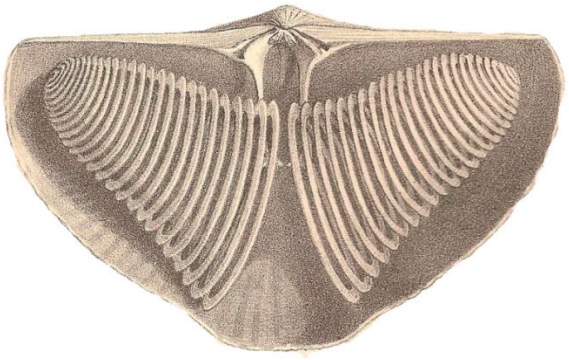
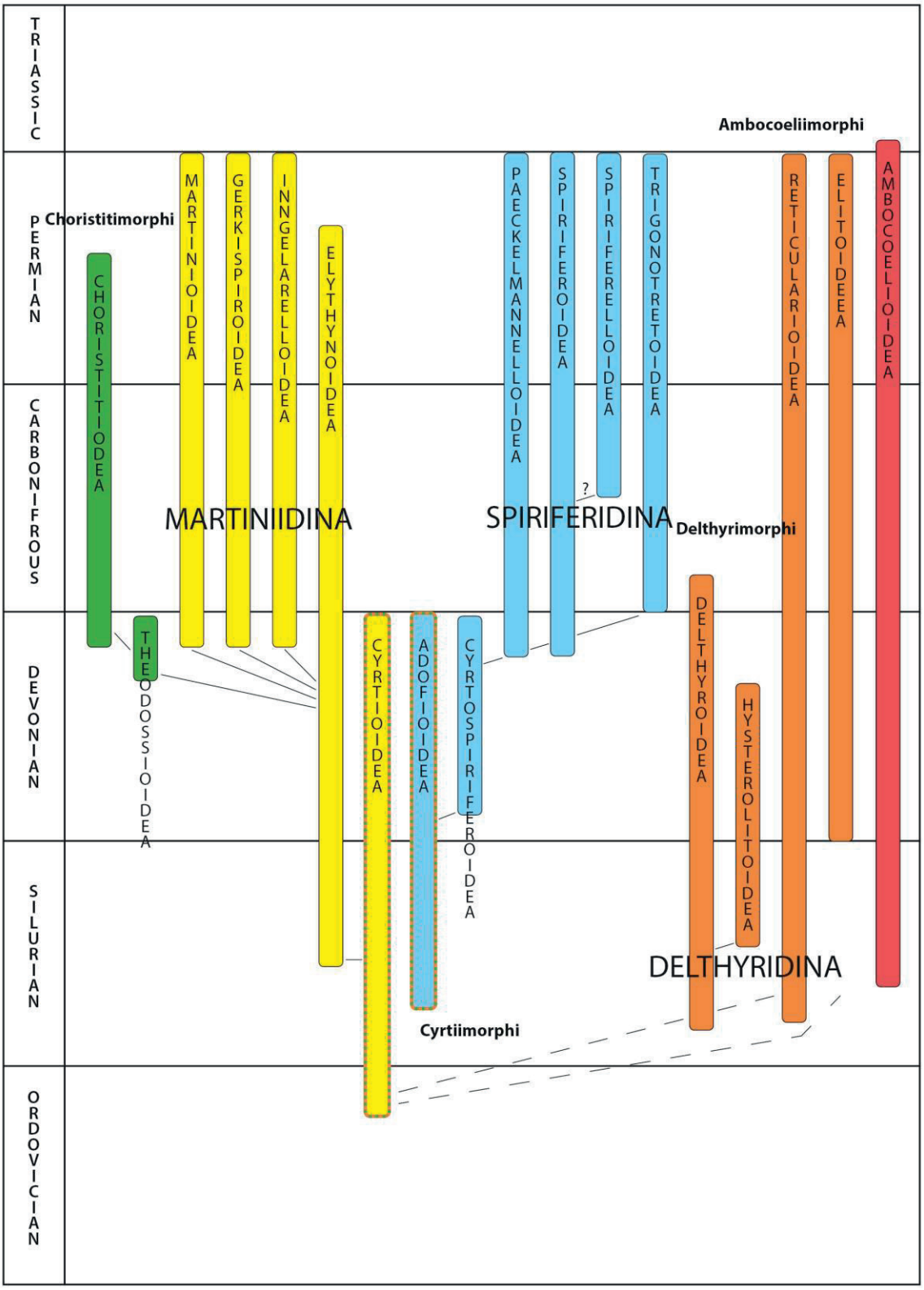
ON THE EVOLUTION AND CLASSIFICATION OF SPIRIFERIDA (BRACHIOPODA)





Frontispiece. Order Spiriferida. The Cyrtioidea and Adolfioidea, members of the Cyrtiimorphi, each gave rise to suborders, along with Delthyridina, also from Cyrtioidea.

ON THE EVOLUTION AND CLASSIFICATION OF SPIRIFERIDA (BRACHIOPODA)

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Earthwise 14

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Dedicated to the memory of Mena Schemm-Gregory, who loved brachiopods, and died all too soon after outstanding research on Devonian brachiopods.

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INTRODUCTION

Spire-bearing Spiriferida ranged from Late Ordovician into Early Triassic time, and so far about 500 genera have been named and described, based on the counts in Curry & Brunton (2007), adjusted upwards to allow for various omissions, further study, and revision. Compared with Productida, Spiriferida were less diversified, and evolved less rapidly. No Spiriferida approached the extreme deviation from the norm exhibited in Productida by richthofeniids or lyttoniids. Yet they offer more difficulties in resolving relationships, quite apart from the unresolved question of origins (Carlson 2016), because internal morphology may be hidden from view, whereas in Productida, the external factors of shape and ornament are relatively much more important. There are further barriers against a ready understanding of the Spiriferida. According to numerous studies on early Spiriferida, of Late Ordovician, Silurian and Devonian age, internal plates and ornament show considerable inconstancy, in what may be termed reiteroplasy, to the extent that Schemm-Gregory (2011a) dismissed the value of attempting cladistic studies to unravel relationships. There are additional reasons why the use of cladistics is crammed with difficulties. Firstly, a number of genera are not well known, and would either have to be left out of evaluation, which means imperfect coverage, unless included with incomplete or neutral data. And furthermore, the last major review of Spiriferida, in the *Revised Brachiopod Treatise* (2006), is inconsistent and partly inaccurate in its description of morphological traits, and unless the original material or at least the descriptions are re-evaluated, the cladistic study will be flawed. But whatever criticisms may be leveled at the *Revised Brachiopod Treatise*, it clearly showed, by implication if not explicitly, that replication of external and internal morphology (that is reiteroplasy) was pervasive amongst different lineages, and that succession and time-control were all important, and must not be homogenized or ignored in classification or metric syntheses.

Any compilation based on a large number of genera, with constraints over time and space for publication, has to conform to certain limitations. In the case of the Treatise publications, and especially the Brachiopod series, the focus had to be the type species, and, deplorably for some groups, “had” to be on the original publication only. No account was possible of taking into consideration the variation shown in different populations of a species, or the variation between different species of the one genus. Even revisions of a type species were not considered. But this was not true of the section on Spiriferida. Members of the team who worked on Spiriferida were unchallegeable experts, and allowed for the variability of genera and species, as much as possible within the permitted limits. The one concern would lie in the lack of anyone who had specialized in Permian faunas, and anyone familiar with southerly as opposed to northerly or paleotropical faunas. I am thinking of someone like the late Neil Archbold, who would have made a valuable addition to the team, or at least could have been consulted over Permian genera. Many of the brachiopod studies mistakenly misrepresented the Permian Period as if had been divided into two, not three. So it had, until the 1980’s, when I launched the proposal that the Permian should be subdivided into three – see Waterhouse 1983c, starting with the Cisuralian Series (my term) of Russia, followed by

Guadalupian Series of United States, and the latest Permian in China, later consolidated as the Lopingian Series. And this was taken up with much skill and documentation by the Permian Subcommission (Jin 1996; Jin et al. 1997). But the *Revised Brachiopod Treatise* continued blithely as if the Permian had never been reinterpreted. Irrelevant Russian divisions were used in the sections on Productida and Spiriferida, based partly on non-marine standards. In the final volume, when catch-up was at last achieved, one lengthy stage was entirely left out (the Wuchiapingian), and the Wordian Stage of mid-Middle Permian age, thought to be Upper Permian in a lengthy article by Curry & Brunton (2007).

And there are further problems. Middle Paleozoic experts on Spiriferida, working on a abundance of diverse material, had stayed with an outmoded nomenclature, with less attention to certain details – a slightly coarser and more conservative approach as a rule, compared with some studies on Permian genera, so that is a disconnect between the two, imperfectly spanned by students on Carboniferous Spiriferida. Over recent times, few brachiodologists have worked on both Permian and Devonian faunas. Yet as I understand Brachiopoda and indeed invertebrate fossils, classification needs in the long run to work from the top down – that is from the youngest down to the oldest, rather than the other way. This is well exemplified by Spiriferida. Looking at Silurian Spiriferida, it is hard to tell what direction evolution will take, which family groups will perish, and which will survive and diversify, and perhaps even give rise to a whole superfamily or infrasuborder. By Permian time, these differences and alliances have become much clearer, and we can see which morphological differences have been consolidated, and which have been amorphosed or lost.

Ideally, each of the major superfamilies should be traceable back through the past to their beginnings or near beginnings, subject to imperfections in the geological record, and inadequacies in the geological and paleontological studies. So to what extent has it been possible to trace established and definitely discrete Permian groups back into the past? One view of the overall history of spiriferid evolution has been summarized in two diagrams by Carter & Gourvennec (2006a, Fig. 1102, 1104). They recognized eleven superfamilies, in two suborders. In their scheme, Martinioidea and Ambocoelioidea were recognized as a somewhat associated group derived from Cyrtioidea. This is modified by removing Ambocoelioidea, recognizing further superfamilies Elythynoidea Fredericks, Ingelarelloidea Campbell and Gerkispiroidea Carter, and associating the superfamilies in a separate Suborder Martiniidina Waterhouse. A question arises about Brachythyridoidea Fredericks, a small group with interior like that of Martinioidea: should this be also placed in Martiniidina? In this study it is concluded that the mantle canal system as well as internal plates, and indeed overall shape point to a close relationship with Martiniidae, and the superfamily Brachythyridoidea is abandoned. (See p. 99).

A separate cluster of superfamilies stemmed from Adolfioidea, possibly through the adolfioid subfamily Callispiriferinae, which evolved into Cyrtospiriferoidea and further diversified into Paeckelmannelloidea, Spiriferoidea, Trigonotretoidea and Spiriferelloidea. This is at odds with an origin from Theodossioidea proposed in the *Revised Brachiopod Treatise*,

but *Theodossia* seems to have been misrepresented in the *Revised Brachiopod Treatise*, judged from revision of the type species. Instead the theodossioids are shown to be linked to Choristitoidea, in a small but long-lived infrasuborder Choristitimorphi.

For Delthyridina, the *Revised Brachiopod Treatise* is substantially modified, one group enlarged by incorporation of all genera with ventral median septum, and further subdivided by additional family groups, with recognition of crucial differences conveyed by the differing natures of the delthyrial apparatus. Ambocoelioidea is regarded as an ally. Does that mean that the study of Spiriferida is complete? Far from it. Carter & Gourvennec (2006a, p. 1692) allowed that "Our knowledge of the evolution of Spiriferida is highly incomplete. For this reason the classification used in this edition of the *Treatise* must be viewed as a temporary progress report….." That remains true. There are some outstanding issues. Were I in were in command of a longer life with good health and ample funds, it is those early Spiriferida that I would choose to reexamine, to explore the number of inadequately circumscribed genera, recheck the ornament in detail, and retest the variability supposedly displayed by internal plates. That is not to downplay the huge contributions from J. G. Johnston, Hou Hong-fei or R. Gourvennec, who in their overviews in the *Revised Brachiopod Treatise* made it clear that early Spiriferida were very different in the constancy and variability of their morphological characteristics from Late Paleozoic Spiriferida.

Classification and taxonomy

The focus of this study is the evolution and development of Spiriferida, best expressed through classification (certainly not through cladistics – p. 22), and centering on family groups, with the nominate group appearing first and followed by other groups in order of age of appearance. Details of genera are covered comprehensively in the *Revised Brachiopod Treatise*, with its provision of illustrations and text, and should be used as a supplement, though a number of descriptions and illustrations are expanded in the present text, because, whatever the broad picture, sight should never be lost of individuals and species.

Studies on Spiriferida are covered up to 2007, with several important additions. Illustrations are provided, and those not attributed have been prepared by me. A word of caution. In the following synopsis, most synonymies of Silurian and Devonian brachiopod genera have been accepted from the *Revised Brachiopod Treatise*. But in a parallel study of Productida discussed in the *Revised Brachiopod Treatise*, it was found, after a great deal of work, that many synonymies had to be revised (Waterhouse 2013). It was not possible to match that degree of thoroughness in this overview, and no doubt students of the brachiopods will wish to test for themselves whether the synonymies are valid are not.

Whereas the *Revised Brachiopod Treatise* in its major subdivision of Spiriferida recognized two suborders, this study recognizes three suborders, and recognizes infrasuborders, as a way of associating superfamilies in a closer bonding, according to interrelationships, so that the superfamilies are packaged in smaller and realistic entities, and families also become clustered – the Treatise arrangement of 38 families can be confusingly unstructured, especially as eight families were grouped under Martinioidea, and five under

Spiriferoidea. Another step is the splitting of families and subfamilies into tribes, a move promulgated successfully by S. S. Lazarev in the Treatise volume 3 on Productida (Productidina and Strophalosiidina). In classification it is desirable to avoid a clutter of families, and the *Revised Brachiopod Treatise* is by no means the only source of family clutter, especially when recognition of subfamilies and tribes would have been more meaningful. Some families and subfamilies in the Treatise study on Spiriferida contain only two genera, or even one. This may be justified in some instances, but in others, tribal recognition should suffice. The result of introducing these two additional ranks is to arrange the classification in a much more structured way that clarifies the paths of relationships and evolution of the order.

An enduring difficulty, to some extent addressed by cladistics, lies in the dual affinities of some family groups. Viewed from a restricted time-span, a family group may be close enough to contemporaries to be classed in the same family or superfamily. But over time, differences became magnified and consolidated, so that the family group can be reassessed as a stem group of a much larger group that differs substantially. In the Productida, Lazarev in Brunton et al. (2000) sought to include the embryonic members of at least some family and superfamily groups (ie. Productoidea and Linoproductoidea), and this was extended to all component groups of Order Productida by Waterhouse (2013). Under a different mode of interpretation, students of Spiriferida in the *Treatise* circumscribed groups horizontally, and included early members of any clade with their contemporaries, rather than their descendents. This is clear from the summary diagram purporting to show the evolution of Spiriferida in Carter & Gourvenec (2006a, Fig. 1104). There is one exception to this observation, because Carter in Carter & Gourvennec (2006a) included Tenellodermidae as source stock within Martinioidea, rather than placing it in Cyrtioidea.

In addition, there were changes to morphology which seemed to have involved different family groups simultaneously, such as changes in the nature of the delthyrial apparatus. Why was this? Something like a shadow evolution, responding to broad environmental and mechanical influences pervaded what seem to have been unrelated groups, affecting details of internal plates, delthyrial apparatus, and micro-ornament, acting in concert, yet at a different tempo from what appear to have been first order genetic changes. Response to certain widespread mechanical needs, such as the advantages of developing a denticulate hinge, or a ctenophoridium modified from a simple cardinal process affected different lineages, more or less simultaneously, and without the implication of common ancestry. The development of a connector plate or stegidia may not have reflected an immediate shared genetic inheritance, though the potential for that change may have built in, and whether it was epigenetic requires further clarification. But however the classification according to morphological and successional analyses is arranged, the groups independently shared subsequent morphological change – often at slightly different tempos. Furthermore it is clear that although some morphological features were permanently lost, others could be temporarily lost, and then regained through reiteroplasy.

In summary, long-lasting superfamilies persisted on the whole through much of the Devonian and all or most of the Carboniferous and Permian Periods, and these arose from closely related stock, and developed in parallel or with subtle differences through time. Many of the changes in morphologies developed, disappeared and developed again reiteratively, involving micro-ornament, plication, costation, delthyrial cover, and cardinal process or ctenophoridium. By and large, tabellae tended to be either retained or lost and not restored within Martiniidina, and permanently lost from Spiriferoidea, but crural plates changed in size and prominence, and appear able to have formed a cruralium or septalium in descendents. Dental plates also changed, rarely forming a spondylium, and adminicula could disappear, temporarily, or permanently. A median septum developed in ventral valves of extremely few genera. Delthyridina were more flexible, and the internal plates arguably less consistent, yet even in that suborder, a ventral median septum may have been restricted to one lineage, which mimicked other lineages in showing high variability in other features.

MORPHOLOGICAL DISTINCTIONS FOR RECOGNITION OF SPIRIFERID FAMILY GROUPS

The most important aspects of morphology in Spiriferida for classification involve the obvious: shape and "build" of the complete shell, as urged to me by the great expert on Brachiopoda, G. A. Cooper. There might seem to be a certain circularity in such an argument, but after all the same applies widely to all animals. Shape and build in turn involve lesser distinctions of umbonal angle and prominence, the width of the hinge, the height and curvature of the interarea, the presence, depth and height and angle of the sulcus and fold, and presence or absence of plication and costation. At lesser ranking comes the nature of the micro-ornament. Ma & Day (2007) and Schemm-Gregory (2011a) have established the value of differences in micro-ornament that apply at least at generic level, and differences that may extend to family groups. In addition, age must be of importance, although it is unwise to discount the possibility of long-lived persistence, in addition to setting aside the so-called Lazarus effect, which at least on occasions can be more of a criticism about the failures in field-work and systematic study than any reflection on the amazing properties of fossils to disappear for a while, and then mysteriously resurrect themselves. Various other attributes are summarized in the following text: they vary in importance and vary between different family groups, but should never be ignored.

Internally, plates have been in the past neglected to a degree, because they are normally less accessible, and because transverse sections are not always simple to interpret (Alvarez & Brunton 2008). Every effort has been made in this study to achieve a consistent nomenclature, missing from parts of the *Revised Brachiopod Treatise*, especially on Silurian and Devonian segments, so that fossils may be more accurately diagnosed and compared. For the ventral valve, teeth, median septum, dental plates and adminicula are all significant, and relatively consistent between family groups, even beyond superfamily level. Dorsal plates have been inconsistently named and interpreted, and hopefully are clarified.

MORPHOLOGICAL TERMS

EXTERNAL ORNAMENT

barchan spine: a small low spine formed by a ramp that increases anteriorly in height, to stop abruptly at the posterior end of a groove or globon (qv). The anterior face is extended laterally forward each side of the globon or surface groove as a low ridge, so that overall the spine is shaped like a barchan, which is an isolated mound of sand that forms a dune of crescentic form, and the horns of the crescent extend forward in advance of the main body (Cotton 1945, p. 269). See Fig. 72B, p. 75.

capillae: used for fine radial threads, similar to fila or lirae.

commargon: a commarginal band with surface concave, flat or gently convex, bordered in front and behind by a growth line, lamellum or growth step. A number of commargons lie over the shell. The term is based on the descriptor commarginal, which is to be preferred as a replacement for “concentric”, applied to growth lines that are parallel to the lateral and anterior margins of the shell, rather than strictly concentric.

costae: There has long been difficulty in conveying exactitude about the nature of radial ribbing, and measurements – so many in 10mm – have not satisfied all workers, who prefer terms that convey mode of origin. The attempt to redefine costa and costella in the *Revised Brachiopod Treatise* (Williams, Brunton & MacKinnon 1997, p. 427) seems logical, but becomes frustrated by the lack of very good preservation over the umbonal region that conceals the mode of costation, and also for some groups in which ribs appear in complex and mutiple successions. The method of counting density is at least objective.

globon: a globon is a small and deep pit on the external shell surface, as a rule weakly elongate, generally deepest posteriorly and shallowing anteriorly, but variable (Waterhouse 1998), representing an extreme form of exopunctation. (See Fig. 89, p. 85).

rib: a useful term for radial ornament that may be as fine as capillae or as coarse as plicae. Schemm-Gregory (2011a) noted how this avoided the controversy and impracticalities caused by Williams, Brunton & MacKinnon (1997) over their newly proposed distinctions and attempted application of terms such as costae and costellae.

tubercle, spinule, micro-spine: significant micro-ornament, may be shown to occur in patterns of specific or generic importance.

DELTHYRIUM

The delthyrium and adjoining and closing structures are important for distinguishing between different genera and family groups, but it is essential to follow a scheme of consistent nomenclature. Anything else will destroy the very bases for comparison and distinction. For that reason, some of the nomenclature in *Revised Brachiopod Treatise* with regards to Spiriferida must be deplored, for the text not only mis-used terms, but ignored definitions set out in the first part of the *Revised Brachiopod Treatise*, by Williams, Brunton & MacKinnon (1997). Perhaps the worst example is offered by the use of pseudodeltidium, a term that should have no role in the description of Spiriferida, because a pseudodeltidium was formed

in a particular way, never achieved by Spiriferida, yet the authors in the section of Spiriferida continually mis-used the term, and it has to be added, in that regard their misuse has been perpetrated by other authors in paleontological studies.

connector plate: a plate that lies under the delthyrium of the ventral valve, and connects the dental plates where they join the adminicula. This term connector plate is used in place of what some studies have termed subdelthyrial plate, and treated as secondary callus in other articles, in each case undefined. This receives further attention on p. 12. The connector plate is especially typical of Spiriferidina, such as Cyrtospiriferoidea, Spiriferoidea, Paeckelmannelloidea and Spiriferelloidea.

delthyrial cover plate: this plate covers the delthyrium, usually as an arched plate, that may be marked by growth-lines, or divided down the middle where deltidial plates have joined. The plate has often been miscalled a pseudodeltidium. The delthyrial cover plate includes forms of different origins. It may have formed by the fusion of two deltidial plates, and if this is deemed likely, it should be called a deltidium (Williams, Brunton & MacKinnon 1997). It may consist in part of secondary tissue that has covered deltidial plates, or stegidial plates. It may consist of a single stegidial plate.

deltidial plates: these arise each side of the delthyrium. They may remain separate, or may develop a median arch or channel where fusing along the mid-line, or leave a line of junction, which may be covered by secondary tissue.

deltidium: a deltidium is formed from the fusion of deltidial plates to cover part or all of the delthyrium.

forked pedicle callist: pleromal ridges may converge posteriorly to unite under the beak at apex of the delthyrium.

pleromal ridge, pleromal tissue: a deposit of shell that partly closes each side of a delthyrium, lying along the inner side of dental plates or the junction of dental plates with adminicula, and may continue forward towards the hinge (Campbell, 1959). It is preferred to regard the pleromal deposit as a thickening or extension, rather than a plate in most cases. In various genera, pleromal thickening passes towards the beak into a connector plate or plug.

plug: in Trigonotretoidea, and some other shells, a massive thickening under the ventral beak may lie above an umbonal cavity, and may pass forward into pleromal tissue. The plug is much thickener than a connector plate.

pseudodeltidium: this plate developed as part of the initial shell, and is solidly attached to the interareas, notably in Productida or Strophomenida. There is no pseudodeltidium in any member of Spiriferida.

stegidium, stegidia: loosely attached platelets that cover the delthyrium, which in some forms amalgamate into one plate, or may be covered by secondary tissue. Stegidia may be pierced by a foramen. They may develop in conjunction with a delthyrial cover plate or with a deltidium. A stegidium may potentially cover the delthyrium without sign of a foramen, or median line of fusion in various genera.

subdelthyrial plate: a somewhat vague term that often is the same as a connector plate, but

provides or stipulates no information about the relationship to dental plates or adminicula.

umbonal callosity: developed under the ventral beak, as in Trigonotretoidea, but also at the umbonal end of a connector plate, as in Gypospiriferinae.

INTERNAL PLATES:

adminicula: plates which support the dental plates, extending to the floor of the ventral valve. Often miscalled dental plates, and in the *Revised Brachiopod Treatise*, inconsistently confused with dental plates.

crural plates: plates which diverge forward from the apex of the dorsal valve, often in front of the ctenophoridium, and which rarely touch the floor of the valve, except at their posterior end. They pass ventrally into inner socket plates, which border the inner side of the dental sockets. Crural plates give rise to the crura at the start of the spiralia, and may or may not be supported by tabellae, the preferred name for what the *Revised Brachiopod Treatise* calls dorsal adminicula in parts of the text. But elsewhere, the crural plates as termed by a number of authors are really tabellae or so-called dorsal adminicula. There is confusion in several sections of the *Revised Brachiopod Treatise*, as outlined by García-Alcade (2005), with further discussion on pp. 15, 16.

crural ridge: the crus at the start of the spire passes back into a ridge or swelling discernible between the crural plate and the tabella, or along the dorsal side of the crural plate, commencing at or near the ctenophoridium.

cruralium: a spoon-shaped structure in the dorsal valve, bearing scars of adductor muscles, and formed by crural plates, according to Williams & Brunton (1997, p. 428), and much more widespread amongst Spiriferida than they indicated. Preservation is often such that muscle imprints cannot be observed, and often, amongst Silurian and Devonian Spiriferida, muscle scars lie in front on the floor of the valve. So the matter of muscle scars was set aside by authors of the systematic sections in the *Revised Brachiopod Treatise*, and their lead is followed herein. For the purposes of this study, the cruralium is made up of crural plates, which rest on the floor of the valve, with the crura arising from virtually the floor of the valve. Or the cruralium may bear the base of the crura above the floor, and the plates between the bases and the socket plates are the crural plates, and form the cruralium. In other examples, the term cruralium has been applied to a structure formed by both crural plates and tabellae, resting on the floor of the valve. Each set of plates may be divided by a low ridge, the crural base, shown as a ridge. This structure is not quite the same as a structure formed only by crural plates, and it is suggested that the structure made up of tabellae plus crural plates be called a tabellarium. (See Fig. 11, p. 18).

ctenophoridium: the seat of the attachment for diductor scars may be a simple or bifid cardinal process, or a more elaborate structure dominated by parallel laminae. The two extremes differ from each other, but many examples are known of intermediate structure, with a cardinal process bearing a few laminae, and this is often called a ctenophoridium in the *Revised Brachiopod Treatise*, a reasonable compromise, often qualified by being termed

rudimentary.

dental plates: plates which support the teeth and dental tracks. Often confused with adminicula, but dental plates do not reach the floor of the valve. For many genera, they have been ignored or thought to have been absent in the Spiriferida section of the *Revised Brachiopod Treatise*. But contrary to the *Revised Brachiopod Treatise*, dental plates are widely present, and may be low or high. And they are genuinely missing from some genera, in which teeth and dental tracks, if present, bear no supporting plate.

hinge plates: often applied to crural plates and tabellae in dorsal valves, but as these plates lie well in front of the hinge, the usefulness of the term seems limited, unless there is enquiry into the various modes of adaptation and change, rather than description and function. The appeal lies principally in tracing the source and development of the plates, no matter what their function and position in the shell. The outer hinge plates represent modification of the crural plates, and the inner hinge plates represent modifications of tabellae. Application of the terms inner and outer hinge plates and used out of deference to the *Revised Brachiopod Treatise* in examples where crural plates and tabellae can be discriminated is too generalized to be informative.

mesopunctae: hollow pores in the middle of the shell in Notospiriferidae. (Fig. 92E, p. 86).

myosepta: a pair of low septa in the posterior of the ventral valve, dividing adductor from diductor impressions, and applicable also to ridges bordering the adductor scars of the dorsal valve. Found in *Cyrella* Archbold (Waterhouse & Chen 2007, p. 57), and possibly in a few Spiriferida.

pleromal thickening: thickening of shell along the inner side of the dorsal edge of the dental plate and possibly ventral edge of the adminicula.

septalium: a term defined as a trough-like structure in the dorsal valve between crural bases, fused medianly and usually supported by median septum, but may be unsupported or sessile, and, according to the definition in the *Revised Brachiopod Treatise*, does not carry adductor scars. But the definition by Williams, Brunton & MacKinnon (1997, p. 437) has not been adhered to in the Treatise section on mid-Paleozoic Spiriferida. As far as Spiriferida are concerned, it seems more practical to restrict the term to a trough-like structure supported by a median septum. The septum supporting the cruralium may have formed from mergence of the tabellae. The Treatise definition really calls for additional terminology to cover various structures with and without septal support, and with or without muscle scars.

sessalium: a sessile cruralium.

tabellae: (plural) named for the plates supporting crural plates in the dorsal valve. Also may be called inner hinge plates, again a term used inconsistently in the *Revised Brachiopod Treatise.* Worse, the tabellae may be called crural plates, which they are not, or they may be called, more clumsily but with better accuracy, dorsal adminicula. The tabellae are clearly not the same as adminicula in the ventral valve, and it is preferred to apply shorter terms to each set of plates.

tabellarium: a cruralium-like structure in the dorsal valve formed by tabellae resting on the

floor of the valve, supporting crural plates, from which they are separated by crural bases (See Fig. 11, p. 18).

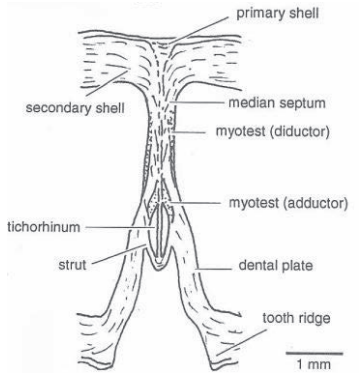


Fig. 1. The tichorhinum in *Cyrtina hibernica* Brunton from the Lower Carboniferous of Ireland. (From Williams, Brunton & MacKinnon 1997).

tichorhinum: defined by Williams & Brunton (1997, p. 439) as a small suboval chamber with or without a median partition, which is formed by struts arising from the dental plates that converge on to a median septum, and possibly accommodated the site of adductor muscles, as illustrated in Fig. 1.

tigillum: heavy rod of thickening along base on sulcus in some ingelarellid genera.

SOME IMPORTANT ASPECTS OF MORPHOLOGY

MICRO-ORNAMENT

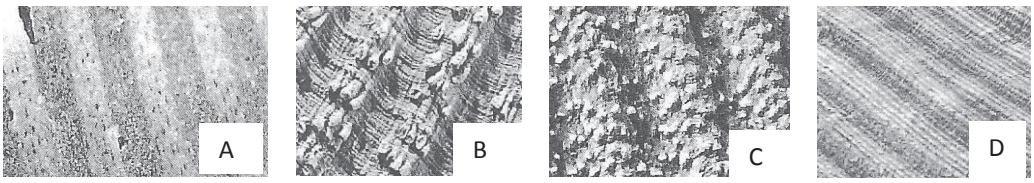


Fig. 2. Micro-ornament x 10. A-C, Cyrtospiriferoidea. A, *Cyrtospirifer*. B, *Lamarckispirifer*. C, *Pseudocyrtiopis*. D, Theodossioidea. *Cyrtiopsis*. (Ma & Day 2007).

Micro-ornament has always been important for helping to classify Spiriferida, featuring especially in the recognition of Delthyridina, and recent studies by Oleneva (2006), Ma & Day (2007) and Schemm-Gregory (2011a) have affirmed the importance of detailed comparisons, to help delineate and circumscribe genera. Ma & Day were able to retrieve several cyrtospiriferoid genera cast into synonymy by the *Revised Brachiopod Treatise,* and Schemm-Gregory (2011a), following years of detailed study on Delthyroidea, indicated that the Treatise classification was deeply flawed, and would have be greatly expanded, and to some extent altered, from her studies on micro-ornament. These workers showed that micro-ornament may be of substantial relevance to the discrimination of genera. What may be unclear, to some extent, is the amount of variation that is to be permitted within families, subfamilies and tribes. At present, variation is deemed acceptable for a number of family-group units amongst the mid-Paleozoic Spiriferida, especially Delthyridina.

As a counter, Ingelarellidae from the Tiverton Formation of Sakmarian age in north-central Queensland, Australia, provides an instructive insight. Here individuals of two species, each of a different genus, developed peculiar c-shaped small barchan spinules (Fig. 72, p. 75) behind the elongate grooves that normally characterize the micro-ornament (see Fig. 79, p. 78). Waterhouse (1998a) named one as type species of a new genus. But it was found that the majority of specimens in each species did not display the spines, as if the spines were merely an exception, not normal to the species, and too scarce to warrant taxonomic recognition: the spines appear to have been a variation, perhaps an ecovariant or still-born genetic change, of infrasubspecific value (Waterhouse 2015a).

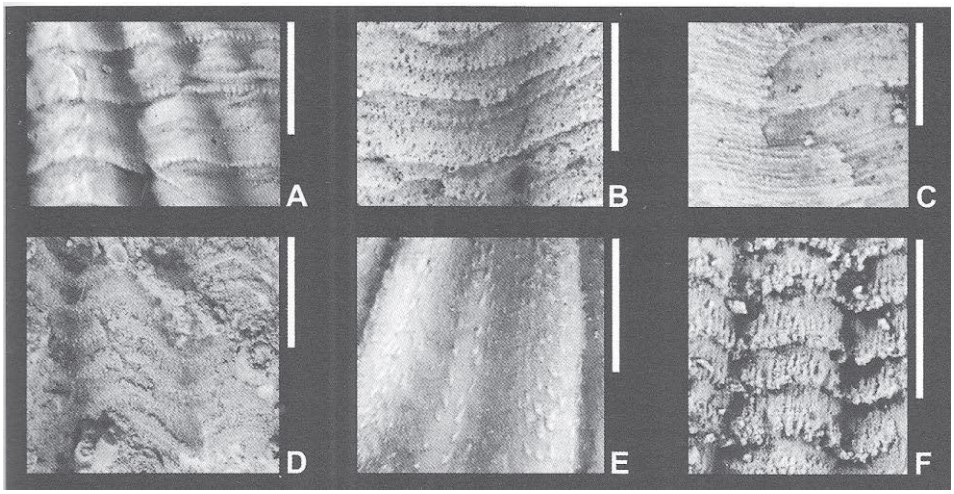


Fig. 3. Micro-ornament in genera from Asia, reproduced from Schemm-Gregory (2011a). A, *Rostrospirifer tonkinenseis* (Mansuy). B, *Frequentispirifer frequens* (Bublitschenko). C, *Intermedites intermedius* (Schlotheim). D, *Otospirifer shipaiensis* (Hou & Xian). E, *Orientospirifer wangi* (Hou). F, *Eospiriferina lachrymosa* Grabau. A-D, fimbriate, E-F, lacrimate. The scale bar is 2mm long.

DELTHYRIAL COVERS, INCLUDING DELTHYRIAL PLATE AND STEGIDIA

The *Revised Brachiopod Treatise* provides definitions for several kinds of delthyrial cover. Discrimination is important, because the kind of delthyrial cover is believed to typify different genera and even family groups. A **delthyrial plate** is defined as a plate within the delthyrial chamber of some spiriferides, and was regarded as a probable homologue of pedicle collar by Williams, Brunton & MacKinnon (1997, p. 428). This definition is set aside, as far as Spiriferida are concerned. It is possible, and indeed necessary to be much more specific on the location of the “delthyrial plate”, and use a less ambiguous term. In many Spiriferida, the plate arises from the junction between the adminicula and dental plates, and connects these four plates. That is not conveyed by the looseness of the term delthyrial plate, and it is suggested that the plate in question be called a **connector plate**. This connector plate has been confused with a delthyrial cover in some accounts, and in other studies is described, more judiciously, as a subdelthyrial plate. The connector plate may pass hingewards (ie. toothwards) into pleromal thickening along the inner edge of the dental plates – pleromal

plates having been proposed by Campbell (1959). The connector plate may adjoin or bear, under the umbo, an umbonal callosity. If the plate joins only the dental plates, this also should be specified in the description. In many genera, secondary thickening fills the space between the plate and floor of the valve with increased age, and secondary thickening comes to bury the adminicula, at least posteriorly. In other Spiriferida, especially Martiniiformi, the pleromal tissue passes apically into an umbonal callosity, without forming a visible connector plate. Available evidence suggests there was never a connector plate, based on study of immature specimens. The same seems to be true of many Trigonotretoidea, in which the dental and adminicular plates of even small specimens with no secondary thickening show no sign of a connector plate.

A **deltidium** is defined as a cover formed by conjunct deltidial plates, with the line of junction visible. This definition should be retained as in the *Revised Brachiopod Treatise*, strictly defined, because it is clear and relevant, although it should be noted that the junction is often masked. For many shells, best exemplified amongst Delthyridina, a convex cover plate lies over the delthyrium. There is no median line of junction. Yet smaller or less mature specimens have deltidal plates or ridges, along the sides of the delthyrium, and these would appear to have joined at maturity to form the cover plate, despite the absence of a visible join. For *Cyrtia*, Boucot (1963) showed that the deltidial plates became covered by secondary shell, to mask any junction between the deltidia, and this may have occurred widely.

A **pseudodeltidium** is defined as a single convex or flat plate covering part or all of the delthyrium (Williams, Brunton & MacKinnon 1997, p. 436), and is well developed in Strophomenida, Chonetida, Productida and Orthotetida. The pseudodeltidium is an arched or flat part of the ventral valve that covers the subapical or all of the median part of the interarea. It is firmly welded to the shell as part of the interarea. But in Spiriferida the plate that covers the delthyrium is not an integral part of the interarea: it may be loose-fitting, and as firm as it may seem in many specimens, is often lost during thanatocoenosis. It usually tucks into the angle left by the dental tracks and interarea. In at least some Spiriferida, the plate may have articulated according to the movement along the pedicle. For this plate, a different term is required, and in this study, the plate is called a **delthyrial cover plate**. This term is not pre-empted in the summary by Williams, Brunton & MacKinnon (1997), which does use **delthyrial plate**, **deltidial cover** and **deltidial plate** and **deltidium** in specific ways, not applicable to all Spiriferida. The difficulty with delineating a delthyrial cover plate as distinct from a convex deltidium arises when neither shows a median join. Then distinction should be revealed by growth stages, to show if deltidial plates later fused across the middle. For Neospiriferidae, the plate is termed a delthyrial cover plate. Because Neospiriferidae never show evidence of having deltidial plates, the cover may have formed from a full deltidium from inception, or from a single stegidial plate.

Amongst Spiriferida, deltidial plates are developed widely in Cyrtioidea, with no such plates in Adolfioidea. Both deltidial plates and connector plate appear in different strands of Theodossioidea and Choristitoidea, and to a minor degree in Martiniidina, whereas most

Spiriferidina display a connector plate, and vary in the presence of deltidia. Delthyridina vary: deltidia are widespread, and it appears likely that a connector plate and pleromal ridges developed in separate and unrelated lineages of Reticularioidea and Elitoidea.

A **stegidium (**plural **stegidia)** is defined as “a convex plate or series of imbricate commarginal plates enclosing the gap between the delthyrial plate and spiriferide dorsal valve…. and with atrophying pedicle migrating dorsally” (Williams, Brunton & MacKinnon 1997, p. 438). That is an imperfect and even misleading definition, because stegidia often develop in Spiriferida where there is no delthyrial plate, or may be separated from the dorsal valve by a delthyrial plate (see Fig. 5, p. 15). And there may be no sign of a peduncle. Stegidia were discussed by Cowen (1968, 1969). The focus of the term is on the nature of the plate, being built up of commarginal bands. There may or may not be what is here defined as a delthyrial cover plate or a connector plate as well. Preservation depended on favorable conditions because stegidia were very fragile (Cooper 1954). Sartenaer (1955) wrote of the

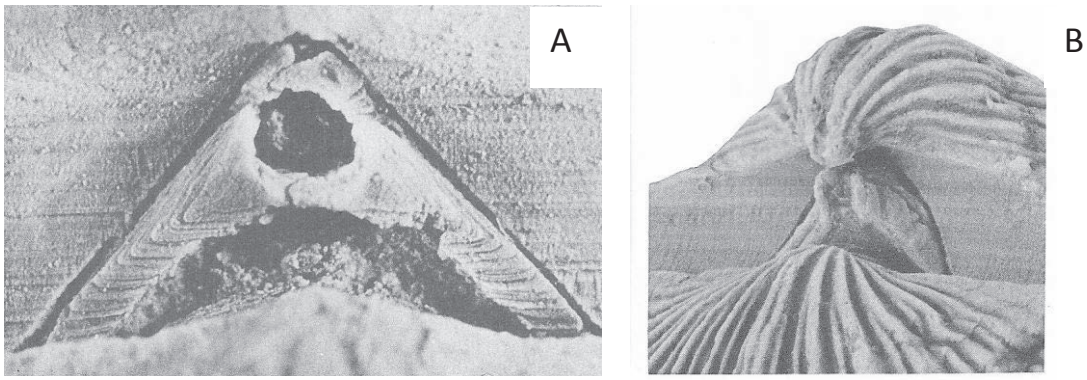


Fig. 4. Growth laminae and peduncular hole. A, *Mucrospirifer mucronatus* (Conrad), showing stegidial plates with, x20. (Cowen 1968a). B, *Neospirifer pattersoni* Sutherland & Harlow (now *Tegulospirifer*), x4, from Gzhelian of New Mexico. (Sutherland & Harlow 1967).

stegidium, differing from Cooper (1954), and noting its occurrence (or preservation) was rare, and reporting the structure in *Cyrtiopsis murchisoniana* of Famennian (Upper Devonian) faunas. A well formed stegidial complex is figured by Sutherland & Harlow (1967, pl. 137, fig. 9f, 12) for shells they called *Neospirifer pattersoni*. Grant (1976) illustrated and discussed in detail the stegidial interlocking platelets on the genus *Tipsispirifer*, preferring to reinterpret some assessments by Cowen. Legrand-Blain (1985b) illustrated growth distortions on stegidia and noted that the gap for the peduncle could become blocked off, as for *Gypospirifer*, suggesting that stegidia still functioned as a cover, but not for the peduncle. Poletaev (1984) described for spiriferids a stegidium which showed no sign of any peduncular gap. That does bring out the problem of distinguishing a convex stegidium from a convex deltidium. Poletaev (1997, p. 308) considered that a groove along the dental track on each side of the delthyrium would indicate the former resting place of a stegidium. All agree that the

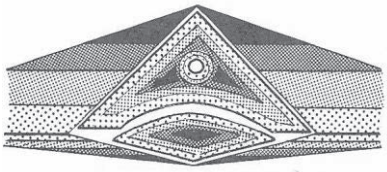


Fig. 5. Ontogenetic sequence in development of stegidial development In *Mucrospirifer mucronatus*, showing stegidial structure overlapping the delthyrial cover plate. (Cowen 1968a).

stegidia were delicate, and that they, as well as the delthyrial cover plate, may be readily lost.

THE INTERNAL PLATES OF SPIRIFERIDA: ADMINICULA AND TABELLAE

In 1953, Brown proposed a new term for plates which supported dental plates within the ventral valve of the Permian spiriferidan genus *Martiniopsis* Waagen. She called the plates **adminicula**, and pointed out that they were not the same as dental plates. Indeed, many genera have dental plates and no adminicula, so that the dental plates are suspended above the floor of the valve. It is the adminicula that extend from the floor of the valve to meet and support the dental plates, as shown by Williams, Brunton & MacKinnon (1997, Fig. 324).

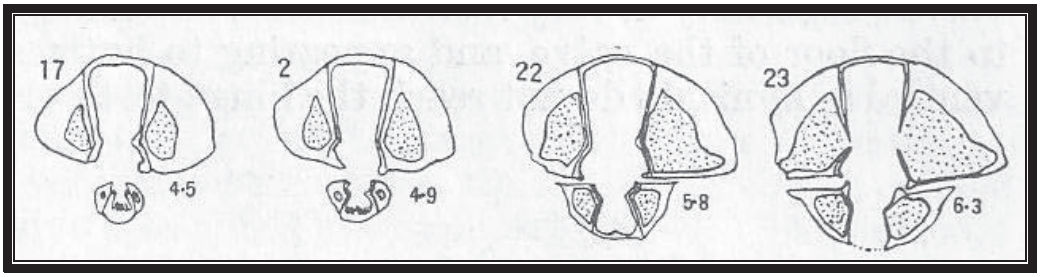


Fig. 6. Transverse serial sections of *Martiniopsis pentagonalis* Waagen, prepared by Ida Brown in the first analysis of internal plates that revealed adminicula as being separate plates supporting the dental plates in the ventral valve. Specimen x1.5, ventral valve on top, distance in mm provided from ventral and dorsal beaks. The specimen was identified by Brown with *M. inflata*, but shape and the source of the specimen indicates *pentagonalis*. From Amb Formation (upper Cisuralian). (Brown 1953).

In the dorsal valve of many genera, there are plates which also extend from the floor of the valve to support crural plates. These plates have been called dorsal adminicula, and Waterhouse (1971a) proposed that they be called **tabellae**, a term endorsed for example by Carter (1974) and Legrand-Blain et al. (1984). Their function differed from that exercised by the adminicula of the ventral valve, in supporting crural plates rather than dental plates. The term is shorter and less clumsy than “dorsal adminicula”, and allows use of adminicula rather than “ventral adminicula” for the supporting plates in the ventral valve. In terms of economy of words, and in being applied to plates with different functions, belonging to different valves, it seems desirable to use tabellae as well as adminicula.

Crural plates extend ventrally from the ridge-like crural bases up from the tabellae to the dental sockets, and may be distinct from the inner side of the sockets, often extending dorsally beyond the socket plates, or merging with the inner side of the sockets. In many

studies of Spiriferida, especially those of Devonian and greater age, the crural plates have been left undescribed.

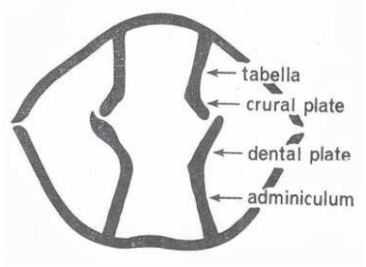


Fig. 7. Diagram illustrating adminicula in Spiriferida, and ignored by too many authorities, who did not distinguish between dental plates and adminicula or between crural plates and tabellae. Dorsal valve on top. (Waterhouse 1971a).

García-Alcade (2005, p. 74), as well as criticizing the Treatise coverage of these plates, outlined a different nomenclatural scheme, with some emphasis on Krans (1965) and other authors rather than Brown (1953). With respect, that scheme is set aside, because it is deemed preferable to outline a three-fold, rather than one or two-fold subdivision of the features involved, and one that may be applied to all Spiriferida.

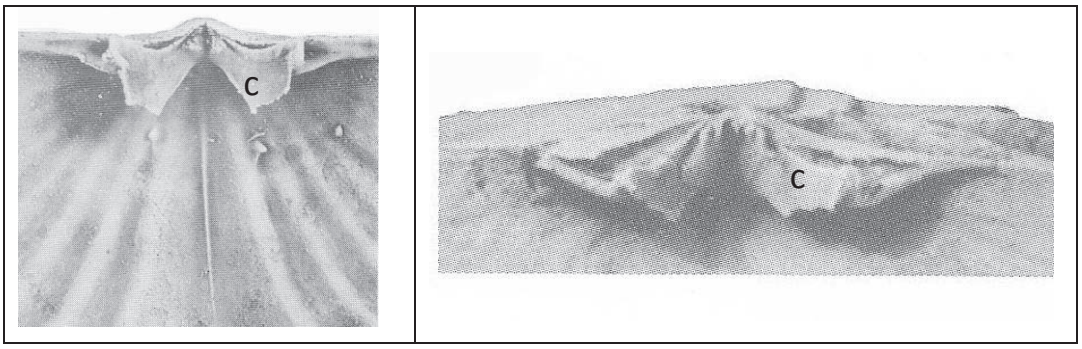
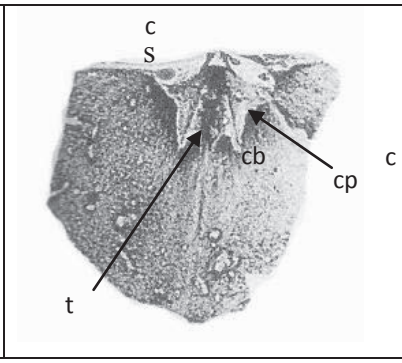


Fig. 8. A, *Spinella passensis ravinia* Flood. dorsal interior with high and well formed crural plates (c). (Strusz et al. 1970). B, *Spirinella caecistriata* Johnson, latex cast of dorsal cardinalia, and well formed crural plates (c), x7. From lower Ludlow of New South Wales. (Strusz 1984).

Fig. 9. *Ladjia saltica* Veevers, dorsal interior showing clear three-fold subdivision of a tabellarium. c – cardinal process; cb – crural base; cp – crural plate; s – dental socket, t – tabella, between the crural base and floor of the valve. (Veevers 1959a, with lettering added).



Williams, Brunton & MacKinnon (1997, Fig. 330.2, p. 370) showed the dorsal cardinalia for *Neospirifer,* in which inner socket plates were recognized, adjoining what was

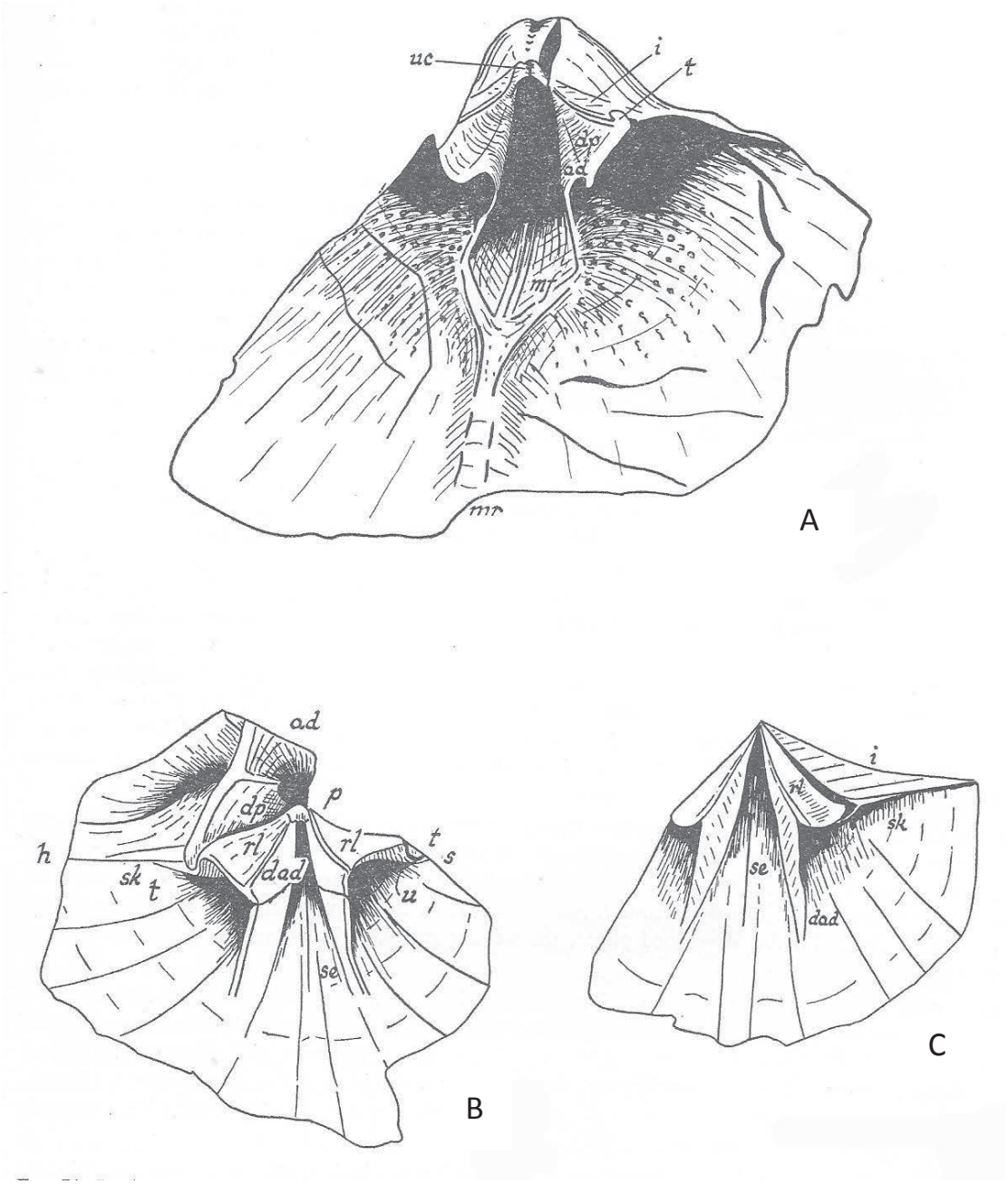


Fig. 10. Sketches of internal plates in *Ingelarella sulcata* Waterhouse, placed in the same subfamily as *Martiniopsis*, for which the term adminicula was first applied A, ventral valve. B, both valves, ventral valve on top, C, dorsal valve. ad – adminicula; dad – tabellae; dp – dental plate; h – hinge; I – interarea; mf – muscle field; mr – median ridge or tigillum lying along the inner side of the sulcus; p – cardinal process; rl – crural plates; s – dental socket; se – dorsal myophragm; sk – socket plate; t – tooth; uc – umbonal callosity. The double line between rl and dad marks the crural base, in the form of a ridge. (Waterhouse 1964).

termed a crural base. It is preferred to call the so-called base a crural plate, because the base of the crura, or crus, is different, forming a ridge as rule that may be seen passing from the spiralia along the edge of the crural plate to the ctenophoridium. Their text (pp. 362-363) is indecisive and gives a mixed message, stating that “dorsal adminicula, which connect crural bases to the dorsal valve floor, as do the better known crural plates,” which may be taken to

imply that crural plates are the same as dorsal adminicula. Their figure (1997, Fig. 324) labelled the crural plate and dorsal adminiculum as one and the same, supporting the so-called crural base, but here is preferred to treat the so-called crural base as the crural plate, supported by the dorsal adminiculum (= tabella) along the line of what is here called the crural base, which forms a perceptible ridge, shown as a swelling in transverse sections. There has been confusion in the *Revised Brachiopod Treatise* over the terms, and in a number of instances, the diagnoses may deny the presence of "dorsal adminicula" and even crural plates, only to be contradicted by the photographs which clearly show the presence of one or both sets of plates. That may imply that the plates are of no significance for classification, but how would one know when the plates are muddled or ignored? Better surely to discriminate them, and analyse the comparative morphologies. A further deplorable aspect of some studies is the reliance on illustrations of internal moulds to depict the species or genus. Internal moulds often do not show the crural or dental plates clearly, and whilst highly informative on tabellae and adminicula and muscle scars and mantle canal systems and gonioglyphes, such moulds need to supplemented by transverse sections, or casts.

Brown's proposal was deemed highly useful, and adminicula was quickly adopted by many paleontologists, especially those working in the southern hemisphere as colleagues of Brown, and those working on Upper Paleozoic faunas. There was more resistance from northern-hemisphere workers, and apparently a complete unawareness on the part of students of mid-Paleozoic brachiopods. This has led to considerable confusion, nowhere greater than in the *Revised Brachiopod Treatise*, in which adminicula are inconsistently termed adminicula and elsewhere dental plates, and the term dental plates may mean dental plates, or may mean adminicula. Similar inconsistencies, ambiguity and confusion is found with regard to crural plates, and the text mentions crural plates when tabellae are clearly present, and sometimes claims no crural plates were present, when they are clearly figured. Nor do the summaries mention crural bases. Examples are mentioned in the following discussion, not to highlight the inconsistencies, but to clarify the actual morphology essential for diagnoses and clarification of the taxa. Even, it has to be said, the diagram purporting to illustrate the morphology of a spiriferid mislabels the internal plates (Carter & Gourvennec 2006a, Fig. 1103), in which adminiculum is called dental plate, the dental plate is left unlabelled, and no crural plate is signified. Internal features cannot be analysed and compared unless there is clear and consistent discrimination.

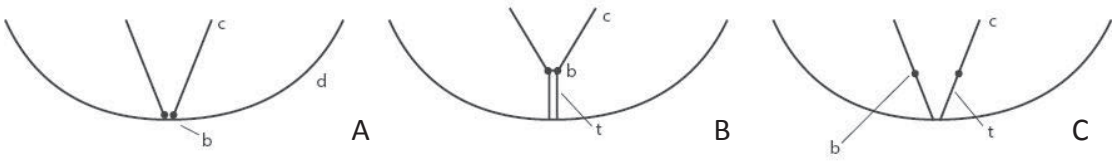


Fig. 11. Diagrams of crural plates and tabellae. A, a cruralium, with crural bases at the floor of the valve. B, a septalium, with crural plates supported by euseptum formed by conjoined tabellae. C, a "tabellarium" formed by diverging tabellae supporting crural plates, separated by crural bases. b – crural base; c – crural plate; d – dorsal valve; t – tabella.

It is partly the analysis of these internal plates, and the significance of their presence or absence, or inconsistent presence, that allows substantial clarification of the evolution and classification of Spiriferida. In this study, it is shown that the crural plates may join medianly, and form a cruralium, and the cruralium may be supported from the floor of the valve by a median septum, to form a septalium. If the septum is a septum duplex, or euseptum (see septal plates in Williams, Brunton & MacKinnon 1997, p. 437), it may represent conjoined tabellae. If the cruralium is sessile, and the crural plates converge towards each other and do not join but rest on the floor of the valve, they allow the possibility of being confused with tabellae, and our limited knowledge of a number of mid-Paleozoic Spiriferida means that a sessile cruralium cannot always be readily distinguished from tabellae. This may be illustrated from serial sections of *Espella* from Kazakhstan, prepared by Nilova (1965), as shown in Fig. 12. The dorsal plates resting on the floor of the valve in the section to the left are crural plates, not tabellae, and further sections to the right reveal that they form a sessalium, which further forward becomes a cruralium, which anteriorly becomes a septalium. Fewer transverse sections could easily convey a misleading description of a complex structure that changed with development.

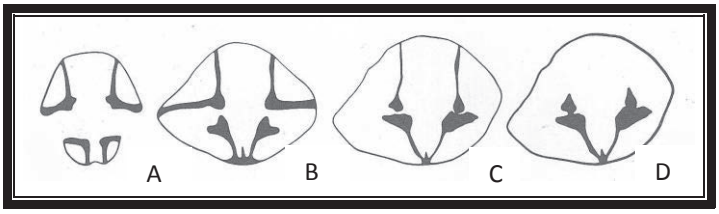


Fig. 12. *Espella kazachstanica* Nilova, from Silurian of Kazakhstan, showing serial transverse sections, progressively distant from the apex from left to right, dorsal valve below. A, are the vertical dorsal plate tabellae? B, no, they converge to the floor and form an imperfect sessalium. C, clarification ensues – the plates form a cruralium, and must be crural plates. D, and now the cruralium rests on a low septum, and forms a septalium. (Nilova 1965).

MANTLE CANAL SYSTEMS

Mantle canal systems are better preserved on the ventral than the dorsal valve, which is less thickened. For martiniids, it was demonstrated that the mantle canal system was dominated by linear channels (Grunt 1977b), and Angiolini (1995) erected a new genus that had developed an openly reticulate pattern. It was found that spiriferids exhibited a field of shallow pits and rises, and choristitids displayed a reticulate pattern (Legrand-Blain 1985a). This pattern was used to assign a subfamily Angiospiriferinae of coarsely ribbed Spiriferida to Choristitidae. Poletaev (1986) has also shown an open slightly distorted reticulate pattern for *Choristites*. The numerous small pits displayed around the anterior muscle field have been interpreted as gonad imprints or gonioglyphes (Vandercammen 1959b), which raises the question of seasonality, and whether such area expanded or contracted during the year. Lazarev & Poletaev (1982, pl. 1, fig. 4) offered a different pattern for *Parachoristites*, but later Vladimir Poletaev advised me that the identification should be changed to *Alphachoristites*

Gatinaud. For *Choristitella*, Legrand-Blain showed a pattern of irregular radial ridges, different again, so that the pattern was found to differ between genera.

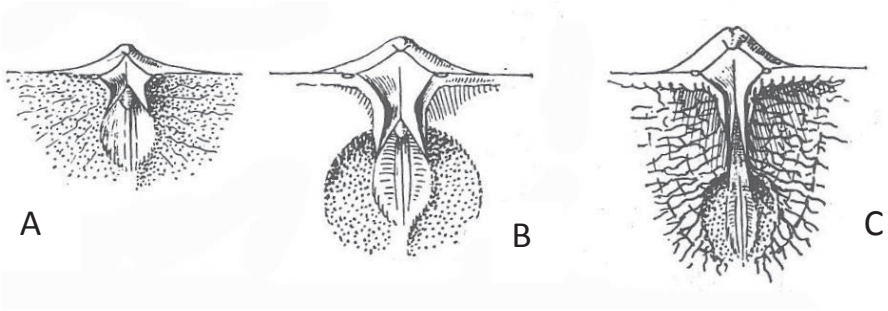


Fig. 13. Ventral interiors of A, *Spirifer,* B, *Parachoristites* and C, *Choristites*, showing dental plates and adminicula behind muscle field, and vascular patterns. (Poletaev 1986).

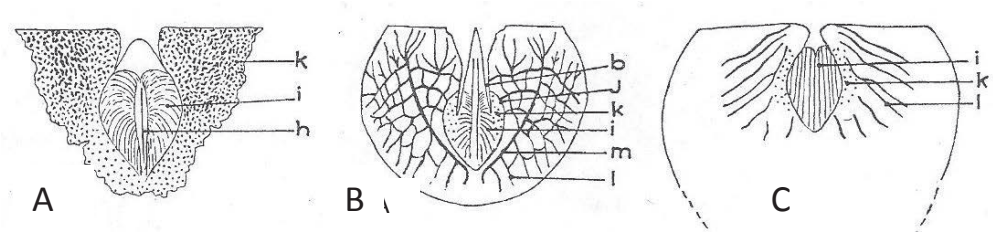


Fig. 14. Internal structures in ventral valves of A, *Spirifer subgrandis* Rotai. B, *Choristites mosquensis* Fischer de Waldheim. C, *Choristitella* sp. b – dental plate; h – adductor; i – muscle scar; j – outer limit of gonoglyphe; k – gonoglyphe; l – angioglyphe (ie. mantle canal system); m – principal canal. (Legrand-Blain 1970).

In Spiriferoidea, such as *Spirifer,* the reticulate pattern is replaced by small closely and evenly spaced pits, but the pattern is not well established for many Spiriferoidea, including *Neospirifer* and *Betaneospirifer*. In addition, there may be slender raised ridges radiating and spreading forward through the pits in Spiriferoidea, as shown in Fig. 13A. This pattern differs from that of Trigonotretoidea or Choristitoidea.

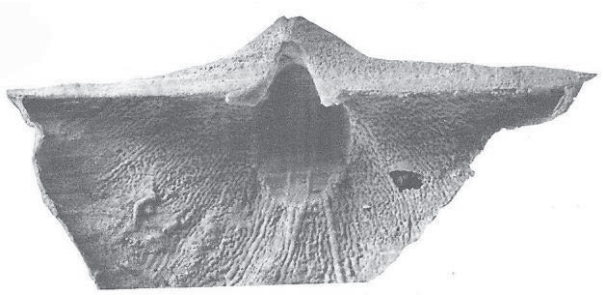


Fig. 15. Mantle canal system in *Spiriferalaria bakeri columbarius* (Cooper & Grant) of Subfamily Spiriferalariinae, Family Spiriferidae. From the Road Canyon Formation (Roadian) of Texas. In addition to the normal dense pattern typical of Spiriferoidea, there are a few radiating linear canals. (Cooper & Grant 1976).

Members of Trigonotretoidea show a pattern somewhat like that of choristitids, and often are dominated by an open, slewed reticulate pattern. A fine example is offered by Fig. 16, which shows the ventral interior, with pits around the anterior muscle field, and extensive subreticulate pattern posteriorly and laterally. This genus, called *Aperispirifer* Waterhouse,

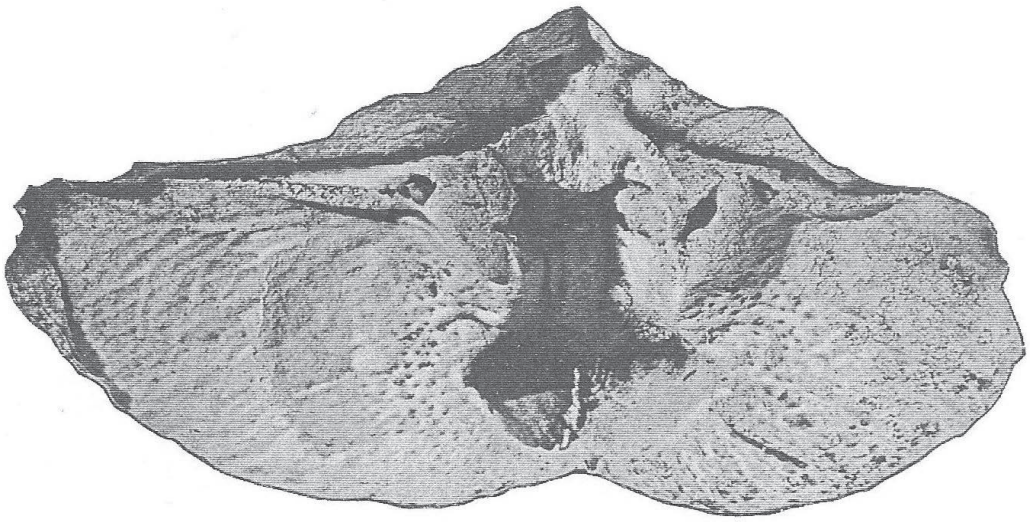


Fig. 16. *Aperispirifer archboldi* Waterhouse, PVC cast of interior, dorsal valve on top. This illustration of a trigonotretid genus shows a distinctively organized mantle canal system complexly branching from a major posterior canal, and anterior possible gonad imprints. Specimen x3. (Waterhouse 1964).

strongly indicates the presence of a posterior main canal, which laterally branches, and branches persist, cross-cutting other branches. *Choristites* has a somewhat similar reticulate pattern, but its main canals lie parallel to the lateral margins of the shell rather than the posterior margin, and branches tend to be directed posteriorly, not laterally (Fig. 14B). The anterior field in *Aperispirifer* displays deep well spaced pits, probably equivalent to gonad or gonioglyph imprints. *Aperispirifer* is of Middle and Late Permian age. An older and probably ancestral genus *Grantonia* Brown shows a smaller posterior network, with less clear main posterior canal. In a still older genus such as *Trigonotreta* Koenig, the posterior network is similar, in a slewed network of canals, directed laterally, and anteriorly there is a somewhat similar pattern of lines or stretched network.

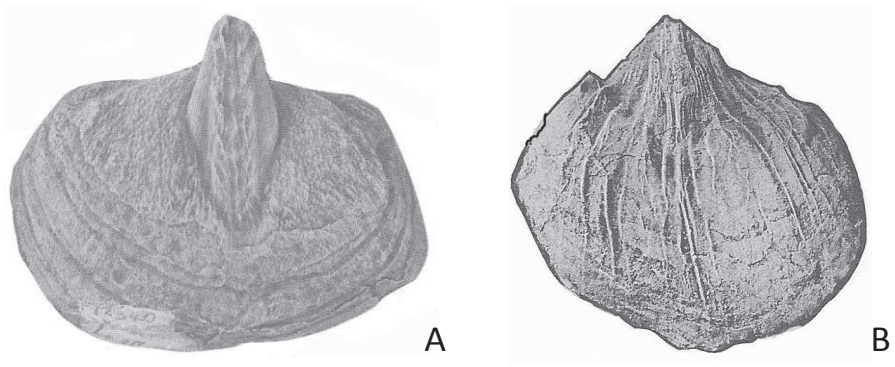


Fig. 17. A, *Johndearia isbelli* (Campbell), internal mould of ventral valve of Ingelarellidae, showing muscle scars surrounded by vascular impressions, directed antero-laterally, x1. From Guadalupian of New South Wales, Australia (McClung 1978). B, long linear canals with a hint of reticulation in the martinioid shell described as *Martinia adentata* Waterhouse, x1.5, from the Artinskian Takitimu Group of New Zealand. The generic position remains unclear. (Waterhouse 1964).

A different pattern is shown by Ingelarelloidea. Fig. 17A presents an overall pattern of shallow broad and well spaced pits near the hinge, and elongate pits anteriorly.

The persistency and constancy of the patterns remain an open question, because for Spiriferida, the mantle canal systems have not been closely studied. In some instances, there is considerable variability, as indicated by some choristitid genera figured above. Whereas the martiniid genus *prolifica* (Waterhouse) from Thailand has a somewhat reticulate pattern, Shi, Leman & Tan (1997) identified specimens of *prolifica* in Malaysia that revealed a simpler radiate pattern (see especially Shi et al. 1997, Fig. 3M).

THE ROLE OF CLADISTICS

Numerous attributes have to be assessed in the classification of Spiriferida. They include, without preparing an exhaustive list, overall shape and size, width of hinge, degree of alation or obtuseness of the cardinal extremities, denticulation or absence of such from the hinge, the nature of the delthyrium, involving presence or absence and size of the teeth, dental bordering rims, the presence and size and profile of a delthyrial cover plate, the presence and size and profile of a deltidium, or separate deltidial plates, and stegidal modes, and foramen, the presence or absence and length of the sulcus, its cross-profile, presence or absence of costae, including median costa, presence or absence of plicae, the presence or absence of a fold, its length and transverse profile, with presence or absence of costae, fascicles and plicae, and the presence or absence of a median channel. The nature of the micro-ornament, with radial capillae, commarginal growth increments or lamellae, the degree of tuberculation, or frilly margins, and presence and distribution of spines, radially aligned, relation to growth increments, their length and density, the degree of fimbriation, the presence or absence of double-barrelled spines, their pattern and any association with single-barrelled spines and/or pustules. Internally, the presence of teeth, the presence or absence and length of dental plates, and of adminicula, and presence or absence, and length and height and position of the median septum, or of a myophragm, and its nature, and presence or absence of a spondylium. Data is also needed for the development of pleromal ridges, position, size and profile of the connector plate, and data on the umbonal callosity or plug. For the dorsal valve, the nature of any notothyrial plate if present, the cardinal process or ctenophoridium, and if it is bilobed or trilobed, the nature and height and elevation of the dental socket plates, the presence and height of the crural plates and crural bases, the absence or presence and height of the tabellae, the absence or presence and length and height of a median dorsal septum or myophragm, and myosepta, and the nature and shape and size and position of the ventral and dorsal adductor impressions and diductor scars in both valves. In addition, the nature of the mantle canal systems, and gonads and other papillation patterns, with marginal ridge if any. As well, the spiralia, including number of coils, their orientation, and presence or absence of an incomplete jugum. Shell structure, including exopunctation, mesopunctation, taleolation, and prismatic structure and secondary thickening provide additional parameters to be calibrated. As well, additional unusual features, and the ontogenetic trajectories of various

morphological structures need to be assessed. These make up more than forty different character states or categories, with subdivisions within them, some of which can be highly variable, with up to ten different discrete states or subdivisions, and more for micro-ornament.

What severely comprises attempts to use cladistics is the all-too-frequent drive to simplify and get rid of information. Of course the number can be legitimately reduced if examination is restricted to one suborder – provided that the suborder has been correctly circumscribed. Programs that use less than some 40 character states are too selective to be of value, and scarcely need to be taken seriously.

Two further major considerations should be assessed. Of these, the prime one is age. Whilst it is understandable that tolerance should be permitted, there are grave considerations against the neglect of age range. To Hennig (1966), in establishing potential valve for cladistics, the need was to explore relationships between living biota. To him, fossil evidence was of negligible value, to my mind a purblind and woefully erroneous assessment, mirroring the one serious blunder by Darwin. A recent cladistic survey declared that *Spiriferella* formed the stem group within Spiriferoidea. Yet *Spiriferella* is much younger than many genera with Spiriferoidea, and it may be a marvel how it therefore defied time to become a stem group for much older genera. Of course, there is an alternative, if unflattering, explanation.

A further and more precarious source of information is provided by association with other genera. In this overview, examples are noted where identification has completely ignored well established distribution studies and major spatially and climatically-controlled assemblages.

Has cladistics been successful amongst Spiriferida in establishing or even supporting classic systematic studies and classifications? So far the answer is no. The problem lies in an egregious process of data-selection, thereby becoming subjective, and substantially reducing the more than forty major categories or character-states, and reducing information to mere presence-absence. To select only some of the categories will severely compromise the analysis, and probably make it worthless. Selecting only some of the genera within a major family group will also compromise the outcome. Cladistics will provide studies of value when all available data is included, and when shortcuts are avoided, whether in the paring down of data to be assessed, the neglect of age, and use of the Treatise to provide the basic information. Original sources must be consulted, and checked.

UNCERTAINTIES

Nomenclature and classification are subject to dilemmas. In taxonomy, the International Subcommission on Zoological Nomenclature 1999, Article 15.1 mandated that the proposal of a specific or generic name must be certain – with no tentativeness is allowed. “A new name or nomenclatural act proposed conditionally and published after 1960 is not thereby made available”. That is understandable. But it raises a problem – what about the merits of scientific caution? Is taxonomy so certain, so confident of perfection, and freedom from possible error, that no reservations can be expressed? Campbell (1965) in proposing the dielasmatoid genus

Hoskingia, wrote that “the distinguishing characters [from *Beecheria*] cannot be stated with complete confidence”, as outlined in Waterhouse 2010a, p. 81. Such caution means that his proposal was conditional, and might therefore be deemed as “not available.” But it could be argued that later workers by recognizing the genus, did ratify Campbell’s name, and make his proposal unconditional. Even someone unscrupulous or ignorant enough to apply his or her own new name with a firm proposal, whilst claiming that Campbell’s proposal was conditional and therefore not available, was thereby recognizing the genus and so ratifying Campbell’s name, which had priority.

For the huge coverage of Spiriferida, as in the *Revised Brachiopod Treatise*, it was impossible to avoid making intelligent choices, according to the best available information, well aware that in some cases, genera had been so poorly circumscribed that it was impossible to assign them with confidence to any given subfamily. Or indeed, that morphological variation was so complex , or poorly understood, that attempts at classification could be no more than provisional – or even experimental, and after all experiments play a major role in science, though not admitted in taxonomy. For the proposal of genera and family groups, a little scientific caution would be appropriate, rather than take the all-too-easy step of conforming with international rules and leave out any whisper of reservation. Nor, unless there is excessive vanity, is it possible to avoid the admission that certainty cannot be justified, given the lack of information on genetics and molecular phylogenetics, the apparent inapplicability of cladistics (at least in a format as unsophisticated as the methology commonly used), and sheer human ignorance and error. There was no place for cautionary remarks in a classification overview such as by the *Revised Brachiopod Treatise*, if only because scientists were well aware of the unwritten presence of such cautions. Even so, Carter & Gourvennec (2006a) did courageously record their reservations, and other writers signalled a degree of provisionality by their use of question marks, and even indicating that figures had been too poor to allow re-use.

The present classification differs from that of the *Revised Brachiopod Treatise*. It pays much more attention to the delthyrium, which although stressed as critical in that study, was treated in a generalized way, by lumping various kinds of delthyrial cover as if they were one sort, or even ignoring or neglecting any form of cover, notably for Cyrtioidea, Adolfioidea and Theodossioidea, as well as various Delthyridina. In this study, stress is laid on the kind of delthyrial cover. But what should we make of a form of delthyrial cover that stands out as exceptional, yet seems to conflict with other morphological attributes? Two examples. Purdonellidae Poletaev has a connector plate, like most members of Spiriferoidea, and unlike most members of Choristitoidea. So it should be classed in Spiriferoidea? But shape and especially ornament, involving a peculiar kind of flat-crested ribs and narrow interspaces, is just like that of choristitids. Which is more important? In this case, the differences in shape and ornament between Spiriferoidea and Choristitoidea are so great, and the choristitoid ornament so consistent, that the ornament is regarded as prime guide. Whether that will prove to be correct remains to be seen.

Another example arises from Delthyridina. There is a scattering of genera amongst Reticularioidea and Elitoidea which have a special kind of delthyrial apparatus, involving pleromal ridges and connector plate, that are absent from most members of these superfamilies. Some genera of Devonian, Carboniferous, and Permian age have a connector plate, unlike other genera that in other respects would appear to belong to the same family group. Should they be reassembled into their own group? The fossil record indicates that the delthyrial apparatus could be recognized as a unifying factor. But there is the strong possibility that the importance of the delthyrium has been overrated, and that the connector plate arose independently in various groups, from time to time.

Ornament has been regarded as a distinguishing feature for the recognition of Delthyridina, which were characterized in the *Revised Brachiopod Treatise* as having fimbriate or frilly micro-ornament. Yet a number of genera and even a whole family do not conform with this kind of micro-ornament. Many instead have a cancellate micro-ornament, or one dominated by radial capillae and commarginal growth lamellae, to the extent that Schemm-Gregory (2011a) declared that their affinities lay with eospiriferids, and she quoted support from the distinguished expert Art Boucot. Should these genera be replaced in Eospiriferidae, or was the ornament variable enough to allow that they had evolved from within Delthyroidea or Hysterolitoidea?

Only limited attention has been paid to mantle canal systems. These were used to justify an alliance between *Angiospirifer* and *Choristites*, in defiance of delthyrial apparatus, shape and ornament, and even the very nature of the mantle canal system. A relationship between *Angiospirifer* and *Trigonotreta* is much more strongly supported, and it is clear that hitherto, the mantle canal system in Trigonotretidae had been ignored.

We are a long way from resolving a full classification of Spiriferida. But there is considerable information of high but unrealized value in many published studies, and of course even more in museums and rocks around the globe. May they become better known to us, and tell us more about the evolution and demise of such a fascinating order. What is important is to be careful in accepting any previous hierachy of classification, and be more willing to explore and discover. The authors of paleontological studies who announce they are adhering to any Treatise classification without critical reassessment are advertising obsolescence and even laziness for their own research. They should allow brachiopods rather than brachiopodologists to speak for themselves. Nor should readers be dismayed that the *Revised Brachiopod Treatise* fails to provide the last word. As Kerrigan (2016) wrote, “The end of any worthwhile book ought to be the start of others”. That said, such admonitions apply to this new classification as well. It is based on extensive review of Spiriferida, includes a number of additional genera omitted or not considered in the *Revised Brachiopod Treatise*, and differs in its attention to micro-ornament, delthyrial apparatus and internal plates. But every classification should be regarded as a springboard for further study.

THE NEW CLASSIFICATION

Order Spiriferida Waagen, 1884

Infrasuborder Cyrtiimorphi new infrasuborder

Superfamily CYRTIOIDEA Fredericks, 1924

Family CYRTIIDAE Fredericks, 1924

Subfamily CYRTIINAE Fredericks, 1924

Subfamily ROCHTEXINAE new subfamily

Family EOSPIRIFERIDAE Schuchert, 1929

Subfamily EOSPIRIFERINAE Schuchert, 1929

Tribe EOSPIRIFERINI Schuchert, 1929

Tribe ESPELLINI new tribe

Subfamily EUREKASPIRIFERINAE Johnson, 1994

Subfamily ALLANELLINAE new subfamily

Family MUCROSPIRIFERIDAE Boucot, 1959

Subfamily MUCROSPIRIFERINAE Boucot, 1959

Subfamily HEDEINOPSINAE Gourvennec, 1990b

Superfamily ADOLFIOIDEA Sartenaer, 1966

Family ADOLFIIDAE Sartenaer, 1966

Subfamily ADOLFIINAE Sartenaer, 1966

Subfamily PINGUISPIRIFERINAE Havlíček, 1971

Subfamily CALLISPIRIFERINAE Johnson, 1994

Family BRANIKIIDAE Johnson & Hou, 1994

Subfamily BRANIKIINAE Johnson & Hou, 1994

Subfamily PARALAZUTKINIINAE new subfamily

Suborder Martiniidina Waterhouse, 2010

Infrasuborder Martiniimorphi Waterhouse, 2010

Superfamily ELYTHYNOIDEA Gourvennec, 1994

Family ELYTHYNIDAE Gourvennec, 1994

Family TENELLODERMIDAE Carter, Johnson & Gourvennec, 1994

Family EOMARTINIOPSIDAE Carter, 1994

Subfamily EOMARTINIOPSINAE Carter, 1994

Subfamily ELIVELLINAE Carter, 1994

Subfamily RALLACOSTINAE new subfamily

Subfamily HETERARIINAE new subfamily

Superfamily INGELARELLOIDEA Campbell, 1959

Family INGELARELLIDAE Campbell, 1959

Subfamily INGELARELLINAE Campbell, 1959

Tribe INGELARELLINI Campbell, 1959

Tribe JOHNDEARIINI new tribe

Subfamily GEOTHOMASIINAE new subfamily

Family RORESPIRIFERIDAE Waterhouse, 1998a

Subfamily RORESPIRIFERINAE Waterhouse, 1998a

Subfamily CRASSUMBINAE Carter, 2006

Superfamily GERKISPIROIDEA Carter, 1985

Family GERKISPIRIDAE Carter, 1985

Family NOTOSPIRIFERIDAE Archbold & Thomas, 1986

Subfamily NOTOSPIRIFERINAE Archbold & Thomas, 1986

Subfamily GLENDONIINAE Clarke, 1992

Subfamily MESOPUNCTIINAE Waterhouse, 1998a

Superfamily MARTINIOIDEA Waagen, 1883

Family MARTINIIDAE Waagen, 1883

Subfamily MARTINIINAE Waagen, 1883

Subfamily PERISSOTHYRINAE Carter, 1994

Subfamily WEININGIINAE new subfamily

Subfamily SPINOMARTINIINAE new subfamily

Family BRACHYTHYRIDAE Fredericks, 1924

Subfamily BRACHYTHYRINAE Fredericks, 1924

Subfamily SKELIDORYGMINAE Carter, 1994

Subfamily PUSTULOPLICINAE Waterhouse, 2004

Infrasuborder Choristitimorphi new infrasuborder

Superfamily THEODOSSIOIDEA Ivanova, 1959

Family THEODOSSIIDAE Ivanova, 1959

Subfamily CYRTIOPSINAE Ivanova, 1972

Tribe CYRTIOPSINI Ivanova, 1972

Tribe UCHTOSPIRIFERINI Johnson & Carter, 1994

Subfamily ENCHONDROSPIRIFERINAE new subfamily

Family PALAEOSPIRIFERIDAE Carter, Johnson & Hou, 1994

Subfamily PALAEOSPIRIFERINAE Carter, Johnson & Hou, 1994

Subfamily HOLLARDOSPIRIFERINAE new subfamily

Superfamily CHORISTITOIDEA Waterhouse, 1968

Family CHORISTITIDAE Waterhouse, 1968

Subfamily CHORISTITINAE Waterhouse, 1968

Subfamily CHORISTITELLINAE new subfamily

Subfamily TANGSHANELLINAE Carter, 1994

Family PALAEOCHORISTITIDAE Carter, 1994

Subfamily PALAEOCHORISTITINAE Carter, 1994

Subfamily AUSTROCHORISTITINAE new subfamily

Subfamily JUNGELOMIINAE new subfamily

Family PURDONELLIDAE Poletaev, 1986

Suborder Spiriferidina Waagen, 1884

Superfamily CYRTOSPIRIFEROIDEA Termier & Termier, 1949

Family CYRTOSPIRIFERIDAE Termier & Termier, 1949

Subfamily CYRTOSPIRIFERINAE Termier & Termier, 1949

Subfamily ECHINOSPIRIFERINAE Liashenko, 1973

Tribe ECHINOSPIRIFERINi Liashenko, 1973

Tribe ULBOSPIRIFERINI Johnson & Carter, 1994

Family SPINOCYRTIIDAE Ivanova, 1959

Family CONISPIRIFERIDAE Ma & Day, 2000

Superfamily PAECKELMANNELLOIDEA Ivanova, 1972

Family PAECKELMANNELLIDAE Ivanova, 1972

Subfamily PAECKELMANNELLINAE Ivanova, 1972

Subfamily SCENESIINAE Carter, 1994

Family STROPHOPLEURIDAE Carter, 1974

Family PTEROSPIRIFERIDAE Waterhouse, 1975

Subfamily PTEROSPIRIFERINAE Waterhouse, 1975

Subfamily VOISEYELLINAE new subfamily

Subfamily BASHKIRIINAE Nalivkin, 1979

Superfamily SPIRIFEROIDEA King, 1846

Family SPIRIFERIDAE King, 1846

Subfamily SPIRIFERINAE King, 1846

Tribe SPIRIFERINI King, 1846

Tribe DONISPIRIFERINI new tribe

Subfamily PROSPIRINAE Carter, 1974

Subfamily SERGOSPIRIFERINAE Carter, 1994

Subfamily WARSAWIINAE new subfamily

Subfamily GYPOSPIRIFERINAE Waterhouse, 2004

Subfamily SPIRIFERALARINAE new subfamily

Subfamily FUSISPIRIFERINAE Waterhouse, 2004

Family NEOSPIRIFERIDAE Waterhouse, 1968

Subfamily NEOSPIRIFERINAE Waterhouse, 1968

Subfamily SEPTOSPIRIFERINAE new subfamily

Subfamily KANINOSPIRIFERINAE Kalashnikov, 1996

Subfamily BLASISPIRIFERINAE new subfamily

Family ALPHANEOSPIRIFERIDAE Waterhouse, 2004

Superfamily SPIRIFERELLOIDEA Waterhouse, 1968

Family SPIRIFERELLIDAE Waterhouse, 1968

Subfamily SPIRIFERELLINAE Waterhouse, 1968

Subfamily ARCULLINAE new subfamily

Subfamily TIMANIELLINAE new subfamily

Family ELIVINIDAE Waterhouse, 2004

Subfamily ELIVININAE Waterhouse, 2004

Subfamily DARBANDIINAE new subfamily

Superfamily TRIGONOTRETOIDEA Schuchert, 1893

Family TRIGONOTRETIDAE Schuchert, 1893

Subfamily TRIGONOTRETINAE Schuchert, 1893

Subfamily COSTULOPLICINAE Waterhouse, 2004

Subfamily GRANTONIINAE Waterhouse, 2004

Family ANGIOSPIRIFERIDAE Legrand-Blain, 1985a

Subfamily ANGIOSPIRIFERINAE Legrand-Blain, 1985a

Subfamily BRACHYTHYRININAE Waterhouse, 2004

Subfamily VARUNINAE new subfamily

Family GEORGINAKINGIIDAE Waterhouse, 2004

Suborder Delthyridina Ivanova, 1972

Infrasuborder Delthyrimorphi Ivanova, 1972

Superfamily DELTHYROIDEA Phillips, 1841

Family DELTHYRIDAE Phillips, 1841

Family CYRTINOPSIDAE Wedekind, 1926

Subfamily CYRTINOPSINAE Wedekind, 1926

Tribe CYRTINOPSINI Wedekind, 1926

Tribe KOZLOWSKIELLININI Boucot, 1957b

Subfamily ARASPIRIFERINAE Johnson, 1994

Subfamily HOWITTIINAE new subfamily

Subfamily TYLOTHYRINAE Carter, 1972

Family XENOMARTINIIDAE Havlíček, 1971

Subfamily XENOMARTINIINAE Havlíček, 1971

Subfamily BOJOTHYRINAE Havlíček, 1990

Tribe BOJOTHYRINI Havlíček,1990

Tribe ALTAJELLINI new tribe

Subfamily QUADRITHYRINAE Gouvennec, 1994

Superfamily HYSTEROLITOIDEA Termier & Termier, 1949

Family HYSTEROLITIDAE Termier & Termier, 1949

Subfamily HYSTEROLITINAE Termier & Termier, 1949

Subfamily PARASPIRIFERINAE Pitrat, 1965

Subfamily ACROSPIRIFERINAE Termier & Termier 1949

Family HOWELLELLIDAE Johnson & Hou, 1994

Subfamily HOWELLELLINAE Johnson & Hou, 1994

Tribe HOWELLELLINI Johnson & Hou, 1994

Tribe FILISPIRIFERINI Schemm-Gregory, 2011b

Tribe A

Tribe B

Tribe AUSTRALOSPIRIFERINI new tribe

Tribe OTOSPIRIFERINI new tribe

Family COSTISPIRIFERIDAE Termier & Termier, 1949

Subfamily COSTISPIRIFERINAE Termier & Termier, 1949

Tribe COSTISPIRIFERINI Termier & Termier, 1949

Tribe MULTISPIRIFERINI Schemm-Gregory, 2008b

Tribe FIMBRISPIRIFERINI Pitrat, 1965

Subfamily PLICONODOSINAE new subfamily

Subfamily ELYMOSPIRIFERINAE Johnson & Hou, 1994

Family SPINELLIDAE Johnson, 1970

Subfamily SPINELLINAE Johnson, 1970

Subfamily EOSPIRIFERININAE new subfamily

Subfamily BREVISPINIFERINAE new subfamily

Superfamily RETICULARIOIDEA Waagen, 1883

Family RETICULARIIDAE Waagen, 1883

Subfamily RETICULARIINAE Waagen, 1883

Subfamily RETICULARIOPSINAE Gouvennec, 1994

Subfamily WARRENELLINAE new subfamily

Subfamily VADUMINAE new subfamily

Subfamily OBESARIINAE Gouvennec, 1994

Subfamily SQUAMULIFERINAE new subfamiy

Family THOMASARIIDAE Cooper & Dutro, 1982

Subfamily THOMASARIINAE Cooper & Dutro, 1982
Subfamily RHENOTHYRINAE Gourvennec, 1994
Subfamily EORETICULARIINAE Gourvennec, 1994

Superfamily ELITOIDEA Fredericks, 1924
Family ELITIDAE Fredericks, 1924
Family TORYNIFERIDAE Carter, 1994
Subfamily TORYNIFERINAE Carter, 1994
Subfamily SPIRELYTHINAE new subfamily
Tribe SPIRELYTHINI new tribe
Tribe KLETSIINI new tribe
Subfamily MARTINOTHYRINAE Carter, 1994
Family PHRICODOTHYRIDAE Caster, 1939
Subfamily PHRICODOTHYRINAE Caster, 1939
Subfamily ANOMALORIINAE Cooper & Grant, 1969
Subfamily ASTEGOSIINAE new subfamily
Family CONDRATHYRIDAE new family

Infrasuborder Ambocoeliimorphi new infrasuborder
Superfamily AMBOCOELIOIDEA George, 1931
Family AMBOCOELIIDAE George, 1931
Subfamily AMBOCOELIINAE George, 1931
Subfamily CRURITHYRINAE Waterhouse, 2010
Subfamily ATTENUOCURVINAE Waterhouse, 2010
Tribe ATTENUOCURVINI Waterhouse, 2010
Tribe EOPLICOPLASIINI new tribe
Tribe OGILVIECOELIINI new tribe
Subfamily JOHNSONONIINAE new subfamily
Family EUDOXINIDAE Nalivkin, 1979
Family LADJIIDAE new family
Subfamily LADJIINAE new subfamily
Subfamily AMBOTHYRINAE new subfamily
Family RHYNCHOSPIRIFERIDAE Paulus, 1957
Subfamily RHYNCHOSPIRIFERINAE Paulus, 1957
Subfamily SUCHANARIINAE new subfamily
Subfamily LAZUTKINIINAE Johnson & Hou, 1994

incerte sedis - Family VERNEUILIIDAE Schuchert, 1929

Repositories: **B** or **BB**: Museum of Natural History, London. **BR**: brachiopod register, Institute of Geological and Nuclear Sciences, Lower Hutt, New Zealand. **GK-D**: Geology Department, Kyushu Universiity, Japan. **GSC**: Geological Survey of Canada, Calgary, Canada. **GSI**: Geological Survey of India, Kolkata (Calcutta), India. **GST**: Geological Survey of Tasmania, Hobart, Australia. **TMF**: Tasmanian Museum, Hobart, Australia. **UQF:** Department of Geology, University of Queensland, kept at Queensland Museum, Hendra, Brisbane, Australia. **USNM**: United States National Museum, Washington, D.C., United States.

AGE DETERMINATIONS FOR CONSTITUENT GROUPS

Age determinations are based on the ranges published in the *Revised Brachiopod Treatise*, with a number corrected especially for Permian groups, from the ages given in the Treatise.

Series subdivisions of the Silurian Period.

"Pridolian'"
Ludlow
Wenlock
Llandovery

International subdivisions for the Perrmian, Carboniferous and Devonian Periods.

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

ACKNOWLEDGEMENTS

This study commenced with the purpose of recording a number of additional genera overlooked by the *Revised Brachiopod Treatise*, and proffering alternate views on the validity of a few Upper Paleozoic brachiopods that had been synonymized in the *Revised Brachiopod*

Treatise. Focus was to be on family groups, with stress on the source of angiospiriferids and an enquiry into the relationships between Martiniidae and Brachythyridae, and taking the opportunity to correct some misplaced illustrations and misdated genera, especially of Permian age. But it became clear that aspects of the Treatise overview had been superseded in critical areas by new and extensive studies, especially for Devonian brachiopods (Oleneva 2006, García-Alcade 2005, Ma & Day 2007, Schemm-Gregory 2008b, 2011a), and examination of internal plates revealed a massive disconnect between Permian and Silurian-Devonian studies. It was therefore necessary to turn to experts world-wide, in an endeavour to clarify various aspects, and I am hugely indebted to a number of colleagues who have most generously responded to questions and requests.

Guang R. Shi, Deakin University of Melbourne, and his colleague Sangmin Lee have kindly send reprints of works not available to me, and provided addresses of further experts. Shen Shu-zhong has sent illustrations of a Tibetan (Xizang) brachiopod. Specific information on genera has been provided by Lucia Angiolini, Milan University, and Vladimir Poletaev, Kiev, and specimens provided by Marie Legrand-Blain have proved highly useful. Tatiana Grunt, formerly of the Paleontological Institute in Moscow, has kindly answered questions and Natalia Oleneva of the Paleontological Institute in Moscow provided information on some Russian studies. Wayne Bamber and Susan Platt, Geological Survey of Canada, have helped with providing access to various publications, and Rémy Gourvennec of Brest, France, gave copies of articles and most helpfully discussed aspects of some genera. Ulrich Jansen of Senckenberg Museum, Frankfurt, also provided copies of articles. Alan Beu, GNS, Lower Hutt, and Ewan Fordyce, University of Otago, New Zealand, responded helpfully to various questions. John Simes, GNS, Lower Hutt, provided duplicates of type Devonian specimens, and many years ago, M. V. Kulikov kindly provided reprints and photographs on critical species. The kindness of numerous colleagues in sending reprints of their studies over many years is also thankfully acknowledged. I am particularly grateful to the late C. H. Crickmay for sending his self-published articles on Devonian brachiopods from western Canada. There is considerable stigma attached to self-published articles (McEwen 2005, p. 276), encouraged of course by the vastly profitable major publishing companies and by some institutions who want control over scientific study with their farcical stress on the need for peer-review, as if that guarantees truth or accuracy, rather than agreement with the prejudices of the peer-reviewer. Crickmay's studies have high validity, and were to a standard higher than that of many contemporary journals, and they conformed with the International Code of Zoological Nomenclature, which is the prime and indeed only standard of reference for taxonomic nomenclature. The *Revised Brachiopod Treatise* accorded full weight to his studies, and took no notice of the bogy over peer review. The one missing but essential item in Crickmay's studies is any indication where the type material is kept. It is now housed at the Paleontological Research Institute at Ithaca, New York, United States.

CLASSICATION AND DIAGNOSES, WITH DESCRIPTION OF NEW TAXA

Superorder SPIRIFERIFORMI Waagen, 1883

[Spiriferiformi Waterhouse, 2010, p. 12].

Spiriferiformi associates Orders Spiriferida and Spiriferinida, which share distinctive internal plates and have laterally directed spiralia in which primary lamellae are parallel and close to the sagital plane. No complete jugum is present.

Order SPIRIFERIDA Waagen, 1883

[Nom. correct. Moore, Lalicker & Fischer 1952, p. 221, pro Order Spiriferacea Kuhn, 1949, p. 104, nom. promoveo ex suborder Spiriferacea Waagen, 1883, p. 447].

Diagnosis: Shell impunctate. High median septum in ventral valve rare. Upper Ordovician to Early Triassic.

Infrasuborder CYRTIIMORPHI new infrasuborder

Diagnosis: Small plicate or rounded (ie. “smooth”), rarely costate, micro-ornament of growth increments and/or radial capillae as a rule, may be pustular, delthyrium open or closed by deltidial plates or delthyrial cover plate, stegidia restricted to one possibly related family, cardinal process or ctenophoridium weakly developed or absent. Internal plates highly varied, with the possibility that they changed within genera and even within species. Upper Ordovician to Upper Devonian.

Discussion: This group constituted the source and stem-group for disparate suborders. The infrasuborder associates two superfamilies Cyrtioidea Fredericks, 1924 and Adolfioidea Sartenaer, 1966, which are of upper Ordovician, Silurian and Devonian age, and involves the root stock of Martiniidina, Delthyridina and Spiriferidina. Constituent genera are small and commonly plicate, but include costate and smooth examples, and micro-ornament is variously capillate, cancellate or tuberculate, including forms with minute scattered or commarginally arranged spines. Dental and adminicular plates in the ventral valve are widespread, and crural plates and tabellae are often present in the dorsal valve, but vary to a high degree and have been deemed to be inconsistent within genera, and surprisingly, even within species. A ventral median septum is rare, but a cruralium is found in a few examples. The cardinal process is absent, simple, or ctenophoridiform, and it appears that different genera in some family groups varied in the nature of the attachment for diductor muscles in the dorsal valve. Muscle scars are as a rule poorly known, and mantle canal systems also poorly displayed. The delthyrium is either open or closed partly or entirely by a delthyrial cover plate or deltidial plates, whereas stegidia are restricted in distribution.

The *Revised Brachiopod Treatise* made a determined effort to circumscribe the two

constituent superfamilies, a difficult task, partly because whatever features are highlit seem to be unstable to a degree, and because many genera are incompletely known. Nonetheless, it is believed that the large array of genera and family group units fall naturally into two major subdivisions, which together formed a natural unit, distinguishable from other mostly Devonian units such as Ambocoelioidea, Cyrtospiriferoidea, Choristitoidea, Delthyroidea, Reticularioidea and Elitoidea. The infrasuborder contains the original sources for many of these and other superfamilies.

Superfamily **CYRTIOIDEA** Fredericks, 1924

[Nom. correct. Johnson, Gourvennec & Hou in Carter et al. 1994, p. 330, pro Superfamily Cyrtiacea Pitrat, 1965, p. 668, nom. transl. ex Cyrtiinae Fredericks, 1924, p. 312].

Diagnosis: Fold and sulcus present, lateral slopes smooth or plicate, micro-ornament of capillae crossed by growth-increments which may be nodose or minutely spinose. Delthyrium closed or partly closed as a rule by deltidial plates, deltidium or delthyrial cover plate. Adminicula and usually tabellae present. Upper Ordovician to Upper Devonian (Frasnian).

Discussion: Several genera or subfamilies that morphologically belong to Cyrtioidea provided the root-stock for other superfamilies, and so have a dual placement. Such duality reflects natural evolutionary affinities.

Johnson & Hou (2006a, p. 1694) defined the superfamily as incorporating genera in which the delthyrium was closed, as prime distinction from Adolfioidea, which lacked such closing plates. Their account did not specify what kind of plate was found in each genus, or even subfamily. As far as can be ascertained, the plates are basically deltidial plates which may later fuse to form a single plate, particularly in Cyrtiidae and Eospiriferidae, and Boucot (1963) provided information about a highly complex arrangement in *Cyrtia*. Regrettably, the Treatise classification in its emphasis on delthyrial plates as confined to Cyrtioidea and absent from Adolfioidea proves to have been far from consistent. For example, *Rochtex* Havlíček was placed within Adolfioidea (Johnson 2006a, p. 1710), yet has a “large imperforate deltidium” that covered the delthyrium. *Howittia* Talent was classed as Adolfiidae, characterized by a supposedly open delthyrium, but the type species *howitti* Chapman has a pair of deltidial plates, one each side of the delthyrium according to Chatterton (1973, p. 110). In this study, any genus with deltidial plates, together with what are considered to be closely allied taxa, are removed from Adolfioidea and placed in Cyrtioidea. This allows classification to become more inherently consistent, but not mechanically so, because genera without cover and believed to be closely allied to others with delthyrial closure are included in the same family group. If emphasis is placed on delthyrial closure, the classification must be more tolerant of variations in the absence or presence of cardinal process or ctenophoridium.

Family **CYRTIIDAE** Fredericks, 1924

[Nom. transl. Ivanova 1959, p. 55 ex Cyrtiinae Fredericks, 1924, p. 312].

Diagnosis: Ventral valve hemipyramidal, high interarea, covered by a deltidium. High

adminicula. Upper Ordovician to Lower Devonian (Emsian).

Subfamily **CYRTIINAE** Fredericks, 1924

[Cyrtiinae Fredericks, 1924, p. 312].

Diagnosis: Delthyrium covered by a deltidium with median foramen. No ctenophoridium, high adminicula and well developed tabellae. Capillae developed as a rule. Upper Ordovician to Lower Devonian (Emsian).

Genera: *Cyrtia* Dalman, *Dongbeiispirifer* Liu, *Plicocyrtia* Boucot.

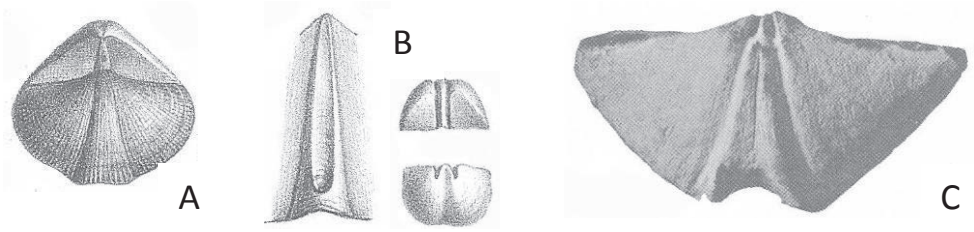


Fig. 18. *Cyrtia exporrectus* (Wahlenberg). A, dorsal aspect. B, delthyrial cover, posterior and dorsal views of ventral valve. C, posterior ventral view. From Wenlock of England. (Davidson 1864-1871).

Discussion: Cyrtiinae is a small group of three genera of unusual hemipyramidal shape, and gently or non-plicate lateral slopes and very fine costellae or capillae. Johnson & Hou (2006a, p. 1695) stated that the family was typified by the absence of delthyrial and stegidial plates, but allowed that the delthyrium was covered by a deltidium. Boucot (1963, p. 701) reported that small specimens of *Cyrtia* showed two discrete deltidial plates, which later joined over the apical half, followed in later ontogeny by a plate that filled the lower half of the delthyrium, with a gap for a small foramen. Then secondary tissue covered the entire structure.

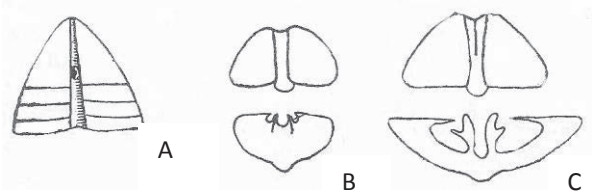


Fig. 19. *Cyrtia exporrectus* (Wahlenberg), posterior view of ventral interarea, and transverse sections, x1.5. (Sarytcheva 1960).

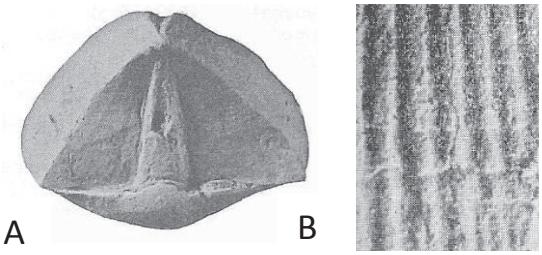


Fig. 20. A, *Cyrtia trapezoidalis* Hisinger, posterior view showing narrow chilidium bordering dorsal margin of the deltidial plate. From Wenlock of England, x2. (Boucot 1963). B, micro-ornament for *Cyrtia exporrecta* (Wahlenberg), x 15, holotype. This figure illustrates fine traces of commarginal fila and fine pustules. (Ivanova 1971).

Subfamily **ROCHTEXINAE** new subfamily

Name genus: *Rochtex* Havlíček in Havlíček & Kukal, 1990, p. 175 from upper Emsian of

Czech Republic, here designated.

Diagnosis: Delthyrial cover plate without foramen. Separate deltidial plates possibly absent. High adminicula, no tabellae. Lower to Upper Devonian (Emsian – Frasnian).

Genera: *Rochtex* Havlíček, *Acutatheca* Stainbrook.

Discussion: *Rochtex* is hemipyramidal with a high narrow delthyrium covered by a convex plate, yet was associated in the *Revised Brachiopod Treatise* with *Callispirifer* Perry, a highly transverse shell with open delthyrium, and to make matters even more dubious, was placed in Adolfioidea which was diagnosed by the lack of a delthyrial plate, yet *Rochtex* has a delthyrial cover plate. The genus is very like members of Cyrtiinae in shape and delthyrial cover, but differs in lacking a delthyrial foramen, and in lacking tabellae. Nor are capillae present, though there are a few open plicae, as in *Plicocyrtia* Boucot. The nature of the cardinal process is uncertain.

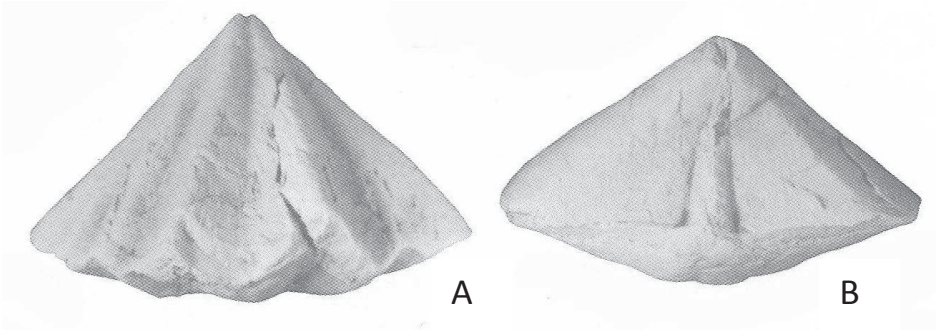


Fig. 21. *Rochtex lissopleura* Havlíček, ventral and posterior aspects, x2. From lower Devonian (upper Emsian) of Czech Republic. (Havlíček & Kukal 1990).

Acutatheca has a convex delthyrial cover plate over part of the delthyrium (Stainbrook 1945), and is of hemipyramidal shape with plicae. It was classed as Adolfiinae in the *Revised Brachiopod Treatise* (Johnson 2006a, p. 1703).

Family **EOSPIRIFERIDAE** Schuchert, 1929

[Nom. transl. hic ex Eospiriferinae Schuchert, 1929, p. 20].

Diagnosis: Biconvex with imperforate deltidium or deltidial plates as a rule, cardinal process or ctenophoridium may be absent, but developed in later members, adminicula present, tabellae usually present. Upper Ordovician to Upper Devonian (Frasnian).

Discussion: This group was treated as a subfamily of Cyrtiidae in the *Revised Brachiopod Treatise*, but workers often refer to the Eospiriferidae, and it is suggested that the distinctive hemipyramidal shape and delthyrial cover for Cyrtiidae with its foramen provide important distinctions.

Subfamily **EOSPIRIFERINAE** Schuchert, 1929

[Eospiriferinae Schuchert, 1929, p. 20].

Diagnosis: Biconvex with curved ventral interarea, deltidial plates usually discrete but may

merge to form a deltidium. Finely to strongly capillate, non-plicate or faintly to moderately plicate, with moderately defined sulcus and fold. Cardinal process or ctenophoridium absent as a rule in early members. Uppermost Ordovician to Lower Devonian (Emsian).

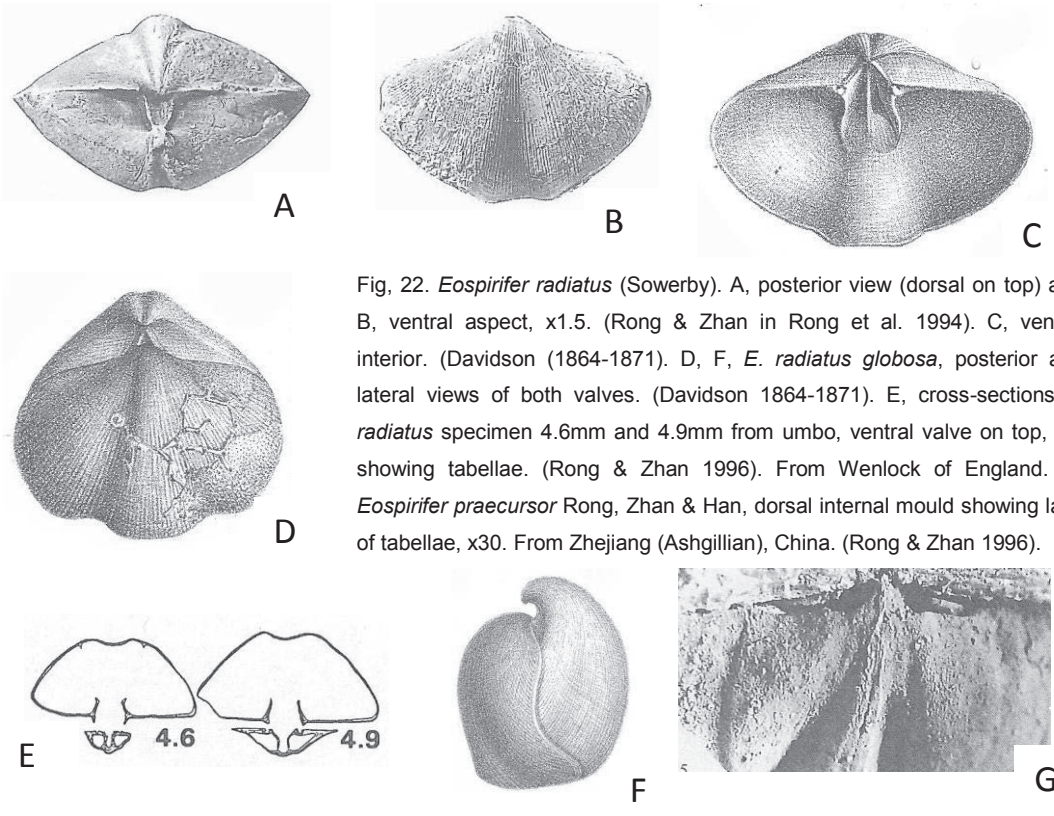
Discussion: Shells are of normal rather than hemipyramidal shape, and the delthyrial cover lacks the distinctive foramen and median convex structure of Cyrtiinae, and ornament as a rule includes distinctive fine to strong radial capillae. Adminicula are invariably present, and tabellae are normally present, although earliest *Eospirifer* lack tabellae.

Tribe **EOSPIRIFERINI** Schuchert, 1929

[Nom. transl. hic ex Eospiriferinae Schuchert, 1929, p. 20].

Diagnosis: Transverse and sulcate with subdued folds in some genera. Uppermost Ordovician to Lower Devonian (Emsian).

Genera: *Eospirifer* Schuchert, *Endospirifer* Tachibana*, Havlicekia* Boucot, *?Lobvia* Breivel & Breivel*, Myriospirifer* Havlíček (= *Acutilineolus* Amsden)*, Nurataella* Larin (syn. *Baterospirifer* Rong, Su & Li), ?*Xinanospirifer* Rong, Xu & Yang.



Fig, 22. *Eospirifer radiatus* (Sowerby). A, posterior view (dorsal on top) and B, ventral aspect, x1.5. (Rong & Zhan in Rong et al. 1994). C, ventral interior. (Davidson (1864-1871). D, F, *E. radiatus globosa*, posterior and lateral views of both valves. (Davidson 1864-1871). E, cross-sections of *radiatus* specimen 4.6mm and 4.9mm from umbo, ventral valve on top, x2, showing tabellae. (Rong & Zhan 1996). From Wenlock of England. G, *Eospirifer praecursor* Rong, Zhan & Han, dorsal internal mould showing lack of tabellae, x30. From Zhejiang (Ashgillian), China. (Rong & Zhan 1996).

Discussion: Shells in this group have sulcus and fold and comparatively smooth flanks without plicae. Strong costae are found in *Xinanospirifer*, covering the entire shell, including moderately distinct sulcus and fold, whereas *Lobvia* has costate flanks and capillate sulcus. *Eospirifer* ranges from uppermost Ordovician to Lower Devonian (Emsian). Its internal plates are as a rule like those of Ingelarellidae, of Upper Carboniferous and Permian age, with

adminicula and tabellae well developed at least in *Eospirifer* and *Xinanospirifer* Rong, Xu & Yang, although Johnson & Hou (2000a, p. 1695) noted that some early members lacked "crural plates" ie. tabellae. Short tabellae were figured in the original proposal of *Xinanospirifer* by Rong, Xu & Yang (1974, pl. 96, fig. 29). Rong & Zhan (1996) described *Eospirifer praecursor* with a small jugal process but no complete jugum. A small striate cardinal process appeared later, so that these authors cast doubt on the significance of whether a ctenophoridium was present or not, contrary to the emphasis in the *Revised Brachiopod Treatise* on its absence as a common diagnostic of Eospiriferinae. Tiny tabellae were figured for *Eospirifer radiatus* (Rong & Zhan 1996, text-fig. 12), whereas Rong, Zhan & Han (1994, Fig. 9.7-11) showed that earliest *Eospirifer* of Ashgillian (upper Ordovician) age had no tabellae, as in Rong & Zhan (1996, text-fig. 4, pl. 1, fig. 15, 16). The studies point to a degree of variability in dorsal cardinalia, reflecting introduction and development of morphological features.

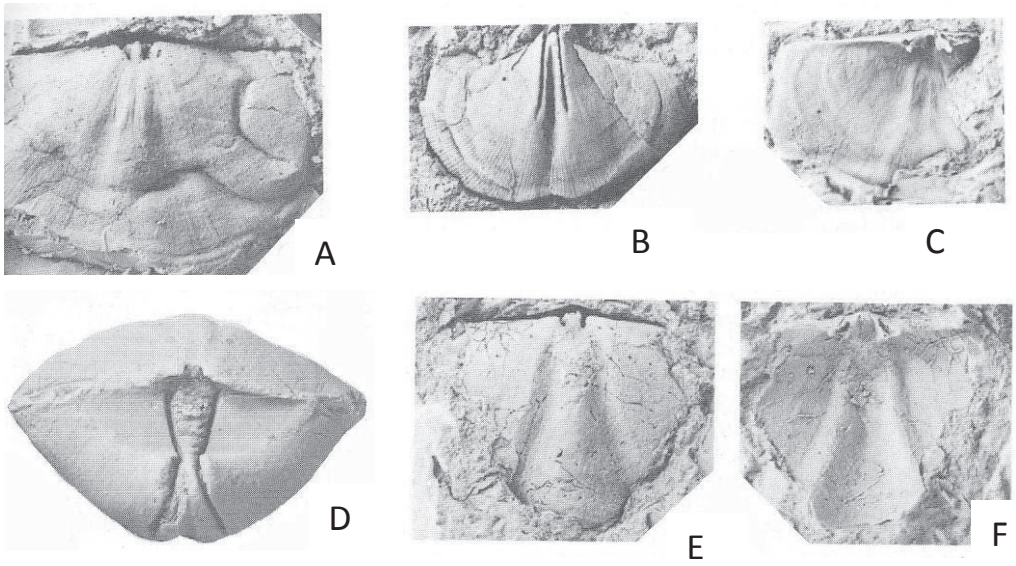


Fig. 23. *Endospirifer anxius* Strusz. A, dorsal interior. B, ventral internal mould. C, latex cast of ventral interior. D, dorsal internal mould, and posterior view. E, F, dorsal internal mould and latex cast. Specimens x4, except E, F, x8. From Wenlock beds near Canberra, Australia. (Strusz 1982).

The sulcate but non-plicate genus *Endospirifer* Tachibana, 1981 of upper Llandovery-Wenlock and possibly Ludlow (Silurian) age, and based on type species *E. nipponicus* Tachibana from possible Ludlow of Japan has long diverging adminicula and comparatively smooth shell apart from sulcus and fold. Figures of the type species are somewhat obscure, but good illustrations of an Australian species were provided by Strusz (1982, Fig. 22A, E, 25, 26), showing the prominent deltidium, delthyrial cover plate, fine capillae with no plicae, cardinal process with several short ridges on the anterior face to indicate a rudimentary ctenophoridium, long adminicula, short tabellae, and slender crural plates with crura at the junction.

Tribe **ESPELLINI** new tribe

Name genus: *Espella* Nilova, 1965, p. 102, type species *E. kazachstanica* Nilova, 1965 from Kazakhstan, here designated.

Diagnosis: Comparatively smooth apart from flattened capillae, thin dental and adminicular plates and crural plates forming cruralium and low median septum. Silurian (Llandovery to Wenlock).

Genus: *Espella* Nilova (syn. *Laevispirifer* Ushatinskaya).

Discussion: The smooth shell of *Espella* suggests a possible source for Devonian families of Ambocoelioidea, which have smooth shell, and well developed cruralium. A few other Middle Paleozoic brachiopods developed a cruralium. For instance the type species of *Ferronia, Spirifer subspeciosus* Verneuil, 1850, has a cruralium and pustulose micro-ornament, but unlike *Espella*, *Ferronia* is strongly plicate, and is distinctly younger than *Espella*, at Emsian (Lower Devonian) age in Spain - see p. 298). It is classed as Delthyridina.

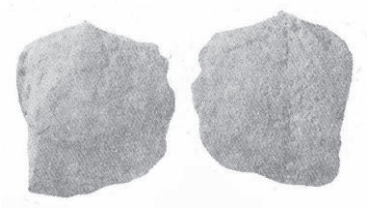


Fig. 24. *Espella kazachstanica* Nilova, from Silurian of Kazakhstan. (Nilova 1965). See also Fig. 12, p. 19.

Subfamily **EUREKASPIRIFERINAE** Johnson, 1994

[Eurekaspiriferinae Johnson in Carter et al., 1994, p. 332].

Diagnosis: Shells usually openly and strongly plicate, with capillae that rarely may be nodose. Deltidial plate may lie each side of delthyrium, but in other genera, the delthyrium is open. Adminicula, dental plates, crural plates and tabellae developed to varying extent, may be well developed, not forming cruralium or tabellarium. Lower Silurian (upper Llandovery) to Lower Devonian (Emsian).

Genera: *Eurekaspirifer* Johnson**,** *Badainjarania* Zhang, *Collinusia* new genus, *Hedeina* Boucot, *Janius* Havlíček, *Macropleura* Boucot (syn. *Ejnespirifer* Fu), *Mictospirifer* Johnson, *Nikiforovaena* Boucot, *Striispirifer* Cooper & Muir-Wood, *Yingwuspirifer* Rong, Xu & Yang.

Discussion: This group involves genera with moderately well developed plicae, fold and sulcus. Members have a bilobed cardinal process and are gently plicate with capillate ornament. *Eurekaspirifer* has long adminicula and long tabellae, and shares capillae with Eospiriferinae. Unlike members of the newly proposed sister subfamily Allanellinae (see p. 42), there is no cruralium, and shells tend to be slightly more strongly plicate.

Although Eurekaspiriferinae was referred as a monogeneric subfamily to Family Adolfiidae Sartenauer, 1966, by Johnson (2006a, p. 1711), the presence of well developed tabellae and the capillate ornament are more consistent with a position in Cyrtioidea, though a bilobed ctenophoridium was recorded, described as a pair of deeply striated lobes in Johnson (1970), and a ctenophoridium was regarded as typical of Adolfioidea in the *Revised*

Brachiopod Treatise. The delthyrium has been portrayed as open, but figures of type *Eurekaspirifer* suggest the presence of two low deltidial plates along the flanks of the delthyrium (see Johnson 1970, pl. 65, fig. 1, pl. 66, fig. 5). Johnson (2006a, p. 1711) reported that the genus has dorsal adminicula and no crural plates, but crural plates according to his usage, meaning tabellae, are clearly present as illustrated by Johnson (2006a, Fig. 1118c, d), and they are long, although one figure in the *Revised Brachiopod Treatise* shows a dorsal valve without tabellae (Johnson 2006a, Fig, 1118d), and similar specimens were figured in his 1970 study. It does seem extraordinary that a single species could vary so much in its internal septation, and it is obvious that this calls for further investigation. By Permian time, internal plates were a comparatively stable feature of species and genera, and Johnson's studies imply that they were much more variable in earlier times. Other genera, including *Warrenella* Crickmay, show similar variability (see pp. 308ff).

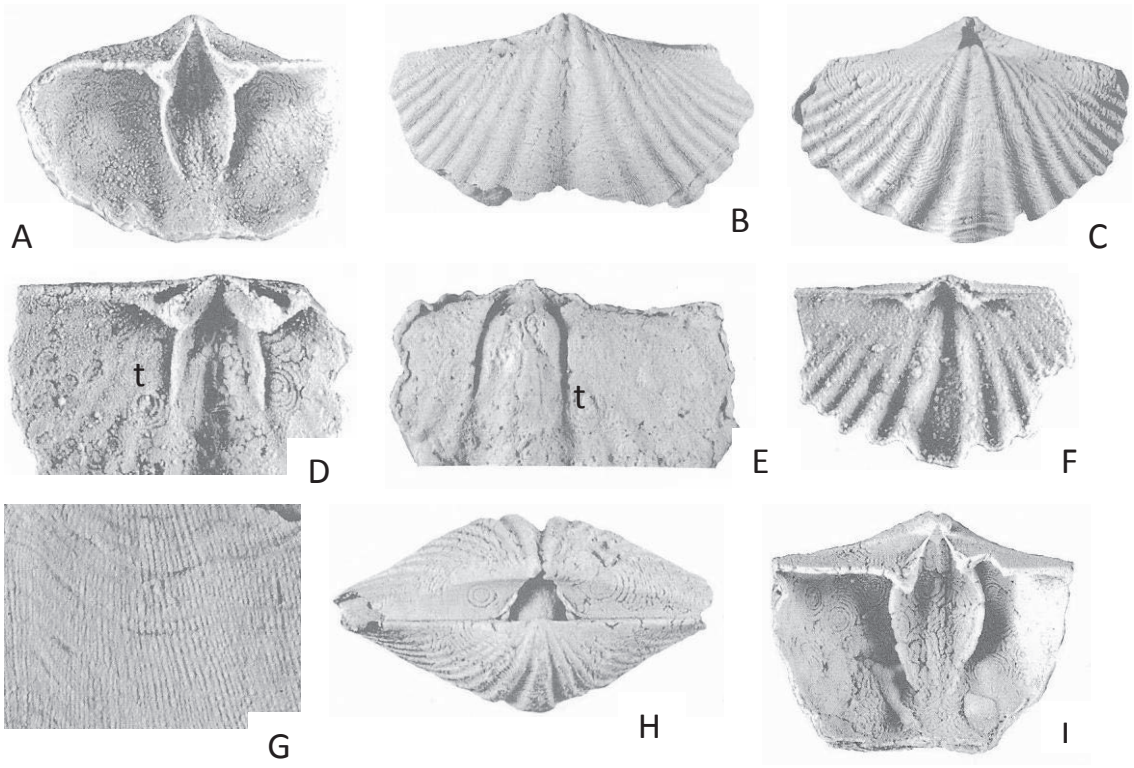


Fig. 25. *Eurekaspirifer pinyonensis* (Meek), type species of the genus. A, ventral interior, x2. B, ventral valve, x2. C, dorsal view, x2. D, E, latex cast and internal mould of dorsal interior, showing tabellae (t), x3. F, dorsal internal cast without tabellae, x4. G, micro-ornament, x5. H, posterior view showing low deltidial plates, x2. I, latex cast of ventral valve showing possible deltidial plates, x1.5. From lower Emsian of Nevada, USA. (Johnson 1970).

Other eospiriferid genera, such *Badainjarania* Zhang, *Hedeina* Boucot, *Janius* Havlíček, *Macropleura* Boucot, *Striispirifer* Cooper & Muir-Wood, *Mictospirifer* Johnson

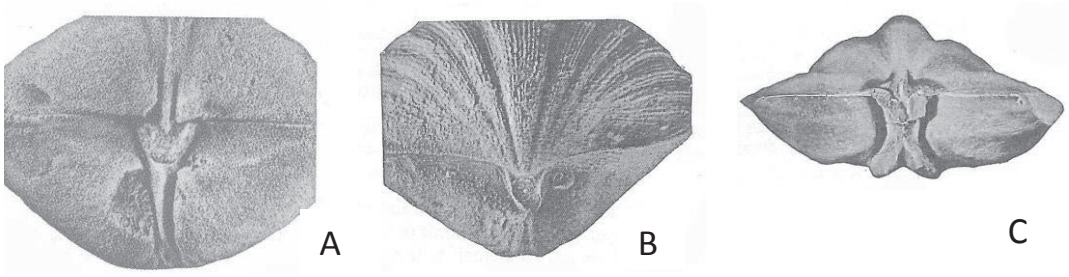


Fig. .26. A, *Striispirifer niagarensis* (Conrad), posterior view of internal cast, dorsal valve on top, x2. From Silurian of New York. B**,** *Striispirifer plicatella* (Linnaeus), posterior view, dorsal view on top, showing narrow deltidial plates projecting each side of delthyrium, x3. From Wenlock of England. C, *Macropleura macropleura* (Conrad), posterior view showing short tabellae in dorsal valve, on top, x1.5. From Lochkovian of Tennessee, USA. (Boucot 1963).

and *Yingwuspirifer* Rong, Xu & Yang are also plicate and display capillae and short tabellae, and were referred in the *Revised Brachiopod Treatise* to Eospiriferinae. *Nikiforovaena* Boucot, 1963 is plicate, with short deltidial plates, and is characterized in part by a median rib along the sulcus. Tabellae and ctenophoridium are present. All these genera are moderately close to *Eurekaspirifer* in general appearance, especially *Badainjarania* and *Striispirifer.* In *Macropleura*, Boucot (1963, p. 690) recorded a pair of narrow deltidial plates, bordering the delthyrium, even though the excellent figures suggest that the delthyrium was open. *Macropleura* shows moderately developed dental and adminicula plates and possible short tabellae, and is of Silurian (upper Llandovery) to Lower Devonian (Emsian) age. Adminicula are long and subparallel in *Striispirifer,* and tabellae are close-set and short. *Striispirifer plicatellus* (Linneaus) has short tabellae (Rong & Zhan 1996, text-fig. 20) and short tabellae are probably also developed in *S. acuminiplicatus* (Rong, Xu & Yang, 1974) of mid-Llandovery age and in *yunnanensis* Rong & Yang of upper Ludlow age.

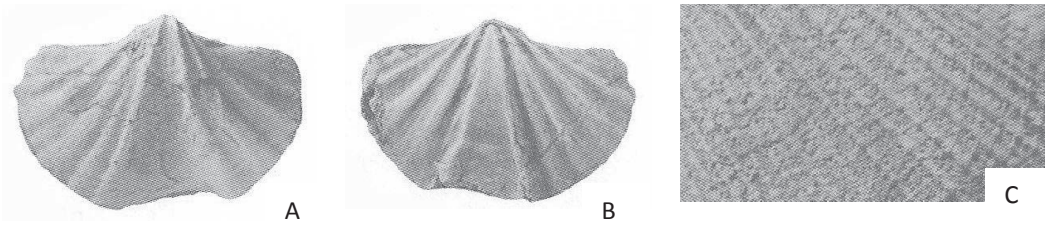


Fig. 27. A, B, *Janius nobilis* (Barrande), type species of the genus, ventral and dorsal views x 1. C, *J. bouskai* Havlíček, micro-ornament, x6. From Wenlock of Bohemia. (Havlíček 1980).

Genus ***Collinusia*** new genus

Name: collinus – of a hill, Lat.

Diagnosis: Small plicate shells with two low subplicae in the sulcus and median channel along the fold, micro-ornament of commarginal growth-lines and radial lira. Deltidial plates, adminicula, dental plates, crural plates and short tabellae.

Type species: *Spinella talenti* Johnson, 1970, p. 205 from Lower Devonian of the Great Basin, United States, here designated.

Discussion: The type species was referred to *Spinella* Talent (see p. 296) by Johnson (1970), but it differs in lacking the micro-spines that help typify *Spinella*, and in having short well formed tabellae in support of the crural plates in the dorsal valve, whereas there are no tabellae in Talent's genus. The species *talenti* Johnson is very close to genera referred herein to Eurekaspiriferinae in shape, ornament and internal plates, and is distinguished by the presence of low sulcal subplicae, and the development of a slender channel traversing along the crest of the dorsal fold. The delthyrial region of the ventral valve shows no sign of the pleromal ridges and connector plate development found in *Spinella* Talent. By contrast, deltidial plates are figured in the present form by Johnson (1970, pl. 64, fig. 11).

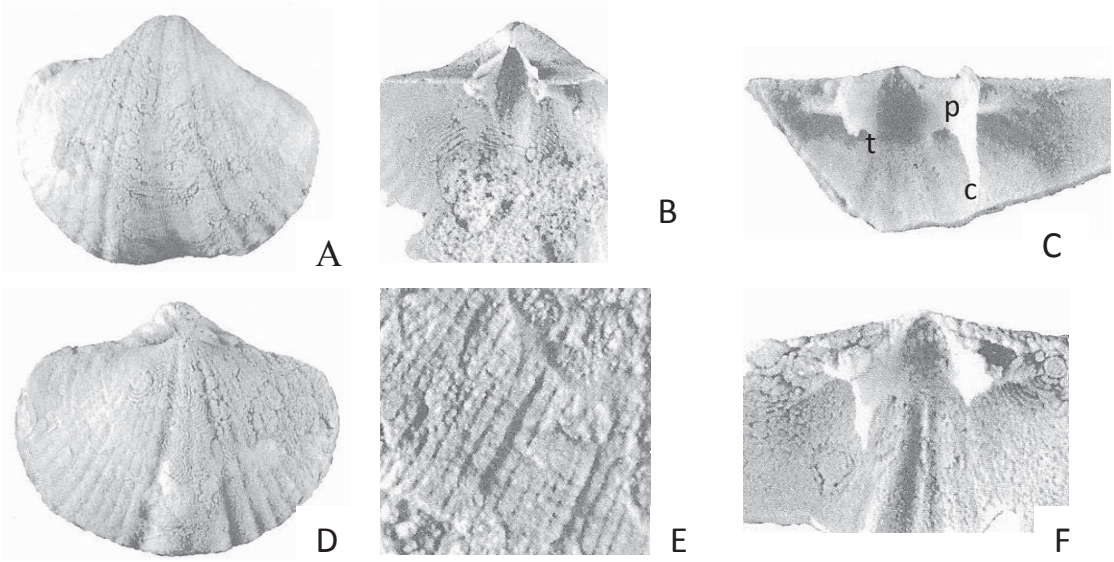


Fig. 28. *Collinusia talenti* (Johnson). A, ventral exterior, x2. B, ventral interior, showing deltidial plates, dental plates and adminicula, x2.5. C, dorsal interior, x5, showing crus (c), crural plate (p), and tabella (t). D, dorsal view, x2. E, micro-ornament, x8. F, dorsal interior, x5. From Lower Devonian of Great Basin, USA. (Johnson 1970).

Subfamily **ALLANELLINAE** new subfamily

Name genus: *Allanella* Crickmay, 1953b, p. 5 from Upper Devonian of Canada, here designated.

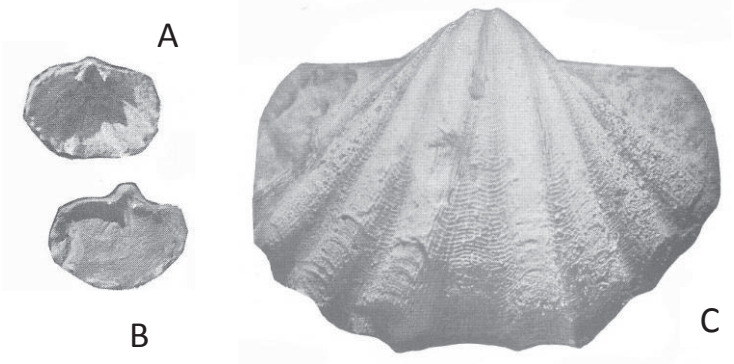


Fig. *29. Minutilla layeri* Crickmay. A, dorsal valve x4. B, ventral valve, x4. C, ventral exterior, x12. Small scattered spines are visible. From Devonian of Western Canada. (Crickmay 1967).

Diagnosis: Small plicate shells with capillate micro-ornament, may be spinulose. Adminicula variably developed, ctenophoridium and usually short cruralium, or short crural plates. Convex delthyrial plate present in *Allanella*. Middle Devonian (Givetian) to Upper Devonian (Frasnian).

Genera: *Allanella* Crickmay (syn. *Allanaria* Crickmay), ?*Fidespirifer* Ljashenko*, Minutilla* Crickmay.

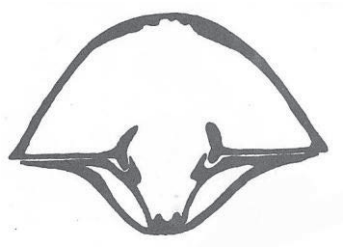


Fig. 30. *Minutilla layeri* (Crickmay), described as type of *Acutatheca (Minutilla)* by Crickmay (1967). From Devonian of Western Canada, x8, 3mm from beak.

Discussion: This group is segregated for plicate genera that have capillate ornament, may display spinules, and differ from Eurekaspiriferinae in displaying a cruralium, or remnants of such a cruralium, such as in *Fidespirifer.* Although the superfamily position of *Fidespirifer* remains insecure, illustrations suggest the possibility of low deltidial plates and short crural plates. *Espella* Nilova is much older, and is not plicate or nodose (p. 39). *Allanella* Crickmay, 1953b was included in the subfamily Adolfiinae by the *Revised Brachiopod Treatise*, but has a delthyrial cover plate. Johnson (2006a, p. 1703) referred *Acutatheca (Minutilla*) Crickmay

Fig. 31. *Allanella decoris* (Crickmay). A, ventral valve, x6. B, dorsal valve, x8. C, dorsal cardinalia, x 20. From Devonian of western Canada. (Crickmay 1967).

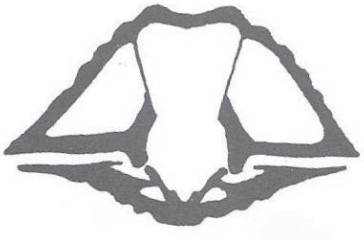


Fig. 32. *Allanella allani* (Warren), cross-section 4.2mm from ventral beak, x3. From Upper Devonian of western Canada. The thickening on the inner side of the cruralium near the base represents the crural bases, to signify that the cruralium is formed solely by crural plates. (Crickmay 1967).

(1967, p. 10, pl. 2, fig. 30-36, pl. 4, fig. 4-7) to synonymy of *Allanella*, and this has similar dorsal plates. The micro-ornament is well preserved, with fine commarginal lirae and

scattered small spines, that are missing from *Allanella*. *Allanella* and *Minutilla* were recorded as having a ctenophoridium in Johnson (2006a, p. 1703), and the cardinal process according to Crickmay (1967, pp. 10, 11) is bifid with a few feeble radial striae.

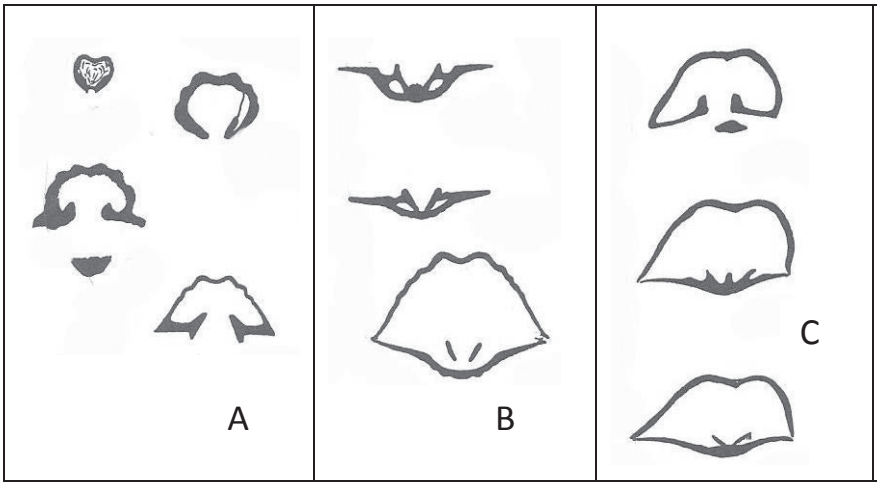


Fig. 33. Serial transverse sections. A, B, *Allanella layeri* (Crickmay). A, figs x5, and x6. B, figs from top to bottom x8, x4 and x2.7. C, *A. decoris* (Crickmay), x3. From Upper Devonian of western Canada. (Crickmay 1967).

Family **MUCROSPIRIFERIDAE** Boucot, 1959

[Nom. transl. Johnson & Carter in Carter et al. 1994, p. 352 ex Mucrospiriferinae Boucot, 1959b, p. 745].

Diagnosis: Cardinal extremities often alate, growth lines lamellose, may be capillate, ctenophoridium present, tabellae may be present, absent as a rule. Delthyrial cover plate and stegidia developed. Middle Devonian (Eifelian) to Upper Devonian (Frasnian).

Discussion: Mucrospiriferidae was classed as Delthyridoidea (= Delthyroidea) in the *Revised Brachiopod Treatise*. From size and general shape, members of Mucrospiriferinae come closer to Hysterolitidae than any member of Cyrtiimorphi, but on the other hand, they are of Devonian age rather than Silurian, and so that their large size is in keeping with the increase in size of brachiopods with the passage of time. Schemm-Gregory (2011a) maintained, with support from senior paleontologists, that some unspecified, but non-"howellellid" brachiopods classed as Delthyroidea by the *Revised Brachiopod Treatise* did not belong to that group but were "eospiriferid". To judge from an extensive overview, Mucrospiriferidae show little in common with typical Delthyridina, other than generalist plication, wide hinge and spiralia. All of the genera so far named fail to show any sign of the particular micro-ornament found in many Delthyridina, apparently in support of the observation by Schemm-Gregory. But a new genus described herein as *Crickmayoria* does indeed show micro-ornament verging on fimbriate (see Fig. 39, p. 47), as if to suggest that a late development with the family could converge on fimbriation, though perhaps only superficially, – or that the family should really be placed in Delthyridina. One further consideration lies in the closeness of Mucrospiriferinae to Hedeinopsinae Gourvennec, of Silurian age, and judged to be closer to its cyrtioidian roots insofar as short tabellae may be present. Aspects of the micro-ornament and the internal plates agree in particular with attributes of Adolfioidea, but the delthyrium is closed by a

delthyrial cover plate, its nature not yet ascertained, and by stegidia, which make their appearance, apparently for the first time, and Johnson & Hou (2006a) placed the group in Cyrtioidea. Provisionally, the family is regarded as representing a flourishing of late Cyrtioidea in developing large size and involved extreme alation.

Subfamily **MUCROSPIRIFERINAE** Boucot, 1959

[Mucrospiriferinae Boucot, 1959, p. 745].

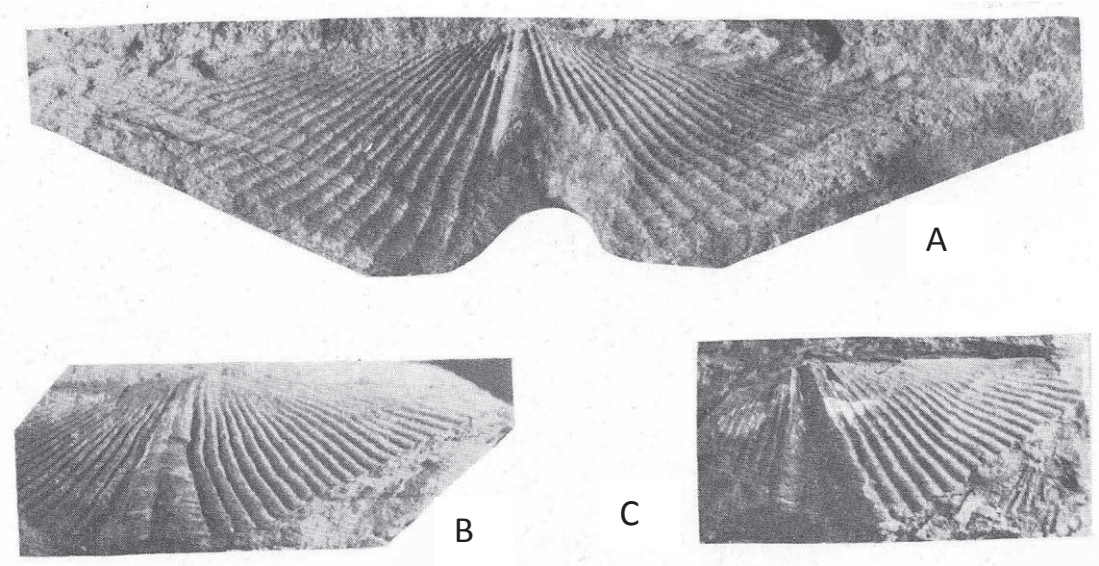


Fig. 34. *Mucrospirifer panduriformis* (Hou), ventral (A, C), and dorsal (B) valves, x 1, from Eifelian-Givetian of northeast China. This was named *Khinganospirifer* Su 1976, p. 221, later synonymized with *Mucrospirifer*. (Su 1976).

Diagnosis: Transverse, multiplicate, with no ventral median septum. Short dental plates and adminicula. Crural plates well developed, may form a cruralium, supported by median dorsal septum in some instances. Micro-ornament of capillae, often tubercular. Lower Devonian (Emsian) to Upper Devonian (Famennian).

Genera: *Mucrospirifer* Grabau (syn. *Lamellispirifer* Conrad, *Khingaspirifer* Su), *Apousiella* Carter (syn. *Bouchardiopsis* Mailleux nom. nud.), *Crickmayoria* new genus, *Cumberlandina* Boucot, *Eleutherokomma* Crickmay (syn. *Dmitrispirifer* Liashenko, ?*Sculptospirifer* Su), *Sulcatospirifer* Maxwell.

Discussion: This is an outstanding group with highly attenuated cardinal extremities in some genera. There are no tabellae, Maxwell (1954, p. 12) noting that plates did not extend along the dorsal floor of the valve in *Sulcatospirifer*, which is characterized by the development of mostly dispersed granules in the micro-ornament. Spines may also be developed in several species of *Eleutherokomma* named by Crickmay, including species *beardi*, *jasperensis* and *killeri,* whereas *scymus*, *impennis* and *aechmophora* (see Crickmay 1963) lack spines. Many transverse sections have been figured in publications, and show short crural plates that in

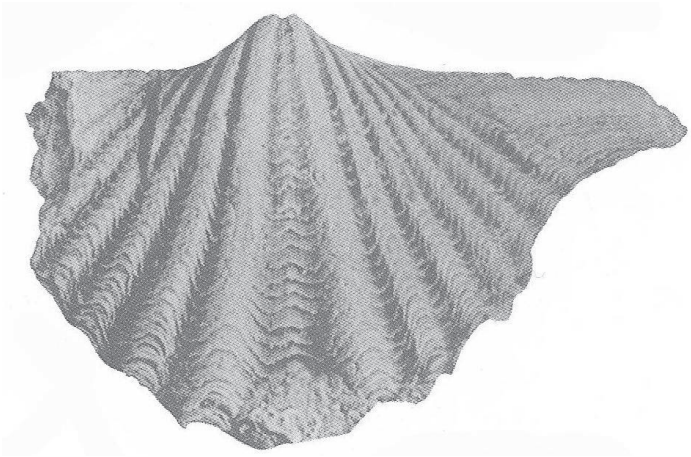


Fig. 35. *Eleutherocomma hamiltoni* Crickmay, type species of the genus, ventral valve, x6, from Givetian of Alberta. (Crickmay 1950).

some individuals at least, or possibly where the section was sited, rest on the floor of the valve, and converge as if forming an incomplete cruralium (see Crickmay 1967, pl. 1, fig. 16, 20, 27, 28). One transverse section of *jasperensis* shows low crural plates converging towards the floor of the valve (Crickmay 1967, pl. 1, fig. 16), and sections for *E. scymus* (pl. 1, fig. 27, 28) show better formed sessile cruralium. The type species *E. hamiltoni* (Crickmay 1967, pl. 1, fig. 16) displays a cruralium resting on a short low thick septum.

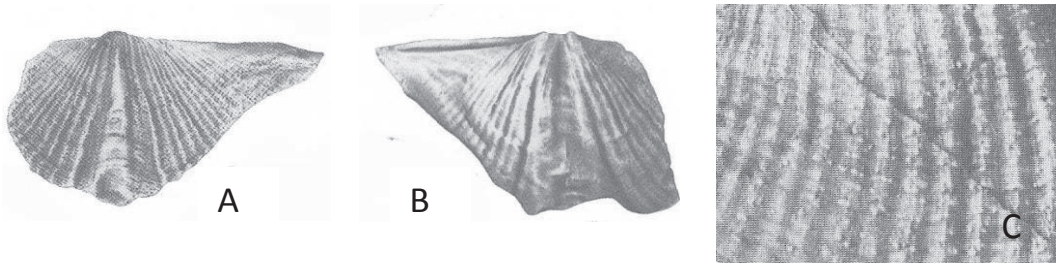


Fig. 36. *Sulcatospirifer primus* Maxwell, internal and external moulds of dorsal valve holotype, x1, and micro-ornament on ventral valve, x7, from Famennian of Queensland. (Maxwell 1954, Johnson & Hou. 2006b).

Cumberlandina Boucot of Pragian (Lower Devonian) age is close in shape and has well defined non-costate sulcus, even-sized costae and the micro-ornament probably capillate, but has a different delthyrium with well-formed posterior apical plate. Schemm-Gregory (2008b, p. 430) favoured placement in Mucrospiriferidae, noting that the genus had a stegidium, and displayed no ribs within sulcus or fold. Its affinities require clarification, and the genus is older at Emsian than any other mucrospiriferin genus.

Although Carter (1972b) and Johnson & Hou (2006b) stated that *Apousiella* has no adminicula and no dental plates, and has sessile socket plates, serial sections provided by Carter (1972b, text-fig. 2) suggest that adminicula could have been present and have been largely buried in secondary shell. (See Fig. 38. 1.4, p. 47). Dorsal plates are inclined outward from the floor of the valve, to enclose the inner side of socket plates. The type species *Spirifer*

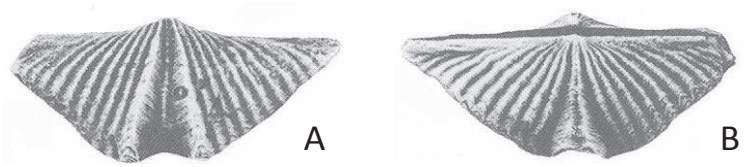


Fig. 37. *Apousiella belliloci* (Rigaux), ventral and dorsal views, x1.5, from Frasnian of France. (Carter 1972b).

bouchardi Murchison has a well defined median groove along the dorsal fold and a narrow sulcal rib. Plicae are well developed and micro-ornament consists of radial and commarginal filae. The genus was allocated to Mucrospiriferidae in the *Revised Brachiopod Treatise*. Carter (1972b) mentioned an apical myophragm, and a cruralium or sessalium is developed.

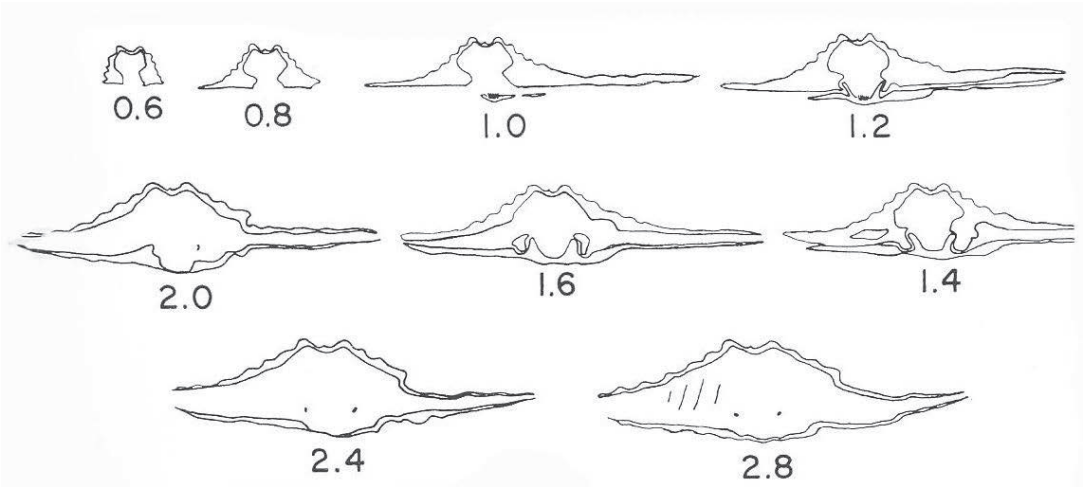


Fig. 38. Transverse sections of *Apousiella bouchardi* (Murchison) from France, with distance indicated in mm from ventral beak, x3. (Carter 1972b).

Genus ***Crickmayoria*** new genus

Name: For C. H. Crickmay.

Diagnosis: Transverse alate and narrowly plicate shells with micro-ornament of spinose capillae crossed by commarginal filae. Dental plates supported by adminicula. Crural plates short but high, converging floorwards.

Type species: *Eleutherokomma beardi* Crickmay, 1950 from Upper Devonian of Alberta, here designated.

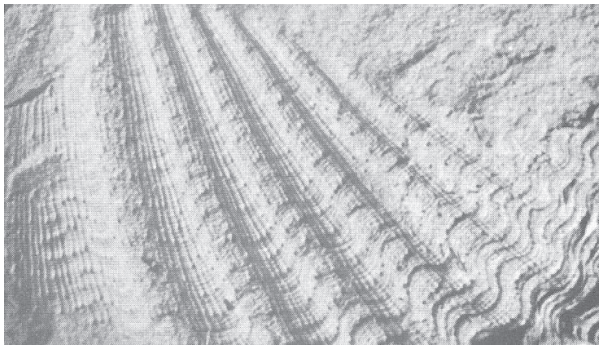


Fig. 39. *Crickmayoria beardi* (Crickmay), detail of micro-ornament, x10. From Upper Devonian of Alberta. (Crickmay 1967).

Discussion: Most species assigned to *Eleutherokomma* have predominant commarginal ornament, with weak radial capillae that are not spinose. The micro-ornament differs in the present form, with slightly weaker commarginals and slightly better developed radial capillae which bear small spinules, approaching fimbriae, but with no evidence that spine bases were prolonged posteriorly. *E. jasperensis* and *E. killeri* also belong to the new genus. The Queensland genus *Sulcatospirifer* Maxwell also has small tubercles, that are much more irregularly disposed, and numerous narrower plicae and fold bearing a deep median channel.

Subfamily **HEDEINOPSINAE** Gourvennec, 1990b

[Hedeinopsinae Gourvennec 1990b, p. 142].

Diagnosis: Plicate, ventribiconvex, with stegidial plates and delthyrial plate, tabellae short or absent. Silurian (Wenlock – Pridoli).

Genera: *Hedeinospis* Gourvennec, *Tannuspirifer* Ivanova.

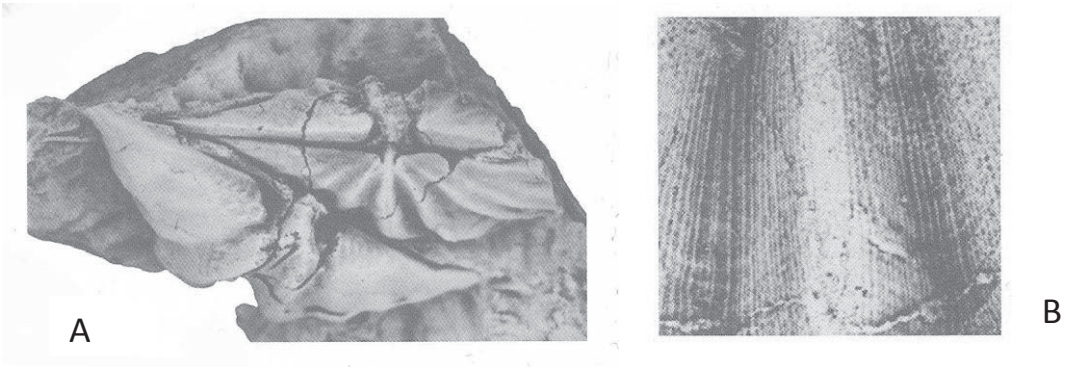


Fig. 40. *Hedeinopsis hispanica disparisulcata* Gourvennec. A, internal moulds, x2. B, detail of of micro-ornament, x10. From Wenlock of Spain. (Gourvennec 1990b).

Discussion: This group was cast in Cyrtioidea as both a family and unnecessarily as a subfamily by Johnson & Hou (2006a, p. 1701), with only two genera and no other subfamily. The two constituent genera have a wide hinge and characteristic shape. *Hedeinopsis* is more transverse and spiriferiform than the subrounded and non-plicate *Eospirifer*. Micro-ornament consists of radial and commarginal fila. Shape approaches that of Spiriferoidea, but costae are lacking, and short tabellae are present. The two genera have a ctenophoridium, unlike the arrangement normal for many although not all Cyrtiidae and Eospiriferidae, so that the family group might seem to be better positioned with Adolfiidae. But on the other hand, the two genera have delthyrial plate (its nature not clarified) and stegidia, and overall shape and micro-ornament are much the same as attributes in Mucrospiriferinae. As well, *Hedeinopsis* appears to have short tabellae, and tabellae are here regarded as a feature more usually although not exclusively found in Cyrtioidea, as compared with Adolfioidea. In addition the strength of the radial capillae points to a further link with *Eospirifer*.

Superfamily **ADOLFIOIDEA** Sartenaer, 1966

[Nom. transl. Johnson 2006a, p. 1703 ex Adolfiinae Sartenauer, 1966, p. 386].

Diagnosis: Shells without prismatic structure and without delthyrial cover plate, deltidia or stegidia. Ctenophoridium usually present. Fold, sulcus and mostly a few well developed plicae, micro-ornament of capillae or pustules and spinules not arranged in commarginal or quincunxial pattern, dental plates supported by short adminicula, socket and crural plates, tabellae short or not developed. Silurian (Wenlock) to Upper Devonian (Frasnian).

Discussion: Cyrtioidea and Adolfioidea are not easily distinguished at first glance, typical members of both superfamilies being small, with somewhat comparable micro-ornament, and the assertion by Johnson (2006a) that a delthyrial plate is lacking from Adolfioidea is endorsed to the extent that some genera are transferred from Adolfioidea to Cyrtioidea. The two groups are often plicate, although some cyrtioids, especially amongst Eospiriferidae, are much less plicate, but have strong radial capillae. Pustules are found in some Cyrtioidea, but are rare if not completely absent from Adolfioidea. Of the genera that bear pustules according to the *Revised Brachiopod Treatise*, a number have delthyrial apparatus, which points to cyrtioid rather than adolfioid affinities, and others have been appraised as delthyroid by Schemm-Gregory (2011a). A cardinal process or ctenophoridium, although considered to be typical of Adolfioidea in the *Revised Brachiopod Treatise*, is also found in Cyrtioidea.

Tabellae feature in many, but not all Cyrtioidea, and feature in only a few Adolfioidea. It is believed that these offer an imperfect means of distinction, because early adolfioids did have short tabellae, which tended to be lost in younger genera.

Family **ADOLFIIDAE** Sartenaer, 1966

[Nom. transl. Johnson 2006a, p. 1703 pro Adolfiinae Sartenaer, 1966, p. 386].

Diagnosis: Multiplicate as a rule, fold and sulcus smooth. Ctenophoridium present as a rule. Devonian (Pragian – Frasnian).

Subfamily **ADOLFIINAE** Sartenaer, 1966

[Adolfiinae Sartenaer, 1966, p. 386].

Diagnosis: Narrowly plicate. Fold and sulcus clearly defined, may lack subplicae or costae. Ventral interarea medium to moderately high, micro-ornament capillate or pustulose. Lower to Upper Devonian (Upper Pragian to Frasnian).

Genera: *Adolfia* Gürich (syn. *Guerichella* Paeckelmann, ?*Changshaispirifer* Zhao in Yang De-li et al.), *Chimaerothyris* Paulus, Struve & Wolfart, ?*Volgospirifer* Shevchenko.

Discussion: Micro-ornament and internal features, as far as they are known, show a degree of variation. Many members are capillate, approaching the micro-ornament known also for some Eospiriferinae (see p. 37). Internally adminicula tend to be short, and tabellae are short or absent. A cruralium is developed in some genera.

Disconcertingly, *Adolfia* would seem to differ from other genera referred to the Adolfiinae in the *Revised Brachiopod Treatise*, because the holotype (Fig. 41) of the type

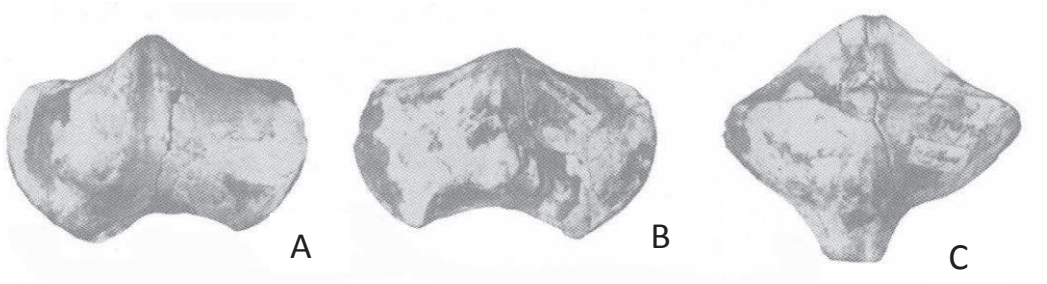


Fig. 41. *Adolfia deflexa* (Roemer), A, ventral, B, ventral anterior and C, dorsal views of holotype, x1. From lower Frasnian of Germany. (Vandercammen 1957).

species seems to have much finer ribbing compared with the ribbing on other genera. Yet what is said to be the same species as figured in the initial *Brachiopod Treatise* has strong plicae, like those of companion genera (Fig. 42). Internally adminicula tend to be short, and tabellae are absent.

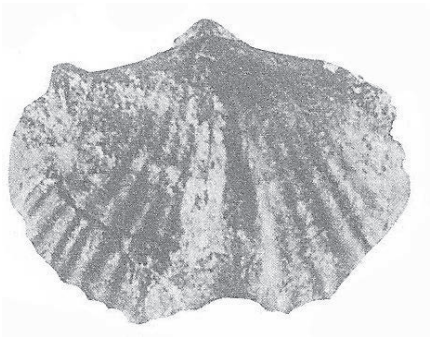


Fig. 42. *Adolfia deflexa* (Roemer), ventral view, figured as typical of *Adolfia* by Pitrat (1965, p. 690), x1.5. From Frasnian of Germany. Plicae are stronger it would appear than in the type species figured in the *Revised Brachiopod Treatise*. Both examples show signs of having a costate sulcus.

Johnson (2006a, p. 1703) synonymized *Changshaispirifer* Zhao in Yang De Li et al. (1977, p. 428) with *Adolfia,* but the type species *C. lianhuaqiaoensis* Zhao (1977, pl. 169, fig. 9, text fig. 34) is a small shell with relatively strong plicae, and indeed looks close to *Chimaerothyris*. Its characters require clarification.

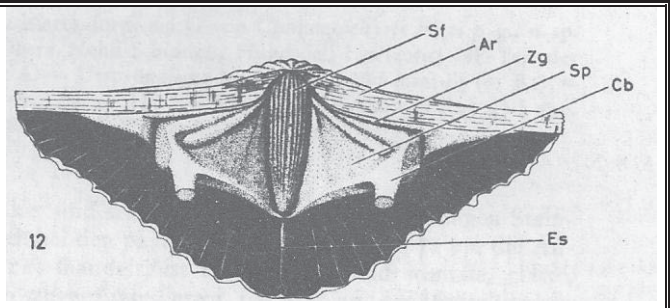


Fig. 43. *Chimaerothyris hotzi* Paulus, Struve & Wolfart, dorsal interior x4. The hinge plate is close to being a cruralium, and the supporting septum may consist of fused tabellae. From Eifelian of the Eifel, Germany. Ar – interarea; Cb – crural base; Es – euseptum; Sf – cardiinal process (ctenophoridium); Sp – hinge plate; Zg – dental socket. (Paulus, Struve & Wolfart 1963).

Subfamily **PINGUISPIRIFERINAE** Havlíček, 1971

[Pinguispiriferinae Havlíček, 1971].

Diagnosis: Openly plicate. Stated to have weak to obscure capillae, crossed by growth fila. Silurian (Wenlock) to Middle Devonian (Eifelian).

Genera: *Pinguispirifer* Havlíček, *Amoenospirifer* Havlíček, *Brevispirifer* Cooper*, Ljudmilispirifer* Cherkesova, *Microttia* García-Alcade, ?*Sergunkovia* Nalivkin*, Spurispirifer* Havlíček.

Fig. 44. A, B, *Pinguispirifer infirmus* (Barrande), ventral and dorsal views, x1. From lower Emsian of Bohemia. (Havlíček 1959). C, *Brevispirifer gregarius* (Clapp), dorsal interior, enlarged. From lower Eifelian of New York. (Cooper 1944).

Discussion: Adolfiinae tend to have higher and more prominent ventral interarea than in Pinguispiriferinae, but its members come very close to *Pinguispirifer* and allies. No clear distinction was offered in the *Revised Brachiopod Treatise,* but it is suggested that the difference in style of plication may offer a distinction. In Pinguispiriferinae, cancellate micro-ornament is developed, dominated by radial capillae, as figured for *Amoenospirifer* Havlíček, 1957 and *Ljudmilispirifer* Cherkesova, 1976 by Johnson (2006a, Fig. 1115.3f, 1116.1c).

Adminicula would appear to be very short (*Pinguispirifer* Havlíček, *Ljudmilispirifer* Cherkesova), and tabellae appear to have been absent. Johnson (2006a, p. 1707) distinguished the subfamily by the presence of weak capillae crossed by fila, and short or no crural (= tabellar) plates, but such a diagnosis does little to discriminate between the two subfamilies, because Adolfiinae is also capillate, and tabellae are not inevitably present in either group.

Ljudmilispirifer Cherkesova of Lower Devonian age (upper Emsian) has ribs in the sulcus, cancellate ornament, and apparent short dental plates and adminicula though stated to be absent by Johnson (2006a, p. 1708). Large pits characterize the mantle canal system in *Ljudmilispirifer*, and were said to be strong in *Amoenospirifer.* Crural plates, without tabellae, are present in *Brevispirifer* Cooper, 1942 (see Johnson 2006a, Fig. 1115.2c). *Brevispirifer cabanillas* (Archiac & Verneuil), as studied by Vandercammen (1959), has fine pustules and a dorsal interior that displays two small lacunae near the umbo, suggestive of very short vertical umbonal plates, with the cardinal process sited on a short rostrum, somewhat approaching a cruralium in appearance. This is not the type species, nor necessarily correctly identified to genus, but does indicate that the umbonal structures may be complex and may carry cryptic information about short or atrophied tabellae, or posteriorly sessile crural plates, or short septum or rostrum. Such detail needs to be clarified in future studies. Given that pustules are

not known in *Brevispirifer,* the apparent spine bases in *cabanillas* suggest *Brevispinifera* García-Alcade of Delthyridina (see p. 299).

Nikiforovaena is moderately like these genera in overall appearance, but Boucot (1963) recorded narrow delthyrial plates in *Nikiforovaena*, and these count as helping close the delthyrium, so the genus is removed to Eurekaspiriferinae, in Cyrtioidea.

Subfamily **CALLISPIRIFERINAE** Johnson, 1994

[Callispiriferinae Johnson in Carter et al, 1994, p. 332].

Diagnosis: Non-capillate with very high almost flat ventral interareas and extended transverse outline, smooth fold and sulcus. Ctenophoridium, no tabellae. Lower Devonian (Emsian).

Genus: *Callispirifer* Perry.

Discussion: Two genera, *Callispirifer* Perry and *Rochtex* Havlíček, were placed in Callispiriferinae by the *Revised Brachiopod Treatise*, but *Rochtex* differs strongly in shape and has a delthyrial cover, close to Cyrtiidae. In view of its transverse outline and high ventral interarea *Callispirifer* could have been forebear of Spiriferidina.

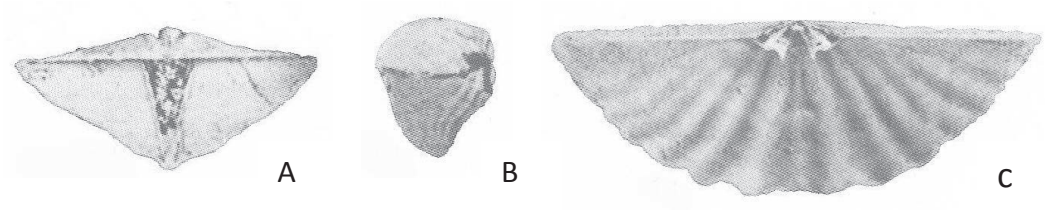


Fig. 45. *Callispirifer teniostrakon* Perry, posterior and lateral views x1.5, and dorsal interior, x2.5. From Lower Devonian (Emsian) of Yukon District, Canada. (Perry 1984). Johnson (2006a, pp. 1709-1710) incorrectly stated Canadian Arctic Islands.

Family **BRANIKIIDAE** Johnson & Hou, 1994

[Nom. transl. hic ex Branikiinae Johnson & Hou in Carter et al. 1994, p. 333].

Diagnosis: Small and plicate shells. Open delthyrium, adminicula, no tabellae. Lower Devonian (Pragian, Emsian).

Discussion: This group was classed as Theodossioidea in the *Revised Brachiopod Treatise*, but genera are much more strongly ribbed. Critics may complain that any definition of a superfamily which placed prime stress on the alleged uniformity of costae or plicae has to be inadequate, and that certainly applies to the placement of *Branikia* and allies in Theodossioidea. *Theodossia* has fine ribs, and *Branikia* has coarse plicae, of two different strengths, so that application as well as definition seems to have been dubious. The definition of the superfamily in the *Revised Brachiopod Treatise* claimed that fold and sulcus were lacking – but this does not apply to *Branikia*. The one correct item in the diagnosis is the statement that a delthyrial plate was lacking. That is correct for Branikiidae, but it is also true of Adolfioidea, with which *Branikia* shows many similarities. Adolfioidea includes a number of

genera which are small, with relatively strong plicae, variably defined sulcus and fold, commarginal micro-ornament, short adminicula, and no tabellae. However Branikiidae does have unique attributes, and for instance, a ctenophoridium is not known, there being a knob-like cardinal process in *Branikia* and a low mound-like process in *Lenzia*. Such features are more characteristic of Cyrtioidea, but delthyrial cover of any sort is missing from Branikiiidae.

Subfamily **BRANIKIINAE** Johnson & Hou, 1994

[Branikiinae Johnson & Hou in Carter et al. 1994, p. 333].

Diagnosis: Non-capillate, small and plicate shells. No ctenophoridium. Lower Devonian (Pragian, Emsian).

Genera: *Branikia* Havlíček (syn. *Bidentatus* Khodalevich & Breivel), ?*Jilinospirifer* Su, *Lenzia* Perry, Boucot & Gabrielse.

Discussion: This group is non-capillate, and plicae vary from fine to coarse in *Lenzia*, whereas *Branikia* has subplicae over the shallow sulcus and channel along the low fold, providing aspects that differ from those in genera of the Adolfiidae. *Branikia* has short dental plates and adminicula and lacks tabellae, like the better preserved *Lenzia* Perry, Boucot & Gabrielse, 1981. But the obscure *Jilinospirifer* Su, 1980 of Middle Devonian age in China, although placed in Branikiinae by Johnson & Hou in Johnson et al. (2006a, p. 1715), probably because of its external similarity to *Lenzia*, is said to lack dental plates (= adminicula). It is of Eifelian (Middle Devonian) age, and its micro-ornament is not known. In short, *Jilinospirifer* needs to be better known before placement in a subfamily is secured. All three genera are somewhat similar to each other externally, and if all conform with *Lenzia* – as is not yet established – then the group may have been a constituent group within Adolfioidea, given the open delthyrium. Any relationship to Theodossiidae would seem to be highly fraught.

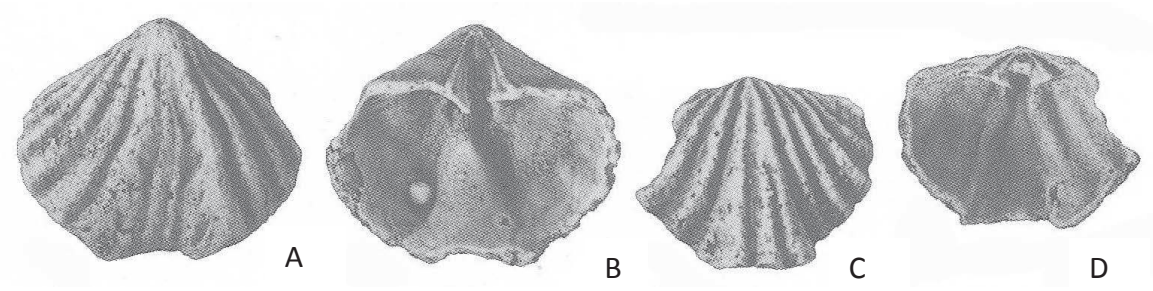


Fig. 46. *Lenzia pachyostrakon* Perry, Boucot & Grabrielse. A, ventral exterior, B, ventral interior, C, dorsal exterior and D, dorsal internal views, x1.8. Note the umbonal callus indicated in B. From Lower Devonian (Emsian) of British Columbia, Canada. (Johnson & Hou 2006).

One genus in the Cyrtioidea called *Collinusia* n. gen. (see p. 41) has subdued subplicae in the sulcus, and a channel along the dorsal fold, reminiscent of aspects found in Branikiinae. It has more plicae than in members of Branikiinae, and has short tabellae and

short tabellae, and well developed deltidial plates, so that it is classed in Eurekaspiriferidae Johnson.

Subfamily **PARALAZUTKINIINAE** new subfamily

Diagnosis: Plicate and capillate, sulcate fold, short dental plates. Median ridge in dorsal valve with cruralium or allied structure, ctenophoridium present. Middle Devonian (Eifelian, Givetian).

Genera: *Paralatzutkinia* Jiang (syn. *Pinghuangella* Jiang), *Urella* Rzhonsnitskaya (syn. *Retzispirifer* Kulkov).

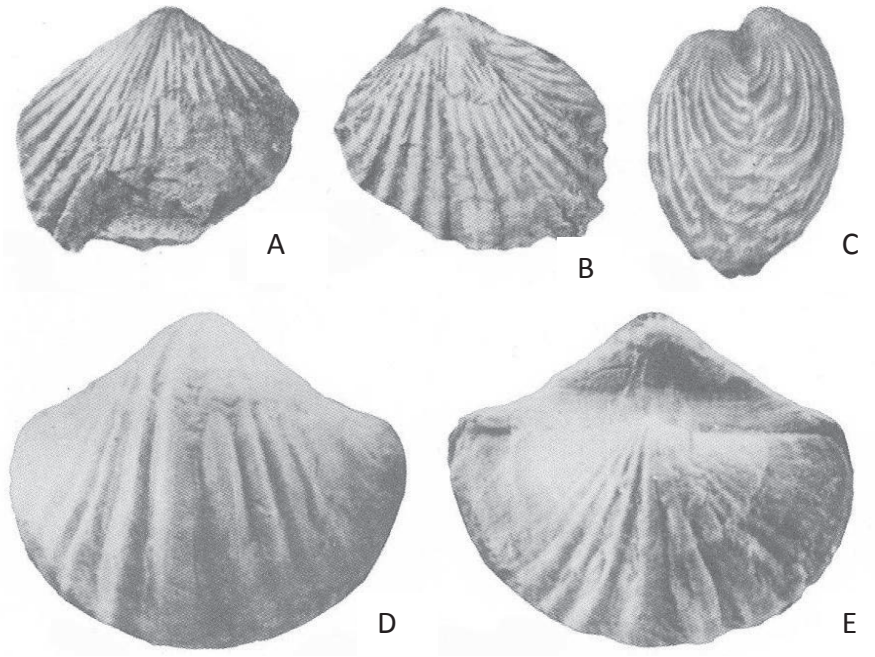


Fig. 47. A, *Urella asiatica* Rhzonsnitskaia, ventral, dorsal and lateral aspects, x1.3. From Middle Devonian of Russia. (Markovski 1960). B, *Paralazukinia pinghuangshanensis* Jiang, x2.2. From Eifelian (Lower Devonian) of southern China. (Xian & Jiang 1978).

Discussion: *Paralatzutkinia* Jiang (Eifelian) and *Urella* Rzhonsnitskaya (Eifelian–Givetian) were placed in Theodossiinae by Johnson et al. (2006a). These genera have shallow sulcus and low sulcate fold, and are plicate with capillate micro-ornament and so approach

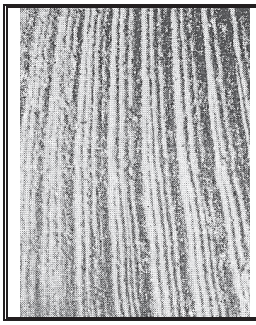


Fig. 48. Micro-ornament of *Urella schmidti* (Stuckenberg), classed as *Retzispirifer* in Ivanova 1971, x 10, from Middle Devonian of Russia.

Adolfiidae. *Paralatzuktkinia* has a cruralium and short median dorsal septum, and the outer hinge plates of *Urella* are attached to a median ridge posteriorly. These features together with a ctenophoridium indicate a separate group, whereas the firm plicae recall aspects of Branikiinae, which differs in lacking capillae, and having no dorsal septum and no ctenophoridium.

Suborder MARTINIIDINA Waterhouse, 2010

[Martiniidina Waterhouse, 2010a, pp. 13, 63].

Diagnosis: Dental plates, adminicula and tabellae highly varied in presence and development. Shells biconvex, smooth or coarsely plicate, some broadly costate, with varied micro-ornament of commarginal and/or radial capillae, spinules, pustules, grooves or pits.

Discussion: A feature of the suborder is the high degree of variation in internal plates, although the variation proceeded along a slender and acceptable range, consonant with external features of shape and micro-ornament, and no genus shows a spondylium, cruralium, or ventral or dorsal medium septum. In many family groups the delthyrium is open, and in smaller groups a connector plate may be developed, with a deltidium or deltidial plates present in one major family. Martiniidiina is diverse, and is subdivided into two major groups, united by the sharing of tabellae in at least some early members. That is proferred as the most conservative of available choices in classification, yet marks a radical departure from the first and second series of *Revised Brachiopod Treatise*. By contrast, Spiriferidina has consistent internal plates, and Delthyridina a differing style of external ornament and plates.

Infrasuborder MARTINIIMORPHI Waterhouse, 2010a

[Nom. transl. hic ex Martiniidina Waterhouse, 2010a, pp. 13, 63].

Diagnosis: Genera smooth or plicate, seldom costate, micro-ornament varied, smooth, pitted, grooved, or minutely spinose. Interior with well developed dental plates and adminicula as a rule, or absent. Dorsal valve with socket and crural plates, tabellae widely present, may be absent. Silurian (Wenlock) to Upper Permian (Changhsingian).

Discussion: To this infrasuborder are referred spiriferidan superfamilies and genera which display adminicula, dental plates and crural plates with tabellae, together with genera deemed to have secondarily lost plates. Overall shape is subrounded, plicae are more or less developed, and micro-ornament is varied, pitted, spinose, or grooved or smooth, with further variations, but without prominent commarginal lamellae, as pointed out by Carter & Gourvennec (2006b, p. 1747), apart from one exception, a new genus *Carteriopsis* (p. 66). The group is moderately well known so far as the Permian constituents are concerned, and contributes information on the variability that may be achieved within a brachiopod group. They stem from Cyrtioidea, which differed in their small size, thin shell, and simple plication with capillae or spinules. Yet unlike Cyrtioidea, few of the known martiniiform genera exhibit deltidial plates or delthyrial cover. Pleromal thickening and a connector plate are developed in some Permian stock, and extensions of the dental plates are seen in Heterariinae (p. 70).

The infrasuborder commenced in Silurian (upper Wenlock) time, and earliest genera displayed a shape and internal plates consonant with members of Eospiriferinae, such as *Endospirifer* Tachibana, *Hedeina* Boucot and *Myriospirifer* Havlíček of Silurian and early Devonian age. These genera differed in their micro-ornament, but overall, shape, internal plates and fossil record display a convincing source for the origin and development of the Elythynoidea, Gerkispiroidea and Ingelarelloidea.

Superfamily **ELYTHYNOIDEA** Gourvennec, 1994d

[Nom. transl. hic ex Elythynidae Gourvennec in Carter et al., 1994, p. 338].

Diagnosis: Dental plates and adminicula varyingly but usually well developed, crural plates present, tabellae absent or feebly to moderately developed. Silurian (Wenlock) to Middle Permian (Guadalupian).

Discussion: This group incorporates genera that differ in their internal plates and ventral muscle field from Martinioidea, and come closer to Ingelarelloidea in the ventral valve, but differ in the nature of the dorsal valve. Tabellae may be strong, yet are definitely absent from some of the better known of species and genera. Full understanding of the various genera and families is hindered by poor knowledge of internal features and even micro-ornament for several genera. The group commenced with stem group Tenellodermidae, succeeded by groups with a ctenophoridium.

Family **ELYTHYNIDAE** Gourvennec, 1994d

[Elythynidae Gourvennec, 1994d in Carter et al. 1994, p. 338].

Diagnosis: Flanks plicate, ornament of pits or pits and spinules or pustules, dental plates and adminicula, ctenophoridium and crural plates. Tabellae present in at least some genera, but apparently absent from others. Lower Devonian (Pragian) to Middle Devonian (Givetian).

Genera: *Elythyna* Rhzonsnitskaya, *Najadospirifer* Havlíĉek (syn. *Naiadospirifer* Havlíček lapsus calami), *Planispirifer* Breivel & Breivel*, Tatjanaspirifer* Cherkesova.

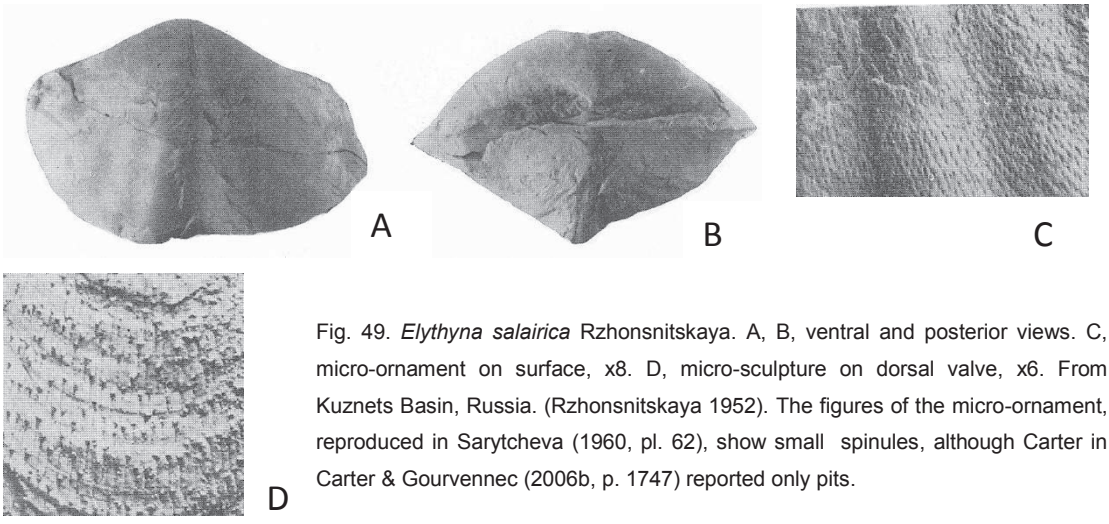


Fig. 49. *Elythyna salairica* Rzhonsnitskaya. A, B, ventral and posterior views. C, micro-ornament on surface, x8. D, micro-sculpture on dorsal valve, x6. From Kuznets Basin, Russia. (Rzhonsnitskaya 1952). The figures of the micro-ornament, reproduced in Sarytcheva (1960, pl. 62), show small spinules, although Carter in Carter & Gourvennec (2006b, p. 1747) reported only pits.

Discussion: This family is chosen as name giver for the superfamily, as genera are moderately well known. The genera share pits and pustules over the surface, broad sulcate shell, and well developed adminicula. The presence of tabellae is well demonstrated by a transverse section for *Elythyna* in Gourvennec in Carter & Gourvennec (2006b, fig. 1148.1j), but otherwise documentation for the genera is incomplete, especially with regards the dorsal interior. The genus has high adminicula, as well as fine pits and pustules. *Najadospirifer*

Havlíček shows a long sulcal tongue and anterior costae, with micro-ornament of pits and tubercles. Adminicula are high, and tabellae ("crural plates") were recorded as short. No tabellae were shown in Fig. 1148.3e of the *Revised Brachiopod Treatise*, possibly because the section lies well in front of the posterior beak. *Tatjanaspirifer* Cherkesova has plicae and short adminicula and tabellae ("crural plates") described as short, with micro-ornament of marginal spines and random coarser spines and very faint capillae. All are of Lower Devonian up to Middle Devonian age. *Planispirifer* Breivel & Breivel, 1999, p. 91 from the lower Devonian (Pragian) of the Urals is large with well developed fold and sulcus and micro-ornament of dense slightly elongate tubercles. Dental plates are developed, and crural plates are free of the floor, indicating that there are no tabellae. Clarification of the dorsal interior as well as reinforced knowledge of micro-ornament for these genera should allow more confident assessment of the group, and allow or rule out subdivision or tolerance of variation.

The family is only moderately close to Crassumbinae Carter in micro-ornament and even further removed from Gerkispiridae of Upper Devonian and basal Carboniferous age in micro-ornament and plication (see p. 82). In such respects the genera come closer to those of Elivellinae and Eomartiniopsinae within the same superfamily, and so are regarded as ancestral, prior to loss of the tabellae, which were seldom more than short. A further question concerns whether the group arose directly from Cyrtioidea or from within Ambocoelioidea (p. 360), the latter possibility asserted by Carter & Gourvennec (2006a). It seems acceptable insofar as members of the ambocoelioid family Rhynchospiriferidae may have dental plates and tabellae, and capillae or more rarely spines, and some genera such as *Havlicekia* Boucot and *Myriospirifer* Havlíček are of similar subrounded shape with smooth surface. Ambocoeliids are pustulose rather than pitted in their micro-ornament, and as a rule lack adminicula, and have reduced if any dental plates, and often have a cruralium. The more critical question concerns the relationship to Adolfiidae. Like Elythynoidea, dental and adminicula plates are present in Adolfiidae, and as a rule crural plates are not supported by tabellae. It is considered that the presence of pitted micro-ornament, and well developed rather than short adminicula and tendency for Adolfiidae to be less rounded in outline with more extended hinge rule against a link, and point to cyrtioidean connections. Ancestors must be sought amongst genera of pre-Wenlockian age, in genera that display adminicula and presumably tabellae, which would favour members of Eospiriferinae, and possibly weakly plicate, such as *Macropleura* and other genera within Eurekaspiriferinae.

Family **TENELLODERMIDAE** Carter, Johnson & Gourvennec, 1994

[Family Tenellodermidae Carter, Johnson & Gourvennec, 1994, p. 338].

Diagnosis: Ctenophoridium absent. Silurian (upper Wenlock) to Middle Devonian (Eifelian).

Genera: *Tenellodermis* Havlíček, *Cingulodermis* Havlíček.

Discussion: In many respects the two genera assigned to this family are close to members of Cyrtiimorphi, being close in size and shape, and either sulcate or gently plicate, and close to Eospiriferidae, except that the delthyrium is open. They also come moderately close to their

successor Family Elythynidae, from which they differ in possessing in place of a ctenophoridium a tubercle as in *Tenellodermis* Havlíček, or occasionally bifid cardinal process as in *Cingulodermis* Havlíček. *Tenellodermis* may be plicate, and has micro-ornament of growth-lines and minute pits, whereas *Cingulodermis* displays growth-lines, and is sulcate without plicae. No pits are developed in members of Cyrtiimorphi. Dental plates were described as long and thin in *Tenellodermis*, and as short in *Cingulodermis*. This genus clearly has adminicula (Gourvennec in Carter & Gourvennec 2006b, Fig. 1147.1e), though

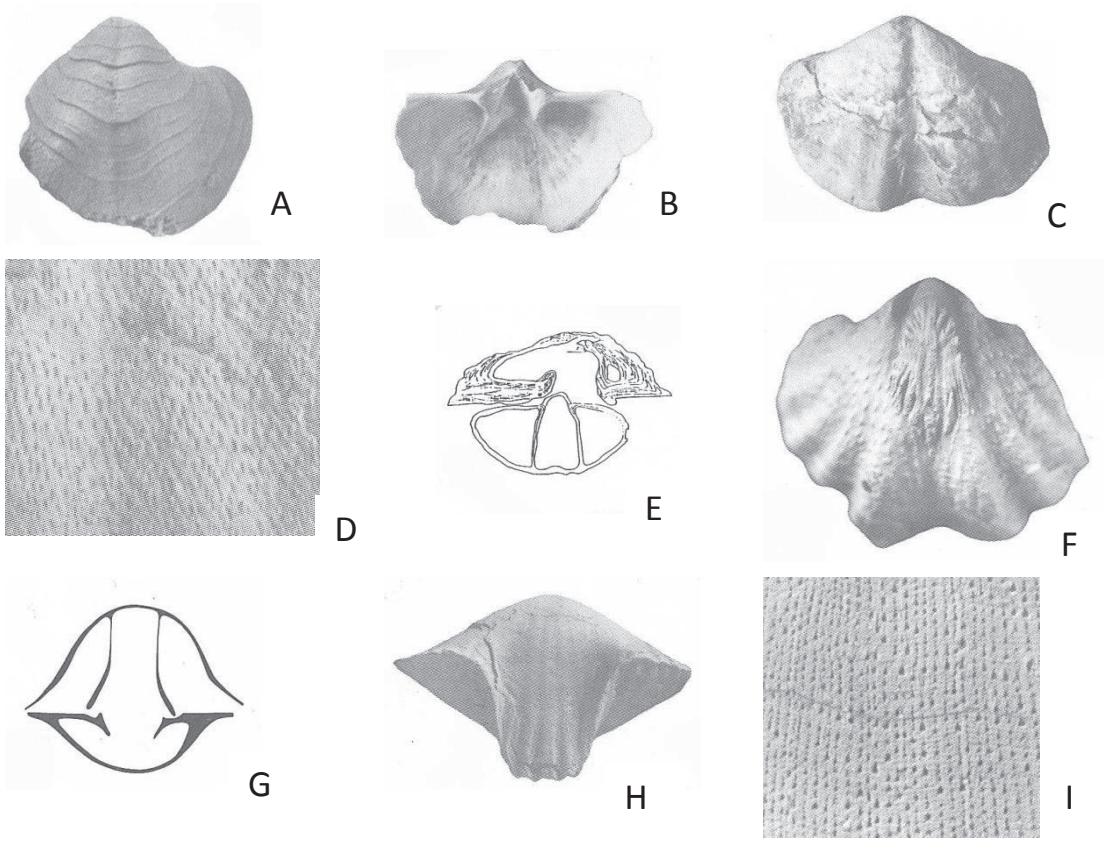


Fig. 50. A, B. *Cingulodermis cinctus* Havlíček, ventral valve, x 2, and ventral interior, x2.6. From Pragian (Devonian) of Czech Republic. (Havlíček 1959). C-E, *Elythyna salairica* Rzhonsnitskaia, C, ventral valve, x0.7. D, micro-ornament, x6. E, cross-section x2, showing high adminicula and tabellae. From Eifelian of Salair. (Rzhonsnitskaya 1952). F, *Tatjanaspirifer variabilis* Cherkesova, ventral interior, x1. From Pragian of Taimyr. (Cherkesova 1991). G-I, *Najadospirifer najadum* (Barrande). G, cross-section x 1.5. H, anterior view x1. I, micro-ornament x12. From Pragian of Czech Republic. (Havlíček 1959, 1971).

not noted in the *Revised Brachiopod Treatise*. The presence of these adminicula means that Martinioidea are a step further away, because they have come to lose such plates. Crural plates (= tabellae) were stated to be absent from *Tenellodermis* and short in *Cingulodermis*. *Tenellodermis* is of Silurian (upper Wenlock) and Lower Devonian (Lochkovian) age, and *Cingulodermis* is of Lower to Middle (Lochkovian to Eifelian) Devonian age.

Family **EOMARTINIOPSIDAE** Carter, 1994

[Nom. transl. hic ex Eomartiniopsinae Carter in Carter et al. 1994, p. 339].

Diagnosis: Lateral slopes may be weakly plicate, micro-ornament of growth lines, capillae or pits, adminicula well developed, tabellae short or absent. Upper Devonian (?Famennian) to Middle Permian (Guadalupian).

Discussion: This family is close to Elythynidae and was not explicitly distinguished from that family in the *Revised Brachiopod Treatise*. The prime distinction appears to lie in the age of Elythynidae, as Lower and Middle Devonian, compared with Eomartiniopsinae which began in the Upper Devonian. In this outline there is some rearrangement of subfamilies and families to better express relationships, centred on a separation from Martiniidae, but further study is needed to validate the distinctions between Elythynidae, Eomartiniopsinae and Elivellinae, given that several genera involved in the family groups are poorly known.

Subfamily **EOMARTINIOPSINAE** Carter, 1994

[Eomartiniopsinae Carter in Carter et al., 1994, p. 339].

Diagnosis: Adminicula moderately to well developed. Tabellae very short or absent. Low radial ribs cover both valves, except in *Eomartiniopsis*. Micro-ornament of pits known for some genera, others less reliably placed have commarginal growth lines. Upper Devonian (?Famennian) to Lower Carboniferous (Visean).

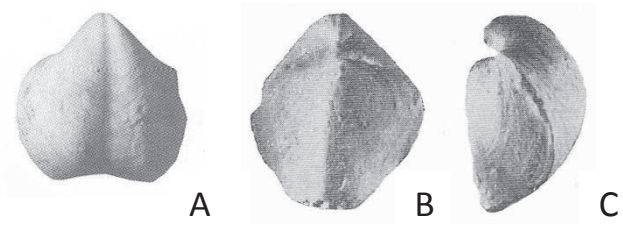


Fig. 51. *Eomartiniopsis elongata* Sokolskaia, ventral, dorsal and lateral views, x1. From Tournaisian of Moscow Basin, Russia. (Carter in Carter & Gourvennec 2006b, Sokolskaya 1941).

Genera: *Eomartiniopsis* Sokolskaya, *Globispirifer* Tachibana, ?*Kisilia* Nalivkin, *Merospirifer* Reed.

Discussion: The listing of the above genera modifies the outline in Carter in Carter & Gourvennec (2006b). Apart from slight differences in the development of the sulcus and fold, and slight differences in the strength of the low external ribbing, genera appear to be similar in internal features and close in age, and the fold of several genera displays a shallow dorsal median groove. What appear to be most significant for family position are facets such as the presence of well formed adminicula as well as dental plates, and a micro-ornament of pits, which helps distinguished the subfamily from Elivellinae with capillae and from Ingelarellidae with elongate grooves, not to mention other groups with small spines.

Inexplicably Eomartiniopsinae was treated as a subfamily of Martiniidae in the Treatise (Carter in Carter & Gourvennec 2006b, p. 1754), but the presence of adminicular plates indicate a ready distinction, and points to an association with Elythynidae and Tenellodermidae.

One of the features of *Eomartiniopsis* is the comparatively smooth shell, with sulcus and fold and only traces, if any, of anterior gentle plicae. *E. waschkuricus* Fredericks (see Aizenberg (1971, pl. 68, fig. 1a, 1b), *E. maximovae* Besnossova in Sarytcheva et al. 1963, *E. waschkuricus osturalicus* Lapina, *E. waschkuricus longus* Kalashnikov, 1974, *E. planosinuata* Poletaev, 1975, *E. grandiformis* Plodowski, 1968, *E. tscherepeti donaica* Poletaev, 1975 and *E. globularis* (Barchatova) are amongst species that are smooth, with no sign of plicae or costae. *E. lakahalensis* Brice (see Brice at al. 2005, pl. 5, fig. 6-21) and *Eomartiniopsis rostrata* (Girty) also lack plicae, the latter illustrated by Carter (1972a, pl. 2, fig. 1-11; 1999, Fig. 15E-X, 16). But micro-ornament of *rostrata* is not known, leaving uncertainty over the generic position.

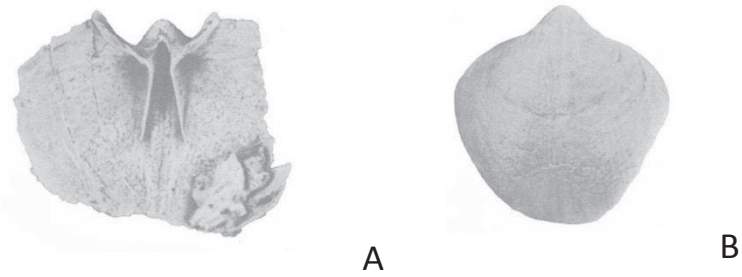


Fig. 52. A, B, *Merospirifer insolita* (Reed), internal and external views of ventral valve, x2, x1. From Visean of Scotland. (Brunton 1984).

Ivanova asserted that the dorsal valve of *Eomartiniopsis* has very short plates of what are herein called tabellae. That was denied by Carter in Carter & Gourvennec (2006b) on the basis of interpretation of figures, but the type material had not been re-examined. Various species identified with *Eomartiniopsis* Sokolskaya in North America (Carter 1972a, Fig. 6; 1987, Fig. 25; 1988, Fig. 25; 1999, Fig. 16) have been sectioned and show no tabellae. Besnossova in Sarytcheva et al. (1963, Fig. 132b) in describing *Eomartiniopsis glaberiformis* Besnossova figured two short plates attached to the floor of the valve, which may be tabellae, or could be interpreted as thick dental socket plates, projecting up from the floor of the valve, and unlike the dental sockets of the North American material, in which the socket floors are subhorizontal, much as in *Ambikella* figured (as *Ingelarella*) by Campbell (1961, Fig. 7). The ventral muscle field is very like that of Ingelarellidae. Superficial pits are present as micro-ornament in at least some species and genera, but micro-ornament is not known for a number of species.

Fig. 53. *Kisilia linguata* Nalivkin, dorsal aspect, x 3. From Tournaisian (Lower Carboniferous) of Urals, Russia. (Carter in Carter & Gourvennec 2006b).

Genera associated with *Eomartiniopsis* in the *Revised Brachiopod Treatise* have low plicae as a rule, and appear to lack tabellae. Such forms include *Globispirifer* Tachibana, 1964, p. 37, of lower Tournaisian age in Japan, with a few anterior plicae, micro-ornament not observed, well developed adminicula, and large crural plates suspended above the dorsal floor (see *Revised Brachiopod Treatise* 2006, Fig. 1153.3d), and no tabellae. The Visean genus *Merospirifer* Reed, 1949 has finely pitted micro-ornament and long adminicula, with small ridges meeting under the beak (Fig. 55), apparently produced at the edge of the delthyrium rather than equivalent to pleromal ridges, a matter to be explored further, and *Kisilia* Nalivkin, 1979, p. 146 of Tournaisian age has fine plicae, short thin adminicula and short thick median ridge. Given that the micro-ornament and dorsal valve are not known, according to Carter in Carter & Gourvennec (2006b, p. 1756), the genus, if it proves to be valid, is possibly to be associated with other genera on the basis of its shape and plicae, though there are approaches to some Elivellinae. On the other hand, *Rallacosta* Cooper & Grant, 1976, p. 2277 from Guadalupian faunas of Texas, although assigned to the subfamily in the *Revised Brachiopod Treatise*, has low plications and costae that may be fasciculate, and shows unusual pleromal development, so that it is assigned to a separate group (p. 67). *Heteraria* Cooper & Grant was included in the subfamily by Carter in Carter & Gourvennec (2006b, p. 1756), but, having unusual plates, is reallocated to its own subfamily (p. 70).

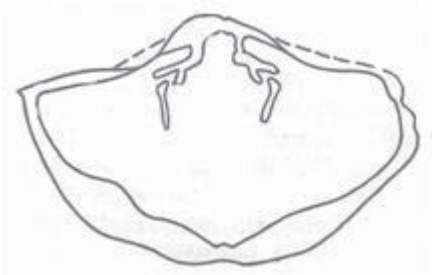


Fig. 54. *Eomartiniopsis waschkuricus waschkuricus* (Fredericks), transverse section x2.5, dorsal valve on top. (Kalashnikov 1974). The plates attached to the floor of the valve could be tabellae.

Subfamily **ELIVELLINAE** Carter, 1994

[Elivellinae Carter in Carter al. 1994, p. 340].

Diagnosis: Ornament of low narrow plicae or costae, ornament of capillae or fine ribs. Dental plates and adminicula short, tabellae absent as a rule. Lower Carboniferous (Tournaisian) to Lower Permian.

Genera: *Elivella* Fredericks, *Besnossoviella* new genus, *Carteriopsis* new genus, *Chuiella* Chen & Shi (possible junior synonym of *Martiniella* Grabau & Tien), *Engania* new genus, *Ushkolia* Martynova & Sverbilova.

Discussion: Carter in Carter & Gourvennec (2006b) stressed the presence of capillae, and and capillation or slightly coarser but fine radial ornament is regarded as the distinguishing feature of the subfamily. *Elivella* Fredericks, 1924, with type species of Cisuralian age, has dental plates and adminicula, both described as short. Costae are low and rounded, the sulcus narrow and shallow and fold narrow and low. Micro-ornament is not clear. *Mouminia* Fredericks, 1924, based on *Martinia incerta* Chernyshev, has narrow hinge line and a

reported dorsal sulcus or groove. Its interior was stated to be like that *Martinia* by Carter in Carter & Gourvennec (2006b, p. 1757), which implies that adminicula and tabellae, and possibly even dental plates, are lacking. That signifies a position within Martiniidae, or given the short hinge and low plicae, a position with Brachythyridae, but there needs to be clarification of the interior, and detail provided for the nature of the micro-ornament.

Chen & Shi (1999, p. 266) proposed a new name *Chuiella* for species previously assigned to *Martiniella* Grabau & Tien, of Mississippian age in China. *Chuiella* has capillae and long adminicula, called dental plates by Chen & Shi. The dorsal interior of *Chuiella* has not been figured but crural plates (or tabellae?) were reported as being short. *Martiniella* Grabau & Tien in Grabau (1931a, p. 420) was proposed as a nomen nudum, with type species *M. nasuta* undescribed. It is capillate, but described as otherwise like *Merospirifer* by Carter in Carter & Gourvennec (2006b, p. 1757). Wang (in Wang et al. 1964) endeavoured to retrieve *Martiniella* by substituting a new type species rendered as *Martiniella chinglungensis* Chu, 1933, and readers will enjoy the verbal gymnastics displayed by Chen & Shi (1999, pp. 267, 269) in rejecting that proposal and seeking to follow procedures mandated by the International Code of Zoological Nomenclature, in order to justify their new generic name. The trouble remains – if *Martiniella* is a valid generic name, as they concluded, then *Chuiella* remains under threat of being a junior synonym, and protestations that the type species cannot be retrieved and recognized may not hold true for ever. If *Martiniella* is a valid generic name, then surely it should be possible to nominate a type species, just as Wang (1964) endeavoured to do. He sought to protect the conception of Grabau, by making up for the errors of omission, which would seem to be a courteous and practical advance that avoided future uncertainties and therefore instability of nomenclature. Otherwise the name should be firmly rejected. The present situation remains unsatisfactory.

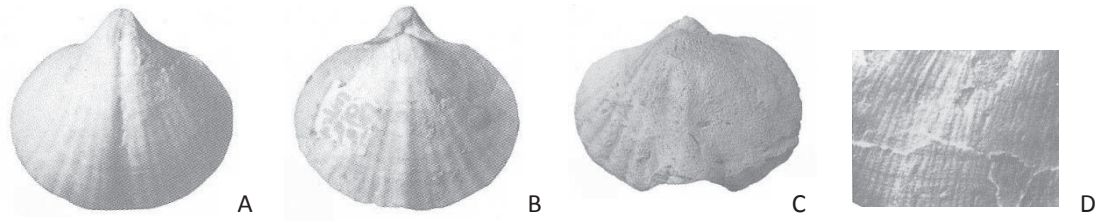


Fig. 55. A, B, *Elivella baschkirica* (Chernyshev), ventral and dorsal aspects, x2. From Cisuralian of Urals. (Carter in Carter & Gourvennec 2006b). C, D, *Ushkolia livinovitchae* Martinova & Sverbilova, dorsal aspect, x0.8, and micro-ornament, x12. From upper Famennian of Kazakhstan. (Carter in Carter & Gourvennec 2006b).

The Upper Devonian genus *Ushkolia* Martynova & Sverbilova, 1969 has simple plicae and long adminicula. This suggests that the genus should be recast as a member of Eomartiniopsinae (cf. *Globispirifer*), but fine capillae are illustrated (Carter in Carter & Gourvennec 2006b, Fig. 1155.3e), whereas small pits are found in some of the genera placed in Eomartiniopsinae. The decision to rely on the presence of capillae for recognition of

Elivellinae is a practical one, given the sparsity of information on the interior. Capillation is also developed in members of the Crassumbinae Carter, of especially Tournaisian age, and these have adminicula and short tabellae, with spinules. Fine capillation is also observed weakly in *Spinospirifer* Martynova, of upper Devonian age and classed in Gerkispiridae Carter. Carter in Carter & Gourvennec (2006b, p. 1756, 1757) stated that dental plates became progressively shorter or absent in younger genera within Elivellinae, and gave a time range for the subfamily of Upper Devonian (upper Famennian) to Lower Permian (Cisuralian).

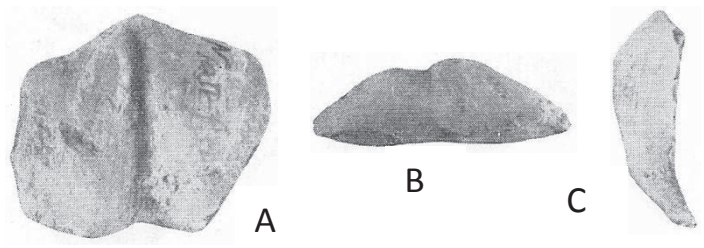


Fig. 56. *Martiniella martiniformis* (Girty) of Chu in Tong & Xian (1978, pl. 91, fig. 5). Showing a ventral valve from ventral (A), posterior (B) and lateral (C) aspects, x1. From Mississippian of China.

Genus ***Engania*** new genus

Name: From Enga Ridge, northern Australia.

Diagnosis: Medium size, moderately well formed sulcus and distinct fold for length of shell, narrow but strong plicae laterally. Micro-ornament of radial capillae and commarginal growth-lines. High dental plates and long adminicula, crural plates but no tabellae.

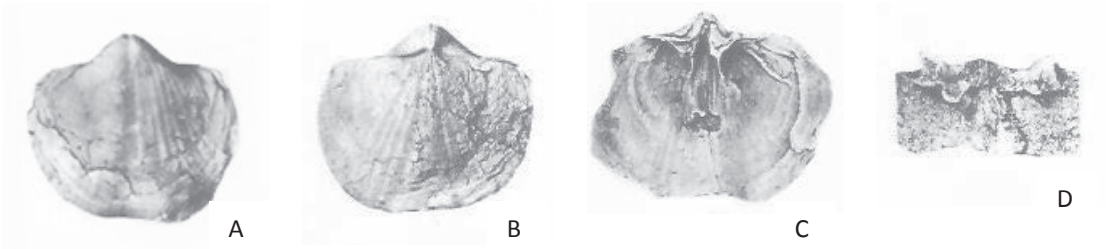


Fig. 57. *Engania costata* (Roberts). A, ventral valve, x1. B. dorsal aspect, x1. C, ventral interior, x2. D, dorsal interior, x1, showing high crural plates without tabellar supports. From Tournaisian of Western Australia. (Roberts 1971).

Type species: *Eomartiniopsis costata* Roberts, 1971, p. 244, from Enga Sandstone (Tournaisian) of northern Australia, here designated.

Discussion: An arched delthyrial plate is recorded below the ventral umbo, and it passes forward into a double ridge, meeting under the umbo and lying along the edges of the delthyrium, although detail is not entirely clear. *Elivella* has less well defined fold and more open plicae, and *Ushkolia* has fewer and open plicae. *Engania* is distinguished from *Eomartiniopsis elongata* Sokolskaya, 1941, type species of *Eomartiniopsis*, by the presence of capillae, and narrower and more sharply defined dorsal fold, and by the presence of over ten pair of narrow plicae each side of the sulcus, with similar plications over the dorsal valve.

Species of *Eomartiniopsis* rarely may display plicae, but they are very faint, and often restricted to the anterior sulcus and fold. As well, the sulcal borders merge more gradually with the lateral flanks. *Globispirifer* Tachibana has a broad fold that merges more subtly with the flanks, and virtually no sulcus, and there are lateral plicae, but no capillae. The shell is thick and muscle field large. This genus comes from the Tournaisian of Japan, and another Tournaisian genus *Kisilia* Nalivkin also has numerous slender ribs, and sulcus limited to the anterior shell, and broad weakly delineated fold. *Merospirifer* Reed from the Visean of Scotland, England and Ireland, is rather similar, and again without capillae, with anterior sulcus, narrow and shallow posteriorly, broad anterior low fold, and very subdued and narrow plicae (like those of *Kisilia*), and well formed crural plates, as revised by Brunton (1984).

Fig. 58. *Brachythyris girtyi* Branson. Dorsal (A), anterior (B) and C, posterior aspects, x1, dorsal valve on top. From Kinderhookian of Missouri and Texas. The genus and micro-ornament are uncertain. (Carter 1967b).

Tournaisian species from the United States are close in shape and plication to the North Australian form, and of similar Tournaisian age, including *Brachythyris girtyi* Branson, 1938, referred to *Eomartiniopsis* by Carter (1967). But the nature of the micro-ornament is insecure, although it is possible that only growth increments were developed. *Eomartiniopsis? susanae* Martínez-Chacón (1978) has low plicae, but micro-ornament is uncertain.

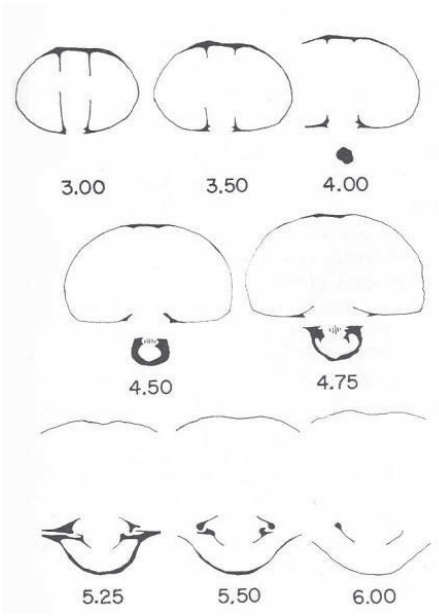


Fig. 59. *Brachythyris girtyi* Branson, serial sections, ventral valve on top, x 1 approx. with distance in mm from ventral beak. From Tournaisian of Texas. See Fig. 58. (Carter 1967b).

Tournaisian-Visean specimens from the Gancaohu area of the southern Tienshan Mountains of China that were assigned to *Brachythyris ovalis* (Phillips) by Chen & Archbold (2000, p. 193, Fig. 5.12, 21-25; Fig. 6) have firm lateral plicae, smooth fold and sulcus, and high adminicula, somewhat as in *Engania*, but there are no capillae.

Genus ***Carteriopsis*** new

Name: For John L. Carter.

Diagnosis: Distinguished by low even commarginal ornament over both valves and very fine radial ribs.

Type species: *Eomartiniopsis kinderhookensis* Carter, 1988 from Kinderhookian of Illinois, USA, here designated.

Discussion: The species has been well described by Carter (1988, p. 66, Fig. 24.35 – 24.47, 25). The presence of fine radial ornament suggests that the genus belongs to Elivellinae, and could have been like a precursor to the subfamily Rallacostinae (see below). There are high adminicula and low crural plates, without tabellae and without a connector plate.

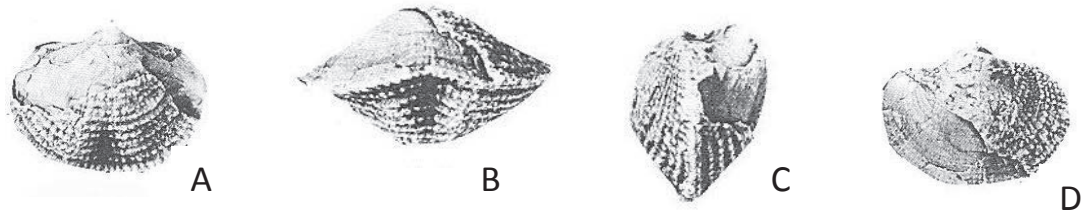


Fig. 60. *Carteriopsis kinderhookensis* (Carter), ventral, anterior, lateral and dorsal aspects, x1.5. From Kinderhookian of Illinois, United States. (Carter 1988).

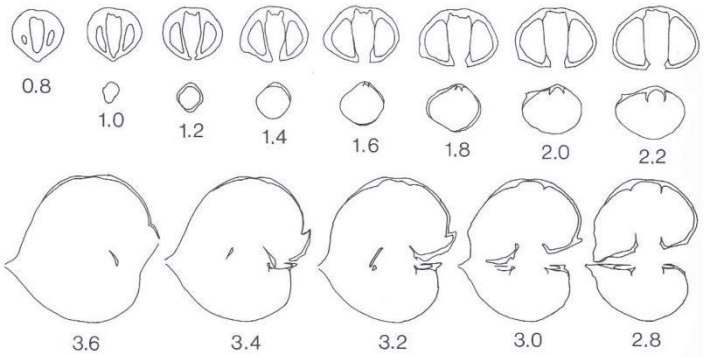


Fig. 61. *Carteriopsis kinderhookensis* (Carter), serial sections, x1. Distance from ventral beak shown in mm, ventral valve on top. From Kinderhookian of Illinois, United States. (Carter 1988).

Genus ***Besnossoviella*** new genus

Name: Named for G. A. Besnossova.

Diagnosis: Small transverse shells with moderately well defined sulcus and sulcate fold, shell covered by fine continuous costae. Adminicula well developed.

Type species: *Eomartiniopsis glaberiformis* Besnossova, 1963, p. 300 from Kuznets Basin (Visean) of Russia, here designated.

Discussion: This genus like *Carteriopsis* is unusual because of the fine ornament, which consists of coarse capillae or fine costae over both valves, unlike that known for any other elythynoid genus. There is clearly some approach, without being identical, with members of Rallocostinae (see below), but the genus is much older, at Lower Carboniferous rather than mostly Middle Permian, and there is no connector plate, so that the genus is not deemed to be closely related. Thick support plates for the socket plates are possible tabellae. *Kisilia* Nalivkin shows fine ribs, but lacks well defined sulcus.

Fig. 62. *Besnossoviella glaberiformis* (Besnossova), ventral valve and, dorsal valve, x1, and transverse sections of ventral valve and dorsal valve, x2.5. From Visean of Kuznets Basin, Russia. (Besnossova 1963).

Subfamily **RALLACOSTINAE** new subfamily

Name genus: *Rallacosta* Cooper & Grant, 1976, p. 2277, from Guadalupian of Texas, USA, here designated.

Diagnosis: Small weakly transverse oval shells with rounded cardinal extremities and low interareas, shell smooth or ornamented by low plicae or costae, sulcus shallow and fold low. Adminicula and dental plates with strong pleromal ridges and small connector plate, low crural plates, no tabellae. Lower to Middle Permian (Cisuralian – Guadalupian).

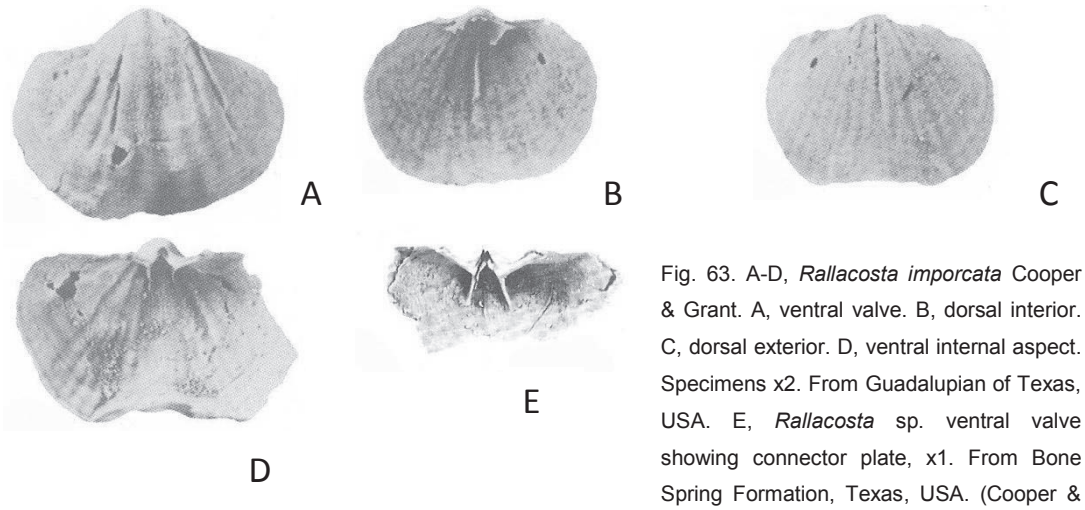


Fig. 63. A-D, *Rallacosta imporcata* Cooper & Grant. A, ventral valve. B, dorsal interior. C, dorsal exterior. D, ventral internal aspect. Specimens x2. From Guadalupian of Texas, USA. E, *Rallacosta* sp. ventral valve showing connector plate, x1. From Bone Spring Formation, Texas, USA. (Cooper & Grant 1976).

Genera: *Rallacosta* Cooper & Grant, *Pulvinoconcha* new genus, *Xysticaria* new genus.

Discussion: *Rallacosta* is a highly unusual genus, limited to the upper Cisuralian and Guadalupian of Texas. It has been interpreted as a member of Eomartiniopsinae by Carter in Carter & Gourvennec (2006b, p. 1754), and there are similarities in shape and short interarea and presence of adminicula. But the genus would have to be regarded as highly exceptional in such a position, because of the presence of well defined radial plicae. More than that, the dental plates and adminicula bear heavy pleromal thickening as described by Cooper & Grant (1976). Such morphology is otherwise scarcely known amongst Martiniimorphi, although some genera placed in Eomartiniopsinae (*Merospirifer*), and Elivellinae (*Engania)* show a ridge along the posterior edges of the delthyrium. Normally the arrangement is a spiriferoid construct. Were that affinity to be established, it would explain the otherwise anomalous radial ornament, and place *Rallocosta* as an exceptional form evolved in paleotropical waters during the late Cisuralian, derived perhaps from gypospiriferin stock. On the other hand, the shortness of the hinge with obtuse cardinal extremities suggests a development from elythynoid or ingelarelloid stock. Micro-ornament is dominated by commarginal growth lines or laminae, stronger in *Xysticaria* than in *Rallacosta*, with no sign of radial capillae, and no sign of the elongate micro-grooves that help typify Ingelarellidae, to rule out any origin from *Martiniopsis* Waagen, even though that genus is of similar shape, and has somewhat allied internal plates, although without any sign of a connector plate.

Genus ***Xysticaria*** new genus

Name: From species name of type species.

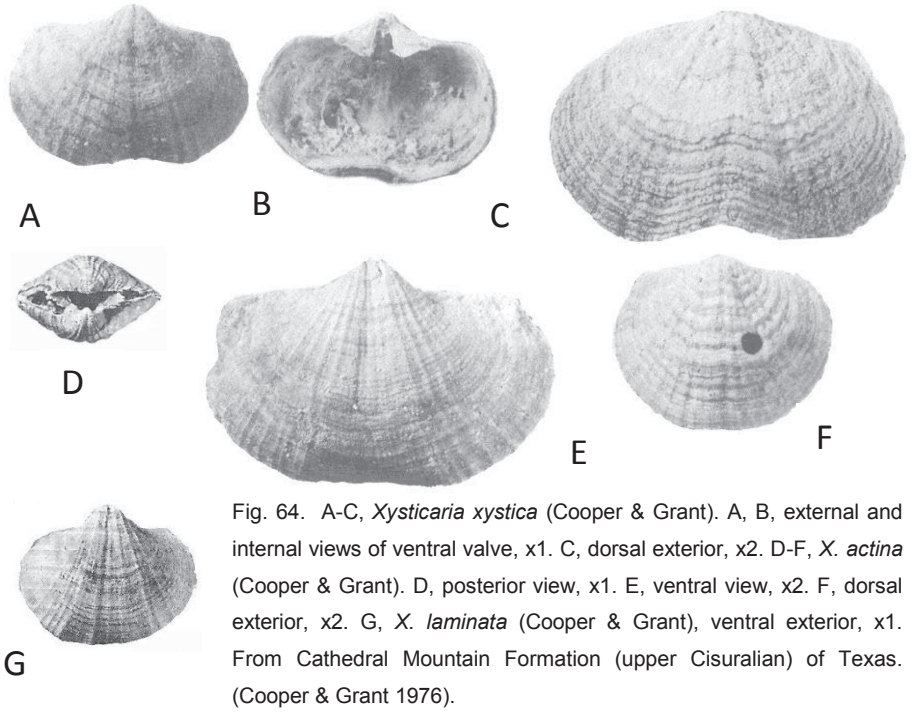


Fig. 64. A-C, *Xysticaria xystica* (Cooper & Grant). A, B, external and internal views of ventral valve, x1. C, dorsal exterior, x2. D-F, *X. actina* (Cooper & Grant). D, posterior view, x1. E, ventral view, x2. F, dorsal exterior, x2. G, *X. laminata* (Cooper & Grant), ventral exterior, x1. From Cathedral Mountain Formation (upper Cisuralian) of Texas. (Cooper & Grant 1976).

Diagnosis: Both valves ornamented by low costae, with low commarginal laminae. Interarea short, adminicula short, with brief connector plate and low umbonal callosity as a rule. Fold broad and low.

Type species: *Rallacosta xystica* Cooper & Grant, 1976, p. 2281 from Cathedral Mountain Formation (Kungurian) of Glass Mountains, Texas, here designated.

Discussion: The type species is comparatively large for the family and has an ornament of round-crested costae crossed by strong commarginal growth laminae. It is readily distinguished from *Rallacosta*, which has an ornament of low broad plicae, but internal detail is much the same in both genera. Two other species from the Cathedral Mountain Formation also belong to *Xysticaria*, named *actina* Cooper & Grant and *laminata* Cooper & Grant.

Genus ***Pulvinoconcha*** new genus

Name: pulvinus – pillow, cushion; concha – shell, Lat.

Diagnosis: Small with oval outline, short hinge, high ventral interarea, weak commarginal ornament, no radial ribbing. Short dental plates and very short adminicula, pleromal thickening diverging anteriorly, low crural plates. Lower and Middle Permian (Cisuralian, Guadalupian).

Type species: *Pulvinoconcha getaway* new species from Cherry Canyon Formation (Guadalupian), Texas, here designated.

Discussion: This genus is readily distinguished by the complete lack of radial ornament. Otherwise it is similar in shape and internal structures to *Rallocosta* and *Xysticaria*. The absence of elongate surface grooves shows that the genus is not the same as *Martiniopsis* Waagen. The genus is highly distinctive, but scarcely represented in the fossil record. Even in the astonishingly rich faunas of the Glass Mountains of Texas, there are a few specimens of of two species, in the Bone Spring and Cherry Canyon Formations, separated by a long interval lasting from late Cisuralian and the early and middle Guadalupian, with no representation yet discovered.

Pulvinoconcha getaway new species

1976 *Rallacosta* species 1 Cooper & Grant, p. 2282, pl. 646, fig. 1-6.

Name: Named from Getaway Member of Cherry Canyon Formation, source of the fossil material.

Diagnosis: Small suboval little inflated shells with shell produced anteriorly by shallow anterior sulcus.

Holotype: USNM 153191a, figured by Cooper & Grant (1976, pl. 646, fig. 4-6) and herein (Fig. 65A, C), here designated.

Description: The species is described by Cooper & Grant (1976). The anterior commissure is broadly uniplicate with shallow broad sulcus that starts at the beak as a narrow depression. The surface is smooth, except for growth lines and varices over the anterior shell. The dorsal valve is gently convex, becoming almost flat anteriorly, with very low broad fold commencing

near midlength. Dental plates are short, supported by very short adminicula, and the muscle field is of an elongate diamond shape, extending to midlength. No myophragm. Shallow socket plates in the dorsal valve. partly covered by growths, small ctenophoridium and very low crural plates.

Discussion: This species is readily distinguished from species of *Rallocosta* and *Xysticaria* by the lack of radial plicae or costae. Similar material is represented from the Bone Spring Formation in the Glass Mountains, of mid-Cisuralian age (Cooper & Grant 1976, p. 2282, pl. 633, fig. 38, pl. 646, fig. 7-9), and this has a prominent median ridge internally, expressed as a median groove externally. This species thus represents the oldest known rallacostin, and it might be taken as the source of the group, persistent from Eomartiniopsinae, or developing as an aberrant ingelarellid from *Martiniopsis*-like stock, which is distinguished by its micro-ornament of closely spaced grooves in quincunx. It must be noted that the prodigious sampling of material in the survey of Glass Mountains brachiopods by G. A. Cooper and R. E. Grant focused on carbonates. The intervening clastic sediments were scarcely collected. (R. E. Grant pers. comm.). A word incidentally on their remarkable studies of Permian brachiopods from the Glass Mountains of Texas. Curry & Brunton (2007, p. 2943) questioned whether the large number of species and genera from that area was “biologically realistic”. That seems presumptious, downplaying the integrity of Cooper & Grant, as if they were not world experts on brachiopods, and as if Curry & Brunton knew what was biologically realistic.

Fig. 65. *Pulvinoconcha getaway* new gen., new sp. A, C, external and internal views of ventral valve holotype, USNM 153191a. B, dorsal interior. Specimens x0.8, from Getaway Member, Cherry Canyon Formation (Capitanian), Texas, USA. (Cooper & Grant 1976).

Subfamily **HETERARIINAE** new subfamily

Name genus: *Heteraria* Cooper & Grant, 1976, p. 2275 from Cathedral Mountain Formation (Kungurian) of Texas, United States, here designated.

Diagnosis: Distinguished from other genera assigned to Elythynoidea by the development of two plates extending horizontally from the edge of the delthyrium, to partly close the delthyrium, without being medianly fused. The plates are attached to the short dental plates and adminicula. Crural plates and tabellae present. Micro-ornament of commarginal growth-lines.

Genus: *Heteraria* Cooper & Grant.

Discussion: Cooper & Grant (1976) have drawn attention to the unusual nature of two plate-like structures that help close the delthyrium in this genus. They wrote that the plates were

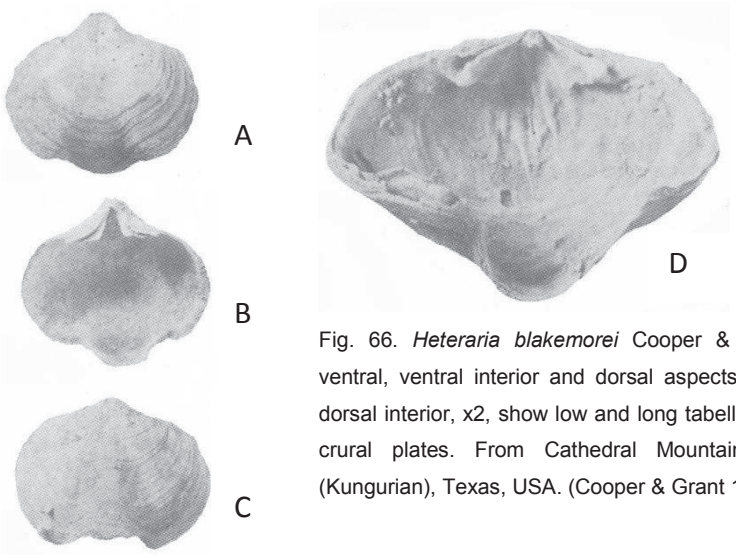


Fig. 66. *Heteraria blakemorei* Cooper & Grant. A-C, ventral, ventral interior and dorsal aspects, x1, and D, dorsal interior, x2, show low and long tabellae below the crural plates. From Cathedral Mountain Formation (Kungurian), Texas, USA. (Cooper & Grant 1976).

horizontal to slightly shelving towards midvalve, and acted like deltidial plates, but are differently oriented, being dorsal to the delthyrial edge rather than flush with it. They are welded to the dental edge, as a prolongation of the tooth in a distal direction and to the dental plates where they buttress the interarea. There is no apical plate, and their nature remains open for clarification, but could match aberrant deltidia or more likely pleromal ridges of other genera.

Fig. 67. *Heteraria blakemorei* Cooper & Grant, holotype ventral interior, x1. From Cathedral Mountain Formation (Kungurian), Texas, USA. (Cooper & Grant 1976).

Carter in Carter & Gourvennec (2006b, p. 1756) referred *Heteraria* to Eomartiniopsinae, and the genus is close to members of that group, but is substantially younger, and has its unique narrowing of the delthyrium. Contrary to the claim by Carter in Carter & Gourvennec (2006b) that micro-ornament was “seemingly absent but poorly known”, the shell is ornamented by fine closely spaced growth increments, without pits or grooves. Tabellae are well represented together with crural plates in the dorsal valve, notwithstanding comments about the absence of such plates by Cooper & Grant (1976), as illustrated in Fig. 66D. But adminicula are short.

Superfamily **INGELARELLOIDEA** Campbell, 1959

[Nom. transl. Waterhouse 1998a, p. 3 ex Ingelarellinae Campbell, 1959, p. 333].

Diagnosis: Smooth to sulcate and often plicate, micro-ornament varied, grooves or spinules being common, shell taleolate and exopunctate, adminicula well developed, tabellae well developed to rarely absent. Upper Devonian (Famennian) to Upper Permian (Changhsingian).

Discussion: The plication and development of adminicula and tabellae seen in Ingelarelloidea are features also well represented amongst genera of Eospiriferinae, including *Eospirifer* Schuchert itself, of latest Ordovician to Lower Devonian age. Some early Cyrtiimorphi look very close to Permian Ingelarellidae, including *Endospirifer* Tachibana, of lower Silurian age in the Eospiriferinae, and *Branikia* Havlíček of subfamily Branikiinae, in Adolfioidea, of Lower to Middle Devonian age. This latter genus is plicate with open delthyrium, umbonal callosity, and well formed adminicula, but the dorsal valve differs. An eospiriferid source seems more likely than that of Ambocoelioidea, in which members have reduced tabellae, and adminicula are frequently lacking. Members of Ingelarelloidea were classed within Martinioidea by Carter & Gourvennec (2006b), but differ in having adminicula and usually tabellae.

Family I**NGELARELLIDAE** Campbell, 1959

[Nom. transl. Archbold & Thomas 1986b, p. 582 ex Ingelarellinae Campbell, 1959, p. 333. Syn. Martiniopsidae nom. transl. Carter in Carter et al. 1994, p. 340 ex Martiniopsinae Kotlyar & Popeko, 1967, p. 182].

Diagnosis: Micro-ornament of grooves in quincunx, adminicula well formed, tabellae short to long, rarely absent. Lower Carboniferous (Visean) to Upper Permian (Changhsingian).

Discussion: The family apparently developed from Rorespiriferidae, an allied but older family, and a number of Permian genera appear to have reverted to an overall build close to that of ancestral Eospiriferinae of latest Ordovician, Silurian and Devonian age, with *Eospirifer, Endospirifer, Havlicekia*, and *Myriospirifer* close in shape, development of fold-sulcus and internal plates to such genera as *Ambikella* and *Ingelarella*, but distinguished from Eospiriferinae by micro-ornament and well developed ctenophoridium.

Subfamily **INGELARELLINAE** Campbell, 1959

[Ingelarellinae Campbell, 1959, p. 333. Syn. Martiniopsinae Kotlyar & Popeko 1967, p. 182].

Diagnosis: Tabellae long. Pennsylvanian to Upper Permian (Changhsingian).

Tribe **INGELARELLINI** Campbell, 1959

[Nom. transl. hic ex Ingelarellinae Campbell, 1959, p. 333].

Diagnosis: Shells smooth or plicate, may be sulcate, smooth or with two subplicae, rarely a median rib. Tabellae and adminicula long. Lower Permian (Cisuralian) to Upper Permian (Changhsingian).

Genera: *Ingelarella* Campbell, *Ambikella S*ahni & Srivastava (syn. *Homevalaria* Waterhouse), *Fredericksia* Paeckelmann (nom. nov. pro *Munia* Fredericks, 1918 non Hodge, 1836),

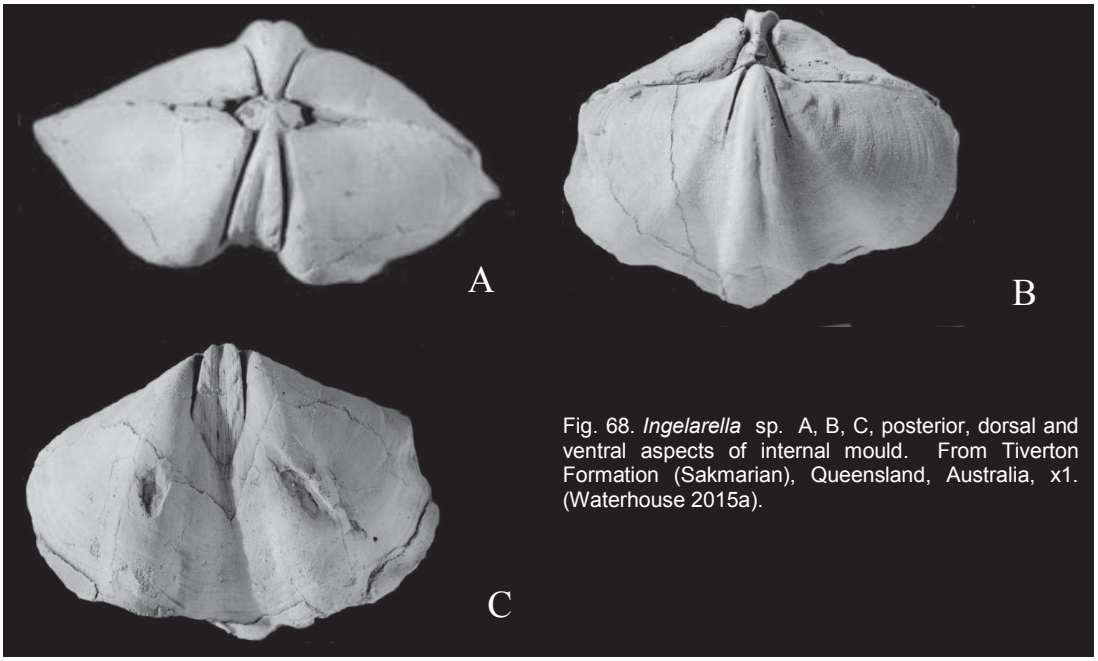


Fig. 68. *Ingelarella* sp. A, B, C, posterior, dorsal and ventral aspects of internal mould. From Tiverton Formation (Sakmarian), Queensland, Australia, x1. (Waterhouse 2015a).

Martiniopsis Waagen, *Tigillumia* Waterhouse, *Validifera* Waterhouse.

Discussion: The development of the internal plates appears to have allowed successful colonization, distribution and diversification more widely and successfully than any other member of Martiniidina: by Permian time the group made up a modest component of boreal faunas and flourished with significant biomass over Gondwana. The development of long tabellae is exceptional for Spiriferida, and the fact that they developed so well marked a return to morphologies in mid-Paleozoic genera such as *Eospirifer* and allies, showing that a morphological feature can be revived. The concentration of genera in high southerly latitudes probably explains why most workers, who study as a rule paleotropical fossil faunas especially each side of the Atlantic, have ignored or misunderstood the significance of the plates and the implications for mid-Paleozoic brachiopod morphology.

Fig. 69. *Ambikella ovata* (Campbell). Dorsal aspect of internal mould, x1.5. From Tiverton Formation (Sakmarian), Queensland, Australia. (Waterhouse 2015a).

Martiniopsis – shells without deep sulcus and high fold, no plicae. Surface grooves, interior with moderately long adminicula and tabellae, no tigillum.

Fredericksia – small, biconvex with sulcus, fold poorly distinguished from lateral slopes except anteriorly, and low plicae. Internal plates well formed, but shorter than in many genera. Micro-ornament not certain.

Tigillumia – shells close to *Martiniopsis* and *Ambikella*, shallow narrow sulcus and round-crested fold, distinguished by long close-set subparallel adminicula and strong tigillum. Tabellae long.

****Tomiopsis*** – low numerous plicae, subplicae within sulcus, channelled fold, moderately long adminicula, short widely diverging tabellae, myophragm, no tigillum as a rule. Deep and crowded long surface grooves and narrow interspaces.

Ambikella – well formed sulcus and fold, sulcal subplicae present or more commonly absent, no fold-channel, plicae present or absent, adminicula moderate to long, moderately closely spaced, tabellae moderate in length (0.3-0.25 of shell length), surface grooves with wide interspaces. No tigillum. Includes *ovata* Campbell, which in some specimens have surface grooves enclosed posteriorly by barchan spines, now assessed as a minor variant.

****Geothomasia*** – shells with well formed sulcus and fold, smooth or plicate, subparallel closely spaced or moderately long and well-spaced adminicula and widely diverging short tabellae.

Validifera – well formed sulcus without subplicae, variable usually low plicae, rounded fold. Characterized by well spaced and divergent adminicula. Tabellae subparallel, moderately long.

Ingelarella – exterior with smooth or plicate shell, smooth or generally subplicate sulcus, surface grooves with wide interspaces, internal plates as in *Ambikella*, distinguished by presence of tigillum, which is a shell thickening of shell along the inner side of the sulcal crest in front of the adductor scars, and by channelled fold.

!Johndearia – large usually non-plicate shells with strong subplicae in broad sulcus, fold round or usually channelled, adminicula and tabellae of moderate length and widely spaced. No tigillum. Very heavy posterior thickening in the ventral valve.

!Oviformia – plicae low or absent, sulcus with anterior median swelling or fold, fold crest rounded, not sulcate. Adminicula and tabellae moderately long. No tigillum.

!Tumulosulcus – fold crest sulcate, otherwise like *Oviformia*.

****Tweedaleia*** – tabellae not developed; sulcus and fold, no plicae, adminicula and crural plates moderately developed.

****Danzania*** – plicate and close to *Tomiopsis*, without strong dorsal myophragm and dorsal adductor ridges. Short tabellae.

Genera of Ingelarellidae. Asterisked genera belong to Geothomasiinae, and !genera to Johndeariini.

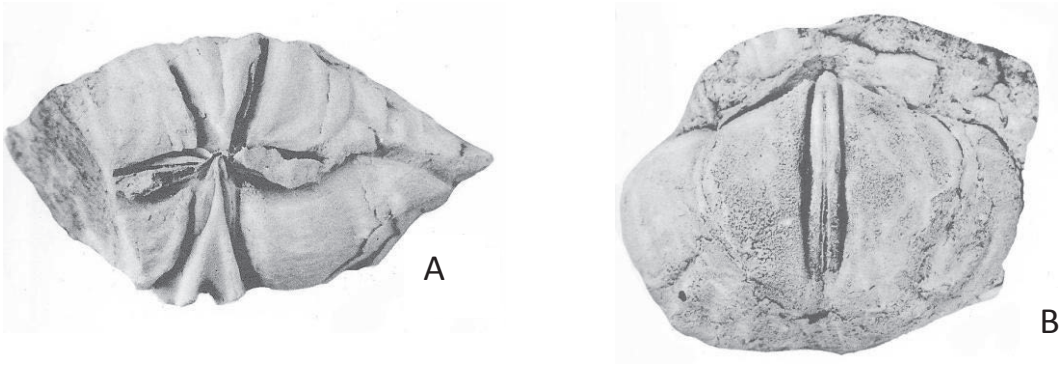


Fig. 70. *Tigillumia parallela* (Waterhouse). A. posterior view, dorsal valve on top, x1.5. B, ventral internal mould, x1. From Changhsingian Kildonan Member, Bagrie Formation, New Zealand. (Waterhouse 1968).

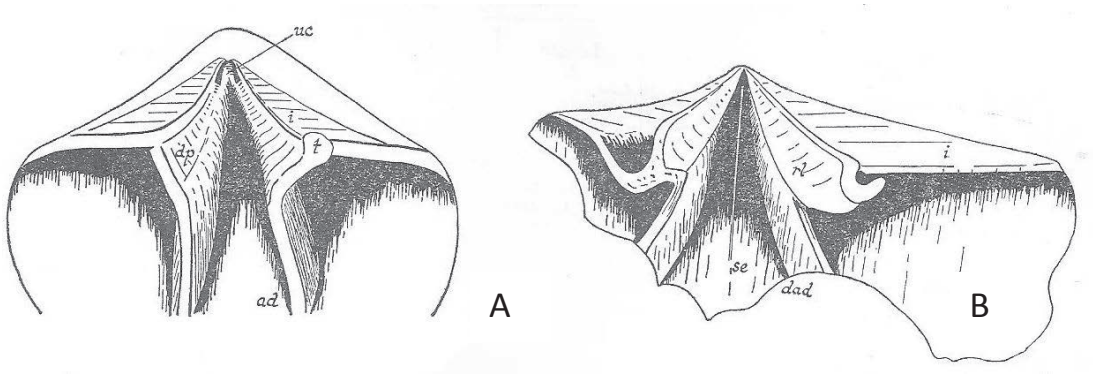


Fig. 71. *Martiniopsis woodi* Waterhouse. Interior of ventral and dorsal valves. In B the crural plate seems to be very short, and the crural plates merge with the inner socket plates. ad – adminicula; dad – tabellae; dp – dental plate; i – interarea; rl – crural plate; se – dorsal septum; t – tooth; uc – umbonal callosity. From Wuchiapingian Earnvale Member, Bagrie Formation, New Zealand. (Waterhouse 1964).

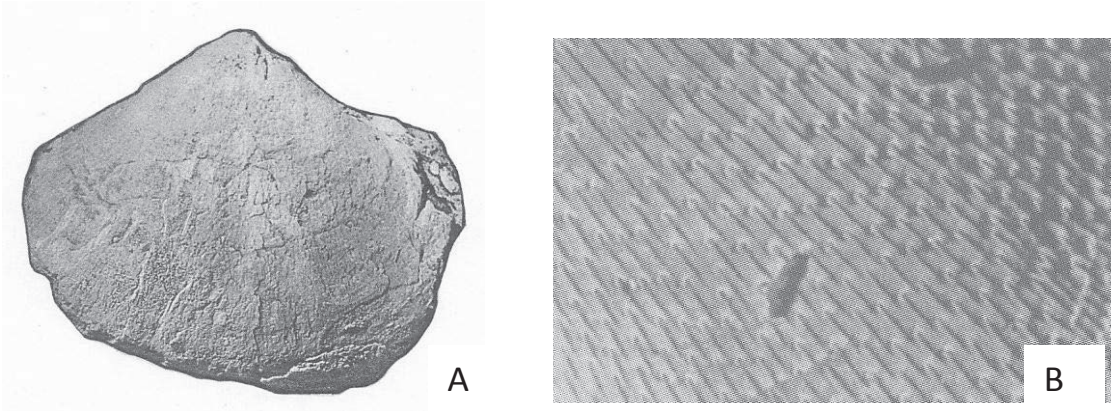


Fig. 72. A, *Martiniopsis woodi* Waterhouse, ventral valve, x1. From Wuchiapingian Earnvale Member, Bagrie Formation, New Zealand. (Waterhouse 1964). B, exceptional micro-ornament in *Geothomasia profunda* (Campbell), x15. From Tiverton Formation (Sakmarian) of Queensland, Australia. (Armstrong 1970b). In most ingelarellids, only the surface grooves are present, without the small barchan spines, and only a few specimens in this species and *Ambikella ovata* show this form of ornament.

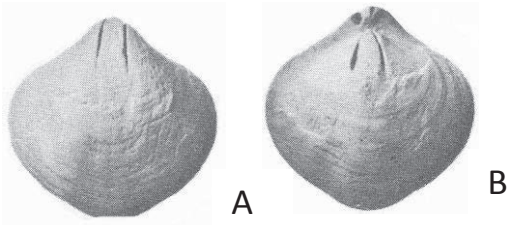


Fig. 73. *Fredericksia simensis* (Chernyshev), dorsal and anterior aspects of internal mould, x2. Upper Carboniferous of northeast Russia. (Grunt 1977b).

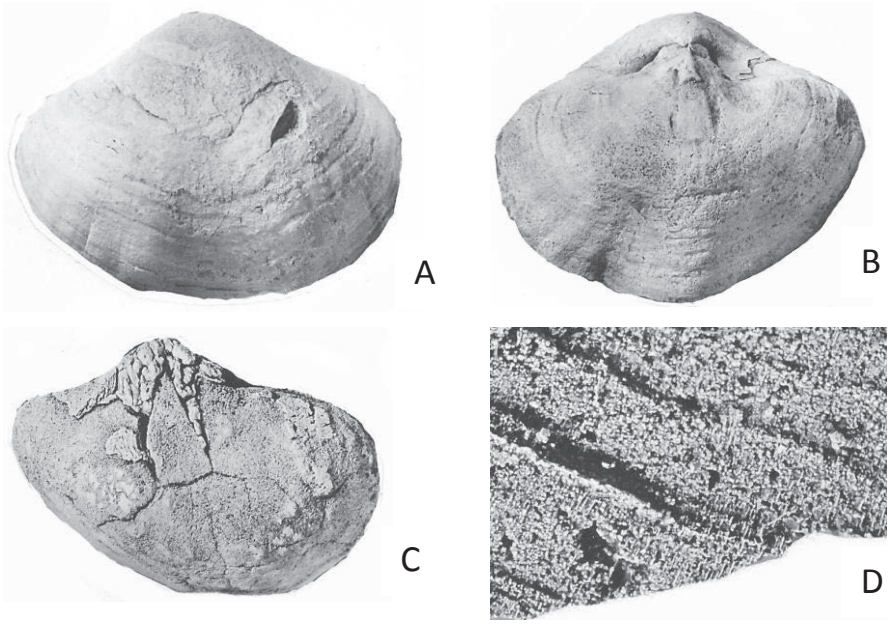


Fig. 74. *Ambikella ovulum* (Waterhouse) from Asselian Kindle Formation of British Columbia. A, ventral valve. B, dorsal valve showing tabellae. C, ventral valve showing adminicula, x1. D, detail of shell showing elongate grooves preserved as moulds on rather worn surface, x15. (Waterhouse 1971a).

Tribe JOHNDEARIINI new tribe

Name genus: *Johndearia* Waterhouse, 1998 p. 18 from Guadalupian of east Australia, here designated.

Diagnosis: Large subquadrate shells with minor or no plication, heavy posterior thickening, anterior sulcus may have medial swelling, adminicula and tabellae of only moderate length and well spaced. Lower to Middle Permian (Asselian to Wordian).

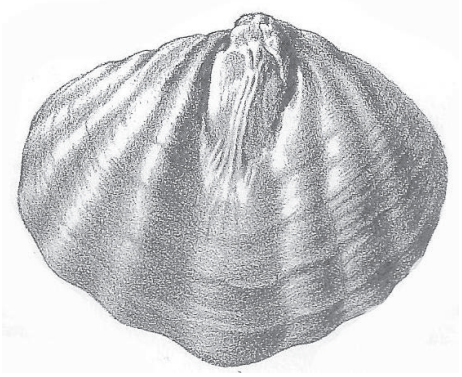


Fig. 75. *Oviformia oviformis* (M'Coy), ventral internal mould x1, from Guadalupian of Hunter Valley, east Australia. (Koninck 1877).

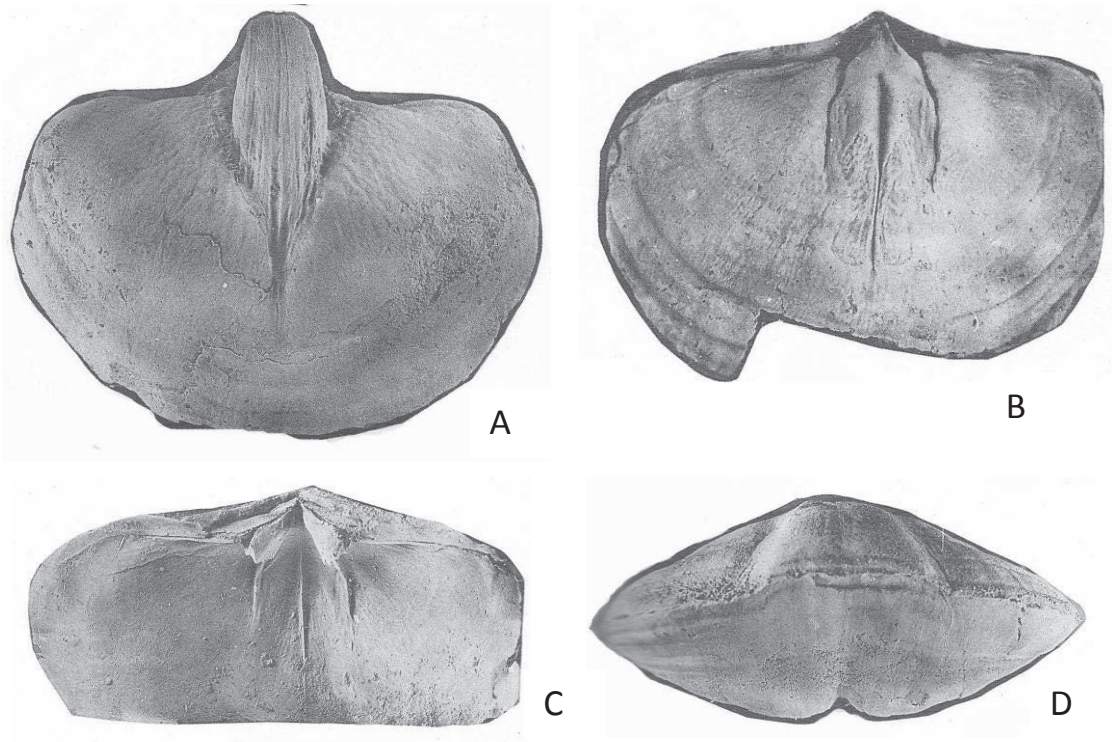


Fig. 76. *Johndearia isbelli* (Campbell). A, ventral internal mould. B, dorsal internal mould, part of holotype. C, internal mould of dorsal valve. D, anterior aspect of specimen with valves conjoined, dorsal valve on top. Specimens x0.8. From Blenheim Group (Wordian) of northern Bowen Basin, Queensland, Australia. (Campbell 1961).

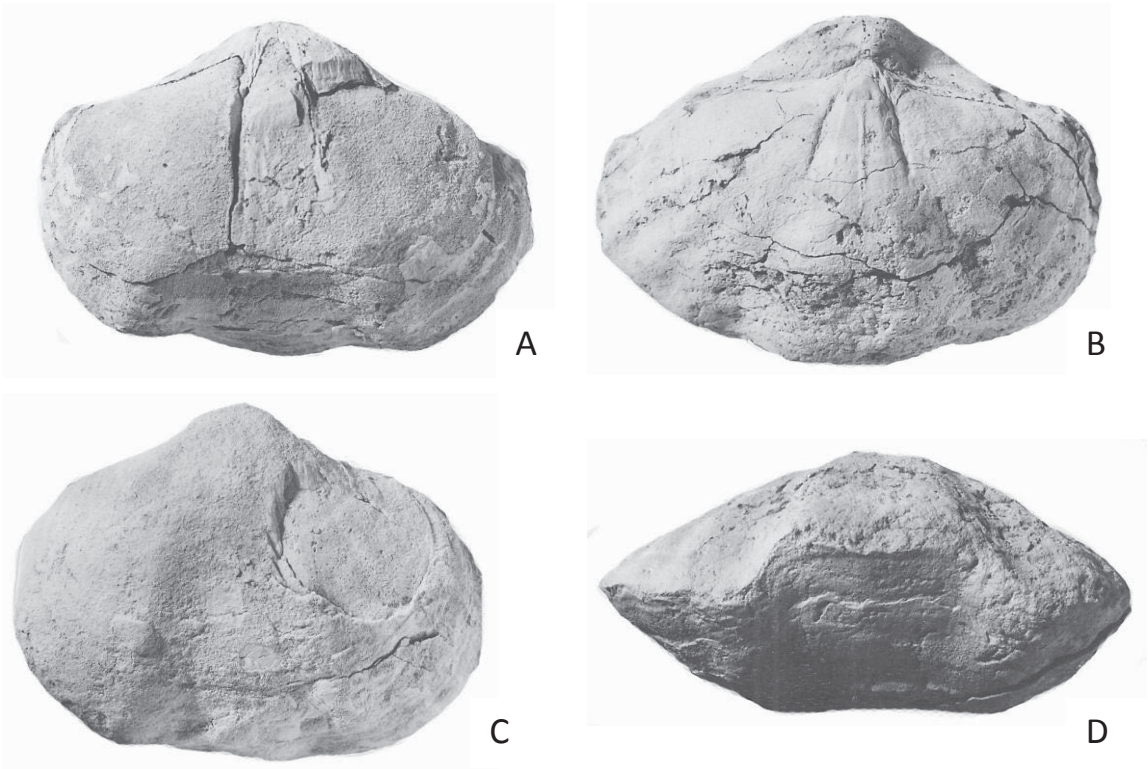


Fig. 77. *Oviformia bamberi* (Waterhouse). A, B, D, ventral, dorsal and anterior views (dorsal valve on top) of holotype. C, ventral valve. From Assistance Formation (Roadian), Melville Island, Canada, x0.8. (Waterhouse 1971a).

Genera: *Johndearia* Waterhouse, *Oviformia* Waterhouse, *Tumulosulcus* Waterhouse.

Discussion: This group is based on a small subset of ingelarellid genera that are limited so far as is known to the Permian of east Australia and Arctic Canada.

Subfamily **GEOTHOMASIINAE** new subfamily

Diagnosis: Tabellae short or not developed. Lower Carboniferous (Visean) to Upper Permian (Wuchiapingian).

Genera: *Geothomasia* Waterhouse*, Danzania* Pavlova*, Tomiopsis* Benediktova, *Tweedaleia* Waterhouse.

Discussion: *Geothomasia* is particularly well represented in Australia, and species have been monographed by McClung (1978), Archbold & Thomas (1986b) and Waterhouse (1998a, 2015a). The genera developed in all probability from *Tomiopsis* stock, which has short tabellae and evolved into larger shells with fewer plicae, with long adminicula and short tabellae, close to *Geothomasia*, and found in Pennsylvanian faunas of northeast Russia. *Geothomasia* radiated into several species especially in east Australia during and after the glacial episodes of the Early and Middle Permian, and evolved into *Tweedaleia* Waterhouse, 2010, of Sakmarian age in east Australia, which is exceptional in having lost its tabellae.

Fig.. 78. *Geothomasia branxtonensis* (Etheridge). A, B, ventral and dorsal aspects of specimens from lower Tiverton Formation (Sakmarian) of Queensland, Australia, x1.5, showing the short tabellae. (Waterhouse 2015a).

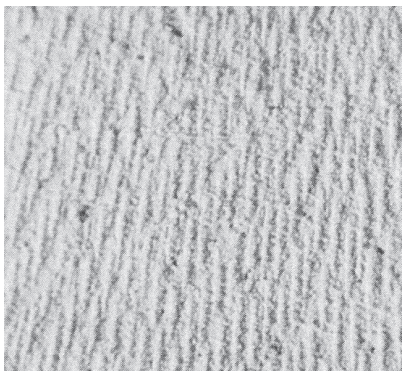


Fig. 79. *Geothomasia symmetrica* (Campbell), external mould of ventral valve, detail of micro-ornament, x 10. Note fine commarginal growth-lines. The raised slender ridges are infillings of surface grooves. From Tiverton Formation (Sakmarian) of Queensland, Australia, (Waterhouse 2015a).

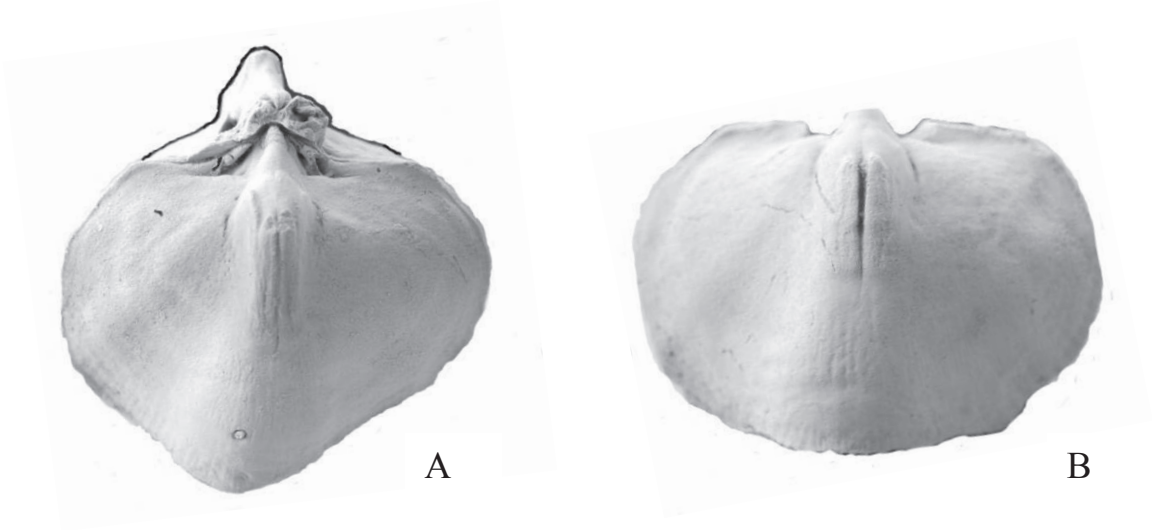


Fig. 80. *Tweedaleia tweedalei* Waterhouse. A, dorsal aspect of holotype, x1. B, dorsal valve, x1.5. Tabellae are not developed. From Tiverton Formation (Sakmarian) of Queensland, Australia. (Waterhouse 2015a).

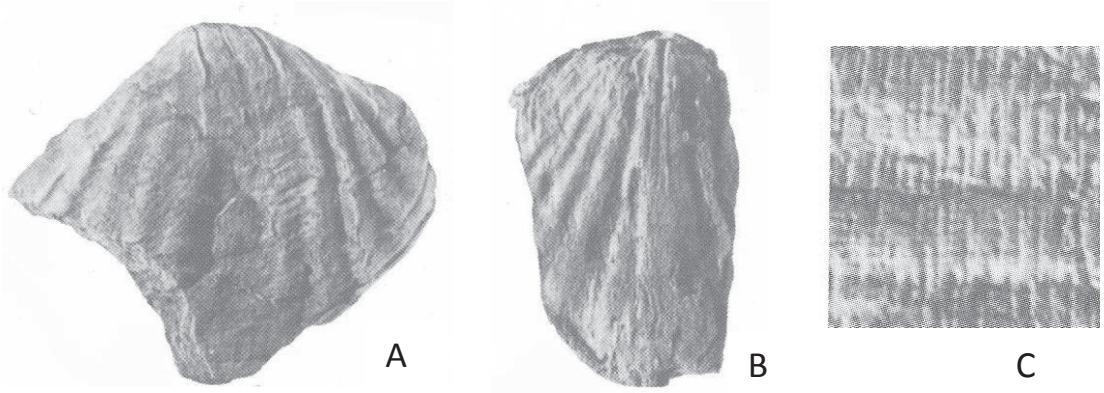


Fig. 81. *Tomiopsis kumpani* (Yanishevsky), ventral and dorsal internal moulds, x1, with micro-ornament, x15. From Early Carboniferous of Kuznets Basin, Russia. (Sokolskaya 1959).

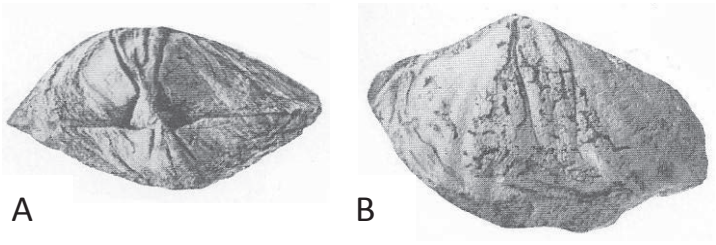


Fig. 82. *Tomiopsis kumpani* (Yanishevsky), ventral and dorsal internal moulds, x1, with micro-ornament, x8. From Early Carboniferous of Kuznets Basin, Russia. (Sarytcheva 1960).

Danzania Pavlova, 1988, based on *D. chalginica* Pavlova, was synonymized with *Tomiopsis* in the *Revised Brachiopod Treatise*. It comes from Visean beds of southern Mongolia, and is figured as Fig. 83. Notably the prominent dorsal myophragm of *Tomiopsis* is not developed.

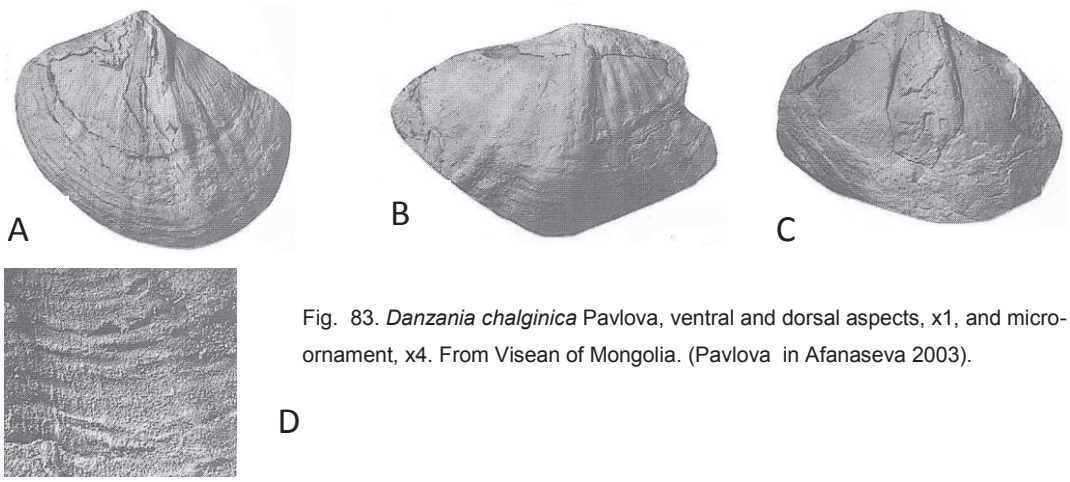


Fig. 83. *Danzania chalginica* Pavlova, ventral and dorsal aspects, x1, and micro-ornament, x4. From Visean of Mongolia. (Pavlova in Afanaseva 2003).

Family **RORESPIRIFERIDAE** Waterhouse, 1998a

[Nom. transl. Waterhouse 2015a, p. 149 ex Rorespiriferinae Waterhouse, 1998a, p. 30].

Diagnosis: Sulcate to plicate shells with micro-ornament of dense spinules or capillae. Interior close to that of Ingelarellidae, or with short tabellae. Upper Devonian (Famennian) to Middle Permian (Wordian).

Discussion: This name assumes priority over Crassumbidae Carter in Carter & Gourvennec, 2006b, p. 1758. *Rorespirifer* was included by Carter in Crassumbidae.

Subfamily **RORESPIRIFERINAE** Waterhouse, 1998a

[Rorespiriferinae Waterhouse, 1998a, p. 30].

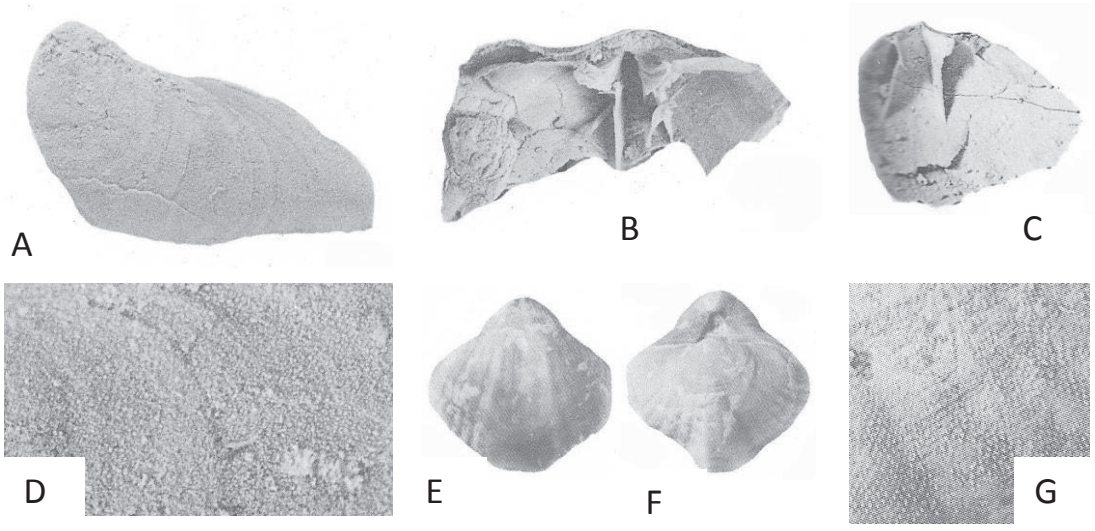


Fig. 84. A-D, *Rorespirifer ruinosus* Waterhouse & Piyasin, external aspect of dorsal valve, x3. B, internal view of ventral valve, x2. C, internal view of dorsal valve, showing tabellae and crural plate, x2. D, micro-ornament of small papillae, x10. From Khao Phrik Limestone (Roadian) of Thailand. (Waterhouse & Piyasin 1970). E-G, *Oiosia putilla* (Stainbrook). E, F, ventral and dorsal views, x2. G, micro-ornament, x5. From New Mexico (upper Famennian), USA. (Cooper & Dutro 1982).

Diagnosis: Surface ornament of minute spinules or papillae. Upper Devonian (upper Famennian) to Middle Permian (Roadian or Wordian).

Genera: *Rorespirifer* Waterhouse & Piyasin, ?*Arktikina* Grunt, *Oiosia* Cooper & Dutro, 1982.

Discussion: *Rorespirifer* comes from the Khao Phrik Limestone of Thailand. The micro-ornament of *Arktikina* Grunt, 1977b from northeast Russia is not known, but the genus is subglobose and of Pennsylvanian age, with long adminicula and tabellae, and so is placed in Rorespiriferinae. The ornament of *Rorespirifer* resembles that of *Oiosia* Cooper & Dutro, 1982, p. 117, an Upper Devonian genus from United States with low plicae and more inflated shell, and short dental plates and adminicula and short tabellae (see Stainbrook 1947, p. 322). *Oiosia* was placed in Gerkispiridae by Carter in Carter & Gourvennec (2006b), a group with stronger more numerous plicae and larger spines. The subfamily stands somewhat apart from Crassumbinae, but better information is required about the internal plates in crassumbin genera before the exact relationships can be consolidated.

Subfamily **CRASSUMBINAE** Carter, 2006

[Nom. transl. Waterhouse 2015a, p. 149 ex Crassumbidae Carter in Carter & Gourvennec, 2006b, p. 1758].

Diagnosis: Non-plicate. Micro-ornament capillate, and may also include papillae. Tabellae short. (Upper Devonian (Famennian) to Lower Carboniferous (Tournaisian).

Genera: *Crassumbo* Carter, *Nodaea* Tachibana.

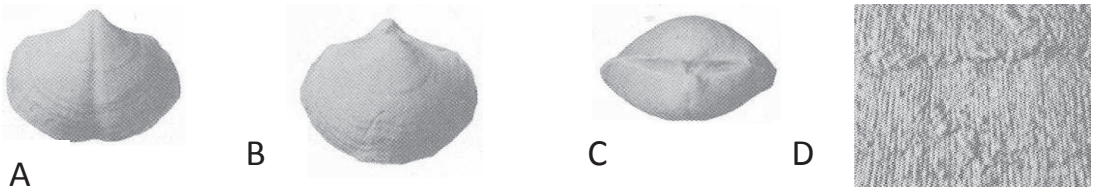


Fig. 85. *Crassumbo inornatus* Carter, ventral, dorsal and posterior aspects (dorsal valve on top), x1, with micro-ornament, x10. From Tournaisian of Texas, USA. (Carter 1967b).

Discussion: The subfamily is based on *Crassumbo* Carter, with capillae and scattered papillae or nodes. *Nodaea* Tachibana, 1981 of Tournaisian age is similar to *Crassumbo* Carter, 1967b and might prove to be a junior synonym, but possibly differs in the lack of papillae. Both type species have well developed adminicula and short tabellae. These are close in time range to the ingelarellid genus *Tomiopsis* Benediktova, which commenced in the Visean.

Superfamily **GERKISPIROIDEA** Carter, 1985

[Nom. transl. hic ex Gerkispiridae Carter, 1985, p. 376].

Diagnosis: Plicate shells with spinose or subspinose micro-ornament. Dental plates and adminicula well developed, crural plates present, short or negligible tabellae. Upper Devonian (Famennian) to Upper Permian (Changhsingian).

Discussion: The group would be better allocated a status lower than that of a superfamily, and higher than a family. It involves closely plicate genera, unlike the smooth or openly folded genera of Elythynoidea or Ingelarelloidea, and the micro-ornament is spinose. Some genera in Infrasuborder Cyrtiimorphi are somewhat similar, and have radial threads, pustules, plicae, open delthyrium, and short tabellae, notably those classed as Allanellinae new subfamily (see p. 42). These brachiopods could be judged as anticipatory for Elythynoidea and Ingelarelloidea, but because the Gerkispiroidea were close to Ingelarelloidea, there must be misgivings about any classification that separates their source genera to any extent.

Family **GERKISPIRIDAE** Carter, 1985

[Gerkispiridae Carter, 1985, p. 376].

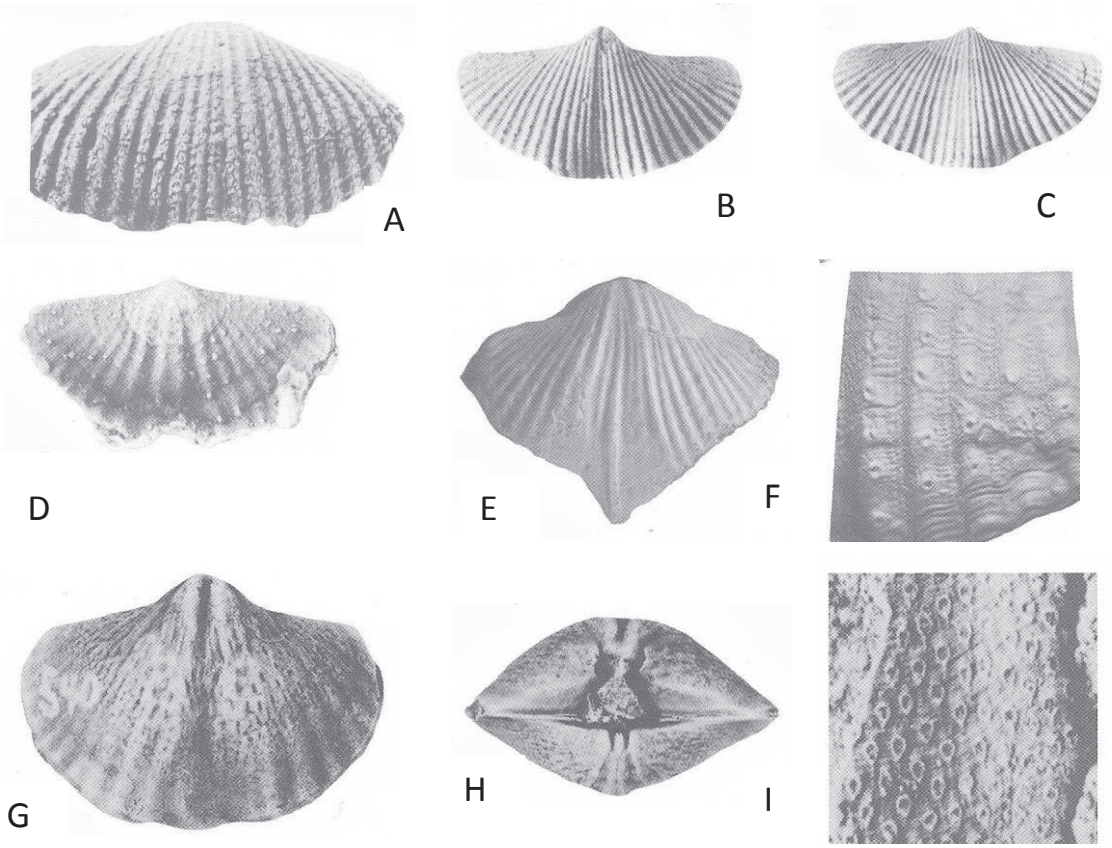


Fig. 86. A-C, *Gerkispirifer spinosa* Carter, detail with micro-ornament, x3.5, ventral valve and dorsal valve, x2. From upper Tournaisian of Iowa, USA. (Carter 1983, in Carter & Gourvennec 2006b). D, *Acanthospirina aciculifera* (Rowley), x6. From Upper Devonian (Famennian) of Missouri, USA. (Carter in Carter & Gourvennec 2006b). E, F, *Spinospirifer nuraensis* (Simorin), ventral valve, x1, and micro-ornament, x12. From Upper Devonian (Famennian) of Kazakhstan. (Carter in Carter & Gourvennec 2006b). G-I, *Punctothyris argus* Hyde, ventral and posterior views, x 3, and micro-ornament, x22. From Tournaisian of USA. (Carter in Carter & Gourvennec 2006b).

Diagnosis: Shells plicate or costate with hollow spines or papillae, short adminicula and short to possibly no tabellae. Upper Devonian (lower Famennian) to Lower Carboniferous (Tournaisian).

Genera: *Gerkispira* Carter, *Acanthospirina* Schuchert & LeVene, *Punctothyris* Hyde, *Spinospirifer* Martynova.

Discussion: *Gerkispirifer* Carter (1983, pl. 3, text-fig. 3) from the Gilmore City Limestone (Visean) of Iowa, United States, has well developed dental plates and adminicula, and short tabellae supporting crural plates. Spine bases are broad and circular, and costae coarse. On the whole, genera of this group are very close to the Permian family Notospiriferidae Archbold & Thomas, subject to the lack of documentation on aspects especially of the dorsal interior for some members of Gerkispiridae. *Acanthospirina* Schuchert & LeVene, 1929 (see Schuchert 1929) is one of the older members of the group, at Upper Devonian (upper Famennian) age, and has spine bases that extend anteriorly as elongate tubes within the primary layer. Other members lack the exopunctae or mesopunctae of Notospiriferidae, but appear to be a possible candidate for source stock, conceivably derived not from Tenellodermidae, but from Allanellinae. Such is no more than speculation at this stage, but if correct would imply that Notospiriferidae and Gerkispiridae form a separate lineage. The genus *Spinospirifer* Martynova of Upper Devonian (lower Famennian) age, shows capillation, as in Elivellinae, and large well-spaced spine bases are present. Faint growth increments. large spine bases short adminicula and miniscule tabellae occur in *Punctothyris,* of Tournaisian age.

Family **NOTOSPIRIFERIDAE** Archbold & Thomas, 1986b

[Nom. transl. Waterhouse 1998a, p. 31 ex Notospiriferinae Archbold & Thomas, 1986b, p. 584].

Diagnosis: Generally small, plicate with sulcus and fold, shell as a rule exopunctate, mesopunctate in one subfamily, ornamented by spines or grooves, or by both spines and grooves. Adminicula well developed, tabellae usually short, rarely absent or well developed. Permian (Asselian to Changshingian).

Discussion: This is a compact but varied group, limited to the Permian of Gondwana, chiefly east Australia and New Zealand. (So-called *Notospirifer bazardarensis* Grunt, 1993 from the Lower Permian of the southeast Pamirs probably belongs to *Ingelarella*). It seems likely that the group developed from Gerkispiridae, agreeing in the shortness of the tabellae, with modification of plicate ornament and micro-ornament. There is a substantial time gap between the two, lasting from Visean to Gzhelian.

Subfamily **NOTOSPIRIFERINAE** Archbold & Thomas, 1986b

[Notospiriferinae Archbold & Thomas, 1986b, p. 584].

Diagnosis: Deep to shallow surface pits as rule, commencing in front of small spines which may be barchanoid or c-shaped. Tabellae very short or rarely absent. Early Permian (Sakmarian) to ?Late Permian (Changhsingian).

Genera: *Notospirifer* Harrington, *Farmerella* Clarke, *Papulinella* Waterhouse.

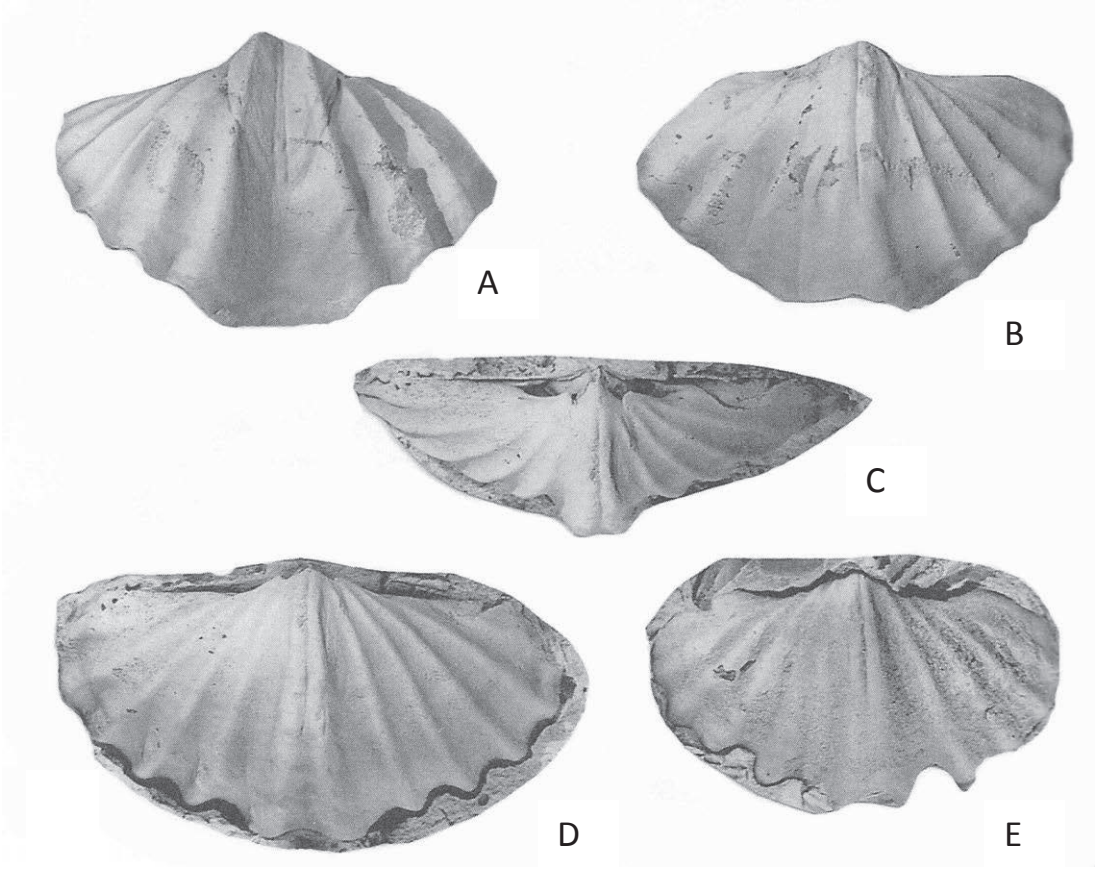


Fig. 87. *Papulinella hillae* (Campbell). A, B, ventral and dorsal aspects of internal mould with valves conjoined, x1. C, D, posterior and dorsal aspects of internal dorsal mould, x1. E, dorsal view. From Tiverton Formation (Sakmarian), Queensland, Australia. (Waterhouse 2015a).

A

Fig. 88. *Papulinella hillae* (Campbell). A, external mould of dorsal valve, x9. B, a fragment of the true exterior of ventral valve, x7. From Tiverton Group, (Sakmarian), Queensland, Australia. (Waterhouse 2015a).

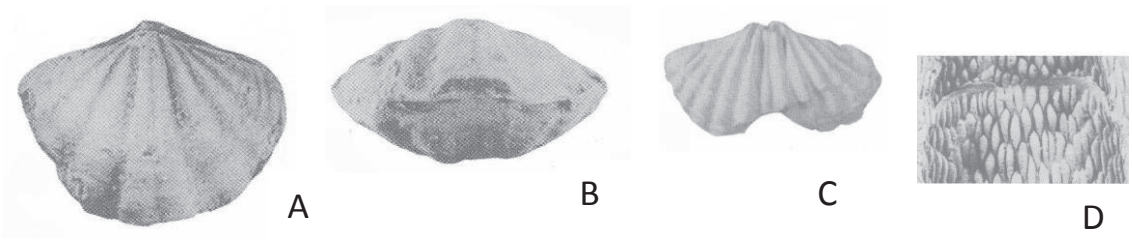


Fig. 89. A, B, *Notospirifer darwini* (Morris), dorsal and anterior aspects (dorsal valve on top), x1. From mid Guadalupian of New South Wales, Australia. (Harrington 1955). C, D, *Farmerella exoporosa* Clarke, ventral valve and subsurface pores, preserved as moulds formed from deep globose hollows called globons, x20. From Cisuralian of Tasmania. (Clarke 1992).

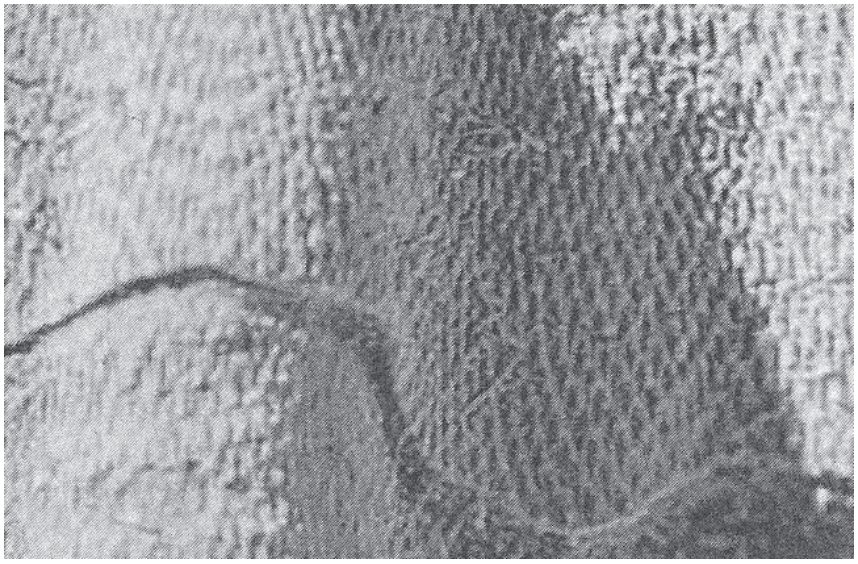


Fig. 90. *Notospirifer triplicata* Waterhouse, detail of latex cast of ventral valve, x10. From Tiverton Formation (Sakmarian), Queensland, Australia. (Waterhouse 2015a).

Subfamily **GLENDONIINAE** Clarke, 1992

[Glendoniinae Clarke, 1992, p. 75].

Diagnosis: Spines well developed behind long and moderately deep surface grooves, and tabellae moderately developed. Early and Middle Permian.

Genera: *Glendonia* McClung & Armstrong, *Birchsella* Clarke, *Monklandia* Waterhouse, *Tabellina* Waterhouse.

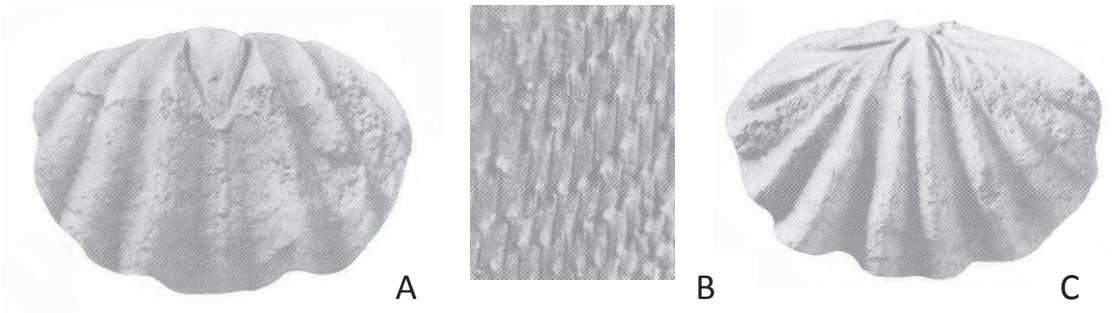


Fig. 91. *Glendonia ulladullaensis* McClung & Armstrong. A, ventral valve, x1. B, micro-ornament of barchan spines, x15. C, dorsal valve, x1. From lower Guadalupian, New South Wales, Australia. (McClung & Armstrong 1978).

Discussion: Ages allocated to notospiriferid genera by Carter in Carter & Gourvennec (2006b, pp. 1762, 1763) are incorrect. For example, *Glendonia* is not Lopingian as claimed, but Guadalupian, and *Birchsella* is not Lopingian, but Cisuralian. For the Permian Period of Australia, original sources and recent summaries as in Shi et al. (2010), Waterhouse (2001, 2002a, 2008, 2015a, b) and Waterhouse & Shi (2011), and New Zealand (Waterhouse 1998b, 2004) should be used for stratigraphic information and ages, rather than the *Revised Brachiopod Treatise*.

Subfamily **MESOPUNCTIINAE** Waterhouse, 1998

[Mesopunctiinae Waterhouse, 1998, p. 40].

Diagnosis: Surface with fine grooves in quincunx or small spines, no deep pits but large pores lie in median shell layer, surface smooth or diversified by capillae, grooves or spines, tabellae short or absent. Early and Middle Permian (Kungurian – Capitanian).

Genera: *Mesopunctia* Waterhouse, *Wairakispirifer* Waterhouse.

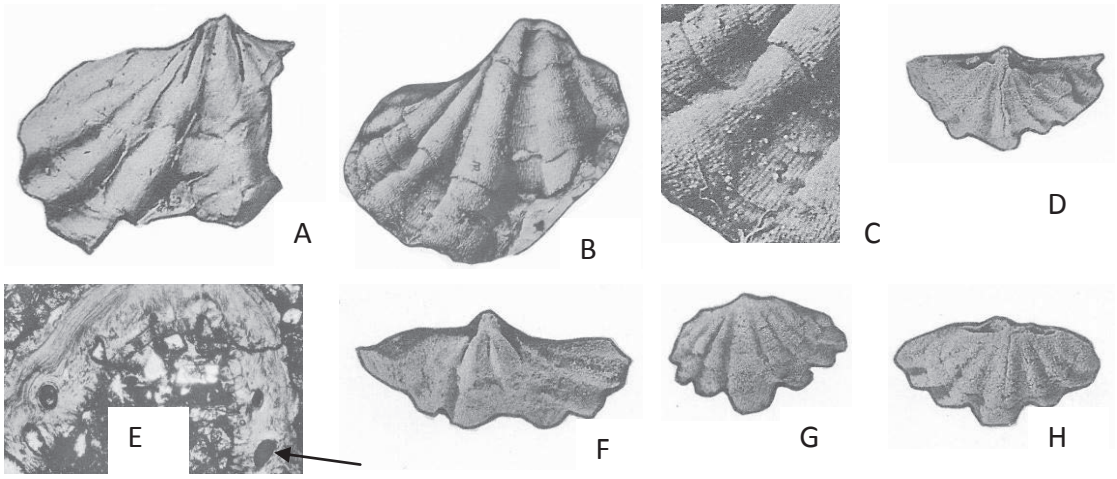


Fig. 92. A-C, *Wairakispirifer microstriatus* (Waterhouse). Internal and external ventral valve, x2, and anterior micro-ornament, x6. D-H, *Mesopunctia macropustulosus* (Waterhouse), D, posterior dorsal valve, x2. E, cross-section of shell structure, showing large mesopunctae as arrowed within the shell, x40. F, posterior ventral internal mould, x2. G, dorsal internal mould x2. H, posterior dorsal internal mould, x2. From Guadalupian of New Zealand. (Waterhouse 1964).

Discussion: In *Acanthospirina* Schuchert & LeVene, placed in Gerkispiridae by Carter in Carter & Gourvennec (2000b, p. 1765), the fine hollow spinules have bases extending longitudinally within the primary layer. The phenomenon of these deep-seated large pores in the shell structure is further discussed in Waterhouse (2013, p. 305).

Superfamily **MARTINIOIDEA** Waagen, 1883

[Nom. correct. Carter, Johnson & Gourvennec in Carter et al. 1994, p. 338, pro Martiniacea Ivanova, 1972, p. 41, nom. promoveo Martiniinae Waagen, 1883, p. 542].

Diagnosis: Suboval biconvex shells, smooth, sulcate and/or plicate, micro-ornament of fine pits, spinules, or commarginal or radial lirae. Dental plates may be reduced or absent, no adminicula; crural plates often reduced, never supported by tabellae (ie. “dorsal adminicula”). Upper Devonian (Famennian) to Upper Permian (Changhsingian).

Discussion: Martinioidea embrace genera that lack adminicula and tabellae, and have moderate varying to virtually no dental plates or distinguishable crural plates. They may have originated from within Ambocoelioidea, as claimed by Carter & Gourvennec (2006a), specifically from within groups with wide hinge and no adminicula, as amongst Crurithyrinae, such as *Crurithyris, Cruricella* and *Echinocoelia*, with change in micro-ornament, from capillae or spinules or tubercles as a rule, rarely only commarginal growth lines, into growth lines and/or pits. But given the time gaps between genera, it seems more likely that martiniids arose from stock close to Elythynoidea, requiring loss of short if any tabellae, a minor change, but also loss of long adminicula, whilst retaining or redeveloping the otherwise rare pitted micro-ornament, that is also found in Tenellodermidae Carter, Johnson & Gourvennec, a family also judged by those authors to have been the immediate source for martiniids. The tenellodermid age is Upper Wenlock (Silurian) and Middle Devonian, and the earliest martiniid appeared in the Tournaisian (Lower Carboniferous). The small size of ambocoeliids, the usual strong representation of dorsal plates, the widespread presence of a deltidial cover plate and the lack of surface pitting and usual presence of dense commarginally aligned spinules suffice to disparage any close tie between Martiniidae and Ambocoelioidea.

Even so, classification imposes something of a quandary. Martiniids make up a very minor part of an overall group that is dominated by shells with short to long adminicula, plates which are entirely missing from martiniids. The martiniid group is really an outlier, but which justifiably takes naming rights over the entire plexus because of a long history of recognition as distinctive from *Spirifer*. Yet despite this long history, *Martinia* itself remains very poorly known as far as dental and crural plates are concerned, and even attributes of micro-ornament have been under contention – this being an all-too-familiar problem of spiriferiform genera based on type species preserved as a rule by exfoliated shells coming from the Early Carboniferous of Great Britain and monographed in the Nineteenth Century. Whilst some genera and species have been clarified through the studies of C. H. C. Brunton (1984) on silicified material from Ireland, and with his colleague D. J. C. Mundy in England, too many genera remain poorly known, including *Martinia,* and much more work is needed, along the lines followed by Legrand-Blain (1985a) and Angiolini et al. (2011).

For Martiniinae, plates and septa were said to be absent from both valves (Carter in Carter & Gourvennec 2006b, p. 1747), which ignores the presence of dental plates, crural plates and socket plates in several genera. The family groups that seem to be most closely related to Martiniidae are Brachythyrinae Fredericks and Perissothyrinae Carter, two

associations which lack adminicula and tabellae, and may have reduced if any dental plates. They have stronger ribs, and the similarity may be due to convergence, but in the favoured interpretation, reflected a modest degree of divergence from allied sources. Several other groups included by Carter & Gourvennec (2006b) in Martinioidea have been segregated as Ingelarelloidea and Gerkispiroidea, including Ingelarellidae Campbell, Notospiriferidae Archbold & Thomas, Gerkispiridae Carter, and Rorespiriferidae Waterhouse. Genera within these families and subfamilies have well formed dental plates and adminicula in the ventral valve and crural plates supported by varyingly developed tabellae in the dorsal valve. By contrast, adminicula and tabellae are completely missing from Martinioidea. With such clear differences in morphology, it is relatively simple to allocate genera to superfamilies, without precluding genera that in their evolution came to lose plates.

Family **MARTINIIDAE** Waagen, 1883

[Nom. promoveo Ivanova 1959, p. 56 ex Martiniinae Waagen, 1883, p. 542].

Diagnosis: As for superfamily. Dental plates present or absent, lateral slopes may be weakly ribbed, or smooth or plicate. Delthyrium may be closed or partly closed by deltidial plates, or rarely, connector plate and pleromal ridges. Lower Carboniferous (Tournaisian) to Upper Permian (Changhsingian).

Discussion: It is difficult to achieve a satisfactory understanding of evolutionary trends within Martiniidae, because dental plates and crural plates remain poorly known for several genera, and even less is known about the variation in these plates within a genus, or from species to species. Not even the micro-ornament is secure for a number of genera. Grunt (1977b) has pointed out the potential value of mantle canal systems, and Angiolini (1995) used the pattern to help define a further genus. That can be risky, unless supported by full analysis of other features in the genus concerned, and even so, allowance has to be made for ontogenetic development, and the possibility of intraspecific variation. For example, whereas the martiniid species *prolifica* Waterhouse from Thailand has a somewhat reticulate pattern, Shi, Leman & Tan (1997) identified specimens of *prolifica* in Malaysia that revealed a much more simple more radiate pattern (see especially Shi et al. 1997, Fig. 3M), and it is not certain whether the differences, involving a number of specimens for each suite, are due to intraspecific variation, ontogenetic development, or subtly different species or even genera.

Small spines are developed in some genera, contradicting the claim by Carter in Carter & Gourvennec (2006b, p. 1748) that all the genera in Martiniinae were characterized by micro-ornament of fine pits only, and these genera are transferred to a new subfamily, and the highly exceptional *Weiningia* is also allocated to a distinct subfamily.

Subfamily **MARTINIINAE** Waagen, 1883

[Martiniinae Waagen, 1883, p. 542].

Diagnosis: Suboval biconvex shells with dental plates in some genera but no adminicula, crural plates small or large, no tabellae. Micro-ornament of pits or commarginal growth lines

common. Mantle canal system linear or complex. Carboniferous (Tournaisian) to Upper Permian (Changhsingian?).

Genera: *Martinia* M'Coy (syn. *Pseudomartinia* Leidholdt, *Paramartinia* Reed), *Beschevella* Poletaev, *Chapursania* Angiolini, *Implexina* Poletaev, *Jilinmartinia* Li & Gu (syn. *Kalitvella* Lazarev & Poletaev), *Krabispirifer* new genus, ?*Ladoplica* Xu & Grant, *Postamartinia* Wang & Yang, *Tiramnia* Grunt.

Discussion: Carter in Carter & Gourvennec (2006b, p. 1748) diagnosed the subfamily as being without plates or septa in either valve. These statements are not correct. Many Martiniinae have dental plates, and most have crural plates, from which the crura arise: the crural plates are also called outer hinge plates in various studies.

Martinia M'Coy 1844, type species *Spirifer glaber* J. Sowerby, 1820, is a large transverse shell of Lower Carboniferous age in the British Isles with weakly defined dorsal fold for the length of the valve, and numerous subparallel radial mantle canals on the surface of the inner shell (George 1931, Muir-Wood 1951, Waterhouse 1981, pl. 30. fig. 3, 6, 7, pl. 31, fig. 1). Yet in the species described as *Martinia balkhashica* Besnossova (1968, pl. 29, fig. 14-16) from the Keregetass Suite of Kazakhstan, small shells have a few radiating vascular markings, and the larger holotype has a broad ventral muscle field surrounded by a narrow field of canals in an irregular network. And "*Martinia*? *semiconcava* Chao" as identified by Poletaev (1975, pl. 10, fig. 7) has a mantle canal system more complex than in any other known "*Martinia"*. (See Fig. 94B, p. 91).

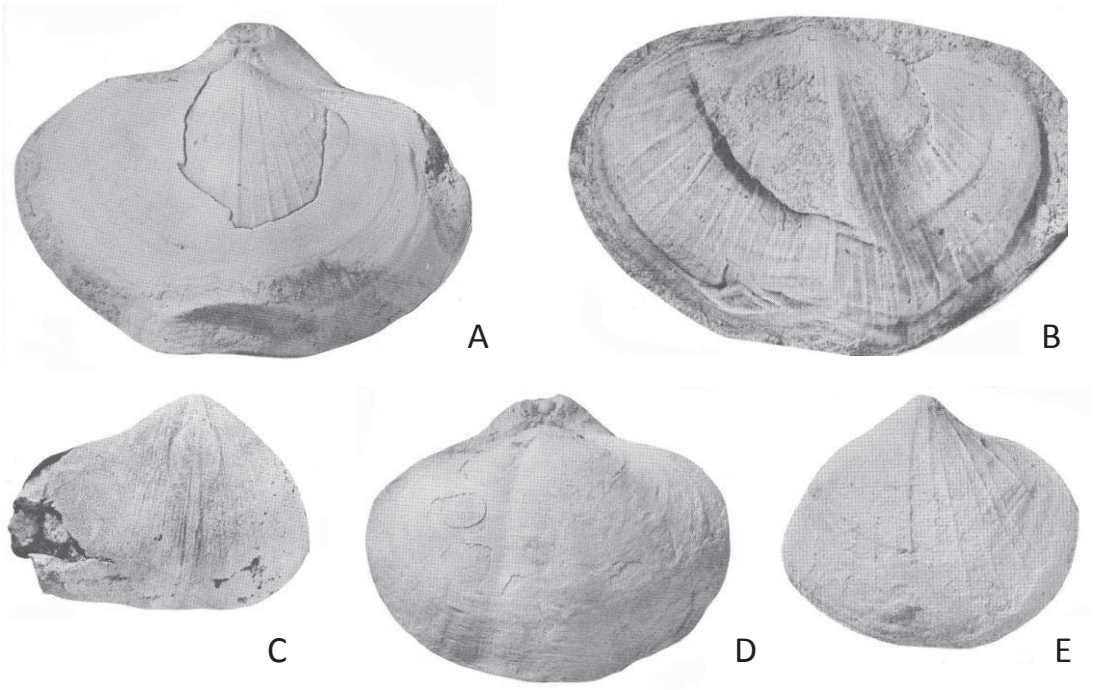


Fig. 93. *Martinia glabra* (Sowerby). A, dorsal aspect of complete specimen, x2. B, dorsal valve x2.5. C, ventral interior, x0.5. D, dorsal view of specimen with valves conjoined, x 0.75. E, ventral interior, x3, Although labelled and shaped as *glaber* at the Museum of Natural History, London, identity is not secure. From Lower Carboniferous (Visean) of England. (Waterhouse 1981).

Internal details have been poorly circumscribed for *Martinia*, and it is not certain whether dental plates and crural plates are present or absent. This is a critical deficiency, and means that well preserved specimens which display internal plates, such as the Namurian internal moulds featured by Martínez-Chacón & Winkler Prins (1977, pl. 11) from Oviedo, Spain, cannot be confidently identified. They may show similar shape, and similar mantle canal pattern, but their internal plates cannot be securely matched or contrasted with those of *Martinia glabra*, the type species. In the Davidson collection at the Museum of Natural History, London, specimen B 14531 from Derbyshire has thick stubby dental plates. But is it truely congeneric with *Martinia glaber*? *Paramartinia* Reed, 1949 was treated as junior synonym of *Martinia* by Carter (in Carter & Gourvennec 2006b, p. 1748), but with incomplete comparison of internal features. *Paramartinia* was reported to lack dental plates by Reed (1949), but he was referring to adminicula rather than dental plates, which are not visible in the sole specimen described, and may be present, suspended above the floor of the valve, or may be absent. *Pseudomartinia* Leidholdt, 1928 is an objective synonym.

Jilinmartinia Li & Gu (1980, pp. 488, 491), type species *Brachythyris shansiensis* Chao (1929, pp. 51-57, pl. 9, fig. 1-3) from the Taiyuan Series of China, was distinguished from *Martinia* by the presence of conspicuous delthyrial ridges, prominent commarginal growth lines and sharply defined sulcus. The diagnosis is far from adequate, and even the type species was described with no dorsal valve, and no internal detail. The external shell is minutely pitted, perhaps indicative of worn prismatic shell. Understanding of the genus was expanded in the *Revised Brachiopod Treatise,* by treating *Jilinmartinia* as senior synonym of *Kalitvella* Lazarev & Poletaev, 1982, type species *Spirifer* (*Brachythyris*) *sokolovi* var. *laevis* Licharew, 1938, p. 83. As a better known form, this also displays well developed commarginal laminae and moderately well formed ventral sulcus, and the interior of the ventral valve displays two vascular media, as opposed to a prominent median canal in several other genera, and reticulate vascular pattern (see Lazarev & Poletaev 1982, pl. 1, fig. 11). Illustrations of the exterior show little difference from various *Martinia*. The main perceptible difference from *Martinia* lies in its narrower sulcus, and not enough is known about various internal details of the genus.

Several other genera of Carboniferous age are much better based. *Implexina* Poletaev, type species *Spirifer (Martiniopsis?) implex* Rotai from the Tournaisian of Ukraine, is distinguished externally by a high ventral interarea, well formed sulcus, low or no dorsal fold and moderately well developed commarginal rugae (Poletaev 1971, pl. 68, fig. 5) and what appear to be small elongate pits in the micro-ornament. Internally the genus has well developed dental plates, large horizontal socket plates and well developed crural plates, suspended above the floor of the valve. The ventral muscle field was described, but its position not located with regards to the posterior wall. The ctenophoridium was recorded as bilobed.

Postamartinia Wang & Yang, 1993, p. 7 is plicate and lacks dental plates. The type species *P. grandplica* Wang & Yang (1993, p. 7, pl. 3, fig. 1a-d, 2a, b, 6; 1998, pl. 23, fig. 15-

17) is transverse with grooved deep ventral sulcus and high fold anteriorly, and well formed anterior plicae. Micro-ornament was recorded as consisting of dense fine commarginal growth-lines. Note should be made of the lack of pits, contrary to the claim by Carter in Carter & Gourvennec (2006b, p. 1748) that pits typified members of Martiniinae. The dorsal interior was said to lack socket plates and medium septum, but this is not illustrated: if correct, the crura must rise from the floor of the valve, but given the lack of precision over dorsal plates, this may be deemed in need of confirmation. The species comes from the upper Baliqliq Formation, considered to be of Kungurian age, in the Qiudayizaya area, Kalpin, Xinjiang, northwest China.

The genus *Tiramnia* Grunt, 1977b is small with or without sulcus, and although said to differ from *Martinia* in its reticulate vascular canals, its mantle canal pattern is in fact close in the pattern to *Martinia*, the type species of which also displays similar rare branching mantle canals, and at early growth stages, similar ventral muscle field. The type species of *Tiramnia* is of Early Permian (Cisuralian) age, and most of the species now ascribed to *Tiramnia* are subelongate, with sulcus and fold restricted to the anterior shell. Internally, dental plates and crural plates are developed, as shown mostly by sections, but aspects of micro-ornament remain obscure. Well preserved material from the Glass Mountains, Texas (Cooper & Grant 1976), and also material from Greenland (Dunbar 1955) and Canada (Shi & Waterhouse 1996) externally, and as far as known internally, could be referable to *Tiramnia*. Secondary thickening is greater in the type species *T. uralica* (Chernyshev, 1902) than in the Glass Mountains species, and the mantle canal pattern varies somewhat, so that shape appears to be a useful criterion. The United States species, best represented by *Martinia globularis* Girty, have a characteristic subpentagonal shape, well developed dental plates, and moderately developed inner socket plates with large crural plates and bases. Exteriors of the United States material show low commarginal growth increments and fine pits that Cooper & Grant (1976) ascribed to slight weathering of the shell surface. The interior displays, for most specimens, a simple linear mantle canal system, but one specimen (Cooper & Grant 1976, pl. 645, fig. 22) is complexly reticulate.

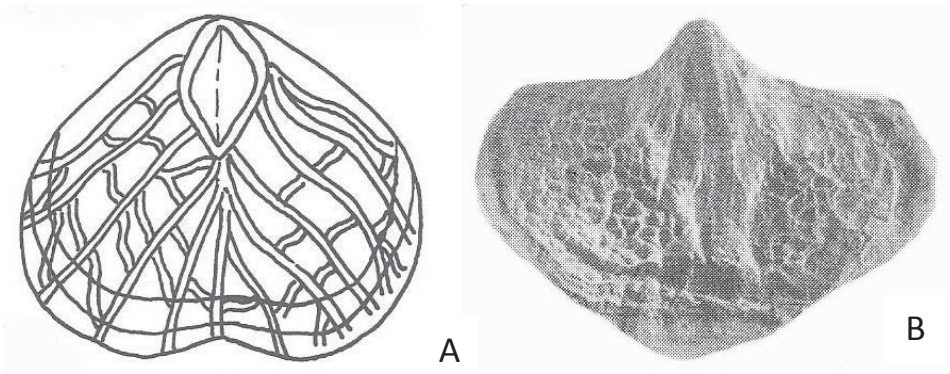


Fig. 94. A, *Chapursania tatianae* Angiolini, diagram of vascular system in ventral valve, x1.5. From Wordian of Pakistan. (Angiolini 1995). B, genus unknown, ventral internal mould, identified as *Martinia* (?) *semiconvexa* Chao, x2, from middle Carboniferous of Donets Basin, Ukraine. (Poletaev 1975).

Chapursania Angiolini, 1995 appears likely to be an ally, but that remains conjectural. The genus was proposed with type species *C. tatianae* Angiolini, 1995 from the Panjshah Formation of the central Karakorum, and further described by Angiolini (2001). The genus was said to be characterized by its thick shell, wide hinge, large muscle field, and coarse sinuous branching vascular imprints connected by cross-bars. No data could be provided on the internal plates, because of extensive recrystallization (Lucia Angiolini pers. comm.). The vascular pattern is more net-like than normal for other martiniid genera. Micro-ornament consists of fine closely spaced growth increments.

Internal detail of the very Late Permian genus *Ladoplica* Xu & Grant, 1996 from China and Salt Range, Pakistan, is poorly known, and the genus is based on the exceptional shape, with angular extended posterior lateral margins and extended ventral tongue.

The mantle canal systems of *Martinia* are essentially linear, radiating forward across the shell, and similar patterns are seen in the genera *Beschevella* Poletaev, 1975, as show in Poletaev (1975, pl. 11, fig. 2b), *Jilinmartinia* Li & Gu and *Postamartinia* Wang & Yang. In *Tiramnia* Grunt, the mantle canals are few and well spaced for the type species, with few branches, much as in mature *Martinia*, and the ventral muscle field is like that of immature *Martinia*. The nature of the mantle canal systems is not secured for several genera, including *Implexina* Poletaev. This genus shares moderately low regular commarginal growth laminae or growth lines with other members of Martiniinae, such as *Beschevella* and *Jilinmartinia*. Some species of these genera, such as *Ladoplica* (see Grant 1970, pl. 3, fig. 4), *Postamartinia* (see Carter & Gourvennec 2006b, Fig. 1151. 2c), and *Implexina* (Carter & Gourvennec 2006b, Fig 1150.2a) show faint radiations in the shell structure, and whether these reflect mantle canal systems is not clear.

Genus ***Krabispirifer*** new genus

Name: Named for Krabi, south Thailand; spirifer – brachiopod genus.

Diagnosis: Distinguished by the development of socket and crural plates on the floor of the dorsal valve rather than suspended above the floor of the valve. Median mantle canal on ventral valve divided by narrow cleft; two or three branches in the canal system in immature shells, later becoming more complexly branching. No array of fine spines externally. Ventral muscle field posteriorly placed.

Type species: *Spinomartinia prolifica* Waterhouse, 1981, p. 107 from Ko Yao Noi Formation (Sterlitamakian) of south Thailand, here designated.

Discussion: As shown by Waterhouse (1981, pl. 29, fig. 7, 8), the outer socket plates rest for their entire length on the posterior floor of the dorsal valve, and the inner hinge plates that border the outer sockets rest for their length on the floor of the valve. By contrast, the socket plates of other martiniids where known project above the floor of the valve and are attached to the floor only at their posterior end. The micro-ornament of *Krabispirifer* consists of subfusc crowded growth increments, and faint suggestions of radial threads, with fine closely and evenly spaced pits along the growth increments. A few very small spine-like projections are

suggested, but it is not clear that they are genuine pustules. The ventral muscle field is placed at the posterior wall, and the mantle canal system in this species becomes more complex with increase in maturity, and shows a single median ventral canal, which may be split in two. Dental plates are low, and crural plates high.

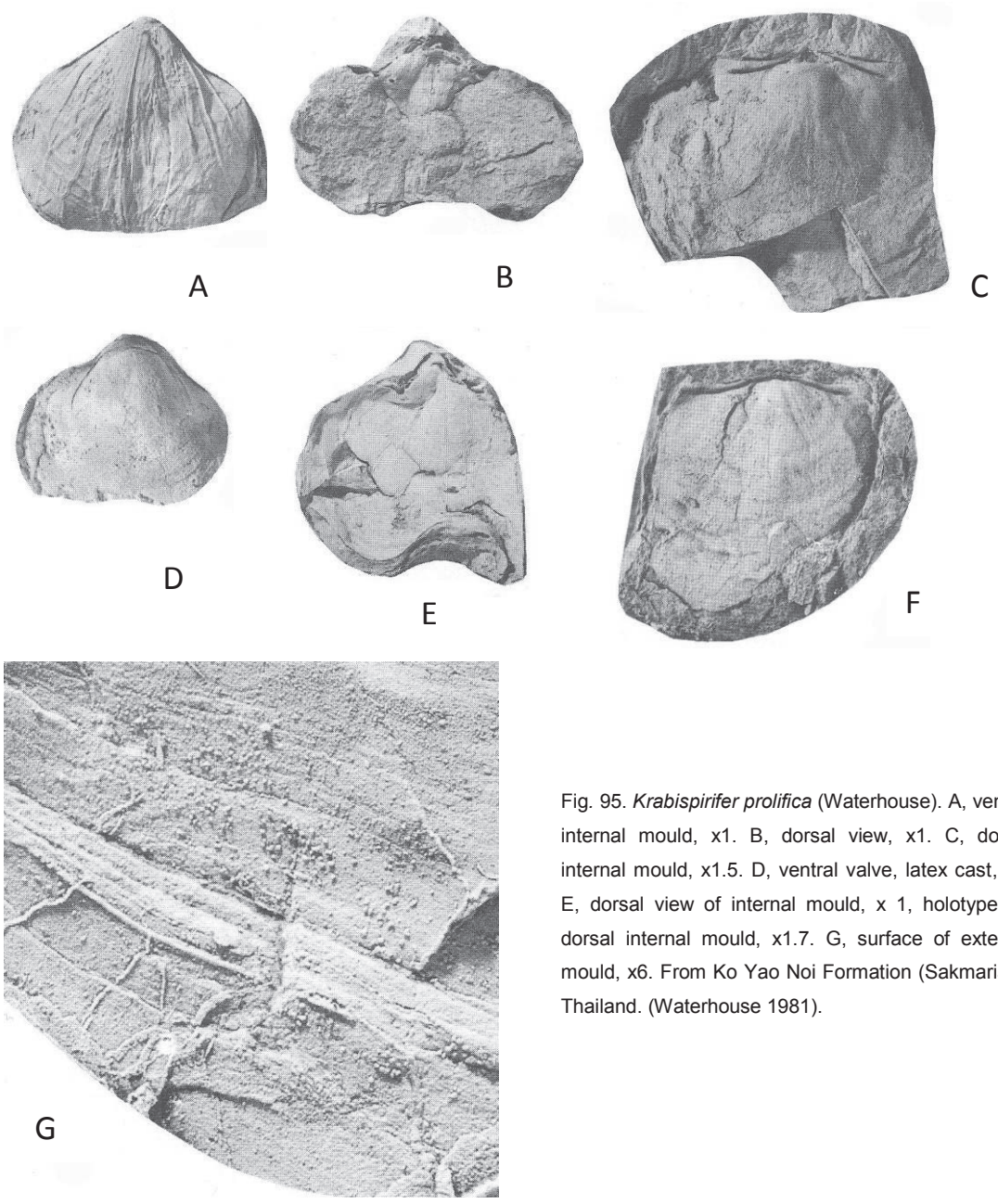


Fig. 95. *Krabispirifer prolifica* (Waterhouse). A, ventral internal mould, x1. B, dorsal view, x1. C, dorsal internal mould, x1.5. D, ventral valve, latex cast, x1. E, dorsal view of internal mould, x 1, holotype. F, dorsal internal mould, x1.7. G, surface of external mould, x6. From Ko Yao Noi Formation (Sakmarian), Thailand. (Waterhouse 1981).

Martinia is readily distinguished by its linear vascular pattern, and *Beschevella* is of subpentagonal shape with deep sulcus, broad fold anteriorly with anterior sulcus, and finely pitted commarginal micro-ornament. Possibly there are no mantle canal imprints. *Implexina* has a narrow groove-like sulcus and very high ventral interarea, with micro-ornament of small elongated pits. The closest genus is *Jilinmartinia* Li & Gu, with low sulcus that is narrow posteriorly and wide in front. Commarginal growth-lines are prominent, and there are faint

narrow lateral plicae, especially on the dorsal valve, unlike the present form. The type species of *Jilinmartinia* was originally described as *Brachythyris shansiensis* Chao, 1929, and possibly *Martinia semiconvexa* of Chao, 1929 from Kansu is congeneric, with less groove-like posterior sulcus, and with broad fold bearing a dorsal channel, and with narrow dorsal plicae. There are two well spaced vascular media in *Kalitvella*, synonymized with *Jilinmartinia*, and a branching reticulate pattern, whereas the median vascular groove in *Krabispirifer* may be singular, or bear a median groove. *Postamartinia* of Permian age has a wide sulcus and sulcal tongue and plicae are present laterally, and the interarea is very low. *Tiramnia* is distinguished by shape and vascular pattern. *Spinomartinia* has external spinules, and *Chapursania* has a stronger vascular network and wider hinge, with a micro-ornament of commarginal growth increments.

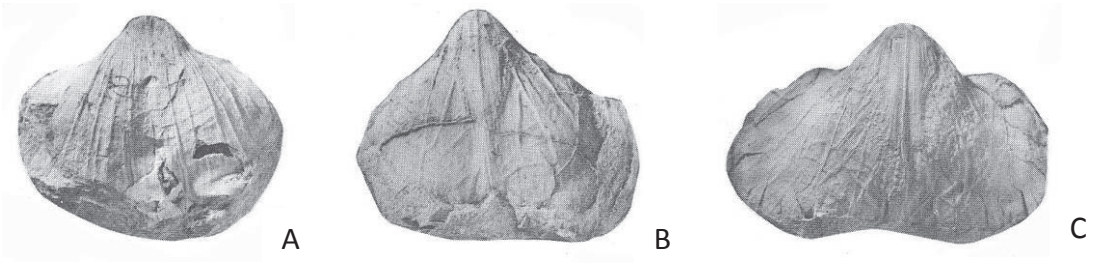


Fig. 96. *Krabispirifer prolifica* (Waterhouse), internal moulds of three ventral valves showing mantle canal systems. Specimens x1, from Ko Yao Noi Formation, Thailand. (Waterhouse 1981).

Subfamily **PERISSOTHYRINAE** Carter, 1994

[Nom. transl. hic ex Perissothyrididae Carter in Carter et al., 1994, p. 342].

Diagnosis: Weakly ribbed shells with sulcus and fold, laterally extended plates extending from valve walls subparallel to commissure. Ventral muscle field clearly defined. Lower Carboniferous (Mississippian).

Genera: *Perissothyris* Carter, *Mongoliopsis* Grunt.

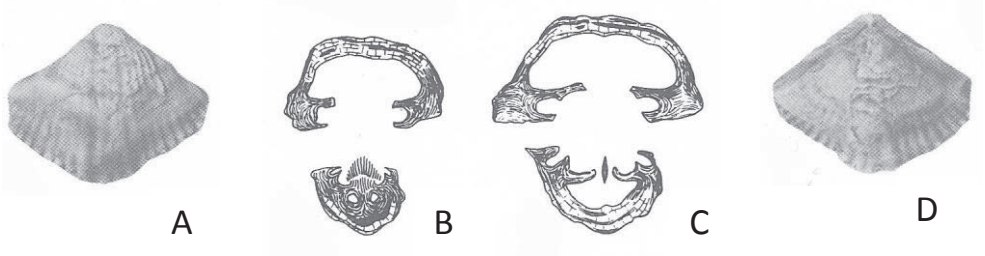


Fig. 97. *Perissothyris masonensis* Carter. A, ventral valve x1. B, C, transverse sections x2.5. D, dorsal aspect, x1. From Visean of Texas, USA. (Carter 1967a)

Discussion: Two genera of Mississippian age have been placed in this unusual group, as followed herein, although the placement in Martiniidae rather than Brachythyridae may be arguable. Adult shells are subpentagonal and transverse, but early growth stages indicate a

less transverse subrounded outline. Carter (1967a) reported subimbricate growth lamellae, and considered that subdelthyrial plates, which may equate to pleromal ridges, turned sharply dorsad as conspicuous flanges. The arrangement is as though the pleromal ridges extended across the delthyrial cavity, without closing the delthyrium completely, like an extreme version of the pleromal ridges and connector plate seen in *Spinomartinia* and *Globosospiniger* (see pp. 96-99), but in *Perissothyris*, there are no dental plates. Teeth are attached directly to the posterior lateral walls of the valve. In the dorsal valve similar extensions extend from the ventromedial edges of the crural bases. There appear to be socket plates. As shown in Fig. 97B, there is the suggestion of a short median septum or sturdy myophragm or pillar in front of the ctenophoridium on a hinge plate in the dorsal valve. Although transverse sections suggested an abbreviated spire, Carter (1967a) stated that there were a dozen or so whorls to each spire. Vascular imprints are not clearly developed, but there are suggestions of slender radiating channels in the ventral valve of *Mongoliopsis*, pointing to a martinioid alliance, just as supported by Carter in Carter & Gourvennec (2006b). Plicae are numerous and well developed, and the ventral muscle field well defined.

Fig. 98. *Perissothyris masonensis* Carter. Posterior view of internal mould, showing pleromal plates converging on a small connector plate in the ventral valve, which lies on top. Specimen x4. From Visean of Texas. (Carter 1967a)

Subfamily **WEININGIINAE** new subfamily

Name genus: *Weiningia* Jin & Liao, 1974, p. 282 from Weiningian beds (Serpukhovian-Bashkirian), of Guizhou, China, here designated.

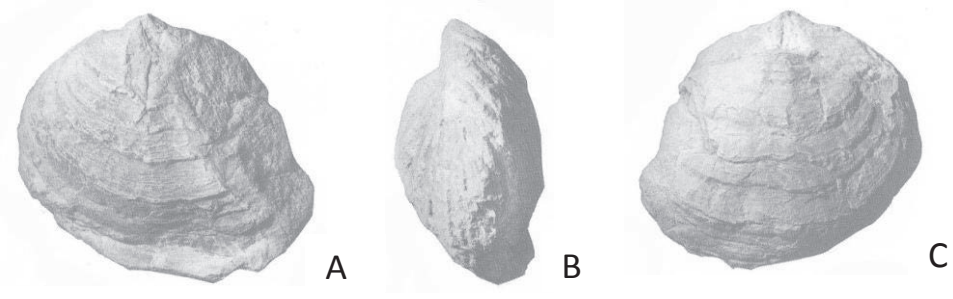


Fig. 99. *Weiningia transversa* Jin & Liao, ventral, dorsal and lateral views, x1. (Carter in Carter & Gourvennec 2006b).

Diagnosis: Suboval with commarginal lamellae and ventral umbo prominent; dental plates

low, crura appear to rise from floor of valve, vascular imprints dense and complex. Lower Carboniferous (Serpukhovian) to Middle Carboniferous (Bashkirian).

Genus: *Weiningia* Jin & Liao (syn. *Elenchus* Alexandrov, 1973 non Curtis 1840).

Discussion: The Carboniferous genus *Weiningia* Jin & Liao, 1974, type species *W. transversa* (= *Elenchus* Alexandrov, 1973, type species *E. areatus*, preoccupied) is an extraordinary genus, far removed from other Martiniidae. Fortunately it is comparatively well known. The hinge is short, the ventral interarea may be high, the dorsal interarea low or absent, and micro-ornament shows growth laminae and growth steps as a rule, and signs of capillae. There may be a ventral sulcus, and dorsal sulcus in some specimens, very thick posterior shell, and weak and narrow radial plicae or ribs (Yanagida & Matsusue 1991). The ventral valve shows two sturdy thick dental flanges, with or without projecting teeth (Alexandrov 1973, pl. 29, fig. 6), and a muscle field divided by a myophragm. The mantle canal system, described as pinnate, is more complex than in martiniids and shows a few strong channels interconnected by a complex of finer reticular impressions (see Alexsandrov 1973, pl. 26, fig. 7). The dorsal interior reveals no internal plates (Yanagida & Matsusue 1991, text-fig. 5) and is clearly shown by Alexandrov (1973, pl. 29, fig. 7) as highly exceptional, with a large swollen cardinal process, low median ridge and two short swellings in front, that might be bases of the crura, or modified crural plates, as also interpreted by Carter in Carter & Gourvennec (2006b, p. 1750). Given the absence of separate socket and crural plates, this genus is like no other martiniid. The genus is widespread, having been reported from China, southern Urals and Japan.

Subfamily **SPINOMARTINIINAE** new subfamily

Name genus: *Spinomartinia spinosa* Waterhouse, 1968, p. 53 from Trig DD Formation (Changhsingian) of New Zealand, here designated.

Diagnosis: Characterized by fine spines. Vascular imprints may be reticulate, especially on ventral valve. Lower Permian (Sakmarian) to Late Permian (Changhsingian).

Genera: *Spinomartinia* Waterhouse*, Duntonia* Waterhouse & Campbell, *Globosospiniger* Waterhouse.

Discussion: Both *Spinomartinia* and *Glosospiniger* have pleromal ridges and small connector plate. The type species of *Spinomartinia*, *S. spinosa* Waterhouse, 1968 from the Changhsingian faunas of New Zealand, is somewhat transverse, with shallow ventral sulcus commencing in front of the umbo, and virtually no dorsal fold, and no anterior ventral tongue. Tiny spines are found over both valves, unmatched in *Martinia* and allies. A narrow subdelthyrial plate lies each side of the delthyrium (Waterhouse 1968, pl. 9, fig. 1, 5), extending ventrally to enclose an inner delthyrial cavity. In another specimen, there is a small sunken connector plate covered by growth lines parallel to the dental tracks (see Waterhouse 1968, pl. 9, fig. 6). The plate is formed by pleromal growth emanating from the inner dental plates – the plates are not of deltidial origin. The ventral muscle field is developed at the posterior wall, not in front. In the dorsal valve, the dental sockets are slender and widely

diverging, contained by horizontal outer plates and subvertical very low inner plates, not in contact with the floor of the valve. The crus of each spire is small and inwardly placed. A low dorsal median myophragm is developed, and the mantle canals are varied, in two to three orders, some anastomosing and branching. The mantle canals in both valves of small specimens are comparatively simple and linear (Waterhouse 1968, pl. 9, fig. 2, 4), spaced only slightly further apart towards the posterior lateral extremities, less than in *Martinia* or *Tiramnia*, and not as closely spaced overall as in *Martinia*. But with increase in size, the canals become stronger and increasingly complex, and almost subreticulate in the ventral valve but not the dorsal valve (Waterhouse 1968, pl. 9, fig. 7, 8). A further difference from *Tiramnia* and *Martinia* is found in the position of the ventral muscle field, which even in small specimens is placed immediately in front of the posterior wall in *Spinomartinia*, and remains comparatively broad and well defined.

Beschevella Poletaev (1975, pl. 11, fig. 1-5), type species *Martinia* (*Ella*) *snjakovii* Rotai of Bashkirian age has a well developed sulcus with ribs, and what appear to be

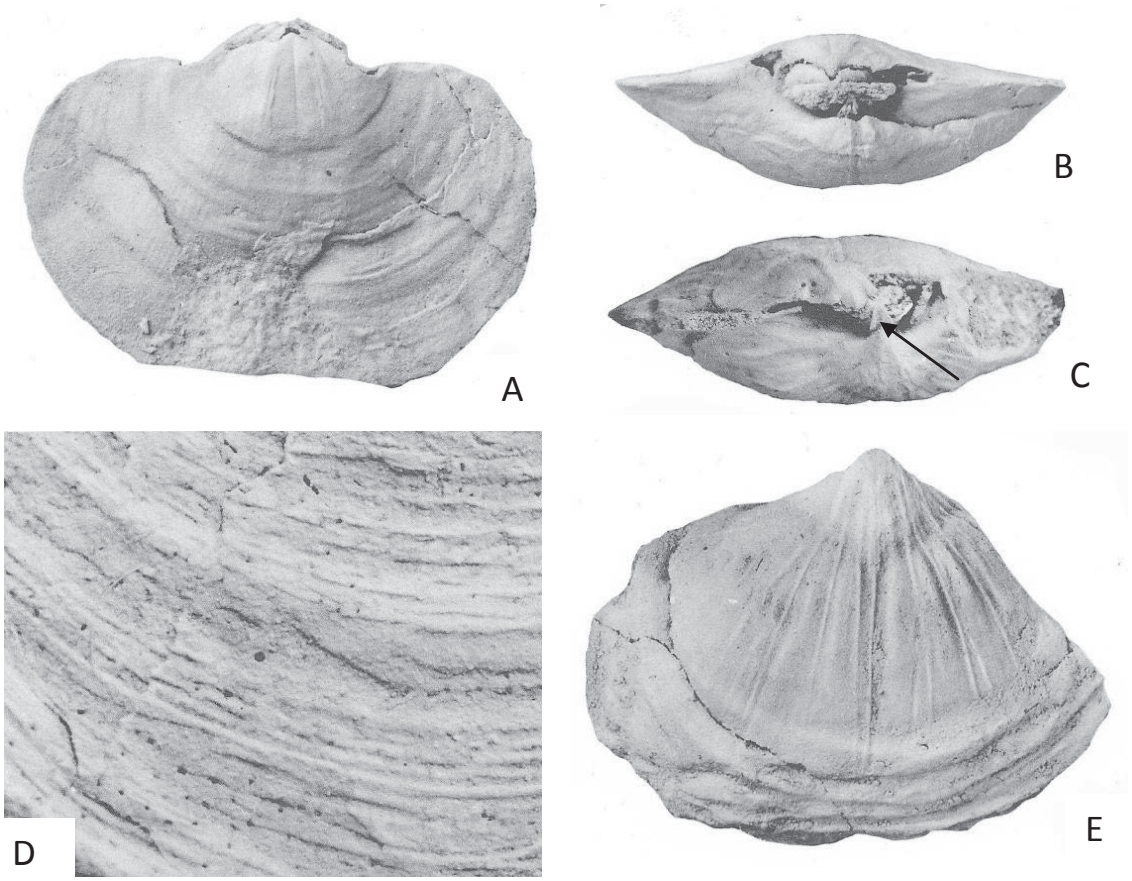


Fig. 100. *Spinomartinia spinosa* Waterhouse. A, B, dorsal and posterior view of holotype, internal mould, x3. C, posterior view of internal mould, dorsal valve on top, x3. The arrow points to the small connector plate. D, micro-ornament as mould, with dark hollows representing spines, x9. E, internal mould of ventral valve, x3. From Trig DD Formation (Changhsingian) of New Zealand. (Waterhouse 1968; 2002, p. 99).

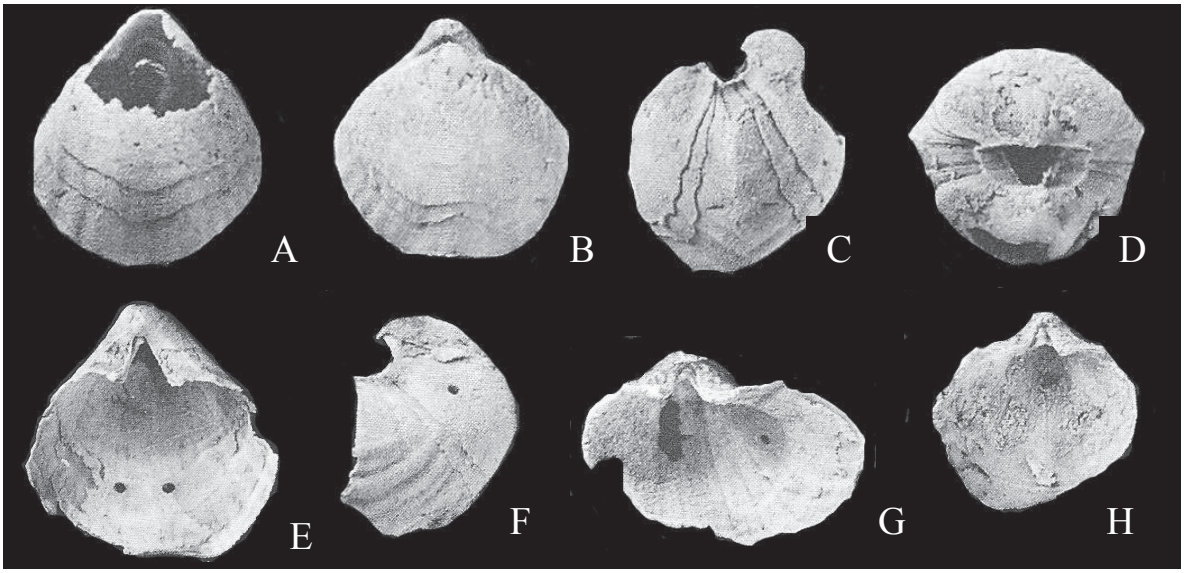


Fig. 101. *Globosospiniger cooperi* Waterhouse. A-D, holotype, x3. E, ventral valve showing delthyrial cover plate, x3. F, G, lateral and dorsal view of small ventral valve, x3.5. G, inner view of ventral valve, x3. From Rat Buri Limestone (Roadian) of southern Thailand. (Grant 1976).

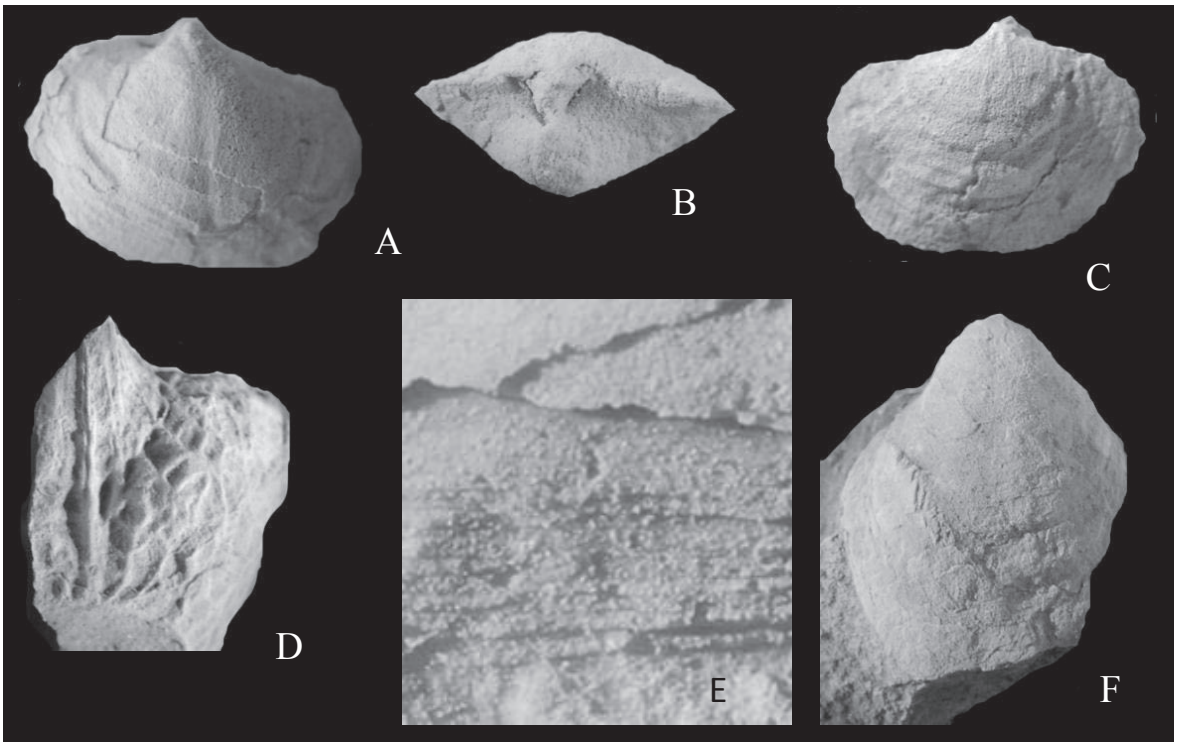


Fig. 102. *Duntonia duntonensis* Waterhouse & Campbell. A-C, ventral posterior and dorsal aspects of small specimen, x4 approx. D, ventral internal mould showing mantle canals, x3. E, detail of micro-ornament on external cast, x7. F, ventral valve, x3. From Takitimu Group (Sterlitamakian), New Zealand.

dense tiny surface pustules in commarginal bands, but they are described as pits. Narrow

deltidial plates extends along the upper edges of the delthyrium.

From the mid-Permian of Thailand, *Globosospiniger* Waterhouse, 2010a, p. 69 is distinctive, of small size with short hinge, anterior sulcus, fold and plicae and micro-ornament of pustules. Both valves are highly inflated. Dental plates are very low, and mantle canals simple, radiating and moderately spaced. Within the socket plates, broad crural bases give rise to spiralia bearing jugal processes, which do not fuse. Both valves are highly inflated, and have low anterior plicae. A short forked callist lies under the ventral umbo - not a convex cover plate, but formed by a subdelthyrial and posterior connector plate or subapical callosity (see Fig. 101E, G, H). The types come from the Rat Buri Limestone in Thailand, of Roadian age, and the hinge lacks denticles, but the inteareas are sharply defined.

Duntonia duntonensis Waterhouse & Campbell from the Takitimu Group of Sakmarian age in the Dunton Range in southern New Zealand is a small elongately or transversely oval form with reduced ventral dental plates and reduced crural and socket plates. In this species the width of the hinge varies from broad to that normal for several other martiniiform genera. The micro-ornament consists of numerous fine pustules, as well as commarginal growth laminae. Unlike the position in *Spinomartinia*, the ventral muscle field lies distinctly in front of the posterior wall. Small pleromal ridges fuse under the apex. The complex network of mantle canals recalls that of *Chapursania* Angiolini (see Fig. 94A, p. 91) from the Middle Permian of Pakistan, but this genus has a consistently wide hinge, and lacks the fine spines typical of *Duntonia*. Unfortunately the interior of *Chapursania* is poorly known, and the nature of delthyrial apparatus requires elucidation. *Duntonia* spines are much finer than those of *Spinomartinia*.

Family **BRACHYTHYRIDAE** Fredericks, 1924

[Nom. correct. hic pro Brachythyrididae Pitrat 1965, p. 706, transl. et correct. ex Brachithyrinae Fredericks, 1924, p. 316].

Diagnosis: Oval usually inflated and biconvex shells with moderately narrow denticulate hinge, ornamented by narrow plicae, radial capillae widespread, but absent from some genera, may be pustular. Delthyrium variably open or covered by subdelthyrial plate, deltidium or stegidial plates, no adminicula or tabellae. Upper Devonian (Famennian) to Upper Permian (Lopingian).

Discussion: Brachythyridoidea was recognized as a superfamily by Carter in Carter et al. (1994), and was placed quite separately from Martinioidea, but still within the massive suborder Spiriferidina. An assessment of the mantle canal system challenges such a long favoured position, because the pattern in type *Brachythyris* is very close to that of type *Martinia*, exhibiting long straight radiating canals in the ventral valve. This is an unusual pattern, differing strongly from the reticulate network of choristitids and trigonotretids, and unlike the densely pitted field typical of spiriferids and the complex mantle canal pattern in ingelarellids. The pattern thus reinforces the information conveyed by the absence of adminicula and tabellae, and severe reduction as a rule in dental plates and crural plates, and

shared type of ctenophoridium. Moreover, although Martiniidae was supposed to differ from Brachythyridae through lacking any form of delthyrial cover, the well preserved genus *Spinomartinia* Waterhouse has subdelthyrial plates, and *Beschevella* Poletaev has a delthyrial cover plate. On the other hand, denticles may be developed along the *Brachythyris* hinge. The *Revised Brachiopod Treatise* stressed the significance of denticulate hinge as being unique to Spiriferoidea. That is clearly not correct, given that the punctate genus *Rastelligera* Hector of Spiriferidina is also strongly denticulate, and indeed the fact that spiriferiforms often have denticulate hinge implies a functional rather than genetic imperative for denticulations.

There is a further pointer to the morphology which needs consideration, and that is in the nature of the micro-ornament. *Brachythyris* itself has faintly cancellate ornament, not different from that of spiriferid and other groups in Spiriferidina, and unlike the often pitted micro-ornament amongst some Martiniidae, although it must be allowed that other Martiniidae do have cancellate or capillate micro-ornament. Genus *Pustuloplica*, allied to brachythyrids though placed in a separate subfamily, has cancellate ornament with scattered well developed pustules. This is a form of ornament developed widely amongst members of Martiniidina, and is found in the earliest genera of Spiriferidina, amongst Cyrtiimorphi. Forms of varied spinose ornament are developed particularly in Gerkispiridae, and in Rorespiriferidae of the Ingelarelloidea, especially in Carboniferous faunas, and in some Martinioidea, such as *Spinomartinia* and *Duntonia*, a number being of Carboniferous and Permian age, whereas subspinose or pustulose ornament is found in spiriferidin groups exclusively in Devonian Cyrtospiriferoidea, and never in the dominant Carboniferous groups such as Spiriferoidea. If brachythyrids are to be regarded as a group independent of martiniids, then they have converged in developing a roughly similar shape, similar internal plates, and similar mantle canal system, and related delthyrial cover. Carter & Gourvennec (2006a, Fig. 1104) derived Brachythyroidea from Theodossioidea. They wrote that denticulation and capillation are suppressed or absent, but this is not fully correct, being contradicted for example by Carter (2006c, p. 1821) in discussing *Brachythyris* itself, in noting the presence of ”faint capillae”. Carter & Gourvennec (2006a, p. 1694) claimed that the interior was devoid of plates, which is not correct, because dental plates and crural plates may be developed. They stated that this was presumably because of paedomorphosis. So what would have been the source? If the *Revised Brachiopod Treatise* interpretation holds true, then a path from Adolfioidea through Theodossioidea into Brachythyroidea holds some possibilities (Carter & Gourvennec 2006a, Fig. 1104), although there is a high degree of exceptionalism, because theodossioids contain few if any species like brachythyrids, and spiriferoids are just as remote: brachythyrid forebears must have constituted a very minor branch which lost costation, plication, internal plates, gained denticulation, duplicated the mantle canal system of Martinioidea, and gained a delthyrial cover plate (for such are missing from some Theodossioidea, fide Johnson, Carter & Hou (2006a, p. 1714). According to such a hypothesis, brachythyrids had changed very markedly from any known source stock. The

preferred alternative is that brachythyrids arose with martiniids from Elythynoidea, either evolving in concert or diverging from a common ancestor, sharing shape, and many but not all aspects of micro-ornament, delthyrial apparatus, loss of internal plates and mantle canal systems, and diverging in the development of denticulate hinge and possibly deltidium. Anyway, the present new scheme can hardly be faulted in terms of unlikelihood or impossibly rapid change – it is much the more conservative of various alternatives.

Brachythyrids are a tiny group, and two families were recognized by Carter (2006c), and another subfamily is added, following Waterhouse (2004). The family groups are united through the lack of adminicula and tabellae, but differ considerably from each other.

Taxonomy: In proposing Brachythyridoidea, Pitrat (1965) inserted the id, and that conforms with recommendations in ICZN 1999. Here it is preferred to delete the id as extraneous for the family ending, and superfamily ending.

Subfamily **BRACHYTHYRINAE** Fredericks, 1924

[Nom. correct. hic pro Brachythyrididae Pitrat 1965, p. 706, nom. correct. pro Brachithyrinae Fredericks, 1924, p. 316].

Diagnosis: Hinge short, cardinal extremities obtuse, interarea high, delthyrium partly closed by convex deltidial plate, ornament of low open plicae, simple or branching, sulcus and fold may be costate. Micro-ornament subdued, variable, commarginal or radial fila. Mantle canal system, at least in type *Brachythyris*, linear. Upper Devonian (Famennian) to Upper Permian (Lopingian).

Genera: *Brachythyris* M'Coy, *Bingleburria* new genus, *Cathayspirina* Liang, *Dalaia* Plodowski, *Ella* Fredericks*, Latibrachythyris* Angiolini, Long & Davies, *Meristorygma* Carter, *Moumina* Fredericks.

Discussion: Carter (in Carter et al. 1994; 2006c, p. 1823) recognized two families in Brachythyridoidea. Brachythyrididae (= Brachythyridae) was characterized by the lack of a median costa from the sulcus, and Skelidorygmidae Carter by the presence of a median costa along the sulcus, and often by presence of additional sulcal costae which bifurcate from sulcus- bounding ribs. Yet such sulcal costae were also described for *Meristorygma* Carter, placed by Carter in Brachythyridae, and occur also in various species assigned to *Brachythyris*. The differences in medial costation are slight, and they appear to be of no more than of subfamilial value, if that. *Brachythyris* M'Coy, 1844 was defined by Carter (2006c, p. 1821) as having a smooth dorsal fold, which is true of the type species *Spirifera ovalis* Phillips, 1836, p. 219, but a number of associated species (such as those now classed as *Latibrachythyris*) in the Carboniferous limestones of Great Britain have narrow plicae over the fold and in some species entering the sulcus. There is considerable variation.

Figures of *Brachythyris* and *Latibrachythyris* from Derbyshire and Isle of Man, England, in Waterhouse (1968, pl. 6, fig. 1, 5, pl. 7, fig. 1, 2) show the short hinge and simple mantle canal system approaching those of *Martinia*. However a figure of the full extent of vascular canals in *Bingleburria elliptica* Roberts (1963, text-fig. 11) shows that the canals bifurcate

terminally, a pattern apparently peculiar to the genus (See Fig. 106, p. 104). Waterhouse (1968, pp. 45, 46) recorded radial capillae in *ovalis*, and showed in a sectioned specimen that the delthyrium is closed by a small convex deltidial plate, to confirm a figure in Davidson (1861, pl. 9. fig. 25, identified as *hemisphaerica* M'Coy) and for *Latibrachythyris pinguis* (Sowerby) from Wales (Waterhouse 1968, pl. 6, fig. 4). There is no knowledge of a connector plate or pleromal ridging. Carter (1974, p. 692) stated that the delthyrium of *Meristorygma* was partly closed by deltidial plates. Genus *Moumina* Fredericks was stated by Carter in Carter & Gourvennec (2006b, p. 1757) to be internally similar to *Martinia*, and it is inflated with short hinge, subdued plicae and capillate micro-ornament, closer to *Brachythyris* than to *Martinia*, whereas Carter referred the genus to Elivellinae, supposedly in Martiniidae.

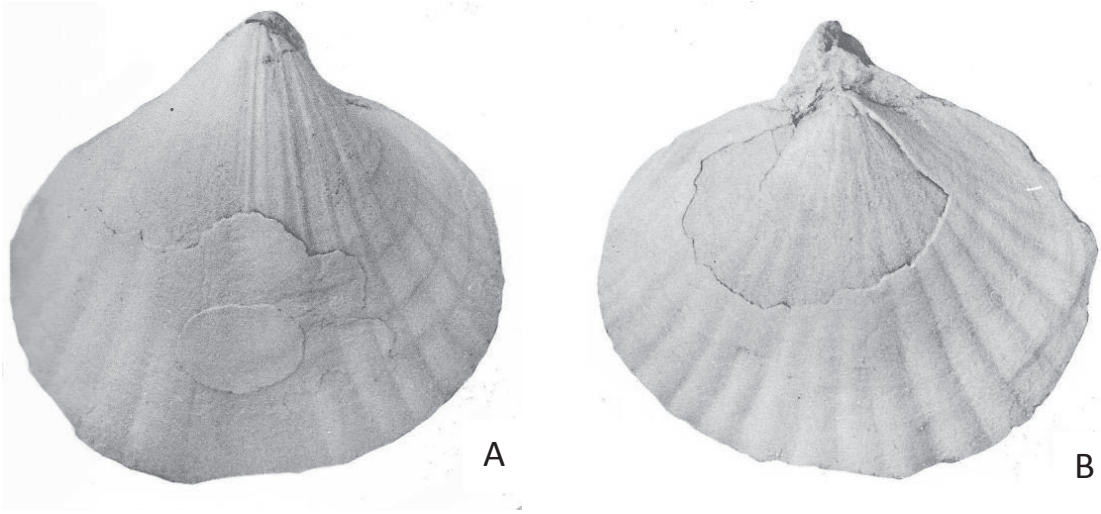


Fig. 103. A, B, *Brachythyris ovalis* (Phillips), ventral and dorsal aspects, x1, showing linear vascular imprints, much as in *Martinia*. C, *Latibrachythyris pinguis* (Sowerby), dorsal view, x1.5, showing delthyrial cover plate. From Visean of England and Wales. (Waterhouse 1968).

Not all genera placed in Brachythyrididae by Carter have fine radial capillae. *Cathayspirina* Liang, 1990 has fine commarginal growth-lines, but Carter (2006c, p. 1821) made no mention of micro-ornament. *Ella* Fredericks, 1918, its micro-ornament not recorded by Carter, has fine cancellate radials and commarginals (Chernyshev 1902, Fig. 51). *Meristorygma* Carter, at least on Canadian material from the Yukon Territory, has fine commarginal growth-lines, though the *Revised Brachiopod Treatise* stated micro-ornament was absent.

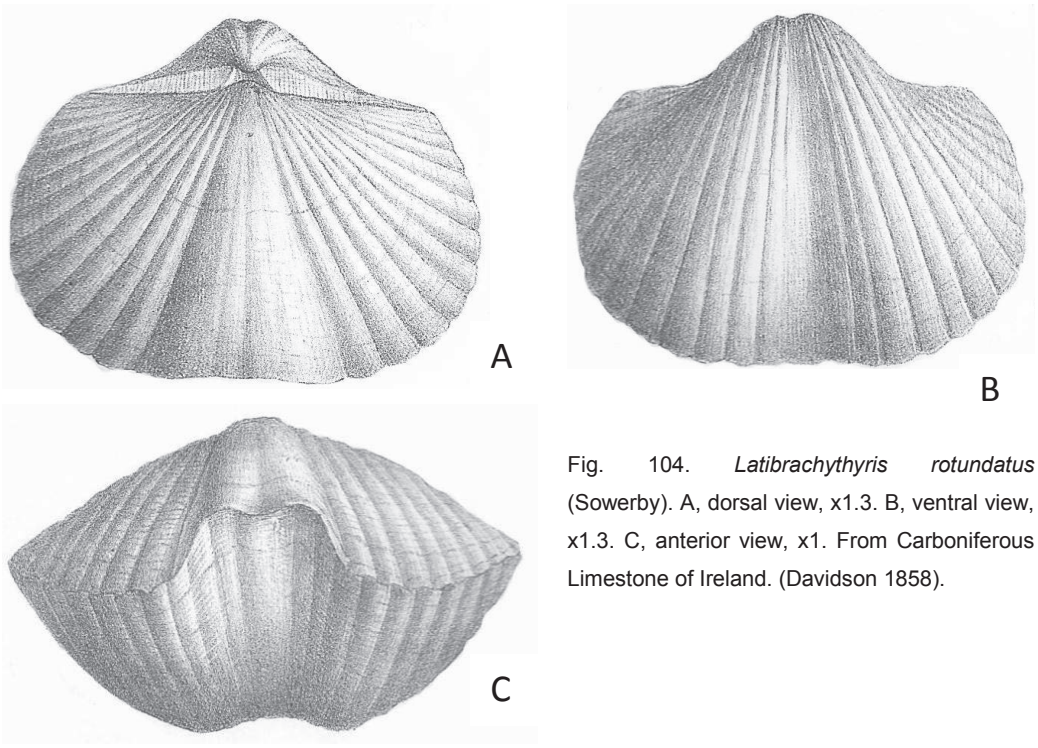


Fig. 104. *Latibrachythyris rotundatus* (Sowerby). A, dorsal view, x1.3. B, ventral view, x1.3. C, anterior view, x1. From Carboniferous Limestone of Ireland. (Davidson 1858).

Genus ***Bingleburria*** new genus

Name: From Bingleburra Formation, source of the material.

Diagnosis: Hinge wide, plicae numerous and weakly divided over lateral slopes, several costae within sulcus, fold divided by cleft.

Type species: *Brachythyris elliptica* Roberts, 1963, p. 17 from Bingleburra Formation (Tournaisian), New South Wales, here designated.

Discussion: This genus is close to *Brachythyris*, but has a broader hinge, that of the type species measuring two thirds of the shell width, compared with less than half the width for *Brachythyris* or the rather similar genus *Ella* Fredericks, 1918. A small deltidium covers the upper delthyrium, forking anteriorly, formed from two deltidial plates centrally merged. Plicae are comparatively numerous and fine, even more than in *Dalaia* Plodowski, 1968 and contrast with the few strong plicae of *Cathayspirina* Liang, 1990. Within the sulcus there are a few fine costae, finer and more numerous than in *Meristorygma* Carter, 1974, and not branching from the sulcal border. There is no median rib. The fold is smooth, apart from suggestions of faint anterior costae, and is traversed by a slender deep cleft. This cleft and the faintness of the radial ornament over the sulcus and fold help distinguish the genus from *Eobrachythyrina* Lazarev & Polataev, 1982, which is found in upper Serpukhovian faunas of the Donets Basin in Ukraine. As well, the ontogenetic trajectory differs, that of *Eobrachythyrina* being much more transverse in early stages. Micro-ornament consists of radial and commarginal fila. Internally there are well developed dental plates and no adminicula, and the muscle field is striate. Mantle canals are highly distinctive. Two pair of adductor scars are present in the

dorsal valve, and a socket plate is well developed each side of the ctenophoridium.

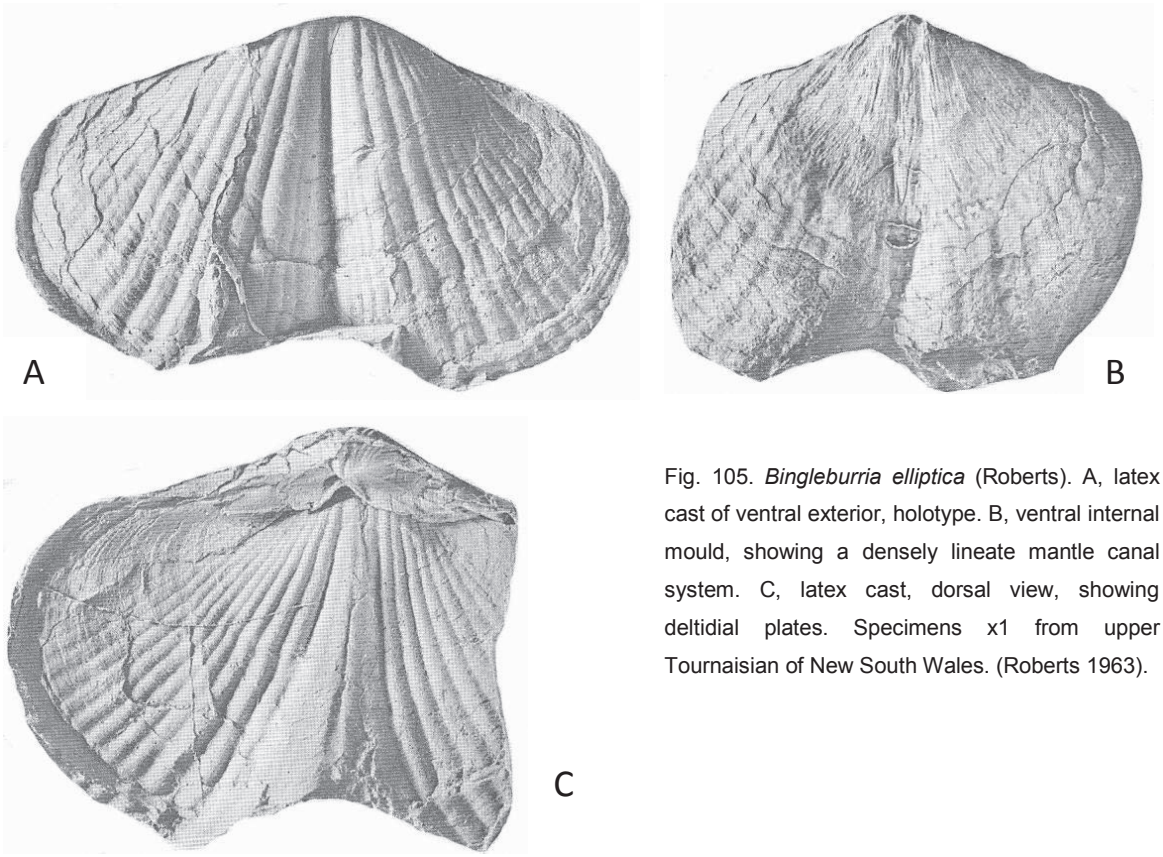


Fig. 105. *Bingleburria elliptica* (Roberts). A, latex cast of ventral exterior, holotype. B, ventral internal mould, showing a densely lineate mantle canal system. C, latex cast, dorsal view, showing deltidial plates. Specimens x1 from upper Tournaisian of New South Wales. (Roberts 1963).

Latibrachythyris pinguis (Sowerby) from the Early Carboniferous of United Kingdom has similar wide hinge and shape and weakly cleft dorsal fold, though with no adventitious sulcal and fold costae, and no tendency for ventral lateral plicae to subdivide. The species described as *Brachythyris suborbicularis* Hall of Weller (1914, pl. 61, fig. 1-8) from

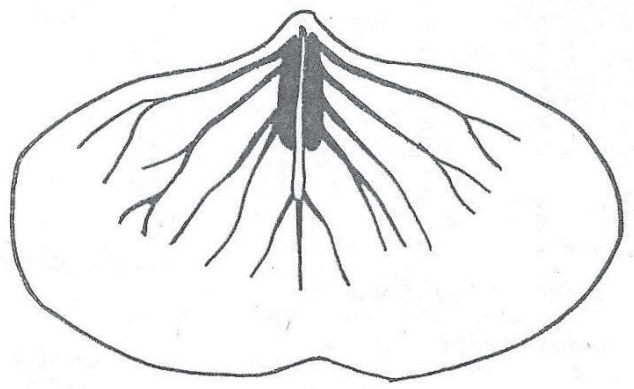


Fig. 106. *Bingleburria elliptica* (Roberts), ventral valve showing mantle canal system. Specimen x1.5 from upper Tournaisian of New South Wales. (Roberts 1963).

Brachythyris suborbicularis Hall of Weller (1914, pl. 61, fig. 1-8) from the Burlington and

Keokuk limestones of Illinois, United States, is somewhat similar. *B. pseudovalis* Campbell (1957, pl. 14, fig. 10-15) from Babbinboon, New South Wales, has even wider hinge and larger deltidial plates. *B. willbourni* Muir-Wood (1948, pl. 8, fig. 1-3) from the Early Carboniferous of Malaya is allied with median cleft along the dorsal fold and numerous narrow plicae laterally.

Subfamily **SKELIDORYGMINAE** Carter, 1994

[Nom. transl. hic ex Family Skelidorygmidae Carter, 1994, p. 349].

Diagnosis: Plicae fine, and approaching costae in strength, occupy sulcus by branching from sulcus-bounding costae in umbonal region, median sulcal costa widely present. Radial capillae absent. No denticulate hinge. Delthyrial cover and mantle canal pattern of radiating canals with posterior pitting. Upper Devonian (Famennian) to Middle Carboniferous (Bashkirian).

Genera: *Skelidorygma* Carter, *Litothyris* Roberts, *Phragmobrachythyris* Poletaev.

Fig. 107. *Phragmobrachythyris stylaensis* Poletaev, ventral valve showing muscle field and mantle canal system, x2. From Visean of Donets Basin, Ukraine. (Lazarev & Poletaev 1970).

Discussion: Two genera were placed in Family Skelidorygmidae by Carter (2000c, p. 1823), *Skelidorygma* Carter, 1974 of upper Tournaisian to Bashkirian age in North America and Russia and *Litothyris* Roberts, 1971 of Upper Devonian age from east Australia. A further genus *Phragmobrachythyris* of Tournaisian and Visean age was described by Poletaev, 1999. The genera are close to brachythyrin genera but have slightly finer plicae and, according to Carter (2006a), a central costa along the sulcus, although that seems minor in *Litothyris*. *Litothyris* is reported as having a short delthyrial plate, *Phragmobrachythyris* Poletaev, 1999 has a reported deltidium, and *Skelidorygma* shows two low deltidial plates with short apical plate. Micro-ornament is described as absent, but it should be noted that the presence of growth-increments was as a rule not rated as ornament in studies by Carter. Internally the morphology is martiniid-brachythyrid, but the mantle canal system, from indications in figures published for *Skelidorygma* by Carter (1974), seems to indicate deep well spaced pits posterolaterally and well spaced canals in front. There does not appear to be any sign of a reticulate network, nor of linear canals. Some uncertainty has to be attached to this interpretation, given that it is based on inspection of figures for *S. bamberi* Carter (1987, pl. 26, fig. 2, 3), which is not the type species. The pattern for *Phragmobrachythyris* was

illustrated by Lazarev & Poletaev (1982, pl. 1, fig. 10) for what was then purported to be *Brachythyris*, and it is moderately similar, showing a more restricted field of posterior pits. There is some agreement with the pattern found on some Ingelarelloidea, because members particularly of Ingelarellidae may show a pattern of posterior well spaced dimples, with an array of fine radiating linear canals in front. Skelidorygminae is slightly older than the oldest known member of Ingelarellidae. *Skelidorygma* itself is of upper Tournaisian age, slightly younger than some genera in Gerkispiridae, and *Acanthospirina* of this latter family started in the upper Devonian. On the other hand, the difference in delthyrial covers would appear to rule out such an alliance. Poletaev (1999) placed *Phragmobrachythyris* in Brachythyrididae, with Skelidorygminae reduced to subfamily status, and that would acceptably accommodate the nature of the delthyrial cover seen in two of the genera. The response by Carter in Gourvennec & Carter (2007, p. 2789) is confusing, because he referred the genus to Subfamily Skelidorygmidae (not Skelidorygminae), leaving the reader to decide which word had been mis-spelled.

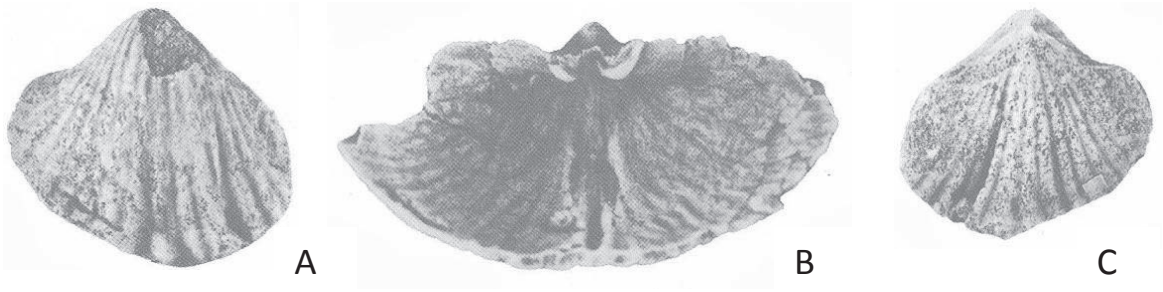


Fig. 108. *Skelidorygma subcardiiformis* (Hall). A, C, ventral and dorsal views of holotype, x1, from Visean of Illinois. (Carter 1974). B, *S. bamberi* Carter, ventral interior x2, from upper Tournaisian of Alberta. (Carter 1987).

Subfamily **PUSTULOPLICINAE** Waterhouse, 2004, p. 234

[Pustuloplicinae Waterhouse 2004, p. 234].

Diagnosis: Small strongly plicate shells with moderately short hinge, costae over sulcus and fold, micro-ornament of commarginal growth increments and radial threads bearing papillae where adequately known. Delthyrium without deltidium or cover plate, bearing low umbonal or pleromal callist that divides in two towards the hinge. No adminicula or tabellae. Upper Carboniferous (Gzhelian) to Upper Permian (Lopingian).

Genera: *Pustuloplica* Waterhouse, ?*Capillispirifer* Zhang, *Zhejiangospirifer* Liang.

Discussion: If Brachythyridae is to include subfamilies that share most attributes and vary mainly in the strength and number of plicae, then Pustuloplinae may need to be upgraded to family status. *Pustuloplica* with its nodose micro-ornament is completely unlike that of the other genera referred to Brachythyridae, and furthermore it lacks a deltidial plate, and has an umbonal callosity that passes forward into low pleromal ridges. So it resembles the delthyrial arrangement in some Spinomartiniinae, and is unique in terms of micro-ornament, composed of radial capillae crossed by commarginal growth increments, and small elongate pustules. As

in Skelidorygminae, hinge denticles are lacking. It has to be conceded that the group should possibly be raised to family status, but whatever arrangement is made, *Pustuloplica* and allies are clearly close to Martiniidae and to Brachythyridae, and belong to the same superfamily.

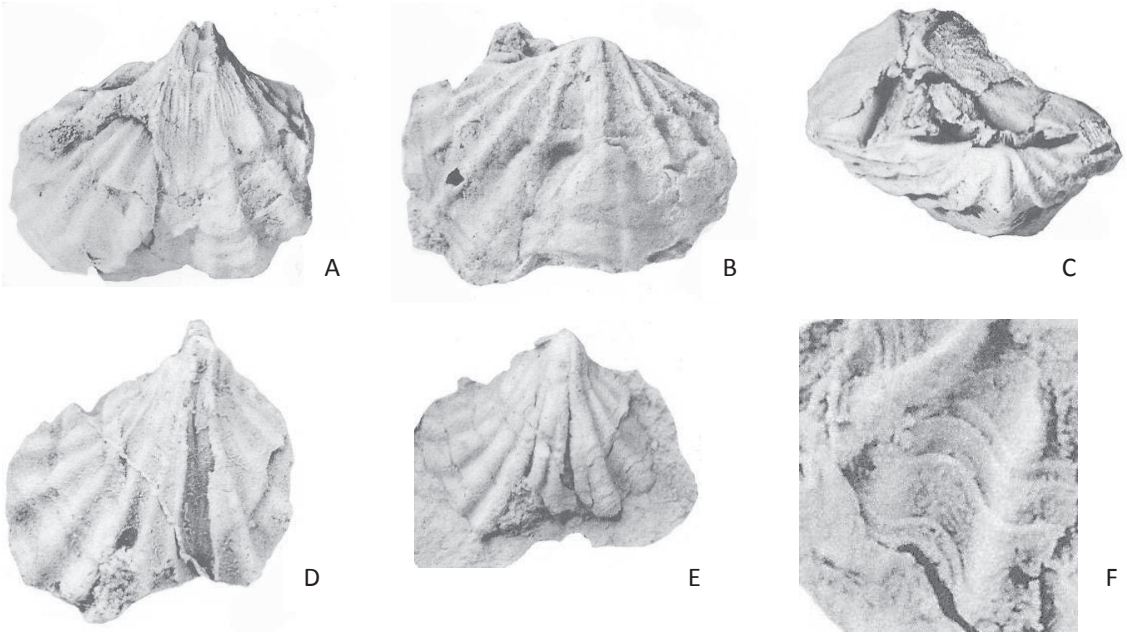


Fig. 109. *Pustuloplica baccata* Waterhouse. A-C, ventral, dorsal and posterior views of holotype internal mould, x2. D, ventral internal mould, x2. From Brunel Formation (Artinskian), New Zealand. E, F, *P. bicostata* Waterhouse. E, latex cast of ventral exterior, x2. F, micro-ornament on external mould of ventral anterior, x6. From Changhsingian boulder, New Zealand. (Waterhouse 1968).

Pustuloplica Waterhouse, 1968, p. 45 comes from Early to Late Permian faunas of New Zealand and east Australia. The small pedicle callist under the umbo, which passes forward into two well developed ridges at the base of the dental plates, is akin to the pleromal ridges and connector plate, represented in Rallacostinae and Spinomartiniinae. *P. baccata* Waterhouse has a median sulcal costa with two further two costae laterally, and *P. bicostata* Waterhouse lacks a median costa, to suggest that the presence or absence of a median costa is of low significance, given that it varies even within one brachythyrid genus, even though the difference was regarded as a leading criterion by Carter (2006c) for *Skelidorygma* and allies. Mantle canals are visible as a dense array of lines around the anterior muscle field, with posterior pitting, and the lines spread further with increased ontogeny, somewhat like the pattern in Skelidorygminae.

Gourvennec in Gourvennec & Carter (2007, p. 2789) objected to the proposal of Pustuloplicinae, stating it led “to a mixture of taxa with different morphologies (eg. delthyrial morphology, deltidial cover, ornament)”. His assertion is difficult to understand. Gourvennec failed to specify exactly what he was writing about, and no wonder. Carter (2006c) had included *Pustuloplica* in Brachythyrididae. Yet it has different micro-ornament and different

delthyrial morphology, including an umbonal callosity and lack of deltidial cover, as well as presence of pustules. Who then is guilty of mixing morphologies? Separation as a subfamily or tribe at least seems amply justified, according to the very criteria that Gourvennec complained about. Just how taxa are mixed through the segregation of *Pustuloplica* is especially mystifying.

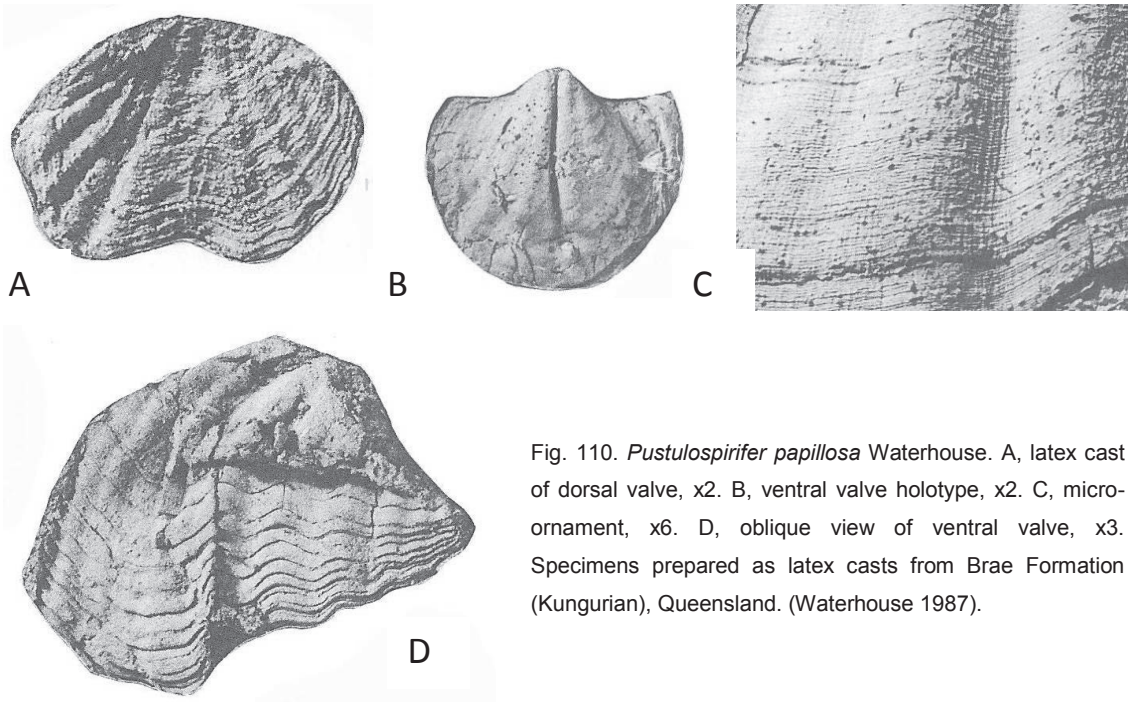


Fig. 110. *Pustulospirifer papillosa* Waterhouse. A, latex cast of dorsal valve, x2. B, ventral valve holotype, x2. C, micro-ornament, x6. D, oblique view of ventral valve, x3. Specimens prepared as latex casts from Brae Formation (Kungurian), Queensland. (Waterhouse 1987).

Angiolini et al. (2011) in discussing *Pustuloplica*, claimed that “the holotype is so poorly preserved that it is not easy to give this taxon a systematic position”. There are several problems with this approach. Firstly, the claim is false. The holotype does show internal detail, and does show external detail. It would seem that those authors failed to check – or they misinterpreted – the original and subsequent studies. Moreover the taxonomic position of a species does not depend solely on the holotype. The holotypes of the species they recorded in their study do not show anything of the internal morphology. That does not negate the classificatory position, which can be adduced from other specimens. Furthermore none of their illustrations convey micro-ornament, which at best reflects on poor preservation of the micro-ornament. In addition, the complaint that it is not easy “to give a systematic position” perhaps expresses an overall dissatisfaction about the taxonomy of Spiriferida. No indeed, taxonomy is not easy – but then, why should it be? It does require a great deal of hard thinking and continual readjustments. In spite of their problems, they agreed that Pustulospiriferinae should be recognized, and possibly include *Zhejiangospirifer* Liang.

Zhejiangospirifer Liang, 1982, 1990, p. 476 from the Lengwu Formation in China, of

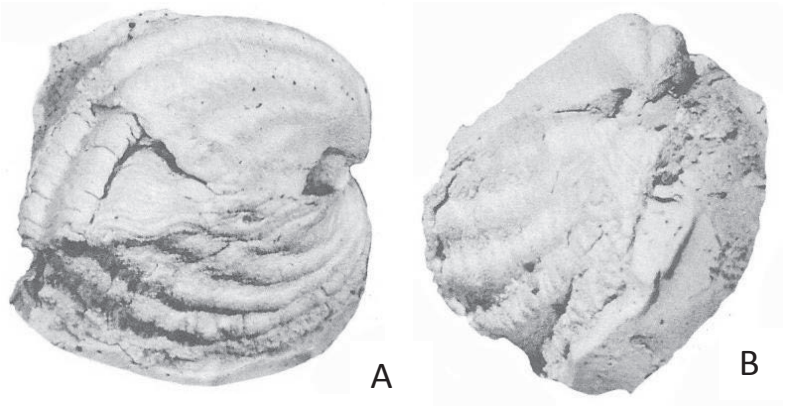


Fig. 111. *Pustuloplica baccata* Waterhouse, lateral and dorsal views of PVC cast, x3. From Takitimu Group (Artinskian), New Zealand. (Waterhouse 1968).

early Lopingian (Late Permian) age, not Cisuralian, as wrongly stated by Carter (2006c, p. 1786), is likely to be another member of the subfamily (Waterhouse 2004, p. 235), having strong plicae, micro-ornament of nodes and no adminicula or tabellae. The delthyrium was described as open, though a cover plate could have been lost, without leaving any sign. Several species were described by Liang (1990), and a median costa is developed along the sulcus in some specimens, and not others, showing variation comparable to that of New Zealand material.

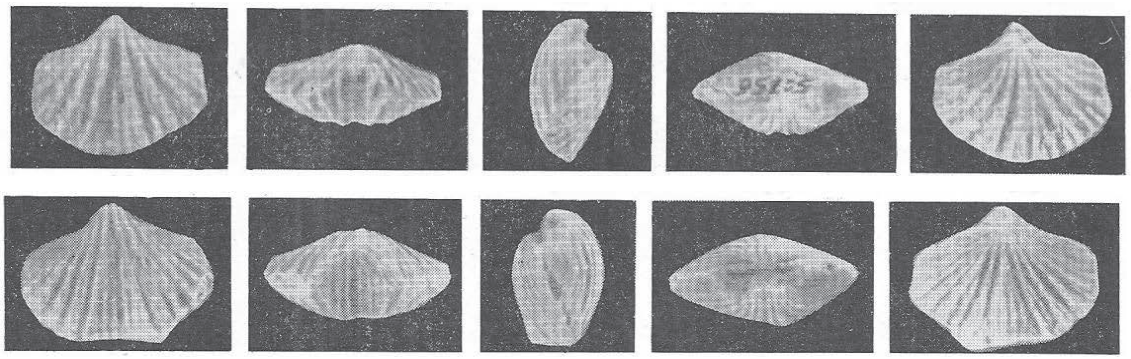


Fig. 112. *Zhejiangospirifer depressus* Liang, showing successive development during early growth phases within the type species, from early Lopingian of Zhejiang Province, China, x1. (Liang 1990). The branching in the plicae is very close to that of *Pustuloplica*.

Zhejiangospirifer is known chiefly from external decorticated specimens, with the interior revealed only by section. Juvenile specimens are close to the mature *Pustuloplica*: the sulcus develops a median costa, followed by more costae; and plicae branch erratically, and the crest of the fold becomes costate. Micro-ornament is not clearly illustrated. Clearly the two are not congeneric, but the internal detail and report of commarginal growth lines and low nodes suggest the likelihood of confamiliarity. Carter classed *Zhejiangospirifer* in Tangshanellidae, and this position was argued by Shen et al. (2003b, p. 242), but their views are not substantiated by numerous aspects of the morphology, involving plication and mode

of increase, delthyrium, and micro-ornament.

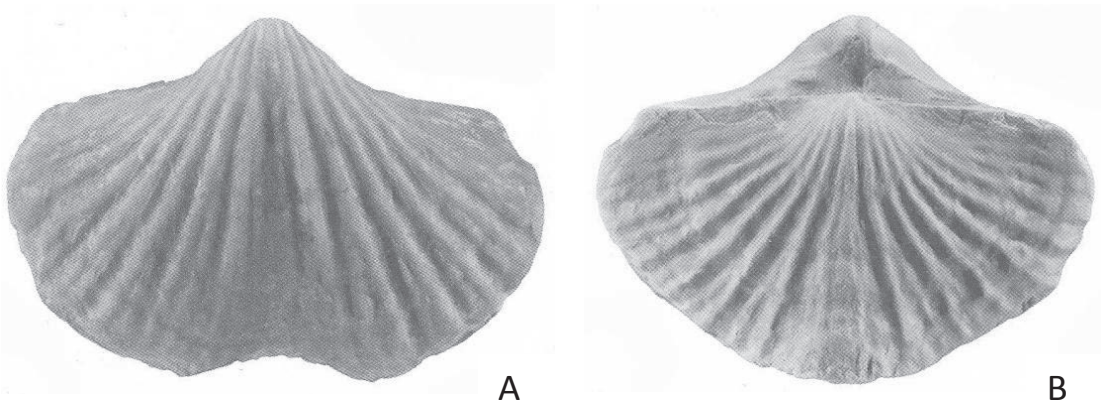


Fig. 113. *Zhejiangospirifer depressus* Liang, ventral and dorsal views, x2. From Wuchiapingian of Zhejiang, China. (Liang 1982).

Liang (1990) considered that specimens described as *Trigonotreta guizhouensis* Liao, 1979, pl. 4, fig. 8-13 from Guizhou in China was likely to be congeneric with *Zhejiangospirifer.* This species comes from beds close to the Carboniferous-Permian boundary. It has plicae that remain simple throughout their length, and whereas the sulcus in one specimen has a single median rib, a larger and more transverse triangular-shaped specimen has three pair of costae in the sulcus, without a median rib, and the fold is anteriorly costate. Whether the Guizhou form really belongs to *Zhejiangospirifer* requires further analysis, and on the whole, seems doubtful.

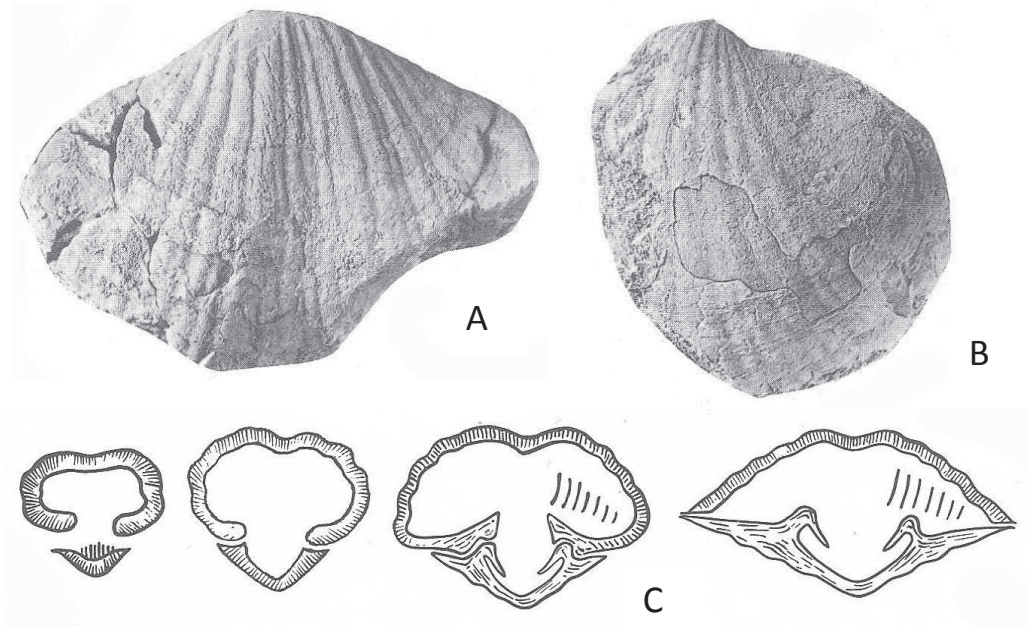


Fig. 114. *Zhejiangospirifer giganteus* Shen, Shi & Archbold. A, B, ventral and dorsal valves, x1, 1.5. From exotic Permian block in Indus-Tsangpo suture, southern Tibet, of Wuchiapingian age. (Shen et al. 2003b). C, *Zhejiangospirifer depressus* Liang, transverse sections, x2. From Zhejiang, China. (Liang 1982).

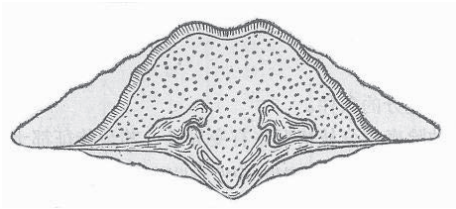


Fig. 115. *Zhejiangospirifer depressus* Liang, showing transverse section 5.5mm ventral beak, x1.75. From Zhejiang Province, China. (Liang 1990).

Capillispirifer Zhang in Zhang Chuan et al. (1983), with better figures provided in Carter (2006a, p. 1786, Fig. 1181a-c) is also close to *Pustulospirifer*, lacking internal plates, having strong plicae, inflated shell, and cancellate ornament.

Fig. 116. *Capillispirifer xinjiangensis* Zhang, ventral, dorsal and lateral views of holotype, x2. From Pennsylvanian of China. (Carter 2006a)

Infrasuborder CHORISTITIMORPHI new infrasuborder

Diagnosis: Shells of characteristic shape, roundly suboval to slightly rectangular or subtriangular in outline, with broad incurved ventral umbones, weakly to moderately defined sulcus and fold, and usually well extended and well rounded antero-lateral margins. Broad or fine subequal strap-like ribs with flat crests and narrow interspaces over entire shell as a rule, may be finer within sulcus and over fold; in many genera posterior broad flat-crested ribs splay anteriorly into a few finer costae; micro-ornament usually of growth increments, may be capillate or pustulose. Delthyrium open or with deltidial or stegidial plates, dental plates usually well developed with supporting adminicula, rarely lost, tabellae long to short or absent; vascular canals may be reticulate and often posteriorly directed, but rarely preserved. Hinge denticles in some younger genera. Upper Devonian (Famennian) to Middle Permian (Roadian).

Discussion: A lengthy but minor lineage may be traced back through Devonian and Carboniferous, before waning through the Permian Period. Origins would appear to have been within Eospiriferinae, insofar as adminicula and tabellae were long in some genera, just as in some Eospiriferinae, and shape was subrounded with well rounded anterior lateral margins, as in a number of eospiriferid genera, such as *Eospirifer*, *Endospirifer, Xinanospirifer, Lobvia* and other genera, which were also close in lacking plicae. But none of these genera have the characteristic choristitid ornament of rather-flat crested narrow ribs which broaden and pass into finer ribs, although *Lobvia* of Emsian (Lower Devonian) age and *Xinanospirifer* Rong, Xu & Yang of Telchian (Silurian) age are costate.

The group is placed in an infrasuborder, and forms part of the Martiniidina, much less diverse and numerous than the Martiniimorphi.

Superfamily **THEODOSSIOIDEA** Ivanova, 1959

[Nom. transl. Johnson, Carter & Hou in Carter et al. 1994, p. 333 ex Theodossiinae Ivanova, 1959, p. 61].

Diagnosis: Shells costate as a rule, sulcus and fold variably developed. Micro-ornament of commarginal fila and radial capillae which may be pustulose. Delthyrium open or closed, adminicula well developed, tabellae short or absent, connector plate present or absent. Inner shell layer may be prismatic. Upper Devonian (Frasnian, Famennian).

Discussion: Theodossioidea as here interpreted have a binary mode, genera with or without prismatic shell and with or without delthyrial cover, and with or without a connector plate. They gave rise in turn to distinct families with or without tabellae and with or without connector plates, but all were united by somewhat similar build of shell, and by macro-ornament.

As interpreted by Johnson, Carter & Hou (2006a, p. 1714), Theodossioidea was deemed to have uniform plicae or costae and indistinct fold and sulcus, with no delthyrial plate. That applies well to genus *Theodossia* in their group Theodossinae, but less to Branikiinae which they classed in the same family, in which plicae and subplicae are

developed in *Lenzia* and *Branikia*, and not to their Ulbospiriferidae, with well developed sulcus and fold, and two orders of ribbing in *Palaeospirifer*. *Palaeochoristites* was included in Theodossioidea, but has ribs of varying strength. Moreover Theodossioidea, diagnosed as lacking a delthyrial cover, was supposed to have included *Cyrtiorina*, with a delthyrial cover. It is almost a constant theme, to discover exception after exception to the prime diagnoses for early family and superfamily groups as treated in the *Revised Brachiopod Treatise*, but Theodossioidea is outstanding for the way it was made to include genus after genus that does not conform with the opening definition. That opens up two options: either the definition was at fault, or the superfamily as presented in the Treatise was polyphyletic, and included disparate groups. Whilst the definition may not have been perfect, it is the second option that is favoured by the evidence.

Eospirifer Schuchert, 1913, name genus for Eospiriferidae in Superfamily Cyrtioidea, ranged from latest Ordovician into Lower Devonian (Emsian) and is close in a number of attributes, shape, sulcus-fold, fine even ribbing, and developed tabellae and long adminicula in younger forms. There are perceptible differences, to some extent in shape and also lack of cardinal process or ctenophoridium, but this genus or kindred stock would appear to have provided potential for ancestral material. There still remains a gap between eospiriferids and theodossioids, but not a lengthy one, because *Eospirifer* persisted into the Lower Devonian, and theodossioids entered the succession in the Upper Devonian.

As arranged in the *Revised Brachiopod Treatise*, Theodossioidea embraced families with and without prismatic shell, and the nominate genus belonged to a family without prismatic shell, so that its relationship to shells with prismatic layer becomes of interest in pointing to an evolutionary change, just as implied by the *Revised Brachiopod Treatise*. Genera assigned to the superfamily in the *Revised Brachiopod Treatise* show such a range of shapes and ornament, to the extent it is difficult to find unifying attributes. The superfamily is very small, the diagnosis does not apply to half the group, and the distinctions from other groups not great. Therefore the superfamily is reinterpreted: partly disbanded, and evidence reassembled to suggest that the superfamily was the ground for the development of Choristitoidea. Genera and family groups that were precursor for Spiriferimorphi, incorporated in Theodossioidea in the *Revised Brachiopod Treatise*, are shown to differ substantially from *Theodossia* and allies, and are removed from the superfamily. Changes are as follows:

Theodossinae appears to have been pre-choristitinoid, and its costae are not choristitinid. But shape is much the same.

Branikiinae is elevated to a family, and regarded as a probable member of Adolfioidea, given the open delthyrium.

Paralazukinia and *Urella,* although lumped with the very different genus *Theodossia* in the *Revised Brachiopod Treatise*, are treated as a separate subfamily close to *Branikia*.

Ulbospiriferinae with prismatic shell is regarded as a member of Cyrtospiriferidae. Its relationships are based partly on the type species, based on a broken and incomplete ventral valve, and on an associated species.

Palaeospiriferidae, also characterized by prismatic shell, has comparatively broad low plicae. It is close to being choristitoid.

Tenisia and *Cyrtiorina*, although regarded as in Ulbospiriferinae, are referred to Hollardospiriferinae new subfamily, in Palaeospiriferidae, characterized by prismatic shell layer, and retained as theodossioid.

These are joined by Cyrtiopsinae Ivanova, transferred from Cyrtospiriferoidea because they lack a connector plate, and by new subfamily Enchondrospiriferinae, based on *Enchondrospirifer* Brice, with pleromal plates and incipient connector plate, and tabellae vestigial from Theodossinae.

Palaeochoristitidae is regarded as a choristitoid family, with addition of other subfamilies.

In summary, *Theodossia* is regarded as an exceptional and prechoristitform genus, distinguished by the shortness or lack of tabellae and presence of slender uniform costae, with extrasinal adminicula. Some of the other groups associated with it in the *Revised Brachiopod Treatise* belong to the same superfamily group, and some display the prismatic shell found in younger choristitids. Theodossiinae seems most likely to have arisen from Eospiriferidae, through the development of fine regular costae, which includes genera amongst Eospiriferinae that were similarly not plicate, and include one genus *Xinanospirifer* Rong, Xu & Yang, 1974 with costate ornament and long well-spaced adminicula and short tabellae. This genus is of Silurian (Telychian) age in southwest China.

Family **THEODOSSIIDAE** Ivanova, 1959

[Nom. transl. Johnson, Carter & Hou in Carter et al. 1994, p. 333 ex Theodossiinae Ivanova, 1959, p. 61].

Diagnosis: Shells without inner prismatic layer. Ornament of costae or exceptionally, fine plicae, gentle if any sulcus and fold. Micro-ornament of commarginal laminae and/or capillae. Long adminicula. Upper Devonian (Frasnian, ?Famennian).

Subfamily **THEODOSSIINAE** Ivanova, 1959

[Theodossiinae Ivanova, 1959, p. 61].

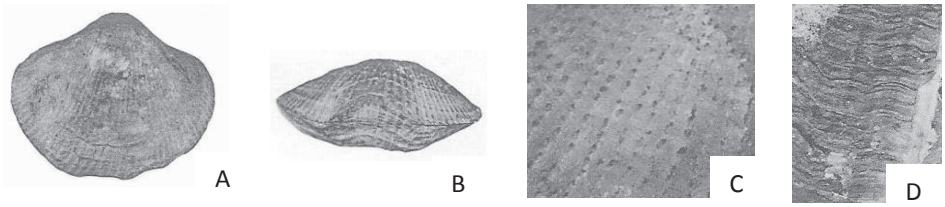


Fig. 117. *Theodossia anossofi* (Murchison, Verneuil & Keyserling). A, ventral view, x1. B, anterior aspect (dorsal valve on top), x1. C, D, micro-ornament, x5, with C thought by Vandercammen to be due to another life-form, and D the real micro-ornament. This is the type species, from Devonian of Russia. (Vandercammen 1959a).

Diagnosis: Shells without inner prismatic layer. Ornament of costae or exceptionally, fine plicae, gentle if any sulcus and fold. Micro-ornament of commarginal laminae and/or capillae. no delthyrial cover plate or deltidia as a rule. Long extrasinal adminicula diverging forward, short tabellae, possibly absent from type genus. Ctenophoridium broad, low. Upper Devonian (Frasnian, Famennian).

Genera: *Theodossia* Nalivkin, ?*Dichospirifer* Brice, ?*Eodmitria* Brice, *Vandergrachtella* Crickmay.

Discussion: *Theodossia* Nalivkin, 1925 is a distinctive finely costate genus of Frasnian (Upper Devonian) age, with shallow anterior sulcus and low fold. The presence of fine regular costae is exceptional amongst Spiriferida in the Devonian Period. Dental plates and long extrasinal adminicula are present.

Theodossia was regarded as senior synonym of *Vandergrachtella* Crickmay, 1953 by Johnson & Hou in Johnson, Carter & Hou (2006a, p. 1715), and the two share shape and costate ornament and large diverging extrasinal adminicula. But micro-ornament in *Theodossia* as illustrated by Vandercammen (1959b) either has aligned pustules, interpreted as due to polyzoa, or prominent commarginal growth increments, whereas Crickmay (1953b) demonstrated strong radial threads without pustules or prominent growth laminae over several species of *Vandergrachtella*. Johnson & Hou claimed that capillate ornament typified *Theodossia,* but this is contradicted by Vandercammen (1959a, pl. 1, fig. 16, 17), both in text and figures for the same material used as typifying *Theodossia* in the *Revised Brachiopod Treatise.*

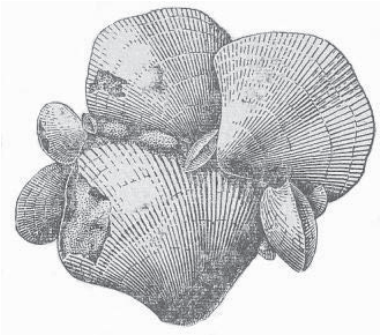


Fig. 118. *Theodossia tanaica* Nalivkin, x1. From Upper Devonian of Russia. (Ivanova 1971).

Johnson & Hou in Johnson et al. (2006a, p. 1715) stated that crural plates (ie. tabellae) were obscured by callus in *Theodossia*, and Vandercammen (1959a, Fig. 5) indicated small socket plates. He provided a detailed sketch for *Theodossia*, which does not show any tabellae, and they must have been extremely short, if present. This possibility is allowed, but confirmation is desirable. Crickmay illustrated several transverse sections for *Vandergrachtella*, and showed vertical and separate plates, apparently tabellae, that extend beyond the ctenophoridium, but possibly not beyond the hinge (see Fig. 121B, p. 117). Overall, there appears to have been confusion over the definitions for the two genera in the *Revised Brachiopod Treatise*, and this is underlined by the *Revised Brachiopod Treatise* text

which stated that figures of *Theodossia* in Johnson, Carter & Hou (2006a, Fig. 1122, 1123) were at natural size, whereas they are in fact nearly four times the natural size.

Eodmitria Brice, 1971, p. 575 has extrasinal adminicula, and no delthyrial cover plate is mentioned. The ctenophoridium is elevated, the fold and sulcus poorly defined, and fine plicae with rounded crests and papillose surface.

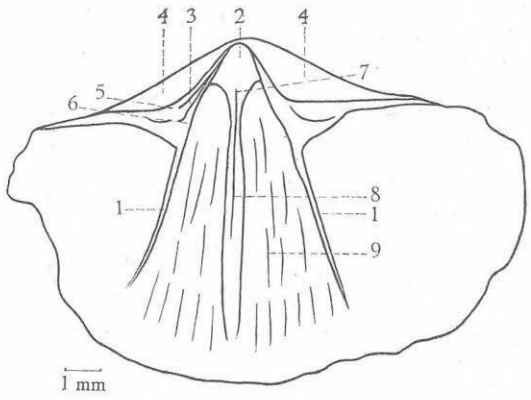


Fig. 4. — *Theodossia anossofi* (M. V. K., 1845).

Schéma du Paratype 5, valve ventrale séparée.

1 : lamelle dentaire. — 2 : petite callosité apicale centrale. — 3 : bourrelet deltidial. — 4 : aréa ventrale. — 5 : rainure deltidiale. — 6 : rainure hypodeltidiale. — 7 : pédonculaire médian. — 8 : adducteurs. — 9 : myoglyphes indiscernables.

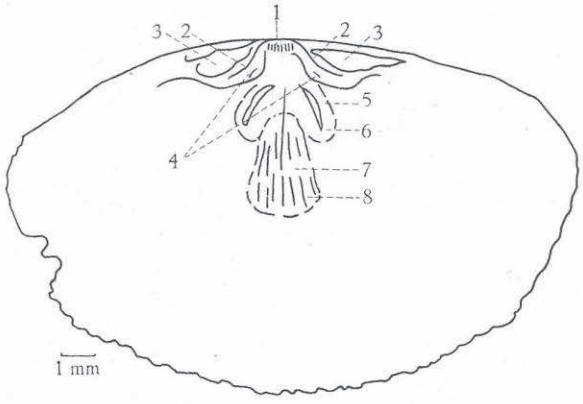


Fig. 5. — *Theodossia anossofi* (M. V. K., 1845).

Schéma du Paratype 6, valve dorsale séparée.

1 : processus cardinal. — 2 : arêtes brachiophoriennes. — 3 : cavité glénoïde. — 4 : pédonculaires dorsaux. — 5 : grosse côte médiane de l'adducteur postérieur. — 6 : adducteur postérieur. — 7 : adducteur antérieur. — 8 : costules longitudinales de l'adducteur antérieur.

Fig. 119. *Theodossia anossofi* (Murchison, Verneuil & Keyserling), as drawn and labelled by Vandercammen (1959a). Note the absence of any plates in the dorsal valve that extend forward from under the cardinal process, and extend along the floor of the valve. If tabellae are present, they must be very short. From Upper Devonian of Russia.

Dichospirifer Brice, 1971, of Famennian (Upper Devonian) age from Afghanistan and reprted from North America is rounded in outline with scarcely any sulcus, close to *Palaeochoristites* in shape. Micro-ornament is capillate with commarginal fila, and a rudimentary delthyrial plate lies under the beak. Extrasinal adminicula and short tabellae are developed. The extrasinal adminicula point to Theodossinae, whereas the delthyrial plate suggests an choristiform development.

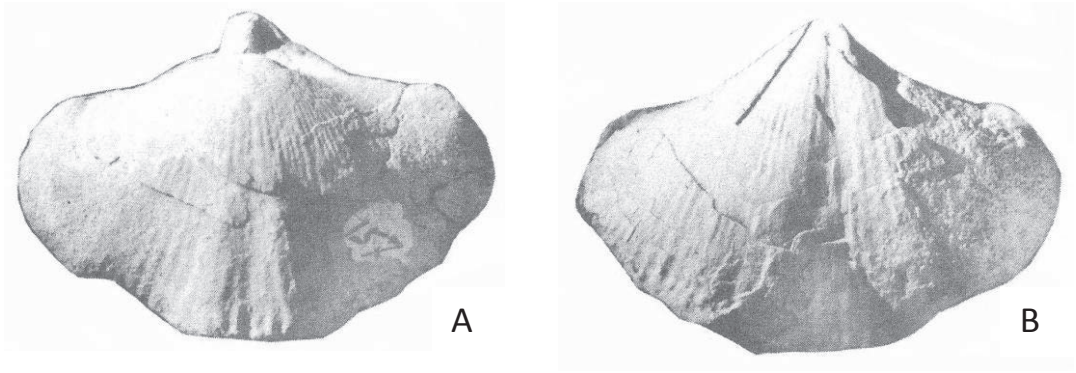


Fig. 120. *Vandergrachtella arcuum* Crickmay, type species, dorsal and ventral views, x1.4. From Upper Devonian of Alberta, Canada. (Crickmay 1953b).

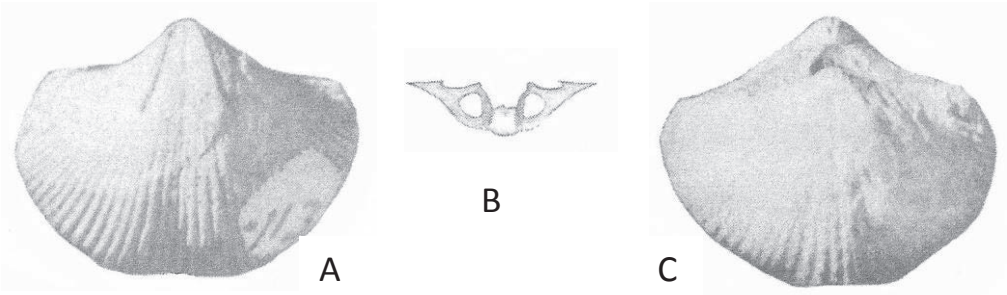


Fig. 121. A, C, *Vandergrachtella keenei* Crickmay, x2.4. A, ventral view. C. dorsal view. B, *V. kobayashi* Crickmay, transverse section of dorsal valve, showing tabellae, x3.2. Upper Devonian of Alberta, Canada. (Crickmay 1953b).

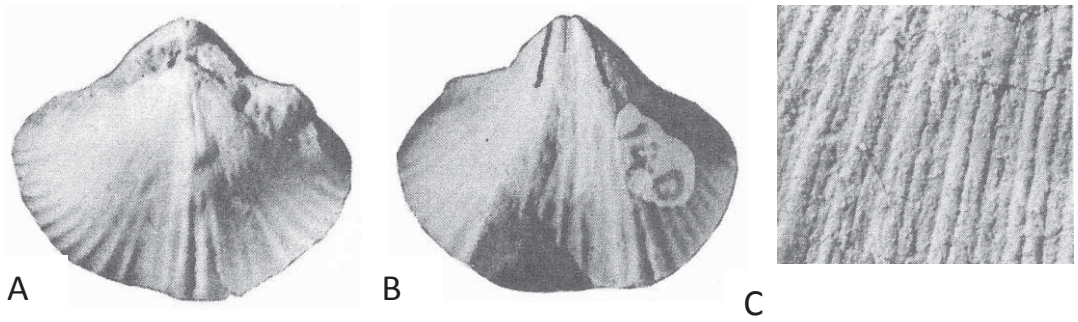


Fig. 122. A, B, *Vandergrachtella kobayashi* Crickmay, dorsal and ventral views, x2. C, micro-ornament of *V. arcuum*, x12. From Devonian of Western Canada. (Crickmay 1953b).

Dichospirifer sp. of Brice (1971, text-fig. 49) shows a well developed connector plate, apparently differing from true *Dichospirifer*, unless both belong to Enchondrospiriferinae.

Genus ***Radinovia*** new genus

Name: From species name *radina*.

Diagnosis: Small with relatively strong and few radial ribs, sulcus extending to beak and narrow and moderately deep, fold differentiated.

Type species: *Vandergrachtella radina* Crickmay, 1953b, p. 9 from central Alberta, Canada, of mid Upper Devonian age, here designated.

Discussion: The type species as described and figured by Crickmay (1953b, pl. 4, fig. 1-8) is notable for the strength of its radial ornament, which consists of some eight narrow plicae, with a few finer costae laterally each side of the sulcus and fold, and usually four more slender ribs within the sulcus, and a median groove along the fold. In species of *Vandergrachtella* Crickmay, radial ribs are of costal strength and well over twice as numerous. Costae are also much more numerous in the sulcus, and number six to ten over the fold, some species or individuals having a median rib, some a median groove. In other respects, the genus is like *Vandergrachtella*, with radial lirae, open delthyrium, and long extrasinal adminicula diverging forward. There is some approach to *Palaeospirifer* (see p. 122) in the coarseness of the ribs, but shape is more transverse, and sulcus and fold less sharply defined, so the genus is distinct, but the family position arguable.

The species *Radinovia radina* preceeded four species of *Vandergrachtella* described by Crickmay from the younger Devonian in Canada. It comes close in shape to *Badainjarania* Zhang Yan and *Striispirifer* Cooper & Muir-Wood of Eospiriferidae.

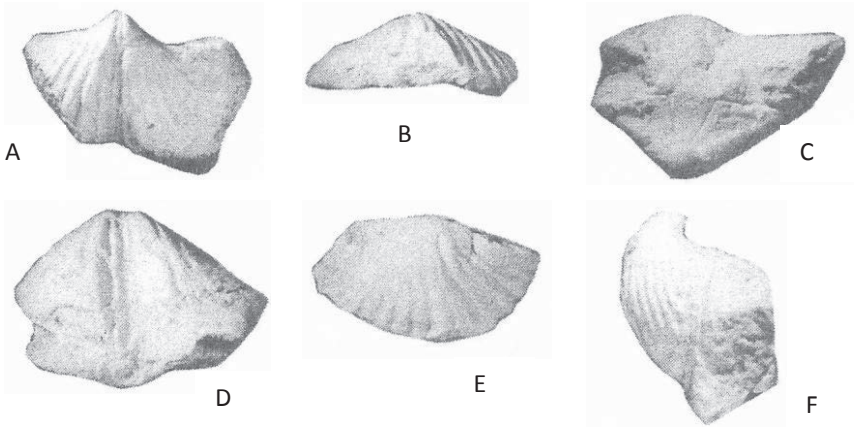


Fig. 123. *Radinovia radina* (Crickmay). A, ventral valve. B, anterior view of dorsal valve. C, posterior view of ventral valve. D, anterior view of ventral valve. E, dorsal valve. F, lateral view of ventral valve. Specimens x2 approx. From Upper Devonian of Alberta, Canada. (Crickmay 1953b).

Subfamily **CYRTIOPSINAE** Ivanova, 1972

[Cyrtiopsinae Ivanova, 1972, p. 33].

Diagnosis: Interarea narrow, cardinal angles narrow or highly obtuse, cover plate may be developed. Sulcus varied. Ribs comparatively fine and uniform. Capillae may bear tubercles. Adminicula intrasinal as a rule, and dental plates well formed but short, no tabellae. Upper Devonian (Famennian).

Genera: *Cyrtiopsis* Grabau (syn. *Grabaucyrtiopsis* Gatinaud, ?*Adolfispirifer* Krylova, *Sinocyrtiopsis* Gatinaud), ?*Platyspirifer* Grabau, ?*Tiocyrspis* Sartenaer.

Discussion: This subfamily has been treated as a member of Cyrtospiriferoidea, and genera show considerable similarities, but cyrtospiriferoids are more transverse with less obtuse cardinal extremities and have well defined sulcus and fold as a rule, as well as shorter adminicula and well developed connector plate. Ma & Day (2007, p. 308) showed that type *Cyrtiopsis,* based on *C. davidsoni* Grabau, 1923, had no connector plate, the delthyrium being covered by a delthyrial cover plate. Amongst various species ascribed to *Cyrtiopsis*, such as forms described by Sidiachenko (1962), some do have connector plate and pleromal ridges, underlining the need for extensive reassessment.

Although Johnson (2006b, p. 1729) stated that radial capillae became tuberculate in *Cyrtiopsis*, Ma & Day (2007, p. 308) showed that type *Cyrtiopsis,* based on *C. davidsoni* Grabau, 1923, had no tubercles, but a lirate micro-ornament (see Fig. 2D, p. 11). Other species ascribed to *Cyrtiopsis* in the literature have lirate micro-ornament, together with high adminicula, no tabellae, and the delthyrium is covered by a delthyrial cover plate or stegidium (Sartenaer 1956a, b, 1957). *Tiocyrspis* has tubercles.

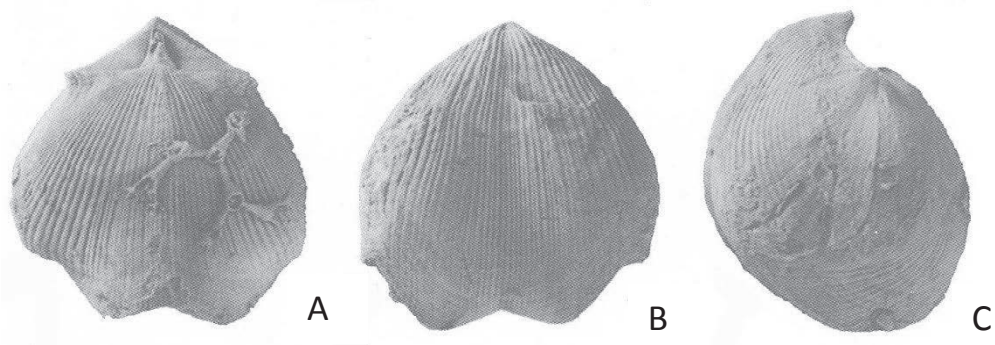


Fig. 124. *Cyrtiopsis davidsoni* Grabau, dorsal, ventral and lateral aspects, x1.5. From Upper Devonian (lower Famennian) of China. (Ma & Day 1999).

Cyrtiopsinae is limited to genera with narrow hinge, and some genera allocated to the group in Johnson (2006b, p. 1729 ff) are moved to Theodossiinae, having similar fine ribs, subdued sulcus and fold, and extrasinal adminicula, whilst others are retained in Cyrtospiriferinae. Johnson (2006b) defined Cyrtiopsinae as characterized by narrow hinge, yet included several genera with wide hinges, such as *Eodmitria* and *Acutella*. These have extrasinal adminicula and so are grouped with Theodossioidea. Another morphological feature is the way in which the cardinal extremities jut laterally at an angle from the body of

the shell in *Cyrtiopsis* and this is also seen in *Eodmitria*, which has a wider hinge, but approaches *Cyrtiopsis* in other respects, though not in the position of its adminicula. To some extent *Pseudocyrtiopsis* Ma & Day (see pp. 149-150), with its rather coarse ribbing and flaring anterior sulcus is similar, but various aspects of the morphology in this genus point to a closer relationship with Cyrtospiriferoidea (p. 139).

Ma & Day (2000) regarded *Geminisulcispirifer* Sartenaer as a possible subgenus of *Cyrtiopsis*, but Sartenaer's genus is more transverse with very different sulcus and fold.

Tiocyrspis Sartenaer, 1994 was referred to Cyrtiopsinae by Gourvennec in Gourvennec & Carter (2007, p. 2774), and has a general appearance like that of choristitids. There is no connector plate or tabellae, but delthyrial cover plate or stegidium and micro-ornament of pustules are developed, which arguably suggests Uchtospiriferini. The hinge is wider than in *Cyrtiopsis*, but the sulcus is gently defined so the genus is provisionally associated. *Dichospirifer* is close in general appearance, with capillate micro-ornament. A rudimentary delthyrial plate suggests a possible relationship to *Cyrtiopsis*, whereas the presence of short tabellae and extrasinal adminicula suggests relationship to Theodossiinae.

Platyspirifer Grabau with capillate micro-ornament and elevated ctenophoridium is distinctive in its subrounded appearance, with somewhat flattened crests of the narrow plicae, and is so poorly circumscribed in the literature that it could belong to Theodossioidea or prove to be an early choristitoid. *Adolfispirifer* Krylova is small with capillae and thickened dental plates, and possibly should be considered as a primitive member of Choristitidae. The presence of tabellae in *Adolfispirifer* is not established, and its family group position highly uncertain.

Uchtospiriferinae Liashenko, 1973, p. 87 was synonymized with Cyrtiopsinae in the *Revised Brachiopod Treatise* (Johnson 2006b, p. 1729), but *Uchtospirifer* has well developed connector plate, as revealed by Oleneva (2004), and so is distinguished, and referred to Cyrtospiriferidae, where indeed it was also placed by Johnson (2006b). See p. 142.

Subfamily **ENCHONDROSPIRIFERINAE** new subfamily

Name genus: *Enchondrospirifer* Brice, 1971, p. 175 from Upper Devonian (upper Famennian) of Afghanistan, here designated.

Diagnosis: Finely costate shells with well formed sulcus and fold, micro-ornament tubercular. Pleromal ridges and connector plate may be present. Intrasinal adminicula, tabellae. Upper Devonian (Frasnian, Upper Famennian).

Genera: *Enchondrospirifer* Brice, *Dmitria* Sidiachenko.

Discussion: *Enchondrospirifer* Brice, 1971 has tubercles, but otherwise the fine ribbing and shape and tabellae ("crural plates") are envisaged as inherited from the likes of *Vandergrachtella*, which has short tabellae. *Enchondrospirifer* has prominent pleromal ledges in the ventral valve between the dental plates and adminicula, pointing to an incipient development of a connector plate. The genus was placed by Johnson (2006a, p. 1711) in Family Echinospiriferidae, but members of this family group have two grades of often stronger

ribbing, and are of different more cyrtospiriferoidean shape (see p. 139), although *Echinospirifer* does lack tabellae and has a connector plate. A specimen from Afghanistan identified by Brice (1971, fig. 49) as *Dichospirifer* shows a well developed connector plate. *Dichospirifer* itself appears to lack a connector plate and is referred to Theodossiinae, although there are also attributes of the related group Cyrtiopsinae Ivanova.

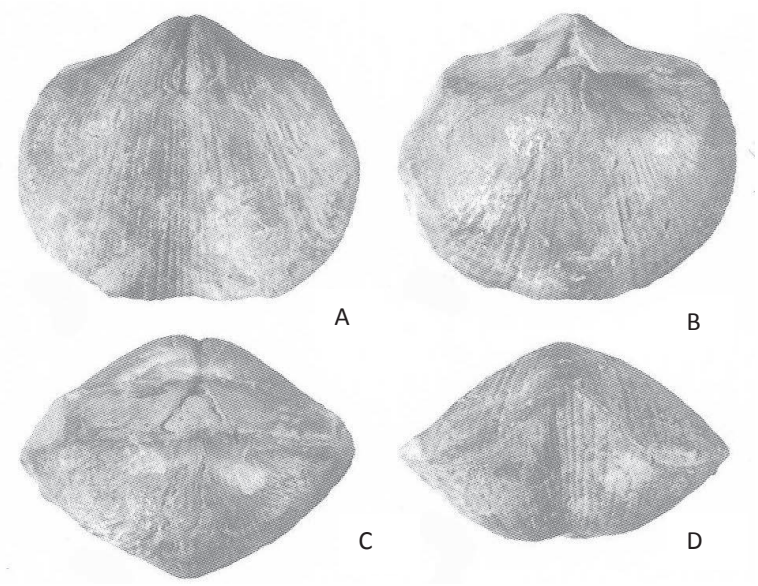


Fig. 126. *Enchondrospirifer ghorensis* Brice, A, ventral, B, dorsal, C, posterior and D, anterior aspects (dorsal valve on top), x1.2. From Famennian (Upper Devonian) of Afghanistan. (Brice 1971).

Dmitria Sidiachenko looks close and has elevated ctenophoridium, capillate micro-ornament, short tabellae and long intrasinal dental plates. Moreover a connector plate is well developed, so that the genus is referred to Enchondrospiriferinae, which has tabellae.

Family **PALAEOSPIRIFERIDAE** Carter, Johnson & Hou, 1994

[Nom. transl. hic ex Palaeospiriferinae Carter, Johnson & Hou in Carter et al. 1994, p. 334].

Diagnosis: Prismatic inner shell layer. Fine to coarse radial ornament. Adminicula short, no tabellae as far as known. Upper Devonian (Famennian).

Subfamily **PALAEOSPIRIFERINAE** Carter, Johnson & Hou, 1994

[Palaeospiriferinae Carter, Johnson & Hou in Carter et al. 1994, p. 334].

Diagnosis: Prismatic inner shell layer. Comparatively broad low plicae. Delthyrium open. Adminicula short. Upper Devonian (upper Famennian).

Genus: *Palaeospirifer* Martynova & Sverbilova (syn, *Goungjunspirifer* Zhang).

Discussion: *Palaeospirifer* is an outstanding genus, and is distinguished by its well defined fold and sulcus, and by its relatively broad plicae, differing in those respects from other Theodossioidea.

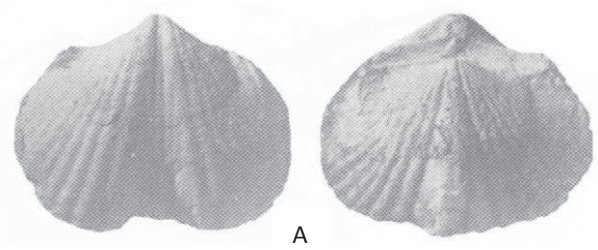


Fig. 127. *Palaeospirifer karagatshicus* (Sverbilova) x1 from Upper Devonian of Kazakhstan. (Martynova & Sverbilova 1968). See Fig. 128A.

Only one genus is known, and relationships to other groups are far from clear. Micro-ornament is capillate, and adminicula high though possibly short: placement of the subfamily in Ulbospiriferidae with its transverse outline and tuberculate micro-ornament advocated in the *Revised Brachiopod Treatise* is set aside, but the genus is retained in Theodossioidea. Tabellae appear to have been absent (Marynova & Sverbilova 1968, Fig. 1), and although the figured holotype displays a choristitinid outline, paratypes show a more prominent ventral umbo, slightly higher plicae, and stronger definition of the sulcus and fold. The ventral muscle field is like that of Spiriferidae. The genus externally approaches *Radinovia* new genus (see p. 118) in having prominent plicae, but is of more fully rounded outline, and *Radinovia* possibly has short tabellae. It is also somewhat like spiriferid genera that as far as known lack tabellae, such as *Andreaspirifer* Abramov & Grigorieva, *Kinghiria* Litvinovich, and *Eobrachythyris* Brice, the latter with well developed capillae, and all of upper Devonian to chiefly Carboniferous age. The prospirin genus *Parallelora* Carter of the same age looks close but has more alate cardinal extremities (see p. 175).

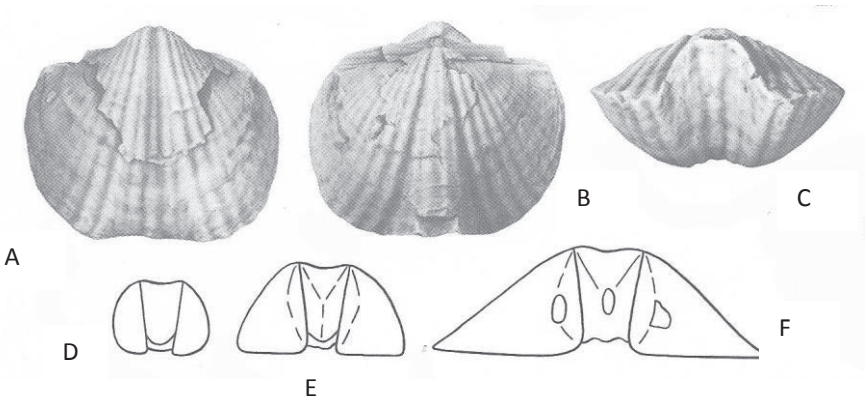


Fig. 128. A-C, *Palaeospirifer sinicus* (Zhang), ventral, dorsal and anterior aspects (dorsal valve on top), x1. (Type species of *Goungiiunspirifer,* synonymized with *Palaeospirifer*). (Zhang Chuan et al. 1983). D-F, *P. karagatshicus* (Sverbilova), transverse sections, x3. (Martynova & Sverbilova 1968).

Subfamily **HOLLARDOSPIRIFERINAE** new subfamily

Name genus: *Hollardospirifer* Nicolin in Brice et al. 2005, p. 111 from Upper Devonian of Morocco.

Diagnosis: Inner shell prismatic. Subrounded in outline with sulcus grading gently on to lateral slopes. Costae fine in place of plicae. Intrasinal adminicula, no tabellae. Upper Devonian (upper Famennian).

Genera: *Hollardospirifer* Nicollin, *Cyrtiorina* Cooper & Dutro, *Tenisia* Marynova (syn. *Omolonospirifer* Simakov in Afanas'eva & Simakov).

Discussion: *Hollardospirifer* Nicollin in Brice et al. (2005, p. 25) was not able to be included in the *Revised Brachiopod Treatise*. It is based on a species from the Late Famennian of Morocco, and has prismatic inner shell, and lacks a dorsal septum or pillar. Ribbing is fine and even. In outline it approaches choristitids, and has open delthyrium, commarginal growth lines and radial capillae, and long adminicula (described as dental plates), with prismatic crystals to right angles to the surface, taken as establishing an ulbospiriferid connection. No information was provided on crural plates or other dorsal internalia, except for the lack of dorsal septum, though a dorsal myophragm was noted. In shape and ornament, and lack of prominent sulcus and transverse outline, this genus is much closer to *Cyrtiorina* and *Tenisia* than to *Ulbospirifer*. *Tenisia* Martynov of Upper Devonian (Famennian) age is moderately close in shape though lacking a sulcus, and has fine ribs and capillae and hinge plates supported by a median ridge.

Cyrtiorina Cooper & Dutro, 1982, p. 111, pl. 32, fig. 35-41, pl. 41, fig. 50), of much the same age as *Hollardospirifer,* has deeper sulcus and long adminicula, and tuberculate micro-ornament. An arched plate lies over the delthyrium, unlike *Theodossia* or *Hollardospirifer.* Johnson, Carter & Hou (2006a, p. 1714) stated that Theodossioidea was to be in part characterized by the lack of a delthyrial plate, yet included *Cyrtiorina* in the superfamily: this may indicate the need to reposition *Cyrtiorina*.

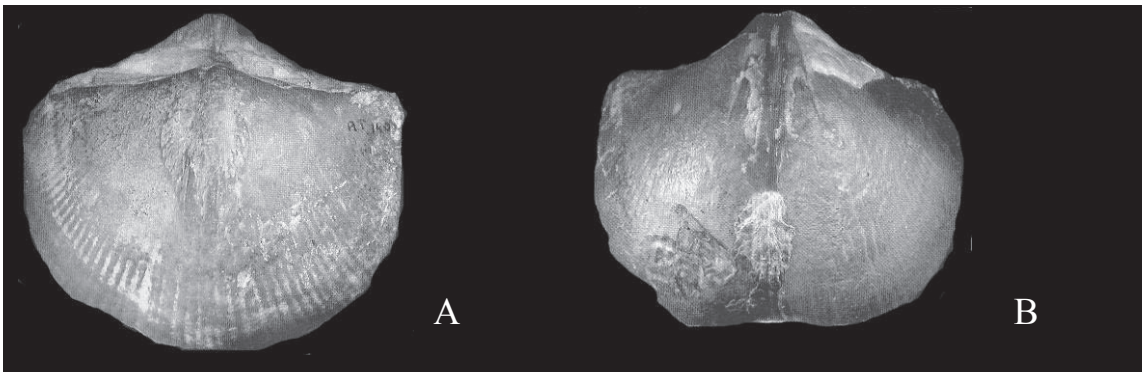


Fig. 129. *Hollardospirifer draensis* Nicollin, dorsal and ventral views, x1. From Late Famennian of Morocco. (Brice et al. 2005).

In the *Revised Brachiopod Treatise*, the presence of an inner prismatic layer was stressed as a distinction between *Theodossia* and genera *Cyrtiorina* and *Tenisia*, which were classed in a different family, Ulbospiriferidae, even though they differ from *Ulbospirifer* in several respects, notably in shape, sulcation and costation. *Ulbospirifer* itself is more

transverse with more strongly defined sulcus and different shape, and has tubercular micro-ornament, thick adminicula and unsupported hinge plates, without tabellae. It is now classed

Fig. 130. *Cyrtiorina kindlei* (Stainbrook), ventral and dorsal aspects, x1. From Famennian (Upper Devonian) of New Mexico, USA. (Cooper & Dutro 1982).

as Cyrtospiriferidae, on the basis of shape, ornament and internal plates, with a companion species better preserved than the type species (pp. 146, 147). Chao (1929) had placed little significance on the variation in secondary shell thickening, and although Poletaev (1984, 1986) gave great value to the feature, Shi & Waterhouse (1996, p. 139) in also discussing choristitoid genera suggested “it is more related to surplus $CaCO_3$, generated under favourable conditions at late maturity”. But until the evolution of spiriferids is fully understood, it is preferred to grant weight to such a distinction.

Superfamily **CHORISTITOIDEA** Waterhouse, 1968

[Nom. transl. et correct. hic ex Choristitidinae Waterhouse, 1968, p. 9].

Diagnosis: Shells may be weakly plicate, usually broadly costate or subcostate, micro-ornament weak, usually of low growth increments and often radial capillae. Dental plates and adminicula variably developed, tabellae may be present. Upper Devonian (Famennian) to Middle Permian (Roadian).

Discussion: This is regarded as a group less varied in shape than members of the superfamily Spiriferoidea, to which members of the group have been referred in past studies. Spiriferoidea are usually plicate and normally strongly costate, with micro-ornament of a meshwork of radial and commarginal fila. Choristitoidea have more and lower broad-crested but low if any plicae, with costae of similar profile, and usually narrow interspaces. Micro-ornament is often dominated by commarginal capillae only. Internally, Spiriferoidea are largely though not entirely immutable with regards to their internal structure, characterized by short adminicula, well formed dental plates, no tabellae, and characteristic pitted mantle canal system. Choristitoidea by contrast varied in the development of adminicula, which may be very long or very short, or absent, and some forms that share the ornament have tabellae, not seen in Spiriferoidea. In at least some genera, the mantle canal system is reticulate in a broad sense, and some ventral valves show two principal canals extending backward from in front of the muscle field, and branching towards the posterior margin (Fig. 14B, p. 20). What is not always clear from either the *Revised Brachiopod Treatise* or the numerous articles on choristitoids is the nature of the delthyrium. It appears that a delthyrial cover plate was developed in some Choristitidae, but its member genera lack a connector plate, unlike genera within Purdonellidae.

The oldest of well established members in the superfamily is Famennian (latest Devonian) in age, when choristitoids were comparatively diverse, presumably sourced from theodossioids, which overlapped early choristitinoids in the Frasnian of Upper Devonian age. *Theodossia* Nalivkin is a shell close externally, with shallow anterior sulcus, fine ribs and capillate micro-ornament, with thin well spaced and diverging adminicula, and little secondary thickening. Broadly, the lack of the characteristic costate ornament and somewhat dissimilar internal plates indicate that if *Theodossia* was related, it was prechoristitoid. Palaeospiriferidae Carter, Johnson & Hou with broad plicae and moderately well defined sulcus is also somewhat similar in shape, and has prismatic inner shell. It is of upper Famennian (Upper Devonian) age.

Family **CHORISTITIDAE** Waterhouse, 1968

[Nom. transl. et correct. Ivanova 1972, p. 40 ex Choristitidinae Waterhouse, 1968, p. 9].

Diagnosis: Shells transverse or elongate, ribbing fine with flattened crests, interspaces narrow as a rule, micro-ornament commonly capillate, denticulate hinge, adminicula usually long, may be short or absent, no tabellae, mantle canal system distinctive. Lower Carboniferous (Tournaisian) to Middle Permian (Roadian).

Discussion: Tabellae are not developed in this family. Carter (2006a, p. 1780) included Angiospiriferinae Legrand-Blain, 1985a, but *Angiospirifer* of Visean to Bashkirian age has different ornament and different mantle canal system and delthyrial arrangement, as discussed on pp. 238ff. Waterhouse (2004, p. 180) showed that the presence and nature of the mantle canal system, apical callosity, and subimbricated micro-sculpture in *Angiospirifer* indicated alliance with Trigonotretidae, rather than Choristitidae.

Subfamily **CHORISTITINAE** Waterhouse, 1968

[Nom. correct. Ivanova 1972, p. 40 pro Choristitidinae Waterhouse, 1968, p. 9].

Diagnosis: Hinge comparatively wide, adminicula subparallel. Early Carboniferous – Permian (Cisuralian).

Genera: *Choristites* Fischer de Waldheim (syn. *Yatsengina* Semichatova, *Betachoristites* Gatinaud, *Jatsengina* Ivanova nom. null.), *Alphachoristites* Gatinaud (syn. *Trautscholdia* Ustritsky), *Prochoristites* Poletaev, *Settedabania* Abramov, *Uralochoristites* Kalashnikov.

Fig. 131. *Choristites mosquensis* Fischer de Waldheim. from the Moscow Basin (Pennsylvanian), x2. Note the long adminicula and the stegidial cover. BR 3215.

Discussion: In some genera there are weak fascicles, and micro-ornament may be capillate or limited to growth increments, and the delthyrium appears to have been open. Mantle canal systems are rarely preserved, and have been found to be reticulate, at least *in Choristites* (Legrand-Blain 1986). There is no connector plate or pleromal ridging.

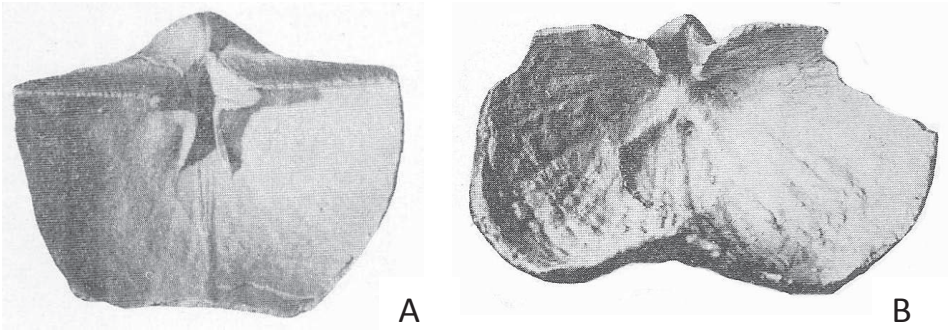


Fig. 132. A, *Choristites sowerbyi* Fischer de Waldheim, ventral interior, x1. B, *Choristitella pachrensis* Ivanova, ventral interior. Specimens x1.2, from Carboniferous of Moscow Basin, Russia. (Sarytcheva 1960).

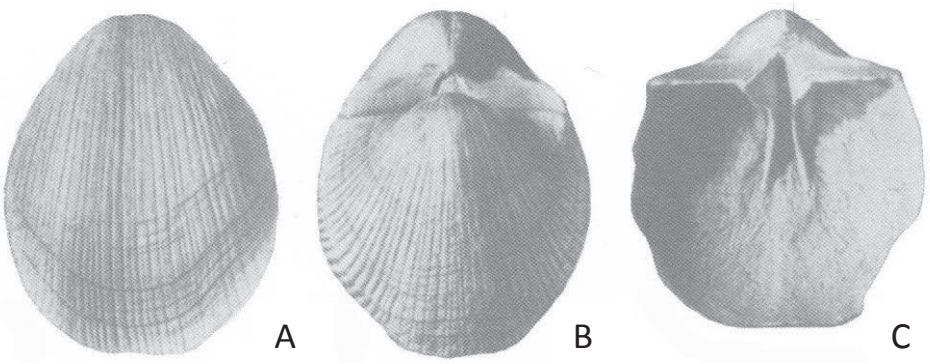


Fig. 133. *Choristites mosquensis* Fischer de Waldheim, ventral and dorsal aspects with ventral interior, x1. From Moscovian of Moscow Basin, Russia. (Ivanov & Ivanova 1937).

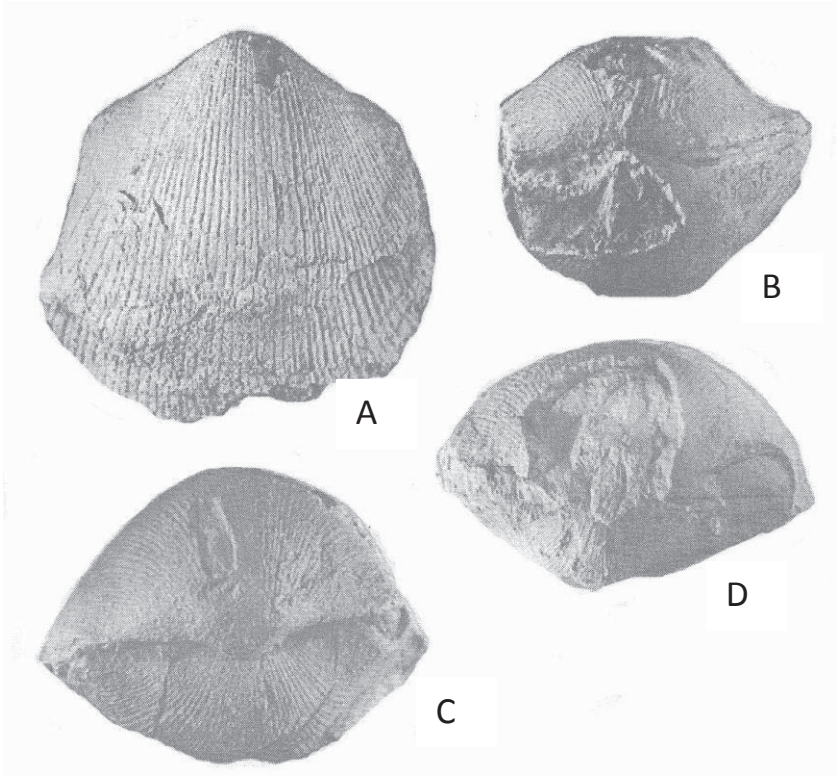


Fig. 134. A-D, *Uralochoristites desinuatus* (Kalashnikov), x1. A, C, holotype. B, D, posterior views of other specimens. From Kosvinsk Horizon, Lower Carboniferous of the Urals, Russia. (Kalashnikov 2003).

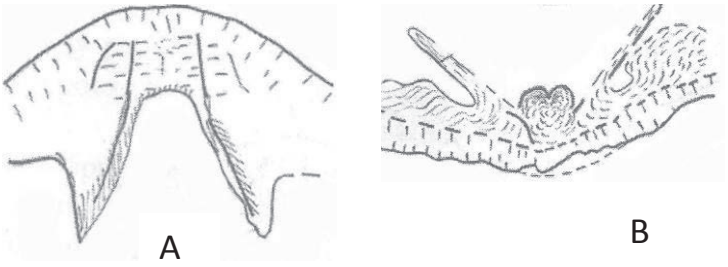


Fig. 135. *Uralochoristites desinuatus* (Kalashnikov), transverse sections x7 of A, ventral valve and B, dorsal valve. From Kosvinsk Horizon (Lower Carboniferous) of the Urals. (Kalashnikov 2003).

Uralochoristites Kalashnikov, 2003, type species *U. desinuatus* Kalashnikov, 1966, was omitted from the *Revised Brachiopod Treatise*. Figures are provided.

Subfamily **CHORISTITELLINAE** new subfamily

Name genus: *Choristitella* Ivanov & Ivanova, 1937, p. 163 from Moscow Basin, Russia, here designated.

Diagnosis: Adminicula very short or not developed, hinge wide. Lower to Upper Carboniferous (Visean, Pennsylvanian).

Genera: *Choristitella* Ivanov & Ivanova, ?*Prochoristitella* Legrand-Blain.

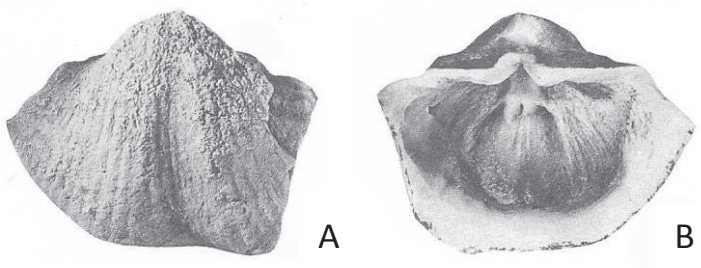


Fig. 136. *Prochoristitella afghanensis* Legrand-Blain, holotype x1, external and internal views of ventral valve. From Carboniferous of Wardak, Afghanistan. (Legrand-Blain 1968).

Subfamily **TANGSHANELLINAE** Carter, 1994

[Tangshanellinae Carter, 1994, p. 345].

Diagnosis: Transverse with well rounded cardinal extremities and multicostate with bifurcations; radial capillae or only growth increments. No adminicula or tabellae, delthyrial apparatus and vascular imprints poorly known, but *Septimusia* has a delthyrial cover plate. Carboniferous (Tournaisian to Pennsylvanian).

Genera: *Tangshanella* Chao, *Septimusia* new genus.

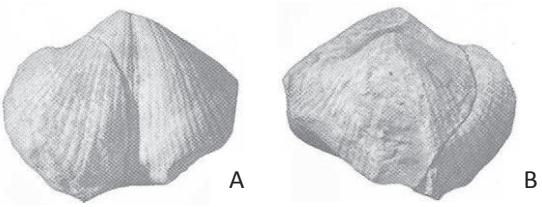


Fig. 137. *Tangshanella kaipingensis* Chao, ventral and dorsal views, from Pennsylvanian of China, x1. (Carter 2006a).

Discussion: This subfamily is regarded as being close to Choristitinae, just as positioned in the *Revised Brachiopod Treatise*, and Roberts (1971) favoured an alliance with *Choristites*. Tangshanellinae is exceptional because dental plates and adminicula have been lost, whilst the shape and ornament have been retained. *Tangshanella* Chao has numerous fine branching costae, and Carter (2006a, p. 1786) allied it with *Alphaneospirifer* Gatinaud, but that genus has a dorsal cruralium and so is distinguished as a separate family Alphaneospiriferidae Waterhouse, 2004 (see p. 209). *Zhejiangospirifer* Liang and *Capillispirifer* Zhang, although included in Tangshanellinae in the *Revised Brachiopod*

Treatise, appear to belong to Pustuloplicinae Waterhouse. These adjustments mean that the group is restricted to Carboniferous faunas, with the age extended downwards to Tournaisian by the description of a new genus from Australia.

Genus ***Septimusia*** new

Derivation: Named from Septimus Limestone, source of the species.

Diagnosis: Medium size with wide hinge and moderately prominent ventral umbo, delthyrium closed by convex plate, sulcus narrow and groove-like, fold with broad rounded crest. Costae wide and strap-like, close to mid-line form fascicles of two or three ribs; micro-ornament of growth increments. Dental ridges, no dental plates, adminicula, or tabellae, ctenophoridium present, hinge denticulate.

Type species: *Tangshanella? fasciculatia* Roberts, 1971, p. 235 from Septimus Limestone (Tournaisian), Bonaparte Gulf Basin, northwest Australia, here designated.

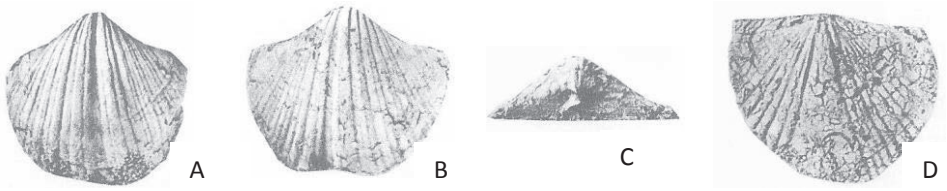


Fig. 138. *Septimusia fasciculata* (Roberts). A, ventral valve holotype. B, ventral valve. C, posterior ventral valve showing convex delthyrial plate. D, dorsal exterior. Specimens x1, from Tournaisian of northwest Australia. (Roberts 1971).

Resemblances: *Tangshanella* Chao, 1929, p. 57, based on *T. kaipingensis* Chao from the Pennsylvanian Tangshan Limestone of China, is moderately close in size and shape and moderately wide hinge, and in interior, but has a broader sulcus and less defined broad fold, with much less fasciculate and narrower ribs. Micro-ornament is capillate. Specimens recorded from a late Bashkirian or Moscovian fauna of the Hare Fiord Formation of the Canadian Arctic at Ellesmere Island are moderately close, though not known internally (Carter & Poletaev 1998).

The present type species is well known thanks to the study by Roberts (1971), who drew attention to the denticulate hinge. Roberts (1971, p. 234) dismissed the view of Waterhouse that the internal plates were important in allocating species and genera, but his views are difficult to follow, being oversimplistic with regard to the complexity and diversity of Spiriferida. After all, he did assign his species to *Tangshanella* based on the similar lack of internal plates, and later Carter in Carter et al. 1994 established a subfamily for the genus. Roberts argued that *Tangshanella* showed an affinity with *Choristites* rather than *Brachythyris* because the latter displayed a micro-ornament of well defined radial lirae, yet his *Tangshanella? fasciculata* lacks radial lirae, and radial lirae are present on *Brachythyris. Brachythyris* also has a denticulate hinge, and displays a convex plate across the delthyrium.

A similar plate, which Roberts (1971) called a pseudodeltidium, is present in *fasciculata*. There is no evidence of a connector plate or deltidial plates, so that the cover plate is possibly a deltidium from inception or of stegidial origin. In overall shape and macro-ornament, the group strongly approaches Choristitidae. The sulcus of *fasciculata* has a median rib.

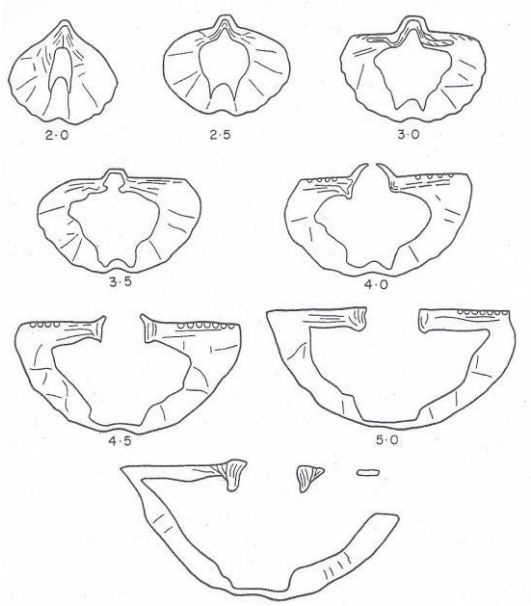


Fig. 139. *Septimusia fasciculata* (Roberts), serial sections with figures indicating distance in mm from ventral beak, x2.5. From Tournaisian of northwest Australia. (Roberts 1971).

Family **PALAEOCHORISTITIDAE** Carter, 1994

[Palaeochoristitidae Carter in Carter et al., 1994, p. 334].

Diagnosis: Ribbing fine, micro-ornament with or without radial fila, may be pustulose. Ctenophoridium, adminicula and tabellae well developed. Delthyrial plate absent or rudimentary. Upper Devonian (Famennian) to Lower Permian (Sakmarian).

Discussion: Palaeochoristitidae is distinguished in part by the presence of tabellae, which is regarded as significant. The definition is broadened from that of the *Revised Brachiopod Treatise*, which restricted the family group to genera without radial fila.

Subfamily **PALAEOCHORISTITINAE** Carter, 1994

[Nom. transl. hic ex Palaeochoristitidae Carter in Carter et al., 1994, p. 334].

Diagnosis: Intrasinal adminicula and tabellae long to moderate in length. No capillae. Upper Devonian (upper Famennian) to Lower Carboniferous (Tournaisian).

Genera: *Palaeochoristites* Sokolskaya, *Eochoristites* Chu (syn. ?*Centrospirifer* Tien).

Discussion: Palaeochoristitids were placed in Theodossioidea Ivanova by Johnson, Carter & Hou (2006a, p. 1720). The mantle canal systems are not known and although micro-ornament was not recorded by Johnson et al. (2006a), there are no capillae or pustules.

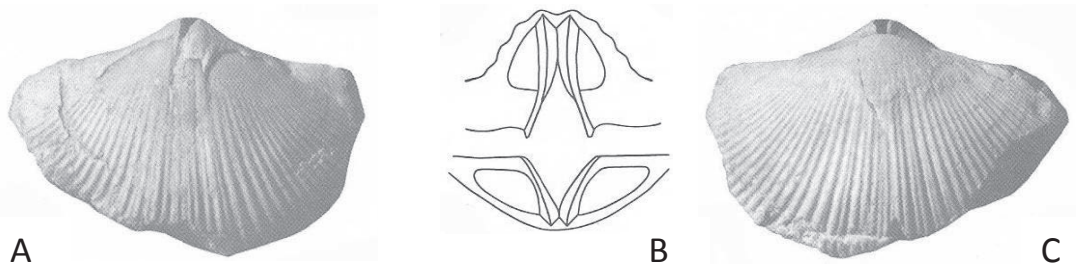


Fig. 140. *Palaeochoristites cinctus* (Keyserling). A, C, ventral and dorsal aspects, x1 (Carter in Johnson et al. 2006a). B, transverse section, x3. From Tournaisian of Russia. (Ivanova 1960).

Subfamily **AUSTROCHORISTITINAE** new

Name genus: *Austrochoristites* Roberts, 1971, p. 230, based on *A. levisulcatus* Roberts, 1971, p. 231 from Burt Range Formation (Tournaisian) of Western Australia, here designated.

Diagnosis: Subelongate with shallow and narrow sulcus and narrow fold, even and fine costae, which may be bundled, hinge wide, micro-ornament with fine radial threads, delthyrium open, denticulate hinge. Adminicula long, tabellae very short. Lower Carboniferous (Tournaisian).

Genera: *Austrochoristites* Roberts, *Ectochoristites* Campbell.

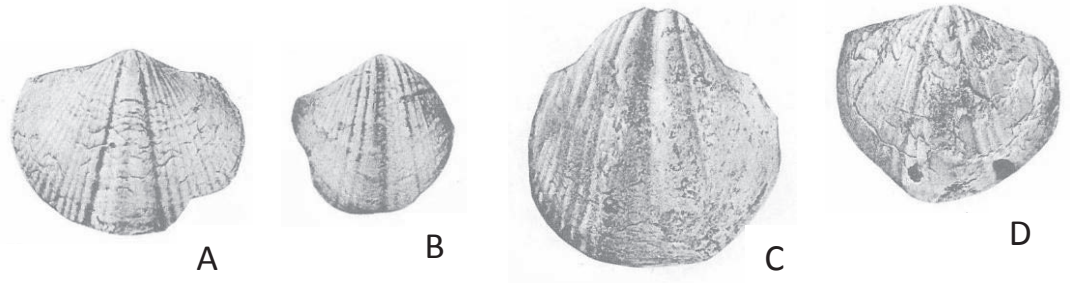


Fig. 141. *Austrochoristites levisulcatus* Roberts, dorsal and ventral aspects, x1, showing weak bundling of costae in some specimens. From Tournaisian of Western Australia. (Roberts 1971).

Discussion: This subfamily is discriminated for genera intermediate between members of Palaeochoristitinae with long tabellae, and Choristitidae with no tabellae. The subfamily is based on *Austrochoristites* Roberts, 1971, together with *Ectochoristites* Campbell, 1957, a genus with fine ribs, and no plicae, of similar age. Both genera were placed in Spiriferidae by Poletaev (2000a), with the claim that adminicula were dorsoventrally subparallel in *Choristites* but were divergent in *Austrochoristites*. This is not deemed to mandate a familial position, given that there is such variation in plate length and angle and presence amongst Choristitoidea (see Fig. 132A, 143B), and the plates in their length and thickness are choristitid in *Austrochoristites*, just as Roberts (1971) realized. Carter (2006a, pp. 1775, 1769) placed Robert's genus in Prospirinae, but members of this subfamily do not have even short

tabellae, and the overall build of the shell and the mode of costation is choristitid, not spiriferidan.

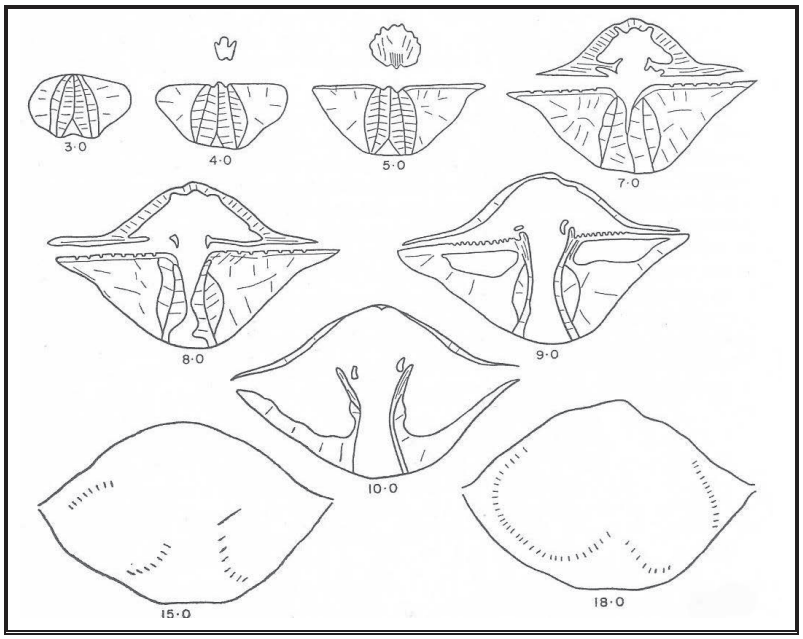


Fig. 142. *Austrochoristites levisulcatus* Roberts, serial sections x1.5. Distance in mm indicated from ventral umbo. Dorsal valve on top. Note the lack of connector plate. From Tournaisian of Western Australia. (Roberts 1971).

Subfamily **JUNGELOMIINAE** new subfamily

Name genus: *Junglelomia* new genus from basal Jungle Creek Formation (Gzhelian) of Yukon Territory, Canada, here designated.

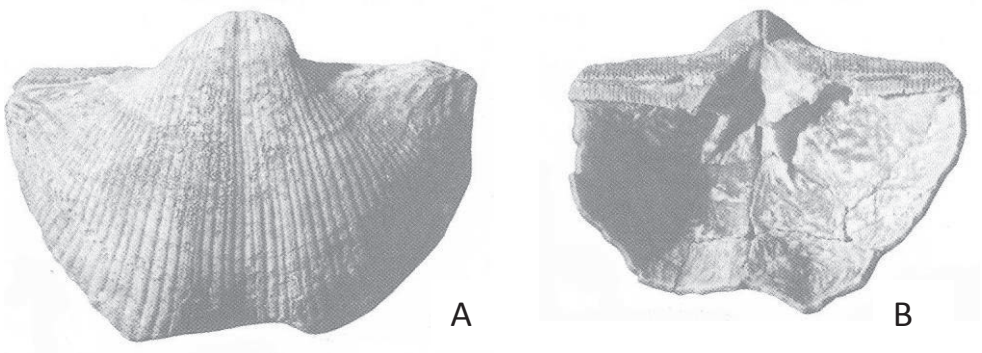


Fig. 143. *Parachoristites volongaensis* Barkhatova, exterior and interior of ventral valve, x1. From Bashkirian of Timan, Russia. (Carter 2006a).

Diagnosis: Shells moderately large with broad hinge and wide-crested costae, and well formed sulcus and fold. Tabellae in the dorsal valve. Pennsylvanian (Bashkirian) to Lower Permian (Sakmarian).

Genus: *Junglelomia* new genus, *Parachoristites* Barkhatova.

Discussion: The subfamily differs from members of Palaeochoristitinae through its well-developed sulcus and fold, and capillate non-pustulose micro-ornament.

Genus ***Jungelomia*** new genus

Name: From Jungle Creek, Ogilvie Mountains, Yukon Territory.

Diagnosis: Hinge wide, broad-topped costae showing minor fasciculation, fold and sulcus well formed and costate. Adminicula short to medium length, tabellae of medium length to long. Upper Carboniferous (Kasimovian) to Lower Permian (Sakmarian).

Type species: *Junglelomia ursus* new genus, new species from basal Jungle Creek Formation (Gzhelian), Yukon Territory, Canada, here designated.

Discussion: This genus is of Pennsylvanian and early Permian age, younger than other described members of Palaeochoristitidae, and is distinguished by the wide hinge and well formed sulcus and fold. One constituent species was initially described as belonging to *Domokhotia* Abramov & Grigorieva, 1983, but this genus does not have tabellae. It appears to have been reidentified as *Neomunella* Ozaki by Carter (2006a, p. 1780), probably because of its wide hinge, but this genus also lacks tabellae. *Parachoristites* Barkhatova, 1968 from Pennsylvanian and Cisuralian faunas of Timan, Russia, has shorter tabellae, and is large in size. It is distinguished by the hinge at maximum width, with alate cardinal extremities through early and early mature growth stages, whereas cardinal extremities are obtuse through all growth stages in the new genus.

Jungelomia ursus n. sp.

1971b Choristitinid Waterhouse in Bamber & Waterhouse, pl. 11, fig. 10.

Derivation: ursus – bear, Lat.

Holotype: GSC 136654, Fig. 147B, here designated.

Diagnosis: Moderately large and transverse shells with broad plicae splitting into two or three costae, sulcus shallow and fold low, both costate.

Material: A number of individual valves and specimens with valve conjoined, from lower Jungle Creek Formation. *Septospirifer tatondukensis* Zone. See Waterhouse in press.

Description: Specimens large and transverse, ventral umbo extended a little beyond hinge and incurved, with angle of 70-85^{o}, ventral interarea of moderate height and curved postero-ventrally, with delthyrium covered only under the umbo by convex delthyrial plate, postero-ventrally inclined; dorsal interarea lower and postero-dorsally inclined, hinge slightly less than maximum width which is placed near mid-length, cardinal extremities overall obtuse, but may be slightly produced. Posterior walls convex in profile, steep posteriorly and becoming low in front; sulcus commences at umbo and in most specimens has an angle between 15^{o} and 25^{o}, but in largest specimen flares out after shell reaches a width of 70mm, and protrudes dorsally as an angular tongue. Dorsal valve much less inflated, close to a third of height of ventral

valve, and in the largest specimen the lateral extremities curve slightly dorsad. The fold is narrow and sharply defined with broad gently rounded crest, widening at an angle of 20°. Ventral ornament consists of some eight primary broad costae (or subplicae – the ribs are coarser than costae, and finer than plicae) with broad gently convex crests and narrow interspaces, although near the umbo the crests are narrow and interspaces may be wider.

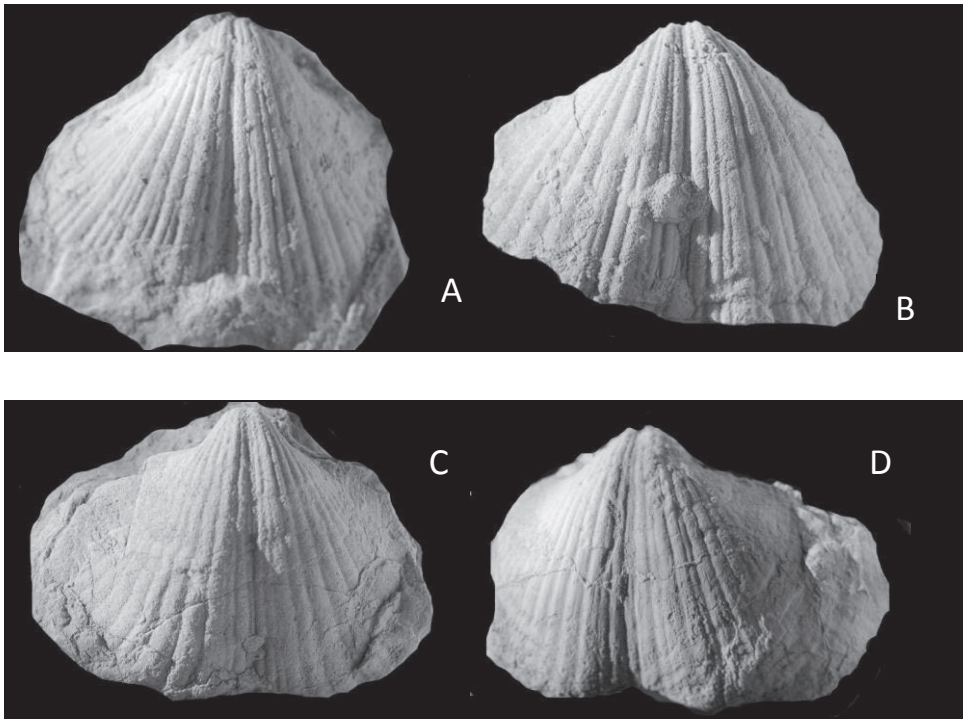


Fig. 144. *Junglelomia ursus* n. gen., n. sp. A-D, ventral valves GSC 136647 - 136650 from basal Jungle Creek Formation (Gzhelian), Yukon Territory, Canada, x1 approx.

A fine costa traverses the sulcus, and the inner primary ribs may subdivide into several much finer costae, somewhat as in *Austrochoristites*, but more markedly. The lateral flanks are comparatively smooth over the immature shell, but may become costate in larger specimens. The plicae become fasciculate anteriorly, so that the ornament is more bundled in some shells than is usual for other species within the genus. Dorsal ornament is similar, and the fold has some four costae, which may be faint. On the largest specimen, there are six additional ribs laterally, but the outermost shell near the cardinal extremities remains smooth. Micro-ornament is cancellate with radial and commarginal capillae. Some specimens suggest the presence of tiny pustules or pits, and these may reflect prismatic structure in the shell.

Delthyrium posteriorly covered by plate, bordered by low ridge which passes into small tooth, supported by low inwardly concave dental plates, converging inwards, supported in turn by adminicula which diverge outwards to the floor of the valve, extending well in front of the teeth. Muscle field compact, placed in front of the adminicula, marked by broad longitudinal ridges and narrow grooves, with limited distinction between adductors and diductor impressions. Secondary thickening fills the umbonal shell cavity, almost burying the

adminicula, and the valve floor carries pits in some specimens each side of the adminicula and vascular ribs in others. No umbonal callosity. Dorsal socket plates enclose narrow sockets, each side of a broad laminate ctenophoridium, which is supported in front by a narrow median ridge that extends over the posterior fourth to third of shell length. Tabellae are well formed, and extend each side of the fold for up to a quarter of the length of the valve. Adductor impressions lie well forward, elongate subrectangular in outline, with light longitudinal striae. Shell floor with little thickening, showing the external ribbing, and bearing light small pustules. Spire with 25 coils.

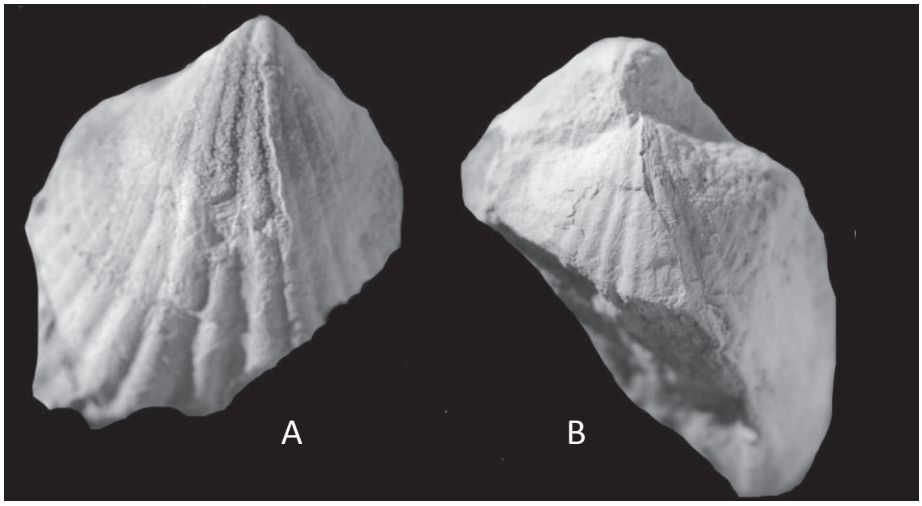


Fig. 145. *Junglelomia ursus* n. gen., n. sp. A, B, ventral and dorsal views of GSC 136651 from basal Jungle Creek Formation (Gzhelian), Yukon Territory, Canada, x1.5.

Resemblances: The closest of species so far described appears to be that described as *Domokhotia junglensis* Shi & Waterhouse, 1996, p. 140 from Jungle Creek Formation (Sakmarian) of Yukon Territory, Canada, with its similarly wide hinge, broad costae and rather long tabellae. The present species has broad costae, which in many individuals do not sub-

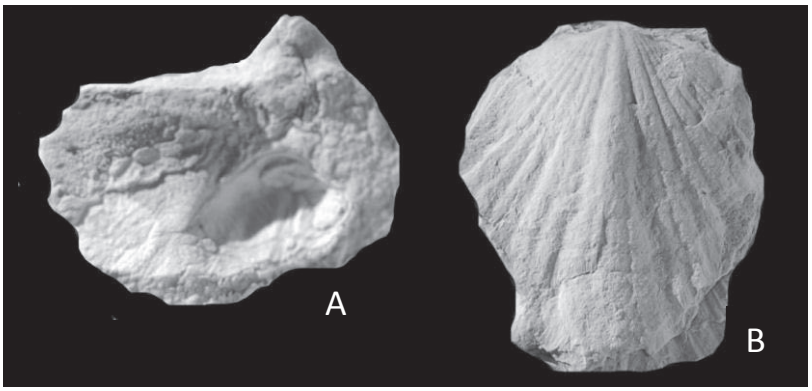


Fig. 146. *Junglelomia ursus* n. gen., n. sp. A, fragment of ventral valve, GSC 136652, x1.5, showing muscle scars and part of mantle canal system. B, dorsal valve, GSC 136653, x1.5. From basal Jungle Creek Formation (Gzhelian), Yukon Territory, Canada.

divide anteriorly, especially on the ventral valve, and the dorsal fold is better defined and higher. Tabellae are shorter in the present form, compared with the tabellae in *junglensis*. The present species also looks moderately close to shells described as *Larispirifer ettrainensis* Shi & Waterhouse (1996, p. 141, pl. 26, fig. 15-20, pl. 27, fig. 1-7, text-fig. 49) from the

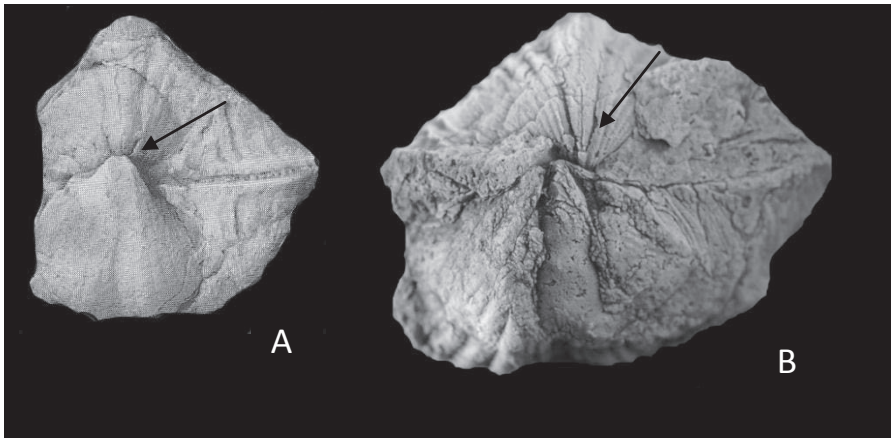


Fig. 147. *Junglelomia ursus* n. gen., n. sp, Posterior view of specimens with both valves splayed open, dorsal valve on top, x1. Arrows point to tabellae. A, From Ettrain Formation (Kasimovian), (Bamber & Waterhouse 1971). B, GSC 136654, holotype, from basal Jungle Creek Formation (Gzhelian), Ogilvie Mountains, Yukon Territory, Canada.

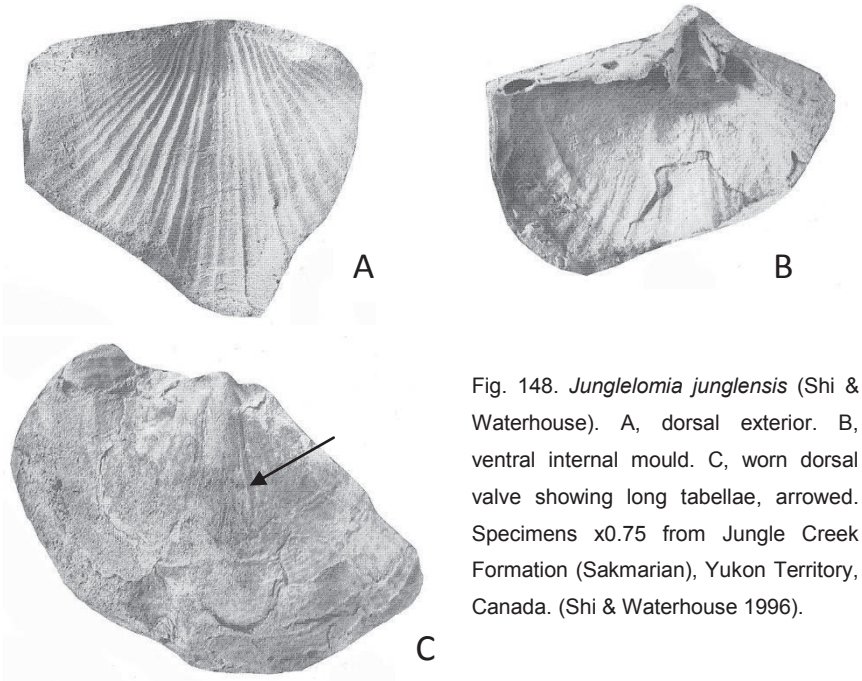


Fig. 148. *Junglelomia junglensis* (Shi & Waterhouse). A, dorsal exterior. B, ventral internal mould. C, worn dorsal valve showing long tabellae, arrowed. Specimens x0.75 from Jungle Creek Formation (Sakmarian), Yukon Territory, Canada. (Shi & Waterhouse 1996).

"*Yakovlevia" transversa* (in fact a muirwoodinin genus – see Waterhouse 2013, p. 343) to *Jakutoproductus verchoyanicus* Zones of the younger Jungle Creek Formation. This species has a slightly deeper ventral sulcus with slightly less emphasized median groove, and the dorsal fold has more costae anteriorly, whereas the fold of the present form tends to

become smooth. As far as is known, there are no tabellae in this species. Older specimens of the genus are found in possible Kasimovian faunas, and these appear to be close to *ursus*, although they await closer comparison.

Family **PURDONELLIDAE** Poletaev, 1986

[Nom. transl. hic ex Purdonellinae Poletaev, 1986, p. 65, nom. nov. pro Munellinae Fredericks, 1924, p. 313, based on invalid homonym].

Diagnosis: Hinge short as a rule, subdelthyrial connector plate, fascicles may be present, surface capillate. Adminicula short to moderate in length. Lower Carboniferous (Tournaisian) to Middle Permian (Roadian).

Genera: *Purdonella* Reed (nom. nov. pro *Munella* Fredericks, 1924 non Bonnier, 1896), *Ala* Nalivkin, *Domokhotia* Abramov & Grigorieva, *Larispirifer* Enokian & Poletaev, *Mirifusella* Carter, *Neomunella* Ozaki, *Podtsheremia* Kalashnikov.

Discussion: The group is distinguished by the presence of a connector plate, and hence has been regarded as a member of Spiriferoidea, in which a connector plate is widely, although not universally, present. But the ornament in most genera is overwhelmingly like that of Choristitoidea, in the way posterior costae are broad with low crests, separated by narrow interspaces, and may subdivide anteriorly into finer costae. That aspect plus the choristitoid shape are considered to overrule the significance of a connector plate, as far as superfamily affiliations are concerned. Throughout much of this study, it is shown that a connector plate developed in the course of ongoing evolution of various spiriferid groups.

Fig. 149. *Purdonella* sp., ventral valve, x2. From lower Jungle Creek Formation (Asselian), Yukon Territory, Canada.

In the presence of a connector plate, the group approaches Enchondrospiriferinae new subfamily, classed as a subdivision of Theodossioidea (p. 120), which shows prominent pleromal ridges (Brice 1971, p. 171) if not a full connector plate, and is found in deposits of Upper Devonian (Frasnian, Famennian) age. Members of Enchondrospiriferinae are more pentagonal in shape with wider sulcus, but open the possibility of a distinct lineage that involves only the two groups.

Purdonella has adminicula and delthyrial plates, and tendency to subfasciculation.

There is some range in morphology amongst the genera placed by Carter (2006a, p. 1780) in Purdonellinae, and some genera (eg. *Ala*) have wide shell, so that the most characteristic genera are limited to *Purdonella* Reed, *Neomunella* Ozaki, and *Domokhotia* Abramov & Grigorieva. The finely costate and plicate *Podtsheremia* Kalashnikov, 1966 also has a subdelthyrial connector plate. In 1984, Poletaev distinguished *Purdonella* by its narrow hinge and well separated and diverging adminicula, and widely spread ovarian impressions, and in 1986, stressed the lack of secondary thickening. In addition to the genera tabulated in Carter 2006a, pp. 1783-1786), *Larispirifer* Enokian & Poletaev is included (Shi & Waterhouse 1996), rather than placed in Spiriferidae as claimed by Poletaev (1986) and Carter (2006a, p. 1771).

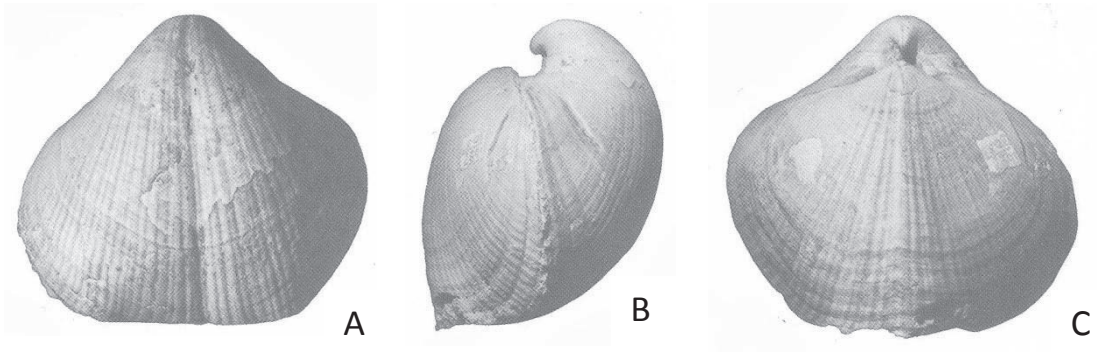


Fig. 150. *Purdonella nikitini* (Chernyshev), ventral, lateral and dorsal aspects, x0.8. (Carter 2006a). Note the nature of the ribs, broad posteriorly, splitting in front, and narrow interspaces.

Mirifusella Carter has long adminicula, and the dorsal fold is sharply defined much as in *Austrochoristites* Roberts, 1971. But there is no sign of the short tabellae reported for *Austrochoristites*, and the ornament differs.

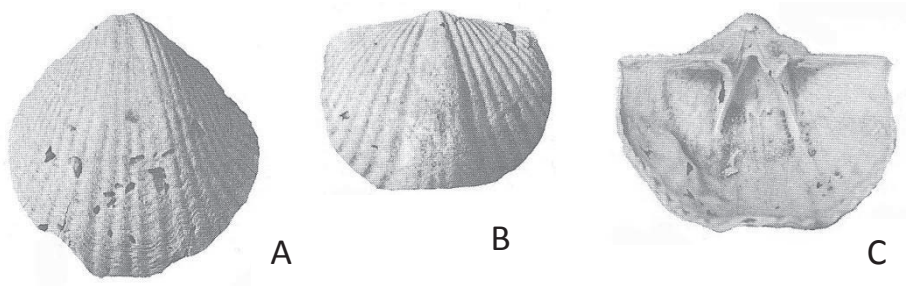


Fig. 151. *Minifusella fortunata* Carter, ventral and dorsal views, x1.5 and ventral interior, x2. From Hampton Formation (Late Kinderhookian) of Iowa, USA. (Carter 1971).

Suborder SPIRIFERIDINA Waagen, 1883

This suborder groups Cyrtospiriferoidea, Paeckelmannoidea, Spiriferoidea, Spiriferelloidea and Trigonotretoidea. They share plicate and often costate ornament with cancellate micro-ornament of radial and commarginal fila, and share ctenophoridium, denticulate hinge, and internal plates, involving dental and adminicula plates, connector plate as a rule (except Trigonotretoidea), ctenophoridium and crural plates but no tabellae, as well as spiralia.

Superfamily **CYRTOSPIRIFEROIDEA** Termier & Termier, 1949

Diagnosis: Usually transverse with well defined sulcus and fold, uniformly ornamented by narrow plicae or stout costae, without fasciculation, micro-ornament capillate, pustulose, or minutely spinose, dental plates and adminicula present, delthyrial cover plate or stegidia well developed as a rule; crural plates and no tabellae. A connector plate is widely developed. Lower Devonian (Emsian) to Upper Devonian (Famennian).

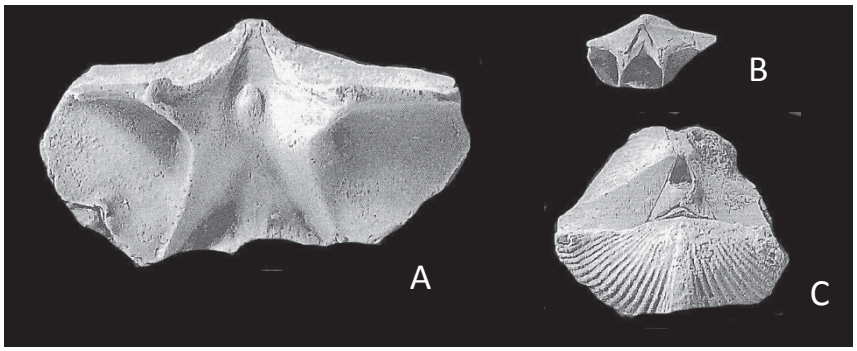


Fig. 152. *Sinospirifer subextensus* Ma & Day. A, ventral interior, x3. B, ventral valve showing pleromal ridges leading to connector plug, x1. From Famennian of Hunan, China. C, *Plicapustula subarchiaci* (Martelli), dorsal view of specimen showing delthyrial (stegidial) covering plate, upper part broken, x1.6. From Famennian of Hunan, China. (Ma & Day 2007).

Discussion: The Devonian superfamily Cyrtospiriferoidea Termier & Termier as interpreted by Johnson (2006b, p. 1722) has adminicula (called dental plates in the *Revised Brachiopod Treatise*), as well as true dental plates, ctenophoridium, and lacking what the *Revised Brachiopod Treatise* frequently called “crural plates,” more precisely termed tabellae. Crural plates as strictly defined are widely present. The superfamily is highly distinctive, and readily recognized. Shape, including alation and height of the ventral interarea, varies within narrow parameters, and a sulcus and fold, and costae or narrow plicae feature in all genera, except in Conispiriferidae with less defined sulcus and fold. Micro-ornament varies only a little, being capillate, cancellate, pustulose or spinose or dominated by commarginal growth laminae. Close study of micro-ornament by Oleneva (2006) showed differing spine development, underlining the need to extend this type of enquiry. The Lower to Upper Devonian Family Spinocyrtiidae Ivanova is alate as a rule, with plicate flanks and smooth sulcus-fold, smooth or with single medial ventral rib and dorsal groove. Stegidial plates are well displayed for

example in *Mediospirifer* Bublichenko, 1956. The Middle and Upper Devonian Family Cyrtospiriferidae Termier & Termier is rather similar, with ribbed sulcus and fold. Cyrtospiriferinae has a wide interarea and acute cardinal extremities. Cyrtiopsinae Ivanova has a narrow interarea and rounded cardinal extremities, and differently defined sulcus, and so is regarded as a member of Choristitimorphi.

From what is known, internal plates are almost fully consistent in nature. The clear exception amongst Cyrtospiriferoidea as far as dorsal interiors is concerned is provided by members of Conispiriferidae Ma & Day of middle to upper Frasnian age, which have a cruralium (or septalium), in genera marked by a high ventral interarea.

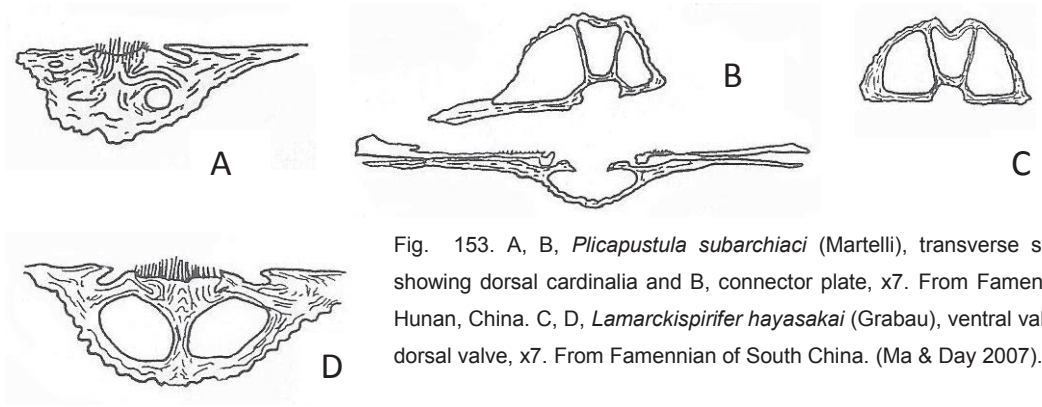


Fig. 153. A, B, *Plicapustula subarchiaci* (Martelli), transverse sections showing dorsal cardinalia and B, connector plate, x7. From Famennian of Hunan, China. C, D, *Lamarckispirifer hayasakai* (Grabau), ventral valve and dorsal valve, x7. From Famennian of South China. (Ma & Day 2007).

It would seem likely, in view of the shape, narrowly plicate ornament, and internal plates, that the oldest Cyrtospiriferoidea, as Spinocyrtiidae, arose from a transverse and plicate shell, with capillae and tubercles. Callispiriferinae Johnson, 1994 of Adolfioidea matches some of these attributes, and although the plicae are relatively fewer and stronger than in cyrtospiriferoids, the fold and sulcus are well defined, whereas its micro-ornament lacks tubercles. *Callispirifer* is of Emsian (Lower Devonian) age, as old as the oldest Spinocyrtiidae. A number of genera within Adolfioidea agree with Cyrtospiriferoidea in the presence of adminicula and lack of tabellae, but are smaller shells with relatively fewer and coarser plicae, and if plates remained stable, they provide the most likely of forebears. It is true that one genus, made the basis of a family in Adolfioidea in the Treatise, is particularly close to Cyrtospiriferoidea, and that is *Echinospirifer* Liashenko, 1973. This genus is transverse, with hinge at maximum width, numerous narrow plicae, tuberculate micro-ornament, and the usual compliment of adminicula, dental plates, and crural plates. However there appears to be a connector plate (Oleneva 2006), indicating that Johnson (2006a) had wrongly placed the genus – it is cyrtospiriferoid. *Callispirifer* of Lower Devonian age seems to offer the mostly likely source, or at least coeval relative.

Family **CYRTOSPIRIFERIDAE** Termier & Termier, 1949

[Nom. transl. Besnossova 1958, p. 17 ex Cyrtospiriferinae Termier & Termier, 1949, p. 99].

Diagnosis: Macro-ornament of costae or fine plicae, sulcus and fold costate. Upper Devonian (Frasnian, Famennian).

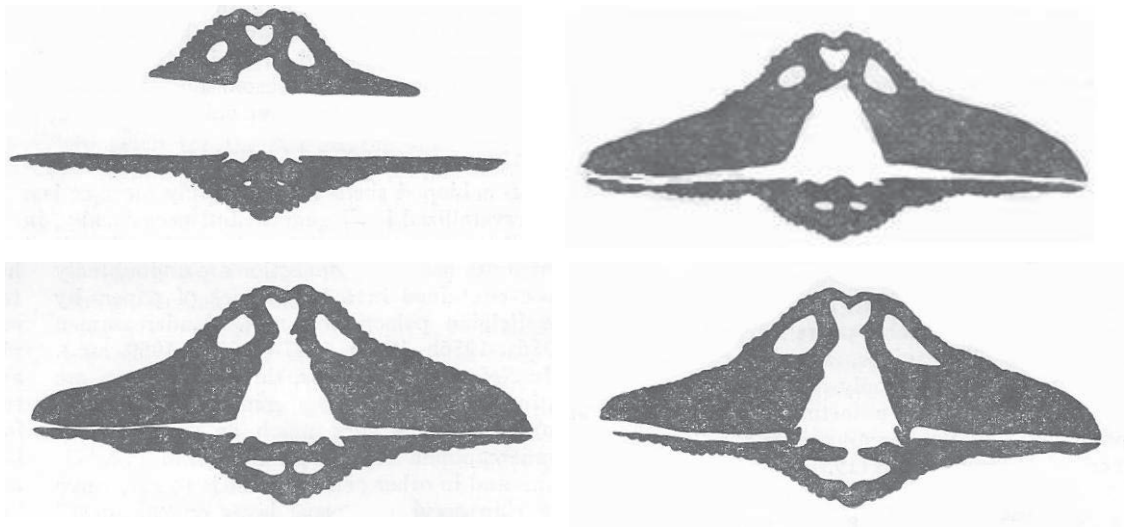


Fig. 154. *Cyrtospirifer iowensis* (Owen), successive transverse sections, with dorsal valve on top, showing connector plate in ventral valve and indicating a short median septal ridge below the ctenophoridium and a brief cardinal shelf formed by the inner hinge plates, with supporting septum, x1. From Devonian of Midwest USA. (Ager & Riggs 1964).

Discussion: Sulcus and fold are well developed, and sulcal and fold costae marginally finer than lateral subplicae. Small granules may be present, as in some members of Spinocyrtiidae.

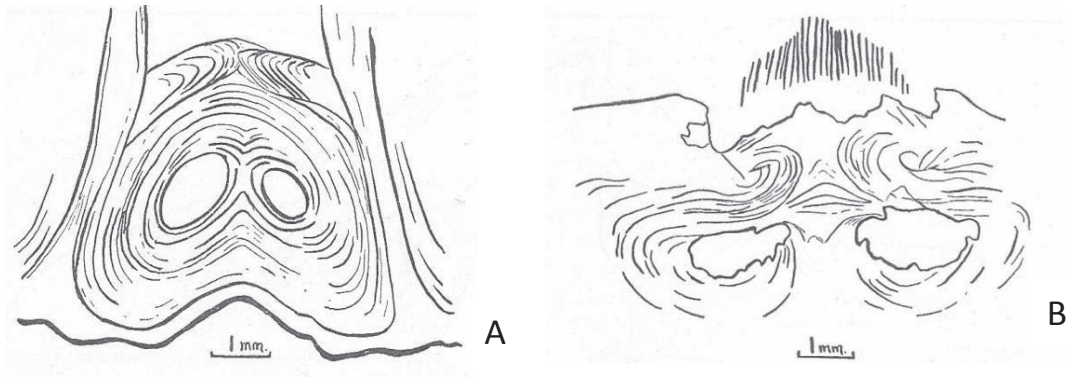


Fig. 155. *Cyrtospirifer iowensis* (Owen), A, ventral valve showing delthyrial plate and septum. B, showing shell structure below the ctenophoridium. From Devonian of Midwest USA. (Ager & Riggs 1964).

Subfamily **CYRTOSPIRIFERINAE** Termier & Termier, 1949

[Cyrtospiriferinae Termier & Termier, 1949, p. 99. Syn. Hunanospiriferinae Besnossova, 1958].

Diagnosis: Wide interarea with acute cardinal angles. No pustules or spinules. Upper Devonian (Frasnian – upper Famennian).

Genera: *Cyrtospirifer* Nalivkin (syn. *Hunanospirifer* Tien, *Grabauispirifer* Gatinaud, *Eurytatospirifer* Gatinaud, *Subquadrangulispirifer* Sartenaer), *Austrospirifer* Glenister, *Deothossia* Gatinaud, *Lamarckispirifer* Gatinaud, *Liraspirifer* Stainbrook, *Nikospirifer* Grechishnikova, *Plicapustula* Ma & Day, *Pripyatispirifer* Pushkin, *Regelia* Crickmay, *Sinospirifer* Grabau, *Syringospira* Kindle, *Tarandrospirifer* Simakov, *Tenticospirifer* Tien, *Validospirifer* Simakov.

Discussion: Ma & Day (2000) have retrieved from synonymy several of the genera cast aside and regarded as the same as *Cyrtospirifer* by Johnson (2006b, p. 1726). They provided detailed analyses, and showed that micro-ornament was particular useful for discriminating and validating various genera. They further indicated a degree of uncertainty about several genera, which were too poorly known to allow confident recognition.

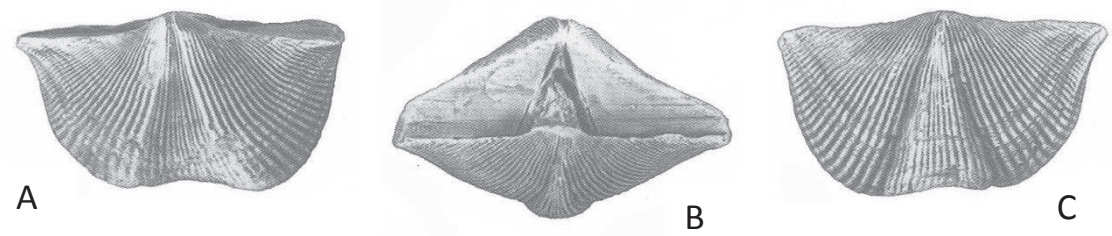


Fig. 156. *Cyrtospirifer verneuili* (Murchison), type species, ventral, posterior (ventral valve on top), with connector plate, and dorsal aspects, x1. From Frasnian of France. (Johnson 2006b).

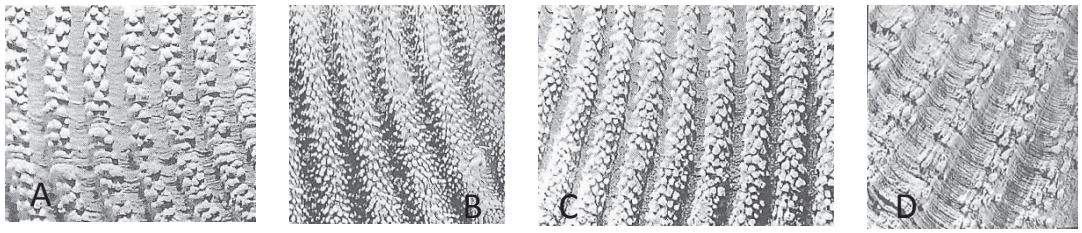


Fig. 157. Micro-ornament x 10 in A, *Plicapustula subarchiaci*, B, *Plicapustula gortanoides*, C, *Sinospirifer subextensus*. D, *Lamarckispirifer hayasakai*. (Ma & Day 2007).

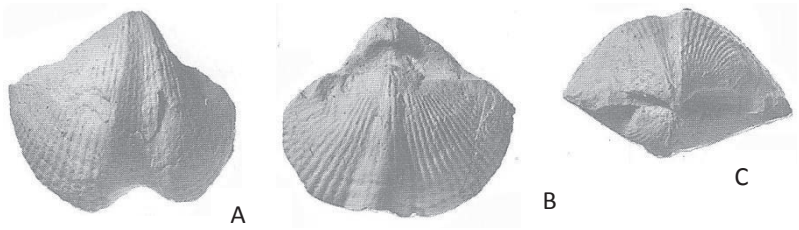


Fig. 158. *Validospirifer validus* Simakova, 1970 from Frasnian (Upper Devonian) of southern Mongolia, x1. (Rozanov 2003).

Subfamily **ECHINOSPIRIFERINAE** Liashenko, 1973

[Nom. transl. hic ex Echinospiriferidae Liashenko, 1973. Syn. Uchtospiriferinae Liashenko, 1973, p. 87, Rigauxiidae Brice, 1988, p. 371].

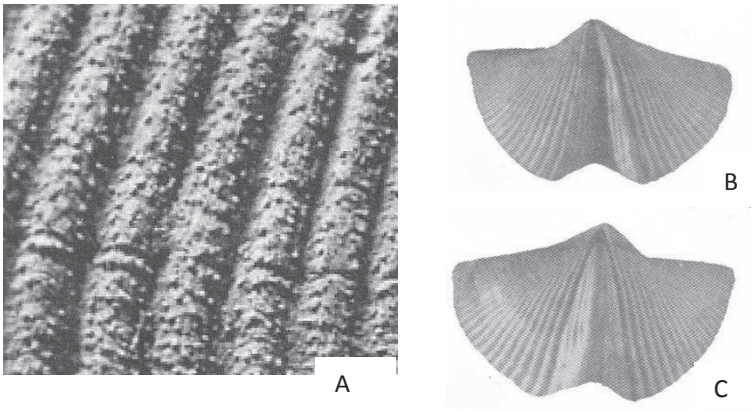


Fig. 159. *Echinospirifer distinctus* Liashenko. A, micro-ornament, x 1, (Oleneva 2006). B, C, ventral and dorsal aspects of complete specimen, x1. From lower Frasnian (upper Devonian) of Timan, Russia. (Liashenko 1973).

Diagnosis: Small shells with cyrtospiriferoid shape and micro-ornament of spinose fila. Narrow plicae cover the shell, with finer ribs over the sulcus and fold. Ctenophoridium developed in at least some genera. Upper Devonian (Frasnian, Famennian).

Tribe **ECHINOSPIRIFERINI** Liashenko, 1973

[Nom. transl. hic ex Echinospiriferidae Liashenko, 1973. Syn. Rigauxiidae Brice, 1988, p. 371].

Diagnosis: Small shells with dense spines. Narrow plicae cover the shell, with finer ribs over the sulcus and fold. Middle Devonian (upper Givetian) to Upper Devonian (Frasnian, Famennian).

Genera: *Echinospirifer* Liashenko, *Arctospirifer* Stainbrook, *Geminisulcispirifer* Sartenaer, ?*Hispidaria* Cooper & Dutro, *Komispirifer* Liashenko (syn. *Mennespirifer* Liashenko), *Petshorospirifer* Fotieva, *Pseudocyrtiopsis* Ma & Day, *Rigauxia* Brice, *Sphenospirifer* Cooper, *Uchtospirifer* Liashenko (syn. *Clivospirifer* Liashenko, *Timanospirifer* Liashenko, *Nordispirifer* Liashenko, *Acutella* Liashenko).

Discussion: *Echinospirifer* Liashenko, 1973 of lower Frasnian (Upper Devonian) age has well defined sulcus and fold and numerous fine lateral plicae, and in shape and size differs considerably from Adolfiidae, where it was classed by Johnson (2006a), being transverse with fine lateral plicae and costate sulcus and fold, bearing fine capillae, with small spines, and indeed Talent & Gratsianova (1988) had synonymized the genus with *Cyrtospirifer.* The genus looks remarkably like members of Cyrtospiriferidae in its transverse shape, extended cardinal extremities, and well defined sulcus and fold, but it was reported to lack any form of delthyrial cover, including a connector plate, as shown by Liashenko (1973, pl. 51, fig. 1) in figures of the type species *E. distinctus* Liashenko. This is contradicted by Oleneva (2006), who stated that the connector plate must have been lost from the particular specimen, and showed a connector plate as present in *E. sublimis* Nilova (2006, Fig. 5), connecting the plates at early growth stages. She further confirmed the absence of tabellae, whereas

Johnson (2006a) had stated that crural plates (= tabellae?) were present. The genus is distinguished principally by its micro-ornament of well developed small spines over ribs along growth lamellae (Oleneva 2006). The genus was classed as a full family in Spinelloidea by Oleneva, but the delthyrial apparatus, and the nature of the sulcus and fold differ considerably. *Spinella* is analysed on pp. 295, 296. Here. largely in agreement with Talent & Gratsianova (1988), the genus is classed within Cyrtospiriferidae, and regarded as a subfamily distinguished by small spines and, as rule, finer costae over the fold and sulcus.

Rigauxia and *Arctospirifer* are also somewhat similar, though with less well defined sulcus, and slightly narrower hinge. Both also are characterized by numerous narrow plicae laterally and costate sulcus-fold, with what appears to be tubercular micro-ornament. *Rigauxia* has apical callus and extrasinal adminicula, and *Arctospirifer* has short adminicula and a small delthyrial plate (Stainbrook 1950, p. 365). Tabellae ("crural plates") are not found in *Arctospirifer,* but have reported as obscured by callus in *Rigauxia*, and this genus has a ctenophoridium, whereas the presence or absence of a ctenophoridium in *Echinospirifer* is not clear. *Geminisulcispirifer* and *Petshorospirifer* also have small spinules. The micro-ornament on these genera is less well known than that of the Russian genera examined by Oleneva (2004, 2006).

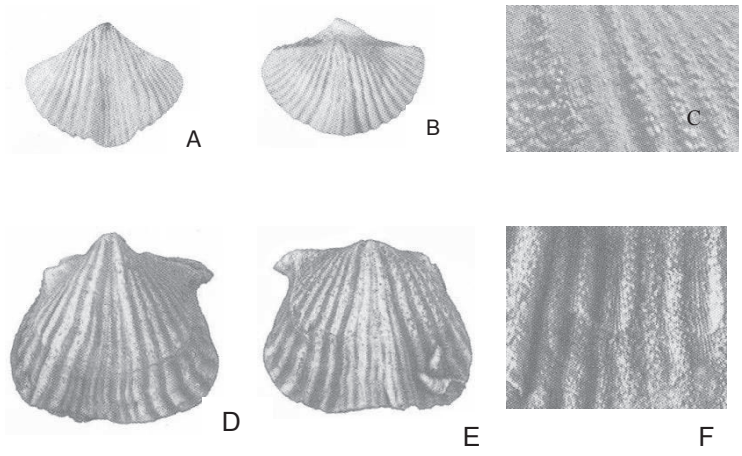


Fig. 160. *Rigauxia acutosinu* (Rigaux), ventral and dorsal views, x2, and micro-ornament, x10. From lower Frasnian of France. (Brice 1988). D – F, *Arctospirifer constrictus* Stainbrook, ventral and dorsal views, x1.5, with micro-ornament x4. From Famennian of Iowa. (Johnson 2006)

Hispidaria Cooper & Dutro, classed as a member of Echinospiriferidae Liashenko in the *Revised Brachiopod Treatise*, is of small size, transversely triangular in shape, with comparable fine ribbing over sulcus and fold and slightly coarser laterally, and micro-ornament appears to be tuberculate, although its nature, as for other genera, needs to be more closely examined. Internal detail is not known, so that the genus is inadequately substantiated, and its position must remain speculative, though transverse shape, wide cardinal extremities and ornament agree well with transverse members of Cyrtospiriferidae.

Sergunkovia Nalivkin is capillate with short adminicula, and of upper Famennian age. It was classed as Echinospiriferidae in the *Revised Brachiopod Treatise*, but is so small that illustrations at x1 are far from adequate. It might be adolfioid, belonging perhaps to Pinguispiriferinae (see p. 51).

Uchtospiriferinae was synonymized with Cyrtiopsinae in the *Revised Brachiopod Treatise* by Johnson (2006b, p. 1729), but *Uchtospirifer* has a connector plate (Oleneva 2004), that is missing from *Cyrtiopsis* (see p. 119). Oleneva (2004) synonymized various genera with *Uchtospirifer,* but it may be noted that whereas *Uchtospirifer* has intrasinal adminicula, *Acutella* has borderline adminicula. The shape and fine ribs do recall aspects of Theodossioidea, where they were classed by Johnson, but constituent genera have a well defined sulcus and fold, and hinge distinctly wider than *Cyrtiopsis* or *Dmitria*, or *Platyspirifer*, which are regarded as the constituents of Cyrtiopsinae, and in a theodossian with wide hinge, such as *Eodmitria* Brice, the sulcus and fold are weakly defined.

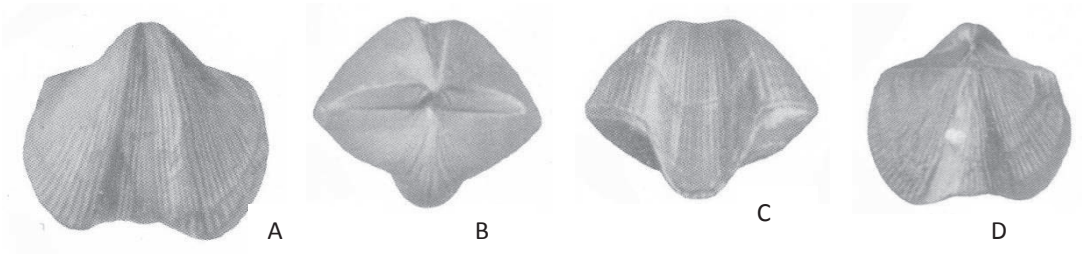


Fig. 125. *Uchtospirifer nalivkini* Liashenko, ventral, posterior (ventral valve on top), anterior and dorsal aspects, x1. From Frasnian of Timan, north Urals. (Liashenko 1957).

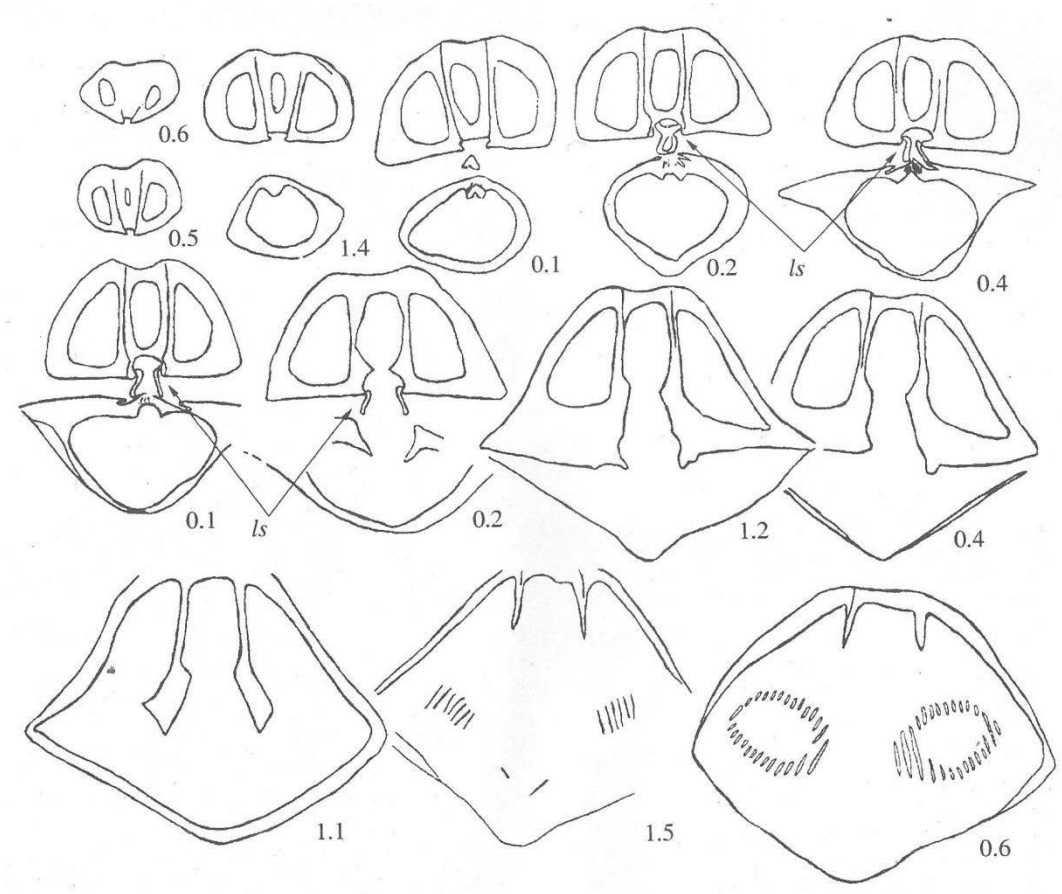


Fig. *Uchtospirifer nalivkini* Liashenko, transverse sections. L (length) = 26.3mm, ls longitudinal section of the high deltidial plate. From lower Frasnian of south Timan, Russia. (Oleneva 2004).

Tribe **ULBOSPIRIFERINI** Johnson & Carter, 1994

[Nom. transl. hic ex Ulbospiriferinae Johnson & Carter, 1994, p. 334].

Diagnosis: Transverse with well defined sulcus, dense and tiny protuberances. Narrow plicae, prismatic inner shell layer. Upper Devonian (upper Famennian).

Genus: *Ulbospirifer* Grechishnikova.

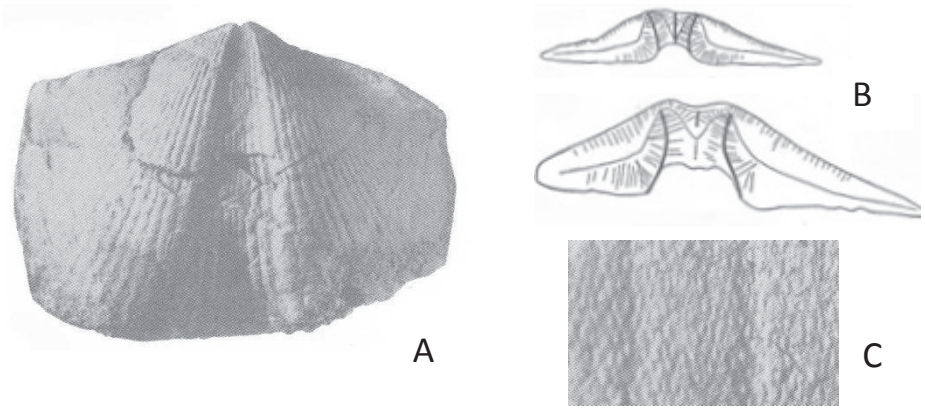


Fig. 162. *Ulbospirifer altaicus* Grechishnikova. A, ventral valve, x1. B, two transverse sections of ventral valve, x1.7. C, micro-ornament, x8. (Grechishnikova 1965).

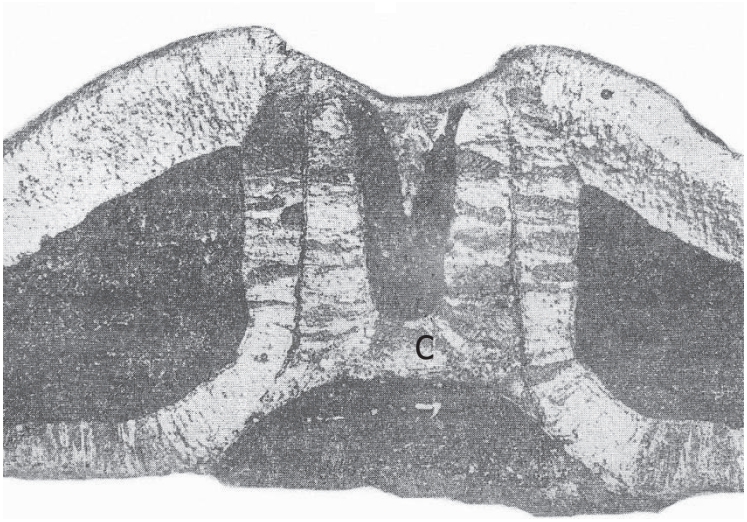


Fig. 163. *Ulbospirifer vulgatus* Grechishnikova, transverse section x10. From Upper Devonian of Rudny Altai, Russia. This is like the transverse sections of the type species (Grechishnikova 1966, pl. 18), but provides a clearer picture. Note the connector plate C supported by a pleromal coat over the adminicula, and the median ridge. (Grechischnikova 1966).

Discussion: This subfamily was recognized as a member of Theodossioidea by Johnson et al. (2006a, p. 1715), but that superfamily is reorganized, with some genera reallocated to Choristitoidea. The thick shell of *Ulbospirifer* with its prismatic structure, and closely spaced costae suggest differences from Adolfioidea. A connector plate was illustrated for the type species *U. nalivkini* by Liashenko (1973, pl. 51, fig. 2a, 2b). *Ulbospirifer* has sturdy close-set tubercular ribs and moderately well defined sulcus, as well as thick dental plates and adminicula, but the only figured material is very incomplete, featuring a broken ventral valve. That it is distinct is of no doubt, but the affinities are difficult to ascertain. Therefore a second

species *vulgatus* assigned to the genus by Grechishnikova (1966) is figured for assessment herein. It is close to the type species in ribs and sulcus, and displays a wide and strongly alate hinge, quite different from *Cyrtiorina* and *Tenisia* that were assigned to the same subfamily by Johnson, Carter & Hou (2006a). There is a connector plate in the ventral valve, as in the norm for Cyrtospiriferoidea, well developed ventral myophragm, and well developed dorsal fold, sharply set off from the lateral flanks. Grechishnikova (1966, p. 125) allocated the genus to Cyrtospiriferidae, and this position seems well judged, in view of the shape and ornament, and connector plate. It would seem to be a very extraordinary morphology to achieve from theodossiid or choristitoid stock.

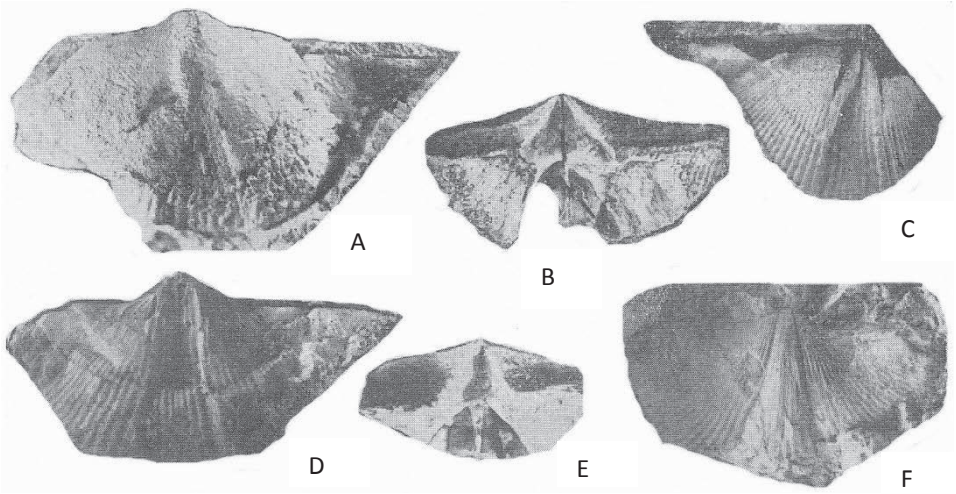


Fig. 164. *Ulbospirifer vulgatus* Grechishnikova. A, ventral valve. B, posterior interior of ventral valve. C, ventral internal mould. D, ventral valve. E, posterior ventral valve. F, dorsal valve. Specimens x 1 from Rudny Altai, Russia, of Upper Devonian age. (Grechishnikova 1966).

Family **SPINOCYRTIIDAE** Ivanova, 1959

[Nom. transl. Pitrat 1965, p. 688 ex Spinocyrtiinae Struve in Paulus, Struve & Wolfart 1963, p. 462, nom. correct. pro Spinocyrtinae Ivanova, 1959, p. 59].

Diagnosis: Fold and sulcus smooth or with one rib, plicate laterally. Micro-ornament granulose. Lower Devonian (Emsian) to Upper Devonian (Frasnian).

Genera: *Spinocyrtia* Fredericks, *Acutoria* Cooper & Dutro, *Alatiformia* Struve, *Carpinaria* Struve, *Duryeella* Boucot, *Eosyringothyris* Stainbrook, *Mediospirifer* Bublichenko, *Orthospirifer* Pitrat, *Platyrachella* Fenton & Fenton.

Fig. 165. *Alatiformia janseni* Gad, internal mould of ventral valve, x1.5, from upper Emsian of Germany. (Jansen 2016)

Discussion: Apart from size, sulcal definition and having many narrow plicae, Spinocyrtiidae stands as a group very close to Adolfiinae, as interpreted by Carter & Gourvennec (2006a, Fig. 1104), with capillate or cancellate micro-ornament, simple fold and sulcus, numerous lateral fine plicae, ctenophoridium, and lack of tabellae. The difference is that a connector

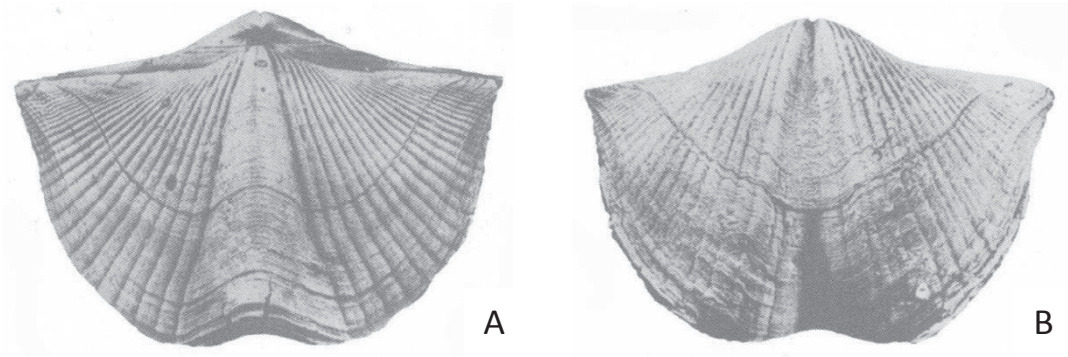


Fig. 166. *Spinocyrtia granulosa* (Conrad), dorsal and ventral aspects, x1. From Givetian of New York, USA. (Ehlers & Wright 1955).

plate is developed in at least some of the genera. Genera are close to each other in many respects. An anterior median spine is developed in the delthyrial plate of *Eosyringothyris*. *Orthospirifer* Pitrat (Johnson 2006b, Fig. 1131.1f) includes a specimen at considerable variance from the others, in the coarseness of the plicae and different fold. It shows short tabellae, but the identification is incorrect, and was not sourced from the cited publication by Pitrat (1975). *Alatiformia* has been classed in this group, although it has unusually well formed plicae, approaching those of *Arduspirifer* in Acrospiriferinae of Hysterolitoidea.

Subcuspidella Mittmeyer, 1965 of Eifelian age in Europe was placed in this group in the *Revised Brachiopod Treatise*, with its non-costate sulcus and nodose growth-lines, but the presence of short tabellae suggest a position within Hysterolitoidea.

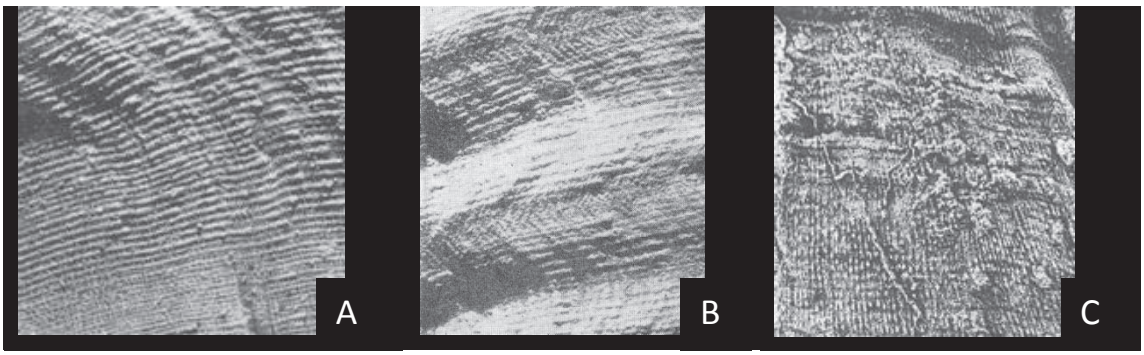


Fig. 167. A, B, *Spinocyrtia martinanofi* (Stuckenberg), micro-ornament x10. From Devonian of Minusinogo Basin. (Ivanova 1972). In type *Spinocyrtia*, the micro-ornament is tuberculate. C, *Spinocyrtia ascendens* (Spriestersbach), latex impression of dorsal exterior showing granules formed at intersection of radial micro-fila and growth lines, x7. From Givetian of Somerset. (Webby 1964).

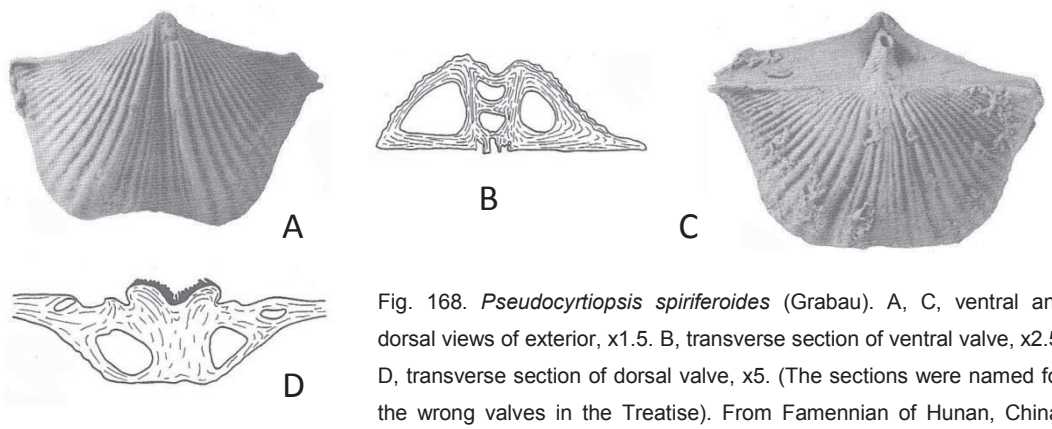


Fig. 168. *Pseudocyrtiopsis spiriferoides* (Grabau). A, C, ventral and dorsal views of exterior, x1.5. B, transverse section of ventral valve, x2.5. D, transverse section of dorsal valve, x5. (The sections were named for the wrong valves in the Treatise). From Famennian of Hunan, China. (Ma & Day 1999). See Echinospiriferini, p. 143.

Family **CONISPIRIFERIDAE** Ma & Day, 2000

[Conispiriferidae Ma & Day, 2000, p. 459].

Diagnosis: Plicate with weak sulcus and fold and very high ventral interarea, short septalium, or cardinal plate on low thick septum. Upper Devonian (?Lower, middle to upper Frasnian).

Genera: *Conispirifer* Ma & Day, *Pyramidaspirifer* Ma & Day.

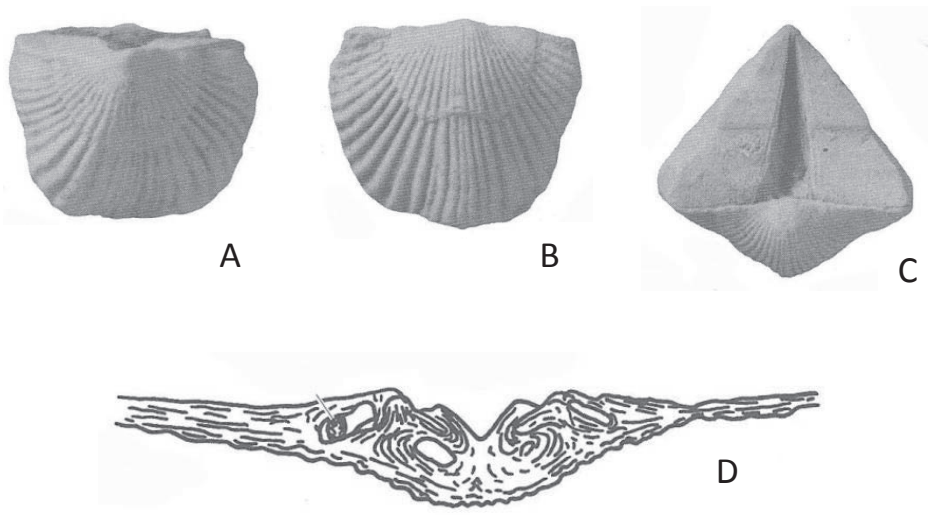


Fig. 169. *Pyramidaspirifer alta* (Fenton & Fenton), A-C, ventral, dorsal and posterior aspects, x2. D, transverse section of dorsal valve, showing septalium, x4. From Upper Devonian (Frasnian) of Iowa, USA. (Ma & Day 2000).

Discussion: The two genera placed in this subfamily by Ma & Day (2000), followed by Gourvennec & Carter (2007, pp. 2774, 2775), look close to Silurian genera of Cyrtiinae Fredericks in their high interarea, and the sulcus is very shallow, reminiscent of that in Cyrtiopsinae, though the genera are younger and are strongly ribbed. *Pyramidaspirifer* Ma & Day has pustulose capillae. The dorsal interior of *Pyramidaspirifer* recalls that of

Alphaneospirifer Gatinaud, which has a low cruralium, and lacks adminicula. For this genus, it is considered that crural plates join dorsally, and in Conispiriferidae the crural plates rest on a broad low septum. Gourvennec in Carter & Gourvennec (2007, p. 2774) classed the family within Cyrtospiriferoidea. The presence of a dorsal septal development, which could have arisen from modification to tabellae, marks out a highly distinct group, but close, it would appear, to several genera of Cyrtospiriferidae which have short posterior median pillar that possibly represents atrophied tabellae, a question requiring further study.

Pseudocyrtiopsis Ma & Day from the lower Famennian of China shows some approach in so far as sections of the dorsal valve reveal a stout median septum or posterior pillar, supporting a cardinal plate with bilobed ctenophoridium. The low septalium of *Pyramidaspirifer* is not developed, but there is some similarity. *Pseudocyrtiopsis* is more transverse with low interarea and better formed sulcus, and has a short connector plate, and there is a substantial delthyrial cover plate with foramen, whereas the delthyrial plate in the other two genera is short.

Superfamily **PAECKELMANNELLOIDEA** Ivanova, 1972

[Nom. correct. Waterhouse 2004, p. 227**,** pro Paeckelmanelloidea Carter in Carter et al. 1994, p. 347, pro Paeckelmanellacea Ivanova, 1981, p. 22, nom. transl. ex Paeckelmanellidae Ivanova, 1972, p. 40].

Diagnosis: Transverse and sulcate, with simple plicae, which become costate in some genera, commarginal growth lamellae often moderately developed, micro-ornament as a rule of radial and commarginal fila, hinge-line denticulate, dental plates and short adminicula, socket and crural plates but no tabellae. Median ventral septum in one group. Upper Devonian (Famennian) to Late Permian (Changhsingian).

Discussion: This superfamily is of modest size and distinctive in its shape, whereas internal plates are usually close to those of Cyrtospiriferoidea, Spiriferoidea, Spiriferelloidea and Trigonotretoidea, and ornament is allied. There are exceptions however, and one group is medianly septate, and another devoid of adminicula, as occurs for some Spiriferoidea. Crural plates are well and widely developed, although Carter (2006b, p. 1812) denied their presence. The delthyrial apparatus appears to be close to that of Spiriferoidea. The distinctive subfamily Callispiriferinae Johnson of Adolfioidea in Carter et al. 1994 involves a genus of Lower Devonian (Emsian) age, *Callispirifer* Perry, which has a high interarea at maximum width of highly transverse shells, and a number of well formed plicae, and the ventral interarea is high. This may well have been involved in the ancestry of Paeckelmannelloidea, which commenced in Famennian (Upper Devonian) time, because, given their age range and morphology, Paeckelmannelloidea commenced before Trigonotretoidea, and at about the same time as Spiriferoidea. But earliest known members are not typical of the superfamily, lacking as they do internal plates, as a temporary suppression, to suggest that there may have been as yet undiscovered contemporary genera more normal for the superfamily. The Middle Devonian interval between *Callispirifer* and first appearance of Paeckelmannelloidea may give pause to any conjecture of ancestral relationship, although it is not insuperably long. Suppositiously, an acceleration in costation could have rapidly transformed members of Paeckelmannelloidea into Spiriferoidea, the shape and internal septation being in close agreement, but Callispiriferinae and earliest Paeckelmannelloidea such as *Strophopleura* Stainbrook have plicae, without costae, whereas the ribs in Prospirinae, earliest subfamily in Spiriferoidea, are much narrower, and in *Prospira* Maxwell and *Parallelora* Carter, the sulcus and fold are more strongly defined. Indeed the Paeckelmannelloidea, being dominated by plicate rather than costate ornament, could have arisen from Spinocyrtiinae, sharing the plicae, wide hinge at maximum width, well defined, but less sharply defined sulcus and fold, and internal plates. They changed by becoming more transverse, and developing other attributes that whilst meriting superfamilial differentiation, were not overwhelming. It does seem that a progression involving minimal though critical changes could have developed from shells moderately like Callispiriferinae, of Family Adolfiidae, into Spinocyrtiidae, to Paeckelmannelloidea, and from Spinocyrtiidae into Prospirinae and Spiriferinae. These genera and groups are all relatively

close to each apart from outliers, and from the fossil record traced pathways of close origin and leap-frogging, in a fractal pattern.

Carter (2006b) has divided Paeckelmannelloidea in a logical way that has to be adjusted, because of a critical study by Poletaev (2001) which showed that *Strophopleura* had been misinterpreted: it lacks the internal plates that Carter thought were present and buried in secondary shell. There are genera with a delthyrial cover plate, such as *Odontospirifer* and *Scenesia*, whereas a connector plate is developed in *Johncarteria* and *Celsifornix*, and *Amesopleura* Carter (now *Voiseyella* Roberts) appears to have a delthyrial cover plate and a connector plate, both short. In some genera, such as *Paeckelmannella* and *Scenesia*, there is a median ventral septum. The micro-ornament seems much the same through all genera, the presence of hinge denticles is shown in well preserved material, but mantle canal systems are obscure. Such variation could well be interpreted as a pointer towards the reality of a variable and real superfamily. Whilst some genera could be dispersed to other superfamilies, most genera, in their transverse outline, high ventral interarea and relatively strong simple plicae, fit readily with no known trigonotretoid or spiriferoid group.

Taxonomy: Licharew (1934) named the genus *Paeckelmanella* after W. Paeckelmann, but mis-spelled the name, and in many articles, including the *Revised Brachiopod Treatise* studies (Carter 2006b), suprageneric categories were similarly mis-spelled, and even though a few authors sought to correct the anomaly, they were overlooked by Ivanova (1972, 1981). Waterhouse (2004, p. 227) underlined the need to correct the spelling, and this was accepted by Gourvennec in Gourvennec & Carter (2007, p. 2786), and in his position as author of a significant contribution, noted that the emendation accorded with the Code for Zoological Nomenclature 1999, Article 33.

Family **PAECKELMANNELLIDAE** Ivanova, 1972

[Nom. correct. Waterhouse 2004, p. 227, pro Paeckelmanellidae Ivanova, 1972, pp. 35, 40].

Diagnosis: Ventral median septum. Lateral ribs simple. Late Carboniferous (Kasimovian) to Late Permian (Changhsingian).

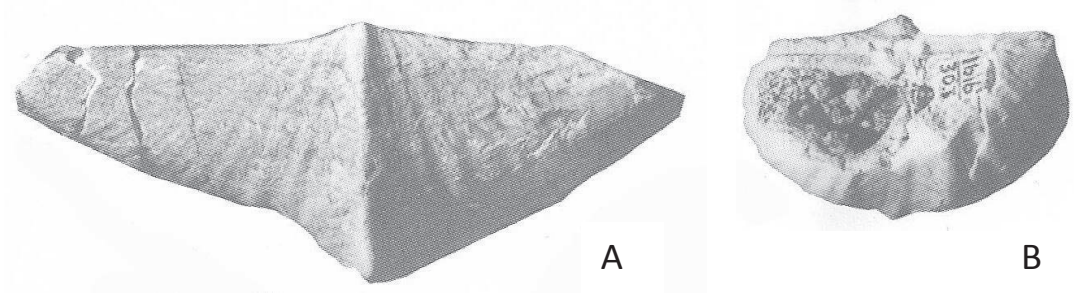


Fig. 170. *Paeckelmannella dieneri* (Chernyshev), dorsal valve and damaged ventral valve from Cisuralian of Urals, x1.5. (Chernyshev 1902, Carter 2006b).

Subfamily **PAECKELMANNELLINAE** Ivanova, 1972

[Nom. correct hic pro Paeckelmanellinae, nom. transl. Waterhouse 1975, p. 15 ex Paeckelmanellidae Ivanova, 1972, p. 40].

Diagnosis: Short divergent adminicula. Late Carboniferous to Permian.

Genera: *Paeckelmannella* Licharew*, Darvasia* Licharew.

Subfamily **SCENESIINAE** Carter, 1994

[Scenesiinae Carter in Carter et al. 1994, p. 348].

Diagnosis: Adminicula very short or absent, ventral median septum present. Lower Permian (Kungurian) to Upper Permian (Changhsingian).

Genera: *Scenesia* Cooper & Grant, *Odontospirifer* Dunbar.

Discussion: Carter in Carter et al. (1994) reinterpreted the genus *Scenesia*, which had been judged as Spiriferidina by Cooper & Grant (1976), although no punctae could be discerned. The genus is only known in the lower Cathedral Mountain Formation of the Glass Mountains. Similarly *Odontospirifer*, although classed as Paeckelmannellinae by Carter (2006b, p. 1818), has only rudimentary adminicula, and may belong here. *Scenesia* has a short delthyrial cover plate, and that was stressed by Carter (2006b). Whether *Odontospirifer* had such a plate is not known for certain, but Dunbar (1955, p. 156) considered it highly likely that an “arched deltidial cover” was present. He also noted a denticulate hinge. *Odontospirifer* is an external homeomorph of *Triangularia* Poletaev, of Early Carboniferous age (see p. 154).

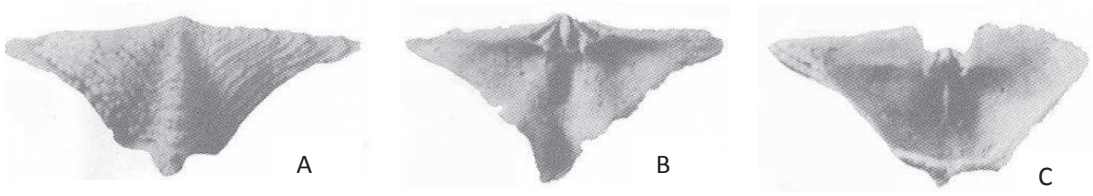


Fig. 171. *Scenesia extensa* Cooper & Grant. A, dorsal exterior, x6. B, interior view, x6. C, ventral interior, x2.5. From Cisuralian of Texas, USA. (Cooper & Grant 1976).

Family **STROPHOPLEURIDAE** Carter, 1974

[Nom. transl. Carter in Carter et al. 1994, p. 347 ex Strophopleurinae Carter, 1974, p. 667].

Diagnosis: Small with simple ribs and sulcus smooth or with median rib. No adminicula or median ventral septum. Upper Devonian (Famennian) to Lower Carboniferous (Serpukhovian). Possibly Upper Permian (Wuchiapingian).

Genera: *Strophopleura* Stainbrook*, Longiusculus* new genus*, Subspirifer* Shan & Zhao (?syn. *Triangularia* Poletaev), ?*Xizispirifer* Liang.

Discussion: Poletaev (2001, p. 42) pointed out that *Strophopleura* appeared to lack adminicula. This marks a very important distinction, even though there is yet to be full

clarification of the interior. *Xizispirifer* Liang, 1990 from the early Wuchiapingian or late Guadalupian of China is an obscure weakly transverse genus with narrow plicae. The nature of the micro-ornament is not known. Denticles occur along the hinge. It lacks a median septum and adminicula, but was classed in Pterospiriferinae in the *Revised Brachiopod Treatise*. Yet from internal data, the genus might represent a late survivor of Strophopleurinae.

Fig. 172. *Strophopleura notabilis* (Kindle). A, dorsal, B, ventral and C, anterior views, x1, from Famennian of New Mexico, Colorado, USA. (Cooper & Dutro 1982).

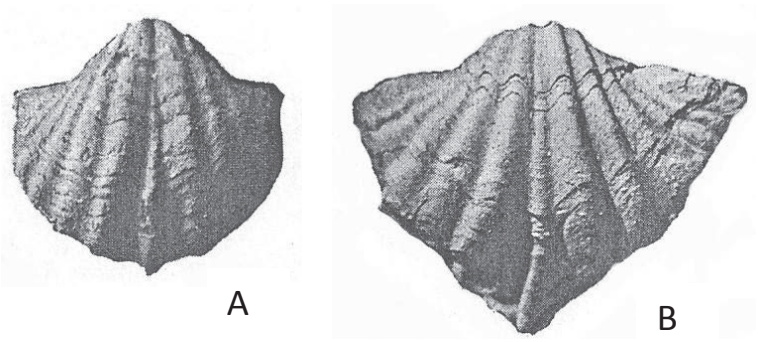


Fig. 173. A, *Triangularia tumida* Poletaev, holotype x1, from Serpukhovian of Donets Basin, Ukraine. B, *T. paratriangularis* Poletaev, x1, from upper Serpukhovian of Donets Basin. (Poletaev 2001). This genus is subjective junior synonym of *Subspirifer* Shan & Zhao.

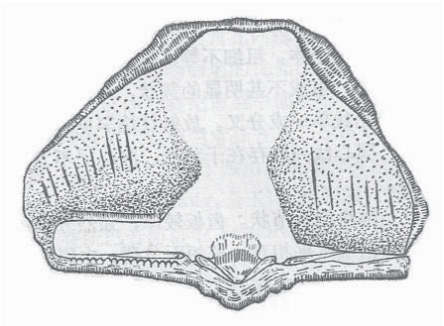


Fig. 174. *Xizispirifer zhejiangensis* Liang, transverse section showing absence of adminicula, dental plates and median septum, x2. From Wuchiapingian of China. (Liang 1990).

Genus ***Longiusculus*** new genus

Name: longiusculus – long, extended, Lat.

Diagnosis: Highly transverse shells with high ventral interarea, alate cardinal extremities, and prominent median plication along the sulcus. Narrow sulcus and fold, smooth shell laterally.

Type species: *Longiusculus yanagidai* new species from late Visean of Akiyoshi, Japan, here designated.

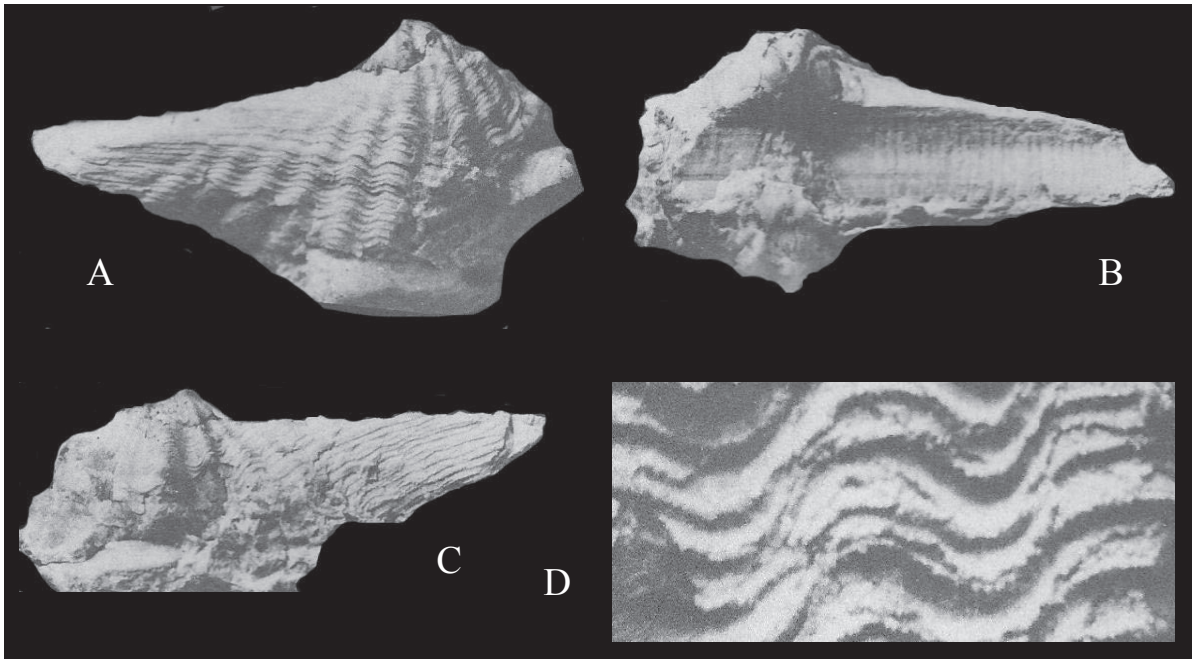


Fig. 175. *Longiusculus yanagidai* n. gen., n. sp. A-C, ventral, posterior and dorsal views, x3.5. D, detail of micro-ornament, x20. From late Visean, Akiyoshi, Japan. (Yanagida 1965).

Discussion: This genus was ascribed to "*Spirifer*" *triangularis* Martin by Yanagida (1965, p. 117), and is close, but has a much wider shape with alate cardinal extremities and strong commarginal laminae. The species *triangularis* belongs to *Triangularia* Poletaev, which appears to be a junior synonym of *Subspirifer* Shan & Zhao. This genus is plicate with median plication along the ventral sulcus, but much less transverse than the new genus. Unfortunately the interior is incompletely known for all of these genera.

Longiusculus yanagidai new species

1965 "*Spirifer*" *triangularis* non Martin, Yanagida, p. 117, pl. 26, fig. 1, 3, text-fig. 2.

Name: For J. Yanagida.

Diagnosis: Transverse with some six pair of plicae and narrow sulcus and fold, extensive smooth outer shell, well developed commarginal laminae.

Holotype: GK-D 30109, from upper Visean of Akiyoshi, southwest Japan, figured as above, and Fig. 175, 176 herein, here designated.

Description: Shell 26mm wide and 10.5mm long, 8mm thick, with slightly incurved ventral umbo and high ventral interarea. Cardinal angle 35-40°. Sulcus narrow with angle of 15°, and bearing a narrow but well formed median plication. Fold narrow and moderately high with narrowly rounded crest. Six or seven pair of plicae developed over lateral slopes, outer shell broad and smooth. Interarea high on ventral valve, with growth lines and denticles, three in 1mm, delthyrium with angle of 40°. Commarginal laminae number three or four in 1mm anteriorly.

Resemblances: The Japanese material is close to a British species revised by Muir-Wood (1951) and she declared that the species *triangularis* was to be credited to J. de C. Sowerby (1827, p. 120, pl. 562, fig. 5) from the original figure by Martin (1809, pl. 36, fig. 2). She assigned the species to *Fusella* (see Muir-Wood 1951, pl. 5, fig. 3a-d). *Fusella* is also a member of Paeckelmannelloidea, and her placement conforms with the assignment of *triangularis* to Strophomenidae by Brunton & Rissoné (1976). *Triangularia* ranged through much of the Lower Carboniferous, because *Fusella jizhongensis* Liu, 1988 from Tournaisian faunas of north China appears to be congeneric. *Subspirifer* Shan & Zhao was misplaced as a member of Prospirinae by Carter (2006a, p. 1776). It is of Visean-Serpukhovian age from Hunan, China, and appears to be senior synonym of *Triangularia*, displaying the same characteristic anterior fold in the centre of the sulcus.

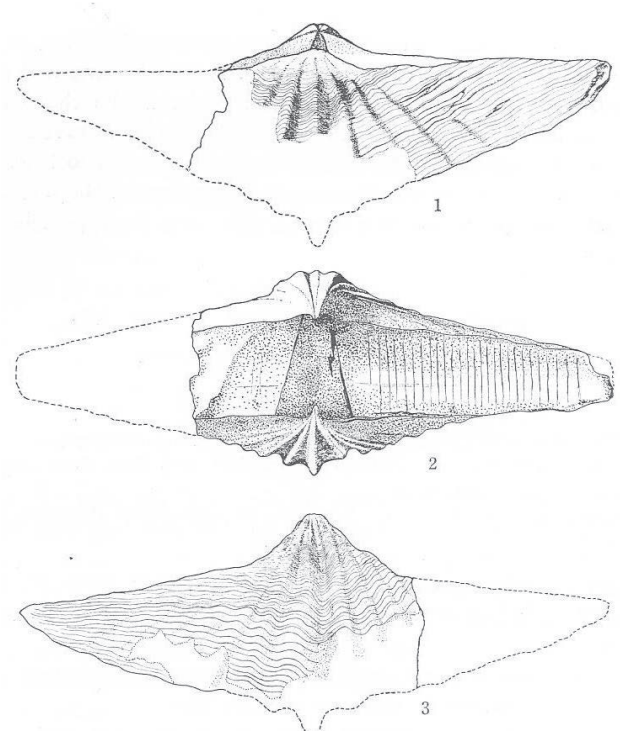


Fig. 176. *Longiusculus yanagidai* n. gen., n. sp. 1-3, ventral, posterior and dorsal views, x4. From late Visean, Akiyoshi, Japan. (Yanagida 1965).

Family **PTEROSPIRIFERIDAE** Waterhouse, 1975

[Nom. transl. hic ex Pterospiriferinae Waterhouse, 1975, p. 15].

Diagnosis: Medium to large, dental plates and adminicula present, no ventral median septum. Flank ribs simple to bifurcating or costate, fold and sulcus with or without median rib, rarely costate. Upper Devonian (Famennian) to Upper Permian (Changhsingian).

Subfamily **PTEROSPIRIFERINAE** Waterhouse, 1975

[Pterospiriferinae Waterhouse, 1975, p. 15].

Diagnosis: Medium to large, flank ribs simple to bifurcating or costate, with or without median rib, rarely costate. Upper Carboniferous (Moscovian) to Upper Permian (Changhsingian).

Genera: *Pterospirifer* Dunbar, ?*Haplospirifer* Li & Gu, *Johncarteria* Waterhouse*, Pteroplecta* Waterhouse, *Spiriferinaella* Fredericks, *Tipsispirifer* Grant.

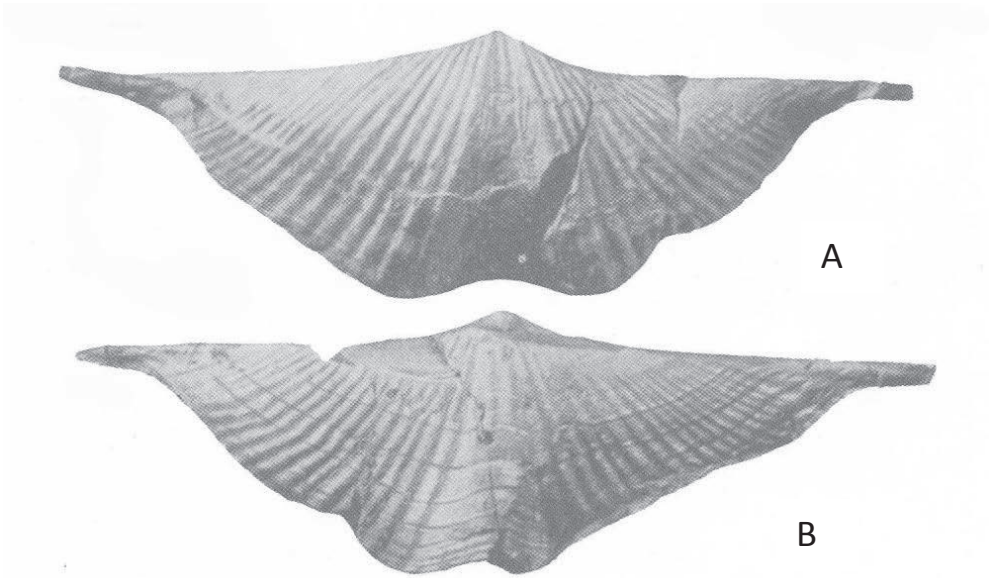


Fig. 177. *Pterospirifer terechovi* Zavodowsky, ventral and dorsal views, x1, from Cisuralian of north-east Russia. (Zavodowsky 1968**).**

Discussion: *Johncarteria* Waterhouse, 2004, p. 230 is based on *Spiriferinaella scalpata* Cooper & Grant (1976, p. 230, pl. 625, fig. 11-28), which was also figured as *Spiriferinaella* by Carter (2006b, Fig. 1205.3b-d) from the Word Formation of the Glass Mountains. *Spiriferinaella* Fredericks, 1926, type species *Spirifer artiensis* Stuckenberg, 1898 from Cisuralian of the Urals, and well figured by Chernyshev (1902, pl. 37, fig. 5-7) and later by Kulikov (1974, pl. 7, fig. 2, 3) with another species in Kulikov (1974, pl. 7, fig. 4) has a simple non-costate sulcus and rather few simple plicae, with high interarea. Specimens assigned

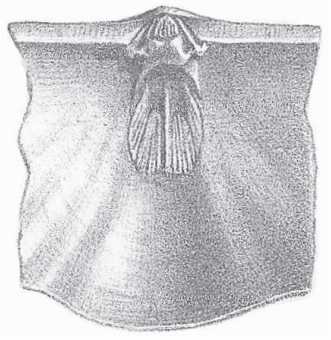


Fig. 178. *Pteroplecta alata* (Schlotheim), cast of dorsal interior. From Late Permian of Humbleton Hill, England. (Davidson 1858a). Size not given, possibly x5.

to *S. artiensis* and to *S. tastubensis* (Chernyshev) by Kalashnikov (1998, pl. 29, fig. 1; pl. 32, fig. 5) and Ustritsky & Chernyak (1963, pl. 42, fig. 1, 2) also lack sulcal costae. So *scalpata* does not belong to *Spiriferinaella*.

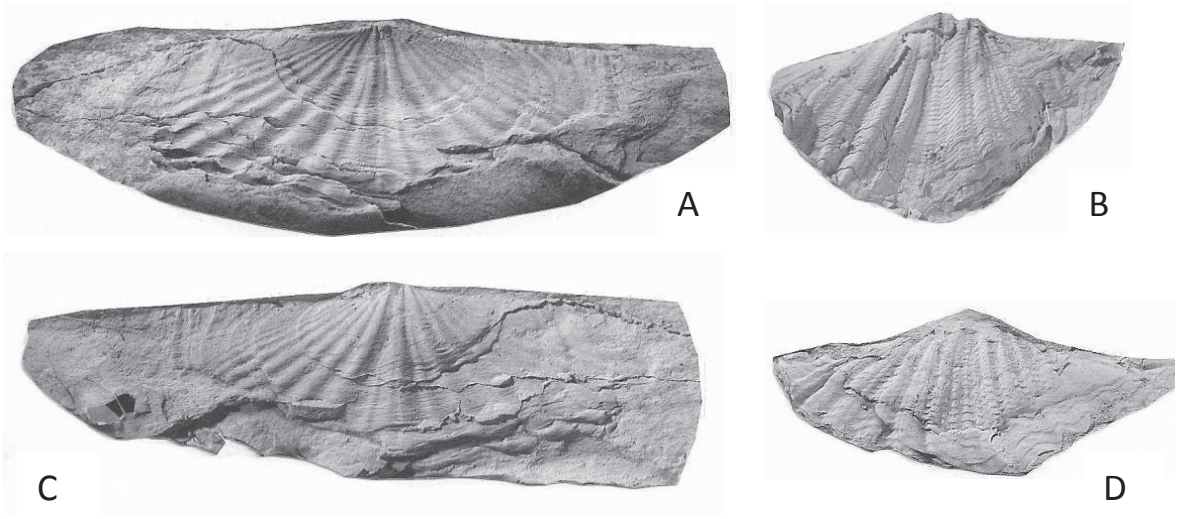


Fig. 179. *Pteroplecta laminatus* Waterhouse. A, C, external mould and latex cast of dorsal valve. B, ventral exterior, latex cast. D, ventral internal mould. D, latex cast of ventral exterior. Specimens x1 from Pija Formation (Changhsingian) in central Nepal. (Waterhouse 1983a).

Later, Carter in Gourvennec & Carter (2007, p. 2787) reassessed *Johncarteria* as being synonymous with *Pteroplecta* Waterhouse, 1978, p. 86, type species *P. laminata* Waterhouse, 1978 from the Changhsinghian of Nepal. This genus is much closer to *Johncarteria* than *Spiriferinaella*, and shares similar prominent commarginal laminae and sulcal and fold costation, with a number of lateral plicae present in both forms. Like *Johncarteria*, *Pteroplecta* has many lateral plicae, a few well formed sulcal costae, and weaker radial capillae. The dorsal fold has a rounded crest. A low but distinct median ridge is developed in each valve, and radial lirae are not strongly developed. The early growth

Fig. 180. *Pteroplecta laminatus* Waterhouse, internal mould of ventral valve, x2. From Pija Formation (Changhsingian) in central Nepal. (Waterhouse 1983a).

stages of *Pteroplecta* do not resemble those of *Johncarteria* in shape, the ontogenetic development being quite different, and one additional difference is the way the plicae split. In *Johncarteria limitata* Cooper & Grant and in an undetermined species (Cooper & Grant 1976, pl. 626, fig. 6-9), the plicae fork to produce two ribs of more or less equal strength. In *Pteroplecta*, the ribs split to produce a prominent and very much subsidiary rib. The delthyrium is partly closed by what appears to be a connector plate between the junctions of

dental plates and adminicula in *Johncarteria*, but such a plate is not known to be present in *Pteroplecta*. The silicified material of the Glass Mountains also has a cover plate (Cooper & Grant 1976, p. 2214) over much of the delthyrium, whereas it appears that the delthyrium was open in the Himalayan and Salt Range species. *Pteroplecta* has a pitted mantle canal system like that of Spiriferoidea.

Fig. 181. *Pteroplecta laminatus* Waterhouse, dorsal exterior, latex cast. Specimen x1 from Pija Formation (Changhsingian) in central Nepal. (Waterhouse 1983a).

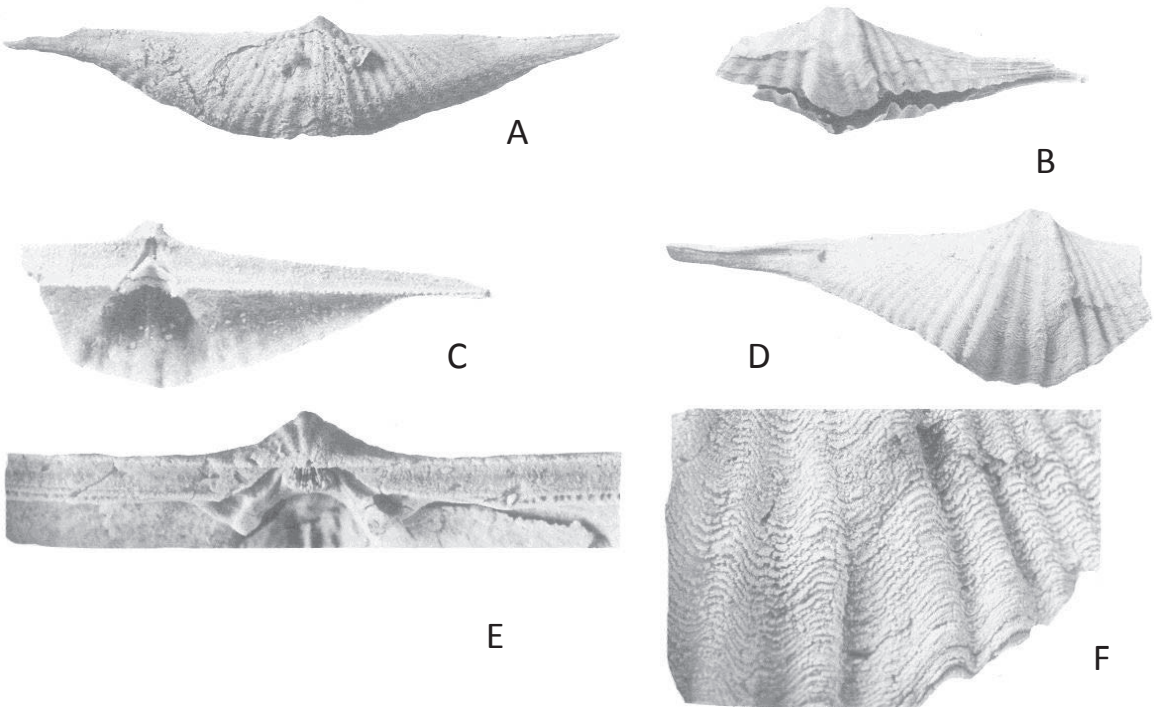


Fig. 182. *Johncarteria scalpata* (Cooper & Grant). A, B, dorsal exterior. B, ventral exterior. C, D, ventral interior with connector plate. D, ventral exterior, x1. E, detail of dorsal cardinalia, x3. F, micro-ornament, x6. From Appel Ranch Member, Texas, USA. (Cooper & Grant 1976).

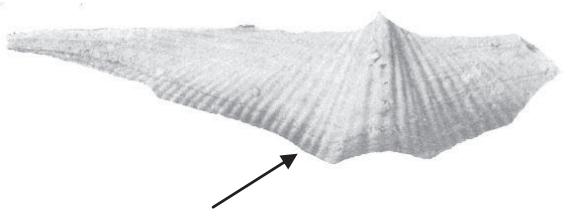


Fig. 183. *Johncarteria limata* (Cooper & Grant), ventral valve showing even subdivision of plicae, as arrowed. From Word Formation, Texas, x1.5. (Cooper & Grant 1976).

Haplospirifer Li & Gu, 1976 from the Cisuralian of China is transverse, and two or three costae of subequal strength arise anteriorly over the plicae, and conceivably the genus is closer to Fusispiriferinae (see p. 193). Published figures are obscure.

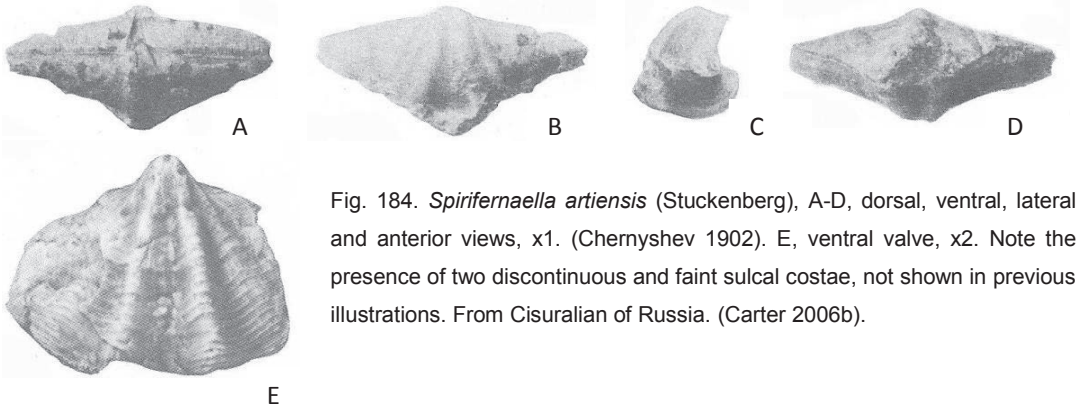


Fig. 184. *Spirifernaella artiensis* (Stuckenberg), A-D, dorsal, ventral, lateral and anterior views, x1. (Chernyshev 1902). E, ventral valve, x2. Note the presence of two discontinuous and faint sulcal costae, not shown in previous illustrations. From Cisuralian of Russia. (Carter 2006b).

Tipsispirifer Grant, 1976, p. 213 may belong to Pterospiriferinae, as assessed by Angiolini (2001, p. 340) and endorsed by Waterhouse & Chen (2007, p. 54). The type species comes from the Rat Buri Limestone of southern Thailand, of Roadian age (Waterhouse & Piyasin 1970), rather than the Artinskian age preferred by Grant (1976) and Carter (2006b). The genus was cast as Cyrtospiriferidae by Grant (1976, p. 213) on the basis of possible, but indefinite micro-ornament of papillae, and was recentred as Spiriferellidae by Carter (2006a, p. 1811). It differs hugely from both these subfamilies, and in its transverse outline,

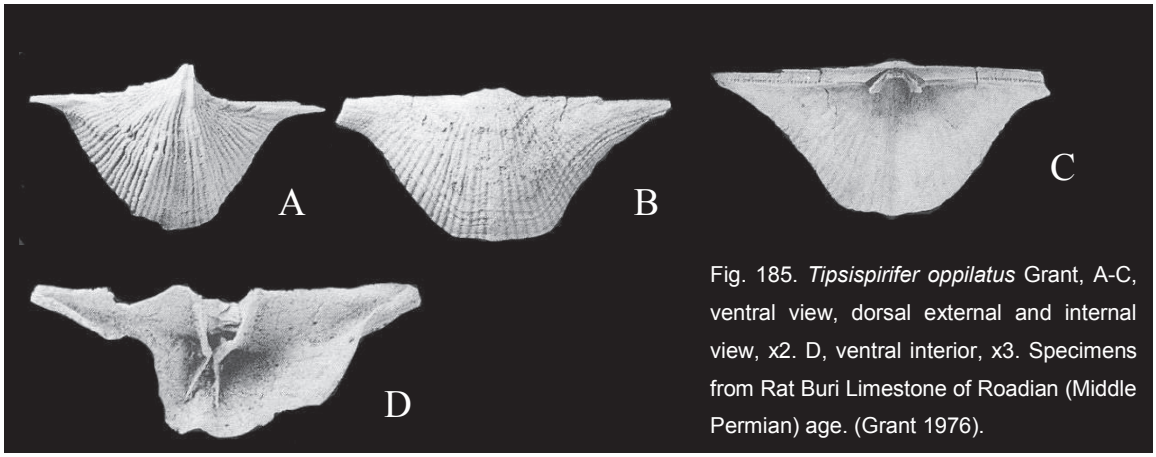


Fig. 185. *Tipsispirifer oppilatus* Grant, A-C, ventral view, dorsal external and internal view, x2. D, ventral interior, x3. Specimens from Rat Buri Limestone of Roadian (Middle Permian) age. (Grant 1976).

high ventral interarea, close-set costae without plication and high ventral plates, comes close to other genera within Paeckelmannelloidea, although costae bifurcate more than usual. Stegidial plates are well developed, but the presence of a connector plate is not certain. The details of costation are unique, and no other form is known to match this genus, so that it certainly reperesents a most interesting genus.

Pterospiriferinae seems to have been further misinterpreted in the *Revised Brachiopod Treatise* through the assignment of the Canadian Permian genus *Yukonospirifer* Shi & Waterhouse, 1996 to the subfamily by Carter in Gouvennec & Carter (2007, p. 2789). This genus, as made clear in the original description and illustrations, is syringothyrid in shape, ornament, interarea, delthyrium and interior. It is exceptional in the fine and weakly fasciculate costation and impunctate shell, implying that it may belong to a new subgroup, perhaps within Licharewiidae, perhaps allied to Syringothyridae, but in no way pterospiriferin, or paeckelmannelloid.

Subfamily **VOISEYELLINAE** new subfamily

Name genus: *Voiseyella* Roberts, 1963, p. 187 from lower Tournaisian – Visean of New South Wales, here designated.

Diagnosis: Small with simple ribs and sulcus smooth or with median rib. Adminicula, no median ventral septum. Crural plates. Upper Devonian (Famennian) to Lower Carboniferous (Serpukhovian).

Genera: *Voiseyella* Roberts (syn. *Amesopleura* Carter), *Acuminothyris* Roberts, *Avisyrinx* Martínez-Chacón, *Calvustrigis* Carter, *Cantabriella* Martínez-Chacón & Rio-García, *?Iwaispirifer* Tachibana, *Poletaevina* new genus.

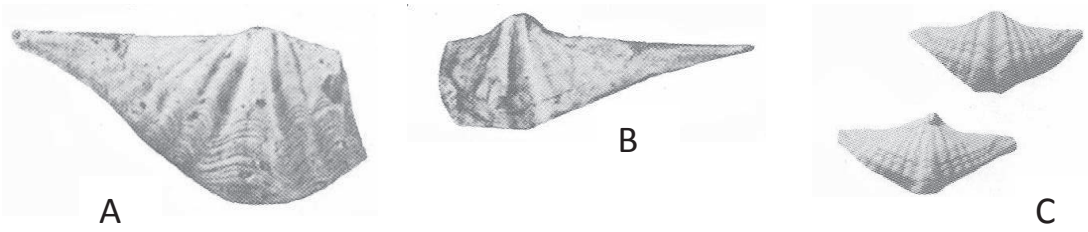


Fig. 186. A, B, *Voiseyella anterosa* (Campbell), dorsal and ventral views, x2. From Visean of New South Wales. (Roberts 1964). C, *V. novamexicana* (Miller), from Tournaisian of New Mexico, x1.5. This was originally proposed as *Amesopleura* Carter. (Carter 1967b).

Discussion: This subfamily is proposed for most of the genera referred to Strophopleurinae in the *Revised Brachiopod Treatise*. Unlike *Strophopleura*, its members have well developed adminicula. *Voiseyella* Roberts is particularly widespread, and its distribution and morphological variation were reviewed by Brice et al. (2005, p. 23). It is especially well known through the study on *Amesopleura*, a junior synonym, by Carter (1967b), which shows a

connector plate in sections. *Calvustrigus* displays a micro-ornament with small nodes at the intersections of radial and commarginal lirae, though Carter (2006b, p. 1812) stated that micro-ornament consisted only of radial capillae, in contradiction or possibly correction of his earlier assessment. There is a subdelthyrial connector plate, high adminicula, low crural plates and well formed spiralia.

The genus *Alatiformia* Struve, 1963 of Devonian (Emsian) age is transverse with long not rounded anterior lateral margins, like voiseyellin genera in shape, but has been classed in Spinocyrtiidae in the Treatise. It has a sulcate fold, like that of several paeckelmannelloid genera, and nodose growth lines close to members of Spinocyrtiidae. (See Fig. 165, p. 147), and also approaches *Arduspirifer* of Paraspiriferinae of Hysterolitoidea.

Genus ***Poletaevina*** new genus

Name: Named for Vladimir Poletaev.

Diagnosis: Transverse with narrow well defined fold bearing median groove, sulcus with or without median rib, interarea high, lateral plicae fine and numerous, rarely subdivide. Ventral interarea high and planar or concave, adminicula and dental plates high, crural plates well formed, myosepta (see Waterhouse & Chen 2007) may be developed.

Type species: *Spirifera rhomboidea* Phillips, 1836, p. 217, pl. 9, fig. 7 from Visean of England, here designated.

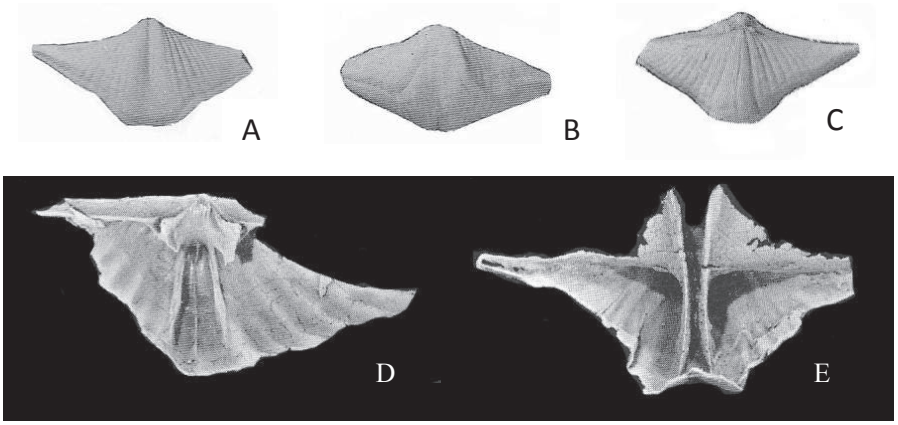


Fig. 187. *Poletaevina rhomboidea* (Phillips). A, ventral, B, anterior, and C, dorsal views of lectotype, x1. D, dorsal interior, x4, with long apparent myosepta. E, ventral interior, x4. From Visean of Yorkshire, England and Co. Fermanagh, Ireland. (Brunton & Rissoné 1976).

Discussion: This genus is well known thanks to study of the lectotype by Brunton & Rissoné (1976, pl. 1, fig. 13-17) with additional figures of specimens from Ireland (pl. 1, fig. 18, 19, text-fig. 1, 2). Those authors assigned the species to *Fusella* M'Coy, but the specimens are more inflated and larger and have a different fold, with more prominent crest divided by a slender median groove, whereas the fold of the type species of *Fusella, Spirifera fusiformis* (Phillips), is low with a broad median sulcus. Plicae of *fusiformis* are fine and low, whereas

plicae of *rhomboidea* are more emphasized and the innermost pair of plicae tends to be bifurcate. *Spirifer distans* J. de C. Sowerby, 1825, p. 152, pl. 12, fig. 3 is allied to *rhomboidea*, and is regarded as congeneric (see Brunton & Rissoné 1976, pl. 1, fig. 1-4). Figures have been repeated in Brunton (1984) and Carter (2006c). Poletaev (2001) pointed out that *rhomboidea* did not appear to be congeneric with *Fusella fusiformis*. Of other genera, the closest appears to be *Voiseyella* Roberts, with finer less marked median dorsal fold groove, lower ventral interarea, undivided inner plicae pair and shorter more divergent adminicula, whilst *Acuminothyris* Roberts is more transverse, and otherwise closer to *Voiseyella*.

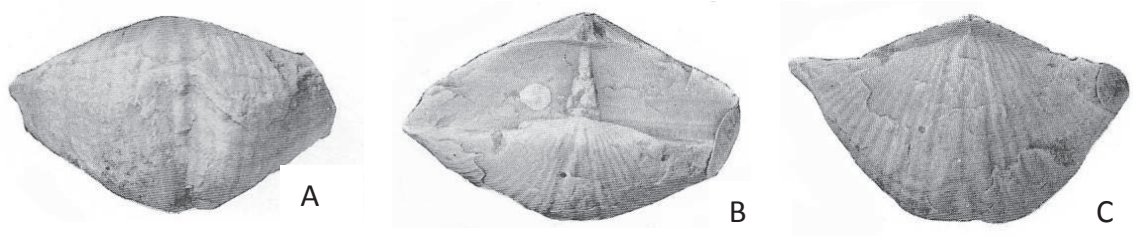


Fig. 188. *Poletaevina distans* (J. de C. Sowerby). A, anterior, B, dorsal posterior and C, dorsal views. From Visean of County Kildare, Ireland. (Brunton & Rissoné 1976).

Subfamily **BASHKIRIINAE** Nalivkin, 1979

[Nom. transl. Carter in Carter et al. 1994, p. 348 ex Bashkiriidae Nalivkin, 1979, p. 143].

Diagnosis: Fold and sulcus prominent with inconspicuous if any ribs, ventral interarea high. Lower Carboniferous (Tournaisian to Visean).

Genera: *Bashkiria* Nalivkin, *Fusella* M'Coy.

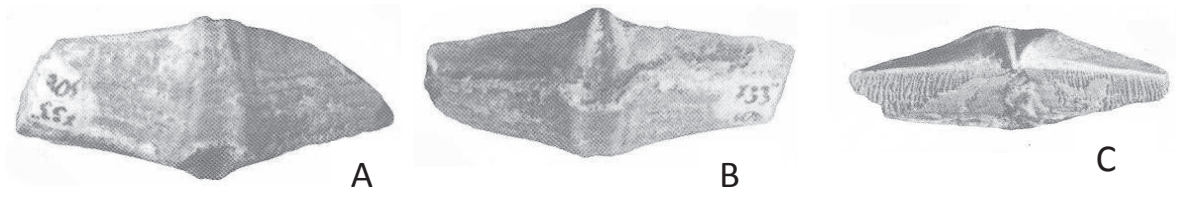


Fig. 189. *Bashkiria gemma* Nalivkin, dorsal, anterior and ventral aspects of holotype, x1. From Tournaisan of southern Urals. (Carter 2006b)

Discussion: The definition of Bashkiriinae in Carter (2006b, p. 1815) noted that lateral ribs were simple, as is true of Strophopleurinae and of Voiseyellinae, and stressed that fold and sulcus were ribbed. But there seem to be no ribs on the fold and sulcus of *Bashkiria* itself, as figured herein, based on the holotype. Carter also gave weight to the height of the ventral interarea, and this, together with the unusually extended shape and smooth sulcate fold and sulcus, would appear to offer the most unusual aspects of the genus. *Fusella* M'Coy is another shell of somewhat comparable appearance and this genus does have faint ribbing over the sulcus and fold. The interior for *Fusella* is not known. It had been extrapolated from a

different species by Brunton & Rissoné (1976) and Brunton (1984), but Poletaev (2001) has expressed doubt, and figures of the two different types in Brunton & Rissoné (1976) strongly suggest he was correct.

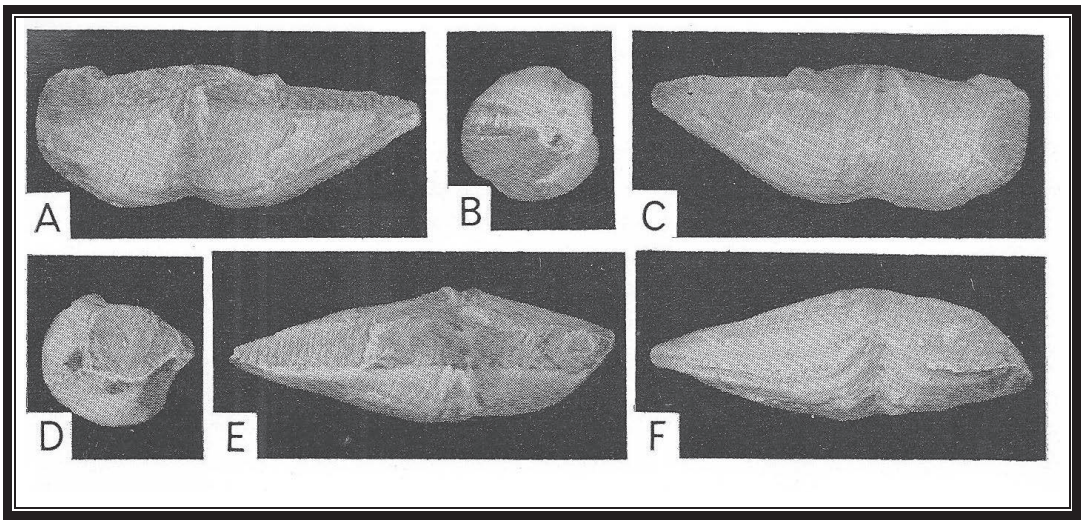


Fig. 190. *Fusella fusiformis* (Phillips), views of the original specimen. A, ventral tilted view. B, lateral view. C, dorsal view, showing sulcate fold. D, lateral view opposed to B. E, posterior view, dorsal valve below. F, anterior view, dorsal valve on top. Specimens x1.2, from Visean of England. (Waterhouse 1970).

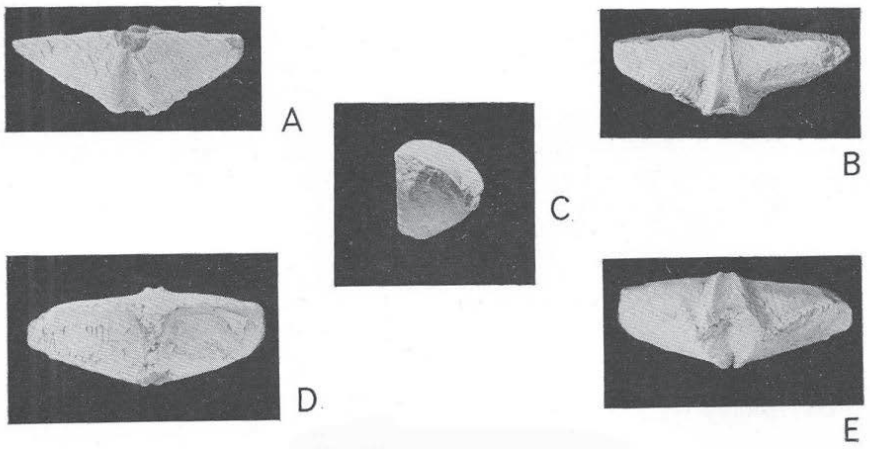


Fig. 191. Unnamed bashkirian species. A, ventral, B, dorsal, C, lateral, D, posterior and E, anterior views. Specimen BB40831 identified in collection as "*Spirifer cuspidatus* Phillips", which is *Syringothyris*, with round-crested fold, whereas the fold of this specimen is closer to that of *Fusella* and especially *Bashkiria*. The shell is impunctate, as confirmed by Brunton & Rissoné (1976, p. 282). Kept at Museum of Natural History, London, from Treak Cliff, Derbyshire, England (Visean). (Waterhouse 1970).

There is some similarity to *Avisyrinx* Martínez-Chacón from the Pennsylvanian of Spain, in that ribbing is subdued, and *Avisyrinx* has a high ventral interarea, although the shape is more triangular. A strong median rib lies along the midline, and adminicula are

very high, like those of *Fusella rhomboidea*. But that genus is retained in Voiseyellinae in view of its high round-crested fold.

Carter (2006b, p. 1815) referred *Adminiculoria* Waterhouse & Gupta (1979) to this subfamily, but *Adminiculoria* has no subdelthyrial plate, or delthyrial plate, displaying a prominent umbonal callosity below the beak, and is judged to belong to Angiospiriferidae Legrand-Blain. The shell is much less transverse and has a ventral interarea very much lower than in *Bashkiria*. Gourvennec in Gourvennec & Carter (2007, p. 2786) endorsed placement of *Adminiculoria* in Bashkirinae, but differences, including the delthyrial structures and vascular pattern, should not be set aside. Gourvennec referred *Varuna* Waterhouse, 2004 to the same subfamily, but this genus, with its costate plicae and well developed umbonal callosity with pleromal extensions, is trigonotretoid, and should not be referred to Strophopleuridae (see p. 247).

Superfamily **SPIRIFEROIDEA** King, 1846

Diagnosis: Transverse with costae and/or plicae, hinge line denticulate as a rule, connector plate and delthyrial cover plate common. Dental plates well developed, adminicula short, crural plates present and no tabellae. Upper Devonian (Famennian) to Upper Permian (Changhsingian).

Discussion: Spiriferoidea are a characteristic Late Paleozoic superfamily, many reaching a comparatively large size, and like other groups in that a wide hinge is common – just as for Cyrtospiriferoidea, Paeckelmannelloidea and Trigonotretoidea. A number of the genera assembled in Superfamily Spiriferoidea King, 1846 in the *Revised Brachiopod Treatise* do not belong to this superfamily, but to a different superfamily Trigonotretoidea, which gradually became costate to closely mimic spiriferoids. The two are largely similar in internal septation, and converge in external appearance, one from a plicate form, the other from costate shells, indicating that they arose from sources which diverged ultimately from a common or related ancestor. In both, sulcus and fold are well developed as a rule. Internally the well formed dental plates are supported by comparatively short adminicula, and socket and crural plates are well developed, with no tabellae. Although the difference between the two was downplayed in the *Revised Brachiopod Treatise*, Carter including Family Trigonotretidae in Spiriferoidea, the difference is further enhanced by the demonstration that trigonotretids have much branched mantle canal systems, approaching those of choristitids, whereas spirifers have a much denser less networked arrangement (Fig. 14, p. 20). In addition, the delthyrium of Spiriferoidea was closed by a delthyrial cover plate, and often a connector plate, whereas Trigonotretoidea had either an open delthyrium or rarely, one with stegidia, and an umbonal callosity, but as far as known never developed a connector plate or delthyrial cover plate. Carter has emphasized that Spiriferoidea possessed a denticulate hinge. But this is true of some Choristitoidea, Trigonotretoidea, and at least some Paeckelmannelloidea, and it appears likely that denticulation arose independently in several streams, including members of a different order, Spiriferinida. Spiriferinae King ranged from Tournaisian to Lopingian (Lower Carboniferous to Upper Permian), with mostly large shells and weakly fasciculate costae, and the more primitive Prospirinae Carter commenced in the upper Famennian. Family Imbrexiidae Carter, 1992, p. 327 was erected for middle to upper Tournaisian genera, but the group is so close to Spiriferinae, with shells more transversely subrectangular to subquadrate in shape, short delthyrial plate, mostly bifurcating costae, and cancellate ornament, and short to moderately long adminicula, that the two are merged: each has only a handful of genera. Gypospiriferinae Waterhouse, 2004 is of varied shape with better formed fascicles posteriorly, which tend to fade over the anterior shell, and the newly recognized subfamily Spiriferalariinae new has well formed persistent plicae. Fusispiriferinae Waterhouse, 2004 embraces very transverse shells, and all these latter groups have a connector plate.

Neospiriferidae Waterhouse is of Pennsylvanian to Permian age, with well formed and costate plicae, and cancellate micro-ornament, divided into Neospiriferinae

Waterhouse, 1968, Septospiriferinae new and Kaninospiriferinae Kalashnikov, 1996, the latter difficult to discriminate, but possibly defensible on the basis of having low dental plates. A delthyrial cover plate is developed, possibly adapted from a stegidium, or a deltidium formed in the delthyrium from inception. Some genera of this group lost their internal plates, and are classed in Alphaneospiriferinae.

The oldest known spiriferoid, in Subfamily Prospirinae Carter, is *Parallelora* Carter, a well known genus that was highly transverse in early growth stages, with well defined sulcus and fold, of uppermost Devonian and Early Carboniferous age. The brachiopods closest in morphology, and of slightly greater age, belong to Cyrtospiriferidae, which have comparable ornament and interior. There are clear differences, involving slightly different shape and high interareas, but the similarities are persuasive.

Family **SPIRIFERIDAE** King, 1846

[Family Spiriferidae King, 1846, p. 28].

Diagnosis: Usually transverse, lateral slopes and fold-sulcus costate or costellate, may be weakly associated in fascicles, micro-ornament of capillae and commarginal fila. Hinge denticulate, delthyrial cover moderately developed as a rule but weak or absent in Early Carboniferous members, better developed in younger members, mantle canal system impressions simple and mostly displaying closely spaced pits, rarely reinforced by a few radiating canals. Upper Devonian (Famennian) to Late Permian (Changhsingian).

Discussion: The presence of fine to coarse costae is characteristic of the family group.

Subfamily **SPIRIFERINAE** King, 1846

[Nom. transl. Waterhouse 1968, p. 9 ex Family Spiriferidae King, 1846, p. 28].

Diagnosis: Transverse, costae plain or in weak and relatively numerous fascicles. Delthyrial plate short to well developed, connector plate. Lower Carboniferous (Tournaisian) to Upper Permian (Changhsingian).

Tribe **SPIRIFERINI** King, 1846

[Nom. transl. hic ex Family Spiriferidae King, 1846, p. 28. Syn. Imbrexiinae Carter, 1992, p. 327].

Diagnosis: Transverse, costae plain or in weak and often numerous fascicles. Lower Carboniferous (Tournaisian) to Upper Permian (Changhsingian).

Genera: *Spirifer* J. Sowerby (subgenera *Grandispirifer* Yang, *Mesochorispira* Carter), *Fasciculatia* Waterhouse, *Fernglenea* Carter, *Imbrexia* Nalivkin, *Kosvaspirifer* Kalashnikov, *Lutuginia* Poletaev, *Tegulocrea* Carter.

Discussion: This tribe is centred on a genus based on large specimens with a short well developed delthyrial plate according to Carter (2006a, p. 1769). Whether this is a delthyrial cover plate was not made clear. Studies of *Spirifer* in various articles (Carter 1967b, Roberts 1971, p. 214) show a well developed connector plate. Thomas (1971, Fig. 27, 28) figured a

connector plate for Tournaisian species from Western Australia, with a fine connector plate illustrated for *Spirifer spiritus* Thomas (1971, p. 62, pl. 3, 3c, b, 4c). As far as is known, the hinge is denticulate. The subfamily would appear to have evolved from Prospirinae (p. 175) by increase in size and development of weak and multiple fasciculation. Only two valid genera were referred to Spiriferinae by Carter (2006a), because other genera referred to Spiriferinae by Carter (2006a, pp. 1769-1775) may be excluded, such as *Ectochoristites* Campbell and *Larispirifer* Enokian & Poletaev, both choristitid. So-called *Unispirifer heshilafuensis* Chen & Shi, 2003 from Visean-Serpukhovian of Kunlun Mountains of China has pleromal ridges, connector plate and is transverse with many fascicles, much as in *Grandispirifer* Yang, 1959 from Visean of China.

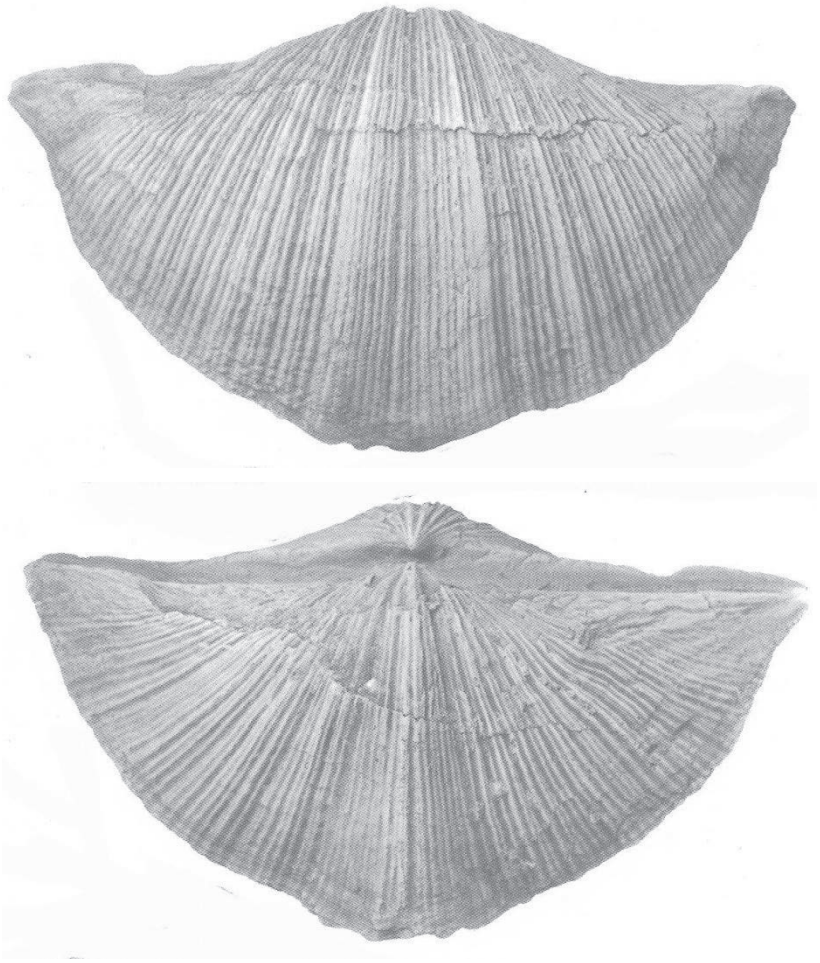


Fig. 192. *Spirifer* (*Spirifer*) *striatus* (Martin), ventral and dorsal views, x1, from Lower Carboniferous of United Kingdom. (Carter 2006a).

It is difficult to find justification for Family Imbrexiidae Carter, 1992, p. 327. This was diagnosed by Carter (2006a, p. 1786) as angularly subrectangular with strong simple or bifurcating costae. Three genera were recognized, *Imbrexia* Nalivkin (upper Tournaisian – Visean), *Fernglenia* Carter (mid to upper Tournaisian) and *Tegulocrea* Carter (upper

Tournaisian), and *Imbrexia* is especially close to *Spirifer*. There are small differences in the nature of the delthyrial development, costation and internal plates, well illustrated by Carter (2006a, Fig. 1182-1184). A short connector plate develops in *Imbrexia* and the other two genera, much as in *Spirifer*. Costae often bifurcate in *Imbrexia*, whereas some – but only some – in *Spirifer* appear to trifurcate, and other costae bifurcate. It is agreed that there is a difference, as far as known from type specimens, and it would certainly be worthwhile establishing the constancy of the pattern, and if it is constant, then *Fasciculatia* may be better placed in *Imbrexia*, which could be rated as a tribe Imbrexini. There are some seven to eight pairs of fascicles in *Imbrexia*, much as in *Spirifer*, and cancellate micro-ornament, strong commarginal laminae, and denticulate hinge. *Lutuginia* Poletaev, 1997 looks moderately like *Tegulispirifer* Poletaev, and has a well developed connector plate with pleromal ridges (Poletaev 1997, Fig. 3). Although classed in Neospiriferinae by Carter (2006a), it is very close to *Spirifer*, and comes from the upper Serpukhovian of the Ukraine.

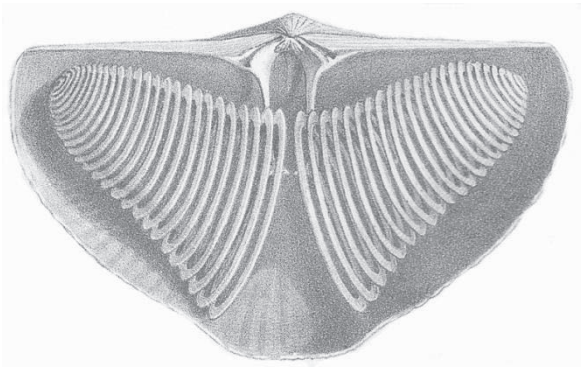


Fig. 193. The dorsal valve figured as *Spirifer striata* Martin var. *attenutata* Sowerby by Davidson (1858b, pl. 2, fig. 19), x1, from the Carbonferous Limestone at Kildare, Ireland. In front of the ctenophoridium lie the crural plates, which give rise to the spiralia. There are no tabellae.

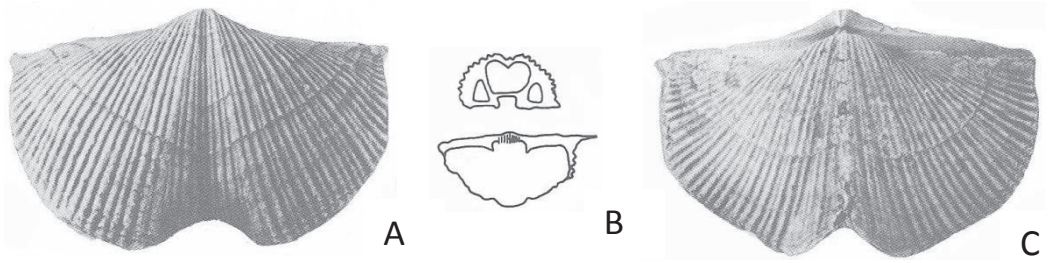


Fig. 194. *Imbrexia imbrex* (Hall). A, C, ventral and dorsal views, x1. B, transverse section, ventral valve on top, x1.5. From Burlington Limestone (Tournaisian), Missouri, USA, (Carter 1974).

Fasciculatia is based on moderately large and well preserved Late Permian

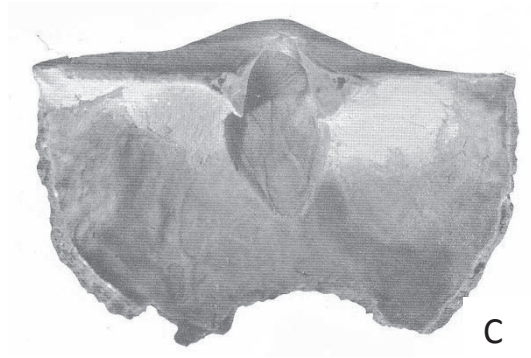


Fig. 195. A, B, *Fasciculatia* sp., internal and external ventral valve, x0.9 and 0.7. From Guadalupian of Arctic Canada. (Allan Miller, photo) C, topotype *Fasciculatia greenlandicus* Waterhouse, x1. From Late Permian Changhsingian of Greenland. (Dunbar 1955).

specimens described by Dunbar as *Spirifer striato-paradoxus* non Toula, and renamed *Fasciculatia greenlandicus* by Waterhouse (2004, pp. 95-99). It was confused with *Kaninospirifer* by Gourvennec in Gourvennec & Carter (2007, p. 1781), but Dunbar realized the similarity of his specimens to *Spirifer*. The fasciculation on the Greenland form is narrow, with six or seven pairs of fascicles, as well as faint subdivision of the broad plication next to the sulcus into three or four narrow fascicles. By contrast, the plication in *Kaninospirifer*, especially well illustrated in Grunt (2006, pl. 14, fig. 1, pl. 15, fig. 1, 2) from Kanin Peninsula, is exemplified by broad rolling plicae in three or four pairs, diminishing in strength laterally, and the innermost pair split, if at all, into two subdivisions only (Fig. 250, p. 204). The difference in plication-fasciculation is marked.

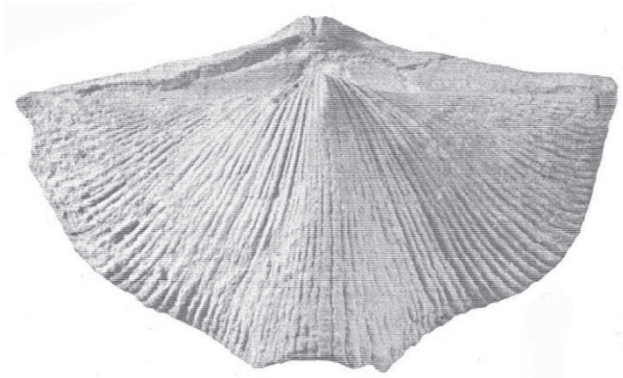


Fig. 196. A, B, *Fasciculatia greendlandicus* Waterhouse, ventral and dorsal views, x0.7 and x1. From Late Permian of Greenland. (Dunbar 1955).

Kosvaspirifer Kalashnikov, 2003, type species *K. kosvensis* (Fotieva in Nalivkin & Fotieva 1973), was omitted from the *Revised Brachiopod Treatise*, and figures are offered. There is no sign of a connector plate, which might be considered to point to Prospirinae (p. 175), but costae are fine and well developed.

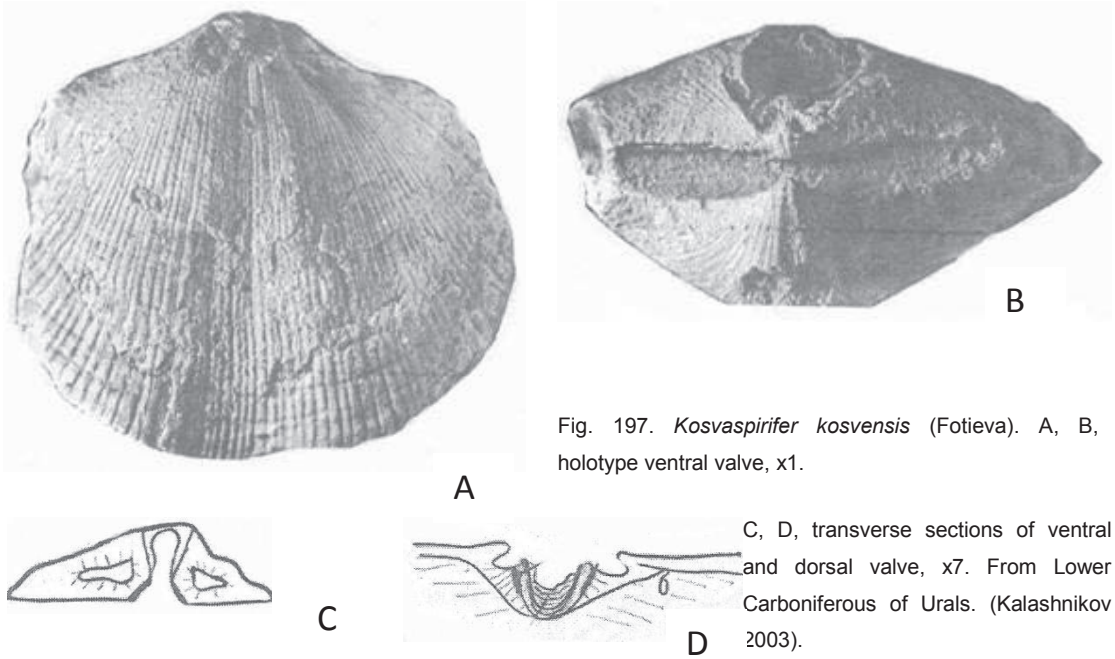


Fig. 197. *Kosvaspirifer kosvensis* (Fotieva). A, B, holotype ventral valve, x1. C, D, transverse sections of ventral and dorsal valve, x7. From Lower Carboniferous of Urals. (Kalashnikov 2003).

Tribe **DONISPIRIFERINI** new tribe

Name genus: *Donispirifer* Poletaev, 2000b, p. 279 from Moscovian beds of Ukraine, here designated.

Diagnosis: Small subrectangular shells, with obtuse cardinal extremities, sturdy ribs and weak fasciculation. Pennsylvanian (Bashkirian to Gzhelian).

Genera: *Donispirifer* Poletaev, *Pristinusia* new genus, *Saltospirifer* Cisterna & Archbold.

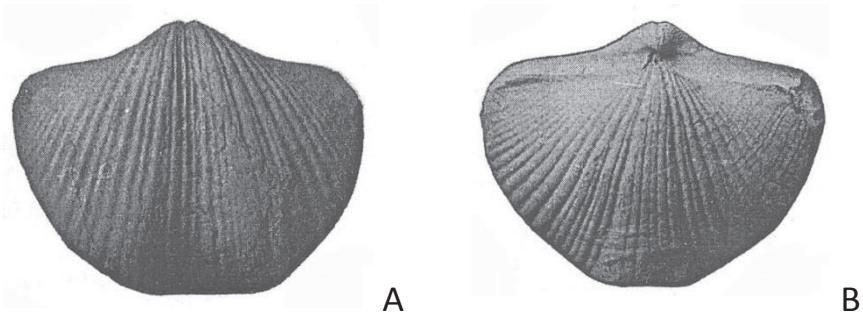


Fig. 198. *Donispirifer toretzensis* Poletaev, ventral and dorsal views of holotype, x1. From Moscovian of Ukraine. (Poletaev 2000b).

Discussion: Genera such as *Donispirifer* and *Pristinusia* differ from *Gypospirifer* in having fascicles that persist as far as or almost as far as the anterior margin. They are of Middle

Carboniferous age, and are close to members of Spiriferini but smaller, with poorly defined fascicles of bifid and even trifid costae.

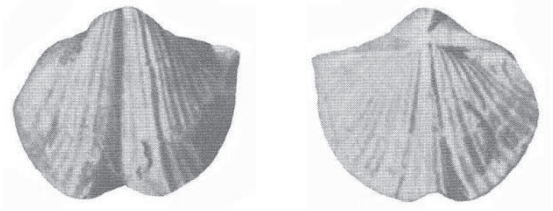


Fig. 199. *Donispirifer baschkovensis* (Rotai), ventral and dorsal views of holotype, x1. From Moscovian of Ukraine. (Carter 2006a).

Saltospirifer Cisterna & Archbold (2007) from Argentina shows a similar number of subdued fascicles, with slightly different costation. It has pleromal plates and thick connector plate. The authors rated the lower Del Salto Formation, source of the genus, as of Sakmarian age. But the formation lies below beds with the palynomorph *Pseudoreticulatispora confluens*, which entered the world succession in late Carboniferous (Stephenson 2009), and is found especially in Asselian (basal Permian) and more rarely in Sakmarian faunas of Australia (Waterhouse 2015a, p. 41, Table 15, p. 36). Del Salto faunas include the Late Carboniferous brachiopod *Auriculispina*. The evidence for a Late Carboniferous is discussed more fully in Waterhouse (2015a, pp. 41, 42), and has radiometric support (Césari et al. 2011).

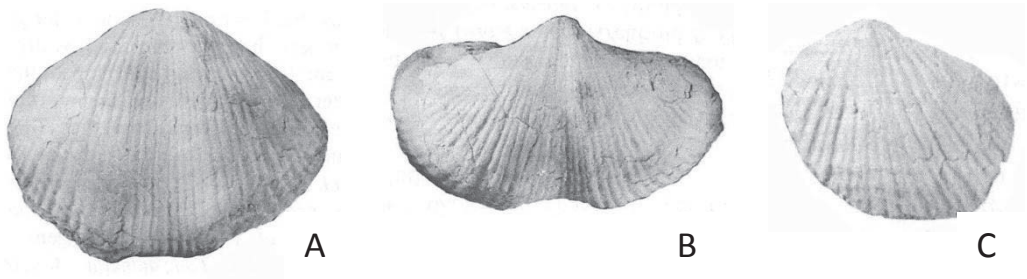


Fig. 200. *Saltospirifer guevarii* Cisterna & Archbold. A, B, ventral valve aspects, x0.9. C, dorsal valve x1. From lower Del Salto Formation, Argentina. (Cisterna & Archbold 2007).

Genus ***Pristinusia*** new genus

Derivation: pristinus – original, pristine, Lat.

Type species: *Neospirifer pristinus* Maxwell, 1951, p. 15 from the lower Branch Creek Formation (Bashkirian-Moscovian?), Yarrol Basin, Queensland, here designated.

Diagnosis: Small subelongate shells with well formed sulcus and moderately distinct fold, obtuse cardinal extremities, numerous costae, weak fascicles with costae splitting into three or usually two near sulcus and fold, especially over anterior shell, delthyrium open, low umbonal callosity in few specimens, dental plates and adminicula low, muscle field impressed in floor of valve, dorsal valve with low crural plates, socket plates, median septum and muscle imprints.

Discussion: *Pristinusia* is close to *Spirifer* Sowerby, 1816 and the subgenus *Grandispirifer* Yang, 1959, but is much less transverse and without strongly alate cardinal extremities and with fewer and less marked fascicles. *Mesochorispira* Carter, 1992 is closer to the new form in its rounded cardinal extremities. These taxa are of Tournaisian and Visean age, whereas the new genus is distinctly younger, at late Serpukhovian or more likely Bashkirian to Moscovian in age. The internal plates are much the same, although the muscle field is less surrounded by high ridges. The presence of an umbonal callosity appears to vary in different specimens, and preservation is such that no delthyrial cover, if it ever existed, has been preserved.

Pristinusia pristinus (Maxwell, 1951)

1951 *Neospirifer pristinus* Maxwell, p. 15, pl. 3, fig. 1-8, pl. 4, fig. 1-4.

1962 *N. pristinus* – Campbell, p. 45, pl. 11, fig. 4-7.

1964 *Spirifer pristinus* – Hill & Woods, pl. 11, fig. 16-18.

1965 *N. pristinus* – McKellar, pl. 4, fig. 10, 11.

1972 *S. pristinus* – Hill, Playford & Woods, pl. 11, fig. 16-18.

1976 *S. pristinus* – Roberts et al., p. 218, Fig. 13.

Holotype: UQF 2005a, b, figured by Maxwell (1951, pl. 3, fig. 4) from Branch Creek Formation (Bashkirian-Moscovian), Yarrol Basin, Australia, OD.

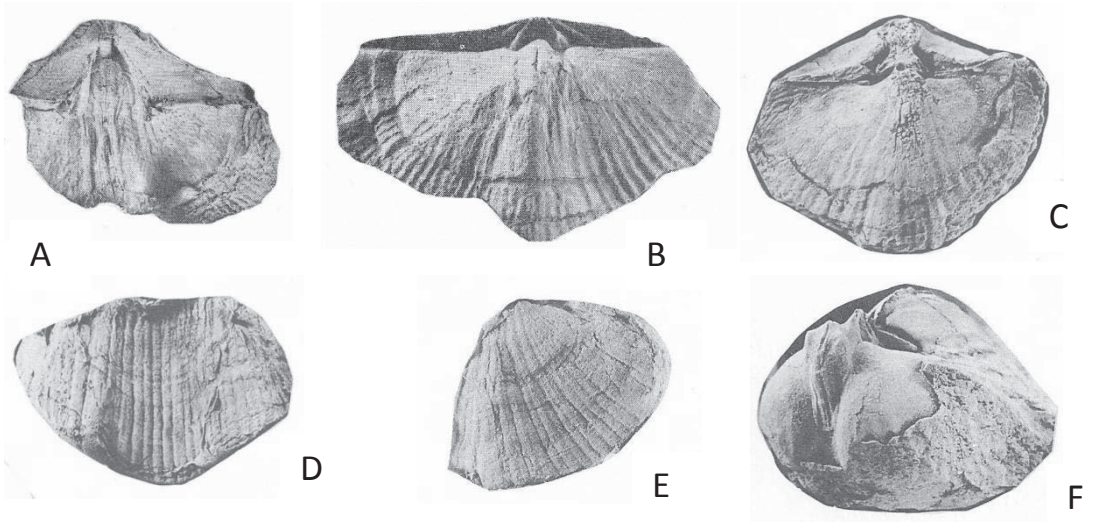


Fig. 201. *Pristinusia pristinus* (Maxwell). A, cast of ventral interior, showing a small umbonal callosity and indicating the lack of delthyrial cover plate. Other specimens lack an umbonal callosity. B, internal dorsal mould. (Hill & Woods 1964). C-F, material from New South Wales. C, D, dorsal view of internal mould and plasticine cast of ventral exterior. E, latex cast of dorsal exterior. F, internal mould of specimen with valves conjoined. Specimens x1. From Middle Carboniferous of east Australia. (Campbell 1962).

Diagnosis: Medium-sized, subelongate, with comparatively short hinge bearing rounded cardinal extremities or slightly produced in small ears, costae entire, trifurcate near sulcus and mostly bifurcate in sulcus and fold, producing very subdued fascicles. Internal ventral valve

ridged along sulcus and each side of muscle field. Short connector plate possibly present, but in need of confirmation.

Discussion: The species has been described and figured as a distinctive form from the Branch Creek and Neerkol Formations of the Yarrol Basin in Queensland, and from the glacial rocks of the Kullatine Series of northeast New South Wales. Specimens from the Yagon Siltstone of New South Wales that were ascribed to the species by Roberts et al. (1976, p. 219, Fig. 13) are a little more transverse with shallower sulcus and more distinct fascicles and ventral muscle field not edged by high ridges. These authors pointed to strong similarities with *Neospirifer tomskiensis* Benediktova as figured by Kotlyar & Popeko (1967, pl. 43, fig. 1-6) from Lake Baikal, and the Baikal specimens are much closer to the Yagon material in shape, although it is true that the ventral muscle field is edged by high ridges. There is considerable approach to material from the Pampa de Tepuel Formation of Argentina that was figured as Spiriferidae indet. spp. by Pagani & Taboada (2010, Fig. 10.1-9).

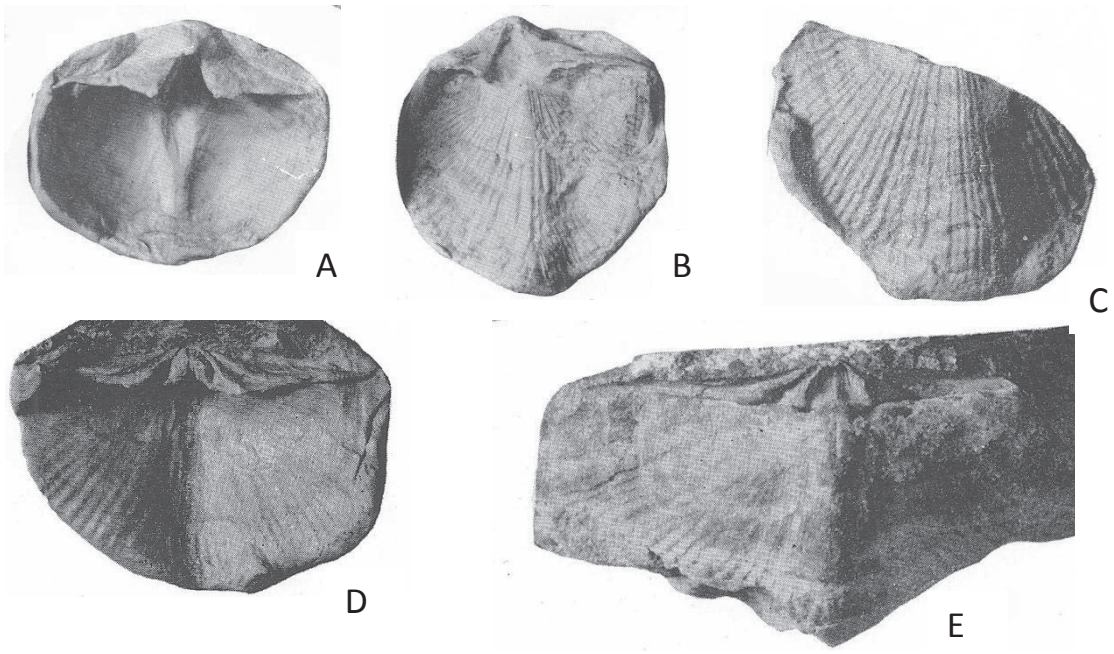


Fig. 202. *Pristinusia pristinus* (Maxwell). A, ventral cast showing interior, x0.75, B, dorsal valve nestling inside ventral valve, x0.75. These specimens lack an umbonal callosity. C, dorsal exterior (stated to be ventral valve in original article), x1. D, internal cast and internal mould of dorsal valve, x1. E, dorsal internal mould, x1. The casts were prepared from plasticine. From mid-Carboniferous (Bashkirian or Moscovian?) of Yarrol Basin, Queensland. (Maxwell 1951).

Donispirifer Poletaev, 2000b, type species *Spirifer* (*Neospirifer*?) *baschkovensis* Rotai from Moscovian beds of the Donets Basin is very close in its ornament, bearing a number of persistent fascicles, and having the ventral muscle field bound by high ridges. The genus was placed in Prospirinae by Carter in Gourvennec & Carter (2007, p. 2781), but is elongate and has a number of weakly defined fascicles, as in Spiriferinae and many Gypospiriferinae. The two genera are moderately similar in shape, but details of costation, fasciculation and sulcus/fold differ. Poletaev (2000b) proposed that the delthyrium was bordered by what he

called hypodeltidial grooves, the inner sides of which fused to form a so-called stegidial platform. The transverse sections suggest that this so-called stegidial platform matches the connector plate in various Spiriferida. It joins the dental plates, and is not related to any stegidial plate.

There is some approach to Lower Carboniferous species, such as that described as *Spirifer esplanadensis* Brown (1952, pl. 5, fig. 1a-e) from Tournaisian beds of the Banff Formation in Canada (Carter 1987, pl. 25, fig. 1-23, Fig. 22), but costae are wide in the Canadian species and divided by narrow grooves, and the sulcus and fold are less developed. A low subdelthyrial plate is developed.

Kinghiria Litvinovich, 1966 of Prospirinae from Visean beds of Kazakhstan is close in overall shape and other detail, but the anterior costae sustain much less splitting.

Subfamily **PROSPIRINAE** Carter, 1974

[Subfamily Prospirinae Carter 1974, p. 680].

Diagnosis: Early growth stages transverse, varying in shape for later growth stages, costae or subplicae simple and moderate in number to numerous. Upper Devonian (upper Famennian) to Middle Carboniferous (Moscovian).

Genera: *Prospira* Maxwell, *Andreaspira* Abramov & Grigorieva, ?*Celsifornix* Carter, *Eobrachythyris* Brice, *Finospirifer* Yin, *Kinghiria* Litvinovich, *Parallelora* Carter (syn. *Mariona* Nalivkin, obj.), *Unispirifer* Campbell, *U*. (*Atylephorus*) Sartenauer & Plodowski, *U*. (*Septimispirifer*) Shi, Chen & Zhan.

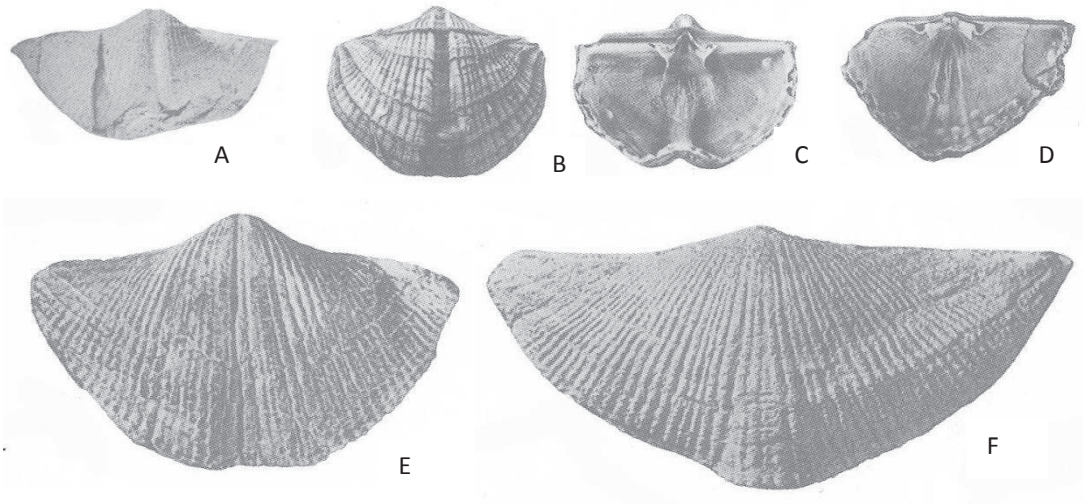


Fig. 203. Members of Prospirinae. A, *Prospira typa* Maxwell, ventral valve x1. From Tournaisian of Yarrol Basin, Queensland, Australia. B-D, *Parallelora marionensis* (Shumard), ventral, ventral interior and dorsal interior views, x1. From Upper Devonian of Missouri, United States. (Carter 1974). E, F, *Unispirifer convolutus* (Benson & Dun), ventral and dorsal aspects, x1. From Tournaisian of New South Wales, Australia. (Campbell 1957).

Discussion: *Prospira* Maxwell is a distinctive Tournaisian genus from east Australia, and has a moderately well defined sulcus and well defined fold, both costate, and ornament of

numerous narrow ribs which become finer laterally, sulcus and fold, and umbonal callus. There are stegidial plates, and pleromal ridges along the inner side of the dental plates, which fuse under the umbo. Whether a connector plate is developed is not clear, and the presence of an umbonal callosity has to be regarded with misgivings, because it raises questions about the relationship to other genera. A connector plate is widely present in other genera, including *Unispirifer*, Campbell (1957, text-fig. 11) showing adminicula that converged inwards from the floor of the valve to fuse medianly, although no broad plate was developed. Carter (1987, pl. 23, fig. 3) illustrated a connector plate for *U. minnewankensis* (Shimer) from Canada, and a connector plate was figured for *Prospira incerta* Thomas by Roberts (1971, fig. 60.29).

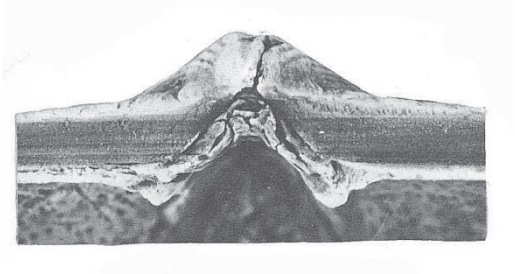


Fig. 204. *Parallelora marionensis* (Shumard), showing fine denticulation on the left side of the figure, and parts of stegidial platelets along borders of the delthyrium, x3. From Louisiana Limestone, Missouri, United States. (Famennian). (Carter 1974).

Carter (2006a, p. 1777) suggested that *Lytha* Fredericks, 1924, based on *Spiriferella tschernyschewiana* Fredericks (1916, p. 30), might prove to be senior synonym of *Unispirifer.* But as figured by Fredericks (1916, pl. 1, fig. 1-5), the Russian genus looks like a syringothyrid, and appears to have a smooth sulcus and large subdelthyrial plate. *Andreaspirifer* Abramov & Grigorieva and *Kinghiria* Litvinovich have strong posterior thickening, as well as distinctly coarse ribbing, like that of *Parallelora* Carter, a well known genus definitely spiriferid in its internal detail. *Subspirifer* Shan & Zhao is different again, and regarded as a member of Paeckelmannelloidea, as senior synonym of *Triangularia* Poletaev, but was included in Prospirinae in the *Revised Brachiopod Treatise.*

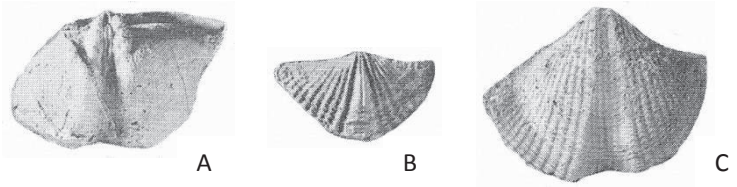


Fig. 205. *Prospira*. A, C, *P. typa* Maxwell. A, ventral internal mould. C, dorsal internal mould. B, *P. typa tellebangensis* Maxwell. Specimens x1, from upper Tournaisian of Queensland. (Hill & Woods 1964).

The presence of hinge denticulation along the hinge is not firmly established for all genera, although Carter (2006a, p. 1769) stipulated that it was a mandatory attribute of the superfamily, and denticulate examples are to be found in *Parallelora*, and in *Unispirifer minnewankensis* (Shimer) as figured by Carter (1987, pl. 23, fig. 2, 3) from Alberta, Canada. Specimens described as *Unispirifer* Campbell from Western Australia by Thomas (1971)

include a number that are denticulate along the hinge (see Thomas 1971, pl. 2, fig. 1, 5; pl. 3, fig, 1a, 1b), unless the denticles are due to a weathering effect, which does seem possible because other specimens lack clearly defined denticles. Shi et al. (2003) recognized two subgenera of *Unispirifer*, *Atylephorus* Sartenauer & Poletaev, 1996 and *Septimispirifer* Shi et al, but neither subgenus was mentioned in the *Revised Brachiopod Treatise*. *Finospirifer* Yin, 1981 is a transverse Tournaisian genus from Hunan, with moderately coarse plicae and a few secondary costae, and high fold. A well developed connector plate lies between the adminicula and dental plates.

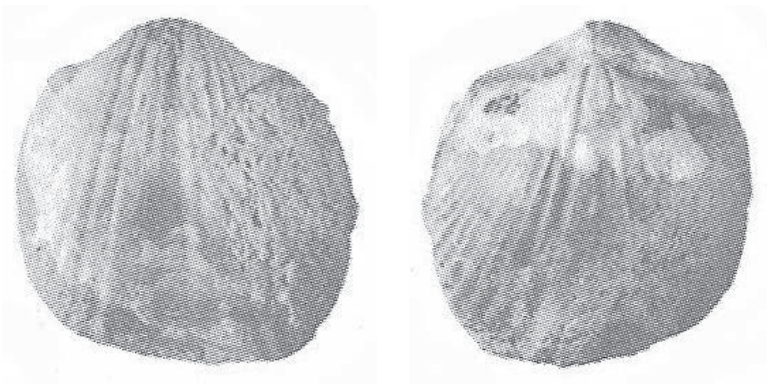


Fig. 206. *Eobrachythyris proovalis* Brice, holotype, ventral and dorsal views x2. From Famennian of Afghanistan. (Carter 2006a).

Brice & Nicollin (2000) and Carter (2006a, p. 1779) referred *Eobrachythris* Brice, 1971 to Sergospiriferinae, as a somewhat rounded shell with weaker plicae and strong radial capillae. Gourvennec in Carter & Gourvennec (2007, p. 2781) reiterated this position and noted that the delthyrial plate was either lacking or rudimentary and buried in apical callus. Brice & Nicollin (2000) had stated that the delthyrial plate (nature unspecified) was absent or rudimentary near the apex, embedded in callosity, which does not read like the connector plate apparatus apparently typical of *Sergospirifer.* The genus ranges from Upper Devonian (Famennian) into Lower Carboniferous (Tournaisian). Prospirinae would seem an equally if not more valid candidate for the genus. It is true that more needs to be known about the delthyrial region for the type species of both subfamilies, and given such uncertainty, it may be preferred to rely at least meanwhile on shape and ornament, two parameters that appear to point to Prospirinae, a position preferred by Brice (1997).

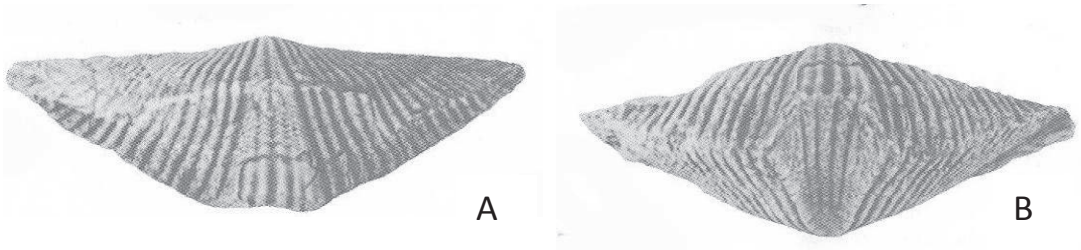


Fig. 207. *Celsifornix rowleyi* Carter, dorsal and anterior views of holotype, x1, from Tournaisian of Missouri, Illinois, United States. (Carter 1974).

Celsifornix Carter, 1974 from Tournaisian beds of Missouri and Illinois is a well preserved closely studied genus with connector plate, rather like the Devonian genus *Hispidaria* Cooper & Dutro in shape and ornament (see p. 145), but without tubercles. *Celsifornix* was classed as Bashkiriinae by Carter (2006b, p. 1815) but has strong ribs, including several over the sulcus and fold, unlike *Bashkiria*. But it is also unlike members of Voiseyellinae, or Strophopleurinae in its strongly costate sulcus and fold, and possibly should be classed in a tribe of its own. In many ways it is rather like members of Cyrtospiriferidae in ribbing, resembling for example *Austrospirifer* Glenister of Famennian age in Western Australia, but may have been closer to *Unispirifer* Campbell.

Subfamily **SERGOSPIRIFERINAE** Carter, 1994

[Sergospiriferinae Carter, 1994, p. 343].

Diagnosis: Cardinal extremities rounded in juveniles. Sulcus and fold ribbed, derived from bounding plicae, lateral slopes with few simple or bifurcating plicae. Micro-ornament of capillae and commarginal lirae. Delthyrium open with more or less developed connector plate. Upper Devonian? (Famennian) to Middle Carboniferous (Moscovian).

Genus: *Sergospirifer* Ivanova (syn. (?) *Anthracospirifer* Lane, *Plicatocyrtia* Gauri).

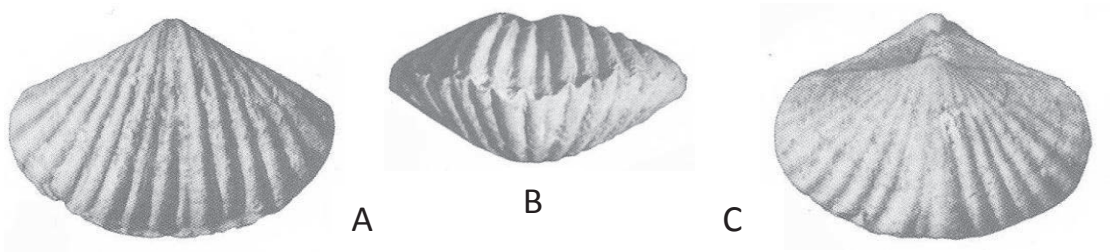


Fig. 208. *Sergospirifer okensis* (Nikitin). A, ventral, B, anterior and C, dorsal views, x2. Note the sulcal rib on the right in A, which commences close to the anterior margin, whereas the rib on the left commences much closer to the umbo. Both branch from the sulcal border rib. From upper Moscovian of the Moscow Basin, Russia. (Carter 2006a).

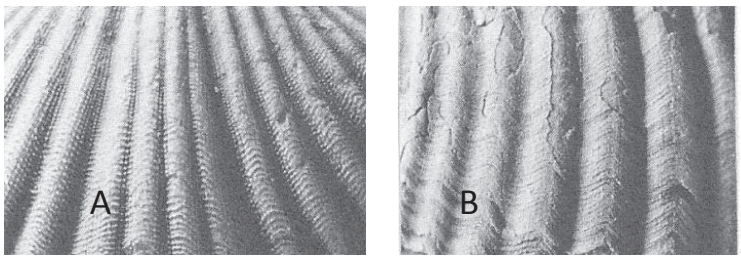


Fig. 209. Micro-ornament x4 for A, *Anthracospirifer curvilateralis tanoensis* and B, *A. curvilateralis chavezae* from Pennsylvanian of New Mexico. Named by Sutherland & Harlow (1973).

Discussion: *Sergospirifer* looks very like members of the Angiospiriferinae Legrand-Blain, with their strong ribbing which covers all of the valve, including sulcus and fold, and arguably, insufficient data has been recorded to distinguish the subfamily from Legrand-Blain's group. Indeed Thomas (1971) considered that *Spirifer bisulcatus* belonged to *Anthracospirifer,* whereas the species is classed now as *Angiospirifer* by Angiolini et al. (2011). Even so,

Thomas (1971, p. 99) recorded a small delthyrial plate in his species *Anthracospirifer milliganensis* from Western Australia, based on interpretation of transverse sections, which it has to be said, are obscure, and which indicate a converging of dental plates, rather than a clear plate – let alone a delthyrial cover plate. If a connector plate is present in *Sergospirifer*, it would suggest a family unit within Spiriferoidea, developed from Prospirinae by strengthening

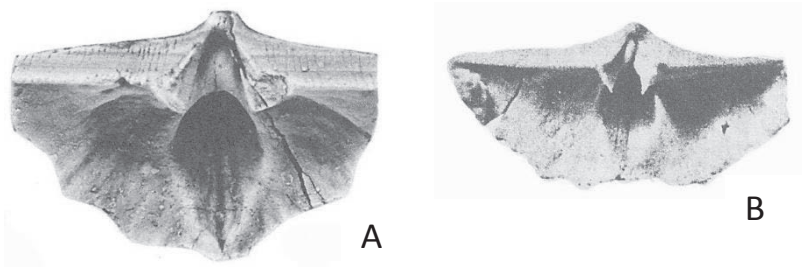


Fig. 210. The delthyrium in *Anthracospirifer*. A, *A. newberryi* Sutherland & Harlow, x3. From lower Pennsylvanian of New Mexico, USA. (Sutherland & Harlow 1973). B, *A. occiduus* (Sadlick). From Nevada, USA. (Lane 1962).

of the ribs, rather than a member of Angiospiriferinae, which generally has an umbonal callosity. A delthyrial plate of unspecified nature was also indicated as characteristic of the *Anthracospirifer* by Legrand-Blain et al. (1984, p. 306). That observation is partly supported by a figure in Sutherland & Harlow (1973, pl. 16, fig. 4), which shows the delthyrium in *Anthracospirifer newberryi* with no umbonal callosity (Fig. 210A). Yet *Anthracospirifer occiduus* (Sadlick) is figured with a well developed umbonal callosity by Lane (1962, pl. 128, fig. 3), as shown in Fig. 210B. Neither species is type of the genus. Some of the species assigned to *Anthracospirifer* may be angiospiriferid, and others close to *Sergospirifer*.

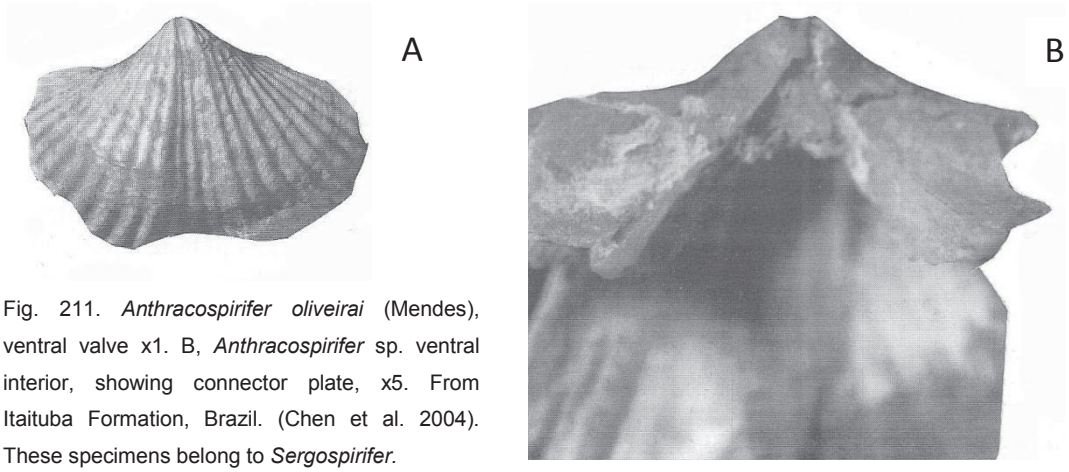


Fig. 211. *Anthracospirifer oliveirai* (Mendes), ventral valve x1. B, *Anthracospirifer* sp. ventral interior, showing connector plate, x5. From Itaituba Formation, Brazil. (Chen et al. 2004). These specimens belong to *Sergospirifer*.

Important evidence is provided by material from the Itaituba Formation of the Amazon Basin in Brazil. Chen et al. (2004) redescribed *Anthracospirifer olivierai* (Mendes, 1956) and *Anthracospirifer* sp. which belong most likely to *Sergospirifer*, and have a well developed connector plate and pleromal ridges lying along the junction between the dental plates and adminicula. The ribs in the various specimens agree closely with the arrangement in type

Sergospirifer. Of course they are not type material, but subject to this provision, do support the validity of Sergospiriferinae and its distinction from Angiospiriferinae.

Carter (2006a, p. 1778-1779) distinguished *Sergospirifer* from *Anthracospirifer* by emphasizing that the costae, which vary in strength from narrow to very strong or even narrow plicae bounding the sulcus "invariably" bifurcated in *Anthracospirifer*, and remained simple in *Sergospirifer.* But even the figures of the two genera in the *Revised Brachiopod Treatise* give pause for thought over this criterion. The figure of type *Sergospirifer* (Carter 2006a, Fig. 1172.1a) shows the rib within and on one side of the sulcus commencing a few mm in front of the ventral umbo, and on the other side, the matching rib commences well in front of the umbo, near the anterior margin. Both branch off from the sulcal bounding rib. The more obvious difference between the two type species lies in the way lateral plicae bifurcate in the type species of *Anthracospirifer, birdspringensis* Lane, with rare lateral splits and even

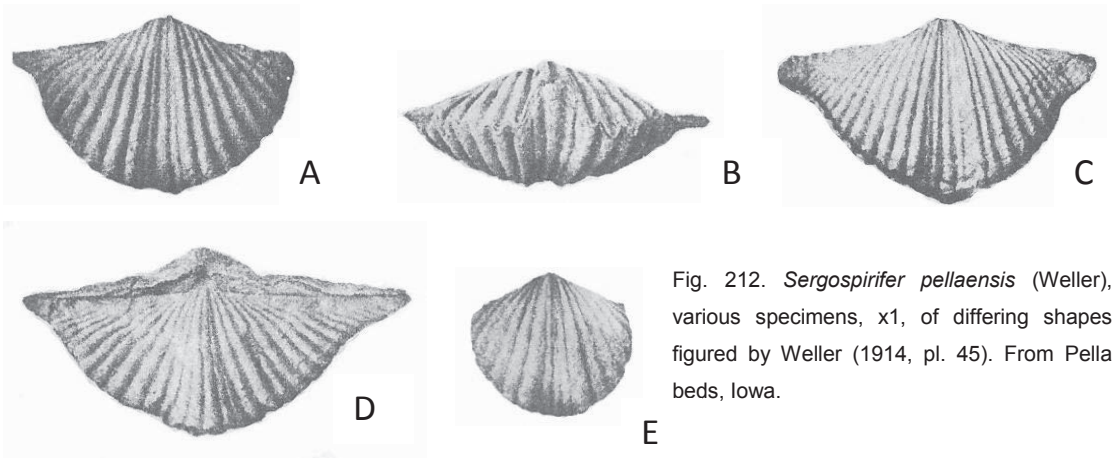


Fig. 212. *Sergospirifer pellaensis* (Weller), various specimens, x1, of differing shapes figured by Weller (1914, pl. 45). From Pella beds, Iowa.

interstitial ribs, but not in *Sergospirifer okensis* Nikitin. Or is this just a criterion of specific importance? Sutherland & Harlow (1973, pl. 15, 16, 17) figured a number of different species and subspecies of *Anthracospirifer* from New Mexico, and in a number of specimens, the ribs inside the sulcus commence very close to the umbo and vary in others. Most but not all have a central rib. Thomas (1971, p. 97) stated that judged from his examination first hand of *Anthracospirifer* species in North America, the ribbing remained simple in many species, or only divided near the umbo. Indeed, he evidently overlooked the genus *Sergospirifer*, to which his species should be referred, according to the definition by Carter (2006a).

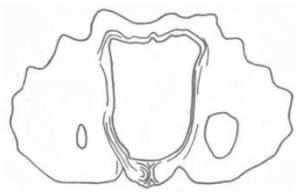


Fig. 213. *Anthracospirifer ouarkzizensis* Legrand-Blain, transverse section through ventral valve, x2. From Serpukhovian of Sahara. Other diagrams show no median join. (Legrand-Blain 1986). The species seems likely to belong to *Sergospirifer.*

In *Spirifer pellaensis* Weller, 1914, which has been assigned to *Anthracospirifer* by Legrand-Bain (1985), there are well spaced commarginal rows of pustules and feeble development of

commarginal laminae. Wulff (1990) has provided statistical analysis of the variation in shape and other criteria for material assigned to the species *pella*. She provided a number of serial sections. The sections do not show the adminicula and seem to pass along the dental plates across the delthyrium.

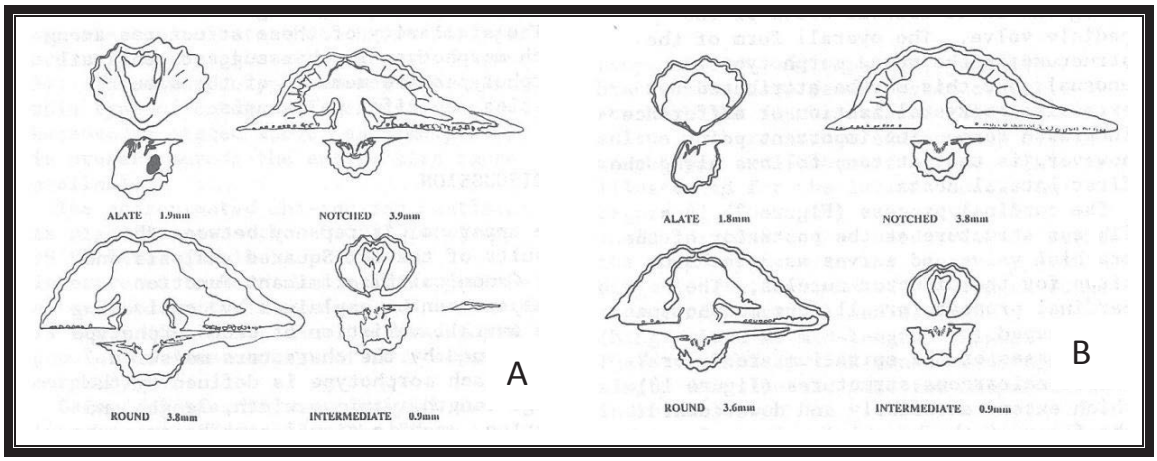


Fig. 214. *Sergospirifer pella* (Weller), transverse sections prepared by Wulff (1990) from material in Pella beds of Iowa (Meramecian, Mississippian).

Spirifer zitteli Schellwien (1892, pl. 4, fig. 6-10), cited as type species of *Plicatocyrtia* by Gauri (1965, p. 55, pl. 2, fig. 10-12) and synonymized with *Anthracospirifer* by Carter (2006a), shows two ventral valves with smooth sulcus. The ribs bordering the sulcus do not branch, whereas some of the lateral costae do (Schellwien 1892, pl. 4, fig. 6, 7). But another specimen has several ribs branching off the sulcal border rib (Schellwien 1892, pl. 4, fig. 10). Gauri (1965) cited the specimen figured in Schellwien (1892, pl. 4, fig. 8) as lectotype for *Plicatocyrtia*, refiguring it (pl. 2, fig. 11, 12) together with another specimen. The ribs over sulcus and fold are finer than in *Sergospirifer-Anthracospirifer*, and so indicate difference from the type species of *Sergospirifer* and *Anthracospirifer.* But ribbing is so variable in species assigned especially to *Anthracospirifer* that more detailed assessment is required. There are likely to be various different arrangements of micro-ornament in the subfamily, and the

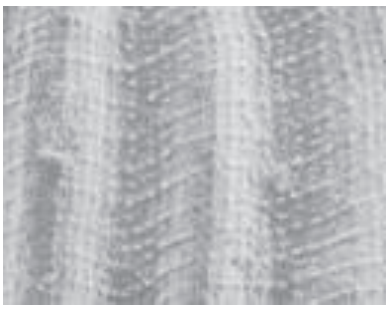


Fig. 215. Micro-ornament in *Anthracospirifer pellaensis* (Weller), x12, from Meramecian of Iowa. (Legrand-Blain 1985a).

patterns need to be clarified for type *Sergospirifer* and type *Anthracospirifer*, as well as for other species. Such detail may well help to distinguish genera, validate or disqualify names

already proposed, and recognize new taxa, to be expected from the large number of species referred currently to *Anthracospirifer*.

Subfamily **WARSAWIINAE** new subfamily

Name genus: *Warsawia* Carter, 1974, p. 684 from middle Visean of United States, here designated.

Diagnosis: Transverse with fine ribs, not fasciculated, well developed over sulcus and fold, both valves with thick callus posteriorly, and no adminicula visible, dental plates slender, ctenophoridium well developed but crural plates not distinct. Lower Carboniferous (mid-Visean).

Genus: *Warsawia* Carter.

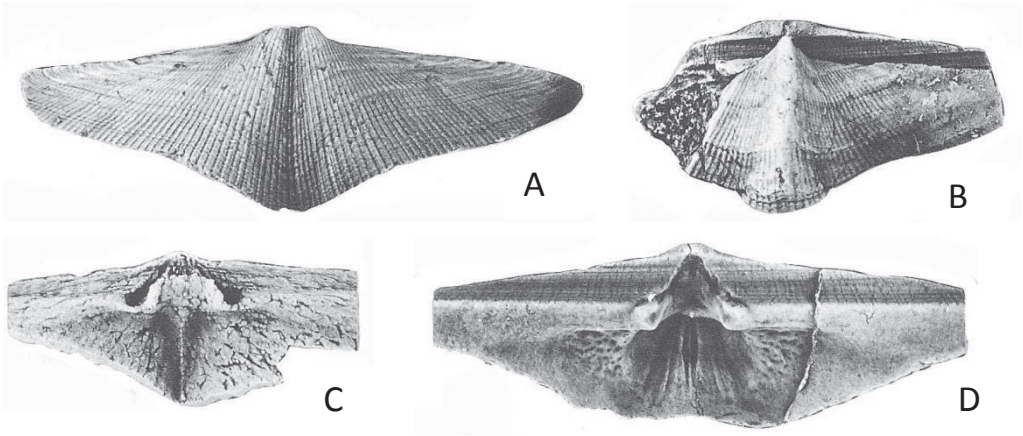


Fig. 216. *Warsawia lateralis* (Hall). A, ventral valve. B, dorsal view. C, dorsal interior. D, ventral interior, showing very slight denticulation, a likely connector plate, and branching mantle canals, unusual for Spiriferoidea. Specimens x2, from Warsaw Formation, Missouri, United States, of Meramecian-Visean age. (Carter 1974).

Discussion: *Warsawia* is one of several remarkable Spiriferida discovered by John Carter in the course of his research on Mississippian brachiopods – *Skelidorygma* and *Perissothyris* are two other highly unusual taxa that he has described and named. *Warsawia* is highly transverse, and has fine ribs that are undifferentiated, and not fascicled, although rare ribs split into two. The shell is as transverse as some Paeckelmannelloidea, and some Fusispiriferinae, but has no plicae. Transverse sections show no adminicula, possibly because they are buried in secondary shell, and dental plates appear to be low and concave, and crural plates are arguably absent or merged with inner socket plates. There is no known delthyrial cover plate, but no umbonal callosity, although one figure suggests the presence of a thick connector plug or plate. The mantle canals appear to form a non-spiriferoid pattern in being moderately complex near the hinge of the ventral valve. In short, affinities are difficult to unravel, and in this study, the genus is referred to a subfamily and treated as a highly exceptional form of Spiriferidae, because of the fine ribbing. It cannot be said that

relationships have been resolved, although it seems possible that the genus arose as an exceptional form from within Prospirinae, or as an early offshoot from Spiriferinae.

Latispirifer Archbold & Thomas, 1986a from the Permian of Western Australia, is large and highly transverse, with slender costae, looking close to *Warsawia*, but it has slender fascicles, especially on the dorsal valve. The possibility remains that it is a descendent, but this cannot yet be established. It may be noted that adminicula are developed in *Latispirifer*, so that this genus is referred to Gypospiriferinae.

Subfamily **GYPOSPIRIFERINAE** Waterhouse, 2004

[Gypospiriferinae Waterhouse 2004, p. 93].

Diagnosis: Transverse as a rule, or slightly elongate, costae increasing by bifurcation or trifurcation, may form weak fascicles but often without plicae. Delthyrium variable, with umbonal callus, or partly or entirely closed by stegidial plates. Dental plates well formed, short adminicula, connector plate, no tabellae. Upper Pennsylvanian (Bashkirian) to Permian (Changhsingian).

Genera: *Gypospirifer* Cooper & Grant, *Cartorhium* Cooper & Grant, *Latispirifer* Archbold & Thomas, *Lepidospirifer* Cooper & Grant, *Ovispirifer* Waterhouse.

Discussion: This subfamily is discussed by Waterhouse (2004). It is very close in most respects to Spiriferinae, but more varied in shape, often with elongate shells or with prominent often extended umbones, and with well developed fascicles posteriorly that usually fade anteriorly, often prominent commarginal laminae, well developed stegidial plates, and in some a low umbonal callosity.

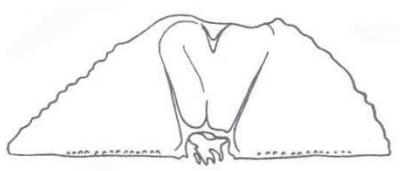


Fig. 217. *Gypospirifer condor* (Orbigny), transverse section through ventral valve showing connector plate and remains of stegidia, x4. From Asselian of Bolivia. (Legrand-Blain 1986).

Grunt (2006) has proposed placement of Gypospiriferinae as a tribe in Kaninospiriferidae (see below, p. 201), but dental plates are not low and plicae not as well formed as in *Kaninospirifer*. Angiolini & Long (2008) transferred Gypospiriferinae to Neospiriferidae, but plicae are not as well formed as a rule, and no single delthyrial cover plate is developed. The presence of a connector plate rules out any alliance with Neospiriferinae.

Cartorhium Cooper & Grant, 1976, p. 2191, type species *C. retusum* Cooper & Grant, is represented by a number of species in the Glass Mountains of Texas, and has well developed facsicles fading anteriorly, and strong costae, with pointed ventral beak. Although judged to belong to Neospiriferinae by Carter (2006a) and Poletaev (1997), the genus looks gypospiriferin because its narrow pointed umbo, and no species in the Glass Mountains was found to have a delthyrial cover plate. Instead, Cooper & Grant (1976)

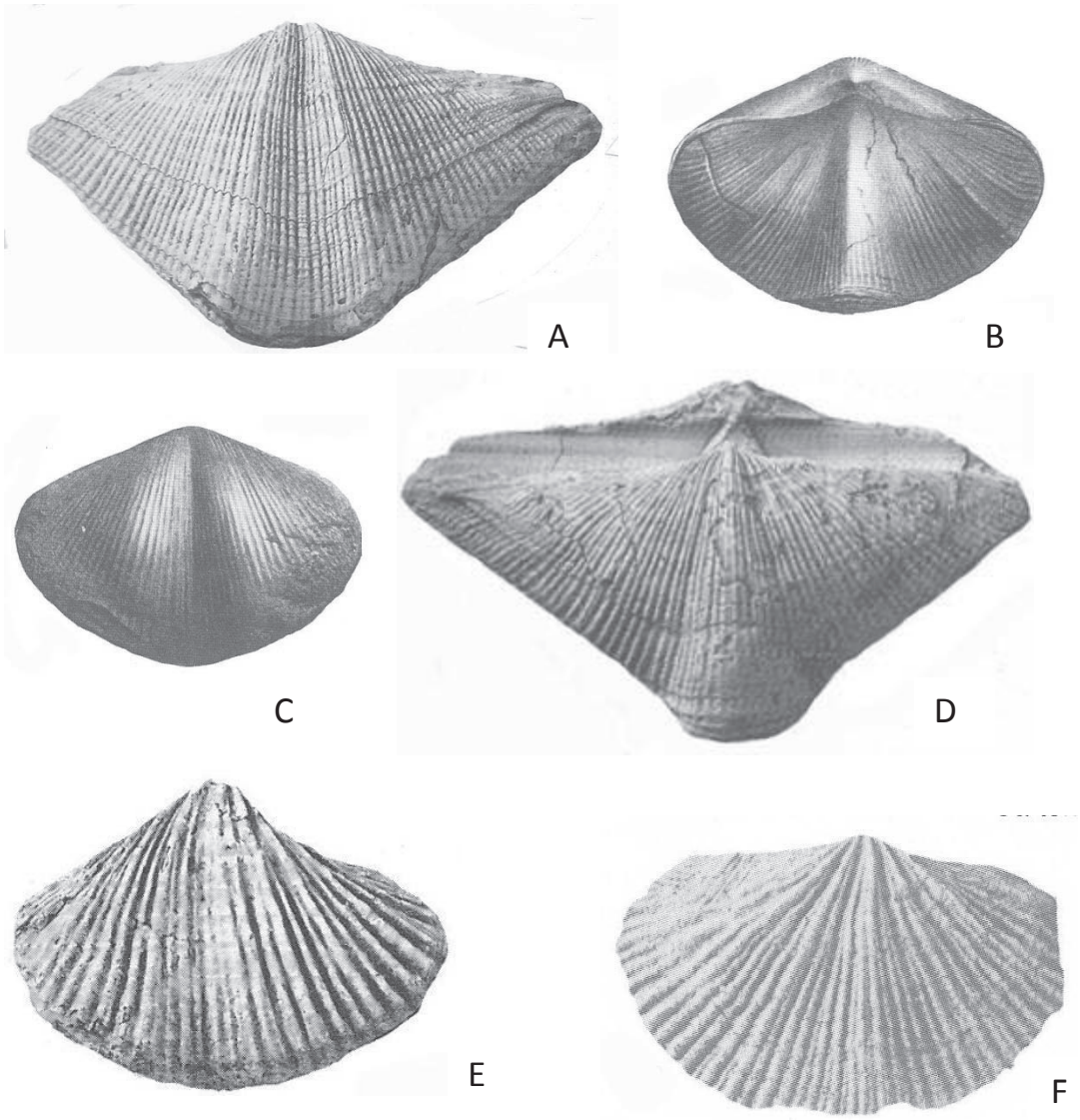


Fig. 218. A, D, *Gypospirifer nelsoni* Cooper & Grant, ventral and dorsal views, x1. From Wolfcampian (Cisuralian) of Texas, USA. (Cooper & Grant 1976). B, C, *Ovispirifer oldhamianus* (Waagen), x1. From lower Guadalupian of Salt Range, Pakistan. (Waagen 1883). E, *Cartorium retusum* Cooper & Grant, dorsal view, x2. F, *C. zoyei* Cooper & Grant, ventral valve, x1. From Guadalupian of Texas. USA. (Cooper & Grant 1976).

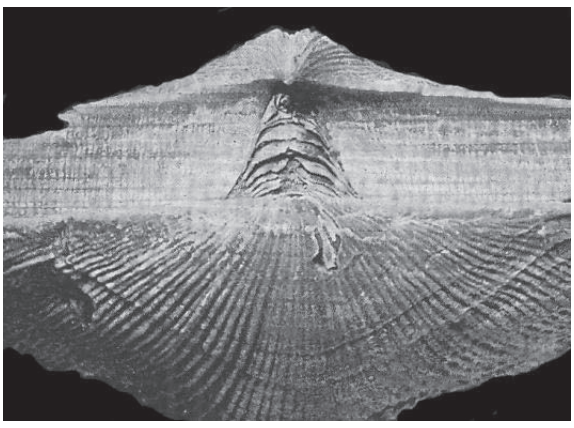


Fig. 219. *Gypospirifer condor* (Orbigny), dorsal aspect showing stegidia filling the delthyrium, x1.5. From Copacabana Group (Asselian) of Bolivia. (Samtleben 1971).

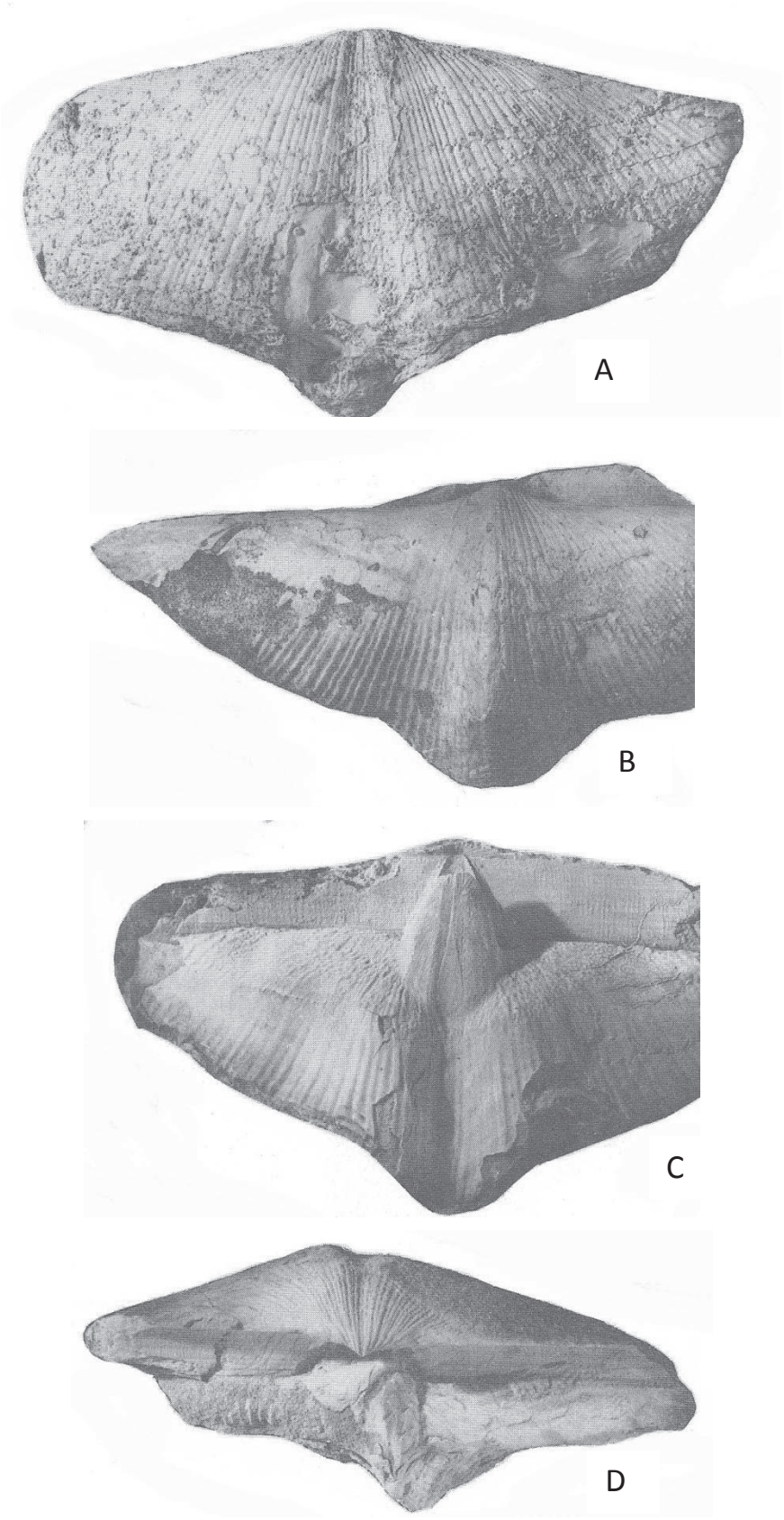


Fig. 220. A, *Latispirifer amplissimus* Archbold & Thomas, ventral valve from Port Keats Group, Western Australia. B-D, *L. callytharrensis* Archbold & Thomas. B, dorsal valve. C, ventral internal mould showing connector plate. D, posterior view, ventral valve on top. Specimens from Callytharra Formation (Sakmarian). x1, from Western Australia. (Archbold & Thomas 1985).

reported a small deep-seated so-called ”pseudodeltidium” or umbonal callosity, and a connector plate diverging forward into two pleromal ridges is well shown by Cooper & Grant (1976, pl. 613, fig. 35).

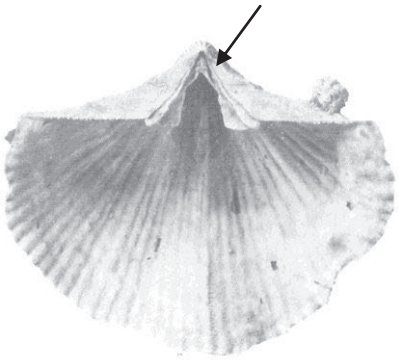


Fig. 221. *Cartorhium chelomatum* Cooper & Grant, internal aspect of ventral valve, showing posterior connector plate as arrowed and pleromal extensions, x1. From Word Formation, Texas, United States. (Cooper & Grant 1976).

Genus *Latispirifer* Archbold & Thomas (Sakmarian to Wuchiapingian) has a well developed connector plate, and a small umbonal callosity, and traces of stegidia (Archbold & Thomas 1985, p. 273, Fig. 3A, D). It is exceptionally transverse, approaching *Warsawia* Carter (p. 182), but has very weak fasciculation. The genus was placed as Spiriferinae in the *Revised Brachiopod Treatise*, although much younger than members of that group.

Subfamily **SPIRIFERALARIINAE** new subfamily

Name genus: *Spiriferalaria* Waterhouse, 2002a, p. 231 from Guadalupian of Texas, USA, here designated.

Diagnosis: Plicae well developed. Lower Carboniferous (Serpukhovian) to Late Permian (Changhsingian).

Genera: *Spiriferalaria* Waterhouse, *Gibbospirifer* Waterhouse, *Simplicisulcus* Waterhouse, *Tegulispirifer* Poletaev.

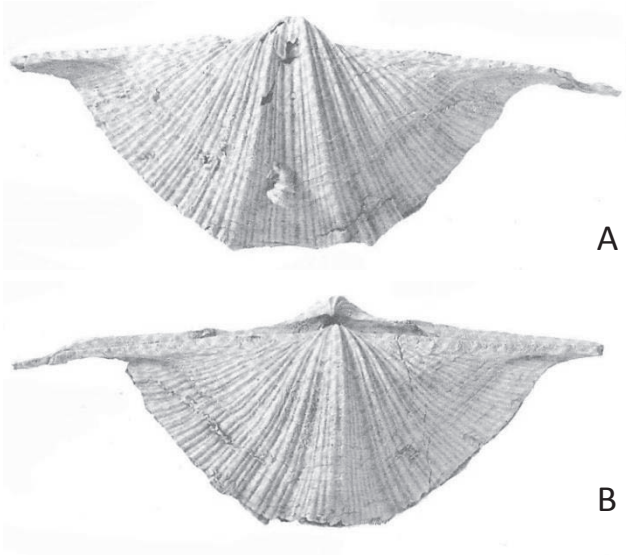


Fig. 222. *Spiriferalaria bakeri bakeri* (King), ventral and dorsal views, x1. From Road Canyon Formation (Roadian), Texas, USA. (Cooper & Grant 1976).

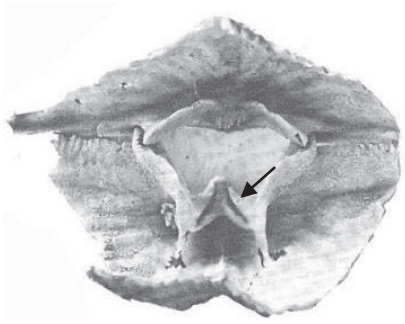


Fig. 223. *Spiriferalaria mansuetus* (Cooper & Grant), internal view of cardinalia, dorsal valve on top, x2.5. Connector plate and pleromal ridges as arrowed. From Cathedral Mountain Formation, Texas, USA. (Cooper & Grant 1976).

Discussion: This tribe includes genera that externally look like Neospiriferidae in being strongly plicate as well as costate, but which differ in having a connector plate like Spiriferidae. Genera are widespread, commencing in the northern hemisphere and found in moderate to high latitudes of both hemispheres at different times.

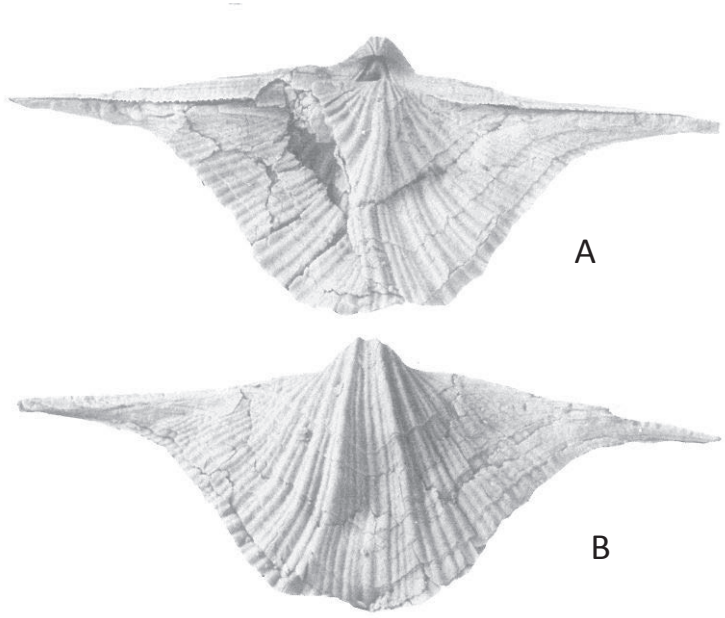


Fig. 224. *Spiriferalaria bakeri columbarius* (Cooper & Grant), dorsal and ventral views, x1.3. From Road Canyon Formation (Roadian), Texas, USA. (Cooper & Grant 1976).

Spiriferalaria Waterhouse is based on *Neospirifer thesculus* Cooper & Grant, 1976, p. 2189, which is allied to several other species from the Glass Mountains of Texas, including *N. mansuetus* and *N. formulosus* named by Cooper & Grant, and *N. bakeri* King. They look close to *Betaneospirifer* Gatinaud, but differ in having a much wider hinge with extremely alate cardinal extremities, as well as having a connector plate.

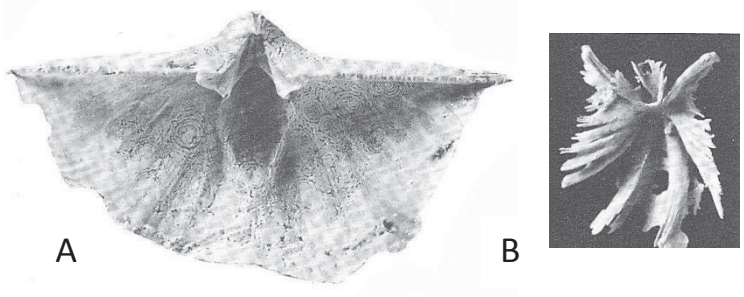


Fig. 225. *Spiriferalaria thesculus* (Cooper & Grant). A, ventral interior, x7. B, buccal plate, x3, a stellate structure between the spiralia of this genus. From Road Canyon Formation (Roadian), Texas, USA. (Cooper & Grant 1976).

Fig. 226. *Spiriferalaria thesculus* (Cooper & Grant) ventral and dorsal views x1, from Road Canyon Formation (Roadian), Texas, USA. (Cooper & Grant 1976).

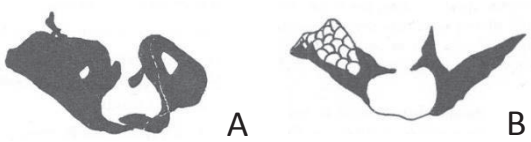


Fig. 227. *Simplicisulcus arthurtonensis* (Waterhouse), transverse sections of two ventral valves at 6.5mm and 7mm from beak, x1.5. From Earnvale Member (Wuchiapingian), New Zealand. (Waterhouse 1968).

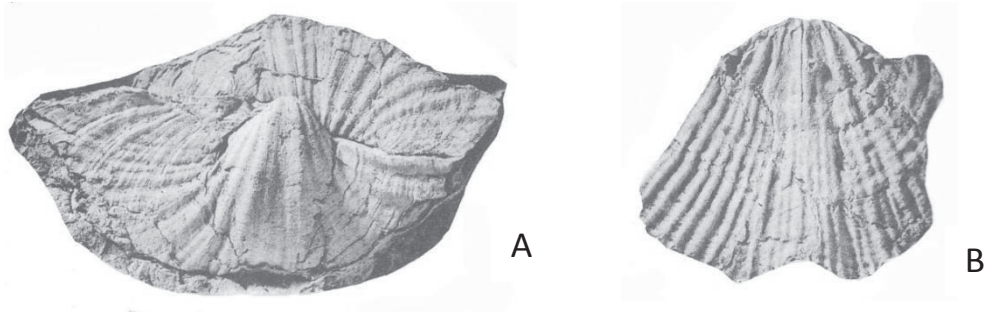


Fig. 228. *Simplicisulcus concentricus* (Waterhouse). A, both valves, ventral valve below. B, dorsal internal mould. Specimens x 1.5. From Brae Formation (Kungurian), Queensland, Australia. (Waterhouse 1987).

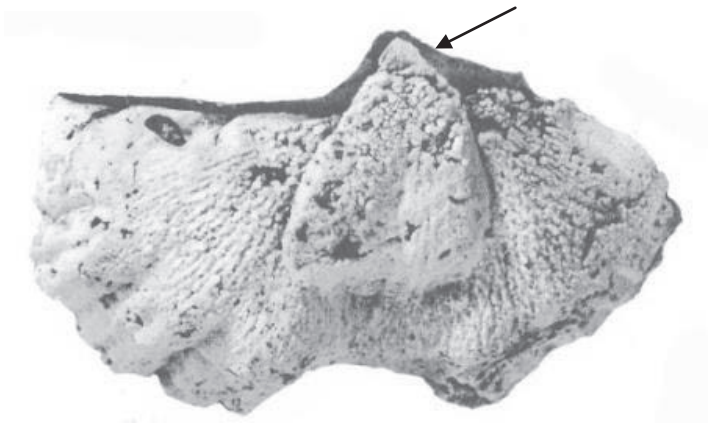


Fig. 229. *Simplicisulcus arthurtonensis* (Waterhouse), ventral internal mould, x2, showing part of connector plate (arrowed) above the muscle field and below the beak, with the vascular pattern of pits. From Earnvale Member (Wuchiapingian) in New Zealand. (Waterhouse 1968).

Genus ***Tegulispirifer*** Poletaev, 2000b

Diagnosis: Medium-sized to large transverse shells with extended hinge and well developed costate plicae, not entering the sulcus, micro-ornament with strong commarginal laminae, and fine radial capillae. Stegidial cover, with small umbonal callosity and connector plate.

Type species: *Spirifer tegulatus* Trautschold, 1876 from Moscovian (Middle Carboniferous) of Moscow Basin, Russia.

Discussion: Poletaev (2000b), followed by the *Revised Brachiopod Treatise*, referred this genus to Trigonotretinae Schuchert. That is an error: Trigonotretinae, and all other genera within the superfamily, lack a connector plate, and seldom show stegidial apparatus. Moreover the style of ornament differs considerably. The misunderstanding demonstrates how difficult it has been for authorities to understand Trigonotretidae, in spite of being the focus of many and some well illustrated studies, mainly no doubt because it has been centred on deep Gondwana.

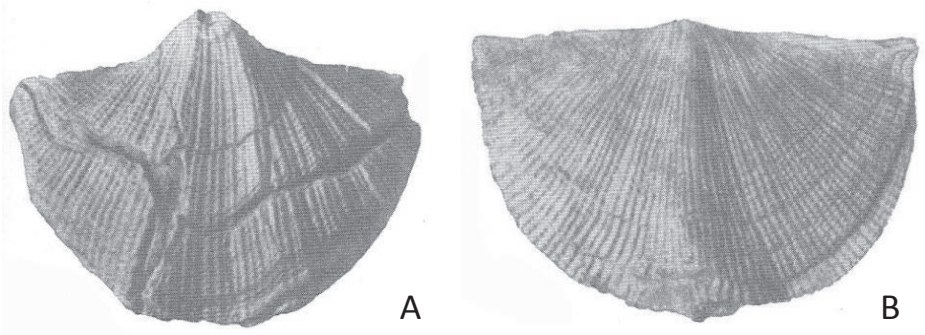


Fig. 230. *Tegulispirifer tegulatus* (Trautschold), ventral and dorsal valves, x1, from Moscow Basin in Russia, of Moscovian-Kasimovian age. (Ivanov & Ivanova 1937).

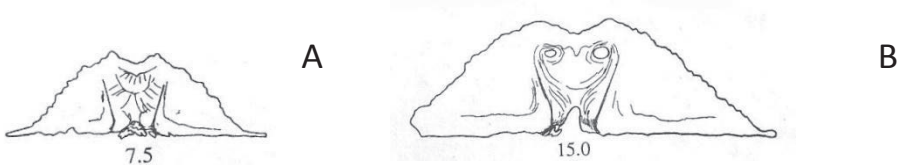


Fig. 231. A, *Tegulispirifer svetlanovoensis* Poletaev, transverse sections, x2.5 with figures showing distance in mm from ventral beak. Specimens x3 from Kasimovian of Donets Basin, Ukraine. (Poletaev 2000b).

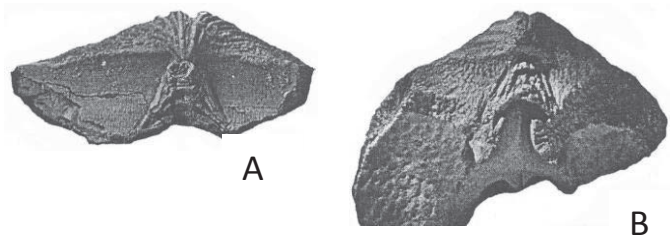


Fig. 232. A, *Tegulispirifer svetlanovoensis* Poletaev, showing delthyrial cover of stegidial apparatus. B, *Tegulispirifer tegulatus* (Trautschold), showing stegidial plate. Specimens x1.5 from Kasimovian of Donets Basin, Ukraine. (Poletaev 2000b).

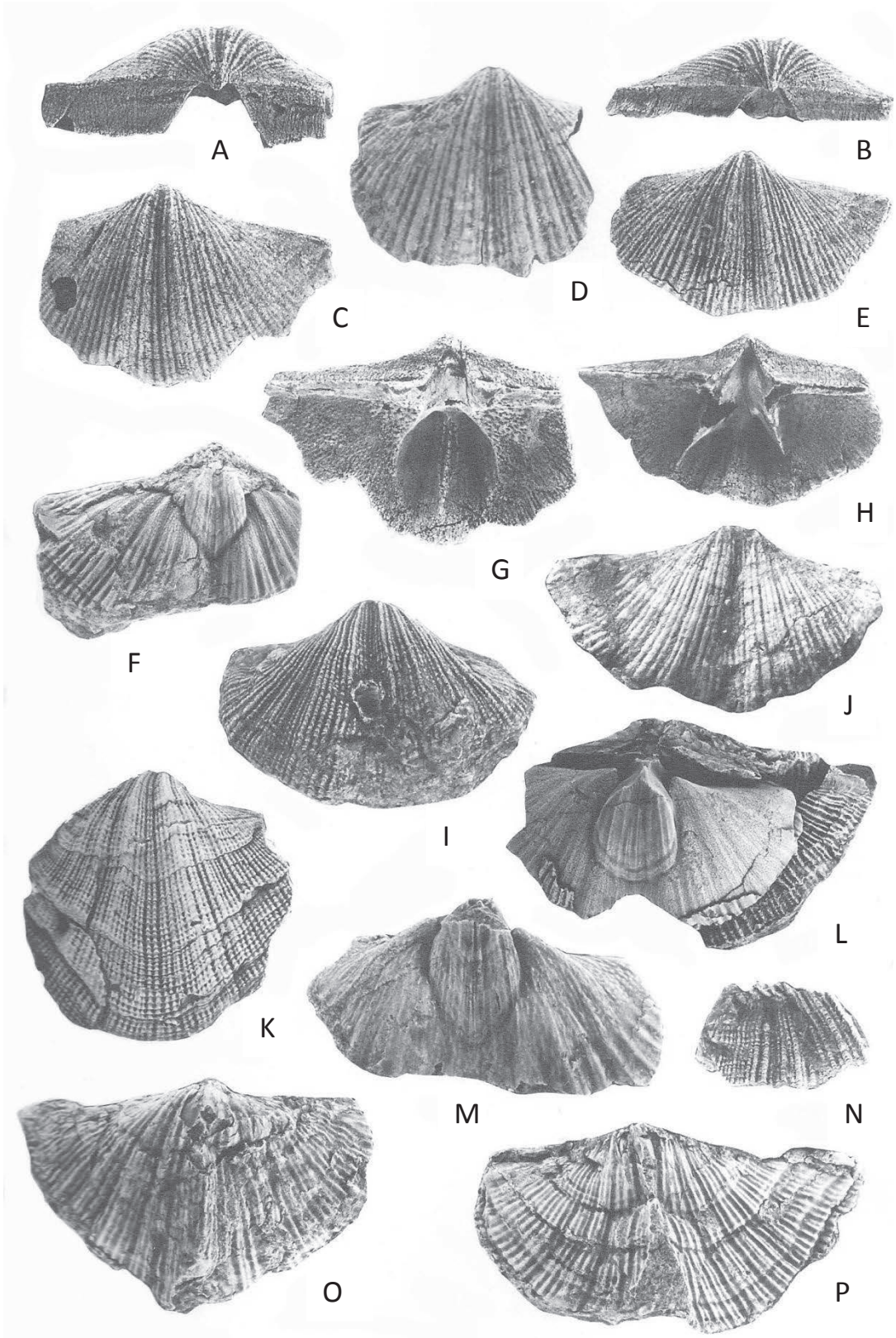


Fig. 233. A-J, L-P, *Tegulospirifer ogilvieensis* n. sp. A, C, G, silicified ventral valve GSC 37429. B, E, H, silicified ventral valve GSC 37431. D, ventral exterior, GSC 37430. F, ventral internal mould, GSC 37432. I, ventral valve GSC 37433. J, ventral valve GSC 37434. L, ventral internal mould GSC 37435. M, ventral internal mould GSC 37437. N, fragment of dorsal valve GSC 37438, showing micro-ornament. O, dorsal valve GSC 37439. P, dorsal valve GSC 37440. Specimens x 1, except Fig. 233M, x2. From the Ettrain Formation (Kasimovian) of Yukon Territory, Canada. K, ventral valve ascribed to *Tegulispirifer tegulatus* (Trautscholdt), BB 8828. (Nazer 1977).

Tegulospirifer ogilvieensis new species

Diagnosis: Medium-sized shells with well formed plicae and moderately strong costae.

Holotype: GSC specimen 37446. Fig. 234A-D, from Ettrain Formation (Kasimovian) of Yukon Territory, Canada, here designated.

Diagnosis: Plicae strong, curve outward, costae fine and branch frequently, and commarginal laminae not as prominent as in some other species. Interarea low with wide delthyrium.

Description: This species is based chiefly on silicified shells etched from the Ettrain Formation of northwest Canada. The shell is of medium size, a ventral valve measuring 62mm wide, 41mm long and up to 80mm wide, with the largest specimen 108mm wide and 65mm long. Maximum width lies at the hinge or a little in front, having a high interarea and largely open delthyrium apart from a small plate, probably part of a stegidium now largely destroyed, lying under the umbo. The sulcus widens at 15-20^{o}, and costae lie in five to six plicae, nine to ten in 10mm, with prominent growth laminae (10-12 in 10mm) and fine radial capillae (eight to ten over a costa). An open notothyrium is present. Inwardly concave dental plates meet adminicula that diverge strongly to the floor of the valve, and a connector plate lies across the valve at the junction of the two sets of plates, and is much more clearly demonstrated than in many other studies. The ctenophoridium lies between crural plates, with no tabellae, and crural plates cannot be readily distinguished from the inner socket plates. Secondary thickening is strong close to the hinge each side of the adminicula, and the floor strongly marked by small pits as is characteristic of Spiriferidae and Neospiriferidae.

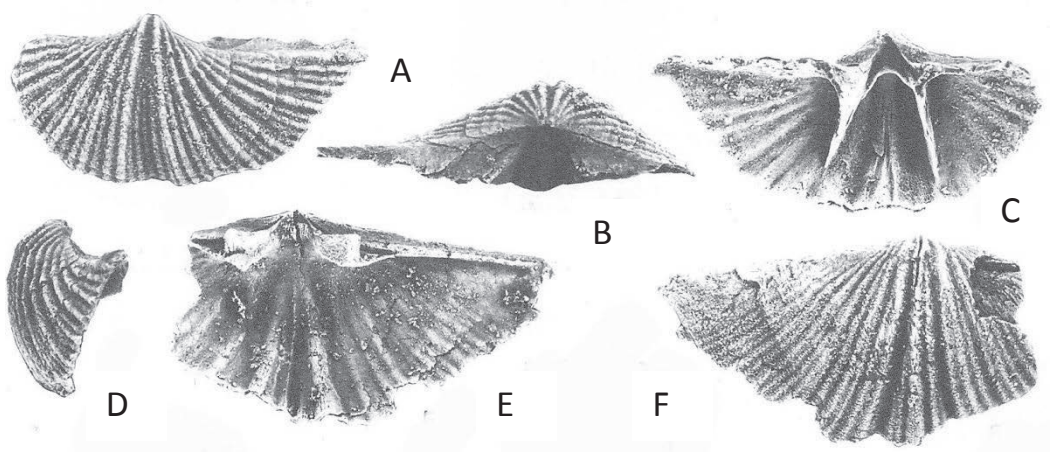


Fig. 234. *Tegulospirifer ogilvieensis* n. sp. A-D, ventral, posterior, internal and lateral views of ventral valve GSC 37446, holotype. E, F, internal and external views of dorsal valve GSC 37447. Specimens x1. From the Kasimovian Ettrain Formation of Yukon Territory, Canada. (Nazer 1977).

Resemblances: There are close resemblances to *Tegulispirifer tegulatus* (Trautschold, 1876) from the Upper Carboniferous of Ukraine and Russia, but plication is a little stronger in the present form, and plicae curve outward more, and commarginal laminae are less prominent, and costae finer and branching more frequently. The interarea is lower and the delthyrium

wider, and the sulcus distinctly narrower. *T. svetlanovoensis* Poletaev, 2000b of Kasimovian age in the Donets Basin of Ukraine is a broader shell with less emphasized plicae and more subdued costae.

Genus ***Gibbospirifer*** Waterhouse, 1971b

Diagnosis: Small subelongate shells with fine costae and low plicae. No deltidia. Small connector plate, with umbonal callosity on a few individuals. Middle and Late Pennsylvanian (Kasimovian, Gzhelian).

Type species: *Gibbospirifer ettrainensis* Waterhouse, 1971b, p. 221 from basal Jungle Creek Formation (Gzhelian), Yukon Territory, Canada.

Discussion: This genus is restricted to Late Carboniferous faunas in western Canada.

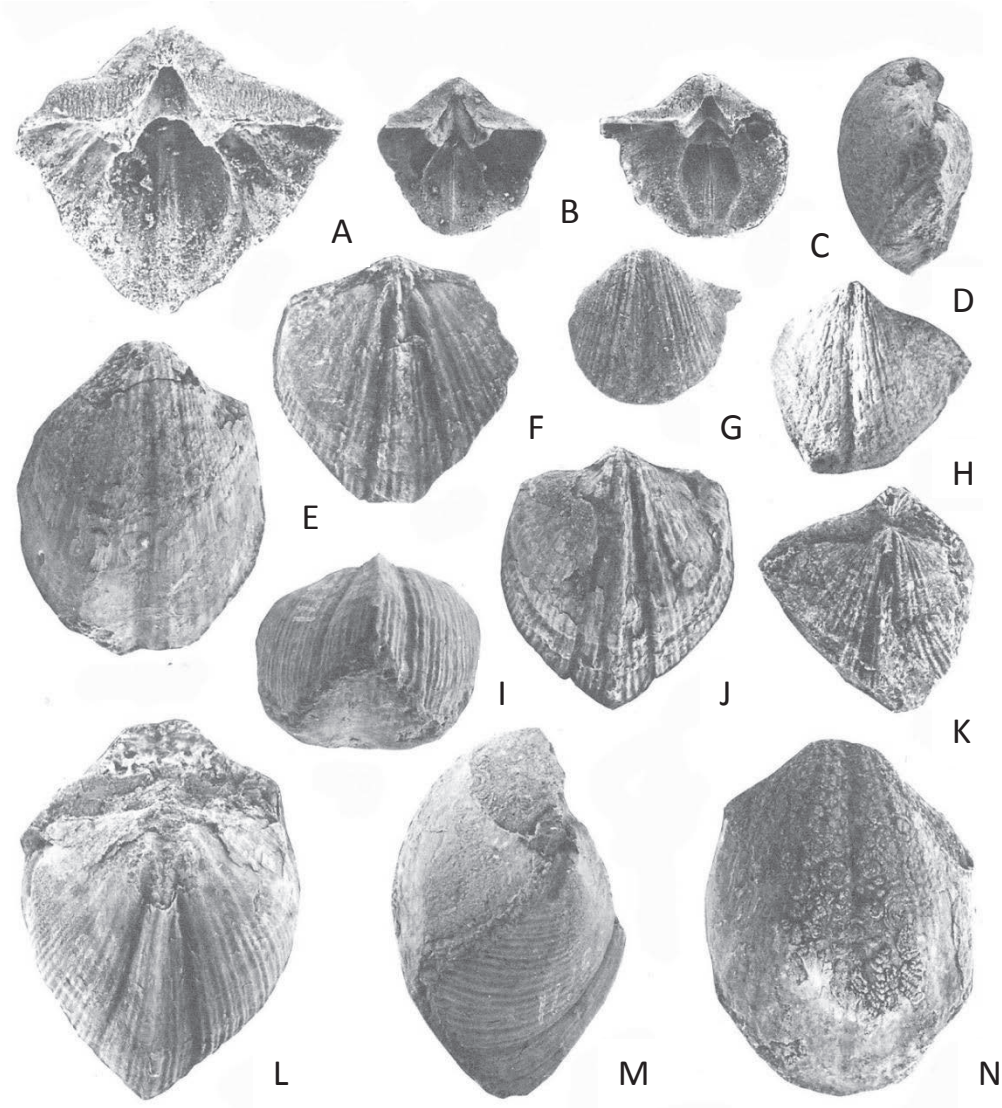


Fig. 235. *Gibbospirifer nazeri* n. sp. A, silicified interior of ventral valve, GSC 37448. B, silicified ventral interior, GSC 37449. C, G, silicified interior and exterior, GSC 37450. D, H, K, lateral, ventral and dorsal views of GSC 37451. E, ventral valve GSC 37452. I, L-N, anterior, dorsal, lateral and ventral views of GSC 37454, holotype. J, dorsal valve GSC 37455. Specimens x1 except fig. A, x2. From upper Ettrain Formation (Kasimovian), Yukon Territory, Canada. (Nazer 1977).

Gibbospirifer nazeri new species

Derivation: Named for Roderick E. Nazer.

Diagnosis: Subelongate with high dorsal fold and moderately defined plicae.

Holotype: GSC 37454, figured in Fig. 236I, L-N, here designated.

Description: Some 35 specimens are available, from the Ettrain Formation, of Kasimovian age. Shells suboval, an example measuring 37mm wide, 51mm long and 32mm high, and the umbonal angle is 105-110°. Maximum width lies at midlength, and the delthyrium is apparently open with angle of 60° and underlain by a connector plate. The sulcus is shallow and narrow, and the fold narrow and high with narrow angular crest. Costae are fine, eight to ten in 10mm at mid-length, in four or five low plicae pairs, with weak capillae and growth increments. Teeth are supported by dental plates and divergent adminicula, buttressed laterally by thick secondary callus. Adductor scars are narrow and diductor scars bear longitudinal striations. The dorsal interior is not known.

Resemblances: This species is distinguished from the slightly younger form *Gibbospirifer ettrainensis* Waterhouse, 1971b from the basal Jungle Creek Formation (Gzhelian) of the Yukon Territory in Canada by its higher fold and slightly stronger costae. Adminicula are longer in the present form.

Subfamily **FUSISPIRIFERINAE** Waterhouse, 2004

[Fusispiriferinae Waterhouse, 2004, p. 143].

Diagnosis: Markedly transverse with slightly variable costation and plication in different genera. Connector plate and small umbonal callosity may be present. Lower Permian (Artinskian) to Upper Permian (Changhsingian).

Genera: *Fusispirifer* Waterhouse, *Cracowspira* Waterhouse, *Cratispirifer* Archbold & Thomas, *Occidalia* Archbold, *Transversaria* Waterhouse & Gupta.

Discussion: This is a very distinctive group, involving highly transverse and plicate shells principally found in southern temperate paleolatitudes of the Permian Period in the Himalaya, Timor and Western Australia, extending rarely into eastern Australia and northeast Russia. *Cracowspira* is characterized by weakly defined fascicles on the dorsal valve, and virtually imperceptible fascicles on the ventral valve, by contrast with the strong fasciculation in *Fusispirifer*. Moreover the costation differs in the two genera. In *Fusispirifer*, the costae are varied, being especially strong along the crests of fascicles, and fine within the sulcus and over the fold, and laterally towards the cardinal extremities. In *Cracowspira*, the costae include fine costae in the sulcus and over the fold, but are uniformly coarse over the fascicles and laterally. Further differences are enumerated in Waterhouse (2004, pp. 151-153). Although Gourvennec in Gourvennec & Carter (2007, p. 2781) synonymized *Cracowspira* with *Fusispirifer*, his view is rejected. It has been demonstrated that one of the short-comings of the studies in the last century, as summarized in the *Revised Brachiopod Treatise* of 2006, has been inadequate attention to details of ornament (Ma & Day 2007, Schemm-Gregory 2011a). There are several species of *Fusispirifer*, all consistent in costation and fasciculation,

including for example *F. nitiensis* (Diener), *F. semiplicata* Jin, and *F. jini* Waterhouse. They all differ from *Cracowspira*. To assign these species to two genera is the best initial way of demonstrating similarities and differences.

Another genus that demonstrates the range of morphology achievable within the subfamily is *Transversaria marcouiformis* (Jin, 1976). It has fine costae and very subdued fascicles, and is characterized principally by the unusually wide anterior fold and sulcus (Waterhouse 2004, pp. 148-150). *Cratispirifer* Archbold & Thomas, and *Occidalia* Archbold, both named from west Australian species, and ranging into Timor and south Asia, and north-

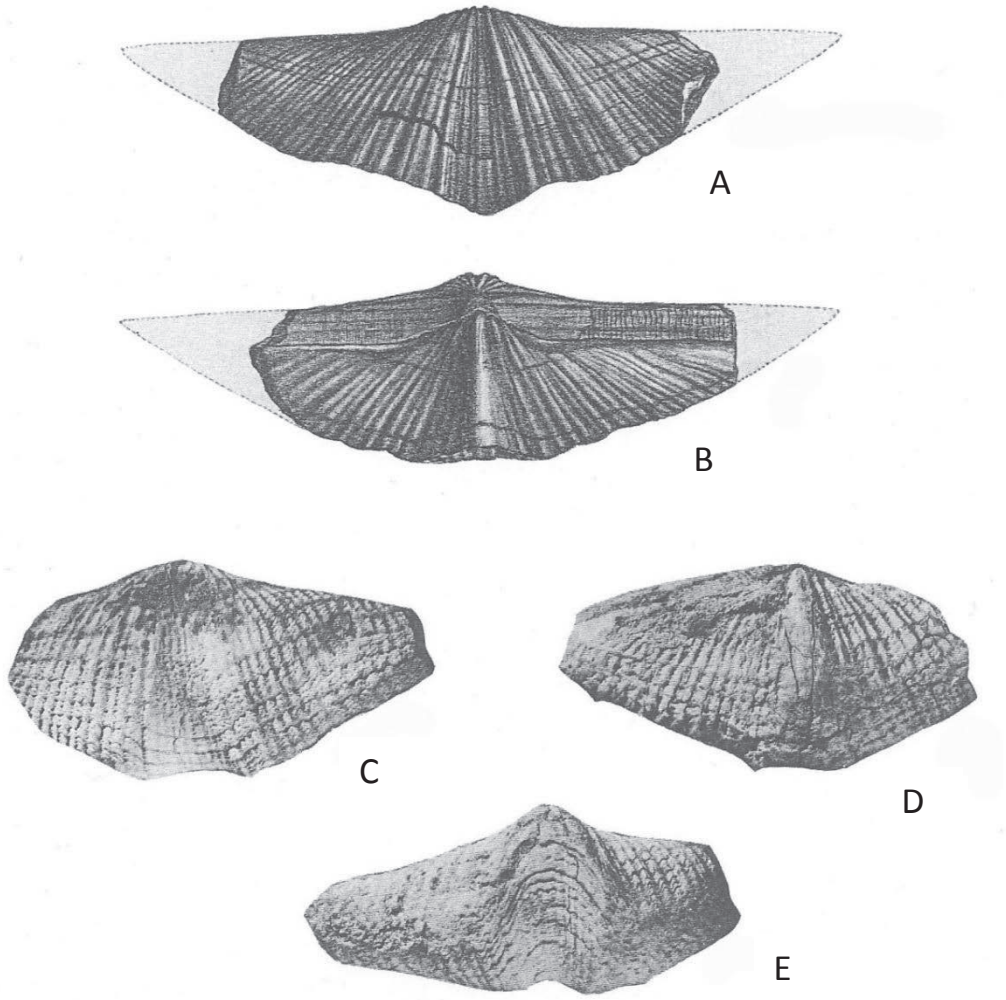


Fig. 236. A, B, *Fusispirifer nitiensis* (Diener, ventral and dorsal aspects, x1. From Spiti (Wuchiapingian) in Himalaya. (Diener 1897b). C-E, *Cracowspira laminata* (Waterhouse, ventral, dorsal and anterior views, x1. From Rose's Pride Formation (Artinksian), Queensland. (Waterhouse 1987).

east Russia, further demonstrate the significance of shape, sulcation, fasciculation and costation in allowing delineation of variation in Fusispiriferinae. It is possible that these genera all have short dental plates, as may be the case for Kaninospiriferinae. But the height of the dental plates in *Fusispirifer* itself is not clear.

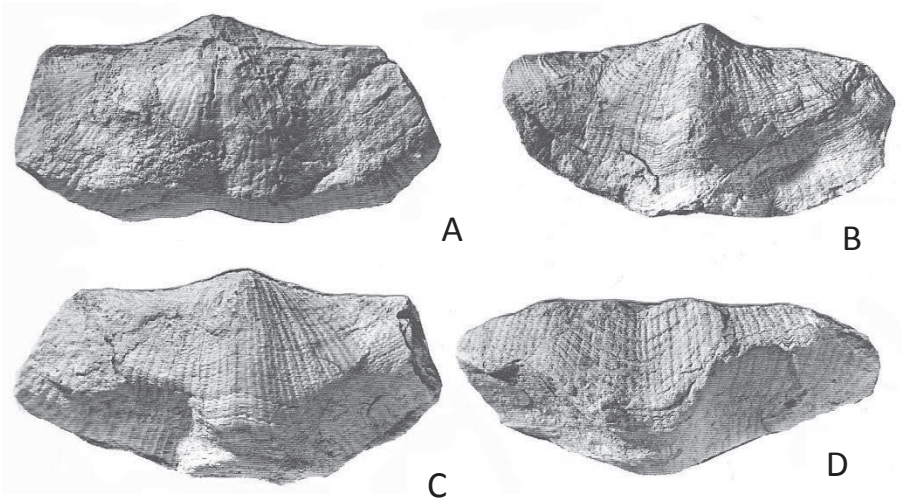


Fig. 237. *Transversaria pauciplicus* (Waterhouse), ventral, dorsal and anterior aspects, x0.75. From Barfield Formation (Wordian) of Queensland, Australia. (Waterhouse 2004).

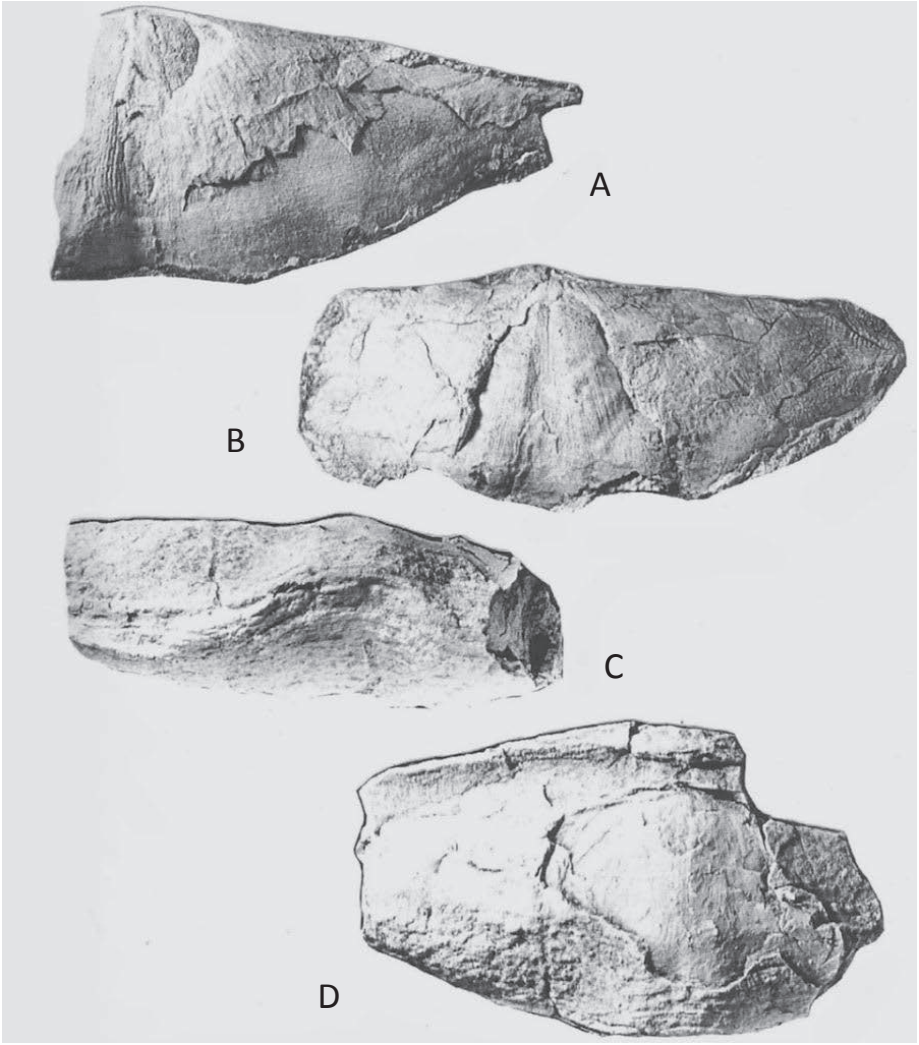


Fig. 238. *Transversaria marcouiformis* (Jin), two ventral views, anterior and dorsal views, x1. From Himalayas (Wuchiapingian) of south Tibet (Xizang), China. (Waterhouse 2004; Shen et al. 2003a).

Gourvennec in Gourvennec & Carter (2007, p. 2781) referred *Spirifera avicula* Morris, 1845 to *Fusispirifer*, but this species belongs to an entirely different lineage, to judge from the delthyrial apparatus and ornamentation, facets which should not be ignored in classification.

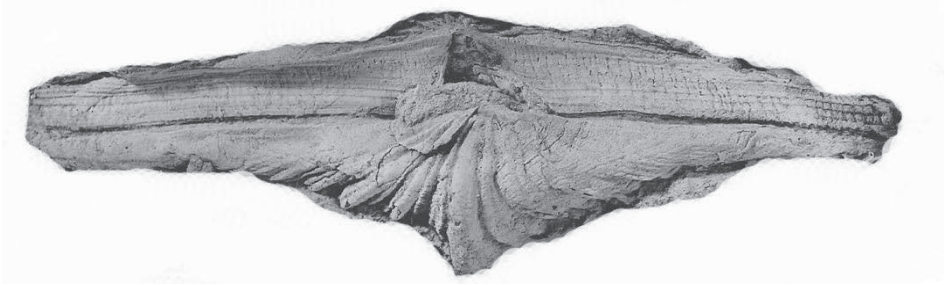


Fig. 239. *Occidalia plicatus* (Waterhouse), dorsal view of latex cast, showing small umbonal callosity and crushed stegidial fragments under the beak, x1. From Agglomeratic Slate, Kashmir (Sakmarian), Himalayas. (Waterhouse 2004).

What is not clear for any of the genera referred to Fusispiriferinae is the nature of the mantle canal system. The delthyrial apparatus appears to be spiriferoid: the descriptions are too generalized to tell, and no figure is informative. For many parts of Gondwana, especially the Himalaya and east Australia, the specimens come from clastic sediments that do not favour the preservation of any delthyrial cover plate or stegidia. But a broad connector plate over the entire delthyrium is developed in a specimen figured by Waterhouse (1966, pl. 11, fig. 1), identified as *Fusispirifer nitiensis* (Diener), and now kept at the Geologische

Fig. 240. *Fusispirifer nitiensis* (Diener), BR 3216, ventral internal mould (plaster duplicate) showing large arrowed connector plate, x2. From Lopingian of western Nepal.

Bundesanstalt in Vienna. The plate is gently concave dorsally, and the plate anteriorly can be seen to lie between the dental plates and the adminicula. Another specimen, identified as *Occidalia plicatus* (Waterhouse) and kept at the Geological Survey of India in Kolkata (Calcutta), registered as GSI 13199, shows a small apparent umbonal callosity below the ventral beak. Both these specimens indicate that Fusispiriferinae is not, as previously supposed, close to Neospiriferidae, but more likely to be related to Spiriferidae, as a group evolved probably from Gypospiriferinae, or more likely Spiriferalariinae.

Family **NEOSPIRIFERIDAE** Waterhouse, 1968

Diagnosis: Ornament of well developed plicae, costae and cancellate micro-ornament. Delthyrial cover plate, and no connector plate. Carboniferous (Visean) to Late Permian (Changhsingian).

Discussion: Members of this family lack a connector plate, and so might have been allied to Trigonotretoidea, which also lacks a connector plate. But the stratigraphic evidence does not favour this view, because plicate and costate neospiriferids are found in beds older than any costate trigonotretid, to suggest that neospiriferids might have arisen independently from spiriferoid stock, through loss of the connector plate. Unlike Trigonotretoidea, an umbonal callosity is not well developed. The delthyrial cover plate is typical of the family, and may have arisen from a single stegidial plate, or from a deltidial plate developed from inception, with no separate deltidial plates at any early stage of development.

Subfamily **NEOSPIRIFERINAE** Waterhouse, 1968

Diagnosis: Plicate and costate shells with sulcus that generally expands to incorporate innermost pair of plicae in many genera. Delthyrium as a rule covered by delthyrial cover plate. Dental plates, short adminicula, without connector plate, socket and crural plates, no tabellae, no median septa. Mantle canal system deeply pitted, but not well known. Carboniferous (Visean) to Permian (Changhsingian).

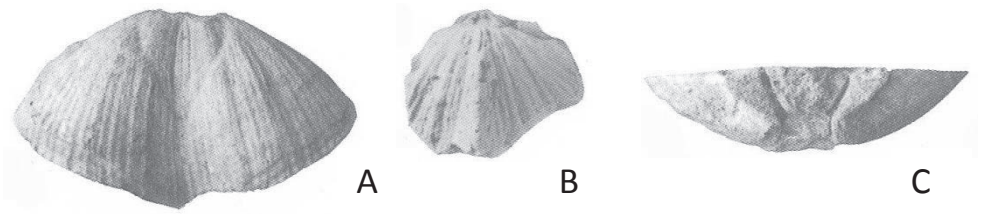


Fig. 241. *Neospirifer fasciger* (Keyserling), A, C, ventral and posterior aspects of ventral valve. B, dorsal valve lectotype. Specimens x1, from lower Cisuralian of Russia. (Carter 2006a).

Genera: *Neospirifer* Fredericks, *Betaneospirifer* Gatinaud, *Frechella* Legrand-Blain, *Pondospirifer* Waterhouse, *Tibetospirifer* Liu & Wang.

Discussion: In shape and ornament, Neospiriferinae appears to have evolved from Spiriferidae, with the development of stronger and restricted plicae rather than low numerous

fascicles, the loss of a connector plate, and the development of a delthyrial cover plate. This plate did not arise from deltidial plates that developed each side of the delthyrium, because no neospiriferid even at immaturity is known to show any sign of deltidial plates. It seems likely that the cover plate was either a specialized form of stegidial plate, lacking any foramen, or a deltidium developed from inception as one plate. Given these differences from Spiriferidae, and some approach to Trigonotretidae, it could be posited that Neospiriferidae are not spiriferoid, although there must be caution because of limited knowledge of type *Neospirifer*. Poletaev (1997, Fig. 1) did show some pleromal thickening inside the dental

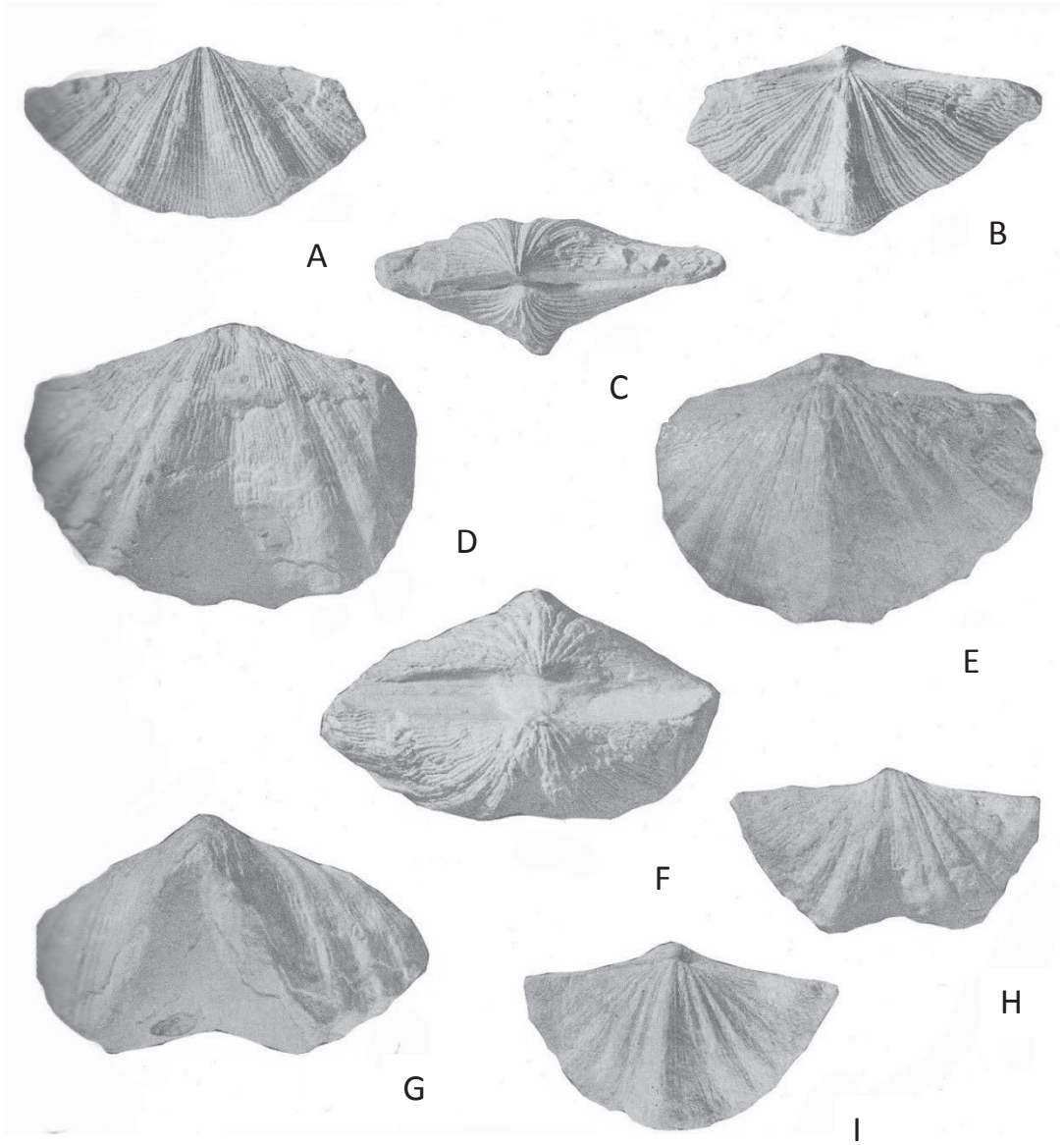


Fig. 242. A-G, *Betaneospirifer moosakhailensis* (Davidson). A, B, C, ventral, dorsal and posterior views of topotype. D-G, ventral, dorsal, posterior and anterior views of lectotype (dorsal valve on top). From Upper Wargal Formation, Salt Range, Pakistan (Wuchiapingian). H, I, *B. ambiensis* (Waagen), posterior ventral and dorsal views. From Amb Formation (lower Guadalupian), Salt Range, Pakistan. Note that even immature specimens have a very long hinge, unlike *Neospirifer*. Specimens x1. (Waterhouse 1978).

plates of *fasciger*. He concluded that *Neospirifer* had a distinct delthyrial plate, and lacked stegidial plates, hypodeltidial grooves and pseudodelthyrial plate.

Licharew (1942) provided an interesting discussion of *moosakhailensis* Davidson and *fasciger*, and regarded the latter as imperfectly represented with the holotype missing, and heterogeneous. Licharew considered that short-hinged specimens ascribed to *moosakhailensis* signified shells at early growth stage, and that hinge width would change with increase in size, but this cannot be firmly established, and it appears that the hinge of *fasciger* is narrow, and that of *Betaneospirifer* very wide. The most comprehensive suite of specimens figured as *Spirifer fasciger*, type species of *Neospirifer* Fredericks, is provided by Poletaev (1997, pl. 4, fig. 2a-c, 3a-d), and he discussed earlier attempts at evaluating the species, including studies by Licharew (1942), Archbold & Thomas (1984a) and Waterhouse (1968), with Waterhouse (2004, pp. 105-108) analyzing the Poletaev overview. One important aspect: although Poletaev claimed that B. K. Licharew had sent a specimen of *Gypospirifer* to Waterhouse for preparing transverse sections (Waterhouse 1968, fig. 8) and reproduced in Poletaev (1997, Fig. 2), the presence of plicae and fascicles in the specimen, as figured in Waterhouse (1968, pl. 16, fig. 7) rule out *Gypospirifer*, although aspects suggest likely identification with *Betaneospirifer* or *Neospirifer*, and given the early Permian age and Russian source of the specimen, evidence seems to point to an accurate determination on the part of B. K. Licharew. Some aspects of the morphological descriptions for *Neospirifer* in the Poletaev article were based not on type *Neospirifer* but on material from the Salt Range, Pakistan, which places a question on reliability, partly because the age of the Salt Range material was misunderstood by Poletaev (1997) to be much older than it is now known to be (Waterhouse 2010b). The likelihood that *Neospirifer fasciger* from the Early Permian of the Urals lasted as a species into the Late Permian of the Salt Range, Pakistan, is remote.

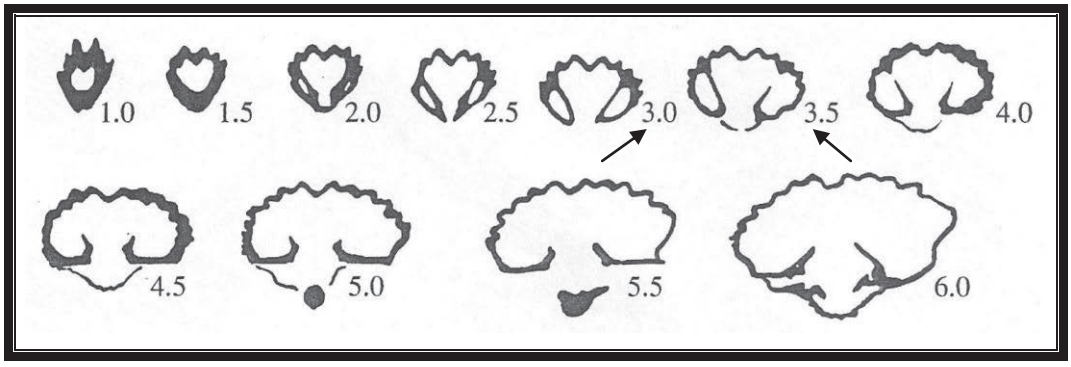


Fig. 243. *Betaneospirifer moosakhailensis* (Davidson), transverse sections with distance from beak in mm, partly rearranged from Waterhouse (1968), and ascribed to *Neospirifer fasciger* non Keyserling by Poletaev (1997). Arrows point to two examples of the delthyrial cover plate. From Kalabagh Member (Wuchiapingian), Salt Range, Pakistan.

Frechella Legrand-Blain, based on *Neospirifer fascicostatus gwinneriformis* Legrand Blain from the upper Visean of Algeria, looks close to *Neospirifer*, apart from having a narrow

sulcus bordered but not entered by the inner pair of plicae, and with micro-ornament prominent. Legrand-Blain (1986, p. 34) recorded that the apical cavity is filled with tissue

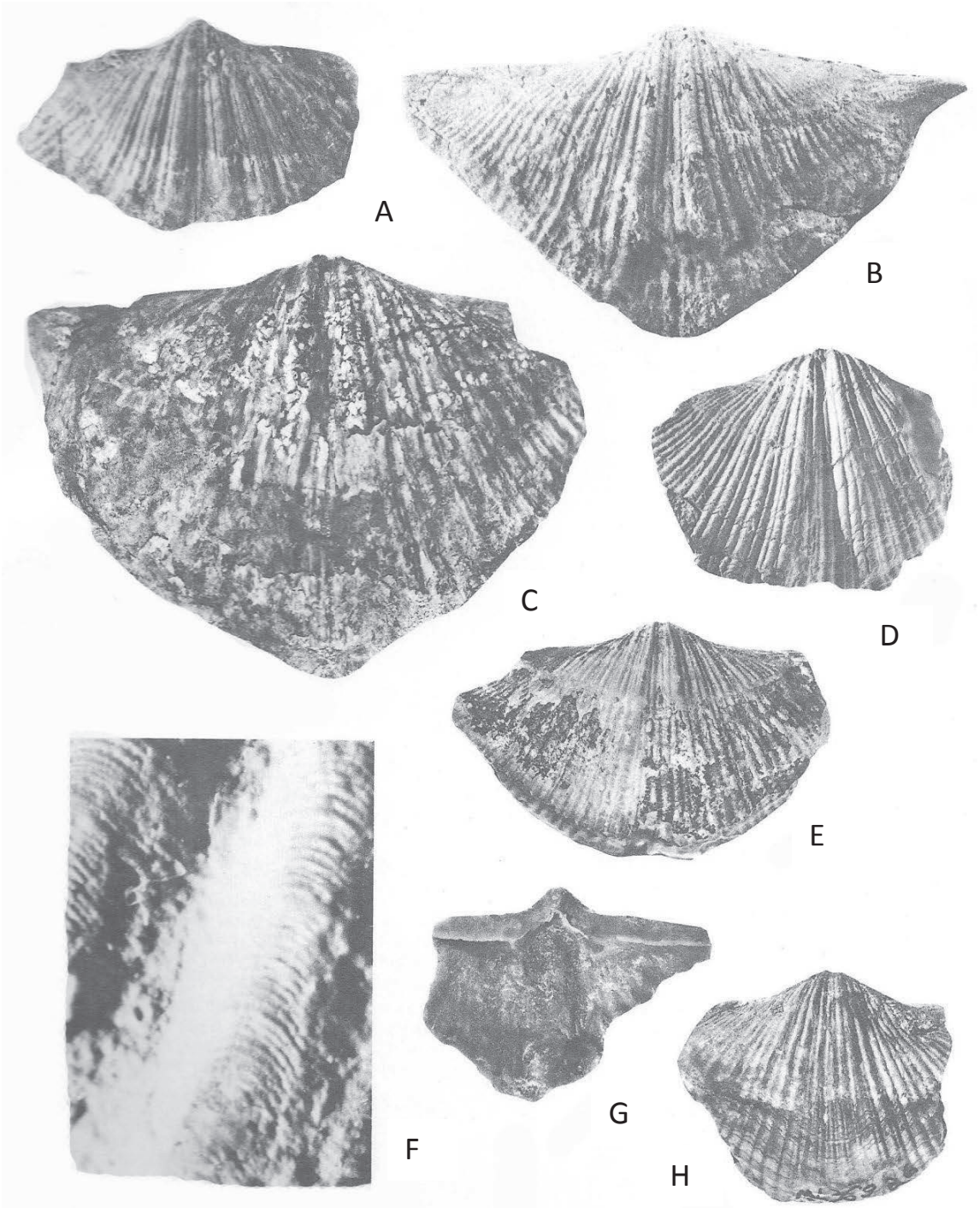


Fig. 244. *Frechella gwinneriformis* (Legrand Blain) from the upper Visean of Algeria, x1 and micro-ornament, x8. (Legrand Blain 1971). Fig. 245G shows a delthyrial cover plate.

(Legrand-Blain 1986, Fig. 13), without forming a prominent apical callosity. A specimen provided to me by Marie Legrand-Blain shows thick apical callus joining the adminicula, with

part of a delthyrial cover plate preserved at the delthyrial apex (Fig. 246). Plicae are well developed with few costae. *Frechella* is older than most other neospiriferid genera, being of Visean to Serpukhovian age, and not all aspects of the genus are known. A slightly older species from the same succession, called *Neospirifer fascicostatus* Menchikoff, includes material with dorsal valves, and some figured specimens show no costae over the plicae. For this species, a laminated plate was illustrated as covering much of the delthyrium (Legrand-Blain 1971, fig. 3), with no peduncular gap. Legrand Blain suggested that *Neospirifer nalivkini* Litvinovich, 1962 from upper Visean-Namurian of Kazakhstan was similar.

Fig. 245. *Frechella fascicostata* (Menchikoff), ventral internal mould, showing vascular pattern typical of Spiriferidae. Specimen x1, from upper Visean of Algeria. (Legrand-Blain 1968).

Other genera are mostly Permian, several extending into late Changhsingian. Occurrences in Pennsylvanian faunas need closer inspection, according to Poletaev (1997), and some forms look close to Spiriferalarinae.

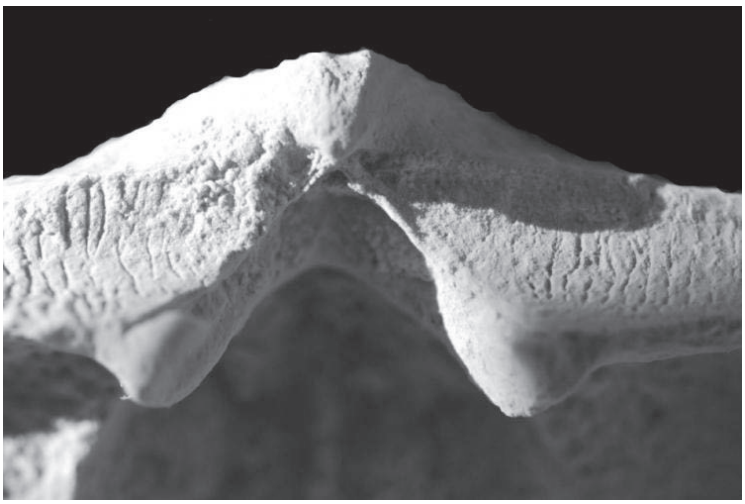


Fig. 246. *Frechella fascicostata* (Menchikoff), BR 3217, delthyrial area showing small cover plate. From late Visean of Algeria, x6.

Subfamily **SEPTOSPIRIFERINAE** new subfamily

Name genus: *Septospirifer* Waterhouse, 1971b from Gzhelian of Yukon Territory, Canada, here designated.

Diagnosis: Typified by median septum in ventral valve. Ventral umbones extended, costae fine. Upper Carboniferous (Gzhelian) to Middle Permian (Roadian).

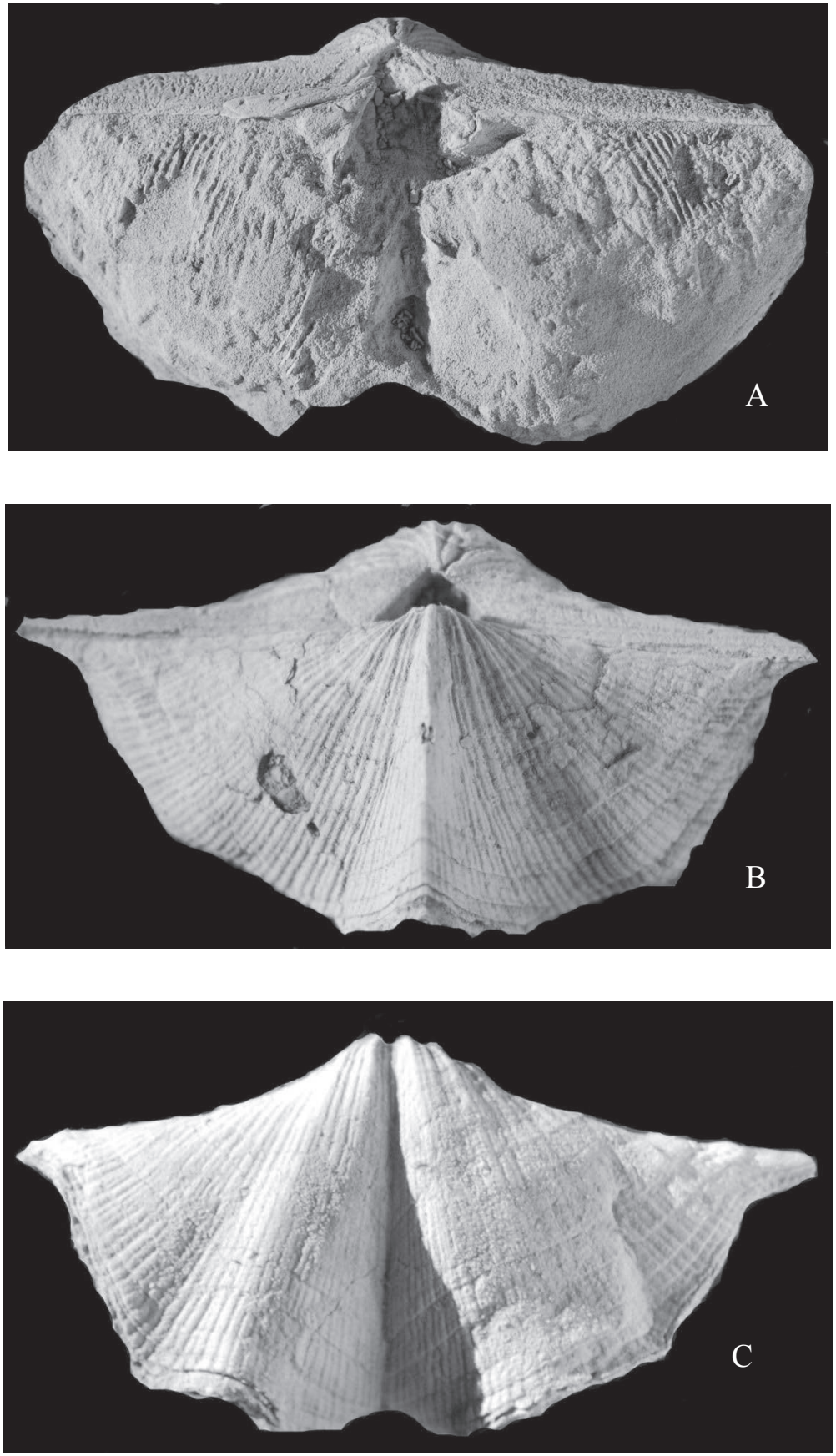


Fig. 247. *Gobbetifera angulata* Waterhouse. A, dorsal view of ventral valve and spiralia, GSC 136655, x1.1. B, C, dorsal and ventral views of exterior, GSC 136656, x1.2. From Assistance Formation (Roadian), Canada, x1,

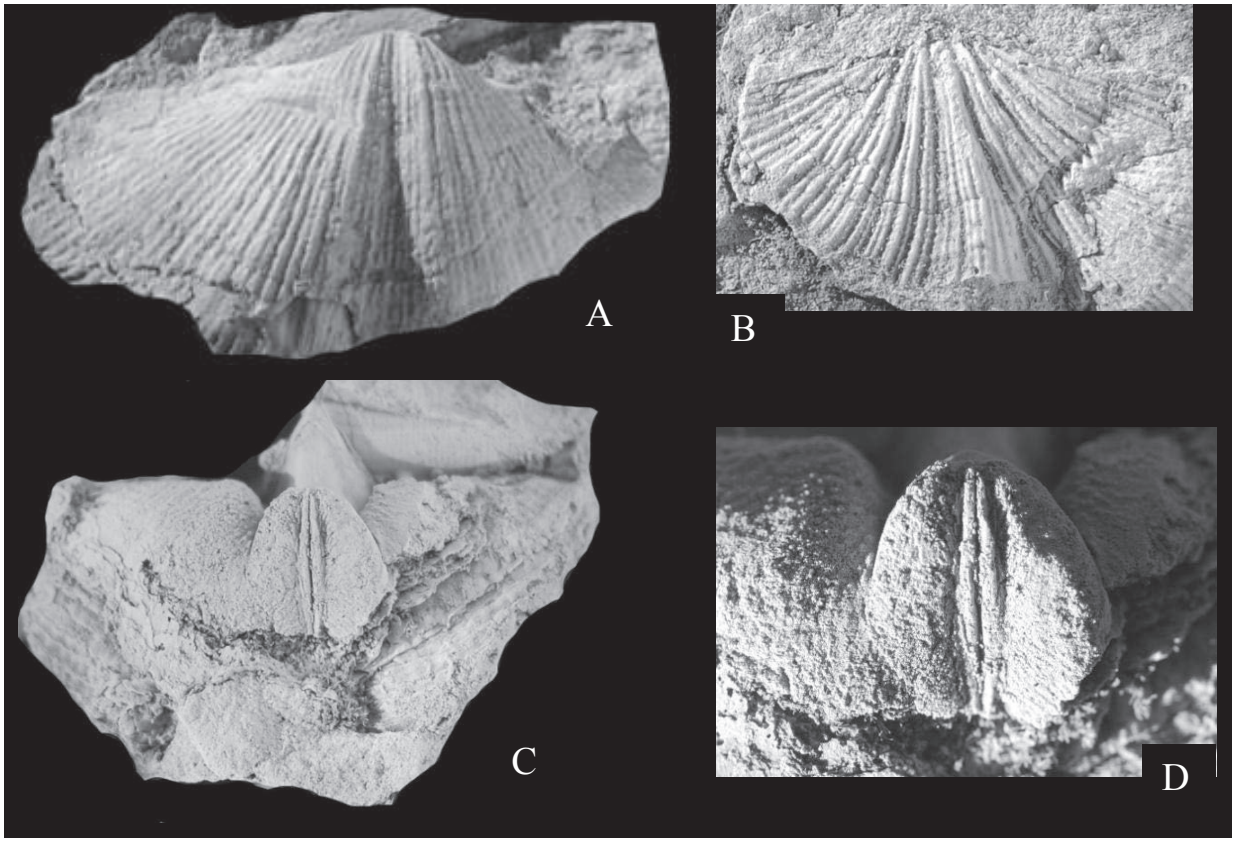


Fig. 248. *Septospirifer tatondukensis* Waterhouse. A, ventral valve GSC 136657, 1. B, dorsal valve, GSC 136658, x2. C, ventral internal mould,GSC 136659, x1.3. D, detail of ventral muscle field of GSC 136659, x3. From lower Jungle Creek Formation (Gzhelian), Yukon Territory, Canada. (Waterhouse, in press)

Genera: *Septospirifer* Waterhouse, *Gobbettifera* Waterhouse.

Discussion: Members of this subfamily are limited so far as is known to northern Canada. *Septospirifer* has somewhat pointed ventral umbo and narrow plicae, whereas the plicae in *Gobbetifera* are few, and the two inner plicae pairs merge to form a broad fold, much as in the type species of *Kaninospirifer*, so that the two genera look very similar to each other. But *Kaninospirifer* lacks the septal development in the ventral valve.

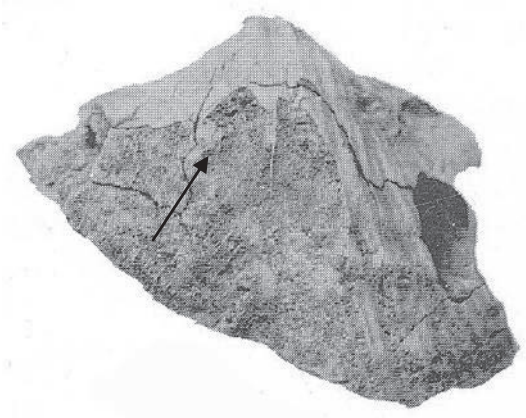


Fig. 249. *Gobbettifera* sp. ventral valve x2, showing high ventral septum, as arrowed, from lower Tatonduk Formation (upper Artinskian), Ogilvie Mountains, Yukon Territory, Canada. (Bamber & Waterhouse 1971).

Gourvennec in Gourvennec & Carter (2007, p. 2781) synonymized *Gobbetifera* with *Septospirifer*, and the two do look very close to each other, even though the type species of one is of Gzhelian age (Late Carboniferous) and the other late Cisuralian to mid-Permian. But the median ventral septum is much higher in the younger form, *Gobbetifera,* than in *Septospirifer.*

Subfamily **KANINOSPIRIFERINAE** Kalashnikov, 1996

[Kaninospiriferinae Kalashnikov, 1996, p. 133].

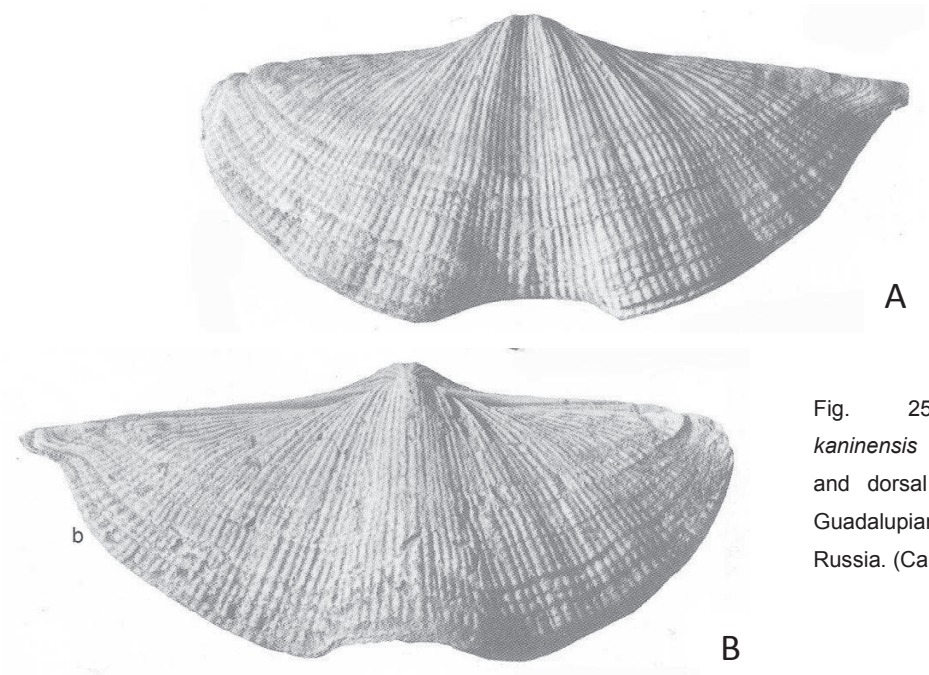


Fig. 250. *Kaninospirifer kaninensis* (Licharew), ventral and dorsal aspects, x1. From Guadalupian of Kanin Peninsula, Russia. (Carter 2006a).

Diagnosis: Weakly transverse shells with costae and plicae. Dental plates very low. Lower Permian (Sakmarian) to Upper Permian (Changhsingian).

Genera: *Kaninospirifer* Kulikov & Stepanov*, Costatispirifer* Archbold & Thomas, *?Crassispirifer* Archbold & Thomas, *Imperiospira* Archbold & Thomas, *Quadrospira* Archbold, *Wadispirifer* Waterhouse.

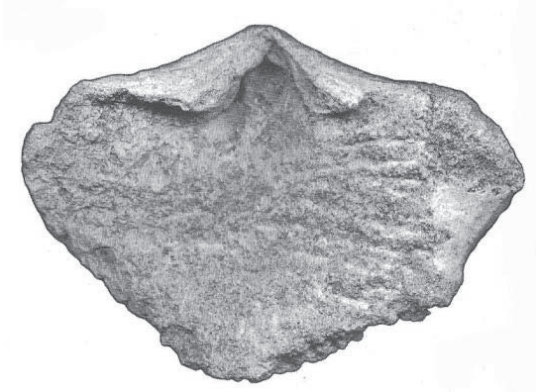


Fig. 251. *Kaninospirifer stepanovi* Grunt, ventral valve, showing low dental plates, x1.5. From Guadalupian of Kanin Peninsula, Russia. (Grunt 2006).

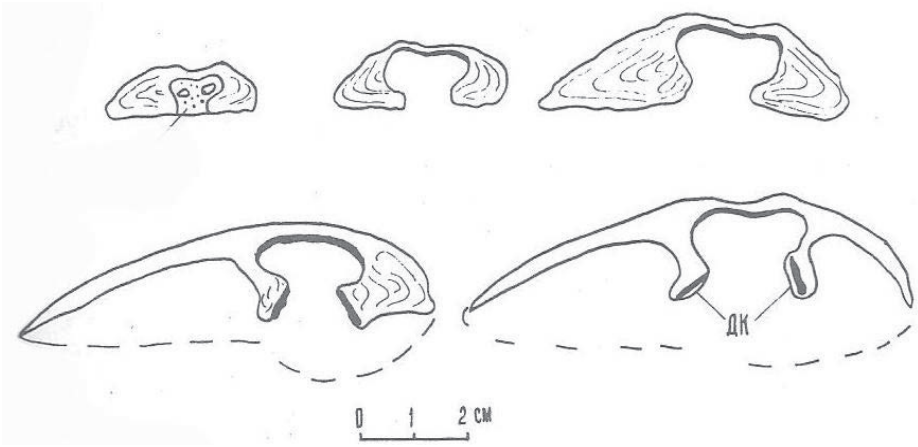


Fig. 252. *Kaninospirifer kaninensis* (Licharew), transverse sections of the ventral valve showing the nature of the low dental plates (DK). From Guadalupian of Kanin Peninsula, Russia. (Kalashnikov 1998).

Discussion: The diagnosis is discussed by Waterhouse (2004, p. 129), and other workers have a different view: they stressed that plicae fade anteriorly as the main criterion. To Waterhouse (2004), the fading of plicae developed independently in other unrelated genera such as *Aperispirifer*, in a trigonotretid lineage (see Waterhouse 1964). Anyway, as shown

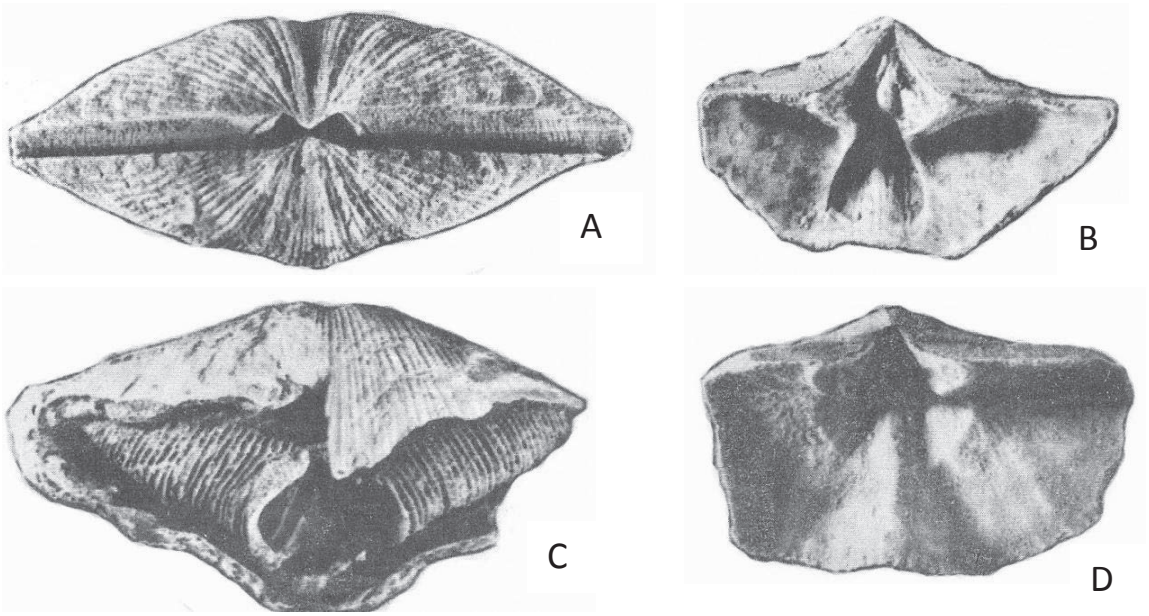


Fig. 253. *Kaninospirifer kaninensis* (Licharew). A, posterior view. B, dorsal valve showing dental plates that seem normal rather than low for Neospiriferinae, and suggestion of eccentric umbonal callosity. C, anterior view showing spiralia. D, ventral valve with low dental plates. From Kanin Peninsula. (Kalashnikov in Molin et al. 1983).

in the accompanying figures of *Kaninospirifer*, the plicae do not seem to fade that much. Some Australian genera, such as *Quadrospira* Archbold, show plicae that vary, either strong

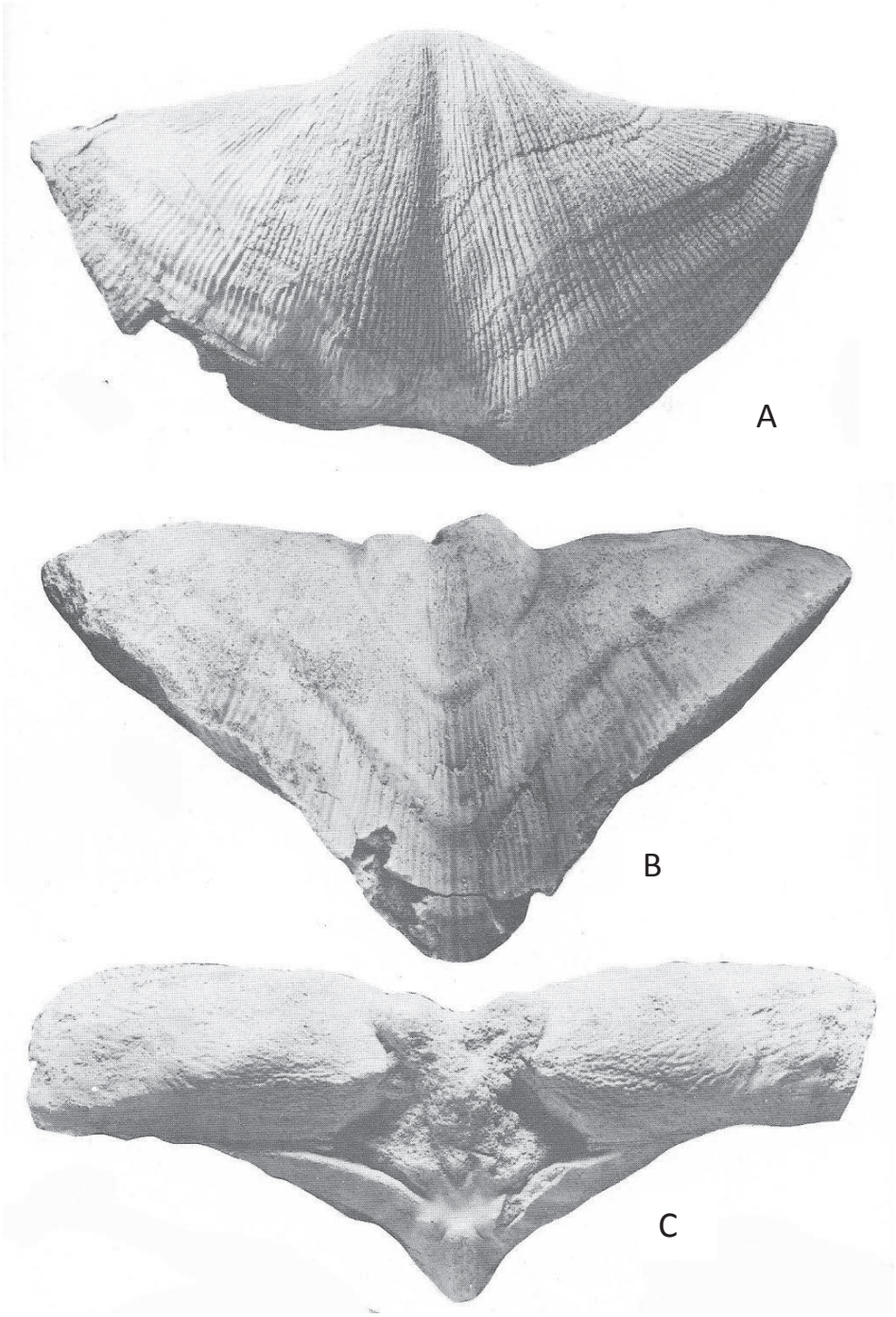


Fig. 254. *Wadispirifer grandis* (Archbold & Thomas). A, ventral valve holotype. B, C, internal mould showing ventral and posterior views. From Hardman Formation (Wuchiapingian), Western Australia. Specimens x1. (Archbold & Thomas 1986).

and persistent, or anteriorly fading. The dental plates are low in Gondwanan genera as figured from Western Australia by Archbold & Thomas (1986), including *Quadrospira*, *Imperiospira*, *Costatispirifer* and *Crassispirifer,* all named by Archbold & Thomas (1986). A small delthyrial plate was reported, under the umbo, and this is probably a small delthyrial cover plate. Species from Kanin Peninsula figured by Grunt (2006), and from Mongolia by Liu

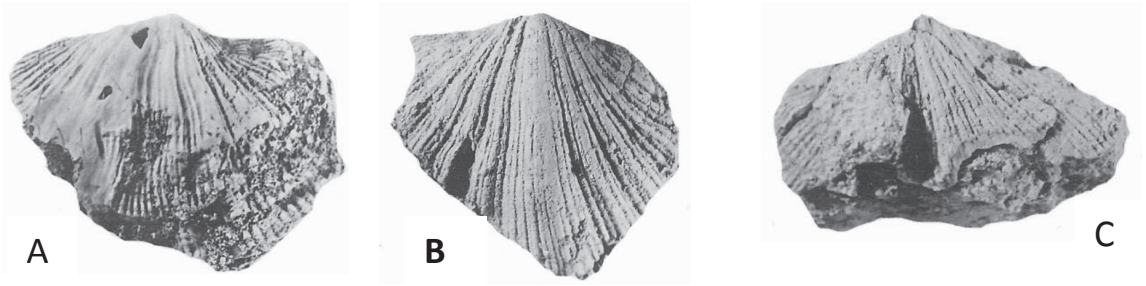


Fig. 255. A, B, *Kaninospirifer borealis* Kulikov & Stepanov, ventral and dorsal valve. C, *K. kaninensis* (Licharew), ventral valve. Specimens from Kanin Peninsula, x1. (Stepanov, Kulikov & Sultanaev 1975). The figures were prepared from photographs also used in the original plate, and provided by M. V. Kulikov.

& Waterhouse (1985), as *adpressum*, and Pavlova (1991) as *latissima,* show broad gently rounded crests for the inner plicae. Shi et al. (2002, p. 294) claimed that adminicula were not developed in *Kaninospirifer*, but adminicula are clearly shown in transverse sections offered by Kalashnikov (1998, text-fig. 6), as repeated in Fig. 253. It was also suggested that the costae of *Kaninospirifer* are distinctively fine and equidimensional – yet the readers may measure for themselves how much finer the costae are on *Kaninospirifer* (see Fig. 255) than in *Neospirifer* or *Betaneospirifer* (see Fig. 241, 242). There does not seem to be much difference, and if there is any, it need not rate as being of subfamilial significance. Figures for the type species that have been published are moderately revealing, and the best appear to have been offered by Kalashnikov in Molin et al. (1993), reproduced herein. Questions still remain over the validity of the subfamily, as distinct from Neospiriferinae, and may

Fig. 256. *Wadispirifer amplus* (Archbold & Thomas), ventral internal mould with typical broad adductor field and very wide sulcus. From Wandagee Formation (Artinskian), Western Australia, x1. (Archbold & Thomas 1986).

depend on the nature of the delthyrial apparatus, which requires further elucidation, and the height of the dental plates, which may have been variable. The appeal of the subfamily may lie in the palaeogeographic distribution, interpreted as indicating a massive flourishing in

Western Australia, as a southerly counterpart to the faunas of northern Russia.

Subfamily **BLASISPIRIFERINAE** new subfamily

Name genus: *Blasispirifer* Kulikov, 1950, p. 6 from Wordian of Russia, here designated.

Diagnosis: Small, costate plicae, no adminicula, possible pleromal development and small connector delthyrial apparatus appears in similar-looking material. Lower and Middle Permian (Kungurian-Wordian).

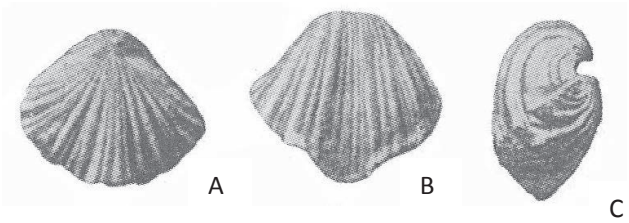


Fig. 257. A-C, *Blasispirifer blasii* (Verneuil), dorsal, ventral and lateral views, x1.5. From western Russia (Kungurian-Roadian). (Licharew 1939),

Genus: *Blasispirifer* Kulikov.

Discussion: *Blasispirifer* Kulikov, based on *Spirifer blasii* Verneuil, 1845, has low dental plates and lacks adminicula. Costae are developed in bundles. Serial sections of *B. multiplicicostatus* (Netschajew) in Gubareva & Boltaeva (1998, text-fig. 1) shows separate dental plates and crural plates, but no adminicula or tabellae. Nor do they show a connector plate, which therefore has to be regarded as poorly developed, or buried in callus, or completely absent, and therefore supporting a position within Neospiriferidae. Indeed Gubareva & Boltaeva (1998) followed by Carter (2006a, p. 1791) allocated the genus to Neospiriferinae, and although the plates may have been buried in secondary shell, this is deemed unlikely, and no delthyrial cover plate, or adminicula or has been reported. There is some approach to *Alphaneospirifer,* which lacks a connector plate, but there is no cruralium in the dorsal valve, unlike the arrangement in *Alphaneospirifer*.

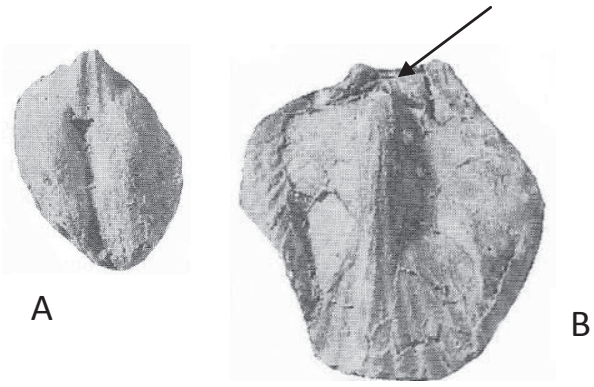


Fig. 258. *Blasispirifer* cf. *reedi* (Licharew), ventral and dorsal internal moulds, x1, x2, with arrow pointing towards what appears to be a connector plate. From Middle Permian at Moribu, central Japan. (Shi & Tazawa 2001).

A specimen figured from Japan by Shi & Tazawa (2001, Fig. 2.6b) suggests a subdelthyrial plate, which challenges the assessment and data provided by Gubareva &

Boltaeva (1998), and invites further study. Given the Japanese material, it would seem possible that *Blasispirifer* developed from Spiriferalariinae by loss of adminicula, and possibly loss or diminution of any connector plate, though that is qualified by the nature of the type material from Russia, which of course may prove not to be congeneric.

Family **ALPHANEOSPIRIFERIDAE** Waterhouse, 2004

[Alphaneospiriferidae Waterhouse, 2004, p. 240].

Diagnosis: Closely costate shells with low plicae, low or no dental plates, no adminicula or subdelthyrial plate, dorsal cruralium sessile on floor of valve. Lower or Middle Carboniferous (Serpukhovian or Bashkirian) to Upper Permian (Wuchiapingian).

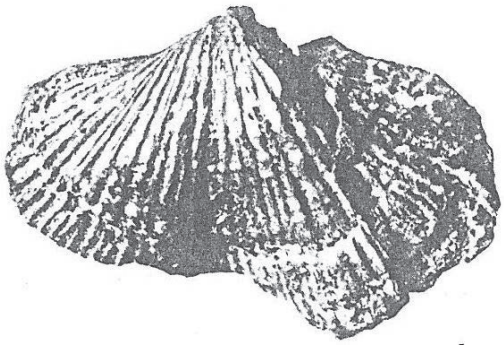


Fig. 259. *Spirifer mahaensis* Huang, type of *Alphaneospirifer*, ventral view, x1.5, from Lopingian (Upper Permian) of China.

Genera: *Alphaneospirifer* Gatinaud (syn. *Semibrachythyrina* Yang & Chang), *Alphaprotinus* new genus.

Discussion: This group is based on the highly unusual genus *Alphaneospirifer* Gatinaud, 1949, which externally looks closest to Neospiriferinae, but internally lacks adminicula, and has a cruralium or sessalium below the dental sockets, formed by crural plates without tabellae.

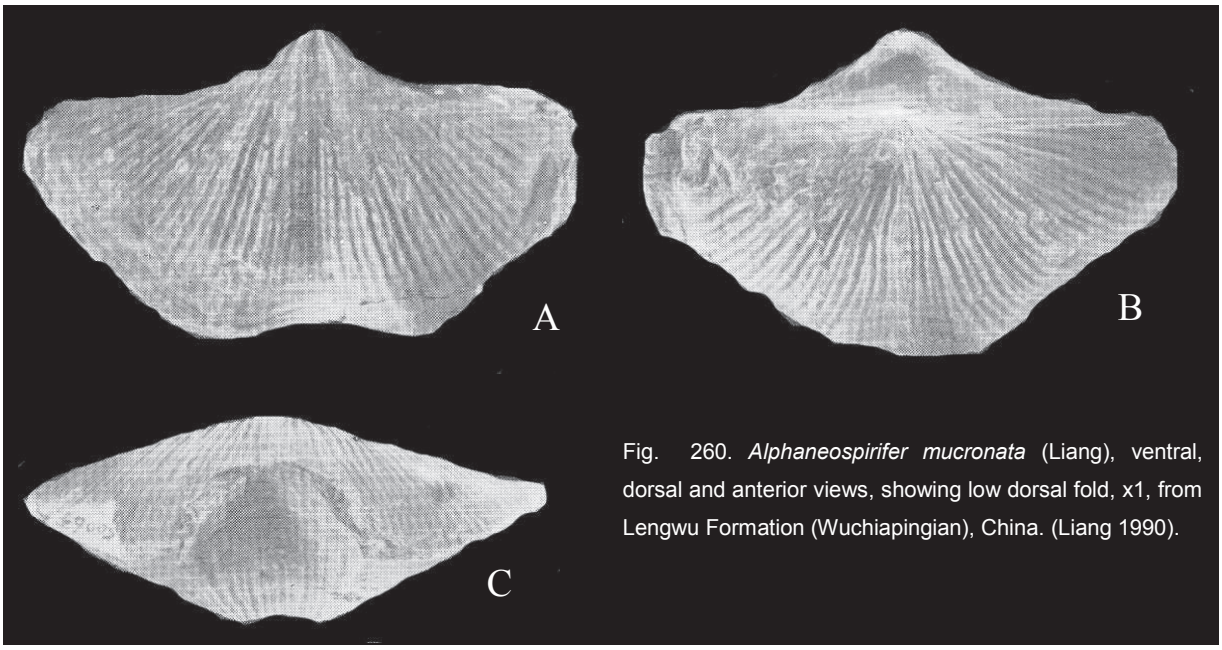


Fig. 260. *Alphaneospirifer mucronata* (Liang), ventral, dorsal and anterior views, showing low dorsal fold, x1, from Lengwu Formation (Wuchiapingian), China. (Liang 1990).

Alphaneospirifer has been described as *Semibrachythyrina* by Yang & Chang in Yang et al., and has cruralium or sessalium below the dental sockets, formed by crural plates without tabellae. *Alphaneospirifer* has been described as *Semibrachythyrina* by Yang & Chang in Yang et al. (1962) and Liang (1990). Because the external appearance is neospiriferid, and there is no connector plate, it is suggested that the genus was derived from such stock with the loss of the adminicula and extension of the crural plates into a cruralium that reached the floor of the valve. Presumably the development of a cruralium to couch the ventral muscles reduced the stress on the dental plates, so that adminicula became redundant. Scattered mid-Paleozoic genera and a few Cyrtospiriferoidea also developed a cruralium, allowing the possibility that *Alphaneospirifer* represented a cryptic Permian survivor, retaining the dorsal interior and developing subfasciculation. But in the absence of information about the nature of the mantle canal system, and even micro-ornament, reliance must be placed on external appearance, so that the genus is judged to be an exceptional offshoot from Neospiriferinae.

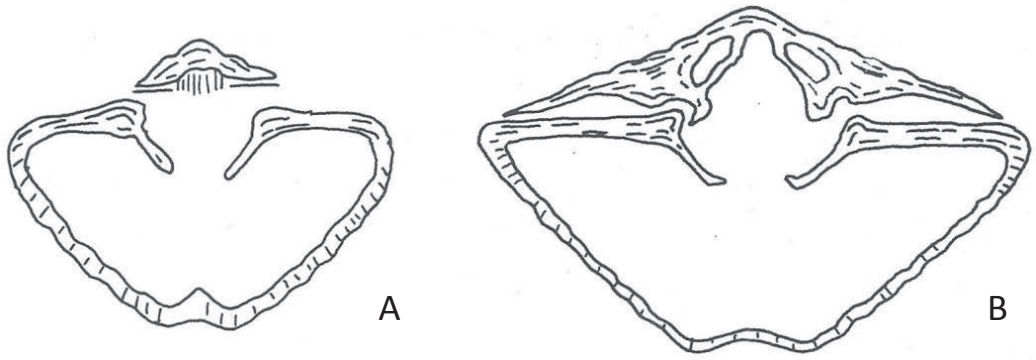


Fig. 261. *Alphaneospirifer pyramidithyris* (Liang), transverse sections dorsal valve on top, x2. From early Wuchiapingian of China. (Liang 1990).

Genus ***Alphaprotinus*** new genus

Derivation: alpha – first, first letter; protinus – further on, Lat.

Diagnosis: Finely costate shells with well defined plicae and high fold bearing narrow abruptly rounded crest.

Type species: *Tangshanella byrangi* Chernyak, 1963, p. 114 from Holodninskaya Suite (Cisuralian) of Taimyr Peninsula, Russia, here designated.

Discussion: Two Late Paleozoic species from Taimyr in northeast Russia, *Tangshanella taimyrica* (Einor, 1939) from the Makarovsky Horizon (Serpukhovian or Bashkirian), initially referred to *Spirifer*, and *T. byrangi* Chernyak in Ustritsky & Chernyak (1963, pp. 113, 114, pl. 41, fig. 2-7) from the Holodninskaya Suite and Evensk Suite (Cisuralian) have wide ventral interareas and have strong narrow costae in distinct fascicles, and are neospiriferid in general appearance. They have a narrower and better defined sulcus than in the type species of *Alphaneospirifer,* and the fold is markedly higher than that of *Alphaneospirifer*, judged from

the illustrations in Huang (1933, p. 41), and figures of *Semibrachythyrina* as proposed by Yang & Chang in Yang et al. (1962, p. 104), with type species *S. fasciculata*, reinforced by illustrations of species described as *Semibrachythyrina mucronata* and *S. pyramidiformis* by Liang (1990). These latter species are of early Wuchiapingian age.

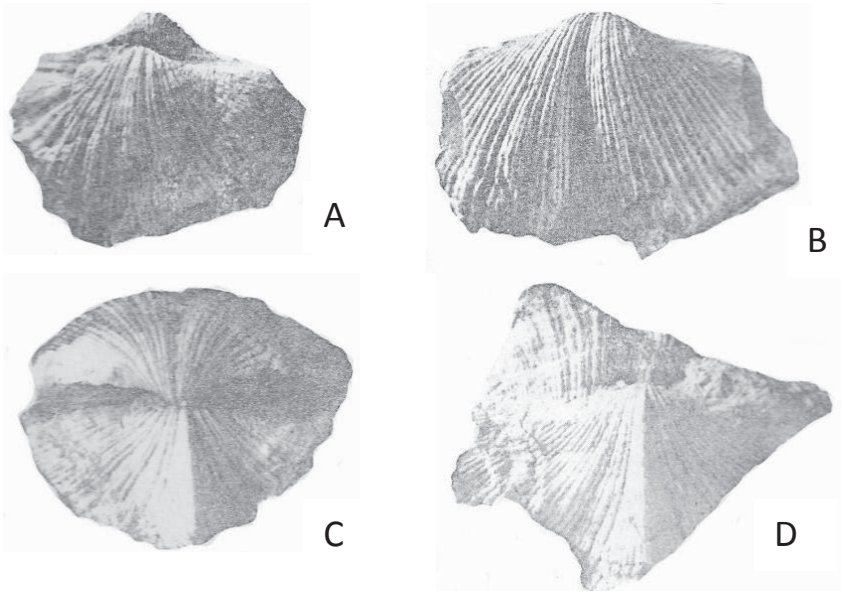


Fig. 262. A, *Alphaprotinus taimyrica* (Einor), dorsal view, from Makarov Suite. B-D, *A. byrangi* (Chernyak) from Holodnin Suite. B, ventral view. C, D, dorsal view, showing high dorsal fold. Specimens from Taimyr Peninsula, x1, of Serpukhovian-Bashkirian and Cisuralian age, respectively. (Ustritsky & Chernyak 1963).

Superfamily **SPIRIFERELLOIDEA** Waterhouse, 1968

[Nom. transl. hic ex Spiriferellinae Waterhouse, 1968, p. 9].

Diagnosis: Medium-small distinctively subpentagonal to subtriangular shape and subelongate with short hinge as a rule, plicate, sulcate, may be costate, with micro-ornament of commarginal and radial fila, often pustulose. Umbonal callosity or delthyrial cover plate and connector plate. Adminicula, dental plates, crural plates. Ventral valve often secondarily thickened. Middle Carboniferous (?Bashkirian or Moscovian) to Upper Permian (Changhsingian).

Fig. 263. *Spiriferella clypeata* Cooper & Grant, x1, showing mantle canal system. From Appel Ranch Member (Wordian – lower Capitanian). (Cooper & Grant 1976).

Discussion: Spiriferelloidea constitute a highly distinctive but not very large group, standing apart from most genera within Cyrtospiriferoidea, Paeckelmannelloidea, and Spiriferoidea in being less transverse with thickened ventral valve and distinctively pustulose micro-ornament. On the other hand, spiralia, denticulate hinge and internal plates are shared with members of those superfamilies. The mantle canal system seems special to Spiriferelloidea, and shows a pattern moderately like that of spiriferids, but coarser in depth and spacing of pits, and in other specimens indicates a closely spaced anastomosing radiating pattern as

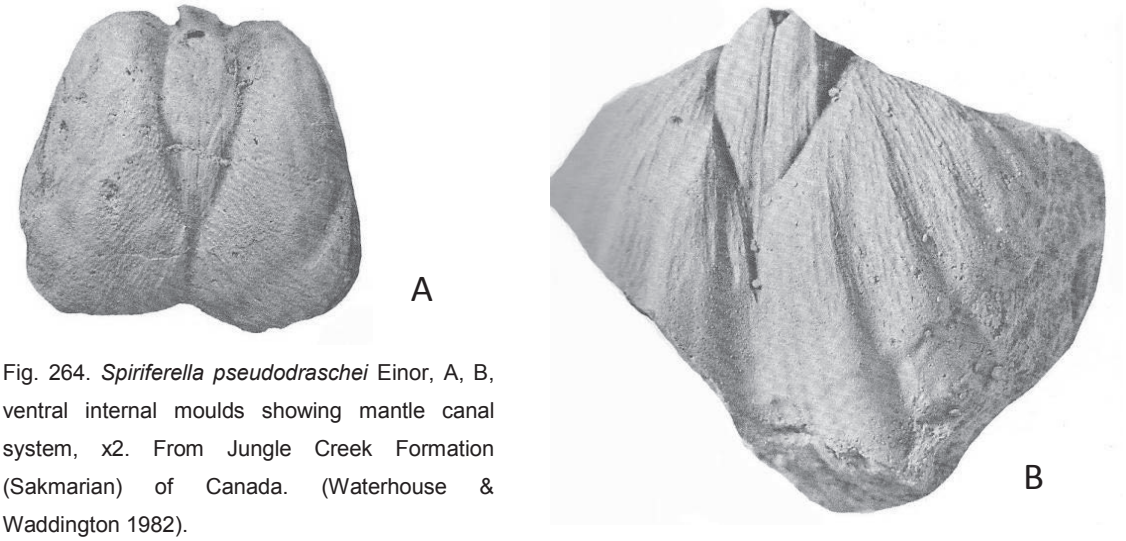


Fig. 264. *Spiriferella pseudodraschei* Einor, A, B, ventral internal moulds showing mantle canal system, x2. From Jungle Creek Formation (Sakmarian) of Canada. (Waterhouse & Waddington 1982).

illustrated in Fig. 263-265, differing from the standard spiriferid pattern, but not forming an open subrectangular network as in choristitids and trigonotretids. There appears to be variation in the development of a delthyrial cover plate, or a prominent umbonal callosity. *Spiriferella* and its allies may exhibit one or other, or both. In spite of often displaying an umbonal callosity, a discrete connector plate is frequently visible, or it has been buried in secondary callus. That is one of the features of many species in the superfamily – the substantial secondary thickening in the ventral valve.

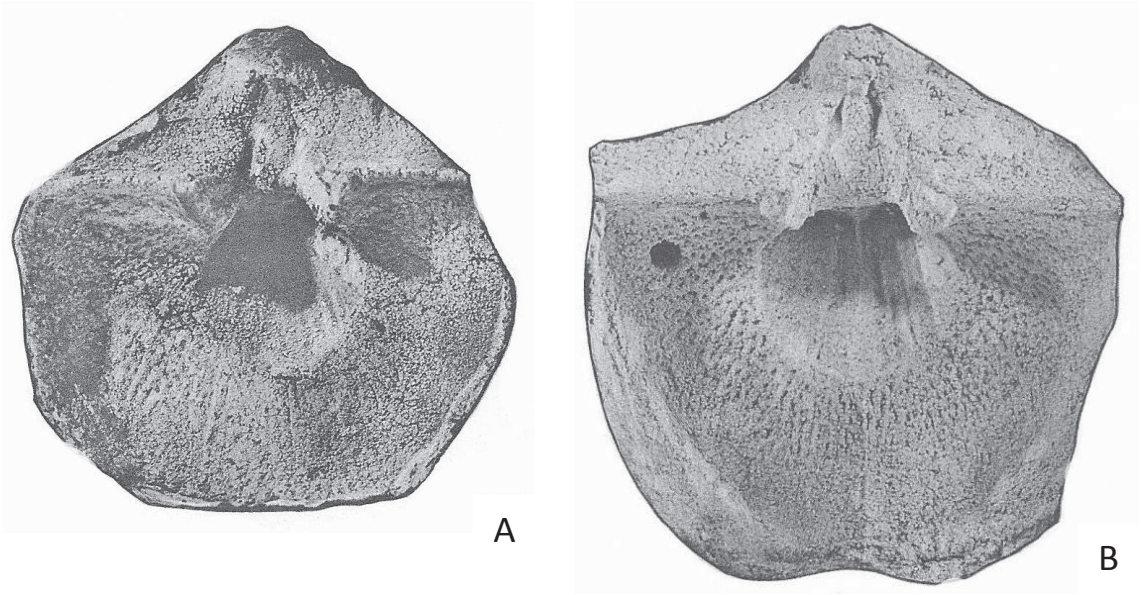


Fig. 265. *Spiriferella supplanta* Waterhouse, ventral valves, x2. A, showing umbonal callus, thick connector plate, floor pits and a few radiating canals, especially near hinge. Note hinge denticles. B, vascular pattern dominated by well spaced pits. From Letham Formation (Kungurian), New Zealand. (Waterhouse 1964).

For origin of the superfamily, there are several possibilities. On the one hand, the group may go all the way back to adolfioid subfamilies with plicae, pustules, and similar internal plates, no younger than of Lower Devonian age, and closely related to Silurian brachiopods. That would mean a lost link lasting through the Middle and Upper Devonian, and Lower Carboniferous, which is a very long time. It seems more likely that Spiriferelloidea branched from Spiriferoidea during mid-Carboniferous time, and that some of the attributes of the early group were revived. On the one hand, there are suggestions of a relationship to Spiriferalarinae through the presence of a connector plate, allowing for modification of the ornament. Yet a closer relationship to Purdonellidae Poletaev may be suggested, through the sharing of a connector plate and similarity in plication with narrow interspaces to some Purdonellidae and various Choristitoidea. But there is little sign of the reticulate mantle canal system typical of some Choristitidae, so the similarity is regarded as due to convergence.

Family **SPIRIFERELLIDAE** Waterhouse, 1968

[Proposed de novo as full family by Termier et al., 1974, p. 136, independent of Spiriferellinae Waterhouse, 1968, p. 10].

Diagnosis: Externally distinctive, with rounded plicae and narrow interspaces, may be smooth or costate, micro-ornament cancellate with pustules. Adminicula short, usually buried in secondary thickening, dental plates, ctenophoridium and crural plates. Posterior ventral valve heavily thickened as a rule. Pennsylvanian (Kasimovian) to Permian (Changhsingian).

Discussion: This is a highly distinctive family, and stands apart from members of Spiriferoidea, as distinct as any superfamily, and showing considerable variation. For example the micro-ornament may be pustulose or cancellate, the plicae may be costate or smooth, the fold varies considerably in prominence and transverse profile, and the delthyrium may be open with umbonal callus, or closed by a delthyrial cover plate as noted by Shen et al. (2001, pp. 165, 167), or may exhibit a connector plate, as in *Bamberina* (see Fig. 272, p. 218). The suite of *Spiriferella* and allied species from the Glass Mountains of Texas, with their favourable preservation of the ventral umbonal shell, establishes that a connector plate was developed, at least in many species, and that it was often buried in secondary shell. Secondary thickening in the ventral valve may be great, much more than in other members of Spiriferidina, and together with extensive postulation, helps define a highly distinctive superfamily group.

Subfamily **SPIRIFERELLINAE** Waterhouse, 1968

[Spiriferellinae Waterhouse, 1968, p. 10. Syn. Hunzininae Angiolini, 2001, p. 332].

Diagnosis: Moderate to well developed dorsal fold, traversed by median groove. Shape weakly transverse to subelongate. Upper Carboniferous (Kasimovian) to Upper Permian (Changhsingian).

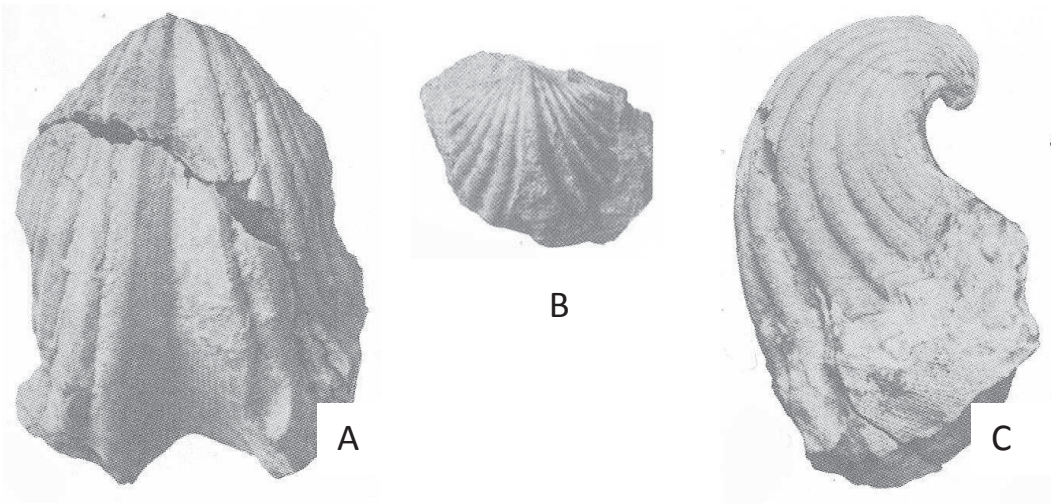


Fig. 266. *Arcullina barchatovae* (Waterhouse & Waddington). Specimens x1, figured as *Spiriferella saranae* by Chernyshev (1902), incorrectly according to first hand re-examination as reported in Waterhouse & Waddington (1982). The same specimens were reproduced as *saranae,* type species of *Spiriferella,* by Carter (2006a).

Genera: *Spiriferella C*hernyshev, *Alispiriferella* Waterhouse & Waddington, *Bamberina* Waterhouse, *Canalisella* Waterhouse, *Eliva* Fredericks, *Eridmatus* Branson, *Hunzina* Angiolini, *Nakmusiella* Shen et al., ?*Spiriferellaoides* Lee, Gu, & Li (syn. *Spiriferelloides* Li, Gu & Li, nom. nud.), ?*Tintoriella* Angiolini.

Discussion: It should be noted that Carter (2006a, Fig. 1198.1) figured as type species for *Spiriferella saranae* (Verneuil) material illustrated by Chernyshev (1902) from the Schwagerinakalk of Sula River. That particular material has been named *Spiriferella barchatovae* by Waterhouse & Waddington (1982), and is evaluated as a species of *Arcullina* Waterhouse, 1986 (see Fig. 266). Type *saranae* comes from younger beds of Artinskian age, as figured by Chernyshev (1902, text-fig. 41-46).

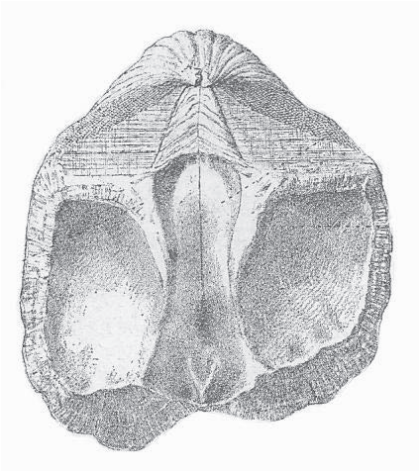


Fig. 267. *Spiriferella saranae* (Verneuil), internal ventral valve figured by Chernyshev (1902, text-fig. 41), showing long adminicula that Angiolini alleged were characteristic of *Tintoriella*, and not found in *Spiriferella*. From Artinskian of Sylwa River, Russia, x1.

Tintoriella Angiolini, type species *Spirifera rajah* Salter, 1865, provides an interesting challenge. It was named at least partly on the basis of comparison with material figured as *Spiriferella* in Chernyshev (1902, pl. 12, fig. 4, pl. 40, fig. 7), which was not type material, and is older than the original material described by Verneuil (1845) and Keyserling (1846). Angiolini reported several distinctions between *Tintoriella* and what she thought was Verneuil's species *saranae*. She noted the presence of what she called a pseudodeltidium (that is a covering plate) in *saranae*, absent from *rajah* of the Himalayas, the presence of an umbonal callosity in *rajah*, and the greater length of adminicula in *rajah* as compared with *saranae*. The latter point would seem to be verified by examination of Canadian specimens assigned to *saranae* by Waterhouse & Waddington (1982, pl. 4, fig. 4, 7, 8, 11), as reproduced in Fig. 268. But figures of larger *saranae* provided by Chernyshev (1902) show long adminicula, as reproduced herein (Fig. 267). The other two distinctions invite a degree of caution, because whilst it is undoubtedly true that some spiriferellids have a well developed delthyrial cover plate and others have an umbonal callosity, it is seldom clear that these features are specifically consistent, and so even more uncertain that the difference is of generic value. Unless of course there were geographic zones in which only an umbonal callosity was developed (outer Gondwana?), and a paleotemperate to paleotropical zone with

an admixture of callosity and delthyrial cover and connector plate. And then the question is whether such a difference reflected generic or geographic influence. Amongst ventral valves figured as *Spiriferella pseudotibetana* Stepanov from the Roadian Assistance Formation of Devon Island in the paleotemperate Canadian Arctic, one has an umbonal callosity, and another has a covering plate (Waterhouse & Waddington 1982, pl. 5, fig. 4, 6). As another example, for *Spiriferella gravis* from the Word Formation of paleotropical Texas, Cooper & Grant (1976, pl. 630, fig. 27) figured a ventral valve with an umbonal callosity, and another ventral valve (pl. 630, fig. 22) with deltidial cover. In instances of material from the Glass Mountains of Texas, the covering plate is clearly formed by deltidia. In material from the Himalayas, the plate seems to be one solid plate, and without first-hand inspection, it is not possible to confirm whether the plate was made up of one stegidial plate, or several, possibly overlain by secondary tissue, as described by Boucot (1963) for *Cyrtia.* In specimens figured by Chernyshev (1902 – see Fig. 267 herein), the covering plate has a median line of junction, as if formed by two deltidial plates, and there are growth lines. Such uncertainities should encourage testing of the distinctions to justify *Tintorella*, although it must be admitted

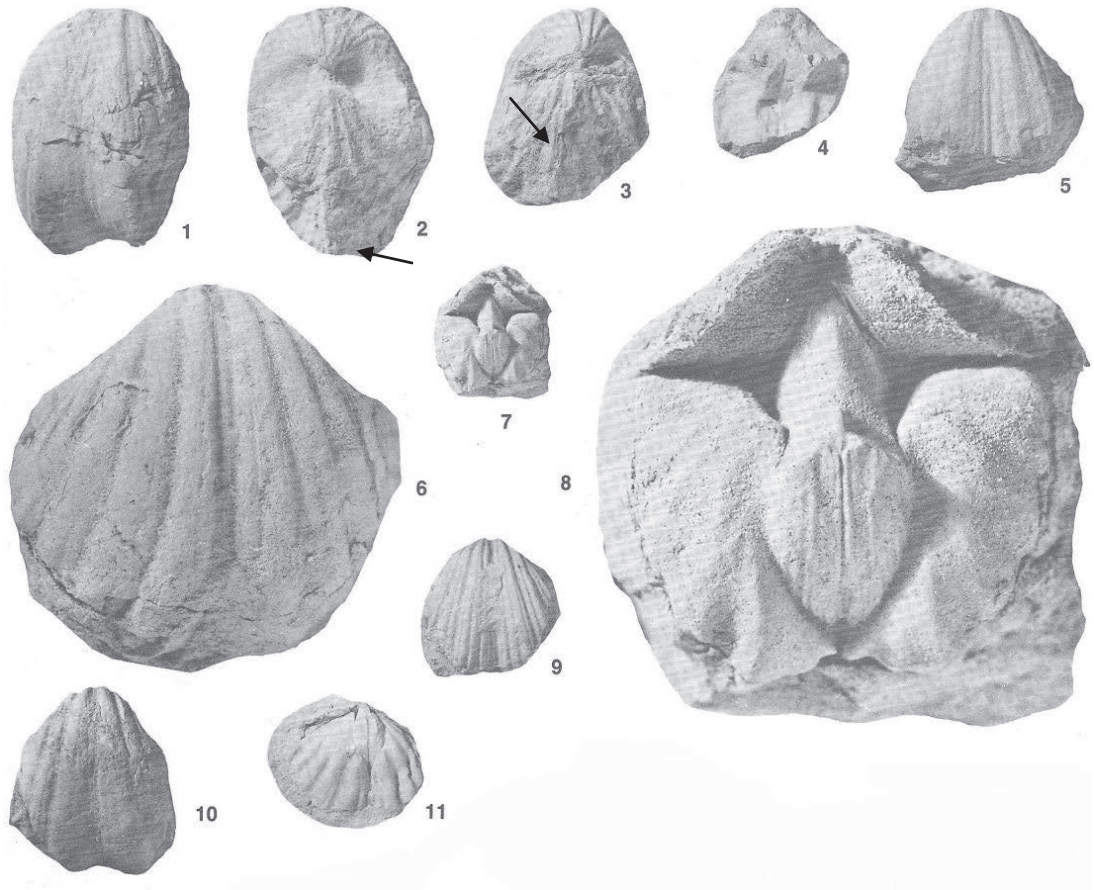


Fig. 268. *Spiriferella saranae* (Verneuil), as figured for Canadian specimens in Waterhouse & Waddington (1982, pl. 4). Fig. 6 x2, fig. 8 x4, other specimens x1. These are not topotypes, but after examination of types at the Chernyshev Museum in St Petersburg (then Leningrad), were considered to conform closely with Verneuil's original material, rather than the Chernyshev material figured as typical by Carter (2006a). The dorsal fold has a slender median groove, as arrowed (Fig. 269.2, 3).

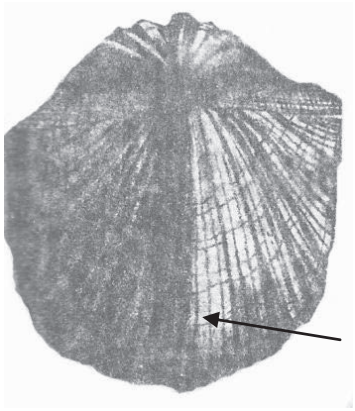


Fig. 269. The original figure of *Spirifer rajah*, from Wuchiapingian of Spiti Pass, Kashmir, x 1. (Salter 1865). Note that the fold is costate and traversed by a slender groove, as arrowed, in contrast to a figure of a different specimen in Davidson (1866, pl. 2, fig. 3), and reproduced in the *Revised Brachiopod Treatise*, which shows a smooth fold without costae or groove (see Fig. 271A). Possibly the fold on the specimen figured by Davidson had been exfoliated, but the specimen in fact still shows a slender median groove.

that Shi & Shen (1997), Shen et al. (2001) and Shi, Shen & Zhan (2003, p. 1062) have discounted its validity.

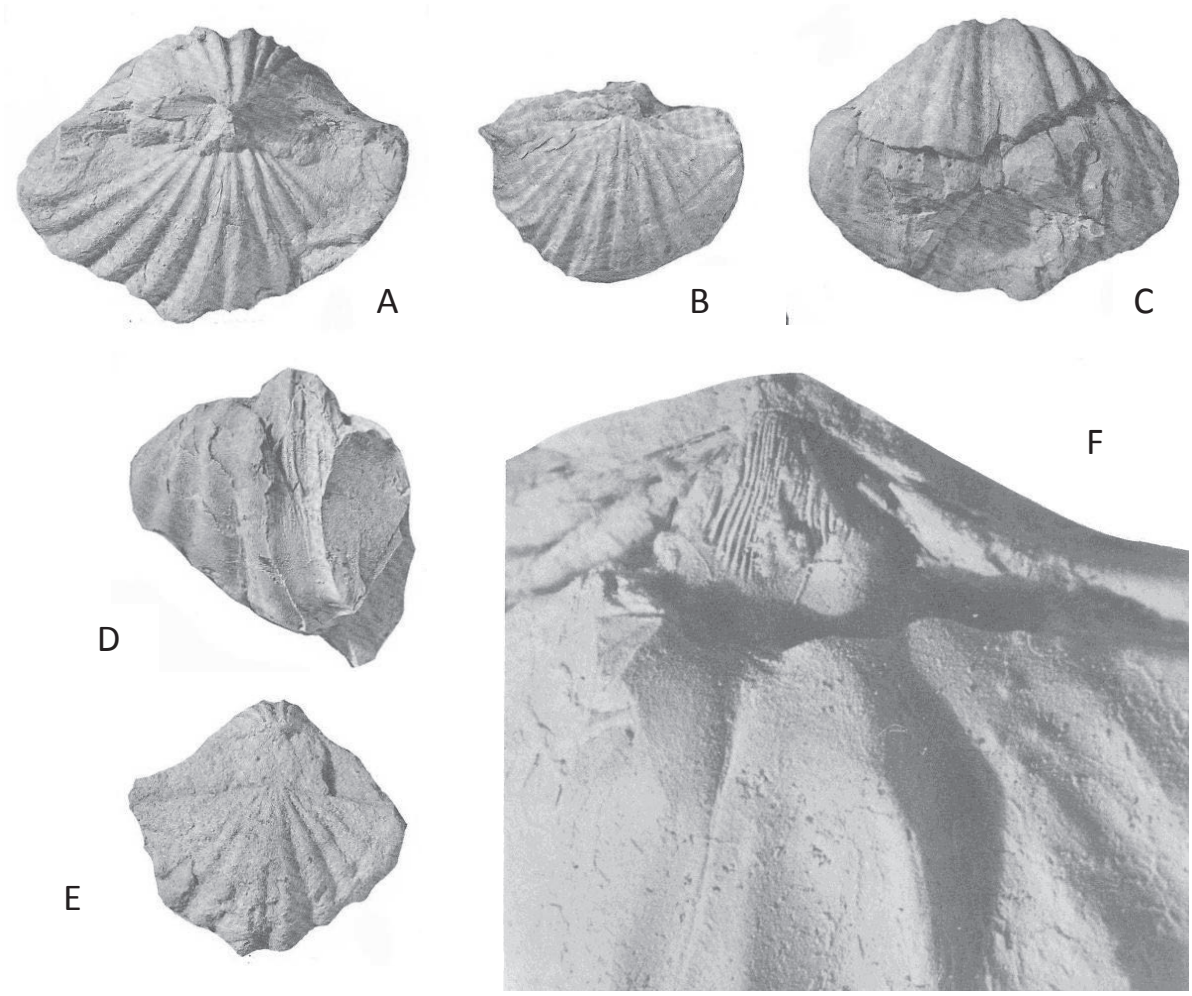


Fig. 270. A, C, D, F, *Canalisella leviplica* (Waterhouse & Waddington). A, dorsal aspect of holotype, x1, showing covering plate across delthyrium and wide dorsal channel. C, ventral valve, x1. D, ventral interior, x1.5. F, dorsal internal mould, posterior part, x4. B, *Alispiriferella ordinaria* (Einor), dorsal view, x1. E, *Canalisella gydanensis* (Zavodowsky), dorsal view, x1. Specimens from Permian of Canada. (Waterhouse & Waddington 1982).

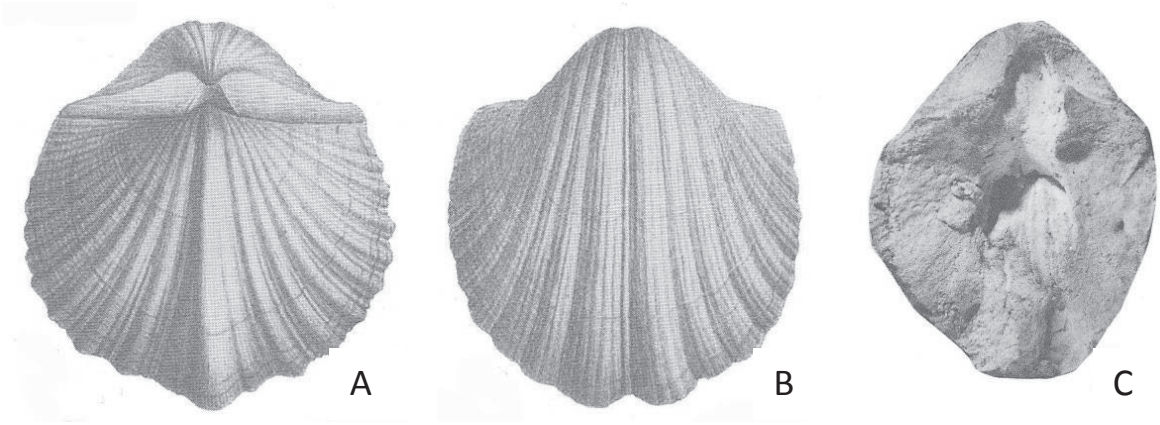


Fig. 271. *Tintoriella rajah* (Davidson). A, B, dorsal and ventral aspects of B 82086, x1. (Davidson 1866). The figures are substantially idealized, and not fully accurate. The specimen in fact shows a slender groove along the crest of the dorsal fold. See also Waterhouse (1978, p. 39). C, ventral interior, x1.5.

Fig. 272. *Bamberina annectens* (Cooper & Grant), ventral interior showing pleromal extensions leading to connector plate, x 2. From Bell Canyon Formation (Capitanian), Texas. (Cooper & Grant 1976).

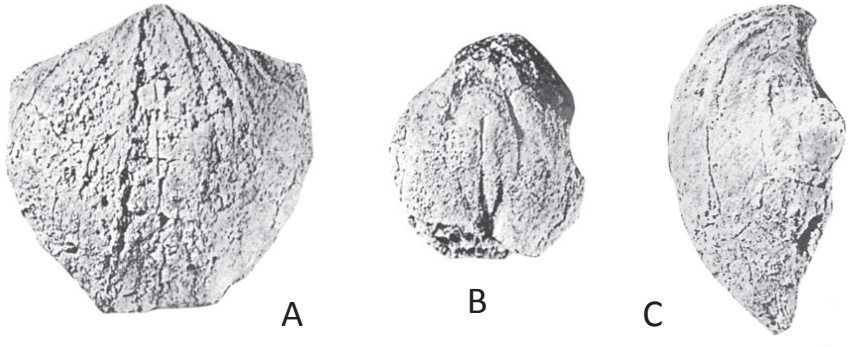


Fig. 273. *Nakmusiella selongensis* Shen et al. 2001, ventral views, x1.5, including holotype (B). From Late Permian of Tibet. (Shen et al. 2001). Courtesy Shen Shuzhong.

The distinctive genus *Nakmusiella* Shen et al. (2001) was left out of the *Revised Brachiopod Treatise*, and is here figured. It has scarcely any ventral sulcus and only low posterior plicae. An occurrence was also recorded in the Changhsingian of New Zealand (Waterhouse 2001, p. 96).

Fig. 274. *Eridmatus texanus* (Meek), dorsal, ventral and anterior aspects (dorsal valve on top), x1, from Desmoinesian of Kansas, United States. (Spenser 1967).

Hunzina Angiolini looks very like members of Spiriferellinae. Angiolini (2001, p. 332) in seeking to justify a separate subfamily for the genus stressed narrow hinge, non-plicate lateral slopes, rare fascicles, and predominantly concentric micro-ornament. It is considered that the last mentioned criterion could prove most useful, if it were correct, because various species allocated to Spiriferellinae vary considerably in plication and costation, but all have pustules. Even for the type species of *Hunzina*, Angiolini (1995, pl. 4, fig. 1-4) illustrated specimens with well developed plicae, and the plicae of a large specimen (Angiolini 1995, pl. 4, fig. 14) are typical of shells like *Spiriferella* and allies. Contrary to the diagnosis of Hunzininae in 2001, Angiolini (1995, p. 186) had reported the presence of pustules, something left out, but not contradicted, by Angiolini (2001). If pustules are present, then the validity of the subfamily becomes highly questionable, and Carter (2006a, p. 2786) agreed that pustules were present.

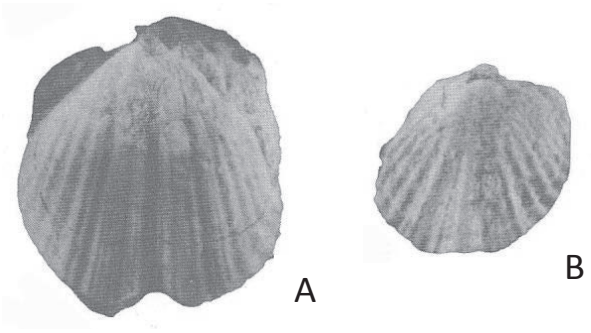


Fig. 275. *Hunzina electa* Angiolini, ventral and dorsal views, x1. From Cisuralian of Pakistan. (Angiolini 1995).

Eliva Fredericks, based on *Spirifer lyra* Kutorga, 1844, and well figured by Chernyshev (1902, pl. 6, fig. 6, 7, pl. 7, fig. 7, pl. 8, fig. 4, 5, text-fig. 150), Kulikov (1974, pl. 7, fig. 1) and Kalashnikov (1998, pl. 12, fig. 4-6) has fine costae in the sulcus and a number of narrow plicae laterally, with or without costae. It is of upper Cisuralian age. The dorsal median groove starts at the umbo and is well defined for the full length of the fold. It is not sure whether pustules are present in this species, which leaves the subfamily position insecure.

Subfamily **ARCULLINAE** new subfamily

Name genus: *Arcullina* Waterhouse, 1986, p. 4 from Arctic Guadalupian, here designated.

Diagnosis: Dorsal fold high with narrow crest and no sign of median groove. Cisuralian to Guadalupian of Urals and Arctic. Upper Pennsylvanian (Kasimovian) to Upper Permian (Changhsingian).

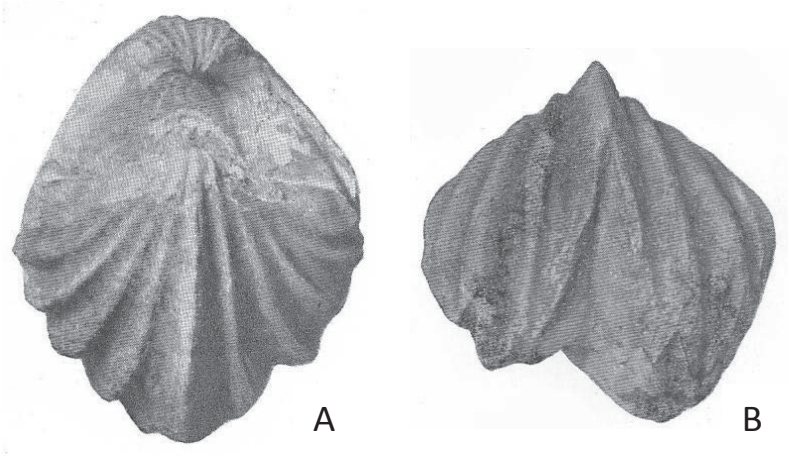


Fig. 276. *Arcullina polaris* (Wiman), dorsal and anterior aspects, showing the narrow dorsal fold crest without a median groove. Specimens x1, from the early Guadalupian or late Cisuralian Spiriferkalk of Spitsbergen. (Wiman 1914).

Genera: *Arcullina* Waterhouse, *Plicatospiriferella* Waterhouse & Waddington.

Discussion: *Arcullina*, based on *Spiriferina polaris* Wiman, 1914, p. 39, has a distinctive high dorsal fold which lacks the median groove or channel that characterizes most of the other genera assigned to Spiriferellidae. The genus is represented by a number of species in the Arctic, and has been especially well illustrated by Grunt (2006). Several species are found in the Late Permian of the Himalaya and Timor (Waterhouse 2004). According to Waterhouse & Waddington (1982, p. 19), the fold has a rounded crest in Chernyshev's so-called *saranae*, and they proposed the name *barchatovae* for the specimens, with the specimen figured by Chernyshev (1902, pl. 12, fig. 4) designated as holotype. Type *saranae* of Verneuil has a fold with a narrow median groove, as indicated in the original figure of a broken posterior dorsal valve (Verneuil 1845, pl. 6, fig. 156), and probable topotypes, or at least specimens from the same horizon, at the Chernyshev Museum of St Petersburg, Russia, have a rounded dorsal fold with a shallow median groove.

Subfamily **TIMANIELLINAE** new subfamily

Name genus: *Timaniella* Barkhatova, 1968, p. 162 from Kungurian-Roadian of Timan, Russia, here designated.

Diagnosis: Wide shells with extended hinge line and alate cardinal extremities. Plicae high with narrow rather than well rounded crests, and broad interspaces. Lower and Middle Permian Cisuralian (Sakmarian) to Guadalupian (Wordian).

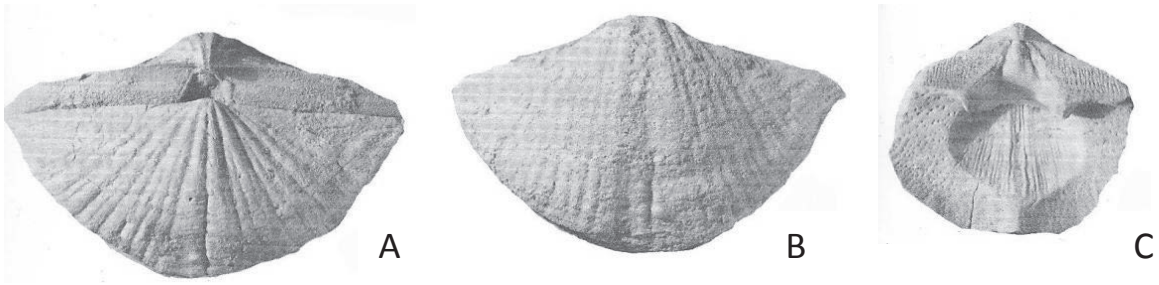


Fig. 277. A-C, *Timaniella harkeri* Waterhouse & Waddington, ventral and dorsal views of holotype, and ventral interior near umbo. Specimens from Guadalupian (Roadian, Wordian) of Canada, x1. (Waterhouse & Waddington 1982).

Genera: *Timaniella* Barkhatova, *Rhombospirifer* Duan & Li.

Discussion: In this subfamily, the hinge is broad and the cardinal extremities alate. Whereas the plicae of Spiriferellinae have broadly rounded crests and narrow groove-like interspaces, the less crowded plicae in these genera are higher medianly and so more angular in section, and the interspaces are not as narrow as in Spiriferellinae. In other respects, members are close to Spiriferellinae, with regard to a well developed groove along the crest of the dorsal fold, and nodose and cancellate micro-ornament.

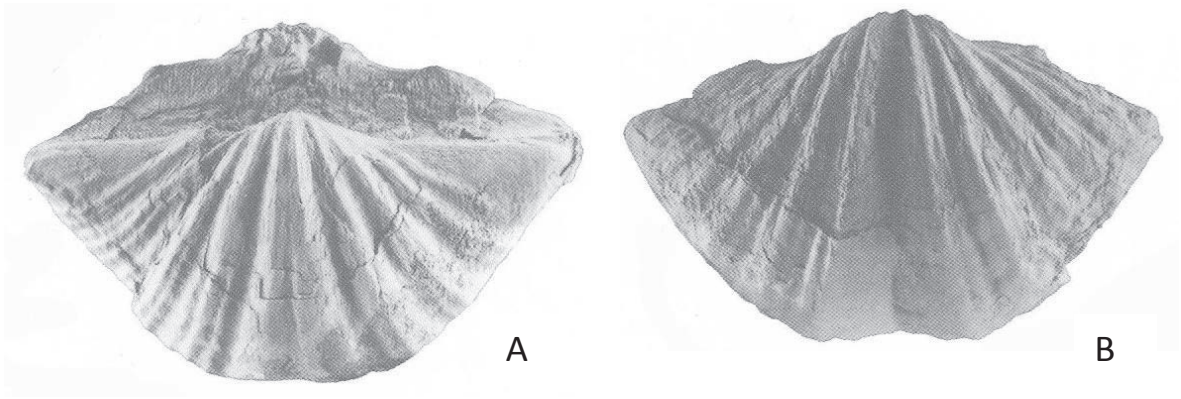


Fig. 278. A, B, *Rhombospirifer zhesiensis* Duan & Li, dorsal and ventral views, x1, from Cisuralian of Inner Mongolia. (Duan & Li 1985).

Family **ELIVINIDAE** Waterhouse, 2004

[Nom. transl. hic ex Elivininae Waterhouse, 2004, p. 223].

Diagnosis: Usually elongate shells, hinge may be narrow, plicae subdued or absent, fold distinctive, commencing posteriorly as a single rib as a rule, which branches into two ribs separated by a distinct but narrow channel. No pustules. Connector plate, but little secondary thickening. Lower Permian (?Asselian) to Late Permian (Changhsingian).

Discussion: This is a very distinctive group, and the differences from *Spiriferella* and allies are great enough to suggest full family rank.

Subfamily **ELIVININAE** Waterhouse, 2004

[Elivininae Waterhouse, 2004, p. 223].

Diagnosis: Plicae subdued or absent, costae fine, may be of varied strength. Connector plate and delthyrial cover plate of deltidium or stegidium; little secondary thickening. Lower Permian (?Asselian) to Late Permian (Changhsingian).

Genera: *Elivina* Fredericks (syn. *Dienerina* Ozaki), *Aequilicosta* Waterhouse, *Dissimiliplica* Waterhouse*, Quispira* Waterhouse.

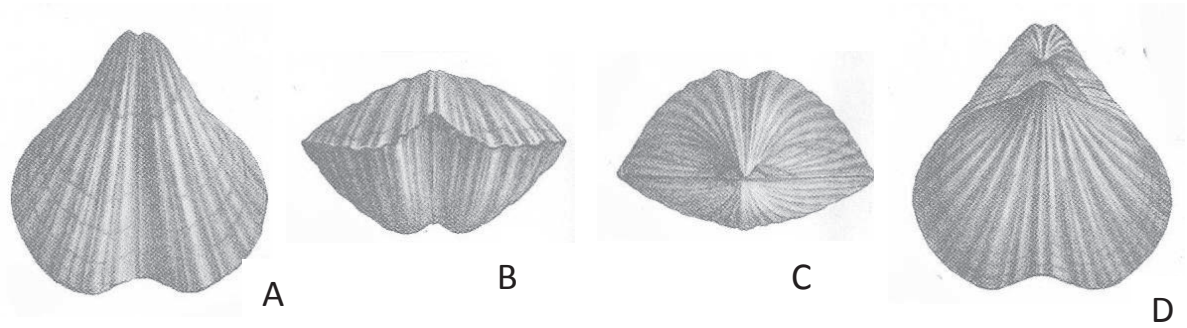


Fig. 279. *Elivina tibetanus* (Diener), ventral, anterior (dorsal valve on top), posterior (ventral valve on top), and dorsal aspects from Late Permian (Wuchiapingian) of Himalayas, x1. (Diener 1897a).

Discussion: The type species *Elivina* Fredericks is based on *Spirifer tibetanus* Diener of Wuchiapingian (Late Permian) age in the Himalayas, although Carter (2006a, p. 1805) asserted that the genus was no younger than Roadian (lower Middle Permian). Evidence for the age is summarized in Waterhouse (2010b). *Elivina tschernyschewi* Waterhouse & Waddington (1982, p. 33) appears to be a typical *Elivina*, with high narrowly grooved dorsal fold and no pustules. It comes from the Schwagerina limestone of the Urals, and was described by Chernyshev (1902, pl. 7, fig. 2-6).

Quispira Waterhouse, 2004, p. 225 is a remarkable genus ornamented by costae rather than plicae, and without pustules, virtually no fold, and with crural plates severely reduced or absent. The delthyrium is open, with a forked connector plate, or pleromal thickening diverging hingewards, and a small umbonal callosity under the beak. This genus also approaches members of Purdonellidae Poletaev, and either exemplifies convergence, or has been misplaced. Differentiation is based on the nature of the fastigium, as discussed by Cooper & Grant (1976) and followed by Waterhouse (2004, p. 223).

In *Dissimiliplica* Waterhouse, 2004, p. 226, the broad plicae of the ventral valve are opposed by slender dorsal costae that fit into the ventral interspaces, and the fold is high and narrow, unlike the less differentiated fold of *Elivina*. The nature of any delthyrial cover has not been determined, whereas a delthyrial cover plate is present in *Elivina*. This genus from

Texas was confused with *Elivina* from the Late Permian of the Himalaya by Gourvennec in Gourvennec & Carter (2007, p. 2786) and it is true that *Elivina* is of overall similar shape, but has subequal ornament on both valves, consisting of low strongly costate subplicae, and broader less upstanding and deeply cleft fold.

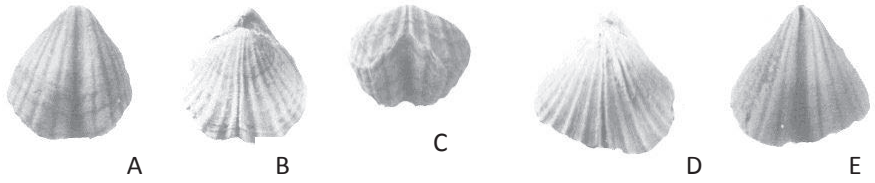


Fig. 280. *Dissimiliplica compacta* (Girty). A-C, ventral, dorsal and anterior views of one specimen. D, E, dorsal and ventral views of another specimen. Note the broad ribs of the ventral valve, and slender ribs of the dorsal valve. Specimens x 1, from Bell Canyon Formation (Capitanian), USA. (Cooper & Grant 1976).

Aequilicosta Waterhouse 2004, p. 193 is based on type species *Eliva inflata* Cooper & Grant, 1976, p. 2239, and with a second species *shumardi* Cooper & Grant, does look close to members of Purdonellidae, because the median channel of the dorsal fold is slender. The fold in *inflata* commences with a single costa, that then splits into two. This is just the same arrangement as in *Elivina* (Diener 1897a, p. 46), although Cooper & Grant (1976, p. 2238) arguably failed to appreciated the similarity, because figured type *Elivina* seems to have two costae commencing at the dorsal beak. A connector plate is developed, as in other members of Eliviniidae.

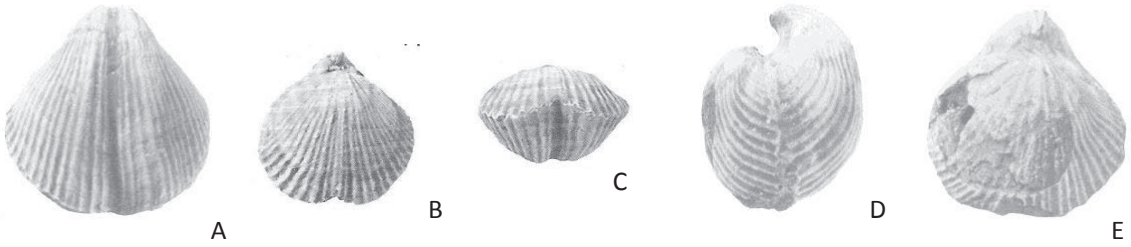


Fig. 281. *Aequilicosta inflata* (Cooper & Grant), ventral, dorsal, anterior (dorsal valve on top), lateral and dorsal views of specimens from Capitan Limestone (Capitanian), USA, x1. (Cooper & Grant 1976).

Eliva Fredericks from the upper Cisuralian of the Urals in Russia was classed in Purdonellidae (see p. 138) in the *Revised Brachiopod Treatise* (2006, p. 1780), but has a wider channel along the fold, suggestive of Spiriferelloidea. Micro-ornament is not clear: Chernyshev (1902) did not report tubercles, so that Purdonellidae is a possible choice, but the fold would be exceptional. What is intriguing is that the ornament in the the choristitoid families Purdonellidae, and allied Choristidae is not entirely dissimilar to that of Elivinidae, in exceptional. What is intriguing is that the ornament in the choristitoid families Purdonellidae,

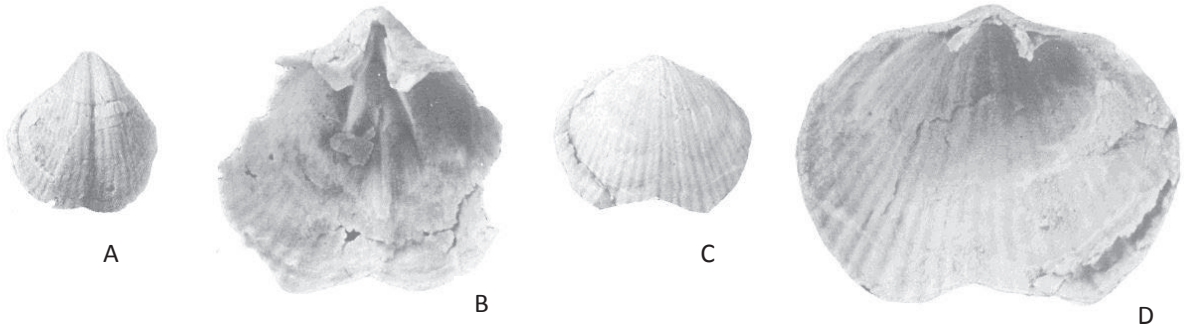


Fig. 282. *Quispira detecta* (Cooper & Grant). A, ventral view, x1. B, ventral interior, showing thick pleromal ridges diverging forward, but without connector plate, x2. C, dorsal exterior x1. D, dorsal interior, x2, from Lamar Member (Capitanian), United States. (Cooper & Grant 1976).

and allied Choristidae is not entirely dissimilar to that of Elivinidae, in consisting of broad gently rounded ribs separated by narrow interspaces. *Aequlicosta* and *Quispira* do strongly approach members of Purdonellidae. Further study may reveal a close relationship, with Spiriferelloidea diverging in the Pennsylvanian from choristitoid stock, with change in costation, plication and micro-ornament, as well as internal changes. But the relationships appear to have been complex, and such possibilities are not favoured, although aspects remain to be explored. Both are narrow and subelongate with narrow interspaces closed up.

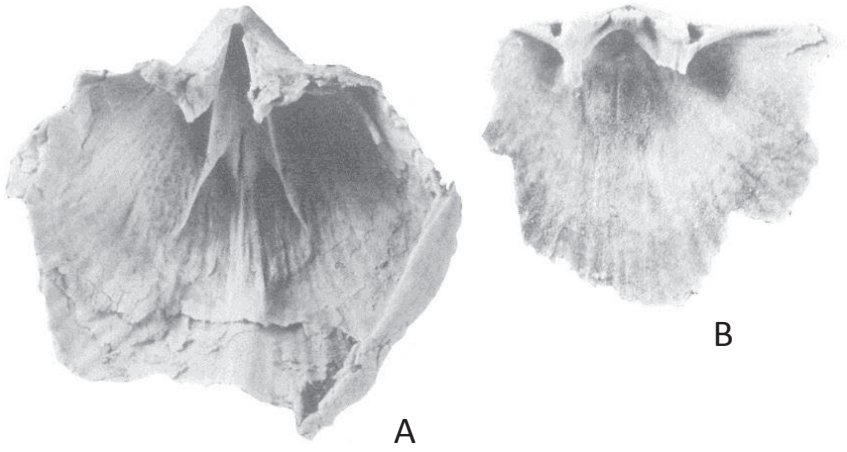


Fig. 283. *Aequilicosta shumardi* (Cooper & Grant), x2. A, ventral interior. B, dorsal interior. From Lamar Member (Capitanian), Texas, USA. (Cooper & Grant 1976).

Subfamily **DARBANDIINAE** new subfamily

Name genus: *Darbandia* Angiolini, 2001, p. 336 from Middle Permian (Wordian) of Pakistan, here designated.

Diagnosis: Large and elongate shells with bifurcating costae forming indistinct fascicles, especially over on the dorsal valve. High interareas, prominent ventral beak. Micro-ornament of growth lamellae, with no pustules. Feeble if any plication, with minor fasciculation. Micro-ornament predominantly commarginal. Apical callosity, no connector plate as far as known. Middle Permian (Wordian).

Genus: *Darbandia* Angiolini.

Discussion: This genus is a member of Elivinidae, judged from shape and micro-ornament, although assigned to Hunzininae Angiolini (synonymous with Spiriferellinae) by Angiolini (2001).

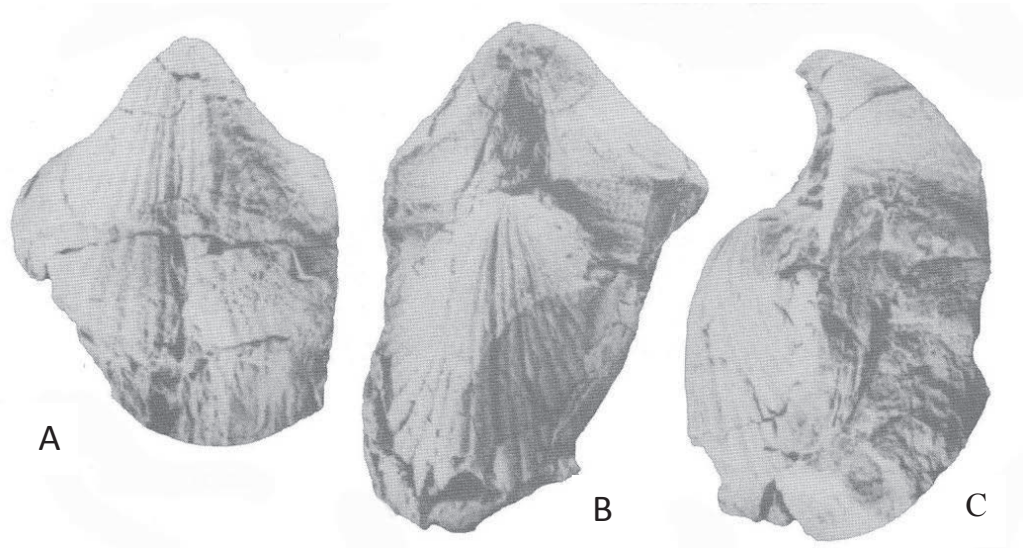


Fig. 284. *Darbandia vagabunda* Angiolini, A, ventral view, B, dorsal view and C, lateral view. Specimens x1 from Wordian of Pakistan. (Angiolini 2001).

Superfamily **TRIGONOTRETOIDEA** Schuchert, 1893

[Nom. transl. hic ex Trigonotretidae Schuchert, 1893, p. 156].

Diagnosis: Plicae and in younger genera costae well developed. No delthyrial plate, no connector plate, small to large umbonal callosity under the ventral beak, in some genera with pleromal extensions along the lower edge of the dental plates, denticular hinge. Adminicula short, and mantle canal systems stretched net-like where known. Radial and commarginal fila well developed as a rule. Lower Carboniferous (Tournaisian) to Upper Permian (Changhsingian).

Discussion: A lineage can be traced from small plicate shells with no delthyrial cover and often cancellate and pustulose micro-ornament, through larger more plicate shells with umbonal callosity and often subplicae or costae over sulcus and fold, with cancellate micro-ornament, to younger groups that developed costae over the plicae, whilst retaining the internal plates and delthyrium of earlier genera. In the Middle and Late Permian, species came to closely resemble Neospiriferidae, apart from minutae of costal development and retention of delthyrial development and mantle canal systems.

Questions to be considered revolve around the relationship of Trigonotretoidea to Choristitoidea, a matter which became highly relevant after Legrand-Blain (1985a, 1986) referred a genus *Angiospirifer* Legrand-Blain to Choristitidae, and was followed in that classification by the *Revised Brachiopod Treatise* and Angiolini et al. (2007). The principal justification was that the mantle canal system of Angiospiriferinae formed an open network, unlike the dense pattern regarded as typical of Spiriferidae. A different relationship was mooted by Waterhouse (2004), in pointing out that Trigonotretidae also displayed reticulate mantle canal systems, and that a delthyrial umbonal callosity was developed in *Angiospirifer*, like the arrangement in trigonotretids, and unlike the delthyrial structure typical of Spiriferidae or Choristitidae.

Legrand-Blain (1986) noted that the hinge of *Angiospirifer* was denticulate. That is also true of trigonotretids. It may be true of at least some choristitinids, because Poletaev (1986, fig. 2) sketched denticles along the hinge of *Choristites*, yet showed none in either *Spirifer or Parachoristites*. On the other hand, *Prochoristitella* as illustrated by Legrand-Blain (1986, Fig. 12) showed no denticles, yet was classed with *Angiospirifer* by Carter (2006a, p. 1783). A variety of choristitinids suggest denticulation, though this could be due to weathering. The specimens indicate that the denticles form at the hinge end of slender vertical rods lying in parallel over the exterior of the interarea. Williams & Rowell (1965) stated they were formed by small crenulations in the primary and secondary shell. So whether choristitids consistently had denticles, or whether they varied, as seems likely, remains to be clarified.

Early trigonotretoids were plicate, weakly transverse, often pustulose, with open delthyrium, or with stegidia, but no delthyrial cover plate, deltidial plates or connector plate as far as known, a large umbonal callosity, and with the usual spiriferidin complement of dental, adminicular and crural plates, and no tabellae. Genera were well established by Visean time,

and probably began in the Tournaisian Stage, of basal Carboniferous age. The early Trigonotretoidea are thus close to the plicate early members of Cyrtospiriferoidea, Paeckelmannelloidea, and less to early Prospirinae, but lacked a connector plate. Spinocyrtiidae were pustulose like members of Angiospiriferidae, and had one evolved into the other, considerable change in shape (being less transverse) and delthyrium and mantle canal system and loss of connector plate would have been involved. But the overall similarities between Paeckelmannelloidea, Spiriferoidea, Trigonotretoidea, and Spiriferelloidea, as well as the reality of the distinctions between each superfamily, encourage a model of ultimately common or near common origin and an intertwining sequence of evolutionary changes, that involved divergences and convergences.

Family **TRIGONOTRETIDAE** Schuchert, 1893

Diagnosis: Characterized by ovally subrectangular shape, may have extended anterior lateral margins. No record of stegidia or deltidial plates. Other morphological attributes as in superfamily. Micro-ornament cancellate as a rule, never tuberculate.

Subfamily **TRIGONOTRETINAE** Schuchert, 1893

[Trigonotretinae Schuchert, 1893, p. 156].

Diagnosis: Comparatively numerous plicae, costae few and coarse, cardinal extremities obtuse. Upper Pennsylvanian (?Moscovian) to early Middle Permian (Roadian).

Genera: *Trigonotreta* Koenig, *Brachythyrinella* Waterhouse & Gupta, *Cancellospirifer* Campbell, *Neilotreta* Waterhouse, *Pericospira* Cisterna & Archbold.

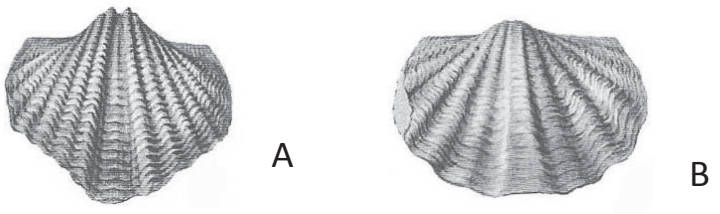


Fig. 285. *Brachythyrinella narsahensis* (Reed), ventral and dorsal views, x1.5. From Lower Permian (Sakmarian) of India. (Reed 1928).

Discussion: Genera are limited in distribution to Gondwana, involving Australia, Indian subcontinent and South America. They have an umbonal callosity, reticulate vascular impressions, and denticulate hinge, but no stegidia or delthyrial cover.

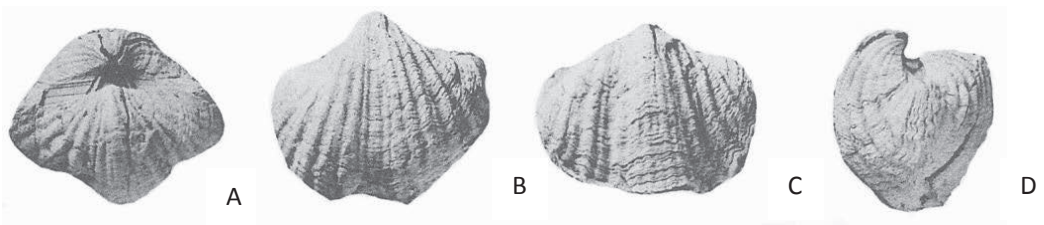


Fig. 286. *Neilotreta occidentalis* (Thomas), dorsal posterior, ventral, dorsal anterior and lateral views of holotype, x1. From upper Lyons Group (Asselian) of Western Australia. (Thomas 1971).

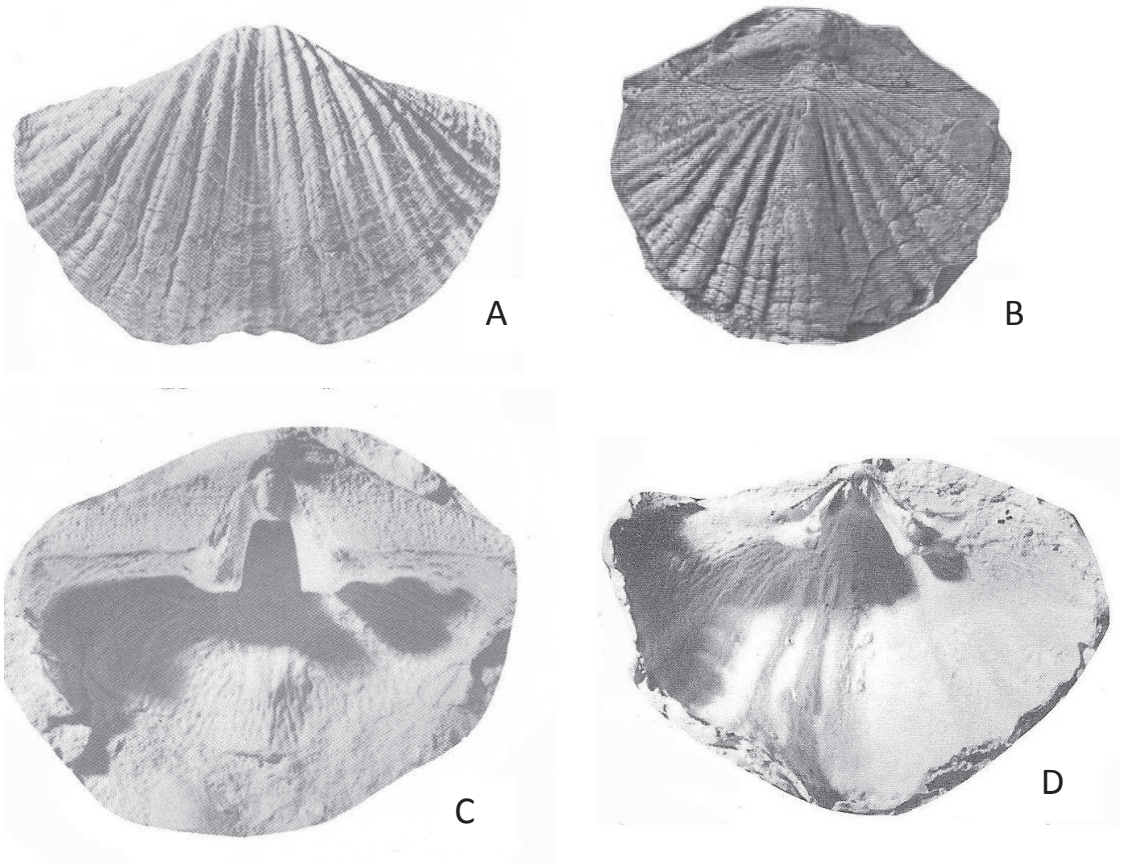


Fig. 287. *Trigonotreta stokes*i Koenig. A, ventral valve. B, lectotype dorsal aspect. C, ventral interior. D, dorsal interior. Specimens x1 and 1.2. From Lower Permian (Asselian) of Tasmania. (Clarke 1979).

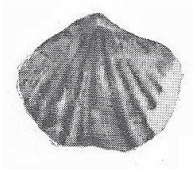
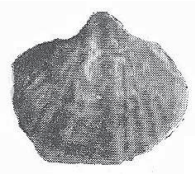

A

Fig. 288. *Cancellospirifer maxwelli* Campbell, x1.5. A, dorsal valve (holotype). B, ventral valve. From Ingelara Formation (Roadian), Queensland. (Campbell 1953).


B

Cancellospirifer Campbell is small with simple plicae and cancellate micro-ornament. It was judged by Carter (2006a, p. 1779) to belong to Sergospiriferine, and there are similarities to *Sergospirifer* and to members of Angiospiriferinae, but the genus is closer in outline and ornament to other members of Trigonotretinae such as *Brachythyrinella* and *Neilotreta*, and is of mid-Permian age. There are more plicae than in species of the trigonotretid genus *Aperispirifer* found in the same general region in beds of the same general age, so the specimens are not juveniles of that genus. Transverse sections of the type species provided by Campbell (1953) and Waterhouse (1968) show that dental plates and adminicula were well developed, and that there was definitely no connector plate even in small specimens, showing it was trigonotretid.

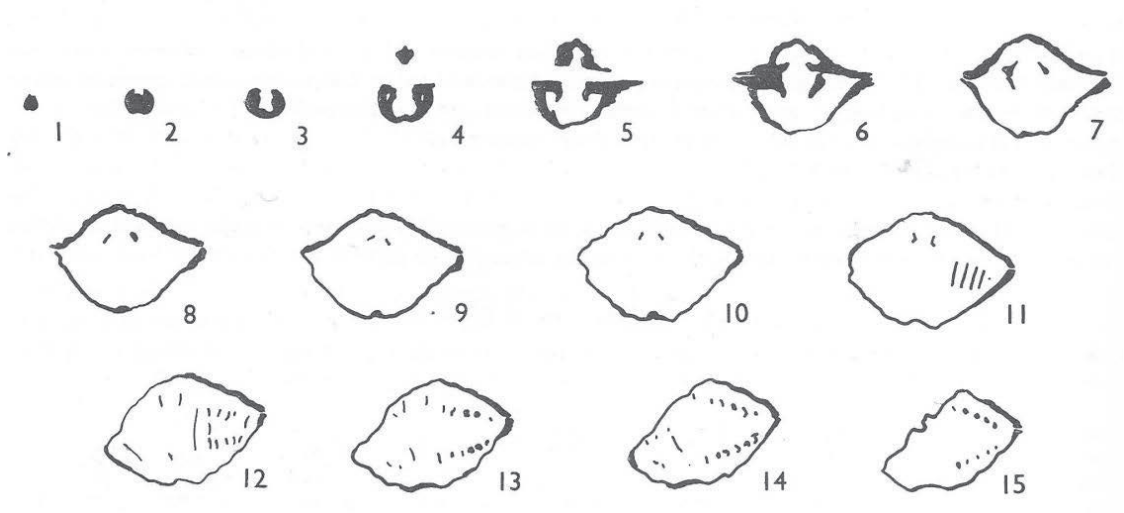


Fig. 289. *Cancellospirifer maxwelli* Campbell, serial sections of the type species, from the Ingelara Formation of Queensland, east Australia, at intervals of 0.5mm, x2. (Waterhouse 1968).

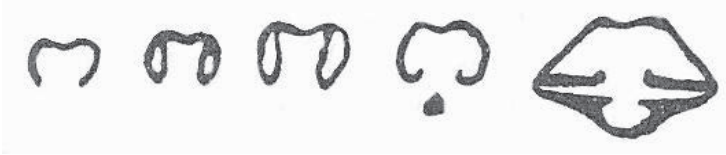


Fig. 290. *Cancellospirifer maxwelli* Campbell, serial sections of the type species, from the Ingelara Formation of east Australia, x2. (Campbell 1953).

Pericospirifer has been recorded from below the *Pseudoreticulatispora confluens* palynomorph Zone in the Tupe Formation and Del Salto Formation of Argentina (Cisterna & Archbold 2007), and is probably mid to late Pennsylvanian (Moscovian or younger).

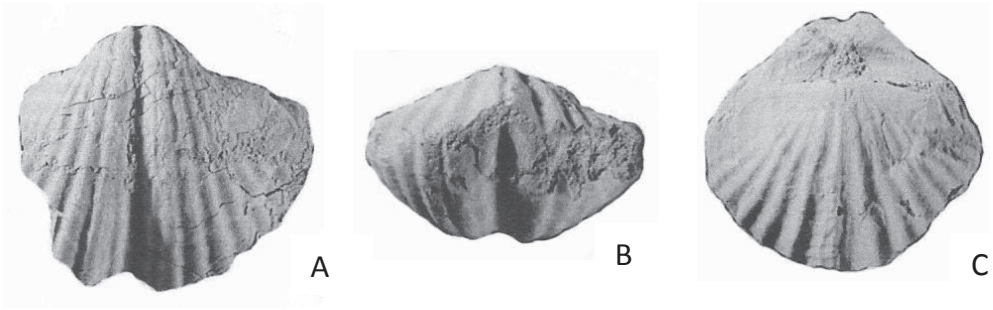


Fig. 291. *Pericospira sanjuanensis* (Lech & Acenolaza). A, ventral view. B, anterior view, dorsal valve on top. C, dorsal view. Specimens x1, from Argentina (mid to upper Pennsylvanian). (Cisterna & Archbold 2007).

Subfamily **COSTULOPLICINAE** Waterhouse, 2004

[Costuloplicinae Waterhouse, 2004, p. 187].

Diagnosis: Small transverse shells with six to nine pair of plicae that may be finely costate anteriorly. Short adminicula and dental plates, micro-ornament of radial and stronger commarginal fila. No well formed delthyrial cover, but small to broad umbonal callosity. Pennsylvanian.

Genera: *Costuloplica* Waterhouse, *Maxwellispirifer* Waterhouse.

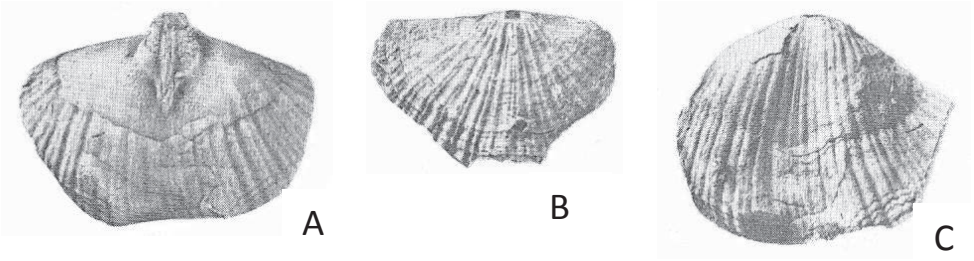


Fig. 292. *Costuloplica campbelli* (Maxwell). A, ventral internal mould. B, dorsal internal mould. C, external cast of anterior ventral valve, x1. From Middle-Carboniferous of Yarrol Basin, Queensland, Australia. (Hill & Woods 1964).

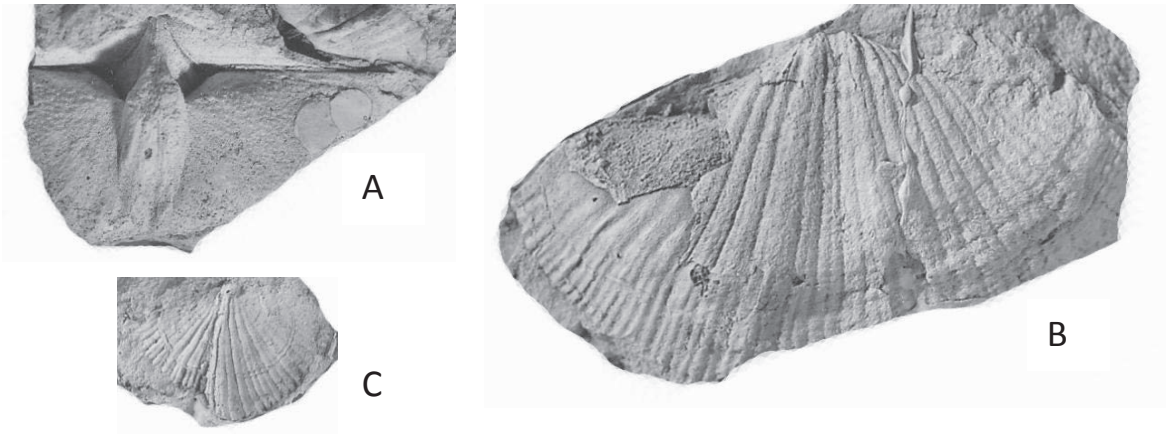


Fig. 293. A, B, *Costuloplica senilis* (Maxwell). A, internal mould of ventral valve, x1. B, ventral view of latex cast, x1.5. C, *C. campbelli* (Maxwell), latex cast of dorsal valve. x1. From Middle-Carboniferous of Yarrol Basin, Queensland, Australia. (Maxwell 1964, JBW).

Discussion: Costuloplicinae is difficult to place, with limited information on family affinities, but the preponderance of evidence points to a trigonotretoid relationship. The nominate genus *Costuloplica* has a high number of low plicae with broad crests, that divide at varying lengths on different species from the umbo, including *C. robertsi* Waterhouse with few costae, and *C. profasciger* Maslennikov, as figured by Kotlyar & Popeko (1967, pl. 44, fig. 6-11) with many costae. The delthyrium provides ambiguous evidence. In the type species, *senilis*, a specimen shows no delthyrial plate and no umbonal callosity (Fig. 293A), whereas a few other specimens of the type species have a small umbonal callosity (Roberts et al. 1976, Fig. 15A),

and the Argentinian species *leoncitensis* Harrington shows an umbonal callosity (Amos et al. 1963, pl. 1, fig. 6, 7), with the species ascribed to *Costuloplica* by Cisterna & Sterren (2008). On the whole, the mantle canal system seems to point to a trigonotretid alliance, the ventral interior figured by Roberts et al. (1976, fig. 16A) suggesting a reticulate pattern. *C. tomskiensis* (Benediktova) of

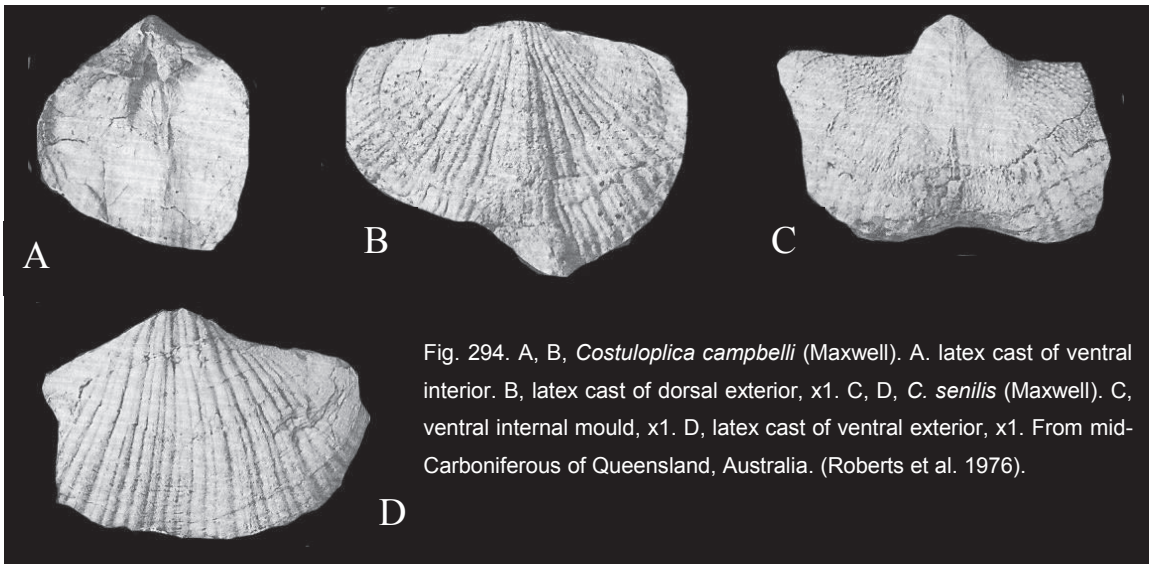


Fig. 294. A, B, *Costuloplica campbelli* (Maxwell). A. latex cast of ventral interior. B, latex cast of dorsal exterior, x1. C, D, *C. senilis* (Maxwell). C, ventral internal mould, x1. D, latex cast of ventral exterior, x1. From mid-Carboniferous of Queensland, Australia. (Roberts et al. 1976).

Kotlyar & Popeka (1967, pl. 43, fig. 3a) from Lake Baikal has a stretched narrowly reticulate pattern with subradiating crowded canals just in front of the ventral muscle field.

A similar pattern is well shown in the type species of *Maxwellispirifer, Neospirifer campbelli exora* (McKellar, 1965, pl. 4, fig. 2b, 4b). A small umbonal callosity was recorded by McKellar (1965, p. 11). This genus is characterized by its coarse broad costae, crossed by fine commarginal laminae. Three pair of prominent plicae and a few finer plicae commence at the umbo and the innermost pair enters the sulcus. The genus has rounded cardinal extremities and few plicae pairs, and tiny ventral plates. A species described below has a

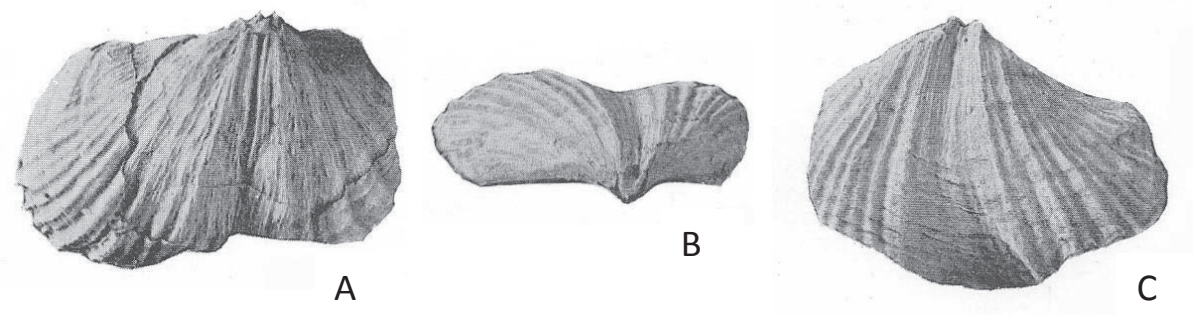


Fig. 295. *Maxwellispirifer exora* (McKellar). internal moulds of ventral valves, x1. A, ventral valve, holotype, B, C, posterior and view views. Specimens from Branch Creek Formation, Middle Carboniferous of Queensland. (McKellar 1965).

more prominent umbonal callosity, developed in late mature specimens.

The appearance of fine subequal costae over the anterior plicae separates the subfamily from Angiospiriferinae. Varuninae (see p. 247), especially *Varuna* with its costae, is closer, with distinctive subtriangular outline and wide hinge, and was probably ancestral.

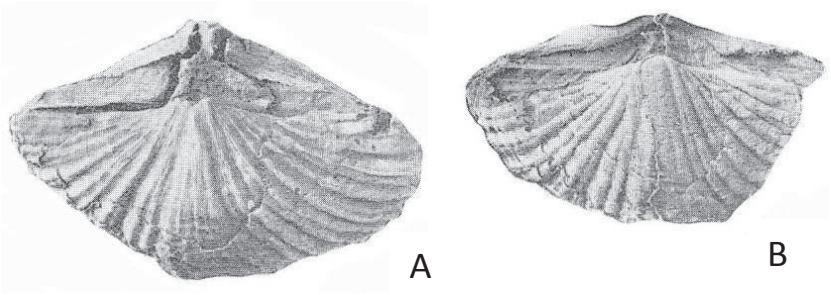


Fig. 296. *Maxwellispirifer exora* (McKellar), dorsal views of internal mould and latex cast, x1.5. Specimens from Branch Creek Formation, Middle Carboniferous of Queensland. (McKellar 1965).

Waterhouse (2004, p. 191) referred *Gibbospirifer* Waterhouse, 1971 to this subfamily, but this is believed to be error. Although some ventral valves of the original collection appeared to show a small delthyrial callosity, formed by pleromal thickening, it is believed that the thickening was in fact contributing to the development of a subdelthyrial connector plate, as illustrated herein in Fig. 235A-C, p. 192, in the course of illustrating a new species of the genus.

In summary, Costuloplicinae represent small costato-plicate genera. It was widespread in the Middle Carboniferous, and would perhaps have arisen from Angiospiriferinae, by the loss of pustules and introduction of costae, or, more likely, from Varuninae by modification of shape, costae and plicae.

Genus ***Maxwellispirifer*** Waterhouse, 2004

Diagnosis: Weakly transverse, sulcus well formed, fold broad anteriorly, ornament of some three prominent pair of plicae with slender additional plicae laterally, totalling six or seven pair, covered by fine or coarse costae, and more costae laterally. Umbonal callosity large and prominent, dental plates and adminicula short and high, low crural plates, thick secondary shell, and well developed sublinear mantle canal system.

Type species: *Neospirifer campbelli exora* (McKellar, 1965, p. 10) from Branch Creek Formation (Bashkirian-Moscovian?), Queensland.

Maxwellispirifer sp.

Description: Shell small, the internal mould of a ventral valve measuring 39mm wide, and 28mm long and 15mm high, and an internal mould of both valves measuring 37m wide, 28mm long and 21mm thick. The ventral umbo is weakly incurved over the hinge, with angle

of 75°, and the interarea is high and extends for the maximum width of the shell, its height approaching a fifth of the length of the shell, and the delthyrium is open, with an angle of 35°. The sulcus is well defined, with angle of 25° and extends as a short tongue anteriorly. The fold has a rounded crest, and broadens anteriorly, grading more evenly onto the lateral slopes and less separated from the lateral shell than the sulcus. Three prominent pairs of plicae are developed on the ventral valve, the plicae not entering the sulcus. Plicae bear fine costae that are slightly angular in profile with narrow crests, increasing to three anteriorly, and seven costae lie in the sulcus anteriorly, between the crest of each bordering plication. The full number of costae over the anterior shell is not known. The shell surface between the plicae and lateral margins is costate. The fold of the dorsal valve bears at least eight fine costae, and the outer slopes of the fold carry a fascicle of two sturdy costae. Three further low plicae lie beyond, with fine costae curving outward, and further costae cover the outer surface.

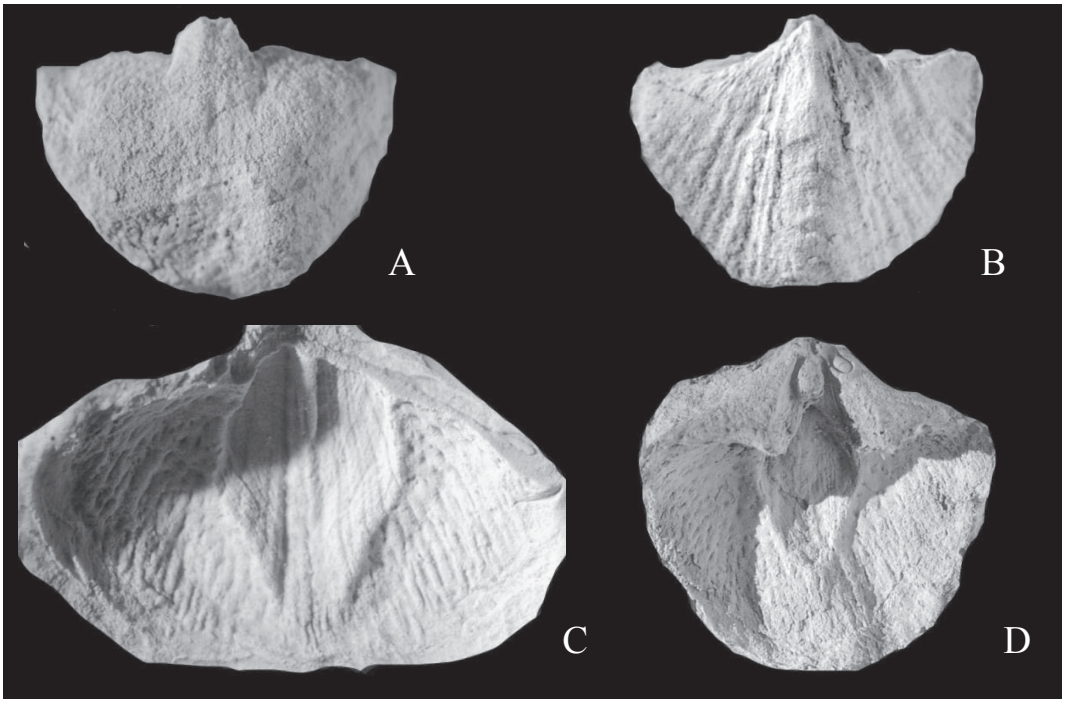


Fig. 297. *Maxwellispirifer* sp. A, B, ventral and dorsal views of internal mould, UQF 12852, x1.5. C, cast of ventral interior, UQF 12850, x2. D, cast of ventral interior and posterior ventral valve, showing large umbonal callosity, x2. From Riversleigh Formation, Mundubbera district, Queensland, Australia.

Teeth are supported by high dental plates which rest at an angle on high short adminicula. The junction between the two plates bears pleromal thickening, which passes into a high umbonal callosity under the beak in mature shells. The ventral muscle field is large and well defined, with two slender adductor ridges, and broad diductor scars bearing longitudinal grooves and ridges. In one specimen, the posterior adductors have been raised into a short high myophragm, bearing a median groove, and the muscle field is bordered by a ridge. The floor of the mature valve in front of the muscle field bears deep irregular grooves, mostly

linear, but anastomosing to some extent, and posteriorly the shell is marked by short ridges and elongate pits. In the dorsal valve, the ctenophoridium is laminate and divided into two by a groove on the anterior face, and low socket plates lie each side. There is a very low myophragm, and muscle scars are not visible.

Resemblances: This species shares with *Maxwellispirifer exora* (McKellar 1965) the broad anterior fold, presence of three or four prominent plicae on each valve, and the heavy ventral myophragm and mantle canal system, but *exora* is more transverse and has much wider costae.

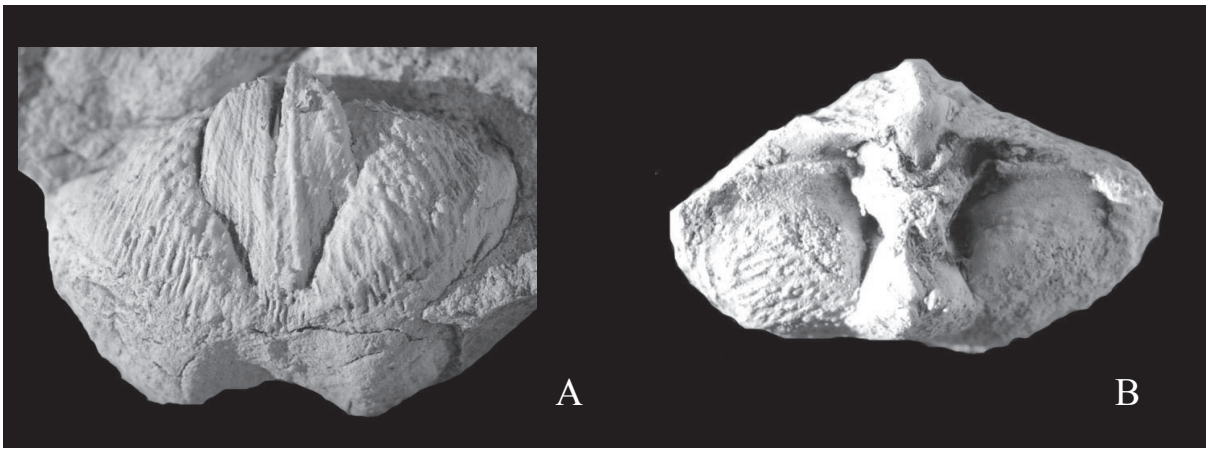


Fig. 298. *Maxwellispirifer* sp. A, ventral internal mould UQF12850. B, posterior view of internal mould UQF 12852. Specimens x1.6. From Riversleigh Formation, Queensland.

Subfamily **GRANTONIINAE** Waterhouse, 2004

[Nom. transl. hic ex Tribe Grantoniini Waterhouse, 2004, p. 170].

Diagnosis: Plicae few, costae well developed, hinge wide. Lower to Upper Permian (Asselian – Changhsingian).

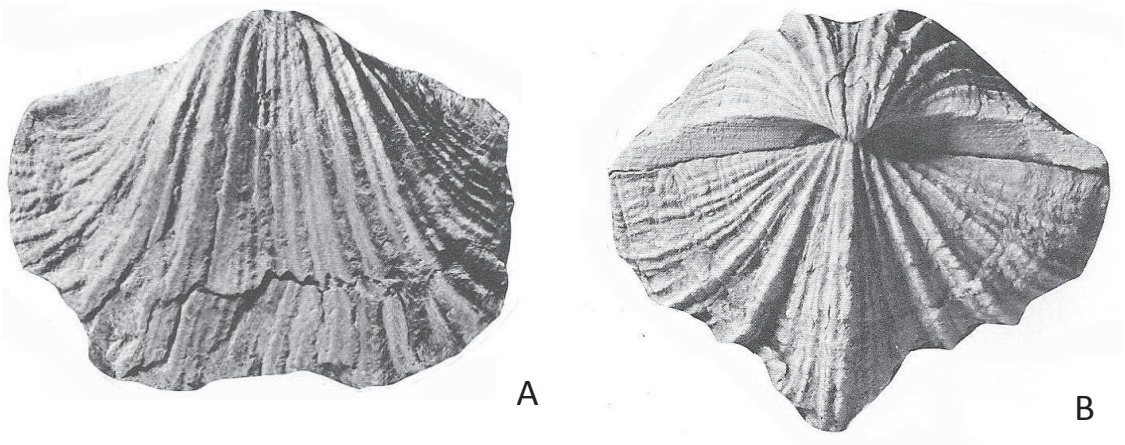


Fig. 299. *Grantonia hobartensis* Brown. A, ventral view, x1.2 and B, dorsal view of holotype, x1.2. From Berriedale Limestone (Artinskian) of Tasmania, Australia. (Clarke 1979).

Genera: *Grantonia* Brown, *Aperispirifer* Waterhouse, *Koenigoria* Waterhouse, *Trigorhium* Waterhouse.

Discussion: Several genera, *Grantonia* Brown, *Aperispirifer* Waterhouse and *Koenigoria* Waterhouse, are found widely in Gondwana, and *Trigorhium* occurs in the mid-Permian or Guadalupian of United States. In many respects, involving ornament, micro-ornament and internal plates, they are like Neospiriferidae, and appear to have converged from non-costate but plicate stock. Prime differences between the two lie in the delthyrial apparatus and mantle canal systems. Compared with Trigonotretinae, plicae are fewer by one to three pair, and costae more numerous and prominent. *Grantonia* Brown was unnecessarily synonymized by Armstrong (1968) and Carter (2006a) with *Trigonotreta* Koenig, which has ornament dominated by plicae, compared with the fewer and stronger plicae and strong costae of *Grantonia*.

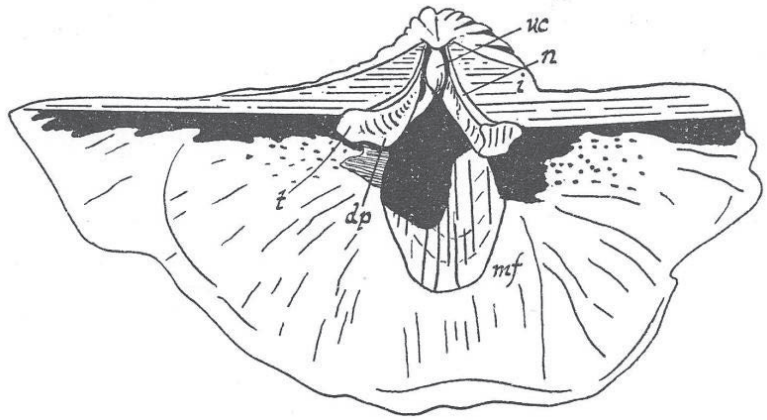


Fig. 300. *Aperispirifer archboldi* Waterhouse, ventral interior, x2. From Letham Formation (Kungurian) of New Zealand. dp – dental plate; i – interarea; mf – muscle field; n – dental flange or dental track; t – tooth; uc – umbonal callosity. (Waterhouse 1964).

Fig. 301. *Grantonia australis* (Bion). ventral interior. Specimen x1.5, from Tiverton Formation (Sakmarian) of Queensland, Australia. (Waterhouse 2015a).

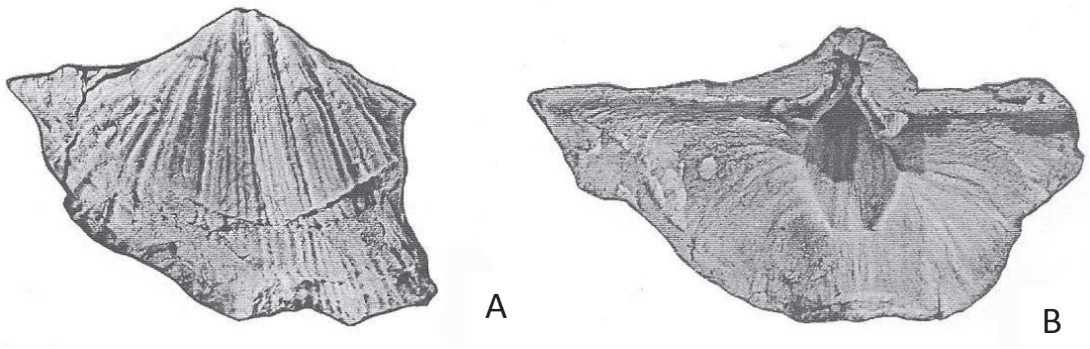


Fig. 302. *Aperispirifer wairakiensis* (Waterhouse), holotype ventral exterior (A), and ventral interior (B), x1.2. From Letham Burn Formation (Roadian), New Zealand. (Waterhouse 1964).

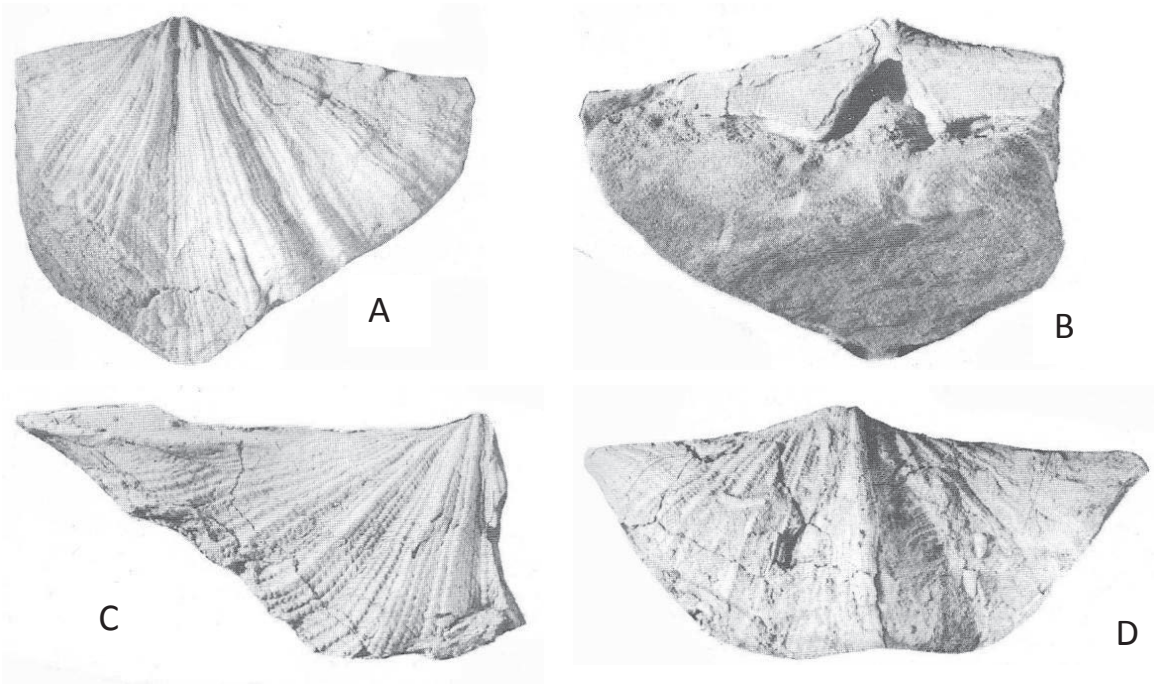


Fig. 303. *Koenigoria neoaustralis* (Archbold & Thomas). A, ventral view, B, posterior view of ventral valve showing small umbonal callosity. C, ventral valve. D, dorsal view. Specimens x1, from Callytharra Formation (Sakmarian), Western Australia. (Archbold & Thomas 1986a).

Koenigoria Waterhouse is closely costate, like *Aperispirifer* Waterhouse. It is based on *Trigonotreta neoaustralis* Archbold & Thomas, 1986a, and unlike *Grantonia*, has a very deep anterior sulcus, and a markedly triangular outline. The plicae fade anteriorly, unlike those of *Trigonotreta* or *Grantonia*, and a pair of sulcal plicae is developed. The genus ranged through much of the Permian Period in Western Australia, and penetrated an offshore region now partly preserved at Gympie of eastern Australia in the late Permian (Waterhouse 2015b, p. 144).

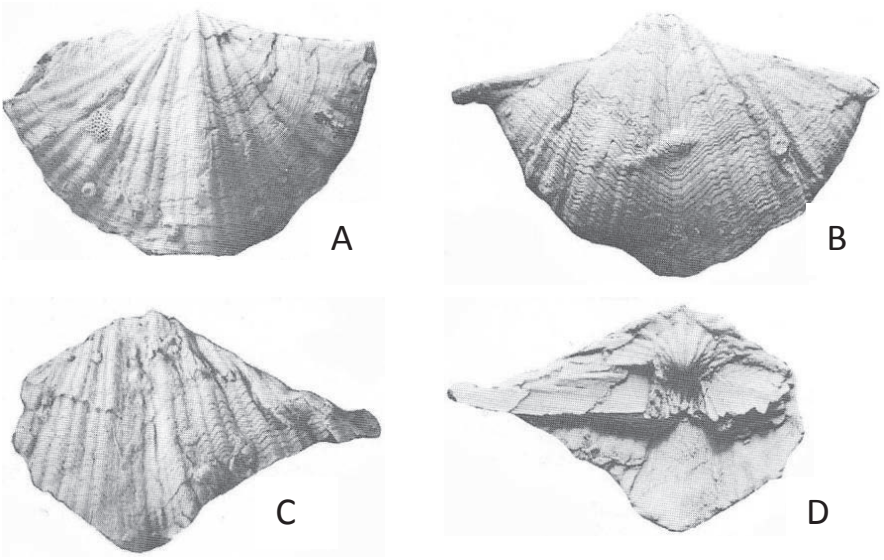


Fig. 304. *Koenigoria dickinsi* (Archbold & Thomas). A, dorsal valve, x1. B, ventral view, x1. C, D, ventral and dorsal aspects of ventral valve, x1.5. Specimens from Nooncanbah Formation (Artinskian), Western Australia. (Archbold & Thomas 1986a).

A possible descendent was *Trighorium* Waterhouse, 2004, based on *Neospirifer amphigyus* Cooper & Grant, 1976, p. 2175 from the China Tank and Appel Ranch Members of the Word Formation in Texas. Unlike spiriferalarians or neospiriferids, there is an open delthyrium, and large umbonal callosity, typical of trigonotretids. Costae are strong, as in *Grantonia*, and plicae are also well developed and persistent, and more numerous than in *Grantonia*, reverting towards the arrangement in *Trigonotreta*. What distinguishes the genus is the presence of a median sulcal plication, unknown in any other Trgonotretidae. The presence of this trigonotretid genus in the substantial paleotropical faunas of west Texas points to a brief incursion of an essentially cold-water spiriferid.

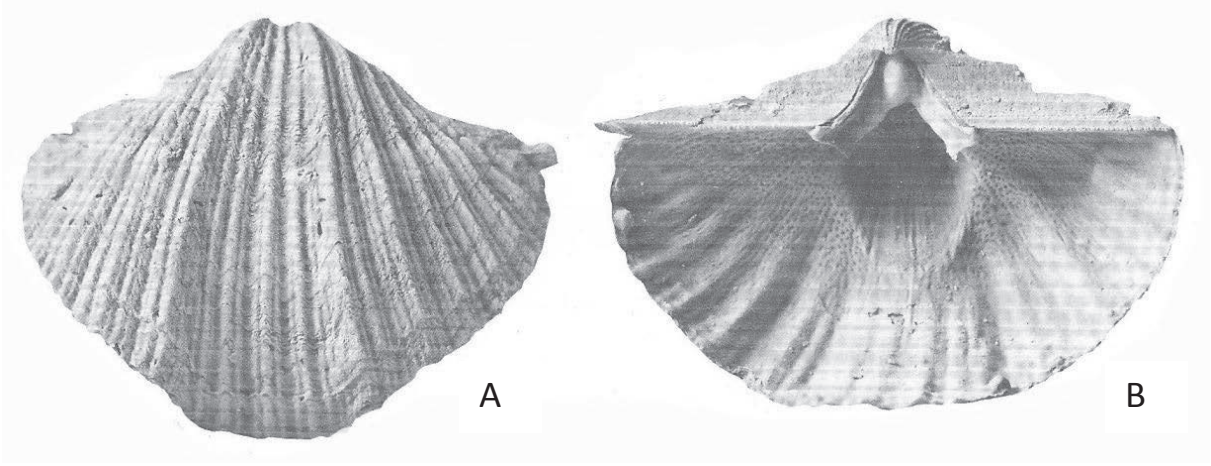


Fig. 305. *Trigorhium amphigyus* (Cooper & Grant), ventral valve exterior (A) and interior (B), showing characteristic three subplicae in the sulcus, and the strong trigonotretid umbonal callosity, x1.2. From Word Formation (Wordian), Texas. (Cooper & Grant 1976).

Family **ANGIOSPIRIFERIDAE** Legrand-Blain, 1985a

[Nom. promoveo hic ex Angiospiriferinae Legrand-Blain, 1985a, p. 574].

Diagnosis: Transverse, small to medium-sized coarsely plicate shells with minor if any costation, micro-ornament cancellate and may be tuberculate, hinge at or close to maximum width, anterior-lateral margins not extended, delthyrium open, usually with umbonal callosity, adminicula short or absent, dental plates and crural plates present, with no connector plate or tabellae. Mantle canal system reticulate.

THE RELATIONSHIP TO CHORISTITIDAE AND TO TRIGONOTRETIDAE

Legrand-Blain (1985a) related Angiospiriferinae to Choristitinae Waterhouse, because both subfamilies displayed a reticulate pattern of mantle canals, and this position was supported in the *Revised Brachiopod Treatise*, and by Angiolini, Long & Davies (2011). On the other hand, it was pointed out that Trigonotretidae also possessed a reticulate mantle canal system (Waterhouse 2004), a matter overlooked by Legrand-Blain as well as the *Revised Brachiopod Treatise*. So which relationship is more likely? The evidence is multilayered, and has to be accompanied by uncertainities and reservations.

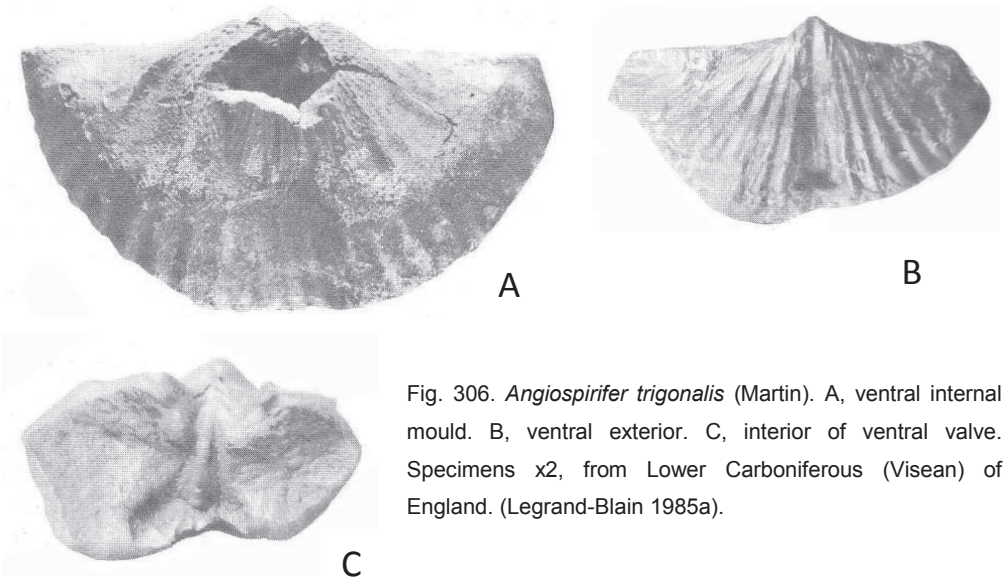


Fig. 306. *Angiospirifer trigonalis* (Martin). A, ventral internal mould. B, ventral exterior. C, interior of ventral valve. Specimens x2, from Lower Carboniferous (Visean) of England. (Legrand-Blain 1985a).

Mantle canal systems

The few examples of choristitid mantle canal systems show a variable pattern. *Choristites* itself, judged from figures in both Legrand-Blain (1986) and Lazarev & Poletaev (1982), shows two major canals lying parallel to the lateral margins of the muscle field, and branching posteriorly towards the hinge (Fig. 307). This differs from the arrangement in *Angiospirifer* and allies, in which the mantle canal system extends laterally parallel to the hinge, and branching towards the posterior lateral margins (Legrand-Blain 1986, fig. 24), as in Fig. 308D, p. 240. The angiospiriferin pattern is somewhat like that found in various Trigonotretidae. The

clearest examples are found in genera younger than *Angiospirifer*, which indicate a main posterior canal, extending laterally and branching towards the posterior lateral margins. Older trigonotretids have a smaller and more closely spaced network of canals, also extending laterally and branching towards the posterior lateral margins. On available evidence, the mantle canal system favours a relationship between Trigonotretidae and Angiospiriferinae, rather than an *Angiospirifer-Choristites* connection.

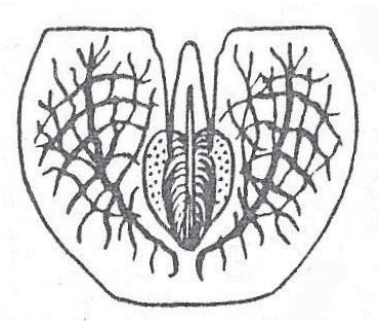


Fig. 307. The mantle canal system in *Choristites*, each side of the muscle scars, pointing and opening posteriorly. By contrast, the mantle canal system open and point laterally in Angiospiriferinae and Trigonotretidae. (Lazarev & Poletaev 1982).

Given the variability of mantle canal systems, especially for choristitids, this is not regarded as completely conclusive, but no angiospiriferid shows a network like that of choristitids, so is a strong pointer in favour of the need to reassess affinities of Angiospiriferinae, and reallocate the group to Trigonotretoidea.

Umbonal callosity

A second approach is provided by the presence or absence of an umbonal callosity. One is developed in a number of specimens allocated to Angiospiriferinae, including *Angiospirifer* Legrand-Blain, and the same is true of the type species of *Trigonotreta* Koenig. The position is more varied amongst Choristitidae. The delthyrium appears to have been open in many choristitids, although there is seldom a well developed umbonal callosity. In Purdonellidae, which looks externally like Choristitidae, a connector plate is common.

Shape

What about the general shape and ornament? Trigonotretids include many transverse genera, with hinge at or close to maximum width, as well as a few genera that are more subelongate in shape. Choristitids are generally equidimensional to slightly elongate, and less commonly transverse, and as a rule, the hinge is shorter than maximum width. Legrand-Blain (1970, pl. 1) figured a number of shells identified as *Choristites* sp. which have relatively wide hinge and are slightly wider than long, yet even so, the anterior lateral margins are well rounded, and the shape no more than a variation of the norm. As illustrated by Legrand-Blain (1985a, text-fig. 1), the type species of *Angiospirifer*, *A. trigonalis*, is transverse with hinge at maximum width, and much closer to the norm for trigonotretid specimens in shape, although *A. bisulcatus* (Sowerby) is only weakly transverse (Angiolini, Long & Davies 2011, Fig. 1). Two trigonotretid genera, *Neilotreta* Waterhouse, 2008 and *Brachythyrinella* Waterhouse & Gupta, 1978 are similar in shape.

Ornament

Ornament does not favour a choristitid relationship. *Angiospirifer* is plicate, like trigonotretids, whereas choristitids are basically costate, often with flattened crests. Even the outstanding species *A. bisulcatus* looks much more like trigonotretids than it does to choristitids. Micro-ornament often involves radial and commarginal capillae in both groups, and Angiospiriferinae is pustulose as a rule, like a number of early Choristitoidea, and unlike Trigonotretidae, but the significance of this difference at superfamily level is negligible, and basically helps offer a point of difference between Angiospiriferidae and Trigonotretidae.

Internal plates

Finally, the nature of the internal plates may be considered. These are consistent, as arranged herein, in both Angiospiriferinae and Trigonotretidae, involving short adminicula, well developed dental plates, and moderate crural plates. By contrast, the same plates in Choristitidae vary considerably in length, and related members of Palaeochoristitidae have tabellae.

Conclusion

In conclusion, the weight of evidence favours a relationship between Trigonotretidae and Angiospiriferinae, and does not favour positioning Angiospiriferinae in Choristitidae, let alone any close kinship with Spiriferoidea, dominated by canals radiating from an imaginary posterior centre, with interspersed pits (possibly reflecting a tiny meshwork) or the simple pattern of martiniids and brachythyrids.

Subfamily **ANGIOSPIRIFERINAE** Legrand-Blain, 1985

[Angiospiriferinae Legrand-Blain 1985a, p. 574].

Diagnosis: Ornament of simple numerous plicae and subplicae or costae in sulcus and fold, micro-ornament cancellate or weakly granulose, or predominantly commarginal. Adminicula short, umbonal callosity well developed, mantle canals reticulate, extending laterally and branching towards the lateral margins. Carboniferous (Visean) to Lower Permian (Cisuralian).

Genera: *Angiospirifer* Legrand-Blain, *Afghanospirifer* Plodowski, *Kasakhstania* Besnossova.

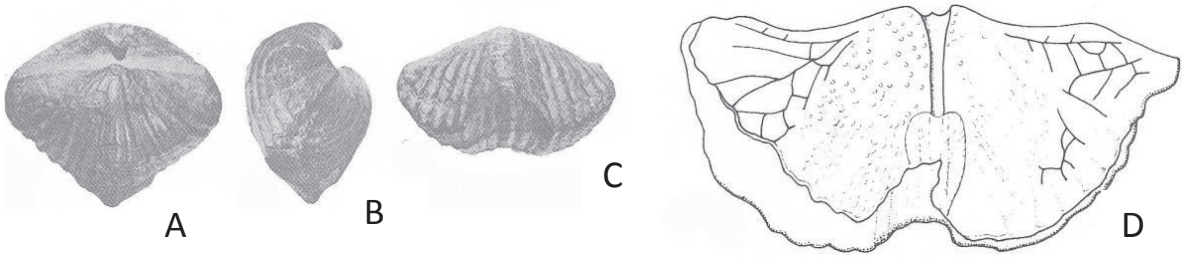


Fig. 308. *Angiospirifer trigonalis* (Martin). A-C, dorsal, lateral and anterior aspects, neotype, x1. (Dunlop 1962). D, vascular markings on ventral valve, x 2.3. (Legrand-Blain 1985a). From Lower Carboniferous (Visean) of British Isles.

Discussion: There are many similarities between Trigonotretinae and Angiospiriferinae

Legrand-Blain, 1985a, with numerous simple or subcostate plicae, cancellate micro-ornament and umbonal callosity. The mantle canal system is ramiform to reticulate, and directed postero-laterally. A stegidium was reported for rare specimens of *Angiospirifer* by Legrand-Blain (1985a, text-fig. 1F). *Angiospirifer* Legrand-Blain, 1985a is of Visean and lower Bashkirian age. Legrand-Blain **(**1986**)** pointed out that the hinge was denticulate, which was considered to rule out a relationship to Brachythyridae, yet brachythyrids may be denticulate. Brunton & Rissoné (1976) suggested that *Spirifer trigonalis* was related to Strophopleuridae, but Legrand-Blain opposed this on the nature of the mantle canal system, though just what the vascular pattern for Paeckelmannelloidea is not clear. A choristitin relationship was favoured by Legrand-Blain.

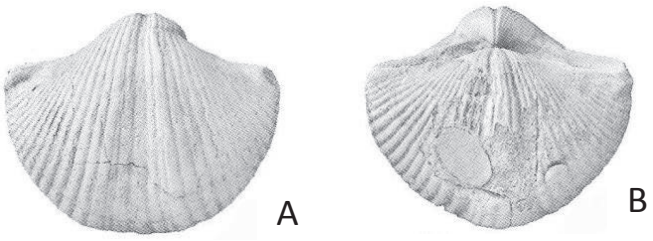


Fig. 309. *Angiospirifer bisulcatus* (Sowerby), ventral and dorsal views of holotype, from Visean of England, x1. (Angiolini et al. 2011).

In a discussion of *Angiospirifer*, Angiolini et al. (2011, p. 74) referred *Spirifer bisulcatus* Sowerby, 1825 to the genus, as a more elongate and oval form, also from the Visean of Britain. Their description of the micro-ornament needs to be clarified. They described it as cancellate with capillae and lamellose growth-lines, as in typical *trigonalis*, and proceeded to mention radially arranged granulose microsculpture. Their illustration does not clarify the situation.

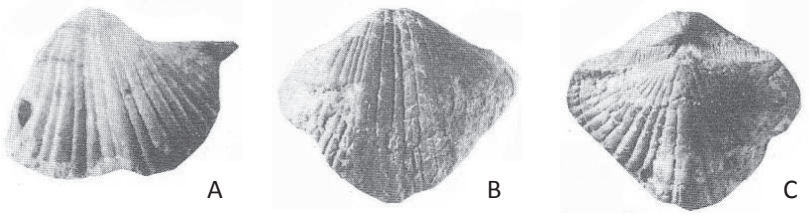


Fig. 310. *Angiospirifer trigonalis* (Martin). Ventral valve and specimen with both valves conjoined, x1, from upper Visean and Serpukhovian in Algeria. (Legrand-Blain 1986).

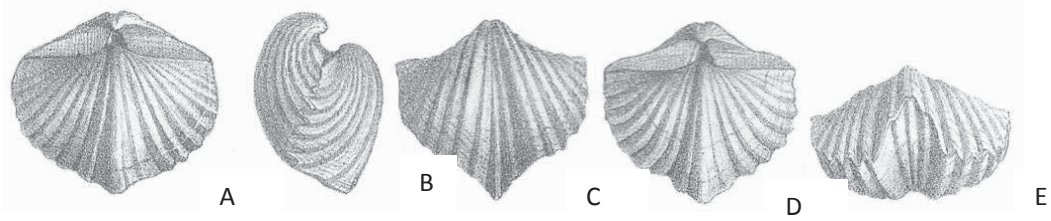


Fig. 311. *Angiospirifer trigonalis* (Martin) as figured from the Lower Carboniferous of England and Scotland, x1. (Davidson 1858b).

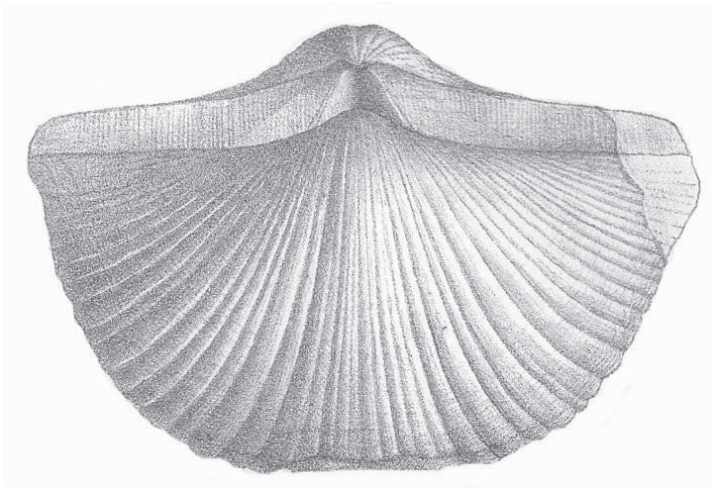


Fig. 312. *Angiospirifer bisulcatus* (Sowerby), dorsal view of large specimen from Lower Carboniferous of Derbyshire, England, x1. (Davidson 1858b).

Kasakhstania Besnossova, of Pennsylvanian age, was shown only as an internal ventral mould in the *Revised Brachiopod Treatise*. It is further illustrated herein as Fig. 313. An umbonal callosity is developed, and micro-ornament is dominated by radial lirae, rather than commarginals typical of Sergospiriferinae, where it was placed by Carter (2006a, p. 1778). The strength of the sulcal ribs show that the genus is closer to Angiospiriferinae than to Trigonotretidae. Adminicula are high.

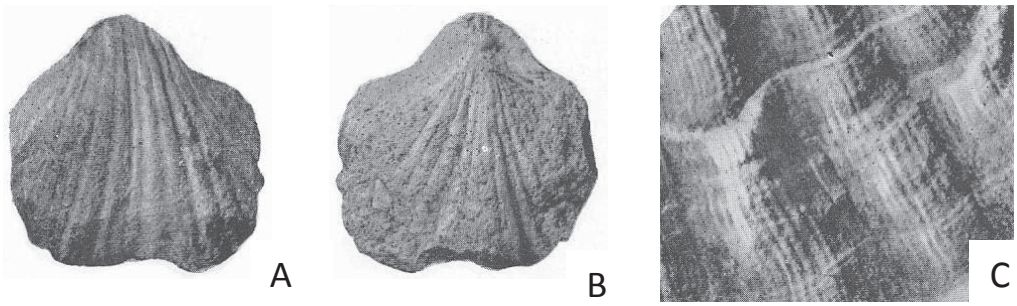


Fig. 313. *Kasakhstania mikunovi* Besnossova, ventral and dorsal views, x1, and micro-ornament, x15. From Pennsylvanian of Kazakhstan. (Besnossova 1968).

Afghanospirifer Plodowski, 1968 has open delthyrium with umbonal callosity, and appears to agree with Angiospiriferinae in all known respects.

Several genera assigned to Angiospiriferinae by Carter (2006a, p. 1783) are excluded. *Prochoristitella* Legrand Blain seems choristitid, and *Brachythyrina* Fredericks, together with *Anthracothyrina* Legrand-Blain, *Elinoria* Cooper & Muir-Wood, and *Quizhouspirifer* Xian Si-yuan have different internal plates and are allocated to Brachythyrininae. *Eobrachythyrina* Brice is judged to belong to Prospirinae. This does result in a severe reduction in the scope of the group, which nonetheless is significant, as the earliest known Trigonotretoidea.

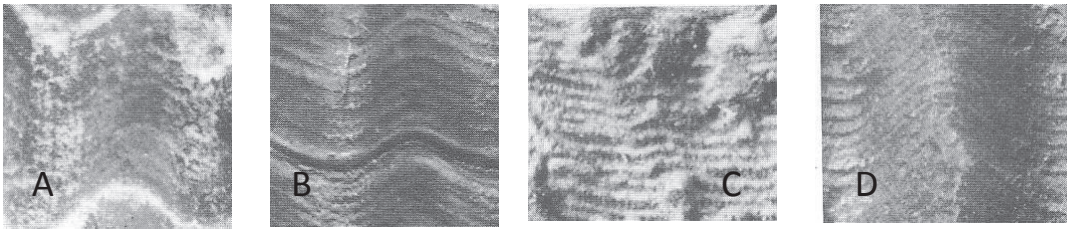


Fig. 314. Micro-ornament. A, *Anthracospirifer libycus* (G. & H. Termier), x13. (See p. 244). B, *Anthracothyrina bressoni* Legrand-Blain, x13. (See p. 244). C, *A. perextensa* Legrand-Blain, x9. D, *Angiospirifer trigonalis* (Martin). Specimens from Visean-Serpukhovian of Algeria. (Legrand-Blain 1986). The strength of the commarginal laminations is striking.

Subfamily **BRACHYTHYRININAE** Waterhouse, 2004

[Nom. transl. hic ex Brachythyrinidae Waterhouse 2004, p. 9, but mis-spelled by Waterhouse 2004, p. 236 as Brachythyridinidae].

Diagnosis: Transverse with wide hinge, plicate with costate sulcus and fold, micro-ornament cancellate or predominantly commarginal, without pustules. Reduced dental, crural and socket plates and no adminicula or tabellae. Delthyrium closed by subdelthyrial shell arching between ends of dental plates and meeting medianly. Lower Carboniferous (Visean) to Lower Permian (Cisuralian).

Genera: *Brachythyrina* (*Brachythyrina*) Fredericks, *Brachythyrina* (*Longathyrina*) Shi, Chen & Zhan, *Anthracothyrina* Legrand-Blain, *Elinoria* Cooper & Muir-Wood (nom. nov. pro *Elina* Fredericks, 1924 non Blanchard 1852), *Eobrachythyrina* Lazarev & Poletaev, *Quizhouspirifer* Xian Si-Yuan, *Vasculumia* new genus.

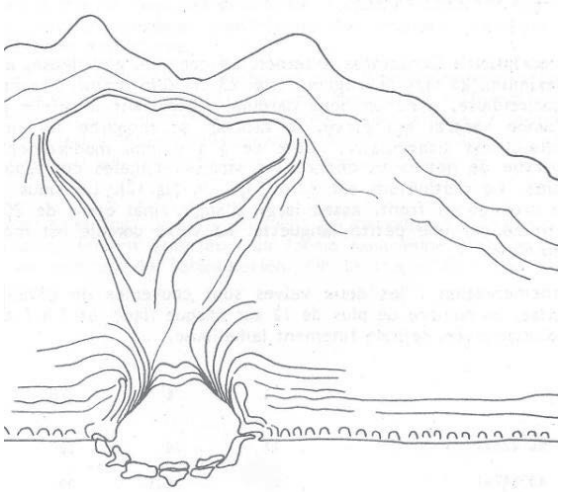


Fig. 315. *Anthracothyrina perextensa* Legrand-Blain, transverse section through ventral apex, x5. From upper Serpukhovian of central Pyrenees of France. (Legrand-Blain 1986).

Discussion: Brachythyrininae has a wide hinge and many fine plicae and costate sulcus and fold. There are reduced dental plates, and no adminicula or tabellae. *Brachythyrina* Fredericks, 1929, based on *Spirifer strangwaysi* Verneuil, 1845 has ramiform vascular

impressions, and *Anthracothyrina* Legrand-Blain, 1984, p. 308, type species *Brachythyrina* (*A.*) *perextensa* Legrand-Blain, has an openly reticulate mantle canal system (Legrand-Blain in Legrand-Blain et al. 1984, text-fig. 2; 1986, Fig. 24E). Micro-ornament consists of commarginal and radial fila, the radials less developed in *Anthracothyrina bressoni* and *perextensa* (Legrand-Blain 1986, pl. 5, fig. 19, 23), and also inconspicuous in some Russian species such as *B. umbonata* Prokofiev, 1969 and *B. declinata* Prokofiev, 1969. Legrand-Blain et al. (1984, p. 307) commented on the absence of radial elements in the micro-ornament in the type species (Besnossova 1968, fig. 96, pl. 28, fig. 11; Prokofiev 1969, pl. 3, fig. 9b, 12b), in contrast to *B. pinica* Martínez-Chacón (1978, pl. 21, fig. 2) from the Bashkirian of Spain, which shows fine radial capillae. The mantle canal system (Ivanova 1960, Lazarev & Poletaev 1982) consists of short branching but not reticulate canals around a small gonoglyphe.

Sections across the umbonal region of *Anthracothyrina* show a double structure developed from the posterior wall and fusing in an arched plug (Legrand-Blain 1986, Fig. 33), covered by stegidia (Legrand-Blain 1986, Fig. 35), and Legrand-Blain et al. (1984, p. 308) noted the presence of a strong apical callosity, and absence of delthyrial plate. There is no connector plate, unlike the arrangement in Spiriferoidea or Cyrtospiriferoidea. The hinge is denticulate, and tabellae absent. Young specimens of *Anthracothyrina* have a mantle canal system close to that of *Brachythyrina*, apart from the absence of a central canal. It was reported that the angioglyphe – that is the mantle canal system - of *Brachythyrina jakovlevi* Gauri (1965, pl. 6, fig. 18) from Gzhelian of Austria, and *B. rectangula* from the Cisuralian of Thailand (Waterhouse 1981, pl. 21, fig. 10, 13, pl. 22, fig. 1) differed in showing finer reticulation than seen in *Anthracothyrina* from the Pyrenees. See p. 245.

Elinoria Cooper & Muir-Wood, based on *Spirifer rectangulus* Kutorga, 1844, and *Eobrachythyrina* Lazarev & Poletaev, 1982, with ramiform vascular impressions in juvenile shells, are similar in most respects. *Quizhouspirifer* Xian Si-Yuan, 1979 also appears to be close, having well developed dental plates, but not all detail is well known.

One genus classed as Bashkiriinae Nalivkin in the Paeckelmannelloidea by Carter (2006b, p. 1815), called *Celsifornix* Carter, is externally close to *Brachythyrina*, but displays a delthyrial connector plate as in Paeckelmannelloidea as well as Spiriferoidea. (See p. 178).

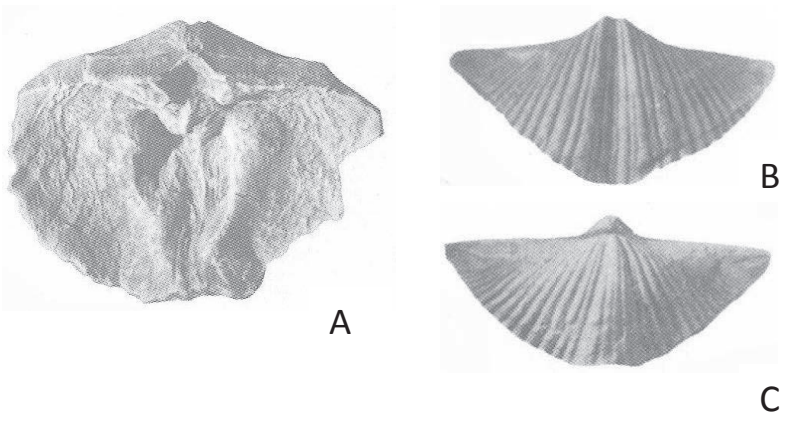


Fig. 316. A, *Eobrachythyrina varians* (Rotai), ventral interior x1.2 from Upper Serpukhovian of Donets Basin. (Carter 2006a). B, C, *Brachythyrina strangwaysi* (Verneuil), ventral and dorsal views x1.2, from Pennsylvanian of Moscow Basin. (Sarytcheva & Sokolskaya 1952).

Carter (2006a) referred most of the preceeding genera to Angiospiriferinae Legrand-Blain, 1985a, and the present position elaborates this relationship. *Angiospirifer* has adminicula, unlike any of the present genera under discussion. All or most share strong plicae, cancellate or commarginal-dominated micro-ornament, and, where known, denticulate hinge and open reticulate vascular impressions. The callosity developed below the ventral umbo in the delthyrial cavity, and presence of a rarely found stegidial plate offers further similarities. But the differences in the internal plates and ventral muscle field are regarded as critical, and are deemed to have marked a further significant development in evolution.

Objections to the recognition of Brachythyrininae were raised by Gourvennec in Gourvennec & Carter (2007, p. 2789), who claimed that the proposal led “to a mixture of taxa with different morphologies (eg. delthyrial morphology, deltidial cover, ornament)”. This author clearly preferred placement of *Brachythyrina* in Angiospiriferinae. Just what was meant by ”mixture” needs further clarification, because according to the accepted meaning of the word, it seems completely inapplicable. If you split a group into two groups that each associate similar genera, and dissociate dissimilar genera, you are not mixing them. Even if you split several similar genera into two groups, you are not mixing them. The claim appears misconceived, and it is support for Carter’s preferred classification that mixes different morphologies, particularly with regard to internal plates. Some of the criteria regarded as critical by Gourvennec in Gourvennec & Carter (2007) do indeed justify the distinction: and in no way leads to a mixture of morphologies. *Angiospirifer* has adminicula. *Brachythyrina* does not. Some contributions to the *Revised Brachiopod Treatise* placed little or no significance on internal plates, and indeed, as shown elsewhere, confused dental plates with adminicula. But no justification has been offered for that stance. Yet, inconsistently, the *Revised Brachiopod Treatise* has recognized their significance by distinguishing Martiniinae from Ingelarellinae, Brachythyridae from Angiospiriferinae, Phricodothyridinae from Toryniferinae, with many other examples.

Genus ***Vasculumia*** new

Name: vasculum – a small vessel, Lat.

Type species: *Brachythyrina boonlomi* Waterhouse, 2004, p. 236 from Ko Yao Noi Formation (Sterlitamakian) of south Thailand, here designated.

Diagnosis: Transverse and plicate with costae over sulcus and fold, micro-ornament of radial and commarginal lirae, no pustules. Hinge weakly denticulate, teeth small, dental plates low and covered by pleromal thickening along the dorsal edges to form an arch which forks under the delthyrium. Mantle canal imprints over ventral valve of two orders, with coarse ramifying set, and intervening space occupied by fine closely reticulate set, opening laterally, not posteriorly.

Discussion: The type species has been described as *Brachythyrina rectangulus* (not Kutorga) by Waterhouse (1981, p. 96, pl. 21, fig. 1-14, pl. 22, fig. 1-8, pl. 23, fig. 1). It is like *Brachythyrina* Fredericks in shape and ornament, and the vascular impressions are

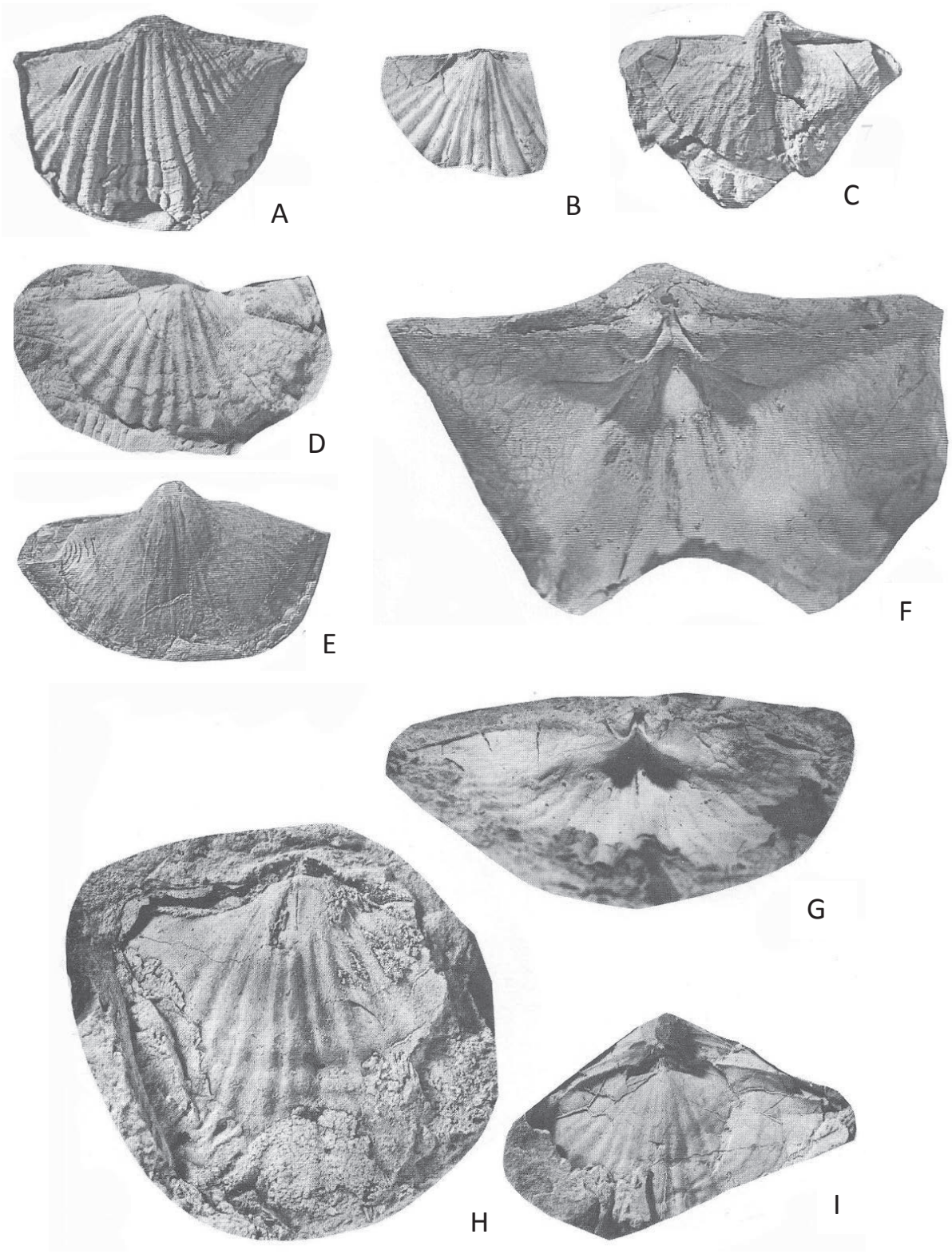


Fig. 317. *Vasculumia boonlomi* (Waterhouse). A, latex cast of ventral valve, holotype, x1. B, internal mould of dorsal valve, x1. C, ventral internal mould, x1. D, dorsal internal mould, x1. E, ventral internal mould, x1. F, G, latex cast of ventral interior, x2. H, dorsal internal mould, x2. I, internal mould of specimen with valves conjoined, x2. From Ko Yao Noi Formation (Sakmarian) of southern Thailand. (Waterhouse 1981).

somewhat comparable, but not the same. *Vasculumia* is also close to *Anthracothyrina* Legrand-Blain in external appearance, and this genus has reticulate vascular impressions, closer to those of the present form, but without the much finer set of reticulate impressions. Because the nature of the vascular impressions has been imparted high significance by Legrand-Blain (1985a) and Carter (2006a), it appears that the present form cannot be referred to either *Brachythyrina* or *Anthracothyrina*, and other genera ascribed to the group have different shape and ribbing. In addition, *Anthracothyrina* has stegidial plates making up a delthyrial cover, nowhere displayed by present material, and a much smaller pedicle callist under the umbo, without the prolonged pleromal thickening. The hinge of *Anthracothyrina* is denticulate (Legrand-Blain 1986, Fig. 35), as in Trigonotretidae, and weak denticles are found in the present form.

Subfamily **VARUNINAE** new subfamily

Name genus: *Varuna* Waterhouse, 2004, p. 186 from Visean-Serpukhovian of Kashmir.

Diagnosis: Small transverse and strongly plicate shells with costae over sulcus and fold as a rule, plicae may be simple or costate, and tend to have angular narrow crests, crossed by predominantly commarginal laminae, with fine radial capillae, no tubercles; narrow cardinal

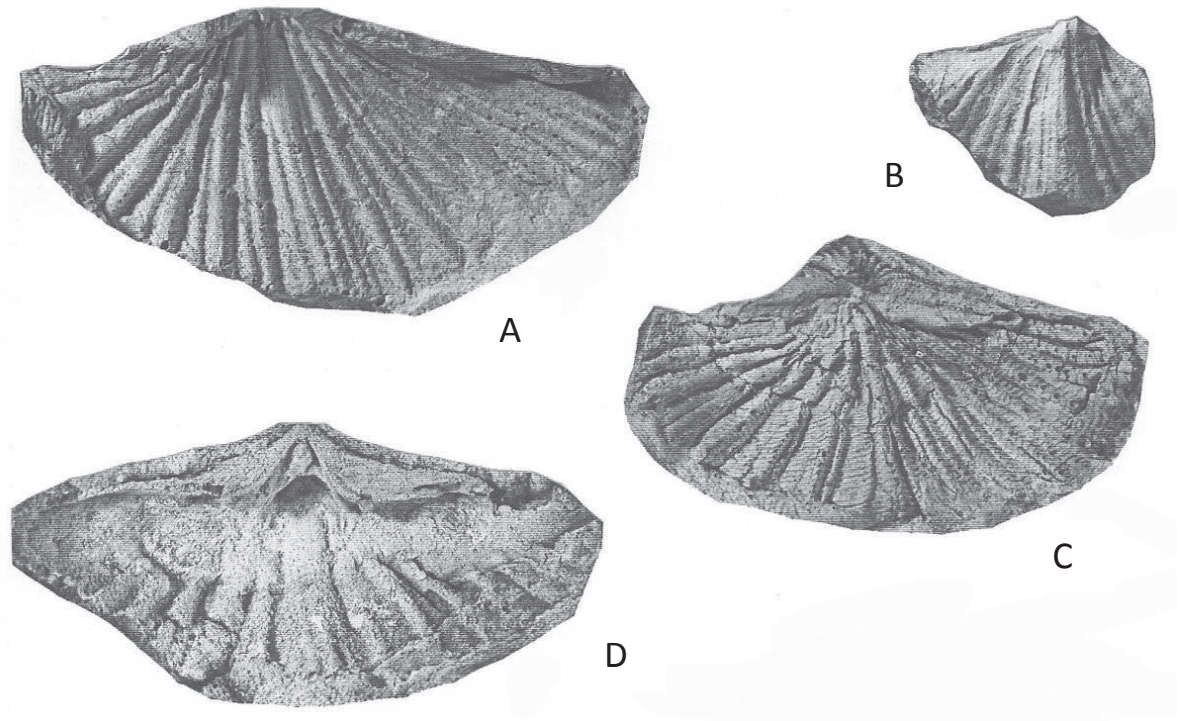


Fig. 318. *Varuna varuna* (Diener), A, latex cast of dorsal valve. B, dorsal internal mould. C, latex cast of dorsal exterior (lectotype). D, latex cast of ventral valve, showing umbonal callosity and pleromal ridges. Specimens x2. From Fenestella Shale (Visean-Serpukhovian) of Kashmir. (Waterhouse 2004). Although reported as Moscovian by some authorities, the so-called Fenestella Shales of the northwest Himalaya in Kashmir and correlative beds in Nepal contain large Rugosochonetidae of mostly Visean age, as confirmed by G. Termier, pers. comm.

extremities, moderately high ventral interarea bearing denticles along the hinge. Internal plates, vascular pattern and umbonal callosity as in the family. Lower Carboniferous (Visean) to Middle Carboniferous (?Moscovian).

Genera: *Varuna* Waterhouse, *Adminiculoria* Waterhouse & Gupta, *Alispirifer* Campbell.

Discussion: The subfamily is distinguished by its small size and highly transverse subtriangular shape. Members are more transverse and more strongly plicate, with shallower sulcus compared with members of Costuloplicinae and Trigonotretinae, closer to members of Angiospiriferinae, but there are no pustules developed over the micro-ornament. Members of this subfamily could have given rise to both Costuloplicinae and Georginakingiidae.

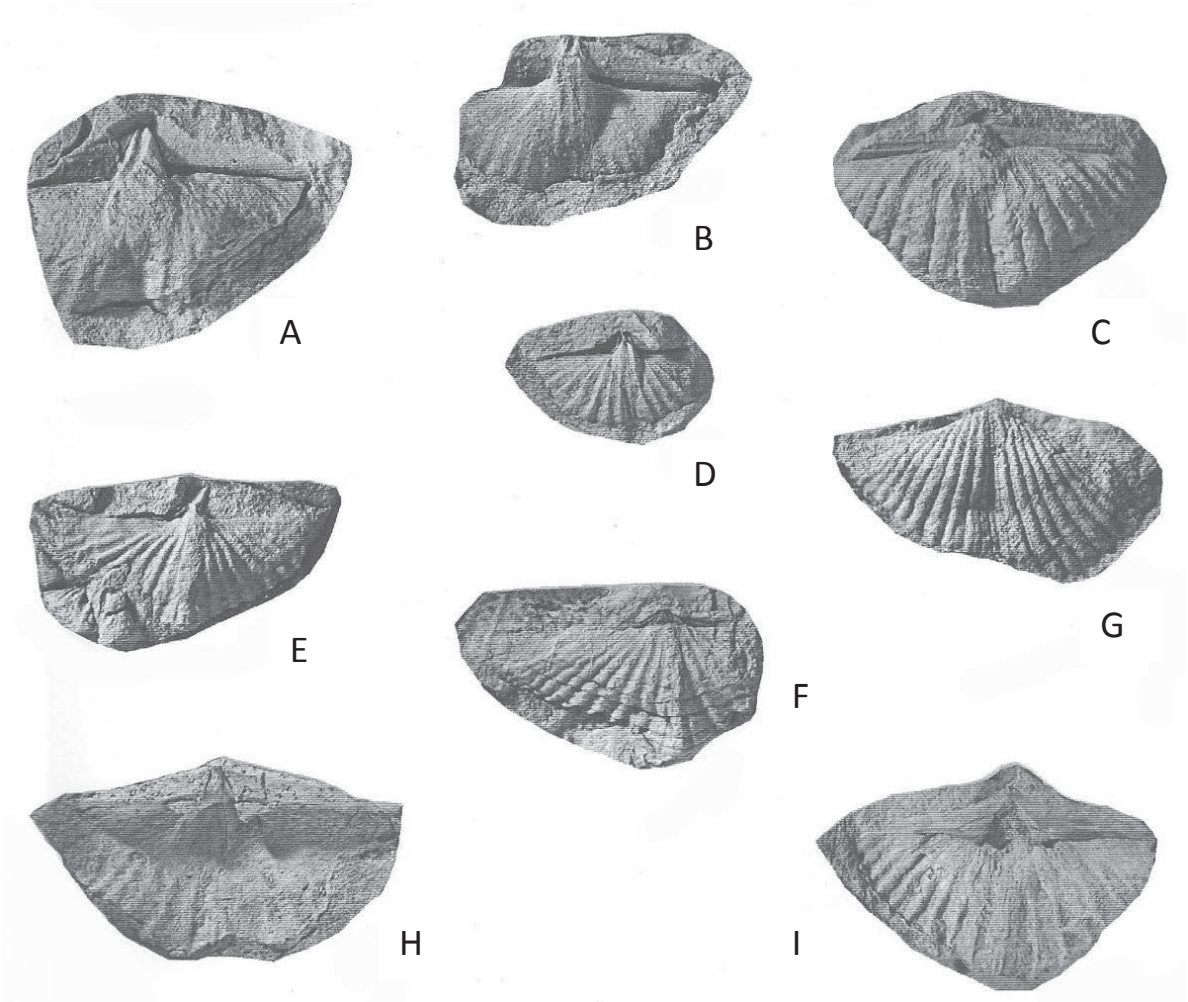


Fig. 319. *Adminiculoria middlemissi* (Diener). A-D, internal moulds of ventral valves. E, F, internal mould of dorsal valve. G, external ventral valve. H, I, latex cast and internal mould of ventral valve. From Fenestella Shales (Visean-Serpukhovian) of Kashmir. Specimens x1. (Waterhouse 2004).

Alispirifer Campbell has been classed as Paeckelmannelloidea, which it superficially resembles, but the genus has a well developed umbonal callosity. It is represented by several species in rocks of Visean to Moscovian age in eastern Australia. Given its southerly position

and age, this genus or allied stock may have given rise to Costuloplicinae and Trigonotretinae.

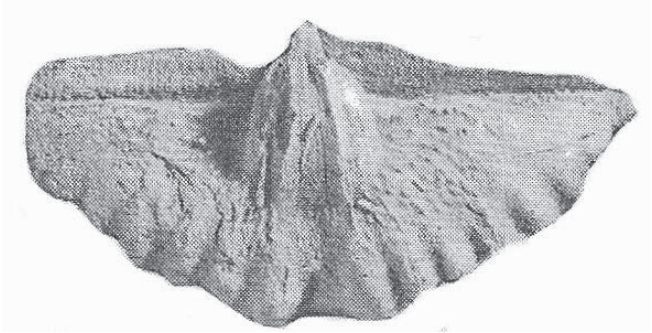


Fig. 320. *Alispirifer laminosus* Campbell, ventral internal mould, x2, from Branch Creek Formation (Middle Carboniferous), Queensland. (Hill & Woods 1964). Note the trigonotretid mantle canal system.

Family **GEORGINAKINGIIDAE** Waterhouse, 2004

[Nom. transl. hic ex Georginakingiini Waterhouse, 2004, p. 184].

Diagnosis: Transverse shells with variable number of strong well-spaced to crowded plicae, usually well rounded in section, but may bear few to several costae arising well in front of umbones. Commarginal lamellae and fine capillae developed, umbonal callosity and denticulate hinge, reticulate vascular impressions. Lower to Upper Permian (Asselian – Changhsingian).

Genera: *Georginakingia* Waterhouse, *Angulispirifer* new genus, *Sulciplica* Waterhouse, *Tasmanospirifer* new genus, *Unicostatina* Waterhouse.

Fig. 321. *Georginakingia aviculiformis* new species. Posterior part of cast BR 3218 prepared from internal mould, figured as *Spirifer avicula* Sowerby by Morris (1845, pl. 17, fig. 6), x1.7, from Eaglehawk Neck (Guadalupian), Tasmania.

Discussion: The family is probably descendent from *Adminiculoria*. *Georginakingia* is a genus of large shells of Guadalupian (Wordian) age most common in eastern Australia, extending

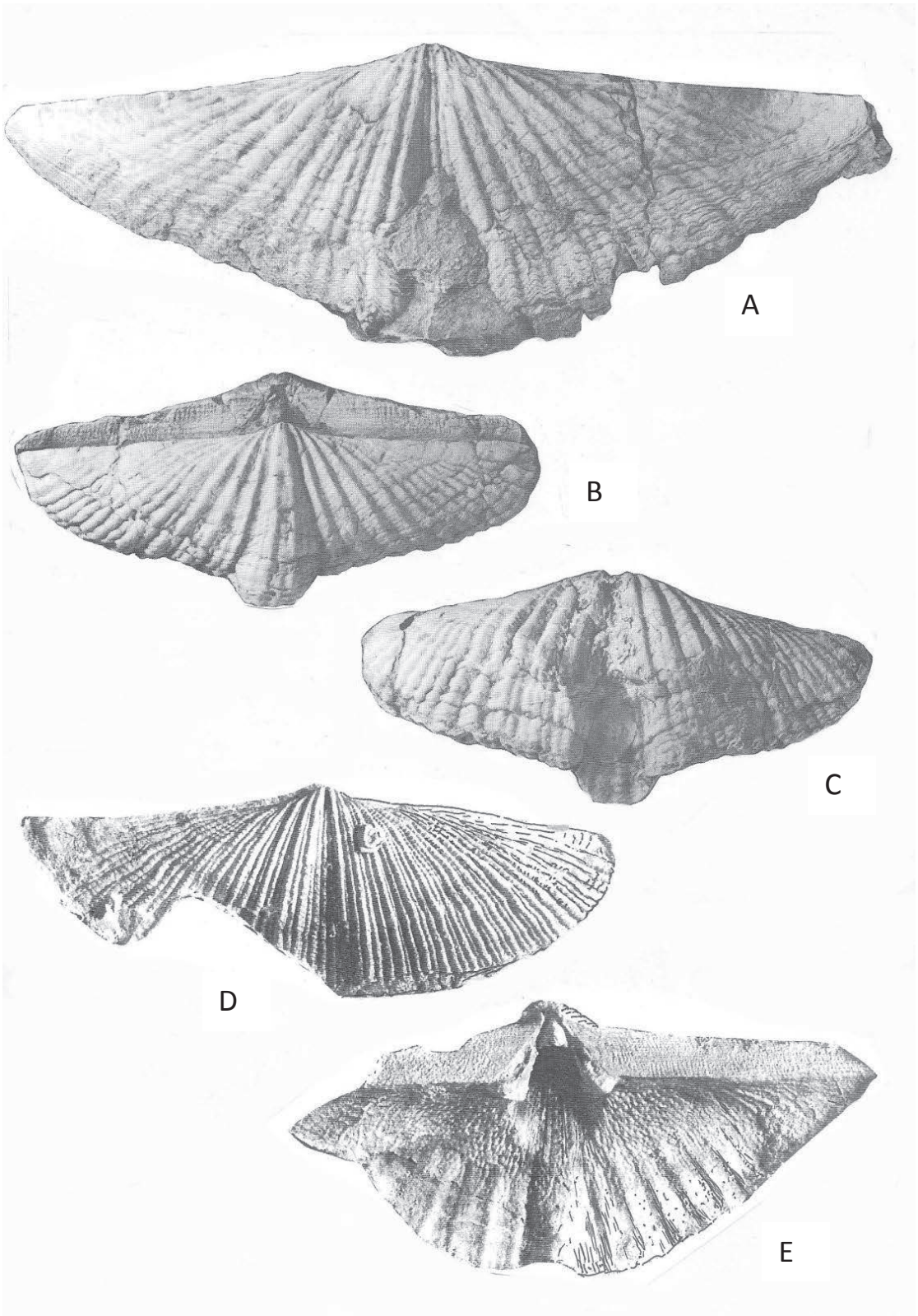


Fig.322. *Georginakingia aviculiformis* new species. A, large ventral valve. B, C, dorsal and ventral aspects of another specimen. D, finely costate ventral valve. E, ventral valve interior, showing bulbous umbonal callosity. Specimens x1, from Guadalupian of Tasmania, Australia. (Clarke 1987).

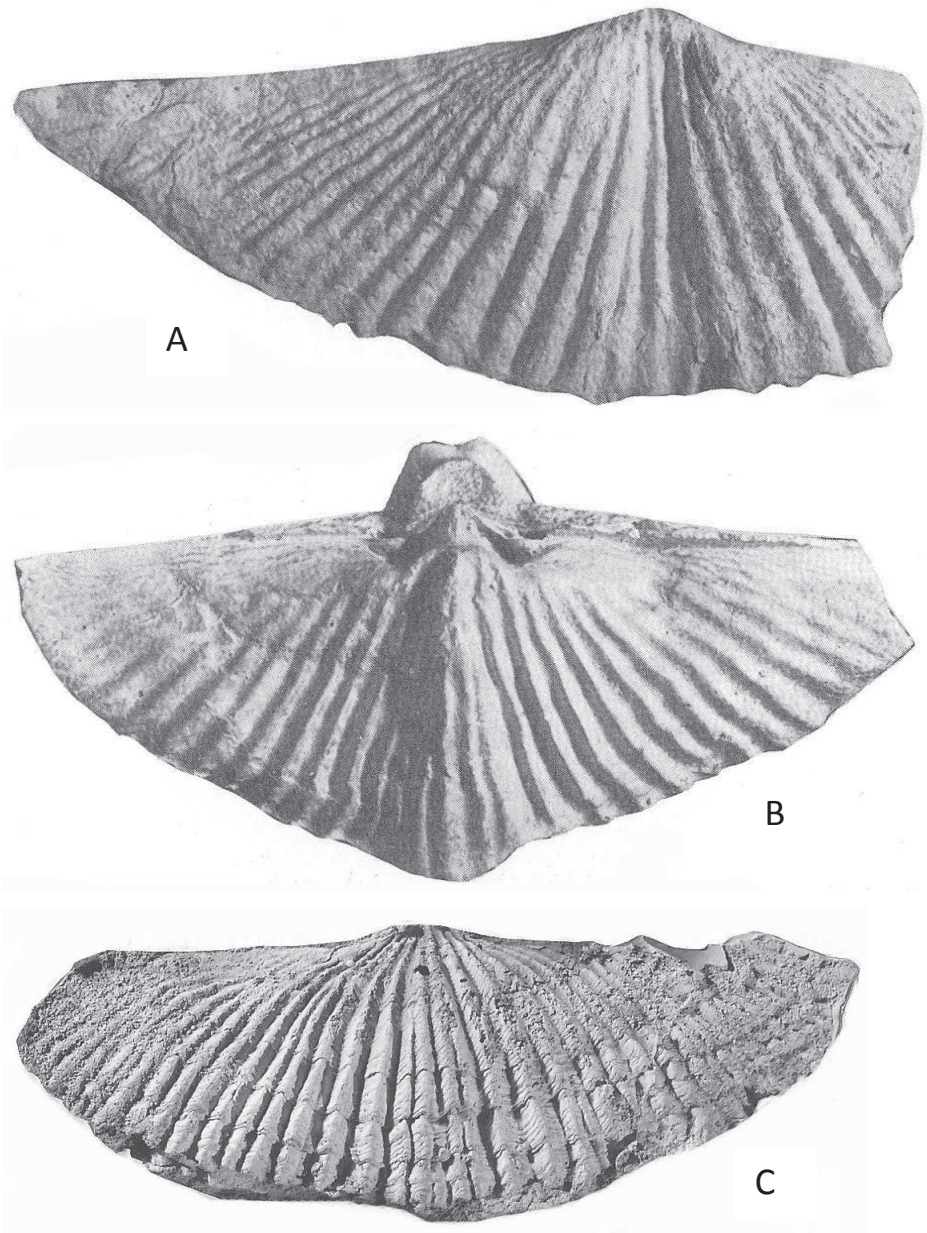


Fig. 323. *Sulciplica transversa* Waterhouse. A, ventral valve exterior, x1. B, dorsal interior, x1. From mid-Guadalupian of Eagle Hawk Neck, Tasmania. (Clarke 1987). C, dorsal exterior, x1.3. From mid-Guadalupian of Blenheim Group, Queensland, Australia. (Waterhouse & Jell 1983).

rarely further west. The genus is ornamented by numerous pairs of strong costate plicae, with sulcal and fold costae, and subcancellate micro- ornament. It shows only a superficial similiarity to *Fusispirifer,* an identification proposed by Clarke (1973, 1987) and endorsed by Gourvennec in Gourvennec & Carter (2007, p. 2781). *Georginakingia* is like *Fusispirifer* in being large and transverse and plicate, but such a comparison lacks rigour. The two genera differ in costation, plication (plicae are much more numerous), mantle canal system and delthyrial appurtenances. The assessment of the genus as trigonotretid is entirely consistent

with ecological and paleolatitudinal assessments (Shi & Waterhouse 2010a). The genus is restricted largely to the marine Permian of east and southeast Australia, a region dominated by trigonotretid genera, whereas members of Fusispiriferinae are rare in the region, and limited to a couple of stratigraphic horizons with evidence for unusually warm waters that lasted for a short interval of time.

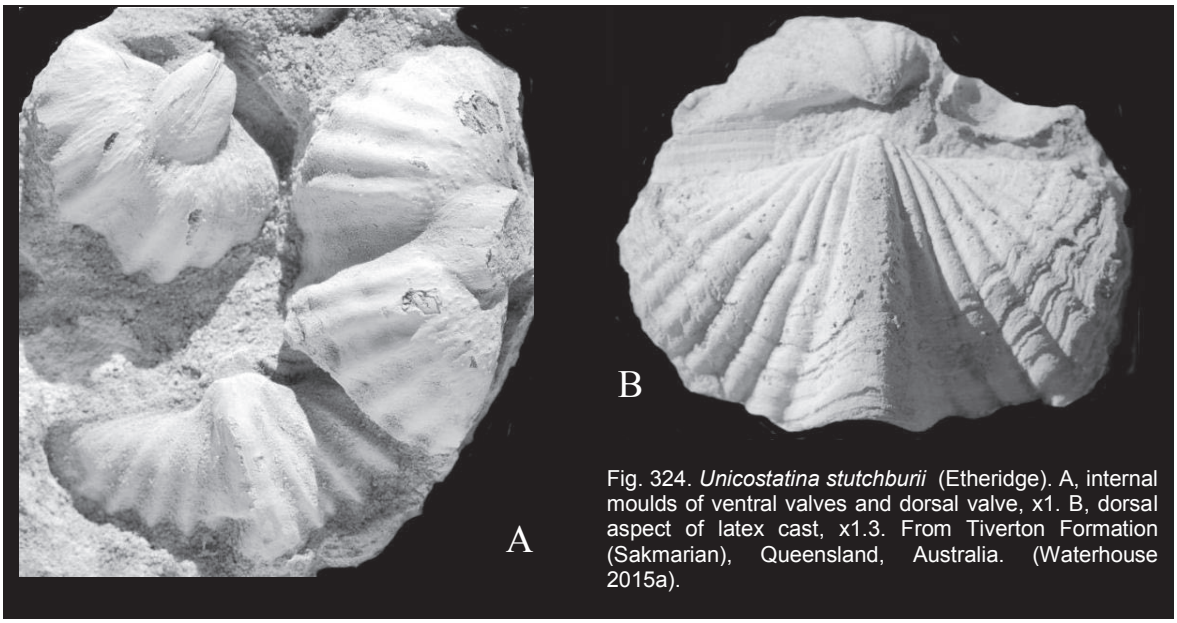


Fig. 324. *Unicostatina stutchburii* (Etheridge). A, internal moulds of ventral valves and dorsal valve, x1. B, dorsal aspect of latex cast, x1.3. From Tiverton Formation (Sakmarian), Queensland, Australia. (Waterhouse 2015a).

Another genus, *Unicostatina* has shorter hinge and obtuse cardinal extremities, and costae are few or absent, apart from a median rib traversing the ventral sulcus. It is most prominent in Cisuralian (Asselian, Sakmarian) faunas of eastern Australia, but survived as *U. chatsworthensis* (Balfe & Waterhouse) in Changhsingian faunas of Gympie, by far the youngest member of the family. *Sulciplica* has numerous plicae with a few subplicae over the sulcus and fold, and extends from Asselian to Capitanian in age in east Australia and New Zealand.

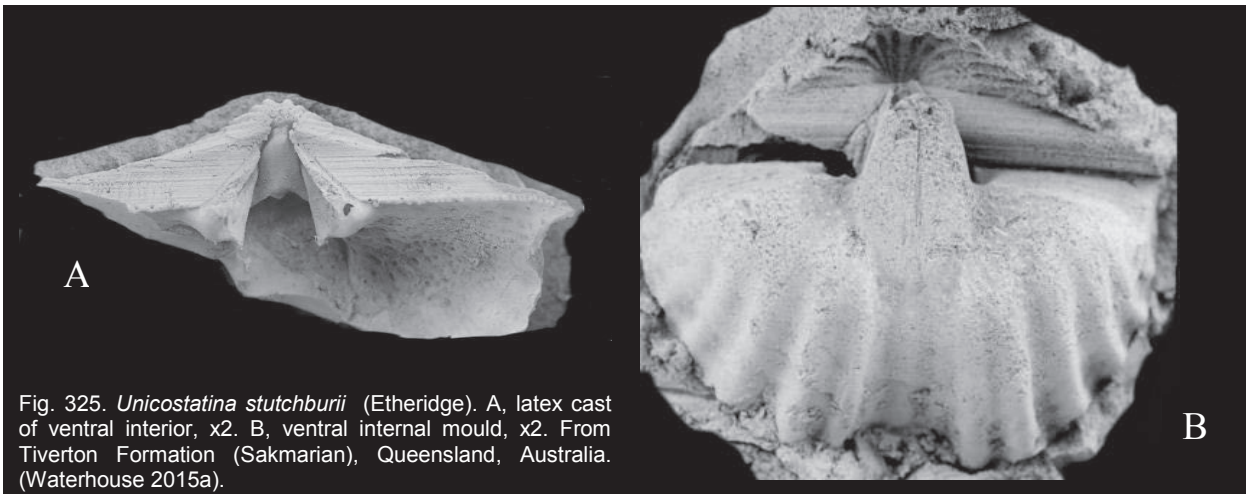


Fig. 325. *Unicostatina stutchburii* (Etheridge). A, latex cast of ventral interior, x2. B, ventral internal mould, x2. From Tiverton Formation (Sakmarian), Queensland, Australia. (Waterhouse 2015a).

Genus ***Georginakingia*** Waterhouse, 2004

Diagnosis: Extremely transverse, numerous pair of plicae with well rounded crests. Open delthyrium, umbonal callosity, low dental plates, short adminicula, ctenophoridium, crural plates, no tabellae, subreticulate mantle canal system.

Type species: *Spirifer avicula* Morris not Sowerby here renamed *Georginakingia aviculiformis* n. sp., in order to place the type species on a firm footing, with available holotype. From Malbina Formation of Tasmania (Guadalupian).

Georginakingia aviculiformis new species

1845 *Spirifer avicula* Morris, p. 282, pl. 17, fig. 6 not G. B. Sowerby 1844, p. 160.

1973 *Fusispirifer avicula* – Clarke, pp. 50, 59.

1987 *F. avicula* – Archbold & Thomas, p. 196, Fig. 12A-D, 13A-G, 14A-C.

1987 *F. avicula* – Clarke, p. 267, Fig. 5A-E.

2004 *Georginakingia avicula* – Waterhouse, p. 184, text-fig. 34.

Name: avis – bird. Named to suggest species name applied to *Spirifer avicula* Morris, 1845 non Sowerby, 1844, relating to topographic expression of source locality.

Diagnosis: Transverse, with numerous plicae bearing fine costae anteriorly, closely spaced growth laminae. Dental plates, short adminicula, well developed umbonal callosity and open delthyrium.

Holotype: GST 887, figured by Clarke (1987, Fig. 5A) from Malbina Formation, Eaglehawk Neck, Tasmania, here designated.

Description: Descriptions are provided by Archbold & Thomas (1987), Clarke (1987) and Waterhouse (2004).

Discussion: The species *Spirifer avicula* as described in recent years is based on *Spirifer avicula* Morris, which was identified with *Spirifer avicula* G. B. Sowerby. This species was described, but not illustrated by Sowerby, and material has long been lost, so that its nature is uncertain. All recent authors have agreed in assigning material to *avicula* Morris not Sowerby, an unsatisfactory situation, so that the taxonomy is regularized by renaming the species, and designating as type a specimen better preserved than the Morris internal mould.

Genus ***Tasmanospirifer*** new genus

Name: From Tasmania, Australia.

Diagnosis: Weakly transverse with well rounded cardinal extremities, and eight to ten pairs of plicae, bearing subangular to rounded crests, fold and sulcus moderately defined, with a few pairs of subplicae, micro-ornament cancellate. Open delthyrium, umbonal callosity, dental plates, short adminicula; ctenophoridium, crural plates, no tabellae, reticulate mantle canal system.

Type species: *Tasmanospirifer clarkei* new species from Berriedale Limestone (Artinskian) of Tasmania, here designated.

Discussion: This genus is readily distinguished from other members of the family by its

distinctive outline and fine plicae. It has more and finer plicae than those of *Unicostatina* from east Australia, and has fewer plicae and is much less transverse than Guadalupian genera *Georginakingia* and *Sulciplica*, also in east Australia, with the latter genus extending into western New Zealand. Clarke & Farmer (1976) recorded species belonging to *Tasmanospirifer* from their late Bernacchian to mid-Lymington Stages in Tasmania, which span Berriedale Limestone to lower Malbina Formation, and are approximately Artinskian to Roadian in age.

Tasmanospirifer clarkei new species

1953 *Trigonotreta stokesii* [not Koenig] – Brown, pl. 5, fig. 5 (part, not fig. 1-4 = *stokesi*).

1968 ''*Spirifer*" *tasmaniensis* [not Morris] – Armstrong, pl. 6, fig. 8-12 (part, not fig. 7 = *tasmaniensis* Morris).

1979 *S. tasmaniensis* – Clarke, p. 206, pl. 4, fig. 1-4, 9, (part, not fig. 5-8 = *tasmaniensis* Morris).

Name: Named for Michael J. Clarke.

Diagnosis: Weakly transverse with subangular plicae and rare additional costae.

Holotype: TMF 36817, figured by Clarke (1979, pl. 4, fig. 2) and herein Fig. 326A, from Berriedale Limestone at Granton's Quarry (Artinskian), Tasmania, here designated.

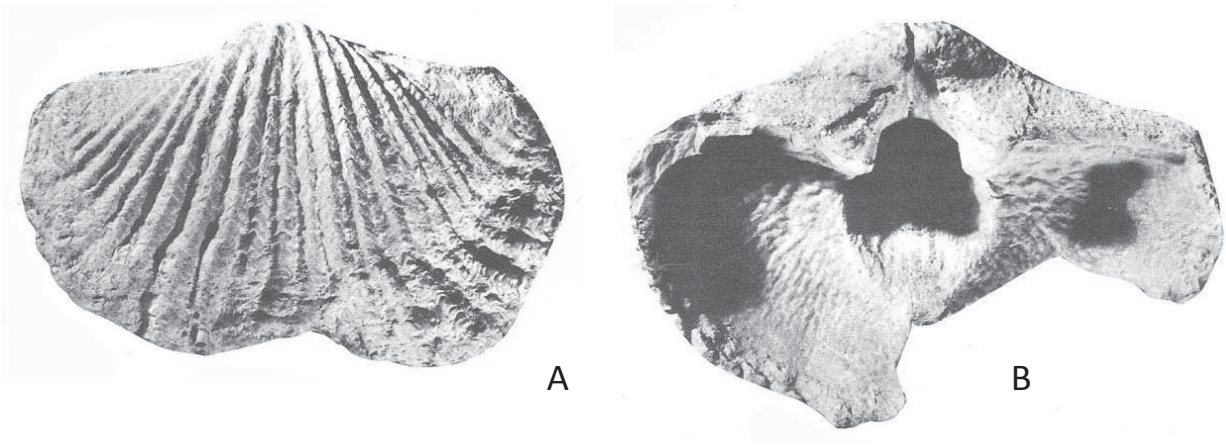


Fig. 326. *Tasmanospirifer clarkei* new species. A, ventral valve holotype TMF 36817. B, interior view of ventral valve. Specimens x1, from Berriedale Limestone (Artinskian), Tasmania, Australia. (Clarke 1987).

Description: This species has been described, chiefly by Clarke (1987), together with *tasmaniensis*, but is distinguished by its larger size, and subangular plicae, whereas the plicae of *tasmaniensis* Morris, 1845, p. 280, pl. 15, fig. 3 have more rounded crests, and also tend to have fewer sharply defined adventitious costae. The species *tasmaniensis* comes from beds younger than the Berriedale Limestone, in an unnamed limestone at Eastern Marshes, rated by Clarke (1979) as mid-Lymingtonian Stage in his local stage scheme for Tasmanian Permian, as compared with the Bernacchian Stage for the Berriedale Lime-

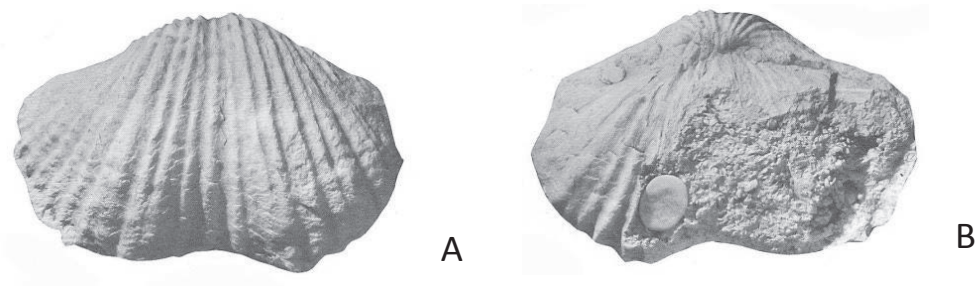


Fig. 327. *Tasmanospirifer tasmaniensis* (Morris), lectotype BB 6246, x1. A, ventral view. B, dorsal view. From unnamed limestone at Eastern Marshes, Tasmania, Australia. (Clarke 1987).

-stone. The comparative ages are Artinskian for *clarkei,* and either Kungurian or Roadian for *tasmaniensis*.

Brachythyrina thailandica Hamada, 1960 from the Lower Permian (Asselian) of southern Thailand, although identified as *Sulciplica* by Waterhouse (1982, p. 347), has narrow costae over the sulcus and fold, and the delthyrium has a connector plate, so cannot belong to *Sulciplica*.

Genus ***Angulispirifer*** new genus

Name: angulus – angle, corner, Lat.

Diagnosis: Transverse with extended cardinal extremities, ornamented by numerous plicae with angular crests and interspaces, prominent commarginal growth laminae. Sulcus narrow with median central rib, and fold with median channel. Prominent ventral umbonal callosity.

Type species: *Spirifer phalaena* Dana, 1849, p. 485 from Guadalupian of Tasmania, here designated.

Fig. 328. *Angulispirifer phalaena* (Dana), external mould BR 3219 of dorsal valve, holotype x1, kept at Museum of Natural History, London. From Eaglehawk Neck, Tasmania, Australia (mid-Guadalupian). (Morris 1845).

Discussion: This genus is distinguished from *Unicostatina* by having more and angular plicae and wide cardinal extremities, and is less transverse than *Sulciplica* or *Georginakingia*, which have more rounded plicae. *Tasmanospirifer* also has a narrower hinge with less extended cardinal extremities and more plicae in the sulcus. The type species has been described as *Spirifer vespertilio* (not Sowerby) by Morris (1845, p. 283, pl. 17, fig. 3), *S. phalaena* Dana (1849, p. 685, ?pl. 2, fig. 4) and Waterhouse & Vella (1965, p. 67, pl. 3, fig. 6) and *S. stutchburii* not Etheridge by Etheridge (1892, p. 232.

Suborder DELTHYRIDINA Ivanova, 1972

[Delthyridina Ivanova, 1972, p. 41].

Diagnosis: Shells smooth or plicate, costae rare, sulcus and fold widespread, commargons or lamellae common, micro-ornament may be distinctively fimbriate, or with frilly laminae in some genera of one superfamily, but also involves closely related genera with capillate or cancellate micro-ornament, finely spinose along commarginal rows in various groups, spines elaborate and double-barrelled in members of another superfamily. Delthyrium variously open, or covered in part or whole by deltidia, or connector plate. Internal plates varied. Silurian (upper Llandovery) to Upper Permian (Changhsingian).

Infrasuborder DELTHYRIMORPHI Ivanova, 1972

[Nom. transl. hic ex Delthyridina Ivanova, 1972, p. 41].

Diagnosis: Highly variable in many aspects of morphology, and typically biconvex and smooth or plicate, by contrast with more limited range of shape and ornament in Ambocoeliimorphi. Silurian (upper Llandovery) to Upper Permian (Changhsingian).

Discussion: Delthyrimorphi are highly variable in many aspects of their morphology. The classification of Delthyridina in the *Revised Brachiopod Treatise* settled on a subdivision into two superfamilies, divided mostly according to whether they were plicate or smooth, and overlapping in micro-ornament and overlapping also with Ambocoelioidea. Although fimbriate or frilly micro-ornament was considered to characterize many Delthyroidea, it was allowed that cancellate or spinose or lamellate micro-ornament also featured strongly, even amongst genera associated in the same subfamily. And although double-barrelled spines were a feature, they only typified a few of the genera even in late members of Reticularioidea. In short, micro-ornament, although readily accessible, could be regarded as reliable only to generic rank, or small family-group units. Variation was also allowed in internal plates, and in delthyrial apparatus. Thus the classification did little to delineate strands of evolution within the two superfamilies. But it is open to debate whether strands can be discerned, because there is so much variation and repetition of morphologies through time, or reiteroplasy. Focus is devoted in the present analysis to several features in an effort to resolve aspects of delthyridin evolution and classification.

The nature of the delthyrial apparatus is of interest. Deltidial closures are widespread, and a number of genera and subfamilies developed pleromal ridges and connector plate. The question is whether these structures signified a strong difference from other Delthyridina and an interrelationship between genera with similar apparatus.

Internal plates assume a major role in classification, beyond the weight allocated to them in the *Revised Brachiopod Treatise*. Most groups are characterized by adminicula, but a few are outstanding in the lack of adminicula. Short tabellae are widespread, but not deemed to be of overwhelming significance, because tabellae vary in presence even within some species and genera, at least from presently available information. Another parameter granted greater weight is the presence or absence of a ventral median septum. This is a feature

readily determined in genera, and deemed to be consistent in genera. In the *Revised Brachiopod Treatise*, the presence or absence of a ventral median septum was claimed to appear sporadically in various family groups thought not to have been closely related. These scattered septate groups are drawn together into one major family group, and allocated a superfamily. That is a major difference from the Treatise scheme, but seems to allow certain consistency in shape and aspects of ornament.

Members differ in micro-ornament – but that is true of all delthyridin families other than those limited to a genus or two. They differ a little in presence or absence of tabellae, which is judged to be of only moderate significance, as in the Treatise. Genera differ to some extent in plication, but so do other major brachiopod groups in Cyrtiimorphii, Martinidina, and many Spiriferidina: in short the prime emphasis on plication in the *Revised Brachiopod Treatise* is regarded with caution, especially as exceptions were allowed. The possibility that the Delthyroidea as newly interpreted is polyphyletic should not be lightly dismissed, despite the appeal of having one concrete attribute to provide the key to its recognition. But it is a stretch to uniquely place principal stress on plication or non-plication, in the face of natural variation in all other groups. Furthermore, micro-ornament clearly does not provide a prime pervasive key, and internal plates are accommodated in the present scheme.

As in other parts of the *Revised Brachiopod Treatise*, there is a problem over the nomenclature and degree of rigour applied to the description of the internal plates, which affects the source of the group. A number of genera in several subfamilies show short nicks in the posterior wall of dorsal internal moulds, where a plate met the posterior wall. The plates scarcely touch the floor, and are either extremely short, vestigial tabellae, or are not tabellae but are crural plates or crural bases. The crural plates (or so-called inner hinge plates) are never supported by long and well defined tabellae, comparable to those for example in Ingelarellidae. The importance of this relates to the source of the Delthyroidea. If the plates are tabellae, and a number of genera have what appear to be short tabellae, then the Delthyroidea probably arose directly from Cyrtioidea, as suggested by Carter & Gourvennec (2006a, Fig. 1104). The fossil record permits derivation, genus *Howellella* appearing in the middle Llandovery (Silurian), according to Carter & Gourvennec (2006a, p. 1694), whilst Johnson & Hou (2006b, p. 1826) assigned an upper Llandovery age to the oldest *Howellella*, and upper Ordovician for *Eospirifer*. Moreover deltidial plates are common in both Cyrtioidea and Delthyridina. The possibility that Delthyroidea arose from early adolfioid stock would seem to be negated by the fact that the oldest adolfioid is of Wenlockian age. Of course such relatively narrow differences in first known occurrences may well be upset in future. But on present evidence, delthyroids arose from Cyrtioidea through both the development of fimbriate ornament, and simultaneously, the reduction and often loss of tabellae.

Classification of delthyroid brachiopods has proven difficult and contentious. There is a high degree of variability amongst leading criteria, and Schemm-Gregory (2008b, p. 401) wrote that the study by Carter et al. (1994) “had been considered controversial … and characterized by certain mistakes in the diagnoses of genera” and that “Most of these errors

were unfortunately adopted in the" *Revised Brachiopod Treatise*. A number of improvements were initiated before Schemm-Gregory's untimely death, and have been pursued by other authors. But Schemm-Gregory did not pursue vital questions over fundamental morphologies of delthyrial cover and tabellae, and in the present overview, the delthyroid brachiopods are viewed much more extensively (beyond what are here called Hysterolitoidea) and within a much larger framework of alliance and conformity-disconformity with other brachiopod groups, which affects the fundamental classification and hierarchy of family groups, so that the clutter of families may be avoided. The following classification therefore marks a further departure from that of the *Revised Brachiopod Treatise*, but nevertheless builds on that classification, which for all its contentious issues, marked a praiseworthy advance over earlier attempts, and deserves respect from the thorough examination of almost all known delthyridin genera in an evolutionary framework.

Superfamily **DELTHYROIDEA** Phillips, 1841

[Delthyroidea Ivanova, 1959, p. 56 nom. transl. ex Delthyridae Phillips, 1841, p. 54].

Diagnosis: Median ventral septum present as a rule, except where secondarily lost. Biconvex, sulcus and fold present with plicate flanks in some genera, growth lamellae prominent, typically but far from always fimbriate, bearing row of spines along edge, but capillate or cancellate in some groups of genera, adminicula and ctenophoridium commonly present. Silurian (upper Llandovery) to Carboniferous (Visean).

Discussion: Delthyroidea is the oldest named superfamily within Delthyridina, with some genera characterized by fimbriate ornament, comprised of elongate fine spine bases in commarginal rows across the entire shell (Gourvennec 1990a). The outstanding feature in comparison with other Delthyridina is the presence of a ventral septum, and such a septum is also present in other groups, that are therefore brought into association. Some genera within the superfamily share much in the way of shape, ornament and internal plates, but lack a median ventral septum. They are classed within the group, because they come so close to other septate genera that they are deemed to have secondarily lost the ventral median septum.

Family **DELTHYRIDAE** Phillips, 1841

[Delthyridae Phillips, 1841, p. 54].

Diagnosis: Small to medium in size, pauciplicate, fimbriate. Ventral median septum, usually with short tabellae ("crural plates" of Johnson & Hou 2006b, p. 1825). Silurian (upper Llandovery? or Wenlock) to Middle Devonian (Eifelian).

Genera: *Delthyris* Dalman, and subgenus *Quadrifarius* Fuchs, *Ivanothyris* Havlíček.

Discussion: The presence of a ventral median septum is considered to be significant. It is uncommon amongst Spiriferida, and very widespread in Spiriferidina, so that its presence potentially signifies relationship rather than spasmodic and unrelated development in different stock. "Crural plates" which often equate to tabellae were said to be present in *Delthyris*

Fig. 329. *Delthyris (Delthyris) elevata* (Dalman). A, ventral, B, dorsal and C, lateral views, x2. From Wenlock of Gotland. (Bassett & Cocks 1974).

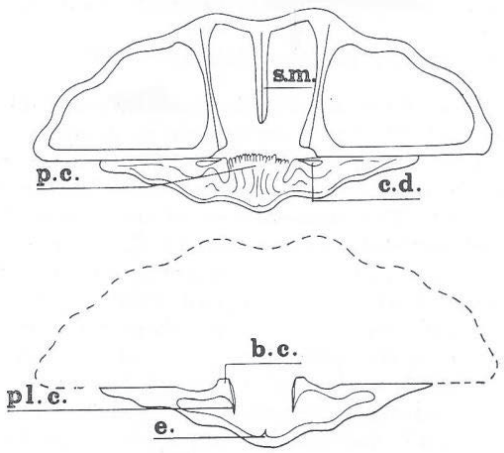


Fig. 330. *Ivanothyris trisecta* (Kayser), as identified and figured by Godefroid (1968, Fig. 3), showing ventral septum and adminicula (not buried in shell as claimed in the *Revised Brachiopod Treatise*), and low dorsal valve with crural bases and very low crural plates. b.c. – crural base; c.d. – dental cavity; e. – euseptum; p.c. – ctenophoridium; pl.c. –- crural plate; sm. – median septum. (Godefroid 1968).

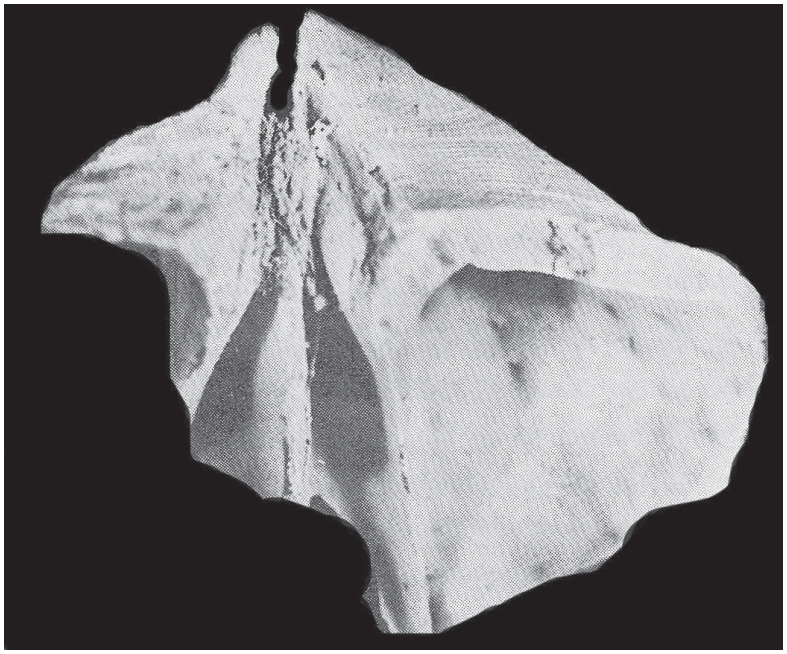


Fig. 331. *Ivanothyris trisecta* (Kayser), ventral interior, x3 approx. From the south of the Dinant Basin, Belgium (lower Couvinan). (Godefroid 1968).

and absent or at least “obsolete” from *Ivanothyris*, but none are clearly present in figures of *Delthyris* provided by Johnson & Hou (2006b, Fig. 1210.2c), unless represented by tiny nicks in the posterior wall of the internal mould, of the sort suggested for *Ivanothyris* in Johnson & Hou (2006b, Fig. 1210.3b).

Delthyridae were made to incorporate Howellellinae Johnson & Hou, 1994, as followed in the *Revised Brachiopod Treatise*, because they are similarly plicate with fimbriate micro-ornament, but the latter group lacks a ventral median septum and is therefore closer to Hysterolitidae. Another group within Delthyroidea is centred on Cyrtinopsidae Wedekind, 1926 (see below), and many genera in this group have a median ventral septum, inviting the proposition that they descended from Delthyridae. Like *Ivanothyris*, they lack tabellae, and unlike *Delthyris* or *Ivanothyris*, they lack fimbriae, displaying frilled micro-ornament. Given the range of types of micro-ornament in Delthyroidea, it defies available evidence to give prime classificatory weight to micro-ornament in this particular superfamily. Were ornament to be treated as prime key to relationships and classification and evolution, then shape and internal plates and delthyrial apparatus would be showing great flexibility and inconstancy.

Family **CYRTINOPSIDAE** Wedekind, 1926

[Nom. transl. Boucot 1957a, p. 38 ex Cyrtinopsinae Wedekind, 1926, p. 198].

Diagnosis: Growth lamellae may be frilly, rarely spinose or fimbriate, capillae interrupted by commarginal growth steps, bilobed cardinal process, ctenophoridium in younger genera. Median ventral septum may be present. Silurian (Wenlock) to Middle Devonian (Givetian).

Discussion: This is a diverse and outstanding family of few genera, with variable internal septation. Plicae are few and well defined. Tabellae are present in the two known genera of Araspiriferinae. The frilly margins to commarginal laminae well developed in *Cyrtinopsis* are not always so clearly developed in other genera, which nonetheless still may display strong and well-spaced commarginal laminae. Schemm-Gregory (2011a, p. 115) appeared to indicate that this family and Family Mucrospiriferidae were derived from eospiriferids, and so should be classed within what is here called Cyrtiimorphi, rather than Delthyridina, although the families were not specifically mentioned. *Cyrtinopsis* possessed a ventral septum, just like *Delthyris* and unlike any member of Cyrtiimorphi, and it is here considered that the cyrtinopsids are close to and probably evolved from Delthyridae. No eospiriferid member is possessed of a ventral median septum, so that Schemm-Gregory’s suggestion is treated with reservations.

Subfamily **CYRTINOPSINAE** Wedekind, 1926

[Cyrtinopsinae Wedekind, 1926, p. 198].

Diagnosis: Ventral median septum and either a spondylium or incomplete spondylium, bilobed cardinal process, becoming striate or ctenophoridiform in younger genera. Silurian (Wenlock) to Middle Devonian (Givetian).

Discussion: Two tribes are recognized.

Tribe **CYRTINOPSINI** Wedekind, 1926

[Nom. transl. hic ex Cyrtinopsinae Wedekind, 1926, p. 198].

Diagnosis: Ventral median septum and spondylium. No tabellae. Silurian (Wenlock) to Middle Devonian (Givetian).

Genera: *Cyrtinopsis* Scupin, *Jehlanaria* Havlíček*, Plicocyrtina* Havlíček.

Discussion: *Cyrtinopsis* Scupin and *Plicocyrtina* Havlíček have a ventral spondylium supported by median septum, and crural plates are large in *Plicocyrtina,* as recorded by Lenz (1972, pl. 1, fig. 16, 17). Figures suggest low deltidial plates along the delthyrium. *Jehlanaria* Havlíček in Havlíček & Vanek, 1998, of Lower Devonian age, lacks lateral plicae other than one obscure pair, and does not show frilled laminae, but does have a ventral spondylium. Narrow deltidial plates fuse under the umbo.

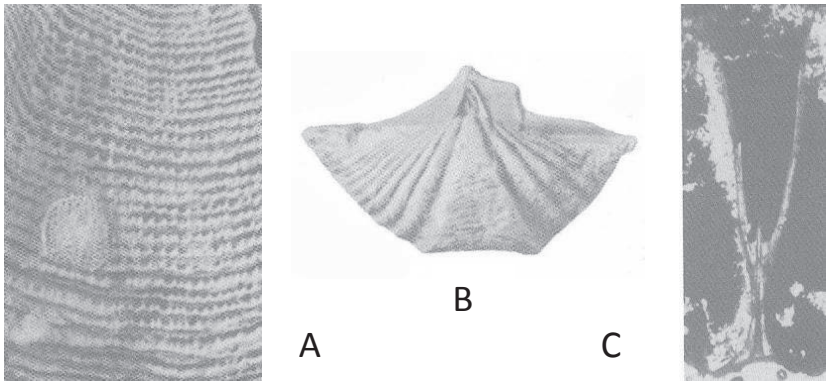


Fig. 332. *Cyrtinopsis undosus* (Schnur). A, frilly micro-ornament, x3. B, dorsal view x1. C, section of ventral valve, x5. From Eifelian of Germany. (Boucot 1957a).

Tribe **KOZLOWSKIELLININI** Boucot, 1957b

[Nom. transl. hic ex Kozlowskiellinae Boucot, 1957b, p. 318, named for *Kozlowskiella* Boucot, 1957b, non Pribyl 1953, and changed to *Kozlowskiellina* Boucot, 1958, p. 1031].

Diagnosis: Adminicula, ventral septum, without fully formed spondylium. Commarginal laminae, strong plicae few and open as in Cyrtinopsini. Silurian (Wenlock) to Middle Devonian (Givetian).

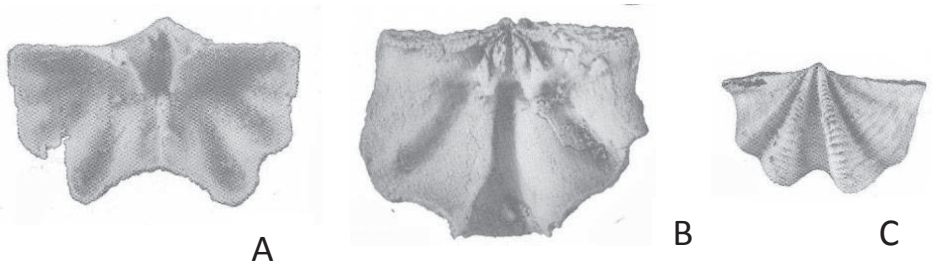


Fig. 333. *Megakozlowskiella magnapleura* Johnson. A, ventral interior, x2. B, dorsal interior, x2. C, dorsal exterior, x1. From Pragian of Nevada, United States. (Johnson 1970).

Genera: *Kozlowskiellina* Boucot*, Megakozlowskiella* Boucot.

Discussion: Because they lack a fully formed spondylium, resting on a septum, *Kozlowskiellina* Boucot and *Megakozlowskiella* Boucot are separated from Cyrtiniopsini. They differ from Araspiniferinae in having a ventral median septum, but are close to that group in possessing strong commarginal lamellae and displaying a quasispondylium. There is a short narrow thick hinge plate in the dorsal valve, supported by a posterior pillar, and no tabellae. Much of the delthyrium is covered by fused deltidial plates, with a foramen below the beak. *Megakozlowskiella* Boucot, 1957b as figured by Johnson & Hou (2006b, Fig. 1225.2c) has a platform in the dorsal valve, containing the sockets, and bilobed cardinal process, with crural bases jutting forward beyond the socket plates. Micro-ornament in both genera involves radial capillae and commarginal fila, rather than fimbriae.

Subfamily **ARASPIRIFERINAE** Johnson, 1994

[Araspiriferinae Johnson in Carter et al., 1994, p. 352].

Diagnosis: Without ventral median septum. Short tabellae. Silurian (Wenlock – Ludlow).

Genera: *Araspirifer* Havlíček*, Boucotiellina* García-Alcalde*, Boucotinskia* Brunton & Cocks.

Fig. 334. A, B, *Araspirifer araneus* Havlíček, ventral and dorsal views, x2, from upper Wenlock of Bohemia. (Havlíček 1959). C, *Boucotinskia sulcata* (von Hisinger), posterior view, dorsal valve below, x2 from Ludlow of Gotland. (Boucot 1957b).

Discussion: Although the interior is distinctive, given the absence of a ventral median septum, the genera externally come close to Cyrtinopsini and Kozlowskiellinini, especially to the latter in the presence of strong commarginal lamellae. Tabellae are absent from the latter tribe, nor known in Cyrtiopsini. *Araspirifer* lacks a ctenophoridium, whereas one is present in *Boucotinskia* (Johnson & Hou 2006, p. 1843). Short tabellae are present in *Boucotinskia* (Boucot 1957b). *Boucotiellina* is externally close to *Boucotinskia*, but has a septalium and rudimentary ctenophoridium.

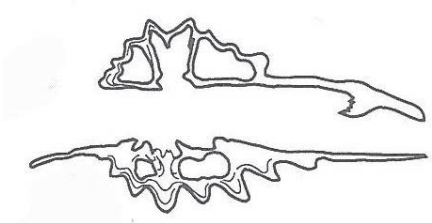


Fig. 335. Transverse section of *Boucotiellina esquerra* (Verneuil), x4, from upper Emsian of northern Spain, with dorsal valve below. (García-Alcalde 2005).

Subfamily **HOWITTIINAE** new subfamily

Name genus: *Howittia* Talent, 1956, p. 34 from Lower Devonian of New South Wales, Australia, here designated.

Diagnosis: Plicate with well formed median septum, no spondylium. Spines closely arrayed in commarginal rows. Lower Devonian (Pragian-Emsian).

Genus: *Howittia* Talent (syn. *Glyptospirifer* Hou & Xian).

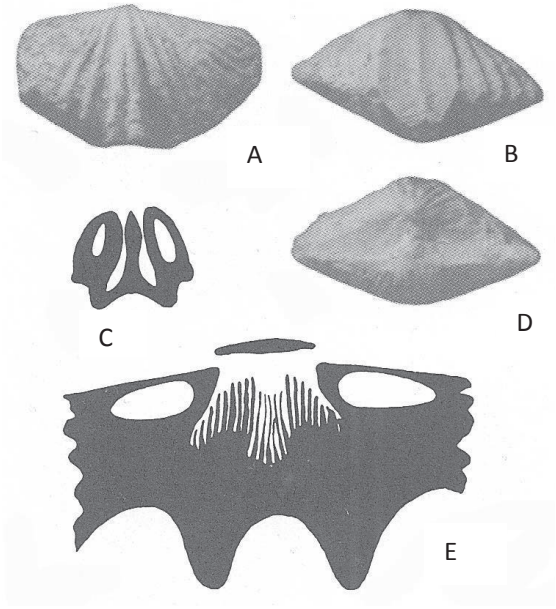


Fig. 336. *Howittia howitti* (Chapman). A, B, D, dorsal, anterior ventral and posterior views with ventral valve on top, x2. C, transverse section of ventral valve, x3, showing adminicula and high median ventral septum. E, section across dorsal valve, x10, showing possible tabellae. From Lower Devonian of New South Wales. (Talent 1956).

Discussion: *Howittia* Talent was placed in Echinospiriferinae Liashenko, Superfamily Adolfioidea, by Johnson (2006a), but is not close to that subfamily, being distinguished by a low to moderately high long ventral median septum, with spines in distinct commarginal rows, and high deltidial plates. Johnson (2006a, p. 1711) stated that micro-ornament consisted of commarginal fila crossed by radial capillae, and that no crural plates (ie. tabellae) were present, but spines and short tabellae are in fact developed (Chatterton 1973, p. 112). There are deltidial plates, and micro-ornament is capillate, with growth laminae, and small spines which appear to be aligned along commarginal rows, although there are no fimbriae. A low ventral septum and two parallel tabellae are developed, separated by a median ridge and well developed ctenophoridium. Chatterton (1973) like previous authors referred the genus to Delthyridina.

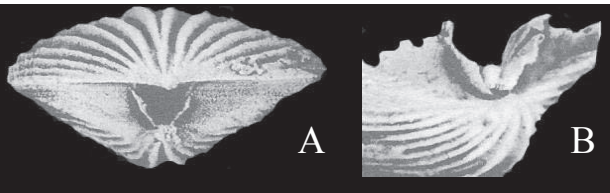


Fig. 337. *Howittia howitti* (Chapman), showing deltidial plates bordering the delthyrium. From Lower Devonian of New South Wales. (Chatterton 1973).

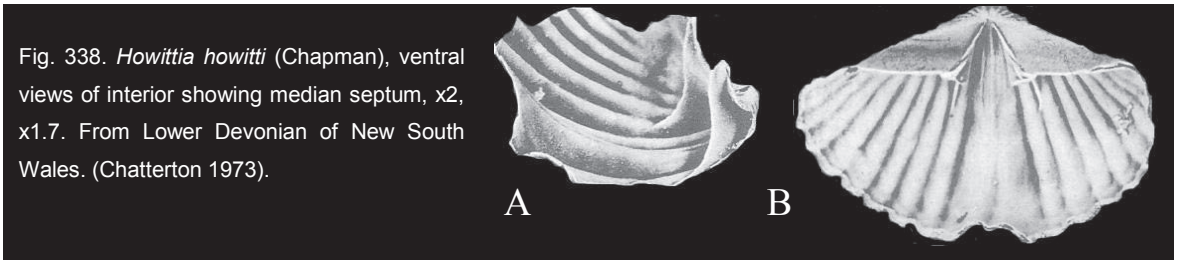


Fig. 338. *Howittia howitti* (Chapman), ventral views of interior showing median septum, x2, x1.7. From Lower Devonian of New South Wales. (Chatterton 1973).

Subfamily **TYLOTHYRINAE** Carter, 1972b

[Nom. correct. pro Tylothyridinae Carter, 1972b, p. 730].

Diagnosis: Moderately numerous plicae, imbricate growth laminae, no radial micro-ornament, adminicula and ventral median septum present, but no tabellae. Middle Devonian (upper Givetian) to Lower Carboniferous (Visean).

Genera: *Tylothyris* North (syn. *Welleria* Mailleux nom. nud.), *Texathyris* Carter.

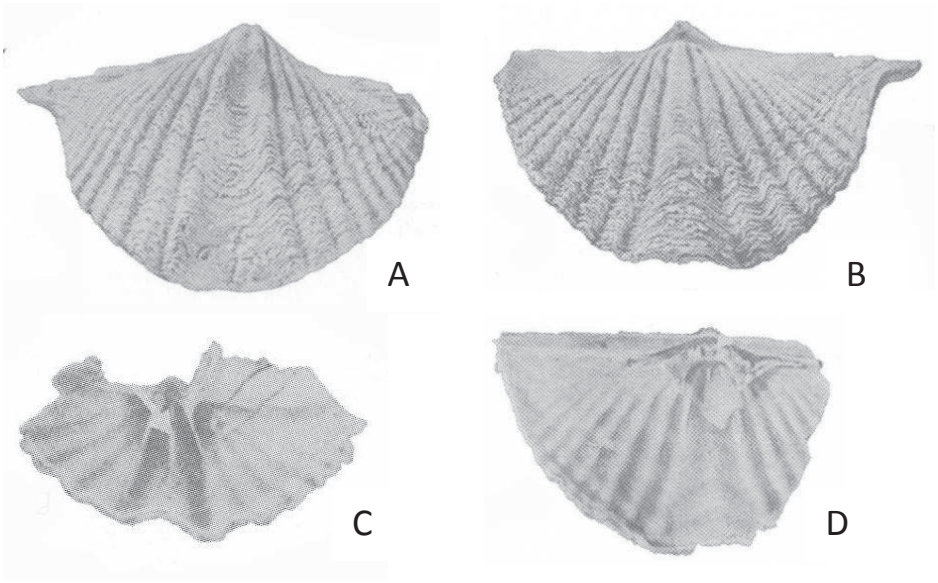


Fig. 339. *Tylothyris laminosa* (M'Coy). A, ventral and B, dorsal exterior views, x1.5. C, ventral interior x3. D, dorsal interior, x1.5. From Visean of Ireland. (Brunton 1984).

Discussion: This subfamily with its ventral median septum approaches Cyrtinopsinae, but lacks capillae, although commarginal growth lamellae are well developed as in Araspiriferinae. It was classed as Mucrospiriferidae in the *Revised Brachiopod Treatise*, but the presence of septum and strong commarginal lamellae are consistent with a cyrtinopsid relationship. Johnson & Hou (2006b, p. 1845) called the plicae of *Tylothyris* costae, whereas for other genera they termed costae plicae. In addition they described dental plates, but ignored or misconstrued the adminicula, which are clearly developed. Serial sections provided by Carter (1972b, text-fig. 1) for *Tylothyris* show high adminicula and high ventral septum, and the socket plates rest high above the dorsal floor. *Tylothyris* has a deltidial cover plate which

leaves a gap nearer the hinge. Brunton (1984, p. 79, Fig. 114) described a wide cardinal process with comb-like structure with deep grooves, and Carter (1972b, p. 730) stated there was a striate cardinal process of four to six plates and no tabellae. *Texathyris* has no ctenophoridium.

Fig. 340. *Tylothyris laminosa* (M'Coy), posterior view showing delthyrial cover plate, x1. From Visean of Ireland. (Brunton 1984).

Family **XENOMARTINIIDAE** Havlíček, 1971

[Xenomartiniidae Havlíček, 1971, p. 24].

Diagnosis: Ventral median septum. May have spondylium. Micro-ornament varied, may be without prominent commarginal laminae. Silurian (upper Wenlock) to Middle Devonian (Givetian).

Discussion: Members of this family display a well developed ventral median septum, the oldest subfamily having high dental plates and adminicula (Quadrithyrinae), succeeded narrowly in time by Bojothyrinae with spondylium, and then Xenomartininae in early Devonian, which has lost the spondylium. There are no delthyrial plates or connector plate. The ornament in a number of the genera allocated to the family in the *Revised Brachiopod Treatise* is cancellate, but a few genera, such as *Spondylothyris, Quadrithyris* and *Uralospirifer,* have marginal spines or fimbriate ornament. Of course, there may be some reservations about mixing genera with cancellate ornament, like that of so many Spiriferida, with genera that have single-barrelled spines arrayed in well developed commarginal rows, typical of many Delthyridina. The justification centres on the presence of the ventral septum in *Quadrithyris* of Quadrithyrinae, with its commarginal spines, that is shared with *Xenomartinia* in Xenomartiniinae, with commarginal lamellae crossed by radial capillae, and *Bojothyris* of Bojothyrinae which has a spondylium, recalling that of Cyrtinopsini, and commarginal growth lines. Whether the sharing of a median septum really justifies merging such different styles of ornament may promote a measure of uncertainty, and there are a few delthyridin subgroups which have ornament, adminicula and dental plates like those of *Quadrithyris*, but lack a septum. On the other hand, Altajellini as recognized herein has a median ventral septum with a spondylium, and its micro-ornament consists of commarginal growth lines, and *Quadrithyrina* has commarginal growth lines, capillae and spines. Two further genera, somewhat like *Bojothyris*, are *Spondylothyris* with marginal spines, and *Uralospirifer* with fimbriate ornament. So the interpretation by Gourvennec in Carter & Gourvennec (2006c) reconciles the development of variable micro-ornament, in genera that also vary in degree of plication, but are united by internal similarities. The transverse smooth shells are not far removed from the gently plicate genus *Ivanothyris* of Delthyridae. And in turn, genera show

various similarities to members of Cyrtinopsidae, internally and externally. There are other ways of classifying the genera, and even allowing more variability in internal plates, but the scheme seems reasonable, and any new arrangement would seem to be retrograde, unless substantiated by compelling evidence. The presence of a ventral median septum strongly suggests that the family should be linked with Delthyridae, to imply that smooth and plicate shells were closely related, as suggested by the presence of plicate Xenomartiniidae such as *Uralospirifer* and *Altajella*, in a family otherwise dominated by smooth genera. Adding to the complexity is the absence of a ctenophoridium from *Xenomartinia*, *Quadrithyris*, and *Quadrithyrina* and presence of a ctenophoridium in *Altajella* and *Spondylothyris*. In shape *Jehlanaria* approaches *Xenomartinia*, yet has a spondylium as in Cyrtinopsinae (see p. 260) and Bojothyrinae.

Subfamily **XENOMARTINIINAE** Havlíček, 1971

[Nom. transl. Gourvennec in Carter et al. 1994, p. 357 ex Xenomartiniidae Havlíček, 1971, p. 24].

Diagnosis: Non-plicate, with low dental plates and no adminicula. Posterior dorsal valve bears socket plates and trilobed cardinal process on thickened posterior wall. Micro-ornament subcancellate with radial and commarginal fila. Lower Devonian (Pragian) to Middle Devonian (Eifelian).

Genus: *Xenomartinia* Havlíček (syn. *Sinothyris* Minato fide Gourvennec in Carter & Gourvennec (2006c, p. 1860). See pp. 323, 324.

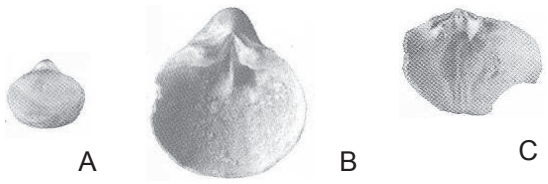


Fig. 341. *Xenomartinia monosepta* Havlíček. A, dorsal view of exterior, x2. B, ventral interior, x3. C, dorsal interior, x3. From Pragian of Czech Republic. (Havlíček 1959).

Discussion: The diagnosis has been rewritten on the basis of figures which partly elaborate the text in Carter & Gourvennec (2006c, pp. 1860, 1861, Fig. 1238.1a-f). *Xenomartinia* is the only known genus. It is ambocoeliiform, with subcancellate ornament and no spines, and although the ventral septum recalls features of Delthyrinae, the genus is not plicate, but does approach members of Bojothrinae. Although the genus is like Cyrtinopsidae in having a median ventral septum, the micro-ornament and shape differ considerably, and the cardinal process is trilobed.

Subfamily **BOJOTHYRINAE** Havlíček, 1990

[Nom. correct. pro Bojothyridinae, nom. transl. Gourvennec in Carter et al., 1994, p. 357 ex Bojothyrididae Havlíček in Havlíček & Kukal, 1990, p. 186].

Diagnosis: Dental plates converge to median septum, to form spondylium or spondylium-like

structure, no connector plate or deltidial development. Silurian (upper Ludlow) to Middle Devonian (Eifelian).

Discussion: There is variation in the micro-ornament, from fimbriate to cancellate or commarginal, with or without minute spines in this subfamily, according to the *Revised Brachiopod Treatise*. According to the present classification, fimbriate ornament is limited as a rule to Delthyroidea and Hysterolitoidea, whereas the *Revised Brachiopod Treatise* classed Bojothyrinae in Reticularioidea. The ventral median septum is double as if formed by fusion of the adminicula.

Tribe **BOJOTHYRINI** Havlíček, 1990

[Nom. correct. et transl. hic ex Bojothyrididae Havlíček in Havlíček & Kukal, 1990, p. 186].

Diagnosis: Shells smooth to gently sulcate. Lower Devonian (Pragian) to Middle Devonian (Eifelian).

Genera: *Bojothyris* Havlíček, *Quadrithyrina* Havlíček, *Spondylothyris* Su.

Fig. 342. *Bojothyris nikiforovae* Havlíček, ventral exterior and internal mould. (Gourvennec in Carter & Gourvennec 2006c). C, transverse section showing spondylium. Specimens x4 approximately. From Eifelian of Czech Republic. (Havlíček 1959). In shape the genus and tribe is reticularioid.

Fig. 343. *Quadrithyrina ivanovae* Havlíček, ventral and dorsal views, x2.5. C, transverse section, x2. From upper Emsian of the Czech Republic. (Havlíček 1959).

Discussion: Small crural plates appear to be developed in *Bojothyris* Havlíček, a shell that has a micro-ornament of fine commarginal growth lines. The spondylium is matched in other Delthyroidea by *Cyrtinopsis*, which is plicate and has frilly margins to the commarginal growth

laminations. *Quadrithyrina* Havlíček has radial and commarginal fila, and ventral median septum with dental plates extending towards, but not reaching it, thus showing some approach to *Xenomartinia.* The genus *Spondylothyris* Su, 1980 with few broad plicae has well formed spondylium and cruralium, and commarginal laminae with marginal spines, aligned in commarginal rows. A ctenophoridium is developed in *Spondylothyris* but not in *Quadrithyrina.*

Tribe **ALTAJELLINI** new tribe

Diagnosis: Strongly plicate. Spondylium and tabellae. Silurian (upper Ludlow) to ?Middle Devonian (?Eifelian).

Genera: *Altajella* Kulkov, *Uralospirifer* Havlíček.

Discussion: Unlike members of Bojothyrini, shells are plicate, and tabellae are developed. Micro-ornament consists of fine commarginal growth lines much as *Bojothyris*. *Uralospirifer* Havlíček is a strongly plicate genus that displays fimbriate ornament and lacks tabellae, and approaches aspects of the delthyroid genus *Cyrtinopsis* (see Carter & Gourvennec 2006c, p. 1840), which is also plicate and has a spondylium, but lacks tabellae. *Cyrtinopsis* differs from *Uralospirifer* in having more plicae, with frilled micro-ornament. *Altajella* has only fine commarginal growth lines, and has a ctenophoridium.

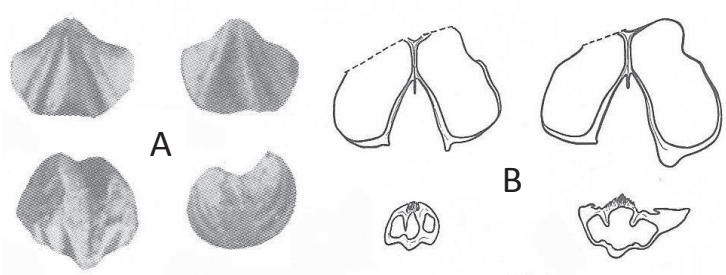


Fig. 344. *Altajella contorta* Kulkov. A, dorsal, ventral, anterior and lateral views, x1. (Kulkov 1963). B, transverse sections (dorsal valve below), x2. (Alekseeva et al. 1970). From Lochovian of Altai.

Subfamily **QUADRITHYRINAE** Gouvennec, 1994

[Nom. correct. hic pro Quadrithyridinae Gourvennec in Carter et al. 1994, p. 358].

Diagnosis: Divergent or subparallel dental and high adminicular plates and median ventral septum, ctenophoridium or multilobed cardinal process present or absent, no tabellae. Micro-ornament of growth lamellae, with or without spinules. Silurian (upper Wenlock) to Middle Devonian (Givetian).

Genera: *Quadrithyris* Havlíček, *Mandageryia* new genus.

Discussion: The diagnosis for this subfamily is elaborated from Gourvennec in Carter & Gourvennec (2006c, p. 1863) on the basis of figures provided by Carter & Gouvennec (2006c, Fig. 1238.2e), which show that adminicula are present, though unmentioned by Gourvennec, and what was reported as a ctenophoridium. Micro-ornament in *Quadrithyris* consists of growth laminae and marginal spine bases aligned along each margin. Johnson (1966a) described species of *Quadrathyris* of similar age from Nevada.

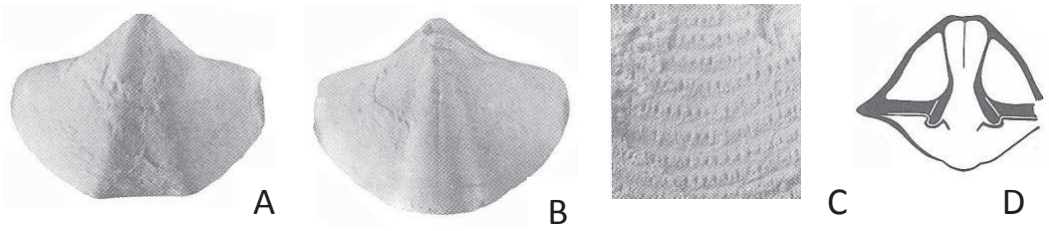


Fig. 345. *Quadrithyris robustus* (Barrande), ventral and dorsal views, x1.5. C, transverse section, x2. From upper Wenlock to Givetian of Czech Republic. (Havlíček 1959).

The general shape of the shell and the presence of a median ventral septum and spines suggest a possible forebear for various Reticularioidea, including Elitidae [Elythidae] Fredericks (see p. 326). These are mostly non-plicate smooth shells with spines and with a long but low median ridge in the ventral valve.

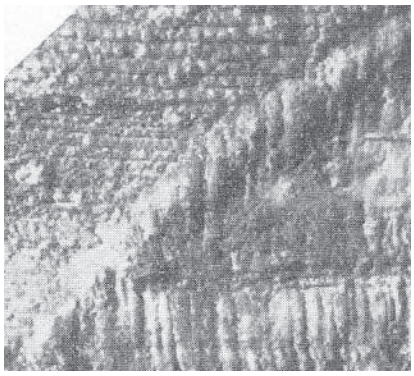


Fig. 346. Micro-ornament of shell ascribed to *Quadrithyris altschedaliensis* (Korov) x10, by Ivanova (1971, pl. 5, fig. 8), from Devonian of Kuzbass, Russia.

A lower Devonian taxon from New South Wales described as *Quadrithyris robusta molongensis* Savage (1969) lacks spines, and so is described as a new genus.

Genus ***Mandageryia*** new genus

Derivation: Named from Mandagery Park Formation, New South Wales, Australia, source of the type material.

Diagnosis: Transverse with prominent sulcus and fold, micro-ornament of growth increments, no spines. Ventral interarea with median septum, dental plates and high adminicula. Dorsal interior with prominent multilobed cardinal process and crural plates, posterior shell traversed by low dorsal median septum.

Type species: *Quadrathyris robusta molongensis* Savage, 1969, p. 473 from Mandagery Park Formation (Siegenian), New South Wales, here designated.

Discussion: *Quadrathyris* Havlíček, 1957, 1959 is very close to the present form, but displays fine marginal spines, and cardinal process. The present form has a low but distinct dorsal septum, and the delthyrium is open, and defined by low bordering rims. A multilobed well rounded cardinal process, equivalent to a rudimentary ctenophoridium, is present.

Fig. 347. *Mandageryia molongensis* (Savage). A, ventral valve, x3. B, dorsal interior, x4. C, ventral interior, x4. From Siegenian of New South Wales, Australia. (Savage 1969).

Superfamily **HYSTEROLITOIDEA** Termier & Termier, 1949

[Nom. transl. hic ex Hysterolitinae Termier & Termier, 1949, p. 95].

Diagnosis: Small to large, fold and sulcus smooth or costate, flanks commonly plicate, micro-ornament fimbriate or in commarginal rows of fine spines, varying to cancellate or capillate. Adminicula, no ventral medium septum, tabellae variably present. Lower Devonian (upper Lochovian) to Middle Devonian (lower Givetian).

Discussion: Members of Hysterolitoidea lack a vental medium septum, and are diverse in size, shape and micro-ornament. They encompass most of the taxa assigned to Delthyridina and typically are moderately large and plicate, and often costate, with varied micro-ornament and with adminicula and often tabellae.

Family **HYSTEROLITIDAE** Termier & Termier, 1949

[Nom. transl. Johnson & Hou in Carter et al., 1994, p. 350 ex Hysterolitinae Termier & Termier, 1949, p. 95].

Diagnosis: Medium to large, fold and sulcus largely smooth or costate, flanks commonly plicate, micro-ornament may be fimbriate, tabellae variably present. No median septum. Lower Devonian (upper Lochkovian) to Middle Devonian (lower Givetian).

Discussion: The distinction between Hysterolitinae and Howellellinae was not made clear in the *Revised Brachiopod Treatise*, with emphasis on features such as size, nature of sulcus and fold, fimbriate micro-ornament and variably present tabellae not matched by the morphological attributes of the various genera assigned to the two subfamilies. It is far from clear why Howellellinae should have been considered to be closer to Delthyridae than to Hysterolitinae. Given that the constituent genera lack a median septum, unlike Delthyrinae, it is more objective to associate Howellellinae Johnson & Hou with Family Hysterolitidae, and distinguish both from Delthyridae. In the following summary, considerable weight is placed on the research by Schemm-Gregory (2008b, 2011a) in tracing alliances. But unlike the partial classifications proferred by Schemm-Gregory (2008b), small associations of genera, and even solitary genera, are not allocated to groups of full family rank. The very chart of generic affiliations summarized by Schemm-Gregory (2011a) shows that a large number of genera stemmed from one genus *Howellella*, which implies that all should be associated in one family or superfamily group. Source is regarded as all-important in classification, and provides a vital clue to the family-group standing of various generic associations. (See Waterhouse 2013).

Schemm-Gregory (2011a) treated Hysterolitidae as if it were a branch of Howellellidae: this cannot be accepted, for Hysterolitidae has long priority. Nor am I entirely convinced that paleogeographic entities were likely to have been so dominant in any purported classification. But the following text attempts to reconcile aspects of the classification in Johnson & Hou (2006b) with the overview by Schemm-Gregory (2011a). She provided a particularly excellent overview of the hysterolitid - howellellid branches, and her diagrams are presented herein. She declined to offer an analysis of family relationships, but set aside the classification in the *Revised Brachiopod Treatise*, and considered that whereas

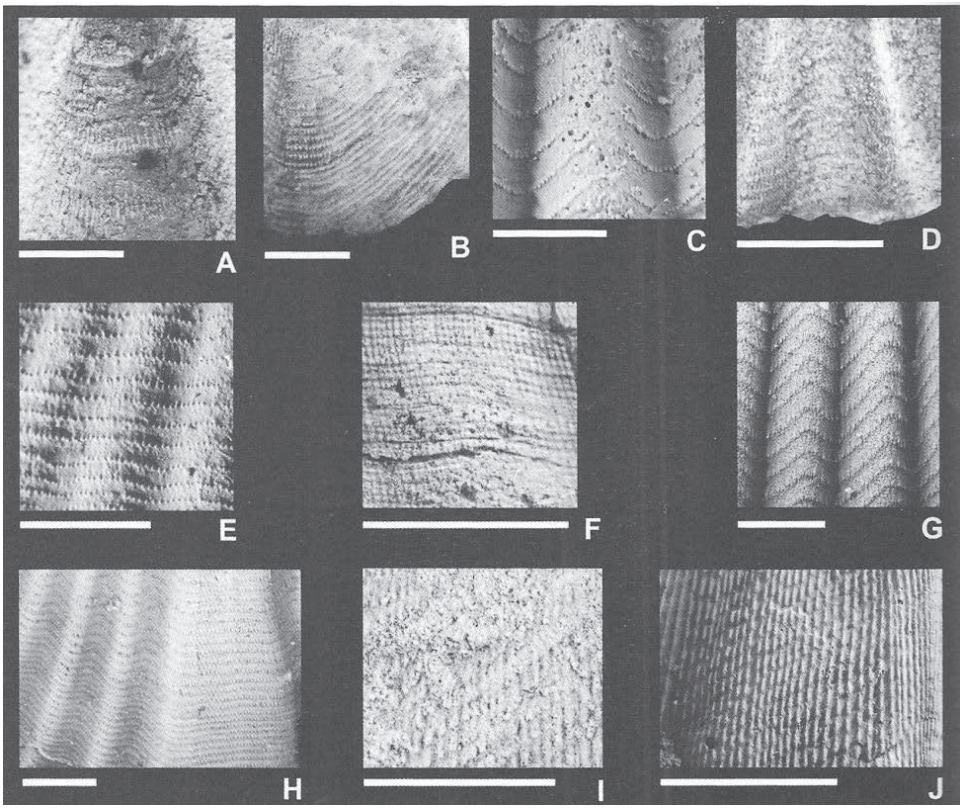


Fig. 348. Micro-ornament in shells from Europe and North America. A, *Hysterohowellella cortazari* (Carls). B, *Iberohowellella hollmanni* (Carls et al.). C, *Arduspirifer arduennensis arduensis* (Schnur). D, Gen. nov. *transversa* (Williams & Breger). E, *Acrospirifer primaevus* (Steininger). F, *Euryspirifer paradoxus* (Schlotheim). G, *Paraspirifer sandbergeri* Solle. H, gen. nov. *engelmanni* (Meek & Worthen). I, *Leonispirifer leonensis* Schemm-Gregory. J, *Filispirifer merzakhsaiensis* Jansen. A-H, fimbriate; I, J, capillate. F, cancellate. Scale bar 2mm long. (Schemm-Gregory 2011a).

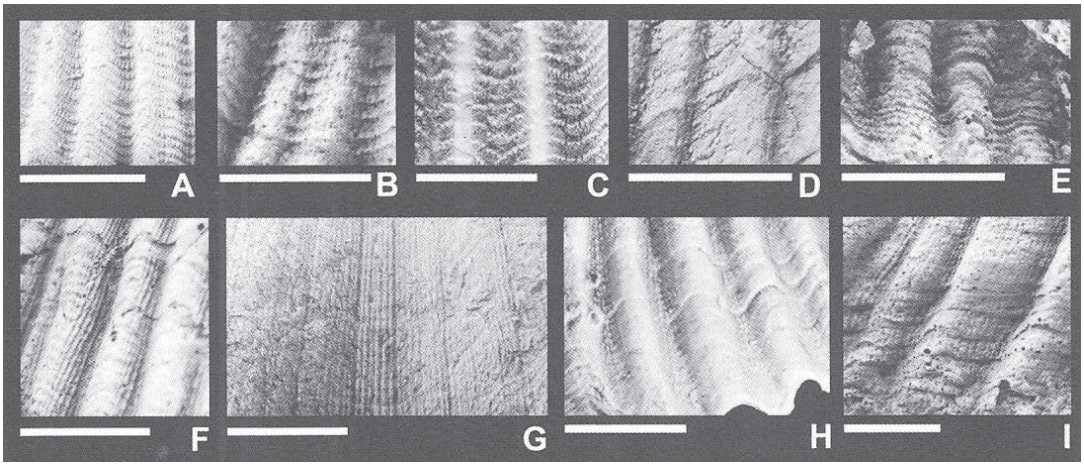


Fig. 349. Micro-ornament. A, *Fimbrispirifer divaricatus* Hall. B, *Struveina daleidensis* (Steininger). C, *Vandercammenina trigeri* (Verneuil). D, *Turcispirifer turciae* Schemm-Gregory. E, *Oventensispirifer ovetensium* (Carls). F, *Multiplicatispirifer foumzguidensis* Schemm-Gregory. G, *Costispirifer arenosus* (Conrad). H, *Elymospirifer kwangsiensis* (Hou). I, *Multispirifer solitarius* (Krantz). Scale bar 2mm, specimens are latex casts. A–E, fimbriate; F, G, capillate without microspines. H, I, capillate with micro-spines. (Schemm-Gregory 2011a).

the branches shown in Fig. 351, p. 274, are true descendents of Howellellinae, other groups classed by the *Revised Brachiopod Treatise* as Delthyroidea evolved from an eospiriferinid, a view shared in personal communications to her by Art Boucot and Zhan Renbin in 2009. In this study, different possibilities are suggested, based on further details of the genera involved. It is also to be noted that not all genera itemized as Hysterolitidae or Howellellinae in the *Revised Brachiopod Treatise* were charted by Schemm-Gregory (2011a), and furthermore, it appears that Russian and Australian genera had been incompletely surveyed, together with an apparent hiatus for South America and southeast Asia.

Subfamily **HYSTEROLITINAE** Termier & Termier, 1949

[Hysterolitinae Termier & Termier, 1949, p. 95].

Diagnosis: Fold and sulcus smooth, flanks plicate, micro-ornament of lamellae and fimbriae, ctenophoridium present, no clearly developed tabellae. Lower and Middle Devonian (Lochkovian to Eifelian).

Genera: *Hysterolites* von Schlotheim, *Arduspirifer* Mittmeyer, *Hysterohowellella* Carls, ?*Iberohowellella* Carls, Meyn & Vespermann, ?*Intermedites* Struve.

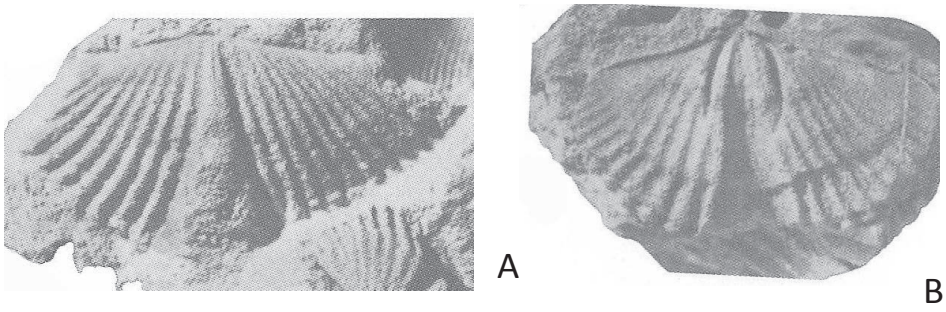


Fig. 350. *Hysterolites hystericus hystericus* von Schlotheim, from Pragian of Germany. A, mould of dorsal interior, x1.7. B, mould of ventral internal mould, x1.7. (Solle 1963).

Discussion: Schemm-Gregory (2011a) showed that *Hysterolites* was associated with a few other genera in a European and North African branch, accompanied by two further associations that are here separated as separate subfamilies. By contrast, Johnson & Hou (2006b, pp. 1830ff) recognized a number of genera in Hysterolitinae, involving *Hysterolites* von Schlotheim, *Antispirifer* Williams & Breger, *Arduspirifer* Mittmeyer, *Australospirifer* Caster, *Brachyspirifer* Wedekind and subgenus *Torosospirifer* Gourvennec, *Costellispirifer* Boucot (syn. *Concinnospirifer* Boucot), *Dixonella* Gourvennec, *Dyticospirifer* Johnson, *Gaspespirifer* Bizzarro & Lespêrance, *Otospirifer* Hou & Xian, *Paraspirifer* Wedekind, *Patriaspirifer Johnson, Rostrospirifer* Grabau (syn. *Neodelthyris* Hou), *Trigonospirifer* Wang, Rong & Chen, *Xerospirifer* Havlíček, and *Xinjiangospirifer* Hou & Zhang. These are dispersed in subfamilies and tribes, in close accord with the scheme outlined in Fig. 351.

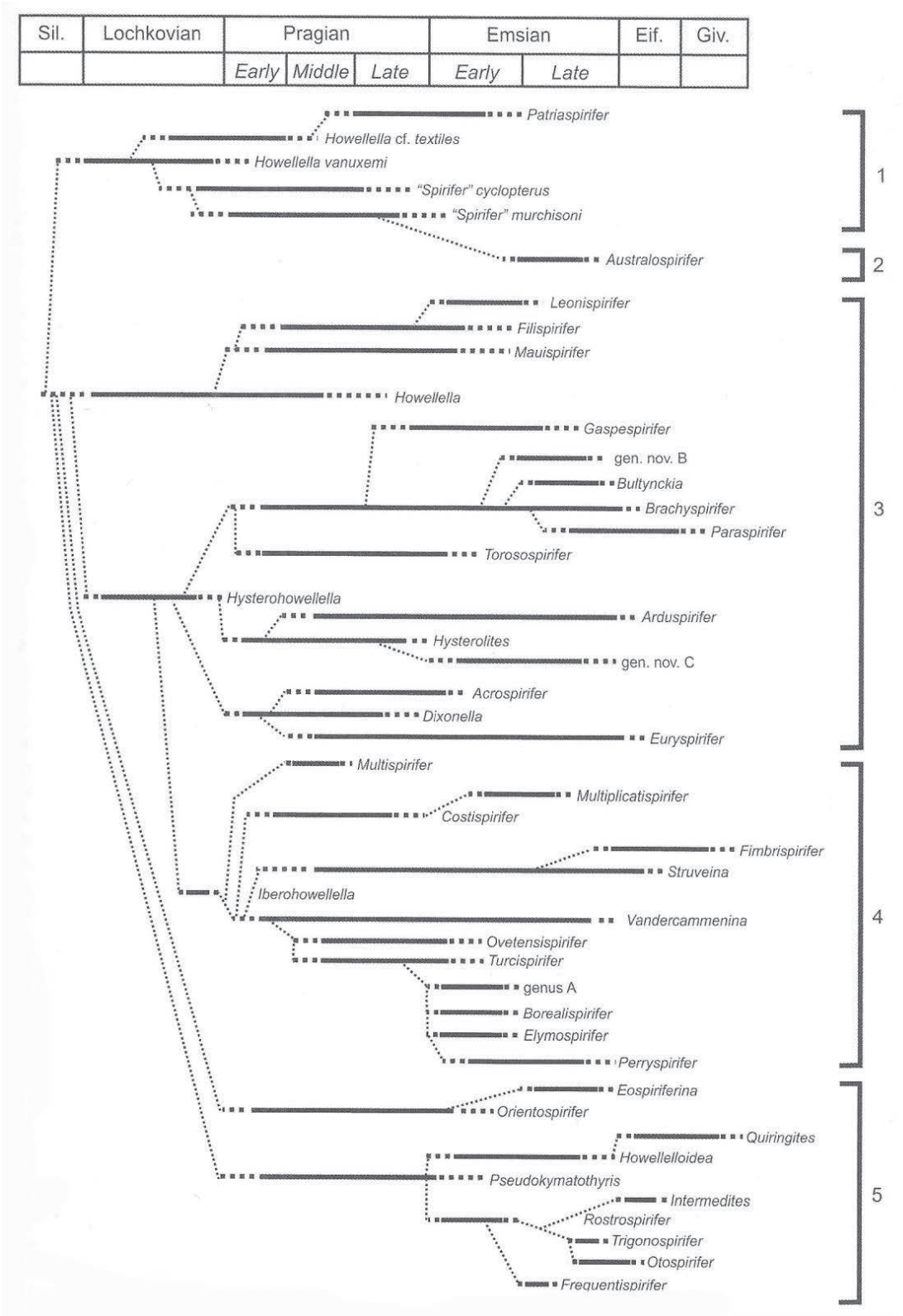


Fig. 351. A chart showing the phylogeny of "howellellid branches" of Delthyroidea, according to Schemm-Gregory (2011a), now treated as branches of Hysterolitoidea. 1 – North America. 2 – Malvinokaffric branch. 3 – European/North African branch. 4 – "delthyroid" multiplicate branch. 5 – Asian branch. Sil. – Silurian; Eif. – Eifelian; Giv. – Givetian.

Subfamily **PARASPIRIFERINAE** Pitrat, 1965

[Paraspiriferinae Pitrat, 1965, p. 684].

Diagnosis: Large, transverse and strongly plicate, with prominent sulcus and fold that are smooth. Micro-ornament of commarginal growth increments and single rows of micro-spines. Adminicula very short to moderately long, tabellae present or absent. Lower and Middle Devonian (Pragian to Emsian, possible Givetian).

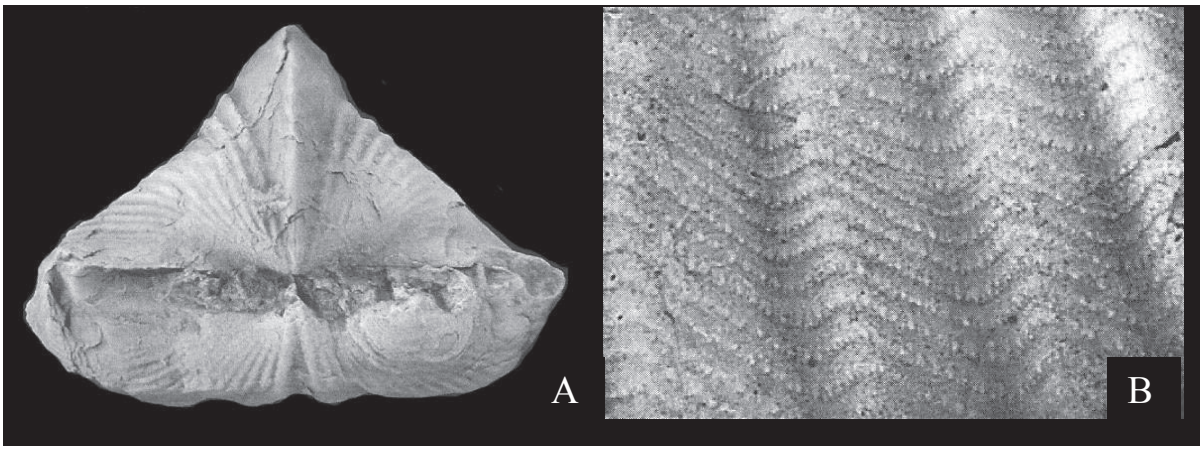


Fig. 352. A, *Paraspirifer* (*Paraspirifer*) *cultrijugatus* (Roemer), posterior view of holotype, x0.9. B, *P.* (*Paraspirifer*) *praecursor* Solle, micro-ornament (latex cast), x7. From Eifelian and Emsian of Germany. (Jansen 2016).

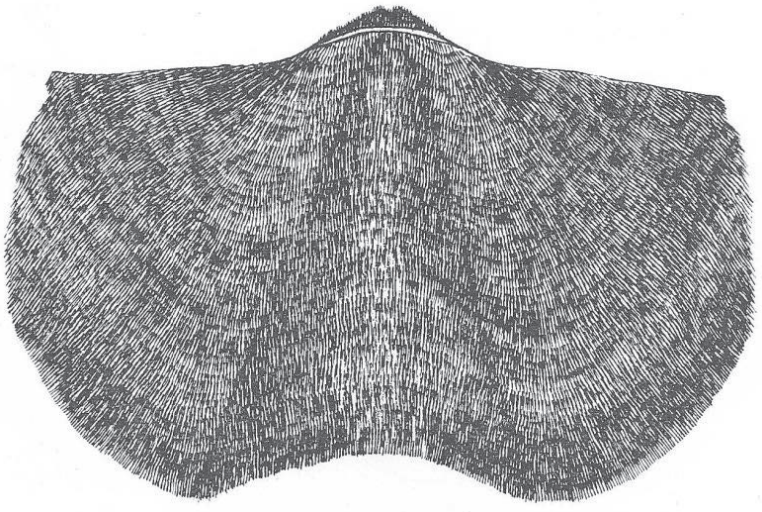


Fig. 353. *Paraspirifer cultrirugatus* (Roemer), type species, reconstruction of spinose ornament, dorsal view, x2. The narrow and numerous plicae have been left out of the reconstruction. From Devonian of Spain. (Vandercammen & Krans 1962).

Genera: *Paraspirifer* Wedekind, *P.* (*Laurentispirifer*) Jansen, *P.* (*Mosellospirifer*) Jansen, *Brachyspirifer* Wedekind, *Bultnyckia* García-Alcade, *Gaspespirifer* Bizzarro & Lespérance, ?*Subcuspidella* Meyer (syn. ?*Tenuicostella* Mittmeyer & Geib), *Torosospirifer* Gourvennec.

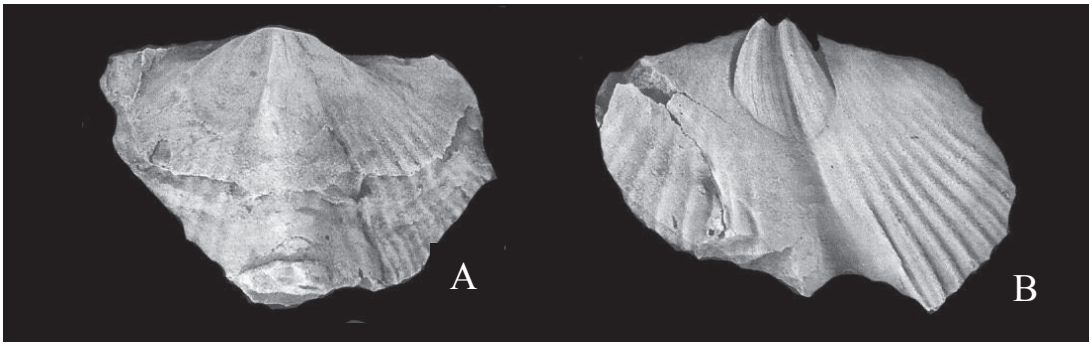


Fig. 354. *Paraspirifer* (*Mosellospirifer*) *sandbergeri* Solle. A, dorsal internal mould. B, ventral internal mould. From upper Emsian of Germany, x1. (Jansen 2016).

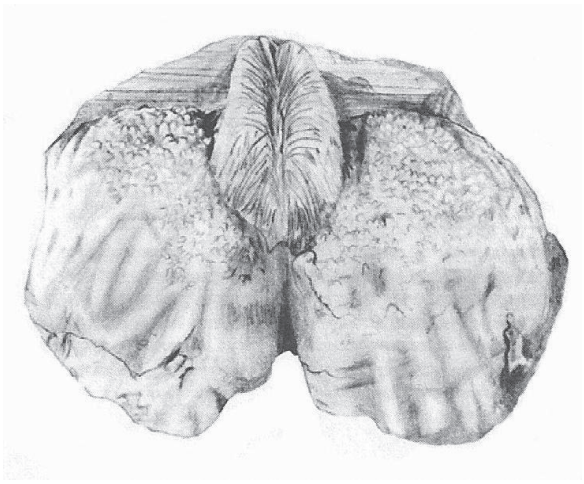


Fig. 355. *Paraspirifer* (*Mosellospirifer*) *sandbergi* Solle, ventral internal mould, x1.5. From Emsian of Germany. (Jansen 1916).

Discussion: The development is traced from genus to genus across western Europe and into North America, and probably North Africa and Turkey by Schemm-Gregory (2011a) and genera are comparatively close to *Hysterolites*.

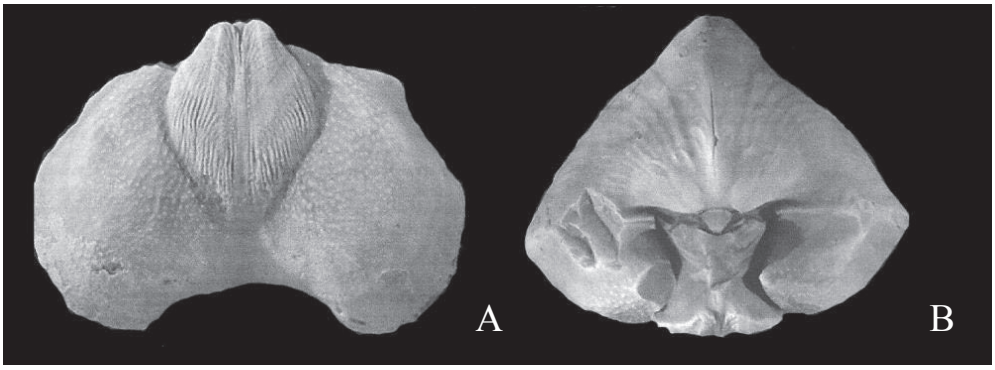


Fig. 356. *Paraspirifer* (*Laurentispirifer*) *conradi* Godefroid & Fagerstrom, x1. A, ventral internal mould. B, posterior view of internal mould, dorsal valve on top. From Eifelian of Indiana, United States. (Jansen 2016).

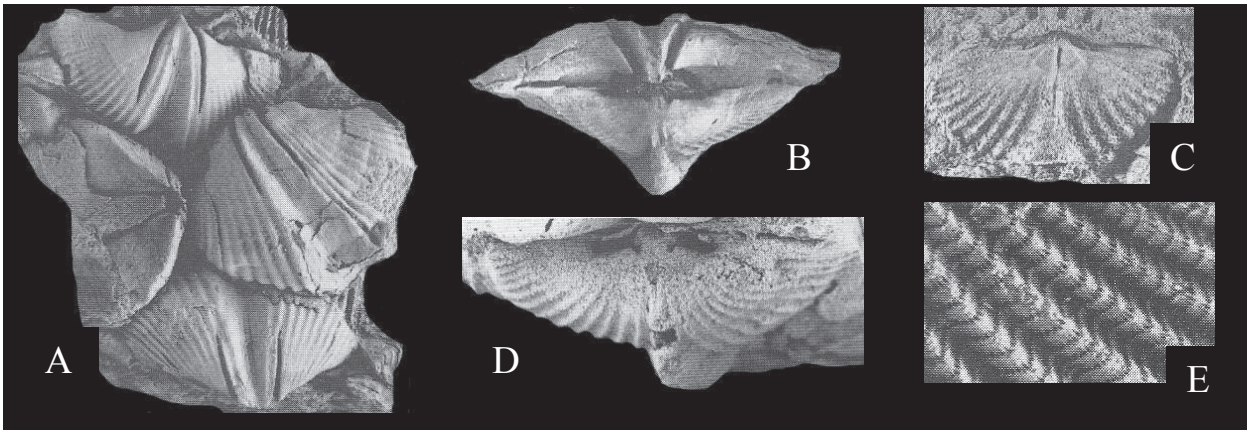


Fig. 357. *Brachyspirifer* species. A, *B. carinatus carinatus* (Scupin) ventral valves, x1. B, *B. mixtus* Godefroid, x1. C, dorsal valve of *B. crassicosta crassicosta* (Scupin). D, *B. minatus* Godefroid, x 1.5, showing short nicks at posterior wall. E, micro-ornament for *B. minatus*, x7. From Lower Devonian and Couvinnian of Dinant, Belgium. (Godefroid 1980).

Vandercammen (1962) analyzed the spines and their mode of emergence from commarginal laminae for *Paraspirifer.* Godefroid & Fagerstrom (1983) described and revised seven species of this genus from the middle Devonian of United States, and of the

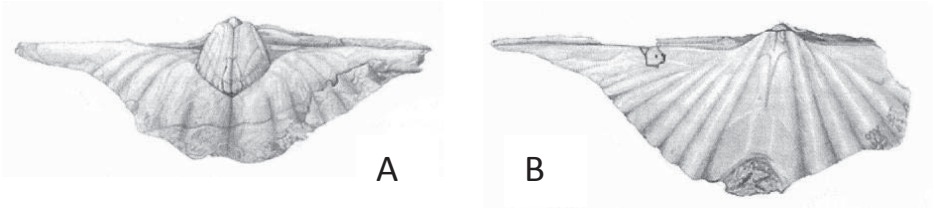


Fig. 358. *Arduspirifer arduennensis treverorum* Schemm-Gregory & Jansen. A. ventral valve holotype. B, dorsal internal mould. From Emsian of Germany, x1. (Jansen 1916).

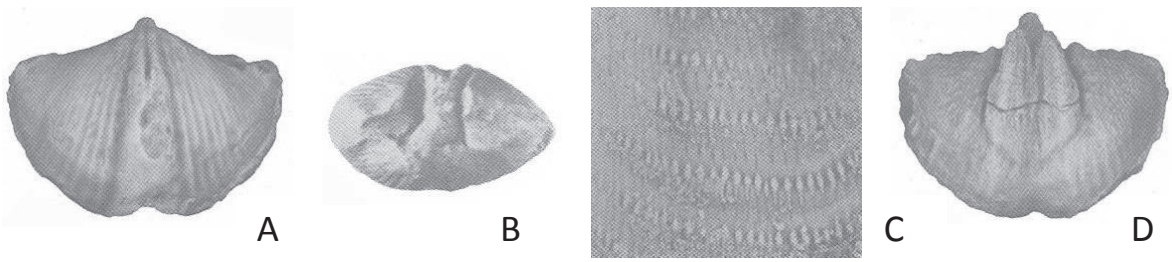


Fig. 359. A, C, D. *Torosospirifer rousseaui* (Rouault), A, dorsal and D, ventral views of neotype, x1.2. C, micro-ornament. From Pragian of France. (Gourvennec 1989). B, *Brachyspirifer (Brachyspirifer) carinatus* (Schnur), posterior view of holotype internal mould, dorsal valve below, x1. From Emsian of Germany. (Vandercammen 1967).

numerous figures provided, in 14 plates, only one internal mould (pl. 12, fig. 3a) indicates the presence of short subparallel posterior vertical plates in front of the cardinal process. The same is true of *Paraspirifer* described by Godefroid (1977) from Belgium, with a specimen of *P. sandbergeri sandbergeri* Solle showing no tabellae (Godefroid 1977, pl. 42, fig. 1b), whereas *P. praecursor* Solle suggests some thickening in the place of tabellae in the figure provided by Godefroid (1977, pl. 44, fig.1d).

A genus described as having short tabellae ("crural plates") and micro-ornament of nodose growth lines is *Subcuspidella* Mittmeyer of Eifelian age, The sulcus is smooth, and Johnson (2006b, p. 1725) pointed out that clarification was required for distinctions between it and *Tenuicostella*. *Subcuspidella* lacks sulcal costae, and falls close to Paraspiriferinae and Acrospiriferinae. The genus had been placed in Cyrtospiriferoidea by Johnson (2006a) but if it has tabellae, comes closer to Delthyridina, and is distinguished in part by its very high ventral interarea.

Subfamily **ACROSPIRIFERINAE** Termier & Termier, 1949

[Acrospiriferinae Termier & Termier, 1949, p. 96].

Diagnosis: Medium to large, capillate with commarginal fila, or fimbriate. No apical deltidium. Lower to Middle Devonian (Pragian – Emsian).

Genera: *Acrospirifer* Helmbrecht & Wedekind, *Dixonella* Gourvennec, *Euryspirifer* Wedekind (syn. *Rhenospirifer* Mittmeyer).

Discussion: This lineage also arose from *Hysterolites*, and was regarded as another of the clusters that typified the European-North African branches by Schemm-Gregory (2011a). The tribe is characterized by increased mucronations and size. Ribs developed in the sulcus, and secondary callus accumulated in the apical region. Micro-ornament varied, from single rows of micro-spines to a net-like (ie. cancellate) appearance in *Euryspirifer*.

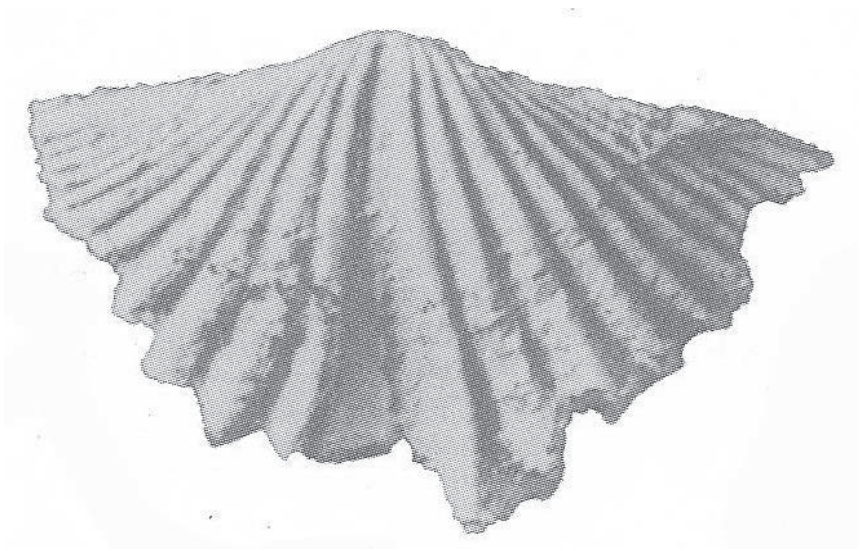


Fig. 360. A, *Acrospirifer primaeva* (Steininger), ventral view, x1.7, from the Lower Devonian (Pragian) of Germany. (Mailleux 1931).

Acrospirifer Helmbrecht & Wedekind, 1923 has well developed crural plates and, as Johnson & Hou (2006b, p. 1836) indicated, tabellae ("crural plates") are variably present. The ornament is figured as being capillate or cancellate, although Johnson (1970) had referred to *Acrospirifer* as displaying subdelthyroid ornament, with commarginally aligned elongate micro-ornament. Gourvennec pointed out that Jansen (2001a) had illustrated spinose shells very close to *Acrospirifer*, whereas the type species of the genus appears to have no spines (Jahke 1971).

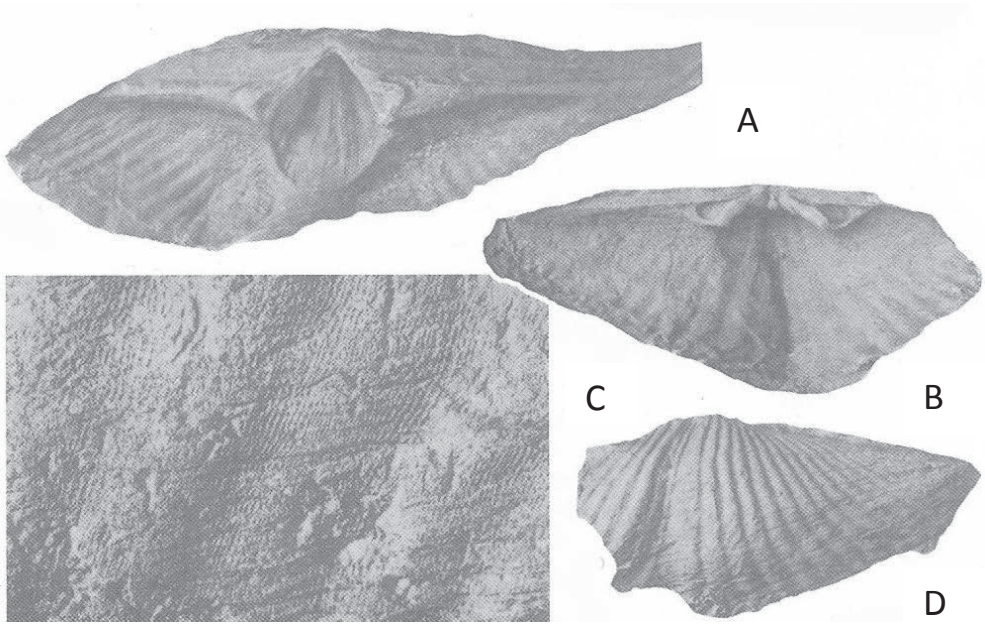


Fig. 361. *Euryspirifer paradoxus* (Schlotheim), A, B, casts of ventral and dorsal interior, x0.8. C, micro-ornament, x5, which is clearly not fimbriate. D, ventral exterior. Specimens x0.8, from Emsian of Belgium. (Vandercammen 1963).

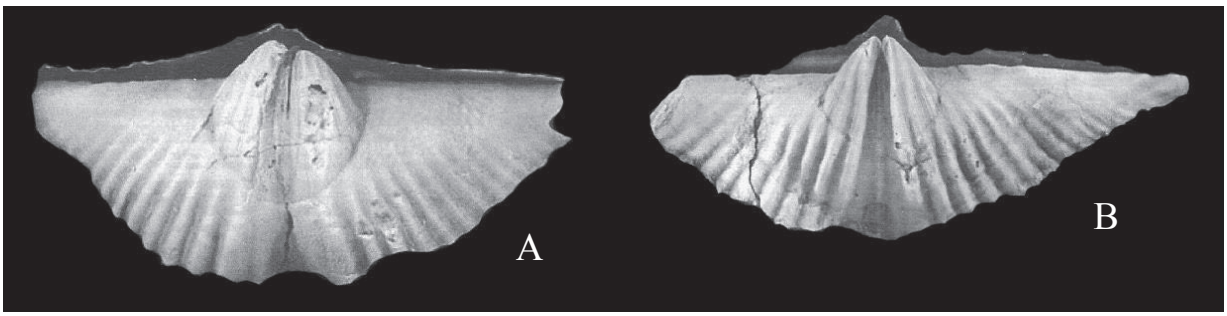


Fig. 362. A, *Euryspirifer* cf. *pelico* (Verneuil & Archiac), ventral internal mould, x0.9. From mid-Emsian of Morocco. B, *E. africanus* Jansen, x0.8. From Siegenian of Morocco. (Jansen et al. 2007).

Family **HOWELLELLIDAE** Johnson & Hou, 1994

[Nom. transl. hic ex Howellellinae Johnson & Hou in Carter et al., 1994, p. 350].

Diagnosis: Small, few to moderate number of plicae, may be costate, dental plates and

adminicula, tabellae often present. Silurian (Wenlock) to Middle Devonian (Givetian).

Discussion: This group made up a second branch of delthyridin genera found especially in Europe and North America. The group, as a subfamily, was associated with Delthyridae in the *Revised Brachiopod Treatise*, but lacks a ventral median septum, and is regarded as completely separate. Discrimination from Hysterolitidae is less readily ascertained, with no clear distinction offered by Johnson & Hou (2006b), but fimbriae and lamellae were stated to be weaker than in hysterolitids, and shells may be smaller and less strongly plicate. The chart of evolution complied by Schemm-Gregory (2011a) depicts an array of related genera that can be traced back to genus *Howellella*, and once allowed, and subject to the constraints imposed by rules of priority, only the ranking of family group units remains to be decided, apart from minutae of generic placements.

Subfamily **HOWELLELLINAE** Johnson & Hou, 1994

[Howellellinae Johnson & Hou in Carter et al., 1994, p. 350].

Diagnosis: Small, few non-costate plicae, dental plates and adminicula present. Silurian (Llandovery) to Middle Devonian (Givetian).

Discussion: Many genera were placed in Howellellinae by Johnson & Hou (2006b, p. 1826) involving *Howellella* Kozlowski (syn. nom. nov. pro *Crispella* Kozlowski not Gray), and subgenera *Hysterohowellella* Carls, and *Iberohowellella* Carls, Meyn & Vespermann, *Acanthospirifer* Menakova, *Aldanispirifer* Alekseeva (syn. *Holcospirifer* Bassett, Cocks & Holland), *Howelloidea* Su, *Orientospirifer* Hou & Xian, *Pseudokymatothyris* Chen, *Qiansispirifer* Yang, *Quiringites* Struve, *Rufispirifer* Havlíček and *Xenospirifer* Hou & Xian. These are now dispersed amongst several groups, with some assigned to Hysterolitidae.

Tribe **HOWELLELLINI** Johnson & Hou, 1994

[Nom. transl. hic ex Howellellinae Johnson & Hou in Carter et al., 1994, p. 350].

Diagnosis: Small, few simple plicae, dental plates and adminicula. Lower Silurian (Llandovery) to Lower Devonian (Pragian).

Genera: *Howellella* Kozlowski, ?*Acanthospirifer* Menakov, ?*Aldanispirifer* Alekseeva (syn. *Holcospirifer* Basset, Cocks & Holland), *Rufispirifer* Havlíček.

Discussion: An overview of *Howellella* is provided in Johnson (1970, p. 184). Species ascribed to *Howellella* by Talent (1956), such as *lirata* (Talent 1956, pl. 10, fig. 4-7, Fig. 2), and *latisulcata* (Talent, 1956, pl. 10, fig. 8, 9) display short tabellae. This is an important aspect of the morphology, but the interior needs to be further inspected. Perry (1984, Fig. 10) illustrated short tabellae and well formed median ventral ridge in shells ascribed to *Howellella* sp. from the Delorme Formation (Lochkovian) of Canada.

As shown in Schemm-Gregory's 2011a chart, *Howellella* occupied a comparatively isolated position with the European complex of howellellin genera, but here *Rufispirifer* of upper Wenlock – Ludlow age is added, as a second European genus of comparatively similar shape and size, with short adminicula and no tabellae, as well as two further genera of

comparable size and plication from Tajikistan and Sette Davan, with further reports from Ireland and the Canadian Arctic.

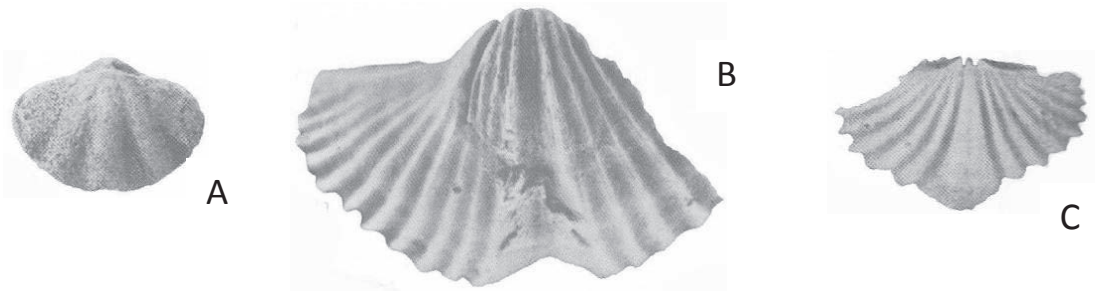


Fig. 363. Important type species for stem genera of family groups in Hysterolitoidea. A, *Howellella elegans* (Muir-Wood), dorsal valve, x4, from upper Llandovery beds of Gotland. (Bassett & Cocks 1974). B, *Iberohowellella hollmanni* Carls, Meyn & Vespermann, ventral internal mould, x1.5 from upper Lochkovian of Spain. (Carls, Meyn & Vespermann 1993). C, *Hysterohowellella coratzari* Carls, x2 from upper Lochkovian of Spain. (Carls 1985).

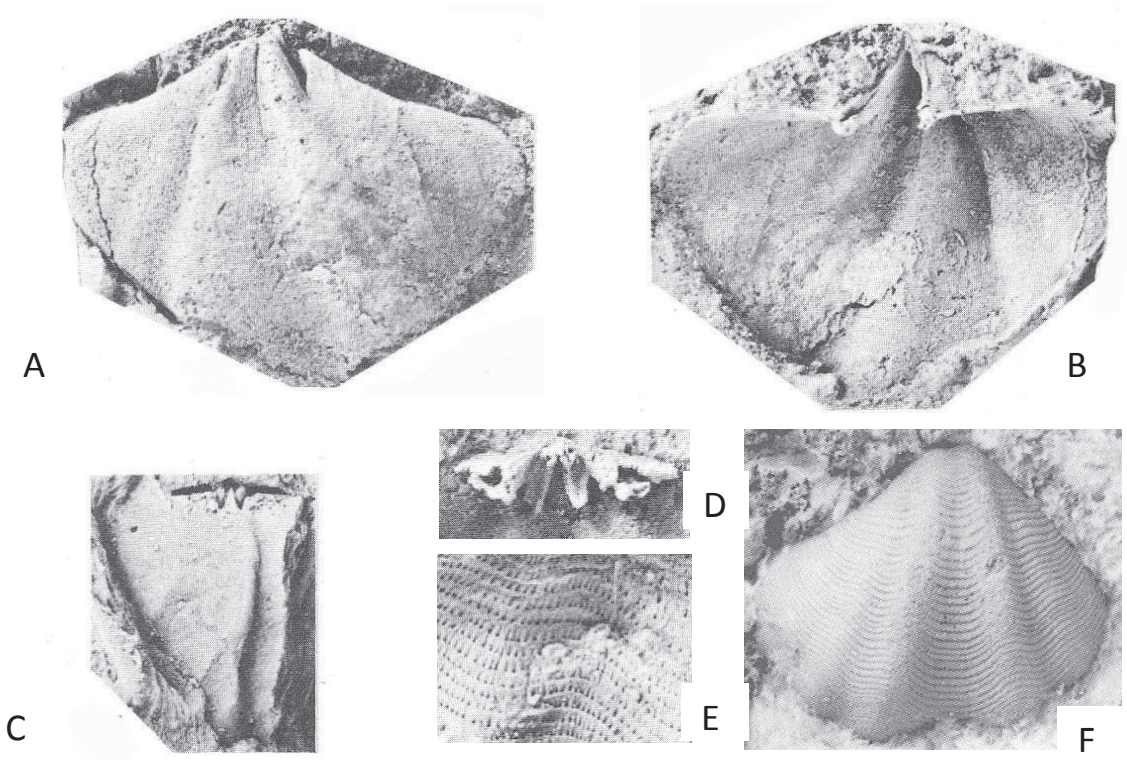


Fig. 364. A-E, *Howellella "nucula* (Barrande)" according to Strusz (1984) from Wenlock or Ludlow of Canberra, Australia. A, B, ventral internal mould and latex cast, showing well-formed myophragm, x6. C, D, dorsal internal mould, x6 and latex cast, x12, showing short tabellae, which seems to rule out *nucula*. E, micro-ornament, x16. F, *Rufispirifer nucula* (Barrande), ventral valve showing micro-ornament, x7.5, from Wenlock of Bohemia. (Havlíček 1959).

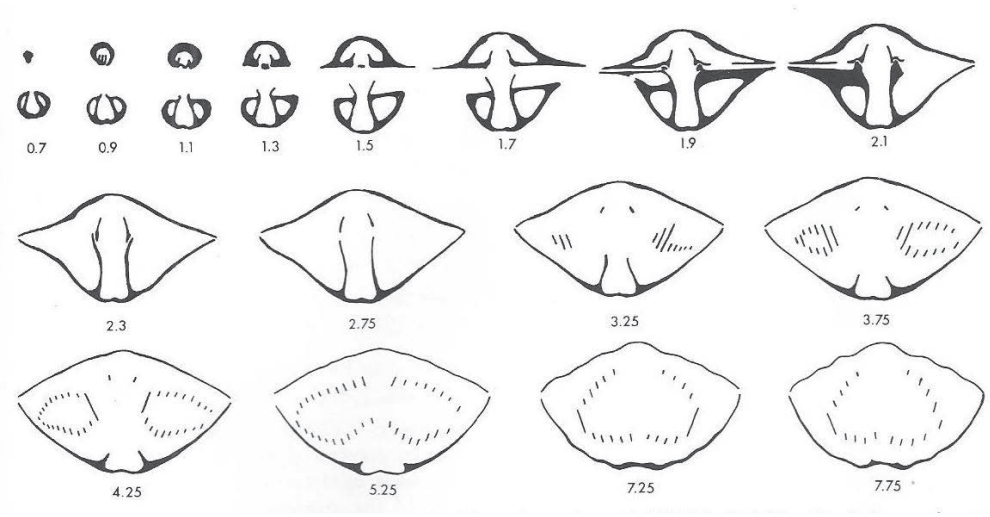


Fig. 365. Transverse sections of *Howellella amsdeni* Savage, from Early Devonian of Alaska, with distance from ventral beak indicated in mm. There are no tabellae in this species, implying an approach to *Rufispirifer*. (Savage 1981).

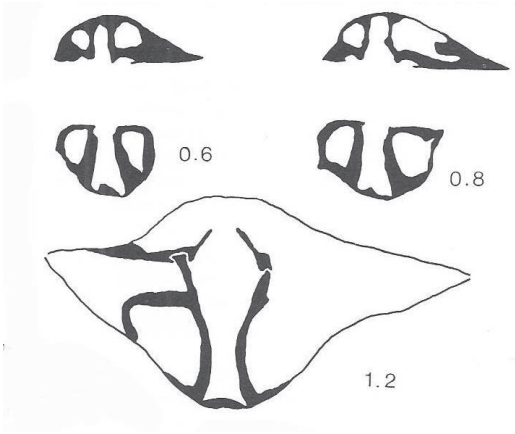


Fig. 366. Transverse section of *Howellella* sp. from the Lochkovian of McKenzie District, northwest Canada, with figures indicating distance in mm from ventral beak. (Perry 1984).

Tribe **FILISPIRIFERINI** Schemm-Gregory, 2008c

[Nom. transl. hic pro Filispiriferidae Schemm-Gregory, 2008c, p. 54].

Diagnosis: Transverse with obtuse cardinal extremities, ornament cancellate with or without pustules, may be semifimbriate. Adminicula present, but probably no tabellae. Lower Devonian (Mid-Pragian, lower Emsian).

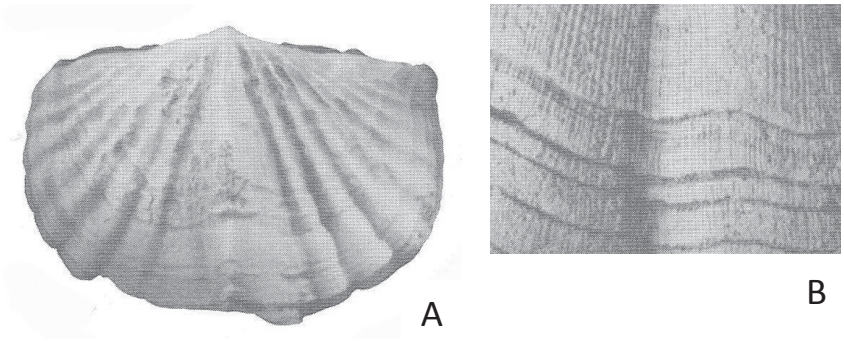


Fig. 367. *Filispirifer merzakhsaiensis* Jansen, dorsal view of holotype, x1 and micro-ornament, x5.2. From Lower Devonian of Morocco. (Jansen 2001b).

Genera*: Filispirifer* Jansen, *Leonispirifer* Schemm-Gregory, *Lusitanispirifer* Schemm-Gregory, *Mauispirifer* Allan, *Xerospirifer* Havlíček.

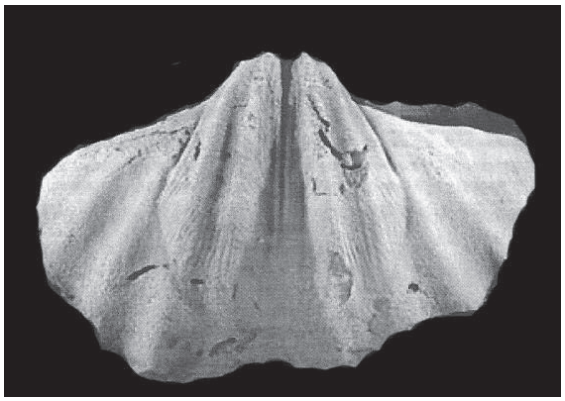
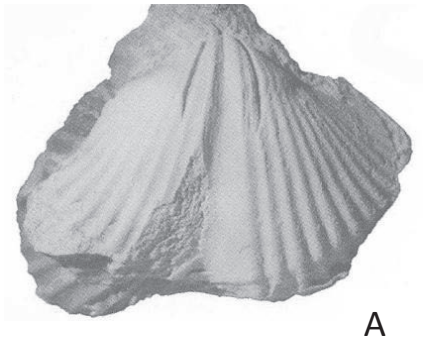


Fig. 368. *Filispirifer merzakhsaiensis* Jansen, internal ventral mould. Specimen x1.3 from middle to upper Siegenian of Morocco. (Jansen et al. 2007).

Discussion: This lineage consists of Gondwanan genera, interpreted as arising from *Howellella*. Gourvennec in Carter & Gourvennec (2006c, p. 2791) pointed out that the capillate micro-ornament in *Filispirifer* Jansen, 2001b tended to show marginal spines, and thus approached *Acrospirifer* in at least some species. But Schemm-Gregory considered that *Acrospirifer* sourced from *Hysterohowellella*, as an ally of *Hysterolites*, and judged that *Filispirifer* was derived from *Howellella*.



A

B

Fig. 369. A, B, *Xerospirifer excelsus* Havlíček, ventral internal mould, x1.8 and micro-ornament x10. From Pragian, Czech Republic. (Havlíček 1978).

Schemm-Gregory (2011a) noted that European species assigned to *Mauispirifer* were probably different from the type species of New Zealand, but it may be pointed out that the micro-ornament of type *Mauispirifer* has to be reinterpreted, because *Mauispirifer* is now known to be nodose. Allan (1947) recorded a pseudofimbriate appearance in *Mauispirifer*, calling the micro-ornament radiate rather than fimbriate and the overall appearance is certainly not fimbriate. The genus has almost sessile crural plates, and lacks tabellae. Micro-ornament of *Xerospirifer* of Pragian age in the Czech Republic is fimbriate.

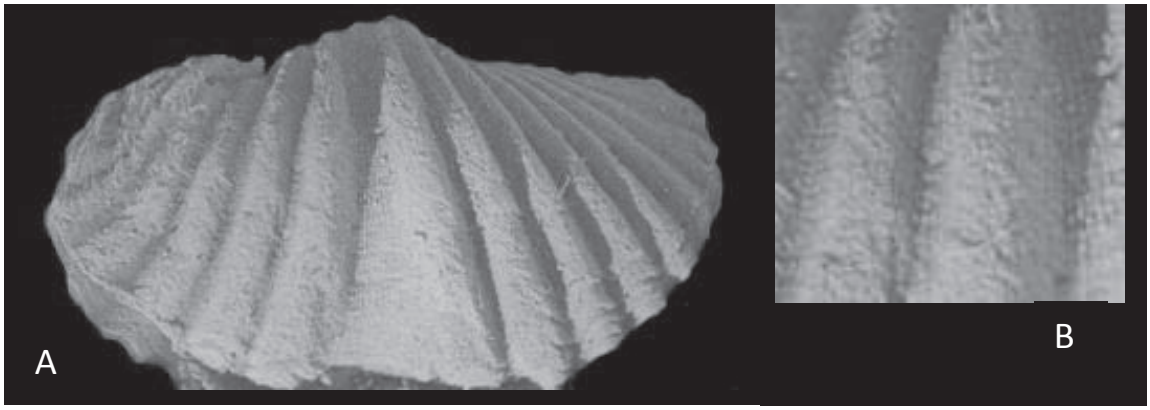


Fig. 370. *Mauispirifer hectori* Allan. A, ventral valve, x3. B, micro-ornament in ventral sulcus and plicae, x9, with pustules present in the interspaces. From Emsian of New Zealand.

Tribe **A**

A distinctive lineage is found in the eastern Americas, with strong development of shell in the apical region, and a fimbriate ornament of single rows of long micro-spines at the edge of each growth lamellum, including *Howellella vanuxemi* Hall, 1859, and "*Spirifer*" *murchisoni* Castelnau, 1843, shown to vary significantly from the genus *Acrospirifer* to which it has been assigned over recent years (Jansen 2001a, b, Schemm-Gregory 2007b, 2008c). The genera need closer study and taxonomic revision, according to Schemm-Gregory (2011a). *Costellispirifer* Boucot (syn. *Concinnispirifer* Boucot) comes from this region, though not included by Schemm-Gregory in her chart, and another likely genus is *Antispirifer* Williams & Breger.

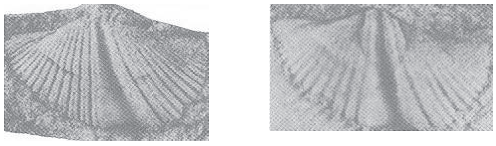


Fig. 371. *Costellispirifer perimele* (Clarke), x1. A, ventral exterior, latex cast. B, ventral internal mould. From lower Emsian of Maine, USA. (Clarke 1907).

Tribe **B**

Patriaspirifer Johnson, 1995, p. 198 from Lower Devonian (Pragian, lower Emsian) of western and central United States and western Canada, or so-called Nevadan Province, is accompanied by a number of other forms in need of closer inspection and formal revision. The species and genera were derived from *Howellella*, being moderately close in plication and display fimbriate ornament, and have much less secondary thickening than genera of the somewhat similar suite of taxa in eastern North America. The group may include *Dyticospirifer* Johnson, 1966b with few well defined plicae, fimbriate micro-ornament and bilobed cardinal process, but this was not included in the Schemm-Gregory chart. The time range is from Lochkovian into early Emsian.

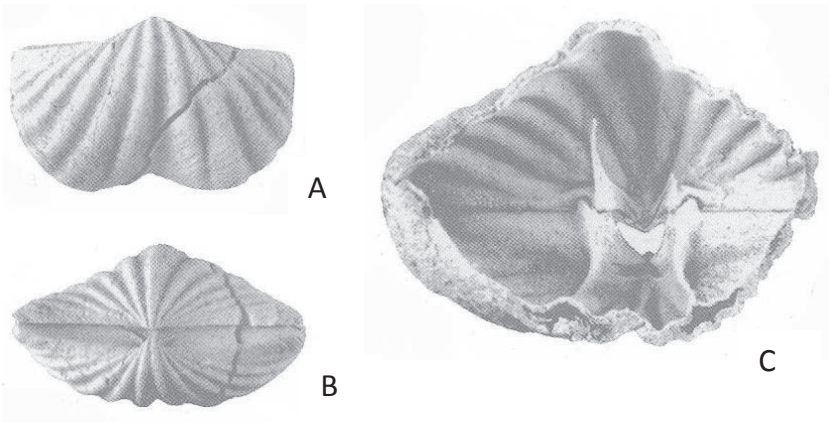


Fig. 372. *Patriaspirifer kobehana* (Merriam), A, ventral view. B, posterior view, x1. C, internal view, x1.5, dorsal valve on top. From Emsian of Nevada. (Johnson 1970).

Genus ***Nevadospirifer*** new genus

Name: From Nevada, United States.

Type species: *Nevadospirifer pulchrum* new genus, new species from Roberts Mountains, Lower Devonian (Siegenian, Emsian), Great Basin, United States, here designated.

Diagnosis: Few open plicae, usually five or six in number, ornamented by commarginal rows of radially aligned ridges, obtuse cardinal extremities, low myophragm, slight pleromal thickening. The micro-ornament is described as consisting of radially aligned ridges in commarginal rows, producing fimbriation (Johnson 1970, pl. 57).

Nevadospirifer pulchrum new genus, new species

1970 *Acrospirifer* aff. *murchisoni* [not Castelnau] Johnson, p. 189, pl. 56, fig. 5-13, pl. 57, fig. 1-6.

Name: pulcher, beautiful, Lat.

Holotype: USNM 157180, figured by Johnson (1970, pl. 57, fig. 1-6) and herein, Fig. 373C, here designated.

Diagnosis: Gently plicate with five to eight plicae on ventral valve, broad open sulcus and fold raised high anteriorly, with broadly rounded crest.

Description: The species has been described by Johnson (1970) from the Roberts Mountains of Nevada, and the nominated holotype is based on a fine specimen well illustrated by Johnson (1970). Johnson drew attention to differences from Castelnau's species *murchisoni,* which extended from the eastern United States as far west as Oklahoma according to Amsden & Ventress (1963, pl. 6), and Johnson noted that the Nevadan form had fewer plicae, counted at three to six pairs, compared with five to eight pairs in the Oklahoman specimens. Schemm-Gregory (2011a) also reported that the Nevadan form show less secondary thickening of the shell. Adminicula in the new form are short, and the ventral muscle field long and narrow in small specimens, whereas the diductor scars become distinctly and relatively larger with increase in shell-size. The ctenophoridium is deeply striate.

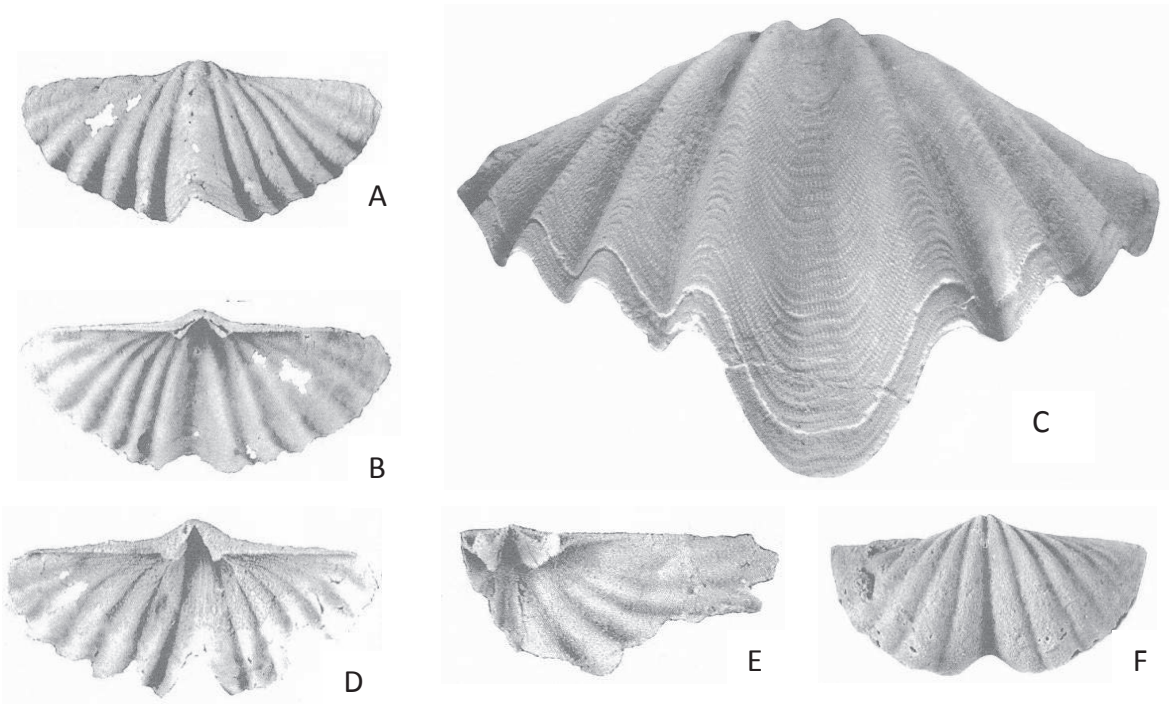


Fig. 373. A-E, *Nevadospirifer pulchrum* n. gen., n. sp. A, B, external and internal views of dorsal valve, x1.5. C, holotype, ventral exterior, x5. D, ventral interior, x1.5. E, dorsal internal view, x3. F, "*Acrospirifer*" *kobehana* (Merriam), ventral valve, x2. From Lower Devonian (Siegenian, Emsian) of Nevada, United States. (Johnson 1970).

An allied species assigned to *Acrospirifer kohebana* (Merriam, 1940) by Johnson (1970, p. 190), which is restricted to one horizon below that of the newly named species, is distinguished by its lower more round-crested plicae and low dorsal fold. This species show well a pair of low deltidial plates, but micro-ornament is obscure.

Tribe **AUSTRALOSPIRIFERINI** new tribe

Name genus: *Australospirifer* Caster, 1939, p. 159 from Lower Devonian of Brazil, here designated.

Diagnosis: Transverse with strong plicae and no costae over the ribs, sulcus and fold subdued, may have median sulcal rib and median fold channel. Fimbriate and capillate micro-ornament, strong secondary thickening in the apical region with umbonal callosity, no tabellae, and as a rule a "large septal pillow". Lower Devonian (Emsian).

Genus: *Australospirifer* Caster.

Discussion: This branch is represented by *Australospirifer* Caster, as typifying the Malvinokaffric realm. The genus is characterized by a combination of fimbriate and capillate micro-ornament, strong secondary thickening in the apical region, as a rule an umbonal callosity, and no tabellae. There is no deltidium, and the dorsal adductor field has what are described as horn-like processes pointing posteriorly and gently elevated (Boucot et al. 1965).

Similar processes were described by Schemm-Gregory (2011b) for *Lusitanispirifer*, judged to belong to Filispiriferini, but showing considerable similarities, due to homoplasy.

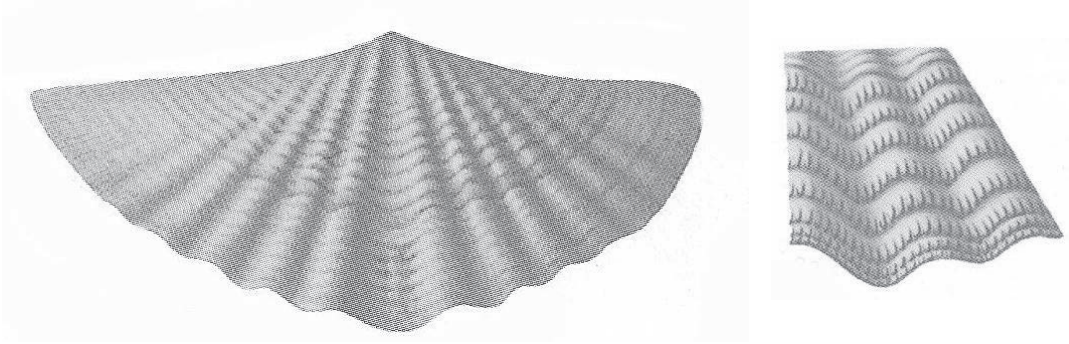


Fig. 374. *Australospirifer keyserianus* (Clarke), ventral view, x1.5 and micro-ornament, x7. Emsian of Brazil. (Clarke 1913).

Tribe **OTOSPIRIFERINI** new tribe

Name genus: *Otospirifer* Hou & Xian, 1975, p. 65 from Lower Devonian (Emsian) of south China, here designated.

Diagnosis: Often large, adminicula varying in length, with or without tabellae, forming an Asian group derived from *Howellella*. Lower Devonian (Pragian) to Middle Devonian (Eifelian). Genera*:* *Otospirifer* Hou & Xian, *Frequentispirifer* Schemm-Gregory, *Howellelloidea* Su, *Pseudokymatothyris* Chen, *Quiringites* Struve. *Rostrospirifer* Grabau, *Trigonospirifer* Wang, *Xenospirifer* Hou & Xian, *Xinjiangospirifer* Hou & Zhang.

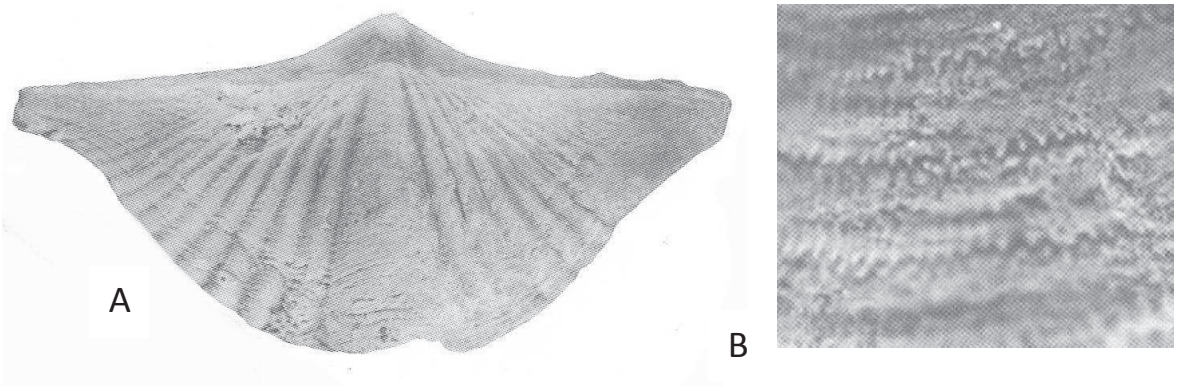


Fig. 375. *Otospirifer shipaiensis* Hou & Xian, dorsal view, x2, and micro-ornament, x7. From Emsian of south China. (Johnson & Hou 2006b).

Discussion: These genera were classed as Howellellinae and Hysterolitinae in the *Revised Brachiopod Treatise*. *Otospirifer* Hou & Xian has crowded rows of pustules, and there are

short or no tabellae. A branch arising from *Pseudokymatothyris* involved the genera *Quiringites* and *Howellelloidea*, genera which also have short tabellae. *Quringites* was deemed exceptional, being capillate with long micro-spines, and has well developed ctenophoridium and short tabellae. *Xinjiangospirifer* is included, though uncharted by Schemm-Gregory (2011a). It is a large subelongate genus from the Lower Devonian of Kazakhstan and China, with rather flattened crests to the plicae and narrow interpaces, and the sulcus may be traversed by a median rib. There is a deltidium, and short adminicula and thick umbonal callus.

Although Talent et al. (2001) considered *Rostrospirifer* to be a synonym of *Euryspirifer*, the two are clearly distinct, *Euryspirifer* having a median sulcal plication, more deeply impressed ventral muscle field, shorter free portions of the dental plates, clearly developed notothyrial shelf, and subdued accessory plicae (Jansen et al. 2008).

Intermedites Struve, 1970 was depicted by Schemm-Gregory (2011a) as belonging to this group, but is here judged to be closer to *Arduspirifer* Mittmeyer in Paraspiriferinae Pitrat (see Fig. 358, p. 277), and the micro-ornament of *Intermedites* lacks pustules.

Family **COSTISPIRIFERIDAE** Termier & Termier, 1949

[Nom. transl. hic ex Costispiriferinae Termier & Termier, 1949, p. 98].

Diagnosis: Plicae covered by costae, micro-ornament capillate with or without micro-spines in single rows, yielding fimbriation. Silurian to Middle Devonian (Eifelian).

Discussion: This family embraces plicate and costate Hysterolitoidea.

Subfamily **COSTISPIRIFERINAE** Termier & Termier, 1949

[Costispiriferinae Termier & Termier, 1949, p. 98].

Diagnosis: Plicae covered by costae, micro-ornament fimbriate with single rows of micro-spines, or capillate without micro-spines. Lower Devonian (Pragian) to Middle Devonian (Eifelian).

Discussion: Family groups are traced through the presence or absence of tabellae, and the simplicity or dividing of ribs.

Tribe **COSTISPIRIFERINI** Termier & Termier, 1949

[Nom. transl. hic ex Costispiriferinae Termier & Termier, 1949, p. 98. Syn. Multiplicatispiriferinae Schemm-Gregory, 2008a, p. 389].

Diagnosis: Capillate without micro-spines, simple low rounded ribs. Lower Devonian (Pragian – Emsian).

Genera*: Costispirifer* Cooper, *Multiplicatispirifer* Schemm-Gregory.

Discussion: The *Revised Brachiopod Treatise* emphasized the broadly arched delthyrium with apical plate, formed by a deltidium, and emphasized that the ctenophoridium was not built up in *Costispirifer* Cooper, 1942. There are no tabellae and only reduced crural plates and

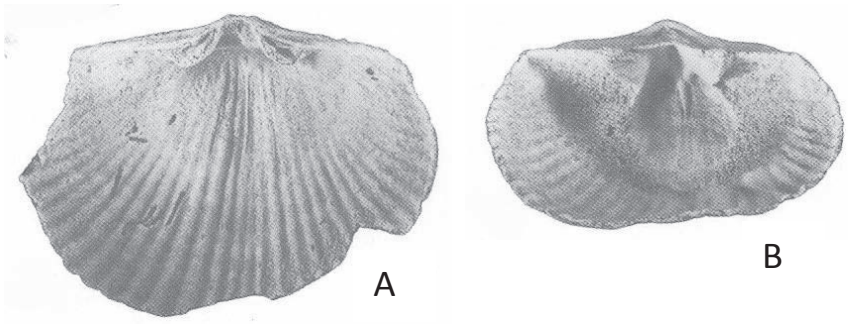


Fig. 376. *Costispirifer arenosus* (Conrad), dorsal and ventral interiors, x1. From Lower Devonian of Maryland, USA. (Johnson & Hou 2006b, p. 1838).

only reduced crural plates, but a delthyrial apical plate is present. It certainly is not a connector plate, because it lies well above the junction of the dental and adminicular plates. Johnson (1970) stated that the genus came close in appearance to *Vandercammenina* Boucot of Fimbrispiriferinae. But its micro-ornament is capillate, and shows no sign of fimbriae or frilly laminae. *Cumberlandina* Boucot was placed in the same subfamily by Johnson & Hou (2006b, Fig. 1222.1c, 2e), and Johnson (1970, p. 193) had drawn attention to some of the differences from *Costispirifer*, but judged that the two were related, because of the somewhat similar delthyrium and apical plate. *Cumberlandina* has no tabellae and only reduced crural plates, and deltidium. It is distinguished by its small posterior platform, sessile probably, with short dorsal septum in front, unlike the dorsal interior of *Costispirifer,* and the sulcus and fold are smooth, unlike the closely costate sulcus and fold of Costispiriferinae. The two hardly seem to be close, in view of such differences, and *Cumberlandina* was rejected from membership of Costispiriferinae by Schemm-Gregory (2008b) and tentatively assigned to Mucrospiriferidae, which shares a stegidium (see Fig. 5, p. 15). Schemm-Gregory (2008b) traced differences elevated to family rank.

Multiplicatispirifer Schemm-Gregory was allocated a subfamily of its own by Schemm-Gregory (2008b), but two subfamilies, each with a solitary genus, poses a question against the weighting of morphological attributes.

Tribe **MULTISPIRIFERINI** Schemm-Gregory, 2008b

[Nom. transl. hic ex Multispiriferidae Schemm-Gregory, 2008a, p. 442].

Diagnosis: Transverse, bundled coarse ribs which bifurcate many times, no median rib in sulcus, capillate and clearly developed micro-spines at edge of each growth lamella. Lower Devonian (Pragian).

Genus: *Multispirifer* Kaplun.

Discussion: This genus is considered to be very close to *Costispirifer*, and so is judged to belong to a tribe rather than a full family. There may indeed be scope for using the category of subtribes for some of the divisions within Howellellidae and Costispiriferidae.

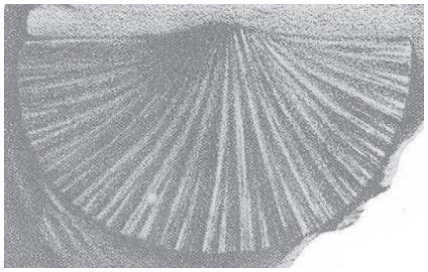


Fig. 377. *Multispirifer solitarius* (Krantz), dorsal valve exterior, x1. From Pragian to lower Emsian of Germany. (Krantz 1857).

Subfamily **PLICONODOSINAE** new subfamily

Name genus: *Pliconodosus* new genus, from Silurian of Gotland, here designated.

Diagnosis: Small shells with narrow moderately high interarea, characterized by strong plicae interspersed with costae, capillae nodose. Short adminicula, short tabellae. Silurian (Ludlow).

Genus: *Pliconodosus* new genus.

Discussion: This tribe is discriminated for an exceptional genus, recognized for a Silurian genus from Gotland. The genus is deemed to mark the first appearance of costate Hysterolitoidea as segregated in Family Costispiriferidae, leading to an interpretation that differs from the overview in Schemm-Gregory (2011a), as shown in Fig. 351, p. 274, which sourced sourced *Costispirifer* and allies from *Iberohowellella*.

Genus ***Pliconodosus*** new genus

Derivation: plico – fold, nodosus – full of knots, Lat.

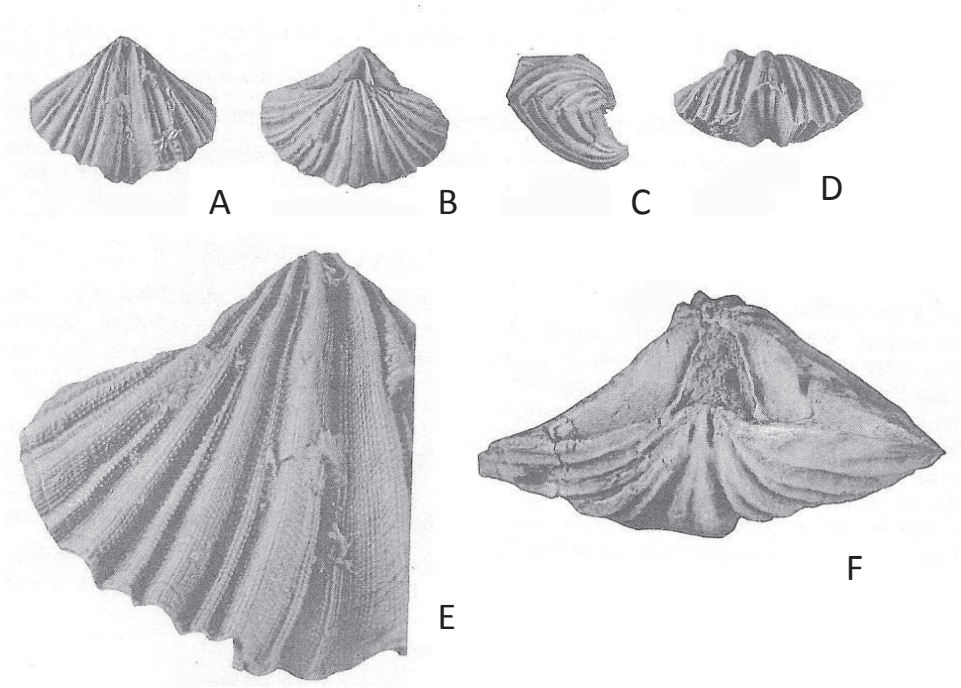


Fig. 378. *Pliconodosus schmidti* (Lindstrom). A-D, ventral, dorsal, lateral and anterior views, dorsal valve on top, x1. E, ventral valve, showing pustular ornament, x3. F, posterior view, showing short tabellae, and suggestions of low deltidia, x3. From Ludlow beds of Gotland. (Boucot 1963).

Diagnosis: Shells with plicae, costae in interspaces and over sulcus, fold grooved. Radial capillae tuberculate. Delthyrium bordered by two deltidial plates which are conjunct under the umbo. Short adminicula and short tabellae. Upper Silurian (Ludlow).

Type species: *Spirifer schmidti* Lindstrom, 1861 from Ludlow beds of Gotland, here designated.

Discussion: The new genus has an apical plate which passes forward into two deltidial plates, bordering the delthyrium. It is closest to members of Elymospiriferinae (p. 292), but displays simpler costae and cleft fold. *Indospirifer* Grabau, 1931b has similar but non-pustulose micro-ornament with commarginal lirae less prominent, and the dorsal plicae are simple rather than costate, and there are very short possible tabellae (p. 294).

Subfamily **FIMBRISPIRIFERINAE** Pitrat, 1965

[Nom. transl. hic ex Fimbrispiriferidae Pitrat, 1965, p. 687].

Diagnosis: Fold, sulcus and flanks costate rather than plicate, and costae may be weakly fasciculate, and may conspicuously bifurcate. Prominent and closely spaced commarginal laminae, which may be zigzag, with marginal spines, open delthyrium. No ventral septum, tabellae may be present. Lower Devonian (Pragian) to Middle Devonian (Eifelian, possibly lower Givetian).

Genera: *Fimbrispirifer* Cooper, *Oventensispirifer* Schemm-Gregory, *Struveina* Boucot, *Turcispirifer* Schemm-Gregory, *Vandercammenina* Boucot.

Discussion: The genera were sourced from *Iberohowellella*, according to Schemm-Gregory (2011a), though this was left out of her family grouping, with the implication that it belonged to an unspecified elsewhere, herein interpreted as Hysterolitidae. The genus *Iberohowellella* is narrowly plicate and unlike other genera, lacks costae, and is not regarded as source for the subfamily, counter to the Schemm-Gregory chart on p. 274.

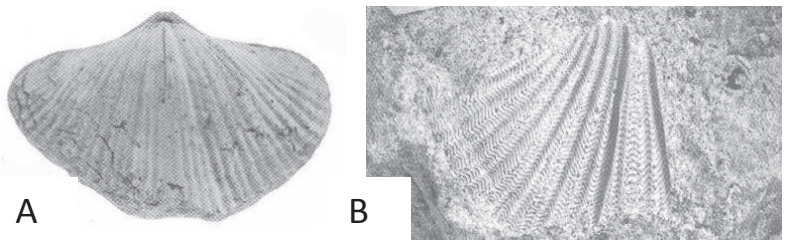


Fig. 379. *Fimbrispirifer venustus* (Hall), dorsal view and ventral external mould showing commarginal ornament over fasciculate costae, x1. From lower Givetian, east USA. (Jones & Boucot 1983).

Johnson & Hou (2006b, p. 1836) stated that crural plates (ie. tabellae?) are variably present, and were recorded for *Fimbrispirifer* Cooper, 1942. No tabellae are visible in the internal moulds of *Fimbrispirifer* figured by Johnson & Hou (2006b, Fig. 1218.1b, 1d), but Jones & Boucot (1983, pl. 2, fig. J) showed that the posterior crural plates touch the posterior wall, reinforcing the report in the *Revised Brachiopod Treatise*. Detail of dorsal cardinalia was

not provided for *Struveina* and *Oventensispirifer*. The diagnosis in the *Revised Brachiopod Treatise* stated that the fold and sulcus were plicate, but it is prefered to call the ornament costate.

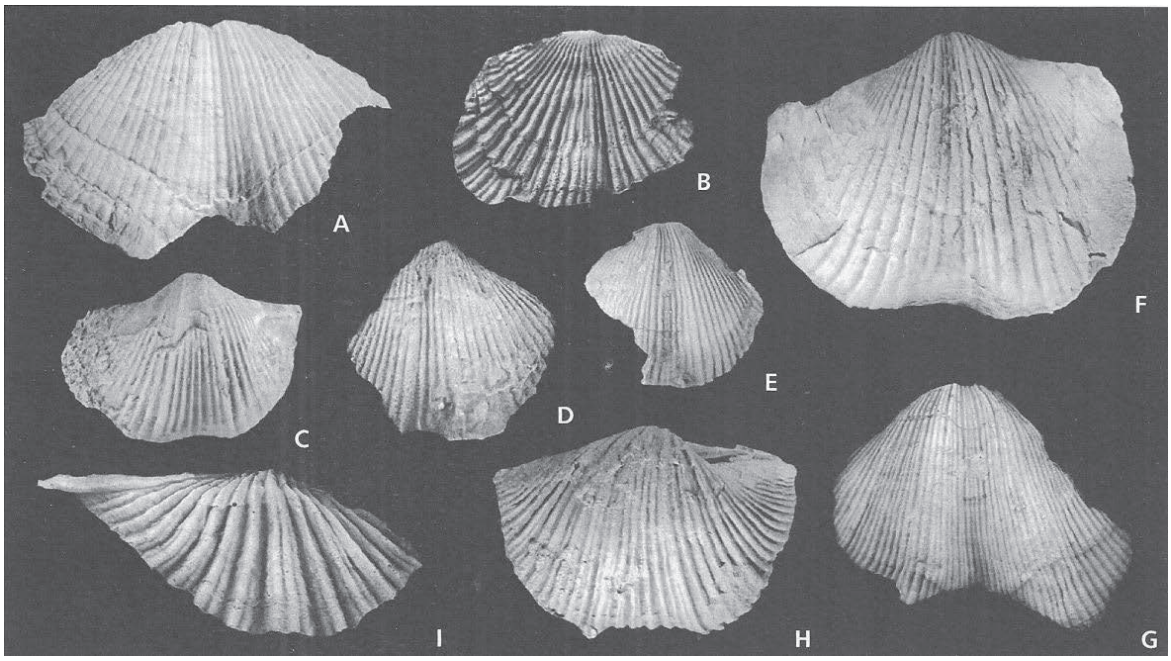


Fig. 380. Examples of finely costate Hysterolioidea, showing differences in costation. A, *Fimbrispirifer divaricatus* (Hall). B, *Struveina daleidensis* (Steininger). C, *Vandercammenina trigeri* (de Verneuil). D, *Oventensispirifer ovetensium* (Carls). E, *Turcispirifer turciae* Schemm-Gregory. F, *Costispirifer arenosus* (Caster). G, *Multiplicatispirifer foumzguidensis* Schemm-Gregory. H, *Elymospirifer kwangsiensis* (Hou). I, *Multispirifer solitarius* (Krantz). Specimens x1. This comparison of ribbing was compiled by Schemm-Gregory (2008b).

Vandercammenina Boucot, 1975, placed in Fimbrispiriferinae in the *Revised Brachiopod Treatise*, displays numerous costae, but is unusual in its long and extrasinal adminicula. Gourvennec (1994c) provided multifactorial analyses for species within this genus.

Subfamily **ELYMOSPIRIFERINAE** Johnson & Hou, 1994

[Elymospiriferinae Johnson & Hou in Carter et al., 1994, p. 352].

Diagnosis: Fold and sulcus costate, flanks with bifurcate and trifurcate costae in fascicles. Micro-ornament capillate, with short rounded micro-spines. No notothyrial cavity, short tabellae common. Lower Devonian (Pragian) to Middle Devonian (Eifelian).

Genera: *Elymospirifer* Wang, *Borealispirifer* Hou & Su, ?*Indospirifer* Grabau, *Perryspirifer* Jones & Boucot.

Discussion: Genera have pronounced deltidial lamellae, and formed a deltidium under the beak, and developed a complicated micro-ornament, cancellate, capillate or fimbriate with one or more rows of spinules at the edge of each growth lamella, or lacrimate with teardrop-

shaped pustules arranged in radial and commarginal rows. (See Johnson & Hou 2006b, Fig. 1223.3e; 1224d and Schemm-Gregory 2011a). Johnson & Hou (2006b, p. 1838) inaccurately described the fold and sulcus as plicate, whereas they are costate, and referred to bifurcating plications laterally for what may be described as fasciculated costae. Short vertical plates like tabellae are present apically in the dorsal valve of *Elymospirifer* Wang in Wang, Yu & Wu, as shown by Jones & Boucot (1983, Fig. 9) and vestigial plates were noted by Johnson & Hou (2006b) in *Borealispirifer* Hou & Su and *Perryspirifer* Jones & Boucot. For the type species of *Elymospirifer,* Jones & Boucot (1983, Fig. 9) illustrated a sectioned topotype which shows two vertical plates inside the outer walls, in the region of the ctenophoridium, extending for approximately 1mm in length. They are difficult to interpret, because the sections do not show clearly defined dental sockets, and suggest that crural plates are severely reduced. The vertical plates might be the outer socket plates, combined with crural plates, and sessile on the floor of the valve.

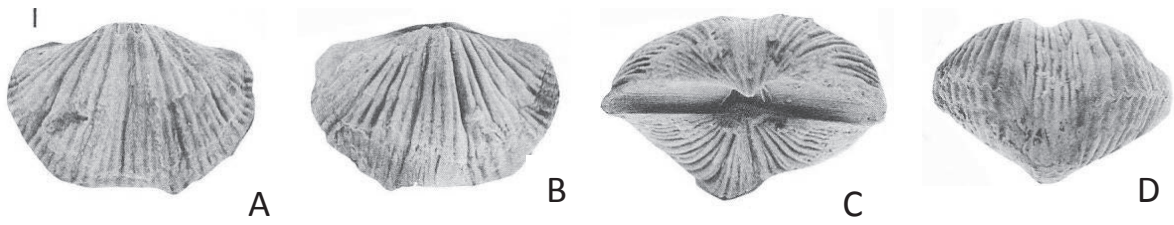


Fig. 381. *Elymospirifer kwangsiensis* Wang, A, ventral view; B, dorsal view; C, posterior view (dorsal valve below) and D, anterior view. Specimens x1. From Guangxi Province, China. (Jones & Boucot 1983).

Jones & Boucot (1983, p. 339) claimed that *Perryspirifer* was characterized by the lack of crural plates, but crural plates as herein defined are developed. Moreover, tabellae are also well represented in a transverse sections of *Perryspirifer* provided by Jones & Boucot (1983, Fig. 4) from the Eids Formation, and absent from a specimen from the Bird Fiord Formation (See Fig. 383, p. 294). The Birds Fiord specimen has a very different dorsal interior, and it is understandable why Johnson & Hou (2006b, p. 1840) declared, counter to Jones & Boucot, that "vestigial crural plates" were present. Indeed, they do not look particularly vestigial in Jones & Boucot (1983, Fig. 4), and further work is required to unravel

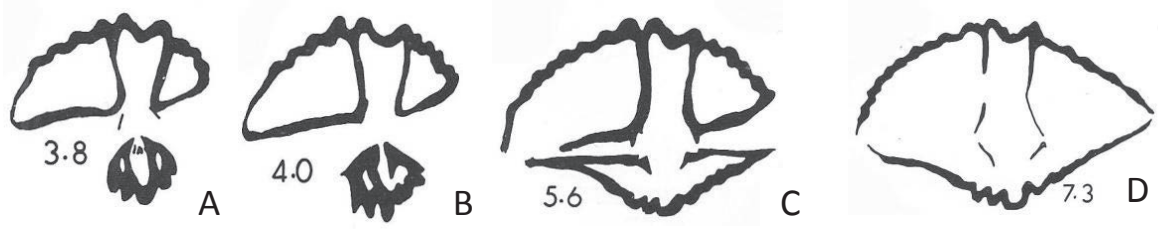


Fig. 382. *Elymospirifer kwangsiensis* Wang, transverse sections, x1.3, dorsal valve below. Distance from beak shown in mm. From Guangxi Province, China. (Jones & Boucot 1983).

the consistency in the dorsal interior of all these genera. A delthyrial cover plate is developed in *Perryspirifer*, and deltidial plates in *Elymospirifer,* and the micro-ornament consists of radial capillae. Stress was laid on the importance of considerable secondary thickening as helping to typify *Perryspirifer*. As shown in Fig. 383B, crural plates diverge strongly, suggestive of a sessile cruralium.

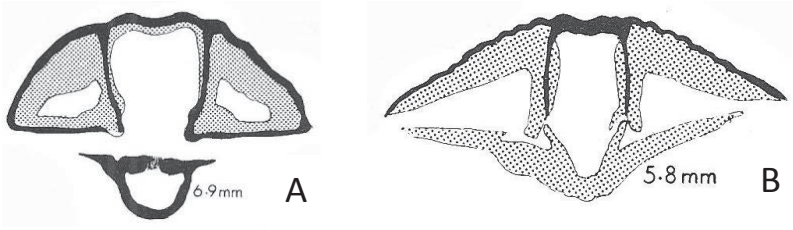


Fig. 383. *Perryspirifer scheii* (Meyer), two differing transverse sections, x1.5 approx, from A, Bird Fiord Formation and B, from Eids Formation, Lower Devonian of Canada. (Jones & Boucot 1983).

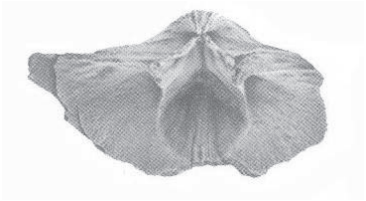


Fig. 384. *Perryspirifer scheii* (Meyer), ventral interior with its strong resemblance to Late Paleozoic spiriferoids. From Lower to Middle Devonian of Canadian Arctic. (Jones & Boucot 1983).

In the complexity of its radial ornament, Elymospiriferinae shows some approach to Pliconodosinae of Silurian age (p. 290). This subfamily has plicae and costae, with capillate or nodose micro-ornament, and tabellae are present. But ornament of Pliconodosinae is not as elaborate as that of Elymospiriferinae.

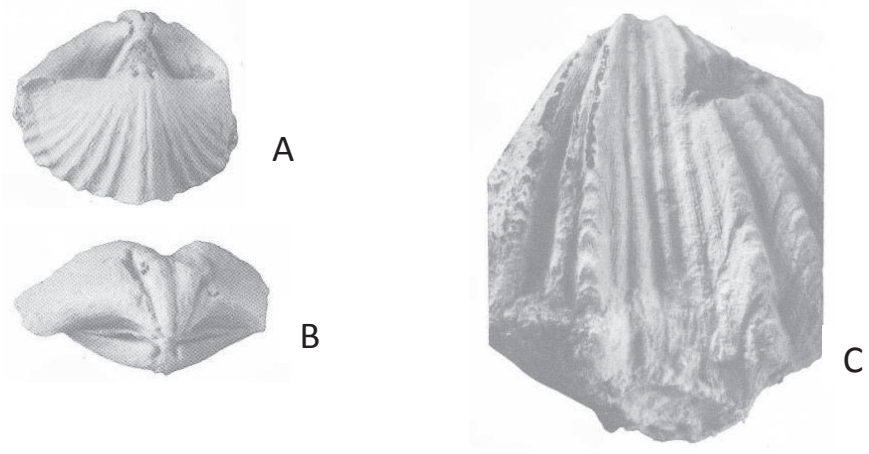


Fig. 385. *Indospirifer padaukpinensis* (Reed). A, B, dorsal and posterior aspects, x3. C, ventral valve, x4. (Anderson, Boucot & Johnson 1969).

Indospirifer Grabau was not mentioned by Schemm-Gregory (2011a), and was regarded as adolfioid by Johnson (2006a). It has cancellate micro-ornament, plicae with ventral costae, adminicula and short tabellae. The genus was discussed by Boucot & Jones (1983) in conjunction with *Perryspirifer*, and the genus, of Lower and Middle Devonian age in Burma, shows some approach Elymospiriferinae in the complexity of the ornament, as noted by Jones & Boucot (1983), and indeed the type species of *Elymospirifer* had originally been referred to *Indospirifer* (*Revised Brachiopod Treatise* 2006, p. 1838). However the ornament is more organized into costate plicae in Elymospiriferinae, and the capillae are not tuberculose. Tabellae may be present in both genera. With its simple dorsal plicae, and strong ventral plicae each side of the costate sulcus, the genus appears to fall within a separate tribe, allied to Costispiriferinae and Elymospiriferinae.

Family **SPINELLIDAE** Johnson, 1970

[Spinellidae Johnson, 1970, p. 205].

Diagnosis: Closely plicate with small spines in commarginal rows. Long adminicula and dental plates and forked subdelthyrial ridge formed by low pleromal ridges passing back into small connector plate. Deltidial plates present in some genera. High crural plates, tabellae very short or absent, feeble or no cruralium. Lower Devonian (Pragian) to Middle Devonian (Eifelian?).

Discussion: This family, named for a genus described by Talent (1956) from the Lower Devonian of east Australia, and coupled with subfamilies from western Europe and from east Asia, is characterized by its micro-ornament of fine spinules in commarginal rows, and in being plicate, approaches members of Cyrtiimorphi in overall shape and size, as well as members of Hysterolitoidea. In the *Revised Brachiopod Treatise*, members have been classified as Adolfioidea, but in the present reinterpretation of that superfamily, no constituent adolfioid genera have such well organized rows of spines, and the presence of a subdelthyrial plate and deltidia in some genera adds further evidence for the need to re-evaluate the family associations. By contrast, Delthyridina does have commarginally arrayed spines. As indeed does Ambocoelioidea, which however is rarely plicate. There are further unusual attributes of the family. A connector plate and pleromal ridges are developed in Spinellinae, and to less extent, with deltidia, in Brevispiriferinae. These are features not known in Adolfioidea, Delthyroidea or Hysterolitidae, but are interpreted as representing a development in Hysterolitoidea, arguably from Howellellidae, and like the delthyrial arrangements which arose independently in various Reticularioidea, Elitoidea and Ambocoelioidea. In addition, a weakly developed cruralium appeared in some Brevispiniferinae, a feature confined to a very few genera in Hysterolitoidea, including *Perryspirifer*, though more common in Ambocoelioidea.

Subfamily **SPINELLINAE** Johnson, 1970

[Nom. transl. hic ex Spinellidae Johnson, 1970, p. 205].

Diagnosis: Closely plicate. Long adminicula and dental plates with low pleromal ridges passing back into small connector plate, leaving a forked subdelthyrial ridge. High crural plates, ctenophoridium, no tabellae, no cruralium. Lower Devonian (Pragian – Emsian).
Genus: *Spinella* Talent.

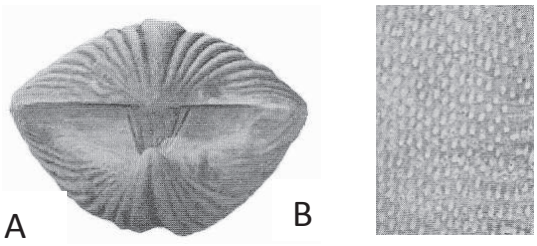


Fig. 386. *Spinella yassensis yassensis* (Koninck), posterior view, x2. *S. buchanensis* (Talent), micro-ornament, x7.5. From Devonian of New South Wales. (Strusz et al. 1970).

Discussion: This family group was abandoned by Johnson (2006a), but is here discriminated for plicate shells with a micro-ornament of commarginal rows of spinules. Deltidium, connector plate and pleromal ridges are developed. The description of *Spinella* Talent by Chatterton (1973, p. 106) greatly clarifies the genus, and recorded that micro-ornament

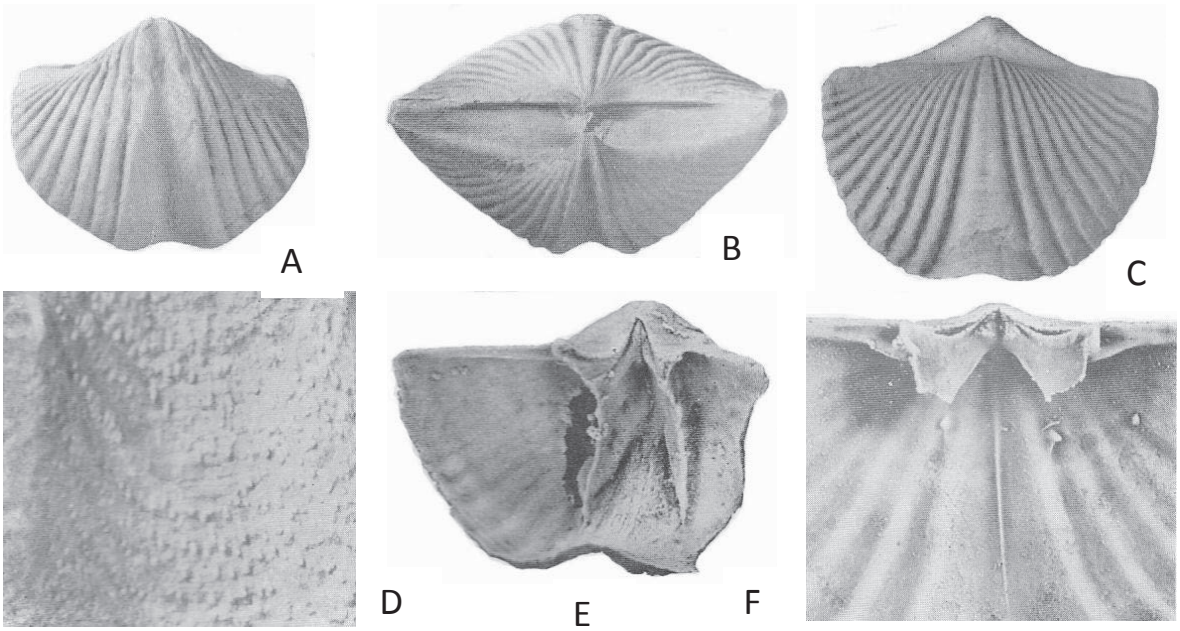


Fig. 387. *Spinella passensis ravinia* Flood. A-C, ventral (neotype), posterior and dorsal aspects of specimens, x2. D, micro-ornament x7.5. E, F, ventral and dorsal interiors with high and well formed crural plates (see Fig. 8A, p. 16), but no visible tabellae, which if present, were very small, as suggested in transverse sections (see Fig. 389A). Specimens from Lower Devonian of Taemas, New South Wales. (Strusz et al. 1970).

became fimbriate at the anterior edges of the growth lamellae. Material shows an umbonal callosity under the open delthyrium, with two pleromal thickenings passing along the lower edge of the dental plates. Well developed adminicula are illustrated for *Spinella* Talent.

Spinella was not mentioned by Schemm-Gregory (2011a), but she had not worked on Australian material, and also may have considered the genus to be non-delthyroid. Yet the ornament shows strong commarginality, and furthermore, pleromal ridges and connector plate are not known to have been developed in Cyrtiidae or Eospiriferidae. The subfamily

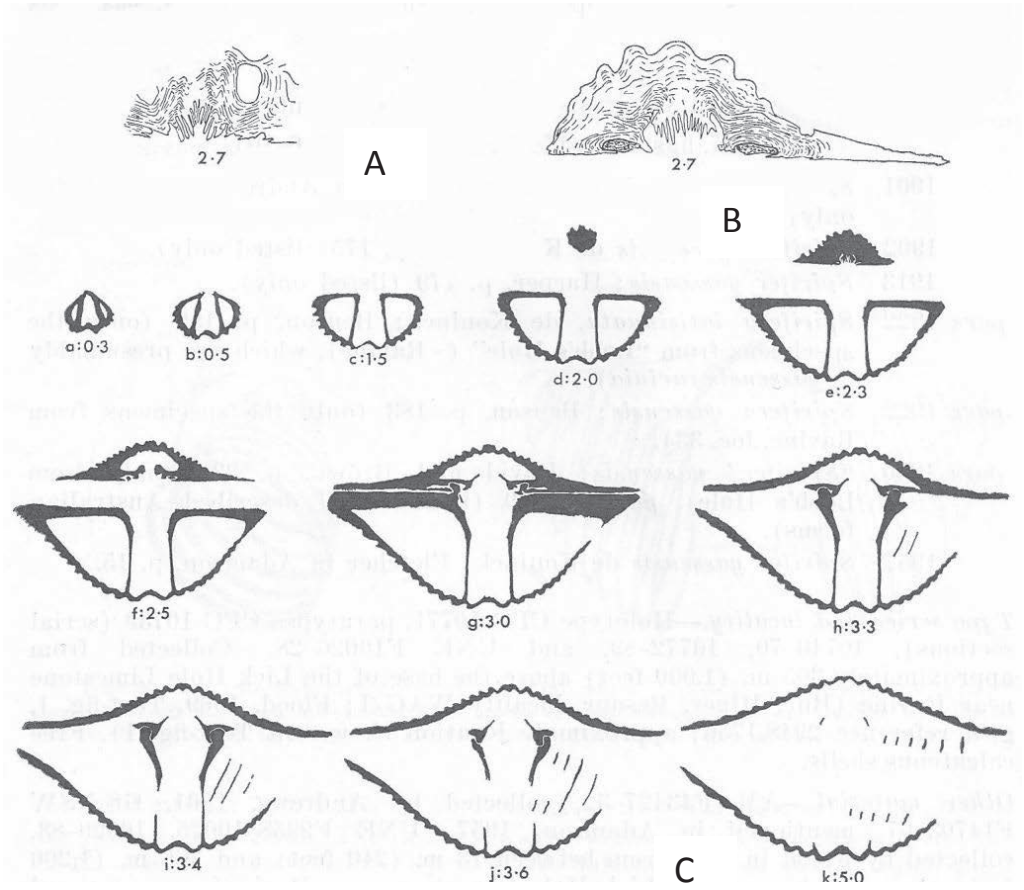


Fig. 388. *Spinella passensis ravinia* Flood. A, B, shell structure in transverse sections at dorsal umbo, x10. Fig. 388A possibly records two very short tabellae. C, transverse sections with distance in mm from ventral beak, x2. Specimens from Lower Devonian of Taemas, New South Wales, Australia. (Strusz et al. 1970).

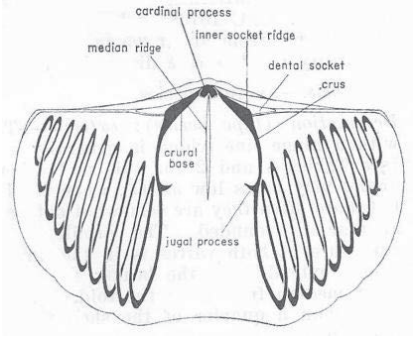


Fig. 389. *Spinella yassensis yassensis* (Koninck), dorsal interior. From Lower Devonian of Taemas, New South Wales, Australia. (Strusz et al. 1970).

has a reduced but nonetheless distinct connector apparatus and partial closure of the delthyrium. Some specimens indicate deltidial plates. The genus was placed in Adolfiidae by

Johnson (2006a, p. 1706), but no adolfioid has such a delthyrial closure – indeed Adolfiidae are supposed to have an open delthyrium. Initial studies by Talent (1956), Strusz et al. (1970) and Chatterton (1973) placed the genus in Delthyridae.

Subfamily **EOSPIRIFERININAE** new subfamily

Name genus: *Eospiriferina* Grabau, 1931b from Lower and Middle Devonian of Guangxi, south China, here designated.

Diagnosis: Small, simple plicae and scattered lacrimate spines with well developed commarginal laminae. No tabellae. Lower Devonian (Pragian) to Middle Devonian (Eifelian).

Genera*: Eospiriferina* Grabau, *Guicyrtia* Wang & Zhu, *Orientospirifer* Hou & Xian.

Fig. 390. *Orientospirifer nakaolingensis* Hou & Xian, ventral, dorsal and lateral views, x 1.5. From Pragian of south China. (Hou & Xian 1975).

Discussion: This small group arose from *Howellella*, and is found in east Asia. It is typified in part by dense spinules in commarginal rows. *Eospiriferina* displays strong thin adminicula and tabellae described as anteriorly convergent. *Orientospirifer* Hou & Xian (1975, pl. 3, fig. 8-10, pl. 3, fig. 7) has well developed adminicula, but no tabellae, and the ctenophoridium is well developed. There are no clearly defined tabellae, but sections are obscure. *Eospiriferina* and *Guicyrtia* were assigned to Adolfioidea by Johnson (2006a, p. 1706), and *Orientospirifer* to Delthyridina, but Schemm-Gregory (2011a) allocated *Eospiriferina* and *Orientospirifer* to an east Asian group of descendents from *Howellella*. The presence of spines in commarginal rows strongly suggests affinity with Spinellidae. *Guicyrtia* Wang & Zhu, 1979 is plicate with closely spaced tear-drop pustules along commarginal growth-lines, but the interior is not known. The genus is limited to Eifelian faunas.

Fig. 391. *Eospiriferina lachrymosa* Grabau. A, ventral internal mould, x1.5. B, dorsal valve, x2. C, micro-ornament, x4. From Emsian-Eifelian of Guangxi, south China. (Grabau 1931b; Johnson 2006a).

Unfortunately the nature of the delthyrial apparatus is poorly known for these genera, and requires clarification before the affinities of the group can be consolidated.

Subfamily **BREVISPINIFERINAE** new subfamily

Name genus: *Brevispinifera* García-Alcade, 2005, p. 81 from lower Emsian of Cantabrian Mountains, Spain, here designated.

Diagnosis: Plicate and pustulose shells with smooth sulcus and fold, high adminicula and either short vertical tabellae or crural plates that may form a cruralium. Reduced pleromal ridges and no connector plate. Lower Devonian (upper Emsian).

Genera: *Brevispinifera* García-Alcalde, *Ferronia* García-Alcade, ?*Mariaspirifer* Cherkesova, *Paillettia* García-Alcalde, ?*Qiansispirifer* Yang.

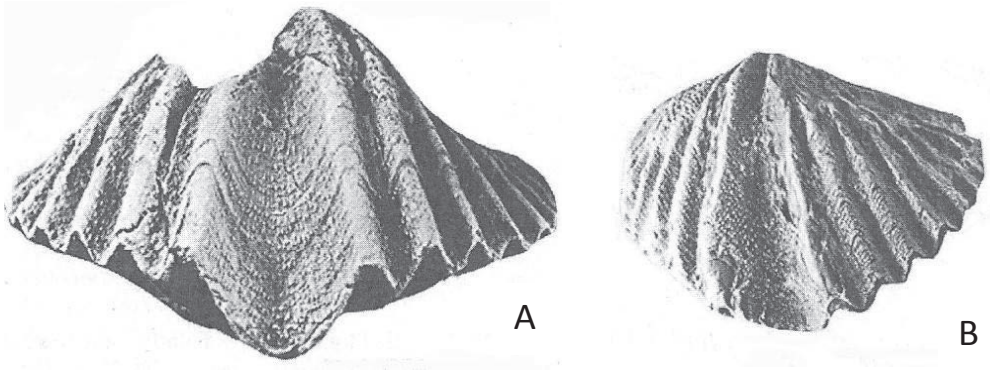


Fig. 392. A, *Ferronia subspeciosa* (Verneuil), ventral views, x6, x5. Note commarginally aligned ornament. From Coladilla Formation (Emsian), Spain. (García-Alcade 2005).

Discussion: These genera were referred by García-Alcade, 2005 to Spinellinae Johnson, Ctenophoridium, crural plates and pleromal ridges are present, although no well developed delthyrial cover plate or connector plate was developed. A pleromal plate and possible apical plate were found in *Ferronia subspeciosa* (Verneuil), and subvertical deltidial plates were reported for *F. arenensis* García-Alcade. For *Pailletia*, García-Alcade reported short lateral outgrowths on the dental plates, like the bases of a delthyrial plate, though no full plate was developed. Short crural bases and distinct tabellae are present. Gourvennec in Gourvennec & Carter (2007, p. 2772) assessed the genera as belonging to Adolfiinae, yet this seems to be denied by the presence of a delthyrial plate or deltidia. The genera are referred to Delthyridina partly because of the reasons proposed for Spinellinae, involving ornament and at least feeble pleromal ridging.

In some respects Allanellinae, a group within Cyrtioidea (p. 42) comes close to Brevispiniferinae, for members have a septalium, as well as less organized or at least less well spaced spinules along commarginal rows. Members of Brevispiniferinae tend to be more transverse with more plicae pairs, and Allanellinae lacks any pleromal development.

Ferronia arenensis García-Alcade, 2005 looks externally like *Ferronia* from the same region, and was ascribed to that genus by García-Alcade (2005). But unlike *Ferronia*, it lacks a full cruralium and short dorsal median septum, and has deltidial plates. The species is much

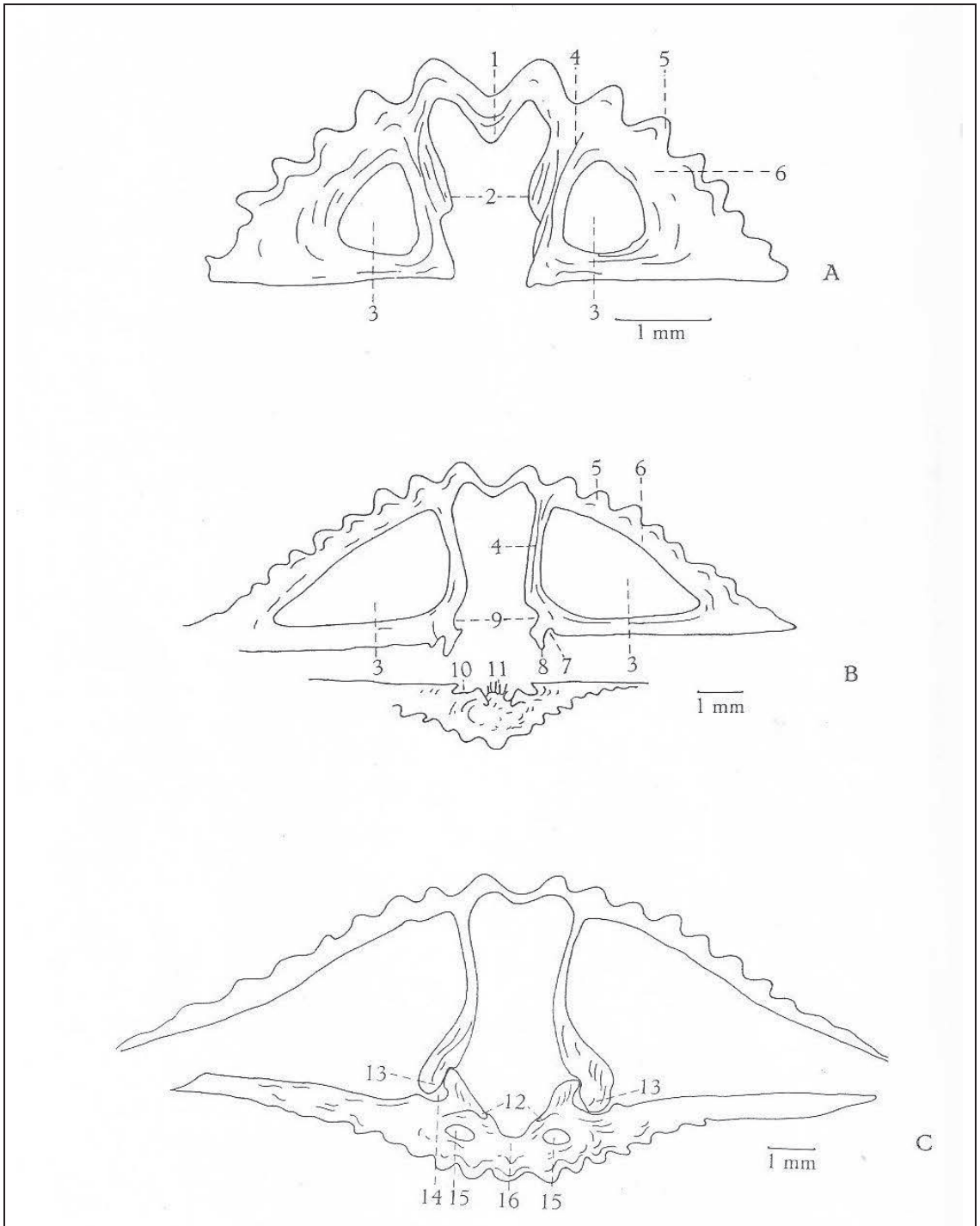


Fig. 3. — *Spinella subspeciosa* (E. VERNEUIL).
Sections successives A, B, C perpendiculaires au plan de symétrie bilatérale dans la région du crochet du spécimen n° 5616 (Effectuées par Th. KRANS) : 1 pédonculaire médian; 2 : bases de la callosité apicale; 3 : cavité apicale latérale ventrale; 4 : prismotest; 5 : fibrotest;6 : callotest; 7 : rainure deltidiale; 8 : bourrelet deltidial; 9 : rainure hypodeltidiale; 10 : cavité glénoïde; 11 : processus cardinal; 12 : lamelles apicales incomplètes; 13 : apophyse articulaire; 14 : cavité glénoïde; 15 : cavité apicale latérale dorsale; 16 : pont callotestaire.

Fig. 393. *Ferronia subspeciosa* (Verneuil), transverse sections. From Lower Devonian of Spain. (Vandercammen & Krans 1964).

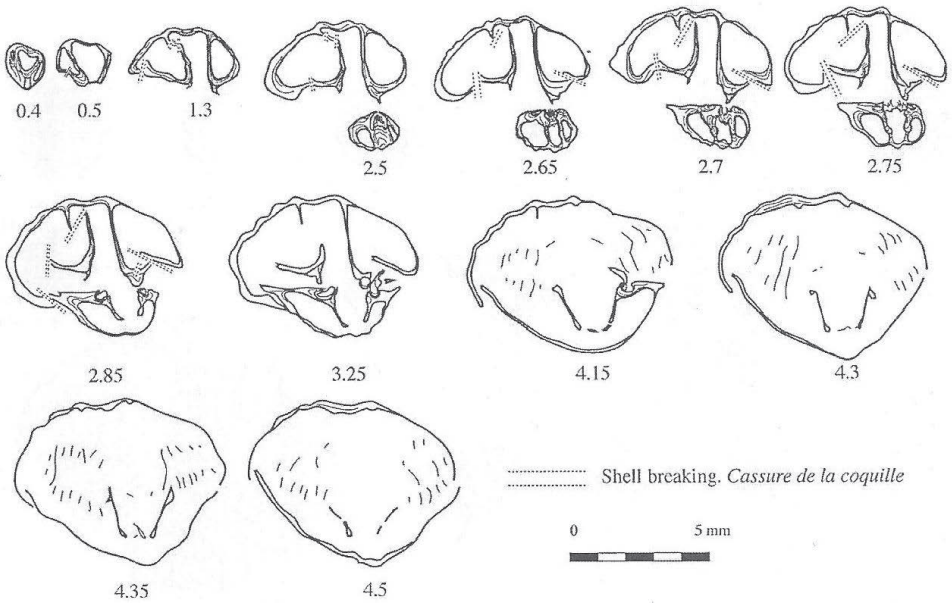


Fig. 394. *Brevispiriferina cabanillas* (Verneuil & Archiac), serial sections with distance from ventral umbo. From Emsian of Cantabrian Mountains, Spain. The crural plate and tabellae are separated by a small bulge representing the crural base in the figure 2.75. (García-Alcade (2005).

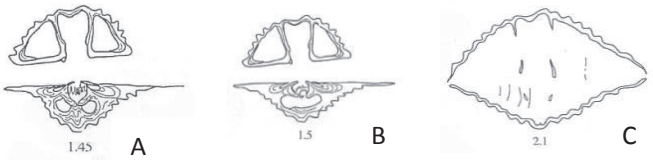


Fig. 395. *Ferronia subspeciosa* (Verneuil), transverse sections at distance measured in mm from ventral beak, x2 approx., from Emsian of Spain. (García-Alcalde 2005).

more transverse than another accompanying genus *Brevispinifera* Garcia-Alcade, with similar ornament and internal structures, and has finer plicae and lower ventral cardinal area. *Badainjarania* Zhan Yan, 1981 of Emsian age of Mongolia is of similar appearance, but lacks spinules.

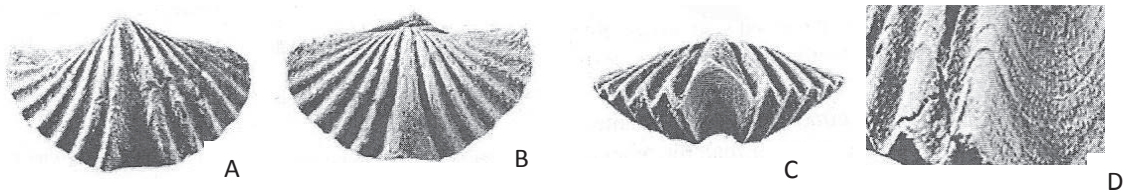


Fig. 396. *Ferronia arenesis* (García-Alcade), ventral, dorsal and anterior views (dorsal valve on top), x2, and detail of micro-ornament, x5. From Emsian of Cantabrian Mountains, Spain. (García-Alcade 2005).

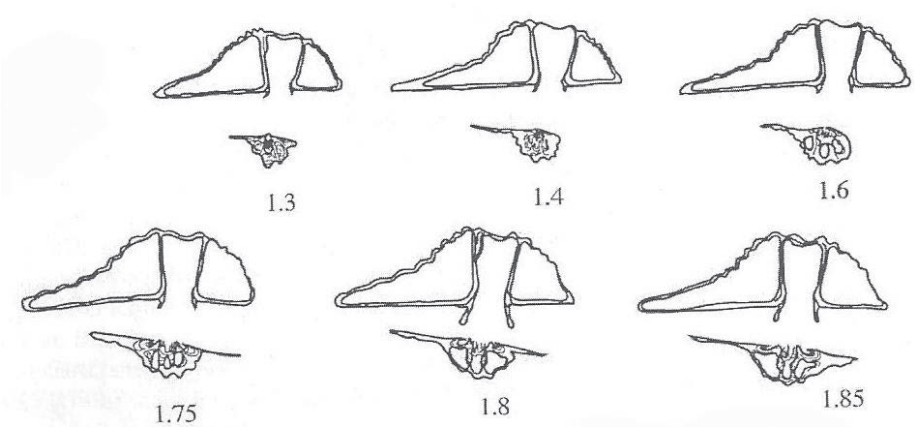
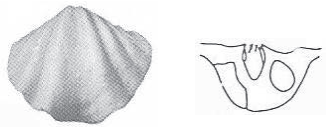


Fig. 397. Serial transverse sections of *Ferronia arenensis* García-Alcade, at distances shown in mm from ventral beak, x5. From Emsian of Spain. (García-Alcalde 2005).

In the small plicate genus *Mariaspirifer* Cherkesova, 1991, the tabellae arise from a massive median ridge, forming a septalium. The genus was referred to Reticulariopsinae by Carter & Gourvennec (2006c), and there is no sign of pleromal ridges or connector plate, though sections may be incomplete. Gourvennec in Carter & Gourvennec (2006c, p. 1852) described the crural plates (ie. tabellae) as long, which is interesting, seeing there was clearly a posterior cruralium. There is a massive ctenophoridium. *Qiansispirifer* Yang in Yang et al. 1977 is somewhat similar internally but needs further study.

Fig. 398. *Mariaspirifer dolganensis* Cherkesova. A, ventral valve x1. B, transverse section (magnification not certain), of dorsal valve from Emsian of Taimyr, Russia. (Cherkesova 1991).



Superfamily **RETICULARIOIDEA** Waagen, 1883

[Nom. correct. Gourvennec & Carter in Carter et al. 1994, p. 353, pro Reticulariacea Pitrat, 1965, p. 717, nom. promoveo ex Reticulariinae Waagen, 1883, p. 538].

Diagnosis: Short hinge, subrounded shape, plicae and costae absent or weak as a rule, micro-ornament of commargons with fine single-barrelled spines or pustules. Silurian (upper Llandovery) to Late Permian (Changhsingian).

Discussion: In the *Revised Brachiopod Treatise*, this superfamily included genera with single-barrelled spines and others with double-barrelled spines. They are separated herein. The superfamily was distinguished from Delthyroidea by Carter & Gourvennec (2006c) partly by the lack of plication, so that members of Reticularioidea tend to be subglobose, and subelongate, whereas members of Delthyroidea are transverse and plicate. This may well be a valid distinction, even though amongst Ingelarellidae of the Martiniimorphi genera varied considerably between plicate and not plicate, and even non-sulcate. Admittedly Carter et al. (1994) did not agree about the variability for ingelarellid genera, wishing to discriminate to family level between the two forms, before (thankfully) abandoning the Family Martiniopsidae Kotlyar & Popeko, 1967 in Carter & Gourvennec 2006b. Most constituent genera in Reticularioidea, unlike those assigned to Delthyroidea and Hysterolitoidea, are transversely oval in outline with shorter hinge and usually less plicate, although exceptions are offered by a number of Devonian genera, such as *Corylispirifer* Gourvennec and perhaps *Paraquadrithyris* Yang, with other examples. Regular commargons are more common than in Hysterolitoidea. Moreover no genera show fimbriate or frilly micro-ornament, and very few genera are capillate. Yet the relationship to Delthyroidea is complex, and there appears to be overlap with some Ambocoelioidea, leaving some uncertainty about the fullness of completely separate relationships. It is hardly surprising that over the years, the classification of Delthyridina has been in the state of flux. Not so long ago, Johnson, Boucot & Murphy (1973) suggested that some delthyrid shells, later regarded by the *Revised Brachiopod Treatise* and Schemm-Gregory (2011a) as at the core of the delthyroid superfamily group, such as *Howellella* (see p. 280), should be assigned to Reticulariidae because of the variable strength and obsolescence of their plications – both common features of early reticulariids. Micro-ornament appears to be very much the same in constituent families. Perry (1984) concluded that there was “no distinctive fine ornament present in most of the early reticulariids to distinguish them from members of the Delthyridae, although a few reticulariids show concentric lamellae that bear spine bases on their anterior edges. These spine bases are not continuous with the radially aligned ridges that cross the entire length of the numerous lamellae. The fine ornament of *Howellella* sp. 1 ….. appears to show radial striae continuous from one lamella to another, supporting the assignment of this species to …” Delthyridae. A number of genera included by the *Revised Brachiopod Treatise* in Reticularioidea, such as Obesarinae, are very close to Ambocoelioidea, and a number of genera such as *Emanuella* and *Ladjia,* that were regarded as ambocoelioid in the *Revised Brachiopod Treatise,* approach reticularioids.

Many members of the superfamily are of Devonian age, with spines finer and possibly shorter than in *Reticularia*, which is of Visean age. A marked change in delthyrial apparatus was introduced in a few members, with the development of a connector plate. Genus *Squamularia* is exceptional in lacking adminicula and tabellae, and is of Middle Permian age.

Family **RETICULARIIDAE** Waagen, 1883

[Nom. transl. Ivanova 1959, p. 59 ex Reticulariinae Waagen, 1883, p. 538].

Diagnosis: Non-plicate, with uniramous spinules. Lacking connector plate and pleromal ridges, adminicula generally present, median ridge but no ventral septum, tabellae present or absent: crural plates present. Silurian (Llandovery) to Middle Permian (Wordian).

Subfamily **RETICULARIINAE** Waagen, 1883

[Reticulariinae Waagen, 1883, p. 538].

Diagnosis: Non-plicate, lacking delthyrial plates or ridges. Uniramous spinules, adminicula present, median ridge but no ventral septum, crural plates present, not forming cardinal plate, no tabellae. Lower Carboniferous (Visean) to Lower Permian (Cisuralian).

Genera: *Reticularia* M'Coy, *Georgethyris* Minato, *Parareticularia* Li & Gu.

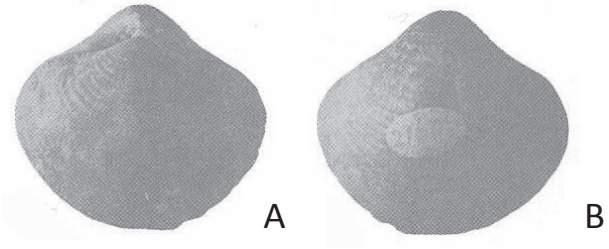


Fig. 399. *Reticularia imbricata* (Sowerby), ventral and dorsal aspects, x1, from Visean of England. (George 1932).

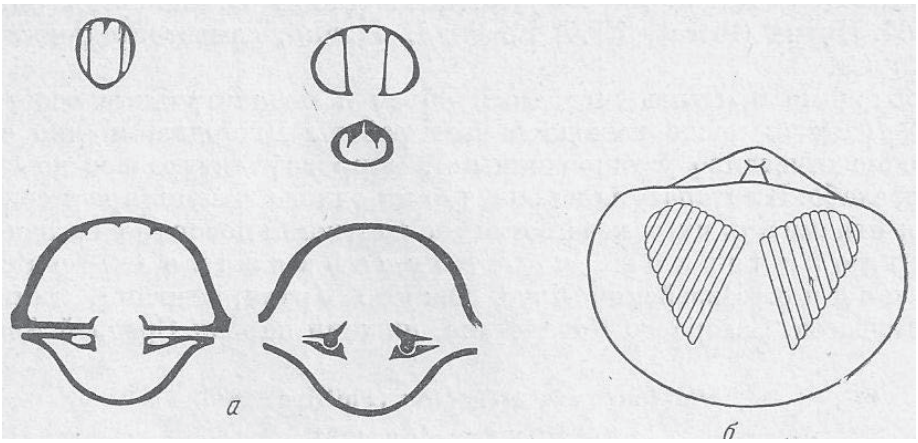


Fig. 400. *Reticularia imbricata* (Sowerby), transverse sections and sketch, dorsal valve below, x1. From Visean of England. (George 1932).

Discussion: The diagnosis is amended from the *Revised Brachiopod Treatise*: no tabellae are present, but crural plates are developed. The subfamily does not include *Squamularia* Gemmellaro, despite the interpretation of this genus by Carter & Gourvennec (2006c, p. 1848). (See p. 319).

Subfamily **RETICULARIOPSINAE** Gouvennec, 1994

[Reticulariopsinae Gourvennec in Carter et al., 1994, p. 355].

Diagnosis: Shells smooth, sulcate or plicate. No delthyrial ridges or plate or apical thickening. Dental plates, adminicula, crural plates, tabellae and ctenophoridium present. Silurian (Wenlock) to Middle Devonian (Givetian).

Genera: *Reticulariopsis* Fredericks (syn. *Tingella* Grabau), *Corylispirifer* Gourvennec, *Kymatothyris* Struve (syn. *Fallaxispirifer* Su), ?*Paraquadrithyris* Yang, *Pavdenia* Breivel & Breivel, *Prosserella* Grabau (syn. *Quasiprosserella* Boucot & Cocks), *Undispirifer* Havlíček (syn. *Nakazatothyris* Minato & Kato, ?*Gerolsteinites* Struve), ?*Undispiriferoides* Xian, *Waddingtonia* new genus, *Yeothyris* Struve.

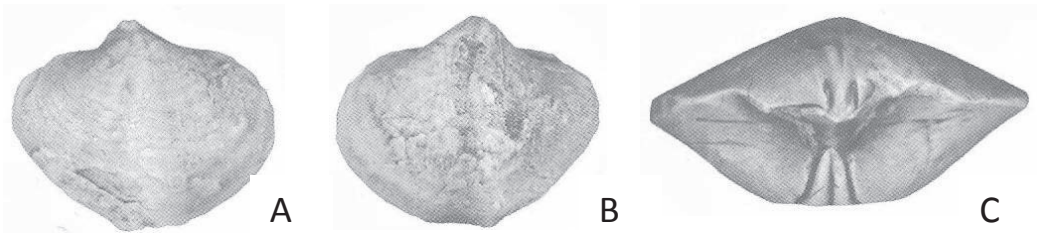


Fig. 401. *Reticulariopsis dereimsi* (Oehlert), dorsal and ventral aspects, x2, and posterior view of internal mould, dorsal valve on top, x3. From Emsian of Spain. (Gourvennec 1994b).

Discussion: A number of family groups flourished principally during the Devonian Period, and gave rise to scattered and much fewer survivors classed as Reticulariidae. Reticulariopsinae was grouped by Gourvennec in Carter & Gourvennec 2006c in the same family as Reticulariinae because both subfamilies lacked any form of delthyrial cover. But in that case it is hard to see why Rhenothyrinae should have also been classed in the same family, because at least some genera classed as Rhenothyrinae in the *Revised Brachiopod Treatise* developed a delthyrial cover or plates. The differences between Reticulariinae and Reticulariopsinae are doubtfully of familial rank, so the Gourvennec subfamily is not upgraded. Nevertheless, given the presence of sulcus and fold or open plicae and short tabellae, Reticulariopsinae is not particularly close to Reticulariinae, even though the two groups both lack delthyrial plates. The type species of *Reticulariopsis* has short tabellae (called crural plates by Gourvennec in Carter & Gourvennec 2006c, p . 1850), and for a well illustrated species from Australia, Strusz (1982, Fig. 28) showed moderately large crural plates, supported by possible very short and low tabellae. *Reticulariopsis* Fredericks,

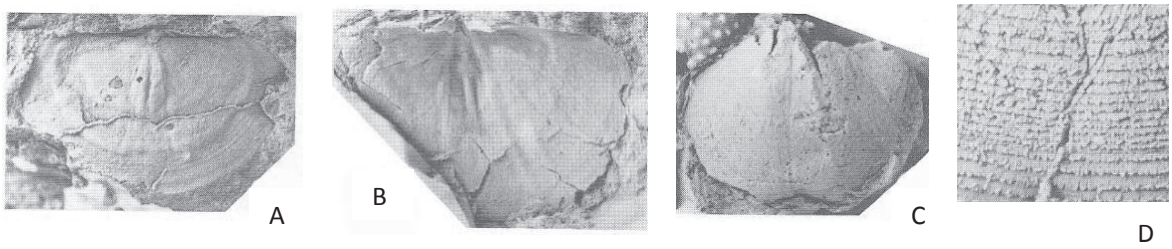


Fig. 402. *Reticulariopsis silurica* Strusz. A, B, internal mould and latex cast of dorsal valve, x5, x4, showing short tabellae in A. C, ventral internal mould, holotype, x5. D, micro-ornament, x15. From Wenlock of New South Wales, Australia. (Strusz 1982).

Corylispirifer Gourvennec, *Pavdenia* Breivel & Breivel, *Undispirifer* Havlíček, *Yeothyris* Struve and *Prosserella* Grabau have short adminicula and ventral septum, and short tabellae supporting the crural plates, whereas tabellae if present must be very short in *Kymatothyris* Struve. *Paraquadrithyris* Yang in Zhang et al., 1983 and ?*Undispiriferoides* Xian in Xian & Jiang (1978, p. 330) are not well known internally.

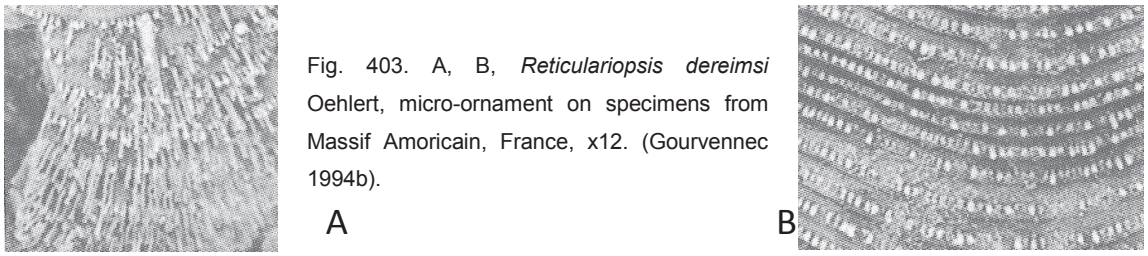


Fig. 403. A, B, *Reticulariopsis dereimsi* Oehlert, micro-ornament on specimens from Massif Amoricain, France, x12. (Gourvennec 1994b).

Prosserella Grabau, based on *P. modestoides* Grabau from the upper Emsian or lower Eifelian of Ontario, Canada, was assigned to the Reticulariopsinae in Carter & Gourvennec (2006c, p. 1850, fig. 1232.3a-f). Their figure (3d) of the ventral valve appears to show a well developed spondylium, but appearances are misleading – the two adminicula have either become conjoined, or matrix has not filled the gap between the two, and the appearance of the spondylium is provided by the edges of the delthyrium. The two other figures (3e, 3f) show long closely spaced adminicula and no spondylium. Tabellae are present, as in Fagerstrom (1971, p. 315). Micro-ornament consists of growth lines.

The genera *Undispirifer* Havlíček, 1957b and *Undispiriferoides* Xian in Xian & Jiang 1978 of Devonian age were included in Reticulariinae by the *Revised Brachiopod Treatise*, but are classed as Reticulariopsinae because it is preferred to exclude plicate shells and tabellate interior from Reticulariinae. Gourvennec in Carter & Gourvennec (2006c, p. 1849) pointed to ongoing research that might alter understanding of *Undispirifer*, mentioning genera that might prove synonymous. Micro-ornament consists of growth laminae and marginal

spines, and tabellae may be absent or short in *Undispirifer* and plate-like in *Undispiriferoides*.

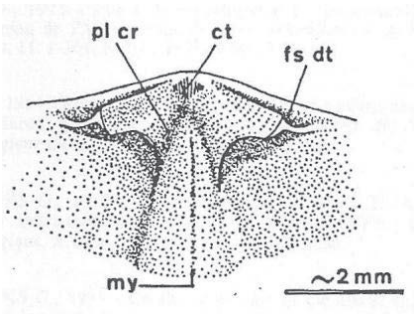
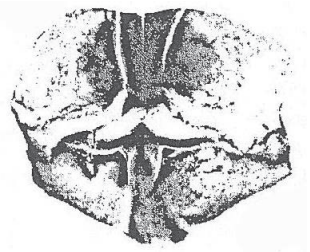


Fig. 404. A, *Reticulariopsis dereimsi* (Oehlert), showing dorsal apical apparatus, as reconstructed by Gourvennec (1994b, Fig. 4). From Emsian of the Amoricain Massif, France, x8. ct – ctenophoridium; fs dt – dental socket; my – myophragm; pl cr – "crural plate", ie. tabella with crural plate above.



B, *Reticulariopsis dereimsi* (Oehlert), showing interior of apex, with the dorsal features of the dorsal (lower) valve figured in Gourvennec (1994b, Fig. 4), as shown above.

Gourvennec in Gourvennec & Carter (2007, p. 2791) synonymized *Quasiprosserella* Boucot & Cocks in Boucot, Cocks & Racheboeuf (1999) with *Prosserella* Grabau. On this page of the *Revised Brachiopod Treatise*, *Prosserella* was shown to be a member of Rhenothyridinae Gourvennec, "as in Carter & Gourvennec (2006c, p. 1852)", but this was an editorial error (Remy Gorvennec, pers. comm.), and *Prosserella* was and is regarded, correctly according to available evidence, as a member of Reticulariopsinae.

Genus ***Waddingtonia*** new genus

Name: Named for Janet Waddington.

Diagnosis: Fine capillae over commargons between growth lamellae, no spines. Adminicula well developed, tabellae very short, ctenophoridium with few laminae, muscle field elongate in both valves.

Type species*: Reticulariopsis*? *warreni* Perry, 1984, p. 121 from Delorme Formation (Lochkovian, Pragian) of Yukon Territory, Canada, here designated.

Discussion: The genus is close to *Reticulariopsis*, and is distinguished principally by the presence of fine capillae over the shell surface, covering the treads of growth laminae that may become well defined anteriorly. In addition the muscle fields are elongate, and the tabellae shorter than in the type species of *Reticulariopsis,* and the ctenophoridium is less developed. These features vary somewhat between genera placed within the subfamily, but no other genus displays radial capillae. Identical material was recorded by Lenz (1977, p. 128), and Perry pointed to specimens with strong capillation that had been described by Johnson (1970, p. 208) from central Nevada, though these appear to have a longer hinge, pointing to a different species.

Commargons are well developed in this genus (see Fig. 405D), suggesting a possible source for Reticulariinae and Squamulariinae, but members of these subfamilies lack capillae.

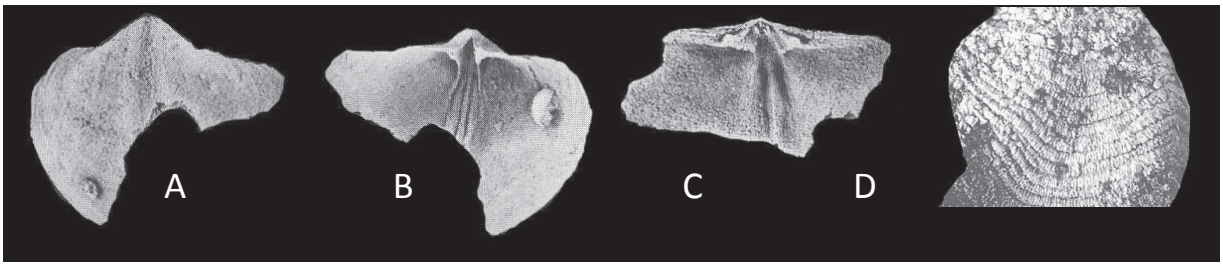
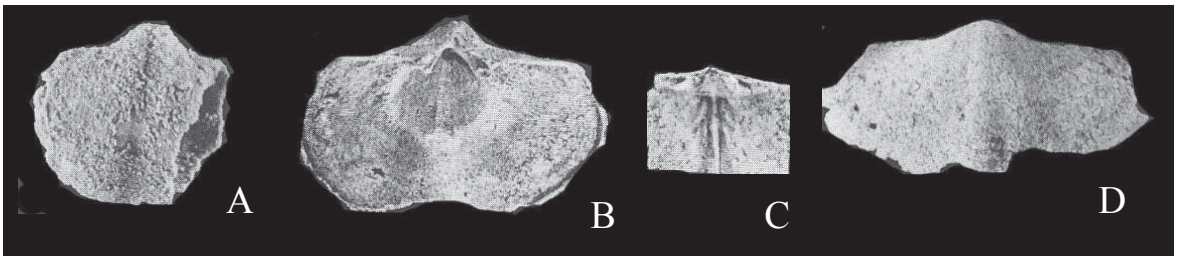


Fig. 405. A-C, *Waddingtonia warreni* (Perry). A, B, external and internal views of ventral valve, x2.5. C, dorsal interior, x2.5. From Delorme Formation (Lochkovian-Pragian), Yukon Territory, Canada. (Perry 1984). D, *Waddingtonia* sp., part of ventral valve, showing external capillae, x3. From Lower Devonian of central Nevada. (Johnson 1970).

Subfamily **WARRENELLINAE** new subfamily

Name genus: *Warrenella* Crickmay, 1953a, p. 596 from Upper Devonian (Frasnian) of Alberta, Canada, here designated.



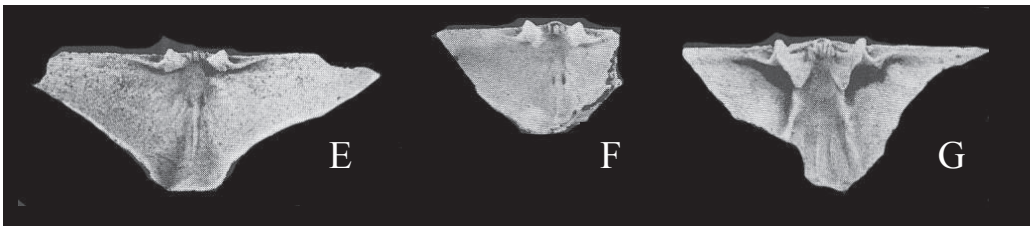


Fig. 406. *Warrenella sekwensis* Ludvigsen & Perry. A, ventral valve, x4.3. B, inner ventral valve, x1.1. C, D, dorsal interior and exterior, x1.1. E, dorsal interior, x1.1. F, G, dorsal interior, x3.3. From Zlichovian (ie. lower Emsian) of Mackenzie district, Canada. (Perry 1984).

Diagnosis: Deltidial plates or deltidium, micro-ornament of tubercles. Ctenophoridium, dental plates, adminicula, short tabellae in some species and genera. Cruralium may be developed. Silurian (upper Llandovery) to Lower Carboniferous (Tournaisian).

Genera: *Warrenella* Crickmay (syn. ?*Minatothyris* Vandercammen), *Warrenella* (*Warrenellina*) Brice*, Deltospirifer* Wang & Rong, ?*Eohowellella* Lopushinskaya, *Gerothyris* Struve,

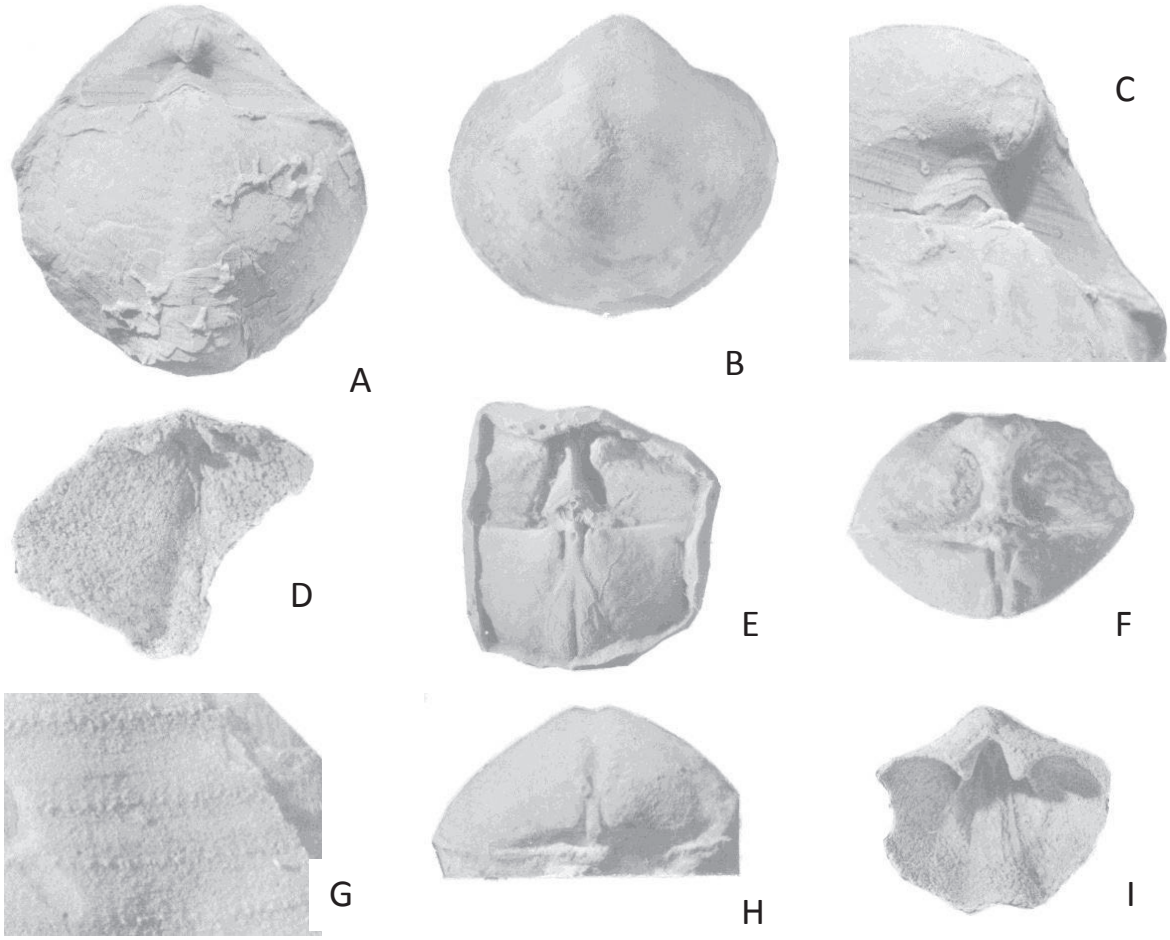


Fig. 407. A-C, E, *Warrenella weigelti meeki* Ludvigsen & Perry. A, dorsal view, x1. B, ventral view, holotype, x1. C, oblique view of hinge, x2. E, internal mould, dorsal valve below, x1. D, 1, *W. sekwensis* Ludvigsen & Perry. D, dorsal interior, x1.25. I, ventral interior, x 1. F, G, H, *W. kirki* (Merriam),D, dorsal interior, x1.25. F, posterior view, internal mould of both valves, x1.25. G, micro-ornament, x12. H, dorsal internal mould with tabellae, x1.5. From Devonian of Western Canada. (Ludvigsen & Perry 1975).

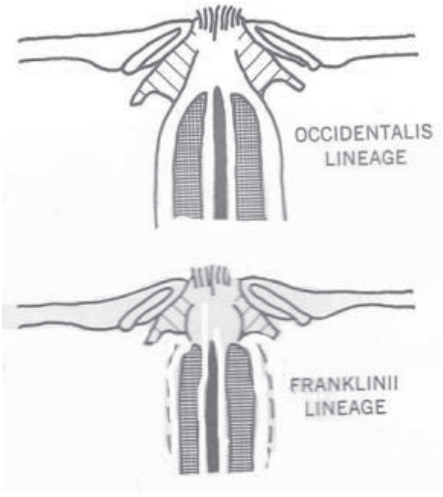


Fig. 408. Schematic diagram in Ludwigsen & Perry (1975) showing differences in disposal of “crural plates” relative to adductor field in lineages of *Warrenella*, which aggregate a number of species.

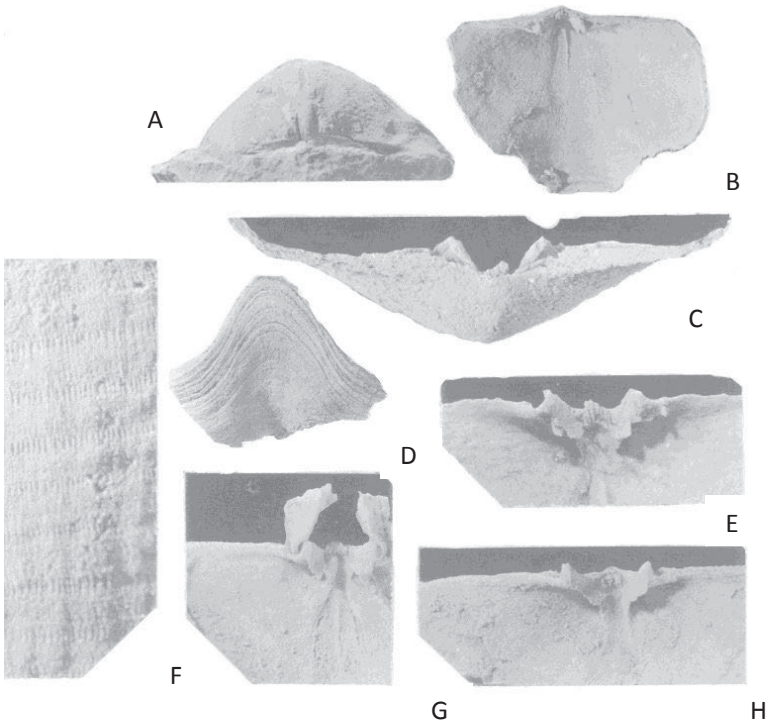


Fig. 409. *Warrenella quadrata* Ludvigsen & Perry. A, internal mould, dorsal valve, x1. B, dorsal interior, x1.2. C, dorsal interior, x2.5. D, fragment of ventral anterior, x1. E, dorsal interior, x2.5. F, micro-ornament, x8. G, dorsal interior x3.5. H, dorsal cardinalia, x3.5. Specimens from Devonian of Western Canada. (Ludvigsen & Perry 1975).

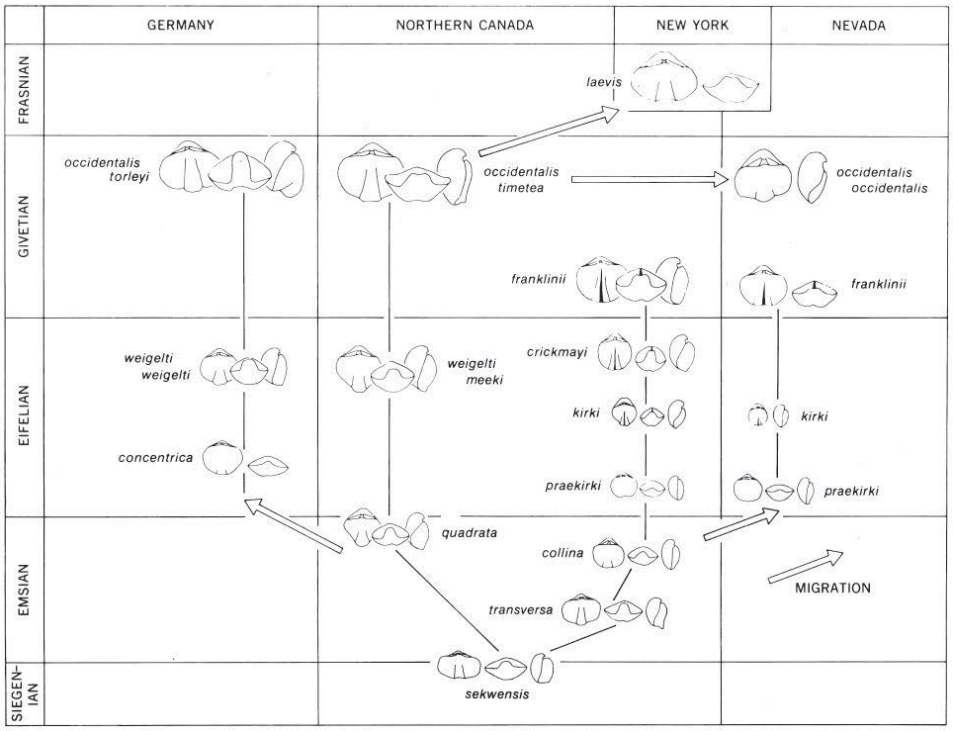


Fig. 410. Chart showing the suggested phylogeny of *Warrenella* lineages, from Ludwigsen & Perry (1975, text-fig. 14).

Fig. 411. *Warrenella eclectea* Crickmay, transverse sections x1.5, dorsal valve underneath, from Frasnian of Alberta, Canada. (Crickmay 1968).

Grebenella Modzalevskaia & Besnossova, ?*Lubricospirifer* Chen & Yao, *Minispinusuria* new genus, *Nordella* Liashenko, ?*Puanospirifer* Jiang, *Spirinella* Johnston (syn. *Ectatoglossa* Chu), *Uexothyris* Struve.

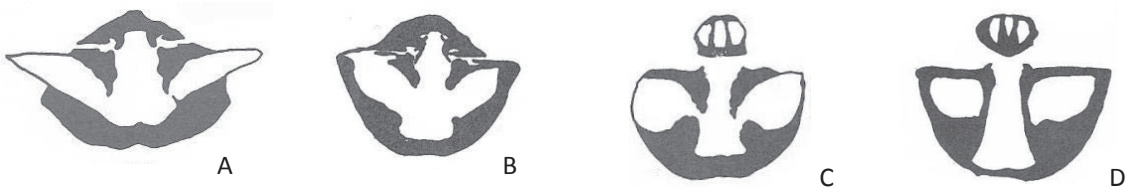


Fig. 412. Transverse sections of *Warrenella* specimens from Devonian of Western Canada, x1. A. *W. transversa* Ludvigsen & Perry, x1. B, *W. crickmayi* Ludwigsen & Perry, x1.5. C, *W. quadrata* Ludwigsen & Perry, x1. D, *W. weigelti meeki* Ludwigsen & Perry, x0.8. (Ludvigsen & Perry 1975).

Discussion: This subfamily is distinguished from Reticulariopsinae by the deltidial plates, and is distinguished from Rhenothyrinae by the lack of pleromal ridges. *Warrenella* Crickmay, 1953a is shown to have highly variable tabellae, and a small cruralium is often developed. Cross-sections of the type species of *Warrenella* provided by Crickmay (1968, pl. 5, fig. 5-15) reveal crural plates and no tabellae in one specimen, and in another, a ctenophoridium on a raised tiny platform, probably the pillar of the process, with sockets and a small cavity each side. There are no tabellae. The type species *W. eclectea* Crickmay shows a small septalium (Fig. 411), and no *Warrenella* shows a connector plate. *Warrenella sekwensis* Ludvigsen & Perry, 1975, further figured by Perry (1984, pl. 41, fig. 1-28) from northwest Canada, shows a long and moderately high ridge each side of the dorsal muscle field (see Perry 1984, pl. 41, fig. 4, 5, 7), absent from other specimens (see pl. 41, fig. 8, 9, 11 etc.). Perry (1984, p. 121) noted that the crural plates joined the “muscle-bounding ridges” in most small specimens, whereas in large specimens the crural plates were mostly free of the valve floor. It was suggested that the muscle-bounding (ie. tabellar) plates were buried by valve thickening in large specimens. Or they could have been resorbed, or equivalent to myosepta (Waterhouse & Chen 2007). In one specimen of *Warrenella sekwensis*, distinct tabellae are developed (Perry 1984, pl. 41, fig. 28, 38). Whether a degree of variation in shape and sulcus-fold in different specimens might encourage discrimination of the material may require further

analysis, although that may be unlikely, because the material has already been intensively studied. A wide convex delthyrial cover is developed (Perry 1984, pl. 41, fig. 15; Ludvigsen & Perry 1975, pl. 18, fig. 9), and deltidial plates are shown in some *Warrenella* (eg. Ludvigsen & Perry 1975, pl. 12, fig. 8,12), to suggest that the cover plate is a deltidium. An apical callus was reported in the *Revised Brachiopod Treatise.* A dorsal septum is moderately developed in at least some specimens.

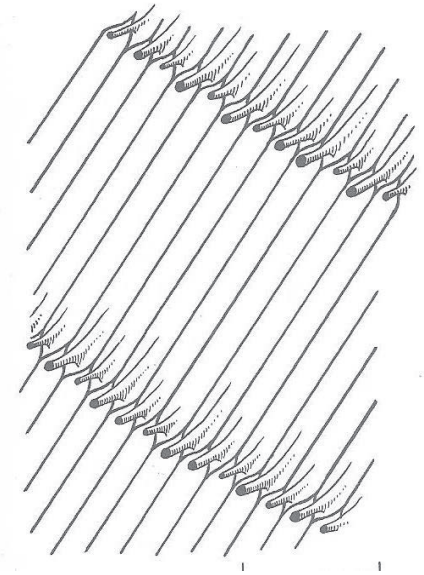


Fig. 413. *Warrenella transversa* Ludvigsen & Perry, showing radial capillae and commarginal rows of spines with slightly prolonged bases, x20. From Devonian of Western Canada. (Ludvigsen & Perry 1975).

Minatothyris Vandercammen was regarded as a possible synonym of *Warrenella* by Gourvennec in Carter & Gourvennec (2006c, p. 1857), and *M. maureri* (Holzappel, not sensu Grabau), now *Minatodina* n. gen., very close to the type species, has a septalium like that indicated for type *Warrenella*. Deltidial plates or convex deltidium are developed in *Minatothyris* as in *Warrenella*. *Deltospirifer* Wang & Rong, 1986 does not seem to have tabellae, unless they have been buried in secondary shell. There are low crural plates. It is deeply sulcate and has an arched delthyrial cover plate across the delthyrium. *Nordella* Liashenko is in the same category, with no tabellae, low crural plates, gentle sulcus and what look like deltidial plates, with a convex deltidium recorded in the *Revised Brachiopod Treatise*. Gourvennec in Carter & Gourvennec (2006c, p. 1855) noted uncertainty over the presence of a ctenophoridium. *Deltospirifer* and *Warrenellina* have signs of plicae, the latter being regarded as a subgenus of *Warrenella*. But as the type species of *Warrenella* (*Warrenella*) also has signs of low plicae on the dorsal valve and near the ventral beak, any distinction between the two taxa according to that criterion, alleged to be of subgeneric standing, seems to be of limited value. *Grebenella* Modzalevskaia & Besnossova, 1992 shows short adminicula and tabellae. Genera are close to each other in micro-ornament, consisting of growth lamellae and marginal spines in *Deltospirifer, Nordella, Spirinella*, and *Warrenella,* with marginal spines in *Puanospirifer*, and marginal papillae in *Uexothyris,* growth lamellae in *Grebenella, and* growth lamellae and radial striae in *Eohowellella*.

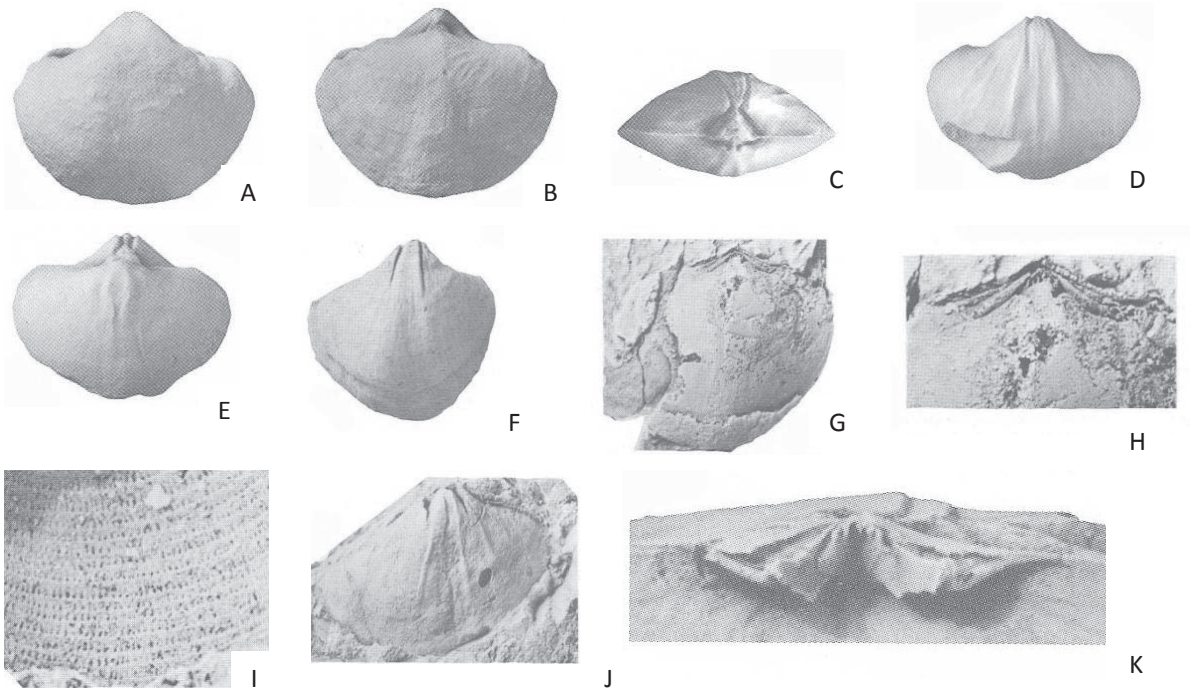


Fig. 414. *Spirinella caecistriata* Johnson. A-B, ventral and dorsal views, x1.5. C-E, posterior, ventral and dorsal views of specimen, x1.5. F, ventral internal mould, x1.5. G, H, dorsal internal moulds, x3 and x6. I, micro-ornament, x16. J, ventral interior, x1.3. K, latex cast of dorsal cardinalia, x7. From lower Ludlow of New South Wales. (Strusz 1984, 1985).

The east Australian genus *Spirinella* Johnston, 1941, revised and illustrated by Strusz (1984), has large crural plates. Strusz (1984, Fig. 19H, I) illustrated the short "nicks" below the ctenophoridium in internal moulds, suggestive of possible very short tabellae or impinging crural plates. Micro-ornament involves closely spaced commarginal laminae with fine spine bases. Unfortunately the delthyrial cover is not preserved, but there appear to be low deltidial plates, and Perry (1984, p. 123) recorded deltidial plates in a Canadian species.

A genus particularly in need of clarification is *Puanospirifer* Jiang, in Xian & Jiang, 1978, said to have apical thickening under the umbo, which might imply a connector plate as in Rhenothyrinae or Eoreticulariinae (see pp. 322, 325), but verification is needed. Gourvennec in Carter & Gourvennec (2006c, p. 1855) suggested that *Puanospirifer* Jiang might be congeneric with *Deltospirifer*, which certainly seems possible, and it also lacks tabellae ("crural plates"). There are growth laminae and marginal spines, short dental plates and adminicula, and no tabellae. *Gerothyris* Struve, 1970, p. 537 from Eifel (Eifelian) of Germany, has micro-ornament of irregular rows of small spinules separated by bands of much finer papillae. It is smooth without sulcus or fold, and does not clearly show any tabellae on the internal mould figured in Carter & Gourvennec (2006a, Fig. 1233.2g). Adminicula ("dental plates") were described as short. Similar micro-ornament was illustrated for *Tingella concentrica* (Schnur, 1853) by Vandercammen (1958, pl. 1, fig. 22, 23) from upper Couvinian of Fond des Valaines, Belgium, a species with similar distinctive short excavated ventral

muscle field, and displaying tabellae (Vandercammen 1958, Fig. 9). *Tingella* Grabau was synonymized by Gourvennec in Carter & Gourvennec (2006c, p. 1850) with *Reticulariopsis* Fredericks, which has short tabellae.

Lubricospirifer Chen & Yao, 1999 is difficult to classify, because of inadequate data over the morphology. It comes from the Lower Devonian (Emsian) of south China. The genus is gently plicate, unlike members of Warrenellinae, but does approach members of this subfamily in the presence ofmarginal spines, adminicula, ctenophoridium, and a septalium. Gourvennec in Gourvennec & Carter (2007, p. 2791) placed the genus in Subfamily Rhenothyridinae, but described the delthyrium as open, and wrote of "faint delthyrial ridges". There is no indication of pleromal ridging or connector plate, nor of tabellae, and Rhenothyrinae includes no plicate genera, being in that respect like Warrenellinae, but differing in delthyrial apparatus and internal cardinalia.

Genus ***Minispinusuria*** new genus

Name: mini – small; spina – thorn, Lat.

Diagnosis: Small shells with ventral interarea of moderate height, delthyrium large, bordered by two deltidial plates which do not fuse medianly, distinct low lateral plicae. Adminicula, short crural plates and tabellae, no cruralium, no connector plate or pleromal ridges.

Type species: ?*Thomasaria voiseyi* Roberts, 1963, p. 21, from Lower Carboniferous Bingleburra Formation (upper Tournaisian), New South Wales, here designated.

Discussion: The type species has been described by Roberts (1963, p. 21, pl. 4, fig. 5-11), with additional material compared to the species by Campbell & Engel (1963). The species has minute spines, lirae, and low subplicae over the lateral slopes, and the sulcus bears a median groove. The delthyrium was said to be like that of Belgium species described as *Thomasaria* by Vandercammen (1956), with a deltidial plate each side, not fused. *Thomasaria alteumbona* Stainbrook, the type species of *Thomasaria*, has a delthyrium which is closed by two apical ridges that fuse medianly, and the remainder of the delthyrium is covered by a separate plate. Type *Thomasaria* has commarginal growth increments and fine spines, whereas *Minispinusuria* has tiny pustules and radial lirae, and the Belgium material has micro-spines in commarginal rows. In *Thomasaria*, there are short flaring socket ridges, and thick crural bases according to Cooper & Dutro (1982). In the new genus, there are two short tabellae, noted as being longer in allied material described by Campbell & Engel (1963) from the same general region. No cruralium has been observed in the Australian material, unlike the cruralium indicated for *T. rockymontana* (Warren) by Crickmay (1967). Crickmay (1967) recorded a convex plate over the delthyrium in *rockymontana*, and reported radial as well as commarginal lirae and minute spinules. The presence of a connector plate or a connector plug in both the North American and Belgium species of *Thomasaria* shows that Roberts' species is very different.

Campbell & Engel (1963) drew attention to two species of Tournaisian age from Queensland that were considered to be close to *Thomasaria voiseyi* of Roberts, and

described as *Dimegelasma elegante* (Maxwell (1954, p. 2, fig. 1-3) and *D. kennedyense* Maxwell (1954, p. 25, pl. 2, fig. 20-22). These have low plicae and fine but strong radial lirae, and adminicula, but the illustrations fail to clarify the nature of the dorsal cardinalia, which possibly differ. The sulcus and fold are conspicuous and broad in these Maxwell species.

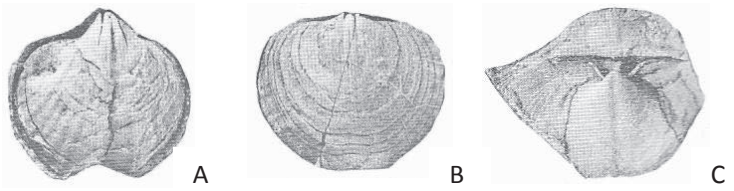


Fig. 415. *Minispinusuria voiseyi* (Roberts), ventral internal mould, x1.5, dorsal internal mould, x1.7 and latex cast of posterior exterior, x2. From Tournaisian of New South Wales, Australia. (Roberts 1963).

The genus is distinguished from other closely related genera by the presence of low regular plicae with narrow sulcus and low broad fold, and is the youngest member of the subfamily.

Subfamily **VADUMINAE** new subfamily

Name genus: *Vadum* Strusz, 1982, p. 136 from Silurian (Wenlock) of New South Wales, Australia, here designated.

Diagnosis: Open delthyrium, short very high adminicula and dental plates, no tabellae, dental sockets. Silurian (Ludlow, Wenlock).

Genera: *Vadum* Strusz, *Chnaurocoelia* Johnson, Boucot & Murphy, ?*Protoreticularia* Su.

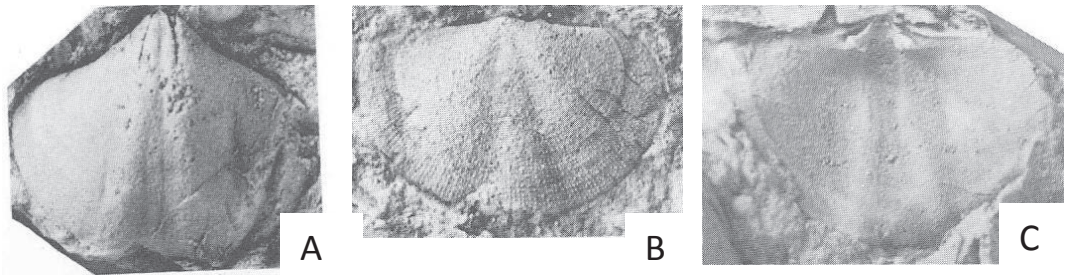


Fig. 416. *Vadum coppinsense* Strusz. A, ventral internal mould. B, latex exterior of dorsal valve, showing micro-ornament. C, latex cast of dorsal interior. Specimens x8. From Wenlock of New South Wales, Australia. (Strusz 1982).

Discussion*: Vadum* Strusz, 1982 has short high adminicula without any clear indication of a connector plate, nor cruralium. The cardinal process is bilobed, and described as crescentic. There are well-formed crural plates which pass into socket plates, labelled outer hinge plates in Strusz (1982, Fig. 31), often resting on the floor, but without visibly discrete tabellae. The

crural bases may be seen at the inner anterior end of the crural plates, and were noted as being occasionally sessile. Small blunt papillae are radially and commarginally arranged.

There are similarities to members of Warrenellinae, but differences include the lack of a ctenophoridium and consistent lack of tabellae and deltidial plates.

Vadum Strusz*, Chnaurocoelia* Johnson, Boucot & Murphy and possibly *Protoreticularia* Su were included in Eoreticulariinae by Gourvennec in Carter & Gourvennec (2006c, p. 1860), but do not have a cruralium, and there is no sign of a connector plate or median dorsal septum. *Chnaurocoelia* has high adminicula and the socket plates and short platform extends along the posterior hinge, with no ctenophoridium and no tabellae. Micro-ornament is not known. In their broadly oval shape the species are reticularioid in appearance, even though the bilobed cardinal process opens the possibility of ambocoeliiform affinities.

Protoreticularia Su, 1980 of Silurian (Ludlow) age might be allied, and although it is poorly known as far as aspects of the internal dorsal valve is concerned, there is no median septum, and almost certainly no cruralium, no median septum and no tabellae. There are either short crural plates or a cardinal plate, but no certainty over either, and micro-ornament was shown by Carter & Gourvennec 2006c, Fig. 1237.2d as having growth lamellae and marginal spines. Givensuch attributes, the genus is moved from Eoreticulariinae as in the *Revised Brachiopod Treatise*. Gourvennec stated that the genus had lateral plicae, not visible in figures.

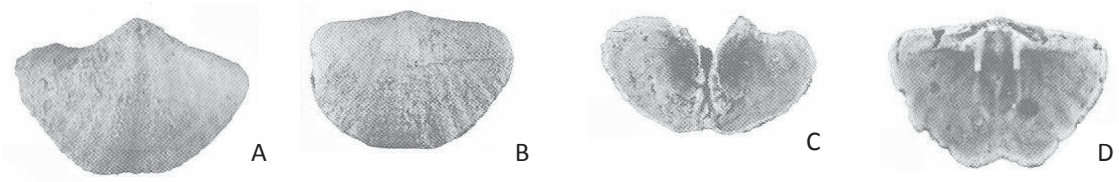


Fig. 417. *Chnaurocoelia transversa* Johnson, Boucot & Murphy, ventral (A), dorsal (B), ventral internal (C) and dorsal internal (D) views, x5. From Ludlow of Nevada, United States. (Johnson, Boucot & Murphy 1976).

Subfamily **OBESARIINAE** Gouvennec, 1994d

[Obesariinae Gourvennec in Carter et al., 1994, p. 356].

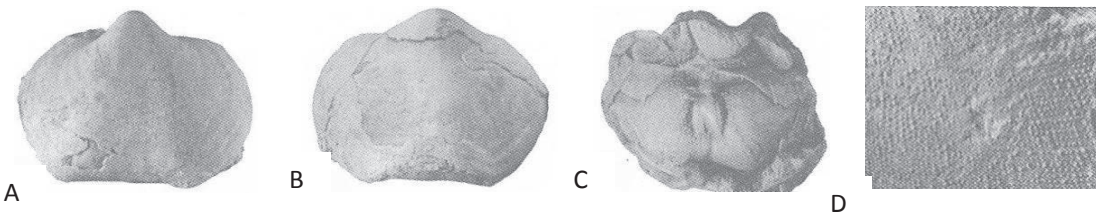


Fig. 418. *Obesaria indifferens obesa* (Barrande). A, B, ventral and dorsal views, x1.5. C, internal mould showing muscle field, x1. D, micro-ornament, x10. From Eifelian of Czech Republic. (Havlíček 1959).

Diagnosis: Non-plicate, radial rows of granules and spinules. Apical thickening in ventral valve, but otherwise open delthyrium. Low dental plates and crural plates. lacking adminicula, tabellae and ctenophoridium. Silurian (upper Wenlock) to Middle Devonian (Eifelian).

Genera: *Obesaria* Havlíček (syn. *Obessaria* Havlíček (lapsus calami)), *Alaskospira* Kirk & Amsden (syn. *Proreticularia* Havlíček), ?*Quasimartinia* Havlíček (syn. *Candispirifer* Havlíček).

Discussion: Members of Obesariinae require further study to determine their nature and true affinities. Four genera were placed in the subfamily in the *Revised Brachiopod Treatise*, as a subfamily in Reticulariidae, and included ?*Echinocoeliopsis* Hamada (syn. *Plicambocoelia* Boucot & Brunton in Wongwanich et al.) which is now moved to Ambocoeliidae (p. 369). Circumscribed by Gourvennec in Carter & Gourvennec (2006c, p. 1827) as lacking dental plates, members of Obesariinae have low dental plates and low crural plates, but no cruralium, tabellae or adminicula. The group differs from most Reticulariidae, and has apical thickening in the ventral valve, of an unspecified nature, which leaves classification possibilities in a vacuum. Critically no cardinal process or ctenophoridium is developed. In addition to the lack of primitive cardinal process let alone more elaborate ctenophoridium, the micro-ornament in *Obesaria* Havlíček consists of minute pustules, spread in radial rows

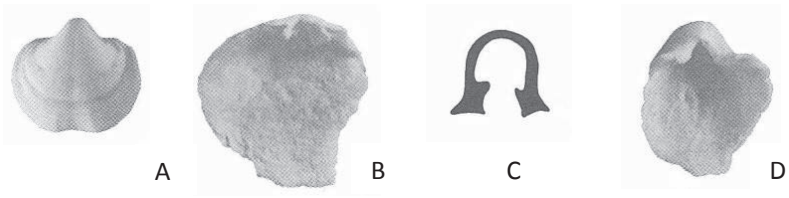


Fig. 419. A, C, *Quasimartinia candida* (Havlíček). A, ventral view, x1.5. C, section of ventral valve, x3. B, D, *Q. rectimarginata* Havlíček. B, dorsal interior, x3.5. D, ventral interior, x3.5. From Pragian of Czech Republic. (Havlíček 1959).

over the surface, as in Ambocoelioidea. There may be reservations over the presence and nature of ventral plates, because the figure in Gourvennec in Carter & Gourvennec (2006c, Fig. 1236.1g) suggests that dental plates and conceivably even adminicula could have been present, largely buried in secondary shell, and comparison may be made between the figure for *Obesaria* in Gourvennec in Carter & Gourvennec (2006c, Fig. 1236.1g) with the figure for *Warrenella* (*Warrenella*) in Gourvennec in Carter & Gourvennec (2006c, fig. 1235.2f), and *Warrenella* has adminicula. But Gourvennec's judgement that there are no adminicula is accepted, and indicates that there has been exceptional secondary thickening. One suggestion of a delthyrimorphian rather than ambocoelimorphian alliance might come from the nature of the ventral muscle field, which could prove to be comparatively broad, rather than elongately linear, but that requires verification.

Other genera associated with *Obesaria* in the *Revised Brachiopod Treatise* do not suggest any possible presence of adminicula or indeed exceptional secondary thickening, so

that members are like or at least mimic members of Ambocoelioidea. *Alaskospira* Kirk & Amsden, one of the oldest members, commencing in upper Wenlock, has dental plates and tiny if any crural plates, and no adminicula or tabellae. Gourvennec's claim that *Alaskospira* Kirk & Amsden has no dental plates is not correct, as shown by transverse sections in Kirk & Amsden (1952). Tiny spines are said to lie in radial rows, like *Obesaria* by Gourvennec in Carter & Gourvennec (2006c, p. 1857), presumably correcting Kirk & Amsden (1952, p. 61) who stated that there were no spines. According to Savage (1969), there were no spines in his material described as *Proreticularia beddiei* Savage, which belongs to a genus synonymized with *Alaskospira*, so that his three figures (pl. 90, fig. 31, 33, 35) that suggest spines must be misleading. But he definitely erred in his claim that there were no dental lamellae, for such are clearly illustrated in Savage (1969, pl. 90, fig. 29). There are very high crural plates, but no tabellae, and a multilobed cardinal process, unlike the arrangement in type *Alaskospira*, which is said to lack a ctenophoridium (Gourvennec in Carter & Gourvennec 2006c, p. 1857). Unfortunately details of the shape and width of the ventral muscle scars were not provided, though the adductor scars seem in an illustration (pl. 90, fig. 29) to be long and slender, and Kirk & Amsden (1952, p. 61) recorded a long ventral median ridge, presumably a seat for adductor scars, and outer narrow deeply impressed diductor scars, as long as a third of the valve in length. Savage (1969) stated that there were two pair of dorsal adductor scars.

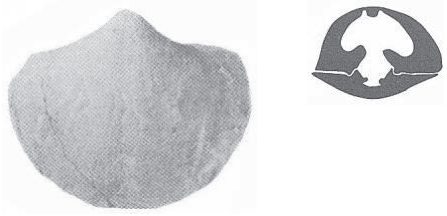


Fig. 420. *Alaskospira dunbari* Kirk & Amsden, ventral view, x2. B, transverse section, dorsal valve below, x1.5. From Wenlock to Emsian, Alaska. (Kirk & Amsden 1952).

Echinocoeliopsis Hamada, 1968b, which ranges from unreliably dated upper Devonian into Mississippian, has similar ornament and sturdy socket plates on a small platform, that looks very close to the arrangement of cardinalia in various ambocoeliids, especially Ogilviecoelini (p. 366), though it was classed as Obesariinae in the *Revised Brachiopod Treatise*. *Quasimartinia* Havlíček could prove to be close to *Echinocoeliopsis*.

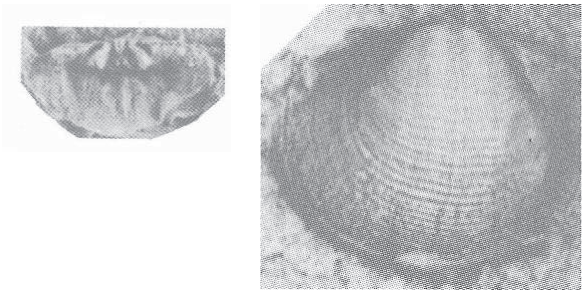


Fig. 421. A, B, *Echinocoeliopsis sculpta* Hamada. A, dorsal interior, x5. B, ventral valve, x5. From Carboniferous of Malaysia. (Hamada 1968b). See also Fig. 495, p. 370.

Subfamily **SQUAMULIFERINAE** new subfamily

Name genus: *Squamulifera* Gemmellaro, 1899, p. 189 from Sicily (Wordian), here designated.

Diagnosis: Single-barrelled spines aligned along anterior edge of each commargon. No adminicula or tabellae. Middle Permian (Wordian).

Genus: *Squamulifera* Gemmellaro.

Discussion: *Squamularia* Gemmellaro is deemed to be allied to Reticulariinae, because as Carter & Gouvennec (2006c, p. 1848) showed, *Squamularia* lacks double-barrelled spines, and is ornamented by growth lamellae fringed by numerous fine uniramous radial spines. Furthermore they contradicted the assertion by Shen et al. (2003a) that the spire was laterally directed: it was said to be postero-laterally directed, just as claimed by Liao (1980). Yet Shen et al. (2003a) were surely correct in pointing to the laterally directed spiralia figured for the type species by Gemmellaro (1899). By contrast, species assigned to *Reticularia* by Gemmellaro (1899, pl. 35) do have spiralia directed postero-laterally. Perhaps there was confusion on the part of Gemmellaro (1899) on the specific identities of two genera – or Carter & Gouvennec (2006c) have confused *Reticularia* with *Squamularia*. Amongst these conflicting views, one must be inclined to accept the interpretation of the *Revised Brachiopod Treatise*, in the hope that the authors were able to re-examine type *Squamularia*, but although the claim was made that their material was topotype, that does not guarantee that the specimens were conspecific or congeneric – and their material clearly differs externally in minor details from Gemmellaro's original specimens. In Carter & Gourvennec (2006c, p. 1866). *Squamularia* was stated to be of Lopingian age: in fact it is Guadalupian, with classic Wordian ammonoids, such as *Waagenoceras*. It is not certain whether or not a connector plate is developed.

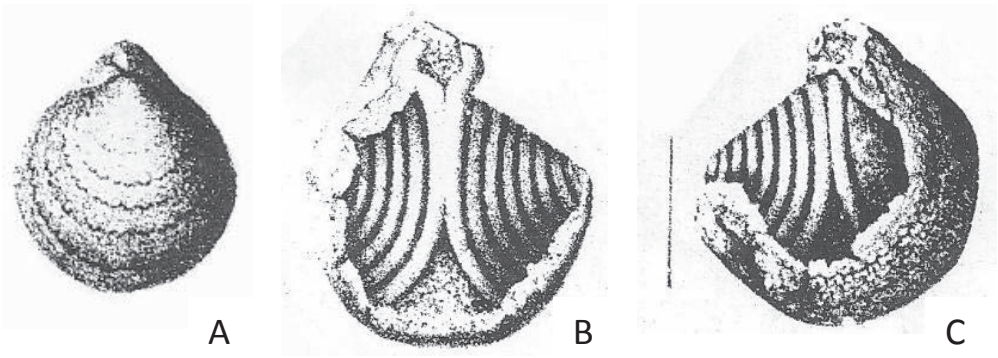


Fig. 422. *Squamularia rotundata* Gemmellaro, specimens x2.5 approx. figured by Gemmellaro (1899), showing laterally coiled spiralia. From Guadalupian of Sicily.

This subfamily is like Obesariinae in lacking adminicula and tabellae, but is much closer to the normal reticulariid ornament in other aspects. There is a clear need for clarification of the genus, given the differing interpretations on the orientation of the spiralia, and what may prove to have confusion over the morphology of the genus.

Family **THOMASARIIDAE** Cooper & Dutro, 1982

[Thomasariidae Cooper & Dutro, 1982, p. 102].

Diagnosis: Single-barrelled spines, distinguished by connector plate or plug, as well as deltidia. Long adminicula, ctenophoridium. Upper Devonian (Frasnian).

Subfamily **THOMASARIINAE** Cooper & Dutro, 1982

[Nom. transl. hic ex Thomasariidae Cooper & Dutro, 1982, p. 102].

Diagnosis: Spinose shells with connector plate or plug, as well as deltidia or deltidial plates. Long adminicula, ctenophoridium and cruralium, no tabellae. Upper Devonian (Frasnian).

Genus: *Thomasaria* Stainbrook.

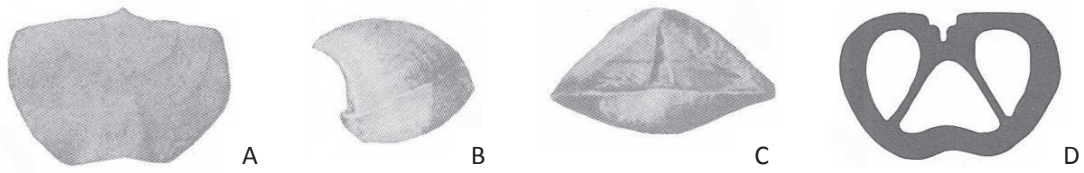


Fig. 423. *Thomasaria altumbona* Stainbrook, dorsal, lateral and posterior views, and transverse section of ventral valve, x1, indicating a connector plate as infilling callus. From Frasnian of mid and western United States, representing type species. (Stainbrook 1945).

Discussion: *Thomasaria* Stainbrook, 1945 is a subpentagonal semipyramidal shell without plicae, and ornament of fine spines. *T. warreni* Cooper & Dutro has fine commarginals and fine pustules, and low subfusc ribs appear anteriorly. The delthyrium in *T. demissum* Cooper & Dutro is partly plugged by a narrow but thick connector plate, deposited on the inner sides of the dental plates, and partly closed by narrow apical plates parallel to the delthyrium, representing deltidial plates. Socket ridges are short and flaring, and crural bases are thick.

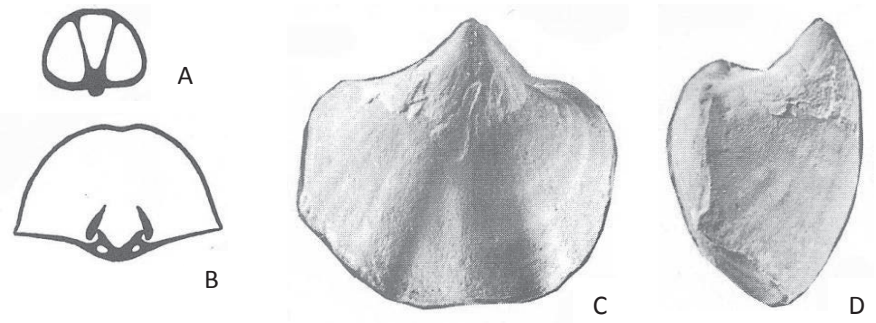


Fig. 424. *Thomasaria rockymontana* (Warren). A, transverse section 1.2mm from ventral beak, x3. B, transverse section 6mm from ventral beak, x3. C, D, ventral and lateral aspects, x4. From Devonian of Western Canada. (Crickmay 1967).

An externally somewhat similar species identified as *Thomasaria rockymontana* (Warren) by Crickmay (1967, pl. 2, fig. 42-44, pl. 3, fig. 22-24) was shown to have a sessile cruralium, recalling the arrangement in some *Warrenella*, and in *Eoreticularia*. Johnson in Carter & Gourvennec (2006c, p. 1864) stated that no crural plates were present, but crural plates are clearly shown in Cooper & Dutro (1982, pl. 43, fig 6). The delthyrium is closed by a convex plate with foramen at the apex.

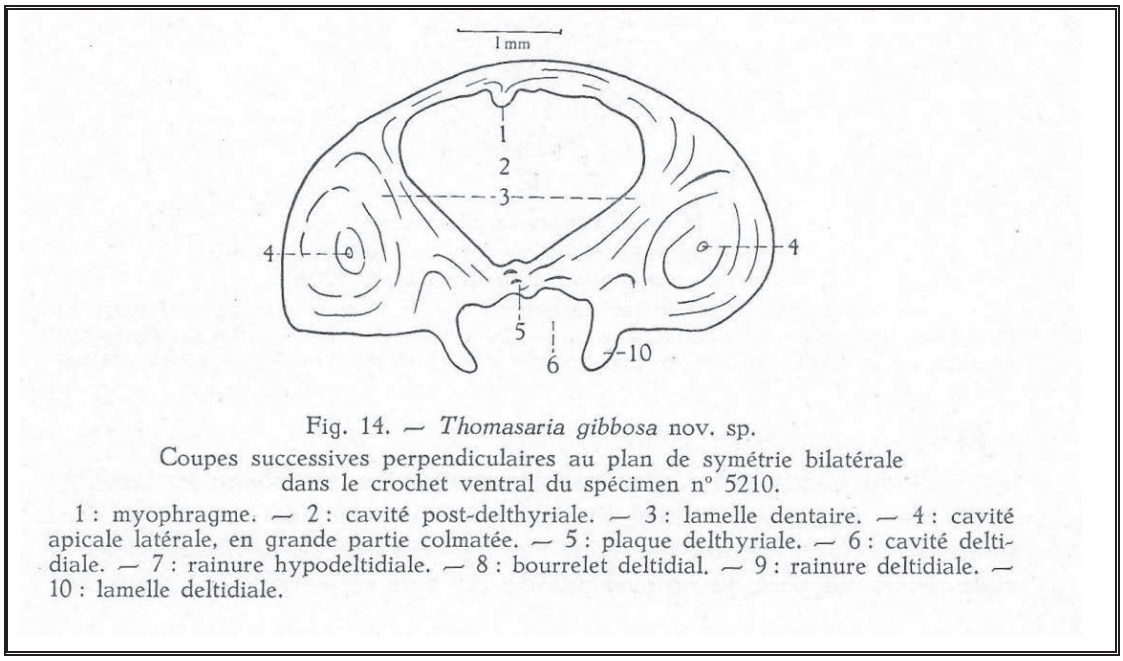


Fig. 14. — *Thomasaria gibbosa* nov. sp.
Coupes successives perpendiculaires au plan de symétrie bilatérale dans le crochet ventral du spécimen n° 5210.
1 : myophragme. — 2 : cavité post-delthyriale. — 3 : lamelle dentaire. — 4 : cavité apicale latérale, en grande partie colmatée. — 5 : plaque delthyriale. — 6 : cavité deltidiale. — 7 : rainure hypodeltidiale. — 8 : bourrelet deltidial. — 9 : rainure deltidiale. — 10 : lamelle deltidiale.

Fig. 425. *Thomasaria gibbosa* Vandercammen, transverse section of ventral valve showing connector plate and deltidial plates. From Tournaisian of Belgium. (Vandercammen 1956).

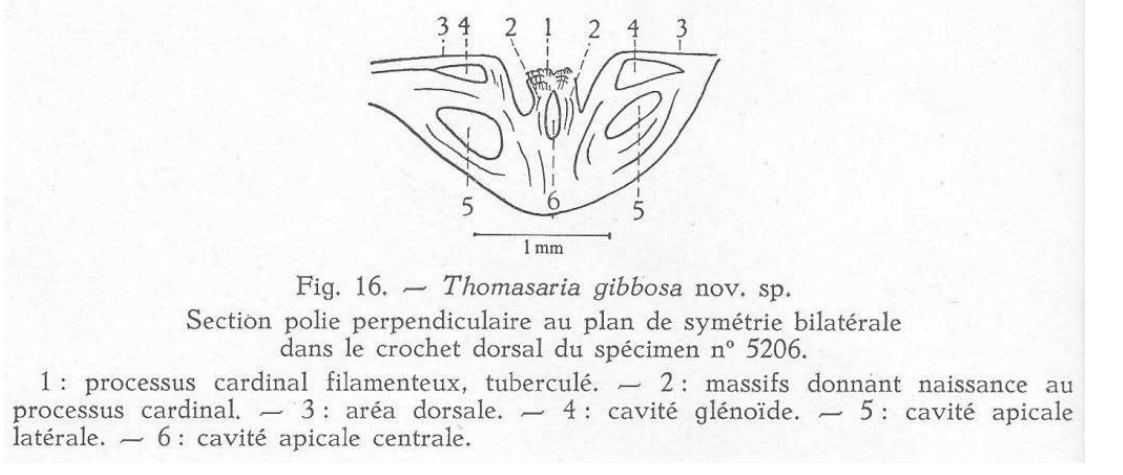


Fig. 16. — *Thomasaria gibbosa* nov. sp.
Section polie perpendiculaire au plan de symétrie bilatérale dans le crochet dorsal du spécimen n° 5206.
1 : processus cardinal filamenteux, tuberculé. — 2 : massifs donnant naissance au processus cardinal. — 3 : aréa dorsale. — 4 : cavité glénoïde. — 5 : cavité apicale latérale. — 6 : cavité apicale centrale.

Fig. 426. *Thomasaria gibbosa* Vandercammen, transverse section of dorsal valve showing cardinal process and median pillar suggestive of tabellae, but no clearly developed cruralium. From Tournaisian of Belgium. (Vandercammen 1956).

Vandercammen (1956) described two species from Belgium, and although Roberts (1963) declared they belonged to a different genus, they come very close to North America *Thomasaria*, and show an apical plate and connector plate, well developed deltidial plates each side of the delthyrium, and dorsal cardinalia only vaguely in the form of a cruralium.

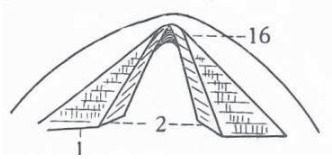


Fig. 427. *Thomasaria gibbosa* Vandercammen, showing ventral interarea (1), with small apical plate (16) and deltidial plates (2). From Tournaisian of Belgium. (Vandercammen 1956).

Subfamily **RHENOTHYRINAE** Gourvennec, 1994

[Rhenothyrinae Gourvennec in Carter et al. 1994, p. 353].

Diagnosis: Non-plicate with commargons bearing row of anterior small spines. Long adminicula and dental plates, low deltidial ridges, and low pleromal ridges passing back into small connector plate, leaving a forked subdelthyrial ridge. Ctenophoridium, high crural plates, very short tabellae, no cruralium. Micro-ornament of slender long spines. Lower and Middle Devonian (Emsian, Eifelian).

Genus: *Rhenothyris* Struve, *Minatodina* new genus, *Pseudoundispirifer* Zhang.

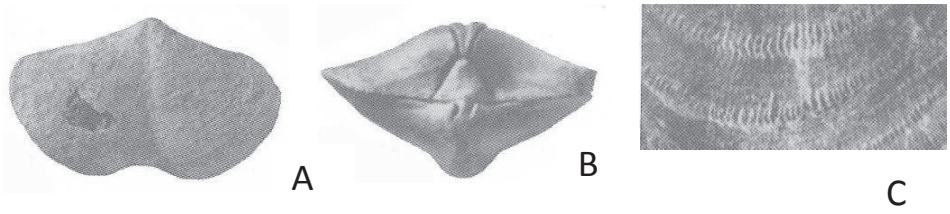


Fig. 428. *Rhenothyris rhenana* Struve, ventral and posterior aspects (dorsal valve below), x1, and micro-ornament, x5. From lower Eifelian of Germany. (Struve 1970**).**

Discussion*: Rhenothyris* Struve shows adminicula and tabellae. The dorsal plates are emphatically not long, to judge from figures, counter to the assertion that *Rhenothyris* had “long thick crural plates” – meaning tabellae – in the *Revised Brachiopod Treatise*. *Rhenothyris* has what the *Revised Brachiopod Treatise* called a “delthyrial plate or ridge or apical thickening” not seen in members allocated to Reticulariopsinae, and low deltidial plates are visible in *Rhenothyris* (Gourvennec in Carter & Gourvennec 2006c, Fig. 1233.1d). Unlike *Eoreticularia*, *Rhenothyris* has a ctenophoridium and lacks a cruralium and micro-ornament is slightly different. Many genera were referred to this subfamily in the *Revised Brachiopod Treatise*, but they lack a connector plate, and most are referred to Warrenellinae new subfamily.

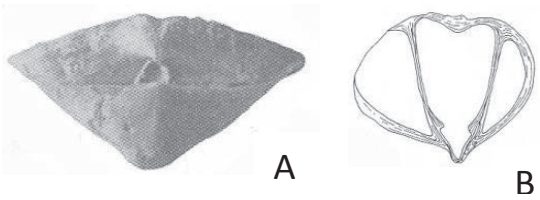


Fig. 429. *Rhenothyris rhenana* Struve, posterior view showing deltidial plates, x1.2, and transverse section of ventral valve showing pleromal ridges, and what may be a deltidial cover plate, x4. From lower Eifelian of Germany. (Struve 1970**).**

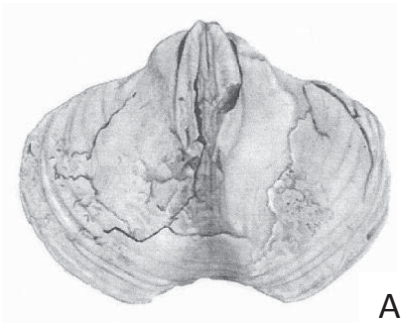
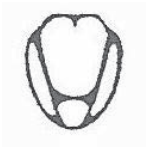


Fig. 430. *Rhenothyris aequabilis tumida* Struve. (holotype) A, ventral internal mould. B, anterior view. From Emsian of Germany, x1. (Jansen 2016).

Pseudoundispirifer Zhang, 1987a from the Middle Devonian (Givetian) of China was suggested as a possible synonym of *Eoreticularia* Nalivkin in Fredericks, 1924 by Carter & Gourvennec (2006c, p. 1855), but *Eoreticularia* has a cruralium (or septalium), not clearly developed in *Pseudoundispirifer*, and unlike *Pseudoundispirifer* lacks a ctenophoridium. Both genera have a connector plate and tabellae. Micro-ornament in *Pseudoundispirifer* consists of growth laminae and marginal spines, and in *Eoreticularia*, micro-ornament consists of growth lamellae and minute granules arranged in radial rows.

Fig. 431. *Pseudoundispirifer yiwaensis* Zhang, anterior aspect x1, and transverse section of ventral valve showing connector plate, x6. From Middle Devonian (Givetian) of China. (Zhang 1987).



Genus ***Minatodina*** new genus

Name: For M. Minato.

Diagnosis: Smooth with micro-ornament of spines varying considerably in diameter, arranged in commarginal rows. Adminicula with connector plug or plate apically. Well developed ctenophoridium and no cruralium. Middle to Upper Devonian (Couvinian, Givetian, Frasnian).

Type species: *Spirifer maureri* Holzapfel, 1896, p. 256 from Middle and Upper Devonian of Belgium, here designated.

Discussion: This genus is distinguished by the development of spines of variable diameter, unlike the arrangement in *Spirifer euryglossa* Schnur, 1851, the type species of *Minatothyris*, or in other genera such as *Warrenella* with rows of spines of uniform diameter, and different from the spines in *Gerothyris* which form bands of spinules differing in diameter.

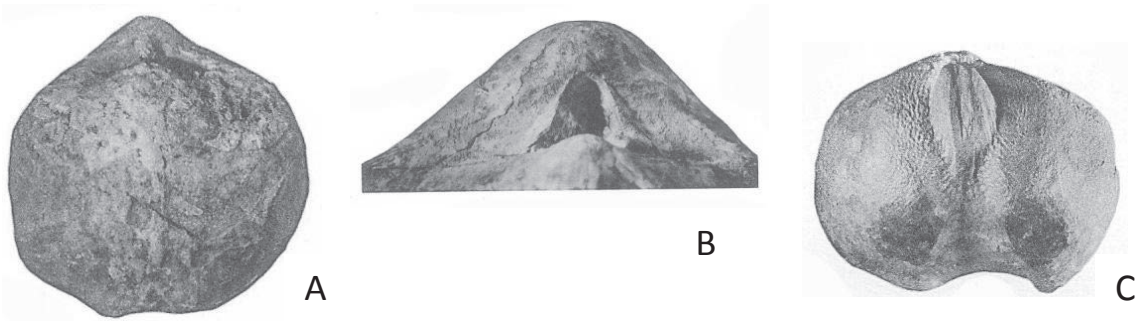


Fig. 432. *Minatodina maureri* (Holzapfel). A, B, dorsal view x1 and dorsal view. x3. C, ventral internal mould x1. From middle Frasnian of Belgium. (Vandercammen 1957).

Vandercammen (1957, p. 9) stated that the diameter along the rows in *maureri* was highly variable and did not seem to follow any pattern. The species *maureri* has been widely reported from England, and Germany as well as Belgium. It approaches *Thomasaria* in having a connector plug and pleromal ridges

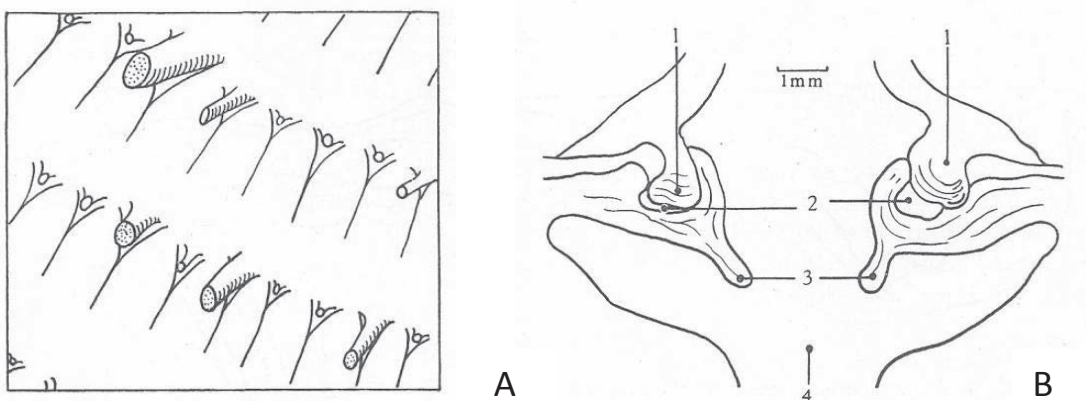


Fig. 433. *Minatodina maureri* (Holzappel), A, micro-ornament of coarse and fine single-barrelled spines, size not stated. B, transverse section showing teeth (1), dental sockets (2) and start of crura (3). From middle Frasnian of Belgium. (Vandercammen 1957).

(Vandercammen 1957, Fig. 3), but lacks a cruralium. Therefore the genus appears to be most closely related to Rhenothyrinae, and is distinguished from other constituent genera by the differentiated spines.

Taxonomy: *Spirifer maureri* Holzapfel was made the type of *Sinothyris* Minato, 1953, p. 68. But Pitrat (1965, p. 717) and Gourvennec in Carter & Gourvennec (2006c, p. 1860) emphasized that *Sinothyris* had been based on *Reticularia maureri* sensu Grabau (1931b, p. 394) non Holzapfel 1896, with a completely different diagnosis. Gourvennec regarded *Sinothyris* as a questionable synonym of *Xenomartinia* Havlicek (see p. 266), which has a median ventral septum. *Spirifer maureri* has no ventral median septum. If truly based on *maureri* Holzapfel, then *Sinothyris* may be regarded as a valid genus, and substituted for

Minatodina, which becomes a junior objective synonym. But diagnosis forms an integral part of any proposed genus, and the diagnosis by Grabua was inapplicable to *maureri.*

Subfamily **EORETICULARIINAE** Gourvennec, 1994

[Eoreticulariinae Gourvennec in Carter et al. 1994, p. 356].

Diagnosis: Connector plate present. Smooth, cardinal platform, cruralium or septalium present, lacking ctenophoridium, adminicula well developed. Micro-ornament of radially arranged minute granules and commarginal growth lamellellae. Lower Devonian (Emsian) to Upper Devonian (Frasnian).

Genus: *Eoreticularia* Nalivkin.

Discussion: The shape, plates, delthyrial apparatus and ornament of *Eoreticularia* are moderately close in those aspects to *Thomasaria* Cooper & Dutro, and the major difference lies in the presence of a ctenophoridium in *Thomasaria*, which is absent from Eoreticulariinae. The significance of this difference remains a question for further study. It is here assessed as meriting no more than subfamily discrimination, because Gourvennec in Carter & Gourvennec (2006c)

Fig. 434. *Eoreticularia indifferens* (Barrande), the type species for the genus. A, B, dorsal and ventral views, x1.5. C, *E. fraterna* (Barrande), transverse section showing connector plate, x3. D, *E. indifferens*, dorsal transverse section, x3. From Emsian of Czech Republic. (Havlíček 1959).

showed that the presence or absence of a ctenophoridium varied within Reticularioidea. On the other hand, Ambocoelioidea is commonly without a ctenophoridium, and distinctions from some genera classed as Reticularioidea in the *Revised Brachiopod Treatise* are not great.

Superfamily **ELITOIDEA** Fredericks, 1924

[Nom. transl. et correct. ex subfamily Elythinae Fredericks, 1924, p. 304].

Diagnosis: Lateral shell smooth or with low plicae, fold and sulcus if present weakly developed, ornament of biramous spines. Lower Devonian (Pragian) to Upper Permian (Changhsingian).

Discussion: Double-barrelled spines are present in various genera that have been classed previously in Reticularioidea. Members were independent since Pragian (Lower Devonian) times.

Family **ELITIDAE** Fredericks, 1924

[Nom. correct. hic pro Elythidae, nom. transl. Pitrat 1965, p. 721 ex subfamily Elythinae Fredericks, 1924, p. 304].

Diagnosis: Lateral shell smooth or with low plicae, fold and sulcus if present weakly developed, ornament of fine biramous spines. Lower Devonian (Pragian) to Lower Carboniferous (Visean).

Discussion: Internal plates show considerably variation between genera within the subfamilies to which they were allocated by Carter in Carter & Gourvennec (2006c), involving the presence or absence of adminicula, low median ridge or septum in either valve, tabellae, and presence or absence of a dorsal hinge plate.

Most genera are not plicate, and show no sign of pleromal ridging or a connector plate, and so appear to form a natural progression parallel to that of non-plicate Reticulariinae and Reticulariopsinae, as outlined in the *Revised Brachiopod Treatise*. Elitinae (Elythinae) have short tabellae and could have developed from Reticulariopsinae, whereas Phricodothyridae have reduced internal plates, no tabellae, no adminicula, and only a weak or more generally absent ventral median septum. There is a range of possible implications over the presence of a low median ridge in both *Elita* and *Phricodothyris,* recalling the median ridge seen in *Reticulariopsis* and in *Reticularia*. Was the ridge newly evolved, or relict from members of Delthyroidea, such as genera within Xenomartiniidae, which included non-plicate shells? That would imply that Reticularioidea evolved from Delthyroidea rather than independently or from Hysterolitoidea.

Taxonomy: It is proposed to substitute Elitinae for Elythinae. The subfamily as proposed by Fredericks 1919 (1924), p. 304 and 1926, p. 406 was based on an unjustifiable emendation, as a mis-spelling, of *Elita* Fredericks, 1918, p. 87, with type species kept as *Delthyris fimbriatus* Conrad, 1842, p. 263. The mis-spelling is corrected, just as Paeckelmannelloidea has been corrected from Paeckelmanelloidea (see p. 152), and Brachythyrinae has been corrected from Brachithyrinae Fredericks (see p. 101). [Note the similarity in confusion between i and y]. This may deviate from rules provided in the International Subcommission of Zoological Nomenclature, which in Article 32.2 writes of preservation of the original spelling, and Article 35.4.6 which writes of “unjustified emendation of the name of the type genus becomes its substitute name”. The latter ruling needs clarification, and requires some form of

defence, rather than a ruling by decree. Early students, in using Elythinae, were convinced that *Elytha* had been the name proposed by Fredericks (Sarytcheva 1960, Pavlova 1969, p. 56), which explains their failure to address the problem. The main point against consolidating a mis-spelling of the genus name in the family group based on that name is that it alienates the genus name from its family-group name. It is deemed preferable to facilitate the relationship between the genus name and family group name, making it complete standard and without exceptions, with adjustment and correction to any deviation, and in no way changing the credit due to the original authorship.

Subfamily **ELITINAE** Fredericks, 1924

[Nom. correct. hic pro Elythinae Fredericks, 1924, p. 304].

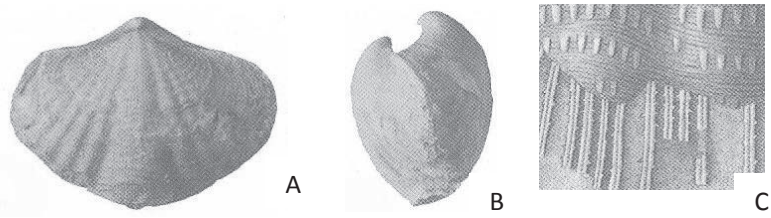


Fig. 435. *Elita fimbriata* (Conrad), type species. A, B, dorsal and lateral views, x1. (Cooper 1944). C, micro-ornament, x4 approx. From Middle Devonian of New York, USA. (Hall & Clarke 1894).

Diagnosis: Small with ornament on both valves of double-barrelled spines in single rows over commargons; may be sulcate or plicate, delthyrium open or closed by convex plate. Characterized by presence of cardinal plate in dorsal valve, bearing ctenophoridium. Adminicula and medium ventral ridge and dorsal median ridge variably developed, but never high. Tabellae short or absent. Lower Devonian (Pragian) to Lower Carboniferous (Visean).

Genera: *Elita* Fredericks, 1918 (mis-spelled *Elytha* Fredericks, 1924), *Kitakamithyris* Minato, ?*Orenburgella* Pavlova.

Discussion: Elythinae according to Carter in Carter & Gouvennec (2006c) contained only two genera, *Elita* and *Kitakamithyris*, said to share biramous spines that were “not elaborate”. The two genera are both of Devonian and Early Carboniferous age. Whilst the spine morphology may not have been elaborate for *Elita* and *Kitakamithyris*, the spines are double-barrelled, and as shown in the discussion of Condrathyridae (p. 348), the spine morphologies may differ considerably in various genera. A bilobed ctenophoridium has been reported for *Elita*. *Elita* was not fully portrayed in the *Revised Brachiopod Treatise*. There are said to be long adminicula and a median septum in the ventral valve, though no high septum is shown in non-type material coming from Russia. It has a massive inconsistently bilobed ctenophoridium on a cardinal platform, short or no crural plates, and strong myophragm. If a ventral septum were developed, this may suggest a relationship to some genera within Xenomartiniidae, but

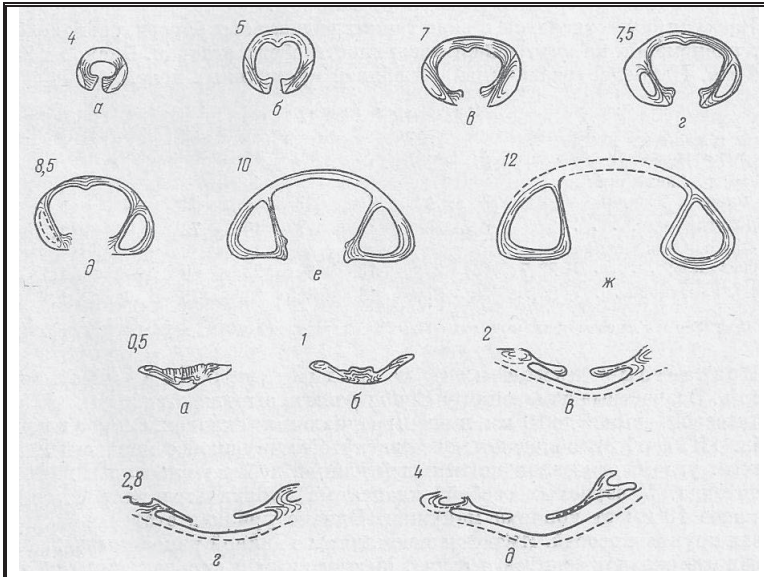


Fig. 436. *Elita granosa* (Verneuil), transverse sections with distance indicated in mm from ventral beak. The sections suggest incipient pleromal ridges but no connector plate. From Frasnian of Russia. (Pavlova 1969).

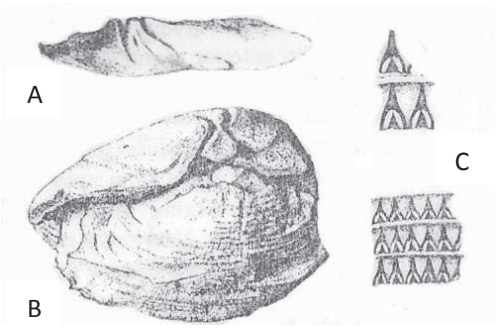


Fig. 437. *Kitakamithyris tyoanjiensis* Minato, posterior ventral and dorsal views, x1, and micro-ornament, x4, x7. From Tournaisian of Japan. (Minato 1951, 1952).

the septal development is very restrained. As interpreted by Pavlova (1969), the spiralia in *Elita* are postero-laterally oriented. The interpretation of internal detail for *Kitakamithyris* by Pavlova (1969) indicated much the same detail, but also was not based on type material. This genus has been incompletely studied, with no transverse sections, and the figure in the *Revised Brachiopod Treatise* has not come out clearly. The originals are reproduced herein, but the types should be rephotographed.

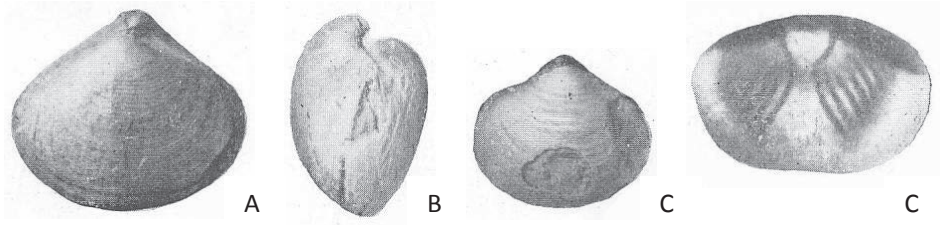


Fig. 438. *Orenburgella uralica* Pavlova, dorsal and lateral views of holotype, x1, ventral view x1, and specimen showing spiralia, x1.5. From Visean of southern Urals, Russia. (Pavlova 1969).

Orenburgella was placed in Martinothyridinae by Carter in Carter & Gourvennec (2006c, p. 1864), but lacks the long tabellae of this subfamily. It does display long adminicula, and has a reduced if any cardinal plate. Low commarginal laminae cross each valve, and spines are double-barrelled but seem comparatively simple, and the spiralia are directed posterolaterally. The genus is provisionally interpreted as a member of Elitinae, and is Visean in age, younger than the upper range of Tournaisian for the other two genera.

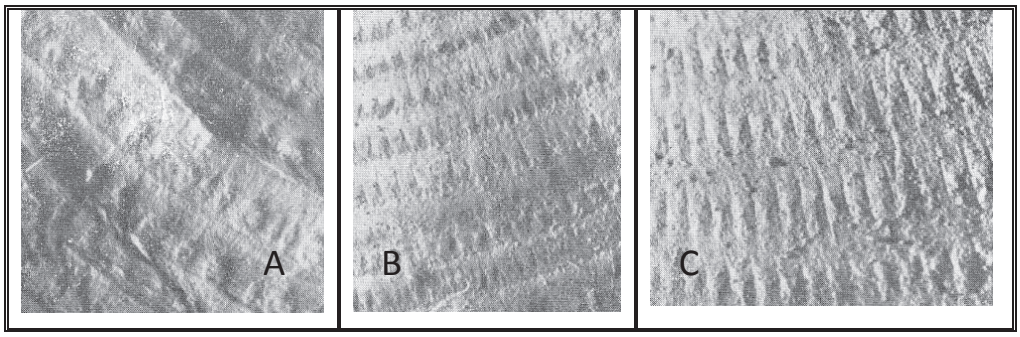


Fig. 439. *Orenburgella uralica* Pavlova, detail of micro-ornament, x15. From Visean of southern Urals. (Pavlova 1969).

Family **TORYNIFERIDAE** Carter, 1994

[Nom. transl. hic ex Toryniferinae Carter in Carter et al. 1994, p. 359].

Diagnosis: Connector plate well developed as a rule. Internal plates varied. Lower Carboniferous (Visean) to Middle Permian (Capitanian?).

Discussion: Reinterpretation of delthyridin genera in the Late Paleozoic arranges the genera according to whether the delthyrial plate involved a connector plate or deltidial plates. As well, it is suggested that internal plates varied, a theme that has largely been endorsed by classification of Delthyridina proposed in the *Revised Brachiopod Treatise*.

Subfamily **TORYNIFERINAE** Carter, 1994

[Toryniferinae Carter in Carter et al. 1994, p. 359].

Diagnosis: Connector plate well developed, adminicula and low median ridge or septum present. Dorsal valve with crural plates forming subhorizontal to concave cardinal plate, may be supported by median septum, no or weakly developed ctenophoridium. Lower Carboniferous (Visean) to Middle Carboniferous (Kasimovian).

Genera: *Torynifer* Hall & Clarke, ?*Plicotorynifer* Abramov, *Toryniferella* Weyer.

Discussion: A subdelthyrial plate, apparently a connector plate, appears in type *Torynifer*, and a ctenophoridium is generally absent. The genus has spine-bearing growth lamellae and lacks plicae. There is a long median ventral ridge, long adminicula, and dorsal concave cardinal plate supported by a median septum of variable height.

Sour-Tovar et al. (2005, p. 477) in discussing specimens identified with the type species of *Torynifer, pseudolineatus* (Hall) from the early Mississippian of Mexico in the

Sierra Madre, pointed out that their specimens showed a small transverse radially striate

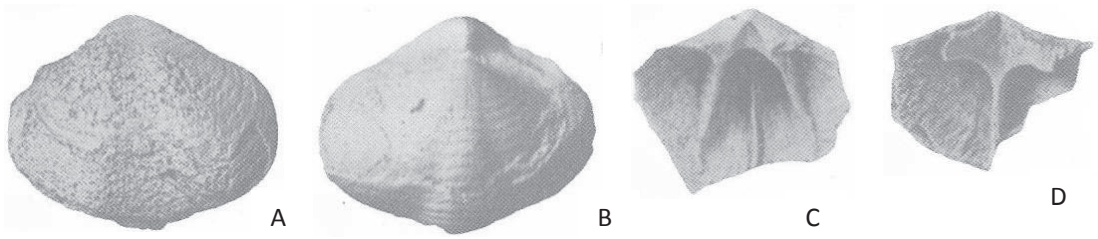


Fig. 440. *Torynifer pseudolineatus* (Hall). A, B, ventral and dorsal views x1. (Weller 1914). C, D, ventral and dorsal interiors, x2. From upper Tournaisian of Iowa, USA. (Cooper 1944).

under the dorsal beak, representing a poorly developed ctenophoridium. Type *Torynifer* shows no sign of a ctenophoridium, according to J. L. Carter, and it was suggested that the lack of a ctenophoridium helped provide the difference between *Torynifer* and *Kitakamithyris*. By contrast, Sour-Tovar et al. (2005) concluded that a ctenophoridium could be present in *Torynifer*. Their figures certainly show the pseudolineation within the shell that typifies *T. pseudolineatus*. But in the *Revised Brachiopod Treatise*, a strong dorsal septum was illustrated, as typical of *T. pseudolineatus*, and credited to Cooper (1944). (See Fig. 440D herein). The figures for the Mexican materal suggest only a slender median ridge, apparently beginning in front of the posterior wall, pointing to variability in septal development. A figure of the dorsal interior in Weller (1914, pl. 74, fig. 11) indicates a relatively sturdy dorsal median septum.

Fig. 441. *Torynifer pseudolineatus* (Hall), cross–section of specimen identified with this species, suggesting a septalium or concave cardinal plate, x5. Note the subdelthyrial connector plate, as in type *Torynifer*. From Kuznets Basin, Russia. (Sarytcheva 1960).

Toryniferella Weyer of upper Visean age in Queensland, Australia, is close to *Torynifer,* but lacks high ventral and dorsal median septa, and no connector plate is revealed in transverse sections (Maxwell 1961). The genus has a dorsal cardinal plate as in *Torynifer.*

Plicotorynifer Abramov & Solomina in Abramov (1970), of Late Carboniferous (Moscovian – Kasimovian) age, has adminicula, low median ventral septum, and dorsal septum. But the presence or absence of a cardinal plate or connector plate cannot be ascertained, and its relationships are therefore uncertain. The original figures are reproduced herein from Abramov (1970, pl. 18, fig. 1-5). The figure in the *Revised Brachiopod Treatise* (Carter in Carter & Gourvennec 2006c, Fig. 1244.6, p. 1869) that purports to be *Plicotorynifer* is in fact an illustration of *Stenoscisma sibirica* Abramov (1970, pl. 19, fig. 1a). No correction

was offered in the updating of Delthyridina in the last volume of the *Revised Brachiopod Treatise*.

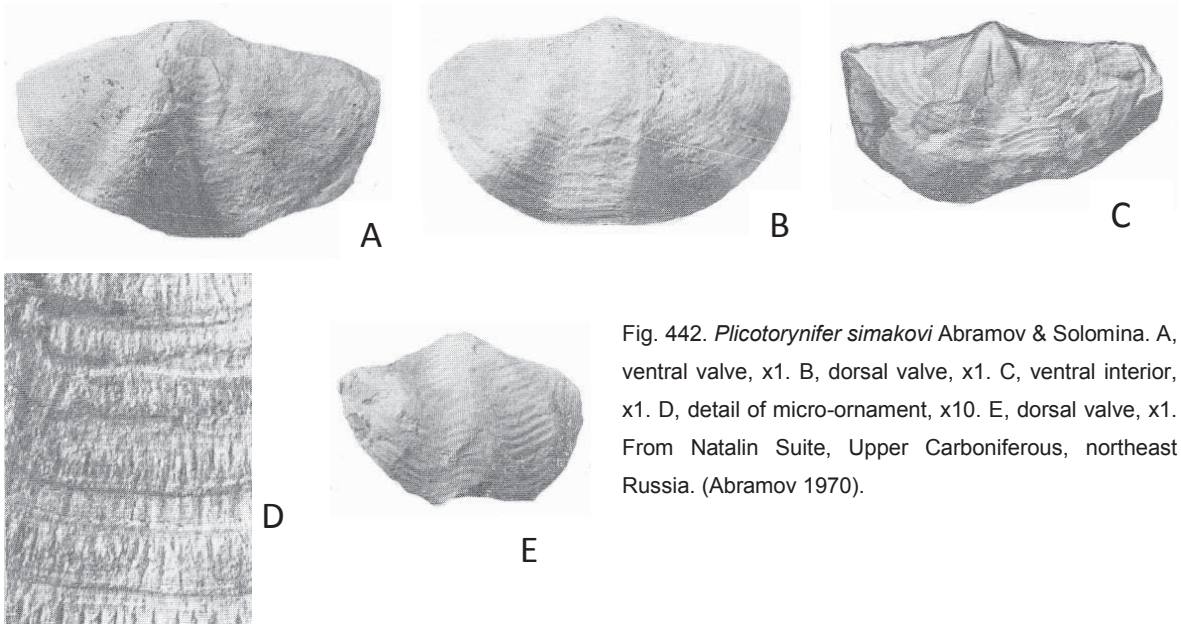


Fig. 442. *Plicotorynifer simakovi* Abramov & Solomina. A, ventral valve, x1. B, dorsal valve, x1. C, ventral interior, x1. D, detail of micro-ornament, x10. E, dorsal valve, x1. From Natalin Suite, Upper Carboniferous, northeast Russia. (Abramov 1970).

Subfamily **SPIRELYTHINAE** new subfamily

Name genus: *Spirelytha* Fredericks, 1924, p. 304 from late Guadalupian of Great Bear Island, Canadian Arctic Archipelago, here designated.

Diagnosis: Distinguished from Toryniferinae by lack of cardinal plate and presence of ctenophoridium. Ornament of double-barrelled spines. Ventral valve with dental plates, adminicula, low well defined median ridge, connector plate and pleromal ridges as a rule. Dorsal valve with crural plates, low median ridge. Upper Pennsylvanian to Middle Permian (Wordian or early Capitanian).

Tribe **SPIRELYTHINI** new tribe

Diagnosis: Distinguished from Toryniferinae by lack of cardinal plate and presence of ctenophoridium. Ornament of double-barrelled spines. Ventral valve with dental plates, adminicula, low well defined median ridge, connector plate and pleromal ridges. Dorsal valve with crural plates, low median ridge. Upper Pennsylvanian to Middle Permian (Wordian or Capitanian).

Genera: *Spirelytha* Fredericks, *Stepanoviina* Zavodowsky, *Taimyrella* Einor.

Discussion: Unlike *Torynifer*, a ctenophoridium is well developed, and a cardinal plate is absent. The type species of *Spirelytha* is comparatively obscure, having been based on *Spirifer scheii* Chernyshev in Chernyshev & Stepanov (1916a, b), not *Spirifer scheii* Meyer, 1913. Potentially, the morphology was clarified by Archbold & Thomas (1984b, p. 313), in pointing out that silicified material from Axel Heiberg Island probably belonged to the genus

and species. This had been described as *Spirelytha* for ventral valves, and *Permophricodothyris* for dorsal valves by Stehli & Grant (1971). The ventral valves show median septum and moderately short adminicula with a posterior connector plate, and the dorsal valves show crural plates and very low if any median septum, with no tabellae. There are indications of a low pleromal ridge along the junction of the dental and adminicular plates, which potentially could have matured into a connector plate.

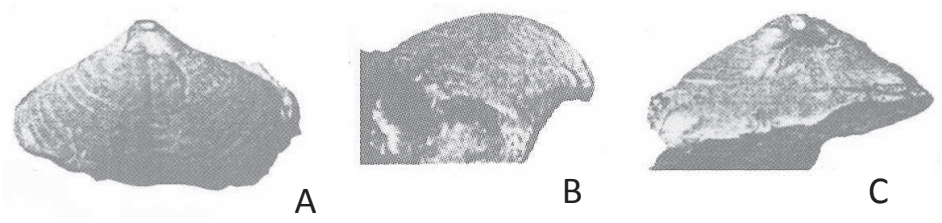


Fig. 443. *Spirelytha pavlovae* Archbold & Thomas, ventral, lateral and posterior aspects of ventral valve lectotype, from Bear Island, Arctic Canada, not Siberia as in *Revised Brachiopod Treatise*, x1. (Chernyshev & Stepanov 1916b).

Archbold & Thomas (1984b) noted that the internal plates resembled those of *Kitakamithyris* Minato, 1951, but hesitated to synonymize the two because the difference in age, and also pointed out that *Kitakamithyris* displayed vascular canals that were not developed in *Spirelytha*. That was adjusted by Klets (1987), who stated the mantle canal markings in *Spirelytha* were net-like rather than radial as in *Kitakamithyris* and *Torynifer*. Moreover Carter (in Carter & Gouvennec 2006c) stated that the spines were less developed, although biramous, in *Kitakamithyris*. Archbold & Thomas (1984b) suggested that the presence of tabellae or “dorsal adminicula” was variable in species of *Spirelytha*, but their interpretation of what constituted tabellae comes under some question, given that they interpreted a cross-section of what appears to be a cruralium in *Spirelytha miloradovichi* (Fig. 3i) as dorsal adminicula. The cruralium is formed by crural plates, not by tabellae, so their definition of “dorsal adminicula” with preference for that term is not reassuring.

Specimens ascribed to *Spirelytha kislakovi* Klets, 1987 from northeast Russia as figured by Klets (2005, pl. 24, fig. 1-10, pl. 25, fig. 1-7) display short adminicula, long ventral median septum, short dorsal median septum, and fine crural plates. Part of the spire appears to touch the floor of the dorsal valve, leaving, after having been dissolved, linear hollows in the internal mould. Specimens illustrated by Klets (2005, pl. 26, fig. 6-11) as *S. fredericksi* Archbold & Thomas have adminicula and ventral median septum, very low dorsal median ridge, and no tabellae. The ornament of single rows of biramous spines is well illustrated for some of the species. An pleromal plug or thick connector plate is illustrated for *S. kislakovi* Klets (2005, pl. 24, fig. 5, 9).

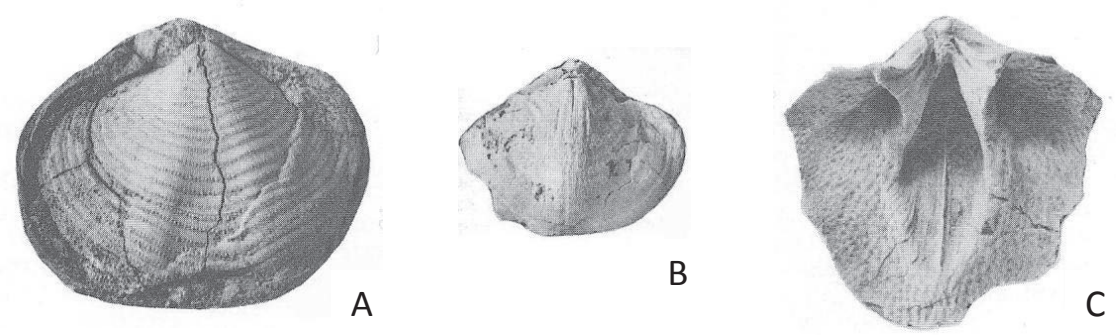


Fig. 444. *Spirelytha fredericksi* Archbold & Thomas, ventral exterior, dorsal view showing internal septum, and ventral interior, x1, from Callytharra Formation (lower mid-Cisuralian), Western Australia. (Archbold & Thomas 1984b). Note the umbonal thickening in C, developed by pleromal thickening close to junction of dental plates and adminicula, and forming a connector plate.

The species called *Kitakamithyris petaliformis* Pavlova in Grunt & Dmitriev (1973, pl. 10, fig. 2-5, text-fig. 38, 39) from the Sakmarian of the Pamirs may be regarded as belonging to *Spirelytha,* and has double-barrelled spines. A connector plate is shown in Grunt & Dmitriev (1973, pl. 10, fig. 3b).

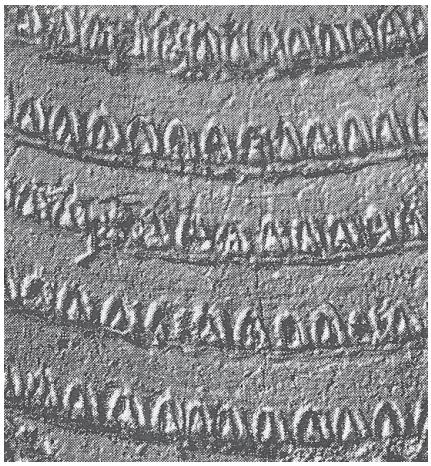


Fig. 445. *Stepanoviina larini* Zavodowsky, micro-ornament x7, from Cisuralian of northeast Russia. (Zavodowsky 1968).

Stepanoviina Zavodowsky, 1968 was recognized by Carter & Gouvennec (2006c), but it is very close to *Spirelytha*, and was synonymized with that genus by Pavlova (1977), Archbold & Thomas (1984b) and Klets (2005). Unlike other genera within the group, it has no ventral septum according to Zavodowsky (1968, Fig. 24, p. 171).

Taimyrella Ustritsky in Ustritsky & Chernyak, 1963 is characterized by its broad lateral plicae. Considered by Carter to be close to *Torynifer*, one specimen assigned to the type species seems to lack adminicula in Ustritsky (in Ustritsky & Chernyak 1963, pl. 43, fig. 2), probably because they are spaced far apart, and another has a high ventral median septum and adminicula. Abramov & Grigorieva (1983, Fig. 54) showed sections of the type species,

T. pseudodarwini (Einor), with connector plate and pleromal ridges. The dorsal valve lacks a cardinal plate but has high crural plates, according to excellent figures of specimens from the Late Carboniferous Mishkinsk Suite of south Verchoyan provided by Klets (2005, pl. 28, fig. 1-3). However the Klets material does not show the plication supposed to be characteristic of *Taimyrella. T. afanasjevi* Abramov & Grigorieva, figured by Klets (2005, pl. 27, fig. 1-13) from the Amonansk Suite (Late Carboniferous) of Lena River, is typically plicate and shows the same dorsal structures. Both species figured by Klets (2005) have a ventral median septum.

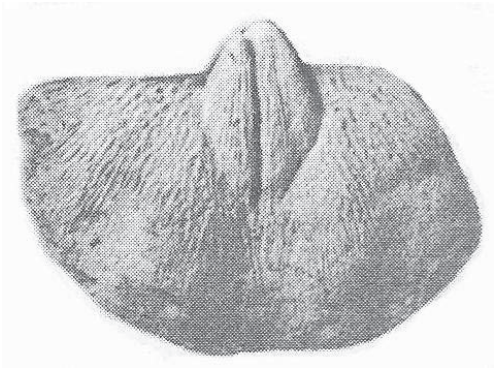


Fig. 446. *Taimyrella pseudodarwini* (Einor), internal ventral internal mould, x1.5, from Upper Carboniferous of Kolyma-Omolon Massif, northeast Russia. (Grunt 1977a).

Genus ***Spirelytha*** Fredericks, 1924

Diagnosis: Suboval shells with shallow ventral sulcus, low fold, lateral slopes smooth, micro-ornament of single row of double-barrelled spines along each commargon. Ventral valve with median septum, teeth and dental plates and short adminicula; connector plate, dorsal interior with very short or negligible median septum, socket plates and no tabellae or cardinal plate.

Type species: *Spirelytha pavlovae* Archbold & Thomas, 1984b, p. 313 (nom. nov. pro *Spirifer scheii* Chernyshev in Chernyshev & Stepanov, 1916b, p. 45, non Meyer 1913) from Store Bjornekap, Ellesmere Island, Arctic Canada.

Spirelytha svartevaegensis n. sp.

1971 *Spirelytha* cf. *S. schei* [not Chernyshev] – Stehli & Grant, p. 518, pl. 63, fig. 3, 5, 6, 9.

1971 *Permophricadothyris*? sp. Stehli & Grant, p. 518, pl. 63, fig. 4, 8, 14-16, 18-20.

Name: Named from Svartevaeg Cliffs, Axel Heiberg Island (Lower Guadalupian, Roadian or early Wordian), source of the material.

Holotype: USNM 166288 from below Svartevaeg Cliff, north Axel Heiberg Island, Canada, figured by Stehli & Grant (1971, pl. 63, fig. 3, 5, 6, 9) and Fig. 447A, C herein, here designated.

Diagnosis: Transverse with shallow anterior sulcus and no clearly defined dorsal fold or dorsal median ridge, ventral median septum long and well defined.

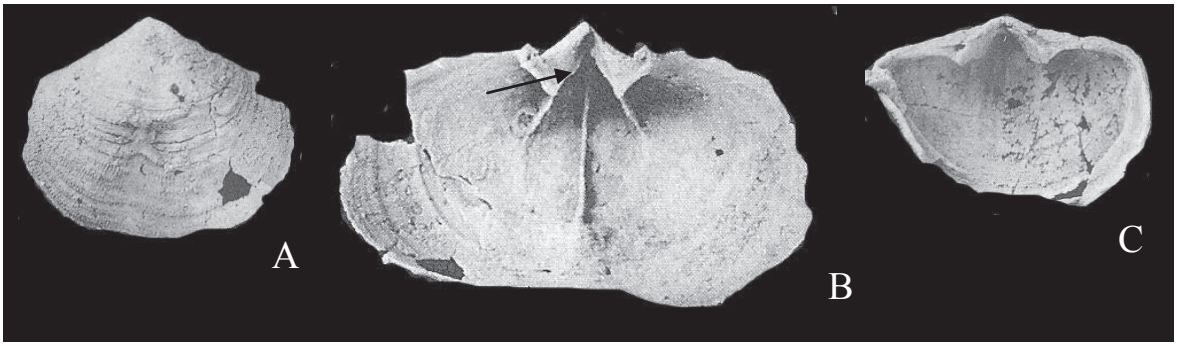


Fig. 447. *Spirelytha svartevaegensis* n. sp. A, B, ventral valve exterior and interior, holotype USNM 166288, x2, x4. C, dorsal interior, x2. From lower Guadalupian of Axel Heiberg Island, Canada. (Stehli & Grant 1971). Note the indications of pleromal ridges (arrowed), and no sign of cruralium or cardinal plate.

Description: The species has been described under two headings by Stehli & Grant (1971). They allocated a ventral valve to *Spirelytha*, and dorsal valves from the locality to *Permophricodothyris*?, but as pointed out by Archbold & Thomas (1984b), the two suites are compatible with each other and belong to one species. Spines are double-barrelled, though poorly preserved, and no delthyrial cover plate is preserved. This reflects the likelihood that the figured ventral valve is not at full maturity. The dorsal valve has socket and inner hinge plates, and no indication of tabellae, and the cardinal process, if present, is small and obscure. A very fine median ridge is present in the dorsal valve (Stehli & Grant 1971, pl. 63, fig. 20).

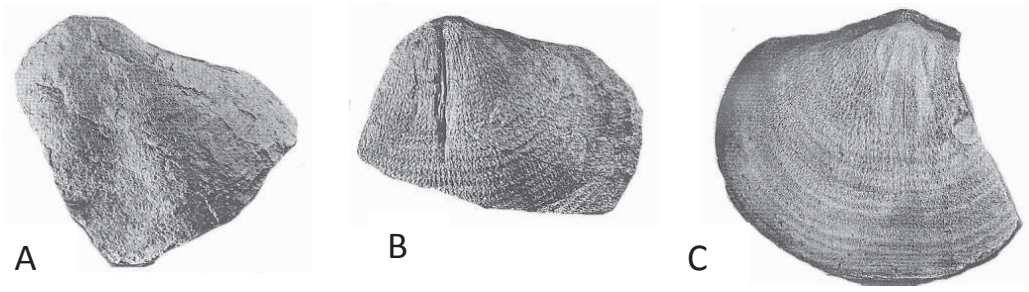


Fig. 448. *Spirelytha grandis* Klets. A, ventral valve, x1. B, internal ventral valve, x1. C, internal dorsal valve, x 1. From Marshrutninsk Suite, northeast Russia. (Klets 2005).

Resemblances: This species is found close to the type of the genus, *Spirelytha pavlovae* from Great Bear Cape, but the ventral valve is less inflated than the type material figured as *Spirifer schei* by Chernyshev & Stepanov (1916a, b, pl. 9, fig. 5-7), with lower ventral interarea, shorter hinge, and shallower ventral sulcus. Further aspects of the morphology cannot be compared. *Spirelytha kislakovi* Klets (see Klets 1987, 2005, pl. 25, fig. 1-7) from an

Early Permian suite of south Verchoyan is similar in its lack of dorsal fold.

Spirelytha grandis Klets (2005, pl. 26, fig. 1-5) from the Middle Permian Marshrutninsk Suite of Cahalichan River, northeast Russia, lacks tabellae and has a dorsal valve close to that the present species, but adminicula are short and widely divergent, and the ventral median ridge is long and sturdy. Specimens figured as *S. fredericksi* Archbold & Thomas by Klets (2005, pl. 26, fig. 6-11) are particularly close to what is understood to be typical *Spirelytha,* with ventral adminicula and median septum. There are well developed double-barrelled spine bases, low median dorsal ridge and no sign of tabellae. A shallow sulcus and low dorsal fold are present. The specimens come from the Early Permian Sigskar Suite of South Verchoyan.

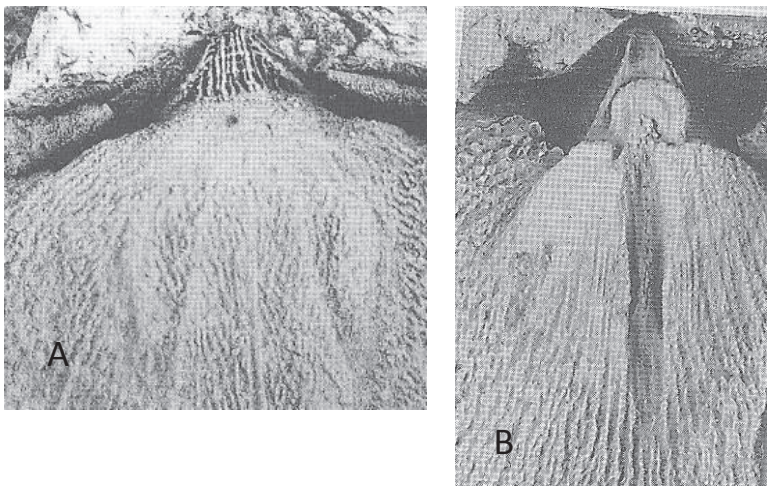


Fig. 449. A, *Spirelytha grandis* Klets, detail of posterior dorsal internal mould, x4. B, *S. kislakovi* Klets, posterior ventral valve, showing connector plug and umbonal callus. From Marshrutninsk Suite and Tartarsk Suites (Guadalupian), northeast Russia. (Klets 2005).

Tribe **KLETSIINI** new tribe

Name genus: *Kletsia* new genus from Wandagee Formation (upper Artinskian) of Western Australia, here designated.

Diagnosis: Shells with double-barrelled spines, ventral septum and adminicula, no connector plate or pleromal ridges. Short and low dorsal ridge, cruralium. Lower Permian (Artinskian).

Genus: *Kletsia* new genus.

Discussion: This subfamily is distinguished from other Permian members by the lack of a connector plate and pleromal ridges, and the presence of a cruralium. Given that the only known genus has adminicula and ventral median septum, the genus may have evolved from *Spirelytha*, through loss of the connector plate and adjustment of the crural plates to form a cruralium.

Genus ***Kletsia*** new genus

Name: For A. G. Klets.

Diagnosis: Medium size, well developed sulcus and fold, spines double-barrelled, adminicula long, without connector plate or pleromal ridges. Crural plates form sessile cruralium.

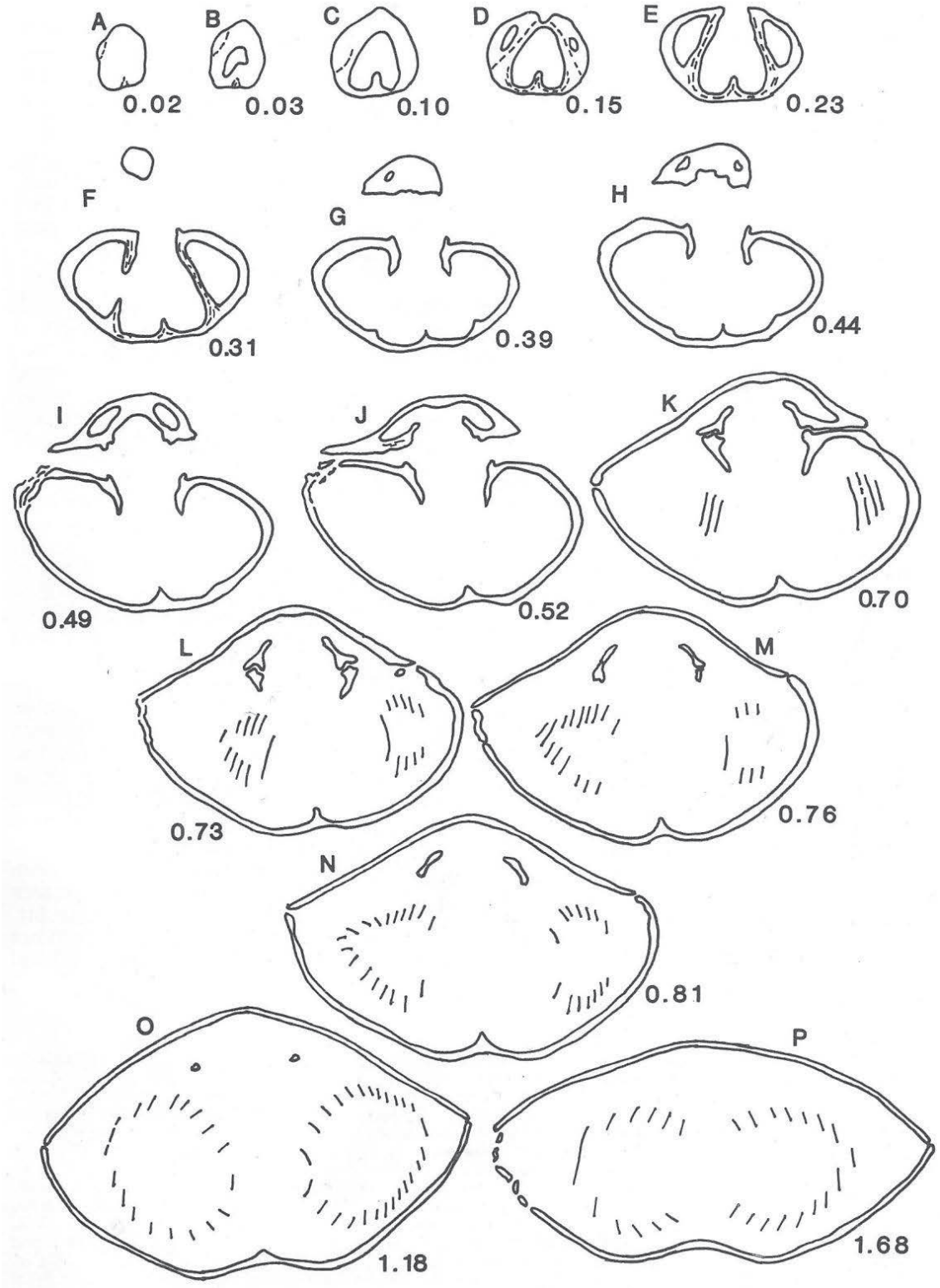


Fig. 450. *Kletsia miloradovichi* (Archbold & Thomas). Transverse sections, with distance from ventral beak indicated in mm, from Archbold & Thomas (1984b). This shows a low ventral septum, remnant cruralium (see 0.49), and no dorsal septum and no connector plate or pleromal ridges. From Wandagee Formation (upper Artinskian), Western Australia.

Type species: *Spirelytha miloradovichi* Archbold & Thomas (1984b, p. 318) from Wandagee Formation (Artinskian) of Western Australia, here designated.

Discussion: This genus is close in morphology to species of *Spirelytha*, with double-barrelled spines, adminicula, median ventral septum, ctenophoridium and low dorsal ridge, but crural plates form a cruralium rather than a broad subhorizontal cardinal plate between the socket plates, and there is no connector plate or pleromal development. Two well formed ridges lie each side of the muscle field (Fig. 451D) in some specimens, and these are assumed to represent myosepta rather than tabellae.

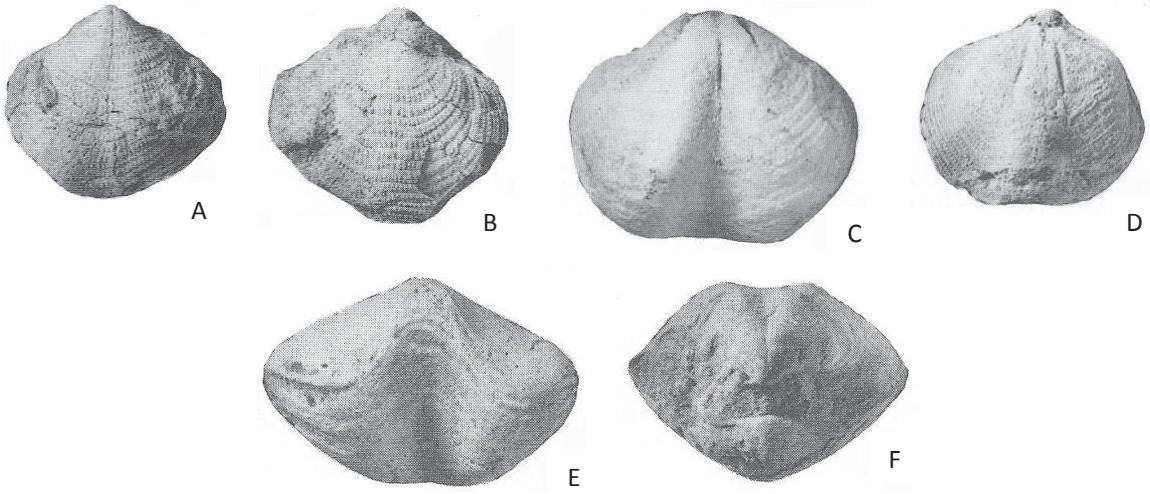


Fig. 451. *Kletsia miloradovichi* Archbold & Thomas. A, B, ventral and dorsal views, x2. C, ventral valve showing inner plates, x1. D, internal mould, dorsal view, x1.5. E, anterior view, x1.5. F, posterior view, dorsal valve below, x1. From upper Cisuralian in Western Australia. (Archbold & Thomas 1984b).

Subfamily **MARTINOTHYRINAE** Carter, 1994

[Nom. correct. hic pro Martinothyridinae Carter, 1994 in Carter et al. 1994, p. 358].

Diagnosis: Adminicula and dental plates with connector plate, tabellae present, no median ventral ridge, spines elaborate. Mississippian to Cisuralian (Lower Permian).

Genera: *Martinothyris* Minato, ?*Latiplecus* Li & Gu.

Discussion: Carter in Carter et al. (1994) recognized a small group of smooth shells with narrow hinge and well developed double-barrelled spines as Martinothyridinae. Minato (1953, Fig. 3) clearly delineated what are now called adminicular and tabellar plates, and low ventral septum (or high myophragm) in type *Martinothyris*, and this is supported by George (1932, fig. 6) in showing a low dorsal ridge, as reproduced by Pavlova (1969, Fig. 48) and see Fig. 452. A connector plate is present with pleromal ridges. Transverse sections of *Orenburgella* in Pavlova (1969, Fig. 49) show adminicula, but no sign of tabellae, and only a very slight suggestion of a median dorsal ridge, so that genus is moved to Elitinae (Elythinae).

Latiplecus is poorly known. It was described by Li & Gu (1976, p. 299, pl. 157, fig. 5-9, 12), and their figures show well developed long adminicula, well developed

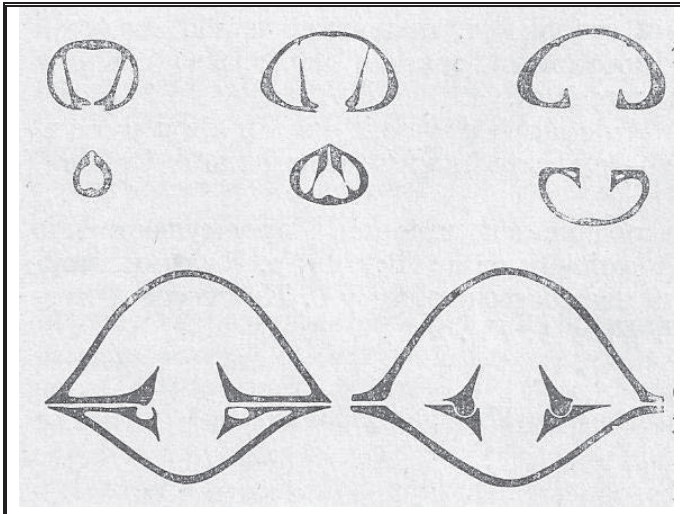


Fig. 452. *Martinothyris lineata* (Sowerby). transverse sections. From Visean of England. (George 1932).

double-barrelled spines, and apparent, but not completely irrefutable, long tabellae. The genus does appear to come close to *Martinothyris,* as in the *Revised Brachiopod Treatise*, but the presence or absence of a connector plate has not been ascertained.

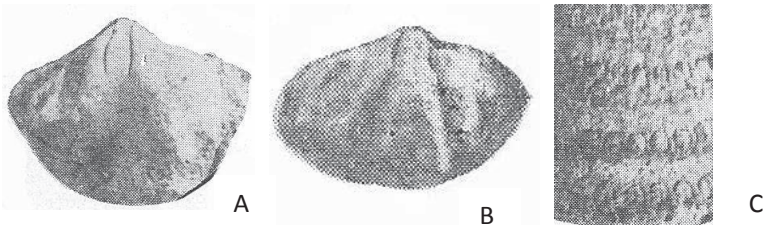


Fig. 453. *Latiplecus typicus* LI & Gu. A, ventral internal mould x1.5. B, dorsal internal mould, x3. C, micro-ornament x5. From Cisuralian of China. (Li & Gu 1976).

Family **PHRICODOTHYRIDAE** Caster, 1939

[Nom. transl. et correct. hic pro Phricodothyriinae Caster, 1939, p. 145].

Diagnosis: Single- and predominantly double-barrelled spines generally in one or often two rows over each commargon. Dental plates reduced, no adminicula. Deltidial plates and connector plate present or absent. No tabellae. Spiralia laterally or postero-laterally directed. Lower Carboniferous (Mississippian) to Upper Permian (Changhsingian).

Discussion: This group is separated as a family from somewhat similar genera referred to Elitidae in the *Revised Brachiopod Treatise*, because of the absence of adminicula. The low ventral median septum tends to be less prominent in *Phricodothyris* and absent from other genera, and is absent from the other subfamilies, Anomaloriinae and Astegosiinae, and no genus displays tabellae. It seems likely that *Phricodothyris* as the oldest genus within the family inherited the median ventral septum along with Elitidae, and later constituents

soon lost the septum. Several genera develop a connector plate.

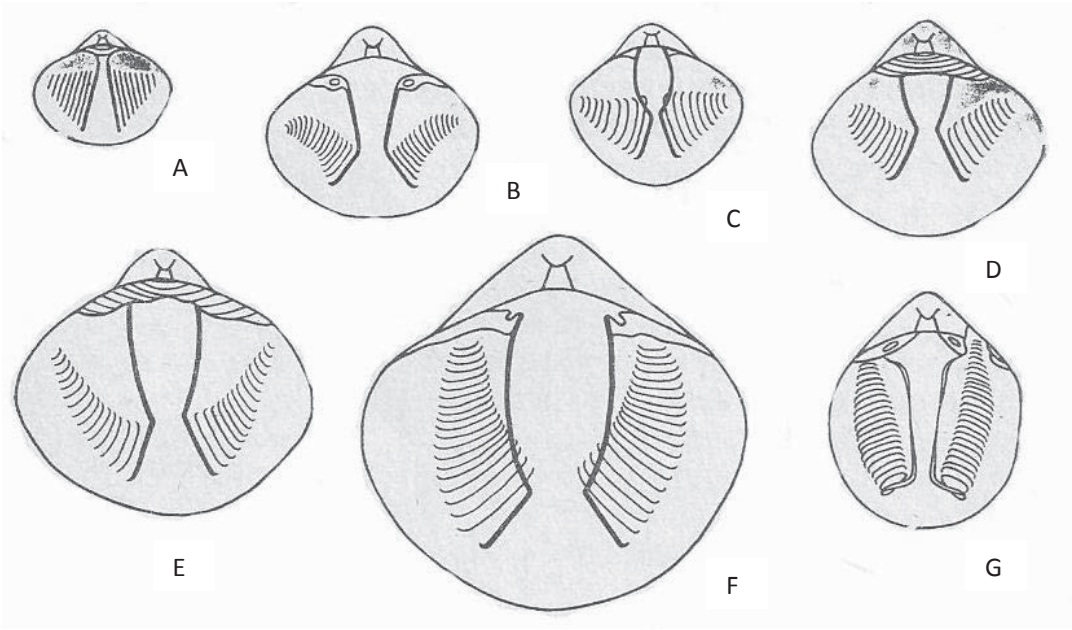


Fig. 454. Spiralia as shown in A, *Eoreticularia kotlubanica* Nalivkin, B, *Elita granosa* (Verneuil). C, *Orenburgella uralica* Pavlova. D, *Phricodothyris verecunda* George. E, *Torynifer asiaticus* Besnossova. F, *Kitakamithyris conquisita* (Monachova). G, *Permophricodothyris ovata* Pavlova. Specimens x0.8, as sketched and identified by Pavlova (1969).

Subfamily **PHRICODOTHYRINAE** Caster, 1939

[Nom. correct. hic pro Phricodothyridinae Carter in Carter et al., 1994, p. 354, nom. correct. pro Phricodothyriinae Caster, 1939, p. 145].

Diagnosis: Ornament of double-barrelled spines generally in one or often two rows over each commargon, of one diameter as a rule. Dental plates reduced, no adminicula. Deltidial plates present, no connector plate. Spiralia laterally or postero-laterally directed. Lower Carboniferous (Visean) to Upper Permian (Changhsingian).

Genera: *Phricodothyris* George*, Bajkuria* Ustritsky*, Bullarina* Jin & Sun, *Catatonaria* new genus, *Nebenothyris* Minato*, Neophricadothyris* Licharew.

Discussion: Phricodothyridae are distinguished by the lack of adminicula and tabellae. If they arose independently of Elitidae from stock like Obesariinae (because Squamulariinae is younger, being of Permian age), the double-barrelled groups would appear to be polyphyletic. But Obesariinae is itself of uncertain relationship, and in addition, the barbed double-barrelled spines are so specialized that multiple sources would seem unlikely. It is thus considered that the barbs and double-barrelled spines developed in Visean time, according to the fossil record, and descendents persisted into the very Late Permian.

The genus *Phricodothyris* George, 1932, type species *Phricodothyris lucerna* George, 1932 from the Visean of England, is applied to subrounded unequally biconvex non-plicate shells with short deltidial plates at high angle to interarea, low dental flanges, and dental

sockets nearly parallel to hinge margin. Crural bases arise from short crural plates in some forms, bulbous ctenophoridium in at least some species, no dorsal septum although a low ridge may be developed, and spiralia directed slightly postero-laterally. Ornament includes fine interspinous pustules or spinules, as well as double-barrelled spines. A low median ventral ridge may be developed. Samtleben (1971, p. 120, pl. 11, fig. 10, 11), in identifying *Phricodothyris guadalupensis* (Shumard, 1860) from the Lower Permian Copacabana Group (Asselian) of Bolivia, illustrated biramous spines in detail, much like those figured by George (1932), allowing for imperfections in preservation. No slender uniramous spines are present in Bolivian *Phricodothyris*. Whilst the material is not type material, it may well be illustrating the persistent nature of ornament for *Phricodothyris,* to judge from accounts of the micro-ornament in *Phricodothyris* from the Early Carboniferous of Great Britain.

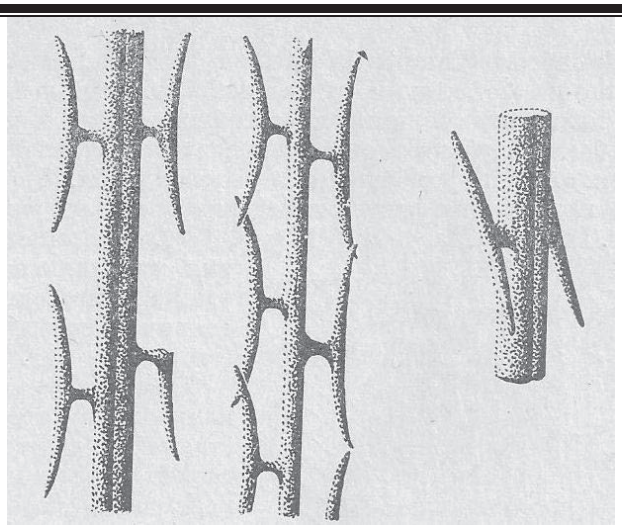


Fig. 455. Detail of the barbed double-barrelled spines in *Phricodothyris*. (George 1932).

Carter in Carter & Gouvennec (2006c, p. 1866) took a broad view of this genus and included several genera in synonymy, including *Neophricadothyris* Licharew, 1934 and *Condrathyris* Minato, 1953. *Condrathyris* was distinguished by Minato (1953) for species with fine and coarser spines, whereas the spines of *Phricodothyris* in the type species are restricted to those of the double-barrelled “coarser” type of spine. García-Alcade & Martínez-Chacón (1988, p. 48) recognized the distinction as valid. The one exception amongst Carboniferous species from the United Kingdom that had been described as *Phricodothyris* by George (1932, Fig. 2f, p. 528) is an unnamed species from the “Upper Limestone Series” of Gower, illustrating double-barrelled spines separated by three pustules, as also shown by Brunton (1984, Fig. 158a, b). Given the difference in ornament, it remains uncertain whether this material is congeneric with *Phricodothyris*, or that pustules are equivalent to single-barrelled spines.

There are several sets of criteria used to discriminate between otherwise closely

related genera. The direction of spiralia offers one criterion. As summarized by Yanagida & Nishikawa (1984, p. 183), *Neophricadothyris*, based on the Carboniferous species *Squamularia asiatica* Chao (Liao 1980), has coiling axes of spiralia extended postero-laterally and dorso-ventrally, following Cooper & Grant (1976). In *Phricodothyris*, the coiling axes extend at a low angle postero-laterally. In *Permophricodothyris*, the spiralia have numerous coils posteriorly extended.

A second facet concerns micro-ornament. In some shells, such as *Phricodothyris*, only biramous spines of uniform large size are found, aligned in single rows on each commarginal band. It means that such species as *perplexa* McChesney, which has a row of

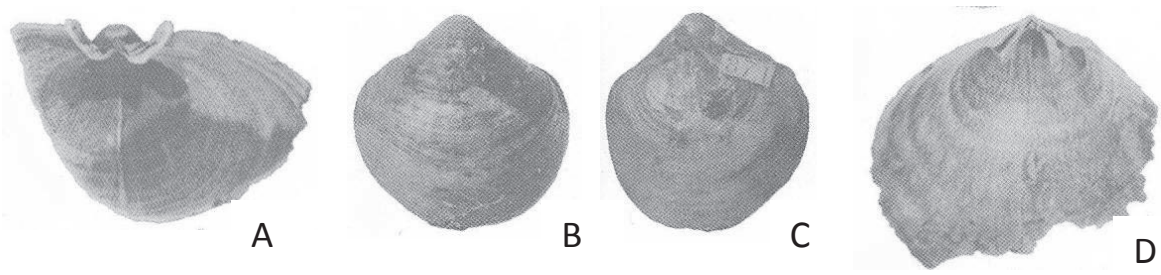


Fig. 456. *Phricodothyris verecunda* George. A, ventral interior, x3. D, dorsal interior, x3. (Brunton 1984). B, C, *P. lucerna* George, ventral and dorsal views of holotype, x1. (George 1932). From Visean of Great Britain.

double-barrelled spines and a row of much more slender double-barrelled spines (Dunbar & Condra 1932, text-fig. 22) are not congeneric. To *Phricodothyris,* Pavlova (1969) assigned various Urals specimens identified with English species, that displayed single as well as double-barrelled spines, but in view of the ornament, these species are not regarded as belonging to *Phricodothyris*. Type *Neophricadothyris*, based on *Squamularia asiatica* Chao, is obscure, given that each commarginal step shows simply a line of parallel ribs and grooves, suggestive of spines pressed against the shell. Associated species appear to show only single rows of double-barrelled spines, without single-barrelled spines, according to figures. For the species *echinata,* Chao (1929, p. 86) recorded double-barrelled spines in one row, with finer spines in front along another row, suggestive of *Phricodothyris* according to Yanagida (1967, p. 74), though that seems doubtful, and is suggestive of *Condrathyris*. The species *ovata* showed somewhat similar ornament. Grabau (1936, p. 186) considered the ornament on his Maping material was well preserved, and described radial striae ending in small spine bases, but in fact detail is far from clear. Overall the preservation for the Chinese material is indifferent, as confirmed by Yanagida (1967), and the reliability of the interpretation low. For *asiatica*, Pavlova (1969, text-fig. 60) illustrated only double-barrelled spines, apparently in two rows for each band. Yanagida (1962, p. 90) offered a strikingly different interpretation, which appeared to be authoritative, although he did not explain whether it was based on reassessment of the type species. He stated that when the surface is worn off,

longitudinal striae appear (as in Chao's figures of *asiatica*). He affirmed that the type species originally had neither biramous barbed spines nor spine bases, but a micro-ornament of fine pustules. But later, on the basis of Thai material deemed to be conspecific, Yanagida (1967, p. 75) referred *asiatica* to *Phricodothyris*, a view also advocated by Yanagida & Nishikawa (1984). In reporting supposed *asiatica* as *Neophricadothyris* from Novaya Zemlya, Licharew & Einor (1939, p. 157, pl. 27, fig. 3) showed an external fragment with prostrate spines and what appear to be finer spines in several rows. Of course the problem with such assessments is that they are not based on type material. In *Squamularia asiatica* Chao, 1929, pl. 11, fig. 12-14, type species of *Neophricadothyris* Licharew (1934, p. 211), the lamellae were described

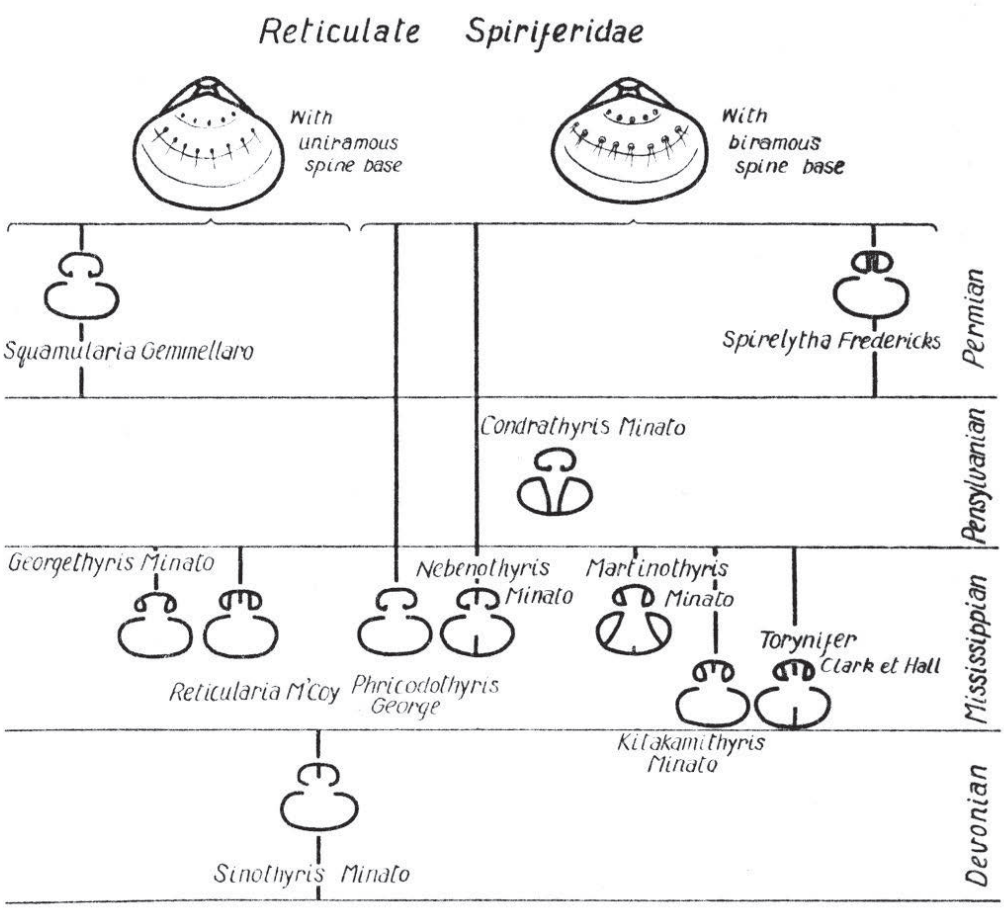


Fig. 457. Chart of relationships proposed by Minato (1953). *Sinothyris* has been synonymized with *Xenomartinia*, and was based on *Reticularia maureri* sensu Grabau not Holzapfel.

as marked by flattish wrinkles separated by grooves, with a row of longitudinal striae, representing, it was considered, the remains of pustules on the actual surface, as confirmed by Wang & Yang (1998). Chao (1929) noted other species that he had assigned to *Squamularia* were ornamented by lamellae with biramous spines or pustules, which he

illustrated for several species. In summary, there have been numerous accounts of the species *asiatica* Chao, and many different views.

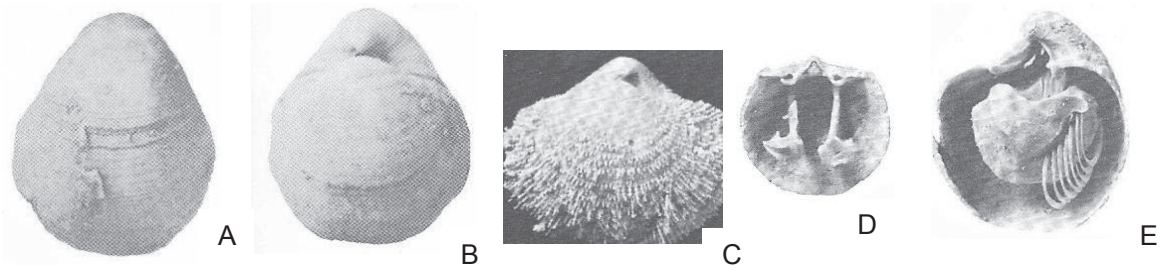


Fig. 458. *Bullarina bullata* (Cooper & Grant), ventral and dorsal views, x1. C, juvenile specimen with spines preserved, x3. D, young dorsal valve, x12. E, oblique view with spire held in undissolved limestone, x1. From lower Guadalupian (Roadian) and upper Cisuralian (Cathedral Mountain beds, Kungurian) of Texas, USA. (Cooper & Grant 1976).

Nebenothyris Minato (1953, p. 72) was proposed for *Spirifer* (*Reticularia*) *lineatus* Nebe, 1911 (not Martin) and Scupin (1900) from the Lower Carboniferous Kulm of Germany. Minato (1953, fig. 3) sketched very high septa in each valve, half the height of the ventral valve and more than half for the dorsal valve (see Fig. 457). But this model is contradicted by Brunton & Mundy (1997), with the demonstration of very low septa in each valve. Based presumably on the interpretation in Brunton & Mundy (1997), who examined well preserved Early Carboniferous specimens from Yorkshire, Carter in Carter & Gouvennec (2006c) treated *Nebenothyris* as a member of Phricodothyrinae, and it may be regarded as a possible progenitor of the Permian form *Bullarina* Jin & Sun, 1981, which shows similarly low but definite median septa in each valve.

Bajkuria Ustritsky in Ustritsky & Chernyak, 1963, p. 116 from Taimyr Peninsula in Arctic Russia is poorly known internally, but according to Carter in Carter & Gourvennec 2006c, p. 1866 has short tabellae (“dorsal adminicula”) and dorsal muscle scars bordered by ridges. The genus was recorded from the Baikursk and Turuzov levels in Taimyr.

Genus ***Catatonaria*** new genus

Derivation: Named from species name.

Diagnosis: Transverse shell with single row of unusually short double-barrelled spines along each commargon. Deltidial plates, no connector plate. Upper and Middle Permian (Cisuralian and Guadalupian).

Type species: *Neophricadothyris catatona* Cooper & Grant from Bone Spring and Skinner Ranch Formations (mid-Cisuralian) of Texas, United States, here designated.

Discussion: *Bullarina* Jin & Sun, 1981 was erected on the basis that the spiralia were directed postero-laterally. There are two further aspects to the morphology. Species have a low but long and clearly developed median ridge in each valve, described and well illustrated by

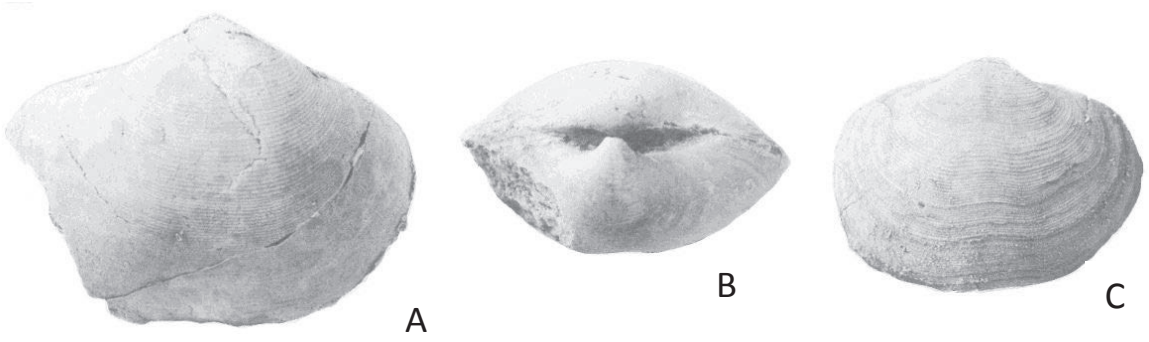


Fig. 459. *Catatonaria catatona* (Cooper & Grant). A, large ventral valve. B, posterior view of holotype. C, dorsal valve. Specimens x1 from Skinner Ranch Formation (lower Kungurian), Texas, United States. (Cooper & Grant 1976a).

Cooper & Grant (1976). The length may vary somewhat: it is weak for *bullata* as figured by Cooper & Grant (1976, pl. 635, fig. 38, 49), strong in *cordata* dorsal valves (Cooper & Grant 1976, pl. 637, fig. 38, 45) and *crassibecca* Cooper & Grant (1976, pl. 638, fig. 31), and not clearly developed in *transversa*, the oldest of the described species, from the Neal Ranch Formation. Furthermore, some species have two rows of double-barrelled spines on the commarginal steps, examples

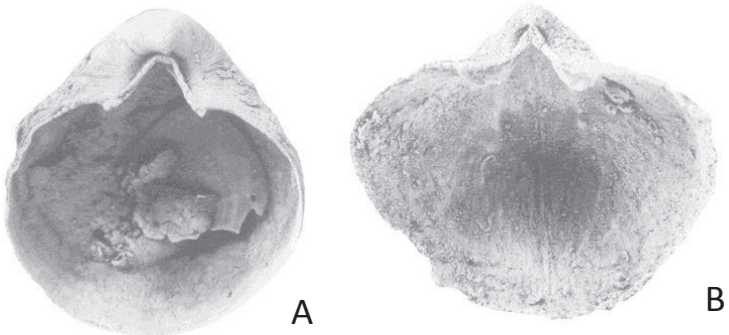


Fig. 460. Deltidial ridges in A, *Bullarina bullata* (Cooper & Grant), and B, *B. cordata* (Cooper & Grant). Specimens x 2, from Road Canyon Formation (Roadian) of Texas, USA. (Cooper & Grant 1976).

being *conara, cordata*, and *bullata*, which are subelongate shells. The species *catatona, crassibecca* and *transversa* are more transverse, and *catatona* and *transversa* are distinguished by the spines, which are short and fine in single rows along each commargon, to indicate two slightly different lineages. A different species, *crassibecca* from the Neal Ranch Formation, comes closest to *Phricodothyris* in its single row of spines and in its feeble if any development of internal median septa. Spiralia are diverge towards the posterior shell. Spiral cones are described as parallel to the median plane in *cordata* by Cooper & Grant (1976), but that may turn out to be less significant that the spination.

The delthyrial covering is well preserved in a number of species belonging to

Bullarina and *Catatonaria*. In *Bullarina bullata*, high ridges project from the delthyrial margin and merge under the beak, like thick low deltidial plates (Cooper & Grant, 1976, pl. 635, fig. 61, 64), and stronger ridges are present in *B. cordata* (Cooper & Grant, 1976, pl. 637, fig. 48) and *B. conara* (Cooper & Grant, 1976, pl. 638, fig. 43). *Catatonaria transversa* (Cooper & Grant, 1976, pl. 639, fig. 18) seems similar.

Subfamily **ASTEGOSIINAE** new subfamily

Name genus: *Astegosia* Cooper & Grant, 1969, p. 16 from Guadalupian of Texas, here designated.

Diagnosis: Double-barrelled spines, no adminicula, low crural plates, no medium septum in either valve. Large connector plate may be developed, no deltidia. Middle Permian.

Genus: *Astegosia* Cooper & Grant.

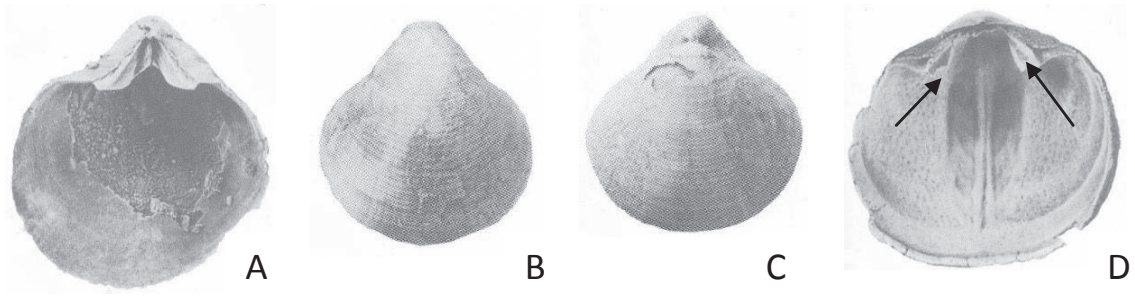


Fig. 461. *Astegosia subquadrata* (Girty). A, ventral interior, x1.5, showing a well developed connector plate. B, C, ventral and dorsal views, x1. D, dorsal interior, with crural plates arrowed, x1.5. From Guadalupian of Texas. (Cooper & Grant 1976).

Discussion: *Astegosia* is highly unusual, because it has a large connector plate. It is allied to Phricodothyrinae, which has a similar interior, that lacks adminicula (see p. 340), and displays double-barrelled spines. Figures of *Astegosia subquadrata* (Girty) as presented in Cooper & Grant (1976, pl. 642) show distinct crural plates below and inside the inner dental socket plates. In the diagnosis of *Astegosia*, Cooper & Grant (1976, p. 2256) described the spines as single-barrelled, but in the description of the one and only species, the spines were recorded as double-barrelled, and as far as known, this is correct.

Subfamily **ANOMALORIINAE** Cooper & Grant, 1969

[Nom. transl. Carter in Carter et al. 1994, p. 359 ex Anomaloriidae Cooper & Grant, 1976, p. 2260].

Diagnosis: Double-barrelled spines. Delthyrium covered by convex delthyrial cover plate. Dorsal interior with notothyrial flanges fused to inner socket plates that may cover dental sockets. No adminicula, or even low median septum, or tabellae. Middle Permian (Guadalupian) to Upper Permian (?Wuchiapingian).

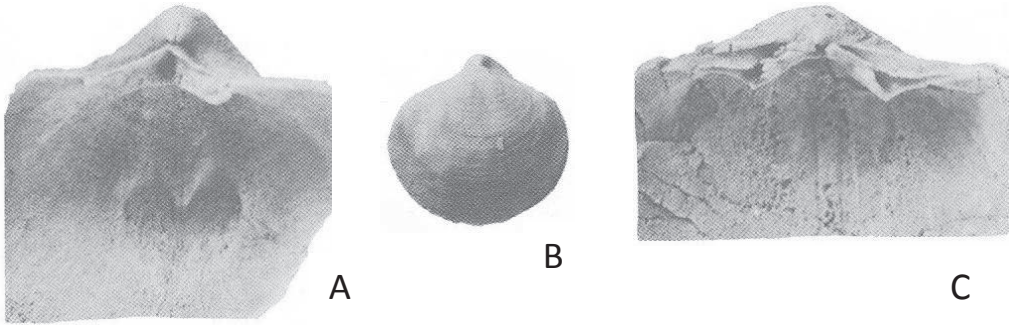


Fig. 462. *Anomaloria anomala* Cooper & Grant. A, ventral interior, x3. B, dorsal view of holotype, x1. C, dorsal interior, x3. From Guadalupian of Texas, United States. (Cooper & Grant 1976).

Genera: *Anomaloria* Cooper & Grant, ?*Zhinania* Liang.

Discussion: This small group is distinguished by the extended flanges which curl over the dental sockets. Whether this marked a discrete subfamily remains open to question, and a genus from Thailand as decribed on p. 356 as *Khaophrikia* has somewhat similar flanges, but is distinguished from *Anomaloria* and *Zhinania* by its spines. Here, greater emphasis is placed on the spines, and that remains a matter for further enquiry.

Carter & Gouvennec (2006c, p. 1870) included the genus *Zhinania* Liang, 1990, p. 308 from the late Guadalupian or more likely early Lopingian (Wuchiapingian Stage) of Zhejiang, China, in the subfamily. The type species *Z. eximiusa* Liang is based on internal moulds which indicate that dental flanges fuse under the umbo, and a large delthyrial cover is figured (Liang

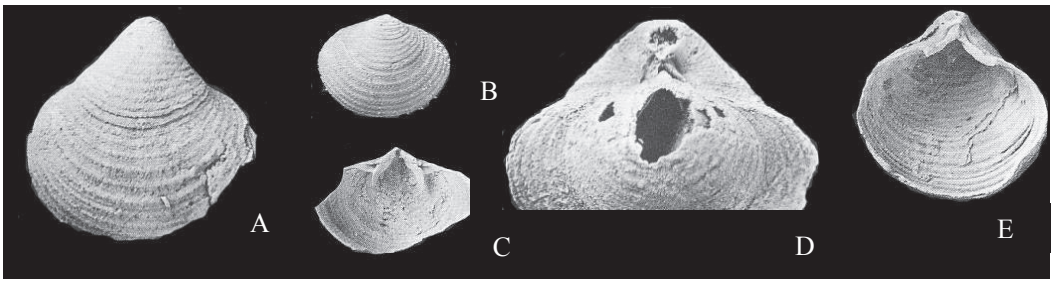


Fig. 463. *Anomaloria glomerosa* Grant. A, ventral exterior, x1. B, dorsal exterior, x1. C, dorsal internal valve, x1. D, dorsal view of specimen with valves conjoined, x3. E, ventral interior, x1, showing a convex deltidial cover plate. From Rat Buri Limestone of Roadian (early Guadalupian) age, Thailand. (Grant 1976).

1990, text fig. 39b), but nothing is known about the nature of notothyrial plates, nor detail of ornament other than presence of double-barrelled spines, nor spire. Liang (1990, p. 473) recorded a circular foramen “at the top end” of the delthyrial cover plate, and stated that short hinge plates were present, their nature not further explained, together with “small and thin

cardinal process". As Liang (1990) noted, the muscle scars also appear to differ substantially from those of *Anomaloria*, notably in the lack of deeply impressed heart-shaped adductor scars typical of *Anomaloria*.

Fig. 464. *Anomaloria anomala* Cooper & Grant), ventral valves showing deltidial cover plate, x 2, from Bell Canyon Formation (Capitanian), Texas, United States. (Cooper & Grant 1976).

Family **CONDRATHYRIDAE** new family

Nominate genus: *Condrathyris* Minato, 1953, p. 69 from Pennsylvanian of United States, here designated.

Diagnosis: Ornament of double-barrelled spines of two different diameters, and single-barrelled slender spines in various combinations. Spiralia laterally or posteriorly directed. Dental plates reduced, flanges may partly close delthyrium, connector plate short or as a rule absent; median ridges subdued or absent. Late Carboniferous to Late Permian (Changhsingian).

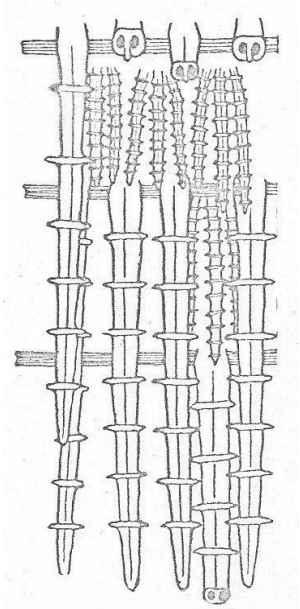


Fig. 465. *Condrathyris perplexa* (McChesney), detail of barbed and double-barrelled spines of two different diameters from Pennsylvanian of mid-United States. (Dunbar & Condra 1932).

Genera: *Condrathyris* Minato, *Biramus* new genus, *Huaitakithyris* new genus, *Khaophrikia* new genus, *Permophricodothyris* Pavlova, *Triramus* new genus.

Discussion: Condrathyridae are a minor lineage delineating a sequence of genera with

double-barrelled spines of two diameters. One of the genera, *Khaophrikia*, is exceptional in that it displays strong and slender double-barrelled spines, but approaches *Anomaloria* in some respects.

Condrathyris Minato (1953, p. 69) was based on *Spirifer perplexa* McChesney (1860, p. 53), figured by Girty (1903, p. 392, pl. 11, fig. 1-3) and Dunbar & Condra (1932, p. 313, pl. 42, fig. 5-8), and has been recognized in northeast China by Hayasaka (1922) and Ozaki (1931), although their descriptions do not clarify the nature of the ornament. The type species has two deltidial plates, and displays biramous spines of two diameters (Dunbar & Condra 1932, text-fig. 22), apparently each in a single row over each commargon. Minato (1953) stressed the presence of a pair of lamellae in the dorsal valve that were interpreted as socket plates, rather than the crural supports as envisaged by Dunbar & Condra.

Phricodothyris pyriformis Pavlova (1969, pl. 8, fig. 1-3, text-fig. 58, 59), and including *Reticularia lineata* of Chernyshev (1902, p. 25, pl. 20, fig. 9-13) and *Neophricadothyris asiatica* of Stepanov (1937, pl. 8, fig. 2) has, according to Pavlova (1969, text-fig. 58), a row of double spines and a row of finer biramous spines, not clustered in threes, and Pavlova (1969, pl. 8, fig. 1b) illustrated one or two rows of coarse spines (the nature unclear), behind one to three rows of single slender spines. The species is of Artinskian age in the Urals, and its spiralia are oriented laterally.

Yanagida (1962, pl. 14, fig. 5b) illustrated a row of coarse double-barrelled spines and a row of finer double-barrelled spines for Japanese specimens from the Carboniferous *Millerella* Zone in southwest Japan. Not all detail is clear, and a row of finer spines seems to be developed in front of the other two along at least one commargon (Yanagida 1962, pl. 14, fig. 5b). The species was mistakenly ascribed to *P. insolita* George, 1932.

Genus ***Biramus*** new genus

Name: bi – two; ramus – a branch, Lat.

Diagnosis: Double-barrelled spines broad, barbed, interspersed with single-barrelled barbed spines. Interior as in *Phricodothyris*.

Type species: *Phricodothyris mosquensis* Ivanova, 1960, pl. 63, fig. 12, 13 from Myachkov Horizon, Moscow Basin, Russia, here designated.

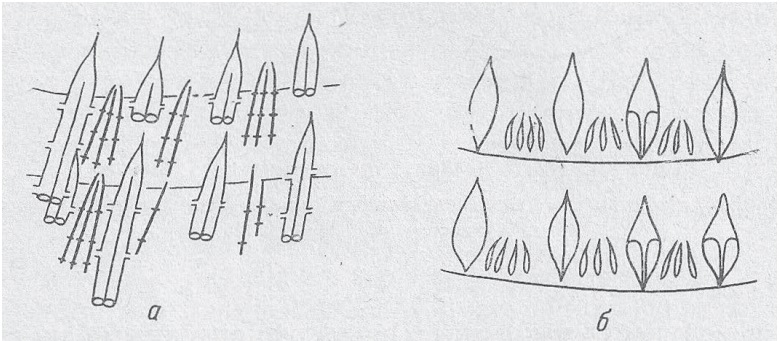


Fig. 466. *Biramus mosquensis* (Ivanova), micro-ornament, x25. From Middle Carboniferous of Moscow Basin, Russia. (Pavlova 1969).

Discussion: The type species has been figured and described by Sarytcheva & Sokoskaya

(1952, p. 223, Ivanova 1960, pl. 63, fig. 12, 13) and especially Pavlova (1969, p. 89, pl. 7, fig. 4, 5, 8-10, text-fig. 55, 56). The broad double-barrelled spines lie in commarginal rows, and single-barrelled spines depicted with barbs lie in clusters of one to three between, as illustrated. Whether the single-barrelled spines have developed barbs from spines originally single-barrelled, or whether they have become single-barrelled by reduction from double-

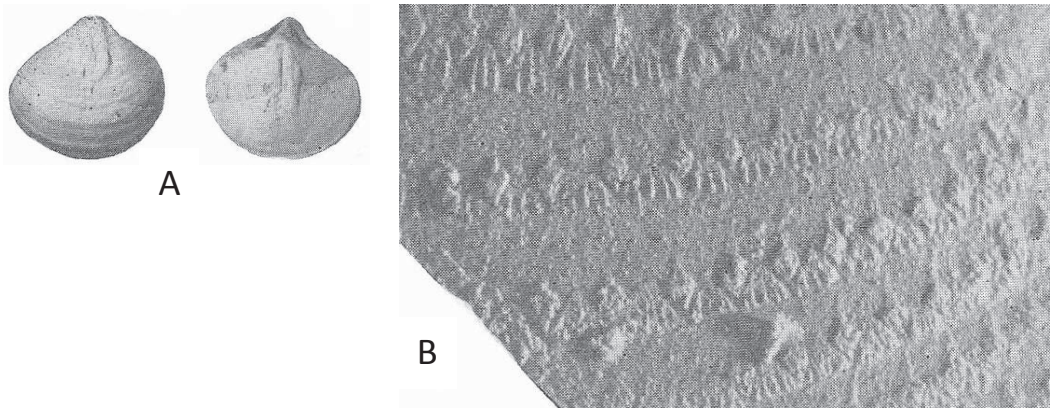


Fig. 467. *Biramus mosquensis* (Ivanova). A, ventral and dorsal aspects, x1. B, micro-ornament, x20. From Middle Carboniferous of Moscow Basin, Russia. (Pavlova 1969).

-barrelled spines, as would seem more likely, requires further study, but the barbs seem so specialized that it is deemed likely that the double-barrelled spines could be reduced in diameter to slender double-barrelled spines, or be further reduced to single-barrelled spines that retained their barbs. An additional similarity to *Condrathyris* lies in the clustering of the single-barrelled spines, which are like the slender double-barrelled spines of *Condrathyris* in being evenly spaced in possible threes along commarginal rows.

Late Carboniferous specimens from the central Pyrenees of France that were referred to *Phricodothyris* aff. *mosquensis* Ivanova, 1960 by Legrand Blain et al. (1984, p. 316, pl. 1, fig. 21) and have spines in two orders, and there have been other reports of *mosquensis* in Russia.

Genus ***Triramus*** new genus

Derivation: tri – triple; ramus – branch, Lat.

Type species: *Triramus canadense* n. sp. from Member D of lower Jungle Creek Formation (Asselian), Yukon Territory, Canada, here designated.

Diagnosis: Oval smooth shells with shallow or imperceptible ventral sulcus and dorsal fold, ornamented over parts of the shell by one or more rows of thick double-barrelled spines, behind one or rarely more rows of evenly spaced single-barrelled spines over low commarginal growth lamellae or growth steps on each valve, as well as scattered slender double-barrelled spines. Teeth with only low dental ridges, median ridge low or absent, no adminicula; dorsal socket and inner hinge plates, low or no median ridge, no tabellae. Spiralia

laterally directed.

Discussion: This genus is very close to *Phricodothyris* George, 1932, but has more elaborate ornament, with rows of single-barrelled spines as well as double-barrelled spines of two diameters. Members of Phricodothyrinae tend to have single rows of biramous spines of subuniform diameter, but are close in internal plates. Compared with *Phricodothyris* as described by Brunton (1984), the present form is distinguished by the presence of a dorsal septal ridge in many but far from all specimens, and open nature of the delthyrium, which is partly closed in *Phricodothyris* by flat deltidial plates. George (1932) emphasized the lack of a dorsal septum from the British type and associated material of *Phricodothyris*, and although it is true that Demanet (1938) reported a ventral septum in material from Belgium, such is less evident in the British material (Campbell 1955). The micro-ornament, as assessed by Pavlova (1969), displays only single rows of double-barrelled spines.

Condrathyris has rows of slender and broader double-barrelled spines, and *Biramus* has broad double-barrelled spines and what appear to be single-barrelled spines in clusters along rows, both sets of spines bearing barbs.

Triramus canadensis n. sp.

Name: Named for Canada.

Holotype: GSC 136662 from lower Jungle Creek Formation, Member D (see Waterhouse 2013, p. 478), of Asselian age, Yukon Territory, Canada, Fig. 468C herein, here designated.

Diagnosis: Small subrounded moderately inflated shells with both valves covered by commarginal growth laminae bearing rows of biramous spines in rows, occasionally preceeded by slender double-barrelled spines, followed anteriorly by a row – rarely more - of single-barrelled spines over parts of the shell.

Material: From lower Jungle Creek Formation. Member D (Asselian), Yukon Territory, Canada.

Description: Biconvex, ventral valve weakly transverse with pointed incurved umbo (angle 80-100^{o}) and concave steep umbonal walls; hinge close to half the width of the valve, with open delthyrium widening at angle of 40-45^{o} and no connector plate or high deltidial ridges; cardinal extremities obtuse, maximum width near or just behind mid-length and no sulcus or plicae. Dorsal valve transverse and convex with inconspicuous slightly protruding umbo and no fold. Both valves covered by low commarginal laminae, just over 1mm wide in ventral valves anteriorly, and bearing as a rule a row of biramous spines, three to five in 1mm medianly, at mid-band, in front of shell marked by fine growth increments. Rarely, a row of short flutings lies over the posterior commarginal lamination behind each larger biramous spine. Laterally the biramous spines are replaced by uniramous spines in some specimens. In front of or sometimes behind the conspicuous spines is occasionally a row, often incomplete, of much smaller biramous spines. Uniramous spines appear in a row or two in front of the larger spines, especially near the anterior margin, with no row of slender biramous spines. Dorsal valves are more worn, and are of similar ornament, though not so well preserved.

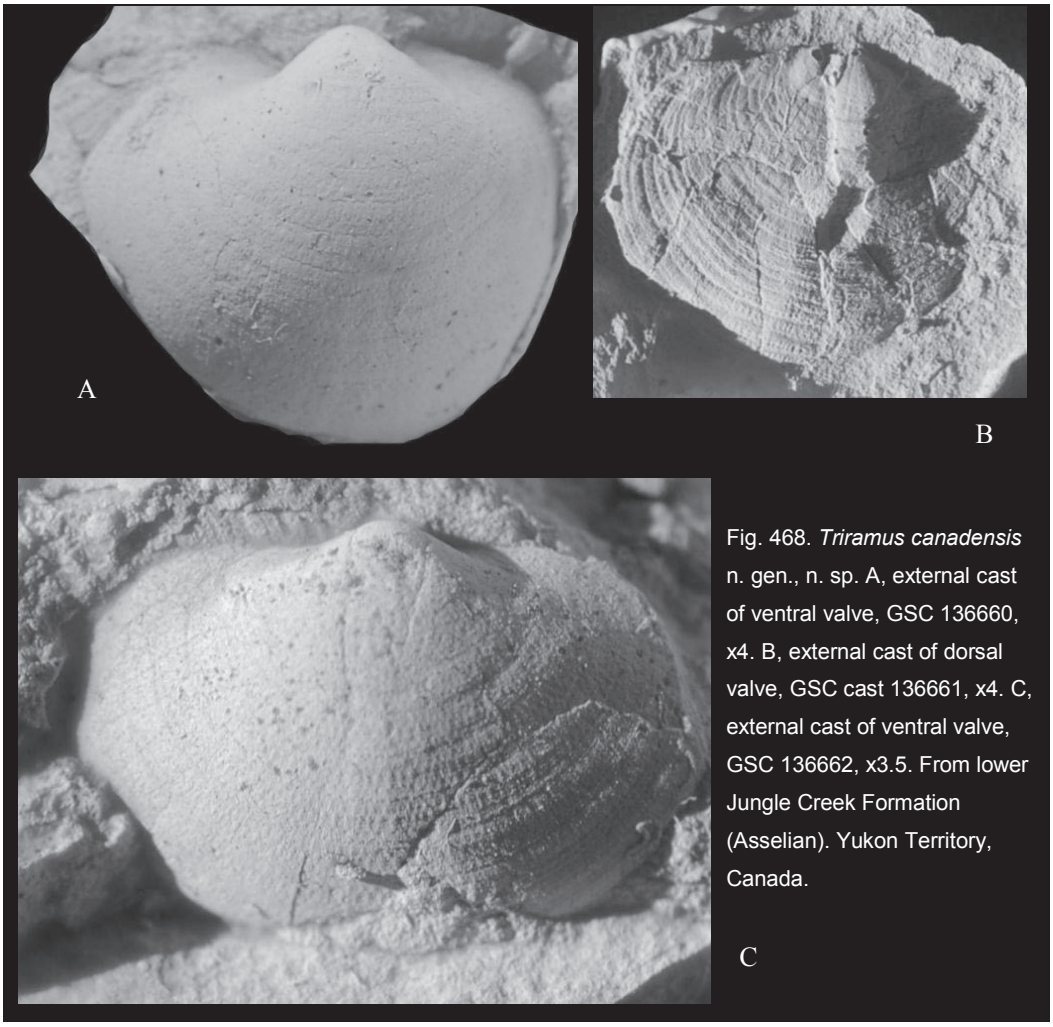


Fig. 468. *Triramus canadensis* n. gen., n. sp. A, external cast of ventral valve, GSC 136660, x4. B, external cast of dorsal valve, GSC cast 136661, x4. C, external cast of ventral valve, GSC 136662, x3.5. From lower Jungle Creek Formation (Asselian). Yukon Territory, Canada.

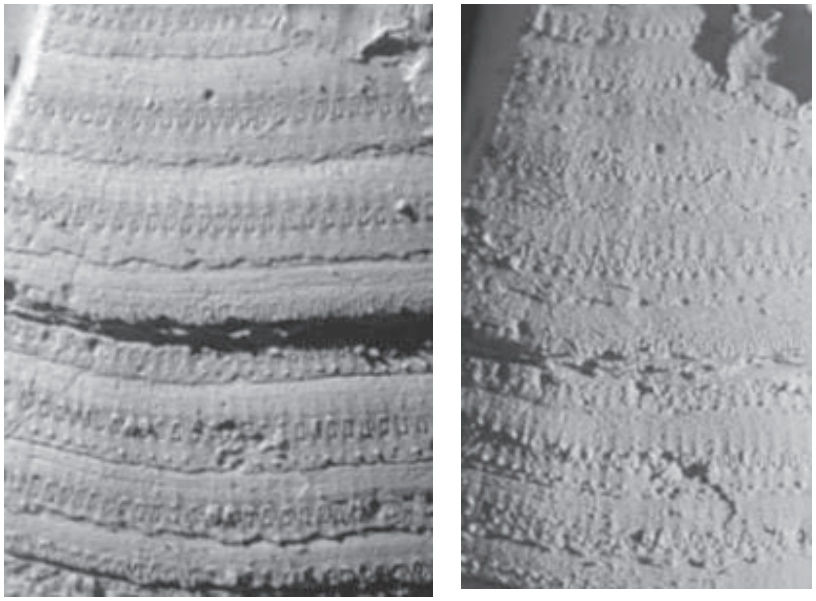


Fig. 469. *Triramus canadensis* n. gen., n. sp. external cast of ventral micro-ornament, GSC 13665, x8. From lower Jungle Creek Formation (Asselian), Yukon Territory, Canada.

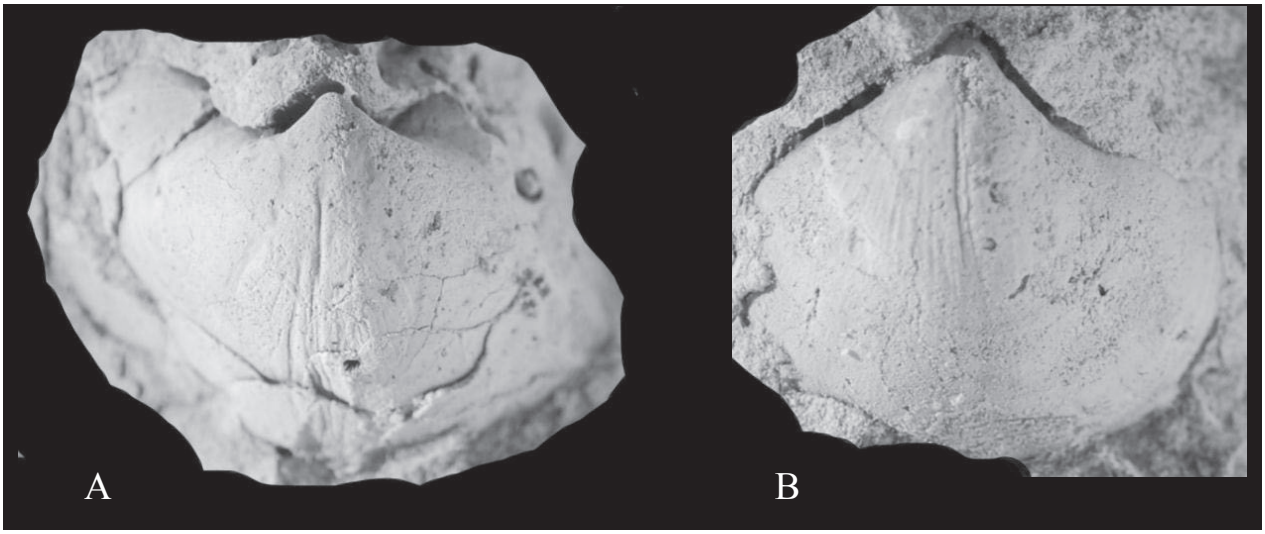


Fig. 470. *Triramus canadensis* n. gen., n. sp. A, internal mould of ventral valve, GSC 136663, x4. B, internal mould of dorsal valve, GSC 136664, x4. From lower Jungle Creek Formation (Asselian), Yukon Territory, Canada.

Fig. 471. *Triramus canadensis* n. gen., n. sp. external mould of ventral micro-ornament, GSC 136665, x20. From lower Jungle Creek Formation (Asselian), Yukon Territory, Canada.

Low dental flanges support the teeth, and there are no adminicula, and no median septum. The adductors appear to be very narrow and extend well forward: they may be bordered by a low ridge each side of a shallow concave trough, or form a slender ridge. Diductor scars also extend well forward and are scarcely impressed, but are marked by fine radial striae. The floor may be smooth or weakly marked by commarginal ridges reflecting the external laminae. The mature ventral valve carries light flexuous radiating vascular impressions, and a very low median ridge is present for much of the length of the valve. The dorsal valve has small dental sockets, and a long but very low median ridge extending from the hinge to beyond mid-length in some specimens, whereas a median groove is present in other specimens. A pair of tear-shaped adductor impressions lies in front of the hinge, bearing light longitudinal striae, and faint radial mantle canals are developed over the floor of the valve. There is no clearly preserved cardinal plate, but crural flanges extend each side of the plates bounding the inner side of the sockets. Spiralia directed laterally.

Resemblances: From the Late Carboniferous Mishkin Suite and lower Akachan Suite of northeast Russia, including south Verchoyan, *Phricodothyris lenaensis* Abramov & Grigorieva (1983, p. 140, pl. 32, fig. 10-12, text-fig. 55) and Klets (2005, pl. 28, fig. 4-8), and judged to include *P. asiatica* of Solomina (1978, p. 120, pl. 11, fig. 10, 11) by Klets (2005, p. 152), is very close in shape but displays only one row of biramous spines along each growth step. Specimens identified as *Phricodothyris asiatica* (Chao, 1929) from the Talatin Suite figured by Kalashnikov (1983, pl. 49, fig. 1-3) show a row of coarse posterior spines and confused bands in front, possibly involving two rows of finer spines. Gobbett (1964, p. 132, pl. 17, fig. 1-3, text-fig. 19) recorded one to three rows of spines, of two sizes, so that his material, identified as *Neophricadothyris asiatica*, and coming from the Cora Limestone and Upper Wordiekammen Limestone of Spitsbergen, could prove to be allied to *Triramus canadensis*. Specimens are of similar shape and size, although figures are too small to allow satisfactory comparison. Specimens from northeast Russia, such as those figured as *Neophricadothyris asiatica* by Kashirtsev (1959, pl. 36, fig. 1, 2) from the Kigiltass Suite of Verchoyan might be closely allied, but detail of the ornament is not available. However Stepanov (1937, pl. 3, fig. 9) illustrated a specimen from the northern Urals with single rows of sturdy spines, and no finer spines. Ozaki (1931) reported the species from northeast China.

Genus ***Permophricodothyris*** Pavlova, 1965

Fig. 472. *Permophricodothyris ovata* Pavlova, dorsal view of species from Djulfian of Armenia, x0.8. (Carter in Carter & Gourvennec 2006c, p. 1866).

In *Permophricodothyris* Pavlova, 1965, the type species *ovata* shows a single row of double-barrelled spines, interspersed with or behind a row of slender biramous spines (Pavlova 1969, p. 98, text-fig. 62). Spiralia are distinctly oriented along a posterior-anterior direction, reflecting the elongate outline of the shell.

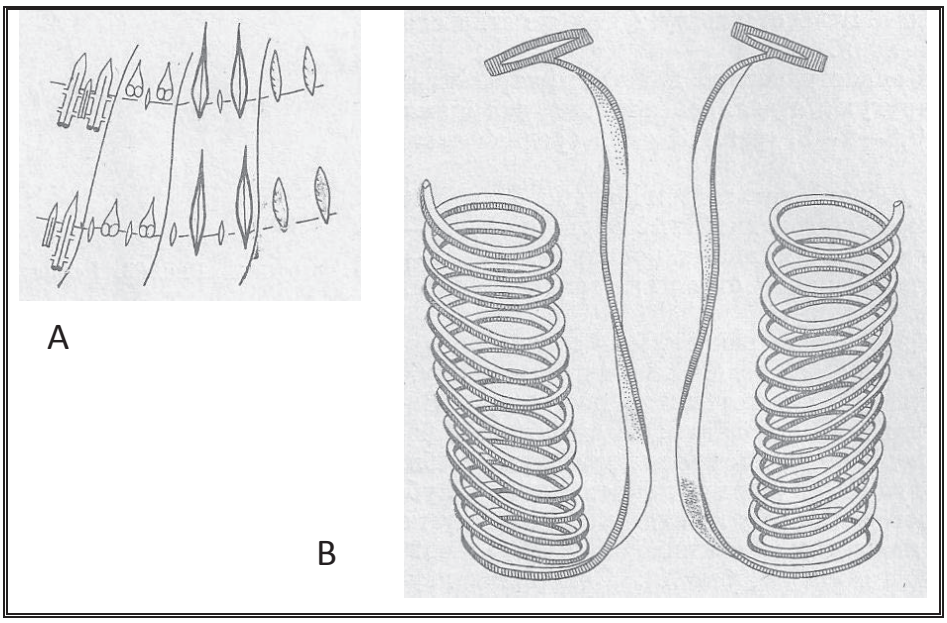


Fig. 473. *Permophricodothyris ovata* Pavlova. A, diagram of external ornament, x25. B, diagram of the spiralia. From Djulfian (Dzhulfian) of Armenia. (Pavlova 1969).

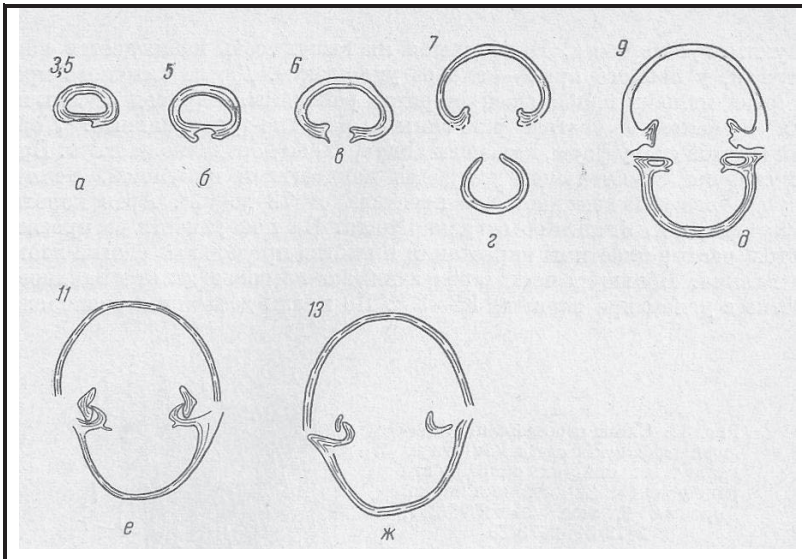


Fig. 474. *Permophricodothyris ovata* Pavlova, transverse sections with distance in mm from ventral beak indicated by figures above each diagram. From Djulfian of Armenia. (Pavlova 1969).

Genus ***Khaophrikia*** new genus

Name: Khao Phrik – Thai place name.

Diagnosis: Suboval to weakly transverse shells with narrow hinge, delthyrium partly closed by convex swollen delthyrial cover plate, notothyrium may be closed by extended socket plates,

growth lamellae bearing row of double-barrelled spines, in front of several rows of slender double-barrelled spines. Small dental plates, well developed ctenophoridium, descending lamellae of spiralia broad, extending from inner socket plates, spiralia probably laterally directed.

Type species: *Khaophrikia ratburiensis* n. sp. from Rat Buri Limestone (lower Guadalupian), Thailand, here designated.

Discussion: This genus is close in some respects to *Anomaloria* Cooper & Grant, 1969, based on *Anomaloria anomala* Cooper & Grant, 1969, p. 16 from the Lamar Member, Bell Canyon Formation, Texas. Like the new genus, *Anomaloria* involves suboval shells with narrow hinge. The delthyrium is partly closed by a convex delthyrial cover plate, and the notothyrium may be closed by extended socket plates. Internally there are small dental plates, and the descending lamellae of spiralia are broad, extending from inner crural plates. In *Anomaloria*, the spiral cones are directed postero-laterally, but the cones are not preserved for the Thai species, although the weakly transverse shape suggest a likely transverse or weakly postero-lateral orientation. Differences are that the external ornament in *Anomaloria* consists solely of double-barrelled spines in single rows along each growth lamellum, whereas in the new form, there are slender double-barrelled spines in one to five rows behind each row of wider double-barrelled spines which lies near the front of each commargon. Internally, a ctenophoridium is well developed (Waterhouse & Piyasin 1970, pl. 26, fig. 13), and the posterior dental sockets become somewhat enclosed, though not to the same degree as in *Anomaloria anomala*, as described and illustrated by Cooper & Grant (1976, pl. 640, fig. 49). Details of the delthyrial cover plate also differ: it is large and covers the external dental tracks in *A. anomala* (Cooper & Grant 1976, pl. 640, fig. 14, 31, 34 etc.), but lies within the dental tracks in the Thai species (Waterhouse & Piyasin 1970, pl. 26, fig. 11). The arrangement of the coarse and slender double spines is unique to this genus.

Zhinania Liang differs in its small ctenophoridium and muscle field, and a foramen lies below the beak in the delthyrial cover plate.

Khaophrikia ratburiensis n. sp.

1970 *Phricodothyris attenuata* [not Reed] – Waterhouse & Piyasin, p. 157, pl. 26, fig. 7-18.

1976 *Anomaloria glomerosa* [not Grant] – not Grant, 1976, p. 220.

Name: Rat Buri, Thai place name.

Diagnosis: Subovoid shells with prominent ventral umbo and distinctive ornament.

Holotype: B 488, kept at Royal Ontario Museum, Toronto, figured by Waterhouse & Piyasin (1970, pl. 26, fig. 14, 18), and Fig. 475D and 476C herein, from Rat Buri Limestone (Roadian), Khao Phrik, Thailand, here designated.

Discussion: This species has been described and figured by Waterhouse & Piyasin (1970). Grant (1976) drew attention to the possible identity with *Anomaloria*, and synonymized most of the figured specimens with his species *Anomaloria glomerosa* Grant (1976, p. 220, pl. 60, fig. 1-42) from limestone of the same age at Ko Muk, an island south of Rat Buri. He

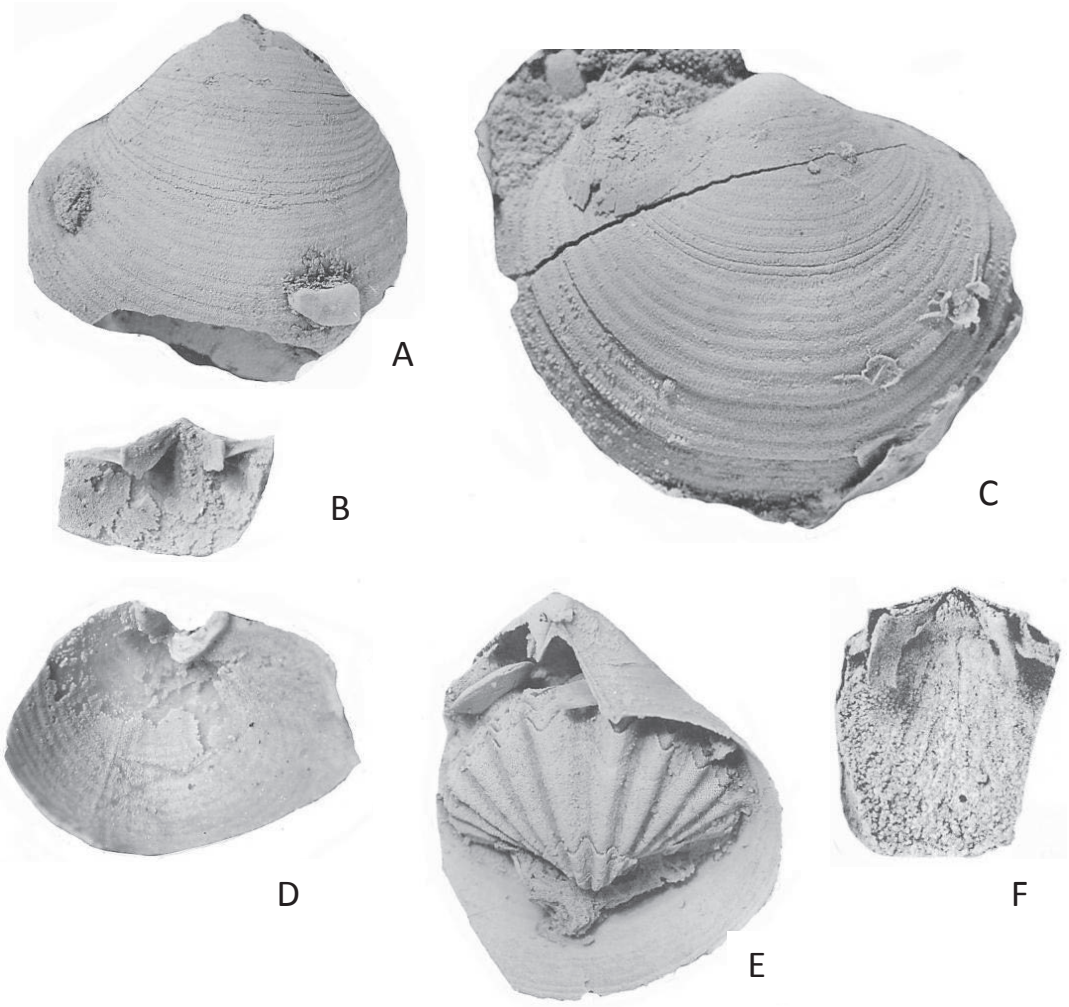


Fig. 475. *Khaophrikia ratburiensis* n. gen., n. sp. A, ventral exterior, x2. B, dorsal cardinalia, x3. C, dorsal exterior, x2. D, holotype, ventral interior, x3. E, ventral interior, x3. F, dorsal cardinalia, x3. Specimens from Rat Buri Limestone of early Guadalupian (Roadian) age, Thailand. (Waterhouse & Piyasin 1970).

omitted some specimens from synonymy, out of caution, in case some were *Permophricodothyris*. He put a few specimens in synonymy with *Permophricodothyris notialasiatica* (Grant 1976, p. 224), enumerating specimens figured by Waterhouse & Piyasin (1970, pl. 26, fig. 7, 8, 10-14, 16, 17), but added “at least”. The specimen of pl. 26, fig. 14 was also doubled up as being *Anomaloria*. His synonymy is set aside. Without needing to detail each specimen, it may be noted that the specimen of pl. 26, fig. 11 shows the delthyrial cover plate typical of the new form and unlike any structure in *Permophricodothyris*, and the specimen of pl. 26, fig. 13 has the extended inner socket plates that mask the posterior dental sockets, unlike structures in *Permophricodothyris*. Some specimens may be judged obscure as to their affinities, but have little bearing on the generic circumscription of the critical species. The micro-ornament figured for various species of *Permophricodothyris* by Pavlova (1965, 1969) does not correspond with the details of micro-ornament in the present form from Thailand. Deltidial ridges coalesce under the umbo, much as in other genera, but

no specimen displays a complete and convex deltidial cover plate.

There are many similarities between the present species and *Anomaloria glomerosa* Grant, but overall shape is somewhat different, the present species being more transverse with ventral posterior walls less concave in outline, and as shown in the dimensions tabulated by Waterhouse & Piyasin (1970, p. 158) as compared with the figures in Grant (1976, pl. 60), the two valves are not so disparate in thickness – though the dorsal valves of *glomerosa* are much less inflated than the ventral valve, whereas the dorsal valves in *ratburiensis* are less inflated than the ventral valve, but not markedly so. No specimens show the complete deltidial cover plate typical of *Anomaloria* and *Zhinania*. Grant (1976) referred only to double-barrelled spines in his description of the ornament in *glomerosa*, and no mention was made of a ctenophoridium or cardinal process. Figures are not fully clear, but seem to suggest that the delthyrial cover plate covers the dental tracks. These aspects, whilst in need of confirmation, strongly suggest that *glomerosa* is true *Anomaloria*.

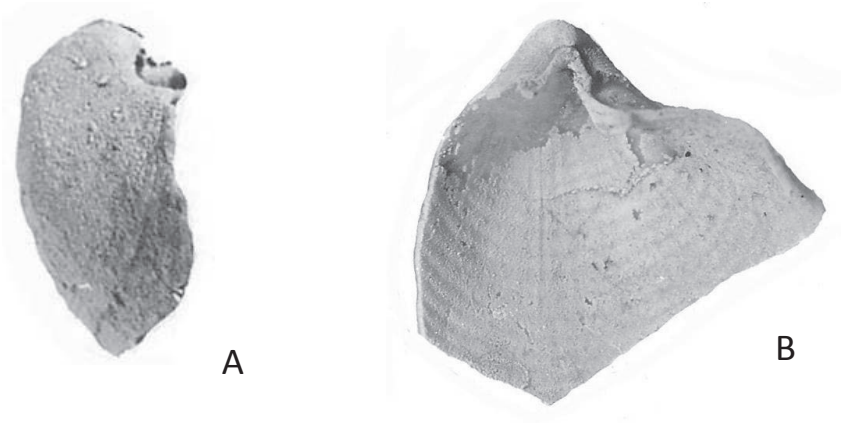


Fig. 476. *Khaophrikia ratburiensis* n. gen., n. sp. A, lateral view of ventral exterior, x3. B, holotype ventral valve x4. See also Fig. 475D. Specimens from Rat Buri Limestone of early Guadalupian (Roadian) age, Thailand. (Waterhouse & Piyasin 1970).

Permophricodothyris notialasiatica Grant 1976, p. 224 is transverse with open delthyrium, rows of double-barrelled spines at the edges of growth lamellae, with spiralia directed postero-laterally. The genus does not belong to *Permophricodothyris*, because no slender double-barrelled spines are present, and the species appears to belong to *Bullarina* Jin & Sun.

Genus ***Huaitakithyris*** new genus

Name: Named from Huai Tak, place name in northern Thailand.

Diagnosis: Subelongate shells distinguished by arrays of double-barrelled spines over posterior and middle shell, succeeded anteriorly by rows of slender single-barrelled spines.

Type species: *Squamularia postgrandis* Waterhouse (1983b, p. 136) from the late Permian (Changhsingian) Huai Tak Formation of Thailand.

Discussion: For so-called *Squamularia postgrandis* from the late Permian Huai Tak Formation of Thailand, Waterhouse (1983b, p. 137) described broad double-barrelled spines in single rows behind each lamellum, with a slender ridge behind each spine. Anterior rows of slender spines, thought to be single-barrelled, lie along close-set laminae, so that the shell, although of elongate oval shape like that of *Permophricodothyris ovalis*, is not be identical with that genus. Further detail of the exterior and internal aspects of both valves were described in Waterhouse (1983b, pp. 136-139, pl. 6, fig. 6-12).

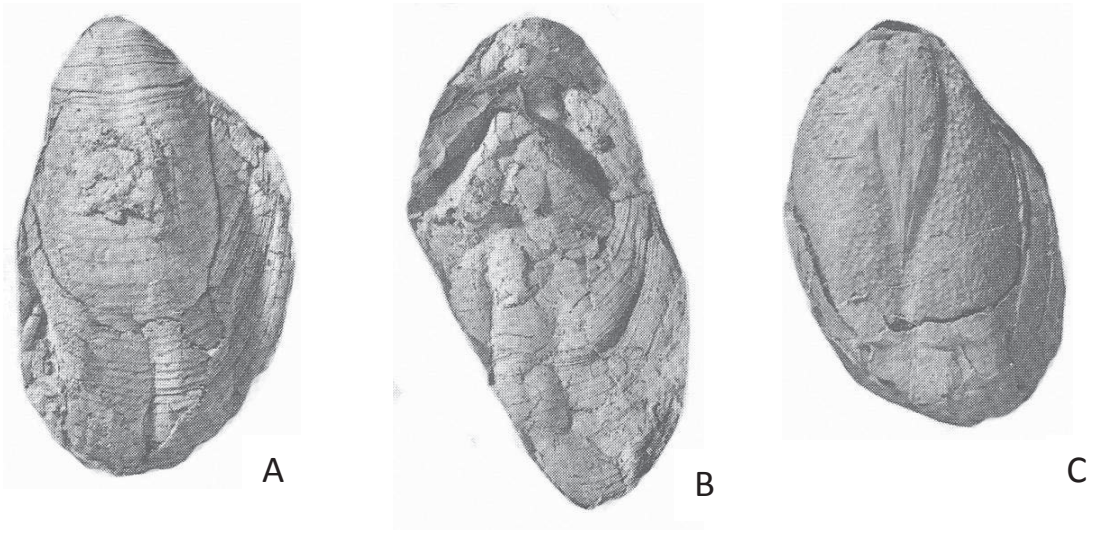


Fig. 477. *Huaitakithyris postgrandis* (Waterhouse). A, holotype, external cast of ventral valve. B, external cast of dorsal valve. C, internal mould of ventral valve. Specimens x1. From Huai Tak Formation (Changhsingian), Thailand. (Waterhouse 1983b).

Infrasuborder AMBOCOELIIMORPHI new

Diagnosis: Small shells, may be biconvex but may tend towards planoconvexity, ornament varied but most often spinose or pustulose, arranged in commarginal rows. Internal plates highly varied, may involve adminicula and/or tabellae, and cruralium widely present, but many genera lack dental plates and adminicula. Most characteristic feature apart from size lies in the simple cardinal process, rather than ctenophoridium of most other than earliest Spiriferida. Radial ornament is comparatively rare. Silurian (Wenlock) to Lower Triassic (Scythian).

Discussion: This is a compact infrasuborder, involving only one superfamily Ambocoelioidea, and so having the identical definition and content. The range of micro-ornament is limited, with no members showing fimbriate or frilled ornament, but the rows of fine uniramous and usually homogeneous spines approach the pattern seen in many Delthyrimorphi.

Superfamily **AMBOCOELIOIDEA** George, 1931

[Nom. promoveo Johnson & Carter in Carter et al. 1994, p. 336 ex Ambocoeliinae George, 1931, p. 42].

Diagnosis: Small plano-convex to biconvex shells lacking deep sulcus and high fold, often without costae or plicae, micro-ornament varied, usually dominated by fine spines or pustules in commarginal rows. The presence of a delthyrial cover plate or deltidium appears variable, present in some genera, apparently absent from others, and as far as can be discerned, derived as a rule from deltidial plates, although a number of genera developed pleromal ridges and connector plate. Adminicula and dental plates not present in Ambocoeliidae, which has crural plates widely present, often supported by tabellae. A spondylium and /or cruralium are developed in other groups. Cardinal process knob-like, tubercular or with few lamellae, brachia simple or spiriform. Silurian (Wenlock) to Lower Triassic (Scythian).

Discussion: Genera of this superfamily show limited variation in micro-ornament, but more in the nature of internal plates. The oldest constituent genera are very slightly younger than some genera within Cyrtiinoidea, for example *Espella* Nilova from middle Llandovery to Wenlock faunas, compared with Wenlock for the oldest ambocoeliid. There is variation in delthyrial apparatus: some genera have a delthyrium closed by a deltidium or partly closed by two deltidial plates, and others have an umbonal callosity, pleromal plates and connector plate. Dorsal muscle scars often form anterior and posterior pair, or inner and outer pair, not the same as those of Productida, but approaching them, because in both groups the dorsal valve is often only gently convex.

The lack of adminicula and widespread absence of dental plates from many genera may reflect the overall build of the shell, in which the dorsal valve is often almost flat and much lighter than the highly convex ventral valve, so that little physical stress was placed on the teeth, with no need for reinforcement or support. Contrary to the understanding of their evolution expressed by Carter & Gourvennec (2006a, Fig. 1104, p. 1693), ambocoelioids did not lose their crural plates as a rule. The presence or absence of tabellae for many genera remains moot, as to whether they are sturdy bases of the crura, or discrete if small tabellae.

There are numerous permutations displayed by genera, involving ornament, presence or absence and nature of dorsal plates, shape and disposition of muscle impressions, and presence or absence of a delthyrial cover. Classification is considerably hindered by the failure to determine all features relevant to each genus for some genera, but the implication remains that various features could vary within subfamilial or tribal clusters.

Possibly the superfamily developed directly from Cyrtioidea. The cyrtiid genus *Dongbeiispirifer* Liu in Liu & Huang (1977, p. 58) was stated to have only short adminicula, and one of the features of early ambocoeliids is the absence of adminicula. This Chinese genus is poorly known, planoconvex, with ill-defined fold. It was classed as Cyrtiinae Fredericks by Johnson & Hou (2006a), and is of Ludlow (Silurian) age. No genus or group amongst Cyrtiimorphi seems to lack adminicula, and their loss marked the major change into Ambocoeliidae within Ambocoeliodea. *Espella* Nilova of middle Llandovery-Wenlock (Silurian) age is smooth like ambocoeliids, and has adminicula and cruralium, like members of Rhynchospiriferidae, but the oldest genera of Rhynchospiriferidae are no older than Lower Devonian (Emsian): the family marked the return of adminicula. In terms of time range, members of the superfamily were amongst the few to survive the extinction shock at the end of the Permian Period, though they did not last long (Chen et al. 2005).

Ambocoelioids arose close to the same time as earliest members of Delthyroidea and Hysterolitoidea, showing a slightly different but allied micro-ornament, and different shape and internal plates. The same can be said of relationships to other Silurian brachiopods of Cyrtiimorphi: Ambocoelioidea differ from all in terms of shape, and plates, but approach Delthyrimorphi in the commarginally prominent finely spinose micro-ornament. It is likely that they shared a common ancestor, or underwent not entirely comparable evolutionary trajectories, differing to some extent in micro-ornament, musculature, spiralia and internal plates. A number of Devonian ambocoelioid genera are delthyridin in attributes, such as *Ladjia* and *Emanuella*. Ornamented by rows of spines aligned commarginally, usually along short commargons, the difference from fimbriation depended on the less pervasive posterior elongation of spine bases forming well developed capillae.

In the *Revised Brachiopod Treatise*, Ambocoelioidea were regarded as progenital stock for Martinioidea (which included Ingelarelloidea). This view is rejected. Martinioidea evolved with Ingelarelloidea from Cyrtioidea.

Family **AMBOCOELIIDAE** George, 1931

[Nom. promoveo Ivanova 1959, p. 56 ex Ambocoeliinae George, 1931, p. 42].

Diagnosis: Ventri-biconvex shells, smooth with varied micro-ornament, no adminicula or dental plates, tabellae stubby or may be absent. Silurian (Wenlock) to basal Triassic (Scythian).

Subfamily **AMBOCOELIINAE** George, 1931

[Ambocoeliinae George, 1931, p. 42].

Fig. 478. *Ambocoelia umbonata* (Hall), ventral valve and spiralia, x2. (Sarytcheva 1960, based on Hall & Clarke 1894). From Devonian of New York State, United States.

Diagnosis: Dorsal adductor scars arranged as posterior and anterior pair. Socket plates and crural plates thick and small, set close to the shell floor. Devonian.
Genera: *Ambocoelia* Hall & Clarke, *Metaplasia* Hall & Clarke.

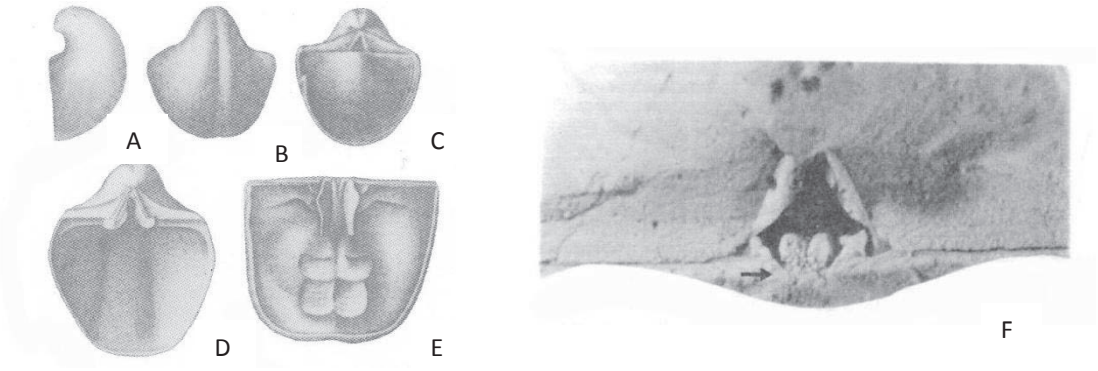


Fig. 479. *Ambocoelia umbonata* (Hall). A, lateral, B, ventral, C, dorsal views of exterior. D, internal view of ventral valve and E, dorsal valve. All x1.5. (Pitrat 1965). F, posterior view, ventral valve on top, x5, showing deltidia and tuberculate cardinal process. (Goldman & Mitchell 1990).From Devonian of New York State, USA.

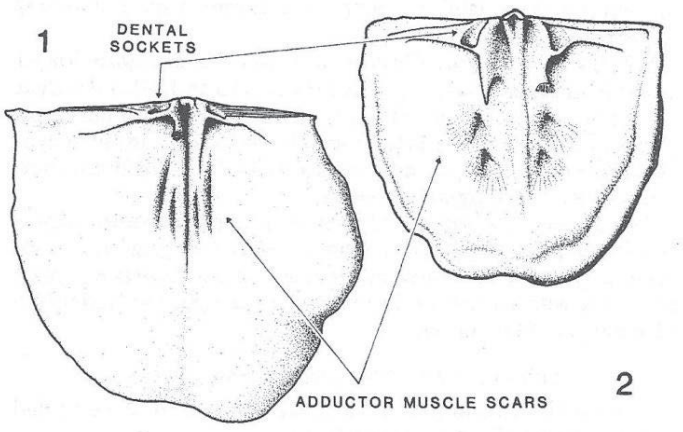


Fig. 480. Dorsal valve interiors of 1, *Crurispina spinosa* (Clarke), and 2, *Ambocoelia umbonata* (Conrad), x7. Note contrast in disposition of dorsal adductor scars. From Devonian of New York State, USA. (Goldman & Mitchell 1990).

Discussion. *Ambocoelia* Hall & Clarke and *Metaplasia* Hall & Clarke are of Devonian age. Dental plates are moderately well developed but adminicula are not developed. Fine growth

lines and weak capillae are present. There are short thick plates, called crural plates by authors, though possibly no more than thick bases to the crura at their inception. Narrow elongate ventral adductors may be divided by a low median ridge.

Subfamily **CRURITHYRINAE** Waterhouse, 2010a

[Crurithyrinae Waterhouse, 2010a, p. 68].

Diagnosis: Dorsal adductor scars laterally arranged. Ventral muscle scars subelongate. Crural plates or bases normally not in contact with floor of valve, often join with tabellae to form cardinal plate as inner and outer hinge plates, spiralia fully formed. Silurian (Wenlock) to Lower Carboniferous (Visean). Upper range uncertain.

Genera: *Crurithyris* George, ?*Aviformia* Xian, *Cyrtinoides* Iudina & Rhzonsnitskaya (syn. *Mucroclipeus* Goldman & Mitchell), *Echinocoelia* Cooper & Williams (syn. *Pyramina* Liashenko), *Guangxiispirifer* Xian, ?*Swaicoelia* Hamada.

Fig. 481. A, B, *Crurithyris urei* (Fleming), ventral and dorsal views. From Visean of Great Britain. (Brunton 1984). C, *Cyrtinoides septata* (Johnson), dorsal interior. From Eifelian of Nevada, USA. (Johnson 1971).

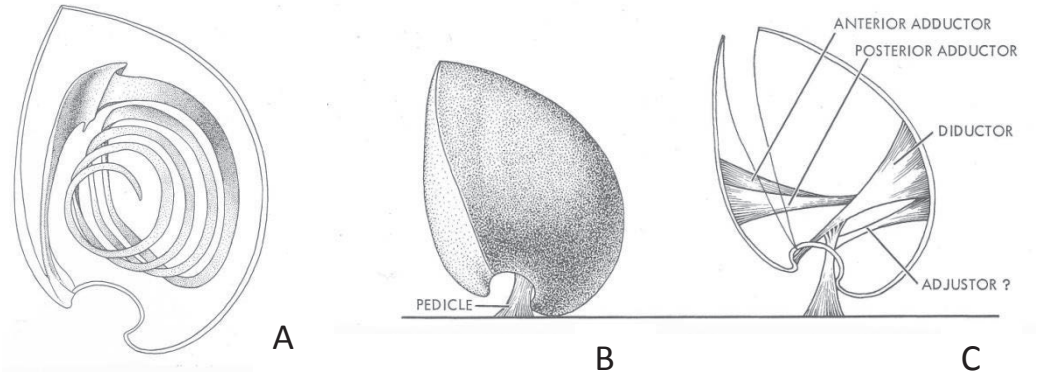


Fig. 482. *Crurithyris*. A, spiralium. B, generalized attachment of ambocoelioid shells. In many genera, there may have been no functional peduncle, with the delthyrium closed by deltidium. C, muscle systems. (Grant 1976).

Discussion: Micro-ornament is highly varied, from spines to capillae, and *Crurithyris* itself has fine spines of varied diameter (Brunton 1984, p. 66, Fig. 86-92). The cardinal process is small

and tubercular, or constitutes a long ridged area on a short notothyrial platform. Three coils in the spiralia were recorded. No delthyrial cover was mentioned by Brunton, so that the delthyrium was presumably open. The inner hinge plates as a rule are subhorizontal rather than meeting the floor. The genus has been reported from Permian faunas, but such species need to be closely examined. For example, specimens from the Magnesian Limestone of northern England (King 1850) that have been assigned to *Crurithyris* have well developed tabellae, and the exact arrangement of the cardinalia needs to be determined. Internal detail for *Aviformia* Xian is not explained by Johnson, Carter & Hou (2006b, p. 1733).

Cyrtinoides Iudina & Rhzonsnitskaya, 1985 has a tichorhinum (Johnson 1971), but crural plates are like those of Crurithyrinae. The genus was treated as senior synonym by Johnson et al. (2006a) of the well described genus *Mucroclipeus* Goldman & Mitchell, which has deltidial plates. In *Echinocoelia*, a cardinal plate was shown in a species *denayensis* recorded by Johnson (1971), whereas a sessile cruralium was figured in the original record of the genus by Cooper & Williams (1935, Fig. 5, p. 845). Johnson, Carter & Hou (2006b, p. 1736) stated that type *Echinocoelia* was too poor to refigure, and provided figures of *E. denayensis* Johnson as a substitute, and also provided figures originally classed in the same species by Johnson (1971) as illustrations of *Cyrtinoides* Iudina & Rhzonitskaya, referring to *C. septata* Johnson, 1971, a name that does not appear in the 1971 publication as itemized, and clearly appeared in a different article. *Swaicoelia* Hamada, 1968b needs further study for validation and assignment of affinities.

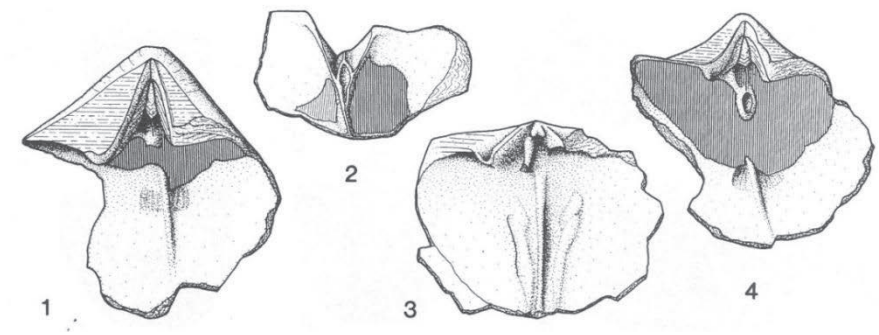


Fig. 483. *Cyrtinoides eleii* (Goldman & Mitchell), diagrams showing the tichorhinum in the ventral valve (1, 2, 4) and the dorsal valve interior (3), x12. Figured as *Mucroclipeus,* which has been synonymized with *Cyrtinoides* in the *Revised Brachiopod Treatise*. From Devonian of New York State, USA. (Goldman & Mitchell 1990).

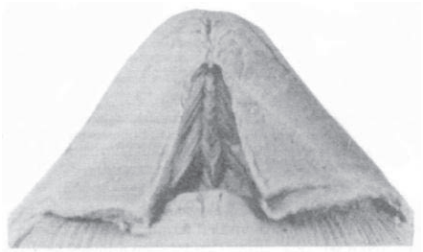


Fig. 484. *Cyrtinoides eleii* (Goldman & Mitchell), ventral valve showing the tichorhinum, x8. Tiny spines define the commarginal growth lines. From Devonian of New York State, USA. (Goldman & Mitchell 1990).

Subfamily **ATTENUOCURVINAE** Waterhouse, 2010a

[Subfamily Attenuocurvinae Waterhouse, 2010a, p. 64].

Diagnosis: No cardinal plate, tabellae small or absent if crural plates are sessile, spire complete or reduced to one coil. Micro-ornament varied, capillate, or pustulose.

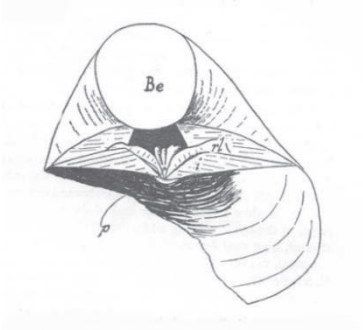


Fig. 485. *Attenuocurvus incurvatus* (Waterhouse), dorsal aspect, showing ventral beak (be), sectioned, above an open delthyrium (the deltidium having been lost), and dorsal valve with crural plate (rl), cardinal process (p) and dorsal interarea (i). A small deltidial plate is normally present over at least the upper delthyrium in *Attenuocurvus*. From Changhsingian of New Zealand. (Waterhouse 1964).

Tribe **ATTENUOCURVINI** Waterhouse, 2010a

[Nom. trans. hic ex Subfamily Attenuocurvinae Waterhouse, 2010a, p. 64].

Diagnosis: Ventral valve highly convex, delthyrium as a rule closed by deltidial plates and median arch. Dorsal valve gently convex to almost flat, micro-ornament of small spines of uniform or varying diameter. Ventral adductor scars on long high ridge, dorsal scars as in *Crurithyris*, more or less laterally arranged. Cardinal process small, tuberculate or feebly lamellate. Crural and socket plates stubby and sessile, tabellae slender and low; spiralia truncated to one coil. Upper Pennsylvanian to Upper Permian (Changhsingian).

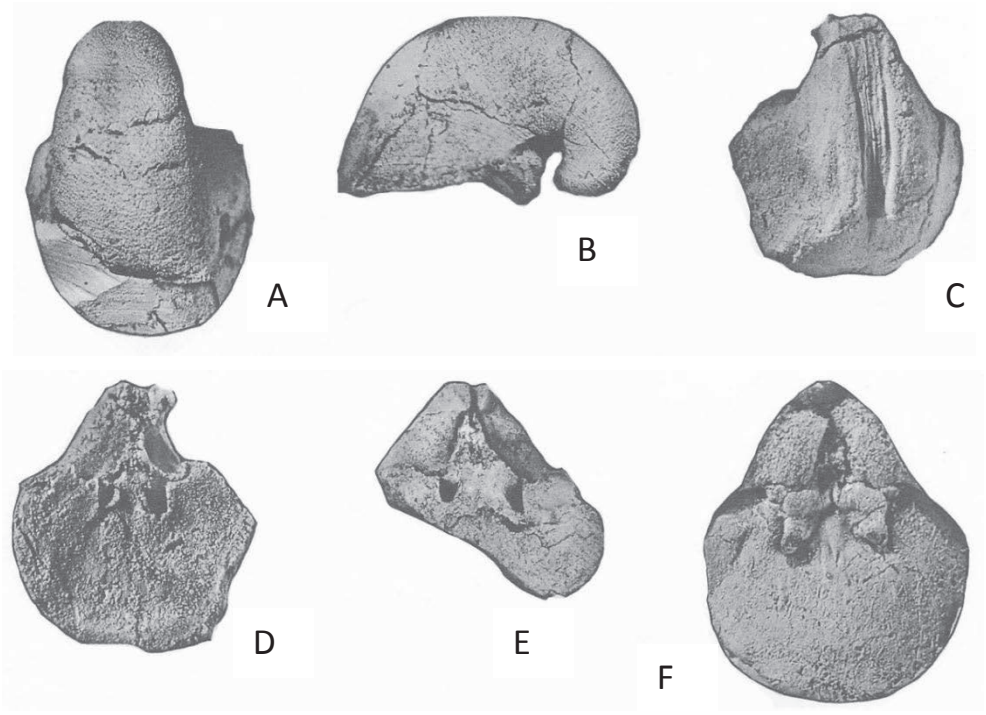


Fig. 486. *Attenuocurvus incurvatus* (Waterhouse). A-C, ventral and lateral aspects, and ventral internal mould. D-F, dorsal aspects of internal moulds, and latex cast of dorsal interior. From Changhsingian (Upper Permian) of New Zealand. (Waterhouse 1964).

Genera: *Attenuacurvus* Waterhouse*, Attenuatella* Stehli, *Biconvexiella* Waterhouse.

Discussion: Genera are limited to Upper Pennsylvanian and Permian. The deltidial plate is well developed in *Attenuocurvus,* formed by two small lateral plates that merge medianly in an arch. *Biconvexiella* is like *Attenuocurvus* in its truncated spire, but has different dorsal adductor scars, a slender posterior pair, and larger overlapping anterior pair. Microspines are differentiated in *Biconvexiella* and *Attenuatella*, as in *Crurithyris* (Brunton 1984), but are uniform in *Attenuocurvus*.

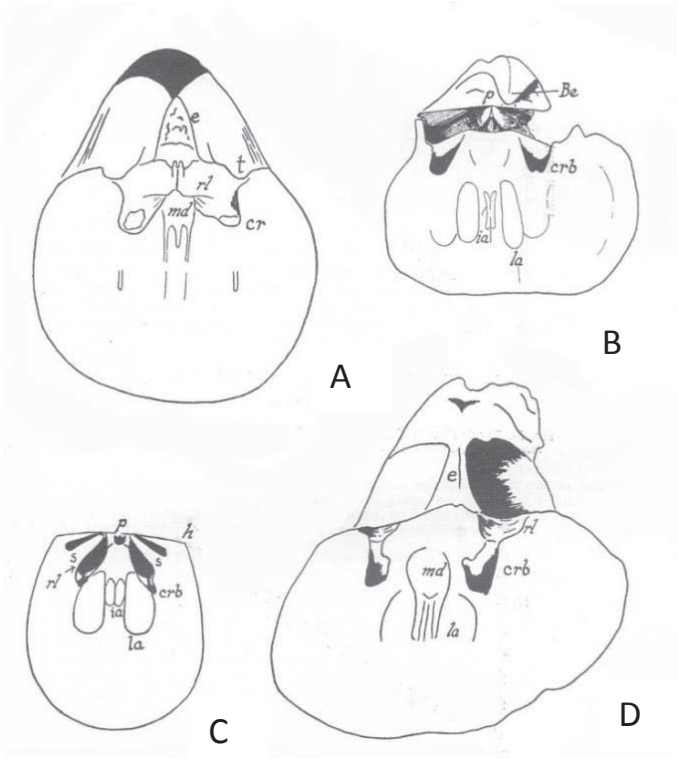


Fig. 487. *Attenuocurvus incurvata* (Waterhouse), dorsal aspects of internal moulds. Be – ventral beak; cr –crus; crb – mould of base of crus; e – delthyrium; h – hinge; ia – inner pair of dorsal adductors; la – lateral adductors; md – median mound; p – cardinal process; rl – crural plate; s – dental socket; t – tooth. From Changshsingian of New Zealand. (Waterhouse 1964).

Tribe **EOPLICOPLASIINI** new tribe

Name genus: *Eoplicoplasia* Johnson & Lenz, 1992, p. 530 based on *Plicoplasia acutiplicata* Lenz, 1972, p. 102 from Yukon Territory (upper Lochkovian), Canada, here designated.

Diagnosis: Shells broadly plicate, micro-ornament of weak capillae and strong commarginals, wide hinge, low dental plates, socket plates wide, crural plates large and rest posteriorly on the floor of the valve, or not developed, no cardinal plate. Silurian (upper Wenlock) to Middle Devonian (Siegenian?).

Genera: *Eoplicoplasia* Johnson & Lenz, ?*Plicoplasia* Boucot, *Pustulatia* Cooper.

Discussion: *Eoplicoplasia* and *Plicoplasia* are exceptional in being plicate shells with hinge at maximum width. They are widely distributed, and of Silurian (Wenlock) to Lower Devonian (Pragian) age. *Eoplicoplasia* is one of the oldest ambocoeliids, and shows links with cyrtioid genera, as suggested by Johnson, Carter & Hou (2006b, p. 1736), indicated by the presence of plicae otherwise rare for the family, capillate micro-ornament, and moderately developed dental plates, low crural plates and a small delthyrial plate. Adminicula and clearly developed tabellae are lacking, in part because the dorsal valve is very shallow. *Plicoplasia* lacks dental

plates.

Pustulatia Cooper, 1956 was regarded as an anoplothecid by Carter et al. (1994, p 371), to the disbelief of Boucot & Brunton in Wongawich et al. (2004, p. 1081), and they

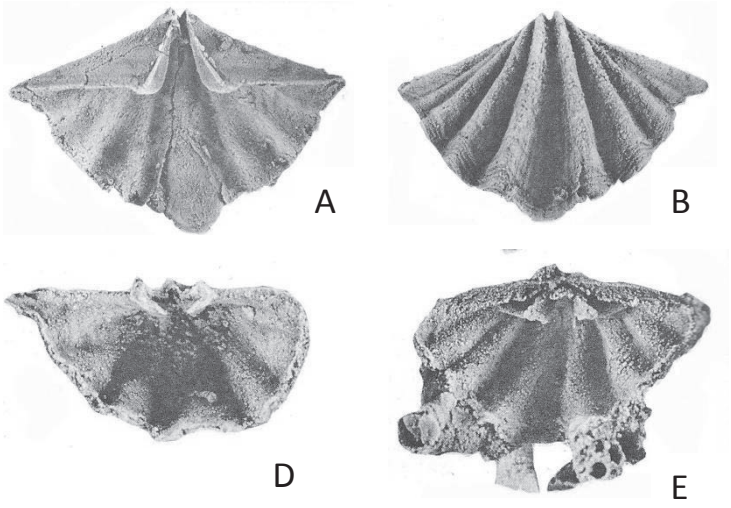


Fig. 488. *Eoplicoplasia acutiplicata* (Lenz). A, ventral interior. B, ventral exterior. C, dorsal exterior. D, ventral interior. E, dorsal interior. From Lochovian of Yukon Territory, Canada. (Lenz 1972).

endorsed the view of Pitrat (1965, p. 675) that it was close to *Plicoplasia*. Curiously, the genus was disregarded in the *Revised Brachiopod Treatise*. It has radial striations and pustules, and approaches members of Johnsononinae (see p. 370) in the shallow and narrow dorsal channel along the fold.

Fig. 489. *Pustulatia pustulosa* (Hall), ventral exterior and dorsal interior and exterior, x3. From Middle Devonian of New York State, USA. (Cooper 1944).

Tribe **OGILVIECOELIINI** new tribe

Name genus: *Ogilviecoelia* Shi & Waterhouse, 1996, p. 119 based on *Ogilviecoelia inflata* Shi & Waterhouse, 1996, p. 119 from Jungle Creek Formation (Sakmarian), Yukon Territory, here designated.

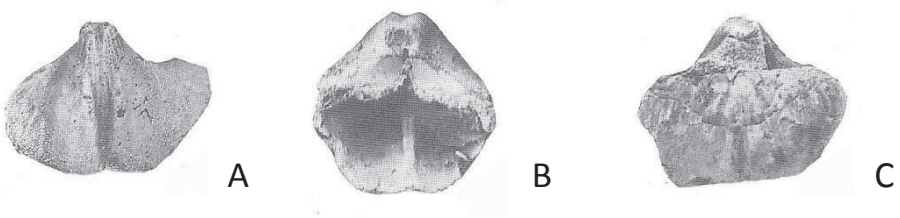


Fig. 490. *Ogilviecoelia inflata* Shi & Waterhouse. A, ventral internal mould. B, dorsal aspect of ventral valve. C, dorsal view of specimen with valves conjoined. From Sakmarian of Yukon Terriotry, Canada. (Shi & Waterhouse 1996).

Diagnosis: Small non-plicate shells with micro-ornament varied, of capillae or spinules, spiralia complete as in crurithyrins, no dental plates, crural plates supported by tabelliform thick short plates. No extensive cardinal plate. Small delthyrial plate, deltidial plate. Lower Devonian (Pragian) to Permian (Changhsingian) and basal Triassic (Scythian).

Genera: *Ogilviecoelia* Shi & Waterhouse, *Cruricella* Grant, *Echinocoeliopsis* Hamada (syn. *Plicambocoelia* Boucot & Brunton in Wongwanich et al.), *Orbicoelia* Waterhouse & Piyasin, *Paracrurithyris* Liao, ?*Spinoplasia* Boucot.

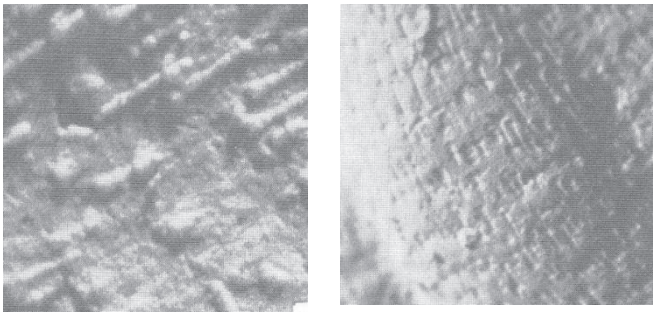


Fig. 491. *Ogilviecoelia inflata* Shi & Waterhouse. A, ventral external mould showing short fine elongate grooves left by spine channels or taleolae, x13. B, latex cast showing short grooves, x9. These appear to be subsurface features, below a spinose periderm. From Sakmarian Jungle Creek Formation, Yukon, Canada. (Shi & Waterhouse 1996).

Discussion: This tribe like Attenuocurvini lacks a dorsal cardinal plate, because the crural plates descend from the socket plates to rest on tabellae that extend to the floor of the valve. The base of the crura commence at or close to the floor of the valve, as in Attenuatellini, but the spire is more complete, like that of *Crurithyris*. *Ogilviecoelia* has a micro-ornament of minute spines and that of *Paracrurithyris* is poorly known. *Ogilviecoelia* and *Paracrurithyris* are of Permian age, ranging from Late Pennsylvanian (Gzhelian), and *Paracrurithyris* survived the Permian-Triassic extinction event into basal Triassic (Chen et al. 2005). The anterior dorsal adductors extend laterally in front of the slender posterior dorsal adductors in *Ogilviecoelia*, somewhat as in *Biconvexiella*, but definitely comprise inner and outer pair.

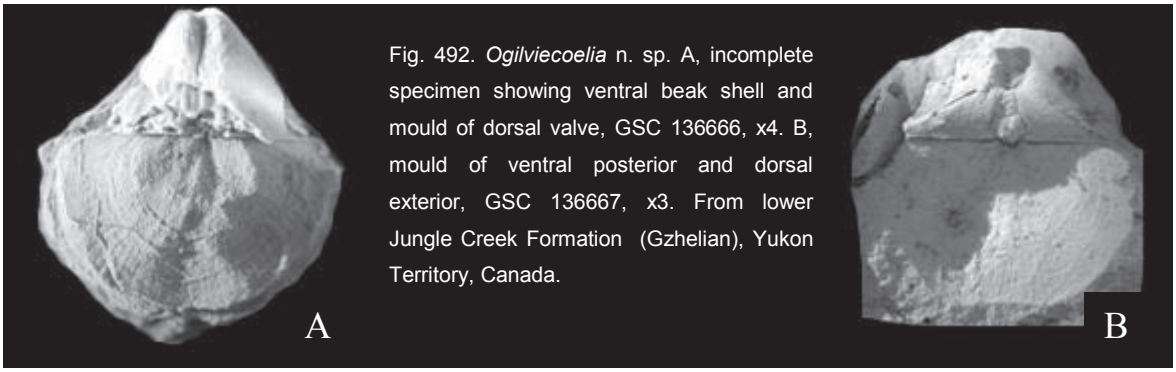


Fig. 492. *Ogilviecoelia* n. sp. A, incomplete specimen showing ventral beak shell and mould of dorsal valve, GSC 136666, x4. B, mould of ventral posterior and dorsal exterior, GSC 136667, x3. From lower Jungle Creek Formation (Gzhelian), Yukon Territory, Canada.

Orbicoelia has an open delthyrium, and two short tabellae support the crural plates from the floor of the valve. Its type species is *O. fraterculus* Waterhouse & Piyasin, not *fraturculus* as recorded in the *Revised Brachiopod Treatise*. The genera range from Lower Devonian to Late Permian, and *Orbicoelia* is reported widely in basal Triassic as a post-

extinction Permian survivor (Chen et al. 2005). The type species *Cruricella* Grant has also been reported from Triassic deposits, and the type species comes from much the same level as *Orbicoelia,* of early Guadalupian age, mis-stated as Lopingian by Johnson, Carter & Hou (2006b, p. 1733).

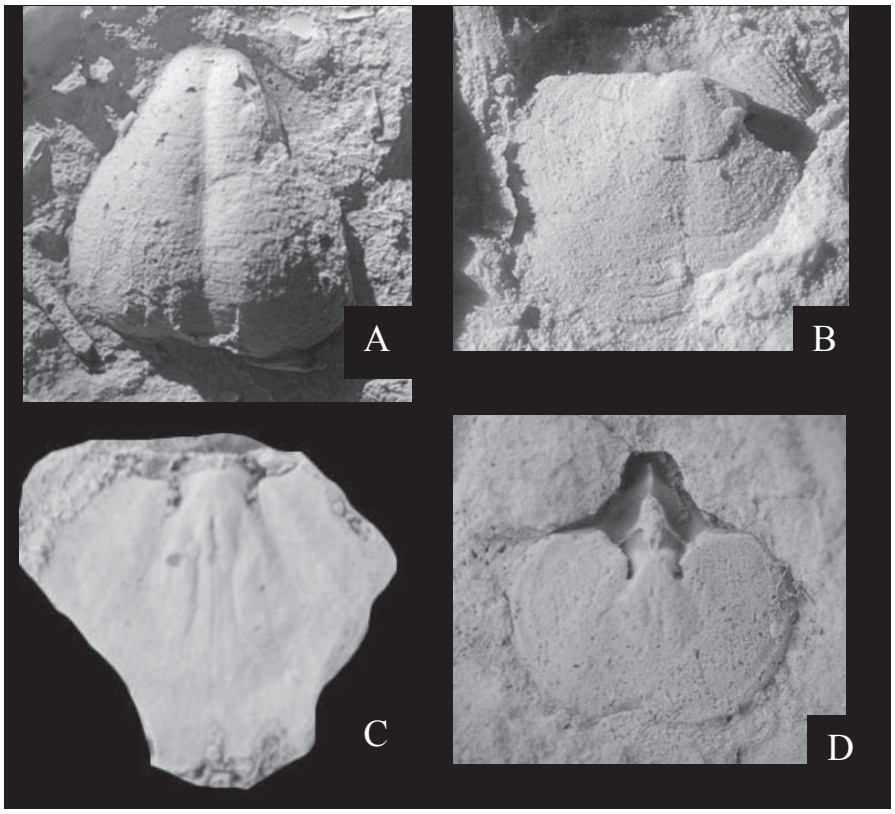


Fig. 493. *Ogilviecoelia* n. sp. A, ventral valve, external cast, GSC 136668. B, external cast of dorsal valve, GSC 136669. C. dorsal internal mould GSC 136670, showing muscle scars. D, dorsal internal mould, GSC 136671. Specimens x4, from lower Jungle Creek Formation (Gzhelian), Yukon Territory, Canada.

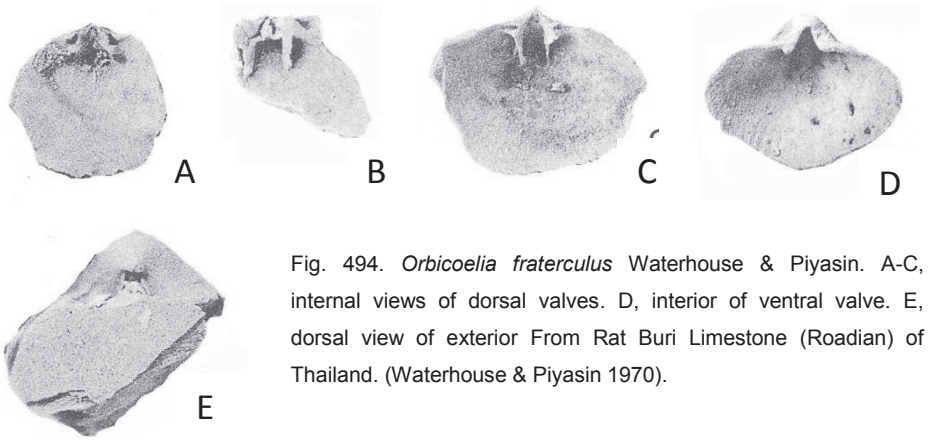


Fig. 494. *Orbicoelia fraterculus* Waterhouse & Piyasin. A-C, internal views of dorsal valves. D, interior of ventral valve. E, dorsal view of exterior From Rat Buri Limestone (Roadian) of Thailand. (Waterhouse & Piyasin 1970).

Johnson, Carter & Hou (2006b, p. 1733) gave an upper range of ?Middle Triassic – ?Upper Triassic for Ambocoeliinae (which involved Crurithyrinae). The only genus in their

summary to possibly have anything like such a range is *Cruricella* Grant, 1976, which occurs in the Mianwali Formation of early Scythian (Lower Triassic) age in the Salt Range, Pakistan.

Echinocoeliopsis Hamada, 1968a from mid-Carboniferous (Namurian) of Malaysia appears to be completely ambocoeliiform, with growth lamellae and tiny marginal spine bases, small teeth without supports, long elongate ventral adductor scars, and dorsal cardinalia featuring sturdy dental sockets and bifid cardinal process. As pointed out by Gourvennec in Gourvennec & Carter (2007, p. 2791), it is senior synonym to *Plicambocoelia* Boucot & Brunton in Wongawich et al. 2004. There may seem to have been uncertainty over the placement of this genus in the *Revised Brachiopod Treatise*, because in 2007, p. 2791, it was stated, by editorial error (Remy Gourvennec pers. comm..), that the genus was placed within Rhenothyridinae, whereas it was put in Obesariinae by Gourvennec in Carter & Gourvennec (2006c, p. 1857). Either way, the the genus was regarded as reticularioid.

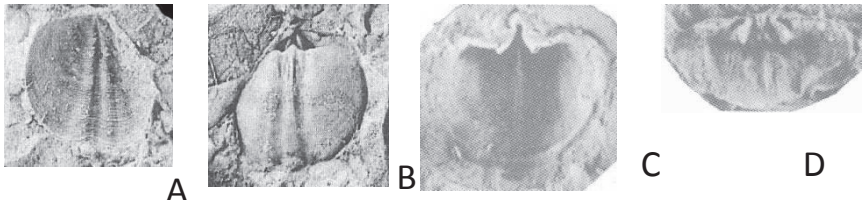


Fig. 495. A, B, *Echinocoeliopsis tansathieni* (Boucot & Brunton). External and internal mould of dorsal valve holotype, x3. (Wongwanich et al. 2004). From Namurian of Thailand. C, *E. scupta* Hamada, dorsal interior x5. D, *E. ladjioidea* Hamada, ventral interior, x3. (Hamada 1968a). From Namurian of Malaysia. See Fig. 421, p. 318. Species and age limits require consolidation. To me they look ambocoelioid, but Gourvennec in Carter & Gourvennec (2006c, p. 1857) and Gourvennec & Carter (2007, p. 2791) classed them as Reticularioidea.

Subfamily **JOHNSONONIINAE** new subfamily

Name genus: *Johnsononia* new genus from Eifelian of Alaska, here designated.

Diagnosis: Shells with deep ventral sulcus opposed by strong dorsal sulcus, each bordered laterally by strong plicae as a rule with a few strong pairs laterally. Micro-ornament of growth increments, no spines. Ventral valve with teeth, dorsal valve with crural plates and tabellae as a rule, tending to form cruralium or tabellarium. [Silurian (Wenlock]; Lower Devonian (Pragian) to Upper Devonian (Frasnian).

Genera: *Johnsononia* new genus, *Bisinocoelia* Havlíček, ?*Choperella* Liashenko, [?*Dicoelospirifer* Zhang], *Nuguschella* Tiazheva.

Discussion: Members of this subfamily have been referred to Verneuiliidae Schuchert, 1929 (see Johnson et al. 2006b), but *Verneuilia* is characterized by deeper more emphasized sulcus in each valve, bordered by sharper keels, and with wide hinge and no lateral plicae. The interior of type *Verneuilia* is not known, and until it is known, it is deemed unwise to regard other genera as congeneric, because Verneuiliidae was proposed before Ambocoeliidae, and must assume precedence for the superfamily name. That would be potentially misleading, until the interior can be shown to be definitely ambocoeliiform.

Fig. 496. *Nuguschella polita* Tiazheva, ventral, dorsal and anterior views, x4. From Middle Devonian (Eifelian) of Urals. (Tiazhev 1960).

Nuguschella has a cruralium, and *Choperella* has short discrete tabellae. *Bisinocoelia* Havlíček from Devonian of Bohemia is bisulcate and shows signs of a sessile and low cruralium, formed by a pair of low ridges that join a low median septum in front, as in many members of Ambothyrinae new subfamily (see p. 379).

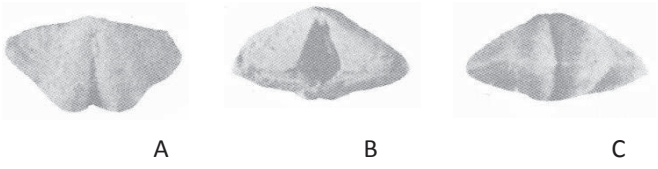


Fig. 497. *Choperella ilmenica* Liashenko, A, ventral, B, posterior and C, anterior views, dorsal valve below, x3. From Middle Devonian (Eifelian) of Russian platform. (Liashenko 1969a).

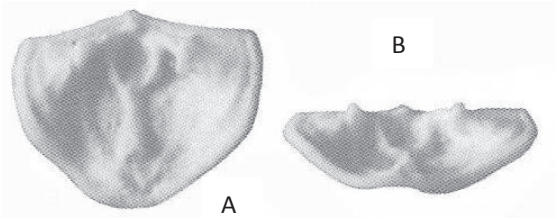


Fig. 498. *Bisinocoelia bisinuata* Havlíček, views of dorsal interior, x10. From Lower & Middle Devonian of Bohemia. (Havlíček 1953).

Dicoelospirifer Zhang Ning (1989, p. 18) from Wenlock (Silurian) of the Canadian Arctic has a wide ventral and dorsal sulcus, commarginal growth-lines, no median septum and no dental plates (Zhang Ning 1989, pl. 10, fig. 37, 41-43) and no cardinal plate, with

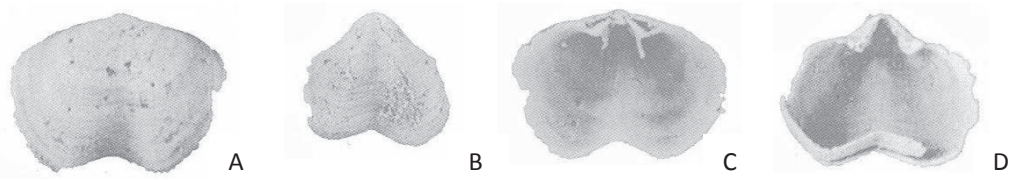


Fig. 499. *Dicoelospirifer dicoelospirifer* Zhang, holotype, A, C, external and internal views of dorsal valve, x8. B, ventral exterior x6. D, ventral interior, x8. From Silurian (Wenlock) of Arctic islands, Canada. (Zhang Ning 1989).

crural bases arising at the end of the socket plates. It probably belongs to a family group of its own, and although with a wide dorsal sulcus, lacks lateral plicae and has no tabellae. It is strongly bisulcate like members of Johnsononinae and has commarginal growth-lines, no median septum and no dental plates, and tiny if any crural plates (Zhang Ning 1989, pl. 10, fig. 37, 41-43). There is no cruralium or sessalium.

Genus ***Johnsononia*** new genus

Name: Named for J. G. Johnson.

Diagnosis: Small, moderately high interarea, one or two lateral plicae each side of median plicae bordering sulcus of either valve. Micro-ornament presumably faint, not known. No dental plates or adminicula. Well formed dental sockets, simple knob-like cardinal process. Low crural plates converge inwards, possibly aligned with tabellae meeting floor of valve, to form a tabellarium.

Type species: *Verneuilia langenstrasseni* Blodgett & Johnson, 1994, p. 1241 from Eifelian of Alaska, here designated.

Discussion: *Nuguschella* Tiazheva, 1960 from the Eifelian of the Urals Mountains is close, with one additional pair of plicae, each plication with well rounded crests, and weakly obtuse cardinal extremities. *Choperella* and *Bisinocoelia* have fewer lateral plicae but are bisulcate, and *Choperella* has a sessile cruralium.

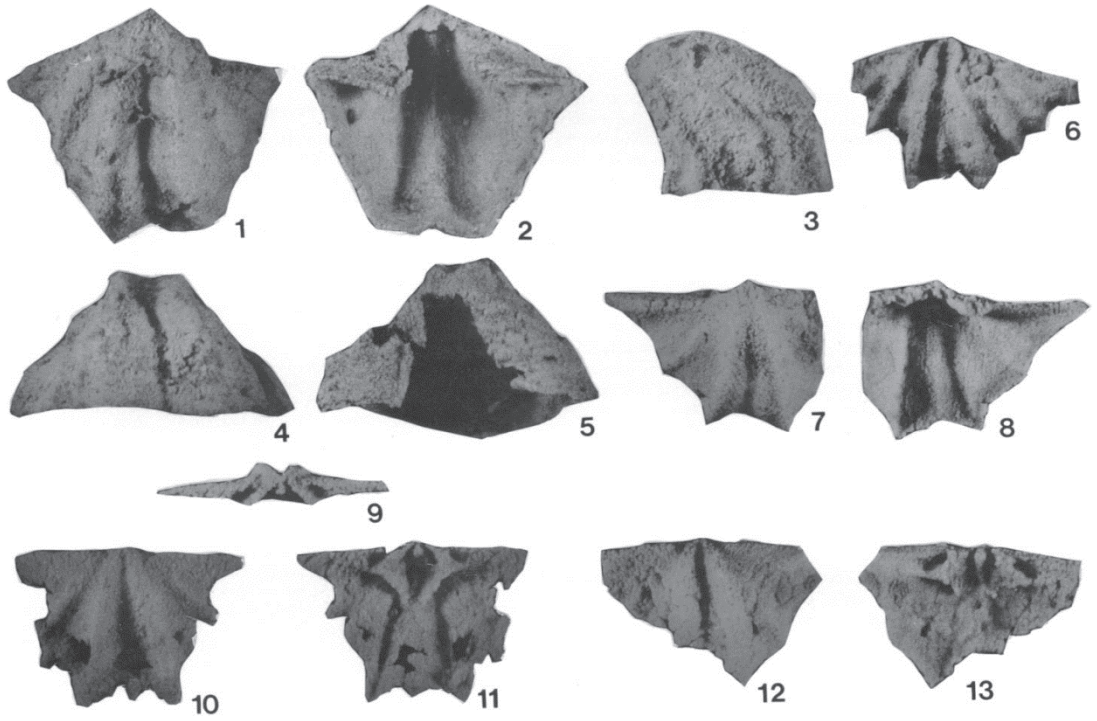


Fig. 500. *Johnsononia langenstrasseni* (Blodgett & Johnson). 1-5, exterior, interior, lateral, anterior and posterior views of ventral valve holotype. 6, exterior of ventral valve. 7, 8, external and internal views of ventral valve. 9-11, posterior, external and internal views of dorsal valve. 12, 13, external and internal views of dorsal valve. Specimens x10. From Cheeneetnuk Limestone (Eifelian), west central Alaska. (Blodgett & Johnson, 1994).

Family **EUDOXINIDAE** Nalivkin, 1979

[Nom. correct. et transl. Carter in Carter et al. 1994, p. 337 ex Eudoxiniinae Nalivkin, 1979, p. 145].

Diagnosis: Biconvex and subglobular shells of rounded outline and short hinge, as a rule, weakly to strongly costate, micro-ornament papillose or lacking, dental plates reduced to narrow or swollen ridges, with crural plates, no adminicula or tabellae. Upper Devonian (Famennian) to Lower or Middle Permian (Kungurian or Roadian).

Genera: *Eudoxina* Fredericks & Kruglov, *Costicrura* Hoover, *Paulonia* Nalivkin, *Wilberrya* Yancey.

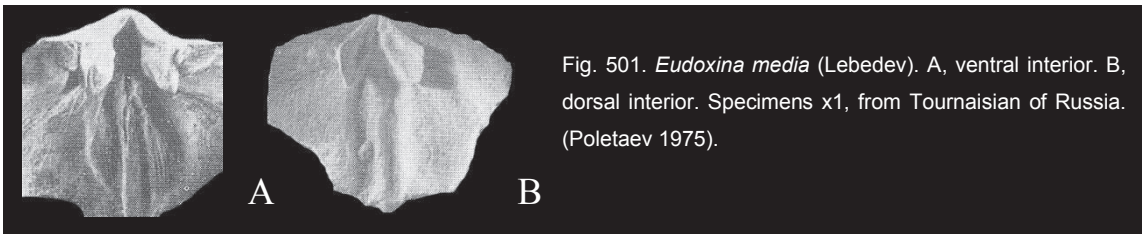


Fig. 501. *Eudoxina media* (Lebedev). A, ventral interior. B, dorsal interior. Specimens x1, from Tournaisian of Russia. (Poletaev 1975).

Discussion: Carter in Johnston, Carter & Hou (2006b, p. 1744) incorporated four genera in this assortment, which all show short somewhat swollen dental projections and supporting ridges, reminiscent of those seen in *Ogilviecoelia* (see p. 367). *Eudoxina* is large for the superfamily, with narrow sulcus, fine branching riblets, no pustules, dental flanges and high

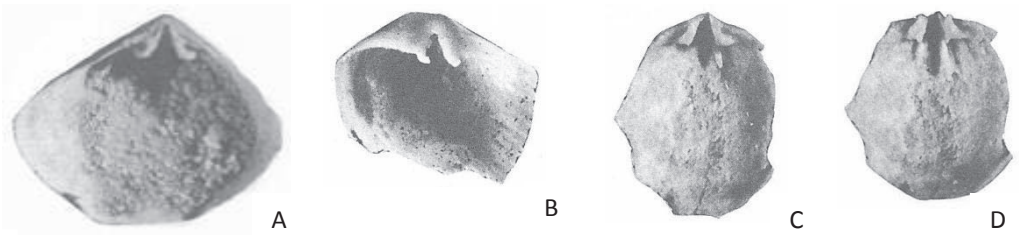


Fig. 502. *Wilberrya fragilis* Yancey. A, internal ventral valve, x5. B, internal view of ventral valve, x4. C,D, internal views of dorsal valve, x6. From upper Cisuralian of western USA. (Yancey 1978).

inner socket ridges. The type species, *E. media* (Lebedev), is of Tournaisian age in Russia. The ctenophoridium is concave and multilaminate in at least some species (see Fig. 504F). *Costicrura* Hoover, 1981 from Venezuela has wide hinge and high interareas, with low anterior ribs, bilobed cardinal process, median septum, and probably no pustular micro-ornament. There are said to be no clearly developed plates in either valve. The age of this genus was stated to be Lopingian in the *Revised Brachiopod Treatise*, but the fauna is either Kungurian (topmost Cisuralian) or Roadian, perhaps Wordian) of the Guadalupian Middle Permian, according to Hoover (1981). *Paulonia* Nalivkin, 1925 of Famennian to Tournaisian age in Ukraine has fine well formed ribs and papillae, and delthyrial plate, but internal septation is not clear, and presumably is absent. *Wilberrya* Yancey, 1978 from the Cisuralian of Nevada, United States, is a swollen shell with narrow hinge and low interareas, and very weak ribbing, and possibly no papillation. There are low dental ridges, no cardinal process,

and crural bases projecting from the edges of inner socket ridges.

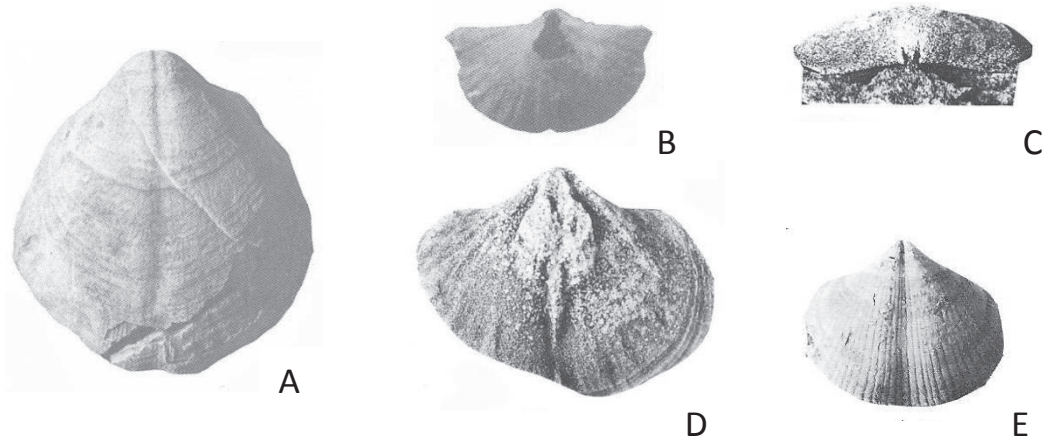


Fig. 503. A, *Eudoxina medius* (Lebedev), ventral valve, x 1. From Tournaisian of Russia. (Carter 2006a, p. 1744). B, *Costicrura minuta* Hoover, dorsal aspect, x10. From Kungurian or Roadian of Venezuela. (Hoover 1981). C-E, *Eudoxina subrotunda* (Weller), posterior dorsal valve, x2, ventral valve internal mould, x2, and ventral valve, x2. From Early Mississippian of Missouri and Illinois. (Carter 1988).

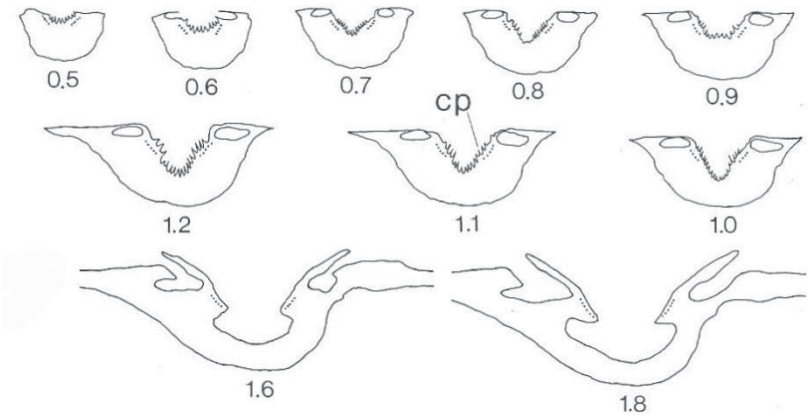


Fig. 504. *Eudoxina subrotunda* (Weller), serial sections with figures to indicate distance in mm from dorsal beak, x3. cp – cardinal process. From Early Mississippian of Iowa, USA. (Carter 1988).

Quasimartinia Havlíček, 1959 (Pragian – Eifelian) from the Czech Republic was placed in Obesariinae by Gourvennec in Carter & Gourvennec (2006c) but shows some approach to Eudoxinae. The genus has thick low dental plates and crural plates, and lacks adminicula and tabellae. But unlike these eudoxinid genera, there are no ribs, and micro-ornament was described as lacking. It cannot be said that the genus is close to most members of Reticularioidea – because even members assigned to groups such as Rhenothyrinae, Reticulariopsinae and Reticulariinae by Gourvennec in Carter & Gourvennec (2006c) differ in having longer ventral plates, a deeper dorsal valve with different cardinalia, and different micro-ornament, generally of close-set spinules in strong commarginal rows along the edge of growth lamellae.

Family **LADJIIDAE** new family

Name genus: *Ladjia* Veevers, 1959a, p. 126 from Frasnian of north Australia, here designated.

Diagnosis: Distinguished by presence of cruralium. Small smooth shells with micro-ornament of fine spines in commarginal rows. Dental plates low, no adminicula. Middle to Upper Devonian (Givetian to Frasnian).

Discussion: Genera placed in this family are characterized by shape, micro-ornament and presence of cruralium, whereas the ventral plates are feeble or lacking.

Subfamily **LADJIINAE** new subfamily

Name genus: *Ladjia* Veevers, 1959a, p. 126 from Upper Devonian of Western Australia, here designated.

Diagnosis: Small smooth shells with very low dental plates, apical plate, no adminicula. Cruralium formed by crural plates and tabellae. Micro-ornament of spines. Middle to Upper Devonian (Givetian – Frasnian).

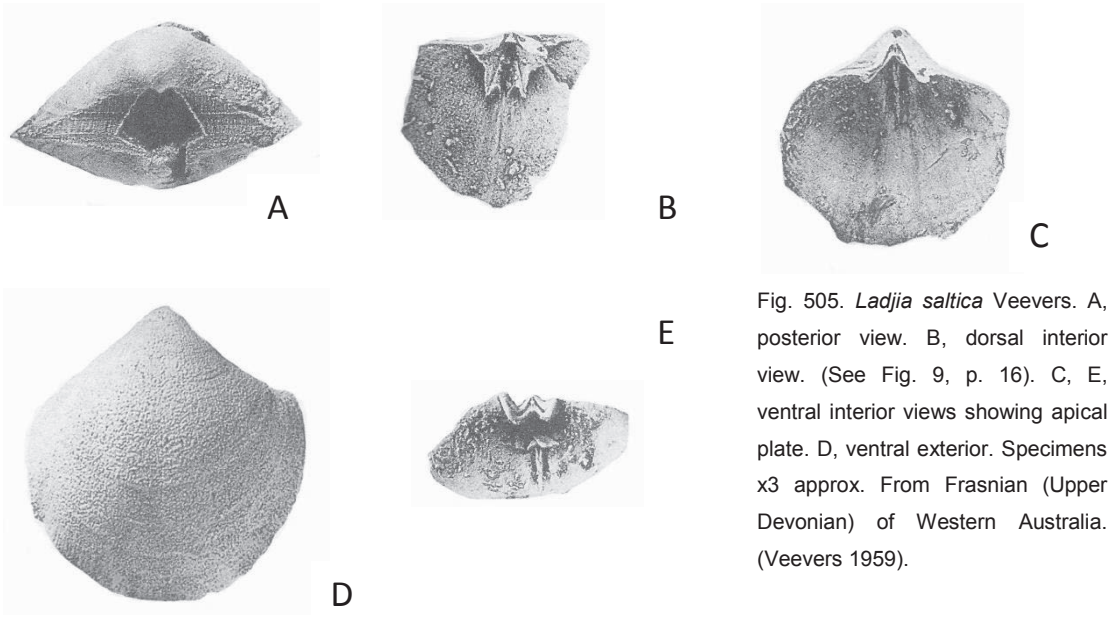


Fig. 505. *Ladjia saltica* Veevers. A, posterior view. B, dorsal interior view. (See Fig. 9, p. 16). C, E, ventral interior views showing apical plate. D, ventral exterior. Specimens x3 approx. From Frasnian (Upper Devonian) of Western Australia. (Veevers 1959).

Genera: *Ladjia* Veevers, *Apenosia* new genus, *Diazoma* Dürkoop (syn. *Kelusia* Mamedov), *Emanuella* Grabau (syn. *Paraemanuella* Yang), *Veeversaria* new genus.

Discussion: *Ladjia* Veevers, 1959a was classed as Rhynchospiriferinae of the Ambocoelioidea by Johnson, Carter & Hou (2006b, p. 1743), because of its cruralium, but is repositioned, because it has subdelthyrial thickening each side of a small apical plate, which closely resembles a connector plate in genera with better developed dental plates and adminicula. The spines lie in well ordered commarginal rows, and a few slender well formed costae on some specimens. Veevers (1959a) noted some variation in the internal plates. Dental flanges only are illustrated in Veevers (1959a, pl. 12, fig. 24), whereas a diagram

Fig. 506. *Ladjia saltica* Veevers, dorsal, ventral, and dorsal view of two specimens showing fine ribs and commarginal spines, x3 approx. From Frasnian (Upper Devonian) of Western Australia. (Veevers 1959).

shows rare dental plates and apparent adminicula (Veevers 1959a, text-fig. 77), and the variation was supposed to be infraspecific by Veevers. Little information has been provided on delthyrial plates, and for some genera, the delthyrium appears to be open, but in type *Ladjia,* narrow thickening is present posteriorly and diverges from a plate under the ventral beak. It approaches Ambothyrinae, which also lacks ventral plates, but has no thickening or apical plate.

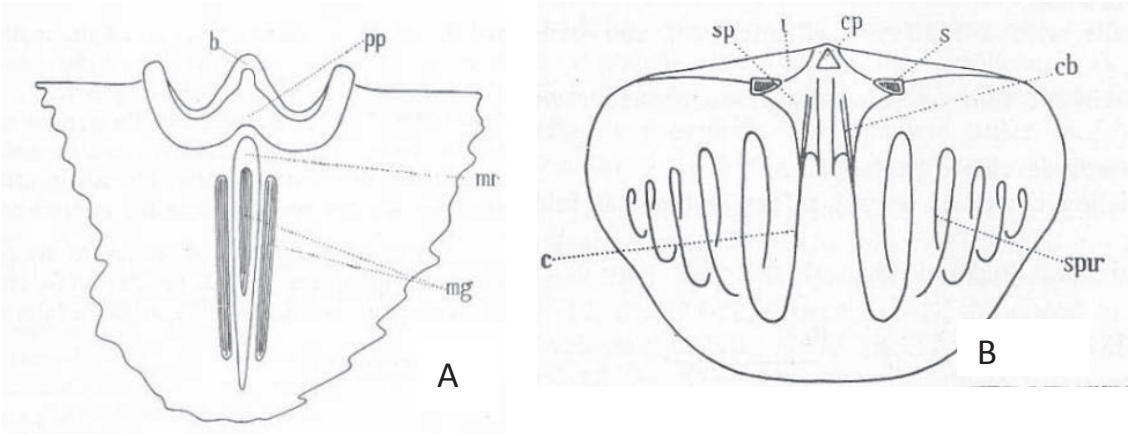


Fig. 507. *Ladjia saltica* Veevers, ventral and dorsal interiors. b – beak; c – crus; cb – crural base; cp – cardinal process; mg – muscle grooves; mr – muscle ridge; pp – pedicle plate; sp – socket plate as labelled but in fact a crural plate; spir – spiralium. From Frasnian (Upper Devonian) of Western Australia. (Veevers 1959).

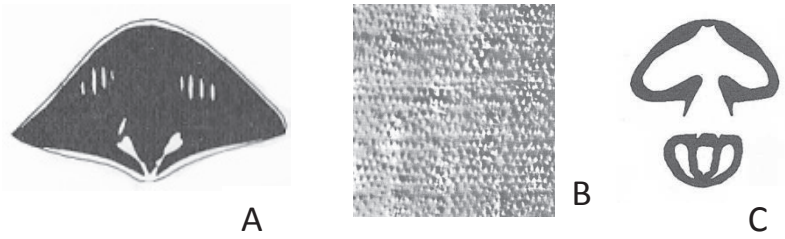


Fig. 508. A, *Emanuella* transverse section, presented by Caldwell (1967, Fig. 5), showing the cruralium at 2.6mm from ventral beak, x3. From Middle Devonian of McKenzie District, Canada. B, *Emanuella meristoides* (Meek), micro-ornament, x30. C, *Emanuella sublineata* (Meek), transverse section 2.6mm from beak, x3. B, C from Middle Devonian of western Canada. (Crickmay 1967).

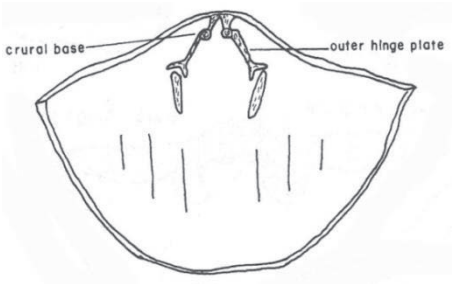


Fig. 509. *Emanuella subumbona* (Hall), transverse section showing crural base, dividing crural plate or so-called outer hinge plate from low tabellae, x5. From Devonian of New York. (Goldman & Mitchell 1990).

Crickmay (1967**)** described and illustrated various Canadian species as *Emanuella* with typical fine spines and sessile cruralium, and no adminicula, and low or no dental plates. Johnson, Carter & Hou (2006b) stated that the crural plates are discrete, but this seems incorrect. These specimens show an apical plate, but its presence needs to be verified for the type species *Nucleospira takwanensis* Kayser from the Givetian of China. The holotype was refigured by Dürkoop (1970, pl. 17, fig. 1), and two taxa ascribed to the genus from Afghanistan show the apical plate, and sessile long cruralium or sessalium for *E. alveosimilis* Dürkoop. Descriptions by Grabau (1923) and Yang (1977) need to be checked to confirm that an apical plate is developed in Chinese material.

Diazoma Dürkoop,1970, Fig. 53, fig. 1) shows a short connector plate in material described from Afghanistan, as well as small spines, pleromal thickening and small connector plate. The genus is based on *Emanuella volhynica* Kelus, 1939 from Pelcza, Volhyniaen.

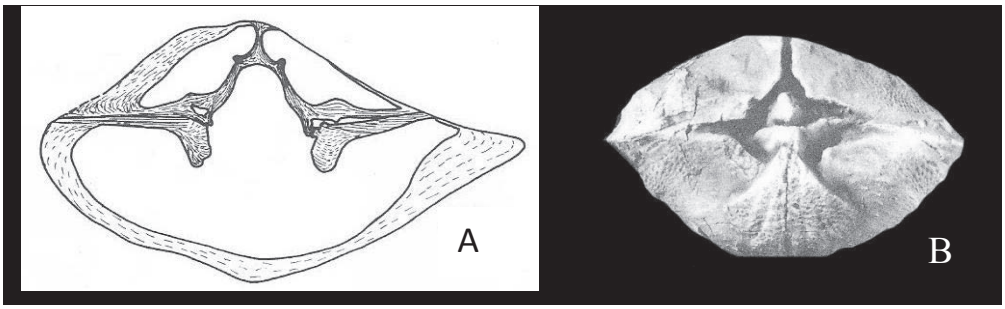


Fig. 510. *Diazoma volhynica* Kelus. A, cross section showing dorsal cruralium, x3.5, at 4.5mm from ventral beak. B, posterior view showing tabellarium, x1.5. From Eifelian of Afghanistan. (Dürkoop 1970).

Fig. 511. Internal moulds of *Diazoma*, showing cardinal plates and muscle impressions. A, B, *D. volhynica* (Kelus), ventral valve, x1.2 and dorsal view, x1.3. C, *D. volhynica oblongula* Dürkoop, posterior view, x1.3. From Eifelian of Afghanistan. (Dürkoop 1970).

Genus ***Apenosia*** new genus

Derivation: from specific name of type species.

Type species: *Crurithyris apena* Veevers, 1959a, p. 133 from Upper Devonian (Frasnian) of Fitzroy Basin, Australia, here designated.

Diagnosis: Micro-ornament of radial and commarginal fila, with shagreen ornament of pits. Dental plates short, no adminicula. Cruralium well formed, without supporting septum.

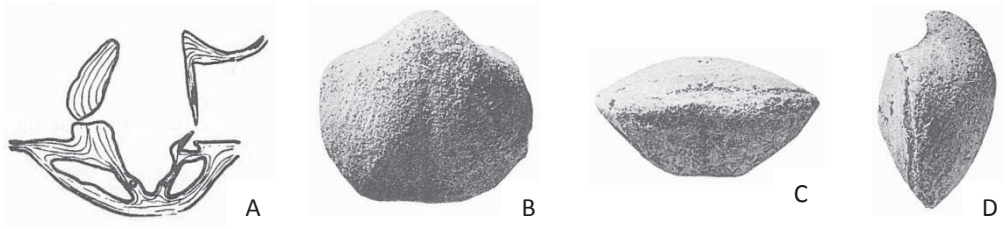


Fig. 512. *Apenosia apena* (Veevers). A, transverse section showing cruralium and dental plates, x10. B, C, D, ventral, anterior and lateral views, x6. Sadler Formation (Frasnian), Fitzroy Basin, Australia. (Veevers 1959a).

Discussion: This genus is distinguished by the cancellate ornament and closely-spaced pits, without spines. Possibly the pits could be due to prismatic shell structure, but this is not confirmed. Deltidial plates are developed, and a small apical plate lies under the ventral beak. Dental plates but no adminicula are developed. The lack of spines means that the genus is readily distinguished from other genera of the Ambothyrinae, and the lack of a dorsal septum below the cruralium provides an additional distinction. *Choperella* Liashenko 1969a from the Middle to Upper Devonian of the Russian Platform and western North America is similar in some of these respects but is transverse with deep sulcus in each valve. (See p. 371).

Genus ***Veeversaria*** new genus

Name: Named for John J. Veevers.

Type species: *Emanuella torrida* Veevers, 1959a, p. 128 from Frasnian of Fitzroy Basin, Australia, here designated.

Diagnosis: Small spinose shells distinguished by sessile dental sockets in the dorsal valve, otherwise close to *Emanuella*.

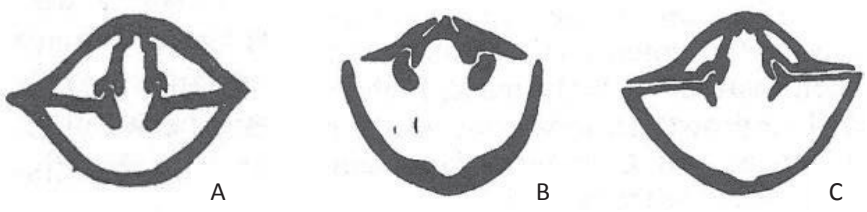


Fig. 513. Comparison of dental socket arrangements in A, *Emanuella takwanensis*, type species of the genus. B, *Veeversaria torrida* (Veevers). C, *E. meristoides* Crickmay. (Goldman & Mitchell 1990).

Discussion: The type species has been well described by Veevers (1959a, pl. 13, fig. 1-9, text-fig. 79-83). The genus has fine spines, and deltidial plates, with an apical plate and umbonal plug under the ventral beak, and dental plates are thick. A cruralium is developed in the dorsal valve, with finely tuberculate cardinal process. The main difference from *Emanuella* Grabau (see Veevers 1959b) is offered by the dental sockets, which are sessile, in contrast to the elevated dental sockets in *Emanuella,* a difference stressed as generically significant by Caldwell (1967) and Goldman & Mitchell (1990, p. 92).

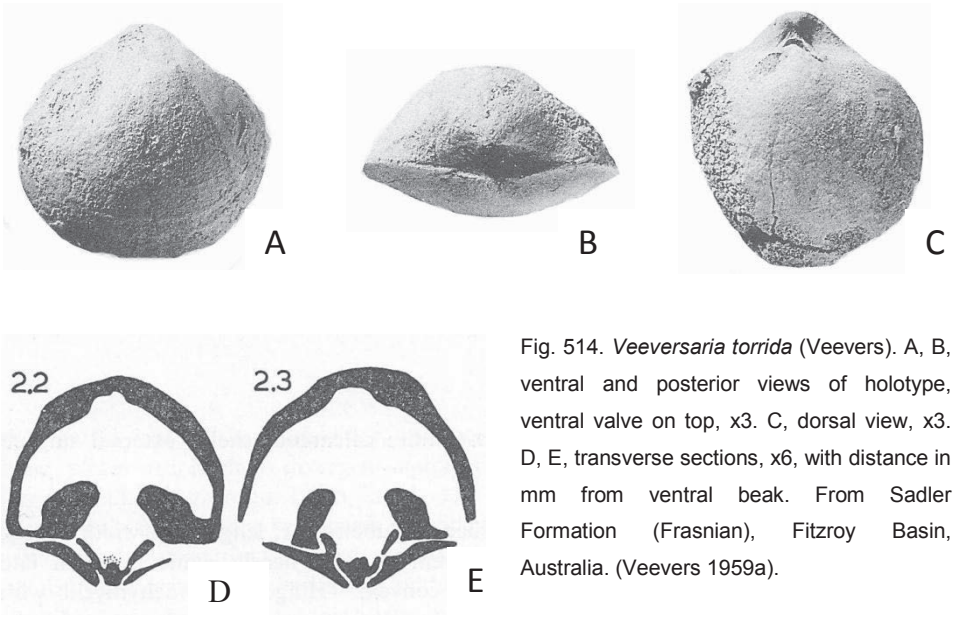


Fig. 514. *Veeversaria torrida* (Veevers). A, B, ventral and posterior views of holotype, ventral valve on top, x3. C, dorsal view, x3. D, E, transverse sections, x6, with distance in mm from ventral beak. From Sadler Formation (Frasnian), Fitzroy Basin, Australia. (Veevers 1959a).

Subfamily **AMBOTHYRINAE** new

Name genus: *Ambothyris* George, 1931, p. 42 from Givetian of Belgium, here designated.

Diagnosis: Shells usually without dental plates, no adminicula, cruralium well to imperfectly developed, micro-ornament varies between capillate and spinose. No apical plate. Middle Devonian to Upper Devonian (Frasnian).

Genera: *Ambothyris* George, *Amboglossa* Wang & Zhu, *Crurispina* Goldman & Mitchell, ?*Ilmospirifer* Ljashenko.

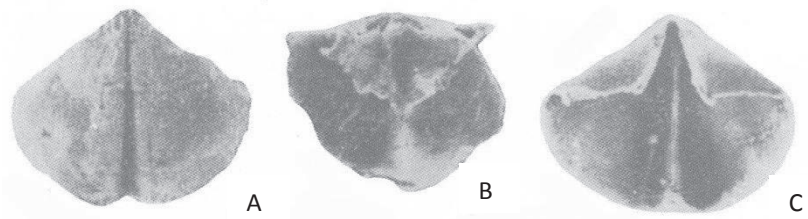


Fig. 515. *Amboglossa transversa* (Wang et al.). A, ventral exterior. B, dorsal interior, x2.5. C, ventral interior, x6. (Johnson & Hou in Johnson, Carter & Hou 2006b).

Discussion: This grouping is based on the lack of adminicula and spondylium, as compared with genera regarded as typical of Rhynchospiriferinae. Johnson & Hou in Johnson, Carter &

Hou (2006b, p. 1739) placed these genera in Rhynchospiriferinae, mixing them with genera that displayed dental plates and adminicula, but it is preferred to stress the difference, rather than amalgamate otherwise disparate genera into a group because they share a cruralium. Unfortunately, the *Revised Brachiopod Treatise* failed to accurately designate true dental plates, which may or may not be developed. Some species are capillate, others are spinose**.** *Amboglossa* Wang & Zu (1979, pl. 33, fig. 9) shows a well defined cruralium (as named by Johnson & Hou rather than a septalium), resting on a dorsal septum. *Ilmospirifer* has a narrow dorsal sulcus.

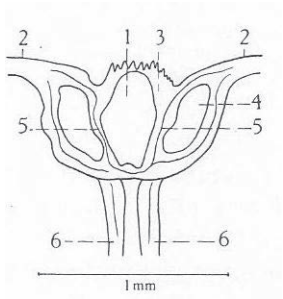


Fig. 516. *Ambothyris infima* (Whidborne), transverse section. 1 – apical dorsal cavity. 2 – dorsal interarea. 3 – cardinal process. 4 – lateral apical cavity. 5 – apical dorsal plate. 6 – apical dorsal lamellae, equivalent to tabellae, are seen through lucid shell. From Devonian of Belgium. (As labelled by Vandercammen 1956).

Family **RHYNCHOSPIRIFERIDAE** Paulus, 1957

[Nom. transl. hic ex Rhynchospiriferinae Paulus, 1957, p. 51].

Diagnosis: Crural plates join to form a cruralium. Dental plates and adminicula developed. Lower Devonian (Emsian) to Upper Devonian (Frasnian).

Discussion: This family is somewhat similar to *Espella* Nilova, a Silurian genus of Llandovery to Wenlock age, which has adminicula and cruralium. However there is no secure data to show that Rhynchospiriferidae developed from *Espella.* That remains a possibility, but the fossil record at present shows that Rhynchospiriferidae did not appear until the Devonian Period.

As a rule, deltidia were involved in partial or complete closure of the delthyrium. But several genera referred to Rhynchospiriferinae in the *Revised Brachiopod Treatise* have pleromal and connector plate development, some with apical callistry. These are segregated as separate subfamilies, judged to have evolved in close concert with subfamily Rhynchospiriferinae.

Subfamily **RHYNCHOSPIRIFERINAE** Paulus, 1957

[Rhynchospiriferinae Paulus, 1957, p. 51. Syn. Ilmeniinae Dürkoop, 1970, p. 203].

Diagnosis: Dental plates and adminicula. Most genera capillate. Lower Devonian (Emsian) to Upper Devonian (Frasnian).

Genera: *Rhynchospirifer* Paulus (= *Biarella* Markovski), *Changtanella* Xian Si-yuan, *Ilmenia* Nalivkin, *Ilmeniopsis* Xian, *Ilmenispina* Havlíček, ?*Levibiseptum* Xian (?), ?*Moravilla* Havlíček, **?***Zhonghuacoelia* Chen.

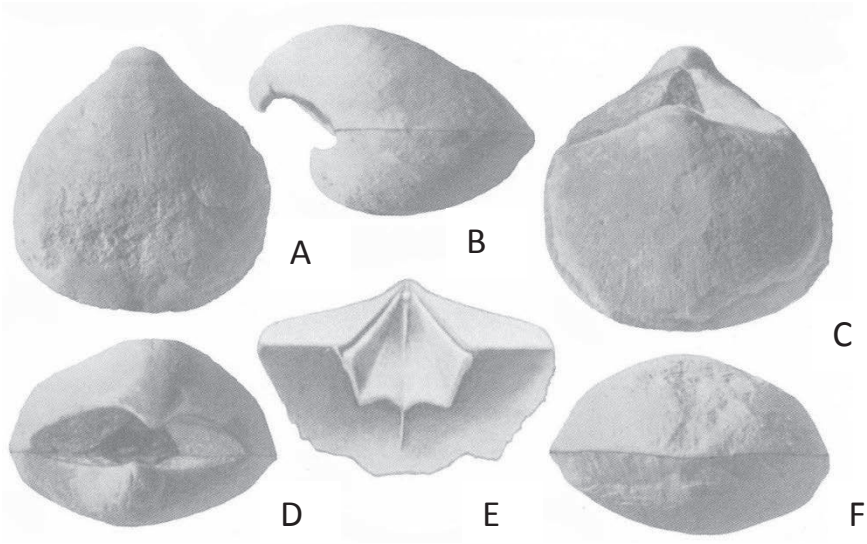


Fig. 517. *Rhynchospirifer hians* (von Buch). A, ventral, B, lateral, C, dorsal, D, posterior and F, anterior views, x1.75, with E, dorsal interior, x3.3. From Eifelian of Germany. (Paulus 1957).

Discussion: The shell is smooth (ie. non-plicate) and micro-ornament cancellate or finely capillate, with open delthyrium and open notothyrium. In *Rhynchospirifer* Paulus, long thin closely spaced dental plates and adminicula are shown (Fig. 518). Other genera have short low adminicula. Little information has been provided on delthyrial plates, and for several genera, the delthyrium appears to have been open. Some of the genera are poorly known, so that attribution is provisional, pending further information. Johnson, Carter & Hou (2006b) stated that the crural plates are discrete in *Moravilla,* yet they form a cup as figured by Havlíček (1953). *Changtanella* Xian Si-yuan, 1983 is outstanding, having a spondylium as well as cruralium and its micro-ornament is capillate, like that of *Rhynchospirifer. Ilmeniopsis* and *Levibiseptum* shows commarginal growth lines and *Zhonghuacoeilia* has small spines: *Ilmenispirifer* has spines as well as capillae.

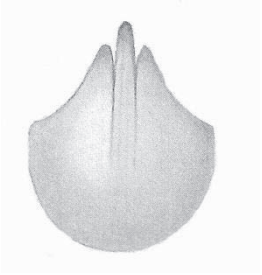


Fig. 518. *Rhynchospirifer hians* (von Buch), ventral internal mould, x2. From Eifelian of Germany. (Paulus 1957).

Dürkoop (1970) proposed Ilmeniinae Dürkoop, 1970, p. 203. The nominate species *Imenia* Nalivkin, 1941, p. 186 was illustrated with figures of a species from Afghanistan that showed well developed pleromal ridges, which are missing from Rhynchospiriferinae. Illustrations of *Ilmenia* in Nalivkin (1941) and Cherkosova (1991) provide no information on delthyrial apparatus, but sections of *Ilmenia hians* Rhzonsnitskaya, the species identified by

Dürkoop in Afghanistan, show no sign of pleromal ridges or connector plate. It is therefore believed that Dürkoop's material from Afghanistan do not belong to *Ilmenia*, but are a taxon yet to named, possibly belonging to Suchanariinae.

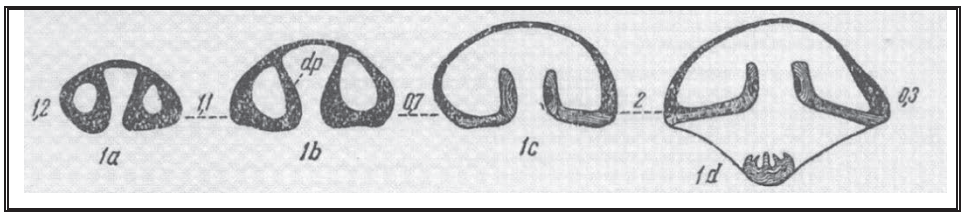


Fig. 519. Transverse sections of *Ilmenia subhians* Rzhonsnitskaya, indicating lack of apical or connector plate and pleromal ridges. Specimens x3. dp – dental plate and adminicula; with figures showing distance in mm from apex. From Middle Devonian of Kuznets Basin, Russia. (Rzhonsnitskaya 1952).

Fig. 520. *Ilmenia altovae* Nalivkin. Ventral and dorsal views, x1. From Middle Devonian of Russia. (Nalivkin 1941).

Subfamily **SUCHANARIINAE** new subfamily

Name genus: *Suchanaria* new genus from Devonian of Fitzroy Basin, Western Australia, here designated.

Diagnosis: Adminicula and connector plate. Smooth, cardinal platform, cruralium or septalium, lacking ctenophoridium. Silurian (Wenlock) to Upper Devonian (Frasnian).

Genera: *Suchanaria* new genus, ?*Kosirium* Ficner & Havlíček.

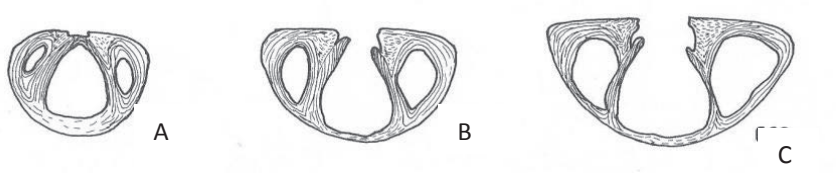


Fig. 521. A-C, transverse sections identified as *Ilmenia subhians* Rhzonsnitskaya, x4, by Dürkoop (1970), but showing pleromal ridges absent from *subhians*. From Lower Devonian of Afghanistan.

Discussion: An Afghan species described as *Ilmenia* by Dürkoop (1970) has pleromal ridges along the junction of the dental and adminicula plates, and may have had a reduced connector plate, or least an incipient plate. This is where ignorance remains a barrier to full understanding, because on the one hand, the pleromal development may have arisen in an ad hoc manner in all sorts of different genera. Or it may have been restricted to a particular lineage, and because the second choice is more easily tested in subsequent research, this is the preferred option. *Imenia* does share a cruralium with Suchanariinae, but lacks pleromal

ridges and so the Afghan material is regarded as belonging to a different taxon.

Kosirium Ficner & Havlíček, 1975 appears to belong to the group, displaying a possible large build-up of tissue between the dental plates. *Emanuella* Grabau has a small apical development, but is retained in Ladjiinae, because it lacks adminicula.

Genus ***Suchanaria*** new genus

Name: souchos – of the crocodile, Greek.

Diagnosis: Oval moderately inflated shells with anterior sulcus and fold, cancellate micro-ornament. Dental plates and short adminicula, low tuberculate cardinal process, cruralium supported by broad median septum. Delthyrium wide, closed by connector plug with heavy pleromal thickening.

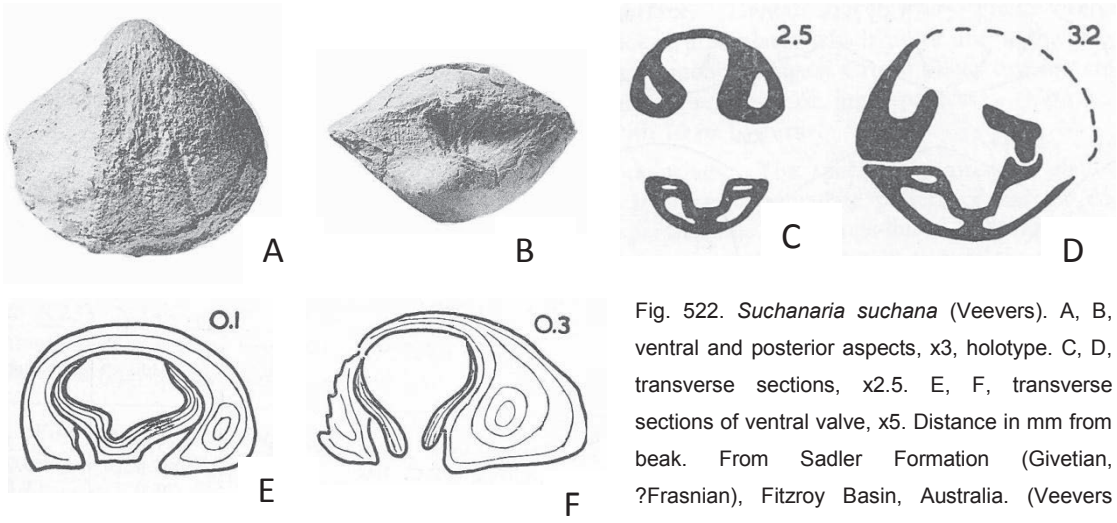


Fig. 522. *Suchanaria suchana* (Veevers). A, B, ventral and posterior aspects, x3, holotype. C, D, transverse sections, x2.5. E, F, transverse sections of ventral valve, x5. Distance in mm from beak. From Sadler Formation (Givetian, ?Frasnian), Fitzroy Basin, Australia. (Veevers 1959a).

Type species: *Tingella suchana* Veevers, 1959a, p. 136 from Givetian and possibly mid-Frasnian of Fitzroy Basin, Australia.

Discussion: This genus is distinguished from *Tingella* Grabau by its cancellate micro-ornament, whereas *Tingella*, synonymized with *Reticulariopsis* Fredericks, has growth lamellae and marginal spines. As well the present genus has pleromal development, and a cruralium.

Subfamily **LAZUTKINIINAE** Johnson & Hou, 1994

[Nom. transl. hic ex Lazutkiniidae Johnson & Hou in Carter et al. 1994, p. 337].

Diagnosis: Strongly and entirely costate to plicate as a rule, without capillae or tubercles. Dental plates, short adminicula and cruralium present. Lower Devonian (Emsian) to Middle Devonian (Givetian).

Genera: *Lazutkinia* Rzhonsnitskaya (syn. *Spirifer* (*Yakorskiella*) Lazutkin nom. nud.), ?*Prolazutkinia* Hou & Xian.

Fig. 523. A, B, *Lazutkinia mamontovensis* Rzhonsnitskaia, dorsal and ventral aspects, x1. From Middle Devonian of Kuznets Basin, Russia. C, D, *Prolazukinia lata* Hou & Xian, x 2. From Lower Devonian (Emsian) of south China. (Rzhonsnitskaia 1955; Johnson & Hou 2006b).

Discussion: Internal features are much as in Rhynchospiriferidae, and *Lazutkinia* has a knob-like cardinal process. Notwithstanding the diagnosis offered by Johnson & Hou in Johnson et al. (2006b, p. 1744), *Lazutkinia* is costate rather than plicate. *Lazutkinia,* although name-giver for a family-group defined by the presence of “dental plates”, which should be corrected to adminicula, was said in some instances to have dental plates that were short and thick, or even lacking. A cruralium on a low median septum is present, as well as commarginal lamellae, as in many members of Rhynchospiriferidae, although it has to be said that neither genus looks particularly close to any other members of Ambocoelioidea. *Prolazutkinia* Hou & Xian in Xian et al. 1983, is only dubiously associated with *Lazutkinia*. It may share costae, but is distinguished by its wide hinge, and subfasciculation. Furthermore long divergent adminicula are present, together with converging tabellae. The only other members of the Ambocoelioidea known to have adminicula are classed within Rhynchospiriferidae, so that the group is deemed to be allied. The subfasciculation of costae in *Prolazutkinia* recalls the elaborate ornament of *Elymospirifer*, classed in Costispiriferidae (p. 293).

Fig. 524. *Lazutkinia mamontovensis* (Lazutkin), x2. Transverse sections from left to right, dorsal valve below, from Middle Devonian of Kuznetz Basin, Russia. (Redrawn from Sarytcheva 1960).

sedis incerte

Family **VERNEUILIIDAE** Schuchert, 1929

[Nom. transl. Brunton 1984, p. 101 ex Verneuiliinae Schuchert, 1929, p. 21].

Diagnosis: Transverse with plicae each side of sulcus opposed on each valve. Middle Devonian (Eifelian) [to Early Carboniferous (Visean)?].

Genus: *Verneuilia* Hall & Clarke.

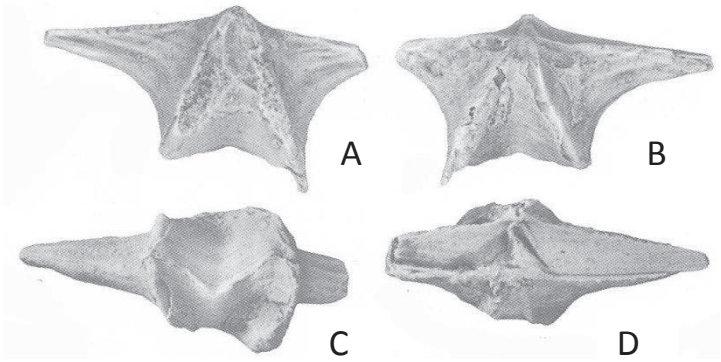


Fig. 525. *Verneuilia cheiropteryx* (Archiac & Verneuil), ventral, dorsal, anterior and posterior aspects, x2. Note the notches, like denticulations, to the upper left of A, due to the horizontal growth increments across the interarea (Rémy Gourvennec, pers. comm.). From Middle Devonian of Germany. (Gourvennec 1994a).

Discussion: Johnson in Johnson et al. (2006b, p. 1746) in the *Revised Brachiopod Treatise* placed this family in Ambocoelioidea, disregarding the fact that in that case, Verneuiliinae Schuchert, 1929 should assume naming rights for the entire superfamily, because it has clear priority over Ambocoeliinae George, 1931. Pitrat (1965) had more judiciously left Verneuiliidae as Superfamily and family uncertain. The trouble is that *Verneuilia* is far from typical for Ambocoelioidea, differing in appearance and micro-ornament. It is of subpentagonal shape (although distorted somewhat as to appear asymmetrical according the examination of the holotype by Gourvennec 1994a), with wide and deep dorsal as well as ventral sulcus, and the sulcus in each valve is bordered by a high carinate plication. Micro-ornament consists of fine growth increments. The hinge is extremely wide, with extended and acute cardinal extremities, and the interarea moderately high. Although Gourvennec stated that the holotype showed nothing of the interior, and added no further detail from other material, Johnson in Johnson, Carter & Hou (2006, p. 1746) asserted that dental plates (meaning adminicula) were lacking, and that short crural plates (tabellae) merged with prominent medianly convergent “hinge plates” that is crural plates, just as in many Ambocoeliidae. No source for this information was provided, but it was probably based on the morphology of material identified with *Verneuilia* by Blodgett & Johnson (1994). The Blodgett-Johnson species is regarded as belonging to another genus, *Johnsononia* n. gen., described on p. 372.

Two further genera were assigned to Verneuiliidae in the *Revised Brachiopod Treatise*, apparently on the basis that they shared the wide sulcus in the dorsal valve. *Nuguschella* Tiazheva, 1960 of Middle Devonian (Eifelian) age of the Ural Mountains in Russia is a transverse form (Fig. 496, p. 371) without the extremely wide hinge, and lacks dental plates and has closely discrete tabellae and medianly convergent crural plates. It is moderately close internally to the species ascribed by Blodgett & Johnson (1994) to *Verneuilia*, incorrectly according to present analysis, for a genus now called *Johnsononia*. The genus has several pairs of plicae, including a pair bordering the sulcus in each valve. Another genus, though not deemed to be allied by Johnson, is *Choperella* Liashenko, 1969a. It has a moderately wide hinge and dorsal sulcus, and so also comes moderately close in external appearance (Fig. 497, p. 371). It was classed as Rhynchospiriferinae in the Treatise, and is capillate with no adminicula, and said to have short “crural plates”. Micro-ornament is capillate. Both are of Middle Devonian age, with *Choperella* ranging into Upper Devonian.

Minythyra Brunton, 1984 from Visean of Ireland has somewhat similar shape with lower interareas, and no median septum. Although assigned to Verneuiliidae by Brunton (1984) as accepted by Johnson in Johnson et al. (2006), it has an extraordinarily short hinge, and family and relationships remain open to question, especially because the jugum appears to have been complete prior to breakage (Fig. 527). No known member of Spiriferida has a complete jugum. Brunton’s genus is close in shape to the Devonian athyrid Plicathyrinae Alvarez, 1990, with sulcus bordered by plicae, and alate cardinal extremities. There are differences, but genera do display tabellae, although usually with a cardinal plate, and dental plates may be missing. A jugum is present in the spiralia.

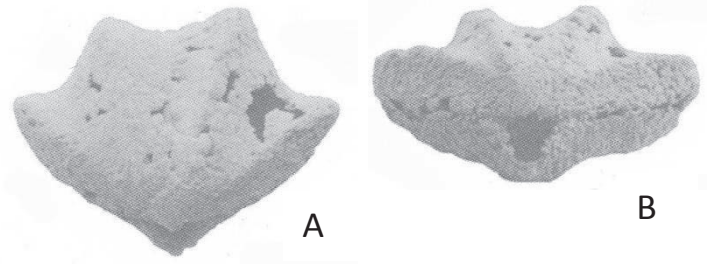


Fig. 526. *Minythyra lopha* Brunton, A, dorsal view, B, posterior view with dorsal valve on top, x20. From Visean of Ireland. (Brunton 1984).

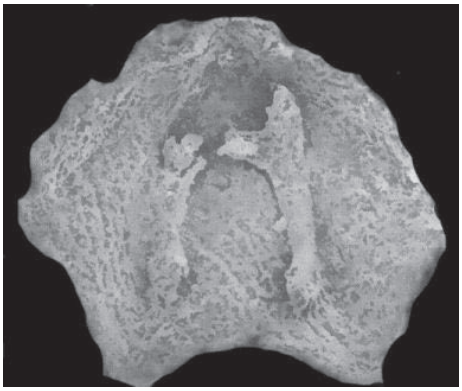


Fig. 527. *Minythyra lopha* Brunton, silicified interior of dorsal valve showing broken but once complete jugum, x25. From Visean of Ireland. (Brunton 1984).

situ speculario et disputando

Verneuilia? oceani Orbigny, 1850

Diagnosis: Small shells with hinge at maximum width, very high ventral interarea, denticulate hinge, ventral valve strongly sulcate with narrow high bordering ridges, dorsal valve deeply sulcate medianly, with high bordering ridges, micro-ornament of commarginal growth lirae and traces of radial capillae. Delthyrial cover plate. Low dental ridges, no adminicula, no connector plate; tabellae present, but apparently no crural plates.

Discussion. The species *oceani* was thoroughly revised by Gourvennec (1994), with extensive synonymy, description and figures, featuring the highly distinctive shape, and providing details of the interior. The dental apparatus is reduced to low ridges each side of the delthyrium, and the cardinal process lies on an elevated cardinal pillar (rather than platform), and is marked by faint striations. To each side lies a tubular crural base as figured in Gourvennec (1994a, Fig. 2), which passes back on the inner side of the dental sockets, and rests each on a low plate, that seems to be a tabella (see Fig. 529).

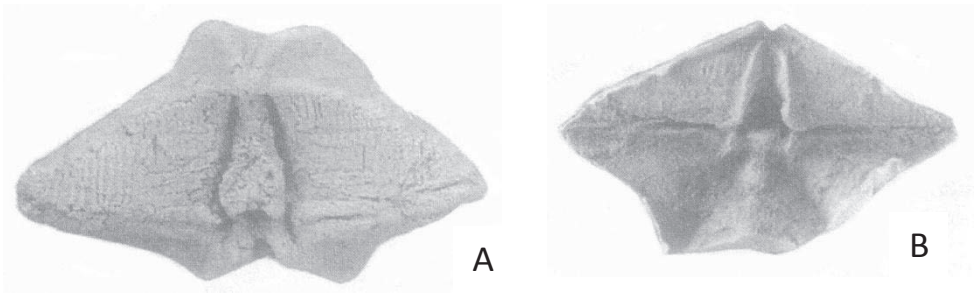


Fig. 528. *Verneuilia*? *oceani* (Orbigny), posterior views of partly decorticated specimen and latex cast, x6. From Visean of Belgium. (Gourvennec 1994a).

Gourvennec (1994a) considered the spiralia and cardinalia in the species *oceani* to be like those of *Cyrtina* and *Cyrtinaella* of Cyrtinidina Carter & Johnston in Carter et al. 1994, These genera overall look somewhat similar in their ventral valve, but lack a dorsal sulcus, and Cyrtinidae has a tichorhinum and spondylium and medium ventral septum. It is true that the Devonian genus *Komiella* Liashenko, 1985, classed in Komiellidae Johnson & Blodget, 1993 as a sole genus-family in the punctate Cyrtinidina, is also bisulcate, and it lacks a tichorhinum. But in various respects, *Komiella* differs considerably from *oceani*.

Brunton (1984, p. 101, Fig. 160) and Gourvennec (1994a, p. 578, Fig. 1, 2, pl. 1, fig. 7-31) referred the species *oceani* to *Verneuilia* Hall & Clarke, 1893, because it externally resembles *Verneuilia cheiropteryx* (Archiac & Verneuil, 1842) in having a deep dorsal median sulcus, and has high narrow ridges bordering this and the ventral sulcus. But Johnson in Johnson et al. (2006b, p. 1746) sharply disagreed, and assigned *Verneuilia*, of Middle Devonian age, to Ambocoelioidea, and *oceani* of Visean age to an unspecified member within Spiriferoidea. He pointed to the strong dental flanges, finely striate cardinal process, with the

implication that it might be a ctenophoridium, and denticulate hinge with supposed perideltidial areas. Mention was made of the lack of crural plates (ie. tabellae), yet tabellae (= crural plates of Johnson) are clearly developed in *oceani*. Ornament consisted of growth striae only. Whether *Verneuilia cheiropteryx* might be the same internally as *oceani* depends on two conflicting assessments. On the one hand, *oceani* and *cheiropteryx* are similar externally in many respects. On the other hand, *oceani* is much younger, at Visean, and there are not many brachiopod genera which survived from Middle Devonian into Lower Carboniferous. Of all the superfamilies in Spiriferidina, *oceani* approaches Paeckelmannelloidea, with its very wide hinge and high striate ventral interarea. Even the presence of the dorsal sulcus is not extraordinary, because *Bashkiria* and *Fusella* also display a dorsal sulcus, and the sulcus of both valves bears high rims, although nowhere near as strong as those of *Verneuilia* or o*ceani.* The capillate micro-ornament of *oceani* would fit, and the low dental rims are close to those of Strophopleurinae. But there is no certain match with aspects of the dorsal interior, due to the absence of crural plates, and presence of tabellae. In several respects, the species is ambocoeliiform, given the lack of dental plates and adminicula, and the presence of tabellae, though there are clearly exceptional aspects, including the absence of crural plates.

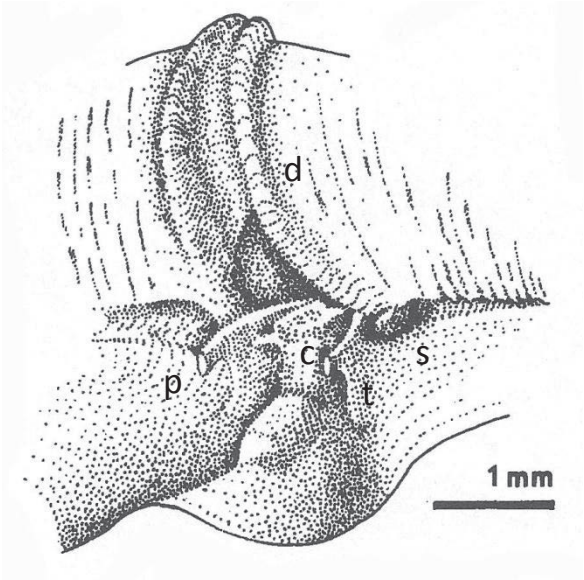


Fig. 529. Reconstruction of apical region of *oceani* (Orbigny), showing dental ridges (d) and adjoining high interarea with vertical striae, and dorsal valve below with dental sockets (s), cardinal pillar with cardinal process (c), start of crural processes (p) and apparent tabellae (t). From Visean of Belgium. (Gourvennec 1994a). Lettering applied.

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