STROPHALOSIIDINA (BRACHIOPODA)

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Earthwise 22

ISSN (PDF): 3021-2111

19 December, 2023

Contents

LIST OF TAXA DISCUSSED IN THIS STUDY. New taxa in bold

PREFACE

Family group and ordinal names are spelled as in the *Revised Brachiopod Treatise*, although I think it would be more serviceable for paleontology to simply add agreed endings to the name of the genus, without changing part of the genus name in order to conform with current rules of Latin grammar (Waterhouse 2022, pp. 3, 4). The addition of et seq. after the record of the original proposal of a family group implies that the same record is to be applied to the same following family group categories.

In an introductory section to the Strophalosiidina, hyporders are introduced, to subdivide the suborder into four divisions, three named for groups treated as much lesser subdivisions in the *Revised Brachiopod Treatise*, and one incorporating the Suborder Lyttoniidina, previously treated as an entity separate from Strophalosiidina. What is believed to be an equivalent name for hyporders is infrasuborders (see Waterhouse 2010, 2015), and it is preferred to try to homogenize ordinal group terms with those used for Class Bivalvia, as set out by Carter et al. (2016), and regard infrasuborders as equivalent to hyporders, and therefore superfluous.

The present study has deficiencies. There are matters beyond present understanding, at least for me, which require insight from meticulous further research. In some cases, there is a shortage of fossil material, in some cases further preparation is required, and one is never free from the suspicion that material is being misinterpreted or that a new discovery will drastically amend previous assumptions. That is Paleontology, free from the artificial certainty that surrounds certain other disciplines which devolves responsibility on to machines or simplistic formulae, instead of endeavouring to reflect and understand the vast complexity displayed by biota and their evolution, through time, and across the globe. This uncertainty encourages for some the use of so-called open nomenclature, as argued by some modern zoologists eg. Sigovini et al. (2016). That is a choice. But it does presume that in future some wonderful practitioner or team will address the question and solve the problems. What if that does not happen? Is it better to proceed step by faltering step, building little by little on what has been already proposed, gradually edging closer to a comprehensive picture. In our present state of uncertainty and caution, imposed by the knowledge that so many fossils remain to be collected and described, there may be room for both procedures.. A number of genera amongst Strophalosiidina remain difficult to place. Should they be set aside and gathered together as a group in open nomenclature, awaiting resolution?

Cladistic diagrams and studies have not been employed in this assessment. I am unimpressed by the diagrams offered in the *Revised Brachiopod Treatise*, and endorse the attitude taken to them by the authors of the studies on Productida, that they would rather do without. The assessment of a mere twenty to thirty character states is nowhere near sufficient for adequate study, and the use of equal weighting for each character state fails to address realities of evolution.

REPOSITORIES

Fossils described throughout this report are housed in the Bulk Storage of the Queensland Museum, Hendra, Brisbane, and are registered individually by number with the prefix **UQF**. They come from localities numbered with the prefix **UQL**. Fossils from other institutions are

AMF for Australian Museum, Sydney, New South Wales, and in Tasmania; **TM** Tasmanian Museum, Hobart, **TMF** Geological Survey of Tasmania, Hobart, and **BR**, for brachiopods kept at the Institute of Nuclear and Geological Sciences, Lower Hutt, New Zealand.

SUMMARY OF HYPORDERS IN STROPHALOSIIDINA

Abstract

Strophalosiidina are subdivided into four hyporders, involving groups previously treated as infrasuborders, and also incorporating lyttoniid brachiopods, which were previously treated as belonging to a higher category called Suborder Lyttoniidina Williams et al., separate from Strophalosiidina.

INTRODUCTION

Many species within Strophalosiidina belong to Hyporder Strophalosiidei, as laterally bisymmetrical shells with swollen ventral valve and concave to flat dorsal valve, attached as a rule by umbonal cicatrix and by spines over the ventral valve. The dorsal valve may be smooth or spinose. Other forms of ornament involve rugae, plicae and very fine radial capillae, comparable in strength to the commarginal growth increments. All these features are moderately consistent within groups of species and genera. Shells articulate through two ventral teeth and two dorsal sockets, and may during life have been further bound through cartilage developed along hinge of each valve, with development of interareas. The valves held together and open and shut through the operation of adductor muscles on each valve, and diductor muscles from the ventral valve attached to a cardinal process at the hinge of the dorsal valve. Feeding brachiophore apparatus developed to leave brachial ridges on the dorsal valve. In the other three hyporders, the teeth and sockets are lost. In Hyporder Aulostegidei, the brachial ridges reduced in size, Richthofeniidei develop a relatively large conical ventral valve and reduced dorsal valve with little known about the feeding apparatus, and in Lyttoniidei the ventral valve is large and dish-like, with very large brachidium and reduced dorsal valve.

Hyporder **STROPHALOSIIDEI** Waterhouse, 1975

[Nom. transl. hic ex Strophalosiidina Waterhouse, 1975, p. 4].

Diagnosis: Teeth developed, with interareas and umbonal cicatrix as a rule. Cardinal process developed as a bilobed, trilobed or quadrilobed shaft. Brachial apparatus simple, large. Devonian to Late Permian.

Discussion: Assuming that Chonopectinoidea belongs here, this is the oldest hyporder in the suborder, with its early development traced in Waterhouse (2013), and by Permian time came to diversify most in the cool to cold waters of east Australia and New Zealand. Four superfamilies are distinguished, Chonopectoidea, Strophalosioidea, Dasyalosiodea and Quadratoidea, as elaborated in the following text (pp. 17-55).

Hyporder **AULOSTEGIDEI** Waterhouse, 2010

[Nom. transl. hic ex Infrasuborder Aulostegimorphii Waterhouse, 2010, p. 13].

Diagnosis: Teeth and sockets are lost, and some genera lack cicatrix, interareas may be reduced or absent. The cardinal process may be large and broad, and brachiophores are reduced in size from the arrangement in Strophalosiidei. Lower Carboniferous (Ivorian) to Late Permian.

Discussion: This group is widely developed, and particularly well known thanks to the study by Cooper & Grant (1975) on occurrences in the Permian of the Glass Mountains in west Texas. It was proposed as an infrasuborder, which appears to be much the same as the category hyporder used by Carter et al. (2011) in the proposed classification of Bivalvia. It is believed that classification should extend across phyla, and therefore a hyporder is substituted for the initial proposed term Aulostegimorphii.

Three superfamilies are recognized, Aulostegoidea Muir-Wood & Cooper, 1960, Institelloidea Muir-Wood & Cooper, 1960, and Scacchinelloidea Licharew, 1928a, b, as promoted in Rozanov (2003) and discussed in Waterhouse (2010, p. 14). An intriguing question remains: the relationship between Scacchinelloidea and Chonopectinoidea. Both are unusual in displaying, for some their genera, a ventral median septum. Does that imply that members of Scacchinelloidea descended from Chonopectinoidea? And if so, does the classification have to be altered? The difficulty is that Chonopectinoidea are mostly Devonian, and Scacchinelloidea mostly Permian. With such a great gap in time, is it not likely that the septum arose anew, as expressed in the present classification? But how good is the fossil record?

Hyporder **RICHTHOFENIIDEI** Waterhouse, 2010

[Nom. reductio hic ex Richthofeniidina Waterhouse, 2010, p. 11].

Diagnosis: Ventral valve conical or sphenoid, with cap-like dorsal valve that may lie below ventral margin, ventral valve may be cemented to substrate or. more rarely. attached by spines. No teeth or interareas, brachiophores not apparent, and their nature unknown, with the question not addressed in the *Revised Brachiopod Treatise* by Wardlaw, Grant & Brunton (2000). Upper Carboniferous (Bashkirian) to Late Permian.

The group evolved from Hyporder Aulostegidei (Sutherland 1996). The group was treated as a suborder by Waterhouse (2010) to fit with the treatment of Lyttoniidina by Williams et al. (2000), but it is preferred to downscale the ranking of both groups and associate them more closely within Suborder Strophalosiidina.

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

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

Diagnosis: Obliquely conical shells with rhizoid spines and no coscinidium. Bashkirian to possibly Late Permian.

Discussion: This is an outstanding family. Cooper & Grant (1975, p. 927) classed *Teguliferina* Schuchert & Le Vene (1929, p. 121) in Strophalosioidea, whereas Williams (1953) and Grant (1993) placed the genus with the orthotetidines. Wardlaw, Grant & Brunton (2000, p. 617) treated the group as a subfamily in Richthofenioidea, following Brunton, Lazarev & Grant (1995, p. 953), and placed the subfamily in Cyclacanthariidae Cooper & Grant (1975, p. 938), even though the proposal of Teguliferinidae Muir-Wood & Cooper, 1960 has priority.

Hyporder **LYTTONIIDEI** Williams, Harper & Grant, 2000

[Nom. reductio hic ex Lyttoniidina Williams, Harper & Grant, 2000, p. 619].

Diagnosis: Dorsal valve reduced, to large lobate brachidial plate with small posterior vestige of original valve, ventral valve rarely spinose, showing posterior flap in some forms, secondary shell pseudopunctate. Early Carboniferous?, Late Carboniferous to Late Permian.

Discussion: Two superfamilies were recognized in the *Revised Brachiopod Treatise,* Lyttonioidea Waagen, 1883 and Permianelloidea He & Zhu, 1979 (nom. transl. Williams et al.

2000, p. 639 ex Permianellidae He & Zhu, 1979, p. 136). However Subfamily Loczyellinae Licharew, 1937, p. 83 seems likely to take priority for the naming of this group, allowing for the judicious caution of its appraisal by Williams et al. (2000, p. 641), and setting aside their failure to provide illustrations for two of the three proposed genera.

A comprehensive summary of the morphology and history of understanding of the group was provided by the *Revised Brachiopod Treatise* by Williams et al. (2000). Caution was expressed over origins for the group, but the discovery of prominent brachiophores in species regarded as strophalosioid by Termier et al. (1966), Termier & Termier (1970) and Grant (1972) helps show that there is a strong linkage between the lyttoniids and strophalosiids, as expressed by Lazarev (1987, p. 48). Grant (1972) had separated Cooperininae Pajaud as Strophalosiacea rather than Lyttoniacea. Earlier, Williams (1953) had proposed Oldhaminidina (as Suborder Oldhaminoidea), a name than potentially could claim priority over Strophalosiidina, but Williams et al. (2000) abandoned this name as failing to recognize that *Lyttonia* was more widely used than *Oldhamina*, Perhaps a better reason would have been that *Lyttonia* provided the basis for family group nomenclature, following Waagen, and it is preferred that ordinal names should be consistent with family group names. It is an awkward fact that *Lyttonia* does not feature as a recognized genus name nowadays (see Williams et al. 2000, p. 631), but as against any possible championing of the Williams-based name, *Strophalosia* would seem to be the much more acceptable provider of the subordinal name rather than the ultraspecialized *Oldhamina.*

Waterhouse (2010) elevated Lyttonidina to a full order, surely an exaggerated upscaling, overly influenced by trying to be consistent with the treatment in the *Revised Brachiopod Treatise* of lyttoniids as forming a distinct suborder, and added a new suborder Cooperinidina Waterhouse (2010, p. 11), based on Cooperinidae Pajaud, 1968, centred on *Cooperina* Termier, Termier & Pajaud, 1966, p. 161, 332 with bilobed or ptycholophous brachidia. This group was placed in Aulostegidae by Brunton et al. (2000, p. 605), and amended to a superfamily in Waterhouse (2013, p. 209). The shell is plane without spines as in lyttoniids, and the brachiophores ptycholophous, suggestive of Lyttoniidae.although the dorsal valve is more complete than in shells of that group.

REFERENCES

BRUNTON, C. H. C., LAZAREV, S. S., GRANT, R. E. 1995: A review and new classification of the brachiopod order Productida. Palaeontology 38 (4): 915-836, fig. 1-4.

CARTER, J. G. + 61 authors: 2011: A synoptical classification of the Bivalvia (Mollusca). Paleont. Contrib. 4: 1-47.

COOPER, G. A., GRANT, R. E. 1975: Permian brachiopods of west Texas 111. Smithson. Contrib. Paleobiol. 19: i-x, 795-1921, pl. 192-502.

GRANT, R. E. 1972: The lophophore and feeding mechanism of the Productidina (Brachiopoda). J. Paleont. 46: 213-248, 9pl.

_____ 1993: The brachiopod family Gemmellaroiidae. J. Paleont. 67: 53-60, fig. 1-7.

LICHAREW, B. K. 1928a: Úber einige seltene und neue Brachiopoden aus dem Unterperm des nordlichen Kaukasus. Paläont. Zeit. 10 (3-4): 258-289.

_____ 1928b: On some rare and new brachiopods from Lower Permian of North Caucasus. Bull. Com. Géol. 47 (3): 261-296, pl. 23, 24. [Russ.]

_____ 1937: Brachiopoda of the Permian System of USSR. Fascicle 1. Permian brachiopods of North Caucasus: Families: Chonetidae Hall & Clarke and Productidae Gray. Mon. Paleont. SSSR 39 (1): 152p., 13pl. [Russ.]

MUIR-WOOD, H. M., COOPER, G. A. 1960: Morphology, classification and life habits of the Productoidea (Brachiopoda). Geol. Soc. Amer. Mem. 81: 1-447, 135pl.

PAJAUD, D. 1968: La néoténie chez les Thécidées (Brachiopodes). C. R. Acad. Sci. (ser. 1) 267: 156-159.

ROZANOV, A. Y. (ed.) 2003: Paleontology of Mongolia. Brachiopoda. Ross. Akad. Nauk. Paleont. Inst., Mongol.: 249p., 64pl. [Russ.]

SCHUCHERT, C., LEVENE, C. M. 1929: Brachiopoda (Generum et genotyporum index et bibliographia). *In* J. E. Pompeckji (ed.) Fossilium Catalogus, vol. 1, Animalia. Pars 42: 140p. W. Junk. Berlin.

SUTHERLAND, P. K. 1996: *Ardomosteges archamus* new genus, new species, in the early Pennsylvanian of Oklahoma – possible ancestor to the richthofenioid brachiopods. J. Paleont. (supplement 2, Paleont. Soc. Mem. 46) 70: 1-25, fig. 1-24.

TERMIER, G., TERMIER, H. 1970: Les Productoides du Djoulfien (Permien supérieur) dans la Tethys orientale: essai sur l'agonie d'un phylum. Soc. Géol. du Nord, Ann. 90 (4): 443-461.

TERMIER, G., TERMIER, H., PAJAUD, D. 1966: Découverte d'une thécidée dans le Permien du Texas. C. R. Hebdom. séances Acad. Sci. 263: 332-335.

WAAGEN, W. 1883: Salt Range Fossils, vol. 1, part 4. Productus Limestone Fossils, Brachiopoda. Palaeont. Indica (ser. 13), fasc. 2*:* 391-546, pl. 29-49.

WARDLAW, B., GRANT, R. E., BRUNTON, C. H. C. 2000: Richthofenioidea. *In* R. L. Kaesler (ed.). Treatise on Invertebrate Paleontology, Part H, Brachiopoda revised, vol. 3, Linguliformea, Craniiformea, and Rhynchonelliformea part: 610-619. Geol. Soc. Amer., Univ. Kansas; Boulder, Colorado & Lawrence, Kansas.

WATERHOUSE, J. B. 1975: New Permian and Triassic brachiopod taxa. Pap. Dep. Geol. Univ. Qld 7 (1): 1-23.

_____2010: New taxa of Late Paleozoic Brachiopoda and Mollusca. Earthwise 9: 1-134.

_____ 2013: The evolution and classification of the Productida. Earthwise 10: 1-535.

WILLIAMS, A. 1953: The morphology and classification of the oldhaminid brachiopods. Wash. Acad. Sci. J. 43: 279-287, 3pl.

WILLIAMS, A., BRUNTON, C. H. C. 1997: Morphological and anatomical terms applied to brachiopods. *In* R. L. Kaesler (ed.). Treatise on Invertebrate Paleontology, Part H, Brachiopoda revised, vol. 1, Introduction: 422-440. Geol. Soc. Amer., Univ. Kansas: Boulder, Colorado & Lawrence, Kansas.

WILLIAMS, A., HARPER, D. A. T., GRANT, R. E. 2000: Lyttoniidina. *In* R. L. Kaesler (ed.). Treatise on Invertebrate Paleontology, Part H, Brachiopoda revised, vol. 3, Linguliformea, Craniiformea, and Rhynchonelliformea part: 619-642. Geol. Soc. Amer., Univ. Kansas: Boulder, Colorado & Lawrence, Kansas.

FAMILY - GROUP CLASSIFICATION FOR STROPHALOSIIDEI

Abstract

The family group classification with Strophalosiidei is summarized, with groups rearranged somewhat to conform better with the morphologies.

INTRODUCTION: AN OVERVIEW OF STROPHALOSIIDEI

According to the *Revised Brachiopoda Treatise* (Brunton et al. 2000), the Strophalosiidina contained one superfamily, Strophalosioidea, divided into three families, the Chonopectidae Muir-Wood & Cooper, 1960 of Upper Devonian and Lower Carboniferous age, Araksalosidae Lazarev, 1989 of Lower Devonian to Lower Carboniferous age, and possibly present in Late Carboniferous, with subfamilies Araksalosiinae, Donalosiinae, Quadratiinae, and Rhytialosiinae, all named by Lazarev in 1989, and Strophalosiidae Schuchert, 1913. This latter family incorporated all the remaining Lower Carboniferous to Permian genera, divided into Strophalosiinae Schuchert, 1913, Dasyalosiinae Brunton, 1966 and Mingenewiinae Archbold, 1980.

Lazarev regarded Strophalosiidina as having been first proposed by Lazarev (1986), though his first valid proposal of the suborder was as late as 1990, and even his manuscript proposal of 1986 was during the same month as that by Waterhouse (1986). He refused to acknowledge the earlier publication of Waterhouse (1975). He regarded the suborder as including lyttoniids, and excluding richthofeniids, unlike Waterhouse (1975, 1986), which was contrary to the treatment in the *Revised Brachiopod Treatise* (Brunton et al. 2000), though the latter publication falsely claimed that it followed Lazarev, not Waterhouse. The *Revised Brachiopod Treatise* pretended that the suborder had been ascribed to Schuchert (1913) by Brunton et al. (1995), but that publication by Brunton et al. (1995) had credited the suborder to Waagen (1883), not Schuchert. Apparently Brunton et al. 2000 deemed it preferable not to admit error. As they no doubt would have had it, a judicious mistake had to be made in the best interests of reputations, if only to ensure confidence in the authors and integrity of the Treatise series. Waagen had only mentioned genus *Strophalosia*, and Schuchert had proposed the subfamily Strophalosiinae. The entire section on Strophalosiidina in the

Revised Brachiopod Treatise fell well below the standards set by that normally profound and impartial series, which may not be inerrant or future-proof, but has normally striven to be as reliable as possible up to the time of publication.

To me, strophalosiiform classification should have been conceived as far more intricate than envisaged by Brunton & Lazarev, authors of the Treatise chapter on Strophalosiidina. (Nominate author R. E. Grant had died several years before, and Jin Yugan had been used only to supply data on Chinese brachiopods). Carboniferous and Permian genera classed as Strophalosiidae in the *Revised Brachiopod Treatise* have well-spaced spines moderately like those of Donalosiinae, classed by Brunton et al. (2000) as Chonopectidae, and of Devonian age. A difficulty against understanding evolution and achieving a satisfactory classification is that there is a long time-gap between the Devonian - Early Carboniferous and Permian occurrences when no such shells have been described, to imply that the Permian shells arose de novo, and replicated morphologies first seen, but later lost, in Devonian time. The question then arises, how good is the Upper Carboniferous fossil record, involving not only preserved fossils, but the scientific knowledge of those fossils. Certainly not perfect, it has to be said, with rather poor records for many parts of the globe, including China, and with the Upper Paleozoic fossils of Alaska, a large state, with only a handful of Late Paleozoic species described, if we set aside mere fossil lists. Indeed no country seems to be able to claim complete and up-to-date coverage.

The assessments of morphological distinctions remain open to further challenge. The distinction applied in Brunton et al. (2000) amongst many of the Permian genera centred on presence or absence of dorsal spines, used to separate Strophalosiinae from Dasyalosiinae, as stressed by Brunton (2007) and upgraded to family level in Waterhouse (2013). This approach requires a measure of caution. *Craspedalosia* Muir-Wood & Cooper lacks dorsal spines, yet in many other respects appears to be closely related to *Melvillosia* Waterhouse, which developed dorsal spines. *Licharewiella* Ustritsky, 1960 has strong ribs, and no dorsal spines, but is close in many respects to *Costalosiella* Waterhouse, which had similar ribs and dorsal spines. There are other examples. Overall such genera arguably suggest that a group of strophalosioid shells differed from donalosiin - strophalosiid shells without dorsal spines and their counterparts with dorsal spines such as *Echinalosia* and *Wyndhamia* in that dorsal spines may appear in some species counted as genera, but not in related species, counted as different genera. It might even be argued that such species with dorsal spines should be classed in the same genus as those without spines, but in the meantime, they are generically distinguished, pace the *Revised Brachiopod Treatise*. *Dasyalosia* itself might well belong to this group. It comes from the Zechstein of Europe and has vermiform spines unlike those of *Echinalosia* or *Eostrophalosia,* so that reference of these latter genera to the same family could be treated as contentious. (See Fig. 16, 17, pp. 29, 30 herein).

A small number of taxa are little larger than spats, and have been treated as full genera by various authors. The first-named example is *Leptalosia* Dunbar & Condra, 1932 of Pennsylvanian age in United States. Another example is *Etherilosia* Archbold, 1993 from Western Australia. That these shells, or some of them, reached full maturity whilst still adnate appears likely. Whether they should be separated from their parent genus may be more arguable. That species derived from different genera should be lumped into one genus, as suspected for *Leptalosia* by Muir-Wood & Cooper 1960 is certainly dubious.

A question that arises in any extensive classification concerns the limits and extent of family groups, and the importance for numbers of units, as against the significance of morphological differences between genera. Early in the development of a major group, it is to be expected that there would be few genera, and in some instances, these few genera may differ substantially from each other to the same degree that recognized subfamilies differ from each other in later times when related taxa were numerous. Several strophalosiid genera were recognized as sole representatives of tribes and subfamilies in Waterhouse (2013), but now I favour bringing them back into the aegis of slightly larger and more variable tribes and subfamilies. What renders either procedure a matter for debate is the conviction, on at least my part, that many more taxa remain to be discovered.

CLASSIFICATION WITHIN HYPORDER STROPHALOSIIDEI

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

[Nom. transl. hic ex Chonopectinae Muir-Wood & Cooper, 1960, p. 156] et seq.

Diagnosis: Ornament typically includes fine radials, with a subset of genera dominated by commarginal rugae and some of these genera losing their radials. Hinge spines usually prominent. No known spine tunnels. Short ventral septum developed in some groups.

Superfamily Chonopectoidea Muir-Wood & Cooper, 1960
- Family Chonopectidae Muir-Wood & Cooper, 1960
  - Subfamily Chonopectinae Muir-Wood & Cooper, 1960
    - Tribe Chonopectini Muir-Wood & Cooper, 1960
    - Tribe Whidbornellini Waterhouse, 2013
  - Subfamily Semenewiinae Muir-Wood, 1962
  - Subfamily Araksalosiinae Lazarev, 1989
- Family Rhytialosiidae Lazarev, 1989

Superfamily Strophalosioidea Schuchert, 1913
- Family Strophalosiidae Schuchert, 1913
  - Subfamily Strophalosiinae Schuchert, 1913
    - Tribe Strophalosiini Schuchert, 1913
    - Tribe Fimbrinialosiini new
  - Subfamily Craspedalosiinae Waterhouse, 2013
- Family Donalosiidae Lazarev, 1989
  - Subfamily Donalosiinae Lazarev, 1989
  - Subfamily Devonalosiinae new
  - Subfamily Crassispinosellinae new

Superfamily Dasyalosioidea Brunton, 1966
- Family Dasyalosiidae Brunton, 1966
- Family Mingenewiidae Archbold, 1980
  - Subfamily Mingenewiinae Archbold, 1980
    - Tribe Mingenewiini Archbold, 1980
    - Tribe Biplatyconchini Waterhouse, 2013
  - Subfamily Bruntonariinae Waterhouse, 2013
  - Subfamily Coronalosiinae new
- Family Truncateniidae Liao, 1982
- Family Ctenalosiidae Muir-Wood & Cooper, 1960

Superfamily Quadratioidea Lazarev, 1989
- Family Quadratiidae Lazarev, 1989
  - Subfamily Quadratiinae Lazarev, 1989
  - Subfamily Acanthatiinae Waterhouse, 2013
- Family Echinalosiidae Waterhouse, 2001
  - Subfamily Echinalosiinae Waterhouse, 2001
  - Subfamily Arcticalosiinae Waterhouse, 2001
    - Tribe Arcticalosiini Waterhouse, 2001
    - Tribe Wyndhamiini Waterhouse, 2010

Table 1. Classification of Strophalosiidei

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

Diagnosis: Transverse with wide hinge and row of hinge spines, bifid cardinal process, long low median dorsal septum. May display fine radial capillae. May have short ventral septum.

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

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

Fig. 1 – 3

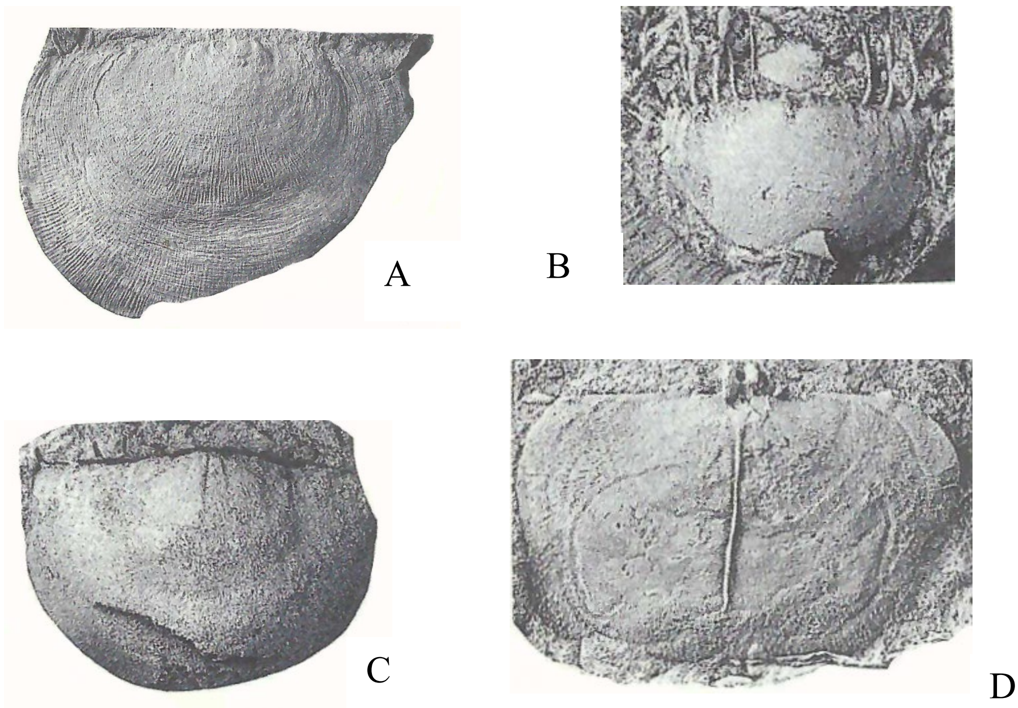


Fig. 1. *Chonopectus fischeri* (Norwood & Pratten). A, ventral exterior, x3. B, replica of ventral exterior, x1.3. C, ventral internal mould, x2. From lower Kinderhookian, Iowa. D, *Chonopectus* sp. dorsal internal mould, x 2. Frwhiom New York. (Muir-Wood & Cooper 1960).

Diagnosis: Transverse, fine radial capillae, row of hinge spines, no commarginal rugae, no dorsal spines. Short posterior ventral septum present as a rule, and low ridge each side.

Genera: *Chonopectus* Hall & Clarke, *Auchmerella* Struve, *Eileenella* Racheboeuf, *Ralia* Lazarev. Lower Devonian (Emsian) to Upper Carboniferous (Bashkirian).

Discussion: Brunton (2007, p. 2667) placed *Eileenella* with *Chonopectus*, but the species appears to have no radial capillae, Instead the shell is largely smooth with ventral hinge spines not extending on to the ears. But the septum between ventral adductors is conspicuous, recalling the septum in *Chonopectus*. The same is true of another obscure genus and species called *Auchmerella* Struve. *Ralia* Lazarev, 1987 of early Devonian (Emsian) age has fine radial capillae on the dorsal valve and the figured ventral valve in Brunton et al. (2000, Fig. 415.1b) suggest fine capillae, as reproduced here in Fig. 2C, though less clearly. Those authors classed the genus in Donalosiinae. There is a mysterious second ridge in this figure (Lazarev 1987, pl. 5, fig. 2), which recalls a ridge or plate shown by Muir-Wood & Cooper (1960) as in Fig. 1C herein. But closer inspection suggests a faint duplication of the ridge on the other side of the figure in Muir-Wood & Cooper, and the ridge seems to have been a ridge along the outer side of the muscle scars each side of the septum. The same is suggested for another Lazarev specimen of *Ralia*, as in Fig. 3 herein, which shows a low ridge each side of the septum. These ridges might be relict from the chonetidin ridge behind the adductor scars, noted by Muir-Wood (1962, pl. 10 fig. 13).

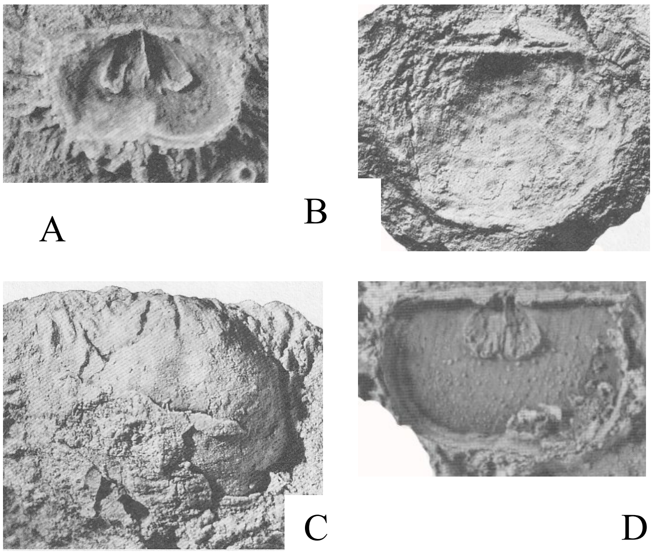


Fig. 2. Obscure strophalosiidin genera, x1. A, *Auchmerella irmingina* Struve, x3, replica from Eifelian of Germany. B, C, *Ralia primigenia* Lazarev. B, dorsal exterior with ventral interarea, holotype, x2.5. C, ventral valve, internal mould posteriorly, x5. From Emsian, Gobi Altai, Mongolia. D, *Eileenella elegans* Racheboeuf, latex ventral internal mould with interarea and hinge spines and median septum, x5, from Bashkirian of Thailand. (Brunton et al. 2000; Lazarev 1987; Wongwanich et al. 2004).

Such interpretations are unfortunately based on figures, and conclusions can only be based on inspection of the actual specimens at the Paleontological Institute in Moscow, to verify or amend the impression given by figures, and published description of the specimens.

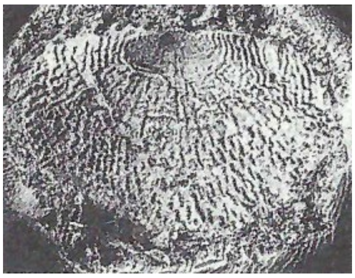
Fig. 3. *Ralia primigenia* Lazarev, posterior aspect of ventral valve, x1, showing median septum flanked each side by a low ridge. From Emsian of Mongolia. (Lazarev 1987).

Tribe **WHIDBORNELLINI** Waterhouse, 2013

Fig. 4

Diagnosis: Ribs firm, moderately spaced. No ventral median septum.

Genera: *Whidbornella* Reed, *Ruthphiala* Carter. Upper Devonian, Lower Carboniferous.



A

B

C

Fig. 4. *Whidbornella caperata* (J. de C. Sowerby). A, ventral external mould. B, replica of dorsal interior. C, ventral external mould. Specimens x1 from top Famennian Pilton beds, Devon. (Muir-Wood & Cooper 1960).

waSubfamily **SEMENEWIINAE** Muir-Wood, 1962

Fig. 5

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

Diagnosis: Ornament of low to strong commarginal wrinkles usually on both valves, fine radials may be present, fine hinge spines, spines small over disc, rarely dorsal spines as well.

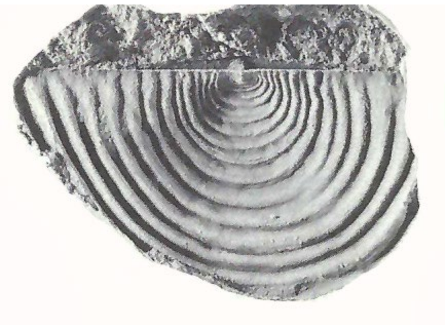


Fig. 5. *Semenewia concentrica* (Koninck), dorsal aspect of replica from Asbian-Brigantian of Visé, lectotype, x2. (Brunton, Racheboeuf & Mundy 1994).

Genera: *Semenewia* Paeckelmann (syn. *Palmerhytis* Brunton & Mundy), *Chonetipustula* Paeckelmann, *Cyphotalosia* Carter, *Dengalosia* Manakov & Pavlova, *Plicaea* Isenberg, *Plicatiferina* Kalashnikov. Lower Carboniferous (Visean) to Upper Carboniferous (Bashkirian or Kasimovian).

Discussion: This group was abandoned by Brunton et al. in the *Revised Brachiopod Treatise* and partly absorbed in Chonopectidae. It is rearranged to provisionally incorporate several genera placed in the Quadratiinae by the *Revised Brachiopod Treatise*. Muir-Wood (1962, p. 92) recorded a long ventral septum in *Chonetes concentricus* Koninck, 1847, p. 186, but Brunton, Racheboeuf & Mundy (1994) denied that a ventral septum was present, and also showed in Fig. 1.1 and Fig. 2.4 that fine radial lineations were present in *Semenewia*. *Dengalosia* has fine capillae and only subdued commarginal rugae, but no ventral septum.

Subfamily **ARAKSALOSIINAE** Lazarev, 1989

Fig. 6

[Nom. transl. hic ex Araksalosiidae Lazarev, 1989, p. 34].

Diagnosis: Spines dense and fine near ventral hinge, no dorsal spines. Fine lineations present. Short ventral median septum and ridge each side (Fig. 6C).

Genera: *Araksalosia* Lazarev, *Hamlingella* Reed. Upper Devonian (Famennian).

Discussion: The ears, though large do not project laterally well beyond the maximum width of the shell placed near mid-length.

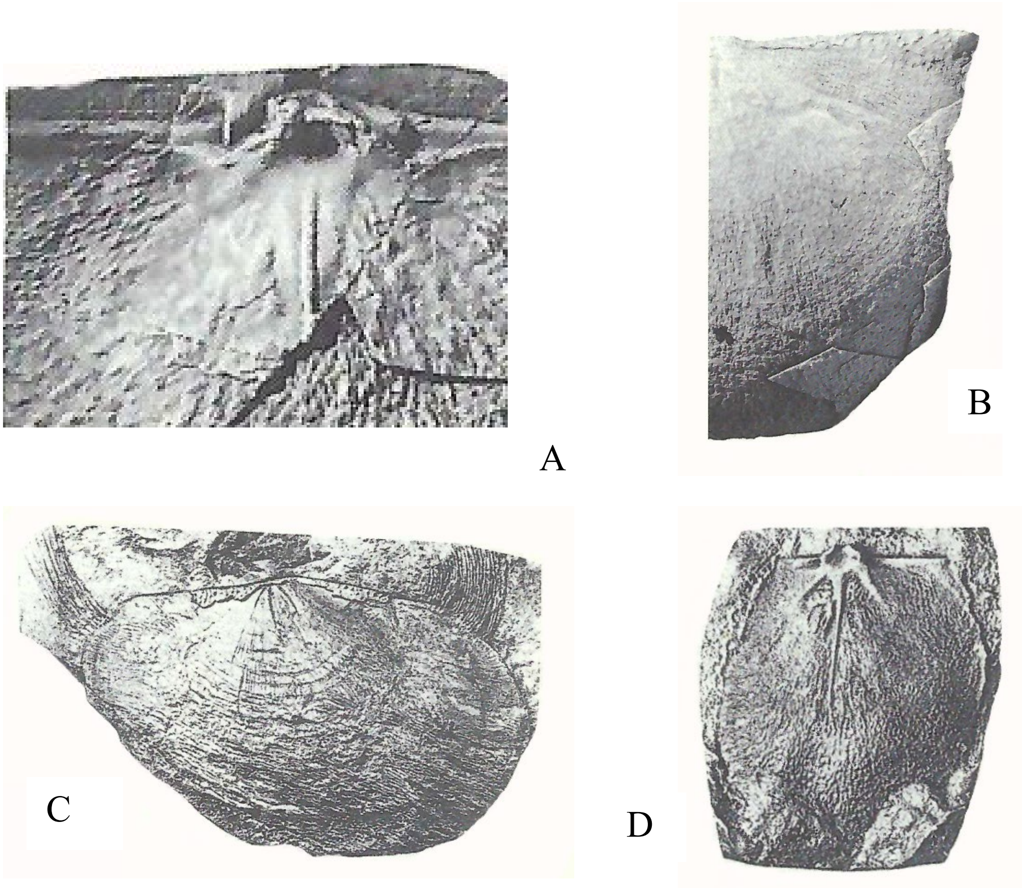


Fig. 6. *Araksalosia maxima* (Abramian). A, panel of dorsal interior, x5. B, partly exfoliated ventral valve showing spine bases, x1.5. From Upper Famennian, Transcausus. (Lazarev 1989). C, D, *Hamlingella georgesi* (Paeckelmann). C, somewhat worn ventral valve, x1. D, dorsal interior, x1. From Etroungt, Rhine. (Paeckelmann 1931).

Family **RHYTIALOSIIDAE** Lazarev, 1989

Fig. 7, 8

[Nom. transl. hic ex Rhytialosiinae Lazarev, 1989, p. 35].

Diagnosis: No radials, low commarginal rugae**.** Dorsal spines are present in *Veeversalosia.* No ventral septum*.*

Genera: *Rhytialosia* Lazarev, *Agrammatia* Sokolskaya (possibly a senior synonym of *Steinhagella* Goldring), *Mckellarosia* Waterhouse, *Myrtlevalia* Waterhouse, *Sinalosia* Ma & Sun, *Steinhagella* Goldring*, Veeveralosia* Lazarev. Middle and Upper Devonian (Frasnian – Famennian).

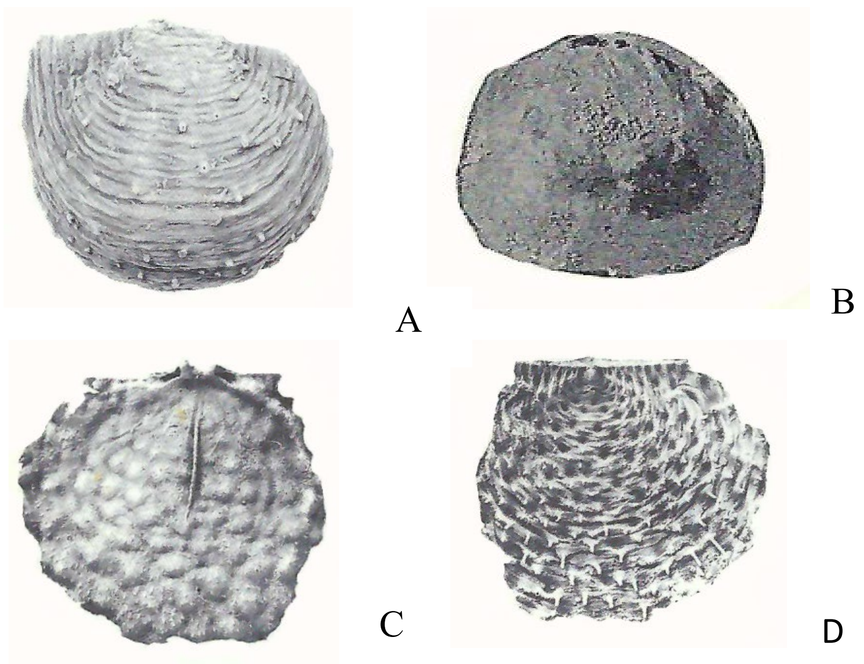


Fig. 7. A, *Rhytialosia petini* (Nalivkin), ventral aspect, mid-Frasnian of Russian Platform, x2. (Lazarev in Brunton et al. 2000). B, C, D, *Veeversalosia numida* (Veevers). B, ventral aspect, CPC 2954 holotype, x1.5. C, D, internal and external aspect of dorsal valve, x3.5. From mid-Frasnian of Fitzroy Basin. (Veevers 1959).

Discussion: The presence of commarginal rugae may suggest that this group gave rise to the Lower Carboniferous Semenewiiinae, and perhaps it was ancestral to some of the Lower Carboniferous genera placed in that group. But authorities have in recent years stressed the relationship between *Semenewia* and Chonopectidae. A few Carboniferous genera such as *Plicaea* Aisenverg, 1992 and *Plicatiferina* Kalashnikov, 1980 show comparable commarginal rugae. Should all these genera be grouped? The differences in rugae, spines and shape are not great, whereas the differences from the subfamily Quadratiinae to which they have been assigned by Brunton et al. (2000, p. 584) are more marked.

The link to other members of the superfamily may be deemed questionable, resting mainly on the presence of commarginal ornament found in Semenewiinae. Further pursuing such possible linkages, it may be wondered if the group did not eventually give rise to Mingenewiinae Archbold through medication of the commarginal rugae into commarginal bands over especially the dorsal valve.

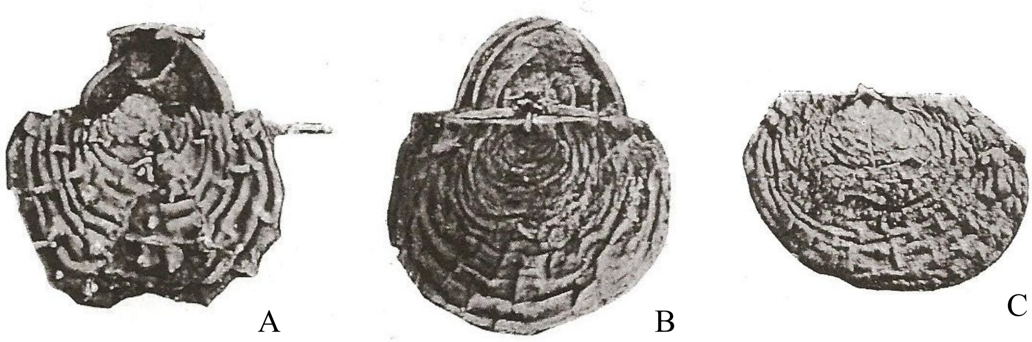


Fig. 8. *Mckellarosia rugosus* (McKellar). A, ventral external latex cast, GSQ F 3644, x4, showing the relatively strong rugae and comparatively few sturdy spines. B, dorsal aspect of specimen with valves conjoined, GSQ F 11489, latex cast, x4. C, dorsal interior, latex cast of GSQ F 11490, x3. From Myrtlevale and Star beds (Famennian), Queensland, Australia. (McKellar 1970).

Superfamily **STROPHALOSIOIDEA** Schuchert, 1913

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

Diagnosis: Shells small to moderate in size, spines varied, usually well spaced. Surface of both valves smooth apart from growth increments and laminae. No ventral spine tunnels, no dorsal spines. No ventral median septum.

Family **STROPHALOSIIDAE** Schuchert, 1913

Subfamily **STROPHALOSIINAE** Schuchert, 1913

Tribe **STROPHALOSIINI** Schuchert, 1913

Fig. 9

Diagnosis: No dorsal spines, no ventral spine tunnels. No dimples or prominent capillae over dorsal valve.

Genera: *Strophalosia* King (syn. *Leptaenalosia* King), *Crenalosia* Waterhouse, *Fortispinalosia* Waterhouse, *Heteralosia* R. H. King, *Kufria* Waterhouse, ?*Leptalosia* Dunbar & Condra Upper Carboniferous and Permian genera. See p. 60 ff for further detail.

Discussion: *Leptalosia* and *Crenalosia* are very small and adnate, deemed likely to have been derived from *Heteralosia* given its presence in the United States.

Fig. 9. *Leptalosia scintilla* (Beecher). A, *Orbinaria* with individuals of attached *Leptalosia scintilla,* x3. B, attached specimen showing anchor spines and smooth dorsal valve, x4. C, D, internal and posterior aspects of dorsal valve, x8. From Louisiana Limestone, Missouri. (Muir-Wood & Cooper 1960).

Tribe **FIMBRINIALOSIINI** new tribe

Diagnosis: Dimples or pits developed along commarginal rows across the dorsal valve. No dorsal spines. See p.

Name genus: *Fimbrinialosia* Waterhouse, 2013, p. 216.

Genera: *Baikuralia* Waterhouse, *Fimbrinialosia* Waterhouse, *Keoghalosia* Waterhouse. Upper Carboniferous, Permian.

Discussion: A possible new genus is to be found in the Karakorum Mountains (p. 70).

Family **DONALOSIIDA**E Lazarev, 1989

[Nom. transl. hic ex Donalosiinae Lazarev, 1989, p. 35].

Diagnosis : Spines subuniform and subevenly spaced over ventral disc.

Subfamily **DONALOSIINAE** Lazarev, 1989

Fig. 10

Diagnosis: Ventral spines numerous and subuniform over disc, crowded posteriorly over the ears and each side of the umbo. No dorsal spines. No other Devonian genera come close in having such numerous and strong posterior lateral spines, though *Auchmerella* Struve, 1964 is so obscure that it might be related, and some Permian genera such as *Pseudostrophalosia* Clarke shows some approach, but have dorsal spines. Various genera referred to Donalosiinae in the *Revised Brachiopod Treatise* have similar dorsal valve without spines, somewhat similar ventral disc spines, but differ in displaying a row of stout hinge spines and a lack of the posterior-lateral brush of spines.

Genus: *Donalosia* Lazarev. Upper Devonian.

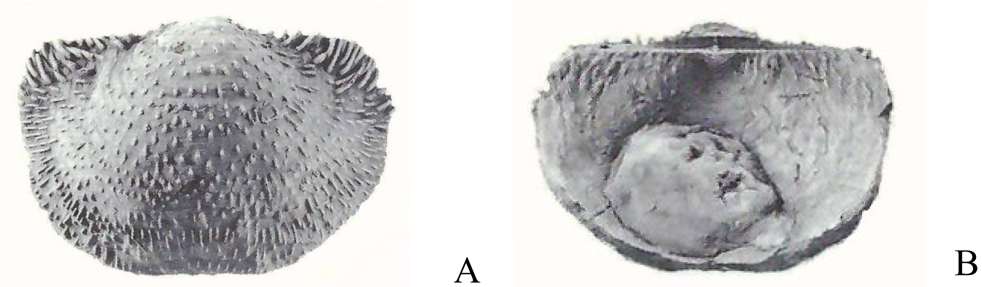


Fig. 10. *Donalosia multispinosa* (Sokolskaya). A, ventral aspect of specimen, x1.5. B, dorsal aspect of specimen with valves conjoined, x1.5. From Upper Devonian of Transcaucasia. (Muir-Wood & Cooper 1960).

Discussion: This subfamily was placed as a unit within Araksalosiidae by Lazarev, 1989 but lacks fine surface ribs and lacks rugae or any sign of a ventral median septum, so that it is judged to be strophalosioid rather than chonopectoid. *Keoghalosia* Waterhouse is similar in various respects, displaying comparable ventral disc spines and a cluster of posterior lateral spines, but the genus is much younger at Early Permian in age, and has numerous pits over the dorsal valve (see p. 67).

Subfamily **DEVONALOSIINAE** new

Fig. 11 - 14

Name genus: *Devonalosia* Muir-Wood & Cooper, 1960, p. 83.

Diagnosis: Moderate to well-developed hinge row of spines, body spines fine and uniform over ventral valve, no ventral ear brush, no dorsal spines or dimples. Cardinal process bifid.

Genera: *Devonalosia* Muir-Wood & Cooper, *Australosia* McKellar, ?*Dichacaena* Cooper &

Dutro, ?*Irboskites* Bekker, *Morganella* McKellar, *Oligorachis* Imbrie, *Rangiara* Waterhouse, *Truncalosia* Imbrie. Middle and Late Devonian.

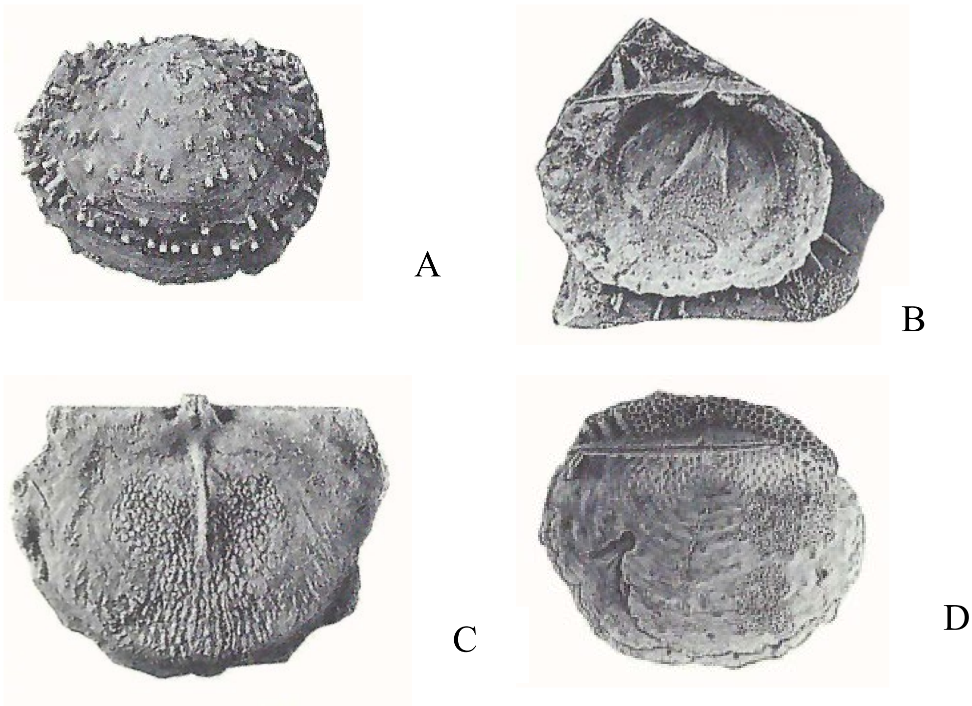


Fig. 11. *Devonalosia wrightorum* Muir-Wood & Cooper. A, ventral aspect, x3. B, ventral interior, x4. C, dorsal interior, x4. D, dorsal aspect of specimen with valves conjoined x4. From Arkona Shale (Givetian), Ontario. (Muir-Wood & Cooper 1960).

Discussion: *Devonalosia* was classed with Donalosiinae in the *Revised Brachiopod Treatise* but has a more distinct row of ventral hinge spines. According to Brunton et al. (2000, p. 582), *Irboskites* (see Fig. 13) might be allied to *Devonalosia* because it shows anteriorly angled teeth. This genus has lost its spines, compelling a search for other indications of family group affinities. *Dichacaena* Cooper & Dutro is close and has no hinge row. *Oligorachis* and *Truncalosia* are small and need to be better known, but have spine attributes of the subfamily and tribe as far as known (Fig. 12, 14). The genus *Australosia* McKellar might be allied, showing a similar hinge row of strong spines. It has strong ventral costae (Fig. 34), as further discussed on pp. 44, 45.

The relationship of Devonalosiinae to *Coronalosia* Waterhouse (see below, p. 37) needs clarification of Carboniferous species and genera. *Coronalosia* is of Permian age and has a well-developed ventral hinge row of spines, but body spines are less robust and may be missing.

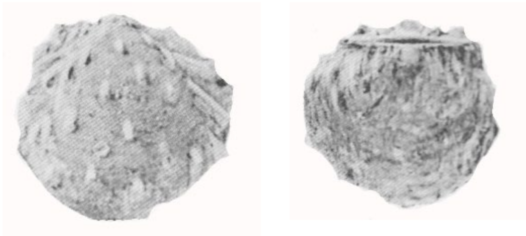


Fig. 12. *Oligorachis oligorachis* Imbrie. A, B. ventral and dorsal views of holotype, x3. From Givetian Gravel Point Formation, Michigan. (Imbrie 1959**).**

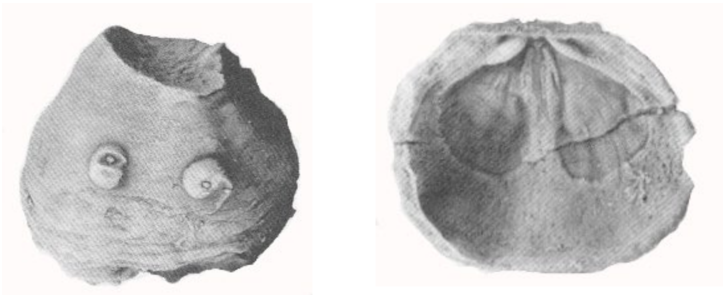


Fig. 13. *Irboskites fixatus* Bekker. A, ventral valve with prominent cicatrix. B, replica of dorsal interior, holotype. From Frasnian Irboska Formation, Estonia, x 2. (Brunton et al. 2000).

Fig. 15. *Truncalosia gibbosa* Imbrie. A, B, ventral and dorsal views of holotype, x2. C, dorsal interior, x3. From Givetian Gravel Point Formation, Michigan. (Imbrie 1959).

Subfamily **CRASSISPINOSELLINAE** new

Fig. 15

Name genus: *Crassispinosella* Waterhouse 2013, p. 218, here designated.

Diagnosis**:** Subuniform ventral spines, no ventral hinge row. No dorsal spines, no capillae, no ventral spine tunnels. Dorsal valve thickened into a wedge in Australian genera.

Genera: *Crassispinosella* Waterhouse, *Etherilosia* Archbold, *Strophalosiaria* Waterhouse, ?*Tupelosia* Simanauskas & Archbold. Upper Carboniferous, Lower Permian.

Discussion: *Etherilosia* is a spat form apparently derived from *Crassispinosella*, allowing a question about its generic status, as to whether it should be categorized as the same genus, or a subgenus, or a separate genus. See p. 76.

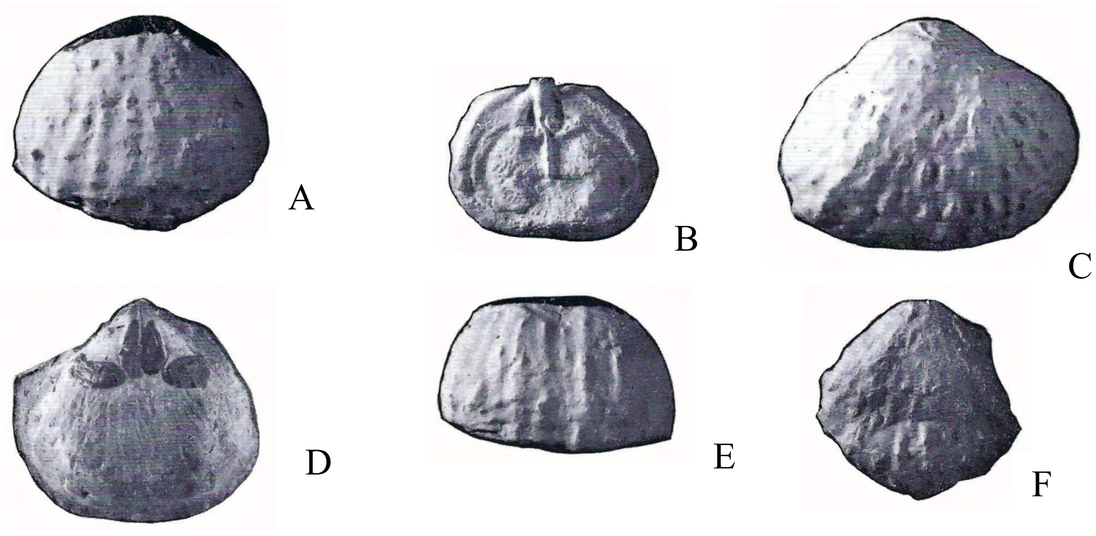


Fig. 15. *Crassispinosella subcircularis* (Clarke), A, syntype TMF 3554. 2, dorsal interior, TMF 3555. C, ventral valve TMF 35115. D, ventral interior TMF 35114. E, anterior aspect of ventral valve TMF 35117. F, worn ventral valve TMF 35118. Specimens x1 approx., from Glencoe Formation, Tasmania. These specimens were described as *Costalosia apicallosa* by Clarke (1969) and are now regarded as belonging to *Crassispinosella subcircularis*.

Superfamily **DASYALOSIOIDEA** Brunton, 1966

[Nom. promoveo hic ex Dasyalosiinae Brunton, 1966, p. 192].

Diagnosis: Spines may be present or absent over dorsal valve, in otherwise closely similar genera. In some genera ventral spines may be vermiform. Attributes vary also in other respects. Some genera are subtriangular in shape with short hinge and many have commarginal bands bordered by laminae across the dorsal valve.

Discussion: This family group is regarded as contentious, as one that embraces genera which may or may not have dorsal spines and are otherwise closely related.

Family **DASYALOSIIDAE** Brunton, 1966

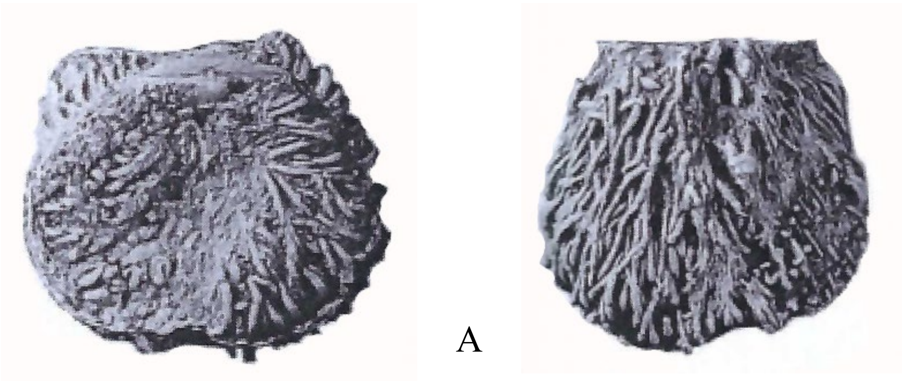
Fig. 16, 17

[Nom. promoveo Waterhouse 2013, p. 225 ex Dasyalosiinae Brunton, 1966, p. 192].

Diagnosis: Dense spines over both valves, or only over ventral valve. Shell subtriangular in shape, with short hinge.

Genera: *Dasyalosia* Muir-Wood & Cooper, *Orthothrix* Muir-Wood & Cooper, *Sphenalosia* Muir-Wood & Cooper. Middle and Upper Permian (Wuchiapingian).

Discussion: *S*pines in *Dasyalosia* are unusually vermiform, possibly reflecting substrate and environment, and so differ strongly from those of many genera. This appears to be a unique feature. Two other genera close in age are similar in having a short hinge and subtriangular shape and they are tentatively associated with *Dasyalosia.*



A B

Fig. 16. *Dasyalosia goldfussi* (Munster). A, B, dorsal and ventral aspects of specimen from Zechstein of Thuringia, Germany, x2. (Muir-Wood & Cooper 1960).

Orthothrix Geinitz, 1847, has crowded spines over both valves, not vermiform, and *Sphenalosia* Muir-Wood & Cooper, 1960 has only coarse ventral spines, some possibly vermiform. The emphasis as far as the family is concerned is placed on shape, and less on the vermiform nature of spines, and presence or absence of spines on the dorsal valve is regarded as infra-subfamilial. There are optional ways of treating this small group, and Brunton (1966, 2000 et al.) chose to regard *Dasyalosia* as typifying a majority of Carboniferous and Permian genera that developed dorsal spines, whilst excluding Carboniferous and Devonian possible allies that had been classed in different groups by Lazarev (1989). The exclusion of such genera seems contentious, but a grouping together of all strophalosiiform genera with dorsal spines would massively disrupt the Lazarev version of the suborder. In trying to achieve a more natural classification of the Strophalosiidina, it is difficult to achieve a final understanding, given the

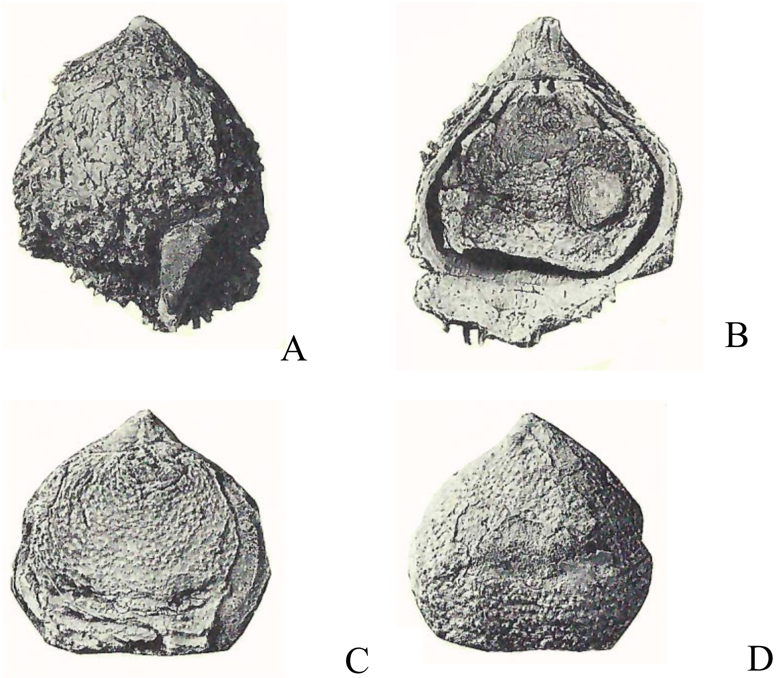


Fig. 17. A, B, *Sphenalosia smedleyi* Muir-Wood & Cooper, ventral and dorsal aspects of holotype, with valves conjoined, x1. From Phosphoria Formation, Wyoming, United States. C, D, *Orthothrix excavata* (Geinitz), dorsal and ventral aspects of a complete specimen, x2, from middle Zechstein of Thuringia, Germany. (Muir-Wood & Cooper 1960).

unknown content of so many faunas, especially of Upper Carboniferous age, which in their absence, give the impression of a great gap between Devonian - Early Carboniferous and Late Carboniferous - Permian Strophalosiidina. Acknowledging this difficulty, it is suggested that to class all upper Carboniferous - Permian Strophalosiidina with dorsal spines as Dasyalosiidae is to conceal origins, trends and evolutionary pathways. It is therefore proposed to confine *Dasyalosia* as name-giver to a restricted group, marked by an ability to generate spines of the dorsal valves of some genera, and not in other closely related genera. That position should help back-track and tentatively delineate the groups that most closely relate to *Daysalosia*. The question remains – how should exceptional groups be accommodated, and to what extent should they dominate zoological classification, when governed as they are by laws of priority.

Family **MINGENEWIIDAE** Archbold, 1980

[Nom. promoveo hic ex Mingenewiinae Archbold, 1980, p. 253] et seq.

Diagnosis: Commarginal bands developed across dorsal valve and in some instances the ventral valve in some of the constituent genera. The presence of spines varies, being present on the dorsal valve of some genera, and absent from others that are close in other respects.

Name genus: *Mingenewia* Archbold, 1980, p. 255 from Mingenew Formation, Perth Basin, Western Australia.

Discussion: This category assembles various differing genera as distinctive in ornament from the previous family groups, with or without dorsal spines, through having strong commarginal laminae, and in some forms fine radial capillae, especially in the dorsal valve. Overall it would seem likely that the members developed from stock with dorsal spines that later in many instances lost those spines. Several genera seem likely to be the only as yet known examples of a tribe or subfamily, to judge from their ornament. These genera in the presence or absence of dorsal spines approach Dasyalosiidae, which differs in lacking dorsal commarginal banding. The question of sources for members of the family cannot as yet be answered, but several older groups show commarginal rugae or rather low rugae bordered by laminae, such as Semenewiinae, and perhaps Rhytialosiidae developed into the commarginal banding seen in Mingenewiidae through the introduction of lamination that borders each rugation.

Subfamily **MINGENEWIINAE** Archbold, 1980

Diagnosis: Prominent commarginal bands across dorsal valve. No apparent spine tunnels, no dimples.

Tribe **MINGENEWIINI** Archbold, 1980

Fig. 18, 19

Diagnosis: May have ventral or dorsal spines. Commarginal ornament prominent.

Genera: *Mingenewia* Archbold, *Cicatricia* Waterhouse, *Quasimingewewia* Waterhouse. Middle and Late Permian.

Discussion: *Mingenewia* Archbold, 1980, comes from the Mingenew Formation of the Perth Basin in Western Australia, of lower Baigendzinian age. There are no spine tunnels. From the Late Permian of Nepal, *Quasimingewewia* Waterhouse 2013, p. 243, Fig. 7.37, 7. 38 is close and lacks the ventral septum or well-formed myophragm and subfusc ribbing of *Mingenewia* (Water-house 2013, p. 243).

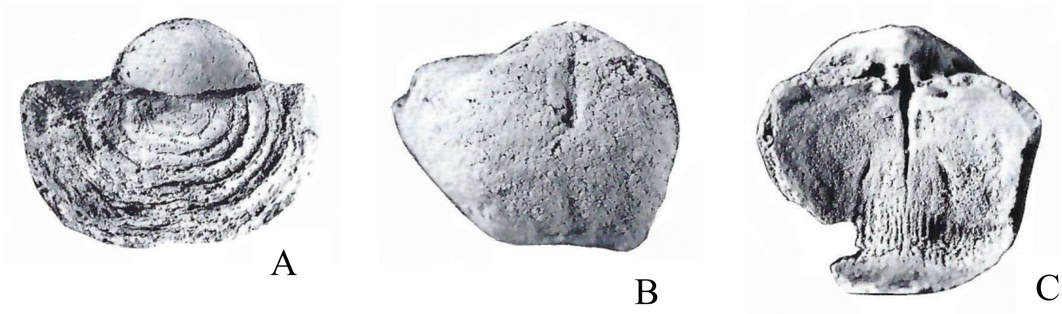


Fig. 18. *Mingenewia anomala* Archbold. A, latex cast, dorsal aspect of specimen with valves conjoined. B, ventral internal mould. C, dorsal aspect of internal mould, holotype. Specimens x4, from Mingenew Formation, Perth Basin, Western Australia. (Archbold 1980).

Cicatricia Waterhouse lacks capillae from the dorsal valve and so is placed here rather than in Coronalosiinae (see p.   ). As well it does not appear to have a hinge row of prominent spines.

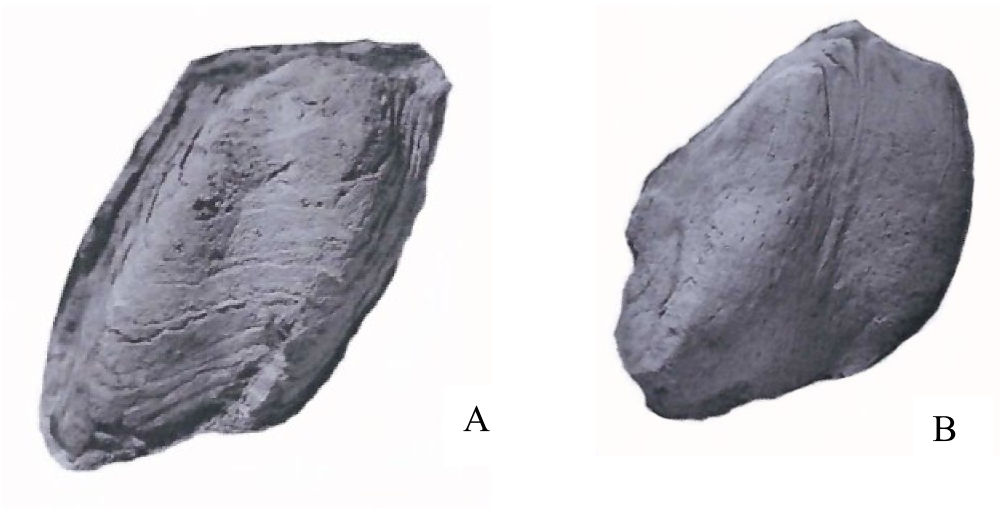


Fig. 19. *Quasimingenewia imperator* Waterhouse. A, dorsal external mould. B, ventral aspect of internal mould, holotype x2 from Braga Formation, north central Nepal. (Waterhouse 2013).

Genus ***Cicatricia*** Waterhouse, 2010

Fig. 20, 21

Cicatricia is based on *Strophalosia hystricula* Girty, 1909, p. 275 from the Willis Ranch Member of the Word Formation in west Texas. Many good figures are provided by Cooper & Grant (1975, pl. 193, fig. 45, 46, pl. 194, fig. 16-31, pl. 195, fig. 1-43). It is distinguished by the large cicatrix

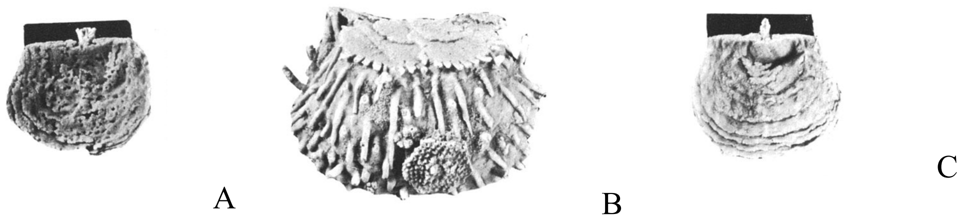


Fig. 20. *Cicatricia hystricula* (Girty). A, dorsal exterior, x2. B, ventral valve, showing spines and large cicatrix, x2. C, dorsal exterior, x2. Specimens lack the short radial ribs and irregularities of *Crenalosia*, from Willis Ranch Member, Texas. (Cooper & Grant 1975).

surrounded by rhizoid spines over the ventral umbo. Other ventral spines are mostly slender or sturdy, usually recumbent, rarely erect, and apparently of subuniform strength. The dorsal valve of *hystricula* is prominently laminate in bands, reminiscent of the arrangement in *Mingenewia* Archbold. The anterior ventral spines are not as coarse or as well-spaced as those of *Etherilosia* Archbold, 1993 (see p. 28) and there is no sign of the row of fine hinge spines which developed in that genus, though they could have been disrupted by the cicatrix.

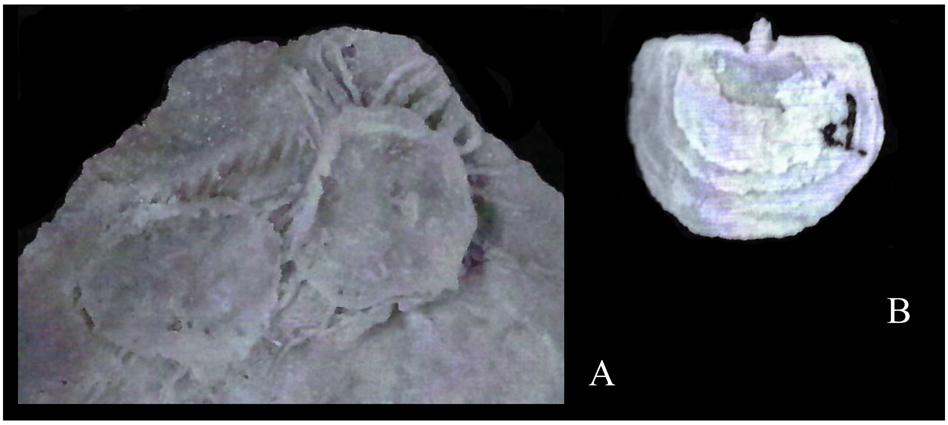


Fig. 21. *Cicatricia hystricula* (Girty). A, ventral valves. B. dorsal exterior. Specimens x4 from Willis Ranch Member, Texas. (Cooper & Grant 1975).

Tribe **BIPLATYCONCHINI** Waterhouse, 2013

Fig. 22, 23

[Biplatyconchini Waterhouse, 2013, p. 232].

Diagnosis: Large shells with numerous fine spines crowded over ventral valve, no dorsal spines, but fine dimples. Dorsal valve slightly thickened anteriorly, with short trail. Commarginal bands prominent over dorsal valve and may be present on ventral valve. No dorsal capillae.

Genera: *Biplatyconcha* Waterhouse, 1983a (nom. nov. pro *Platyconcha* Waterhouse, 1975 not Longstaff, 1933, syn. *Megalosia* Waterhouse, 1988); *Subtaeniothaerus* Solomina. Late Permian.

Discussion: Waterhouse (2013, p. 232) suggested that members of this tribe may have been derived from *Marginalosia* Waterhouse through loss of dorsal spines, rather than descend directly from strophalosiid stock, as interpreted in Brunton et al. (2000). But the presence of dorsal commarginal bands and large size and lack of marginal ridges indicate that Biplatyconchini with regular commarginal bands is much closer to Mingenewiinae Archbold, and distinguished by the presence of numerous ventral spines.

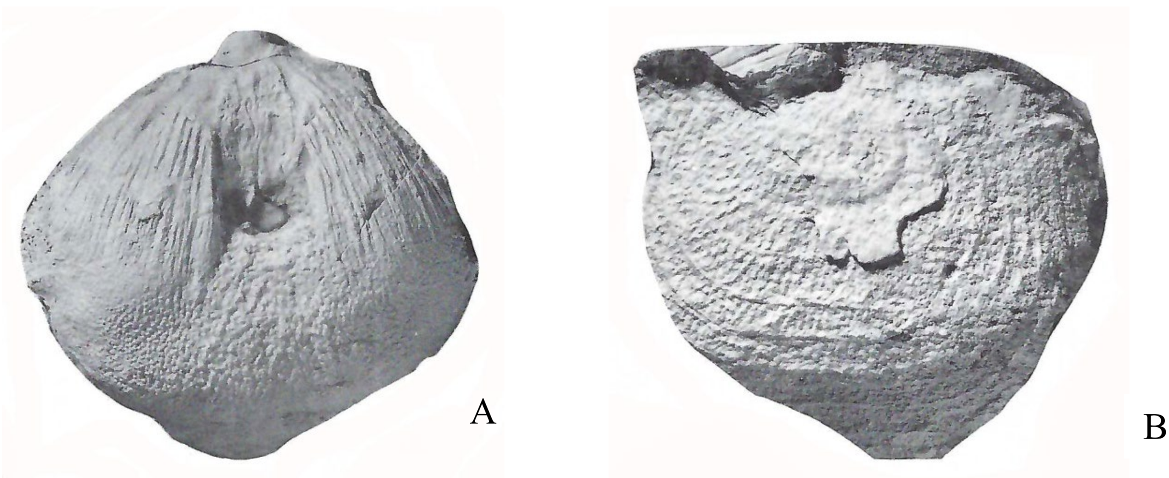


Fig. 22. *Biplatyconcha grandis* (Waterhouse). A, ventral internal mould, UQF 68995. B, dorsal external mould, UQF 68902. From Nisal Member, Senja Formation, Nepal. x1. (Waterhouse 1978).

Originally Waterhouse thought the genus was waagenoconchid in view of the fine spines, and indeed Solomina (1988) leaned towards a comparable interpretation for her genus *Subtaeniothaerus*. Waterhouse then prepared hinges of the genus to show strophalosiiform affinities. Briggs (1998) improperly took advantage of this preparation to announce that it was he rather than Waterhouse had “discovered” the strophalosioid attributes.

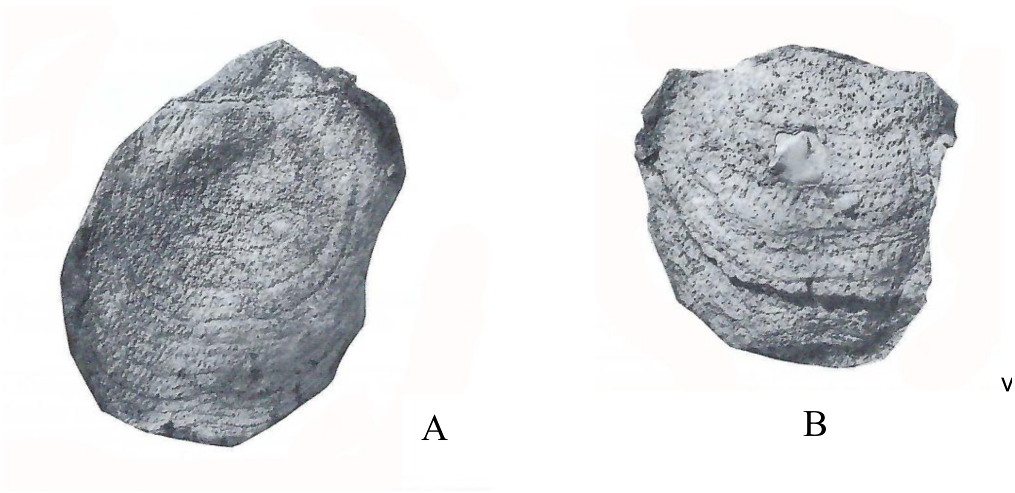


Fig. 23. *Biplatyconcha* (?) *grandis* (Waterhouse). A, dorsal view of conjoined specimen UQF 76010. B, latex cast of ventral valve UQF 76009. Specimens x1 from the Nisal Member of the Senja Formation, late Changhsingian of north central Nepal, showing ventral as well as dorsal banding, and originally described as *Megalosia*. (Waterhouse 1988). Questions arise. Is this really *Biplatyconcha*, given the ventral banding, and should its relationship to *Subtaeniothaerus* be clarified, noting the close similarity in publication dates.

Strophalosia enantiensis Archbold, 1996 from the Mingenew Formation of the Perth Basin in Western Australia appears to belong to *Biplatyconcha*. *Subtaeniothaerus* has a short hinge and low commarginal rugae over the ventral as well as dorsal valve, but is very close to *Biplatyconcha. Megalosia* shows a few ventral growth stops, but is regarded as a synonym of *Biplatyconcha* (Fig. 22), though as the caption notes, further clarification is needed.

Subfamily **BRUNTONARIINAE** Waterhouse, 2013

Fig. 24, 25

[Bruntonariinae Waterhouse, 2013, p. 242].

Diagnosis: Spines not vermiform, numerous over both valves. Commarginal laminae well developed over both valves. No dorsal dimples, no capillae, possible ventral spine tunnels.

Genera: *Bruntonaria* Waterhouse, *Crossalosia* Muir-Wood & Cooper. Lower Carboniferous (Visean).

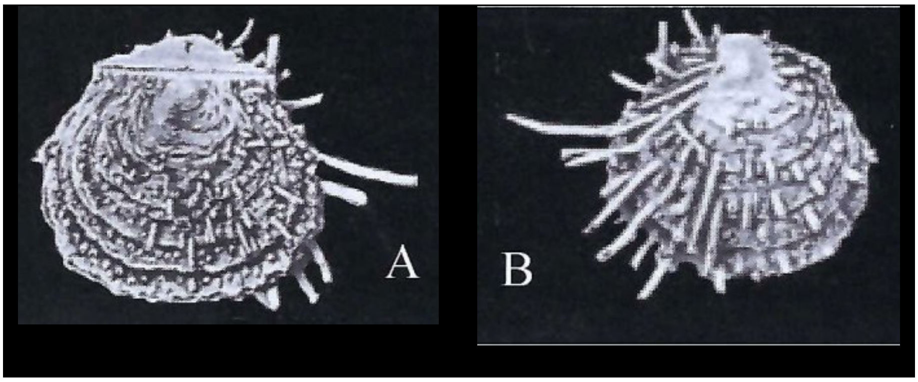


Fig. 24. *Bruntonaria panicula* (Brunton). A, B, ventral and dorsal aspects of silicified specimen with valves conjoined, x8. From Lower Carboniferous of Ireland. Brunton (2007, p. 2663) wrote that there was no difference between these figures and those of Fig. 16, p. 29 herein which illustrates *Dasyalosia* Muir-Wood & Cooper. (Brunton 1966).

Discussion: Bruntonariinae Waterhouse (2001, p. 85) is based on a Lower Carboniferous genus from Ireland, called *Dasyalosia panicula* by Brunton (1966) and renamed *Bruntonaria* by Waterhouse (2001, p. 85). The type species has a strongly lamellate dorsal valve, distinguished by the presence of numerous dorsal spines, as well as spinose and lamellate ventral lamellae with long erect ventral spines. The species had originally been assigned by Brunton (1966) in describing a silicified fauna from Northern Ireland to a species of the upper Permian genus *Dasyalosia* Muir-Wood & Cooper, 1960, and Brunton (2007, p. 2663) insisted this had been the correct generic identification. But *Dasyalosia* differs substantially from the species *panicula* Brunton. It has crowded vermiform spines over both valves, and lacks the prominent commarginal laminae over each valve found in *Bruntonaria*. Similar laminae are also found in Mingenewiinae including Biplatyconchini, and Craspedalosiinae.

Crossalosia Muir-Wood & Cooper, 1960, based on the species *Productus buchianus* Koninck, 1847 from Visean of Belgium has lamellae and spines over both valves, including a posterior brush of spines on the dorsal ears, and the faint suggestion of spine tunnels (Muir-Wood & Cooper 1960, pl. 5, fig. 2). So-called *Dasyalosia panicula* Brunton is much closer to this genus than to *Dasyalosia*, and Brunton & Mundy (1988, p. 64) even synonymized their earlier reference of *panicula* with Koninck's species: though they were recording material from Yorkshire, not Ireland.

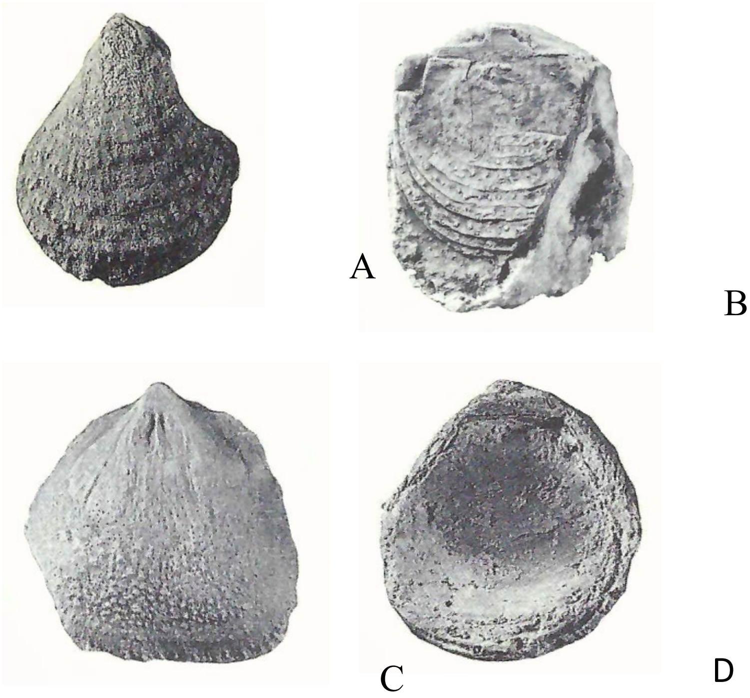


Fig. 25. *Crossalosia buchiana* (Koninck). A, ventral exterior, x3. A ventral internal mould, x3. B, dorsal aspect of specimen with valves conjoined, size not indicated. C, ventral internal mould showing a few spine tunnels, x2. D, dorsal internal mould, showing spine bases posteriorly, x2. A, C, D from Visé, Belgium. (Muir-Wood & Cooper, 1960). B from north Yorkshire (Brunton & Mundy, 1988).

Subfamily **CORONALOSIINAE** new subfamily

Name genus: *Coronalosia* Waterhouse & Gupta, 1978, p. 451, here designated.

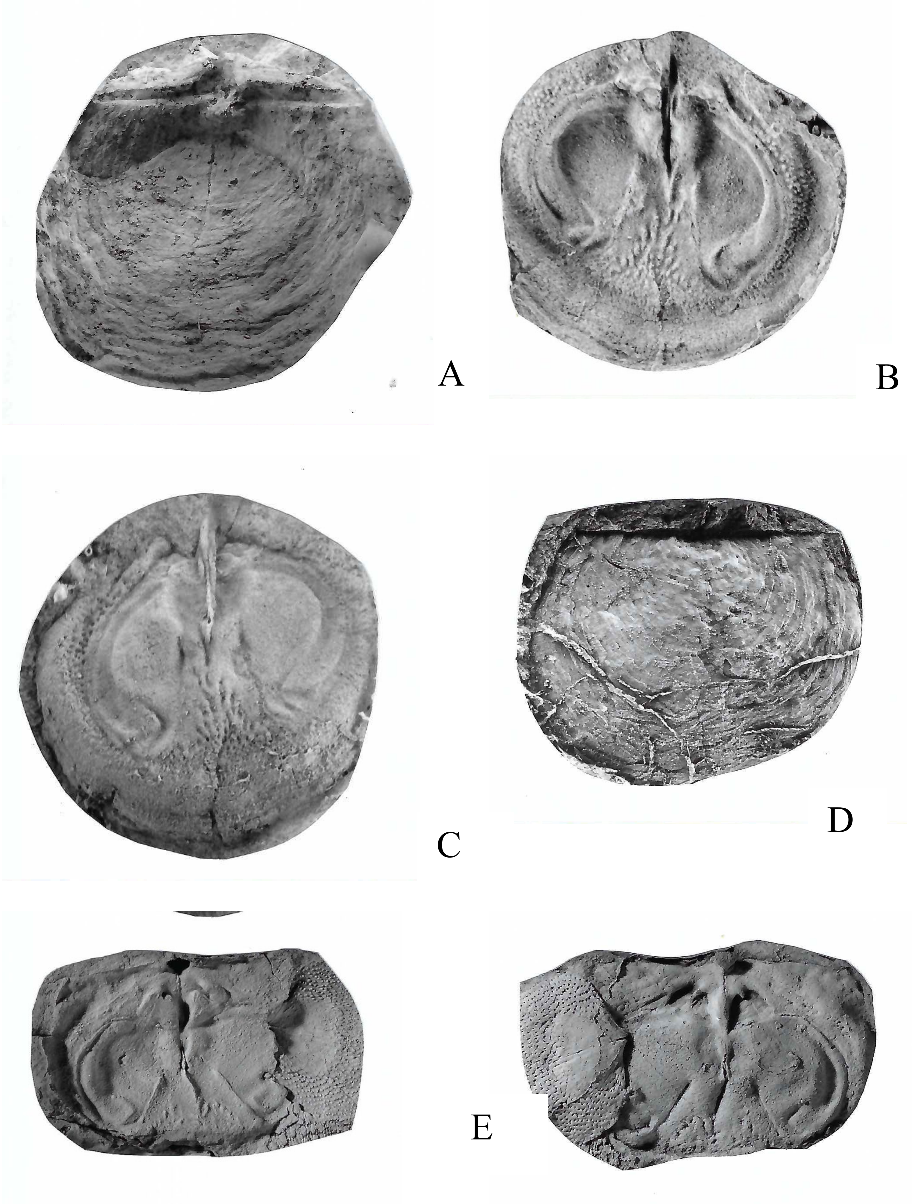
Diagnosis: Shells typified by well-developed row of spines along the ventral hinge. Ventral disc spines well-spaced, uniform, dorsal spines on only one of the known genera, called *Capillaria*. fine dorsal capillae widespread, a few dorsal dimples. Cardinal process trifid.

Genera: *Coronalosia* Waterhouse & Gupta, *Capillaria* Waterhouse, *Lialosia* Muir-Wood & Cooper, *Liveringia* Archbold. Permian.

Genus ***Coronalosia*** Waterhouse & Gupta, 1978

Fig. 26, 27

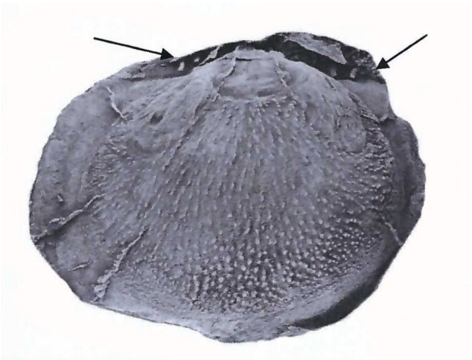
Diagnosis: Ventral spines over the disc are slender, subrecumbent, and well-spaced along somewhat irregular commarginal rows. No dorsal spines. The distinctive feature of the genus lies in the well-developed hinge row of sturdy erect spines.



A B C D E F

Fig. 26. *Coronalosia blijniensis* Waterhouse & Gupta. A, dorsal aspect of conjoined specimen. B, C. dorsal internal mould and latex cast. D, dorsal external mould. E, F, dorsal internal mould and latex cast. From Bijni tectonic unit, Garwhal Himalaya. (Waterhouse 2013).

Discussion: This appears to be a group limited to Gondwana, with species and genera found in India, Australia and New Zealand. *Lialosia* has lost most of its ventral spines. The presence of dorsal dimples suggest a relationship to Fimbrinialosiini (see p. 24), and various species show very fine radial dorsal capillae, including *Coronalosia* (Waterhouse & Gupta 1978, p. 413). Three genera listed above lack dorsal spines, but *Capillaria* has both a well-developed ventral hinge row of spines, and numerous dorsal spines as well, so that Coronalosiinae are judged to be dasyalosioid. Dorsal sub-banding is also developed in *Capillaria*, and ventral rugation is found in some Queensland material.



A

Fig. 27. *Coronalosia blijniensis* Waterhouse & Gupta. A, ventral internal mould with arrow pointing to row of cardinal spines, x1.5. From Bijni tectonic unit, Garwhal Himalaya. (Waterhouse 2013).

The type species was described from the Bijni tectonic unit of the Garwhal Himalaya by Waterhouse & Gupta (1978, p. 417, pl. 1, fig. 4, pl. 2, fig. 1-6, pl. 3, fig. 1-6), and the poor reproduction of figures was addressed by Waterhouse (2001, pl. 4, fig. 17-21; 2013, Fig. 2.11, 7.13). The species described as *Strophalosia* (*Heteralosia*) *irwinensis* Coleman (1957) from Western Australia is congeneric with *Coronalosia*, even though used to exemplify *Strophalosia* by Brunton et al. (2000, Fig. 400.1d-f). The dorsal valve has fine radial capillae and dimples appear on a few specimens.

Genus ***Liveringia*** Archbold, 1987

Fig. 28

Diagnosis: Spines form hinge row, and are few over the ventral valve. Elongate dimples and prominent capillae over dorsal valve, no dorsal spines or commarginal ornament other than growth increments, but prominent elongate dorsal dimples. Marginal ridge in each valve.

Type species: *Liveringia magnifica* Archbold, 1987 from the Hardman Member of Western Australia, stated to be upper Capitanian by Brunton et al. (2000, p. 569), but more likely Wuchiapingian in age.

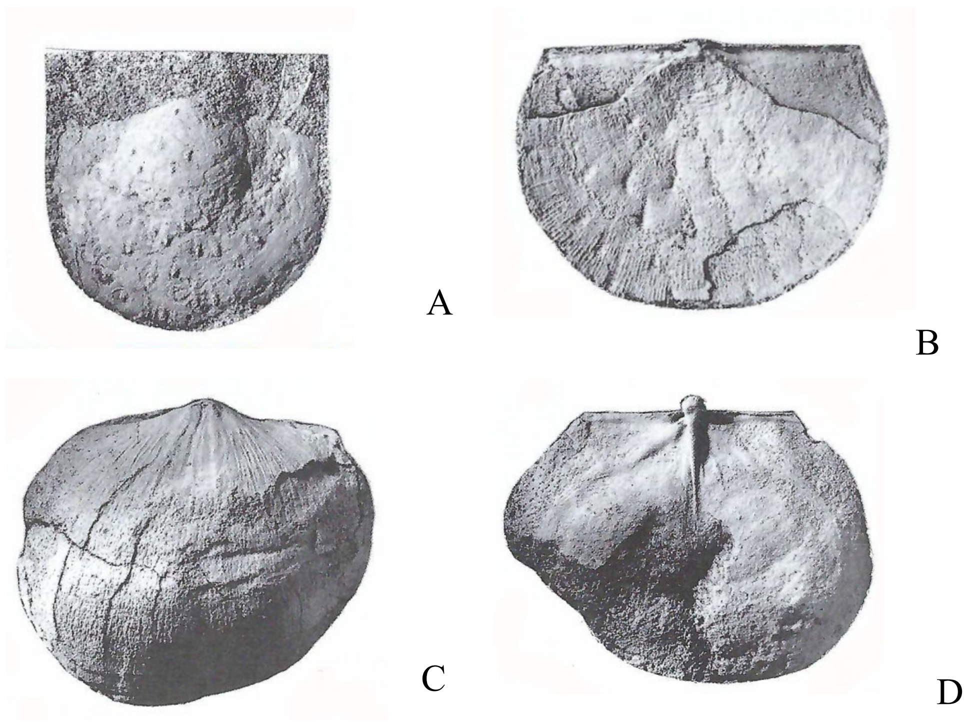


Fig. 28. *Liveringia magnifica* Archbold. A, ventral exterior. B, dorsal valve showing characteristic exterior. C, ventral internal mould. D, dorsal internal mould. Specimens x1 from the Hardman Member, Canning Basin, Western Australia. (Archbold 1987).

Discussion: The cardinal process appears to be trifid. There are no spine tunnels as such in the ventral valve, but the posterior floor each side of the adductor scars bears fine striae (Archbold 1987, Fig. 6H, L).

Genus ***Lialosia*** Muir-Wood & Cooper, 1960

Fig. 29

Diagnosis: Spines limited to rows near the ventral hinge, remainder of both valves with low commarginal growth increments, capillae faint. Dorsal disc thickened, no commarginal rugae. Cardinal process stated to be bifid from inner aspect, each lobe folded into two.

Type species: *Strophalosia kimberleyensis* Prendergast, 1943, p. 47 from the Wandagee Formation of the Carnarvon Basin, Western Australia, of Baigendzinian age, to refine the Artinskian-Kungurian age proferred by Brunton et al. (2000, p. 569). Muir-Wood & Cooper (1960, p. 87) mentioned concentric (= commarginal) ornament and traces of fine capillation in both valves.

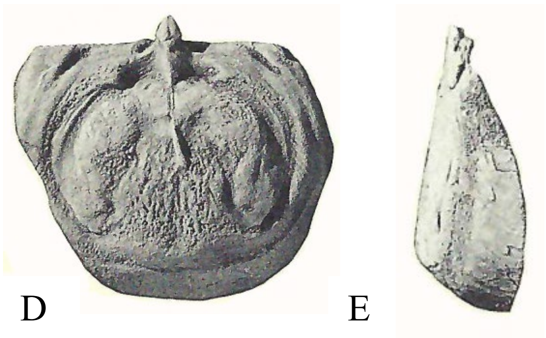


Fig. 29. *Lialosia kimberleyensis* (Prendergast). A, B, dorsal and ventral views of exterior complete specimen. C, ventral interior. D, ventral internal aspect and E, lateral aspect of dorsal valve. Specimens x1.5 from Wandagee Formation, Western Australia. (Muir-Wood & Cooper, 1960).

Subfamily **CRASPEDALOSIINAE** Waterhouse, 2013

Fig. 30 - 32

[Craspedalosiinae Waterhouse, 2013, p. 245].

Diagnosis: Ventral spines vermiform like those of *Dasyalosia*. Dorsal ornament of strong commarginal laminae, and fine to strong radial capillae. One of the two known genera developed robust dorsal spines.

Genera: *Craspedalosia* Muir-Wood & Cooper, *Melvillosia* Waterhouse. Middle and Upper Permian (Capitanian, Wuchiapingian).

Discussion: *Craspedalosia pulchella* Dunbar 1955) has ventral spine tunnels as in Echinalosiidae. Such are absent from Strophalosiidae. *Melvillosia* has dorsal spines, but is otherwise like *Craspedalosia* apart from having stronger radial capillae.

Craspedalosia lacks dorsal spines, so was regarded as belonging to Strophalosiinae by Brunton et al. (2000, pp. 565, 569). But this position may require adjustment. A species remarkably similar to *Craspedalosia* from Melville Island, Canada, and of slightly greater age, called *Melvillosa canadense* Waterhouse, 2001, p. 56, develops anterior dorsal spines (Fig. 31). Moreover a ventral valve of *Craspedalosia pulchella* (Dunbar) from Wuchiapingian beds of

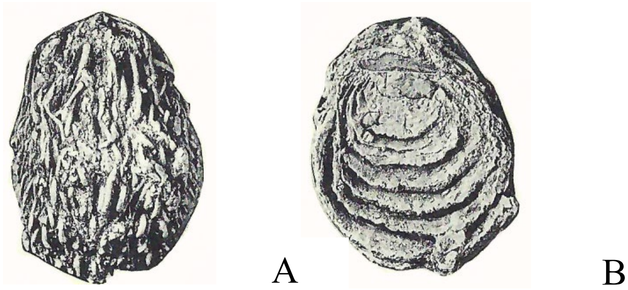


Fig. 30. A, B, *Craspedalosia lamellosa* (Geinitz). A, ventral valve. B, dorsal aspect. From lower Zechstein, Thuringia, Germany, x1.5. Note faint suggestions of possible fine and worn capillation in B. (Muir-Wood & Cooper 1960).

Greenland, and assigned to the genus by Muir-Wood & Cooper (1960, p. 82), shows spine tunnels over the interior of the ventral valve. Ventral spine tunnels are not known in any well established strophalosiid genus or species, but are found in many genera of Dasyalosioidea and Quadratioidea. Brunton (2007, p. 2667) objected to the association between *Craspedalosia* and *Melvillosia* on the basis that the latter genus has fine capillation, stronger than in *Craspedalosia*. But Muir-Wood & Cooper (1960, p. 82) did record rare capillation on a single lamellum in *Craspedalosia*, and Dunbar (1955, pl. 7, fig. 20) showed capillae (on the left side) in *C. pulchella*. The difference in capillation between the two genera is therefore one of degree and preservation. The vermiform ventral spines of *Craspedalosia* recalls the vermiform spines over both valves of *Dasyalosia*, whereas the dorsal commarginal bands are found in Mingenewiidae and in Bruntonariinae, pointing to association with all these genera.

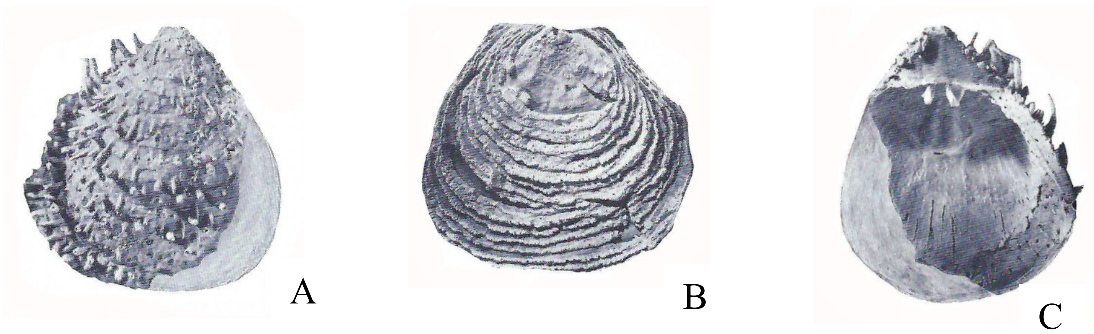


Fig. 31. *Craspedalosia pulchella* (Dunbar). A, C, ventral external and internal aspects, suggesting presence of spine tunnels in C. B, dorsal exterior. Specimens x 1.5, from northeast Greenland. (Dunbar 1955). Note suggestions of capillation on left side in B.

There seem to be a number of alternative explanations in trying to reconcile these observations with the classification. Any proposition that the particular specimens were highly exceptional and should be ignored offers no rational escape from the demands of taxonomy. But given the adaptability and variable options available for evolution, the simplest immediate explanation may in the feasibility that some dasyalosiids lost their dorsal spines, if only temporarily. Thus, to follow the stratigraphic record so far available, *Melvillosia* developed a distinctive micro-ornament and subtriangular shape, and retained its dorsal spines. It then evolved jnto *Craspedalosia*, losing its dorsal spines, but at least for some ventral valves, retained its spine tunnels.

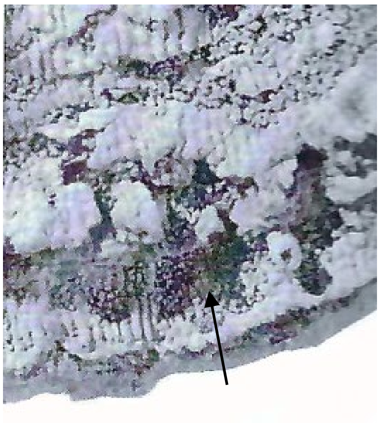


Fig. 32. *Melvillosia canadense* Waterhouse, anterior part of dorsal valve, showing well-formed spine, as arrowed, x4. From Trold Fiord Formation, Melville Island, Canada. Radial capillae are well developed, and also appear more faintly in *Craspedalosia*, and both genera have commarginal laminae. (Waterhouse 2020).

Family **TRUNCATENIIDAE** Liao, 1982

Fig. 33

[Nom. transl. hic ex Truncateniinae Liao, 1982, p. 539 = Licharewiellinae Archbold, 1986, p. 98].

Diagnosis: Both valves strongly costate. *Licharewiella* Ustritsky has only ventral spines, whereas *Costalosiella* Waterhouse also has dorsal spines.

Fig. 33. *Truncatinia heshanensis* Liao, ventral valve x2, from Late Permian of South China. (Liao 1982). Now referred to *Licharewiella*.

Genera: *Licharewiella* Ustritsky (syn. *Costalosia* Waterhouse & Shah, *Truncatenia* Liao), *Costalosiella* Waterhouse, Middle and Upper Permian. Possibly *Australosia* McKellar, 1970 from the Famennian of Queensland with its well developed ribs was ancestral (see Fig. 34). This genus was classed in Donalosiinae by Brunton et al. (2000, p. 580) and has a row of prominent hinge spines, recalling Devonalosiinae and also Coronalosiinae.

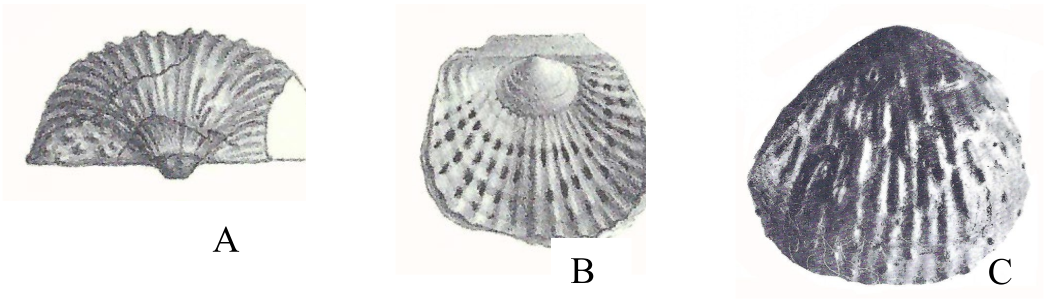


Fig. 33. A, B, *Licharewiella costata* (Waagen). A, dorsal aspect of specimen with valves conjoined. B, posterior ventral aspect of ventral valve. Specimens x2 from Amb Formation, Salt Range, Pakistan. (Waagen 1884). C, *Costalosiella argentea* (Waterhouse & Shah) x4 from Malakabad, Iran. This has dorsal spines. (Douglas 1936, Waterhouse & Shah 1966).

Discussion: *Costalosiella* Waterhouse, 1983b is based on *Costalosia argentea* Waterhouse & Shah 1966, p. 2 named for material from Iran described by Douglas (1936). It has dorsal spines as well. But the dorsal valve has not been illustrated, and needs assistance from the Geological Survey of India, Calcutta, where the material is stored. Commarginal laminae are missing from these genera.

Truncatiinae Liao (1982, p. 539) associates genera that are typified by having strong costae. The two Permian genera are very close to each other in general appearance, but one has no dorsal spines, the other many dorsal spines. Other than the presence in one form of dorsal spines, and absence of such spines in the other form, there is little in the respective morphologies to indicate linkage with Dasyalosioidea, so that affinities require further study. From the Famennian of Queensland, *Australosia* McKellar, 1970 has a ventral hinge row of spines, a bifid cardinal process, and firm ventral costae. *Australosia* was placed in Donalosiinae Lazarev in the *Revised Brachiopod Treatise* (Brunton et al. 2000, p. 580), and is close to this group and

Fig. 34. *Australosia starensis* McKellar, internal aspect of ventral valve, GSQF 11324, x3, holotype. From Star beds (Famennian) of Queensland. Note the presence of a ventral hinge row of spines. (Brunton et al. 2000).

especially Devonalosiinae, and so could have been ancestral for Truncateniinae. Given the sharing of ribs with *Australosia* McKellar, the group may have stemmed from this genus classed in Devonalosiinae, some members of which have dorsal spines, and others lack them. That would imply that this group should be transferred to Donalosiidae, but is regarded as speculative, given the long time gap between McKellar's genus and the Permian occurrences, and the presence of a prominent row of ventral hinge spines not seen in Truncatiinae. Nevertheless the possibility remains, and that would demand a degree of rearranging, and dasyalosiids broadened to involve Devonalosiinae. Moreover the alliance between genera with and without dorsal spines would be clearly associated with Devonian groups, and open up questions about the realities and limits of superfamily Dasyalosioidea.

Superfamily **QUADRATIOIDEA** Lazarev, 1989

[Nom. promoveo hic ex Quadratiinae Lazarev, 1989, p. 38] et seq.

Diagnosis: Spines over both valves. Radial ornament may be capillate, no dorsal dimples as a rule.

Family **QUADRATIIDAE** Lazarev, 1989

Diagnosis: Spines fine and evenly dispersed over both valves. Dorsal valve with subeven spines, shell not thickened, dorsal valve laminate, without well-defined commarginal bands.

Discussion: This family is characterized by an ovally rectangular transverse shape, low inflation and fine spines, and shares attributes with Echinalosiidae – perhaps it was the source family, though some Devonian and younger genera are also echinalosiid in shape and spine detail. Two minor groups are associated with Quadratiinae, as tribes. There are no ventral spine tunnels as far as known.

Subfamily **QUADRATIINAE** Lazarev, 1989

Fig. 37, 38

Diagnosis: Transverse shells, fine spines, ventral spines may be in two series, may include weak hinge row, dorsal spines present, as a rule of one erect series. Commarginal ornament subdued, limited to growth stops and increments, shell not regularly undulose, no dorsal dimples. Marginal ridges may be present. Cardinal process possibly bilobed, described as knob-like by Muir-Wood & Cooper (1960).

Genera: *Quadratia* Muir-Wood & Cooper, *Chonetipustula* Paeckelmann, Cyphotalosia Carter, *Quadralosia* Waterhouse. Lower Carboniferous.

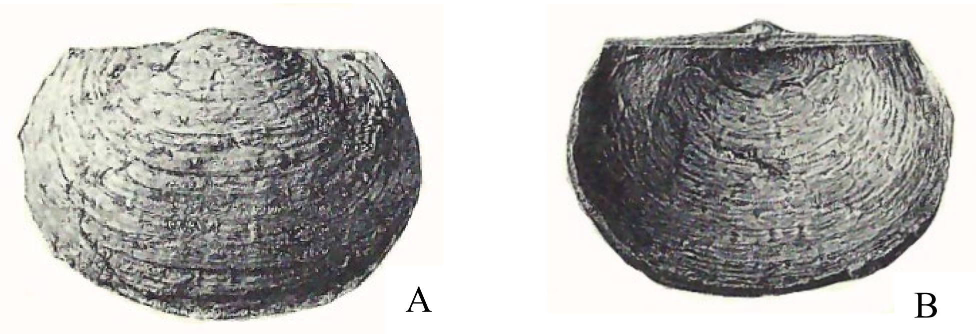


Fig. 37. *Quadratia hirsuteformis* (Walcott). A, B, ventral and dorsal aspects of specimen with valves conjoined, x1.5, from Chesterian of Oklahoma.(Muir-Wood & Cooper 1960).

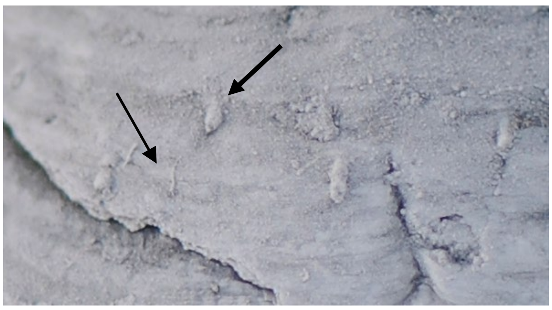


Fig. 38. *Quadralosia delicata* Waterhouse, GSC 133257 holotype x8 from Hart River Formation, Yukon Territory. Thicker arrow points to larger diameter spine; finer arrow to slender spine. (Waterhouse 2013).

Subfamily **ACANTHATIINAE** Waterhouse, 2013

Fig. 39, 40

[Acanthatiinae Waterhouse, 2013, p. 240. Syn. Eostrophalosiini Waterhouse 2013, p. 227].

Diagnosis: Transverse semicircular to oval outline, characterized by displaying a modest row of hinge spines. Dorsal spines rare as a rule, no pits and only commarginal growth lines. Pit in front of bifid cardinal process, which is supported by lateral buttress ridges.

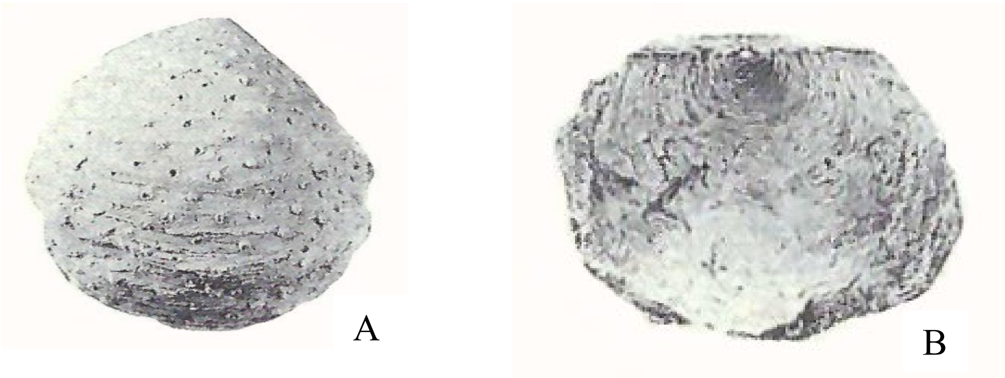


Fig. 39. *Acanthatia nupera* (Stainbrook). A, ventral exterior, x1.5. B, dorsal aspect of specimen with valves conjoined, x2. From upper Famennian Percha Shale, New Mexico. (Muir-Wood & Cooper 1960, Brunton et al. 2000).

Genera: *Acanthatia* Muir-Wood & Cooper, *Eostrophalosia* Stainbrook, ?*Kahlella* Legrand-Blain. Upper Devonian to Lower Carboniferous (upper Famennian to Tournaisian).

Discussion: This group is close to Donalosiidae, especially Devonalosiinae, in its ventral spines, but has dorsal spines. *Acanthatia* was placed in Araksalosiidae by the *Revised Brachiopod*

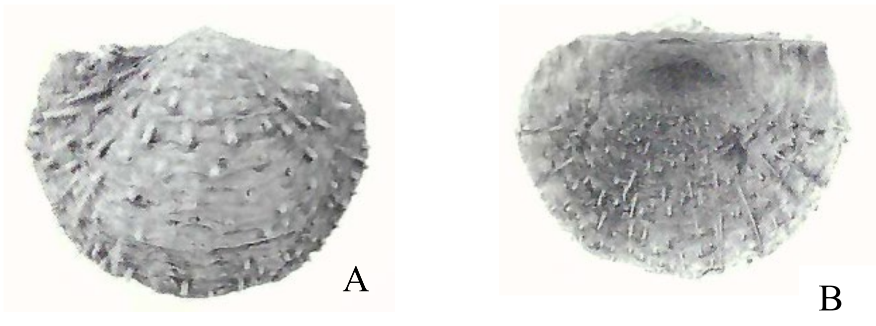


Fig. 40. *Eostrophalosia rockfordensis* (Hall & Clarke). A, B, ventral and dorsal aspects of specimen with conjoined valves x3. From Frasnian Hackberry Formation, Iowa. (Brunton et al. 2000).

Treatise by Brunton et al. (2000, p 576), but *Acanthatia* shows no radial capillae, and body spines are moderately well developed. It is close to *Eostrophalosia*, which has less delicate spines, that are few over the dorsal valve. Although this genus was proposed as a separate tribe Eostrophalosiini by Waterhouse (2013, p. 227), no comparable genera are known, so the tribe is suppressed. The group is of minor importance, differing from Quadratiinae through its well-defined ventral hinge row of spines.

Family **ECHINALOSIIDAE** Waterhouse, 2001

[Echinalosiinae Waterhouse, 2001, p. 57] et seq.

Diagnosis: Usually transverse, ventral valve moderately arched, ventral spines well-spaced and regular as a rule, but varies, from uniform to diverse, well-spaced, or crowded and irregular. One series is often fine and prostrate, no prominent hinge row as a rule, irregular in thickness and dense in one tribe, may be clustered over ears or absent from ears. Dorsal spines vary throughout the family, but usually of one series, fine and erect. Dorsal dimples often developed, capillae and/or dimples in some genera. In ventral valve, spine tunnels may be present and cardinal process trilobed. Marginal ridges common.

Discussion: The spines are stronger in both valves than in Quadratiidae and are more clearly differentiated as a rule over the ventral valve into two series, but evolution within Echinalosiidae displays what is interpreted as secondary convergence with Devonian strophalosiiform genera.

Subfamily **ECHINALOSIINAE** Waterhouse, 2001

Diagnosis: Dorsal valve concave, not thickened.

Tribe **ECHINALOSIINI** Waterhouse 2001

Fig. 41

Diagnosis: Ventral spines in two series, thicker series dominant as a rule.

Genera: *Echinalosia* Waterhouse (pro *Multispinula* Waterhouse, 1966 not Rowell, 1962), with subgenera *Glabauria* Waterhouse, *Unicusia* Waterhouse, also *Hontorialosia* Martinez Chacon, *Nothalosina* Waterhouse, *Yukonolasia* Waterhouse. Basal Permian (Asselian) to Late Permian (Wuchiapingian). Earlier occurrences of *Echinalosia* in the Arctic seem possible.

Discussion: *Yukonalosia* is an early and somewhat exceptional member from Arctic Canada.

Most ventral spines are coarse and erect (Fig. 41A). Fig. B shows that dorsal spines are in a coarse and fine erect series. Echinalosiini are especially numerous and diverse in east Australia and New Zealand, as summarized in a forthcoming volume of Earthwise.

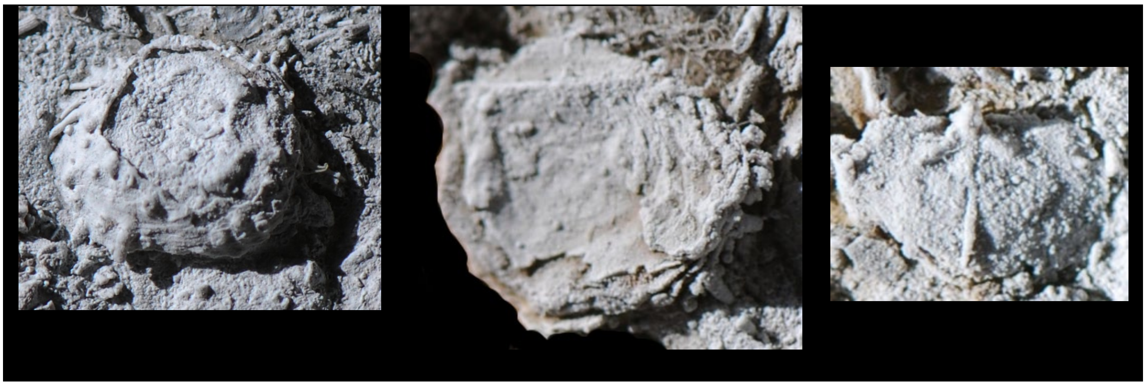


Fig. 41. *Yukonalosia arctica* Waterhouse, an early and somewhat exceptional member of Echinalosiini. A, ventral aspect of specimen with valves conjoined, GSC 136878 x4, with most spines coarse and erect. B, dorsal aspect of specimen with valves conjoined, GSC 136875 x4 showing spines in two series. C, dorsal valve interior, GSC 137263 x5. From Member A, Jungle Creek Formation, Yukon Territory, Canada. (Waterhouse 2018).

Tribe **MARGINALOSIINI** Waterhouse, 2013

[Marginalosiini Waterhouse, 2013, p. 229].

Diagnosis: Ventral spines numerous and fine, of one series. Dorsal valve may be thickened, trail short. Marginal ridge well-developed in *Marginalosia*.

Genera: *Marginalosia* Waterhouse, ?*Guadalupelosia* Archbold & Simanauskas (syn. *Muirwoodicia* Waterhouse). Middle (Capitanian) and Late Permian.

Tribe **ACANTHALOSIINI** new

Name genus: *Acanthalosia* Waterhouse, 1986, p. 31.

Diagnosis: Ventral and dorsal spines numerous and diameter variable.

Genera: *Acanthalosia* Waterhouse, *Maxwellosia* Waterhouse. Lower and Middle Permian.

Subfamily **ARCTICALOSIINAE** Waterhouse, 2001

[Arcticalosiinae Waterhouse, 2001, p. 82].

Diagnosis: Large, may have thick body corpus, dorsal valve thickened to wedge-shape.

Tribe **ARCTICALOSIINI** Waterhouse, 2001

Fig. 42, 43

Diagnosis: Ventral spines subuniform and fine, crowded over disc, trail and ears. Dorsal valve gently concave to flat, and wedge-shaped.

Genus: *Arcticalosia* Waterhouse. Middle or upper Early and early Middle Permian of Canada and Western Australia.

Fig. 42. *Arcticalosia unispinosa* (Waterhouse). A, ventral valve holotype. B, dorsal exterior. From Trold Fiord Formation, Melville Island and Ellesmere Island, Canada, x1. (Waterhouse 1969).

Discussion: There is an alternative position for this tribe: that it should be associated with Biplatyconchini, because of the subfusc commarginal bands suggested over the shell. Here these are interpreted as irregularly placed growth-stops. The dorsal valve is wedge-shaped, as in Wyndhamiini, rather than the unthickened dorsal valve of *Biplatyconcha*.

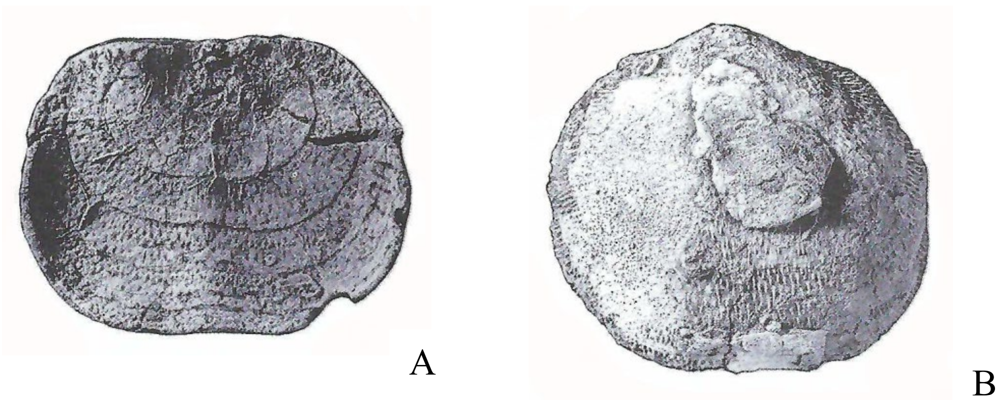


Fig. 43. *Arcticalosia multispinifera* (Prendergast). A, dorsal valve CPC 26431. B, ventral valve. Specimens x1 from Nooncanbah Formation, Western Australia. (Archbold 1987).

Tribe **WYNDHAMIINI** Waterhouse, 2010

[Wyndhamiini Waterhouse 2010, p. 53].

Diagnosis: Ventral spines in two series.

Genera: *Wyndhamia* Booker (syn. *Branxtonia* Booker), *Nonauria* Waterhouse, *Pseudostrophalosia* Clarke (syn. *Notolosia* Archbold, 1986?). Lower and Middle Permian.

Discussion: Briggs (1998) defended the validity of *Notolosia* on the grounds that the scar of attachment supposedly remained functional for longer than for *Pseudostrophalosia*.

A GENUS THAT IS NOT STROPHALOSIID

Enigmalosia Czarniecki, 1969, type species *E. sarytchevae* Czarniecki, 1969 was treated as a doubtful member of Donalosiinae by Brunton et al. (2000, p. 582), but it lacks teeth and has buttress plates, suggesting a position within Rhamnariidae, as discussed in the next Earthwise volume.

REFERENCES

AISENBERG, D. E. 1992: A new Visean productid genus from the Donbass. Paleont. Zhurn. 1992 (2): 130-132, 1 fig. [Russ.]

ARCHBOLD, N. W. 1980: *Mingenewia* n. gen. (Strophalosiidina, Brachiopoda) from the Western Australian Permian. J. Paleont. 54: 253-258, 1 pl.

_____1986: Studies on Western Australian Permian brachiopods 6. The genera *Strophalosia* King, 1844, *Heteralosia* King, 1938 and *Echinalosia* Waterhouse, 1967. Proc. Roy. Soc. Victoria 98: 97-119.

_____ 1987: Studies on Western Australian Permian brachiopods 7. The strophalosiid genera *Wyndhamia* Booker, 1929, *Lialosia* Muir-Wood and Cooper, 1960 and *Liveringia* gen. nov. Proc. Roy. Soc. Victoria 99: 19-35.

_____1993: Studies on Western Australian Permian brachiopods 11. New genera, species and records. Proc. Roy. Soc. Victoria 105: 1-29.

_____ 1996: Studies on Western Australian Permian brachiopods 13. The fauna of the Artinskian Mingenew Formation, Perth Basin. Proc. Roy. Soc. Victoria 108 (1): 17-42.

BRIGGS, J. D. C. 1998: Permian Productidina and Strophalosiidina from the Sydney-Bowen

Basin and the New England orogen: systematics and biostratigraphic significance. Mem. Assoc. Aust'asian Palaeont. 19: 1-258.

BRUNTON, C. H. C. 1966: Silicified productoids from the Visean of County Fermanagh. Bull. Brit. Mus. (Nat. Hist.) Geol. 12 (5): 155-243.

_____ 2007: Productidina. Strophalosiidina. *In* P. A. Selden (ed.). Treatise on Invertebrate Paleontology, Part H, Brachiopoda revised, vol. 6 Supplement: 2639-2676. Geol. Soc. Amer., Univ. Kansas; Boulder, Colorado & Lawrence, Kansas.

BRUNTON, C. H. C., LAZAREV, S. S., GRANT, R. E. 1995: A review and new classification of the brachiopod order Productida. Palaeontology 38 (4): 915-836, fig. 1-4.

BRUNTON, C. H. C., LAZAREV, S. S., GRANT, R. E., JIN YUGAN 2000: Productidina. [Includes Strophalosiidina, except for Richthofenioidea]. *In* R. L. Kaesler (ed.). Treatise on Invertebrate Paleontology, Part H, Brachiopoda revised, vol. 3 Linguliformea, Craniiformea, and Rhynchonelliformea part: 442-609. Geol. Soc. Amer., Univ. Kansas; Boulder, Colorado & Lawrence, Kansas.

BRUNTON, C. H. C., MUNDY, D. J. C. 1988: Strophalosiacean and Aulostegacean productoids (Brachiopoda) from the Craven Reef Belt (late Visean) of North Yorkshire. Proc. Yorkshire Geol. Soc. 47 (1): 55-88, Fig. 1-14.

BRUNTON, C. H. C., RACHEBOEUF, P. R., MUNDY, D. J. C. 1994: Reclassification of *Semenewia concentrica* (de Koninck, 1847) (Brachiopoda, Lower Carboniferous). Geobios 27 (1): 51-60, 3 fig.

CARTER, J. G. + 61 authors: 2011: A synoptical classification of the Bivalvia (Mollusca). Paleont. Contrib. 4: 1-47.

COLEMAN, P. J. 1957: Permian Productacea of Western Australia. Bull. Bur. Mineral. Res. Geol. Geophys. 40: 1-148, 21pl.

COOPER, G. A., GRANT, R. E. 1975: Permian brachiopods of west Texas. 111. Smithson. Contrib. Paleobiol. No. 19: 795-1298, pl. 192-502.

DOUGLAS, J. A. 1936: A Permo-Carboniferous Fauna from South-west Persia (Iran). Palaeont. Ind. 22 (6): 1-59.

DUNBAR, C. O. 1955: Permian brachiopod faunas of central east Greenland. Medd. om Grønland 110 (3): 1-169, 32pl.

DUNBAR, C. O., CONDRA, G. E. 1932: Brachiopoda of the Pennsylvanian System in Nebraska. Nebraska Geol. Surv. Bull. (ser. 2) 5: 1-377, 44 pl., 25 fig.

GEINITZ, H. B. 1847: *Orthothrix* Geinitz. Soc. Imperial. des Naturalistes Moscou Bull. 20: 84-86.

GIRTY, G. H. 1909: The Guadalupian fauna. U. S. Geol. Surv. Prof. Pap. 58: 651p., 31pl.

GREGORIO, A. de 1930: Sul Permiana di Sicilia (fossili del calcare con Fusulina di Palazzo Adriano non descritti del Prof. Gemmellaro conservati nel mio private gabinetto). Ann. Géol. et de Paléont. Palermo 52: 18-32, pl. 4-11.

KALASHNIKOV, N. V. 1980: Brachiopods of the Upper Paleozoic of the European North of the USSR. Nauka Leningrad, 136p., 39pl. [Russ.]

KONINCK, L. G. de 1847: Recherches sur les animaux fossiles. Part 1. Monographie des genres *Productus* et *Chonetes* . H. dessain. Liège : 246p., 20pl.

LAZAREV, S. S. 1986: The main direction of the evolution and systematics in Suborder Productidina. Avtoreferat dissertatsii na soiskanie ushenoi stepeni doktora biologicheskikh. Akad. Nauk SSSR. Paleont. Inst.: 1-41. [Russ.]. (Unpub.).

_____ 1987: Origin and systematic position of the main groups of Productida (brachiopods). Paleont. Zhurn. 1987 (4): 41-52, pl. 5. [Russ.]

_____ 1989: Systematics of Devonian brachiopods of Suborder Strophalosiidina. Paleont. Zhurn. 1989 (2): 27-39, pl. 3. [Russ.]

_____ 1990: Evolution and systematics of Productida. Acad. Nauk. SSSR. Tr. Paleont. Inst. 242: 171p., 40pl. [Russ.]

LIAO ZHUO-TING 1982: New genera and species of Aulostegacea (Brachiopoda). Acta Palaeont. Sin. 21: 537-541, 2pl. [Chin.]

LONGSTAFF, J. 1933: A revision of the British Carboniferous members of the family Loxonematidae with descriptions of new forms. Quart. J. Geol. Soc. London 89 (2): 87-124, pl. 7-12.

MANANKOV, I. N., PAVLOVA, E. E. 1976: *Mongolosia* – new genus of Permian brachiopod. Akad. Nauk SSSR, Tr. Akad. Nauk MNR Paleont. Biostrat. Mongolii 3: 354-357. [Russ.]

McKELLAR, R. G. 1970: The Devonian productoid brachiopod faunas of Queensland. Geol. Surv. Qld (Palaeont. Pap.) 3442: 1-40, pl. 1-12.

MUIR-WOOD, H. M. 1962: On the morphology and classification of the brachiopod suborder Chonetoidea. Brit. Mus. (Nat. Hist.): 132p., 16pl. William Clowes & Sons, London & Beccles.

MUIR-WOOD, H. M., COOPER, G. A. 1960: Morphology, classification and life habits of the Productoidea (Brachiopoda). Geol. Soc. Amer. Mem. 81: 1-447, 135pl.

PAECKELMANN, W. 1931: Die Fauna des deutschen Unterkarbons. 11: die Brachiopoden des deutschen Unterkarbons. Part 2. Die Productinae und Productus-ähnlichen Chonetinae. König-Preuss. Geol. Landes, Abh. (n. s.) 136: 440p., 41pl.

ROWELL, A. J. 1962: The genera of the brachiopod superfamilies Obolellacea and Siphotretacea. J. Paleont. 36: 136-152, 2pl.

SCHUCHERT, C. 1913: Class 2. Brachiopoda. *In* ZITTEL, K. A. von Text-book of Paleontology, vol. 1, part 1, 2nd ed., translated and edited by C. R. Eastman: 355-420, fig. 526-636. MacMillan & Co. Ltd, London.

SOLOMINA, R. V. 1988: New brachiopods from the Permian of the Verchoyan area. Paleont. Zhurn. 1988: 40-49, 2pl. [Russ.]

STRUVE, W. 1964: Stromungs-Orientierung bei Bodenverwachsenen, Schlosstragenden Brachiopoden. Natur und Museum 94 (12): 515-529, fig. 1-13.

SUTHERLAND, P. K. 1996: *Ardomosteges archamus* new genus, new species, in the early Pennsylvanian of Oklahoma – possible ancestor to the richthofenioid brachiopods. J. Paleont. (supplement 2, Paleont. Soc. Mem. 46) 70: 1-25, fig. 1-24.

USTRITSKY, V. I. 1963: *In* USTRITSKY, V. I. & CHERNYAK, G. E, Biostratigraphy and brachiopods of the Upper Paleozoic of Taimyr. Tr. Nauchno-Issled Geol. Arkt. Inst. (NIIGA) 134: 139p., 47pl. [Russ.]

VEEVERS, J. J. 1959: Devonian brachiopods from the Fitzroy Basin, Western Australia. Bur. Mineral Res., Geol. Geophys. Bull. 45: 220p., 18pl.

WAAGEN, W. 1883: Salt Range Fossils, vol. 1, part 4. Productus Limestone Fossils, Brachiopoda. Palaeont. Indica (ser. 13) fasc. 2: 391-546, pl. 29-49.

_____ 1884: Salt Range Fossils, vol. 1, part 4. Productus Limestone fossils. Brachiopoda. Palaeont. Indica (ser. 13) fasc. 5: 729- 770. Pl. 50-81.

WATERHOUSE, J. B. 1966: Lower Carboniferous and Upper Permian Brachiopods from Nepal. Jb. Geol. B. A. Sonder. 12: 5-99, 16pl.

_____ 1969: Permian Strophalosiidae (Brachiopoda) from the Canadian Arctic Archipelago. J. Paleont. 43: 28-40, pl. 7-10.

_____ 1975: New Permian and Triassic brachiopod taxa. Pap. Dep. Geol. Univ. Qld 7 (1): 1-23.

_____ 1978: Permian Brachiopoda and Mollusca from north-west Nepal. Palaeontographica A 160: 1-175, 26pl.

_____1983a: Permian brachiopods from Pija Member, Senja Formation, in Manang District of Nepal, with new brachiopod genera and species from other regions. Bull. Ind. Geol. Assoc. 16: 11-151.

_____ 1983b: *In* WATERHOUSE, J. B., & GUPTA, V. J. An early Djulfian (Permian) brachiopod faunule from upper Shyok Valley, Karakorum Range, and the implications for dating of allied faunas from Iran and Pakistan. Contrib. Himal. Geol. 2: 188-233, pl. 1-4.

_____ 1986: *In* WATERHOUSE, J, B, & BRIGGS, D. J. C. Late Palaeozoic Scyphozoa and Brachiopoda (Inarticulata, Strophomenida, Productida and Rhynchonellida) from the southeast Bowen Basin, Australia. Palaeontographica A 193 (1-4): 1-76.

_____ 1988: *Megalosia,* a new strophalosiid (Brachiopoda) genus from the Late Permian Nisal Member, Manang district, Nepal. J. Paleont. 62: 41-45, 1pl.

_____ 2001: Late Paleozoic Brachiopoda and Mollusca, chiefly from Wairaki Downs, New Zealand, with notes on Scyphozoa and Triassic ammonoids and new classifications of Linoproductoidea (Brachiopoda) and Pectinida (Bivalvia). Earthwise 3: 1-195.

_____ 2010: New taxa of Late Paleozoic Brachiopoda and Mollusca. Earthwise 9: 1-134.

_____ 2013: The evolution and classification of the Productida. Earthwise 10: 1-535.

_____ 2020: Permian brachiopods (Upper Artinskian to Wordian) from the Canadian Arctic. Earthwise 17: 1-477.

WATERHOUSE, J. B., GUPTA, V. J. 1978: Early Permian fossils from the Bijni tectonic unit, Garwhal Himalaya. Rec. Res. Geol. 4: 410-437, pl. 1-4.

WATERHOUSE, J. B., SHAH, S. C. 1966: *Costalosia*, a new strophalosiid genus (Brachiopoda) from the Permian of south Asia. Trans. Roy. Soc. N. Z. 4: (12): 229-234, 2pl. (Earth Sciences).

WONGWANICH, T. A., BOUCOT, A. J., BRUNTON, C. H. C., HOUSE, M. R., RACHEBOUEF, P. R. 2004: Namurian fossils (Brachiopods, Goniatites) from Satun Province, southern Thailand. J. Paleont. 78: 1072-1089.

1b. A REVIEW OF BRACHIOPOD GENERA CLASSED AS STROPHALOSIIDAE SCHUCHERT, 1913

Abstract

Strophalosia and allied genera are summarized from the fossil record.

CLASSIFICATION

Superfamily **STROPHALOSI0IDEA** Schuchert, 1913

Diagnosis: Shells as a rule with cicatrix, ventral and dorsal interareas, articulate by means of teeth and interareas considered to have supported cartilage as soft binding tissue, attached by umbonal cicatrix and spines. Ventral valve spinose, dorsal valve smooth without spines, may be tubercular and pitted by dimples, may be radially capillate. No spine tunnels.

Discussion: The cardinal process may appear to be bifid or trifid, but is not well known for a number of genera, so that its nature and uncertainties prevent weight being given for purposes of classification.

Family **STROPHALOSIIDAE** Schuchert, 1913

Diagnosis: Shells without dorsal spines.

Subfamily **STROPHALOSIINAE** Schuchert, 1913

Diagnosis: Ventral spines present and evenly cover entire valve as a rule, somewhat variable in strength and diameter, and vary from prostrate to erect, not forming a prominent hinge row as a rule.

Tribe **STROPHALOSIINI** Schuchert, 1913

Diagnosis: Dorsal valve without crowded pits or dimples.

Genera: *Strophalosia* King, *Crenalosia* Waterhouse, *Fortispinalosia* Waterhouse, *Heteralosia* Hinchey & Ray, *Kufria* Waterhouse, *Leptalosia* Dunbar & Condra. Upper Carboniferous and Permian.

Discussion: *Leptalosia* Dunbar & Condra 1932, p. 260 is based on *Strophalosia scintilla* Beecher, 1890 from the Louisiana Limestone of Missouri, of Lower Carboniferous (Hastarian) age, and is shown in Fig. 9, p. 24.

Genus ***Strophalosia*** King, 1844

Fig. 1 - 4

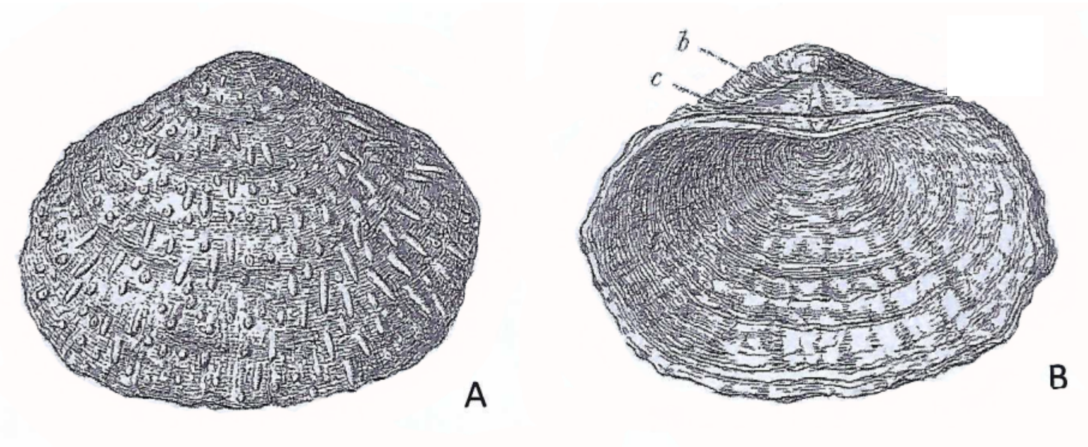


Fig. 1. *Strophalosia gerardi* King, holotype. A, ventral and B, dorsal aspects. From Ladakh Himalaya, age and locality uncertain, but deemed to be of Late Permian age. Specimen as figured by King (1850, pl. 19, fig. 6, 7), x1.5. b – pseudodeltidium, c- dorsal interarea.

The landmark examination of Productida by Muir-Wood & Cooper (1960) hugely increased the number of genera and families in the Productida and Strophalosiidina that made up the Order Productida, but *Strophalosia*, based on *Strophalosia gerardi* King (see herein Fig. 1 - 3) was misinterpreted by Muir-Wood & Cooper (1960) as having dorsal spines. A different view was expressed in a Ph. D. thesis by Waterhouse in 1958 after inspection of the type specimen and a dorsal valve topotype housed at the Department of Geology in the university at Galway, Ireland. With H. M. Muir-Wood as one of the examiners for the degree, Waterhouse (1964, p. 28) was persuaded to retain *Strophalosia* by Muir-Wood, as understood by the Muir-Wood & Cooper study, a mistake corrected eventually by Brunton (1966) who also examined the holotype (but not the better preserved dorsal valve). The species has sturdy ventral spines, no specialized row of spines along the hinge or over the ears, and the dorsal valve is deeply concave, with moderately developed commarginal

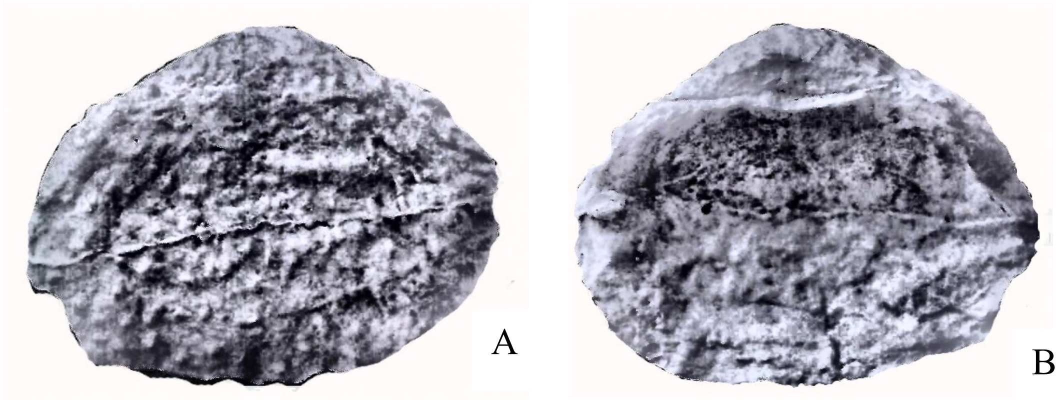


Fig. 2. *Strophalosia gerardi* King, ventral and dorsal views of holotype BR 2068 (as plaster cast), reproduced by local equalization, x1.5. Kept at National University of Ireland, Galway. The fissure is an artifact, on the plaster cast prepared for me at the University of Galway. but not on the actual specimen. (Modified from Waterhouse 2013).

laminae but no regular commarginal bands, and scattered well-developed tubercles, but no conspicuous capillae or dimples. Other species with these attributes include *Strophalosia sublamellata* Reed, 1944 from the upper Cisuralian Amb Formation of the Salt Range, Pakistan, originally described as *S.* (*Heteralosia*) *sublamellata* (see Fig. 4). Specimens from the early Changhsingian *Lazarevonia arcuata* Zone (Pija Member) in north central Nepal as recorded in Waterhouse (1983, p. 118, pl. 2, fig. 1, 2) and Waterhouse (2004, p. 73, pl. 2, fig. 2, 4: 2013, p. 213, Fig. 7.3 B, D) have a short hinge like that of *S. gerardi*, but the dorsal valve is less deeply concave. The claim that spines were finer (Briggs 1998) than in *gerardi* is not entirely correct, but spines are less crowded, and it appears that the species is distinct, though closely related to *gerardi*. Its dorsal exterior is comparatively free of tubercles and pits and shows no capillae, and subdued commarginal growth laminae cover the entire valve.

Many other taxa have been ascribed to *Strophalosia* and most differ in the nature of the ornament, including spacing and diameter of spines, and other detail of shape, and of course, most such generic placements were made before the appearance of the *Revised Brachiopod Treatise*, which discounted the presence of dorsal spines. A species *S. kharaedensis* Manankov, 1998, pl. 8, fig. 1a-g, 2) from Mongolia appears to be very close, allowing for the somewhat broken specimens and small scale of figures (Fig. 5). Manankov noted an approach to *Strophalosia pulchra* Lee, Gu & Li, 1983. The likely age would appear to be Capitanian.

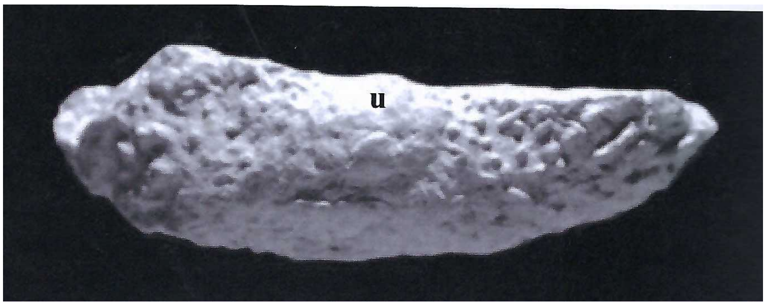


Fig. 3. *Strophalosia gerardi* King, posterior view of plaster cast BR 2068, x2, of holotype kept at National University of Ireland, Galway. u = ventral umbo. (Waterhouse 2013).

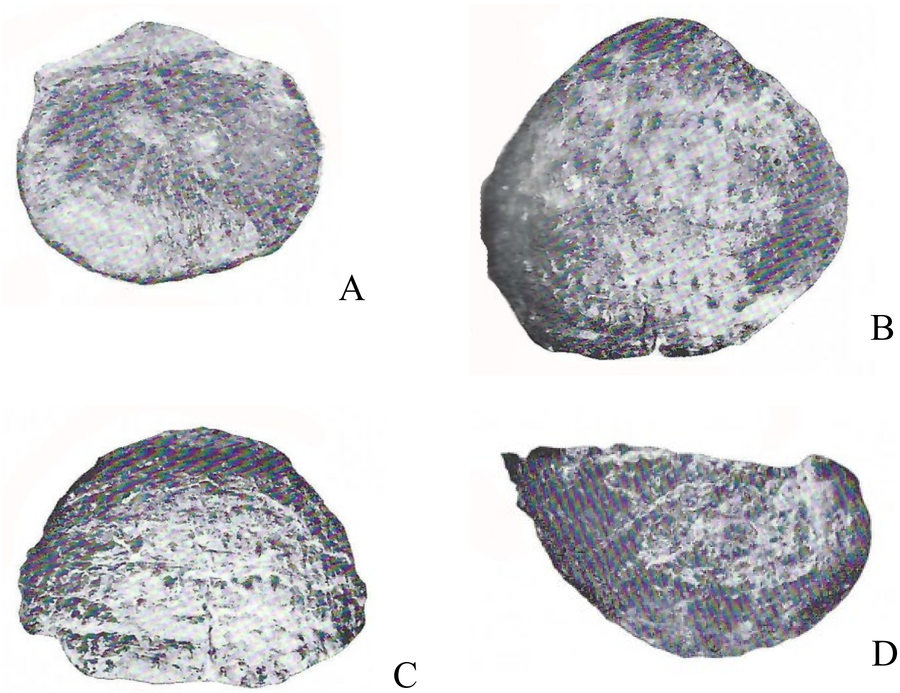


Fig. 4. *Strophalosia sublamellata* Reed, A, dorsal aspect of complete specimen, here nominated as lectotype. B, C, D, ventral, anterior and lateral aspects of specimen with valves conjoined. Specimens x 1.5, from Amb Limestone, Salt Range, Pakistan. (Reed 1944).

Fig. 5. *Strophalosia*? *kharaerdensis* Manankov, cast of ventral valve, from *Echinauris jisuensis* Zone, Mongolia, x1. (Manankov 1998).

Genus ***Crenalosia*** Waterhouse, 2010

Fig. 6

The type species is *Heteralosia paucispinosa* Cooper & Grant, 1975, a highly vaulted shell with large umbonal cicatrix surrounded by rhizoid spines, and thick erect or semi-recumbent ventral spines arising from ridges as a rule anteriorly. The dorsal valve lacks spines and is strongly crinkled and bears dimples and ridges. Several species from Texas belong to the genus (Waterhouse 2010, p. 48), including *Heteralosia magnispina* Cooper & Grant, 1975 and *H. tenuispina* Cooper & Grant, 1975 and probably arose from *Heteralosia*, to judge from the nature of the ventral spines.

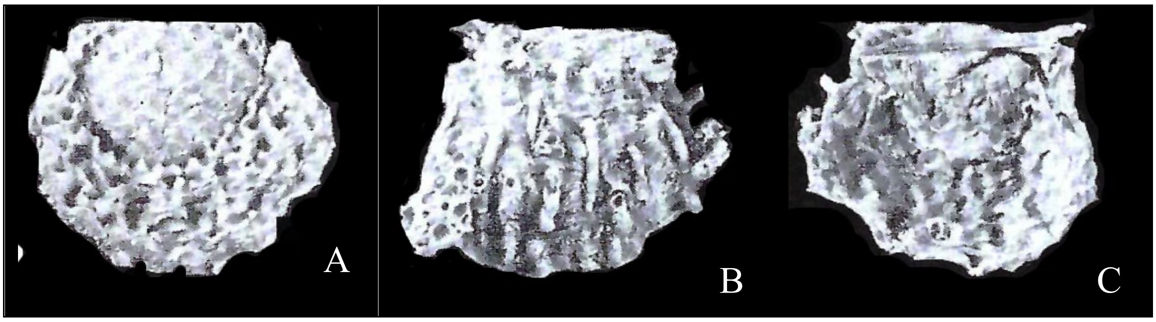


Fig. 6. A, *Crenalosia paucispinosa* (Cooper & Grant), dorsal aspect of specimen from Lamar Limestone, Bell Canyon Formation, Texas, x6. B, C, *Crenalosia magnispina* (Cooper & Grant), ventral and dorsal external aspects of specimen from Getaway Member, Cherry Canyon Formation, x4. (Cooper & Grant 1975).

Genus ***Fortispinalosia*** Waterhouse, 2013

Fig. 7

Fortispinalosia Waterhouse (2013, p. 215) is based on *Strophalosia fortispinosa* Hinchey & Ray, 1935 from the Warsaw Formation of Mississippian age in United States. Ventral spines consist of a predominant coarse and a subsidiary semirecumbent slightly sinuous series and finer scattered prostrate spines, with no elongate spine bases comparable to those of *Kufria* (see below) and more differentiated than those of *Strophalosia* or *Heteralosia*. The dorsal exterior shows short laminae and low elongate rises, with no capillae or dimples. The dorsal interior features short well-developed lateral buttress ridges that support the bifid cardinal process. The spines are not like those of *Strophalosia*, in having much more of a mix of spines, in two series, thick and thin, and the supporting ridges for the cardinal process are unusually prominent.

Other strophalosioid species featured by Hinchey & Ray (1935) and may be congeneric, but lack these buttress plates.

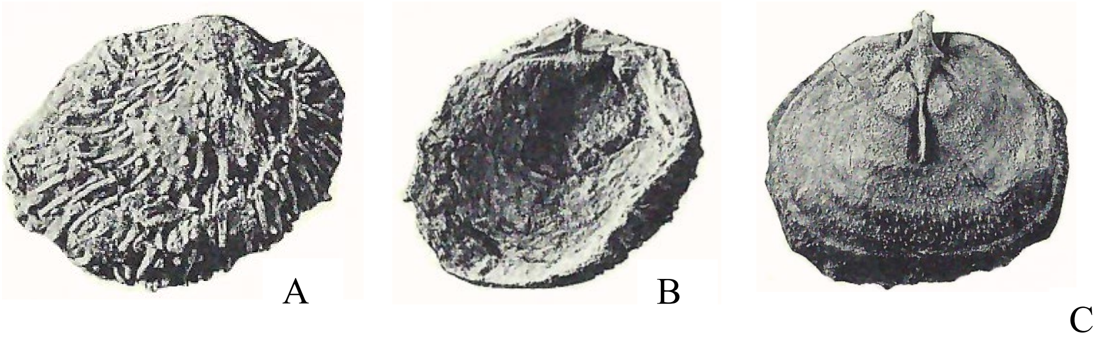


Fig. 7. *Fortispinulosia fortispinosa* Hinchey & Ray), formerly A, ventral valve. B, dorsal view of conjoined valves. C, dorsal interior. Specimens x3 from Warsaw Formation (Mississippian) of Missouri, United States. (Muir-Wood & Cooper 1960).

Genus ***Heteralosia*** R. H. King, 1938

Fig. 8

Heteralosia R. H. King, 1938 with type species *H. slocomi* King from the Graham Formation of Texas has been widely regarded as a synonym of *Strophalosia*, as reviewed by Briggs (1998, p. 66). Species of Carboniferous age have been assigned to the taxon, and do not seem to differ significantly from *Heteralosia*. The ventral spines in this genus are a little less regularly dispersed and possibly more irregular in diameter than in *Strophalosia*, and the spines are less crowded. The lamellate projections over the dorsal exterior have been judged not to be spines, because they do not form hollow tubes. Dorsal laminae with no dorsal dimples are much better developed than in type *Strophalosia*. Whether this is a subfamilial distinction remains open for assessment, but is regarded as doubtful. Muir-Wood & Cooper (1960, p. 80) proposed the subfamily Heteralosiinae and there are certainly differences in the ornament of both valves between the type species of *Strophalosia* and *Heteralosia*, here not deemed to be of subfamily or tribal ranking. Their proposal hinged on the belief that *Strophalosia* had dorsal spines. Whether the cardinal process differs critically in the two genera requires further study.

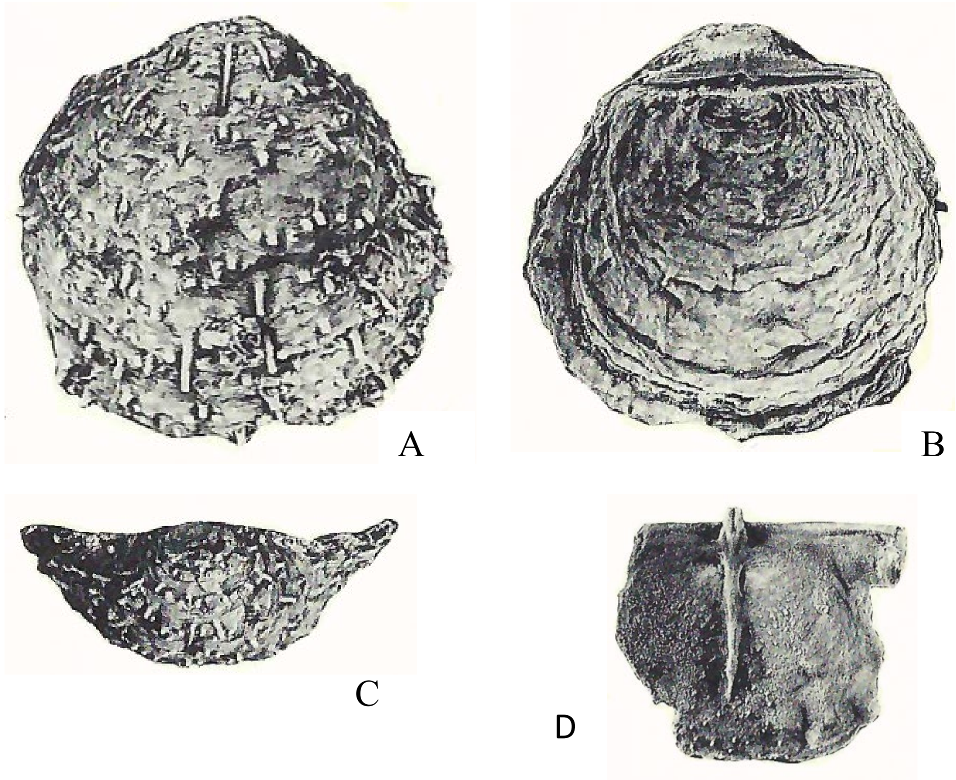


Fig. 8. *Heteralosia slocomi* R. H. King. A-C, ventral, dorsal and posterior aspects of specimen with valves conjoined. D, interior of dorsal valve, showing a bifid cardinal process. Specimens x3, from Wayland shale, Graham Formation, Texas. (Muir-Wood & Cooper 1960).

Genus ***Kufria*** Waterhouse, 2002

Fig. 9

1944 *Strophalosia blanfordi* Reed, p. 104, pl. 6, fig. 3, 3a
2002 *Kufria* Waterhouse, p. 53.

Diagnosis: Ventral valve spines arising at anterior end of swollen and elongate spine bases.

Holotype: *Strophalosia blanfordi* Reed, 1944, p. 104, pl. 6, fig. 3, 3a from uppermost Wargal or basal Chhidru Formation, Salt Range, Pakistan, OD.

Discussion: The holotype has an abraded dorsal valve, so that dorsal spinosity is not clear. Reed compared his species with a shell from Warcha, misidentified as *Productus abichi* (see also Reed 1931, pl. 3, fig. 4; Brunton 2007, Fig. 1771c, d) and Reed (1944, p. 104) also compared *blanfordi* with *Strophalosia gerardi* King. Other Salt Range species that appear to have somewhat comparable ventral ornament were described by Reed (1944) as *S. excavata remota* Reed and *S. salmunensis* Reed. For the latter species, Reed (1944, p. 106) recorded tubercles and pits and a smooth flat band of uniform width around the lateral and anterior margins for the dorsal valve. The problem remains: the scarcity of well-preserved let alone well-illustrated dorsal valves. The long spine bases suggest the possibility of placement within Aulostegidae, but Reed was well aware of such genera and did not favour such an alliance.

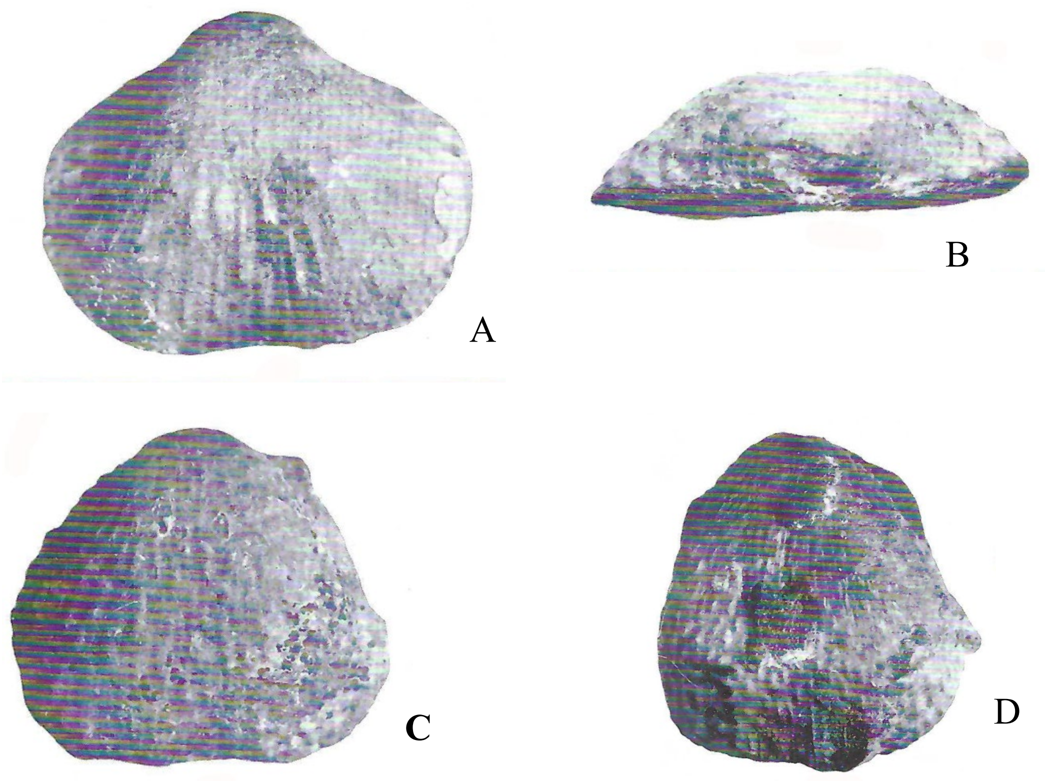


Fig. 9. *Kufria blanfordi* (Reed). A, B, ventral and posterior ventral aspects of holotype, x1.5, from Amb Limestone. C, *K. remota* (Reed) ventral aspect, from Wargal limestone, x2.5. D, *K. salmunensis* (Reed) from Chhidru Limestone, ventral aspect, x2. Specimens from Salt Range, Pakistan. (Reed 1944).

Tribe **FIMBRINIALOSIINI** new tribe

Name genus: *Fimbrinialosia* Waterhouse, 2013, p. 216 from Bap Formation (Asselian) of southern India, here designated.

Diagnosis: Dorsal valve without spines but with numerous dorsal pits in quincunx along commarginal rows.

Genus ***Baikuralia*** Waterhouse, 2013

Fig. 10

The designated type species *Strophalosia*? *bajkurica* Ustritsky in Ustritsky & Chernyak, 1963, p. 96 from the Baikur Suite of northeast Russia has dense comparatively uniform and fine ventral spines, and crowded slightly elongate dorsal dimples much denser and deeper than those of *Fortispinulosia* or *Fimbrianalosia*. *Krotovia tolli* Fredericks, 1931 and *Strophalosia*? *grandis* Tolmachov, 1912 from northeast Russia are congeneric.

Fig. 10. *Baikuralia bajkurica* (Ustritsky), x1. A, ventral valve. B, dorsal aspect of specimen with valves conjoined. C, dorsal exterior. From Omolon Suite, northeast Russia. (Sarytcheva 1977).

Genus ***Fimbrianalosia*** Waterhouse, 2013

Fig. 11, 12

Unlike *Strophalosia*, this genus has a wide hinge and well-developed dorsal capillae. with crowded ventral spines involving many that are sturdy and suberect, and others that are finer and more prostrate. The suggestion by Lee in Lee et al. (2023) that the genus was the same as *Strophalosia* is based on a misinterpretation of the ventral ornament, and Dr S. Lee has not examined any of the relevant specimens, including all those classed as *Fimbrinialosia* or indeed *Strophalosia*. The authority available to those who have never inspected the types at first hand seems tenuous, and details of ornament should be properly evaluated instead of dismissed as variable and of no significance. The ventral spines in *Strophalosia* are of more uniform diameter and lack the long prostrate spines. Dorsal capillae and dimples are much better developed in *Fimbriniaalosia* than in *Heteralosia, Fortispinulosa* or *Strophalosia*, and the set of thick spines tends to be semirecumbent and the set of prostrate spines tends to be subsinuous. The cardinal supports of *Fimbrinialosia* are much less prominent than in *Fortispinalosia.* The type species of *Fimbrianalosia* is *Strophalosia perfecta* Waterhouse &

Rao, 1989, p. 28 from the Bap Formation of Peninsula India, of Asselian age. Another and a rather similar species was described as *F. ettrainensis* Nazer & Waterhouse in Water-

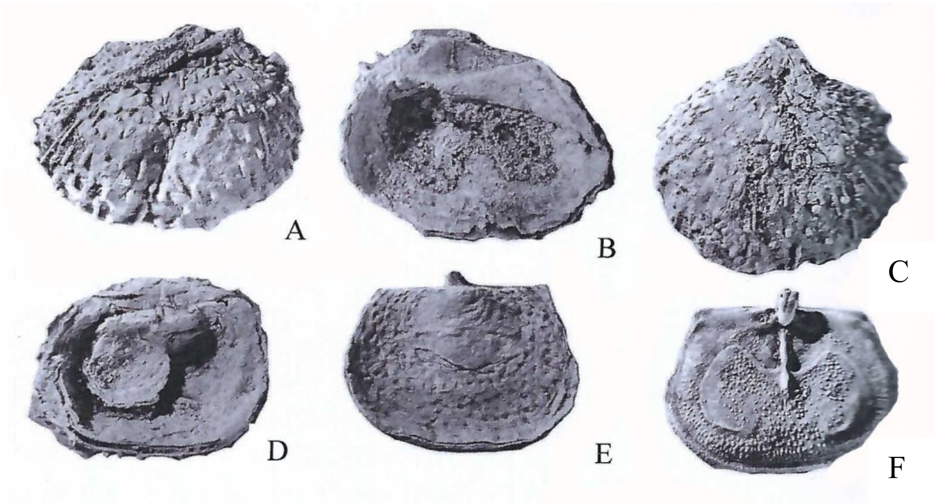


Fig. 11. *Fimbrianalosia perfecta* (Waterhouse & Rao). A, B, ventral and dorsal aspects of holotype. C, ventral valve. D, dorsal aspect with juvenile specimen attached. E, F, external and internal aspects of dorsal valve. Specimens x 2 from Bap Formation, India. (Waterhouse & Rao 1989).

house (2013, p. 216, Fig. 7.7, 7.8) from the Late Carboniferous part of the Ettrain Formation in the Yukon Territory, Canada, but for neither species is the nature of the cardinal process completely clear, though it seems to be most likely trifid.

Fig. 12. A, C, *Fimbrinialosia ettrainensis* Nazer & Waterhouse. A, ventral exterior. C, ventral internal mould. Note the absence of spine tunnels. Specimens x 2 from Kasimovian part of Ettrain Formation, Yukon Territory, Canada. B, *F. perfecta* (Waterhouse & Rao), exterior of dorsal valve x3. (Waterhouse 2013; Waterhouse & Rao 1989).

Genus ***Keoghalosia*** Waterhouse, 2010

Fig. 13

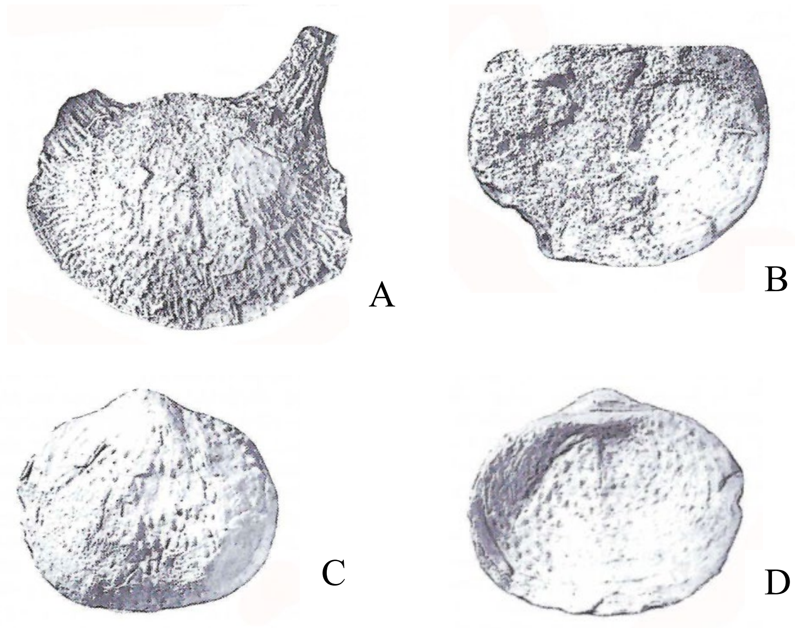


Fig. 13. *Keoghalosia onegumensis* Waterhouse. A, ventral valve holotype. B, dorsal exterior. From One Gum Formation, Carnarvon Basin, x1. C, D, *K. jimbaensis* (Archbold), ventral and dorsal aspects of holotype, x1. From Jimba Jimba Calcarenite, Carnarvon Basin, Western Australia. (Archbold 1986).

Keoghalosia is based on *K. onegumensis* Waterhouse, 2010, proposed for *Strophalosia* cf. *jimbaensis* [not Archbold] of Archbold (1986, p. 104, Fig. 2H-O) from the Carnarvon Basin of Western Australia. It is generically characterized by a brush of moderately thick ventral ear spines, reminiscent of that feature found in *Pseudostrophalosia* Clarke, 1970. Ventral spines are otherwise low angle recumbent to prostrate and closely spaced, with some finer prostrate spines. There are no dorsal spines, according to Archbold (1986). The dorsal valve appears to be closely and regularly dimpled, and the genus is close to *Bajkuralia* from northeast Russia (see pp. 64, 65), but has more crowded spines over the ventral ears. There are no ventral spine tunnels.

The closely related and better preserved *Strophalosia jimbaensis* Archbold, 1986 has similar ventral spines packed along commarginal rows and subuniform in diameter in the lower Artinskian of Western Australia. The dorsal valve is not thickened and is concave with a short trail, and its ornament diversified by numerous evenly distributed pits and fine capillae. The cardinal process has not been described.

Strophalosia diadema, a new genus?

Fig. 14

1983 *Strophalosia diadema* Waterhouse in Waterhouse & Gupta, p. 237, pl. 1, fig. 6-9, pl. 3, fig. 2-4.

Diagnosis: Characterized by relatively fine and closely spaced spines over the ventral valve, becoming sturdy anteriorly. Dorsal valve with conspicuous large dimples, no spines.

Discussion: A possible new genus is represented by *Strophalosia diadema* Waterhouse in Waterhouse & Gupta (1983, p. 237) from the *Lamnimargus himalayensis* Zone of Wuchiapingian age in the south Karakorum, for which the geology is described by Bhandari et al. 1983. Material is kept at Centre for Advanced Studies in Geology, Panjab University, Chandigarh, India, and figured in Waterhouse & Gupta (1983). This species shows well developed dorsal pits and wide hinge, and the dorsal valve is almost flat with short trail (Waterhouse & Gupta 1983, pl. 3, fig. 2; Waterhouse 2013, Fig. 7.3A, C). The ventral valve appears to have coarse anterior spines as well as rather fine closely spaced spines posteriorly, unusual in appearance (Waterhouse & Gupta (1983, pl. 3, fig. 3). But better figures and more material are required to justify the separation of a genus.

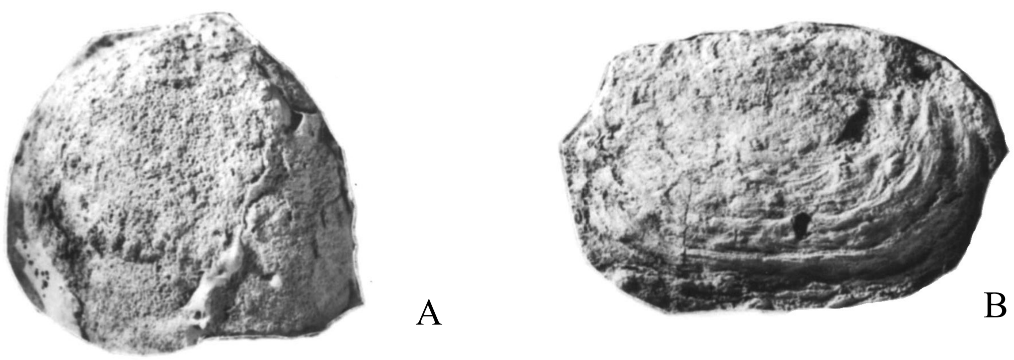


Fig. 14. *Strophalosia diadema* Waterhouse & Gupta. A, ventral valve, showing fine spines over much of disc. B, dorsal exterior, showing dimples, holotype. Specimens x2, from upper Shyok valley, southern Karakorum Range, kept at Centre for Advanced Studies in Geology, Panjab University, Chandigarh, India. (Waterhouse & Gupta 1983).

Subfamily **CRASSISPINOSELLINAE** new subfamily (see p. herein)

Diagnosis: Ventral spines subuniform, fine or sturdy. Dorsal valve thickened, may be wedge-shaped.

Discussion: This family group is limited to the Late Paleozoic faunas of Gondwana and is characteristic of Early Permian faunas in Australia, especially east Australia. Possibly it commenced in the Argentine during Late Carboniferous time with *Tupelosia* Archbold & Simanauskas, 2001, when the dorsal valve became thickened. *Tupelosia* has only a very short trail, without apparently developing a wedge shape for the dorsal valve.

Given that dorsal dimples are developed in *Crassispinosella* and *Strophalosiaria*, it would appear that the group may have evolved from Fimbrianialosiini (see above, p. 64). But *Tupelosia* Simanauska & Archbold which is included in the group shows only subfusc traces of dimples, and so may not have been related.

Genus ***Crassispinosella*** Waterhouse, 2013

Fig. 15 - 19

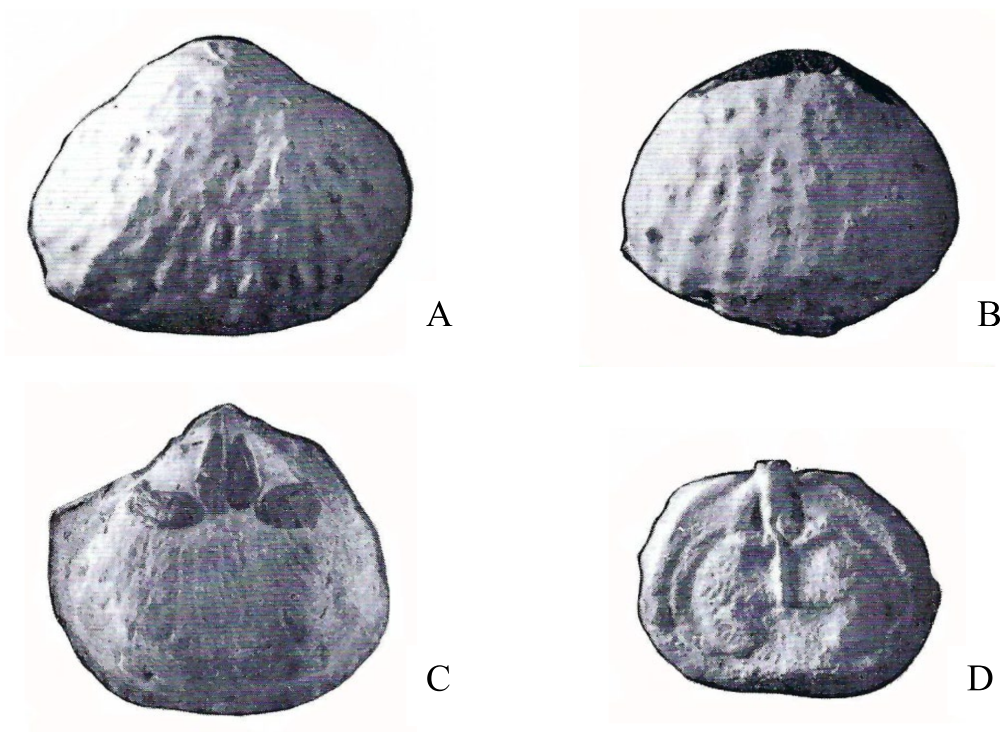


Fig. 15. *Crassispinosella subcircularis* (Clarke), Originally described as *Costalosia apicallosa* Clarke, 1969. A, TMF 35115, ventral aspect, x1.20. B, ventral valve TMF 3554, x1.40. C, ventral interior TMF 35113, x1.33. D, dorsal interior, TMF 3555, x1.33. From Glencoe Formation, Tasmania. (Clarke 1969).

Discussion: Based on the type species *Strophalosia subcircularis* Clarke, 1969, p. 22 from the Asselian Glencoe Formation of Tasmania, this genus is characterized by stout and well-spaced erect ventral spines, and deeply concave dorsal valve, bearing radial capillae and regularly spaced dimples. A myophragm lies between the ventral adductor scars.

Fig. 16. *Crassispinosella subcircularis* (Clarke), dorsal aspect of internal mould BR 3013 with valves conjoined, from Glencoe Formation, x1.5. (Waterhouse 2013).

The cardinal process is trifid. The genus is close in various respects to *Strophalosia*, which differs in having more crowded ventral spines, and lacking dorsal capillae and dimples and no wedge-like dorsal valve. Some specimens develop low radial rugae and these were recognized as *Costalosia* – later corrected to *Licharewiella* – *apicalosia* Clarke, 1969, 1992 and *L. brevicardinalis* Clarke (1990, 1992), but all were deemed to be conspecific and members of *Strophalosia* by Briggs (1998). What seems to be another variant was named *Wyndhamia* ? *irregularis* Clarke, 1969.

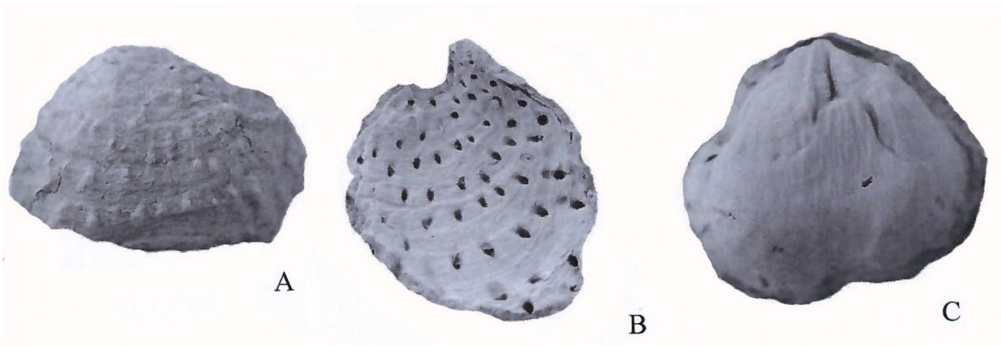


Fig. 17. *Crassispinosella subcircularis* (Clarke), ventral valves from Glencoe Formation, Tasmania, x1.5. A, ventral valve exterior BR 3014. B, ventral external mould BR 3011 showing spine bases, x2. C, ventral interior BR 3024 showing prominent myophragm, x2. The ventral spine pattern differs strongly from that of *Strophalosia* in its uniformity and regularity of distribution. (Waterhouse 2013).

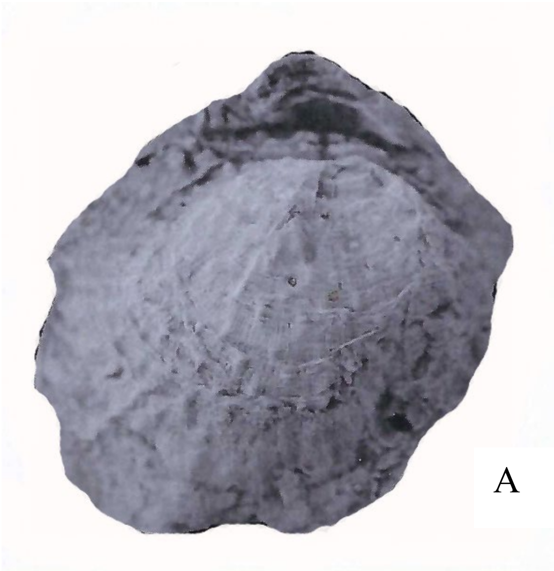
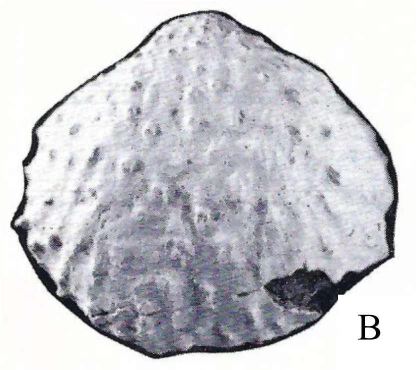
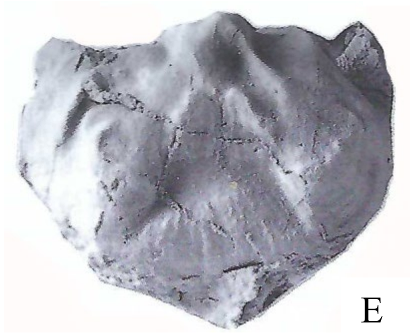


Fig. 18. *Crassispinosella subcircularis* (Clarke) from Tasmania. A, dorsal aspect of conjoined specimen BR 3016 x2 from Glencoe Formation. B, ventral exterior, TMF 3595, x1.3, from Glencoe Formation. C, latex cast of ventral valve, UQF 49044, x2, from upper Quamby or basal Golden Valley Group. D, E, ventral internal moulds UQF 65731 and 65733, x2, text not clear on source. (A, Waterhouse 2013, B, Clarke 1969; C-E, Briggs 1998).





Etherilosia calytrixi Archbold, 1995 from the Calytrix Formation of the Barbwire Terrace Formation in the Canning Basin of Western Australia, of basal Permian age, shows some approach but its spines are less regularly arranged (Waterhouse 2015, p. 33).

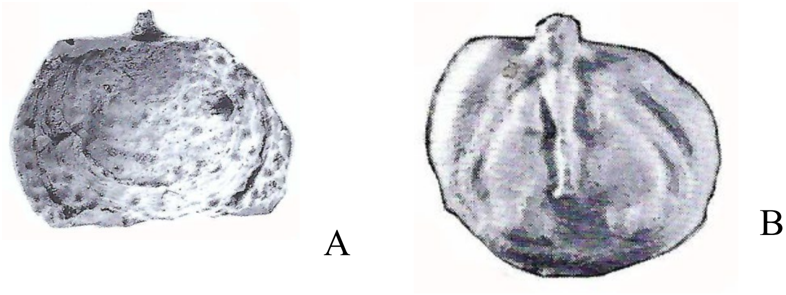


Fig. 19. *Crassispinosella subcircularis* (Clarke), dorsal valves. A, dorsal exterior AM 96218 from Alum Rock, New South Wales, x1.5. B, dorsal interior TM 35120 x 1.25 from Glencoe Formation, Tasmania. (Briggs 1998; Clarke 1969).

Genus ***Strophalosiaria*** Waterhouse, 2013

Fig. 20

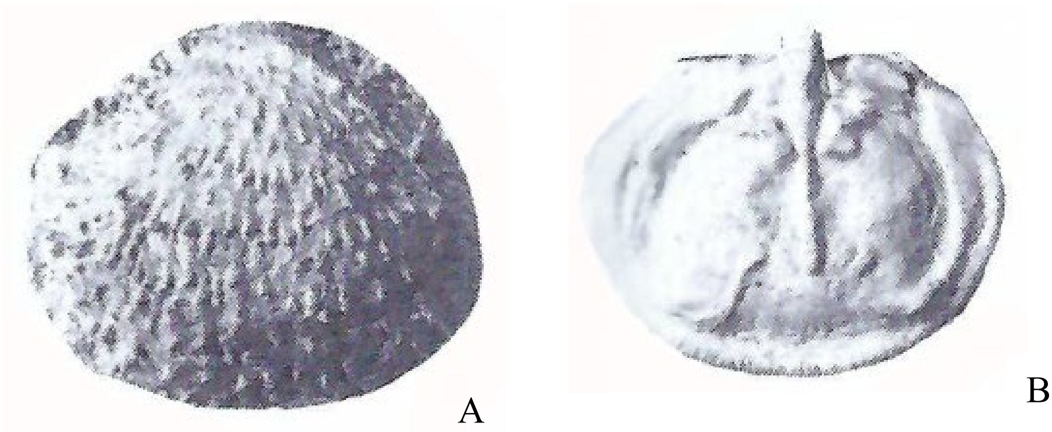


Fig. 20. *Strophalosiaria concentrica* (Clarke). A ventral exterior, GST 14113, x2. B, dorsal interior, GST 14117, x2. From Kansas Creek Formation, Tasmania. (Clarke 1992).

The species described as *Strophalosia concentrica* Clarke, 1990 from the Kansas Creek Formation of Asselian age in Tasmania is like the slightly younger *Crassispinosella subcircularis* Clarke, in having a wedge-shaped dorsal valve. The ventral spines are fine, suberect and closely spaced, but not entirely uniform, involving mostly fine spines, mixed with some that are thicker. There are dorsal dimples and capillae. It may be argued that the difference in spine densities between that of *Crassispinosella* and *Strophalosiaria* is of specific rather than generic ranking, although on the whole, in view of diversity found in members of the much more numerous Echinalosiidae, two genera seem more likely. But this remains open for further examination.

Genus ***Tupelosia*** Archbold & Simanauskas, 2001

Fig. 21

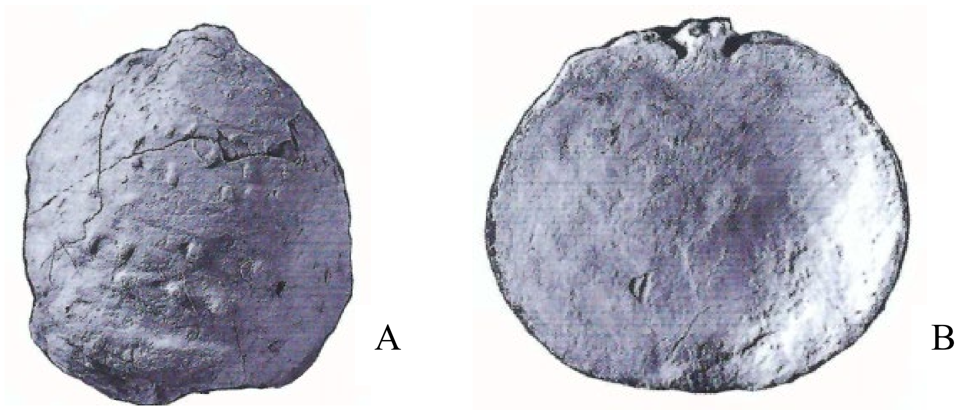


Fig. 21. *Tupelosia paganzoensis* Archbold & Simanauskas. A ventral exterior. B, C, external and internal aspects of dorsal valve holotype. Specimens x3, from Tupe Formation, Argentine. (Archbold & Simanauska 2001).

Tupelosia as based on type species *T. paganzoensis* Archbold & Simanauskas, 2001, p. 222 comes from the Tupe Formation of the Paganzo Basin of Argentine and is highly distinctive with narrow hinge, short dorsal septum, and thickened dorsal valve without a free-standing trail, not showing capillae or dimples, though wear may have been involved. Ventral adductors are raised, long and smooth. Archbold & Simanauskas (2001, p. 223) stated that there were no dimples, and that the cardinal process was weakly bilobed. The age of the Tupe Formation appears to be Late Carboniferous, although Cisterna et al. (2002), Archbold et al. (2004) and Taboada (2010) regarded the age as Asselian. But the type species lies well below the first entry of the critical palynomorph *Converrucosporites confluens* (Archangelsky & Garnerro), of basal Asselian if not slightly greater age (Stephenson 2009), and Cesari et al. (2011) recorded Moscovian radiometric values. Argentine material identified as *Heteralosia cornelliana* [not Derby] from the Quebrada Largo, Rio Blanco, San Juan by Antelo (1972, p. 164, pl. 2, fig. 1-5) has a gently concave dorsal valve and may prove to belong to *Tupelosia*. The Tupe species described as *Coronalosia argentinensis* Archbold & Simanauskas (2001, Fig. 3A-N, 4A-F) shows considerable approach in some respects to *Tupelosia*, and the species certainly does not belong to *Coronalosia*, because there appears to be no sign of the ventral hinge row of strong spines typical of this genus, as figured in Cisterna et al. (2002, Fig. 7A-E). The Cisterna et al. (2002, Fig. 7D) specimens are shaped like *Crassispinosella* of Tasmania.

Genus ***Etherilosia*** Archbold, 1993

Fig. 22

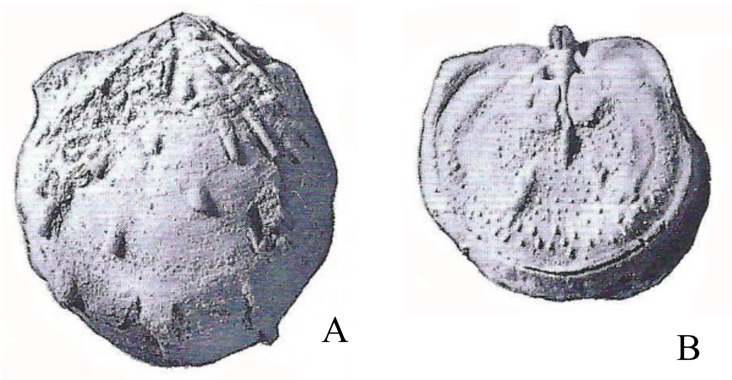


Fig. 22. *Etherilosia etheridgei* (Prendergast) from Callytharra Formation, Western Australia, A, ventral valve, x3.5. B, dorsal interior, x4.5. (Archbold 1986).

Based on *Strophalosia etheridgei* Prendergast (1943, p. 43, pl. 5, fig. 5-12) from the Callytharra Limestone of the Basin in Western Australia, this genus is small with relatively coarse and well-spaced ventral spines, and only gently concave and thickened dorsal valve. es and the dorsal valve is thin and deeply concave. Some individuals amongst the type species *etheridgei* and in *E, prendergastae* Archbold, 1993 have a row of fine ventral hinge spines, as if derived from *Coronalosia*, unless they are indicating a new development within Crassispinosellinae. Some specimens have only a few coarse hinge spines, few in number (Archbold 1986, pl. 3, fig. 5), and others have none (Archbold 1986, pl. 3, fig. P, V). Perhaps the hinge spines developed independently of Coronalosiinae, a matter requiring further enquiry.

REFERENCES

ANTELO, B. 1972: Los brachiopodas del Carbonifero superior de la Quebrada Larga, en las cabeceras del Rio Blano, Provincia de San Juana. Ameghiniana 9 (2): 159-172.

ARCHBOLD, N. W. 1986: Studies on Western Australian Permian brachiopods 6. The genera *Strophalosia* King, 1844, *Heteralosia* King, 1938 and *Echinalosia* Waterhouse, 1967. Proc. Roy. Soc. Victoria 98: 97-119.

_____ 1987: Studies on Western Australian Permian brachiopods 7. The strophalosiid genera *Wyndhamia* Booker, 1929, *Lialosia* Muir-Wood and Cooper, 1960 and *Liveringia* gen. nov. Proc. Roy. Soc. Victoria 99: 19-35.

_____1993: Studies on Western Australian Permian brachiopods 11. New genera, species and records. Proc. Roy. Soc. Victoria 105: 1-29.

_____1995: Studies on Western Australian Permian brachiopods 12. Additions to the late Asselian-Tastubian faunas. Proc. Roy. Soc. Victoria 107: 95-112.

ARCHBOLD, N. W., CISTERNA, G., SIMANAUSKAS, T. 2004: The Gondwana Carboniferous-Permian boundary revisited: new data from Australia. Gondwana Research 7: 125-133.

ARCHBOLD, N. W., SIMANAUSKAS, T. 2001: New Strophalosiidae (Brachiopoda) from the early Permian of Argentina. Proc. Roy. Soc. Victoria 113: 217-227.

BHANDARI, A. K., GUPTA, V. J., AHLUWALIA, A. D., SEIMAL, N., CHAKRABORTY, S. K. 1983: Permian Fusulinids from Karakroum Region, Ladakh Himalaya, India. Contrib. Himal. Geol. 2: 33-38, 3pl.

BEECHER, C. E. 1890: North American species of *Strophalosia*. Amer. J. Sci. (ser. 3) 40: 240-246, pl. 9.

BRIGGS, D. J. C. 1998: Permian Productidina and Strophalosiidina from the Sydney-Bowen Basin and the New England orogen: systematics and biostratigraphic significance. Mem. Assoc. Aust'asian Palaeont. 19: 258p.

BRUNTON, C. H. C. 1966: Silicified productoids from the Viséan of County Fermanagh. 11. Bull. Brit. Mus. (Nat. Hist.) Geol. 12 (5): 173-243, pl. 1-19.

_____ 2007: Productidina. Strophalosiidina. *In* P. A. Selden (ed.). Treatise on Invertebrate Paleontology, Part H, Brachiopoda revised, vol. 6 Supplement: 2639-2676. Geol. Soc. Amer., Univ. Kansas; Boulder, Colorado & Lawrence, Kansas.

BRUNTON, C. H. C., LAZAREV, S. S., GRANT, R. E., JIN YUGAN 2000: Productidina. [Includes Strophalosiidina, except for Richthofenioidea]. *In* R. L. Kaesler (ed.). Treatise on Invertebrate Paleontology, Part H, Brachiopoda revised, vol. 3, Linguliformea, Craniiformea, and Rhynchonelliformea part: 442-609. Geol. Soc. Amer., Univ. Kansas; Boulder, Colorado & Lawrence, Kansas.

CESARI, S. N., LIMARINO, C. A., GULBRANSON, E. L. 2011: An Upper Paleozoic bio-chronostratigraphic scheme for the western margin of Gondwana. Earth-Science Reviews 106 (2011): 149-160.

CISTERNA, G. A., SIMANAUSKAS, T., ARCHBOLD, N. W. 2002: Permian brachiopods from the Tupe Formation, San Juan Province, Precordillera, Argentina. Alcheringa 26: 177-200.

CLARKE, M. J. 1969: Tasmanian Strophalosiidae. Tasmanian Dep. Mines, Geol. Surv. Rec. 10: 1-51, 8pl.

_____ 1970: A new Permian strophalosiid brachiopod genus from eastern Australia. J. Paleont. 44: 986-987.

_____ 1990: Late Palaeozoic (Tamarian: Late Carboniferous - Early Permian) cold-water brachiopods from Tasmania. Alcheringa 14: 53-76.

_____ 1992: Hellyerian and Tamarian (Late Carboniferous - Lower Permian) invertebrate faunas from Tasmania. Bull. Geol. Surv. Tasmania 69: 1-52.

COOPER, G. A., GRANT, R. E. 1975: Permian brachiopods of west Texas. 111. Smithson. Contrib. Paleobiol. No. 19: 795-1298, pl. 192-502.

DUNBAR, C. O., CONDRA, G. E. 1932: Brachiopoda of the Pennsylvanian System in Nebraska. Nebraska Geol. Surv. Bull. (ser. 2) 5: 1-377, 44pl.

FREDERICKS, G. 1931: The Upper Paleozoic fauna of Kharaulakh Mountains. Akad. Nauk SSR. Otdel. Mat. Estestven. Nauk, Izvest. 2: 199-228, 4pl. [Russ.]

HINCHEY, N., RAY, L. L. 1935: New Mississippian species of *Strophalosia* from Missouri. J. Paleont. 9: 247-250, pl. 25.

IMBRIE, J. 1959: Brachiopods of the Traverse Group (Devonian) of Michigan. Part 1. Dalmanellacea, Pentameracea, Strophomenacea, Orthotetacea, Chonetacea and Productacea. Amer. Mus. Nat. Hist. Bull. 116 (4): 349-409, pl. 48-67.

KING, R. H. 1938: New Chonetidae and Productidae from Pennsylvanian and Permian strata of north-central Texas. J. Paleont. 12: 257-279, pl. 36-39.

KING, W. 1844: On a new genus of Palaeozoic shells. Ann. Mag. Nat. Hist. (ser. 1) 14: 313-317.

_____1850: A monograph of the Permian fossils of England. Palaeont. Soc. Mon. 3: xxxvii + 258p, 29pl.

LEE LI, GU FENG, LI MEN-GUO 1983: Early Permian productids from Xi Ujmgin Gi, Nei Mongol Autonomous. Prof. Pap. Strat. Paleont. Beijing: 11: 71-78. Geol. Publ. Hosde.

LEE, SANGMIN, SHI, G. R., RUNNEGAR, B. W., WATERHOUSE, J. B. 2023: Kungurian (Cisuralian/Early Permian) brachiopods from the Snapper Point Formation, southern Sydney Basin, southeastern Australia. Alcheringa: 47: 62-108.

MANANKOV, L. N. 1998: Late Permian Productida (Brachiopoda) from southeastern Mongolia. Paleont. Zhurn. 5 1998: 49-55. [Russ.]

MUIR-WOOD, H. M., COOPER, G. A. 1960: Morphology, classification and life habits of the Productoidea (Brachiopoda). Geol. Soc. Amer. Mem. 81: 1-447, 135pl.

PRENDERGAST, K. L. 1943: Permian Productinae and Strophalosiinae of Western Australia. J. Roy. Soc. West. Aust. 28: 1-73, 6pl.

REED, F. R. C. 1931: New fossils from the Productus limestones of the Salt Range. Palaeont. Indica (n. s.) 17: 1-56, pl. 1-8.

_____1944: Brachiopoda and Mollusca of the Productus limestones of the Salt Range. Palaeont. Indica 23 (1): 1-678, 65pl.

SCHUCHERT, C. 1913: Class 2. Brachiopoda. *In* ZITTEL, K. A. von Text-book of Paleontology, vol. 1, part 1, 2nd ed., translated and edited by C. R. Eastman: 355-420, fig.

526-636. MacMillan & Co. Ltd, London.

STEPHENSON, M. H. 2009: The age of the Carboniferous-Permian *Converrucosporites confluens* Oppel Zone: new data from the Ganigobis Shale member (Dwyka Group) of Namibia. Palynology 33: 167-177.

TABOADA, A. C. 2010: Mississippian-Early Permian brachiopods from western Argentina: tools from middle- to high-latitude correlation, biogeographic and paleoclimatic reconstruction. Paleogeog. Paleoclim. Paleoecol. 298 (2010): 152-173.

TOLMACHOFF, I. P. 1912: Materials for understanding of the Paleozoic beds of north-east Siberia. Tr. Geol. Mus. 6 (5): 123-150, pl. 4, 5. [Russ.].

USTRITSKY, V. I., CHERNYAK, G. E. 1963: Biostratigraphy and brachiopods of the Upper Paleozoic of Taimyr. Tr. Nauchno-Issled Geol. Arkt. Inst. (NIIGA) 134: 139p., 47pl. [Russ.]

WATERHOUSE, J. B. 1964: Permian brachiopods of New Zealand. N. Z. Geol. Surv. Paleont. Bull. 35: 1-288, 37pl.

_____1983: Permian brachiopods from Pija Member, Senja Formation, in Manang District of Nepal, with new brachiopod genera and species from other regions. Bull. Ind. Geol. Assoc. 16: 111-151, pl. 1-8.

_____ 2002: The stratigraphic succession and structure of Wairaki Downs, New Zealand, and its implications for Permian biostratigraphy of New Zealand and marine Permian of eastern Australia and Gondwana. Earthwise 4: 1-260.

_____2004: Some new subfamilies, genera and species of Suborder Productidina (Brachiopoda). Earthwise 7: 1-46.

_____ 2010: New Late Paleozoic brachiopods and molluscs. Earthwise 9: 1-134.

_____ 2013: The evolution and classification of the Productida. Earthwise 10: 1-535.

_____ 2015: Early Permian Conulariida, Brachiopoda and Mollusca from Homevale, central Queensland. Earthwise 11: 1-390.

WATERHOUSE, J. B., GUPTA, V. J. 1983: A faunule from the *Lamnimargus himalayensis* Zone in the upper Shyok Valley, southern Karakorum Range. Contrib. Himal. Geol. 2: 234-245, 3pl.

WATERHOUSE, J. B., RANGA RAO, A. 1989: Early Permian brachiopod and molluscan species from the Bap Formation of Peninsula India. Paläont. Zeit. 63 : 25-39, 7 fig.

INDEX

Selected index for family groups, genera and species highlit in the text.