PERMIAN GENERA AND SPECIES
OF STROPHALOSIIDINA (BRACHIOPODA) FROM
EAST AUSTRALIA AND NEW ZEALAND

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Contents

[Some titles abbreviated]

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

PREFACE

This study summarizes the occurrences of the major brachiopod suborder Strophalosiidina in Permian deposits of east Australia and New Zealand, for families, subfamilies and tribes, species by species, with synonymy, diagnosis, holotypes and neotypes, morphological distinctions and stratigraphic range, together with facets that require further clarification. Overall procedure is to provide a diagnosis for the family group, followed by discussion with figures for the nominate genus and its constituent species, then discussion of related genera ordered alphabetically, and their constituent species. The species within each genus are ordered by stratigraphic occurrence as a rule, starting with the oldest species, apart from a few exceptions. 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 to save repetition.

Synonymies are attempted, but it is not easy to deal with some of the earlier proposed taxa, given uncertainties over the stratigraphic and even geographic source, and for some forms, the subsequent loss of even the figured specimens, a problem that besets not only some early descriptions of the nineteenth century, but even a recent monograph published just before the close of the twentieth century. (See last article in the text). Useful and indeed critical catalogues of type material kept at institutions, as by Crespin (1964), Fletcher (1971) and Parfrey (1996) are set aside. Also minor reports of genera unidentified to species are mostly omitted.

A few illustrations are provided for each taxon, to facilitate comparison and differentiation between species. There are problems over some illustrations. Photographs do much to help reinforce the published descriptions and diagnosis, but may still be wanting in critical detail. The illustrations are the best available to me, reproduced by rescanning published photographs, not all of which are satisfactory, and are duely credited. In some cases, printing was poor, especially up to the 1990's with publishers apparently unable or unwilling to afford the costs of reasonable reproduction, a restriction all too often imposed by poverty of funding by government. And even today, there are a few authors who persist in providing dismal original photographs marked by poor lighting and inadequately enlarged, though fortunately these authors are becoming increasingly rare. Some specimens, though of great interest and importance, are not well preserved, or have a very obscure morphology, but nonetheless are significant. Some – even a number – of species await the discovery of further and better-preserved material, so that obscure species provide a challenge for further work. It is deplorable that even contributors to the *Revised Brachiopod Treatise* (2007, p. 2781) should imply that the recognition of genera should depend on published illustrations. Not so. Genera depend on actual specimens, not on illustrations. Paleontologists may prefer to rely only on illustrations and descriptions, especially those who are financially constrained or restricted for other reasons, but that is an unreliable methodology, even though currently as in the nineteenth century, many workers do not visit museums and check specimens at first hand.

But without spending time at the great institutions, such as the Smithsonian Institute of Washington D.C., the American Museum of Natural History, New York, the Geological Survey of Canada at Ottawa, the Museum of Natural History in London, the Sedgwick Museum at Cambridge, the Paleontological Institute at Moscow, the Tschernyschew Museum at St Petersburg, the Geologisches Bundesanstahlt at Vienna, the Geological Survey of India at Kolkata and the institutions at Nanjing and Beijing, to mention some of the most critical centres, the study by paleontologists on Permian fossils is likely to prove an incomplete construct of human thoughts, insights and errors and fantasies, deeply inadequate, with at best an erratic relevance to actual brachiopod fossils. And of course, for the present project, the institutions in east Australia, mentioned below as Repositories, and including centres in New Zealand. As well, the Museum of Natural History in London and Sedgwick Museum at Cambridge and Smithsonian Institution at Washington D. C. which hold Australian fossils have to be regarded as critical. Even that modest number of repositories seem to have been beyond the aspirations of some practitioners.

There is an unusual aspect to the present study. Throughout the history of paleontology, most students do not revisit their earlier work in other than a minor way. G. A. Cooper, surely one of the greatest of paleontologists, moved from massive faunal study to massive faunal study, usually each from a different period. But without in any way being able to emulate the great G. A. Cooper, I have taken a different path, focusing mostly on Permian faunas, and concentrating as far as brachiopods are concerned, substantially on faunas from east Australia and New Zealand, reinforced by work on faunas from Arctic Canada, as well as the Himalaya and also Thailand. This has meant revisiting earlier work, again and again, to reveal previous inadequacies, and outright errors. These I try to show clearly, through synonymies. There have had to be corrections. Some were due to the collection of new faunas, or to improved study by various authors – including me on occasion – and being influenced and corrected by especially the major works as in the *Revised Brachiopod Treatise* and the massive study of Glass Mountains brachiopods by G. A. Cooper and R. E. Grant, and outstanding monographs especially by Russian authorities. The present study owes so much to some outstanding paleontologists who worked on Permian faunas in east

Australia. The remarkable R. Etheridge Jnr was followed, just before and overlapping with me by two inspiring workers, W. G. H. Maxwell and K. S. W. Campbell, who in the 1950's and 1960's set a remarkably high standard, in their fields not even excelled by G. A. Cooper. I would hope that in my work, I follow the lead of these students in focusing on the specimens, not on the publications, let alone reputations, or slavish adherence to whatever was understood by the writers of the *Revised Brachiopod Treatise*. The fact that I have had to change my conclusions from time to time of course makes my work suspect. But that is better than pretending all earlier work was and is infallible, even to the point of lying about it, as regrettably has proven to be the case for some authors.

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 another institution are mentioned, involving **GSQ**, Geological Survey of Queensland, also stored at the Queensland Museum at Hendra, Brisbane, together with Queensland Museum material, **QM.** In New South Wales, repositories include **AMF** for Australian Museum, Sydney; **ANU** Australia National University, Canberra, ACT; **CPC** – now **AGSO**, former Bureau of Mineral Resources – at Canberra ACT; **MM** Mining Museum, Sydney; **SUP** Department of Geology, Sydney University; **UNE** Department of Geology, University of New England, Armidale, with material transferred to the Australian Museum. For Victoria, **MVP** Museum of Victoria, Melbourne. In Tasmania; **TM** Tasmanian Museum, Hobart; **TMF** Geological Survey of Tasmania, Hobart; **UT** Department of Geology, University of Tasmania, Hobart, and for Western Australia, **UWA** University of Western Australia, Perth. New Zealand repositories involve **CM** Canterbury Museum, Christchurch; **OU** Department of Geology, Otago University, Dunedin; and **BR** for brachiopods kept at the Institute of Nuclear and Geological Sciences, Lower Hutt. From further afield, **BMNH** and **BB** refer to collections at the Museum of Natural History, London, and **SM** to the Sedgwick Museum, Cambridge, England; **GSC** Geological Survey of Canada, Ottawa, Canada; **PIN** Paleontological Institute, Moscow, Russia, and **USNM** United States National Museum, Washington D. C., USA.

ACKNOWLEDGEMENTS

Throughout this series of studies, Kristen Spring at the Queensland Museum (Bulk Storage, Brisbane) has provided advice over locality details and registration numbers. This has not always been a straightforward matter, because of confusion and even replication or duplication of numbers, requiring much patience, and her help is acknowledged with gratitude. Marianna Terezow at GNS in Lower Hutt, New Zealand, has also readily helped over the registration of type specimens from New Zealand. I have also received help from time to time from Dr Sangmin Lee and Prof. Guang Shi at the University of Wollongong in New South Wales. For one study that appears in this volume of Earthwise, I have drawn on a B. Sc. Honours thesis by Dr D. J. C. Briggs. This thesis provides some illuminating photographs of the dorsal interior of what he called aulostegids and I have reused and credited these photographs. Unfortunately I have been unable to get in touch with him – no one that I have approached now knows his present whereabouts, but all agree he has now abandoned Paleontology.

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WATERHOUSE, J. B. 2022: Description of some Early Permian and mostly Middle Permian Conulariida, Brachiopoda and Mollusca from east Australia, chiefly the Bowen Basin of Queensland. Earthwise 20.

STROPHALOSIARIA, CRASSISPINOSELLA AND *CAPILLARIA*, STROPHALOSIIDIN GENERA FROM THE PERMIAN OF EAST AUSTRALIA AND NEW ZEALAND

Abstract

Species of the brachiopod genera *Crassispinosella, Strophalosiaria* and *Capillaria* are described from east Australia and New Zealand. The first two genera belong to Strophalosiidae, with only ventral spines, and for *Capillaria*, species are characterized by a row of hinge spines, spines over both valves, and at least n some species, radial capillae over the dorsal valve.

SYSTEMATICS

Suborder STROPHALOSIIDINA Waterhouse, 1975

Hyporder STROPHALOSIIDEI Waterhouse, 1975

Superfamily **STROPHALOSIODEA** Schuchert, 1913

Family **STROPHALOSIIDAE** SCHUCHERT, 1913

Subfamily **CRASSISPINOSELLINAE** Waterhouse, 2013

[Crassispinosellinae Waterhouse 2023, p. 27]

Diagnosis: Spines limited to ventral valve, often few well-spaced and robust. Dorsal valve thick and may be wedge-shaped.

Discussion: Two species from Tasmania that belong to this family provide the key species for the two oldest Permian macrofaunal zones for east Australia. Both were named by Clarke (1990, 1992), who not only described the species but provided a comprehensive insight into the full accompanying faunas, with attention to other brachiopods and to Mollusca.

Genus ***Strophalosiaria*** Waterhouse 2013

Diagnosis: Spines closely spaced over ventral valve and semi-recumbent, rarely erect, vary somewhat in diameter and spacing. Brachial shields large. Dorsal dimples and capillae.

Type species: *Strophalosia concentrica* Clarke, 1990 from Tasmania, OD.

Strophalosiaria concentrica (Clarke, 1990)

Fig. 1

1990 *Strophalosia concentrica* Clarke, p. 60, Fig. 5H-R.
1992 *S. concentrica* – Clarke, p. 16, Fig. 5H-R.
1998 *S. concentrica* – Briggs, p. 67, Fig. 36A-C.
2013 *Strophalosiaria concentrica* – Waterhouse, p. 220.
2014 *Strophalosia concentrica* – Cisterna & Shi, p. 536, Fig. 5.1, 5.2.
2023 *Strophalosiaria concentrica* Waterhouse, p. 74, Fig. 20.

Diagnosis: As for genus.

Holotype: GST 14112 from middle part of Kansas Creek Formation, Tasmania, figured by Clarke (1990, Fig. 5I; 1992, Fig. 5I) and herein as Fig. 1A, OD.

Morphology: A good selection of specimens were figured by Clarke (1990) and repeated in 1992. Dorsal valves have dimples and at least traces of radial capillae, and bthe ventral valve lacked spine tunnels.

Stratigraphy: The species is found widely in Tasmania in what Clarke (1990) termed the rocks of Early Tamarian age, with stratigraphic detail added in Clarke (1992, p. 13). Nillsen (1982) discovered what was determined to be the same species in the lower Wasp Head Formation of the southern Sydney Basin, as endorsed by Cisterna & Shi (2014).

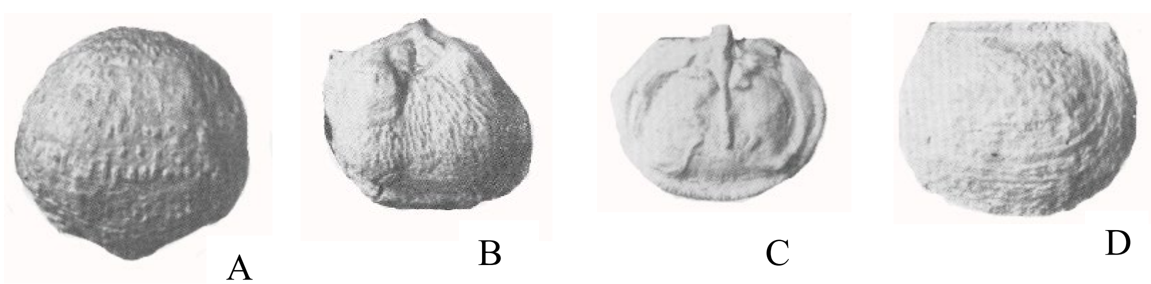

Fig. 1. *Strophalosiaria concentrica* (Clarke). A, ventral valve GST 14112, holotype. B, ventral interior, GST 14115. C, dorsal interior, GST 8272. D, dorsal exterior, GST 14118. From Glencoe Formation, except D from basal Bundella Formation, Tasmania, all x1. (Clarke 1990).

Genus ***Crassispinosella*** Waterhouse, 2013

Diagnosis: Ventral spines stout and subuniform, well-spaced, no dorsal spines. Dorsal valve thickened but externally concave.

Type species: *Strophalosia subcircularis* Clarke, 1969 from Glencoe Formation, Tasmania, OD.

Discussion: Ventral spines are stronger and better spaced than in *Strophalosia* King, and are comparatively uniform. The dorsal valve of *Crassispinosella* is capillate and dimpled unlike *Strophalosia*, and although thickened is more concave than *Strophalosiaria*.

Crassispinosella subcircularis (Clarke, 1969)

Fig. 2

1969 "*Strophalosia* cf. *gerardi*" [not King] – Brunton, p. 188, pl. 1, fig. 5, 6.
1969 *S. subcircularis* Clarke, p. 22, pl. 1, fig. 1-8, pl. 2, fig. 1-8, pl. 3, fig. 1-8, pl. 4, fig. 1-9, text-fig. 4, 6 (1), 7, 11 (1-6), 15 (4).
1969 *S. subcircularis tumida* Clarke, p. 27, pl. 5, fig. 1-4, text-fig. 5.
1969 *S. subcircularis brevicardinalis* Clarke, p. 28, pl. 6, fig. 1, 24, text-fig. 6.2-4.
1969 *Costalosia apicallosa* Clarke, p. 37, pl. 6, fig. 9-11, pl. 7, fig. 1-8, text-fig. 11.7, 8, 13, 15.5.
1969 *Wyndhamia irregularis* Clarke, p. 45, pl. 4, fig. 5-8, text-fig. 16.
1990 *S. subcircularis* – Clarke p. 58, Fig. 5A-G.
1990 *Licharewiella apicallosa* – Clarke, p. 61, Fig. 6A-H.
1992 *S. subcircularis* – Clarke, p. 16, Fig. 5A-G.
1992 *Licharewiella apicallosa* – Clarke, p. 16, Fig. 6A-H.
1998 *S. subcircularis* – Briggs, p. 69, Fig. 36D-L.
2013 *Crassispinosella subcircularis* – Waterhouse, p. 218, Fig. 7-10.
2014 *S. subcircularis* – Cisterna & Shi, p. 537, Fig. 5.3-5.5.
2023 *Crassispinosella subcircularis* – Waterhouse, p. 28ff, Fig. 15, p. 71, Fig. 15-19.

Diagnosis: Medium-size suboval and weakly transverse shells with concave dorsal valve thickened into wedge, ventral spines subuniform, well-spaced, stout and erect.

Lectotype: GST 3545 figured by Clarke (1969, pl. 4, fig. 1, 2; 1992, Fig. 5E) from Glencoe Formation, Tasmania, SD Clarke (1990, p. 59 caption).

Morphology: The species has been profusely illustrated by Clarke (1969, 1990, 1992) and Waterhouse (2013, 2023).

Stratigraphy: This species is found widely in a restricted biozone of Tasmania, and was discovered in the middle Wasp Head Formation of the south Sydney Basin by Nillsen (1982), with further discoveries in New South Wales further north by Briggs (1998, p. 70) at Alum Rocks of the Texas block and Kensington Formation of the Peel Fault zone.

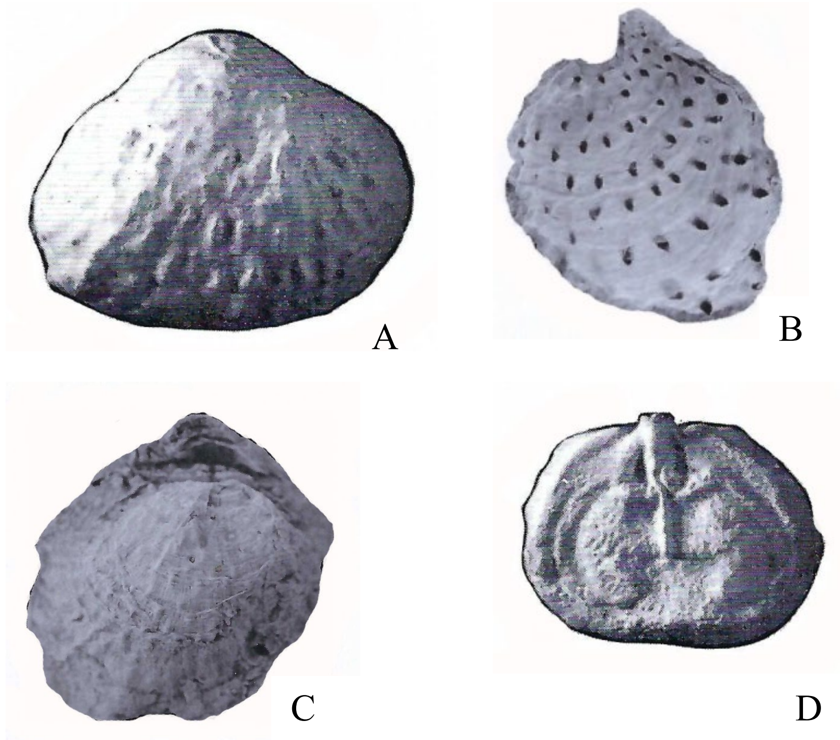

Fig. 2. *Crassispinosella subcircularis* (Clarke), A, TMF 35115, ventral aspect, x1.20. B, ventral external mould showing spine bases, BR 3011, x2. C, dorsal aspect of conjoined specimen BR 3016 x1. D, dorsal interior, TMF 3555, x1.33. From Glencoe Formation, Tasmania. (A, D, Clarke 1969; B, C, Waterhouse 2013).

Superfamily **DASYALOSIOIDEA** Brunton, 1966

Family **MINGENEWIIDAE** Archbold, 1980

Subfamily **CORONALOSIINAE** Waterhouse, 2023

Genus ***Capillaria*** Waterhouse, 2001

Diagnosis: Ventral row of hinge spines well developed. Other ventral spines distributed subevenly, dominated by strong erect spines, also with fine erect spines. Dorsal spines fine, erect, largely of one series, dorsal valve with moderately developed commarginal bands.

Type species: *Strophalosia preovalis* var. *warwicki* Maxwell, 1954, p. 54 from the Tiverton Formation of the north Bowen Basin, Queensland. OD.

Capillaria warwicki (Maxwell, 1954)

Fig. 3

1954 *Strophalosia preovalis* var. *warwicki* Maxwell, p. 543, pl. 54, fig. 16-19.
?1954 *S. preovalis* [not Maxwell], p. 44, pl. 7, fig. 16,17 fide Briggs 1998.
?1981 *E. preovalis* – Dickins, pl. 4, fig. 3 but deemed more likely to be *cenula* - see p. 34, (part, not pl. 4, fig. 1, 2, 4, 5 = *discinia* fide Briggs 1998,
1986a *S. warwickensis* Waterhouse, p. 1.
1986b *S. warwickensis* Waterhouse, p. 24.
1987 *Echinalosia warwicki* – Briggs, p. 137.
1998 *E. warwicki* – Briggs, p. 74, Fig. 39.
2001 *Capillaria warwicki* – Waterhouse, p. 67.

Diagnosis: Ventral spines arranged in quincunx, slightly variable in diameter, most a little finer than in younger species, capillate ornament well developed on dorsal valve.

Holotype: UQF 15626 from *Eurydesma* beds of Stanthorpe Road fault block, Queensland, figured by Maxwell (1954, pl. 54, fig. 16, 17) and Briggs (1998, Fig. 39E), OD.

Morphology: A lengthy synonymy provided by Briggs (1998) is reduced herein, because various ventral valves, some with a wide hinge, were included, without evidence on the presence of a hinge row of prominent spines in the ventral valve or capillate ornament of the dorsal valve. For example Briggs (1998) included a ventral internal mould from the Tiverton Formation that had been ascribed to *preovalis* by Hill & Woods (1964, pl. 4, fig. 9) as in Hill et al. (1972), but to establish identification with *warwicki*, it is preferred to demonstrate that the ventral valve had a hinge row of spines and dorsal valve showed fine dorsal capillae, or at least establish the development of a strong muscle adductor field and well-formed tunnels in the ventral valve. For few of the specimens figured by Briggs (1998), what may be parts of a ventral hinge row are suggested, as in Briggs (1998, Fig. 39E – see Fig. 3C herein). But several of the identifications proferred by Briggs (1998) in his synonymy lack signs of radial capillae and show no evident row of ventral hinge spines, including those provided by Maxwell (1954, pl. 54, fig. 4, 5; 1964, pl. 7, fig. 11, 12), Dickins 1981, pl. 4, fig. 3) and McClung (1980, pl. 19.1, fig. 1. The dorsal valves figured in Waterhouse et al. (1983, pl. 1, fig. 4, 5) lack any sign of radial capillae. The other specimens figured in Waterhouse et al. (1983) could belong, but need not. Specimens figured as *preovalis* in Maxwell (1964, pl. 7, fig. 11, 12) from the Yarrol beds and synonymized with *warwicki* by Briggs (1998) might belong, but uncertainty remains.

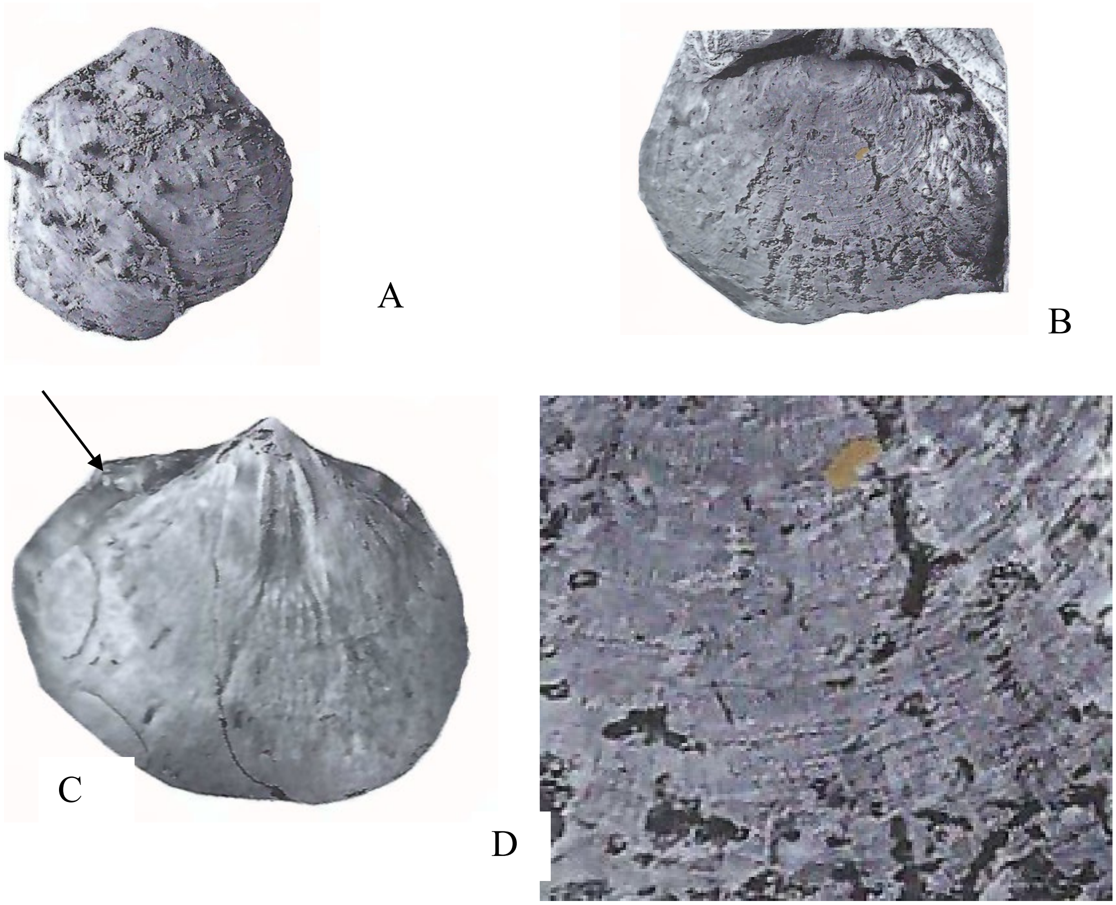

Fig. 3. *Capillaria warwicki* (Maxwell). A, latex cast of ventral exterior, UQF 75201. B, D, dorsal external mould, UQF 15629, x2, and panel x6, showing radial capillae. C, ventral internal mould, UQF 15626, holotype, x2.5, with signs of a remnant hinge row of stout spines as arrowed. From *Eurydesma* beds, Stanthorpe Road block, south Queensland. (Briggs 1998).

Stratigraphy: The claim by Briggs (1998) that the species typified a biozone below that of *Echinalosia preovalis*, including *E. curvata*, and above that of *curtosa* is regarded as feasible. The report that *warwicki* occurs in the Farley Formation above *curtosa* may be correct – little evidence was provided – but that would not rule out the presence of *warwicki* in beds correlative with those containing *Echinalosia curvata*, or overlapping perhaps only part of the previously discriminated *curvata* Zone, now assigned to the *Magniplicatina undulata* Zone, and possibly extending into older beds.

Taxonomy: In 1986a, Waterhouse proposed a new species name for Maxwell's species. The proposal followed the procedures understood at that time, based on Stoll (1961), that varieties of species should enjoy no systematic standing. This was changed in 1985, by which time Waterhouse had in manuscript proposed to refer the Maxwell material called var. *warwicki* to a full species *warwickensis*. Clearly the change in official taxonomic procedure rendered this name redundant, and Briggs (1998), apparently ignorant of past ICZN rulings, criticized Waterhouse, just as he had criticized Dear (1971) as discussed in Waterhouse (2022, p. 138). But Briggs did point out that dorsal spines were present and so amended the Maxwell and Waterhouse understanding that the species belonged to *Strophalosia*.

Capillaria conata (Waterhouse, 2001)

Fig. 4, 5

1964 *Strophalosia prideri* [not Coleman] – Waterhouse, p. 213.
1982 *Echinalosia prideri* [not Coleman] – Waterhouse, p. 31, pl. 23, fig. I, text-fig. 19A, B.
1998 *E*. cf. *mcclungi* [not Briggs] – Briggs, p. 80 (part, not Fig. 41 = *mcclungi*).
2001 *E. conata* Waterhouse, p. 58, pl. 3, fig. 12-22, text-fig. 5e.

Fig. 4. *Capillaria conata* (Waterhouse), internal mould of ventral valve BR 1480, x1.5, upper Takitimu Group. (Waterhouse 1982).

Diagnosis: Somewhat triangular in shape, high massive posterior walls at maturity, maximum width near mid-length, dorsal valve gently concave with trail at high angle. Well-formed row of hinge spines in ventral valve. Ventral disc spines erect, moderately close-set, but unevenly spaced, diameter varies, prostrate spines rare. Dorsal spines erect and sturdy, up to 0.25mm in diameter, irregularly dispersed, valve crossed by several laminate bands, radial capillae visible on some specimens. Dorsal medium septum poorly developed.

Holotype: OU 18750 from McLean Peaks Formation, upper Takitimu Group, figured by Waterhouse (2001, pl. 4, fig. 21) and Fig. 5E herein, OD.

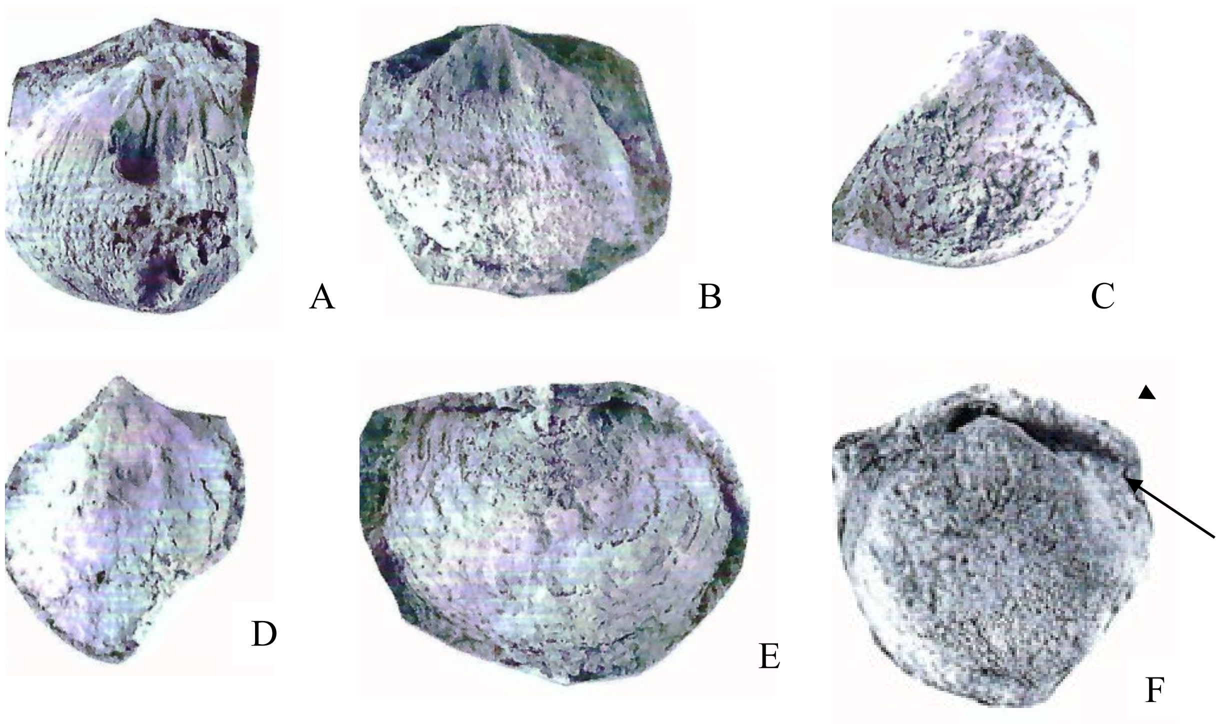

Fig. 5. *Capillaria conata* (Waterhouse). A, internal mould OU 18753 of mature ventral valve, x1.5. B, ventral internal mould OU 18749, x1.5. C, obscure ventral external mould OU 18748, showing spine bases, x1.5. D, ventral internal mould OU 18745, x1.5. E, dorsal external mould OU 18750, holotype, x1.5. F, anterior and ventral aspects of ventral internal mould OU 18747, x1, showing bases of hinge row of spines, arrowed. From upper Takitimu Group, New Zealand (Waterhouse 2001).

Morphology: This is a very distinctive species. Aspects of the text in Waterhouse (2001) indicated that *Echinalosia* was not the most appropriate receptor, given the presence of irregularly distributed mostly erect spines of varying diameter over the ventral valve, and the presence of subfusc commarginal bands with faint capillae over the dorsal valve, and the presence of a ventral hinge row. Unfortunately the published figures, prepared for me by an outside organization, are poor – so poor that they made me realize I must learn how to use a digital camera. But the types are in good order, kept at the University of Otago in the Department of Geology. Briggs (1998, p. 81) asserted that the specimens belonged to *Echinalosia mcclungi* Briggs from the Snapper Point Formation of the south Sydney Basin, but the dorsal valve is almost flat in this species, and the ventral posterior lateral slopes carry large spines (see p. 143 herein) that are not organized in a hinge row. The Takitimu species is superficially like *Strophalosia* (*now Echinalosia*) *prideri* Coleman (1957, p. 116, pl. 18, fig. 15, 16, pl. 19, fig. 1-19) from the Bulgadoo Shale in the Byro Group of the Carnarvon Basin, of Baigendzinian age. This species is of subtriangular shape with low interareas and sturdy ventral spines, loosely arranged in commarginal rows and rare much finer spines, all erect, and scattered dorsal spines, some comparatively stout. The dorsal valve is concave, and commarginal laminae and bands subdued, and no hinge row of spines is developed in this species.

Stratigraphy: The species is found at several localities in the upper Takitimu Group of the Takitimu Mountains (Waterhouse 2001, p. 58) and is treated as name-giver to the faunal zone in those rocks. There is no species in east Australia that is like this species, and other species found in New Zealand with *conata* are also absent from east Australia. This and the stratigraphic position and attribution of underlying and following faunal zones strongly suggests that the *conata* zone of New Zealand is represented by widespread non-marine beds in east Australia. Briggs and other east Australian geologists have never realized the significance of this gap in the marine sedimentary and faunal sequence, and their transcontinental let alone international correlations are in disarray. In Western Australia, the same time interval is also well represented by marine rocks and faunas.

Capillaria floodi (Waterhouse, 2001)

Fig. 6

2001 *Echinalosia floodi* Waterhouse, p. 59, pl. 4, fig. 1-5, cf. pl. 5, fig. 17.
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Diagnosis: Small subequidimensional shells with ventral ornament of relatively large and scattered erect spines interspersed with more slender erect and prostrate spines, spine tunnels inconspicuous. Ventral hinge row of spines. Dorsal spines fine and erect, commarginal laminae strong but commarginal banding weak. Posterior ventral adductor scars tend to be long.

Holotype: AMF 117369 as figured in Waterhouse (2001, pl. 4, fig. 2) from Elderslie Formation, north Sydney Basin, OD.

Morphology: Ventral adductor scars are divided into two pairs, the anterior pair oval to rounded, and may be separated by distinct myophragm; dorsal adductor anterior elements are rounded. The presence of dorsal capillae is not established.

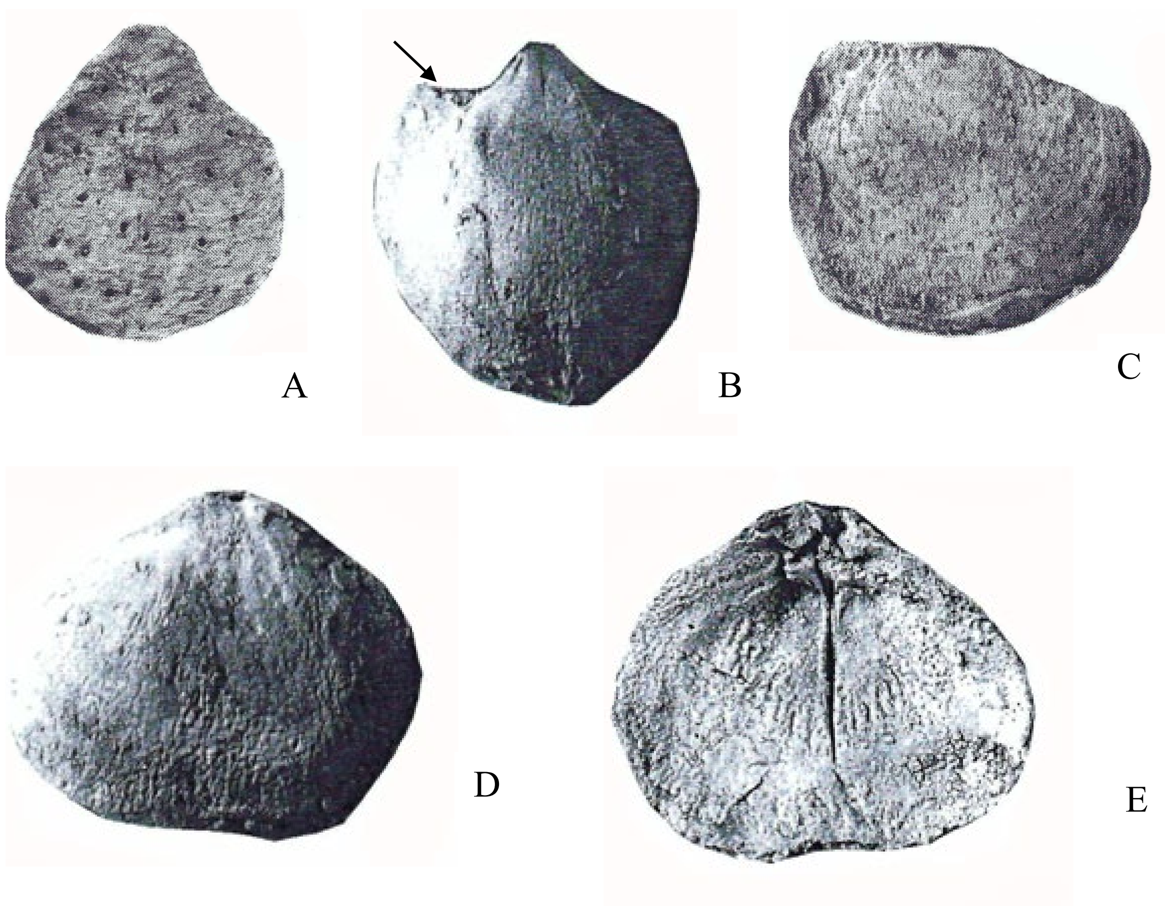

Fig. 6. *Capillaria floodi* (Waterhouse). A, external mould showing ventral spine bases. AMF 117370, x2. B, ventral internal mould AMF 117369, with hinge spines arrowed. C, dorsal external mould AMF 117368. D, E, ventral and dorsal aspects of internal mould AMF 117367. Specimens x2, from Elderslie Formation, north Sydney Basin. (Waterhouse 2001).

Stratigraphy: This species entered the Permian succession above the Greta Coal Measures in the Elderslie Formation of the north Bowen Basin (Waterhouse 2001), and persisted into the upper Elderslie Formation or basal Fenestella Shale. The ventral valve of *Capillaria floodi* is less arched than that of *E. preovalis* (Maxwell), and the ventral adductor scars are longer, not to mention the presence of the hinge row of spines. Dorsal spines are relatively coarse. The closeness to the older species *Capillaria conata* shows that the genus persisted, and the precise age of its oldest members is of interest, but needs clarification. Possibly the beds with early specimens were correlative with part of the Greta Coal Measures, but specimens appear to have persisted into younger beds.

Capillaria denmeadi (Waterhouse, 2015)

Fig. 7, 8

1969 *Wyndhamia preovalis* var. *warwicki* [not Maxwell] – Runnegar & Ferguson, pl. 2. fig. 10-12, 14 (part, not fig. 13 = sp. indet.).
1987 *Echinalosia* sp. Waterhouse & Balfe, p. 32, pl. 2, fig. 4, 5.
1998 *Echinalosia preovalis* [not Maxwell] – Briggs, p. 76.
2015 *E. denmeadi* Waterhouse, pp. 84, 140, 148, Fig. 26I, 57, 67.

Diagnosis: Small concavo-convex moderately transverse shells with ventral hinge row of spines, other ventral spines slightly stronger postero-laterally, dorsal spines fine, often numerous. Commarginal rugae may be prominent over ventral valve. Ventral muscle scars small to moderately elongate, and posteriorly placed.

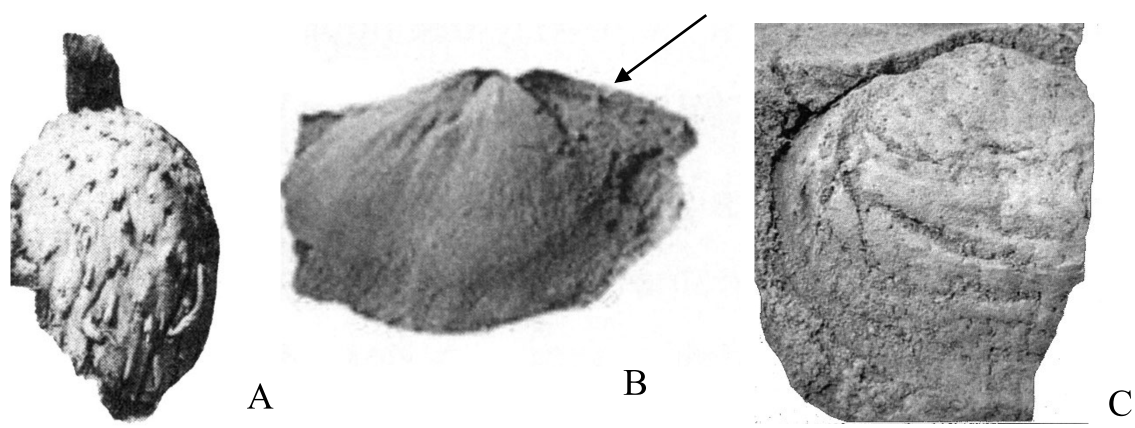

Fig. 7. *Capillaria denmeadi* (Waterhouse). A, latex of ventral valve, UQF 45414. B, ventral internal mould, UQF 69249, with row of hinge spines arrowed. C, dorsal external mould UQF 46710. Specimens x2 from South Curra Limestone, southeast Queensland. (A, Runnegar & Ferguson 1969; B, C, Waterhouse 2015).

Holotype: UQF 45409 from South Curra Limestone, Gympie, Queensland, figured by Runnegar & Ferguson (1969, pl. 2, fig. 10), OD. This was a poor choice of type, and other specimens show attributes of the species much better.

Morphology: A dorsal valve from the Gigoomgan Limestone near Gympie that was assigned to the species in Waterhouse (2015, Fig. 67) and Fig. 7C herein has commarginal rugae as well as fine spines, and its taxonomic position is not certain, though specimens from elsewhere show signs of commarginal rugae (see Fig. 8B). The presence of strong ventral spines near the hinge, the less steep posterior ventral walls, the difference in ventral adductor scars, and variable presence of capillae suggest that the Gympie form *denmeadi* is not specifically related to *warwicki,* nor to *preovalis*, despite the reports in Runnegar & Ferguson (1969) and the assessment by Briggs (1998).

Stratigraphy: The species is found in the lower South Curra Limestone and nearby Gigoomgan Limestone of the Gympie region of southeast Queensland, as well as the Gundiah Bridge Greywacke of Brown (1964), an informal and unpublished unit in the same area.

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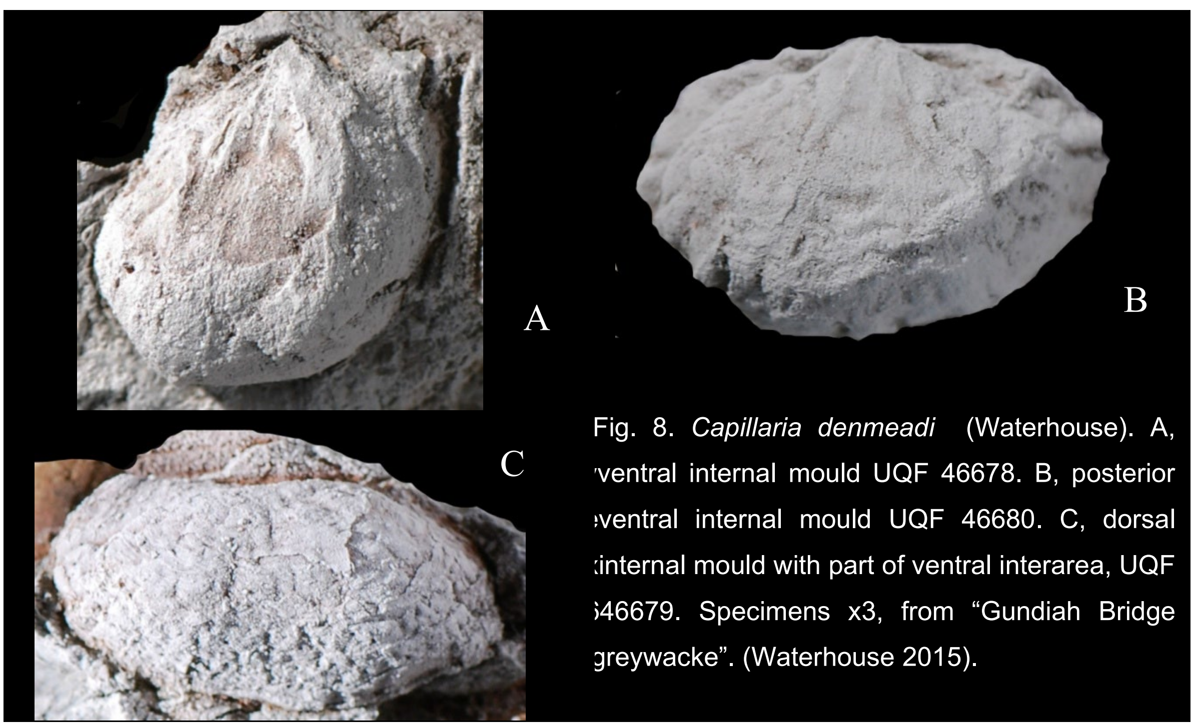

Fig. 8. *Capillaria denmeadi* (Waterhouse). A, ventral internal mould UQF 46678. B, posterior ventral internal mould UQF 46680. C, dorsal internal mould with part of ventral interarea, UQF 46679. Specimens x3, from “Gundiah Bridge greywacke”. (Waterhouse 2015).

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A FRENZY OF EVOLUTION: ECHINALOSIIN BRACHIOPODS IN THE PERMIAN OF EAST AUSTRALIA AND NEW ZEALAND

Abstract

Echinalosiinae entered Permian sediments of east Australia in Sakmarian times, after the especially cold Asselian Stage, and were represented by only a few species throughout the Sakmarian and lower Artinskian stages, with a hiatus in marine sedimentation during the upper Artinskian (Baigendzinian) Stage, a critical gap represented by marine sediments and faunas in Western Australia and in New Zealand. Throughout the Kungurian Stage and the Roadian to Capitanian Stages of the Middle Permian Guadalupian Series in east Australia, Echinalosiinae underwent rapid changes, resulting in a number of separate lineages, and involving populations of rather limited distribution, so that some species are of little interest for purposes of wide-ranging correlation. More than fifty taxa are recognized, and associated in several distinct groupings, treated as genera and subgenera, which are illustrated and summarized for their morphological attributes and known stratigraphic occurrences.

INTRODUCTION

Echinalosiinae Waterhouse are an association of brachiopods characterized by dorsal spines which are usually of one series, and ventral spines which are commonly found in two series. The dorsal valves maybe a little thickened but are not wedge-shaped. The shells are allied to Strophalosiidae Schuchert, 1913, which like Echinalosiidae have teeth and sockets and umbonal cicatrix, but Echinalosiidae differ from those of Strophalosiidae in possessing dorsal spines, a feature which in the past has been regarded as bringing them close to Dasyalosiinae Brunton, 1966. *Daysyalosia* has crowded and vermiform spines of several orders over both the ventral and dorsal valve, whereas spines in Echinalosiinae are more regular in diameter and spacing as a rule. Variations in spine density and format appeared in related genera that are found in east Australia and New Zealand, but are conform more to the pattern seen in *Echinalosia* rather than *Dasyalosia*. Echinalosiinae may be divided into three tribes, Echinalosiini, Marginalosiini with thickening of the dorsal valve and

Series	Stage	East Australasian biozone
LOPINGIAN	Changhsingian	*Wairakiella rostrata*
		**Marginalosia planata*
		Spinomartinia spinosa
		***Capillaria denmeadi* !**
	Wuchiapingian	*Mytilidesmatella sivelli*
		Martiniopsis woodi
		------------??-------------
GUADALUPIAN	Capitanian	***Ingelarella costata***
		****Echinalosia minima***
		****Pseudostrophalosia clarkei***
	Wordian	****Ps. blakei***
	Roadian	****Echinalosia maxwelli***
CISURALIAN	Kungurian	****Echinalosa discinia***
		****Wyndhamia typica***
		Glendella dickinsi
	Artinskian	*Capillaria conata* !
		Martinia adentata
		****Echinalosia preovalis***
		Notostrophia zealandicus
	Sakmarian	***Taeniothaerus subquadratus*** !
		Magniplicatina undulata
		Bookeria pollex
	Asselian	***Bandoproductus macrospina***
		***Crassispinosella subcircularis* !**
		***Strophalosiaria concentrica* !**

Table 1. The succession of marine macro-invertebrate biozones of east Australia (bold) and additional zones found only in New Zealand (regular), mostly correlative with non-marine intervals in east Australia, modified from Waterhouse (2008, 2010, 2021d). Several zones are designated after echinalosiin species, as asterisked, and allied strophalosiidin species are signified by !.

reduction in spine disparity over the ventral valve, and a new tribe Acanthalosiini, illustrating the development of various morphological differences amongst a thriving diversity of closely related strophalosiiform taxa.

A major study of echinalosiids was incorporated in a monograph on Productida from the Permian sediments of east Australia by Briggs (1998). Briggs named many echinalosiid species, and assigned most of them to a single genus *Echinalosia*, in an attempt to assign the rocks and macro-faunas east Australia to biozones. He provided critical information on a number of species, and gave important detail on various stratigraphic occurrences. But the effort was not entirely successful. He endeavoured to correlate the successions purely on the basis of literary and local geological surveys, without ever inspecting any of the world stratotypes, and never examined many of the critical species first hand at museums and geological surveys across the world. In east Australia, he assumed without proof that the east Australian successions were complete without major sedimentary gaps, though he had enjoyed no experience of the world successions, including stratotypes, and failed to accurately assess the impact of the coal measures on the marine sequences, and misinterpreted the Late Permian sequences of the Gympie Province in southeast Queensland, judging them to be Middle Permian. It is revealing that not once in his lengthy monograph of east Australian Productida did he ever present a geological map. Rather the geological aspect of his study was presented as idealized stratigraphic sections, showing the presence of species, and some of the sections were somewhat interpretative, if not fanciful, as expressed to me by Dr G. McClung in expressing reservations over the interpretation of parts of the north Sydney Basin. The Briggs rendition of the sequence of species in the northern part of the Bowen Basin is particularly maladroit, where he had completely misrepresented the sequence involving the species *clarkei, typica, crassa, ingelarensis*, and *ovalis*, basing his views on ill-judged species identifications, misinterpretation of the geological map in Waterhouse & Jell (1983), and deprecation of various paleontological descriptions by various other paleontologists. Understandably, some experts in and beyond Australia adopted his zonal scheme, because they thought it was the “latest and most up-to-date” alternative. Nor did Briggs establish that his zonal species were to be found in every major fauna throughout east Australia. More gravely, many of his type specimens have gone missing. It appears that the types were never securely deposited in any institution, and it appears that the editor for his monograph, published by the Association of Australasian Palaeontologists, never checked that the type material had been securely deposited. A further disconcerting feature is that the lost material was mostly, though not entirely, registered through published specimen numbers as belonging to the Australian Museum in Sydney, so that in the following text and illustrations, such specimens so credited may well now have disappeared, and whether the actual numbers were ever applied to the specimens is not known. Many if not all of these specimens belonged in fact to the Queensland Museum and were taken by Briggs from that institution, but were registered by AMF numbers by Briggs as if the specimens belonged to the Australian Museum, certainly without permission from the Queensland Museum which provided the specimens to Briggs (S. M. Parfrey, pers. comm.). Yet the editor of the Briggs memoir published on behalf of the Australasian Association of Palaeontologists and the referees selected to check his manuscript before publication offered no demurral. Some later scholars have even left open the possibility that it was perhaps the Australian Museum which was responsible for the disappearance of the specimens. Desultory efforts to find the missing material have yielded nothing: these specimens cannot be found. They are recorded in the following text, and the photographs are real enough, but the specimens have now "disappeared". Fortunately, a number of the types, registered with UQ numbers, were uplifted from Briggs by Dr Peter Jell and taken back to Queensland, so that they remain in safe custody. Whether the missing specimens will ever be found remains at best, an open question. Near the end of this monograph, a summary is provided of uncertainties in the Briggs interpretation of correlations based on his interpretation of echinalosin species, and a summary of Middle and Late Permian macro-faunal zones and correlations will follow in a forthcoming volume of Earthwise.

A SUMMARY OF THE EVOLUTION OF ECHINALOSIIN SPECIES DURING THE PERMIAN PERIOD IN EAST AUSTRALIA

It was W. G. H. Maxwell while at the University of Queensland who provided the first critical study of Strophalosiidina in the Permian of east Australia. He recognized and compared a number of species, chiefly in the Bowen Basin of Queensland, and his types are still extant.

Earliest *Echinalosia* in east Australia are represented by the middle Sakmarian species *dejecta*, *sulcata*, *curvata* and *cenula*, all named by Waterhouse, and then *preovalis* (Maxwell), with *curvata* found beyond Queensland in New Zealand and possibly in New South Wales. A major change in the extent of species occurred during the Middle Permian. For the Kungurian Stage, placed by geopolitical rather than faunal and environmental considerations at the top of the Cisuralian or Early Permian Period, although faunally much more closely related to the faunas of the Middle Permian or Guadalupian Series. *Echinalosia briggsi* is followed by *Echinalosia discinia* Waterhouse in the Sydney Basin, and *discinia* occurs as well in the Bowen Basin, possibly the New England orogen at Warwick, and in New Zealand. Whether it ranged into Tasmania is uncertain, because of the paucity of faunal descriptions of that region. A short-lived *E*. *denisoni* Archbold within the range of *discinia* is also found in the Sydney and Bowen Basins, and New Zealand. The overlying species *E. maxwelli* (Waterhouse) is also widespread, occurring in New Zealand, with its closely allied subspecies *robusta* Briggs, found in the Sydney and Bowen Basins. But the following species became more limited in their geographic range. In the overlying faunal assemblage, now referable to a *Maxwellosia ovalis* Superzone because it involved three contemporaneous taxa, which were related to *Echinalosia* but chiefly of a different tribe, *Maxwellosia ovalis* (Maxwell), limited to the southwest Bowen Basin, *M. ovalis wassi* Briggs in the Sydney Basin and southeast Bowen Basin, and arguably in the Narrabri core of the Sydney Basin, and reported from New Zealand by Briggs (1998), and *Nothalosina*? *glabra* (Briggs), limited to the southeast Bowen Basin. In the Sydney Basin, approximately if not exactly correlative faunas include *E*. (*Glabauria*) *telfordi* Briggs followed by E. (*Glabauria*) *hanloni* Briggs and slightly younger faunas of the Sydney Basin contain *E.* (*Glabauria) runnegari* Briggs. No *Glabauria* have been recognized in either the Bowen Basin or in New Zealand. *Echinalosia* (*Unicusia*) *minima* (Maxwell) is found not only in the northern Bowen Basin, but possibly in northwest Nelson, New Zealand, marking the only occurrence in New Zealand of the subgenus. At the top of the marine succession, in the northern Bowen Basin, *Pseudostrophalosia* shows similarities to a species from the correlative *Ingelarella costata* Zone of New Zealand, though further material is desirable to consolidate the link. In summary, for much of the Middle Permian in east Australia and New Zealand, widespread zonal correlation, particularly between the Sydney and Bowen Basins, cannot completely rely on echinalosiid species being pervasive throughout east Australia for brief successive intervals of time. Other brachiopods, as well as molluscs, were much less restricted in their geographic range, and so remain useful for intercorrelation.

Late Permian faunas in eastern Australia are limited to those of Gympie, and lacked *Echinalosia* ss. *Capillaria denmeadi* (Waterhouse, 2015b) is found in the South Curra Limestone, as well as Gundiah Bridge Greywacke of Brown (1964) and Gigoomgan Limestone of the Gigoomgan area near Gympie. Younger species *Marginalosia sulcata* n. sp. and *M. planata* (Waterhouse) are restricted to New Zealand, when coal measures prevailed in east Australia.

SYSTEMATIC DESCRIPTIONS

with notes on relationships and stratigraphic occurrence

PHYLUM BRACHIOPODA Duméril, 1806

Class Strophomenata Williams et al., 1996

Superorder PRODUCTIFORMII Waagen, 1883

Order PRODUCTIDA Waagen, 1883

Suborder STROPHALOSIIDINA Waterhouse, 1975

Superfamily **QUADRATIOIDEA** Lazarev, 1989

Family **ECHINALOSIIDAE** Waterhouse, 2001

[Nom. promoveo hic ex Echinalosiinae Waterhouse, 2001, p. 57] et seq.

Diagnosis: Ventral valve usually has spines of one or two series, rarely more diverse, generally one series erect and the other recumbent, rarely sinuous in most constituent genera, no conspicuous hinge row. Spines mostly uniform and erect over the dorsal valve. Fine commarginal growth increments and also lamellae and dimples commonly developed on dorsal valve, radial capillae generally faint or usually absent. Spine tunnels well-developed as a rule in ventral valve. Ventral attachment scar, teeth and sockets, interareas, dorsal median septum and muscle scars as in the suborder. Cardinal process trifid.

Subfamily **ECHINALOSIINAE** Waterhouse, 2001

Diagnosis: Dorsal valve concave, not wedge-shaped, rarely thickened. Ventral spines regular and of two series. Dorsal spines regular, in one series.

Tribe **ECHINALOSIINI** Waterhouse, 2001

Diagnosis: Ventral spines in two series, more or less quincunxially arranged; dorsal spines in single fine erect series as a rule.

Genus ***Echinalosia*** Waterhouse, 1967a

Diagnosis: Spines of two series interspersed over ventral valve, simple, not normally sinuous or arranged in special rows or aggregated to form a posterior lateral brush, spines present over ventral ears; spine cores over middle valve may extend well forward from spine base as a rule, leaving spine tunnels in many specimens. Dorsal spines fine and erect, without prolonged bases. Capillae faint or absent, commarginal rugae and laminae subdued or absent, growth increments well developed, dorsal dimples in a number of species. Marginal ridges subdued or absent.

Type species: *Strophalosia maxwelli* Waterhouse, 1964, p. 32 from Letham Burn Formation, New Zealand, OD.

Subgenus ***Echinalosia*** Waterhouse, 1967a

Diagnosis: As above. Ventral ears spinose, marginal ridges not well developed, dorsal valve not thickened, ventral spines in two series, thick and thin.

Discussion: Table 1, p. 24 presents a summary of the stratigraphic units in different parts of the Sydney and Bowen Basins of New South Wales and Queensland, with the succession at Wairaki Downs, New Zealand, as representing the Highbury and Brook Street volcanic arc segments and overlying sediments of southeast Queensland and New Zealand. Table. 2, p. 51, summarizes the presentation of east Australian species of *Echinalosia* according to Briggs (1998), following his order of appearance, with proposed adjustments to his identifications.

Echinalosia (***Echinalosia***) ***dejecta*** Waterhouse, 1986b

Fig. 1

1986b *Echinalosia dejecta* Waterhouse, p. 25, pl. 3, fig. 15-24.
1989 *E. dejecta* – Waterhouse, pl. 1c.
1998 *E. preovalis* [not Maxwell] – Briggs, p. 76.
2015a *E. dejecta* – Waterhouse, p. 78.

Diagnosis: Small subrounded shells with broad incurved ventral umbo, moderately wide hinge, sturdy ventral spines, some of which are rhizoid. Dorsal spines moderately thick for size of shell, at 0.3mm diameter.

Holotype: UQF 73955 from Dresden Limestone, southeast Bowen Basin, figured by Waterhouse (1986b, pl. 3, fig. 20, 24), OD.

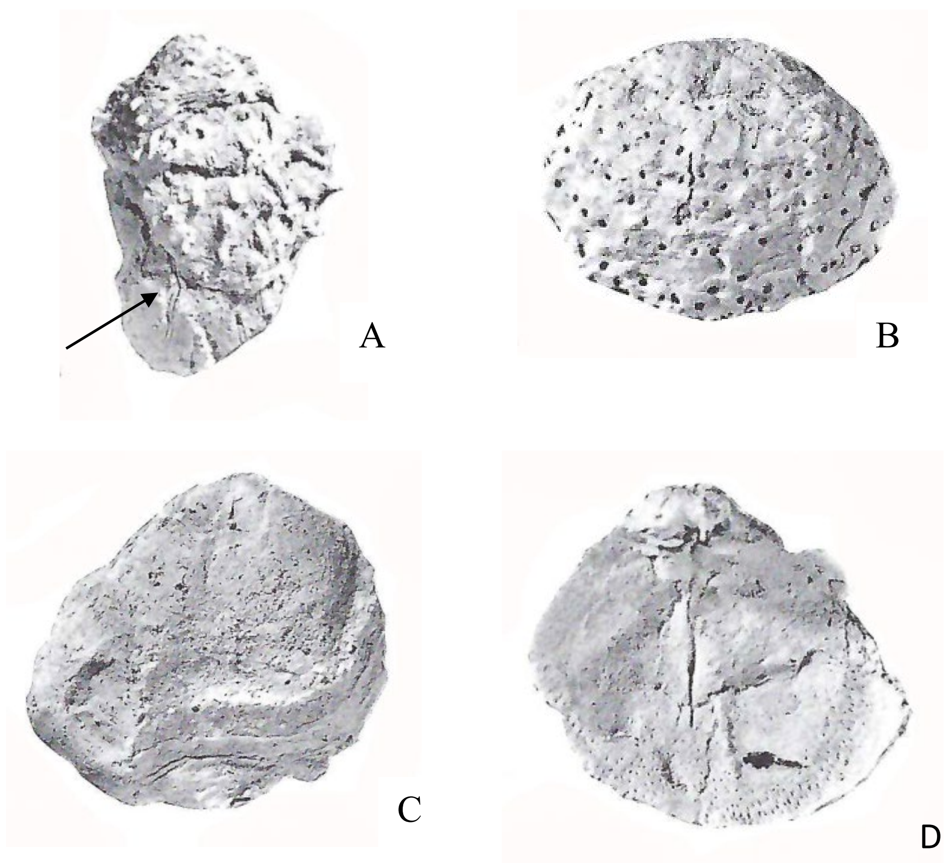


Fig. 1. *Echinalosia* (*Echinalosia*) *dejecta* Waterhouse. A, ventral latex cast, UQF 73950, arrow pointing to sinuous spine. B, dorsal external mould, UQF 73953. C, D, ventral and dorsal aspects of internal mould of specimen with valves conjoined, UQF 73955, holotype. Specimens x3 from Dresden Formation, southeast Bowen Basin. (Waterhouse 1986b).

Morphology: Ventral spines are in two series, somewhat disorganized and scattered. Briggs (1998) declared that this species was conspecific with *preovalis* Maxwell, but Waterhouse (1986b) had noted that unlike *preovalis*, *dejecta* had well differentiated ventral spines, short hinge, and moderately long ventral adductors. Dorsal spines anteriorly are unusually thick and robust. These differences from *preovalis* as well as the much lesser convexity were ignored by Briggs (1998), and further differences were added by Waterhouse (2015a, p. 78). Ventral spines in type *dejecta* may be rhizoid (see Waterhouse (1986b, pl. 3, fig. 15) and even thick over the anterior shell.

It was reported in Waterhouse (2015a) that ventral interiors figured as *preovalis* from calc-rich beds of the Yarrol Formation, Yarrol Basin, that were figured by Maxwell (1964, pl. 7, fig. 11, 12) might be related because an accompanying unfigured specimen has similar sturdy recumbent rhizoid spines, as if the calcareous nature of the substrate may have influenced the development of *Echinalosia* in both the Bowen and Yarrol Basins. But the Yarrol specimens are not necessarily the same as *dejecta:* because they show a short dorsal median septum, and have spine tunnels, unlike type *dejecta*. It is not certain that such features are taxonomically significant: they may depend on the degree of maturity of the specimen. Whether spine tunnels are absent from *dejecta* is not certain, because of uncertainty over the maturity of the specimens figured.

Stratigraphy: The species is limited to the Dresden Limestone of the southeast Bowen Basin.

Echinalosia*? *(Echinalosia) sulcata Waterhouse, 2015a

Fig. 2, 3

1983 *Strophalosia* cf. *subcircularis* [not Clarke] – Waterhouse et al., p. 126, pl. 1, fig. 4, 5.
?1998 *Echinalosia curtosa* [not Waterhouse] – Briggs, p. 72, Fig. 38A (part, not Fig. 38B-H = *curtosa*).
2015a *Echinalosia curtosa sulcata* Waterhouse, p. 70, Fig. 19-21.

Fig. 2. ?*Echinalosia* (*Echinalosia*) *sulcata* (Waterhouse), latex cast of ventral valve UQF 75203 x2 from Farley Formation, north Sydney Basin, New South Wales. (Briggs 1998).

Diagnosis: Equidimensional moderately inflated well-rounded shells, ventral valve with shallow sulcus as a rule, no cicatrix, ornamented by spines 0.3-0.6 up to 1.2mm in diameter, often not numerous, mostly suberect, some specimens prostrate, a few sturdy posterior lateral spines, dorsal valve deeply concave and feebly marked by radial capillae, with variable number of rare to numerous erect spines, dimples scattered and usually well-formed, commarginal laminae moderately to scarcely developed. Ventral muscle adductor impressions well defined and elongate as a rule. Dorsal interior not exceptional.

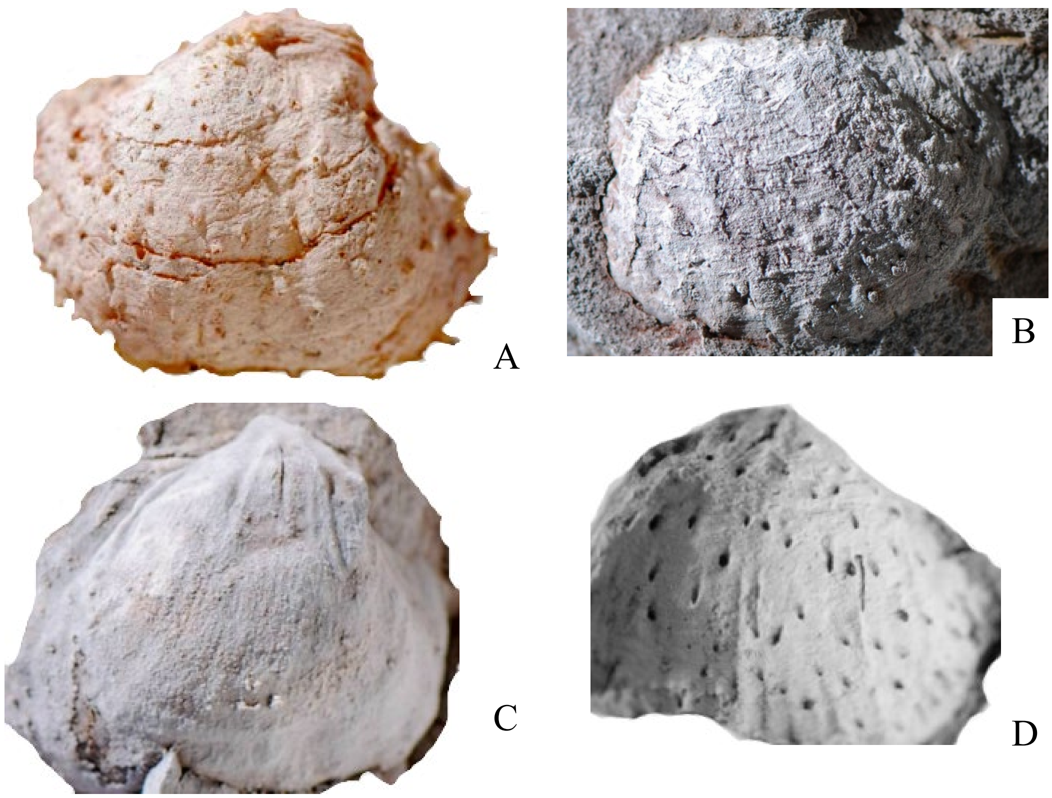


Fig. 3. *Echinalosia* (*Echinalosia*) *sulcata* (Waterhouse). A, latex cast of ventral valve UQF 81260, holotype. B, dorsal external mould UQF 81373. C, external mould of ventral valve, UQF 81445. D, ventral external mould UQF 81258. Specimens x2 from lower Tiverton Formation, north Bowen Basin. (Waterhouse 2015a).

Holotype: UQF 81260 from lower (but not basal) Tiverton Formation, figured by Waterhouse (2015a, Fig. 19A, B, 21A-D) and herein as Fig. 3A, OD.

Morphology: Specimens from the lower Tiverton Formation in the north Bowen Basin have been described in Waterhouse (2015a) as a subspecies of *Echinalosia curtosa*. They are broader and more sulcate than *curtosa* from the Fairyland Formation, and have a number of fine erect spines, unlike ventral spines in *E. curvata*, but approaching species of *Echinalosia.* The taxon is not represented by many specimens, which handicaps its generic placement. *Echinalosia curtosa* has mostly coarse erect spines (see p. 72), suggesting genus *Maxwellosia*

Stratigraphy: The material was described from the lower Tiverton Formation in the north Bowen Basin. A specimen figured from the Farley Formation by Briggs (1998, Fig. 38A) as shown in Fig. 2 herein shows some similarities, though the fine ventral spines are recumbent rather than erect.

Echinalosia* (*Echinalosia*) *curvata Waterhouse, 1986b

Fig. 4

1986b *Echinalosia preovalis curvata* Waterhouse, p. 26, pl. 3, fig. 25-29, pl. 4, fig. 1-5.
?1998 *E. preovalis* [not Maxwell] – Briggs, p. 76, Fig. A, F (part, not Fig. 40B-E, G-M = *preovalis*).
2015a *E. curvata* – Waterhouse, p. 82, Fig. 30-33.
2021c *E. curvata* – Waterhouse, p. 107, Fig. 2-4.
2021 *E. curvata* – Waterhouse & Campbell, p. 10, Fig. 2-4.

Diagnosis: Large, usually transverse and moderately concavo-convex shells with numerous regularly arranged spines over both valves.

Holotype: UQF 73959 from Elvinia Formation, southeast Bowen Basin, figured by Waterhouse (1986b, pl. 4, fig. 2, 5), OD.

Morphology: Spacing of ventral spines is regular. This species is based on transverse specimens, readily distinguished from *Echinalosia preovalis* (Maxwell) which is applied to smaller specimens with highly arched ventral valve and small posteriorly placed adductor scars.

Stratigraphy: *Echinalosia* (*Echinalosia*) *curvata* is regarded as a widespread marker species, occurring in the Elvinia Formation of the southeast Bowen Basin, the lower middle Tiverton Formation of the north Bowen Basin, the Lakes Creek Formation of the New England Orogen in Queensland, the

Farley Formation of the north Sydney Basin, and Eglinton volcanics of the Dunton Range in New Zealand. The species was incorrectly synonymized with *preovalis* by Briggs (1998), which is smaller, narrower and more arched. He thereby masked the correlation potential for the species *curvata*, and at the same time exaggerated the correlation potential for the species *preovalis*.

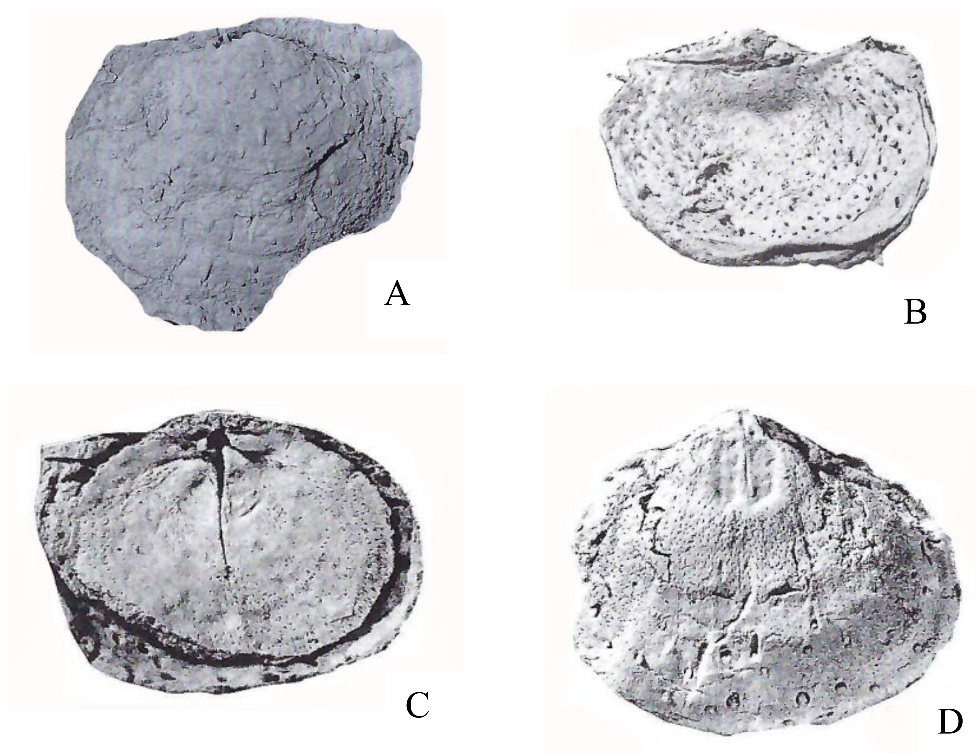


Fig. 4. *Echinalosia* (*Echinalosia*) *curvata* Waterhouse. A, latex cast of ventral exterior UQF 140 x2.5, from Lakes Creek Formation. B, dorsal view of latex cast of specimen with valves conjoined, x2. C, internal dorsal mould, x3. D, ventral internal mould, x3. B-D from Elvinia Formation, southeast Bowen Basin. (Waterhouse 1986b, 2021).

Echinalosia (***Echinalosia***) ***cenula*** Waterhouse, 2015a

Fig. 5, 6

?1954 *Strophalosia preovalis* Maxwell, p. 542, pl. 54, fig. 4, 5 (part, not 1-3, 6-11 = *preovalis*).
?1981 *Echinalosia preovalis* [not Maxwell] – Dickins, pl. 4, fig. 3 (part, not fig. 1, 2, 4, 5 = *discinia* Waterhouse, fide Briggs 1998).
1998 *E. warwicki* [not Maxwell] – Briggs, p. 76 (part, not p. 77, Fig. 39 = *warwicki*).
2015a *E. cenula* Waterhouse, p. 74, Fig. 22-29.

Diagnosis: Small highly convex shells with deeply concave dorsal valve, not showing geniculation, ventral spines in a coarse series 0.3 to 0.6mm up to 1mm in diameter, and recumbent series 0.3-0.4mm in diameter. Dorsal spines rare, 0.2 to 0.4mm in diameter, dorsal dimples and commarginal laminae, no capillae.

Holotype: UQF 81820 from lower middle Tiverton Formation, figured in Waterhouse (2015a, Fig. 26A) and herein as Fig. 32C, OD.

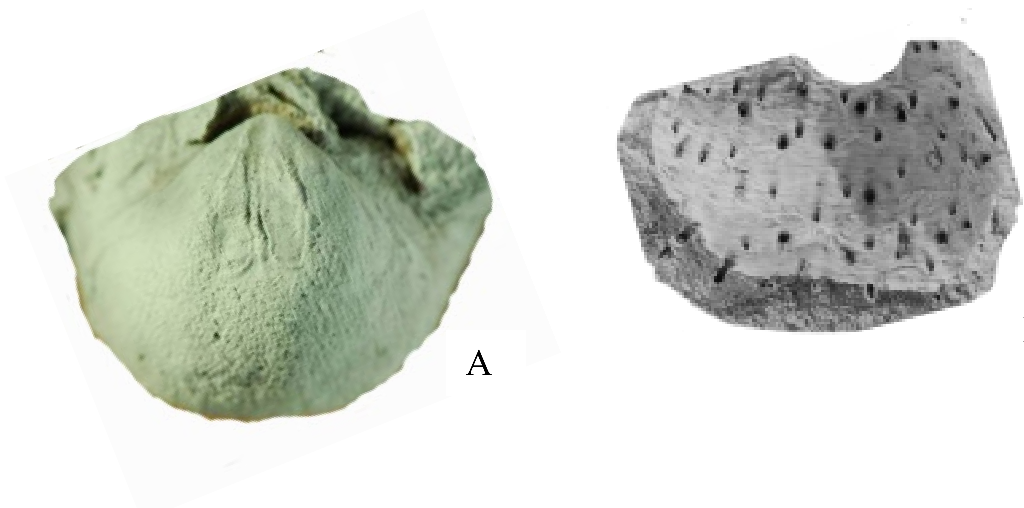


Fig. 5. *Echinalosia* (*Echinalosia*) *cenula* (Waterhouse). A, ventral internal mould UQF 81266, x2.5. B, ventral external mould UQF 81253, x3. Tiverton Formation. (Waterhouse 2015a).

Morphology: The ventral valve is moderately arched, and the dorsal spines are consistently fine and uniform, though somewhat rare. Judged from shape and curvature, it appears that the specimens are not simply immature representatives of other named species in the formation. They are close in some respects to *Maxwellosia. curtosa* (Waterhouse), but are less inflated and have more diverse ventral spines. They are also close to *Echinalosia* (*Echinalosia*) *sulcata* from the lower Tiverton Formation, a species that is less transverse and less sulcate, but close in ventral spines.

Stratigraphy: The types come from the *Magniplicatina undulata* Zone, in the lower middle Tiverton Formation of the Bowen Basin.

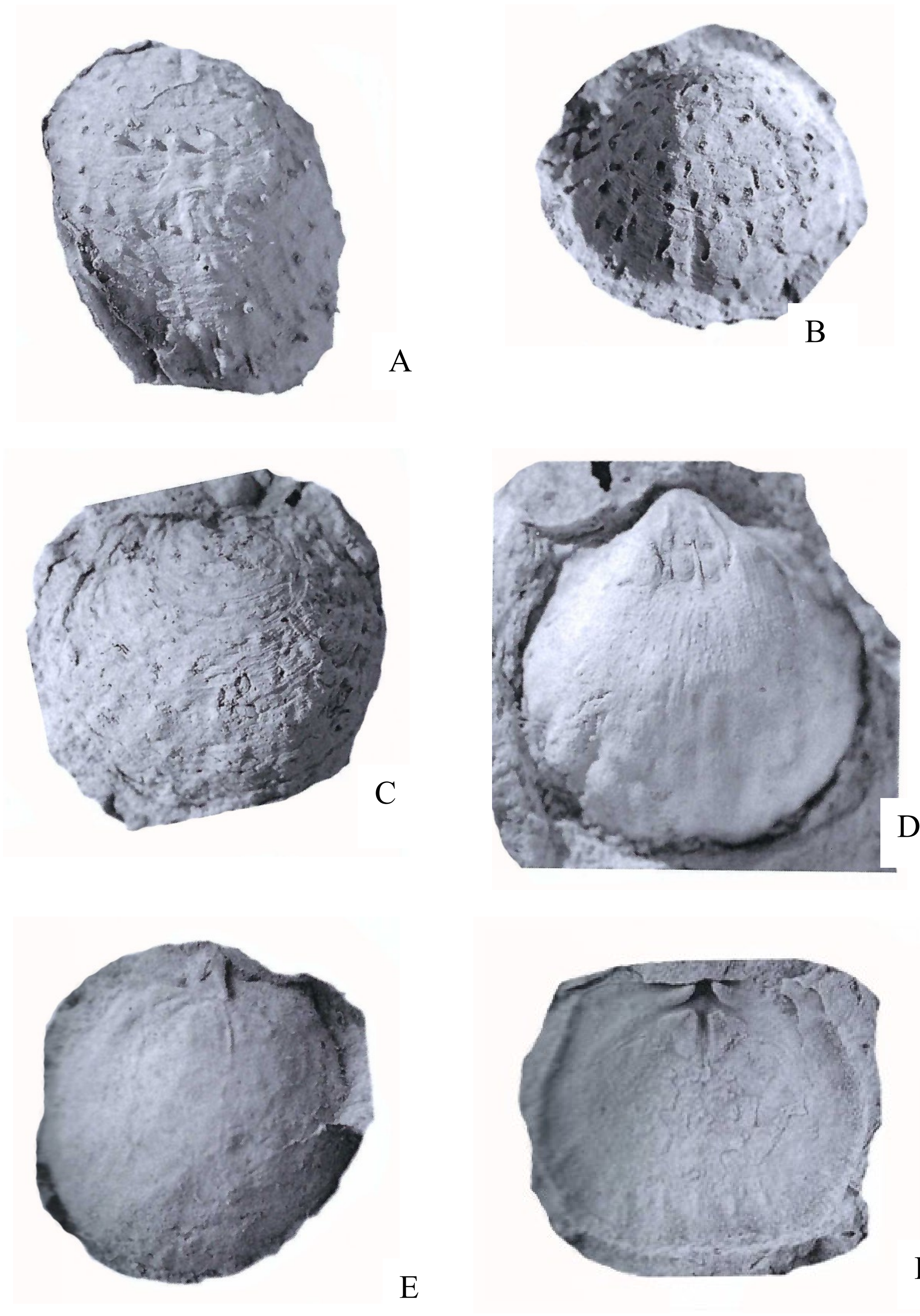


Fig. 6. *Echinalosia* (*Echinalosia*) *cenula* (Waterhouse). A, latex cast of ventral exterior, UQF 81445, x2. B, ventral external mould, UQF 81262, x3. C, external mould of dorsal valve UQF 81820, holotype, x3. D, ventral internal mould UQF 81827, x3. E, latex cast of dorsal interior, UQF 81292, x2. F, dorsal internal mould UQF 81823, x3. From lower middle Tiverton Formation, north Bowen Basin. (Waterhouse 2015a).

Echinalosia* (*Echinalosia*) *preovalis (Maxwell, 1954)

Fig. 7, 8

1954 *Strophalosia preovalis* Maxwell, p. 542, pl. 54, fig. 1-3, 6-11 (part, not fig. 4, 5 from older beds in the Tiverton Formation, indet., could be *cenula*).
1964 *S. preovalis* – Hill & Woods, pl. P4, fig. 6-8 (part, not fig. 9 = *Maxwellosia bryani*).
1969 *Wyndhamia preovalis* – Clarke, pl. 6, fig. 7, fig. 8?
1972 *Echinalosia preovalis* – Hill et al., pl. P4, fig. 6-8 (part, not fig. 9 = *Maxwellosia bryani*).
1983 *Echinalosia* cf. *preovalis* – Waterhouse, p. 156, pl. 1, fig. 1, 2.
1986 *E. preovalis* – Waterhouse, pl. 4, fig. 6.
1998 *E. preovalis* – Briggs, p. 76, Fig. 40B-E, G-M (part, not Fig. Fig. 40A, F possibly = *curvata*).

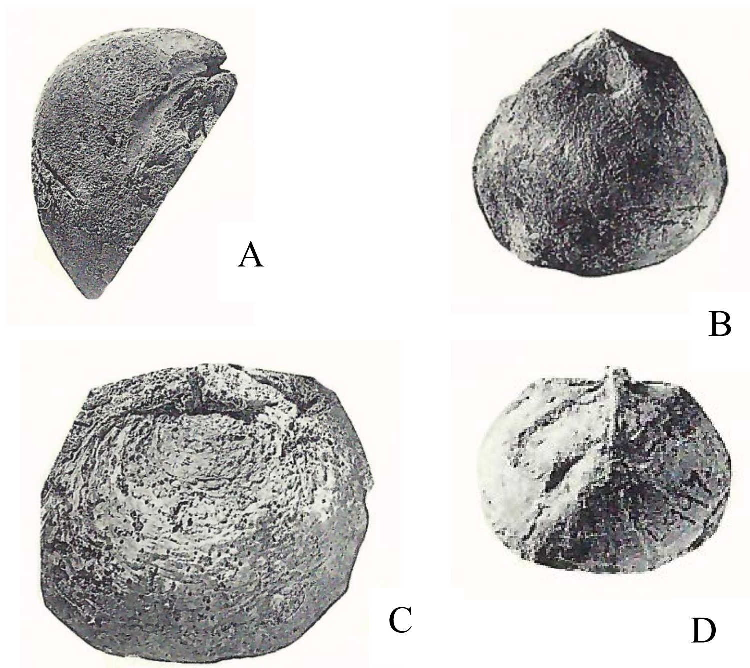


Fig. 7. *Echinalosia* (*Echinalosia*) *preovalis* (Maxwell). A, B, lateral and ventral aspects of ventral internal mould, UQF 15622, holotype, x1 approx.. C, external mould of dorsal valve, UQF 14625, x1.5. D, dorsal interior UQF 15620, x1.5. Cattle Creek Formation, southwest Bowen Basin. (Maxwell 1954).

Diagnosis: Equilateral to subelongate shells as a rule, with highly arched ventral valve and incurved ventral umbo. Ventral spines arranged in quincunx or with commarginal rows prominent, prostrate and suberect, small, in two series, comparatively slender, reaching diameters of 0.3mm and 0.5mm. Dorsal disc strongly concave, spines numerous and fine, in two series with diameters of 0.1 and 0.2mm over trail according to Briggs (1998). Ventral muscle scars small and posteriorly placed until late in ontogeny, dorsal septum short.

Holotype: UQF 15622 from upper Cattle Creek Formation, southwest Bowen Basin, figured by Maxwell (1954, pl. 4, fig. 1-3) and Fig. 7A, B herein, OD.

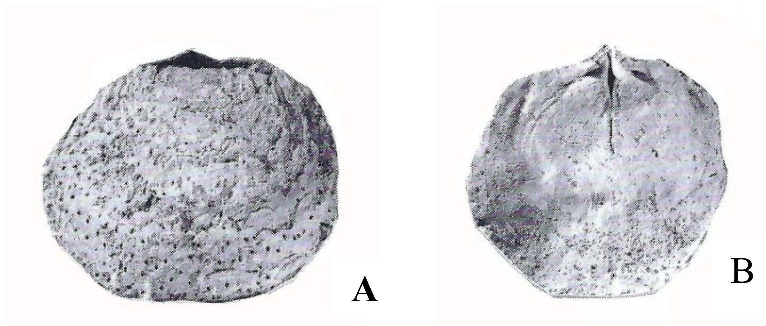


Fig. 8. *Echinalosia* (*Echinalosia*) *preovalis* (Maxwell). A, B, dorsal external and internal mould UQF 70037 x2 from upper Tiverton Formation. (Waterhouse 1983).

Morphology: Briggs (1998, Fig. 40A, F) included two less elongate specimens with fine ventral spines in synonymy, and perhaps they were unusual specimens, or belonged to a different more transverse species. They look to be very close to *Echinalosia curvata* Waterhouse, coming apparently from the older Cattle Creek Formation in the southwest Bowen Basin, and from Rokeby close to the Queensland border. A ventral interior figured as *preovalis* by Hill & Woods (1964, pl. P4, fig. 9) and Hill, Playford & Woods (1972) from the Tiverton Formation might belong to *Maxwellosia bryani*, given its thick posterior shell, emphasized muscle scars, and strong spine bases on the ears, and it has strong spine tunnels. The specimen was apparently found in the chonetid band of the Tiverton Formation (Hill & Woods (1964), which is older than beds with *E. preovalis* (Waterhouse 2015a), and is known to contain *bryani* (Waterhouse 2015a). The material figured as *preovalis* by Maxwell (1954, pl. 54, fig. 4, 5) from slightly older beds compared with the types are shaped like *preovalis* in the figures, but show no spines and could be *Maxwellosia cenula*. Indeed Briggs (1998) treated them as belonging to *warwicki*, though the figures provide no clear mandate for such an identification. Clearly further material and first-hand inspection are required to determine the identity.

The specimen figured as *preovalis* by Clarke (1969, p. 47, pl. 6, fig. 7) was transferred to *warwicki* by Briggs (1998, p. 74), yet it was indicated as a topotype specimen of *preovalis* by Clarke (1969), which is younger than *warwicki.* The source for Clarke's other figured specimen (Clarke 1969, pl. 6, fig. 8) was not provided, and is poorly known, being an internal mould, but has muscle scars close to those of *preovali*s.

Stratigraphy: As far as known, *Echinalosia preovalis* is limited to the upper Cattle Creek Formation of the southwest Bowen Basin, and correlative levels in the upper Tiverton Formation of the north Bowen Basin, and Roses Pride Formation of the southeast Bowen Basin. Likely specimens also come from the Hastings Block and possibly other rocks near the Queensland - New South Wales border, in an area of diverse formations and various faunas, in need of up-to-date mapping and clarification with expert paleontological support. Briggs (1998, pp. 78, 79) included various other species in the same taxon, to considerably distort his preferred correlation scheme. Whereas *Echinalosia preovalis* is judged to be Aktastinian in age, he included *E. dejecta* of earlier Sakmarian age, though it is less inflated than *preovalis* and has robust ventral spines, some rhizoid. He also included *E. curvata*, a large and transverse shell with well-ordered ventral spines, of middle to later Sakmarian age, immediately older than *preovalis*, and he included *Capillaria floodi*, from the Elderslie Formation and Pebbley Beach Formation, units which are probably of Kungurian age. *C. floodi* is less arched than *preovalis*, and has a row of prominent hinge spines and coarser fewer ventral disc spines. And he included Gympie specimens described as *preovalis warwicki* by Runnegar & Ferguson (1969, pl. 2, fig. 10-14). These are likely to belong to *Capillaria denmeadi*, of Changhsingian age. Unlike *preovalis*, they have a ventral hinge row of spines.

Echinalosia (***Echinalosia***) ***briggsi*** Waterhouse, 2001

Fig. 9

1998 *Echinalosia maxwelli* [not Waterhouse] – Briggs, p. 81, Fig. 42A-G.
2001 *E. discinia briggsi* Waterhouse, p. 61.

Diagnosis: Small transverse little inflated shells, with somewhat unevenly distributed ventral spines in two orders, and numerous fine erect dorsal spines. No row of well-developed hinge spines. Spine tunnels and dorsal dimples moderately developed.

Holotype: UQF 75219 figured by Briggs (1998, Fig. 42A) and Fig. 9B herein from Wandrawandian Formation, south Sydney Basin, OD.

Morphology: The ventral valve of *Echinalosia* (*Echinalosia*) *.briggsi* is less arched than that of *E.* (*E.*) *preovalis* (Maxwell), and the ventral ornament shows better defined spine series than in *E.* (*E.*) *maxwelli* (Waterhouse), with coarser stout spines predominant, but less regularly arranged than in *maxwelli*, and more scattered fine erect spines. The ventral interarea is higher, and the ventral adductor scars longer than in *maxwelli*, and the ventral adductor scars are longer. Unlike *Capillaria floodi*, there is no hinge row of sturdy ventral spines.

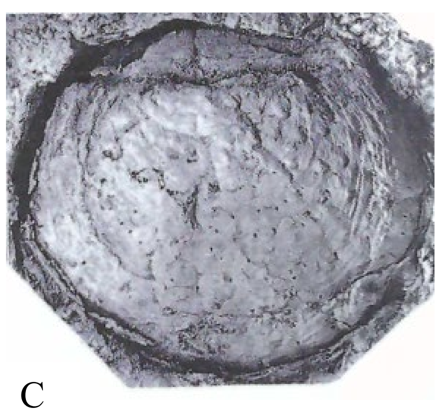


Fig. 9. *Echinalosia* (*Echinalosia*) *briggsi* Waterhouse. A, part of external mould of large ventral valve, UQF 75218. B, latex cast of ventral exterior, UQF 75219, holotype. C, dorsal aspect, external mould of specimen with valves conjoined, UQF 75220. Specimens from Wandrawandian Formation, Ulladulla, x2. These were misidentified with *E. maxwelli* by Briggs. (Briggs 1998).

Stratigraphy: This is the first well-established member of *Echinalosia* to enter the Permian succession in the Wandrawandian Formation at Warden Head in the south Sydney Basin, above the level equivalent to the Greta Coal Measures. *Paucispinauria paucispinosa* and *Aperispirifer archboldi* were reported to occur also with the species by Waterhouse (2001, p. 60), consistent with a pre-*maxwelli* stratigraphic position. But the relationship to *discinia* requires consolidation.

Echinalosia (***Echinalosia***) ***discinia*** Waterhouse, 1986b

Fig. 10, 11

1981 *Echinalosia preovalis* [not Maxwell] – Dickins, p. 30, pl. 4, fig. 1, 2, 4, 5 = *discinia* (part, not fig. 3 = *warwicki* fide Briggs 1998, pp. 74, 86).
1986b *E. discinia* Waterhouse, p. 28, pl. 4, fig. 7-17.
1998 *E. discinia* – Briggs, p. 86, Fig. 45A-H.
2001 *E. discinia* – Waterhouse, p. 60, pl. 4, fig. 6, 7, 10-12.
2008 *E. discinia* – Waterhouse, p. 361, Fig. 6G, J.

Diagnosis: Transverse to subcircular shells with fine and numerous spines over both valves, up to 0.4mm diameter in ventral valve, with a number of spines only half that diameter.

Holotype: UQF 70303 figured in Waterhouse (1986b, pl. 4, fig. 12) from Brae Formation, southwest Bowen Basin, OD.

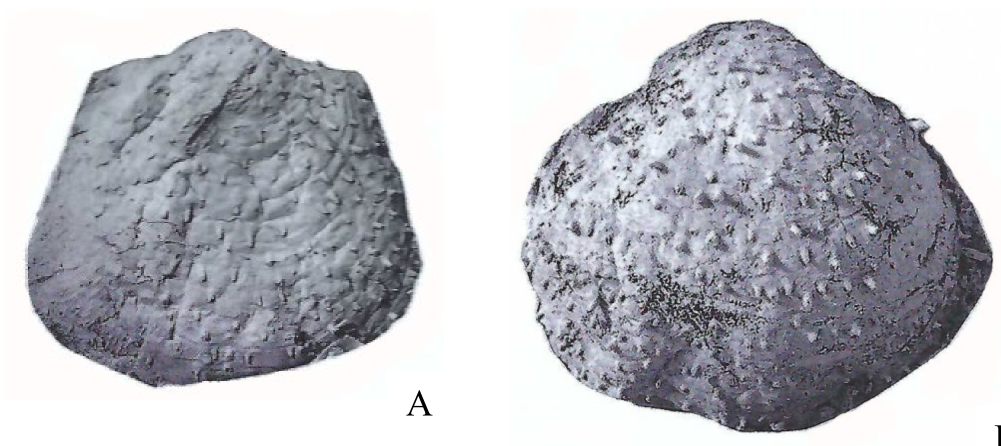


Fig. 10. *Echinalosia* (*Echinalosia*) *discinia* Waterhouse. A, latex cast of ventral exterior, UQF 75241 from Wandrawandian Formation, south Sydney Basin. B, latex cast of ventral exterior, AMF 96230, x2 from Brae Formation, southeast Bowen Basin. Specimens x2. (Briggs 1998).

Morphology: Specimens recorded as *Echinalosia preovalis* [not Maxwell] by Dickins (1981, p. 30, pl. 4, fig. 1, 2, 4, 5) from near Warwick in southeast Queensland, were assigned to *E. discinia* by Briggs (1998,

p. 86). Spines are not shown in the figures presented by Dickins, so that the likely identification will be helped by assessment of the accompanying species, not to mention examination of specimens with spines and ears preserved. The decorticated internal moulds resemble those of several species. But otherwise, the identification with *discinia* seems feasible.

Stratigraphy: This species is found in the upper Letham Formation of New Zealand and, together with other species and genera, helps affirm correlation with the Brae Formation of the southeast Bowen Basin. Briggs (1998) argued that *Echinalosia* in the upper Brae Formation belonged to *Echinalosia robusta* rather than *discinia*, and shared that species with the overlying Oxtrack Formation. But the two faunas have little in common, as may be seen from comparing the faunal lists compiled from fully described faunas from a number of localities from the two formations in Waterhouse (1987, Table 12, p. 213) from the Brae Formation, including upper Brae as UQL 4108 in a very large collection, to be contrasted with Table 14, p. 214 for fossils from the Oxtrack Formation. The specimen highlit by Briggs (1998) from upper Brae (Waterhouse, 1986b, pl. 4, fig. 9) is more mature than other specimens figured by Waterhouse, and is close to the Brae specimen figured as *discinia* by Briggs (1998, Fig. 45C) and herein as Fig. 11B in the coarseness of its spines. Critically, the posterior lateral spines are finer than in the species *robusta* Briggs. See also p. 49 herein.

Fig. 11. *Echinalosia* (*Echinalosia*) *discinia* Waterhouse. A, dorsal view of latex cast of specimen with valves conjoined, UQF 70755. B, ventral view, latex cast UQF 70758, possibly *denisoni*. C, ventral internal mould, UQF 70296. Specimens x2 from Brae Formation. (Waterhouse 1986b).

Echinalosia (_Echinalosia_) _denisoni_ Archbold, 1987

Fig. 12

1983 *Echinalosia* sp. nov. McClung, p. 71, Fig. 13: 1-12.
?1986 *E. discinia* [not Waterhouse?] - Waterhouse, pl. 4, fig. 9 (part, remainder = *discinia*).
1987 *E. denisoni* Archbold, p. 34.
1998 *E. denisoni* – Briggs, p. 98 (part, not Fig. 51A-D = *Maxwellosia ovalis wassi*?)
2001 *E. denisoni* – Waterhouse, p. 6, pl. 4, fig. 8, 9?.

Diagnosis: Small in size as far as known, ventral spines over much of disc sturdy and erect, finer and semirecumbent posteriorly, dorsal spines relatively sturdy and erect. Ventral adductor platform comparatively long and high. Dimples are lacking and the internal ventral moulds do not show spine tunnels.

Holotype: GSQF 12465 figured by McClung (1983, Fig. 13.12) and Fig. 12A herein from interval C of GSQ Eddystone 1 core, Bowen Basin, OD.

Morphology: The principal feature of this species is the presence of strong and erect spines over much of the ventral valve, as well as strong dorsal spines. That recalls the ornament of *Echinalosia bookeri*

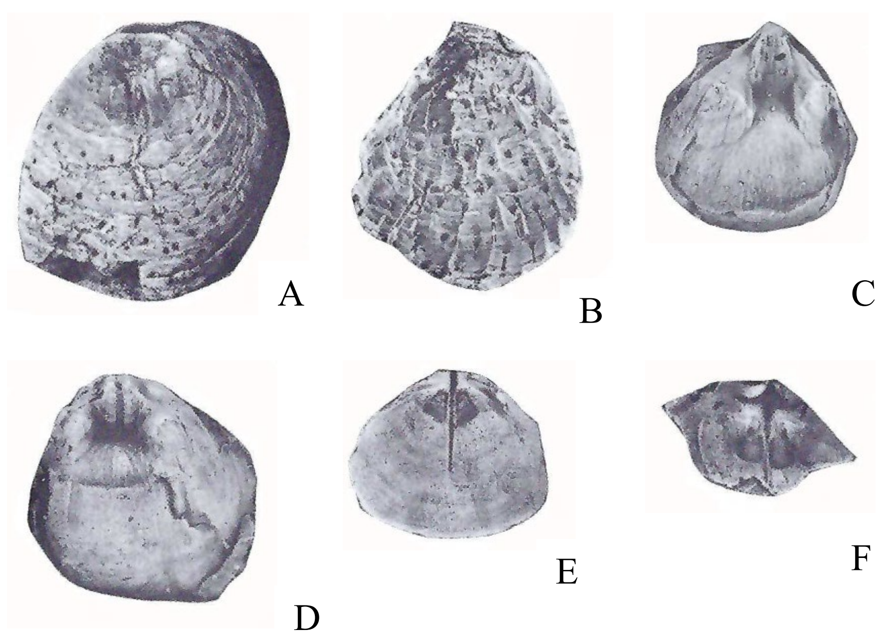


Fig. 12. *Echinalosia* (*Echinalosia*) *denisoni* Archbold. A, dorsal external mould, GSQF 12465, holotype. B, ventral external mould GSQF 12472. C, ventral internal mould GSQF 12470. D, ventral internal mould GSQF 12474. E, dorsal internal mould GSQF 12469. F, dorsal internal mould GSQF 12468. Specimens x1 (except F x2) from level C, GSQ Eddystone 1. (McClung 1983).

Briggs, 1998 found at two localities in the Branxton Subgroup and Fenestella Shale of the north Sydney Basin, as in the following Fig. 13. Dorsal spines are stronger than in *E*. (*Echinalosia*) *briggsi,* and no spine tunnels are developed in ventral interiors. Briggs (1998, Fig. 51) figured different-looking specimens as *denisoni* from DM Narrabi, showing a mix of thick erect spines and long more slender mixed with thicker recumbent spines, approaching the ornament on *E. wassi* Briggs (now *Maxwellosia ovalis wassi*) as shown in Fig. 43 herein**.** From the Brae Formation of the southeast Bowen Basin, Waterhouse (2001) assigned a specimen that to some extent approaches *E.* (*E.*) *denisoni*, as refigured in Fig. 11B herein. Material reported from the upper Letham Formation of New Zealand was considered to have spines like those of *denisoni* but the published figures do not show ventral spinosity, an omission that needs to be remedied. Briggs referred specimens figured as *ovalis* (Maxwell) by Waterhouse & Jell (1983, pl. 1, fig. 1-6) from the lower Blenheim Formation just below the Scottville Member to *denisoni,* but spines are more crowded, and although mostly if not entirely erect, the ventral spines vary somewhat in diameter, more as in *Maxwellosia ovalis* (Maxwell). (See Fig. 38, p. 79). *E. denisoni* shows considerable approach to *Echinalosia* (*Echinalosia*) *briggsi* (see Fig. 9, p. **36**) but shells are less transverse with fewer fine erect spines and coarser dorsal spines.

Stratigraphy: Briggs (1998) wished to interpret the species *denisoni* as younger than it really is, according to stratigraphic information and according to the fossils associated with *denisoni.* The species comes from Member C in the Eddystone 1 drill core, and accompanies the species *Tumulosulcus undulosa* (Campbell) and *Angulospirifer phalaena* (Sowerby) according to McClung (1983). These fossils point to an upper Kungurian age, which would fit with the possible occurrences in the Brae Formation and upper Letham Formation. It is also consistent with the Ingelara age proffered by Briggs (1998) for the overlying beds with *Pseudostrophalosia crassa* Briggs.

Echinalosia (***Echinalosia***) ***bookeri*** Briggs, 1998

Fig. 13

1987 *Echinalosia* n. sp. 2 Briggs, p. 138.
1998 *Echinalosia bookeri* Briggs, p. 86, Fig. 44A-I.

Diagnosis: Ventral spines coarse, most semirecumbent, a few slender. Dorsal spines also comparatively robust.

Holotype: UQF 75231 figured in Briggs (1998, Fig. 44B, E) from Branxton Subgroup, OD.

Morphology: *Echinalosia bookeri* Briggs, 1998 was proposed for material from localities near the top of the Fenestella Shale and at an unspecified level of the Branxton Subgroup. It was understood by Briggs to involve medium-sized subcircular shells with ventral spines supposedly of two coarse series, although some of the prostrate spines are comparatively slender (Briggs 1998, Fig. 44A, G). Apart from the low angle of the ventral spines, the specimens somewhat approach *Echinalosia denisoni* which has strong but erect rather than recumbent ventral spines, which opens up the question of whether the angle of the spines with the shell surface is a genetic and specific feature, or whether it is caused by environmental parameters. Dorsal spines are also robust, ventral adductor scars long in both *denisoni* and *bookeri* and the dorsal median septum of similar length in both named taxa. That does leave a question over the implications for specific distinction if based largely on recumbency or otherwise for ventral spines.

Stratigraphy: The species is apparently rare and of limited occurrence, from top of the Fenestella Shale and in an unspecified level of the Branxton Subgroup.

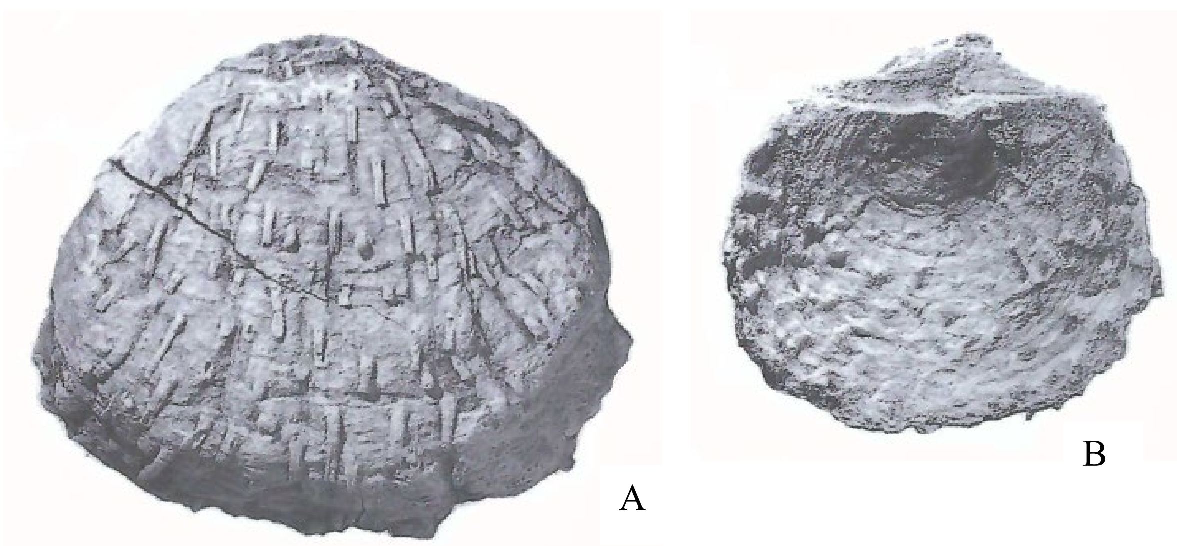


Fig. 13. *Echinalosia* (*Echinalosia*) *bookeri* Briggs. A, ventral valve of conjoined specimen UQF 75232. B, dorsal aspect of conjoined UQF 75230, with sturdy spines shown on the left side. Specimens x2, from Fenestella Shale and Branxton Subgroup. (Briggs 1998).

Echinalosia* (*Echinalosia*) *maxwelli (Waterhouse, 1964)

Fig. 14 - 16

1964 *Strophalosia maxwelli* Waterhouse, p. 32, pl. 4, fig. 6-11, pl. 5, pl. 6, pl. 7, fig. 1-3, pl. 36, fig. 5, 6, text-fig. 7a, c, e, 8b, 9a-m, 10a, b, 11, 12a-d, 13, 14.
1967 *Echinalosia maxwelli* Waterhouse, p. 167, nom nov. pro *Multispinula* Waterhouse, 1966, p. 11 non Rowell, 1962, p. 147.
1982 *E. maxwelli* – Waterhouse, p. 32, pl. 19, fig. a-d, pl. 23, fig. 1-d, text-fig. 20-23A, 28.
2000 *E. maxwelli* – Brunton et al., p. 571, Fig. 405.2a-d.
2008 *E. maxwelli* – Waterhouse, p. 363, Fig. 7E.
2010 *E. maxwelli* – Waterhouse, Fig. 17A-C (D = *maxwelli robusta*).
2013 *E. maxwelli* – Waterhouse, p. 229, Fig. 7.20.

Diagnosis: Highly variable in shape and may include narrow specimens with short hinge, but typically transverse, spines with two well-defined series as a rule and evenly arranged over the ventral shell, but locally exceptional, and number and width of erect spines may vary, dorsal spines fine, erect and as a rule dense, though there are exceptions. Interarea of moderate height, ventral adductor platform of moderate height and length. Median dorsal septum sturdy, up to two thirds of the valve in length.

Holotype: BR 253 figured by Waterhouse (1964, pl. 4, fig. 8, 9, pl. 5, fig. 5, pl. 6, fig. 5) and Fig. 15A, D herein from Letham Burn Member, Wairaki Downs, New Zealand, OD.

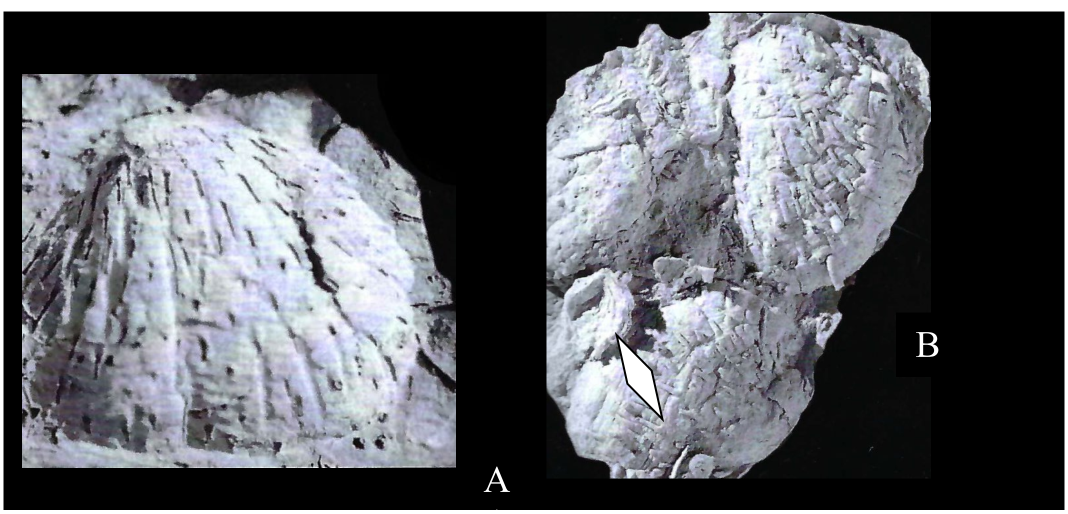


Fig. 14. *Echinalosia maxwelli* (Waterhouse). A, ventral external mould of BR 2728, x3. B, latex casts from external moulds, BR 2728 (below) and 2729, with juvenile specimen BR 2731 indicated at the diamond, x1.5. Topotypes, Letham Burn Formation, New Zealand. (Waterhouse 2010).

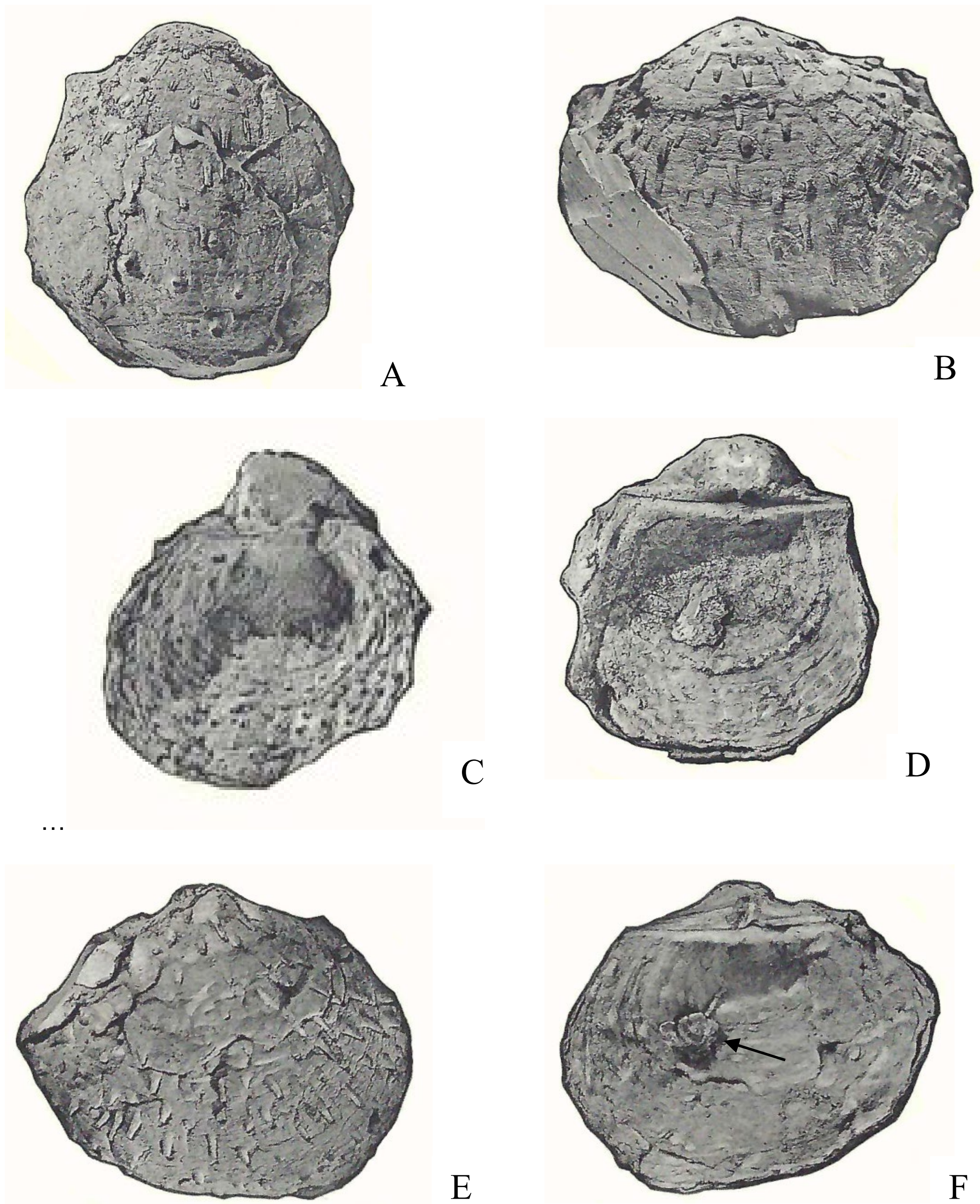


Fig. 15. *Echinalosia* (*Echinalosia*) *maxwelli* (Waterhouse). A, D, holotype BR 253, ventral and dorsal aspects of PVC cast. B, ventral aspect of PVC cast of conjoined specimen BR 272. See also Fig. 4, p. 142. C, dorsal aspect, immature conjoined specimen, BR 279. E, F, ventral and dorsal aspects of PVC cast of conjoined specimen BR 270, with spat arrowed on F. Type and topotype specimens from Letham Burn Member, New Zealand, x2, except C, x3. (Waterhouse 1964).

Morphology: Many individuals are known for this species, enabling a large number of figures, and even so, not all the variants have been figured. Particular attention has been paid to the changes in morphology with increased maturity (Waterhouse 1959, 1982, pp. 32-37), an aspect which should not be ignored in taxonomic studies.

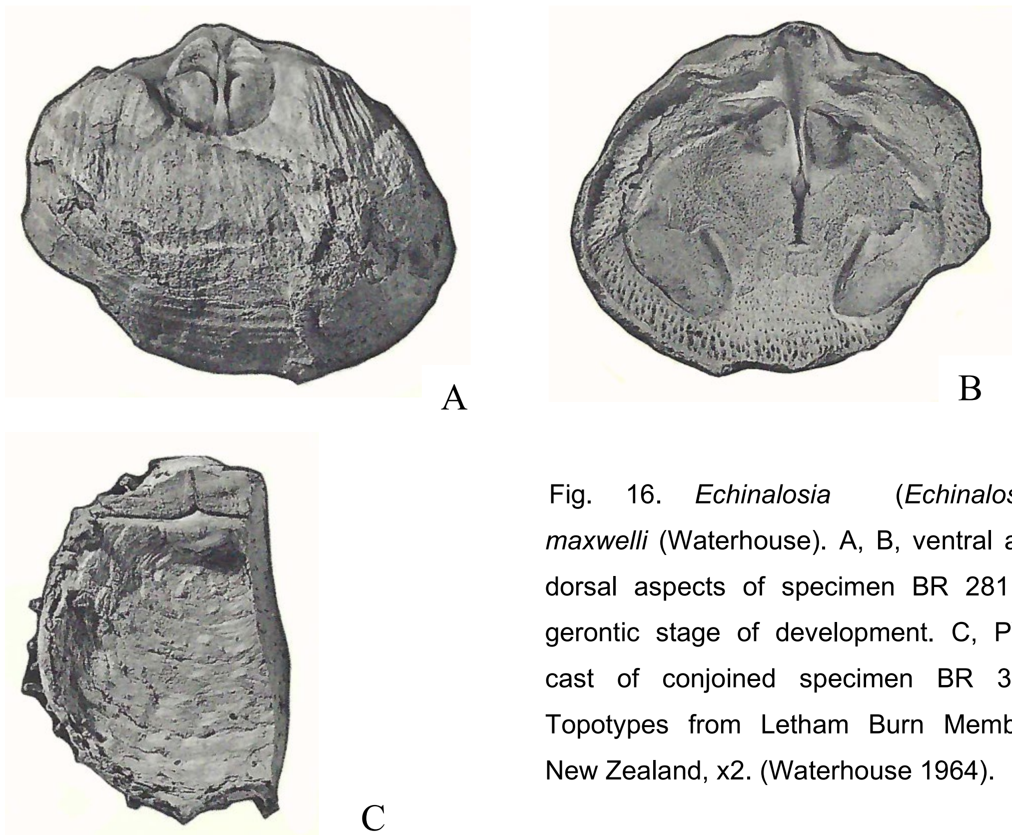


Fig. 16. *Echinalosia* (*Echinalosia*) *maxwelli* (Waterhouse). A, B, ventral and dorsal aspects of specimen BR 281 at gerontic stage of development. C, PVC cast of conjoined specimen BR 330. Topotypes from Letham Burn Member, New Zealand, x2. (Waterhouse 1964).

The extent to which Briggs (1998) has misrepresented and distorted fossil species and their positions in the stratigraphic column is well illustrated in his Fig. 11, which purports to show the succession of zonal species of *Echinalosia*. He showed a box for *E. maxwelli*, and matched it with *Terrakea dickinsi* shown as occurring in the Caravan Formation of Wairaki Downs in New Zealand. Above, he showed *Terrakea concava* (as *T. concavum*) in the lower Letham Formation. His biostratigraphy is fictitious. *E. maxwelli* is found with *T. concava* in Wairaki Downs, at the same registered, mapped and photographed localities. They occur together, not in separate zones, both in the Letham Burn Member distinctly above the Letham Formation and well above the Caravan Formation. *E. maxwelli* occurs stratigraphically far above the shells ascribed to *T. dickinsi*, which was sourced from the Brunel Formation, well over 1000m stratigraphically below the Caravan Formation. Presumably this strange version of New Zealand biostratigraphy was devised to support his highly inaccurate depictions of east Australian biostratigraphy and misidentified fossil species. All too often, the Briggs presentation of stratigraphy and fossils is completely unreliable. Fossil sequences are a very complex subject, and so easy to misinterpret.

Echinalosia **(*Echinalosia*)** ***maxwelli robusta*** Briggs, 1998

Fig. 17, ?18

1964 *Strophalosia clarkei minima* – Hill & Woods, pl. P4, fig. 14 (part, 13a, b (part, not fig. 14 = *minima*).
1972 *Echinalosia minima* – Hill & al., pl. P4, fig. 14 (part, not 13a, b = *minima*).
1986b *E. maxwelli* – Waterhouse, p. 30, pl. 4, fig. 18-22, pl. 5, fig. 1, 2.
1998 *E. robusta* Briggs, p. 88, Fig. 46A-I.

Diagnosis: Medium size, subcircular to transverse, with many prostrate ventral spines (0.35-0.45mm diameter) and erect ventral spines up to 1mm in diameter, but variation considerable. Some Belford specimens have a posterior and posterior lateral row of coarse spines, without forming a hinge row (Briggs 1998, Fig. 46A, C, E). Dorsal spines are fine, erect and as a rule dense, though there are exceptions. The Interarea is of moderate height, the ventral adductor platform of moderate height and length, and median dorsal septum sturdy, up to two thirds of the valve in length.

Holotype: UQF 75235 figured by Briggs (1998, Fig. 46A) from Belford Formation, north Sydney Basin, OD.


A


B

Fig. 17. *Echinalosia* (*Echinalosia*) *maxwelli robusta* Briggs. A, ventral valve UQF 75238, x2. B, dorsal aspect of conjoined shell, UQF 75242, x2. From Belford Formation, north Sydney Basin. (Briggs 1998).

Morphology: Briggs (1998, p. 90) alleged that this taxon *robusta* was a species to be distingushed by its larger size from *Echinalosia maxwelli* of New Zealand, but size within populations depends on suitable or difficult environmental parameters, and the shape and basic features or ornament and internal musculature and septum are much the same in both *robusta* and *maxwelli.* The claim by Briggs that dorsal spines are more numerous in *robusta* than in *maxwelli* ignores the variation in both suites (see Waterhouse 1964, pl. 4, fig. 8, 10 for New Zealand specimens with numerous dorsal spines, and Briggs 1998, Fig. 46B, F for specimens with fewer dorsal spines than in Fig. 46D). According to Briggs (1998), New Zealand specimens assigned to *maxwelli* have fewer large erect spines than in *robusta*, but this is hard to sustain. The one real difference appears to lie in the presence of a number of sturdy erect spines lying over the posterior ventral shoulders in Belford and Oxtrack specimens that can only be matched in a few of the New Zealand specimens belonging to *maxwelli.* On that basis, *robusta* is recognized as a subspecies. There is intergradation of various features, and it would seem that essentially the two taxa are conspecific, as geographic variants.

Fig. 18. *Echinalosia* (*Echinalosia*) *maxwelli robusta* Briggs, ventral valve UQF 70536 x3, of debatable identity, referred variously to *discinia*, *robusta* or *denisoni.* The taxon *robusta* appears to be the most acceptable. Oxtrack Formation, southwest Bowen Basin, (Waterhouse 1986b, pl. 4, fig. 18).

Stratigraphy: The Letham Burn Member of New Zealand and the Belford Formation of the Sydney Basin share the same stratigraphic position above the faunas with *Echinalosia discinia* in the upper Letham Formation and Brae Formation and Elderslie Formation, and share important faunal elements, including *Paucispinauria concava*, and possible *Aperispirifer wairakiensis*. The Briggs interpretation that *E. maxwelli* is two zones older must be set aside. Briggs (1998) recorded *robusta* as extending into the overlying Nowra and Muree Formations of the Sydney Basin. That would be beyond the range achieved by *maxwelli maxwelli*, in Queensland and New Zealand, extending in those regions into the following *Pseudostrophalosia blakei* (= *ingelarensis*) Zone, and requires further study to support the claim, but is of interest in suggesting latitudinal differences that were controlling the time ranges for specimens in New South Wales as compared with Queensland. Provisionally this discrepancy between the Sydney Basin and the Bowen Basin with New Zealand is regarded as feasible, because *Ps. blakei* is absent from the Sydney Basin, and it is suggested that sediments with the same time span rocks were occupied by *robusta* with an extended range in New South Wales, as compared with Queensland.

Echinalosia maxwelli (Waterhouse). See *Echinalosia* (*Echinalosia*) *briggsi* Waterhouse.
Echinalosia davidi Briggs. See *Echinalosia* (*Glabauria*) *davidi.*
Echinalosia bookeri Briggs. Close to *Echinalosia* (*Echinalosia*) *denisoni* Archbold?.
Echinalosia discinia Waterhouse.
Echinalosia robusta Briggs. See *E.* (*Echinalosia*) *maxwelli robusta.*
Echinalosia hanloni Briggs. See *Echinalosia* (*Glabauria*) *hanloni.*
Echinalosia telfordi Briggs. See *Echinalosia* (*Glabauria*) *telfordi*.
Echinalosia runnegari Briggs. See *Echinalosia* (*Glabauria*) *runnegari.*
Echinalosia wassi Briggs. *See Maxwellosia ovalis wassi.*
Echinalosia denisoni Archbold.
Echinalosia minima (Maxwell), See *Echinalosia (Unicusia) minima.*
Echinalosia deari Briggs. See *Acanthalosia deari*
Echinalosia glabra Briggs. See *Nothalosina glabra*.
Echinalosia ovalis (Maxwell). See *Maxwellosia ovalis*.
Echinalosia voiseyi Briggs. See *Nothalosina voiseyi*.
Table 2. Summary of species, in order as described by Briggs (1998) from east Australian faunas judged to range from Kungurian to upper Capitanian in age.

SUBGENERA OF *ECHINALOSIA*

Subgenus ***Glabauria*** Waterhouse, 2010

Diagnosis: Ventral ears smooth apart from growth increments, ventral spines mostly or entirely recumbent and uniform or subuniform.

Type species: *Echinalosia runnegari* Briggs, 1998 from Mulbring Formation, north Sydney Basin, OD.

Discussion: This subgenus appears to have developed only in the Sydney Basin, subject of course to the content of undescribed faunas especially from Tasmania and New England Orogen. The largely spine-free ventral ears constitute a contrast with shells that bear a hinge row of stout spines, or bear several scattered spines.

Echinalosia (***Glabauria***) ***davidi*** Briggs, 1998

Fig. 19

1929 *Strophalosia gerardi* [not King]? – Booker, pl. 1, fig. 6, 7.
1998 *Echinalosia davidi* Briggs, p. 83, Fig. 43A-G.
2010 *E*. (*Glabauria*) *davidi* – Waterhouse, p. 51, Fig. 19A.

Diagnosis: Transversely oval to subcircular with short well-spaced prostrate spines, erect spines rare to absent. Dorsal spines fine, semirecumbent.

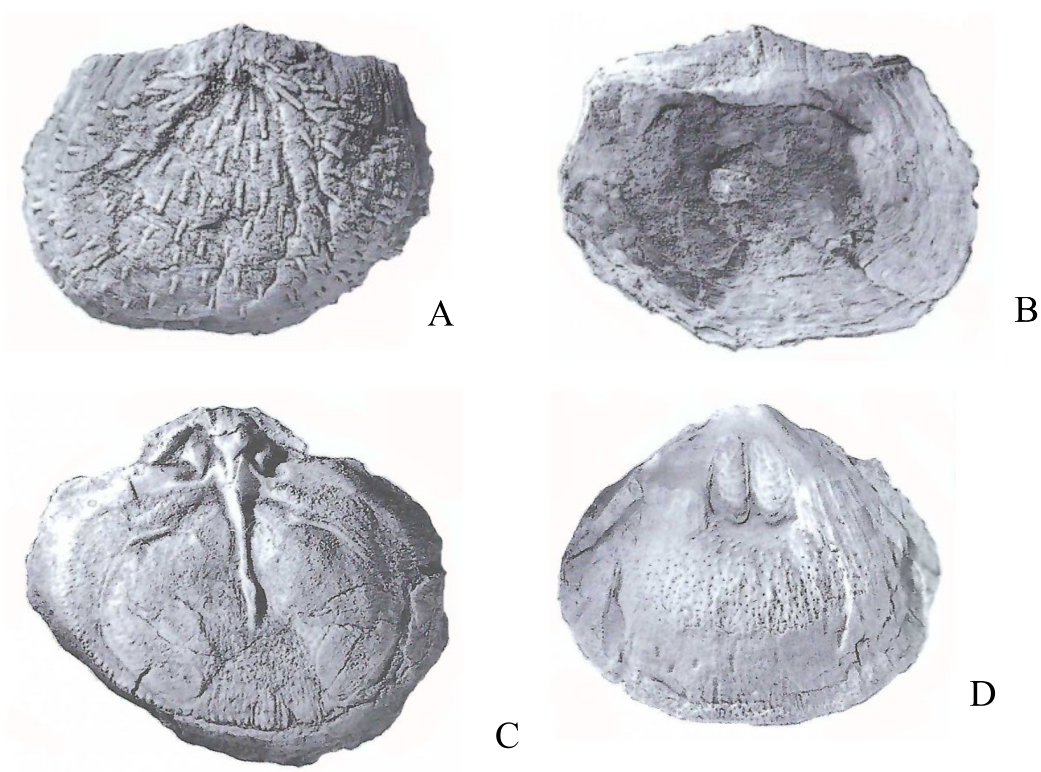


Fig. 19. *Echinalosia* (*Glabauria*) *davidi* Briggs. A, B, ventral and dorsal aspects of UQF 75224, holotype. C, dorsal interior UQF 75228. D, ventral internal mould UQF 75227. Specimens x2, from Fenestella Shale, Sydney Basin. (Briggs 1998).

Holotype: UQF 75224 figured by Briggs (1998, Fig. 43A, B) and Fig. 19A, B herein from Fenestella Shale, south Sydney Basin, OD.

Stratigraphy: This species is found in the Branxton Subgroup and Wandrawandian Formation of the Sydney Basin.

Echinalosia **(*Glabauria*)** ***hanloni*** Briggs, 1998

Fig. 20

1987 *Echinalosia* n. sp. no. 3 Briggs, p. 139.
1990 *Echinalosia* n. sp. C Briggs *in* Draper et al., p. 27.
1998 *Echinalosia hanloni* Briggs, p. 90, Fig. 47A-J.

Diagnosis: Medium in size, as a rule subequidimensional, weakly elongate to weakly transverse, with mostly moderately stout but varying recumbent ventral spines up to 0.8mm in diameter and few if any erect spines. Outer ventral ears free of spines. Dorsal spines fine and vary from erect to recumbent.

Holotype: UQF 75247 figured by Briggs (1998, Fig. 47B) and Fig. 20F herein from the Muree Formation of the north Sydney Basin, OD.

Morphology: Briggs emphasized that ventral spines were of a single recumbent series, but there is some variation in diameter, and although he stated that dorsal spines were recumbent, there appear to be a number that are erect (Briggs 1998, Fig. 47E). Unlike the type species of *Glabauria*, many of the ventral spines in *hanloni* are coarse, especially anteriorly. The affinities therefore are somewhat mixed, close to *Glabauria* in several respects, unique in other respects, as is to be expected where evolution is proceeding exuberantly along unrestricted lines. The dorsal shell is thickened in *hanloni* and in Tasmanian shells referred by Briggs (1998) to *hanloni,* but now reassigned to *Echinalosia* (*Unicusia*) *tasmantia* (see p. 56), and the shape is close in both suites, and spine tunnels few, but full comparison is frustrated by the differing modes of preservation. The ventral spines on the Tasmanian shells are slightly finer, **some four in 5mm, compared with three in 5mm** (assuming the Tasmanian figures are magnified at x1, a matter not stated). Clarke (1987, p. 264) provided no synonymy, claiming that would take too much space, and did not describe or illustrate the external ears. The dorsal valve was reported to have a flat disc and geniculate to short trail. (See Waterhouse 2001, p. 67). There appear to be no recumbent spines in the Tasmanian ventral valves.

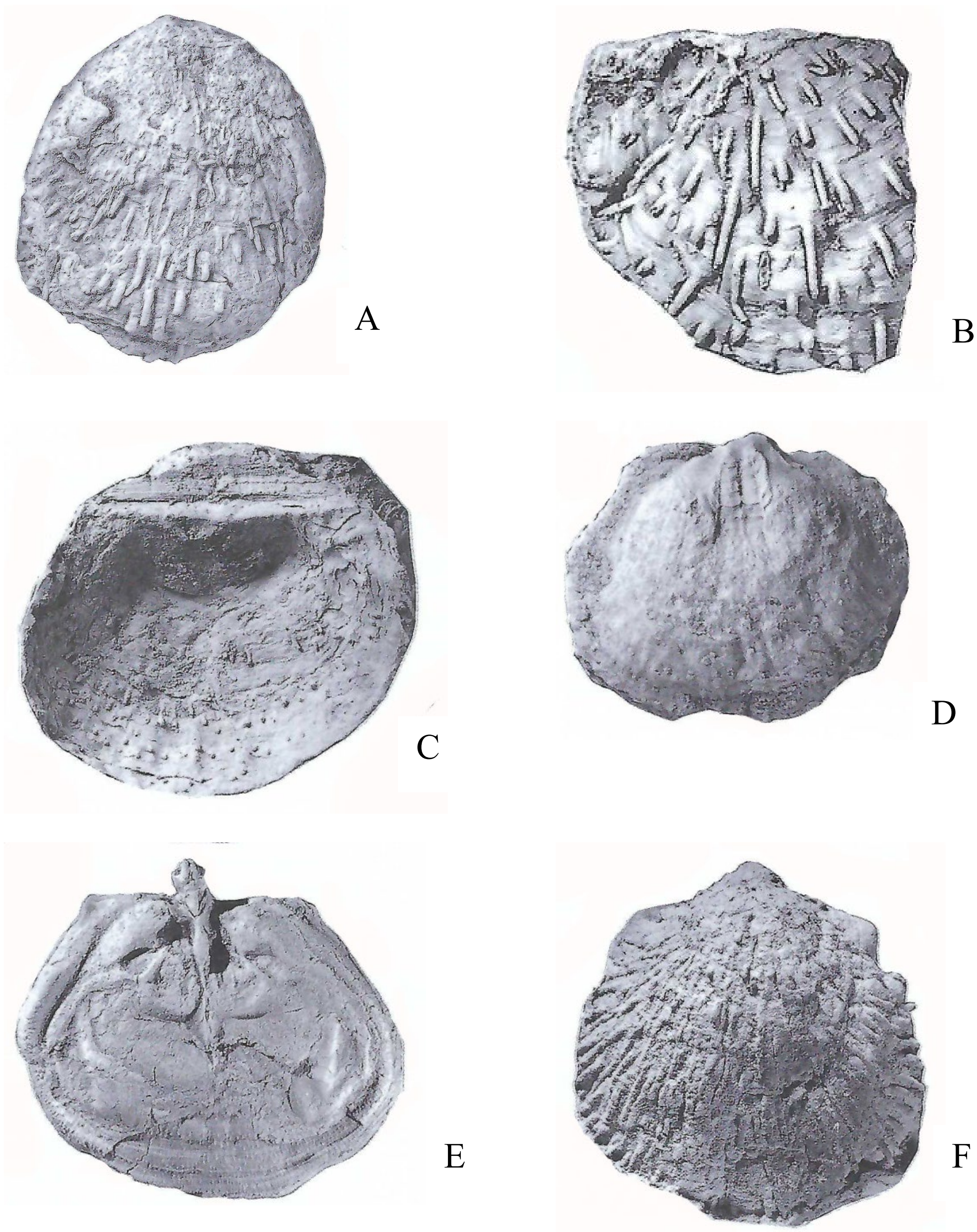


Fig. 20. *Echinalosia* (*Glabauria*) *hanloni* Briggs. A, ventral valve latex cast, MMF 2395, x1. B, part of posterior ventral exterior, latex cast associated with SUP 25553, x2.5. C, dorsal aspect of latex cast of specimen with valves conjoined, UQF 75249. D, ventral internal mould SUP 25539, x2. E, dorsal internal aspect UQF 75253, x1.5. F, latex cast of ventral exterior, UQF 75247 holotype, x2. A, C, E, F from Muree Formation, B and D from South Marulan. (Briggs 1998).

Stratigraphy: The species *hanloni* is found chiefly in the Muree Formation of the north Sydney Basin and has been reported in the Porcupine Formation of the Gunnedah Basin and in the Nowra Sandstone of the south Sydney Basin. There was also an unsubstantiated report of the species in the Belford Formation. Briggs (1998) referred material figured by Wass & Gould (1969, pl. 14, fig. 19) from South Marulan to the species, and although no ventral spines are shown in their figures, Briggs figured material that does show spines. The Tasmanian material described by Clarke (1987) from Malbina E has very different spines, so that the proven geographic range of the species appears to have been less than claimed by Briggs (1998).

Echinalosia (***Glabauria***) ***runnegari*** Briggs, 1998

Fig. 21

1998 *Echinalosia runnegari* Briggs, p. 93, Fig. 49A-I.
2010 *E*. (*Glabauria*) *runnegari* – Waterhouse, p. 51, Fig. 19B.

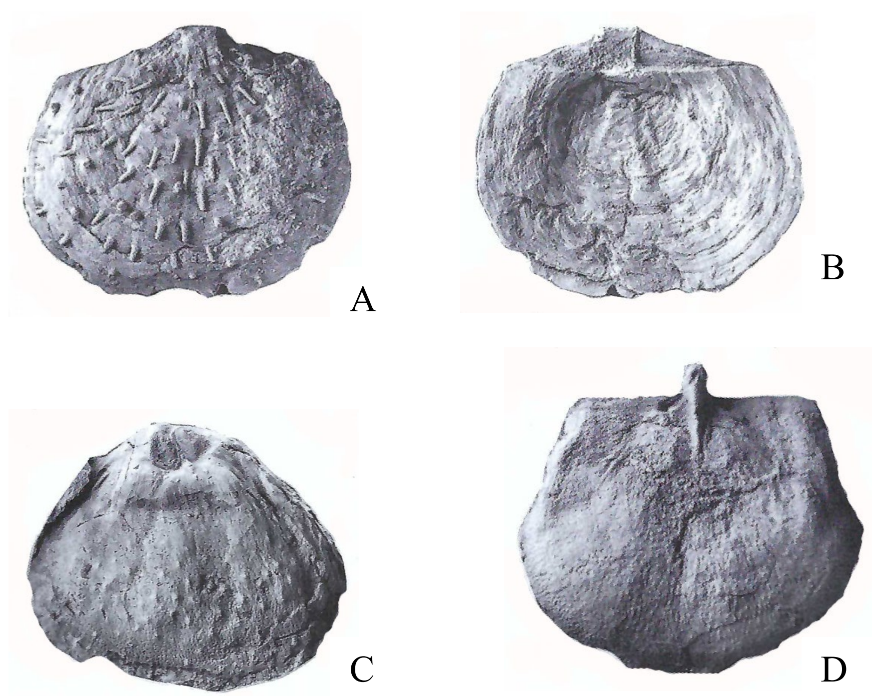


Fig. 21. *Echinalosia* (*Glabauria*) *runnegari* Briggs. A, B, dorsal and ventral aspects of conjoined shell, UQF 75258, x1.5. C, ventral internal mould, UQF 75262, x2, judged to be at early maturity. D, dorsal internal valve UQF 75263, x1.5. From Mulbring Formation. (Briggs 1998).

Diagnosis: Moderately large, ventral spines subuniform, distinguished by Briggs as one series that is prostrate to embedded, 0.3-0.5mm diameter, and another series as slightly coarser and rarer, varying from recumbent to suberect. However illustrations show that a few ventral spines are erect, and a few very thin. Dorsal spines up to 0.15mm in diameter anteriorly, described by Briggs (1998) as medium-angle recumbent, arranged in irregular transverse rows.

Holotype: UQF 75256 figured by Briggs (1998, Fig. 49A) from Berry Formation, south Sydney Basin, OD.

Stratigraphy: This species is typical of the younger Middle Permian faunas in the Sydney Basin, coming from the upper Nowra Formation, and overlying Berry Formation in the south Sydney Basin, as well as Mulbring Formation of the north Sydney Basin, and the Blue Mountains Shelf.

Subgenus ***Unicusia*** Waterhouse, 2022c

Diagnosis: Ventral valve tending to have subevenly spaced suberect and sturdy spines in commarginal rows; slender suberect spines rare over ventral valve. Marginal ridge well developed in both valves.

Type species: *Strophalosia clarkei* var. *minima* Maxwell, 1954, p. 547 from north Bowen Basin, OD.

Discussion: This subgenus incorporates species previously treated as members of *Echinalosia* ss. Ventral spines differ from those typical of that genus, in having fewer and inconspicuous slender spines over the ventral valve: most of the spines, indeed in some specimens all of the spines, are suberect and sturdy, and regularly spaced along commarginal rows. It appears that the lineage, a minor one, developed from *Echinalosia* (*Echinalosia*). The subgenus may well have given rise to the genus *Marginalosia* Waterhouse, 1978, which is mostly of Late Permian age, found in Nepal and New Zealand. This genus has no slender ventral spines: the spines are uniform and suberect, and the dorsal valve tended to become somewhat thickened, without being wedge-shaped. Dorsal spines are slender and erect, as in *Unicusia*, and dorsal dimples are well developed, and as in *Unicusia*, the marginal ridge is developed in both valves. Genus *Marginalosia* is treated as member of a separate tribe, Marginalosiini by Waterhouse (2013), because of the uniform nature of the ventral spines. See p. 84ff.

Echinalosia (***Unicusia?***) ***tasmantia*** (Waterhouse, 2001)

Fig. 22

1969 *Wyndhamia ovalis* [not Maxwell] – Clarke, p. 45, pl. 8, fig. 6.
1987 *Echinalosia ovalis* [not Maxwell] – Clarke, p. 264, Fig. 2A-L.
1998 *E. hanloni* [not Briggs] – Briggs, p. 91.
2001 *E. ovalis tasmantia* Waterhouse, p. 67.

Diagnosis: Medium-sized shells with convex weakly subpentagonal ventral valve displaying moderately wide hinge, spines crowded and subuniform, dorsal valve externally gently concave and slightly thickened, almost flat internally. Ventral adductors well-developed, low marginal ridge, dorsal valve with scattered erect and slender spines, interior with well-developed marginal ridge and large brachial shields.

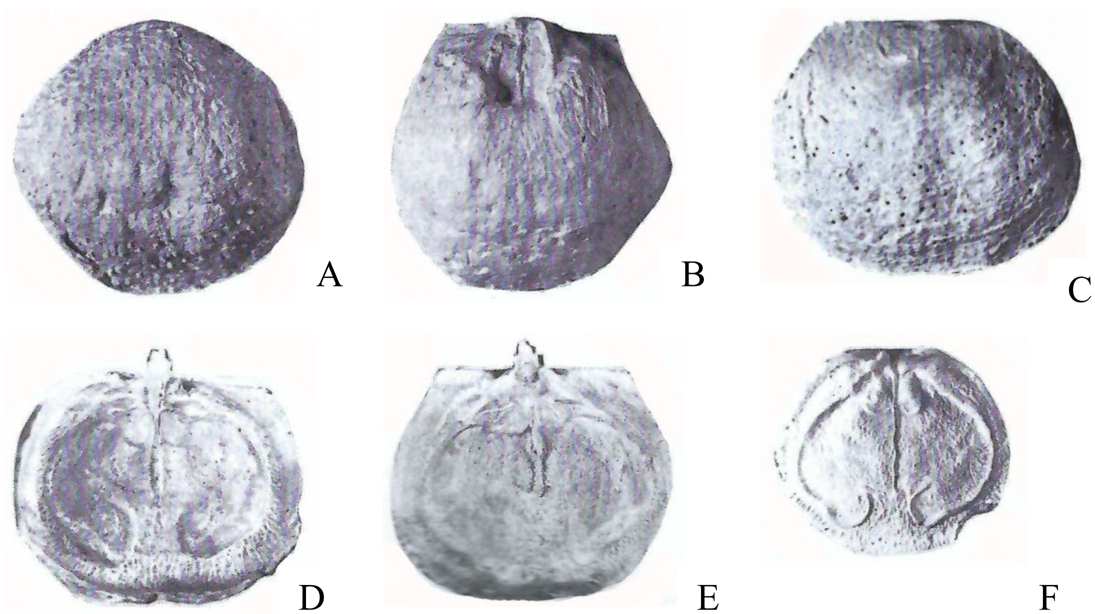


Fig. 22. *Echinalosia* (*Unicusia*)? *tasmantia* Waterhouse. A, latex cast showing ventral exterior, GST 14006A, holotype. B, ventral internal mould and same specimen. C, dorsal external mould GST 14005. D, dorsal internal mould GST 14007. E, latex cast of same specimen. F, internal mould of dorsal interior, GST 14009. Specimens from Malbina Formation, Member E, Tasmania. Size not specified, presumably x1. (Clarke 1987).

Holotype: GST 14006 figured by Clarke (1987, text-fig. 2A, B) and Fig. 22A, B herein from Malbina Member E, Tasmania, OD.

Morphology: This species was identified by Clarke (1969, 1987) as *Echinalosia ovalis*, but that species has now been shown to belong to *Maxwellosia*, whereas the ventral spine detail for *tasmantia*, as far as it is known, is close to that of *Echinalosia* (*Unicusia*), to judge from the nominated holotype, which shows closely spaced spines of uniformly fine size. Internally, both valves of the taxon show a marginal ridge, and the dorsal valve appears to be somewhat thickened anteriorly. The taxon approaches *Strophalosiara* (see p. 8) from the earlier Permian of Tasmania in its relatively fine and crowded ventral spines and thickened dorsal valve, but has dorsal spines, with apparently few and shallow dimples (Clarke 1987, Fig. 2H). Briggs (1998) referred the present specimens to *Echinalosia hanloni* Briggs, but his figures for *hanloni* show thick and thin spines for the ventral valve, long and recumbent but less crowded, so that any such comparison is not supported by what is known about the nature of the ornament in the Tasmanian material. The one available figure of the exterior for *tasmantia* shows erect spines, closely spaced and fine, 0.4 to little more than 0.6mm thick, apart from a very few thicker protuberances of uncertain nature. That leads to uncertainty. Is the figured specimen exceptional? Or was ornament variable? Or are there two species involved? Not satisfactory, but nothing can be done until the Tasmanian collections can be examined, and more precise, reliable and figured examples offered of spine ornament, and data on the ventral ears provided.

Stratigraphy: The species is known only from the upper Malbina Formation of Tasmania.

Echinalosia (***Unicusia***) ***telfordi*** Briggs, 1998

Fig. 23

1976 *Echinalosia ovalis* [not Maxwell] – Telford in Thomson (part, pp. 165, 166), fide Briggs (1998).
1998 *E. telfordi* Briggs, p. 91, Fig. 48A-F.
2022c *E.* (*Unicusia*) *telfordi* – Waterhouse, p. 138.

Diagnosis: Small subcircular shells, ventral valve with mostly suberect numerous and evenly spaced spines of subuniform diameter, increasing in size and spacing slightly from the umbo to the anterior margin, though becoming finer and more closely spaced anteriorly in the one figured ventral exterior. Dorsal spines finer, numerous and erect. Ventral muscle adductors compact and well-developed, dorsal marginal ridge prominent.

Holotype: UQF 75254 figured in Briggs (1998, Fig. 48F) and Fig. 23C herein from beds correlative with the Nowra Sandstone, south Sydney Basin, OD.

Morphology: Although Briggs (1998) reported slender prostrate ventral spines, very few are shown in the one figure provided by Briggs. Specimens examined by the author at the University of New England, Armidale, indicate that ventral spines are mostly subuniform and erect. Nor is his report of low to medium angle recumbent dorsal spines verified from his few provided figures, apart from a very few and rare examples involving a few spines, tending to be in small clusters.

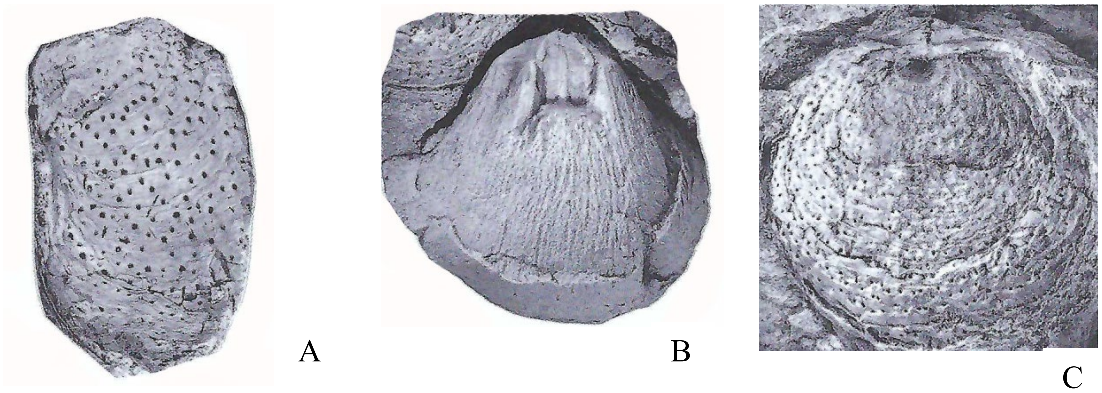


Fig. 23. *Echinalosia* (*Unicusia*) *telfordi* Briggs. A, part of ventral external mould, UQF 60649, x2. B, ventral internal mould UQF 60648, x2. C, dorsal aspect, external mould of specimen with valves conjoined, UQF 75254, holotype, x2. D, dorsal interior, latex cast UQF 75255, x4. From correlate of Nowra Sandstone, south Sydney Basin. (Briggs 1998).

Stratigraphy: The species was reported mostly from the Nowra Sandstone and correlative beds on the Illawarra Shelf and Ulladulla Shelf in the south Sydney Basin (Briggs 1998, p. 93). After examining collections at the University of New England at Armidale, Waterhouse (2002, p. 179) confirmed the occurrences in the Nowra Sandstone, and suggested the species appeared to range into the Berry Sandstone of the south Sydney Basin, and possibly into the Muree Sandstone of the north Sydney Basin.

Echinalosia* (*Unicusia*) *minima (Maxwell, 1954)

Fig. 24

1954 *Strophalosia clarkei* var. *minima* n. var. Maxwell, p. 547, pl. 56, fig. 9-11.
1954 *Strophalosia ovalis* Maxwell, p. 548, pl. 57, fig. 10-12 (part, not fig. 4-9, 13 = *clarkei*).
1964 *S. clarkei minima* – Hill & Woods, pl. P4, fig. 13a, b (part, not fig. 14 = *maxwelli robusta*).
1965 *S. minima* – Waterhouse & Vella, p. 62, pl. 2, fig. 4.
1971 *Echinalosia minima* – Dear, p. 7, pl. 3, fig. 11-16.
1972 *E. minima* – Hill & al., pl. P4, fig. 13a, b (part, not fig. 14 = *maxwelli robusta*).
1980 *E. minima* or *E. maxwelli* – McClung photo 19.1, fig. 2.
1987 *Wyndhamia minima* – Briggs, p. 140 (part).
1998 *E. minima* – Briggs, p. 99, Fig. 52A-F.
2022c *Echinalosia* (*Unicusia*) *minima* – Waterhouse, p. 130, Fig. 3-10.

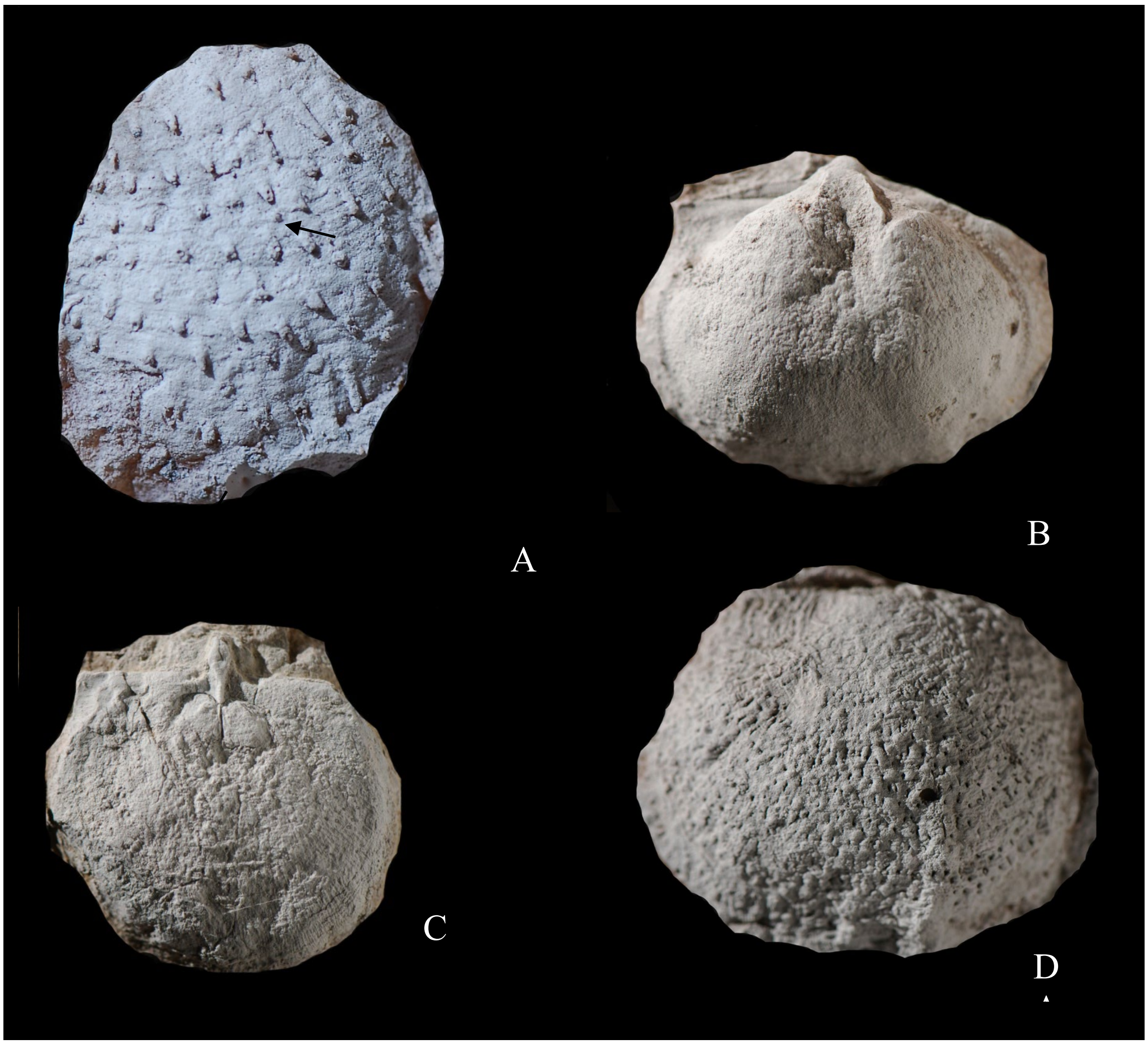


Fig. 24. *Echinalosia* (*Unicusia*) *minima* (Maxwell). A, latex cast of part of the ventral valve, showing the characteristic subevenly spaced semirecumbent spines typical of the subgenus. Arrow points to a rare fine spine. UQF 82625, x3.5. B, ventral internal mould UQF 82630, x1.2. C, dorsal interior UQF 82641, x2, with alveolus in cardinal process. D, dorsal external mould UQF 82638, x1.5. Blenheim Formation. (Waterhouse 2022c).

Diagnosis: Transverse to subcircular, wide hinge, often weakly sulcate, moderately high subelongate ventral adductor field. Ventral spines predominantly suberect, not coarse, regularly arranged in commarginal rows, rare and in some specimens no fine prostrate spines, dorsal valve sublamellate with moderately firm erect spines, and numerous regularly arranged pits which may be slightly elongate. Well-developed internal marginal ridge on both valves.

Holotype: UQF 16262 from Pelican Creek band, north Bowen Basin, figured by Maxwell (1954, pl. 56, fig. 9, 10), Hill & Woods (1964, pl. P4, fig. 13a, b) and Hill et al. (1972, pl. P4, fig. 13a, b), OD.

Morphology: This species is highly distinctive, generally but not always with a very wide hinge, well-spaced ventral spines, and well-developed marginal ridge in each valve. The dorsal valve may be slightly thickened. The species is further described and illustrated, with extensive synonymy, in Waterhouse (2022c, p. 130 ff). On p. 121-122 a discussion is provided of an attempted re-interpretation by Briggs (1998) of a ventral valve figured by Maxwell (1954, pl. 57, fig. 10-12) and accepted by Dear (1971). The Briggs version appears to be contradicted by the appearance of the internal ventral mould figured herein as Fig. 24B.

Stratigraphy: The species characterizes a zone in the late Middle Permian of the northern Bowen Basin, extending from above the Scottville Member to take in the Pelican Creek fauna according to the biostratigraphic terms proposed by Dear (1972). Admittedly Hill & Woods (1964) and Dear (1971) implied that *minima* appeared in the “Big Strophalosia Zone”, but I have not been able to confirm this, and find that the species first appears immediately above, in a band with *Pseudostrophalosia furcalina* Waterhouse, that may have been confused with *Ps. clarkei* which betokens the Big Strophalosia Zone. The species is also found in the Flowers Formation of northwest Nelson, New Zealand.

Genus ***Nothalosina*** Waterhouse, 2010

Diagnosis: Distinctively shaped, ovally transverse, wide high ventral interarea, ventral spines of disc and trail in two series, one of low angle recumbent spines, usually thick, but varying a little, arranged in regular commarginal rows, interspersed with a series of numerous short fine erect or semi-recumbent prostrate spines. Hinge row of erect spines, including up to three large lateral spines on ears. Dorsal spines fine, erect, subevenly dispersed over disc and trail, up to 0.2mm in diameter. No radial capillae, apparently no dorsal dimples.

Type species: *Echinalosia voiseyi* Briggs, 1998, p. 105 from Gilgurry beds of New England, New South Wales, OD.

Discussion: This genus is outstanding in the arrangement of the ventral spines, and its ancestral stock is far from clear, although presumably some form of *Echinalosia* was involved. "*Echinalosia*" *mcclungi* Briggs, which may well prove to belong to *Nothalosina*. As discussed on pp. 143-145, this species from the Snapper Point Formation shows a diversity of ventral spines, including strong posterior lateral spines, and a mix of dorsal spines, and examination of *mcclungi* is required to consolidate or refute this possibility.

Nothalosina voiseyi (Briggs, 1998)

Fig. 25, 26

1998 *Echinalosia voiseyi* Briggs, p. 105, Fig. 56A-E.
2010 *Nothalosina voiseyi* – Waterhouse, p. 52, Fig. 20A, B, 21A-C.

Diagnosis: Transverse shells with gently concave dorsal valves, strong spines over ventral posterior lateral slopes, ventral disc spines in two series and dorsal spines fine and erect.

Holotype: UQF 75273 figured by Briggs (1998, Fig. 56C) from Gilgurry Mudstone, OD.

Fig. 25. *Nothalosina voiseyi* (Briggs). latex cast of ventral exterior UQF 75270, x2.5, showing massive ear spine as arrowed and two series of spines along uneven commarginal rows From Gilgurry Mudstone. (Briggs 1998).

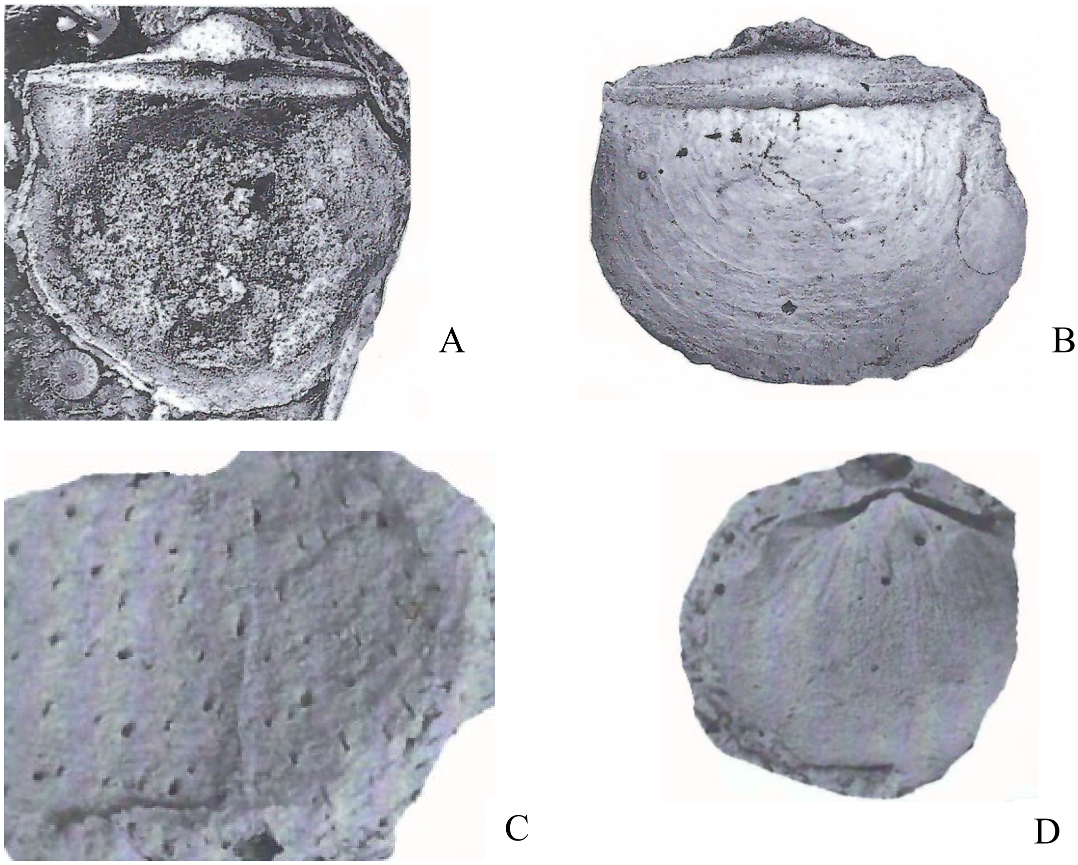


Fig. 26. *Nothalosina voiseyi* (Briggs). A, dorsal aspect of specimen with valves conjoined, latex cast, UQF 75272, x2. B, dorsal aspect of external mould, valves conjoined, UQF 58928, x2. C, ventral external mould UQF 75270 x2. D, ventral internal mould UQF 75271, x2. Specimens from Gilgurry Mudstone, northern New South Wales. (A, B, Briggs 1998; C, D, Waterhouse 2010).

Morphology: Briggs (1998, p. 107) recorded ventral spines as being in two series "both extremely fine", one series prostrate, reaching 0.2mm diameter and 1mm long, and the other series low angle recumbent, half as numerous, reaching 0.25 mm diameter. But Fig. 25 and 26 herein show that this may not be correct. In these figures all spines are erect, and either fine (0.2-0.3mm) or coarse (0.5-0.6mm) in diameter, and the relative numbers judged from the figures seem questionable. There appear to be about twenty five spines along a commarginal row in the ventral valve and possibly as many as forty in the dorsal valve.

Stratigraphy: This genus and species has only been reported up to now from the Gilgurry Mudstone of northern New South Wales. The age has been subject to some dispute. Briggs (1998) regarded the species as younger than *Echinalosia* (now *Maxwellosia*) *ovalis*, basing his claim on the speculation that his species *Lethamia condaminensis* from the *voiseyi* Zone of the Condamine Block near Warwick, south Queensland, could be the same as *Lethamia collina* from the Arthurton rocks of New Zealand, which is placed in the *Martiniopsis woodi* Zone of Wuchiapingian age. But *collina* is more hunched with higher posterior walls, and the two species do not appear to be conspecific (Waterhouse 2023, pp. 73. 74).

Questions were also raised by Armstrong & Telford (1967, p. 116) about the possible relationship and conspecity of *Attenuatella multispinosa* Waterhouse, 1967b from the Gilgurry Mudstone near Drake, New South Wales, with *A. incurvatus* Waterhouse, 1964 from the *Plekonella multicostata* Zone of lower Changhsingian age in New Zealand. The similarity could be generic rather than specific. The two species, originally assigned to *Attenuatella* Stehli are now referred to *Attenuocurvus* Waterhouse, because they have uniformly fine spines, in contrast to the diversely spinose condition of *Attenuatella*. The age for the Gilgurry fauna remains unclear, and clarification would be aided by attention to the whole fauna. Armstrong throughout his brief but promising career as a paleontologist was determined, despite the lack of evidence, to homogenize the sequences of east Australia with those of New Zealand, and make them identical.

As a possibility, it could be conjectured that the Gilgurry beds and fauna are of early or middle Wuchiapingian age, equivalent to thick beds of the Glendale Formation and equivalent limestones and clastics in southern New Zealand which lack any wide-ranging or numerous fossils that might serve as zonal indices.

Nothalosina? glabra **(**Briggs, 1998)

Fig. 27, 28

1892 *Strophalosia gerardi* [not King] – Etheridge Jnr, p. 260, pl. 40, fig. 7 only.
1986b *Echinalosia ovalis* [not Maxwell] – Waterhouse, p. 31, pl. 5, fig. 3-8 (fide Briggs 1998).
1998 *E. glabra* Briggs, p. 103, Fig. 54A-G.

Diagnosis: Medium-large transverse shells with rounded cardinal extremities and fine ventral spines in two series, a fine recumbent series 0.1 to 0.15 mm in diameter, and a slightly thicker erect series, with about thirty spines along a commarginal row near mid-length of the ventral valve. Distinctly stronger

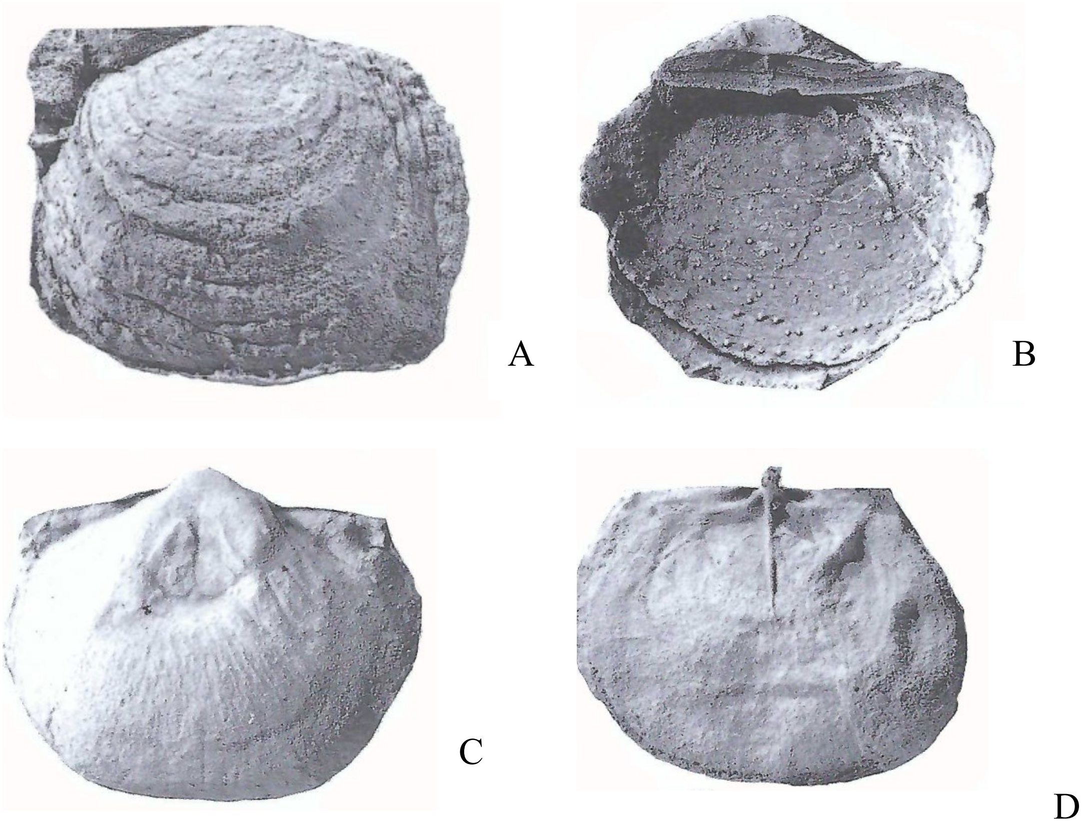


Fig. 27. *Nothalosina*? *glabra* (Briggs). A, latex cast of ventral exterior, UQF 27677, holotype. B, dorsal aspect of latex cast of specimen with valves conjoined, AMF 96236. C, ventral internal mould AMF 96235. D, dorsal interior GSQF 13476. Specimens from Flat Top Formation, x2. (Briggs 1998).

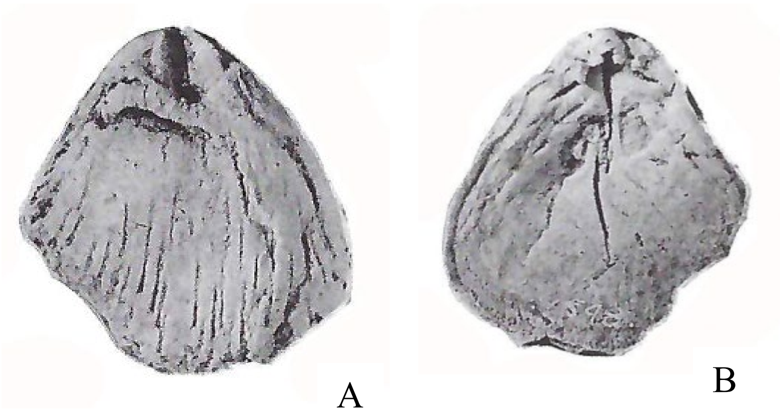
spines in two or three rows lie close to the lateral margins, Briggs mentioning “about eight spines of erect series concentrated in loose group near each ear”, and spines are slightly finer anteriorly, with over forty in a row along the dorsal anterior. Dorsal spines fine, 0.2mm diameter, erect and moderately numerous, no dorsal dimples. Ventral interarea high, ventral adductors broad and well developed.

Holotype: UQF 27677 figured by Briggs (1998, Fig. 54B) and Fig. 27A herein, Flat Top Formation, southeast Bowen Basin, OD.

Morphology: No fold is present in the dorsal valve of Briggs figured material, nor in the specimen figured by Waterhouse (1986b, pl. 5, fig. 4). An internal mould figured from ventral and dorsal aspects by Waterhouse (1986b, pl. 5, fig. 7, 8) is much narrower that the now lost specimens of *glabra* figured by Briggs (1998). *Echinalosia* species, notably including the type species *E.* (*E.*) *maxwelli*, vary in width, so these particular Flat Top specimens cannot be confidently excluded from synonymy with other specimens in the same collection (see Fig. 28). Despite Briggs' opinion that such specimens belonged to *deari* Briggs, type *deari* has a less concave dorsal valve and different spines over both valves, and as far as is known, *deari* lacks spine tunnels, being now referred to *Acanthalosia*. (See p. 70).

The Etheridge specimen mentioned in the synonymy, adopted from Briggs (1998), is a transverse dorsal valve with fold from Banana Creek in Queensland. Although it suggests *minima*, this form is not known in the Banana Creek area, so the proposal that the figure represents *glabra* is reasonable.

Briggs (1998, p. 103) gave slightly differing synonymies for the Waterhouse 1986b specimens, as pl. 5, fig. 3, 5-8 in the text and pl. 5, fig. 3, 4, ?5, 8 in his synonymy.



A B

Fig. 28. .Possible *Nothalosina*? *glabra* Briggs. A, B, ventral and dorsal aspects of internal mould UQF 73974 x1.5, from lower Flat Top Formation, southeast Bowen Basin. Briggs (1998) judged this specimen to belong to *deari* Briggs, but the concavity of the dorsal valve and presence of spine tunnels suggests it belongs to *E. glabra* or even *Maxwellosia ovalis.* (Waterhouse 1986b).

Stratigraphy: This species, judged from the associated fauna, is largely contemporaneous with the Mantuan fauna bearing *Maxwellosia ovalis*, which as analyzed on p. **77** ff is clearly a different strophalosioid genus.

Tribe **ACANTHALOSIINI** new tribe

Name genus: *Acanthalosia* Waterhouse, 1986b from Fairyland Formation, Bowen Basin, Queensland, here designated.

Diagnosis: Ventral spines crowded, many long, of varying diameters, linear and not vermiform. Dorsal spines also vary somewhat in diameter, crowded but may be less diverse than those of ventral valve.

Discussion: Two genera are assigned to the tribe. These two were originally classed as Dasyalosiinae Brunton in Brunton et al. (2000, p. 569) and Waterhouse (2013, 2015a).

Genus ***Acanthalosia*** Waterhouse, 1986b

Diagnosis: Ventral spines of differing diameters, densely packed and with uneven spacing, varyingly erect to recumbent. Dorsal valve very gently concave, spines dense and vary from prostrate to suberect, and of varying diameters. The ventral valve in the type species of this genus appears to lack spine channels, at least in available material.

Type species: *Acanthalosia domina* Waterhouse from Fairyland Formation, southeast Bowen Basin, OD.

Discussion: The genus *Acanthalosia* has dense spines of varying diameters over both valves, and its dorsal valve is only gently concave externally. Just three species are known, the type species, found in the Bowen Basin, *A. mysteriosa* Waterhouse from the Cattle Creek Formation (Aktastinian) of the southwest Bowen Basin, and *A. deari* (Briggs) of early Capitanian age in the southeast Bowen Basin. Members of the genus are readily distinguished from species related to *Echinalosia* by their dorsal valve, which is of low concavity, as well as the nature of the spines and the apparent lack of ventral spine channels. Spines are crowded over both valves as in *Dasyalosia* Muir-Wood & Cooper, but the spines of *Acanthalosia* are not vermiform, to suggest that the two genera need not be closely related.

Acanthalosia domina Waterhouse, 1986b

Fig. 29, 30

1986b *Acanthalosia domina* Waterhouse, p. 32, pl. 5, fig 9-18, pl. 15, fig. 8.
1998 *A. domina* – Briggs, p. 108.
2000 *A. domina* – Brunton et al., p. 569, Fig. 405.1a-d.
2008 *A. domina* – Waterhouse, p. 356, Fig. 3I, J.

Diagnosis: Subequidimensional shells, ventral valve gently arched, dorsal valve gently concave and a little thickened. Ventral spines diverse and crowded, erect spines varying as rule in diameter between 0.7mm and 1.1mm and not regularly disposed over the valve, but crowded in patches, fine slender prostrate spines as well. Dorsal spines comparatively numerous, may be prostrate but usually suberect, somewhat varied in diameter, up to 0.5mm or more anteriorly. No dorsal dimples. Spine tunnels apparently absent from ventral valve.

Holotype: UQF 73978 from Fairyland Formation, southeast Bowen Basin, figured by Waterhouse (1986b, pl. 5, fig. 11), OD.

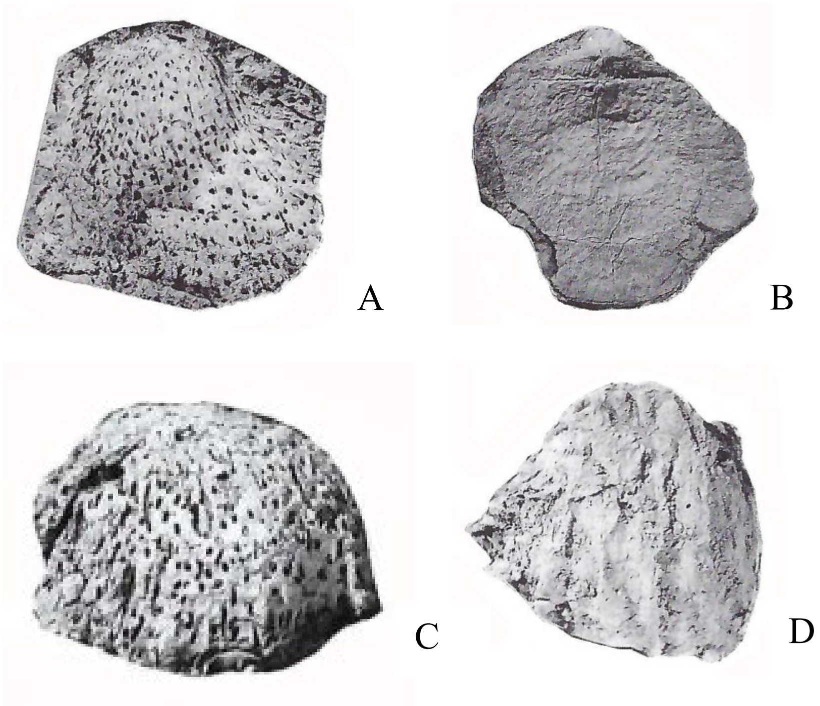


Fig. 29. *Acanthalosia domina* Waterhouse. A, external mould of ventral valve UQF 73976. B, dorsal aspect of specimen with valves conjoined, UQF 73981. C, external mould of dorsal valve UQF 73969 x1.5,. D, ventral internal mould UQF 73983. From Fairyland Formation, southeast Bowen Basin, x1. (Waterhouse 1986b).

Morphology: Briggs (1988) asserted that ventral spines occur in only two series, but the spinosity is much more complex, and show a range of diameters.

Stratigraphy: The species so far is limited to the Fairyland Formation. The scattering of other Queensland occurrences reported by Briggs (1998) need to be supported by illustrations and text, because it has been found that so many of his observations require adjustment so they must remain in limbo until well substantiated and preferably supported by figures. Certainly the Briggs claim that the species is present in the Roses Pride Formation must be rejected – a different species is found there, with finer spines.

Acanthalosia mysteriosa Waterhouse, 2010

Fig. 30

1977 *Echinalosia* sp. nov. McClung, p. 575.
1986b ?*Echinalosia* cf. *brittoni* [not Maxwell] – Waterhouse, p. 27, pl. 5, fig. 19-23, pl. 15, fig. 6, 7.
1987 *Acanthalosia* Waterhouse, p. 212, Table 11.
1998 *Acanthalosia* n. sp. Briggs, p. 111, Fig. 58.
1998 *Pseudostrophalosia brittoni* [not Maxwell], Briggs, p. 113 (part).
2010 *Acanthalosia mysteriosa* Waterhouse, p. 57, Fig. 24.

Diagnosis: Ventral valve moderately convex, dorsal valve almost flat. Ventral spines dense and crowded, varying considerably in diameter but all relatively fine, measuring 0.5 - 0.7mm in diameter, and mostly though not entirely erect. The dorsal valve is moderately concave to almost flat, and its spines are numerous and erect**.**

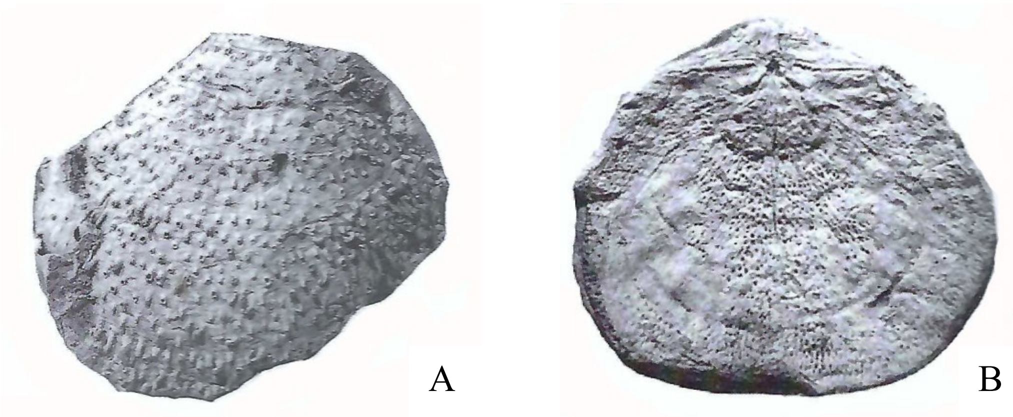


Fig. 30. *Acanthalosia*? *mysteriosa* Waterhouse. A, ventral valve GSQF 13485, x4. B, dorsal aspect, worn specimen with valves conjoined, UQF 73990, x2. Roses Pride Formation. A, Briggs 1998, B, Waterhouse 2010).

Holotype: UQF 73985 from Roses Pride Formation, southeast Bowen Basin, figured by Waterhouse (1986b, pl. 5, fig. 19, 20), OD.

Morphology: Although few specimens have been described or illustrated, this species is abundantly represented in the southwest Bowen Basin of Queensland and in collections at the Queensland Museum. The ventral spines are less evenly spaced than in *Echinalosia* (*Unicusia*) *tasmantia* (see p. 56**)** from the somewhat younger Malbina E beds of Tasmania and are arguably more diversified in diameter. Certainly there is some approach between the two species, including almost flat dorsal exterior and fine spines, so that more work is advisable to clarify the relationship between the two taxa, and confirm or rule out the possibility that separate genus or subgenus is involved.

Stratigraphy: The species is found in the Roses Pride and Cattle Creek Formations of southeast and southwest Bowen Basin. This level is understood to be somewhat older than that of *tasmantia*.

Acanthalosia deari (Briggs, 1998)

Fig. 31

1971 *Wyndhamia ingelarensis* [not Dear] – Dear, p. 12, pl. 3, fig. 10 (part, not fig. 5-9 = *ingelarensis-blakei* Dear).
1986b *W. blakei* [not Dear] – Waterhouse, p. 33, pl. 5, fig. 24, 29, 30, pl. 6, fig. 1, 2, pl. 15, fig. 10 (part, not pl. 5, fig. 25, 26?, 28 = *Nonauria parfreyi* (Waterhouse).
1998 *E. deari* Briggs, p. 101, Fig. 53A-C (part, not *N. parfreyi* as above).
2001 *Acanthalosia deari* – Waterhouse, p. 83.
2008 *A. deari* – Waterhouse, p. 366, Fig. 8B, C.

Diagnosis: Small subelongate shells with gently concave ventral valve and very gently concave dorsal valve, narrow hinge, both valves ornamented by dense comparatively fine spines which are moderately variable over ventral valve. No dorsal dimples, no spine tunnels.

Holotype: UQF 73991 from lower Flat Top Formation figured by Waterhouse (1986b, pl. 5, fig. 24, 29) and Fig. 31A herein, OD.

Morphology: The almost flat but not wedge-shaped dorsal valve and the dense spination indicate a species far removed from typical *Echinalosia*.

Stratigraphy: The species is limited to the lower Flat Top Formation and the Barfield Formation. Claims by Briggs (1998) that the species occurred in the Eddystone 1 core

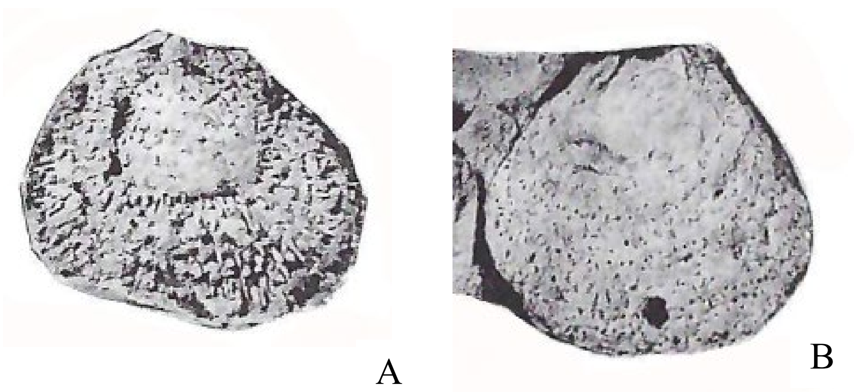


Fig. 31. *Acanthalosia deari* (Briggs). A, latex cast of ventral exterior, UQF 73991, holotype. B, external mould of dorsal valve UQF 73992. Specimens x2 from lower Flat Top Formation. (Waterhouse 1986b).

described by McClung (1983, Fig. 14.3-5, 7, 8) and in the lower middle Flat Top faunas (eg. Waterhouse 1986b, pl. 5, fig. 6, 7), as urged by Briggs, cannot be sustained. The McClung specimens appear to belong to *Pseudostrophalosia blakei/ingelarensis,* and the lower middle Flat top specimens come from with a large suite with species differing from those associated with type *deari,* His so-called *deari* from these faunas have a much more concave dorsal valve, and different spine ornament. See p. 66, and Fig. 28.

Genus ***Maxwellosia*** Waterhouse, 2013

Diagnosis: Moderately concavo-convex, dorsal valve deeply concave, shells medium-sized to large for the genus with crowded erect spines in several orders over ventral valve, many spines in commarginal rows, but many also irregularly disposed, and may be in clumps, prostrate spines thin to almost as strong as erect or suberect series, but rare as a rule. Dorsal spines also crowded and largely erect, varying slightly to considerably in diameter; no dimples. Ventral interior with moderately prominent spine tunnels.

Type species: *Strophalosia jukesi concava* Maxwell, 1954, p. 551 from the Wallaby rocks of southeast Queensland, OD.

Discussion: Type *Echinalosia* has ventral spines of two series, and dorsal spines of a single erect series, whereas the arrangement in *Maxwellosia* involves an array of ventral spines displaying different diameters, somewhat irregularly arranged, and mostly to entirely erect. Dorsal spines are somewhat differentiated and erect to semirecumbent. The dorsal valve is deeply concave, in contrast to the flat or gently concave dorsal valve of *Acanthalosia* Waterhouse, 1986b.

Amongst the species assigned herein to the genus, that named *curtosa* is particularly inflated with ventral spines that are mostly sturdy and erect, whereas the other species are broader with less arched discs and more ventral spines are slender and erect.

Maxwellosia curtosa (Waterhouse, 1986b)

Fig. 32

1986b *Echinalosia curtosa* Waterhouse, p. 24, pl. 3, fig. 5-14, pl. 15, fig. 9.
1989 *E. curtosa* – Waterhouse, pl. 1d.
1998 *E. curtosa* – Briggs, p. 72, Fig. 38B-H (part?, 33A close to *sulcata*).
2008 *E. curtosa* – Waterhouse, p. 355, Fig. 3E-G.

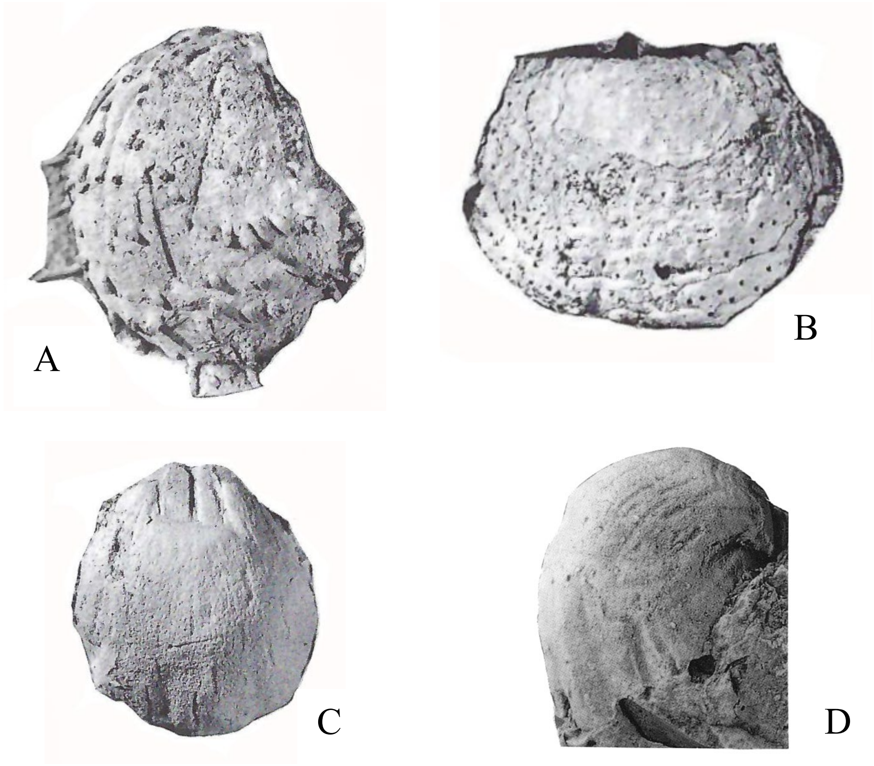


Fig. 32. *Maxwellosia curtosa* (Waterhouse). A, latex cast, ventral valve, UQF 73944, x2. B, dorsal external mould, UQF 73945, x1.25. C, ventral internal mould, UQF 73947, x1.75. D, ventral internal mould CPC 31669, showing high inflation From Fairyland Formation, southeast Bowen Formation. (A-C, Waterhouse 1986b; D, Briggs 1998).

Diagnosis: Subelongate arched shells, ventral spines up to 0.8mm in diameter and mixed suberect and prostrate, dorsal spines about 0.3mm in diameter, erect, crowded. A few short spine tunnels. Ventral muscle scars elongate.

Holotype: UQF 74270 from Fairyland Formation, southeast Bowen Basin, figured in Waterhouse (1986b, pl. 3, fig. 5, 6, 10, 11), OD.

Morphology: Although Briggs (1998) claimed that spine tunnels were restricted to the posterior part of the ventral valve, this does not appear to true of several specimens, as shown by the specimen figured by Waterhouse (1986b, pl. 3, fig. 10) and, reproduced herein as Fig. 33C. Shallow dimples are common in the dorsal valve.

Stratigraphy: This species is found in the Bowen Formation in the Fairyland Formation, of early Sakmarian age. Briggs (1998) reported specimens in the Farley Formation at the Lochinvar Anticline, though one of his figures suggests *Echinalosia* (*E.*) *sulcata* (see p. 33).

Maxwellosia bryani Waterhouse, 2015a

Fig. 33

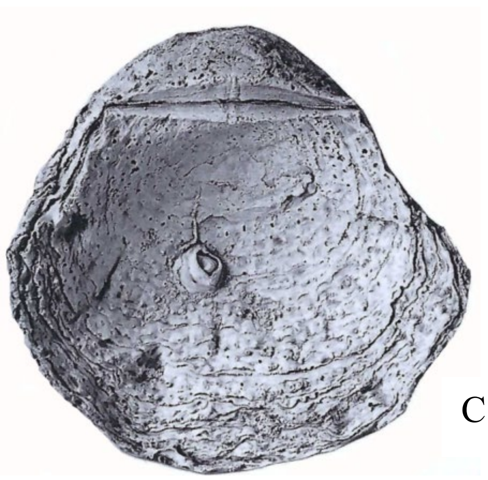
2013 *Maxwellosia* n. sp. Waterhouse, p. 226, Fig. 7.17, 7.18.
2015a *Maxwellosia bryani* Waterhouse, p. 92, Fig. 42-49.

Diagnosis: Ventral valve highly convex, ornamented by coarse erect spines 0.8mm to 1.5mm in diameter, and moderate number of recumbent spines 0.3mm to 0.8mm in diameter, width variable. Dorsal valve with erect spines 0.4-0.5mm in diameter and rare to moderately numerous low angle recumbent spines of similar diameter. Ventral spine tunnels well developed.

Holotype: UQF 81269 from middle Tiverton Formation, north Bowen Basin, figured in Waterhouse (2015a, Fig. 43) and herein as Fig. 33C, OD.

\ A

B



C

Fig. 33. *Maxwellosia bryani* Waterhouse. A, part of latex cast of ventral exterior, UQF 81804, x2. B, part of ventral external mould showing spine bases, UQF 81804, x7. C, dorsal aspect of latex cast of specimen with valves conjoined, UQF 81269, x1.5, holotype. From middle Tiverton Formation. (Waterhouse 2015a).

Morphology: A range of specimens are described and figured in Waterhouse (2015a). Uncertainty surrounds the ventral internal mould figured as *Strophalosia preovalis* [not

Maxwell] by Hill & Woods (1964, pl. P4, fig. 9 (part, not fig. 6-8 = *preovalis)* and as *Echinalosia preovalis* by Hill, Playford & Woods (1972, pl. P4, fig. 9 (part, not fig. 6-8 = *preovalis*). Also the ventral external mould figured by Hill & Woods (1964, pl. P4, fig. 10) shows the ornament somewhat poorly, and shows little of the ears, and of course nothing of the dorsal valve, and so is of uncertain allegiance, but possibly belonging to *Pseudostrophalosia brittoni*. Briggs (1998, p. 108) assigned Fig. 10 to *Acanthalosia domina*, and Hill & Woods (1964, pl. 4, fig. 9) to *Echinalosia warwicki*. The identifications are feasible and require first hand validation, and a different view is expressed on p. 38.

Stratigraphy: This species is found in the lower and upper middle Tiverton Formation, in the *Magniplicatina undulata* and *Taeniothaerus subquadratus* Zones (see Waterhouse 2021d). Few macrofaunas of this age have been comprehensively described from these levels throughout east Australia, so that the full stratigraphic extent of the species is yet to be established.

Maxwellosia concava (Maxwell, 1954)

Fig. 34, 35

1924 *Strophalosia jukesi* [not Etheridge] – Richards & Bryan, pl. 20, fig. 4.
1954 *S. jukesi* var. *concava* Maxwell, p. 551, pl. 56, fig. 23, 24, pl. 57, fig. 1-3.
1964 *S. jukesi* var. *concava* – Hill & Woods, pl. P4, fig. 15.
1972 *Wyndhamia jukesi* [not Etheridge] – Hill. Playford & Woods, pl. P4, fig. 15.
1986b *Acanthalosia domina stanthorpensis* Waterhouse, p. 33.
1998 *A. concava* – Briggs, p. 108, Fig. 57A-I.
2010 *A. concava* – Waterhouse, p. 57, Fig. 23.

Diagnosis: Moderately large with dense ventral spines of differing diameters, densely packed and with uneven spacing, varyingly erect through recumbent. Dorsal valve deeply concave, spines dense and vary from prostrate to suberect, and of varying diameters, less variable than those of ventral valve. Ventral adductors long, spine tunnels developed in ventral valve.

Holotype: UQF 15638 from higher beds of "Wallaby Rocks", Stanthorpe Road Block, south Queensland, figured by Maxwell (1954, pl. 57, fig. 2, 3), OD.

Morphology: The presence of many recumbent moderately thick spines over the ventral valve recalls those of *Echinalosia* (*Glabauria*) *hanloni* from Tasmania, but the ears of the present species are spinose, and the diameter of the ventral spines is more varied.

Stratigraphy: The question of stratigraphic units and accompanying fossils in the Stanthorpe

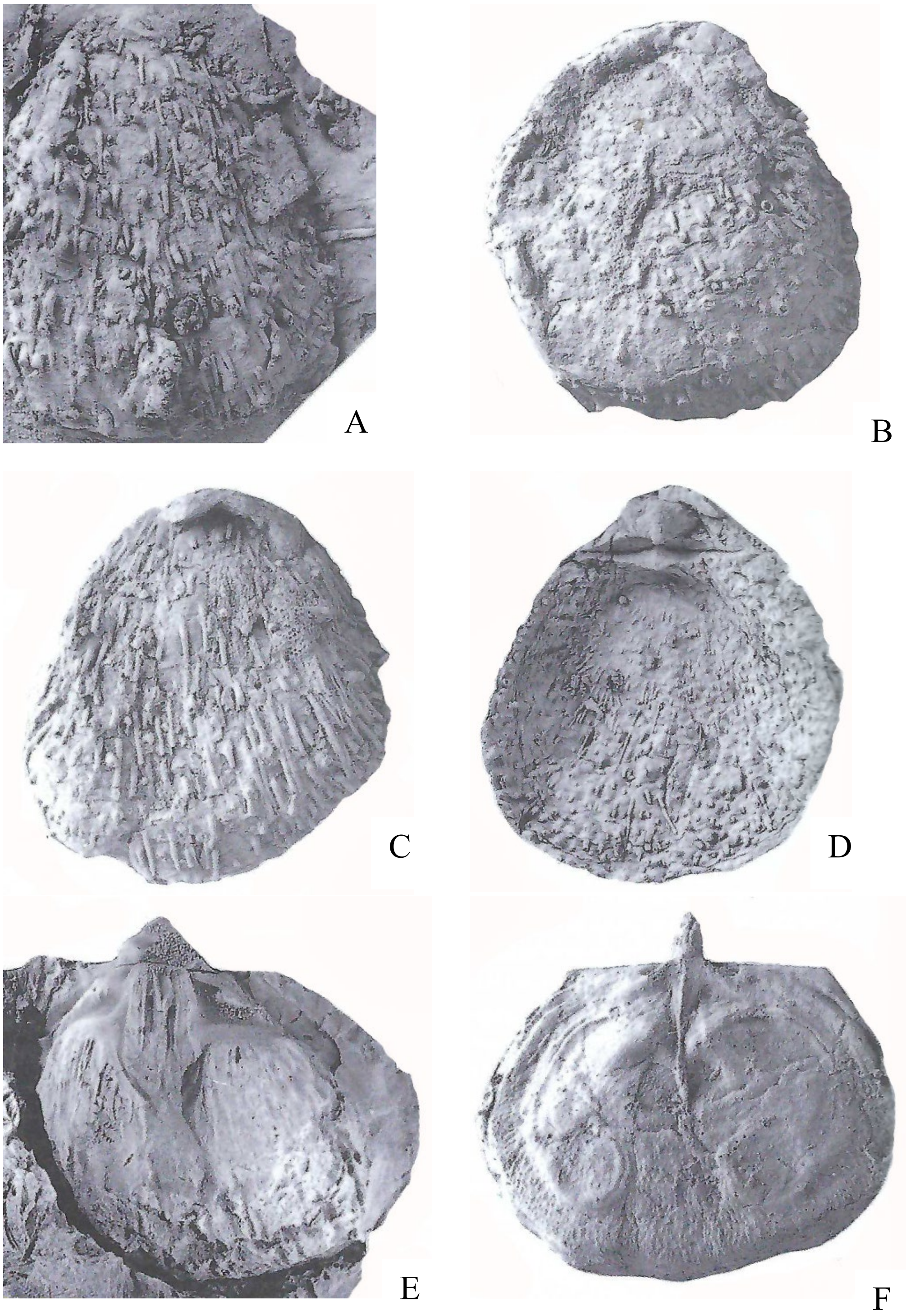
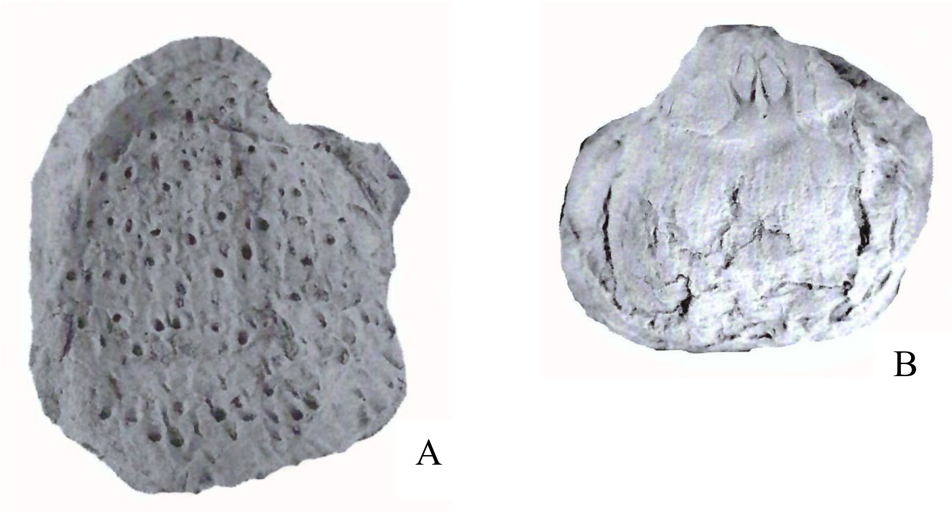


Fig. 34. *Maxwellosia concava* (Maxwell). A, latex cast of ventral valve, UQF 75212. B, latex cast of ventral valve of specimen with valves conjoined, UQF 75213. C, latex cast of specimen with valves conjoined, ventral aspect, UQF 40279. D, dorsal aspect of specimen with valves conjoined, UQF 15640. E, ventral internal mould UQF 8628. F, latex cast, dorsal interior, UQF 75214. Specimens x2, A, D, E, F from Wallaby Rocks, B, C, from (presumably lower) Cattle Creek Formation, Springsure. (Briggs 1998).



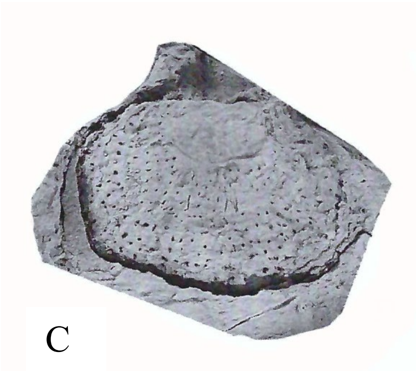


Fig. 35. *Maxwellosia concava* (Maxwell). A, part of external mould of ventral valve, UQF 8509. B, ventral internal mould, UQF 40167. C, dorsal external mould UQF 4016. Specimens x1.5, from upper Wallaby Rocks, southeast Queensland. (Waterhouse 2010).

Road Block is still to be addressed adequately, and I am not sure of the relative stratigraphic position for *concava*: I assume it would be equivalent to or a little older than that of *Echinalosia preovalis*, but this remains to be consolidated. Briggs (1998, p. 111) reported the species from various localities in and near the Wallaby Rocks near the border between Queensland and New South Wales, and added various other occurrences without adequate documention. For instance he claimed without providing reference numbers or figures that the species was to be found possibly in the South Curra Limestone of Gympie, southeast Queensland, from rocks deemed from available evidence to be of Late Permian age.

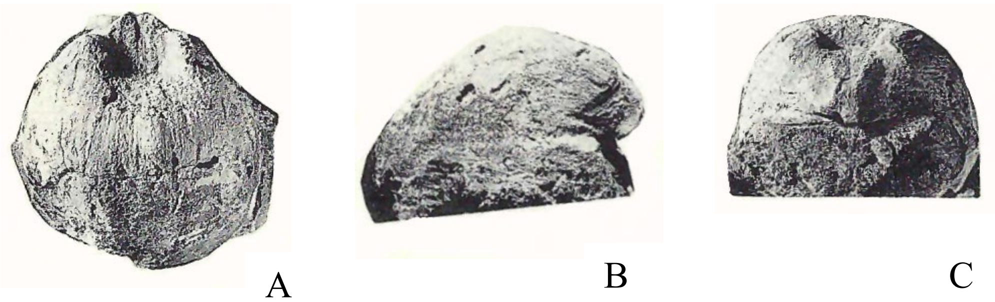
Taxonomy: Maxwell's type was renamed *stanthorpensis* by Waterhouse (1986b), in following the then current interpretation of the ICZN with regards to varieties, as explained on p. 14. This interpretation was changed in 1985, after the article had been submitted, and the name *stanthorpensis* is clearly redundant.

Maxwellosia ovalis (Maxwell, 1954)

Fig. 36 - 41

1954 *Strophalosia ovalis* Maxwell, p. 548, pl. 57, fig. 4-9, 13 (part, not fig. 10-12 = *minima*).
1964 *S. ovalis* – Hill & Woods, pl. P4, fig. 16, pl. P5, fig. 1, 2.
1970 *Wyndhamia clarkei* [not Etheridge Snr] – Armstrong, pl. 3, pl. 4, fig. 1-5, pl. 5, fig. 1-5.
1971 *Echinalosia ovalis* – Dear, pp. 8, 9.
1972 *Echinalosia ovalis* – Hill et al., pl. P4, fig. 16, pl. P5, fig. 1, 2.
?1975 *Wyndhamia ovalis* – Runnegar & McClung, pl. 31.2, fig. 1-3.
1980 *E. ovalis* – McClung, pl. 19.1, fig. 3.
1983 *E. ovalis* – Waterhouse & Jell, p. 241, pl. 1, fig. 1-6.
1998 *E. ovalis* – Briggs, p. 103, Fig. 55A-G.
2008 *E. ovalis* – Waterhouse, p. 366, Fig. H, I.
2022 *Maxwellosia ovalis* – Waterhouse, p. 64, Fig. 1-6.

Diagnosis: Medium-large shells weakly transverse to weakly subelongate, moderately wide hinge, cardinal extremities extended or obtuse, well-formed ventral interarea, large and variably shaped umbonal cicatrix in some shells, dorsal valve moderately concave, not wedge-shaped or thickened, curving evenly like that of the ventral valve into a short trail. Ventral spines largely of subuniform strength, semi-arranged in commarginal rows, but with substantial irregularity in spacing, may be fine close to anterior margin, and in some specimens fine over much of the valve, interspersed with much coarser spines, vary from erect to semi-recumbent. Dorsal spines preserved as fine and erect in patches; in two or



A B C

Fig. 36. *Maxwellosia ovalis* (Maxwell). A-C, ventral, lateral and posterior aspects of ventral internal mould, UQF 15630, holotype x1, from Mantuan Member, southwest Bowen Basin (Maxwell 1954).

more series, substantial irregularity in spacing, may be fine close to anterior margin, vary from erect to semi-recumbent. Dorsal spines preserved as fine and erect in patches; in two or more series, commarginal growth steps and rugae well-developed over both valves, no dimples. Ventral adductor platform long and high, and dorsal adductor platform also high, moderately large. Spine tunnels in many specimens.

Holotype: UQF 15630 figured by Maxwell (1954, pl. 57, fig. 5-7) and herein as Fig. 37A-C from Mantuan Member, southwest Bowen Basin, OD.

Morphology: It has been assumed for many years that *Strophalosia ovalis* Maxwell was a member of the genus *Echinalosia*, an assumption aided by the failure of Maxwell to figure

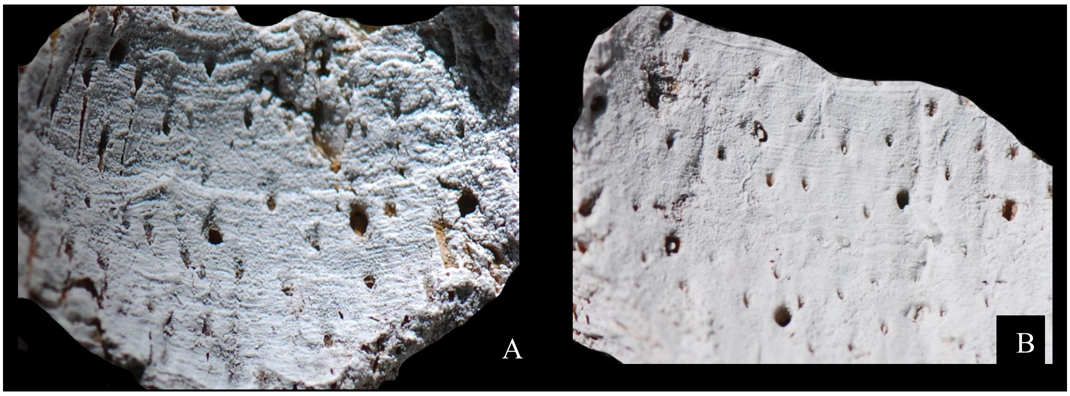


Fig. 37. *Maxwellosia ovalis* (Maxwell), external moulds showing distribution and nature of spines bases, x4 approx. A, UQF 82841. B, UQF specimen, not registered**.** Specimens x2, from the Mantuan Member, southwest Bowen Basin. (Waterhouse 2022a).

external ornament, and the fact that *Echinalosia* species were predominant amongst strophalosiids in the Permian of east Australia. A figure published for the external ventral ornament for *ovalis* by Briggs (1998, Fig. 55A) and reproduced as Fig. 38A, B herein strongly suggests that the ventral ornament is not that typical of *Echinalosia*, and comes much closer to that of *Maxwellosia*. This is not entirely supported by figures for the dorsal valve (Briggs 1998, Fig. 55B, C), which show a number of spines in regular commarginal rows, though the anterior part for Fig. 55C would fit. Specimens provided from the Mantuan Member by Elliott as described in Waterhouse (2022a, p. 64 ff) agree in their detail of spines: ventral external moulds show the irregular spacing range of diameters typical of ventral valve ornament for *Maxwellosia*, and other details, including the elongate and large ventral adductor platform are consistent.

Stratigraphy: The species *ovalis* was originally described from the Mantuan Member in the Southwest Bowen Basin, and material from the lower Blenheim Formation is comparable

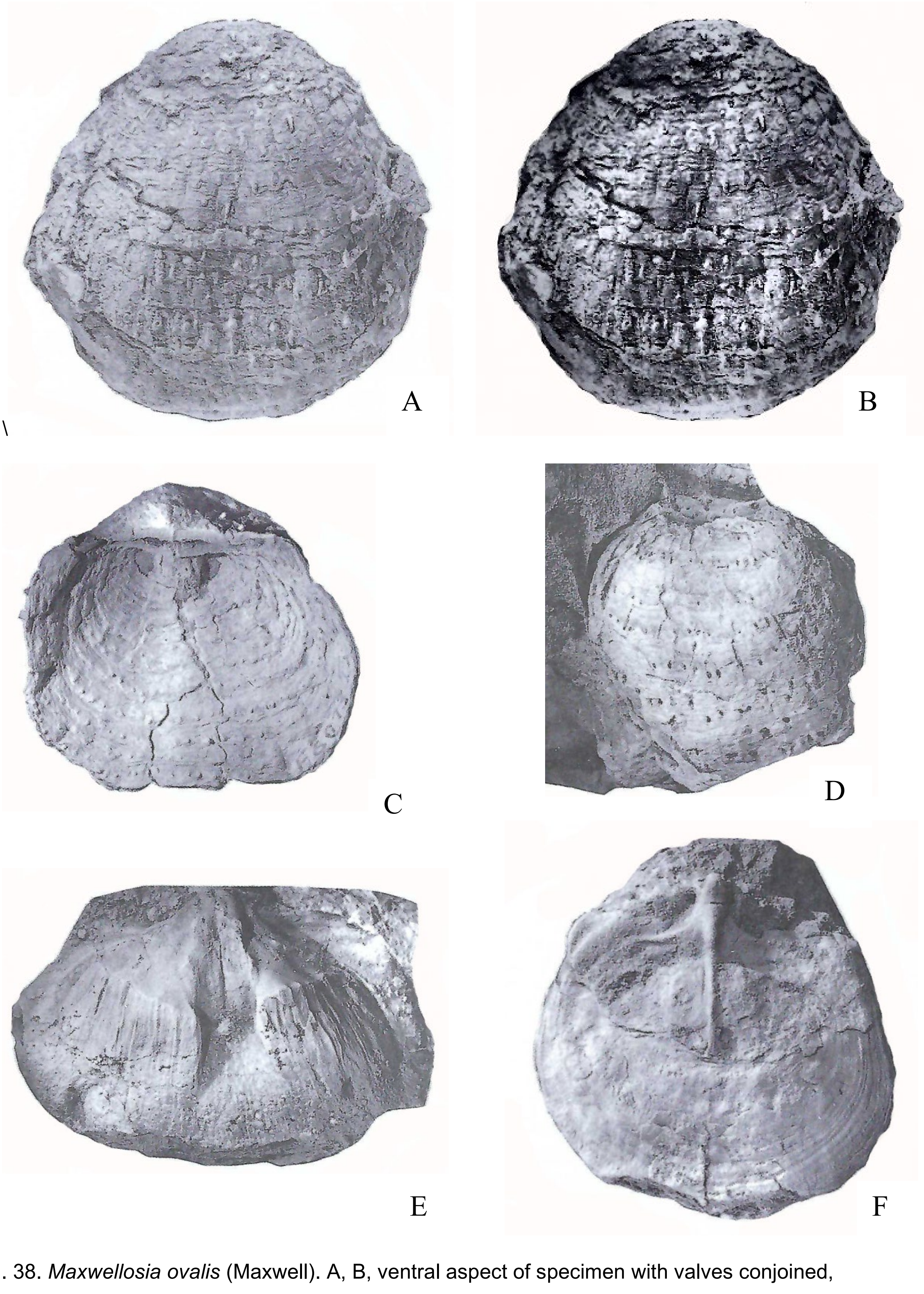


Fig. 38. *Maxwellosia ovalis* (Maxwell). A, B, ventral aspect of specimen with valves conjoined, UQF 60736, with B reproduced by local equalization, x1.5. C, dorsal aspect, conjoined shell UQF 60735, x1.5. D, dorsal external mould, AMF 96239, x1.5. E, ventral internal mould, UQF 62541, x1.5. F, dorsal interior, AMF 96240, x1.5. Mantuan Member, Bowen Basin. (Briggs 1998).

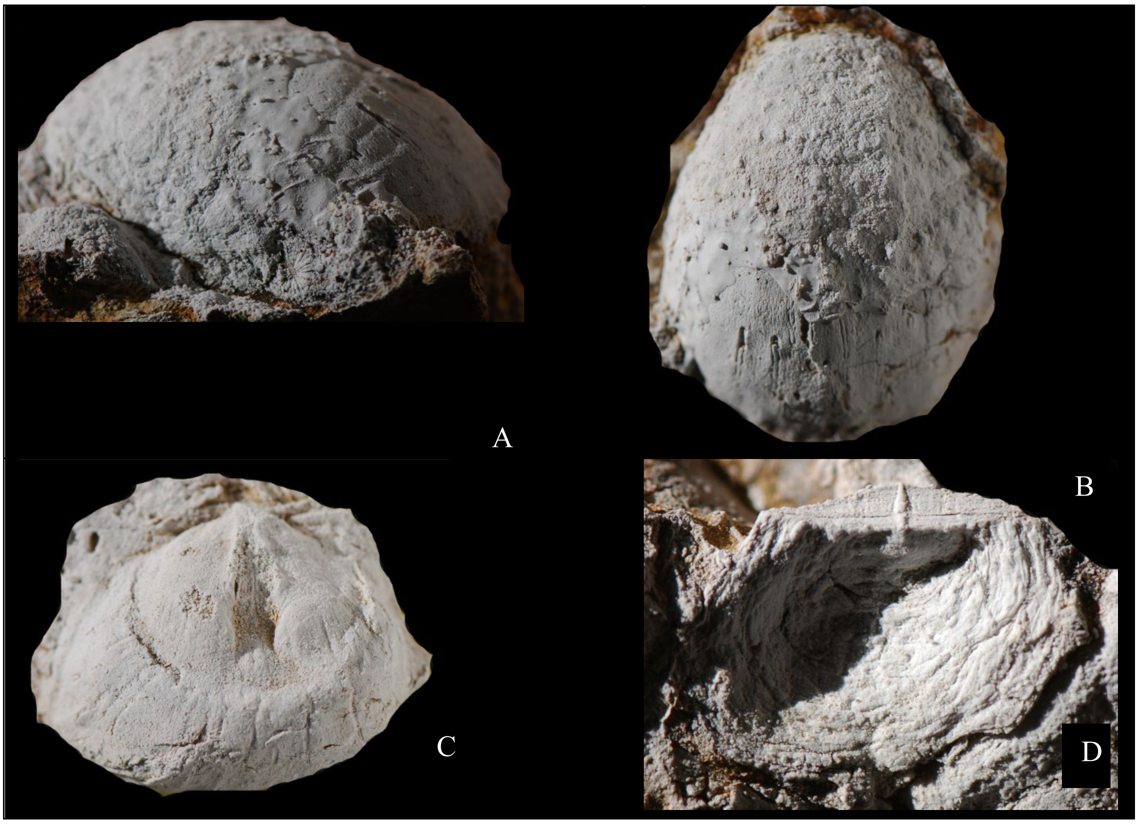


Fig. 39. *Maxwellosia ovalis* (Maxwell). A, B, lateral and ventral aspects of ventral valve, UQF 82729, x1.5. C, ventral internal mould, UQF 82730, x1.5. D, dorsal aspect of conjoined specimen, UQF 82731, x2.5. Specimens collected by L. G. Elliott from the Mantuan Member, southwest Bowen Basin. (Waterhouse 2022a).

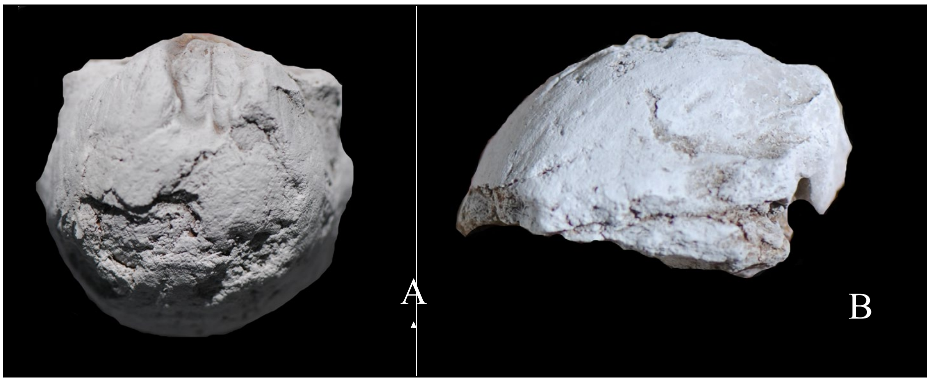


Fig. 40. *Maxwellosia ovalis* (Maxwell). A, B, ventral and lateral aspects of UQF 82772 from UQL 998, Mantuan Formation, x1.2. (New).

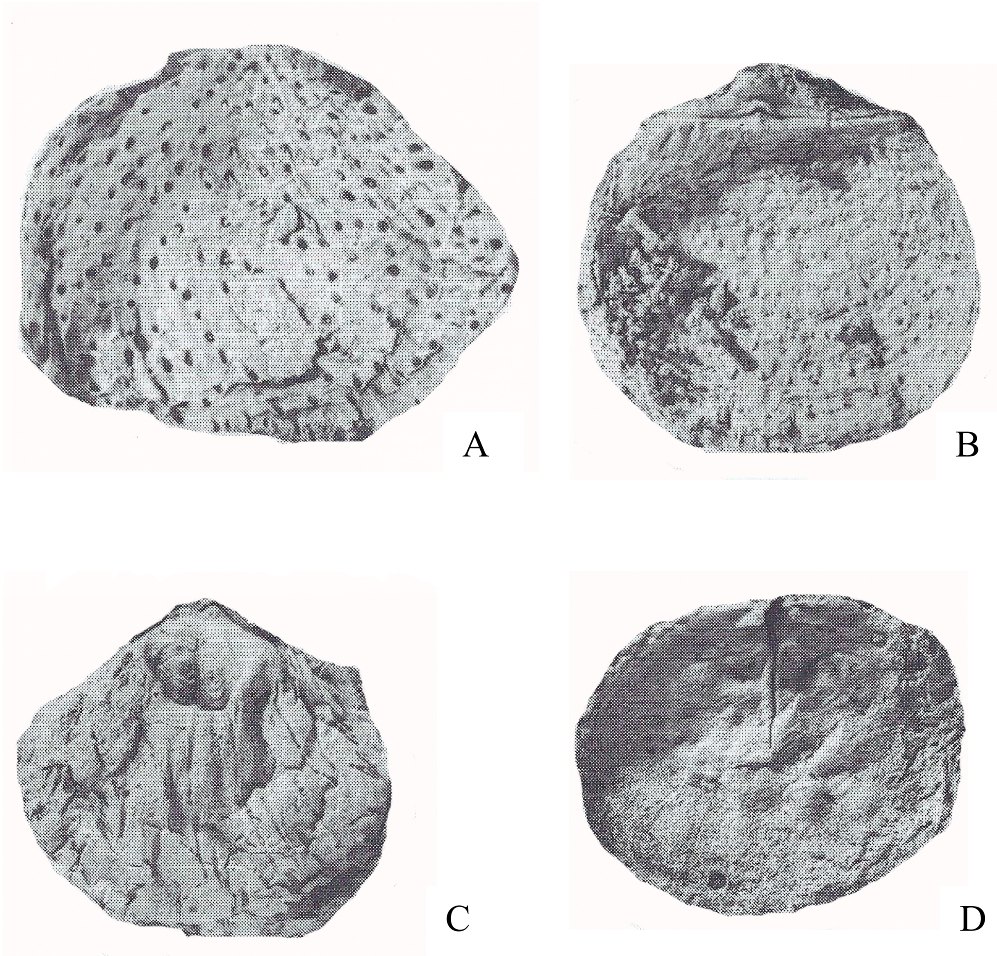


Fig. 41. *Maxwellosia ovalis* (Maxwell). A, C, ventral external and internal mould, UQF 73176, x2.5, x2. B, dorsal aspect of specimen with valves conjoined, latex cast, UQF 73196, x2. D, dorsal internal mould, UQF 73200, x2. Specimens from Blenheim Formation just below Scottville Member. (Waterhouse & Jell 1983).

(Waterhouse & Jell 1983), though mistakenly considered to be close to *Echinalosia denisoni* by Briggs (1998, pp. 98, 99). Briggs (1998) referred various specimens figured by Etheridge Jnr to *ovalis* (1892, pl. 13, fig. 14; pl. 40, fig. 8) and Etheridge Snr (1872, pl. 18, fig. 4, 4a) to *ovalis*, perhaps with the advantage of first-hand inspection, and questioned the assignment of material to *ovalis* by Runnegar & McClung (1975) to the species,presumably because they only figured internal moulds. But those two authors were well aware of the occurrence of ovalis in the Mantuan Member, and had ready access to large collections of the species at the University of Queensland, so that the identification of their material needs to be checked.

Maxwellosia ovalis wassi (Briggs, 1998)

Fig. 42?, 43

1982 *Echinalosia ovalis* [not Maxwell] – Waterhouse, p. 37, fig. 7a-f (fide Briggs 1998, p. 96).
1987 *Echinalosia* n. sp. 6 Briggs, p. 139.
1990 *Echinalosia* n. sp. D Briggs in Draper et al., p. 27.
1998 *E. wassi* Briggs, p. 96, Fig. 50A-H.
?1998 *E. denisoni* [not Archbold] – Briggs, Fig. 51A, B.

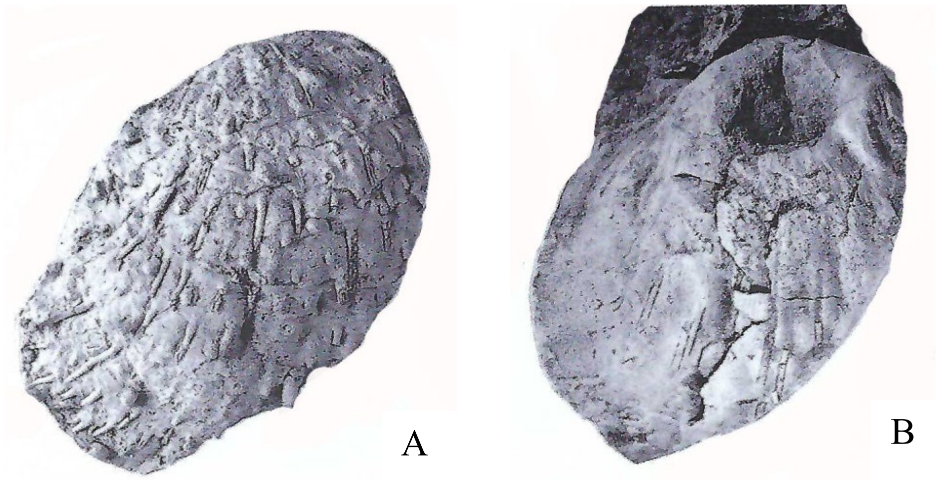


Fig. 42. Possible *Maxwellosia ovalis wassi* (Briggs). Specimens ascribed to *E. denisoni* [not Archbold] by Briggs (1998, Fig. 51]. A, latex cast of ventral exterior, and B, ventral internal mould of MMF 27828, x2 approx., from DM Narrabri, 646.6m. But the ventral adductor platform is shorter and wider than normal for this taxon. (Briggs 1998).

Diagnosis: Moderately large subequidimensional to transverse shells with coarse suberect spines up to 0.8mm in diameter over mid-disc and 1 to 1.2mm over the trail, interspersed with robust often tapering prostrate spines up to 0.55mm in diameter over mid-disc, somewhat irregular in distribution though tending to lie in commarginal bands. Dorsal spines moderately strong, weakly differentiated into a spectrum of diameters rather than forming two series 0.25 and 0.5 mm in diameter anteriorly as suggested by Briggs (1998, p. 96), and at least three "series" may be recognized. A few dorsal dimples, and ventral spine tunnels.

Holotype: UQF 75264 figured by Briggs (1998, Fig. 50B) and Fig. 43A herein, from upper Shoalhaven Group, OD.

Morphology: This is a distinctive form with characteristic ventral spine pattern somewhat less regular than in various species more closely allied to *Echinalosia maxwelli*, and so

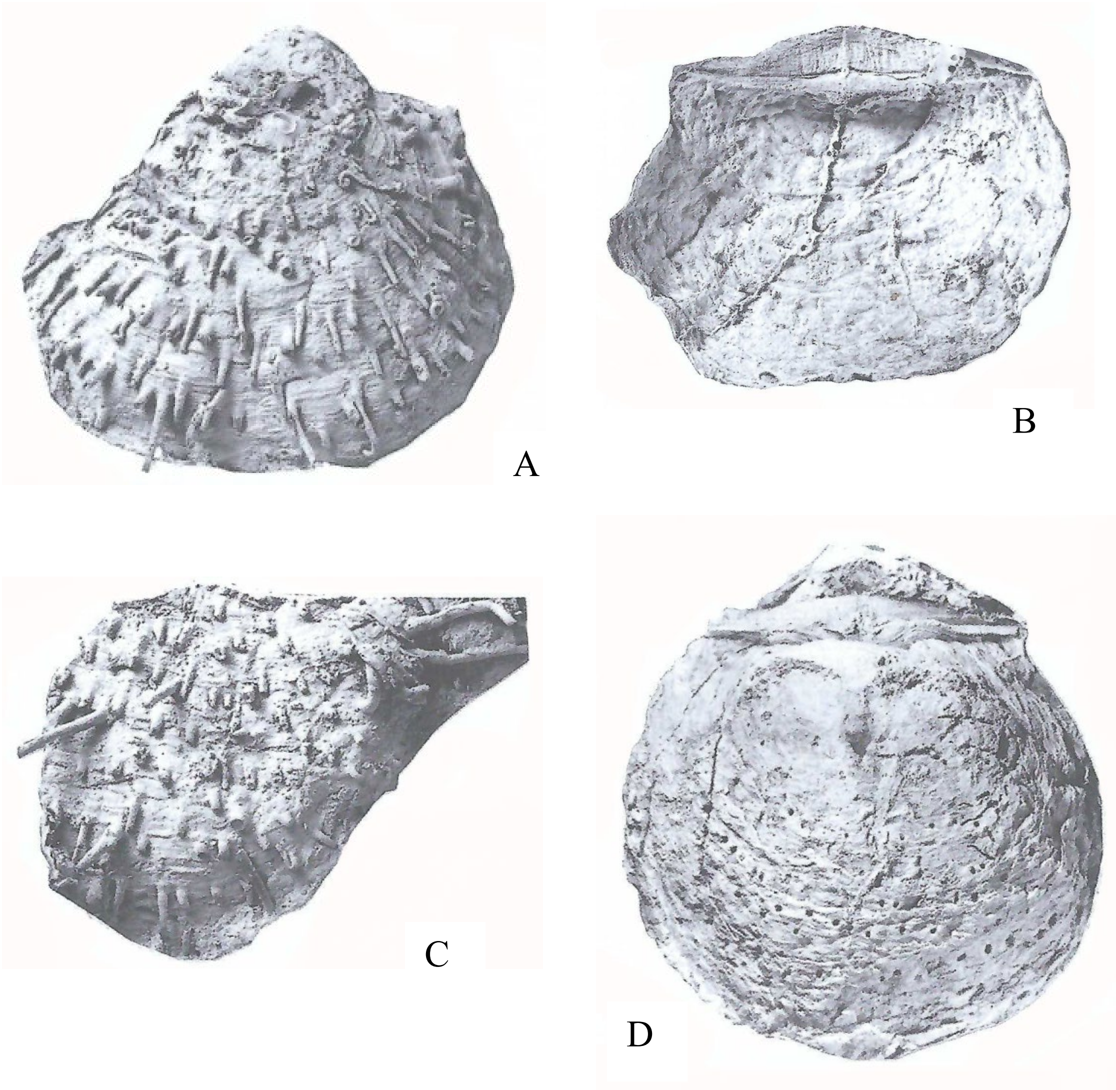


Fig. 43. *Maxwellosia ovalis wassi* (Briggs). A, latex cast of ventral exterior, UQF 75264, holotype, x2. B, latex cast of specimen with conjoined valves, UQF 75287, x1.5. C, part of latex cast of ventral valve, UQF 75265, UNE 675, x2. D, dorsal aspect of external mould with valves conjoined, UQF 75267, x2. A, C, from Berry Formation or correlative. B from Broughton Formation, D from unspecified part of the Shoalhaven Group, Sydney Basin. (Briggs 1998).

approaching *Maxwellosia ovalis*. It was reported from the upper Shoalhaven Group of the south Sydney Basin, in the Berry and Broughton Formations, and sediments of the Gunnedah Basin and Blue Mountains shelf. Briggs (1998) declared that the species was represented in the upper Mangarewa Formation of New Zealand, refining the identification of *E. ovalis* in that zone. Waterhouse failed to figure any satisfactory external moulds or casts of the ventral ornament, but prepared moulds that were inspected by Briggs, which presumably were critical for his identification, though he cited no particular specimens.

It would appear possible from figures provided by Briggs (1998) and replicated herein as Fig. 42 that specimens of *wassi* had been misidentified with *E. denisoni* Archbold. These came from a drill-core Narrabri, and appear to have misled Briggs into assigning an age younger than type *denisoni*, which unlike the Narrabri material is of greater age, and has sturdy suberect ventral spines (see p. 43). The ventral adductor platform is broader than usual however, whereas the platform for *wassi* (Briggs 1998, Fig. 50G) is closer to that of *ovalis*.

Stratigraphy: This form is regarded as essentially correlative with *Maxwellosia ovalis*. However Briggs (1998, Fig. 2, 10, 11) had a different view, placing a "*wassi* Zone" below the zones of *blakei* and *clarkei* and much older than *ovalis*. The accompanying faunas, as summarized for the southeast Bowen Basin in Waterhouse (1987), but never analyzed by Briggs (1998), do not agree. As favoured herein, the correlation is indeed close to or possibly a little younger than that of *runnegari.*

Tribe **MARGINALOSIINI** Waterhouse, 2013

Diagnosis: Ventral spines of one series.

Genus ***Marginalosia*** Waterhouse, 1978

Diagnosis: Spines fine and largely but not entirely uniform and suberect over ventral valve, seldom differentiated and without swollen or prolonged bases, arranged along commarginal rows, dorsal spines numerous and may be moderately thick for the subfamily, uniform, dorsal pits common. Umbonal cicatrix small or not developed, ventral interarea relatively high. Both valves with marginal ridge, dorsal valve may be slightly thickened. Ventral spine tunnels present.

Type species: *Echinalosia*? *kalikotei* Waterhouse, 1975 from Nisal Member, northwest Nepal (Changhsingian), OD.

Discussion: The genus *Marginalosia* Waterhouse is typical of the Late Permian Lopingian zones in the Himalayas and New Zealand. It has been reported from northeast Russia, but verification of that occurrence seems to require further evidence. The genus *Guadalupelosia* Archbold & Simanauskas is judged to have converged in its similarity to *Marginalosia*, rather than evolved into it, because it is older and is found in low paleolatitudes rather than the moderately high paleolatitudes inhabited by *Marginalosia*.

Marginalosia is distinctive, largely restricted to paleotemperate to cold-water faunas of Late Permian age. The species *minima* Maxwell has largely uniform ventral spines in regular rows, approaching the arrangement in type *Marginalosia*, but the ventral valve does tend to show a very few fine prostrate spines suggestive of an adaption of the ornament typical of the genus *Echinalosia,* and recognized as the subgenus *Unicusia* Waterhouse, 2022c. Dorsal dimples typical of *Marginalosia* are also prominent in *Echinalosia* (*Unicusia*) (Briggs 1998, Fig. 52C), and *Marginalosia* has a prominent marginal ridge in each valve, just as in the subgenus *Unicusia*. Like most specimens of *Echinalosia* (*Unicusia*) *minima*, *M. kalikotei* (Waterhouse) from Nepal has a wide hinge, but the trail is considerably longer. *M*. *planata* (Waterhouse, 1964) from the Pig Valley Limestone of New Zealand has a shorter trail and hinge of variable width, with similar ventral spines spaced well apart. The dorsal valve is slightly thickened anteriorly in these species, without being wedge-shaped. Specimens of *Marginalosia* which show a distinct sulcus are found in the slightly older *Spinomartinia spinosa* Zone of the Hilton Limestone in New Zealand.

Marginalosia sulcata n. sp.

Fig. 44

2001 *Marginalosia*? sp. Waterhouse, p. 89, pl. 5, fig. 1-3, text-fig. 5f.

Diagnosis: Thick body cavity, ventral valve sulcate, dorsal valve gently concave with strongly geniculate short trail.

Holotype: OU 2388 figured from the Nemo Formation at Wether Hill, Southland, by Waterhouse (2001, pl. 5, fig. 2 and herein as Fig. 44A, here designated.

Morphology: Some ventral valves are sulcate and the cardinal extremities tend to be rounded rounded. Spines are fine and arranged in quincunx, and of uniform diameter. Dorsal spines moderately thick. The dorsal valve is slightly thickened with low geniculate trail (Waterhouse 2001, text-fig. 5f). Although many features are distinguishable, overall preservation and number of specimens were judged not good enough to warrant recognition as a distinct taxon, but in the context of distinctiveness, it is now preferred to name the species.

Stratigraphy: These specimens apparently mark the first appearance of the genus in New

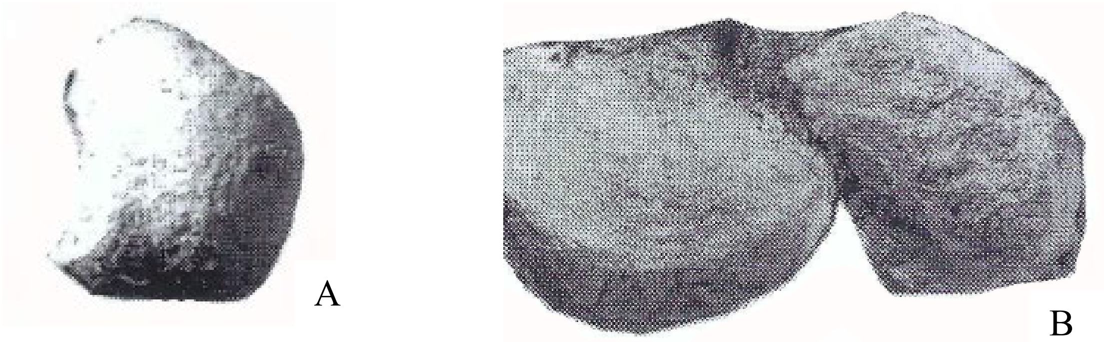


Fig. 44. *Marginalosia sulcata* n. sp. A, ventral valve BR 2388, holotype. B, two dorsal valves BR 2386 and 2387. From Nemo Limestone, x1.5. (Waterhouse 2001).

Zealand Permian, and are judged to be of mid-Changhsingian age. They are found in the *Spinomartinia spinosa* Zone in the Nemo Limestone at Wether Hill Station, and possibly in the Hilton Limestone at Coral Bluff, Wairaki Downs, western Southland in New Zealand. These two limestones though named separately appear likely to be part of the same stratigraphic unit, exposed in different areas.

Marginalosia planata (Waterhouse, 1964)

Fig. 45

1917 *Strophalosia* sp. cf. *gerardi* [not King] – Trechmann, p. 58, pl. 5, fig. 4, 5.
1964 *Strophalosia planata* Waterhouse, p. 41, pl. 7, fig. 4-11, pl. 8, fig. 1, 2. Fig. 8A, 12E, F, 14, 15D, E.

Diagnosis: Oval to ovally transverse with well-rounded cardinal extremities, hinge narrow to wide, high ventral interarea, inflated visceral disc, dorsal disc often flat posteriorly, and slightly thickened. Ventral spines subuniform, well-spaced, tend to be arranged in quincunx rather than solely in commarginal rows. Ventral spine tunnels. Dorsal spines rare, no dimples.

Holotype: Specimen BR 363 from Pig Valley Limestone, Nelson, figured in Waterhouse (1964, pl. 7, fig. 6) and Fig. 45D herein, OD.

Morphology: This species is moderately well known, and differs from *Echinalosia* by developing a slightly thickened dorsal valve that tends to be flat posteriorly, and ventral spines are subequal and arranged in quincunx along commarginal rows. Dorsal spines are rare. Cardinal extremities are well rounded. The dorsal septum is short.

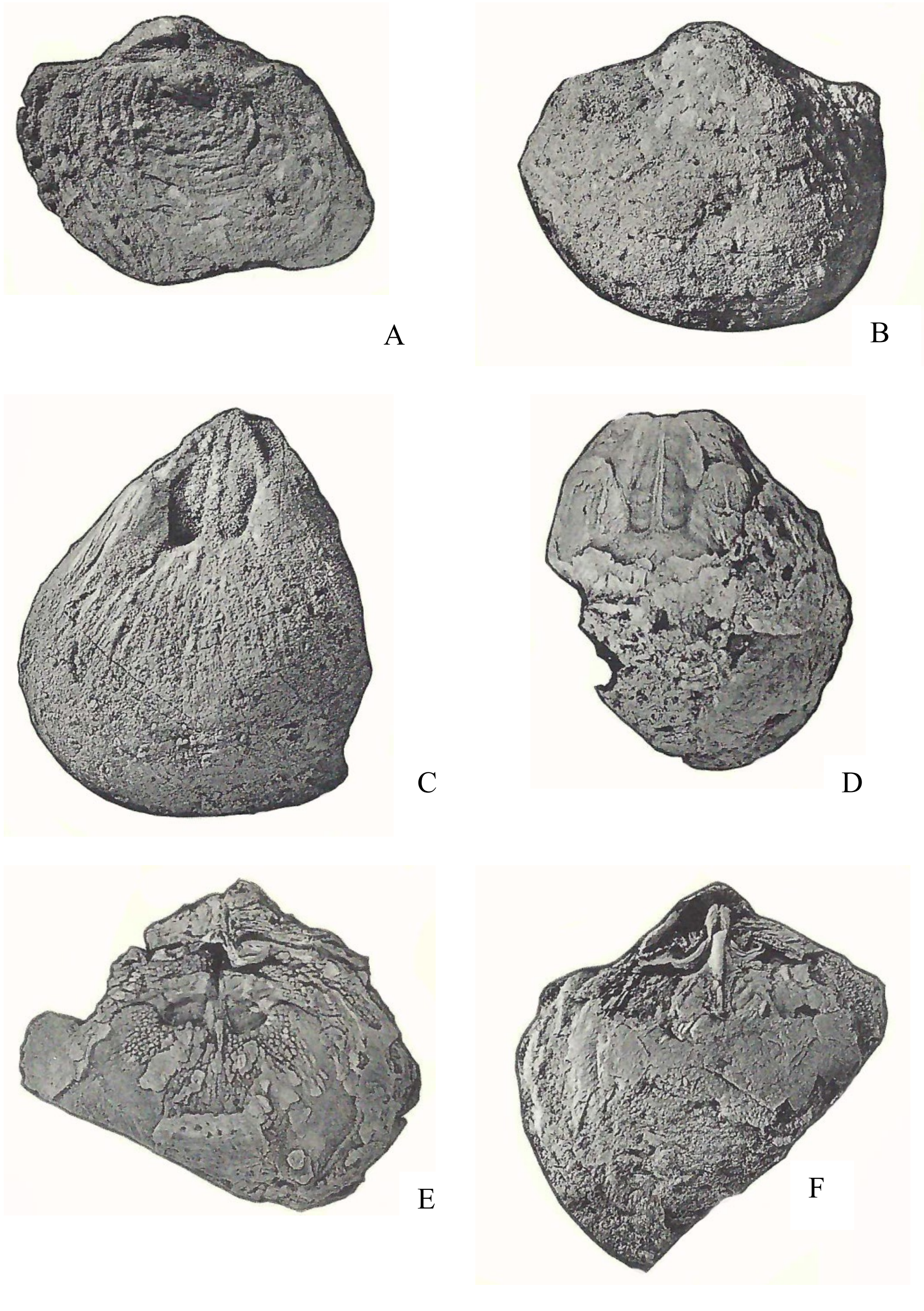


Fig. 45. *Marginalosia planata* (Waterhouse). A, PVC cast of specimen with valves conjoined, BR 354. B, PVC cast of exterior ventral valve, BR 361. C, ventral internal mould BR 918. D, zeolitized interior of ventral valve BR 363, holotype. E, dorsal aspect of zeolitized interior of specimen with both valves conjoined, BR 356. F, zeolitized interior of specimen with valves conjoined, showing dorsal posterior and part of dorsal exterior, BR 376. Specimens x2, from Pig Valley Limestone, Nelson. (Waterhouse 1964).

Runnegar (1968) substantially distorted the observation in Waterhouse (1964) that *planata* shared some attributes with *Echinalosia ovalis,* and he ignored the distinctions made in Waterhouse (1964) between the two species and the justifications that *planata* was a new and distinct species, by asserting that the two suites were conspecific, which would imply that the Mantuan Member of Queensland was correlative with the Pig Valley Limestone of New Zealand. He disregarded paleontological and stratigraphic evidence to assert, in essence, that the New Zealand Permian was the same as the Australian Permian. He could not believe that the realm of east Australia did not contain vastly superior fossils of every last biozone represented in New Zealand. Similar in many respects, but not identical would be a better-informed assessment. It never seems to have occurred to him that the coal measures of east Australia were not developed in New Zealand, and that that signified a considerable difference in the stratigraphic and biozonal succession.

Stratigraphy: The species is abundant over patches of the Pig Valley Limestone, which is developed as large lenses near the base of the Goat Hill Group (Waterhouse 2002). This is of Late Permian age, younger than any marine deposits of east Australia, including the South Curra Limestone and Tamaree Formation of Gympie, Queensland (Waterhouse 2021a, pp. 113, 114).

Marginalosia kalikotei (Waterhouse, 1975)

Fig. 46, 47

1966 ?*Marginifera* sp. Waterhouse, p. 17, pl. 3, fig. 5 (part, not pl. 3, fig. 3, 4).
1975 *Echinalosia kalikotei* Waterhouse, p. 4, pl. 1, fig. 4-7.
1978 *Marginalosia kalikotei* – Waterhouse, pp. 64, 115, pl. 7, fig. 21-26, pl. 8, fig. 1-15, pl. 9, fig. 13, pl. 10, fig. 2.
2007 *M. kalikotei* – Waterhouse & Chen, p. 25, pl. 4, fig. 18, 19.
2010b *M. kalikotei* – Waterhouse, p. 276, Fig. 7M, O, P.

Diagnosis: Moderately large shells, variably developed sulcus and fold, moderately concave dorsal disc, obtuse cardinal extremities, moderately long subgeniculate trail. Ventral spines subuniform, 0.3 - 0.7mm in diameter, erect and arranged in quincunx. Dorsal spines numerous, erect, 0.5mm in diameter, arranged erratically along commarginal rows. Pits well developed over dorsal disc. Marginal ridge well developed in dorsal valve.

Holotype: Specimen UQF 68854 figured in Waterhouse (1975, pl. 1, fig. 4, 5; 1978, pl. 7, fig. 22) and Fig. 46D herein from Nisal Member, Senja Formation, west Nepal.

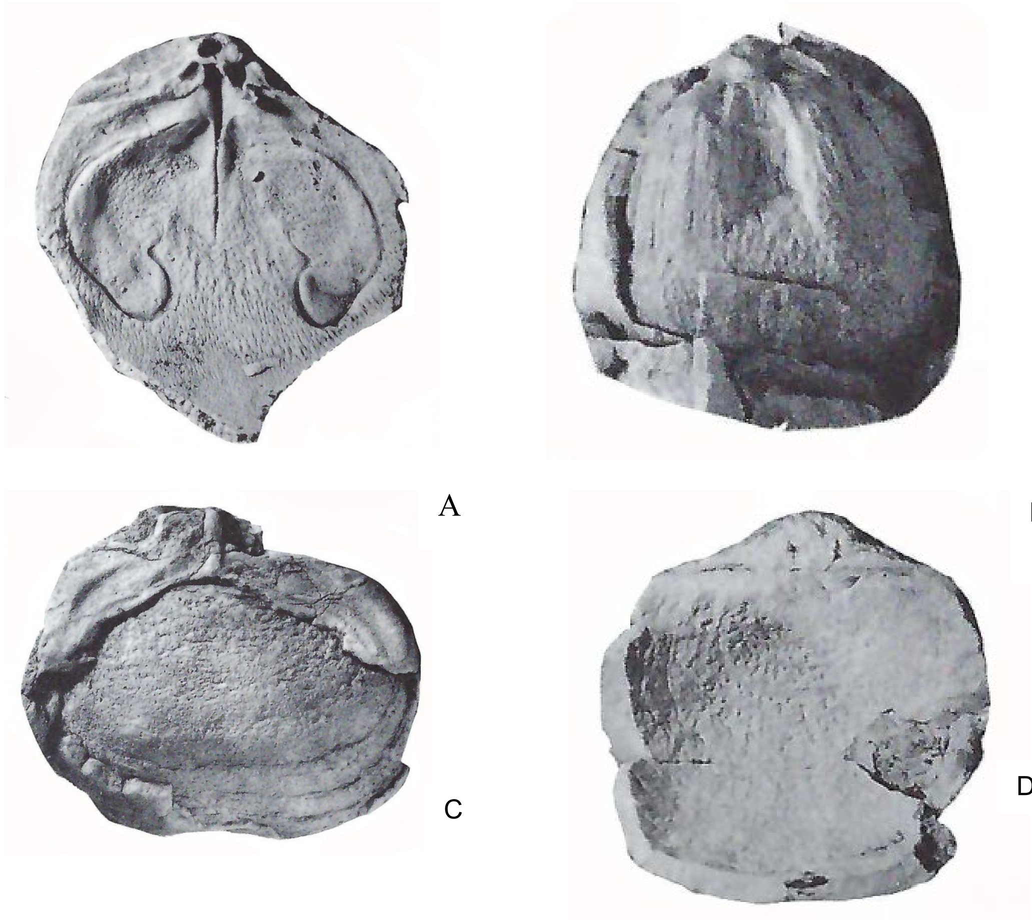


Fig. 46. *Marginalosia kalikotei* (Waterhouse). A, dorsal view of internal mould of specimen with valves conjoined, UQF 68861, x1.5. B, decorticated ventral valve showing internal muscle impressions, UQF 68865, x1.5. C, dorsal internal mould UQF 68869, x 1.5. D, holotype, dorsal aspect of specimen with valves conjoined, UQF 68854, x1.5. Nisal Member, Nepal. (Waterhouse 1978).

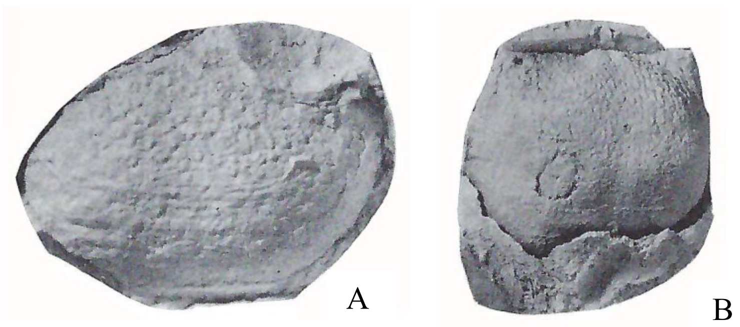


Fig. 47. *Marginalosia kalikotei* (Waterhouse). A, anterior ventral exterior, UQF 68856 x1. B, external mould of dorsal valve UQF 68852 x1 with attached spat UQF 68853 and showing the ventral interarea. Nisal Member, Nepal. (Waterhouse 1978).

Stratigraphy: This species is abundant in the Nisal and Luri Members of the *Marginalosia kalikotei* Zone (originally subzone) in upper Changhsingian deposits and faunas of northwest Nepal and further east in north-central Nepal, in the Puchenpra, Galte and Ngawal Members, also classed as belonging to the Senja Formation. The zone is comparatively thick and rich in fossils, and is approximately correlative with the Pig Valley limestones and *Marginalosia planata* Zone in New Zealand, to mark a well-developed cool to cold-water phase in the development of late Permian faunas, at least in the southern paleohemisphere.

Marginalosia*? *magna Abramov & Grigorieva, 1988

Fig. 48

A

Fig. 48. *Marginalosia*? *magna* Abramov & Grigorieva. A, dorsal aspect showing decorticated specimen PIN 4065/204 with both valves conjoined dorsal interior from South Verchoyan. B, PIN 4065/201 dorsal internal mould, from South Verchoyan. C, holotype ventral internal mould PIN 4065/327, from West Verchoyan. Specimens x1. (Abramov & Grigorieva 1988).

B

C

Diagnosis: Not enough is known at least to me of the ornament to be able to provide a critical diagnosis.

Holotype: PIN 4065/325 figured by Abramov & Grigorieva (1988, pl. 3, fig. 3) and Fig. 48C herein from Kolyma River, South Verchoyan, northeast Russia, OD.

Discussion: The lack of figures of the ventral ornament for this species makes placement in a genus difficult, and clarification of the nature of the dorsal valve would be an advantage. At present, there seems to be no clear indication that the species conclusively belongs to *Marginalosia*, but I have not inspected the material at first hand, which is a severe disadvantage in assessing the generic position.

Genus ***Guadalupelosia*** Archbold & Simanauskas, 2001

Diagnosis: Spines fine, erect and comparatively uniform over both valves, ventral interarea high and plane, marginal ridge present over both valves.

Type species: *Strophalosia inexpectans* Cooper & Grant (1975, p. 796) from the Getaway Member of the Cherry Canyon Formation of the Guadalupe Mountains in west Texas, OD.

Discussion: The genus appears to be very close to *Marginalosia*, though distinguished by its more delicate shell and finer spines, suggestive of climatic influence due to warmer climate. The same species was nominated as type of a new genus, clearly as a junior synonym, by Waterhouse (2002, p. 54), called *Muirwoodicia,* and was compared with other strophalosioid genera. The genus differs from *Marginalosia* in having more numerous spines, including some rhizoid posterior ventral spines, and smooth dorsal exterior with no pits or prominent growth steps of laminae, and no geniculate trail. Its spines are fine, erect and comparatively uniform over both valves. The ventral interarea is high and planar, and a marginal ridge is present in both valves.

Guadalupelosia inexpectans (Cooper & Grant, 1975)

Fig. 49

1975 *Strophalosia inexpectans* Cooper & Grant, p. 795, pl. 269, fig. 13-30.
2001 *Guadalupelosia inexpectans* – Archbold & Simanauskas, p. 223.
2002b *Muirwoodicia inexpectans* – Waterhouse, p. 54.

Diagnosis: As for genus.

Holotype: USNM 151229b, figured by Cooper & Grant (1975, pl. 269, fig. 17-21) and Fig. 49C herein from Getaway Member, Cherry Canyon Formation, OD.

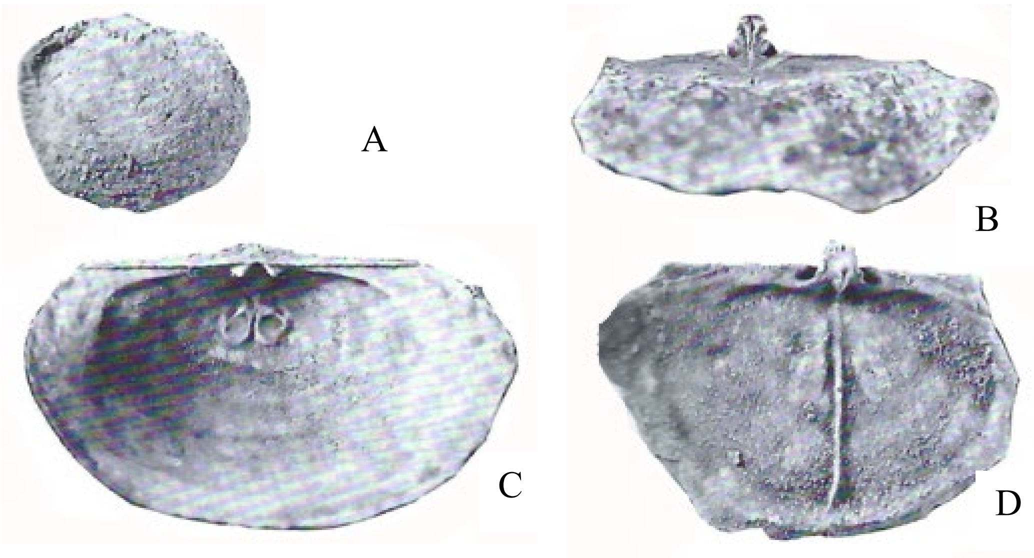


Fig. 49. *Guadalupelosia inexpectans (*Cooper & Grant). A, ventral exterior, USNM 151229a, x1. B, dorsal valve USNM 151229d, x3. C, interior of holotype, USNM 151229b, x3. D, dorsal interior, USNM51229d, showing long median septum, and low marginal ridge, x3. Specimens from Getaway Member, Cherry Canyon Formation, west Texas. (Cooper & Grant 1975).

Stratigraphy: Getaway Member, Cherry Canyon Formation, Texas.

Discussion: Cooper & Grant (1975, p. 796) showed that this species was very rare – one of the rarest amongst Permian faunas in the Guadalupe Mountains.

The similarities to *Marginalosia* would, from a pragmatic viewpoint, appear to be due to convergence. The American species is older than the established species of *Marginalosia*, and if it were closely related, would be regarded as progenital stock. A more likely ancestral stock for *Marginalosia*, from the point of view of morphology and geographic distribution seems to be *Echinalosia* (*Unicusia*), given that this genus developed at relatively high latitudes, moderately close to those younger occurrences of *Marginalosia*, and very different from the tropical faunas which contained rare *Guadalupelosia*. But the complexities of evolution mean that such a source cannot be conclusively ruled out.

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SUBFAMILY ARCTICALOSIINAE, TRIBE WYNDHAMIINI (BRACHIOPODA) IN THE PERMIAN OF EASTERN AUSTRALIA AND NEW ZEALAND

Abstract

Known species of Tribe Wyndhamiini are summarized from the Permian of eastern Australia and New Zealand. Members of the tribe are rare elsewhere in the world, with likely species limited to Arctic Canada and perhaps Mongolia, according to present knowledge.

INTRODUCTION

Members of Wyndhamiini were first recognized as a genus distinct from strophalosiids and echinalosiins by Booker (1929), with the description of *Wyndhamia*. Three genera are now classed as Wyndhamiini, involving largely simple lineages of successive species. All three display the particular features which characterize members of the tribe: the wedge-shaped thickened dorsal valve, and the mix of coarse and slender spines which cover much or all of the ventral valve, as well as largely uniform fine spines over the dorsal valve. They are deemed to allied to Arcticalosiini, which in common with Wyndhamiini has a wedge-shaped dorsal valve, but which differs through displaying only fine and crowded ventral spines of uniform fine diameter. Some authorities, such as Briggs (1998), have discounted the significance of the thickened dorsal valve in *Pseudostrophalosia* and *Wyndhamia*, but *Echinalosia* and its array of species and related subgenera never have a thickened dorsal valve, any more than a number of other strophalosioid species and genera. Brunton et al. (2000, p. 574) synonymized *Arcticalosia* with *Wyndhamia,* but the ornament of the ventral valve differs substantially.

Wyndhamia has ventral ears largely to entirely free of spines, and the dorsal valve is wedge-shaped. The earliest known *Wyndhamia* Booker, 1929 is found in the late Sakmarian Berriedale Limestone of Tasmania as *W. jukesi* (Etheridge, 1880), followed by *W. typica* Booker, 1929 (initially described as *Branxtonia typica*, *Wyndhamia dalwoodensis* Booker, 1929 and *W. valida* Booker, 1929) in the Elderslie Formation of the north Sydney Basin, with possible occurrences elsewhere. In these species most ventral spines are comparatively coarse. Two taxa close in age to *W. typica* include *W. typica clarkeina* Waterhouse (2001, p. 75) with an unusual number of slender ventral spines, found widely in Malbina A beds and correlates of Tasmania, and *W. typica crassispina* Waterhouse, 2001, p. 72 from the Freitag Formation of the southwest Bowen Basin in Queensland. This species has fine spines over the first-formed shell to a width of 20 to 25mm, and spines then become large in patches and around the periphery.

The companion genus *Pseudostrophalosia* Clarke, 1970 also has wedge-shaped dorsal valve but the ventral ears are crowded with spines. The oldest species *Ps. brittoni* (Maxwell) is found in the Sakmarian Tiverton Formation. *Ps. blakei* (Dear, 1971) comes from the lower Blenheim Formation, amended to upper Moonlight Formation, and could well be senior synonym to *Ps. ingelarensis* (Dear, 1971) by page appearance from the correlative Ingelara-Catherine-Sandstone and Barfield Formation of the southern Bowen Basin. *Ps. crassa* Briggs, 1998 comes from a bore-hole, and is followed by *Ps. clarkei* (Etheridge Snr, 1872) from the Scottville Member, overlain by *Ps. furcalina* Waterhouse, 2022c from above the Scottville Member and taking in the Pelican Creek fauna of Dear (1972) in the north Bowen Basin. The topmost *Pseudostrophalosia* in the marine sequences of Queensland is described as *Ps. cryptica* Waterhouse, 2022d, contemporaneous with *Ps. routi* Waterhouse, 2022e at the top of the Mangarewa Formation in New Zealand. The spine thickness varied in these species, and one significant aspect of the genus is that no species is yet known to have come from Middle Permian deposits of New South Wales or Tasmania.

Nonauria was derived from *Wyndhamia* by loss of ears, and of course loss of ear spines, with two species, *N. parfreyi* (Waterhouse, 2001) in the Barfield Formation of Queensland, and *N. laminata* Waterhouse (2022e) in the Kulnura marine tongue of New South Wales, correlative with upper Blenheim Formation of the Bowen Basin.

Tribe **WYNDHAMIINI** Waterhouse, 2010

Diagnosis: Ventral body spines mostly coarse, semirecumbent, prostrate spines thin and often rare. Dorsal valve thickened and wedge-like with fine spines of one series, and often crinkled surface.

Discussion: This group associates *Wyndhamia*, *Pseudostrophalosia* and *Nonauria.* The three genera are close to Arcticalosiini, but have some fine ventral prostrate spines, which are missing from *Arcticalosia* Waterhouse: this genus has only one series of largely uniform and usually erect spines on each valve. That contrasts with the ventral spines of Wyndhamiini, which may be varied in diameter, and include very sturdy spines either over the ventral disc or postero-laterally.

Genus ***Wyndhamia*** Booker, 1929

Diagnosis: Ventral valve swollen, dorsal valve gently concave, with thick body corpus, and dorsal valve thickened anteriorly, leading into short trail. Ventral spines in two series, few over the ears, dorsal spines in one series.

Type species: *Wyndhamia typica* Booker, 1929, p. 24, the synonymy involving *Branxtonia typica* and *Wyndhamia dalwoodensis* Booker and *W. valida* Booker, thanks to what some may consider to be contentious decisions by Maxwell (1954) and Muir-Wood & Cooper (1960), not in disputing the synonymy, but regrettably making *typica* the type.

Discussion: For Wyndhamiini, the genera will be ordered according to date of proposal.

Wyndhamia jukesii (Etheridge, 1880)

Fig. 1, 2

1880 *Strophalosia jukesii* Etheridge Jnr, p. 307, pl. 13, fig. 39-43.
1884 *S. jukesii* – Etheridge Jnr, p. 88.
1888 *S. jukesii* – Johnston, pl. 14, fig. 7.
1954 *S. jukesi* – Maxwell, p. 550, pl. 56, fig. 12-22.
1969 *Wyndhamia jukesi* – Clarke, p. 43, pl. 8, fig. 1-3, 7.
1969 *W. dalwoodensis* – Clarke, p. 43, pl. 8, fig. 5 (part, not fig. 4 = *typica*).
1998 *W. jukesii* – Briggs, p. 126.

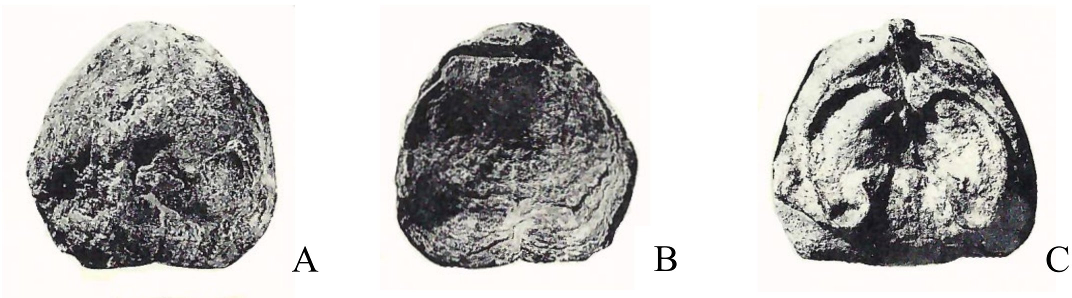


Fig. 1. *Pseudostrophalosia jukesi* (Etheridge). A, B, ventral and dorsal aspects of holotype, BMNH BB 9807. C, dorsal valve, internal aspect BB 9806. From Berriedale Limestone, Tasmania, x1. (Maxwell 1954).

Diagnosis: Shells small, ventral spines low angle recumbent, as well as slender prostrate, dorsal valve strongly wedge-shaped and externally of low concavity, internally almost flat.

Lectotype: BB 9807, exact locality not known, presumably from Berriedale Limestone or equivalent in Tasmania, figured by Etheridge Jnr (1880, pl. 13, fig. 39, 40) and Maxwell (1954, pl. 56, fig. 14, 15), repeated herein as Fig. 1, SD Maxwell (1954, p. 550).

Morphology: More attention to this species is needed. The claim by Briggs (1998, p. 126) that ventral spines were prostrate rather than low and medium angle recumbent appears to be questionable, because some spines appear to be semi-recumbent with others semi-erect.

Stratigraphy: From what is known, the species appears to be limited to late Sakmarian faunas of Tasmania, and found in the Berriedale Limestone.

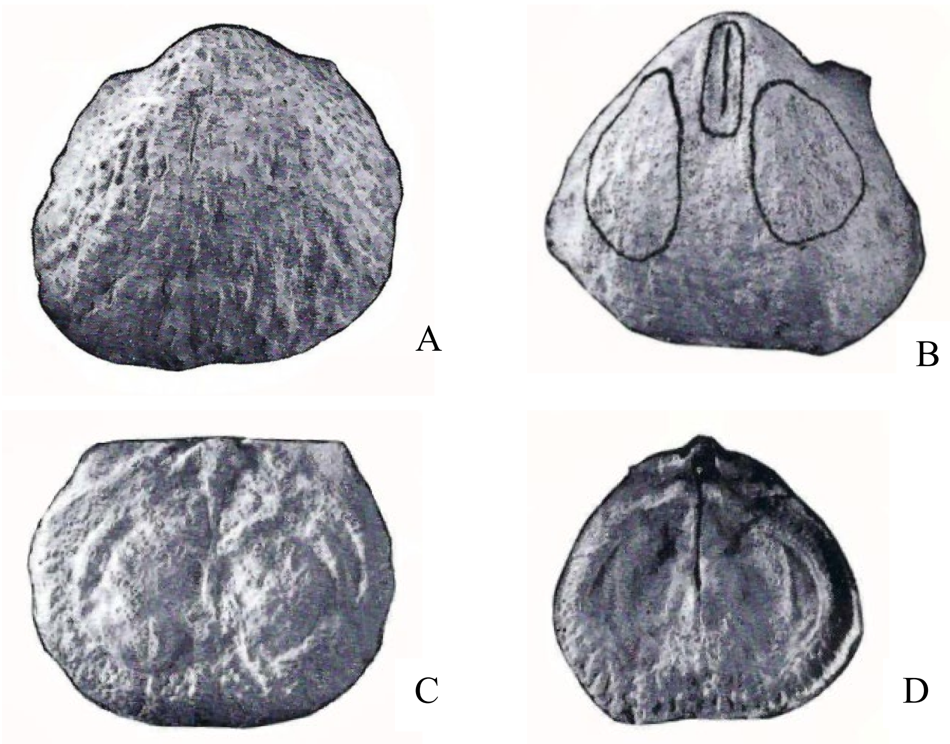


Fig. 2. *Wyndhamia jukesii* (Etheridge Jnr). A, ventral valve TMF P20Z104 x1.4, named as *Strophalosia gerardi tasmaniensis* Prendergast but only in manuscript. B, ventral internal mould UTF 28044, x1.2. C, dorsal interior, TMF 3587, x1.2. D, internal mould of dorsal valve, TMF 3585 x1.3. From Berriedale Limestone except D from “Main Limestone.” (Clarke 1969).

***Wyndhamia*? sp.**

Fig. 3

1964 ?*Wyndhamia* sp. aff. *jukesi* [not Etheridge] – Waterhouse, p. 48, text-fig. 16, 17.
1982 ?*Wyndhamia jukesi* [not Etheridge] – Waterhouse, p. 39, pl. 7, fig. g, l, k.
2001 *Wyndhamia*? sp. – Waterhouse, p. 71.

Diagnosis: Small shells, ventral valve gently convex, posterior walls low, ventral spines few and suberect, with rare prostrate slender spines, absent from ears and postero-laterally. Dorsal valve with flat disc, scattered erect spines and strong commarginal laminae, with pits.

Morphology: Ventral spines are subuniform, with few slender and prostrate, but not adequately known. Dorsal spines are comparatively few, erect and slender.

Stratigraphy: The specimens come from a zone found in beds of a distinctive stratigraphic unit, miscalled upper Brunel Formation in Campbell et al. (1990), but including much conglomerate, and so differing from beds typical of the underlying Brunel Formation. Youngest specimens come from towards the top of the Chimney Peaks Formation. The level is regarded as lower Baigendzinian in age, younger than the late Sakmarian age deemed appropriate for the Berriedale Limestone of Tasmania. The paucity of specimens makes a full assessment of the species impossible at present.

Fig. 3. *Wyndhamia*? sp. A, ventral internal mould, BR 1472, x3. B, latex cast of dorsal interior BR 650, x2. From Chimney Peaks Formation. (Waterhouse 1982).

Wyndhamia typica typica (Booker, 1929)

Fig. 4

1877 *Productus Clarkei* [not Etheridge Snr] – Koninck, p. 203, pl. 11, fig. 11 only.
1929 *Strophalosia* (*Wyndhamia*) *dalwoodensis* Booker, p. 25, pl. 1, fig. 1-5, pl. 3, fig. 5, 7.
1929 *S.* (*Wyndhamia*) *valida* Booker, p. 26, pl. 2, fig. 1-5, pl. 3, fig. 4, 6.
1929 *Productus* (*Branxtonia) typica* Booker, p. 30, pl. 3, fig. 1-3.
1950 S*. clarkei* [not Etheridge Snr] – David, pl. 34b.

1954 *S. typica* – Maxwell, p. 545, pl. 55, fig. 8-14.
1957 *S. clarkei* [not Etheridge Snr] – Coleman, pl. 18, fig. 1, 2.
1960 *Wyndhamia jukesi* [not Etheridge] – Muir-Wood & Cooper, p. 90, pl. 5, fig. 6, 8.
1960 *Branxtonia typica* = *Wyndhamia typica* – Muir-Wood & Cooper, p. 89, pl. 5, fig. 11-13.
1960 *W. valida* – Muir-Wood & Cooper, p. 90.
1964 *W. dalwoodensis* – Waterhouse, p. 50, pl. 8, fig. 3, 4.
1965 *W. dalwoodensis* Muir-Wood p. 452 (part, not Fig. 307.3a-c = *W. typica clarkeina*).
1969 *W. dalwoodensis* – Clarke, p. 43, pl. 8, fig. 4 (part, not fig. 5 = *jukesi*).
1987 *W. dalwoodensis* – Archbold, p. 19.
1998 *W. typica* – Briggs, p 125, Fig. 64A-H.
2001 *W. typica* – Waterhouse, p. 70.
2008 *W. typica* – Waterhouse, pp. 358, 361, Fig. 6E, I.
cf. 2023 *W*. cf. *typica* - Lee in Lee et al., p. 10, Fig. 4W-Y, 5.

Diagnosis: Moderately large shells with thick body cavity, ventral valve may be weakly sulcate, dorsal valve with short trail in early growth stages, becoming thickened into wedge-shape with increased maturity. Ventral disc spines largely semi-recumbent subuniform and 0.5 to 0.8mm in diameter, rarely erect, interspersed with rare slender prostrate spines. Ears with few if any spines. Dorsal ornament of low angle recumbent spines, about 0.25mm in diameter, lost during maturity from posterior valve and so concentrated over anterior shell, closely spaced shallow dimples.

Lectotype: AMF 41763 from Elderslie Formation, north Sydney Basin, figured by Booker (1929, pl. 3, fig. 1-3); Maxwell (1954, pl. 55, fig. 9, 10), and Muir-Wood & Cooper (1960, pl. 5, fig. 11-13), SD Maxwell (1954, p. 545).

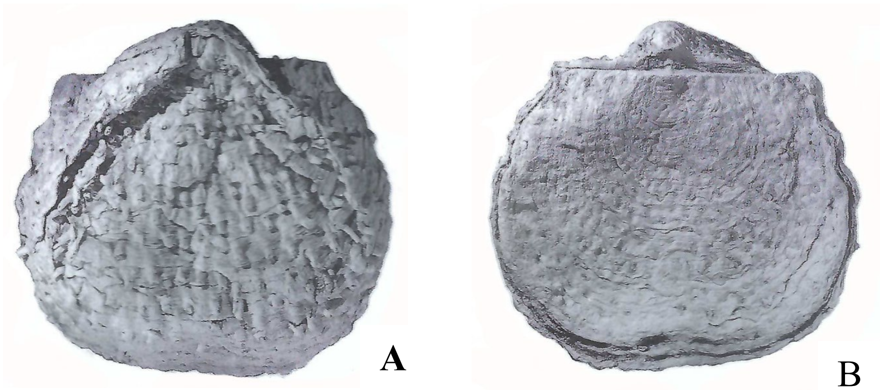


Fig. 4. *Wyndhamia typica typica* (Booker). A, B, ventral and dorsal aspects of conjoined specimen, UQF 49386 x1 from Elderslie Formation. (Briggs 1998).

Morphology: Features of this species include the common though not ubiquitous presence of a shallow ventral sulcus, and a hinge that is a little less than maximum width, with small well-defined ears, bearing few erect spines. It may well be that the morphotypes described below are no more than varieties within the species, but that requires further study. It was shown on the basis of an extensive examination of *Wyndhamia typica* as summarized in Waterhouse (2001) that Briggs (1998) had inadequately diagnosed *Wyndhamia* by ignoring or overlooking the widespread presence of prostrate fine ventral spines, and in neglecting the fact that ears in a number of specimens lack spines.

Briggs (1998, p. 125) regarded Queensland specimens from the Bowen River coal-field at Parrot Creek that had been figured by Etheridge Jnr (1880, pl. 9, fig. 21, pl. 10, fig. 22) and Etheridge Jnr (1892, pl. 13, fig. 15) as belonging to *Wyndhamia typica*, but no evidence was provided to distinguish the specimens from *Pseudostrophalosia clarkei*, or possibly *Ps. furcalina.* His misidentifications considerably distorted the distribution and correlation for *W. typica,* and miscorrelated the sequences in the Bowen Basin of Queensland with those of the Sydney Basin in New South Wales.

Stratigraphy: The type species comes from the Elderslie Formation. Other specimens, including individuals from approximately correlative lower Letham beds in New Zealand, upper Aldebaran and Freitag beds of the southwest Bowen Basin, and Grange Mudstone and lower Malbina beds of Tasmania show differences that are of uncertain significance, provisionally evaluated as of no more than subspecific ranking.

Wyndhamia typica crassiconcha Waterhouse, 2001

Fig. 5

1998 *Pseudostrophalosia clarkei* [not Etheridge] – Briggs, p. 116, text-fig. 29 column for GSQ Eddystone 1.
2001 *Wyndhamia typica crassiconcha* Waterhouse, p. 72, pl. 5, fig. 12-16, (part, not fig. 17? = *Echinalosia*?).

Diagnosis: Large shells, ventral valve with very shallow sulcus or median reduction in curvature, dorsal valve externally weakly concave in early maturity, becoming wedge-shaped with almost flat internal disc. Ventral spines somewhat variable in diameter, rare or absent from ears, aligned in commarginal rows as a rule but may be more irregular, rare slender spines, overall suberect rather than semirecumbent, many 0.8mm to just over 1mm in diameter. Spines crowded over three quarters of the one known dorsal valve, erect, up to 0.6mm in diameter in Waterhouse (2001, pl. 5, fig. 117; Fig. 5B herein), but the identity of this specimen is not certain – it could belong to *Echinalosia*, unless the spines were present at early maturity and then lost.

Holotype: UQF 65481 from Freitag Formation, southwest Bowen Basin, figured in Waterhouse (2001, pl. 5, fig. 14-16) and herein Fig. 5D, OD.

Morphology: The ventral spines are not quite the same as those of *Wyndhamia typica*, but differences are not fully consistent, as discussed in Waterhouse (2001, p. 73). In the Freitag suite, the lateral spines are somewhat coarser than in type *W. typica*. It was noted than the Freitag specimens are closer in shape to the material described by Waterhouse (1964) from the middle Letham Formation of New Zealand.

Stratigraphy: Similar specimens are also found in the upper Aldebaran Sandstone, below the Freitag Formation, as recorded by Waterhouse (2001, p. 74). They also occur through the

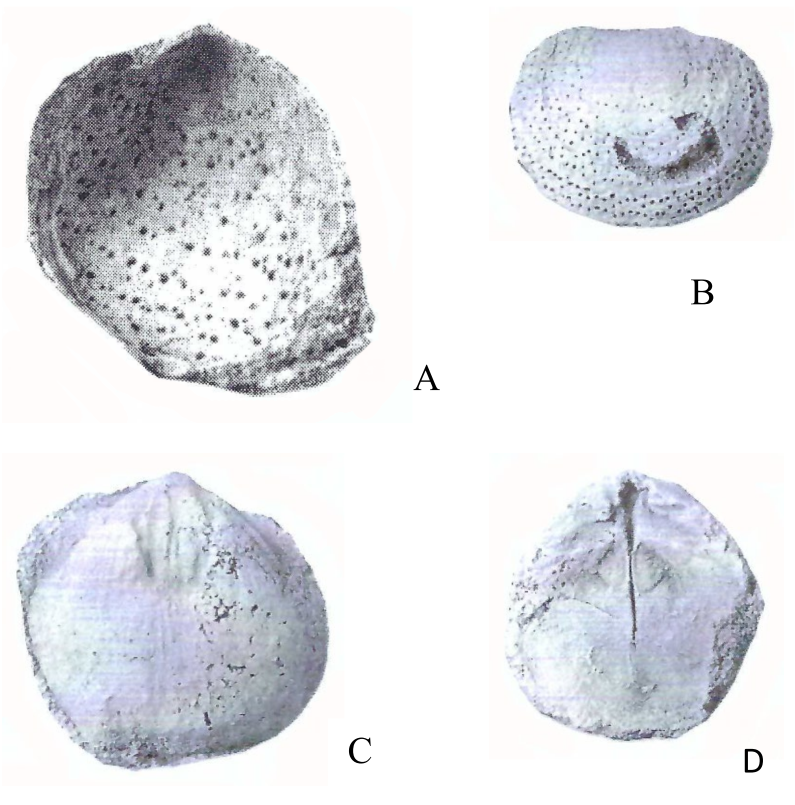


Fig. 5. A, C, D. *Wyndhamia typica crassiconcha* Waterhouse. A, ventral external mould UQF 65492. C, ventral internal mould UQF 65480. D, dorsal aspect of internal mould with valves conjoined, UQF 65481, part of holotype. B, dorsal external mould possibly of *Echinalosia* sp., UQF 65482. From Freitag Formation, west Bowen Basin, x1. (Waterhouse 2001).

Freitag Formation in the GSQ Eddystone 1 core, as examined in Waterhouse (2001, pp. 73, 74). They were identified as *Pseudostrophalosia clarkei* by Briggs (1998, text-fig. 29), but do not belong to *Pseudostrophalosia* because the ventral ears have few or no spines.

Wyndhamia typica clarkeina Waterhouse, 2001

Fig. 6

1960 *Wyndhamia dalwoodensis* [not Booker] – Muir-Wood & Cooper, p. 90, pl. 5, fig. 7, 9, 10.
1965 *W. dalwoodensis* – Muir-Wood, p. 452, text-fig. 307.3a-c.
1969 *W. dalwoodensis* – Clarke, p. 43, pl. 8, fig. 4 (part, not fig. 5 = *W. jukesii*).
1998 *W. jukesii* [not Etheridge] – Briggs, p. 126 (part).
2000 *W. dalwoodensis* [not Booker] – Brunton, Lazarev, Grant & Jin, p. 574, text-fig. 405.3a-c.
2001 *W. clarkeina* Waterhouse, p. 75.

Diagnosis: Anterior ventral valve with numerous prostrate and slender spines.

Holotype: USNM 112138d from Collinsville Road Quarry near Granton, Hobart, Tasmania, figured by Muir-Wood & Cooper (1960, pl. 5, fig. 10), Muir-Wood (1965, text-fig. 307.3a), Brunton et al. (2000, text-fig. 405.3a), and herein as Fig. 6A, OD.

Morphology: Briggs (1998, p. 127) excluded the Muir-Wood & Cooper specimens treated herein as *clarkeina* from *Wyndhamia typica*. He claimed that these specimens belonged to *jukesi*, as spines were deemed to be prostrate, but size and shape indicate *typica*. There would appear to be justification to treat the Tasmanian form as a subspecies rather than full species. Judged from figures, ear spines are few or not developed.

Fig. 6. *Wyndhamia typica clarkeina* Waterhouse. A, part of exterior of ventral valve, latex cast, USNM 112138d, holotype, x2. B. dorsal aspect of specimen with valves conjoined, USNM 112138a x1. C, latex cast of dorsal interior, USNM 112138c, x1. From Grange Mudstone at Collinsvale Road near Hobart, Tasmania. (Muir-Wood & Cooper 1960).

Stratigraphy. This form has been observed in the Granton Mudstone, and in the overlying Malbina A and B levels in Tasmania (Clarke 1969, Waterhouse 1970)

Genus ***Pseudostrophalosia*** Clarke, 1970

Diagnosis: Medium-sized suboval shells, the ventral valve moderately to well-inflated with small cicatrix and dense more or less semirecumbent to recumbent spines generally arranged in commarginal rows, in two series over disc and trail, and, as prime characteristic, close-set spines clustered over ears. Dorsal valve with numerous fine spines. Internal features heavily thickened, especially over the anterior disc.

Type species: *Strophalosia brittoni* Maxwell, 1954, p. 543 from Tiverton Formation, Bowen Basin, OD.

Discussion: *Pseudostrophalosia* is the oldest member of Wyndhamini. The source of the genus is not clear: it obviously arose from stock different from that *of Echinalosia* (*Echinalosia*) *preovalis* and *E*. (*E*.) *curvata*, and perhaps, if it arose from within Australian faunas, ancestry lies with the species described as *Maxwellosia curtosa* (Waterhouse, 1986b) from the Fairyland Formation, because this species is highly convex with sturdy spines, and has strongly impressed muscle scars. On the other hand, *Crassispinosella* from the early Permian of east Australia (Waterhouse 2023, pp. 27, 69) has a thick dorsal valve, though it lacks dorsal spines and ventral spines are of largely uniform diameter. Waterhouse (1986, p. 28) had pointed out that *brittoni* has a large number of ear spines in contrast to the ears of *Wyndhamia*, and later Briggs (1998) on this basis established that species of *Pseudostrophalosia* should not be referred to *Wyndhamia* Booker, 1929, which lacks the cluster of ventral ear-spines.

Pseudostrophalosia appears to be very close to *Notolosia* Archbold, 1986, type species *N. dickinsi* Archbold, 1986 from the Hardman Member of Wuchiapingian age in the Canning Basin, Western Australia, with similar burst of ventral ear spines (see Waterhouse 2013, p. 230) and wedge-shaped dorsal valve. *Notolosia* was proposed as a subgenus of *Echinalosia*, and was treated as a full genus by Brunton et al. (2000, p. 574) with a burst of “unusually prominent” ear spines. Briggs (1998) suggested that the halteroid subvermiform ventral spines are more persistent and numerous than those in *Wyndhamia* or *Pseudostrophalosia*, which might validate its status as a subgenus of *Pseudostrophalosia,* but reservations remain over the validity of any separation from *Pseudostrophalosia.*

Pseudostrophalosia brittoni (Maxwell, 1954)

Fig. 7, 8

1954 *Strophalosia brittoni* Maxwell, p. 543, pl. 54, fig. 20-22, pl. 55, fig. 1-3.
?1964 *Strophalosia* sp. Hill & Woods, pl. P4, fig. 10.
1970 *Pseudostrophalosia brittoni* – Clarke, p. 987.
1970 *Wyndhamia enorme* Clarke, p. 987.
?1972 *W. enorme* – Hill, Playford & Woods, pl. P4, fig. 10.
1998 *Ps. brittoni* – Briggs, p. 113, Fig. 60A-F.
2007 *Ps. brittoni* – Brunton, p. 2666, Fig. 1774a-e.
2015 *Ps. brittoni* – Waterhouse, p. 86, Fig. 34-40.

Diagnosis: Moderately large and inflated shells with weakly concave dorsal valve which may bear low median fold, moderately wide hinge, ventral spines close-set, of two series, usually in commarginal rows, low angle recumbent spines about 0.2m in diameter and much more common semi-recumbent spines some 0.6mm in diameter that are inclined at 30° from the shell surface, coarse at over 0.7m diameter over ears and forming brush, which extends anteriorly over posterior lateral slopes. Dorsal spines closely spaced, 0.2mm in diameter, prominent commarginal lamellae and crowded small dimples. Posterior ventral valve heavily thickened, elongate adductor scars, buttressed large teeth. Dorsal valve with raised brachial ridges, thickened anteriorly.

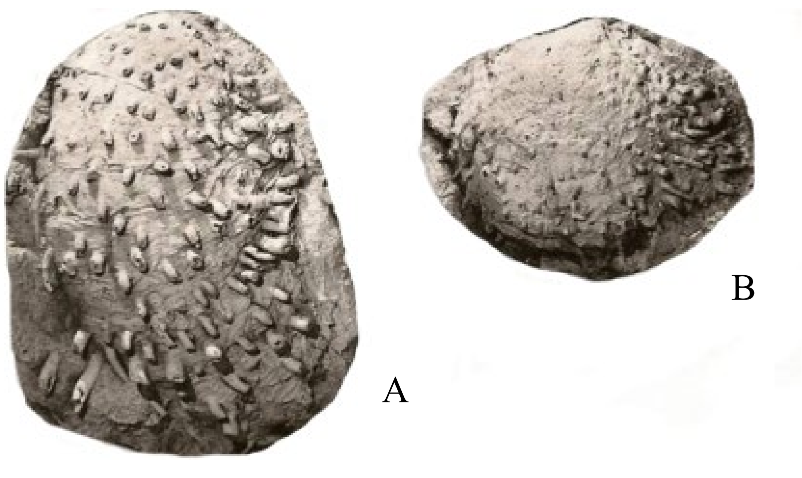


Fig. 7. *Pseudostrophalosia brittoni* (Maxwell). A, latex cast of ventral valve UQF 81295, x2. B, latex cast of ventral valve UQF 81296, x1.5. From middle Tiverton Formation. (Waterhouse 2015a).

Holotype: UQF 15657 from Tiverton Formation, figured by Maxwell (1954, pl. 54, fig. 20-22), OD. Holotype for *enorme*, specimen UQF 16258 from Tiverton Formation at Homevale, figured by Maxwell (1954, pl. 55, fig. 1, 2), designated by Clarke 1970, p. 987), OD.

Morphology: Shells large for family, up to 45mm wide, gently arched ventrally, flat medianly, only moderately concavo-convex, and may show a dorsal fold. The ventral valve is gently inflated with moderately wide hinge. Ventral spines open into the ears and anterior trail, but spine tunnels are seen over the disc chiefly in immature specimens, though one mature specimen is reported by Waterhouse (2015) to have short channels about 2mm long.

Stratigraphy: The species is abundant in the middle Tiverton Formation and correlates of the north Bowen Basin, occurring abundantly in the *Taeniothaerus subquadratus* Zone, and rarely in the *Capillonia armstrongi* Subzone. Briggs (1998) recognized the species only at one locality in the Tiverton Formation, and wrongly identified *Acanthalosia mysteriosa* from the Roses Pride Formation as *Pseudostrophalosia brittoni*, though it has no burst of ear spines.

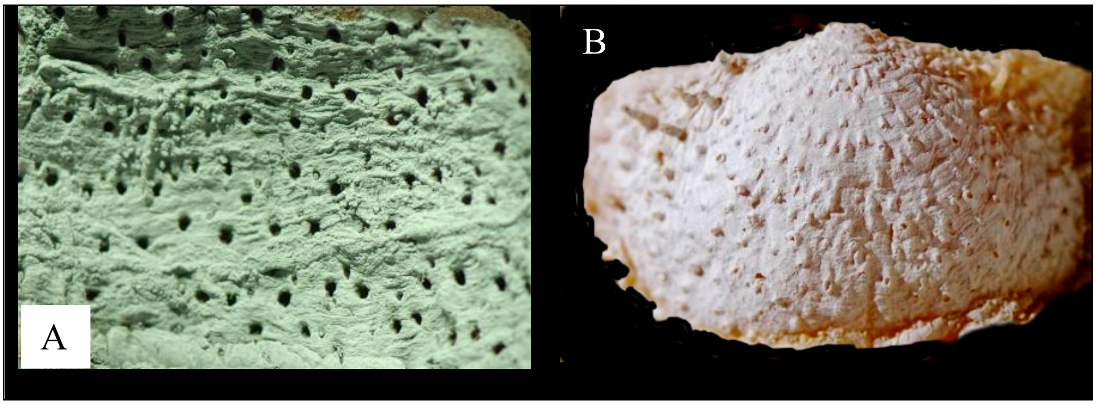


Fig. 8. *Pseudostrophalosia brittoni* (Maxwell). A, detail of anterior ventral external mould, UQF 81280, x3.5. B, latex cast of ventral valve UQF 81282, x2. From middle Tiverton Formation, north Bowen Basin. (Waterhouse 2015).

Pseudostrophalosia blakei (Dear, 1971)

Fig. 9 - 11

1971 *Wyndhamia blakei* Dear, p. 9, pl. 2, fig. 10, 11, pl. 3, fig. 1-4.
1983 *W. ingelarensis* – Waterhouse & Jell, p. 241, pl. 1, fig. 7, 8, pl. 6, fig. 1.
1983 *Echinalosia maxwelli* [not Waterhouse] – McClung, p. 72, text-fig. 14.1, 2, 6.
1983 *W. ingelarensis* – McClung, p. 73, Fig. 14.3-5, 7, 8.
1998 *Pseudostrophalosia blakei* – Briggs, p. 115 (part).
1998 *Echinalosia deari* [not Briggs] – Briggs, p. 101 (part).
2001 *Ps*. cf. *blakei* – Waterhouse, p. 76, pl. 5, fig. 6-11.

2008 *Ps. blakei* – Waterhouse, p. 365, Fig. 7G.

This is the preferred version: a modified alternative follows on p. 113.

Diagnosis: Small to medium in size, ventral valve elongate, sulcus of variable strength, may be absent, ventral interarea of moderate height, often but not always narrow, ventral spines numerous, recumbent and often erect, both sets up to 0.75mm in diameter, short spine tunnels. Dorsal valve weakly concave, weakly wedge-shaped, spines fine, erect.

Holotype: GSQF 11623 from upper Moonlight Sandstone, [with boundary shifted upwards to incorporate lower Blenheim Formation of Dear 1971, as based on faunal content summarized in Waterhouse & Jell 1983], figured by Dear (1971, pl. 2, fig. 10), OD.

Morphology: Waterhouse & Jell (1983) suggested that the taxon *blakei* was basically the same as *ingelarensis* Dear, and later Waterhouse noted the name had page priority over that of *ingelarensis*. The species *ingelarensis* is shaped moderately like *blakei* and may display a

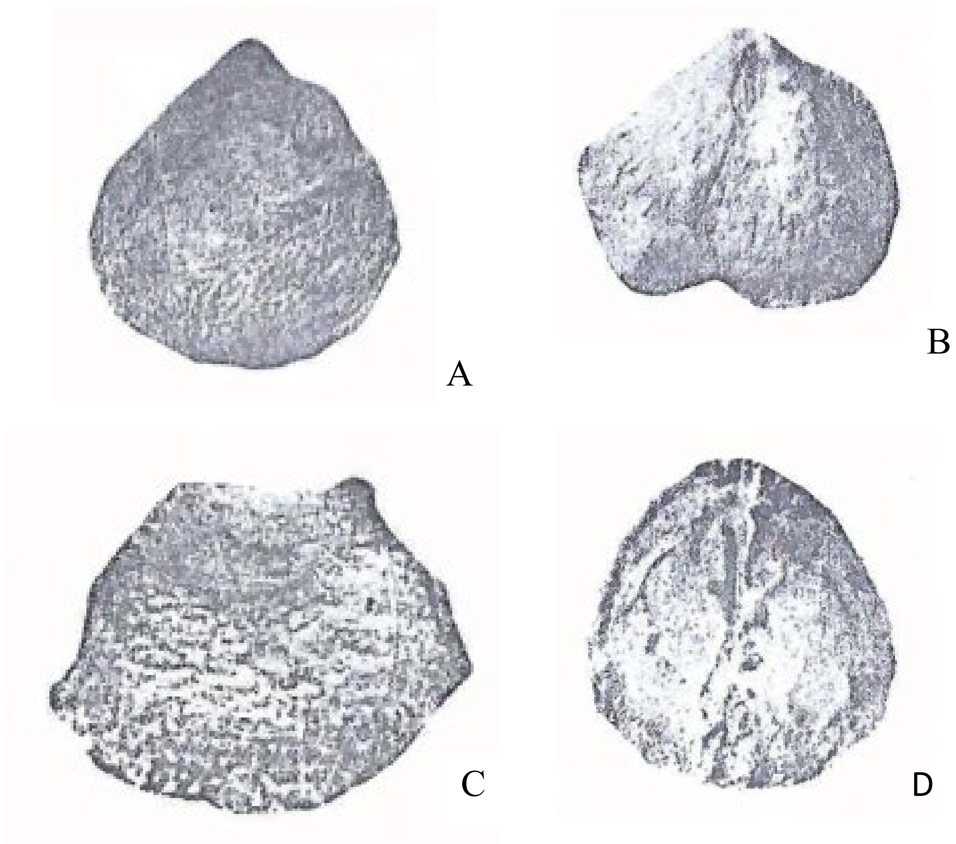
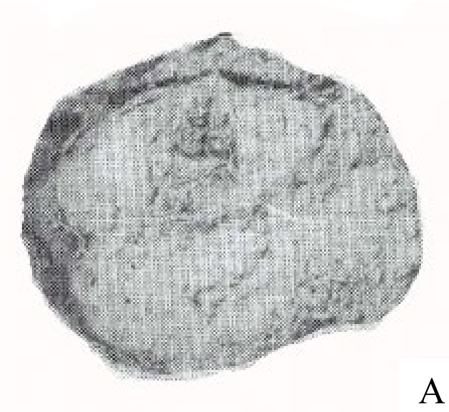


Fig. 9. *Pseudostrophalosia blakei* (Dear). A, latex cast of dorsal exterior, GSQF 11699. B, ventral internal mould, GSQF 11622. C, dorsal external mould GSQF 11700. D, latex cast of dorsal interior, GSQF 11697. Specimens x1.5 from Moonlight Sandstone (formerly lower Blenheim Formation), north Bowen Basin. (Dear 1971).

sulcus. The identity of the two names appears to be substantiated by examination of the collections at the Geological Survey of Queensland, now kept at the Queensland Museum bulk storage unit at Hendra, Brisbane. These show that specimens vary well beyond the narrow limits stressed by Briggs (1998) in insisting that *blakei* had a narrow elongate shape with narrow hinge and was in part distinguished by its sulcate ventral valve. Many *blakei* in the bulk collection have a wide hinge, and may be non-sulcate. This is shown by the synonymy of Waterhouse & Jell specimens made by Briggs, which though assigned to *blakei,* have wide hinge, and no ventral sulcus, counter to the Briggs definition. Only small specimens of *blakei* were selected by some authors to diagnose the species, whereas some larger specimens were featured in attempts to circumscribe *ingelarensis,* to give a misleading impression of the two species. Internal moulds figured by McClung (1983, Fig. 14.1, 2, ?6) as *Echinalosia maxwelli* from locality LD96 could well prove to be *blakei.* Only internal moulds were figured for the ventral valve, and the exterior would be helpful in determining the species.



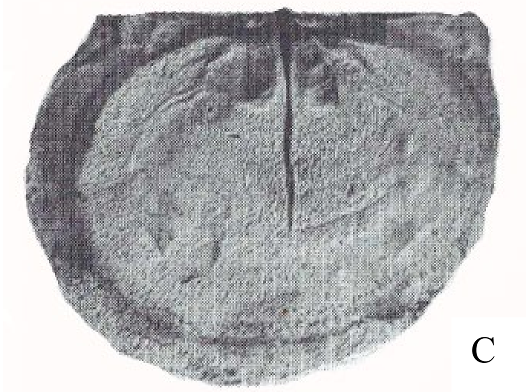


Fig. 10. *Pseudostrophalosia blakei* (Dear). A, ventral internal mould UQF 73260, x3. B, dorsal external mould UQF 73202, x1.5. C, dorsal internal mould UQF 73201. Specimens x2 from upper Moonlight Sandstone, north Bowen Basin. (Waterhouse & Jell 1983).

Stratigraphy: The species *blakei* is represented in the lower and especially upper Moonlight

Sandstone of the north Bowen Basin, the Barfield Formation of the southeast Bowen Basin, and lower Peawaddy Formation (formerly ascribed to Ingelara Shale) and Catherine Sandstone of the southwest Bowen Basin. Poorly preserved material from New Zealand appears to belong to *blakei.* It comes from above the *Echinalosia maxwelli* Zone and below the *Maxwellosia ovalis wassi* Zone in the Mangarewa Formation at Wairaki Downs, above the Letham Burn Member with *Echinalosia maxwelli*.

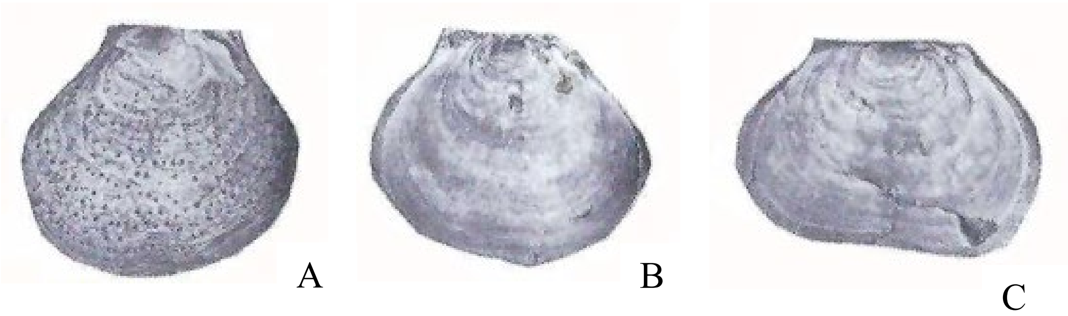


Fig. 11. *Pseudostrophalosia blakei (*Dear)?. A, external mould of dorsal valve, GSQF 12538 12538. B, decorticated dorsal valve GSQF 11707. C, decorticated dorsal valve GSQF 11703. The specimens were referred to *Echinalosia* (now *Acanthalosia*) *deari* by Briggs (1998). Specimens x1.5 from GSQ LD 96, lower Catherine Sandstone or just below. (McClung 1983).

Pseudostrophalosia blakei ingelarensis (Dear, 1971)

Fig. 12, 13

1971 *Wyndhamia ingelarensis* Dear, p. 12, pl. 3, fig. 5-10.
1986 *W. blakei* –Waterhouse, p. 33, pl. 5, fig. 25, 27, pl. 6, fig. 1, 2, pl. 15, fig. 10 (part, not pl. 5, fig. 26, 28, 30 = *Nonauria parfreyi,* not pl. 5, fig. 24, 29, 30 = *Acanthalosia deari*).
1998 *Pseudostrophalosia ingelarensis* – Briggs, p. 118, Fig. 62A-D, H (part, not E, F, G, I = *furcalina* (if genuinely from UQL 3135).

Diagnosis: Possibly with earlier growth stages more rounded and less elongate than in *blakei,* though this needs further exploration.

Holotype: UQF 15651 from the lower fossiliferous sandstone of the Ingelara Formation, southwest Bowen Basin, figured by Dear (1971, pl. 3, fig. 5a, b) and Fig. 13C herein, OD.

Morphology: Out of deference to the assessments of Dear (1971), Briggs (1998) and others, the form entitled *ingelarensis* may be considered as a subspecies of species *blakei.* But I remain doubtful about the validity or usefulness of the taxon and prefer the synonymy to be integrated with that of *blakei.* On the other hand it must be allowed that the accompanying faunas do not show a great deal in common with those species that accompany *Pseudostrophalosia blakei* in the Moonlight Formation of the north Bowen Basin, and the productids and ingelarellids differ, suggesting a difference in ages, unless facies were involved, inviting further study.

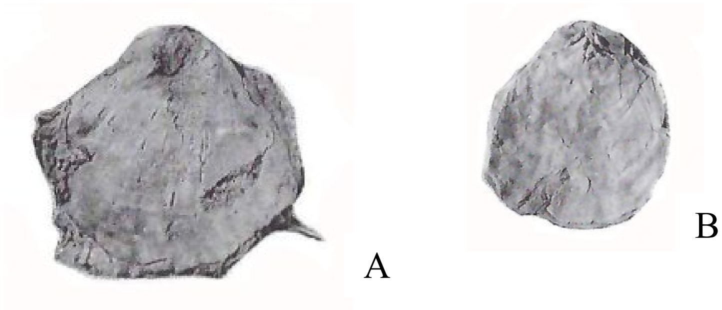


Fig. 12. *Pseudostrophalosia blakei ingelarensis* (Dear). A, ventral internal mould, UQF 43429. B, dorsal aspect of decorticated specimen with valves conjoined, UQF 73988. Specimens x1 from Barfield Formation, southeast Bowen Formation. (Waterhouse 1986b).

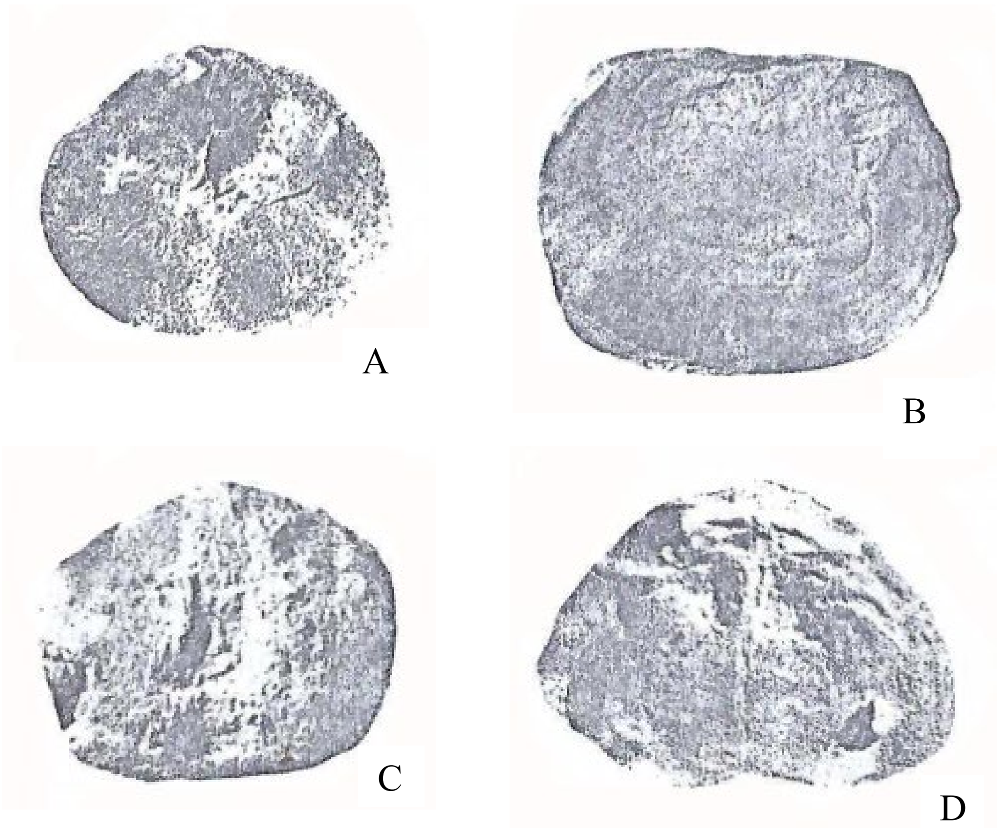


Fig. 13. *Pseudostrophalosia blakei ingelarensis* (Dear). A, ventral internal mould UQF 59651, holotype. B, dorsal external mould UQF 59994. C, ventral valve with exterior spines largely preserved, UQF 15651, holotype. D, dorsal aspect, internal mould of both valves, UQF 59995. Specimens x1.5 from Ingelara Formation, southwest Bowen Basin. (Dear 1971).

Pseudostrophalosia crassa Briggs, 1998

Fig. 14, 15?

1983 *Wyndhamia* cf. *ingelarensis* [not Dear] – McClung, p. 73, Fig. 15.1-20.
1998 *Ps. crassa* [not Briggs] – Briggs, p. 119, Fig. 63D (part, not Fig. 63A-C, E-G = *clarkei*?).
2001 *Ps. crassa* – Waterhouse, p. 81.

Diagnosis: Ventral valves with coarse erect spines, in some individuals the coarse erect spines are mixed with fine erect spines, unlike the arrangement in other species such as *Pseudostrophalosia clarkei*. Dorsal valve with hinge and prominent ears rather like the build in small specimens of *Ps. blakei.*

No diagnosis was offered by Briggs (1998) for his proposed species, relying instead on a partial condensed description, which was entitled diagnosis, but contained no explicit means of discriminating the taxon from other species. This technique, useful for avoiding accurate assessments of species, was widely employed by Briggs (1998) and accepted by the editor and referees, but doubtfully conforms with the stipulation by the ICZN Article 13 that the diagnosis should differentiate the taxon from other related or similar taxa. However comparisons with other species may sit awkwardly at times with a diagnosis, so herein comparisons may be made in the discussion under the heading Morphology, and Briggs did the same for some of proposed species in his Remarks, but this was not done for *crassa*.

Holotype: GSQF 12493, stated without reasons to be from Ingelara equivalents by Briggs (1998), figured by McClung (1983, Fig. 15.16) and herein as Fig. 14C herein, OD. Briggs also cited a second holotype as Briggs (1998, Fig. 63A), CPC 31675, from a younger stratigraphic level, but this has to be discounted.

Morphology: Much of the material included by Briggs (1998) is obviously close in terms of shape, size and spine detail to *Pseudostrophalosia clarkei* (Etheridge, Snr), and various specimens included by Briggs (1998) in his synonymy for *crassa* were originally described as *clarkei by* Etheridge Jnr (1880). These show no spine detail, to imply that the reason for identification was purely stratigraphic not morphological. Possibly the fact that ventral spines are coarse in one of the two Briggs versions of *crassa* provided a distinction between *crassa* and *clarkei,* but one figure of *clarkei* in Briggs (1998, Fig. 61D) shows that *clarkei* spines can be robust, as reaffirmed by Waterhouse (2022b). Briggs (1998, p. 121) asserted that successive populations of *crassa* "showed a marked coarsening of the spinose ornament in both valves upward" [ie. stratigraphically], based on the figures provided by McClung (1983, Fig. 15). The three figures provided for ventral external moulds came from levels at 682m (McClung 1983, Fig. 15.20) which is the holotype, 701m (McClung 1983, Fig. 15.16) and 702m (McClung 1983, Fig. 15.11), as refigured herein (Fig. 14A). The anterior spines in McClung (1983, Fig. 15.20), the highest specimens stratigraphically, are a little coarser than in the figures from older localities, and from the low-placed specimen at 702m there are numerous fine erect spines, much less evident in other figures. The assessments are based on solitary specimens, with no confirmation that other specimens from the same levels were exactly the same, so that the assertion remains possible but needs to be better established, not easy when specimens are known only from a borehole. Briggs referred to McClung

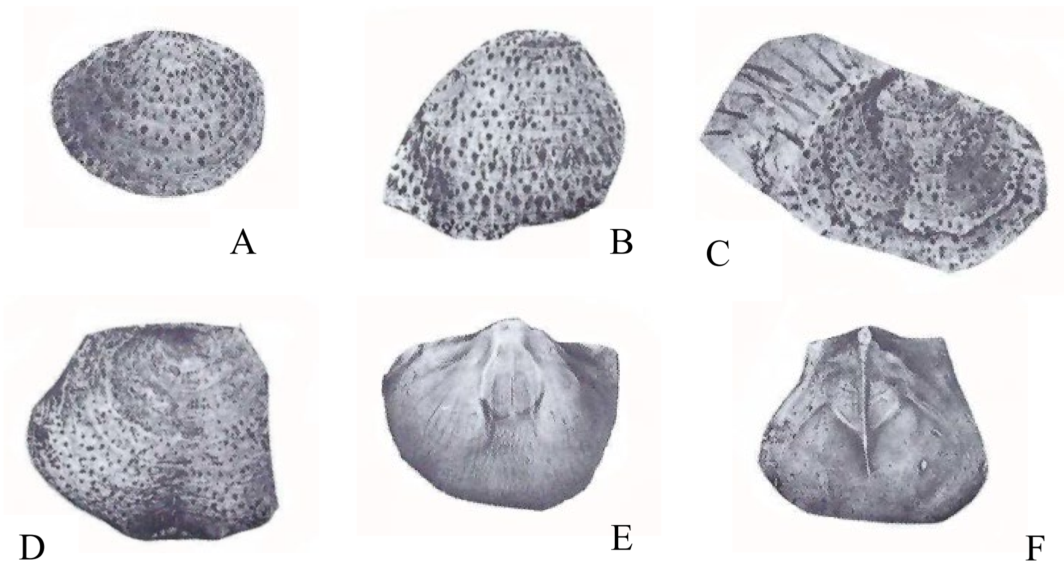


Fig. 14. *Pseudostrophalosia crassa* Briggs. A, ventral external mould GSQF 12497, 701.7m. B, ventral external mould, GSQF 12523, 682m, C, ventral external mould, GSQF 125493, 701.7m, holotype, not showing many fine erect spines, unlike 14A. D, dorsal external mould GSQF 12574. E, ventral internal mould GSQF 12495. F, latex cast of dorsal interior, GSQF 12520. Specimens x1 from Eddystone 1 core, with thickness measured from the surface, north Bowen Basin. The specimen in F shows large projecting ears, deemed by some authors to typify *blakei*. (McClung 1983).

(1983, pl. 15, meaning Fig. 15). In addition, he included specimens of Dickins (1989) from the upper Blenheim Formation and equivalents in the northern Bowen Basin in synonymy as

Pseudostrophalosia. The Dickins material has no ears and no pseudostrophalosian ear-spines, and so is clearly not *crassa*. Is it possible that Briggs realized that *Pseudostrophalosia* at least somewhat like *clarkei* was definitely to be found well above the stratigraphic position he had allocated to *clarkei,* and had to be allocated to a species? To call them *clarkei* would never do – that would undercut his understanding and advocacy for a low stratigraphic position for *clarkei*. So he came up with *Ps. crassa*. That might well indicate that *crassa* should be synonymized with *clarkei.* But such a step might prove premature, given the inadequate description by Briggs, and at least two unusual features in the McClung material, involving the high number of fine erect ventral spines in one specimen (McClung 1983, Fig. 15.11), as shown herein in Fig. 14A, and the presence of some dorsal valves shaped somewhat like some dorsal valves of *Ps. blakei*, which could even support the correlation of the faunal level with the Ingelara Formation, proposed by Briggs (1998). Is the specimen of Fig. 14A exceptional, and are the rest of the specimens to be interpreted as *Ps. blakei / ingelarensis*? This cannot be ruled out, and it should be remembered that *crassa* cannot be reliably found anywhere else in east Australia.

Briggs (1998, p. 121) took exception to the interpretation by Maxwell (1954, pl. 57, fig. 10-12), who had refigured one of the Etheridge specimens as *Strophalosia ovalis*, as accepted by Dear (1971). Briggs argued that anterior ventral tunnels were significant, and added that the ventral adductor scars were relatively elongate. But the scars of *ovalis* and its ventral tunnels may also be long. I cannot reliably reinterpret the specimen reallocated by Maxwell and Dear because it is not to hand, but see no reason why it should be identified as *crassa*, and indeed the internal mould is remarkably similar to a ventral internal mould figured herein (see Fig. 20B) on p. 56 as *Echinalosia* (*Unicusia*) *minima* (Maxwell) from faunas overlying the Scottville Member. Briggs followed M. J. Clarke in refusing to recognize that wedge-shaped dorsal valves were developed in *Pseudostrophalosia* and *Wyndhamia*, but never found in *Echinalosia* or related taxa.

Stratigraphy: *Pseudostrophalosia crassa* comes from what McClung (1983) recognized as faunal level E in the GSQ Eddystone 1 core, drilled in the Denison Trough of the southwest Bowen Basin. He listed twenty six species from level E, illustrating only a few, without

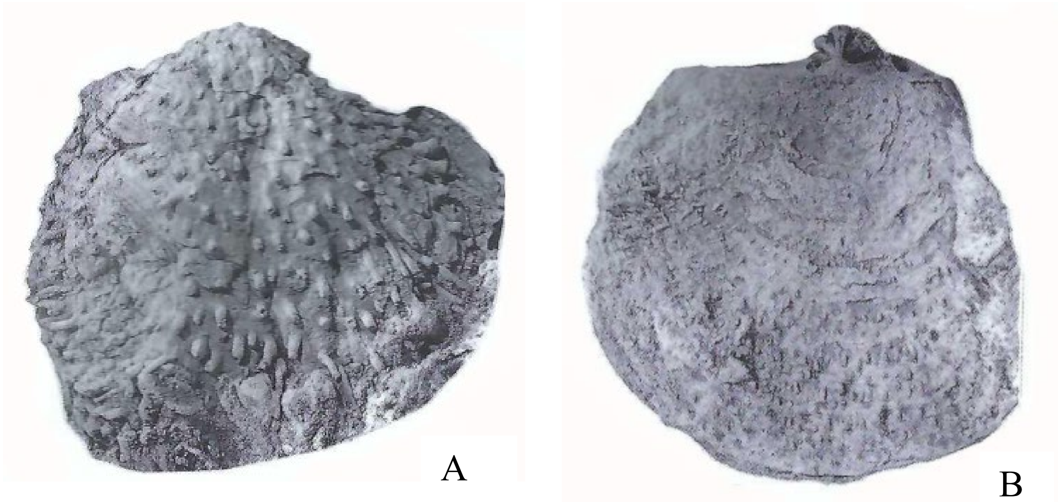


Fig. 15. *Pseudostrophalosia "crassa* Briggs". A, latex cast of ventral valve CPC 31675. B, latex cast of dorsal exterior. Specimens x1.5 from "Back Creek Group" (= Scottville Member or post-Scottville), Clermont, north Bowen Basin. (Briggs 1998). These specimens are tentatively regarded as belonging to *Ps. clarkei* (Etheridge) and occur with Briggs' second and therefore redundantly chosen holotype.

describing any to modern standards, so the age is difficult to determine without re-examination of the collections. The figures include *Ingelarella mantuanensis* as identified by McClung (1983, Fig. 7.3, 4), interesting because the dorsal valve allows that identification whereas the ventral valve approaches *Tigillumia*; worn so-called *Trigonotreta* sp. (McClung 1983, Fig. 9.5, 6) which are subrectangular transverse specimens with low if any plicae could be *Aperispirifer lethamensis, A. hillae* or *A. parfreyi*; *Cancrinella* (now *Magniplicatina*) *magniplica* (McClung 1983, Fig. 16.1, 2) with subdued and fine rugae; and *Terrakea* cf. *brachythaera* (McClung 1983, Fig. 18), which shows considerable approach to *Terrakea exmoorensis*. The fauna, to judge from McClung's faunal list, is clearly large enough to allow a better correlation from first-hand examination. At present, in view of the stratigraphic position, one possible position would seem to be equivalent to part of the Peawaddy Formation, which might accommodate the recognition of dorsal valves of *Pseudostrophalosia* approaching *blakei* in appearance. Figures of the Eddystone fauna E provided by McClung (1983) could also suggest a possible match with Ingelara Shale or early Peawaddy Formation. This is where figures have to be treated with caution, and are not a satisfactory substitute for first-hand examination. Certainly, Briggs' second choice of holotype would suggest Scottville Member and the possibility that *crassa* should be synonymized with *clarkei* or even a contemporaneous companion species. In summary, the few fossils illustrated by McClung (1983) make it difficult to rule out correlation with the Ingelara Formation, just as interpreted by Briggs (1998), and suggest that *crassa* could be a subspecies or variant of *Pseudostrophalosia blakei.*

Pseudostrophalosia clarkei (Etheridge Snr, 1872)

Fig. 15?, 16 - 19

1872 *Productus Clarkei* Etheridge Snr, p. 334, pl. 17, fig. 2, a, b.
?1877 *P. Clarkei* – Koninck, p. 203, pl. 10, fig. 5 (part).
1880 *Strophalosia Clarkei* – Etheridge, p. 289, pl. 9, fig. 18a, 19, 20, 21, pl. 10, fig. 22-25, 28-31, pl. 12, fig. 32, 33? (pl. 10, fig. 23-25, pl. 11, fig. 29-31 = *ovalis* fide Dear 1971, but probably *clarkei*).
1892 *S. Clarkei* – Etheridge, p. 258, pl. 13, fig. 12,13, 15,16, 17, pl. 14, fig. 19 (part, not pl. 13, fig. 14, 16, 17 = *ovalis* fide Dear 1971 but probably *clarkei*). Briggs considered that pl. 13, fig. 12, 16, 17 = *crassa*).
1892 *S. Gerardi* [not King] – Etheridge, p. 260, pl. 13, fig. 14, pl. 14, fig. 18 (part, not pl. 40, fig. 7, 8 (7 = possible *glabra* and 8 = possibly *ovalis* s. l. as in Briggs 1998, p. 103).
1929 *S. clarkei* – Reid, fig. 28.
1954 *S. clarkei* – Maxwell, p. 546, pl. 56, fig. 1-7.
1964 *S. clarkei* – Hill & Woods, pl. P4, fig. 11, 12.
1970 *Wyndhamia clarkei* – Armstrong, p. 13, pl. 1-3, text-fig. 1.
1971 *W. clarkei* – Dear, p. 11.
1972 *W. clarkei* – Hill et al., pl. P4, fig. 11, 12.
1983 *W. clarkei* – Waterhouse & Jell, pp. 236, 238.
1998 *Pseudostrophalosia clarkei* – Briggs, p. 116, Fig. 61A-F.
?1998 *Ps. crassa* Briggs, p. 119 Fig. 63A-C, E-G (part, not Fig. 63D = *crassa* or *blakei*).
2001 *Ps. clarkei* – Waterhouse, p. 79.
2008 *Ps. clarkei* – Waterhouse, p. 367.
2022b *Ps. clarkei* – Waterhouse, p. 101, Fig. 2 - 6.

Comment: The synonymies provided for *clarkei* by Maxwell (1954), Dear (1971) and Briggs (1998) differ from author to author and so seem to include a few omissions and errors. The specimens need to be re-examined at first hand, a task beyond the scope of the present study, and although tentative synonymies for nineteenth century references are suggested in the synonymy, they are highly provisional, and not based on first-hand inspection.

Diagnosis: Moderately large for the genus, ventral valve convex but not strongly inflated with median curvature diminished in a number of specimens, dorsal valve wedge-shaped and gently concave to flat, sharply separated from remainder of disc in both valves, ear spines moderately numerous. Ventral spines in two series, one series fine and low-angle recumbent, the other series coarse and erect, especially prominent posteriorly, spines may be varied in

Fig. 16. *Pseudostrophalosia clarkei* (Etheridge), internal and external aspects of dorsal valve, damaged but showing aspects of morphology, UQF 82800 from UQL 4654. Note the complete secondary loss of dorsal spines. (Waterhouse 2022b).

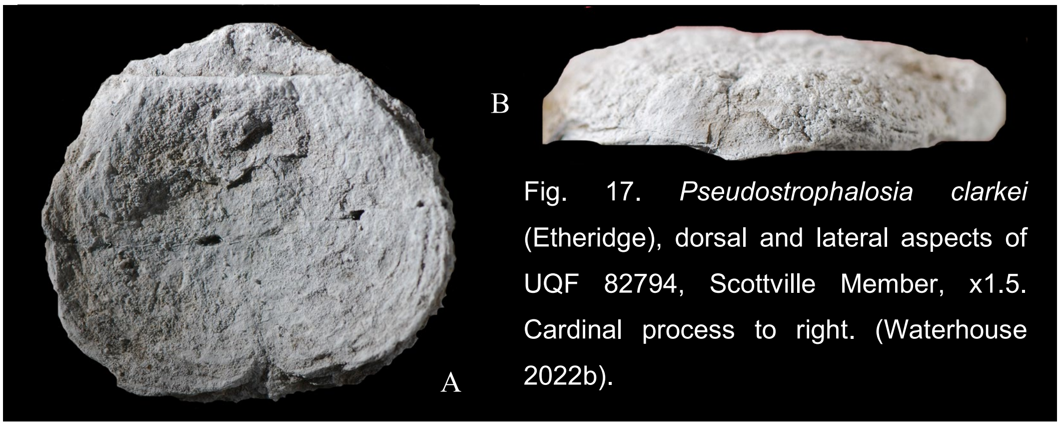


Fig. 17. *Pseudostrophalosia clarkei* (Etheridge), dorsal and lateral aspects of UQF 82794, Scottville Member, x1.5. Cardinal process to right. (Waterhouse 2022b).

apparently different species as *crassa*, and had nominated two different type specimens. A glance at the material figured as *Wyndhamia* cf. *ingelarensis* by McClung (1983, Fig. 15) shows that spine tunnels are not particularly strong in what is now the chosen type for *crassa*, any more than they appear to be in *blakei* or type *ingelarensis*. Well-developed tunnels may typify *clarkei*, and are even stronger in *Ps. furcalina* Waterhouse, as shown shortly.

Briggs (1998, p. 125) regarded Queensland specimens from the Bowen River coal-field at Parrot Creek that had been figured by Etheridge Jnr (1880, pl. 9, fig. 21, pl. 10, fig. 22) and Etheridge Jnr (1892, pl. 13, fig. 15) as belonging to *Wyndhamia typica*. They surely belong to *clarkei.*

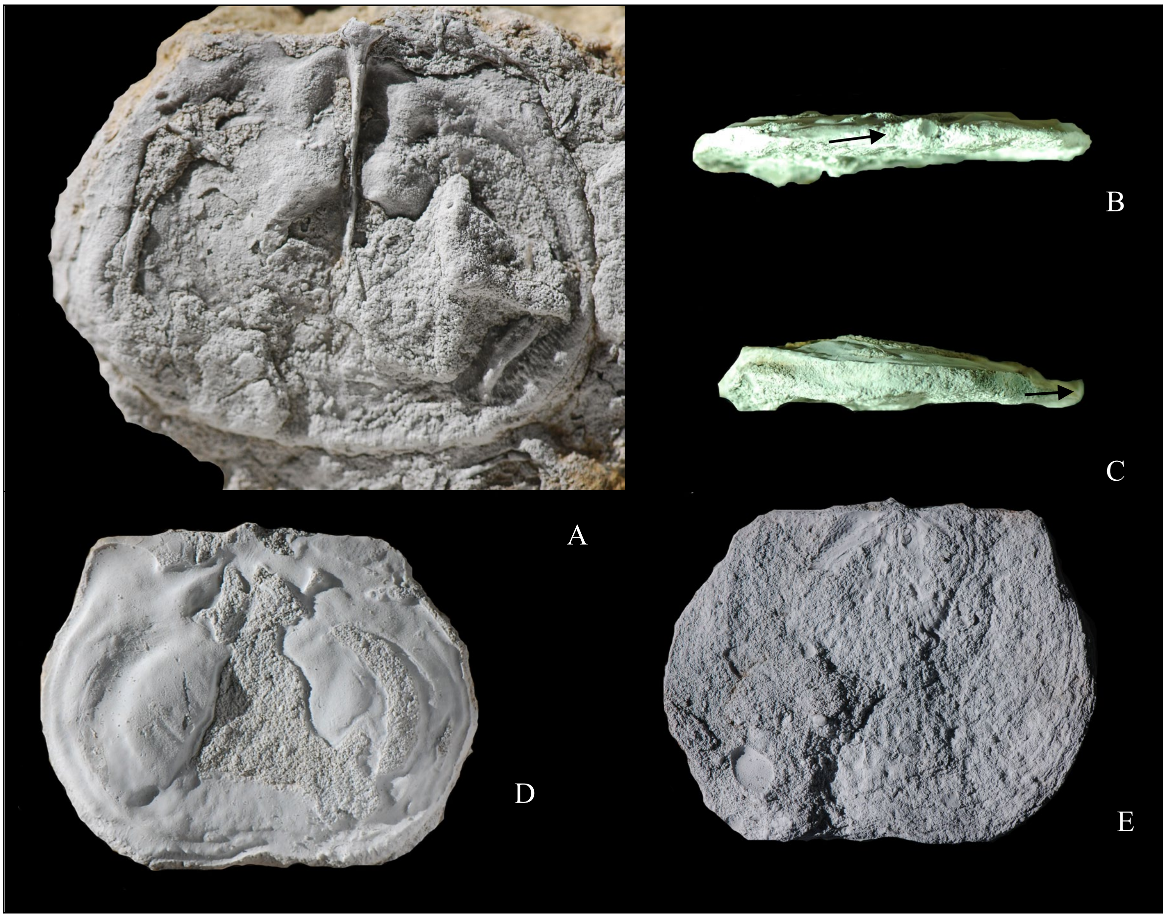


Fig. 18. *Pseudostrophalosia clarkei* (Etheridge) from Scottville Member, UQL 4657, x1. A, dorsal valve UQF 82799, x1.5. B-E, dorsal valve UQF 82793, x1. B, posterior aspect, cardinal process arrowed. C, lateral aspect of same specimen, with cardinal process to right, as arrowed. D, E, dorsal external and internal aspects. (Waterhouse 2022b).

Dear (1971) referred specimens figured by Etheridge (1880, pl. 10, fig. 23-25; pl. 11, fig. 29-31; 1892, pl. 13, fig. 14, 16, 17) to *Echinalosia ovalis*, but the specimens are judged to be *clarkei. Strophalosia Gerardi* [not King] of Etheridge (1880, p. 32, pl. 12, fig. 34-37, pl. 13, fig. 38) was referred to *clarkei* by Dear (1971), but the specimens show a concave dorsal valve. They come from Parrot Creek and Pelican Creek, and are less transverse than most specimens of *Echinalosia* (*Unicusia*) *minima*, in shape coming closest to *Pseudostrophalosia furcalina* Waterhouse. Muir-Wood & Cooper (1960, p. 87) even tentatively referred *clarkei* to *Lialosia*, a genus with spines limited to a ventral hinge row, which shows how shells can become decorticated and lose their spines, but those authors did realize that their material was decorticated, and so made the suggestion with due caution.

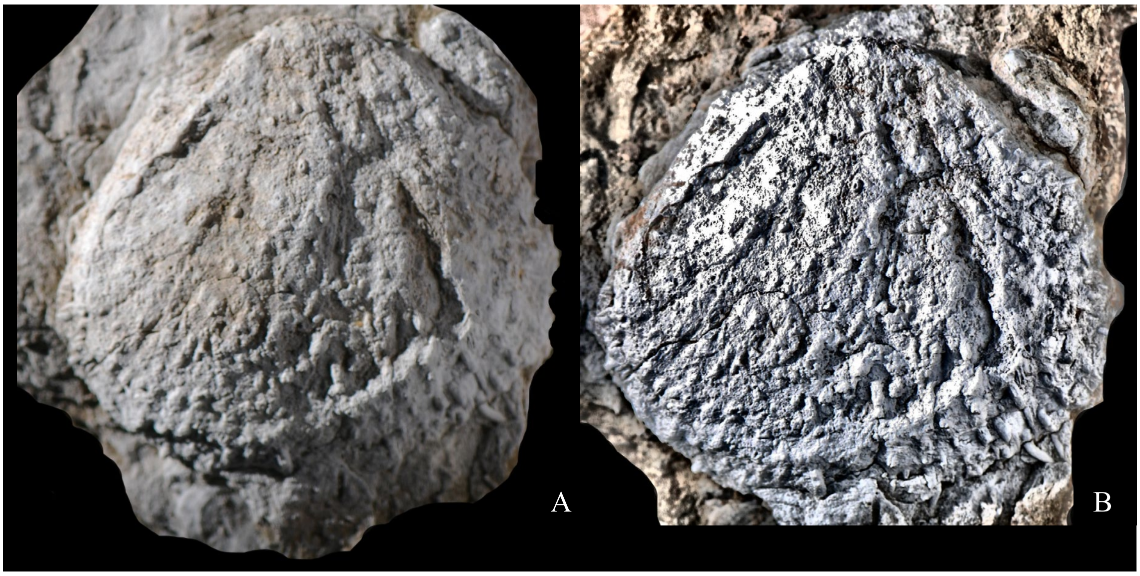


Fig. 19. *Pseudostrophalosia clarkei* (Etheridge) from Scottville Member, ventral valve UQF 82792 from UQL 4657, x1.5, B reproduced by local equalization. (Waterhouse 2022b).

Stratigraphy: One of the first taxa to be recognized amongst strophalosioid species in east Australia, this taxon appears to be limited to the Scottville Member in the north Bowen Basin, and apparently represents sediments and fossils accumulated during a brief cold – glacial – interval. Briggs (1998) misrepresented its occurrence, reporting it from drill-core collections in the Freitag Formation of the southwest Bowen Basin, below *Pseudostrophalosia ingelarensis*, but the Freitag collections are judged to be older, belonging to *Wyndhamia typica* s.l., and was surveyed from the same core material by Waterhouse (2001, p. 74). These specimens lack spines from the ventral ears and are accompanied by further brachiopod species which reinforce this correlation, involving *Tumulosulcus undulosa*, as verified by McLoughin (1988), and *Aperispirifer lethamensis*. Generically related taxa found with *clarkei* in the Scottville Member are completely different.

Pseudostrophalosia gattoni Maxwell, 1954

Fig. 20

1954 *Strophalosia brittoni* var. *gattoni* Maxwell, p. 544, pl. 55, fig. 4-7.
1971 *Wyndhamia clarkei gattoni* Dear, p. 12.
1998 *Pseudostrophalosia clarkei* [not Etheridge] – Briggs, p. 116.

Diagnosis: Ventral valve highly inflated, dental buttresses well-developed, no clearly developed spine tunnels, ventral adductor platform of moderate height. Dorsal valve thick and wedge-shaped. Otherwise poorly known.

Holotype: UQF 15655 from lower Scottville Member, north Bowen Basin, figured by Maxwell (1954, pl. 55, fig. 4-6) and herein as Fig. 20A, B, OD.

Morphology: The type of *gattoni* somewhat approaches *brittoni* Maxwell (1954, pl. 54, fig. 20-22, pl. 55, fig. 1-3) from the Tiverton Formation in lacking conspicuous ventral spine tunnels from the interior of the ventral valve, but this feature is also shared with some specimens of *clarkei.* This similarity to *brittoni* appears to be reinforced by the strong dental buttresses recorded by Dear, whereas the dental buttresses in *clarkei* are not as robust. The taxon called *gattoni* is closer to *brittoni* in having steep lateral walls and being more inflated than type *clarkei*, as appreciated by Maxwell (1954).

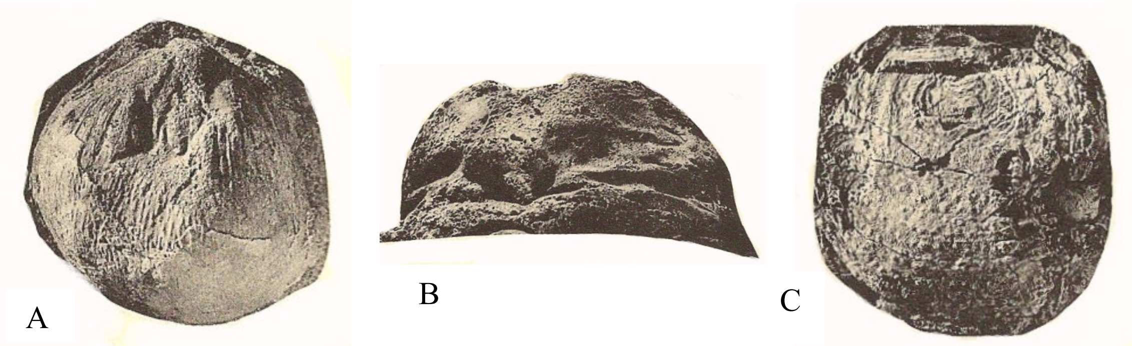


Fig. 20. *Pseudostrophalosia gattoni* (Maxwell). A, B, ventral and posterior aspects of holotype, ventral internal mould, UQF 15655 x1 approx. C, dorsal external mould UQF 15656. Specimens from Scottville Member, north Bowen Basin, x1 approx. (Maxwell 1954).

Stratigraphy: Dear (1971) stated that *gattoni* ranged from the lower Big Strophalosia Band (= Scottville Member) up to the *Streptorhynchus pelicanensis* band, and it would be desirable to support this through the provision of figures.

Pseudostrophalosia furcalina Waterhouse, 2022c

Fig. 21, 22

?1880 *Strophalosia Gerardi* [not King] of Etheridge (1880, p. 32, pl. 12, fig. 34-37, pl. 13, fig. 38).

?1998 *Pseudostrophalosia ingelarensis* [not Dear] – Briggs, Fig. 62E-G, I (or = *ingelarensis*, from a different locality not the one cited by Briggs).
2022c *Ps. furcalina* Waterhouse, p. 139, Fig. 11-19.

Diagnosis: Moderately inflated gently arched shells characterized by shape and especially by

Fig. 21. *Pseudostrophalosia furcalina* Waterhouse, ventral internal moulds. A, UQF 82654, x1.5. B, UQF 82655, x4. C, UQF 82657, x2. D, UQF 82654, x2. Band above Scottville Member, north Bowen Basin. (Waterhouse 2022c).

numerous close-set spine tunnels over the ventral internal surface. Ventral spines dense and of varied diameter, many erect, may be stronger laterally.

Holotype: Specimen UQF 82752 figured by Waterhouse (2022c, Fig. 12B) and herein as Fig. 22B, from just above the Scottville Member, OD.

Morphology: Many specimens are described and illustrated in Waterhouse (2022c). Ventral spines appear to be finer than those found in *Pseudostrophalosia clarkei* and other species. The spines on the ventral ears are moderately numerous, but not outstandingly coarse, and the dorsal valve is gently concave, not as externally flat like the dorsal valve of *Ps. clarkei,* approaching in this respect the dorsal valve of *Ps. gattoni* and *Ps. blakei*.

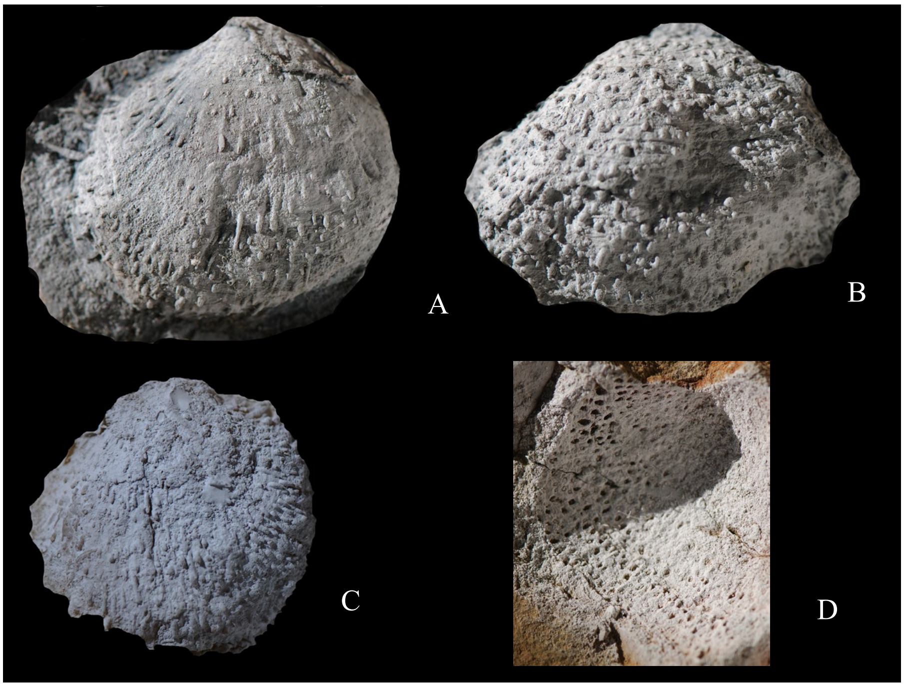


Fig. 22. *Pseudostrophalosia furcalina* Waterhouse. A, external ventral latex cast, UQF 82644. B, external ventral latex cast, UQF 82752, holotype. C, latex cast of ventral valve UQF 82648. D, detail of ventral spines entering external mould, UQF 82649. Specimens x1, from just above Scottville Member, north Bowen Basin, Queensland. (Waterhouse 2022c).

Stratigraphy: This is not quite the youngest of known species of *Pseudostrophalosia*. It is represented by specimens crowded in the narrow band of sediment just above the Scottville Member in the Bowen Basin. But so far, the species is not known elsewhere in east Australia. Briggs (1998) regarded specimens from the band as *ingelarensis*, but this is incorrect, as explained by Waterhouse (2022c, p. 247). It is noteworthy that his supposed *ingelarensis* ventral valves from UQL 3135 are not sulcate and are shaped like *furcalina*, transversely oval and arched. The types and other specimens often sulcate often sulcate, of *ingelarensis* come from the Ingelara and lower Peawaddy beds of the southwest Bowen Basin and may be matched with *Ps. blakei* in the Moonlight Sandstone in the north Bowen Basin, well below the band with *Ps. furcalina* just above the Scottville Member. This match is reinforced by various other taxa described by Campbell (1953), McClung (1978) and Waterhouse (1986, 1987a, b, 2022c, d; Waterhouse & Jell 1983).

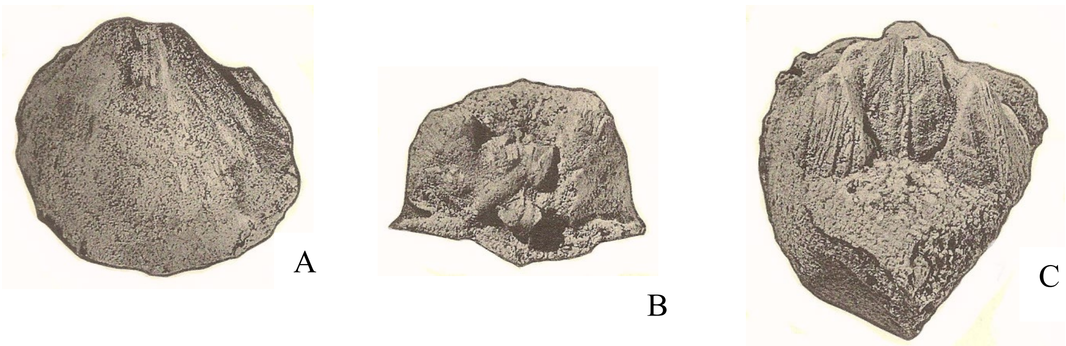
Pseudostrophalosia routi Waterhouse, 2021

Fig. 23 - 26

1964 *Wyndhamia clarkei* [not Etheridge Snr] – Waterhouse, p. 51, pl. 8, fig. 5-9, pl. 37, fig. 5, Fig. 7I, J, 8C, 15A-C, 18, 19.
1982 *Wyndhamia* sp. aff. *clarkei* – Waterhouse, p. 39, pl. 7h, j.
2001 *Pseudostrophalosia clarkei* [not Etheridge Snr] – Waterhouse, p. 79.
2013 *Ps. clarkei* – Waterhouse, Fig. 7.23.
2021 *Ps. routi* – Waterhouse, p. 124, Fig. 1-5.

Diagnosis: Shells characterized by wide hinge, mature shells considerably inflated with steep lateral walls, dorsal valve flatly concave and wedge-shaped with coarse erect spines, high marginal ridge at maturity. Ventral valve without strong spine tunnels, raised muscle platform with elongate ventral adductors, dental buttresses low or not developed.

Holotype: BR 221, figured by Waterhouse (1964, pl. 8, fig. 6, 7) and herein as Fig. 23B, C from upper Mangarewa Formation, New Zealand, OD.



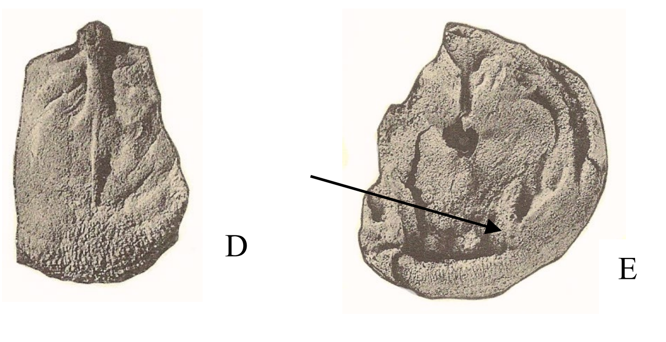


Fig. 23 *Pseudostrophalosia routi* Waterhouse. A, internal mould of ventral valve, BR 219. B, C, posterior and ventral aspects of ventral internal mould, BR 221, holotype. D, PVC cast, interior of dorsal valve BR 316. E, PVC cast of interior dorsal valve BR 222, with anterior hook of brachial sheld indicated by arrow. (See Fig. 26A). Upper Mangarewa Formation, New Zealand, x1.5. (Waterhouse 1964).

Morphology: In the mature dorsal valve, the cardinal process (Fig. 25) bears prominent muscle apophyses. The marginal ridge is high laterally and in front in mature specimens, and the brachial ridges describe an anterior hook (Fig. 23E, 26A) which is anteriorly placed and more abruptly recurved than the corresponding feature in *Echinalosia*. The dorsal valve is thickened and wedge-shaped. The overall shape is close to that of *gattoni*, but buttress plates are much more subdued.

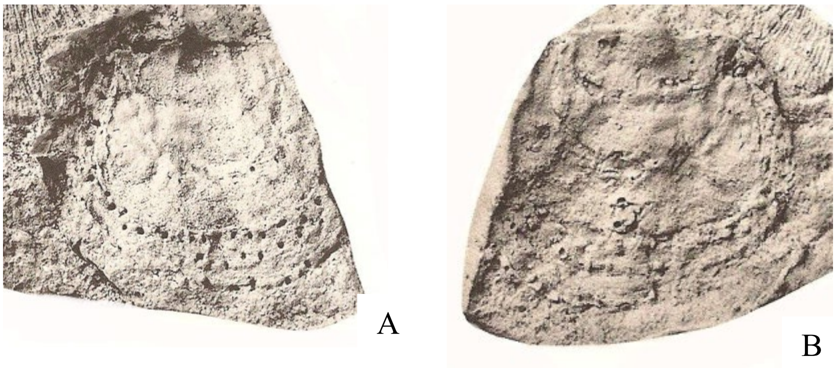


Fig. 24. *Pseudostrophalosia routi* Waterhouse. A, B, external mould and latex cast of dorsal valve BR 1177, upper Mangarewa Formation, New Zealand, x2. (Waterhouse 1982). [B mislabelled in 1982].

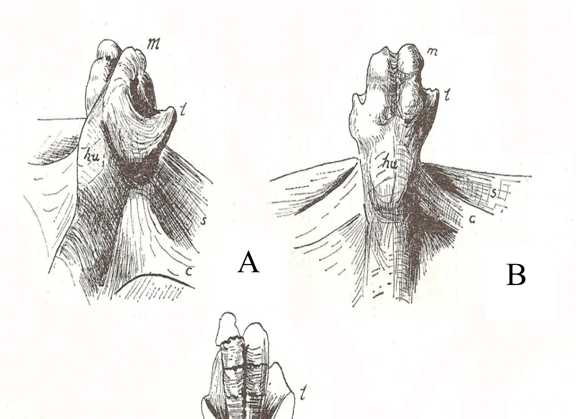


Fig. 25. *Pseudostrophalosia routi* Waterhouse, cardinal process in BR 316, x4 approx. A, anterior oblique view, B, anterior aspect and C, posterior aspect, x9. Upper Mangarewa Formation, New Zealand (Waterhouse 1964). c = supporting ridge for cardinal process, hu = anterior hump, l = lateral lobe, m = muscle apophyses, s = dental socket, t = lateral lobe of cardinal process.

A critical facet concerns the nature of the ventral ornament. None of the ventral valves display any spines, and this is believed to be connected with the advanced maturity of shells, which may lead to decortication. Specimens have been recorded from a number of localities (Waterhouse 2002, 2021), and it seems highly probable that these will afford the necessary information.

Stratigraphy: The species comes from the upper Mangarewa Formation at Wairaki Downs, New Zealand.

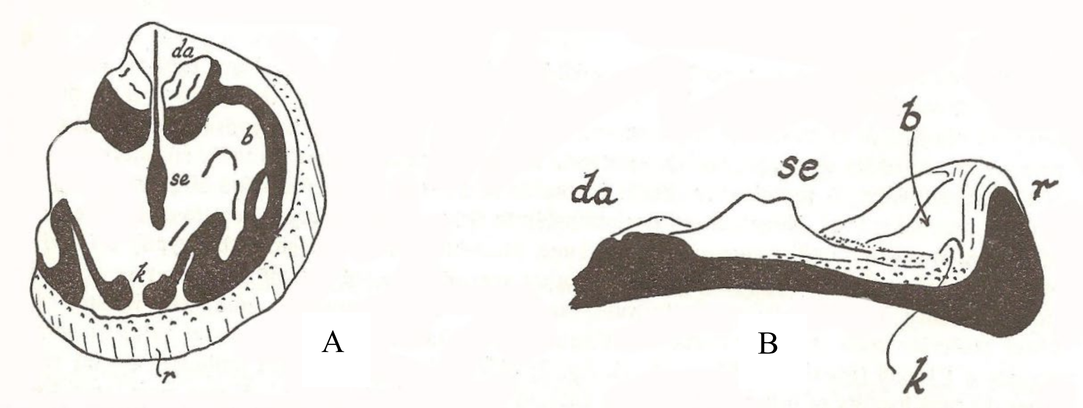


Fig. 26. *Pseudostrophalosia routi* Waterhouse. A, dorsal interior. B, transverse section through dorsal valve, BR 222, x2, x3. Upper Mangarewa Formation, New Zealand. b = brachial ridge, da = dorsal adductor platform, k = knob at which brachial ridges appear to terminate, r = marginal ridge and trail, se = median septum. (Waterhouse 1964).

Pseudostrophalosia cryptica Waterhouse, 2022d

Fig. 27

1989 *Echinalosia* cf. *minima* [not Dear] – Dickins, p. 75, pl. 3, fig. 2-5, 11 (part, not fig. 1, 6? = *Terrakea densispinosa*; not pl. 3, fig. 10, 12-21 = *Nonauria laminata*).
2022d *Pseudostrophalosia cryptica* Waterhouse, p. 272, Fig. 1, 2.

Diagnosis: Small shells with wide hinge, no sulcus or fold, ventral spines subuniform and erect, evenly spaced in quincunx over the disc, coarse over the ears, dorsal spines fine, erect, irregularly arranged.

Holotype: CPC 25287 figured by Dickins (1989, pl. 3, fig. 4) and Fig. 27A herein, from upper Blenheim Subgroup, Mt Coolon, OD.

Morphology: Ventral spines over the disc are mostly in two series, one up to 0.6mm, the other up to 1mm in diameter, and regularly spaced over the disc in quincunx, with only a few thinner and recumbent spines irregularly disposed. The posterior lateral spines are coarse and few.

Stratigraphy: The species comes from the upper Blenheim Subgroup of the north Bowen

Basin. Conjecturally, the specimens could be regarded as a subspecies of *Pseudostrophalosia routi* Waterhouse (2021, p. 124, Fig. 1-5) from the *Ingelarella costata* Zone in the upper Mangarewa Formation of New Zealand. The present form shares the generic position and age, and wide hinge with *routi*, but is much smaller, possibly reflecting environmental conditions. The possibility needs further study to be resolved.

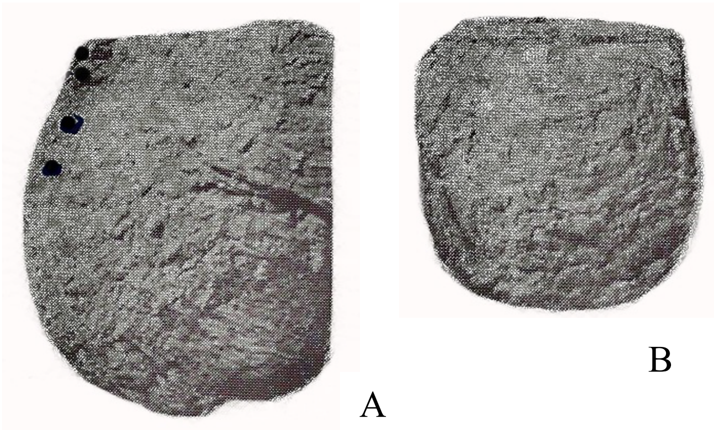


Fig. 27. *Pseudostrophalosia cryptica* Waterhouse. A, ventral valve holotype CPC 25287, x2. Black dots show position of large spines. B, dorsal external mould CPC 25290, x2. From upper Blenheim Formation, reproduced by local equalization. (Dickins 1989).

Genus ***Nonauria*** Waterhouse, 2022a

Diagnosis: Close to *Wyndhamia*, distinguished by lack of ears from either valve.

Type species: *Wyndhamia parfreyi* (Waterhouse, 2001, p. 84) from Barfield Formation, southeast Bowen Basin, Queensland.

Discussion: This genus is close to *Wyndhamia* Booker and *Pseudostrophalosia* Clarke, but unlike these genera, lacks ears for either valve. *Wyndhamia* has few spines over the ears, and *Pseudostrophalosia* has numerous long and well-developed ear spines over the ventral ears. To judge from the fossil record, *Pseudostrophalosia* was the oldest of these genera, and evolved into *Wyndhamia* by substantial diminution of ear spines, and *Nonauria* was the last genus to appear, with the loss of the ears.

Nonauria parfreyi (Waterhouse, 2001)

Fig. 28

1986 *Wyndhamia blakei* [not Dear] – Waterhouse, p. 33, pl. 5, fig. 26, 27, 28 (part, not pl. 5, fig. 24, 29, 30, pl. 6, fig. 1, 2, pl. 15, fig. 10 = *Acanthalosia deari* (Briggs).
1988 *Echinalosia* sp. Parfrey, p. 12, pl. 2, fig. 14-17, 19.
1988 *Wyndhamia* sp. Parfrey, p. 13, pl. 2, fig. 18.
1998 *Echinalosia deari* [not Briggs] – Briggs, p. 101 (part, referring the Waterhouse 1986 specimens assigned to *blakei* to *deari* in the synonymy. These now regarded as *parfreyi*).
2008 *Echinalosia*? *parfreyi* – Waterhouse, pl. 7F, p. 365.
2010 *Wyndhamia parfreyi* – Waterhouse, p. 54, Fig. 22.
2022e *Nonauria parfreyi* – Waterhouse, p. 60, Fig. 1.

Diagnosis: Small-medium shells with evenly spaced spines, coarse over ventral valve apart from a few very thin prostrate spines, fine and erect over dorsal valve. Interareas low, and no ears developed.

Holotype: GSQF 12983 figured by Parfrey (1988, pl. 2, fig. 14, 19) from Barfield Formation, southeast Bowen Basin, Queensland, OD.

Morphology: The ventral ornament with swollen but not extended spine bases is highly distinctive.

Stratigraphy: The species is found only in a limited part of the Barfield Formation, ca. 138-140m below the top, in about the middle of the formation (Parfrey 1988, Fig. 4).

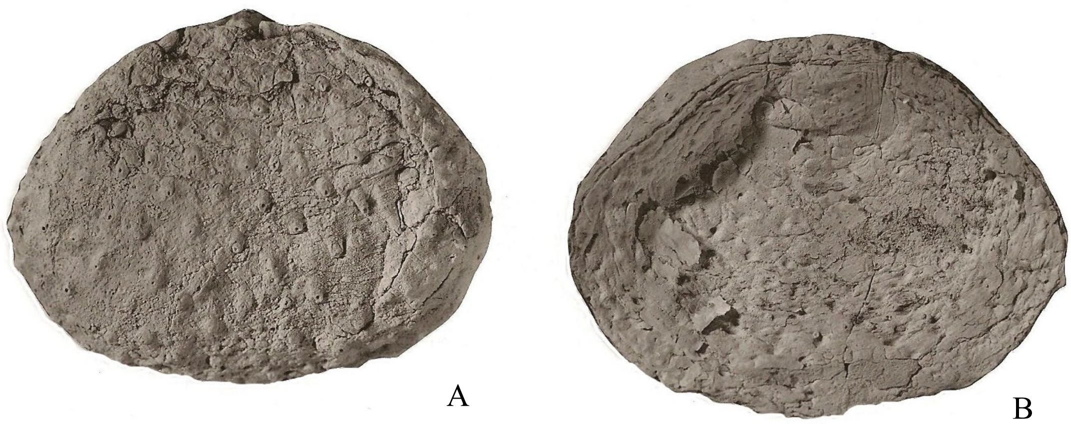


Fig. 28. *Nonauria parfreyi* (Waterhouse). A, B, ventral and dorsal aspects of UQF 69888 frtom Barfield Formation, southeast Bowen Basin, x2. (Waterhouse 1986).

Nonauria laminata Waterhouse, 2022e

Fig. 29

1989 *Echinalosia* cf. *minima* [not Dear] – Dickins, p. 75, pl. 3, fig. 10, 12-21 (part, not fig. 1, 6? = *Terrakea densispinosa* Waterhouse, not pl. 3, fig. 2-5, 11 = *Pseudostrophalosia*

cryptica Waterhouse.
1998 *Pseudostrophalosia crassa* [not Briggs] – Briggs, p. 119 (part).
2022e *Nonauria laminata* Waterhouse, p. 302, Fig. 1.

Diagnosis: Anterior ventral valve with numerous recumbent spines. Dorsal valve with strong commarginal laminae and many erect spines.

Holotype: Specimen figured by Dickins (1989, pl. 3, fig. 17, 18) as reproduced in Waterhouse (2022e, Fig. 1C, F), and herein as Fig. 29C, F, from Kulnura beds, NSW Geological Survey bore DDH3, New South Wales, OD.

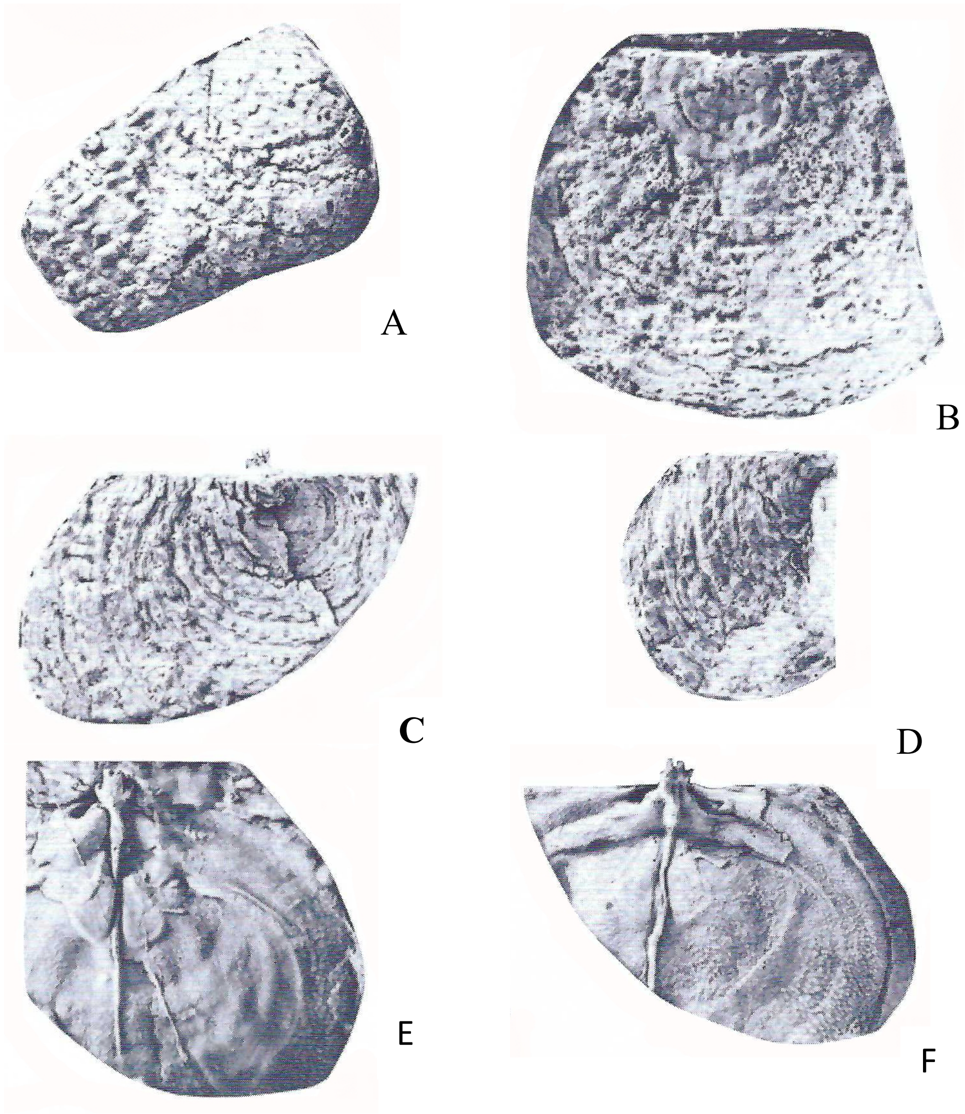


Fig. 29. *Nonauria laminata* Waterhouse. A, ventral valve. B, exterior of dorsal valve. C, F, external and internal aspects of dorsal valve, holotype. D, external cast of dorsal valve. F latex cast of interior. E, latex cast of interior of dorsal valve, with faintly preserved brachial ridge. Specimens from New South Wales Bore DDH3, x2. (Dickins 1989). Registration numbers not provided.

Holotype: Specimen figured by Dickins (1989, pl. 3, fig. 17, 18) as reproduced in Waterhouse (2022e, Fig. 1C, F), and herein as Fig. 29C, F, from Kulnura beds, NSW Geological Survey bore DDH3, New South Wales, OD.

Morphology: Ventral spines are semirecumbent and crowded, many coarse, some slightly narrower, and a few comparatively slender. Dorsal spines are also crowded, commarginally aligned, suberect and comparatively strong and suberect. The external dorsal valve is particularly striking because of the well-developed commarginal laminae. This species is like the older species *Nonaura parfreyi* in its lack of ears, but has more diverse spines, and conspicuous commarginal laminae, especially over the dorsal valve. Briggs (1998) assigned the material to *Pseudostrophalosia crassa*, even though the Dickins specimens have no ears and differ considerably in spination.

Stratigraphy: Specimens come from the Kulnura marine tongue derived from the DDH3 bore in the Newcastle Sheet area. (See Dickins 1989, p. 77). This level is younger than the Mulbring Formation.

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_____ 2022a: A new strophalosioid genus from the Barfield Formation, southeast Bowen Basin, Queensland. Earthwise 20: 59-61.

_____ 2022b: Brachiopods and molluscs from the Scottville Member, *Pseudostrophalosia clarkei* Zone, north Bowen Basin, Queensland. Earthwise 20: 97-123.

_____ 2022c: Brachiopods and molluscs from the *Echinalosia* (*Unicusia*) *minima* Zone, upper Blenheim Formation, north Bowen Basin, Queensland. Earthwise 20:125-266.

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STROPHALOSIIDIN SPECIES IN EAST AUSTRALIA AND NEW ZEALAND THAT ARE HARD TO PLACE GENERICALLY

Abstract

Strophalosia preovalis pristina Maxwell, *Echinalosia ardua* Waterhouse, *Strophalosia yalwalensis* Briggs and *Echinalosia mcclungi* Briggs are discussed as species hard to assign to any known genus.

SYSTEMATIC DISCUSSION

Strophalosia pristina Maxwell, 1954

Fig. 1

1954 *Strophalosia preovalis* var. *pristina* Maxwell, p. 543, pl. 54, fig. 12-15.
1998 *Echinalosia preovalis* – Briggs, p. 76 (part).

Diagnosis: Shells small, subequilateral, may have rounded outline, dorsal valve moderately concave. Both valves spinose, but nature of spines not established.

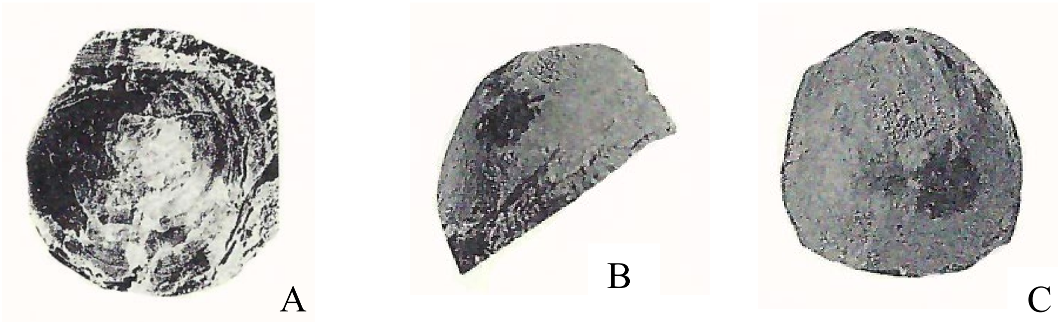

Fig. 1. *Echinalosia*? *pristina* (Maxwell). A, dorsal view of GSQF 2093, holotype. B, C, lateral and ventral views of ventral internal mould, GSQF 2088. Specimens x1.5 from Dilly, southwest Bowen Basin. (Maxwell 1954).

Holotype: GSQF 2093 from Dilly beds, southwest Bowen Basin, as figured by Maxwell (1954, pl. 54, fig. 1, 2) and Fig. 1A herein, OD.

Morphology: The only figures ever provided for this taxon are reproduced herein and indicate how poorly the taxon is understood, though Maxwell (1954) was able to provide further detail on the morphology. Briggs (1998) summarily placed the form in synonymy with *Echinalosia preovalis* Maxwell. His view was that *preovalis* was a long-lived and apparently a highly variable species but evidence does not support such an interpretation, based on consideration of the morphology and variation displayed by topotypes and other specimens from exactly correlative horizons, as explained on pp. 37, 38. He ignored and/or was unaware of evidence provided by numerous other fossils from the same stratigraphic levels.

Stratigraphy: The taxon came from the Dilly beds, regarded as slightly older than the Cattle Creek beds of the southwest Bowen Basin. It could even prove to be of the same age as, and remotely, a senior synonym to *Echinalosia* (*Echinalosia*) *curvata* or more likely *E. (E.*) *cenula*, to judge from size and shape, but at present, the morphological limits are poorly known, though the taxon might well prove to be *Echinalosia* (*Echinalosia).* Further stratigraphic occurrences of the taxon are not known. Under the constraints imposed by the ICZN (1999), it might reasonably be regarded as a variety, and without standing, and in our present stage of knowledge, this appears to be a preferable option. But the source of the material is established, and with the potential that the name may yet legitimately replaced one of the currently better-known species names, it should be possible to collect and examine further material, to clarify the nature of the taxon. Specimens may well have been collected by the Geological Survey of Queensland and kept in the bulk storage unit of the Queensland Museum, to allow closer inspection of specimens from the same locality as original *pristina*.

Echinalosia ardua Waterhouse, 1982

Fig. 2

?1964 *Strophalosia* aff. *preovalis* [not Maxwell] – Waterhouse, p. 29, pl. 4, fig. 3-5, text-fig. 7B, D.
1982 *Echinalosia ardua* Waterhouse, p. 30, pl. 6d-i.
1998 ?*Acanthalosia ardua* – Briggs, p. 109.
2001 *Acanthalosia*? *ardua* – Waterhouse, p. 83.

Diagnosis: Dorsal exterior complex, with spines of two series and surface somewhat rugged, possibly dimpled, ventral ornament not fully known and so in need of clarification.

Holotype: BR 1476 from Takitimu Group, Brunel Formation, figured by Waterhouse (1982, pl. 6, fig. f), OD.

Morphology: The ventral ornament needs to be better known, which will require further examination of material kept at GNS and Department of Geology at Otago University, and/or

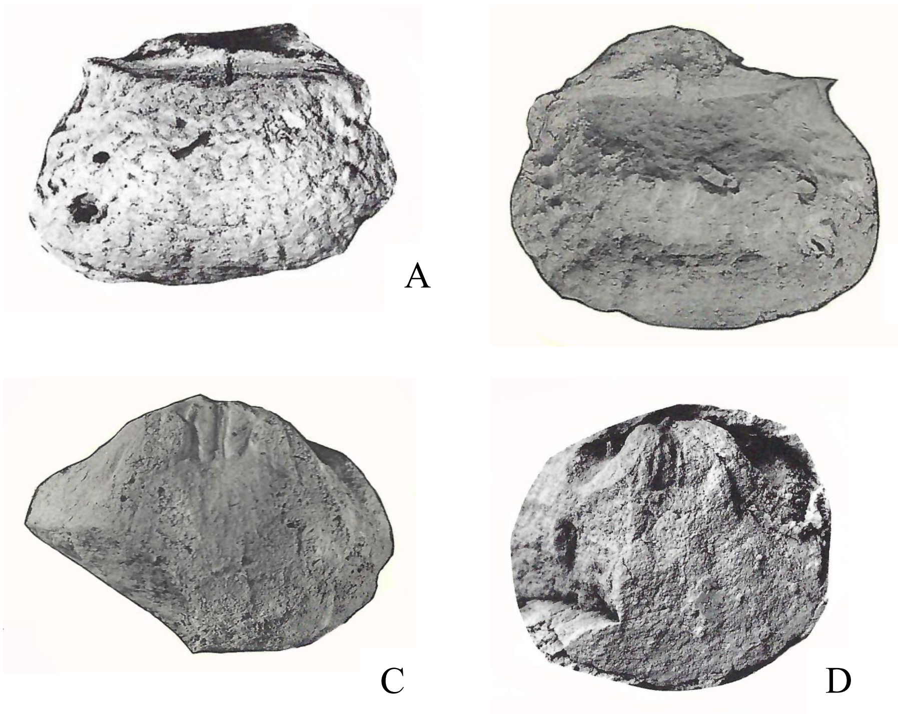

Fig. 2. *Echinalosia ardua* Waterhouse. A, B, external mould and latex cast from same mould, BR 384, x2. C, ventral internal mould BR 386, x1.5. D, ventral internal mould, BR 1528, x4. From Brunel Formation, D from the top, 1-C from underlying beds. (Waterhouse 1964, 1982).

more material being collected from the Brunel Formation. According to Waterhouse (1964, p. 30), ventral spines near the umbo on specimens from the older zone are some 0.4mm in diameter, and involve spines 0.7mm in diameter anteriorly, where they are arranged in quincunx, 1.5mm apart along rows 2mm apart. A ventral sulcus may be developed, and the posterior lateral margins are auriculate. The dorsal valve is somewhat thickened, without being wedge-shaped. More detailed descriptions provided in Waterhouse (2001, p. 83) for material from the younger of the two zones in the Brunel Formation suggest *Maxwellosia*, given the deeply concave dorsal valve, and lead to the question of whether the specimens are really conspecific with those of the older zone. At least two series of spine diameters are developed on each valve, with fullest description in Waterhouse (2001, p. 83), unfortunately not reinforced by figures, but with specific references to numbered specimens that are kept at GNS in Lower Hutt, New Zealand. Briggs (1998, p. 109) also noted ornament details, without citing the relevant specimen number. He suggested that specimens were possibly conspecific with what is now called *Maxwellosia concava* (Maxwell). This taxon appears to be of much the same age, and therefore his suggestion deserves closer enquiry, though aspects of what is known of spines over both valves from the older zone suggest *Echinalosia* rather than *Acanthalosia* or *Maxwellosia*. The species *concava* appears to be more elongate that the New Zealand specimens, and possibly has a greater range of spine diameters, but this needs to be checked. A species of *Acanthalosia* is found in the correlative Cattle Creek and Roses Pride Formations, described as *A. mysteriosa* Waterhouse. It is distinguished by its numerous fine erect spines and flatter dorsal valve, and therefore is unlikely to be conspecific. Begg & Ballard (1991, Fig. 5) figured a strophalosiidin from correlative beds in the Mantle Volcanics Formation in the Skipper Range of New Zealand, and their figure suggests *Echinalosia* (certainly not *Wyndhamia*, nor *Maxwellosia*), close to *Echinalosia* (*Echinalosia*) *preovalis* (Maxwell), though more transverse, and with dimples.

Strophalosia yalwalensis Briggs, 1998

Fig. 3

1998 *Strophalosia yalwalensis* Briggs, p. 70, Fig. 37.
2023 *S. yalwalensis* Lee & Shi *in* Lee et al., p. 7, Fig. 4A-V, 5.

Diagnosis: Moderately large, ventral valve ornamented by closely spaced subuniform semi-recumbent spines, with rare erect spines preserved, interspersed with fewer and more slender recumbent spines. Dorsal valve worn, gently concave, somewhat thickened, weakly dimpled, several specimens have a short trail and a few spines at least within the dorsal shell. Ventral interior characterized by spine tunnels.

Neotype: AMF 158966 from Snapper Point Formation, south Sydney Basin, figured in Lee et al. (2023, Fig. 4A, B), SD Lee et al. (2023, p. 7).

Morphology: The morphology is not fully known, with uncertainly surrounding the nature of the dorsal ornament. Specimens described by Lee (2023) have lost their exolayer, so that most of the specimens now show the ends of prisms which make up most of the shell. This means that it is no longer possible to tell if radial capillae were present – they would have been removed, if ever present, by wear, and the claim in Lee et al. (2023) that radial capillae were not developed must be questioned – it is not possible to be sure, given the absence of the exolayer, which was not assessed, with S. Lee by email considering that the presence of a few laminae established that the exolayer was present. Laminae are much larger, and so should never be confused with a single growth increment. The loss of the exolayer also suggests that spines would have been removed, if they were ever present. But Lee in Lee et al. (2023) has discovered remnants of a few dorsal spines, exceptional because they appear to be prostrate and embedded in the shell. He deduced that this did not require that the Briggs identification as *Strophalosia* should be challenged: rather it provided a challenge to the classification by the *Revised Brachiopod Treatise* in Brunton et al. (2000) of

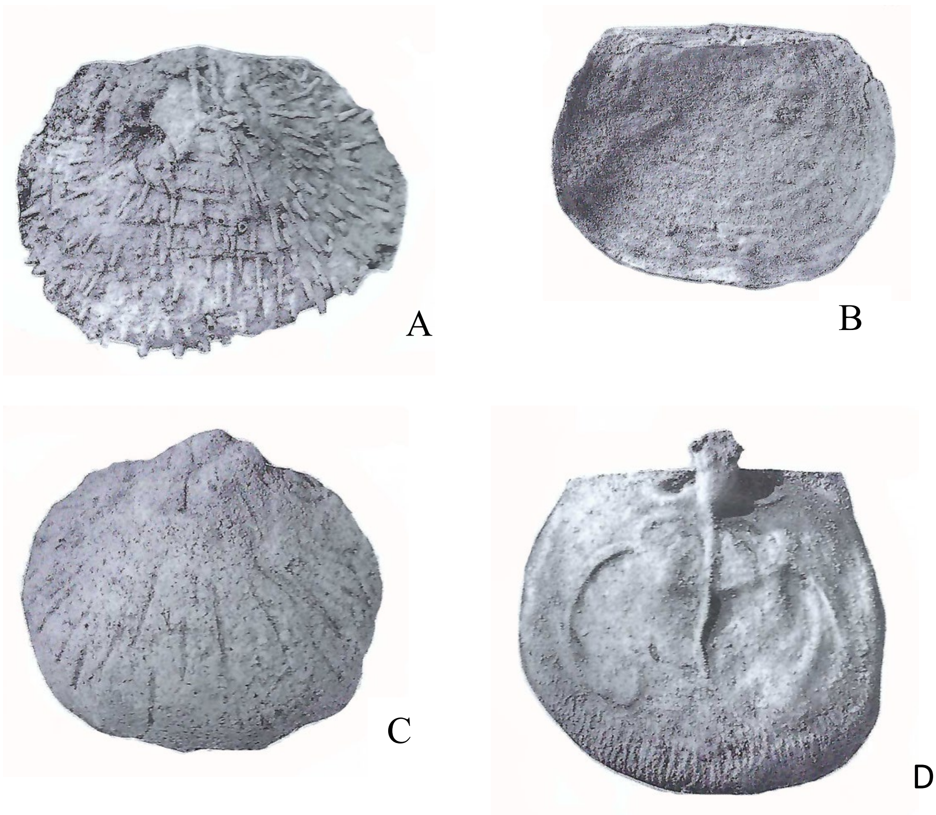

Fig. 3. *Strophalosia yalwalensis* Briggs. A, ventral exterior latex cast AMF 96221. B, dorsal aspect of latex cast AMF 96222. C, ventral internal mould MMF 11446. D, latex cast of dorsal interior, AMF 96223. Specimens x1.5, from Snapper Point Formation. The AM specimens were never deposited at the Australian Museum and appear to have disappeared, justifying the citation of a neotype in Lee et al. 2023. The assignment to *Strophalosia* is doubtful, given the presence of ventral spine tunnels (see Fig. 3C). (Briggs 1998).

various strophalosioid genera into family groups with dorsal spines and a family group without dorsal spines. Clearly there are alternatives to this interpretation, including the most obvious one, that the specimens were not ever free of dorsal spines until post-mortal fossilization, when the dorsal ornament was heavily modified by erosion. Indeed we know that well-preserved *Pseudostrophalosia clarkei* in the Scottville Member of the north Bowen Basin has dorsal spines, but the spines have been removed from many of the specimens, so that they now mimic a strophalosiid species (Waterhouse 2022, Fig. 4, 5), leading Muir-Wood & Cooper (1960) to suggest that *clarkei* belonged to *Lialosia* (see p. 121 herein). One convincing line of evidence is provided by a figure in Briggs (1998, Fig. 37I), as reproduced herein in Fig. 3C. This clearly shows spine tunnels in the ventral valve, and further figures demonstrating the presence of ventral spine tunnels are provided in Lee et al. (2023, Fig. 4E, G). No member species or genus within Strophalosiidae ever shows spine tunnels, as far as is known (Waterhouse 2023). The presence of spine tunnels in Snapper Point specimens indicates that the specimens were likely to have been non-strophalosiid, as understood by Brunton et al. 2000, Brunton 2007) and in general amongst brachiopod experts. In our present state of knowledge, it could be that Dr S. Lee is pioneering a new understanding of the groups and hopefully further evidence will be provided..

Fig. 4. *Echinalosia maxwelli* (Waterhouse), dorsal aspect of conjoined specimen BR 272, x 2, a topotype from which dorsal spines have been removed from all but the anterior edge of the shell. For the ventral view, see Fig. 15B, p. 47. Some workers might suggest the dorsal valve is strophalosiid, and noticing the anterior spines, declare strophalosiids could develop a few dorsal spines. In this specimen, growth increments have been removed, proving that the dorsal surface has been eroded. Moreover the ventral valve shows internal spine tunnels, which are never developed in Strophalosiidae. Letham Burn Member, New Zealand. (Waterhouse 1964).

Pending any such study, and on present understanding, what is the genus? There are indications that the genus could be *Wyndhamia* and the species might belong to *W. typica* Booker. The general shape is close and the ventral ornament suggestive of that of the *Wyndhamia* ventral valve, especially of specimens at early maturity. The density of ventral spines is somewhat similar, but the thickness of spines in the late mature material figured by Briggs (1998, Fig. 64A) is greater than that of the spines figured in Lee et al. (2023). One possible difference is that *W. typica* tends to be weakly sulcate, and no sulcus is visible in the specimens figured as *yalwalensis*. The dorsal valve is somewhat thickened, and Lee in Lee et al. (2023) has shown that the rarely preserved spine bases of the dorsal valve are recumbent rather than erect, and intra-shell, matters that substantiate further enquiry. Certainly the trail although short is longer than in mature *W. typica*, but this is also the case for immature *Wyndhamia*, which developed a concave shell, with moderate trail, and then began to accrete shell on the inner side, to build up a wedge, whilst the outer trail became worn and often disappeared. Lee in Lee et al. (2023, Fig. 5) provided a diagram to prove that *yalwalensis* differed in the mode of its regression line of its dimensions from those of *W. typica*. It would be instructive to prepare detailed analyses of growth trajectories and morphological changes followed by the species during ontogeny, not only for the species as a whole, but for different collections from different localities. Possibly the species will prove to be a species of *Wyndhamia*, contemporary with *W. typica*.

Echinalosia mcclungi Briggs, 1998

Fig. 5

1987 *Wyndhamia* n. sp. Briggs, p. 138.
1998 *Echinalosia mcclungi* Briggs, p. 79, Fig. 41A-H.

Diagnosis: Subequilateral shells with ventral spines comparatively dense and in two series, one up to 0.5mm in diameter, and stronger and erect postero-laterally, interspersed with fine more numerous prostrate spines about 0.2mm in diameter. The dorsal valve is gently concave to flat, and ornamented by a few erect spines about 0.2mm in diameter “and perhaps interspersed finer spines” according to Briggs, 1998.

Holotype: MMF 28944G-H from Pebbley Beach Formation, figured by Briggs (1998, Fig. 41A, C), and herein, Fig. 5B, D, OD.

Morphology: The diversity and distribution of ventral spines is outstanding, the latex cast figured by Briggs suggesting that ventral spines are distributed in bands, with interspersed thick and thin suberect spines, though the external mould (Fig. 5D) shows few slender spines. This specimen displays strong posterior lateral spines. The dorsal valve (Fig. 5B) arguably points to *Acanthalosia*, as supported by the shallowly concave nature of the dorsal valve. Or does the species belong to a separate genus, so far unnamed? More material is required, to unravel the nature of the ornament on both valves. The very gently concave dorsal valve and thick posterior lateral ventral spines point against any affinity with the genus

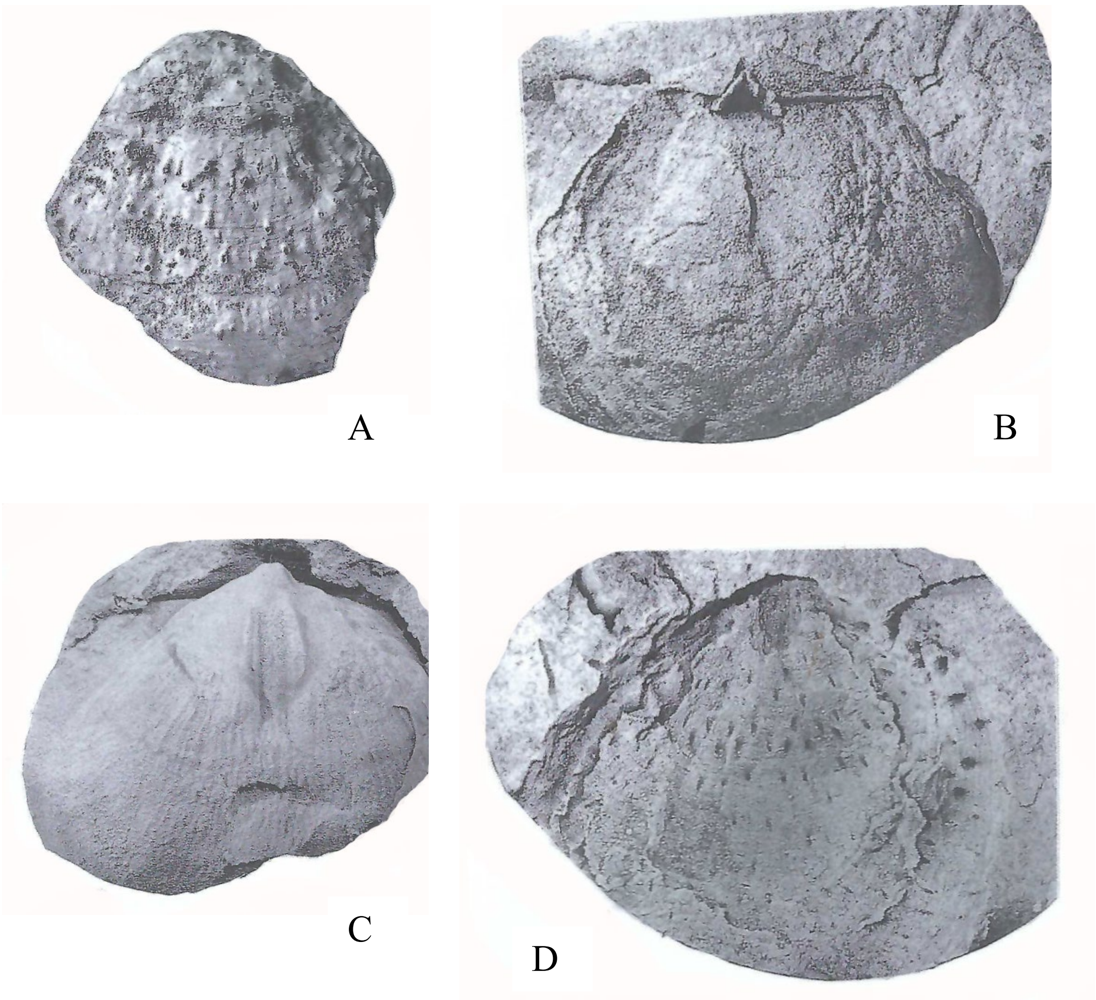

Fig. 5. *Echinalosia mcclungi* Briggs. A, latex cast of ventral exterior, MMF 28940c, x1.5. B, D, dorsal and ventral views of external moulds of holotype, MMF 28944G, H, x2. C, Ventral internal mould MMF 289441a, x1.5. From Pebbly Beach Formation DM Callala DDH1. (Briggs 1998).

Echinalosia, but the suggestion of ventral spine tunnels indicates a taxon that varies from known members of *Acanthalosia*, which appear to lack spine tunnels.

A possible and indeed likely link with *Nothalosina* Waterhouse, 2010 (see p. 61) is suggested by the unusual nature of the coarse posterior lateral spines on the ventral valve, and the report of fine erect ventral spines in Briggs (1998). These features of *mcclungi* are also found in *Nothalosina voiseyi* (Briggs), though this species, deemed to be somewhat younger, has many more spines along a commarginal row. The concavity of the dorsal valve is low in *yalwalensis*, which is more elongate than *voiseyi,* as a different species, and the relationship may repay further exploration. One item from Briggs (1998, p. 79) needs to be checked: his report of "perhaps finer dorsal spines" for such is not known in *Nothalosina*.

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AULOSTEGID BRACHIOPODS FROM THE PERMIAN BEDS OF EAST AUSTRALIA AND NEW ZEALAND

Abstract

A modest diversity of Aulostegoidea are developed in east Australia and New Zealand, chiefly in early Permian deposits.

INTRODUCTION

The first aulostegid from east Australia was recorded but not figured by Morris (1845) and a long time ensued before Fletcher (1945) described a different species, Hill (1950) issued a more comprehensive coverage for species in Queensland, and Briggs (1979, 1983, 1986, 1998) contributed a new genus and several new species.

SYSTEMATIC STUDIES

Hyporder **AULOSTEGIDEI** Waterhouse, 2010

[Nom. transf. Infrasuborder AULOSTEGIMORPHII Waterhouse, 2010, p. 10].

This hyporder is derived from within Strophalosioidea, and involves superfamilies Aulostegoidea and Scacchinelloidea. Its derivative hyporder Richthofenioidei is not known in east Australia or New Zealand.

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

[Nom. transl. Brunton, Lazarev & Grant 1995, p. 93 ex Aulostegidae Muir-Wood & Cooper 1960, p. 94].

Discussion: The general relationships of Aulostegoidea are summarized by Waterhouse (2013, Fig. 10.1). Many authorities have preferred an alliance with *Strophalosia* (Strophalosiidina), as in Muir-Wood & Cooper (1960) and Brunton et al. (2000), following the pioneering studies of the nineteenth century, whereas Coleman (1957, p. 34), Waterhouse (1983b, 2001), Brunton & Mundy (1988), Briggs (1998) and Archbold (2001) placed the superfamily with Productidina. In particular the nature of the brachial ridges is productin (Waterhouse 1983b, p. 192), as is the

Superfamily Aulostegoidea Muir-Wood & Cooper, 1960

Spines dominant in ornament and tend to form ventral ear-cluster.

Family Aulostegoidea Muir-Wood & Cooper, 1960

Dorsal spines as a rule. Spine bases may be elongate. Buttress plates not extending lateral to adductors.

Subfamily Aulosteginae Muir-Wood & Cooper, 1960

Subfamily Taeniothaerinae Waterhouse, 2002b

Subfamily Septasteginae Waterhouse , 2002b

Tribe Septastegini Waterhouse 2002b

Tribe Saeptathaerini new

Family Echinostegidae Muir-Wood & Cooper, 1960

No dorsal spines, no buttress plates.

Subfamily Echinosteginae Muir-Wood & Cooper, 1960

Subfamily Aglesiinae Muir-Wood & Cooper, 1960

Superfamily Institelloidea Muir-Wood & Cooper, 1960

Ribbing usually prominent. Spines ventral and often sparse, no prolonged bases, no ear clusters as a rule.

Family Institellidae Muir-Wood & Cooper, 1960

Strongly ribbed or reticulate.

Subfamily Institellinae Muir-Wood & Cooper, 1960

Subfamily Sinuatellinae Muir-Wood & Cooper, 1960

Subfamily Institininae Muir-Wood & Cooper, 1960

Family Chonostegidae Muir-Wood & Cooper, 1960

Strongly geniculate with complex valve margins.

Family Gondolinidae Jin, Brunton & Lazarev, 1998

Homeomorph of *Striatera* with rhizoid umbonal spines.

Subfamily Gondolininae Jin, Brunton & Lazarev, 1998

Subfamily Sphenosteginae Waterhouse, 2002b

Superfamily Scacchinelloidea Licharew, 1928a, b

Fine spines, no ribs, long buttress plates. Median ventral septum.

Family Scacchinellidae Licharew, 1928a, b

Conical ventral valve with transverse partitions, lid-like dorsal valve, strong ventral median septum.

Family Tschernyschewiidae Muir-Wood & Cooper, 1960

Concavo-convex, externally like *Waagenoconcha*, with dense and fine erect spines on both valves. Ventral septum high.

Family Rhamnariidae Muir-Wood & Cooper, 1960

Dorsal valve with long buttress plates extending from cardinal process each side of adductor scars. Dorsal spines. Ventral septum less developed.

TABLE 1. Classification of the Aulostegidei.

nature of the broad cardinal supports and the dorsal adductor scars, with further similarities, well documented by Briggs (1998). But as suggested in Waterhouse (2013, pp. 273-275), Aulostegoidea were apparently derived from Strophalosioidea, Family Rhytialosiidae Lazarev, and must be classed in the same suborder, even though members developed a morphology that became productiform in several aspects.

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

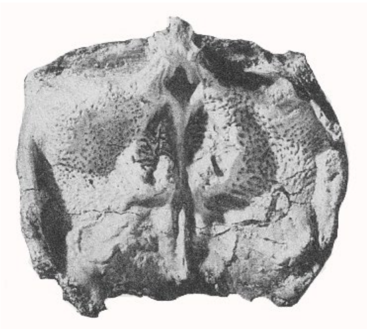


Fig. 1. *Aulosteges wangenheimi* (de Verneuil), dorsal interior, NH BB 3279, x1, showing diverging buttress ridges. Mid-Permian of Russia. Muir-Wood & Cooper 1960).

Subfamily **TAENIOTHAERINAE** Waterhouse, 2002b

Diagnosis: Large shells with erect and/or prostrate spines on both valves, not rhizoid on dorsal valve, spine bases variable and patterns vary. Interior with large ventral muscle scars that often include small ancillary scars lateral to the adductors. Buttress ridges placed behind the dorsal adductor scars, subparallel rather than diverging as in *Aulosteges* (Fig 1).

Tribe **TAENIOTHAERINI** Waterhouse, 2002b

Diagnosis: Elongate spine bases developed over both valves.

Genera*: Taeniothaerus* Whitehouse, *Colemanosteges* Waterhouse (see Fig. 33, p. 180 herein), *Lipanteris* Briggs.

Discussion: *Ctenalosia* Cooper & Stehli 1955 has a somewhat similar cardinal process with subparallel buttress supports extending in front of the cardinal process and behind the dorsal adductor scars (Fig. 2A, C). It is classed in Ctenalosiidae Muir-Wood & Cooper, 1960, and unlike *Taeniothaerus* has a short ventral median septum, recalling that of both *Rhamnaria* Muir-Wood & Cooper, 1960 and Chonopectidae as discussed in Waterhouse (2023, pp. 17-21).

Ctenalosia is further distinguished by its numerous hinge denticles (Fig. 2A, C, Fig. 3B, D herein). Muir-Wood & Cooper (1960) proposed a strophalosioid subfamily Ctenalosiinae for the

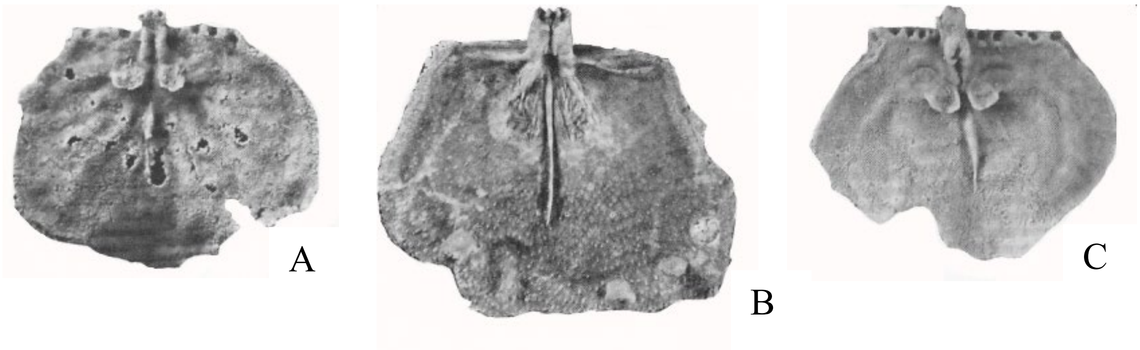


Fig. 2. *Ctenalosia transversa* Cooper & Grant. A, dorsal interior, unregistered, x3. C, dorsal interior USNM 154134a, x3. Franson Member, Park City Formation, United States. B, *Rhamnaria tenuispinosa* Cooper & Grant, dorsal interior USNM 149373b x1, showing widely diverging buttress supports. From Cathedral Mountain Formation, United States. (Cooper & Grant 1975).

genus, and Brunton et al. (2000, p. 593) treated the subfamily as aulostegid although the brachial shields are large rathe than small. *Mongolasia* Manankov & Pavlov, 1976 was added to the subfamily, because of its hinge (Fig. 3E, F), although it lacks a ventral septum. Both genera lack dorsal spines, and *Mongolosia* has dorsal radial ribs, and ventral ribs are present in *Ctenalosia*. *Mongolasia* recalls Devonian strophalosioids such as *Chonopectus* (see Waterhouse 2023b, pp. 17-21) with its large brachial shields, hinge row of spines and emphazised outer borders to the ventral adductor scars. In some respects the interior recalls aspects of the dorsal interior of *Juresania* Tschernyschew, in which two closely juxtaposed ridges lie in front of the cardinal process and between the adductor scars.

Girlasia de Gregorio, 1930 from Sosio of Sicily has hinge crenulations, and dorsal spines, but would seem to be an exceptional member of a different group, given its ornament and shape. It was classed as the aulostegid Echinosteginae Muir-Wood & Cooper in the *Revised Brachiopod Treatise*, and it would be useful to understand the internal features of this genus.

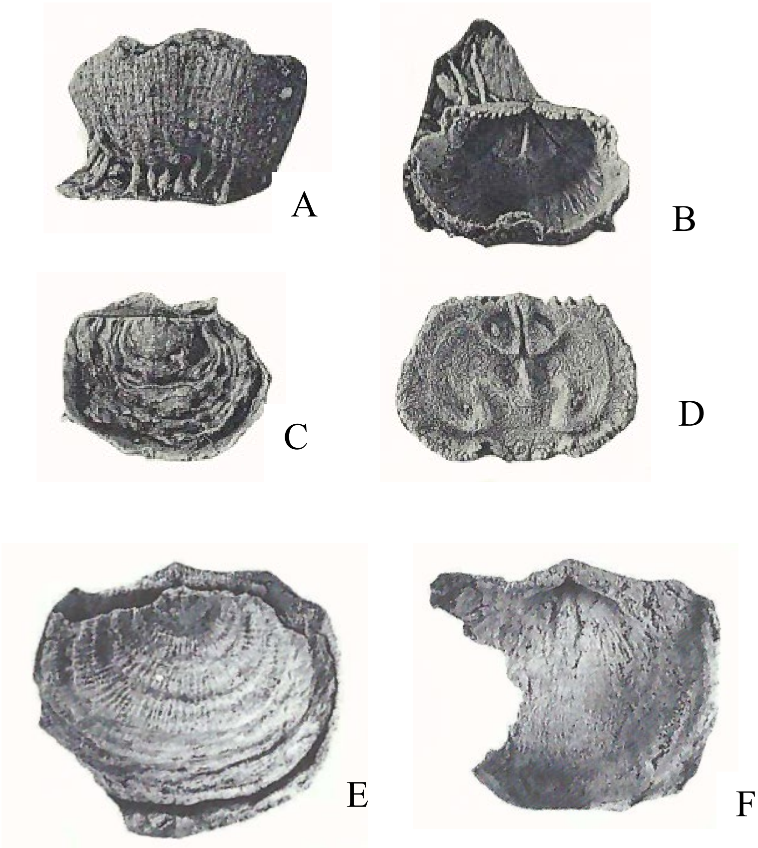


Fig. 3A-D. *Ctenalosia fixata* Cooper & Stehli A, B, anterior and interior views of ventral valve. C, dorsal aspect of specimen with valves conjoined, holotype. D, dorsal interior showing large brachial shields. Specimens x 3, from Word 2, west Texas. (Muir-Wood & Cooper, 1960). E, F *Mongolosia morenkovi* Manankov & Pavlova. A, dorsal aspect, holotype. B, ventral internal mould. Specimens x1, from Roadian- Wordian of central Mongolia. (Manankov & Pavola 1976).

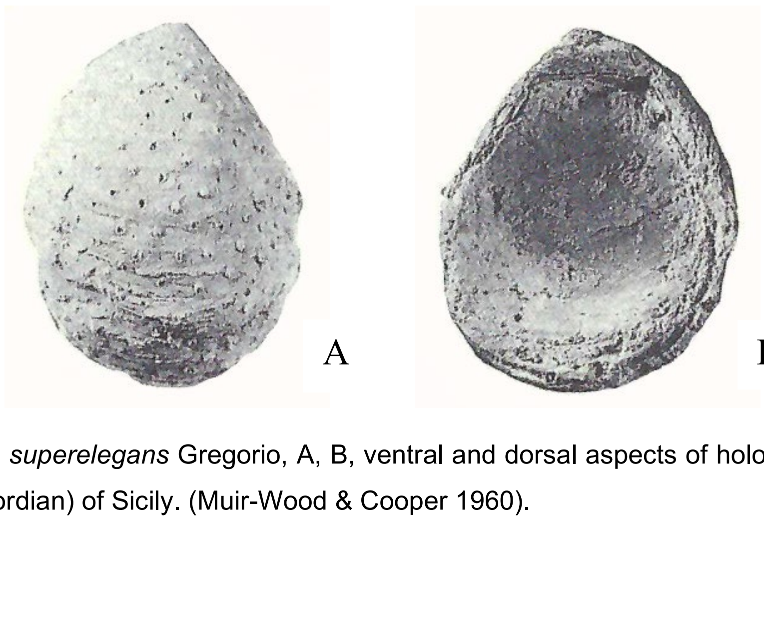


Fig. 4. *Girlasia superelegans* Gregorio, A, B, ventral and dorsal aspects of holotype, from Sosio Limestone (Wordian) of Sicily. (Muir-Wood & Cooper 1960).

Genus ***Taeniothaerus*** Whitehouse, 1928

Diagnosis: Shells distinguished from allied genera by wide hinge, low to moderately high ventral interarea, spines numerous on venter, may include fine erect spines generally arising from short to long spine tubercles or ridges, spine cores extend anteriorly from base within shell over median part of valve, spines crowded on posterior flanks and form halteroid brushes. Dorsal valve with regular closely spaced elongate dimples and tubercles, spines comparatively uniform or in two series, erect or semi-recumbent, arising from pustules, may be finer and arranged in rows anteriorly. Cardinal process not deeply embayed or strongly incurved. Buttress plates short in front of the cardinal process, subparallel and placed behind the dorsal adductor scars.

Type species: *Productus subquadratus* Morris, 1845, p. 284, from Berriedale Limestone (upper Sakmarian) of Tasmania, OD.

Discussion: *Taeniothaerus* was discussed and illustrated by Brunton et al. (2000) partly on the basis of a species later made the type species of *Carilya* Archbold, 2001b, and Brunton (2007, p. 2670) issued a fresh diagnosis with illustrations, based on the type species. Included in the revised diagnosis was the observation that the “dorsal adductor scars posteriorly bordered by ridges extending from cardinal process shaft”. Inspection of the figure in Brunton (2007, text-fig. 1778.d) shows that the ridges extend forward from the base of the shaft, and that the ridges lie behind the adductor scars, rather than in a lateral or bordering position. Archbold (2001b, p. 370) reported that the posterior portions of the dorsal scars were smooth in one specimen figured from the Berriedale Limestone, Tasmania, by Parfrey (1983, fig. 4), and noted that it was not known if this was a feature of the species and genus. Tiverton material suggests that such was an aspect of ontogenetic development, with the posterior scars becoming dendritic in large specimens, and indeed merging with the anterior part of the adductor scars. Briggs (1998) failed to acknowledge the revision of *Taeniothaerus subquadratus* by Parfrey (1983), based on topotype material from the Berriedale Limestone, Tasmania. Parfrey (1983, Fig. 3B) noted fine and coarse spines interspersed near the ventral anterior margin.

Taeniothaerus subquadratus (Morris, 1845)

Fig. 5 - 10

1845 *Productus subquadratus* Morris, p. 284.
1892 *P. subquadratus* – Etheridge, p. 252, pl. 37, fig. 18, pl. 38, fig. 7-10, pl. 40, fig. 5?
1909 *P.* (?) *subquadratus* – Etheridge & Dun, p. 300, pl. 16, fig. 1 (part, not fig. 2-5 = *homevalensis* Briggs).
1928 *Taeniothaerus subquadratus* Whitehouse, p. 281.
1950 *Aulosteges* (*Taeniothaerus*) *subquadratus* – Hill, p. 6, pl. 1, fig. 1 (part, not pl. 5, fig. 1, 2 = *Saeptathaerus homevalensis*; pl. 6, fig. 4 = *S? farleyensis*).
1957 *Taeniothaerus subquadratus* – Coleman, p. 87, pl. 15, fig. 1-7.
1983 *T. subquadratus* – Briggs, p. 126, pl. 1, fig. 11.
1983 *T. subquadratus* – Parfrey, p. 291, Fig. 2-4.
1998 *T. subquadratus* – Briggs, p. 139.
2015a *T. subquadratus* – Waterhouse, p. 100, Fig. 50-53.

Diagnosis: Large elongately oval shells with sulcate venter, low dorsal fold, moderately wide hinge, spines coarse for genus, up to 1.5mm in diameter anteriorly, bases weakly prolonged, well-developed halteroid brush, coarse elongate spine ridges, dorsal spines 0.2-0.7mm in diameter anteriorly, reaching 1mm, dimples elongate and closely spaced, interspersed with some fine spines at start of trail.

Fig. 5. *Taeniothaerus subquadratus* Whitehouse, lectotype, BMNH 91171, x1 from Berriedale Limestone, Tasmania. (Hill 1950).

Lectotype: NHM 91171 from Berriedale Limestone at either Mt Wellington or Mt Dromedary, Hobart, figured by Etheridge & Dun (1909, pl. 41, fig. 1), Hill (1950, pl. 1, fig. 1), Coleman (1957, pl. 15, fig. 1, 2), and Fig. 1 herein, SD Prendergast (1943, p. 27). See Parfrey (1983, p. 293).

Morphology: The species is characterized by its large and well-spaced posteriorly elongated spine bases over both valves, as well illustrated by Hill (1950), Coleman (1957) and Parfrey (1983). They may be some 12mm long in Tasmanian specimens as figured by Parfrey (1983) and over 7mm long in Tiverton specimens. The spines themselves may be large, often exceeding 1mm in diameter on both valves, and reaching 1.5mm on the ventral valve. Over the middle shell, spines are extended in front of the base through the shell as tunnels. Dorsal spines as a rule 0.3-0.5mm in diameter. Tasmanian dorsal valves figured by Parfrey (1983) are less dimpled than dorsal valves from the Tiverton Formation.

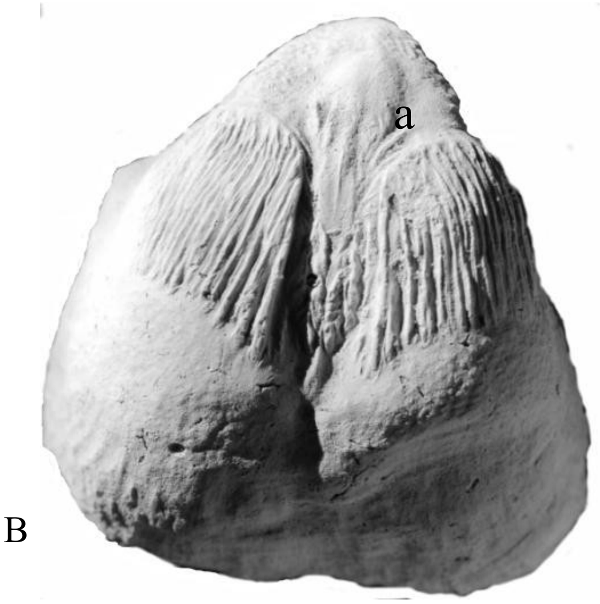


Fig. 6. *Taeniothaerus subquadratus* (Morris). A, dorsal external mould of UQF 81276, x1. B, Ventral internal mould UQF 81191, x1.5. Note ancillary muscle scars (a) each side of posterior adductors. From upper middle Tiverton Formation. (Waterhouse 2015a).

Stratigraphy: Briggs in Waterhouse et al. (1983) limited *Taeniothaerus subquadratus* to the upper middle Tiverton Formation. There are older specimens from additional localities in the Tiverton Formation, too poorly preserved to be sure of the species. The Tiverton material is identified with *Taeniothaerus subquadratus* from the Berriedale Limestone of Tasmania, and in a number of Tasmanian specimens the ventral spine bases are shorter and spaced further apart, but they are very long in other specimens. Material close to *subquadratus* is kept at the National Museum of Victoria, collected by G. A. Thomas from the Callytharra Formation in the K52 Range, north of the main road, at Middalya Station, Carnarvon Basin. Sturdy thick ventral spines with short bases are up to 2mm wide, with fine radial threads over parts of the shell, and dorsal dimples are present. Coleman (1957, pl. 15, fig. 8-12) reported somewhat similar internal moulds from the Fossil Cliff Formation of Western Australia, but these need the external ornament as well to permit specific identification.

Fig. 7. *Taeniothaerus subquadratus* (Morris), A, B, detail of dorsal external mould near start of trail, showing spine bases as black circles, UQF 81426, x6. From upper middle Tiverton Formation. (Waterhouse 2015a).

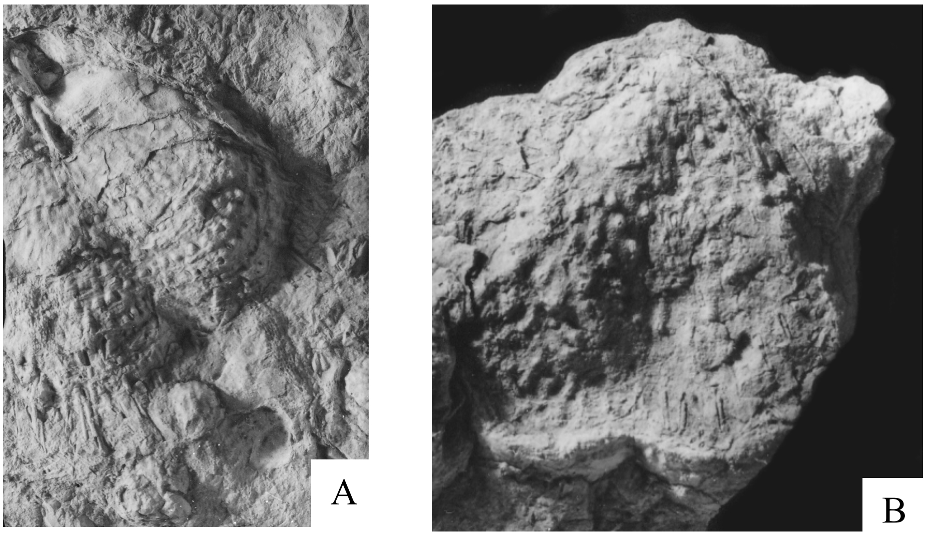


Fig. 8. *Taeniothaerus subquadratus* (Morris). A, Juvenile specimen showing part of posterior dorsal valve and part of anterior ventral valve, with spines, UQF 11050 from Granton Quarry, x0.5. B, crushed ventral valve from Maria Island, UQF 49271, x1. From Berriedale Limestone, Tasmania. (Briggs 1979).

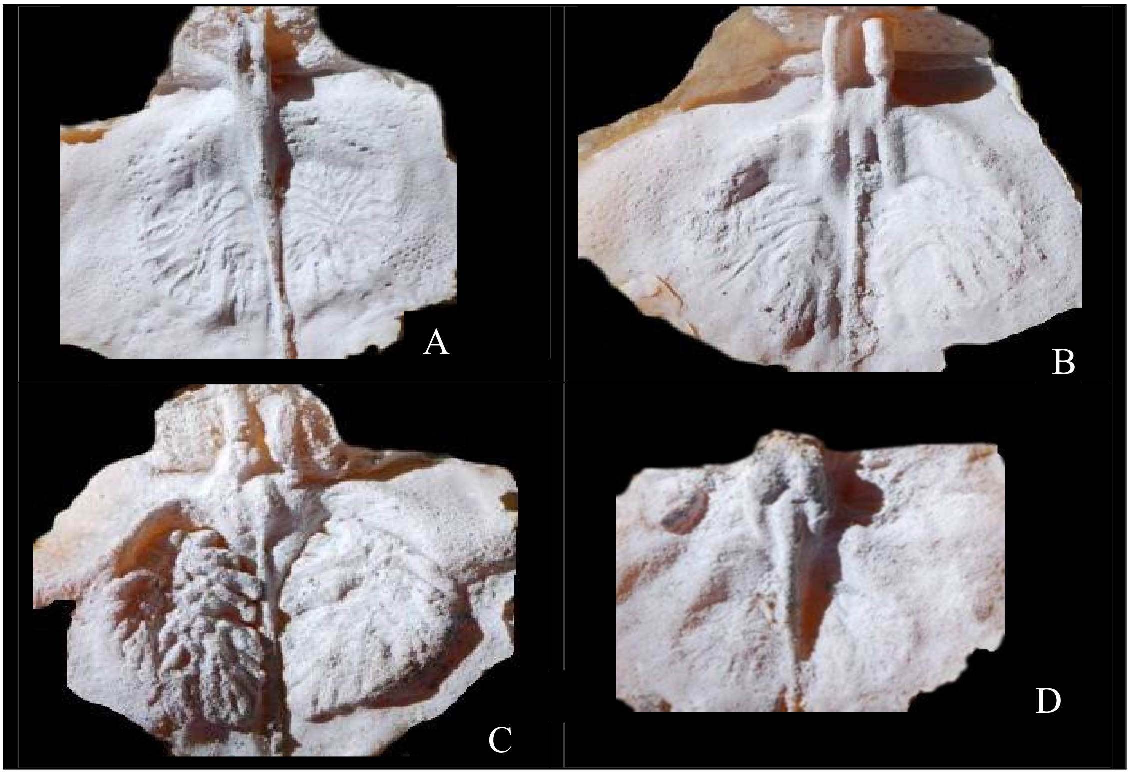


Fig. 9. *Taeniothaerus subquadratus* (Morris), latex casts of cardinalia of dorsal valve. A, UQF 81189, x1. B, UQF 81211, x1. C, UQF 81190, x1.5. D, UQF 81193, x1. From upper middle Tiverton Formation. (Waterhouse 2015a).

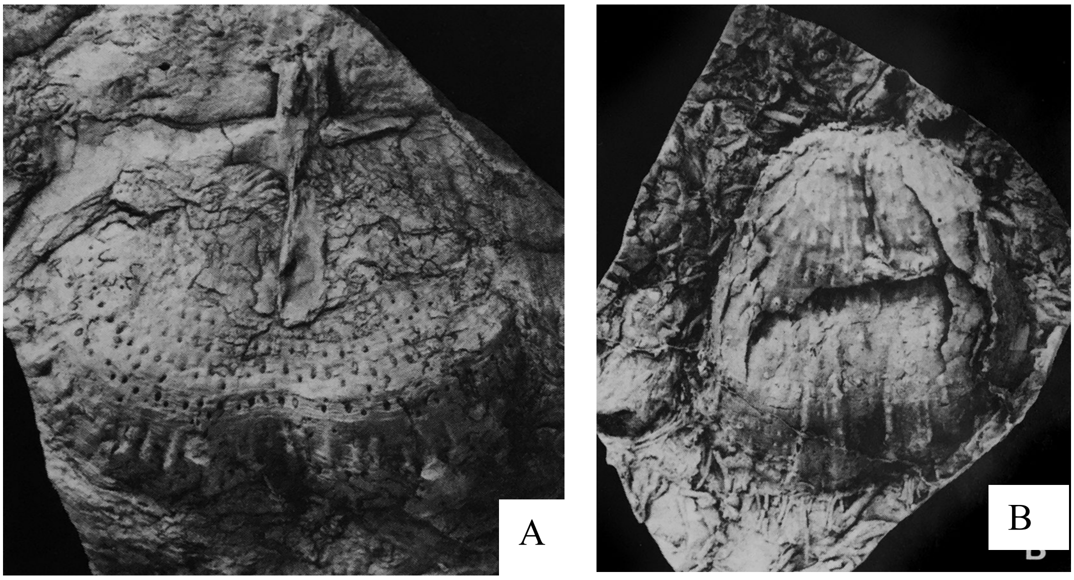


Fig. 10. *Taeniothaerus subquadratus* (Morris). A, dorsal valve UT 21553A, x1. B, ventral valve UT 90138a, x0.6. From Rathbone's Quarry, near Granton, Enstone Park Limestone, Elephant Pass, Tasmania. (Parfrey 1983).

An internal mould from the Tiverton Formation of the Mt Britton Goldfield figured as *subquadratus* by Etheridge (1892) was referred to *Taeniothaerus homevalensis* by Briggs (1998, p. 139), but has coarse spine bases like those of *subquadratus*, and a second internal mould (Etheridge 1892, pl. 38, fig. 10) is possibly conspecific. The posterior fragment of a ventral valve figured by Etheridge (1892, pl. 40, fig. 5) is difficult to assign specifically. Briggs (1998, p. 139) referred *Productus* sp. indet. (e) of Etheridge (1892, p. 256, pl. 37, fig. 18) from Mt Britton Goldfield to *subquadratus*, which is feasible, because a burst of ear-spines is shown.

Taeniothaerus subquadratus quadratus n. subsp.

Fig. 11, 12

1983 *Megasteges* cf. *randsi* [not Hill] – Briggs in Waterhouse et al. p. 13, pl. 3, fig. 1.
1986 *Megasteges* cf. *randsi* [not Hill] – Briggs, p. 39, pl. 8, fig. 6?, 9, 10 (part, not fig. 7, 8 = *Lipanteris*? *sulcata*).

Derivation: quadratus – square, quadrate (Lat.).

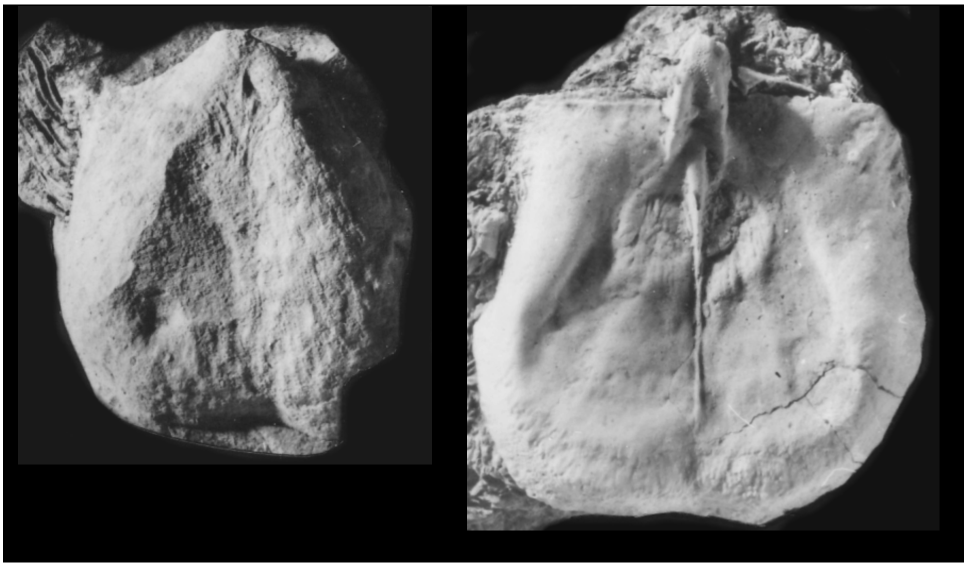


Fig. 11. *Taeniothaerus subquadratus quadratus* n. subsp. A, ventral valve UQF 20972 from Campbell's bed 6, Tiverton Formation, near Homevale Station, north Bowen Basin, x1. B, dorsal valve UQF 40286 from Cattle Creek Formation, x1. (Briggs 1979).

Diagnosis: Small shell, weakly elongate to subequilateral in outline, with well-defined ventral sulcus commencing at the beak, low distinct dorsal fold, fine mostly erect spines. Ventral spines have slender elongate bases, distinct ear cluster, less developed than in *subquadratus*.

Holotype: UQF 74431 from Roses Pride Formation, southeast Bowen Basin, figured by Briggs (1986, pl. 8, fig. 9, 10) and Fig. 12B, C herein, here designated.

Morphology: An unregistered ventral valve and UQF 74431 do not show ornament well, and a sulcus commences at the umbo rather than well in front. Although the specimens were treated as possible *Megasteges randsi* by Briggs (1986), they were left out of synonymy by him in 1998. They come from the Roses Pride Formation of the south-east Bowen Basin. Cattle Creek material shows the presence of a posterior lateral brush of spines, as well as

A

Fig. 12. *Taeniothaerus subquadratus quadrata* n. subsp. A, unregistered ventral valve. B, C, dorsal and ventral views of UQF 74431, holotype. Specimens x1 from Roses Pride Formation. (Briggs 1986).

B

C

elongate ventral spine bases. The subspecies is smaller than *Taeniothaerus subquadratus* and has a better-defined ventral sulcus. The ventral interarea is moderately well-formed for the genus.

Stratigraphy: The species is found in the Roses Pride Formation of the southeast Bowen Basin, in the *Echinalosia preovalis - Ingelarella plica* Zone. The specimens are close to a ventral valve from Campbell's (1961) band 6 in the Tiverton Formation, as figured and described by Briggs in Waterhouse et al. (1983). Further specimens are found in the lower Cattle Creek Formation in the southwest Bowen Basin, from "the limestone hill" near 2km from Mt Serocold, Reid's Dome.

***Taeniothaerus*? spp.**

Fragments and incomplete specimens likely to belong to *Taeniothaerus* have been reported from the *Echinalosia preovalis - Ingelarella plica* Zone in the upper Tiverton Formation in the north Bowen Basin (Waterhouse 1983a), the *Martinia*? *adentata* Zone of the Takitimu Group**,** including the Chimney Peaks Formation of New Zealand (Waterhouse 1982, p. 41) and other stations.

Genus ***Lipanteris*** Briggs, 1986

Diagnosis: Large subquadrate shells with enrolled ventral umbo and narrow hinge bearing short ventral interarea, dorsal valve geniculate. Ventral spines in one or two series, moderately erect, arising from very short spine ridges that become elongate near anterior margin, some spines fine, most moderately thick, spine tunnels present, spines project laterally from the flanks, without forming postero-lateral brushes, few over the trail. Dorsal spines in two orders, fine at 0.2- 0.3mm diameter and coarse up to 0.7mm near edge of disc. Cardinal process with deep embayment on the inner (ventral) side, curved dorsally.

Type species: *Aulosteges* (*Taeniothaerus*) *subquadratus* var. *cracowensis* Hill, 1950, p. 8 from Fairyland Formation (Sakmarian), southeast Bowen Basin, Queensland, OD.

Lipanteris cracowensis (Hill, 1950)

Fig. 13, 14

1950 *Aulosteges* (*Taeniothaerus*) *subquadratus* var. *cracowensis* Hill, p. 6, pl. 3, fig. 1, 2, ?3, pl. 4, fig. 1, 2, pl. 6, fig. ?2, 3 (part?, possibly not pl. 4, fig. 3a-c = *sparsispinosus* fide Briggs but no apparently divergent buttress ridges, suggesting his identification is wrong. See Fig. 3A herein).
1986 *Lipanteris cracowensis* Briggs, p. 37, pl. 7, fig. 1-4.
1998 *L. cracowensis* – Briggs, p. 134.

Diagnosis: Large strongly enrolled shells, coarse and fine series of interspersed ventral spines, prolonged spine bases, costae on flanks, dorsal spines recumbent to erect 0.7mm diameter and fine recumbent 0.2 to 0.3mm diameter, coarse sparse trail spines.

Holotype: UQF 10741 from Fairyland Formation, southeast Bowen Basin, figured by Hill (1950, pl. 3, fig. 1a, b, pl. 4, fig. 1a, b) and Fig. 13C herein, OD.

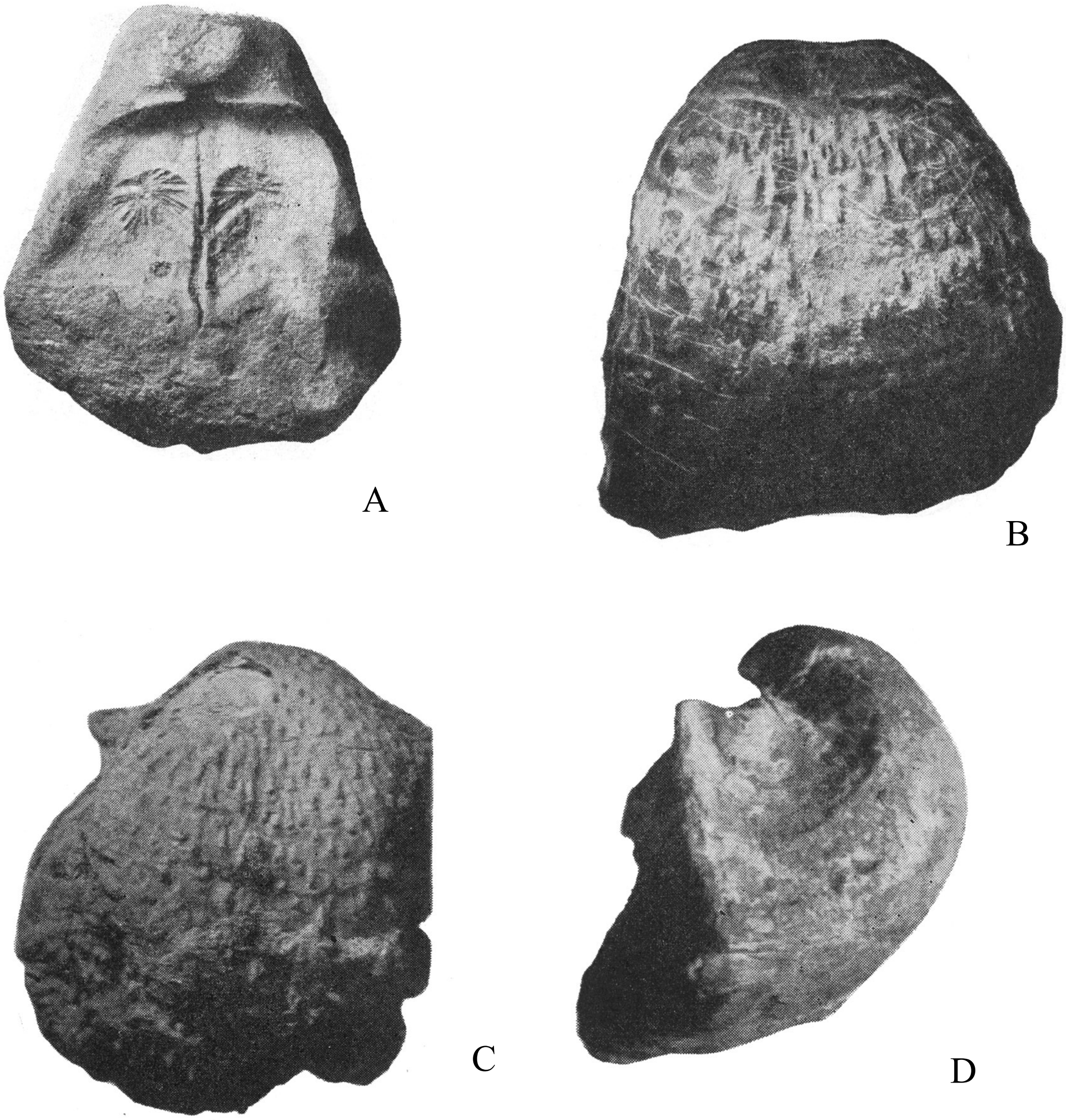


Fig. 13. *Lipanteris cracowensis* (Hill). A, dorsal aspect of internal mould, UQF 10743, rated as possibly *sparsispinosus* by Briggs (1998, p. 135). B, ventral aspect of exterior, UQF 10739. C, external aspect of ventral valve UQF 10741, holotype. D, lateral aspect of internal mould UQF 10738. Specimens x1, from Fairyland Formation, southeast Bowen Basin. (Hill 1950).

Morphology: The lack of ventral lateral spine brushes is a prime feature, and ventral spine bases are moderately like those of *Taeniothaerus*.

Stratigraphy: The species is found only in the Fairyland Formation, in the *Maxwellosia curtosa* Zone.

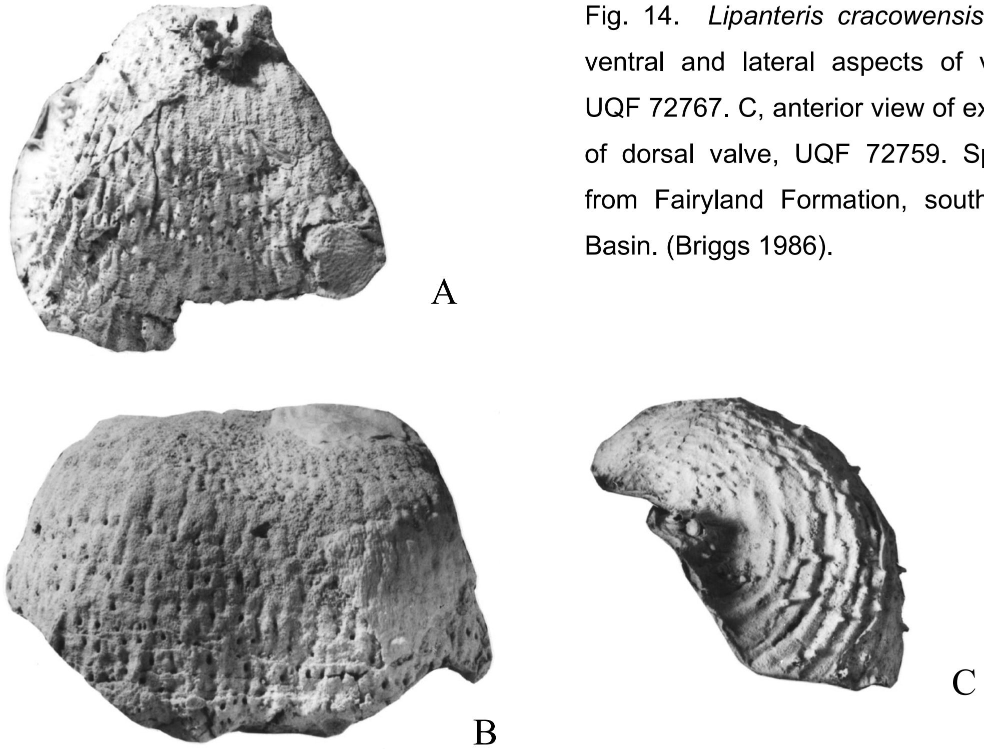


Fig. 14. *Lipanteris cracowensis* (Hill). A, B, ventral and lateral aspects of ventral valve UQF 72767. C, anterior view of external mould of dorsal valve, UQF 72759. Specimens x1 from Fairyland Formation, southeast Bowen Basin. (Briggs 1986).

Lipanteris enigmosus n. sp.

Fig. 15, 16

2015a *Lipanteris anotos* [not Briggs] – Waterhouse, p. 109ff (part), Fig. 60A-F.

Derivation: enigma – uncertain, mysterious (Lat.)

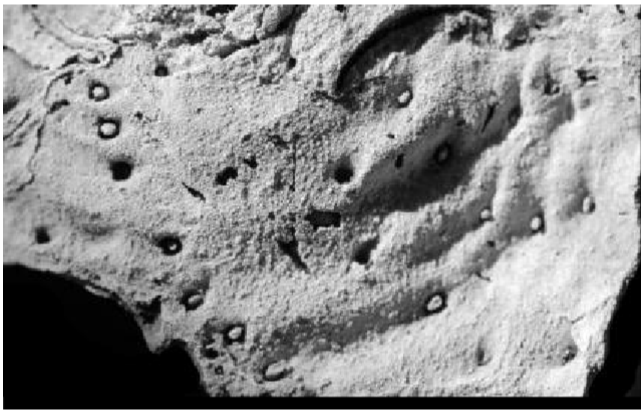


Fig. 15. *Lipanteris enigmosus* n. sp., fragment of lateral external mould UQF 81584, x1.5. Upper middle Tiverton Formation, UQL 4515, x1.5.

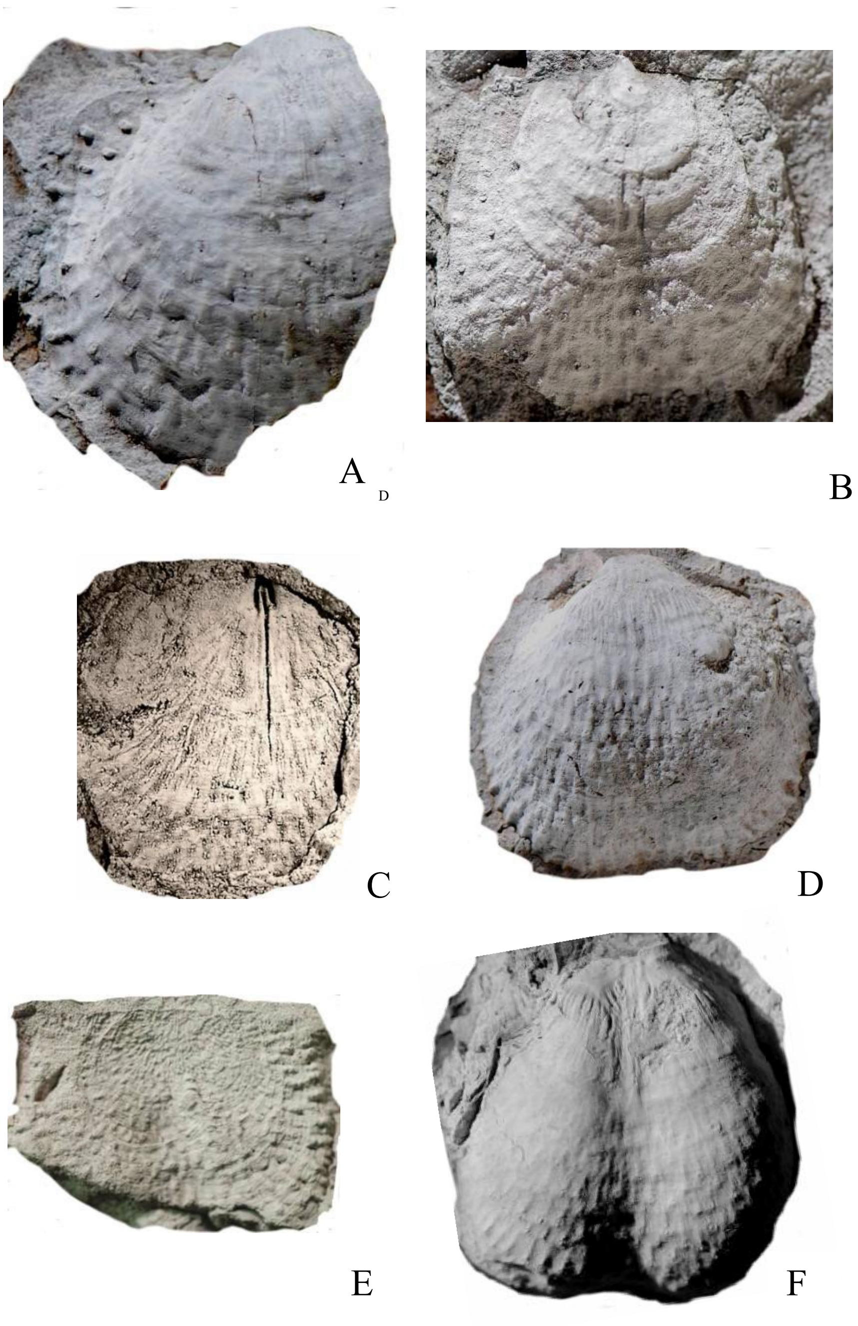


Fig. 16. *Lipanteris enigmosus* n. sp. A, ventral valve UQF 81199, x1.5. B, ventral valve UQF 81198, holotype x2. C, dorsal valve internal mould UQF 81201, x2. D, ventral valve UQF 81200, x1. E, external mould of ventral valve UQF 81203, x1. F, ventral internal mould UQF 81202, x1. Upper middle Tiverton Formation. (Waterhouse 2015a).

Diagnosis: Small, subelongate short bases to ventral spines, no posterior-lateral ear brush but evenly distributed moderately robust ear spines. Short parallel buttress ridges behind adductor scars. Shape subquadrate, ventral sulcus shallow, may be deep anteriorly, fold low.

Holotype: UQF 81198 from Tiverton Formation, north Bowen Basin, figured in Waterhouse (2015a, Fig. 60B) and herein as Fig. 16B, here designated.

Stratigraphy: The species ranges from the upper middle *Magniplicatina undulata* Zone well into the *Taeniothaerus subquadratus* Zone of the Tiverton Formation.

Lipanteris*? *sulcata (Waterhouse, 2015a).

Fig. 17

?1983 *Megasteges* cf. *randsi* [not Hill] - Briggs, p. 131, pl. 3, fig. 1.
1986 *Megasteges* cf. *randsi* [not Hill] – Briggs, p. 39, pl. 8, fig. 7, 8 (part, not fig. 6, 9, 10 = *Taeniothaerus subquadratus quadratus* n. subsp.)
2015a *Lakismatia sulcata* Waterhouse, p. 107, Fig. 57.

Diagnosis: Ventral umbo elongate and distorted, ventral interarea high, ventral sulcus well developed. No apparent ear cluster of ventral spines, ventral spines have short bases.

Holotype: UQF 81205 from the *Capillonia armstrongi* Subzone at the base of the *Taeniothaerus subquadratus* Zone, Tiverton Formation, figured in Waterhouse (2015a, Fig. 57A) and herein as Fig. 17A, OD.

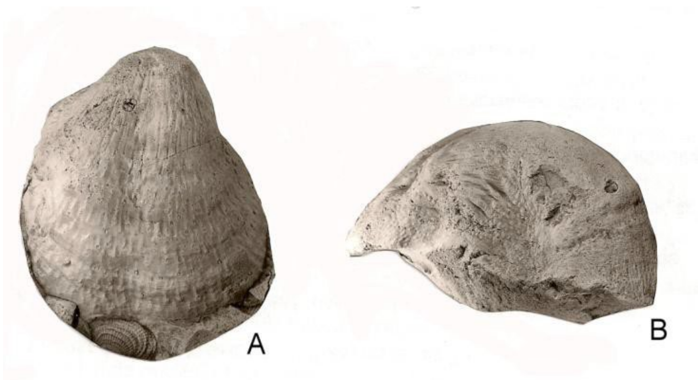


Fig. 17. *Lipanteris*? *sulcata* (Waterhouse). A, ventral valve holotype UQF 81205, x0.66. B, lateral aspect of ventral valve UQF 81204, x0.66. From Tiverton Formation. (Waterhouse 2015a).

Morphology: The ornament needs to be better known, and dorsal valve better understood. The species is close to *Lakismatia lakismatos* in shape, but spine bases are elongate. Posterior lateral spines are obscure in available photographs, and the dorsal valve has a median fold. Briggs (1983, 1986) referred the specimens with a query to *Megasteges*

Waterhouse, which differs in lacking the elongate spine bases.

Stratigraphy: The type comes from the middle Tiverton Formation of the north Bowen Basin, and specimens close in shape come from the Roses Pride Formation of the southeast Bowen Basin.

Tribe **MEGASTEGINI** Waterhouse, 2013

[Megastegini Waterhouse, 2013, p. 282].

Diagnosis: Spines suberect to subprostrate in both valves, without prolonged bases and without rhizoid spines. Ventral interarea low to moderately high, ventral umbo irregular in shape. Short buttress plates supporting cardinal process and placed behind the dorsal adductor scars. Permian (Sakmarian to Changhsingian).

Name genus: *Megasteges* Waterhouse, 1975, p. 6 from Nisal Member (Changshingian), Senja Formation, Nepal, OD**.**

Genera: *Megasteges* Waterhouse, *Austrothaerus* Waterhouse, *Lakismatia* Waterhouse. Permian.

Discussion: These genera are distinguished by the nature of the spines on both valves, which differ from those of Aulosteginae with its thick or thin rhizoid spines and Taeniothaerinae, with slightly prolonged spine bases. The dorsal valve of *Megasteges* is gently convex over much of the venter, whereas that of *Austrothaerus* and *Lakismatia* is concave., and all three genera have much the same dorsal cardinalia as in Taeniothaerini. *Austrothaerus* Waterhouse (2010, p. 15) from the Sakmarian or early Artinskian Camila Formation of Queensland, Australia, has a moderately developed ear-brush, and the ventral spines are comparatively uniform in size and erect, apart from fine prostrate spines anteriorly. Dorsal spines are in two high-angled series, 0.1-0.2mm diameter and 0.4mm diameter. In *Megasteges*, the ear brush is less developed, and ventral spines are erect and of varying diameters, and dorsal spines are uniformly thin and of one series. This genus is found chiefly in Lopingian deposits of Nepal and Tibet, and is not of Capitanian age as claimed by Brunton et al. (2000), nor especially close to *Wyatkina* Fredericks with its fine spines, possibly missing from the dorsal valve, and different cardinal process. The types of *Megasteges* and *Austrothaerus* are kept at the bulk storage unit of the Queensland

Museum, Hendra, Brisbane, rather than “repository unknown” as alleged by Brunton et al. (2000, p. 587) for *Megasteges*. (See Waterhouse 1978, p. 69). *Lakismatia* is shaped more like *Taeniothaerus*, with bulky ventral valve and concave dorsal valve, and its spines, like those of *Megasteges* and *Austrothaerus,* arise directly from the shell, without posteriorly prolonged bases.

Genus ***Megasteges*** Waterhouse, 1975

Diagnosis: Large shells, ventral valve asymmetric, high ventral interarea and elytridium, ventral sulcus, sessile and erect spines, no posterior lateral brush of spines. Dorsal valve variable in profile, may be convex near hinge and concave anteriorly, geniculate, ornamented by pustules and small erect spines. Ventral adductor scars long and narrow, surrounded partly or completely by diductor scars, cardinal process with two anterior short buttress plates, medium septum, dendritic adductor scars.

Type species: *Megasteges nepalensis* Waterhouse, 1975 from Senja Formation of Late Permian age in west Nepal, OD.

Discussion: The presence of this genus in east Australia and New Zealand remains uncertain, because possible specimens are rare and too incomplete to allow a positive identification. Perhaps further work in east Australia will resolve the question: New Zealand outcrops appear to have been closely examined, so that future prospects are poor for finding definite occurrences of the genus in New Zealand, although one never knows.

Megasteges? sp. A

Fig. 18

1998 Aulostegid, genus and species uncertain Briggs, p. 141, Fig. 71A, B.

UQF 58891 from the upper Drake Series of Boorook and also Cataract River Formation AMF 36345 possibly belongs to *Megasteges*, given the elongate outline of the shell, the moderately high ventral interarea, and crowded erect spines without elongate bases over the dorsal valve anterior. Much of the dorsal disc is gently convex, and anteriorly appears to become concave, together with the trail, recalling the build of the shell in *Megasteges*.

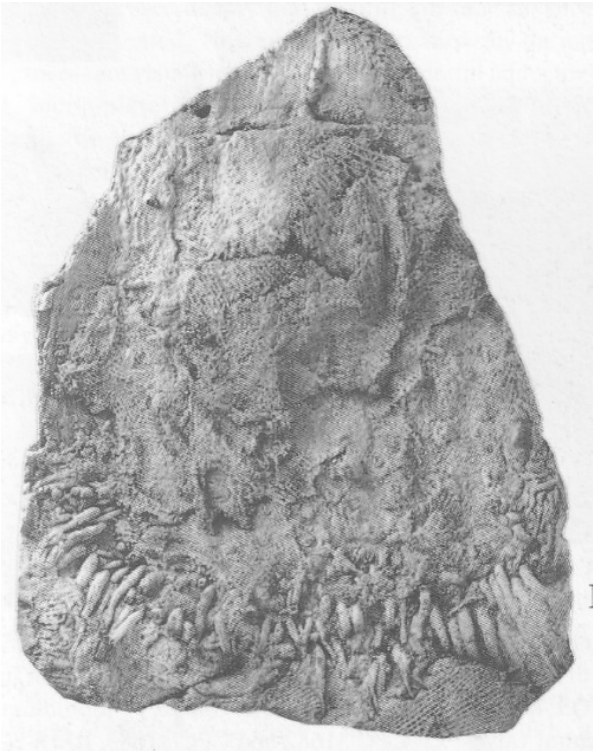


Fig. 18. *Megasteges*? sp. A, dorsal aspect showing high ventral interarea and coarse anterior dorsal spines, UQF 38891, x1. Possibly from Cataract River Formation. (Briggs 1998).

***Megasteges*? sp. B**

Fig. 19

2001 *Megasteges*? sp. Waterhouse, p. 85, pl. 5, fig. 18, text-fig. 5i, j, k.

A single worn ventral valve OU 18758 comes from the Hilton limestone at Wairaki Downs, New Zealand. It has the overall shape of *Megasteges*, gently convex dorsal disc and the lateral spines do not appear to form a brush, unlike those of *Austrothaerus*.

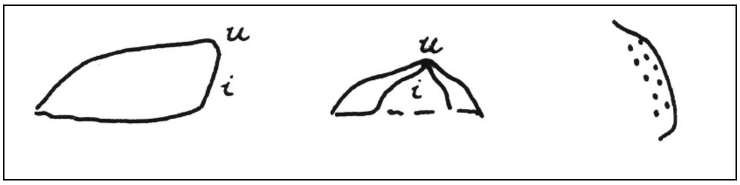


Fig. 19. *Megasteges*? sp. B. A, lateral view of OU 18302. A, lateral view, x1.25. B, posterior view showing interarea, x1. C, spine bases on lateral side of the specimen, x1. i = interarea; u = umbo. From Hilton Limestone, Wairaki Downs, New Zealand. (Waterhouse 2001).

Austrothaerus Waterhouse, 2010, p. 15

Diagnosis: Distinguished from *Megasteges* Waterhouse, 1975 by the development of an ear brush, whereas *Megasteges* lacks an ear-brush. Ventral spines in two series anteriorly, compared with the slightly more varied but subuniform diameters of ventral spines in *Megasteges*. Dorsal valve concave.

Type species: *Aulosteges* (*Taeniothaerus*) *randsi* Hill, 1950, OD.

Discussion: Several species from Western Australia are also asymmetric in shape with extended or distorted ventral umbones. *Aulosteges ingens* Hosking (1931, pl. 5, fig. 1, pl. 6, fig. 2) from the lower Byro Group of Western Australia is a large and asymmetric species with coarse ventral spines that may be of a single order, and fine more erect dorsal spines. Unfortunately, the dorsal interior is not entirely clear. Coleman (1957, pl. 3, fig. 5) figured one specimen with lateral buttress plates, and another seemingly without (Coleman 1957, pl. 3, fig. 7). Neither of the dorsal valves are topotypes, and the specimen with buttress plates is closer in shape to type *ingens*. A similar dorsal interior with buttress plates was figured by Archbold (1997, Fig. 3H) and was ascribed to *ingens*.

Austrothaerus randsi (Hill, 1950)

Fig. 20, 21

1950 *Aulosteges* (?*Aulosteges*) *randsi* Hill, p. 6, pl. 6, fig. 1a-d.
1998 *Megasteges randsi* – Briggs, p. 140, Fig. 70A-F.
2010 *Austrothaerus randsi* – Waterhouse, p. 17.

Diagnosis: Moderate in size, ventral interarea high, with slightly distorted umbo, shallow ventral sulcus anteriorly. Ventral spines erect without prolonged bases, in two series, one erect to high angle recumbent, and the other of rare thin spines appearing anteriorly, small ear brush. Dorsal spines in two series.

Holotype: GSQF 1991a, b figured by Hill (1950, pl. 6, fig. 1a-d) and Fig. 19A-C herein from Camila Formation near Wilangi Station, Yarrol Basin, Queensland, OD.

Morphology: Tiverton and Rose's Pride material was regarded by Briggs (1983; 1986, pl. 8, fig. 6-10; 1998, Fig. 70A-F) as comparable to *Megasteges* (now *Austrothaerus*) *randsi* (Hill, 1950, pl. 6, fig. 1a-d), and the Tiverton ventral valves resemble *randsi* in characteristic features of overall shape, large size, distorted umbonal region, well-developed ventral sulcus and high interarea. Specimens are more irregular in shape with high ventral interareas, compared with *Taeniothaerus*, and the high arched pseudodeltidium appears to have a

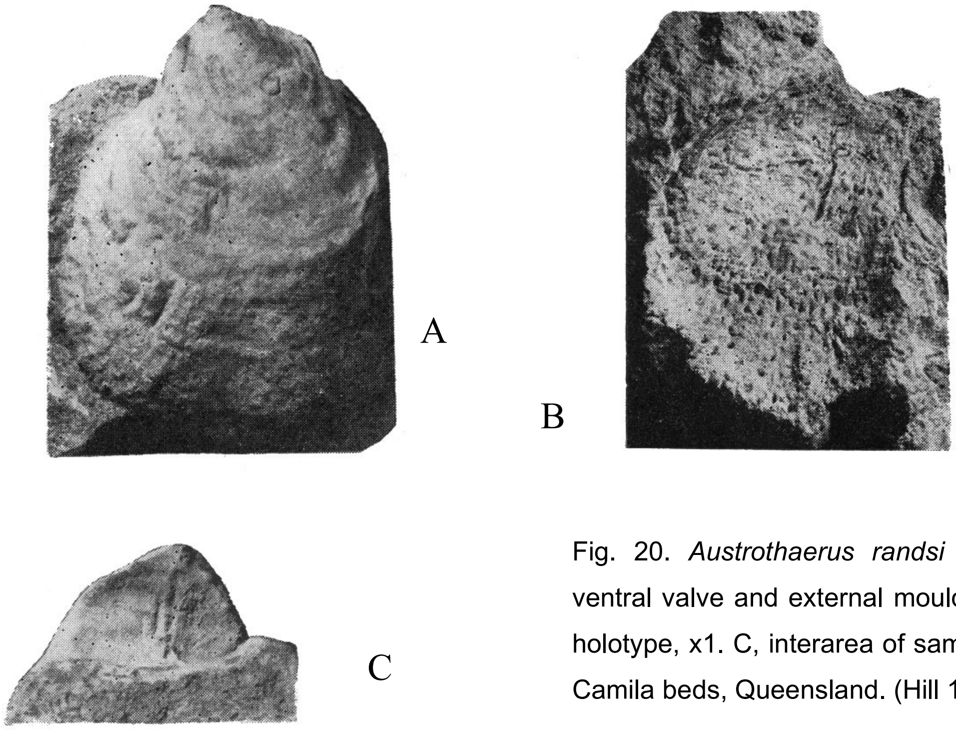
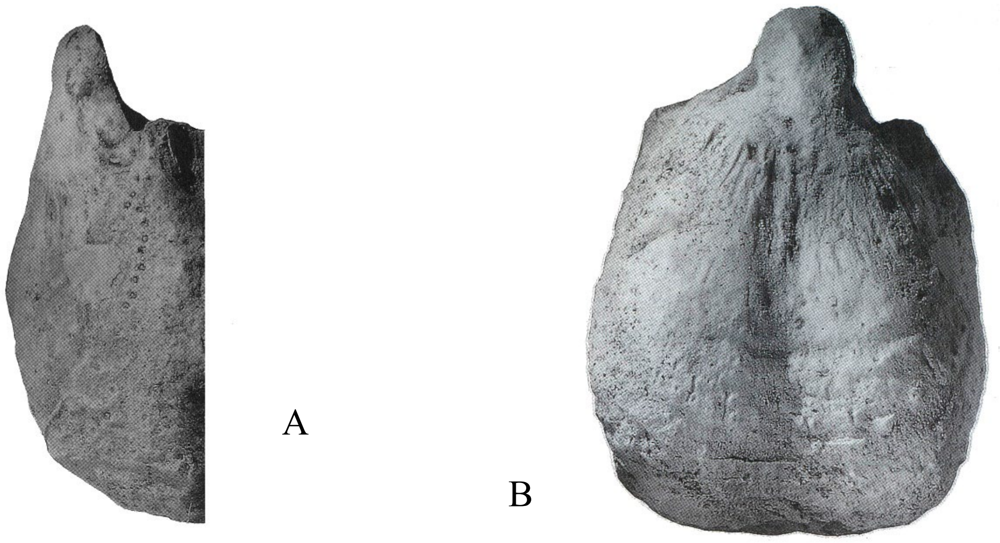


Fig. 20. *Austrothaerus randsi* (Hill). A, B, ventral valve and external mould, UQF 1991 holotype, x1. C, interarea of same specimen. Camila beds, Queensland. (Hill 1950).

median channel along its length (see Fig. 20C), but this is not seen in other specimens ascribed to *randsi*. Briggs (1986, 1998) did not include in his synonymy for “*randsi*” the material he had compared to that species in Waterhouse et al. (1983, p. 131, pl. 3, fig. 1) from the Tiverton Formation. His figured specimen shows a well-formed sulcus and cluster of posterior lateral spines, and spines in two orders, and overall quadrate shape, and it is now assigned to *Taeniothaerus subquadratus quadratus* n. subsp. His Roses Pride material of 1986 was also excluded, and is now divided between *T. subquadratus quadratus* and *Lipanteris*? *sulcata*.. One specimen (Briggs 1998, Fig. 70F) was figured from the Lizzie Creek volcanics of the northern Bowen Basin, but only a panel of the ornament is shown, with erect spines.

Stratigraphy: The species is found in the Camila beds of the Yarrol Basin, Queensland, and possibly occurs in the Lizzie Creek Volcanics of the northern Bowen Basin.



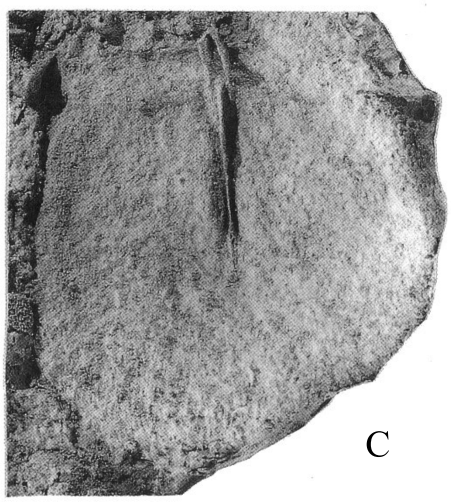


Fig. 21. *Austrothaerus randsi* (Hill). A, B, lateral and ventral aspects of ventral internal mould GSQF 13474, x1.5. C, latex cast of dorsal interior, CPC 31681, x1.5. From Camila beds, Star River, Queensland. (Briggs 1998).

Genus ***Lakismatia*** Waterhouse, 2010

Diagnosis: Elongate with high ventral interarea, ventral and dorsal spines though said by Briggs (1998) for *lakismatos* to be each in two orders, are dominated by suberect to erect spines of subuniform diameter, fine spiines tending to be prostrate, coarse spines variably inclined, spine bases very short, usually absent. No apparent halteroid brush over posterior flanks, buttress ridges behind the dorsal adductors. The shell is often subsymmetrical with extended ventral umbo.

Type species: *Taeniothaerus lakismatos* Briggs, 1986, p. 40 from Elvinia Formation (Sakmarian) of southeast Bowen Basin, OD.

Discussion: This genus is very close to *Taeniothaerus*, but is regarded as of distinct generic rank, given the difference in spines, which are dense over both valves in the type species and have very short if any posterior bases. There is no apparent posterior lateral ventral brush, although spines are dense just as over the rest of the valve in the type speces.

Lakismatia lakismatos (Briggs, 1998)

Fig. 22, 23

1986 *Taeniothaerus lakismatos* Briggs, p. 40, pl. 8, fig. 1-5.
1998 *T. homevalensis* [not Briggs] – Briggs, p. 137.
2010 *Lakismatia lakismatos* – Waterhouse, p. 18, Fig. 2.
2013 *Taeniothaerus* (*Lakismatia*) – Waterhouse, p. 277.

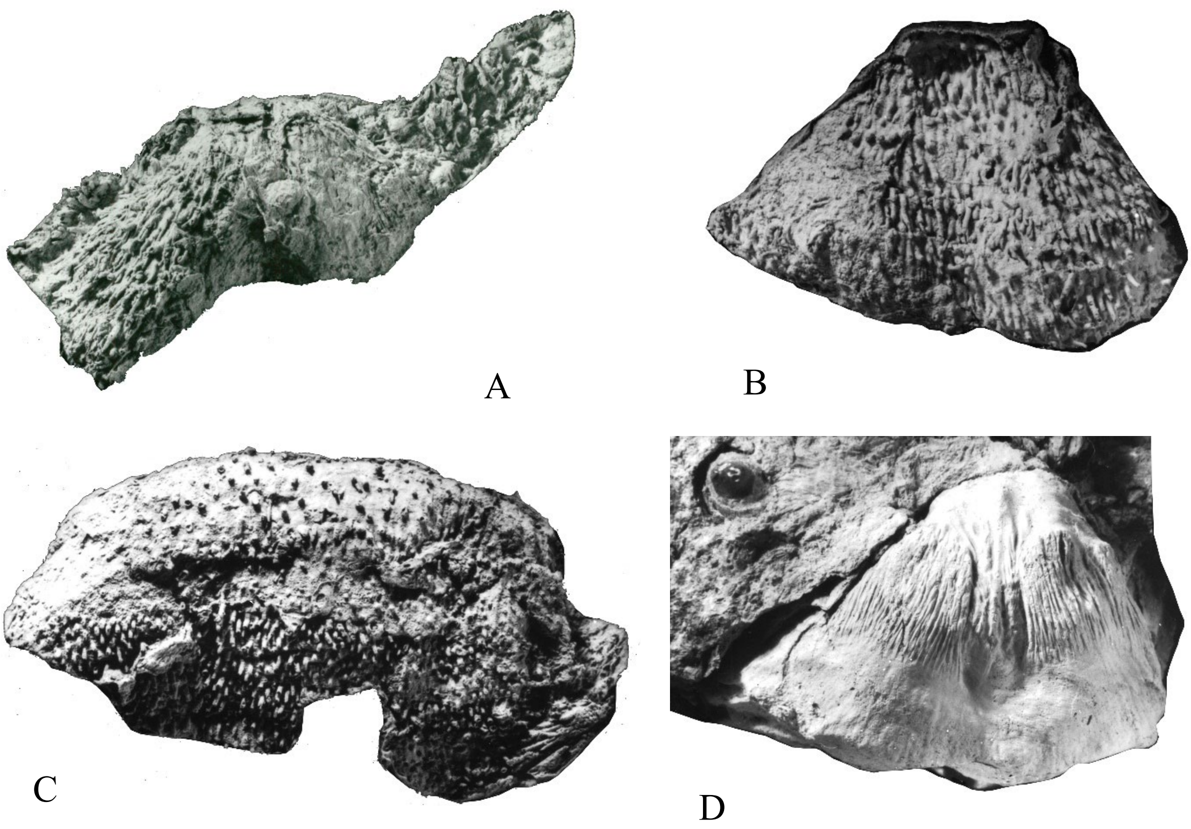


Fig. 22. *Lakismatia lakismatos* (Briggs). A, ventral latex cast, UQF 72751. B, latex cast of ventral valve UQF 7274650. C, E, anterior latex cast of ventral exterior and ventral internal mould, UQF 72747. From basal Elvinia Formation, southeast Bowen Basin, x0.9 to 1. (Briggs 1979).

Diagnosis: Shell narrow and highly arched. Spines dense over both valves, most erect and in two series, one fine and prostrate on the ventral valve and semirecumbent over the dorsal valve, the other series coarse, erect to variably inclined, predominant, especially over ventral valve. Low, short or no spine bases, weak costae developed anteriorly. Posterior lateral brush not apparent, because the spines are of similar density over entire valve. Two subparallel septa lie in front of the cardinal process (Fig. 23B).

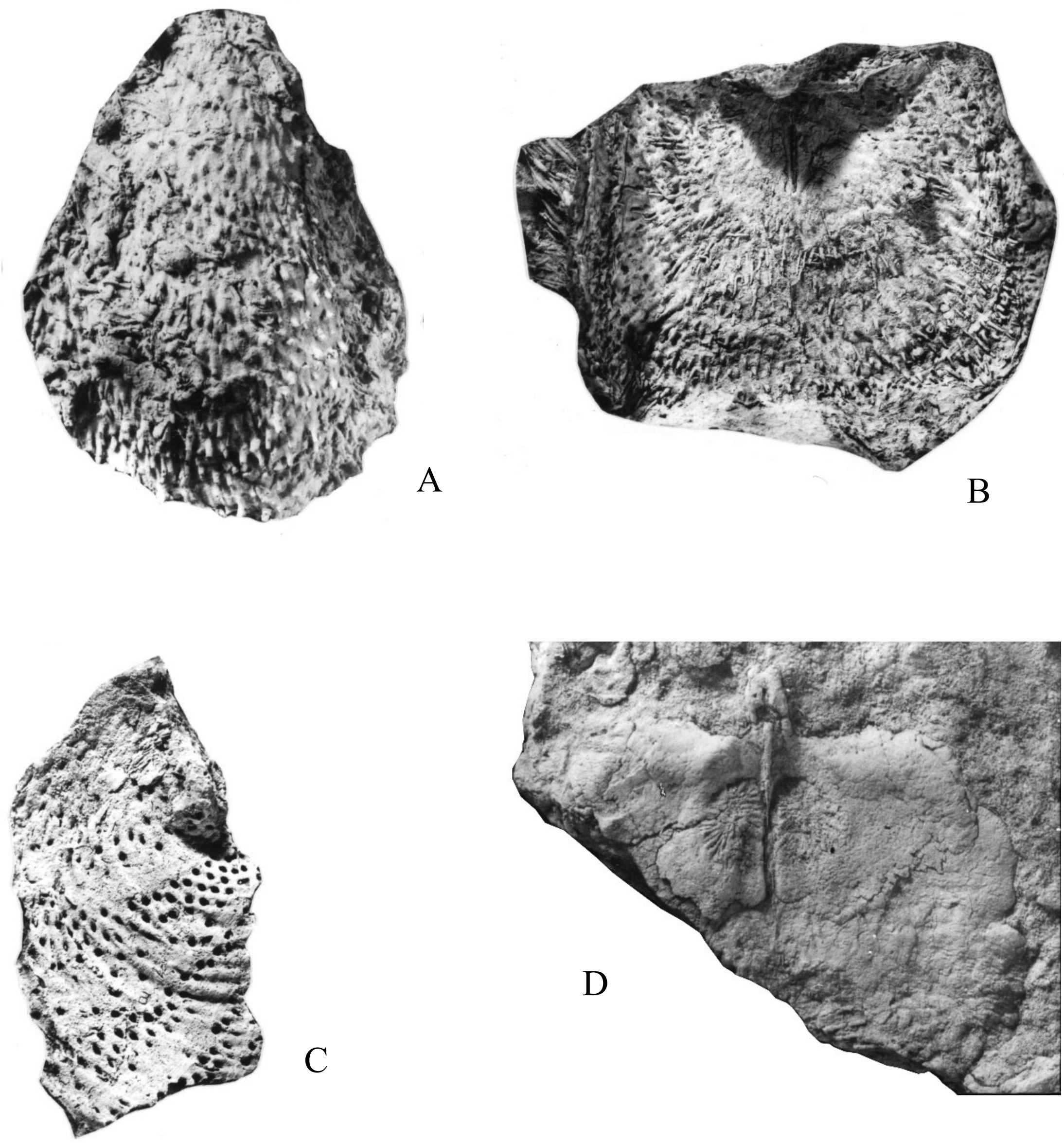


Fig. 23. *Lakismatia lakismatos* (Briggs). A, C, latex cast and external mould of ventral valve UQF 72750. B, internal aspect of dorsal valve, UQF 72743. D, dorsal aspect of conjoined specimen, latex cast, UQF 72749. From basal Elvinia Formation, southeast Bowen Basin, x1. (Briggs A-C, 1979; B, 1986).

Holotype: UQF 40445 figured by Briggs (1986, pl. 8, fig. 1, 4) from basal Elvinia Formation, southeast Bowen Basin, OD.

Morphology: The spines over both valves are dense, and laterally ventral spines are coarse, and prostrate spines more numerous.

The genus is possibly represented in the Carnarvon Basin by *Aulosteges lyndonensis* Coleman (1957, p. 46, pl. 4, fig. 1-10) from beds originally mapped as Bulgadoo Shale and considered to be Madeleine (= Coyrie) Formation by Archbold (1986, p. 113). The age is Baigendzinian, younger than the mid-Sakmarian age attributed to *Lakismatia lakismakos*. This species is ventrally sulcate with high ventral interarea and sturdy anterior shafts extending forward from the anterior flanks of the cardinal process. Further attributes were analyzed in Coleman (1957) and Waterhouse (2010, p. 19).

Stratigraphy: The species is found in the lower Elvinia Formation and in the Camboon Volcanics of the southeast Bowen Basin, and possibly is present in the Yarrol Basin of Queensland (Waterhouse 2015a, p. 104).

Lakismatia sparsispinosa (Briggs, 1986)

Fig. 24, 25

?1950 *Aulosteges* (*Taeniothaerus*) *subquadratus* var. *cracowensis* Hill, p. 6, pl. 4, fig. 3? (part, not pl. 3, fig. 1, 2, ?3, pl. 4, fig. 1, 2, pl. 6, fig. ?2, ?3 = *cracowensis*).
1960 *Taeniothaerus subquadratus* [not Morris] – Muir-Wood & Cooper, pl. 11, fig. 2 fide Briggs (part, not 1, 3-6 = *Carilya*).
1986 *Lipanteris sparsispinosus* Briggs, p. 38, pl. 7, fig. 5-10.
1998 *L. sparsispinosus* – Briggs, p. 135.

Diagnosis: Ventral valve with low interarea and shallow sulcus, spines coarse and erect and slightly finer semi-recumbent series, ribs present over flanks, coarse ribs with spines along crest over trail. Dorsal valve geniculate, spines in coarse erect series (0.75mm) continuing onto trail and fine mostly recumbent series 0.15 to 0.3mm in diameter.

Holotype: UQF 72797 from Fairyland Formation, figured by Briggs (1986, pl. 7, fig. 6-9) and Fig. 24A, B, D herein, OD.

Morphology: This species is highly distinctive, without ribs and without prolonged spinal bases. It will be interesting in future to see if other species are discovered to show the same pattern of well-spaced coarse spines, or if this form was simply a one-off: the spacing of the spines and the definite lack of any lateral brush of spines are highly distinctive features.

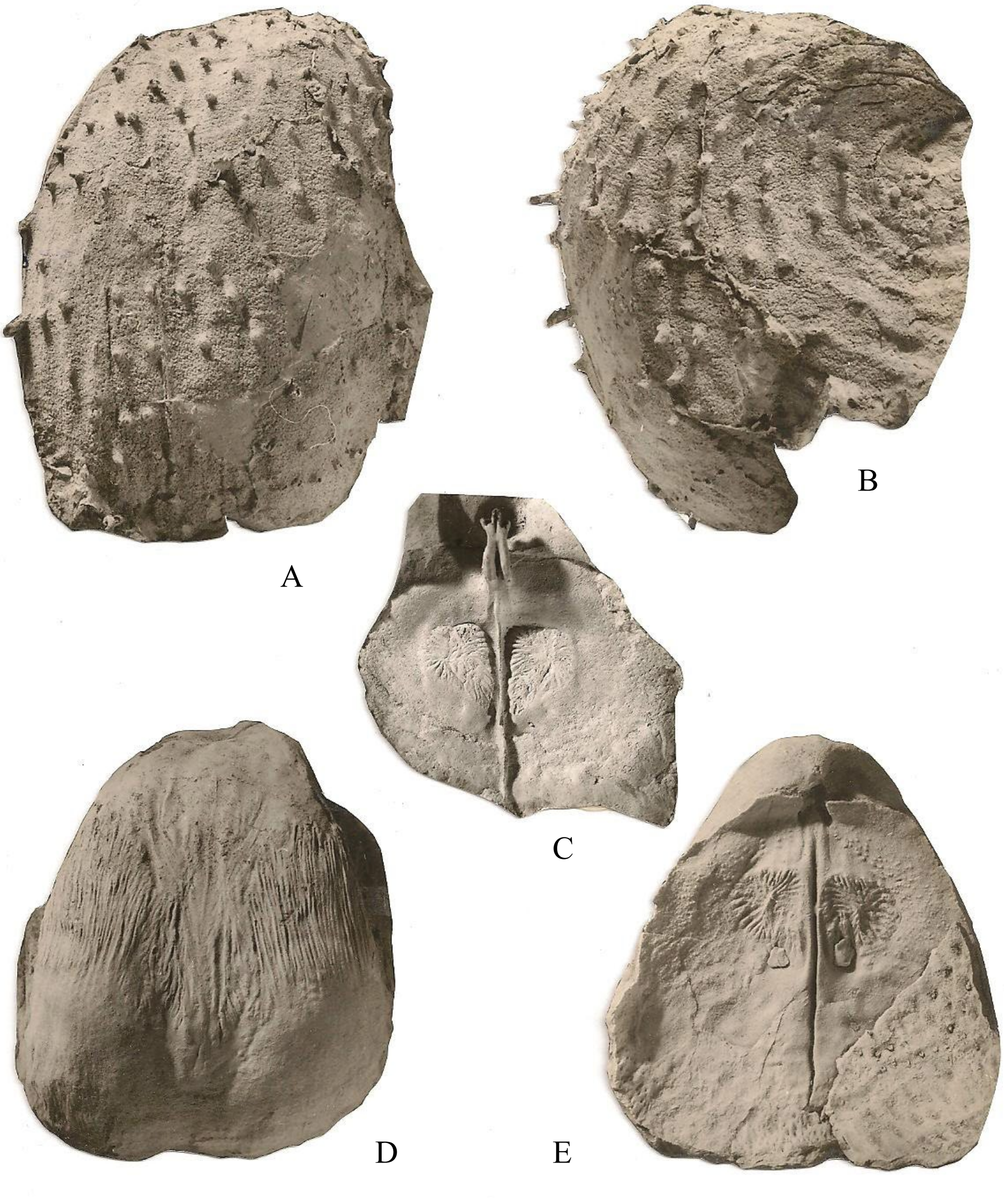


Fig. 23. *Lakismatia sparsispinosus* (Briggs). A, B, ventral and lateral aspects of UQF 72797, holotype. C, latex cast of dorsal interior, UQF 72796. D, ventral aspect of internal mould, holotype, UQF 72797. E, dorsal aspect of internal mould, UQF 72801. Specimens x1 from Fairyland Formation, Queensland, x1. (Briggs 1986).

Stratigraphy: The species is found only in the Fairyland Formation of the southeast Bowen Basin in Queensland.

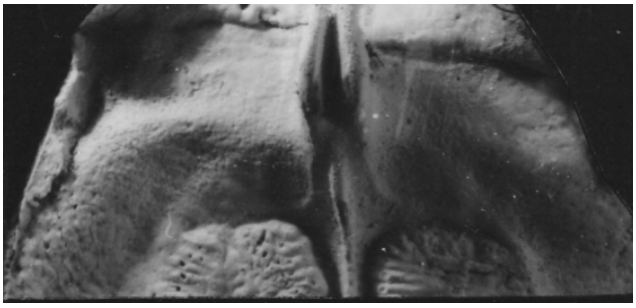


Fig. 25. *Lakismatia sparsispinosus* (Briggs), latex cast of dorsal interior, UQF 72796 from Fairyland Sandstone southeast Bowen Basin, x2. (Briggs 1979).

Aulostegid gen. and sp. indet.

Fig. 26

1984 Aulostegidae gen. indet. Campbell et al., Fig. 6.14.

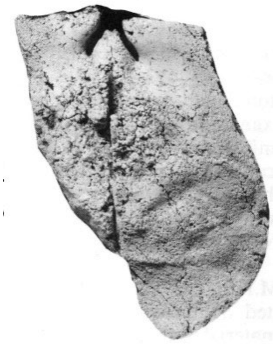


Fig. 26. Aulostegid gen. and sp. indet., dorsal internal mould BR 1644 x 1 from boulder at Stephens Island, New Zealand. (Campbell et al. 1984).

The internal mould of a dorsal valve BR 1644 was figured from a boulder in the Stephens Formation at D'Urville Island, to show two sturdy diverging buttress supports. These recall the short strongly diverging and robust buttress plates of a Nepal specimen figured by Waterhouse & Chen (2007, pl. 2, fig. 3). Moreover the dic of this Nepal specimen is convex, and surrounded by an outer concave shell, much as in the New Zealand specimen. The Nepal specimen was ascribed, with hesitation, to possible *Megasteges*, but Waterhouse & Chen expressed reservations. Ornament is not known for the New Zealand specimen, and the plates are exceptionally thickened, and diverge strongly. The age is likely to be late Early Permian (see Briggs & Campbell, 1993; Waterhouse 2021b). But a spectrum of possible identifications means that the species, genus and even family are indeterminate. In *Megasteges*, the buttress supports are normally close-set and subparallel, unlike those of the specimens from Stephens Island and Nepal, and the buttress supports approach those found in *Aulosteges*. (See Fig. 1 herein).

Subfamily **SEPTASTEGINAE** Waterhouse, 2002b

[Septasteginae Waterhouse, 2002b, p. 28]

Diagnosis: Dorsal buttress plates long in front of the cardinal process, extending outside the dorsal adductor scars.

Discussion: According to Grant (1976), *Septasteges* named for a species from Thailand is a junior synonym of *Bilotina* Reed, 1944, named for a species of the Salt Range India. This may or may not be correct. Unfortunately the dorsal interior of the Salt Range form, figured by Grant (1976) from silicified material, has lost its internal structures. Grant did establish that the report of a ventral septum in *Bilotina* by Reed (1944) and accepted by Muir-Wood & Cooper (1960) was incorrect – there is no median septum, which means in that regard it is close to the form from Thailand.

Tribe **SAEPTATHAERINI** new

Diagnosis: Dorsal buttress ridges long and well developed, each side of adductor scars, and commencing at the base of the cardinal process. No ventral median septum. Spines cover both valves, may have slightly elongate bases.

Genera include *Geniculatusia, Guadaluposteges, Koyaonoia*, *Saeptathaerus* and *Shuzhongia,* all named by Waterhouse.

Discussion: *Bilotina* Reed might belong, but the presence and nature of buttress plates is uncertain. The type species has a ventral septum according to Reed (1944) and Muir-Wood & Cooper (1960) to suggest Rhamnariinae, but this was not substantiated by Grant (1976, pl. 36, fig. 37-39). Unfortunately Grant's silicified dorsal valves (pl. 37, fig. 29, 30) fail to show the dorsal interior adequately. But Grant's excellent figures of what Waterhouse & Piyasin called *Septasteges* and named *Septasteges praeclarus* Waterhouse (2002b, p. 50) show high buttress plates developed from the buttress ridges, typical of Tribe Septastegini in Subfamily Septasteginae Waterhouse, 2002b**.** *Buxtoniella* Abramov & Grigorieva, 1986 of Visean age, has somewhat similar median dorsal ridges that diverge from a short double ridge in front of the cardinal process, Other authors have ignored the presence of long buttress ridges and assigned species to *Taeniothaerus*, but such examples have to be repositioned (Fig. 27, 28),.

Rhamnaria Muir-Wood & Cooper, 1960 differs in having shorter and more widely divergent buttress pates in front of the cardinal process, and in having a ventral median septum, as in *Minisaeptosa* Waterhouse, and *Ramavectus* Stehli, and possibly *Ramovsina* Sremac. *Shumardoria* Waterhouse has well-developed buttress ridges and what was called a well-developed myophragm between the ventral adductors. *Cactosteges* Cooper & Grant, 1975 and *Spuriosia* Cooper & Grant, 1975 were included in Rhamnariidae by its authors, and in Rhamnariinae by Brunton et al. (2000, p. 605) but display neither ventral septum nor long buttress ridges.

A B

Fig. 27. *Shuzhongia densipustulata* (Shen, Archbold, Shi & Chen). A, ventral valve holotype, NMV P148857, x1. B, dorsal interior, NMV P148859, x1, showing long buttress ridges, as arrowed. This species was originally ascribed to *Taeniothaerus*, and renamed *Shuzhongia,* as endorsed in Rong Jiayu et al. (2017, p. 713). From south Tibet. (Shen et al. 2000).

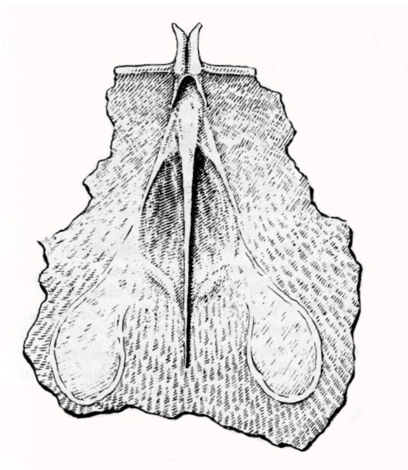


Fig. 28. *Taeniothaerus rusticus* Grunt, dorsal interior x1.4, showing the long buttress plates which are not developed in Taeniothaerinae. Sakmarian of Pamirs. The species apparently belongs to *Saeptathaerus.* (Grunt & Dmitriev 1973).

Genus ***Anechinotsia*** n. gen.

Derivation: an – not, without, echina – spiny, otos – ear, referring to ear brush of spines (Greek).

Diagnosis: Large shells both valves spinose, ventral spines with elongate bases. Dorsal buttress ridges extend each side of the adductor scars. Few posterior-lateral or ventral ear spines.

Type species: *Taeniothaerus anotos* Briggs, 1983 from Tiverton Formation, north Bowen Basin, Queensland, here designated.

Discussion: The dorsal interior is like that of *Saeptathaerus* (see below), but the ventral exterior differs in that the brush of spines is not developed over the ears. Despite the Briggs name of *anotos*, the type species is not without ears.

Anechinotsia anotos (Briggs, 1983)

Fig. 29, 30

1983 *Taeniothaerus anotos* Briggs *in* Waterhouse et al., p. 130, pl. 1, fig. 6-10.
1998 *Lipanteris anotos* – Briggs, p. 135.
2015a *L. anotos* – Waterhouse, p. 109, Fig. 59 - 61.

Holotype: UQF 72790 from Fairyland Tiverton Formation, figured in Briggs (1983, pl. 1, fig. 6, 7), Waterhouse (2015a, Fig. 59A, B) and Fig. 30A, B herein, OD.

Stratigraphy: The species is found in the upper middle Tiverton Formation of the north Bowen Basin in Queensland.

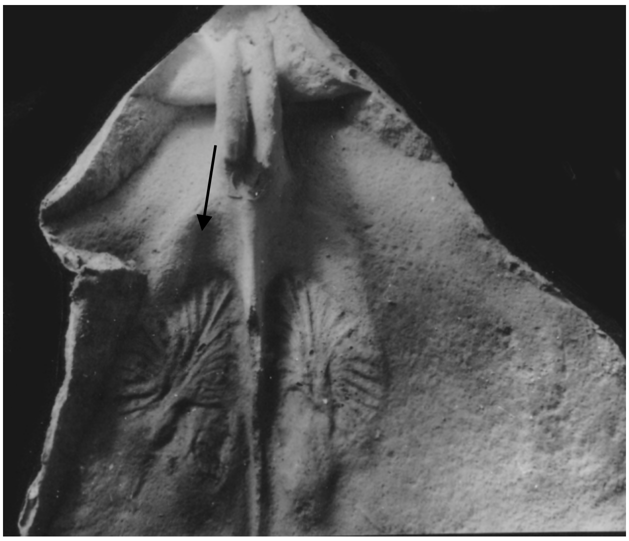


Fig. 29. *Anechinotsia anotos* (Briggs), latex cast of dorsal interior showing low buttress plates, as arrowed, UQF 72786, x 1.8. Tiverton Formation. (Briggs 1979).

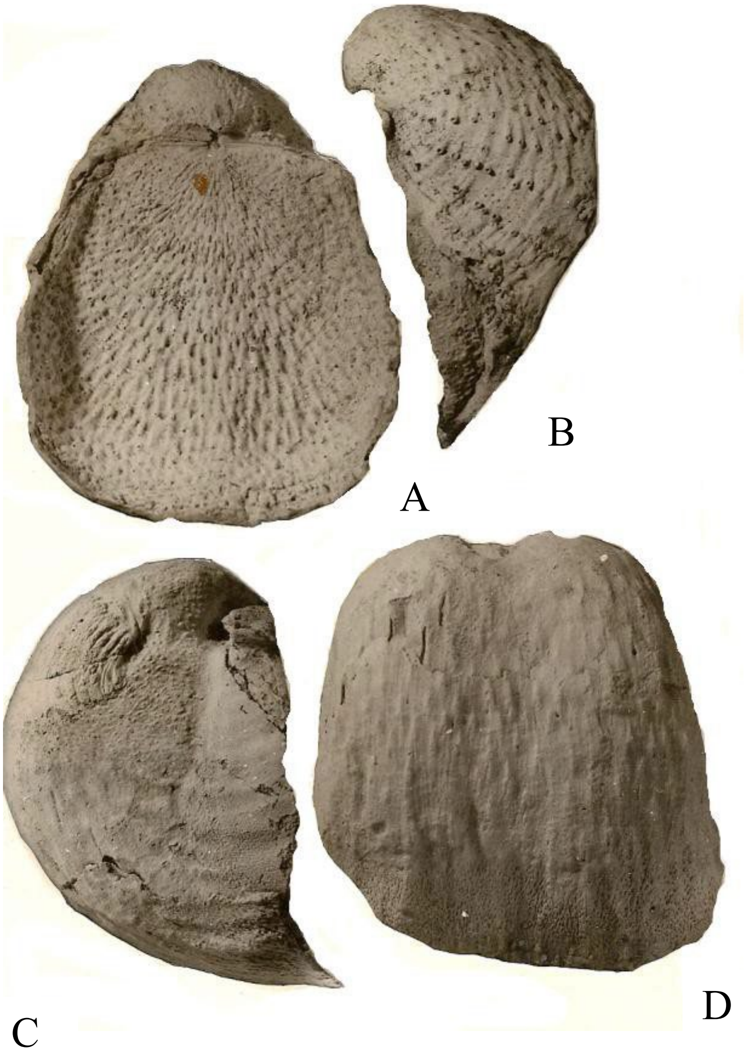


Fig. 30. *Anechinotsia anotos* (Briggs). A, B, dorsal and lateral aspects of holotype UQF 72790, x1. C, D, lateral and ventral aspects of internal mould UQF 72787, x 1. From upper middle Tiverton Formation. (Briggs 1983).

Genus ***Carilya*** Archbold, 2001

Fig. 31A

Diagnosis: Large subquadrate shells with shallow ventral sulcus, both valves covered by uniformly very fine spines which may arise from low ridges.

Holotype: *Taeniothaerus miniliensis* Coleman, 1957, p. 96 trom the Wandagee Formation, Carnarvon Basin, Western Australia, OD.

Discussion. The presence or absence of buttress plates is not entirely clear. Coleman (1957, pl. 13, fig. 7, 9) shows dorsal interiors with very low ridges passing forward from the lateral ridge-like flanks of the cardinal process, which could be subdued buttress plates, but reservations may be retained pending first-hand examination. *Miniliconcha* Waterhouse 2004, p. 71) was proposed for the same species and so is an objective synonym. *Balkhasheconcha* Lazarev, 1985, p. 68 [66] has fine and numerous crowded spines. It is of Upper Carboniferous age in northeast Russia, but has much more closely associated and long buttress plates.

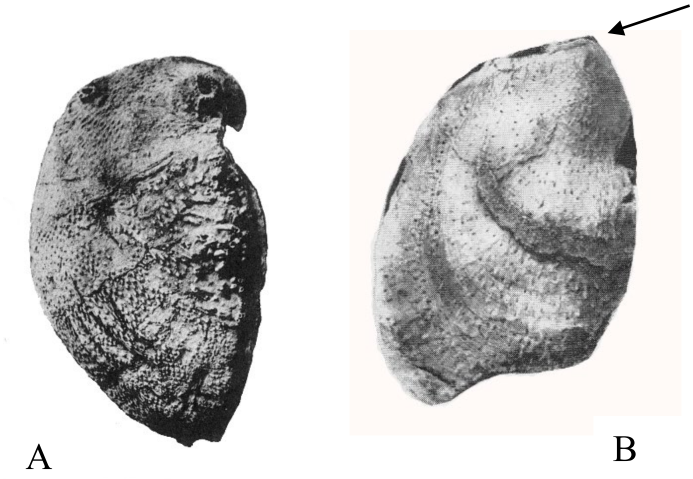


Fig. 31. A, *Carilya miniliensis* (Coleman), lateral aspect of ventral valve, x1, from Wandagee Formation, Carnarvon Basin, Western Australia. (Coleman 1957). B, *Carilya*? sp. A, external mould of part of a dorsal valve UQF 43047 x1 from Yarrol Formation, Yarrol Basin, Queensland. Cardinal process arrowed. (Maxwell 1964).

***Carilya*? sp. A**

Fig. 31B

1964 *Taeniothaerus subquadratus* [not Morris] – Maxwell, p. 44, pl. 7, fig. 35.
1998 *T. farleyensis* [not Briggs] – Briggs, p. 136.

Briggs (1998) referred a Yarrol specimen of Maxwell (1964, pl. 7, fig. 35) to *Taeniothaerus farleyensis*, but it has much finer and denser spines, and possibly approaches *Carilya* Archbold, 2001b.

***Carilya*? sp. B**

1982 ?*Taeniothaerus* cf*. miniliensis* Coleman – Waterhouse, p. 41.

An unregistered ventral valve reported from the upper Takitimu Group of New Zealand was considered to be of similar shape and ornament to *Carilya miniliensis*. It is of much the same age, at Baigendzinian - upper Artinskian.

Genus ***Saeptathaerus*** Waterhouse, 2002a

Fig. 32, 33

Diagnosis: Medium large shells with wide hinge and high wide ventral interarea, gently concave dorsal valve. Ventral spines with short bases, ear-brush of spines. Two buttress ridges diverge, lying outside the dorsal adductor scars.

Type species: *Saeptathaerus fairbridgei* (Coleman, 1957, p. 40) from Hardman Member, Western Australia, OD (Waterhouse 2002a, p. 230).

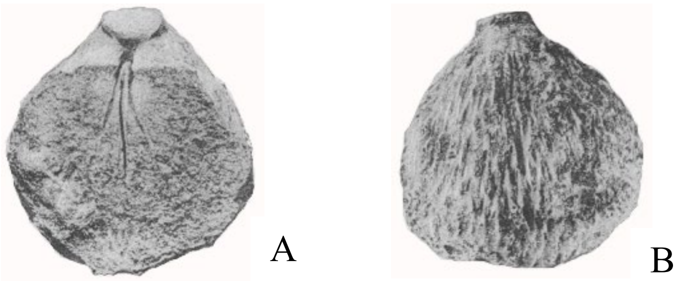


Fig. 32. *Saeptathaerus fairbridgei* (Coleman). A, B, dorsal and ventral aspects of topotype internal mould UWA 29438b, x1. Hardman Member. (Coleman 1957).

Genus *Colemanosteges* Waterhouse (2002b, p. 49) from the same member looks somewhat similar but has clusters of fine erect spines and the buttress supports are close-set, though flaring anteriorly (Fig. 33).

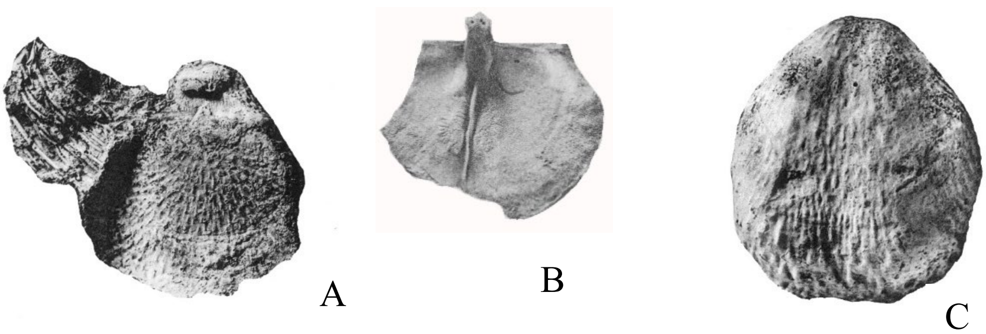


Fig. 33. *Colemanosteges fletcheri* (Coleman). A, dorsal aspect of specimen UWA 24444 with valves conjoined, x0.6. B, posterior dorsal valve with cardinal process, CPC 1955, x2. C, ventral valve UWA 29427, x0.75. A, C, Hardman Member, B, Liveringa Formation, Western Australia. (Coleman 1957).

Saeptathaerus acanthophorus (Fletcher, 1945)

Fig. 34, 35

1945 *Aulosteges acanthophorus* Fletcher, p. 314, pl. 23, fig. 1-3.
1950 *Aulosteges* (*Taeniothaerus*) *subquadratus* var. *acanthophorus* – Hill, p. 7, pl. 2, fig. 3-4, ?5a, b, ?6a, b.
1964 *Taeniothaerus subquadratus* var. *acanthophorus* – Hill & Woods, pl. 5, fig. 3 (part, not fig. 4 = ?*homevalensis*).
1972 *T. subquadratus* [not Morris] – Hill, Playford & Woods, pl. 5, fig. 3 (part, not fig. 4 = ?*homevalensis*).
1998 *T. subquadratus* – Briggs, pp. 139, 140 (part).

Diagnosis: Large subquadrate shells with shallow sulcus and low dorsal fold, moderately wide hinge, ventral spines coarse for genus, tend to be well-spaced over disc, well-developed halteroid brush, coarse elongate spine ridges, intermixed with fine prostrate spines, spines usually erect anteriorly. Erect and semi-recumbent spines on dorsal valve. Lateral buttress ridges low.

Holotype: UQF 10747 figured by Fletcher (1945, pl. 23, fig. 1-3), Hill (1950, pl. 2, fig. 3) and Fig. 34A-C herein from Riverstone Sandstone Member, Cattle Creek Formation, OD.

Morphology: Briggs (1983, 1998) and Parfrey (1983) synonymized the taxon *acanthophorus* Fletcher, 1945 from the lower Cattle Creek Formation with *Taeniothaerus subquadratus*. The two certainly look similar, and the spacing of the ventral spines is close to that of Berriedale specimens of *subquadratus,* but spine bases are less prolonged. The type specimen of *acanthophorus* and specimen UQF 1994 (Hill 1950, pl. 2, fig. 4) have short spine-bases that swell to a width of 1.5mm and comparably coarse semi-recumbent ventral spines, which appear to be less regularly disposed over the venter than in Tiverton *subquadratus*. The spines making up the lateral brush are fewer than in typical *subquadratus*, but are close-set (Fletcher 1945, pl. 23, fig. 1-3; Hill 1950, pl. 2, fig. 3-6; Hill & Wood 1964, pl. P5, fig. 3; Hill, Playford & Wood 1972, pl. P5, fig. 3). Ventral anterior spines are coarse. Spine bases are coarse and elongate (often 5mm), less regularly in quincunx than in *subquadratus*, and erect anteriorly, and they are mixed with more slender and subprostrate spines. The dorsal exterior of *acanthophorus* is poorly preserved and dorsal spines appear to involve sets of erect and semi-recumbent spines, whereas dorsal spines are uniform and erect or high-angle recumbent on *T. subquadratus* from Homevale. The dorsal interior figured by Fletcher (1945, pl. 23, fig. 2)

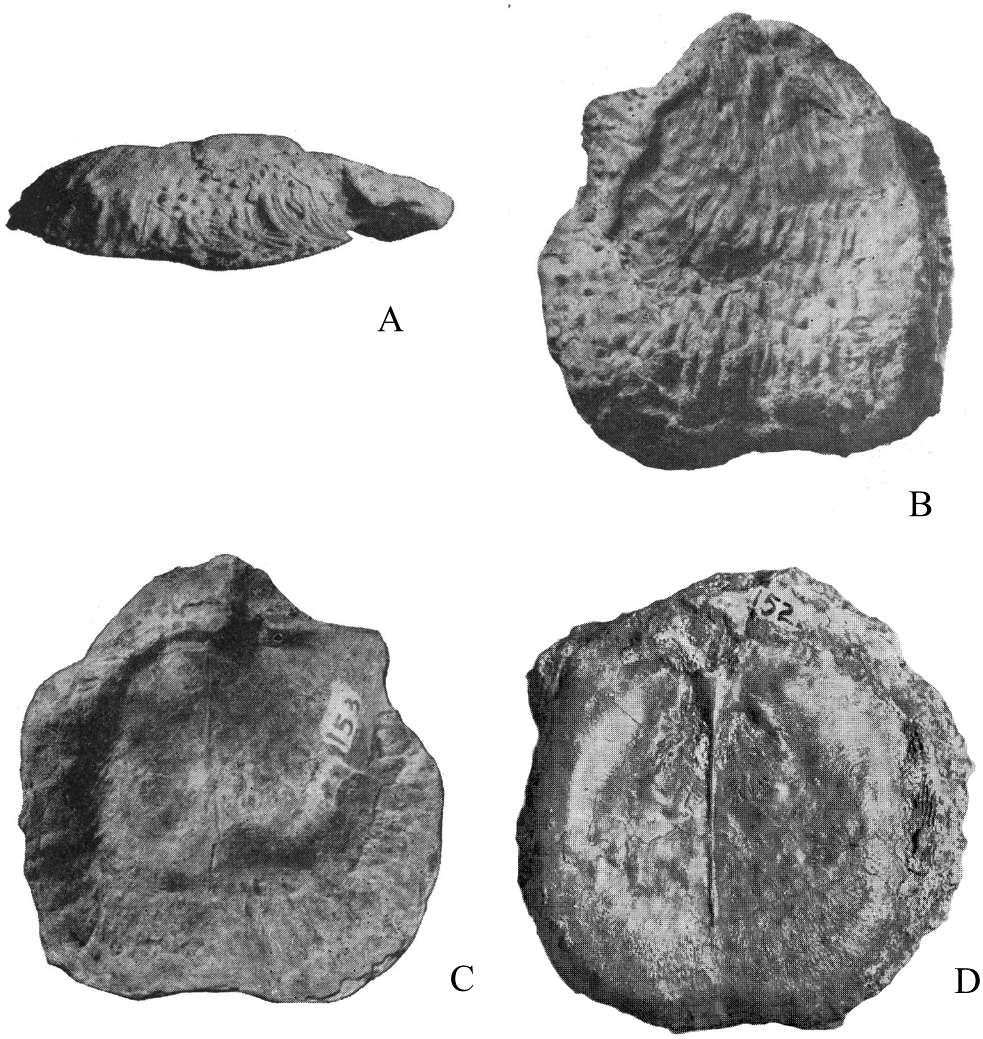


Fig. 34. *Saeptathaerus acanthophorus* (Fletcher). A-C, lateral, ventral and dorsal aspects of holotype, UQF 10747. D, dorsal interior UQF 152. Specimens x1 approx., from Riverstone Formation, southwest Bowen Basin. A-C, Hill 1950; D – Fletcher 1945).

suggests the presence of lateral buttress plates, a feature absent from *Taeniothaerus*, but present in *Saeptathaerus* Waterhouse, 2002a, p. 230. The species *acanthophorus* appears closest to *Saeptathaerus*, given the similarity in spines and the presence of lateral buttress plates.

Fragments figured by Hill (1950, pl. 2, fig. 5a, b) are too small to be identified with confidence, and need not belong to *acanthophorus*, though they come from much the same stratigraphic horizon. On one, there are buttress supports which converge anteriorly as in *Taeniothaerus*.

Fig. 35. *Saeptathaerus acanthophorus* (Fletcher). A, ventral valve UQF 72728 from Lizzie Creek Volcanics, north Bowen Basin. B, ventral valve UQF 21667 from Cattle Creek Formation, Reid's Dome, southwest Bowen Basin.. Specimens x1. Briggs (1979).

Material from the Yarrol Basin includes specimens UQF 12413-4 labelled *Aulosteges* (*Taeniothaerus*) *subquadratus* var. *acanthophorus* (Fletcher) as identified by Fletcher (1945, p. 315) from UQL 591 at Yarrol Station above the Burnett River bank west of the homestead. A ventral fragment shows evenly spaced semi-recumbent to erect spines 0.7 to 1.2mm in diameter, with small or no posterior bases, and more close-set anteriorly. The dorsal valve has dense fine spines 0.2-0.4mm in diameter, most prostrate but a number erect. A high blade is suggested in the dorsal shell structure, and appears to be a medium septum.

Saeptathaerus homevalensis (Briggs, 1983)

Fig. 36 - 38

1909 *Productus subquadratus* [not Morris] – Etheridge & Dun, p. 300, pl. 41, fig. 2-5 (part, not fig. 1 = *subquadratus*).
1950 *Aulosteges* (*Taeniothaerus*) *subquadratus* – Hill, p. 6, pl. 5, fig. 1, 2 (part, not pl. 1, fig. 1 = *subquadratus*; not pl. 6, fig. 4 = *farleyensis* Briggs).
1964 *T. subquadratus* – Hill & Woods, p. 10, pl. P5, fig. 5, 6.

1964 *T. subquadratus* var. *acanthophorus* [not Fletcher] – Hill & Woods, pl. P. 5, fig. ?4 (part, not pl. P5, fig. 3 = *acanthophorus*).
1972 *T. subquadratus* – Hill, Playford & Woods, p. 10, pl. P5, fig. ?4, 5, 6 (part, not fig. 3 = *acanthophorus?*).
1974 *T. subquadratus* – McCarthy et al., Fig. 4c.
1983 *T. homevalensis* Briggs, p. 127, pl. 2, fig. 1-7.
1986 *T. homevalensis* – Parfrey, p. 59, Fig. 2.1a, b.
1998 *T. homevalensis* – Briggs, p. 137, Fig. 67A, B.
2015a *T. homevalensis* – Waterhouse, p. 105, Fig. 55, 56.
2015b *T. homevalensis* – Waterhouse, p. 131, Fig. 49, 50A, C, D.

Diagnosis: Distinguished by body spines largely of one series and finer than those of *subquadratus*, few if any interspersed finer spines, spine ridges short, closely spaced for genus, well-defined lateral halteroid brush of spines, broad low fold on dorsal valve, with spines in single series, erect or high-angle recumbent. Low low widely diverging buttress plates.

Holotype: UQF 72738 from Tiverton Formation, figured in Waterhouse et al. (1983, pl. 2, fig. 1-7) and Fig. 37A-G herein, OD.

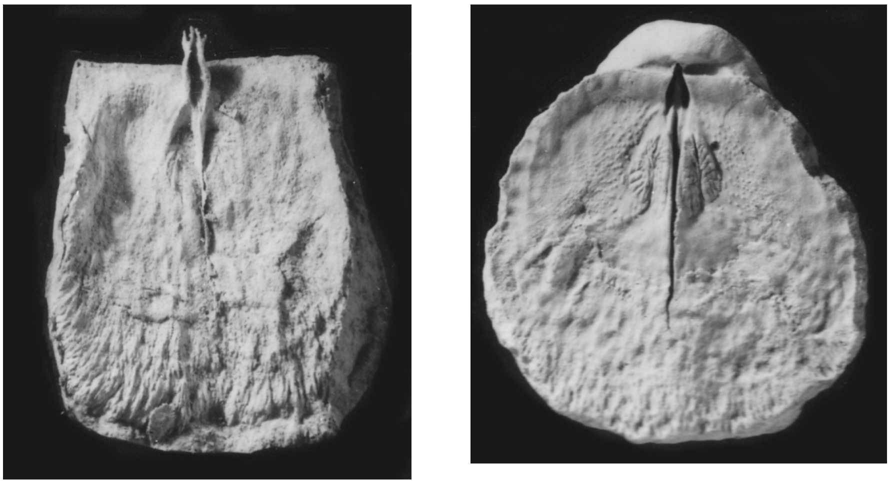


Fig. 36. *Saeptathaerus homevalensis* (Briggs). A, dorsal valve UQF 72729 from Lizzie Creek Volcanics, x1. B, dorsal internal mould, UQF 72736, from Tiverton Formation. Specimens x1 from north Bowen Basin. (Briggs 1979).

Morphology: Briggs (1979, 1983, 1998) ignored or overlooked the nature of the dorsal interior in his proposal of *homevalensis*, not recording the inner pair of buttress ridges, though they are shown in his 1979 photographs and one of his original published figures. Externally, this species is close in overall shape to *Taeniothaerus subquadratus*, and was distinguished primarily

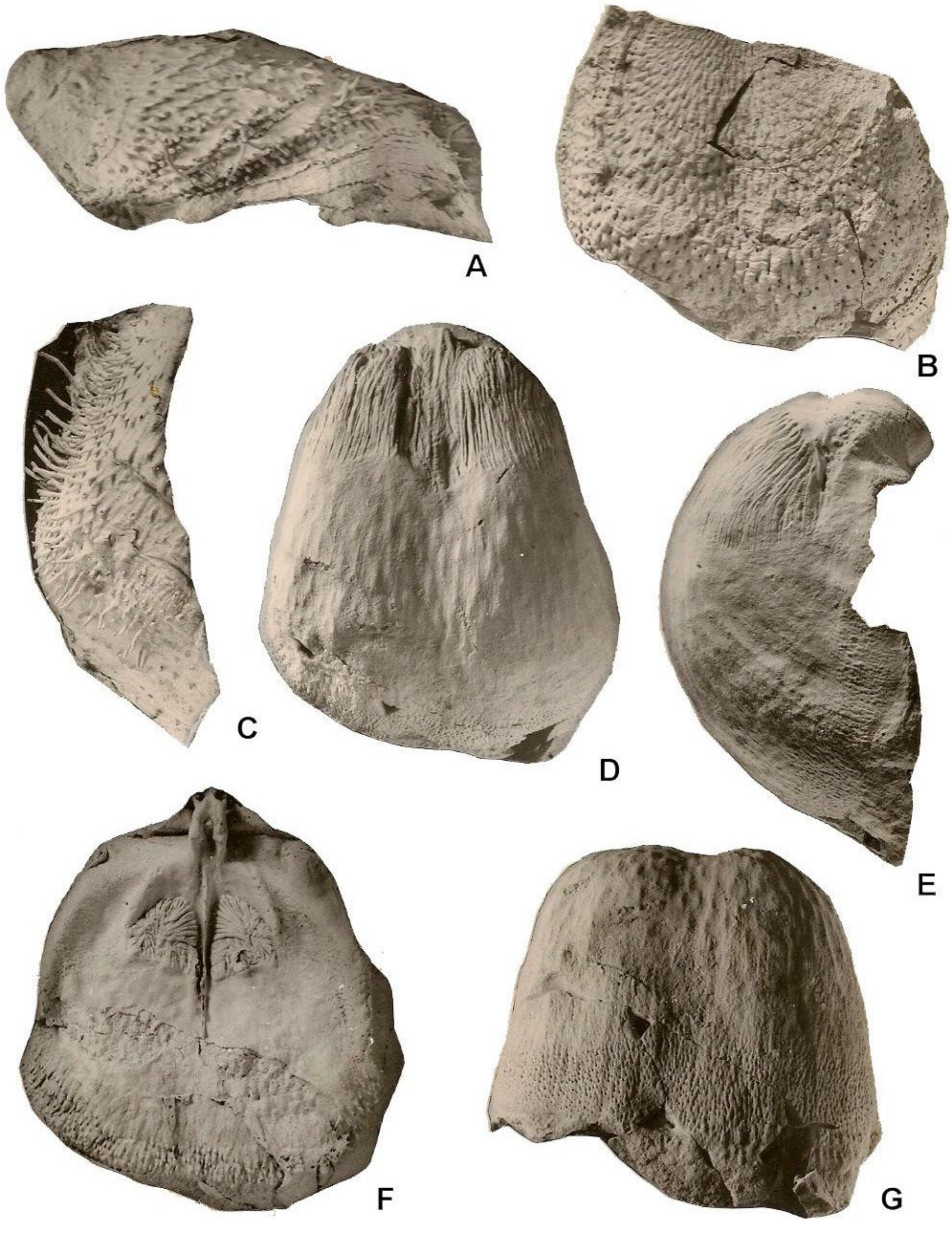


Fig. 37. *Saeptathaerus homevalensis (*Briggs). Holotype UQF 72738, x0.75. A, C, lateral and ventral view of ventral exterior. B, dorsal external mould. D, E, G, ventral, lateral and anterior aspects of ventral internal mould. F, latex cast of dorsal interior. From upper middle Tiverton Formation. (Briggs 1983).

through its ventral spines that are rarely up to 0.8mm in diameter, according to Briggs, as compared with coarser spines up to 1.4mm in diameter over the disc anteriorly and in the lateral halteroid brushes of *subquadratus*. Spine bases are less closely spaced and coarser in

T. subquadratus, especially over the dorsal valve and anterior ventral valve spines are 0.4-0.5mm in diameter in *homevalensis*, thinner than in *subquadratus*, and they vary in spacing and distribution over different specimens, and may cover all of the valve, or lie concentrated over the anterior disc and trail, often in commarginal rows, erect or high-angle recumbent. Spines may be thick or thin in the halteroid brush, and the spine bases are more crowded, lower and thinner than in specimens assigned to *Taeniothaerus subquadratus*.

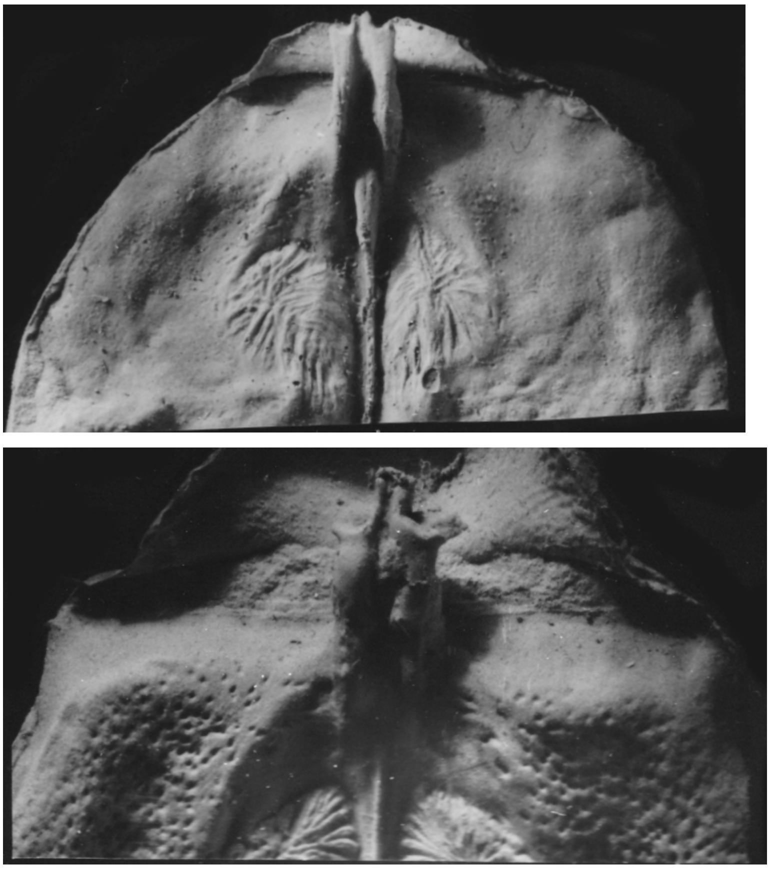


Fig. 38. *Saeptathaerus homevalensis* (Briggs). A, posterior view of dorsal interior, latex cast UQF 72732 x1 From bed 11 of Campbell 1961. B, posterior view of dorsal interior, latex cast UQF 72733 from Campbell's bed 12. Tiverton Formation, north Bowen Basin, Queensland. (Briggs 1979). See also Briggs (1998, Fig. 67A, B).

Stratigraphy: Collections come from the upper middle Tiverton Formation at UQL 4517-4520, as well as UQL 1630 and 2631, but it is difficult to differentiate species without knowledge of the interior, and good preservation for the ornament. Briggs (1998) limited the species to UQL 4517-

4519, but such limitations do not reflect the nature of the material. Present collections, although imperfect, show some range in density and diameter of spines and in density, width and length of spine bases. *Saeptathaerus homevalensis* is represented by large specimens (UQF 46685, 46713, 46714, 46716, 46717) with well formed ventral sulcus and comparatively coarse spines in the Teebar Formation of Cranfield (1989) near Gigoomgan north of Gympie at Teebar Creek, recorded as being "on the north bank of Ten Chain Road", and another as "half a mile north of Glenbar Station" as elaborated in Waterhouse (2015b).

Saeptathaerus*? *farleyensis (Briggs, 1998)

Fig. 39 - 41

1909 *Productus subquadratus* [not Morris] – Etheridge & Dun, p. 9 (part).
1950 A*ulosteges* (*Taeniothaerus*) *subquadratus* [not Morris] – Hill, p. 6, pl. 6, fig. 4 fide Briggs 1998 (part, not pl. 1, fig. 1 = *subquadratus*; pl. 5, fig. 1, 2 = *homevalensis*).
1998 *Taeniothaerus farleyensis* Briggs, p. 136, Fig. 69A-F.
1998 *T. homevalensis* [not Briggs] – Briggs, p. 137 [referred the specimen of Hill 1950, pl. 6, fig. 4 to *homevalensis,* and on the same page, and p. 136, the same specimen to *farleyensis.*
2013 *T. farleyensis* – Waterhouse, p. 277, Fig. 10.5-10.7.
2021 *T. farleyensis* – Waterhouse, p. 110, Fig. 5, 6.

Diagnosis: Large with shallow ventral sulcus and low fold, beak not distorted, interarea well-formed, also developed in dorsal valve, ventral spine bases long and slender, dorsal ornament of elongate dimples and crowded fine spines with subdued bases.

Holotype: UQF 75291 from Farley Formation, Sydney Basin, New South Wales, Australia, figured by Briggs (1998, Fig. 69A, B, D), OD.

Generic position: The interior of the dorsal valve is rarely preserved for this species and the only figure available is that provided for a specimen from the Lakes Creek Formation of eastern Queensland, which is nowhere near topotype material and indeed appears to be a little younger than type material, although some uncertainy remains because of the inadequate information on precise stratigraphic position and nature of accompanying fauna . The one dorsal interior that is available, as refigured herein as Fig. 41A, suggests two low buttress supporting ridges leading forward from the lateral cardinal process.

Morphology: Ventral ornament over the umbo consists of fine erect spines 0.4-0.5mm in diameter, and erect spines lie up to 2-3mm apart along commarginal rows up to 7mm apart anteriorly, reaching a diameter of 0.8mm, but usually slightly less. Very low spine ridges extend

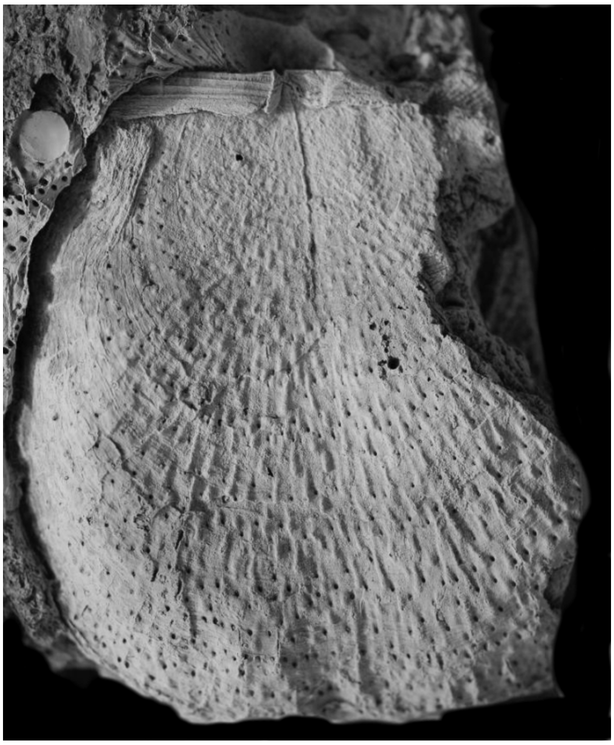


Fig. 39. *Saeptathaerus*? *farleyensis* (Briggs), external mould of dorsal valve and ventral beak UQF 13543 from Nerimberah Quarry, Lakes Creek Group, Queensland, x1. (Waterhouse 2013)

posteriorly towards the preceeding spine row, 3mm up to 7mm long: they gradually increase forward in height and width to terminate anteriorly where the spine projects out from the shell. Some ridges are present without spines. Dorsal spines are fine over the entire valve, anteriorly becoming as coarse as those of the ventral valve, up to 2 to 2.5mm apart along rows 2-4mm apart. Spine-bases are less conspicuous than in the ventral valve, but intervening dimples are well-formed and elongate.

Saeptathaerus? *farleyensis* is strongly arched, and although Briggs (1998) stressed that the hinge of *farleyensis* was unusually short, this is not confirmed from the figure of the holotype UQF 75291 (Briggs 1998, Fig. 69B) According to the Briggs' text, ventral spines in *farleyensis* are usually 0.6mm in diameter and dorsal spines are 0.3-0.4mm in diameter, compared with up to 0.8mm in the ventral valve and 0.4-0.5mm in the dorsal valve of *homevalensis* Briggs, 1983, but spines are up to 1mm in diameter with bases 3-5mm long in the *farleyensis* topotype UQF 75290 (Briggs 1998, Fig. 69F). Over the ventral ears, spine bases are only 0.6mm thick in UQF 75289, and form rows of closely spaced spines in curtains, but another external mould has more numerous spines, and those of UQF 75292 have many fine spines in clumps. The

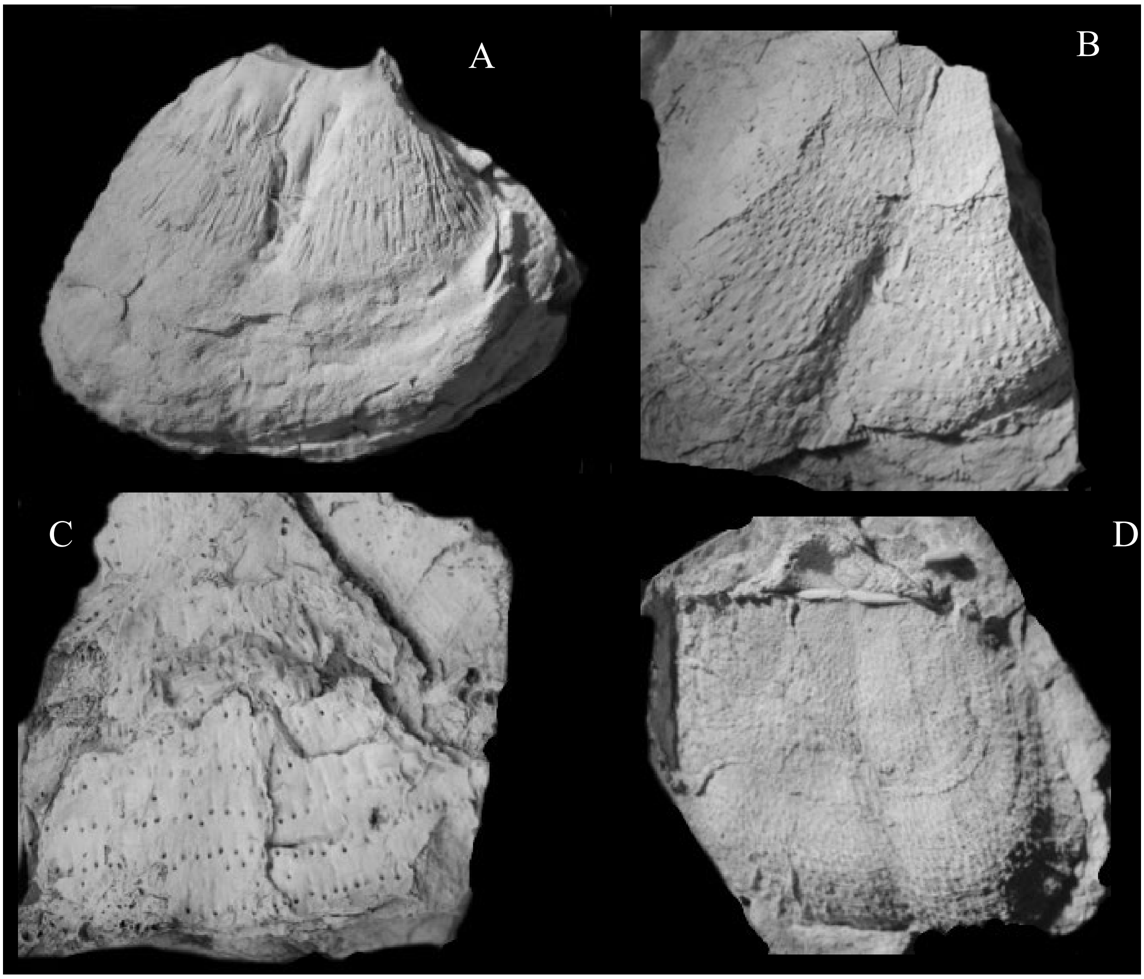


Fig. 40. *Saeptathaerus*? *farleyensis* (Briggs). A, ventral internal mould UQF 13540, x0.66. B, dorsal external mould UQF 26439, x0.66. C, external mould of ventral valve UQF 26439, x0.75. D, dorsal external mould with ventral umbo, UQF 13535, x0.66. From Lakes Creek Group, east Queensland. (Waterhouse 2013).

spine-bases as figured for *farleyensis* are not as as coarse as those over the venter of *homevalensis*, but are just as numerous. On the other hand, dorsal spines are finer and spaced further apart in *farleyensis*, and the dorsal valve is less dimpled, and the ventral muscle field smaller.

Stratigraphy: Adequate information on the stratigraphic position of type *farleyensis* was not provided by Briggs, and may not be available. The specimen figured by Hill (1950, pl. 6, fig. 4) from Lakes Creek, Rockhampton, was referred by Briggs (1998, pp. 136, 137) to both

Taeniothaerus farleyensis and to *T. homevalensis.* The specimen is judged to belong to *farleyensis* (Waterhouse 2021, p. 110 ff). Further material is also found in the Lakes Creek Group, Rockhampton, Queensland, Australia. (See Crouch & Parfrey 1998, p. 17).

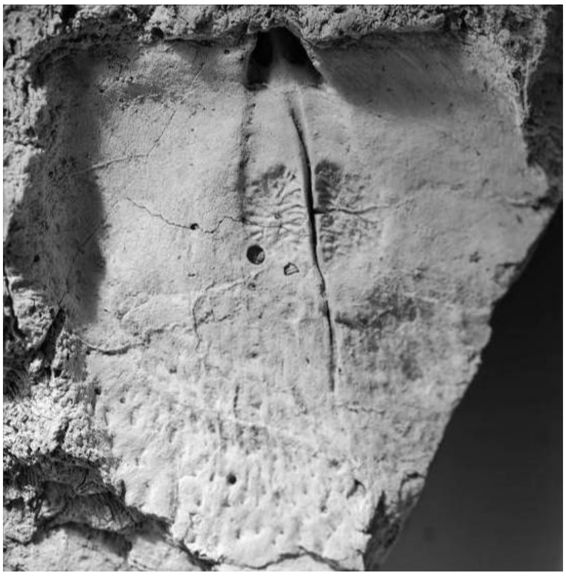


Fig. 41. *Saeptathaerus*? *farleyensis* (Briggs). A, dorsal internal mould UQF 13534 from Lakes Creek Group, Queensland, x1. (Waterhouse 2013). B, latex cast of anterior ventral valve, UQF 75290 x1 from Farley Formation, New South Wales. (Briggs 1998).

A ventral valve from Cessnock, New South Wales, figured as *Reedoconcha* sp. by Briggs (1998, Fig. 68) is badly preserved and poorly known. It has very long spines bases stated to exceed 15mm in length, suggestive of an approach to *farleyensis* Briggs. *Reedoconcha* Kotlyar, 1964 is supposedly distinguished by the lack of a ventral interarea (Waterhouse 2013, p. 281), but Briggs did not record whether an interarea was present or absent, though he did state that the ventral umbo did not extend far beyond the hinge. His figures do not clarify the situation.

Briggs (1998, p. 137) stated that *Taeniothaerus* cf. *subquadratus* of Coleman (1957, p. 15, pl. 9, fig. 8-12) from the basal High Cliff Sandstone of the Perth Basin was somewhat like *farleyensis*. The cited figures in Coleman shows shells identified as *Marginifera gratiodentalis* Grabau. In the same paragraph, he referred to *T.* cf *subquadratus* of Coleman (1957, p. 15, pl. 9, fig. 8-12), stating that fine spines were visible laterally in fig. 8 like those of *farleyensis*. Although he referred to Coleman 1957, p. 15, that page has only a diagrammatic cross-section of *Taeniothaerus* (Coleman 1957, Fig. 3.1). The correct page in Coleman (1957) for cf. *subquadratus* is p. 102.

Genus ***Reedoconcha*** Kotlyar, 1964

Fig. 42A

Diagnosis: Ventral interarea low, ventral ornament of long spine ridges, spines said to include halteroid brushes. Buttress supports preserved in dorsal valve.

Type species: *Productus* (*Taeniothaerus*) *permixtus* Reed, 1932 from Nagmarg Formation, Kashmir, OD.

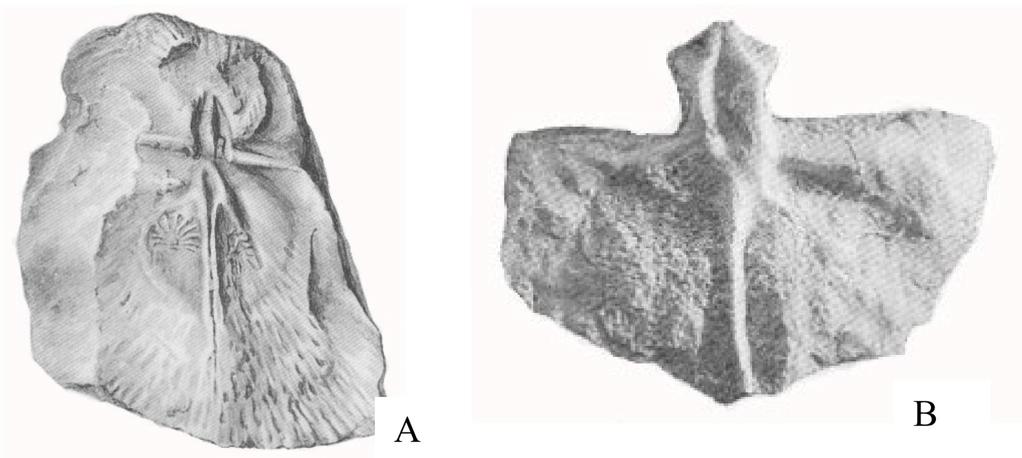


Fig. 42. A, *Reedoconcha permixtus* (Reed), dorsal aspect of internal mould showing buttress plate. From Agglomeratic Slate, Kashmir, x1. (Reed 1932). B, taeniotherin x2, dorsal interior suggesting absence of anterior buttress plates, though identified as *Reedoconcha*. Perhaps the interior has been worn, to remove the buttress ridges. Saiwan Formation, Oman. (Brunton et al. 2000).

Discussion: To Briggs (1998) goes the credit of recognizing a possible occurrence of this genus in the north Sydney Basin. Principal indication of the genus as far as the ventral valve is concerned appears to be the presence of only what at best must be a very low ventral interarea.

Brunton et al. (2000, p. 587, Fig, 419a-f) stated that the interarea was short, occupying only half the width of the hinge, but did not state that the interarea was very low.

?Reedoconcha sp.

Fig. 43

1909 *Productus subquadratus* [not Morris] – Etheridge & Dun, p. 9.
1998 *Reedoconcha* sp. Briggs, p. 133, Fig. 68A-C.

A single possible specimen is available, illustrated by Briggs (1998), but , inadequately known. It comes from the Lochinvar Anticline in the north Sydney Basin, with matrix thought by Briggs to match that of the Farley Formation. He compared the spine ridges with those of a fragment from the Jimba Jimba Calcarenite in the Carnarvon Basin of Western Australia that had been identified as *Reedoconcha*? sp. by Archbold & Shi (1993, Fig. 3A). Only the exterior of a ventral valve was shown. There must be severe reservations about the reality of both identifications, because for generic and familial placement, knowledge of the dorsal interior is essential. The dorsal valve shows that the Reed species is saeptothaerin (Fig. 42A), not taeniothaerin, but without the dorsal valve of the Farley and the west Australian species, there at present seems little hope of determining even the subfamily allegiance. There is no surety that specimens so far reported from Western Australia or New South Wales belong to *Reedoconcha*.

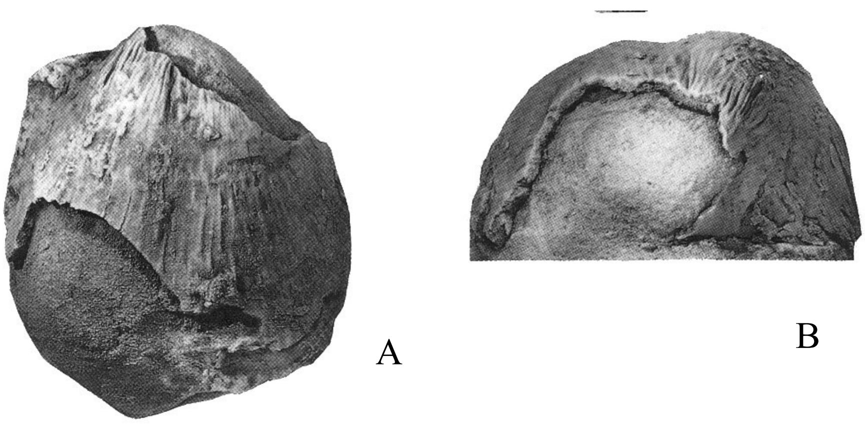


Fig. 43. *Reedoconcha* sp. A, B ventral and posterior aspects of ventral valve MMF 8044 x1 from Farley Formation, Sydney Basin. (Briggs 1998).

FOSSIL LOCALITIES

UQL no. Description of localities in Tiverton Formation, north Bowen Basin, Queensland.

Colllection by K. S. W. Campbell & G. W. Tweedale

1630 Homevale bed no. 13.

Collection by F. W. Whitehouse.

2631 Homevale Bed 11. Upper part of middle of three ridges, extending down its SW flank, to the bench.

Collections by P. Balfe , D. J. C. Briggs & J. B. Waterhouse

4515 2m stratigraphic thickness at gulch NE of molasses tank. Abundant *Capillonia armstrongi.*

4517 Road leading to molasses tank on Homevale fossil hill.

4518 3m including 0.7m calcareous bed below road leading to molasses tank.

4519 5-6m stratigraphic thickness up the hill bearing the molasses tank.

4520 Base of the hill bearing the molasses tank.

More information is provided on these localities by Campbell (1961) and Waterhouse (2015a).

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FLAWS IN THE BRIGGS SCHEME FOR MACRO-FAUNAL ZONATION OF THE PERMIAN IN EAST AUSTRALIA

Abstract

The scheme proposed by Briggs (1998) for dividing the marine Permian of east Australia into macro-faunal zones, mostly on the basis of selected Productida, is appraised, on the basis of preceeding and more recent studies. It is concluded that there were too many errors and wrong assumptions to encourage use of the scheme, and that there are better alternatives.

INTRODUCTION

Briggs (1991, 1998) proposed to subdivide the marine Permian deposits of east Australia into twenty one biozones. The scheme is far from adequate. Some workers have adopted the scheme, possibly in denial that many of the Briggs species are based on Queensland Museum specimens that were improperly never returned. They had been ascribed to collections in the Australian Museum, and have since “disappeared” so that technically, several of his key species could be regarded as nomen nuda. Not to mention collections from other institutions, “borrowed”, and never returned. And beyond those difficulties, several of the proposed zones do not withstand close scrutiny. Misidentifications, inadequate documentation, and incorrect representations of the stratigraphic succession litter the Briggs model, to the extent that even if the Briggs species could be properly sustained with collections safely esconsed in a trusted institution – and one still hopes that may be possible – the Briggs model is simply not good enough but is deeply flawed. Partly this is due to misconceptions over the range and dispersal of some brachiopod species, and partly due to his unwarranted dismissal of the correlation value for so many fossil species, not only amongst Brachiopoda, but many Mollusca as well, with the value of Foraminifera, and Bryozoa still largely unexplored.

DISCUSSION OF EACH BRIGGS ZONE

In this overview, each of the Briggs zones will be briefly discussed in order of age.

***Lyonia bourkei* Zone**

The zone is based on a very few species, with uncertain stratigraphic support, as made clear by Briggs (1998, p. 23) in a realistic appraisal. The proposed zone is yet to be consolidated.

***Strophalosia concentrica* Zone**

Thanks to studies in Tasmania by Clarke, completed in 1990 and 1992, a faunal assemblage zone was recognized (Waterhouse 1987) that is reliably of Early Permian age. Briggs (1998, p. 28) endorsed the correlation value of *Eurydesma burnettensis* Waterhouse, 1987b, noting its presence not only in the Yarrol Basin and in the lower *Strophalosia concentrica* beds in the Quamby Group of Tasmania but in the Lochinvar and Cranky Corner beds of New South Wales. The nominate species *Strophalosia concentrica* is referred to *Strophalosiaria*. (See herein, p. 9).

***Strophalosia subcircularis* Zone**

This zone too is based on studies by Clarke (1969, 1990, 1992) in Tasmania, with recognition by Runnegar (1969) and Waterhouse (1987). The nominate species is now referred to *Crassispinosella.* (See herein, p. 10).

***Bandoproductus walkomi* Zone**

First recognized as the *Bandoproductus macrospina* Zone (erroneously miscalled *crassicostata* in Waterhouse (1987, p. 197), Briggs (1998, p. 31) substituted his own species, *B. walkomi* as name-giver, though in my opinion *walkomi* which occurs widely with *macrospina* is no more than a subspecies, and Briggs (1987) had earlier confused the taxon with *Auriculispina*. Fuller documentation of the macro-faunal content was provided eventually and the stratigraphic place in the faunal succession clearly indicated by Waterhouse (2015b, pp. 44-73) in a monograph on the Permian faunas near Gympie in southeast Queensland, whereas Briggs (1998) placed most emphasis on scattered and somewhat obscure occurrences in New South Wales.

***Tomiopsis strzeleckii* Zone**

This zone was interpreted by Briggs (1998) from deposits and faunas in the upper Rammutt Formation near Gympie, southeast Queensland, as recorded in preliminary fashion by Waterhouse & Balfe (1987). Briggs (1998) accepted the improper designation by McClung (1978) of the taxon *strzeleckii*, despite the challenge by Campbell (1960, p. 1111) who concluded that the specimens designated as *strzeleckii* by Koninck definitely differed from the specimens treated as *strzeleckii* by McClung. The Gympie zone with McClung's so-called *strezleckii* was interpreted by Waterhouse (2015b) as correlative with the *Strophalosia subcircularis* Zone of Clarke (1990), thanks to a few brachiopods, including *Permasyrinx allandalensis* (Armstrong, 1970) and a number of bivalves, shared with the Allandale Formation (Waterhouse 2015b), to indicate that the so-called *strzeleckii* zone was not separate from the Allandale or *Strophalosia subcircularis* entity, and is to be regarded as

	***Echinalosia preovalis* Zone**	**Zone extended far beyond range of key species.**
?	***Echinalosia warwicki* Zone**	**Probably overlaps much or all of *Echinalosia curvata* Zone of Waterhouse (1987 etc.).**
	***Echinalosia curtosa* Zone**	**As establshed by Waterhouse (1987b).**
	***Tomiopsis strzeleckii* Zone**	**So-called zone matches *Strophalosia subcircularis.* Wrong stratigraphic position.**
	***Bandoproductus walkomi* Zone**	**Established by Waterhouse (1987) and especially 2015b, under a more appropriate name.**
	Strophalosia subcircularis Zone	**Well established by Clarke (1990).**
	***Strophalosia concentrica* Zone**	**Well established by Clarke (1990).**
?	***Lyonia bourkei* Zone**	**Stratigraphic position and fauna need more information.**

Fig. 1. Summary of Early Permian productid zones proposed by Briggs (1998). In the left-hand column, ? refers to zones of insecure boundaries, stratigraphic position and faunal content, green refers to zones already established by other workers, black covers a zone placed in the wrong stratigraphic position, and red-orange signals a zone extended well beyond its natural limits.

as non-existent as a separate entity. Just as disturbingly, so- called Gympie *strzeleckii* comes from below, not above, beds with *Bandoproductus macrospina, B. macrospina walkomi*, and other taxa that characterize the upper Rammutt Formation. The upper Rammutt beds lie above the middle Rammutt Formation, which contains the Briggs-McClung version of *strzeleckii*, now named *Monklandia gympiensis.* Real *strzeleckii* comes from the Middle Permian of New South Wales (Campbell 1960, McClung 1978, p. 48). Briggs (1998) tried to underpin his version by identifying his false *strzeleckii* with specimens figured by McClung (1978, pl. 4, fig. 6-8) in the upper Rutherford Formation of the north Sydney Basin. This seemed to reinforce the Briggs misconstruction of stratigraphic succession. But the McClung specimens from the Rutherford Formation have fewer plicae than the Gympie "*strzeleckii*", and belong to *Monklandia mcclungi* Waterhouse (2015b, p. 171), not *gympiensis*, let alone *strzeleckii*, so that misidentification as well as stratigraphic misrepresentation and taxonomic distortion have added to the imbroglio.

***Echinalosia curtosa* Zone**

Briggs (1998) followed Waterhouse (1987) in recognizing this zone, as represented in the Fairyland Formation of the southeast Bowen Basin. He preferred to accept the interpretation of Draper (1985) in calling Fairyland a member, to accommodate the pioneering placement by Wass (1965) of the beds as part of an overall Buffel Formation, but the units proposed and mapped by Waterhouse (1983a, 1986) incorporate members, and it is not normal for "members" to include "members" – such members have to be upscaled to formations, or at least subformations. Briggs 1998, p. 35) contributed to understanding of the zone by pointing out other regions that appeared to contain similar faunal elements, in the Sydney Basin (lower Farley Formation) and Tasmania (possible Hickmann Formation)

***Echinalosia warwicki* Zone**

The *Echinalosia warwicki* Zone was used by Briggs (1998) as a partial replacement for the *Acanthalosia domina* Zone of Waterhouse (1987, p. 204) as well as to some extent the *Echinalosia curvata* Zone of Waterhouse (1987). Briggs (1998) believed that *warwicki* was more widespread. I retain reservations. The taxon *warwicki* is distinguished by its ventral hinge row of stout spines and strong dorsal capillae, facets which Briggs (1998) failed to recognize, so that many of his reported occurrences are not adequately reinforced by description or figures. That is in contrast to the species *domina* and *curvata* which are highly distinctive. However it would be premature to rule out the usefulness of the *warwicki* Zone. There is however cause for considerable reservations over the Briggs version of faunas. This is provided by his Fig. 22, p. 36, which purports to represent the equivalents of the *curtosa, warwicki* and *preovalis* Zones in the Tiverton Formation of the north Bowen Basin. It is this formation which has had the faunas monographed in Waterhouse (1983b, 2015a). Following these publications and the earlier studies by Campbell and others, it is clear than several of the species are more or less accurately tabulated by Briggs, based on their studies, whereas a number, involving "*Tivertonia*" *yarrolensis, "Echinalosia" warwicki, Echinalosia preovalis, Acanthalosia domina,* and *Terrakea dickinsi*, are wrong, in other words, the Productida on which Briggs worked are the ones which have been misidentified and/or their supposed ranges inaccurately depicted. Waterhouse (2015a) profusely illustrated species where possible and the types and other figured specimens, all registered, are safely esconsed at the Queensland Museum, so that the identifications may be checked, unlike the widespread reports of *warwicki* by Briggs, let alone the reports of other species in Briggs (1998, Fig. 22).

***Echinalosia preovalis* Zone**

The *Echinalosia preovalis* Zone was modified from the *Echinalosia preovalis* - *Ingelarella plica* Zone of Waterhouse (1983b, 1987, p. 212) and *Ingelarella plana* Zone of Runnegar & McClung (1975) by including a major lower division, developed in the "upper part of the lower Tiverton Formation", according to Briggs (1998, p. 37). This is a major error, based on several misidentified species summarized in Briggs (1998, Fig. 22) and discussed previously (pp. 38, 39). He showed limited understanding of the nominate species *E. preovalis*, identifying shells with discrepant morphologies from the upper Middle Tiverton Formation, as well as the Dresden Formation of the southeast Bowen Basin, and obliterating the important and widespread form *Echinalosia curvata*, which he fancied matched *E. preovalis*, in spite of substantial differences in size and shape. That mistake has affected the correlations known for various members of the Taeniothaerinae and Balkhasheconchinae, and wiped out the much better based zone based on *Ingelarella* (now *Ambikella*) *ovata* of Runnegar & McClung (1975). As a result, the Dresden and Elvinia Formations of the southeast Bowen Basin were miscorrelated with this *Echinalosia preovalis* Zone, whereas they are distinctly older.

Furthermore Briggs (1998, p. 41) included the *Martinia*? *adentata* and "*Echinalosia prideri"* (now *Capillaria conata*) zones of Waterhouse (1982a) from New Zealand. These overlie the New Zealand equivalents of the *Echinalosia preovalis* Zone in both New Zealand and east Australia. Worse – he matched this *Capillaria conata* species with "*Echinalosia*" *mcclungi* from the Snapper Point Formation of the south Sydney Basin, a blunder, because the two have very different morphologies, involving spine pattern and other detail (see p. 14ff and p. 143ff). There is not a single species link between these particular New Zealand faunas with the *E. preovalis* zone faunas: they are younger, lying over the *preovalis*-zone faunas. As a consequence, Briggs failed to recognize a major faunal gap in the marine faunas of east Australia, coinciding with the development of non-marine beds including coal throughout east Australia. In short, the Briggs reshaping of the *Echinalosia preovalis* Zone is highly inaccurate and has to be rejected.

Echinalosia maxwelli and _E. davidi_ Zones

The *Echinalosia maxwelli* Zone was extended into east Australia by Waterhouse (1987) from the zonal equivalent in New Zealand, as coeval and essentially the same zone as *Terrakea concavum* Zone. The types of the two named species come from one and the same locality, whereas Briggs (1998) claimed they came from different localities separated by many hundreds of metres stratigraphically. (See pp. 48, 49 herein). The New Zealand zone was found in deposits of the Letham Burn Formation at Wairaki Downs, and the east Australian equivalent placed as the Oxtrack Formation in the southeast Bowen Basin (see Flood et al. 1983). But Briggs placed the *maxwelli* Zone in somewhat older beds, the Elderslie Formation of the north Sydney Basin, though he included *Echinalosia davidi*, found in the Fenestella Shale above the Elderslie beds, which is more likely to match or at least come close to type *maxwelli*. The east Australian faunas placed wrongly in the *maxwelli* Zone by Briggs included the pre-*maxwelli* species *Wyndhamia typica*, which is a mistake: that species occurs distinctly below *Echinalosia* (*Echinalosia*) *maxwelli.* Briggs so-called *maxwelli* has an ornament distinctive from that of *maxwelli,* which is exceptionally well preserved. Briggs ignored the evidence provided by the ingelarellids and by *Aperispirifer*, and various bivalves and gastropods.

A false match was postulated by Briggs (1998, p. 42) with the claim that the faunas were different because of facies differences and domination by bivalves. That was his interpretation, an excuse. In fact some brachiopods are found, and they can be found also in the Pebbley Beach and Snapper Point Formations of the south Sydney Basin (Shi et al. 2021. Lee et al. 2023). There are also shared species with the middle Letham Formation of New Zealand, including *Wyndhamia typica* (Waterhouse 2002, 2008) but Briggs denied this similarity, because he wanted correlation to be with the younger Letham Burn Formation. *Terrakea rylstonensis* Briggs, one of many species now lost, was described initially from equivalents of the Snapper Point Formation in the Sydney Basin, and appears to be closely allied to New Zealand material from the Queens Beach boulder at Stephens Island, and the lower Letham Formation at Wairaki Downs. But reliance is now on figures, for Briggs has failed to return these specimens borrowed from the New Zealand Geological Survey (now GNS), and they are now appear to be lost.

In short, Briggs applied the wrong name, assigning a well-established zonal name to beds and faunas much older than the *Echinalosia maxwelli* Zone. He did allow that Waterhouse (1991) had indicated the stratigraphic succession, which is correct, but of course that did not suit, so he ignored the 1991 summary. The geographic range of *Echinalosia* (*Glabauria*) *davidi* is very limited, and the relationship to *Echinalosia* (*Echinalosia*) *discinia* promulgated by Briggs (1998) is challengeable - it may be younger, not older.

***Echinalosia discinia* Zone**

Established for the fauna chiefly from the Brae Formation of the southeast Bowen Basin by Waterhouse (1987, p. 214), this zone conforms moderately well with the treatment by Briggs (1998, p. 48) and is well known in the Bowen and Sydney Basins, with Briggs (1998) pointing to co-occurrences in the lower Wandsworth Volcanic Group in the southern New England Orogen, near Warwick, Drake and Texas Block.

***Echinalosia robusta* and *E. hanloni* Zones**

These zones, as delimited by Briggs (1998, p. 48) were stated to occur in a scattering of localities, most reliably in the Sydney Basin, in the upper Muree and Mulbring Formations and Nowra Sandstone. But the report by Briggs (1998) of *hanloni* in Tasmania is not reliable, and his identification of the poorly delimited *Terrakea etheridgei* Briggs in northwest Nelson of New Zealand is unconvincing, and indeed unlikely. *E. robusta* seems to be no more than a

?	***Echinalosia voiseyi***	**Stratigraphic position needs confirmation. The zone is redundant, matching well-known *Plekonella multicostata* Zone of Gympie & NZ.**
	Echinalosia ovalis	**Well established long known zone, older not younger than *clarkei.***
	Echinalosia deari	**Minor zone extended well beyond natural limits, and older not younger than *clarkei.***
	Pseudostrophalosia ingelarensis	**Zone placed well above natural position.**
?	***Pseudostrophalosia crassa***	**Validity highly uncertain.**
	Pseudostrophalosia clarkei	**Well known long-established fauna, badly miscorrelated, said to have *Wyndhamia typica.***
	Pseudostrophalosia blakei	**Match with other faunas challengeable.**
	Echinalosia runnegari & E. wassi	**Likely to be correlative with Bowen Basin faunas of *ovalis* & *deari* zones. Too localized.**
	Echinalosia robusta & E. hanloni	***robusta* probably matches *maxwelli, hanloni* local and short-lived, possibly matches *deari* of Queensland.**
	Echinalosia discinia	**Previously well-established fauna.**
	Echinalosia maxwelli, E. davidi	***maxwelli* placed too low, *davidi* minor and limited in time and space.**

Fig. 2. Middle Permian zones and possibly Late Permian *voiseyi* Zone of Briggs (1998), proposed for Permian macro-faunas of east Australia. Black signifies zone out of place in his construction; green zones following earlier workers; yellow, apparently redundant zones correlative with already proposed zones; ? signifying present uncertainty about the reality and correlation of the zone, especially regarding the *crassa* zone. The *voiseyi* zone if aged as in Briggs (1998 should be replaced by the much better zone and widely correlated New Zealand and Gympie equivalent, but needs full faunal description.

variety of *maxwelli,* and largely if not entirely contemporaneous with *maxwelli*.

***Echinalosia runnegari* & *E. wassi* Zones**

These zones are developed most clearly in successive stratigraphic levels in the south Sydney Basin, in the Berry Formation and possibly overlying upper Nowra Sandstone followed by *wassi* in the Broughton Formation. Leaving aside various aspects, some contentious, promulgated by Briggs (1998), the fact is that these two zones, and the underlying two as proposed by Briggs, are of very limited extent, and there seems to be no evidence that the zones ever extended in contemporaneous marine sediments right throughout east Australia. They appear rather to have been short-lived entities, centred in the Sydney Basin, sometimes extending further afield and not representing widespread faunal assemblages, though important in some faunas, mostly in New South Wales.

Terrakea brachythaera is common in the Broughton beds. Briggs reported this species from the lower Moonlight Sandstone in the north Bowen Basin, but the Moonlight specimens are older and belong to *T. exmoorensis* Dear. The Moonlight beds are the source of type *exmoorensis*, not *brachythaera*. He noted the presence of *wassi* in New Zealand, in higher Mangarewa beds regarded herein as likely to match the Broughton beds. The species *wassi* can be found the south Sydney Basin and New Zealand, and *runnegari* is restricted to the south Sydney Basin. This latter species is not geographically very extensive, even for a regional zone, and accompanying faunas suggest the critical species were localized and developed in a broader assemblage of more widely shared species.

***Pseudostrophalosia blakei* Zone**

This zone is developed in the Moonlight beds of the north Bowen Basin, with other species including *Terrakea exmoorensis, Ingelarella isbelli, I. magna* (now *Tumulosulcus*) and a number of other species, including many bivalves. Waterhouse & Jell (1983) considered after inspection of the large collections then at the Geological Survey of Queensland that *blakei* was the same as *Pseudostrophalosia ingelarensis* from the southwest Bowen Basin, which shares *Marinurnula mantuanensis* (though that species persists into higher beds) and has *Magniplicatina magniplica*. *Ps. ingelarensis*, described initially from the southwest Bowen Basin, is also known in the Barfield Formation of the southwest Bowen Basin, sharing several species (cf. Parfrey 1988, Fig, 15; Waterhouse 1987, Table 15). However, the faunas from the three regions of the Bowen Basin each differ to considerable extent, suggesting either a slight difference in age and biofacies, as here interpreted, or as favoured by Briggs (1998) complete disparity in age. In New Zealand, unit 5 of the Mangarewa Formation at Wairaki Downs has yielded *Pseudostrophalosia blakei, Terrakea exmoorensis* and *Magniplicatina magniplica.* Although the fauna according to Briggs (1998, p. 50) is limited largely to the north Bowen Basin with the lens in New Zealand, ingelarellids with a limited time range in Queensland, such as *Ingelarella isbelli* and *Tumulosulcus magna,* are well known in the Sydney Basin (McClung 1978) and in Tasmania (Clarke 1987). In the Sydney Basin, *magna* is found in the uppermost Snapper Point Formation and ranges into the middle Wandrawandian Siltstone according to McClung (1978, p. 48), equivalent to the *I. undulosa* and *I. brevis* zones in Queensland. *I. isbelli* overlaps in Tasmania as middle and late Lymingtonian, and was reported by McClung (1978) as being common in the Belford and Muree Formations of the Sydney Basin from the north Sydney Basin, and Nowra Sandstone, Berry Formation and Gerringong Volcanics in the south Sydney Basin, to suggest an extended range (McClung (1978, p. 52), so that disparate time ranges for these particular ingelarellids undercut their reliability as time indices, but still indicate general correlation.

***Pseudostrophalosia clarkei* Zone**

The *clarkei* Zone is based on fossils from the Scottville Member of the north Bowen Basin. Briggs claimed that material from nearly 100m below the Scottville also belonged to the species. They were never described or figured, and had been identified as *Pseudostrophalosia ingelarensis* (now *blakei*) by Waterhouse & Jell (1983), so the assertion is at best unproven, and seems very unlikely. In Briggs (1998, Fig. 29), *Ps. clarkei* was indicated as occurring in the uppermost Aldebaran Sandstone above the Cattle Creek beds, and similar specimens are found in the overlying Freitag Formation. These specimens have been described as *Wyndhamia typica crassiconcha* by Waterhouse (2001, p. 72, pl. 5, fig. 12-16, 17?). The ventral ears lack the large dense ear spines typical of *Pseudostrophalosia*: they should not be assigned to *Pseudostrophalosia,* despite Briggs. Moreover the specimens are accompanied by *Ingelarella undulosa* as identified by McLoughlin (1988) and Waterhouse (2001). The species is distinctly older than *Ps. clarkei*. It is found with *typica* in New South Wales and occurs in the Gebbie Member of the north Bowen Basin. Briggs (1998) also identified *Wyndhamia typica* in the *clarkei* band of the north Bowen Basin (see herein, p. 105), a most unlikely occurrence, and not supported by the figures he quoted.

As a valuable contribution, Briggs (1998, p. 52) pointed out that *Terrakea elongata* occurred in the Speldon Formation of the Avon Coal Measures in the Gloucester Syncline of New South Wales, regarded as correlative with the lower Tomago Coal Measures in New South Wales. He took a broad view of *Terrakea elongata*, which is now divided into subspecies, including *elongata elongata* in the Scottville Member, and *elongata planidisca* in the overlying beds within his so-called *ingelarensis* and *crassa* zones.

***Pseudostrophalosia ingelarensis* Zone**

Pseudostrophalosia ingelarensis was named for a species appearing in the Ingelara Formation of the southwest Bowen Basin, and persisting to the overlying Catherine Sandstone, and widely recognized in the Barfield Formation of the southeast Bowen Basin. This zone was placed hugely out of stratigraphic position by Briggs (1998, p. 118ff). He supposed that it followed the *Pseudostrophalosia clarkei* Zone on the basis of two lines of evidence, first the misidentification of *clarkei* in the Freitag and Aldebaran beds below the Ingelara Formation, and secondly, the identification of *Ps. ingelarensis* in beds immediately above the *Ps. clarkei* band or Scottville Member in the north Bowen Basin. The first identification is wrong: because the specimens do not belong to *Pseudostrophalosia* but to *Wyndhamia*. The second identification is wrong, because the species has been described on the basis of substantial material (rather than the handful reported by Briggs), from the same locality, and shown to belong to a distinct species, *Ps. furcalina* Waterhouse, 2022. Immature specimens of *furcalina* do approach *ingelarensis*, and perhaps Briggs had few specimens for study, unless he selected only those specimens which suited his model.

Briggs (1998, p. 52) noted the occurrence of *Echinalosia minima*, now *Echinalosia* (*Unicusia*) *minima*, which does appear as an important species above the Scottville Member, and also noted *Streptorhynchus pelicanensis* and *Ingelarella havilensis*. These reports are correct: they are found with *minima*, but do not occur with *Ps. ingelarensis*. As a result of his misidentification, he has wrongly interpreted the placement of the zone, and its faunal content.

***Pseudostrophalosia crassa* Zone**

This species is found in the Eddystone 1 core within interval E of McClung (1983), as summarized by Briggs (1998, p. 52). In the systematic section, he introduced a second type species based on specimens from the *clarkei* band or younger, but this is discounted. He reported supposedly identical specimens from the Ingelara Formation of the southwest Bowen Basin, and upper Blenheim Formation. Moreover he identified *crassa* with *Echinalosia* cf. *minima* of Dickins (1989, pl. 3, fig. 10-21) from the Kulnura marine tongue of New South Wales. The Dickins specimens are not *Pseudostrophalosia*, because they not only lack ventral ears with stout erect spines, but they lack the ears themselves, and are placed in a different genus *Nonauria laminata* Waterhouse.

Even the species *crassa* requires further substantiation. If there was such a zone, it still remains difficult to place in the hierachy and succession, and in the well-known sequences found in the north and southeast Bowen Basin, and New Zealand, there is no definite *crassa*. That is implying that at best *crassa* was a short-lived and geographically very limited form. It could well prove to be a minor variant within the species *Pseudostrophalosia blakei* (Dear).

***Echinalosia deari* Zone**

Echinalosia deari, now corrected to *Acanthalosia* (which is a genus recognized by Briggs 1998) occurs at the base of the Flat Top Formation, with a distinctive fauna delineated by Waterhouse (1986, 1987a, b). Material from the overlying more abundant faunas of the Flat Top Formation were allocated to *deari* by Briggs (1998, p. 55) but these specimens have a more deeply concave dorsal valve and less diverse ventral spines, so that it appears that Briggs has exaggerated the extent of the zone and greatly expanded its faunal content, with many of the species he listed coming from the middle Flat Top rather than lower Flat Top beds. Moreover he dubiously identified *deari* from specimens identified more accurately as "*Wyndhamia" ingelarensis* by McClung (1983, Fig. 14.3-5, 7, 8) from GSQ LD 96, equivalent to Catherine Sandstone approximately. The zone is much more limited than presented by Briggs, virtually confined to the southeast Bowen Basin, and the fauna may rate as a local geographically limited development above the *Pseudostrophalosia ingelarensis* faunas. The most prominent constituent of the fauna is *Ingelarella dissimilis* Waterhouse, which is also found in a comparable stratigraphic position in the lower Mangarewa Formation (unit 6) of New Zealand. But no *deari* is to be found in New Zealand, and the species *dissimilis* does

Zone favoured herein	Interpretation re Briggs (1998)	
Wairakiella sella	Not found in east Australia.	
Marginalosia planata	Not found in east Australia.	**UPPER**
Spinomartinia spinosa	In upper South Curra Limestone as well as New Zealand Miscorrelated by Briggs as much older zone.	
Echinalosia denmeadi	Miscorrelated by Briggs with much older zone.	**PERMIAN**
Martiniopsis woodi	Not in east Australia.	
Terrakea densispinosa	High in marine Bowen Basin, thought older by Briggs.	
E. (Unicusia) minima	Mismatched by Briggs with part of *ingelarensis* and *ovalis* Zones.	
Pseudostrophalosia clarkei	Miscorrelated with much older faunas in Freitag and Aldebaran Formations of southwest Bowen Basin.	
Maxwellosia ovalis	Placed too high by Briggs,and is found below *clarkei*, not above.	
Pseudostrophalosia blakei & Ps. Ingelarensis	*Ps ingelarensis* placed as substitute for *minima* by Briggs.	**MIDDLE**
Echinalosia maxwelli	Placed too low by Briggs in defiance of stratigraphic & faunal evidence. Wrongly separated from subspecies *robusta.*	**PERMIAN**
Lethamia ligurritus	Briggs largely follows Waterhouse (1987b), except for stratigraphic position.	
Wyndhamia typica	Briggs wrongly reported the species to be with *clarkei* in the north Bowen Basin.	
?Terrakea rylstonensis	Possible equivalent of Briggs species, but Briggs has lost or destroyed east Australian types and New Zealand material.	
Attenuocurvus beds	Informal unit, tiny fauna, limited to New Zealand.	
Capillaria conata	Misassigned by Briggs to ***maxwelli*** *preovalis* Zone.	**LOWER**
Martinia? adentata	Zone ignored.	
Echinalosia preovalis ……………………………………	Extended by Briggs well below the range of the type species and associated faunas in Queensland and New Zealand.	
Magniplicatina undulata	Divided between *preovalis* and *warwicki* zones as interpreted by Briggs, mixing too different faunas.	
Maxwellosia curtosa	Much as in Waterhouse (1986, 1987a).	
Bandoproductus macrospina	Misinterpreted by Briggs as being older than his "*Tomiopsis strzeleckii*" Zone, which should be regarded as part of *S. subcircularis* Zone.	
Crassispinosella subcircularis	Largely follows Clarke (1990).	**PERMIAN**
Strophalosiaria concentrica	Largely follows Clarke (1990).	

Fig. 3. The left hand column shows the sequence of macro-faunal zones as in Waterhouse (2002, 2008, 2021) and herein, with comments to the left on the interpretations of the sequence in Briggs (1998).

range sparsely into higher beds. At least Briggs placed the zone in its correct position, below the *Echinalosia ovalis* (now *Maxwellosia ovalis*) Zone, because the overlying middle Flat Top faunas are broadly correlative with that faunal assemblage (Waterhouse 1987b, 2002). Briggs (1998, p. 56) included faunas from the upper South Curra Limestone near Gympie in the zone. The inclusion is fanciful: the faunas are much younger. But his inclusion of *Filiconcha hillae* is generically correct: just the species name is wrong, with ornament distinguished from that of *hillae* by the strength of capillae and the nature of the ventral spines: the material belongs to *auricula* Waterhouse, not *hillae* Dear.

***Echinalosia ovalis* Zone**

This zone as typified by the Mantuan band of the upper Peawaddy Formation has long been recognized, but Briggs narrowed the range of the zone to the Bowen Basin and the Condamine Block near Warwick south Queensland, with no mention of faunas regarded as correlative, including for instance those of Tasmania or New Zealand. The accompanying faunas including echinalosiids say otherwise.

***Echinalosia voiseyi* Zone**

The *Echinalosia voiseyi* Zone was named for the faunas found in the Gilgurry Mudstone of the Drake Syncline in northern New South Wales, and regarded as including " the youngest productoid-bearing faunas known from eastern Australia" (Briggs 1998, p. 57). Briggs stressed the presence of several species considered to be close to species found in the *Plekonella multicostata* Zone of New Zealand (Waterhouse 1982), with *Capillaria denmeadi* and . *Tigillumia parallela* and *Oviformia alteplicata.* Correlation for *voiseyi* needs confirmation, and awaits full monographic treatment of the fauna. But if it is correct, and Briggs reported a number of species found also in the *Plekonella multicostata* Zone (now *Paucispinauria verecunda*) Zone, then the zone in the Gilgurry beds should be referred to that New Zealand zone, where the zone is much more fossiliferous and is developed in clear stratigraphic succession, to resolve the uncertainties surrounding the so-called *Echinalosia* (now renamed *Nothalosina*) *voiseyi* Zone. Briggs failed to recognize the development of the *Plekonella multicostata* - *Paucispinauria verecunda* Zone at Gympie, where there is no sign of the so-called *Echinalosia voiseyi* Zone (Waterhouse 2015b).

THE STRATIGRAPHY AND FAUNAS OF THE EARLY MIDDLE PERMIAN AT EXMOOR STATION, NORTH BOWEN BASIN

It is revealing than in all his publications, Briggs never provided any photographs or sketches of fossil localities, and never offered a single geological map to reveal spatial relations of fossil localities. Geological stratigraphy was not a discipline he undertook. Yet that is an integral part of faunal zonation, far more important and challenging than the provision of sections, which restrict relationships to one plane. That may be why he so severely misconstrued the study by Waterhouse & Jell (1983) in the north Bowen Basin on some of the rocks and macro-fossils. That publication provided a geological map, reinforced by an aerial photograph with fossil localities marked, and tables with faunal lists, and fossil descriptions and illustrations. He claimed (1998, p. 45, caption to Fig. 28) that Waterhouse & Jell were inconsistent. He offered several points. First, he stated that his charted "level A" was indicated by Waterhouse & Jell, table 8. That is wrong: it is Table 9 in Waterhouse & Jell that matches Briggs (1998, Fig. 28, A). He moreover claimed that his level A was the top of the Moonlight Sandstone: not so: it is as shown in Briggs 1998, Fig. 28). Second point, “level B" is indicated in Waterhouse & Jell 1983, Fig. 4. That is correct and agrees with Waterhouse & Jell 1983, tables 8 and 9. Third point, "level C" of Briggs (1998, Fig. 28), is consistent with the other points in Waterhouse & Jell (1983). His fourth point was raised by Briggs (1998, Fig. 28, caption) that "level D" is implied by the locality in index in Waterhouse & Jell (1983). This involves localities UQL 4654 and UQL 4643. Yet Waterhouse & Jell (1983, Table 11, p. 255) stated that UQL 4654 came from the Blenheim Formation, not as Briggs stated, the Moonlight Sandstone. UQL 4643 came from the Moonlight Sandstone, according to Waterhouse & Jell 1983), and was not in the mapped area. In short, it is Briggs (1998) who erred. I would certainly not claim that Waterhouse & Jell (1983) were infallible, corrections are and were required, but the Briggs mistakes even in assessing an article of so long ago, were on another order of magnitude. No wonder that the Briggs interpretation of the stratigraphy and faunas of the north Bowen Basin was so removed from the actual rocks and faunas. He never achieved a sound understanding of those rocks and faunas, relying on his laboratory-based identifications of fossils rather than field-based interpretations reinforced by fossil study. His errors over the relevance of the Waterhouse-Jell faunal lists to the rock units extended into younger marine faunas, in particular involving the identification of *Wyndhamia typica* from faunas in the Scottville Member and gross misplacement of the *Pseudostrophalosia ingelarensis* Zone.

The numerous errors in the Briggs account of Permian stratigraphy in east Australia led to a further gross distortion, with the claim that marine sedimentation paused for a lengthy interval in the Bowen Basin, while continuing in the Sydney Basin. Thus various zones, involving the zones based on *Echinalosia hanloni* to *E. wassi* accumulated in the Sydney Basin during a still-stand in the Bowen Basin, and further zones, from *Pseudostrophalosia blakei* to *Echinalosia ovalis* accumulated in the Bowen Basin, with no or very limited marine representation during this interval in the Sydney Basin. There is very limited evidence to support this hypothesis. Especially geologically – no evidence of an still-stand or paraconformity has ever been uncovered over many years of mapping in any part of the Bowen Basin. Briggs ignored the evidence from a number of species shared between the two basins. Notably amongst the Ingelarellidae, for example, *Ingelarella mantuanensis* is found in the *Maxwellosia ovalis* Zone of the Mantuan Member in the Bowen Basin, and in the Muree and Nowra and Berry beds of the Sydney Basin (McClung 1978, p. 54). Shared bivalves, notably amongst *Etheripecten, Striochondria, Vacunella, Myonia* and others were completely ignored, but are summarized by Runnegar (1968) and Waterhouse (1969, 1982b etc,). Briggs claimed that his model fitted that of evidence provided by palynomorphs as then interpreted, and only a little adjusted since (Smith et al. (2016). The presently favoured palynomorph interpretation is indeed curious, because reliance has been placed on *Dulhuntysporites parvithola*, which in Queensland ranged throughout most of the Middle Permian and all of the upper Permian, as one zone, to me a zone of preposterous duration, and virtually useless. The palynomorph has been recognized in the early Middle Permian Aldebaran and Freitag beds of the southwest Bowen Basin, as well as the Brae and Oxtrack Formations of the southeast Bowen Basin and persists through the overlying Permian successions. The Freitag level shares *Wyndhamia typica* with Elderslie beds in the Sydney Basin. *Echinalosia* (*Echinalosia*) *maxwelli robusta* is shared between the Belford and Nowra Formations of the Sydney Basin with the Oxtrack Formation of the Bowen Basin (Briggs 1998, p. 90), even though the palynomorph assemblages differ (Smith et al. 2016), in contradiction of the Briggs Great (but non-existent) Gap. The Briggs Gap is there sure enough, but only in Briggs' interpretation of productid fossils. The disparities in both palynomorph assemblages and in the distribution of several genera of Productida reflect not differences in sedimentation, but climatic control, with the climate warmer in the north (Bowen Basin), leading to a greater generic diversity in that basin. There are many more facets. One involves the New Zealand succession, so profoundly misrepresented by Briggs (1998). The New Zealand succession is very close to the overall sequences of the Bowen Basin, apart from including marine intervals in place of non-marine sediments. But it shares several critical fossils with the Sydney Basin, notably *Maxwellosia ovalis wassi* (Briggs, p. 98), otherwise found in the Berry equivalents and Broughton Formation of the Sydney Basin, equivalent to sediments supposedly absent from the Bowen Basin.

In conclusion, the Briggs memoir has contributed a great deal of information, and involved a great deal of meticulous study on the Permian fossils of east Australia. But for all that, its major contributions have been negative: especially wrong in discounting so much macro-fossil evidence. Wrong in the placement and correlation for several biozones, and delinquent in the naming of a number of fossil species based on material that appears to be no longer extant. As for the calamity over the improper registration of Queensland Museum fossils as belonging to the Australian Museum, and their disappearance, the original problem surely arose over funding to meet the costs of their return to Queensland. Was no one able to help in this regard - perhaps just the cost of driving them by car from Sydney to Brisbane? Not good.

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