral shell of *Auritusinia* has long hollow spine bases, also seen in *Magniplicatina*, and better developed than in *Costatumulus*.

Auritusinia tazawai (Shen et al. 2000)

2000 *Costatumulus tazawai* Shen, Archbold, Shi & Chen, p. 744, text-fig. 12.1-8, 11-14.

Holotype: NMV P148917, figured by Shen et al. (2000, text-fig. 12.2) from bed 5, Selong Group, Selong Xishan section, Tibet.

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

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

Genus ***Choanoproductus*** Termier & Termier, 1970

Type species: *Choanoproductus gubleri* Termier & Termier, 1970.

Discussion: *Choanoproductus* is judged to be a synonym of *Monticulifera* Muir-Wood & Cooper, 1960. It was figured as interiors, with the ventral ginglymus and umbo by Termier & Termier (1970), and was considered to be indeterminate by Brunton et al. (2000, p. 643), "possibly representing a strophalosiidine". But in all internal detail, involving cardinal process, muscle field, brachial ridges, as well as wide hinge, overall outline and ginglymus, and locality and age, the species *gubleri* agrees with *Monticulifera*. Moreover *Productus* cf. *sumatrensis* of Mansuy (1914, p. 18, pl. 2, fig. 12) from Ta Kreem, regarded as conspecific by Termier & Termier (1970), shows monticules, and Termier & Termier (1970) confirmed this ornament in their discussion.

According to Brunton et al. (2000, p. 643), the name was proposed by Termier & Termier (1966, p. 609) and described and illustrated in 1970, based on material from Sisophon, Cambodia. The 1970 article refers to a publication of 1968, with no authors, but cites p. 109, fig. 215, p. 116, and does not provide diagnosis or data on holotype.

Family **STROPHALOSIIDAE** Schuchert, 1913

Subfamily **STROPHALOSIINAE** Schuchert, 1913

Tribe **TRUNCATENIINI** Liao, 1982

Genus ***Kufria*** new

Derivation: Kufri, Pakistan town in Salt Range, Pakistan.

Type species: *Strophalosia blanfordi* Reed, 1944, p. 104, here designated.

Diagnosis: Medium-sized shells, gently convex ventral valve and dorsal valve almost flat over disc, with low geniculate trail. Narrow hinge, wide ventral sulcus and low anterior dorsal fold. Ventral ornament distinguishes the genus, with long ridges tapering posteriorly, 5-7mm long over middle of shell, with small suberect spine at anterior end of each ridge, distribution somewhat irregular; spines with shorter or no bases postero-laterally. Ribs stop at anterior end of spine, but one or two slender tapered ribs may resume in front. No dorsal spines, surface irregular.

Discussion: The genus is characterized by its long spine ridges. *Licharewiella* Ustritsky has much stronger costae, and spines arise from crests, not ends.

Kufria blanfordi (Reed, 1944)

1944 *Strophalosia blanfordi* Reed, p. 104, pl. 6, fig. 3, 3a.

Holotype: GSI 16884, figured as above, by monotypy.

Discussion: The holotype is moderately well preserved, but interareas are destroyed, and the cardinal process, typical of *Strophalosia* and allies, is revealed. No cicatrix is preserved, and if it was destroyed, it must have been small. The dorsal exterior has low well formed long tubercles. The type comes from the Kufri Member of the Chhidru Formation, Salt Range. Reed (1944) compared the species with *Strophalosia gerardi* King, but this form has short spine bases. He also noted an approach to a specimen figured as *Productus abichi* by Reed (1931, pl. 3, fig. 4) from Warccha, Salt Range. This has shorter though elongate ridges, and seems close, though first-hand examination is required.

Subfamily **ECHINALOSIINAE** Waterhouse, 2001
Tribe **ECHINALOSIINI** Waterhouse, 2001
Genus ***Muirwoodicia*** new

Derivation: Named for H. M. Muir-Wood.

Type species: *Strophalosia inexpectans* Cooper & Grant, 1975, p. 795, here designated.

Diagnosis: Characterized by very fine erect or suberect spines evenly distributed over most of ventral valve, slender rhizoid spines over ears, umbonal and postero-lateral slopes; dorsal spines delicate. Ventral valve gently convex with small poorly defined ears and wide hinge, dorsal valve very gently concave. Ridge lies across ventral ears internally, teeth small and close-set, ventral adductors clearly subdivided; dorsal valve with very long median septum and low hinge and marginal ridges.

Discussion: Although the type species was described as having dorsal spines, Cooper & Grant (1975) allowed that *Strophalosia* lacked dorsal spines, yet referred the species to *Strophalosia*: they admitted that Australian species were similar in having dorsal spines, yet would not countenance or even admit the by-then established use of genus *Echinalosia* (eg. Dear 1971) to receive such species. They use the terms dorsal as well as brachial in their account. But the description of the species, and its illustrations (Cooper & Grant 1975, pl. 269, fig. 13-20) are more than adequate. Holotype USNM 151229b.

The species is the only such form known in United States, and comes from the Getaway Member of the Cherry Canyon Member, in west Texas. Spines are more widely present than in *Lialosia* Muir-Wood & Cooper, 1960, which has only posterior spines on the ventral valve. *Liveringia* Archbold has few ventral spines at the hinge and ears, and scattered widely over the ventral exterior, as somewhat sessile spines, and radial capillae are present. In the new form spines are finer, more numerous and more erect, and dorsal spines are present, and there are no capillae. The dorsal interior of *Liveringia* has somewhat comparable marginal ridge, and externally lacks spines. *Echinalosia* is readily distinguished by its mix of coarse and fine ventral spines, and various other features.

The closest genus to *Muirwoodicia* appears to be *Marginalosia* Waterhouse, 1978, a widespread genus found in Himalaya, Australia, New Zealand and possibly Siberia (Waterhouse 2001, p. 68). This genus has fine ventral and dorsal spines, and gently concave dorsal valve, and somewhat comparable marginal ridge in each valve. *Muirwoodicia* has finer more numerous ventral spines, including rhizoid posterior spines, and otherwise comparatively smooth ventral valve, and smooth dorsal exterior with no pits or prominent growth steps and laminae, and no geniculate trail: overall the dorsal valve is much flatter. Internally the ventral ear baffles are prominent compared with those of *Marginalosia*, and the muscle scars divided in the ventral valve, and the septum longer in the dorsal valve.

E. ALPHABETICAL INDEX T0 CLASSIFICATION OF GENERA WITHIN PRODUCTIDINA AND STROPHALOSIIDINA

Genera ordered alphabetically, followed by code as in Tables 1-8 and in text.
1 - superfamily; 2 - (second number) family; A - subfamily; a - tribe, including subtribe. Junior homonyms shown in regular type, mis-spelled versions omitted.

A

Absenticosta 1.3Bb, *Acanthatia* 8.3A, *Acanthocosta* 4.3B, *Acanthalosia* 8.1C, *Acanthoplecta* 3.1Ba, *Acanthoproductus* 1.1Ba, *Achunoproductus* 7.1Aa, *Acritosia* 10.3A, *Adairia* 4.2C, *Admodorugosus* 3.1Ba, *Agelesia* 6.2D, *Agramatia* 8.3E, *Akatchania* 7.1C, *Alatoproductus* 5.1Aa, *Alexenia* 4.1C, *Alitaria* 2.2Ab, *Ametoria* 5.1Ba, *Anemonaria* 2.2Aa, *Anidanthus* 7.1C, *Ansehia* 9.1A, *Antiquatonia* 4.1B, *Araksalosia* 8.3A, *Araxilevis* 3.1Bc, *Archaiosteges* 6.2F, *Archboldina* 1.2Ba, *Arcticalosia* 8.1Bb, *Ardmosteges* 10.3A, *Ardviscus* 3.1Aa, *Argentiproductus* 1.4A, *Aseptella* 1.3Ba, *Asioproductus* 2.1A, *Asperlinus* 7.1Ab, *Aspinosella* 4.1B, *Atelestegastus* 9.1A, *Auchmerella* 8.3B, *Auloprotonia* 4.2Ba, *Aulosteges* 6.1A, *Auriculispina* 7.2Ca, *Auritusinia* 7.2Dc, *Australosia* 8.3B, *Avonia* 1.2Aa, *Azygidium* 2.1A.

B

Bagrasia 5.3Ab, *Baillenia* 3.2A, *Baissalosteges* 6.2B, *Balakhonia* 7.1Aa, *Balkasheconcha* 5.2Ab, *Bandoproductus* 7.2Cb, *Barunkhuraya* 1.2Bb, *Bathymyonia* 5.1Bb, *Beleutella* 7.1Da, *Bellaclathrus* 4.3Aa, *Bibatiola* 2.2B, *Bilotina* 6.1D, *Biplatyconcha* 8.1Aa, *Bispinoproductus* 3.1Aa, *Bothrionia* 2.2B,

Brasilioproductus 4.3B, *Breileenia* 1.2Aa, *Bruntonaria* 8.1C, *Bulahdelia* 1.2Bb, *Buntoxia* 5.1Bb, *Burovia* 3.2A, *Buxtonia* 4.3Aa, *Buxtoniella* 5.2Ab, *Buxtonioides* 4.3Aa.

C

Cactosteges 6.1C, *Calliprotonia* 5.1Aa, *Calliomarginatia* 4.1B, *Callyconcha* 2.1B, *Callytharrella* 4.2Ba, *Cancrinella* 7.2Dc, *Cancrinelloides* 7.2Cb, *Capillifera* 7.3A, *Caricula* 2.2Aa, *Carilya* 6.1B, *Carlinia* 4.1Ab, *Carringtonia* 1.2Bc, *Cathaysia* 2.2Ab, *Caucasiproductus* 8.3C, *Caucasoproductus* 2.1A, *Celebetes* 1.4B, *Ceocypea* 9.1C, *Chaoiella* 4.2Ba, *Chattertonia* 1.1Aa, *Chenxianoproductus* 5.1Aa, *Chianella* 7.1Ab, *Chilianshania* 7.3A, *Choanoproductus* 7.3A, *Chonetella* 1.4B, *Chonetipustula* 8.2B, *Chonopectella* 3.-, *Chonopectoides* 7.1B, Chonopectoides 3.-, *Chonopectus* 8.2A, *Chonosteges* 6.2C, *Chonostegoidella* 5.1Aa, *Chonostegoides* 6.2C, *Cimmeriella* 7.1Ab, *Cinctifera* 1.2Ab, *Colemanosteges* 6.1C, *Collumatus* 10.3Bb, *Companteris* 4.1Ab, *Compressoproductus* 7.1Eb, *Comuquia* 2.1B, *Connectoproductus* 7.1Aa, *Contraspina* 5.2Aa, *Coolkilella* 7.2Db, *Cooperina* 9.1A, *Cora* 7.1Aa, *Coronalosia* 8.1Aa, *Coscinarina* 10.1, *Costalosia* 8.1Ab, *Costalosiella* 8.1Ab, *Costatumulus* 7.2Ca, Costellaria 6.2Eb, *Costellarina* 6.2Eb, *Costiferina* 4.2Ba, *Costispinifera* 2.3A, *Costisteges* 6.2C, *Craspedalosia* 8.4C, *Craspedona* 6.2Ea, *Crossacantha* 1.3Bb, *Crossalosia* 8.1Ba, *Ctenalosia* 8.4A, *Cubacola* 5.1Bb, *Cymoproductus* 2.1A, *Cyndalia* 10.4, *Cyclacantharia* 10.3Ba, *Cyphotalosia* 8.3D, *Cyrtalosia* 2.1B.

D

Darlinuria 1.3Ab, *Dasysaria* 4.2A, *Dasyalosia* 8.1C, *Datangia* 7.1Da, *Dengalosia* 8.2A, *Densepustula* 5.1Ba, *Derbyella* 6.3, *Desmoinesia* 2.3B, *Devonalosia* 8.3B, *Devonoproductus* 7.1B, *Diaphragmus* 4.1Ab, *Dichacaenia* 8.3B, *Dictyoclostoidea* 7.1Aa, *Dictyoclostus* 4.2A, *Donalosia* 8.3B, *Dorashamia* 1.3Ab, *Dorsirugatia* 1.4A, *Dotswoodia* 8.3B, *Dowhatania* 4.1Ab, *Duartea* 7.4, *Dyschrestia* 2.3A.

E

Echinalosia 8.1Ba, *Echinaria* 5.1Aa, *Echinauriella* 2.3C, *Echinauris* 2.3A, *Echinoconchella* 5.1Ab, *Echinoconchus* 5.1Aa, *Echinosteges* 6.2A, *Edriosteges* 6.2A, *Elliotella* 2.1A, *Enigmalosia* 8.1Ab, *Entacanthadus* 2.1A, *Eomarginifera* 2.2Ab, *Eomarginiferina* 2.2B, *Eoproductella* 7.2B, *Eostrophalosia* 8.3C, *Epicelia* 9.1C, *Ericiatia* 5.3Ab, *Etheridgina* 5.2B, *Etherilosia* 8.1Aa, *Euproductus* 7.1Aa.

F

Falafer 9.1B, *Fallaxoproductus* 7.1Eb, *Ferganoproductus* 1.3Bb, *Filiconcha* 7.2Cc, Fimbriaria 1.3Aa, *Fimbrinia* 1.3Aa, *Flexaria* 4.3Aa, *Fluctuaria* 7.1Ac, *Fostericoncha* 5.2Aa, *Fusiproductus* 7.1C.

G

Galeatella 3.1Ab, *Gemmellaroia* 10.4, *Gemmellaroiella* 10.4, *Gemmulicosta* 4.3Aa, *Geniculifera* 3.1Bb, *Gigantoproductus* 7.1Da, *Girlasia* 8.4A, *Globiella* 7.1Ab, *Globosobucina* 10.1, *Globosoproductus* 7.1Da, *Glyptosteges* 6.2Eb, *Gondolina* 6.2G, *Grandaurispina* 7.2Da, *Grandiproductella* 3.1Ab, *Gratiosina* 2.1A, *Gruntoconcha* 5.2Aa, *Guangia* 1.3Ab, *Guizhouella* 7.2A.

H

Hamlingella 8.3A, *Hanaeproductus* 7.2B, *Haydenella* 1.4B, *Helaspis* 1.1Aa, *Helenaeproductus* 7.2Dc, *Hercosia* 10.2, *Hercosestria* 10.2, *Heteralosia* 8.1Aa, *Holotricharina* 2.3A, *Hontorialosia* 8.1Ba, *Horridonia* 3.2A, *Howseia* 6.2A, *Huatangia* 2.2Ab, *Hubeiproductus* 4.1Aa, *Hunanoproductus* 3.1Ab, *Hypolinoproductus* 7.1Aa, *Hystriculina* 2.1A.

I

Impiacus 1.2Bb, *Incisius* 2.1B, *Indigia* 7.1Aa, *Inflatia* 4.2C, *Iniproductus* 1.2Bc, *Institella* 6.2Ea, *Institifera* 1.3Bc, *Institina* 6.2F, *Irboskites* 8.3B.

J

Jakutella 5.3Aa, *Jakutoproductus* 1.2Bb, *Jiguliconcha* 2.1A, *Jipuproductus* 2.1A, *Juresania* 5.1Ba.

K

Kadraliproductus 3.1Ba, *Kahlella* 8.3A, *Kansuella* 7.2A, *Karavankina* 5.1Ab, *Kasetia* 7.2Db, *Kavesia* 3.1Ab, *Kelamelia* 4.2C, *Keokukia* 4.2C, *Kochiproductus* 4.3Aa, *Kozlowskia* 2.2Ab, *Krotovia* 1.2Ba, *Kueichowella* 7.2A, *Kufria* 8.1Ab, *Kunlunia* 4.2A, *Kurtomarginifera* 2.1A, *Kutorginella* 4.1B, *Kuvelousia* 7.1C.

L

Labriproductus 4.3Aa, *Laminatia* 5.1Aa, *Lamiproductus* 7.1Ab, *Lamnimargus* 2.2Aa, *Lampangella* 2.1A, *Lanipustula* 1.2Bb, *Latiproductus* 7.1Db, *Lazarevonia* 1.2Aa, *Leioproductus* 3.1Aa, *Leptaenalosia* 8.1Aa, *Leptalosia* 8.1Aa, *Lercarella* 6.2A, *Lethamia* 3.2B, *Levipustula* 1.2Bb, *Levisapicus* 7.1Aa, *Levitusia* 3.1Ba,

Lialosia 8.1Aa, *Libys* 4.3Ab, *Licharewiella* 8.1Ab, *Limbella* 6.2A, *Limbifera* 6.2Ea, *Linoproductus* 7.1Aa, *Linoprotonia* 7.1Aa, *Liolimbella* 6.2D, *Liosotella* 2.1A, *Lipanteris* 6.1B, *Liraplecta* 4.2A, *Liraria* 7.1Ab, *Liveringia* 8.1Aa, *Lomatiphora* 1.1Bb, *Longyania* 7.1Ab, *Lopasnia* 4.1Ab, *Lyonia* 7.2Cb.

M

Maemia 1.2Ab, *Magadania* 7.2Db, *Magnaurinia* 7.2Cc, *Magniderbyia* 8.1Ab, *Magniplicatina* 7.2Dc, *Magnumbonella* 3.1Bb, *Malloproductus* 5.3Aa, *Margaritiproductus* 1.1Bb, *Marginalosia* 8.1Ba, *Marginatia* 4.3B, *Marginicinctus* 4.3Aa, *Marginifera* 2.1A, *Marginirugus* 7.1Aa, *Marginoproductus* 4.2C, *Marginovatia* 7.1Aa, *Markamia* 5.3Aa, *Megalosia* 8.1Aa, Megarhynchus 10.4, *Megasteges* 6.1C, *Megatschernyschewia* 6.4, *Megousia* 7.1C, *Melvillosia* 8.4C, *Mesoplica* 3.1Aa, *Mingenewia* 8.4B, *Minispina* 2.1A, *Mistproductus* 7.2Ca, *Moderatoproductus* 7.1Da, *Mongolosia* 8.4A, *Monticulifera* 7.3A, *Morganella* 8.3B, *Muirwoodia* 7.4, *Muirwoodicia* 8.1Ba, Multispinula 8.1Ba.

N

Nambdoania 7.2Cb, *Neoedriosteges* 6.2A, *Neopugilis* 4.1B, *Neoplicatifera* 2.3C, *Neorichthofenia* 10.2, *Nigerinoplica* 1.1Bb, *Nigeroplica* 1.1Bb, *Nisalaria* 7.2Ca, *Niutoushania* 4.3Ab, *Nothokuvelousia* 7.1C, *Notolosia* 8.1Ba, *Nudauris* 4.2Bb, *Nudymia* 1.2Bb.

O

Ogbinia 1.4B, *Oligorachis* 8.3B, *Oncosarina* 2.1A, *Onavia* 1.2Aa, *Onopordumaria* 2.3C, *Orbinaria* 1.1Ab, *Orthothrix* 8.1Bb, *Otariella* 2.1A, *Ovatia* 7.1Aa, *Overtonia* 1.3Aa, *Overtoniina* 1.2Ab, *Ozora* 4.2Ba.

P

Palmerhytis 8.2B, *Papiliolinus* 7.2Ca, *Parachonetella* 1.4B, *Parajuresania* 5.1Ba, *Parakansuella* 7.2A, *Paramarginatia* 4.3B, *Paramarginifera* 2.2Ab, *Paramonticulifera* 7.3B, *Paramuirwoodia* 2.2Ab, *Paraplicatifera* 2.3A, *Parmephrix* 8.2B, *Paryphella* 2.2Ab, *Paucispinauria* 7.2Da, *Paucispinifera* 2.2Aa, *Peniculauris* 4.3Ac, *Permundaria* 7.2Ca, *Pharcidodiscus* 1.2Ab, *Piatnitzkaya* 1.2Bb, *Piloricilla* 4.3Ab, *Pinegeria* 7.2Da, *Planihaydenella* 1.4B, *Planispina* 10.3A, *Planoproductus* 1.2Bc, *Platycancrinella* 7.2Ca, Platyconcha 8.1Aa, *Platyselma* 1.3Bb, *Pleurohorridonia* 3.2A, *Plicaea* 8.2B, *Plicatifera* 1.3Ba, *Plicatiferina* 8.2B, *Plicoproductus* 7.2B, *Polymorpharia* 6.2Ea, *Poloniproductus* 7.1B, *Praehorridonia* 3.2A, *Praewaagenoconcha* 8.3C, *Probolionia* 2.2Ab, *Proboscidella* 7.1F, *Productella* 1.1Aa, *Productellana* 1.1Aa, *Productellina* 1.4A, *Productelloides* 3.1Ab, *Productina* 1.4A, *Productus* 4.1Aa, *Promarginifera* 4.1B, *Protanidanthus* 7.1C, *Proteguliferina* 10.3A, *Protoanidanthus* 7.1C, *Protonia* 4.1Aa, *Protoniella* 2.1A, *Pseudoantiquatonia* 4.3C, *Pseudoavonia* 2.3A, *Pseudohaydenella* 1.4B, *Pseudomarginifera* 7.1C, *Pseudomonticulifera* 7.3A, *Pseudostrophalosia* 8.1Ba, *Pugilis* 4.2A, *Pulchratia* 5.1Ba, *Pustula* 5.2B, *Pyxis* 4.1Aa.

Q

Quadratia 8.3D, *Quasiavonia* 1.2Aa.

R

Ralia 8.3B, *Ramavectus* 6.1C, *Ramovsina* 6.1C, *Reedoconcha* 6.1B, *Reedosepta* 6.4, *Regrantia* 7.1Eb, *Retaria* 4.1B, *Reticulatia* 4.2A, *Retimarginifera* 2.2Aa, *Retroplexus* 6.2F, *Rhamnaria* 6.1C, *Rhytialosia* 8.3E, *Rhytibulbus* 6.2D, *Rhytiophora* 1.1Ba, *Rhytisia* 2.1B, *Richthofenia* 10.1, *Rudinia* 2.3B, *Rugatia* 4.2Bb, *Rugauris* 1.2Bc, *Rugicostella* 6.2F, *Rugivestis* 2.2Ab, *Rugoclostus* 3.2B, *Ruthenia* 5.2Aa, *Rugoconcha* 1.3Ba, *Ruthiphiala* 8.3A.

S

Saeptathaerus 6.1C, *Saetosina* 7.2Da, *Sajakella* 7.4, *Sandia* 2.3B, *Sarytchevinella* 7.1Eb, *Scacchinella* 6.3, *Scapharina* 2.1B, *Schrenkiella* 7.1Aa, *Scissicosta* 4.3Ab, *Scoloconcha* 1.2Ba, *Scutepustula* 5.2B, *Semenewia* 8.2B, *Semicostella* 1.2Ab, *Semilunataproductus* 4.2Ba, *Seminucella* 1.1Bb, *Semiplanella* 7.1Db, *Semiplanus* 7.1Db, *Semiproductus* 1.1Ba, *Sentosia* 5.3Aa, *Sentosioides* 5.3Aa, *Septarinia* 5.1Bb, *Septasteges* 6.1D, *Septiconcha* 5.1Bb, *Septoproductus* 5.2Aa, *Serbarinia* 7.1Da, *Sesloidia* 10.1, *Sestropoma* 10.3Ba, *Setigerites* 4.3Aa, *Shanxiproductus* 2.1A, *Sicularia* 10.2, *Simplicarina* 2.1B, *Sinoproductella* 1.1Aa, *Sinuatella* 6.2Eb, *Siphonosia* 7.2Cd, *Sowerbina* 3.2A, *Spargospinosa* 7.2Da, *Sphenalosia* 8.1Aa, *Sphenosteges* 6.2B, *Spinarella* 4.2Bb, *Spinauris* 5.2Aa, *Spinifrons* 4.3Ac, *Spinocarinifera* 1.1Bb, *Spinomarginifera* 2.3C, *Spinoparyphella* 2.2Ab, *Spinorugifera* 3.1Bb, *Spinosteges* 1.2Ab, *Spinulicosta* 1.1Aa, *Spirisosium* 6.2B, *Spitzbergenia* 7.2Cc, *Spuriosa* 6.1C, *Spyridiophora* 4.1C, *Squamaria* 4.3Ab, *Stegacanthia* 5.3Aa, *Steinhagella* 8.3E, *Stelckia* 3.1Aa, *Stepanoconchus* 5.1Aa, *Stepanoviella* 7.1Ab, *Stereochia* 4.2Ba, *Stictozoster* 1.3Ab, *Stipulina* 6.2F, *Striatifera* 7.1Ea, *Striatoproductella* 7.2B, *Striatoproductus* 7.1B, *Striatospica* 7.1Aa, *Strigospina*

2.1A, *Striirichthofenia* 10.1, *Strophalosiella* 6.2B, *Strophalosiina* 6.2C, *Strophalosia* 8.1Aa, *Strophoproductus* 8.3C, *Strophorichthofenia* 10.2, *Substriatifera* 7.1Eb, *Subtaeniothaerus* 8.1Aa, *Svalbardoproductus* 4.1B.

T

Taeniothaerus 6.1B, *Talasoproductus* 7.1Db, *Taphrosestria* 10.3Ba, *Teguliferina* 10.3A, *Teleoproductus* 7.1Ac, *Tenaspinus* 4.2C, *Terrakea* 7.2Da, *Tesuquea* 4.1B, *Thamnosia* 4.1B, *Thomasella* 1.3Bc, *Thuleproductus* 4.1B, *Titanaria* 7.1Da, *Tityrophoria* 3.2A, *Tolmachoffia* 4.3Ab, *Tomilia* 4.3B, *Tomiproductus* 4.3Ab, *Tongluella* 7.3B, *Transennatia* 2.1A, *Trigonoproductus* 6.4, *Truncalosia* 8.3B, *Truncatenia* 8.1Ab, *Tschernyschewia* 6.4, *Tubaria* 4.1B, *Tuberculatella* 1.2Aa, *Tuberella* 5.3Aa, *Tubersulculus* 1.2Ba, *Tyloplecta* 4.3C.

U

Umboanctus 4.3B, *Uncisteges* 6.2C, *Undaria* 7.2Ce, *Undellaria* 1.2Ba, *Uraloconchus* 5.3Aa, *Urushtenia* 6.2C, *Urushtenoidea* 6.2C.

V

Vediproductus 5.1Bb, *Veeversalosia* 8.3E, *Verchojania* 1.2Bb, *Vitiliproductus* 7.1Da.

W

Waagenoconcha 5.2Aa, *Whidbornella* 8.3A, *Wimanoconcha* 5.2Aa, *Wooramella* 3.2B, Worthenella 4.3Aa, *Wyatkina* 6.1B, *Wyndhamia* 8.1Ba.

X, Y, Z

Xenosteges 6.2D, *Xestosia* 4.2Bb, *Xinjiangiproductus* 7.1Da, *Xinshaoproductus* 4.3Ab. *Yakovlevia* 7.4, *Yanguania* 1.1Bb.

Zalvera 10.3C, *Zhejiangoproductus* 7.3B, *Zhenania* 7.3A, *Zhuaconcha* 2.3C, *Zia* 4.2Ba.

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Table 9. Families of Productidina and Strophalosiidina.

Suborder Productidina Waagen, 1883

Superfamily Productelloidea Schuchert, 1929
- Family Productellidae Schuchert, 1929
- Family Avoniidae Sarytcheva, 1960
- Family Overtoniidae Muir-Wood & Cooper, 1960
- Family Productinidae Muir-Wood & Cooper, 1960

Superfamily Marginiferoidea Stehli, 1954
- Family Marginiferidae Stehli, 1954
- Family Paucispiniferidae Muir-Wood & Cooper, 1960
- Family Costispiniferidae Muir-Wood & Cooper, 1960

Superfamily Horridonioidea Muir-Wood & Cooper, 1960
- Family Leioproductidae Muir-Wood & Cooper, 1960
- Family Horridoniidae Muir-Wood & Cooper, 1960

Superfamily Productoidea Gray, 1840
- Family Productidae Gray, 1840
- Family Dictyoclostidae Stehli, 1954
- Family Buxtoniidae Muir-Wood & Cooper, 1960

Superfamily Echinoconchoidea Stehli, 1954
- Family Echinoconchidae Stehli, 1954
- Family Waagenoconchidae Muir-Wood & Cooper, 1960
- Family Sentosiidae McKellar, 1970

Superfamily Aulostegoidea Muir-Wood & Cooper, 1960
- Family Aulostegidae Muir-Wood & Cooper, 1960
- Family Echinostegidae Muir-Wood & Cooper, 1960
- Family Scacchinellidae Licharew, 1928
- Family Tschernyschewiidae Muir-Wood & Cooper, 1960

Superfamily Linoproductoidea Stehli, 1954
- Family Linoproductidae Stehli, 1954
- Family Kansuellidae Muir-Wood & Cooper, 1960
- Family Monticuliferidae Muir-Wood & Cooper, 1960
- Family Yakovleviidae Waterhouse, 1975

Suborder Strophalosiidina Waterhouse, 1975

Superfamily Strophalosioidea Schuchert, 1913
- Family Strophalosiidae Schuchert, 1913
- Family Chonopectidae Muir-Wood & Cooper, 1960
- Family Araksalosiidae Lazarev, 1989
- Family Ctenalosiidae Muir-Wood & Cooper, 1960

Superfamily Cooperinoidea Pajaud, 1968
- Family Cooperinidae Pajaud, 1968

Superfamily Richthofenioidea Waagen, 1885
- Family Richthofeniidae Waagen, 1885
- Family Hercosiidae Cooper & Grant, 1975
- Family Teguliferinidae Muir-Wood & Cooper, 1960
- Family Gemmellaroiidae Williams, 1953