THE EVOLUTION AND CLASSIFICATION OF PRODUCTIDA (BRACHIOPODA)

by

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PART ONE

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Preamble

This text may used as a reference for genera: consult the index for genera at the back of the monograph, and thereby be enabled to allocate the family relationships, and in a number of instances, be provided with figures and text, especially for new or revised genera, for which there are more than a hundred and fifty examples, no small component of the whole corpus of Productida. For such purposes, the monograph should be used in concert with the *Revised Brachiopod Treatise* (Brunton et al. 2000; Brunton 2007), which provides so much in the way of useful illustrations and references. Many paleontological studies are used in that way, as a means of identifying fossils, and pinning down at least the generic affinities, before embarking on a determination of specific limits and age of the fauna. But as well, this text is a narrative of the Productida, tracing the evolution of its numerous family branches, their origination and development, through the Devonian, Carboniferous and Permian periods, with the gradual, indeed spasmodic proliferations and set backs, until the grand catastrophe at the end of the Permian Period – not a history of slow decline, as some would maintain from flawed evaluations, but a truly extinction shock, which more than decimated promising new developments in the evolution of the order. By way of explanation, there never was a weirder form of brachiopod than the Lyttonioidea, and these had gained substantial biomass towards the end of the Permian Period. Yet they perished. There seldom was a time of more rapid proliferation amongst genera in some parts of the globe in Late Permian (Waterhouse 2011), but these genera were short-lived, wiped out. Leading up to the final climax were a series of diversifications, including a great flourishing in Early Carboniferous and a steady proliferation of life in Late Carboniferous and Early Permian specially adapted to high paleolatitudes, long winters and often cold conditions, and this specialized life from time to time invaded paleotropical waters. Under such a narrative, the application of simplistic generalizations, often spuriously supported by heavily selected data, and gross lumping of faunas into stages, becomes an embarrassment. Life was not simple, evolution was hugely complex, trends multilinear and seldom unidirectional, other than in tiny clades, both time-controlled and space-controlled, indeed event-controlled, as well as genetically governed.

As far as possible, all named productid genera are named and assessed in terms of their relationships, and classed in tribes and families, and stress is placed on lines of descent, so that ancestry becomes an important factor in classification. Superfamilies become the main building block. Yet it is still deemed that populations and species are the most significant and accessible component of biota, and therefore many species are described, both individually or in terms of evolutionary development, as a means of retaining contact with actual fossil faunas. Incidentally, although some myopic biologists sneer at the reality of fossil species, those species at least reveal all-important data on their full duration, and potentially their descendents, which is more than current species can do.

For illustrations, the reader must consult the numerous initial and subsequent publications on species, and the *Revised Treatise on Brachiopoda* provides invaluable documentation on the initial proposals of genera. But revisions should not be set aside or ignored, nor indeed accepted critically. Illustrations are critical, and are not always satisfactory, the paleontologist often being let down by cheap or unsatisfactory reproduction. That is not the paleontologist's fault. The journal Palaeontology has provided an excellent standard since commencement, and has been joined over recent years by a number of other publications, though a number remain deficient. Because productids tend to be small, it is my own personal preference to enlarge the size of reproduction – squinting at small specimens that are justifiably discriminated on minutae of ornament becomes ridiculous, and the small size does little to enhance the fascinating variations in shape and ornament. Nat Beatus, Brian O'Donovan and John Coker have been of great help in assisting with photography. My own photographs are based on an SLX Nikon, with photographs prepared in direct sunlight. Whilst I like hard copy because of the ease of comparing multiple publications concurrently, PDF's do allow image enhancement at wonderful scales of magnification and clarity.

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Abstract

The evolution of Productida is discussed in terms of four suborders, Productidina, Strophalosiidina, Oldhaminidina (= Lyttoniidina), and Linoproductidina (new). The morphology of the oldest Productida is strophalosiiform in terms of presence of teeth, sockets, interareas and large brachial shields, and in Productidina and Linoproductidina, this phase was comparatively short-lived, through evolving into a productiform morphology which lost those particular attributes. The two suborders arose each from different chonetid ancestors, one smooth, the other ribbed. Strophalosiidina had different ancestry, closer to that of Productidina, and although some streams retained a strophalosiiform construct, some descendents also developed a morphology that was productiform or partly productiform. In turn, Oldhaminidina evolved from Strophalosiidina. The membership in each suborder is assembled through chronomorphic analysis, involving successive species and genera, which establish that lineages underwent substantial morphological change during their evolution. Superfamilies classed as suborder Productidina, namely Overtonioidea, Marginiferoidea, Horridonioidea, and Productoidea, grouped as Productimorphi, arose from Productellidae within Productelloidea, which commenced as a strophalosiiform group that possessed interareas, teeth, smooth non-dendritic muscle scars and large brachial shields during Devonian time, lacking an umbonal cicatrix, and displaying chonetid anderidia in the earliest subfamily. In later Devonian time, Echinoconchoidea stemmed from the strophalosiiform Caucasiproductidae, a separate component of Productelloidea. Strophalosiidina arose from an allied group, characterized by presence of ventral cicatrix, and a diverse superfamily Strophalosioidea persisted until the end of the Permian Period. The group gave rise through loss of strophalosiiform accoutrements to Aulostegoidea in the Visean (Lower Carboniferous), directly from the Upper Devonian Subfamily Rhytialosiinae (Frasnian – Fammennian) within Strophalosioidea. Aulostegoidea branched during mid-Carboniferous into Richthofenioidea and the two are grouped as Aulostegimorphi. Scacchinelloidea (Lower Carboniferous – Visean) arose from the strophalosioid Araksalosiidae (Upper Devonian – Fammenian), also by losing teeth and sockets in developing towards a productiform morphology. A restricted Superfamily Strophalosioidea gave rise in the Late Carboniferous to Cooperinoidea, and to Suborder Oldhaminidina. Within Suborder Linoproductidina, which arose from a ribbed rather than smooth chonetid, Paucispiniferoidea emerged from the strophalosiiform Subfamily Devonoproductinae, and two main branches Linoproductoidea and Proboscidelloidea arose each separately from other Devonian strophalosiiform subfamilies within Devonoproductidae.

Although the evolution is complex, and does not conform other than broadly to any simple pattern, it strongly suggests that diverse superfamilies arose independently from allied stock, not from any shared point source, and the superfamilies may be traced back in time through considerable morphological change, with evolution proceeding independently, but in similar directions, through the loss of several strophalosiiform character-states. A moderately diverse classification seems necessary to express the origins and interrelationships between the superfamilies. The classification is based on morphologies, source stock, sequential development and geographic distributions.

Critical new species, genera, tribes and subfamilies are proposed across the spectrum of Productidina, Strophalosiidina, Oldhaminidina and Linoproductidina, from various parts of the globe, including England, Scotland, Ireland, Belgium, Germany, Armenia, Russia, Kazakhstan, Canada, United States, Bolivia, Brazil, Argentina, Japan, China, Mongolia, Malaysia, Thailand, Pakistan, India, Nepal, west Papua (Irian Jaya), Australia and New Zealand, ranging from Devonian to Permian in age. Amongst other proposals that affect classification, Scacchinelloidea are differentiated from Aulostegoidea through the presence of lateral buttress plates, and Paucispiniferoidea are recognized as a major group that changed significantly during evolution. Yakovleviidae are evaluated as paucispiniferoid, and Monticuliferidae are allocated to Aulostegoidea.

A summary of newly named taxa is provided in Appendix B (p. 481), and a classificatory key set out in Appendix C (p. 486). The references (p. 496) are followed by an index for genera (p. 526).

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INTRODUCTION

Genera *Strophalosia* and *Productus*

This study enquires into the brachiopod Order Productida, building on the summaries of brachiopod genera and classification in volumes of the *Treatise of Invertebrate Paleontology*, and endeavouring to reconcile classification with evolution. There are two principal and long known genera on which the order is founded: *Strophalosia* King, 1844 from an uncertain locality of Permian age in Ladakh of Northwest India, and *Productus* Sowerby, 1814 from the Early Carboniferous faunas of England. *Strophalosia* (Fig. 1, Fig. 2) and its close allies are bivalved, with concave dorsal valve lacking spines, and opposed to a convex and spine-bearing ventral valve which may be further attached through a cicatrix over the umbo in a number of allied genera, although not always in *Strophalosia* itself. Both valves bear interareas along the hinge, with articulation aided by two teeth in the ventral valve fitting into sockets along the dorsal hinge. Muscles were attached to smooth ventral adductor scars imprinted on the inner shell, partly enclosed laterally by longitudinally striate diductor scars, and two pair of smooth dorsal adductor scars, divided by a median septum which extends forward from a small cardinal process, made up of prominent high shaft, the knob at top divided in two and small lateral lobe to each side (Fig. 6A-G, p. 11). The feeding apparatus leaves two very large brachial shields on the floor of the dorsal valve, and the interior of both valves is covered by a pattern of papillae and pits. This brief and incomplete summary of aspects of the genus is illustrated in Fig. 1, Fig. 2 , Fig. 7.2, p. 212, and internal morphology is illustrated from a related genus *Crassispinosella subcircularis* (Clarke) in Fig. 7. 9 (p. 219).

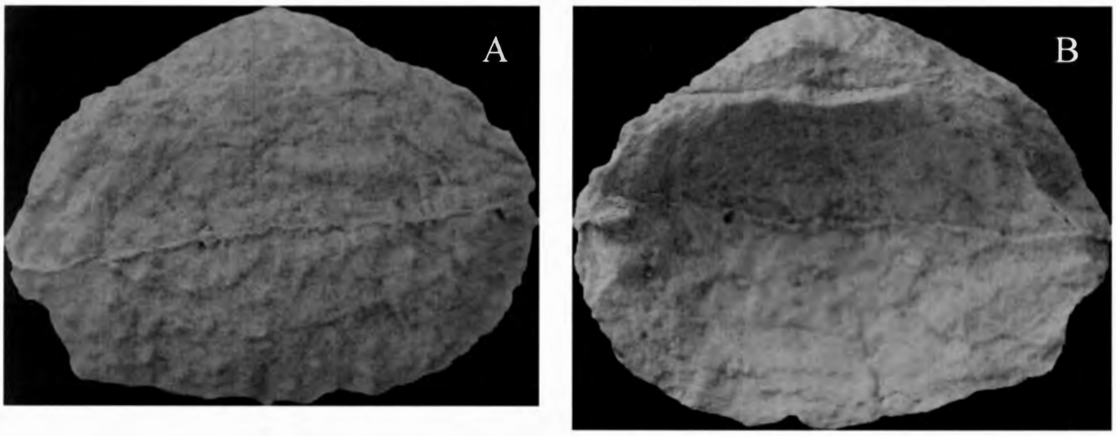

Fig.1. *Strophalosia gerardi* King, plaster mould BR 3068 of holotype prepared by J. Mitchell, University College, Galway (now National University of Ireland, Galway). A, B, ventral and dorsal views x1.9. See also Fig. 7.2, p. 212. Specimen from Upper Permian of ?Laddakh, northwest India. JBW photo.

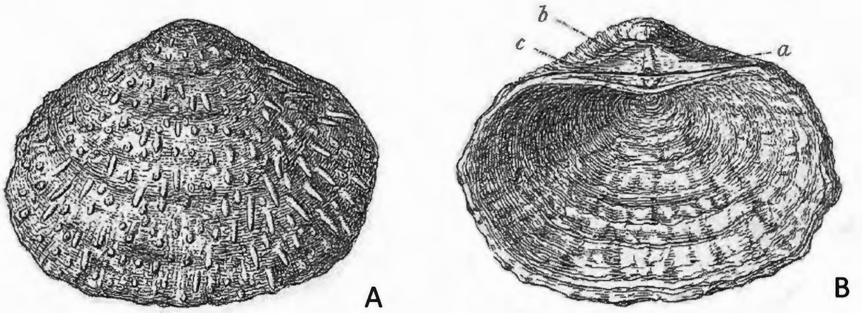

Fig. 2. *Strophalosia gerardi* King, holotype, A, ventral and B, dorsal aspects as figured by King (1850, pl. 19, fig. 6, 7), x1.2. Some morphological features indicated by King (1850), are as follows: a – ventral interarea, b - pseudodeltidium, c- dorsal interarea.

Fig. 3. *Productus productus* (Martin) figured as *Producta martini* by Sowerby (1814, p. 73, pl. 36, fig. 1), x1, from Carboniferous limestone of England.

Productids are of much the same size, with similar convex ventral valve and concave dorsal valve (see Fig. 3, 4). Ventral spines are retained and modified, but the external appearance is altered through simplification: the interareas of *Strophalosia* are lost, and any umbonal cicatrix has disappeared. Internally, the teeth and sockets have also disappeared, and the muscle scars are often no longer smooth, but are dendritic. The brachial shields are much reduced in area (Fig. 5H-J). These changes are substantial, and visible both externally and internally. In addition, there are more subtle changes to the cardinal process, often with deep median division and more prominent lateral lobes, as elaborated by Sutton & Summerson (1943) and Muir-Wood & Cooper (1960, pp. 27-31). A high diaphragm is developed around the dorsal disc, a feature more peculiar to *Productus*. These aspects are illustrated for *Productus* in the *Revised Brachiopod Treatise* (Brunton et al. 2000, Fig. 313.1a-f).

From these features the soft part morphology may be reconstructed with some authority. The overall anatomy of brachiopods is discussed by Williams et al. (1997), and living habits especially for Productida suggested by Muir-Wood & Cooper (1960, pp. 40-47), Brunton (1966), Rudwick (1970), Grant (1972) and Brunton, Lazarev & Grant (2000). The genera in question lived on the sea-floor, usually on sediment or on other shells, attached as a rule by the ventral valve through spines and to lesser extent cicatrix in the case of many Strophalosiidina, especially Strophalosioidea, and fed by opening the two valves, which were articulated by means of teeth and sockets in the case of Strophalosioidea, whereas these were lost in most Productoidea (ie. Infrasuborder Productimorphi), and in descendent members of Strophalosioidea, namely Aulostegoidea, Richthofenioidea, Scacchinelloidea and Cooperinoidea.

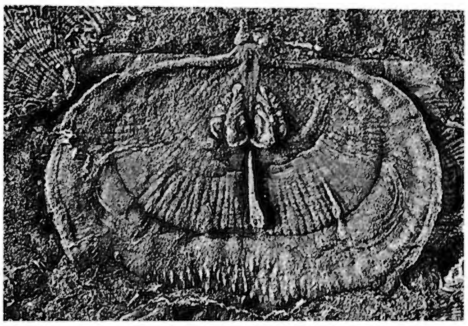

Fig.4. *Productus carbonarius* Koninck, latex impression of interior showing broad diaphragm, dendritic adductor scars, cardinal process, medium septum and brachial ridges, GSGB 4772, x2, from Millstone Grit, Yorkshire, England. See Muir-Wood & Cooper (1960).

The two allied but different genera, *Strophalosia* King and *Productus* Sowerby, are classified respectively as Suborder Strophalosiidina Waterhouse and Suborder Productidina Gray. Productidina is a very large group with hundreds of genera and several superfamilies; members exhibit a form of quasi-entropic evolution: reduction and simplification in part, coupled with elaboration of surviving parts. But there is a clash between the morphological attributes and the classification offered in the *Revised Brachiopod Treatise* and more recent studies (Williams, Carlson & Brunton 2000; Brunton et al. 2000, Brunton 2007; Waterhouse 2002b, 2004b). Some genera which gave rise to several of the superfamilies of Productidina, and were included in Productoidea, Linoproductoidea, and Echinoconchoidea by the *Revised Brachiopod Treatise*, are strophalosiiform in morphology, not productiform. That is, they display ventral and dorsal interareas, and have teeth and sockets, and large brachial shields. Careful analysis of morphological attributes and change through the fossil record allows the superfamilies to be tracked back through time from a productiform morphology into an older strophalosiiform morphology, and these productiforms did not arise from a point source, but from a "seed bed" made up of a number of different strophalosiiform genera, tribes and subfamilies. Such analyses have been conducted by a number of different authorities, those of the past few decades including Stehli (1954), Muir-Wood & Cooper (1960), Sarytcheva (1960, 1977), Lazarev (1987, 1989, 1990), Brunton et al. (1995, 2000) and the present writer (Waterhouse 1978, 2002b, 2004a). Authorities agree that whereas build and ornament discriminates between genera, families and even superfamilies within Productidina and Strophalosiidina, it may remain similar for groups across the morphological boundary between strophalosiiform and productiform Productida. It appears from analysis that the presence of teeth and sockets, and less inevitably, interareas, was related to the size and nature of brachial imprints, and their presence somehow inhibited the achievable variation in shape and ornament: once lost, genera could evolve with much greater diversity.

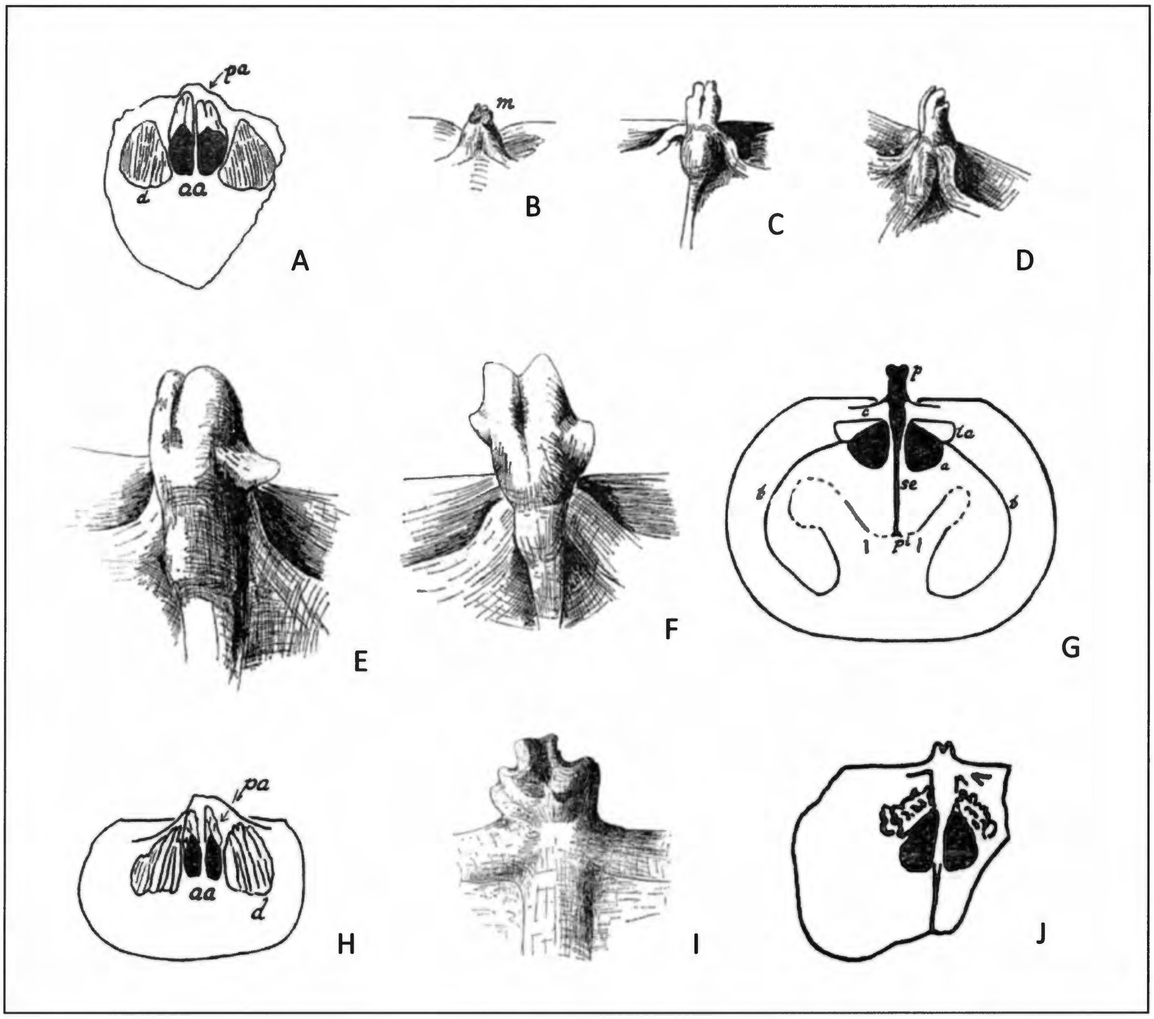

Fig. 5. A-G, internal aspects of strophalosiiform specimens. A, ventral muscle scars in *Pseudostrophalosia clarkei* (Etheridge), BR 221, x 1.2. B-G, *Echinalosia maxwelli* (Waterhouse). B-F, cardinal processes. B, anterior aspect at early neanic stage, without median lobe. Two strong lateral lobes continue into the cardinal or hinge ridges. Median septum arises well in front – and is absent from small shells. BR 333, 7.5mm wide. C, D, anterior and anterior oblique aspects of process in neanic shell 10mm wide, median lobe well formed and lateral lobes small. Septum continues into process, BR 348. E, F, oblique and anterior aspects of BR 925, 22mm wide, at early maturity. G, dorsal valve showing outline of brachial ridges, BR 281, x1.5. Specimens from Letham Burn Formation (Roadian), Wairaki Downs, New Zealand.
H, J, internal aspects of productiform specimens. H, J, *Terrakea brachythaera* (Morris). H, imprint of ventral muscle scars on ventral interior, BR 940, x1, Mangarewa Formation (Capitanian), Wairaki Downs. J, imprint of dorsal muscle scars on interior, BR 922 from the same locality, x1.5. I, *Paucispinauria concava* (Waterhouse), BR 788 from Letham Burn Formation, cardinal process, lateral hinge ridges and median septum, anterior view, x5. See Waterhouse (1964).
a = dorsal anterior adductor scar; aa = ventral anterior adductor scar, b = brachial ridge; c, dental socket ridge; la = posterior lateral dorsal adductor scar; d = diductor scar, m = myophore on cardinal process, p = cardinal process; pa = posterior ventral adductor scar; pi = pillar at anterior end of septum; se = median septum.

The question is, should these progenital genera be classed as Strophalosiidina on the basis of articulation and feeding apparatus, or as early members of the productiform superfamilies? The latter model was followed in the *Revised Brachiopod Treatise*, notably for what were called Productoidea, Linoproductoidea, and Echinoconchoidea, but not for Aulostegoidea or Scacchinelloidea ("Scacchinellidae"). That classification reflected an attempt to squeeze the evolution of Productida into the widely accepted model of evolution branching from a point-source, with each superfamily and suborder tidy in its origins. Their view was summarized by Brunton, Lazarev & Grant (2000, Fig. 233), to show five "original" families springing from one unknown chonetidine ancestor called X. There is what seems to be an artificial split between Strophalosioidea, which was shown as holding only one family, and various other families that are strophalosiiform in all attributes, apart from a mysterious Monticuliferidae for which the time range does not conform with known data, and Productidae. Yet although it might seem to be more objective to draw the boundary between Productidina and Strophalosiidina at the morphological change, it is preferred to incorporate the progenital stock in separate superfamilies. Some might argue it would be better to merge the two suborders, but that would be a retrograde destruction of information. Difficulties do arise from the approach followed in the *Revised Brachiopod Treatise*. The first problem is that cladistics appears to be subverted, or at least set aside. It is believed by students of Productida that family groups involve substantial change in their early history: it is like looking at a stick passing from air into water, where the stick appears to bend. The morphology and therefore an objective analysis of character states does change, but the stick, or the evolutionary group, is ultimately one and same, before and after the change in morphology. Analysis of such change requires controlled sequencing of morphological change, or chronomorphic analysis, rather than rely on a narrow and indeed reductionist focus centred on character states with no components of time or succession. So it remains arguable where to draw the boundary between Strophalosiidina and Productidina. Does the lineage start within the strophalosiiform group or within the oldest productiform member? And how are the diagnoses to be arranged? In the *Revised Brachiopod Treatise*, they are frequently conflicted – or even irrelevant – because of what appears to be an inconsistent treatment of morphological traits.

Two further key genera: *Linoproductus* Chao and *Leptodus* Frech

At first sight, *Linoproductus* Chao, 1927, based on *Productus cora* d'Orbigny, 1842, is close to *Productus* Sowerby, (Fig. 6), for it lacks teeth, sockets and interareas, and has small brachial shields. It has ribs and spines not so very different from those of *Productus*, and therefore has long been classed as an ally, and put in the same suborder in the *Revised Brachiopod Treatise*. But that is denied by the need to express origins of family groups. *Linoproductus* and its allies may be traced back to Devonoproductidae Muir-Wood & Cooper, which differed from their smooth and non-ribbed contemporary Productida by displaying ribs, and belonged to a distinct Linoproductidina. Such ornament implies that Devonoproductidae arose from a ribbed chonetid, in contrast to productid and strophalosiid brachiopods which arose from smooth non-ribbed chonetids. Devonoproductidae and descendents followed the same path as that taken by productids and strophalosiids, changing from a strophalosiiform morphology to a productiform morphology, but these changes were independent of the other major groups.

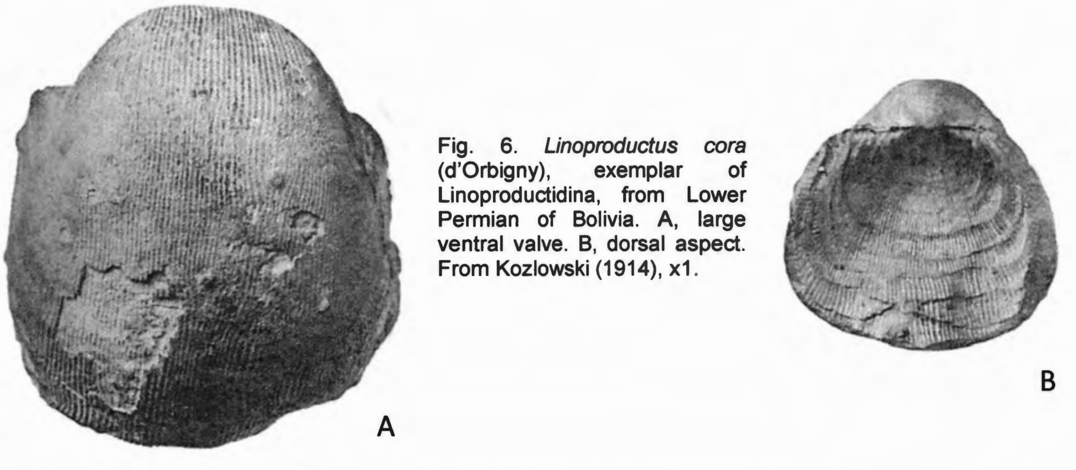
Fig. 6. *Linoproductus cora* (d'Orbigny), exemplar of Linoproductidina, from Lower Permian of Bolivia. A, large ventral valve. B, dorsal aspect. From Kozlowski (1914), x1.

Oldhamina Waagen, 1883, type species *Bellerophon decipiens* de Koninck looks neither productiform nor strophalosiiform (Fig. 7). The ventral valve is a simple convex dish-like structure, and the dorsal valve is severely reduced, largely to the elaborate feeding apparatus. But its origins may be traced to Strophalosiidina, even though subordinal status is mandated by the highly distinctive morphology. It typifies Oldhaminidina.

The need for elaborate classification

The complexity in relationships between family groups cannot be fully conveyed by use of the classification provided in the *Revised Brachiopod Treatise.* That study used these relevant categories: Class, Order, Suborder, Superfamily, Family, Tribe. To these Waterhouse (2001, 2004b) and Lazarev (2005b) have added Subtribe as a means of expressing divisions within tribes, by clustering genera of allied morphology believed to have been closely related: which is simple enough. But the categories recognized in the *Revised Brachiopod Treatise* beyond superfamily are too few, and it is deemed desirable to introduce categories that reflect relationships, both at superfamily and higher level. Within Productidina, four superfamilies are close to each other in so far as Overtonioidea, Marginiferoidea, Horridonioidea and Productoidea arose, each separately, from Productelloidea. That may be expressed by clustering them in Infrasuborder Productimorphi Gray. Echinoconchoidea arose separately from a different family in the same Superfamily Productelloidea, and is a member of Productidina, but stands somewhat apart. Linoproductoidea, Proboscidelloidea and Paucispiniferoidea arose separately, each directly from different strophalosiiform genera classed as Devonoproductidae (Brunton et al. 2000, pp. 545-550; Waterhouse 2004b, pp. 42, 43), and therefore should stand on their own as Linoproductidina. Fossil evidence and sequence-streaming strongly suggest that Cooperinoidea, Scacchinelloidea and Aulostegoidea arose independently, each directly from different Strophalosioidea, and Richthofenioidea evolved later from Aulostegoidea: the latter two are placed as Aulostegimorphi Waterhouse. Such a classification expresses no more than a bare minimum of adjustment to the classification of Productida. It may be allowed that further elaboration of brachiopod classification would bring the phylum into better harmony with the proposed classification of Bivalvia (J. G. Carter et al. 2011), for which it is planned to use various categories far more elaborate than set forth in the *Revised Brachiopod Treatise*, involving such terms as cohort, subcohort, infrasubcohort, hyporder and minorder, in order to express concepts of interrelationships and evolution. Phylum Brachiopoda is somewhat similar in aspects of its complexity.

Fig. 7. *Oldhamina squamosa* Huang, exemplar of Oldhaminidina, block of specimens BR 3073, x1. From Huai Tak Formation (Changhsingian), northern Thailand. JBW photo.

The significance of morphological space in the *Revised Brachiopod Treatise* classification of Productida has already been underlined by the treatment of oldhaminid brachiopods (Fig. 7). These are highly specialized paleotropical brachiopods in which the ventral valve has become large and dish-like, cemented to substrate, and the dorsal valve has mostly disappeared, except for an articulatory area and a large ptycholophous brachidium (Termier & Termier 1949). Williams (1953, 1965) expressed the substantial difference from other and ancestral stock by classing the group as Suborder Oldhaminoidea, the name amended later to Lyttoniidina (Williams, Harper & Grant 2000). All available evidence points to a source from Strophalosioidea (Waterhouse 2010a), but the morphological distance from Strophalosiidina is so great that at least subordinal standing is well justified. Few if any other brachiopods have lost most of the dorsal valve.

There is another group, called Cooperinidae in the *Revised Brachiopod Treatise* (Brunton et al. 2000, pp.

605-607), and only discovered in the mid 1960's (Termier, Termier & Pajaud 1966), which has outstanding morphology, intermediate between that of Strophalosioidea and Lyttonioidea. They are strophalosiiform in the presence of large cementing cicatrix, spines, and dorsal valve, but several genera have developed multilobed brachial supports which may become ptycholophous, approaching those of Oldhaminidina, to suggest an intermediary stage of evolution between Strophalosioidea and Lyttonioidea, even though the fossil record is such that Cooperinoidea are actually found in faunas of mostly Permian age. It seems highly likely that Lyttonioidea evolved from cooperinid-like stock, and arguably this exceptionality and likely source position should be expressed by raising the standing of the group. Certainly retention of Cooperinidae as a mere family in Aulostegoidea (Brunton et al. 2000) does not express adequately the evolutionary relationships with either Strophalosioidea, for which families are recognized principally on distinctions in ornament, or Oldhaminidina, distinguished mainly by the feeding apparatus.

Two alternatives

There are several alternative ways of understanding Productida, and the two main options involve on the one hand prime stress on morphology, and an alternative scheme which emphasizes descent and association. One of these alternatives at subordinal level could stress the sharing of teeth, sockets, interareas and large brachial shields as being requisites for Strophalosiidina, and the absence of these features as requisites for Productidina. It thereby would keep Strophalosiidina as a diverse but interrelated group which gave rise from different groupings to different streams of Productidina, that shared morphologies, but not ancestry, at least in some cases. It may be suspected that cladistics would support such a view, but if it did, would it be correct? To judge from the paleontological evidence, the associations and paths of apparent descent would not be truely phylogenetic.

The alternative would be to consider morphology as less constant, and allow suborders to have undergone comparable change in losing teeth, sockets, interareas and change in brachial ridges. With that degree of tolerance, Productidina would form a somewhat shrunken group, embracing Overtonioidea, Horridonioidea, Marginiferoidea, Productoidea and Echinoconchoidea, all descended from various members of Productelloidea, which are classed as essentially smooth-shelled spinose strophalosiiform genera, characterized in part by the lack of a ventral cicatrix. Strophalosiidina include forms close to early Productidina, differing in the presence of an umbonal cicatrix on the ventral valve. Major groups retained a strophalosiiform morphology, but some followed the trend of Productidina, and began to lose various strophalosiiform aspects, to evolve into Aulostegoidea, Scacchinelloidea, and Cooperinoidea. The morphology for some groups thus overlaps with that of Productidina, but their sources may be traced into Strophalosioidea rather than Productelloidea. Ultimately, the sources of the two suborders were comparatively close, stemming from perhaps different genera or different subfamilies within Chonetida (Family Anopliidae), the difference expressed in the presence of a cicatrix on earliest Strophalosioidea. It is widely agreed that Oldhaminidina arose from Strophalosiidina. But the proposal of Linoproductidina is new, based on tracking origins of the constituents to an entirely different chonetid group, distinguished by its close-set fine ribbing. This ribbing persisted throughout most members of the suborder, but in other respects, the morphology, especially for articulation and feeding, matches that of Productidina and various Strophalosiidina. Overall, the classification reflects change from different chonetid groups into first a strophalosiiform morphology, which in turn changed into a more or less productiform morphology. Such a pattern may not have been predictable, nor projected according to some popular models of evolution, but is substantiated in the following summaries for Productida.

Sequence for classification

Tthe succession of genera and family groups provided in the *Revised Brachiopod Treatise* is followed to some extent, and as far as possible. That work provides much basic information and remains a prime source for illustrations and references. The linearity of text provides a problem: for three dimensions through time would provide a more realistic rendition, and in some ways it would be more convenient to place Linoproductidina at the start of the analysis, rather than end, because these are in terms of origin a more stand-alone group, even though they followed fairly closely, although in some respects more expansively, the course of evolution traced by Productidina. The latest major groups to have evolved, Richthofenioidea, Cooperinoidea, and Lyttoniidina came last in the evolution of the order, and it would have been advantageous in explaining origins and setting out classification in an orderly sequence which followed the passage of time. But it is traditional to begin the analysis of classification with the nominate group, which was more closely related to Strophalosiidina and Lyttoniidina than to Linoproductidina, in terms of origin. The succession for further genera usually proceeds by age, but may follow in alphabetical order.

Age of genera

The age of various genera is taken especially for the Devonian Period from the *Revised Brachiopod Treatise*, the Carboniferous and especially Permian Periods partly from the *Revised Brachiopod Treatise* and partly from additional literature. The ages are summarized in Table 2 (see p. 29), with cautions expressed on p. 474.

Authorship of ordinal categories

In this study, authorship for all ordinal categories is ascribed to the author who was first to propose an ordinal group, as in Waterhouse (2010a). This follows the practise established for family group names, and greatly simplifies procedures, and is being followed for the Treatise series on Bivalvia. To adhere to the system championed by some writers, in which the ordinal level and its authorship is under constant change with adjustments in understanding, is clumsy, and was not followed with full consistency by the *Revised Brachiopod Treatise*. Whilst that approach does have the advantage of potentially if cryptically indicating which interpretation is being favoured, such a procedure, which seeks to couple authorship with definition, may encourage a freeze on progress, in order to achieve constancy.

Rigidity of Classification

The higher orders of classification seem comparatively rigid: the lower levels are more flexible and open to shifts up or down the hierachy. In that regard, there is scope for recalibrating especially tribal and infrafamilial groupings to ever more accurately express relationships and ongoing evolution. Even so, it is deemed desirable to allow some flexibility, and acknowledge that evolution did not always play by whatever current interpretations are in fashion, so that a parameter normally critical for a tribe or subfamily may be weakly developed or absent from a genus very close in other attributes to a given tribe or subfamily. These are what may be termed varions, defined as a genus that shares many characters with other genera, yet lacks what is normally a critical feature displayed by the other genera, thereby displaying flexigenesis. Examples may be found for example amongst Paucispinauriini (eg. *Vagarea* with the loss of ventral capillae) or Kozlowskiinai (eg. *Opiparia*, with the loss of mutiple trails), or Desmoinesiinae (*Hexiproductus* with the loss of dorsal spines). Such may or may not indicate a new tribe or subfamily in embryo: it also provides static for cladistics. In the course of this enquiry, some genera – not many – simply do not fit well in any category so far recognized, and as a rule, these are "shoe-horned" into a tribe or subfamily which provides the closest fit, with a query. That poses a challenge, to improve the classification – or uncover more of the fossil record! But it also may have been a real phenomenon, because evolution may not have been constrained in whatever way it is interpreted, and may have outflexed any applied program. The need remains to compare the classification as based on evolutionary trends, against a model based on cladistics, to see if the parameters of time and geography, left out of cladistics, make any difference. From the study of over 700 genera, it is concluded that in trying to unravel the course of evolution, it is essential to be cautious in applying techniques that constrain as well as unravel evolution: all too easily, the medium becomes the message.

A "Widow" family

One family is set apart from the superfamily groups, because it was a transition group, related to, yet differing substantially from, the ancestral and descendent superfamilies, namely Devonoproductidae, a family progenital to three productiform superfamilies of Linoproductidina, but differing from all three in its strophalosiiform accoutrements. It could be subdivided into three, corresponding with its constituent subfamilies, with each third placed as the earliest member of its descendent superfamily, but then there would be three widowed subfamilies, for any higher ranking would seem to be excessive.

Acknowledgements

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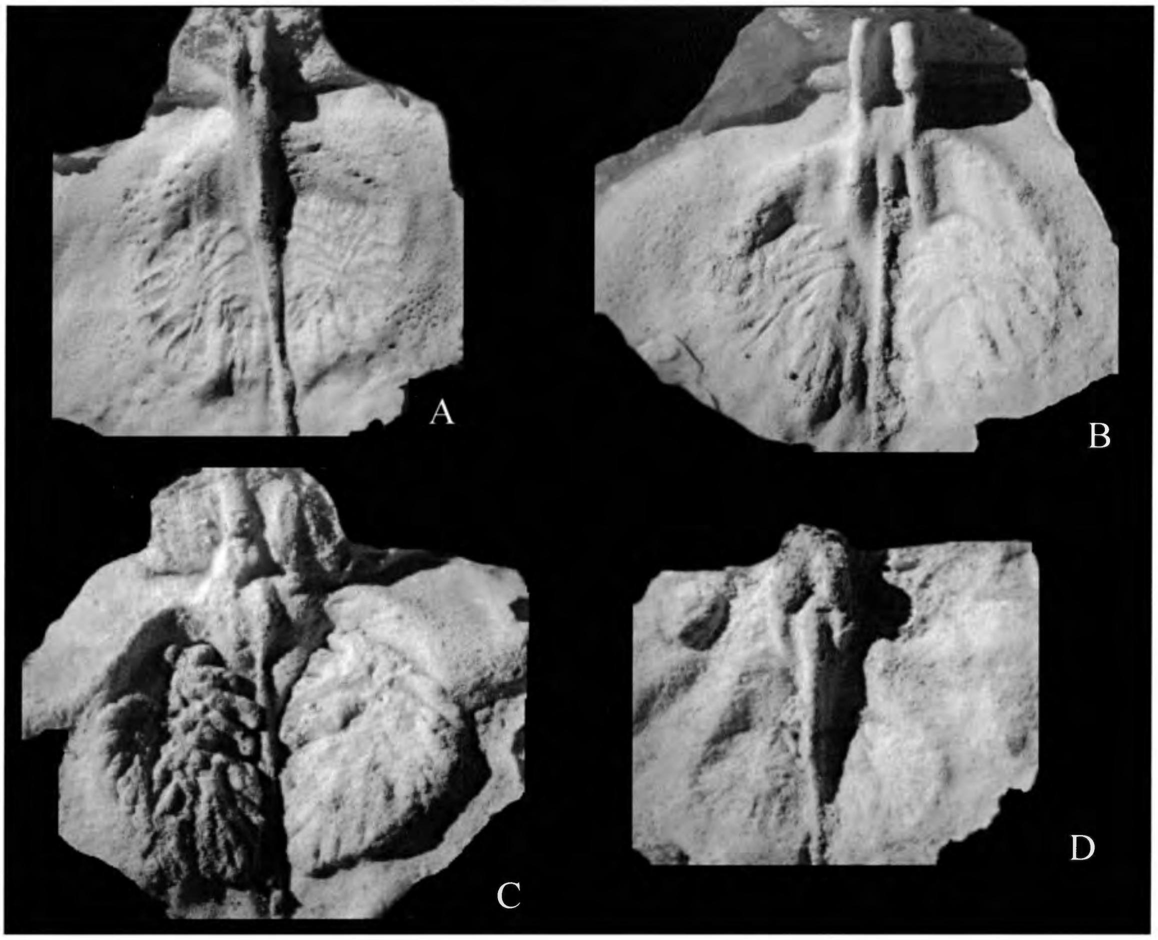

Fig. 8. *Taeniothaerus subquadratus* (Morris), buttress plates as shown by latex casts of cardinalia of dorsal valve. A, UQF 81189, x1.5. B, UQF 81211, x1.5. C, UQF 81190, x2. D, UQF 81193, x1.5. Specimens from middle Tiverton Formation (Artinskian), Bowen Basin, Queensland, Australia. JBW photo.

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MORPHOLOGICAL TERMS

1. Specific terms

Alveolus: The term alveolus was applied by H. M. Muir-Wood in Williams & Rowell (1965, p. 139) to a pit in front of the internal face of the cardinal process, but was deprecated by Williams & Brunton (1997, pp. 424, 426). No reason was provided, but perhaps the term was abandoned because it is applied widely and with different meanings across phyla. On the other hand Russian translations into English continue to use the term as applied to Productida.

Anderidia: Low septa or ridges in dorsal valve placed between the anterior and posterior pairs of adductor scars.

Buttress plates: Two short ridges immediately in front of cardinal process, usually parallel, and placed behind dorsal adductor scars. (See Fig. 8).

Buttress mounds: Broad small domes or mounds one each side of the dorsal septum and in front of the cardinal process, may be in place of lateral buttress plates (q. v.).

Commarginal (new): It is common for descriptions of brachiopods to mention concentric rugae, growth lines, etc. But commarginal seems a more accurate term, and this is used throughout the text, not to the exclusion of concentricity, because there does not seem any need to be completely rigorous. Commarginals may involve solid costae, rugae or wrinkles, lamellae, growth stops, each kind significant and often distinct.

Commargon (new): A commarginal band of shell, concave or convex, bordered posteriorly and anteriorly by growth steps, growth lamellae, ridges or interspaces.

Double septum: In various Productida, two septa lie side by side over the posterior dorsal valve, in front of the cardinal process, and separated usually by a groove, or in other instances by the median septum.

Growth step, growth stop, growth pause (new): Although omitted from the glossary of descriptive terms for Brachiopoda in the *Revised Brachiopod Treatise*, growth steps and growth pauses or growth stops are commonly exhibited by many brachiopod shells.

Lateral buttress plates (new): Two ridges diverging from in front of the cardinal process outside of and lateral to the posterior adductor scars. Called buttress plates in some studies. (See Fig. 9).

Morphological congruence (new): This is a term to be preferred over the commonly used reference "convergence", which has developed teleological implications.

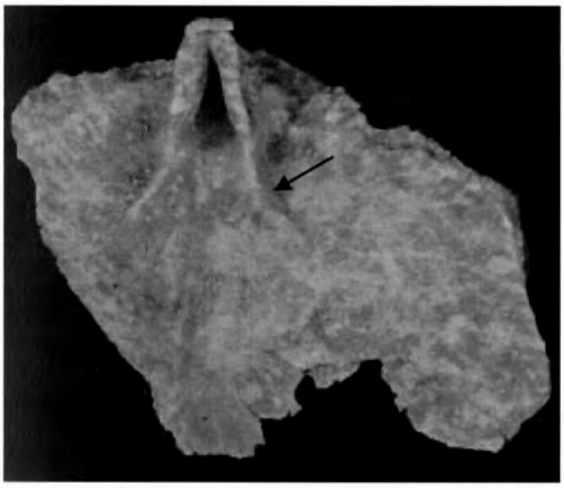


Fig. 9. Lateral buttress plates as arrowed in *Guadaluposteges guadalupensis* (Shumard), USNM 154181, x2.2, from Bell Canyon Formation (Capitanian), Texas, photo courtesy M. Brett-Surman, Smithsonian Institution, Washington D.C.

Shagreen: Shagreen structure or texture has been applied in two different ways to brachiopods. Waagen (1883) followed by many paleontologists so described the *external* pattern of smooth shell marked by shallow pits or exopunctae, usually in quincunx or regular pattern, in *Martinia* or allied Spiriferida. Ignoring this application, Lazarev & Carter (2000) and translations of Lazarev (2000a, b) have used the same term for *internal* pustulation in Productidina, that may look somewhat like sandpaper. It is undesirable to duplicate the term with such different meanings, and throughout this text, the reference to the studies by Lazarev that use his meaning of shagreen is in no way intended to endorse the duplication of Waagen's application in a different sense.

Spine base: Refers to the base of the productid or strophalosiid spine where it emerges from the body of the shell. In a number of genera the shell surface behind the base is elongately raised, and this may also be termed a spine base.

Spine tunnel: The hollow core of the spine may be prolonged anteriorly and/or posteriorly from the base of the spine through the shell, and may leave an elongate tube, or channel internally. This is termed spine tunnel. (See Fig. 10).

Split septum: Applied to dorsal septum in front of the cardinal process if it is divided by a short slit. (See Fig. 4, p. 10).

Strut spine: Strut spines are long, thick and rigid spines limited to the ventral valve, usually numbering three or six. Earlier strut spines may become atrophied. They differ from halteroid spines in being linear and much fewer, symmetrically arranged, and so functioned as balancing props, rather than attached or halteroid. They are largely limited to Families Paucispiniferidae and Yakovleviidae, with some Retariinae. (See Fig. 15.31, p. 344).

2. Discussion of buttress plates

For the dorsal interior of productid and strophalosiid brachiopods, there have been slight inconsistencies in terminology, and usage of the terms herein follows that illustrated in Fig. 8 and 9. The term buttress plate has been applied in different ways, and here it is used solely for two short ridges connected usually to the cardinal process and lying behind the adductor scars. In some descriptions, as for juresaniids and buxtoniids, a split septum has been also labelled as buttress plates. That does not fully describe the appearance of the plates.

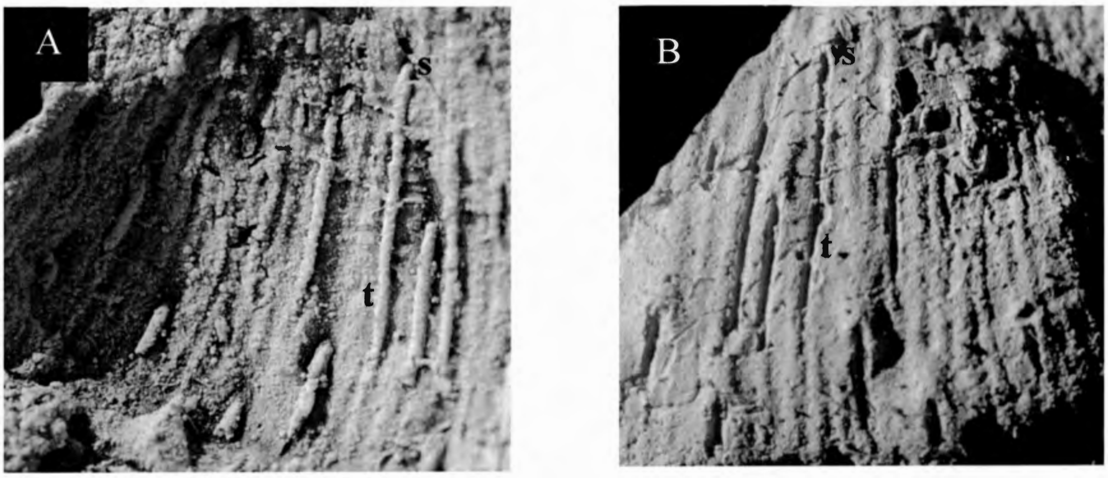


Fig. 10. *Paucispinauria geniculata* Waterhouse. A, latex cast of inner ventral anterior shell, showing spine base (s) which is extended forward each by a hollow tunnel (t) within the shell which presumably connected the interior of the spine with the growing mantle until filled in. UQF 81813, x6. B, internal mould of the same specimen. The anterior spine channels are not visible in intact shells, but here the shell has been worn out to leave open gutters on the internal mould. The top of each figure is the posterior part of the shell. Letham Burn Member (Roadian), New Zealand. JBW photo.

In some groups such as Rhamnariinae Muir-Wood & Cooper and Balkhasheconchinae Waterhouse, two slender ridges diverge forward from in front of the cardinal process to lie outside the outer adductor scars. These have also been called buttress plates, but are somewhat longer and differently arranged, and are called lateral buttress plates herein. Authors may refer to accessory plates in the dorsal valve, and in a number of instances, these can be more precisely named, as anderidia (q. v.) or lateral buttress plates. Lateral buttress plates that pass forward from the base of the cardinal process are developed in Araksalosiidae, Leioproductinae, and all members of Scacchinelloidea. Lateral buttress plates pass forward at an angle from long buttress plates in Levipustulini, or from the posterior medium septum in some Gigantoproductidae.

Some species amongst Dictyoclostidae (pp. 161-165) and Linoproductidae (pp. 360-363, 389-395) have short lateral buttress plates or buttress mounds, and these are provisionally assigned a degree of significance for helping to distinguish a few genera. The significance appears to be enhanced by further similarities shared between the genera concerned.

3. Discussion of "shagreen" texture (Fig. 11 - 14).

In several studies, Lazarev (2000a, b) has emphasized the significance of what he called shagreen surface, comprised of dense and small pits and/or conical mammillate tubercles, found widely in brachiopods and commonly termed pustules or tubercles, or papillae in brachiopod literature. To them, Lazarev applied a Russian term for what has been translated as "shagreen" texture, and repeated in English language publications such as that by Lazarev &

Carter (2000). That is not to be confused with shagreen surface or shagreen applied by paleontologists to describe the external micro-ornament of martiniid brachiopods. Waagen (1883, p. 529) and Leidhold (1928) referred to "chagrin sculpture" like "chagrin leather" and correctly interpreted by Dunbar (1955, p. 152) to mean "shagreen". The term has not dropped out of use, and was for example mentioned by Cooper & Grant (1976, p. 2264). But Waagen's shagreen is in no way comparable to the application proposed by Lazarev and mentioned by Brunton (2007), and the copying of Waagen's term with a different application must be deemed regrettable: the sooner the terminology is clarified, and consistency achieved, the better. Indeed the term "papillation" would suffice, as a name already in wide usage, and it could be specified as "posterior central papillation" to convey what Lazarev intended to convey by the term "shagreen". An additional problem with the term shagreen as translated from Lazarev is not only that it duplicates a Waagen term in a different sense – it is a junior homonym – but his "shagreen" is not always different from similar papillation to the side or in front – only its location is important, and the term "shagreen" is non-directional and non-locational, except according to an artificial definition. I suggest that instead emphasis should be placed on

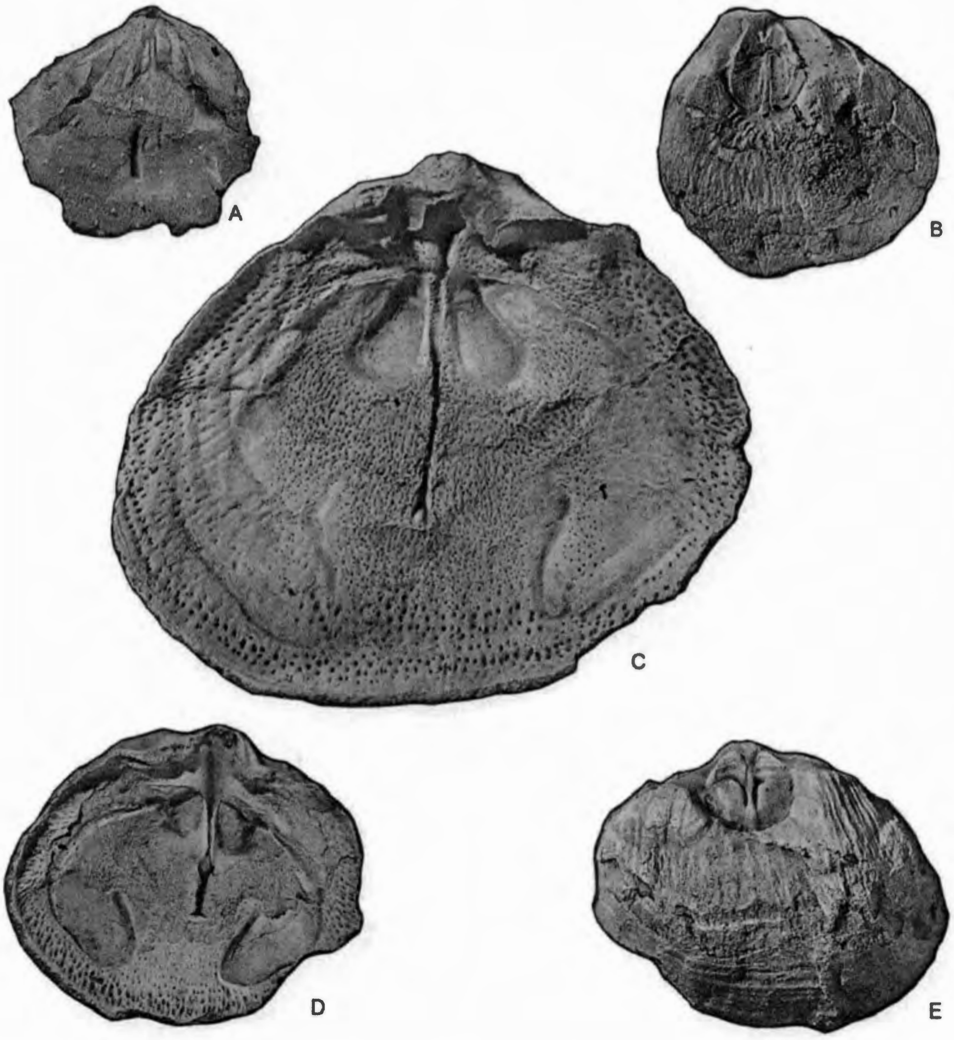


Fig. 11. "Shagreen" or posterior central papillation in *Echinalosia maxwelli* (Waterhouse). A, internal mould of immature ventral valve BR 270, with extensive shagreen pattern. B, internal mould of mature ventral valve BR 272, having lost shagreen pattern from posterior shell. The very fine pits are an artefact of the printing process. C, dorsal aspect of mature internal mould BR 246, showing retention of shagreen pattern. D, dorsal aspect of internal mould of gerontic specimen, BR 281, showing reduction of shagreen pattern. E, internal mould of gerontic ventral valve BR 281, also without shagreen pattern posteriorly. Specimens x1.8, except Fig. 11C, x3.5, from Letham Burn Formation, (Roadian), New Zealand. In summary, shagreen pattern is well developed in both valves at immature stage of growth, and disappears or is reduced from mature ventral valves, but is retained in mature dorsal valves until late in maturity. S. N. Beatus & JBW photo.

the opposite "non-shagreen" phenomenon, the "posterior central smooth" shell, because this can be exceptional, and need not be replicated to either side (at least according to Lazarev, though this may be questionable). The basic observations have strong prospects of holding value, provided that the concept is qualified, and applied to fully mature shells, a stipulation never proposed by Lazarev. Throughout this text, the term shagreen is used sensu Lazarev, together with "posterior central papillation". Ideally, a new and brief term should be introduced, with the focus on the smooth and non-papillate surface, for it is this that may be deemed exceptional. The phrase "Lazarevian surface" might be appropriate, in view of the contribution by that author, to replace "posterior (central) smooth surface". Alternatively, a different English rendition of the Russian word could be used, to impart a special application, for of course Lazarev was communicating in Russian a concept somewhat unfortunately translated into English as "shagreen".

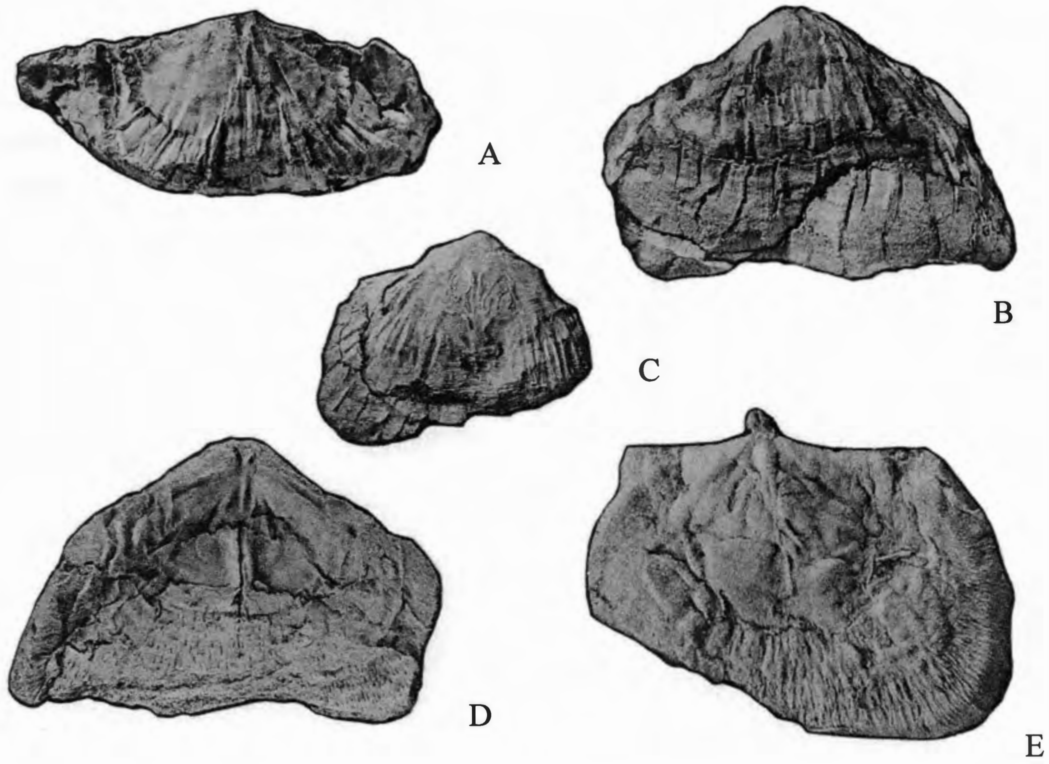


Fig. 12. "Shagreen" pattern in *Paucispinauria concava* (Waterhouse). A, B, posterior and ventral aspects of internal mould BR 200 (holotype), showing lack of posterior papillation in fully mature specimen. C, ventral aspect of immature internal mould, BR 213, also lacking papillation posteriorly. D, dorsal aspect of BR 200 (holotype), showing very weak and fine posterior papillation. E, latex cast of dorsal interior, BR 788, with very weak posterior papillation. As in *Echinalosia*, the dorsal and ventral valves differ slightly in presence of shagreen pattern, even in a single specimen. From Letham Downs Member (Roadian), New Zealand. All specimens x2. S. N. Beatus & JBW photo.

According to Lazarev, the pits and pustules of the productidan interior served as bases for the papillae-bearing cilia. The presence of this posterior central papillation was taken by Lazarev to show that the surface contacted the bilayered epithelium restricting the mantle cavity, whereas the visceral (coelomic) cavity corresponded to the smooth part without papillae of the umbonal part of the valves and muscle scars. It was deemed that the pattern indicated that the mantle cavity extended into the centre of the umbonal part of the base of the ventral valve. The lack of such papillation posterior to the muscle scars was alleged to belong to more conservative lineages, exemplified by Yakovleviinae (Lazarev 2000b, p. 495). Using these observations, Lazarev (2000b, p. 496) noted that Buxtoniinae lacked posterior central papillation, whereas Productinae displayed posterior central papillation. Such would imply that Buxtoniidae proceeded Productidae, which accords with the interpretation in this study, but unfortunately other presence/absence data is not always so accommodating. His classification of Yakovleviinae emphasized the lack of posterior central papillation as an important shared character. However it may be noted that it was not deemed so significant that it mandated an association with Buxtoniinae, which also lacks "shagreen" pattern. That in turn allows the possibility that whatever the nature of papillation, other criteria – including, it is here believed, ornament and shape, as explained by Waterhouse (2001, 2002b) – are more significant. It is here deemed that counter to Lazarev, the posterior central inner shell of so-called "advanced" productidans may become smooth as in so-called "conservative" productidans during the individual life cycle, and that conclusions need to be reinforced by ontogenetic and ecological studies. Indeed the nomenclature should be reversed, because ontogenetic development records change from papillate to smooth. And Yakovleviidae with posterior central smooth patch are shown to be an advanced rather than conservative member of Paucispiniferoidea (pp. 336ff).

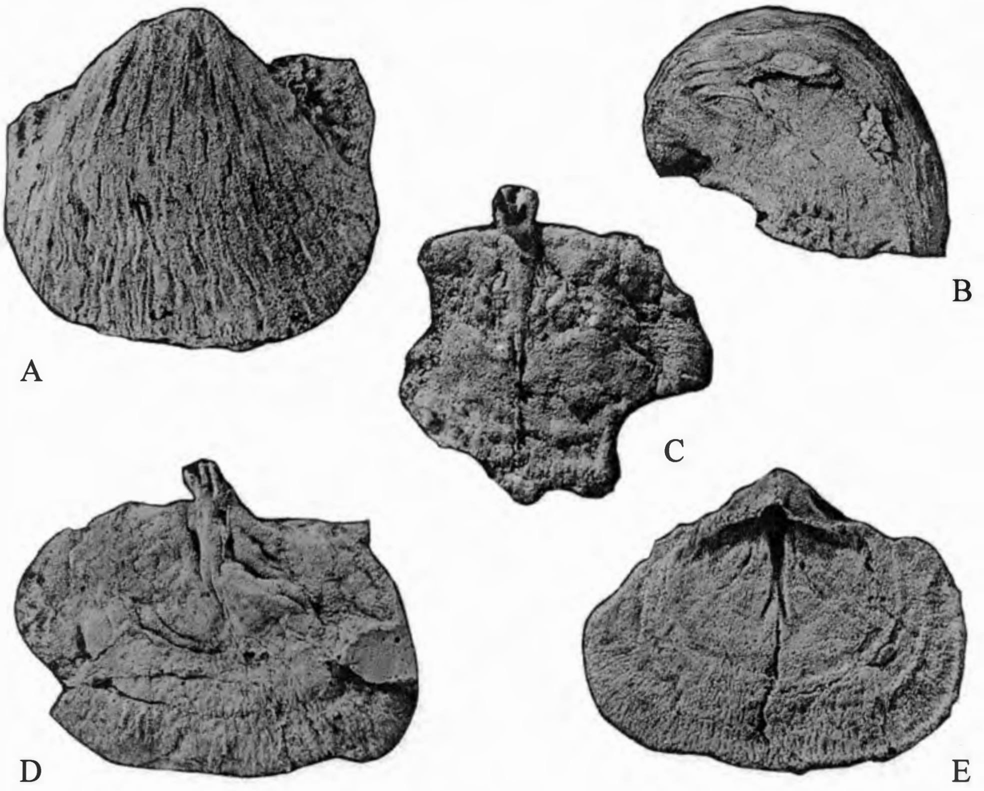


Fig. 13. *Terrakea brachythaera* (Morris). A, internal mould of immature specimen BR 159. B, lateral aspect of ventral valve BR 162. C, PVC cast of dorsal interior BR 936. D, PVC cast of dorsal interior BR 65. E, dorsal aspect of internal mould BR 163. Specimens x 2, from upper Mangarewa Formation (Capitanian), New Zealand. Posterior papillation is more strongly developed than in *Paucispinauria concava* (see Fig. 12), possibly reflective of more active bottom conditions and accumulation in coarse sandstone as opposed to siltstone. S. N. Beatus & JBW photo.

For detecting posterior central papillation or "shagreen" pattern, Lazarev (2000b) stressed that it was difficult to determine the nature of the umbonal surface in the ventral valve, and so indicated reliance on the dorsal interior. He seems to have been unaware of the value of internal moulds, which in fine siltstone or shale, preserve fine detail much better than silicified material and even shell material, because shell material of calcium carbonate can dissolve away, and because silicification often is imperfect and blurs detail. Examination of Productida dissolved in dilute HCl acid and preserved as internal and external moulds reveals some challenging aspects, especially in material so well preserved that every growth increment is superbly preserved, which is more than can be said of the few examples mentioned by Lazarev. For the genus *Echinalosia* of Family Strophalosiidae (Fig. 11), immature ventral valves of the type species *E. maxwelli* have papillation over the entire posterior shell and the papillation pattern disappears with increased maturity. In other words, juvenile and immature *Echinalosia* are "advanced" and then in late maturity become "conservative", which does not seem to be in accord with the Lazarev dictum, by implying a regression in ontogenetic development. The dorsal valve has posterior central papillation into maturity, and a gerontic specimen has lost it from the ventral valve and has almost lost it from the dorsal valve, with only very fine traces remaining. Moreover an extended surface of the posterior valve may be affected. *Lethamia*, member of Lethamiini Waterhouse in Family Sentosiidae, has posterior central papillation which tends to be less marked in fully mature specimens (late mature Waterhouse 1964, pl. 9, fig. 1 cs. Waterhouse 1982a, pl. 9c, f, i). For *Paucispinauria concava* (Family Paucispinauriidae), immature and late mature ventral valves lack "shagreen" pattern (Fig. 12). But a species within the closely allied genus *Terrakea brachythaera* has conspicuous posterior central papillation into late maturity (Fig. 13). Significantly, these specimens lived in a more turbulent environment than *concava*. Yet in *Terrakea dickinsi* Dear from volcanic breccia, the "shagreen" pattern is lost at maturity (Fig. 14).

These observations suggest that Lazarevian shagreening varies: it may disappear late in ontogeny: it may disappear from one valve and not the other, and it may vary in intensity and presence depending on ecological conditions. For it to be regarded as a prime discriminant may prove to be correct within some lineages, but that has yet to be established by ontogenetic study, from a range of habitats and a range of specimens, thereby avoiding extrapolations from a handful of specimens. Reliance on a paucity of samples, with the unproven assumption that each may typify an entire family or tribal group would seem hazardous, given the proven plasticity and variation displayed by biota at different growth stages, in different environments. As shown subsequently, the speculation that lack of Lazarev's "shagreen" pattern has established the nature and affinities of Yakovleviidae appears to be contradicted by various morphological attributes, and indeed specimens at early maturity have posterior papillation, and lose it in mature *Elucidatea*, a new yakovleviid genus (p. 339). Moreover specimens of the yakovleviid *Harkeria* new genus from Arctic Canada appear to lack posterior central papillation, but close scrutiny shows very fine papillation, preserved in a very fine matrix (see p. 351). Such fine papillation might not be observable in an ordinary shell or coarse matrix. The gradual disappearance of "shagreen" texture exhibited in specimens of various genera, tribes and families may suggest that the smooth shell reflects late ontogenetic smoothing by secondary shell deposition, or an area impinged in some way by muscles. But this is also speculation, needing further exploration.

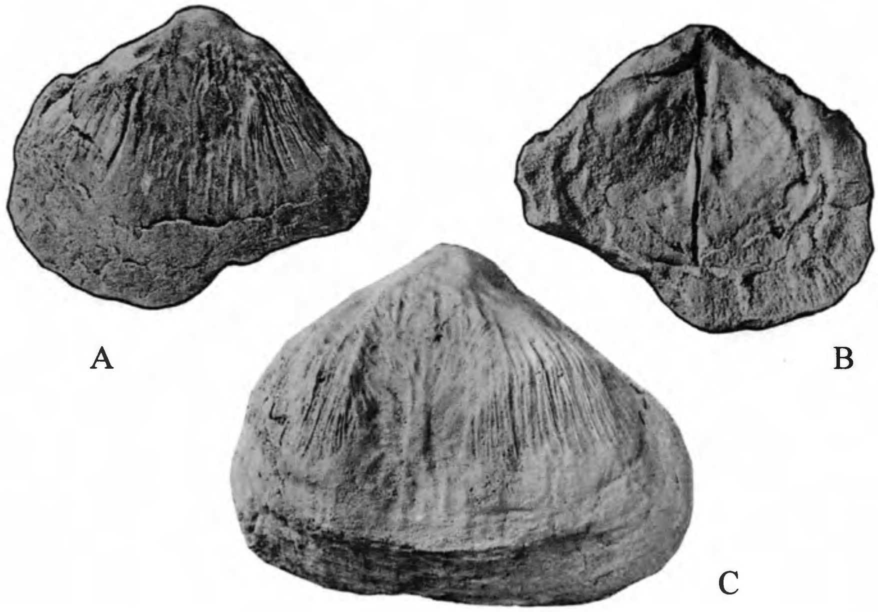


Fig. 14. *Terrakea dickinsi aurispina* Waterhouse. A, B, fine "shagreen" pattern in ventral and dorsal valves of internal mould BR 217. C, ventral view of internal mould BR 1486. Specimens x 1.8, from Brunel Formation (Artinskian), New Zealand. The enclosing sediment is of coarse volcanic breccia, and the posterior papillation is lost in the fully mature specimen BR 1486. S. N. Beatus & JBW photo.

4. **Ontogeny.**

The development and loss of posterior central papillation for at least some brachiopods clearly depends on ontogeny, and this field remains to be more widely explored. Although ignored in many studies, different ontogenetic pathways

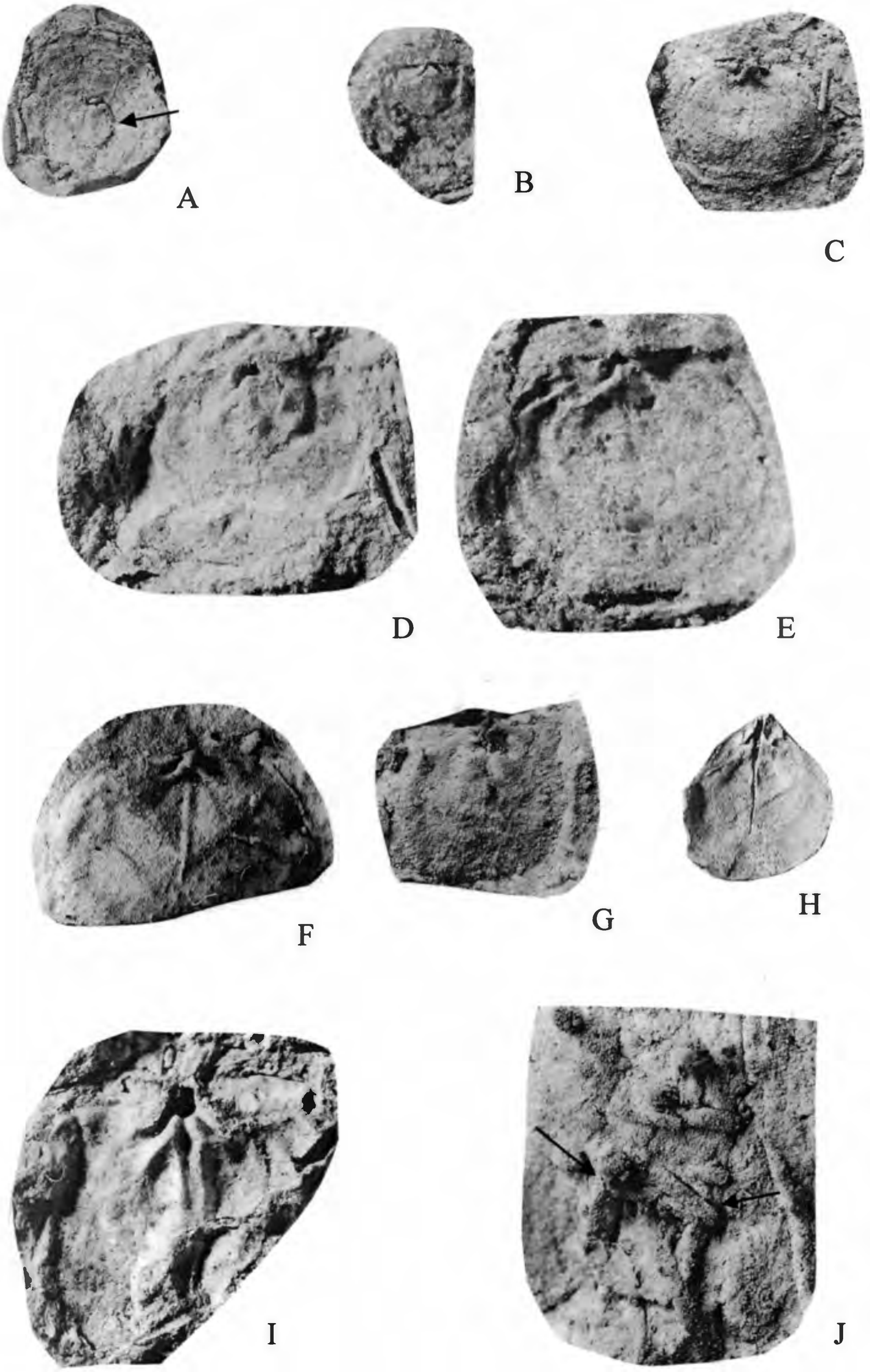


Fig. 15. Early growth stages in the strophalosiid genus and species *Echinalosia maxwelli*. Nepionic dorsal valves are convex, and then change into a neanic phase as the shell becomes larger and concave. A, Juvenile specimen BR 322 as arrowed, showing dorsal exterior and ventral spines and ventral umbo, attached to mature *E. maxwelli*, with its hinge down, PVC cast, x1.2. B, internal mould of nepionic dorsal valve, x2. Note absence of median septum, and prominent cardinal process and dental socket plates. C, PVC cast of juvenile dorsal valve BR 300, x5. D, internal mould of nepionic dorsal valve, x7. E, internal mould of early neanic dorsal valve, x4, with incipient dorsal septum. F, PVC cast of dorsal interior at early immaturity, BR 323, x4.5. G, PVC cast of dorsal interior, cardinal process damaged, at early immaturity, BR 315, x2.5. H, dorsal view of internal mould at early immature stage, x1.5. I, dorsal view of internal mould at early maturity, x1.5. J, Find the specimen! A minute ventral valve BR 324 x4.5, with arrows pointing to the ends of the hinge area, attached to surface and spines of mature *E. maxwelli*. PVC cast. The interarea, now open delthyrium and teeth are visible. Specimens from Letham Burn Member (Roadian), New Zealand. See Waterhouse (1959, 1982a). JBW photo.

provide significant indications for different specific, generic and family group allegiances. For example, although many linoproductidin brachiopods end their life cycle with dendritic adductor scars, some develop such scars only late in ontogeny, after phases when adductor scars are smooth or striate, whereas the scars in other forms are dendritic from an early growth stage (Waterhouse 1986a, p. 2; 1986b, p. 57; 2010a, pp. 33, 39). On the other hand, Tims & Brunton (1991) showed how *Plicatifera* developed a trail at varying sizes in the one species. The development of species may involve the gradual introduction of septa, as for *Echinalosia* (Fig. 15), and it has been tempting to recognise spat as fully fledged and distinctive species and even genera because they lack the dorsal median septum of more mature specimens. Some authors regard the spines over the early formed shell in a mature specimen as recording the ontogenetic record. This is certainly not always correct for brachiopods as far as spines are concerned: it may be, it may be not. Spines retain living tissue, and when a spine becomes redundant, as may occur for early-formed spines, the spine may break or drop off, and the lumen through the shell may be secondarily sealed. There is no substitute in ontogenetic studies for obtaining a range in size for specimens, even though a few authors ignore this and deduce from mature shells a supposedly progressive introduction of spines along the hinge. Their conclusions remain to be verified from a range of specimens at various stages of development.

5. Build of the shell.

Although more than 700 genera are now known for Productida, there are a rather limited range of shell types, some minor, some exceptional, some subject to numerous permutations.

Type 1. Chonetiform shells with wide hinge and row of ventral hinge spines, no sulcus or fold. Rare examples only, such as *Chonopectus*.

Type 2. Chonetid derivatives as the earliest Productida, with interareas preserved, and rounded cardinal margins, such as Productelloidea.

Type 3. Mostly as spat of Strophalosiidae, with flat ventral valve adpressed against substrate, the shell then developing at high angle. Includes various mature but small Strophalosiidae such as *Etherilosia* Archbold.

Type 4. Interareas lost. Trail externally indiscernible from disc. Includes numerous genera, especially amongst Overtonioidea. In addition various genera and subfamilies developed a much larger size, but retained comparatively slender visceral disc and externally imperceptible trails, such as Gigantoproductidae, Schrenkiellinae or some Waagenoconchidae (eg. *Patellamia*).

Type 5. Trail at angle and often long. Many Productoidea and Linoproductoidea.

Type 6. Dorsal disc gently concave, ventral valve of low convexity, trail at high angle. Includes Paucispiniferidae, Yakovleviidae, some Aulostegidae.

Type 7. Dorsal valve externally flat, thickened towards anterior to form wedge. Several dasyalosiid groups, also *Wimanoconcha* of Echinoconchoidea, and *Archboldina* of Yakovleviidae.

Type 8. Ventral valve very long and irregular. *Proboscidella*.

Type 9. Ventral valve forms long coral-like tube. Richthofenioidea, Scacchinellidae.

Type 10. Ventral valve dish-like, enclosing brachial feeding apparatus. Lyttoniidae.

Type 11. Ventral valve bilobed, reduced dorsal valve. Permianellidae.

Type 12. Ventral valve attached by spines and cementation, no interareas or teeth. Dorsal valve enclosed. Cooperinidae.

Other minor variations are developed. Spination also falls in a number of well developed categories, generally restricted to different subfamilial and family and high group categories.

Abbreviations

OD – by original designation. SD – by subsequent designation. The nomination of a type species for a genus is by original designation unless otherwise indicated.

In the synonymies for descriptions of species, use of square brackets […] enclose the conclusion that the attribution of species and author was incorrect. Square brackets may also used to indicate page numbers for summaries in English of Chinese or Russian articles.

Repositories

The following abreviations signify the repository of brachiopod type specimens.

AMF – Australian Museum, Sydney, Australia; **ANU** – Australian National University, Canberra, Australia; **B, BB, BD** or other permutations – The Natural History Museum, London, England; **BR** – GNS Science, Lower Hutt, New

Zealand; **CM** – Carnegie Museum of Natural History, Pittsburgh, United States; **CPC** – Australian Geosciences, Canberra; **E** – Sedgwick Museum, Cambridge, England; **FML** – Palaeontological Institute, Miguel Lillo Foundation, Tucumán, Argentina; **GBGS** – Geological Survey of Great Britain, Keyworth, Nottinghamshire, England; **GK-D** – Department of Geology, Kyushu University, Japan; **GSC** – Geological Survey of Canada, Ottawa and Calgary; **GSI** – Geological Survey of India, Kolkata (Calcutta); **GSQ** – Geological Survey of Queensland, Queensland Museum bulk storage, Hendra, Brisbane, Australia; **IGPS** – Institute of Geology & Palaeontology, Tohoku University, housed in Natural History Museum of Tohoku University, Sendai, Japan; **IGS** – Illinois Geological Survey, United States; **MEF** – Museo Paleontológico Egidio Feruglio, Trelew, Argentina; **NMV** – Museum of Victoria, Melbourne, Australia; **NIGP** – Nanjing Institute of Geology & Palaeontology, Nanjing, China; **NU-B** – Department of Geology, Niigata University, Niigata, Japan; **NUF** – University of Newcastle, New South Wales, Australia; **OCG** – Oil and Gas Commission, Dehra Dun, India; **NYSM** – New York State Museum, Albany, United States; **OU** – University of Oklahoma, United States; **pe** – Bundesanstalt fur Bodenforschung, Germany; **PRI** – Paleontological Research Institute, Ithaca, New York, United States; **ROM** – Royal Ontario Museum, Toronto, Canada; **TBR** – Geological Survey Division, Department of Mineral Resources, Bangkok, Thailand; **TMF** – Geological Survey of Tasmania, Hobart, Australia; **UC** – University of Calgary, Alberta, Canada; **UHR** – Department of Geology & Mineralogy, Hokkaido University, Japan; **UQF** – Queensland Museum bulk storage, Hendra, Brisbane, Australia; **UKM** – Department of Geology, University of Malaysia, Kuala Lumpur, Malaysia; **UNE** – University of New England, Armidale, Australia; **USNM** – Smithsonian Institution, Washington D.C., United States; **YPM** – Peabody Museum, Yale University, United States. Other repositories are explained in the text.

Note on Early Triassic Productida

A few Productida, especially amongst Productidina, are found in Early Triassic deposits, including for example one Canadian sample that looks somewhat like Avoniinae, apart from a median ventral rib that recalls Leioproductinae (Waterhouse 1972). The ammonoid *Vavilovites sverdrupi* (Tozer) is found in the same beds, indicative of a Dienerian age in Canadian terms, or the *Gyronites* faunas found above the *Otoceras* and *Ophiceras* ammonoid assemblages of basal Triassic age in the Himalaya of India , Tibet and Nepal. Extensive overviews of Productida and other brachiopods near the Permian – Triassic boundary are provided by Chen et al. (2005a, b, 2006), and used as a preliminary guide for the range charts, but up-to-date and closer scrutiny is required to verify several of the generic determinations, and the larger classification in those publications only follows the *Revised Brachiopod Treatise*. Thus the upper age limits for productid tribes and superfamilies remain open for further study.

THE ORIGINS OF MAJOR SUPERFAMILIES

1. Introduction

An illustrated compendium of productid genera is provided in the *Revised Brachiopod Treatise* by Brunton et al. (2000) and Brunton (2007), followed by summaries that revised or expanded classification in Waterhouse (2002b, 2004b). The *Treatise* publications, justifiably expensive, should be available in major scientific or geological libraries. The present Earthwise publication is deposited in a few major geological libraries and institutions, including The Natural History Museum, London and Sedgwick Museum, Cambridge, England; GNS, Lower Hutt, and Hocken Library, University of Otago, New Zealand; Paleontological Institute, Moscow, Russia; Institute of Sedimentary and Petroleum Geology, Geological Survey of Canada, Calgary and Geological Survey of Canada, Ottawa, and Department of Geology, University of Toronto, Canada; Smithsonian Institution, Washington DC., and University of North Carolina, United States; Nanjing Institute of Geology and Palaeontology, Nanjing, and Wuhan School of Geology and Geological Institute of Palaeontology, Wuhan, P. R. China; Dorothy Hill Library, University of Queensland and Queensland Museum Bulk Storage at Hendra, Brisbane; School of Environmental and Life Science, Deakin University, Melbourne Campus, Melbourne, and Australian Museum, Sydney, Australia. Copies may be obtained from the author.

There are more than 700 genera of productid genera, in the time span of Early Devonian to Late Permian and earliest Triassic. Almost 540 genera were listed by Curry & Brunton (2007), and since the time that text was written (closure was mostly about halfway through 2004 according to C. H. C. Brunton, pers. comm.), there have been a number of further additions and a number of corrections. Many of the genera are reasonably well known, with data on the exterior and interior of both valves described and figured, within the limits of paleontology. The advantages of world-wide coverage, reinforced by the all-significant dimension of time as well as space, offer a detailed overview of the way the order developed in morphology and distribution, with substantial information on environment and climate that is beyond the reach of cladistics or molecular clock theory, and so discounted by their accolytes. In this summary, focus is on the roots of major groups, Superfamilies Productelloidea Schuchert, Overtonioidea Muir-Wood & Cooper, Marginiferoidea Stehli, Horridonioidea Muir-Wood & Cooper, Productoidea Gray, Echinoconchoidea Muir-Wood & Cooper in Productidina, Strophalosioidea Schuchert, Cooperinoidea Pajaud, Aulostegoidea Muir-Wood & Cooper, Richthofenioidea Waagen and Scacchinelloidea Licharew in Strophalosiidina, Lyttonioidea Waagen and Loczyelloidea Licharew in Suborder Oldhaminidiina (= Lyttoniidina) Williams, and Devonoproductidae Muir-Wood & Cooper, Paucispiniferoidea Muir-Wood & Cooper, Linoproductoidea Stehli and Proboscidelloidea Muir-Wood & Cooper in Linoproductidina. Historically, the classification of these groups has been substantially "top down" – from the Permian "canopy," strongly influenced by the segregation and distinctiveness of each group in Permian faunas, as expressed in the first major and comprehensive overview of the Productidina, Strophalosiidina and Linoproductidina and excluding Lyttoniidina, by Muir-Wood & Cooper (1960). This overview was accompanied by Russian studies as in Licharew (1960) and Sarytcheva (1960), and elaborated by Brunton et al. (2000), Brunton (2007) and Waterhouse (2002b, 2004b). Genera and family groups are distinguished principally by ornament and shape, and by back-tracking through time, it is found that genera and family groups gain strophalosiiform attributes such as interareas, teeth and sockets, large brachial fields, often a strongly divided cardinal process, and smooth adductor scars. Reversing the direction of enquiry, as time passed from Devonian into Carboniferous, features were modified in a number of groups that retained or modified shape and ornament – the teeth and sockets and interareas disappeared, the adductor scars became dendritic, and the brachial scars changed in outline and size. Under a different and more gradual tempo, the cardinal process changed from bifid to trifid or quadrifid. The challenge that faced systematists was to determine whether to allocate major weight to internal or external features, and essentially, Muir-Wood & Cooper (1960), in constructing a classification far more elaborate than that of earlier studies, gave prime weight to ornament and shell construct – or "build" as G. A. Cooper used to say. This gained even more weight when Lazarev (eg. 1987, 1989, 1990) extended the time range of some superfamilies and families into ancestral stock. The morphology of virtually all early productids was strophalosiiform, in so far as that morphology was preserved into Late Permian by Strophalosiidae. The productiform groups, with their lack of interarea, teeth and sockets, small brachial shields and often dendritic or other specialized adductor scars are distinct enough in the Permian, but they seem to have originated from within strophalosiiform sources in the Devonian Period. It has been long and correctly asserted that the Strophalosiidae can be distinguished from stock ancestral to Productidina by the presence of a scar of attachment, and (in some studies) by the lack of a pseudodeltidium. A classification based objectively and solely on morphology might wish to re-assign a number of the Devonian genera referred to productid groups by Muir-Wood & Cooper (1960) and Brunton et al. (2000) to Strophalosiidina, and start the component superfamilies of Productidina in either late Devonian or especially Carboniferous. On the other hand, that would frustrate the natural desire to seek beginnings, to understand how each productidan superfamily started, and in which particular stock. There is thus some tension in how to classify productids. It may be objective to rely solely on morphology. On the other hand, it would seem most informative if the superfamilies are traced as far back in time as possible, meaning that lineages, even though distinguishable and parental to strongly separated groups, shared at their beginning more character states than later. It appears to have been this approach that was partly adopted in Brunton et al. (2000). There is a duality in the phylogeny, and there must be caution in applying only simplistically invariant characterization to a full megalineage. If that is followed, then the outline of each productiform superfamily should be accompanied with a discussion of its immediate ancestry. That is done herein. The ancestors are retained as Productidina, even though their morphology is strophalosiiform.

(SUBORDER PRODUCTIDINA WAAGEN, 1883)
Superfamily Productelloidea Schuchert, 1929
Family Productellidae Schuchert, 1929
Subfamily Productellinae Schuchert, 1929 → **Productoidea**
Subfamily Dotswoodiinae new → **Overtonioidea**
Subfamily Helaspinae new → Tribe Ardviscini → **Horridonioidea**
Subfamily Chattertoniinae Waterhouse, 2002b → other Productelloidea
Subfamily Orbinariinae new → **Marginiferoidea**
Family Caucasiproductidae Lazarev, 1987 → **Echinoconchoidea**

(SUBORDER STROPHALOSIIDINA Waterhouse, 1975)
Superfamily Strophalosioidea Schuchert, 1913
Family Strophalosiidae Schuchert, 1913
Subfamily Strophalosiinae Schuchert, 1913
Subfamily Donalosiinae Lazarev, 1989
Family Dasyalosiidae Brunton, 1966
Subfamily Dasyalosiinae Brunton, 1966
Subfamily Eostrophalosiinae new subfamily
Subfamily Echinalosiinae Waterhouse, 2001→ **Cooperinoidea**?
Subfamily Arcticalosiinae Waterhouse, 2001
Family Chonopectidae Muir-Wood & Cooper, 1960
Subfamily Chonopectinae Muir-Wood & Cooper, 1960
Subfamily Rhytialosiinae Lazarev, 1989 → **Aulostegoidea**
Subfamily Quadratiinae Lazarev, 1989
Family Araksalosiidae Lazarev, 1989
Subfamily Araksalosiinae Lazarev, 1989 → **Scacchinelloidea**
Subfamily Whidbornellinae new
Subfamily Acanthatiinae new
Family Ctenalosiidae Muir-Wood & Cooper, 1960
Subfamily Ctenalosiinae Muir-Wood & Cooper, 1960
Subfamily Mingenewiinae Archbold, 1980
Subfamily Bruntonariinae new
Subfamily Craspedalosiinae Waterhouse, 2010a
Superfamily Cooperinioidea Pajaud, 1968 Ж **Suborder Lyttoniidina?**
Superfamily Scacchinelloidea Licharew, 1928

(SUBORDER LINOPRODUCTIDINA new)
Family Devonoproductidae Muir-Wood & Cooper, 1960
Subfamily Devonoproductinae Muir-Wood & Cooper, 1960→ **Paucispiniferoidea**
Subfamily Eoproductellinae Lazarev, 1987 → **Linoproductoidea**
Subfamily Plicoproductinae Waterhouse, 2004b → **Proboscidelloidea**

Table 1. Strophalosiiform superfamilies, families and subfamilies (regular font) and their productiform descendents (bold font). The symbol Ж signifies uncertain but apparent interrelationships.

Each lineage, with rare exceptions, is remarkably distinct, and convergences may be traced through morphologic sequencing. Only in very rare instances is it possible to point to shared ancestry. The oldest pure Strophalosiidina are the Donalosiinae, which commenced in the Emsian (i.e. early Devonian). The root-stock of Horridonioidea commenced in Famennian, or possibly Givetian; Echinoconchoidea in Fammenian and Givetian;

linoproductidin strains can be traced to Eifelian for Devonoproductidae, Pragian for Linoproductoidea and Eifelian for Proboscidelloidea. (See Table 2, p. 29 for the summary of stages in the Upper Paleozoic). Productoidea appear to have possibly commenced (pre-Buxtoniidae) in the Famennian, and Marginiferoidea go back to root-stock Orbinariinae (Eifelian), though the earliest marginiferid senso stricto is only early Carboniferous. Aulostegoidea may go back to the strophalosiid group Rhytialosiinae, of Famennian – Frasnian age. More distinctive groups arose in the later Paleozoic, in further waves of significant evolution, the gigantoproductids during Early Carboniferous from strands within Linoproductoidea to display large size, and development of brachial cones, Scacchinelloidea from early Carboniferous roots, Richthofenioidea during Upper Carboniferous from Aulostegoidea and Cooperinoidea (Upper Carboniferous) and Oldhaminidina (Carboniferous – Lower? or more likely Upper) arose from Strophalosioidea. The latter groups, Scacchinelloidea, Richthofenioidea, Cooperinoidea and Oldhaminidina, differ strikingly from other Productida, but perished with their older allies virtually at the end of the Paleozoic Era.

2. Summary of beginnings

ORDER PRODUCTIDA WAAGEN, 1883

Order Productida arose from Order Chonetida Bronn during Devonian time, commencing with members which retained the articulatory apparatus of teeth, sockets and interareas of Chonetida, kept or modified the hinge spines and developed spines over the rest of the ventral valve, added often an umbonal cicatrix, and expanded the dorsal feeding apparatus, with other modifications.

SUBORDER PRODUCTIDINA WAAGEN, 1883

Earliest Productidina retained chonetiform anderidia, which are two plates subdividing the dorsal adductor scars, and are classed in Subfamily Chattertoniinae new subfamily, within Productelloidea. These evolved into Productellinae through loss of the anderidia and development of an alveolus, and developed into several other subfamilies that provided root-stock for various Productidina. One major aspect of Chattertoniinae was the comparatively smooth shell, apart from spines, to suggest a source possibly within the chonetiform Anopliinae Muir-Wood, 1962, which commenced in basal Devonian (Lochovian) time, or involved genus *Squamatina* Havlíček & Racheboeuf (see Racheboeuf 2000, p. 380) of Lower Devonian (Pragian) age.

Superfamily Productelloidea Schuchert, 1929

Earliest members of Productidina belong to Superfamily Productelloidea Schuchert, 1929, characterized by mostly simple spine patterns, distributed in quincunx or commarginally. Rarely commarginal rugae may be prominent, and radial ornament is variable. Several internal features are inherited from or at least shared with Chonetida, such as interareas, teeth, sockets, non-dendritic smooth adductor scars as a rule, and narrow body corpus of modest size. The brachial ridges have come to enclose large areas, but marginal ridges are usually low or absent, as in most Chonetida. There is a close approach between Productelloidea and Strophalosioidea: separation is based on the lack of a cicatrix of attachment, a difference that cannot be applied always to strophalosiids, but is generally true, and presence or absence of a pseudodeltidium. For many constituent genera, radial and concentric ornament is more developed than in Strophalosioidea, but there are close similarities, further brought out by the shape of the brachial ridges, which appear to be large and like those of strophalosiids (eg. *Helaspis* Imbrie, 1959). *Orbinaria* Muir-Wood & Cooper (1960, p. 149, pl. 35) appears similar with large brachial shields, and distinguished by its heavy marginal ridge, classed as Orbinariinae Waterhouse within Productellidae.

Two families are placed in Productelloidea, Productellidae Schuchert, and Caucasiproductidae Lazarev, the latter distinguished by the presence of numerous fine dorsal spines, and both distinguished from Strophalosiidina by the lack of an umbonal cicatrix. Productellidae are believed to have given rise to the productiform superfamilies Overtonioidea, Horridonioidea, Marginiferoidea, and Productoidea, all grouped in Infrasuborder Productimorphi. The other family Caucasiproductidae gave rise to Echinoconchoidea Stehli, which has overall ornament close to that of Caucasiproductidae, but lack strophalosiiform attributes. Summaries are provided by Brunton et al. (2000, pp. 424-426, 526, 527).

INFRASUBORDER PRODUCTIMORPHI WAAGEN, 1883

There are four major superfamilies in Infrasuborder Productimorphi Waagen, 1883, as recognized by Waterhouse

(2010a) and modified herein, Overtonioidea, Horridonioidea, Marginiferoidea and Productoidea, which evolved from the strophalosiiform family Productellidae.

Period	Series	Stage
PERMIAN	Lopingian	Changhsingian
		Wuchiapingian
	Guadalupian	Capitanian
		Wordian
		Roadian
	Cisuralian	Kungurian
		Artinskian
		Sakmarian
		Asselian
(Pennsylvanian) CARBONIFEROUS (Mississippian)	Upper	Gzhelian
		Kasimovian
	Middle	Moscovian
	Lower	Bashkirian
	Upper	Serpukhovian
	Middle	Visean
	Lower	Tournaisian
DEVONIAN	Upper	Famennian
		Frasnian
	Middle	Givetian
		Eifelian
	Lower	Emsian
		Pragian
		Lochkovian

Table 2. International stages for the Devonian, Carboniferous and Permian Periods.

Lower Carboniferous divisions allocated for some genera in the Treatise are Hastarian at the base, followed by Ivorian for Tournaisian, and Chadian, Arundian, Holkerian, Asbian and Brigantian for Visean. The Permian subdivisions are set out by Jin et al. (1997), and Carboniferous subdivisions by Heckel (2004). Pennsylvanian and Mississippian are used as subsystems for Upper and Lower Carboniferous. However the value of splitting of the Carboniferous stages into two sets of lower through middle to upper seems a little dubious. The Mississippian divisions for the mid-continental United States are Kinderhookian, Osagean, Meramecian and Chesterian, followed Pennsylvanian divisions Morrowan, Atokan, Desmoinesian, Missourian and Virgilian. Radiometric values may be adduced from Menning et al. (2006) and Menning & Hendrich (2012).

Superfamily Overtonioidea Muir-Wood & Cooper, 1960

Overtonioids are amongst the oldest of true productiform brachiopods, and evolved from Superfamily Productelloidea, becoming, especially in Overtoniidae, more elaborate in ornament, through the development of commarginal rugae and lamellae, but losing interareas, teeth and sockets, and reducing the size and changing the shape of the brachial shields. They remained rather small shells, and the adductor scars remained smooth as a rule. Most genera are of Lower Carboniferous ranging into Permian and earliest Triassic in age. The overtonioid genera in Rugaurini and Semiproductini have rugae and spines finer than in either *Poloniproductus* or *Overtonia*, as if evolved from Dotswoodiinae of Productellidae.

Tribes within Avoniidae Sarytcheva are mostly Early Carboniferous, persisting into Late Permian. These also have more or less productiform as opposed to strophalosioid internal morphology, though sharing the smooth adductors. Although most genera display predominantly spinose ornament and weak to strong radial ornament, rather than commarginal ornament, which might suggests origination from Productellinae, what is believed to be the earliest known genus *Barunkharaya* Lazarev has fine rugae, and it is suggested that these were lost or weakened in younger genera, but the basic original stock was close to that of Overtoniidae, descended from Dotswoodiinae.

The group, unlike Productelloidea, continued to flourish until the end of the Permian Period. The families and tribes were lumped as Productoidea by Brunton et al. (2000, pp. 426-464).

Superfamily Horridonioidea Muir-Wood & Cooper, 1960

Superfamily Horridonioidea has ornament dominated by spines, well spaced and often thick, with minor radial and commarginal ornament and usually no heavy marginal ridges. Adductor muscle scars are dendritic as a rule, and numerous rows of large papillae are developed anteriorly. The superfamily can be traced from Upper Devonian into Late Permian, and was a relatively small group, but there was a substantial increase in individual size for a number of genera, compared with Overtonioidea and Productelloidea. The earliest horridonioids, Leioproductini Muir-Wood & Cooper, arose from Ardviscini, of Upper Devonian (lower Famennian) age, and in turn, Ardviscini appear to have been derived from Helaspini of Middle and Upper Devonian age, in Productellidae. The brachial shields are seldom displayed, but those of the upper Devonian genus *Leioproductus* Stainbrook, 1947 are smaller than in strophalosiids, and appear to be slightly larger than is normal for productiform genera. Members of Leioproductini have a median row of spines down the centre of the ventral valve, whereas members of Hunanoproductini Liang, 1990 lack the row. Levitusiinae are regarded as descendents of Leioproductinae, and have lost traces of their strophalosiiform ancestry: they ranged from Tournaisian to Late Permian.

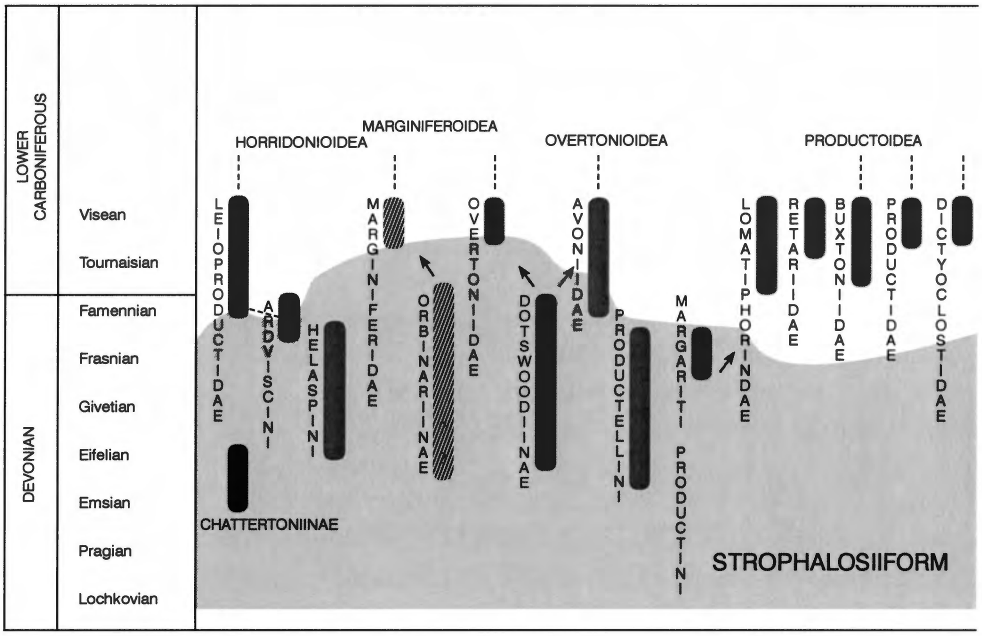


Fig. 17. The passage of strophalosiiform Productida (shaded) into productiform

Most Horridoniidae are share a comparatively smooth shell apart from spines, and spines are well developed and often well spaced, with well developed erect spines along the ventral and often the dorsal hinge. Members of the superfamily are outlined and figured in Brunton et al. (2000, pp. 453-459, 475-483).

Superfamily Marginiferoidea Stehli, 1954

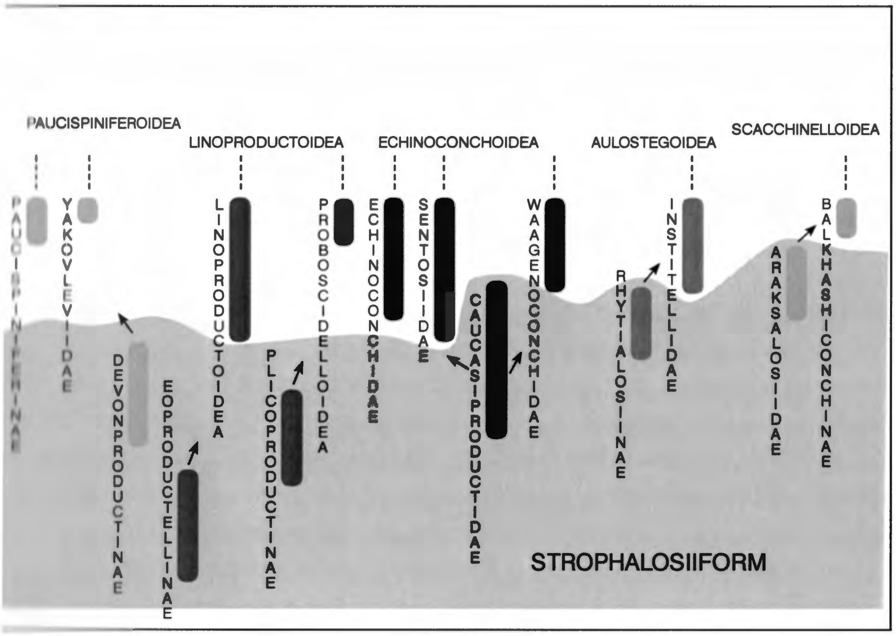
Superfamily Marginiferoidea Stehli, 1954 has specialized and often varied spines, often mutiple trails, and as a rule well developed marginal ridges and ear-baffles. Muscle scars usually remain smooth, and internal papillation is often distinctive, with few rows of large papillae anteriorly. Origination appears to have been from the Upper Devonian and Lower Carboniferous genus (Famennian-Hastarian) *Orbinaria* Muir-Wood & Cooper, 1960, Subfamily Orbinariinae, Family Productellidae, which has coarse ventral spines, fine dorsal spines, low interareas, teeth and sockets, large brachial shields and sturdy dorsal marginal ridge covered in strong papillae. There is a small gap in the fossil record before the first appearance of marginiferids. The superfamily was well established by Visean time and flourished in the Permian and is completely productiform in the lack of teeth and sockets and the presence of small brachial shields, but retained smooth adductor scars as a rule.

The constituent groups are summarized in Brunton et al. (2000, pp. 439-450, 464-467, 469-472).

Superfamily Productoidea Gray, 1840

A small group, separate from Overtoniidae and Avoniidae although sharing some features, is centred on Lomatiphoridae Roberts, 1971. The presence and nature of ribs and spines, and internal lateral buttress plates in genera such as *Lomatiphora* Roberts and *Spinocarinifera* Roberts indicate precursory links to the slightly younger buxtoniids, productids and dictyoclostids. *Lomatiphora* and allies appear to have been derived from only slightly older members of Margaritiproductini (Upper Devonian, Famennian), which share at least some strophalosiid attributes in having teeth, and appear to have evolved from Productellini, in view of similarities in the dorsal interior.

The main constituent families of Superfamily Productoidea are Productidae, Retariidae, Dictyoclostidae and Buxtoniidae, many of the species being of comparatively large size, with long trail. Families are distinguished by their ornament, Productidae with predominantly linear ornament with posterior reticulation, Retariidae with reticulate disc and posterior spine rows, Buxtoniidae with ribs that swell where bearing spines, and Dictyoclostidae by their reticulate disc ornament and no umbonal slope row spines. Spines tend to be mostly subuniform in nature and distribution, and muscle scars are dendritic, and cardinal process possessed of a well developed median shaft. According to Brunton et al. (2000, p. 501), the oldest buxtoniids *Labriproductus* Cooper & Muir-Wood, 1951 and *Setigerites* Girty, 1939 are of upper Tournaisian (basal Carboniferous) age, and these two genera are close in external appearance and ornament and internally with their posterior close-set lateral buttress plates to their ancestral members of Lomatophoridae (lower Tournaisian, lower Visean), derived in turn from Margaritiproductini (Upper Devonian – Famennian) of subfamily Productellinae. Buxtoniids developed an abundance of dorsal spines and posterior lateral ventral spines. Many buxtoniids also displayed commarginal rugae, and the fossil record suggests that productids, retariids and dictyoclostids, well established by Visean time, evolved from buxtoniids. The families are outlined by Brunton et al. (2000, pp. 467-469, 472-475, 485-509), with other sections.



Productida across the late Devonian and early Carboniferous.

Superfamily Echinoconchoidea Stehli, 1954

Superfamily Echinoconchoidea Stehli, 1954 is a compact group characterized by close-set fine spines, often arranged in commarginal bands and virtually no radial ornament. Adductors are usually dendritic except in Sentosiidae, and the median septum may be subdivided or buttress plates present. Echinoconchoidea did not develop through the intermediacy of Productelloidea or Overtonioidea, but arose directly from the strophalosiiform Caucasiproductidae Lazarev, 1987. This family was assigned to Sentosiidae as the oldest echinoconchid (Brunton et al. 2000, p. 526), but in morphology, it is strophalosiiform. It commenced in the middle Devonian, and with fine spines, its genera may have given rise to both Sentosiidae and Waagenoconchidae. Waagenoconchidae were derived from members of Sentosiinae McKellar, 1970, of Upper Devonian age. *Praelaminatia* new genus and *Laminatia* Muir-Wood & Cooper, 1960, of Upper Devonian (Fammenian) age, are regarded as early members of Echinoconchidae because of their ornament.

The superfamily is outlined by Brunton et al. (2000, pp. 509-526).

SUBORDER STROPHALOSIIDINA WATERHOUSE, 1975

Superfamily Strophalosioidea Schuchert, 1913

Strophalosioidea are characterized by a ventral umbonal cicatrix as a rule, simple and unspecialized spines on ventral or both valves, usually with little radial ornament, and commarginal ornament in only some genera. Interareas were developed, and articulation aided by teeth and sockets. Brachial ridges enclosed a large area on the floor of the dorsal valve, and adductor scars werenormally smooth. Most genera fall within Strophalosiidae, which largely lacks dorsal spines, and in Dasyalosiidae, which usually has spines on both valves. Strophalosiinae appears to have arisen from Donalosiinae Lazarev. This could in turn have evolved from genus *Ralia* Lazarev, classed within Chattertoniinae, earliest group of the Productelloidea, but that remains far from certain, given the need to clarify a number of early Strophalosioidea. A small Late Paleozoic family centred on Ctenalosiidae displays more prominent commarginal lamellae. Specialized and short-lived mostly Devonian to Early Carboniferous families involved Chonopectidae, including *Chonopectus* which is very like chonetids in general appearance, and Araksalosiidae, with ornament of prominent hinge spines as a rule and elongate spines or fine ribs, and lateral buttress plates internally. (See Brunton et al. 2000, pp. 565-587).

Superfamily Scacchinelloidea Licharew, 1928a, b

Members of Scacchinellidae are highly unusual with long conical ventral valve and lid-like dorsal valve, and further characterized by having a high ventral median septum, and dorsal adductor scars resting on thickened short lateral buttress plates. *Tschernyschewia* of Tschernyschewiidae is similar to the extent that it also has a high ventral median septum and well formed lateral buttress plates: the genus is much less conical. Spines cover both valves in Scacchinellidae and Tschernyschewiidae, mostly of Permian age. Genera within Rhamnariidae display long lateral buttress plates and have ornament somewhat similar to that of Tschernyschewiidae, and although most lack the median ventral septum, a short ventral septum is displayed early in ontogeny in new genus *Minisaeptosa* (p. 252). Ancestral stock is provided by Balkhasheconchinae, also with lateral buttress plates and somewhat allied spines on each valve. The spinose ornament is particularly characteristic on two genera *Balkhasheconcha* Lazarev and *Buxtoniella* Abramov & Grigorieva, in which spines are fine and crowded, and have long and slender posterior bases. *Buxtoniella* is of Lower Carboniferous (middle Visean) age, the same age as an Australian new genus *Campbelliconcha*, with shorter spine bases. It is proposed that these genera were derived from the strophalosiiform group Araksalosiidae, based on genera of Upper Devonian (Famennian) age, which display similar ventral ornament over the disc, and similar lateral buttress plates. In other respects the araksalosiid genera differ, for they are strophalosiiform in the presence of interareas with pseudodeltidium, teeth and sockets, though adductors may be somewhat dendritic, and several araksalosiid genera have dorsal spines.

Aspects of the superfamily constituents are mentioned by Brunton et al. (2000, pp. 518, 604, 605, 607-609).

Superfamily Cooperinoidea Pajaud, 1968

This is a very small group, close to Strophalosioidea in the presence of interareas and large cicatrix, with swollen ventral valve, high brachial ridges, and ptycholophous or schizolophous brachidia. The outstanding brachial apparatus differs substantially from that of Productelloidea and Strophalosioidea, and is far removed from that of Aulostegoidea, with which the group was associated by Brunton et al. (2000, pp. 605-607). In different subfamilies of Cooperinidae, the brachial apparatus approaches that of different groups within Oldhaminidina (p. 269). Shells evolved from Dasyalosiidae close to Echinalosiinae, and shells like Cooperinidae could have given rise to Suborder Oldhaminidina (= Lyttoniidina). Most forms within the superfamily are limited to the Permian Period, but there are

Pennsylvanian occurrences.

INFRASUBORDER AULOSTEGIMORPHI WATERHOUSE, 2010

Aulostegimorphi associates superfamilies Aulostegoidea Muir-Wood & Cooper and Richthofenioidea Waagen: Richthofenioidea did not arise directly from Strophalosioidea, unlike Aulostegoidea, Scacchinelloidea and Cooperinoidea.

Superfamily Aulostegoidea Muir-Wood & Cooper, 1960

Aulostegoid genera are highly diverse, with elaborate ornament, often reticulate or commarginally rugose, and with luxuriant spines, and in some genera elaborate trails. Relict strophalosiiform characters may be preserved as high interareas, and some have smooth adductor scars, and some were attached by an umbonal cicatrix, so that there has been dispute about whether the group is productiform or strophalosiiform. Most arguments in favour of a productiform relationship have been summarized by Briggs (1998), and the most critical morphology in favour of a productiform alliance is offered by the productiform brachial shields (Waterhouse 1983b, p. 192). It is believed from analysis of the fossil record and changes in morphology that aulostegoids branched independently from Strophalosioidea, and tended to follow productiform trends in morphological change. The aulostegoid subfamily Institininae Muir-Wood & Cooper, 1960 includes a number of genera that appeared in Lower Carboniferous, including *Institina* Muir-Wood & Cooper and *Stipulina* Muir-Wood & Cooper which have low dorsal commarginal rugae, and swollen ventral spine bases and no dorsal spines or teeth. *Archaiosteges* Carter of Tournaisian age is of similar external appearance and the dorsal valve looks very like that of strophalosiids with high dorsal marginal ridge and large brachial shields, even though teeth and interareas are lacking. Commarginal rugae are developed and erect ventral spines have swollen bases. Such commarginal rugae are also observed in *Rhytialosia* Lazarev, 1989 of upper Devonian age, Subfamily Rhytialosiinae Lazarev, and this subfamily is strophalosioid with scar of attachment, teeth and sockets and interarea; *Veeversalosia* Lazarev and *Mckellarosia* new genus are related. None of the Devonian productelloidean genera appear to offer any alternative source, because the concentrically rugose Rugaurini developed into a very different suite of genera, classed as Overtonioidea.

Aulostegoidea gave rise to Richthofenioidea during the Upper Carboniferous. The superfamily is summarized in Brunton et al. (2000, pp. 587-606).

Superfamily Richthofenioidea Waagen, 1885

Richthofeniids are highly exceptional: the ventral valve is high and conical, with no interarea, and cemented to substrate or attached by rhizoid spines,and the dorsal valve is reduced to a cap. Amongst other Brachiopoda, only Scacchinellidae and Lyttoniidina approach Richthofenioidea in exceptionality, and in all three groups it is the ventral valve that grew substantially in size and changed shape. In richthofeniids the ventral valve became high and conical to look like a solitary coral, and special structures are developed, such as coscinidium (p. 293). In terms of morphology, with origins in mind, the group is exceptional enough to be regarded as belonging to a rank higher than that of superfamily, but ranking below a subordinal category (Waterhouse 2010a). Origins have been traced by Wardlaw, Grant & Brunton (2000), based on invaluable observations in Sutherland (1996), which showed that early growth stages were aulostegid-like, and the brachial shields are shaped like those of aulostegids rather than strophalosiids. Arising in the middle Carboniferous, richthofeniids are amongst the youngest of productidan superfamilies. The superfamily is summarized well by Wardlaw, Grant & Brunton (2000, pp. 610-619).

SUBORDER OLDHAMINIDINA (= LYTTONIIDINA) WILLIAMS, 1953

Lyttoniids are outstanding: the ventral valve formed a shallow to deep dish, often cemented to substrate, and the dorsal valve was reduced to little more than articulatory structures, whilst the brachial apparatus became ptycholophous or lobate, and very large. The suborder is largely of Permian age, but early occurrences are known in the Carboniferous. There is an obvious similarity to Cooperinoidea, which are smaller, with more of the dorsal valve preserved, as if they were intermediate between Strophalosiidina and Oldhaminidina, although this is not adequately confirmed by the fossil record, possibly because preservation of cooperinoids and their delicate brachidia is highly fraught. Whilst the relationship to Strophalosiidina is clear, the morphological distance from that group ensures that subordinal standing is well justified. Most genera and family groups fall within Lyttonioidea Waagen, and a small exceptional group Locyzyelloidea (= Permanelloidea) is bilobed in shape.

The suborder is outlined by Williams, Harper & Grant (2000, pp. 619-642).

SUBORDER LINOPRODUCTIDINA NEW

This infrasuborder involves three superfamilies, Linoproductoidea, Proboscidelloidea and Paucispiniferoidea, that shared a common ancestry in the strophalosiiform Family Devonoproductidae, and diverged substantially in many aspects of their respective morphologies. Devonoproductidae are characterized in part by fine ribbing, which allows the possibility of a sourcing from a wide range of finely ribbed chonetids, including Strophochonetidae Muir-Wood, 1962, some Anopliinae Muir-Wood, 1962, Eodevonariinae Sokolskaya, 1960, Chonetidae Bronn, 1862 or Chonostrophiidae Muir-Wood, 1962. Most genera in these families have anderidia, although members of Chonetidae may have weaker anderidia, and anderidia are not developed in Devonoproductidae. One subfamily within Devonoproductidae gave rise to the productiform Paucispiniferoidea, and the other two subfamilies to major superfamilies Linoproductoidea and Proboscidelloidea, each characterized by distinct ribs, laminae and ventral spines first displayed in Devonoproductidae. Devonoproductidae is retained as an isolated and ancestral group, standing on its own, though it may be argued it would be better split into three with each subfamily assigned to its descendent superfamily. The family is summarized in Brunton et al. (2000, pp. 546-550).

Superfamily Paucispiniferoidea Muir-Wood & Cooper, 1960

This is a newly recognized association, based on back-tracking through time the gradual change of morphologies from groups that appear unrelated from a Permian perspective. Paucispiniferidae itself with moderately developed marginal ridge and often strut spines may be traced into Visean (Carboniferous) members of Bibatiolinae, which arose in turn from Productininae of Upper Devonian (Famennian) to Lower Carboniferous (Visean) age. Productininae are commonly ribbed with few spines that may include symmetrically arranged strut spines. The ventral ribs are coarse, and the dorsal valve has strong concentric laminae, reminiscent of Devonoproductinae (Middle and Upper Devonian, Givetian to Frasnian). Devonoproductinae has finely costate ventral valve and many spines, similarly lamellate dorsal valve, and smooth adductor scars and low internal marginal ridges, as well as teeth and sockets and interareas that are lost from Productininae. A finely ribbed family Yakovleviidae commenced in the Visean and also has specialized ventral strut spines, allied to those of Paucispiniferidae, and some of the genera have high and others very reduced marginal ridges. In another family, Anidanthidae Waterhouse, Subfamily Anidanthinae (Upper Carboniferous) displays costellate ventral valve and lamellate dorsal valve and smooth adductors, and also arose from Devonoproductinae, with which it shares many features. A sister Permian family Larariinae new subfamily is close in attributes of the ventral valve, but differs in lacking dorsal laminae.

Scattered references to genera within these groups are provided in Brunton et al. (2000, pp. 429, 443-450, 464-466 and 530-533).

Superfamily Linoproductoidea Stehli, 1954

Superfamily Linoproductoidea incorporates a bundle of lineages extending well into the Devonian Period. The oldest family, Ovatiidae Lazarev, is first found in Upper Devonian (Famennian) faunas (Carter 1988, Lazarev 2004). Progenital stock is provided by the strophalosiiform genus *Eoproductella* Rzhonsnitzkaya, 1980, classed as Subfamily Eoproductellinae Lazarev, 1987, Family Devonoproductidae, of Lower Devonian (Pragian – Emsian) age. This genus has fine ribbing on both valves, with erect ventral spines, teeth and sockets.

Superfamily Proboscidelloidea Muir-Wood & Cooper, 1960

Another major group within Linoproductidina is characterized by ribs and by ventral spines with elongate bases, and bases prolonged forward and back within the shell (Waterhouse 2010a, p. 32). The earliest known source genus appears to be the strophalosiiform genus *Plicoproductus* Ljaschenko, 1969 of Middle Devonian (Eifelian) age, with costae and striae and ventral spines with long posterior ramps. It is classed as Plicoproductinae Waterhouse, 2004b, p. 42. The upper Givetian genus *Striatoproductella* Krylova, 1962 is allied, with somewhat swollen ventral spine bases and coarse and fine ribs on both valves. Teeth and sockets are present in both genera, with very low interareas. The oldest member of Proboscidelloidea is *Dawesionia*, of Upper Devonian (Famennian) age.

Thus the major groupings Paucispiniferoidea, Linoproductoidea and Proboscidelloidea can be traced to progenitors of Devonian age. Linoproductidina links various families which arose from different genera in different subfamilies of Devonoproductidae. Each remained distinct, but shared a number of features. The latter two superfamilies are outlined in part by Brunton et al. (2000, pp. 526, 533-546 and 550-563).

The relationship between productids and strophalosiids

Muir-Wood & Cooper, 1960, p. 10 reported that the lower Devonian "productid" *Spinulicosta* Nalivkin, 1937 (Lower to Middle Devonian) and strophalosiid *Devonalosia* Muir-Wood & Cooper (Middle Devonian, Eifelian – Givetian) shared interareas with pseudodeltidium (but no chilidium), teeth and sockets, and smooth adductor scars. They dismissed the concept that they had evolved from chonetids, and suggested possible derivation from strophomenoids, such as *Leptaenisca* (Muir-Wood & Cooper, 1960, p. 48). But that appraisal is not acceptable (Perry 1984), and there is little doubt that chonetids gave rise to strophalosiiiforms, which evolved into productiform brachiopods. Muir-Wood & Cooper, 1960, p. 71 offered a general diagnosis for Strophalosioidea which stressed cementation by the ventral umbo, a stress well justified, because parental chonetids show no such cicatrix, so that its development was new, and exceptional. Their outline was largely followed by Waterhouse (1975, 1978) in proposing Suborder Strophalosiidina, and by Brunton et al. (2000, p. 565). Yet other than the development of early umbonal cementation, Strophalosioidea are close to Productidina, and would appear to have arisen either from the same or a very closely related chonetiform group, whereas Linoproductidina had a related but separate source.

Infrasuborders

The introduction of Infrasuborders allows better reflection of interrelationships. In an initial appraisal of Productida, Waterhouse (2010a) suggested that the spiny superfamilies be associated and separated from the superfamilies with predominantly costate ornament. But closer analysis based on lineages, sources and evolutionary trends suggests a refined arrangement:

Productimorphi involves transition and fully productiform genera. It commenced with Overtonioidea, followed by Horridonioidea, Marginiferoidea and Productoidea. The infrasuborder is associated with Superfamily Echinoconchoidea, derived from a separate family within Productelloidea, called Caucasiproductidae Lazarev.

Aulostegimorphi, involving aulostegids and richthofeniids appear to have arisen directly from within strophalosioids – Institininae (Aulostegidae) from Rhytialosiinae of Chonopectinidae (Strophalosioidea). Although the morphology of Richthofenioidea is productiform, the descent traces back to Strophalosioidea, but indirectly, unlke the origins of Aulostegoidea, Scacchinelloidea or Cooperinoidea.

CLASSIFICATION

EVOLUTION OR PHYLOGENESIS

At the commencement of this survey, it was planned to cladiscate the Productida from data provided in the *Revised Brachiopod Treatise*, in order to present a phylogenetic overview of the order. But as preliminary compilation progressed, it became evident that the hope was premature: there were far too many errors of morphological summary in Brunton et al. (2000), and inspection showed that synonymies were far from trustworthy. All had to be reinspected, partly from literature, partly from specimens. In addition, it was clear that many species of Late Devonian and Carboniferous age had evaded revision since the mid-nineteenth century, and that many genera had been assigned to tribes and subfamilies from which they diverged considerably. Thus the study has morphed into an overview of genera and their classification, and hopefully now provides the basic data for cladistic summaries.

The family group terms of classification fail to convey mode of origin, and clearly need to be supplemented by the qualifiers such as those introduced by Hennig (1966) and elaborated over subsequent decades (Carter et al. 2012). The highly expressive and useful terms applied to phylogenetic systematics should be based on evolutionary analysis of morphology and succession, reinforced by subjective and objective cladistics,involving prejudged selection of already delineated genera (or higher categories) to test if the pattern conforms with classification, together with analysis of an array of genera (or higher categories) without prejudgement or preference.

SYSTEMATICSUMMARY

Phylum **BRACHIOPODA** Duméril, 1806

Class **STROPHOMENATA** Williams et al., 1996

Lazarev (1987, p. 47) proposed to refer productiform and strophalosiiform brachiopods to Subclass Concavoconvexa Lazarev, with orders Strophomenida, Chonetida, and Productida. Productida was subdivided into Productidina and Strophalosiidina (which he asserted was new, disregarding the prior proposal by Waterhouse 1975, 1978), and he included Lyttonioidea (as Lyttoniacea) in Strophalosiidina, ignoring or rejecting Williams (1953, 1965), although offering no explanation. No attention has been granted to this proposal, and the *Revised Brachiopod Treatise* used a very different scheme. Nonetheless there is value in using a non-generic stem for classes and subclasses, just as for phylum Mollusca, and there also may be value in a ranking of subclass, rather than class.

A slightly different approach was taken by Afanasieva & Dagys (1989) who subdivided Class Articulata Huxley, 1869, into several subclasses, including Strophomenata Afanasieva & Dagys, to receive orders Strophomenida Opik, 1934, Chonetida Nalivkin, 1979 [ie. Muir-Wood 1962], and Productida Sarytcheva & Sokolskaya, 1959 [ie. Waagen, 1883]. Williams et al. 1996 also ignored this analysis, although it was used in Rozanov (2003), and the Williams et al. proposal is reinforced by the prestige of the *Revised Brachiopod Treatise*. Nonetheless the question of higher categories and their authorship relevant to Productida should not be regarded as sttled, because higher level relationships are open to further enquiry.

Liang (1990, pp. 368, 480) proposed a new order, Punctoproductida, for “productoids with test endopunctate, without endospines”. He recognized two suborders. Punctoproductidina were provided with endopunctae, but no pseudopunctae, represented by one genus, *Punctoproductus* Liang (1990, pl. 21, fig. 15 – 20). There are no spines, and the dorsal valve seems to be convex. It is difficult to accept that the genus is productid or in any way closely related to productids. Suborder Dipunctellidina Liang was proposed for shells with endopunctae and pseudopunctae and appears to involve shells mostly referred herein to Loczyelloidea, or permianellids, as discussed in fuller detail on pp. 301-306, and a comparable phenomenon is displayed by some Spiriferida, as discussed by Waterhouse (1998), though not realised by Williams (1997). To Waterhouse, the phenomenon did not merit subordinal discrimination.

Superorder PRODUCTIFORMI Waagen, 1883

[Nom. transl. hic ex suborder Productacea Waagen, 1883, p. 447].

Diagnosis: Small to large strophomenates with dorsal valve smaller than ventral valve, commonly concavo-convex to plano-convex, ears and trails commonly prominent. Spines tubular and usually over ventral valve, may be restricted to hinge or absent, often present on dorsal valve. Dental plates absent, cardinal process prominent, shell structure

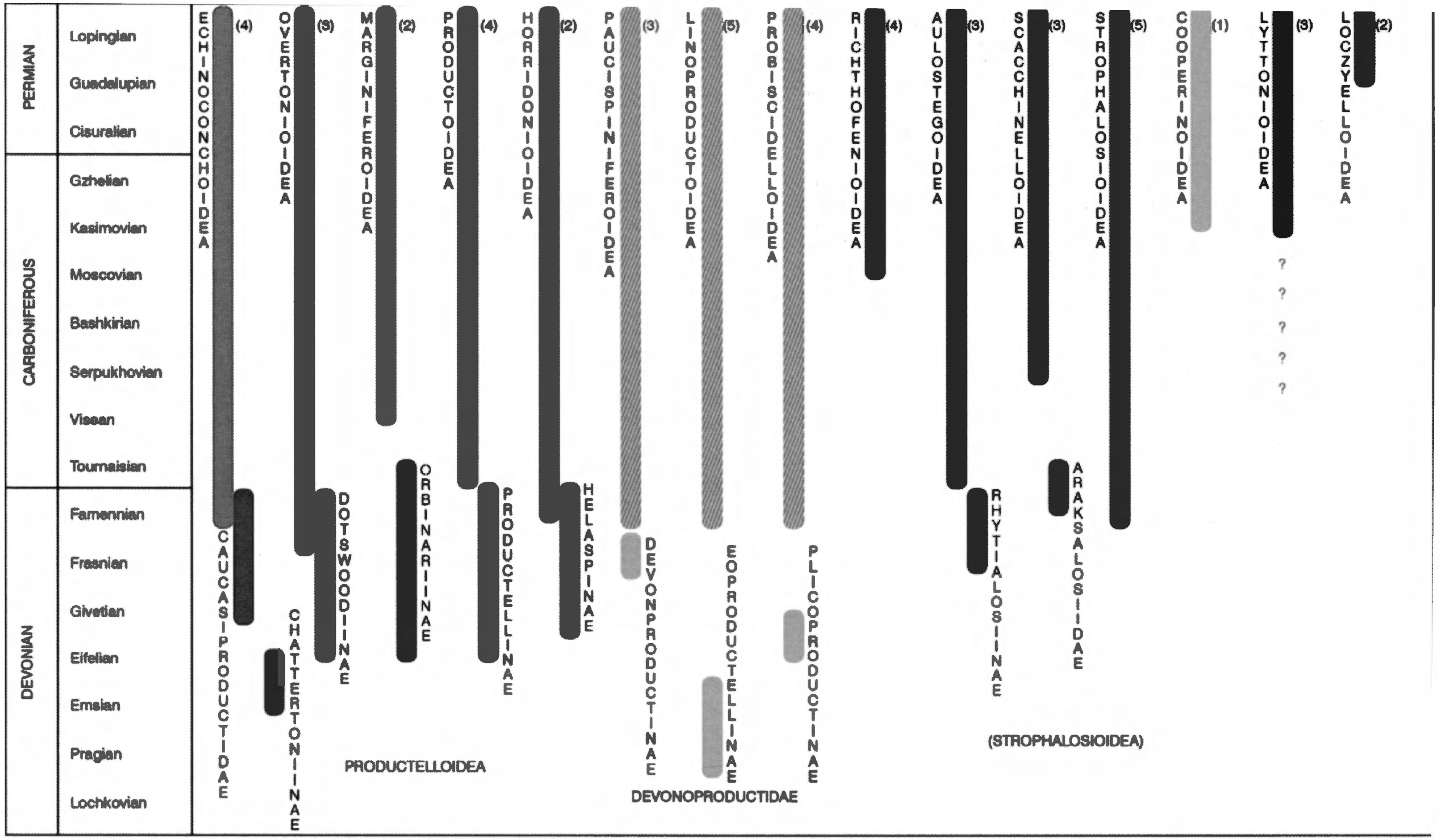


Fig. 1.1. Range chart for Order Productida, with four suborders, and the number of constituent families indicated in brackets for eachsuperfamily. Progenital subfamilies are indicated as members of Productelloidea, Devonoproductidae and Strophalosioidea

crested to cross-bladed laminar with pseudopuncate having taleolae. Upper Ordovician to eariest Triassic.

Discussion: This superorder combines Chonetida and Productida. Such a category is useful for combining chonetids and productids in the broad sense, just as it is useful to combine Orders Spiriferida and Spiriferidina in a Superorder Spiriferiformi Waagen, 1883. Productidina, Strophalosiidina and Lyttoniidina were grouped with Chonetidina as Productida in the *Revised Brachiopod Treatise*, but the chonetids stand apart as a group, and do not show nearly the same amount of morphological traits and evolutionary intergradations. It is far preferable to follow the lead of various Russian authorities and recognise Chonetida as a separate order.

Order PRODUCTIDAWaagen, 1883

[Nom. transl. Sarytcheva & Sokolskaya, 1959 pro suborder Productacea Waagen, 1883, p. 447].

Diagnosis: Concavo- or plano-convex genera with well formed hinge, may have umbonal cicatrix, ornament of spines which are not limited to ventral hinge as a rule, interior with adductor and diductor muscle scars and cardinal process, no vascular media, and simple to semi-elaborate brachiophore feeding apparatus of a simple schizolophe ranging to more strongly folded ptycholophous falafer style of lophophore (see Williams et al. 1997, pp. 110-120).

Discussion: Chonetida differ in having a more limited shape, lacking scar of attachment or cementation, having either a row of ventral hinge spines which angle through the hinge shell, or no spines, possessing long ventral median septum and ventral vascular media passing forward from the adductor scars, and different papillation. The dorsal valve never has spines, and is not geniculate. The cardinal process differs, and the brachial shields are usually not defined.

SUBORDER PRODUCTIDINA WAAGEN, 1883

[Nom. correct. Muir-Wood, 1965, p. 448, pro suborder Productacea Waagen, 1883, p. 447. Mailleux 1940, p. 3 proposed suborder Productoidea for Productidae and Chonetidae, and disavowed his proposal in 1941, p. 8].

Diagnosis: May be attached during early ontogeny by pedicle, less commonly by cementation, usually by spines. All but the earliest genera have no teeth or sockets, interareas and pseudodeltidium, and the brachiophores except in earliest genera normally leave a simple and small loop on the floor of the dorsal valve. All genera belong to or descended from Productelloidea.

Discussion: Prime distinctions from Strophalosiidina lie in the lack of interareas from both valves in many but not all superfamilies, lack of teeth and sockets, and development of much smaller brachial shields as a rule, and lack of umbonal cicatrix. Some of these morphological attributes were not limited to Productidina, for they developed across a wide range of Productida, including later Strophalosiidina, most Linoproductidina, and in many respects Oldhaminidina. The prime requisite is inclusion within or descent from the strophalosiiform Superfamily Productelloidea. Productidina make up a highly diverse group with numerous variations in macro-morphology. Classification has been influenced by three major advances, a for-then comprehensive overview (excepting Oldhaminidina (=Lyttonidina) by Muir-Wood & Cooper (1960), with the recognition of numerous subfamilies and families, the arrangement of families into superfamilies (Waterhouse 1978), and the splitting of subfamilies into tribes (Lazarev in Brunton et al. 1995, 2000). The importance of recognising tribes amongst Productidina has not been acknowledged, but marked a substantial gain in understanding, and was due to the insight of S. S. Lazarev.

1. Superfamily **PRODUCTELLOIDEA** Schuchert, 1929

Fig. 1.2

[Nom. transl. Waterhouse 1978, p. 20 ex Productellinae Schuchert, 1929, p. 17].

Diagnosis: Small shells with spines on ventral or less commonly both valves, ornament varied, interareas, teeth and sockets and large brachial shields present, cardinal process typically bifid, trail simple, comparatively short as a rule and not geniculate. Shell not attached by umbonal cicatrix, and pseudodeltidium often reported as missing.

Discussion: This superfamily associates two early strophalosiiform families, which included significant progenital stock for later Productidina. Superfamily members have long been treated as productiform by workers who regarded *Strophalosia* and allies as a minor and mainly Permian group, and Muir-Wood & Cooper (1960) and Muir-Wood (1965) found some difficulty in separating the genera from strophalosiids, except at a generic level. Placement of Productelloideaas Strophalosiidina would reflect many aspects of the morphology, but would obscure the position of the superfamily as the only source for other superfamilies within Productidina, such as Overtonioidea, Horridonioidea, Marginiferoidea, Productoidea and Echinoconchoidea. The superfamily was a significant and indeed only link between parental Chonetida and descendent Productidina, and source for younger families and superfamilies.

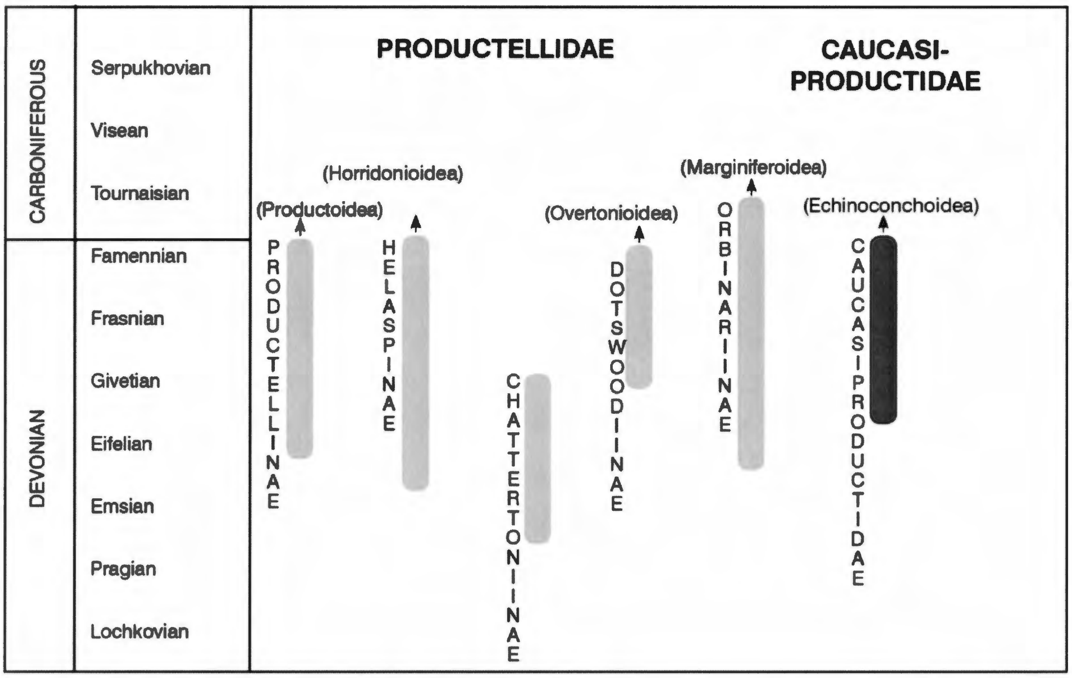


Fig. 1.2. Constituent groups in ProductelloideaSchuchert, 1913. Derived superfamilies shown in brackets.

The component members of Productelloidea differ to large extent although not entirely from early Strophalosioidea in usually being more ornamented (although that is not true for all genera), and in not being attached by umbonal cicatrix. In instances where the umbonal cicatrix is absent from Strophalosiidina, the taxon is close in other morphological attributes to species and genera which do not have an umbonal cicatrix. The hinge spines inherited from Chonetida are not markedly strong as a rule, unlike those of a few early groups within Strophalosioidea, such as Donalosiinae Lazarev, Chonopectidae Muir-Wood & Cooper, and Araksalosiidae Lazarev.

Family **PRODUCTELLIDAE** Schuchert, 1929

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

Diagnosis: Small shells with varying radial ornament, spines usually restricted to ventral valve, arranged in quincunx, not clustered. Body cavity slender.

Discussion: In the following arrangement, attention is focused on differences amongst the constituent genera, to enable assessment of genera as potential progenitors for different productiform groups.

Subfamily **PRODUCTELLINAE** Schuchert, 1929

[Productellinae Schuchert, 1929, p. 17].

Diagnosis: Shells small with simple ventral spines, may have dorsal spines, and in some genera, radial ribs. Teeth and sockets present, cardinal process lobes divergent, V-shaped from dorsal aspect, cardinal process pit (= alveolus) present. Muscle scars not dendritic. Corpus cavity shallow.

Tribe **PRODUCTELLINI** Schuchert, 1929

Fig. 1.3

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

Diagnosis: Spines usually but not always limited to ventral valve, low interareas, lateral ridges each side of cardinal process, alveolus well developed, no slit in dorsal medium septum, no accessory plates. Middle Devonian (Eifelian) to Upper Devonian (Famennian).

Genera: *Productella* Hall, *Productellana* Stainbrook, *Spinellicosta* new genus, *Spinulicosta* Nalivkin.

Discussion: Spines are erect in *Productella* Hall & Clarke, including along the hinge, or arise from swollen or slightly extended bases over the disc, and no commarginal ornament other than growth-lines is developed. The brachial shields of *Productella* are more obliquely directed than in strophalosiids, but larger than in productids (Muir-Wood & Cooper 1960, pl. 32, fig. 12, 13, 15, 16). There are no ear baffles or heavy marginal ridging, and the cardinal process tends to be high with divergent small lobes and prominent alveolus. In most descriptions it is stated that a cicatrix is not developed, and although Veevers (1959, p. 80) reported that some specimens of ?*Productella* sp. from the Fitzroy Basin, Western Australia, showed signs of a supra-apical cicatrix, his specimens are strophalosioid. The upper Middle and Upper Devonian (Givetian to Famennian) age of *Productella*, and its well developed dorsal alveolus and lack of anderidia strongly suggest derivation from the slightly older and new genus *Nahannilusia*, from an Eifelian (early Middle Devonian) fauna in Canada, and this is classed in Chattertoniinae, a productellid subfamily distinguished by the presence of anderidia in the dorsal valve (p. 43). *Productellana* Stainbrook, 1950, well figured in Brunton et al. (2000, Fig. 362.2a-e), and of Famennian age, is similar in ventral spines but has well spaced few dorsal spines, like some *Productella* (Muir-Wood & Cooper, 1960, p. 151), and only short interareas. Although the genus was placed in Sentosiini as an early echinoconchid by Brunton et al. (2000, p. 522), and in spite of some reports that teeth are lacking (unconfirmed), as if it were a transition genus from Productellini, the ornament is very like that of *Productella*. The genus is poorly known internally, and remains difficult to distinguish from *Productella*. It is provisionally treated as discrete from Caucasiproductidae because the spines are so much better spaced, fewer and stronger. Low ventral ribs or spine bases and dorsal dimples are present in *Spinulicosta* Nalivkin, 1937, p. 49. This genus has a well developed alveolus and wide hinge ridges, and costae are developed to varying degree.

Family Productellidae Schuchert, 1929
- Subfamily Productellinae Schuchert, 1929
  - Tribe Productellini Schuchert, 1929
  - Tribe Margaritiproductini new tribe
- Subfamily Chattertoniinae new subfamily
- Subfamily Helaspinae new subfamily
  - Tribe Helaspini new tribe
  - Tribe Ardviscini new tribe
- Subfamily Orbinariinae Waterhouse, 2002b
- Subfamily Dotswoodiinae new subfamily

Family Caucasiproductidae Lazarev, 1987

Table 3. Classification of Productelloidea Schuchert, 1913.

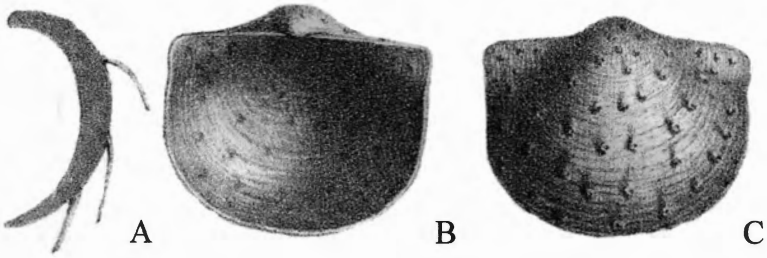


Fig. 1.3. *Productella subaculeata* (Murchison), ventral and dorsal aspects, x2, specimen figured by Davidson (1871, pl. 20, fig. 2) from Middle Devonian of north Devon, England.

Genus *Spinellicosta* new genus

Fig. 1.4

Derivation: spina – thorn; costa – rib, Lat.

Type species: *Spinulicosta dotswoodae* McKellar, 1970, p. 19 from Myrtlevale Formation(Famennian), Burdekin Basin, Queensland, Australia, here designated. See Appendix A, part A, p. 477.

Diagnosis: Ventral spines fine and numerous, concentrated over mid-valve, and usually in dense row aligned along median rib, ventral and dorsal ribs thick, branching.

Discussion: In many respects this genus is close to *Spinulicosta*Nalivkin, named for *Productus spinulicostus* Hall,1857, p. 173 from Eifelian beds of United States. Weak teeth and sockets and very low interareas are present, and the dorsal interior displays a bifid cardinal process, deep alveolus, and slender median septum. The ventral valve in both forms is costate, and the dorsal valve somewhat more costate in *Spinellicosta*. The significant difference between the two lies in the nature of the spines. In *Spinulicosta spinulicosta*, the spines are well organized and arise singly at regular intervals from the crests of costae, or more typically from short spine ridges, as well as forming a row or two near the hinge, and a weak cluster postero-laterally. Other species assigned to the genus vary a little in spine and rib detail, but show the same basic pattern. In *Spinellicosta*, ribs are strong and may bifurcate anteriorly, and spines are much more numerous. As well as a posterior small cluster, they lie as a rule in a closely spaced row or rows along the mid-line, and are suberect, without seeming to be so closely connected to the ribbing as in *Spinulicosta,* fortwo or three spines arise along a growth line across a single rib, and spines may arise in the interspace between two ribs. Brunton et al. (2000, p. 426) stated that the range of *Spinulicosta* was Lower Devonian to Middle Devonian (Eifelian). The age of *Spinellicosta* is Upper Devonian (Famennian).

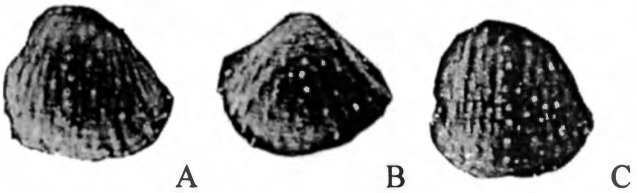


Fig. 1.4. *Spinellicosta dotswoodae* (McKellar), ventral valve latex casts. A, GSQF 11298. B, GSQF 11296. C, GSQF 11295. Specimens x2 approx. from Myrtlevale Formation (Famennian), Queensland, Australia. See McKellar (1970, pl. 2).

Tribe **MARGARITIPRODUCTINI** new tribe

Name genus: *Margaritiproductus* Lazarev, 1986b, p. 67 from late Devonian of Kazakhstan, here designated.

Diagnosis: Spines near hinge may lie in well formed row, ventral spines well spaced and arise from ribs with prolonged bases, or erect, ribs limited to trail of both valves, relict simple teeth and sockets, dorsal valve usually with hinge ridges, deep alveolus. Upper Devonian (Famennian).

Genera: *Margaritiproductus* Lazarev, *Nalivkininius* new genus, *Nigerinoplica* Lazarev, *Proteusiella* new genus.

Discussion: Although these genera as named were included within Semiproductini McKellar by Brunton et al. (2000), they lack the fine rugae and fine numerous ventral spines with slightly elongate bases typical of Semiproductini, and they also lack the moderately well formed and closely spaced ribs of Lomatiphoridae Roberts – ribs if present tend to be restricted to the trail, and are short and discontinuous. The dorsal interior is not quite the same either, and genera show a deep alveolus in front of the cardinal process, and have teeth and sockets that are small and apparently relict. The Eifelian (mid-Devonian) genus *Spinulicosta* Muir-Wood & Cooper (1960) of Tribe Productellini, Family Productellidae, has a deep pit in front of the cardinal process, and tends to develop elongate spine bases, to seem the most likely ancestral stock for *Margaritiproductus* Lazarev, and provides a feasible link back through time. Margaritiproductini is apparently a transition tribe, with some strophalosiiform attributes shown weakly in the form of teeth, the strophalosiiform attributes being vestigial compared with those of Productellini. The similarity to the younger group Buxtoniidae is conveyed by the illustrations of *Buxtonia* s. l. by Easton (1962, pl. 8, fig. 1-6).

Margaritiproductus was originally treated as a member of Dictyoclostidae, in Semiproductinae, and dendritic posterior dorsal adductors and teeth were recorded, and figures indicate possible weakly developed or incipient low lateral buttress plates (see Brunton et al. 2000, Fig. 328.3c). Lazarev (1986b) in proposing *Nigerinoplica* as a member of Productellidae, reported very narrow interareas and dendritic posterior dorsal adductor scars, and teeth and sockets. Lazarev (1990, pl. 7, fig. 1-12) showed that a median ridge with larger spines was developed on some ventral valves of *Nigerinoplica*. Most species have been figured only from a dorsal aspect, masking the nature of ventral ornament. An exception is provided by *N. halli* Pushkin in Lazarev & Pushkin (1986, p. 48, pl. 5, fig. 13-16) in which ventral spines are shown. The type species *N. nigerina* (Martynova, 1961) exhibits similar but fewer and more prominent slightly swollen bases to the dorsal spines, and closely spaced commarginal rugae and growth-lines, similar to those of *N. meisteri* sensu Martynova, 1961 (Lazarev 1990, pl. 7, fig. 1-9) and *N. praelonga* sensu Martynova, 1961 (Lazarev 1990, pl. 7, fig. 10-12). *N.variplicata* (Martynova, 1970; Lazarev 1990, pl. 9, fig. 4-7) shows little in the way of ventral spines, rugae and internal dorsal dimples, with signs of anterior disc plicae. Specimens of *N. naidovense* Pushkin in Lazarev & Pushkin (1986, pl. 5, fig. 3-7) are comparatively smooth shells with erect spines. But *Nigerinoplica parva* Pushkin in Lazarev & Pushkin (1986, p. 46, pl. 5, fig. 9-11) displays short ventral ribsanteriorly,and *N. nalivkini* Pushkin (in Lazarev & Pushkin, 1986, p. 48, pl. 5, fig. 17-21 has numerous ventral spines and subfusc anterior ventral ribs or elongate spine bases.

Genus ***Nalivkininius*** new genus

Derivation: Named for D. V. Nalivkin.

Type species: *Nigerinoplica nalivkini* Pushkin in Lazarev & Pushkin, 1986, p. 48 from the Eletski Horizon (lower Famennian), southern Prozdov, Russia, here designated.

Diagnosis: Small with fine spines and low discontinuous ribs over anterior ventral valve. Bifid cardinal process and cardinal pit.

Discussion: This species (holotype AN SSR No. 4067/128 - Academy of Science) together with *Nigerinoplica parva* Pushkin in Lazarev & Pushkin, 1986 was described from Famennian beds of Russia. The species are close internally to *Nigerinoplica* Lazarev, but have finer spines and closely spaced discontinuous anterior ribs. The ribs are more subdued than in *Seminucella* Carter, 1987 from the Tournaisian Banff Formation of Alberta, Canada, which also has a cardinal pit, and displays a hinge ridge. *Seminucella* shows no trace of teeth, but it has to be said that sockets and teeth are not clearly developed in Pushkin's material, though the dorsal hinge is sturdy and thickened.

Genus ***Proteusiella*** new genus

Fig. 1.5

Derivation: Named from species name.

Type species:*Avonia proteus* Veevers, 1959, p. 80 from Fairfield Beds (Famennian), south of Barramundi Range, Fitzroy Basin, Western Australia, here designated.

Diagnosis: Ventral ornament includes fine linear filae, dorsal ornament of rounded pits. Dorsal interior with two short posterior septa, in front of cardinal process and behind median septum, and two anterior grooves.

Fig. 1.5. *Proteusiella proteus* (Veevers), ventral view of holotype, CPC 2959, x1.3. From Fairfield beds, Fitzroy Basin, Australia. See Veevers (1959, pl. 8). Fine radials faintlyvisible over mid-length.

Discussion: The species described as *Avonia proteus* Veevers from the upper Famennian faunas of the Fitzroy Basin, Western Australia, displays low interareas, and the dorsal interior shows some unusual aspects, as described by Veevers (1959, p. 81), with two ridges developed in parallel in front of the cardinal process, and median dorsal septum commencing well in front of the cardinal process, as well as pair of submedian grooves, and extended dental sockets (Veevers 1959, text-fig. 44), with brachial shields well rounded in outline. Unlike *Avonia*, to which the type species was originally referred, there are fine filae between the major ventral spine bases in the holotype (Veevers 1959, pl. 8, fig. 2). The pits over the dorsal exterior are round rather than elongate.

The type species was referred to *Nigerinoplica* by Lazarev (1986b, p. 45). This genus is of the same age, but its ventral exterior lacks fine ribs, although the dorsal exterior is more or less similar in both forms. Internally,*proteus* has a cardinal pit and double septum close to that of *Nigerinoplica*, but in addition has a pair of anterior grooves, not seen in *Nigerinoplica*.

Subfamily **CHATTERTONIINAE** new subfamily

Name genus: *Chattertonia* Johnson, 1976, p. 789 from Murrumbidgee Group (Emsian) of New South Wales, here designated.

Diagnosis: Shells with slightly extended spine bases varying to ribs on ventral valve, spines subuniform and arranged subevenly over valve, well spaced and more numerous close to hinge. Distinguished by presence of long slender myophragm in ventral valve as a rule and anderidia in dorsal valve. Lower Devonian (Emsian) to Middle Devonian (Eifelian).

Genera: *Chattertonia* Johnson, *Costatonia* new genus, *Nahannilusia* new genus, *Ralia* Lazarev.

Discussion: *Chattertonia* is outstanding in the presence of well developed accessory septa in the dorsal valve. These have been called anderidia by Chatterton (1973, p. 79), Perry (1984, p. 65) and Brunton et al. (2000, p. 424), as an apparent analogue with the anderidia of chonetids. By definition, anderidia are low ridges that pass between the two pair of dorsal adductor scars (Racheboeuf 2000, 2007). Chatterton (1973, p. 79, pl. 18, fig. 5) noted that the ridges terminated each in a short protuberance, to imply a relationship with feeding apparatus. Johnson (1976, text-fig. 1A) pointed to the implications of a chonetid-productid link in the presence of the accessory septa, as elaborated by Perry (1984), and this is enhanced by the presence of a long ventral myophragmal septumin *Chattertonia, Costatonia* and *Ralia*, recalling the median ventral septum common in Chonetida.

Ralia Lazarev, 1987 from the Emsian of Mongolia is obscure, but there are ventral hinge spines and smooth dorsal valve with fine capillae, the figure in Lazarev (1987, pl. 5, fig. 1) being much clearer than in Brunton et al. (2000, Fig. 415.1a). Another figure suggests the presence of a ventral myophragm, and Lazarev reported anderidia. Although included in Donalosiinae by Brunton et al. (2000, p. 582), the genus is distinctive. Arguably the presence of spines along the ventral hinge suggests the potential for developing into Donalosiinae (p. 224), the oldest subfamily within Strophalosiidae, which would mean that Productelloidea gave rise not only to Productidina, but to Strophalosioidea. But this remains conjectural pending clarification of *Ralia* and further study of Devonian strophalosians.

Genus ***Costatonia*** new genus

Fig. 1.6

Derivation: costa – rib, Lat.

Type species: *Chattertonia mackenzia* Perry, 1984, p. 65 from Delorme Formation (lower Emsian) of MacKenzie Mountains, Yukon Territory, here designated.

Diagnosis: Fine ribbing developed on ventral valve and stronger ribbing on dorsal valve.

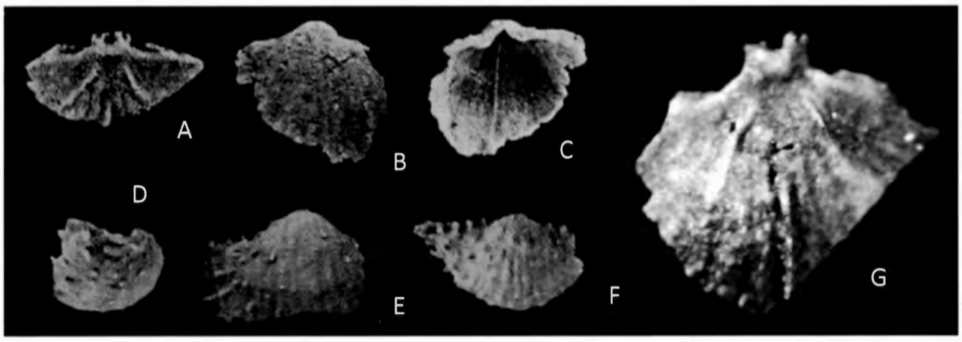


Fig. 1.6. *Costatonia mackenzia* (Perry). A, posterior view of dorsal interior, holotype ROM 33620, x5 approx. B, C, external and internal aspects of ventral valve, ROM 33621, x2.8. D, E, F, lateral, ventral and ventral posterior views of ventral valve ROM 33623, x 2.8. G, internal view of dorsal valve holotype ROM 33620-1, x10 approx. See Perry (1984). From Delorme Formation, Yukon Territory, Canada. Photograph Fig. 1.6G courtesy of Janet Waddington.

Discussion: *Costatoniamackenzia* (Perry) is close to *Chattertonia campbelli* (Chatterton) in internal features, sharing the significant long ventral myophragm and distinctive accessory septa. Perry (1984) noted that cardinal process lobes were less divergent and emerged from a less distinct basal column and that socket ridges were more divergent, compared with *Chattertonia*. The critical differences from *Chattertonia* centre on the external appearance. In type *Chattertonia*, the two valves are essentially smooth and disrupted by extended but short spine bases on the ventral valve, like those of *Spinulicosta*, which lacks dorsal accessory septa. In the new genus, even the immature dorsal valve bears strong simple ribs, which split into more slender secondary ribs anteriorly. The ventral valve is also ribbed, with coarse primary ribs and fine secondary ribs, and the ventral spines arise from the crests of the primary ribs. As Perry (1984) reported, the appearance of the spines differs on the two species, due to their more complete preservation on the Australian form, whereas those of the Canadian species are represented only by their bases.

Genus ***Nahannilusia*** new genus

Derivation: Named for Nahanni River, northwest Canada.

Type species: *Spinulicosta prima* Chatterton & Perry, 1978, p. 34 from Funeral Formation (Eifelian), Northwest Territory, Canada, here designated.

Diagnosis: Small shells with densely spinose ventral valve, weakly prolonged spine bases, no ventral myophragm, cardinal process bifid with two lobes joined ventrally by yoke, well formed alveolus and weak anderidia.

Discussion: This genus is like *Chattertonia* Johnson and *Costatonia* new genus in possessing anderidia, although they are more weakly developed, and in having a yoke-like structure joining the two lobes of the cardinal process, but unlike these genera, the cardinal process of the dorsal valve has a well developed alveolus. In that regard, it is closer to the Middle Devonian genus *Spinulicosta* Muir-Wood & Cooper, 1960, which lacks the cardinal yoke and anderidia, but has well developed alveolus. There is no sign of a myophragm which is developed in *Chattertonia* and *Costatonia*, but not in *Spinulicosta*. The ventral spines show signs of differentiation into thin and thicker, but all follow a similar course, and there is some development of hinge spines and the suggestion of a clasping ring. The bases are scarcely prolonged, somewhat as in *Chattertonia*, and lack the extended bases and often anterior costae of *Spinulicosta*, or the well formed costae of *Costatonia*. *Nahannilusia,* of Eifelian age, is the youngest genus within the subfamily, the other three being of Emsian (Lower Devonian) age, and the type species comes from north of the North Nahanni River, Northwest Territories, Canada. The delthyrium is open, both valves show low interareas, teeth are small and thin, and the dorsal exterior is pitted and irregular, with no ribs or spines. Type material is kept at the University of Alberta, Edmonton, Canada. *Spinulicosta mutocosta* Imbrie, 1959 of Middle Devonian (Givetian) age in the Traverse Group of Michigan bears an alveolus, and indications of weak anderidia.

Subfamily **HELASPINAE** new subfamily

Name genus: *Helaspis* Imbrie, 1959, p. 400 from Givetian fauna of Michigan, United States, here designated.

Diagnosis: Ventral spines erect or with slightly elongate bases, to appear like short costae. Dorsal valve with short costae and prominent pits. No alveolus, no anderidia.

Tribe **HELASPINI** new tribe

Name genus: *Helaspis* Imbrie, 1959, p. 400 from Givetian fauna of Michigan, United States, here designated.

Diagnosis: Ventral spines erect or with slightly elongate bases. Dorsal valve with short disrupted costae and prominent pits. Middle Devonian (Eifelian) to Upper Devonian (Famennian).

Genera: *Helaspis* Imbrie, *Sinoproductella* Wang.

Discussion: A prime distinction from Productellinae lies in the absence of an alveolus at the base of the cardinal process, and there are no anderidia. Brachial shields are large in *Helaspis*(Brunton et al. 2000, text-fig. 278.3c). *Sinoproductella* Wang looks externally close to *Productella*, but lacks an alveolus (Tien 1938, Wang 1955). Its ventral ornament of spines emerging with only slightly elongate bases from otherwise smooth shell, and dorsal dimples, suggest potential for evolving into genera such as Ardviscini (see below). *Helaspis*is distinguished by its ornament, with prominent ventral spine bases and strongly textured dorsal exterior ornamented by elongate dimples and pustules and weak commarginal rugae.

Tribe **ARDVISCINI** new tribe

Name genus: *Ardviscus* Lazarev in Lazarev & Pushkin, 1986 from lower Famennian of Eurasia and possibly North America, here designated.

Diagnosis: Small comparatively smooth shells with rather fine ventral spines, dorsal valve smooth or with commarginal rugae, apparently no external pits, dorsal interior may have low lateral buttress ridges, no cardinal process pit as a rule. Upper Devonian (Famennian).

Genera: *Ardviscus* Lazarev, *Grandiproductella* Lazarev, *Productelloides* Kotlyar.

Discussion: These genera were assigned to Leioproductini by Brunton et al. (2000), and to Leioproductidae by Lazarev in Lazarev & Pushkin (1986) and Lazarev & Simakov (1987). That assessment is strongly supported by the morphologies involved, and here the genera under consideration are segregated, because they possess interareas, teeth and sockets, but are regarded as ancestral to Leioproductini. They do not show any sign of an umbonal cicatrix.

The simple and well spaced spinose ornament of the ventral valve and single dorsal septum of the three genera involved come closest in such respects to morphologies in the members of Helaspini of Middle and Upper Devonian age.

Genus ***Ardviscus*** Lazarev, 1986b

Ardviscus is exemplified by type species *A. naidovense* Pushkin from lower Famennian (Upper Devonian) beds of Belorussia (Lazarev & Pushkin, 1986, Fig. 1, 2a, b, pl. 5, fig. 3-7), and the specimen in pl. 5, fig. 7 appears to indicate a low ridge slanting behind the dorsal adductors, suggestive of a weak lateral buttress plate, and there is no cardinal process pit (ie. alveolus). The presence of a weak median ventral external ridge and well spaced spines justifies the assessment of Biernat & Lazarev (1988) that *Ardviscus* developed into Leioproductidae.

Genus ***Grandiproductella*** Lazarev, 1987

Grandiproductella Lazarev in Lazarev & Simakov, 1987 was included in Leioproductidae by Lazarev, and in Leioproductini by Brunton et al. (2000, p. 477). The genus is of Famennian age, and shows low commarginal rugae, as in Geniculiferini Waterhouse (p. 74), but unlike genera in this tribe, has low interareas, strong teeth and long dorsal septum with socket ridges parallel to the hinge margin. No mention is made of lateral buttress ridges, but no figure provided in their publications shows the dorsal interior. Unlike *Leioproductus*, the ventral valve lacks a median external ventral ridge, but has a shallow anterior ventral sulcus. Ventral spines are rare and small.

Genus***Productelloides*** Kotlyar, 1985

In *Productelloides* O. E. Kotlyar, 1985, there are not only small teeth but thin linear interareas and scattered erect fine ventral spines, with a short row along the hinge, and oblique row on the umbonal slopes. There is no median external ventral ridge, and no regular ventral commarginal rugae. The outer dorsal adductor scars are weakly dendritic. Kotlyar described a dorsal cardinal pit, though its presence is ambiguous in Brunton et al. (2000, Fig. 322.3d), andreported fine accessory septa which could be lateral buttress plates. This genus was placed as Tribe Leioproductini by Brunton et al. (2000, p. 480), but appears to be productellid, as originally assessed by Kotlyar (1985).

Kavesia Lazarev in Lazarev & Simakov, 1987 is of very late Devonian and lower Tournaisian age, and has lateral buttress mounds passing into plates, but lacks teeth, and so is classed as Leioproductini.

Subfamily **ORBINARIINAE** Waterhouse, 2002b

Fig. 1.7, Fig. 1.8

[Nom. transl. hic ex Orbinariini Waterhouse, 2002b, p. 8].

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. ?Middle Devonian (Eifelian), Upper Devonian (Famennian) to Lower Carboniferous (?Hastarian).

Genera: *Orbinaria* Muir-Wood &Cooper, ?*Poloniproductus* Biernat & Lazarev.

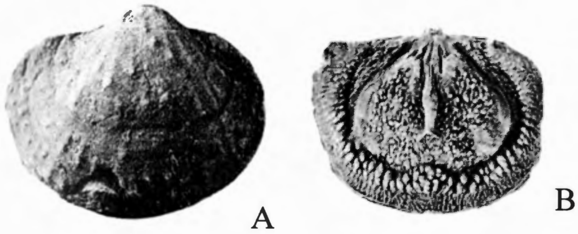


Fig. 1.7. *Orbinaria pyxidata* (Hall). A, ventral view of USNM 123933a. B, dorsal interior, USNM 123932f. From Louisiana Limestone (Famennian),Louisiana and Pike County, Missouri, United States, x2. See Muir-Wood & Cooper (1960, pl. 35).

Discussion: *Orbinaria* is regarded as productellid, as in Muir-Wood & Cooper (1960, p. 149), although treated as a member of the Overtonioidea, Tribe Rugaurini, by Brunton et al. (2000, p. 461). Unlike Rugaurini, it lacks fine regular commarginal rugae and has teeth and sockets. The genus has a time range of Famennian to Hastarian, and was attached during early growth by a ventral umbonal spine ring (Muir-Wood & Cooper 1960, pl. 35, fig. 20-22, 25).

There are no dorsal spines according to Muir-Wood & Cooper (1960), yet rare dorsal spines were recorded and figured by Brunton et al. (2000, Fig. 305.3c). *Orbinaria* has attributes of productellids and strophalosiids, with its teeth, interareas, and brachial ridges, but lacks a cicatrix, as in productellids. The group is raised to subfamilial standing, because of its exceptionally well developed dorsal marginal ridge, unmatched in other known productelloid subfamilies, which encloses the visceral disc and provides an unusually strong border between the visceral disc and trail. Although most genera of Productellidae lack such a well developed marginal ridge, they are close to *Orbinaria* in their strophalosiiform aspects and share rather similar ornament. The strongly developed marginal ridge potentially anticipated the marginal ridge in Marginiferoidea, and shape and spine detail suggest aspects of this superfamily, the ventral spines being erect and well spaced with moderately developed row close to the hinge.

It might be conjectured that *Orbinaria* is a junior synonym of *Leptalosia* Dunbar & Condra, 1932, p. 260. The type species of *Leptalosia,Strophalosia scintilla* Beecher (1890, p. 263), was figured by Muir-Wood & Cooper (1960, p. 85, pl. 2, fig. 1-7) as resting on the dorsal valve of mature *Orbinaria* from the Louisiana Limestone of Pike County, to open the possibility that *Leptalosia* could be spat of*Orbinaria*.But *Orbinaria* lacks an umbonal cicatrix, whereas such is large on *Leptalosia*.

There is some approach to the Middle Devonian (Eifelian) genus *Poloniproductus* Biernat & Lazarev, 1988, a genus with large more regular concentrically arranged ventral spines, aligned between growth laminae, with suggestion of hinge row (Brunton et al. 2000, Fig. 383.3b), and the dorsal valve shows lamellae and some suggestion of dimples. (See Fig. 1.8). Such ornament is surprisingly complex for so old a genus. The interior is strophalosioid, though the marginal ridge is not as high or thick as in *Orbinaria*, but the dorsal trail is strongly distinguished internally, again unusual for so old a genus. The genus was treated as a member of Devonoproductinae by Brunton et al. (2000), but it lacks any sign of radial ribs. The regularly arranged spines of *Poloniproductus* do not indicate a potential source for Marginiferoidea, but the arrangement of strong spines on commargons, defined between growth lamellae, do strongly suggest an approach to Overtoniinae, which appeared in upper Visean time. In Overtoniinae the dorsal valve is also sublamellate and usually has spines, and the dorsal valve in *Poloniproductus* has low to moderate marginal ridge and fine closely spaced laminae and elongate pits, but Overtoniinae has lost the teeth, sockets, large brachial shields, and interareas of *Poloniproductus*. Even so, the overtoniids of intermediate age have finer rugae and finer and more numerous spines, and are classed in Rugaurini Lazarev.

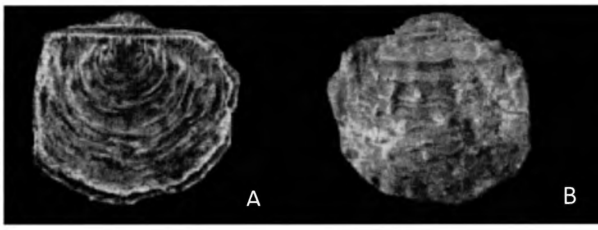


Fig. 1.8. *Poloniproductus varians* (Biernat). A, B, dorsal and ventral aspects, x1.5, from Middle Devonian of Poland. See Biernat & Lazarev (1988).

Subfamily **DOTSWOODIINAE** new subfamily

Fig. 1.9

Name genus: *Dotswoodia* McKellar, 1970, p. 19 from Myrtlevale Formation of the Burdekin-Star shelf (Famennian), Queensland, Australia, here designated. See Appendix A, part A, p. 477.

Diagnosis: Ventral valve raised medianly, dorsal valve deeply concave. Interareas slender, no umbonal cicatrix. Spines restricted to ventral valve, along posterior margin and ears, and along the median ridge, rare and recumbent on flanks and near anterior margin. Additional ornament of ribs disrupted by commarginal growth pauses and low closely spaced rugae, imparting a feebly reticulate pattern. Middle Devonian (Givetian) to Upper Devonian (Famennian).

Genera: *Dotswoodia* McKellar, *Stelckia* Crickmay.

Discussion: *Stelckia* is distinguished by its unusual trigonal shape with extended anterior lateral margins and by its unusual ornament. Further detail has been provided by Crickmay (1963), including observations on the short teeth, large dental sockets, papillation, nature of the cardinal process and the breviseptum, which does not show any slit or sign of buttress plates.

Dotswoodia McKellar, 1970, p. 19 of Upper Devonian (Famennian) age in Queensland, and also reported from western Europe, is of more normal shape, and moderately close in its textured ornament, with less conspicuous dorsal grooves and slightly more swollen ventral spine-bases or riblets, and more prominent rugae, compared with *Stelckia*. It also lacks a cicatrix, and has interareas, teeth and sockets, entire dorsal septum and no alveolus. Fine and closely spaced concentric growth-lines and rugae are more prominent. The genus was classed by Brunton et al. (2000, p. 582, Fig. 413) in Subfamily Donalosiinae Lazarev, Family Araksalosiidae Lazarev, but given that the ornament is so different from that of other members of Donalosiinae, the genus may be placed with *Stelckia*, with which it shares most aspects of the ornament, even including a median row of spines occasionally.

The low rugae typical of the two genera suggest the low commarginal rugae typical of early members of Overtonioidea, of upper Devonian and lower Carboniferous age.

Fig. 1.9. A, *Dotswoodia wyatti* (McKellar), GSQF 11477 latex cast of exterior, x1.5, from Myrtlevale Formation, (Famennian), Queensland. See McKellar (1970). B, *Stelckia galearius* Crickmay, dorsal aspect of holotype, PRI 27111. From Upper Ramparts Formation, western Canada, x1.25. See Crickmay (1963).

Family **CAUCASIPRODUCTIDAE** Lazarev, 1987

Fig. 1.10

[Nom. transl. hic ex Caucasiproductinae Lazarev, 1987, p. 49].

Diagnosis: Ventral spines fine and of even size and regular spacing, no strong hinge row, dorsal spines fine and often close-set, cardinal process of two lobes internally. Middle Devonian (Givetian) to ?Lower Carboniferous (Tournaisian).

Genera: *Caucasiproductus* Lazarev, *Praewaagenoconcha* Sokolskaya, *Stainbrookia* new.

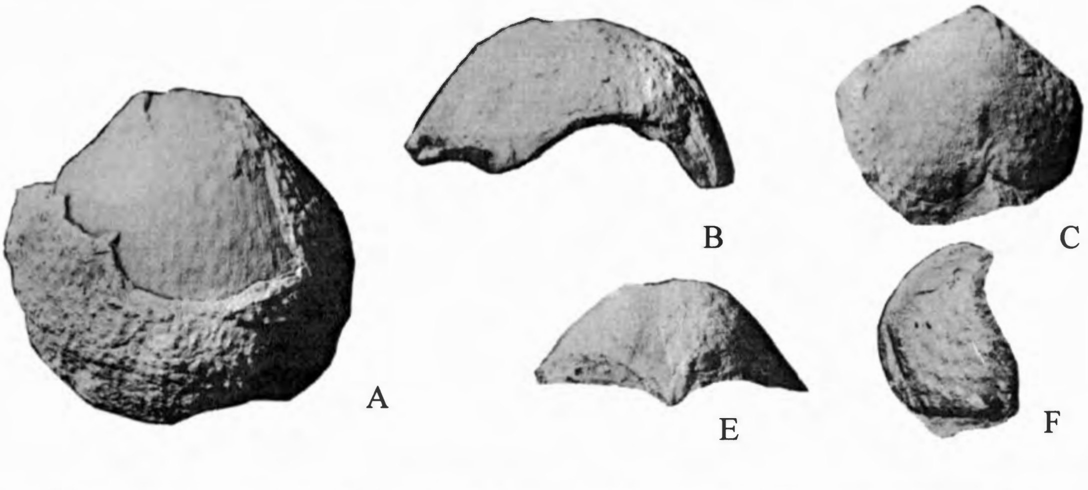


Fig. 1.10. *Caucasiproductus caurina* (Crickmay). A, B, holotype PRI 27122. C-E, paratopotype PRI 27123, as figured by Crickmay (1963, pl. 12, fig. 20-24) from Ramparts Formation (Givetian) of western Canada. Specimens x 2. See Crickmay (1963).

Discussion: These genera lack cicatrix and were assigned to Sentosiidae Muir-Wood & Cooper, within Productidina, by Brunton et al. (2000, p. 516), an assessment defensible in terms of evolutionary development of the

Echinoconchoidea, even though they have teeth and sockets and low interareas. They are now regarded as related to Productellidae, with which they share approximate age and overall body structure, including the absence of anyumbonal cicatrix, and are differentiated by the presence of numerous fine dorsal spines.

Brachial ridges are poorly known but appear strophalosioid in *Caucasiproductus* Lazarev, 1987, a genus which was said to have a short ventral median septum, although none is visible in available figures, and assuming that is correct and not a myophragm, the septal development raises possibilities of a relationship to Scacchinellidae, but more certainly anticipated the presence of a ventral septum in Septariniini, based on *Septarinia* Muir-Wood & Cooper, 1960, a genus related to Juresaniinae which arose ultimately from Caucasiproductidae (p. 182).

The nature of the crowded and erect and somewhat homogeneous spines in genus *Praewaagenoconcha* Sokolskaya, 1948 suggests a relationship to *Spinauris* Roberts, 1971, Waagenoconchiinae Stehli, 1954 and possibly Pustulinae Waterhouse, 1981, as well as Echinalosiinae and its derivatives. *Strophoproductus* Nalivkin, 1937 was included in Caucasiproductinae by Brunton et al. (2000), but has better developed rugae and appears to be closer to Rhytialosiinae Lazarev. A newly named genus *Stainbrookia* shares very closely spaced and numerous fine ventral and dorsal spines with *Praewaagenoconcha* and *Caucasiproductus*, and is of Lower Carboniferous age. *Productellana* Stainbrook has dorsal spines, but they are few and well spaced (see p. 40).

Genus ***Stainbrookia*** new genus

Derivation: Named for M. A. Stainbrook.

Type species: *Strophalosia butlerensis* Stainbrook, 1950, p. 375 from Aplington Formation (Lower Mississippian), Iowa, United States, here designated.

Diagnosis: Medium in size, ventral valve with crowded fine subprostrate spines, no conspicuous hinge row, dorsal spines very fine, crowded and suberect. Commarginal rugae subdued and somewhat irregularly spaced.

Discussion: Compared with the new genus, *Caucasiproductus* Lazarev, 1987, p. 50 from the Middle Devonian (Givetian) of the Transcaucasus has more crowded fine spines with slightly bolder bases and more vaulted ventral valve, whereas the Upper Devonian (Famennian) genus *Praewaagenoconcha* Sokolskaya, 1948, p. 132 from the Moscow Basin of Russia has slightly stronger ventral spines, fewer (but numerous) dorsal spines and is also well vaulted with median ventral spine ridge in some specimens. *Strophoproductus* Nalivkin, 1937, p. 46 from Frasnian faunas of North America and Eurasia is less vaulted, but has slightly fewer and less crowded spines and better developed rugae over both valves, pointing to a rhytialosiid relationship, although referred to Caucasiproductinae in Brunton et al. (2000, p. 526).

This new genus is close in many respects to the Lower Carboniferous genus *Quadratia* Muir-Wood & Cooper, 1960, but has finer and more numerous spines and less developed rugae. *Eostrophalosia* Stainbrook, 1943, p. 58 is also close in general morphology, and slightly greater in age at Frasnian (early Upper Devonian), but has coarser spines spaced further apart, and an umbonal cicatrix (see p. 227).The ventral umbo of *Stainbrookiabutlerensis* is small and projecting, with no sign of cicatrix.

INFRASUBORDER PRODUCTIMORPHI WAAGEN, 1883

Fig. 1.1, Fig. 2.1, Fig. 5.52, pp. 173, 174

[Nom. transl. Waterhouse 2010a, pp. 10, 11 ex Order Productacea Waagen, 1883, p. 447].

Diagnosis: Shells varied in morphology, arose from various Productelloidea, often with ribs and/or commarginal growth steps or rugae over both valves, spines of general or moderately specialized nature, smooth, dendritic or striate muscle impressions.

2. Superfamily **OVERTONIOIDEA** Muir-Wood & Cooper, 1960

Fig. 2.1

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

Diagnosis: Genera productiform in lack of teeth and sockets, interareas, umbonal attachment scar and often pseudodeltidium, apart from relict structures in rare instances. Shells small, without differentiated spines or marginal ridges, spine bases may be prolonged, ribbing subdued or absent, rugation strong to fine or absent, trail simple and not geniculate. Muscle impressions commonly smooth, cardinal process commonly bifid, even in members of Upper Permian age.

Discussion: The major constituents in terms of genera and tribes form a natural grouping, centred on the families Avoniidae and Overtoniidae. The two families were reduced to a subfamily and tribe by Brunton et al. (2000), and submerged amongst a formidable array of tribes and subfamilies classed as Productoidea in Brunton et al. (2000), and these are separated into distinct superfamilies, Overtonioidea, Horridonioidea, Marginiferoidea, and Productoidea. For Avoniidae, ornament is dominated by spines and radial if any ornament, which may be discontinuous. For Overtoniidae, spines are prominent together with concentric rugae or lamellae. A small family Lomatiphoridae is close in some respects to Overtonioidea, but having arisen from a different productellid subfamily, is classed in Productoidea.

Family Overtoniidae Muir-Wood & Cooper, 1960
- Subfamily Overtoniinae Muir-Wood & Cooper, 1960
- Subfamily Plicatiferinae Muir-Wood & Cooper, 1960
  - Tribe Plicatiferini Muir-Wood & Cooper, 1960
  - Tribe Absenticostini Waterhouse, 2002b
  - Tribe Crossacanthiini new tribe
  - Tribe Institiferini Muir-Wood & Cooper, 1960
- Subfamily Semiproductinae McKellar, 1970
  - Tribe Semiproductini McKellar, 1970
  - Tribe Rugaurini Lazarev, 1990
- Subfamily Levipustulinae Lazarev, 1985
  - Tribe Levipustulini Lazarev, 1985
  - Tribe Lanipustulini new tribe

Family Avoniidae Sarytcheva, 1960
- Subfamily Avoniinae Sarytcheva, 1960
- Subfamily Semicostellinae Nalivkin, 1979

Table 4. Superfamily Overtonioidea Muir-Wood & Cooper, 1960.

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

[Nom. transl. Waterhouse 2002b, p. 11 ex Overtoniinae Muir-Wood & Cooper, 1960, p. 183].

Diagnosis: Commarginal ornament well developed on both valves, radial ornament subdued or lacking. Spines on both valves or only ventral valve, subuniform in size except for a few distinctive genera, and arranged in quincunx, with short or no extended bases. No interareas, teeth or buttress supports, adductor scars smooth as a rule and may become dendritic, brachial shields tend to be productiform, low to moderately defined cardinal ridges, dorsal endospines fine and numerous.

Discussion: This family is characterized in part by strong commarginal ornament, and separated on that basis from Avoniidae. But evolution seldom proceeded along a single track, and later tribes and subfamilies developed or lost commarginal ornament, leading to potential confusion, and the position of some groups remains contentious.

The middle Devonian strophalosiiform genus *Poloniproductus* Biernat & Lazarev, 1988, treated tentatively as an ally of Orbinariinae, Family Productellidae, has strong ventral spines in concentric rows, separated by laminae,

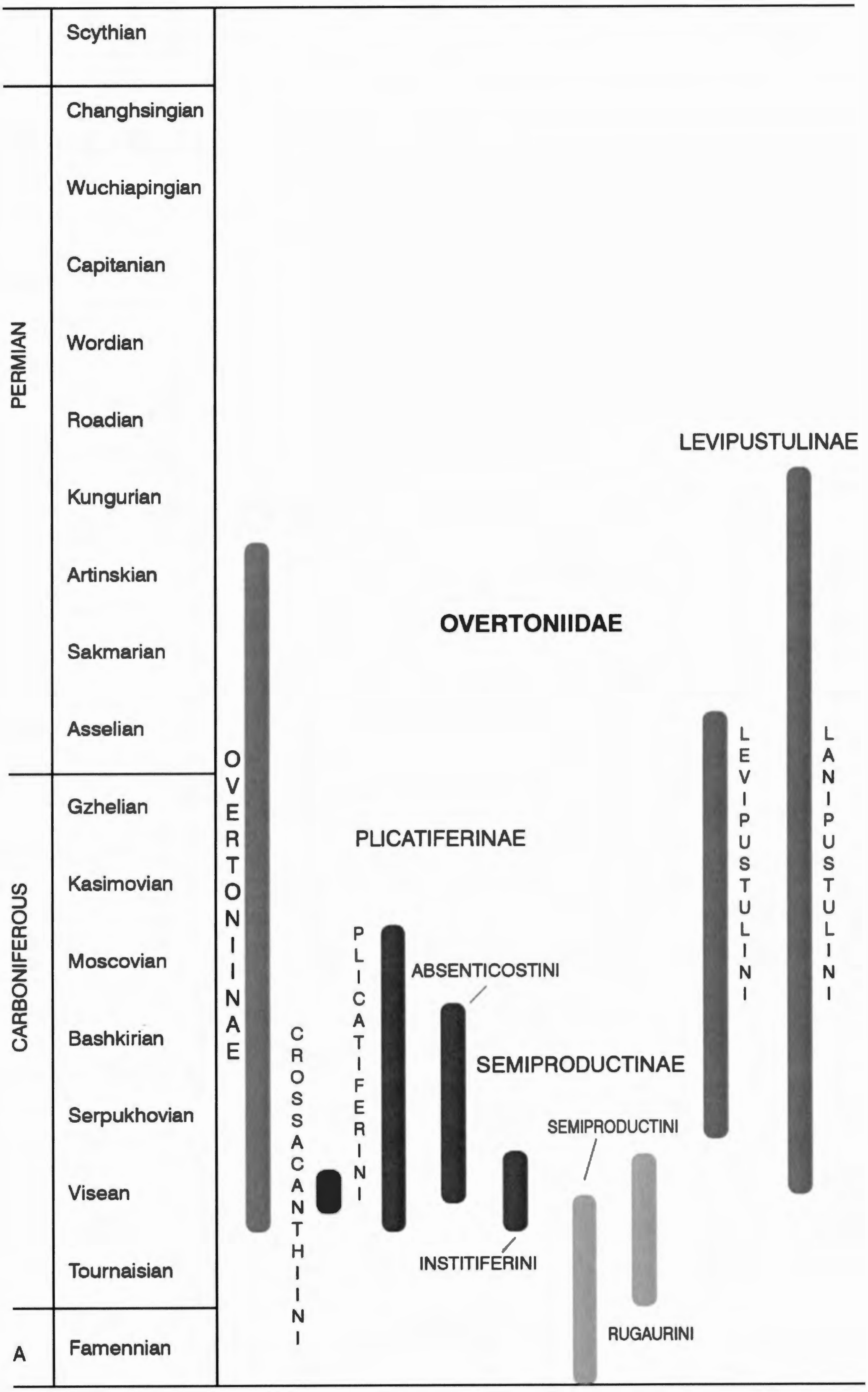


Fig. 2.1. Range chart for Overtonioidea.

and offers a possible source for Overtoniinae, although given the time constraints, the two appear to have arisen independently.

Of all potential progenitors, Dotswoodiinae (Middle and Upper Devonian, Givetian to Famennian) displays fine rugae, approaching though not as regular as those of Rugaurini of Upper Devonian (Famennian) to Lower Carboniferous (Visean) age. Rugaurini are classed in Plicatiferinae, Family Overtoniidae.

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

Fig. 2.2A-C

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

Diagnosis: Moderately strong spines arranged in commarginal 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 (upper Visean) to Lower Permian (Artinskian).

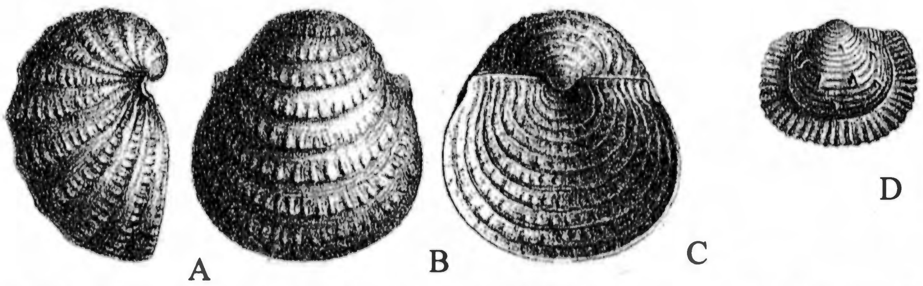


Fig. 2.2A-C. *Overtonia fimbriatus* (Sowerby), as figured by Davidson (1861, pl. 33, fig. 13), from Lower Carboniferous at Settle, Yorkshire, England, specimens x1 approx. Fig. 2.2D. *Thomasella wrightii* (Davidson) as figured by Davidson (1861, pl. 33, fig. 6) from Lower Carboniferous at Middleton, near Cork, Ireland, x 3. See Tribe Institiferini, p. 56.

Genera: *Overtonia* Thomas, *Fimbrinia* Cooper (nom. nov. pro *Fimbriaria* Muir-Wood & Cooper, 1960 non Froelich, 1802 Naturforscher 29: 13), *Fimbrininia* new genus, *Fimbrinusia* new genus, *Jakutella* Abramov, ?*Overtoniina* Grunt.

Discussion: There is a weak suggestion of lateral buttress plates in *Overtonia* and *Fimbrinia* (Muir-Wood & Cooper 1960, pl. 46, fig. 8, 20), and in the new genus *Fimbrininia transversa* (Shi & Waterhouse, 1996, pl. 4, fig. 19), but the appearance seems insignificant, and none are shown in the silicified material of *Fimbrinia* that was figured by Brunton (1966, pl. 9, fig. 7-9, pl. 10, fig. 2, 3). *Jakutella* Abramov, 1970 has elongate ventral spine bases in quincunx posteriorly and more or less in rows anteriorly, and fine dorsal spines interspersed with dimples. It is of Moscovian and Kasimovian (Upper Carboniferous age) in Yakutsk, northeast Russia. Although classed as Sentosiinae by Brunton et al. (2000, p. 522), the figures suggest little similarity to this subfamily, but the position of the genus is difficult to decipher without first-hand examination. Lazarev (2005a) suggested that the genus was close to *Horridonia* and allies. *Overtoniina* Grunt is supposed to have broad costae over the trail according to Brunton et al. (2000, p. 464). But none were figured (Grunt in Grunt & Dmitriev 1973, pl. 5, fig. 8, 9, fig. 19; Brunton et al. 2000, Fig. 308.1a-d), and Grunt (op. cit., pp. 94, 96) stated that "the trails of both ventral and dorsal valves are smooth, sometimes with weak ribs and fine growth lines, and fine spines," as verified by e-mail. Low broad pustules in commarginal rows over the ventral valve suggest that the genus is overtoniin.

Genus ***Fimbrininia*** new genus

Derivation: fimbriae – threads, fringe, Lat.; alt. Fimbrinia, name of allied genus.

Type species: *Fimbrininia spinosa* new species from lower Jungle Creek Formation (Asselian), Yukon Territory, here designated.

Diagnosis: Subelongate shells with sturdy spines emerging from the crests of commarginal rugae over ventral valve.

Discussion: This genus is very closely related in most aspects to *Fimbrinia* Cooper, 1972, based on *Overtonia plummeri* King, 1938 from the Gaptank Formation (*Uddenites*-bearing Shale Member) and the Neal Ranch Formation of west Texas, United States. The difference lies in the ventral spines. These emerge from the crests of the commarginal rugae or close by in the present form, whereas the spine bases are stronger and longer, emerging from the interspaces or treads between the rugal crests in *Fimbrinia*, as illustrated by R. E. King (1931, pl. 20, fig. 1-3), R. H. King (1938, pl. 39, fig. 19-22), Muir-Wood & Cooper (1960, pl. 46, fig. 1-9), Cooper & Grant (1975, pl. 311, fig. 5-14) and Brunton et al. (2000, Fig. 283.2a-e). Texan forms such as *Fimbrinia* spp. from the Cibolo Formation and Lenox Hills Formation are typical *Fimbrinia*, as is possiby *F. ovata* Cooper & Grant, 1975 from the Bone Spring Formation. On the other hand various Russian species are congeneric with the Canadian genus.

Fimbrininia spinosa new species

Fig. 2.3

Derivation: spina – a thorn, Lat.

Holotype: GSC 133266 from JBW locality 581, Member D (Asselian), Jungle Creek Formation, Ogilvie Mountains, Yukon Territory, Canada, figured as Fig. 2.3A, here designated.

Diagnosis: Comparatively transverse shells with some twelve spines along each of the concentric rugae of the ventral valve.

Material: More than twenty specimens from Member D (early Asselian), Jungle Creek Formation, Ogilvie Mountains, Yukon Territory, Canada. See Appendix A, Part C, p. 478.

Description: Shell large for genus, up to 17mm long, 19mm wide and 8mm high, with incurved prominent ventral umbo, steep posterior walls, large ears which are weakly alate with acute extremities, and maximum width sited towards anterior third of shell length. The dorsal valve is gently concave so that the visceral disc is thick, and the dorsal ears are gently concave with alate extremities. The trail is slender, curving smoothly from the disc. Ornament is strong, made up of some twelve or more prominent commarginal rugae on the ventral valve, increasing in spacing and strength from the umbo, and becoming lower and more closely spaced over the anterior third of the shell length. Some twelve spines emerge from the crest of each rugation that crosses the shell, increasing in size towards the middle, with swollen bases over 1mm across that extend only slightly back over the dorsal ramp of each rugation. There are ten to twelve growth increments per mm over mid-length. Concentric rugae are not so regular and high over the dorsal valve, and the shell surface is diversified by low radial folds, which are less persistent laterally over the anterior shell, as well as concentric laminae, dimples and pits and numerous spines in at least 25 concentric rows. The dorsal spines are erect and up to 0.25mm in diameter. They form a well defined row in front of the dorsal ears along the junction with the visceral disc, and the ears lack spines.

The ventral adductor platform is small and only slightly longer than wide: on one specimen the scars are marked by irregular subdendritic growth lines. Diductor scars are small, anteriorly placed, and marked by faint longitudinal striae and lines parallel to the anterior margin. The posterior floor is smooth, and small pustules lie in front, in bands behind and in front of the spine rows. One shell has a low forked ridge across the umbo.

In the dorsal valve the medium septum extends for about half the length of the valve and the anterior adductor scars are large and tear-shaped, with faint markings parallel to the anterior margin. Posterior adductors are very small and are bordered each side by a low oblique ridge. A stronger ridge lies close to the hinge, and a broad platform lies in front of the cardinal process. Brachial scars are not visible. The posterior shell bears fine closely spaced pustules, and larger pustules lie in front of the septum around the anterior shell.

Resemblances: This species is closely allied to the slightly younger form described as *Fimbrinia transversa* Shi & Waterhouse (1996, p. 55, pl. 4, fig. 9-20), now referred to *Fimbrininia,* and coming from the so-called *Yakovlevia* (now *Muirwoodia*) *transversa* to *Jakutoproductus verchoyanicus* Zones in the Jungle Creek Formation of the Ogilvie Mountains in northwest Canada. Differences are that the younger shells are slightly narrower, and have eight to ten spines as a rule along the commarginal rugae, fewer than in the present form. The dorsal valve as figured by Shi & Waterhouse (1996, pl. 4, fig. 12, 17) is smoother, with more subdued commarginal ornament other than a few prominent layers, and apparently fewer spines. According to the text there are only some four to five growth increments per mm, much fewer than in present material. Ventral spines emerge from the crests of the rugae in both species. A short ridge in the position of the lateral buttress ridge was shown for *transversa* by Shi & Waterhouse (1996, pl. 4, fig. 19), and a similar ridge is present in an older species of *Fimbrininia*, yet to be described, from Member A (Gzhelian) in the Jungle Creek Formation of Canada.

Fimbrinia? gracilis Abramov & Grigorieva (1983, pl. 3, fig. 10-14) from the Upper Carboniferous of the southern Verchoyan Mountains, northeast Russia, cited as Moscovian by Klets (2005, p. 44), is close in the number of ventral spines along the rugae, but is more transverse with fewer rugae. *Overtonia gijigensis* Zavodowsky (1970, pl. 35, fig. 1-3) from the Sakmarian Irbichan Suite of the Kolyma-Omolon massif of northeast Russia is very transverse, with further specimens assigned to the species from the lower Kigiltass Suite of Verchoyan by Abramov & Grigorieva (1983, pl. 3, fig. 15-17). *"Fimbriaria" kolymaensis* Zavodowsky (1970, pl. 37, fig. 8-10) from the Sakmarian Yasachnin Suite of the same region is also moderately transverse. Details in figures for these two species are obscure, and none of the Russian forms show much of the interior or dorsal valve.

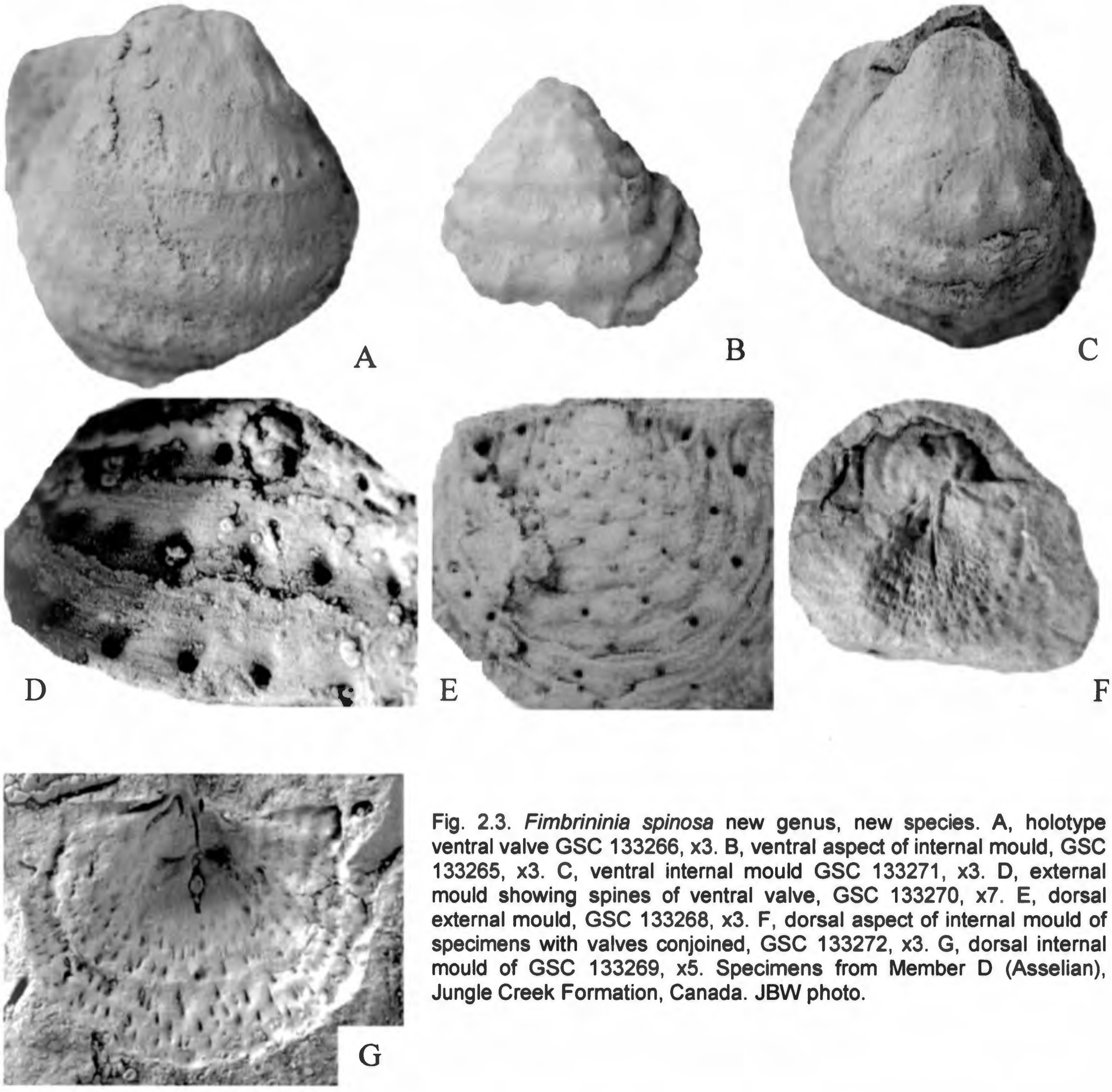


Fig. 2.3. *Fimbrininia spinosa* new genus, new species. A, holotype ventral valve GSC 133266, x3. B, ventral aspect of internal mould, GSC 133265, x3. C, ventral internal mould GSC 133271, x3. D, external mould showing spines of ventral valve, GSC 133270, x7. E, dorsal external mould, GSC 133268, x3. F, dorsal aspect of internal mould of specimens with valves conjoined, GSC 133272, x3. G, dorsal internal mould of GSC 133269, x5. Specimens from Member D (Asselian), Jungle Creek Formation, Canada. JBW photo.

Productus cristatotuberculata Kozlowski (1914, pl. 2, fig. 61, 62), also figured by Branisa (1965, pl. 66, fig. 34–35a), from the Asselian Copacabana Group of Bolivia, differs in having fewer concentric rugae. The nature of the spine bases is not clear in figures but the text indicates that the spines are like those of *Fimbrinia.* Specimens from Kazakhstan that were ascribed to this species in Sarytcheva (1968, pl. 6, fig. 5-10) are small and subelongate, with few concentric rugae, although the spines do commence over the posterior part of each rugation, whereas spines arise from the crests in Kigiltass specimens from west Verchoyan figured (wrongly) as *cristatotuberculatus* by Kashirtsev (1959, pl. 15, fig. 6, 7), as do the spines in Turuzov specimens assigned to the species by Ustritsky & Chernyak (1963, pl. 4, fig. 11, 12), together with material figured by Einor (1946, pl. 4, fig. 8, pl. 5, fig. 7-9) from Taimyr, north Russia.

Genus ***Fimbrinusia*** new genus

Derivation: Name variation from *Fimbrinia* Cooper, 1972, allied genus.

Type species: *Fimbrinia*? *borealis* Carter & Poletaev (1998, p. 123) from the Hare Fiord Formation (Atokan), Ellesmere Island, Canada, here designated.

Diagnosis: Ventral valve strongly rugose with scattered spines emerging from crests of rugae; dorsal valve rugose, without spines.

Discussion: This genus is distinguished by the lack of dorsal spines. It is closer in other respects to *Fimbrininia* than to *Fimbrinia*.

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

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

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

Discussion: A striking characteristic of Plicatiferinae is the development of closely spaced, even and well defined commarginal rugae with rounded crests, which dominate the ornament. This is a feature that appears in various unrelated members of Productida, examples including *Admodorugus* Brunton & Mundy, 1993, a member of the horridonioid tribe Levitusiini, and *Scutepustula* Sarytcheva, 1963, a member of Pustulinae in Waagenoconchidae. Strophalosioid examples are offered by *Parmephrix* Brunton & Mundy in Brunton, Rachboeuf & Mundy, 1994 and *Semenewia* Paeckelmann, 1930 of Tribe Semenewiini Muir-Wood & Cooper in Family Chonopectidae, and *Rhytialosia* Lazarev, 1989, *Steinhagella* Goldring, 1957 to a degree and *Veeversalosia* Lazarev, 1989 in Rhytialosiinae Lazarev. Aulostegoid genera believed to be descendent from this subfamily Rhytialosiinae include *Rugicostella* Muir-Wood & Cooper, 1960, *Retroplexus* Brunton & Mundy, 1988b and *Institina* Muir-Wood & Cooper, 1960 of Institinini Muir-Wood & Cooper in Family Institellidae Muir-Wood & Cooper. In this study, it is preferred to associate such regularly rugose genera in tribes or subfamilies, to imply that rugation arose independently in different stock, and indicate that rugose genera within a subfamily were likely to be closely related, rather than representative of random emergence of rugation amongst scattered genera within a group.

Taking into consideration the constraints of time as well as various aspects of morphological development, it would appear most likely that Plicatiferinae together with other overtoniids arose from Dotswoodiinae, a Devonian subfamily of Productellidae.

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

Fig. 2.4

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

Diagnosis: Commarginal rugae strong as a rule. Spines over ventral valve may involve a few stout well spaced halteroid spines near hinge, flanks and anterior, and may include additional fine spines, though they are not numerous or dense; no dorsal spines. Gently convex ventral disc and geniculate trail, ribbing anterior only or usually not developed but disrupted swellings along concentric crests may be radially aligned. Ear baffles and posterior hinge ridges well developed on dorsal valve, dorsal anterior pustules inconspicuous. Lower Carboniferous (middle Visean) to Upper Carboniferous (Moscovian).

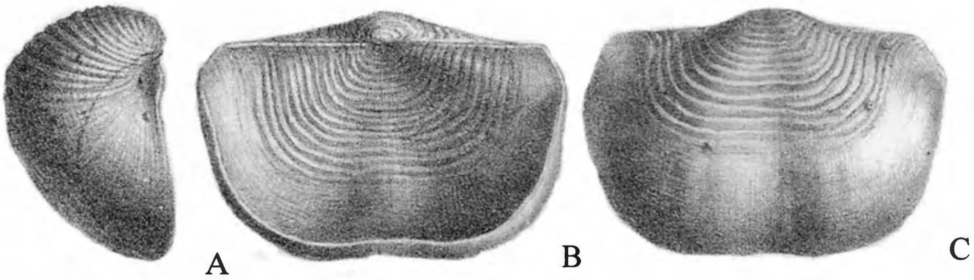


Fig. 2.4. *Plicatifera plicatilis* (Sowerby), lateral, ventral and dorsal aspects, as figured in Davidson (1861, pl. 31, fig. 3) from Carboniferous Limestone of Derbyshire, England, x1.

Genera: *Plicatifera* Chao, *Aseptella* Martínez Chacón & Winkler Prins, *Lazarevia* Carter & Poletaev, ?*Rugoconcha* Jin & Sun.

Discussion: *Lazarevia* Carter & Poletaev, 1998 is very close to *Plicatifera*, but is slightly younger, with slightly different arrangement of ventral spines. *Rugoconcha* is poorly known, and its position requires consolidation from further study. Brunton (2007, p. 2644) considered that *Labaella* Kotlyar, Zakharov & Polubotko, 2004 belonged to Plicatiferini, although it is late Changhsingian (Upper Permian) in age, much younger than the otherwise Carboniferous members of the tribe. Brunton (2007, p. 2644) mistakenly asserted that it was smaller than *Lazarevia*: in fact it is more than twice as large, and in general shape looks dictyoclostid, with fine reticulate ornament close to although not the same as that of *Rigrantia* Lazarev, 2000b, a genus which has more spines and has dorsal dimples. Spines in *Labaella* are limited to a row along the ventral hinge. Radial ornament in *Labaella* is more prominent and commarginal rugation close-set but less regular than in Plicatiferini, lateral ears are much larger than in any Lower Carboniferous member of Plicatiferini, and dorsal adductors are broad and dendritic. Lazarev (2010) regarded *Labaella*, so far as his text can be interpreted, as closely related to *Linoproductus*, which is certainly more acceptable than the proposed plicatiferin position. But here the genus is placed as a separate tribe in Dictyoclostidae (p. 161).

Aseptella Martínez Chacón & Winkler Prins, 1977 from the Visean to Bashkirian faunas of Spain is a distinctive genus, with *A. patricias* Simanauskas, 1996 (and see Martínez Chacón & Winkler Prins, 1999) from Argentina, allegedly Permian in age, but more likely to be Upper Carboniferous. A Bashkirian species from Thailand (Wongwanich et al. 2004, p. 1075), described as *Aseptella satunensis* Brunton, is close to type *Aseptella*, and one specimen (Wongawanich et al. 2004, Fig. 4.12) shows clearly an outer hinge ridge (much as in Crossacanthiini new tribe) and brachial shield outer ridge passing into the dorsal adductor scars. The species has a dorsal median septum, unlike mature *A. asturica* from Spain, but *A. beetsi* Winkler Prins & Martínez Chacón of Visean age from Spain shows a weak dorsal septum, and the type species and the Argentinian species have a dorsal septum at earlier growth phases. Martínez Chacón & Winkler Prins (1999) considered that the Spanish occurrence is found in deep-water and therefore cold conditions, helping to explain the later appearance of the genus in relatively cold waters of Thailand and Argentina.

Tribe **ABSENTICOSTINI** Waterhouse, 2002b

[Absenticostini Waterhouse, 2002b, p. 12].

Diagnosis: Close to *Plicatifera* with concentric laminae or fine rugae, spines even in size, numerous and close-set over ventral valve, present more sparsely on dorsal valve. Lower Carboniferous (middle Visean) to Upper Carboniferous (Bashkirian or younger).

Genera: *Absenticosta* Lazarev, *Ferganoproductus* Galitskaya, *Taboadaia* new genus.

Discussion: Commarginal ornament is less strong than in Plicatiferini, dorsal spines are present, at least rarely, and a double septum may be developed in the dorsal valve. No lateral buttress plates are known in *Absenticosta* (see Lazarev 1991, pl. 4, fig. 6): the other genera are less well known with regard to internal detail. *Absenticosta* Lazarev, 1991 is of Visean age in Mongolia, and *Ferganoproductus* is reported from upper Visean to Bashkirian faunas of eastern Europe and Asia, according to Brunton et al. (2000, p. 452). New genus *Taboadaia* is found in the late Visean of Argentina, and possibly in Mongolia.

Genus ***Taboadaia*** new genus

Fig. 2.5

Derivation: Named for Arturo C. Taboada.

Type species: *Absenticosta bruntoneileenae* Taboada & Shi (2011, p. 105) from El Paso Member of San Eduardo Formation (latest Visean), Argentina, here designated.

Diagnosis: Small medium in size, transverse with scattered ventral spines over the visceral disc that have elongate bases, spines rare and erect near hinge and over trail; spines minute and erect over dorsal visceral disc. Commarginal rugae fine and closely spaced over both valves.

Discussion: This genus is very close to *Absenticosta* Lazarev in Lazarev & Suur'suren 1991, p. 58 from the ?middle and upper Visean of Mongolia, but differs in the nature of the ventral spines over the visceral disc, for these have extended bases, whereas ventral spines of characteristic *Absenticosta* are erect, without prolonged bases. The type species of *Absenticosta* lacks cardinal spines, and a single spine is present on each auricle of the type species of *Taboadaia*. As pointed out by Taboada & Shi (2011, p. 106), this does not constitute a significant difference, because younger species of *Absenticosta* have auricular spines. Lazarev (1991) assigned such species to *Impiacus* Lazarev & Suur'suren in Afanasieva et al. 1988, p. 53, but as noted by Taboada & Shi (2011), such species show the fine rugation characteristic of *Absenticosta*, rather than *Impiacus*. One fragmentary ventral valve figured as *Absenticosta* by Lazarev (1991, pl. 4, fig. 7) shows elongate spine bases, suggesting that the genus was also present in Mongolia.

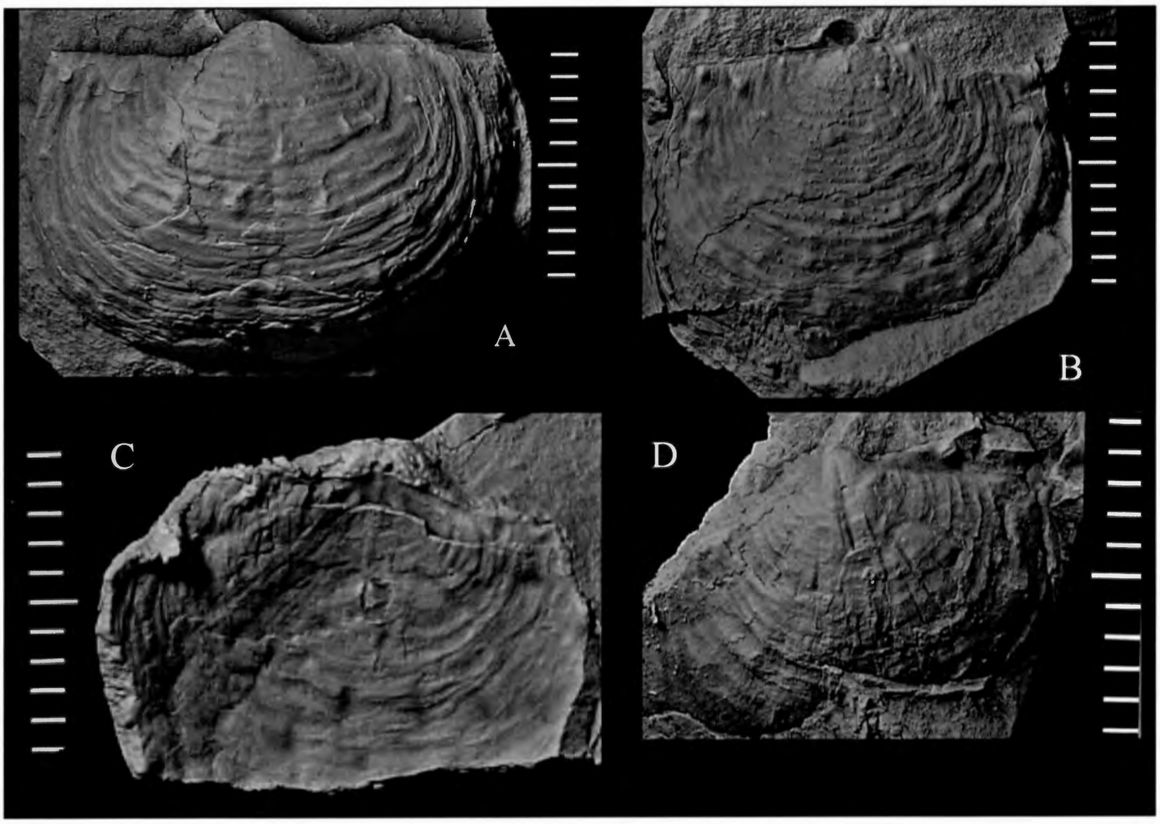


Fig. 2.5. *Taboadaia bruntoneileenae* (Taboada & Shi). A, holotype ventral valve exterior FML-PI 1201-1. B, dorsal external mould FML-PI 1201-4. C, FML-PI 1204-3, dorsal aspect. D, internal mould of ventral valve FML-PI 1204-4. Specimens from El Paso Member of San Eduardo Formation (late Visean), Argentina. Scale bar in mm. Photos courtesy of A. C. Taboada.

Tribe **CROSSACANTHIINI** new tribe

Name genus: *Crossacanthia* Gordon, 1966, p. 580 from Missouri (middle Visean), United States, here designated.

Diagnosis: Small subpentagonal to subcircular shells, ventral spines numerous to few, dorsal spines absent or possibly present, low commarginal rugae or growth steps. Dorsal valve with thick lateral buttress plates, and double septum anteriorly, well formed marginal ridge, peg-like unifid cardinal process. Lower Carboniferous (middle Visean).

Genera: *Crossacanthia* Gordon, *Platyselma* Gordon.

Discussion: *Plicatiferina* differs in having a long dorsal median septum, and no sign of the double anterior septa, or ridges diverging from in front of the cardinal process. The mid-Visean *Platyselma* Gordon has erect ventral spines, possible but not certain dorsal spines, and subdued dorsal concentric lamellae, but no teeth or interarea. It carries apparent lateral buttress plates either side of the swollen dorsal adductor scars, and a low double ridge in front of the dorsal adductor scars, not seen in *Plicatifera*. The dorsal valve resembles that of *Crossacanthia* externally, and this latter genus also shares thick lateral buttress plates.

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

Fig. 2.2D

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

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

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

Subfamily **SEMIPRODUCTINAE** McKellar, 1970

[Semiproductinae McKellar, 1970, p. 26].

Diagnosis: Medium size with relatively long trails. Spine bases long on ventral disc, quincunxially arranged, ribs begin on disc and present on trail. Lateral hinge ridges short, no marginal ridges, teeth in early genus.

Discussion: This subfamily has finer rugae and more numerous spines than in Overtoniinae, and genera are older. If *Poloniproductus* Biernat & Lazarev of Eifelian age was ancestral to *Overtonia*, then *Semiproductus* and allies seem likely to have formed an older and different suite, distinct from Overtoniinae, and apparently modified from Dotswoodiinae. It seems more likely that *Poloniproductus* was an isolated one-off derivative.

Tribe **SEMIPRODUCTINI** McKellar, 1970

Fig. 2.6

[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 commarginal wrinkles, posterior dorsal septum cleft. Deep body cavity. Upper Devonian (Famennian) to Lower Carboniferous (upper Visean).

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

Discussion: Semiproductini McKellar, 1970 is centred on *Semiproductus* Bublichenko, 1956, for which the best preserved material comes from Queensland, Australia (McKellar 1970). The genus shows short elongate ventral spine bases and low commarginal rugae, shells not very different in ornament from Rugaurini Lazarev (see below), but with thicker corpus cavity. Members have a dorsal marginal ridge as in Rugaurini, but display a distinctive split dorsal septum. Lazarev (1986b, p. 42) stressed that the body cavity was relatively large, and the dorsal trail geniculate, with costae on the trail.

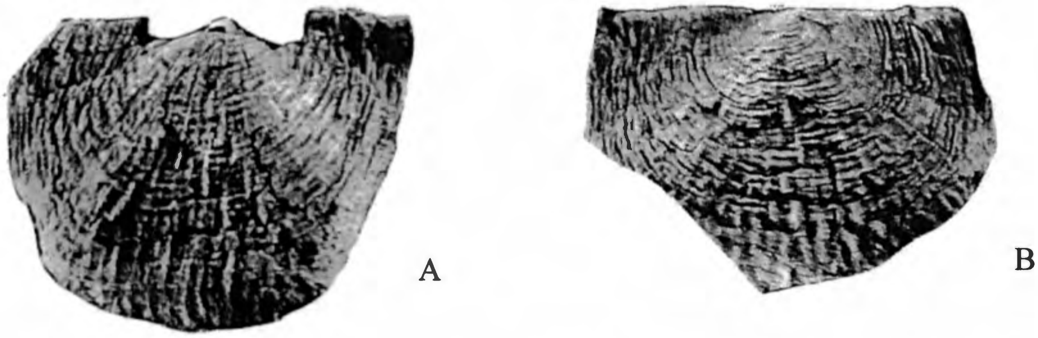


Fig. 2.6. *Semiproductus etheridgei* McKellar. A, ventral valve GSQ F 11546. B, external mould of dorsal valve GSQ F 11548, from upper Famennian of Queensland, Australia, x1.5 approx. See McKellar (1970, pl. 8).

The Lower Carboniferous (Hastarian) genus *Rhytiophora* Muir-Wood & Cooper, 1960, p. 192 was transferred to Semiproductini McKellar by Waterhouse (2002b, p. 8) from Tribe Semicostellini Nalivkin, where it was classed by Brunton et al. (2000, p. 464), because it shows fine commarginal rugae and numerous fine spines including dorsal spines, and weakly cleft posterior dorsal median septum typical of Semiproductini. Ribs vary in definition on different species (Muir-Wood & Cooper 1960, pl. 51, fig. 15; Roberts 1971).

Genus ***Acanthoproductus*** Martynova, 1970

Acanthoproductus of Upper Devonian (upper Famennian) age was included in Semiproductini by Brunton et al. (2000, p. 484, Fig. 326.2a-d). The genus is somewhat like Leioproductinae Muir-Wood & Cooper (Horridonioidea, see p. 69), because it displays a median spinose fold on the ventral valve, and dorsal median groove with pits, whereas its close-set spines and fine crowded rugae are like those of *Semiproductus*. Martynova (1970) placed the genus in

Leioproductidae and stressed the distinctiveness of radial striae on the dorsal valve, well figured by Lazarev (1990, pl. 6, fig. 3-5). The dorsal valve is very gently concave, helping to enclose a thick body corpus, and ventral adductors are obscurely striate. There are short dorsal cardinal ridges and cardinal pit, and although the dorsal septum is split, no buttress plates are present. Teeth were reported, but brachial shields are not visible. The genus in its median rib shows some approach to *Stelckia* Crickmay, 1963 of Middle Devonian (Givetian) age, though unlike that older genus, it seems to lack interareas. The ornament is also like that of Rugaurini Lazarev, but Rugaurini lacks the split posterior dorsal septum and its ventral spines are more concentrically arranged.

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 wrongly ascribed to Muir-Wood & Cooper (1960) by Brunton et al. (1995, p. 927).

Diagnosis: Commarginal 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. No teeth or ear baffles or submarginal ridges, or cleft posterior dorsal median septum, posterior hinge ridge well developed. Corpus cavity shallow. Upper Devonian (upper Famennian) to Lower Carboniferous (upper Visean).

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

Discussion: This tribe is distinguished by its thin visceral disc, whereas the fine numerous often somewhat commarginally aligned ventral spines and very low close-set commarginal wrinkles are close to those of Semiproductini. Ventral and dorsal spines are found in *Rugauris*, but only ventral spines are known in the other genera. Commarginal rugae are finer than in Plicatiferini, and spines are fine and usually closely spaced, but the dorsal septum is somewhat like that of Plicatiferini, and not doubled. The definition for Rugaurini in Brunton et al. (2000, p. 459) states that there are "no ear baffles". Yet *Rugauris* itself has a low but well formed posterior hinge ridge and ear baffles (Brunton et al. 2000, Fig. 305.1f), and *Orbinaria* Muir-Wood & Cooper with its high and well formed dorsal marginal ridge was placed in the same tribe. *Orbinaria* differs in having less regular concentric wrinkles and fewer coarser spines, and also teeth and large marginal ridge, features that it shares with Productellidae (see Orbinariinae, p. 45).

In the upper Famennian genus *Iniproductus* Lazarev, 1990, spines are spaced further apart than in *Rugauris*, with elongate bases and limited to the ventral valve, approaching ventral spines of Levipustulini, but close-set commarginal rugae point to Rugaurini. There are no dorsal spines but elongate pits are prominent.

Subfamily **LEVIPUSTULINAE** Lazarev, 1985

[Levipustulinae Lazarev, 1985, p. 72].

Diagnosis: Spines in quincunx with elongate or swollen bases, absent dorsally from some Devonian and Permian genera. Commarginal ornament subdued, mostly lamellate or in growth steps. Median septum may be broad in front of cardinal process, or divided in two, low posterior hinge ridge, marginal ridges low or absent, lateral buttress plates present or absent. Corpus cavity variable in depth.

Discussion: A summary of the varying interpretations of *Levipustula* and allies by Lazarev (1986a, 1987, 1990) and Brunton et al. (1995, 2000) is provided by Waterhouse (2001, p. 18). Taboada & Shi (2011) derived the levipustulin genera *Lanipustula* → *Verchojania* → *Jakutoproductus* → *Piatnitzkya* from *Absenticosta* in Patagonia, in parallel to a lineage of *Absenticosta* → *Impiacus* → *Lanipustula* in northeast Russia, urged by Lazarev (1991). It should be noted that these authors referred to "phylogenetic lineages" but no cladistics were employed – the lineages were based on morphologies, rather than statistically assessed. The gradation between *Absenticosta* and *Impiacus* postulated by Lazarev (1991) was described in terms of gradual loss of rugation and gradual insertion of posterior spines towards the *Impiacus* model, but there is a disturbing lack of quantitative data with no provision of number of specimens involved, nor any data on measured distance or sediment thickness between successive specimens. Subject to this lack of data, it seems that some shells assigned to *Impiacus* could more readily be assigned to *Absenticosta*, because they display well developed commarginal rugae, a point also stressed by Taboada & Shi (2011), and some species, including *arateliensis* Lazarev figured by Brunton et al. (2000, Fig. 299.2d), lack the elongate spine bases

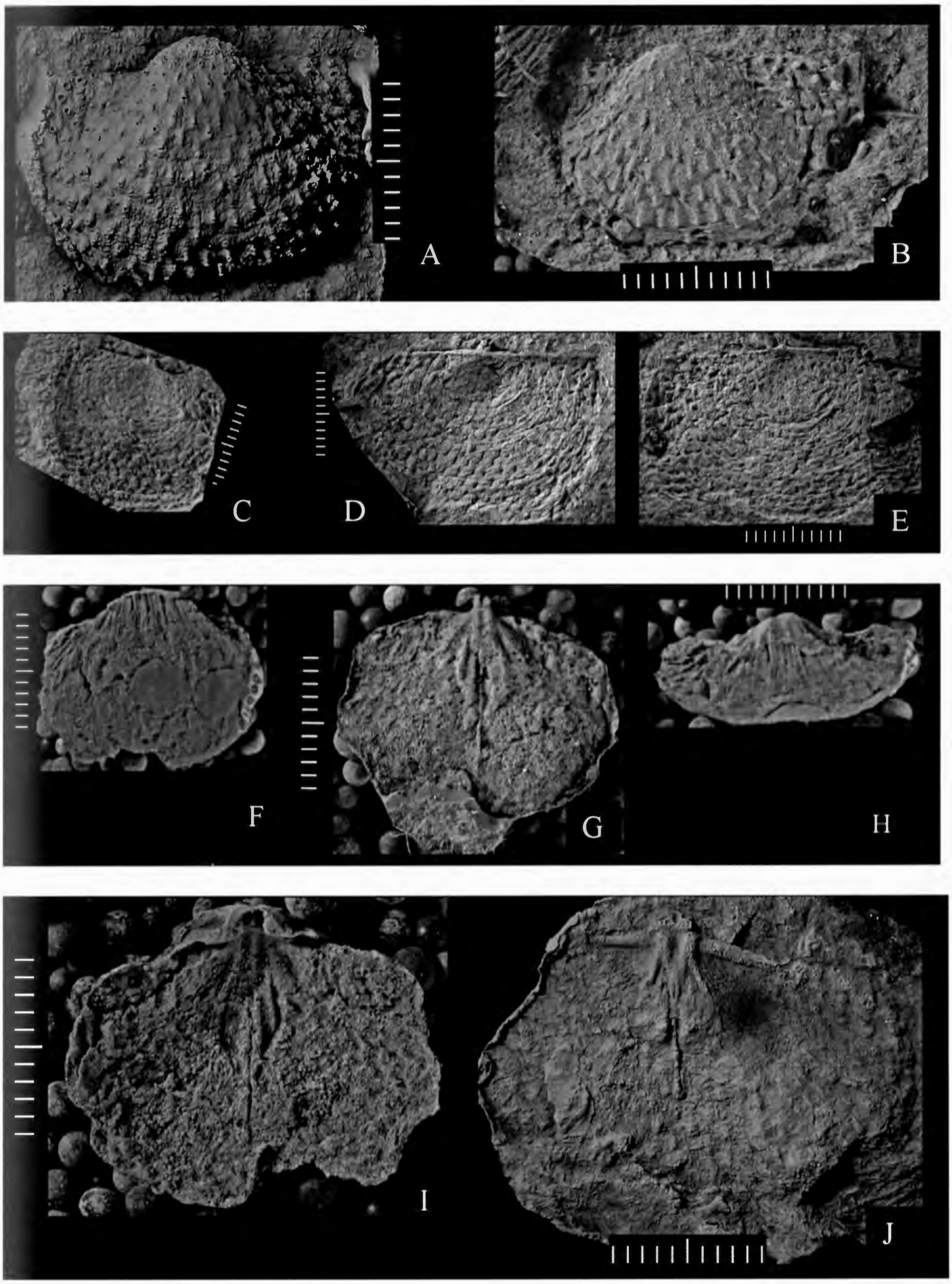


Fig. 2.7. *Levipustula levis* Maxwell. A, latex cast of ventral exterior, UQF 11909. B, latex cast of ventral exterior, UQF 11967. C, latex cast, dorsal exterior FML-PI 3558-3. D, latex cast of dorsal exterior FML-PI3. E, latex cast of dorsal exterior FML-PI 3560. F, H, ventral and posterior ventral views of internal mould, holotype UQF 11900. G, I, latex cast and dorsal internal mould of holotype. J, latex cast of dorsal interior, UQF 11915. Scale bar: 10mm. Upper Carboniferous specimens from eastern Queensland, Australia. Photographs supplied by A. C. Taboada. See Taboada & Shi (2011).

found in type *Impiacus*. There remains a gap in morphology between such specimens and the first incontrovertible *Impiacus*, which is here characterized by the lack of well defined commarginal rugae and presence of elongate spine bases over the ventral visceral disc. This gap is partly closed, at least in theory, by the recognition of a new genus *Taboadaia*, which also has elongate spine bases over the ventral disc. But the difference in rugation remains. That implies that the *Absenticosta* - *Impiacus* link remains open for further analysis.

A further step in the understanding of the origins of Levipustulini is the recognition of a new genus *Austroboreas* for species hitherto referred to *Lanipustula*, but distinguished by the presence of lateral buttress plates. Restricted *Lanipustula* appears in upper Visean and/or Bashkirian faunas, including the Amonoman Suite of Serpukhovian and Bashkirian age in Russia, and the genus comes very close in most detail to *Austroboreas*, and therefore may have constituted short-lived parental stock. *Austroboreas* includes *Lanipustula tolaensis* Lazarev, 1991 of upper Visean age, and eventually may have given rise to *Levipustula* of mainly Moscovian – Kasimovian age. The genera were not apparently forming a lineage of successive short-lived forms which were quickly replaced, but an overlapping complex of somewhat persistent genera that lasted until the end of the Early Permian Cisuralian Series. A feasible modification in postulating the evolutionary chain would be to posit *Absenticosta* → *Taboadaia* → *Lanipustula* → *Austroboreas* → *Levipustula*. That more or less accords with the succession in Argentina, except that *Lanipustula* is left out: the dating of first appearances of each generic strand is possibly not yet refined enough to firmly establish FAD, so that biological progression rather than tightly controlled stratigraphic succession becomes significant. But it will be noted that *Impiacus* Lazarev is omitted from the chain. In some respects this genus is close to *Lanipustula* in lacking lateral buttress plates and close-set rugae, and spines are relatively strong. Later Lazarev (2005a) suggested that *Impiacus* was ancestral to horridonians (Horridoniidae herein). Whether Lazarev wished to retain *Impiacus* as also close to *Levipustula* was not made clear. From available evidence, it is concluded that *Impiacus* was not ancestral to horridonians, differing in the nature of its spines, which have short elongate bases, and the lack of costellae, and other features.

Tribe **LEVIPUSTULINI** Lazarev, 1985

Fig. 2.7

[Nom. transl. Brunton, Lazarev & Grant in Brunton et al. 2000, p. 452 ex Levipustulinae Lazarev, 1985, p. 72].

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

Diagnosis: Elongate ventral spine bases, distinguished by presence of lateral buttress plates, and their descendents. Lower Carboniferous (Visean) to Lower Permian (Kungurian).

Genera: *Levipustula* Maxwell, *Austroboreas* new genus, *Piatnitzkya* Taboada.

Discussion: Members of this tribe are characterized by the possession of elongate ventral spine bases over the visceral disc, and by the possession of lateral buttress plates in the dorsal interior. The lateral buttress plates are unusual in that they often divert forward from long buttress plates, whereas lateral buttress plates in Araksalosiidae, Leioproductidae and Scacchinelloidea pass forward from the base of the cardinal process, without the intervention of buttress plates.

The dorsal median septum of *Piatnitzkya* from Argentina is cleft posteriorly and carries weak suggestions of lateral buttress plates, and the genus is discussed briefly by Waterhouse (2001, p. 22). Brunton et al. (2000, p. 453) had suggested that fine ribbing was present, counter to the actual material, but this is rejected by Dr A. C. Taboada (pers. comm.).

Genus ***Austroboreas*** new genus

Fig. 2.8

Derivation: auster – south wind, australis – southern; boreas – the north wind, Boreas – god of the north, Lat.

Type species: *Lanipustula kletsi* Taboada & Shi, 2011, p. 103 from the upper Las Salinas Formation (Moscovian) of Argentina, here designated.

Diagnosis: Medium-small with spines bearing elongate bases in quincunx over ventral disc, marginal spines erect, ventral ear spines slender; dorsal spines erect and mostly antero-lateral in distribution, with well defined pits, commarginal rugae and/or laminae moderately well developed. Lateral buttress plates well developed.

Discussion: This genus includes *Lanipustula patagonensis* Simanauskas, 1996, Fig. 3A-E from the Pampa de Tepuel Formation and lower Las Salinas Formation, of approximately upper Serpukhovian and Bashkirian age in Argentina.

The genus also includes several species that were previously referred to *Lanipustula* Klets, 1983, including

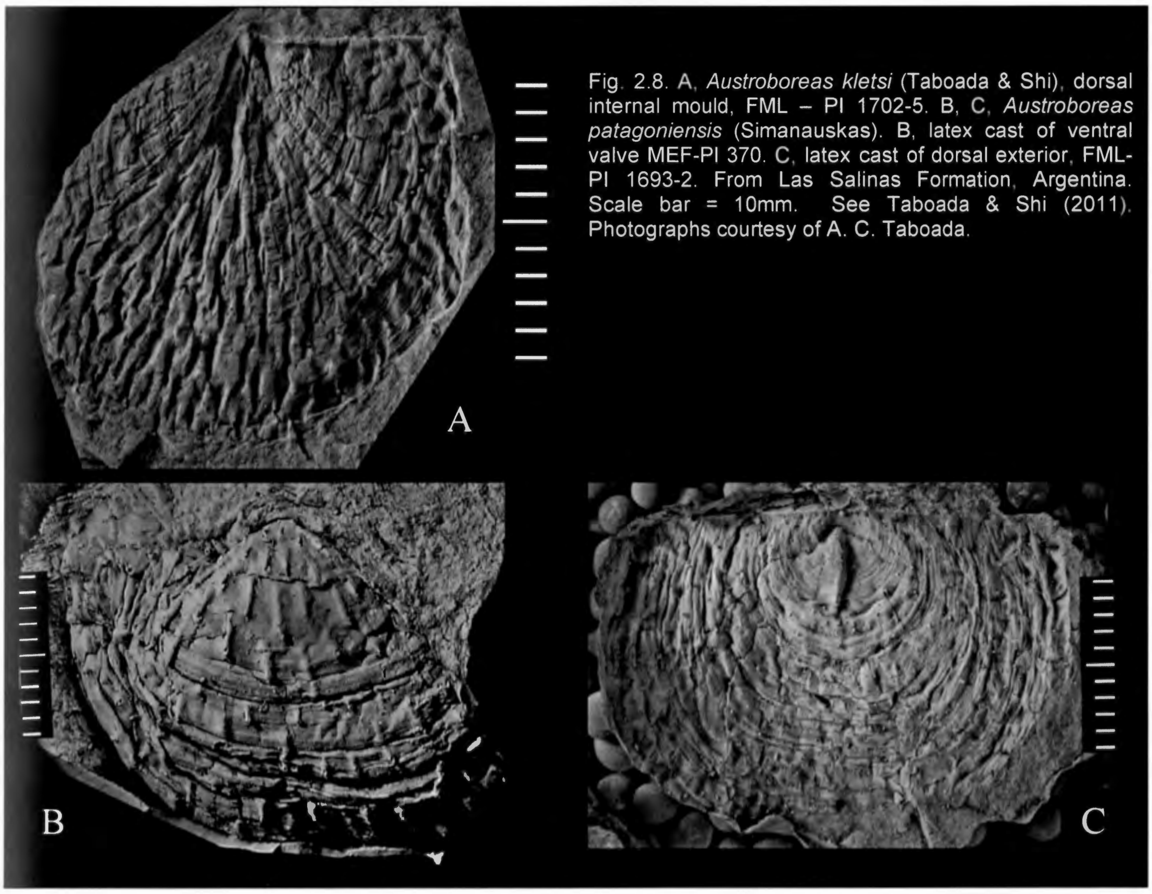


Fig. 2.8. A, *Austroboreas kletsi* (Taboada & Shi), dorsal internal mould, FML – PI 1702-5. B, C, *Austroboreas patagoniensis* (Simanauskas). B, latex cast of ventral valve MEF-PI 370. C, latex cast of dorsal exterior, FML-PI 1693-2. From Las Salinas Formation, Argentina. Scale bar = 10mm. See Taboada & Shi (2011). Photographs courtesy of A. C. Taboada.

species from the Carboniferous of Verchoyan, northeast Russia, Mongolia, and possibly Europe, as summarized by Taboada & Shi (2011, p. 99). The distinctions from *Levipustula* Maxwell that were ascribed to *Lanipustula* by Klets (1983), involving dorsal adductor scars and disposition of the posterior dorsal hinge ridge, have been discounted through extensive survey of material by Taboada (2006) and Taboada & Shi (2011), but the abundance of dorsal spines is much greater than in *Levipustula* (Brunton et al. 2000, p. 453) and commarginal rugae and/or lamination stronger than in *Levipustula* (Taboada & Shi 2011, p. 100). In these external attributes, these particular species strongly approach *Lanipustula* Klets, which is based on the upper Visean species *Pustula baicalensis* Maslennikov, 1960, p. 341 from Transbaikal, east Russia. This species is especially well figured by Klets (2005, pl. 8, fig. 1-9) from the Anomonan Suite (Serpukhovian, Bashkirian), and apart from specific differences, displays one critical difference, in that lateral buttress plates are not developed, a facet first pointed out by Lazarev (1991). Taboada & Shi (2011, pp. 94, 102) showed that *Lanipustula* Klets, 1983 was very close in many respects to *Levipustula* Maxwell, but lacked or at least had few dorsal spines (as was indeed noted for Australian specimens by Maxwell, 1951), and reassigned to *Lanipustula* various specimens from New South Wales, Australia, that had been described as type *Levipustula levis* by Muir-Wood & Cooper (1960), Muir-Wood (1965) and Brunton et al. (2000). Such specimens are now reallocated to *Austroboreas*.

Tribe **LANIPUSTULINI** new tribe

Fig. 2.9, Fig. 2.10

Name genus: *Lanipustula* Klets, 1983, p. 75 from Transbaikal (Bashkirian) of Russia, here designated.

Diagnosis: Shells externally and internally close to Levipustulini, but lack lateral buttress plates. Lower Carboniferous (Visean) to Upper Carboniferous (Bashkirian).

Genera: *Lanipustula* Klets, *Impiacus* Lazarev & Suur'suren (syn. *Nudymia* Lazarev), *Jakutoproductus* Kashirtsev, *Verchojania* Abramov.

Discussion: The relationship with Levipustulini is outlined in the preceeding text. *Lanipustula* appears to have buttress plates, apparently missing from *Impiacus*.

Fig. 2.9. *Jakutoproductus* sp., ventral valve BR 3052 from Member D (JBW 581), Jungle Creek Formation (Asselian), Yukon Territory, Canada, x2.5. JBW photo.

Genus *Impiacus* Lazarev, 1988

Impiacus Lazarus & Suur'suren in Afanasieva et al. (1988, p. 53) and refigured well in Rozanov (2003, pl. 46, fig. 7-9) from the upper Visean of Mongolia has been placed in Levipustulini, and has been deemed to have been the oldest genus in that tribe, though it has coarser wrinkles and ventral spines with only moderately elongate bases that tend to be in less regular quincunx. The dorsal posterior median septum is not divided in *Impiacus*, but is divided in *Absenticosta* (Lazarev 1991, pl. 4, fig. 6). *Impiacus* has cardinal ridges which may extend laterally as ear baffles. Knowledge of the type species of *Impiacus* is greatly enhanced by being synonymized with *Nudymia* Lazarev, 1990, based on *Bailliena nudymiensis* Sarytcheva (1977, p. 116, pl. 16, fig. 6, 7, pl. 17, fig. 1-3; Fig. 69, 70) from Magarsk beds of Lower Carboniferous age, in the Russian Arctic, as a much better illustrated and described form, thanks to the study by Sarytcheva (1977). The species *nudymiensis* has strong ventral spines in somewhat irregular quincunx and erect dorsal spines and dimples, remotely suggestive of *Levipustula*, with a single dorsal septum and ridge inside the inner ears (Sarytcheva 1977, pl. 16, fig. 6b, pl. 17, fig. 2b). Unlike either of these species, *Impiacus arateliensis* Lazarev, 1991, used as partial illustration for the genus by Brunton et al. (2000, Fig. 299.2d,e), and *Impiacus minutus* Lazarev, 1991 have fine rugae on both valves, more as in *Absenticosta* and members of Rugaurini, and Lazarev allowed that these early species were close to *Absenticosta* in their commarginal rugation. A minutely detailed appraisal of the spine patterns suggested to Lazarev that the early species were trending from *Absenticosta* towards *Impiacus*.

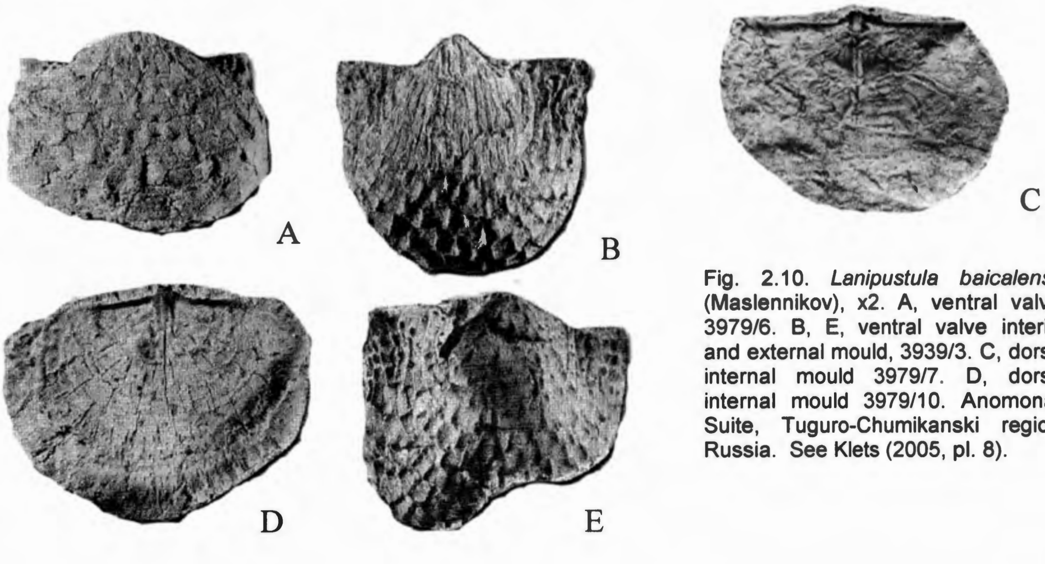


Fig. 2.10. *Lanipustula baicalensis* (Maslennikov), x2. A, ventral valve. 3979/6. B, E, ventral valve interior and external mould, 3939/3. C, dorsal internal mould 3979/7. D, dorsal internal mould 3979/10. Anomonan Suite, Tuguro-Chumikanski region, Russia. See Klets (2005, pl. 8).

Family **AVONIIDAE** Sarytcheva, 1960

[Avoniidae Sarytcheva, 1960, p. 226].

Diagnosis: Ornament dominated by spines, well spaced to close-set, especially on ventral valve, with bases swollen or prolonged, may be weakly aligned concentrically, low commarginal laminae and low or anterior ribs only as a rule. No teeth, sockets or interareas, adductor scars not dendritic, brachial ridges productiform.

Discussion: Avoniids appear to have evolved from productelliform shells, losing interareas, teeth and sockets, and reducing the size of the brachial shields. They retained a predominantly spinose ornament, but developed ribs to varying degree, the bases in some groups short and impersistent, in others becoming longer and more prominent. Although treated as a mere tribe by Brunton et al. (2000), the group is considered to incorporate those productiform tribes and subfamilies with commarginal lamination much less marked than in Overtoniidae. The prolonged spine bases over the ventral valve may suggest a source close to Helaspinae, but the low commarginal rugae of the earliest Avoniinae, coupled with the single dorsal septum, suggests that the family commenced from Dotswoodiinae, close to Overtoniidae, and unlike that family, reduced the ornament of commarginal rugae with more emphasis on spines and elongate bases, and introduction of more linear ornament and alveolus.

Subfamily **AVONIINAE** Sarytcheva, 1960

Fig. 2.11

[Nom. transl. Waterhouse 2002b, p. 9 ex Avoniidae Sarytcheva, 1960, p. 226].

Diagnosis: Well spaced subcommarginal 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, cardinal process pit as a rule, corpus cavity shallow to moderate in depth. Upper Devonian (Famennian) to Upper Permian (Changhsingian), possibly mid-Scythian.

Genera: *Avonia* Thomas, *Barunkhuraya* Lazarev, *Bulahdelia* Roberts, *Costavonia* new genus, *Lazarevonia* Waterhouse, *Onavia* Lazarev, *Quasiavonia* Brunton, ?*Sentosioides* Lazarev.

Discussion: Externally, genera come close to members of Productellinae, other than in the lack of interareas, teeth and strophalosiiform brachial ridges. *Avonia* and allies display much less concentric ornament than in Overtoniidae.

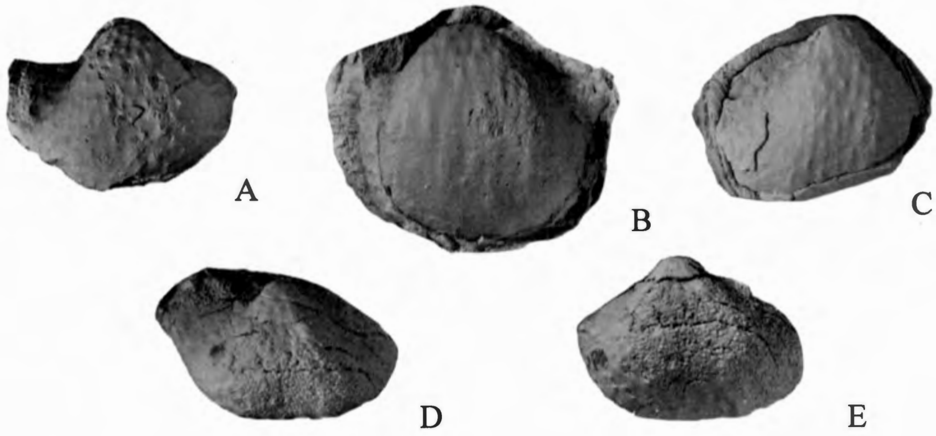


Fig. 2.11. *Lazarevonia arcuata* (Waterhouse). ventral valves. A, UQF 68814. B, holotype UQF 68815. C, UQF 68817. D, E, posterior ventral and ventral internal mould UQF 68819. From Pija Member (Changhsingian), Senja Formation, Nepal. x2. J. Coker & JBW photo. See Waterhouse (1978, pl. 6).

Sentosioides Lazarev in Lazarev & Suur'suren, 1992, p. 62 from faunas of Upper Devonian (upper Famennian) age in Russia and Asia shows elongate spine bases described as present on both valves, and figures of external moulds indicate that elongate dorsal dimples are characteristic, together with fine growth-lines. In many respects this genus appears to be of overtonioid appearance, rather than sentosiid (Echinoconchoidea, p. 185) as claimed by Brunton et al. (2000, p. 523), because anterior ventral spines have elongate bases, arranged in quincunx, certainly not as dense as in *Sentosia*.

Barunkhuraya Lazarev in Lazarev & Pushkin (1986) of upper Famennian (Upper Devonian) age from Mongolia also requires consideration. This genus was placed in Avoniini by Brunton et al. (2000, p. 433), and it developed a large cardinal pit. Its ventral spines are sublevipustulin, with elongate bases, and dorsal spines are lacking, and commarginals moderately well developed on both valves, unlike *Avonia* itself, and indeed somewhat reminiscent of the more regularly and closely developed rugae in Rugaurini. Unlike a number of levipustulin shells in Semiproductinae, *Barunkhuraya* does not have a split or double dorsal septum, and there are no lateral buttress plates. Its position is such that it somewhat approaches Levipustulinae in the nature of its elongate ventral disc spines, but otherwise appears to be avoniid, and the development of commarginal rugae must raise the question of whether the genus shared ancestry with Overtoniidae, and began a deviation that culminated in Avoniidae. In the nature of the ventral spines, *Barunkhurarya* appears to have been progenital to *Buhladelia* Roberts in Roberts et al. 1976, p. 213 of upper Visean age in New South Wales, Australia. The ventral spines of *Buhladelia* are regularly arranged, with slightly elongate bases. Dorsal spines are limited to lamellae over the anterior shell. The dorsal interior is avoniid, having a pit in front of the cardinal process and single dorsal septum, without the posterior double septum or lateral buttress plates of Levipustulini, although the shape, less transverse than normal for Levipustulini, was interpreted as levipustulin by Brunton et al. (2000, p. 453). The present interpretation signifies that Avoniidae shared common ancestry with Overtoniidae, arising from Devonian Productellidae such as *Dotswoodia* McKellar, 1970.

Genus **Costavonia** new genus

Fig. 2.12

Derivation: costa – rib, Lat., Avonia – brachiopod name.

Type species: *Productus minnewankensis* Shimer, 1926 p. 40, from Banff Formation (Tournaisian), western Canada, here designated.

Diagnosis: Subelongate shells, may be ornamented by strong ribs which increase through bifurcation and intercalation, erect ventral spines along hinge and array of spines curving forward along flanks, with a few spines towards lateral extremities; spines also over disc and trail. Scattered dorsal spines. Body cavity apparently deep, lateral ridges well developed and extending to about mid-length.

Description: Spines are numerous over the lateral slopes of the ventral valve. They are arranged in somewhat irregular commarginal rows, emerging from elongate bases and subprostrate on costae over disc, and tending to be more erect anteriorly. In the type species, ventral costae arise 2.5mm in front of the umbonal tip. The dorsal valve displays bifurcating costae, with dimples over ears, scattered fine erect spines, and deep corpus. Costae begin a little in front of the ventral umbo, which is ornamented mostly by fine spines and weak commarginals. The cardinal process is bilobed, with alveolus (Carter 1987, pl. 7, fig. 10-13), and the median dorsal septum arises in front, without slit. Lateral marginal ridges are well developed, with rim across ears, extending to mid-valve.

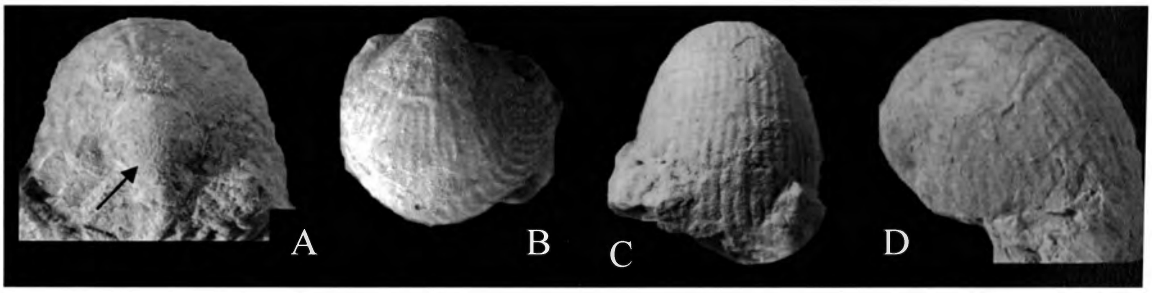


Fig. 2.12. *Costavonia minnewankensis* (Shimer). A, posterior view showing tiny spine bases near umbo, as arrowed, x5. B, C, D, posterior, anterior and lateral aspects. Specimen GSC 4551a, x3.5 approx., from Banff Formation (Tournaisian), Lake Minnewanka, Alberta, Canada. JBW photo.

Discussion: The type species is distinguished primarily by the numerous spines over the umbonal slopes, and it and some allied species also share strongly developed costae, which cover both valves and conspicuously bifurcate. A strong hinge ridge is developed in the dorsal valve, which suggests Semicostellinae, but on the other hand the elongate shape and dorsal alveolus are typical of Avoniinae. *Productus minnewankensis* Shimer was regarded as senior synonym of *Avonia linospinosa* Sutton, 1942, p. 466 from the Burlington Limestone (Tournaisian) of Illinois by Carter (1987, p. 31), but has slightly coarser costae and is more tumid, and *Avonia* sp. of Carter (1987, pl. 6, fig. 15-18) is similar. Carter (1987) also synonymized *A. minuta* Sutton, 1942 with *linospinosa*.

None of the other genera referred to Avoniinae or indeed Semicostellinae has such well formed costae, so that the genus is readily distinguished. There is a further and more significant distinction, in the nature of the band of erect spines developed on the lateral flanks of the ventral valve, these being more numerous than in *Avonia* or *Quasiavonia*, or other genera. Somewhat similar spines are developed in *Avonia canyonensis* Carter, 1987, p. 30, pl. 6, fig. 19-24 from the Banff Formation, and this species has much less well developed ribs. It belongs to *Costavonia*, even though the costation is less continuous and not as strong as in *C. linospinosa* and is more like characteristic Avoniinae. Some doubt pertains to the identity of the material from the St Joe Formation of Oklahoma, United States, that was ascribed to *minnewankensis* by Carter (1999, Fig. 2A-N), because there appear to be fewer spines over the lateral flanks of the ventral valve, and probably the material belongs to a different species, modified from *Costavonia* or some other genus.

Semicostella Muir-Wood & Cooper, 1960, p. 195 of Subfamily Semicostellinae Nalivkin has well developed ribs on long trails, as in *Costavonia*, and a deep corpus cavity. Marginal ridges are developed on both valves, and extend around the anterior dorsal valve, but the umbonal flank spines are not developed. The posterior dorsal septum is broad without split or alveolus, unlike the present genus.

In external appearance, the new genus approaches *Seminucella* Carter, 1987, but this genus lacks dorsal spines and has buttress plates and deep alveolus: it is classed as Lomatiphoridae. Carter (1999, p. 99) and Shi, Chen & Tong (2008, p. 292) referred the species *minnewankensis* Shimer as figured by Carter (1987) to *Breileenia* Brunton in Brunton & Lazarev, 1997, but there is little similarity, *minnewankensis* and associate species being much more vaulted, with different less branching ribs, and displaying numerous spines along the ventral umbonal slopes. *Breileenia* apparently belongs to Semicostellinae Nalivkin, although Brunton et al. (2000) preferred a relationship to the marginiferid *Desmoinesia*. *Spinocarinifera* Roberts, 1971 looks somewhat similar to the new genus, due its costae and numerous ventral spines, but lacks dorsal spines and differs internally, so that it is classed in Lomatiphoridae Roberts.

Subfamily **SEMICOSTELLINAE** Nalivkin, 1979

[Semicostellinae Nalivkin, 1979, p. 67. ?Syn. Breileeniini Brunton in Brunton & Lazarev, 1997, p. 389].

Diagnosis: Concentric rugae fine, subprominent, costae on long trails, often geniculate. The dorsal valves have discontinuous or anterior ribs and pits. Spines of moderate number on both valves in several genera, bases may be extended in ventral valve. Low to moderately developed hinge ridge and often marginal ridges may be present. No cardinal process pit or septal slit. Corpus cavity moderate to deep. Lower Carboniferous (Tournaisian – Serpukhovian).

Genera: *Semicostella* Muir-Wood & Cooper, ?*Breileenia* Brunton, *Cinctifera* Muir-Wood & Cooper, *Maemia* Lazarev, *Tuberculatella* Waterhouse, *Waggononia* new genus.

Discussion: This subfamily is very close to Avoniinae and some distinctions may seem slight or inconsistent. Some genera have a more transverse shape, and pits and ribs are more evident on the dorsal valve. Members have a thick corpus cavity, costae on long trails, and strong tendency to develop marginal ridges. Members of Semiproductinae also have a deep corpus cavity, but internal marginal structures are limited to the posterior dorsal ridge, and a split posterior dorsal septum is developed. Ornament of Semiproductinae tends to differ from that of Avoniinae, the latter being dominated by crowded ventral spines over disc and trail, but members of Avoniinae often have ribbed trails.

Although Brunton et al. (2000, p. 463) included *Limbifera* Brunton & Mundy of upper Visean age in Semicostellini, the posterior disc of this genus is reticulate, and spines few, with a well developed row along the ventral hinge. The ventral muscle field is elevated and the genus is transferred to the aulostegoid tribe Institellini. *Spinosteges* Liang was also included in Semicostellini by Brunton et al. (2000, p. 464), but has an apparently geniculate ventral valve and strong commarginal rugae reminiscent of *Limbifera,* and so is also classed as a member of Institellini (p. 287).

Genus *Waggononia* new genus

Fig. 2.13

Derivation: Named from Waggon Creek, source of the fossils.

Type species: *Protoniella? waggonensis* Roberts, 1971, p. 116 from unnamed breccia (Tournaisian), Bonaparte Gulf, northwest Australia, here designated.

Diagnosis: Small moderately arched ventral valve, ventral spines numerous, especially prominent over inner ears, only feebly arranged in concentric rows, arise from short bases over much of shell medianly, and from rib-like swellings anteriorly. Dorsal valve with weak ribs, low commarginal rugae over disc, and spines. Dorsal valve with hinge ridge, long septum, no lateral or anterior marginal ridges, but weak lateral mounds, no alveolus or septal slit, more or less smooth adductor scars.

Discussion: The type species was described by Roberts (1971, p. 116, pl. 26, fig. 1-24, text-fig. 25) from the Bonaparte Gulf of Australia. It was assigned with a query to *Protoniella* Bell, 1929 from Nova Scotia, but ribs are much more prominent in Bell's genus, and dorsal spines are absent, and there are two to four rows of larger spines on the posterior lateral extremities, with further differences in shape. Roberts (1971, p. 115) prepared a topotype of *Protoniella*, as figured by Bell (1929, pl. 15, fig. 12), to clarify the nature of the cardinal process, and concluded that Bell's genus was overtoniid, although aspects of the overall appearance do not agree, given the nature of the ribs and spines which form a row along the hinge and along the umbonal slopes, and in view of the presence of a dorsal marginal ridge along the hinge and across the ears, according to Muir-Wood & Cooper (1960, p. 265). The genus *Protoniella* is here assigned to Retariidae (p. 120).

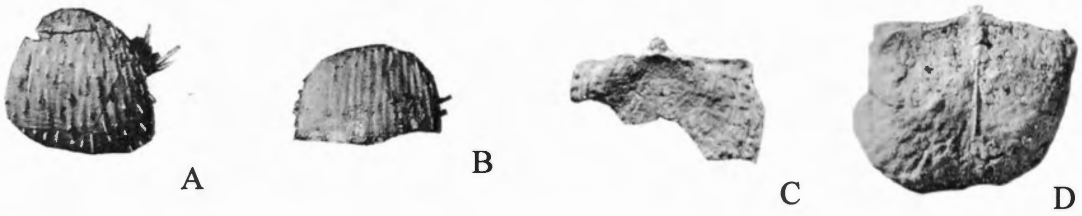


Fig. 2.13. *Waggononia waggonensis* (Roberts). A, anterior of dorsal valve CPC 8597, x1. B, anterior view of holotype CPC 8588, x1. C, external view of dorsal valve CPC 8594, x2. D, interior view of dorsal valve CPC 8595, x2. From unnamed Tournaisian breccia, Bonaparte Gulf, Australia. See Roberts (1971).

The species *waggonensis* is not overtoniid, in that the spines are not arranged in marked concentric rows, and anterior ribbing is developed on the ventral valve, and weakly over the dorsal valve, with low commarginal rugae. In such respects, the species comes close to *Semicostella* Muir-Wood & Cooper, 1960, recorded widely from the Lower Carboniferous of North America and Asia. This genus has similar but firmer anterior ventral ribs, weaker dorsal ribs, and lower commarginal dorsal rugae, and although spinose over both valves, lacks strong postero-lateral spines. Internally there is a comparable cardinal process, and anterior platform which gives off two broad short ridges, mirrored occasionally in the new genus (Roberts 1971, pl. 26, fig. 17), but often absent, more or less smooth adductors, and sturdy hinge ridge. A marginal flange is well developed around the visceral disc of *Semicostella* (see Muir-Wood & Cooper 1960, pl. 62, fig. 6, 10, 11), unlike the dorsal interior of the present form, and an anterior cincture is developed in the ventral valve of *Semicostella*.

Genus *Breileenia* Brunton, 1997

Genus *Breileenia* Brunton, of upper Tournaisian to upper Serpukhovian age, was separated as Tribe Breileeniini by Brunton in Brunton & Lazarev, 1997. Ribs arise over the corpus, and spines lie on both valves, including the ventral hinge, and ventrally have elongate bases posteriorly. Low concentric growth pauses or lamellae are present. *Breileenia* was linked with marginiferids *Desmoinesia* Hoare, 1960 and *Sandia* Sutherland & Harlow, 1973 by Brunton et al. (2000, p. 440), and with *Desmoinesia* by Brunton & Lazarev (1997), but given the paucity of data on the interior of *Breileenia*, the link is speculative, and it was claimed that *Breileenia* was like "ribbed Avoniini," although in fact members of Avoniinae are more vaulted. There is considerable approach to the contemporaneous Visean genus *Cinctifera* Muir-Wood & Cooper, 1960, classed as Semicostellinae McKellar, but *Cinctifera* has a flatter dorsal valve. The position of *Breileenia* remains uncertain, requiring further clarification of the internal morphology, and even the report of the genus from Pennsylvanian faunas of the Geumcheon-Jangseong Formation of Korea by Lee et al. (2010, Fig. 4.1-5) has added no further information. The elongate spine-bases or short ribs also somewhat approach features of *Sentosioides* Lazarev in Lazarev & Suur'suren, 1992 of Famennian age in Mongolia, allowing for some uncertainty because the posterior ornament of *Sentosioides* was not figured, and both genera have a high postero-lateral dorsal ridge. Further comparison is provided on p. 102.

Genus ***Maemia*** Lazarev, 1997 and ***Tuberculatella*** Waterhouse, 1982b

Fig. 2.14, Fig. 2.15

Fig. 2. 14. *Tuberculatella tubertella* Waterhouse, external mould of dorsal valve TBR 584, reregistered as BR 3012, from Huai Bun Nak , Khao Luak Formation (Moscovian), Thailand, x4. See also Waterhouse (1982b, Fig. 2.6). Note slightly larger size of spines over outer ears.

Genus *Maemia* Lazarev, in Brunton & Lazarev, 1997 of Bashkirian – lower Moscovian age was named for small shells from Cape Chayka, Yugorsky Peninsula, in the Barents Sea at the northern extremity of the Ural Mountains (not Mongolia as in Brunton et al. 2000, p. 463), with spines and elongate tubercles over both valves, low radial ribs over anterior ventral valve, low concentric lamellae or rugae, very weak marginal ridges and ear baffles, and comparatively thick body corpus. Although the genus shares a number of attributes with species of Tournaisian age assigned to *Avonia* by Sarytcheva et al. (1963, pl. 14), it was classed in Semicostellini Nalivkin by Brunton et al. (2000, p. 463). *Maemia* is particularly close to *Tuberculatella* Waterhouse, 1982b of Late Carboniferous (Moscovian) to Lower Permian (Asselian) age. This was named for small medium-sized shells, with ventral ornament of well spaced large more or less elongate tubercles each bearing a spine, dorsal spines arising from tubercles or between dimples, concentric lamellae moderately developed, and short irregular radial ridges anteriorly on the ventral valve. The genus is widely distributed, from Asia, Canada, Argentina and Spain. The adductor scars are smooth in both valves, and the floor of the valve is densely covered by sharply pointed pustules, of two orders in the dorsal valve. There is a very weak marginal ridge, and short bifid cardinal process, and simple median dorsal septum, without obvious alveolus. Unfortunately the genus was omitted from the *Revised Brachiopod Treatise* by Brunton et al. (2000), and eventually acknowledged by Brunton (2007, p. 2641): no note of the genus was made by Lazarev in Brunton & Lazarev (1997). The species *Maemia gelida* Carter & Poletaev (1998, p. 127) from an Atokan fauna on Ellesmere Island, Canada, is very like *Tuberculatella,* as far as it has been described and illustrated, and shows no regular radial ribs on the ventral valve, but only irregular low and short radial riblets. *Maemia archboldi* Martínez Chacón & Winkler Prins (2008, Fig. 2) from a Bashkirian fauna of north Spain has ventral spine bases slightly shorter than those of *Tuberculatella tubertella* Waterhouse, the type species, and clearly belongs to *Tuberculatella. Maemia* may be confused with *Tuberculatella.* The type species of *Tuberculatella* has irregular long radial swellings anteriorly, and although they are less regular than in type *Maemia*, they suggest a position intermediate between type *Maemia* and *M. gelida*, suggesting that there was an irregular cline of species that varied in the development of anterior costae, within one genus, but the dorsal adductor scars in *Maemia* bear high rims, not seen in *Tuberculatella*. In

Tuberculatella, the dorsal spines arise from pustules between dimples, much it seems as in In *Maemia*. In *Tuberculatella*, the internal pustules are both dense, and in two grades, fine and dense, better spaced and coarser. The arrangement is, so far, obscure for type *Maemia*. *Maemia* appears to be a close ally of *Tuberculatella*, distinguished by its adductoral rims.

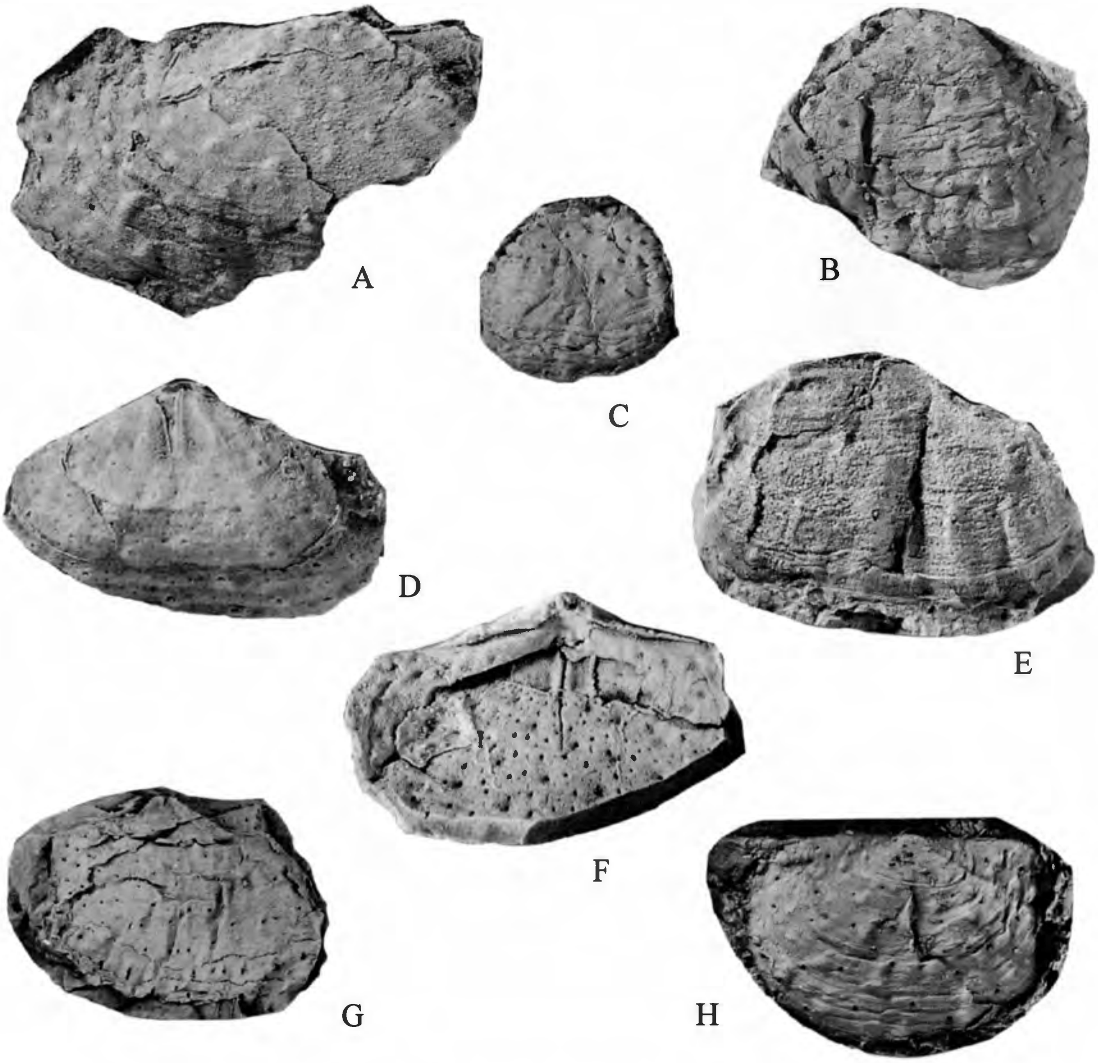


Fig. 2.15. *Tuberculatella tubertella* Waterhouse. A, dorsal external mould of holotype, TBR 579, x3. B, latex cast of ventral valve TBR 580, x2. C, latex cast of anterior ventral valve TBR 583, x 1. D, F, ventral and dorsal aspects of internal mould TBR 579, holotype, x2. E, ventral internal mould, TBR 581, x2. G, dorsal external mould TBR 585, x2. H, dorsal external mould TBR 584, reregistered as BR 3012, x2. From Huai Bun Nak, Loei, north Thailand. Khao Luak Formation (Moscovian). See Waterhouse (1982b). J. Coker & JBW photo.

A question remains about the affinities of *Tuberculatella*. Brunton (2007) referred the genus to Lethamiini Waterhouse, and there is considerable approach, although spines are spaced further apart and ventral spine bases more swollen. A comparison of the different examples figured as Lethamiini by Brunton (2007, Fig. 1754) shows that *Tuberculatella* differs considerably in appearance, with much coarser and fewer ventral spines and low discontinuous radial ribs, and different internal pustulation. Waterhouse (2002b, p. 9) referred the genus to Avoniini Sarytcheva, based on external appearance, but the lack of an alveolus, just as in *Maemia*, points to a position within Semicostellinae, which is characterized in part by the lack of an alveolus. Several genera in Semicostellinae have stronger ribbing, but at the immature stage, specimens are close in appearance to *Maemia* and *Tuberculatella*.

3. Superfamily **HORRIDONIOIDEA** Muir-Wood & Cooper, 1960 (Table 4)

Fig. 5.51, pp. 172-173

[Nom. transl. Waterhouse 2002b, p. 16 ex Horridoniinae Muir-Wood & Cooper, 1960, p. 292].

Diagnosis: Ornament characteristic, with minor radial and concentric ornament, spines few to moderately numerous and well spaced, may be specialized and very stout along the hinge, on ventral, dorsal or both valves, may be aligned along ventral mid-line. Corpus cavity generally but not always thick. Trail well developed in younger forms and may be geniculate. Fine numerous pustules internally, no heavy marginal ridges.

Discussion: Of minor significance numerically, this group formed an independent lineage that commenced in Devonian time with strophalosiiform genera bearing teeth, and lasted until Upper Permian. Given the comparatively smooth or finely pustular inner shell and somewhat organized distribution of ventral spines in Leioproductidae, which appeared first in Late Devonian (upper Famennian) faunas, Horridonioidea probably sourced from Tribe Ardviscini, Subfamily Helaspinae, found in faunas of Early (Emsian) and Middle (Givetian) Devonian age.

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

- **Family Leioproductidae Muir-Wood & Cooper, 1960**
  - Subfamily Leioproductinae Muir-Wood & Cooper, 1960
    - Tribe Leioproductini Muir-Wood & Cooper, 1960
      - Subtribe Leioproductinai Muir-Wood & Cooper, 1960
      - Subtribe Costadoniinai new subtribe
    - Tribe Hunanoproductini Liang, 1990
  - Subfamily Levitusiinae Muir-Wood & Cooper, 1960
    - Tribe Levitusiini Muir-Wood & Cooper, 1960
    - Tribe Geniculiferini Waterhouse, 2002b
    - Tribe Araxilevini Waterhouse, 2002b

- **Family Horridoniidae Muir-Wood & Cooper, 1960**
  - Subfamily Horridoniinae Muir-Wood & Cooper, 1960
  - Subfamily Baillieninae new subfamily
  - Subfamily Sowerbininae Lazarev, 2005b
    - Tribe Sowerbiniini Lazarev, 2005b
    - Tribe Karnelliini new tribe

Table 5. Superfamily Horridonioidea Muir-Wood & Cooper, 1960.

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, not at beak, scattered ventral spines, posterior spines may lie in row along or inclined from hinge but often absent, dorsal spines as a rule absent. Cardinal process usually bilobed, with pit or groove in front in some genera, dorsal hinge ridge may be developed.

Discussion: Biernat & Lazarev (1988, Fig. 1) derived Leioproductidae from *Ardiviscus*, evolved in turn from *Productella*. *Ardviscus* is here classed as Ardviscini in Productellinae, and endorsed as ancestral stock for Leioproductidae.

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

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

Diagnosis: Concentric wrinkles weak or absent, shells small.

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, commarginal rugae weak or absent, scattered ventral spines; lateral buttress plates.

Discussion: The ventral median fold with line of spines on the ventral valve is an unusual feature for Productidina, and is developed in several of the genera that were incorporated within Leioproductini by Brunton et al. (2000).

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

[Nom. transl. hic ex Leioproductinae Muir-Wood & Cooper, 1960, p. 168].

Diagnosis: Dorsal median septum may be posteriorly cleft, lateral buttress supports. Upper Devonian (Famennian) to Lower Carboniferous (Tournaisian).

Genera: *Leioproductus* Stainbrook, *Bispinoproductus* Stainbrook, *Engasia* new genus.

Discussion: There is a split septum and cardinal process supports in *Leioproductus* (Muir-Wood & Cooper 1960, pl. 40, fig. 8, 10 - 12), and productiform brachial shields, and the supports are independent of the brachial shields. The cardinal process is sessile and bilobed, and may be posteriorly joined by a short median lobe. Each lateral lobe may be notched on the posterior face, and the external face is bilobate or quadrilobate (see Brunton et al. 2000, Fig. 321.1f). *Bispinoproductus* Stainbrook, 1947 has split dorsal septum and lateral buttress plates.

Stelckia Crickmay, 1963 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, but apart from the median row of ventral spines, the ornament is not like that of any horridonioid. The allied genus *Dotswoodia* McKellar is of upper Devonian (Famennian) age, and both *Dotswoodia* and *Stelckia* seem more likely to have been ancestral to finely rugose plicatiferins such as Semiproductini and Rugaurini.

Genus ***Engasia*** new genus

Fig. 3.1

Derivation: Named from Enga Ridge, source of the fossils.

Type species: *Magnumbonella prolata* Roberts, 1971, p. 112 from Enga Formation (Tournaisian), Bonaparte Gulf, Australia, here designated.

Diagnosis: Average size for tribe, narrow and inflated with incurved ventral umbo, median ventral ridge with bordering grooves somewhat variable in development, ventral spines scattered and moderately numerous and fine, not forming well defined hinge row or median row; dorsal valve with fine commarginal rugae over disc, no dorsal median ridge, no row of median spines. Median dorsal septum broad without groove posteriorly, posterior adductor scars strongly dendritic; weak lateral buttress plates.

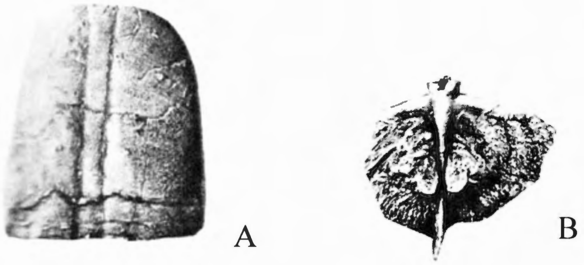


Fig. 3.1. *Engasia prolata* (Roberts). A, anterior view of ventral valve CPC 8501, x1. B, dorsal interior, CPC 8503, x2. From Enga Sandstone, (Tournaisian), Bonaparte Gulf, Australia. See Roberts (1971).

Resemblances: Externally, *Engasia* is close to *Leioproductus* Stainbrook, 1947, based on *L. plicatus* (Kindle) of uppermost Famennian age in New Mexico, a genus which consistently has a more persistent median plication along both ventral and dorsal valve, and somewhat coarser and more regularly spaced ventral spines, including a median row and a further row near the hinge. Low dorsal rugae are present, much as in the new form. The median dorsal septum of *Leioproductus* carries a well defined slit, and there are low lateral buttress plates, and weak striae or dendritic markings over the posterior dorsal adductors, whereas the median dorsal septum of the new genus is like that of *Costadonia* (see below) in lacking a septal slit: there is therefore tension as to whether tribal allegiances are better indicated by external appearance, or by the dorsal interior. But the cardinal process of *Engasia* is like that of *Leioproductus*, and was well figured in Roberts (1971, pl. 25, fig. 14-17), and lateral buttress plates are suggested in Roberts (1971, pl. 25, fig. 16). Roberts (1971, p. 91) compared *prolata* with *Leioproductus buttonensis* Roberts, 1971 from the Button Beds in the same region of Australia, noting that *buttonensis* had a divided median septum and a row of spines along the ventral flanks.

Roberts (1971) referred the species *prolata* to *Magnumbonella* Carter, 1968, p. 1145 from the Lower Carboniferous of central North America. But unlike *Engasia*, *Magnumbonella* shows no sign of a median ventral plication, and commarginal rugae are more evident across the ventral umbonal region. There is a row of spines near the ventral hinge, and muscle scars are not as strongly developed, with further differences enumerated by Roberts (1971, p. 114), not that all are of generic significance. Otherwise the two are close in shape and size and share a comparable dorsal interior.

Bispinoproductus Stainbrook, 1947 of similar age has finer and more numerous spines than in *Leioproductus* or the new genus, and dimples are numerous as well as rugae on the dorsal valve. The median ridges in the ventral and dorsal valves, the ventral ridge with prominent spines as a rule, and the slit dorsal septum and low lateral buttress plates are present as in *Leioproductus.*

Ardviscus Lazarev in Lazarev & Pushkin, 1986 of lower Famennian age has teeth and no cardinal process pit. A low median ventral ridge is present and spines are slightly coarser than in the new genus. From the upper Famennian of England, *Mesoplica* Reed, 1943 is narrow with a swollen ventral valve and no slit septum, and shows incipient ribbing either anteriorly or over much of the ventral valve. It has a low median fold in the ventral valve, and thicker spines. Stronger ribbing is developed in *Costadonia* new genus, so that these two genera differ externally from *Engasia*, yet share a somewhat similar posterior dorsal septum, without septal slit.

Subtribe **COSTADONIINAI** new subtribe

Name genus: *Costadonia* new genus from Myrtlevale Formation (Famennian), Burdekin Basin, Queensland, Australia, here designated.

Diagnosis: Dorsal median septum simple, without cleft, no lateral buttress supports. Upper Devonian (Famennian) to Lower Carboniferous (Tournaisian).

Genera: *Costadonia* new genus, *Mesoplica* Reed.

Discussion: The large and simple spines and comparatively smooth shell strongly suggest derivation from *Ardviscus* and allies in Tribe Ardviscini, Subfamily Helaspinae. *Ardviscus* Lazarev in Lazarev & Pushkin, 1986, of lower Famennian age, has a low median ventral ridge and teeth and sockets, and there is no cardinal process pit, although one has been reported but not clearly illustrated for the allied genus *Productelloides* Kotlyar. *Mesoplica* Reed, 1943 shows no lateral buttress plates and a simple septum, even though it has a median ventral fold. This genus has short to long ribs and spine bases over the ventral valve and pits over the dorsal valve.

Genus ***Costadonia*** new genus

Fig. 3.2

Derivation: costa – rib, Lat.

Type species: *Mesoplica*? *hillae* McKellar, 1970, p. 23 from Myrtlevale Formation (Famennian), Burdekin Basin, Queensland, Australia, here designated. See Appendix A, Part A, p. 477.

Diagnosis: Small, transverse, ornamented by strong costae in front of umbones, with weak commarginal rugae. Rare hinge and inner ear spines on the ventral valve, further spines along the mid-line and over costae, no dorsal spines, dorsal pits. Bifid cardinal process, deep alveolus, short hinge ridges and short dorsal median septum.

Discussion: This genus, based on a species described by McKellar (1970, pl. 7, fig. 14-26) from the Famennian *Sentosia* (now *Spinauricula*) *profunda, minuta* and *transversa* Zones of the Burdekin Basin in Queensland, is judged to be leioproductin, judged from spine pattern and interior, a position moderately close to that assigned by McKellar (1970), who pointed out the similarity to *Mesoplica* Reed from the Upper Devonian of Scotland. There are ventral spines in a row along the hinge, a small cluster on the posterior flanks and inner ears, a row along the mid-line, and scattered and small and erect spines over the costae and rugae. There are no dorsal spines, but shallow pits are present. The dominant ornament is provided by costae which arise in front of posterior smooth shell on both valves, and there are suggestions of a low ventral median ridge on some specimens, made up of one or two costae and in some bearing large anterior spines. The cardinal process is low and bifid with well formed alveolus, and median septum extending to approximately mid-length. There is no median slit, and no lateral buttress plates. A low hinge ridge extends each side of the cardinal process, not for the full length of the hinge. A degree of transitionality is indicated by the presence of dental sockets in a very few dorsal valves. Another species, as yet unnamed, was recorded by McKellar (1970, p. 25) from the Yarrol Basin of Queensland. This form has more numerous and persistent ribbing, and somewhat approaches *Mesoplica variplicata* Martynova (1970, pl. 3, fig. 7, 8) from the

Famennian Munar beds of central Kazakhstan. A second Queensland species assigned to *Mesoplica*? by McKellar (1970, p. 25) is assigned to a different genus, *Dawesionia* new genus (see p. 411).

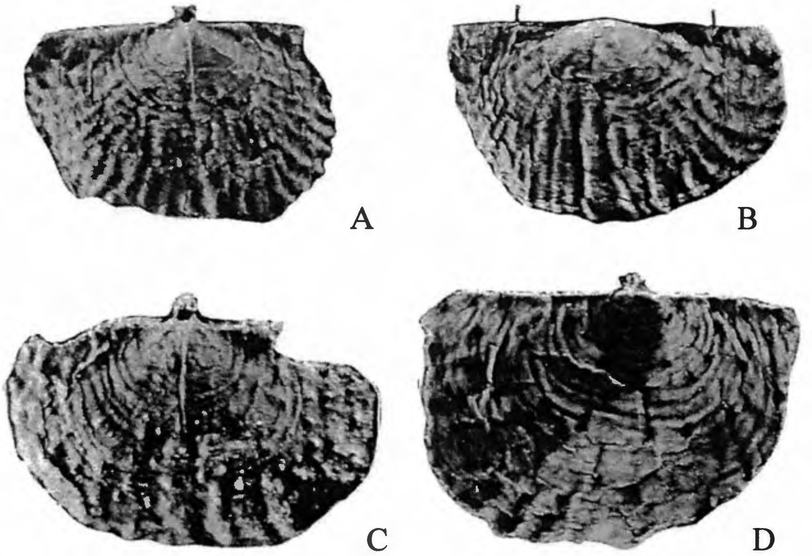


Fig. 3.2. *Costadonia hillae* (McKellar). A, holotype, dorsal interior, latex cast, GSQ F 11511, x2. B, dorsal valve exterior latex mould with ventral spines, GSQ F 11508, x 2. C, latex cast, dorsal interior, GSQ F 11509, x3. D, latex cast of dorsal exterior, GSQ F 11513, x3. From Myrtlevale Formation (Famennian), Queensland, Australia. See McKellar (1970, pl. 7).

Mesoplica Reed, 1943, p. 97, initially described from the Upper Devonian of Devonshire, England, is moderately close, with higher ventral median ridge, lower ventral costae, and dorsal pits, and without conspicuous dorsal costae. Ventral spines were described by Muir-Wood & Cooper (1960, p. 175) as forming a group on the ears, a row along the median ridge, a single spine on each flank, and small spines emerging from costae and from rugae over the visceral disc. The dorsal valve bears a row of spines close to the hinge. Although there is considerable difference in appearance and spination, the dorsal interior is comparable in the two genera, with hinge ridge and single median septum, but no alveolus in *Mesoplica*.

Tribe **HUNANOPRODUCTINI** Liang, 1990

[Nom. transl. Waterhouse 2002b, p. 17 ex Hunanoproductinae Liang, 1990, p. 197 (465)].

Diagnosis: Shells smooth, or with gentle sulcus, no median ventral fold, lacking pronounced concentric wrinkles, ventral spines variously in row along hinge or scattered and well spaced, no median row, dorsal spines rarely present, lateral buttress plates in at least two of three genera. Upper Devonian (Famennian) to Lower Carboniferous (Tournaisian).

Genera: *Hunanoproductus* Hou Hong-Fei, *Galeatella* Muir-Wood & Cooper, *Kavesia* Lazarev.

Discussion: This is a small assemblage of diverse but simple leioproductiform genera, which are allied to *Leioproductus*, but lack the median ventral fold and spine row, and also lack commarginal rugae. The cardinal process where known is like that of *Leioproductus*, with median lobe. The nominate genus *Hunanoproductus* Hou Hong-fei, 1965 has ventral spines along the hinge. In a specimen registered as BB 61924 at the Natural History Museum, London, England, a row of large spines lies along the ventral hinge, and fine commarginal lirae and growth increments are developed. *Kavesia* Lazarev in Lazarev & Simakov, 1987, of very late Devonian and early Carboniferous age, has low irregular commarginal rugae, row of hinge spines and other fine scattered ventral spines, and no median ventral ridge. There is no cardinal process pit. *Kavesia* and *Galeatella* Muir-Wood & Cooper, 1960 have lateral buttress supports as in Leioproductini, and in *Galeatella* Muir-Wood & Cooper, 1960, the supports form the inner posterior part of exceptional posteriorly placed brachial shields. Teeth are not known in any of the genera. Because the interior of *Hunanoproductus* is not known, interpretation of the genus and contingent tribe must remain speculative to a degree.

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

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

Diagnosis: Shells of medium to large size, ventral spines scattered or in quincunx, row of spines along the hinge in only some forms, commarginal wrinkles prominent and regular. Cardinal process large, trilobate to quadrilobate. No slit in dorsal septum, no lateral buttress plates.

Discussion: The subfamily is close to Leioproductinae, but shells are larger and more typically productiform, and have regular commarginal rugae and long trails, and no lateral buttress plates, unlke various Leioproductinae. Whereas Muir-Wood & Cooper (1960) placed Levitusiinae as a member of Dictyoclostidae, Brunton & Mundy (1993, p. 109) regarded Levitusiinae as a subfamily of Plicatiferidae, and were followed by Brunton et al. (2000, p. 453), treating it as a tribe together with Levipustulini, which is here judged to belong to Plicatiferinae. Leioproductini Muir-Wood & Cooper (1960) was separated by Brunton et al. (2000) as a unit in Productidae. Yet spine patterns, median rib, and commarginal ornament of Leioproductini and Levitusiinae are close, and members of the genera *Admodorugosus* Brunton & Mundy, 1993 and *Acanthoplecta* Muir-Wood & Cooper, 1960 are similar in many respects to both *Levitusia* Muir-Wood & Cooper and *Leioproductus* Stainbrook. All lack the strong dorsal marginal ridges or ear baffles of *Plicatifera,* and may have a median ventral spine row.

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

Fig. 3.3

[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), but that was incorrect.

Diagnosis: Genera of relatively large size with regular commarginal wrinkles at least over disc, moderate to deep body corpus, no radial ribs or striae, spines sparse, usually thin, spine row on median ridge as a rule, also spine row in front of ears, and suggested along or inclined from hinge, dorsal spines absent or rare. Weak cardinal ridges, no lateral buttress plates or cardinal pit or septal slit. Lower Carboniferous (Tournaisian – upper Visean).

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

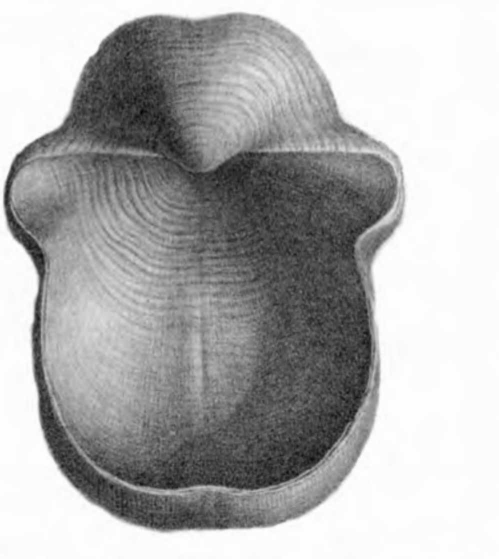


Fig. 3.3. *Levitusia sublaevis* (de Koninck), ventral valve as figured by Davidson (1861, pl. 31, fig. 2) from Carboniferous of Clitheroe, Lancashire, England, x1.

Discussion*:* *Admodorugosus* and *Kadraliproductus* have well defined commarginal wrinkles, median ventral ridge, and scattered ventral spines as in *Levitusia*. The ventral median fold and/or median row of ventral spines are shared with *Leioproductus*, which is regarded as closely allied. Whilst it may be true that the ventral fold and ventral spine row and rugae are somewhat evanescent features in populations and in allied species (Lazarev 1992), even so they 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*. The cardinal process is large, developed from that of Leioproductinae with median shaft developed and divided at the posterior end. The genera have lost the lateral buttress plates and any slit of the median dorsal septum, and are much larger than members of Leioproductinae. Teeth are not known in any of the genera within Levitusiini.

Levistusia is much larger than constituents of Leioproductinae, often exceeding 70mm in length, but is similar in having well spaced spines, without displaying prominent hinge spines, and ornamented by characteristic very fine lirae as figured by Brunton et. al. (2000, fig. 302G). Internal features include small brachial shields, large cardinal process and dendritic dorsal adductor scars, as well illustrated by Muir-Wood & Cooper (1960). The trail is well developed, and *Acanthoplecta* Muir-Wood & Cooper may have a gutter. Unlike other genera, *Kadraliproductus* Galitskaya has low radial ribbing.

Tribe **GENICULIFERINI** Waterhouse, 2002b

Fig. 3.4

[Geniculiferini Waterhouse, 2002b, p. 18].

Diagnosis: Small arched shells, wide hinge, low regular concentric wrinkles and lamellae, spines well distributed over ventral valve, no median ventral fold or sulcus, no median row of spines or hinge spines but spines may appear at cardinal extremities of ventral valve, dorsal spines often present; no marginal ridges or lateral buttress plates, low hinge ridges. Lower Carboniferous (Tournaisian – Visean).

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

Fig. 3.4. *Geniculifera boonensis* (Branson), ventral posterior aspect of USNM 124017, x2. From Caballeo Formation (Mississippian), United States. See Muir-Wood & Cooper (1960).

Discussion: These shells are small and lack cardinal pit, septal slit, or lateral buttress plates, and display low regular and well spaced commarginal rugae. There are a small number of ventral spines near the hinge, scattered prostrate spines over the ventral disc, and fine dorsal spines. The cardinal process is bilobed in *Geniculifera* and *Spinorugifera*. These two genera were included by Brunton et al. (2000, pp. 456ff) in Levitusiini, and have somewhat comparable spines and internal dense pustules, but show less emphasized comarginal 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 Avoniinae, 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 association grouped as Hunanoproductini in the presence of commarginal rugae. Cardinal supports are lacking from *Magnumbonella, Spinorugifera* and *Geniculifera*, and internal pustulation is dense at least in *Geniculifera*. *Magnumbonella* has rare dorsal spines, low rugae, and no pit in front of the cardinal process.

This group of shells appears to have been forerunner of Horridoniidae. The cardinal process is simpler than in Levitusiini, believed to reflect the difference in size, but the low rugae and lack of lateral buttress plates suggest a close relationship.

Tribe **ARAXILEVINI** Waterhouse, 2002b

Fig. 3.5, Fig. 3.6

[Araxilevini Waterhouse, 2002b, p. 18].

Diagnosis: Little or no radial ornament, shells may have subdued but distinct concentric wrinkles, no median ridge or spine row, ventral spines fine and numerous, disposed in quincunx over disc, usually in row diverging from hinge, scattered on trail, rarely clustered on ears. No dorsal spines. Upper Permian (Wuchiapingian – Changhsingian).

Genus: *Araxilevis* Sarytcheva, *Howesia* Logan

Discussion: *Araxilevis*, found in Djulfian (ie. Wuchiapingian) faunas of Armenia and Iran (Stepanov et al. 1969), was referred to Levitusiinae by Sarytcheva (1965) as repeated in Akopyarna (1974), and the genus is distinguished by the numerous and fine ventral spines organized in a regular pattern, without any median row, and without strong spines along the hinge of either valve. There are short numerous trails and fine dense pustules internally. Commarginal wrinkles are low but regular, and decorticated shell indicates radial striae. This led Brunton et al. (2000) to suggest a position with the productoid Tyloplectinae, but *Tyloplecta* has no ear spines other than in a row along the hinge. The lectotype of the type species of *Araxilevis*, *A. intermedius* (Abich) as figured by Sarytcheva (1965, pl. 36, fig. 4) has moderately dense spines over the ventral ears, lateral flanks and venter, with faint radial lirae. On another figured specimen (Sarytcheva 1965, pl. 36, fig. 1), spines are spaced further apart and lie also in quincunx over most of the valve, and there is a hinge row and row in front over the ears: the other figured ventral valve (Sarytcheva 1965, pl. 35, fig. 4) is somewhat similar. So is the specimen BR 3022 as figured herein (Fig. 3.5, Fig. 3.6), with a row of spines along the hinge and an oblique row of spines in front, crossing the ears. Two rows lie over the umbonal flanks, and spines are numerous over the outer ears. Internally the dorsal septum may be split, and the dorsal adductors are relatively small and not raised on a platform.

The Zechstein *Horridonia geranus* Eisel, 1909 may be congeneric, depending on the nature of its dorsal spines.

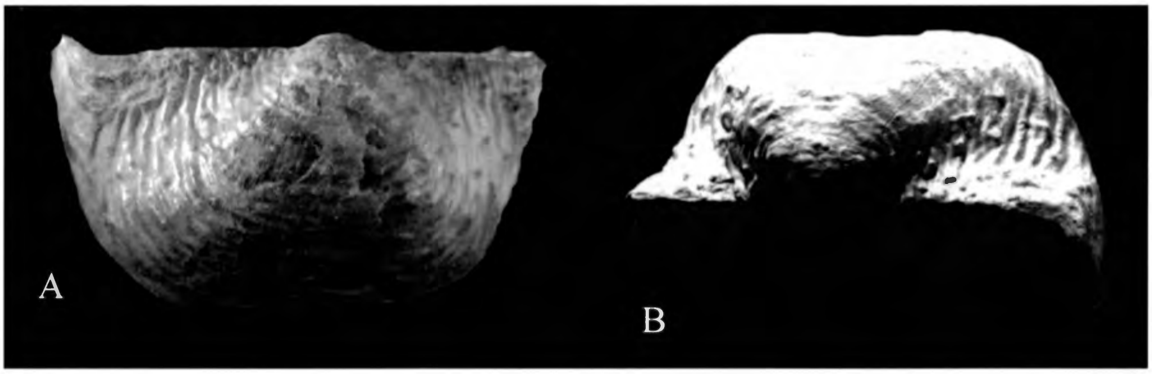


Fig. 3.6. *Araxilevis intermedius* (Abich). Ventral posterior aspects of BR 3022 from Djulfian fauna of Armenia, x1.25. B is highlit to bring out spine base distribution. JBW photo.

Bailliena Nelson & Johnson, 1968 from the Ettrain Formation (Kasimovian), Yukon Territory, Canada, has numerous and undifferentiated spines over ventral valve, but differs in displaying anterior dorsal spines and costae. *Praehorridonia* Ustritsky, 1962 (and see Sarytcheva 1977, p. 112) is rather similar with anterior dorsal spines, and both show fine ribs, though *Bailliena* has well defined dorsal pits, not so far clearly indicated for *Praehorridonia*. Full comparison is hindered by the poor preservation and apparently decorticated nature of the ventral disc of *Praehorridonia*, and poor preservation, suggesting decortication of its dorsal exterior.

Genus ***Howseia*** Logan, 1963

Fig. 3.7

Type species: *Productus latirostratus* Howse, 1848, p. 256 from Magnesian Limestone (Wuchiapingian), England.

Diagnosis: Two or three rows of sturdy non-rhizoid spines posteriorly on the ventral valve, scattered moderately numerous comparatively fine to moderate body spines, otherwise smooth, and commarginal ornament subdued but apparently regular, dorsal valve without spines. Ventral adductors dendritic, dorsal adductor scars striate. Cardinal process somewhat bilobate, thanks to a deep cleft in the median posterior lobe, which is bent dorsally. Floor of valves with numerous fine endospines, and larger papillae mostly around anterior margin.

Discussion: With some hesitation, Logan (1963) assigned this genus to Aulostegidae, in noting a number of differences from *Horridonia*, including a more upright cardinal process and reduced hinge with no ventral ears, and no dorsal spines. Hill (1950, p. 5) had already suggested that *umbonillatus* King (= *latirostratus* Howse) was aulostegid, close to the opinion of King (1856), whereas Trechmann (1945, p. 349), Mahlzahn (1937) and Branson (1948, p. 369) somewhat favoured a horridoniid approach. Although Muir-Wood (pers. comm. to A. Logan) could not decide between a horridoniid or aulostegid alliance, Logan (1963) opted in favour of an aulostegoid alliance and tentatively referred *Howseia* to Subfamily Echinosteginae Muir-Wood & Cooper, 1960. But the overall appearance of *Howseia* Logan is here deemed to be horridonioid, especially taking into consideration the smooth shell, small or undifferentiated ears, and strong but non-rhizoid posterior spines. The cardinal process is matched in other horridoniids, particularly in *Burovia* as figured in Brunton et al. (2000, Fig. 324.c), and is quadrifid, with median shaft deeply divided. No aulostegoid is very close, and although Logan (1963, p. 758) pointed to some similarities with *Xenosteges* Muir-Wood & Cooper, the much larger ventral ears, strong rugae, and thick rhizoid spines of *Xenosteges* make for strong distinctions, whilst acknowledging some internal similarities. *Xenosteges* shows considerable approach to Agelesiinae Muir-Wood & Cooper, 1960. The distribution of ventral spines in *Howseia*, although not perfectly preserved, appears to be close to that of *Araxilevis* over the ventral disc and anterior.

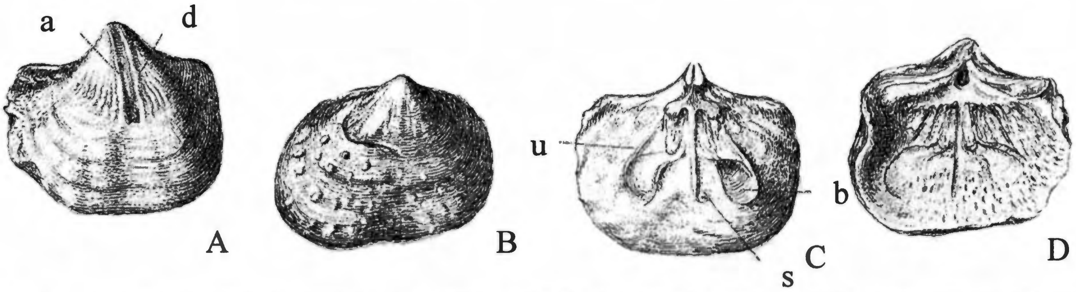


Fig. 3.7. *Howseia latirostratus* (Howse). A, D, ventral and dorsal aspects of internal mould of specimens with valves conjoined. B, ventral valve. C, dorsal view of internal mould. Specimens figured as *Productus umbonillatus* King (1850, pl. 11, fig. 14 - 16), from Magnesian Limestone (Wuchiapingian), England, x1. a – ventral adductor scars, b – brachial shield, d – diductor scars, s – dorsal septum, u – dorsal adductor scar. From King (1850, pl. 4), labelled a little differently.

The type species of *Howseia* was named *Productus latirostratus* by Howse (1848), and not described and illustrated by that author until Howse (1857, p. 46, pl. 4, fig. 1, 2) and Howse (1858, p. 18, pl. 11, fig. 1, 2). In the meantime King (1848, p. 8), and King (1856, pl. 12, fig. 6) had named the same form *umbonillatus*, but Davidson (1858, p. 36, pl. 4, fig. 1-12) considered that *latirostratus* had priority.

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

[Horridoniinae Muir-Wood & Cooper 1960, p. 292; Horridoniidae Sarytcheva, 1960, p. 234.].

Diagnosis: Medium to large shells as a rule, with spines well spaced and erect, often on both valves and along hinge. Limited radial or concentric ornament as a rule, no ventral median rib, minor internal thickening, may show dense pustulation over both valves. Cardinal process broad, may be squat, usually trilobed, but median lobe usually deeply cleft on dorsal side; no lateral buttress plates and no dorsal hinge ridge as a rule.

Discussion: This is a small family varying within constraints over the distribution and thickness of spines. *Horridonia* itself has a row of moderate to large spines developed along the hinge in both valves. In some species and genera, spines are developed in regular quincunx over the ventral valve, in others over the dorsal valve as well; in others rows of posterior spines are the only prominent ornament, and the development of auricular spines also varies. A few genera show costation, and several are also pustular to varying degree. In the present overview what may be a simplistic subdivision is provided by comparison of the different patterns of spine development. Members of the group are of particular interest in so far as spines may be strongly developed along the dorsal hinge, and Lazarev (2005a, b) has drawn attention to the way the shell could be anchored by dorsal spines, with a posterior hinge row diverging in one direction, and anterior (and fewer) spines in a row diverging in another direction. Both sets of spines, though unmentioned, would have acted like legs of a trestle. He considered that when the valves opened, the posterior dorsal spines moved through the sediment. Indeed he postulated that the valves would open by 90°, and this model, together with the supposed movement of dorsal hinge spines backwards and forwards through enclosing sediment would seem to require further consideration. Certainly caution is required with regards at least some Horridoniinae. Jordan (1966, Fig. 11) figured specimens of *Productus (Horridonia) horridus bufoninus* Eisel in which the dorsal hinge spines do not project at a high angle beyond the shell, but curve within the concavity of the dorsal valve, and lie below the commissure. A similar arrangement is suggested for a horridoniid figured by Koninck (1847, pl. 15, fig. 1b). The butt end of spines in some Canadian material indicates that dorsal ear spines lay close to the plane of the commissure. On the other hand Davidson (1861, pl. 54, fig. 44) illustrated a specimen with the hinge row of spines on both valves projecting into matrix, with two anterior ventral spines projecting from the outer ears, and the dorsal spines in *Burovia* Ustritsky and *Bruntonia* Angiolini & Long project strongly beyond the dorsal valve. The degree of opening close to 90° as proposed for horridoniids may also be questioned: it seems far too high. A careful analysis of the degree of opening possible for a waagenoconchid by Shiino & Suzuki (2007) showed an opening possible up to 6° only, and the authors dismissed postulations that favoured a much higher amount, and their analysis bears weight quite apart from the doubtful generic identification and claim over diductor scars. Furthermore, for some horridoniids, the ventral umbo is so long and incurved that slight opening of the valves brings the ventral umbo hard against the dorsal valve, preventing further opening. As far as those genera with only dorsal spines are concerned, it would seem likely that the shell was anchored by its dorsal hinge spines, and the ventral valve could have been the one that opened and closed.

Sources for the family are here believed to have lain within the Lower Carboniferous subfamily Levitusiinae. Somewhat similar spine distributions, and overall smooth shell and interior are found for example in *Acanthoplecta* Muir-Wood & Cooper of Levitusiini, which does however have a median ventral ridge, and in *Geniculifera* Muir-Wood & Cooper, of Geniculiferini, which lacks the median ventral ridge.

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

Fig. 3.8

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

Diagnosis: Row of spines close to hinge along ventral and dorsal valves, scattered few to numerous other spines, spines may be in one or more rows near hinge of either or both valves. External surface may be pustular. No lateral buttress plates. Upper Carboniferous (Moscovian) to Upper Permian (Changhsingian).

Genera: *Horridonia* Chao, *Calvadonia new genus, Inflatusia* new genus, *Pleurohorridonia* Dunbar, *Sangredonia* new genus.

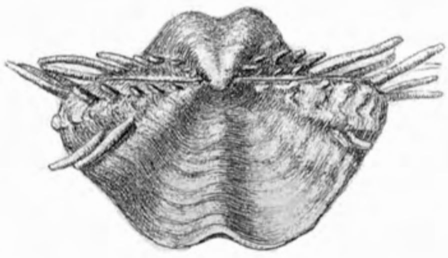


Fig. 3.8. *Horridonia horrida* (J. de C. Sowerby), ventral and dorsal aspects of original specimen of Sowerby (1823) ,x1, as figured by King (1850, pl. 11, fig. 2) from Magnesian Limestone (Wuchiapingian), England.

Discussion: The most characteristic horridoniins develop large ventral spines along the hinge, and the range of variation in *Horridonia* Chao, 1927, p. 24 and allies is well exemplified by King (1850), Eisel (1909), Malzahn (1937) and Jordan (1966). Some early names have been applied to horridoniids from north Europe, such as *Producta Hoppi* Koenig (1825, pl. 9, fig. 108), but for this specimen no spines were shown, and the likely relationships remain difficult to decipher. True *Horridonia*, as based on the original specimen named and figured by Sowerby (1823) from the Magnesian Limestone of northern England, and well illustrated by King (1850, pl. 11, fig. 2), has three rows of stout spines on the dorsal valve close to the hinge, with a transverse fold on the ears, and the anterior row composed of two stout prostrate spines. There are two rows of well formed ventral hinge spines, and a short third row, and few other spines. *Pleurohorridonia* Dunbar from the Late Permian of Greenland is very close, but has only two rows of dorsal hinge-ear spines, and the anterior row comprises only two large spines that project in the plane of the commissure, and passes into a row of pits towards the umbo, and the ear-fold is missing. The type species of *Pleurohorridonia* also displays ventral pustules and anterior costae: the presence of pustules was regarded as significant by Lazarev (2005b), but is moderately widespread in non-Russian forms. *Horridonia grandis* new species from the late Middle Permian of Arctic Canada has better developed second row of dorsal hinge ear spines, and an incipient third dorsal row. Ventral spines are rare except in two well developed hinge rows, and costae, plicae, and pustules are developed. The material figured as *Horridonia horrida* [not Sowerby] by Muir-Wood & Cooper (1960, pl. 108, fig. 1-6), and largely repeated by Brunton et al. (2000, Fig. 323.1a-e) differs. There is one row of dorsal spines along the hinge, and a very large prostrate spine lies in a second row laterally, with pits continuing inwards from this spine, in front of the hinge row. The ventral spines lie in a row at the base of the umbonal slopes, sloping forward laterally from the hinge. There are few other spines, and no costae, and possibly no pustules, although this is not certain. These specimens are not topotypes of *Horridonia horrida*, but come from the Zechstein of Germany. One further specimen that was figured (Muir-Wood & Cooper 1960, pl. 108, fig. 7) shows signs of a row of fine ventral spines lying closer to the hinge. Another figured specimen is mostly of the dorsal interior, from the Magnesian Limestone of England (Muir-Wood & Cooper 1960, pl. 108, fig. 8), and shows nothing of the ornament.

Sangredonia new genus has simplified ornament of spines on both valves and could have been progenital to *Inflatusia* new genus and *Horridonia*. It is of Desmoinesian age, and has fewer spines on either valve than in *Bailliena* Nelson & Johnson or *Praehorridonia* Ustritsky (see Baillieninae new subfamily), but both valves are spinose and a row of ventral spines is developed, with an imperfect row along the umbonal slopes, and fewer dorsal spines, some close to the hinge. *Inflatusia* new genus has a well formed row of spines close to the hinge along the ventral and dorsal valves, and scattered ventral spines, and commarginal ornament more subdued than in *Sangredonia*.

Zhejiangoproductus Liang, 1990, pp. 196, 464, pl. 30, fig. 5-11 from Middle Permian of China was regarded by its author as a horridoniid, but from shape appears to be more likely a member of Monticuliferidae (see p. 292).

Genus **Horridonia** Chao, 1927b

Type species: *Productus horridus* Sowerby, 1823, p. 17 from Magnesian Limestone (Wuchiapingian), England.

Diagnosis: Large, three rows of spines close to ventral hinge and few scattered erect anterior spines; spines in two rows over dorsal ears, of subequal strength, short third row, few or no other dorsal spines. Low pustules may be present, and low costae and plicae. Low fold on dorsal ears.

Discussion: *Horridonia* has spines close to the hinge in both valves. Shells ascribed to *Horridonia horrida* by Muir-Wood & Cooper (1960) and Brunton et al. (2000), wrongly referring to Sowerby (1822), are based mostly on Zechstein material, deemed to belong to at least one different genus. *Horridonia horrida* (Sowerby), as interpreted from the type specimen as figured by Sowerby (1823, pl. 319, fig. 1) and King (1850, pl. 11, fig. 2) and additional specimens from Derbyshire and Humbleton Hill (Durham) figured by King (1850, pl. 11, fig. 3, 6, 7), has two thick spines in an anterior dorsal ear row, and a better developed median row, and comparable dorsal hinge row, and displays a transverse fold across the dorsal ears. Whereas the first ventral row in a new Canadian species consists of a few thin spines and does not extend far from the ventral umbo, the row in *Horridonia horrida* extends to the lateral margin, with lateral spines becoming large. The second row in the Canadian species commences well away from the ventral umbo and consists of three or four spines, developed only on the ears. The second row in *Horridonia horrida* commences close to the umbo on the umbonal slopes, and extends to the lateral margin. Nodes suggest an incipient third row on the Canadian species, and in *Horridonia horrida* the few spines of the third row are stronger. *Horridonia horrida* lacks plicae and costae, and the degree of papillation is not known. Spines are more numerous over the ventral disc, and low radial plicae may be developed (King 1850, pl. 11, fig. 3).

Pleurohorridonia scoresbyensis Dunbar (1955) from the Late Permian of Greenland is close, having two rows of posterior ventral spines, the posterior row close to the hinge being relatively complete, unlike the row in the Canadian species of *Horridonia*. No specimen show signs of a third row, and spines in the anterior row on the dorsal ears are few (one to two, rarely three) and are much broader than spines along the posterior row, and pass towards the hinge into a row of pits. A low fold lies on the dorsal ears of *Horridonia*, but there is no corresponding fold in *Pleurohorridonia*. Spines over the ventral disc are possibly slightly more numerous in the type species of *Pleurohorridonia*, but not, it appears, to any significant degree. Pustules are present, and the decorticated anterior shell of *Pleurohorridonia* suggests the possible presence of costate plicae, although not so clearly as in the new Canadian species of *Horridonia*. The type species of *Pleurohorridonia* is distinguished from *Horridonia* by possessing one fewer row of spines near the hinge, a pair of thick dorsal spines on the anterior dorsal ear, and lack of fold on the dorsal ears, and less developed costae and plicae. The dorsal valve in front of the hinge is smooth. It is believed to be of late Changhsingian age, younger than known *Horridonia.*

Horridonia grandis new species

Fig. 3.9, Fig. 13.10

Derivation: grandis – large, Lat.

Holotype: Specimen GSC 36835 (see Fig. 3.9, Fig. 3.10) from C-13356, Trold Fiord Formation (Capitanian), Ellesmere Island, Canada, here designated. See Appendix A, part C, p. 479.

Diagnosis: Large, with long sulcus and convex ears, ventral posterior with short row of small spines close to umbo and hinge, second row laterally over ears, low incipient spines or mounds in front in third row on ears, a few scattered erect fine spines over disc and trail. Dorsal spines form two rows over ears, six or seven in posterior row, five or six in next row, with one or two spines or spinose nodes in front, forming a feeble third row; a few dorsal dimples. Shell plicate, bearing costae over anterior ventral disc and trail, and dorsal trail.

Dimensions in mm for GSC 36835:

Width	Length	Height	Umbonal angle	Sulcal angle
78	56	38	65°	30°

Description: Shell large and transverse, with strongly incurved ventral umbo, steep umbonal flanks, and sulcus commencing close to tip of umbo. The trail is long and curves through more than 180°. The dorsal valve is deeply concave and curves smoothly into the trail, which is about a third of the length of the shell. A narrow median fold commences some 8mm in front of the hinge. Ears are large, highly convex on the ventral valve, more gently concave on the dorsal valve, which carries a low median fold that extends along each ear parallel to the hinge. The posterior ventral valve is comparatively smooth, with low growth lines, some three or four in 1.5mm, low growth steps and pauses. Low costae commence over the anterior disc, and are often paired, numbering five or six in 5mm, and developed over low plicae, one narrow pair within the sulcus, two pair that are broad over the sulcal borders, and three poorly discriminated pairs laterally. The costae also cover the anterior ears, which are sharply separated anteriorly from the umbonal flanks. Growth lines over the trail vary between three and five per millimetre, and the ventral surface is covered by fine pustules, three per mm anteriorly, and less evenly arranged over the posterior shell; some shell patches without pustules. The dorsal disc is smooth and costae commence at the start of the trail, and vary in strength, between three and five per 5mm at the anterior margin. Plicae are less noticeable than on the ventral valve. Although growth lines are visible, there are no well developed pustules, but the shell surface is rather irregular with small pustules and pits in parts. Ventral spines form a short row of six spines close to the hinge and each side of the umbo, and this row does not persist laterally. Three stronger spines lie in a second row, up to 2.2mm in diameter, limited to the ears. A third potential row lies in front, represented by two or three swellings, that have not produced spines. There are a few other erect or prostrate spines, no more than 1mm in diameter, over the disc and trail. Dorsal spines are well developed over the ears. Some six erect spines lie close to the hinge, and a second row of five lies in front on the mid-ear swelling. The third row represented by a spine or node lies in front close to the anterior edge of each ear. Spines of each row include some roughly comparable in thickness to thickest spines of other rows. On one side the second and last spine from the outer margin is 2mm in diameter, and one spine fourth from inner side on the posterior row is 2mm wide, and the outermost spine of this row is 2.5mm in diameter. The posterior spines on the other ear tend to be finer, whereas the middle row includes at least two spines 2mm in diameter. There are no definitely developed spines over the dorsal disc and trail, or they have been lost through silicification, and any such spines must have been rare and fine.

Resemblances: The present form is moderately close to the specimen figured as *Productus horrida* Sowerby by King (1850, pl. 11, fig. 2), originally figured by Sowerby (1823, pl. cccxix, fig. 1) from Derbyshire, England. This specimen is kept at the Natural History Museum, London, and registered as B 60971. The dorsal ears show a similar median transverse fold, with an outwardly inclined posterior row of at least five spines, and a poorly developed median row of spines or knobs, and two anterior spines, and the fold is placed between the hinge row and median spine row of the holotype. Two rows of spines are shown close to the hinge on the ventral valve, with outer spines stronger than on the dorsal valve. There appear to have been a number of other spines over the visceral disc of the ventral valve, to judge from King's figures. Differences from the Canadian species lie in the better development of an anterior (third) row of dorsal ear spines, more strongly developed and longer rows of ventral hinge spines, more spines over the venter, and the lack of costae or rarer presence of few and simple plicae: other facets, such as the presence of ventral pustules, are obscure.

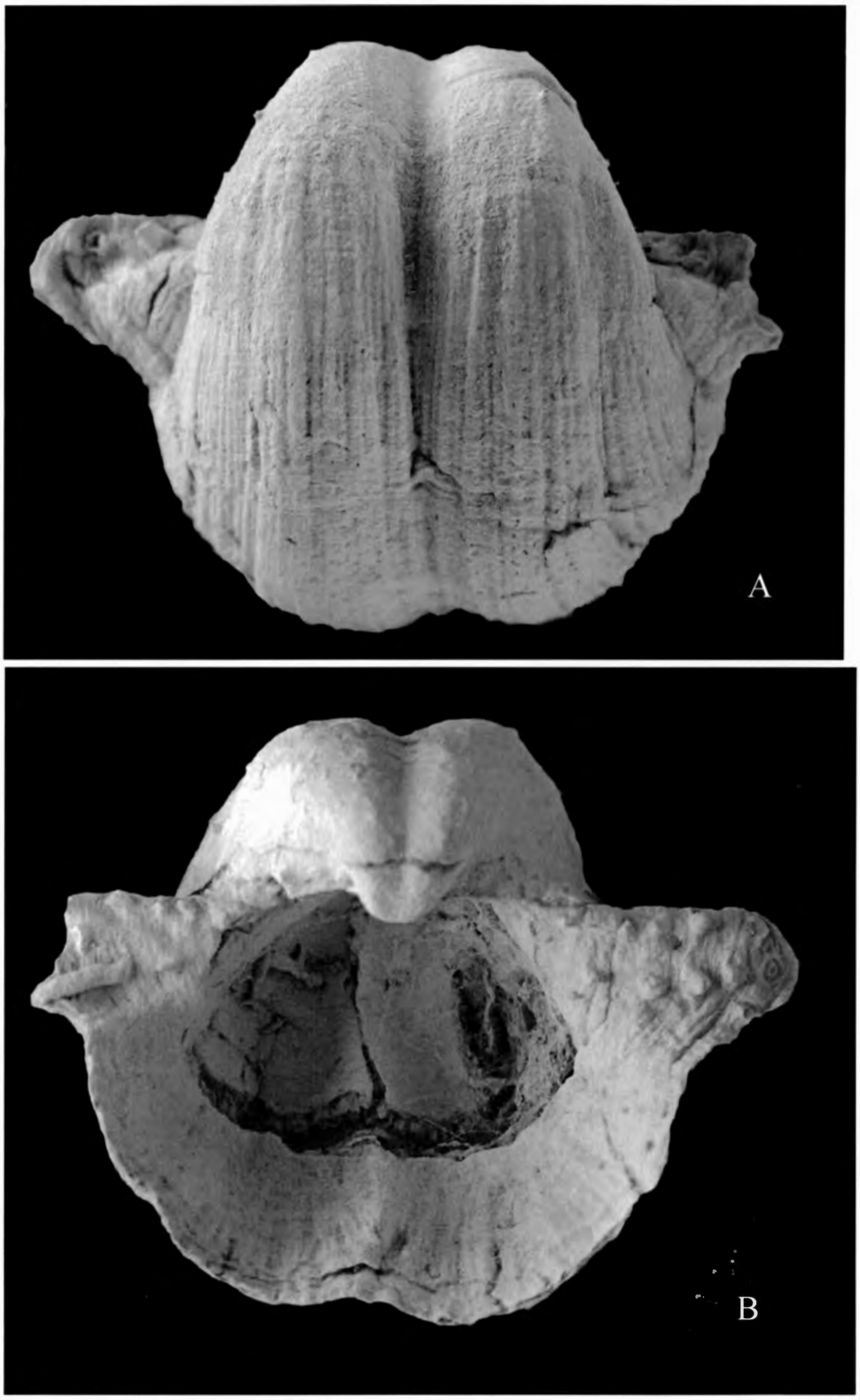


Fig. 3.9. *Horridonia grandis* new species. A, B. holotype, ventral and dorsal aspects of GSC 36825, x1.5, from GSC loc. C-13356, Trold Fiord Formation (Capitanian), Ellesmere Island, Canada. JBW photo.

Horridonia horridus bufoninus Eisel (1909) has a row of fine ventral spines and fewer but larger row spines in front, and the dorsal valve has a different anterior row of spines with no pits. There are more body spines. In some respects *buffoninus* is similar to *hoppieanus* Eisel. The form *auritulus* Eisel appears to show one row of ventral spines at the umbonal slope base, and a row of dorsal hinge spines and a row of pits, but no outer ear spines. Jordan (1966, Fig. 1b) considered that *Producta calva* Sowerby (1829, pl. 560, fig. 2-4) was senior synonym of *auritulus*, *bufoninus* and some *initialis*, which seems doubtful because most Zechstein taxa have thick anterior dorsal ear spines and often numerous ventral spines over the disc.

Stratigraphic position: According to Liao Zhuo-ting in Nakamura et al. (1992, p. 83), conodonts from the upper Trold Fiord Formation indicate a Capitanian age, which, from the overview of Canadian Arctic faunas in Bamber & Waterhouse (1971) and Waterhouse & Waddington (1981), seems eminently acceptable.

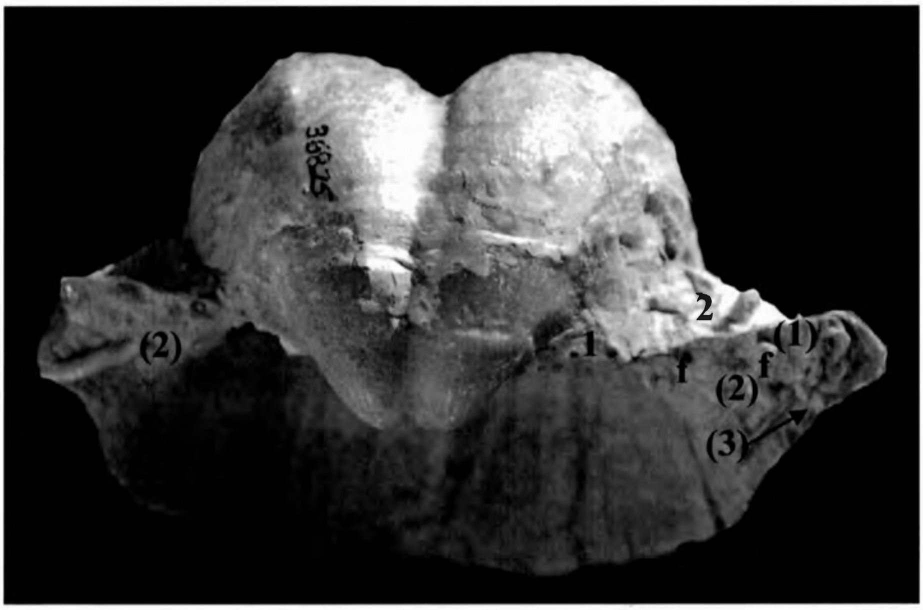


Fig. 3.10. *Horridonia grandis* new species, holotype GSC 36825 x 1.5, back-lit to show spine rows, numbered one and two along ventral hinge, and the mid-ear fold f – f along the dorsal ears. Numbers in brackets refer to first and second hinge rows and feeble third row on dorsal valve. From Trold Fiord Formation (Capitanian), Ellesmere Island, Canada. JBW photo.

Genus ***Sangredonia*** new genus

Fig. 3.11

Derivation: Named from Sangre de Cristo Mountains, New Mexico.

Type species: *Horridonia*? *daltonensis* Sutherland & Harlow, 1973, p. 55 from middle La Pasad Formation (early Desmoinesian), New Mexico, United States, here designated.

Fig. 3.11. *Sangredonia daltonensis* (Sutherland & Harlow) from La Prasad Formation (Moscovian), New Mexico, United States, x 3. A, posterior view of ventral valve holotype OU 7766. B, dorsal aspect of OU 7768. See Sutherland & Harlow (1973, pl. 11).

Diagnosis: Small in size, transverse with shallow anterior ventral sulcus and broad low anterior dorsal fold, ventral spines erect, in irregular row close to hinge, a row along the umbonal slopes, and scattered rarely over remainder of valve, dorsal spines few and close to hinge. No large spines are developed in either valve. Surface of both valves smooth to granular with pustules of varying size, and small irregular growth steps, more closely spaced on dorsal valve, and more prominent than in other horridoniids.

Discussion: The ventral adductor platform is elongate and elevated, and the cardinal process is close to that of younger horridoniids, broad, short, bilobed anteriorly and trilobed posteriorly. Internal dorsal pustules are large anteriorly, just like those of several other horridoniid genera, and there is no marginal ridge. In ornament the form is close to horridoniids, especially in its spine distribution, for spines are comparatively few and well ordered, suggesting source stock for Horridoniinae and Sowerbininae, and dorsal spines lie near the hinge. Widespread external papillae are present, with broad faint costae anteriorly, and lack of marginal ridges. The genus comes moderately close to *Horridonia* Chao, 1927, *Burovia* Ustritsky, 1980 and *Bailliena* Nelson & Johnson, 1968, but has less well defined hinge spines on each valve, and has a moderately well defined row of spines along the ventral umbonal slopes. As well, the shape is more transverse and the growth steps more defined, as if descended from Geniculiferini.

Genus ***Inflatusia*** new genus

Derivation: inflatus – swollen, puffed up, Lat.

Type species: *Inflatusia ogilviensis* new species from Member A (Gzhelian), Jungle Creek Formation, Yukon Territory, Canada, here designated.

Diagnosis: Medium size, ventral valve highly swollen, dorsal valve gently concave over disc, well defined ventral sulcus and low dorsal fold, long trail. Row of spines close to hinge of each valve, other spines limited to ventral valve, as strong as those of the outer ventral hinge.

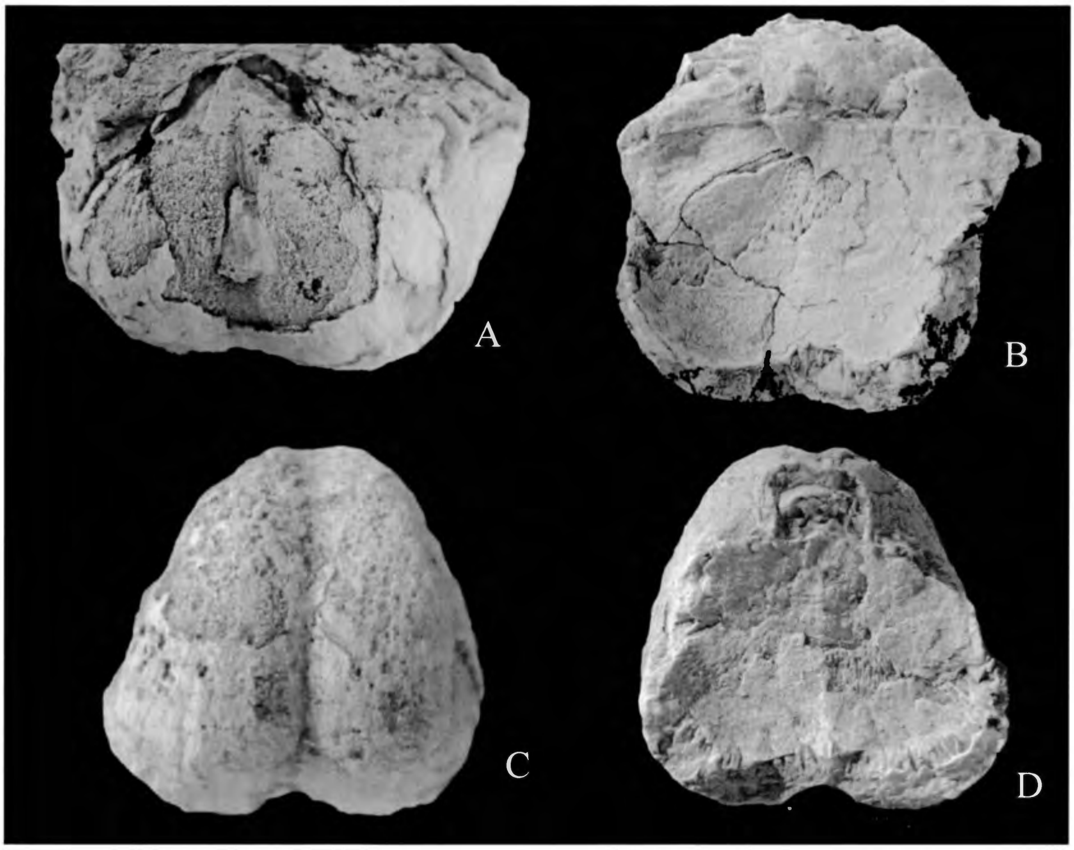


Fig. 3.12 *Inflatusia ogilviensis* new genus, new species. A, posterior view of ventral valve GSC 133289. B, dorsal aspect of GSC 133281. C, D, ventral and dorsal aspects of specimen with conjoined valves, GSC 133282. Specimens x1.5, from Member A (Gzhelian), Jungle Creek Formation, Canada. JBW photo.

Discussion: *Sangredonia* new genus from the Late Carboniferous of United States is distinguished from *Inflatusia* by its lower inflation, and presence of more ventral spines, with a row along the lower ventral umbonal flanks. Commarginal rugae, growth laminae, and growth stops are moderately defined on the two valves, and small pustules are developed over the shell surface. The genus *Horridonia* Sowerby is readily distinguished by the presence of more spine rows close to the hinge of each valve, and *Pleurohorridonia* Dunbar is somewhat similar, and largely of Late Permian age. *"Productus" calva* Sowerby (see below) as described from the Late Permian of England is much closer, though less inflated, and is assigned to new genus *Calvadonia*. Various taxa named from the Zechstein (Late Permian) of Germany by Eisel (1909) and Jordan (1966) are close, but have one or more very thick spines in front of the hinge row of dorsal spines, sited on the ear.

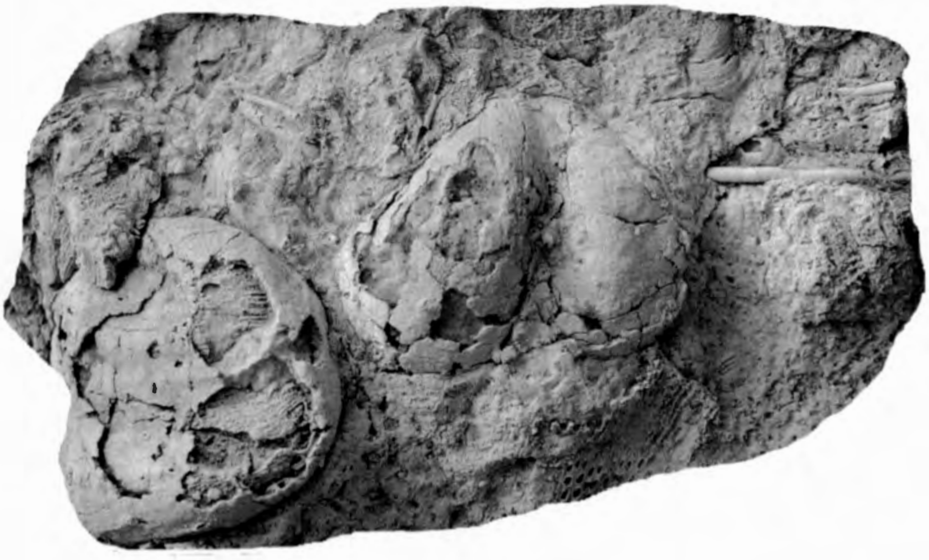


Fig. 3.13. *Inflatusia ogilviensis* new genus, new species. GSC 133361 in centre, showing faint ventral costae, and GSC 133362 to left, x1. From lower Jungle Creek Formation (Gzhelian), Yukon Territory, Canada. JBW photo.

Inflatusia ogilviensis new species

Fig. 3.12 - Fig. 3.15

Derivation: Named from Ogilvie Mountains, Yukon Territory.

Holotype: GSC 136036, figured in Fig. 3.15A, B, from Member A (Gzhelian), Jungle Creek Formation, Canada, here designated.

Diagnosis: Ventral valve highly arched and body corpus thick, ventral hinge row of spines becoming thick and long laterally, spines almost as stout on anterior trail, low radial costae anteriorly, and sulcus well formed. Dorsal valve smooth over disc, trail may be weakly costate, fold low.

Material. Some twenty specimens, mostly of valves conjoined, from Member A (Gzhelian), Jungle Creek Formation, Canada. See Appendix A, part C, p. 478.

Dimensions in mm:

Specimen GSC	Width	Length	Height	
136036	19	14	7	holotype
136037	24	22	15	
133282	35	34	23	
133281	39	37	28	
133209	42	37	22	
136038	40	38	25	

Description: Mature shells highly inflated and of medium size, with only moderately wide hinge and subangular to abruptly rounded cardinal extremities, and maximum width well forward near anterior quarter of length. The ventral umbo is strongly incurved, with angle of 90-110°. The sulcus is well defined, commencing just in front of the umbonal tip, with angle of 22-25°, and narrow subangular floor, and the fold of the dorsal valve is less conspicuous, with very narrow to broad gently rounded to subangular crest. Ventral ears are small and convex. Shell 1mm thick, and up to 1.6mm thick in a large specimen. Some ventral valves are smooth apart from spines, whereas a few have low broad-crested costae, eleven to eighteen each side of the sulcus, and on some shells of even strength, on others, of two or three orders, whereas dorsal valves are smooth, or in some specimens faintly ribbed. Fine pustules are present in the sulcus of the holotype, but for the most part the surface seems too worn to preserve pustules. Fine pustules cover the surface of the dorsal valve, but whether they are true surface ornament seems doubtful. Very low and irregular growth lines are present on some dorsal valves, but otherwise are not pronounced. Spines form a hinge row just front of the hinge on the ventral valve, numbering eight or nine each side of the umbo. They are less than 1mm in diameter until full maturity, when outer spines become up to 1.5mm in diameter and over 20mm long. Spines cover the ventral disc and trail, and are thick anteriorly, up to 2.5mm in diameter. The spines are most prominent along the high flanks each side of the sulcus, whereas spines are missing from the sulcus itself. On the small and immature holotype, 17mm wide, only two spines are developed along the hinge, and erect spines are developed on the flanks, 2-2.5mm apart anteriorly. Three well developed spines lie along the dorsal hinge, inclined postero-laterally, the outer spines 0.6mm in diameter. No other spines are developed. A larger dorsal valve 26mm wide has nine spines each side of the umbo, and the outermost spine is just over 1mm wide.

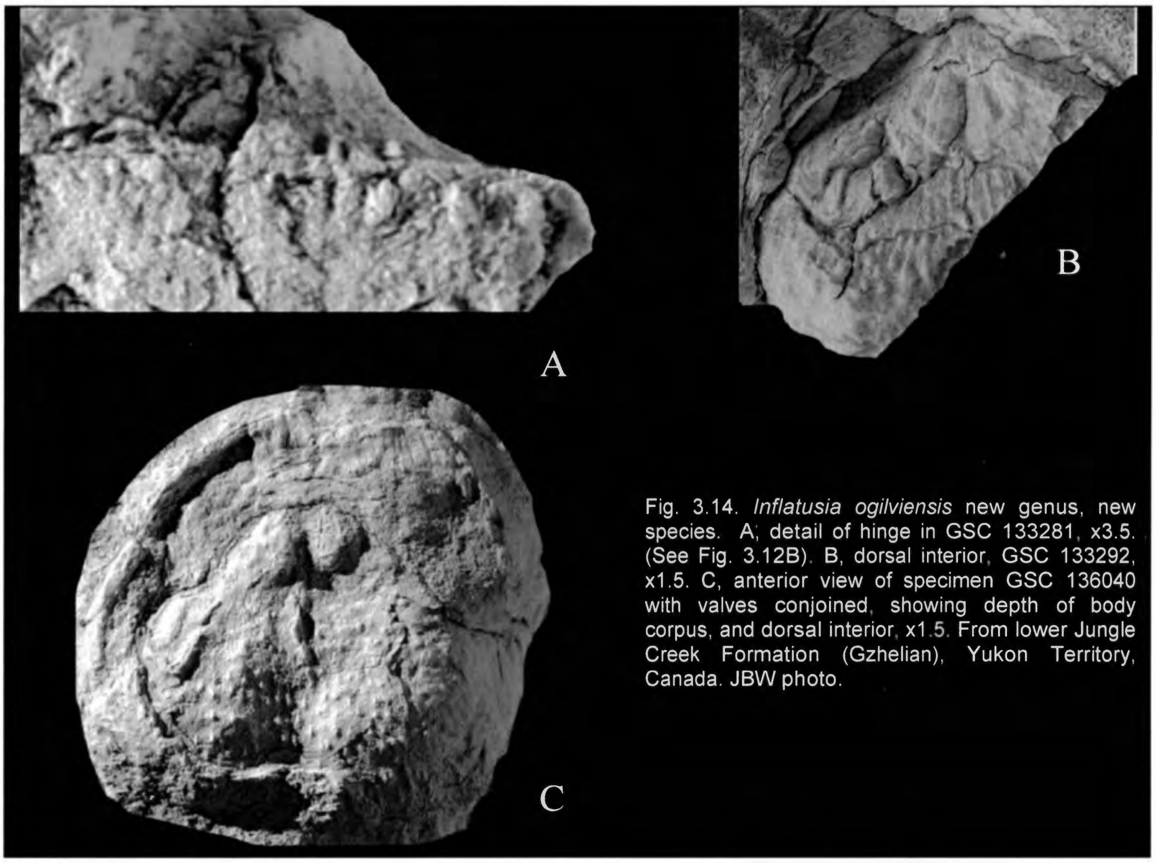


Fig. 3.14. *Inflatusia ogilviensis* new genus, new species. A, detail of hinge in GSC 133281, x3.5. (See Fig. 3.12B). B, dorsal interior, GSC 133292, x1.5. C, anterior view of specimen GSC 136040 with valves conjoined, showing depth of body corpus, and dorsal interior, x1.5. From lower Jungle Creek Formation (Gzhelian), Yukon Territory, Canada. JBW photo.

The adductor platform in a large mature ventral valve is over 15mm long and 3.5mm wide in a specimen nearly 40mm long, raised on a platform, with low median ridge and shallow groove each side. Diductor scars are large with longitudinal striae, commencing near the posterior third of the adductor platform and extending moderately well in front. Cardinal process obscure, base juts out slightly externally; low and slender median dorsal septum, extends close to anterior edge of visceral disc, dorsal adductor scars raised, and outer pair slightly lower and more slender. The brachial shields are visible, and heavy pustules are concentrated over the anterior disc, and fine papillae only lie over the trail. In a late mature specimen low ridges lie behind the anterior disc pustules. There is no lateral marginal ridge and no posterior marginal hinge ridge, but the papillae build up thickened shell.

Resemblances. *Calvadonia* new genus, based on *Producta calva* Sowerby from Wuchiapingian of England has a row of spines close to the hinge of each valve, and few other ventral spines. The dorsal valve is more concave, the ventral hinge row more inclined from the hinge, and its spines are finer, and low ribbing is present. There are also internal differences; the dorsal adductors are larger and less raised, and brachial ridges more extended.

In *Pleurohorridonia* Dunbar, 1955 from the Late Permian of Greenland, dorsal spines lie in a row along the hinge, and in front there are two thick prostrate spines, not seen in *Inflatusia*, and a line of pits that continues inwards.

Ventral spines lie in a row at the base of the umbonal slopes and another row closer to the hinge. Body spines are few and fine pustules are developed over the shell surface, and anterior coarse but irregular ribbing is developed. Ventral adductor scars are broader posteriorly and more dendritic in *Pleurohorridonia*, as shown in Dunbar (1955, pl. 11, fig. 8) compared with those of *Inflatusia* (see Fig. 3.12A herein).

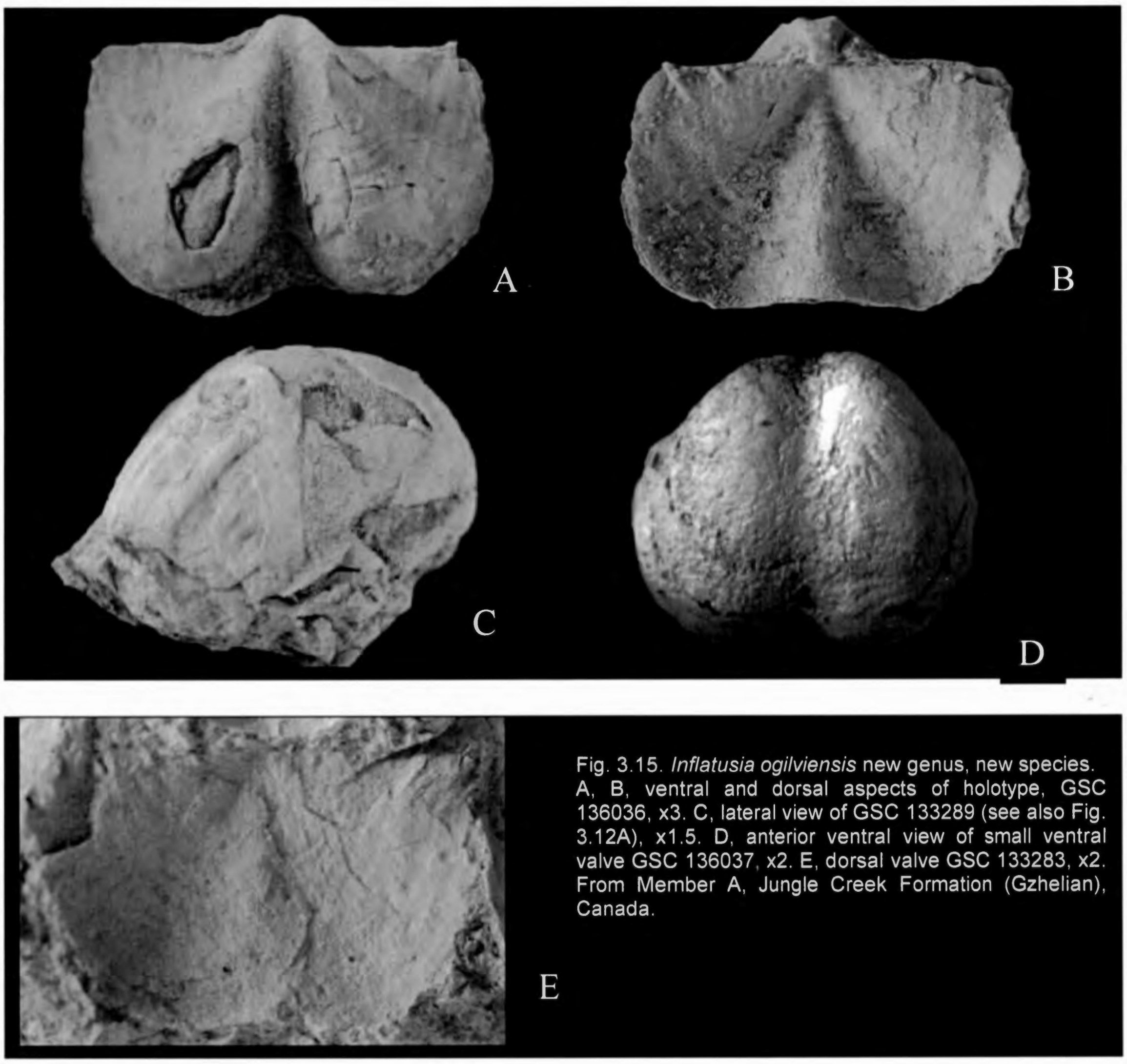


Fig. 3.15. *Inflatusia ogilviensis* new genus, new species. A, B, ventral and dorsal aspects of holotype, GSC 136036, x3. C, lateral view of GSC 133289 (see also Fig. 3.12A), x1.5. D, anterior ventral view of small ventral valve GSC 136037, x2. E, dorsal valve GSC 133283, x2. From Member A, Jungle Creek Formation (Gzhelian), Canada.

Genus ***Calvadonia*** new genus

Fig. 3.16

Derivation: Named from name of type species, calva.

Type species: *Producta calva* Sowerby, 1829, p. 115, from the Magnesian Limestone (Wuchiapingian) of England, here designated.

Diagnosis: Small shells with row of moderately fine spines close to hinge of each valve, a few other well spaced spines over ventral disc and trail, no costae.

Discussion: *Producta calva* Sowerby, 1829, p. 115, pl. 560, fig. ?3, 4, ?5, 6 from the Magnesian Limestone (Wuchiapingian) of England is based on subelongate shells with thick disc and little to moderately extended ears, broad shallow sulcus and low fold. Ventral spines lie in a row close to the base of umbonal slopes, further from the hinge than in other genera, and scattered over the visceral disc and trail; dorsal spines lie in a row along the hinge. Specimens are kept at the Natural History Museum, London, including B 60976 (Sowerby 1829, pl. 560, fig. 2) and B 5816 (fig. 3). *Horridonia horridus* (Sowerby) has three dorsal ear rows, and two or three well developed ventral hinge rows. Shells similar to Sowerby's *calva* have been illustrated and described as *Productus horridus* [not Sowerby] by

King (1850, pl. 10, fig. 29-31) from Garmundsway, and by Davidson (1858, p. 33, pl. 4, fig. 13-26) from Tunstall Hill and Humbleton, and parts of the Magnesian Limestone in northern England. They are kept at the Natural History Museum, London, and some may be composites, such as fig. 19, based essentially on B 5816, and fig. 26 may be B 13791 (Zoë Hughes, pers. comm.). The specimens are subequilateral, and the ventral umbo broad and incurved; the sulcus commences close to the umbonal tip and becomes broader and shallower anteriorly. The dorsal valve is subplanar, with low fold commencing near the umbo, and a comparatively short trail. A row of ventral spines slopes forward in front of the hinge and lies close to the base of the umbonal slopes. There are few if any other spines (Davidson 1858, pl. 4, fig. 14, 18), and no costae, but there are growth stops and laminae. The dorsal spines are limited to a row close to the hinge. Both Fig. 4 and Fig. 6 in Davidson (1858, pl. 4) show a row of spines along the ventral hinge and another along the dorsal hinge, but ears are incomplete. The interior is well preserved, with thick pustules in front of the brachial scars and median septum, near the start of the trail, approaching those of *Inflatusia* new genus. The dorsal interior figured by Muir-Wood & Cooper (1960, pl. 108, fig. 8) from Raisley Hill, Durham, England, shows dendritic adductor scars, well defined brachial ridges, strong anterior pustules, and a trifid cardinal process, but its identity is insecure.

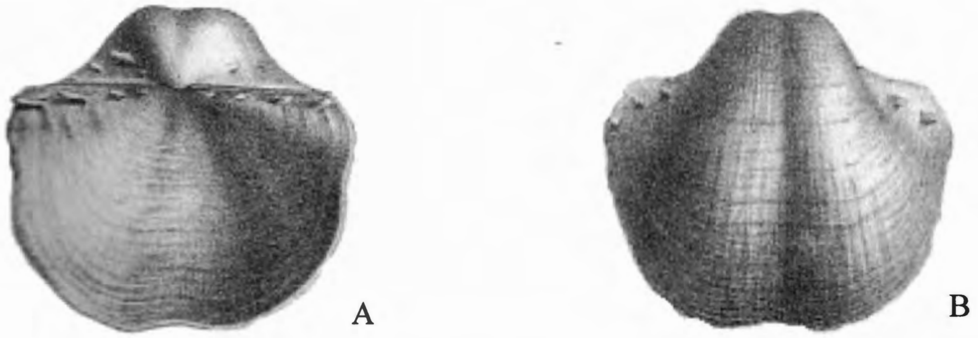


Fig. 3.16. *Calvadonia calva* (Sowerby). A, B, specimen figured as *Horridonia horridus* by Davidson (1858, pl. 4, fig. 16, 16a) from Upper Permian Magnesian Limestone (Wuchiapingian), Tunstall Hill, northern England, x1.2.

Calvadonia is readily distinguished from *Sangredonia* new genus through lacking prominent commarginal ornament and lacking the ventral umbonal slope row of spines, and having fewer ventral spines over the disc. *Inflatusia* new genus has low costae, and thicker ventral spines a little further from the hinge, and different dorsal interior, with other differences. *Horridonia* Sowerby and *Pleurohorridonia* Dunbar have more rows of spines close to the hinge in each valve, with further differences.

Of the Zechstein varieties named by Eisel (1909) and studied by Mahlzahn (1937) and Jordan (1966) for forms found in the Wuchiapingian of Germany, *bufoninus* is close with signs of a second posterior ventral hinge row and two spines in the anterior dorsal row, and more ventral disc spines. Pustules are very fine. A large number of forms is found in the Zechstein, distinguished as a rule by having two rows of dorsal spines in front of the hinge with at least one anterior hinge spine very large, as figured by Muir-Wood & Cooper (1960, pl. 108, fig. 6), repeated in Brunton et al. (2000, Fig. 323.1a-e). Such a large anterior ear spine or spines betoken a separate genus, being studied by T. Grunt and D. Meyer.

Subfamily **BAILLIENINAE** new subfamily

Name genus: *Bailliena* Nelson & Johnson, 1968, p. 723 from Ettrain Formation (Kasimovian) of Yukon Territory, Canada, here designated.

Diagnosis: Ventral spines moderately numerous over valve, dorsal valve bearing spines over anterior valve and trail. Costae moderately well developed, on either ventral or dorsal valve, or both. Hinge and ear spines not strongly specialized on either valve. Lateral buttress plates may be present. Upper Carboniferous (Bashkirian – Gzhelian).

Genera: *Bailliena* Nelson & Johnson, *Praehorridonia* Ustritsky (spelled *Praechorridonia* by Lazarev 2011, English version).

Discussion: The presence of numerous spines on both valves and well ordered costae provides a ready distinction from Horridoniinae Muir-Wood & Cooper and Sowerbininae Lazarev. *Bailliena* has been chosen as name bearer, because *Praehorridonia*, although profusely illustrated by Ustritsky in Ustritsky & Chernyak (1963), seems to be based on somewhat decorticated specimens, as implied by the much greater detail preserved on external moulds, such as that in Ustritsky (1963, pl. 21, fig. 3v), which show far more numerous spines than indicated for most of the ventral valves, including the counterpart figured by Ustritsky (1963, pl. 21, fig. 3b). Despite the implication from specimens figured by Brunton et al. (2000, Fig. 325.1) and its vaguely worded diagnosis, ventral spines are denser, at least on the ventral trail of *Praehorridonia* than in *Baillenia*. *Baillenia* has dorsal pits; their presence is not sure for *Praehorridonia*.

Horridoniinae has more specialized spines over the dorsal and sometimes ventral ears; Sowerbininae has only dorsal spines over the ears, and Araxileviinae has only ventral spines over the entire shell. Costae are moderately well developed in *Bailliena* and *Praehorridonia*.

The subfamily shows some resemblance to *Impiacus* Lazarev & Suur'suren in Afanasieva et al. 1988, p. 53 from upper Visean beds of Mongolia, and indeed Lazarev (2005a) suggested that *Impiacus* provided source stock. The type material of *Impiacus* is poorly preserved with regard to the ventral exterior posteriorly, and shows the dorsal exterior as pitted and bearing numerous fine spines and only moderately defined commarginal sublamellar growth pauses. The genus was synonymized with *Nudymia* Lazarev, 1990, p. 93, based on type species *Bailliena nudymiensis* Sarytcheva (1977, p. 116, pl. 16, fig. 6, 7, pl. 17, fig. 1-3, text-fig. 69, 70) from the Makarov beds of South Verchoyan, northeast Russia, of Bashkirian age. The dorsal valve of this species (Sarytcheva 1977, pl. 16, fig. 6b, 7, pl. 17, fig. 2b) certainly looks moderately close to that of the type species of *Impiacus*, *I. dzhinsetuensis* Lazarev & Suur'suren in Afanasieva et al. (1988) of upper Visean (Lower Carboniferous) age of the Gobai Altai, as further figured in Rozanov (2003, pl. 46, fig. 7, 8) and Brunton et al. (2000, Fig. 299.2c), and although the anterior spines only are preserved in type material for *Impiacus*, more of the ventral exterior is shown in *nudymiensis* by Sarytcheva (1977, pl. 17, fig. 1a, b, 2a-c). But there are many differences between *Impiacus* and *Bailliena-Praehorridonia*. *Impiacus* appears to lack a hinge row of ventral spines, and body and trail spines have somewhat elongated bases, whereas ventral spines in *Bailliena* and at least on the trail of *Praehorridonia* are erect. Dorsal spines are more numerous in *Impiacus*, and elongate pits are conspicuous: dorsal spines are restricted to the anterior half in *Bailliena*, and pits are round, not elongate. Costellae and rugae are not found in *Impiacus*, but are common in *Bailliena* and *Praehorridonia*. The ventral adductors of type *Impiacus* are striate and poorly separated from diductor scars, whereas the ventral adductor platform is usually well defined and not striate in *Bailliena* (see Fig. 3.18D herein). The dorsal interiors are poorly known for some of these genera, though note may be made of the well preserved posterior interior for *Bailliena*, as shown in Fig. 3.18G herein, to illustrate the presence of lateral buttress plates. The brachial shields in *Bailliena* and especially *Praehorridonia* seem smaller than in *Impiacus,* the cardinal process much larger, and a marginal hinge ridge apparently not developed, but the dorsal median septum is single in both suites. On available evidence, it is deemed likely that Baillieninae developed from Leioproductidae, certainly as a side branch from the main trend in evolution as displayed by Horridoniinae and Sowerbininae, and not from *Impiacus*. Although *Impiacus* shows some similarity to *Bailliena*, especially in its dorsal exterior, it appears to fall within Levipustulinae.

Genus **Bailliena** Nelson & Johnson, 1968

Type species: *Bailliena yukonensis* Nelson & Johnson, 1968, p. 723 from Ettrain Formation (Kasimovian) of Yukon Territory, Canada.

Diagnosis: Well inflated subequilateral shells, ventral valve covered by spines, including hinge row, dorsal valve with spines and pits over anterior disc and trail, no spines very broad, costae may be developed anteriorly. Lateral buttress plates.

Bailliena yukonensis Nelson & Johnson, 1968

Fig. 3.17, Fig. 3.18

1961 *Pleurohorridonia scoresbyensis* [not Dunbar] – Nelson, pl. 28, fig. 9, 10.
1962 Horridonid (sic) sp. Nelson, pl. 1, fig. 1a-e.
1968 *Bailliena yukonensis* Nelson & Johnson, p. 723, pl. 90, fig. 1-11, pl. 91, fig. 13, 14, text-fig. 3a, b.
1971a *Praehorridonia yukonensis* – Waterhouse, pl. 5, fig. 2, 3, pl. 7, fig. 4.
2000 *B. yukonensis* – Brunton et al., p. 480, Fig. 323.2a-d.

Holotype: UC F1088, figured by Nelson & Johnson (1968, pl. 90, fig. 1-3), OD, from Ettrain Formation equivalents at Peel River rapids, northern Yukon Territory, Canada. See Appendix A, part C, p. 478.

Discussion: This species is widely represented in the Ettrain Formation of the Yukon Territory, and figures prepared by R. E. Nazer are here provided as further exemplars of the species and genus . The genus was well described by Nelson & Johnson (1968) whereas the diagnosis of *Praehorridonia* provided by Brunton et al. (2000, p. 480), and the figures of decorticated ventral valves provide few accurate or meaningful means of distinction. Lazarev (2005a) declared the two genera were readily distinguished, but failed to specify the differences. A clear description and good figures of *Praehorridonia* were provided by Sarytcheva (1977, p. 112, pl. 16, fig. 1-5). Figures show a hinge row of ventral spines, what appear to be fewer disc spines, and more numerous trail spines over the costate trail on the ventral valve, compared with that of *Bailliena*. The dorsal valve is similarly costate anteriorly, and has many spines, and the dorsal disc has traces of costae and growth lamellae and few or no pits, compared with *Bailliena*. These differences are established by means of the external moulds, which except in Ustritsky & Chernyak (1963, pl. 21, fig. 3v) were rarely figured, and the external moulds differ considerably in costation and density of spines when compared with the mostly decorticated internal moulds figured by Ustrtitsky (1962, in Ustritsky & Cheryak 1963, p.

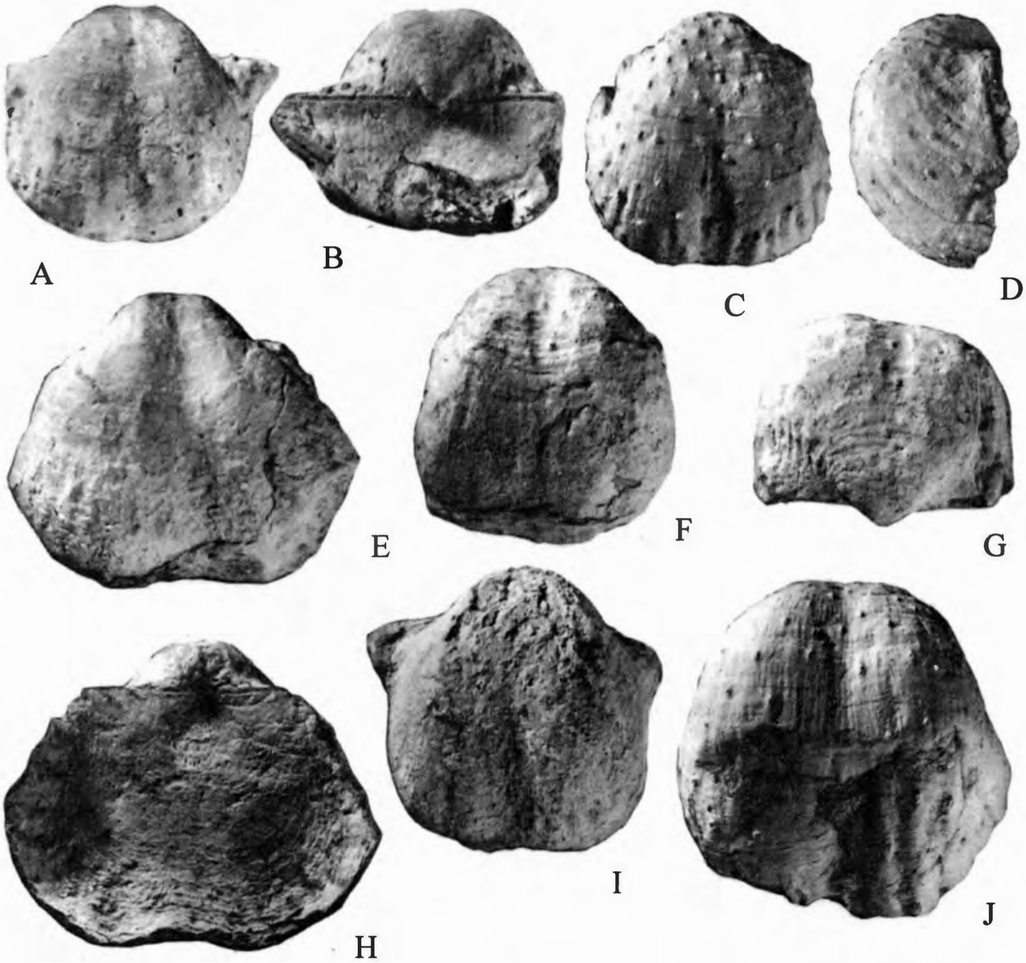


Fig. 3.17. *Bailliena yukonensis* Nelson & Johnson. A, B, ventral and dorsal views of GSC 37228 from near GSC loc. 53728. C, D, ventral and lateral views of ventral valve GSC 37229 from same locality. E, H, ventral and dorsal views of conjoined specimen GSC 37230 from GSC loc. 53690. F, G, ventral and posterior views of ventral valve GSC 37231 from near GSC loc. 53728. I, ventral valve GSC 37232 from GSC loc. 53811. J, ventral valve GSC 37233 from near GSC loc. 53728. Specimens x1 except H, x1.2. From Ettrain Formation (Kasimovian), Yukon Territory, Canada. R.E. Nazer, photo.

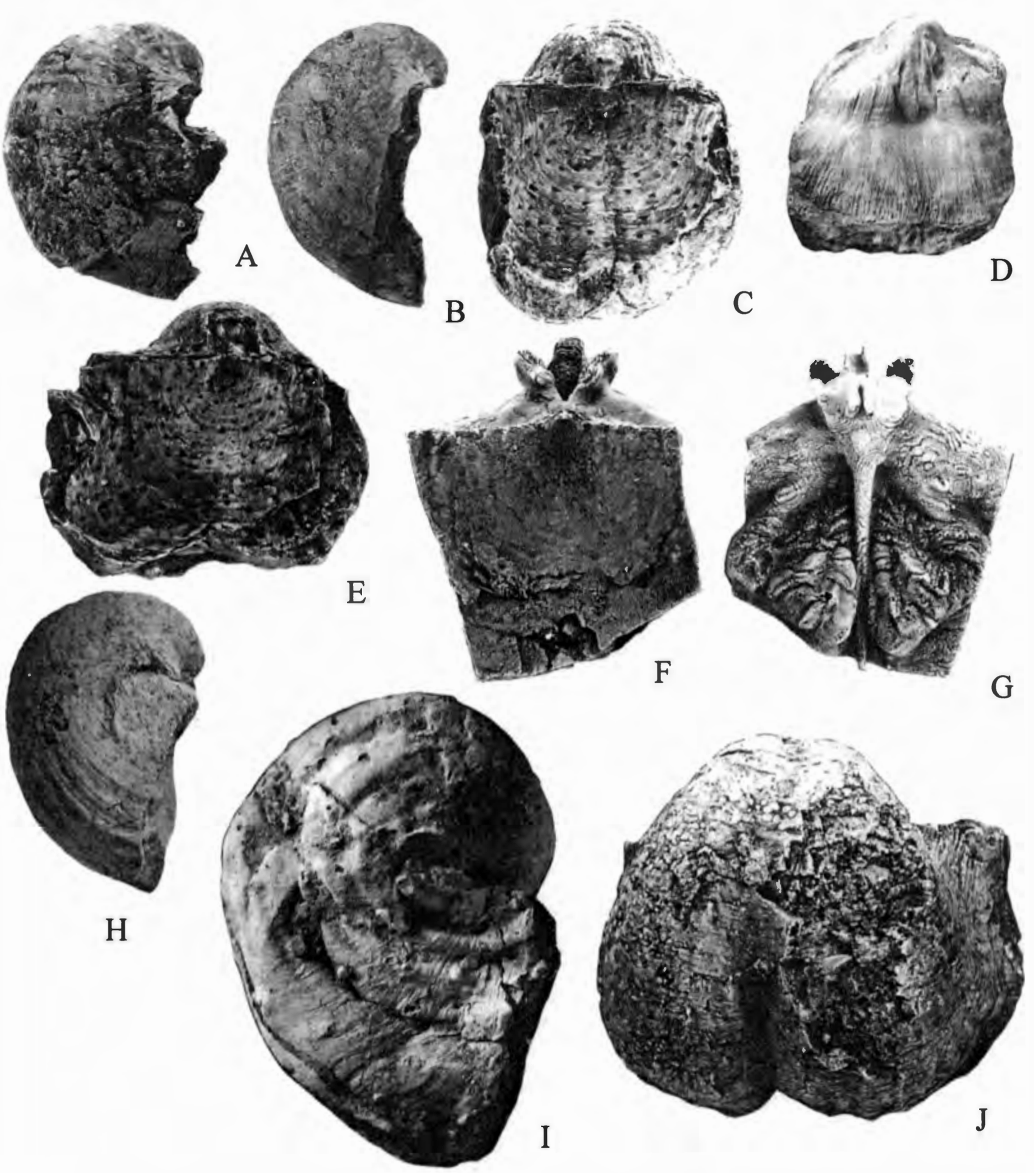


Fig. 3.18. *Bailliena yukonensis* Nelson & Johnson. A, E, lateral and dorsal views of conjoined specimen GSC 37235 from near GSC loc. 53728. B, C, lateral and dorsal views of conjoined specimen GSC 37236 from same locality. D, natural mould of ventral interior GSC 37237 from same locality. F, G, ventral and internal views of incomplete silicified dorsal valve GSC 37328 with lateral buttress plates, from GSC loc. 53984. H, lateral view of ventral valve GSC 37239 from near GSC loc. 53728. I, lateral view of ventral valve GSC 37329 from near GSC loc. 53728. J, ventral valve GSC 37240 from GSC loc. 53690. Specimens x1 except F and G, x2, from Ettrain Formation (Kasimovian), northwest Canada. R. E. Nazer, photo.

95) and Brunton et al. (2000). Brunton et al. (2000) referred to thick spine bases, valve not stated, in *Bailliena*, but such are visible only in one specimen according to Nelson & Johnson (1968) and are not evident on more than 100 specimens surveyed by Nazer (1977). Although Brunton et al. (2000) stressed the presence of a thick dorsal hinge ridge in *Praehorridonia*, a similar ridge in present in *Bailliena*.

Reference to this text and figures on *Bailliena* should be to joint authors R. E. Nazer and J. B. Waterhouse.

Genus ***Praehorridonia*** Ustritsky, 1963

Praehorridonia Ustritsky (1962a, p. 52) from the Siberian Arctic has been extensively figured, especially in Ustritsky & Chernyak (1963, pl. 18, fig. 7, pl. 19, fig. 1-3, pl. 20, fig. 1-4, pl. 21, fig. 1, 2, 4, 5). In shape the genus is usually elongate like *Bailliena*, but has stronger longer costae. There is no sign of lateral buttress plates in Fig. 18, fig. 7, or in the dorsal interior figured in Sarytcheva (1977, pl. 17, fig. 3). but a pair may be developed in Ustritsky & Chernyak 1963, pl. 21, fig. 5. A dorsal interior of a specimen of *Bailliena* shows short lateral buttress plates (see Fig. 3.18G). The visceral disc is very thick, as in some horridoniids, with long trail and high angle (Sarytcheva 1977, pl. 16, fig. 5a). Lazarev (2011) considered that the costation over *Praehorridonia* indicated a chaoiellin relationship, but subdued costae are developed in many horridoniid species and specimens, including *Bailliena, Inflatusia, Pleurohorridonia,* some *Horridonia* and other forms. Whilst it is true that some *Praehorridonia* show more persistent and regular costation than usual for horridoniids, the costation may be lost from even slightly decorticated specimens, as figured by Ustritsky & Chernyak (1963) and Sarytcheva (1977), whereas costation tends to remain stronger in decorticated *Chaoiella* and allies. Members of Chaoiellini are more transverse with larger ears than in *Praehorridonia*, and a strong dorsal hinge ridge is not developed (Ustritsky & Chernyak, 1963, pl. 18, fig. 7, pl. 21, fig. 5).

Subfamily **SOWERBININAE** Lazarev, 2005b

[Nom. transl. hic ex Subtribe Sowerbinina Lazarev, 2005b, p. 47].

Diagnosis: No ventral spines in row along hinge, but present submedianly; dorsal spines very large along hinge or outer hinge and anterior ears. Lower Permian (Sakmarian?) to Upper Permian (Changhsingian).

Tribe **SOWERBININI** Lazarev, 2005b

Fig. 3.19, Fig. 3.20

[Nom. transl. hic ex Subtribe Sowerbinina Lazarev, 2005b, p. 47].

Diagnosis: No ventral spines; dorsal spines very large along hinge or outer hinge and anterior ears. Lower Permian (Sakmarian?) to Upper Permian (Changhsingian).

Genera: *Sowerbina* Fredericks, *Bruntonia* Angiolini & Long, *Burovia* Ustritsky, *Sowburia* Lazarev.

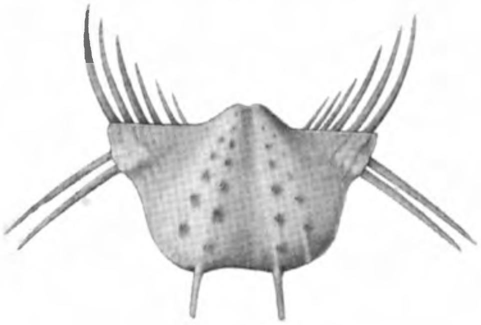


Fig.3.19. *Bruntonia maynci* (Dunbar) as reconstructed by Dunbar (1955, Fig. 20) from the "Productus Limestone" at Kap Stosch and the "Martinia-Productus limestone" (Changhsingian) of Gauss Halvo etc, Greenland, approx. x1.

Discussion: *Productus timanicus* Stuckenberg (1875, p. 86) from Indiga River, Timan, is the type species of *Sowerbina*, with the specimen in Stuckenberg (1875, pl. 1, fig. 3a, b, c) later cited as lectotype for *Sowerbina*, but Lazarev (2005a) declared that this specimen had been lost in 1974, and so nominated a dorsal valve figured by Stuckenberg (1875, pl. 1, fig. 2c, no. 24/43) as replacement. *Sowerbina* has been usually synonymized with *Horridonia*, as urged by Muir-Wood & Cooper (1960), Stepanov (1963), Logan (1966), Brunton et al. (2000) and Angiolini & Long (2008). By contrast, Sarytcheva (1960, p. 235), Gobbett (1964, pp. 95-97) and Waterhouse (1971a, p. 214) claimed that no ventral hinge row of spines was developed. Although this appears to be contradicted by a figure in Stuckenberg (1875), we argued that Stuckenberg's figure was based on a misinterpretation of the specimen, an observation ignored in other studies. Lazarev (2005a, b) showed that *Sowerbina* and allies have large spines confined to the dorsal hinge area, and allowed that *Sowerbina* has indeed no ventral hinge spines, just as claimed by Gobbett (1964) and others, although no acknowledgement of the earlier and preceeding correct observations was offered by Lazarev. On the basis of possessing dorsal hinge spines, *Sowerbina* was justifiably made the name bearer for a family group by Lazarev (2005a, b), treated in his study as a subtribe in Horridoniini.

Sowburia was recognized by Lazarev for Ufimian or lower Kazanian species with zygidium and more surface granules, and other minor features. Strikingly, he was able to point to an American species *Horridonia texana*

King, 1931, that was congeneric, and occurred in the Roadian fauna of west Texas, of much the same age. *Burovia* Ustritsky is of slightly younger age, with very thick dorsal ear spines, well formed zygidium and large pustules, and two or three rows of trail spines. Its character is masked in the *Revised Brachiopod Treatise*, because Brunton et al. (2000, Fig. 324.b) mislabelled a dorsal valve as a ventral valve.

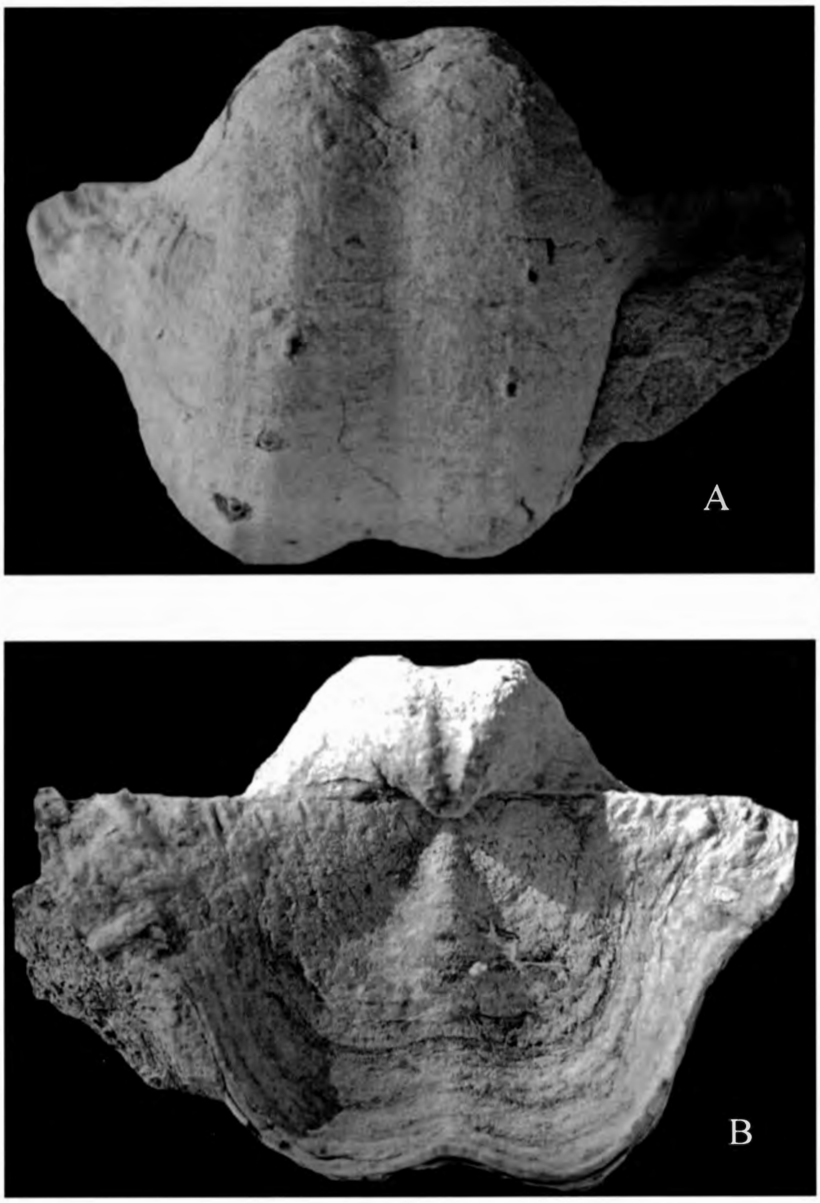


Fig. 3,20. *Bruntonia* cf. *rudis* (Dunbar), ventral and dorsal aspects of GSC 36826 from GSC loc. 57687, Trold Fiord Formation (Capitanian), Canadian Arctic, x1.5. JBW photo. (The sulcus is narrower than in type *rudis*).

Bruntonia Angiolini & Long, 2008, based on material from Spitsbergen, clearly belongs to Sowerbinini, with no ventral hinge spines, and few well developed dorsal spines in a few linear rows, as best illustrated by Dunbar (1955). In some specimens an anterior ear spine may be thicker than others, as in *Bruntonia rudis* figured by Dunbar (1955, pl. 14, fig. 7), its diameter as measured from photographs being 4.5mm compared with 3.4mm in the posterior row. Granules are well developed. The cardinal process was considered to be distinguished by being sessile in *Burovia*. Stress was also placed on the absence of a strong marginal ridge from *Bruntonia,* but that is normal for various Horridoniidae. The presence or absence of a zygidium was not determined, and although in many respects

Bruntonia falls close to *Burovia*, it has fewer ventral spines. The authors ignored the studies by Lazarev (2005a, b), and regarded *Sowerbina* as a synonym of *Horridonia*.

Tribe **KARNELLIINI** new tribe

Name genus: *Karnellia* Lazarev, 2005b, p. 47 from Djigdalin Suite (upper Artinskian), northeast Russia, here designated.

Diagnosis: No ventral spines in row along hinge; dorsal spines very large along second row of outer hinge and anterior ears. Lower Permian (Artinskian – Kungurian).

Genera: *Karnellia* Lazarev, *Vigdalia* Lazarev.

Discussion: One aspect of horridoniid morphology stressed by Lazarev (2005b) centred on the relative thickness of dorsal hinge spines, and he considered that the spines were of much the same thickness in both rows in *Sowerbina* and allies, or that the last (outermost) spine of the first row and at least one spine of the second row was of approximately equal thickness (allowing for some small latitude), whereas spines in the second dorsal ear row in "horridoniins" were one and a half to twice as thick as spines in the first row. This led to two newly proposed genera, *Vigdalia* Lazarev, 2005b and *Karnellia* Lazarev, 2005b, being treated as allied to *Horridonia*, rather than *Sowerbina*. But in type *Horridonia horridus*, as figured by King (1850, pl. 11, fig. 2), the spines in the anterior dorsal row are only slightly thicker than those of the posterior row, certainly not one and a half to twice as thick. It appears that Lazarev interpreted *Horridonia horridus* (Sowerby) from specimens figured by Muir-Wood & Cooper (1960) and Brunton et al. (2000, Fig. 323.1e), in which the spine in the anterior or second row of spines along the dorsal hinge may be at least twice as thick as spines of the first row. The figures are not of the type species, and indicate a different genus. *Karnellia* Lazarev and *Vigdalia* Lazarev, of Artinskian and Kungurian age in northeast Russia, lack ventral hinge spines, and have no pustules. They are here regarded as Sowerbininae, even though the spines in the second ear row are comparatively thick, because the absence of ventral hinge spines is considered in this study to be of greater classificatory significance than differences in dorsal ear spine thickness. Moreover it has to be noted that there is some variation in ear spine numbers and their relative thickness, particularly in faunas from Arctic Canada and from the Zechstein and Magnesian Limestone in northwest Europe.

4. Superfamily MARGINIFEROIDEA Stehli, 1954

Fig. 5.51, p. 172

[Nom. transl. Waterhouse 2002b, p. 13 ex Marginiferidae Stehli, 1954, p. 321].

Diagnosis: Genera with specialized and varied spines, especially on ventral valve, often arranged in rows along hinge and umbonal slopes, may have a number of trails. Cardinal process trilobed, the median lobe extending dorsally over the posterior grooves, adductor scars usually smooth, well developed marginal ridges and ear-baffles.

Discussion: Members of this superfamily are small and distinguished by their variously distinctive spine patterns. In Costispiniferidae spines generally occur on both valves and are comparatively uniform, fine and dense, whereas spines are ventral only as a rule and arranged in a posterior row or rows in Marginiferidae, as well as over disc and trail. 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, pp. 28, 29, Fig. 5B), often with zygidium, and dorsal anterior pustules often well developed and comparatively few in number. Dorsal adductors are generally not dendritic, and brachial shields are productiform.

- **Family Marginiferidae Stehli, 1954**
  - Subfamily Marginiferinae Stehli, 1954
    - Tribe Marginiferini Stehli, 1954
    - Tribe Pseudoavoniini new tribe
    - Tribe Caucasoproductini Kotlyar, 1989
  - Subfamily Desmoinesiinae Waterhouse, 2002b
  - Subfamily Scapharininae Cooper & Grant, 1975

- **Family Costispiniferidae Muir-Wood & Cooper, 1960**
  - Subfamily Costispiniferinae Muir-Wood & Cooper, 1960
    - Tribe Costispiniferini Muir-Wood & Cooper, 1960
    - Tribe Onopordumariini new tribe
  - Subfamily Spinomarginiferinae Waterhouse, 2002b

Table 6. Superfamily Marginiferoidea Stehli, 1954.

Family **MARGINIFERIDAE** Stehli, 1954

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

Diagnosis: Spines usually restricted to ventral valve, form row along hinge and/or umbonal slopes as a rule, of modest number, many halteroid; radial ribs and concentric rugae may be present. Heavy marginal ridges, dorsal trails simple or mutiple.

Discussion: The smooth ventral valve and well spaced well developed spines of some marginiferid genera in Marginiferinae and Scapharininae resemble the general appearance of Productellinae. *Orbinaria* (see p. 45) has moderately similar but finer and closer-set spines, said to be present on both valves (as in Costispiniferidae), and displays a thick dorsal marginal ridge. That suggests Costispiniferidae was derived from Orbinariinae, and gave rise to Marginiferidae, but the latter group has a fuller and more extended fossil record, and indeed some Marginiferidae, such as in Desmoinesiinae, have dorsal spines.

Subfamily **MARGINIFERINAE** Stehli, 1954

[Marginiferinae Stehli, 1954, p. 321].

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.

Tribe **MARGINIFERINI** Stehli, 1954

Fig. 4.1 - Fig. 4.2

[Nom. transl. Brunton, Lazarev & Grant, 1995, p. 927 ex Marginiferinae Stehli, 1954, p. 321. Syn. Jiguliconchinae Lazarev, 1990, p. 81; Hystriculininae Lazarev, 1990, p. 82].

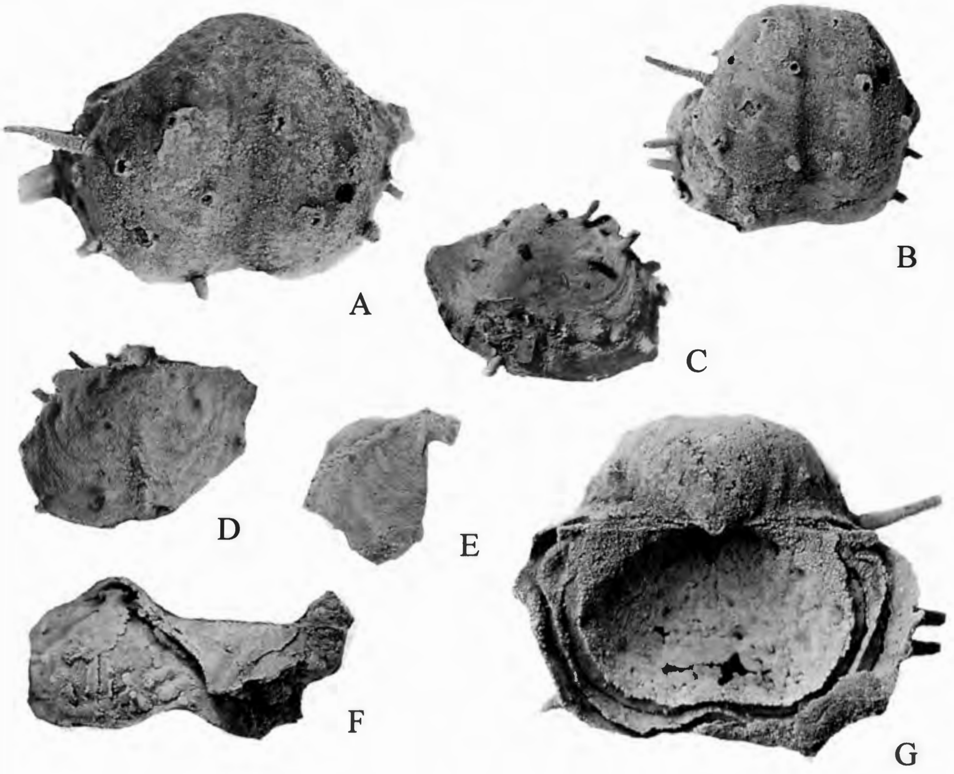


Fig. 4.1. *Otariella otaria* (Grant). A, B, G, posterior ventral, ventral anterior, and dorsal aspects of specimen with valves conjoined, ROM 32142 (formerly B20), x 2.5, x2, and x2.5. C, ventral exterior B675, x3. D, dorsal aspect of specimen with valves conjoined, B 675, x3. E, interior of broken dorsal valve, ROM 32153 (formerly B 578), x3. F, broken specimen showing part of dorsal interior, ROM 32152 (formerly B 577) x3. The extravagant ear extensions are lost, but are well illustrated in Grant (1976) and Brunton et al. (2000). Specimens silicified, from Rat Buri Limestone (Roadian), Khao Phrik, southern Thailand. All kept at Royal Ontario Museum, Toronto. B. O'Donovan and JBW photo.

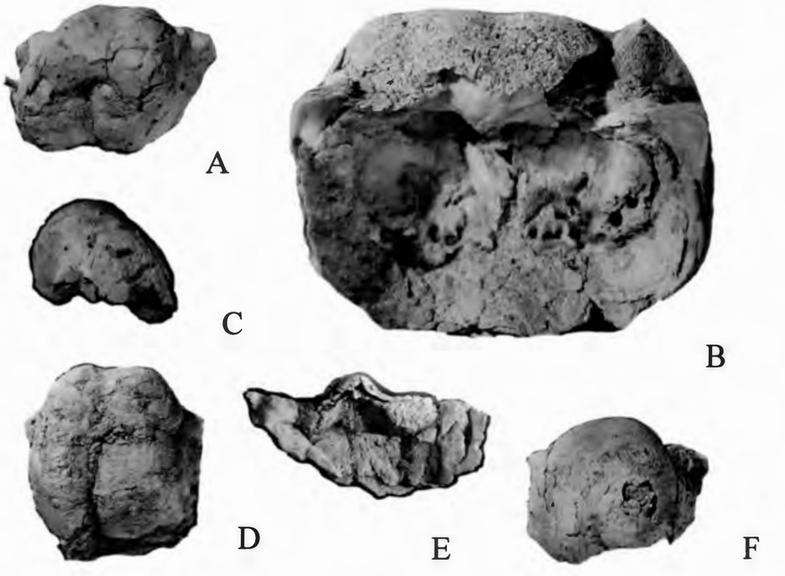


Fig. 4.2. *Azygidium mitis* (Hill). A, ventral valve, unregistered, x1. B, dorsal aspect of specimen with valves conjoined, UQF 74000, x2. C, lateral view of ventral valve UQF 73998, x 1. D, anterior ventral aspect of specimen with valves conjoined, unregistered, x1. E, dorsal aspect, UQF 73996 x 2. F, ventral valve UQF 74001 x 1. From Dresden Limestone (Sakmarian), central Queensland, Australia. All kept at Queensland Museum. J. Coker & JBW photo.

Taxonomy: Lazarev (1986a) listed his subfamily names Jiguliconchinae and Hystriculininae with no description or clarification. *Jiguloconcha*, name genus for Jiguloconchinae, was not even described until Lazarev (1990): in 1986a 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. *Jiguloconcha* is close to *Hystriculina*. Lazarev included in the family group dictyoclostid genera now referred to Spinarellini Waterhouse (see p. 165). Jiguliconchinae Lazarev and Hystriculininae Lazarev were synonymized with Paucispiniferinae Muir-Wood & Cooper, 1960 by Brunton et al. (2000, p. 443), but the nominate genera lack the strut spines typical of the latter family group.

Diagnosis: Spines on ventral valve well formed, may include row along umbonal flanks, and generally along hinge. Radial ornament subdued to well defined, concentric ornament subdued to moderate. Corpus cavity shallow to deep. Upper Carboniferous (Kasimovian) to Upper Permian (Changhsingian).

Genera: *Marginifera* (*Marginifera*) Waagen (syn. *Strigospina* Liao), *M.* (*Arenaria*) Chen & Shi, *M.* (*Nesiotia*) Chen & Shi, *Azygidium* Waterhouse, *Disparatia* new genus, *Entacanthadus* Grant, *Gadikao* new genus, *Hystriculina* Muir-Wood & Cooper, *Jiguliconcha* Lazarev, *Lampangella* Waterhouse, *Otariella* Waterhouse, *Shanxiproductus* Duan & Li.

Discussion: These genera are associated because of their shell which varies from smooth to bearing low moderately spaced ribbing. *Strigospina* Liao (1979, p. 535) was synonymized with *Marginifera* by Brunton et al. (2000, p. 439), correctly as far as can be discerned.

Genus ***Disparatia*** new genus

Derivation: dispar – unlike, dissimilar, Lat.

Type species: *Disparatia nassichuki* new species from Canyon Fiord Formation (Upper Carboniferous), Ellesmere Island, Arctic Canada, here designated.

Diagnosis: Small with swollen ventral valve and gently concave dorsal valve, thick corpus. Light radial ribs over ventral valve and low commarginal rugae over ventral disc; dorsal valve smooth or with fine rugae. Spines limited to ventral valve, in row along hinge and another row along umbonal slopes, fine and scattered over remainder of valve. Dorsal marginal ridge high, composed of numerous trails.

Discussion: This new genus is moderately close to *Hystriculina* Muir-Wood & Cooper (1960, p. 210), a genus based on *H. texana* Muir-Wood & Cooper, and ranging from upper Kasimovian to Permian. The ribs are slightly stronger in *Hystriculina*, and present over the dorsal as well as ventral valve. Commarginal rugae are virtually absent from *Hystriculina*, and the spines are coarser, and, as stated by Muir-Wood & Cooper (1960), do not form a hinge row, although a few hinge spines are visible rarely, as for example in Brunton et al. (2000, Fig. 293.3a, b). By comparison, the hinge row is well developed in *Disparatia*. As well the dorsal marginal ridge is much higher anteriorly in the new genus, and the overall shape is more elongate with more swollen and non-sulcate ventral valve.

Marginifera Waagen, 1884 of Permian age is moderately like the present form, with umbonal slope row of spines, and no hinge spine row, and larger ears: subgenera were described by Chen & Shi (2006). The basic ornament of low ribs and rugae is close apart from the lack of hinge row, but the arrangement of trails is different.

In shape, the new genus comes close to *Caruthia* Lazarev & Carter, 2000, based on *C. borealis* Lazarev & Carter from Prince of Wales Island, southeast Alaska. This has low ribs on both valves, and at least signs of low less regular commarginal rugae. (Photographs of the species are rather dark). Unlike the present form, there is no row of hinge spines, and thick spines are recorded, their position not described, but seeming to involve strut spines anteriorly as a pair (see Lazarev & Carter 2000, Fig. 1 Q, R, Y).

Disparatia nassichuki new species

Fig. 4.3, Fig. 4.4

Derivation: Named for W. W. Nassichuk.

Holotype: GSC 133296 (Fig. 4.3A, B, C) from GSC loc. 58959, Canyon Fiord Formation (Late Carboniferous), Ellesmere Island, Canada, here designated.

Diagnosis: Subelongate but with transverse visceral disc, low commarginal rugae on ventral disc, dorsal valve almost smooth or with only weak rugae and ribs; dorsal marginal ridge high anteriorly.

Material: Six specimens from GSC loc. 58959, Canyon Fiord Formation (?Upper Carboniferous), Bjorne Peninsula, Ellesmere Island, Canada. See Appendix A, Part C, p. 479.

Dimensions in mm: both valves

Specimen GSC	Width	Length	Height	
133296	20	18	11	holotype
133295	21	19	12	
133294	22.5	19.5	14	

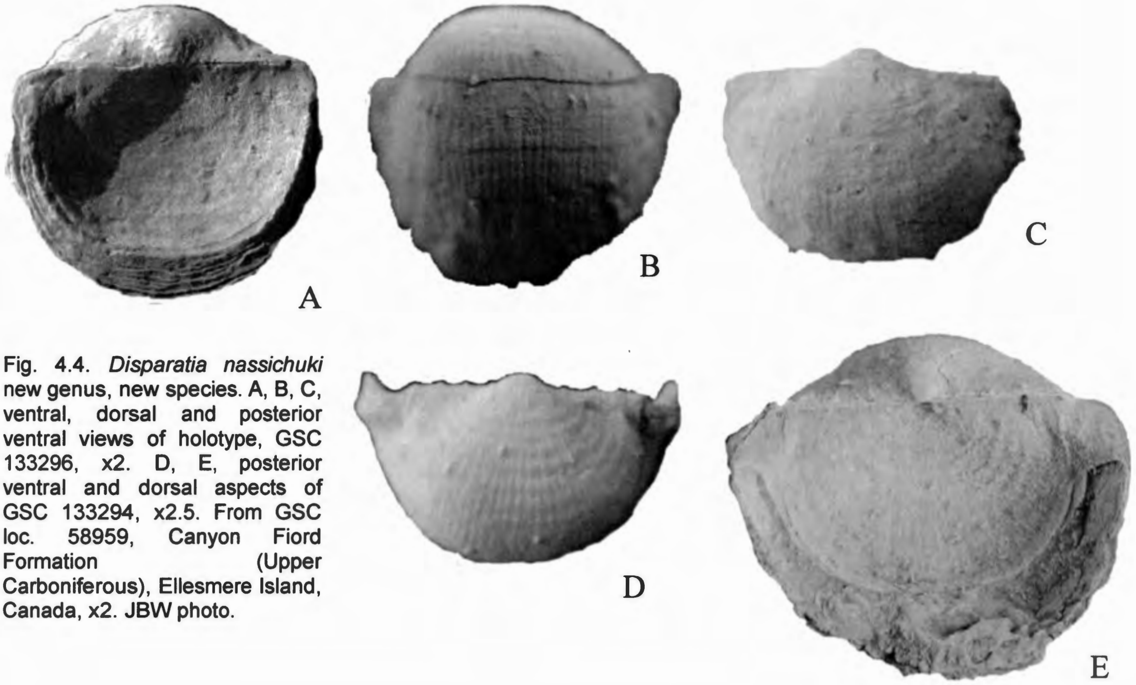


Fig. 4.4. *Disparatia nassichuki* new genus, new species. A, B, C, ventral, dorsal and posterior ventral views of holotype, GSC 133296, x2. D, E, posterior ventral and dorsal aspects of GSC 133294, x2.5. From GSC loc. 58959, Canyon Fiord Formation (Upper Carboniferous), Ellesmere Island, Canada, x2. JBW photo.

Description: Shells small with low ventral umbo, umbonal angle close to 100°, extending a little beyond the hinge but little incurved, umbonal slopes convex and merging imperceptibly with small ill-defined ears (which may have been slightly reduced by damage), disc less convex medianly, but trail long and fully convex medianly. The trail extends the valve in several growth phases, each terminating in a growth step, and changes the shape of the shell from transverse to elongate during ontogenetic development. The dorsal valve is gently concave with moderately well defined concave ears, and the trails are mutiple, and extend the valve length only slightly. The ventral disc and trail are covered by fine costellae, numbering about six in 5mm, and these are absent from the ears, and are very subdued or in different specimens absent from the dorsal valve. Very low commarginal rugae are present over the disc of both valves, but are absent from the ventral trails, which leave growth steps, compared with laminae on the dorsal valve. Spines are limited to the ventral valve. They form a row along the hinge, about seven each side of the

Fig. 4.4. *Disparatia nassichuki* new genus, new species, posterior tilted view of GSC 133298, x3. From GSC loc. 58959, Canyon Fiord Formation (Upper Carboniferous), Ellesmere Island, Canada. JBW photo.

umbo and directed laterally, and a well-spaced erect row lies along the umbonal slopes. A few other spines are scattered over the disc and trail, and tend to form a commarginal row on the anterior trail.

Resemblances: There appear to be no other species that come close. Marginiferids in the Late Carboniferous and Early Permian of the Yukon Territory in Canada show similar rows of hinge and umbonal slope spines, none quite the same, but they have different trails and have strut spines approaching those of *Paucispinifera* Muir-Wood & Cooper, 1960. *Anemonaria* Cooper & Grant, 1969 from the mid-Permian of Texas has an umbonal slope row of spines and other scattered ventral spines (see Fig. 15.6A, B, p. 315), and there are a few strong spines that suggest strut spines, placed with slight variation.

Genus **Gadikao** new genus

Fig. 4.5

Derivation: Named after Gadikao Formation, China, source of the type species.

Type species: *Spinomarginifera concentrica* He & Shi, 2008, p. 851 from Gadikao Formation (Kungurian), Qinghai, northwest China, here designated.

Diagnosis: Medium-sized shells with distinctive ornament of commarginal rugae over the disc and coarse radial ribs anteriorly and over the trail of both valves, about four in 5mm. Spines limited to ventral valve, moderately numerous, and of moderate strength, arising from crests of commarginal rugae, arranged roughly in quincunx, and in rows along the flanks, no hinge row. Dorsal valve geniculate and bears prominent marginal ridge.

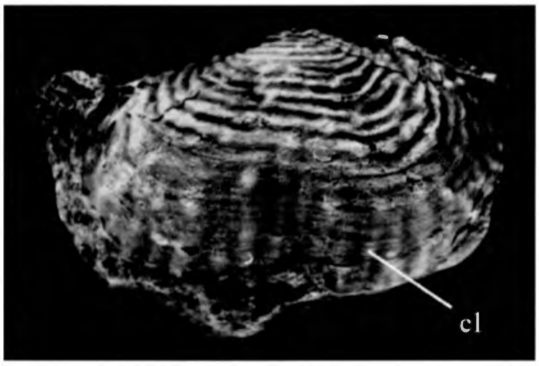


Fig. 4.5. *Gadikao concentrica* (He & Shi), holotype dorsal valve D-1f-4, x6 approx. from Gadikao Formation, South Qinghai, China. cl = concentric lines. See He et al. (2008, Fig. 3). Photo courtesy of He Weihong. Kept at China University of Geosciences, Wuhan, China.

Discussion: This genus is characterized by its striking ornament of commarginal rugae over the disc and radial ribs over the trail. The genus thus somewhat approaches *Caricula* Grant, 1976 in appearance, but has even more strongly bimodal ornament. *Caricula* bears a few strong strut spines, and belongs to Paucispiniferidae, whereas *Gadikao* has spines that are fine and of moderately even strength over the disc and in well defined rows over the flanks. The genus is readily distinguished from *Spinomarginifera* Huang, 1932 (see p. 106) by the lack of dorsal spines and the lack of fine and numerous ventral spines. Further detail is provided by He & Shi (2008).

There is a degree of similarity to the shells described as *Tyloplecta persica* Sestini & Glaus (1966, p. 907, pl. 64, fig. 2, 3) from the Upper Permian (Wuchiapingian) Nesen Formation of north Iran, in that the ventral valve of this species displays strong commarginal ornament over the disc, and radiating ribs over the trail, but unlike *Gadikao*, the ribs commence on the disc.

Tribe **PSEUDOAVONIINI** new tribe

Fig. 4.6

Name genus: *Pseudavonia* Wang in Zhang et al. 1983 from Lower Permian of Kun Lun Mountains, northwest China.

Diagnosis: Shells close to *Marginifera*, distinguished by sturdy ribs. Lower to Upper Permian (Sakmarian – Wuchiapingian.

Genera: *Pseudoavonia* Wang, *Elliottella* Stehli (nom. nov. pro *Psilonotus* Stehli, 1954 non Walker, 1834), *Jipuproductus* Sun, *Liosotella* Cooper, *Paraplicatifera* Zhao & Tan.

Discussion: These genera are distinguished by their strong ribs, and are limited to east Asia and North America, in paleotropical faunas of Permian age. The Asian genera were poorly known at the time of the *Revised Brachiopod*

Treatise, but now may be shown to belong to Marginiferinae, because they lack dorsal spines and have one or two well developed rows of spines along the ventral umbonal slopes.

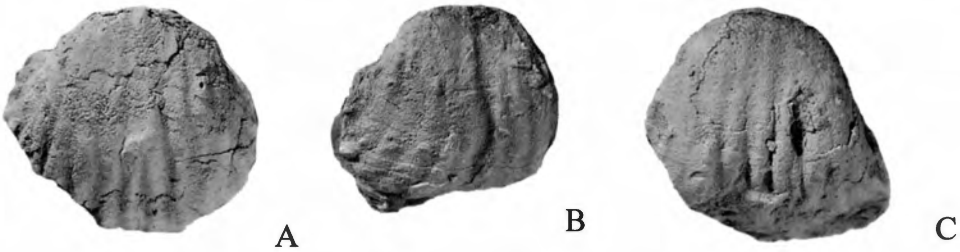


Fig. 4.6. *Liosotella multiplicata* Waterhouse. Three ventral valves from Late Permian (Wuchiapingian) of upper Shyok Valley, northwest India. See Waterhouse in Waterhouse & Gupta (1983). Kept at Centre of Advanced studies in Geology, Chandigarh, India. J. Coker & JBW photo.

Genus ***Pseudoavonia*** Wang in Zhang et al. 1983

Fig. 4.7

Type species: *Marginifera lopingensiformis* Ustritsky, 1960, p. 28, junior synonym of *M. lopingensis* var. *kunlunensis* Terra, 1932 (fide Chen & Shi 2006, p. 138) from upper Lower Permian of Kun Lun Mountains, northwest China.

Diagnosis: Small, anteriorly ribbed, geniculate, spines form two rows along umbonal flanks, as well as moderately dense over umbo and anterior, no dorsal spines.

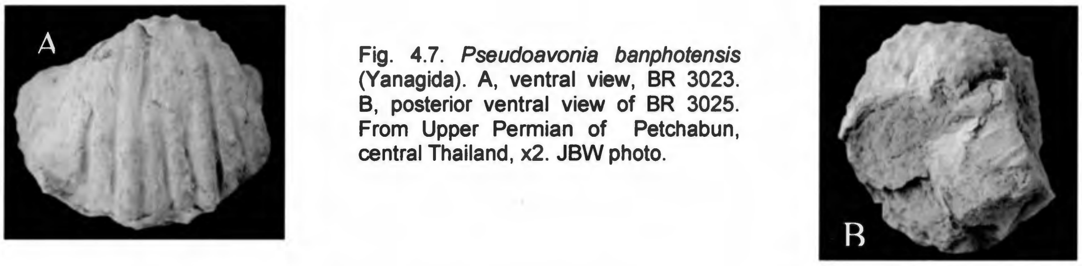


Fig. 4.7. *Pseudoavonia banphotensis* (Yanagida). A, ventral view, BR 3023. B, posterior ventral view of BR 3025. From Upper Permian of Petchabun, central Thailand, x2. JBW photo.

Discussion: *Pseudoavonia* was assigned to Costispiniferini by Brunton et al. (2000), but has been revised by Chen & Shi (2006, p. 138 ff, pl. 4, fig. 1-18, pl. 8, fig. 13, text-fig. 11) to show that two rows of ventral spines are developed along the umbonal slopes, and that there were no dorsal spines. In the discussion of the genus the diductor scars were described as dendritic by Chen & Shi (2006), but this was amended in the species description, to specify that the anterior ventral adductor scars were weakly dendritic.

Marginifera banphotensis Yanagida, 1964, pl. 3, fig. 2, 3 from the younger Permian of Thailand near Petchabun is possibly congeneric, although the dorsal valve is not well known. The ventral spines are more numerous posteriorly than in the Chinese species, but costae are similarly strong in front of an umbonal smooth portion, and a double row of spines is well developed along the ventral umbonal flanks.

Genus ***Paraplicatifera*** Zhao & Tan, 1984

Type species: *Paraplicatifera* Zhao & Tan, 1984, p. 26 from Lower to Middle Permian of China.

Diagnosis: Subelongate shells with strong ribs.

Discussion: The poorly known known genus *Paraplicatifera*, with dorsal valve not preserved, was included in Costispiniferini by Brunton et al. (2000, p. 436). But Sone et al. (2009, p. 805) described *P. thaica* from the Wordian of central Thailand to show that dorsal spines were absent. Moreover a ventral umbonal slope row of spines is well developed, and dorsal pits opposed the ventral umbonal slope row. Although Sone et al. (2009) continued to refer the genus to Costispiniferini, the distribution of spines clear shows that the genus is a member of Marginiferinae. It has posterior rugae and strong ribs anteriorly.

Genus *Jipuproductus* Sun, 1983

Type species: *Jipuproductus jipuensis* Sun, 1983, p. 124, pl. 16, fig. 4, 5 from Artinskian of Xizang, China.

Discussion: This genus was not figured in Brunton et al. (2000), and is not well known. But it has strong ribs and so appears to be a member of this tribe. Figures show strong dorsal hinge ridges and ear baffles, but spinosity is unclear and the relationship to other members of the tribe is obscure.

Tribe **CAUCASOPRODUCTINI** Kotlyar, 1989

[Nom. transl. hic ex Caucasoproductinae Kotlyar, 1989, p. 121. Syn. Asioproductinae Liang, 1990, p. 161].

Taxonomy: Caucasoproductinae was synonymized with Paucispiniferinae Muir-Wood & Cooper, 1960 by Brunton et al. (2000, p. 443), but unlike *Paucispinifera* and allies, *Caucasoproductus* lacks strut spines (see Kotlyar 1989, p. 121; Kotlyar et al. 2004, p. 521). With its closely reticulate disc, and dorsal external pits, it looks like some dictyoclostids, such as Rigrantiini Lazarev (p. 121), but also resembles *Transennatia* Waterhouse and *Asioproductus* Zhan. On the other hand, Kotlyar in Kotlyar et al. (2004) referred to the genus as sole representative of Family Caucasoproductidae, regarded as somewhat allied to *Diaphragmus* Girty (see p. 112), and offered no rebuttal of the assessment by Brunton et al. (2000). The genus remains less well known than other genera in the tribe, and further evaluation may challenge the present interpretation.

Diagnosis: Marginiferinae with ornament dominated by closely spaced ribs and low posterior rugae. Upper Carboniferous (Moscovian?) to Upper Permian (Changhsingian).

Genera: *Caucasoproductus* Kotlyar, *Asioproductus* Zhan, *Cymoproductus* Xu, ?*Jinomarginifera* Shen, Shi & Archbold, *Minispina* Waterhouse, *Oncosarina* Cooper & Grant, *Transennatia* Waterhouse (syn. *Gratiosina* Grant).

Discussion: *Caucasoproductus, Asioproductus* and *Transennatia* were treated as Paucispiniferini by Brunton et al. (2000, pp. 444 - 447), and Asioproductinae Liang left unmentioned by Brunton et al. (2000). Unlike Paucispiniferini, strut spines are missing from these genera.

Jinomarginifera Shen, Shi & Archbold, 2003 has well formed ribs and feeble ventral spines, and no anterior dorsal marginal ridge. It was classed as Paucispiniferini by Brunton (2007, p. 2642), but appears to lack strut spines and indeed looks, at least superficially in terms of its radial ornament, like Retariinae, although retariin spine patterns are not displayed.

Genus ***Minispina*** Waterhouse, 1982b

Fig. 4.8

Type species: *Minispina alata* Waterhouse, 1982b, p. 46 from Khao Luak Formation (early Moscovian) of north Thailand.

Fig. 4.8. *Minispina alata* Waterhouse, external mould of dorsal valve BR 3026, x5 approx. From Khao Luak Formation (early Moscovian), Huai Bun Nak, central north Thailand. JBW photo.

Diagnosis: Small transverse shells with large ears and wide hinge, strong radial and concentric ornament, spines limited to ventral valve, in row along hinge and along umbonal flanks, rare and fine over disc and trail.

Discussion: The radial and concentric ornament of *Minispina* somewhat approaches that of Desmoinesiinae (see p. 101) of similar Upper Carboniferous age, but *Minispina* lacks dorsal spines. The genus appears to resemble Lower Permian and younger genera such as *Retimarginifera* Waterhouse, known from Australia, southeast Asia and China, but *Retimarginifera* has strut spines. *Transennatia* Waterhouse, 1975, type species *Productus gratiosus* Waagen, 1884, p. 691 is closer in spine detail, but is small with less developed ears and strong ribs differently arranged. The type species of *Transennatia* has a row of spines along the hinge and another along the umbonal flanks (Grant 1976, pl. 33, fig. 24), even though Grant (1976) in correctly allocating *gratiosus* to Marginiferinae, made no mention of a row developed along the hinge.

Strangely, Brunton et al. (2000, pp. 469, 470) considered *Minispina* to be "similar to *Kozlowskia*, possibly differing by having no dorsal trails". *Kozlowskia* obviously has smaller ears and less emphasized commarginal rugae, and moreover has conspicuous strut spines that are not developed on *Minispina*, as was made clear in the original description and diagnosis. Specimen BR 3026 shows well the large smooth ventral ears. Spines are well spaced along the hinge, and are also well spaced in a row at the junction between the inner ears and umbonal slopes, unlike the arrangement in *Kozlowskia*. A trail is present, despite the assertion in Brunton et al. (2000) that there were possibly "no trails."

Genus **Asioproductus** Chan (=Zhan), 1979

Type species: *Asioproductus bellus* Chan (=Zhan) in Hou, Zhan & Chen, 1979, p. 85 from Late Permian of Guangtung, China.

Diagnosis: Small shells with costae crossed over the disc by commarginal rugae, ventral spines form row along umbonal slopes and scattered and moderately numerous over ventral valve.

Discussion: *Asioproductus* was synonymized by Brunton et al. (2000) with *Transennatia* Waterhouse, 1975, based on *Productus gratiosus* Waagen, 1884 from the Upper Permian (Wuchiapingian) of the Salt Range, Pakistan, and this synonymy appears to be well justified by the general similarity in size and shape, ribs, rugae and spines. But the type species of *Asioproductus* appears to lack a hinge row of spines, whereas a row is developed in type *gratiosus*, as revealed by inspection of the types at the Geological Survey of India, Calcutta. The lectotype GSI 3687 (Waagen 1884, pl. 72, fig. 3a-d) as designated by Waterhouse (1975, p. 10) has an umbonal slope row near the umbo, with the diameter of the spines increasing laterally, and a possible hinge row, as in GSI 3688 (Waagen 1884, pl. 72, fig. 4a-d), and although the hinge row is not mentioned in the text, two hinge spines are indicated in fig. 4c (Waterhouse 1978, p. 118). A figure in Grant (1976, pl. 33, fig. 24) confirms that the type species has a row of spines along the hinge and another along the umbonal slopes. Basleo (Wuchiapingian) specimens from Timor were referred to *gratiosus* by Broili (1916, pl. 2, fig. 4, 5, 11) and the specimen in fig. 5 shows a hinge row: the ribs differ from those of the Salt Range, to suggest a specific difference. (Reference of the Timor material to *Spyridiophora* with a query by Termier & Termier 1970b, p. 58 may be doubted because Broili's specimens are more reticulate than the Cambodian types). Bitauni specimens so named (Broili 1916, pl. 2, fig. 12, 13) appear to belong to *Retimarginifera*. The Changhsingian species *Transennatia pitakpaivani* Waterhouse (1983d, pl. 3, fig. 4-10) – see Fig. 4.9 – also has a hinge row of spines, a few additional spines on the ears and a few along the umbonal slopes and disc.

In *Asioproductus*, one row of spines is developed along the umbonal slopes, and no spines are visible along the hinge. This arrangement is close to that described for *Gratiosina insculpta* Grant (1976, p. 135, pl. 32, fig. 1-37, pl. 33, fig. 1-16) from the early Middle Permian Rat Buri Formation of Thailand. Grant (1976, p. 131) had allocated the Thai species to the same genus as *Productus gratiosus*, and referred that species to *Gratiosina*, which was considered in page proof to be a junior objective synonym of *Transennatia*. The species *insculpta* is closer to *Asioproductus* in spine detail. Indeed on present evidence, *insculpta* was the older form, and both persisted into younger faunas.

In *Transennatia gratiosus* figured by Reed (1944, pl. 19, fig. 6, 7a) and Grant (1976, pl. 33, fig. 23), the septum is short and brachial shields extend well beyond, whereas in *Asioproductus bellus* the septum is very long, extending to the start of the trail (Zhan 1979, Fig. 18). But in *Asioproductus insculpta* (Grant) the septum is very short, and in *T. pitakpaivani* (see Fig. 4.9) so short that it lies totally behind the brachial shields. The length of the dorsal septum and relationship to brachial shields, deemed critical for genus separation amongst linoproductiform genera by Lazarev (2010), would appear to be less significant for these marginiferoids.

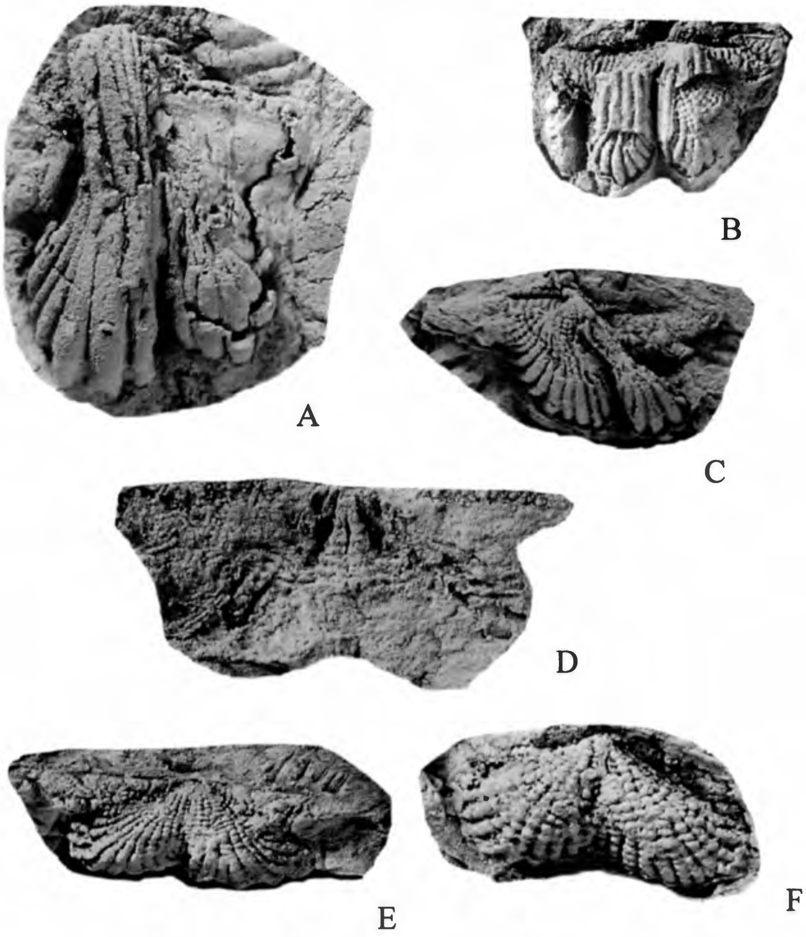


Fig. 4.9. *Transennatia pitakpaivani* Waterhouse. A, ventral valve latex cast of exterior, TBR 421, x3. B, dorsal external mould of holotype, TBR 417, x1.8. C, dorsal external mould TBR 418, x2. D, dorsal internal mould TBR 419, x2.5. E, external mould of dorsal valve TBR 420, x1.5. F, external mould of dorsal valve, TBR 416, x2. From Huai Tak Formation (Lopingian), northwest Thailand. See Waterhouse (1983d). J. Coker & JBW photo.

Subfamily **DESMOINESIINAE** Waterhouse, 2002b

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

Diagnosis: Spines on ventral valve somewhat like those of Marginiferinae with umbonal slope or hinge rows, tending to be multiple; may display moderate number of dorsal spines. Ribs and concentric rugae moderately developed. Upper Carboniferous (Moscovian).

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

Discussion: *Desmoinesia* is close to marginiferins externally and internally, but the single spine rows have become slightly diffused by the presence of more spines, and dorsal spines are present in two genera. *Desmoinesia* is marginiferid internally. *Sandia* is not so close and has less developed dorsal marginal ridge (Sutherland & Harlow 1973). The group would appear to have provided source material for younger and more spinose Costispiniferidae.

Genus ***Hexiproductus*** Chen & Shi, 2008

Fig. 4.10

Hexiproductus Chen & Shi in Shi et al. (2008) is close to *Desmoinesia*, and was distinguished on the basis of having narrower and less consistent costae, and no dorsal spines. Shi et al. (2008) provided an interesting summary of the distribution through time of the genus, which they regarded as monospecific. The migration tracks through time that were analyzed by Shi et al. (2008) help demonstrate the precariousness of any evolutionary study that is geographically limited to one part of the earth's crust. *Hexiproductus* was referred to Paucispiniferini by Chen & Shi in Shi et al. (2008), but the spine pattern is quite different, and no strut spines are present on *Hexiproductus*. The lack of dorsal spines from *Hexiproductus* may imply marginiferin links, but the distinctive ribbing so close to although not the same as that of *Desmoinesia* and the nature and distribution of ventral spines suggest a desmoinesiin alliance, with secondary loss of the dorsal spines. *Desmoinesia* was placed in Breileenini Brunton by Brunton et al. (2000, p. 441) but Chen & Shi in Shi et al. (2008) did not recognize the validity of the tribe.

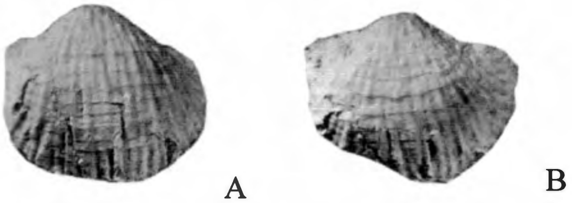


Fig. 4.10. *Hexiproductus echidniformis* (Grabau). A, B, antero-ventral and postero-ventral aspects of NMV P309596 from Hexi Corridor Terrane (Gzhelian), north China, x1.5. See Shi, Chen & Tong Jin-nan (2008).

Breileenia Brunton in Brunton & Lazarev (1997, p. 389) is too poorly known internally to be sure of its family affinities. The genus is of upper Tournaisian – Serpukhovian age and has weak ribs and elongate ventral spine bases. It externally shows a degree of similarity to *Desmoinesia* Hoare of Upper Carboniferous age: both genera have dorsal spines, and moderately concave dorsal valve. *Desmoinesia* is clearly marginiferoid, bearing hinge and umbonal slope row of ventral spines (see Muir-Wood & Cooper 1960, p. 229 re *Rudinia*, an objective synonym). Unfortunately Brunton failed to provide a detailed description of the ventral spines in his two species of *Breileenia*, but implied that spines are arranged fairly regularly over the venter and trail: there is no indication that hinge or umbonal slope rows of spines are developed, whereas the ventral valve of *Desmoinesia* has a hinge row of spines and one or two umbonal slope rows of spines. The interior of *Breileenia* is poorly known but does show dorsal lateral ridges at the ears; whether it was close to *Desmoinesia* remains uncertain, and indeed if reliance is to be placed on Brunton's exposition of ventral spines, seems unlikely. Its spine pattern differs and ventral ribs are less continuous and less crossed by concentric rugae, but does, to a degree, recall that of the English material assigned to the Visean genus *Cinctifera* Muir-Wood & Cooper, 1960 (see Brunton et al. 2000, pp. 462-463). But type *Cinctifera* Muir-Wood & Cooper has more prominent ribbing, and as well its dorsal valve is flatter over the disc and more geniculate anteriorly. There needs to be more analysis to demonstrate that *Breileenia* is not avoniid, through comparative description of the ventral spinosity, and discovery of internal detail.

Subfamily **SCAPHARININAE** Cooper & Grant, 1975

Fig. 4.11

[Nom. transl. hic ex Scapharinidae Cooper & Grant, 1975, p. 895].

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. Middle Permian (Roadian) to Upper Permian (Changhsingian).

Genera: *Scapharina* Cooper & Grant, *Callyconcha* Waterhouse, *Rhytisia* Cooper & Grant, *Simplicarina* Cooper & Grant.

Discussion: Brunton et al. (2000, p. 441) amalgamated most of the genera as Incisiini Grant, and included *Scapharina* without realizing the family group implications: Scapharininae if cofamilial has priority over Incisiinae. *Cyrtalosia* and *Incisius* are of similar and unusual shape, and *Incisius* has the extended brachial ridges characteristic of Cooperinae Pajaud, and is interpreted quite differently from the position in Marginiferinae that was allocated by Brunton et al. (2000, p. 441). Scapharininae remains marginiferid. The position of *Incisius* and *Cyrtalosia* are further discussed on p. 271 and p. 303. Liang (1990) treated Incisiini as a member of his Order Punctoproductida, Suborder

Dipunctellidina Liang, as outlined on p. 271, the subtriangular shape of *Incisius* suggesting an approach to Loczyelloidea.

Callyconcha Waterhouse was put in Costispiniferini by Brunton (2007, p. 2639), but lacks dorsal spines and has few ventral spines, clustered laterally, and clearly belongs to Scapharininae. Spines tend to be rather few but as a rule form a variably discriminated row along the ventral umbonal slopes.

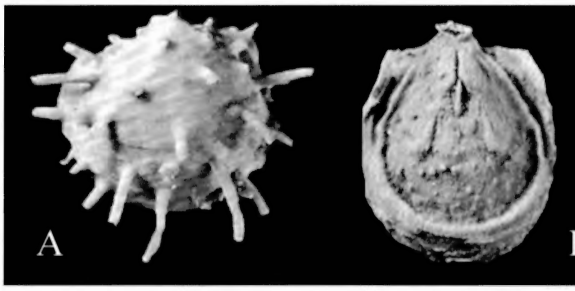


Fig. 4.11. A, *Rhytisia rugosa* Cooper & Grant, ventral valve USNM 154000b, x3 approx., from Road Canyon Formation (Roadian), United States. B, *Scapharina rugosa* Cooper & Grant, dorsal interior USNM 154227h, x4 approx., from Hegler Member (Capitanian), Bell Canyon Formation, United States. See Cooper & Grant (1976).

It is true that the spine arrangements in this subfamily are less organized than in other groups attributed to the family, and that may be secondary, or may indicate that the subfamily should be classed as allied to Costispiniferidae. There may be a case for treating the group as a distinct family.

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

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

Diagnosis: Spines numerous and on both valves. No distinct ventral hinge or umbonal slope rows.

Discussion: Like *Orbinaria* Muir-Wood & Cooper, 1960, members of this family have dorsal as well as ventral spines. *Orbinaria* is of upper Famennian to possibly Hastarian age, and the oldest known member of Costispiniferidae is much younger, at Upper Carboniferous, so that Costispiniferidae possibly redeveloped dorsal spines in evolving from Marginiferidae. But members lost the well formed posterior rows of ventral spines which help typify Marginiferidae.

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

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

Diagnosis: Subquadrate to suboval shells with spines on both valves, rugae not well developed. No dorsal adductoral septa.

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

Fig. 4.12

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

Diagnosis: Ventral spines may be differentiated, many coarse and halteroid, ventral ribs and dorsal pits 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. Lower Permian (Sakmarian) to Upper Permian (Wuchiapingian).

Genera: *Costispinifera* Muir-Wood & Cooper, *Comuquia* Grant, *Dyschrestia* Grant, *Echinauris* Muir-Wood & Cooper, *Nempemarginifera* new genus.

Genus ***Nempemarginifera*** new genus

Fig. 4.12

Derivation: nempe – without doubt, Lat.; Marginifera – brachiopod genus.

Type species: *Productus spinoso-costatus* Abich, 1878, p. 41 from Wuchiapingian (Djulfian) of Armenia, here designated.

Diagnosis: Small, transverse, swollen ventral valve, ventral spines spaced well apart with low rises continuing forward from spine base, and spine tunnels within shell, dorsal spines fine. Commarginal rugae fine and irregular on dorsal valve. Dorsal marginal ridge thick, adductor bordering ridges low or absent.

Discussion: A small group of species from the Djulfian of Armenia, described by Abich (1878), and revised by Sarytcheva (1965) as *helica, spinosocostata*, and possibly *labaensis* Licharew and *pygmaea* Sarytcheva, differ from *Spinomarginifera* of China and southeast Asia in displaying much less regular commarginal rugae, the ventral valves of *helica* and *spinosocostata* being particularly smooth, with low rugae faintly visible on *pygmaea* and irregularly present over the dorsal valve of *labaensis*. The ventral spines are also spaced further apart and are coarser, and the anterior development of fine ribs on many *Spinomarginifera* is missing. There are no well defined rows of spines along the ventral hinge or umbonal slopes. Internally, there are less conspicuous rims to the dorsal adductor scars, although low rims are visible in a dorsal valve ascribed to *labaensis* (Licharew) by Sarytcheva (1965, pl. 37, fig. 5b). The dorsal marginal ridge is especially thick (Sarytcheva 1965, pl. 37, fig. 8), and spine tunnels are visible on the internal mould of the ventral valve in Sarytcheva (1965, pl. 37, fig. 5a). The genus is found in southeast Europe and extends through Armenia and Iran as far east as the Karakorum Range in northwest India (Sarytcheva 1965, Waterhouse 1983b, Angiolini et al. 2010).

Fig. 4.12. *Nempemarginifera spinosocostatus* (Abich). A, ventral valve lectotype PIN no. 35/99 from Armenia. B, C, *N. helica* Abich), ventral and dorsal aspects of valve PIN 1649/12 from Armenia. See Sarytcheva (1965, pl. 37). Specimens of Wuchiapingian age, x1.

The genus is characterized by the short spine ridges of the ventral valve. *Comuquia* Grant, 1976 and *Dyschrestia* Grant, 1976 from Roadian faunas of south Thailand have a smooth shell and strong erect spines, and *Echinauris* Muir-Wood & Cooper from Wordian of Texas, United States, is moderately close but lacks extended ventral spine bases. *Costispinifera* Muir-Wood & Cooper from Roadian and Wordian faunas of Texas, United States displays strong costae. These genera tend to have more swollen ventral valves and more concave dorsal disc.

Tribe **ONOPORDUMARIINI** new tribe

Fig. 4.13, Fig. 4.14

Name genus: *Onopordumaria* Waterhouse in Bamber & Waterhouse (1971, p. 205 from Ettrain Formation (Kasimovian), Yukon Territory, Canada, here designated.

Fig. 4.13. *Onopordumaria punctura* Waterhouse. A, ventral valve holotype GSC 26396, x1.5. B, internal moulds of two ventral valves, GSC 26398 and GSC 26399, x1. C, dorsal internal mould GSC 26401, x1.5. Specimens from Ettrain equivalents (Upper Carboniferous), Peel River, Yukon Territory, Canada. B. O'Donovan & JBW photo.

Diagnosis: Suboval to subquadrate shells with dorsal geniculation as a rule, characterized by very fine and closely spaced spines on both valves, aligned commarginally, ventral ornament may include some slightly stronger spines, dorsal valve with regular dimples and pits, but no regular concentric rugae. Marginal ridges well developed, especially on dorsal valve. Upper Carboniferous (Kasimovian) to Upper Permian (Changhsingian).

Genera: *Onopordumaria* Waterhouse, *Ciliciumia* new genus, *Neoplicatifera* Jin, Liao & Hou, *Zhuaconcha* Liang.

Discussion: *Onopordumaria* was misplaced in Levipustulini by Brunton et al. (2000, p. 453) but differs in ornament and internal detail. Its dorsal spine bases are not noticeably swollen, although stated to be so by Brunton et al. (2000) – see Bamber & Waterhouse (1971, pl. 23, fig. 15). The genus has two or three rows of large marginiferoid dorsal pustules internally. *Zhuaconcha* Liang, 1990, centred on *Z. hirsutispina* Liang (1990, pl. 28, fig. 1-18, text-fig. 25) from mid-Permian of China, was judged to be waagenoconchin by its author, and costispiniferin by Brunton et al. (2000, p. 436). It appears to have high dorsal marginal ridge and fine spines over both valves, and very subdued and fine even dorsal rugae. *Echinauriella* Lazarev in Brunton & Lazarev, 1997 is close to *Onopordumaria* Waterhouse, 1971a in its fine numerous spines over both valves, and has a high dorsal posterior lateral internal ridge as in *Tubersulculus* and *Krotovia* (see p. 188).

Neoplicatifera Jin, Liao & Hou, 1974, p. 309 is assigned to Onopordumariini. The genus has low growth rugae and numerous spines over both valves, much as *Spinomarginifera*, but the dorsal marginal ridge does not extend completely around the visceral disc, according to He et al. (2008), although the marginal ridge could be complete in the original specimen of *minor* figured by Huang (1932, pl. 3, fig. 3a). The species *minor* non Schellwien as identified by Huang (1932) was renamed *huangi* by Ustritsky (in Ustritsky, Hu and Chan 1960), and made the type species of *Neoplicatifera*. Wuchiapingian material referred to the genus by Shen & Zhang (2008, Fig. 4.4) shows high posterior ear baffles. Best information on the genus is provided by Huang (1932, pp. 38-41, pl. 3, fig. 1-4). Only one figure in Huang (1932) indicates the nature of the dorsal adductor scars, and these appear to be raised, without bordering platelets, unlike the arrangement in Spinomarginiferinae. Brunton et al al. (2000) suggested that the genus should be reassigned to Semicostellini within Plicatiferinae if geniculation was strong and ribs occurred on the trail, but this scenario is rejected.

Fig. 4.14. *Neoplicatifera huangi* (Ustritsky), ventral valve BR 3027, x4, from middle Permian of China. JBW photo.

Genus ***Ciliciumia*** new genus

Derivation: cilicium – covering, originally of goat's hair, Lat.

Type species: *Ciliciumia cilicia* new species from Djulfian (Wuchiapingian) of Armenia, here designated.

Diagnosis: Ventral spines very fine, low anterior radial ventral ribs, no regular commarginal rugae. Dorsal spines fine, subdued irregular commarginal growth steps and rugae. High dorsal marginal ridge.

Discussion: This is a very distinctive genus, with very fine ventral spines. The genus is found in the Lesser Caucasus of Armenia, extending through Iran (Sestini & Glaus, 1966, p. 903) to the Upper Shyok valley of northwest India (Waterhouse 1983b). There are no well defined rows of spines along the ventral hinge or umbonal slopes. The small size and density of spines is matched to some extent by *Echinauriella jisuensiformis* (Sarytcheva, 1965, pl. 34, fig. 5-

8) from Guadalupian or early Lopingian faunas of Armenia, and this genus, as proposed by Lazarev in Brunton & Lazarev (1997), has a more vaulted and much narrower ventral valve, and strong posterior dorsal ridges. Shells of *Echinauriella* have much finer spines at close to ten in 5mm, compared with five in 5mm in *Ciliciumia*, and show oblique inner ridges in the dorsal valve (Sarytcheva 1965, pl. 34, fig. 8), unlike *Ciliciumia* (Sarytcheva 1965, pl. 37, fig. 12g).

Ciliciumia cilicia new species

Fig. 4.15

1965 *Spinomarginifera ciliata* [not Arthaber] – Sarytcheva, p. 386, pl. 37, fig. 12a, b, v, z.
1966 *S. ciliata* – Sestini & Glaus, p. 903, pl. 64, fig. 7.
1983 *S. ciliata* – Waterhouse, p. 197, pl. 3, fig. 1.
2010 *S. ciliata* – Angiolini et al. Fig. 3.1.

Derivation: cilicium – covering, Lat.

Holotype: PIN no. 1649/15, figured by Sarytcheva in Ruzencev & Sarytcheva (1965, pl. 12a, b, v, z) from Djulfian of Armenia, here designated.

Diagnosis: Small, highly arched, geniculate, with fine closely spaced spines (five in 5mm) over both valves, weak spine ridges over trail, no strong commarginal rugae but weak concentric markings over dorsal disc, very shallow if any ventral sulcus, high dorsal marginal ridge.

Fig. 4.15. *Ciliciumia cilicia* new genus, new species. A – C, PIN no. 1649/15, ventral, ventral posterior and dorsal aspects of holotype, x1, from Wuchiapingian of Armenia. See Sarytcheva (1965, pl. 37). D immature ventral valve x2, from Wuchiapingian fauna of upper Shyok Valley, NW India. See Waterhouse (1983b). Kept at Centre of Advanced Studies in Geology, Chandigarh, India.

Description: The holotype is 20mm wide, 17mm long and about 12.5mm thick, as estimated from figures. The ventral umbo is broad, the hinge wide with weakly alate cardinal extremities well preserved, and very shallow sulcus commencing in front of the ventral umbo. The dorsal valve is only gently concave over the disc and curves abruptly into a long trail. Ventral spines are erect, fine and closely spaced, estimated from the figure to be some five in 5mm over mid-disc, and the trail is crossed by fine radial ribs, three or four in 5mm. The dorsal spines are also fine and erect, some six in 5mm anteriorly, with a very slightly rise anteriorly rather than a distinct fold. The cardinal process has two widely splayed lobes and the marginal ridge is very thick (see Sarytcheva 1965, pl. 37, fig. 12b).

The same taxon was reported from the Wuchiapingian Nesen Formation of north Iran by Sestini & Glaus (1966), with fine ventral spines counted as four to mostly five in 5mm (as estimated from the figure), very shallow ventral sulcus or none, and short spine ridges anteriorly. Sestini & Glaus reported that the dorsal valve was ornamented by dimples, and it is possible that spines would have been present on well preserved material. A ventral valve was described from the Wuchiapingian faunas of the upper Shyok valley in northwest India by Waterhouse (1983), with five to six ventral spines in 5mm. No spine ridges were recorded, apparently because the specimen had not reached full maturity.

Resemblances: The type specimen was figured as *Spinomarginifera ciliata* by Sarytcheva, but its spines are much finer and more numerous than shown for *Marginifera spinosocostata* var. *ciliata* Arthaber (1900, p. 264, pl. 20, fig. 9a-c) from much the same faunas in Armenia. Nor is there any indication in the description by Arthaber that the spines are unusually fine and numerous. As illustrated by Arthaber, the ventral spines number only three to three and a half in 5mm, which is certainly finer than in his other material allocated to *spinosocostata* (mostly two in 5mm), but not nearly as fine as those of the Sarytcheva material. The ventral valve shows a shallow sulcus and no radial ribs, and is less vaulted, and the dorsal valve as figured has similar commarginal laminae and fine spines, less numerous than in the present type, and lower dorsal marginal ridge. Perhaps the specimen was less mature, but that would not explain the difference in spination, although as Arthaber's figures are drawings, there may have been some inaccuracy. Sarytcheva (1965) identified, but did not describe, her material, and listed the species from the *Oldhamina* and *Haydenella* beds of the upper Djulfian (= largely Wuchiapingian) Stage. Somewhat similar fine spines were illustrated for a shell figured as *Spinomarginifera helica* from the upper Barabash beds of Primoyr by Licharew & Kotlyar (1978, pl. 20, fig. 21, 22). The material figured as *ciliata* by Licharew (1936, pl. 10, fig. 35, 36) appears to have fewer spines than in the present form, more as in type *ciliata*. Taraz et al. (1981, p. 121) listed *ciliata* from the lower Abadeh Formation of early Djulfian age in central Iran, but provided no data on spine spacing, and Angiolini et al (2010) illustrated a well preserved specimen from the Nesen Formation of north Iran.

Subfamily **SPINOMARGINIFERINAE** Waterhouse, 2002b

Fig. 4.16

[Spinomarginiferinae Waterhouse, 2002b, p. 16.]

Diagnosis: Suboval to subquadrate shells with dorsal geniculation as a rule, characterized by very fine and closely spaced spines on both valves, aligned commarginally, ventral ornament may include some slightly stronger spines. Dorsal valve with regular dimples and pits and regular commarginal rugae; rugae may develop over ventral valve. Marginal ridges well developed, especially on dorsal valve, dorsal adductor scars bordered or divided by short platelets. Middle Permian (?Capitanian) to Upper Permian (Changhsingian), possibly basal Triassic.

Genera: *Spinomarginifera* Huang (syn. *Rugosomarginifera* Xu), *Piyasinia* new genus.

Discussion: The inner side of the dorsal adductor scars is raised as a slender ridge in various *Spinomargifera* from China, Japan and southeast Asia, as shown in illustrations of various species by Li & Shen (2008), Liao (1980a, b), Shi & Shen (1998) and Tazawa (2012), to mention a few of the more recent studies, although it is true that the rims could be anderidia, for muscle scars are not that clearly impressed. These ridges do not extend as far back as the base of the cardinal process as a rule, but in an example figured by Tazawa (2012, Fig. 4.3a), intersect the medium septum. In a Thai species, it is clearly the outer rim of the dorsal adductor scars that is raised (Waterhouse 1983d).

Rugosomarginifera Xu, 1987 as based on *Marginifera jisuensis* Chao, 1927, p. 149 is characterized by rugae over both valves, but so is *Spinomarginifera*.

Fig. 4.16. *Spinomarginifera* sp. Internal moulds of two dorsal valves, BR 3159 and BR 3162, showing cardinal process, marginal ridge, median septum, and high septa inside the dorsal adductor scars, with brachial ridges in B, prominent row of pustules in front, and bordering trail. The ears and hinge of the ventral valve are visible, and fine ventral spines are visible as tiny dark holes to the right in B, as arrowed, representing spine bases on the external mould. From northern Thailand, of Changhsingian age. JBW photo.

Spinomarginifera has been reported from basal Triassic beds in Italy (Chen et al. 2006), but the nature of the internal dorsal valve may need verification.

Genus ***Piyasinia*** new genus

Fig. 4.17

Derivation: Named for Sangat Piyasin.

Type species: *Spinomarginifera plana* Waterhouse, 1983d, p. 124 from Huai Tak Formation (Changhsingian), north Thailand, here designated.

Diagnosis: Characterized by having short diverging plates bordering posterior sides of dorsal adductor scars. Ventral valve spines moderately strong, well spaced, with fine growth lines, commarginal rugae very fine, dorsal spines numerous and fine.

Discussion: As noted previously, *Spinomarginifera* and allies have adductoral plates in front of or within the adductor scars: those of this genus lie behind. The holotype is TBR 423, figured in Waterhouse (1983d, pl. 3, fig. 1, 2). The ventral spines are comparatively sparse and well spaced, approaching those of *Nempemarginifera* (see above) from Armenia, and also display spine tunnels within the shell, but the Armenian genus lacks adductoral plates. The dorsal interior shows well developed and few high anterior pustules, as developed in other members of the group. Shi & Shen (1998, p. 509) considered that the species *plana* was comparable in size and outline to *Spinomarginifera chenyaoyanensis* Huang (1932, p. 63, pl. 5, fig. 18, 19) from the Upper Permian of China, but Huang's specimens appear to have commarginal rugae and denser ventral spines. In the specimens so identified by Shi & Shen (1998, Fig. 4.8-10) the dorsal adductoral plates lie in front of the scars, not behind.

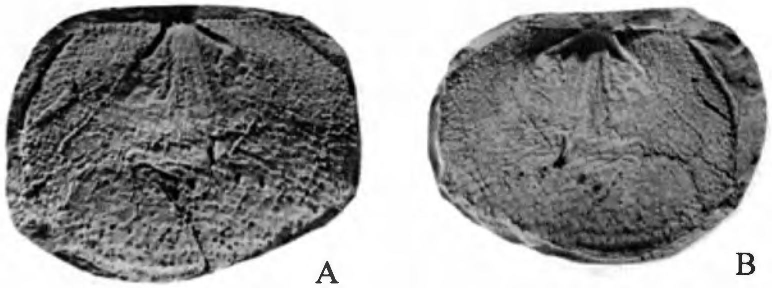


Fig. 4.17. *Piyasinia plana* (Waterhouse), internal mould and latex cast of dorsal valve TBR 428, showing plates outside of adductor scars, x5. From Huai Tak Formation (Changhsingian), north Thailand. J. Coker & JBW photo.

5. Superfamily **PRODUCTOIDEA** Gray, 1840

Fig. 5.51, pp. 172, 173

[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, strong in some groups, may be numerous over dorsal valve. Radial ornament prominent, commarginal ornament varied but present and usually strong, shells small to large in size, simple to moderately elaborate and often geniculate trails. Corpus cavity shallow to deep, muscle adductor scars generally dendritic, marginal ridges moderate to high in Productidae and variably developed in other families.

Discussion: The characteristic ribbing that gives rise to prominent spine bases suggests derivation for Productoidea from amongst *Lomatiphora* Roberts (Tournaisian), *Seminucella* Carter and *Spinocarinifera* Roberts (lower Tournaisian), classed as Lomatiphoridae Roberts, and preceeded by *Margaritiproductus* Lazarev (upper Famennian), classed in Margaritiproductini, Subfamily Productellinae. These genera may display cardinal pit and lateral buttress plates, and subdued costae bearing spines of varying description. They are only slightly older than earliest Buxtoniidae of Tournaisian age, and are small, and given what is known of age and morphologies, likely to have arisen from the Lower to Middle Devonian Tribe Productellini, Subfamily Productellinae of Superfamily Productelloidea, distinguished from Productoidea through the presence of teeth and sockets and low interareas.

It is true that *Productus* and allies of Productinae also show attributes of Linoproductinae in the prominence of radial ribbing and erect ventral spines. This possible source is judged less likely, on the basis that *Productus* also displays low regular posterior costiform rugation, indicating kinship with Dictyoclostidae, and also weakly developed in *Lomatiphora* and Buxtoniidae, and a split dorsal septum. The linoproductid ribs are more slender than those of *Productus*. Therefore Productoidea are at present viewed as a unified group, which arose in early Carboniferous time from productellid stock.

Family Lomatiphoridae Roberts , 1971

Family Productidae Gray, 1840
- Subfamily Productinae Gray, 1840
- Subfamily Diaphragminae Waterhouse, 2002b

Family Retariidae Muir-Wood & Cooper, 1960
- Subfamily Retariinae Muir-Wood & Cooper, 1960
  - Tribe Retariini Muir-Wood & Cooper, 1960
  - Tribe Protoniellini new tribe
  - Tribe Rigrantiini Lazarev, 2000b
    - Subtribe Rigrantiinai Lazarev, 2000b
    - Subtribe Antiquatoniinai new subtribe
  - Tribe Spyridiophorini Muir-Wood & Cooper, 1960
- Subfamily Reticulatiinae Lazarev, 2000b

Family Buxtoniidae Muir-Wood & Cooper, 1960
- Subfamily Buxtoniinae Muir-Wood & Cooper, 1960
  - Tribe Buxtoniini Muir-Wood & Cooper, 1960
  - Tribe Spinifronsini Waterhouse, 1981
  - Tribe Dowhataniini new tribe
- Subfamily Tolmachoffiinae Sarytcheva, 1963
- Subfamily Marginatiinae Waterhouse, 2002b
- Subfamily Tyloplectinae Termier & Termier, 1970

Family Dictyoclostidae Stehli, 1954
- Subfamily Dictyoclostinae Stehli, 1954
  - Tribe Dictyoclostini Stehli, 1954
  - Tribe Inflatiini Sarytcheva, 1977
  - Tribe Liraplectini Chen & Shi, 2000
  - Tribe Labaellini Kotlyar, Zakharov & Polutbotko, 2004
- Subfamily Reticulumiinae new subfamily
- Subfamily Spinarellinae Waterhouse, 2002b
  - Tribe Spinarellini Waterhouse, 2002b
  - Tribe Chaoiellini Lazarev, 2011

Table 7. Superfamily Productoidea Gray, 1840.

Family **LOMATIPHORIDAE** Roberts, 1971

Fig. 5.1, Fig. 5.2

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

Diagnosis: Spines near hinge may lie in distinct row, ventral spines well spaced and arise from ribs with prolonged bases, or erect, no dorsal spines, both valves covered by ribs. No teeth or sockets, dorsal valve usually with hinge ridges, alveolus, lateral buttress plates may be present. Corpus cavity moderate to deep. Lower Carboniferous (Tournaisian, Visean).

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

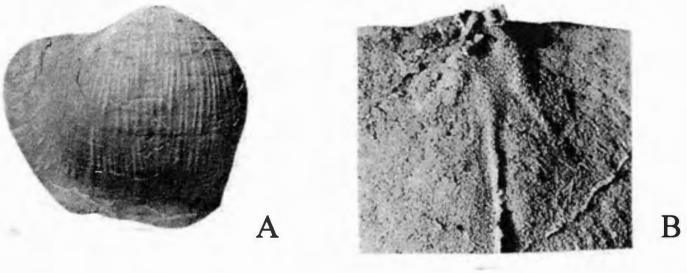


Fig. 5.1. *Lomatiphora aquila* Roberts. A, ventral valve CPC 8632, x1. B, latex mould of dorsal interior, CPC 8623, x7. From Roberts (1971).

Discussion: This is an outstanding group, with ribbed ventral valve bearing few spines, which may include a row near the hinge as in *Lomatiphora*, and somewhat lamellose and non-spinose dorsal valve. *Lomatiphora* has large substrophalosiid brachial ridges inclined obliquely forward, an alveolus, and broad lateral buttress mounds or ridges in some specimens. Overtonioidea are close in several aspects but come from a different source.

Whereas members of Lomatiphoridae were merged with Semiproductini McKellar by Brunton et al. (2000, pp. 484-485), the morphological traits are highly distinctive, and moreover strongly point to an evolutionary pathway from Chattertoniinae through Productellinae followed by Lomatiphoridae, then by Buxtoniidae, succeeded by Productidae, Retariidae and Dictyoclostidae. The constituent genera share some characteristics with Semiproductinae, in displaying a somewhat similar dorsal interior, *Semiproductus* having a split dorsal septum, and *Lomatiphora* having short diverging lateral buttress plates. The two differ in ornament, for there is little or no sign of commarginal rugae, and more emphasized radial ribbing in *Lomatiphora*, and spines are few over the disc and not subprostrate. Amongst Productellidae, *Helaspis* of Middle Devonian age (Helaspinae) has elongate ventral spine bases, although the single dorsal median septum passes forward from the cardinal process with no sign of alveolus or buttress plates, meaning that the dorsal interior of Lomatiphoridae would have had to have developed de novo, were the family to have been derived from this source. But one striking aspect of genera precursor to Lomatiphoridae is provided by Margaritiproductini (Subfamily Productellinae), regarded as a transition group because the genera display feeble teeth and sockets. In this tribe, some ribbing is developed, and the dorsal interior has an substantial pit in front of the cardinal process, bordered more or less by ridges, and not very different from the interior of *Lomatiphora* and allies, which lack the teeth and sockets. This would suggest an alliance with Productellinae, and this origin is preferred. It means that classification, if sources are considered as well as morphology, should separate *Lomatiphora* and allies from Overtoniidae and Avoniidae, which arose from Dotswoodinae. Lomatiphoridae was a small and somewhat isolated group, arguably too small to justify a separate family, yet fitting in neither with Productellidae, nor Overtoniidae or Avoniidae. The constituent genera appear to have been ancestral to Productoidea, giving rise to Buxtoniidae, showing split or divided dorsal median septum, and moderately developed spinose ribs over the ventral valve, although no dorsal spines are present, unlike the arrangement in many Buxtoniidae. The poorly known *Yanguania* Yang Shi-pu, 1978 of Tournaisian age has spines with traces of costae.

Genus ***Pharcidodiscus*** Roberts, 1976

Pharcidodiscus Roberts, 1976, p. 46 from the lower Tournaisian of Queensland is comparatively transverse and not highly tumid, with short low costae and only a low dorsal marginal ridge: no lateral or anterior marginal ridge is indicated clearly in figures and ear baffles are definitely absent, whilst there is a distinct cardinal process pit, such as is not found in Semicostellinae, and single dorsal septum. It appears to belong to Lomatophoridae rather than Semicostellini as claimed by Brunton et al. (2000), even though the ribbing approaches that of Semicostellinae.

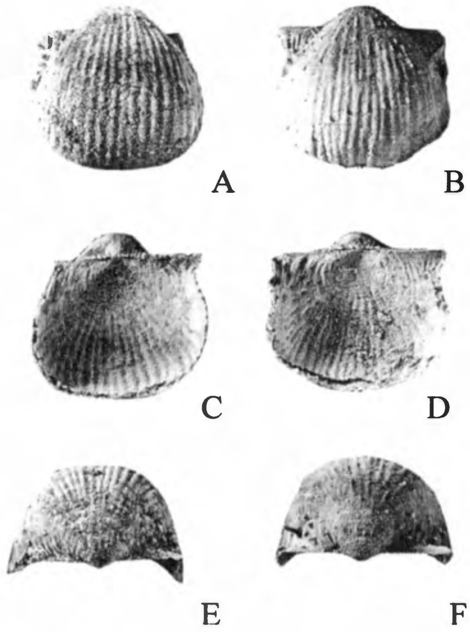


Fig. 5.2. *Spinocarinifera adunata* Roberts, x1.5. A, B, ventral and posterior ventral valve CPC 8562. C, E, dorsal and posterior ventral views of CPC 8563. D, F, dorsal and posterior ventral views of holotype, CPC 8564. From Burt Range Formation (Tournaisian), Bonaparte Gulf, Australia. See Roberts (1971).

Family **PRODUCTIDAE** Gray, 1840

[Productidae Gray, 1840, p. 151].

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

Discussion: The family is divided between genera like *Productus* which have few ear spines, and several genera which have a cluster of ear spines.

Subfamily **PRODUCTINAE** Gray, 1840

Fig. 4, Fig. 5

[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, concentric ornament weak, diaphragm and trails well developed. No dorsal pits over the dorsal exterior, possibly no posterior central papillation at maturity. Lower Carboniferous (upper Visean) to ?Upper Carboniferous (?Bashkirian).

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

Discussion: Two rows of spines were reported to lie along the ventral hinge of *Productus* by Muir-Wood & Cooper (1960, p. 239), with other spines scattered over the ventral valve. The exterior of *Productus* has been figured in various studies, notably by Muir-Wood (1928, pl. 1, fig. 1-6, text-fig. 6, 11), as well as Paeckelmann (1930) and Böger & Fiebig (1963). *Hubeiproductus* Yang De-li, 1984, p. 229 [p. 331], pl. 33, fig. 15, text-fig. 5-10, based on *H. guanyinyanensis* Yang De-li, of Lower Carboniferous age from China, was synonymized with *Productus* by Brunton et al. (2000). It has one or two rows of spines extending along the hinge, with further spines over the flanks and anterior, and no dorsal spines, and apparently no ear burst of ventral spines. There are mutiple trails. The high diaphragm does not extend across the postero-lateral interior, and this is presumably not due to breakage, because the feature was firmly regarded as providing a distinction from *Productus* by Yang De-li (1984), together with the absence of the flared anterior ventral valve typical of *Productus*. On the other hand, C. H. C. Brunton would have had good access to collections of typical *Productus* for comparison, and it seems likely that he determined that the differences were of little significance.

Subfamily **DIAPHRAGMINAE** Waterhouse, 2002b

[Nom. transl. hic ex Diaphragmini Waterhouse, 2002b, p. 20].

Diagnosis: Distinguished from Productinae by cluster of erect spines on ears or lateral umbonal slopes, other ventral spines numerous to rare. Lower Carboniferous (upper Visean) to Upper Carboniferous (Gzhelian).

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

Discussion: Various genera referred to Productini by Brunton et al. (2000, pp. 467, 469) differ from *Productus* in the details of spinose ornament. *Marginovatia* Gordon & Henry, included in Productini by Brunton et al. (2000), is placed in Ovatiinae Lazarev, and *Dowhatania* Waterhouse referred to Buxtoniidae.

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

[Nom. transl. Sarytcheva 1971, p. 35 ex Retariinae Muir-Wood & Cooper, 1960, p. 230].

Diagnosis: Medium to large shells with well formed reticulate ornament, spines form distinct row along ventral umbonal slopes.

Discussion: This family is large and varied, with well formed reticulate ornament, and lacks the diaphragm of Productidae, but is otherwise close.

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

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

Diagnosis: Medium-sized shells with large ears as a rule, dorsal spines commonly present. Dorsal median septum long, marginal ridge and ear baffles usually high in dorsal valve.

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

Fig. 5.3, Fig. 5.4

[Nom. transl. Brunton, Lazarev & Grant 1995, p. 928 ex Retariinae Muir-Wood & Cooper, 1960, p. 230].

Diagnosis: Generally somewhat transverse shells with large ears and reticulate disc, may have strong spines at base of ventral umbonal flanks or anterior, dorsal spines commonly present. External dorsal pits present in many genera. Dorsal adductor platform not high and cup-like. Upper Carboniferous (Kasimovian) to Upper Permian (Wuchiapingian?).

Genera: *Retaria* Muir-Wood & Cooper, *Aspinosella* Waterhouse, *Calliomarginatia* Jin, *Kutorginella* Ivanova, *Nasutusia* new genus, *Pitakpaivania* Waterhouse, ?*Svalbardoproductus* Ustritsky, *Thamnosia* Cooper & Grant (possible junior synonym of *Svalbardoproductus*), *Thuleproductus* Sarytcheva & Waterhouse (possible alternative junior synonym of *Svalbardoproductus*), *Tubaria* Muir-Wood & Cooper.

Discussion: The synonymy provided by Brunton et al. (2000, p. 472) is modified. *Calliomarginatia* Jin in Zhang & Jin, 1976, p. 181 from the Permian of Tibet is regarded as typified by the lack of dorsal spines, and so resembles *Aspinosella* Waterhouse (1982b, p. 47) from Permian of United States. Both were synonymized with *Kutorginella* by Brunton et al. (2000, p. 472), and this is judged to be in error. *Calliomarginatia* is close to *Kutorginella*, but lacks dorsal spines, and ventral spines are few other than in well formed rows along the hinge and umbonal flanks. The dorsal marginal ridge appears to be limited to the posterior valve. *Aspinosella* somewhat approaches *Thamnosia* Cooper & Grant, 1969 with its more numerous ventral spines, and lacks dorsal spines and strut spines. It has few spines at the ventral hinge, and a row along the umbonal flanks. *Thamnosia* Cooper & Grant, 1969 has numerous spines on ventral lateral slopes and ears, and numerous spines on the anterior shell, and a number of dorsal spines. *Pitakpaivania* Waterhouse 2004b, p. 69 is allied to *Kutorginella* and *Retaria* Muir-Wood & Cooper, 1960, and is based on *K. aprica* Grant (1976, p. 143, pl. 38, fig. 1-18) from the early Middle Permian of south Thailand. It is distinguished by the weak development of a hinge row and umbonal slope row of ventral spines, presence of numerous spines over the venter and admixed coarse halteroid and very fine spines over the anterior ventral valve: dorsal spines are fine. In these respects *Pitakpaivania* differs from the array of species that belong to *Retaria* from the Permian of the Glass Mountains in Texas, described as *Kutorginella* by Cooper & Grant (1975), and although they share strut spines, these in *Pitakpaivania* are differently placed from those of the American species, with the anterior pair lying further from the mid-line. The coarser ribs and better developed sulcus and fold of the United States species help to circumscribe a set of species distinguishable as genus *Retaria* Muir-Wood & Cooper. Russian and Canadian species lack the large strut spines and have better developed umbonal slope and hinge spines as a rule, and moderately well formed sulcus and fold, and so form another subset, referable to *Kutorginella*. Another close ally is *Tubaria* Muir-Wood & Cooper, 1960, characterized by its extended and tubiform anterior margin.

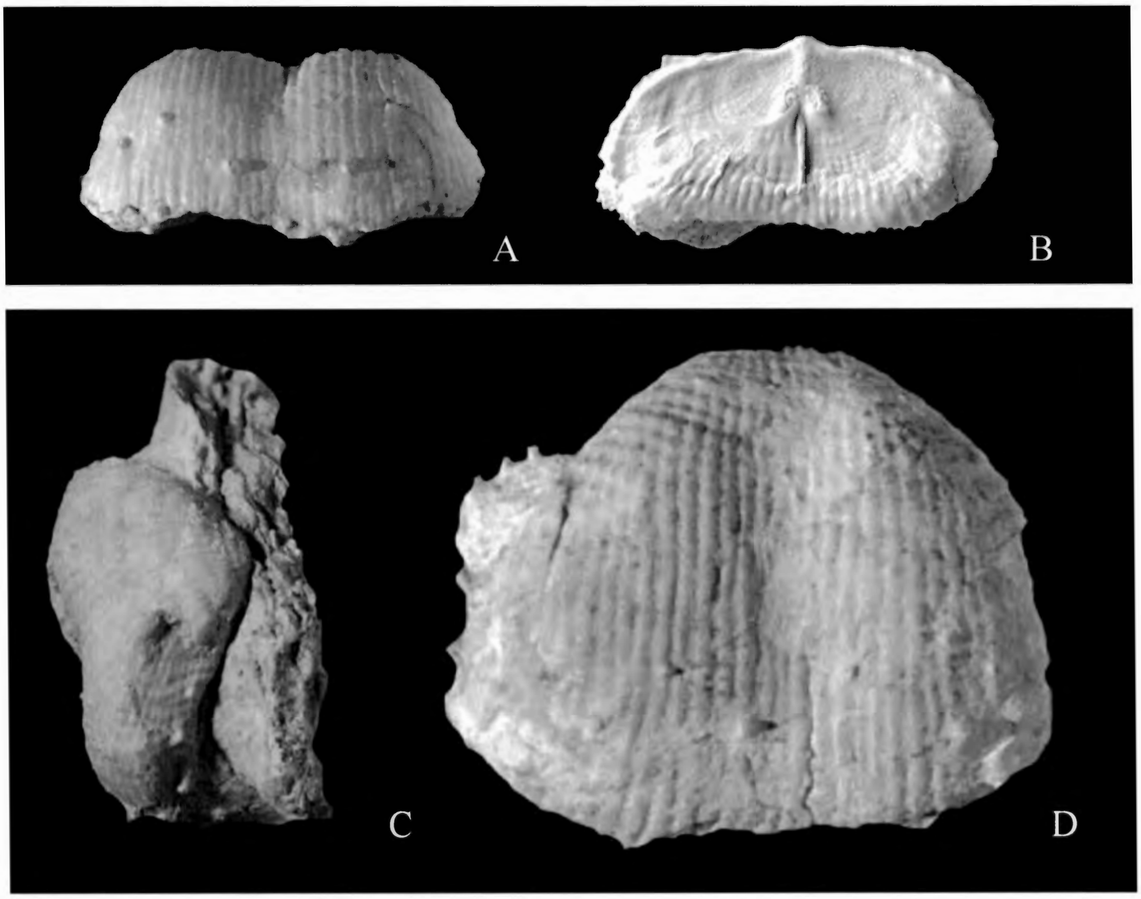


Fig. 5.3. *Kutorginella mosquensis* Ivanov. A, anterior ventral valve BR 3009, x2. B, dorsal valve interior, BR 3031, x2. C, oblique view of ventral valve BR 3030, showing umbonal slope row of spines, X3. D, ventral valve BR 3010, x3. Specimens from upper Carboniferous Kasimovian beds, Moscow Basin, Russia. JBW photo.

Other genera allocated to Tribe Retariini by Brunton et al. (2000) are further removed from *Retaria* and *Kutorginella*. *Keokukia* Carter, 1990 is not particularly close, and on available evidence appears to be allied to *Inflatia* Sarytcheva. The well described *Promarginifera* Shiells, 1966, another Early Carboniferous genus, stands apart, especially in terms of ornament. It has proportionately thicker ribs than usual, but reticulate posterior disc, high inner hinge ridge, dendritic adductors and long dorsal septum suggest retariin affinities, as in Brunton et al. (2000, p. 475), and it is classed in a small precursor group Protoniellini new tribe. Pits from which spines arise appear to be present over the dorsal valve. *Tesuquea* Sutherland & Harlow, 1973 has fine ribs and a prominent row of spines over the umbonal slopes, and with its small ears is also classed in Protoniellini. *Kelamelia* Zhang Zi-xin in Zhang et al. 1983 is poorly known, being based on decorticated material with obscure spinosity, and seems moderately close to *Inflatia* Muir-Wood & Cooper, 1960 and Inflatiini Sarytcheva, whilst *Marginoproductus* Tan Zhen-xiu, 1986 shows little similarity to *Retaria*. Brunton et al. (2000) suggested that the genus might be closer to Tolmatchoffiinae, even though this seems to be ruled out by the presence of dorsal pits, normally lacking from Tolmatchoffinae (p. 149), and the genus is provisionally placed in Marginatinae Waterhouse (p. 151). *Antiquatonia* Miloradovich, 1945 is also of uncertain position, in so far as the shape and ornament suggest alliance with dictyoclostids, and there is no complete dorsal marginal ridge, unlike the arrangement in many retariin genera. It has a well defined row of spines along the ventral umbonal slopes, placed on a ridge as in Rigrantiini Lazarev (see p. 122), and spines lie in a row in front of the hinge and scattered over the ventral valve (see p. 124ff).

An aspect to be further explored is the presence or absence of pits over the dorsal exterior. Judging from

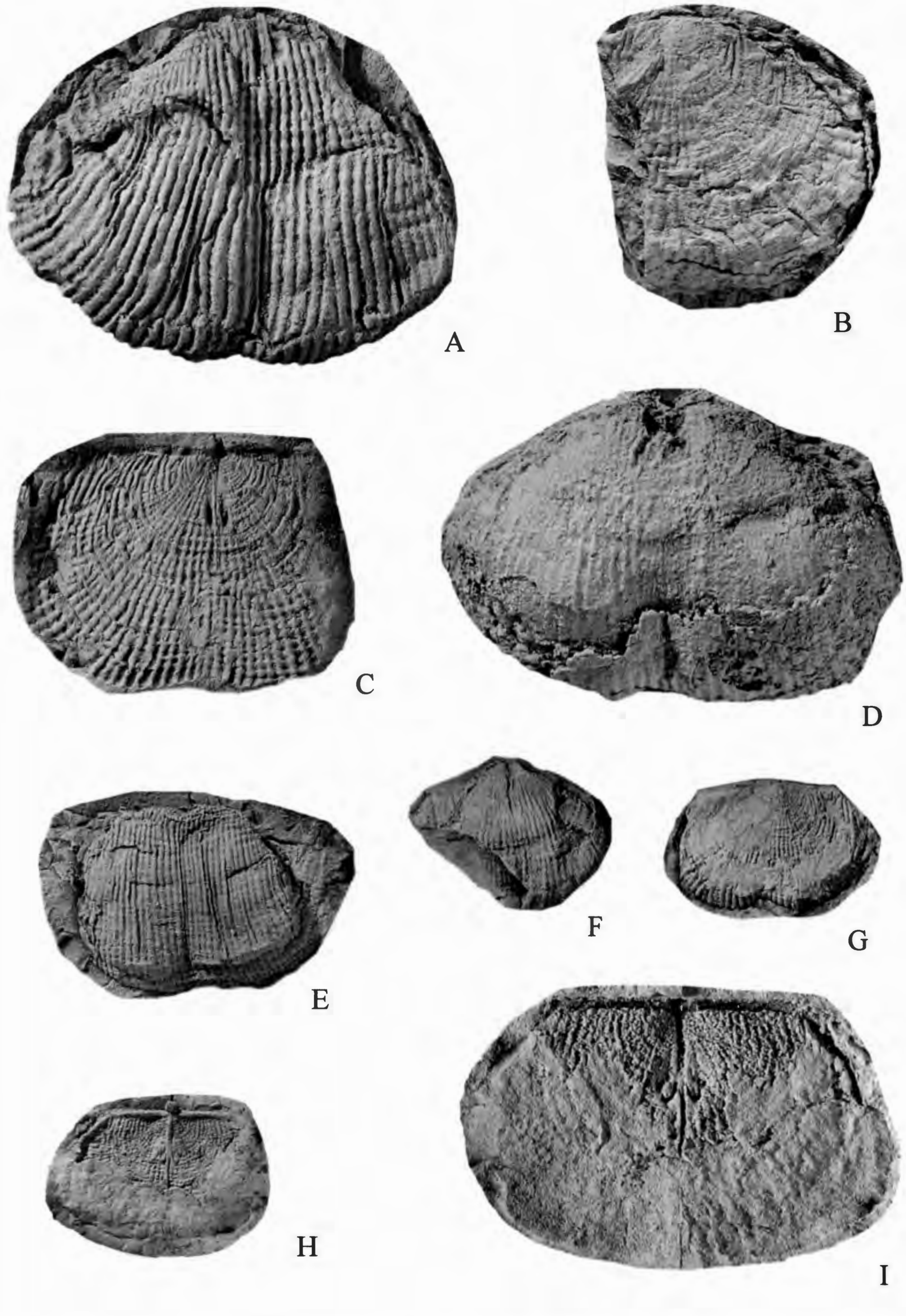


Fig. 5.4. *Calliomarginatia sinauris* (Waterhouse). A, ventral valve TBR 589, x2. B, external mould of dorsal valve, TBR 591, x2. C, dorsal internal mould from TBR 592, x2. D, ventral internal mould TBR 588, x2. E, holotype, ventral valve TBR 587, renumbered BR 3157, x1. F, ventral internal mould TBR 590, x1. G, dorsal external mould TBR 594, x1. H, I, latex cast and dorsal internal mould of TBR 593, x1, x2. From Huai Tak Formation (Upper Carboniferous), northwest Thailand. (See Waterhouse 1982b). J. Coker & JBW photo.

illustrations, dorsal pits are present in *Thamnosia, Thuleproductus, and Nasutusia,* and questionably in *Aspinosella* and *Calliomarginatia*. The development of posterior central papillation or "shagreen" is not so clearly present in type *Kutorginella, Retaria, Tubaria*?, and only questionably in *Aspinosella* and *Calliomarginatia*. Knowledge of the development of posterior central papillation is not certain for all genera, but a few pits are present over the posterior septum in a figure of *Retaria* by Muir-Wood & Cooper (1960, pl. 70, fig. 14), coarse like pits over the dorsal floor to each side of the median septum, whereas the posterior septal area in Canadian *Kutorginella* is smooth immediately in front of the cardinal process.

Genus ***Svalbardoproductus*** Ustritsky, 1962

Fig. 5.5

Ustritsky (1979, pp. 127, 128) has forcefully claimed that *Thuleproductus* Sarytcheva & Waterhouse is a synonym of *Svalbardoproductus* Ustritsky (1962). I am greatly obliged to Dr Tatiana Grunt for translating his published opinion, and for providing translations of his earlier work on the subject. He claimed that his material of *S. striatoauritus* from the basal horizon of the Cape Starotsin Formation on Svalbard had been passed on the Paleontological Institute in Moscow, and that it had been redescribed as *Tuleproductus* (sic) *subarcticus* Sarytcheva (1977 – see pp. 78, 79, pl. 9, fig. 1-3, text-fig. 48). It was further considered that the Spitsbergen outcrops yield a succession of species, *subarcticus* = *striatoauritus*, followed by *arcticus* Whitfield, followed in the Selander Formation by *crassauritus* Sarytcheva & Waterhouse, all three belonging to the one genus.

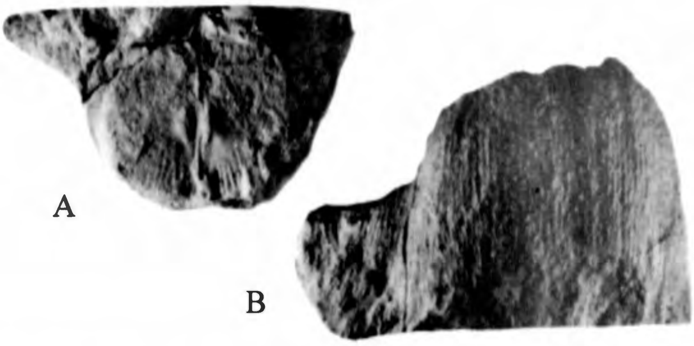


Fig. 5.5. *Svalbardoproductus striatoauritus* Ustritsky. Reproduction of two of the original figures of Ustritsky (1962, pl. 2, fig. 1, 2), provided by Tatiana Grunt, showing interior of dorsal valve (A) and anterior view of ventral valve (B), suggestive of numerous small anterior spines. From Cape Starotsin Formation (Roadian) of Spitsbergen.

But certainty is still lacking, although it may well prove that Ustritsky is right. Here are the difficulties. In the first place, the species *subarcticus* was based on material from River Kozhim, Pechora Basin, not Spitsbergen, and even in the Sarytcheva account, the exterior of the dorsal valve is not illustrated. That does not disprove the stratigraphic position of *subarcticus* in Spitzbergen, but reliance solely on the nature of the ventral valve may be deemed precarious. It is very difficult to reconcile the original description of *Svalbardoproductus* by Ustritsky (1962) with the description of *Thuleproductus* Sarytcheva & Waterhouse, 1972. Ustritsky (1962) emphasized the lack of concentric ornament from the ventral ears of *Svalbardoproductus striatoauritus*, but it might prove somewhat variable, because concentric ornament is visible on at least the inner ears in the type of *subarcticus* Sarytcheva (1977, pl. 9, fig. 1a, 1b). Ustritsky (1962) stated that spines were absent from the ears in *striatoauritus*, and Brunton et al. (2000, p. 475) repeated this observation, stating that *Svalbardoproductus* was " lacking spine clusters from ears" and noting that ribs were indistinct anteriorly. These observations were not qualified in any way by Ustritsky (1979), to imply they did not need changing. Yet these aspects of the description of *Svalbardoproductus* are completely different from the ornament in *Thuleproductus crassauritus*, which has numerous spines over the ventral ears, and firm and coarser ribbing to the anterior margin. Finally, Ustritsky (1962) rated his genus as being closest to *Peniculauris* Muir-Wood & Cooper (1960), apart from the lack of ear spines. It is doubful if anyone would confuse *Thuleproductus* with *Peniculauris,* a buxtoniid rather than retariid. Somehow, were Ustritsky (1979) correct, *Svalbardoproductus* Ustritsky, 1962 has morphed over the years into *Thuleproductus* Sarytcheva & Waterhouse, 1972. The name *Thuleproductus* goes, but the description stays. The name *Svalbardoproductus* stays, but the description goes. That is by no means impossible, for paleontological descriptions are not infallible. Yet Ustritsky (1979) did not adjust his description.

In summary, it may well prove necessary to synonymize *Thuleproductus* with *Svalbardoproductus*. But first, there have to be corrections to the original description of *Svalbardoproductus*, and acceptance that ear spines are numerous, not absent as asserted by Ustritsky, and that ribs do not necessarily disappear or become very faint at the anterior margin. And that there is little similarity to *Peniculauris*. And of equal importance, the nature of the dorsal exterior needs to be determined, to clarify the nature of the spines. The ignorance concerning dorsal spinosity for *subarcticus* is bad enough, but the ignorance for a proposed genus, *Svalbardoproductus*, is crippling. Why? Because various genera in Retariinae have been recognized partly on the basis of dorsal spinosity. *Svalbardoproductus* might be senior synonym for *Thuleproductus*. But it equally might be senior synonym for *Thamnosia* Cooper & Grant, 1969, which differs from *Thuleproductus* in having fewer dorsal spines, especially over the ears. Until clarification, we can only guess at the limits of *Svalbardoproductus*, because *Kutorginella, Thamnosia* and *Thuleproductus* all potentially occur in Arctic faunas.

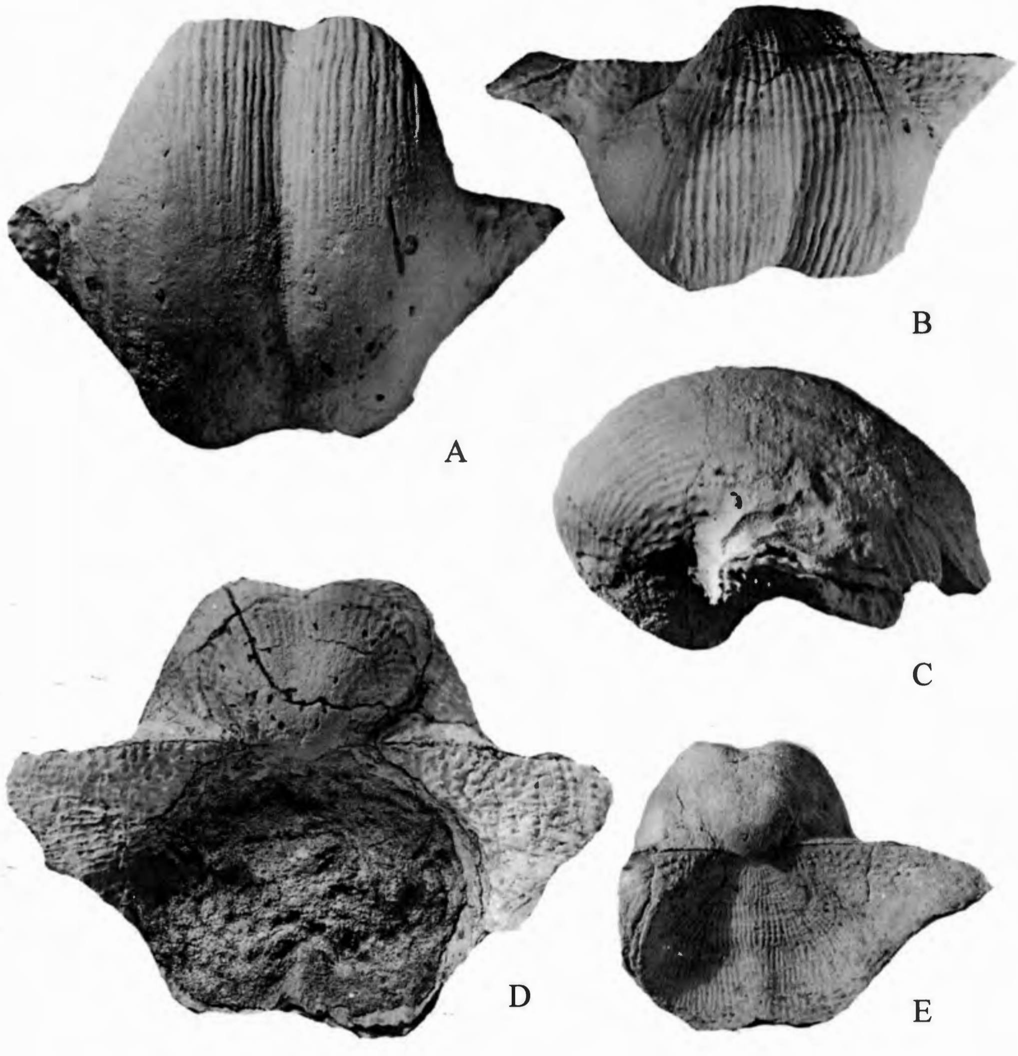


Fig. 5.6. *Thuleproductus crassauritus* Sarytcheva & Waterhouse. A – C, ventral, posterior ventral and lateral aspects of ventral valve GSC 26374 from GSC loc. 35316. See Sarytcheva & Waterhouse (1972, pl. 8). D, dorsal aspect of GSC 26376 from GSC loc. 76029. E, dorsal aspect of GSC 36773 from GSC loc. 35316. Trold Fiord Formation (Capitanian). A. Miller, B. O'Donovan & JBW photo. Specimens x0.75 natural size.

A dorsal valve figured as *Svalbardoproductus* sp. from Timan, Russia, by Lazarev (1990, pl. 19, fig. 10) is small with well formed marginal ridge and numerous pustules over the inner ventral ears, suggestive of spines, but the dorsal exterior and most of the ventral valve are not shown, and the identity insecure.

Genus **Thuleproductus** Sarytcheva & Waterhouse, 1972

Fig. 5.6, Fig. 5.7

Brunton et al. (2000, p. 475) synonymized the genus *Thuleproductus* Sarytcheva & Waterhouse, 1972, p. 67 with *Thamnosia* Cooper & Grant, 1969, p. 10. This is a mistake. The type species of *Thamnosia, T. anterospinosa* has been examined and compared at the Smithsonian Institution, Washington, D. C., and is large with numerous spines over the ventral ears and umbonal flanks, and near the anterior margin. Dorsal spines are not very numerous. *Thuleproductus* is based on a very large species, much larger than any Texan species of *Thamnosia,* and has much larger ears than in the type species *Thamnosia anterospinosa*, and notably far more numerous spines over the dorsal ears. Spines are much less numerous over the ventral flanks and ears than in *anterospinosa*, but are numerous over the dorsal valve anteriorly. Internally the dorsal marginal ridge is high posteriorly and laterally, but stops short of the anterior margin, whereas the ridge persists around the anterior in a number of well preserved *Thamnosia*. Of other species from the Permian of Texas that belong to *Thamnosia, T. phragmophora* Cooper & Grant (1975) has moderately large ears, and largish anterior lateral ventral spines (Cooper & Grant 1975, pl. 346, fig. 19) but the dorsal ear spines are not fully clear. *T. parvispinosa* (Stehli) certainly has moderately large ears and numerous ventral spines, so many that lateral rows are not clearly observable, and as in *T. anterospinosa*, dorsal spines are not nearly as numerous as in *Thuleproductus*. Although smaller, *T. silicica* Cooper & Grant, 1975, p. 1036, pl. 351, fig. 1-18 from the Hess Formation of the Glass Mountains Texas, is closer to *Thuleproductus crassauritus* in some respects, in

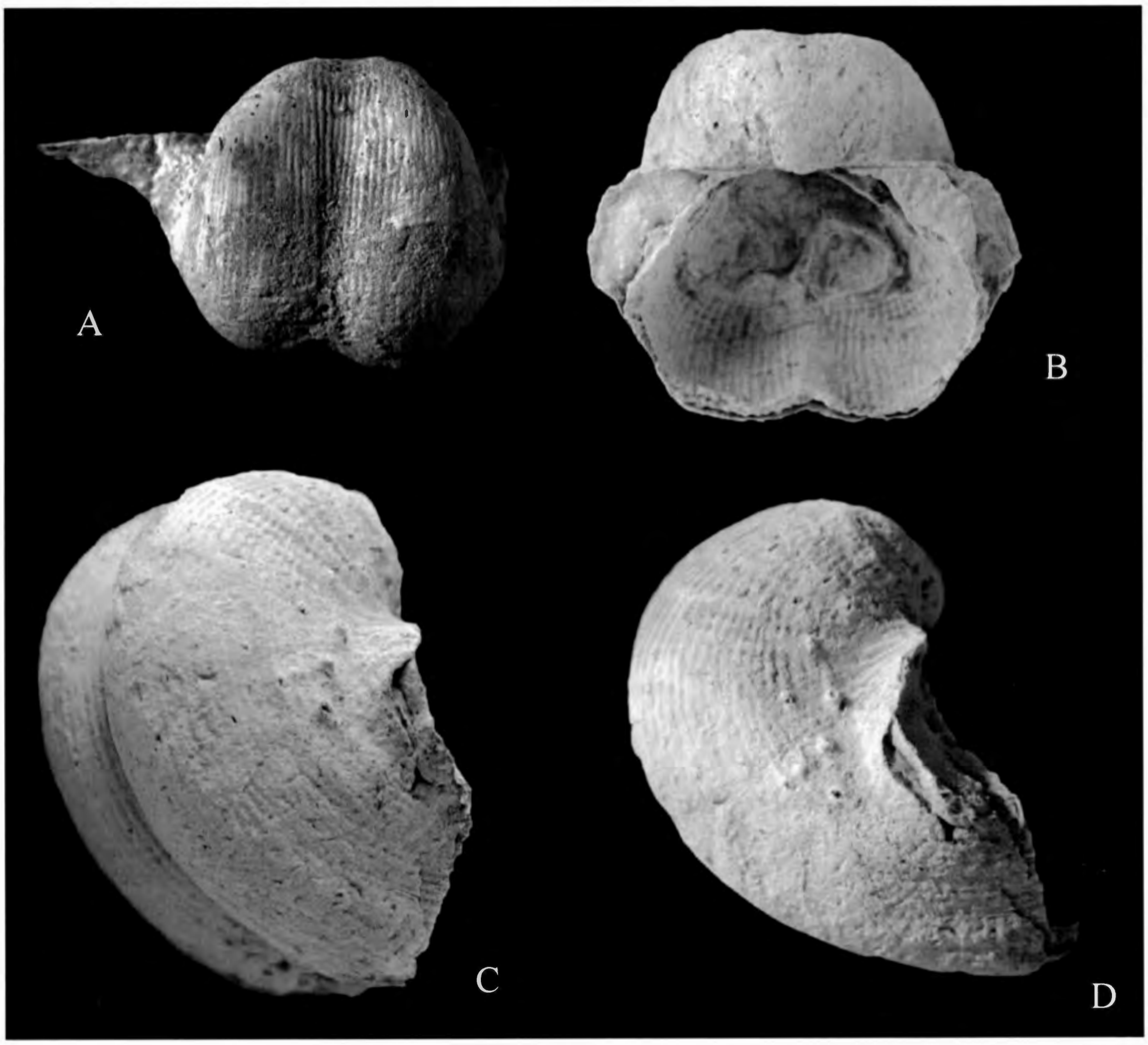


Fig. 5.8. *Thuleproductus crassauritus* Sarytcheva & Waterhouse. A, ventral aspect of GSC 36773 from GSC loc. 35316, x1. B, C, D, dorsal and oblique lateral aspects of specimen with valves conjoined, GSC 36795 from uncertain locality, = ?Trold Fiord Formation, x1, x1.5, x1.3 respectively. Capitanian. From Melville Island, Canada. JBW photo.

that spines are numerous over the dorsal valve, including, it appears, the ears, and also numerous over the anterior dorsal valve and over the ventral valve, including fine numerous spines over the lateral slopes. It may be identified as *Thuleproductus silicica* (Cooper & Grant), ancestral to younger *Thuleproductus* and to *Thamnosia* through loss of numerous ear spines. Or is it *Svalbardoproductus*? Of course, if *Thamnosia* is senior synonym of *Thuleproductus*, as proposed by Brunton et al. (2000), and if *Svalbardoproductus* is senior synonym of *Thuleproductus*, as analyzed by Ustritsky (1979), then *Svalbardoproductus* must be senior synonym of *Thamnosia* as well. I suspect that *Thamnosia* will prove valid, and *Svalbardoproductus* will likely to be senior synonym of *Thuleproductus*. But that is only a suspicion: evidence is needed.

Thuleproductus arcticus (Whitfield, 1908)

Fig. 5.8

1908 *Productus semireticulatis arcticus* Whitfield, p. 54, pl. 1, fig. 2, pl. 2, fig. 8-10.
1914 *Productus boliviensis* [not d'Orbigny] – Wiman, p. 63, pl. 13, fig. 7-10.
1914 *P. inflatus* [not McChesney] – Wiman, p. 66, pl. 14, fig. 1, 2, pl. 15, fig. 5.
1936 *P. arcticus* – Stepanov, p. 115, pl. 1, fig. 1-4.
1960 *Dictyoclostus* cf. *neoinflatus* [not Licharew] – Harker & Thorsteinnson, p. 55, pl. 17, fig. 1-4.
1964 *Costinifera* (sic) *arctica* – Gobbett, p. 91, pl. 9, fig. 2-6, text-fig. 15.
1972 *Thuleproductus arcticus* – Sarytcheva & Waterhouse, p. 71, pl. 7, fig. 9, pl. 8, fig. 4, 5.
1977 *T. arcticus* – Sarytcheva, p. 74, pl. 7, fig. 6-8, text-fig. 44, 45.
2008 *Thamnosia arctica* – Angiolini & Long, p. 81, Fig. 3F-I, 4A-D.

Lectotype: Specimen figured by Whitfield (1908, pl. 2, fig. 8, 9) and Stepanov (1936, pl. 1, fig. 3, 4) from Cape Sheridan, northeast Ellesmere Island, Canada, designated by Solomina (1960, p. 58) and later by Gobbett (1964, p. 91).

Diagnosis: Moderately large with large ears, moderately defined narrow ventral sulcus, persistent ribs, two or three rows of erect spines along umbonal flanks of ventral valve; gently concave dorsal disc, geniculate trail.

Resemblances: This species is smaller than *Thuleproductus crassauritus* Sarytcheva & Waterhouse, 1972 from the Trold Fiord Formation of the Canadian Arctic Archipelago, but shares the numerous spines over the ears of both valves. The ribs are firmer in *crassauritus* and do not fade anteriorly, and up to four rows of well developed spines lie along the ventral lateral flanks of the ventral valve. These are strongly reminiscent of umbonal slope spines that are developed in *Kutorginella* Ivanov and *Retaria* Muir-Wood & Cooper and related genera. The original figures of *arcticus* Whitfield, kept at the American Museum of Natural History, New York, show only ventral valves, indicating large size and strong ribs and narrow sulcus like aspects of the present material, and were reproduced by Stepanov (1936, pl. 1, fig. 3, 4). But there is no data on the ventral ears or the dorsal valve. However Whitfield (1908, pl. 2, fig. 9) showed two well developed spines on the flanks, akin to lateral spines in the present specimens.

Specimens from Selandar Cape of west Spitsbergen that were assigned to *crassauritus* by Sarytcheva (1977, pl. 8, fig. 1-4) are larger, and show coarser ribs than in the present species. From the Cape Starotsin Suite of west Spitsbergen, specimens allocated to *Thuleproductus arcticus* (Whitfield) by Sarytcheva (1977, pl. 7, fig. 6-8, Fig. 44, 45) are close in size, and the specimen in fig. 6a shows some coarse erect spines over the umbonal flank, though not clearly aligned in an umbonal slope row. The lack of information about ear spinosity for both valves leaves uncertainty. The same applies to the specimens in the synonymy of *arcticus* Whitfield provided by Sarytcheva (1977) and Sarytcheva & Waterhouse (1972). Figures suggest that there is general agreement in size and shape as a rule, though few if any show the same extended ears, probably due to breakage, and very few show the dorsal valve adequately. In the specimen figured by Licharew & Einor (1939, pl. 7, fig. 11a) there are strong erect spines, somewhat disordered, on the lateral slopes, but no information about the ears and the shape is not close. The specimen comes from the western coast of the North Island, Novaya Zemlya, Russia. Specimens figured from the Assistance Formation of Devon Island, Canada, by Harker & Thorsteinsson (1960, pl. 17, fig. 1-4) show nothing of ears or lateral slopes, so that identity depends on size, strong ribs, parallel lateral flanks and narrow sulcus. The various Spitsbergen specimens illustrated by Wiman (1914), as in the synonymy provided by Sarytcheva & Waterhouse (1972), show specimens poorly, but one ventral valve illustrated in side view (Wiman 1914, pl. 14, fig. 2) shows rather fine erect spines in a short row along the lower umbonal slopes. Further Spitsbergen material figured by Gobbett (1964, pl. 9, fig. 2-6) as *Costinifera* (sic = *Costiferina*) *arcticus* is close in shape, fails to show the dorsal valve, but includes a lateral view with a few erect moderately coarse spines. Material figured by some other authors, such as Solomina (1960, p. 58, pl. 10, fig. 1-8) reveals little similarity. *T. subarcticus* Sarytcheva (1977, pl. 9, fig. 1-3) shows nothing of the dorsal spinosity, nor any sign that strong erect spines are present laterally on the ventral valve.

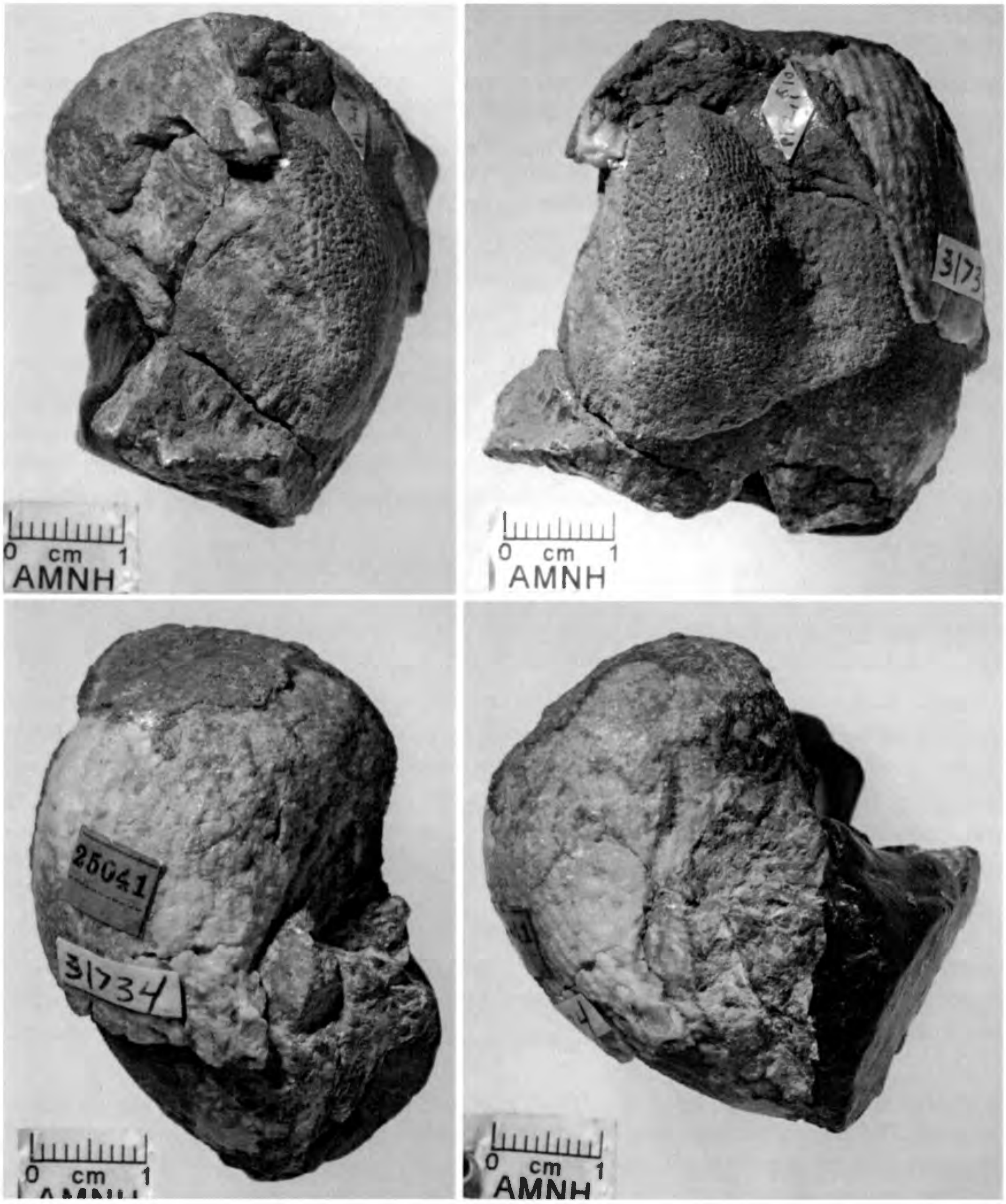


Fig. 5.8. *Thuleproductus articus* (Whitfield), lectotype, ventral valve AMNH 31734, from Cape Sheridan, Ellesemere Island, Canada. Photographs kindly supplied by Steve Thurston through Bushra Hussaini, American Museum of Natural History, New York.

Specimens of so-called *Thamnosia* cf. *arctica* of Stehli & Grant (1971, p. 511, pl. 62, fig. 1-14) from Axel Heiberg Island in the Canadian Arctic have shallower ventral sulcus and more commarginal rugae over the disc compared with *arcticus*, especially in the specimens figured by Stehli & Grant (1971, pl. 62, fig. 1, 2), which have small ears and which may not be conspecific with their other specimens figured as *arctica*. The other specimens could belong to *Thuleproductus*, but the species is questionable, with *subarcticus* a contender. The material figured as cf. *arctica* by Brabb & Grant (1971) from the Takhandit Formation of Alaska is only moderately close, and the specifc identification not supportable from the inadequate preservation. Much better preserved specimens that offer the best available insights to the species were described from Svalbard by Angiolini & Long (2008). These show moderately sturdy ribs, shallower ventral sulcus than in *crassauritus*, a number of anterior ventral spines, and comparatively flat dorsal disc. Ventral ears are not well preserved, and are best shown in specimens figured by Gobbett (1964, pl. 2, fig. 2, 5).

Genus ***Nasutusia*** new genus

Derivation: nasutus - nose, Lat.

Type species: *Productus semireticulatus* var. *capitanensis* Girty, 1909, p. 254 from Capitan and Bell Canyon Formations (Capitanian), Texas, United States, here designated.

Diagnosis: Large transverse shells with strongly reticulate disc and strongly geniculate trail, moderately deep ventral sulcus, strongly nasute anterior, spines thin and crowded over ventral umbonal flanks, may be rare elsewhere, and inconspicuous or absent from dorsal valve, dorsal pits present. Dorsal marginal ridge low anteriorly.

Discussion: This species has been described and figured by Girty (1909, p. 254, pl. 12, fig. 1-3b, pl. 20, fig. 8, 8a), King (1931, p. 66, pl. 10, fig. 15) and Cooper & Grant (1975, p. 1033, pl. 345, fig. 1-17, pl. 349, fig. 6-19). It is outstanding in view of its large size, nasute anterior, and crowded spines over the ventral umbonal flanks, extending well forward. Unlike *Thamnosia*, which is not nasute, spines are not crowded over the anterior ventral valve, and are few over the disc and apparently outer ears, and are rare if present over the dorsal valve. *Thuleproductus* Sarytcheva & Waterhouse from principally the Arctic Permian is readily distinguished by its more numerous dorsal ear spines, and by somewhat fewer ventral umbonal flank spines. What appears to be a somewhat similar species from the Permian of west Texas, *Thuleproductus silicica* (Cooper & Grant, 1975), has numerous spines over the ventral umbonal flanks, but spines are also numerous over the ears and anterior ventral valve and over the dorsal valve, and the dorsal marginal ridge is well developed anteriorly.

In the nasute nature of the ventral anterior, the species *capitanensis* resembles some species of *Kutorginella* Ivanova and *Retaria* Muir-Wood & Cooper, but these genera have rows of spines posteriorly and laterally, rather than an extended burst of fine spines. *Aspinosella* Waterhouse, 1982b, based on *Kutorginella uddeni* Cooper & Grant, 1975, p. 1029 from the Gaptank and Neal Ranch Formations (Gzhelian and Asselian) of west Texas, United States, is similar in that spines are lacking from the dorsal valve. Ventral spines are few along the hinge, form a row at the base of the lateral flanks, and are scattered to moderately numerous over the disc and especially trail. It is likely that *Aspinosella* evolved into the younger genus *Nasutusia*, becoming large and nasute.

Tribe **PROTONIELLINI** new tribe

Name genus: *Protoniella* Bell, 1929 from Windsor Group (Visean), Nova Scotia, Canada.

Diagnosis: Small with subdued row of spines along umbonal slopes, further disc, trail and hinge spines on ventral valve, may have dorsal spines; ribbing fine to strong, posterior dorsal hinge ridge and low ridge may be developed across anterior dorsal ears, ears small. Lower Carboniferous (Visean) to Middle Carboniferous (Bashkirian).

Genera: *Protoniella* Bell, *Promarginifera* Shiells, *Tesuquea* Sutherland & Harlow.

Discussion: This is a small group of early retariin shells, lacking the diaphragm of Productidae, and displaying somewhat similar spines, with umbonal slope row, often spines closer to the hinge, and scattered disc and trail spines. Ears are comparatively small, unlike those of typical Retariini. There are no dorsal spines in *Protoniella*, but a few dorsal spines are present in *Promarginifera*. The genera represent an early development of Retariinae, as small shells, tending to be elongate and less transverse with smaller ears than in later Retariinae, and display less developed dorsal inner ridges.

Genus ***Protoniella*** Bell, 1929

Fig. 5.9

This genus was named for small strongly ribbed shells from the Visean Windsor Group of Nova Scotia, Canada. Present assessment is based on well prepared plaster duplicates of the figured types, kept at the Geological Survey of Canada, Ottawa, and somewhat amends what was known about the distribution of posterior spines, and the nature of the dorsal interior. The ribs are crossed by very subdued commarginal rugae over the umbonal part of the ventral valve. Spines are limited to the ventral valve, and form a row along the hinge, and a row along the base of the umbonal flanks in GSC 7954d (Bell 1929, pl. 15, fig. 10). These two rows strongly suggest a relationship to members of Retariinae, such as *Kutorginella* Ivanova, 1951, and although dorsal spines are lacking, whereas they are present in most genera of Retariini, the genus seems likely to have been a forerunner of Retariini. The flank row is less clear in GSC 7954b (Bell 1929, pl. 15, fig. 14) and spines form a small cluster on the ear on the left side – that of the right side ear is obscure. In the ventral valve of the specimen figured by Bell (1929, pl. 15, fig. 13), the hinge and flank rows are clearly formed and separated by another row. Spines of the umbonal shell are weakly prostrate, and over the remainder of the valve are erect, arising from costal crests. There are no external dorsal pits.

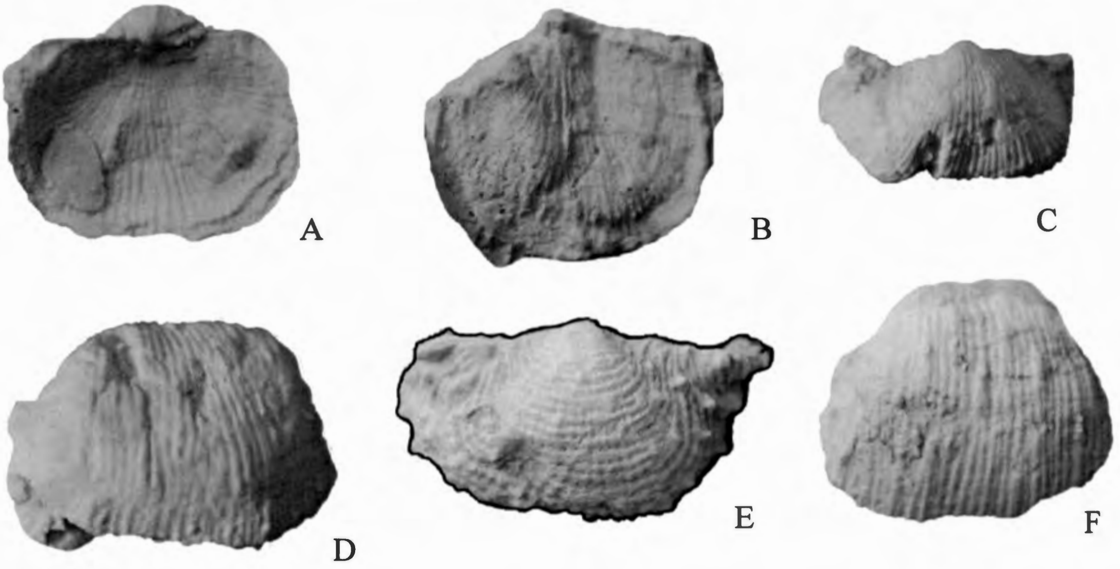


Fig. 5.9. *Protoniella beedei* Bell. Photographs of different plaster casts kept at GNS, Lower Hutt, New Zealand, and prepared from Bell's types which are kept at the Geological Survey of Canada, Ottawa. A, dorsal aspect of BR 3095, = GSC 7954, x2.5. B, dorsal aspect of BR 3096 (= GSC 7954a), x2. C, D, posterior and anterior ventral aspects of BR 3097 (= GSC 7954b), x2. E, F, posterior and anterior aspects of ventral valve, BR 3098 (= GSC 7954d), x3, x2.5. From Lower Carboniferous Windsor Group, Nova Scotia, Canada. JBW photo.

For the dorsal interior, Bell (1929) and Muir-Wood & Cooper (1960, p. 265) have described a split median septum and a distinct ridge along the hinge. In addition, the plaster mould indicates that the ridge continues around the entire visceral disc, its height increased by juxtaposition to a commarginal furrow behind and within the ridge. It was presumably the presence of this ridge that led Bell (1929) to argue for a marginiferid relationship, whereas Muir-Wood & Cooper (1960) regarded *Protoniella* as buxtoniid, based probably on the split dorsal septum. Brunton et al. (2000, p. 431) more or less returned to the Bell assessment, placing the genus with a query in Paramarginiferini Lazarev, 1986a (sic – an invalid designation), together with a mix of genera, many marginiferid, although *Paramarginifera* itself may be yakovleviid (see p. 352). Roberts (1971, p. 115) examined and partly prepared the dorsal valve of Bell (1929, pl. 15, fig. 12) and deduced that the genus was a member of Overtoniinae, which may seem justifiable on the basis of some dorsal internal features, but is clearly dissonant with the external ornament and the nature of the trail. Both spine detail, involving the lack of strut spines and presence of erect rather narrow body spines, and the alveolus plus split dorsal septum indicate that *Protoniella* is no ally of *Paramarginifera* nor paucispiniferiform genera such as *Bibatiola* or *Eomarginiferina*. Rather Muir-Wood & Cooper (1960) were more accurate in their assessment, with a moderate approach to Buxtoniidae. On the other hand the ventral spines do not typify those of buxtoniid genera, in which costae swell at the base of each ventral spine. Instead the ornament of ribs, low posterior rugae, spine distribution and nature, and dorsal interior, including split septum and high marginal ridge (cf. Brunton et al. 2000, Fig. 313.1f), suggest a relationship to Retariidae Muir-Wood & Cooper. The marginal ridge is moderately high, despite the report of it being low by Roberts (1971).

Tribe **RIGRANTIINI** Lazarev, 2000b

[Rigrantiini Lazarev, 2000b, p. 28].

Diagnosis: Spines well developed in single rows along hinge and base of umbonal flanks, arising from low ridge; reticulate ornament over entire disc. Dorsal dimples in some genera. Lower Carboniferous (Visean) to Middle Permian (Wordian).

Subtribe **RIGRANTIINAI** Lazarev, 2000b

Fig. 5.10 – Fig. 5.12

[Nom. transl. hic ex Rigrantiini Lazarev, 2000b, p. 28].

Diagnosis: Medium size, dorsal ears bordered anteriorly by groove, and dorsal dimples distinct. Middle Carboniferous (?Moscovian) to Middle Permian (Wordian).

Genera: *Rigrantia* Lazarev, *Bicarteria* Lazarev, *Pseudantiquatonia* Zhan & Wu.

Discussion: This tribe has been proposed by Lazarev (2000b) and briefly summarized by Brunton (2007). The constituent genera were believed to be distinguished by having a rib traversing the ventral slope each side of the umbo. In other respects, the genera come moderately close in ornament to Retariinae, in having reticulate ornament over at least part of the visceral disc, and in possessing a row of spines along the hinge, another row arising from the ridge each side of the umbo, and spines over the disc and trail. Elongate pits are moderately well developed over the dorsal valve. They certainly show little approach to *Yakovlevia*, even though classed with that genus as a tribe within Yakovleviinae by both Lazarev (2000b) and Brunton (2007). These authors overlooked the even closer approach of *Rigrantia* and allies, in terms of ornament and interior, to members of Spyridiophorini and Retariini, and the tribe is therefore transferred to Family Retariidae.

Fig. 5. 10. *Rigrantia planumbona* (Stehli), dorsal valve USNM 148988a, showing groove bounding each anterior dorsal ear. From Bone Spring Formation (Kungurian), west Texas, United States. See Cooper & Grant (1975, pl. 390), x1.

The genus *Rigrantia* Lazarev, 2000b is based on *Antiquatonia planumbona* Stehli, 1954, p. 316 from the Bone Spring Formation (Kungurian) of western United States. The ventral valve is very like that of *Antiquatonia* in a general sense. Ventral spines form a distinct row along ears and another along umbonal slopes above an external ear ridge, and scattered over remainder of ventral valve, and the visceral disc is finely reticulate. The dorsal valve is also reticulate and lacks spines but as a rule has dorsal pits. Lazarev (2000b) asserted that the row of spines along the hinge were similar in their moderately great diameter to spines in the row along the base of the flanks. However this is contradicted for some specimens of the type species, with figures by Cooper & Grant (1975, pl. 390, fig. 17, 18, 19, 20) establishing that the outer spines of the umbonal slope row could be substantially thicker than any spines of the hinge row. Yet the observation does hold true for another specimen (Cooper & Grant 1975, pl. 390, fig. 8). For some of the other species evaluated as belonging to *Rigrantia* by Lazarev, too little is known of the hinge spines especially to enable any assessment, but *hessensis* King appears to show stronger spines along the umbonal slope row than along the hinge. Lazarev (2000b) also stated that the dorsal ears were sometimes delineated internally by cardinal and lateral ridges, but this is not true of the type species (see Cooper & Grant 1975, pl. 390, fig. 14). Of the other species allocated to *Rigrantia,* only *hessensis* (King, 1931) shows anything of the dorsal interior, and this has a posterior hinge ridge (Cooper & Grant 1975, pl. 391, fig. 15). The facets that are not known to vary involve the general

Fig. 5. 11. *Bicarteria hermosana* (Girty), dorsal aspect showing ear groove, OU 7757 from lower Desmoinesian of New Mexico, United States, x1. See Sutherland & Harlow (1973, pl. 11).

distribution of spines, the general presence of ventral umbonal slope ridges, the dorsal external pits, and the finely reticulate ornament. One apparent distinction from *Antiquatonia* lies in the presence of a strong groove along the anterior margin of each dorsal ear (Cooper & Grant 1975, pl. 390, fig. 13, 15, 16). Such a groove is more ambiguously present on *hessensis* King, missing from an external surface (Cooper & Grant 1975, pl. 391) but suggested from internal views (pl. 391, fig. 15, 17). For other species assigned to *Rigrantia* by Lazarev (2000b), the dorsal valve is not known.

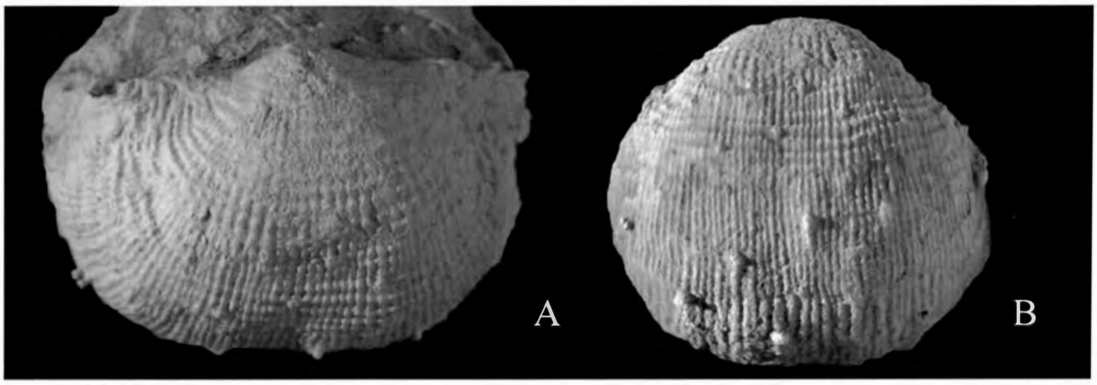


Fig. 5.12. *Bicarteria hermosana* (Girty), A, B, posterior and anterior aspects of ventral valve BR 3158, x2, x1.5, from Frensley Limestone (Upper Carboniferous), Oklahoma, United States. JBW photo.

Genus *Bicarteria* Lazarev, 2000b (see Fig. 5.12, Fig. 5.13) is based on type species *Productus semireticulatus* var. *hermosanus* Girty, 1903, p. 359 from Colorado of Bashkirian age, United States. There is a row of spines along the ventral hinge and over the ridge at the base of the umbonal slopes, and spines may be larger over disc and trail. Costae may be coarse anteriorly, and reticulation with commarginals covers part or all of disc. Although Lazarev (2000b) relied on the thinness of spines along the hinge compared with those along the umbonal slopes to distinguish *Bicarteria* from *Rigrantia*, this difference may be deemed precarious, both because of variability even in the type species of *Rigrantia*, and because the relative thickness is often obscure. But the hinge spines are indeed slender in *hermosana*, and the umbonal slope spines not very thick. The larger size of type and some other *Bicarteria*, and the coarser anterior ribs are noteworthy. A groove along the anterior inner margin of the dorsal ear is displayed by *hermosana*, as in *B. blackwelderi* MacKenzie Gordon (1975, pl. 5, fig. 16, 19). Pennsylvanian species such as *coloradensis* Girty and *portlockianus* Norwood & Pratten are likely to be congeneric, though not well preserved and with several aspects poorly known, and Lazarev (2000b) judged *inflatoventra* Cooper & Grant from the *Uddenites* Shale to be congeneric. In this species, reticulation is well developed, but umbonal slope spines are possibly stronger than those few spines preserved along the hinge, although it should be noted that the specimen in Cooper & Grant (1975, pl. 386, fig. 9) appears to have a strong spine along the outer hinge. The preservation of posterior ventral spines in these various species is seldom adequate for generic discrimination.

Antiquatonia jemezensis Sutherland & Harlow, 1967, pl. 135 from Jemez Springs Shale Member of late Carboniferous age (Virgilian) in New Mexico, United States is small and transverse with well developed reticulation, indicative of *Rigrantia*, but has spines along the umbonal slope ridge that are substantially stronger than those along the hinge, more as in *Bicarteria hermosana*. A dorsal ear groove is developed. If this is *Rigrantia*, then the definition of *Rigrantia* must be adjusted. And if it is *Bicarteria*, the definition focused on hinge and umbonal slope spines as in Lazarev may be accepted, and the variation in ribs and rugae accommodated.

Pseudantiquatonia Zhan & Wu, 1982 from the Xiala Formation of Wordian age in central Xizang (Tibet) has a distinctive ridge at the base of the ventral umbonal slopes, but was ignored by Lazarev (2000b) and misinterpreted by Brunton et al. (2000, p. 488) as a member of Tyloplectini Termier & Termier (see p. 151). As shown in the original study, and confirmed by Shi & Shen (2001, p. 244) and Shi & Chen (2003, p. 778), *Pseudantiquatonia* lacks capillae and lateral buttress plates which help characterize *Tyloplecta*. The genus may be placed in Rigrantiini, and is distinguished by its strong costae, and lack of conspicuous external dorsal pits. Dorsal valve exteriors are incomplete but appear to indicate the presence of a dorsal ear groove. Spines along the umbonal slope ridge are comparatively fine, but the nature of hinge spination is not well described or illustrated. The genus remains in contention as senior synonym for *Rigrantia*, unless stress is placed on the emphatic posterior reticulation that is marked in type *Rigrantia*, but less so for other species from the United States. *Pseudantiquatonia* has no dorsal spines but seems to have an anterior dorsal ear groove, though ears of both valves are poorly preserved (Zhan & Wu 1982, pl. 3, fig. ?4, 14). Shi & Shen (2001, p. 244) expressed some doubt about the presence of a umbonal slope ridge, but seemed to indicate one in their pl. 1, fig 10, 14. The costae are strong, and reticulation not as pronounced as in some forms. Poor preservation conceals the nature of the hinge spines, and the umbonal ridge spines are not very robust.

The species described as *Antiquatonia cooperi* Shi, 1990 by Shi & Waterhouse (1996, pl. 13, fig. 3-11) from the *Yakovlevia transversa* Zone of the Jungle Creek Formation of northwest Canada has larger ears and coarser costae and transverse rugae. A row of spines is developed along the hinge and another over the umbonal slopes, but the ventral valve appears to be more convex and the ornament less markedly reticulate than normal for *Rigrantia*. No figure shows if a dorsal ear-groove is present. The types were described from the Coyotte Butte Formation of Oregon by Cooper (1957, p. 35, pl. 5C, fig. 18-22) as *Antiquatonia sulcata* Cooper [non *sulcata* Sowerby, 1821], and renamed *cooperi* by Shi (1990). The species is elongate, but is close in long trail and convex ventral valve to *hessensis,* and a dorsal ear-groove appears to be present.

Subtribe **ANTIQUATONIINAI** new subtribe

Name genus: *Antiquatonia* Miloradovich, 1945, p. 496 from Carboniferous limestone (Visean) of Derbyshire, England, here designated.

Diagnosis: Medium to large, dorsal ears without bordering anterior groove, dimples developed in some forms. Lower Carboniferous (Visean) to Lower Permian (Sakmarian).

Genera: *Antiquatonia* Miloradovich, *Costacondraia* new genus, *Nazeriproductus* new genus.

Discussion: *Antiquatonia* Miloradovich is a Carboniferous genus known from many species, and displays reticulate ornament over the disc, scattered ventral spines, a row of spines along the ridge that is developed along the lower umbonal flanks of the ventral valve, just as in *Rigrantia*, and a row of spines close to the hinge. The dorsal valve, rarely figured or described, has a few dorsal spines according to Muir-Wood & Cooper (1960, p. 270), and appears to lack dorsal external pits. It was classed in Dictyoclostidae by Muir-Wood & Cooper (1960), and in Tribe Retariini by Brunton et al. (2000, p. 472). The genus is close in size and many aspects of ornament to Retariini, whilst noting that many Retariini have dorsal external pits, and often more dorsal spines. But no Retariini have a ventral external ridge, and the dorsal marginal ridge that is usually well developed in members of Retariini may be missing, although the posterior hinge ridge is well displayed each side of the cardinal process. Type *Rigrantia* lacks an internal marginal ridge and hinge ridges, but hinge ridges are developed in *Bicarteria*, and in some other species of *Rigrantia*. There is also some similarity to *Spyridiophora* Cooper & Grant (see p. 130), classed in Spyridiophorini and close to Retariini. *Spyridiophora* shows reticulate ornament, ventral spines, pits on some dorsal exteriors, and often has a ridge along the lower umbonal slopes of the ventral valve. Any emphasis on the significance of dorsal dimples must be treated with caution. Pits are present or absent in type *Reticulatia* (p. 132), and appear to have disappeared at maturity from *Costiferina* (p. 138). Given that the external ventral ridge along the umbonal slopes is a rare feature, and given that many morphological features are shared by *Rigrantia, Bicarteria* and *Antiquatonia*, it is deemed possible that *Antiquatonia* evolved within Family Retariidae by developing an external ridge along the ventral umbonal slopes, and changed through time into *Bicarteria*, followed by *Rigrantia*.

Genus ***Antiquatonia*** Miloradovich, 1949

Fig. 5.13, Fig. 5.14

Type species: *Productus antiquatus* Sowerby, 1821, p. 15 from Lower Carboniferous of England.

Diagnosis: Ventral spines form distinct row along ears and another along umbonal slopes above internal ear ridge, scattered over remainder of ventral valve, visceral disc finely reticulate. Dorsal valve reticulate and usually without spines. Inner anterior margin of each ear grades smoothly on to dorsal visceral disc, without being bordered by groove.

Discussion: Morphology of the ventral valve indicates a close relationship to Rigrantiini, because of the reticulate ornament and row of spines along the ventral hinge and base of the umbonal slopes, that emerge from a distinct ridge. A principal distinction from allied genera appears to lie in the nature of the dorsal ears, which are not bordered anteriorly by a distinct groove, as may be seen in illustration of Lower Carboniferous species ascribed to *Antiquatonia*, such as *A. antiquatus* (Sowerby) figured by Muir-Wood (1928, pl. 7, fig. 2), *A. insculptus* Muir-Wood, figured by Muir-Wood (1928, pl. 3, fig. 12), or *A. sulcatus* (Sowerby) figured by Muir-Wood (1928, pl. 10, fig. 4), or *A. insculpta* of Sarytcheva in Sarytcheva et al. (1963, pl. 35, fig. 7a). *Antiquatonia* sp. of Brunton (1966, pl. 17, fig. 8) shows a narrow bordering groove. In the original figures of the species provided by Sowerby (1821, pl. 317, fig. 1) there is a line of pits. However it has to be noted that dorsal views of *Antiquatonia* are seldom illustrated, and even Muir-Wood (1965) and Brunton et al. (2000) failed to provide any figures of dorsal valves, and no confirmatory text on the nature of the border for the dorsal ears. But although some reservation must be retained over the reality and persistence of the feature as a diagnostic criterion, dorsal valves as here figured lack the dorsal ear-groove, as well as strong dorsal pitting.

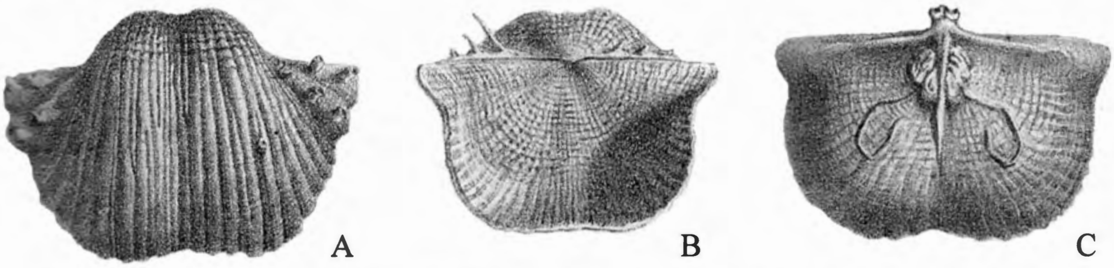


Fig. 5. 13. *Antiquatonia costatus* (Sowerby), as figured by Davidson (1861, pl. 32, fig. 3, 6, 8). A, ventral valve. B, dorsal aspect. C, dorsal interior. From Lower Carboniferous at Settle, Richmond, and Lanarkshire, England and Scotland, x1.

Lazarev & Carter (2000, pp. 17-20, Fig. 3) stressed that *Antiquatonia* belonged a lineage quite separate from that of *Rigrantia* and *Bicarteria*, pointing to umbonal shagreening, as distinct from the younger genera which lacked such papillation. Caution is needed however, because *A. insculpta* (Muir-Wood) of Sarytcheva et al. (1963, pl. 35, fig. 6v) lacks papillation, and dorsal valves of type *Spinocarinifera*, deemed by these authorities to be in the same lineage as *Antiquatonia*, also appear to lack papillation (Roberts 1971, pl. 19, fig. 16, pl. 20, fig. 16), perhaps indicative of the loss of papillation with increased maturity, as for New Zealand Productida (see pp. 18-22). Papillation is developed over the posterior septum in *Bicarteria hermosana* figured by Sutherland & Harlow (1973, pl. 11, fig. 10) and possibly in *Bicarteria coloradoensis* (Sutherland & Harlow 1973, pl. 11, fig. 3, 4). But the papillation is finer than that found laterally and anteriorly. What is striking about these genera is the very strong papillation developed over both valves in *Keokukia, Tesuquea, Spinocarinifera* and *Antiquatonia*. It recalls the equally strong papillation developed in *Lethamia* Waterhouse (see Waterhouse (1982a, pl. 8, fig. c, e, pl. 9, fig. c). This papillation weakened in more mature specimens of *Lethamia*. Strong papillation comparable with that of *Antiquatonia* is developed over much of the floor of both valves in *Bicarteria* (Sutherland & Harlow 1973, pl. 11, fig. 9) and *Rigrantia* (Cooper & Grant 1975, pl. 386, fig. 7, pl. 390, fig. 14). In short, the interrelationships of these genera do not appear to have been conclusively demonstrated by the distribution, nature and change through ontogeny of posterior papillation,

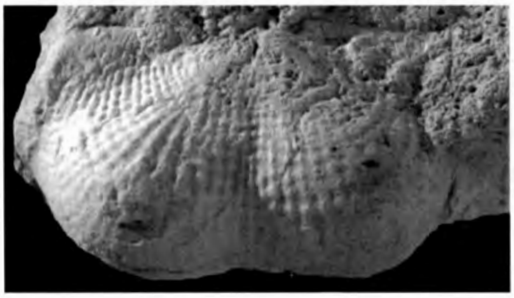


Fig. 5. 14. *Antiquatonia insculpta* (Muir-Wood), dorsal valve BR 3160 from zone B2 (*Beyrichoceras*), Visean of Castleton, Derbyshire, England, x3. JBW photo.

Genus **Costacondraia** new genus

Fig. 5.15

Derivation: costa – rib, Lat.; condraia, named for G. E. Condra.

Type species: *Dictyoclostus portlockianus crassicostatus* Dunbar & Condra 1932, p. 217 from Desmoines beds and overlying Pennsylvanian in Nebraska, United States, here designated.

Lectotype: YPM 13568 from near Kiewitz Quarry, near Meadow, Nebraska, United States, figured by Dunbar & Condra (1932, pl. 33, fig. 6), SD Sutherland & Harlow (1967, p. 1077).

Diagnosis: Small strongly reticulate shells with ventral costae broadening anteriorly, ventral spines sturdy, as strong or slightly stronger along hinge compared with umbonal slope spines. Thickest spines lie over trail, moderately thick along hinge and thinner over umbonal ridge. Ventral umbonal slope ridge well developed. Dorsal valve without spines or pits, and apparently without groove along anterior border of ears.

Discussion: This genus would appear to be descendent from *Antiquatonia*, and differs in the strength of its ventral spines and costae, and the way in which the row of hinge spines is short and arises virtually at the hinge, rather than in a row sloping forwards over the posterior ear. The type species in a general way looks moderately close to *Antiquatonia costatus* (Sowerby), though less transverse with smaller ears and stronger hinge spines diverging less from the hinge. The two were distinguished by Muir-Wood (1928, p. 143) and Dunbar & Condra (1932, p. 218). The dorsal valve is poorly known, but as figured by Dunbar & Condra (1932, pl. 33, fig. 7b), shows costae that are distinctly finer and more numerous than those of the ventral valve, and points to the absence of a groove along the inner anterior margin of the dorsal ears. Caliche covers the dorsal valve of the two specimens figured in Fig. 5.15, and the dorsal costae are only obscurely indicated.

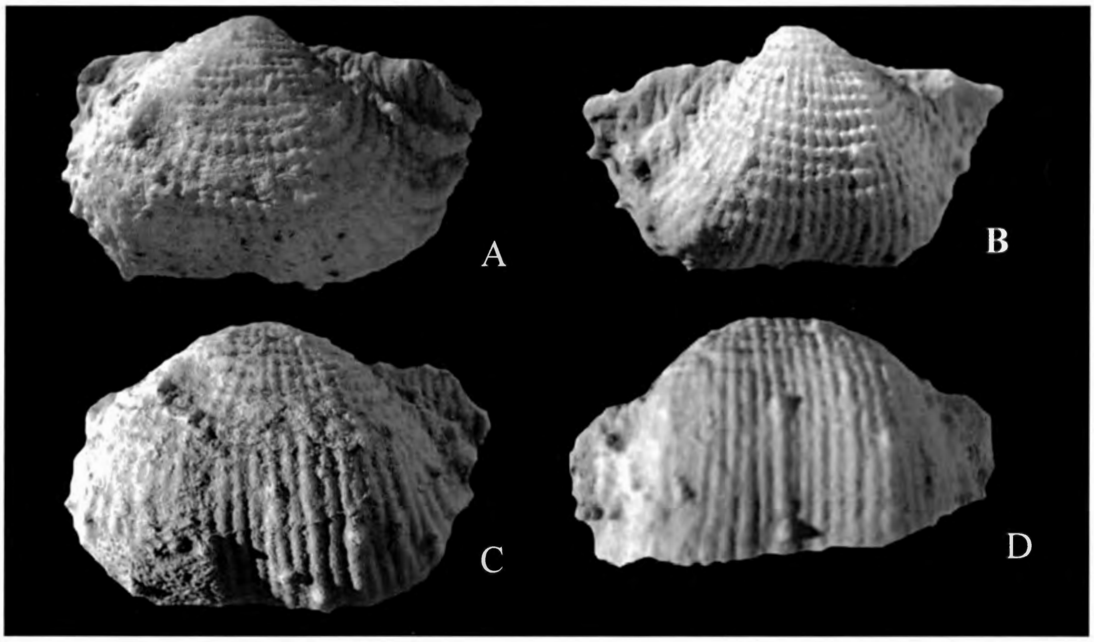


Fig. 5.15. *Costacondraia crassicostata* (Dunbar & Condra). A, C, ventral posterior and anterior aspects of ventral valve BR 3161. B, D, ventral posterior and anterior aspects of ventral valve BR 3051. Specimens from Spring Hill Member, Plattsburg Limestone (Missourian), Langsing Group near Louisville, Nebraska, United States, x3. JBW photo.

Genus ***Nazeriproductus*** new genus

Derivation: Named for R. E. Nazer.

Type species: *Nazeriproductus nazeri* new species from Ettrain Formation (Kasimovian), Yukon Territory, Canada, here designated.

Diagnosis: Large with extended ears, reticulate over much of disc, hinge and umbonal slope of spines moderately developed, varying to thin, body spines rare, scattered, mostly posterior, usually thin. Umbonal slope ridge in many but far from all specimens, dorsal ears without bordering groove, and disc bears pits.

Discussion: This new genus is much larger than species allocated to *Antiquatonia*, and has dorsal pits and extended ears. Species presently assigned to *Antiquatonia* are of Lower Carboniferous age as a rule, and lack dorsal pits and ear groove, and vary considerably in the detail of spine thickness and distribution.

Nazeriproductus nazeri new species

Fig. 5.16, Fig. 5.17

1971 ?*Reticulatia* sp. Waterhouse in Bamber & Waterhouse, pl. 5, fig. 1?, pl. 9, fig. 1, 2 only.

Derivation: Named for Roderick E. Nazer.

Holotype: GSC 37196 from near GSC loc. 53727, Ettrain Formation (Kasimovian), Canada, figured as Fig. 5.16B, C, D, here designated.

Diagnosis: Large with wide ears, strong ribs and posterior commarginals, spines in row along hinge and along ridge on lower umbonal slopes, very large and few spines on anterior valve.

Material: Some fifty mostly ventral valves and specimens with valves conjoined from GSC loc. 53693, 53727, 56931 and 57069. See Appendix A, part C, p. 478.

Dimensions in mm:

Specimen GSC	Width	Length	Height
37202	80	70	36
37208	88	64	42
37195	86	63	44
37200	86	60	41

Description: Large and transverse shells, ventral valve strongly convex, ventral umbo slightly incurved with angle of 95-110°, and slightly extended beyond the hinge. Ventral ears very large and extended, almost tubular in their convexity. The sulcus commences 10-20mm in front of the umbonal tip, and becomes 20-25mm wide and only 1-3mm deep over the trail. Costae strong, numbering six to eight in 10mm over the trail, with rounded crests and interspaces of comparable width; may branch anteriorly on trail. Commarginal rugae rib-like and firm, may not cover entire disc, and a little variable in extent, cover the ears, or least inner ears, extending radially from the hinge. In some specimens the radial ribs cover the ears, and for other specimens, the ears are comparatively smooth. Dorsal valve gently concave over broad disc, no groove in front of the ears, and trail subgeniculate. Ribs strong and disc covered by commarginal ornament, but posterior shell in front of the hinge may be smooth. A row of stout erect spines lies close to the ventral hinge, and another row of spines, close in diameter, or slightly thicker, extends along a ridge developed along the umbonal flanks, though a number of specimens do not show this ridge. Halteroid spines scattered over the disc and trail, and a few very large spines lie on the trail, one to three in number. The dorsal exterior has elongate pits over the disc, often with a line of pits corresponding with the umbonal flank row of spines.

Ventral adductor scars on low platform and dendritic; diductor scars long (30mm) each side, striate. Secondary shell thickens the valve posteriorly, but not to any great extent. Cardinal process large and ventrally bilobed, supported by strong median septum extending for about two thirds of the length of the visceral disc. Hinge ridges diverge laterally, extending for little more than half the width of the valve, and bend forward over the inner ear and continue forward a short distance around the margin of the disc. Posterior adductor scars large and dendritic, anterior scars small, raised and more or less smooth. Brachial ridges extend horizontally from between the adductor pair, and form small smooth brachial shields. Papillation strong in both valves.

Resemblances: These specimens look as though they belong to a form of *Reticulatia* Muir-Wood & Cooper, but several have a well defined external ridge along the base of the ventral umbonal slopes. The type species of *Bicarteria, B. hermosanus* Girty (1903) from a Bashkirian fauna of Colorado, United States, is moderately close, showing bifurcating anterior ventral costae, and long and dorsally geniculate trail. The size is smaller, and the ears are not as large, possibly because of breakage, and have anterior ear grooves. Reticulation is a little fainter, and although rare anterior spines are large, they are not as strong as those of the Canadian species. Sutherland & Harlow (1973, p. 51, pl. 11, fig. 6-12) recorded *hermosanus* from the lower to middle Desmoinesian of New Mexico. The interior of a ventral valve at late maturity shows fine striae covering the posterior floor, much as in *Reticulatia oldershawi* (see p. 133), whereas a dorsal valve interior posteriorly has either very fine papillation, or is smooth (Sutherland & Harlow 1973, pl. 11, fig. 10, 12). Specimens of Pennsylvanian age from New Mexico were also figured as *Antiquatonia* by Muir-Wood & Cooper (1960, pl. 94, fig. 10, pl. 95, fig. 4, 5).

Antiquatonia coloradoensis Girty (1910, p. 216) was proposed as a replacement name for *Productus inflatus* Girty non McChesney from the basal Hermosana Formation of Colorado, and the species was also reported from the Morrowan and lower Atokan of New Mexico by Sutherland & Harlow (1973, p. 51, pl. 11, fig. 1-5). Reticulation is finer and size smaller, compared with *hermosana*, but both Girty and Sutherland & Harlow agreed that there was a degree of gradation between the two. *Bicarteria portlockiana* (Norwood & Pratten), described further by Dunbar & Condra (1932, p. 215, pl. 33, fig. 1-3), Sturgeon & Hoare (1968, p. 46, pl. 11, fig. 8-13) and Sutherland &

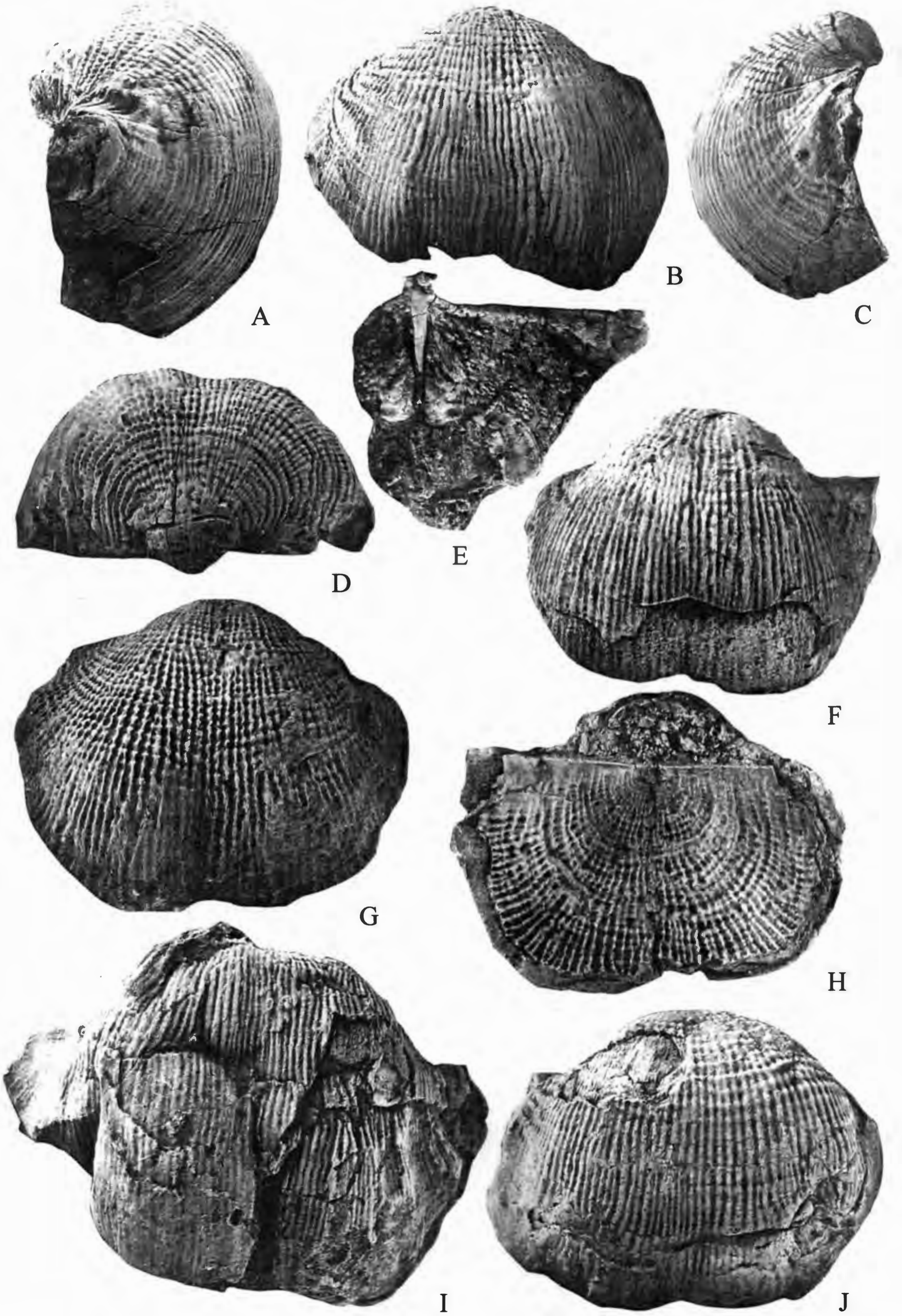


Fig. 5.16. A-F, H-J, *Nazeriproductus nazeri* new species. A, ventral valve GSC 37195. B-D, holotype, ventral, lateral and posterior aspects of a conjoined specimen, GSC 37196. E, dorsal interior, GSC 37197. F, H, ventral and dorsal aspects of GSC 37198. I, ventral view of GSC 37201. J, ventral GSC 37201 from same locality. G, *Reticulatia* sp. ventral view of GSC 37200. Specimens from GSC loc. 53727, and Fig. 5.13 G from nearby. Ettrain Formation, Yukon Territory, Canada, x1. See Appendix A, part C, p. 478. R. E. Nazer, photo.

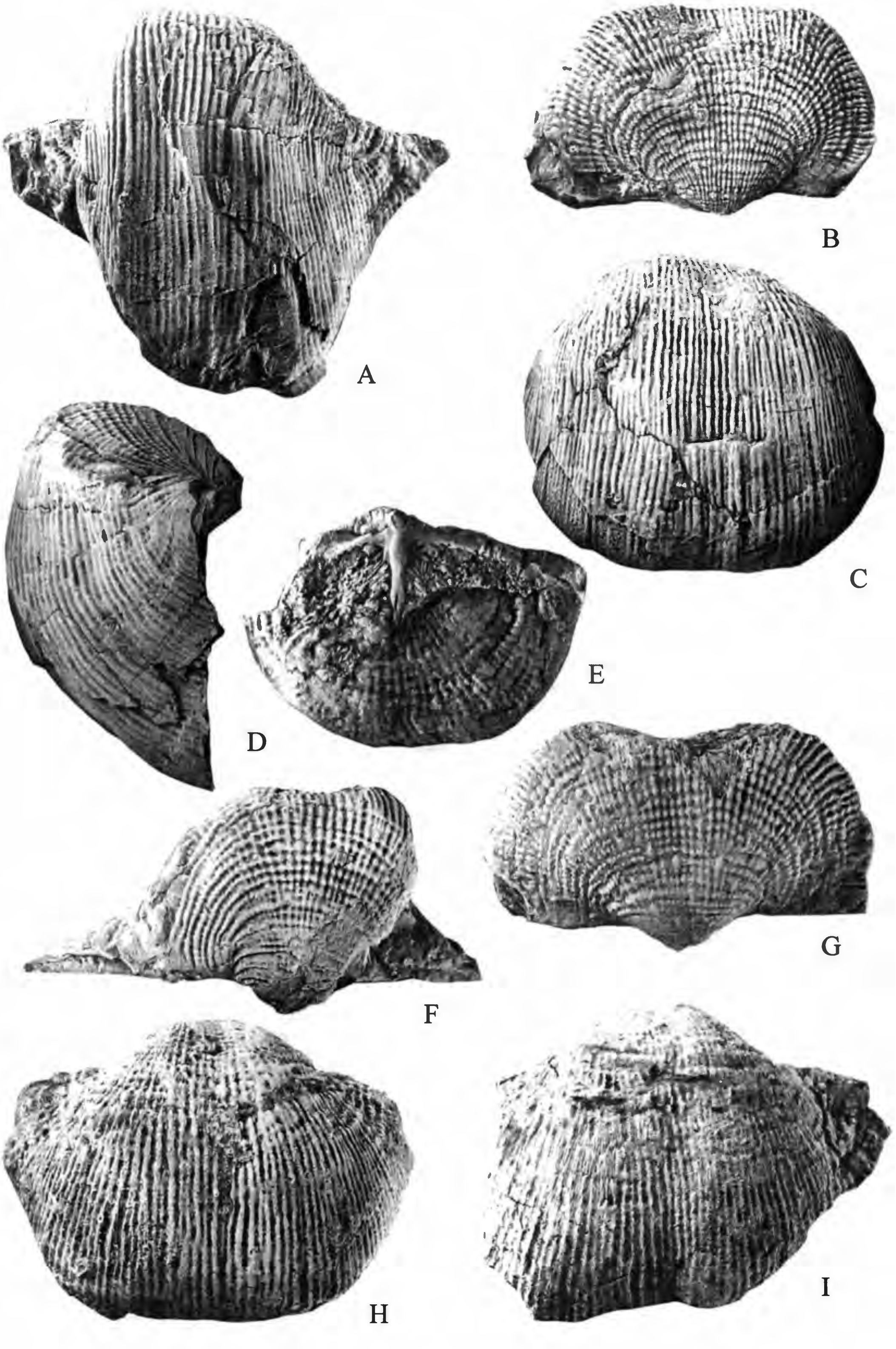


Fig. 5.17. *Nazeriproductus nazeri* new species. A, D, F, ventral, lateral and posterior views of partly crushed ventral valve GSC 37202 from GSC loc. 56931. B, C, posterior and anterior ventral aspects of ventral valve, GSC 37203 from near GSC loc. 53727. E, dorsal interior, GSC 37204 from same locality. G, posterior view of ventral valve GSC 37205 from the same locality. H, ventral view of ventral valve GSC 37206 from GSC loc. 53693. I, ventral view of ventral valve GSC 37207 from GSC loc. 57069. Ettrain Formation, Yukon Territory, Canada, x1. See Appendix A, part C, p. 478. R. E. Nazer, photo.

Harlow 1973, p. 52, pl. 11, fig. 13) is small with coarse costae. The general age is Desmoinesian, but Sturgeon & Hoare (1968) believed that the species ranged into Missourian and possibly lower Virgilian.

In many respects the species *nazeri* approaches species of *Reticulatia*, and study of large populations of species allocated to the two genera is needed to clarify morphological constraints.

Antiquatonia reticulata Cooper (1957, p. 34, pl. 3, fig. 1-9) from the Sakmarian Coyotte Butte Formation of Oregon, United States, is apparently congeneric, with comparable reticulate ornament and no ear groove and ventral umbonal slope ridge. The shell is smaller and less elongate than the Canadian species. So-called *A. cooperi* Shi from the same beds is less reticulate with coarser ornament, and has an ear groove.

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

Fig. 5.18

[Nom. transl. Brunton, Lazarev & Grant, 1995, p. 928 ex Spyridiophoridae Muir-Wood & Cooper, 1960, p. 230].

Diagnosis: Coarse ribs with spine row on each arched ventral ear, high internal ridge posteriorly in both valves, but no diaphragm or series of dorsal trails. Two septa present in dorsal valve, may form an elevated cup or spyridium. Upper Carboniferous (Moscovian) to Upper Permian (Wuchiapingian).

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

Discussion: These exceptional genera are regarded as a tribe within Retariinae, which they resemble externally in their ribbing and distribution of spines and commarginal ornament, and are distinguished by the development of two dorsal septa and in one genus a spyridium, consisting of a subvertical dorsal platform bearing the seat of the dorsal adductor muscles. Brunton et al. (2000, p. 475) treated Spyridiophorini as a tribe with Retariini in Productinae. Scattered dorsal pits are present in some specimens. The Texan forms may show a ventral umbonal slope external ridge, recalling that of Rigrantini (see above).

The time range given by Brunton et al. 2000 for the group was Lower Permian (?Artinskian), but Termier & Termier (1970b) named new species *Spyridiophora timorensis, S. gubleri* and *S. tenuicostatata* from what they stated were Djulfian (= Wuchiapingian) beds of Cambodia: they are notably less reticulate over the posterior ventral valve than the types of the genus.

Fig. 5.18. A, C, *Spyridiophora reticulata* (King). A, ventral valve USNM 149321a, x1. C, dorsal interior USNM 24118b, x2, from Poplar Tank Member and Taylor Ranch Members (Lower Permian), west Texas, United States. B, *S. distincta* Cooper & Stehli, dorsal aspect of USNM 124116b, x1.5, from Neal Ranch Formation (Asselian), Texas. See Cooper & Grant (1975, pl. 251, 252).

Subfamily **RETICULATIINAE** Lazarev, 2000a

[Nom. promoveo hic ex Reticulatiini Lazarev, 2000a, p. 40. Syn. Latispiniferini Lazarev, 2000b, p. 26; Callytharrellini Waterhouse, 2002b, p. 21].

Diagnosis: Mostly large shells with relatively small ears as a rule, strongly reticulate disc with spines usually sparse, usually in row around base of flanks, spines may be more numerous on ears, moderate to rare over venter and trail, may include a few strong anterior spines. No external ridge at base of umbonal slopes. Dorsal disc with no spines, dimples as a rule, matching positions of ventral spines. Moderate to low if any marginal ridge, internal posterior papillation arguably not developed. Lower Carboniferous (Tournaisian) to Middle Permian (Wordian).

Genus: *Reticulatia* Muir-Wood & Cooper, *Admoskovia* Lazarev, *Bogabbria* new genus, *Bruntonella* Chen & Shi, *Callytharrella* Archbold, ?*Chaoina* Jin, *Costiferina* Muir-Wood & Cooper, 1960, *Dasysaria* Cooper & Grant, *Kunlunia* Wang Zhi, *Latispinifera* Lazarev, *Neopugilis* Li, *Robertsina* new genus, *Stereochia* Grant, ?*Tenaspinus* Brunton & Mundy, *Zia* Sutherland & Harlow (syn. ?*Semilunataproductus* Han Tong-xiang in Han et al.).

Discussion: There is a modest number of ventral spines, variously disposed, but not numerous, and in some genera including stout spines on the ears and anterior disc or trail. As a rule, dorsal dimples are also present. Compared with Retariinae, the size is generally larger, the shape less transverse, with less extended ears, and there is no high marginal ridge around the dorsal interior. Members of Family Dictyoclostidae are rather similar in general appearance (see pp. 154 - 174), but lack the row of spines along the base of the umbonal slopes, and reticulation is a little less sharply defined.

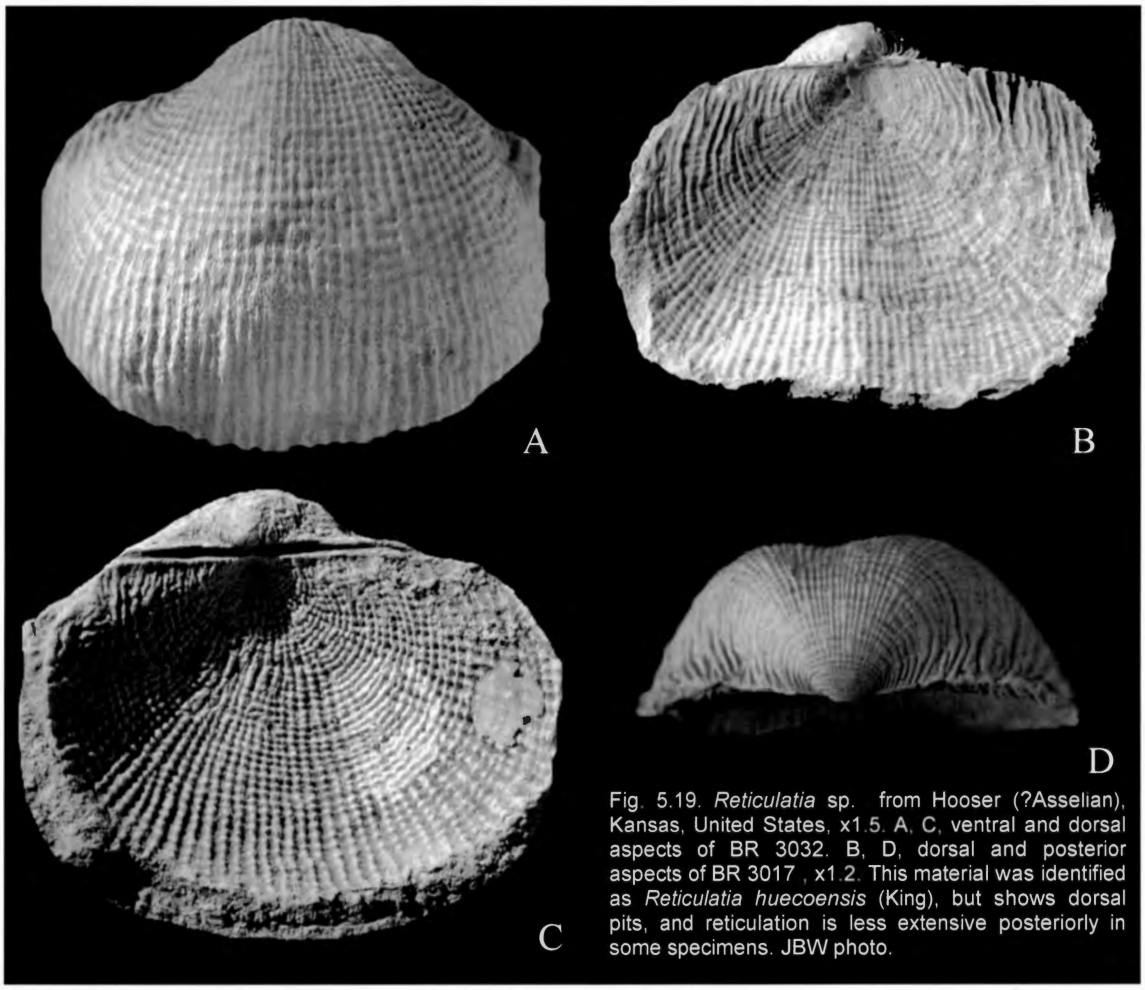


Fig. 5.19. *Reticulatia* sp. from Hooser (?Asselian), Kansas, United States, x1.5. A, C, ventral and dorsal aspects of BR 3032. B, D, dorsal and posterior aspects of BR 3017 , x1.2. This material was identified as *Reticulatia huecoensis* (King), but shows dorsal pits, and reticulation is less extensive posteriorly in some specimens. JBW photo.

Lazarev (2000b) separated a somewhat similar group of dictyoclostiform genera as Latispiniferini, which he regarded as a fellow tribe within Yakovleviinae. As well as *Latispinifera,* genera included *Callytharella* Archbold, *Stereochia* Grant, and *Costiferina* Muir-Wood & Cooper. The tribe was defined as differing from other tribes by the presence of well developed narrow spines at the base of the ventral umbonal flanks, continuing over the geniculation, and further distinguished from Reticulatiini in the presence of pits over the disc of the dorsal valve. Such differences between *Reticulatia* and *Latispinifera* are not easy to establish. The ventral spines overall are fairly similar in species of the two genera, and both certainly have a row of spines at the base of the umbonal flanks. Spines are present in figures of *Reticulatia* presented by Muir-Wood & Cooper (1960, pl. 104, fig. 5; pl. 105, fig. 1), and are obscure, if present, in the type species of *Latispinifera*, as figured by Sarytcheva (1977) and Brunton (2007). Whether they cross the trail in this genus as reported by Lazarev (2000b) is not clearly explained, and not explictly figured. On *Reticulatia* from Hooser, Kansas, the flank row passes forward into a more generally spinose trail, passing around the trail rather than across the trail. Dorsal dimples are strikingly present in *Latispinifera*, and are more variably present in *Reticulatia*, as illustrated by Muir-Wood & Cooper (1960, pl. 104, fig. 3, 4) with no apparent dimples, and in Muir-Wood & Cooper (1960, pl. 105, fig. 2) with a few small dimples. Such variation is found also in *Reticulatia*, and

Costiferina Muir-Wood & Cooper, included in Latispiniferini by Lazarev (2000b), also varies in the presence or absence of dorsal pits, as shown below. Given the lack of detail, and apparent variation in some aspects, and given the overall similarity in many details, it appears that Reticulatiini and Latispiniferini are cotribal. It may be allowed, however, that better illustrations for *Latispinifera* would establish a clearer tribal distinction, but in the meantime, differences appear to lie within the limits of tribal variation. An outstanding genus *Admoskovia* Lazarev 2000b, p. 28 from the Upper Carboniferous differs more clearly from both *Reticulatia* and *Latispinifera*, in having rows of very coarse spines near the ventral hinge and over the wide ears, and no dorsal pits are developed. Classed as Reticulatiini by Lazarev (2000b, 2000c) and Brunton (2007), it is highly distinctive. However the uncertainty over posterior central papillation is resolved, the presence of external dorsal dimples at least in most genera marks no more than a tenuous distinction from Dictyoclostini. The difference in ventral spinosity from Dictyoclostini other than the presence of an umbonal slope row is not great, and is poorly conveyed in various figures of *Latispinifera*.

Tenaspinus Brunton & Mundy (1994) from the Visean of north England is small and reticulate with row of spines along the hinge and further spines over the anterior ear margins, which possibly equates to a row along the umbonal slopes, and also ventral disc, and dimples are scattered over the dorsal disc. The corpus is thick, but the interior is poorly known and the degree of maturity uncertain. There is thus some possibility that the genus represents an early member of Reticulatiinae. Originally the genus was classed as Inflatiini in Leioproductinae, a placement defying analysis, and later the genus was repositioned in Yakovleviini in Brunton et al. (2000, p. 467), though there is little similarity to *Yakovlevia* and allies. *Chaoina* Jin in Jin, Liao & Hou (1974, pl. 162, fig. 7, 8) is also small with ventral spines, and is discussed on p. 457.

Brunton (2007, p. 2648) did not accept the placement of *Callytharrella* Archbold, 1985 in Latispiniferini, retaining it in Dictyoclostinae, but the genus is close to *Latispinifera*, as also assessed by Lazarev (2000b).

Genus ***Reticulatia*** Muir-Wood & Cooper, 1960

Type species: *Productus huecoensis* King, 1931, p. 68 from Hughes Creek Shale (Lower Permian), Nebraska, United States.

Diagnosis: Large with reticulate ornament, ginglymus, ventral spines in variable row along hinge and another along base of umbonal slopes, often more but not very numerous spines on outer ears and over disc and trail, no spines and variable and often small pits on dorsal valve, moderate hinge ridge and low dorsal marginal ridge. There is no ridge along the ventral umbonal slopes or groove along the anterior inner margin of the dorsal ears.

Discussion: Although Lazarev (2000a, p. 40) insisted that *Reticulatia* was restricted to Permian deposits, a species close to the genus is represented in Upper Carboniferous faunas of Canada, including Member A at the base of the Jungle Creek Formation.

Admoskovia Lazarev, 2000b was regarded as allied to *Reticulatia* by Lazarev. The hinge is well preserved in *Admoskovia*, with hinge row and a number of stout spines over the ventral ears, but more strongly developed, and dorsal pits are not developed.

Reticulatia oldershawi new species

Fig. 5.20, Fig. 5.21

Derivation: Named for A. Oldershaw.

Holotype: GSC 136049 figured as Fig. 5.20C from Member A, Jungle Creek Formation, Yukon Territory, Canada, here designated.

Diagnosis: Large and weakly transverse with moderately large ears and high trail. Ventral spines few and lie in row along hinge, another row along base of umbonal slopes, rare over venter and trail. Sulcus and fold moderately well formed anteriorly. Concentric fine wrinkles form crenulate pattern, dorsal pits not clearly defined.

Material: Numerous single ventral valves and specimens with valves conjoined from Member A, lower Jungle Creek Formation. *Septospirifer tatondukensis* Zone, Canada. See Appendix A, part A, p. 478.

Dimensions in mm:

Specimen GSC	Width	Length	Height	
136049	75	50	28	holotype
136052	70	49	27	
136048	63	52	29	

Description: Shells large, weakly transverse as a rule and high with long trail. Ventral umbo weakly incurved, umbonal angle of 100-120°, umbonal walls steeply convex and of moderate height, ears large and convex, with obtuse cardinal extremities. A well formed ginglymus is developed along the hinge. Sulcus commences some 12-15mm in front of umbonal tip, and widens at angle of 27-30°, deepest over the trail, with concave floor. Dorsal valve gently concave over disc, with concave ears and median fold commencing close to hinge and persisting on to a trail which is as long as the disc, and subgeniculate. A dorsal ginglymus is developed. Ventral spines are comparatively inconspicuous, forming an oblique row close to the hinge, with umbonal slope row of finer spines, and a few over outer ears, and scattered rarely over the visceral disc and trail, where spines are rarely 1.8mm in diameter, and usually 0.8-0.9mm in diameter, compared with diameter of 1.5mm along the outer hinge. There are no dorsal spines. The predominant ornament is formed by well formed costae crossed by commarginal rugae, four to five radial in 5mm and three commarginals in 5mm at about 20mm from the umbo, and two to three radials and two commarginals in 5mm at 40mm from the umbo. Ribs are round-crested, and separated by interspaces just as wide, with concave floors; the commarginals form nodes, or slightly crescentic ridges arching posteriorly, over the costae. Ears are free of costae, but display commarginal ornament. The commarginals are not developed over the trail, and fade over the anterior disc, but the ribs continue with gradually increasing strength, and in some specimens the ribs become bundled, or arranged over broad low plicae. A few may converge at the start of the trail, and a very few costae may arise by intercalation near the anterior margin. Dorsal ornament of ribs and commarginals is similar to that of the ventral valve, with some variation shown in relative strength of the commarginals and radials. On some specimens the costae increase by intercalation near the anterior margin. Visceral disc of only moderate thickness, close to 10mm in large specimens, and no conspicuous pits lie over the disc of the dorsal valve.

Ventral adductor scars are placed on a high narrow platform, divided by a low myophragm, with posterior dendritic scars, that flare postero-laterally, and narrow anterior scars bearing low linear ridges. Diductor scars are only moderately impressed and deeply grooved, and very wide, extending as far as the lateral umbonal slopes. The floor of the valve behind the scars is lightly marked by fine more or less commarginal lines, and the shell floor behind the adductor scars is marked by short and low irregular ridges, more or less commarginal, with fine pits, and no development of smooth surface. Shell some 8mm thick posteriorly, due to secondary thickening.

Cardinal process large and trilobed, with narrow median shaft bent ventrally, and high lateral lobes directed posteriorly and well separated from the median lobe. The process is supported by a short broad platform, joined laterally by a ridge along the hinge, and leading forward into a slender median septum that extends to anterior third or fourth of the visceral disc, but ends behind mid-length in one specimen from JBW 141. Posterior adductors are large with dendritic markings, and anterior adductors are more raised, and may be smooth or bear dendritic ridges. Brachial shields small, not clearly outlined, and placed far behind the anterior terminus of the septum. Posterior shell smooth, anterior shell with pustules, which become very large (JBW 141).

Resemblances: This species is like type *Reticulatia* in its reticulate ornament and more or less in spine detail, except that ear spines are more numerous in one specimen figured by Muir-Wood & Cooper (1960, pl. 105, fig. 1), and in one specimen of *americana* (Dunbar & Condra) figured by Branson (1964, pl. 1, fig. 3), although spines are fewer in other figured specimens (Muir-Wood & Cooper 1960, pl. 105, fig. 4; Branson 1964, pl. 1, fig. 1). The present material does not show the fine external dorsal pits seen in at least some type *Reticulatia* (Muir-Wood & Cooper 1960, pl. 105, fig. 2), has a narrower median lobe in the cardinal process and lateral lobes inclined posteriorly rather than more laterally, and apparently lacks a marginal ridge. The ventral interior was not figured by Muir-Wood & Cooper (1960) or Brunton et al. (2000). In overall shape, the Canadian species has a longer trail and is more sulcate. The dorsal interior of the Canadian species is too imperfect to show if papillation was developed. Type *Latispinifera* Lazarev is similar and differs in many of the same aspects: the one clear difference lies in the lack of large and elongate dorsal pits from the Canadian form, and type *Reticulatia* has small if any dorsal pits. Type *Latispinifera* as figured by Sarytcheva (1977) may show more reticulation over the anterior disc and dorsal pitting, but details of its posterior spination are obscure, and whether an internal marginal ridge was developed is not clear.

Specimens from the *Yakovlevia transversa* to *Jakutoproductus verchoyanicus* Zones of the younger Jungle Creek Formation that were described as *Reticulatia uralica* (Tschernyschew) by Shi & Waterhouse (1996, pl. 11, fig. 11, pl. 12, fig. 1-11, pl. 13, fig. 1, 2, pl. 32, fig. 1) are also large with somewhat comparable radial and transverse ornament. They have smaller ears, a shallower ventral sulcus, and more ventral spines over the visceral disc and umbonal slopes, and larger spines along the hinge. Overall the general appearance of size, shape and reticulate ornament is close. There is no dorsal marginal ridge, and a shorter dorsal septum. The species *uralica*, as represented by Tschernyschew (1902, pl. 33, fig. 1) from the Early Permian of Urals, and type specimen selected by Volgin (1960, p. 91), has large ears with more spines than in the Canadian species, but is close in reticulation and in its long trail and presence of ventral sulcus.

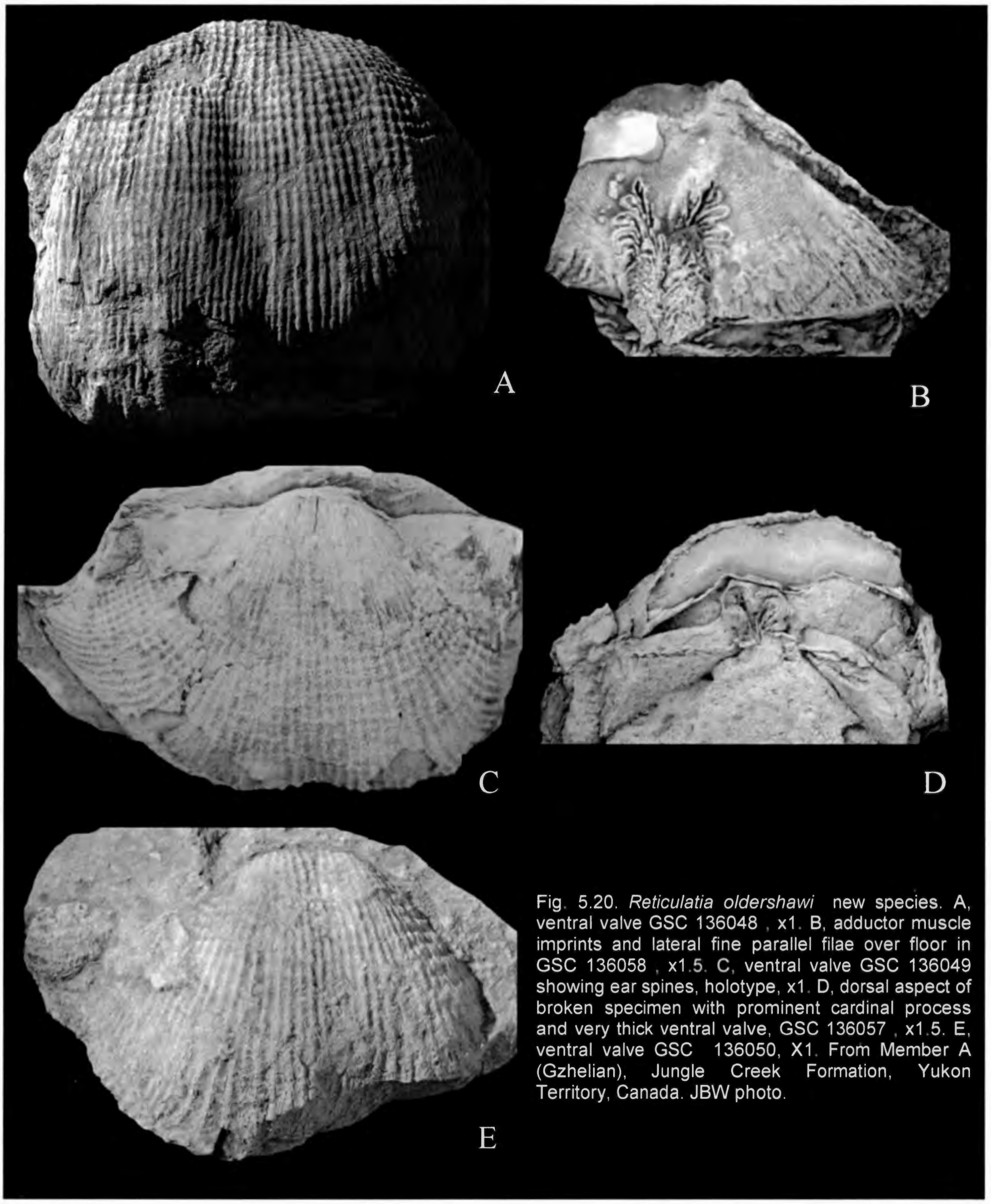
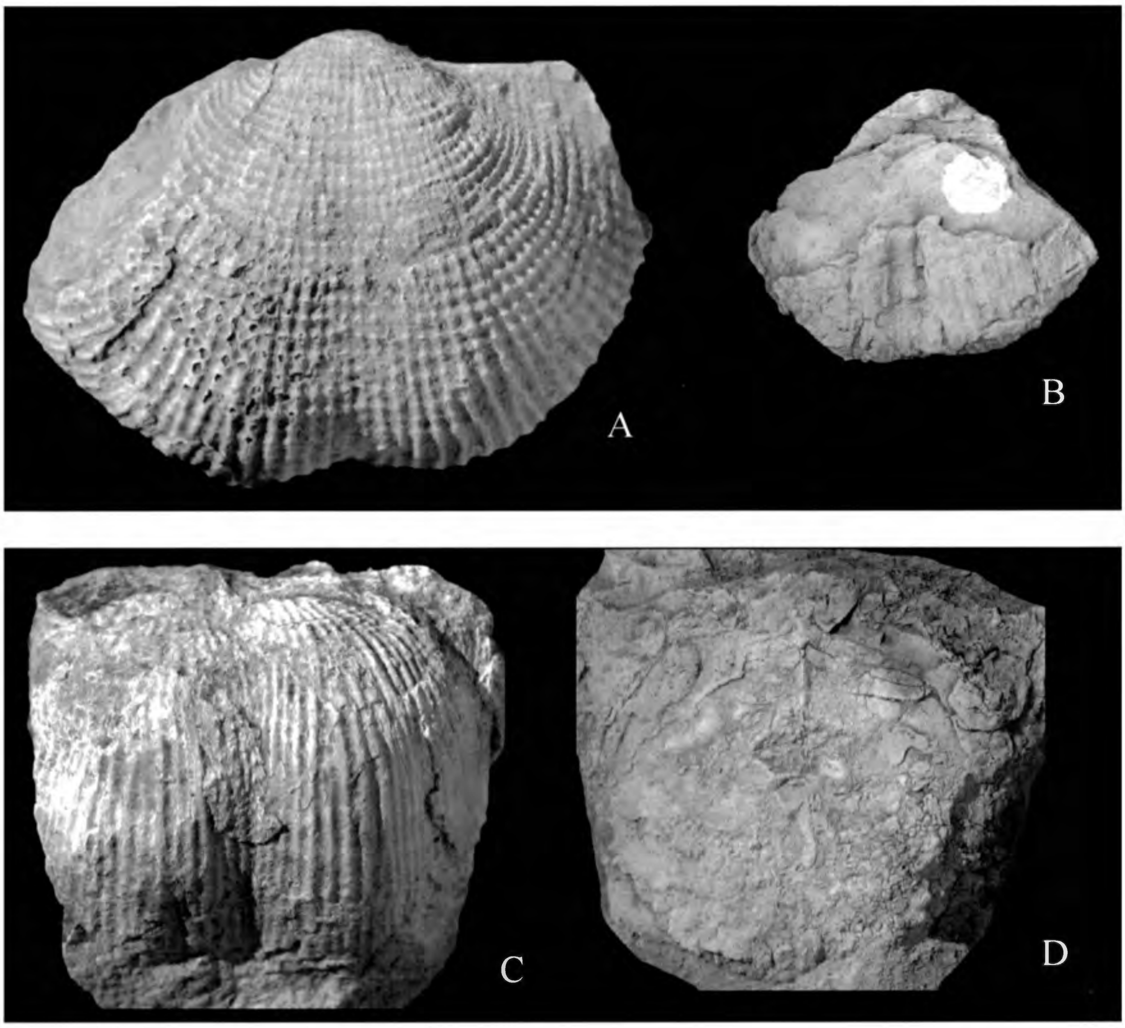


Fig. 5.20. *Reticulatia oldershawi* new species. A, ventral valve GSC 136048 , x1. B, adductor muscle imprints and lateral fine parallel filae over floor in GSC 136058 , x1.5. C, ventral valve GSC 136049 showing ear spines, holotype, x1. D, dorsal aspect of broken specimen with prominent cardinal process and very thick ventral valve, GSC 136057 , x1.5. E, ventral valve GSC 136050, X1. From Member A (Gzhelian), Jungle Creek Formation, Yukon Territory, Canada. JBW photo.

Opposite page:
Fig. 5.21. *Reticulatia oldershawi* new species. A, ventral valve showing spines along hinge and umbonal slope, GSC 136052, x1.3. B, ventral valve, the trail recurved by distortion and showing broad anterior ribbed subplicae, as well as high ginglymus, GSC 136053 , x0.7. C, anterior dorsal valve showing high geniculate trail, GSC 136054, x1. D, dorsal interior, nested within ventral valve, GSC 136056, x0.8. From Member A (Gzhelian), Jungle Ceek Formaton, Canada. JBW photo.



Reticulatia americana Dunbar & Condra (1932, pl. 34, fig. 3-6), treated as a synomym of *R. huecoensis* not King of Muir-Wood & Cooper (1960, pl. 104, 105) by Cooper & Grant (1975, pl. 383, fig. 14-22), but opposed by Branson (1964), is slightly smaller and more equilateral in shape, and with finer costellae, especially on the dorsal valve. It is found widely in the United States in Nebraska, Kansas, Oklahoma and Neal Ranch Formation of west Texas, in beds of Wolfcampian age. *R. robusta* Cooper & Grant (1975, p. 1088, pl. 386, fig. 1, pl. 392, fig. 1-6) is closer to the present species in the strength of the ribbing, but the shell is smaller and less sulcate, and anterior spines are coarser.

Reticulatia magna Sarytcheva (1977, pl. 13, fig. 4, pl. 14, fig. 1, text-fig. 60) from the Moscovian Stage of Moscow Basin, Russia, is close in size and ornament to the present species: both sets of specimens show strong concentric ornament, but many details for the Russian species remain poorly known. The species *ivanovi* (Lapina, 1957, pl. 13, fig. 1-4) from the Kashirian and Kirov levels of the Urals has finer ornament as figured in Stepanov (1975, pl. 77, fig. 5), but Upper Carboniferous specimens from the Arctic as figured in Sarytcheva (1977, p. 90, pl. 11, fig. 1-6, text-fig. 54, 55) are moderately close in ornament and shape, although smaller with shallower sulcus. Lapina's species was referred to *Latispinifera* by Lazarev (2000b), together, as a possibility, with *posthindi* Solomina. The species *ivanovi* has been reported extensively from Russian faunas, of Bashkirian – Moscovian and slightly younger age, and was considered to include *R. moelleri* of Winkler Prins (1968, pl. 7, fig. 7, 8) from Spain. The Spitsbergen species *Reticulatia holtedahli* Gobbett (1964, pl. 8, fig. 1-5, text-fig. 13) from the Passage Beds, Lower Gypsiferous Series and Ambigua beds is readily distinguished, with more rounded venter and less conspicuous ornament. *R. pamirica* Grunt in Grunt & Dmitriev (1973, pl. 6, fig. 1-4, pl. 7, fig. 1, text-fig. 20) from the Sakmarian to lower Artinskian Bazardarin Suite of the Pamirs has a more triangular outline with slightly deeper sulcus. *Antiquatonia bublitchenkoi* Sarytcheva (1968, p. 128, pl. 16, fig. 5-7) from the Kokpektin Complex of Kazakhstan has spines in hinge and umbonal slope rows that become very strong laterally, although the costae are slightly coarser, the commarginals weaker, and trail long, whilst the shape is transverse. The generic placement by Sarytcheva (1968) implies the present of ventral slope ridges, though none are visible in illustrations.

Genus ***Boggabria*** new genus

Derivation: Named from Boggabri district where the type species is found.

Type species: *Antiquatonia spinulicosta* Roberts, 1976, p. 69 from Namoi Formation (late Tournaisian to early Visean), New South Wales, east Australia, here designated.

Diagnosis: Small with short trail and small ears, weakly reticulate over disc, a row or group of about four spines along ventral hinge and better developed row along base of umbonal slopes, smaller but numerous spines over disc and trail, emerging from elongate bases anteriorly, except near the anterior margin, where spines are erect. Dorsal pits slender and elongate. Dorsal adductors smooth, at least until late in ontogeny.

Discussion: Types are kept at the Australian Museum, Sydney, with AMF 57036 as holotype. Referred to *Antiquatonia* Miloradovich by Roberts (1976), there is no apparent sign of a ridge along the umbonal slope base each side of the umbo, although the row of slope spines is well developed. Roberts pointed out that the dorsal hinge ridge did not diverge from the hinge in his species, and that the adductor scars were smooth rather than dendritic, and the dorsal medium septum was comparatively short. Costae fade anteriorly, and the spines along the hinge, although moderately sturdy, are few and not always in one clearly defined row. The principal diagnostic feature lies in the ventral disc spines, which are very numerous, and have rather elongate bases, tapering posteriorly. Their nature suggests an approach to spines in *Buxtonia* and allies. But there are many differences from this group, in the lack of spine-base swelling, no tuft of posterior lateral spines, no dorsal spines, and no dorsal septal slit. The genus is tentatively placed as Reticulatiinae, but its position is not secure. *Retiarisia* new genus, based on *Dictyoclostus simplex* Cambell, 1957 has no umbonal slope row or hinge row of ventral spines, and displays often a split dorsal septum and lateral buttress plates. (See p. 163).

Genus ***Robertsina*** new genus

Fig. 5.22

Derivation: Named for John Roberts.

Type species: *Marginatia patersonensis* Roberts, 1965, p. 63 from Bonnington Siltstone (Visean), in Gresford-Dungog district, New South Wales, Australia, here designated.

Diagnosis: Transverse, moderately inflated, costellae moderate in strength, reticulate over visceral disc, ventral spines in hinge row and umbonal slope row, scattered over disc and trail, long and halteroid on trail. External dorsal pits well defined. Dorsal hinge ridges well defined, medium septum narrow, dorsal adductors becoming dendritic in later growth stages.

Discussion: The species *patersonensis* Roberts is based on holotype UNE 6813, now kept at the Australian Museum, Sydney, Australia, and reregistered as AMF 77942. The species was referred to *Marginatia* Muir-Wood & Cooper, but is more transverse and less inflated, with a hinge row of spines, and without an alveolus or slit in the posterior dorsal septum: the interior is dictyclostiform rather than buxtoniiform. The lower Visean genus *Ozora* Carter (1990) from United States is somewhat similar in shape, apart from being more inflated, and has ventral spines close to the hinge and a scattering of anterior ventral spines, but ornament is coarser in *Ozora*, and the dorsal valve surrounded by a marginal ridge, and the cardinal process buttressed anteriorly by mounds. *Tenaspinus* Brunton & Mundy, 1994 from the Asbian of Yorkshire is small, and strongly reticulate, with less clearly defined rows of posterior spines (see below). Other genera within the tribe are of Permian age, and are as a rule larger with stronger reticulation and often stout spines.

The type material for *Robertsina* is very well preserved, and has been described and illustrated in detail by Roberts (1965, p. 63, pl. 10, fig. 1-5; 1976, p. 67, pl. 12, fig. 1-10). Posterior central papillation is not entirely clear, but seems to be absent in figures of the posterior dorsal septum.

The genus is substantially older than species referred to *Reticulatia* and *Latispinifera*, but shows a row of spines at the base of the umbonal flanks, a row of hinge spines, and stouter anterior spines on the posterior trail. The dorsal valve has no spines, and has conspicuous slightly elongate dorsal pits.

Fig. 5.22. *Robertsina patersonensis* (Roberts), latex cast of ventral valve, from Bonnington Siltstone (Visean), Clarencetown, New South Wales, Australia, now kept at Australian Museum as AMF 57098, x 1. See Roberts (1976, pl. 12, fig. 6).

Genus **Tenaspinus** Brunton & Mundy, 1994

Tenaspinus, type species *T. smarti* Brunton & Mundy (1994, Fig. 2-5) from the late Asbian (Visean) of north England is small and strongly reticulate, with dorsal pits. There are posterior ventral halteroid spines, but their nature requires elucidation. Brunton & Mundy wrote of five strong rhizoid spines near the hinge, and a cluster at the antero-median edges of the ears. In their diagram of Fig. 5, the posterior spines are shown as being implanted in a somewhat irregular row in front of the hinge and well behind the base of the umbonal slope, but the photograph of Brunton & Mundy (1994, Fig. 3.12) shows a row of erect spines along the base of the ventral umbonal slope, with further spines nearer the hinge on the outer ear. There appears to be a degree of inaccuracy in Fig. 5 and vagueness in the written description, and it appears likely that *Tenaspinus* is close to *Reticulatia* and especially *Latispinifera*. Brunton et al. (2000) placed the genus in Yakovleviini Waterhouse, an unlikely position, given the different shape and ornament.

Genus ***Zia*** Sutherland & Harlow, 1973

Zia Sutherland & Harlow, 1973, p. 59 from Morrowan faunas of New Mexico, United States, is close in fine costae and commarginals. There is an umbonal slope row of fine spines and other spines over the umbonal slopes, and there appear to be faint signs of a row of very fine spines along the hinge in illustrations. Sutherland & Harlow (1973, p. 60) reported a row of medium-sized spines along the hinge, and a single large spine projecting from each ear. Scattered body spines are comparatively numerous, as in *Bruntonella* (see below). Dorsal pits are present, but small. It was suggested by Brunton et al. (2000) that the genus was a senior synonym for *Semilunataproductus* Han in Han et al. (1987), but the type for this is only 4mm wide, and as such, hardly able to be compared adequately. Arguably the presence of micro-forms and spats amongst Brachiopoda requires much further enquiry. Both genera were referred to Anidanthinae Waterhouse by Brunton et al. (2000, p. 533), but show little resemblance. Sutherland & Harlow (1973) related the genus to linoproductids. Fine reticulation is developed over both valves, and commarginal ornament is more in the form of ribs rather than rugae.

The genus resembles in its close reticulation members of Caucasoproductinae Kotlyar, but the interior of this tribe is marginiferiform. Labaellini Kotlyar et al. (p. 161) is also somewhat similar in its fine ornament, but does not have the same arrangement of spines.

Genus **Neopugilis** Li in Ding et al., 1991

Neopugilis Li in Ding et al. (1991, p. 159 [p. 186] was proposed for several species from Carboniferous-Permian boundary faunas of the Xikou area in the eastern Qinling Range in China. The genus is distinguished by finely reticulate disc and costate anterior disc and trail, some ten spines over the ventral ears and disc spines with swollen bases from which up to four ribs continue forward. The dorsal valve has dimples rather than spines, and the anterior flank margins are recurved with a frill. Internally, lateral ridges divert forward from the hinge and extend to mid-length. The genus resembles *Pugilis* Sarytcheva, but has dorsal dimples, and resembles *Chaoiella* Fredericks, but spine bases are stronger, ear spines more numerous and dorsal dimples more numerous.

Neopugilis was synonymized with *Thamnosia* Cooper & Grant of Retariinae by Brunton et al. (2000, p. 475), but this is highly unlikely. *Thamnosia* has dorsal spines that are missing from *Neopugilis*, and is much larger with proportionately larger ears, and tendency for lateral ventral spines to form rows. Ventral spine bases are different, and dorsal pits less well developed, and costae are coarser with coarser commarginal rugae in *Thamnosia*, these distinctions also applying to *Calliomarginatia* Jin and *Aspinosella* Waterhouse. In size and shape, *Neopugilis* approaches several genera classed within Retariinae, but provisionally the genus is classed in Reticulatiinae because hinge and umbonal slope spines do not appear to be as well developed as in Retariinae.

Genus *Bruntonella* Chen & Shi, 2006

Bruntonella Chen & Shi (2006, pl. 9, fig. 1-15, 18, 19, 23, pl. 10, fig. 2-7, 9, 10, 17, pl. 11, fig. 1-7, 9-14, text-fig. 14) from the upper Lower Permian of the Tarim Basin, northwest China, shows fine and reticulate ribs and rugae, row of coarse spines along the hinge, three cardinal spines on each ear, fine disc spines, and elongate dimples on the dorsal valve. A row of spines lies along the umbonal slopes as illustrated in Chen & Shi (2006, pl. 9, fig. 5), but such a row is not indicated in other specimens, and it appears that the umbonal slopes carried spines in various dispositions, without well formed umbonal slope row, and the careful description confirms that the umbonal slope row was not consistently present. The basic pattern and overall appearance is very close to that of *Rigrantia* Lazarev, but unlike this genus, there is no development of a posterior lateral ridge each side of the umbo which bears the flank row of spines, and there is no dorsal ear groove. The outer hinge spines are much coarser than those along the umbonal slopes, and there are some anterior coarse spines. Some internal detail is available, but the anterior smooth dorsal adductors displayed by most reticulate genera are not visible. The presence of an internal dorsal marginal ridge was reported and illustrated by Chen & Shi (2006, p. 151, text-fig. 14B).

Genus *Costiferina* Muir-Wood & Cooper, 1960

Fig. 5.23

Costiferina is best known from the younger Permian of the Salt Range, Pakistan, where Waagen (1884) described several species, and other occurrences are reported from the Himalayas, southeast Asia, China and Western Australia. A row of spines lies along the umbonal slopes, and another close to the hinge, sometimes sporadic, and a few individual spines lie over the disc and trail of the ventral valve. Costae are strong and may become broad anteriorly, and internally the cardinal process is broad, and a wide if low marginal ridge is developed around the dorsal interior, at least in the type species, a feature not seen in *Dictyoclostus* but weakly developed in type *Reticulatia* Muir-Wood & Cooper, and in *Pugilis* Sarytcheva. It was perhaps the presence of this marginal ridge that led Brunton et al. (2000, p. 444), to class the genus as a member of Paucispiniferini, a most unlikely position, given the complete absence of strut spines. Muir-Wood & Cooper (1960, p. 277) placed the genus in Dictyoclostinae, and Lazarev (2000b) put the genus in Latispiniferini, as accepted by Brunton (2007, p. 2648). The genus over the last few years has thus been put in Productellidae, and in Yakovleviinae – both positions scarcely tenable, when compared with the assessment by Muir-Wood & Cooper (1960). The general ornament, and the nature of the dorsal anterior papillae underscore the probability of a productoid relationship. Figures in Muir-Wood & Cooper (1960) suggest that posterior papillae in front of the cardinal process are absent, or too fine to have been shown. But in large ventral

Fig. 5.23. *Costiferina alata* Waterhouse. Dorsal view of plaster cast of holotype, BR 3034, x1. Original kept at Geologisches Bundesanstahlt, Vienna. From Senja Formation (Wuchiapingian), Dolpo, Nepal. See Waterhouse (1966). JBW photo.

valves figured by Waterhouse (1966, pl. 5, fig. 1, pl. 7, fig. 3), there are very low and fine papillae over the umbonal interior. The presence of pits over the dorsal exterior is not entirely clear: the dorsal exterior not being shown in figures by Muir-Wood & Cooper (1960) or Brunton et al. (2000). For the species described by Waagen (1884, pl. 70, fig. 2b, 4b), one tiny dorsal valve shows external pits, and the other has pits only along the anterior ears, opposite the spines of the ventral valve. The small specimen is too small to have been identified with confidence, and there is arguably no reason to suppose it belongs to *Costiferina*. Equally, it might be signifying that pits present in young specimens disappear with increased maturity. The material assigned to *Costiferina* in Waterhouse (1966) and Zhang & Ching (Jin) (1976) show no dorsal pits, significant because dorsal external moulds are large and well preserved (Zhang & Jin 1976, pl. 6, fig. 5, 12; Waterhouse 1966, pl. 5, fig. 4, 5, pl. 6, fig. 2, 3, pl. 7, fig. 3, pl. 8, fig. 3; 1978, pl. 3, fig. 2, 4). The genus is nonetheless regarded as reticulatiin, because coarse spines lie in a row over the lower umbonal slopes (see Muir-Wood & Cooper 1960, pl. 95, fig. 7).

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

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

Diagnosis: Large shells with deep body corpus as a rule, ribs over both valves somewhat irregular, costae may swell in front of and behind especially ventral spines, no strut spines, dorsal spines and pits generally present and spines often numerous. Concentric ornament moderate to subdued. Narrow elongate cardinal pit and generally long posterior split in the dorsal septum. Adductor scars dendritic, dorsal endospines large and numerous across anterior shell, marginal ridges generally subdued but hinge ridge or lateral cincture developed in some genera.

Members of the Upper Devonian to Lower Carboniferous Family Lomatiphoridae are deemed to have been ancestral, because such genera as *Lomatiphora* and *Spinocarinifera* have short diverging lateral buttress plates or median slit in the posterior dorsal median septum, and spines in *Spinocarinifera* are erect and arise from ribs, though without the basal swelling typical of Buxtoniidae. They lack dorsal spines and clusters of ventral ears, and so approach members of Marginatiini, a group within Buxtoniinae.

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

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

Diagnosis: Spines on both valves as a rule.

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

Fig. 5.24

[Nom. transl. Brunton et al. 1995, p. 928 ex Buxtoniinae Muir-Wood & Cooper, 1960, p. 255].

Diagnosis: Ventral spines crowded on lateral umbonal slopes and inner to outer ears; dorsal spines usually numerous. Radial ribs well formed, commarginal rugae moderate to inconspicuous, dorsal pits present as a rule. Lower Carboniferous (Tournaisian) to Upper Carboniferous (Kasimovian).

Genera: *Buxtonia* Thomas, *Flexaria* Muir-Wood & Cooper, *Gemmulicosta* Waterhouse, *Labriproductus* Cooper & Muir-Wood (nom. nov. pro *Worthenella* Girty, 1938 not Walcott, 1901), *Libys* Massa, Termier & Termier, *Marginicinctus* Sutton, *Piloricilla* Carter, *Setigerites* Girty.

Discussion: Buxtoniini includes *Marginicinctus* Sutton, of chiefly Early Carboniferous age, with sinuous and spinose ribs and commarginal rugae. *Flexaria* Muir-Wood & Cooper, *Labriproductus* Cooper & Muir-Wood, and *Setigerites* Girty have similar spinose ribs and subdued if any commarginal rugae, and the ventral ears bear a dense cluster of fine erect spines. They are of Early Carboniferous age, extending into Serpukhovian. A similar cluster of ventral spines is present on the ears of the small *Tomiproductus* Sarytcheva, 1963, p. 201 from early Carboniferous of Kazakhstan, and this genus has two broad posterior dorsal ridges like swollen buttress plates, and apparent dorsal pits, although ventral spines are rather like those of *Tolmatchoffia* (see Fig. 15.31).

Gemmulicosta Waterhouse in Bamber & Waterhouse, 1971 (Fig. 5.24) was synonymized with *Buxtonioides* by Brunton et al. (2000, p. 407), but has longer swellings behind spine bases, whereas *Buxtonioides* has ribs with slight rounded swellings at the base of the spines. Indeed *Gemmulicosta* is closer in that regard to *Buxtonia* itself. The confusion is well illustrated by their claim that *Gemmulicosta* came from western Alberta (Brunton et al. 2000, pp. 497-498). It does not – it comes from Yukon Territory, well to the north.

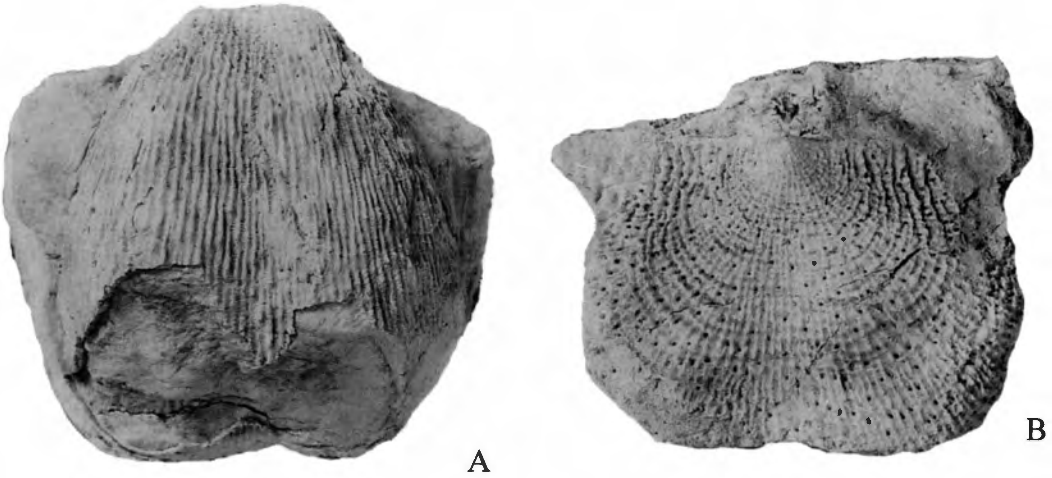


Fig. 5. 24. *Gemmulicosta gemma* Waterhouse. A, ventral valve GSC 26405. Ears are slightly decorticated, but are closely spinose. B, dorsal valve external mould GSC 26408. Specimens x 1 approx., from Ettrain equivalents (Moscovian) at Peel River, Yukon Territory, Canada. See Bamber & Waterhouse (1971). B. O'Donovan & JBW photo.

Affinities of *Xinshaoproductus* Tan Zhen-xiu (1986, pp. 433, 442, pl. 1, fig. 5-13) from the basal Lower Carboniferous of Hunan, China, remain uncertain. Although placed as a member of Buxtoniini by Brunton et al. (2000, p. 508), a well preserved dorsal interior shows well developed lateral buttress plates (Tan Zhen-xiu (1986, pl. 1, fig. 13), and possible plates are developed in the other two figures of the dorsal interior (pl. 1, fig. 11, 12). There are fine numerous ventral spines over the anterior lateral flanks, and a split dorsal septum in one of the specimens. The dorsal exterior is not known, but ventral spine bases were described as elongate, suggesting Buxtoniinae. *Neoyanguania* Shi Xiao-yong, 1988, p. 348 [352], type species *N. quadrata*, was synonymized with *Xinshaoproductus* by Brunton et al. (2000). The latter type species also comes from the late Tournaisian of Hunan, and figures (Shi Xiao-yong (1988, pl. 1, fig. 1a-d; 2a-d) of two reported species show a row of spines along the hinge and group of spines over the ears. A text-figure (Fig. 1A-C) illustrates the lateral buttress plates. (See also p. 162). *Xinshaoproductus* is classed as Reticulumiini.

Tribe **SPINIFRONSINI** Waterhouse , 1981

[Nom. transl. hic ex Spinifronsinae Waterhouse, 1981, p. 82. Syn. Kochiproductini Lazarev, 1985, p. 67].

Diagnosis: Costae well defined to rarely erratic in course, crossed by low but defined concentric ribs which leave low nodes or ridges over costae, from which spines may arise. Spines scattered over disc and trail of both valves, crowded over ventral ears, and wider, as wide, or narrower than costae. Dorsal pits. Upper Carboniferous (Kasimovian or older) to Upper Permian (Changhsingian).

Genera: *Spinifrons* Stehli, ?*Bellaclathratus* Winters, *Kochiproductus* Dunbar (= *Tschernyschewiella* Fredericks, 1924 not Toll, 1899), *Kochiproductus* (*Dunbarovia*) new subgenus, *Peniculauris* Muir-Wood & Cooper, ?*Rugoclostus* Easton, *Squamaria* Muir-Wood & Cooper.

Discussion: This is a distinctive group characterized by varied and complex ribbing. The group was initially proposed on the basis that costae may be somewhat irregular in course, and this is particularly true of *Spinifrons* and of *Kochiproductus* (*Dunbarovia*). Otherwise members of the tribe are close overall in most attributes to Buxtoniini. In Buxtoniini, the spine bases are elongate, and spines emerge gradually from the shell, or from costal swellings. In Spinifronsini, the spines tend to emerge with less prolonged bases, and the rises along the costae are caused by crossing points with the rib-like commarginal ornament, and spines often arise at the intersections. *Peniculauris* Muir-Wood & Cooper, which may display slightly erratic costae on individuals, is particularly close in ornament to *Kochiproductus*, and indeed Stehli & Grant (1970, pl. 13, fig. 1-7) identified as *Kochiproductus*? sp., well preserved material from Guatemala that belongs to *Peniculauris*. The ornament is largely similar, but in *Peniculauris* as distinct from *Kochiproductus,* the ear spines are coarser and the flare of the ears does not continue far forward. As Stehli

& Grant (1970, p. 33) explained, the "bumpy" ornament, caused by commarginals crossing radials is characteristic of both genera, and of other allies.

Rugoclostus was regarded as ?Horridoniini by Brunton et al. (2000, p. 480) and Lazarev (2005a), and as possible Chaoiellini by Lazarev (2011), but has scattered dorsal and ventral spines and weakly reticulate ornament, approaching the morphology of *Squamaria* Muir-Wood & Cooper, 1960.

Spinifronsini has dorsal pits that are missing from Tolmatchoffinae, although at a grosser scale, both are largely similar in many details, including interior. Kochiproductini, as proposed by Lazarev (1985), was synonymized with Buxtoniini by Brunton et al. (2000, p. 496).

Genus *Kochiproductus* Dunbar, 1955

Subgenus *Kochiproductus* (*Kochiproductus*) Dunbar, 1955

Type species: *Productus porrectus* Kutorga, 1844, p. 96 from Lower Permian (Asselian, lower Sakmarian) of Urals, Russia. SD Muir-Wood & Cooper 1960, p. 260.

Diagnosis: Large shells with large ears, prominent costae which do not anastomose anteriorly, dominated over disc by closely spaced elongate spine bases, costae crossed posteriorly by prominent commarginal rugae, spines numerous over both valves, semi-erect over ears and trail. Cardinal ridges long.

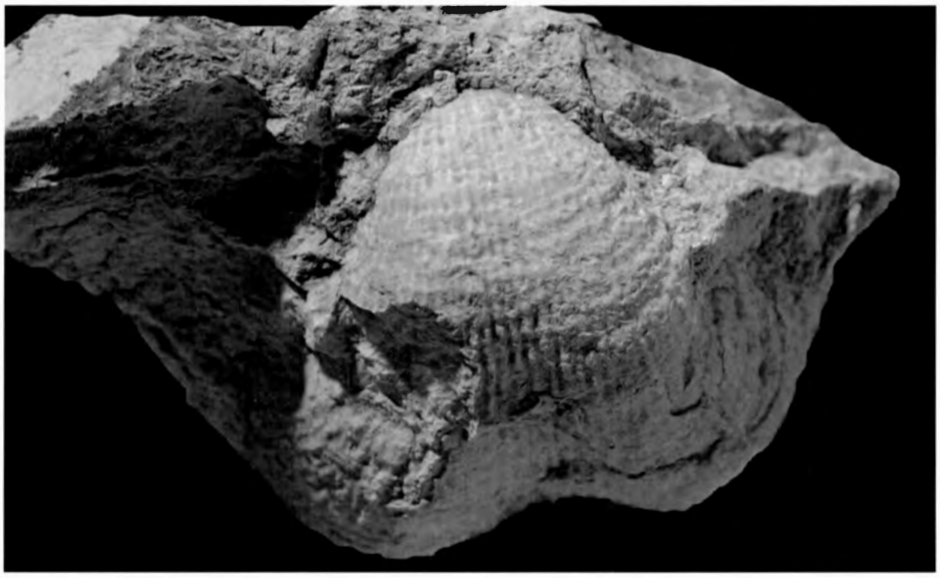


Fig. 5.25. *Kochiproductus imperiosus* new species, slightly tilted because of the lump of matrix, posterior ventral aspect of ventral valve holotype GSC 133304 x1 from Member B (basal Asselian), lower Jungle Creek Formation, Yukon Territory, Canada. JBW photo.

Discussion: Dunbar (1955, p. 107) regarded his name *Kochiproductus* as a replacement for *Tschernyschewiella* Fredericks, 1924, p. 20, named for *Productus porrectus* Kutorga, 1844, not *Tschernyschewiella* Toll, 1899. But Dunbar proposed a new type species for his *Kochiproductus, K. plexicostatus.* Although Ustritsky (1960, p. 8) accepted *plexicostatus* as type, Muir-Wood & Cooper (1960, p. 260) emphatically declared this procedure invalid, and because *Kochiproductus* was proposed as a substitute name, considered that the type species had to be retained as *Productus porrectus* Kutorga. This has been followed ever since in all available literature, including the *Revised Brachiopod Treatise*. Dunbar's species *flexicostatus* is not in fact completely identical with *porrectus*, and is here assigned to a new subgenus. Some authorities may consider that *flexicostatus* should remain type species as originally proposed for *Kochiproductus* s.s., with a new name proposed for *porrectus*. In that case the newly proposed subgenus will have to be set aside, a new subgeneric name found for *porrectus*, and *Kochiproductus flexicostatus* restored as type species for *Kochiproductus*. The present course follows what appears to be established precedent.

Kochiproductus* (*Kochiproductus*) *imperiosus new species

Fig. 5.25 – Fig. 5.31

Derivation: imperiosus – mighty, powerful, Lat.

Holotype: GSC 133304 figured as Fig. 5.25, Fig. 5.26 and Fig. 5.29 from Member A, Jungle Creek Formation, Canada, here designated. The dorsal valve is present but buried in matrix.

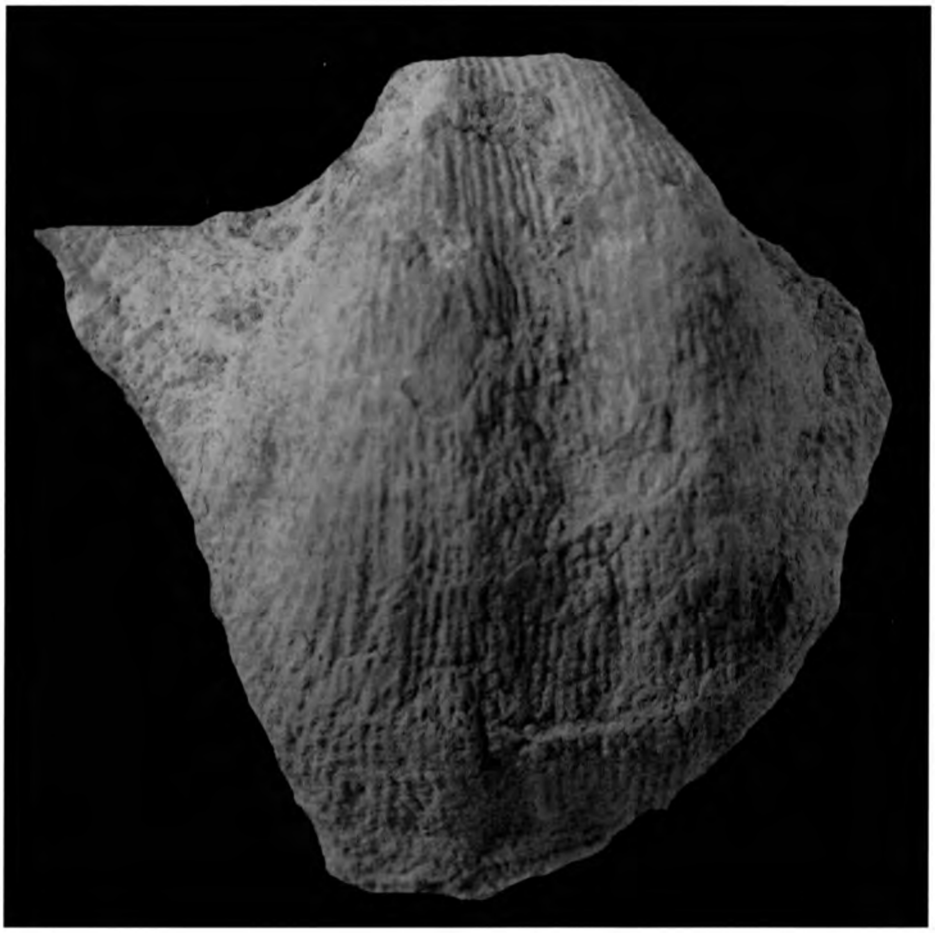


Fig. 5.26. *Kochiproductus imperiosus* new species, ventral valve holotype GSC 133304, x1 from Member B, lower Jungle Creek Formation (basal Asselian), Yukon Territory, Canada. JBW photo.

Diagnosis: Large, elongate with moderately well formed ventral sulcus, moderate fold, wide ears and strong ornament. Commarginal rugae restricted to posterior shell and relatively weak.

Material: More than twenty specimens, mostly with valves conjoined, from Member B (Asselian), lower Jungle Creek Formation, Yukon Territory, Canada. See Appendix A, part C, p. 478.

Dimensions in mm:

Specimen GSC	Width	Length	height	
133303	75	79	40	
Unregistered	81	76	43	
133304	106	91	58	holotype

Description: Specimens very large, ventral valve highly convex, with broad incurved umbo and umbonal walls high and steeply convex, diverging at 60-70°, and very large gently convex ears at maximum width though with obtuse extremities; sulcus well defined, commences some 10-15mm in front of umbonal tip and widens at angle of 30°. Dorsal valve almost flat across disc apart from subdued narrow fold which varies in strength on different specimens, very large concave ears, and high geniculate trail almost as long as the disc. The body cavity is extremely thick.

Ornament on ventral valve of low costae, some four in 10mm at 45mm from the beak, and five to six anteriorly, with five in 10mm on the anterior flanks, increasing mainly if not entirely by intercalation with rounded crests and interspaces of similar width. There are numerous fine erect spines with very slightly swollen and moderately prolonged bases, arising from the costal crests with little perturbation over the disc and umbonal flanks, and as shown by the specimen from JBW 815, a cluster of ear spines extend posteriorly, 0.5mm in diameter and 55mm long. The shell is crossed by low rugae, 2mm apart posteriorly, increasing to 2.5mm anteriorly, and strengthening over the umbonal walls. The intersections of rugae and spinose ribs impart a particular and peculiar spinifronsin texture to the shell surface, termed "bumpy" by Stehli & Grant (1970). The dorsal ornament is similar, except that concentric rugae are slightly more prominent and spines less common, largely restricted to the anterior disc and trail at maturity, with only a few slender erect spines over the dorsal ears of mature shells.

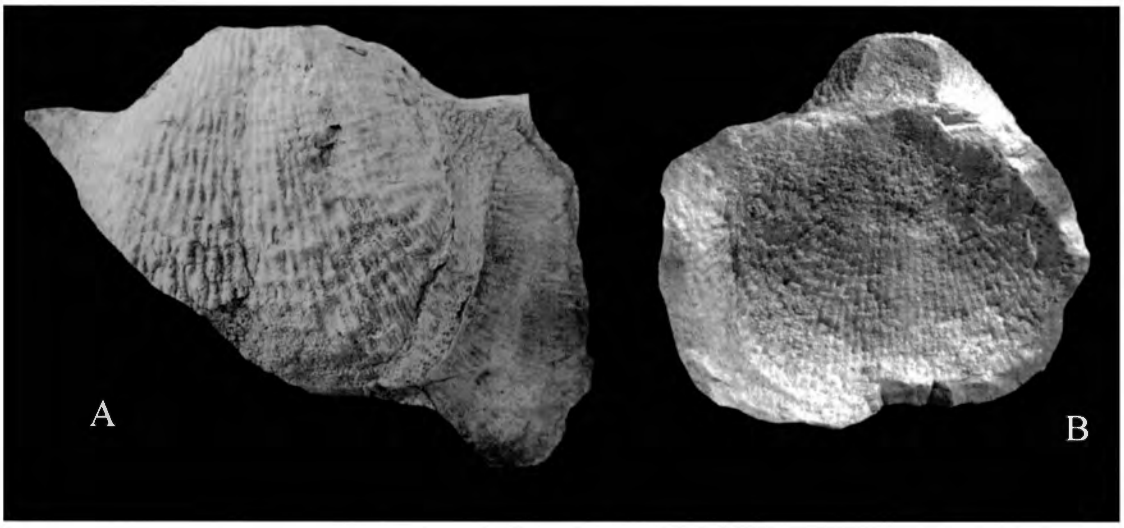


Fig. 5.27. *Kochiproductus imperiosus* new species. A, ventral valve, showing skirt, GSC 133306. x0.8 B, dorsal valve GSC 133309, x0.9. Specimens from Member B, lower Jungle Creek Formation (basal Asselian), Ogilvie Mountains, Yukon Territory, Canada. JBW photo.

The adductor scars are narrow and the diductor scars large and oval and moderately impressed, but are not well known. The cardinal process is slender and bilobed, with a sturdy ridge extending in front along each side of the hinge, and the median septum continues as a narrow blade as far as the start of the trail.

Resemblances: Specimens ascribed to *Kochiproductus porrectus* (Kutorga 1844, p. 26, pl. 10, fig. 3) from the *Muirwoodia transversa* to *Jakutoproductus verchoyanicus* Zones in the younger Jungle Creek Formation by Shi & Waterhouse (1996, pl. 10, fig. 5-12, pl. 11, fig. 1-6, Fig. 28) are smaller with finer ornament, compared with the present material, involving seven to eight ribs in 10mm, and have shallower sulcus and high dorsal fold. They are not as large or as coarsely costate, and have weaker wrinkles than the Russian species, but the lack of true external ornament makes them difficult to assess. The species *porrectus* as interpreted from material figured by Tschernyschew (1902, pl. 32, fig. 4, pl. 55, fig. 1, pl. 56, fig. 4; Sarytcheva 1952, pl. 36, fig. 4; 1960, Fig. 216, 217) is very close in shape, size and ornament to the present form, displaying some five or usually six costae and four concentrics in 10mm over mid-ventral valve, but the ventral sulcus is deeper especially over the disc anteriorly in the present form and costae are slightly coarser. The specimen figured by Tschernyschew (1902, pl. 62, fig. 2) has distinctly finer costae. Some features, such as the large ears of the Canadian material, or the fold over the dorsal trail, are not preserved in Tschernyschew's material. Internal fragments were figured as aff. *porrectus* by Gerassimov (1953, pl. 7, fig. 4, pl. 8, fig. 1, 2), difficult to assess. A suite of specimens was figured by Solomina (1960, p. 41, pl. 5, fig. 5-10, pl. 6, fig. 1-3) from the Talatin Suite of Pai Hoi, of late Early Permian age. Solomina (1960, p. 41) included in synonymy *P.* (*Buxtonia*) *lesnikowae* Stepanov (1934, p. 24, pl. 2, fig. 8-10) and *P.* (*Buxtonia*) *freboldi* Stepanov (1937, p. 122, pl. 2, fig. 2). Of other specimens referred to *porrectus* from Russian outcrops, those of Abramov (1970, pl. 13, fig. 1-5) from the Verchoyan Suite of Verchoyan, northeast Russia, are smaller with broad shallow sulcus and fine ornament, not closely allied to the Urals species, whereas the large Taimyr specimens figured by Ustritsky &

Chernyak (1963, pl. 9, fig. 4, 5) from the Holodnin Suite (C_2^b according to the text), show considerable approach to the Canadian specimens in the depth of ventral sulcus and coarseness of costae: the dorsal fold seems low, much as in present material. A rather damaged specimen from the Urals that was illustrated by Kulikov (1974, pl. 2, fig. 6) does suggest the presence of large ears, and a Talatin Formation specimen figured by Kalashnikov (1990, pl. 1, fig. 10) as *porrectus* lacks strong transverse ornament and has such prominent spine bases that it looks taeniothaerin (see p. 277). The specimen reported by Tschernyschew & Stepanov (1916, p. 41, pl. 5, pl. 8, fig. 5) as *porrectus* from Great Bear Cape, Arctic Russia, is less inflated with deeper sulcus.

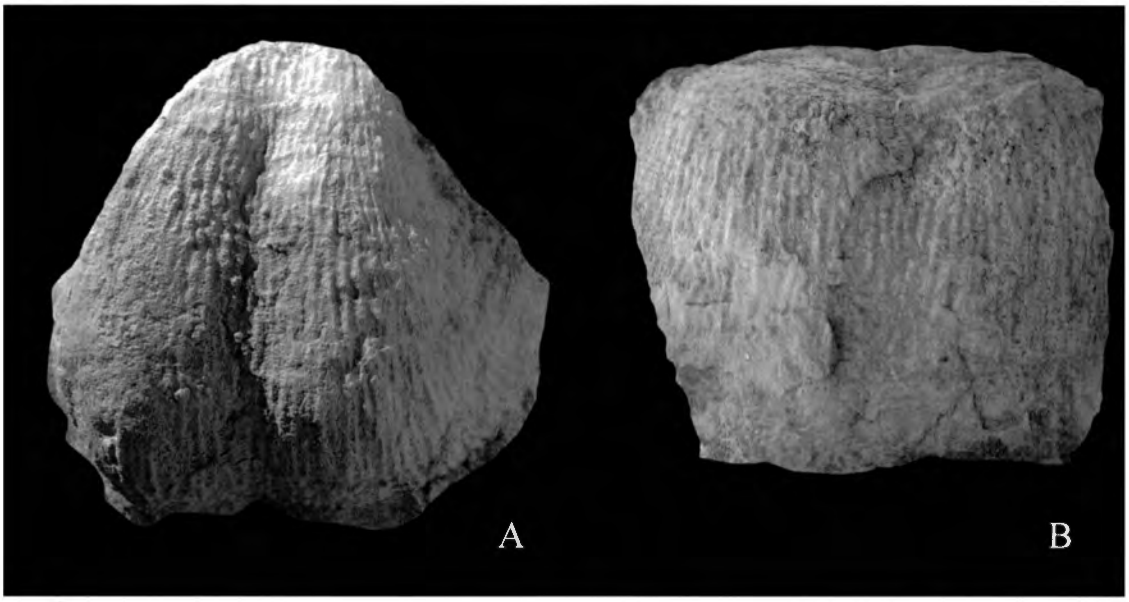


Fig. 5.28. *Kochiproductus imperiosus* new species. A, ventral valve GSC 133303, x0.8. B, trail of dorsal valve, decorticated, inner view, GSC 133319, x0.8. Specimens from Member B, lower Jungle Creek Formation (basal Asselian), Yukon Territory, Canada. JBW photo.

There have been various specimens identified as *Kochiproductus porrectus*, or compared with *porrectus*, that appear to be based mostly on generic similarity of the "bumpy" ornament. Examples include Grabau (1931, p. 295, pl. 1, fig. 10), and Ustritsky et al. (1963, p. 9, pl. 1, fig. 4, 5) from west Gansu, China. Mansuy (1913, pl. 3, fig. 10) figured a supposed specimen from the Early Permian of Kham-Kheut, Laos, that shows only the posterior part of a dorsal valve. *K. egragius* Lee & Gu (1976, p. 254, pl. 182, fig. 3, 4) from the Early Permian of Mongolia is very incomplete, with somewhat decorticated surface, and the outer hinge apparently lost. It appears to be more transverse than the present species. So called *porrectus* of Grabau (1936, pl. 6, fig. 1) from the Maping Limestone of China may be related but is an exfoliated fragment, difficult to identity.

Gobbett (1964, pl. 7, fig. 1-3) described broken specimens from the Spirifer Limestone of Spitsbergen that are only moderately close, having more nodose ribs, but it is difficult to compare the material fully. Gobbett (1964, p. 80) included some material originally described as *Productus payeri* Toula (1874, pl. 4, fig. 1, 3) in possible synonymy with *porrectus*, as well as *Productus* (*Buxtonia*) *freboldi* Stepanov (1937, p. 122, 176, pl. 2, fig. 4, part) as also figured by Harker in Harker & Thorsteinsson (1960, pl. 17, fig. 5, 6) from the Assistance Formation of Canada. The material is likely to belong to *Kochiproductus* (*Dunbarovia*), as described below. Harker's material shows more nodose ribs, and subequidimensional shell with wide shallow sulcus. No ears are preserved. The taxon *freboldi* appears to be a valid species, younger than *porrectus* or the present species. *K. flexicostatus* Dunbar (1955, pl. 17, fig. 1-6, pl. 18, fig. 1-6) is rather similar. These species belong to *Kochiproductus* (*Dunbarovia*). Gobbett (1964) reported that the other Toula specimens, labelled as *payeri* at the Natural History Museum in Vienna, Austria, resembled *Waagenoconcha irginae* (Stuckenberg) and *Horridonia timanicus* (Stuckenberg). Dunbar (1955, p. 85) ascribed all Toula material to *Waagenoconcha payeri* (Toula), but only that of Toula (1874, pl. 4, fig. 2) seems likely to belong to Waagenoconchidae. No holotype for *payeri* has yet been cited.

Specimens identified as *Kochiproductus saraneanus* (Fredericks) by Shi & Waterhouse (1996, pl. 11, fig. 8-10, 12) from the younger Jungle Creek Formation in Yukon Territory, Canada, are close in size, though not as elongate, and have large ears. The sulcus is not as deep as in the present species, but the ribs are comparable at the anterior edge of the disc: much of the material is exfoliated and so difficult to compare further. As noted by Shi & Waterhouse (1996), the anterior costae in type and Yukon *saraneanus* become fine with frequent bifurcation, but in present material the costae continue at strength to the anterior margin. Type *saraneanus* was figured from the Urals by Tschernyschew (1902, pl. 27, fig. 2, pl. 34, fig. 4, pl. 35, fig. 2) as *Productus longus* (not Meek) and shows large ears and coarse costae, less sulcate ventral valve and wide dorsal valve: the ears are similarly large. Further material was figured as *Buxtonia saraneana* by Fredericks (1933, pl. 5, fig. 1) and Kulikov (1974, pl. 2, fig. 7). A Kungurian specimen assigned to *saraneanus* by Ifanova in Ifanova & Semenova (1972, pl. 4, fig. 1) is elongate. *Buxtonia peruvianus* not d'Orbigny of Fredericks (1915, p. 26, pl. 3, fig. 1) was included in synonymy by Solomina (1960, p. 43), together with references to the species by Licharew (1939, p. 86, pl. 17, fig. 12, pl. 18, fig. 1, 2; Licharew & Einor 1939 p. 37, pl. 5, fig. 1) from Taimyr, and compared to *P. theodossianus* Gerassimov (1953, p. 44, pl. 6, fig. 1, 2) and *P. georgianus* Gerassimov (1953, p. 52, pl. 6, fig. 1-3).

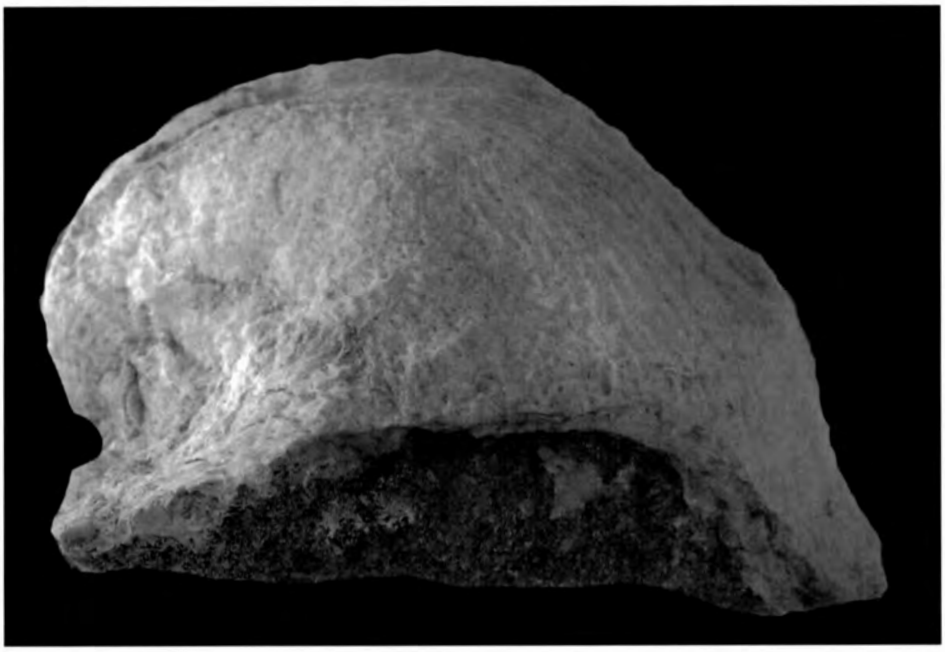


Fig. 5.29. *Kochiproductus imperiosus* new species, lateral view of ventral valve GSC 133304, holotype, x1. See Fig. 5.25 and Fig. 5.26. Specimen from Member B, lower Jungle Creek Formation (basal Asselian), Yukon Territory, Canada. JBW photo.

Kochiproductus levinsonlessingi Zavodowsky (1970, pl. 5, fig. 1) from the Asselian Burgali Horizon of northeast Russia is wide with virtually no sulcus and finer ribs. *K. sultanaevi* Kulikov & Stepanov in Stepanov et al. (1975) of Middle Permian age from the Kanin Peninsula, Russia, is not well known with regards its anterior costae. Kalashnikov (1983, pl. 54, fig. 1-3) figured worn specimens with coarse ornament and shallow sulcus from the Talatin Suite of the Pechora Basin, northwest Russia.

Other species include *Productus peruvianus* d'Orbigny (1842, p. 52, pl. 4, fig. 4; Kozlowski 1914, p. 38, pl. 5, fig. 1-4, text-fig. 7) from the Copacabana Group of Bolivia. The specimens are smaller with more prominent spine bases. Muir-Wood & Cooper (1960, pl. 75, fig. 13-15, pl. 77, fig. 1-7) provided figures for specimens from the Hueco and Hess limestones of Texas, United States, of smaller size, with less sulcate ventral valve and finer nodose ribs. From west Texas, *Kochiproductus occidentalis* (King, 1931, pl. 17, fig. 20, 21; Cooper & Grant 1975, pl. 358, fig. 7-9) from the Neal Ranch Formation is moderately close in shape, but is too worn and damaged to allow adequate comparison. *K. elongatus* Cooper & Grant (1975, pl. 358, fig. 4-6) from the Skinner Ranch Formation of west Texas lacks firm radial ribs, and is described as a new genus, *Glabrispinus* in Echinoconchoidea (see p. 196). *K. quadratus* Cooper & Grant, 1975 from the Hueco Canyon Formation is large with finer and more nodose ribs, and *K. victoriensis* (King, 1931, pl. 19, fig. 1; Cooper & Grant, 1975, pl. 360, fig. 8-12) is similar in shape and other aspects but has finer ornament, shallower sulcus and more transverse outline. It comes from the Victorio Peak Member of the Bone Spring Formation in west Texas.

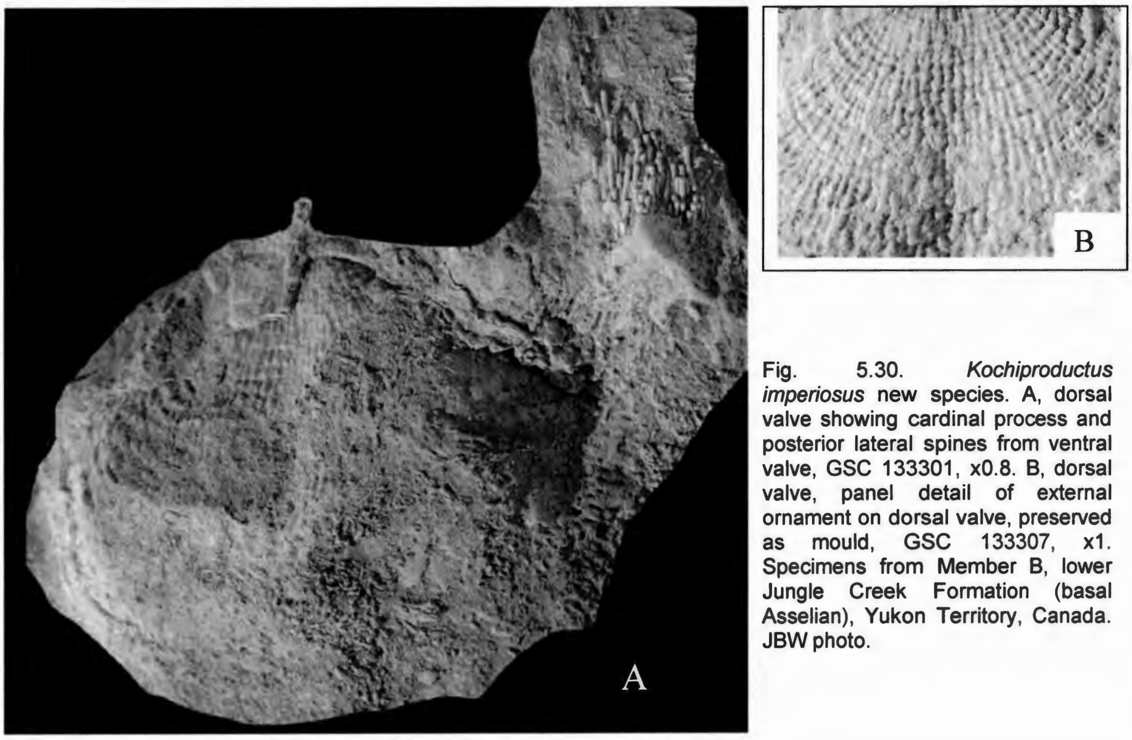


Fig. 5.30. *Kochiproductus imperiosus* new species. A, dorsal valve showing cardinal process and posterior lateral spines from ventral valve, GSC 133301, x0.8. B, dorsal valve, panel detail of external ornament on dorsal valve, preserved as mould, GSC 133307, x1. Specimens from Member B, lower Jungle Creek Formation (basal Asselian), Yukon Territory, Canada. JBW photo.

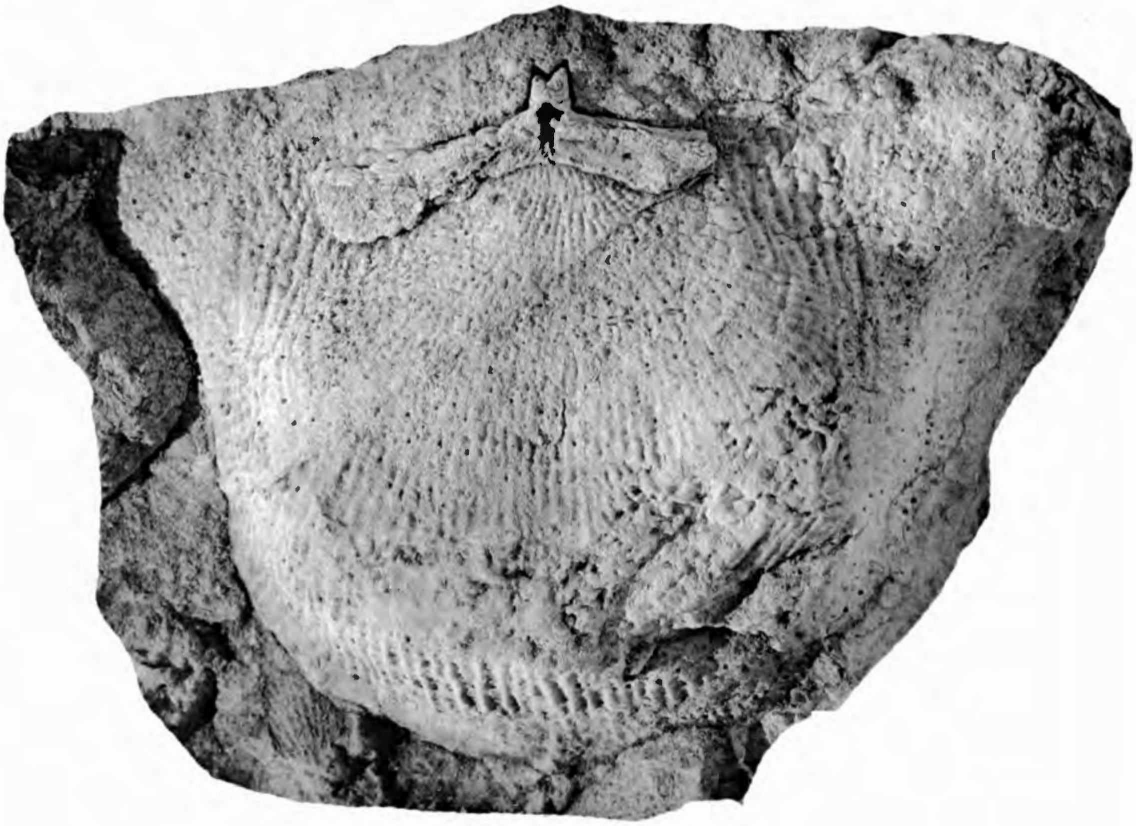


Fig. 5.31. *Kochiproductus imperiosus* new species, dorsal valve external mould and posterior interior, GSC 133302, x1. Specimen from Member B, lower Jungle Creek Formation (basal Asselian), Yukon Territory, Canada. JBW photo.

***Kochiproductus* (*Dunbarovia*) new subgenus**

Fig. 5.32

Derivation: Named for C. O. Dunbar.

Type species: *Kochiproductus plexicostatus* Dunbar, 1955, p. 107 from Kap Stosch Formation (Changhsingian) of Greenland.

Diagnosis: Large shells with large ears, prominent costae which anastomose anteriorly, dominated by closely spaced elongate spine bases, costae crossed posteriorly by prominent commarginal rugae, spines numerous over both valves, semi-erect over ears and trail. Cardinal ridges long, possibly the median septum not split.

Discussion: In *Kochiproductus plexicostatus* Dunbar (1955, p. 109) from Late Permian (Changhsingian) of Greenland, and unlike older species referred to *Kochiproductus* (*Kochiproductus*), the anterior costae show irregular swellings and branchings. The same irregularies are displayed in other younger Permian species, such as the early Middle Permian species *Productus* (*Buxtonia*) *freboldi* Stepanov (1937, pp. 122, 176, pl. 2, fig. 4) from the Brachiopod Limestone of Spitsbergen, a species also identified from the Assistance Formation of Roadian age, Devon Island, Canada, by Harker in Harker & Thorsteinsson (1960, pl. 17, fig. 5, 6). None of these species display the split dorsal septum or short buttress plates of older species and genera. Although this may be because no immature specimens have been described or figured, specimens of *Kochiproductus* sp. 6 of Cooper & Grant (1975, pl. 361, fig. 16-19) from the Cathedral Mountain Formation (Kungurian) of west Texas are comparatively small and do not show any split. But nor do the specimens show anterior anastomosing costae, although one specimen (Cooper & Grant 1975, pl. 360, fig. 1, 2) is moderately large. There is thus uncertainty about the nature of the dorsal septum in younger species assigned to *Kochiproductus*. Should there prove to be a difference in ontogeny, generic separation would be warranted, but at present, pending full knowledge about early ontogeny, the difference in anterior costation is judge to be of no more than subgeneric importance, affecting Middle and Upper Permian species from the Arctic.

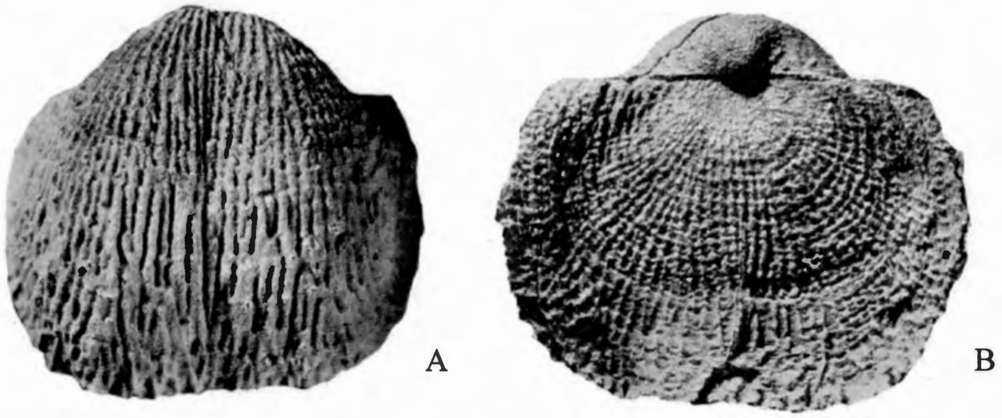


Fig. 5.32. *Kochiproductus (Dunbarovia) plexicostatus* Dunbar. Holotype as figured by Dunbar (1955, pl. 17, fig. 1, 2), x1. From Kap Stosch (Changhsingian), Greenland.

Tribe **DOWHATANIINI** new tribe

Name genus: *Dowhatania* Waterhouse in Waterhouse & Gupta, 1979a, p. 127 from Fenestella Shales, India.

Diagnosis: Spines limited to ventral valve, crowded postero-laterally, with slightly swollen bases over disc, ribbing sturdy over both valves, commarginals subdued, dorsal valve capillate. Dorsal septum cleft posteriorly. Lower Carboniferous (Visean or lower Serpukhovian).

Genus: *Dowhatania* Waterhouse.

Discussion: *Dowhatania* Waterhouse in Waterhouse & Gupta, 1979a, p. 127, type species *Productus dowhatensis* Diener, 1915, p. 27, was referred to Buxtoniinae in Waterhouse & Gupta, and transferred to Productini by Brunton et al. (2000, p. 469). The genus shows somewhat swollen ventral spine bases that rule out a productid alliance, and point to Buxtoniidae. There are numerous ear spines and shallow dorsal dimples, and divided posterior dorsal septum, with no high marginal ridge just as in Buxtoniini, but unlike buxtoniins, dorsal spines are missing and capillae appear over the dorsal valve. These two attributes suggest Tyloplectinae Termier & Termier (see p. 153), but *Tyloplecta* has fewer ventral spines, and has lateral buttress plates. Both genera are highly exceptional, and *Dowhatania* could have been anticipatory of Tyloplectinae, which is restricted to the Permian Period.

Brunton et al. (2000, p. 469) had stated that *Parabuxtonia* Yang & Zhang, 1982 and synonymous *Shishapangmaella* Yang from the Visean of China were the same as *Dowhatania*, but this is rejected, because capillae are absent over the costae, and lateral buttress plates are well developed in *Parabuxtonia*.

A ?Bashkirian age was assigned by Brunton et al. (2000, p. 469) to the Fenestella Shales, but the evidence for such an age seems poorly based, judging from studies by the writer on both the faunas and field evidence. Several brachiopod genera and species from the Fenestella Shales and equivalents in Nepal have yet to be described, including a gigantoproductid, belonging to a group not known above the Lower Carboniferous.

Genus **Dowhatania** Waterhouse in Waterhouse & Gupta, 1979a

Type species: *Productus dowhatensis* Diener, p. 27 from Fenestella Shales, Kashmir.

Diagnosis: Dorsal valve capillate, no dorsal spines, dorsal septum medianly cleft.

Dowhatania dowhatensis (Diener, 1915)

Fig. 5.33

Cf. 1899 *Strophalosia* sp. indet. aff. *S. costata* [non Waagen] Diener, p. 28, pl. 1, fig. 15, 16.
1915 *Productus dowhatensis* Diener, p. 27, pl. 2, fig. 8-11, not pl. 3, fig. 1.
1977 ?*Setigerites dowhatensis* – Waterhouse & Gupta, p. 155, pl. 2, fig. 4, 5.
1979a *Dowhatania dowhatensis* – Waterhouse & Gupta, p. 127, pl. 10, fig. 3-6.
2000 *D. dowhatensis* – Brunton et al. p. 469, Fig. 314.2a-c.

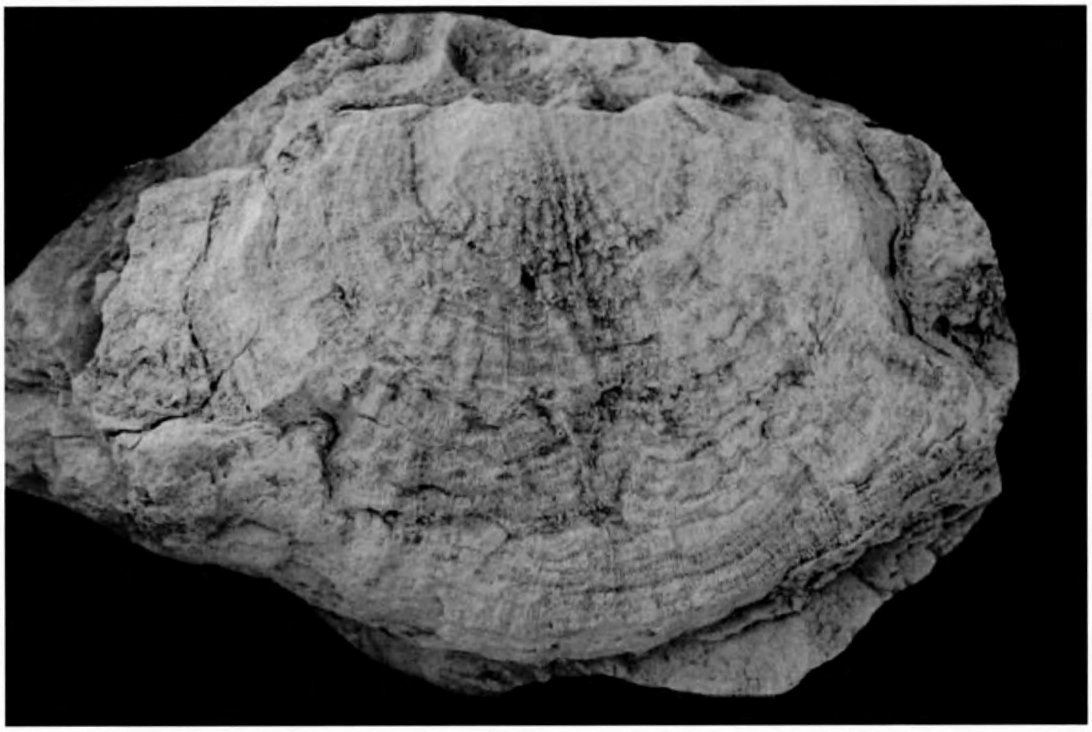


Fig. 5.33. *Dowhatania dowhatensis* (Diener), external mould of dorsal valve BR 3082 from Fenestella Shale, (Serpukhovian?), Kashmir, showing capillae and shallow dorsal pits, x2. JBW photo.

Lectotype: GSI 11069 figured by Diener (1915, pl. 2, fig. 8), from Fenestella Shales, India, designated by Waterhouse & Gupta (1977, p. 155).

Diagnosis: Moderate size with numerous ventral postero-lateral spines, and fine dorsal capillae over well formed costae.

Discussion: There is little to add to the description of the species and genus in Waterhouse & Gupta (1979a), where attention was drawn to the unusual nature of the dorsal valve, in which costae, three or four anteriorly in 5mm, bear fine capillae, numbering five to six in 1mm. There are shallow pits, and no spines. Yet the ventral valve is like that of Buxtoniini, with spines over the umbonal slopes and inner ears, and slightly swollen bases over the disc and trail.

Subfamily **TOLMATCHOFFIINAE** Sarytcheva, 1963

Fig. 5.34

[Nom. transl. hic ex Tolmatchoffiidae Sarytcheva, 1963, p. 168].

Diagnosis: Spines on ventral valve not uniformly distributed, may be crowded on ears or postero-laterally, spine bases fine, not prolonged posteriorly or swollen at the base, dorsal spines present as a rule. Rugae often low or inconspicuous; no external dorsal pits as a rule. Lower Carboniferous (Tournaisian) to Upper Carboniferous (?Moscovian).

Genera: *Tolmatchoffia* Fredericks, *Buxtonioides* Mendes, *Coronatonia* new genus, *Kadelia* Waterhouse, ?*Parabuxtonia* Yang & Zhang (syn. *Shishapangmaella* Yang in Yang & Fan), *Scissicosta* Lazarev, *Tomilia* Sarytcheva, ?*Tomiproductus* Sarytcheva.

Discussion: Members of this tribe are difficult to separate from Buxtoniini, and the *Revised Brachiopod Treatise* (pp. 501, 502) offered no clear nor accurate distinction, asserting that rugae "are commonly absent", which is not entirely true, because *Tolmatchoffia* has low commarginal rugae over the ventral disc and crowded rugae over the dorsal disc, and they stated that as a further discriminant, there is "commonly an elongate cardinal process pit", true also of at least some Buxtoniini. For example, *Buxtonia* itself has a long slit in the posterior septum (Brunton et al. 2000, Fig. 338.3e), and several genera allocated (albeit contentiously) by those authors to Tolmatchoffini lack the slit (eg. *Peniculauris* (Brunton et al. 2000, Fig. 345.1e) or *Squamaria* (Brunton et al. 2000, Fig. 345.1f). It was noted that spines on the ventral valve were not uniformly distributed, but they are nonetheless numerous, and the distribution difficult to quantify and compare with any surety that the matter is of more than generic significance. *Tolmatchoffia* itself is large, with faint commarginals and fine spines that may be numerous but arise from costae with little swelling and no prolongation at the base. Spines are not as crowded as those on some genera of Buxtoniinae, but may form small clumps laterally, either on the ears or the umbonal slopes. There is scope for subdivision of the subfamily, but the distribution of spines is poorly known for several of the genera. Here a further distinction is added: the lack of pits from the dorsal valve as a rule, whereas pits are well developed in Buxtoniinae.

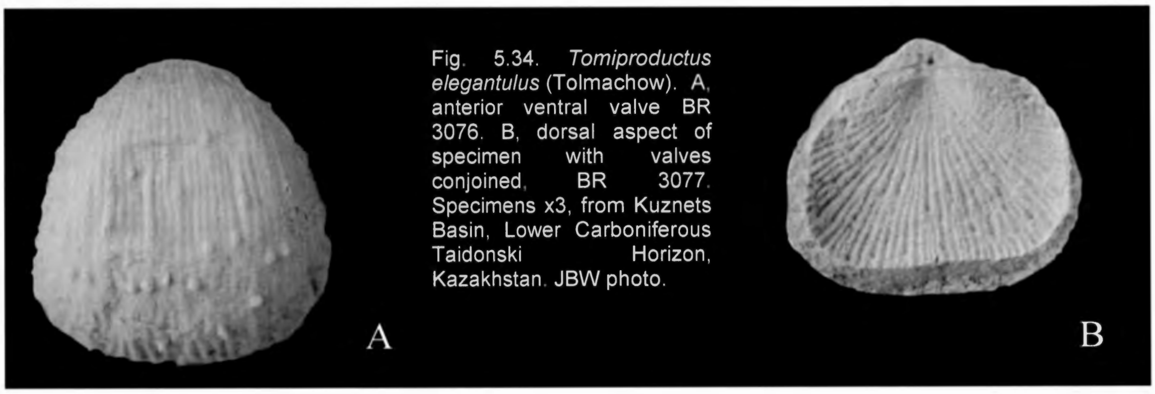


Fig. 5.34. *Tomiproductus elegantulus* (Tolmachow). A, anterior ventral valve BR 3076. B, dorsal aspect of specimen with valves conjoined, BR 3077. Specimens x3, from Kuznets Basin, Lower Carboniferous Taidonski Horizon, Kazakhstan. JBW photo.

Tomiproductus Sarytcheva is difficult to evaluate. Dorsal valves of the type species *T. elegantulus* (Tolmachoff) as figured by Sarytcheva (1963, pl. 31, fig. 8, pl. 32, fig. 3v) lack pits. But of a dozen specimens presented to me by Tatiana Sarytcheva, a couple have rare and scattered pits, rare posteriorly over the dorsal valve, and very few and scattered pits over the disc and trail, pointing to a possible relationship with Buxtoniini. Brunton et al. 2000 classed the genus as Tolmatchoffinae, following Sarytcheva (1963), and there is similarity in shape and spination. Conceivably the pits are due to slight inflections and spine bases, or their significance is not so great.

Genus ***Coronatonia*** new genus

Derivation: corona – wreath, garland, Lat.

Type species: *Kochiproductus coronus* Shiells, 1968, p. 479 from limestone (upper Visean) of Ayreshire, Scotland, here designated.

Diagnosis: Large shells with fine and numerous spines over both valves, especially crowded over inner ventral ears. Ventral ribs fine and crossed by numerous low rugae, dorsal valve more reticulate, without dorsal pits. Long marginal flange. Dorsal septum single without median slit.

Discussion: Shiells (1968) described the type species in detail and analyzed the function of the flange. He ascribed the species to *Kochiproductus*, in spite of its Visean age, whereas Brunton et al. (2000) stated that *Kochiproductus* was limited to the Permian Period. This is not quite correct, for there are several species found in the Upper Carboniferous of Russia and Canada, though none are known so far to be as old as Lower Carboniferous. The Shiells species does have the flange found in some *Kochiproductus*, and has spines on both valves, but the ribs are more continuous than in the disrupted pattern displayed by *Kochiproductus*, in which ribs may swell and constrict. Indeed the continuous nature of the ventral ribs is one of the outstanding features of *Coronatonia*, because spine bases are fine, somewhat as in *Tolmatchoffia* itself, and costae do not swell at the base of spines. Moreover the dorsal valve is markedly reticulate, even more than in *Tolmatchoffia*. In *Buxtonia* Thomas, costae especially on the ventral valve are much more disrupted by spines, and the dorsal valve less reticulate. A very few members of Buxtoniini show similar ribs, such as *Setigerites* Girty, 1939 from North America, Eurasia and possibly North Africa, which has very fine ribs, and spines that are dense posteriorly as well as numerous elsewhere, but commarginal rugae are much less evident. *Labriproductus* Cooper & Muir-Wood, 1951 from central United States has stronger ribs and short flange, and little in the way of commarginal rugae.

The close reticulation of the dorsal valve shows pits between the costae and rugae, but they do not seem to be the same as the dorsal pits displayed at greater spacing by members of Buxtoniinae. *Kochiproductus* and *K.* (*Dunbarovia*) have similar dorsal reticulation, but also show well spaced dorsal pits.

Genus ***Parabuxtonia*** Yang & Zhang, 1982

Parabuxtonia, type species *kongjingensis* Yang & Zhang (1982, p. 305, pl. 2, fig. 1-4, pl. 3, fig. 10, 11, Fig. 2) from the Early Carboniferous of southern Tibet is large with predominant radial ornament, weak and fine commarginal rugae, and numerous spines, clustered over the ventral ears (Yang & Zhang 1982, pl. 3, fig. 10), and arising from costae over the disc and trail, without swollen or prolonged bases. There are no dorsal external pits, so that the genus is included in Tolmatchoffinae, but is exceptional in having well developed lateral buttress plates. The genus is much larger with stronger ribs and fewer ventral spines than in *Xinshaoproductus* Tan Zhen-Xiu, 1986, and although this genus also has lateral buttress plates, it is assessed as being dictyoclostid (see p. 162). *Buxtonioides itaitubensis* Chen, Tazawa & Shi (2004, Fig. 4I-K, 5, 7E) from the Upper Carboniferous (Bashkirian) Itaituba Group of Brazil is closely related, and has somewhat similar exterior, with less commarginal ornament, and similar lateral buttress plates. The posterior ventral valve has rather coarse spine bases, and possibly there are ventral spines with elongate bases anteriorly. This could be approaching the ventral ornament of *Parabuxtonia*, but again, detail is yet to be clarified. *Buxtonioides* Mendes, 1959, type species *amazonicus* (Katzer), also comes from the Itaituba Group of Brazil, and is deemed to lack lateral buttress plates, and although there may seem to be scope for revision of the two species, to determine more about the nature of the dorsal valves, and demonstrate that of type *Buxtonioides* has been correctly described, the studies by Mendes (1959) and Chen, Tazawa & Shi (2004) do not support such a possibility. *Shishapangmaella* Yang in Yang & Fang (1983, p. 273, pl. 2, fig. 15, 16) is an objective synonym of *Parabuxtonia*.

The genus *Parabuxtonia* was synonymized with *Dowhatania* Waterhouse from the Fenestella Shales of Kashmir by Brunton et al. (2000, p. 469), but is readily distinguished by its lateral buttress plates, which are absent from *Dowhatania*, and by the lack of capillae over the costae, which are present in *Dowhatania*. Although *Tyloplecta* also has lateral buttress plates, it has a capillate dorsal costae, and larger more ventral disc spines.

Genus ***Buxtonioides*** Mendes, 1959

Buxtonioides Mendes (1959, pl. 2, fig. 1, pl. 3, fig. 1a, b, 2, text-fig. 10, 11, 13, 14) from Itaituba, Brazil, was confused with *Gemmulicosta* Waterhouse, 1971a by Brunton et al. (2000, p. 496) but has more or less simple ventral ribs with slightly swollen and not elongate spine bases, as may be seen by comparing the figures in Brunton et al. (2000, Fig. 339c – *Buxtonioides*, with Brunton et al. (2000, Fig. 339.d – *Gemmulicosta*). The best illustration of the type species of *Buxtonioides, B. amazonicus* (Katzer, 1903), is provided by Rocha Campos & Archangelsky (1985, pl. 6, fig. 6), which clearly shows the ventral valve with costae little disturbed by spines, low posterior commarginal rugae, and numerous spine bases especially over the ears and posterior shell and disc: a very different appearance from that of *Gemmulicosta*. Another high quality illustration of the ventral valve was provided by Derby (1874, pl. 4, fig. 8), which shows numerous fine erect spines over the ears and lateral slopes, with fine body spines, arising with little disturbance to the costae over the disc. Brunton et al. (2000) speculated that *Buxtonioides* lacked the bordering flange of *Kochiproductus*, but this is unproven, and the flange is not always shown in *Kochiproductus*. Those authors also emphasized that *Buxtonioides* lacks adult buttress plates. So does *Kochiproductus*. Mendes (1959, Fig. 12, 13) illustrated the dorsal interior, to show a split septum (Fig. 12) and no split septum (Fig. 13), and no lateral buttress plates. Several fragmentary dorsal interiors were illustrated by Derby (1874) and one - pl. 6, fig. 18 – suggests a lateral buttress plate on the left side, whereas the valve in pl. 7, fig. 5 definitely indicates an absence of lateral buttress plates, so that the specific identity of the fragments may need closer examination. In USNM 86174, examined at the Smithsonian Institution, Washington D.C., ribs persist well with slight swelling at the base of spines. Spines are numerous over the ventral beak and anteriorly and over the dorsal valve. Reticulation is moderately firm, and no dorsal pits are apparent. Anterior dorsal pustules are large.

Subfamily **MARGINATIINAE** Waterhouse, 2002b

Fig. 5.35

[Marginatiinae Waterhouse, 2002b, p. 23].

Diagnosis: Distinguished by lack of postero-lateral cluster of spines over ears, spines may form row close to ventral hinge, dorsal spines may be rare, external dorsal pits present, disc of both valves usually reticulate. Ribs and interior as in *Buxtonia*. Lower Carboniferous (Tournaisian) to Upper Carboniferous (Moscovian).

Genera: *Marginatia* Muir-Wood & Cooper, ?*Acanthocosta* Roberts, *Agirovia* new genus, *Anamarginatia* new genus, *Brasilioproductus* Mendes, *Paramarginatia* Yang Shi-Pu (syn. *Marginoproductus* Tan Zhen-xiu), *Umboanctus* Waterhouse.

Discussion: The subfamily is close to Buxtoniini, but is distinguished by the lack of a ventral cluster of spines and tendency of dorsal spines to be rare or absent. The lower Visean genus *Marginoproductus* Tan Zhen-xiu, 1986, p. 435 [p. 443] from Hunan, south China, is highly vaulted and narrow with signs of a hinge row, and bears possible dorsal pits, although Brunton et al. (2000, p. 474) suggested that the genus closely resembled Tolmatchoffinae, and yet referred the genus to Retariini. The distinction from Retariini is readily ascertained when comparing the name-giving genera of the two family groups. The genus needs further inspection, but the overall shape and aspects of interior and ornament certainly appear to come close to *Paramarginatia*, which Brunton et al. synonymized with *Marginatia*. *Paramarginatia* has a cleft dorsal septum and otherwise somewhat approaches *Inflatia* (see p. 157).

Genus ***Anamarginatia*** new genus

Derivation: an – or, Lat., Marginatia, brachiopod genus.

Type species: *Marginatia mimica* Roberts, 1971, p. 120 from Enga Sandstone (Tournaisian), Bonaparte Gulf Basin, Australia, here designated.

Diagnosis: Ventral spines form row along hinge, scattered over disc and larger over trail, few over ears, may form cluster in front of ears, no dorsal spines. Dorsal disc strongly reticulate.

Discussion: The type species has been well described and figured by Roberts (1971, pl. 28, fig. 1-20, Fig. 26) and shows a dorsal hinge ridge extending into a marginal ridge which stops short of the anterior margin, and a dorsal septum with antron in small forms. Ribs are well developed on both valves, and dorsal pits are present over the dorsal exterior, which lacks spines. Ventral disc spines have slightly elongate bases, and sturdy trail spines are erect. Commarginal rugae are subdued, and cover more of the dorsal valve than the ventral valve. Internal features were described and illustrated in detail by Roberts (1971). The species ranges from upper Tournaisian into Visean beds. *Marginatia* Muir-Wood & Cooper, 1960, type species *Productus fernglenensis* Weller, 1909 of Osagean age has a few dorsal spines, no cluster of spines postero-laterally, no hinge row of spines, and only a few ear spines. Internally the genus is close to Roberts' form. *Paramarginatia* Yang Shi-Pu, 1978, type species *P. weiningensis* Yang from Visean of China (Yang 1978, pl. 25, fig. 1-9, text-fig. 23), with another species *P. gesuoensis* Yang (1978, pl. 25, fig. 10-13) is also close: it shows no cluster over the ears or postero-lateral flanks, and was synonymized with *Marginatia* by Brunton et al. (2000, p. 502), yet lacks dorsal spines. Another Australian genus of Tournaisian age, *Acanthacosta* Roberts, 1971, p. 104, has numerous dorsal spines, and ventral spines show elongate bases posteriorly. Flank spines are moderately numerous, but ventral ear spines are few, and hinge spines missing. *Umboanctus* Waterhouse 1971a, p. 212 from lower Pennsylvanian of Yukon Territory, Canada, has numerous ventral spines, including a hinge row, but no posterior lateral cluster, and no strong erect trail spines. Dorsal spines are not developed.

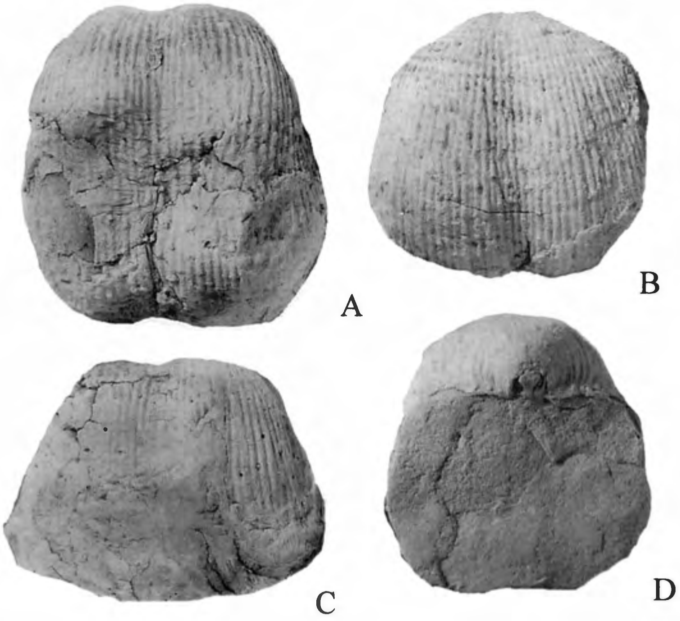


Fig. 5.35. *Umboanctus spinosus* Waterhouse. A, ventral valve GSC 26410. B, D, ventral valve GSC 26411, holotype. C, anterior external mould of dorsal valve GSC 26412. Specimens x1, from Peel River, Yukon Territory, Canada, Ettrain Formation equivalents (Moscovian). B. O'Donovan & JBW photo.

Genus ***Agirovia*** new genus

Fig. 5.36

Derivation: Named from Flöz Agir, source of the genus and species.

Type species: *Tolmatchoffia demaneti* Böger & Fiebig, 1963, p. 133 from marine horizon above Flöz Agir (Westphalian C), Germany, here designated.

Diagnosis: Moderately large in size, ribs well developed and crossed by a number of inconspicuous rugae. Spines prominent only along the hinge in one row, increasing to two rows laterally, long and curving inwards as if to enclose object.

Discussion: In some respects this genus approaches *Schrenkiella* Barchatova, 1973 (see p. 379) in the way the ventral spines emerge from the ventral hinge, but the ventral valve is moderately inflated, and may bear an anterior shallow sulcus, and commarginal rugae are present over both valves. Anteriorly some ventral costae split, as if bearing small spines at or behind the junction. Dorsal spines are not obviously developed.

Tolmatchoffia Fredericks, 1933, p. 28, based on *Productus robustus* Tolmatchoff, 1924, p. 230 from the upper Tournaisian of Russia, has numerous fine spines on both valves, and coarse spines are concentrated on the anterior inner ears and umbonal slopes of the ventral valve, and hinge spines are few and inconspicuous. *Bellaclathratus* Winters, 1963 of Pennsylvanian age in the United States has somewhat similar hinge spines, but the shell is smaller and other spines, rugae and ribs more prominent. Other genera related to *Tolmatchoffia*, such as *Kadelia* Waterhouse, 2010a have a more prominent ventral cluster of posterior or postero-lateral spines.

In the prominence of hinge spines and lack of a postero-lateral cluster of spines, the new genus comes moderately close to *Marginatia* Muir-Wood & Cooper, 1960, type species *Productus fernglenensis* Weller, 1909, p. 299 from lower Visean of North America , but has more and larger spines postero-laterally, and lacks the external pits of the dorsal valve, and moderately numerous spines over the ventral disc and trail. The Tournaisian genus from north Australia called *Acanthocosta* Roberts, 1971, p. 104 displays less continuous ribs punctuated by rugae and spines, and *Brasilioproductus* Mendes, 1959, p. 48 from Upper Carboniferous of Brazil and North America has scattered larger ventral spines. On the other hand *Umboanctus* Waterhouse, 1971a from Upper Carboniferous in northern Canada has numerous fine ventral spines over the ventral disc and trail, as well as a row of spines along the hinge, and rugae are moderately prominent. Costae on the new form are moderately close to those of *Tomilia* Sarytcheva, 1963, p. 220 from the lower Visean of Kuzbass, Kazakhstan, but *Tomilia* is much more vaulted and lacks the prominent ventral hinge spines. Possibly that is true also of *Scissocosta* Lazarev in Lazarev & Suur'suren, 1992 from Tournaisian of Mongolia. This genus was said to resemble *Tolmatchoffia*, and has scattered dorsal spines.

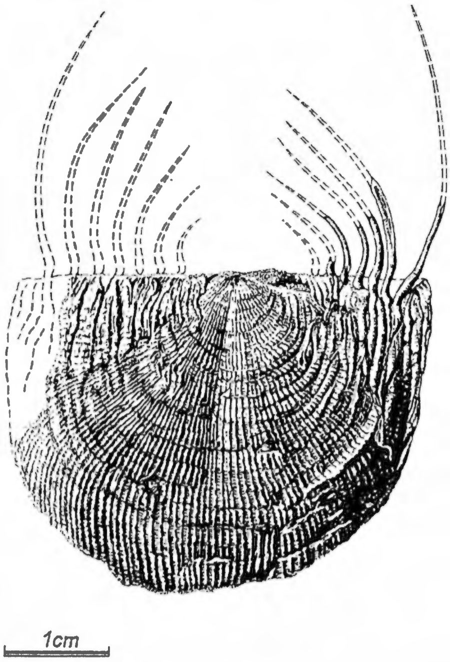


Fig. 5.36. *Agirovia demaneti* (Böger & Fiebig), ventral valve as sketched by Böger & Fiebig (1963), from Westphalian C, Germany.

Subfamily TYLOPLECTINAE Termier & Termier, 1970

[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-slope ear-channel rows, not clustered. Dorsal valve with pits, no spines, ribs striate. Lateral buttress developed. Lower Permian (Kungurian) to Upper Permian (Changhsingian).

Genera: *Tyloplecta* Muir-Wood & Cooper.

Discussion: The relationship of *Tyloplecta* to Buxtoniidae is based on a fresh assessment of the ventral valve ornament. The presence of strong ribs with dorsal striae recalls aspects of Liraplectini Chen & Shi (2000), but *Liraplecta* is dictyoclostid, whereas the irregular and swollen spines bases along ventral costae of *Tyloplecta* suggest a buxtoniid alliance. There are lateral buttress mounds in the dorsal valve. *Tyloplecta* was discussed by Shi & Chen (2003) in terms of its distribution as controlled by water temperatures and availability of migration pathways. *Araxilevis* Sarytcheva, referred to the group in Brunton et al. (2000), has different ornament, though radial striae are visible within and not externally over the shell structure (Termier & Termier 1970a, pl. 31, fig. 1, 3). (See p. 74).

Pseudoantiquatonia Zhan & Wu, 1982 was also assigned to the group by Brunton et al. (2000, p. 488) but lacks capillate dorsal valve and lacks lateral buttress plates. It is placed in Rigrantiini (p. 123).

. Chen et al. (2004, p. 445, Fig. 4I-K, 5, 7E) described *Buxtonioides itaitubensis* as a new species from the type region to show more buxtoniid-type ventral spine bases over the umbonal region such as are not seen in type

Buxtonioides, and apparently no commarginal rugae, to imply ontogenetic degeneration from a buxtoniid ornament during the growth cycle. But the species also displays widely divergent lateral buttress plates (Fig. 4K, 5), whereas type *Buxtonioides* has an entire or split median dorsal septum (Mendes 1959, Fig. 12, 13), and no lateral buttress plates (p. 151). The species *itaitubensis* belongs to a different genus, possibly related to *Tyloplecta*, but the nature of the dorsal exterior was not illustrated or described, so that it is not known if the dorsal valve is capillate.

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 reticulated by commarginal growth rugae over disc, spines limited to ventral valve as a rule, may be large and halteroid, no umbonal slope row. Internal posterior hinge ridge generally well formed, marginal ridges low, may be broad, trails long and simple as a rule, or may be multiple.

Discussion: The family appears to have evolved during the Early Carboniferous from a buxtoniid, such as *Coronatonia* new genus, because this genus has persistent and moderately reticulate ribs, no or few dorsal pits and non-cleft dorsal septum (see p. 149).Reticulation is less well developed than in Retariidae, including Reticulatiinae, and a row of spines along the base of the ventral umbonal slopes is not developed.This constitutes a readily determinable difference from Retariidae, including genera within Reticulatiinae, which otherwise are somewhat similar in size and reticulation, athough the reticulation is slightly better defined.

One matter to be pursued in questions over classification for Dictyoclostidae centres on the significance or otherwise of posterior central papillation or Lazarev's "shagreen texture" (not Waagen's). A number ofdictyoclostid-like genera as judged on the basis of reticulate or subreticulate ornament, were discriminated from Dictyoclostidae and assigned by Lazarev (2000a, b, etc.) to Yakovleviinae, which he later came to regard as a subfamily of Productidae rather than tribe in Plicatiferinae as in Brunton et al. (2000). Both these assessments marked considerable reassessment of earlier positions. The move to Plicatiferinae was based, it was said, on meronomic analysis, deemed to be a major revelatory advance on previous procedures. Within a few years, that meronomic analysis was overturned, again by meronomic analysis. The re-assessment was based on the absence of Lazarev's "shagreen" or sandpaper texture from the posterior dorsal and ventral valves in some genera. By contrast, *Dictyoclostus* itself has posterior central papillation. Throughout this study, it is deemed that caution is required over the significance of posterior central papillation, because well preserved New Zealand material shows that it changes during ontogeny and with substrate.

Subfamily **DICTYOCLOSTINAE** Stehli, 1954

[Dictyoclostinae Stehli, 1954, p. 316. Syn. Reticulariini Lazarev, 2000a, p. 40].

Diagnosis: Medium-sized to large shells with reticulate ornament, ventral spines varying in distribution, feeble or no dorsal pits, reducing towards maturity, and dorsal spines rarely present.

Tribe **DICTYOCLOSTINI** Stehli, 1954

[Nom. transl. hic ex Dictyoclostinae Stehli, 1954, p. 316].

Diagnosis: Large reticulate shells with spines as a rule clustered laterally in very small brush or array on slope between ears and umbonal slope, or outer ears, may be numerous over trail, not forming a row along base of umbonal slopes. Lower Carboniferous (Visean).

Genera: *Dictyoclostus* Muir-Wood, *Auloprotonia* Muir-Wood & Cooper, *Pugilis* Sarytcheva (mis-spelled *Pugilus* Sarytcheva).

Discussion: This group is more restricted than shown in the *Revised Brachiopod Treatise*, and is partly defined by the small cluster of spines on the ears, and spines close to the hinge, with a few anterior spines, and lack of a row of spines along the umbonal slopes. There are a few dorsal spines in *Dictyoclostus*, visible in specimens kept at the Smithsonian Institution of Washington D.C. Fine pits are present postero-laterally in the dorsal valve (see Muir-Wood & Cooper 1960, pl. 93, fig. 5, 6), a matter ignored in some studies, but in Canadian Arctic specimens the pits disappear or are reduced in relative extent with increased maturity (Fig. 5.37).The decorticated nature of figured type *Dictyoclostus*is of limited value in helping to circumscribe the genus, and the dark figures of *Latispinifera*Lazarev, with obscure hinge detail, although claimed to help delineate a dictyoclostiform group at least superficially close to *Dictyoclostus*, add to the uncertainty of tribal limits. As a result, the limits of Dictyoclostini, and two at least superficially similar groups proposed by Lazarev (2000a, 2000b) as Reticulatini and Latispiniferini remain cloudy, but are enhanced in part by the limits for better known groups, such as those of Inflatiini, Spinarellinae and Liraplectini.Tribe Reticulatiini Lazarev was distinguished from Dictyoclostinae by Lazarev (2000a, p. 40), as followed by Chen & Shi (2006) and Brunton (2007, p. 2648), Lazarev asserting that *Reticulatia* was to be distinguished from *Dictyoclostus* through the absence of posterior central papillation over the posterior and inner parts of the dorsaland ventral valves. The difference is shown in comparing the "shagreened" dorsal interior of *Dictyoclostus* (Brunton et al. 2000, Fig. 331e) with the posterior smooth central shell surface of the dorsal interior in *Reticulatia* Muir-Wood & Cooper (1960, pl. 105, fig. 8; Brunton et al. 2000, Fig. 335, 2e). However in the latter figure, there seems to be more papillation on the shaded side of the figure, rather than on the left and overlit side of the figure, just behind the dorsal adductor scars. Indeed there appear to be numerous but very fine papillae over this central posterior area, and one is left to wonder about the reliability of interpretations of the photographs. The value of the discriminant is discussed in the Introductory section on morphology (see pp. 18-22) and further discussed for the genus *Yakovlevia* and Yakovleviinae, which also show, allegedly like *Reticulatia,* a lack of posterior central papillation, leading Lazarev to class *Reticulatia* within Yakovleviinae (see pp. 336-339). There appear to be two substantial cautions with regard to the Lazarev interpretation. As shown in the opening discussion on morphology, Lazarev's "shagreen" pattern in very well preserved New Zealand Productida changes during ontogeny, and varies between the dorsal and ventral valves, and varies in closely related species and genera. The very good preservation, and availability of numerous specimens, stands in contrast to the paucity of material available to Lazarev (2000a), who emphasized how difficult it was to confirm the presence or absence of posterior central papillation, and who conducted no studies on ontogenetic change or the influence of bottom facies. But that was because he relied on shells which are normally filled with matrix, instead of using internal moulds that clearly show internal detail, or, at second best, using silicified material etched from matrix. Moreover, "shagreen" patterns are present or absent in different strands and lineages. "Shagreen" presence or absence is not an overriding and unique morphological trait restricted to very closely related taxa. It appears as acknowledged by Lazarev (2000a) in *Schrenkiella, Productus*, and *Dictyoclostus* and is absent (ie. smooth or non-shagreen) from *Buxtonia, Reticulatia* and *Yakovlevia*, or at least in the specimens that Lazarev examined. Such a wide distribution means that other criteria need to be used for tribal, subfamilial, and even superfamilial discrimination. Evidence for disassociation between *Reticulatia* and *Yakovlevia* is meagre – the two are deemed to have such different shape, visceral disc, muscle scars and ornament that a close relationship is ruled out, and *Yakovlevia* is deemed to be close to *Paucispinifera* and members of Linoproductidina, whereas *Reticulatia* is as it looks, a member of Productidina, but, as adjudged by Lazarev, somewhat removed from Dictyoclostidae, in spite of the similarity in appearance – yet another example of morphological congruence. Lazarev (2000a, p. 496) asserted that shagreened shells could not give rise to non-shagreened shells, but this is denied in ontogenetic study of single species, which can show that immature shells with posterior central papillation become smooth in later maturity. The assertion is just that, an assertion, disproved by actual material.

If, however, the "shagreen" texture proves to be of constant value amongst dictyoclostiform genera at maturity, there might be a group already proposed for shells that allegedly lack posterior central papillation, because the name genus was included as a synonym of Yakovleviini. The family group is called Inflatiinae Sarytcheva, 1977, which clearly predates Reticulariini Lazarev, 2000a. But whether posterior central papillation is really missing from *Inflatia* Muir-Wood & Cooper is uncertain, as discussed on p. 157.External dorsal pitting is arguably present in some Inflatiinae, as in Dictyoclostidae, but it is not clear that such pitting is diagnostic, given the apparent variation in Dictyoclostidae.

Chen & Shi (2006, p. 148) recognized Reticulatiini Lazarev, and repeated the "shagreen" interpretation, without analysis, but treated the tribe as a member of Dictyoclostidae, not Yakovleviinae. They added further aspects to the summary of Reticulatini, but the observations (medium and large size, deep shell cavity, reticulate disc, halteroid spines), apply equally to Dictyoclostini. The allegedly "rare" geniculation ascribed to *Dictyoclostus* in contrast to *Reticularia* seems mostly a matter of different preservation: well preserved *Dictyoclostus* is at least subgeniculate. For the comparison with *Dictyoclostus*, they stated that *Reticulatia* differed in the presence of a ginglymus, and overlapping lamellae near the ventral margin. These authors (2006, p. 150) also mentioned that

Dictyoclostus had fewer dorsal spines than in their new genus *Bruntonella*, though they diagnosed *Bruntonella* as having no dorsal spines (Chen & Shi 2006, pp. 149, 151). But they also commented on the more "perfect" reticulation

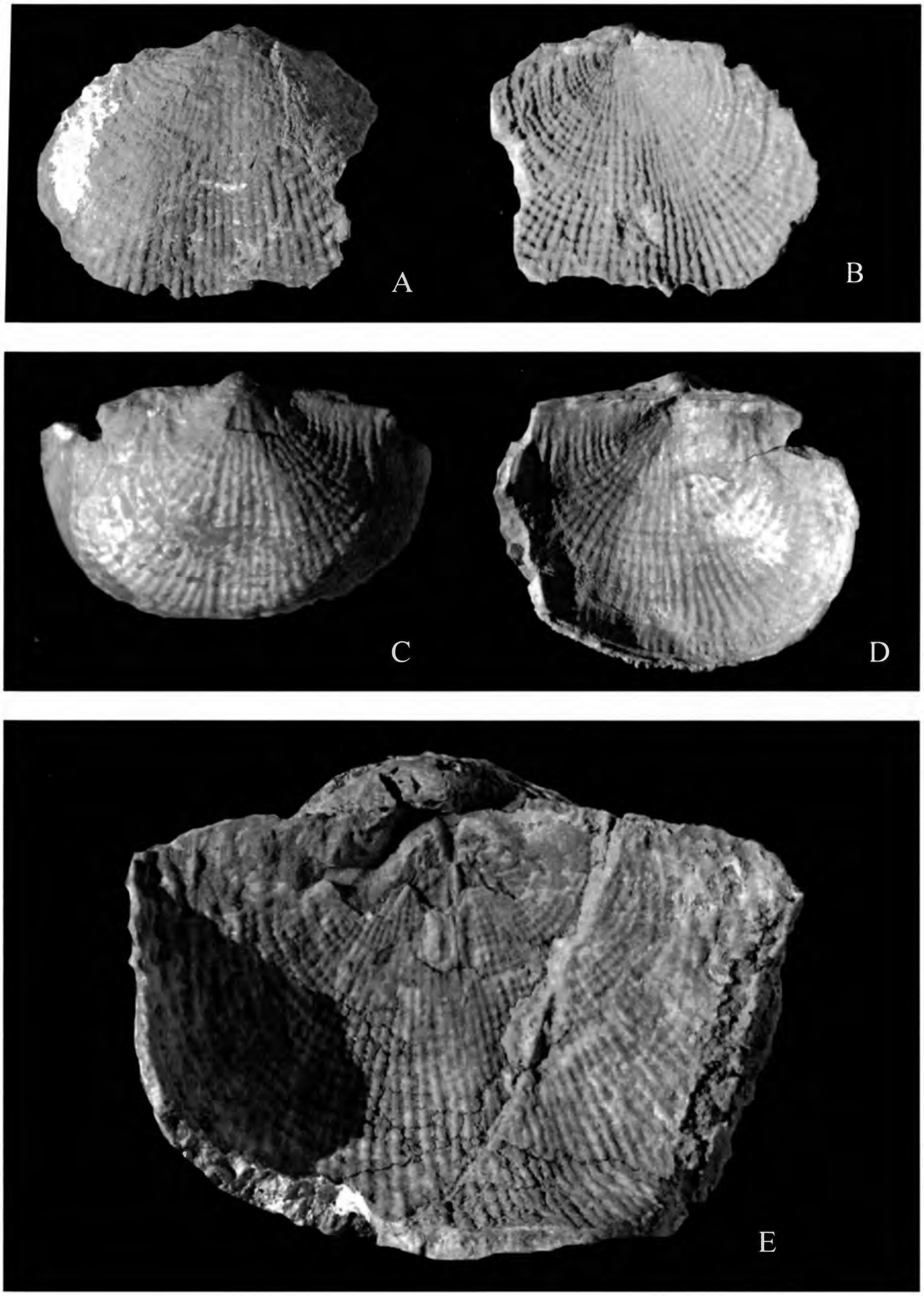


Fig. 5.37. Illustrations of a dictyoclostin genus from the Canadian Arctic, showing some degree of disappearance of dorsal external pits during ontogeny. A, B, ventral and dorsal aspects of small immature specimen GSC 136075 33mm wide. C, D, ventral and dorsal aspects of GSC 136076 40mm wide. E, mature dorsal valve GSC 13607468mm wide. JBW photo.

on the ventral discof *Reticulatia* and allies, a perspicaeous insight deemed to be a valid distinction.On the other hand, *Reticulatia* is close to *Dictyoclostus* in many respects, including lack of dorsal dimples externally in some species, and the few differences that can be enumerated, such as the presence of a ginglymus and stronger reticulation may be of little more than generic value. Muir-Wood & Cooper (1960, p. 285) noted that the spines formed a patch on the umbonal flanks in *Dictyoclostus,* and a row along the hinge and another along the sulcus inside the ears in *Reticulatia*. The figures provided for *Dictyoclostus* by Muir-Wood & Cooper (1960), or by Brunton et al. (2000) do not show the patch very clearly, but the description should be accepted. Only two figures show the ventral posterior spines clearly (Muir-Wood & Cooper 1960, pl. 105, fig. 1, 4) for *Reticulatia huecoensis*, the type species, and these suggest a weak hinge row, and a small number of spines over the ears, with signs of a row of fine spines along the inner ear channel, and although fine, and not clear all specimens, theumbonal slope spine rows are considered to point to a significant difference between the two genera, because no such row appears to be developed in *Dictyoclostus*. For *Dictyoclostus semireticulatus*, a few spines are indicated on the ventral ears (Muir-Wood & Cooper 1960, pl. 92, fig. 1; Muir-Wood 1928, pl. 4, fig. 2a, b), and a row was recorded near the hinge. Brunton et al. (2000, Fig. 331.a; Fig. 335. 2a) showed a number of ear spines for *Dictyoclostus*, and slightly fewer for *Reticulatia*. Overall the two are very similar in ornament, size and shape and disc, and of course there are differences, many more individual rather than species or genus-wide. As for the difference in distribution of internal papillae, it is not entirely convincing for figured *Reticulatia*, as discussed previously. Given the indications that "shagreen" presence and absence depended at least in some stock on the stage of maturity, and varied in other stock considerably between individuals and species, it seems more objective to note external and overall internal similarities as providing the chief guide for tribal classification, and refer *Reticulatia*toProductoidea rather than Yakovleviidae. Chen & Shi (2006, p. 147ff) also dismissed any close relationship to Yakovleviinae, seeming to place little credence on the Lazarev interpretations. Throughout this study, there is certainly no objection to the recognition of tribes, but it is believed that these must be defensible, and applicable on consistent differences in morphology that hopefully apply to a number of genera, thereby establishing that the criteria are of more than generic rank. The exception is where at least one aspect of the morphology of a single genus is strikingly different from otherwise similar genera.To Lazarev, posterior papillation was such a feature, but doubts remain.

Tribe **INFLATIINI** Sarytcheva, 1977

Fig. 5.38

[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, forming hinge rowas a rule, no umbonal slope row. Deep corpus cavity, hinge ridge, well developed cardinal process. Lower Carboniferous (Visean) to Upper Carboniferous (Moscovian).

Genera: *Inflatia* Muir-Wood & Cooper (syn. *Adairia* Gordon, Henry & Treworgy), *Costaglobus* new genus, ?*Kelamelia* Zhang Zi-Lin, *Keokukia* Carter.

Discussion: *Inflatia* Muir-Wood & Cooper, 1960 is well figured by Muir-Wood & Cooper (1960, pl. 55, fig. 1-13) andGordon et al. (1993), and Russian material is shown in Sarytcheva (1977, pl. 14, fig. 2-6; pl. 15, fig. 1-3). The shells are tumid and inflated, with moderately strong reticulate ornament, and ventral hinge row of spines and scattered other ventral spines. The presence or absence of external dorsal pits in *Inflatia* is not entirely certain. If present they are very fine, and not as clear as in Rigrantiini Lazarev. The interior is dictyoclostid, with sturdy cardinal process bearing posterior cleft, usually no sign of buttress plates or anderidia, nor cleft dorsal septum, and pustules are high and close-set in many rows anteriorly, starting near the anterior end of the disc and continuing over the trail. Central papillation is developed posteriorly, each side of the dorsal septum, but not over the posterior septum, to judge from figures in Muir-Wood & Cooper (1960, pl. 55, fig. 7, 13, 14), although some low relief pits and pustules are faintly visible, whilst it is true that the figures of *Inflatia* in Sarytcheva (1977, pl. 14, fig. 5, 6) suggest a smooth posterior central part, possibly because published figures are not of high quality. The ventral valve figured by Muir-Wood & Cooper (1960, pl. 55, fig. 7) is more clearly pitted behind the ventral muscle field, and conceivably these specimens are not fully mature. Lazarev (1996), followed by Brunton et al. (2000), lumped Inflatiini with Yakovleviinae, which appears to lack posterior central papillation at maturity (Muir-Wood & Cooper 1960, pl. 120, fig. 5, 7), but *Inflatia* and *Yakovlevia* differ considerably in spine distribution and ornament. The relationship is further elaborated under Yakovleviidae (pp. 336 ff), and it is concluded that *Inflatia* is dictyoclostid. Both *Dictyoclostus* and *Inflatia* lack conspicuous external dorsal pits as a rule, but at least some *Inflatia* appear to show posterior central papillation, yet were classed in the "non-shagreen" Yakovleviini. According to present evidence, *Yakovlevia* and its close allies constitute a distinct family within Paucispiniferoidea, characterized by symmetrically disposed strut spines and low marginal ridges. Certainly there are some similarities between *Inflatia* and *Yakovlevia* in shape, length of trail, flat thin visceral disc and to some extent radial ornament, and row of ventral hinge spines, but *Inflatia* has a reticulate disc, not developed in *Yakovlevia* or *Muirwoodia*, and lacks strong strut spines, and has different ventral muscle scars, with wide dendritic adductor imprints and anteriorly placed diductor scars (Gordon et al. 1993) and different anterior papillae internally. It is perhaps significant that Lazarev (2011) omitted any reference to *Inflatia* in elaborating on his previous analyses of early yakovlevin genera.

Apart from being less transverse, *Keokukia* Carter, 1990 externally approaches *Kutorginella*, and it together with *Kelamelia* Zhang Xi-lin in Zhang et al. 1983, pl. 131, fig. 6 was referred to Tribe Retariini by Brunton et al. (2000, p. 474). A row of spines is developed along the ventral hinge. Internally *Keokukia* differs from *Kutorginella* and *Retaria*, and is more dictyoctostid than retariin, with a high posterior hinge ridge in the dorsal valve, subdued marginal ridge and only moderately developed anterior dorsal pustules. *Kelamelia* isless well known, but appears to be close. Small and scattered pits are possibly present over the dorsal exterior, especially trail, of *Keokukia*, but not in figures of*Kelamelia*.

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

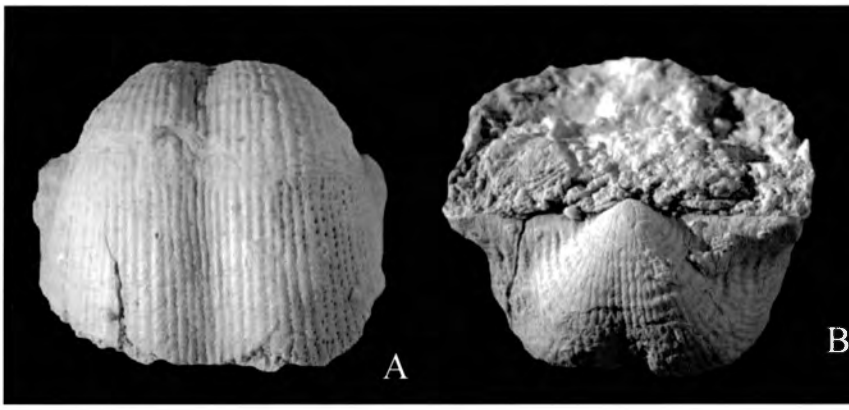


Fig. 5.38. *Inflatia inflata* (McChesney).A, anterior view, BR 3036. B, posterior view showing hinge spines, BR 3033 From Fayetteville Formation (Chesterian), Oklahoma, x1.75. JBW photo.

Genus ***Costaglobus*** new genus

Fig. 5.39

Derivation: costa – rib; globus – globular, Lat.

Type species: *Inflatia engeli* Roberts, 1976, p. 61, from Copeland Road Formation (late Visean), New South Wales, here designated.

Diagnosis: Relatively small and inflated, with usually no or few ventral hinge spines but large pair of spines at cardinalextremities and a few large anterior spines.

Discussion: *Costaglobus* is close to *Inflatia* Muir-Wood & Cooper, 1960, and lacks conspicuous dorsal pits, and internal shell appears to lack posterior central papillation (Roberts 1976, pl. 12, fig. 13, 15, 27, 28). The present genus lacks the well developed row of spines close to the ventral hinge that characterizes *Inflatia*, and instead may have a large spine projecting from the cardinal extremity, and a few spines lie over the flanks and trail, the anterior spines numbering one to six and quite strong. Internally the dorsal valve shows short hinge ridges and usually a well developed alveolus or median slit. The type material is very well preserved, and closely described. Roberts (1976) noted that *Inflatia elegans* Roberts (1964b, pp. 202-204, pl. 2, fig. 1-18) from the underlying fauna differs in having spines along the hinge, finer costae, fewer rugae, a single pair of platform-like ventral adductor scars and brachial ridges which originate almost horizontally from the muscle field, a coarsely pustular internal dorsal trail, and no sign of alveolus or septal slit.

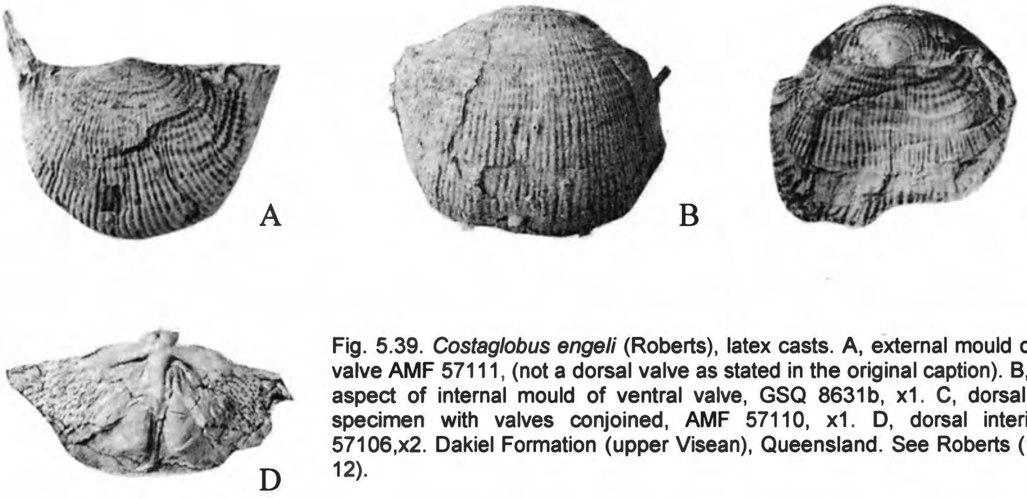


Fig. 5.39. *Costaglobus engeli* (Roberts), latex casts. A, external mould of ventral valve AMF 57111, (not a dorsal valve as stated in the original caption). B, anterior aspect of internal mould of ventral valve, GSQ 8631b, x1. C, dorsal view of specimen with valves conjoined, AMF 57110, x1. D, dorsal interior AMF 57106,x2. Dakiel Formation (upper Visean), Queensland. See Roberts (1976, pl. 12).

Other members of the tribe are close in shape but tend to poorly known. The type species of *Kelamelia* Zhang Zi-xin in Zhang et al. (1983), *K. typica* from the Moscovian of Xinjiang, China, has thin scattered disc and trail spines, and spines close to the hinge, but assessment of such poor material is difficult. It was rated as Retariini by Brunton et al. (2000, p. 473). *Keokukia* Carter, 1990 of lower Visean age in Illinois is better preserved and has a low marginal ridge and what seems to be a coarsely pitted posterior dorsal septum, without alveolus. Spines are few and more slender than in the present genus, but include a hinge row of five spines each side of the umbo, and there are no dorsal spines, and arguably a limited number of small scatteredexternal dorsal pits.

Tribe **LIRAPLECTINI** Chen & Shi, 2000

[Liraplectini Chen & Shi, 2000, p. 329].

Diagnosis: Dorsal ribs finely capillate. No dorsal dimples. Lower Permian (Sakmarian) to Middle Permian (?Wordian).

Genera: *Liraplecta* Jin & Sun, *Dictyoclostoidea* Jin & Hu (syn. ?*Hypolinoproductus* Liang), *Kepingia* Wang & Yang, *Tarimplecta* Chen & Shi.

Discussion: The type species of *Liraplecta* Jin & Sun, 1981 is well preserved and strongly dictyoclostid, but *Tarimplecta* Chen & Shi, 2000 is based on somewhat decorticated specimens with strong costae very like those of *Kunlunia* Wang Zhi, 1983, p. 308, which has been classed as Dictyoclostinae. No capillae are visible in the figures but the text is quite clear that capillae are present in *Tarimplecta*. The presence or absence of posterior central papillation is not known.

Kepingia Wang & Yang, 1998, type species *Costiferina pumila* Wang & Yang, 1993, from the younger Lower Permian of the Tarim Basin, northwest China, was overlooked in the *Revised Brachiopod Treatise*, but has been clarified by Chen & Shi (2006, p. 153), and both valves are capillate.

Genus ***Dictyoclostoidea*** Jin & Hu, 1978

Fig. 5.40, Fig. 5.41

Genus *Dictyoclostoidea* was referred to Schrenkiellinae Lazarev by Brunton et al. (2000, p. 562), but is obviously dictyoclostid with ribs and matching rugae over the disc. A slender ginglymus is developed, and the dorsal ribscarryfine lirae. The type species *Dictyoclostoidea kiangsiensis* Wang & Jin in Wang, Jin & Fang, 1966, p. 437 comes from the Xiaojiangbian Limestone of Jiangxi, central east China, of approximately latest Early Permian and Middle Permian – Kungurian to Wordian – age. Brunton et al. (2000) stated that ventral spines were rare, but one specimen with valves conjoined, as illustrated herein, has numerous fine erect spines over the ventral trail, arising from costellae. There seem to be similar tubercles or spine bases in the Wang & Jin figures of *Dictyoclostoidea*, suggesting that Brunton et al. erred in their diagnosis.

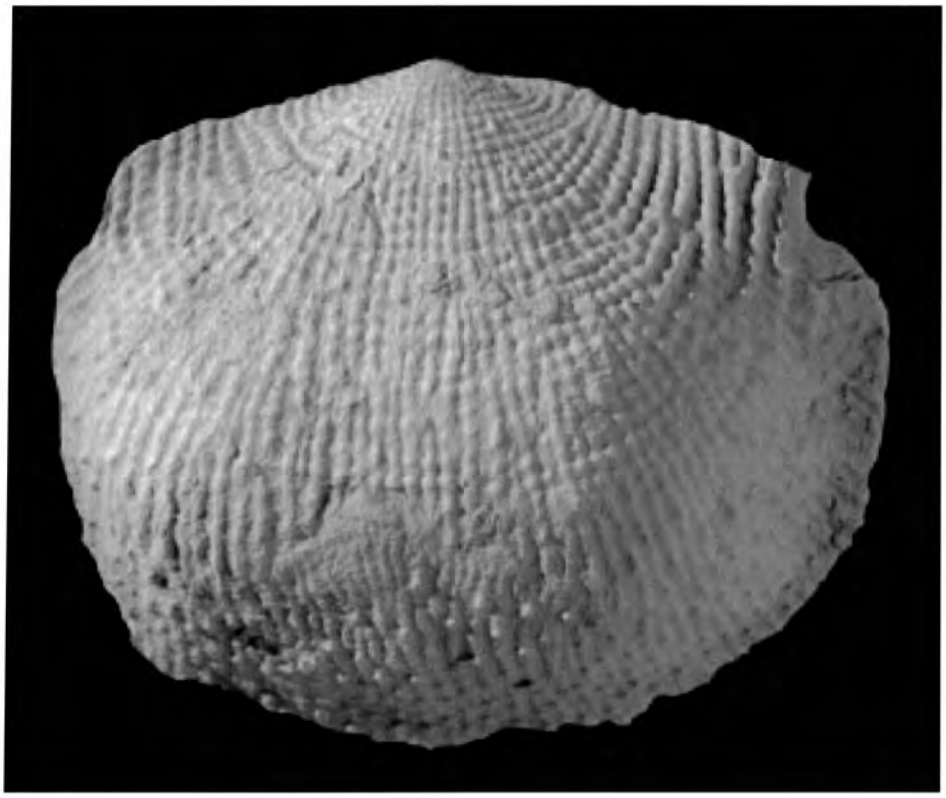


Fig.5.40.*Dictyoclostoidea kiangsiensis* Wang & Jin, ventral aspect of BR 3035 from late Early to Middle Permian of Jiangxi, South China, x2.5. Note anterior spines. JBW photo.

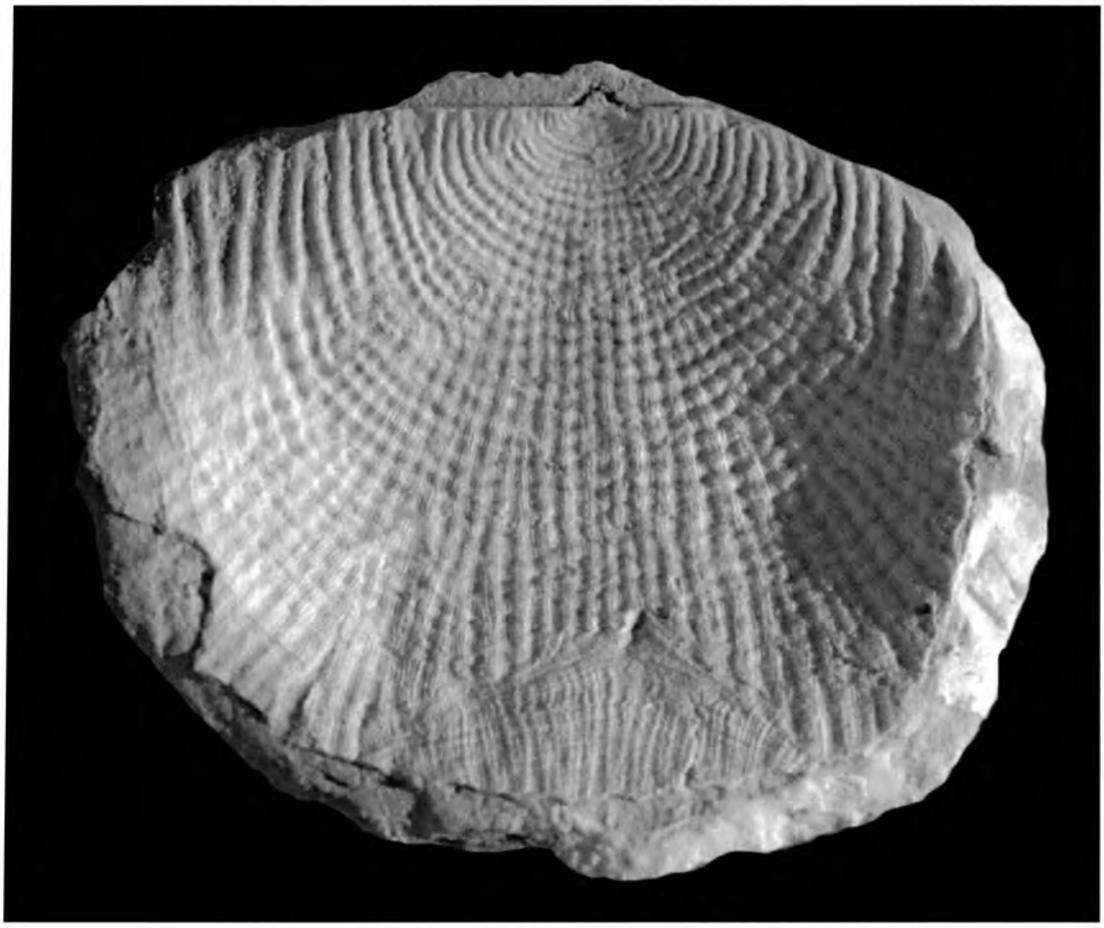


Fig. 5.41. *Dictyoclostoidea kiangsiensis* Wang & Jin, dorsal aspect of BR 3035, x3 approx., to show dorsal capillae. From Jiangxi, South China. JBW photo.

Genus *Hypolinoproductus* Liang, 1982

Fig. 5.42

*Hypolinoproductus*Liang(1982, p. 212, pl. 98, fig. 13-15), based on *H. changxingensis* Liang from the ChihsiaFormation (Sakmarian – Artinskian) of Anhui, China, does not appear to have such spines, even though synonymized with *Dictyoclostoidea* by Brunton et al. (2000, Fig. 397.2e). The trail is moderately long, and capillae over costae are shown in Liang (1990, pl. 98, fig. 15). Low commarginal rugae are developed over both valves. Ribs are coarser and fewer than in *Dictyoclostoidea kiangsiensis*, as also shown in Brunton (2000, Fig. 397.2e, f). Material provided for me by Liao Zhuo-ting is close in other respects (Fig. 5.42), showing a ginglymus and traces of the dorsal capillae over ribs, which supports the synonymy proposed by Brunton et al., and there are obscure signs of numerous ventral spines anteriorly.

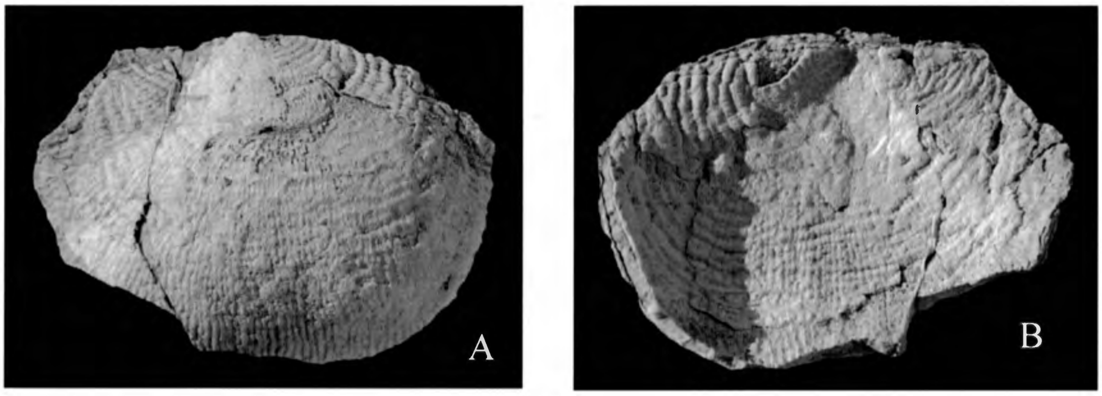


Fig. 5.42. *Hypolinoproductus changxingensis* Liang, ventral and dorsal aspects of BR 3037 from Chihsia Limestone, Anhui, South China, x1.2. There are obscure signs of anterior ventral spines. JBW photo.

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

[Nom. transl. hic ex Labaellidae Kotlyar, Zhakarov & Polubotko, 2004, p. 517].

Diagnosis: Large transverse shells with large ears and fine reticulate ornament. Hinge row of ventral spines, also ear spines and rare body spines, no umbonal slope row of spines, no dorsal pits. Upper Permian (Changhsingian).

Genus: *Labaella* Kotlyar, Zakharov & Polutbotko.

Discussion: Only one genus was assigned to this group, from the Nikitin Formation (Changhsingian) of North Caucasus Mountains, Russia, and it is close to linoproductids in fine ribs and row of hinge spines, but has closely spaced irregular and not very strong commarginal fine rugae over the disc. In some respects the genus looks like Rigrantini (see p. 122), because of the densely reticulate ornament but dorsal pits are lacking from the disc and spinosity differs. Brunton (2007, p. 2644) regarded the genus as a member of Plicatiferini, a Lower Carboniferous overtoniid group, and such an assignment would greatly extend the time range of that tribe. That extension seems unlikely in view of the ornament, which is much less dominated by commarginal rugae compared with Plicatiferini, and Lazarev (2010) regarded the genus as close to *Linoproductus* and *Sublinoproductus*.

Subfamily **RETICULUMIINAE** new subfamily

Name genus: *Reticulumia* new genus from Branch Creek Formation (Visean), Yarrol Basin, Queensland, Australia, here designated.

Diagnosis: Moderately large and reticulate over disc, dorsal valve with pits, ventral spines few, aligned along hinge,rare over disc and trail. Dorsal platform lies in front of cardinal process, leading to medium septum and accessory septa suggestive of anderidia and lateral buttress plates. Lower Carboniferous (lower Visean) to Lower Permian (Asselian).

Genera: *Reticulumia* new genus, *Ozora* Carter, *Retiarisia* new genus, ?*Xinshaoproductus* Tan Zhen-xiu (syn. *Neoyanguania* Shi Xiao-yong), *Niutoushania* Liao, 1984, *Yacotania* new genus.

Discussion: This subfamily is characterized in part by the ventral spines, which form a row along the hinge, but not along the base of the umbonal flanks. Internally, a well developed platform lies at the base of the dorsal cardinal process, and to varying degree projects forward into slender plates like truncated anderidia and lateral buttress plates. Reticulation is weak because commarginals are subdued. Dorsal external pits are well developed over the exterior of the dorsal valve, and a few specimens indicate there were no central papillae in the dorsal valve at maturity. These factors suggest a mix of categories used to discriminate between various dictyoclostid groupings, and it is considered that on the whole the groupfalls closer to Dictyoclostinae than to Reticulatiinae.

In some respects, similarities are shared with *Marginirugus* Sutton, 1938, a widespread genus of similar shape with wide hinge, flattish disc and short trail, and row of hinge spines. There are similar hinge and lateral marginal ridges, similar cardinal process, somewhat similar muscle scars, dense pustulation, lateral buttress mounds, and short ridges over the anterior dorsal disc. *Marginirugus* has closely spaced radial ribs, and displays more ventral spines especially near the start of the trail, and the rugae are weak and irregular, unlike those of *Reticulumia*. Present interpretation, based on shape, ornament and internal detail, is that *Marginirugus* belongs to Linoproductoidea, and is distinguished by its closely spaced rugae and weakly reticulate visceral disc, spines with erect or slightly elongate bases and no dorsal pits.

Xinshaoproductus Tan Zhen-xiu (1986, pp. 433, 442, pl. 1, fig. 5-13) from the basal Lower Carboniferous of Hunan, China, has a well developed row of hinge spines, and numerous other ventral spines: the dorsal exterior was not figured. A well preserved dorsal interior shows well developed lateral buttress plates (pl. 1, fig. 13), and possible plates are developed in the other two figures of the dorsal interior (pl. 1, fig. 11, 12). The genus was placed as a member of Buxtoniini by Brunton et al. (2000, p. 508), but more likely the genus should be placed in Reticulumiini. It is shaped most like *Ozora* Carter, 1990, and is distinguished by its more numerous spines. Figures of the genus are too poor to conclusively show whether the genus is buxtoniid or dictyoclostid.

Genus ***Reticulumia*** new genus

Fig. 5.43

Derivation: reticulum – little net, Lat.

Type species: *Reticulatia cinctifera* Roberts, 1976, p. 71 from the Branch Creek Formation (Bashkirian), Yarrol Basin, Queensland, Australia, here designated.

Diagnosis: Medium-large with wide hinge, shallow disc and short trail, both valves costellate, disc finely reticulate, spines limited to a row along the ventral hinge, scattered small dorsal pits. Lateral buttress mounds developed in front of cardinal process in dorsal valve.

Description: The type species has been described by Roberts (1976) from the Yarrol Basin, Queensland, where it is accompanied by *Levipustula levis* Maxwell, and is also found in northern New South Wales, Australia. The ears are large, and the dorsal valve almost flat, with short trail. Costae are narrow, 13-15 in 10mm at 20mm from the umbo, and 10-12 in 10mm at the anterior margin, increase mostly by branching, and fine commarginal rugae lie over the disc of both valves. Spines are only moderately thick and limited to a row close to the hinge, which bears a ginglymus. What look like anterior spines are suggested in the figure of Roberts (1976, pl. 13, fig. 1) but Roberts was emphatic that only hinge spines were developed. The posterior ventral adductor scars are dendritic, and anterior scars smooth and lineate; the outer dorsal adductors are strongly dendritic, and the anterior adductors smooth and raised. The cardinal process is quadrifid, with deep median cavity in the central shaft. The median septum arises in front of a moderately large smooth mound in front of the cardinal process, and two extended lateral buttress mounds extend obliquely forward, one each side. There are no anderidia. Further detail together with illustrations is provided by Roberts (1976, pl. 13, fig. 1-15).

Discussion: The species is readily distinguished from *Reticulatia* Muir-Wood & Cooper (1960, p. 284), having finer reticulation, a much shorter trail, and spines limited to a hinge row, whereas *Reticulatia* has a row along the umbonal flanks, several spines over the ventral ears, and scattered spines over the visceral disc and trail. Internally there are no buttress mounds in *Reticulatia*, and there are a number of pustules at the anterior disc, unlike the new genus which has a few elongate ridges. The spines, shape and ornament differ from those of the various genera assigned to Dictyoclostidae by Brunton et al. (2000).

One genus that comes close is *Ozora* Carter (1990, Fig. 4, 5) from the Osagean of Missouri, UnitedStates, based on slightly smaller shells with stronger costae and more emphasized reticulation, displaying a row of spines along the hinge and a few anterior erect spines, and a few dorsal pits. The ventral interior is poorly known, but the dorsal interior shows a similar broad rounded platform in front of the cardinal process with septa projecting forward, and a low broad marginal ridge. For both genera the presence of posterior central papillation is not clear, but the American form does display a few coarse pits and seems to have fine pits, and the Australian genus, as represented by the specimen in Roberts (1976, pl. 13, fig. 5, 14) possibly but uncertainly suggests fine posterior central papillation. The dorsal valve bears external pits. *Yacotania* new genus from the early Permian of Bolivia also shares the internal structures, but has stronger commarginal rugae, longer trail and more elongate shell. Ear spines are present and coarser spines moderately numerous over the anterior disc and trail.

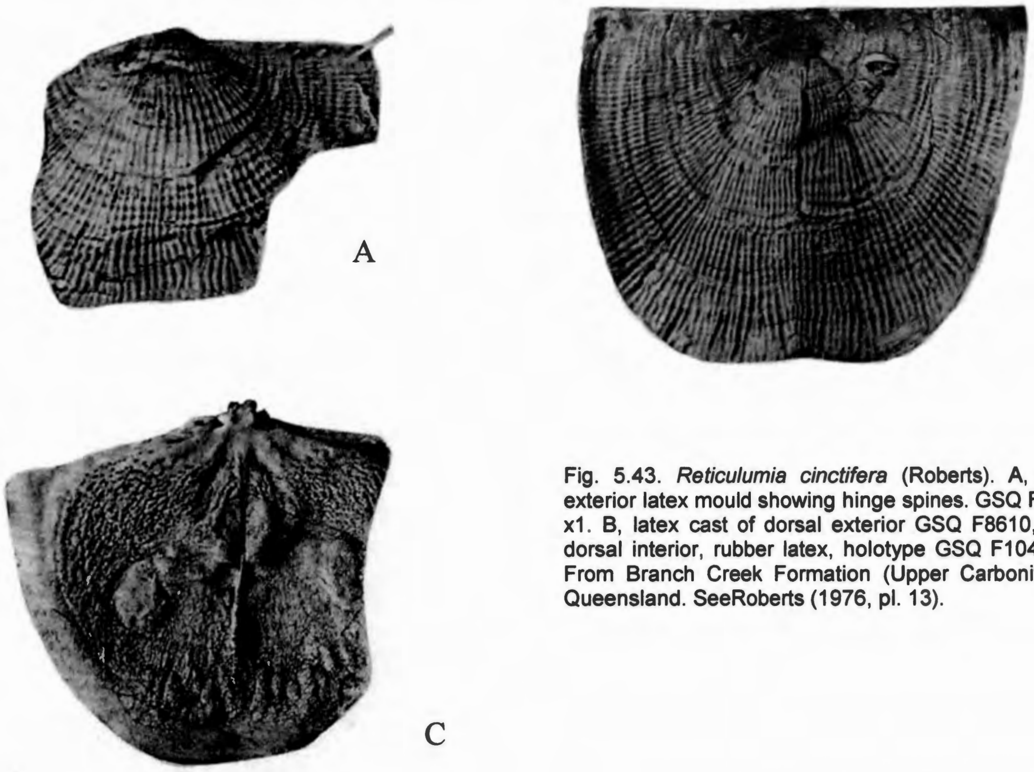


Fig. 5.43. *Reticulumia cinctifera* (Roberts). A, ventral exterior latex mould showing hinge spines. GSQ F8612a, x1. B, latex cast of dorsal exterior GSQ F8610, x1. C, dorsal interior, rubber latex, holotype GSQ F10468, x2. From Branch Creek Formation (Upper Carboniferous), Queensland. SeeRoberts (1976, pl. 13).

Genus ***Retiarisia*** new genus

Derivation: retiarius – a gladiator with a net to entangle the foe, Lat.

Type species: *Dictyoclostus simplex* Campbell, 1957, p. 57 from Watts, Babbinboon (upper Tournaisian), New South Wales, Australia, here designated.

Diagnosis: Small with moderately reticulate pattern over disc, ribs persisting over trail, dorsal commarginal rugae relatively strong. Spines characteristic, limited to ventral valve, none along hinge margins or inner umbonal slopes, relatively large spines arranged at posterior trail in front of cardinal extremity and three to five on anterior trail, as well as rare fine spines arising from costae. No dorsal dimples. Dorsal hinge ridge well developed and may extend across the inner ears. Lateral buttress plates.

Discussion: In *Dictyoclostus* Muir-Wood, 1930, spines form a row near the hinge and may form a patch on the flanks and sometimes a band anteriorly. The present genus lacks hinge spines and inner umbonal slope spines. Lateral buttress plates appear to be developed. *D. vaughani* (Muir-Wood, 1928, pl. 2, fig. 12, 13) from northern Europe was thought by Campbell (1957) to be the closest of British species, but has two rows of spines on the cardinal slopes, and spines lie along the hinge and are numerous over disc and trail. A closer form was believed by Campbell (1957) to be represented by upper Visean forms from Germany, described as *Productus* (*Dictyoclostus*) sp. 2 (see Paeckelmann 1931, pl. 35, fig. 5, pl. 36, fig. 3, 4) and sp. 3 aff. *pugilis* Phillips (Paeckelmann 1931, pl. 36, fig. 5a-d). The German species are externally close, but poorly known internally. *Dictyoclostus paradoxus* Campbell (1957, pl. 13, fig. 9-17) which also belongs to *Retiarisia* was compared by Campbell (1957) with *D. bergicus* Paeckelmann

(1931, pl. 39, fig. 2, 3) from the upper Visean of Rattingen, Germany, but the interior of the German species is not well known.

It was suggested that *Dictyoclostus burlingtonensis* Hall as figured by Weller (1914, p. 104, pl. 9, fig. 1-10) from the upper Tournaisian Burlington Limestone was also similar. This species was later assigned to *Marginatia* Muir-Wood & Cooper (1960, p. 263), type species *Productus fernglenensis* Weller, 1909, p. 299, from the Fern Glen Formation of lower Visean age. Both radial and commarginal ornament are prominent over the ears of both valves in the Australian species, whereas the ears in North American species lack the radial ribs. The Australian genus has rather few ventral spines, and the spines are differently distributed. In *Marginatia*, Muir-Wood & Cooper (1960, p. 263) reported one or two erect spines on the ears, a few in the depression separating the ears from the umbonal slopes, and larger spines over the trail. There is slight swelling of costae in front of the spines. In *Retiarisia*, one or two spines of large diameter, which leave visible signs internally, are present at the posterior end of the trail just in front of each cardinal extremity, and three to five similar spines are present over the anterior trail. Very small spines are scattered over the valve, leaving no internal trace. The descriptions indicate a considerable measure of similarity, with some differences over the distribution of posterior spines. *Marginatia* lacks lateral buttress plates.

Genus **Yacotania** new genus

Fig. 5.44

Derivation: Named from Yaco, Bolivia, source of some of the fossils.

Type species: *Reticulatia globosa* Samtleben, 1971, p. 71 from Copacabana Formation (Asselian), Bolivia, here designated.

Diagnosis: Medium size with closely reticulate visceral disc and moderately long trail; fine spines along the ventral hinge, a few over ears and spines moderately numerous and large over anterior disc and trail, dorsal valve with external pits. Prominent dorsal septum, strong dorsal hinge ridge, lateral buttress plates.

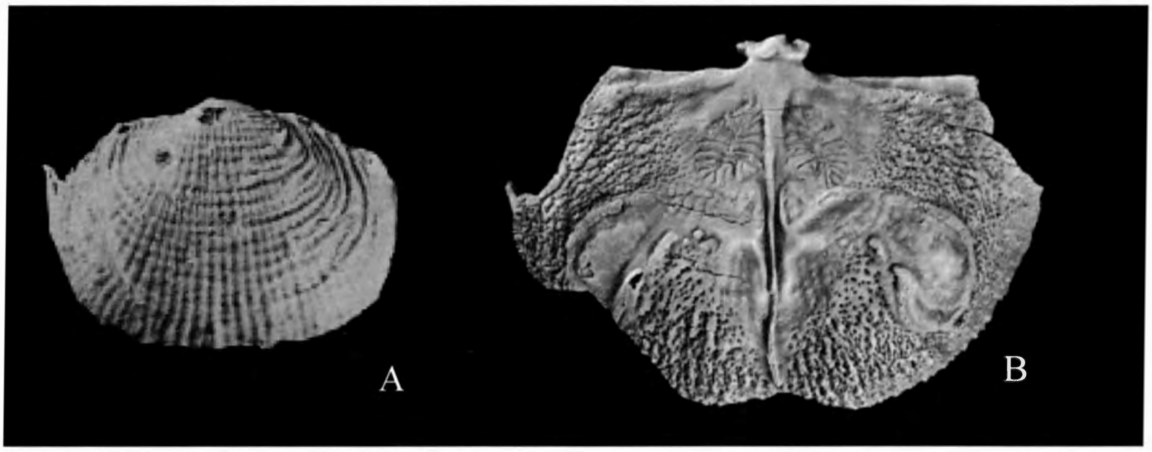


Fig. 5.44. *Yacotania inca* (d'Orbigny). A, ventral valve pe 191 x1.5. B, dorsal valve pe 197, x1.5, from Copacabana Formation, Bolivia. See Samtleben (1971). Photograph B kindly provided by Christian Samtleben.

Discussion: *Yacotania* is much younger than the other two genera of the tribe. The genus is represented by several species in the Early Permian Copacabana Group of Bolivia, including *Reticulatia globosa* Samtleben, *R. oblonga* Samtleben, and *Productus inca* d'Orbigny, 1842, p. 51. The commarginal rugae are stronger, the trail is longer and the shell more elongate than in *Reticulumia* new genus, and ear spines are present and coarser spines moderately numerous over the anterior disc and trail. The dorsal valve has similar lateral buttress mounds and fine anderidia are possibly suggested in *oblonga* Samtleben (1971, pl. 4, fig. 6c), and the cardinal process is basically similar to that of *Reticulumia*, with deep median ventral incision and lateral lobes that become more discrete in some specimens. There are possibly no posterior central papillae in the dorsal valve. *Ozora* Carter is close in that its trail is long and commarginal rugaemore emphasized than in *Reticulumia*, and stouter spines are developed over the ventral ears.

Both *Ozora* and *Reticulumia* have a low marginal ridge around the entire dorsal disc, whereas *Yacotania.* has onlya dorsal hinge ridge.

Genus ***Niutoushania***Liao, 1984

Niutoushania Liao, 1984, p. 281 from the Late Permian Longtan Formation of Anhui, China,was transferred fromDictyoclostiini (Brunton et al. 2000, p. 494, with query) to Tolmatchoffini by Waterhouse (2002b, p. 23), probably an error based on the crinkled nature of ribs in one ventral valve. According to Brunton et al. (2000, p. 494), it supposedly lacks reticulate ornament and spines are limited to the ventral hinge (Liao 1984, p. 281), although Hu Shi-Zhong (1987, pl. 1, fig. 3) figured very fine commarginal rugae over the ventral disc, and slightly stronger rugae over the dorsal disc. Moreover postero-lateral rugae are firmly developed in the orginal types. The presence of dorsal spines and dorsal pits requires clarification, though dorsal spines seem to be absent, and the presence of pits dubious. A single row of hinge spines and rare coarse and fine disc spines are developed, even though Brunton et al. (2000) claimed that spines were limited to the hinge region. The brachial shields and well rounded in outline. A further species was described as *N. chongqingensis* Chen in Chen et al. (2005, p. 355), from the Longtan Formation of Wuchiapingian age in south China. Short lateral buttress plates are present, and the anterior dorsal adductor scars are very slender. But dorsal ornament and posterior exterior of the ventral valve, including the ears, were not described or illustrated.

In ribs and shape the genus is moderately close to *Yacotania* new genus, but anterior and posterior spines are stronger, commarginal ornament less pronounced, and shells more tumid.

Subfamily SPINARELLINAE Waterhouse, 2002b

[Nom. transl. hic ex Spinarellini Waterhouse, 2002b, p. 21.]

Diagnosis: Medium-sized transverse shells with large ears and subdued reticulate ornament. Dorsal valve tends to be gently concave to almost flat, and curves often abruptly into trail. Row of spines inclined forward laterally from the ventral hinge, and scattered other ventral spines, no umbonal slope row of spines and no dorsal spines or external dorsal pits. Hinge ridge well developed, marginal ridges low or not developed, long dorsal median septum, anterior dorsal pustules moderately numerous. Cardinal process trifid and short.

Tribe **SPINARELLINI** Waterhouse, 2002b

[Spinarellini Waterhouse, 2002b, p. 21. Syn. Rugatiini Lazarev, 2011, p. 30].

Diagnosis: Medium-sized transverse shells with large ears and subdued reticulate ornament, no dorsal spines. Row of ventral spines near hinge, and scattered other ventral spines. Hinge ridge well developed, marginal ridges low or not developed, long dorsal median septum, anterior dorsal pustules moderately numerous. Cardinal process short. Lower Permian (Asselian) to Middle Permian (Roadian).

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

Discussion: This embraces a subset of genera reported from the Early to Middle Permian of United States. *Spinarella* Cooper & Grant, 1975, type species *S. perfecta* Cooper & Grant, has a row of spines in front of the ventral hinge, spines becomingprogressively stronger laterally, other ventral body spines, weak costation, depressed ventral adductor scars and sessile inconspicuous cardinal process.There is no umbonal slope row of spines. Additional ear spines are found in the type species only according to Cooper & Grant, but also appear to be present in S. *paulula* Cooper & Grant (1975, see pl. 379, fig. 4). *Xestosia* Cooper & Grant has a more dictyoclostid cardinal process and adductor scars, and more and larger ear spines. *Rugatia* Muir-Wood & Cooper, 1960 has a tuft of ear-spines and strong costae, and the visceral disc is comparatively thick (see Cooper & Grant 1975, pl. 374, fig. 1). *Nudauris* Stehli, 1954 is characterized by its thick and thin ribs, especially over the ventral trail, and moderate sparse spines. Cooper & Grant (1975) have added numerous additional points of difference and similarities between the genera in question. Various specimens show small dorsal external pits, yet other specimens show none, amongst the excellent figures provided by Cooper & Grant (1975). Therefore the significance of the external pits is open to question, at least amongst Spinarellini, and implies that the criterion may be of less than prime value in related groups.

The posterior mature dorsal valve of *Nudauris*, as figured by Cooper & Grant (1975, pl. 370, fig. 17, pl. 371, fig. 12) carries short shallow grooves, as if to suggest an unusual form of posterior central papillation, but the appearance could be due to an artifact of silicification. The posterior region in front of the short cardinal process in *Spinarella* appears to be possibly pustulose and pitted (Cooper & Grant 1975, pl. 380, fig. 14, 17, pl. 381, fig. 7), although detail is not strikingly clear. For *Rugatia*, lines are developed over the posterior median septum in front of the cardinal process in Cooper & Grant (1975, pl. 374, fig. 17), but otherwise this part is shown as smooth in Cooper & Grant (1975, pl. 374, fig. 14, pl. 375, fig. 12, pl. 376, fig. 2, pl. 377, fig. 42, 46).

Amongst this galaxy of species and genera, *Nudauris linospina* Cooper & Grant (1975, p. 1069, pl. 368, fig. 1-29, pl. 369, fig. 21-29, pl. 410, fig. 1-8) from the Cathedral Mountain Formation of west Texas stands out as dissonant with the description, for the posterior ventral valve bears two posterior rows of erect spines, thickening and inclined forward from the hinge laterally (Cooper & Grant1975, pl. 368, fig. 16, 18, 22, pl. 369, fig. 26, 29), though more obscure on the holotype (pl. 368, fig. 25, 28), which seems to have a few additional ear spines. Even though the text insisted on the presence of only one row, there are two rows, which mark a strong distinction. *Xestosia schucherti* (King) and *X. obsolescens* Cooper & Grant are closest in this regard, having more of a cluster of ear spines, without the two well formed rows diverging from the hinge. In the elevated dorsal adductors and sunken myophore of the cardinal process, the species *linospina*approaches *Xestosia*.

Rugatia was referred to Dictyoclostinae by Brunton et al. (2000, p. 496),and*Spinarella, Xestosia* and *Nudauris* were placed in Paucispiniferini (p. 447), but they lack strut spines and have low marginal ridges, and are interpreted as dictyoclostid, distinguished by small size, transverse outline and subdued ornament as a rule, although some species have strongly reticulate ornament posteriorly, and others show strong ribbing especially over the trail. The dorsal pustules over much of the floor of the valve, apart from a band of coarser pustules around the start of the trail, are fine and dense, reminiscent of those in horridoniids and dictyoclostids. Lazarev (1990, p. 81) referred *Nudauris, Spinarella* and *Xestosia* to Jiguliconchinae Lazarev, 1990, a subfamily synonymized with Paucispiniferini by Brunton et al. (2000, p. 443). *Jiguliconcha* Lazarev, 1990 is poorly known, with no figured dorsal exterior or ventral interior, but appears marginiferid, with its small ears and marginiferid spine distribution and a few large anterior dorsal pustules. Later Lazarev (2011) assigned the very same genera to his Tribe Rugatiini new. He argued for descent from Plicatiferinae, which he placed in Family Productellidae. But ornament and shape reinforced by age point to a dictyoclostid association, as indicated by the posterior reticulate ornament well shown for *Nudauris diabloensis* Stehli (Cooper & Grant 1975, pl. 372, fig.10, 18) or *N. enigmatica* Cooper & Grant (1975, pl. 371, fig. 5, 8), or *Rugatia mckeei* Cooper & Grant (1975, pl. 376, fig. 6, 10) and *Spinarella paulula* Cooper & Grant (1975, pl. 379, fig. 4, 5, 15) or *S. lobata* Cooper & Grant (1975, pl. 381, fig. 22, 23), with a number of other examples. These show that the ribs and rugae are fainter than in *Dictyoclostus* or *Reticulatia*, but modified from such patterns, and papillation and cardinal process are close to aspects of Dictyoclostidae and allied in the nature of muscle scars (see Cooper & Grant 1975, pl. 374, fig. 14, 17), and simple median dorsal septum, broad in front of the cardinal process. Throughout their text, Cooper & Grant (1975) indicated various dictyoclostiform features for each genus.

Of other groups proposed amongst dictyoclostiform genera, Rigrantiini Lazarev, 2000b, p. 28 is close, with *Rigrantia* especially close in shape apart from slightly smaller ears. The reticulate ornament is more strongly developed in *Rigrantia*, and pits are conspicuous on the dorsal valve – whereas these are weak or lacking from Spinarellini. There is a row of spines at the base of the ventral flanks, and spines become very thick and arise from a prominent ridge in *Rigrantia*. No ridge or umbonal flank row of spines is developed in Spinarellini, whereas Inflatiini Sarytcheva has a row of spines near the ventral hinge, and arguably lacks external dorsal pits as a rule, and shells are more elongate: they tend to be Carboniferous and are more widespread, whereas Spinarellini are restricted to the Permian of North America.

Genus ***Bilinospina*** new genus

Fig. 5.45

Derivation: bi – two; lino – aligned; spina – thorn, Lat.

Type species: *Nudauris linospina* Cooper & Grant (1975, p. 1069) from Cathedral Mountain Formation (Kungurian) ofGlass Mountains, Texas, here designated.

Diagnosis: Subquadrate shells with fine ribbing, faint posteriorly, commarginal rugae over posterior slopes, and discobscurely reticulate, ventral spines form two distinct rows inclined forward laterally from hinge and a few extra spines on outer ears, strongest furthest from umbo, other large halteroid spines on trail, body spines fine.

Discussion: The vental adductor platform is raised, and diductor scars narrow and elongate. The cardinal process is broad and very low, and dorsal adductors strongly dendritic although little raised. In *Xestosia*, closest of allied genera, the ventral adductors are only slightly raised, and the diductor scars described as flabellate and striate. Cooper & Grant (1975, p. 1064) noted the degree of similarity between *linospina* and *Xestosia*, but stressed the much greater width of species of *Xestosia*, and noted that the posterior spine patterns differed, although *linospina* has two rows of posterior spines, not just the one reported in their description. Figures of *Xestosia* variously show one row of spines near the hinge, traces of a very fine second row, and a cluster of ear spines, especially fine in *X. schucherti* (King). Two distinct rows of stronger spines in *linospina*traverse the ears for most of their width, arising close to the umbo.

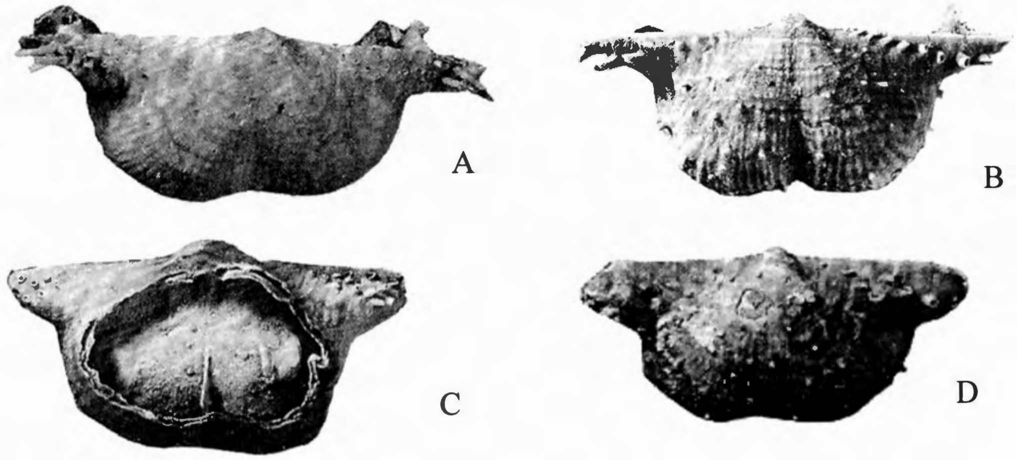


Fig. 5.45. A, *Xestosia obsolescens* Cooper & Grant, ventral aspect of holotype, USNM 148861b from Cathedral Mountain Formation (Kungurian), x 1.2. B, *Nudauris diabloensis* Stehli, ventral aspect of USNM 152748a, Bone Spring Formation (Kungurian), x 1. C, D, *Bilinospina linospina* (Cooper & Grant), ventral aspect of USNM 153982b and 148856c, Cathedral Mountain Formation (Kungurian), x1.2. From United States, see Cooper & Grant (1975, pl. 368, 369, 372, 382).

Tribe **CHAOIELLINI** Lazarev, 2011

[Tribe Chaoiellini Lazarev, 2011, p. 28].

Diagnosis: Weakly transverse shells with subdued radial ribs and weak commarginal rugae, row of spines close to ventral hinge, not becoming strong laterally, and spines as strong over trail. Corpus cavity varies from low to high in different genera. Upper Carboniferous (Serpukhovian or lowermost Bashkirian) to Lower Permian (Artinskian).

Genera: *Chaoiella* Fredericks, *Altaiproductus* Lazarev, *Tityrophoria* Waterhouse (syn. *Alpavlia* Lazarev).

Discussion: *Chaoiella* Fredericks was included in Dictyoclostinae by Brunton et al. (2000, p. 489), but Lazarev (2011) pointed out that costation took a different form, and was weaker, together with commarginal ornament. He included with a query the genus *Rugoclostus* Easton, 1962, not a well known genus, and placed for some reason that must remain totally obscure in Horridoniini by Brunton et al. (2000, p. 480). But *Rugoclostus* does not show a strongly developed row of spines close to the ventral hinge, and with relatively small ears and moderately strong commarginal rugae over the disc, may at best be a highly deviant member of Chaoiellini. The genus is, pending clarification, placed as ashrivelled member of Retariiinae. *Praehorridonia* Ustritsky was also included in Chaoiellini by Lazarev (2011), but is regarded as Horridoniidae, given its usually elongate outline, and apparent lack of posterior hinge ridge (Ustritsky & Chernyak 1963, pl. 18, fig. 7, pl. 21, fig. 5). Members of Chaoiellini are comparatively close to Spinarellini, which have more prominent posterior spines especially strong on the ears, and on some forms stronger ribs on the trail. The body corpus is more slender, and diductor scars are placed at almost the same distance from the hinge as the adductor scars, a point emphasized by Lazarev (2011), but similar dispositions of ventral muscle scars are observable in many Productoidea, including *Retaria, Kutorginella, Thuleproductus, Antiquatonia* etc. Papillae are distinctly finer and more numerous at the start of the trail than in members of Chaoiellini. The gently concave dorsal disc, and longitudinal profile of many genera classed as Productoidea are close to features of

Chaoiella and allies. Shallow and scattered pits may be present over the dorsal exterior in *Chaoiella*, but are not strongly developed, and there is no well developed row of spines along the umbonal slopes.

Genus ***Tityrophoria***Waterhouse, 1971a

Type species: *Tityrophoria nelsoni* Waterhouse, 1971a, p. 214 from upper Jungle Creek Formation (Artinskian), Yukon Territory, Canada.

Diagnosis: Shells with spines largely limited to row close to ventral hinge, may be large along outer hinge, genus further distinguished by presence of fine radial costellae, especially over ventral valve.

Discussion: The spines in this genus are limited to the ventral hinge, with a few over the anterior ventral valve, as well shown in the original description and figures (Waterhouse 1971, pl. 25, fig. 12, 13), reinforced by a diagram in Shi & Waterhouse (1996, Fig. 30A). Ribbing is fine and consistent over both valves (Waterhouse 1971, pl. 25, fig. 12, 13, 14; Shi & Waterhouse 1996, pl. 15, fig. 1, 3). Internal pustulation and dorsal interior are well shown inWaterhouse (1971, pl. 25, fig. 10, 11, 15) and Shi & Waterhouse added clear information of the posterior hinge ridge and ventral musculature. Brunton et al. (2000, p. 483) claimed that dorsal spines were rare or absent in *Tityrophoria*, but no specimen is known to have dorsal spines. The type species is found in Sakmarian and Artinskian deposits of the Jungle Creek Formation. In a Late Carboniferous species from Canada, the hinge row of spines is stronger, and the surface is similarly marked by fine ribbing, especially prominent on the ventral valve; anterior plicae also appear. In its fine costellae, *Tityrophoria* shows some approach to *Nudauris* Stehli and allies of the Spinarellini Waterhouse, which have ventral spines, including an umbonal slope row, and spines that are not excessively robust, and ears are large, and the corpus slender.

Lazarev (2011) evaluated *Tityrophoria* as a member of Chaoiellini. He noted that *Tityrophoria* has five spines each side of the umbo compared with three in *Chaoiella* (in fact the number varies up to eight or more), and that the posterior row was more steeply inclined forward from the hinge in *Chaoiella*, and indicated that anterior trail spines were possibly thicker than the last spines on the ears in *Chaoiella*, and this observation is reinforced byadditional Canadian material. Commarginal ornament is more marked in *Chaoiella*, but is present, although slightly variable and often subfusc in *Tityrophoria*. One particular aspect that requires attention lies in the apparent variation displayed by the disposition of the ventral muscle scars. Shi & Waterhouse (1996, pl. 15, fig. 2, Fig. 30C) illustrated narrow long adductor scars with rounded diductor scars well in front of most of the adductors. But another specimen shows an adductor platform that extends almost as far forward as the anterior diductor scars (Shi & Waterhouse 1996, pl. 15, fig. 5). Similar variation is displayed in material described below as a new species.

Tityrophoria zimmermani new species

Fig. 5.46 – Fig. 5.50, Fig. 5.52

Derivation: Named for Ray Zimmerman.

Holotype: GSC 133300, figured as Fig. 5.52A, B from Member A (Gzhelian), Jungle Creek Formation, Canada, here designated.

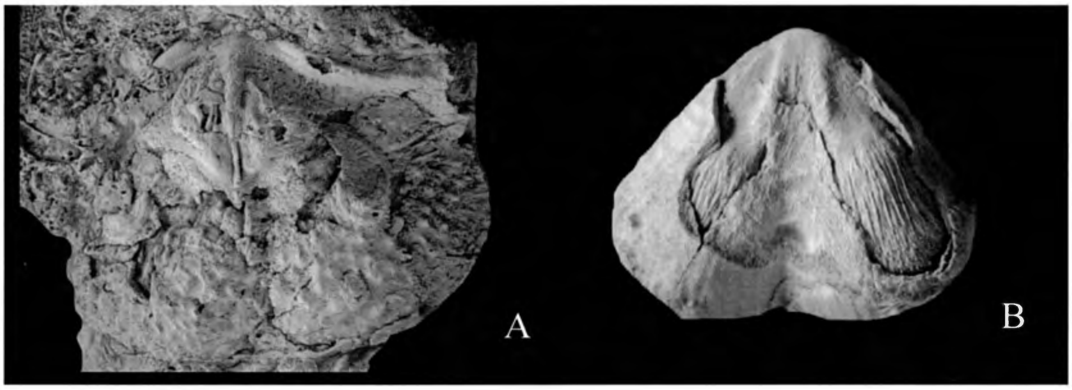


Fig.5.46. *Tityrophoria zimmermani* new species. A, dorsal interior, GSC 136044, x1.5. B, internal mould of ventral valve GSC 136045, x2. From Member A (Gzhelian), Jungle Creek Formation, Canada. JBW photo.

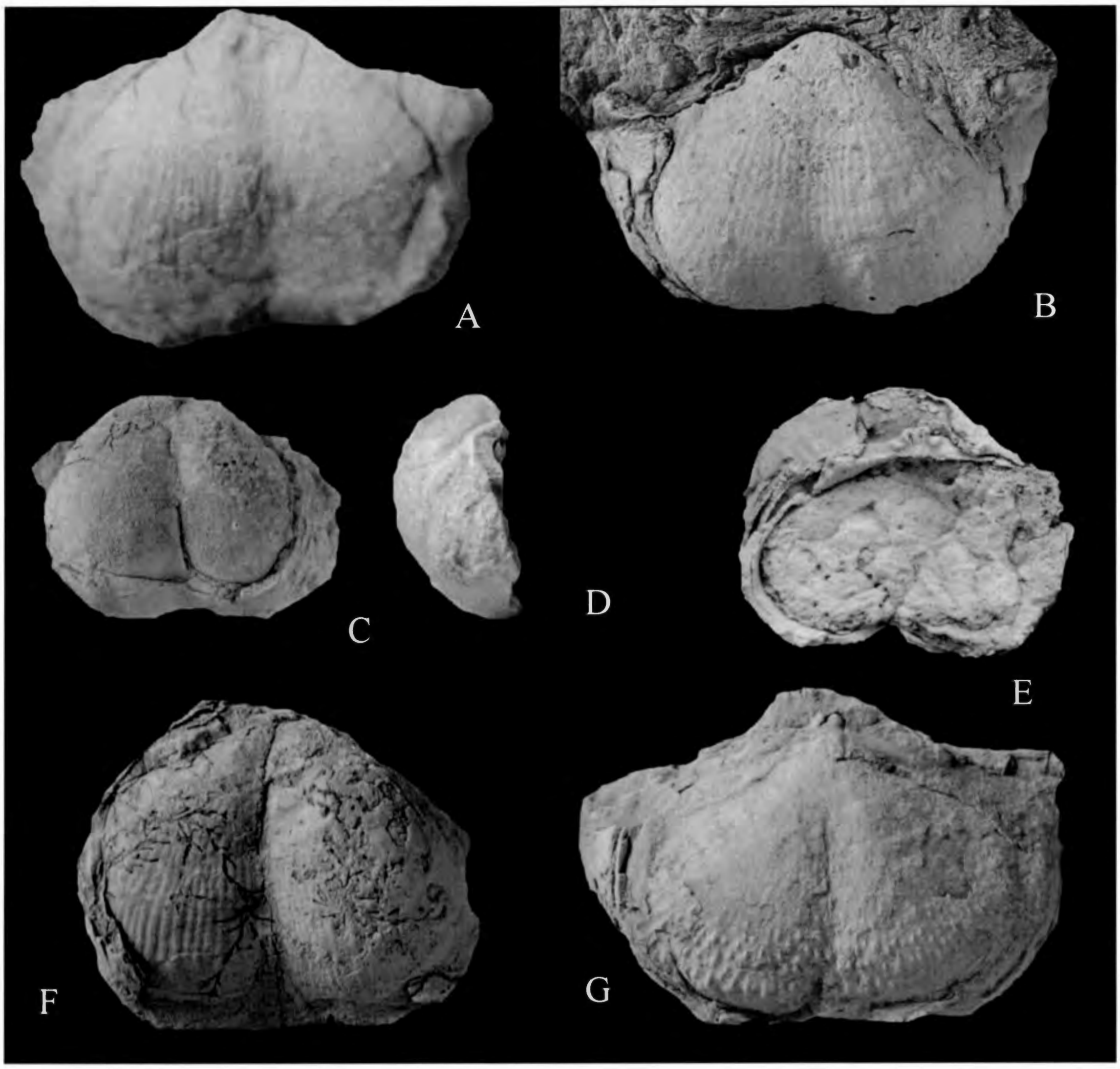


Fig. 5.47. *Tityrophoria zimmermani* new species. A, ventral valve, largely internal mould, GSC133291, x1.3. B, ventral valve GSC 133293, x1.3. C, D, ventral and lateral aspects ofGSC 136042, x1. E, dorsal aspect of specimen with valves conjoined, GSC 133390, x1.F, dorsal interior of GSC 133287, x1.5. G, decorticated dorsal valve with surrounding ventral valve, GSC 136041, x0.9.From Member A (Gzhelian), Jungle Creek Formation, Ogilvie Mountains, Yukon Territory, Canada. JBW photo.

Diagnosis: Moderately large with thick visceral disc, spines form a row along the ventral hinge, scattered and few over the remainder of the ventral valve. Ribs low and even, six in 5mm anteriorly.

Material: Some twenty ventral valves, one dorsal valve and ten specimens with valves conjoined from Member A (Gzhelian), lower Jungle Creek Formation, Ogilvie Mountains, Yukon Territory, Canada. See Appendix A, part C, p. 478.

Dimensions in mm:

Specimen GSC	Width	Length	Height	
133300	47	34	19	holotype
133291	46	35	19	
136041	52	36	17	
133248	54	35	23	
136047	55	32	23	

Description: Moderately large transverse shells with thick visceral disc. Ventral umbo incurved, umbonal angle close to 90°, steep but not extremely high umbonal walls and large gently convex ears with obtuse cardinal extremities, broken short in many specimens, but placed at maximum width; the shell is also wide near the anterior third of the shell length. A well formed ventral sulcus commences a little in front of the umbo and widens at 20°, with subangular or more rarely trench-like median trough, and gently convex lateral walls. The dorsal valve is gently concave over the disc, with large concave ears, and is subgeniculate, curving steeply into a moderately long trail that as preserved is usually half the length of the visceral disc, but in well preserved more complete specimens is as long as the disc. The fold commences mid-disc or in front over the trail, and remains low, and scarcely visible in some specimens. Ventral spines form a row that passes obliquely forward over the ears from the hinge, with individual outer spines more than 1.8mm in diameter. A few fine or strong spines up to 1.8 mm in diameter lie over the ventral disc and trail, but there are also finer spines less than 1mm thick anteriorly. A few radial rugae are developed anteriorly on some specimens, as well as weakly differentiated concentric bands. The dorsal valve has no spines. Ribs are low and even, numbering six in 5mm anteriorly on the ventral valve, commencing within 2-3mm of the umbonal tip, and five in 5mm on the dorsal valve: the ribs become subdued on large specimens towards the anterior margin. No ribs on ears, which are either smooth in some specimens or bear low commarginal wrinkles in others, and ribs often missing from umbonal flanks. Pustulation is not clear, because the shell has been silicified and the surface possibly worn, so that although pustules appear, they may not reflect the true nature of the original exterior.

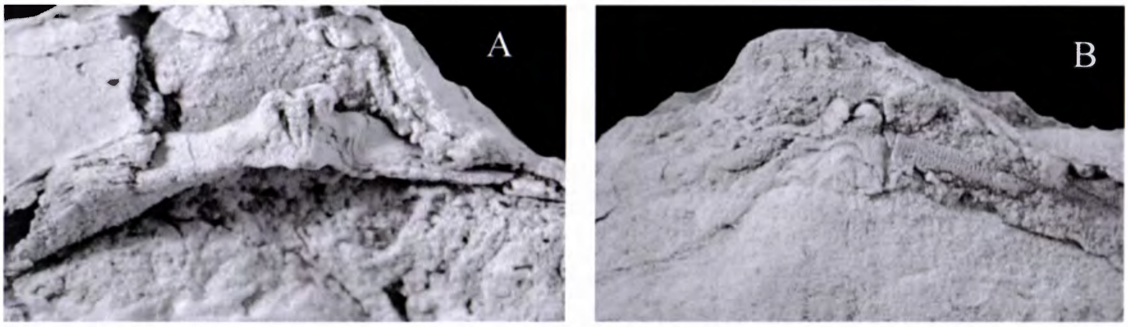


Fig. 5.48. *Tityrophoria zimmermani* new species. A, external aspect of cardinal process, GSC 133290, x3. (See Fig. 5.47E). B, dorsal aspect of cardinal process, GSC 136041, x2.5. (See Fig. 5.47G). From Member A (Gzhelian), Jungle Creek Formation, Ogilvie Mountains, Yukon Territory, Canada. JBW photo.

Fig. 5.49. *Tityrophoria zimmermani* new species, ventral valve GSC 133298, x1.5 from Member A (Gzhelian), lower Jungle Creek Formation, Ogilvie Mountains, Yukon Territory, Canada, x1. JBW photo.

The ventral adductor platform is high and elongate, and diductor scars strongly grooved. In one specimen the diductor scars commence in front of the adductors, but in another the two pair lie side by side. Papillae over the floor of the valve are fine and even. The cardinal process lies in the plane of the commissure and has a deep cleft on the ventral side, with two broad lateral lobes, and two deep dorsal clefts: there is no zygidium. The median lobe from a dorsal aspect is convex, and shows a slit nearer the base in one specimen, but the slit is missing from another shell. The median septum is sturdy posteriorly and extends for three quarters of the disc length in a fully mature specimen, for less than half the length of the disc in an immature specimen, and for nearly two thirds of the length in a specimen at early maturity. Dorsal adductor scars are large, not highly raised, somewhat tear-shaped, and largely smooth at immaturity into early maturity, and become highly raised, with somewhat dendritic outer posterior division and irregular but semi-smooth inner anterior portion. Brachial shields are well defined at maturity, and a stout posterior ridge extends along the hinge, but in a less mature specimen the brachial shields lie further from the median septum. Only low fine papillae lie over most of the floor at early maturity, with a band of stouter pustules at the start of the trail, curving hingewards to meet the anterior dorsal septum. Papillae are large and slightly elongate at maturity in the anterior band, numbering four or five irregular rows, and the trail bears finer pustules. The ventral shell is 2mm thick under the sulcal crests, and may be thinner anteriorly; the dorsal shell is as thick, though thin over the ears.

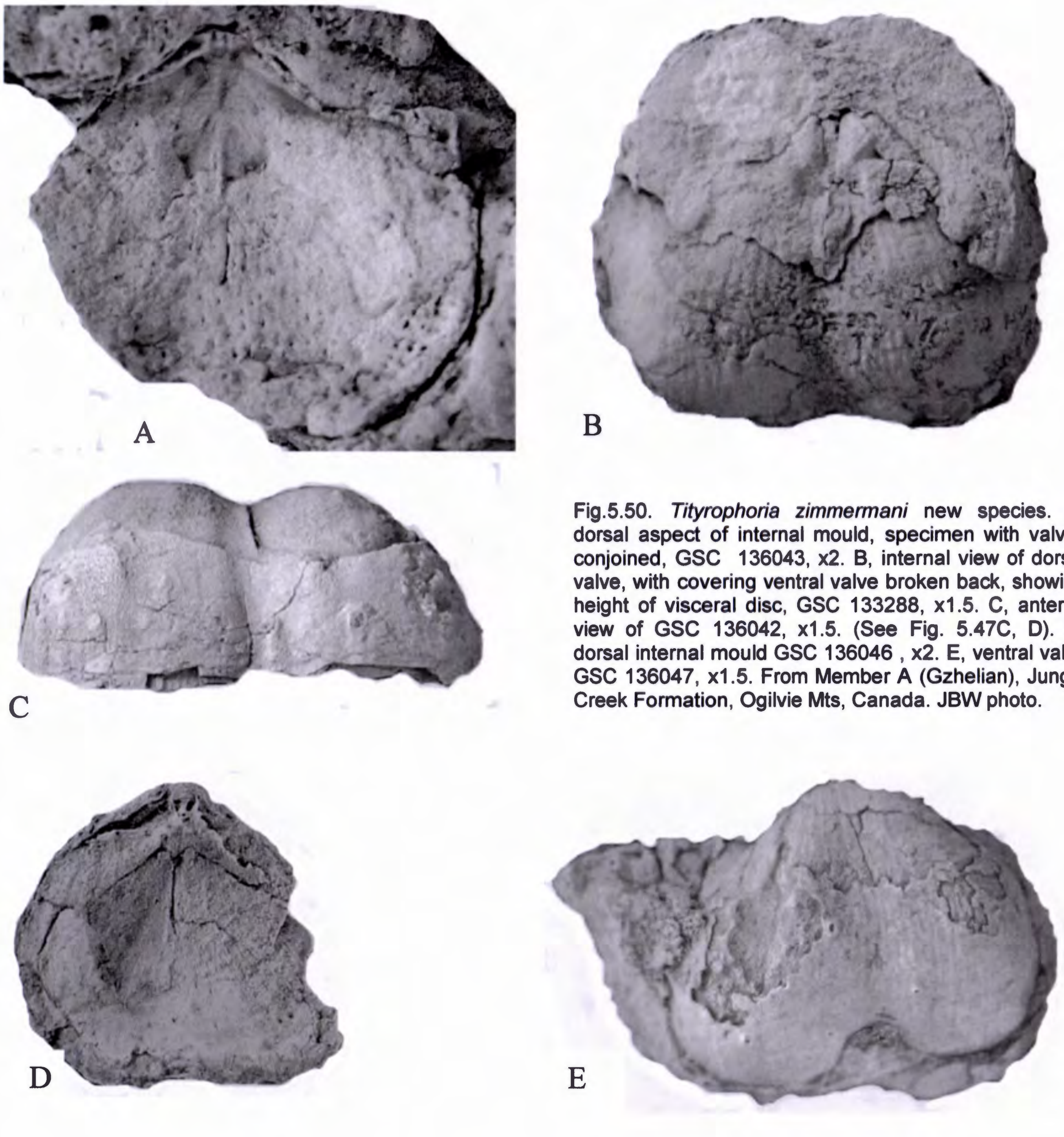


Fig.5.50. *Tityrophoria zimmermani* new species. A, dorsal aspect of internal mould, specimen with valves conjoined, GSC 136043, x2. B, internal view of dorsal valve, with covering ventral valve broken back, showing height of visceral disc, GSC 133288, x1.5. C, anterior view of GSC 136042, x1.5. (See Fig. 5.47C, D). D, dorsal internal mould GSC 136046 , x2. E, ventral valve GSC 136047, x1.5. From Member A (Gzhelian), Jungle Creek Formation, Ogilvie Mts, Canada. JBW photo.

Resemblances: This species is characterized by wide shell and ears of moderate size (usually incomplete because they are broken laterally), well formed ribs and by having a single row of spines along the ventral hinge, with the disc

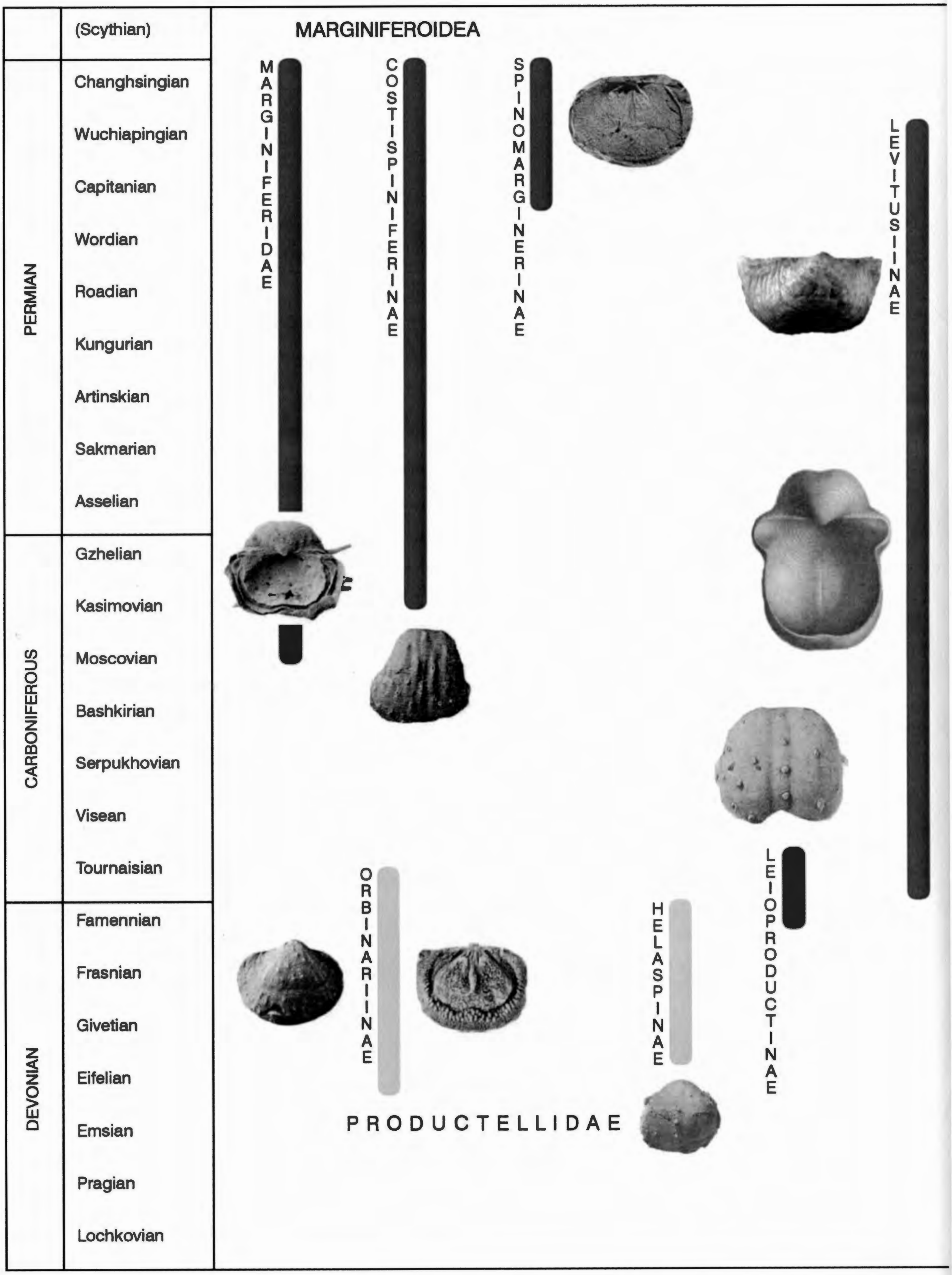
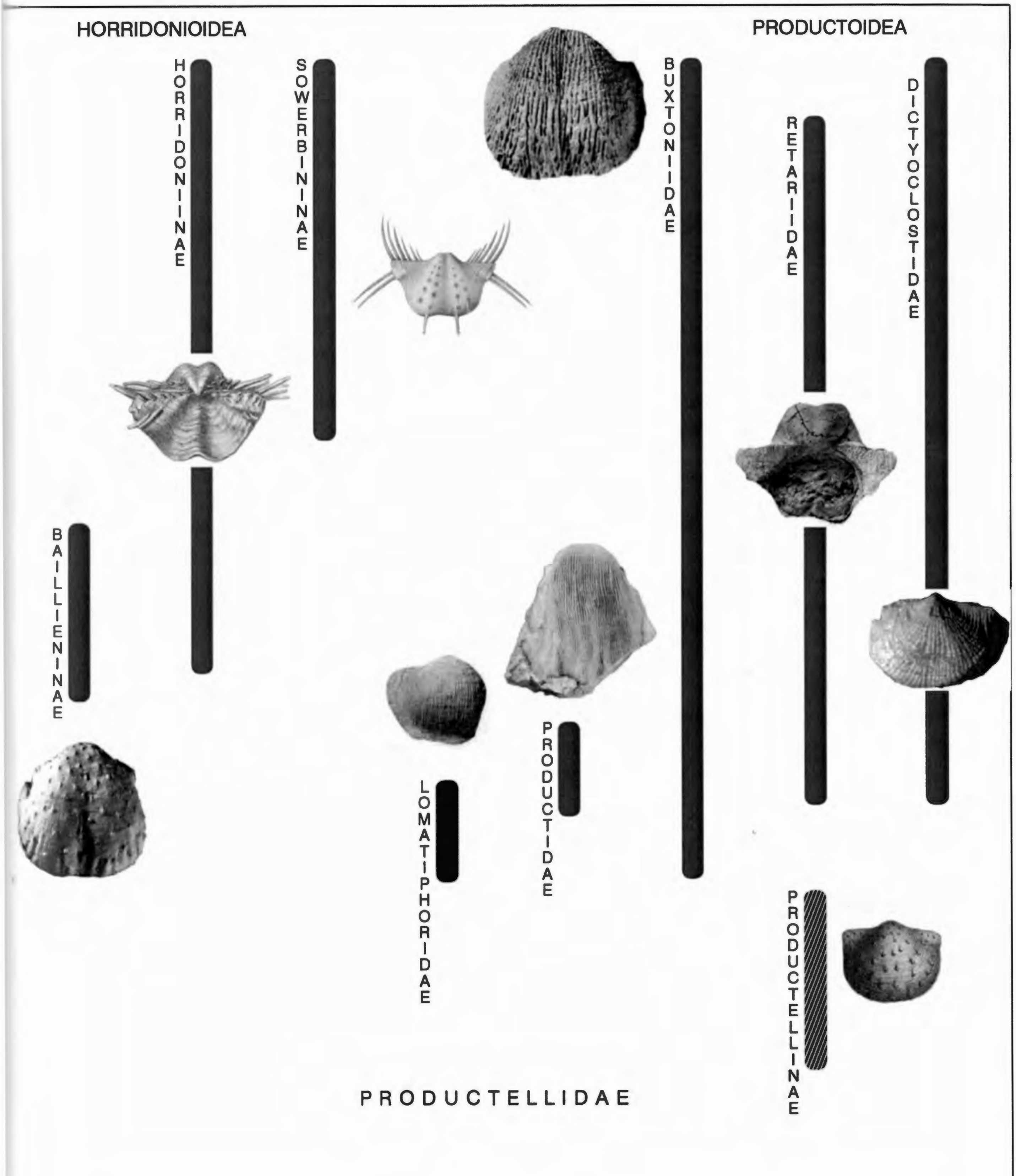


Fig. 5.51. Major constituent groups of Superfamily Productelloidea and their descendent superfamilies Marginiferodea, HForridonioidea and Productoidea.


HORRIDONIOIDEA
PRODUCTOIDEA
HORRIDONIINAE
SOWERBININAE
BUXTONIIDAE
RETARIIDAE
DICTYOCLOSTIDAE
BAILLIENINAE
PRODUCTIDAE
LOMATIPHORIDAE
PRODUCTELLINAE
PRODUCTELLIDAE

marked by costellae, reinforced anteriorly by coarse subplicae. *Tityrophoria nelsoni* Waterhouse in Bamber & Waterhouse (1971, pl. 25, fig. 1-11; Shi & Waterhouse 1996, p. 91, pl. 14, fig. 22-26, pl. 15, fig. 1-8, text-fig. 30; Brunton et al. 2000, Fig. 323.3a-c) from higher members in the Jungle Creek Formation of northern Canada is smaller with narrower ribs and finer hinge spines and better defined ventral sulcus.

Horridonia geniculata Gobbett (1964, p. 97, pl. 10, fig. 5-7) has a row of ventral hinge spines and has fine radial threads and anterior rugations. Only two ventral valves were available, and no dorsal valves known. The species comes from the Cora Limestone of Bear island. The radials of Gobbett's species are slightly finer than in the Canadian species. Unfortunately many details remain unknown, but provisionally the species is regarded as belonging to *Tityrophoria*.

The species described as *Alpavlia gzheliensis*by Lazarev (2011, pl. 4, fig. 1-13) from Gzhelian of theMoscow Basin in Russia is moderately close, but has wider ears, with ventral costae commencing a little further from the beak, and ventral hinge row of spines that slopes slightly more forward laterally from the hinge. The median septum is consistently long and brachial shields lie well away from the mid-line. There are various additional differences, arguably specific rather than generic.

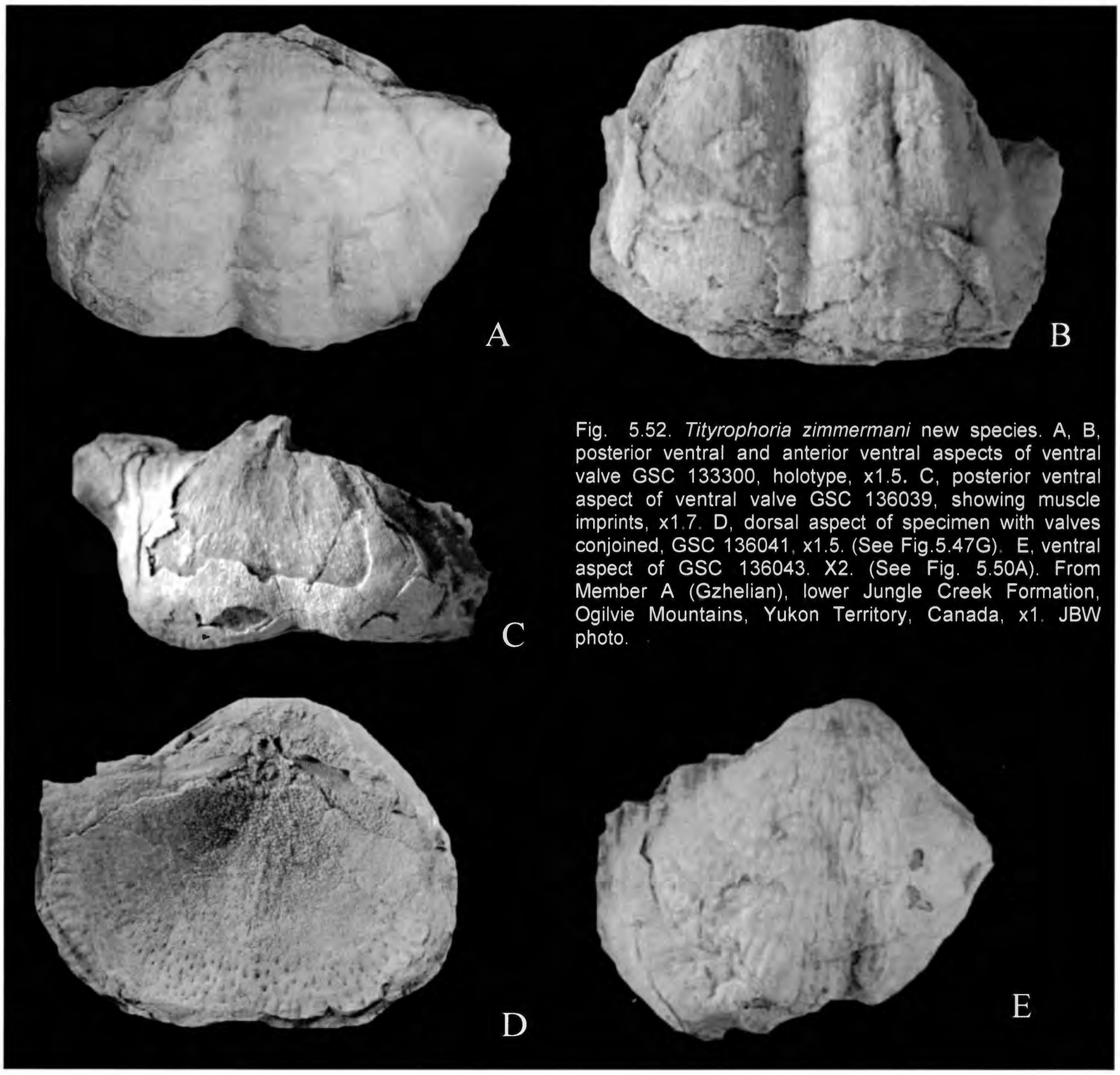


Fig. 5.52. *Tityrophoria zimmermani* new species. A, B, posterior ventral and anterior ventral aspects of ventral valve GSC 133300, holotype, x1.5. C, posterior ventral aspect of ventral valve GSC 136039, showing muscle imprints, x1.7. D, dorsal aspect of specimen with valves conjoined, GSC 136041, x1.5. (See Fig.5.47G). E, ventral aspect of GSC 136043. X2. (See Fig. 5.50A). From Member A (Gzhelian), lower Jungle Creek Formation, Ogilvie Mountains, Yukon Territory, Canada, x1. JBW photo.

6. Superfamily ECHINOCONCHOIDEA Stehli, 1954

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

Taxonomy: Brunton et al. (2000) attributed the elevation in rank to Brunton et al. (1995, p. 928).

Diagnosis: Spines numerous and fine over both valves, commonly in commarginal bands, may be varied in diameter but not strongly halteroid, rhizoid or strut, no radial ribs. Maximum width in front of hinge, posterior dorsal septum may be cleft, adductors dendritic, marginal ridges low, dorsal endospines seldom very large but may be crowded.

Discussion: Understanding of the evolutionary course followed by this superfamily is refined from the scheme advocated by Lazarev (1987) and Brunton et al. (2000). In their model, the earliest family was Sentosiidae McKellar, ornamented by fine even spines, which gave rise to Echinoconchidae with spine bands, and included Waagenoconchini with little banding and spines of mainly one or two diameters as a rule. The genus *Laminatia* Muir-Wood & Cooper, 1960 has spine bands as in Echinochonchinae, but was included in Sentosiidae. Of uppermost Famennian age, it presumably was interpreted as a forerunner of echinoconchs, but not in the path of direct ancestry – it was a deviant sentosiid. But herein, as in Waterhouse (2002b), the genus is classed as Echinoconchidae, which extends the range of the subfamily from upper Visean into late Devonian, much the same age as the supposedly oldest Sentosiinae. A closely related new genus *Praelaminatia* has similar laminae, but has only a single row of spines along each lamination. The two genera appear to indicate likely sources for the slightly younger ordinary echinoconchs, in which laminae have morphed into spinose commargons, and adductor scars have become more dendritic, and whether *Praelaminatia* arose from Sentosiinae is not at present clear, although it seems likely, because there are subfusc laminae in *Sentosia*. In addition, the interpretation of Caucasiproductinae Lazarev is altered. The two genera *Caucasiproductus* and *Praewaagenoconcha* particularly characteristic of this subfamily are strophalosiiform with interareas, teeth and sockets, and short lateral ridges that diverge anteriorly, but critically, no cicatrix. The ventral spines are moderately spaced and erect, approaching the fine and crowded and prostrate spines of Sentosiinae. These caucasiproductin genera are not similar to Sentosiinae other than in ornament, and their inclusion as a subfamily within Sentosiidae is rejected. They are classed as Productelloidea, as a full family distinguished from Productellidae through the presence of numerous dorsal spines, and distinguished from even early Strophalosiidina by the lack of a ventral umbonal cicatrix. The fossil record, if interpreted from a morphogenic temporal ie. morphochronic basis, shows that there were several separate streams: Waagenoconchidae, starting in Tournaisian and perhaps arising through *Praewaagenoconcha* (Famennian, or late Devonian) of Caucasiproductidae, which was also possible source or near-source of Pustulinae (Tournaisian); Sentosiidae, starting in Famenian, from the strophalosioid *Caucasiproductus* of Middle Devonian (Givetian) age, and Echinoconchidae, from *Laminatia* and *Praelaminatia* (upper Famennian), without any obvious progenitor at generic level, but close to Sentosiidae.

- **Family Echinoconchidae Stehli, 1954**
  - Subfamily Echinoconchinae Stehli, 1954
    - Tribe Echinoconchini Stehli, 1954
    - Tribe Karavankinini Ramovš, 1969
  - Subfamily Juresaniinae Muir-Wood & Cooper, 1960
    - Tribe Juresaniini Muir-Wood & Cooper, 1960
    - Tribe Bathymyoniini Lazarev, 1990
  - Subfamily Septariniinae new subfamily
    - Tribe Septariniini new tribe
    - Tribe Alatoproductini new tribe
- **Family Sentosiidae McKellar, 1970**
  - Subfamily Sentosiinae McKellar, 1970
  - Subfamily Bagrasiinae Nalivkin, 1979
  - Subfamily Tubersulculinae Waterhouse, 1971
    - Tribe Tubersulculcini Waterhouse, 1971
    - Tribe Lethamiini Waterhouse, 2001
  - Subfamily Stictozosterinae Waterhouse, 2002b
- **Family Waagenoconchidae Muir-Wood & Cooper, 1960**
  - Subfamily Waagenoconchinae Muir-Wood & Cooper, 1960
    - Tribe Waagenoconchini Muir-Wood & Cooper, 1960
    - Tribe Wimanoconchini new tribe
  - Subfamily Pustulinae Waterhouse, 1981

Table 8. Superfamily Echinoconchoidea Stehli, 1954.

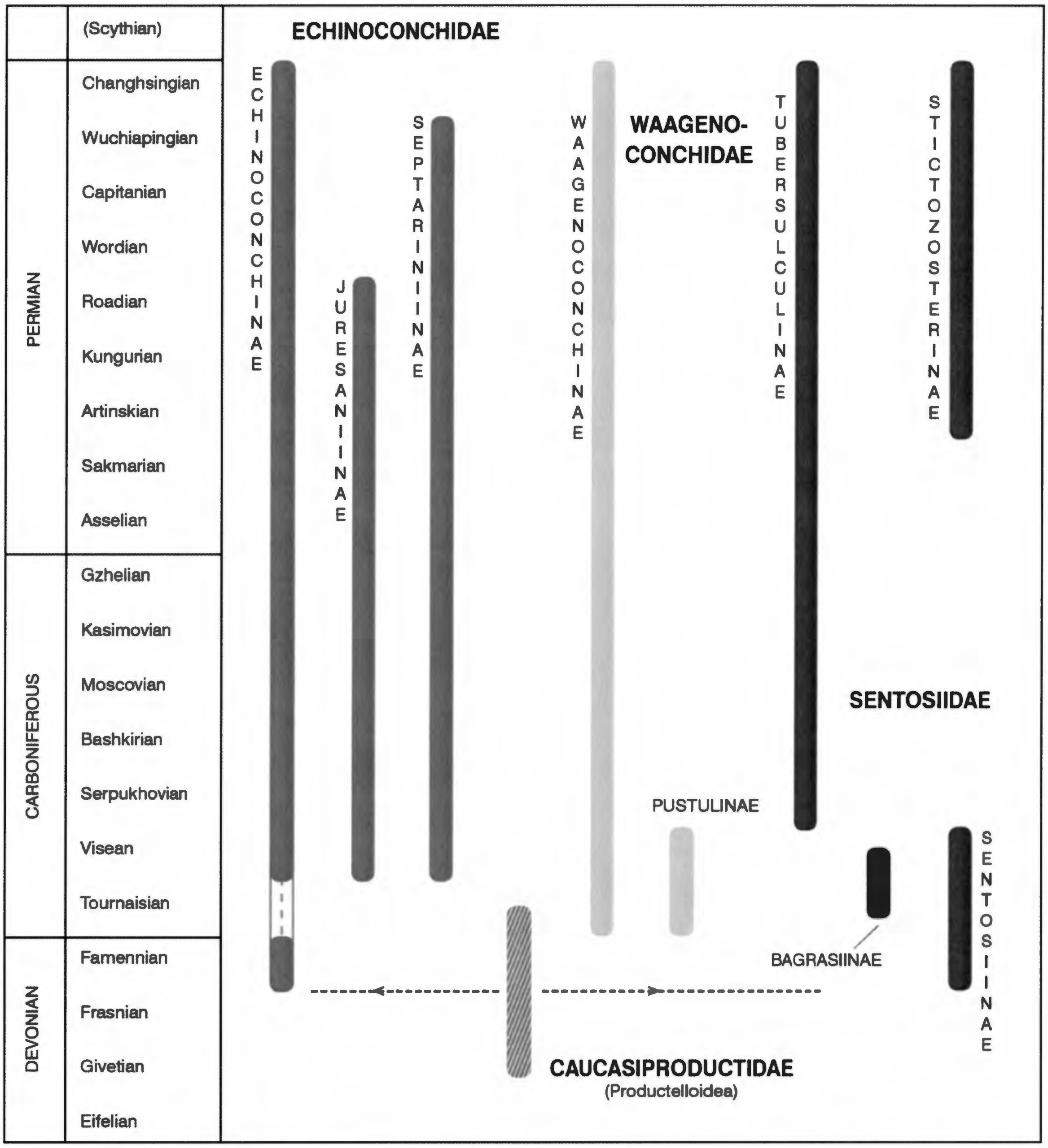


Fig. 6.1. Range chart for Superfamily Echinoconchoidea. Although a comparatively large superfamily with numerous genera and infrafamily groupings, change centred on a few kinds of limited distributions in spine patterns, and the spines remained subuniform, or distinguished as only two series, and as a rule covered both valves, varying only a little in being erect or prostrate, with short elongate bases. Little in the way of rugae was developed, but some groups displayed short smooth strips of shell between spine bands, and commargons were developed widely. Any form of ribbing or radial plication was extremely limited. The anterior margin remained simple, and some later forms even reduced or lost the trail. Internally the morphology was also nothing out of the ordinary, apart from *Stepanoconchus*, which developed two long plates in the dorsal valve, presumably for muscle supports.

It may seem dubious that so many sources are indicated for what are believed to be closely related members within a single superfamily, although that is the pattern which emerges from study of the species and genera in Productidina, Strophalosiidina and Linoproductidina. It is certainly not point-source evolution, but an ongoing divergence and proliferation that proceeded from closely related sources in similar directions.

Family **ECHINOCONCHIDAE** Stehli, 1954

[Echinoconchidae Stehli, 1954, p. 326].

Diagnosis: Planoconvex profile, short dorsal trail, spines slender and erect to recumbent, in commarginal bands. Corpus cavity generally deep.

Subfamily **ECHINOCONCHINAE** Stehli, 1954

[Nom. transl. Muir-Wood & Cooper, 1960, p. 243, ex Echinoconchidae Stehli, 1954, p. 326].

Diagnosis: Spines erect, differentiated in size as a rule, no buttress plates or cardinal pit.

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, smooth posteriorly, spines differentiated in size along narrow concentric bands called commargons, thicker in a few spine rows posteriorly and thin in rows anteriorly over each commargon, often subprostrate. Lower Carboniferous (upper Visean) to Lower Permian (Artinskian), with Upper Devonian (Famennian) forebears.

Genera: *Echinoconchus* Weller, *Calliprotonia* Muir-Wood & Cooper, *Echinaria* Muir-Wood & Cooper, *Laminatia* Muir-Wood & Cooper, *Praelaminatia* new genus, *Stepanoconchus* Lazarev, *Uraloconchus* 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: it is synonymized with Echinoconchini. *Laminatia* is included on the basis of its similar ornament with two series of spines in laminate commargons over both valves (Muir-Wood & Cooper 1960, p. 189, pl. 41, fig. 1-14), though it should be noted that dorsal ornament is not as differentiated as in *Echinoconchus* and other allies, and unlike some but not all other Echinoconchini it has non-dendritic dorsal adductor scars, as in Sentosiidae. *Laminatia* is of Upper Devonian (upper Famennian) age, and was assigned by Brunton et al. (2000, p. 522) to Sentosiinae, which has simple spines and bands.

Uraloconchus Lazarev, 1990, based on *Productus jakovlevi* Tschernyschew (1902, pp. 300, 633, pl. 56, fig. 17-19) is close to the stictozosterin genus *Markhamia* Jin & Shi (see p. 192) and was placed in synonymy with this genus by Brunton et al. 2000, p. 522, but has more numerous spines, as confirmed by a detailed illustration in Lazarev (1990, pl. 25, fig. 8a), in which one commargon bears a row of broader spines behind one to three rows of finer spines, or even more, and bands of smooth shell. *Stepanoconchus* Lazarev has high dorsal muscle supports, as discussed on p. 267.

Several genera within Sentosiinae have fine spines on both valves and a tendency for commarginal lamination, and so would seem to be the most likely source for giving rise to *Laminatia*, although little older. But the discovery of a new genus *Praelaminatia* indicates a more complicated history. *Praelaminatia* has only one series of spines, arranged in commarginal rows, one per ventral lamellum, and would seem to have been precursor to *Laminatia*, by later developing an additional series of finer spines. That would in turn could imply an origin segregated from *Sentosia*, *Waagenoconcha* and *Spinauris* etc. There is little detailed stratigraphic support as yet for this model, and some might prefer to regard *Praelaminatia* as a later, simplified descendent from *Laminatia*.

Genus ***Praelaminatia*** new genus

Fig. 6.2

Derivation: prae – before, in front of, Lat.; Laminatia – genus name.

Type species: *Laminatia jacki* McKellar, 1970, p. 34 from Star beds (now Myrtlevale Formation, Famennian), Burdekin Basin, Queensland, Australia, here designated. See Appendix A, part A, p. 477.

Diagnosis: Small, ventral spines subprostrate, aligned in single rows each over a lamination, subuniform, dorsal valve laminate, with similar or slightly finer spines.

Discussion: The type species was described and figured by McKellar (1970, pl. 7, fig. 1-13) from the younger Famennian faunas west of Collinsville, Queensland, Australia. The valves are covered by slightly overlapping laminae, and laterally directed spines lie in a row close to the ventral hinge, some six each side of the umbo. Each lamination is crossed by short spine ridges, which terminate each in a fine almost prostrate spine. A single spine row also lies close to the cardinal margin of the dorsal valve, and spines and ridges are developed over the valve. There is no differentiated trail, the cardinal process is bilobate, and dorsal adductor scars are smooth and not divided into anterior and posterior pair. *Laminatia salebrosa* Martynova (1970, pl. 3, fig. 9-12) from the Famennian Munar beds of central Kazakhstan appears to be somewhat similar. According to Martynova (1970), recesses on the dorsal valve correspond with "pustules" (=ridges?) of the ventral valve, and thin oblique spines emerge from the anterior margin of the laminae, between the recesses. This is not exactly the same as but is close to the dorsal ornament of *Praelaminatia jacki*, in which the dorsal spine bases cross each lamination and project from the anterior edge of each lamination.

This genus is very close to *Laminatia* Muir-Wood & Cooper, 1960 from the upper Devonian Box Member in the Percha Formation of New Mexico and Chafee Formation of Oklahoma, United States, in size, laminate valves and bifid cardinal process. But two series of spines are developed on each valve of *Laminatia*, whereas only one series is developed on the two valves of *Praelaminatia*. Muir-Wood & Cooper reported a small cicatrix on some specimens of *Laminatia*, but no cicatrix is visible in any of the specimens of *Praelaminatia* or figured *Laminatia*.

Fig. 6.2. *Praelaminatia jacki* (McKellar). A, dorsal exterior, latex cast of GSQ F 11558, x 4. B, ventral internal mould, GSQ F 11556, x 6. C, latex cast of dorsal interior, GSQ F 11560, x 6. From Myrtlevale Formation (Famennian), Queensland, Australia. See McKellar (1970, pl. 7).

Genus ***Calliprotonia*** Muir-Wood & Cooper, 1960

Type species: *Calliprotonia renfrarum* Muir-Wood & Cooper, 1960, p. 247 from the Finis Shale (Upper Pennsylvanian), Texas, United States.

Diagnosis: Small to median in size, spines of two sizes over concentric bands on each valve, tend to be uniform posteriorly and anteriorly on shell, marginal ridge high.

Discussion: The spinose ornament is more complex on a new Canadian species than in the type form, and varies also in another Canadian species described by Shi & Waterhouse (1996).

Calliprotonia mclareni new species

Fig. 6.3, Fig. 6.4

Derivation: Named for Digby J. McLaren.

Holotype: GSC 133333 figured herein as Fig. 6.3A, Fig. 6.4A, from Member D (Asselian), Jungle Creek Formation, here designated.

Diagnosis: Ventral valve with shallow or no anterior sulcus and low anterior dorsal fold. Three rows of coarse spines as a rule and two or three up to five rows of fine spines over each commarginal band.

Material: Mostly single ventral valves, three dorsal valves and a specimen with valves conjoined, Member D, lower Jungle Creek Formation, Ogilvie Mountains, Yukon Territory, Canada. See Appendix A, part C, p. 478.

Description: Shells small, subquadrate in outline with broad ventral umbo and small ears with obtuse cardinal extremities. Ventral valve holotype GSC 133333 measures 28mm in width, 22mm in length, and 14mm in height. The venter is gently rounded with no sulcus, or very weakly sulcate. The dorsal valve is comparatively flat, with weakly differentiated ears, and gently concave disc which becomes broadly and gently convex anteriorly, and the lateral and anterior shell curves steeply at right angles, to form a subgeniculate trail. The ventral valve is crossed by a series of concentric bands separated by growth-stops, and posteriorly each of these bear crowded fine erect spines in three or four rows, and over most of the shell there are some three or rows rows of erect spines, six to seven in 5mm, arranged in rows and fairly regularly in quincunx, and slightly inclined forward with traces of faint posterior bases; the anterior part of each commargon, about 1mm across, bears a further three or more rows of much finer spines. Anteriorly the spine pattern may be less regular, and this part of the shell in some specimens has single rows of

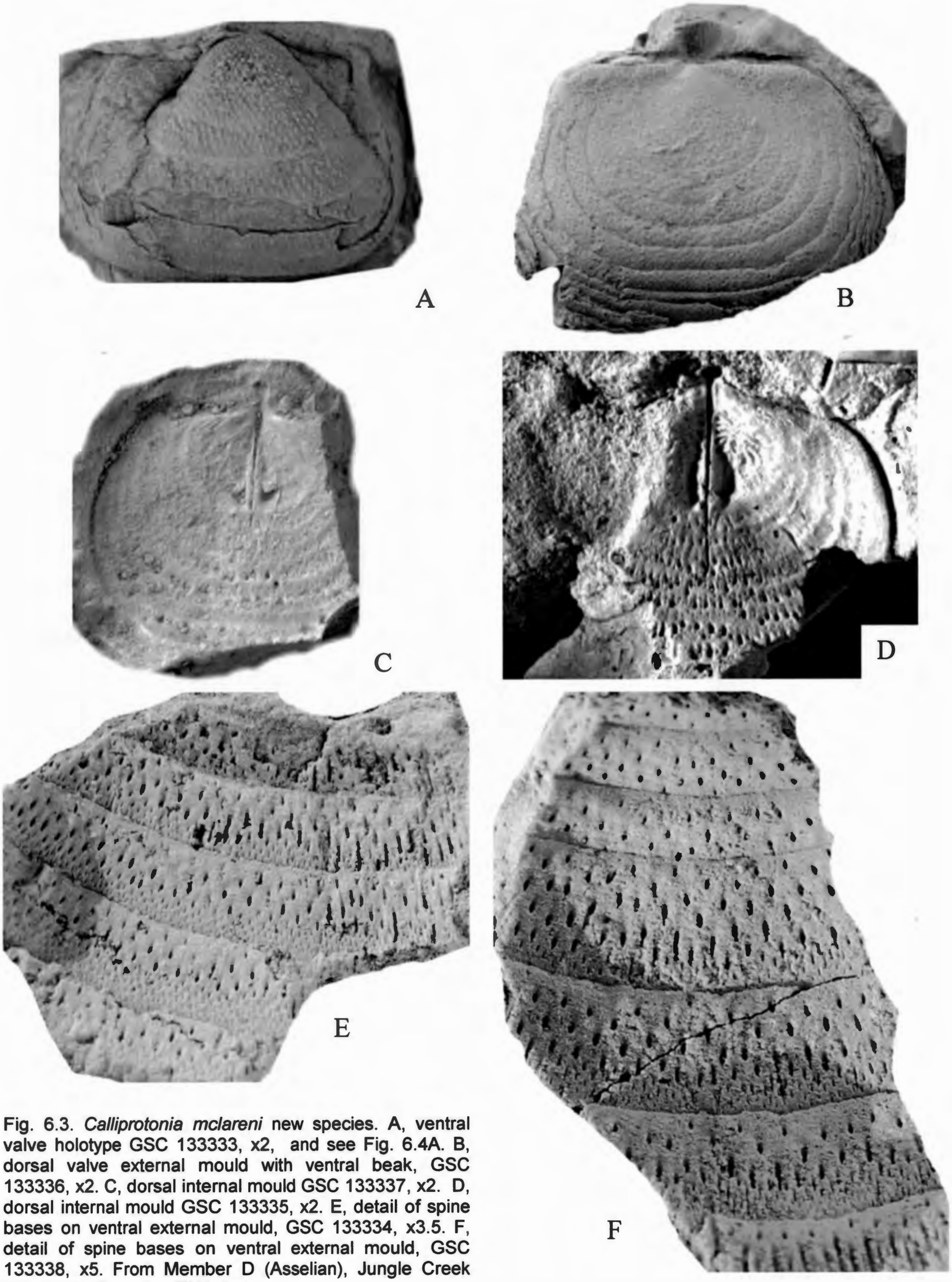


Fig. 6.3. *Calliprotonia mclareni* new species. A, ventral valve holotype GSC 133333, x2, and see Fig. 6.4A. B, dorsal valve external mould with ventral beak, GSC 133336, x2. C, dorsal internal mould GSC 133337, x2. D, dorsal internal mould GSC 133335, x2. E, detail of spine bases on ventral external mould, GSC 133334, x3.5. F, detail of spine bases on ventral external mould, GSC 133338, x5. From Member D (Asselian), Jungle Creek Formation, Canada. JBW photo.

coarse spines, or fewer rows of coarser spines and none or only few fine spines; rarely fine spine bases are interspersed with the coarser spines. On the dorsal valve the posterior nepionic shell is convex with evenly spaced fine erect spines, and the concentric bands bear fairly uniform spines close in size to the coarser series on the ventral valve, and anterior commargons bear spines in two or three rows posteriorly and three to five rows of finer spines anteriorly. The anterior bands are usually ornamented only by growth lines, and are narrow, less than 1mm across. Very fine spines appear anteriorly on one or two bands, and the outermost band carries no spines in one specimen.

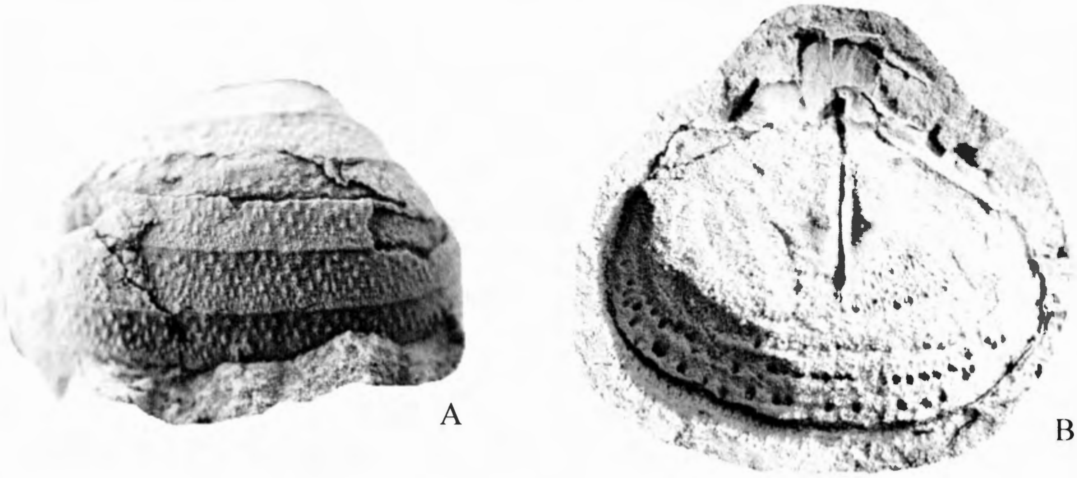


Fig. 6.4. *Calliprotonia mclareni* new species. A, anterior ventral valve GSC 133333, holotype. (See Fig. 6.3A). B, dorsal view of internal mould of specimen with valves conjoined, GSC 133339. Specimens x2, from Member A (Asselian), Jungle Creek Formation, Yukon Territory, Canada. JBW photo.

The ventral interior is poorly known, with small and weakly delineated muscle scars, and floor pitted by pustules that reflect the external bands and spines. The dorsal valve has a low shafted cardinal process and medium septum extending just past half length of the shell in one specimen but much longer in another. Posterior adductors are dendritic and small, and anterior tear-shaped adductors are marked by low growth lines parallel to the anterior margin. In a more mature specimen the posterior adductors are very narrow and comparatively smooth and the anterior adductors weakly dendritic. The posterior floor is closely pustulose and pitted and the posterior marginal ridge high. Brachial impressions are faint, forming slender shields inclined obliquely forward. A ridge extends along the hinge, and around the lateral slopes. The floor is marked by pustules related to the spine bases, as well as linear striae that may be reflecting spines adpressed against the shell, and the posterior lateral shell carries well spaced pustules.

Resemblances: This new species is moderately like the material from younger Jungle Creek beds that was identified as *Calliprotonia inexpectans* (Cooper, 1957), and overall, interiors are similar. Although the dorsal septum was shown to be unusually long for the species, one specimen possesses a short septum (Shi & Waterhouse 1996, pl. 8, fig. 26). The dorsal marginal ridge is present but low, unlike that of type *Calliprotonia.* The ventral spines possibly differ, in so far as the finer spine rows were shown to occupy a steep anterior slope in front of each band (Shi & Waterhouse 1996, Fig. 27B), whereas in the present material they occupy the anterior only moderately sloping part of each band behind the growth step, just as figured by Shi & Waterhouse (1996, pl. 8, fig. 23). The fine spines were described for Yukon *inexpectans* as occurring in only one or two rows, compared with three up to five rows in present material.

The relationship to the Oregon material originally described as *Echinoconchus inexpectans* Cooper (1957, p. 48, pl. 8c, fig. 13-26) is far from certain. Overall shape and interior are much the same, but neither figures nor text provided in Cooper (1957) clearly indicate the presence of rows of finer spines along the anterior part of the ventral bands, but suggest that commargons have relatively thick spines anteriorly: however figures are not good enough or clear enough to allow full understanding. The overall similarity of shape and age compatibility suggest the species is congeneric with the Yukon material, but doubtfully conspecific, and the morphology for the types of *inexpectans* requires clarification.

Tribe **KARAVANKININI** Ramovš, 1969

[Nom. transl. Brunton et al. 1995, p. 929 ex Karavankininae Ramovš, 1969, p. 261].

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

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

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

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

Diagnosis: Commarginal 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, buttress plates may be present in Carboniferous juveniles. Dorsal spines are more homogeneous and not in bands as distinctive as those of Echinoconchinae.

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

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

Diagnosis: Quincunxial elongate pustules and spine bases posteriorly, commarginal bands as a rule limited to anterior of both valves, poorly differentiated. Upper Carboniferous (Kasimovian) to Middle Permian (Roadian?).

Genera: *Juresania* Fredericks (?syn. *Parajuresania* Lazarev), *Ametoria* Cooper & Grant, *Densepustula* Lazarev, ?*Septiconcha* Termier et al.

Discussion: *Septiconcha* Termier et al. (1974, p. 125, pl. 23, fig. 4-6) from the lower Murghabian of Afghanistan is possibly a member of Juresaniini, but is difficult to circumscribe. The dorsal ornament appears to be not known. The question of relationship between Juresanini and Septasteginae Waterhouse is discussed on p. 266.

Genus ***Parajuresania*** Lazarev, 1982

Fig. 6.5, Fig. 6.6

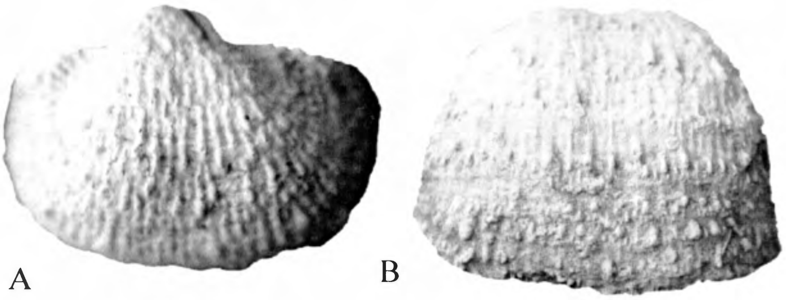


Fig. 6.5. *Juresania nebraskensis* (Owen). A, posterior ventral aspect of BR 3061, x1.6. B, anterior ventral and dorsal aspects of BR 3062, x2. Specimens from Nebraska (Pennsylvanian), United States. JBW photo.

Parajuresania Lazarev, 1982, p. 70 was erected for *Productus nebraskensis* Owen, 1852 from the Iowa Point Shale (Virgilian) of Kansas, because it showed a small cicatrix, and differentiated spines appear only anteriorly, and buttress plates are subparallel at a juvenile phase (see Muir-Wood & Cooper 1960, pl. 79, fig. 15), as accepted by Brunton et al. (2000, p. 514). Yet the finer of the two orders of spines appears moderately early in *nebrascensis*, and no available figures have been published to establish that fine spines appear over the actual ventral umbo of *Juresania juresanensis*: figures in Lazarev (1982, pl. 8, fig. 9, 10) indicate only coarse spines posteriorly in this species. The detailed description for the spine detail of *nebraskensis* provided by Dunbar & Condra (1932, p. 196) reads like that for *Juresania*. There is a small cicatrix on the ventral valve of some but far from all specimens of *nebrascensis*, and low interareas are found in *Juresania* and *Parajuresania* (see Muir-Wood & Cooper 1960, pl. 79, fig. 16). Fine anterior spines appear to be common in *nebraskensis* (see Muir-Wood & Cooper 1960, pl. 80, fig. 1; Mudge & Yochelson 1962, pl. 14, fig. 6-8) and in *Juresania juresanensis* (Lazarev 1990, pl. 33, fig. 8). Unfortunately the ornament over the ventral ears is poorly known for *juresanensis*, but well displayed for *nebraskensis* (Muir-Wood & Cooper 1960, pl. 80, fig. 1; Mudge & Yochelson 1962, pl. 14, fig. 6), and posterior spination illustrated for *nebraskensis* by Gehrig (1958, pl. 2, fig. 13-16) does not seem to differ from that in *Juresania juresanensis.* Small buttress plates are developed in immature dorsal valves, and the buttress plates unite anteriorly in *juresanensis*. Given the degree of overlap and uncertainty, it is not surprising that Martínez Chacón & Winkler-Prins (1985, p. 439) disputed the validity of the differences, and synonymized *Parajuresania* with *Juresania*, to imply that the differences were of no more than specific rank.

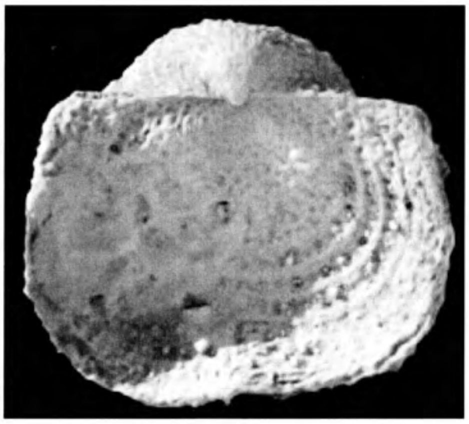


Fig. 6.6. *Juresania nebraskensis* (Owen), dorsal aspect of BR 3062. Specimen from Nebraska (Pennsylvanian), United States, x2. (See Fig. 6.5B). JBW photo.

Tribe **BATHYMYONIINI** Lazarev, 1990

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

Diagnosis: *Juresania*-like ornament posteriorly and subechinoconchiform ornament anteriorly in marked commargons. Lower Carboniferous (Visean – ?Asbian) to Middle Permian (?Roadian).

Genera: *Bathymyonia* Muir-Wood & Cooper, *Buntoxia* Lazarev, *Cubacola* Lazarev, *Pulchratia* Muir-Wood & Cooper, *Vediproductus* Sarytcheva.

Discussion: This group, initially proposed as a nomen nudum by Lazarev (1986a, p. 29), was synonymized with Juresaniini by Brunton et al. (2000, p. 521). It is very close to *Juresania* and allies, but the anterior shell bears well defined commargons, which are much less conspicuous in Juresaniini.

Subfamily **SEPTARINIINAE** new subfamily

Name genus: *Septarinia* Muir-Wood & Cooper, 1960, p. 251, here designated.

Diagnosis: Ventral ornament close to that of *Juresania*, with anterior commargons bearing two spine series on ventral valve. Dorsal ornament comparatively uniform.

Discussion: The lack of commargons from the anterior dorsal valve provides the prime distinction from Juresaniinae coming close to Sentosiidae , whereas the ventral ornament is closer to that of Juresaniinae.

Tribe **SEPTARINIINI** new tribe

Name genus: *Septarinia* Muir-Wood & Cooper, 1960, p. 251, here designated.

Diagnosis: Distinguished by presence of long ventral septum. Anterior commargons bearing two spine series on ventral valve, dorsal ornament comparatively uniform. Lower Carboniferous (Visean) to Upper Permian (Wuchiapingian).

Genera: *Septarinia* Muir-Wood & Cooper, *Septumusia* new genus.

Discussion: *Septarinia* was classed with a query in Pustulinae Waterhouse by Brunton et al. (2000, p. 521), but the ventral ornament is closer to that of Juresaniinae. What distinguishes the genus is the presence of a long septum in the ventral valve, as well as subuniform ornament on the dorsal valve. *Septarinia* is described from rare specimens from Lower Carboniferous faunas of Western Europe, Belgium, Ireland and England, and a new genus is reported in Upper Permian faunas of Pakistan.

The posterior ventral valve of *Productus* (*Tschernyschewia*) *vicinalis* Reed (1944, p. 85, pl. 6, fig. 11, 11a, pl. 17, fig. 1, 1a, pl. 18, fig. 9) from the Wargal and Chhidru Formations (Upper Permian) of the Salt Range, Pakistan, bears spines like those of *Tschernyschewia*, and there is a thin median septum extending for the length of the valve.

But the anterior shell bears bands (commargons) with a row of posterior relatively large erect spines, and anterior rows of finer erect spines. Such ornament suggests a *Juresania*-like form, but *Juresania* and allied genera lack such a long median ventral septum. Although Muir-Wood & Cooper (1960) could not ascertain the nature of the interior for type *Juresania*, there is definitely no median ventral septum in Canadian members of the same genus. Reed's species is now assigned to the new tribe Septariniini.

Genus ***Septumusia*** new genus

Derivation: septum – fence, Lat.

Type species: *Productus* (*Tschernyschewia*) *vicinalis* Reed (1944, p. 85) from Kalabagh Member (Wuchiapingian), Wargal Formation, Salt Range, Pakistan, here designated.

Diagnosis: Moderately large elongate shells, ventral ornament over posterior and median shell of subeven spines with slightly elongated bases, not strongly aligned along rows separated by commarginal laminae, anterior commargons with posterior row of stronger longer spines and anterior rows of fine erect spines. Dorsal spines uniform, erect and fine. Ventral median septum extends to anterior margin.

Discussion: The only known species in *Septarinia* Muir-Wood & Cooper is *Productus leuchtenbergensis* Koninck (1846, p. 226, pl. 14, fig. 3, 3a-d) from Visean (Asbian), of western Europe, described by Muir-Wood & Cooper (1960, p. 251, pl. 59, fig. 1-3, pl. 88, fig. 1-10), and further revised by Mundy & Brunton (1983). In this genus the ventral spines lie mostly in slightly irregular commarginal rows, described as spine ridges by Muir-Wood & Cooper (1960), and anteriorly the lamellation becomes stronger with two series of spines, as well illustrated by Mundy & Brunton (1983) and Brunton et al. (2000, Fig. 2f). In the new genus, the posterior spines lie in very irregular commarginal rows, without intervening lamellation or ridges. The anterior commargons cover about half the length of the valve – more than in *Septarinia* – and the coarser spines are distinctly finer than those over the posterior shell, and more differentiated than in those of *Septarinia*. The dorsal valve of *Septarinia* has finer spines and moderately conspicuous lamellae, and no anterior commargons with two spine series are distinguished. The dorsal valve in the new genus appears to be much the same. The ventral median septum extends for half of the length of the valve in *Septarinia*, and for the full length of the valve in the new genus.

Septumusia vicinalis (Reed, 1944)

Fig. 6.7

1944 *Productus* (*Tschernyschewia*) *vicinalis* Reed, p. 85, pl. 6, fig. 11, 11a, pl. 17, fig. 1, 1a, pl. 18, fig. 9.

Lectotype: Specimen GSI 16854, figured by Reed (1944, pl. 17, fig. 1, 1a) from Kalabagh Member (Wuchiapingian), Wargal Formation, Salt Range, Pakistan, here designated. Reed (1944, p. 86) cited this as his best specimen.

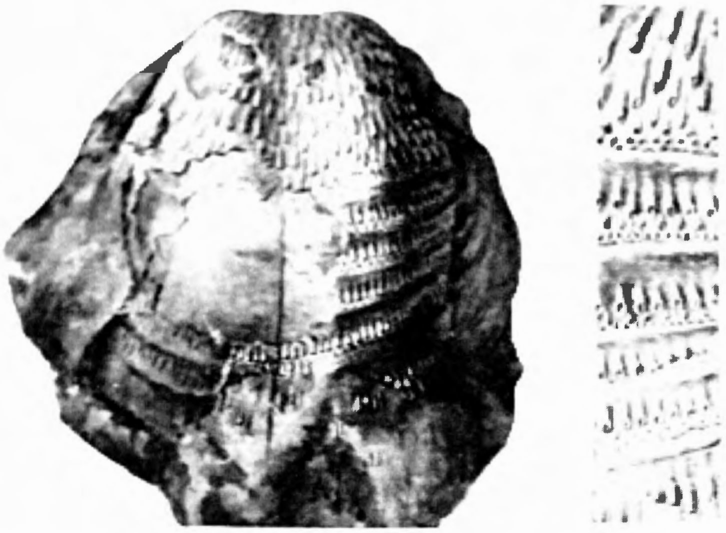


Fig. 6.7. *Septumusia vicinalis* (Reed), holotype GSI 16854, x1, showing ventral valve with long median septum and detail of ornament. From Wargal Formation (Wuchiapingian), Pakistan. See Reed (1944).

Diagnosis: Moderately elongate shells with long median ventral septum, commargons over anterior half of ventral valve.

Discussion: The species has been described by Reed (1944), figuring specimens from the Kalabagh Member and noting that the species extended into the overlying "Upper Productus Limestone", now treated as the Kufri Member of the Chhidru Formation. Several other Salt Range species were ascribed to *Tschernyschewia* by Reed (1944), but none show the anterior commargons. Reed (1944) drew attention to the similarity of *Buxtonia kweichowensis* Chao (1928, p. 57, pl. 5, fig. 21) from the early Permian of Kweichow, China, but the ventral interior and dorsal valve are not known for the Chinese specimen.

Tribe **ALATOPRODUCTINI** new tribe

Name genus: *Alatoproductus* Jin & Zhu in Jin & Hu, 1978, p. 120 from early Middle Permian Kuhfeng Formation, China, here designated.

Diagnosis: Small, slender ventral bands with thicker spines giving way to fine spines over each anterior commargon, dorsal valve with uniform fine erect spines, no dorsal commarginal bands. No ventral septum. Middle Permian (?Wordian) to Upper Permian (Changhsingian).

Genus: *Alatoproductus* Jin & Zhu (syn. *Chenxianoproductus* Liao & Meng).

Discussion: Like Echinoconchinae, the ventral valve has concentric bands with differentiated spines, but unlike genera of that tribe and Juresaniinae, the dorsal valve lacks such bands and is ornamented by uniform fine erect spines, thus approaching the arrangement in Septariniini.

Genus ***Alatoproductus*** Jin & Zhu, 1978

Fig. 6.8

Alatoproductus Jin & Zhu, in Jin & Hu (1978, pl. 3, fig. 5-7) from the approximately Middle Permian Kuhfeng Formation of Anhui, China, has ventral spine bands like those of *Bathymyonia* according to Liao & Meng 1986, in describing material from Hunan. The posterior ornament is arranged in feebly distinguished spinose bands, less differentiated than anteriorly. The dorsal valve figured by Jin & Zhu (1978) clearly shows the dorsal spines, which are subuniform and become more closely spaced anteriorly, with no bands and no differentiation in size. The dorsal marginal ridge is high posteriorly and a substantial cardinal pit is developed, unlike the arrangement in *Bathymyonia*, whereas *Buntoxia* Lazarev and *Cubacula* Lazarev, both of Upper Carboniferous age, have a slit septum or narrow cardinal pit. *Alatoproductus* was classed as Sentosiini by Brunton et al. (2000, p. 522), but members of this group are much older and show less differentiated spine bands over the ventral valve, and none show a cardinal pit or slit dorsal septum. One difficulty in understanding the genus stems from the failure to figure the ventral external ornament, but the authors were clear in the text that there were fine suberect spines posteriorly and bands with prostrate spines anteriorly.

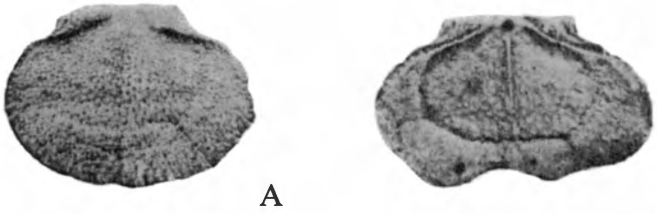


Fig. 6.8. A, B, *Alatoproductus truncatus* Jin & Hu, dorsal valve external mould and interior. Specimens from Kuhfeng Formation of Anhui and Upper Permian of Hunan, China, x1 approx. See Jin & Hu (1978).

Chenxianoproductus Liao & Meng 1986, p. 79, type species *C. nitens* Liao & Meng, was judged to be congeneric with *Alatoproductus* in Brunton et al. (2000, p. 522), possibly on fresh assessment by Jin Yugan, as one of the authors in the *Revised Brachiopod Treatise,* although he did not write any diagnoses (Brunton et al. 2000a). One figure (Liao & Meng 1986, pl. 2, fig. 15) as repeated by Brunton et al. (2000, Fig. 361.2c) shows anterior differentiated ventral bands of spines. *Chonostegoidella* Li & Yang, 1986 in Li, Yang & Feng, 1986, p. 219, was also placed in synonymy with *Alatoproductus* by Brunton et al. (2000, p. 522) but apparently belongs to Stictozosterini (see p. 194).

Family **SENTOSIIDAE** McKellar, 1970

[Sentosiidae McKellar, 1970, p. 27].

Diagnosis: Shallow corpus cavity, fine and closely spaced spines on ventral valve, spines little differentiated as a rule, dorsal spines crowded. Cardinal process bifid, externally quadrifid.

Discussion: The source favoured by Lazarev (1987) and Brunton et al. (2000) for Sentosiidae is Caucasiproductinae Lazarev, a strophalosiiform group, and *Caucasiproductus* itself is small and has very fine spines. Although the suggestion of low broad internal swellings may be indicated posteriorly in the dorsal valve of *Sentosia* Muir-Wood & Cooper (1960, pl. 43, fig. 21, Brunton et al. 2000, Fig. 361.1e), such are not shown by *Caucasiproductus* (see Brunton et al. 2000, Fig. 364.2e), and no other genera allocated to Sentosiinae are known to possess buttress plates or buttress mounds.

Subfamily **SENTOSIINAE** McKellar, 1970

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

Diagnosis: Spines thin and numerous, may have elongate bases. In most genera the median septum is entire. Concentric rugae or lamellae may form bands anteriorly. Upper Devonian (Famennian) to Lower Carboniferous (Visean).

Genera: *Sentosia* Muir-Wood & Cooper, *Malloproductus* Tachibana (nom. nov. pro *Nodella* Tachibana, 1964, non Zaspelova, 1952), *Parasentosia* new genus, *Plicosentosia* new genus, *Spinauricula* new genus, *Stegacanthia* Muir-Wood & Cooper.

Discussion: This subfamily is typified by late Devonian and early Carboniferous shells with fine spines over both valves, often arranged in weak somewhat commarginal rows, with ventral spines of *Stegacanthia* displaying elongate bases set on lamellae. The cardinal process is low, sturdy, and bifid. *Malloproductus* is close in much detail to *Sentosia*, but is larger and has fine long spines.

The amount of variation between genera classed in Sentosiinae by Brunton et al. (2000) is very considerable, and variant genera are here excluded. *Laminatia* Muir-Wood & Cooper has bands with diversified spines on both valves, 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). But in terms of critical ornament, it is echinoconchid, whereas in musculature and age, it is more but not exclusively sentosiid. *Productellana* Stainbrook, 1950, p. 373 of Famennian age, classed in Sentosiini by Brunton et al. (2000, p. 522), appears to be productellid in ornament, having well spaced large ventral spines and there are interareas but allegedly no teeth: it is like no sentosiid genus, and deviates from other productellids in having some dorsal spines. *Jakutella* Abramov is transferred to Overtoniinae (p. 51), and *Sentosioides* Lazarev is difficult to place, perhaps avoniin, given its elongate ventral spine bases and dorsal dimples, but not close to *Sentosia*. The only Upper Permian member allocated to Sentosiidae by Brunton et al. (2000, p. 522) was *Alatoproductus* Jin & Zhu in Jin & Hu, 1978 of ?Early to Late Permian age in China, a remarkable form with sentosiid-like dense subequal dorsal spines, and ventral ornament of commarginal bands with fine apparently differentiated spines. It is herein transferred to Tribe Alatoproductini (p. 184).

Genus ***Spinauricula*** new genus

Fig. 6.9

Derivation: spina – spine, thorn; auricula – ear, Lat.

Type species: *Sentosia profunda* McKellar (1970, p. 28) from Myrtlevale Formation (Famennian), Burdekin Basin, Queensland, Australia, here designated. See Appendix A, part A, p. 477.

Diagnosis: Spines close to hinge up to twice the diameter of body spines, especially on ventral valve.

Discussion: Spines tend to arise from minute spine ridges over the ventral valve, and spines are fine or recumbent. Spines are larger and erect along the hinge, and in a patch over the slender but not well differentiated ears. On the dorsal valve minute spine ridges tend to be separated by pits, or pits may coalesce and be separated by ridges, and fine commarginal rugae are developed over both valves. Detail of the ventral interior, cardinal process and septum and adductor scars are provided by McKellar (1970). In a number of dorsal interiors, there appear to be slender anderidia between the dorsal adductors (McKellar 1970, pl. 9, fig. 10b – *profunda*; pl. 10, fig. 6 – *minuta*; possibly pl. 11, fig. 2a – *transversa*), and there is a broad band of large endospines across the anterior dorsal valve, becoming finer laterally. Another form, treated as a subspecies *transversa deari* McKellar, was named for a larger form from the

Yarrol Basin of Queensland, and is probably a separate and full species, given the differences itemized by McKellar (1970, p. 30).

Details of the ornament differ from that of *Sentosia* and *Malloproductus*, these genera lacking the strong spines of the postero-lateral shell, and the spine bases are not as elongate as those of *Stegacanthia* or *Parasentosia*.

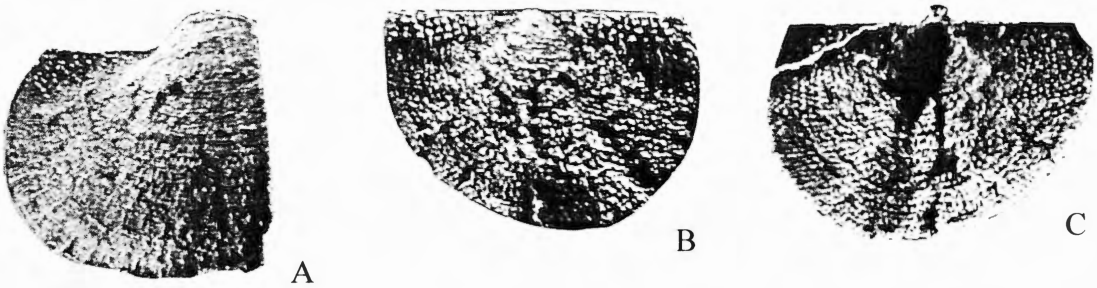


Fig. 6.9. A, *Spinauricula transversa* (McKellar), ventral valve latex cast of exterior, GSQ F 11537 x 1.5. B, C, *S. minuta* (McKellar), external mould and latex cast of dorsal valve GSQ F 11526, x3. From Myrtlevale Formation (Famennian), Burdekin Basin, Queensland, Australia. See McKellar (1970).

Genus ***Plicosentosia*** new genus

Fig. 6.10

Derivation: plico – fold, Lat.; Sentosia – brachiopod name.

Type species: *Sentosia plicata* McKellar, 1970, p. 33 from topmost Myrtlevale Formation (upper Famennian) of Burdekin Basin, Queensland, Australia, here designated. See Appendix A, part A, p. 477.

Diagnosis: Transverse shells with wide ventral sulcus and broad dorsal fold. Postero-lateral spines as fine as those over body of shell; dorsal endospines restricted to region of fold.

Discussion: This sentosiin genus is outstanding in having a wide and distinctly bordered ventral sulcus and dorsal fold. The postero-lateral spines are like those of type *Sentosia* in being as fine as the spines over the disc, unlike the spines in the new genus *Spinauricula*, and the dorsal endospines are restricted to the inner surface of the fold, whereas endospines in *Spinauricula* extend much further laterally. McKellar (1970) noted that the species also occurred in the Denny Gully Member of the Dawes Range Formation in the Yarrol Basin of Queensland.

Fig. 6.10. *Plicosentosia plicata* (McKellar). A, ventral valve, latex cast of exterior, GSQ F 11464, x0.9. B, ventral valve latex cast of exterior, GSQ F 27271, x1. C, dorsal external mould GSQ F 3656, x0.75. Specimens from Myrtlevale Formation (Famennian), Burdekin Basin, Queensland, Australia. See McKellar (1970).

The species *Sentosia transversa caniensis* McKellar, 1970, p. 33 from the Denny Gully Member of the Dawes Range Formation in the Yarrol Basin Formation appears to mark a transitional phase from *Spinauricula* towards *Plicosentosia*. It shows a subdued and broad ventral sulcus and medial reduction in dorsal concavity. Postero-lateral ventral spines include a few stronger than those over the rest of the valve, and dorsal endospines are stronger medianly. McKellar (1970, p. 33) concluded that "The inconstant development of a median flattening or sulcation anteriorly in the pedicle (ie. ventral) valve suggests that the form is a little more advanced than *S.* (= now *Spinauricula*) *transversa* (of McKellar) and more nearly approaches the strongly sinuate condition of *Sentosia* (now *Plicosentosia*) *plicata*...." (bracketed words inserted).

Genus *Parasentosia* new genus

Fig. 6.11

Derivation: par – equal, Lat.; Sentosia, brachiopod name.

Type species: *Sentosia*? *ignota* Carter, 1988, p. 39 from Glen Park Formation (Tournaisian) of Illinois, United States, here designated.

Diagnosis: Ventral spines with elongate bases that tend to coalesce anteriorly, dorsal spines fine and scattered, slightly elongate dimples in quincunx.

Discussion: *Sentosia* Muir-Wood & Cooper, 1960, type species *Krotovia praecursor* Stainbrook (1947, p. 313, pl. 46, fig. 11-15) from the Upper Devonian Box Member of the Percha Formation, New Mexico, United States, is distinguished by its ornament, the ventral spines being erect without prolonged bases, and the dorsal spines more numerous, and no dorsal pits. *Malloproductus* Tachibana, 1981, p. 62, based on the Famennian species *M. pexus* (Tachibana, 1964) of Japan appears to be very close, with "possibly longer fine spines, extending almost radially" according to Brunton et al. (2000, p. 522) and the dorsal valve appears to indicate fine closely spaced spine bases. The cardinal process is long. Much longer spine bases are developed on both valves – not just the ventral valve – in *Stegacanthia* Muir-Wood & Cooper, 1960, type species *S. bowsheri* Muir-Wood & Cooper, 1960, p. 199, pl. 48, fig. 1-12 from the Lake Valley Formation (Mississippian, Ivorian) of New Mexico. The ventral spine bases lie in parallel along concentric bands terminating in a lamellar edge, whereas bases are thicker and less organized in the new genus, with commarginal lamellae less conspicuous.

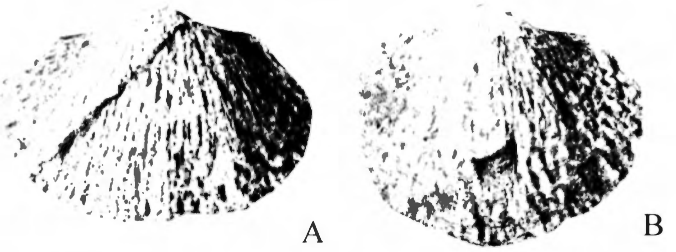


Fig. 6.11. *Parasentosia ignota* (Carter), ventral valves CM 34663 and IGS 80P37, x2. From Glen Park Formation (Tournaisian), Pike County, Illinois, United States. From Carter (1988).

Carter (1988, p. 41) drew attention to two Russian species that are similar in ornament, although differing in shape: *Sentosia kysarkensis* Nalivkin, 1979 from the Famennian of the southern Urals, and *Productus* (*Waagenoconcha*) *nurensis* Nalivkin, as described by Litvinovich et al (1975) from the lower Tournaisian of Kazakhstan, the latter species bearing weak ribs on the ventral trail.

Subfamily **BAGRASIINAE** Nalivkin, 1979

[Bagrasiinae Nalivkin, 1979, p. 109].

Diagnosis: Elongate crowded spine bases, simulating ribs, on both valves. Short low buttress swellings. Lower Carboniferous (upper Tournaisian – lower Visean).

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

Discussion: The nature of the lightly ribbed valves with numerous spines on both valves and the somewhat subdued and vague suggestions of broad buttress mounds (ie. lateral swellings) in front of the cardinal process recall swellings weakly indicated in *Sentosia* (Muir-Wood & Cooper 1960, pl. 43, fig. 21).

Ericatia is moderately close to *Stegacanthia* Muir-Wood & Cooper, but the latter has no buttress mounds.

Subfamily **TUBERSULCULINAE** Waterhouse, 1971

[Tubersulculinae Waterhouse in Bamber & Waterhouse, 1971, p. 205].

Diagnosis: Spines arranged in quincunx on the ventral valve, uniformly fine except postero-laterally where they may be coarser, bases short to elongate, dorsal spines erect and numerous as a rule. Radial ornament not developed, commarginal ornament limited, trail short. Corpus slender, cardinal process bifid where known. Dorsal marginal ridges subdued to moderately developed, high postero-laterally, posterior dorsal septum almost always entire, dorsal pustules fine or moderately large, crowded in front of dorsal septum.

Tribe **TUBERSULCULINI** Waterhouse, 1971a

[Nom. transl. hic ex Tubersulculinae Waterhouse, 1971a, 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 (Visean) to Lower Permian (Kungurian).

Genera: *Tubersulculus* Waterhouse, *Archboldina* Waterhouse, *Echinauriella* Lazarev, *Krotovia* Fredericks, ?*Scoloconcha* Gordon.

Discussion: As pointed out by Waterhouse (2001), the genus *Tubersulculus* lacks specialized and varied ventral spines, and lacks heavy marginal ridge around the anterior dorsal disc, high cardinal process with zygidium, and large few anterior dorsal pustules. These and other attributes indicate that *Tubersulculus* does not belong to Costispiniferini, Subfamily Overtoniinae, counter to Brunton et al. (1995, 2000). *Tubersulculus* is very close to *Krotovia* and current study on Late Carboniferous species of *Tubersulculus* from Canada shows a gradual but step-wise divergence from species to species upwards through time from *Krotovia*. *Scoloconcha* Gordon, 1966 of middle Visean age is small with smooth ventral valve and erect fine spines. It has a high dorsal posterior lateral ridge, just as in *Tubersulculus* (see Shi & Waterhouse 1996, pl. 4, fig. 27), to reinforce the external similarities in the nature of spines and distribution. *Echinauriella* has a smooth ventral ear sector, fewer dorsal spines, high inner dorsal oblique ridges, and lacks an anterior thick marginal ridge (see p. 105).

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Genus ***Tubersulculus*** Waterhouse, 1971a

Type species: *Tubersulculus maximus* Waterhouse, 1971a, p. 209 from *Muirwoodia transversa* Zone, Jungle Creek Formation (Tastubian), Ogilvie Mountains, Yukon Territory, Canada.

Diagnosis: Deeply concavo-convex with ventral sulcus and dorsal fold producing or incipiently producing tubiform trail, regular ribbing absent but ventral valve may display faint longitudinal ridging, low commarginal lamellae, spines numerous over both valves in quincunx and in commarginal rows, with weakly swollen bases, lateral ridges cross ears, dorsal endospines strong and numerous.

Discussion: Notably, the genus is lacking from paleotropical Permian faunas of Pamirs (Grunt & Dmitriev 1973) or Texas (Cooper & Grant 1975), as well as from Gondwana, but its precursor genus *Krotovia* Fredericks is well represented in paleotropical faunas of Lower Carboniferous age.

Tubersulcus reidi new species

Fig. 6.12, Fig. 6.13

Derivation: Named for Hugh Reid.

Holotype: GSC 133278 figured herein as Fig. 6.12A, from Member D, Jungle Creek Formation, Canada, here designated.

Diagnosis: Weakly transverse with wide hinge and gentle ventral sulcus over median length, ventral spines fine and closely spaced, may be coarse near start of trail and very fine in bands over trail, dorsal spines fine and especially numerous over ears and trail. Myophragm well developed.

Material: From Member D (late Asselian), lower Jungle Creek Formation, Ogilvie Mountains, Yukon Territory, Canada. See Appendix A, part C, p. 478.

Dimensions in mm:

Specimen GSC	Width	Length	Height
133278	28	22	8
133277	30	22	12
133276	32	27	11.5

Description: Shells transverse, ventral valve gently convex with sulcus having an angle of 30°, commencing six or seven per mm in front of umbonal tip, narrowing and shallowing anteriorly over trail and may persist to anterior margin, which is extended. Dorsal fold reflects ventral sulcus, becoming low and narrow anteriorly over trail. Ventral umbo broad with angle of 100°, slightly extended beyond hinge, which is wide, with obtuse cardinal extremities as a rule, although a few specimens have tiny alate acute extremities. Very low interareas are developed along the hinge in each valve, marked by growth striae parallel to the hinge, but it is not certain that a ginglymus is developed on all specimens. The postero-lateral shell is weakly convex for the ventral valve, and concave in the corresponding part of the dorsal valve. Ornament is spinose. Ventral spines are arranged in close-set commarginal rows, seven in 5mm at

5mm from the umbo, five in 5mm at 12mm from the umbo, with rows 1 to 1.7mm apart. In some specimens rows are 3mm apart with some seven spines in 5mm; in rare specimens spines are in rows 2.5mm apart and coarse, at only four in 5mm. In front over the anterior shell and involving the trail, spine development varies, but as a rule spines are fine with seven to ten in 5mm along rows 1 to 3mm apart. Low and short radial ridges appear, often in front of the spines, and dimples may develop, especially laterally. There are eight to ten growth laminae per mm at mid-length, and coarser subfusc concentric rugae present, numbering more than 50. The dorsal valve is more dimpled than the ventral valve, and dorsal spines are finer and more close-set over the postero-lateral ears, and spines at the posterior cardinal extremities are slightly larger and spaced further apart. As in the ventral valve spines form a few well developed commarginal rows at the start of the trail, with ten to twelve in 5mm, and are fine and variably spaced over the trail.

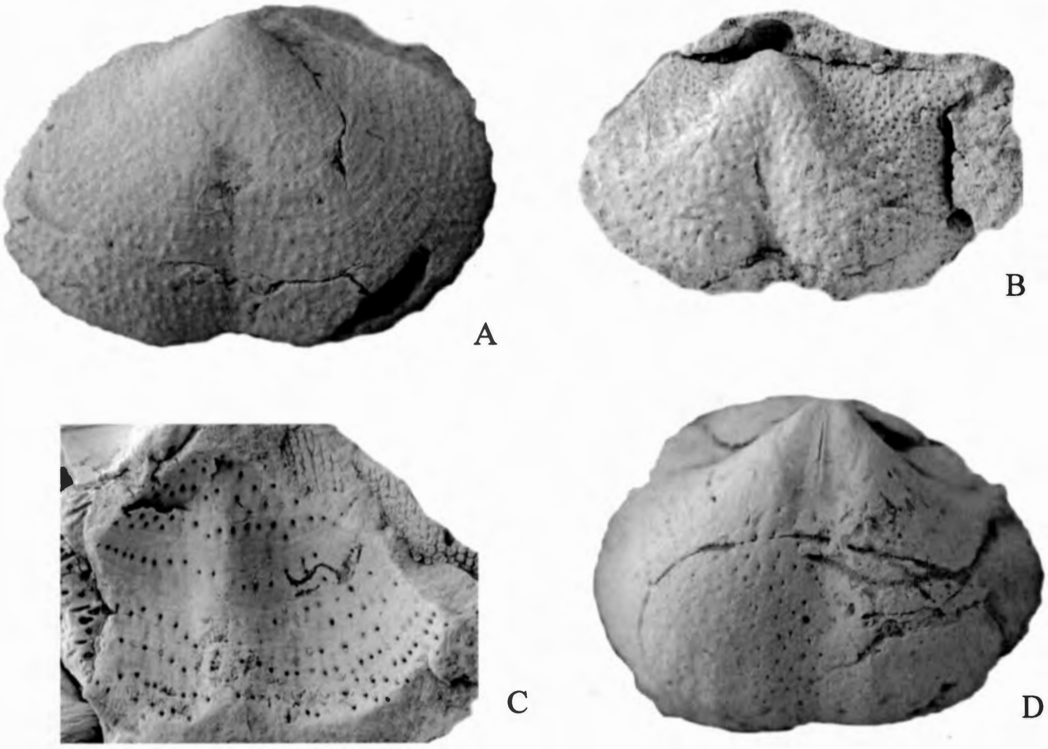

Fig. 6.12. *Tubersulculus reidi* new species. A, ventral valve holotype GSC 133278. B, dorsal aspect of external mould showing dorsal exterior and ventral beak, GSC 133279. C, external mould of ventral anterior, GSC 133340. D, internal mould of ventral valve GSC 133277. From Member D (Asselian), Jungle Creek Formation, Ogilvie Mountains, Yukon Territory, Canada, x2. JBW photo.

Ventral adductors are large and smooth, apart from weak growth rugae parallel to the rounded anterior, and elongately oval in shape, and divided by a narrow but comparatively high myophragm, with a narrow groove each side. The diductor scars are very faintly impressed and are suboval and small, and anteriorly placed, overlapping only the anterior part of the adductor scars. A short ridge crosses the floor of the valve at the anterior margin of the ears, and the floor of the valve bears sharp pustules and small pits, coarse near the muscle scars and finer in front. In the dorsal valve, a medium septum extends to mid-length, broad posteriorly and narrow between the adductors and in front. The posterior adductors are small, subrectangular and smooth, the anterior adductors large, suboval, elongate, marked in one specimen by growth-lines parallel to the rounded anterior margin. In a well preserved small specimen a short well defined ridge lies postero-laterally to the adductors, and a higher ridge extends along the hinge. The cardinal process is not preserved, and the brachial ridges are not clearly visible, but one large mature specimen shows a single fine ridge extending forward from just behind the end of the median septum, representing the inner arm of the brachial ridge, comparable in outline with that figured in Shi & Waterhouse (1996, pl. 4, fig. 25, 27). Large pustules are developed over the floor of the valve.

Resemblances: This species is very close to the type species of the genus, *Tubersulculus maximus* from the *Muirwoodia transversa* to *Jakutoproductus verchoyanicus* Zones of the upper Jungle Creek Formation, Yukon Territory, Canada, as described by Waterhouse (1971a, pl. 23, fig. 1-11) and Shi & Waterhouse (1996, pl. 4, fig. 24-29, pl. 5, fig. 1-9), but most specimens of *reidi* are more transverse, and have a shallower broader ventral sulcus, and the sulcus persists to the anterior margin, whereas it is replaced by a fold in *T. maximus*. Ventral spines are less varied in spacing on *maximus*: the spacing is similar at five to six in 5mm at 5mm from the umbo, but spines become more close-set in front, often six or seven in 5mm, with some well spaced rows, and finer and denser over the anterior shell and trail, at eight or nine in 5mm. Dorsal spines are more close-set posteriorly, and dense over the trail. Internally the myophragm is better developed in the ventral valve of the present form. The species *maximus* is slightly younger than *reidi*, being Sakmarian – Artinskian, whereas *reidi* is found in underlying beds and is considered to be upper Asselian in age.

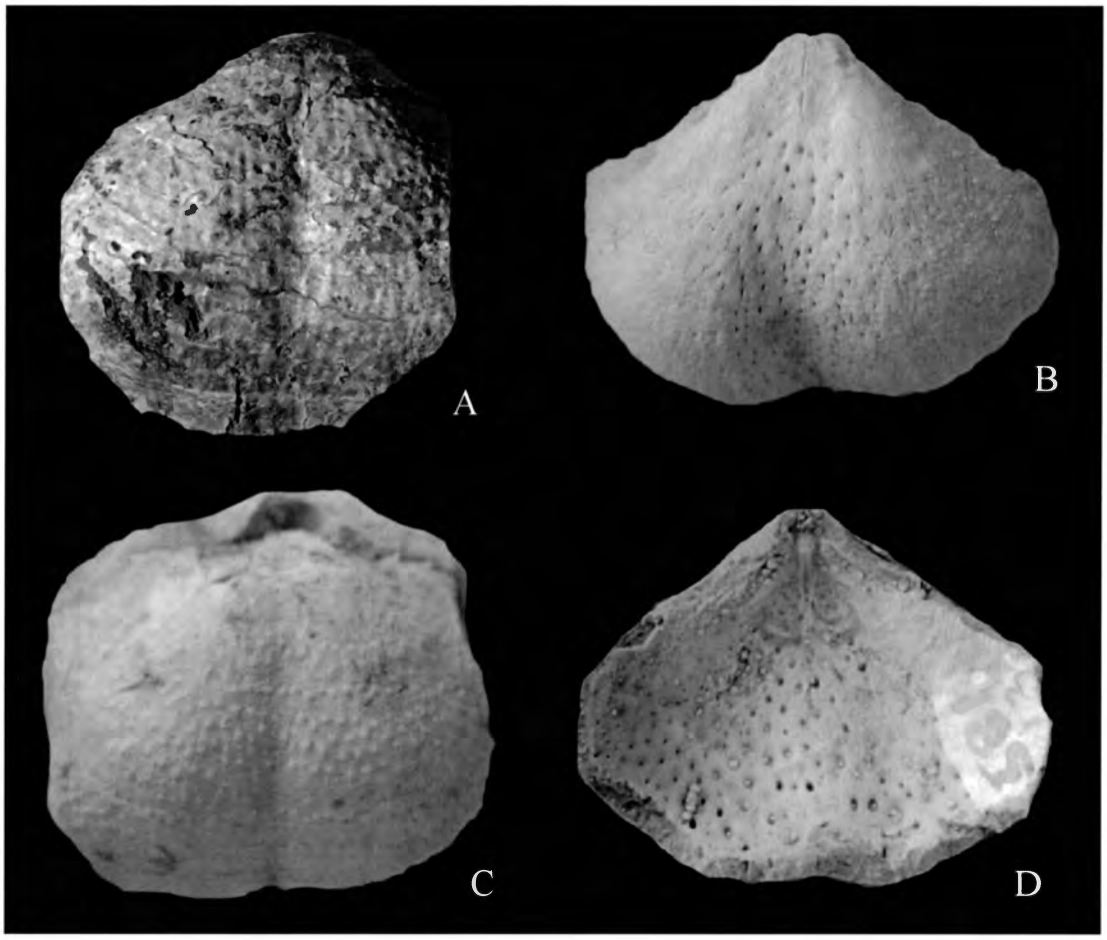

Fig. 6.13. *Tubersulcus reidi* new species. A, ventral valve GSC 133276, x2. B, D, ventral and dorsal aspects of internal mould GSC 133275, x2.5. C, dorsal view of specimen with valves conjoined, GSC 133280, x2. A thin calcite coating covers much of the surface, but spine bases are visible over the trail. From Member D (Asselian), Jungle Creek Formation, Ogilvie Mountains, Yukon Territory, Canada, x2. JBW photo.

Russian specimens figured as *Productus pseudoaculeatus* Krotow by Tschernyschew (1902, p. 615, pl. 30, fig. 7, pl. 53, fig. 10-12) suggest a sulcus like that of the present species, similar to the ventral valve figured as *pseudoaculeatus* by Kalashnikov (1983, p. 209, pl. 47, fig. 9) from the late Early Permian Talatin Suite of the Pechora Basin. The original specimen figured by Krotow (1888, pl. 1, fig. 8) and further specimens (Stepanov 1934, pl. 3, fig. 1-8) have a more tubiform trail, and are closer to *Tubersulculus maximus* than the present species, and are of Sakmarian age. Figures identified as this species in Gerassimov (1953, pl. 10, fig. 4-8, 10, 18 aff. 13) are poorly reproduced, but suggest a ventral sulcus and tubiform trail, though they are small. *Productus tundrae* Fredericks

(1926, p. 87, pl. 3, fig. 7-9) from Sakmarian beds in Kejim-Terovey River, north Urals, has a tubiform trail and more emphasized concentric rugae.

Tribe **LETHAMIINI** Waterhouse, 2001

Fig. 6.14, Fig. 6.15

[Lethamiini Waterhouse, 2001, p. 17].

Diagnosis: Spines numerous and evenly spaced over both valves, no special hinge row, no high postero-lateral internal dorsal ridge. Lower Permian (Sakmarian) to Upper Permian (basal Changhsingian).

Genera: *Lethamia* Waterhouse, *Amosia* Simanauskas, *Undellaria* Cooper & Grant, *Wooramella* Archbold.

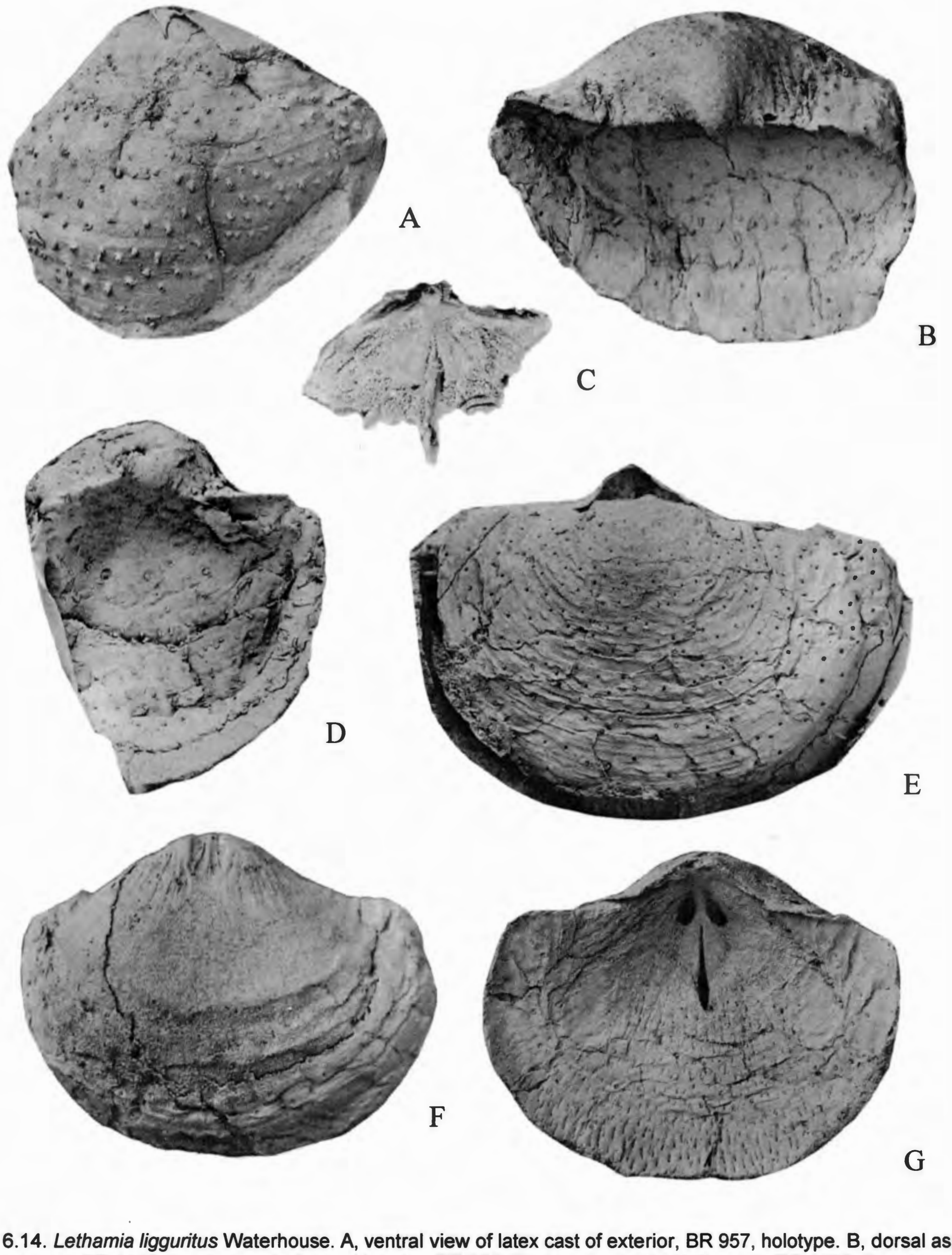

Fig. 6.14. *Lethamia ligguritus* Waterhouse. A, ventral view of latex cast of exterior, BR 957, holotype. B, dorsal aspect of latex cast, BR 1440. C, latex cast of dorsal interior, BR 956. D, dorsal aspect of latex cast, BR 1438. E, external mould of dorsal valve BR 1441. F, G, ventral and dorsal view of internal mould of same specimen. Specimens x2, from Letham Formation (upper Kungurian), Wairaki Downs, New Zealand. See Waterhouse (1982a). Photo S. N. Beatus & JBW.

Discussion: The cardinal process of *Lethamia* is low and broad, apparently bilobed, with deeply recessed median lobe and prominent lateral lobes. The process is bilobed in *Wooramella* (Archbold in Hogeboom & Archbold 1999, p. 260). In general appearance *Lethamia* and allies look close to *Tubersulculus* and *Krotovia*, classed as Tubersulculinae Waterhouse. Waterhouse (2002b, p. 19) had suggested that Lethamiini should be linked with *Horridonia* and *Leioproductus* because of the dense internal pustulation and reduced ornament other than spines. Lethamian shells are moderately close to *Galeatella* Muir-Wood & Cooper, 1960, but unlike that genus, dorsal spines are numerous. The horridoniid *Araxilevis* Sarytcheva, 1965 is close in ventral ornament and has dense internal pustulation. On the other hand the ventral adductor scars in *Lethamia* are striate and the dorsal adductor scars almost smooth, unlike the dendritic adductors typical of Horridoniidae. Therefore the tribe is regarded as a member of Tubersulculinae, moderately close to the assessment by Brunton (2007, p. 2640).

Fig. 6.15. *Lethamia ligguritus* Waterhouse, detail of dorsal posterior, from BR 1441, upper Letham Formation (upper Kungurian), New Zealand, x4. Photo kindly supplied by John Simes, GNS Science, Lower Hutt, New Zealand.

Genus ***Undellaria*** Cooper & Grant, 1975

Undellaria Cooper & Grant, 1975, pl. 467, fig. 14-19 from the Bone Spring Formation (Artinskian) of west Texas, United States, has undulate non-costate valves and delicate spines without prolonged bases on either valve. The ventral adductors are elongate with a few longtudinal grooves, and the dorsal adductor scars are smooth. Low dorsal hinge ridges are present, and the cardinal process is strongly bifid, much as in *Krotovia* (that of *Tubersulculus* is still not known). Such features would suggest a relationship close to Tubersulculinae, and Lethamiini in particular. Yet Cooper & Grant (1975, p. 1158) insisted "That this genus belongs to Linoproductidae there can be no doubt", a view modified only slightly by Brunton et al. (2000, p. 546) in referring the genus to Auriculispininae Waterhouse. There appear to have been two reasons (none were explicitly mentioned): the nature of the cardinal process, and the group of slightly stronger spines over the postero-lateral ventral valve. The cardinal process is bilobed from a ventral view, but the two lobes are born on a low broad shaft. It is not particularly linoproductoid – indeed it differs substantially, but on the other hand is not very close to the cardinal process of largely Carboniferous overtonioids. In my opinion, the cardinal process has evolved, and in this Permian genus, developed beyond that of Carboniferous genera, without becoming linoproductoid. The lack of costellae, the nature of the ventral spine bases, and the nature of the muscle scars all tell against a linoproductoid affinity, and are reinforced by the nature of the dorsal papillae, which form a broad band of endospines less developed than in Linoproductoidea, and not so circumscribed, extending almost to anterior margin, whereas in Linoproductoidea, the coarse papillae in front of the brachial shields are followed as a rule by a band of finer papillae. The slightly coarser spines developed at the postero-lateral ventral valve mark another development for a genus in Tubersulculinae, and are nowhere near as strong as those of Paucispinauriinae in west Texas. Waterhouse (2002b, p. 10) therefore referred the genus to Tubersulculini, and noted that *Krotovia*

Fredericks also tended to develop slightly coarser spines postero-laterally. The cardinal process is bilobed, the dorsal adductors raised and tiny, the dorsal hinge ridge low, and posterior ventral spines slightly thicker than in *Lethamia*.

Genus ***Amosia*** Simanauskas, 1996

Fig. 6.16

Brunton (2007) classed *Amosia* (Sakmarian) from Argentina as Lethamiini Waterhouse: its spine pattern is close, and although there appear to be a few slender spines found in front of the prominent ventral spines along each commargon, as if modified from a stictozosterin ornament, the spines on the whole are well spaced.

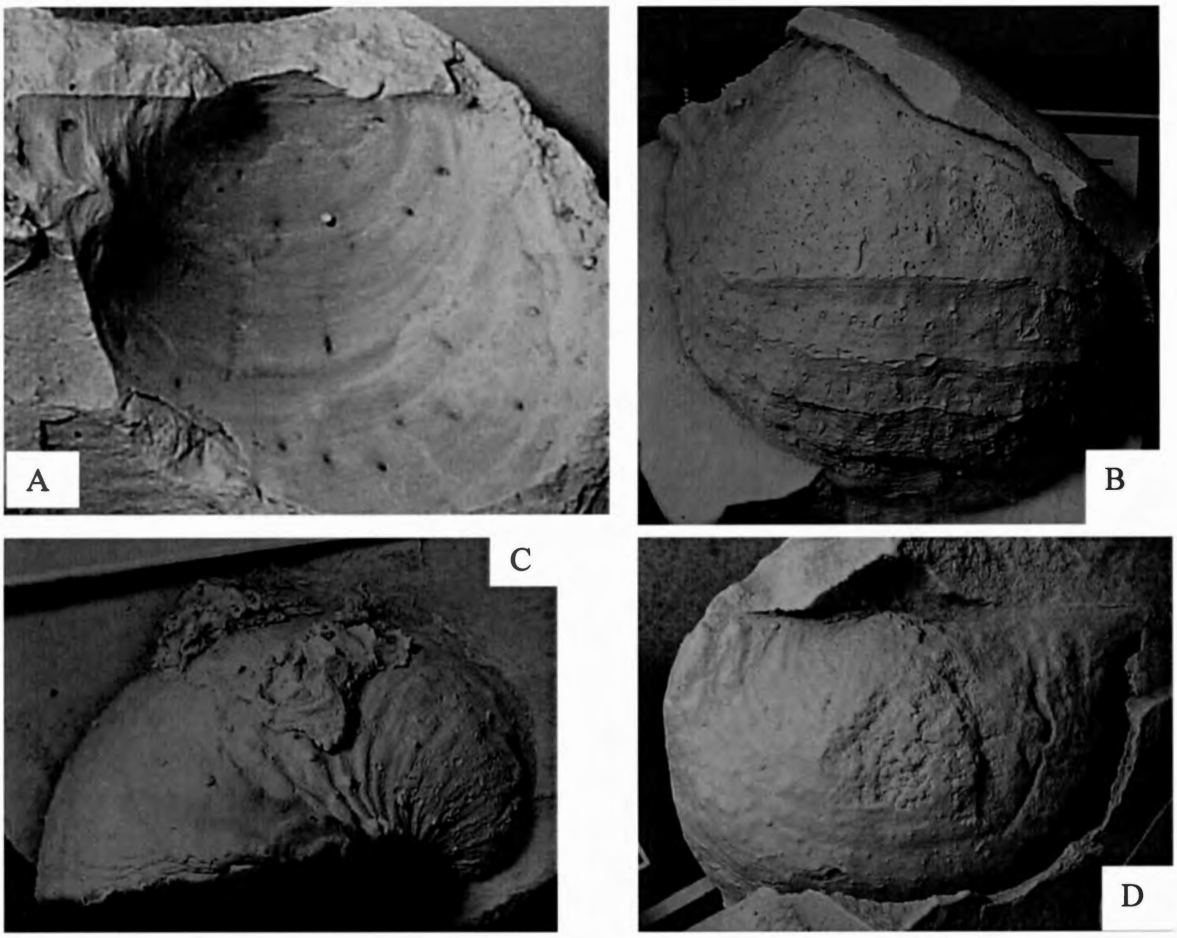

Fig. 6 16. *Amosia sueroi* Simanauskas A, ventral external mould, x4 approx. B, anterior aspect of ventral cast, x4 approx. C, lateral aspect of ventral valve cast, x3.2. D, dorsal valve and ventral beak of external mould, x3. From Lower Permian of Chubut, Argentina, 43°32'25.8"S, 070°43'36.3"E. Photographs supplied by A. C. Taboada.

Subfamily **STICTOZOSTERINAE** Waterhouse, 2002b

Fig. 6.17

[Nom. transl. hic ex Stictozosterini Waterhouse, 2002b, p. 11].

Diagnosis: Small, spines of uniform size 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 commarginal bands in front of small growth intervals. Slender corpus cavity, marginal ridges lightly if at all developed. Lower Permian (Sakmarian) to Upper Permian (Changhsingian).

Genera: *Stictozoster* Grant, *Chonostegoidella* Li & Yang, *Darlinuria* Li & Gu, *Dorashamia* Sarytcheva, *Guangia* Waterhouse, *Markhamia* Jin & Shi (syn. *Tuberella* Li in Li, Yang & Feng).

Discussion: This subfamily differs from Sentosiinae in having smooth commarginal bands between the spinose bands. Grant (1976), in erecting the distinctive genus *Stictozoster*, pointed out that the genus showed some attributes of Echinoconchidae in its concentric banding, although he considered that internal features differed from echinoconchiform genera and approached those of Productellidae (Overtonioidea herein). *Stictozoster* is characterized by numerous fine spines, arranged generally in concentric bands, and separated by short smooth bands. The cardinal process appears bifid from a ventral aspect, each lateral lobe subdivided posteriorly, and with deep alveolus, as if inherited and preserved from sentosiid stock. Genera of Costispiniferini Muir-Wood & Cooper, to which *Stictozoster* and others were referred by Brunton et al. (2000), lack narrow and smooth concentric banding and have internal marginal ridges to varying degree.

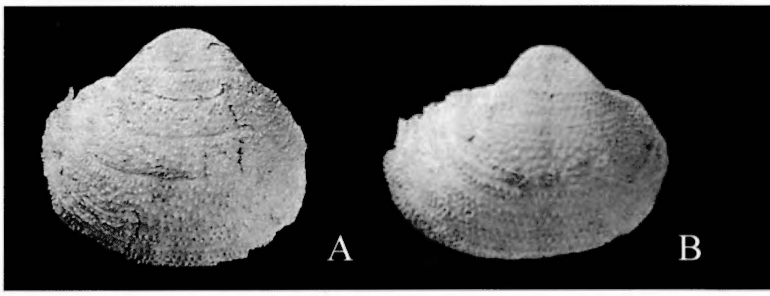

Fig. 6.17. *Stictozoster leptus* Grant. A, ventral valve USNM 212110 and B, tilted posterior ventral valve, USNM 212104, x2. From Rat Buri Limestone (Roadian), south Thailand. See Grant (1976).

Markhamia Jin & Shi in Jin et al. (1985, p. 192) of Late Carboniferous to Early Permian (Gzhelian to Artinskian) age is typified by fine prostrate spines in commarginal rows separated by narrow smooth bands on the ventral valve, and fine dorsal spines, with low commarginal rugae indicated in figures. This appears to be the same pattern as found in *Stictozoster* Grant. Another genus *Tuberella* Li in Li, Yang & Feng, 1986, p. 222, pl. 2, fig. 12-14, based on two species, including the type, *T. typica* Li, appears to be congeneric. Unfortunately the interior is not known for these taxa, but their external similarity to *Stictozoster*, though overlooked or ignored by previous authors, is hard to gainsay. Brunton et al. (2000, p. 522) regarded *Markhamia* and allies as members of Sentosiini. The pattern of spines does indicate a possible relationship, and *Sentosia* of Famennian age does have subdued commarginal spine bands, but lacks the smooth sectors.

Compared with *Stictozoster*, *Dalinuria* from Inner Mongolia has coarser, fewer spines, and commarginal ridges. *Dorashamia* has commarginal ridges over the ventral valve at least, but spines are few.

Genus **Guangia** Waterhouse, 2002b

Guangia Waterhouse, 2002b, type species *Krotovia inflata* Shen et al. (2000, p. 739) from the Late Permian of Tibet has both valves covered by spines with swollen bases arranged in commarginal rows and separated by narrow commarginal bands (see Shen, Archbold, Shi & Chen 2000, Fig. 9.19-22). Brunton (2007, p. 2638) reallocated the type species to *Krotovia* Fredericks, 1928. However commarginal banding is not developed to the same extent on *Krotovia*, and *Guangia* belongs to a different family, Stictozosterinae, whereas *Krotovia* belongs to Tubersulculinae, the latter readily discriminated by the absence of banding, and presence of the high postero-lateral dorsal ridge.

Chonostegoidella Li & Yang, 1986

Chonostegoidella Li & Yang, 1986 in Li, Yang & Feng, 1986, p. 219, type species *C. longlinensis* Li & Yang (1986, p. 219, pl. 1, fig. 14-16) from the Late Permian of China, was placed in synonymy with *Alatoproductus* by Brunton et al. (2000, p. 522), but the anterior differentiated ventral spine rows cannot be seen clearly in the figures, nor in *C. minor* Li & Yang in Li, Yang & Feng (1986, pl. 1, fig. 25). The taxon appears to been interpreted differently by Chen et al. (2005, pp. 357, 358, Fig. 7K, 10B, 14). Well preserved material was described and figured as comparable to the type species, *C. changxingensis* Liao & Meng, 1986, and the ornament of closely spaced subuniform ventral spines separated by commarginal strips of smooth shell is close to the ornament of *Stictozoster* Grant and *Markamia* Jin & Shi. Chen et al. (2005) added invaluable comments on material described by Kayser (1883) and Chao (1927).

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

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

Diagnosis: Spines may vary in size, but are subuniform over different parts of the shell, not associated in numerous repeated patterns of commargons. Spines dense and uniform on dorsal valve. Cardinal process with high shaft.

Discussion: The family group was downgraded to a tribe by Brunton et al. (2000), but its ornament differs considerably from Echinoconchidae in lacking bands with differentiated spines. Furthermore the source may have been different, stemming from *Praewaagenoconcha* of Caucasiproductinae through Sentosiinae, whereas Echinoconchidae may have arisen from *Praelaminatia* and *Laminatia*, and although these genera seem likely to have shared a common ancestry with Sentosiidae, Waagenoconchidae is closer to Sentosiidae in morphology.

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

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

Diagnosis: Spines fine, suberect to erect, may vary in size but crowded and subuniform over different parts of the shell and not associated in repeated patterns over commarginal bands. Cardinal process without buttress supports.

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

Fig. 6.18

[Nom. transl. Brunton, Lazarev & Grant 1995, p. 929 ex Waagenoconchinae Muir-Wood & Cooper, 1960, p. 252].

Diagnosis: Spines fine, suberect to erect, may vary in size but crowded and subuniform over different parts of the shell. Dorsal disc subplanar, curving into short trail. Lower Carboniferous (Tournaisian) to Upper Permian (Changhsingian).

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

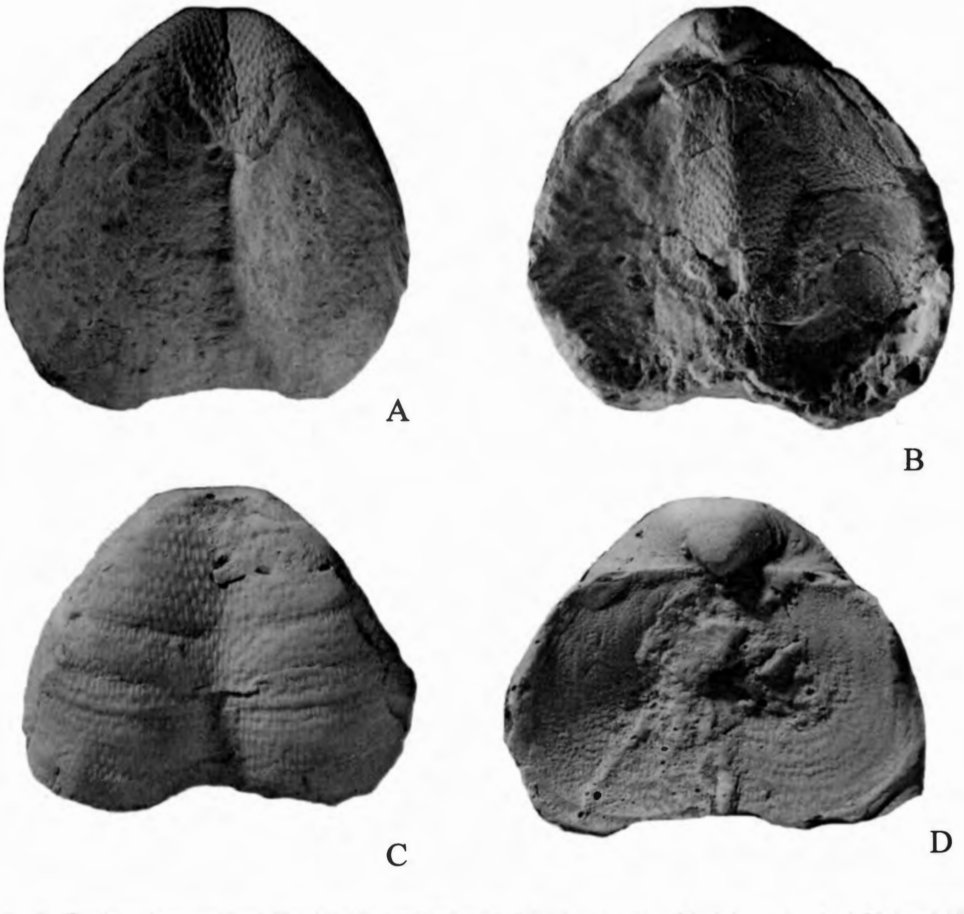

Fig. 6.18. A, B, *Contraspina purdoni* (Davidson), ventral and dorsal aspects of holotype, kept at Natural History Museum, London. Plaster cast BR 3053. From Salt Range (Kalabagh Member, Wuchiapingian), Pakistan, x1. C, D, *Quenstedtenia rugosa* Waterhouse, ventral and dorsal aspects of holotype, from Basleo beds (Wuchiapingian) of Timor, x1. Plaster cast BR 3055. Original kept at Free University, Amsterdam, Netherlands, transferred to Nationaal Natuurhistorisch Museum, Leiden (Winkler Prins 2008). JBW photo.

Discussion: Frech (1911, pp. 57, 132), when 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 intermediate between *Waagenoconcha* Chao, 1927 and *Gruntoconcha* as analyzed by Angiolini (1995) and Brunton et al. (2000, p. 517). Thus one or other of these genera stands under threat of synonymy, unless the prior proposal of *Septoproductus* is set aside. On the other hand, *Septoconcha* could simply replace *Gruntoconcha*, which is hardly an overwhelming change. My personal view is that in this instance the rules of zoological nomenclature should 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, Kolkata, are in fine shape, so there is no need for ambiguity over the nature of the taxon.

Contraspina Waterhouse, 2002b, p. 46, based on *Productus purdoni* Davidson, 1862 from Wuchiapingian faunas of the Salt Range, Pakistan, has small erect spines over the posterior ventral valve and more elongate bases in front, with a band of finer spines in front on large specimens, but no close-set rugae or growth steps. *Productus humboldti* (d'Orbigny), the type species of *Waagenoconcha* from the Lower Permian Asselian Stage of Bolivia, has more elongate spine bases over the posterior ventral valve (see Muir-Wood & Cooper 1960, pl. 89, fig. 6-10) with erect spines over an extensive band in front, and *Gruntoconcha* Angiolini, 1995, type species *W.* (*Gruntoconcha*) *macrotuberculata* Angiolini, 1995 from the Karakorum Range, has coarse and swollen spine bases, as figured by Angiolini (1995, p. 206, Brunton et al. 2000, fig. 357.2a). *W. abichi* Waagen from the Salt Range, Pakistan, is intermediate in its spine base size and spacing between *humboldti* and *macrotuberculata*, which supports no more than a subgeneric standing for *Gruntoconcha*, as proposed by Angiolini and maintained by Brunton et al. (2000). *Fostericoncha* Waterhouse, 2002b is based on *Waagenoconcha*? *gigantea* Waterhouse, 1983a, p. 125 from the Pija Shale Member of Wuchiapingian age in Nepal, and has wide hinge and large erect spines postero-laterally, and fine erect spines over most of the ventral valve. *Spinauris* Roberts, 1971 was described from Tournaisian (basal Carboniferous) beds of Australia, with even spines becoming slightly finer anteriorly, and moderately small in size, with weak cardinal ridges and low submarginal ridge.

Genus ***Glabrispinus*** new genus

Derivation: glabri – smooth; spinus – thorn, Lat.

Type species: *Kochiproductus elongatus* Cooper & Grant, 1975, p. 1049 from Skinner Ranch and Bone Spring Formations (lower and upper Kungurian), Glass Mountains, Texas, United States, here designated.

Diagnosis: Large elongate shells with sulcus and fold, narrow to moderately wide hinge, characterized by ventral ornament of well-spaced short elongate spine bases giving rise anteriorly to fine spines, dorsal valve with fine spines and dimples. No ginglymus or interarea. Dorsal interior with high and humped cardinal process which lacks anterior supporting or buttress plates, hinge ridge high, passing into high marginal ridge.

Discussion: Material on which the type species is based, as well as *Glabrispinus kingi* new species and *Buxtonia occidentalis* King, 1931 from the same region, were referred to the genus *Kochiproductus* Dunbar, 1955 by Cooper & Grant (1975). But the species are readily distinguished from that genus by having a much narrower hinge with much smaller ears, more elongate shape, and lack of ribs and commarginal rugae which form a reticulate pattern over the visceral disc. Furthermore the spines on both valves have elongate bases, more distinctively than the spine bases in *Kochiproductus.* In *Kochiproductus*, as well shown by material figured in Cooper & Grant (1975), the cardinal process varies somewhat: it may be supported by two short buttress plates like those of *Taeniothaerus*, or lack buttress plates, and pass anteriorly into two adpressed ridges separated by a slit. In some specimens, the cardinal process carries a median trough on the ventral side to appear bifid, but in none is the cardinal process as slender and tall as in *Glabrispinus.*

The species somewhat approach Taeniothaerini Waterhouse, 2002b, best known in the Permian of east Australia, and extending into south Asia. In the nature of its spines, which are of largely uniform diameter, and rise from elongate bases that swell towards the spine over the ventral valve, the Texan species come close to *Taeniothaerus* Whitehouse, 1928, and the dorsal ornament is also moderately close, with short bases, erect spines and small crowded dimples. Differences are that a ventral interarea is missing from the Glass Mountains species, and the dorsal interior differs in the nature of the cardinal process, which has a single high shaft without the two lateral sheaths, and without the short anterior supporting ridges or plates that are developed in *Taeniothaerus*. Good examples of taeniothaerin cardinal processes are figured in Coleman (1957) from Western Australia (see also Fig. 9, p. 16 herein), and their generic position discussed in Waterhouse (2002b, 2004b). Such differences raise the possibility that the present form is indeed an exceptional derivative from *Kochiproductus*, which has converged in external appearance on *Taeniothaerus*. But the similarity to waagenoconchins is even more marked as far the cardinal process is concerned, because these Texan species lack any form of buttress plates, and the dorsal medium septum need not be slit or divided. Normally, it is considered that internal structures are comparatively conservative, and slow to change, so that this possibility can be by no means set aside. Yet no known species or genus within Waagenoconchinae is shaped like the shell of *Glabrispinus*, with its moderately short hinge, and thick body corpus, and especially the somewhat elongate, slightly swollen, and well spaced ventral spine bases.

Body shape and ornament resemble in several aspects genera allocated to Bathymyonini, such as *Buntoxia* Lazarev, 1986b, p. 94 or *Bathymyonia* Muir-Wood & Cooper, 1960, p. 244, but *Glabrispinus* lacks the anterior bands with thick and fine spines which help characterize members of this tribe. As well, most genera display a posterior groove in the dorsal septum, of which there is no sign in *Glabrispinus*. Admittedly the cardinal process in the genus *Bathymyonia* as described by Muir-Wood & Cooper (1960, p. 244, pl. 82, fig. 1-7, pl. 109, fig. 1) and Cooper & Grant (1975, pl. 353, fig. 12-17) from the Park City Formation of western United States lacks a groove or alveolus and so is moderately close to that of *Glabrispinus*. It may be conjectured that *Glabrispinus* could be interpreted as related, a descendent of Bathymyonini which has lost its anterior commargons with differentiated spines, and somewhat changed the nature of the cardinal process, but showing considerable approach otherwise in shape and ornament to *Bathymyonia*, which is found in the same general region. But there is no conclusive proof of this possibility, and the genus is judged to be waagenoconchin. From the Wuchiapingian faunas of the Salt Range, Pakistan, several species were ascribed to *Productus* (*Ruthenia*) that have well spaced ventral spines with protracted bases, such as *P.* (*Ruthenia*) *vagans* Reed (1944, pl. 16, fig. 3) from the middle Wargal Formation, and *P.* (*Ruthenia*) *purdoni prolongata* Reed (1944, pl. 14, fig. 1, 2) from the base of the Kufri Member or top of the Kalabagh Member. The material described as *P.* (*Waagenoconcha*) *cylindricus discreta* Reed (1944, pl. 14, fig. 7, 8) from the Kufri Member shows well spaced spines over the posterior ventral valve, followed by bands of coarse and fine spines, suggesting bathymyoniin links.

Glabrispinus elongatus (Cooper & Grant, 1975)

1975 *Kochiproductus elongatus* Cooper & Grant, p. 1049, pl. 358, fig. 4-6 (part, not *K.* aff. *elongatus* Cooper & Grant, pl. 360, fig. 3, pl. 361, fig. 9-11 = *Glabrispinus kingi* new species).
1975 *Kochiproductus* sp. 5 Cooper & Grant, p. 1054, pl. 361, fig. 3-8.

Holotype: USNM 152732 figured by Cooper & Grant (1975, pl. 358, fig. 4-6) from Skinner Ranch Formation (Kungurian), Glass Mountains, west Texas, United States, here designated.

Discussion: This species was also reported from the Bone Spring Formation. A ventral valve figured as *Kochiproductus* sp. 5 by Cooper & Grant (1975, pl. 361, fig. 3) from the Sullivan Peak Member of the Skinner Ranch Formation is similar in ornament and probably conspecific, together with some smaller dorsal valves (Cooper & Grant 1975, pl. 361, fig. 4-8) that confirm the nature of the interior.

Glabrispinus kingi new species

Fig. 6.19

1931 *Waagenoconcha leonardensis* [not King] – King, p. 80, pl. 19, fig. 2a, b (part, not fig. 3, 4 = *Waagenoconcha* & *Rhamnaria*).
1975 *Kochiproductus* aff. *elongatus* [not Cooper & Grant] – Cooper & Grant, pl. 360, fig. 3, pl. 361, fig. 9-11.

Derivation: Named for R. E. King.

Holotype: USNM 153903a, from Cathedral Mountain Formation (Kungurian), figured by Cooper & Grant (1975, pl. 361, fig. 9, 10), here designated.

Diagnosis: Small subelongate shells with comparatively wide hinge for the genus, no ginglymus or interarea, ventral spines fine, well spaced along commarginal rows, bases short, slightly elongate; dorsal spines fine, arising from low swellings interspersed with dimples.

Description: Shell of moderate size with incurved ventral umbo, shallow ventral sulcus, low dorsal fold, and hinge as wide or almost as wide as maximum width, which is placed well forward. In one specimen the sulcus is narrow and deep. Trail short. Spines as described previously. The ventral interior is not known, but the dorsal interior is well preserved, with single-shafted and internally humped cardinal process, and from a posterior aspect the flanks curve around the central shaft. A well developed ridge just inside the hinge extends laterally into high marginal ridges, and the median septum is long and sturdy, dividing large and dendritic muscle scars. Brachial ridges cannot be discerned, and the floor of the valve bears dense fine pits posteriorly, and large pustules in a number of rows anteriorly.

Resemblances: *Kochiproductus* (now *Glabrispinus*) *elongatus* Cooper & Grant (1975) from the Skinner Ranch Formation of the Glass Mountains is much larger, with relatively narrower hinge and better formed sulcus and fold, and coarser spines spaced further apart. *Buxtonia occidentalis* King, 1931 from probably the Neal Ranch Formation is more transverse, with conspicuous dorsal pits. The holotype of *Waagenoconcha leonardensis* King (1931, pl. 19, fig. 3a, b) is an incomplete waagenoconchid, too incomplete for Cooper & Grant (1975, p. 1044) to identify with any of their material, and it has close-set spines not like those of *Glabrispinus*.

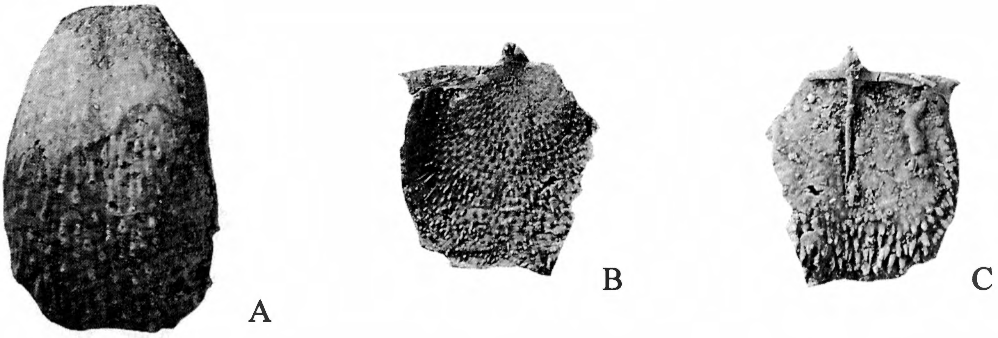

Fig. 6.19. *Glabrispinus kingi* new genus, new species. A, ventral exterior, USNM 153903b. B, C, internal and external views of holotype, USNM 153903a. Specimens from Cathedral Mountain Formation (Kungurian), west Texas, United States, x1. See Cooper & Grant (1975).

Tribe **WIMANOCONCHINI** new tribe

Fig. 6.18C, D, Fig. 6.20, Fig. 6.22

Name genus: *Wimanoconcha* Waterhouse, 1983a, p. 125 from Spitsbergen, here designated.

Diagnosis: Usually large, with dorsal valve that is almost flat, varying to gently concave, without externally distinct trail or geniculation. Middle Permian (Roadian) to ?Upper Permian (Wuchiapingian?).

Genera: *Wimanoconcha* Waterhouse, *Patellamia* new genus, *Quenstedtenia* Waterhouse, *Villaconcha* Waterhouse.

Discussion: Genera placed in Waagenoconchini have a dorsal valve that is flat over the disc, and a geniculate to subgeniculate distinct dorsal trail. By contrast, the dorsal valves in genera of Wimanoconchini have a flat or gently concave visceral disc and very short or no trail, or no perceptible trail: the dorsal trail as a rule cannot be distinguished from the disc externally. *Wimanoconcha* Waterhouse, based on *Ruthenia wimani* Fredericks, 1934 from Middle Permian of Spitsbergen has a thickened dorsal valve with no external trail. Ventral spines are posteriorly fine with slender elongate bases, and anteriorly the bases are short and broad. *Wimanoconcha* is distinguished by its flat dorsal valve that is thickened into a wedge, and is found in Arctic Permian faunas (Kalashnikov 1986, Grunt 2006), and reported from Western Australia by Archbold (1993). Brunton et al. (2000, p. 517) synonymized *Wimanoconcha* with *Waagenoconcha*, claiming to rely on a study by Archbold (1993). They completely misrepresented Archbold (1993, p. 20), who wrote "Based on the new material illustrated herein, the Western Australian species *Waagenoconcha imperfecta* Prendergast is assigned to *Wimanoconcha* on the basis of the morphology of mature specimens". Archbold certainly did not synonymize the two genera, and the allegation by Brunton et al. (2000) was wrong. *Villaconcha* Waterhouse, 2004b, p. 13, type species *Waagenoconcha magnifica* Cooper & Grant (1975, p. 1044, pl. 354, fig. 1-15) from the Willis Ranch, China Tank and Appel Ranch Members (Word, early Capitanian, or Middle Permian) of Texas, United States, has uniformly fine spines over the ventral valve, with no elongate bases, and no bands of spines with different diameters. The shape is distinctive with wide hinge, and the dorsal valve almost flat, with short trail. *W. platys* Cooper & Grant from the Road Canyon Formation (Roadian Stage) is congeneric. *Patellamia* new genus is close, but has a gently concave and unthickened dorsal valve. It appears in that respect to be close to *Quenstedtenia* Waterhouse 2004b, p. 12, type species *Q. rugosa* Waterhouse from the Basleo beds (Wuchiapingian or Upper Permian) of Timor. This genus has close-set rugae and growth steps, and elongate spine bases over most of the ventral valve, with erect spines restricted to the posterior

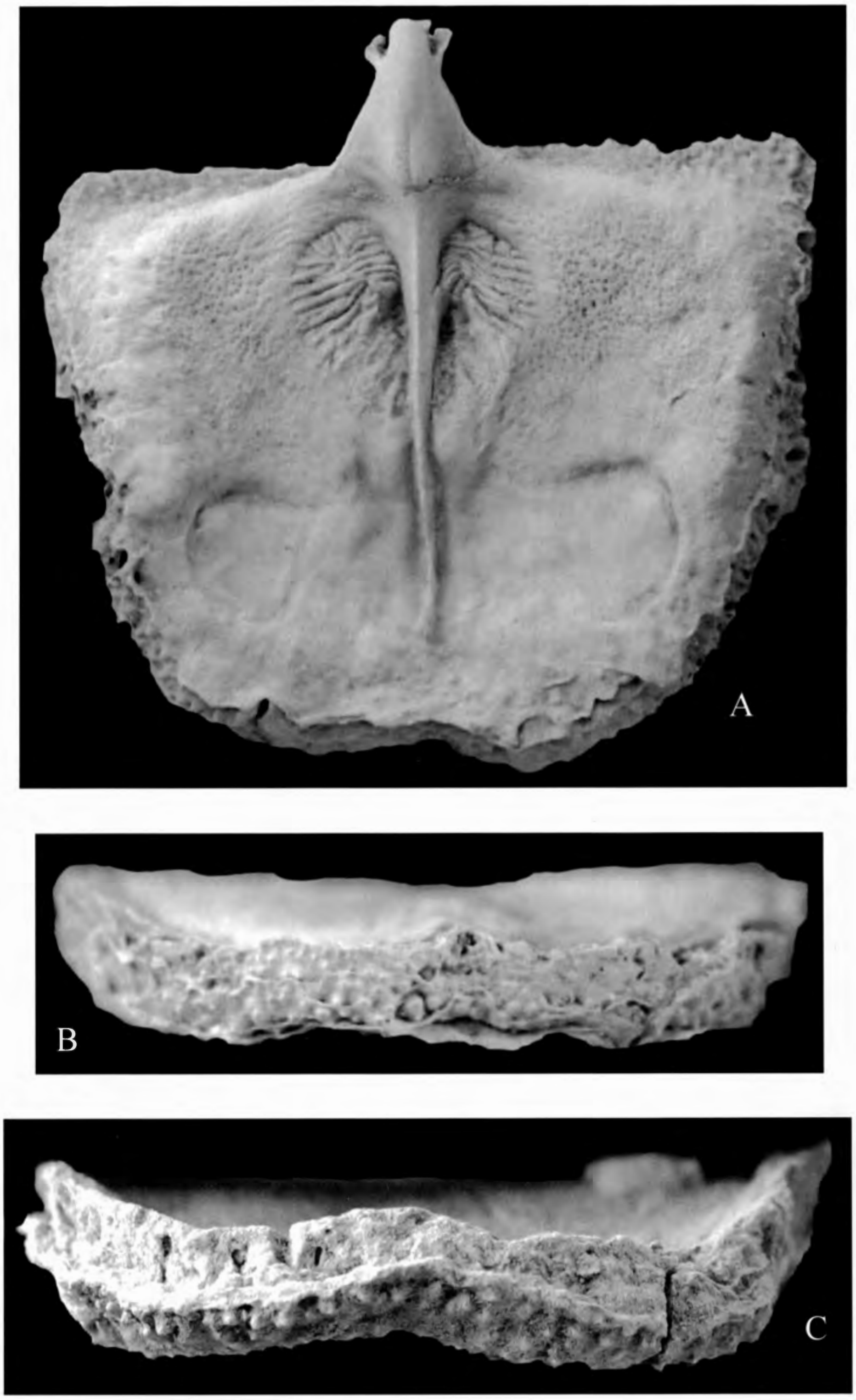

Fig. 6.20. *Wimanoconcha* sp. A, B, dorsal interior and anterior aspect of GSC 36800, inner side below, x2. C, anterior view of dorsal valve GSC 36801, showing anterior edge of dorsal valve, inner side below. From GSC loc. C-13356, Trold Fiord Formation (Capitanian), Melville Island, Canada, x1.5. (See p. 480). JBW photo.

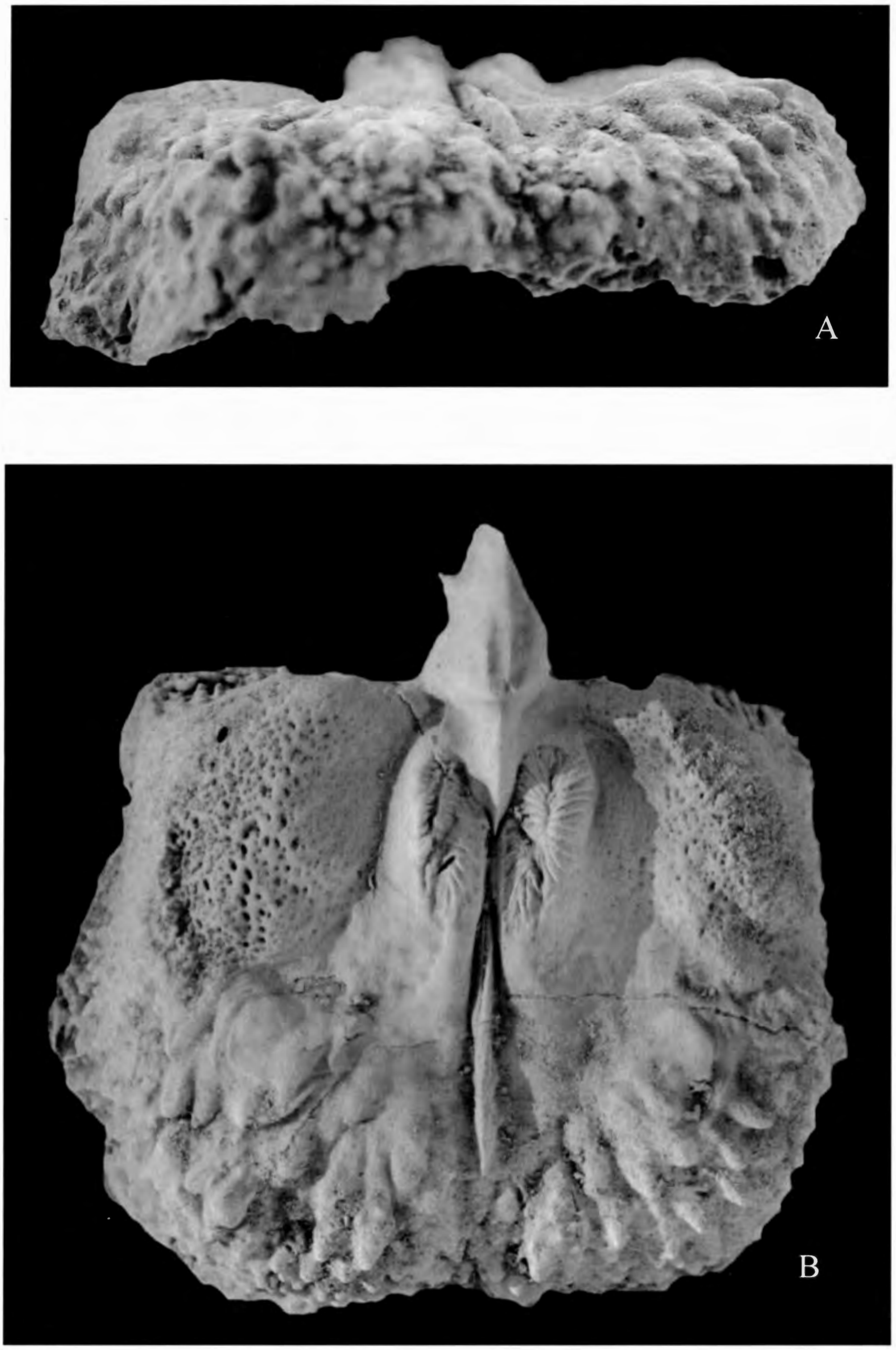

Fig. 6.21. *Wimanoconcha* sp. A, anterior edge (with inner side uppermost) and dorsal interior of GSC 133341 from GSC loc. C-13356, Trold Fiord Formation (Capitanian), Melville Island, Canada, x1.5. JBW photo.

shell. Dorsal spine bases are also elongate. Fine specimens have also been figured by Hamlet (1928, pl. 4, fig. 1a-c, pl. 5, fig. 1a-c) from Basleo-Wesleo in Timor, and additional material by Rothpletz (1892, pl. 10, fig. 20) and Archbold & Bird (1989, text-fig. 3C, D). The dorsal valve is gently concave, and no specimen shows sign of a geniculate trail. *Waagenoconcha delectus* Waterhouse & Gupta (1979b, pl. 2, fig. 11-16, pl. 3, fig 1-8) from the Wuchiapingian of the Himalayas is close but has a very short trail.

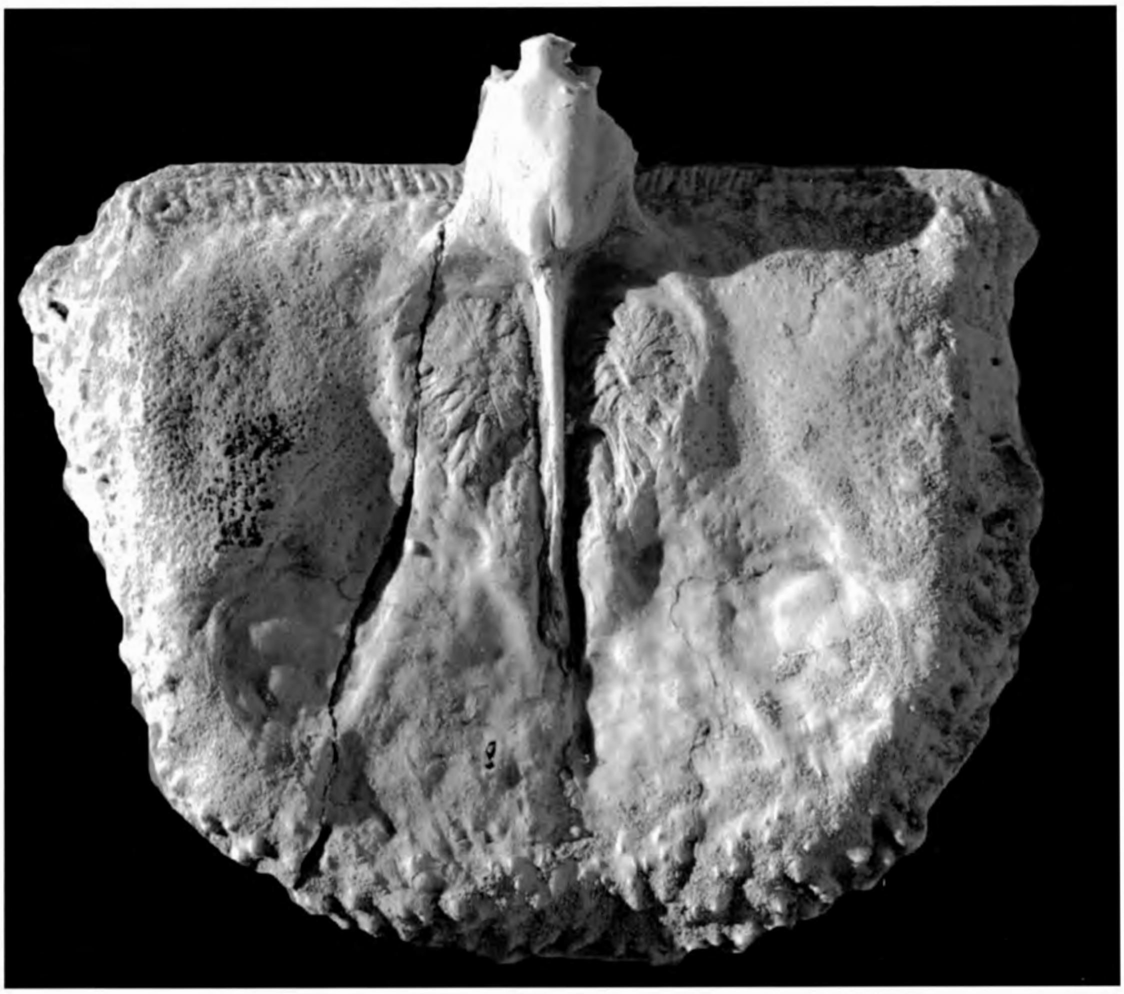

Fig. 6.22. *Wimanoconcha* sp. dorsal interior, GSC 36801 from GSC C-13356, x1.7. Trold Fiord Formation (Capitanian), Melville Island, Arctic Canada, x1. JBW photo.

Genus ***Patellamia*** new genus

Derivation: patella – small dish, Lat.

Type species: *Patellamia confinis* new species from Trold Fiord Formation, Melville Island, Canada, here designated.

Diagnosis: Medium to large, narrow body corpus and gently convex ventral valve, gently concave dorsal valve without flat disc or geniculate trail, spines over both valves fine and suberect, with only short bases.

Discussion: The genera *Waagenoconcha* Chao, *Waagenoconcha* (*Gruntoconcha*) Angiolini, *Fostericoncha* Waterhouse and *Contraspina* Waterhouse all have a somewhat similar shape in which the ventral valve is moderately arched, and the dorsal valve gently concave over the visceral disc, and curving more or less abruptly into a usually short trail at high angle. The differences between genera are revealed by different spine patterns, that are particularly consistent for the most widespread of these genera, namely *Waagenoconcha* Chao. *Villaconcha* Waterhouse and *Wimanoconcha* Waterhouse differ in having a dorsal valve that is largely flat or gently concave externally, with no trail, or only a very reduced trail, and in the latter genus the valve is considerably thickened. The present species and genus is like these two genera in that there is virtually no visible dorsal trail, the trail curving forward imperceptibly from the disc margin, but the dorsal valve is more concave, and the ventral valve is of very low convexity. Spines are fine on both valves, with very short elongate bases, especially posteriorly, and many spines are erect anteriorly. A second species is also recognized, also in the Permian of the Canadian Arctic, with very large size, and presence of distinct ears, sulcus and fold. *Quenstedtenia* Waterhouse is somewhat closer in that the dorsal valve is not thickened into a wedge, and is gently concave, curving imperceptibly into a short trail. The genus has long ventral spine bases and marked commarginal growth-stops.

Patellamia confinis new species

Fig. 6.23A, Fig. 6.24A-C, E

Derivation: confinium – a confine (geographic restriction), Lat.

Holotype: GSC 36818 figured herein as Fig. 6.23A, Fig. 6.24B from GSC loc. C-13356, Trold Fiord Formation (Capitanian), Melville Island, Canada, here designated.

Diagnosis: Large shells with slender corpus, gently convex ventral valve, shallowly concave dorsal valve without externally distinct trail, spines very fine on both valves, with short elongate bases posteriorly, erect anteriorly.

Material: Two complete specimens and ventral valve from GSC C-13356, two specimens from C-4025, ventral and dorsal valve from C-4026, single specimens from C-4005 and C-4006. Trold Fiord Formation (Capitanian), Melville Island, Arctic Canada. Single specimen from GSC loc. 58951, ?Assistance Formation, Melville Island. See Appendix A, part C, p. 479.

Dimensions in mm: ventral valve

GSC	Width	Length	Height
36824	89	76	18
36818	85	78	17.5
36817	90	70	27

Description: Shells gently concavo-convex, with trail not externally distinguished from visceral disc. The ventral umbo protrudes slightly beyond the hinge, with angle of 90-100° and incurved, hinge moderately wide, well rounded cardinal extremities and no differentiated ears. The dorsal valve is gently concave, without differentiated ears, being gently concave over the posterior disc, and curving imperceptibly into a trail, with no geniculation or subgeniculation. Ventral spines over the umbo and in front have short elongate bases up to 1mm long, numbering some ten in 5mm along a growth line, and with shorter bases or often erect, some fifteen in 10mm anteriorly, counted some 60mm in front of the umbo. Posterior dorsal spine bases are 1 to 1.5mm long, over 2mm long in front of mid-length, and shorter close to the anterior margin. Both valves, especially the dorsal valve, have low ragged growth lamellae, becoming growth steps posteriorly, and as close as five in 5mm over parts of the shell. There are also subdued radial ventral plicae anteriorly, but erratic and not evenly distributed.

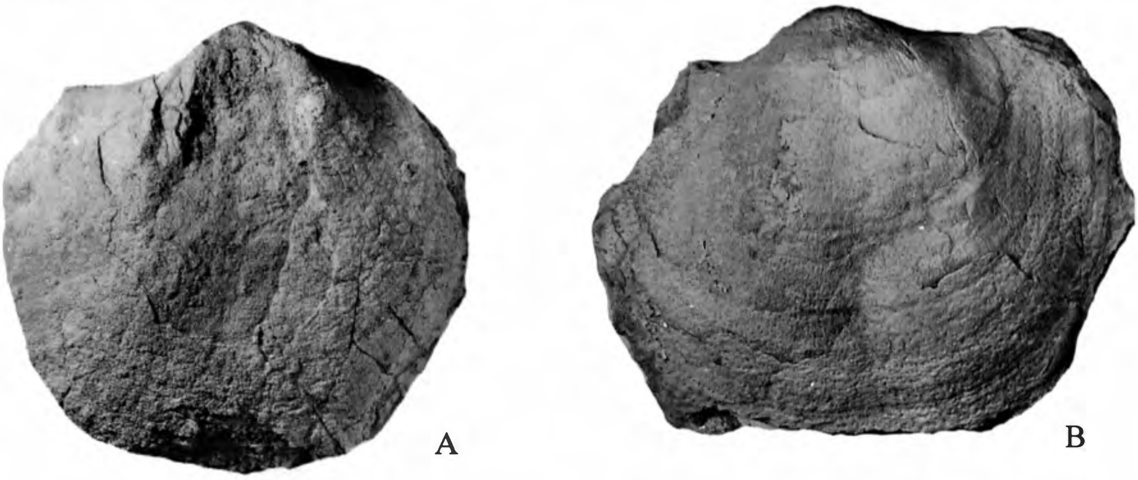

Fig. 6.23. *Patellamia confinis* new genus, new species. A, ventral aspect of holotype GSC 36818 from C-13356, x0.7. From Trold Fiord Formation (Capitanian), Melville island, Arctic Canada. B, *P. sulcata* new species, ventral aspect of GSC 36823 from GSC loc. 47846, x0.8, with slightly crushed venter, ?Degerbols Formation (Capitanian), Ellesmere Island, Arctic Canada. JBW photo.

The ventral adductor platform is impressed onto the dorsal exterior in GSC 36818, and forms a narrow long platform extending over the posterior third.

Resemblances: There appear to be no described species that resemble this form, which as far as is known is limited to the Permian deposits of Arctic Canada. The west Texas species *Waagenoconcha* (now *Villaconcha*) *platys* Cooper & Grant, 1975 from the Road Canyon Formation (Roadian) is somewhat similar in having low height, but its dorsal valve is almost flat, with upturned periphery, not gently concave. The hinge is wide and spines uniformly fine. The figure of the dorsal interior (Cooper & Grant 1975, pl. 355, fig. 11) suggests the possibility of a lateral buttress plate on one side, but this is not confirmed in the text, and is apparently an artifact, due to shell damage. Shells from the Canadian Arctic Assistance Formation ascribed to *Waagenoconcha payeri*? (Toula) by Harker & Thorsteinnson (1960, pl. 9, fig. 9-11) have longer umbonal spine bases and subgeniculate trail, much as in type *Waagenoconcha*.

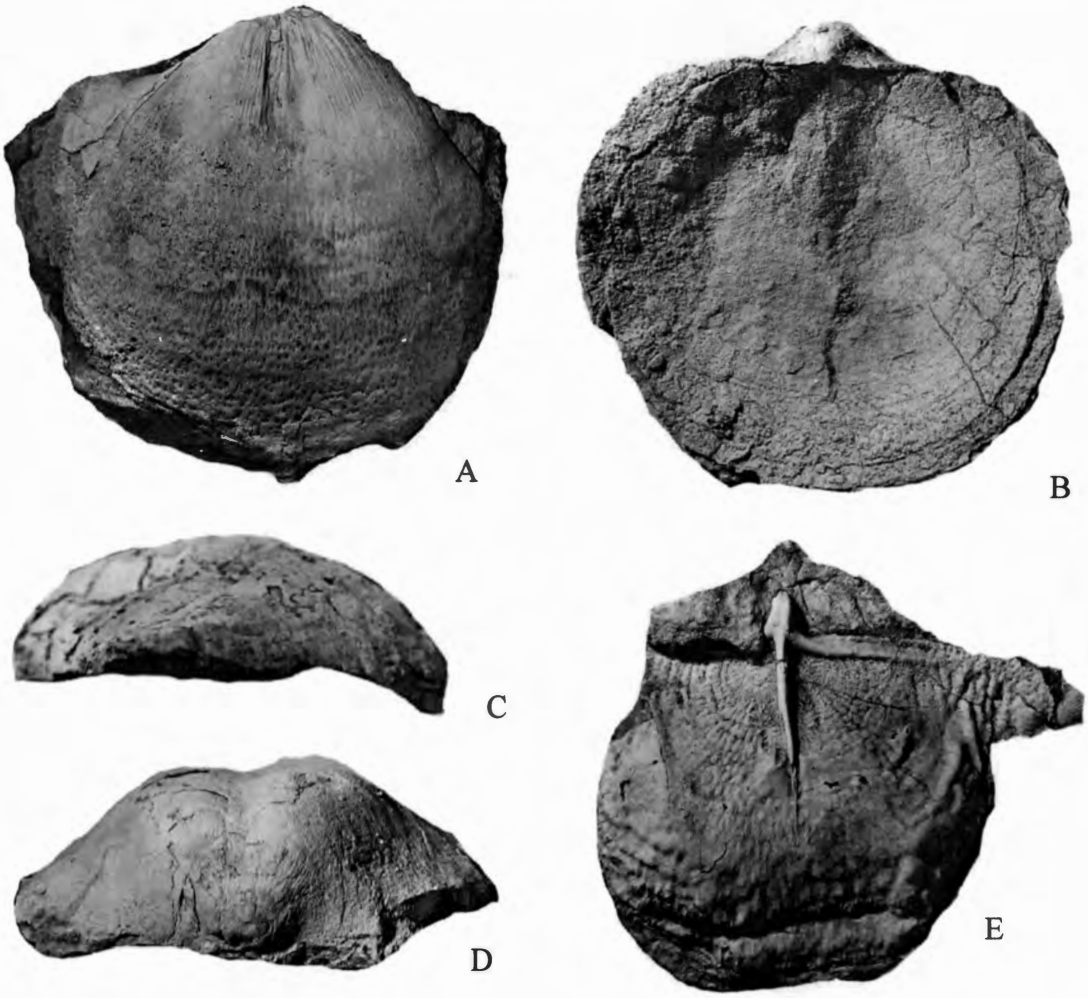

Fig. 6.24. A-C, E, *Patellamia confinis* new genus, new species A, internal mould of ventral valve GSC 36809 from C-4006, x0.9. B, dorsal aspect of specimen with valves conjoined, holotype GSC 36818 from GSC loc. C-13356, x0.8. C, lateral aspect of GSC 36824 from GSC loc. C-13356, x0.8. Trold Fiord Formation (Capitanian). E, interior of dorsal valve, GSC 36819 from GSC loc. 58951, x 0.8.?Assistance Formation (Kungurian). D, *P. sulcata* new species, posterior aspect of GSC 36823 from GSC loc. 47846, x0.8, ?Degerbols Formation. (See Fig. 6.23B). Specimens from Arctic Canada, see pp. 479, 480. A. Miller, B. O'Donovan & JBW photo.

Patellamia sulcata new species

Fig. 6 23B, Fig. 6.24D, Fig. 6.25 - 27

Derivation: sulcus – furrow, Lat.

Holotype: GSC 36811 from C-4095, Degerbols Formation, figured as Fig. 6.27B, here designated.

Diagnosis: Large shells with narrow ventral sulcus and dorsal fold.

Material: A ventral valve and dorsal valve from C-4095, Ellesmere Island, and ventral valve from GSC loc. 47856, Melville Island, Degebols Formation. Ventral and dorsal valve from C-4026, Trold Fiord Formation, Melville Island. Arctic Canada. See Appendix A, part C, p. 479.

Dimensions in mm: ventral valve, GSC 36811

GSC	Width	Length	Height
	140	120	36
dorsal valve GSC 36813			
	124	112.5	8

Description: Specimens very large, ventral umbo broad, with umbonal angle of 100°, hinge wide with small convex ears, disc broadly convex with shallow sulcus commencing at umbo and with angle slightly less than 20°, no external distinction from trail. On the dorsal fragment GSC 36810 from C-4026, the plicae are better developed, and appear to have covered the anterior half to third of the valve, probably coinciding with the extent of the trail. Spine bases short, fine and crowded over both valves.

Adductor platform in GSC 36811 long and narrow, diductor scars large and striate, band of coarse pustules around anterior margin. The platform is very long in the specimen from C-4026, extending for more than the posterior third of the shell length, and diductor scars do not extend as far forward. Behind them, each side of the posterior adductors, lie small lateral scars. Papillae cover much of the valve, and a low ridge lies under the umbonal slopes. Dorsal valve with no clearly differentiated ears, narrow fold commencing close to hinge, moderately conspicuous commarginal laminae, no trail. Medium septum short, moderately strong pustules laterally, becoming coarse in front.

Fig. 6.25. *Patellamia sulcata* new genus, new species, incomplete dorsal exterior, GSC 36810, x1. from C-4026, Trold Fiord Formation (Capitanian), Ellesmere Island, Arctic Canada. JBW photo.

Resemblances: This species clearly belongs to *Patellamia*, and is distinguished from the type species *P. confinis* by its larger size, presence of small ventral ears, and presence of shallow sulcus and low dorsal fold.

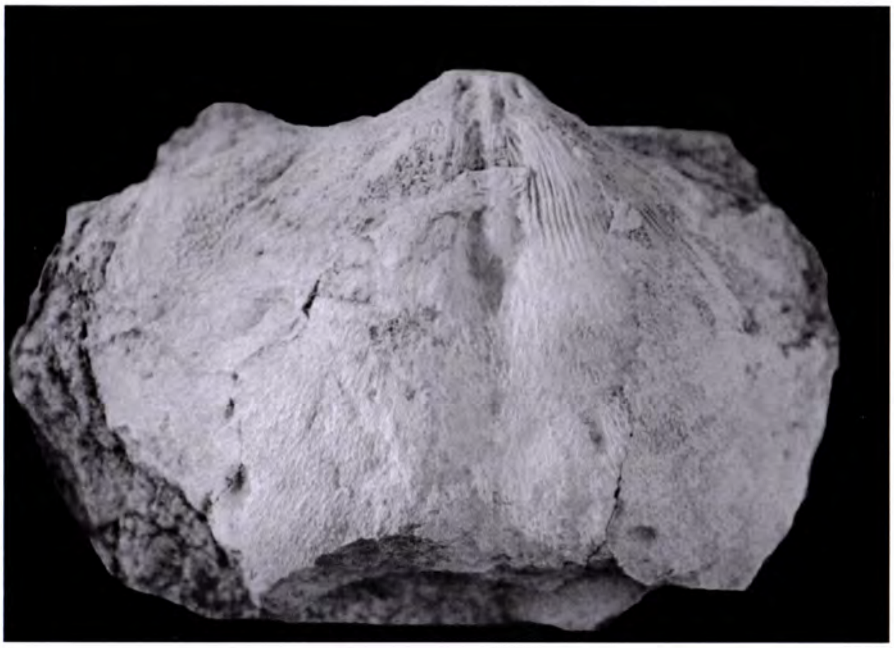

Fig. 6.26. *Patellamia sulcata* new genus new species, ventral aspect of GSC 36809, x1.2, from C-4026, Trold Fiord Formation (Capitanian), Ellesmere Island, Arctic Canada. JBW photo.

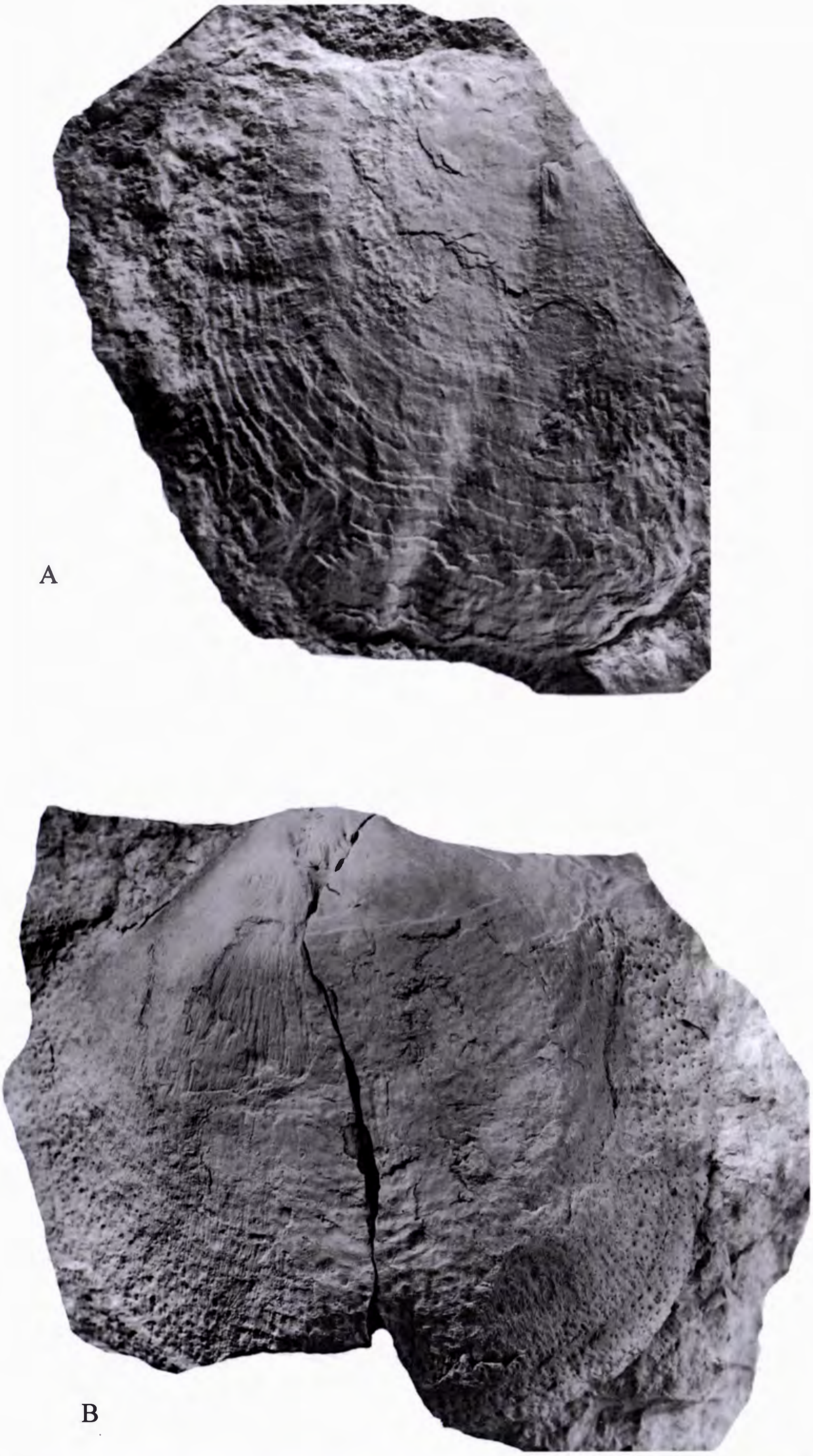

Fig. 6.27. *Patellamia sulcata* new genus, new species. A, worn interior of dorsal valve, GSC 36813, x0.8. B, ventral valve, GSC 36811, holotype, x0.7. From C-4095, Degebols Formation (Capitanian), Ellesmere Island, Arctic Canada. A. Miller & B. O'Donovan photo.

Subfamily **PUSTULINAE** Waterhouse, 1981

Fig. 6.28

[Pustulinae Waterhouse, 1981, p. 71].

Diagnosis: Medium to moderately large shells with low rugae, spines uniform and arranged in weakly defined commarginal rows, no cardinal pit or buttress plates. Lower Carboniferous (Tournaisian – Visean).

Genera: *Pustula* Thomas, ?*Etheridgina* Oehlert, *Putapustula* new genus, *Putusia* new genus, *Scutepustula* Sarytcheva.

Discussion: *Pustula* is a wide-ranging genus of Lower Carboniferous age. A number of species from the United Kingdom were described by Thomas (1914) and reassessed in Muir-Wood & Cooper (1960). The type species *Producta pustulosa* Phillips, 1836 has comparatively well spaced erect ventral spines in slightly irregular concentric rows, and Thomas (1914, p. 262) described dorsal ornament of ribs (ie. rib-like commarginal rugae) with intervening grooves that showed pittings corresponding with the spine bases on the opposite valve, and this pattern is confirmed by good figures provided for the type species by Muir-Wood & Cooper (1960, pl. 84, fig. 2, pl. 85, fig. 10) or Brunton et al. (2000, Fig. 359.2e). Brunton (1966, p. 238) noted that the ventral spines on *Pustula* were pustule-like without elongate bases, except anteriorly, but figures in Muir-Wood & Cooper (1960) and Brunton et al. (2000) do indicate weakly elongated bases which emerge gradually from the shell. The cardinal process of *P. pustulosa* is humped internally (Muir-Wood & Cooper 1960, pl. 84, fig. 5), as in some waagenoconchins.

Specimens of *Pustula multispinosa* Roberts (1963, pl. 5, fig. 9-14) from New South Wales, Australia, have regular elongate ventral spine bases in commarginal rows, one row for each commargon, approaching the arrangement in *P. pyxidiformis* (de Koninck, 1847, pl. 11, fig. 7?, pl. 12, fig. 1a, b, pl. 16, fig. 2) of Belgium and United Kingdom. In the Australian species, dorsal spines are fine, erect and closely spaced, not so obviously in single rows for each commargon, except posteriorly where they approach the arrangement in the type species *P. pustulosa*, as illustrated by Muir-Wood & Cooper (1960).

In two species described as *Pustula kenwoodensis* Carter and especially *P. oklahomae* Carter (1999, p. 105, Fig. 5D-L) from Oklahoma, United States, the ventral spines are like those of type *Pustula*, and the dorsal valve bears prominent and elongate pits arranged in regular quincunx. The dorsal posterior adductors are long and dendritic, and anterior adductors are smaller and smoother. There is a simple dorsal median septum, without buttress plates.

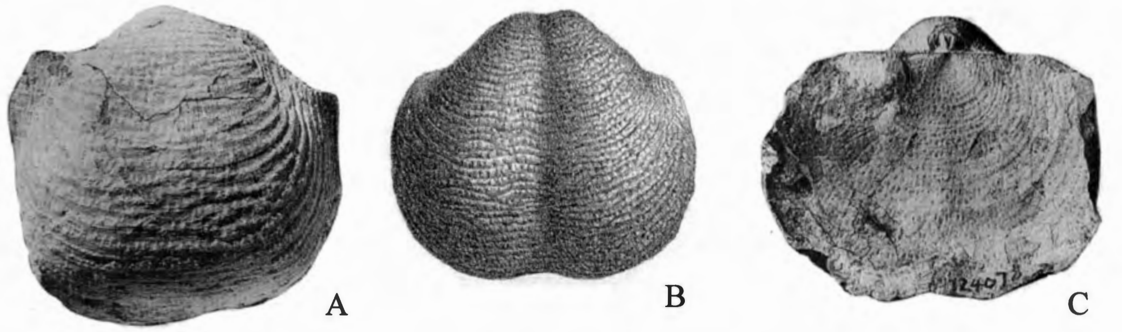

Fig. 6.28. *Pustula pustulosa* (Phillips). A, ventral valve holotype B 419, from Muir-Wood & Cooper (1960, pl. 85, fig. 7). from Bolland, Yorkshire, x0.8. B, ventral valve as figured by Davidson (1861, pl. 42, fig. 1) from County Kildare, Ireland, x 0.5. C, dorsal aspect, USNM 124078 as figured by Muir-Wood & Cooper (1960, pl. 84, fig. 2), from Narrowdale, Staffordshire, Specimens of Lower Carboniferous (Visean) age, from England, x0.6.

A possible forebear for *Pustula* is the waagenoconchin genus *Spinauris* Roberts, 1971, p. 107 from the Burt Range Formation of Tournaisian age in the Bonaparte Gulf of northwest Australia. Both valves are densely spinose with short elongate spine bases posteriorly, and a short trail. Roberts (1971) reported an antron in the dorsal septum, and some figures suggest, faintly, the possible presence of extremely low ridges, inconsistent in strength and length, comparable in position to the lateral septa of Balkhasheconchinae (see Roberts 1971, pl. 20, fig. 3, 4, pl. 21, fig. 1, 4, pl. 22, fig. 3). That as well as the presence of a posterior lateral tuft of spines reminiscent of those in

Araksalosia (see pp. 239-240), raises the possibility that descendents of *Spinauris*, though treated as Waagenoconchini by Brunton et al. (2000, p. 518), should be reclassed as early Balkhasheconchinae which gave rise to *Campbelliconcha* and *Buxtoniella* (p. 258). But the ridges are weak, and show little consistency in their presence or distribution.

Genus ***Putapustula*** new genus

Fig. 6.29

Derivation: puta – suppose, Lat.; Pustula – brachiopod genus.

Type species: *Pustula multispinata* Roberts, 1963, p. 13 from Bingleburra Formation (upper Tournaisian) of New South Wales, Australia, here designated. Kept at Australian Museum, Sydney.

Diagnosis: Shells of medium size, ventral spines closely arranged in single rows along narrow commargons, with prolonged spine-bases. Dorsal spines erect, tend to be arranged in commarginal rows and more than one row anteriorly over commargons.

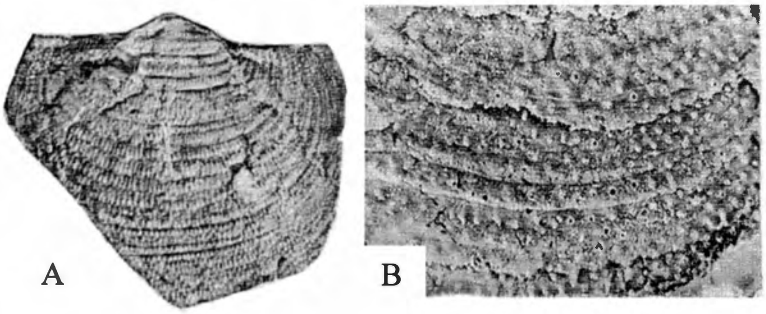

Fig. 6.29. *Putapustula multispinata* (Roberts). A, latex mould of ventral exterior, AMF 75658 (formerly UNE 5221), x1.5. B, latex mould of dorsal exterior of same specimen, x6. Note distinctive fine pustules. See Roberts (1963, pl. 5). From Bingleburra Formation (upper Tournaisian), New South Wales, Australia.

Discussion: The type species has been fully described by Roberts (1963). The dorsal septum is simple, with no buttress plates, and posterior dorsal adductors are smooth, whereas the posterior dorsal adductors are dendritic in type *Pustula*. The main distinction from type *Pustula* lies in the nature of the ventral spines, which are more irregularly and sparsely arranged and erect with less prolonged bases along the commarginal bands in type *Pustula* and allied species, numbering three or rarely four in 5mm, and somewhat quincuncial in arrangement, whereas those of *Putapustula* are closely packed, at seven in 5mm and close-set in concentric rows, with short elongate bases. Spines are more closely spaced posteriorly over the umbonal region in *Pustula*. Very fine dorsal pustules or spinules are also visible over the dorsal exterior (see Fig. 6.29B). *P. abbotti* Campbell (1956, p. 476, pl. 49, fig. 4-6) from upper Tournaisian faunas of the Lower Burindi beds in New South Wales is congeneric with *multispinata*, and also lacks dendritic posterior dorsal adductor scars. *Pustula pilosa* Thomas (1914, p. 284, pl. 20, fig. 3, 4) from the Carboniferous Limestone of Little Island, Cork, Ireland, has what were described as elongated closely packed spine bases, close to other species such as *Productus pyxidiformis* Koninck (1847, p. 116, pl. 9, fig. 7?, pl. 12, fig. 1a, b, pl. 16, fig. 2) from Visé, Belgium. But the dorsal valve of *pyxidiformis* as figured by Koninck (1847, pl. 12, fig. 1a) and Thomas (1914, pl. 18, fig. 6) shows broad and dendritic posterior adductor scars, and so is likely to be of a different lineage from the Australian material.

Genus ***Putusia*** new genus

Fig. 6.30

Derivation: putus – bright, splendid, Lat.

Type species: *Pustula oklahomae* Carter, 1999, p. 105 from St Joe Formation (upper Tournaisian), Oklahoma, United States, here designated.

Diagnosis: Ventral spines erect, arranged in slightly irregular commarginal rows, one row each along commargon. Dorsal valve ornamented by erect, very slender scattered spines and regular dimples in quincunx.

Discussion: The ventral ornament is close to that of *Pustula*, and the dorsal valve is characterized by less conspicuous spines that are erect and usually emerge at the anterior end of slightly elongate dimples, arranged in regular quincunx. The dimples are regular in spacing and form a conspicuous part of the dorsal ornament. *P. kenwoodensis* Carter, 1999, p. 102 from the same beds is congeneric. *Pustula morrocreekensis* Carter (1987, p. 38, pl. 11, fig. 24-32) from the Lower Carboniferous Banff Formation of western Alberta, Canada, is congeneric, and its ventral spines have more elongate bases.

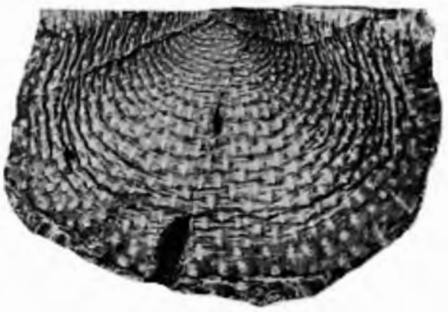

Fig. 6.30. *Putusia oklahomae* (Carter), dorsal valve exterior, CM 45026 from St Joe Formation (upper Tournaisian), Oklahoma, United States, as figured by Carter (1999, Fig. 5D), x1.5.

SUBORDER STROPHALOSIIDINA WATERHOUSE, 1975

Fig. 7.1

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 *Strophalosia*: instead he had included it in Chonetinae. Without explicitly correcting the statement, Brunton et al. (2000, p. 565) shifted ground and ascribed the suborder to Schuchert (1913, p. 389), claiming that that step was made by Brunton et al. 1995. Not so. Moreover Schuchert (1913) had never proposed an ordinal grouping for *Strophalosia* – he had regarded it as a subfamily. Separately, a chapter by 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, p. 365). Yet this later text (in small print) claimed that it preferred to follow Lazarev. Lazarev (1987, p. 48) in fact had excluded Richthofenioidea from the suborder. Indeed Lazarev (1987, p. 48; 1990, p. 77) included Lyttoniacea [Oldhaminidina or Lyttoniidina], which is excluded from Strophalosiidina by Brunton et al. (2000), as in Waterhouse (1978). In Strophalosiidina "sensu Lazarev 1989", explicitly asserted by Brunton et al. (2000, p. 365 in small print) as containing the understanding of Strophalosiidina in the *Revised Brachiopod Treatise*, the article by Lazarev referred only to what is regarded as Strophalosioidea. 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). Brunton et al. (2000, p. 595) misrepresented the prior proposals by Waterhouse, ascribed the suborder to Schuchert long after the suborder had already been proposed by a different author, 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. Lazarev (2003, p. 492) later complained about the first section on Strophalosiidina (ie. Brunton, Lazarev & Grant 2000), which he evidently regarded as less than acceptable, and wrote that he took no part in it. That means C. H. C. Brunton wrote the entire section (for by that time, Grant had died). The version in which Lazarev says he took no part (Brunton, Lazarev & Grant, 2000) was far more accurate than the second account (eg. Brunton et al. 2000). So who wrote the second part? According to Lazarev, it was R. E. Grant, which may not accord fully with the statement by Brunton (p. 362) that Permian Productida being written up by Grant had to be redistributed between Brunton and Lazarev after Grant's death. That confusion prevailed is possibly implied by the title to the section in the *Revised Brachiopod Treatise* by Brunton et al. (2000, p. 424). The section is headed "Productidina". Yet it includes not only Productidina (p. 424), but Strophalosiidina (p. 565) as well, signifying perhaps a change of mind during publication, or oversight.

Diagnosis: Genera either exhibiting well formed hinge apparatus with cardinal areas, teeth and sockets, and ventral cicatrix, pseudodeltidium usually present, or evolved from such genera. Ornament of spines which may be halteroid or rhizoid but no strut spines, spines as a rule arranged in quincunx, but may involve ventral cardinal spines, adductor scars usually only slightly or not dendritic, cardinal process distinctive. Simple to semi-elaborate brachiophore feeding apparatus of various constructs, generally occupying large part of dorsal floor in ancestral superfamily, morphing into productiform or sublyttoniid construct in later superfamilies.

Discussion: As will be seen from this study, the arrangements in the *Revised Brachiopod Treatise* are partly recast, to better express evolutionary relationships. Cooperinidae, treated as a mere family within Aulostegoidea by Brunton et al. (2000, pp. 605-606), is elevated in standing to express its morphological separateness (Waterhouse 2002b, p. 44, 2010a), and shown to be close to Strophalosioidea and to Oldhaminidina.

2. Superfamily **STROPHALOSIOIDEA** Schuchert, 1913

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

Diagnosis: Well formed cardinal areas, teeth and sockets, ventral cicatrix, spines halteroid or rhizoid but no strut spines, spines as a rule arranged in quincunx, but may involve ventral cardinal spines, adductor scars usually only slightly or not dendritic, cardinal process distinctive. Brachiophore feeding apparatus generally occupying large part of dorsal floor.

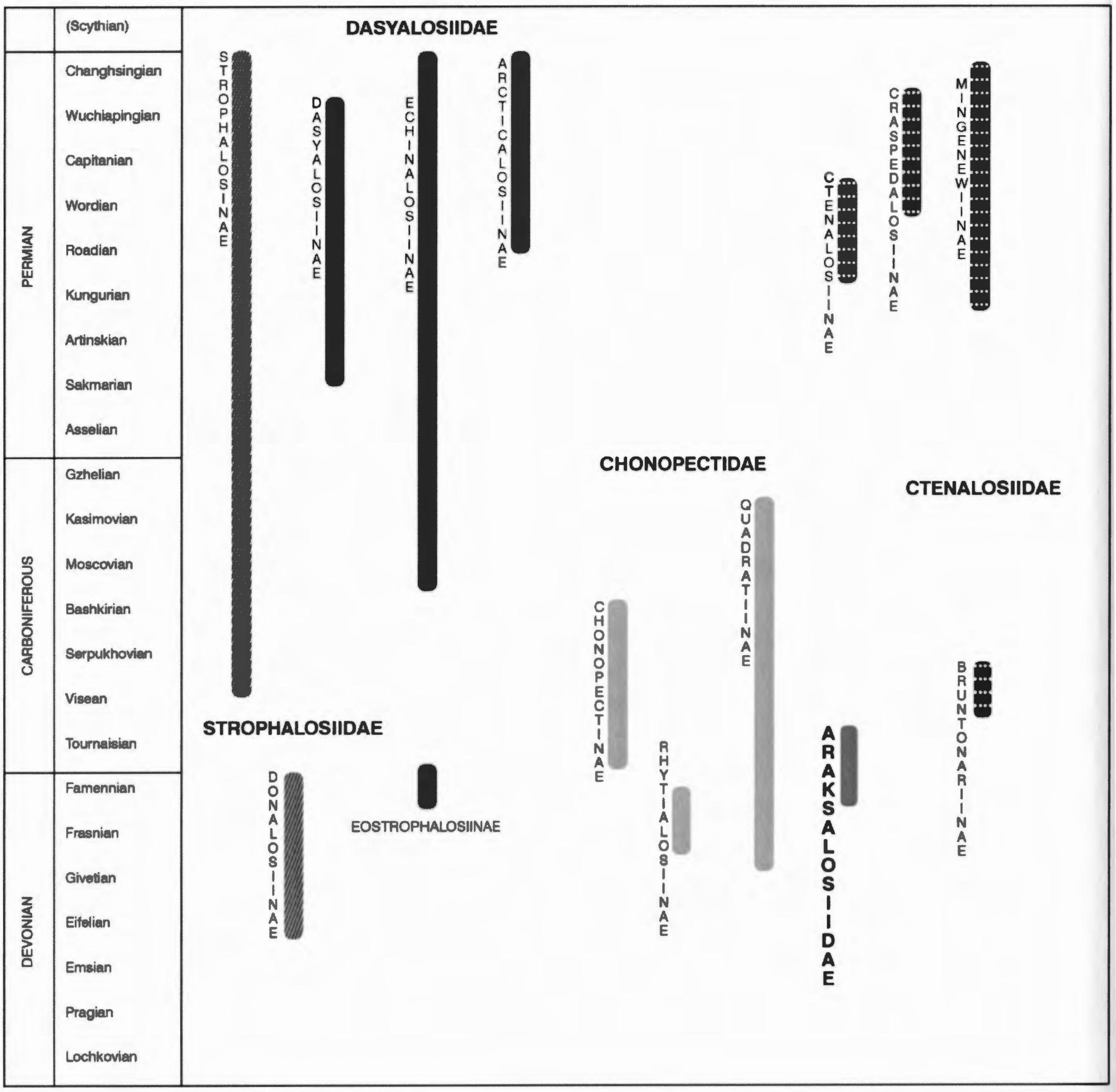

Fig. 7.1A. Range chart for Superfamily Strophalosioidea.

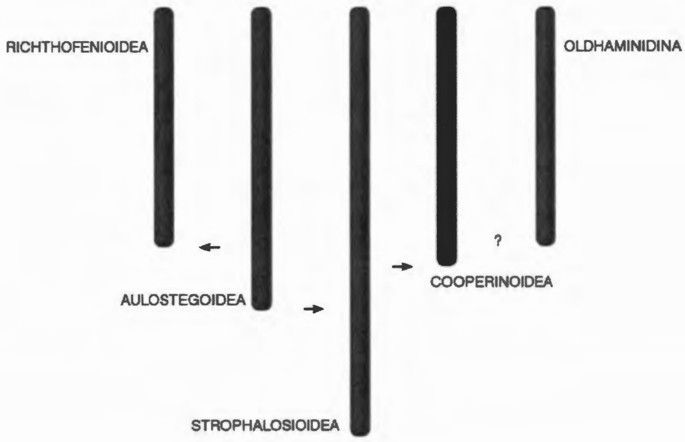

Fig. 7.1B. Overview of interrelationships within and between superfamilies of Strophalosiidina and Oldhaminidina, during the Carboniferous followed by the Permian Period..

- **Family Strophalosiidae Schuchert, 1913**
  - Subfamily Strophalosiinae Schuchert, 1913
    - Tribe Strophalosiini Schuchert, 1913
    - Tribe Truncateniini Liao, 1982
  - Subfamily Donalosiinae Lazarev, 1989
- **Family Dasyalosiidae Brunton, 1966**
  - Subfamily Dasyalosiinae Brunton, 1966
  - Subfamily Eostrophalosiinae new subfamily
  - Subfamily Echinalosiinae Waterhouse, 2001
    - Tribe Echinalosiini Waterhouse, 2001
    - Tribe Marginalosiini new tribe
    - Tribe Wyndhamiini Waterhouse, 2010a
  - Subfamily Arcticalosiinae Waterhouse, 2001
    - Tribe Arcticalosiini Waterhouse, 2001
    - Tribe Biplatyconchini new tribe
- **Family Chonopectidae Muir-Wood & Cooper, 1960**
  - Subfamily Chonopectinae Muir-Wood & Cooper, 1960
    - Tribe Chonopectini Muir-Wood & Cooper, 1960
    - Tribe Semenewiini Muir-Wood, 1962
  - Subfamily Quadratiinae Lazarev, 1989
  - Subfamily Rhytialosiinae Lazarev, 1989
- **Family Araksalosiidae Lazarev, 1989**
  - Subfamily Araksalosiinae Lazarev, 1989
  - Subfamily Whidbornellinae new subfamily
  - Subfamily Acanthatiinae new subfamily
- **Family Ctenalosiidae Muir-Wood & Cooper, 1960**
  - Subfamily Ctenalosiinae Muir-Wood & Cooper, 1960
  - Subfamily Bruntonariinae new subfamily
  - Subfamily Mingenewiinae Archbold, 1980
  - Subfamily Craspedalosiinae Waterhouse, 2002b

Table 9. Superfamily Strophalosioidea Schuchert, 1913.

Discussion: It is necessary to change some aspects of the classification of Strophalosioidea offered by Brunton et al. (2000). Diagnoses offered particularly for Devonian groups fail to offer any means of discrimination from the principal family Strophalosiidae – other than age, and there is no reason to assume that strophalosiids did not commence early in the history of the superfamily. Statements purporting to differentiate strophalosiiform groups of Devonian age, especially amongst Araksalosiidae, such as "presence of pseudodeltidium and chilidium", "cicatrix present, marginal structures absent, concentric ornament may be lamellose, visceral disc thin, dorsal spines absent " (Brunton et al. 2000, p. 576), offer no means of distinction from Strophalosiidae, and no positive observations were provided to reinforce the distinctions of Araksalosiidae and other Devonian strophalosioids from Family Strophalosiidae.

Two morphological attributes require continuing assessment for evolutionary significance, both concerned with the dorsal valve in Strophalosiidae and allied families. One involves the nature of the valve as a whole, whether it is thickened in a wedge with short or no trail, or is more concave and less thickened anteriorly, with long trail as a rule. The two morphotypes are readily distinguishable, and consistent in large populations from single fossil localities, and widely across a sedimentary basin at the same stratigraphic level. As a working hypothesis, the difference is judged to be of generic significance. But whether that is correct will require ongoing evaluation. Nor is the cause clear, although it is noteworthy that in east Australia, the wedge-shaped dorsal valves are characteristic of cold-climate lithosubstrates, which bear glacial drop-stones and are characterized by low faunal diversity (Waterhouse & Shi 2010). These genera and species with wedge-shaped dorsal valves may alternate through the stratigraphic column with genera and species which lack wedge-like dorsal valves, and may be found in zones with indices for warmer waters (Waterhouse 2011), though this may not always be true. Provisionally some tribes have been recognized for genera with wedge-like dorsal valves, but this does not preclude the possibility of some wedge-like dorsal-valved genera arising independently within other tribes and subfamilies.

Archbold & Simanauskas (2001, p. 221) suggested that presence or absence of dorsal spines was useful at generic level, but "unlikely to be a feature of subfamilial importance", but by assembling strophalosiiform genera in clusters characterized in part through having or lacking dorsal spines, it is clear that the assemblages are natural, because they also share attributes of ventral ornament, internal detail, and nature of the dorsal valve. That in no way removes the possibility that exceptional species and genera arose occasionally within the ranks of a tribe characterized by presence or absence of dorsal spines. For example, *Melvillosia* Waterhouse has scattered and rare dorsal spines, but is otherwise very close to *Craspedalosia* Muir-Wood & Cooper, which lacks spines, and is therefore classed with that genus in Craspedalosiinae.

Family **STROPHALOSIIDAE** Schuchert, 1913

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

Diagnosis: No dorsal spines, short trails. No lateral buttress plates as a rule, although exceptions occur.

Discussion: The family is further defined by the nature of other families, as outlined below.

Subfamily **STROPHALOSIINAE** Schuchert, 1913

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

Diagnosis: Ventral spines only as a rule, usually irregular, may be differentiated as sturdy suberect and fine subprostrate spines, no strongly developed ventral hinge row of spines as a rule. Cardinal process with tall shaft, terminally trifid or quadrifid.

Discussion: Heteralosiinae Muir-Wood & Cooper, 1960 is synonymized with Strophalosiinae. Differences are slight, and no consistent discrimination can be found. The only apparent difference between *Strophalosia* King, 1844 and *Heteralosia* R. H. King, 1938 lies in the possible absence of dorsal dimples from *Heteralosia*, and that is treated as a generic rather than subfamilial distinction, in the context of the particular family group. Brunton (1966, p. 188) regarded the two genera as indistinguishable except for age and geographic distribution, parameters deemed herein to be significant, but in this case not supporting subfamilial distinction.

Tribe **STROPHALOSIINI** Schuchert, 1913

Fig. 7.2, Fig. 7.3

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

Diagnosis: Shells tending to have capillae and often dimples on dorsal valve; dimples may form deep network. Lower Carboniferous (Asbian) to Upper Permian (Changhsingian).

Genera: *Strophalosia* King (syn. *Leptaenalosia* King), *Baikuralia* new genus, *Cicatrixia* Waterhouse, *Coronalosia* Waterhouse & Gupta, *Crassispinosella* new genus, *Crenalosia* Waterhouse, *Etherilosia* Archbold, *Fimbrianalosia* new genus, *Fortispinalosia* new genus, *Heteralosia* King, *Keoghalosia* Waterhouse, *Leptalosia* Dunbar & Condra, *Lialosia* Muir-Wood & Cooper, *Liveringia* Archbold, *Sphenalosia* Muir-Wood & Cooper, *Strophalosiaria* new genus, *Tupelosia* Archbold & Simanauskas.

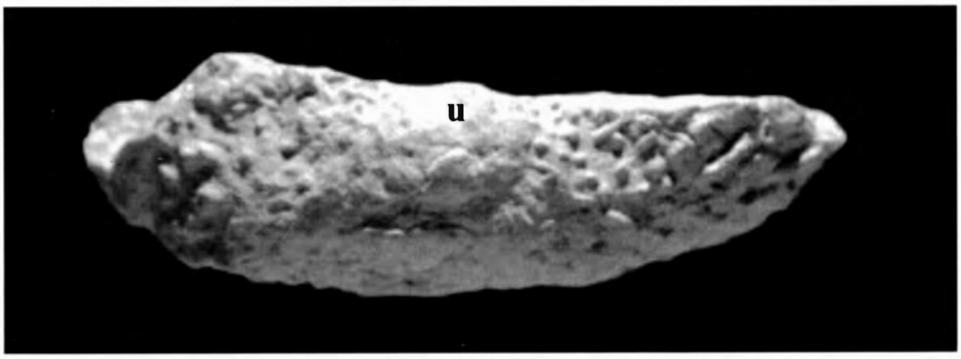

Fig. 7.2. *Strophalosia gerardi* King, plaster mould BR 3068 of holotype prepared by J. Mitchell, University College, Galway (now National University of Ireland, Galway), posterior view, x3. Specimen from ?Laddakh, northwest India. u = umbo. See also Fig. 1 and Fig. 2, p. 9. JBW photo.

Discussion: *Lialosia* and *Liverynga* are genera with few ventral spines, so that although difficult to determine their tribal position, they are regarded as members of the tribe, reduced in ornament.

Strophalosia King, 1844, p. 313, type species *S. gerardi* King, 1846, and figured by King (1850, p. 96, pl. 19, fig. 6, 7), is based on two specimens (Fig. 2, 3, p. 9, Fig. 7.2), believed to come from Ladakh, northwest India, and no further topotype material is known. From personal observation, the most widespread of fossiliferous Permian faunas in the Himalayan region belongs to the *Lamnimargus himalayensis* Zone, of Wuchiapingian (Lopingian) age. For the holotype of *S. gerardi*, the ventral exterior is moderately well preserved, whereas the dorsal valve is rather worn, and of questionable reliability. The second specimen is a dorsal valve, examined and discussed by Waterhouse (1964) and Brunton (1966), and shown to lack spines. Of particular interest is the detail of its ornament, in particular the presence or absence of radial capillae, and the presence or absence of elongate or rounded pits, which may be arranged in quincunx. Waterhouse (1964) and Brunton (1966, pl. 1, fig. 7) recorded tubercles and pits or dimples, but no capillae in type *gerardi*. Another species from the region that may be ascribed to *Strophalosia* includes *Strophalosia* (*Heteralosia*) *sublamellata* Reed (1944, p. 107, pl. 6, fig. 6, 6a, pl. 7, fig. 8, 8a, 9, 9a) from the "Lower Productus Limestone" or Amb Formation, Salt Range, Pakistan. This shows some suggestion of tubercles and no capillae on a worn surface. From the *Lamnimargus himalayensis* Zone of the upper Shyok Valley of the south Karakorum Range in northwest India, close to the source of *S. gerardi* King, *S. diadema* Waterhouse in Waterhouse & Gupta (1983, p. 237, pl. 1, fig. 6-9, pl. 3, fig. 2-4) has ventral valves close in outline to that of *gerardi*, and somewhat less concave dorsal valve. Ventral spines are coarser posteriorly in *gerardi* and similar anteriorly, and the dorsal valve has distinct pits, but no capillae or spines. Reproduction of figures was poor in Waterhouse & Gupta (1983), so that two of the figures are represented herein as Fig. 7.3A, C. Further material (Fig. 7.3B, D) from the Himalaya comes from central Nepal, in the *Lazarevonia arcuata* Zone of the Pija Member, of Changhsingian age (Waterhouse 1983a, p. 118, pl. 2, fig. 1, 2; 2004a, p. 73, pl. 2, fig. 2, 4). The material was tentatively identified as *Strophalosia gerardi* (?), on the basis that the hinge was comparatively short and dorsal valve moderately concave. Ventral spines are moderately close, although spaced further apart in some specimens, including the figured specimen, and closely comparable in other specimens. There is a degree of wishful thinking in the identification, because so much study in the Himalaya has still failed to definitely find topotype or exactly identical material of *S. gerardi*, and Waterhouse (1983a) admitted that the Pija material was not completely identical, because the figured dorsal valve is smooth, without capillae or tubercles or pits, although growth increments are well preserved. Possibly the dimples developed later, but were capillae present, they should be observable.

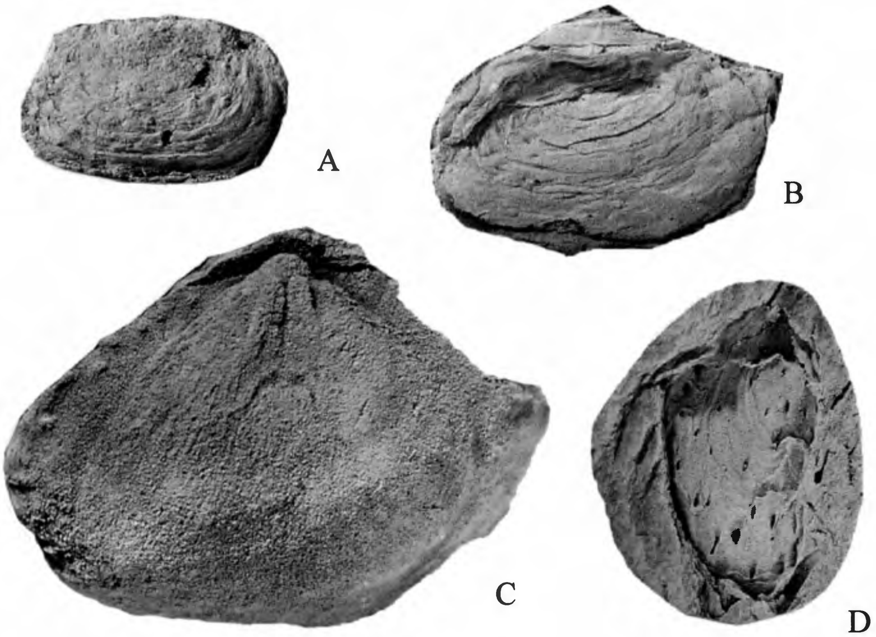

Fig. 7.3. A, C, *Strophalosia diadema* Waterhouse. A, dorsal valve holotype, x1. C, internal mould of ventral valve, x2. From *Lamnimargus himalayensis* Zone (Wuchiapingian), upper Shyok Valley, northwest India. Kept at CASG, Chandigarh, India. B, D. *Strophalosia gerardi* King (?) of Waterhouse (1983a). B, dorsal aspect of latex cast, valves conjoined, UQF 73603. D, external mould of ventral valve, UQF 73604. Specimens x2, from Pija Formation (Changhsingian), north-central Nepal. J. Coker & JBW photo.

From the Bap Formation of Rajasthan, north India, *Strophalosia perfecta* Waterhouse & Rao (1989, p. 28, Fig. 4) is well preserved. The ventral spines are erect and rarely prostrate, moderately close overall to those of *S. gerardi*, and the dorsal valve bears capillae and regularly spaced dimples (Fig. 7.5, Fig. 7.6).

A number of Permian species from Australia have been assigned to *Strophalosia*, but belong to different genera, including specimens figured as *Strophalosia* by Brunton et al. (2000, Fig. 400.1d-f), that belong in fact to *Coronalosia* Waterhouse & Gupta, 1978 – see Waterhouse (2004a, p. 55, pl. 4, fig. 17-21) and herein (Fig. 7.11 to 7.13). Two species from the Early Permian of Tasmania that were described by Clarke (1969, 1990, 1992) as *S. subcircularis* and *S. concentrica* are close in a general and tribal way to *S. gerardi*. On the ventral valve of *subcircularis*, the spines as compared with those of type *gerardi* are spaced slightly further apart, and are largely uniform in diameter, slightly thicker (often close to 1mm) than ventral spines in *S. gerardi* with a diameter close to 0.6mm, and there are no prostrate spines. By contrast, *S. gerardi* has scattered albeit few prostrate spines, and more crowded and fine spines over the umbonal region. For *S. concentrica*, spines are thinner, with a few to many prostrate spines. The dorsal valve of *subcircularis* is regularly dimpled, and where well preserved, marked by close-set capillae, often three per mm, much as in *S. perfecta* from Rajasthan. *S. concentrica* also has regular dimples (Clarke 1990, Fig. 5N), but capillae are rare according to Clarke (1990). The dorsal valve of *concentrica* is wedge-shaped, rather than externally concave, and the ventral disc is bordered by a low broad marginal ridge, morphological facets which appear to signify significant differences.

Another species from east Australia was described as *Strophalosia yalwalensis* Briggs (1998, p. 70, Fig. 37A-I) from the basal Snapper Point Formation, New South Wales, of uncertain age, possibly early Middle Permian, possibly older. As Briggs (1998) pointed out, the ventral spines are varied, many stout and others prostrate, with spine tunnels over mid-valve internally, and the dorsal valve is comparatively smooth apart from commarginal growth rugae and very shallow and indistinct postero-lateral dimples. No capillae are present. It is somewhat similar to *Strophalosia* but appears to be a little closer to *Keoghalosia* Waterhouse, 2010a, p. 45, based on *K. onegumensis* Waterhouse, 2010a from the One Gum Formation (Artinskian), Carnarvon Basin, Western Australia. This genus is characterized especially by a burst of ventral spines over the ears. Spines over the disc and trail are very similar to those of *yalwalensis*, which however does not clearly show a spine burst. *K. onegumensis* has numerous shallow dimples over the dorsal valve (Archbold 1986, Fig. 2N), and no dorsal capillae.

From the Calytrix Formation of the Grant Group in the Canning Basin, a species described as *Etherilosia calytrixi* Archbold (1995, p. 102, Fig. 5J-Q) and also recorded by Foster & Waterhouse (1988, p. 155, Fig. 7c, 8a-c) appears to be close to *Strophalosia gerardi*, especially in the nature of its ventral spines, which are moderately varied in diameter, and suberect to subprostrate, and the dorsal valve shows rare but no clear scattered dimples and only traces of capillae. Whilst Archbold (1995) treated the species as *Etherilosia* Archbold, 1993, which is small with only ventral spines, some rhizoid, Briggs (1998, p. 67) regarded the form as close to the Tasmanian species assigned to *subcircularis*. *Etherilosia carolynae* Archbold (1995) from the Carolyn Formation of the Grant Group has a large umbonal cicatrix, fine ventral spines, and shallow dimples and fine capillae on the dorsal valve, as in the Indian species *perfecta*. The type species of *Etherilosia, Strophalosia etheridgei* Prendergast, 1943, p. 43 as figured by Archbold (1986, Fig. 3; 1993, Fig. 7) appears to be an offshoot from *Coronalosia*, and some specimens display the hinge row of spines typical of that genus (Waterhouse 2010a, p. 46). Dorsal valves may display capillae and dimples, just as shown in *Coronalosia jimbaensis* (Archbold) and *C. irwinensis* (Coleman), as figured in Archbold (1986). But *Etherilosia convexa* Shen, Shi & Archbold (2003, p. 68, pl. 3, fig. 4-15) from the Late Permian Qubuerga Formation of southern Tibet shows the crinkled and deeply pitted dorsal valve seen in *Crenalosia* Waterhouse, based on Capitanian (Middle Permian) material from Texas, United States. In short, small-sized species that adhered by large cicatrix appear to have arisen from a range of genera.

From the Tupe Formation of the Paganzo Basin, Argentina, Archbold & Simanauskas (2001, p. 221, Fig. 3A-N, 4A-F) described *Coronalosia argentinensis*, with widely and unevenly spaced suberect ventral spines, not particularly like those of *Strophalosia*, and although there is some approach to the body spines of west Australian *Coronalosia*, there is no row of ventral hinge spines. The dorsal valve, according to the authors, lacks not only spines, but shows no dimples and no capillae. In many respects the species *argentinensis* approaches *Tupelosia* Archbold & Simanauskas, 2001, based on *T. paganzoensis* Simanauskas & Archbold from the same beds. *Tupelosia* is very distinctive with narrow hinge, short dorsal septum and thickened dorsal valve without trail, worn and not showing capillae or dimples, and distinctive ventral adductors. The cardinal process is squat, described as weakly bilobed, but with signs of a broad median shaft and small lobe to each side (Archbold & Simanauskas 2001, Fig. 4B, C). The species *argentinensis* shows similar ornament but slightly different internal detail and shape. It comes from the so-called *Tivertonia jachalensis* – *Streptorhynchus inaequiornatus* Zone (both genera in need of reassessment) in the San Juan Province, and was regarded as being of basal Permian age (Asselian) age by Cisterna, Simanauskas & Archbold (2002), Archbold et al. (2004) and Taboada (2010, pp. 167, 168). But radiometric ages indicate a Moscovian age according to Césari et al. (2011), and the species lies well below the first entry of the palynomorph *Converrucosporites confluens* (Archangelsky & Gamerro), which is largely Asselian in age and entered successions in very late Carboniferous (Stephenson 2009). According to Archbold & Simanauskas (2001), Argentine material described as *Heteralosiacornelliana* [not Derby] from the Quebrada Largo, Rio Blanco, San Juan by Antelo (1972, p. 164, pl. 2, fig. 1-5) is congeneric with *argentinensis*, but has finer spines, and the dorsal valve shows rare capillae. It has a gently concave dorsal valve and may prove to belong to *Tupelosia*.

In northern Canada, the upper Ettrain Formation of Kasimovian age contains a distinct strophalosiid species with dorsal valve ornamented very like the Tasmanian species *subcircularis* and even closer to that of *perfecta* from Rajasthan, India. Ventral spines are mostly subprostrate and of two diameters, like those of *perfecta* and *gerardi* rather than *subcircularis*, and the dorsal valve lacks spines and displays regular dimples and capillae. Internal detail is unremarkable, other than the presence of spine tunnels over the middle interior of the ventral valve. Strophalosiids are curiously absent from Cisuralian deposits of northern Canada, even though these are extensive and very fossiliferous, with innumerable brachiopods. But strophalosiids reappear in Canadian Permian deposits during Guadalupian time. A somewhat similar pattern appears to be the case in northern Russia, where outcrops are extensive, richly fossiliferous, and extensively described, with a number of Middle and Upper Permian forms recognized in Sarytcheva (1977). Several species are characterized by closely spaced uniform subprostrate spines over the ventral valve and comparatively dense pustules and knobs over the dorsal valve. They come closest to the west Australian strophalosiid genus *Keoghalosia* Waterhouse from the Jimba Jimba Calcarenite, of Artinskian age, but lack the postero-lateral ear burst of spines, and have more uniform spines, and so come even closer to "*Strophalosia*" *yalwalensis* Briggs from the basal Snapper Point Formation of New South Wales, Australia.

Genus ***Fortispinalosia*** new genus

Fig. 7.4

Derivation: forti – strong; spina – thorn, Lat.; alos – disc, Grk.

Type species: *Strophalosia fortispinosa* Hinchey & Ray, 1935, p. 249 from Warsaw Formation (Mississippian), Missouri, United States, here designated.

Diagnosis: Spines limited to ventral valve, in two series, fine prostrate series moderately numerous, no dorsal spines, capillae or dimples. Distinguished by thick lateral buttress plates in dorsal interior.

Discussion: The type species of this new genus was described as *Strophalosia* by Hinchey & Ray (1935, pl. 25, fig. 13-21), and later transferred to *Heteralosia* King by Muir-Wood & Cooper (1960, p. 81). It is close to these genera, especially *Strophalosia*, in the nature of ventral spines, which consist of a predominant coarse and less common subprostrate series, and finer scattered prostrate spines. The dorsal exterior is diversified by short laminae and low elongate rises, with no apparent dimples nor radial capillae. The internal dorsal valve of *fortispinosa* as figured by Hinchey & Ray (1935, pl. 25, fig. 15) and Muir-Wood & Cooper (1960, pl. 3, fig. 3, 5) is distinguished from *Heteralosia* and *Strophalosia* by having well defined broad lateral buttress plates lying behind and each side of the posterior adductor scars, and extending in front of low recurved dental socket ridges. Such lateral buttress plates are not observed in *Heteralosia, Strophalosia*, or other genera in the tribe. The posterior faintly visible brachial shields suggest that the posterior end terminates in front of the anterior end of the lateral buttress plates, between the anterior adductors and slim posterior adductor scars. The cardinal process is strophalosiid, comprised mostly of a tall main shaft bearing a posterior slit. A distinct albeit low dorsal marginal ridge circumscribes the visceral disc, with a short trail, curving forward from the disc.

A number of other Missisippian species of strophalosiid species are known, described as *Strophalosiaorbiculata* Hinchy & Ray, *S. subelliptica* Hinchey & Ray, *S. ? beecheri* Rowley, 1893 and *S. cymbula* Hall

& Clarke, 1893, showing less dense ventral spines, and where known, no lateral buttress plates. There are thus no other species yet known to belong to this genus.

Fig. 7.4. *Fortispinosella fortispinosa* (Hinchey & Ray), dorsal interior USNM 136341, x3, from Warwsaw Formtion (Mississippian), United States. See Hinchey & Ray (1935).

Genus ***Fimbrianalosia*** new genus

Fig. 7.5, Fig. 7.6

Derivation: fimbriae – threads, fringe, Lat.; alos –disc, Grk.

Type species: *Strophalosia perfecta* Waterhouse & Rao, 1989, p. 28 from the Bap Formation (Asselian), India, here designated.

Diagnosis: Ventral cicatrix small or absent, ventral spines mixed, of sturdy suberect and finer more prostrate spines; no dorsal spines, but dimples and fine capillae well developed.

Discussion: This genus is allied to *Strophalosia* W. King and*Heteralosia* R. H. King in the nature of its ventral spines, and has dorsal dimples like those of these genera, but in addition has well developed and persistent radial capillae over the dorsal valve.

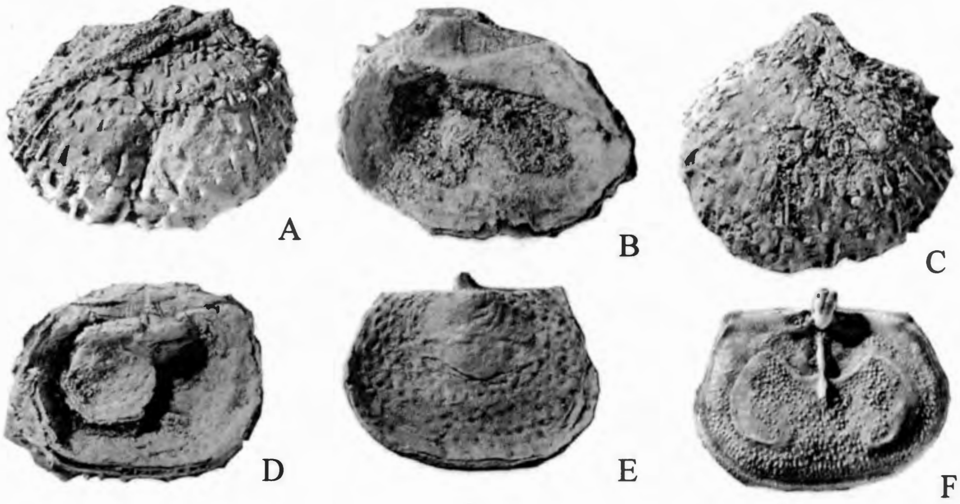

Fig. 7.5. *Fimbrianalosia perfecta* (Waterhouse & Rao). A, B, ventral and dorsal aspects of holotype OGC F5. C, ventral valve OCG F6. D, dorsal aspect of OGC F7, with juvenile specimen attached. E, F, external and internal views of dorsal valve OGC F8. Specimens x 2, from Bap Formation (Asselian), India.Photo J. Coker & JBW.

Fig. 7.6. *Fimbrianalosia perfecta* (Waterhouse& Rao), external view of dorsal valve OGC F 8, enlarged x3 to show traces of capillae. See Fig. 7.5E. Photo J. Coker & JBW

Fimbrianalosia ettrainensis Nazer & Waterhouse new species

Fig. 7.7, Fig. 7.8

1971 *Heteralosia* sp. Bamber & Waterhouse, pl. 1, fig. 3.

Derivation: Named for Ettrain Creek, north Ogilvie Mountains, Yukon Territory, Canada.

Holotype: GSC 37042 from GSC loc. 53727, figured in Fig. 7.7A, here designated.

Diagnosis: Moderate size, weakly transverse, small cicatrix, dorsal fine capillae and regularly spaced dimples.

Material: Some 400 specimens, including a few from GSC loc. 53727, 150 specimens from GSC loc. 53728 and 76 specimens at GSC loc. 57069, and several specimens from GSC loc. 57071. Common in silty beds throughout Ettrain Formation and equivalents of Yukon Territory. See Appendix A, Part C, p. 478.

Dimensions in mm:

Specimen	valve	width	length	height
GSC 37039	ventral	15.5	16.0	6?
GSC 37040	ventral	15.2	16	5?

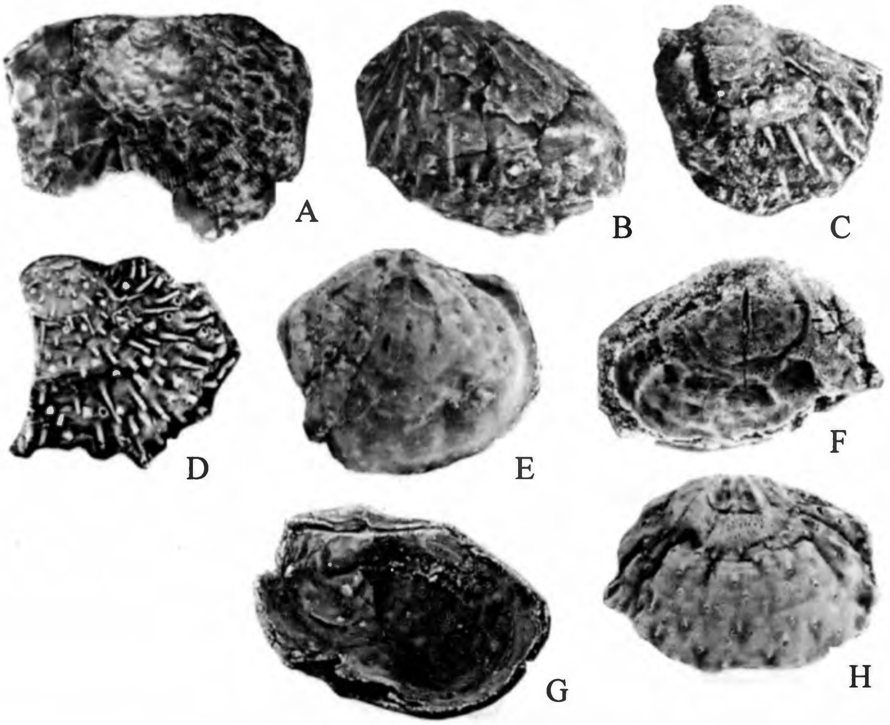

Fig. 7.7. *Fimbrianalosia ettrainensis* new species. A, dorsal view of holotype, GSC 37042, from GSC loc. 53727. B, ventral valve GSC 37043 from GSC loc. 53728. C, ventral valve GSC 37044 from same locality. D, latex cast of ventral exterior, GSC 37045 from same locality. E, natural mould of ventral interior, GSC 37046 from same locality. F, H, dorsal and ventral views of natural internal mould, GSC 37047 from same locality. G, latex cast of dorsal exterior and ventral beak, GSC 37048, from GSC loc. 53728. Specimens from Ettrain Formation (Kasimovian), Yukon Territory, Canada, x2. R. E. Nazer & B. O'Donovan, photo.

Description: Shell small to medium in size, subcircular to subquadrate in outline. Umbonal cicatrix usually present, and shell growth frequently irregular. Ears weakly developed, maximum width close to mid-length. Ventral interarea apsacline, up to 1.5mm high, delthyrium narrow with angle of 25°, mostly covered by convex pseudodeltidium. Dorsal interarea anacline and very narrow. Ventral valve ornamented by spines of two series, erect and prostrate, 0.3-0.6mm in diameter, mostly in quincunx, 1-2mm apart. The trail is short and non-geniculate. Weak irregular plicae up to 1.7mm across may develop near the anterior margin. Surface otherwise smooth, apart from fine inconspicuous growth lines. Dorsal exterior with fine uniform capillae, five or six per mm, and uniformly distributed dimples 0.7mm in diameter and 1mm apart, except for early growth stages, where shell is weakly rugose; no dorsal spines.

Ventral adductor scars located on low subtriangular platforms, and diductor scars weakly impressed. Three rows of endospines lie in front of the adductors. Teeth simple. Thin callus covers the posterior valve, and external spine bases may be visible over much of the valve. Dorsal median septum thin, extending for almost the length of the subtriangular platforms, which are smooth and divided into two sets. Brachial shields large, weakly impressed, extending in front of visceral disc, cardinal process slightly inclined ventrally and small, short socket ridges. Adductor scars raised.

Resemblances: *Fimbrinialosia perfecta* (Waterhouse & Rao) has a higher ventral interarea and slightly longer trail and more numerous dorsal dimples, and shorter dorsal septum. In other respects, the two are close. *F. carolynae* (Archbold, 1995, Fig. 4A-I) from Western Australia is smaller with wide hinge and more numerous prostrate spines. The dorsal valve bears faint to strong capillae and dimples.

This species was originally described as a new species of *Strophalosia* by Nazer (1977), on the basis of material collected by E. W. Bamber and J. B. Waterhouse.

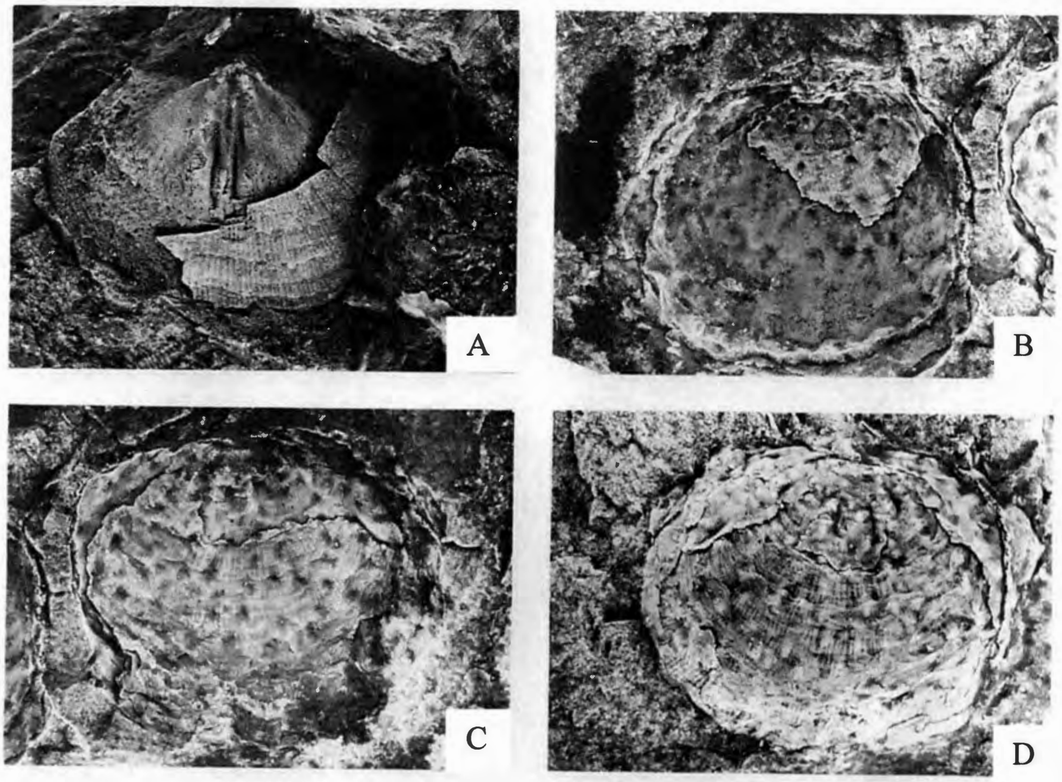

Fig. 7.8. *Fimbrianalosia ettrainensis* new species. A, vental valve interior overlain by fragment of dorsal valve, GSC 37039. B, dorsal view of conjoined specimen GSC 37040. C, external mould of dorsal interior, GSC 37401. D, unregistered interior of dorsal valve, decorticated to show external surface. Specimens from GSC loc. 57071, x3. Ettrain Formation (Kasimovian), Yukon Territory, Canada. R. E. Nazer& B. O'Donovan photo.

Genus ***Crassispinosella*** new genus

Fig.7.9, Fig. 7.10

Derivation: crassus – thick, stout; spina – thorn, Lat.

Type species: *Strophalosia subcircularis* Clarke, 1969, p. 22 from Glencoe Formation (Asselian), Tasmania, here designated.

Diagnosis: Highly convex ventral valve with spines of one series, mostly erect, dorsal valve deeply concave and ornamented by regular dimples in quincunx, fine radial filae common, but may be faint. Ventral myophragm often well developed.

Discussion: The type species of *Strophalosia, S. gerardi* King, 1846 from an uncertain Permian level of the Indian subcontinent in Ladakh (probably Late Permian), is represented by two specimens described by Brunton (1966) and Waterhouse (1964) and kept at the National University of Ireland, Galway. There are differences in the ventral spines on *gerardi* and *subcircularis*. On *gerardi*, posterior spines are crowded, and 0.3-0.4mm in diameter, and most are erect but some are finer and subprostrate: they are figured herein, and it will be noted there is no well developedhinge row. Spines over most of the shell are arranged in irregular commarginal rows, and are usually subprostrate, and range in diameter from 0.3 to 0.6mm, some erect, some completely prostrate. On *subcircularis*, spines are perceptibly different, being less crowded posteriorly, and more uniform and usually more erect with more space between rows. They range from 0.9 to 1.3mm in diameter. The surface of the dorsal valve of the type specimen of *gerardi* is very irregular, with low especially anterior growth steps, some growth increments, and erratically disposed short ridges and scattered depressions. The paratype of *gerardi*, a dorsal valve figured by Brunton (1966, pl. 1, fig. 9; Brunton et al. 2000, Fig. 400.1c), shows shallow pits more or less in quincunx over part of the valve. This is close to the arrangement of *subcircularis*, in which mature dorsal valves bear a small gently convex nepionic region with low commarginal rugae, and slightly elongate pits in quincunx, but smaller and immature *subcircularis* may lack these dimples. The species *subcircularis* also bears weak to strong radial capillae, numbering four to five in 1mm. *Fimbrianalosiaperfecta* (Waterhouse & Rao, 1989, Fig. 4) has fine dorsal capillae approaching those of *subcircularis*, but the ventral spines are more like those of *Strophalosia gerardi*. Because *Fimbrianalosia* is older than *Crassispinosella*, dating back to at least Kasimovian, it seems likely to given rise to *Crassispinosella*, through strengthening of the suberect ventral spines and loss of the prostrate spines, coupled with a weakening in the radial dorsal capillae.

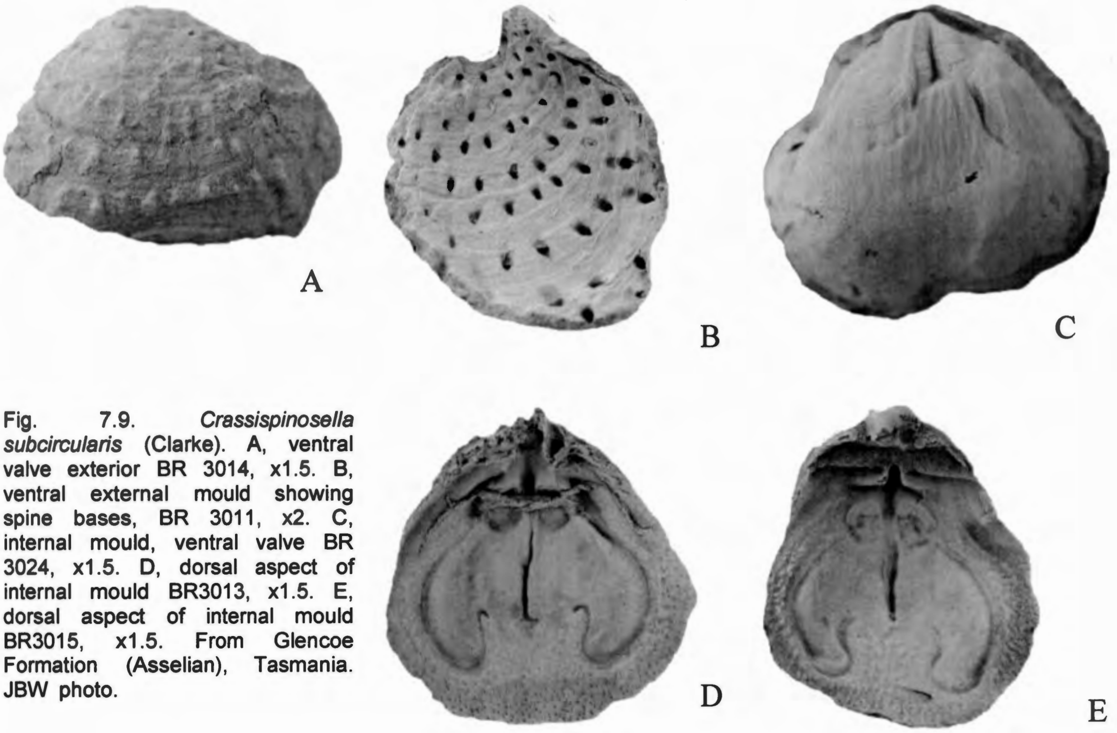

Fig. 7.9. *Crassispinosella subcircularis* (Clarke). A, ventral valve exterior BR 3014, x1.5. B, ventral external mould showing spine bases, BR 3011, x2. C, internal mould, ventral valve BR 3024, x1.5. D, dorsal aspect of internal mould BR3013, x1.5. E, dorsal aspect of internal mould BR3015, x1.5. From Glencoe Formation (Asselian), Tasmania. JBW photo.

Internal detail for the Tasmanian species has been closely described by Clarke (1969). One striking aspect is the strong development of a myophragm in many of the ventral valves (See Fig. 7.9C). As in many strophalosiids, the dorsal septum appears to be connected with the posterior inner end of the brachial shields, and so does not extend far forward. Low ridges lie outside the dorsal adductor impressions in some specimens (see Clarke 1969, pl. 2, fig. 5) so as to approach the lateral buttress plates in *Fortispinalosia* new genus (see p. 215), though the two genera differ considerably in the nature of the ventral spination, much larger posterior adductors in *Crassispinosella* (the posterior adductors are no more than a slender posterior lateral strip in *Fortispinalosia* – if present), and various other details. In *Fortispinalosia*, the posterior lateral ridges of the brachial shields pass into the lateral side of the anterior adductors, possibly to the junction with the putative posterior adductors, and the arrangement is more definite in *Crassispinosella*. But exceptionally in *Crassispinosella*, the lateral brachial ridges appear to pass outside the adductor scars, as in TMF 3547, figured by Clarke (1969, pl. 4, fig. 6; 1990, Fig. 5E), to apparently continue into socket ridges.

A number of specimens bear anterior radial rugae, and these were segregated as *Costalosia apicallosa* Clarke, 1969, later revised to *Licharewiella apicallosa* by Clarke (1990, 1992). Another variant was named *Wyndhamia*? *irregularis* Clarke, 1969, and two varieties *tumida* and *brevicardinalis* with *subcircularis* were recognized by Clarke (1969). All were synonymized with *subcircularis* by Briggs (1998, p. 69), but not by Clarke (1990, 1992), and it would be advantageous to learn more about the specimens identified by Clarke with *Wyndhamia*.

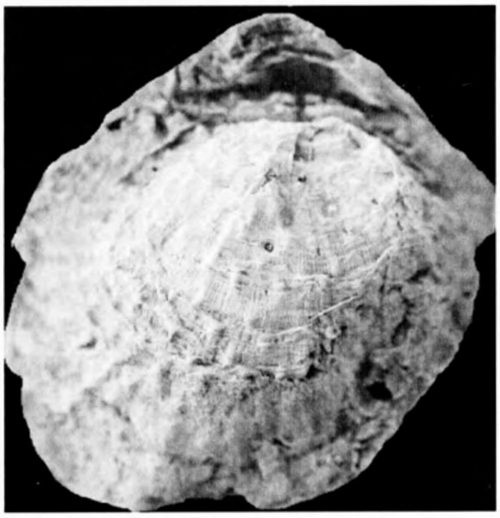

Fig. 7.10. *Crassispinosella subcircularis* (Clarke), dorsal aspect of external mould, BR 3016, x2, showing fine capillae. From Glencoe Formation (Asselian), Tasmania. JBW photo.

Genus ***Strophalosiaria*** new genus

Derivation: variation for name of brachiopod.

Type species: *Strophalosia concentrica* Clarke, 1990, p. 60 from Kansas Creek Formation (Asselian), Western Bluff, Tasmania, Australia, here designated.

Diagnosis: Small planoconvex shells with fine suberect spines and finer prostrate spines of varying diameter on ventral valve, dorsal valve wedge-shaped with no extended free trail, dorsal ornament of commarginal growth laminae, dimples and some capillae, no spines.

Discussion: Although this species was referred to *Strophalosia* by Clarke (1990, p. 60, Fig. 5H-R; replicated in 1992, p. 16, Fig. 5H-R) and Briggs (1998, p. 67, Fig. 36A-C), it differs strongly in general appearance from the type and other species referred to *Strophalosia*, including the slightly younger Tasmanian species *Crassispinosella subcircularis* (Clarke). Whereas the dorsal valves of *Strophalosia gerardi* King, type species of the genus, and *Crassispinosellasubcircularis* (Clarke) have a long trail and deeply concave disc, and the dorsal disc is surrounded by a very low if any marginal ridge, the dorsal valve of *concentrica* is wedge-shaped, strongly thickened anteriorly, with very short and only internal trail, not projecting beyond the visceral disc, and high marginal ridge around the disc. Ventral spines are distinctly finer in *concentrica* than in *gerardi* or *subcircularis*, with more slender prostrate spines, as also noticed by Briggs (1998). There is no sign of lateral buttress plates in the dorsal valve. As well, there are subtle internal differences between *concentrica* and *subcircularis*, but it is difficult to evaluate the significance of these features, given the natural variation within populations, and the limited geographic range of the two species.

Strophalosia yalwalensis Briggs, 1998, p. 70 shows considerable approach, in displaying ventral spines of varying diameter, somewhat coarser than those of *concentrica*, and leaving ventral spine tunnels. The dorsal valve appears to be gently concave externally, and possibly, but not securely, wedge-shaped, though that is neither confirmed or denied in the Briggs description, and it lacks dorsal capillae and pits.The species comes from the basal Snapper Point Formation, New South Wales, of uncertain age.

Genus ***Coronalosia*** Waterhouse & Gupta, 1978

Fig. 7.11 - Fig. 7.13

Type species: *Coronalosia blijniensis* Waterhouse & Gupta, 1978, p. 417, from Bijni Tectonic Unit, Garwhal Himalaya (Sakmarian), north India.

Diagnosis: Spines limited to ventral valve, fine and well spaced, row of spines along hinge and in some specimens around the anterior margin of mature shells. Dorsal valve without spines, may be radially striate.

Discussion: The genus was further discussed in Waterhouse (2001, pp. 54, 55), and figures are provided herein to compensate for the poor quality reproduction in the original publication. Brunton et al. (2000, Fig. 400d, e) figured the taxon *irwinensis*Coleman, 1957 as an example for *Strophalosia*. But, as shown by Briggs (1998, pp. 66, 67), *Strophalosiairwinensis* Coleman, 1957 and *S. jimbaensis* Archbold, 1986 belong to *Coronalosia* Waterhouse & Gupta. However the genus is not so far known in Argentina, despite reports by Archbold & Simanauskas (2001), and the various species from Tasmania, mistakenly assigned to *Coronalosia* by Cisterna et al. (2002), differ in morphology.

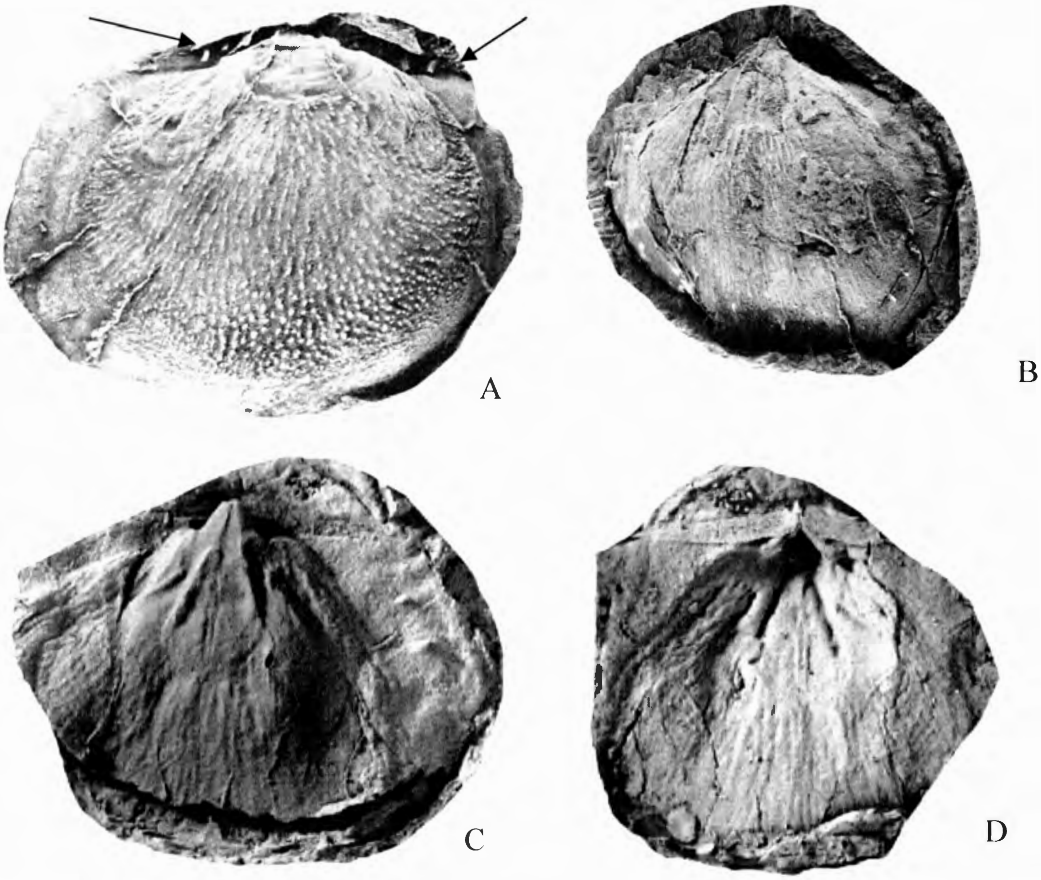

Fig. 7.11. *Coronalosia blijniensis* Waterhouse & Gupta. A, holotype, ventral valve, mostly internal mould, showing prominent row of hollow spine tubes along hinge between arrows, BR 3019, formerly CASGF 526. B, ventral internal mould, showing open spine bases around the margin. C, D, latex cast and mould of ventral valve, internal view. Specimens from Bijni tectonic unit (Sakmarian), Garwhal Himalaya, x2. See Waterhouse & Gupta (1978). Material includes unregistered material kept at Centre of Advanced Studies in Geology, Chandigarh, India. J. Coker, JBW photo.

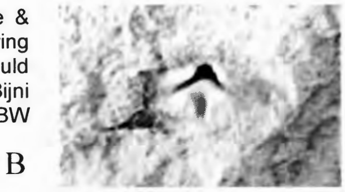

Fig. 7.12. *Coronalosia blijniensis* Waterhouse & Gupta.A, external mould of ventral valve showing ornament, BR 3089, x2. B, posterior internal mould of juvenile dorsal valve, BR 3090, x3. From Bijni tectonic unit (Sakmarian), Garwhal Himalaya. JBW photo

Unlike most species of Strophalosiidae, *Coronalosia* has a moderately well developed ventral row of hinge spines, suggesting reversion to a more chonetid-like morphology. In that regard, the genus approaches Subfamily Donalosiinae Lazarev, a subfamily limited, so far as known, largely to Devonian time. At present, the hinge row is believed to have arisen independently in a few strophalosiid and dasyalosiid genera, but further examination of Carboniferous genera may close the time gap and provide further examples of genera with row of hinge spines, to imply persistence of donalosiin stock. It may be that if the significance of the hinge row is emphazed,Donalosiinae could be interpreted as a subfamily within Chonopectidae Muir-Wood & Cooper, 1960, and *Coronalosia* regarded as a surviving member.

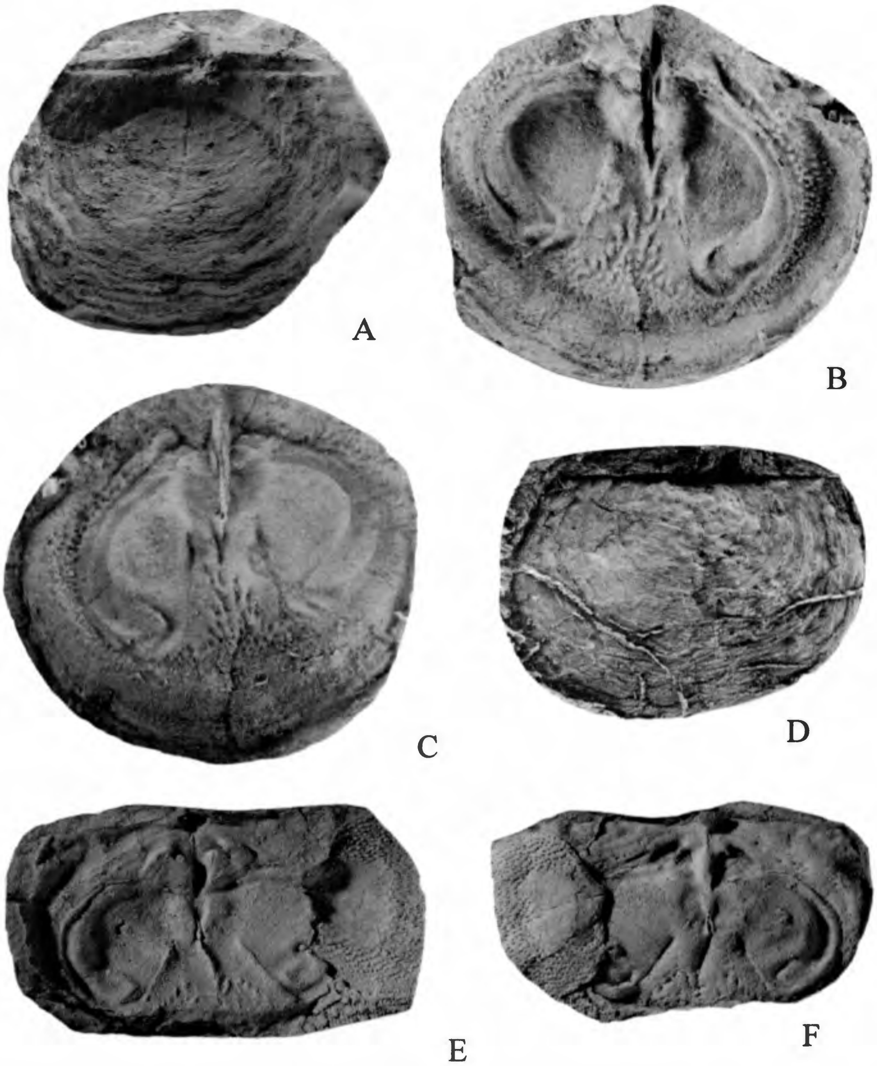

Fig. 7.13. *Coronalosia blijniensis* Waterhouse & Gupta. A, latex cast of specimen with valves conjoined, dorsal view, x2 approx.B, C, dorsal internal mould and latex cast, CASGF 589, reregistered as BR 3020, x1.8. D, dorsal external mould, x2 approx. E, F, external mould and latex cast of dorsal valve BR 3018 (formerly CASGF 532), x 1.2. Chonetid (*Svalbardia*?) attached. Specimens from Bijni tectonic unit (Sakmarian), Garwhal Himalaya, x2. Unregistered specimens kept at Centre of Advanced Study in Geology, Chandigarh, India. See Waterhouse & Gupta (1978). J. Coker & JBW photo

Genus ***Baikuralia*** new genus

Fig. 7.14

Derivation: Named from species name, based on the Permian Baikur faunas and beds of northeast Russia.

Type species: *Strophalosia*? *bajkurica* Ustritsky in Ustritsky & Chernyak, 1963, p. 96 from Baikur Suite (Capitanian), northeast Russia, here designated.

Diagnosis: Average size for tribe, no conspicuous cicatrix, well formed interareas. Ventral spines dense over entire valve, generally uniform and comparatively fine, subprostrate without ear-burst; dorsal valve covered by dense slightly elongated dimples, low growth steps and laminae. Ventral muscle field well defined.

Discussion: This genus is distinguished by the nature of its ventral spines and dorsal dimples, which aredense. Internal detail for *Baikuralia* seems largely unexceptional: the ventral adductor platform is well developed, and there are no lateral buttress plates in the dorsal valve. There are no specialized hinge spines as in *Coronalosia* Waterhouse, or large cicatrix and rhizoid spines and crenulate or lamellate patterns over the dorsal valve as in

Cicatrixia Waterhouse or *Crenalosia* Waterhouse, nor large cicatrix, ventral hinge row, and dorsal dimples and capillae as in *Etherilosia* Archbold. The spines do not resemble the two clearly defined series of spines as in *Fortispinalosia* new genus, nor are radial capillae prominent as in *Fimbrinialosia*. The dorsal valve is not thickened into a wedge shape, as in *Strophalosiaria*. The ornament is thus closer to that of *Strophalosia* King and *Heteralosia* King, but spines are more uniform and crowded and dorsal pits are much more crowded with rows along commarginal bands, and slightly elongate. Such dimples are faint or missing from the South American genus *Tupelosia* Archbold & Simanauskas. The closest genus appears to be *Keoghalosia* Waterhouse, type species *K. onegumensis* Waterhouse, 2010a from the Artinskian One Gum Formation of the Carnarvon Basin, Western Australia. This species has comparatively dense ventral spines, less uniform than in the Russian genus, with a number of very fine prostrate spines, and a brush over the outer ventral ears. Dorsal dimples are comparatively dense and in commarginal rows, but are shallower than in *Baikuralia*and not elongate. *Strophalosia yalwalensis* Briggs, 1998, Fig. 37 from the basal Snapper Point Formation of New South Wales, Australia, is somewhat similar, with dense and subprostrate ventral spines, and possibly there is no brush over the ears. But spines are a little coarser and more spaced than in the Russian form, although similarly varied in diameter, and the dorsal valve of *yalwalensis*is smooth apart from low growth wrinkles. Internally the ventral muscle platform is not as emphasized, but spine tunnels are developed as in the Russian form. The type species of *Baikuralia* is found in the Baikur Suite of Taimyr and Omolon Horizon of Kolyma-Omolon, northeast Russia. *Krotovia tolli* Fredericks, 1931, p. 213, transferred to *Strophalosia* in Sarytcheva (1977, p. 46) in being reported from Taimyr and the Kolyma-Omolon Massif of northeast Russia, is similar in having more uniform but dense ventral spines and strong crowded dorsal pits, and *Strophalosia*? *grandis* Tolmachov, 1912 from the same region is also congeneric.

Fig. 7.14. *Baikuralia bajkurica* (Ustritsky), x1. A, ventral valve PIN No. 3824/513. B, dorsal aspect of PIN No. 3824/531. C, dorsal external mould PIN No. 2834/530. From Omolon Suite (Capitanian), northeast Russia. See Sarytcheva (1977, pl. 4).

Tribe **TRUNCATENIINI** Liao, 1982

Fig. 7.15A

[Nom. transl. Waterhouse 2002b, p. 41 ex Truncateniinae Liao, 1982, p. 539. Syn. Licharewiellinae Archbold, 1986, p. 98].

Diagnosis: Strong radial ornament on both valves. Permian (Roadian – Wuchiapingian).

Genera: *Truncatenia* Liao, *Costalosiella* Waterhouse, *Kufria* Waterhouse, *Licharewiella* Ustritsky (syn. *Costalosia* Waterhouse & Shah).

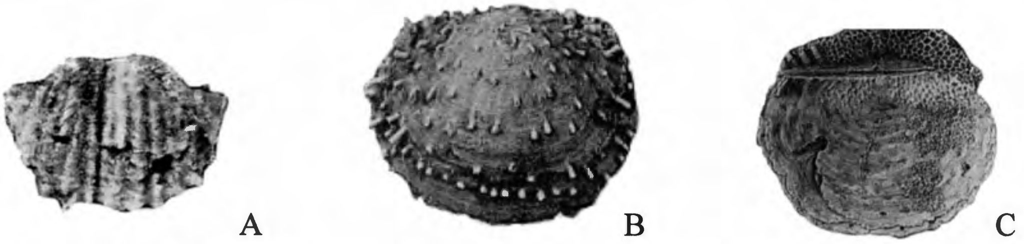

Fig. 7.15. A,*Truncatinia heshanensis* Liao, ventral valve x2. From Late Permian of South China. See Liao (1982). B, C, *Devonalosia wrightorum* Muir-Wood & Cooper from Middle Devonian Arkona Shale, Ontario, Canada, x3. B, ventral view of holotype USNM 123431. C, dorsal aspect of USNM123432d. See Muir-Wood & Cooper (1960, pl. 1, fig. 2, 9).

Taxonomy: Sokolskaya (1960, p. 219) proposed the name *Licharewiella* for an orthotetoid, later than *Licharewiella* Ustritsky in Ustritsky, Hun & Chan 1960, p. 47. Ting (1965, p. 265) proposed replacing *Licharewiella* Sokolskaya with the name *Magniderbyia*, and figured a derbyiid as an illustration. Brunton et al. (2000, p. 569) however registered *Magniderbyia* as a synonym of *Licharewiella* Ustritsky.

Discussion: This group is distinguished by its strong costae, and the cardinal process is like that of Strophalosiini. *Truncatenia* Liaois provisionally regarded as valid, counter to Brunton et al. (2000), because it lacks the cluster of posterior ventral spines characteristic of *Licharewiella* Ustritsky. It has well developed marginal ridges, not so far confirmed for *Licharewiella,* which is based on externals only. The genus *Costalosiella* Waterhouse is included in the tribe, because it shares the distinctive ribs with *Truncatenia* and *Licharewiella*, yet has a few strong dorsal spines.

Subfamily **DONALOSIINAE** Lazarev, 1989

Fig. 7.15B, C

[Donalosiinae Lazarev, 1989, p. 35].

Diagnosis: Spines relatively stout near hinge, uniform over the visceral disc, erect and usually only on ventral valve, commarginal ornament may be lamellose. Pseudodeltidium and chilidium present, commonly with large cicatrix. No lateral buttress plates, pit in front of cardinal process, cardinal process tends to bifid appearance from ventral aspect. Middle Devonian (Eifelian) to Upper Devonian (Famennian).

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

Discussion: This subfamily was regarded as a member of Araksalosiidae Lazarev by Brunton et al. (2000), but although the two may share a strong ventral hinge row of spines, Araksalosiidae differs in its distinctive spine ornament, and presence of lateral buttress plates. Given what is known of the morphological parameters, Donalosiinae is repositioned, and treated as an early constituent of Strophalosiidae. The diagnosis provided by Brunton et al. (2000, p. 579) for Donalosiinae makes no distinction from Strophalosiidae or Strophalosiinae. It reads " Pseudodeltidium, chilidium present; cicatrix present, may be extensive; spines relatively thick, commonly only on ventral valve; concentric ornament may be lamellose; radial ornament rare on trails". Here *Donalosia* and allies are distinguished from Strophalosiinae by the stouter hinge spines, rather uniform other spines, and bifid cardinal process. There are a few Permian genera, such as *Capillaria* Waterhouse, *Coronalosia* Waterhouse & Gupta, and *Nothalosina* Waterhouse, that also display a hinge row of ventral spines, and the hinge row is presently interpreted as having arisen independently from various stock. Such genera differ in having trilobed strophalosiin cardinal process but the affinities remain open for further assessment.

Donalosia Lazarev, 1989, p. 35, of Upper Devonian age (Frasnian, Famennian) from east Europe and Russia, has sturdy erect ventral spines, crowded and strong along the ventral hinge, no dorsal spines or ventral prostrate spines, light dorsal commarginal laminae and rugae, long dorsal septum and pit in front of the cardinal process, which persists as a cleft to the end of the process (see Brunton et al. 2000, Fig. 413.1d), imparting a bifid appearance. The presence or absence of lateral buttress plates is not fully clear, but it is assumed that they are absent. The ventral adductor scars are broad with light dendritic markings.

A diverse assortment of genera was referred to the subfamily in Brunton et al. (2000, pp. 580 - 582), and some are close enough to be regarded as allied, and several show a deep ventral notch on the bifid cardinal process. *Australosia* McKellar, 1970, a well known genus of Famennian age from Queensland, Australia, is similar in ventral spines, apart from the lack of an ear-burst. There are no dorsal spines, and ventral spines form a prominent row along the hinge: there might be such a row in *Donalosia*, but this is obscured by the presence of additional spines close to the hinge. Lateral ridges pass into the brachial scars, and there are no lateral buttress plates. *Australosia* has strong ribs over the ventral valve and over the anterior dorsal valve, suggestive of Truncateniini, but the much greater age and long gap in time before the earliest member of Truncateniini suggests the likelihood of independent development. A probable ally *Devonalosia* Muir-Wood & Cooper, 1960 of Middle Devonian age, has spines near the ventral hinge, a deep median notch in the cardinal process from a ventral aspect, and lacks lateral buttress plates. *Morganella* McKellar, 1970 of lower Famennian age also has a row of ventral hinge spines, and cardinal process with deep wide ventral notch. These genera are treated as constituting the core membership of the subfamily, which is diagnosed accordingly. Genera may display a low dorsal marginal ridge, and the trail is short and curves evenly on from the visceral disc.

Other Devonian genera are possibly close, but may lack strongly developed ventral hinge spines and vary widely in attributes: were they more fully known, they potentially could be ascribed to different family groupings. *Irboskites* Bekker, 1924 of Frasnian age is smooth without spines, and so is exceptional, but shows similarities in shape to *Devonalosia* Muir-Wood & Cooper. *Truncalosia* Imbrie, 1959 of Givetian age has what appear to be oblique supporting dorsal ridges, possibly socket plates, and its ornament is not like that of Araksalosiinae, explaining the reference to Donalosiinae by Brunton et al. (2000). It needs to be recalled that a study of ontogenetic development by Waterhouse (1959) showed that early growth stages of *Echinalosia* start with wide supporting ridges for the cardinal process, followed by the appearance of the median septum, then followed by the disappearance of the supporting ridges. (See Fig. 6A, p. 11, Fig. 16B, C, p. 23). Given the very small size of *Truncalosia,* it seems possible that the genus is based on immature specimens, and although spines lie along the hinge, they are not strong. Otherwise it is based on rare mature specimens, with relationships still to be determined. *Oligorhachis* Imbrie, 1959 of Givetian age is also probably allied, with ventral spines close to the hinge, but not strong. Some of the genera listed from Brunton et al. (2000) are even less certain. *Auchmerella* Struve, 1964 is a mid-Devonian genus only known as a cemented ventral valve. *Dotswoodia* McKellar, 1970 is reassigned to Dotswoodiini, Productellidae, and *Enigmalosia* Czarniecki, 1969, though included in Donalosiinae by Brunton et al. (2000), is judged to belong to Septasteginae (Scacchinelloidea), given its strong ribs and lack of teeth and sockets and presence of long accessory dorsal plates (p. 263). *Ralia* Lazarev, 1987 is reassigned to Chattertoniinae, because of the presence of anderidia.*Dichacaena* Cooper & Dutro is replaced in Quadratiinae, and *Eostrophalosia* Stainbrook is replaced inEostrophalosiinae.

Family **DASYALOSIIDAE** Brunton, 1966

[Nom. promoveo hic ex Dasyalosiinae Brunton, 1966, p. 192].

Diagnosis: Both valves spinose as a rule, ribs and concentric lamellae subdued as a rule.

Discussion: The present grouping associates subfamilies and genera that do not differ greatly from each other, and dissociates subfamilies classed it would appear more by age than by morphology in the *Revised Brachiopod Treatise.* At an individual level, members of Dasyalosiidae are themost prolific of all strophalosiiform families, and it is members of this family that gave rise to several of the productoid superfamilies, Rhytialosiinae to Aulostegoidea, and possibly Echinalosiinae to Cooperinoidea.

The presence of dorsal spines is not completely mandatory, and it is evident in surveying the range of tribes and genera allocated to the family that some forms lost the dorsal spines, but show enough of other significant features to point to close alliance with dorsally spined genera and tribes, avoiding thereby a mechanistic classification devoid of biological reality. Most genera lack a prominent row of ventral hinge spines, unlike typical Donalosiinae, but it should be recalled that several genera assigned to Donalosiinae are poorly known.

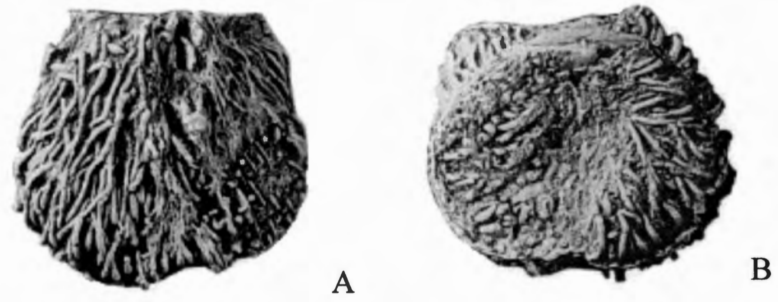

Fig. 7.16. *Dasyalosia goldfussi* (Műnster). A, B, ventral and dorsal views of USNM 6230a, from Zechstein (Wuchiapingian) of Thuringia, Germany, x2. See Muir-Wood & Cooper (1960, pl. 6).

Subfamily **DASYALOSIINAE** Brunton, 1966

Fig. 7.16

[Dasyalosiinae Brunton, 1966, p. 192].

Diagnosis: Crowded spines of at least two orders on both dorsal and ventral valves. Dorsal disc usually of low concavity, develops short to long trail at high angle. Lower Permian (Sakmarian) to Upper Permian (Wuchiapingian).

Genera: *Dasyalosia* Muir-Wood & Cooper, *Acanthalosia* Waterhouse, *Maxwellosia* new genus.

Discussion: Although the dorsal valve of *Dasyalosia* was described as "deeply concave" and defining a thin body cavity by Muir-Wood & Cooper (1960, p. 76), Brunton (2007) insisted that the dorsal disc was comparatively flat (Brunton 2007, Fig. 1772. 3a, 3b). He provided no explanation of the nature of the trail, nor reconciliation with the Muir-Wood & Cooper statement.

Genus ***Maxwellosia*** new genus

Fig. 7.17 , Fig.7.18

Derivation: Named for W. G. H. Maxwell.

Type species: *Strophalosia jukesi concava* Maxwell, 1954, p. 551 from upper Wallaby Formation (Artinskian), south Queensland, Australia, here designated.

Diagnosis: Two series of thick and thin spines on ventral valve, less markedly different two series of spines on dorsal valve, a varying number prostrate. Dorsal valve moderately to strongly concave.

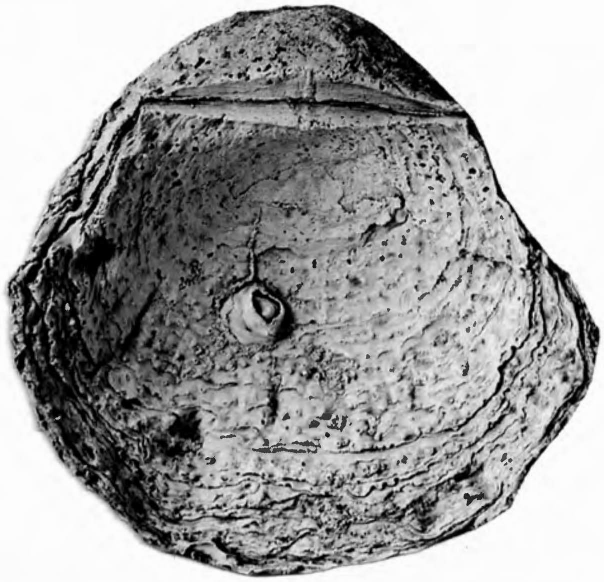

Fig. 7.17.*Maxwellosia*n. sp., dorsal view of latex cast of UQF 81289 fromTiverton Formation (Sakmarian), Bowen Basin, Queensland, x2. D. J. C. Briggs & JBW photo.

Discussion: The type species of *Acanthalosia* possesses comparatively flat dorsal valves. But an allied species, initially described as a "variety" *concava* Maxwell, and transferred to a full species of *Acanthalosia* by Briggs (1998, p. 108) and Waterhouse (1986b, p. 33; 2010a, p. 57), has a dorsal valve that is deeply concave (see Briggs 1998, Fig. 57G). Maxwell's *concava*was assigned to *Acanthalosia*by these authors, because there are two series of spines on each valve, just as in *Dasyalosia* and type *Acanthalosia*, though the thicker spines are usually rare if present over the dorsal disc and are found chiefly round the margins (Briggs 1998, p. 109). Another species, *Acanthalosia*n. sp. from the middle Tiverton Formation (upper Sakmarian) of the Bowen Basin, Queensland, also has a deeply concave dorsal valve, and somewhat fewer prostrate dorsal spines. The two species therefore pose a conundrum. Have they developed from the slightly older species *Acanthalosia domina* Waterhouse, changing one of the morphological aspects normal to Dasyalosiinae through alteration to the dorsal valve profile? Or have echinalosiin specimens (see below, p. 228) developed a slightly larger size, and changed the dorsal spines of one series into two series? Present evidence appears to favour the first alternative, because some specimens amongst the collections have only a gently concave visceral disc, as shown by Briggs (1998, Fig. 57F, I) and Waterhouse (2010a, Fig. 23C, D), it being the trail that is long, although most specimens have a more concave disc, as shown in a cross-section for *concava*by Maxwell (1954, pl. 56, fig. 24). In the Tiverton new species, to be described in Waterhouse & Shi (in press), the dorsal valve is more deeply concave than in *concava*. *Acanthalosia* as narrowly defined continued higher in the Permian succession, with two distinct species A. *mysteriosa* Waterhouse and *A. deari* (Briggs) bearing dorsal valves that are comparatively flat, but not strongly wedge-shaped.

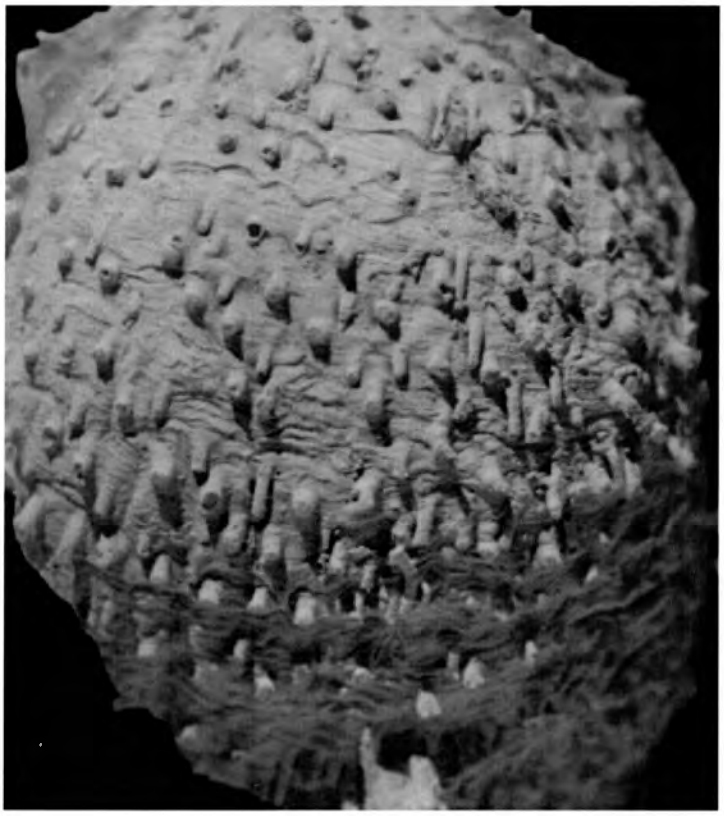

Fig. 7.18. *Maxwellosian*. sp., latex cast of ventral exterior UQF 81804, Tiverton Formation (Sakmarian), Bowen Basin, Queensland, x3. JBW photo.

Subfamily **EOSTROPHALOSIINAE** new subfamily

Name genus: *Eostrophalosia* Stainbrook, 1943, p. 58 from the Hackberry-Cerro Gordo Member (Frasnian), Iowa, United States, here designated.

Diagnosis: Spines in quincunx over ventral valve, subuniform to hints of two series, no prominent ventral hinge row, dorsal spines fine, erect and numerous. Cardinal process bilobed. Upper Devonian (Frasnian – Famennian).

Genera: *Eostrophalosia* Stainbrook, *Myrtlevalia* new genus.

Discussion: These genera are closely spinose over both valves, and somewhat resemble the much younger genera of Permian age that are classed in Echinalosiinae Waterhouse. They differ in having a bilobed cardinal process. Both valves are sublaminate, thereby differing from members of Chonopectidae Muir-Wood & Cooper, which have low to coarse commarginal rugae and prominent ventral hinge spines as a rule.In other respects members of Chonopectidae come close, especially genera within the subfamily Rhytialosiinae Lazarev, which may have spines over both valves, but have low very regular rugae and tend to have prominent spines along the ventral hinge. Ventral spines are otherwise more uniform over the ventral valve in Rhytialosiinae. The recognition of the subfamily implies that Dasyalosiidae appeared early in the evolution of Strophalosiidina, overlapping in some aspects with Chonopectidae, but discrete.

Eostrophalosia Stainbrook, 1943 of Frasnian age has well developed dorsal spines, unlike members of Donalosiinae where it was classed in Brunton et al. (2000, p. 582). The ventral spines are mostly comparatively thick and subuniformover most of the disc, but thin and subrostrate spines are developed anteriorly; the dorsal spines are thin and subprostrate, and ventral hinge spines are not noticeably strong, though slightly thicker in *E. pedderi* Crickmay, 1963.The dorsal interior is shown by Cooper & Dutro (1982, pl. 19, fig. 2). The cardinal process is widely bilobed, as in Caucasiproductinae, which also has numerous dorsal spines. Members of Caucasiproductidae do not display an umbonal cicatrix, indicating membership of Productidina.

Genus ***Myrtlevalia*** new genus

Fig. 7.19

Derivation: Named from Myrtlevale Formation, source of the species.

Type species: *Acanthatia fragilis* McKellar, 1970, p. 17 from Myrtlevale Formation (Famennian), Burdekin Basin, Queensland, Australia, here designated. See Appendix A, part A, p. 477.

Diagnosis: Small with wide hinge and strong ventral lamellae, weaker dorsal fine rugae, not very strong hinge row of ventral spines, ventral spines over disc and trail uniform and arranged in single rows along each lamellum, subprostrate, dorsal spines numerous and just as strong. No visible trail.

Discussion: The type species has been described in detail by McKellar (1970), from the *Sentosia* (now *Spinauricula*) *minuta* Zone in the Myrtlevale beds of the Burdekin Basin west of Collinsville, Queensland. Pseudodeltidium and chilidium are present, and trail not discriminated.

Acanthatia Muir-Wood & Cooper, 1960 shows limited similariities, having a much stronger row of hinge spines and finer body spines, and lacking commarginal ventral laminae or dorsal rugae, and has well developed lateral buttress plates, pointing to Araksalosiidae. The new genus is close to *Eostrophalosia* Stainbrook, 1943 as far as that genus is known, and like that genus has dorsal spines and has moderately low ventral and dorsal interareas, but lacks an umbonal cicatrix. The hinge is similarly wide, and interareas low, and laminae grading into discontinuous rugae present, shared by both genera. The new genus is distinguished from the type species *Eostrophalosia rockfordensis* (Hall & Clarke) in having a wider hinge with slightly better formed hinge row of ventral spines, though these are little stronger than spines over the ventral disc. The ventral valve of *Myrtlevalia*is lamellate, and prostrate or subprostrate spines lie in a single row over each lamellum, whereas the ventral valve of *Eostrophalosia* is less lamellate, and spines are arranged more in quincunx. The dorsal valve of the new genus is more rugose, though rugae are fine, and spines cover all of the valve, apart from the convex nepionic shell. Internal detail is preserved: ventral teeth are small, and muscle scars small and posteriorly placed. There is a small widely bilobed cardinal process, and well formed median septum extending to mid-length. Adductor scars are small, with a conspicuous anterior and subrounded pair with smooth surface. Fine and crowded endospines cover the anterior half of the valve, but brachial shields are not clearly displayed. There is no visible hinge ridge or ear baffles.

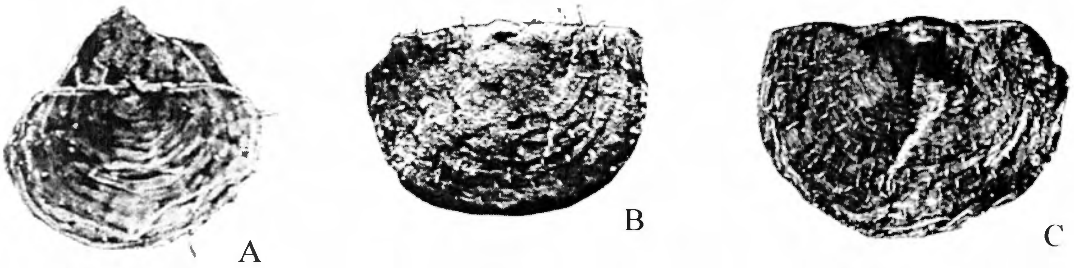

Fig. 7.19. *Myrtlevalia fragilis* (McKellar). A, dorsal aspect, GSQF 11492 with valves conjoined, latex cast, x3. B, latex cast of ventral exterior, GSQF 11495, x2.5. C, dorsal exterior, latex cast of GSQF 11502, x2.5. From Myrtlevale Formation (Famennian), Queensland, Australia. See McKellar (1970, pl. 6).

Subfamily **ECHINALOSIINAE** Waterhouse, 2001

[Echinalosiinae Waterhouse, 2001, p. 57].

Diagnosis: Shells distinguished from other members of the family by usually possessing erect spines of one series over dorsal valve, spines usually of two series on ventral valve. Commarginal lamellae developed to varying but never marked degree, radial filae generally weak or absent. Cardinal process usually trifid.

Discussion: The template outlined in the diagnosis was modified during the evolution and radiation of species and genera within this subfamily, some forms changing the nature of ventral spines, and others losing the dorsal spines, or changing the nature of the dorsal valve into a wedgeshape. Such changes are substantial, but are supported by detailed study of sequential change and geographic distribution.It appears likely that members of the subfamily developed from ancestors close to Eostrophalosiinae, rather than genera within Chonopectidae, which apart from often having a row of prominent ventral hinge spines, display low to high and very regular commarginal rugae over both valves. Although this proposal implies a gap in the fossil record, between Upper Devonian and Upper Carboniferous, there are various strophalosioid occurrences in Lower Carboniferous faunas that require evaluation.

A summary of the evolution is provided on p. 464.

Tribe **ECHINALOSIINI** Waterhouse, 2001

Fig. 10, Fig. 7.20

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

Diagnosis: Ventral valve with two series of spines as a rule. Dorsal valve thin, with trail and erect slender spines. Upper Carboniferous (Moscovian) to Upper Permian (Changhsingian).

Genera: *Echinalosia* Waterhouse (nom. nov. pro *Multispinula* Waterhouse, 1966 not Rowell, 1962), *Echinalosia* (*Capillaria*) Waterhouse, *Echinalosia* (*Glabauria*) Waterhouse, ?*Hontorialosia* Martínez Chacón, *Nothalosiina* Waterhouse.

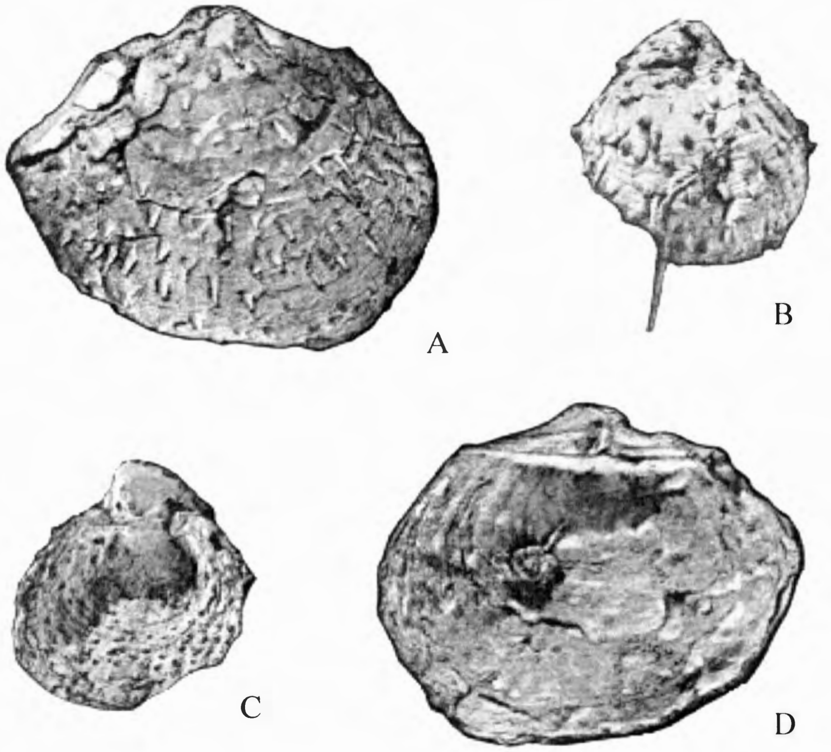

Fig. 7.20. *Echinalosia maxwelli* (Waterhouse). A, D, PVC cast of exterior, ventral and dorsal aspects of mature specimen BR 270; most dorsal spines have been lost. B, C, ventral and dorsal aspects of PVC external cast of BR 279 at early maturity. Specimens x2.5 from Letham Burn Formation (Roadian), Wairaki Downs, New Zealand. (See Waterhouse 1964). S. N. Beatus & JBW photo.

Discussion: *Echinalosia*is mainly found in the Lower and Middle Permian of Australia and New Zealand, with likely occurrences in the Salt Range of Pakistan. The subgenus *Capillaria* is unusual in having well developed spines along the ventral hinge. *Hontorialosia* isnot fully understood: its ventral spines appear from photographs to include thick and thin.

Tribe **MARGINALOSIINI** new tribe

Fig.7.21

Name genus: *Marginalosia* Waterhouse, 1978, p. 64 from Nisal Member (Changhsingian) of Nepal, here designated.

Diagnosis: Ventral spines closely spaced and mostly fine; dorsal valve with gently concave disc and curving into moderate to short trail, valve may be slightly thickened, fine spines. Middle Permian (late Capitanian) to Upper Permian (Changhsingian).

Genera: *Marginalosia* Waterhouse, *Guadalupelosia* Archbold & Simanauskas (syn. *Muirwoodicia* Waterhouse).

Discussion: These genera appear to have evolved during the younger Permian from Echinalosiini through reduction in spine disparity over the ventral valve, and thickening of the dorsal valve, and became moderately widespread,*Marginalosia*occurring in Nepal, east Australia and New Zealand, and possibly northeast Russia.

Fig. 7.21. *Marginalosia planata* (Waterhouse), ventral valve PVC mould of topotype, BR 361, from Pig Valley Limestone (Changhsingian), New Zealand, x2. (See Waterhouse 1964). S. N. Beatus & JBW photo.

Genus *Guadalupelosia* Archbold & Simanauskas, 2001

Guadalupelosia Archbold & Simanauskas, 2001, p. 223 from the Cherry Canyon Formation of the Glass Mountains, Texas, United States, has fine spines on both valves and moderate ventral and dorsal marginal ridges. Waterhouse (2002b) assigned a different name to the same type species. Although Cooper & Grant (1975, p. 796) described the dorsal valve of the type species, *inexpectans*, as moderately concave, Brunton (2007, p. 2663) drew attention to the comparatively low concavity of the dorsal valve, with surrounding rim behind the short trail, and strongly advocated a close approach to *Dasyalosia*. Yet the spines of *Guadalupelosia* are very different from those of Dasyalosiinae, being of uniform nature on both valves, and fine, delicate and recumbent. Short delicate rhizoid spines lie over the ears and umbonal and lateral slopes of the ventral valve. There is a considerable approach to *Marginalosia* Waterhouse of late Guadalupian and Changhsingian age in the Himalayas, New Zealand and east Australia. This genus has a somewhat flattened and slightly thickened dorsal valve and fine comparatively homogenous ventral spines, and the two genera are separable to a degree from *Echinalosia* and close allies.

Tribe **WYNDHAMIINI** Waterhouse, 2010a

Fig. 7.22, Fig. 7.23

Diagnosis: Ventral body spines mostly coarse, semirecumbent, prostrate spines thin and often rare. Dorsal valve thickened and wedge-like, with fine spines of one series. Lower Permian (Sakmarian) to Middle Permian (Capitanian).

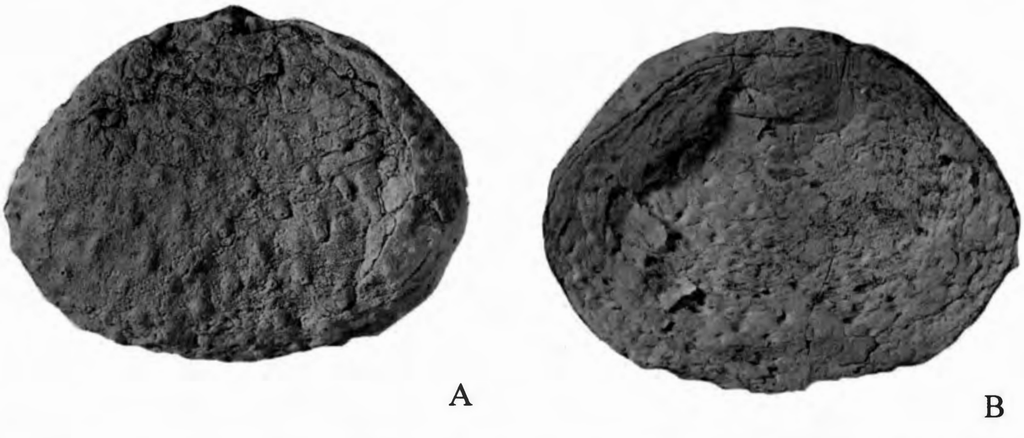

Fig. 7.22. *Wyndhamia parfreyi* (Waterhouse), ventral and dorsal aspects of UQF 69888 from Barfield Formation (Roadian), Queensland, Australia, x2. (See Waterhouse 2001). J. Coker & JBW photo.

Genera: *Wyndhamia* Booker (syn. *Branxtonia* Booker), *Pseudostrophalosia* Clarke (syn. *Notolosia* Archbold).

Discussion: This is a small subset of shells reliably known only in Australia and New Zealand, with reports from northeast Russia seemingly dubious, those species being more echinalosiin.

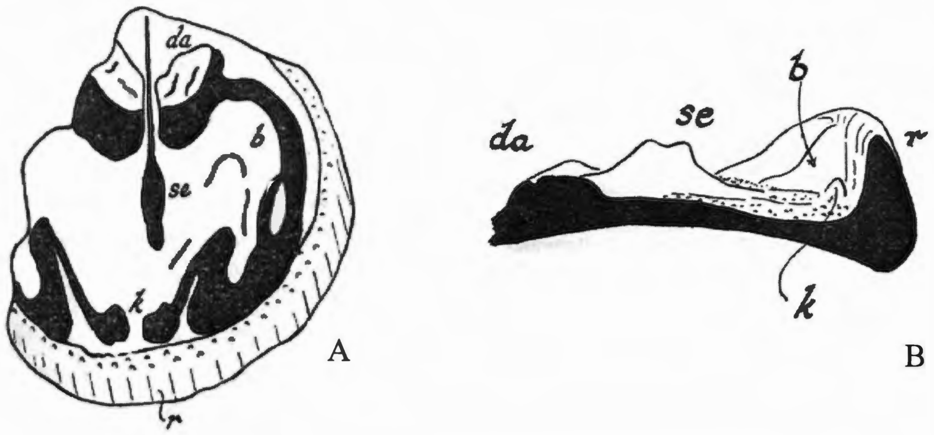

Fig. 7.23. *Wyndhamia clarkei* (Etheridge), A, dorsal interior, x1.5. B, transverse section through dorsal valve, x1.7, posterior part not shown. BR 222 from Mangarewa Formation (Capitanian), Wairaki Downs, New Zealand. JBW del. b = brachial ridge, with branch; da = dorsal adductor platform with ridges on the posterior part; k = knob at which brachial ridges appear to terminate; r = marginal ridge; se = median septum.

Subfamily **ARCTICALOSIINAE** Waterhouse, 2001

[Nom. transl. hic ex Arcticalosiini Waterhouse, 2001, p. 82].

Diagnosis: Ventral spines uniform to subuniform and crowded over entire disc and trail. Dorsal valve comparatively flat and usually wedge-like.

Discussion: The ventral spine pattern is distinctive.

Tribe **ARCTICALOSIINI** Waterhouse, 2001

Fig. 7.24, Fig. 7.25

[Arcticalosiini Waterhouse, 2001, p. 82].

Diagnosis: Ventral and dorsal spines of one order as a rule, fine, numerous and closely spaced. Middle Permian (Wordian) to Upper Permian (Wuchiapingian).

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

Fig. 7.24. *Arcticalosia sphenarctica* (Waterhouse), dorsal interior, GSC 23812 from GSC loc. 76029, Trold Fiord Formation (Capitanian), Cameron Island, Canada, x2.5. B. O'Donovan & JBW photo.

Orthothrix has an almost flat dorsal valve. Whether or not the dorsal valve is wedge-shaped is not known, but it seems possible.

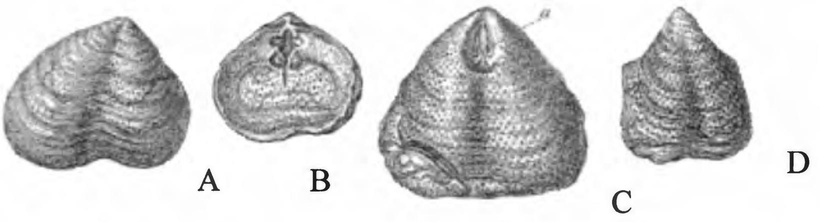

Fig. 7.25. *Orthothrix excavata* (Geinitz). Figures of specimens from the Magnesian Limestone (Wuchiapingian) of north England, illustrated by King (1850, pl. 12, fig. 1-11) as *Strophalosia goldfussi* (Műnster), showing fine erect and crowded spines over both valves. a = adductor scars.

Tribe **BIPLATYCONCHINI** new tribe

Fig. 7.26

Name genus: *Biplatyconcha* Waterhouse, 1983c, p. 125 from Nisal Member (Changhsingian), west Nepal, here designated.

Diagnosis: Large shells with numerous fine spines crowded over ventral valve, no dorsal spines, dorsal valve tends to be thickened anteriorly, without long trail. Upper Permian (Wuchiapingian – Changsingian).

Genus: *Biplatyconcha* Waterhouse (nom. nov. pro *Platyconcha* Waterhouse, 1975 not Longstaff, 1933; syn. *Megalosia* Waterhouse, 1988), *Subtaeniothaerus* Solomina.

Discussion: The ventral ornament is moderately close to that of Arcticalosiini, which unlike Biplatyconchini has dorsal spines. Genera of this tribe, despite differing in their spine detail from most genera assigned to Dasyalosiidae in their lack of dorsal spines, are believed from most aspects of their morphology to have arisen through Arcticalosiini. *Subtaeniothaerus* Solomina, 1988, p. 40 from the lower Lopingian Dulgalakh beds of Verchoyan, northeast Russia, appears to be closely allied to *Biplatyconcha*, but its spines vary more in diameter.

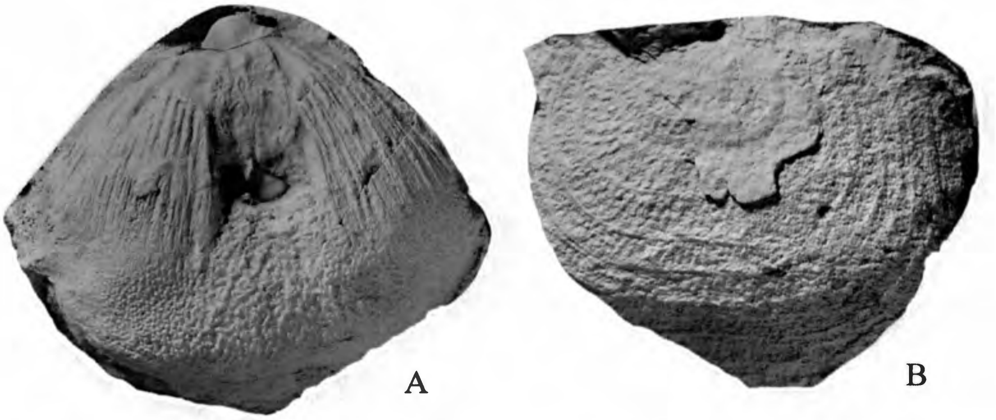

Fig. 7.26. *Biplatyconcha grandis* (Waterhouse). A, internal mould of ventral valve UQF 68895. B, external mould of dorsal valve UQF 68902. Specimens from Nisal Member (Changhsingian), west Nepal, x1. See Waterhouse (1978, 2004a). J. Coker & JBW photo.

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 fine to strong commarginal ornament, cicatrix varied, hinge long and shell semicircular in outline, low corpus cavity. Dorsal spines rare. Median septum simple, alveolus may be present.

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

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

Diagnosis: Transverse with wide hinge and prominent row of hinge spines, bifid cardinal process, long low dorsal septum.

Discussion: The possibility may be raised that Donalosiinae could prove to be related to Chonopectidae, through the presence of a row of ventral hinge spines (p. 224), though because the hinge spines are better developed in *Chonopectus* than in *Donalosia*, and commarginal rugae better organized in the closely related tribe Semenewiini, the putative relationship is set aside.

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

[Nom. transl. hic ex Chonopectinae Muir-Wood & Cooper, 1960, p. 157].

Diagnosis: No commarginal rugae, no dorsal spines. Upper Devonian (Famennian?) to Upper Carboniferous (Bashkirian).

Genus: *Chonopectus* Hall & Clarke, *Eileenella* Racheboeuf.

Discussion: *Chonopectus* strongly approaches chonetids in external appearance through its fine radial ornament and row of ventral hinge spines, with no other spines. But the genus is not particularly old, appearing only late in the Devonian and ranging into Lower Carboniferous. One characteristic of the genus is the fine radial striae, crossed by only slightly weaker commarginals. *Eileenia* Racheboeuf in Wongawich et al. (2004) was referred to the same group, agreeing in shape and other aspects, but having anterior ventral spines as well. The shell surface is mostly devoid of ornament, possibly due to poor preservation, but does show anterior fine commarginal growth-lines (Rachebouef in Wongawich et al. 2004, p. 1078). An alveolus, present in *Chonopectus*, is not developed in *Eileenella*.

Tribe **SEMENEWIINI** Muir-Wood, 1962

Fig. 7.27

[Nom. transl. hic ex Semenewiinae Muir-Wood, 1962, p. 33].

Diagnosis: Ornament of low to strong commarginal wrinkles, usually on both valves, fine radials present as a rule, ventral spines along hinge and small over rugae, rarely dorsal spines as well. Lower Carboniferous (Visean) to Upper Carboniferous (Bashkirian or Kasimovian).

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

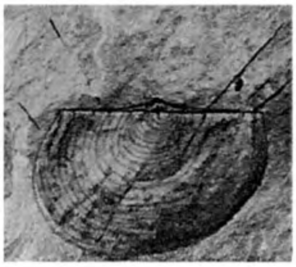

Fig. 7.27. *Chonetipustula plicata* (Sarres), impression from Posidonienschiefer, Aprath, Rhine Province, Germany, x1.5. See Paeckelmann (1931, pl. 1, fig. 6).

Discussion: Semenewiinae was synonymized with Chonopectidae Muir-Wood & Cooper by Brunton et al. (2000, p. 576), even though *Chonopectus* Hall & Clarke lacks strong rugae, but there is a sharing of strong ventral hinge spines, and *Semenewia* and *Dengalosia* are like *Chonopectus* in having fine radial and commarginal filae (Brunton, Racheboeuf & Mundy, 1994, Fig. 1; Manankov & Pavlova 1981). Such micro-ornament is less developed in the junior synonym *Palmerhytis* Brunton & Mundy, in Brunton et al. 1994, and in *Chonetipustula* there are only traces of fine radial filae, and commarginal ornament is overwhelmingly rugose. *Chonopectus* is kept provisionally separate from *Semenewia* and allies, because of the obvious external differences in rugation, and the relationship is expressed as tribal, in deference to the studies by Brunton and colleagues. *Dengalosia* Manankov & Pavlova, 1981 has a few dorsal spines, and low rugae on both valves and fine radial ribbing. It was put in Chonopectidae by Brunton et al. (2000) and is close to Semenewiini. The Visean genus *Chonetipustula* Paeckelmann, 1931 is assigned to this group. It has prominent spines along the ventral hinge, comparatively well defined commarginal lamellar rugae and recumbent ventral body spines and rare dorsal spines. The genus was placed as Quadratiinae in Brunton et al. (2000, p. 584), but differs considerably in having a more prominent row of ventral hinge spines, pronounced commarginal ornament and shape close to that of *Semenewia*.

The membership of *Plicaea* Aisenverg, 1992 (Visean) and *Plicatiferina* Kalashnikov, 1980 (Kasimovian) of

Lower and Upper Carboniferous age respectively requires better knowledge of their spine distribution and interior. Both show commarginal wrinkles as in Semenewiini, coupled with slightly narrower hinge. The hinge is also at less than maximum width in in early growth stages as indicated by growth-lines of *Semenewia* and *Parmephrix* Brunton & Mundy in Brunton, Racheboeuf & Mundy, 1994, 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. There are spines along the hinge, few body spines, and extremely fine radial threads.

Subfamily **QUADRATIINAE** Lazarev, 1989

[Quadratiinae Lazarev, 1989, p. 38].

Diagnosis: Ventral body spines at low angle, weak row of spines near hinge, dorsal spines variable, numerous, rare or absent, subdued regular rugae on both valves; marginal ridges may be present. Middle Devonian (Givetian) to Upper Carboniferous (Kasimovian).

Genera: *Quadratia* Muir-Wood & Cooper, *Cyphotalosia* Carter, *Dichacaena* Cooper & Dutro, *Quadralosia* new genus.

Discussion: This subfamily was classed in Araksalosiidae by Lazarev (1989) and Brunton et al. (2000, p. 582) but is similar only in terms of being of nearly the same age: it lacks the lateral buttress plates and usually elongate ventral spine bases which characterize that family. *Quadratia* is widespread and well preserved, and fails to show any umbonal cicatrix, and although Brunton et al. (2000, p. 582) stated that a pseudodeltidium was absent, one was observed in type *Quadratia* by Campbell (1966), one was figured for *Q. egregia* by Carter (1967), and one is here figured for a related genus from Canada (Fig. 7.30). The ventral valve carries numerous fine ventral spines, including a rather weakly defined row close to the ventral hinge, rare dorsal spines, and subdued commarginal laminae and very low rugae on both valves, and overall looks externally very like members of Echinalosiinae Waterhouse, 2001, apart from the fine rugae and, as a rule, uniformly fine spines. The genus is distinguished principally by its wide hinge, low interareas, fine spines, and low crowded commarginals, less conspicuous than in Rhytialosiinae, but nonetheless present, even though they are somewhat masked by commarginal laminae on the ventral valve of the name genus and type species, *Quadratia hirsutiformis*. This species has a heavy internal ventral posterior ridge, not seen in all of the associated genera as far as is known, but also not well displayed by other species of *Quadratia*. A dorsal pit lies in front of the broad sub-bifid cardinal process.

Dichacaena Cooper & Dutro, 1982 of Givetian (Middle Devonian) age has weak commarginal growth laminae and rugae, and fine recumbent ventral spines but no conspicuous hinge row of spines and no dorsal spines. As stressed by Cooper & Dutro (1982), the bifid cardinal process (which is well known for the associated rather than type species) is like that of *Eostrophalosia* Stainbrook, 1943, and also *Caucasiproductus* and *Strophoproductus*, genera which have numerous dorsal spines. The figure in Cooper & Dutro (1982, pl. 12, fig. 54) suggests dorsal spine bases, though this is presumably incorrect, but *Quadratia egregia* Carter, 1967, p. 284 also lacks dorsal spines. *Dichacaena* has suggestions of closely spaced commarginal rugae approaching those of Quadratiinae, and indeed the rugae are not always clearly defined in species of *Quadratia* itself, including the type species. Heavy ear baffles are present in *Dichacaena* as in type *Quadratia*.

Genus ***Quadralosia*** new genus

Derivation: quadra – quadrate, Lat.; alos – disc, Greek.

Type species: *Quadralosia delicata* new species, from Hart River Formation (Late Mississippian – Chesterian) of Yukon Territory, Canada, here designated.

Diagnosis: Transverse shells with wide and short interareas, subdued wrinkles, fine spines of two distinct diameters over ventral valve, including erect row along hinge, dorsal spines fewer and erect.

Discussion: A Canadian species from the Yukon Territory shows some differences from *Quadratia* Muir-Wood & Cooper, 1960, in so far as the semiprostrate spines of one size over the ventral valve, shared with *Quadratia,* are accompanied by additional much finer erect and prostrate spines. The more prominent spines are 0.2 to 0.3mm in diameter, and appear to be ordered over most of the valve in commarginal rows, although in detail they are not regularly arranged, protruding from different growth lines and rugae, and somewhat more disordered over the trail. In addition, there are much more slender spines less than 0.1mm in diameter, disordered in distribution, usually over the anterior half of the valve, and prostrate over the median valve, and tending to be more erect near the margin. They may be bunched as two to four in a cluster. According to available descriptions, as confirmed by figures, *Quadratia* is typified by spines of subuniform diameter.

Quadralosia delicata new species

Fig. 7.28 - Fig. 7.32

1971 *Quadratia* cf. *hirsuteformis* (sic = *hirsutiformis*) [not Walcott] – Waterhouse in Bamber & Waterhouse, p. 110, pl. 1, fig. 1-4.

Derivation: delicatus – alluring, Lat.

Holotype: GSC 133257 from GSC loc. 53743, Hart River Formation (upper Visean), Yukon Territory, Canada, figured as Fig. 7.28 and Fig. 7.32C, here designated.

Diagnosis: Shells with thin body corpus, slightly upturned ventral ears, ventral umbo with small cicatrix, ventral interarea low with pseudodeltidium, posterior lateral ridges not high. Well defined row of ventral hinge spines, major ventral spines thin and loosely arranged in commarginal rows, but moderately irregular, additional much more slender spines, prostrate over shell and becoming erect over trail. Dorsal spines concentrated on ears.

Material: Some twenty specimens with valves conjoined from GSC loc. 53743, and ten from GSC loc. 53745, and fragments from GSC loc. 53749, Hart River Formation (upper Visean), Yukon Territory, Canada. See Appendix A, part C, pp. 477, 478.

Dimensions in mm:

Specimen GSC	Width	Length	Height	
133257	34	24	9.5	holotype
133252	24	15.5	4.5	
133251	29	19	11.5	distorted
133260	32	28	10	
133262	32	22	?5	
133274	27	19	5	

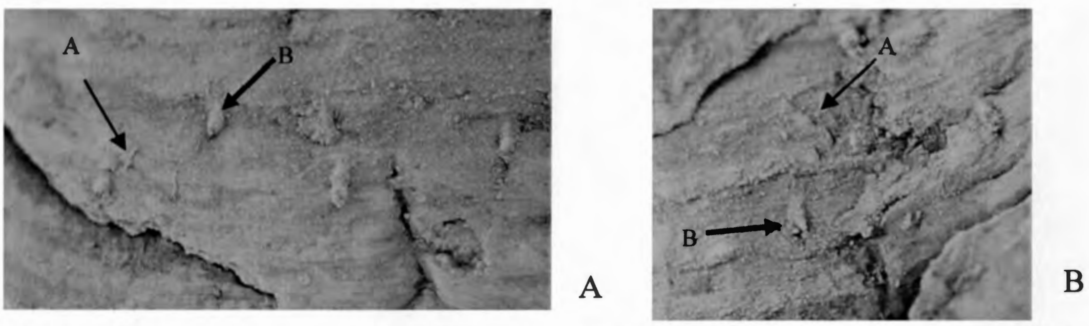

Fig. 7.28. *Quadralosia delicata* new genus, new species, detail of ornament on ventral valve, holotype GSC 133257, x8, from GSC loc. 53743. Arrows pointing to slender (A) and thicker (B) spines. From Hart River Formation (upper Visean), Yukon Territory, Canada. JBW photo.

Description: Shells of moderate size, up to 35mm wide and 28mm long, with very thin visceral disc and trail curving smoothly forward. Maximum width lies toward the anterior quarter of the shell length, and the hinge is almost as wide, with an extremely low ventral interarea bearing a narrow arched pseudodeltidium that may be lost in later ontogeny, and low dorsal interarea, standing at high angle to disc, bearing low horizontal markings and broad chilidium marked by outward sloping ridges. A very small smoothly convex nepionic part lies in front of the notothyrium on the dorsal valve. The cardinal extremities are acute and the ventral ears slightly upturned. There is no sulcus or fold, and umbonal slopes are low and short. Ventral spines cover the valve, small and erect without prolonged or swollen bases. The spines at the hinge seem to form part of a row that follows a growth line or rugation, and the spines are no thicker than elsewhere. But they project posteriorly and are erect, whereas those over the disc and trail are semi-prostrate and project forwards, and may cause short grooves in the exterior, where external shell partly enwrapped an overlying prostrate spine. The thicker spines are about 2 to 2.5mm apart with 2-3mm between rows anteriorly, usually 0.2 to 0.3mm in diameter, rarely 0.4mm, and the thinner spines more irregularly dispersed, 0.1mm in diameter or slightly less, with further detail provided in the generic description and in figures. Dorsal spines are like those of the thicker ventral spines and are suberect with a number over the ears. Both valves are covered by very low and regular commarginal growth increments, some ten in 1mm, superimposed over low irregular rugae, with commarginal growth lamellae. Internal detail is not well known. Specimens show very small teeth and small lightly impressed adductor scars. There is no prominent hinge ridge across the ears.

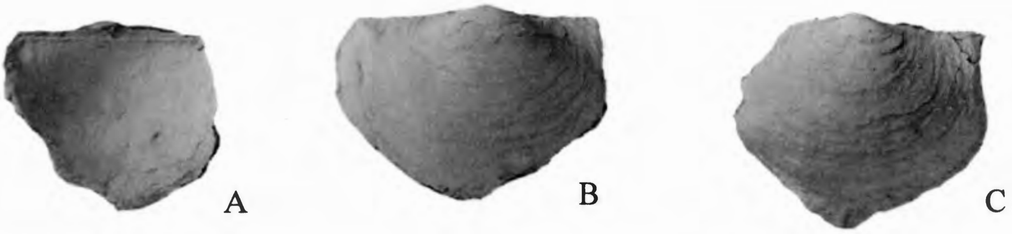

Fig. 7.29. *Quadralosia delicata* new species. A, ventral valve GSC 26438 from GSC loc. 53745. B, ventral valve GSC 26439 from GSC loc. 53743. C, ventral view of GSC 26440 from GSC loc. 53743. Specimens x 1, from Hart River Formation (upper Visean), Yukon Territory, Canada. B. O'Donovan & JBW photo.

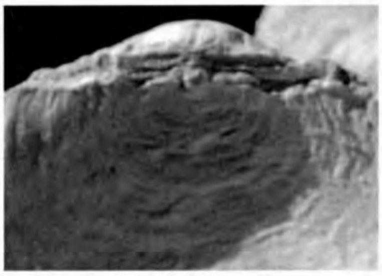

Fig. 7.30. *Quadralosia delicata* new species, posterior detail of GSC 133260, from GSC loc. 53743, x3, showing pseudodeltidium. Hart River Formation, Yukon Territory, Canada. JBW photo.

Resemblances: This species is very close in most known detail to *Quadratia hirsutiformis* (Walcott 1884, p. 133) from lower Chesterian of Oklahoma, United States, as revised by Muir-Wood & Cooper (1960). External differences are that the cardinal extremities are more pointed in the Canadian species, and the spines more closely spaced, with about five per 10mm in the Canadian form, compared with three in 10mm in Walcott's species, and dorsal spines may be more common. The critical difference lies in the nature of the ventral spines, those of *Quadratia* being of uniform diameter, as far as described, those of the new genus being of two differing diameters. Muir-Wood & Cooper (1960, p. 161) stated that a pseudodeltidium was absent from *hirsutiformis*, whereas it is definitely present in the Canadian form. However Campbell (1966) challenged the observation for *hirsutiformis*, asserting that one was present in at least some specimens. No chilidium was reported for *hirsutiformis*, but this may reflect a change in

Fig. 7.31. *Quadralosia delicata* new genus, new species. GSC 133274, from GSC loc. 53749, showing detail of ornament, x10, with slender arrow pointing to a fine spine, and thicker arrow pointing to a more sturdy spine. Hart River Formation, Yukon Territory, Canada. JBW photo.

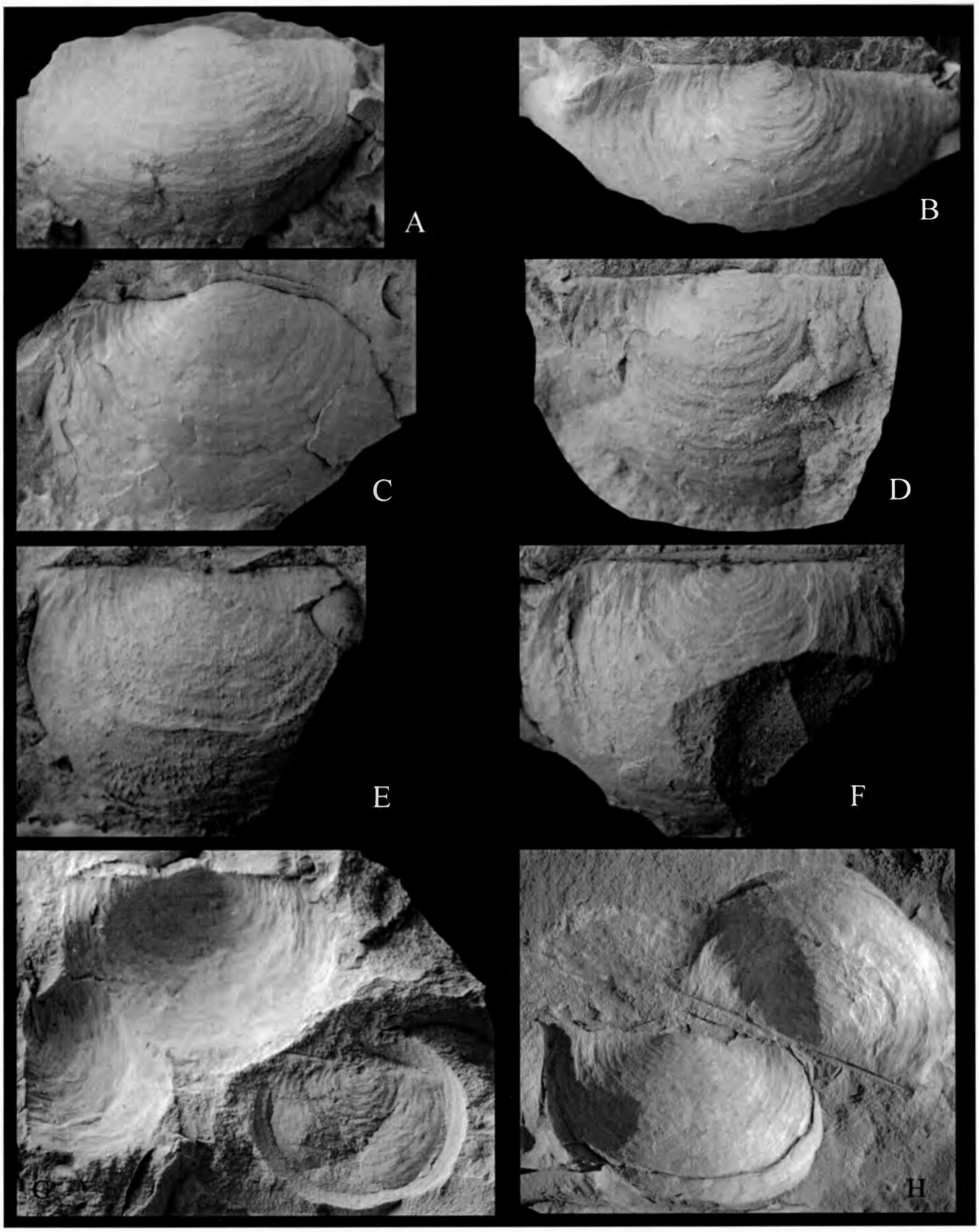

Fig. 7. 32. *Quadralosia delicata* new species. A, B, ventral and posterior ventral aspects of GSC 133254 from GSC loc. 53745, x1.8. C, holotype, ventral valve GSC 133257, from GSC loc. 53743, x1.7. D, ventral valve GSC 133252 from GSC loc. 53743, x3. E, decorticated dorsal valve (ventral aspect) BR 133255 from GSC loc. 53749, x2. F, decorticated external mould of a dorsal valve GSC 133263 from GSC loc. 53745, x3. G, dorsal aspects of ventral valves and a specimen with valves conjoined, GSC 133256 and 133257, from GSC loc. 53743, x2. H, dorsal views of two specimens with valves conjoined, GSC 133261 and 133262, from GSC loc. 53743, x1.6. Hart River Formation (upper Visean),Yukon Territory, Canada. JBW photo.

specimens with increased maturity, the chilidium being displaced by the cardinal process. Commarginal rugae are low and fine in the Canadian form. Walcott's species has larger ventral adductor scars, and a heavy posterior ridge that continues across the ears, but no comparable ridge is seen in the Canadian form. *Productus hirsutiformis* *batesvillensis* Girty (1911, p. 51, pl. 3, fig. 5) from the Moorefield Shale or northern Arkansas, United States, is a wider shell with well developed ears and sparsely developed spines. *Quadratia patula* (Girty, 1915b, p. 13, pl. 1, fig. 1-16, 2) from the Mississippian Boone Limestone of Arkansas, United States, is close in shape but has stronger and regular commarginal rugae in both valves, approaching those of *Plicatiferina* Kalashnikov, 1980, p. 15 from Kasimovian faunas of Bashkiria, Russia. *Q. alifera* (Girty, 1899, p. 530, pl. 68, fig. 10a-c) from the Madison Limestone of Yellowstone Park, Wyoming, United States, shows more visible spines, subdued commarginal rugae and prominent alar extensions to the hinge. From the Chappel Limestone of late Kinderhookian and possibly early Osagean age in central Texas, United States, *Quadratia egregia* Carter, 1967, p. 284, pl. 17, fig. 1a-8 has more marked commarginal rugae, and diductor scars are bordered each by a ventral marginal ridge extending from the umbo for half of the length of the shell, diverging more narrowly than in type *Quadratia*. Dorsal spines are lacking.

Subfamily **RHYTIALOSIINAE** Lazarev, 1989

[Rhytialosiinae Lazarev, 1989, p. 38].

Diagnosis: Undulose rugae prominent and discontinuous on both valves; spines dense on ventral valve, fewer on dorsal valve. Upper Devonian (middle Frasnian – Famennian).

Genera: *Rhytialosia* Lazarev, *Agramatia* Sokolskaya, *Mckellarosia* new genus, *Sinalosia* Ma & Sun, *Steinhagella* Goldring, ?*Strophoproductus* Nalivkin, *Veeversalosia* Lazarev.

Discussion: This is an outstanding group, readily distinguished by its ornament, to suggest, from age, ancestral stock for similarly rugose Institinini Muir-Wood & Cooper of Visean age, which is amongst the oldest of Aulostegoidea. Spines may develop close to the hinge, but not consistently within the subfamily. Rhytialosiinae is completely strophalosiiform, whereas genera of Institinini lack teeth and sockets, and are rarely cicatrixed, but do have interareas, illustrating the overlap and duality of relationships within Productida.

The subfamily was classed as a member of Araksalosiidae Lazarev by Brunton et al. (2000), but shows no particularly close affinity, other than age: the distinctive elongate spine bases, and lateral buttress plates of Araksalosiidae are not developed, although a strong row of spines are developed in some genera, as in Araksalosiidae. *Sinalosia* Ma & Sun in Ma et al., 2002 has regular very fine commarginal rugae suggestive of Rhytialosiinae, but is tiny in size. It has widely diverging cardinal supports enclosing the dorsal sockets, leading to questions over ontogenetic development and degree of maturity. Subfamily Quadratiinae is moderately close in the possession of close-set commarginal rugae and well spaced small especially ventral spines, and varying development of ventral hinge spines.

Genus ***Mckellarosia*** new genus

Fig. 7.33

Derivation: Named for R. G. McKellar.

Type species: *Strophoproductus rugosus* McKellar, 1970, p. 16 from Myrtlevale and Star beds (Famennian), Burdekin Basin, Queensland, Australia, here designated. See Appendix A, part A, p. 477.

Diagnosis: Small with wide hinge and otherwise well rounded outline, both valves closely and strongly rugose commarginally, ventral hinge spines number about four each side, posteriorly directed, ventral body spines uniform, well and subevenly spaced in quincunx, suberect posteriorly, nearly prostrate anteriorly, in front of posterior ridges extending over one or two lamellae, marginal fringe of short costae or spine ridges in some specimens. Dorsal valve with conspicuous elongate pits and rare spines. Cardinal process bilobed with widely splayed hinge ridges, median septum extends for half length of valve.

Discussion: The shape and rugation of this genus are close to features of two genera classed within Rhytialosiinae: *Rhytialosia* Lazarev, 1989 and *Veeversalosia* Lazarev, 1989. *Rhytialosia*, described from the middle Frasnian of Europe, has relatively finer rugae, a ventral cicatrix that is missing from the Australian form, long dorsal median septum, and no clear dorsal pits. *Veeversalosia* differs more, in having numerous dorsal spines and much finer rugae, but there are similarities in the lack of cicatrix, length of median septum, and numerous but more rounded dorsal pits. *Mckellarosia* is found in the *Sentosia* (now *Spinauricula*) *minuta* Zone of the Burdekin Basin, west of Collinsville, Queensland.

Strophoproductus Nalivkin, 1937, p. 46, proposed for *Productella hystricula* Hall, 1867, p. 178 from the Upper Devonian (Frasnian) of New York and Eurasia, does show some similarities, although rugae and spines are finer and less prominent, with dorsal papillae elongate and numerous over the anterior shell. Muir-Wood & Cooper (1960, p. 155) described ventral spines as arranged in one or two rows near the hinge and two curved rows down the flanks, which is not the same as the distribution in the present form. Most spines are arranged along spine ridges as in the present genus, and there are dorsal spines. The genus *Strophoproductus* was classed as Caucasiproductinae Lazarev, 1987 by Brunton et al. (2000, p. 526), but does not appear to be close to other members of that subfamily, given the prominence of fine rugae.

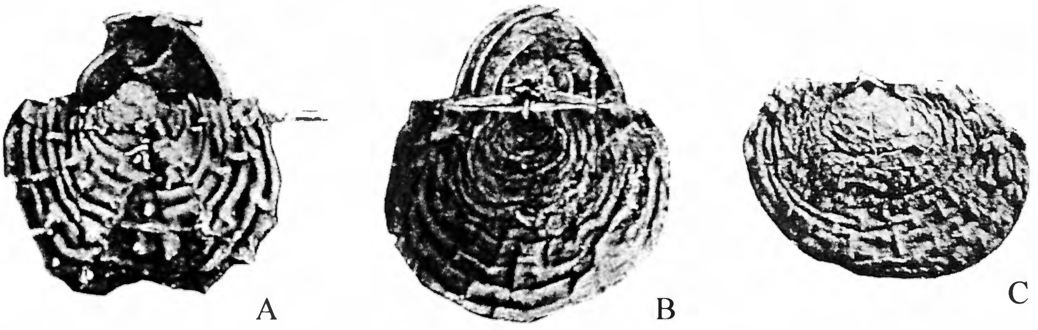

Fig. 7.33. *Mckellarosia rugosus* (McKellar). A, ventral external latex cast, GSQ F 3644, x4. B, dorsal aspect of specimen with valves conjoined, GSQ F 11489, latex cast, x4. C, dorsal interior, latex cast of GSQ F 11490, x3. From Myrtlevale and Star beds (Famennian), Queensland, Australia. See McKellar (1970, pl. 4).

Family **ARAKSALOSIIDAE** Lazarev, 1989

[Araksalosiidae Lazarev, 1989, p. 34].

Diagnosis: Radial ornament present or absent, short interareas, shallow corpus cavity, well developed lateral buttress plates, cardinal process pit may be present, marginal ridges commonly absent.

Discussion: The diagnosis for Araksalosiidae provided by Brunton et al. (2000, p. 576) – "interareas short, concavo-convex, shallow corpus cavity, radial ornament commonly absent, cardinal process with pit, marginal ridges commonly absent " is little better than meaningless in the context of Strophalosioidea. Even for Araksalosiinae, one of the prime diagnostic features – the presence of lateral buttress plates – is not mentioned. But this criticism applies to all of the Devonian strophalosiid groups, leaving the classification in the *Revised Brachiopod Treatise* as a less than adequate guide: the pictures in the *Revised Brachiopod Treatise* are much more useful, provided they are critically evaluated.

Aspects of the distinctive ornament and well developed lateral buttress plates in Araksalosiidae suggest that constituent genera were progenital to Balkhasheconchinae, a distinct group within Scacchinelloidea, so that there rises the problem of dual affinities, *Araksalosia* and allies being undoubtedly strophalosioid in morphology, and their descendents productiform. Just as Brunton et al. (2000) and Lazarev (1987) quite logically treated strophalosiiform genera such as *Devonoproductus* and *Eoproductella* as primitive Linoproductoidea, or *Productella* as primitive Productoidea, then *Araksalosia* needs in an evolutionary sense to be treated as a forerunner of Scacchinelloidea, although itself fully strophalosioid.

It may be speculated that Araksalosiinae arose from Chattertoniinae, a subfamily within Productellidae which is characterized in part by the possible presence of dorsal accessory septa. But the lateral buttress plates of Araksalosiidae lie outside the dorsal adductor scars, whereas the accessory septa of Chattertoniinae lie between the adductor scars, and correspond with the anderidia of Chonetida. *Fortispinalosia* new genus of Mississippian age in the United States (p. 215) is excluded from the family, because its lateral buttress plates are thicker, and the spine pattern completely like that of Strophalosiidae, without the strongly patterned distribution and usual elongate bases, and without any conspicuous row of strong ventral hinge spines found in many Araksalosiidae.

Subfamily **ARAKSALOSIINAE** Lazarev, 1989

Fig. 7.34A, B

[Araksalosiinae Lazarev, 1989, p. 35].

Diagnosis: Mat of spines on ventral or both valves, elongate spine bases. Lateral buttress plates. Upper Devonian (upper Famennian) to basal Carboniferous (lower Tournaisian).

Fig. 7.34. A, B, *Hamlingella goergesi* (Paeckelmann), A, ventral valve, x0.85. B, dorsal valve, showing lateral buttress plates, x1. From Etroungt beds (Lower Carboniferous), near Ratingen, Rhine Province, Germany. See Paeckelmann (1931, pl. 2, fig. 1, 2). C, *Whidbornella caperata radiata* (Paeckelmann), from Etroeungt beds, Germany, x1. See Paeckelmann (1931, pl. 3, fig. 7).

Genera: *Araksalosia* Lazarev, *Hamlingella* Reed, *Kahlella* Legrand-Blain.

Discussion: Spines are notably fine along the ventral hinge in *Araksalosia*, but are stronger in *Hamlingella*. Although no dorsal spines are developed on *Araksalosia* according to Brunton et al. (2000), fine dorsal spines are numerous on *Hamlingella* as shown by Reed (1943) and Muir-Wood & Cooper (1960). Semenewiini has prominent ventral hinge spines, prominent commarginal rugae, and lacks prolonged ventral spine bases and lateral buttress plates.

Subfamily **WHIDBORNELLINAE** new subfamily

Fig. 7.34 C

Name genus: *Whidbornella* Reed, 1943, p. 71 from Pilton Beds (upper Famennian), England, here designated.

Diagnosis: Mat of spines on ventral or both valves, elongate spine bases form very fine ribs, spines strong along ventral hinge, truncated lateral buttress plates. Upper Devonian (upper Famennian) to basal Carboniferous (lower Tournaisian).

Genera: *Whidbornella* Reed, *Ruthiphiala* Carter.

Discussion: These genera are close to *Araksalosia* and the better known and more fully described genus *Hamlingella*, and have very fine ventral ribs and spine bases. *Whidbornella* has numerous dorsal spines. Its lateral buttress plates are shorter than in *Hamlingella* but closer to those of *Araksalosia*.

Subfamily **ACANTHATIINAE** new subfamily

Name genus: *Acanthatia* Muir-Wood & Cooper, 1960 from Percha Shale (uppermost Famennian), New Mexico, United States, here designated.

Diagnosis: Transverse, semicircular to oval outline, small cicatrix, row of strong ventral hinge spines, other fine to coarse spines in quincunx over ventral valve, dorsal spines rare or absent, no ribs or elongate bases or prominent commarginal ornament other than low closely spaced growth lines. Dorsal valve with pit in front of cardinal process, which is supported by diverging lateral buttress plates. Upper Devonian (upper Famennian) to Lower Carboniferous (Tournaisian).

Genera: *Acanthatia* Muir-Wood & Cooper, *Rangaria* new genus.

Discussion: Two of the most significant aspects of Araksalosiidae as interpreted herein are developed in Acanthatiinae, involving prominent ventral hinge spines and strong supports for the cardinal process, extending into lateral buttress plates. The ornament does not display the short spine bases aligned in rows that typify *Araksalosia* and allies, nor any sign of the fine ribbing of Whidbornellinae.

Genus ***Rangaria*** new genus

Fig. 7.35

Derivation: Named from Rangari Limestone, source of the type species.

Type species: *Acanthatia*? *rangariensis* Campbell & Engel (1963, p. 70) from Rangari Limestone (Tournaisian), northern New South Wales, Australia, here designated.

Diagnosis: Transverse little inflated shells with row of sturdy diverging spines along the ventral hinge and moderately strong and semi-recumbent spines in quincunx over the remainder of the valve, no dorsal spines. Lateral buttress supports long and sturdy in the dorsal valve.

Discussion: The type species has been described by Campbell & Engel (1963, pl. 2, fig. 17-33), with holotype UNE 7204 (pl. 2, fig. 26, 27), now reregistered and kept at the Australian Museum, Sydney as AMF 76011. Other specimens registered as UNE numbers in the publication are re-registered as follows: UNE 7212 (AMF 75965), UNE 7215 (AMF 75964), UNE 7214 (AMF 75966) and UNE 7243 (AMF 76102). The shell outline is almost semi-circular, and interareas low but well developed, with moderately arched pseudodeltidium, and small cicatrix on the ventral umbo, and delicate chilidium. Spines along the hinge bend sharply outwards near the umbo, and the surface of the shell bears low growth increments. A low marginal ridge passes laterally from each tooth and curves around the valve, and muscle scars are undivided and small. The cardinal process is small, broad and sub-bifid, with lateral hinge ridges that may continue forward across part of the ears, no cardinal process pit and a massive breviseptum. Lateral buttress plates extend moderately far forward, and are shown in an internal mould as impinging on the ventral valve through post-mortal compression (Fig. 7.35C), lying each side of the ventral muscle field (Campbell & Engel 1963, pl. 2, fig. 33). Endospines are dense.

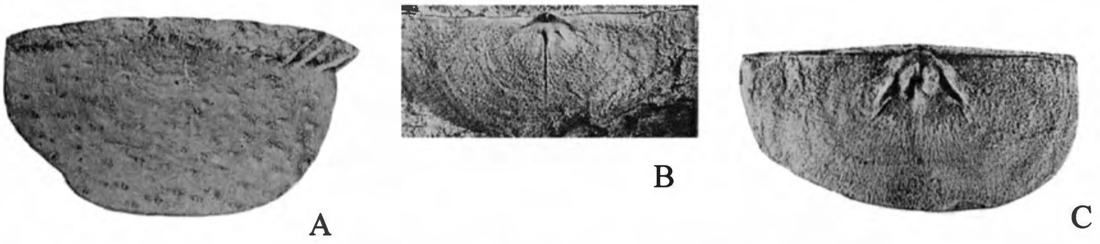

Fig. 7.35. *Rangaria rangariensis* (Campbell & Engel) from Rangari Limestone (Tournaisian), New South Wales, Australia. A, latex cast of ventral valve holotype, AMF 76011 (formerly UNE F 7204). B, internal mould of dorsal valve, UNE 7310. C, internal mould of ventral valve AMF 75964 (formerly UNE 7215) with imprints of lateral buttress plates from dorsal valve. Specimens x0.8 approx. See Campbell & Engel (1963, pl. 2).

A moderately close genus is *Acanthatia* Muir-Wood & Cooper (1960, p. 158, pl. 38, fig. 1-14), based on a type species of Upper Devonian age in New Mexico, United States. This genus is more rounded in outline, and the ventral hinge row of spines is equally well developed but ventral body spines are much finer and more closely spaced, and there are at least occasional dorsal spines. Teeth are present, and the ventral adductors were described as not divided into two scars, and in the dorsal valve the breviseptum is thin, the lateral buttress plates are much shorter and finer, and marginal and hinge ridges were reported as absent. Other aspects are also comparable, including a small cicatrix, pseudodeltidium and chilidium, bilobed cardinal process and alveolus between the socket plates, which is infilled by a broad septum in more mature specimens of *Rangaria* (Campbell & Engel 1963, pl. 2, fig. 28). According to Brunton et al. (2000, p. 576), *Acanthatia* is found in North America, Europe, ?northern Africa and ?Asia, and was not mentioned as coming from Australia.

Campbell (1966) reallocated the species *rangariensis* to *Quadratia* Muir-Wood & Cooper (1960, p. 161, pl. 39, fig. 1-13). Campbell & Engel (1963) had stressed that the presence of a pseudodeltidium and chilidium in their species *Acanthatia? rangariensis* provided a clear distinction from *Quadratia*, and indeed according to Brunton et al. (2000, p. 582), a pseudodeltidium and chilidium are commonly absent from members of Quadratiinae. But Campbell (1966) found on inspection that the type species of *Quadratia, Q. hirsutiformis* (Walcott), has a pseudodeltidium and chilidium, just like *Acanthatia*. The new form is close to *Quadratia*, but lacks dorsal spines, which are frequently but not always present in *Quadratia,* and has lateral buttress plates. *Rangaria* has a much more conspicuous row of ventral hinge spines and less developed commarginal growth rugae and laminae, especially on the ventral valve. The ventral adductors of *Quadratia* are divided into anterior and posterior pair, unlike those of the new genus, and the ventral hinge ridge is strong in at least the type species of *Quadratia* but absent from *Rangaria* and *Acanthatia*.

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 denticulate hinge.

Discussion: This group differs strongly from Strophalosiidae and Araksalosiidae in its ornament of dorsal lamellae bearing fine radial filae as a rule, with spines less prominent.

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

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

Diagnosis: Ventral ribs, short interarea, dorsal lamellae, dorsal spines present or absent, hinge 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, Fig. 423.1e). *Girlasia* Gregorio, 1930 is placed here because of its reportedly denticulate hinge. It looks strophalosioid in morphology, but was classed in Echinosteginae Muir-Wood & Cooper of Aulostegoidea by Brunton et al. (2000, p. 595). *Girlasia* has dorsal spines, *Mongolosia* has dorsal radials, and *Ctenalosia* no radials or dorsal spines.

Subfamily **BRUNTONARIINAE** new subfamily

Name genus: *Bruntonaria* Waterhouse, 2001, p. 85 from Carrick Lough and Bunnahone, Derrygonnelly (Visean), North Ireland, here designated.

Diagnosis: Commarginal laminae over both valves. Dorsal valve planar, two orders of spine. Lower Carboniferous (Visean).

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

Discussion: This subfamily is placed in Ctenalosiidae because of the well developed lamellae on both valves. In other respects, the genera are distinguished from associated subfamilies through the rather flat dorsal valve and comparatively abundant spines on both valves and lack of radial capillae. Internal detail is well established, especially for the silicified material described from Northern Ireland by Brunton (1966).

Genus ***Bruntonaria*** Waterhouse, 2001

Fig. 7.36

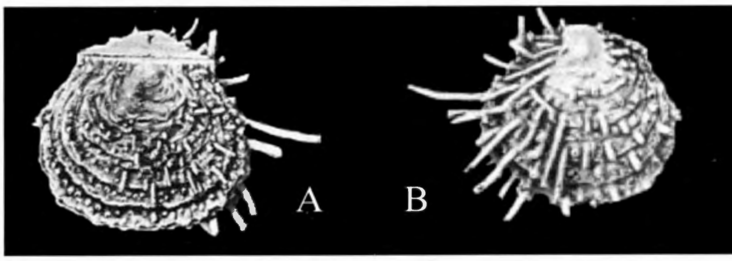

Fig. 7.36. *Bruntonaria panicula* (Brunton). A, B, dorsal and ventral aspects of BB 52796, x 8, from Visean of County Fermanagh, Ireland. See Brunton (1966, pl. 2, fig. 14, 15).

Discussion: *Bruntonaria* Waterhouse was confused with *Dasyalosia* Muir-Wood & Cooper by Brunton (1966, cf. Brunton et al. 2000, Fig. 404.1a-c with Fig. 404.1d, e; 2007, p. 2663), but is readily distinguished by the much more strongly developed and regularly disposed concentric lamellae on each valve, with less tangled and less vermiform spines and stronger supporting ridges for the cardinal process. Brunton (2007) in trying to justify his original misidentification of a Lower Carboniferous brachiopod with an Upper Permian form, ignored the strong differences in nature of the spines and the degree of concentric laminae, and made much of the fact that the cardinal process in a specimen figured by Muir-Wood & Cooper (1960) was broken, bypassing the fact that no classificatory significance was attached to the nature of the cardinal process by Waterhouse (2001), although he did comment that its apparently small size might indicate immaturity.

Acanthalosia Waterhouse of Dasyalosiinae is close to *Bruntonaria* in that the two share major ventral spines directed forwards at a very low angle from the shell surface, whereas the major spines in *Dasyalosia* are much more vermiform. As well, the cardinal supports (ie. socket plates) for the cardinal process are strong in both genera, and weak in *Dasyalosia*. On the other hand commarginal laminae are strong only in *Bruntonaria*.

Genus **Crossalosia** Muir-Wood & Cooper, 1960

Although placed as Dasyalosiinae by Brunton et al. (2000, p. 570), *Crossalosia* has lamellae over both valves, with ventral spines in single rows (see Muir-Wood & Cooper 1960, p. 75, pl. 5, fig. 1), and dorsal spines are not as uniform as in younger genera, the figure in Brunton et al. (2000, Fig. 404.2d) suggesting two orders of spine. There are additional spines near the hinge on both valves. In that it lacks radial capillae, the genus is readily distinguished from most other genera assigned to Ctenalosiinae. The ventral spines are of one order, whereas those of *Bruntonaria* are more crowded and in two distinct orders. The dorsal valves in the two genera appear closer. Internal detail is well known for both genera.

Subfamily **MINGENEWIINAE** Archbold, 1980

[Mingenewiinae Archbold, 1980, p. 255].

Diagnosis: No cicatrix, no spines on either valve. Dorsal valve has radial capillae and lamellae. Lower Permian (Artinskian) to Upper Permian (Changhsingian).

Genus: *Mingenewia* Archbold, *Quasimingenewia* new genus.

Discussion: *Mingenewia* has low ribs on the ventral valve, and ventral median septum. A new genus from the Upper Permian of Nepal has no ventral ornament, nor ventral septum.

Genus ***Quasimingenewia*** new genus

Derivation: quasi – near, Lat.; Mingenewia – strophalosioid genus.

Type species: *Quasimingenewia imperator* new species from Manang Group (Changhsingian) of north-central Nepal, here designated.

Diagnosis: Medium-sized with no ventral cicatrix and no ventral or dorsal spines, no ventral ribs, dorsal valve weakly lamellate with faint radial markings. No ventral septum.

Discussion: This genus was reported as *Mingenewia* Archbold (1980) by Waterhouse & Shi (1991), but differs from the only known species of that genus in the lack of a sturdy septum in the posterior ventral valve. Topotypes of the type species of *Mingenewia*, inspected at the Natural History Museum, London, England, are small with well developed and radially striate dorsal lamellae, and heavy dorsal anterior marginal ridge. The ventral valve has been described as smooth, as verified by figures of the umbonal surface (Archbold 1980, pl. 1, fig. 13, 14, 19), but faint costae or radial lineations are visible over the anterior internal mould (Archbold 1980, pl. 1, fig. 2, 12). The Nepal specimens differ in several respects from *Mingenewia*, involving especially the lack of subfusc costae and the lack of a ventral septum, and are much younger than the Australian species, which comes from the Early Permian Mingenew Formation of the Perth Basin, Western Australia.

Quasimingenewia imperator new species

Fig. 7.37, Fig. 7.38

1991 *Mingenewia* n. sp. Waterhouse & Shi, p. 382.
2010b aff. *Mingenewia* n. sp. Waterhouse, p. 278, Figure 10 F, G.

Derivation: imperator - ruler, Lat.

Holotype: Specimen 2006.81.259 figured herein as Fig. 7.37A, B, C from PMb5, Braga Member (Changhsingian), Nepal, here designated. Kept at Canterbury Museum, Christchurch, New Zealand.

Diagnosis: Medium-sized subquadrate to subrectangular specimens with massive umbo and steep posterior shoulders, ventral sulcus deep and well formed, dorsal fold low, hinge wide. Shell without spines or umbonal cicatrix, dorsal laminae subdued and marked by fine radial lirae.

Material: Five specimens with valves conjoined and two ventral valves from BMb5, single specimens with valves conjoined from PM1 and PM5, Braga Member and undifferentiated Marsyangdi Formation, northern Nepal. One dorsal valve UQF 45875 from Marsyangdi Formation, Kali Gandaki valley, Nepal. See Appendix A, part G, p. 480.

Dimensions in mm:

Width	Length ventral	Length dorsal	Height	Hinge width	
23	34	25	16	16	holotype
27	?21	18	-	?20	
34	21	7.5	-	?22	

Description: Specimens vary from elongate to transverse, partly due to deformation, umbo massive, incurved, without cicatrix. Ventral interarea moderately concave, lying in plane of commissure, with horizontal markings and slender pseudodeltidium, dorsal interarea moderately well formed, flat, sloping gently forward dorsally from the commissure. Cardinal extremities minutely alate, or asymmetric with one rounded, the other alate; maximum shell width lies well in front of hinge. Ventral posterior walls massive and high; ventral sulcus commences well in front of umbo and becomes wide and deep with steep lateral walls. Dorsal valve moderately concave, with no clearly discriminated nepionic part, fold commencing near posterior third of shell length and widening at angle of 27°, trail non-geniculate, passing straight on from disc in holotype, but steeply inclined in two dorsal valves, without geniculation. Ventral valve poorly preserved externally, but nowhere shows spines, ribs, or other form of ornament; dorsal valve non-spinose, with 16-20 subdued lamellae, marked by fine uneven growth-lines, up to eight to ten per mm, and irregular radial capillae, six to eight per mm.

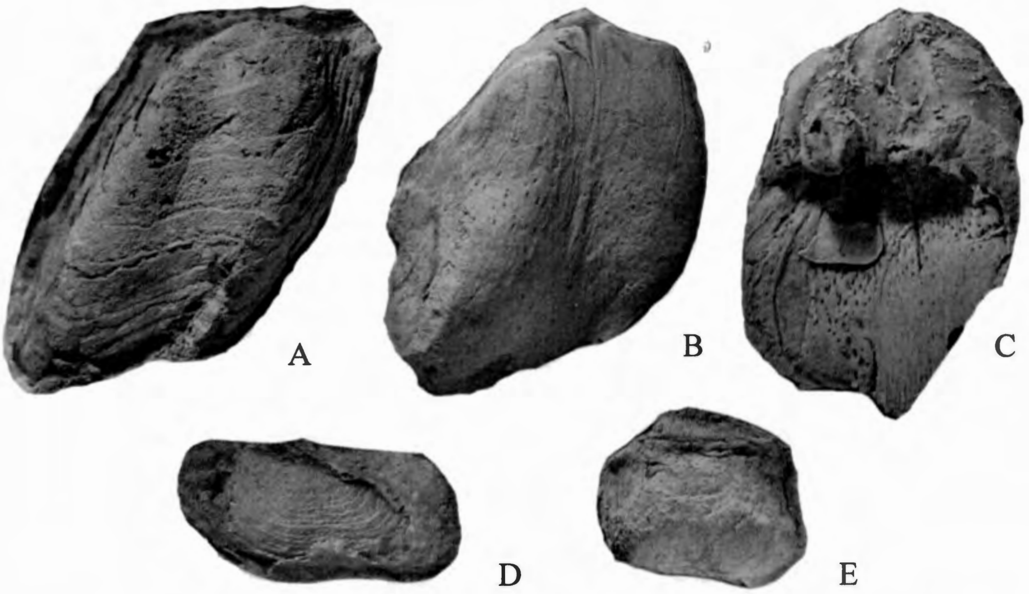

Fig. 7.37.*Quasimingenewia imperator* new genus, new species from north-central Nepal. A, B, C, holotype, specimen no. 2006.81.259 dorsal external mould and ventral and dorsal views of internal mould, from PMb5, Braga Member, x2. D, dorsal external mould and ventral valve anteriorly, with marginal ridge, UQF 45875, from Marsyangdi Formation, Kali Gandaki Valley. E, dorsal aspect of specimen with valves conjoined, decorticated dorsal valve and ventral interarea, from PM5, undifferentiated Marsyangdi Formation, Valley of Lakes, x1. Specimens of Changhsingian age, kept at Canterbury Museum, Christchurch, New Zealand. J. Coker, N. Hiller & JBW photo.

Ventral teeth of moderate size, not well preserved, ventral adductors smooth and concave, subdivided intosmall posterior pair and elongate anterior pair, divided medianly by two fine ridges. Diductors large and elongately oval, marked by several irregular longitudinal grooves less evenly spaced than in many strophalosiids. Large elongate or round pustules lie in front of the muscle field below the sulcus, rare over lateral walls. Very fine even pits and pustules also present over valve floor. There is no median septum or prominent myophragm.

Cardinal process massive, trifid, supported by strong median septum, extending to mid-length. Socket ridges short. Dorsal adductors divided into almost smooth oval posterior lateral pair and subrounded smooth anterior pair. Brachial ridges extend from posterior adductors well forward, and curve back to terminate not far from the anterior end of the median septum. Floor of valve marked by fine pits and well spaced pustules like those of the ventral valve. No anterior or lateral marginal ridge. Thin inner shell layer present.

Resemblances: The only remotely similar species, *Mingenewia anomala* Archbold (1980), is readily distinguished by its smaller size, more transverse outline, shallower sulcus, faint internal ventral ribbing anteriorly, more prominent dorsal lamellae, substantial ventral septum and massive anterior marginal dorsal ridge, with other differences.

Fig. 7.38.*Quasimingenewia imperator* new genus, new species. A, B, ventral and dorsal aspects of BR 3029 x2 from PM5, Marsyangdi Formation (Changhsingian), Nepal. The shell is decorticated, but shows the lack of internal costae visible in *Mingenewia*. JBW photo.

Mongolosia Manankov & Pavlova, 1976 is somewhat similar especially in its dorsal valve, which has radial filae over lamellae and lacks spines, but the genus also has ventral spines, cicatrix, and hinge denticles. It is classed in Ctenalosiinae, but also approaches Craspedalosiinae in the nature of the dorsal valve – the ventral valve of Craspedalosiinae has rhizoid spines.

Subfamily **CRASPEDALOSIINAE** Waterhouse, 2002b

[Craspedalosiinae Waterhouse, 2002b, p. 44].

Diagnosis: Ventral valve with rhizoid spines, dorsal spines absent or rare, dorsal valve lamellate with radial capillae present, faint, or absent. Hinge not denticulate. Middle Permian (Wordian) to Upper Permian (Wuchiapingian or Changhsingian).

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

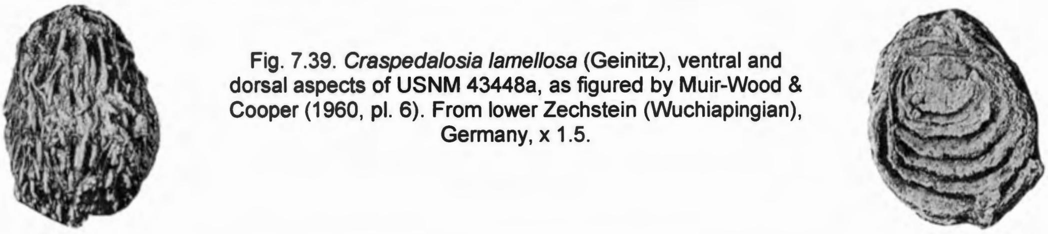

Fig. 7.39. *Craspedalosia lamellosa* (Geinitz), ventral and dorsal aspects of USNM 43448a, as figured by Muir-Wood & Cooper (1960, pl. 6). From lower Zechstein (Wuchiapingian), Germany, x 1.5.

Discussion: For these genera, Brunton (2007, p. 2667) claimed that Waterhouse (1969, 2001) had overlooked the significance of radial capillae, and did not consider the presence of dorsal spines on *Melvillosia* as significant, yet the diagnosis for *Melvillosia* in Waterhouse (2001, p. 56) reads "Close to *Craspedalosia*, distinguished by the presence of rare dorsal spines", and radial capillae were diagnosed as an essential characteristic of *Craspedalosia* and *Melvillosia* (Waterhouse 2001, 2002b). There are numerous examples of this kind of mis-statement or ambiguity throughout the texts by Brunton et al. (2000) and Brunton (2007), underlining the need for caution in quoting or accepting statements from those publications, and the need for careful checking of the original literature, not to mention critical evaluation of figures. Brunton (2007) proceeded to suggest that the presence of dorsal spines in *Melvillosia* might suggest an approach to *Orthothrix* Geinitz, 1847. *Orthothrix* is readily distinguished by having numerous fine and non-rhizoid spines over both valves, and lacks capillae, as well illustrated by Muir-Wood & Cooper (1960, pl. 7, fig. 7-16) and Brunton et al. (2000, Fig. 406.3a-d), to suggest a position in Arcticalosiini. *Melvillosia* is not close to *Orthothrix*, and is certainly close to *Craspedalosia*.

Bruntonariinae are close, but have non-rhizoid ventral spines and numerous diverse dorsal spines.

8. **SuperamilySCACCHINELLOIDEA Licharew, 1928a, b**

Fig. 8.1

[Nom. transl. Rozanov 2003, p. 112 ex Scacchinellinae Licharew, 1928b, p. 265].

Diagnosis: Well developed lateral buttress plates. Spines subprostrate, suberect or usually erect and with short posteriorly prolonged bases, dorsal valve usually spinose. Interareas as a rule, no teeth or sockets. Widely bilobed cardinal process and median ventral septum prominent in two families. Lower Carboniferous (Visean) to Middle Permian (Capitanian).

Discussion: The superfamily is named from *Scacchinella* Gemmellaro which has an extraordinary morphology, in which the ventral valve becomes very deep, to lift the aperture high above the substrate, and develops a median septum. There is thus a degree of convergence, or what might be termed morphological congruence with Richthofenioidea, which also developed a conical ventral valve, and indeed the richthofeniid Hercosiidae Cooper & Grant has a high median ventral septum. Richthofenioidea evolved from Aulostegoidea, evolved in turn from Rhytialosiinae of the strophalosiiform family Chonopectidae. *Scacchinella* and allies were derived ultimately from Araksalosiidae, an outstanding strophalosiiform group typified by fine even ventral disc spines, often with elongate bases over disc and trail, and well developed lateral buttress plates. The scacchinellid morphology is described by Licharew (1928a, b), Muir-Wood & Cooper (1960, p. 129) and Rudwick & Cowen (1967), and is especially well illustrated for United States species by Cooper & Grant (1975). Two papers were authored by Licharew in 1928a, b on *Scacchinella*, but the Russian version was ignored by Muir-Wood & Cooper (1960) and Brunton et al. (2000).

The seniority of Scacchinelloidea Licharew, 1928a, b was overlooked by Brunton et al. (2000, p. 607) and Waterhouse (2002b), who referred Scacchinellidae to Superfamily Aulostegoidea Muir-Wood & Cooper, 1960, but the superfamily was acknowledged in Rozanov (2003, p. 112), as including Aulostegidae Muir-Wood & Cooper and Cooperinidae Pajaud, simply granting seniority without changing the relationships envisaged in the *Revised Brachiopod Treatise*. The seniority was also recognized by Waterhouse (2010a). Its evolution is summarized on p.465.

An appraisal of the ornament for *Scacchinella* shows that both valves are spinose, those of the dorsal valve fine and erect, those of the ventral valve fine and including halteroid spines which helped to anchor the ventral valve. The spines are moderately like those of aulostegoids, and also especially close to those echinoconchoids which have erect spines, such as Waagenoconchinae and Pustulinae. Members of Tschernyschewiidae are instructive in this regard. *Tschernyschewia* is regarded as an ally of *Scacchinella* because it also has a high ventral median septum. Several genera are known, each distinguished by the nature of its spines. *Tschernyschewia* itself is comparatively close to *Waagenoconcha*, whereas the ally *Reedosepta* has elongate swollen ventral spine bases, approaching those of *Juresania* and *Taeniothaerus*. A double row of rhizoid spines lies along the ventral hinge in *Trigonoproductus*, and the ventral disc bears low ribs with numerous somewhat swollen short spine bases, whereas a network of rather coarse ventral spines and dorsal dimples characterize the new genus *Sierradiabloa*. These genera thus show a range of ornament styles close to those found in some echinoconchoids and to lesser extent, aulostegoids.

Family Scacchinellidae Licharev, 1928

Family Rhamnariidae Muir-Wood & Cooper, 1960
- Subfamily Rhamnariinae Muir-Wood & Cooper, 1960
- Subfamily Balkhasheconchinae Waterhouse, 2002b
- Subfamily Septasteginae Waterhouse, 2002b

Family Tschernyschewiidae Muir-Wood & Cooper, 1960

Table 10. Superfamily Scacchinelloidea Licharew, 1928.

There is an additional internal feature which is unusual, and that is the presence of lateral buttress plates in the dorsal valve. These are variably developed in Tschernyschewiidae, but always present, and in *Scacchinella*, the plates are thicker and more closely placed, to support the adductor muscle scars. That allows consideration of further possible alliances. Rhamnariinae Muir-Wood & Cooper, 1960 has well developed lateral buttress plates, as well as

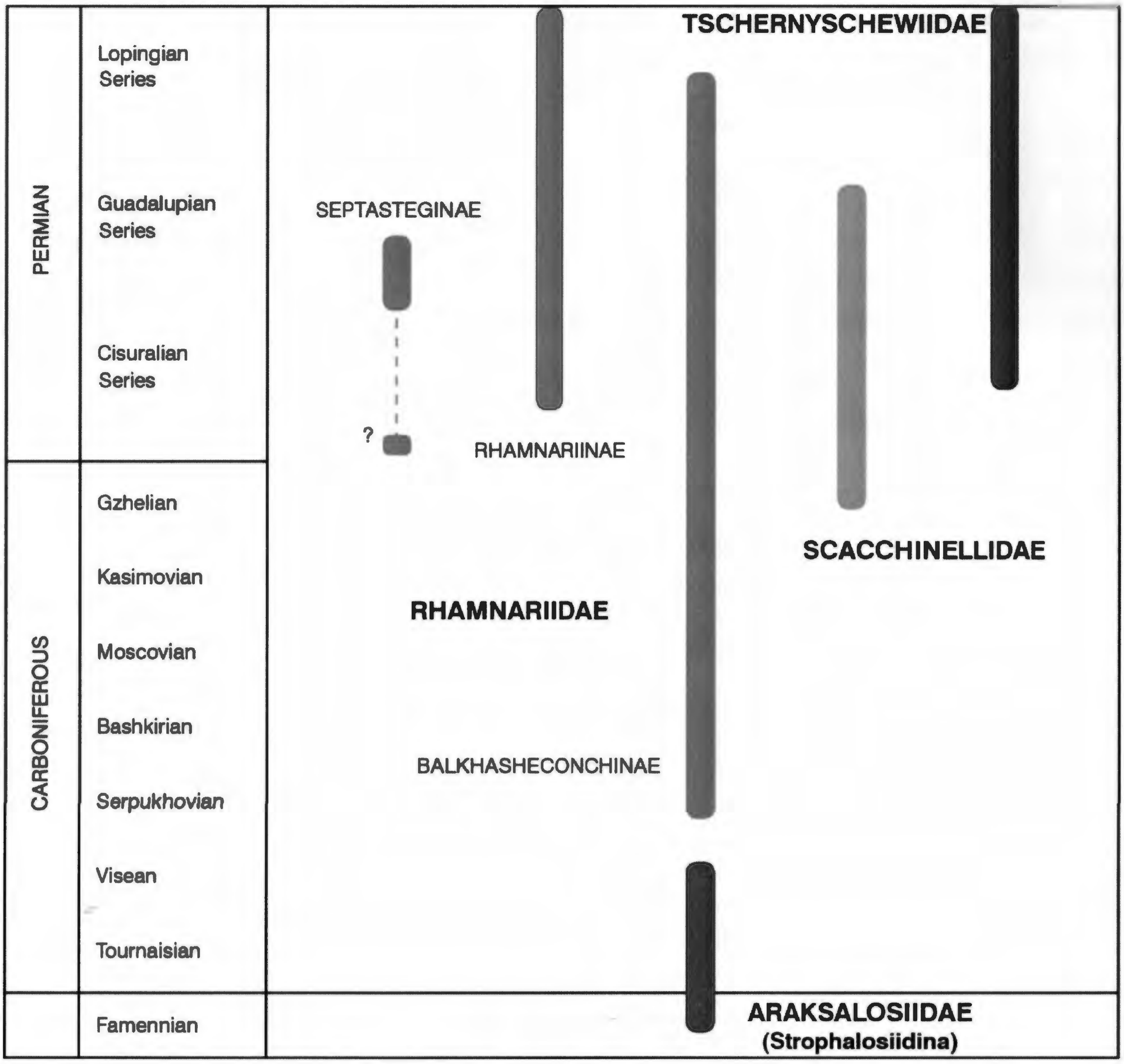

Fig. 8.1. Range chart for Superfamily Scacchinelloidea and progenital family Araksalosiidae.

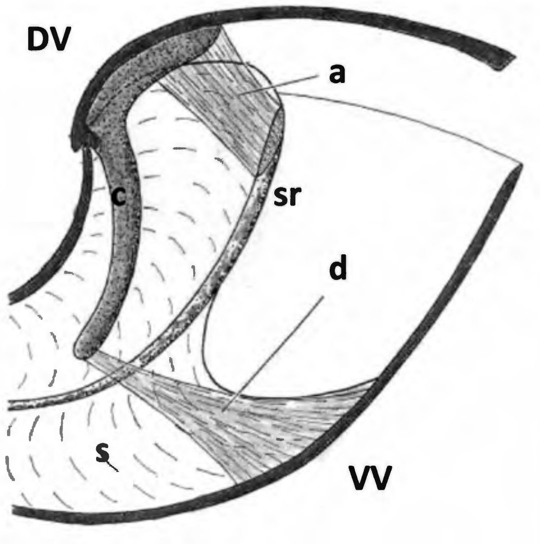

Fig. 8.2. *Scaccchinella variabilis* Gemmellaro, section through specimen as rearranged from Rudwick & Cowen (1967, text-fig. 5). From Sosio valley, Sicily, of Wordian age.
a, adductor muscle; c, prong of cardinal process;
d, diductor muscle; DV, dorsal valve; s, anterior septum; sr, septal rod; VV, ventral valve.

mostly erect spines, fine to coarse or mixed, and variably developed ventral interarea. This group is therefore incorporated as a family in Scacchinelloidea. The group Septasteginae Waterhouse, 2002b also has longaccessory plates. Neither of these groups has a high ventral median septum (with rare rhamnariid exceptions, such as a genus called *Minisaeptosa* new), but are close in basic ornament and other internal detail to Tschernyschewiidae. No genus or family group member of Aulostegoidea or Echinoconchoidea shows such lateral buttress plates. A further group with lateral buttress plates was named Balkhasheconchini Waterhouse, 2002b, originally classed within Waagenoconchidae, and with closely spaced fine ventral spines, either erect or with posteriorly elongate bases. These groups are amalgamated with Scacchinellidae and Tschernyschewiidae, united by the presence of closely spaced spines on both valves, common presence of ventral interareas, and development of lateral buttress plates. Aulostegidae and Cooperinidae are excluded from the superfamily, because they differ externally and internally.

Family **SCACCHINELLIDAE** Licharew, 1928

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

Diagnosis: Conical ventral valve often with transverse partitions apically, deep corpus cavity, high interarea and lid-like dorsal valve. Dorsal and ventral spines fine and numerous, including ventral rhizoid spines. Prominent ventral median septum, widely bilobed cardinal process, lateral buttress plates. Upper Carboniferous (Gzhelian) to Middle Permian (Wordian).

Genera: *Scacchinella* Gemmellaro, *Derbyella* Grabau, *Titanisia* new genus.

Discussion: Given the nature of its spines and interior, it appears likely that Scacchinellidae could have evolved from a rhamnariid source. Whilst it is true that no rhamnariin genus is yet known to be older than Permian in age, so that *Campbelliconcha* (Balkhasheconchinae) from Visean faunas of east Australia, may have offered an alternate source, the rhamnariinnew genus *Minisaeptosa* developed a ventral septum early in ontogeny, to suggest a likely link.

The small size and cap-like nature of the dorsal valve in Scacchinellidae and Tschernyschewiidae is only to be expected, given the depth of the ventral valve. It may be wondered whether the two valves developed pari passu, in concert, or whether one led the other. In Balkhasheconchinae, the dorsal trail was very short, and indeed one Canadian species of basal Permian age appears to have an almost flat dorsal valve, without trail, suggesting the potential to form a flat dorsal valve and deep ventral valve.

Genus ***Titanisia*** new genus

Fig. 8.3

Derivation: Titanis, of the Titans, Lat.

Type species: *Scacchinella titan* Cooper & Grant, 1975, p. 923 from Decie Ranch Member, Skinner Ranch Formation (lower Kungurian), Texas, United States, here designated.

Diagnosis: Ventral valve with vescicular filling and plates, ventral septum lacks septal rod, dorsal adductors supported on short plates.

Discussion: The type species is very large, with specimens measured up to 15cm in length, and has been profusely illustrated by Cooper & Grant (1975). Some four fifths of the ventral valve is infilled with vesicular tissue, whereas the type species of *Scacchinella*, *S. variabilis* Gemmellaro, 1896 from Sicily, has little or no such tissue, or what Rudwick & Cowen (1967, p. 131) called tabulae. Vesicular tissue is also developed in *S. gigantea* Schellwien, 1900 from the European Alps, and in other North American species such as *S. americana* Stehli, 1954 and *S. exasperata* Cooper & Grant, 1975 with very little in *S. primitiva* Cooper & Grant, 1975 from the basal Permian Gaptank Formation of Texas. By contrast, *S. triangulata* Cooper & Grant, 1975 from the late Carboniferous *Uddenites* Shale of Texas virtually lacks vesicular tissue. The dorsal adductor scars are sited on two elevated platforms which appear to be modified lateral buttress plates, raised laterally, excavated medianly in *Titanisia*. Similar plates are well developed in *S. americana*, but the platforms are small and closely spaced in *S. primitiva*, and seem to be sessile in *S. triangulata*. A further difference involves the presence in type *Scacchinella* of what Rudwick & Cowen (1967) called a septal rod, which thickened the edge of the ventral median septum. No such rod is visible in figures of *Titanisia* provided by Cooper & Grant (1975, pl. 273, fig. 10, pl. 282, fig. 19), whereas a bordering rod is suggested for *S. triangulata* in Cooper & Grant (1975, pl. 271, fig. 1), the same species that also lacks vesicular tissue and so resembles type *Scacchinella*.

Derbyella Grabau, 1931 from the Jisu Honguer Limestone of Mongolia is small and with ribs. Although poorly known, it shows little resemblance to the new genus.

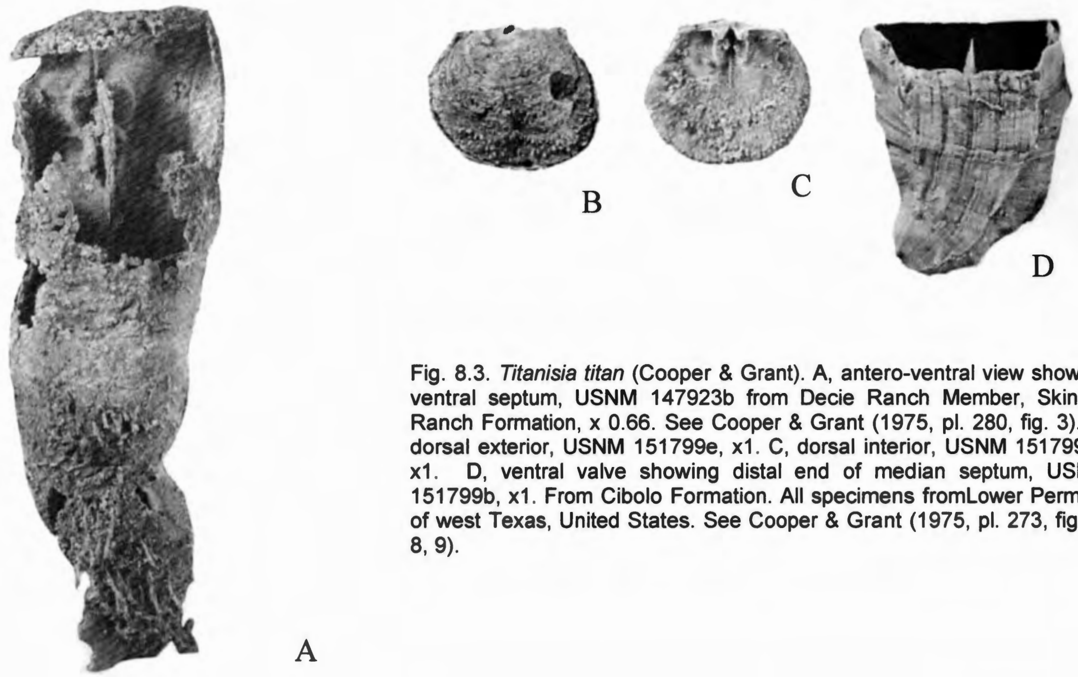

Fig. 8.3. *Titanisia titan* (Cooper & Grant). A, antero-ventral view showing ventral septum, USNM 147923b from Decie Ranch Member, Skinner Ranch Formation, x 0.66. See Cooper & Grant (1975, pl. 280, fig. 3). B, dorsal exterior, USNM 151799e, x1. C, dorsal interior, USNM 151799m, x1. D, ventral valve showing distal end of median septum, USNM 151799b, x1. From Cibolo Formation. All specimens fromLower Permian of west Texas, United States. See Cooper & Grant (1975, pl. 273, fig. 4, 8, 9).

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

[Nom. transl. hic ex Rhamnariinae Muir-Wood & Cooper, 1960, p. 119].

Diagnosis: Variable spine development on both valves, with or without elongate spine bases, cicatrix may be prominent, interarea absent to moderately high, cardinal process supported by long buttress plates.

Discussion: As discussed in the introductory remarks on Scacchinelloidea, rhamnariids are now regarded as allies of *Scacchinella*, through the presence of well developed lateral buttress plates. Judged from the fossil record, Rhamnariinae evolved from subfamily Balkhasheconchinae, changing the spinose ornament to a degree and restoring the ventral interarea and short trail. Rhamnariinae gave rise to a more specialized group Septasteginae, characterized by increased height of the lateral buttress plates which supported the dorsal adductors, and further distinguished by the increased height of the marginal ridge which is present in various genera within Rhamnariinae.

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

Fig. 8.4, Fig. 8.5

[Rhamnariinae Muir-Wood & Cooper, 1960, p. 119. Possible syn. Ramovsinidae Sremac, 1986, p. 14. Brunton et al. 2000, p. 604 spelled the name Ramovsiinidae].

Diagnosis: Variable spine development on both valves, interarea as a rule well developed, dorsal marginal ridge low. Cardinal process may appear bilobed, but basically quadrilobed, broad. Lower Permian (Sakmarian) to Upper Permian (Changhsingian).

Genera: *Rhamnaria* Muir-Wood & Cooper, *Colemanosteges* Waterhouse, *Geniculatusia* new genus, *Guadaluposteges* Waterhouse, *Koyaonoia* new genus, *Minisaeptosa* new genus, *Ramavectus* Stehli, ?*Ramovsina* Sremac, *Saeptathaerus* Waterhouse, *Shumardoria* new genus, *Shuzhongia* Waterhouse.

Discussion: Rhamnariinae Muir-Wood & Cooper, 1960 involves genera that display interareas as a rule and long lateral buttress plates, and the ornament, somewhat variable between different genera, is by no means completely different from that displayed by Scacchinellidae or Tschernyschewiidae, although in several genera the ventral spines are more differentiated. *Septarinia* Muir-Wood & Cooper, 1960, a Lower Carboniferous (Asbian) genus close to

Pustulinae and Juresaniinae in ornament, has a ventral septum, recalling that of Tschernyschewiidae and Scacchinellidae, and there is little in the way of a trail, but also displays a simple dorsal median septum with no sign of lateral buttress plates, and so is considered to be unrelated. (See p. 182).

Fig. 8.4. *Colemanosteges fairbridgei* (Coleman), dorsal aspect of internal mould AMF 44781. Specimen x 1 from Hardman Member (Wuchiapingian), Western Australia. See Coleman (1957).

The lateral buttress plates extend either side of the dorsal adductor scars, not like the extended plates attached to the anterior cardinal process which lie behind the adductor platform on *Taeniothaerus* and were termed buttress plates by Briggs (1998, text-fig. 67). *Rhamnaria* Muir-Wood & Cooper, 1960 has a cicatrix on the ventral umbo and shows brachial ridges, whereas one peculiar feature of *Saeptathaerus* Waterhouse, 2002b is that no specimens appear to show outlines of the brachial ridges. *Ramovsina* Sremac, 1986is poorly known, and its placement is based on the assessment by Brunton et al. (2000, p. 605). *Spuriosa* Cooper & Grant, 1975, although placed in Rhamnariinae by Cooper & Grant and by Brunton et al. (2000), lacks lateral buttress plates and is treated as a member of Echinosteginae (p. 284).*Cactosteges* in Cooper & Grant (1975, pl. 230, 231) lacks true lateral buttress plates (see p. 284), and the genus also approaches *Edriosteges* and *Echinosteges*, but has dorsal spines.

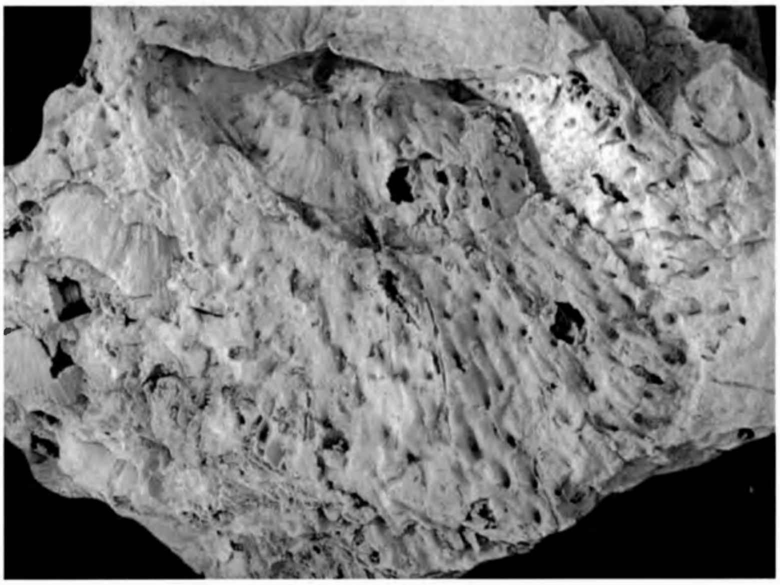

Fig. 8.5. *Colemanosteges transversa* (Ching = Jin), exterior of ventral valve showing prostrate spines with elongate bases, and erect spines, and interarea. BR 3070 from Zewan Formation (Wuchiapingian), Kashmir, x2. JBW photo.

In most genera, including *Rhamnaria, Ramavectus, Minisaeptosa, Ramovsina* and *Koyaonoia*, ventral spines are of two series, or even more varied, and these are largely paleotropical in distribution, with *Koyaonoia* exceptional in lackinga well formed ventral interarea.*Saeptathaerus* and *Colemanosteges* have much coarser ornament on the whole, and come from southerly mostly temperate Permian paleolatitudes of Oman, Himalaya and Western Australia, and their spines are sturdy with elongate bases on both valves.From the Himalaya, *Shuzhongia* is distinguished by its very fine spines. *Guadaluposteges* from Texas has largely uniform and numerous spines, without elongate bases. There is thus an array of attributes, considerable geographic clustering, but also some exceptional genera.

Genus *Koyaonoia* new genus

Fig. 8.6, Fig. 8.7

Derivation: Named from Ko Yao Noi, an island in the Andaman Sea, north of Phuket, Thailand.

Type species: *Juresania? dissimilis* Waterhouse, 1981b, p. 71 from Ko Yao Noi Formation (Sakmarian) of south Thailand, here designated.

Diagnosis: Moderately large shells for group, dorsal valve with simple trail, ventral spines in a range of sizes, coarser spines usually erect, some spines with elongate bases, not crowded close to hinge; dorsal valve spines crowded, suberect, largely in two orders with additional variants, commarginal laminae and low rugae. Low ventral interarea, no internal dorsal hinge ridge, slender lateral buttress plates.

Fig. 8.6. *Koyaonoia dissimilis* (Waterhouse). A, dorsal view of holotype, TBR 33. B, internal mould of dorsal valve TBR 48. Specimens x2 approx., from Ko Yao Noi Formation (Sakmarian), south Thailand. (See Waterhouse 1981b). J. Coker & JBW photo.

Discussion: This genus is close to two genera from the early Permian of west Texas, United States, *Ramavectus* Stehli, 1954, and *Rhamnaria* Muir-Wood & Cooper, 1960. Like these genera, the dorsal valve has lateral buttress plates, and the spines are diverse and numerous. Both genera are readily distinguished from the new form by possessing higher interareas, and an abundance of halteroid spines close to the ventral hinge, whereas spines are few along the hinge and over the ears of *Koyaonoia* (cf. Waterhouse 1981b, pl. 7, fig. 2). *Rhamnaria* often displays an umbonal cicatrix, not seen in the new genus, and ventral spines often have slightly elongate bases, and dimples are more conspicuous over the dorsal valve. *Ramavectus* is a little closer to the Thai genus, with no cicatrix, and ventral spines have short elongate bases. In both genera, spines are less obviously arranged in concentric rows, and the dorsal hinge ridge is better developed. The ornament on the present genus is complexly spinose, as illustrated for the dorsal valve, and in addition, broad rugae may develop over mid-length in both valves. *Minisaeptosa* new genus is distinguished by developing a distinct median septum at early phases of growth, and has ornament of crowded fine spines in two series over the ventral valve and fine single series over the dorsal valve. But *Shumardoria* new genus from the same region has more uniform spines over both valves, and a short median ventral septum is developed at an early growth phase. From the same Ko Yao Noi deposits, *Rhamnaria bunopasi* Waterhouse, 1981 is congeneric, and has better defined ventral sulcus and dorsal fold than *dissimilis*.

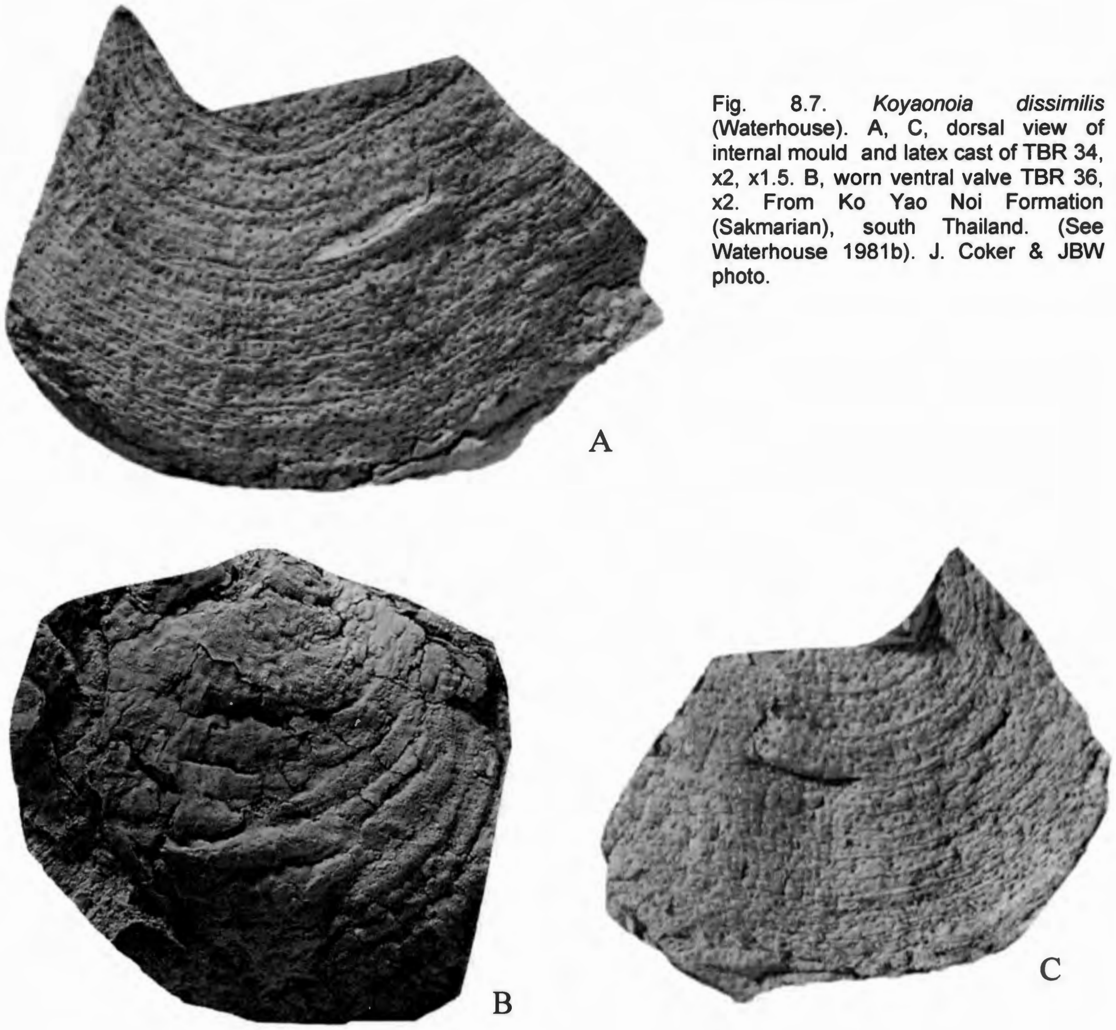

Fig. 8.7. *Koyaonoia dissimilis* (Waterhouse). A, C, dorsal view of internal mould and latex cast of TBR 34, x2, x1.5. B, worn ventral valve TBR 36, x2. From Ko Yao Noi Formation (Sakmarian), south Thailand. (See Waterhouse 1981b). J. Coker & JBW photo.

Genus ***Minisaeptosa*** new genus

Fig. 8.8

Derivation: minimus – smallest, minute; saepta – fence, Lat.

Type species: *Rhamnaria tenuispinosa* Cooper & Grant, 1975, p. 911 from Cathedral and Road Canyon Formations (Kungurian, Roadian) of west Texas, United States, here designated.

Diagnosis: Short median septum in ventral valve, best developed at early growth stages. Spines crowded, fine and delicate, of two orders on ventral valve, fine over dorsal valve.

Discussion: The type species has been extensively illustrated, and figures in Cooper & Grant (1975, pl. 259, fig. 24, pl. 261, fig. 27, 28) show the presence of a short median septum under the ventral umbo of small specimens, which gradually disappears with age. The lateral buttress plates of *Minisaeptosa* are rather short in small specimens and become more prominent with increased maturity. Spines are moderately coarse near the ventral hinge, and the dorsal valve carries somewhat regular pits in rows, as well as dimples and spines. The ventral interarea is very low. *R. kingorum delicata* Cooper & Grant, 1975, p. 908 also belongs to the new genus, and should be upgraded to a full species. It has finer and more numerous spines than in *kingorum*, which belongs to *Rhamnaria*. The text in Cooper & Grant (1975) stated that the taxon came from the Cathedral Mountain Formation, whereas the caption to the illustrations (pl. 263) stated that the material came from the China Tank Member of the Word Formation, and Cooper & Grant (1977) tabulated *delicata* from the China Tank Member, Willis Ranch Member and Road Canyon Formation.

No species of *Rhamnaria* shows such a septum, even in early growth stages, but the septum is much smaller than that of *Tschernyschewia* and allies of Tschernyschewiidae. The present form, in view of its age, could on the one hand be a surviving member of a genus intermediate between Rhamnariidae and Tschernyschewiidae, or represent a deviation or Lazarus feature: whatever the interpretation, it helps endorse the likelihood of an ultimate alliance between Rhamnariidae and Tschernyschewiidae.

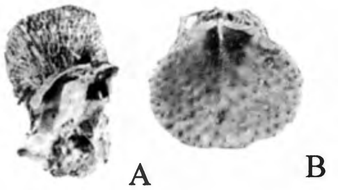

Fig. 8.8. *Minisaeptosa tenuispinosa* (Cooper & Grant). A, ventral view of small attached specimen USNM 154216b. B, interior of immature ventral valve showing small septum, USNM 154531. From Cathedral Mountain Formation (Kungurian), west Texas, United States, x1. See Cooper & Grant (1975, pl. 261, fig. 26, 28).

Genus ***Shumardoria*** new genus

Fig. 8.9

Derivation: Named for B. F. Shumard.

Type species: *Aulostegesguadalupensis* Shumard, 1860, p. 292 from Capitan Formation (Capitanian), New Mexico, United States, here designated.

Diagnosis: Low to extended ventral umbo without cicatrix, well formed ventral interarea, moderately fine subprostrate and subuniform ventral spines, dense fine dorsal spines and dorsal pits. Cardinal process high and slender with two extended shafts, without massive bulbation, posterior hinge ridge low or absent.

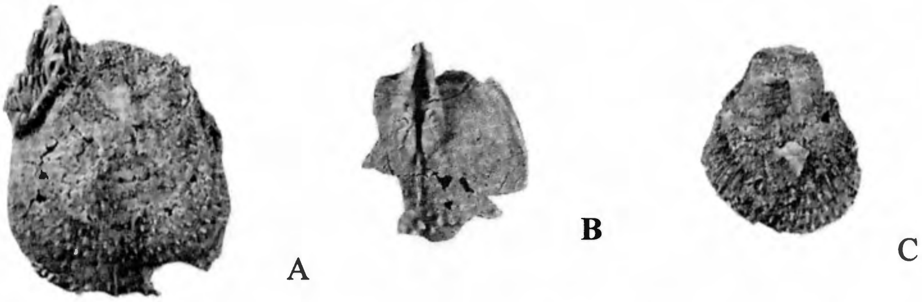

Fig. 8.9. *Shumardoria guadalupensis* (Shumard). A, ventral valve USNM 152652a. B, dorsal valve interior, USNM 154182a. The external dimples have left a mottled appearance to the interior. C, ventral valve USNM 152652c, with long umbonal walls as in the original figure. Specimens x1, from Bell Canyon Formation (Capitanian), Guadalupe Mountains, United States, as figured in Cooper & Grant (1975, pl. 229).

Discussion: This genus is based on *Echinosteges guadalupensis* (Shumard) as figured by Cooper & Grant (1975, p. 847, pl. 229, fig. 1-19, pl. 244, fig. 28, 29, pl. 258, fig. 30, pl. 267, fig. 1-4). These specimens have long lateral buttress plates, as in Rhamnariinae. The ventral spines are subuniform, and subprostrate, with a dense array over the ventral ears. The ventral spines of *Rhamnaria* Muir-Wood & Cooper, mostly of Wordian age, are of less uniform diameter, with thick and thin suberect spines, larger ear spines, well developed umbonal cicatrix, and more massive and elaborate cardinal process with well developed hinge ridges. *Ramavectus* Stehli from older faunas in west Texasalso has differentiated ventral spines, fine and numerous ear spines, no cicatrix, less massive cardinal process, and sturdy hinge ridge. The original specimen of *guadalupensis*was described by Shumard (1858, p. 292;1859, p. 390, pl. 11, fig. 5a, b) and another by Girty (1909, p. 277, pl. 20, fig. 22, 22a), and thedrawings of their specimens are close in shape, but detail of the ventral ornament is poorly shown, and deemed to be not fully accurate. A second species was recorded as *Rhamnaria shumardi* Cooper & Grant, 1975, p. 910, also from the Capitan and Bell Canyon Formations: this species is similar in ornament, with broader ventral umbo, and the two taxacould be interpreted as belonging to one variable species. Cooper & Grant (1975) noted that youthfulindividuals of *shumardi* from the Bell Canyon Formation have a small median septum in the ventral apex, but *Minisaeptosa* (see above) has more varied spines, cicatrix, dorsal hinge ridges, and cardinal process close to that of *Rhamnaria*.

Genus *Geniculatusia* new genus

Fig. 8.10, Fig. 8.11

Derivation: geniculatus – having joints, Lat.

Type species: *Productus gangeticus* Diener, 1897, p. 23 from "Productus Shales" (Wuchiapingian) of northwest India, here designated.

Diagnosis: Moderately large, low or usually no ventral interarea, dorsal valve with flat disc and distinct geniculate trail, ventral spines well spaced with elongate bases, dorsal spines fewer and erect, dorsal elongate dimples.

Discussion: This genus is distinguished by its lack of well formed ventral interarea, strongly geniculate dorsal valve and ornament of elongate well spaced spine bases over the ventral valve, and dimples over the dorsal valve, with erect spine bases, mostly over the trail. *Geniculatusia* differs from most Rhamnariinae in rarely displaying a ventral interarea, but on the other hand is like other genera placed in this group by having spines that differ on the ventral as compared with the dorsal valve, and having a short but well formed trail. The shape is moderately distinctive, with flat dorsal disc, ventral sulcus and low dorsal fold. Diener (1897, p. 24) recorded a low interarea in one specimen, but such an occurrence is rare. The lateral buttress plates are well developed. The genus is found in the *Lamnimargus* *himalayensis* Zone of Wuchiapingian (early Lopingian) age in the Himalayas. Diener (1897, pl. 1, fig. 1, 2, pl. 2, fig. 3) first described the species from the Productus Shales of the Kumwaon and Garwhal Himalayas, with lectotype designated by Waterhouse (1978, p. 26) as that figured in Diener (1897, pl. 1, fig. 1). Diener's specimens of so-called *P. purdoni* [non Davidson] are probably conspecific. Further material was recorded from the central Himalayas by Diener (1903, pp. 72, 103, 181), and figured from the Zewan beds of Kashmir by Diener (1915, pl. 8, fig. 6), together with so-called *Productus* sp. aff. *porrecto* [non Kutorga] as figured by Diener (1915, p. 78, pl. 8, fig. 7, 8). From the Karakorum Range, Merla (1934, p. 265, pl. 25, fig. 27) recorded a specimen that has long spine bases, but his specimen appears to lack a distinct sulcus. Muir-Wood (1941, p. 24, pl. 1, fig. 15a, b) assigned a worn ventral valve from the Lachi Series of Sikkim to *humboldti*. It does not belong to *gangeticus*, because although the specimen is

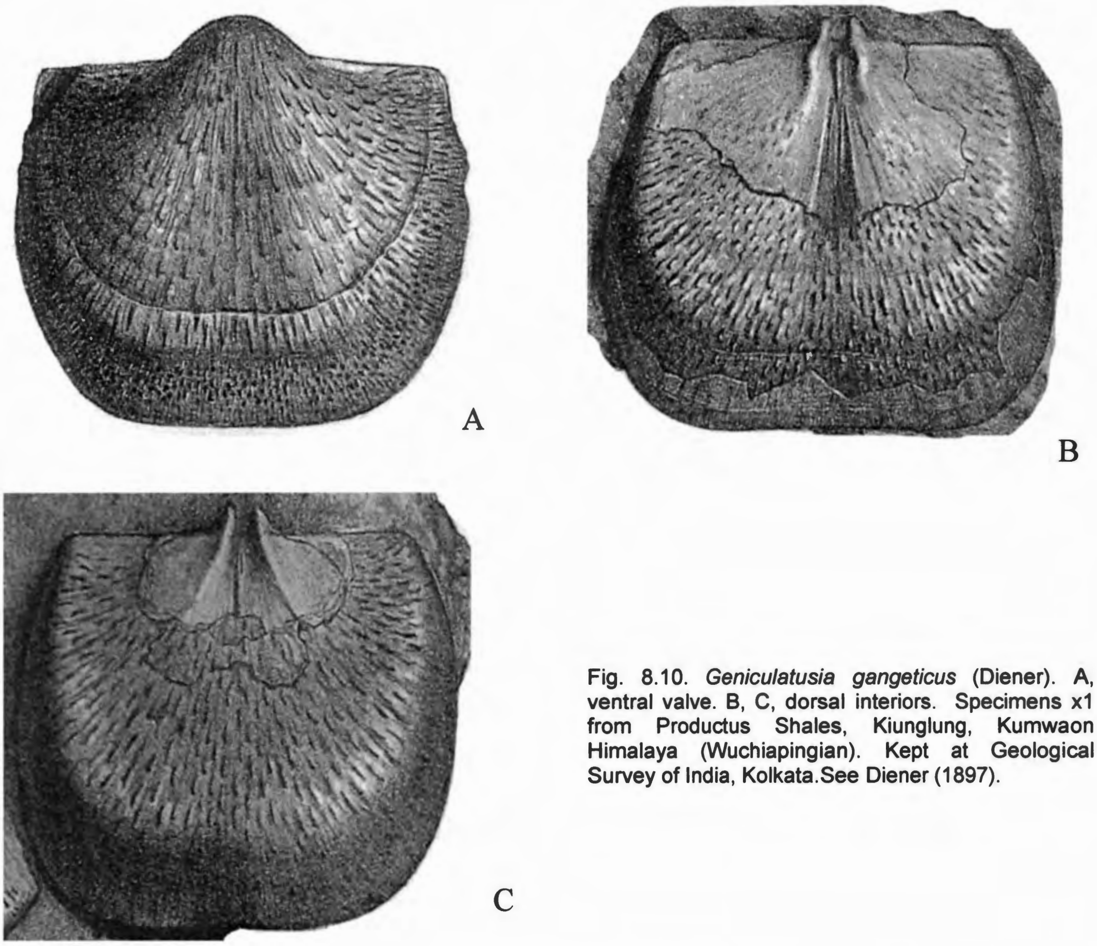

Fig. 8.10. *Geniculatusia gangeticus* (Diener). A, ventral valve. B, C, dorsal interiors. Specimens x1 from Productus Shales, Kiunglung, Kumwaon Himalaya (Wuchiapingian). Kept at Geological Survey of India, Kolkata.See Diener (1897).

poorly preserved, it shows signs of numerous and very fine spines. Specimens of so-called *Waagenoconcha purdoni* [non Davidson] of Waterhouse (1966, p. 23, pl. 4, fig. 4, fig. 2, 3, pl. 5, fig. 2, 3) from the *Lamnimargus himalayensis*Zone in west Nepal have similar shape, with well formed ventral sulcus, flat dorsal disc and geniculate trail, and elongate ventral spine bases, but no specimens show the dorsal interior, and external ornament is also poorly preserved. The external dorsal valve has subelongate dorsal mounds and dimples and fine anterior erect disc spines, and erect spines over the dorsal trail (Waterhouse 1966, pl. 5, fig. 2). A further ventral valve from west Nepal was figured as *gangeticus* by Waterhouse (1978, p. 26, pl. 1, fig. 23). Clearly, the best material was described by Diener (1897), but the distinctive and usually sulcate ventral valve and geniculate dorsal valve help signal thelikelihood of widespread occurrence of the species throughout the Wuchiapingian faunas of the Himalayas. A specimen is figured herein from the Zewan Formation of Kashmir, the first report of the genus in this formation.

Saeptathaerus Waterhouse, 2002b, p. 49, based on *Aulosteges fairbridgei* Coleman, 1957, p. 91 from the Hardman Member and Port Keats Group of Western Australia, is also of Wuchiapingian age, and is close and has comparatively uniform spines with elongate bases especially on the ventral valve, and erect halteroid spines over the ventral ears. *Aulosteges spinosus* Hosking, 1931, p. 17 from the Callytharra and Fossil Cliff Formations of Western Australia, of early Artinskian age, is closely allied. This genus has elongate ventral spine bases and long lateral buttress plates, and anterior ventral spines are erect, as in the present form. Differences are that an umbonal cicatrix is often developed in *Saeptathaerus*, and the ventral interarea is high and well developed. Over the dorsal valve, crowded spines are slender with slightly elongate bases, and the trail is apparently less developed. *Saeptathaerus latus* Waterhouse & Chen (2007, p. 11, pl. 2, fig. 5-12, pl. 3, fig. 1, 2) from Puchenpra and Galte Members of the Changhsingian Senja Formation in north-central Nepal is sulcate with broad slightly distorted ventral umbo, and ventral interarea, and short geniculate trail. The ventral spines have bases somewhat shorter than in *Geniculatusia*, more as in *Saeptathaerus*.Given such ornament, these genera, *Geniculatusia, Saeptathaerus*, and also *Colemanosteges* Waterhouse, belong to a subgroup, arguably a tribe.

Fig.8.11. *Geniculatusia gangeticus* (Diener), worn dorsal valve interior, BR 3072, x1.5. From Zewan Formation (Wuchiapingian), Kashmir. JBW photo.

Balkhasheconcha Lazarev has a gently concave or flat dorsal valve with a trail that is difficult to discriminate externally, curving gently from the visceral disc, and other allied genera are somewhat similar. The ventral spines in the present genus have elongate bases, close to those of *Balkhasheconcha*, but more spaced and more prominent, and as in *Balkhasheconcha*, anterior and lateral spines are finer and more erect. Dorsal ornament in *Balkhasheconcha* is much like that of the ventral valve.

A number of brachiopod species from the Himalayas are shared with the diverse faunas of the Salt Range, Pakistan, but none appear to belong to *Geniculatusia*. The closest have been described as *Productus* (*Ruthenia*) *purdoni mirkalanensis* Reed (1944, pl. 13, fig. 1, 2) from the top Wargal or lower Chhidru faunas, *P.* (*Ruthenia*) *purdoni prolongata* Reed (1944, pl. 13, fig. 4, 5) from the topmost Kalabagh Member and from the Kufri Member, and *P.* (*Ruthenia*) *purdoni circularis* Reed (1944, pl. 13, fig. 6) from the Wargal Formation, genera of Wuchiapingian age. (The stratigraphic names are updated, as explained in Waterhouse 2010b). These forms have somewhat elongate ventral spine bases as in *gangeticus*, but they also show commarginal growth stops and suggest a short gently angled trail, as in the waagenoconchin genus *Quenstedtenia* Waterhouse from Timor (see pp. 195, 199). As well, a long dorsal median septum is portrayed by Reed (1944), with no trace of lateral buttress plates, again supporting a waagenoconchin position.

Subfamily **BALKHASHECONCHINAE** Waterhouse, 2002b

[Nom. transl. hic ex Balkhasheconchini, nom. correct. hic ex Balkasheconchini Waterhouse, 2002b, p. 25].

Diagnosis: Waagenoconchiform shells with lateral buttress supports in the dorsal valve, extending each side of dorsal adductors. No interareas, no cicatrix, trail very short. Spines over both valves subprostrate or erect especially around margins, largely uniform in bands. Cardinal process with tall shaft. Lower Carboniferous (Visean) to Upper Permian (Wuchiapingian).

Genera: *Balkhasheconcha* Lazarev, *Buxtoniella* Abramov & Grigorieva, *Campbelliconcha* new genus, *Ramaliconcha* new genus.

Discussion: The treatment of this group offers a marked change from Lazarev (1985) and Brunton et al. (2000, p. 518). These authors placed constituent genera within Tribe Waagenoconchini, butthe genera were discriminated as distinctive within Waagenoconchinae by Waterhouse (2002b). Yet even this may not suffice. The external ornament is moderately characteristic, dominated as a rule by spines which are mostly subprostrate with elongate bases, arranged in quincunx over the ventral and dorsal valves. The interior is even more distinctive, with well formed lateral buttress plates. Such plates are absent from any genus within Echinoconchidae, Waagenoconchidae, and Sentosiidae. It is possible to go further with the *Balkhasheconcha* group. Araksalosiinae Lazarev, 1989 has disc and trail spines over the ventral valve like those of Balkhasheconchinae, and internally displays lateral buttress plates. Araksalosiinae clearly differs from *Balkhasheconcha* and allies in having interareas, teeth and sockets, and a row of strong ventral hinge spines in several genera. Araksalosiin genera are of Upper Devonian (Famennian) to Lower Carboniferous (lower Tournaisian) age, whereas the earliest known balkhasheconch genera are of Visean age. The closest of known Araksalosiinae likely to have provided a progenital source is *Hamlingella* Reed, 1943 of upper Devonian age. This species has moderately strong hinge spines, fine spines on both valves and similar dorsal interior with dendritic posterior dorsal adductors and long lateral buttress plates.

The predominantly spinose ornament and the presence of lateral buttress plates in the dorsal valve of Balkhasheconchinae are aspects shared with members of Rhamnariinae Muir-Wood & Cooper, 1960, and agree in displaying mostly elongate spine bases with southerly members of Rhamnariinae, such as *Saeptasteges, Colemanosteges*, and *Geniculatusia*, which do have longer lateral buttress plates.Members of Rhamnariinae display attributes of Aulostegoidea, and have moderately high interareas, and a cicatrix on some specimens, and a distinctive cardinal process. Members of Balkhasheconchinae do not show the same aulostegoid attributes, lacking interareas and cicatrix, and having a non-aulostegoid cardinal process, and in shape approaching the build of Waagenoconchidae. Rhamnariinaeis younger than early Balkhasheconchinae, and has reverted through regaining interareas and cicatrix to features typical of Strophalosiidina. Theorists may discount such possibilities, claiming that reversion is impossible, and progression always linear in one direction, but the fossil record yields examples across a number of phyla and classes.

Balkhasheconchins approach Scacchinellidae and Tschernyschewiidae to some extent in their ornament,and in the presence of lateral buttress plates, but lack ventral interareas and show no sign of a ventral median septum. Whilst the present outline offers a minimalist rendition of Scacchinelloidea, there are similarities amongst members of Juresaniinae and Pustulinae, classed as Echinoconchoidea, which might encourage expansion of the superfamily at the expense of Echinoconchoidea, but such genera lack lateral buttress plates.

Genus ***Balkhasheconcha*** Lazarev, 1985

Type species: *Waagenoconcha balkhashensis* Nasikanova in Sarytcheva 1968, p. 106 from Keregetass Formation (Bashkirian?), Kazakhstan.

Diagnosis: Fine erect or subprostrate spines over both valves, fine (rarely coarse) and erect anteriorly on ventral valve, short lateral buttress plates.

Discussion: *Buxtoniella* Abramov & Grigorieva (1986, p. 94) of middle Visean age in Verchoyan, northeast Russia, is said to lack the anterior band of thinner spines on the ventral valve, although a number of fine spines are present.

Campbelliconcha new genus from middle Visean of east Australia has fine spines posteriorly, and very fine spines anteriorly: none have notably elongate bases. The present species of *Balkhasheconcha*is exceptional for the genus insofar as the anterior fine spines form a double band, a posterior band of very fine erect spines, as in other species of *Balkhasheconcha*, bordered by an outer band of coarser erect spines on at least one specimen.(See Fig. 8.12).

Balkhasheconcha bamberi new species

Fig. 8.12– Fig. 8.14

cf. 1968 *Waagenoconcha* cf. *abichi* [not Waagen]–Logan & McGugan, p. 1133, pl. 141, fig. 7-10.

Derivation: Named for E. W. Bamber.

Holotype: GSC 133343figured herein as Fig. 8.14A, from Member D (Asselian), lower Jungle Creek Formation, Ogilvie Mountains, Yukon Territory, Canada, here designated.

Diagnosis: Medium-sized shells characterized by well formed ventral sulcus and commarginal rugae over ventral valve.

Material: Approximately twenty specimens from Member D (upper Asselian), lower Jungle Creek Formation. See Appendix A, part C, p. 478.

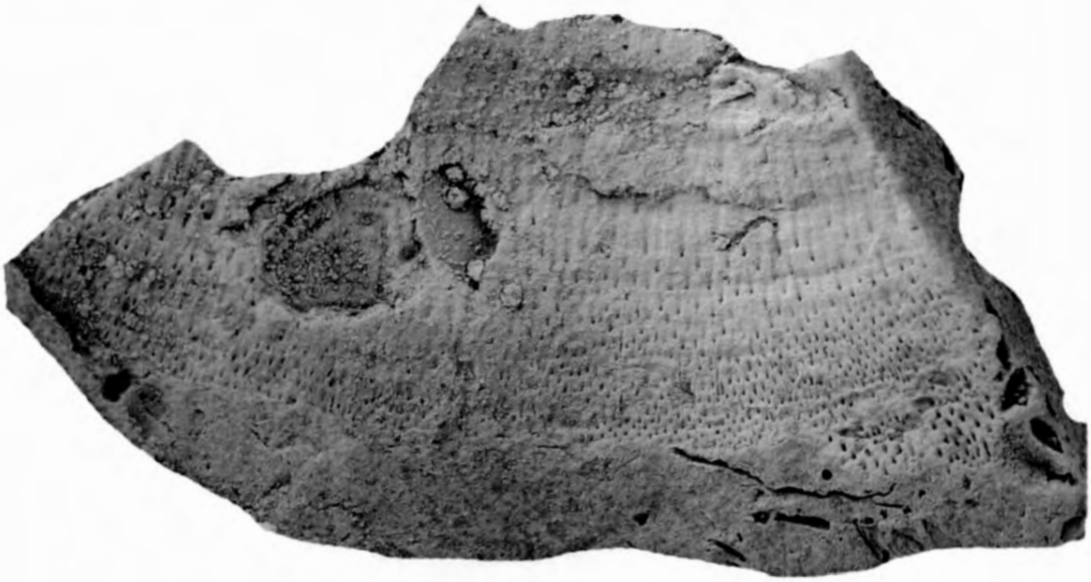

Fig. 8.12. *Balkhasheconcha bamberi* new species. External mould showing elongate spine bases giving way to erect spines anteriorly, GSC 133347, x6.Note the outer band of coarse erect spines, in front of the band of fine erect spines, exceptional for *Balkhasheconcha*. From Member D (Asselian), Jungle Creek Formation, Yukon Territory, Canada. JBW photo.

Dimensions in mm: (specimens incomplete and preserved as internal moulds)

Specimen GSC	Width	Length	Height	
133344	53	35	20	
133343	42	37	10	holotype
133346	34	34?	14	

Description: Plano-convex shells, ventral umbo incurved, with angle of 60-70°, umbonal walls steeply to gently convex in profile and persist well forward, hinge wide and cardinal extremities obtuse, ears not clearly distinguished, but slightly upturned laterally. A sulcus commences a little in front of the umbonal tip and widens at 25-30°, with gently concave floor. Dorsal valve almost flat, with very low fold broadening from posterior third of shell length, leaving a shallow depression each side. There is no geniculate trail. Entire ventral valve ornamented by spines, 0.5mm in diameter posteriorly, arranged in quincunx and emerging from short raised spine bases 2mm long posteriorly and 7mm long anteriorly and little more than 1mm apart: there are some irregularities and some erect spines without extended bases. In some specimens the bases are aligned in semicontinuous ridges, and in one specimen the lateral shell has only erect spines. Anteriorly there is a band of slender, crowded and erect spines, about three per mm, and in one ventral valve, as figured (Fig. 8.12), there is a band of stouter spines, unlike the ornament of other known species. The valve is crossed by firm commarginal rugae, faint posteriorly, and strongest over mid-length. The dorsal valve is densely ornamented by erect spines with short elongate bases 1.5mm long, separated by elongate pits, crossed by fine growth increments numbering nine per mm anteriorly, and fine close-set growth rugae, overall imparting a very rough texture to the surface. The commarginal rugae are not as prominent as those of the ventral valve.

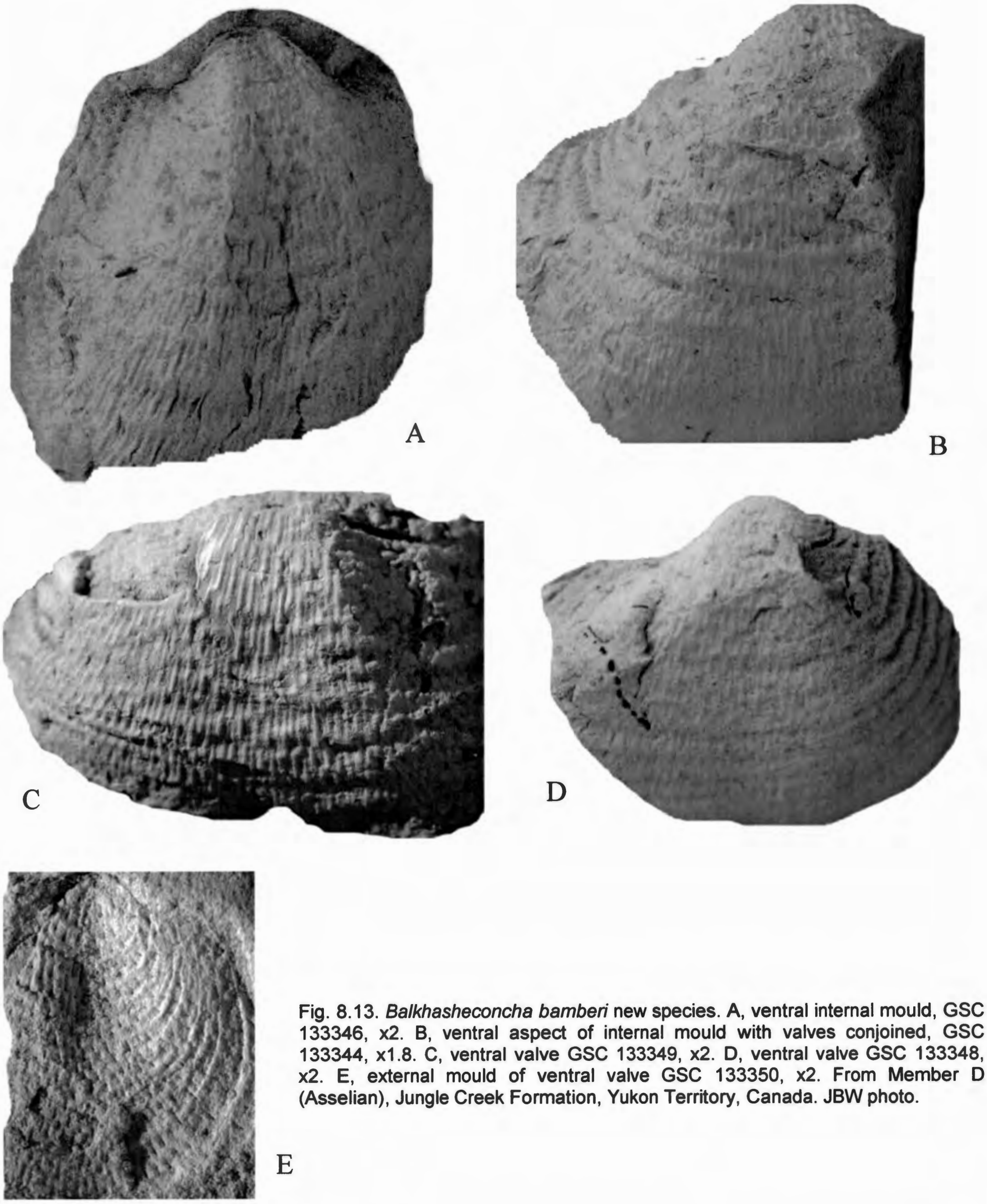

Fig. 8.13. *Balkhasheconcha bamberi* new species. A, ventral internal mould, GSC 133346, x2. B, ventral aspect of internal mould with valves conjoined, GSC 133344, x1.8. C, ventral valve GSC 133349, x2. D, ventral valve GSC 133348, x2. E, external mould of ventral valve GSC 133350, x2. From Member D (Asselian), Jungle Creek Formation, Yukon Territory, Canada. JBW photo.

The shell is very thin and the ventral valve reflects the external ornament, to the extent that muscle scars are obscure, with only faint signs of adductor scars. In the dorsal valve the cardinal process is slender, and the median septum extends beyond mid-length. A broad low smooth platform lies in front of the cardinal process, and a low slender lateral buttress plate extends obliquely from the platform each side of the posterior adductor scars, which are faintly impressed with irregular ridges, behind slender elongate smooth anterior adductor impressions. Brachial ridges are not visible. The floor is marked by crowded sharp pustules and dimples, and a strong ridge lies along the hinge.

Resemblances: This species is distinguished by its moderately well-formed ventral sulcus and strong concentric rugae, and detail of its spine pattern. Specimens from the Mt Greene beds of northeast British Columbia are similar (Logan & McGugan 1968). The closest ally in the younger Jungle Creek Formation was described as*Waagenoconcha permocarbonica* Ustritsky by Shi & Waterhouse (1996, p. 77, pl. 9, fig. 4-15, pl. 10, fig. 1-4) from the *Yakovlevia* (= *Muirwoodia*) *transversa, Ogilviecoeliainflata* and *Jakutoproductus verchoyanicus* Zones. These specimens should be transferred to *Balkhasheconcha*. Compared with *B. bamberi*, they are of larger size, and haveshallow ventral sulcus, less prominent concentric ornament and less elongate spine bases and dimples on the dorsal valve. Ustritsky's species *permocarbonica* (Ustritsky & Chernyak, 1963, pl. 7, fig. 6, pl. 8, fig. 1-3) and his so-called *wimani* [not Fredericks] (pl. 6, fig. 6, pl. 7, fig. 1) differ in much the same way, although the dorsal valve does show more elongate spine bases. The types come from the Upper Carboniferous Makarov Horizon (Bashkirian) of western Taimyr, north Russia.

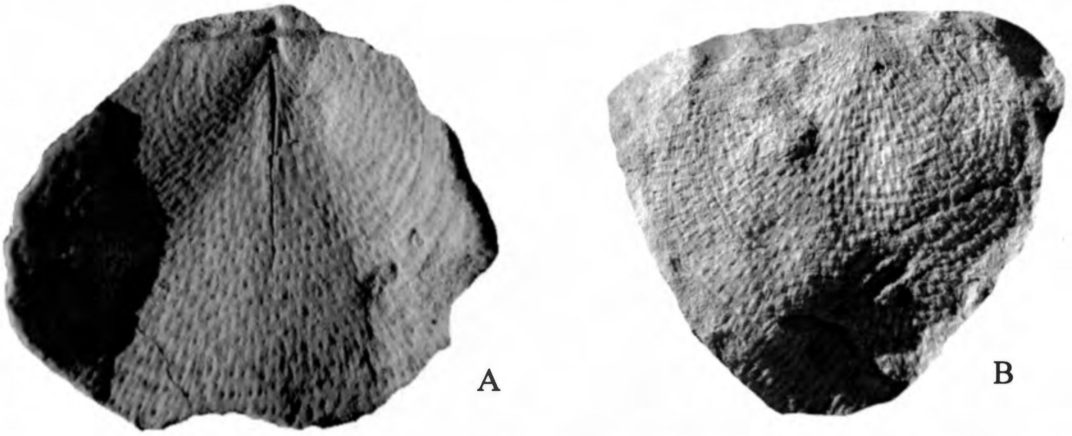

Fig. 8.14. *Balkhasheconcha bamberi* new species. A, internal mould of specimen with both valves conjoined, holotype, at early maturity, dorsal aspect, GSC 133343, x1.5. B, dorsal external mould GSC 133342, x2. From Member D (Asselian), Jungle Creek Formation, Yukon Territory, Canada. JBW photo.

The type species of the genus, *Balkhasheconcha balkhashensis* Nasikanova in Sarytcheva (1968, p. 106, pl. 9, fig. 1-4; Ganelin 1984, pl. 12, fig. 1-3) from the Upper Carboniferous Keregetass Suite of north pre-Balkhash and Makar Suite of the Kolyma Basin, northeast Russia, is larger with shallower sulcus and less conspicuous growth steps. The original types are moderately close, but ventral spine bases are shorter. The species was also figured by Lazarev (1990, pl. 34, fig. 1-3). *B. gigantea* (Ganelin, 1984, pl. 18, fig. 4, 5, pl. 19, fig. 1-4, pl. 20, fig. 1-7, pl. 21, fig. 1-5; Lazarev, 1990, pl. 35, fig. 1-4) from the same level, in the Hayran Suite, is even larger, but otherwise close to the type species: both show spines like those of the present form. Various specimens referred to *Waagenoconcha irginaeformis* Stepanov are somewhat similar to the present species, including those described by Abramov & Grigorieva (1983, pl. 3, fig. 26-29; 1988, pl. 6, fig. 9) from the early Permian Echi Suite of west Verchoyan, northeast Russia, whereas Gobbett (1964, p. 76) referred the species to synonymy of *irginae* Stuckenberg. Sarytcheva (1968, pl. 10, fig. 1-8) in figuring Kazakhstan material included both a dorsal interior apparently without lateral buttress plates (Fig. 46) and shells with lateral buttress plates (Fig. 47) as belonging to *irginaeformis*.Judged from the figure, the dorsal plates in the latter form diverge very narrowly, more like anderidia than lateral buttress plates, but clarity is required over the width and nature of the muscle scars, although they do seem to be completely enclosed by the plates. The original specimens of *irginaeformis* (Stepanov 1937, p. 124, pl. 6, fig. 4, 5) – see also Licharew (1939, p. 84, pl. 21, fig. 5) –belong to Waagenoconchidae. Kulikov (1974, pl. 3, fig. 5) illustrated a specimen from the west Urals: he kept *irginae* separate. Specimens assigned to *W. irginae* (Stuckenberg) by Ifanova & Semenova (1972, pl. 3, fig. 14-16) from upper Artinskian and Kungurian beds of Pechora are moderately close, but whether or not they belong to*Balkhasheconcha*is not clear from figures. The specimens lack the conspicuous concentric ornament of the present form. *Waagenoconcha asiatica* Zavodowsky (1970, p. 89, pl. 3, fig. 1, 2) from the Burgali Suite (Asselian)of northeast Russia has elongate spine bases but differs in size and shape from the Canadian species.

Genus ***Campbelliconcha*** new genus

Fig. 8.15

Derivation: Named for K. S. W. Campbell.

Type species: *Waagenoconcha delicatula* Campbell, 1956, p. 471 from Greenhills (middle Visean, mostly Asbian), New South Wales, here designated.

Diagnosis: Ventral valve ornamented by moderately fine spines over posterior third, with very short bases, most of valve covered by very fine erect spines. Lateral buttress plates well developed.

Description: The type species, kept at Australian Museum, Sydney, is roundly subpentagonal in outline, of average size for the family, with ventral sulcus and low dorsal fold. The gently concave dorsal valve is thickened around the margins, and has virtually no trail. Ventral spine bases are fine posteriorly, and very fine over most of the shell. Numerous fine spines lie over the ventral ears and dorsal spines are fine posteriorly, coarser medianly, and fine laterally and anteriorly. In the ventral valve, faintly dendritic adductors lie on low narrow platforms, divided by a low myophragm. Dorsal adductor scars are large and dendritic at maturity, the anterior scars smooth in immature specimens, divided by a low median septum, in front of a sturdy cardinal process, bifid from a postero-ventral aspect, trifid on its dorsal surface, between two well formed hinge ridges that continue into marginal thickening around the entire valve (Campbell 1956, text-fig. 4). Two distinct lateral buttress plates arise close to the junction of the hinge ridges and median septum (Campbell 1956, pl. 50, fig. 6), most clearly illustrated by Roberts (1964a, pl. 3, fig. 14b, c, Fig. 3A). Brachial ridges and shields are illustrated by Roberts (1964a, Fig. 3), and details of pustulation are described by Campbell (1956), with regular and evenly spaced pustules prominent over the middle and anterior shell of the dorsal interior.

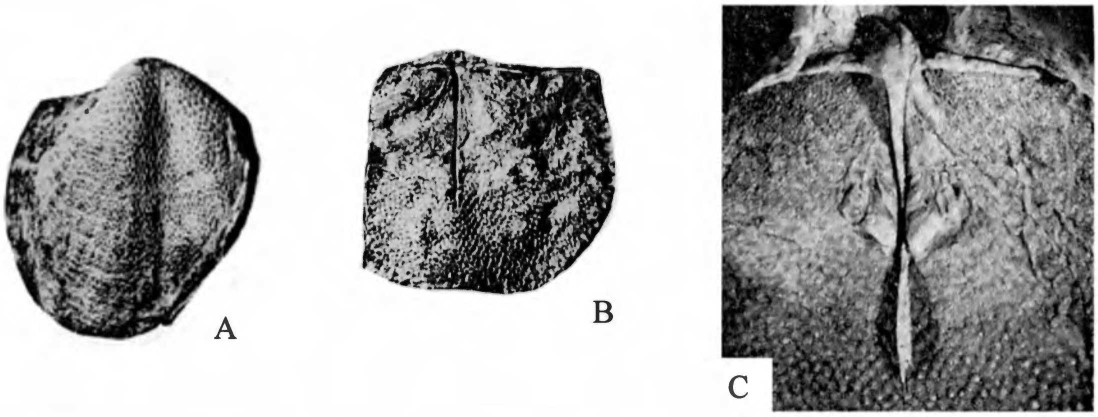

Fig. 8.15. *Campbelliconcha delicatula* (Campbell). A, plaster cast of ventral exterior of holotype, AMF 79395, formerly UNE 6827. B, dorsal internal mould UNE 1399. Specimens x1 from Babbinboon (Visean), New South Wales,Australia, x1, figured by Campbell (1956). C, latex cast of dorsal interior, AMF 75658, formerly UNE 6827, x2, from Greenhills, New South Wales. See Roberts (1964a, pl. 3, fig. 14).

Discussion: The type species as described by Campbell (1956) and Roberts (1964a) is exceptionally well preserved. The genus is close in most details to *Buxtoniella* Abramov & Grigorieva, 1986, p. 94 from mid-Visean faunas of Kazakhstan, and *Balkhasheconcha* Lazarev, 1985, p. 68 from Bashkirian to Asselian faunas of north Russia and Canada. But it lacks the highly distinctive elongate spine bases and prostrate spines of those two genera, and comes closest in age to *Buxtoniella*. The appearance of two related but different genera in Kazakhstan and east Australia implies very rapid migration on the part of ancestral stock, or an incompleteness of the fossil record in which stock gradually diverged and migrated. So-called *Waagenoconcha wimani* [not Fredericks] of Sarytcheva (1968, p. 112, pl. 11, fig. 1-8) from the Kokpectin Suite (Visean, Serpukhovian) of Kazakhstan is perhaps the closest of species, showing fine closely spaced spines but with short distinctly elongate bases. There are anterior commarginal growth steps and rugae and well defined adductor scars and heavy dorsal marginal thickening. Lateral buttress plates are well developed. *Pustula* (*Waagenoconcha*) *pseudoirginae* Huang (1932, pl. 4, fig. 1, 2) from the Late Permian of Kueichow, China, is sulcate with crowded spines, the bases a little longer than those of *Campbelliconcha*.

Genus ***Ramaliconcha*** new genus

Derivation: ramalia – twigs, sticks; concha – shell, Lat.

Type species: *Ramaliconcha bitteri* new species from Member A, Jungle Creek Formation (Gzhelian), Ogilvie Mountains, Yukon Territory, Canada, here designated.

Diagnosis: Small, both valves ornamented by raised, elongate and crowded spine-bases, spines erect only over posterior lateral ventral valve; low trail. Lateral buttress plates may be short, narrowly diverging in type species.

Discussion: *Buxtoniella* Abramov & Grigorieva (1986, p. 94) of middle Visean age in Verchoyan, northeast Asia, is said to lack the anterior band of thinner spines on the ventral valve, although a number of fine spines are present, scattered over the venter and anteriorly. The spine bases are lower, shorter and less conspicuous than in the new genus. *Balkhasheconcha* also has more subdued spine-bases and anterior spines are erect. *Campbelliconcha* new genus from middle Visean of east Australia has fine spines posteriorly, and very fine spines anteriorly: none have very elongate bases. The dorsal valve is slightly thickened.

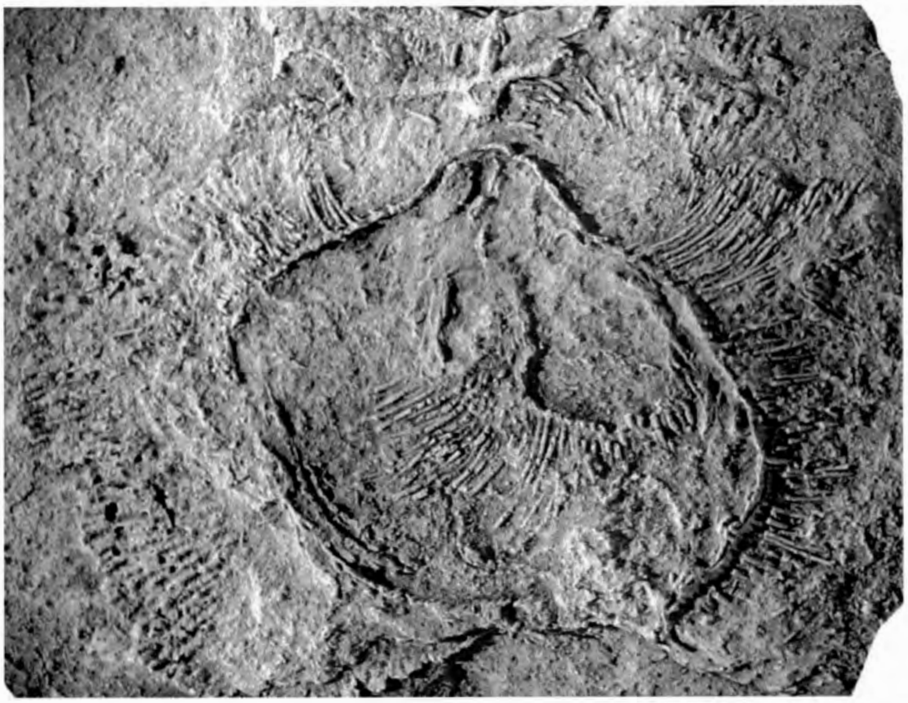

Fig. 8.16. *Ramaliconcha bitteri* new genus,new species. GSC 133360, x2, showing several valves and array of ventral spines. From Member A (Gzhelian), Jungle Creek Formation, Yukon Territory, Canada. JBW photo.

Ramaliconcha bitteri new species

Fig. 8.16 - Fig. 8.20

Derivation: Named for Peter von Bitter.

Holotype: GSC 133352 figured herein as Fig. 8.17A, from Member A, Jungle Creek Formation, Canada, here designated.

Diagnosis: Small shells with ventral sulcus and semigeniculate short trail, spine bases coarse and elongate over both valves, with no erect spine bases.

Material: About forty specimens from Member A (Gzhelian), basal Jungle Creek Formation, Ogilvie Mountains, Yukon Territory, Canada. See Appendix A, part C, p. 478.

Dimensions in mm:

Specimen GSC	Width	Length	Height	
133357	30	22	9.5	holotype
136060	28	28	7	
133360	42	35	10?	
133359	29	23	9	

Description: Moderate to large in size, a specimen from JBW 802 measuring 58mm wide, 39mm long and 17mm high, without the trail preserved. The ventral umbo is broad with angle of 110°, and not strongly incurved, and the maximum width is placed towards the anterior third of the shell length, with obtuse cardinal extremities and low umbonal walls. A median sulcus commences 10-15mm in front of the umbonal tip and widens at 20-25°, and ventral ears are not well defined. The dorsal valve is very gently concave with low median swelling over the anterior disc and trail, ears are weakly defined, and the disc curves steeply into the very short trail. Ventral ornament consists of crowded elongate spine bases, widening forward, up to 3.5mm long anteriorly, numbering five in 5mm, and these are shorter anteriorly over the first formed part of the trail, and short over the ears. Dorsal ornament is similar: in both valves the bases are comparatively high and crowded.

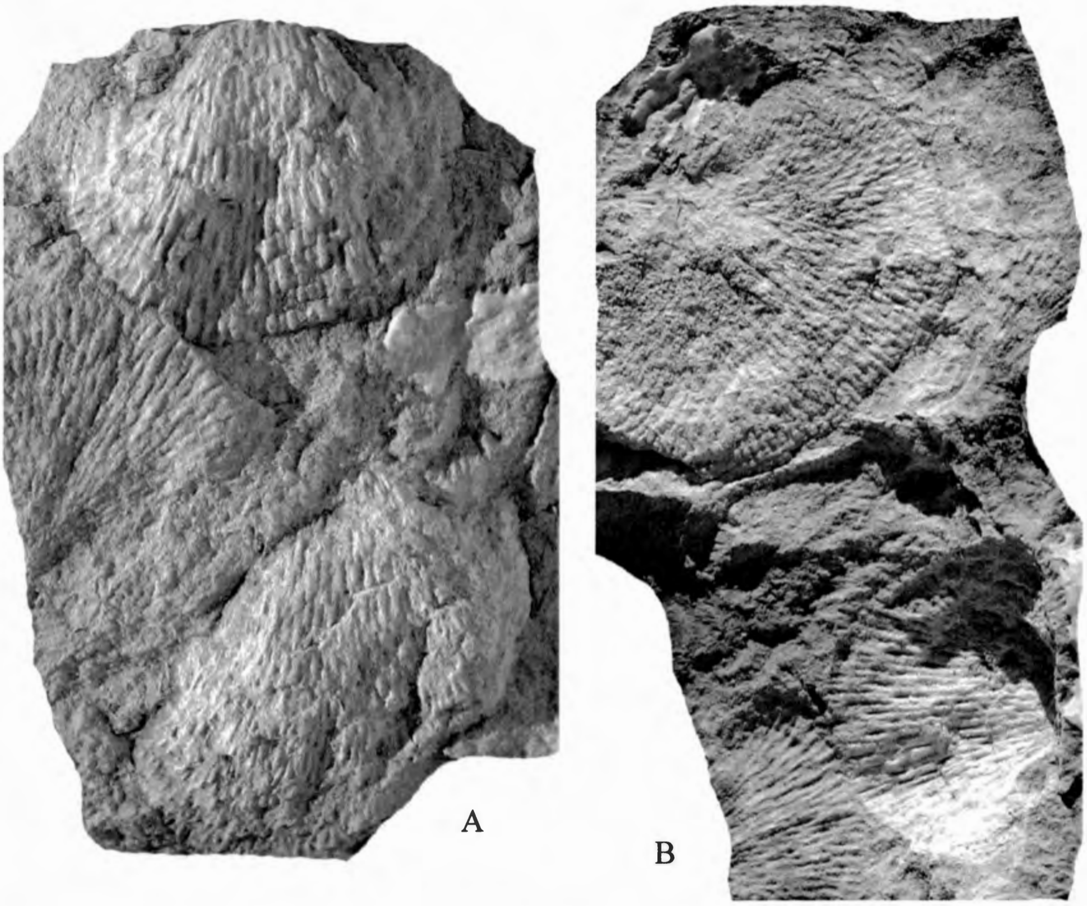

Fig. 8.17. *Ramaliconcha bitteri* new genus,new species. A, ventral valves holotype GSC 133352 (above) and GSC 136069, with part of dorsal valve, x2. B, dorsal valve interior GSC 133358and external mould of ventral valve GSC 133359, x1.5. From Member A (Gzhelian), Jungle Creek Formation, Yukon Territory, Canada. JBW photo.

Details of the ventral interior are masked by ornament from the exterior. Dorsal valve with low cardinal process supported by two high cardinal ridges, median septum extending to the posterior third and in some shells to the anterior third of the length. The dorsal adductors form two elongate weakly raised platforms, bordered by low and narrowly diverging lateral buttress plates, which commence over the ventral face of the cardinal process and are short in many specimens, longer in a few.

Resemblances: The ventral valve is more convex and the visceral disc thicker than in *Balkhasheconcha bamberi* new species and the ornament coarser, and the dorsal valve moderately concave. Externally the species is particularly close to material described as *Waagenoconcha skinderi* Sarytcheva (1968, p. 111, pl. 9, fig. 7-12), sharing similar ventral spines and spine bases that are prolonged and swollen. The species *skinderi* comes from the Kokpektin Suite of west Kazakhstan. Klets (2005, p. 40) recorded the species as *Waagenoconcha skinderi* from the Kasimovian Stage, and tabulated the Kokpektin Complex as Serpukhovian and Visean (Klets 2005, Fig. 36). The lateral spines are finer in the Russian species and the sulcus shallower, and growth steps more defined. No dorsal valves were figured, so that the generic position is not necessarily the same as the Canadian form, and the assessment by Klets (2005) indicates that it is not congeneric. Another larger possible ally with slightly thinner ventral spines was named as *Waagenoconcha infima* Ganelin in Ganelin & Kotlyar (1984), of early Carboniferous age in the Hayarmsk Suite of northeast Russia.

Fig. 8.18. *Ramaliconcha bitteri* new genus, new species. Slab of mostly dorsal valves, from MemberA, Jungle Creek Formation (Gzhelian), Yukon Territory, Canada, x1.2. JBW photo.

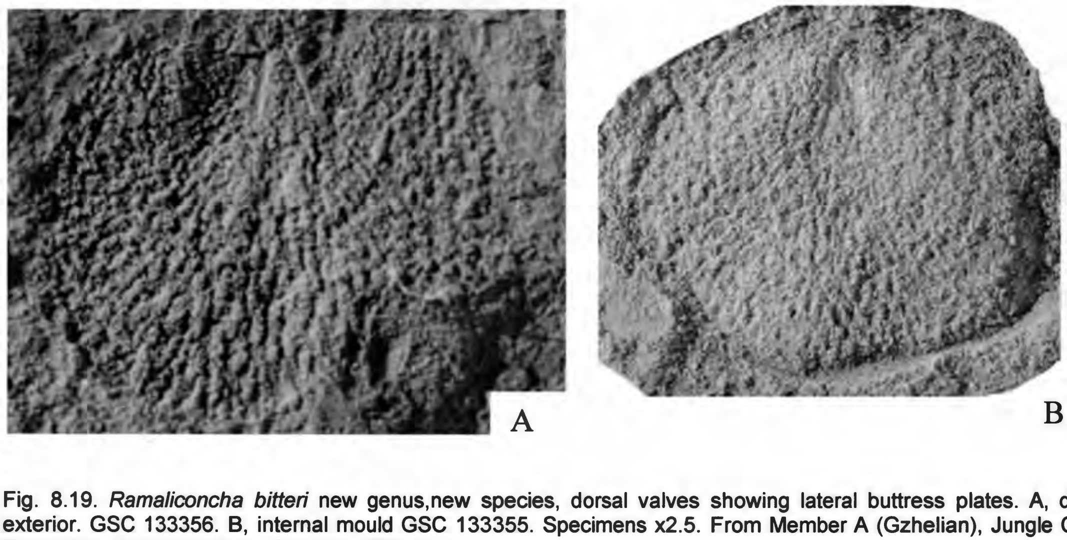

Fig. 8.19. *Ramaliconcha bitteri* new genus,new species, dorsal valves showing lateral buttress plates. A, dorsal exterior. GSC 133356. B, internal mould GSC 133355. Specimens x2.5. From Member A (Gzhelian), Jungle Creek Formation, Yukon Territory, Canada. JBW photo.

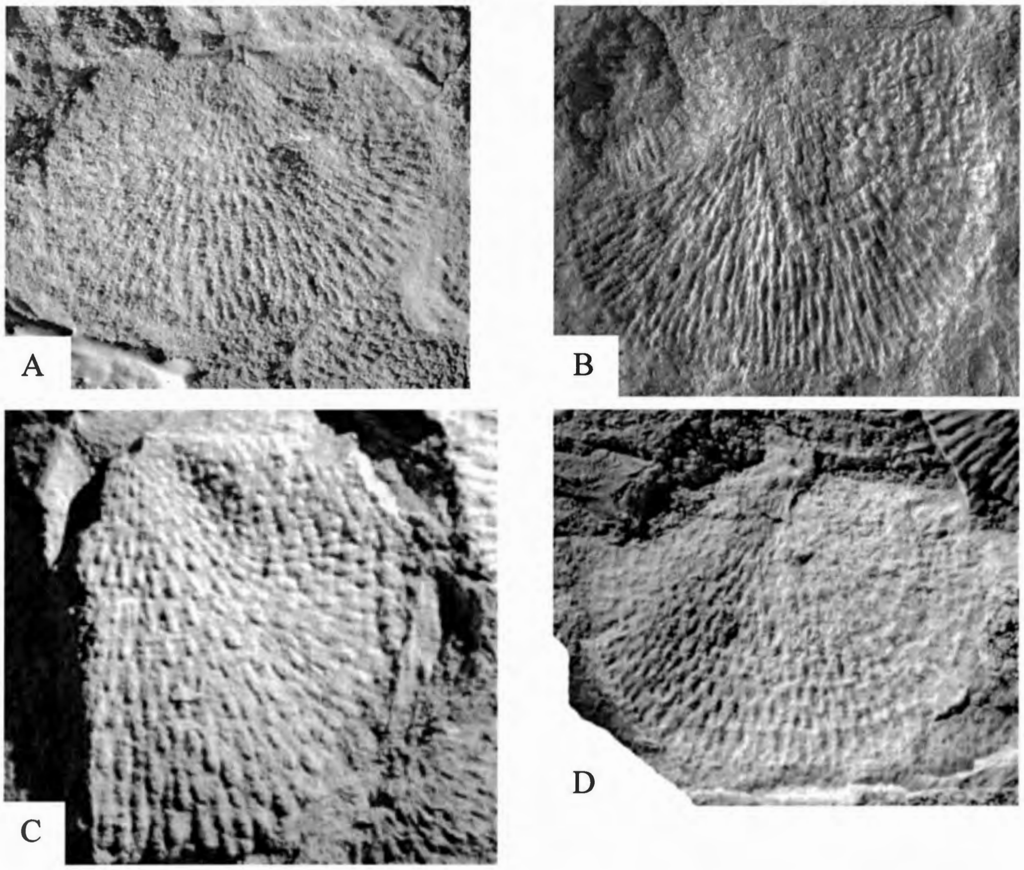

Fig. 8.20. *Ramaliconcha bitteri* new genus,new species, dorsal valves. A, interior of GSC 133354, x1.7. B, exterior of GSC 133357, x1.7. C, part of dorsal exterior, GSC 136071, x2. D, dorsal interior of GSC 133351, x2.2. From Member A (Gzhelian), Jungle Creek Formation, Yukon Territory, Canada. JBW photo.

Waagenoconcha irginaeformis of Sarytcheva (1968, pl. 10, fig. 1-8, fig. 44, 45, ?46, 47) from Kazakhstan has rather similar lateral buttress plates in Fig. 47, and though none were shown in Fig. 46, perhaps they were worn from the specimen, or more likely the figure illustrates a different taxon. The ventral spines are much finer than in the present species, but figures of the internal dorsal valve (pl. 10, fig. 4b, 5-8) show coarse internal ridges like those of *Ramaliconcha bitteri*.

Ramaliconcha guryulensis new species

Fig. 8.21

1932 *Productus* (*Taeniothaerus*) *permixtus* Reed, p. 12, pl. 1, fig. 4) [part only]. (GSI 15499).
1932 Untitled Reed, pl. 4, fig. 11. (GSI 15519).
2007 ?*Reedoconcha permixtus*[not Reed?] – Waterhouse & Chen, p. 13, pl. 3, fig. 4. (GSI 15499).
2007 uncertain Waterhouse & Chen, p. 13, pl. 3, fig. 8. (GSI 15519)

Derivation: Named from Guryul Ravine, Vihi District, Kashmir.

Holotype: BR 3071 from Agglomeratic Slate (late Sakmarian) of Kashmir, here designated. See Fig. 8.21.

Diagnosis: Small to medium transverse shells with ventral sulcus and dorsal fold, no ventral interarea, spine bases prostrate with long bases, dorsal spines equally crowded with slightly shorter bases.

Description: Holotype 37mm wide and 28mm long and disc 9.5mm high, ventral umbo low and incurved with posterior walls diverging at 110°, no cicatrix, sulcus commences a little in front of the umbo, widens at 25°, hinge short at about a third of the width, dorsal fold very low and commences near mid-length. Trail semi-geniculate and short. Ventral spines crowded and prostrate with bases 4mm long and anteriorly 8-9mm long. Dorsal spines also crowded but bases appear to be no longer than 4mm, and are mostly short and spines more erect postero-laterally. A few irregular rugations cross the ventral valve, and the dorsal valve bears more low growth stops and rugae, especially over the trail. Ventral muscle scars cannot be clearly discerned. Cardinal process high, with median lobe bearing central groove, and lateral lobes splayed apart. Median septum strong, extends beyond mid-length, with indications of posterior median groove. Well formed lateral buttress plates diverge to each side, enclosing striate adductor scars. Brachial impressionsanteriorly placed.

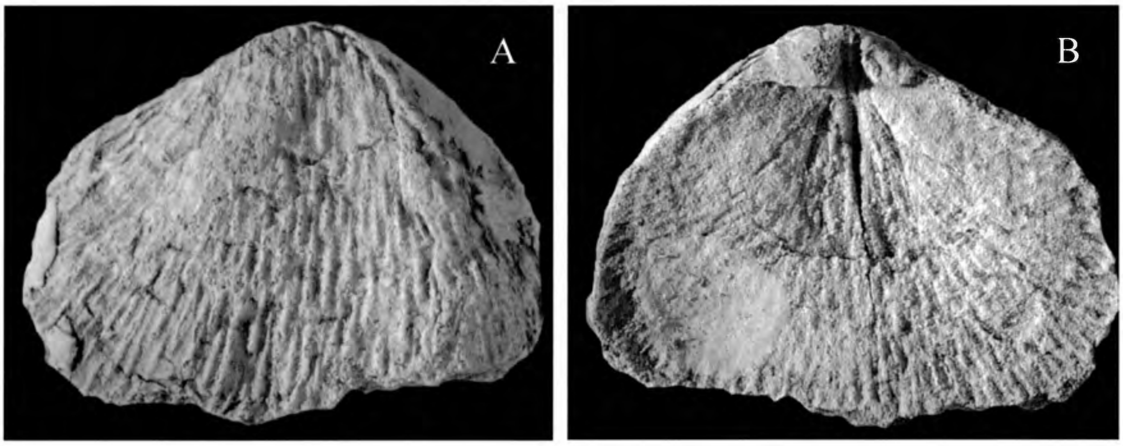

Fig. 8.21. *Ramaliconcha guryulensis*new genus, new species. A, B, ventral and dorsal aspects of holotype, BR 3071 from Agglomeratic Slate (Sakmarian) of Kashmir, x2 approx. JBW photo.

Resemblances: This species is represented by relatively rare specimens in the Agglomeratic Slate of Kashmir, northwest India.Two of the species of *Reedoconcha* Kotlyar,namely *permixtus* Reed and *brenensis* Reed, that are found in the Agglomeratic Slate of Kashmir, have similar ornament, ventral sulcus and lack of ventral interarea, but are larger and more elongate, and a well preserved dorsal interior lacks lateral buttress plates, so that, as reviewed on p. 281, the species are considered to belong to Taeniothaerini, which is an aulostegoid rather than scacchinelloid group. A third species, *Productus* (*Buxtonia*) *kashmiricus* Reed (1932) is transverse and sulcate, closer to the present form, but nearly twice as large. One dorsal interior (Reed 1932, pl. 2, fig. 6 – GSI 15508) has a median septum much longer than in the present species, and the other (Reed 1932, pl. 2, fig. 7 – GSI 15509) lacks lateral buttress plates.

The species has a thicker visceral disc and greater body cavity than *Balkhasheconcha*, with more sturdy ventral and dorsal spine bases, and no erect anterior spines on either valve, unlike *Balkhasheconcha* or *Buxtoniella*. The spine bases are somewhat more spaced and longer than in *Ramaliconcha bitteri* new species from the Late Carboniferous lower Jungle Creek Formation of Yukon Territory, Canada, and the dorsal disc is more evenly concave, rather than almost flat with median low fold, and the ventral sulcus is better defined, compared with the Canadian species, and the lateral buttress plates diverge more.

Subfamily **SEPTASTEGINAE** Waterhouse, 2002b

Fig. 8.22

[Septasteginae Waterhouse, 2002b, p. 28].

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,elevated septa in front of the broad cardinal process, which has four posterior lobes. Lower Permian (Asselian?) to Middle Permian (Roadian).

Genera: *Septasteges* Waterhouse & Piyasin, *Bilotina* Reed, ?*Enigmalosia* Czarniecki.

Discussion: This group is provisionally referred to Rhamnariidae, although the ornament is not like that of most Rhamnariinae, because members display ribs or elongate spine bases over the ventral valve, approaching the spine bases in *Ramaliconcha*new genus, and the dorsal ornament differs. Septasteginae has prominent septa in the dorsal valve, one each side of the dorsal medium septum. However dorsal muscle imprints have not been ascertained, perhaps because the best preserved material is silicified. To judge from well-preserved *Septasteges* (Waterhouse & Piyasin 1970, pl. 19, fig. 20, 21), the muscles would have had to have been implanted on the *outside* of the plates because of the way the plates bend inwards away from the shell floor, pointing to a shift in their position from that of Rhamnariinae, in which muscle scars lie on the inner side of the lateral buttress plates. A low to moderate interarea and small to large umbonal cicatrix are present, as in some Rhamnariinae.

The relationship preferred in previous studies has been with *Juresania* and allies, suggested to some extent by the ribs with long spine bases. Although *Juresania* does not have two high dorsal septa, it does display two low ridges in many specimens, and these potentially could have increased in height. The cardinal process in Septasteginae appears to indicate a rhamnariid relationship. It has been extensively figured by Grant (1976, pl. 37), to show a broad process, largely concave on the ventral face, and bordered in some specimens by two ridges that pass into the lateral septa. It thus somewhat approaches the cardinal process in *Rhamnaria,* as for instance in Cooper & Grant (1975, pl. 257, fig. 13, 16). In juresanin cardinal processes figured by Muir-Wood & Cooper (1960, pl. 50), the two ridges, one each side of the cardinal process on the ventral face, converge anteriorly to form a prow, rather than continue into the posterior ridges each side of the median septum.

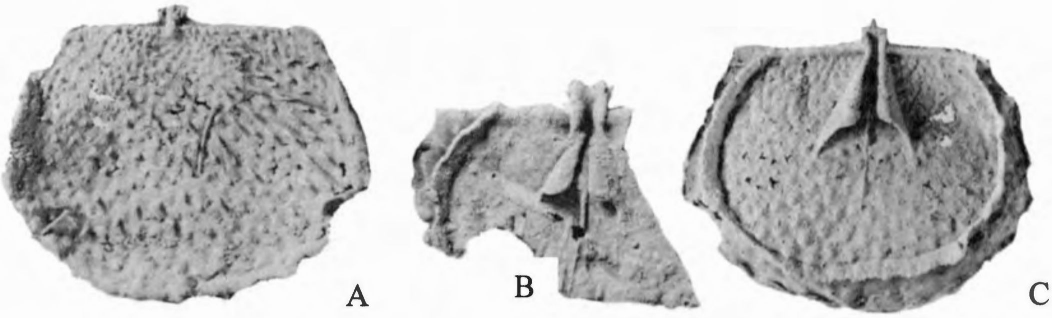

Fig. 8.22. *Septasteges acanthus* Waterhouse & Piyasin. A, C, external and internal aspects of immature dorsal valve B 301, x3. B, interior of dorsal valve B 305, now ROM 31991, x3. From Rat Buri Limestone (Roadian) at Khao Phrik, south Thailand. Kept at Royal Ontario Museum, Toronto. B. O'Donovan & JBW photo.

In Septasteginae, there is no sign of concentric anterior banding which helps characterize Juresaniinae of Echinoconchoidea. Rather the interarea, spines, costae and internal marginal ridge approach features of Aulostegoidea. The genera are 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, implying that the dorsal adductors rested on lateral buttress plates. *Septasteges* was described from the early Middle Permian of Thailand. Grant (1976) pointed out that the genus approached*Strophalosia (Bilotina) subtecta* Reed from the Amb Formation, Salt Range (Pakistan) of approximately Artinskian or Kungurian age. This form was well described by Reed (1944, p. 109, pl. 8, fig. 1-8), and Grant (1976) was able to prepare some Amb Formation material from the Khisor Range of Pakistan. Ventral valves of *Bilotina* are inflated and elongate, laterally compressed, parallel-sided, with steep lateral walls, and shallow sulcus for the full length, differing somewhat from the much less inflated Thai form. The ventral umbo in *Bilotina* is strongly enrolled, with cicatrix and low interarea, and there are small elongate pustules over the ventral umbo and posterior ventral valve, whereas *Septasteges* has spines arising directly from the umbonal shell. Anteriorly, spine bases in *Bilotinasubtecta* are very crowded and only moderately prolonged, and arranged in dense quincunx. For the ornament of Thai ventral valves over most of the shell except posteriorly and laterally, the spines are aligned and rare, emerging from ribs. The ribs pass from the posterior shell to the anterior margin, with occasional introduction of a 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 *Septasteges*, the spines arise from either an almost smooth shell (*S. acanthus* Waterhouse & Piyasin), or from small pustules (*S. praeclarus* Waterhouse). In *Bilotina*, the dorsal valve is heavily pitted and pustuled, and larger tubercles are developed laterally. There is contradictory evidence on the nature of septation in *Bilotina*. Reed (1944) recorded both a ventral and dorsal medium septum in *Bilotina*, whereas the Thai species has no ventral septum, and Grant (1976) suggested that the ventral valve of type *Bilotina* also lacked a septum, and argued that the absence of the septum from Grant's dorsal valve of *B. subtecta* was due to preservation.

Genus ***Enigmalosia*** Czarniecki, 1969

Fig. 8.23

The poorly known genus *Enigmalosia* from Spitsbergen has ventral ribs bearing spines, large umbonal cicatrix, indistinct interareas, capillate dorsal valve and costate trail, divided cardinal process, and no teeth. There are long 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) favoured a late Carboniferous age, but an Asselian age appears possible, judged from Canadian faunas found in Member B of the Jungle Creek Formation (see p. 478).

The genus was classed in the strophalosiidin subfamily Donalosiinae by Brunton et al. (2000, p. 582), but shows little similarity, because of the lack of teeth and unusual dorsal interior of *Enigmalosia*. Scouting possibilities, the genus could be aulostegoid, perhaps close to Chonosteginae, of which some genera develop ribs, but Scacchinelloidea seems more likely, because the long plates in front of the cardinal process seem to be lateral buttress plates or rather their equivalent. They converge anteriorly, rather than diverge as in *Septasteges* and Rhamnariinae. In addition, the bilobed cardinal process is like that of some Scacchinelloidea. In that case, *Enigmalosia* may prove to be a member of Septasteginae, reinforced by its large cicatrix (approaching that of*Septasteges*), and distinguished by convergent internal dorsal plates and coarse bases to the ventral spines.

There is some approach in the dorsal interior to that of *Stepanoconchus* Lazarev, 1985, p. 69, based on *Echinoconchus postpunctatus* Stepanov in Volgin (1960, p. 62, pl. 6, fig. 1a, b), and clearly echinoconchiform.The genus is distinguished by having two plates which arise close to the median septum, and terminally spread outwards to presumably provide muscle supports for the adductors (see Lazarev 1990, pl. 6, fig. 1; Brunton et al. 2000, Fig. 350.1b). These plates arose independently, apart from the scacchinelloid template. Perhaps *Enigmalosia* is also an independent development. Even the nature of the plates in *Septasteges* and *Bilotina* is not secure.

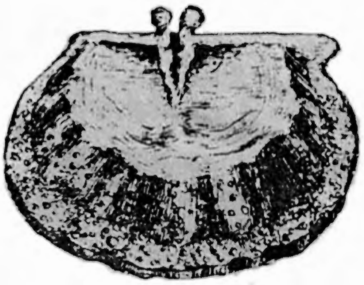

Fig. 8.23. *Enigmalosia sarytchevae* Czarniecki, dorsal interior from Treskelloden Beds (?Asselian), Spitsbergen, x8, sketched by Czarniecki (1969, Fig. 29).

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

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

Taxonomy: Brunton et al. (2000, p. 608) mistakenly averred that Muir-Wood & Cooper (1960) had proposed Tschernyschewiinae only as a subfamily, but that is not correct.

Diagnosis: Ornament somewhat waagenoconchid varying to pustular, cicatrix often present, interarea variable and may be high, profile concavo-convex, cicatrix common with support spines. Cardinal process bilobed and high. Lower Permian (Sakmarian or Artinskian) to Upper Permian (Changhsingian).

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

Discussion: Muir-Wood & Cooper (1960) and Cooper & Grant (1975) evaluated Tschernyschewiidae as a full family, as supported by substantial differences in ornament and nature of the dorsal valve from Sccachinellidae.

There are well developed lateral buttress plates in *Tschernyschewia* (Stoyanow (1915 [1916], pl. 2, fig. 9; Muir-Wood & Cooper 1960, pl. 25, fig. 7), and the nature of the spines and the dorsal interior suggest an origin from within Rhamnariidae. The publication date for *Tschernyschewia* Stoyanow remains debatable, and although possibly in 1916, as discussed on p. 386, Sone (2009) preferred the date of 1915.

Genus ***Tschernyschewia*** Stoyanow, 1910b

Type species: *Tschernyschewia typica* Stoyanow, 1910b from Wuchiapingian of Armenia.

Diagnosis: Hinge narrow with low ventral interarea, closely spaced spines with short elongate bases over the ventral valve, bases slightly shorter and spines more erect over the dorsal valve, medium ventral septum high.

Tschernyschewia geniculata Zhan, 1979

Fig. 8.24

1979 *Tschernyschewia geniculata* Zhan in Hou et al., p. 78, pl. 12, fig. 1-5, text-fig. 15.
1983d *T. geniculata* – Waterhouse, p. 120, pl. 2, fig. 14, 16.
2005 *T. geniculata* – Campi et al., p. 123, pl. 3, fig. V, X, Y.

Discussion: This species was described from the Lopingian of China, Thailand and Malaysia.

Fig. 8.24. *Tschernyschewia geniculata* Zhan, internal mould TBR 410, x1 from Huai Tak Formation (Changhsingian), north Thailand.See Waterhouse (1983d). JBW photo.

Genus ***Sierradiabloa*** new genus

Fig. 8.25

Derivation: Named after Sierra Diablo, the range that provided the fossils.

Type species: *Tschernyschewia americana* Cooper & Grant, 1975, p. 914 from Bone Spring Formation (Artinskian), Sierra Diablo, Texas, United States, here designated.

Diagnosis: Small with coarse erect ventral spines, dorsal valve with prominent closely spaced dimples and fine spines. Lateral buttress plates short.

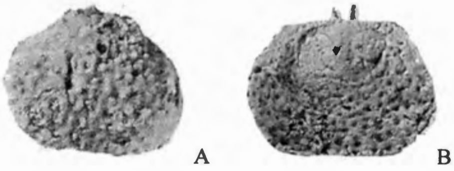

Fig. 8.25. *Sierradiabloa americana* (Cooper & Grant). A, ventral view of USNM 149434b, x1.7. B, dorsal exterior of USNM 152683b. From Bone Spring Formation (upper Kungurian), west Texas, United States, x2. See Cooper & Grant (1975, pl. 268, fig. 8, 14).

Discussion: This genus is distinguished by ornament. *Tschernyschewia* Stoyanow, 1910b has very fine and dense spines, with slightly elongated slender bases on the ventral valve and fine pits and pustules over the dorsal valve. Ventral spine bases in the new form are coarser, as a rule without elongate bases, and dorsal dimples and pustules are larger and more prominent in the dorsal valve. Lateral buttress plates in the new genus are distinct but very short (Cooper & Grant 1975, pl. 268, fig. 5, 7). *Megatschernyschewia* Sremac, 1986 from the Guadalupian of the Velebit Mountains, Croatia, was based simply on large size, but its ventral spines are very fine and crowded, and dorsal spines subprostrate. From the Taylor Ranch Member of the Hess Formation in Texas, *Trigonoproductus* Waterhouse,2002b is of trigonal shape with coarse ventral hinge spines in a double row, somewhat diversified ventral spines and elongate spine bases that are semicontinuous to suggest ribs. Dorsal pits are less conspicuous than in the new genus, and lateral buttress plates are moderately well formed (Brunton 2007, p. 2672, Fig. 1781.2a-f). *Reedosepta* Waterhouse, 2002b, p. 50 is distinguished by its swollen and aligned spine bases, with more erect spines over the postero-lateral slopes and ears, and the ventral septum is high (Brunton 2007, p. 2672, Fig. 1781.1a-f). It comes from the Wargal Formation of the Salt Range, Pakistan, and is of Wuchiapingian age (lower Lopingian), not Capitanian as claimed by Brunton (2007, p. 2672).

9. Superfamily **COOPERINOIDEA** Pajaud, 1968

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

Diagnosis: Ventral valve attached and comparatively high, brachial apparatus specialized. No teeth or sockets.

Discussion: Family Cooperinidae was classed as Aulostegoidea by Brunton et al. (2000, p. 605), but brachial shields are large and appear to have been modified from strophalosioid stock. The brachial apparatus is so unusual that the genera are separated as a distinct superfamily, characterized by distinctive bilobed or ptycholophous lophophores. Shells are small with large cicatrix, and spines in some genera, moderately high interarea, and no teeth or pseudodeltidium. Brunton et al. (2000, p. 605) outlined a different morphology, claiming that the family was in part defined by the presence of "hinge teeth", but this is incorrect, Grant (1972, pp. 217, 244) and Cooper & Grant (1975, pp. 823, 829) explicitly stating that no teeth were developed in four of the prominent genera. The brachiophores together with cardinal process are quite different from the arrangement in Aulostegoidea, to which Brunton et al. (2000) had referred the family, and differ from Strophalosioidea, which otherwise is allied in several respects. In that regard, Williams, Harper & Grant (2000, Fig. 454) appear to have disagreed with Brunton et al. (2000), and showed Lyttoniidina (= Oldhaminidina) as sourcing from the cooperinoid genus *Falafer*, which was treated as a derivative from strophalosioids, not aulostegoids as in Brunton et al. (2000). Cooperinoidea are readily distinguished from Oldhaminidina, in which the dorsal valve is reduced mainly to a lobate brachial plate (Termier & Termier 1949), and in which the presence of any spines, limited to the ventral valve, is extremely rare, apart from *Laterispina* Wang & Jin of Permianellidae (see p. 304), in which there are spinose protrusions, not exactly like ordinary productid spines. According to Williams, Harper & Grant (2000), spines are completely absent from Lyttonioidea. Known members of Cooperinoidea are no older than Lyttonioidea, but the lobate or ptycholophous brachidia suggest they could have been intermediate between the two: conceivably they are surviving members of a group which commenced in Carboniferous, although scarcely represented in the fossil record for that period. One possible exception, according to Cooper & Grant (1975, p. 828) is offered by *Leptalosia spondyliformis* (White & St John) from Pennsylvanian rocks of Iowa and Nebraska, United States.

Family Cooperinidae Pajaud, 1968
- Subfamily Cooperininae Pajaud, 1968
    - Tribe Cooperinini Pajaud, 1968
    - Tribe Incisiini Grant, 1976
- Subfamily Falaferinae Waterhouse, 2002b
- Subfamily Epiceliinae Grant, 1972

Table 11. Superfamily Cooperinoidea Pajaud, 1968.

The question remains as to whether Cooperinoidea should be classed as Strophalosiidina or Oldhaminidina (Lyttoniidina). On the one hand, *Cooperina* and allies differ from *Oldhamina* and allies in the presence of ventral spines for most genera, the presence of interarea, and a relatively complete dorsal valve, to mention only some of the differences. On the other hand, there is a three-fold division in Cooperinoidea which is crudely mirrored amongst groups in Oldhaminidina, and most genera display a ventral internal ridge around the valve which, earlier matched with the marginal ridge of Marginiferidae, approximates and could have developed into, or less likely, given the spinose ornament, degenerated from, the vallum of Lyttonioidea. The broad similarities may be outlined as follows:

Cooperiinae displays elongate brachiophores, recalling those of the more extreme oldhaminidin group *Permianella*, and allies, and the sulcate shape in *Incisius* and *Cyrtalosia* recalls that of *Caninella*(cf. Fig. 9.3, p. 271 with Fig. 13.3, p. 303).

Epicelia Grant and *Ceocypea* Grant display multilobed brachiophores, with deep lobes orientated obliquely along the much of the length of the dorsal valve. This arrangement somewhat recalls the arrangement in *Rigbyella*Stehli, classed as Rigbyellidae Williams, Harper & Grant in Lyttonioidea (compare Fig. 9.5, p. 272 with Fig. 12.6, p. 300).

Falafer Grant has an elaborate ptycholophous brachidia, arguably suggestive of the brachidia in Lyttoniidae (see Fig. 9.4, p. 272, and Fig. 12.2B, Fig. 12.3, Fig. 12.4, on pp. 298-299). The difference is that the brachidial structure affects both valves much more profoundly in Oldhaminidina than in Cooperinoidea.

The similarities across different groupings raise the possibility that the small subdivisions within Cooperinoidea should be reassembled as offshoots, or primitive survivors of of the main groupings within Oldhaminidina (=Lyttoniidina). But this can only be a suggestion. Too little is known for the brachiophores of various other Productida, and probably the fossil record of Cooperinoidea is too imperfect to allow reclassification at this stage.

Family **COOPERINIDAE** Pajaud, 1968

Fig. 12.1 (p. 297)

[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, no hinge teeth, no pseudodeltidium, brachial ridges prominent.

Subfamily **COOPERININAE** Pajaud, 1968

Fig. 9.1

[Cooperininae Pajaud, 1968, p. 158].

Diagnosis: Small shells with ventral spines, brachidia as simple schizolophes.

Tribe **COOPERININI** Pajaud, 1968

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

Diagnosis: Small shells with cicatrix surrounded by rhizoid spines, dorsal muscle platform short, brachidia as simple schizolophes. Lower Permian (Asselian) to Middle Permian (Capitanian).

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

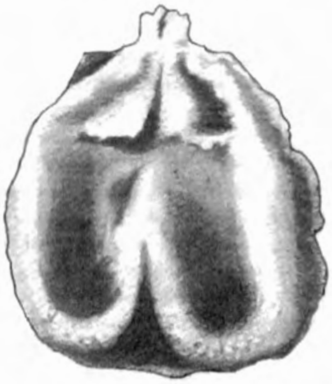

Fig. 9.1. *Cooperina inexpectata* Termier, Termier & Pajaud from Willis Ranch Member, Word Formation (Wordian), west Texas, United States, dorsal interior, redrawn from Cooper & Grant (1975, pl. 210, fig. 37), x13. JBW del.

Discussion: The oldest known genus in this subfamily is *Atelestegatus* Cooper & Grant from the Neal Ranch Formation (Asselian) of west Texas, with ventral spines that are mostly erect and of slightly different diameters, and rhizoid over the umbo. Dorsal spines are fine. The ornament and shape suggest a possibly source from within Echinalosiinae, although this subfamily is not common in North America. Younger genera, notably *Ansehia* Termier & Termier, may lack dorsal spines and have deeper ventral valve.

Genus ***Cooperinoides*** new genus

Fig. 9.2

Derivation: Named for G. A. Cooper.

Fig. 9.2. *Cooperinoides triangulata* (Cooper & Grant), dorsal interior, USNM 154139a, Neal Ranch Formation (Asselian), Texas, United States, x24.Redrawn from Cooper & Grant (1975, pl. 209, fig. 34). JBW del.

Type species: *Cooperina triangulata* Cooper & Grant, 1975, p. 827 from Neal Ranch Formation (Asselian), Glass Mountains, United States, here designated.

Diagnosis: Triangular shells with dorsal lateral flanges becoming lower anteriorly and converging, without uniting to form a median ridge.

Discussion: This genus is very close to *Cooperina* Pajaud et al 1968, but is more triangular in shape with narrow hinge, and diverging lateral margins. The dorsal margin is bordered each by a high flange or ridge that extends to the anterior margin, the two sides curving inwards to the centre and passing posteriorly in parallel. In *Cooperina*, the two ridges fuse. In *Cooperinoides* the ridges do not fuse, but remain separate. Several species of *Cooperina* are found in the Permian of Texas, but the only other species so far known for *Cooperinoides* is *polytreta* (Grant, 1976, p. 87, pl. 19, fig. 1-24) from the Rat Buri Limestone (Roadian) of south Thailand. The shell of this species is perforate in parts. Full detail of the two species is provided by Cooper & Grant (1975) and by Grant (1976).

Tribe **INCISIINI** Grant, 1976

Fig. 9.3

[Nom. transl. hic ex Incisiidae Grant, 1976, p. 103].

Diagnosis: Ventral spines well spaced or apparently absent, no cicatrix,no dorsal spines, ventral sulcus well developed, shells elongate.

Middle Permian (Roadian) to Upper Permian (?Wuchiapingian), possibly late Middle Permian (Capitanian).

Genera: *Incisius* Grant.

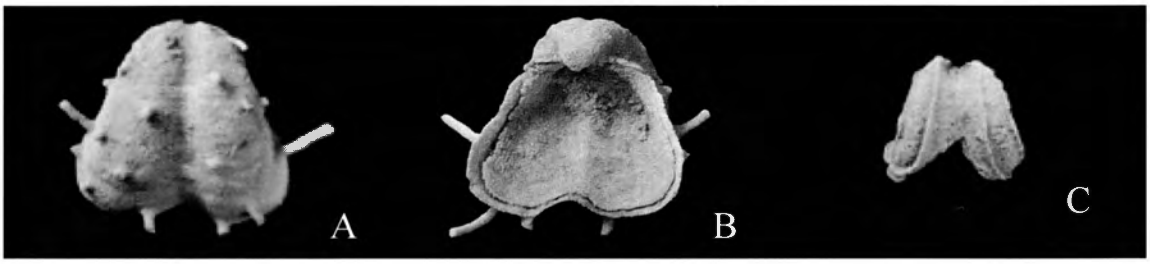

Fig. 9.3. *Incisius concisus* Grant. A, B, ventral and dorsal aspects of USNM 212184, x4. C, interior of dorsal valve, USNM 212201, x5. From Rat Buri Limestone (Roadian) of Ko Muk, Thailand. See Grant (1976, pl. 23).

Discussion: Although the shape and to some extent ventral spines would allow a position close to Scapharininae Cooper & Grant, 1975– see p. 102– the long and raised brachial ridges that edge the brachial shields rule out such an allegiance, and instead point to a close relationship with *Cooperina* Pajaud et al. Whether the genus really merits tribal separation may be deemed debatable, but is based principally on the much closer distribution of more numerous ventral spines in Cooperinini, and presence of a cicatrix surrounded by somewhat rhizoid spines. *Incisius* is sulcate, but so is *Ansehia* Termier & Termier, which has numerous ventral spines.

Cyrtalosia Termier & Termier, 1970 is shaped very like *Incisius*, and Grant (1972) included it in his Incisiidae. The genus lacks spines apparently, although Grant considered they may have been lost through silicification, and has better developed hinge. Given that the interior is not known, the position remains uncertain, and illustrations and discussion are provided later, on p. 303 under the heading Locyzellidae.

The species *spondyliformis* White & St John

White & St John (1868) described a tiny species as *Aulosteges spondyliformis* from the Demoinesian of Iowa, United States, close to 2.5mm wide, and subtriangular in shape, with high triangular interareas, and spines on both valves. Dunbar & Condra (1932, p. 262, pl.32, fig. 10, 11) repeated the original figure and added another specimen from the basal Plattsmouth limestone of Nebraska. They disputed the presence of dorsal spines. Cooper & Grant (1975, p. 828) pointed out the similarity to Cooperinidae.

The subtriangular shape is suggestive of Incisini, but the nature of the brachiophores, and resolution of the distribution of spines, need to be resolved: it seems highly likely that a new genus is involved. The minute size acts as a reminder that there may be many such forms, as yet undescribed.

Subfamily **FALAFERINAE** Waterhouse, 2002b

Fig. 9.4

[Falaferinae Waterhouse.2002b, p. 44].

Fig. 9.4. *Falafer epidelus* Grant. Dorsal interior of USNM 169763, showing paired crenulated ptycholophous brachidia, from Episkope Limestone (Changhsingian), Hydra, Greece. X15. Redrawn from Grant (1972, pl. 2, fig. 20). JBW del.

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

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. The ventral valve is deep and marginal ridge high. The unique position of *Falafer* is confirmed in a cladogram presented by Williams et al. (2000, Fig. 453).

Subfamily **EPICELIINAE** Grant, 1972

Fig. 9.5

[Epicelinae Grant, 1972, p. 223].

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

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

Discussion: Dorsal spines may be present in *Epicelia*, but are absent from *Ceocyea*, and the latter genus has simpler bilobed brachidia, whereas the brachidia form three lobes in *Epicelia*.

Fig. 9.5. *Epicelia episcopiensis* Grant, dorsal interior USNM 169749 from Rat Buri Limestone (Roadian), Thailand, x7. Redrawn from Grant (1972). JBW del.

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