A SUMMARY OF BRACHIOPOD SPECIES BELONGING TO LINGULIDA, STROPHOMENIDA, CHONETIDINA AND PRODUCTIDINA FROM THE PERMIAN FAUNAS OF EAST AUSTRALIA AND NEW ZEALAND

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With the proposal of a new genus *Hiranesania* by

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Earthwise 21

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LIST OF INDIVIDUAL SPECIES DESCRIBED AND FIGURED. New taxa in bold.

Genera beyond east Australia and New Zealand

INTRODUCTION

This is the first of volumes planned to summarize the occurrences, diagnosis, morphological range and stratigraphic occurrences for brachiopod species so far named in the Permian deposits of eastern Australia and New Zealand. As far as I am aware, it has been preceeded by the remarkable set of studies by Davidson, starting in 1853, on brachiopods from throughout the stratigraphic record in Great Britain, and of course the evolutionary record is now more complete and much more elaborate than in his day, but it would be difficult to match let alone excel his superb illustrations. In much more recent times, two volumes have appeared on the brachiopod genera found throughout the fossil record in China (Tong Jiayu (2017). The present set of studies focuses on species, rather than genera, because it is species that set the limit for genera, and the emphasis on only type species in particular for a genus may fail to convey a great deal of valuable information.

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. In New South Wales, repositories include **AMF** for Australian Museum, Sydney; **ANU** Australian 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; and **UT** Department of Geology, University of Tasmania, Hobart. New Zealand repositories involve **BR** for brachiopods kept at the Institute of Nuclear and Geological Sciences, Lower Hutt; **CM** Canterbury Museum, Christchurch; **OU** Department of Geology, Otago University, Dunedin. From further afield, **BMNH** refers to collections at the Museum of Natural History, London, and **SM** to the Sedgwick Museum, Cambridge; **GSC** Geological Survey of Canada, Ottawa, Canada; **PIN** Paleontological Institute, Moscow, Russia, and **USNM** United States National Museum, Washington D. C., USA. **NU-B** refers to the Department of Geology, Faculty of Science, Nigata University, Japan.

ACKNOWLEDGEMENTS

Throughout this study, Kristen Spring at the Queensland Museum (Bulk Storage, Brisbane) has provided advise 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.

REFERENCES

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RONG JIAYU 2017 Editor in Chief, with associate editors JIN YUGAN, SHEN SHUZHONG & ZHAN RENBIN: Phanerozoic Brachiopod genera of China, vol. 1, 2: i-xviii, 1-1096. Science Press, Beijing.

PERMIAN SPECIES OF LINGULIDA AND STROPHOMENIFORMII FROM EAST AUSTRALIA AND NEW ZEALAND

Abstract

Described species of the brachiopod groups Lingulida and Strophomeniiformii are summarized from the marine faunas of Permian age in east Australia and New Zealand.

SYSTEMATIC SUMMARY

Phylum Brachiopoda Duméril, 1806

Subphylum Linguliformea Williams et al., 1996

Class Lingulata Gorjansky & Popov, 1985

Order LINGULIDA Waagen, 1885

Superfamily **DISCINOIDEA** Gray, 1840

Family **DISCINIDAE** Gray, 1840

Genus ***Orbiculoidea*** d'Orbigny, 1847

Diagnosis: Dorsibiconvex to convexoplane shell, subcircular in outline, both valves ornamented by concentric fila, dorsal valve conical to subconical, apex variably positioned, ventral valve low subconical to gently concave. Pedicle track narrow, closed anteriorly by listrium continued internally by tube to open in front of posterior margin.

Type species: *Orbicula forbesi* Davidson 1848, p. 334 from Wenlock of England (ICZN opinion 722, 1965).

Orbiculoidea rotularia Waterhouse, 1986

Fig. 1A, B

1986 *Orbiculoidea rotularia* Waterhouse, p. 18, pl. 1, fig. 8, 11.

Diagnosis: Well-defined concentric fila, two in 2m with fine discontinuous radial capillae, pedicle notch placed close to outer margin, closed by listrium with two diverging ridges not reaching outer margin. Apex closed placed very close to outer margin

Holotype: UQF 73912 figured in Waterhouse (1986, pl. 1, fig. 8, 11) and herein as Fig. 1A, B, OD.

Stratigraphy: The species is limited to the Elvinia Formation of the southeast Bowen Basin, Queensland, equivalent to the *Magniplicatina undulata* Zone, and is named because it marks the exceptional occurrence of a genus otherwise not known in the Permian of east Australia.

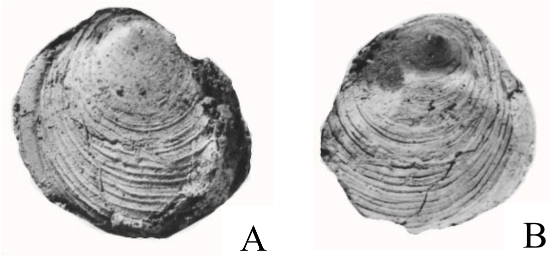

Fig. 1. *Orbiculoidea rotularia* Waterhouse, latex cast and external mould of holotype UQF 73912 x2 from Elvinia Formation, southeast Bowen Basin. (Waterhouse 1986).

Orbiculoidea clintonensis Waterhouse, 1986

Fig. 2

1982 *Orbiculoidea* sp. Waterhouse, p. 23, pl. 1a.
1986 *O. clintonensis* Waterhouse, p. 18.

Fig. 2. *Orbiculoidea clintonensis* Waterhouse, ventral valve, BR 1180, x8. Trig. D Formation. (Waterhouse 1982).

Diagnosis: Subcircular in outline, with V-shaped pedicle interior opening in the midst of a long broad posterior ridge. Subconical dorsal valve with apex halfway between posterior margin and centre of the valve. Ornament of concentric fila of two series, the stronger numbering two to three in 1mm, with finer ones as well, visible on the only available dorsal valve.

Holotype: BR 1180 from Trig. D Formation, New Zealand, figured by Waterhouse (1982, pl. 1a) and herein as Fig. 2, OD.

Morphology: The species is rare in New Zealand, and was named to mark its exceptional distribution. Aspects of the morphology and variability are not known.

Stratigraphy: The species is found in the Trig D Formation, of upper middle Changhsingian age.

Subphylum Rhynchonelliformea Williams et al., 1996

Class Strophomenata Williams et al., 1996

Superorder STROPHOMENIFORMII Őpik, 1934

[Nom. transl. Waterhouse 2010, p. 8 ex suborder Strophomenoidea Őpik, 1934, p. 75].

This superorder includes Strophomenida and Triplesiida, for which nomenclatural background and critical aspects of morphology were discussed in the *Revised Brachiopod Treatise* by Cocks & Rong (2000, p. 216 ff.) and Williams & Brunton (2000, p. 644 ff.). In spite of differences in shell structure, association between the two orders is strongly suggested by many aspects of shape, ornament and internal structures, just has been done in numerous studies prior to the somewhat radical treatment by Williams & Brunton (2000). It is further proposed that the Clitambonitida Őpik, 1934 should be included in the same group. Cocks & Rong (2000) considered that the Plectambonitoidea probably evolved from the Billingselloidea, and gave rise to Strophomenoidea. In Williams & Harper (2000), the Billingselloidea were classed as a distinct Order Billingsellida "Schuchert" (corrected to Clitambonitida Őpik), which helps justify amalgamation of these orders in one superorder.

Order TRIPLESIIDA Moore, 1952

This order was treated as a suborder of Orthotetida "Waagen, 1884" by Wright (2000), but Waagen proposed no such ordinal group, and the constituent first recognized as having ordinal ranking was Triplesiida Moore (1952, p. 221), as clarified in Waterhouse (2010, p. 9).

Suborder ORTHOTETIDINA Cooper & Grant, 1974

Williams & Brunton (2000, p. 644) referred to Order Orthotetida Waagen, 1884, but Waagen neither proposed such an order or suborder, referring instead to a subfamily. Cooper & Grant (1974, p. 276) were first to promote Orthotetidina from Subfamily Orthotetinae Waagen, 1884, p. 576, and as it was they who first interpreted the group as meriting subordinal status, they should be credited with the proposal. The change of rank from Suborder to Order was promulgated by Williams & Brunton (2000), based on their reassessment of the significance of shell structure. (See Waterhouse 2010, p. 9; Waterhouse & Campbell 2021, p. 8)

Superfamily **ORTHOTETOIDEA** Waagen, 1884

Family **SCHUCHERTELLIDAE** Williams, 1953

Subfamily **STREPTORHYNCHINAE** Stehli, 1954

Tribe **STREPTORHYNCHINI** Stehli, 1954

Diagnosis: Generally medium-sized with fine branching ribs, high ventral interarea with convex pseudodeltidium and as a rule a perideltidium, linear dorsal interarea with chilidium. No ventral median septum, long cardinal shaft, long lobes with erismata, low dorsal septum. Shell extropunctate.

Type genus: *Streptorhynchus* King, 1850 from the Zechstein of Germany, OD.

Genera: *Streptorhynchus* King, *Chelononia* Cooper & Grant, *Erismatina* Waterhouse and *Kiangsiella* Grabau & Chao. *Lepius* de Gregorio, 1930 and *Mammosum* de Gregorio, 1930 remain to be properly assessed.

Discussion: This subfamily is discussed by Waterhouse & Chen (2007), in revising the interpretation offered by Williams & Brunton (2000), and in noting the need for more comparative diagnoses to provide clear distinctions between genera, which Williams & Brunton had failed to provide. The long and slender plates extending in front of the cardinal process along each side of the muscle field were described as erismata by Cooper & Grant (1974), and are typical of Streptorhynchini in their considerable length.

A major contribution by Williams (1997) and Williams & Brunton (1993, 2000) has been on shell structure, aspects of which have been severely criticized by Afanasieva (2002) because of a focus that ignored or deprecated much of the literature, especially outside of that published in English, though the Williams-Brunton version must be judged as far better than others available in English studies. But overall, their work, as concluded by Afanasieva, “is remarkable in its inadequacy”, which hardly provides a sound basis for the two of them to castigate the work by other students. An additional source of contention lies in the way Williams & Brunton (2000) sought to apply a terminology to morphological parts that was highly interpretative in stressing supposed origin rather than function, and further studies of ontogeny, shell structure and paleogeographic variation are required to substantiate some of their proposals. By contrast, Cooper & Grant (1974) applied terms relating only to Orthotetidina, an approach may have been more objective, though arguably, less instructive – or speculative. Moreover the question remains – if plates have changed in function, it is not clear why should they be given the same name as applied to the structure from which they were derived.

Tribe **TROPIDELASMINI** Waterhouse, 1983

[Nom. reductio hic ex Tropidelasminae Waterhouse, 1983, p. 117].

Diagnosis: Without erismata. As a rule, the pseudodeltidium bears a monticule, which may be channelled, and the ventral interarea lacks perideltidia. Teeth ridges may be connected to the floor of the valve especially in early growth phases of some genera.

Name genus: *Tropidelasma* Cooper & Grant, 1969, p. 3 from Glass Mountains, Texas, OD.

Genera: *Tropidelasma* Cooper & Grant, *Arctitreta* Whitfield, *Bothrostegium* Cooper & Grant, *Fissulina* Waterhouse, *Grumantia* Ustritsky if valid, or arguably a subgenus of *Arctitreta*, *Isbellina* Waterhouse*, Notostrophia* Waterhouse.

Discussion: The two genera found in east Australia and New Zealand are characterized in part by the absence of perideltidial areas, and the lack of erismata, a lack which they share with Arctic forms, such as *Arctitreta* Whitfield, and differ notably in the absence of these features from *Streptorhynchus* King. *Tropidelasma* lacks erismata, yet a somewhat similar genus *Erismatina* has long erismata. (Waterhouse 1983; Waterhouse & Chen 2007). To Waterhouse (1983), *Tropidelasma* and *Erismata* were distinguished by their prominent monticule, much more emphasized than in otherwise related forms, so as to justify recognition of a separate group. But now it is preferred to change the emphasis, and base the group, reduced to a tribe, on the lack of erismata. That suggests the Tropidelasmini involve the genera as listed above, bringing together genera that have no erismata and no perideltidia, whereas these features are developed in *Streptorhynchus.*

Genus ***Isbellina*** Waterhouse, 2022

Diagnosis: Elongately subpentagonal shells ornamented by weakly differentiated costellae, ventral interarea high, lacking perideltidium, bearing broadly convex pseudodeltidium with only a low monticule, bordered by teeth ridges, vestigial or no dorsal interarea, tooth ridges not supported by plates, cardinal process high and quadrifid, crural supporting plates short, no erismata.

Type species: *Streptorhynchus pelicanensis* Fletcher, 1952, p. 8 from Pelican Creek band, north Bowen Basin, of Dear (1972), OD.

Discussion: Compared with other Permian genera, this genus is distinguished from *Streptorhynchus* King, 1850 through the lack of perideltidia, and lack of erismata. In these regards, the genus is close to *Arctitreta,* type species *A. pearyi* Whitfield, 1908, p. 57 from the Canadian Arctic Archipelago, as discussed and illustrated in Waterhouse (2020, p. 26ff, Fig. 8A, B, 9-12). Note that the interpretation of *Arctitreta* by Waterhouse & Chen (2007) needs to be updated by the study of that genus and Arctic allies in Waterhouse (2020). The known species of *Arctitreta* have more differentiated ribbing than in *Isbellina*, and in the ventral valve the dental ridges are supported by slender plates which extend to the floor of the valve, at least in immature specimens. Such plates are not known for *Isbellina*. A low monticule lies over the pseudodeltidium in *Arctitreta* as well as in *Isbellina (*see Fig. 2A). Similar structures are visible in *Grumantia* Ustritsky, 1963, a genus of questionable validity, arguably distinguished from *Arctitreta* by its wide hinge. *Fissulina* Waterhouse, 2020 is an Arctic genus distinguished by having a channel down the middle of the pseudodeltidium. Dental supporting plates are present in *Fissulina*, but not in *Bothrostegium* Cooper & Grant, 1974, which as a rule lacks erismata, but differs from *Isbellina* in having a pseudodeltidial channel like that of *Fissulina*. One further genus found in east Australia and New Zealand is *Notostrophia* Waterhouse 1973, 1982, which also lacks erismata, but unlike *Isbellina*, the ventral interarea in *Notostrophia* is not very high as a rule. In several species of *Notostrophia*, the ribs on the dorsal valve are coarser than those of the ventral valve.

Isbellina pelicanensis (Fletcher, 1952)

Fig. 3, 4

1880 *Orthotetes crenistria* var. *senilis* [not Phillips] – Etheridge Jnr, p. 282, pl. 8, fig. 12-15.
1892 *Derbyia senilis* [not Phillips] – Etheridge Jnr, p. 246, pl. 12, fig. 1-6.
1929 *D. senilis* [not Phillips] – Reid, Fig. 36.1.
cf. 1952 *Streptorhynchus pelicanensis* Fletcher, p. 8, pl. 1, fig. 2.
1964 *S. pelicanensis* – Hill & Woods, pl. P4, fig. 2, 3.
cf. 1964a *S. pelicanensis* – Waterhouse, p. 17, pl. 1, fig. 1, 2.
1969 *S. pelicanensis* – Armstrong, pp. 310-320, pl. 57, fig. 1-6, pl. 58, fig. 3-5, pl. 60, fig. 1, 2.
1971 *S. pelicanensis* – Dear, p. 2, pl. 1, fig. 1-8.
1972 *S. pelicanensis* – Hill et al., pl. P4, fig. 2, 3.
cf. 1982 *Grumantia*? sp. – Waterhouse, p. 24, pl. 1b.
cf. 1982 *Grumantia*? *pelicanensis* – Waterhouse, p. 24, pl. 1c.
1990 *G. pelicanensis* – Clarke, Fig. 4N.
2022 *Isbellina pelicanensis* – Waterhouse, p. 127, Fig. 1, 2.

Diagnosis: Large and elongate shells with high ventral interarea, ribs fine and in several orders, but only weakly differentiated.

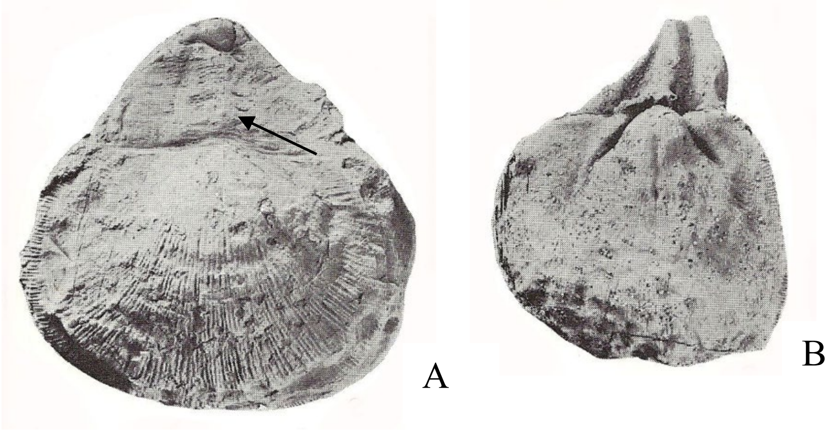

Fig. 3. *Isbellina pelicanensis* (Fletcher). A, holotype GSQF 1451 from Pelican Creek Member, Rosella Creek, showing very low monticule, as arrowed. B, dorsal aspect of internal mould, GSQF 1452 from Pelican Creek. Specimens x1 from north Bowen Basin. (Hill & Woods 1964).

Holotype: Specimen GSQ F1451 from Havilah Byerwin Road, south of Rosella Creek crossing, "*Streptorhynchus* bed", high in Blenheim Subgroup, north Bowen Basin, Queensland, figured by Etheridge Jnr (1880, pl. 7, fig. 12), Etheridge Jnr (1892, pl. 12, fig. 1), Hill & Woods (1964, pl. P4, fig. 2) and Hill et al. (1972, pl. P4, fig. 2), OD. See Fig. 3A and 4A, B herein.

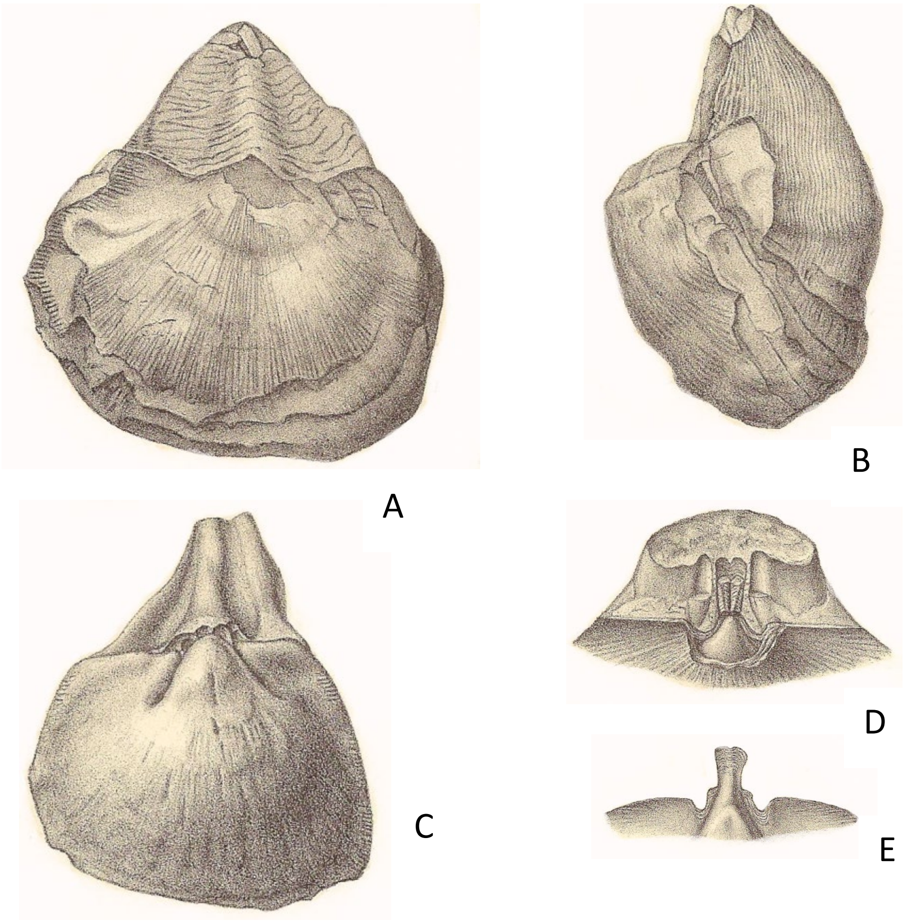

Fig. 4. *Isbellina pelicanensis* (Fletcher). A, B, ventral and lateral aspects of holotype GSQF 1451. C. dorsal aspect of specimen with valves conjoined, GSQF 1452. These two specimens were refigured by Hill & Woods 1964, as in Fig. 3 herein. D, posterior internal mould with part of umbonal region removed. E, cardinal process. Specimens x0.8 approx. from the Pelican Creek band, Bowen Basin. (Etheridge Jnr 1892).

Stratigraphy: This species is an outstanding member amongst brachiopod species found high in the marine Permian faunas of the north Bowen Basin. Specimens that are probably congeneric have been reported from slightly older faunas, as reviewed by Dear (1971, p. 4), and include specimens from the Barfield Formation, figured by Waterhouse (1986, pl. 2, fig. 5, 6). These have a less extended ventral umbo and are unlikely to be conspecific, but better preserved material is required to consolidate their generic position, though they appear to be related. Somewhat similar specimens were reported from the Mangarewa Formation of New Zealand (Fletcher 1952; Waterhouse 1964a, 1982), but the specimens are incomplete and not fully known. *Streptorhynchus* sp. of McClung (1983, p. 69, Fig. 12.1) from interval E of the

Eddystone 1 GSQ bore possibly belongs to the genus, but with only the dorsal interior figured, is difficult to compare further without further information.

Genus ***Notostrophia*** Waterhouse, 1973

Diagnosis: Large ventribiconvex non-plicate non-auriculate shells, dorsal valve may have recurved anterior portion that is finely costate, and rest of dorsal valve coarsely costate in type and other species, but recurved portion not developed in some otherwise similar species. Pseudodeltidium broad and convex, low monticule, no perideltidium. Chilidium plate-like. Teeth with low ridges, restricted to ridges along delthyrial sides, not supported by plates, no erismata. Ventral muscle scars flabellate with dividing myophragm, cardinal process broad with lobes at base, low ridge may lie as a cardinal collar across outer face of process.

Discussion: In the original diagnosis, and as an error not repeated in the main and leading diagnosis by 1982, Waterhouse (1973) referred to pseudopunctae in the shell – following a number of other authors for related genera. This misreport, for what Williams & Brunton (1993) twenty years later called extropunctae, was used by Williams & Brunton (2000, p. 670) to excoriate the Waterhouse diagnosis for failing to anticipate the Williams-Brunton discovery of exopunctae and so they claimed that the family position of *Notostrophia* could not be recognized. Such errors I have made. Fortunately those two authors, who controlled the publication and content of the *Revised Brachiopod Treatise*, did not apply the same strictures to other authors, which included Thomas (1958), Williams (1965, p. 409), Cooper & Grant (1974) and Grant (1976) who had wrongly reported pseudopunctae. That the list even includes Williams himself may seem peculiar, but of course he has written so prolifically that he may be excused for the lapse of memory – unless Brunton was responsible for the criticism. They also deplored the lack of information about the pseudodeltidium for *Nototrophia*, because it was not preserved, but did not criticize other authors, when the pseudodeltidium was not preserved, for failing to describe the pseudodeltidium. Their problem was only with me. One of the difficulties for Williams and Brunton was that they had little experience with Permian faunas, and no familiarity at all with Permian brachiopods from Australia or New Zealand. It was natural, given the time constraints, that they focused solely on the nature of the type species of *Notostrophia*, and it is not surprising, no matter how disappointing, that they were not aware of other species of *Notostrophia* which in their morphology demand adjustments to the understanding of the genus that were promulgated in its original definition. Perhaps that requires a much broader approach to the writing of Treatise studies, with a broader field of genuine experts, showing much less willingness to denigrate those they quite unnecessarily imagined were rivals. The real concern still centres on the shell structure of *Notostrophia* and allies. Waterhouse (1982, p. 28) noted the presence of pores in the shell BR 1505, about two per millimetre. That recalls the report on west Australian fossils by Thomas (1958, pp. 44, 49) of numerous fine punctae in species he described as *Streptorhynchus costatus* and *S. crassimurus* from the Nooncanbah Formation of the Fitzroy Basin in Western Australia. The two species are likely to belong to *Notostrophia*. But no mention was made of such punctae by Williams & Brunton (2000) or in their earlier and rather circumscribed studies.

Type species: *Notostrophia homeri* Waterhouse, 1973, p. 35 from Brunel Formation of Takitimu Group, New Zealand, OD.

Notostrophia costellata (Clarke, 1990)

Fig. 5

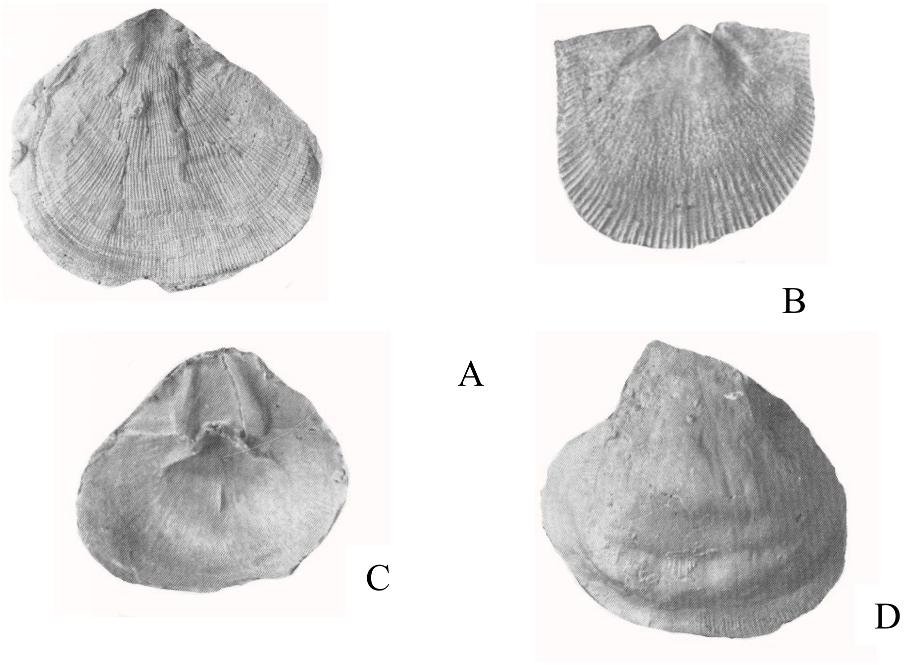

Fig. 5. *Notostrophia costellata* (Clarke). A, latex cast of ventral exterior, GST 14101, x0.6. B, dorsal internal mould, GST 14109, x2. C, latex cast of dorsal interior and ventral interarea, GST 8334A, holotype, x1. D, ventral valve internal mould GST 14108, x1. Bundella Formation and *Tasmanites* oil shale (B). (Clarke 1990).

1990 *Grumantia costellata* Clarke, 56, Fig. 4A-M
1992 *G. costellata* – Clarke, p. 14, Fig. 4A-K.

Diagnosis: Large shells up to 60mm wide and 70mm long, with thick shell described – or misdescribed – as pseudopunctate, and with coarse taleolae, ventral valve more inflated than dorsal valve.

Holotype: GST 8334A-B figured by Clarke (1990, Fig. 4G, H; 1992, Fig. 4G, H) and herein as Fig. 5C from basal Bundella Formation, Tasmania, OD.

Morphology: A good selection of specimens was figured by Clarke (1990) and repeated in 1992.

Stratigraphy: The species is found in the widely in the basal Bundella Formation and in the *Tasmanites* oil shale. (See Clarke 1992, Fig. 1, 3), largely within the range of *Strophalosiaria concentrica* (Clarke), key species to the oldest Permian macro-faunal zone known in east Australia.

Notostrophia bifurcata Waterhouse, 1986

Fig. 6

1986 *Notostrophia bifurcata* Waterhouse, p. 20, pl. 2, fig. 9-19.

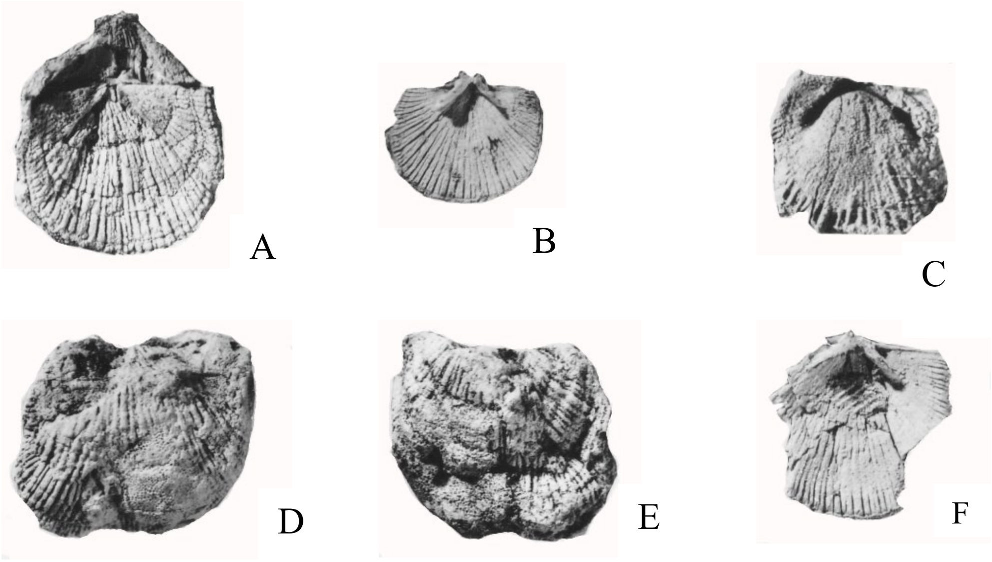

Fig. 6. *Notostrophia bifurcata* Waterhouse. A, dorsal view of specimen with valves conjoined, UQF 73923, holotype. B, dorsal interior, UQF 73922. C, dorsal internal mould, UQF 13708, x1. D, E, dorsal and ventral views of UQF 73927, x1. F, dorsal interior, UQF 73925. Specimens x2, C-E from Fairyland Formation, A, B, F from Dresden Formation. (Waterhouse 1986).

Diagnosis: Small with broad ventral umbo, ventral sulcus, dorsal fold, costae moderately strong, numbering twelve in 5mm over ventral valve and six in 5mm for dorsal valve at anterior margin.

Holotype: UQF 73923 figured by Waterhouse (1986, pl. 2, fig. 10) and herein as Fig. 6A from Dresden Formation, southeast Bowen Basin, Queensland, OD.

Morphology: The species is distinguished by its small size. Ventral ribs are fine, especially posteriorly, and dorsal ribs increase by bifurcation, with intercalation rare.

Stratigraphy: The species found in the Dresden Formation and Fairyland Formation of the southeast Bowen Basin, Queensland.

Notostrophia simplicata n. sp.

Fig. 7

2021: *Notostrophia* sp. Waterhouse & Campbell, p. 9, Fig. 1.

Derivation: simplex – plain, uncompounded (Lat.)

Diagnosis: Moderately large shells with prominent ventral umbo, ribs simple, coarser on dorsal valve, weak sulcus may be present in some specimens of both dorsal and ventral valves.

Holotype: BR 2429 from Eglinton Volcanics in Dunton Range, New Zealand, figured in Waterhouse & Campbell (2021, Fig. 1B) and herein as Fig. 7B, here designated.

Morphology: This species is so far not well represented in the fossil collections, but more material is available for collecting. It has been decided to name the form, because it represents an interval otherwise not covered in the array of *Notostrophia* species, and available evidence indicates that it does not match other described species.

The largest specimen BR 2429 is estimated to measure 56mm wide, 40mm long and approximately 12mm high. The dorsal valve is more inflated and transverse, with wide hinge and obtuse cardinal extremities, one measuring 40mm in width. Ventral costae number six in 5mm near mid-line anteriorly, with broad crests and narrow interspaces, and number thirteen to fifteen in 5mm laterally in BR 2429. Dorsal costae stronger, five in 5mm medianly, the number of costae increasing anteriorly, with subdivision of some costa by median slit. The ventral valve has several commarginal growth steps. No dental supports for the teeth. In the dorsal valve the high and curved cardinal process is supported by sturdy socket ridges, but further detail is not clear. The dorsal shell is at least 1.5mm thick, compared with ventral shell 0.5mm thick, apart from the ventral interarea, which is over 1mm thick.

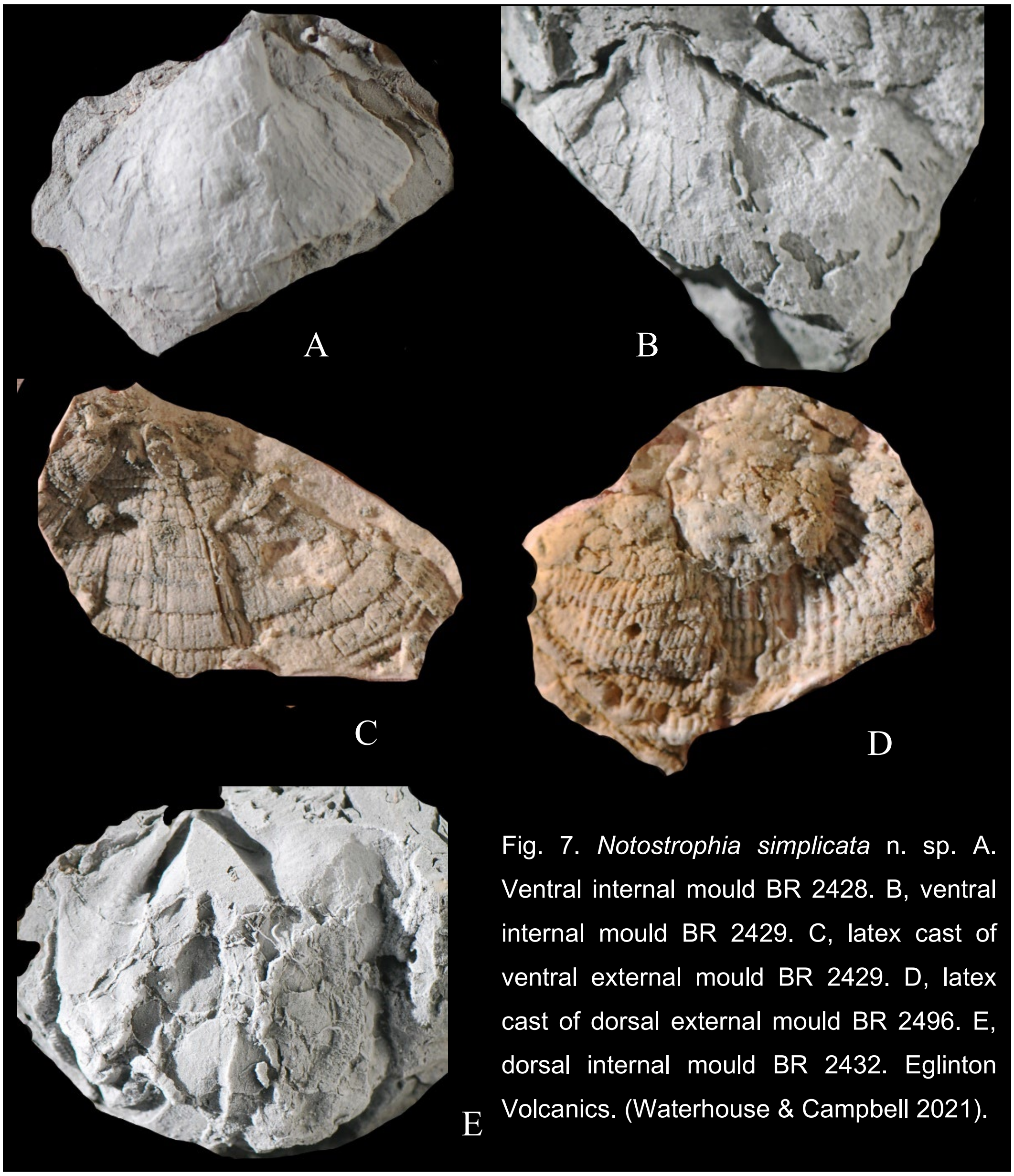

Fig. 7. *Notostrophia simplicata* n. sp. A. Ventral internal mould BR 2428. B, ventral internal mould BR 2429. C, latex cast of ventral external mould BR 2429. D, latex cast of dorsal external mould BR 2496. E, dorsal internal mould BR 2432. Eglinton Volcanics. (Waterhouse & Campbell 2021).

These specimens are characterized by long and varyingly divergent posterior walls for the ventral valve, with fine ventral costae and slightly broader higher dorsal costae. *Notostrophia zealandicus* Waterhouse (1982, p. 24, pl. 1d-l, 2a-f, Fig. 17B, C, 18) from the Brunel Formation, Takitimu Group, of south New Zealand, is the closest of known species in terms of ornament and has a reflexed dorsal anterior shell. The slightly younger species *N. homeri* Waterhouse (1973, 1982, p. 26, pl. 3a-h, 4a-d, 5a, Fig. 17D) from overlying beds in the Takitimu Range has a less inflated dorsal valve, with strong but narrow costae. The two New Zealand species are younger than the present form (Waterhouse 2002, p. 193). *N. laticostata* Waterhouse (2015, p. 57, Fig. 7-9) from the *Taeniothaerus subquadratus* Zone in the Tiverton Formation of the Bowen Basin, Queensland, has broad dorsal ribs that may be clustered into mutiples and lacks a reflexed ventral anterior. *N. bifurcata* Waterhouse (1986, p. 20, pl. 2, fig. 9-19) from the Fairyland and Dresden Formations of Sakmarian age in the southeast Bowen Basin is a smaller more elongate species with fine ventral ribs and dorsal ribs that are broad-crested. From the Roses Pride Formation of the southeast Bowen Basin, *N. alta* Waterhouse (1986, p. 20, pl. 2, fig. 20-24) is a very elongate shell with high ventral interarea, very fine ventral ribs and strong dorsal ribs, broader than those of the Dunton species, and likely to have been a contemporary of the New Zealand species *N. homeri*. The Tasmanian species *N. costellata* (Clarke, 1990) from the Early Permian basal Bundella Mudstone and *Tasmanites* oil shale of early Asselian age shows diversified ribbing and more widely divergent cardinal supports.

Stratigraphy: The species is limited so far as is known to the Eglinton Volcanics, in the *Magniplicatina undulata* Zone (Waterhouse & Campbell 2021, p. 54).

Notostrophia laticostata Waterhouse, 2015

Fig. 8 – 10

2015 *Notostrophia laticostata* Waterhouse, p. 57, Fig. 7-9.

Fig. 8. *Notostrophia laticostata* Waterhouse, latex cast of ventral valve UQF 81448 from Tiverton Formation, x1.3. (Waterhouse 2015)

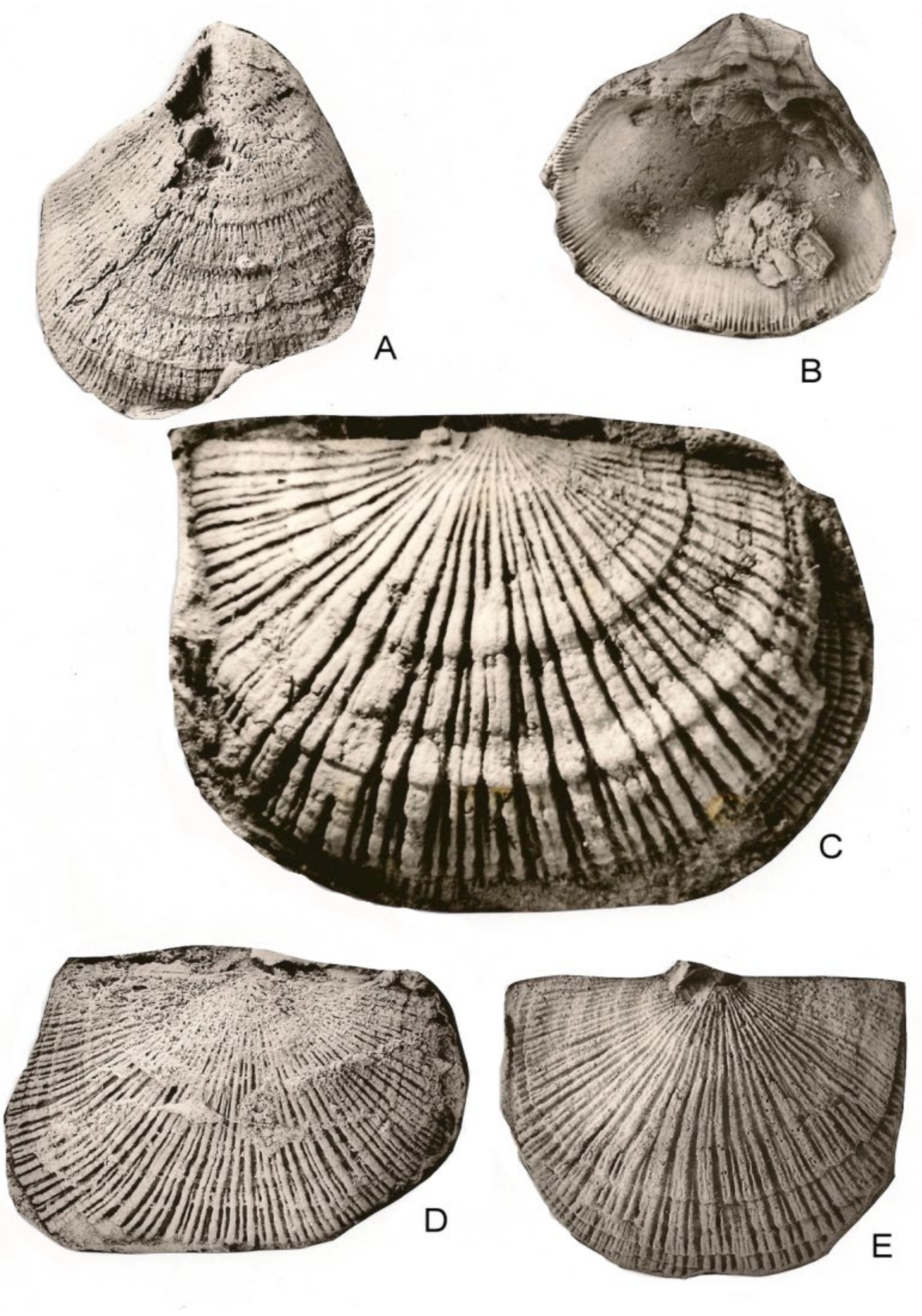

Fig. 9. *Notostrophia laticosta* Waterhouse. A, latex cast of ventral valve UQF 21057, x1.5. B, aspect of latex cast of ventral valve UQF 81299, x2. C, holotype, latex cast of dorsal exterior, UQF 54551, x2.5. D. latex cast of dorsal exterior UQF 21076, x2. E, latex cast of dorsal exterior UQF 43478, x1.5. Tiverton Formation. (Waterhouse 2015).

Diagnosis: Dorsal costae low and broad, split anteriorly into finer ribs, ventral costae fine, anterior dorsal valve not known to be anteriorly reflexed.

Holotype: Specimen UQF 54551 from upper middle Tiverton Formation, figured in Waterhouse (2015, Fig. 8C) and herein Fig. 9C, OD.

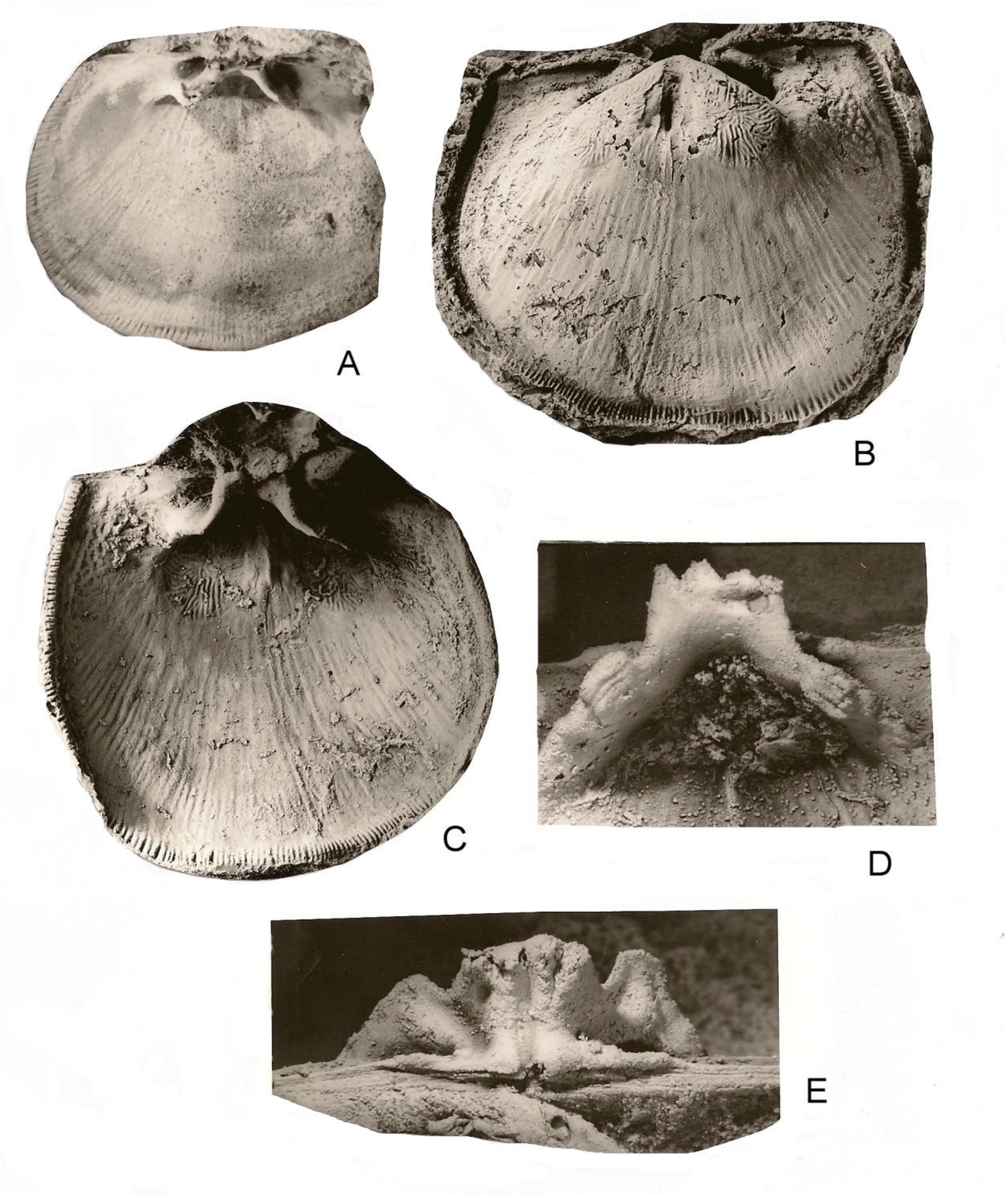

Fig. 10. *Notostrophia laticostata* Waterhouse. A, latex cast of dorsal interior UQF 81301, x2. D, E, detail of cardinal process, internal (ventral) and dorsal aspects, same specimen, x5. E shows the cardinal collar along the hinge. B, C, dorsal internal mould and latex cast of UQF 21375, x2. Tiverton Formation. (Waterhouse 2015).

Morphology: Shell moderately large and biconvex. Ventral valve subpentagonal with slightly extended ventral umbo and posterior walls diverging at 150 -160°, maximum width near mid-length. Interarea high, pseudodeltidium broad and convex, with hint of irregular median raised convex ridge indicative of a damaged monticule: both share low growth steps parallel to commissure and fine impersistent vertical striae. Costae distinctive, arranged in subfascicles, increase by intercalation and branching in four successive bands, primaries and secondaries develop broad flat crests with narrow interspaces, and two anterior sets of costae retain narrow crests.

Ventral interior without dental supports, other interior markings not clear. Cardinal process of dorsal valve high, adjoined anteriorly by sturdy support plates diverging at 100°. These were called socket plates by Williams & Brunton (2000) and unlike the socket plates of various brachiopods, extend well in front of the dental sockets, to constitute significant internal supports for the cardinal process, as well as helping at their posterior end to contain the teeth from the ventral valve. In some respects they compare well with the lateral buttress plates of some Productida (cf. Waterhouse 2013, p. 17, although the productids lack teeth).

A low anterior ridge lies at base of exterior process (Fig. 10E). Dorsal adductor scars marked by distinctive grooves, the inner grooves linear from hinge to anterior, the lateral grooves recurving back from near centre, divided by low broad variable ridge. Shell finely extropunctate, a thick outer layer rippled by costae and also pierced by open pores in short rows; thin inner impunctate layer. This species is characterized by its broad dorsal ribs that may be clustered into mutiples and by lack of reflexed ventral anterior.

Stratigraphy: The species comes from the middle Tiverton Formation, in the *Magniplicatina undulata* Zone.

Notostrophia zealandicus Waterhouse, 1982

Fig. 11, 12, 13A, B

1964a *Streptorhynchus* sp. Waterhouse, p. 71.
1964b *Streptorhynchus* sp. Waterhouse, p. 210.
1982 *Notostrophia zealandicus* Waterhouse, p. 24, pl. 1d-l, 2a-f; text-fig. 17B, C, 18.

Diagnosis: Strong dorsal costae crossed by almost regular commarginal wrinkles, fold present in some specimens, low interarea. Ventral costae finer, moderately high interarea.

Holotype: BR 8 from high in Brunel Formation, Takitimu Group, New Zealand, figured by Waterhouse (1982, pl. 1d, 2c, f) and herein as Fig. 12C, F, OD.

Morphology: The ventral costae are definitely finer than those of the dorsal valve, ten in 5mm at 20mm from the umbo on the ventral valve, compared with five or six in 5mm at 20mm from the dorsal umbo, with more measurements provided in Waterhouse (1982, p. 26). The socket supports are sturdy and short, and a socket ridge projection as named by Thomas (1958) lies close to the posterior margin of each socket plate, but there is no cardinal collar.

Stratigraphy: The species typifies the *Notostrophia zealandicus* Zone, with an array of species not found elsewhere either in New Zealand or east Australia, and evidently marking a short-lived and possibly geographically very restricted fauna, slightly older than the *Echinalosia preovalis* Zone.

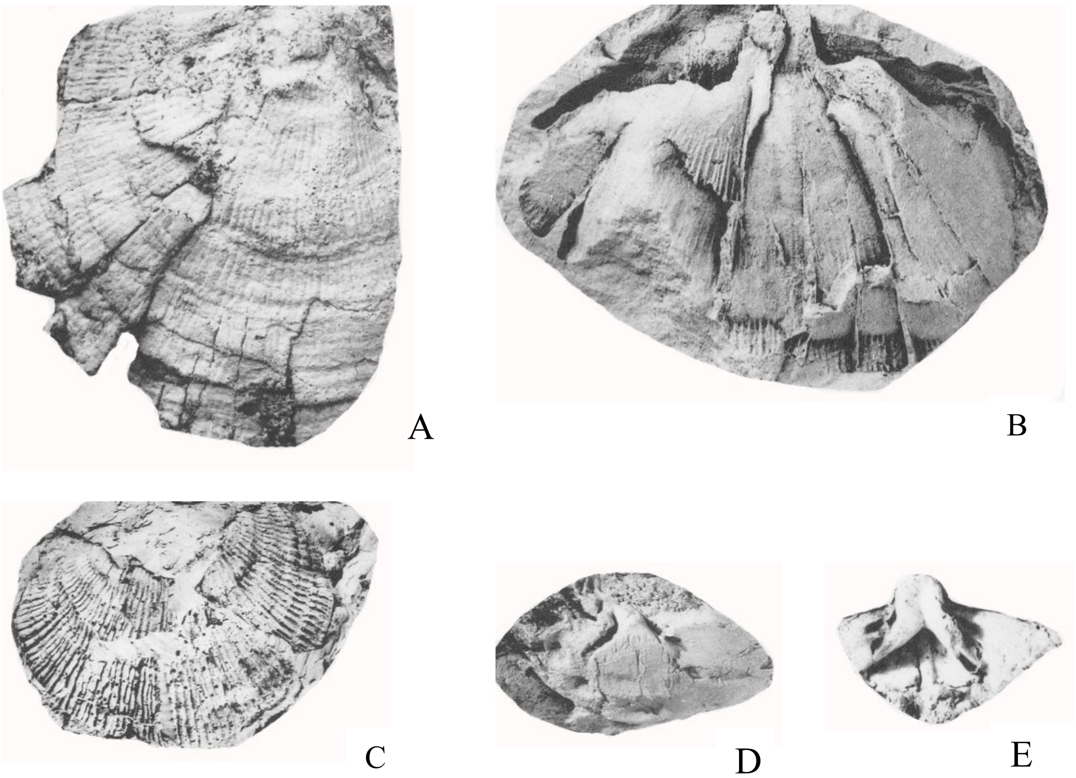

Fig. 11. *Notostrophia zealandicus* Waterhouse. A, latex cast of ventral exterior, BR 944, x2. B, mould of ventral interior and interarea, BR 945, x2. C, PVC cast of dorsal exterior, BR 7 x1. D, posterior aspect of dorsal internal mould BR 5, x1. E, latex cast of cardinalia in immature dorsal valve BR 3, x2. Brunel Formation, New Zealand. (Waterhouse 1982).

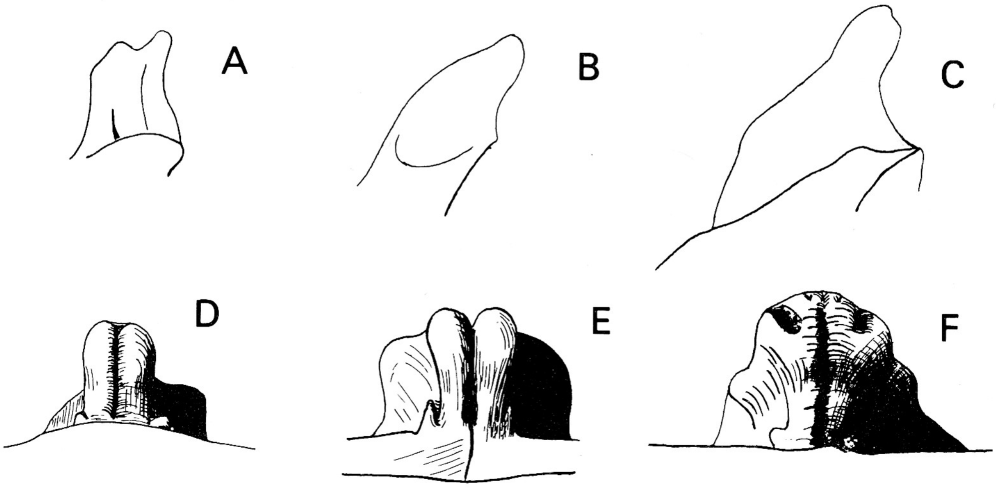

Fig. 12. *Notostrophia zealandicus* Waterhouse, lateral and posterior views of cardinal process, x4. A, BR 3. B, BR 5. C, BR 8, D, E, F corresponding posterior views. Brunel Formation. (Waterhouse 1982).

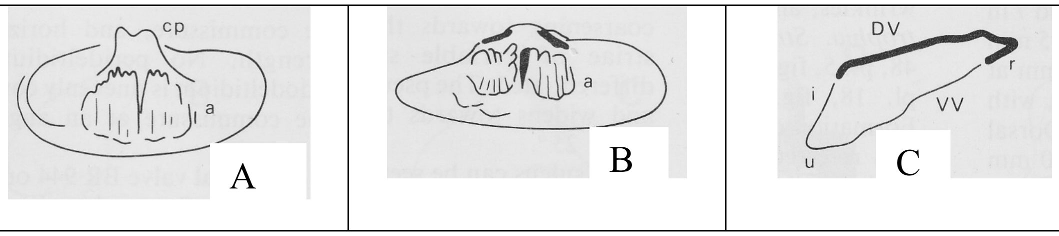

Fig. 13. A, B, *Notostrophia zealandicus* Waterhouse. A, latex cast of dorsal interior, BR 5, x1.3. B, internal mould of dorsal interior BR 7, x1. C, *N. homeri* Waterhouse, lateral cross-section, dorsal valve on top, in heavy black line, in concept, x1. Brunel Formation. (Waterhouse 1982).

Notostrophia homeri Waterhouse, 1982

Fig. 13C, 14 - 16

1973 *Notostrophia homeri* Waterhouse, p. 36, fig. 1, 2: no. 1, 3, 6.
1982 *N. homeri* Waterhouse, p. 26, pl. 3a – h, pl. 4a – d, pl. 5a, text-fig. 17D.
1991 *N.* cf. *homeri* – Begg & Ballard, p. 146, Fig. 2, 3.

Diagnosis: Ventral valve high, dorsal valve little inflated, recurved posteriorly from anterior margin, no fold. Ribs fine over ventral valve, coarse over dorsal valve except for recurved portion. Cardinal process broad.

Holotype: BR 1472 figured in Waterhouse (1982, pl. 4d) and herein as Fig. 15A from Brunel Formation, New Zealand, OD.

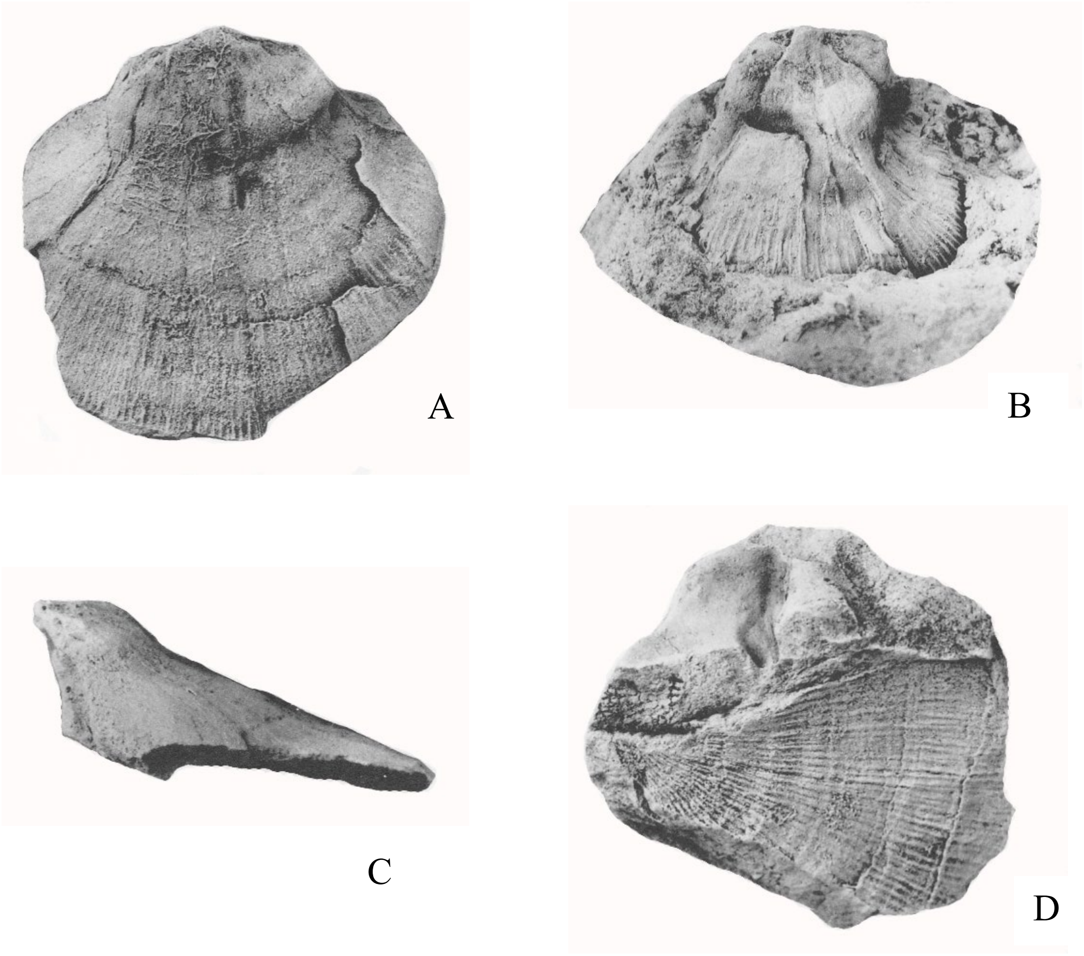

Fig. 14. *Notostrophia homeri* Waterhouse. A, C, ventral and lateral aspects of internal mould BR 1506. B, ventral internal mould BR 1526. D, posterior dorsal view of BR 1506 showing teeth and cardinal area, overlain by external mould of a different ventral valve showing the fine ribbing. Specimens x2. Brunel Formation. (Waterhouse 1982).

Morphology: Dorsal costae number six to seven in 5mm at about 5mm from the umbo, five in 5mm at 20mm from the umbo and four to six in 5mm near the anterior margin, where several costae appear by intercalation. About ten costae are present at the anterior margin of the ventral valve and eight costae in 5mm at 15mm from the umbo in another ventral valve, with eleven in 5mm anteriorly on another specimen. There are fine radial striae as well.

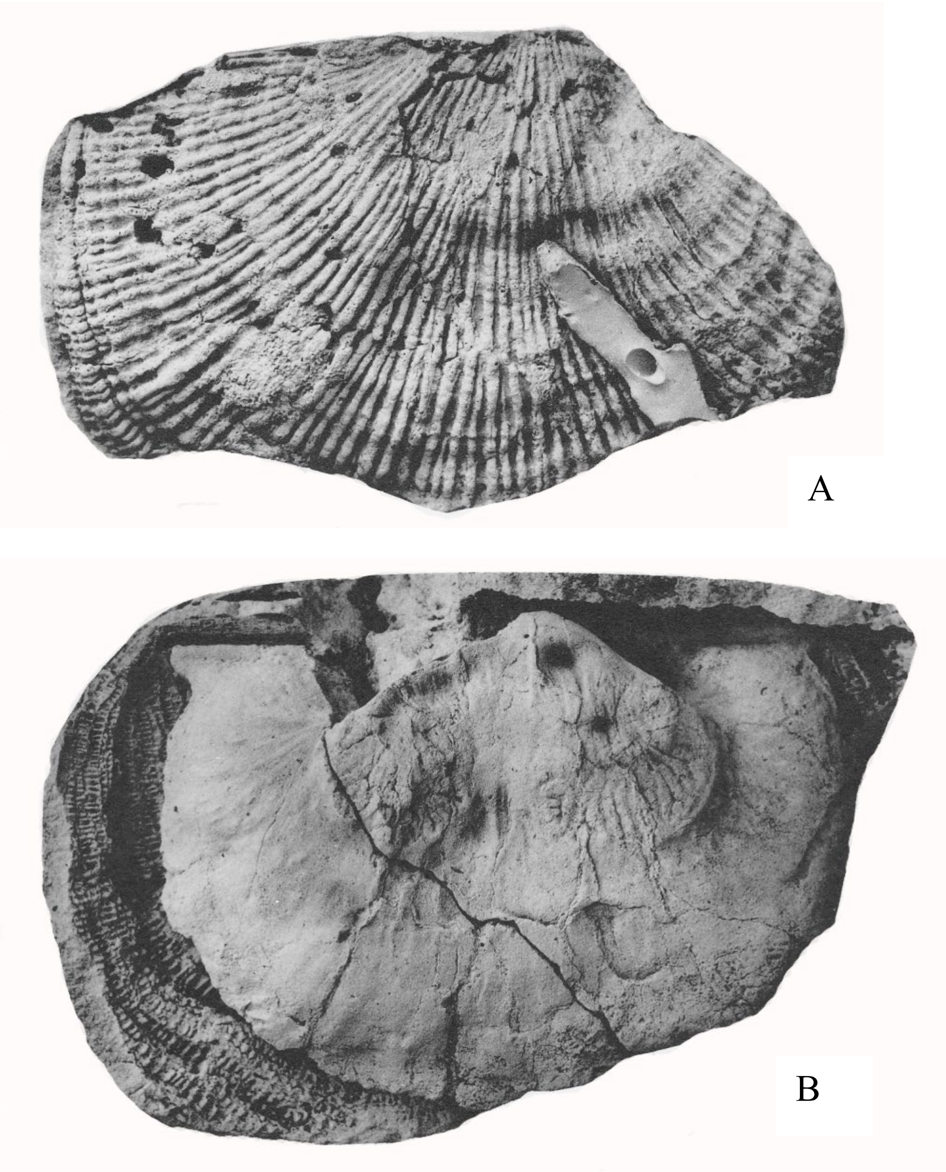

Fig. 15. *Notostrophia homeri* Waterhouse. A, latex cast of dorsal exterior, BR 1472 holotype. B, internal mould of holotype showing muscle scars and fine costae anteriorly from recurved anterior dorsal valve. Specimens x2 from Brunel Formation, New Zealand. (Waterhouse 1982).

Stratigraphy: The type material comes from the upper Brunel Formation of the Takitimu Range, above the *Notostrophia zealandicus* Zone, in a faunal assemblage related to that of the *Echinalosia preovalis* Zone in east Australia. Begg & Ballard (1991) reported the species from an equivalent fauna in the Mantle Volcanics of the Skippers Range to the west.

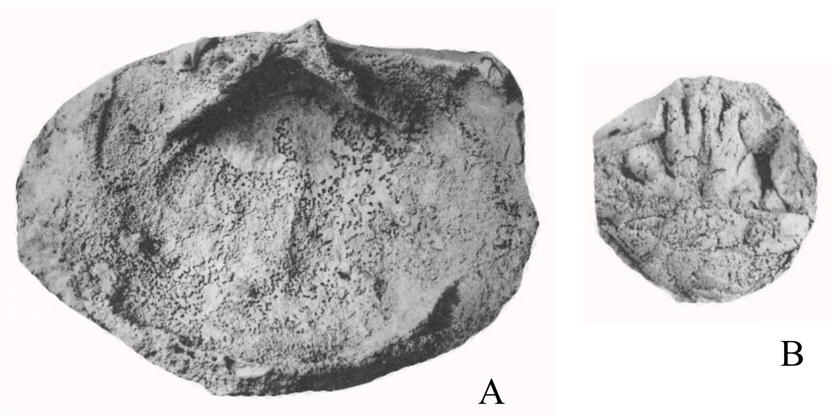

Fig. 16. *Notostrophia homeri* Waterhouse. A, latex cast of dorsal interior, BR 1470. B, posterior aspect of cardinal process (registration number not available). Specimens x2 from Brunel Formation. (Waterhouse 1982).

Notostrophia alta Waterhouse, 1986

Fig. 17

1986 *Notostrophia alta* Waterhouse, p. 20, pl. 2, fig. 20-24.

Diagnosis: Elongate small shells with prominent ventral umbo, high flat ventral interarea, fine costae close to twelve in 5mm, dorsal valve gently convex with shallow anterior sulcus and coarse costae, numbering five to six in 5mm.

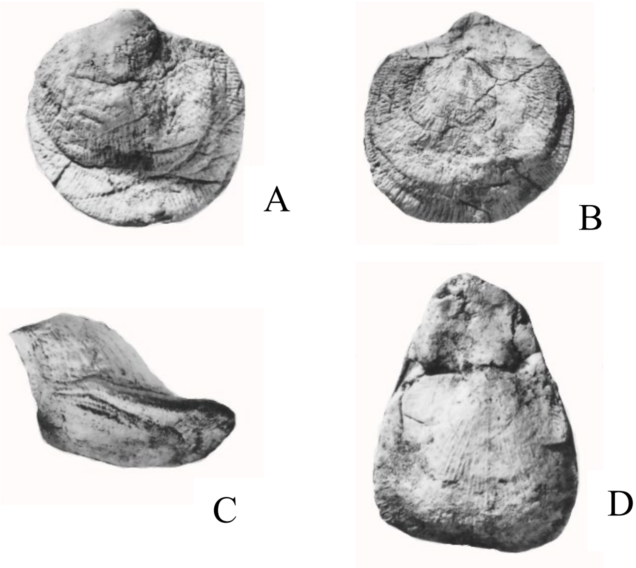

Fig. 17. *Notostrophia alta* Waterhouse. A, B, C, ventral, dorsal and lateral aspects of holotype, UQF 73933. D, dorsal aspect of specimen with valves conjoined, UQF 73934. Specimens x1, from Roses Pride Formation, southeast Bowen Basin. (Waterhouse 1986).

Holotype: UQF 73933 from Roses Pride Formation, figured by Waterhouse (1986, pl. 2, fig. 21, 22, 24) and herein as Fig. 17A, B, C, OD.

Stratigraphy: Although of the same age as *Notostrophia homeri* in New Zealand, this species involves much smaller specimens with more elongate shape and high ventral interarea, with other differences. Following a number of species in the Early Permian, the genus seems to have disappeared from the fossil record in both east Australia and New Zealand.

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A SUMMARY OF CHONETIDINA (BRACHIOPODA) FROM THE PERMIAN FAUNAS OF EAST AUSTRALIA AND NEW ZEALAND

Abstract

Chonetid species and specimens are described from Permian macro-faunas of east Australia and New Zealand. There are no more than six genera and subgenera, but one or two species occur in overwhelming abundance in bands at a couple of horizons.

INTRODUCTION

The most significant paleontological contributions by N. W. Archbold, based at Deakin University in Melbourne, have been in Western Australia, but he has extended his studies into east Australia with analyses of chonetid brachiopods from Permian deposits. Not that there are many species involved, as far as is presently known. There is a scattering of forms, ranging from Sakmarian into middle Changhsingian, and they appear to be limited to a handful of genera. Anopliids are represented only by very few specimens, too few to allow even the genus to be determined with confidence, and the remainder centre around the genera *Svalbardia* Barchatova, *Neochonetes* Muir-Wood, and *Capillonia* Waterhouse, with a poorly known form *Tivertonia* Archbold, based on a poorly preserved type species *Lissochonetes yarrolensis* Maxwell, as well as a distinctive genus *Gympietes* from the Early Permian at Gympie, southeast Queensland. The differences between species, and variation within species, are not straightforward, and the entire group could benefit from closer study.

SYSTEMATIC SUMMARIES

Phylum Brachiopoda Duméril, 1806

Class Strophomenata Williams et al., 1996

Superorder PRODUCTIFORMII Waagen, 1883

Order CHONETIDA Muir-Wood, 1962

Discussion: Chonetids have spines limited to the ventral valve, especially along the hinge, and never have dorsal spines. The trail is not strongly discriminated, and internally teeth and a ventral septum is developed with vascular trunks, and there are usually dorsal sockets, accessory septa and relatively small brachial shields. Russian authorities have long recognized the validity of Chonetida as distinct from Productida, as further discussed in Waterhouse (2013), Nalivkin (1979) treating the chonetids as a full order.

Superfamily **CHONETOIDEA** Bronn, 1862

Family **ANOPLIIDAE** Muir-Wood, 1962

Subfamily **ANOPLIINAE** Muir-Wood, 1962

Diagnosis: Small strongly concavoconvex anopllids with smooth exterior.

Anopliin gen. & sp. indet. A

Fig. 1B, ?C

1964 *Lissochonetes yarrolensis* Maxwell, pl. 6, fig. 10, 12 (part, not fig. 9, 11, 13, 14 = *Tivertonia yarrolensis*).
1983 *Tivertonia yarrolensis* – Archbold, p. 71.

Fig. 1. Anopliin specimens. A, Anopliin gen. & sp. B, ventral valve BR 2380 from Hilton Limestone, New Zealand. B, ?C, Anopliid gen. & sp. A, ventral valve UQF 43044 x2. ?C, small ribbed specimen of uncertain affinities, UQF 43040 x2. From Yarrol Limestone, Queensland. (Waterhouse 2001, Maxwell 1964).

Maxwell (1964) figured two specimens from the Yarrol Limestone of the Yarrol Basin in Queensland of which at least one appears to be anopliid, judged from the swollen ventral valve (Fig. 1B). But the identity of the specimen in Fig. 1C is more doubtful. Its ornament consists of well-defined ribs, and Permian anopliin specimens are not known to be ribbed, as summarized by Racheboeuf (2000). There needs to be more material and closer study to determine the nature of the species and generic affinities.

Stratigraphy: The species is likely to be of middle Sakmarian age.

Anopliin gen. & sp. B

Fig. 1 A

2001 Anopliin? gen. & sp. indet. Waterhouse, p. 16, pl. 1, fig. 9, text-fig. 4.

A small transverse ventral valve 12mm wide comes from the Hilton Limestone at Wairaki Downs, New Zealand. The shell surface is smooth. No dorsal valve is known.

Stratigraphy: The Hilton Limestone belongs to the *Spinomartinia spinosa* macro-faunal Zone, of approximately upper middle Changhsingian (Late Permian) age.

Family **RUGOSOCHONETIDAE** Muir-Wood, 1962

[Nom. transl. Cooper & Grant 1975, p. 1212 ex Rugosochonetinae Muir-Wood, 1962] et seq.

Subfamily **RUGOSOCHONETINAE** Muir-Wood, 1962

Genus ***Neochonetes*** Muir-Wood, 1962, p. 87

Diagnosis: Transverse weakly concavoconvex shells with firm ribs and numerous spines. May be weakly sulcate. Ventral valve with median septum and teeth, dorsal valve with two lateral septa.

Type species: *Chonetes dominus* R. H. King, 1938, p. 259 from Upper Carboniferous Marble Falls Limestone, Texas, OD.

Neochonetes beatusi Waterhouse, 1964

Fig. 2

1952 *Chonetes* sp. ?n. sp. Fletcher, p. 10, pl. 1, fig. 7, 8.
1964 *Neochonetes beatusi* Waterhouse, p. 18, pl. 1, fig. 3-6.

Diagnosis: Moderately transverse large shells with alate hinge and roundly subrectangular outline, most ventral valves weakly sulcate.

Holotype: BR 743 figured in Waterhouse (1964, pl. 1, fig. 4) and herein as Fig. 2A from middle Mangarewa Formation, New Zealand, OD.

Morphology: Although Fletcher (1952) stated that his figured specimens were brachial (= dorsal) valves, they are in fact ventral valves, with teeth and cardinal spines, and gentle convexity.

Stratigraphy: The species is found in the *Maxwellosia ovalis wassi* fauna, part of the *ovalis* Superzone.

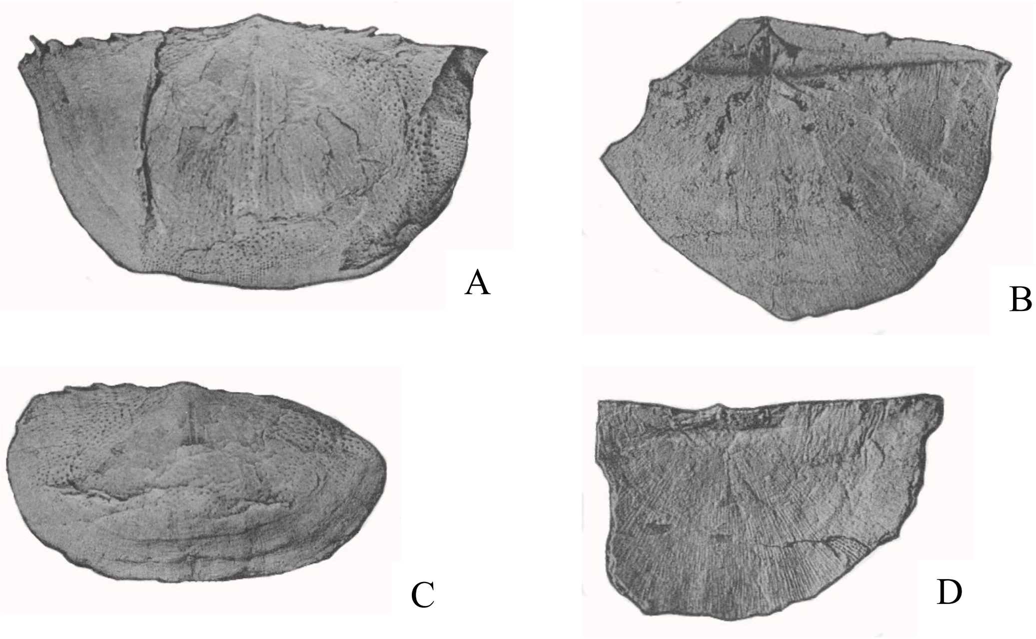

Fig. 2. *Neochonetes beatusi* Waterhouse. A, ventral valve BR 743, holotype. B, external mould of dorsal valve and posterior ventral valve, BR 741. C, decorticated ventral valve, also figured by Fletcher (1952), BR 11. D, dorsal external mould, BR 931. Specimens x2, from middle Mangarewa Formation, New Zealand. (Waterhouse 1964).

Subfamily **SVALBARDIINAE** Archbold, 1982

Diagnosis: Small to medium shells without ribs, ventral hinge spines.

Genus ***Svalbardia*** Barchatova, 1970

Diagnosis: Shell smooth, transverse, with no more than a shallow if any ventral sulcus or low dorsal fold, ventral valve gently convex, dorsal valve concave or almost flat, cardinal extremities weakly alate or obtuse, maximum width usually in front of the hinge, hinge spines thin and lying at moderate angle to hinge. Ventral interior with teeth, small adductor scars, large weakly impressed diductor scars, slender pair of vascular trunk ridges, divided posteriorly and usually anteriorly by long median septum, most vascular pustules evenly spread and of subequal size, tend to be stronger near anterior margin. Dorsal cardinal process low and broad, with pit or broad platform in front, behind long median septum, inner anterior adductor scars well defined, outer posterior adductor impressions may be faint, divided by short pair of anderidia, which broaden at maturity, lateral cardinal ridges well developed, joining or separate from lateral posterior ridges, brachial shields well developed, anterior pustules numerous.

Type species: *Chonetes capitolinus* Toula, 1875, p. 26 from Spirifer Limestone (late Artinskian) of Svalbard, OD.

Discussion: Gobbett (1964, pl. 15, fig. 11-13) and Ifanova (1972, pl. 2, fig. 33-35) have provided figures of shells identified with the type species, to reinforce the original description.

Svalbardia*? *cracowensis (Etheridge Snr, 1872)

Fig. 3

1872 *Chonetes cracowensis* Etheridge Snr, p. 336, pl. 18, fig. 2.
1892 *C. cracowensis* – Etheridge Jnr, p. 262, pl. 13, fig. 9.
1986a *Svalbardia cracowensis* – Waterhouse, p. 21, pl. 2, fig. 25-32.

Diagnosis: Small slightly transverse shells normally with rounded non-alate cardinal extremities.

Lectotype: Sole specimen figured by Etheridge Snr (1872), by monotypy, from Fairyland Formation, SD Waterhouse (1986a, p. 21).

Morphology: *Chonetes cracowensis* Etheridge Snr (1872, p. 336, pl. 18, fig. 2) was ascribed to *Svalbardia* by Waterhouse (1986a, p. 21, pl. 2, fig. 25-32). This species has maximum width near mid-length and lacks a sulcus, and its dorsal valve is moderately flat with a band of large pustules between the brachial shields, and conspicuous circle of pustules in front of the brachial shields as in Ifanova's specimens from the Petchora Basin. The ventral septum tends to be shorter than in *Capillonia armstrongi* (see p. 43), and the dorsal septum is only moderately long, and strong pustules lie between the brachial shields. Maximum width varies from hinge to mid-length.

The species is a comparatively early representative of the genus, and is compared with other species in Waterhouse (1986a, p. 22). The generic position is insecure. *Svalbardia* as illustrated by Toula (1875), Gobbett (1964) and Ifanova (1972) and further interpreted from better preserved material from Western Australia by Archbold (1982) has rounded cardinal extremities, an almost flat dorsal valve, and very strong dorsal median septum. Most of the figures of *cracowensis* in Waterhouse (1986a) conform with this description, but that of Fig. 3D shows a more concave dorsal valve, and the dorsal septum in Fig. 3F is not overwhelmingly long.

Stratigraphy: The species is limited to the Fairyland Formation, in the southeast Bowen Basin.

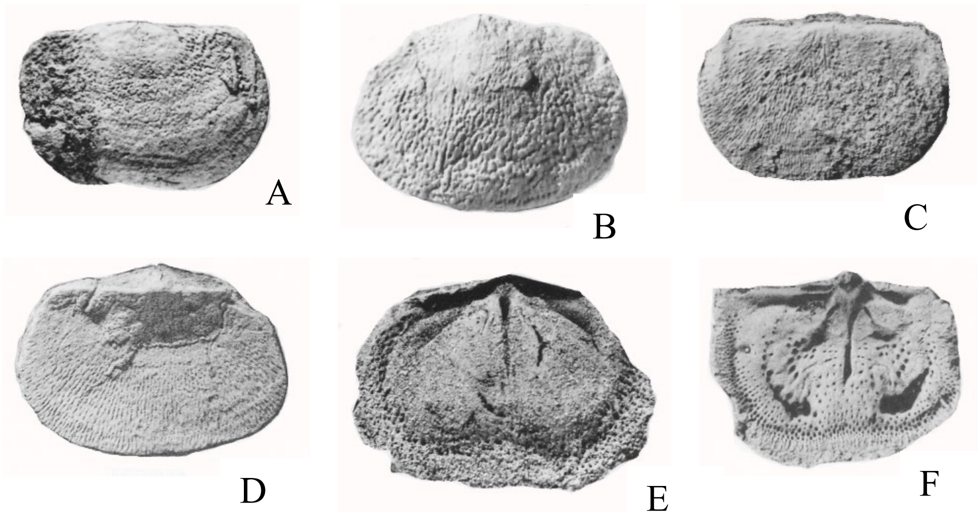

Fig. 3. *Svalbardia cracowensis* (Etheridge). A, C, worn ventral and dorsal exteriors, UQF 26203. B, D, ventral exterior and dorsal aspect, UQF 43402. E, ventral internal mould, UQF 73935, F, dorsal internal mould, UQF 73938. Specimens x2 from Fairyland Formation. (Waterhouse 1986a).

Genus and subgenus ***Capillonia*** (***Capillonia***) Waterhouse, 1973

Diagnosis: Ventral valve smooth, dorsal valve concave, possibly weakly capillate, cardinal extremities slightly produced and acute, spines orthomorph oblique, thin dorsal median septum, short anderidia.

Type species: *Lissochonetes brevisulcus* Waterhouse, 1964a from Kildonan Member and Trig D Formation, Arthurton Group, New Zealand, OD.

Discussion: This genus is characteristic, given its extended hinge and regular gently concave dorsal valve. Uncertainty still surrounds the nature of the dorsal surface. Waterhouse (1973) believed that the dorsal valve showed very fine capillae, but Archbold (1981) and Racheboeuf (2000) have expressed their opinion that the effect could be due to wear on the surface of a smooth shell, and at present this feature therefore remains of uncertain value. A number of Australian species that have been referred to different genera are apparently closely related to *Capillonia*. Unlike *Svalbardia*, they have a more concave dorsal valve, and the cardinal extremities are often produced and acute, although this is not always clear, because preservation is not as good as it is for the New Zealand type material. This is a significant factor in the validity or otherwise of the genus *Tivertonia* Archbold. The proposed type species *Lissochonetes yarrolensis* Maxwell, 1964 is poorly illustrated and not very well preserved by comparison with *brevisulcus*. The one apparent difference from type *Capillonia* lies in the broader deeper ventral sulcus found in several specimens of *yarrolensis*. On this basis, the name *Tivertonia* is treated as a subgenus of *Capillonia*, but reservations remain. Archbold based his distinctions for *Tivertonia* on non-type material from the Tiverton and Farley Formations, as described herein as *armstrongi* and *saeptata*, and these are illustrated below to allow pictorial assessments

Capillonia (***Capillonia***) ***armstrongi*** (Waterhouse, 2015a)

Fig. 4 - 8

1892 *Chonetes* sp. ind. (d) Etheridge, p. 264, pl. 37, fig. 19.
1964 *Lissochonetes* sp. Hill & Woods, p. 8, pl. 4, fig. 4.
1972 *L. australis* Maxwell – Hill, Playford & Woods, p. 8, pl. 4, fig. 4.
1983 *Tivertonia yarrolensis* [not Maxwell] – Archbold, Fig. 2A-P.
1983 *L. yarrolensis* [not Maxwell] – Waterhouse, Briggs & Parfrey, p. 126, pl. 1, fig. 1-3.
1983 *Tivertonia yarrolensis* – Archbold, p. 71, pl. 2, fig. A-P.
cf. 1991 *T.* cf. *yarrolensis* [not Maxwell] – Begg & Ballard, p. 146, Fig. 4.
2000 *T. yarrolensis* [not Maxwell] – Racheboeuf, p. 420, Fig. 275a-c.
2015a *Svalbardia armstrongi* Waterhouse, p. 62, Fig. 10-18.

Diagnosis: Moderately large with gently convex ventral valve, maximum width at hinge or near mid-length, dorsal valve flat or very gently to moderately concave, thickened, internal septa well developed.

Holotype: UQF 81627 from UQL 4515, figured in Waterhouse (2015a, Fig. 12A, B, Fig. 14A) and herein as Fig. 5A, B from Tiverton Formation, OD.

Fig. 4. *Capillonia* (*Capillonia*) *armstrongi* (Waterhouse) UQF 81379, x6 from Tiverton Formation. (Waterhouse 2015a).

Morphology: The species has been described by Archbold (1983) as well as Waterhouse (2015a). Surface detail is poorly preserved, and the surface now worn to show radial rows of pustules. The full length of ventral hinge spines is seldom displayed. Archbold (1986) suggested that the hinge spines were short, but a specimen at early maturity has spines at least 8mm long, which is not unduely short. Most specimens suggest that maximum width lay close to the hinge throughout most of ontogeny, but a number of specimens are widest near mid-length during at least part of shell development. A few dorsal valves have a low slender median fold anteriorly, and some show growth steps. Others have a flat rather than gently concave disc, and curve into the short trail, but available evidence does not otherwise distinguish these as a discrete taxon. One ventral valve has a median sulcus, close to that in the Yarrol ventral valve figured by Maxwell (1964, pl. 6, fig. 14), but most other detail is obscured by weathering. Whether it is a variant of the present species or not is therefore uncertain.

Within the ventral valve, the strength of the ventral septum varies, and rarely the septum is short and is high posteriorly. In the dorsal valve, the posterior hinge and teeth and cardinal process ridges vary somewhat, and the medium septum also varies in strength: often it is broad posteriorly, where it may be divided by a groove, and the septum is long and thin in front. A broad platform lies in front of the cardinal process, and bears a well-developed alveolus in mature specimens.

The species is crowded in a band now called the *Capillonia armstrongi* band near Homevale high in the middle level of the Tiverton Formation in the Bowen Basin. The Homevale material was originally identified with the species *yarrolensis* Maxwell (1964) from the Yarrol Basin. The Yarrol specimens belong to two different genera, and those closer to the Homevale specimens, including the holotype, are small, similar to the Homevale specimens in shape, and distinguished by the wider and deeper ventral sulcus, short ventral septum and different vascular pustules.

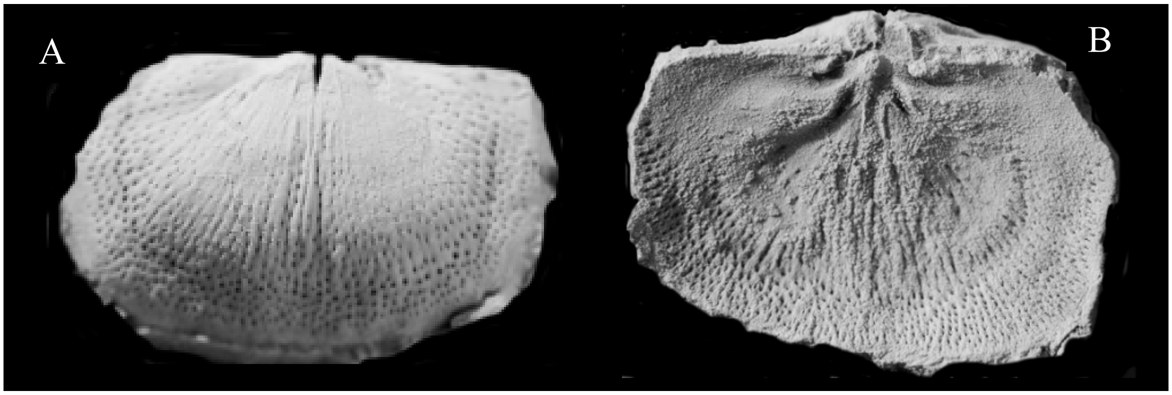

Fig. 5. *Capillonia* (*Capillonia*) *armstrongi* (Waterhouse), holotype, ventral and dorsal views of internal mould UQF 81627 from Tiverton Formation, x3.5. (Waterhouse 2015a).

Etheridge (1892) figured a ventral valve UQF 1486 from the Tiverton Formation of the Mt Britton Goldfield. Another Tiverton taxon *Bookeria drysdalei* Waterhouse is present on the same rock sample (p. 126).

Occurrences of a chonetid were also noted in the Sydney Basin by Waterhouse (1970, p. 389) and Waterhouse et al. (1983), as confirmed and illustrated by Archbold (1986), and this taxon is identified as a different taxon (see *saeptata* herein, p. 56). Farley specimens tend to have the maximum width near mid-length, as in some of the Homevale specimens, whereas most Homevale specimens are widest at the hinge. Farley specimens tend to have fewer hinge spines (Archbold 1986, Fig. 1L), and long but variable ventral median septum and long dorsal median septum.

The indeterminate chonetid recorded by Waterhouse (1964a, pl. 4, fig. 1, 2) from the correlative *Notostrophia zealandicus* Zone of the Takitimu Group in Southland has a short septum in the ventral valve, and in several respects, the New Zealand material is closer to *Capillonia* than to *Svalbardia,* and it might prove to be conspecific with or closely allied to *armstrongi*.

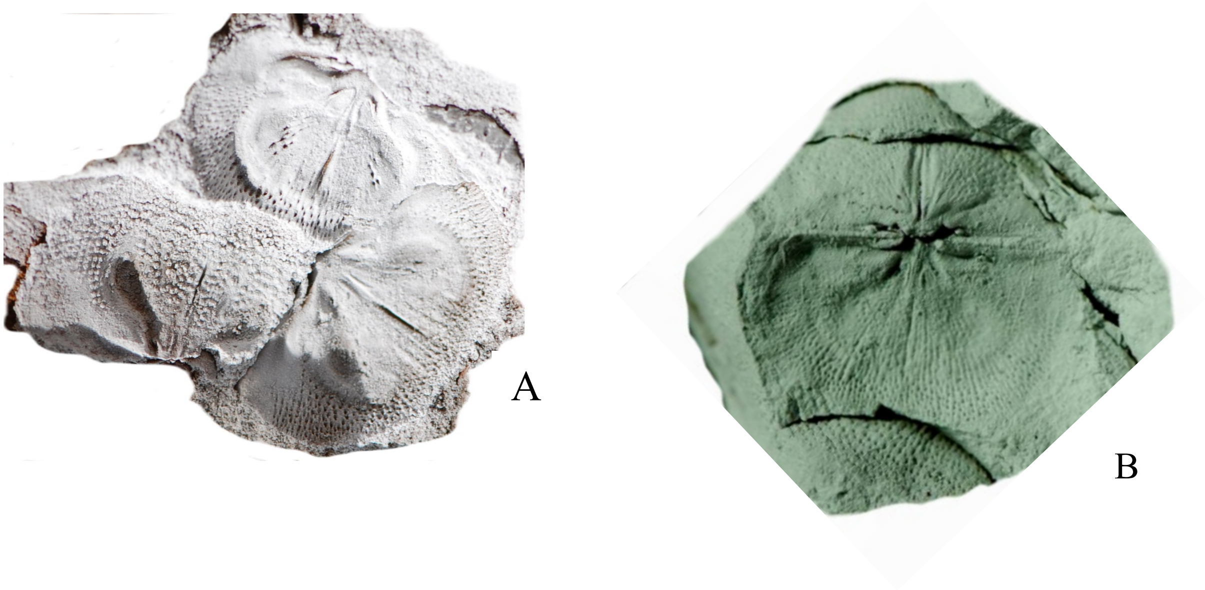

Fig. 6. *Capillonia* (*Capillonia*) *armstrongi* (Waterhouse). A, internal moulds of dorsal valves UQF 81376 and UQF 81377, x3. B, internal mould of dorsal and ventral valve UQF 81184, x3. From Tiverton Formation. (Waterhouse 2015).

Taxonomy: Hill et al. (1972) referred to *Lissochonetes australis* Maxwell, but this name was never published by Maxwell. Whether this name was applied originally by Maxwell to the Yarrol species in his unpublished Ph. D. thesis, or separately to the Tiverton form, is not known, but either way, the name has no validity.

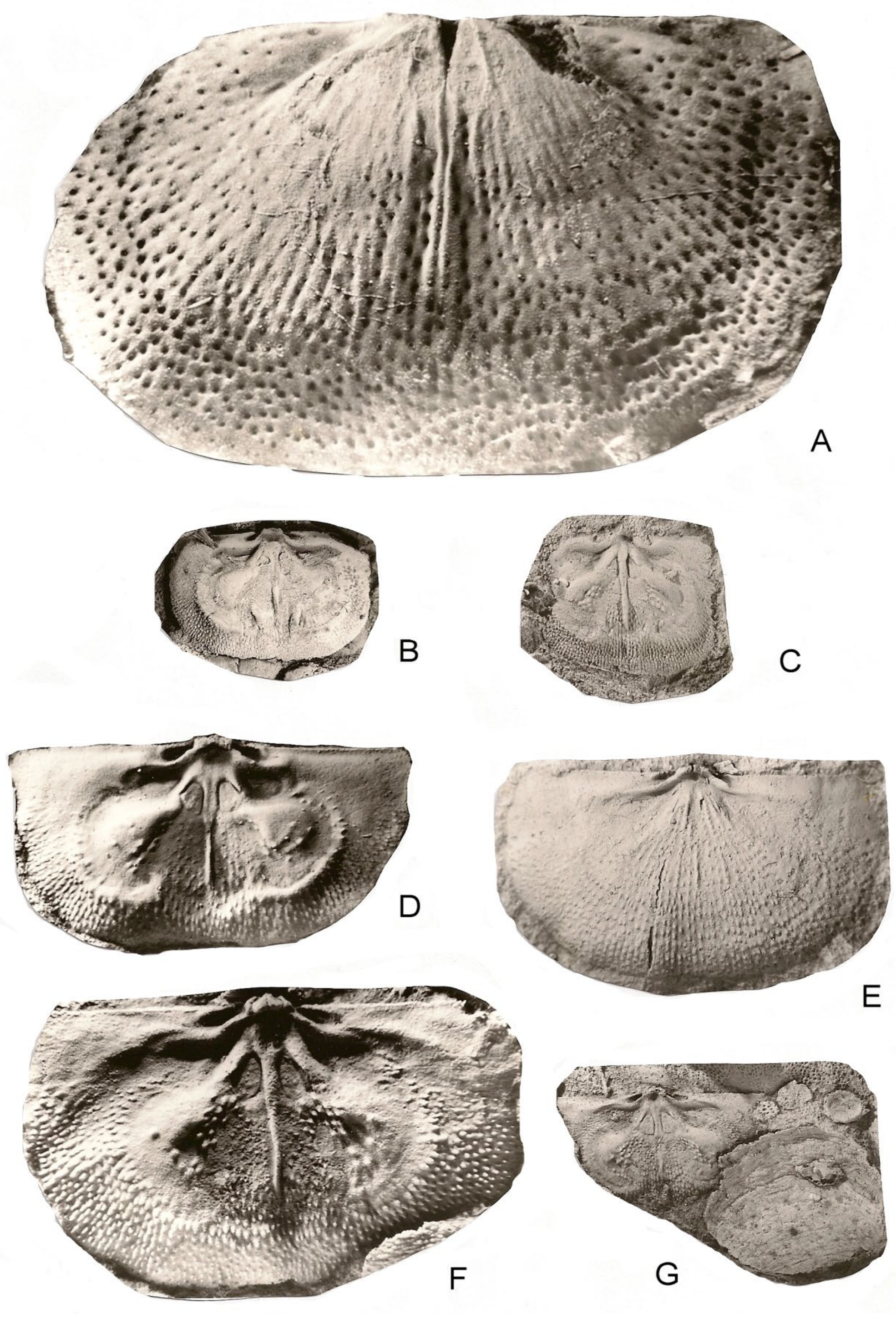

Fig. 7. *Capillonia* (*Capillonia*) *armstrongi* (Waterhouse). A, holotype, ventral internal mould UQF 81627, x6. B, latex cast of dorsal interior, near UQF 20871, x1.6. C, latex dorsal internal mould UQF 81181, x1.5. D, latex cast of dorsal interior, UQF 21000, x3. E, latex cast of immature dorsal interior, UQF 81183, x3. F, latex cast of dorsal interior, UQF 20913, x3. G, latex dorsal internal cast UQF 81182 with part of dorsal cast of *Maxwellosia cenula*, x1.5. From Tiverton Formation. (Waterhouse 2015a).

Fig. 8. *Capillonia* (*Capillonia*) *armstrongi* (Waterhouse), latex preparation from the bedding plane of a slab, showing dorsal interiors UQF 81181 and 81182, x1.3. From Tiverton Formation. (Waterhouse 2015a).

Capillonia (***Capillonia***) ***semicircularis*** (Campbell, 1953)

Fig. 9, 10

1953 *Lissochonetes semicircularis* Campbell, p. 6. Pl. 1, fig. 10-13.
1971 *L. semicircularis* – Dear, p. 4, pl. 2, fig. 9.
?1983 "*Lissochonetes*" *semicircularis* – McClung, p. 70, Fig. 12,2.
1983 *Capillonia semicircularis* – Archbold, p. 67.
1986a *Capillonia*? *semicircularis* – Waterhouse, p. 22, pl. 2, fig. 34, pl. 15, fig. 2, 4 (part, not pl. 2, fig. 33, 35, pl. 3, fig. 1-4, pl. 15, fig. 3, 5 = *solida*).
1988 *C. semicircularis* – Parfrey, p. 12, pl. 2, fig. 11-13.

Diagnosis: Somewhat rectangular in outline, and less alate than *brevisulcus*.

Holotype : UQF 14621 from lower Peawaddy Formation, figured by Campbell (1953, pl. 1, fig. 10, 11) and Fig. 9A herein, OD.

Morphology: The species was described mostly by Campbell (1953) and Waterhouse (1986a), but the original types were poorly figured. Archbold (1983) assigned the species to *Capillonia*.

Stratigraphy: The species is found in the lower Peawaddy Formation and Catherine Sandstone of the southwest Bowen Basin and Barfield Formation of the southeast Bowen Basin, Queensland.

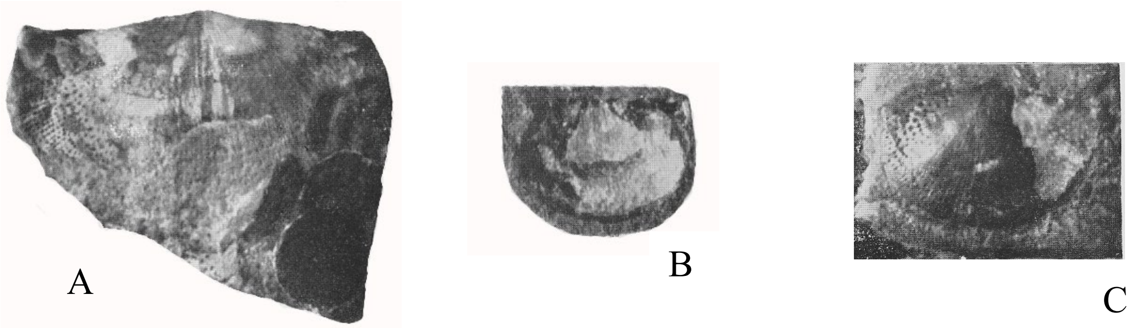

Fig. 9. *Capillonia* (*Capillonia*) *semicircularis* (Campbell), ventral valves. A, UQF 14261, holotype x3. B, UQF 14262, x3. C, UQF 14263. Specimens x3 from mudstone of lower Peawaddy Formation, southwest Bowen Basin. (Campbell 1953).

Fig. 10. *Capillonia* (*Capillonia*) *semicircularis* (Campbell). A*,* ventral internal mould UQF 73937. B, dorsal aspect UQF 69986. C, dorsal aspect, UQF 69984. Specimens x2 from Barfield Formation (Waterhouse 1986a).

Capillonia (***Capillonia***) ***solida*** (Dear, 1971)

Fig. 11, 12

1964 *Lissochonetes* sp. Hill & Woods, pl. P4, fig. 5,
1971 *Lissochonetes semicircularis solida* Dear, p. 5, pl. 2, fig. 1-8.
1972 *L. semicircularis* subsp. *solida* – Hill et al., pl. P4, fig. 5.

1983 *Capillonia semicircularis solida* – Archbold, p. 67.
1986a ?*Capillonia semicircularis* [not Campbell] – Waterhouse, p. 22, pl. 2, fig. 33, 35, pl. 3, fig. 1-4, pl. 15, fig. 3, 5 (part, not pl. 2, fig. 34, pl. 15, fig. 2, 4 = *semicircularis*).
1988 *Capillonia solida* – Parfrey, p. 12.

Diagnosis : Like *semicircularis* in shape, distinguished by shallow ventral sulcus and low dorsal fold, strong dorsal septum, shell thick.

Holotype: GSQF 5535 from Flat Top Formation, figured by Dear (1971, pl. 2, fig. 1), Hill & Woods (1964), Hill et al. (1972) and herein as Fig. 11C, D, OD.

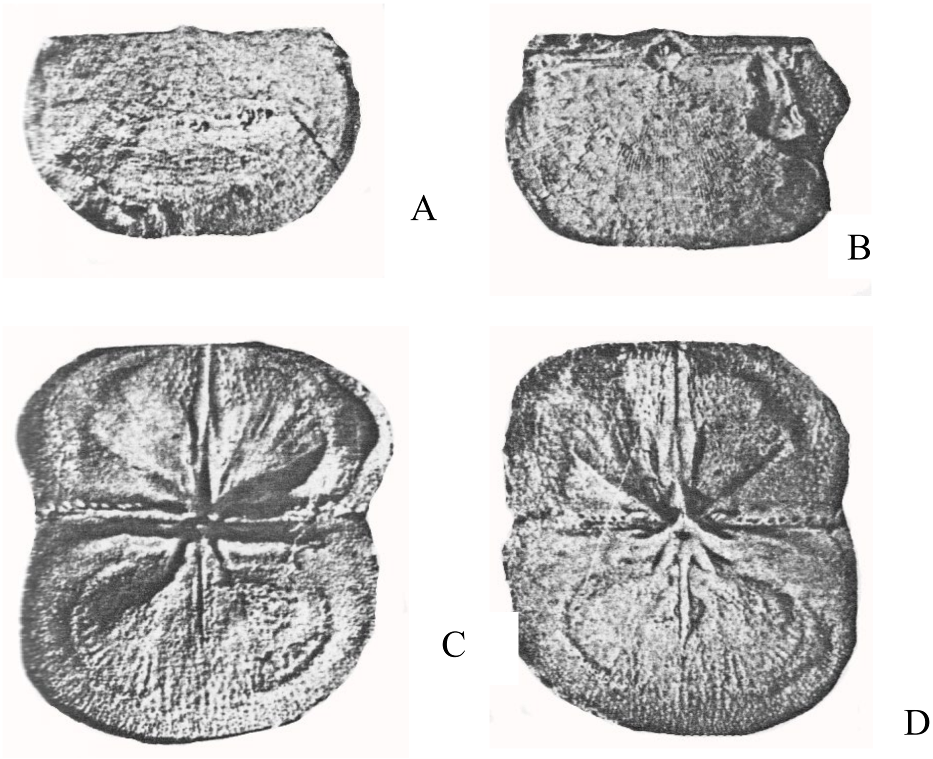

Fig. 11. *Capillonia* (*Capillonia*) *solida* (Dear). A, ventral valve GSQF 11063, latex cast. B, dorsal valve GSQF 11078, latex cast. C, D, internal mould and latex cast of both valves, holotype, GSQF 5535. Specimens x2, from lower middle Flat Top Formation. (Dear 1971).

Morphology: This form is very like *semicircularis* in shape. But collections of the same age show the same disconcerting variability over shape, sulcation and septation as other suites, to imply that the collections either involved one highly variable suite of specimens, or involved several populations that belonged to different varieties, subspecies and even so-called genera.

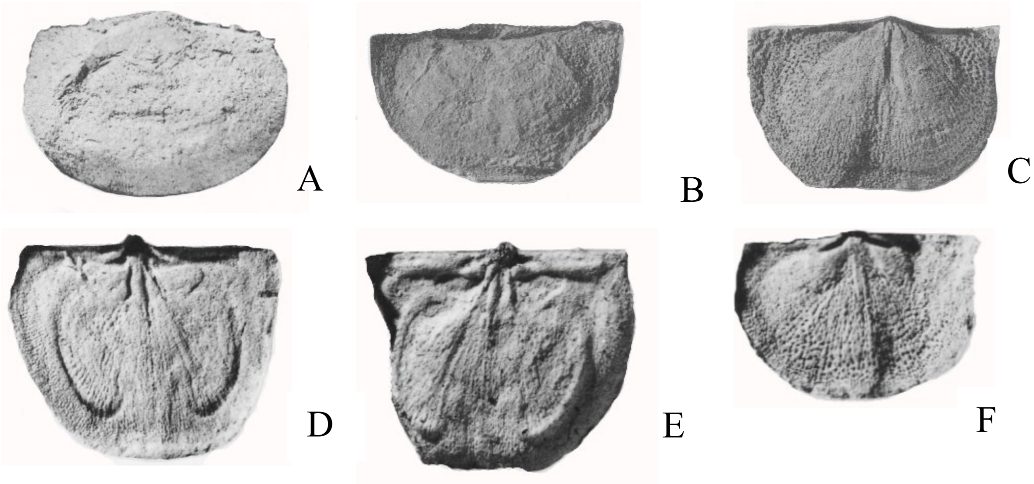

Fig. 12. *Capillonia* (*Capillonia*) *solida* (Dear) from the Flat Top Formation. A, ventral valve UQF 73939, B, dorsal external mould UQF 74268. C, ventral internal mould, UQF 73937. D, E, dorsal internal mould and latex cast, UQF 73942. F dorsal internal mould UQF 73943. Specimens x2, from Flat Top Formation. (Waterhouse 1986).

Stratigraphy: The species is limited to the Flat Top Formation of the southeast Bowen Basin in Queensland. But the exact limits of the taxon in terms of both morphology and stratigraphy need to be better defined, as indicated by Waterhouse (1986a, p. 22), because the presence and definition of the ventral sulcus seem to vary in both Flat Top and Barfield specimens, even though Parfrey (1988) claimed that the form was defined by its sulcus. Some specimens are sulcate, pointing towards *Tivertonia yarrolensis*, others are not. Archbold referred the species to *Capillonia* rather than *Tivertonia*.

Capillonia (***Capillonia***) ***brevisulcus*** (Waterhouse, 1964)

Fig. 13, 14

1925 *Chonetes* cf. *vishnu* [not Salter] – Marwick, p. 362, text-fig. 2-5.
1956 *Chonetes* aff. *vishnu* [not Salter] – Marwick in Wood, p. 47.
1964 *Lissochonetes brevisulcus* Waterhouse, p. 21, pl. 1, fig. 7-11, pl. 2, fig. 1-8, pl. 3, fig. 1-12, pl. 36, fig. 3, 4, text-fig. 2-5.

1969 *Lissochonetes* cf. *yarrolensis* [not Maxwell] – Runnegar & Ferguson, pl. 2, fig. 24-25.
1969 *Lissochonetes* sp. Runnegar & Ferguson, pl. 5, fig. 8.
1973 *Capillonia brevisulcus* – Waterhouse, p. 37.
1978 *C. brevisulcus* – Waterhouse & Mutch, p. 517, Fig. 3-6.
1978 *C. brevisulcus* – Suggate et al. text-fig. 4.7, fig. 6, 10.
1981 *C. brevisulcus* – Speden & Keyes, pl. 7, fig. 6, 10.
1982 *C. brevisulcus* – Waterhouse, p. 29, pl. 6c.
1987 *Capillonia*? *semicircularis* [not Campbell] – Waterhouse & Balfe, p. 32, pl. 2, fig. 3.
2000 *C. brevisulcus* – Racheboeuf, p. 415, Fig. 271.2a-c.
2001 *C. brevisulcus* – Waterhouse, p. 15, pl. 1, fig. 2-9.
2015b *C. brevisulcus* – Waterhouse, pp. 81, ?108, 148, Fig. 66.

Diagnosis: Transverse shells with cardinal extremities at maximum shell width and acute as a rule, ventral valve normally non-sulcate, dorsal valve concave, without fold. Ventral septum as a rule short, but long in some specimens, dorsal septum moderately low and varies in length. Ventral valve smooth, dorsal valve often has faint capillation, whether original or due to wear not secure.

Holotype: BR 917 from Trig D Formation, figured in Waterhouse (1964, pl. 2, fig. 4, pl. 3, fig. 2, 3) and herein as Fig. 14F, OD.

Morphology: Numerous well-preserved specimens are available and have been described and figured. There is a somewhat disconcerting amount of variation amongst the collections, involving sulcation, fold, and the strength and length of the median septum in each valve. Specimens from the upper South Curra Limestone of the Gympie district were compared with *yarrolensis* by Runnegar & Ferguson (1969, pl. 2, fig. 24-25), but differ in inflation and development of the dorsal septum from the Tiverton material, and were identified as *Capillonia brevisulcus* in Waterhouse (2015b).

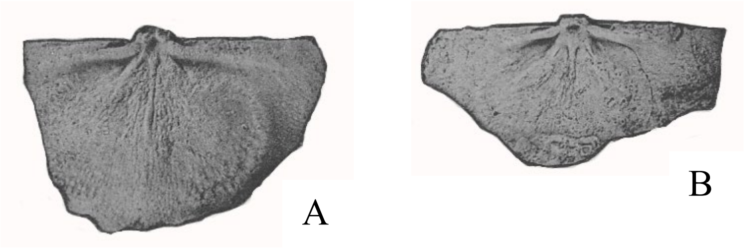

Fig. 13. *Capillonia* (*Capillonia*) *brevisulcus* (Waterhouse). A, dorsal interior, PVC cast BR 25. B, latex cast of dorsal interior BR 938. Specimens x2, from Trig D Formation. (Waterhouse 1964).

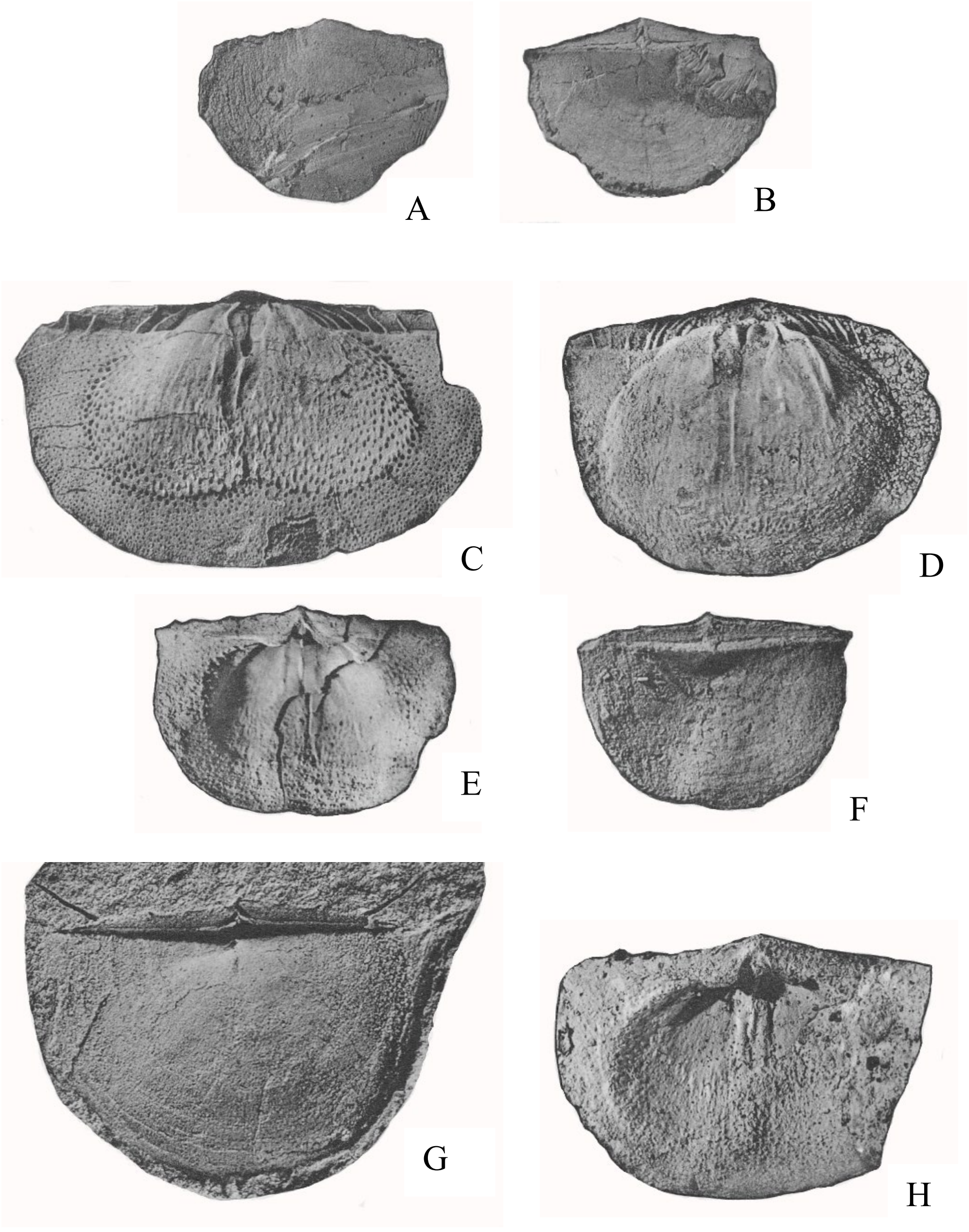

Fig. 14. *Capillonia* (*Capillonia*) *brevisulcus* (Waterhouse). A, B, ventral and dorsal aspects of conjoined specimen, PVC cast, BR 16. C, ventral internal mould, BR 35. D, ventral internal mould BR 21. E, ventral interior, PVC cast BR 24. F, latex cast of conjoined specimen, dorsal aspect, BR 917, holotype. G, dorsal aspect, internal mould of specimen with valves conjoined, OU 2205. H, ventral interior, PVC cast BR 30. Specimens x2 except G, from Kildonan Member, x4. This specimen comes from the Bagrie Formation and remainder from Trig D Formation. (Waterhouse 1964).

Stratigraphy: The species is found in the Kildonan Member, Bagrie Formation, and in the overlying Trig D Formation in New Zealand. The species is also found in the lower South Curra Limestone and Gigoomgan Limestone of the Gympie region in southeast Queensland.

Subgenus ***Tivertonia*** Archbold, 1983

Diagnosis: Transverse shells, maximum width as rule at hinge, sulcus broad as a rule though comparatively shallow in many specimens, narrow dorsal fold, surface uncertain, appears to be essentially smooth. Ventral median septum high posteriorly, short to medium in length, vascular trunks narrow and inconspicuous, internal pustules may form band close to margin. In dorsal valve medium septum extends beyond mid-length, anderidia present, pustules numerous in front of brachial shields.

Type species: *Lissochonetes yarrolensis* Maxwell, 1964, p. 35 from Yarrol Formation (Sakmarian) of Yarrol Basin, Queensland, OD.

Discussion: This taxon, which one wonders why it was not called *Yarrolia*, differs from the Tiverton chonetid previously assigned to the species and now described as *Capillonia armstrongi* through the smaller size, deeper and wider ventral sulcus, and short ventral septum, judged from examination of topotypes as specified in Waterhouse (2015a). Aspects of the shape, including length of hinge and nature of external ornament and consistency in the internal septa remain obscure. There are points of distinction from such genera as *Leurosina* Cooper & Grant, 1975, *Quadrochonetes* Stehli, 1954, *Lissochonetes* Dunbar & Condra, 1932 and *Dyoros* Stehli, 1954, but species ascribed to these genera do vary. *Lissochonetes* is close in shape, but is more transverse and has distinctly longer ventral median septum, and apparently less developed anderidia. *Capillonia* Waterhouse is closer in internal features and is close in shape. This genus is common in Middle Permian faunas of Queensland. The species *cracowensis* Etheridge Snr, 1872 from the Fairyland Formation of the southeast Bowen Basin near Cracow and revised in Waterhouse (1986a, p. 21, pl. 2, fig. 25-32) is externally like *Svalbardia*, and has obscure vascular trunks, and the ventral median septum is not long, and the length of the dorsal median septum medium to long.

Available topotype material of *Tivertonia* seems too sparse to rule out synonymy with *Capillonia*. The one obvious difference between the two type species, *brevisulcus* and *yarrolensis* appears to be that some but not all *yarrolensis* have a broad ventral sulcus, whereas most *brevisulcus* have no ventral sulcus or only a short sulcus. That arguably provides a basis for recognizing *yarrolensis* as a distinct strand, and that is done herein, making *Tivertonia yarrolensis* as a subgenus of *Capillonia*. This step is contentious, because a few specimens of *yarrolensis* lack the sulcus, and a few *brevisulcus* have a sulcus, though narrower than in *yarrolensis*. Archbold described the dorsal septum as strong and long, yet Maxwell (1964) described it as obsolete. It is wished to protect the Archbold name, but there must remain questions. These are exacerbated by the poor preservation and limited illustrations of *yarrolensis*, and it is clear that more and better material is required to consolidate any generic distinction.

Capillonia **(*Tivertonia*)** ***yarrolensis*** (Maxwell, 1964)

Fig. 15

1964 *Lissochonetes yarrolensis* Maxwell, p. 35, pl. 6, fig. 9, 11, 13, 14 (part, not fig. 10 = anopliin, fig. 12 indet..).
1983 *Tivertonia yarrolensis* – Archbold, p. 71.
2000 *Tivertonia yarrolensis* – Racheboeuf, p. 420 (part, not Fig. 275.1a-c = *armstrongi*).

Diagnosis: Poorly known, Ventral valve may be widely sulcate, dorsal valve concave, without or without median fold. Ventral septum short to moderately long, low as a rule. Dorsal septum moderately long, not very strong.

Holotype: UQF 43037 figured by Maxwell (1964, pl. 6, fig. 9) and herein as Fig. 15A, from Yarrol Formation, Queensland, OD.

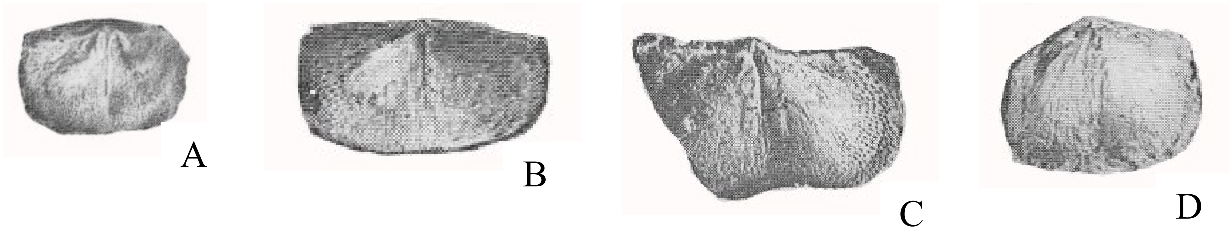

Fig. 15. *Capillonia* (*Tivertonia*) *yarrolensis* (Maxwell). A, internal mould of dorsal valve UQF 43037, holotype, x1.5. B, ventral internal mould UQF 43041, x2. C, ventral internal mould UQF 43158, x1.5. D, Ventral internal mould UQF 43039 x1.5. From Yarrol Formation, Queensland. (Maxwell 1964).

Morphology: Reliance must be placed on a few inadequate figures by Maxwell (1964), and although I examined the material, it was some time ago. Archbold (1983) as accepted by Racheboeuf (2000) presented a full plate of figures of specimens from the Tiverton Formation that were claimed to represent *yarrolensis*, but they differ in being much less sulcate and belong to *Capillonia armstrongi*. The cardinal extremities are now rounded in the types and in the Archbold material, but there appears to have been attrition. The median ventral septum is long in one figured *yarrolensis* type (Fig. 11D herein) but extends only to mid-length in two other specimens (Fig. 11B, C herein). In type *Capillonia brevisulcus*, the ventral median septum is often short (Waterhouse 1964a, pl. 1, fig. 11, pl. 2, fig. 3, 8) but arguably long in pl. 2, fig. 2 and 5).

Racheboeuf (2000) stated the species name *yarrolensis* was published by Maxwell (1954), but the correct date is 1964.

Stratigraphy: The form comes from the Yarrol Formation of Queensland, probably of Sakmarian age and equivalent to the *Magniplicatina undulata* Zone.

Capillonia (***Tivertonia***?) ***saeptata*** (Waterhouse, 2015a)

Fig. 16

1986 *Tivertonia yarrolensis* [not Maxwell] – Archbold, p. 413, Fig. 1A-N.
2015a *Svalbardia saeptata* – Waterhouse, p. 68.

Diagnosis: Median septum of each valve very long, especially that of the ventral valve. Ventral sulcus broad in at least some specimens.

Holotype: Specimen MMF 2386A from Farley Formation, New South Wales, figured by Archbold (1986, Fig. 1F) and Fig. 16A herein, OD.

Morphology: This species is recognized for material from the Farley Formation of the Sydney Basin, because the ventral septum is especially long, and the septa in both valves are longer than in the Tiverton or possibly Yarrol material. In addition, the maximum width is for some specimens placed near mid-length rather than along the hinge, a number of specimens are sulcate, and there may be fewer spines along the ventral hinge row, although this varies. These differences are substantial enough to suggest at least varietal if not specific or subspecific discrimination from the Tiverton material called *Svalbardia armstrongi* Waterhouse, 2015a, but arguably a subspecific ranking might be preferable.

Stratigraphy: The form is limited to the chonetid band in the Farley Formation of the north Sydney Basin.

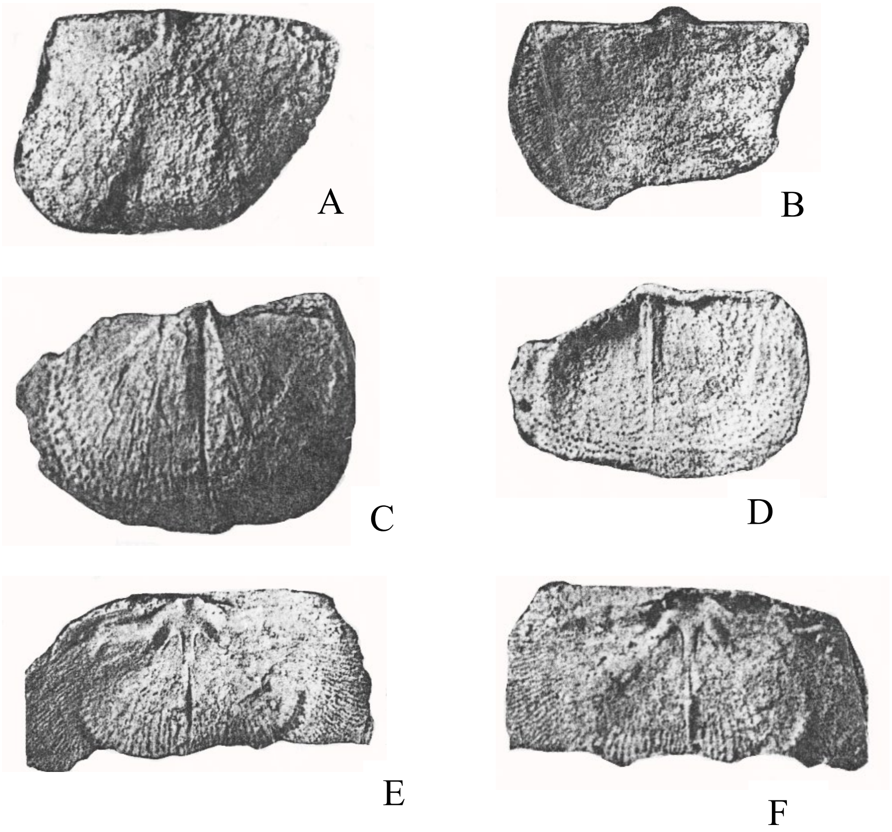

Fig. 16. *Capillonia* (*Tivertonia*?) *saeptata* (Waterhouse). A, latex cast of ventral exterior, MMF 2386A, x2.5, holotype. B, latex cast showing dorsal exterior, MMF 2385C, x2. C, ventral internal mould MMF 2385H, x2.5. D, latex cast of ventral interior, MMF 2385B, x2. E, F, dorsal internal mould and latex cast, MMF 2385A, x2.5. From Farley Formation. (Archbold 1986).

Genus ***Gympietes*** Waterhouse, 2015b

Diagnosis: Smooth shells with obtuse cardinal extremities, cardinal row of spines, no body spines, ventral valve little inflated, dorsal valve almost flat. Ventral interior with short median septum and pair of low median vascular trunks as a rule, may be absent; dorsal valve with cardinal process, curved socket ridges, brachial shields, slightly impressed adductor scars, rarely with median septum even in large shells, no clearly defined anderidia or lateral septa.

Type species: *Gympietes aseptus* Waterhouse, 2015b from Rammutt Formation (Asselian), Gympie, southeast Queensland, OD.

Discussion: The genus is known from the middle Rammutt Formation in the Gympie Basin, of Early Permian age, and there is a possible occurrence in the overlying *Bandoproductus* fauna in the upper Rammutt Formation, although this specimen is poorly preserved and generically insecure, possibly even belonging to *Capillonia*, a genus also found in the South Curra limestone at Gympie and in the early and middle Permian of the Bowen Basin. *Gympietes* is like *Svalbardia* Barkhatova, 1970, type species *Chonetes capitolinus* Toula from Spitsbergen, in its smooth exterior and flat dorsal valve but has a short ventral septum and no dorsal septa, except rarely for a very short posterior median ridge in some specimens. No body spines appear to be developed. The smooth genus *Komiella* Barkhatova, 1970, type species *Chonetes omolonensis* Licharew from northeast Russia, as discussed by Archbold (1981), has prominent dorsal medium and lateral septa. The chonetid *Sandrella* Waterhouse, 1986b, type species *S. platina* Waterhouse from the Wuchiapingian lower Testha Sandstone Member of the Gungri Formation, Zanskar Himalaya, is similar externally in its gently convex ventral valve, obtuse cardinal extremities, and flat dorsal valve, but this form lacks hinge spines and has five septa in the dorsal valve.

From Lower Carboniferous (Visean) faunas of New South Wales, *Leiochonetes* Roberts, 1976, type species *L. salisburyensis* Roberts, with its semicircular outline and pointed cardinal extremities is moderately close to the new genus in its lack of sulcus and fold and presence of short ventral median septum, though shape and septation differ. There is a short dorsal septum, short anderidia, and no vascular ridges. Amongst Svalbardiinae, *Gympietes* is the only one with comparably reduced internal septation, so that there needs to be consideration as to whether the specimens have failed to reach a mature stage of development. Nonetheless shape and septation differ in available material.

Gympietes aseptus n. sp.

Fig. 17, 18

1987 Chonetid Waterhouse & Balfe, p. 30, pl. 1, fig. 1, 2.
2015b *Gympietes aseptus* Waterhouse, p. 14, Fig. 4B-0.

Diagnosis: Transverse shells with rounded cardinal extremities, generally with median flattening or shallow sulcus over little inflated ventral valve.

Holotype: GSQF 13182 from Rammutt Formation, Gympie, figured in Waterhouse (2015b, Fig. 4K), and herein as Fig. 17A, OD.

Morphology: Shells transverse to almost subquadrate in outline and little inflated. The cardinal extremities are obtuse throughout ontogeny, ventral valve gently inflated, maximum width just behind or in front of mid-length; median shell gently arched or flattened, rarely sulcate with angle of about 25°, but variable. Dorsal valve very weakly concave, almost flat over disc, and slightly upturned anterior margin, indicating a short trail. Cardinal spines emerge from ventral hinge in prominent row, number twelve to fifteen each side, turn abruptly within interarea. External surface of both valves smooth apart from low growth lamellae; no body spines are visible.

Ventral teeth large and extend along hinge; median septum usually short, thick and high, mostly only a sixth of length of shell between hinge and anterior margin, but reaching mid-length in about 10% of sample and in one specimen beyond; similar number of shells have no median septum.

Dorsal cardinal process narrow, supported by low socket ridges extending laterally in front of narrow dental sockets, not reaching lateral margin of shell. No dorsal median septum or lateral septa is developed, except for low anterior septum in two out of twenty specimens.

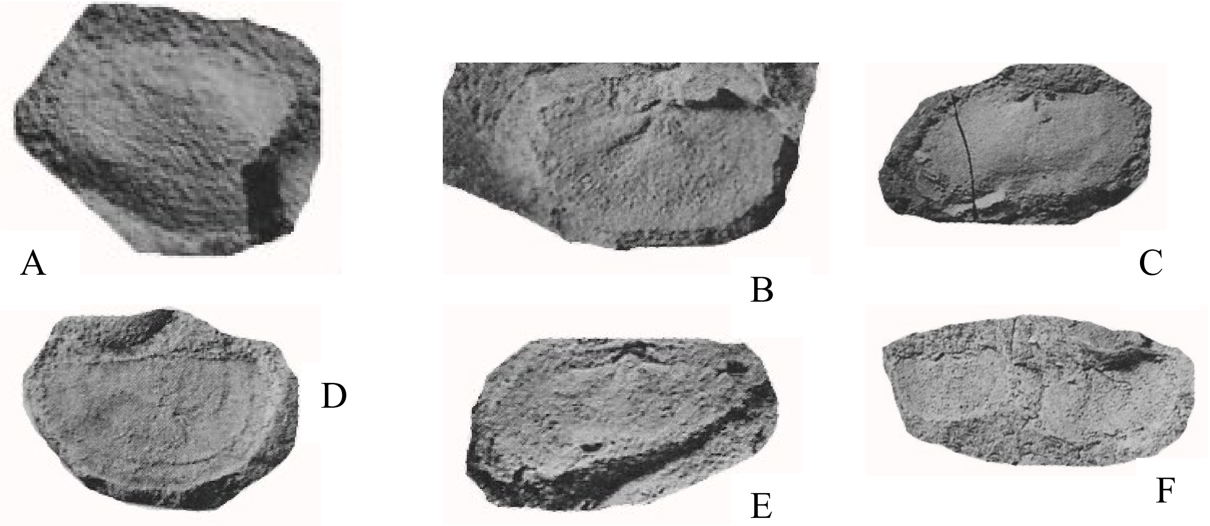

Fig. 17. *Gympietes aseptus* Waterhouse. A, ventral exterior (to left), GSQF 13180, x2. B, dorsal internal mould, GSQF 13137, x1.5. C, small ventral internal mould GSQF 13139, x1. D, dorsal valve external mould GSQF 13179, x1.5. E, dorsal internal mould GSQF 13183, x1.5. F, dorsal internal mould, GSQF 13143, x 1. From Rammutt Formation, Gympie, southeast Queensland. (Waterhouse 2015b).

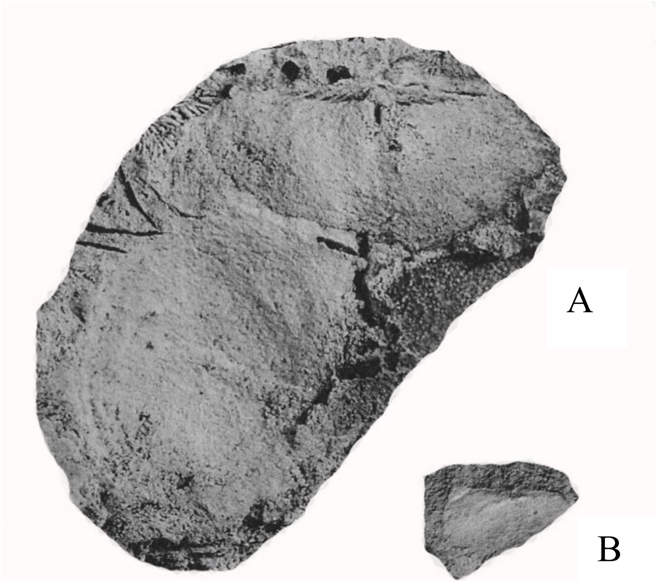

Fig. 18. *Gympietes aseptus* Waterhouse. *A,* ventral internal mould, holotype GSQ F 13182, above ventral external mould, x2. B, dorsal external mould GSQF 13140, x1. Rammutt Formation, Gympie, southeast Queensland. (Waterhouse 2015b).

Stratigraphy: The species is known only from the Rammutt Formation, of Asselian age.

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BRACHIOPOD SPECIES OF SUBORDER PRODUCTIDINA IN THE PERMIAN OF EAST AUSTRALIA AND NEW ZEALAND

Abstract

Species of a marginiferid, Lethamiini, and a waagenoconchid are summarized from the marine Permian of east Australia and New Zealand.

SYSTEMATIC SUMMARY

Order PRODUCTIDA Waagen, 1883

Suborder PRODUCTIDINA Waagen, 1883

Superfamily **MARGINIFEROIDEA** Stehli, 1954

Family **MARGINIFERIDAE** Stehli, 1954

Subfamily **MARGINIFERINAE** Stehli, 1954

Tribe **MARGINIFERINI** Stehli, 1954

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

Diagnosis: Spines on ventral valve well formed, may include row along umbonal flanks, and generally along hinge, no large strut spines. Radial ornament subdued to well-defined, commarginal ornament subdued to moderate. Corpus cavity shallow to deep. Upper Carboniferous (Kasimovian) to Upper Permian (Changhsingian).

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

Genus ***Azygidium*** Waterhouse, 1983

Diagnosis: Highly arched shells with umbonal row of spines and scattered disc spines, no strut spines or dorsal spines. Low ribs. No zygidium.

Type species: *Horridonia mitis* Hill, 1950, p. 17 from Dresden Limestone of southeast Bowen Basin, Queensland.

Discussion: The genus *Azygidium* was named for a distinctive marginiferid, based on familiarity with European and North American collections of various marginiferid genera. Briggs declared that the Hill species *mitis* belonged to *Anemonaria* Cooper & Grant, 1969, but he failed to observe that *Anemonaria* possesses strut spines, as in Paucispiniferidae, not Marginiferidae including *mitis*, and he declared that *mitis* just might have a zygidium. But his supposed zygidium (Briggs 1998, Fig. 72A, B) seems to possibly be a broken fragment of shell. He had never examined any material beyond Australia, other than in publications.

Azygidium mitis (Hill, 1950)

Fig. 1

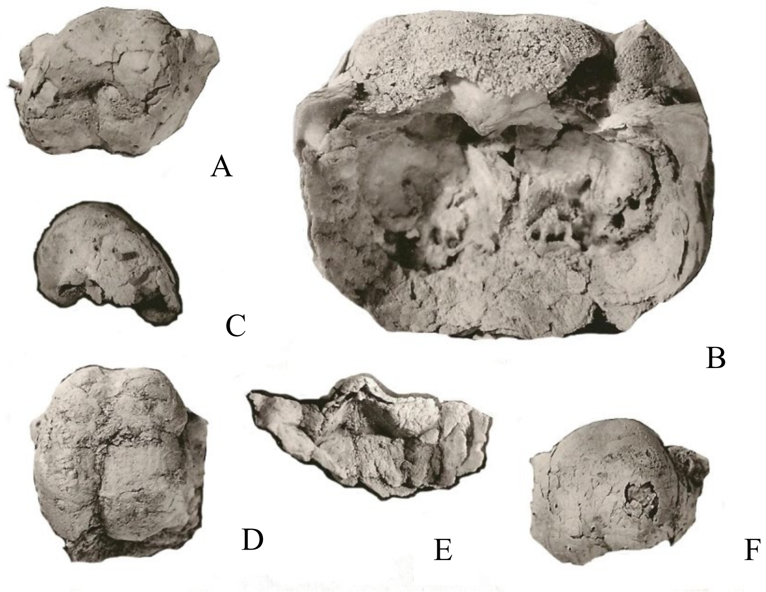

Fig. 1. *Azygidium mitis* (Hill). A, ventral valve, unregistered, x1. B, dorsal aspect of specimen with valves conjoined, UQF 74000, x2. C, lateral view of ventral valve UQF 73998, x 1. D, anterior ventral aspect of specimen with valves conjoined, unregistered, x1. E, dorsal aspect, UQF 73996 x 2. F, ventral valve UQF 74001 x 1. From Dresden Limestone, southeast Bowen Basin, central Queensland. (Waterhouse 2013).

1950 *Horridonia mitis* Hill, p. 17, pl. 8, fig. 7-10, pl. 9, fig. 1.
1965 *Horridonia mitis* – Wass, p. 166.
1983 *Azygidium mitis* – Waterhouse, p. 153.

1986 *A. mitis* – Waterhouse, p. 43, pl. 6, fig. 6, 12-19, pl. 7, fig. 11, 12, pl. 9, fig. 1-4, pl. 15, fig. 11, text-fig. 8.
1989 *A. mitis* – Waterhouse, pl. 1, fig. e, f.
1998 *Anemonaria mitis* – Briggs, p. 143, Fig. 72A-F.
2013 *Azygidium mitis* – Waterhouse, p. 95, Fig. 4.2.

Diagnosis: Subelongate shells with deep sulcus and moderate fold, shell smooth, spines in row along umbonal slopes and scattered over ventral disc, no dorsal spines, no strut spines. Dorsal interior with large pustules close to anterior brachial supports.

Holotype: UQF 10772 from Dresden Limestone, southeast Bowen Basin, figured by Hill (1950, pl. 8, fig. 7), OD.

Stratigraphy: The species is limited to the limestones of the lower Dresden Formation.

Superfamily **ECHINOCONCHOIDEA** Stehli, 1954

?Family **SENTOSIIDAE** McKellar, 1970

Subfamily **TUBERSULCULINAE** Waterhouse, 1971

These higher category classificatory positions proposed in Waterhouse (2013) need confirmation , because *Tubersulculus* and *Lethamia* appear close to Productimorphii Waagen. Brunton (2007, p. 2640 ff) provided a convincing assemblage of genera for Lethamiini and classed the tribe in Productellidae. Waterhouse (2013, p. 188) on the other hand argued that the lack of heavy marginal ridge and various other features pointed to an association with Echinoconchoidea.

Tribe **LETHAMIINI** Waterhouse, 2001

[Lethamiini Waterhouse, 2001, p. 17].

Diagnosis: Spines numerous and evenly spaced over both valves, no special hinge row, no high posterior lateral internal dorsal ridge. Sakmarian to lower Changhsingian.

Genera: *Lethamia* Waterhouse, *Amosia* Simanauskas, *Undellaria* Cooper & Grant, *Wooramella* Archbold.

Genus ***Lethamia*** Waterhouse, 1973

Diagnosis: Spines evenly distributed over both valves, in quincunx, stouter over ventral valve but still relatively fine, crowded over both valves.

Type species: *Lethamia ligurritus* Waterhouse, 1973 from upper Letham Formation, Wairaki Downs, New Zealand, OD.

Lethamia rara Briggs, 1998

Fig. 2

1972 *Krotovia*? sp. nov. Dear, p. 7.
1998 *Lethamia rara* Briggs, p. 127, Fig. 65A-F.

Diagnosis: Small transverse specimens with arched ventral valve, ventral spines fine and erect, up to 0.35mm in diameter, slightly coarser (0.4mm diameter) and more crowded over ears and posterior flanks, low commarginal rugae. Dorsal valve deeply concave, spines most numerous anteriorly, erect.

Holotype: GSQF 13478 from Yarrol Formation, figured by Briggs (1998, Fig. 65A, C) and herein as Fig. 2A, OD.

Stratigraphy: The species was described by Briggs (1998) as coming from the Yarrol Formation of the Yarrol Basin. He recorded the species also from the Dresden Formation of the southeast Bowen Basin (see Overtoniid gen. & sp. indet. in Waterhouse 1986, p. 36) but no figure or detailed description is available.

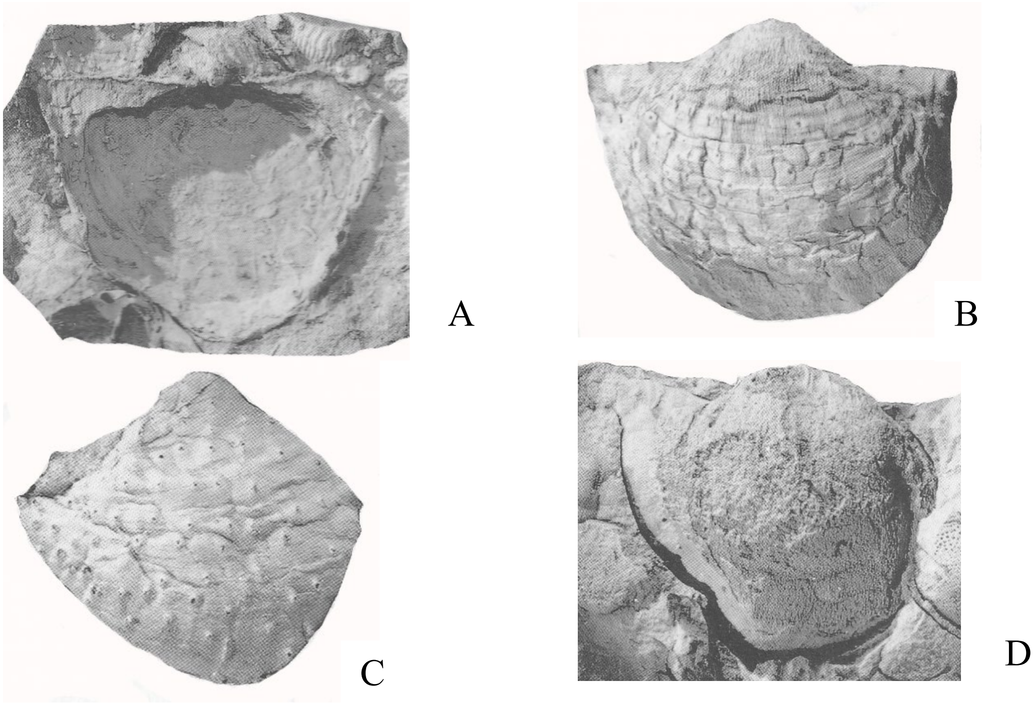

Fig. 2. *Lethamia rara* Briggs. A, latex cast, dorsal aspect, GSQF 13478, holotype, x1.5. B, ventral valve GSQF 13479, x1.5. C, latex cast of part of ventral valve. GSQF 13480, x2. D, ventral valve interior, GSQF 13481, x1.5. From Yarrol Formation. (Briggs 1998).

Lethamia sp.

1964a ?*Krotovia* sp. Waterhouse, p. 72.
1964b *Krotovia* sp. Waterhouse, p. 57.
1969 *Krotovia* n. sp. Waterhouse, p. 726.
1982 *Lethamia* sp. Waterhouse, p. 42, pl. 8b.

A few poorly preserved ventral valves come from GS 6070 in the middle Letham Formation, as recorded in Waterhouse (1982, p. 42).

Fig. 3. *Lethamia* sp. ventral internal mould BR 1155, x2. From middle Letham Formation, Wairaki Downs, New Zealand. (Waterhouse 1982).

Lethamia ligurritus Waterhouse, 1973

Fig. 4, 5

1969 *Krotovia* n. sp. Waterhouse, p. 726.
1973 *Lethamia ligurritus* Waterhouse, p. 38, Fig. 2, no. 4, 5.
1982 *L. ligurritus* – Waterhouse, p. 42, pl. 8c-l, 9a-j.
2000 ?*Lethamia* – Brunton et al., p. 436.
2007 *L. ligurritus* – Brunton, p. 2640 Fig. 1753.1a-e.
2013 *L. ligurritus* – Waterhouse, p. 191, Fig. 6.14, 6.15.

Fig. 4. *Lethamia ligurritus* Waterhouse, detail of dorsal posterior, BR 1441, from upper Letham Formation (upper Kungurian), New Zealand, x3. (Waterhouse 2013)

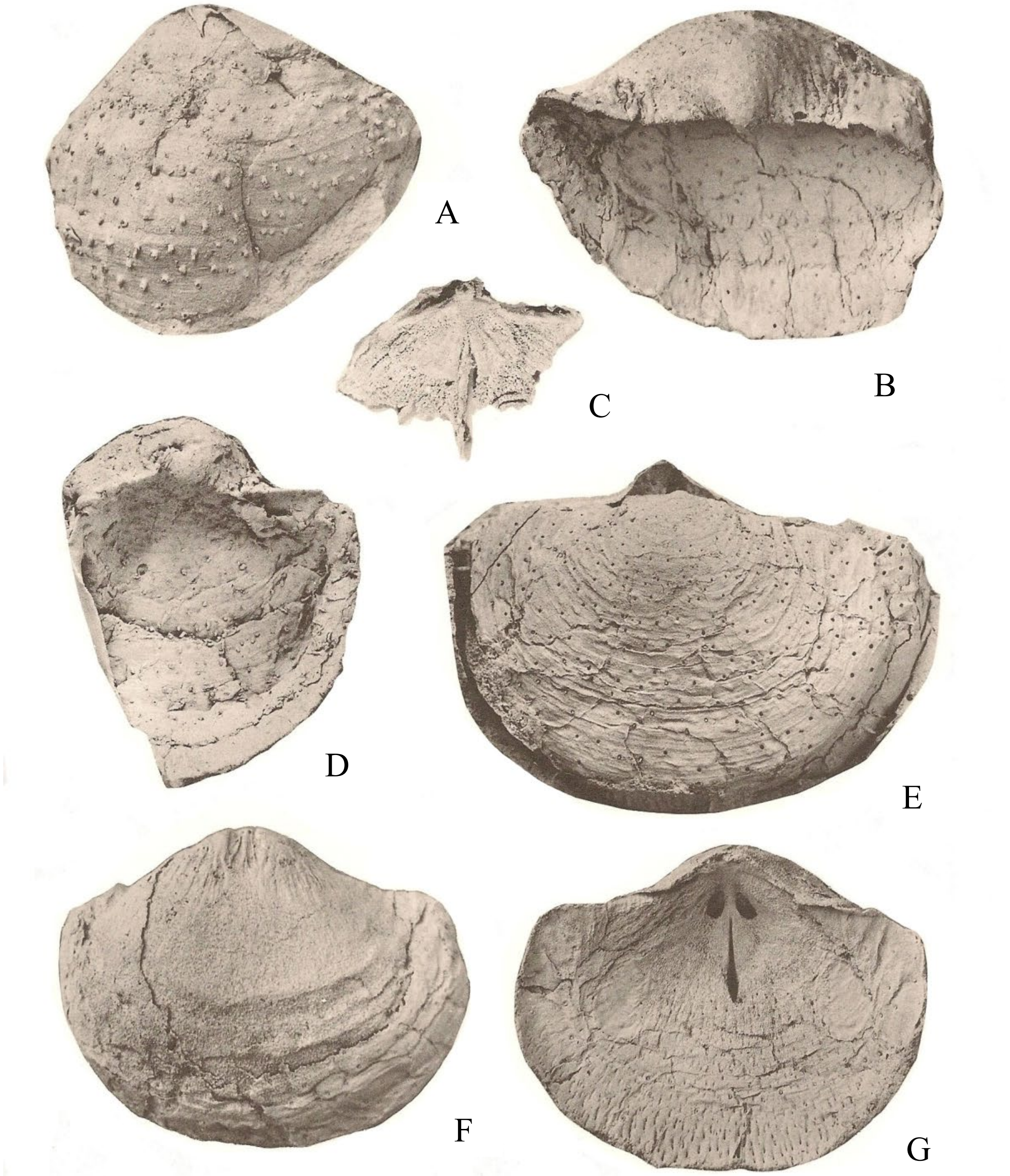

Fig. 5. *Lethamia ligurritus* Waterhouse. A, ventral view of latex cast of exterior, BR 957, holotype. B, dorsal aspect of latex cast, BR 1440. C, latex cast of dorsal interior, BR 956. D, dorsal aspect of latex cast, BR 1438. E, external mould of dorsal valve BR 1441. F, G, ventral and dorsal views of internal mould of same specimen. Specimens x2, from upper Letham Formation, Wairaki Downs, New Zealand. (Waterhouse 1982).

Diagnosis: Shells moderately concavo-convex, maximum width near mid-length. Spines fine and evenly distributed.

Holotype: BR 957 figured by Waterhouse (1973, Fig. 2, no. 4, 5; 1982, pl. 8c, d, i. pl. 9e. g) and Fig. 5A herein from upper Letham Formation, Wairaki Downs, New Zealand, OD.

Morphology: Material is well-preserved. This species and genus were shabbily treated in Brunton et al. (2000) by ignoring the description and good figures in Waterhouse (1982). Brunton (2007) made amends.

Stratigraphy: The species is limited to the upper Letham Formation at Wairaki Downs.

Lethamia hillae Waterhouse, 1986

Fig. 6

1986 *Lethamia hillae* Waterhouse, p. 35, pl. 6, fig. 3-5, 7-11.
1998 *L. hillae* – Briggs, p. 129.

Diagnosis: Transverse shells with gently convex venter, inconspicuous ventral umbo, ventral spines of even size, slightly stronger than in *ligurritus*.

Holotype: UQF 70064 from upper Brae Formation, figured by Waterhouse (1986, pl. 6, fig. 3) and herein as Fig. 6A, OD.

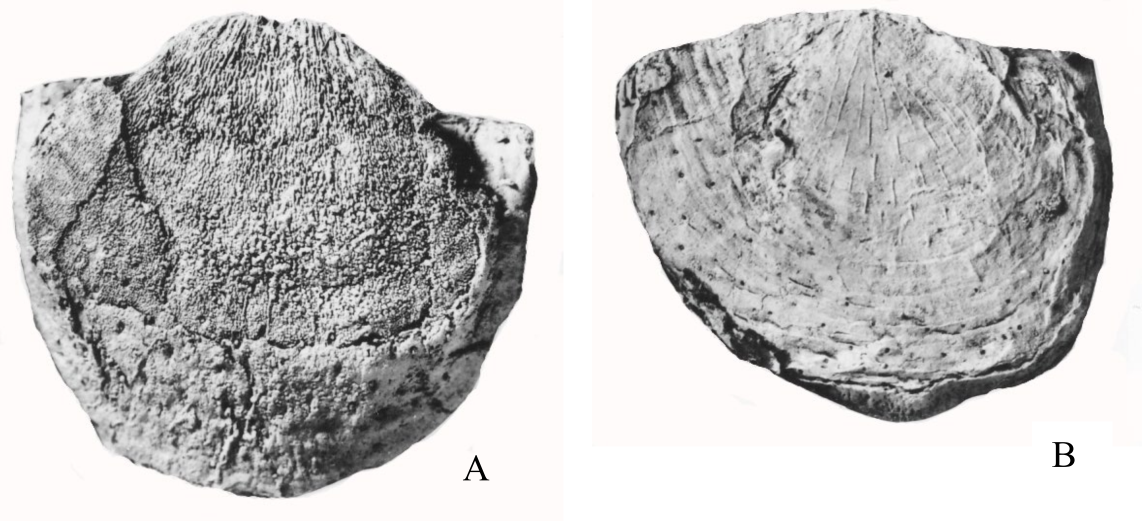

Fig. 6. *Lethamia hillae* Waterhouse. A, ventral valve holotype, UQF 70064, x2. B, latex composite mould of ventral and dorsal valve UQF 70065, x2. Brae Formation. (Waterhouse 1986).

Morphology: This species is very close to *Lethamia ligurritus*, but is more consistently transverse in shape with less incurved ventral umbo and ventral spines of more consistent and greater diameter. Overall, the differences appear to reflect some geographic distance between the two taxa, which are believed to have been contemporaneous. So that the status as a full species is open to question.

Stratigraphy: The species is limited to the upper Brae Formation of the southeast Bowen Basin.

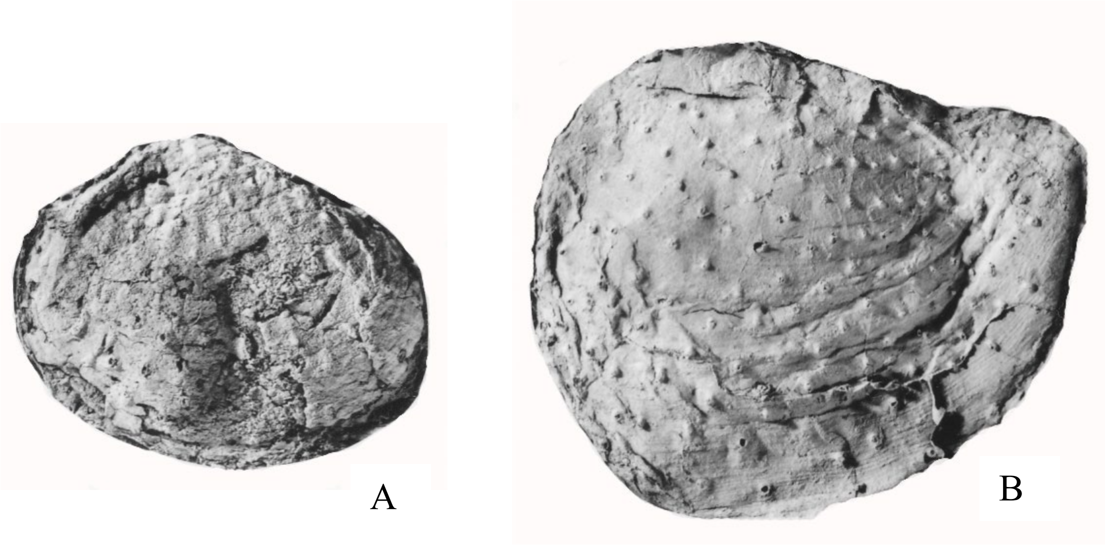

Fig. 7. *Lethamia hillae* Waterhouse. A, ventral internal mould UQF 70059, x1. B, dorsal aspect of specimen with valves conjoined, UQF 70061, x2. Brae Formation. (Waterhouse 1986).

Lethamia condaminensis Briggs, 1998

Fig. 8

1998 *Lethamia condaminensis* Briggs, p. 129, Fig, 66A-G.

Diagnosis: Small, highly arched, transverse to less commonly elongate, with wide hinge and enrolled umbo, spines fine over disc, only 0.2mm in diameter, and a little coarser postero-laterally between venter and ears. Dorsal disc deeply concave posteriorly, geniculate, trail short, spines fine, up to 0.1mm diameter.

Holotype: UQF 75286 from Condamine beds, figured by Briggs (1998, Fig. 66A, E) and herein as Fig. 8A, C, OD.

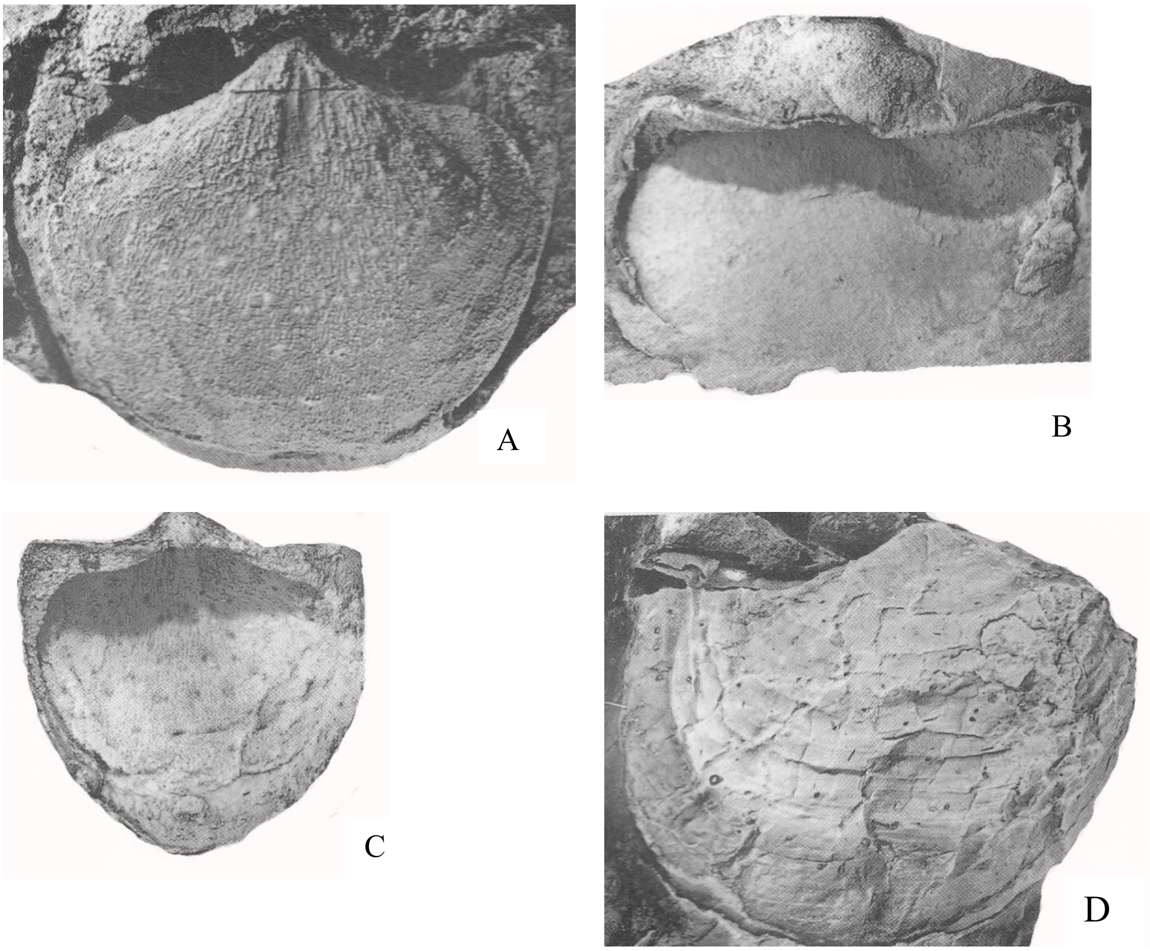

Fig. 8. *Lethamia condaminensis* Briggs. A, C, ventral internal mould x3 and latex cast x2 of UQF 75286, holotype. B, latex cast of posterior conjoined specimen UQF 75283, x2. D, external mould of conjoined specimen showing dorsal valve UQF 75284, x2. Condamine beds, Queensland. (Briggs 1998).

Morphology: Briggs (1998, p. 131) was uncertain that this taxon was new, considering that it approached *Lethamia collina* from New Zealand, and suggested that the uncertainty was due to the poor preservation of the New Zealand material. However the New Zealand species appears to have a higher posterior ventral valve, more enrolled umbonally, and ventral spines near the hinge are 1mm in diameter, whereas only one specimen of the Briggs collection suggested relatively coarse spines, placed well forward on the lateral slopes, thinner than those of the New Zealand species. Clearly more and better preserved material should be sought for both suites, but in the meantime, the two appear to be distinct, judged from both shape and ventral spination.

Stratigraphy: The species is limited to the Condamine beds of the Condamine block near Warwick, southeast Queensland. These beds share according to Briggs (1998, p. 108) the distinctive species *Echinalosia* (now *Nothalosiina*) *voiseyi* with the Gilgurry Mudstone. Such distinctive species are not matched elsewhere, suggesting the possibility that they characterize a distinctive zone, which I speculate matches unfossiliferous or poorly fossiliferous marine beds of lower Wuchiapingian age in New Zealand, below the upper Wuchiapingian *Martiniopsis woodi* Zone.

Lethamia collina Waterhouse, 1982

Fig. 9, 10

1956 *Productus* sp. Marwick in Wood, pp. 47, 48.
1964b *Horridonia* n. sp. Waterhouse, p. 58, pl. 8, fig. 11, pl. 9, fig. 1, 2, text-fig. 21.
1982 *Lethamia collina* Waterhouse, p. 43, pl. 10a, b, Fig. 17G.

Diagnosis: Mature shells with wide hinge and steep high posterior ventral slopes, lending a hunched appearance to specimens. Spines are few along the hinge and scattered over the venter. Sulcus shallow.

Holotype: `BR 51, figured in Waterhouse (1964b, pl. 8, fig. 11, pl. 9, fig. 1, 2) and herein as Fig. 10A-C, from Kildonan Member, Bagrie Formation, New Zealand, OD.

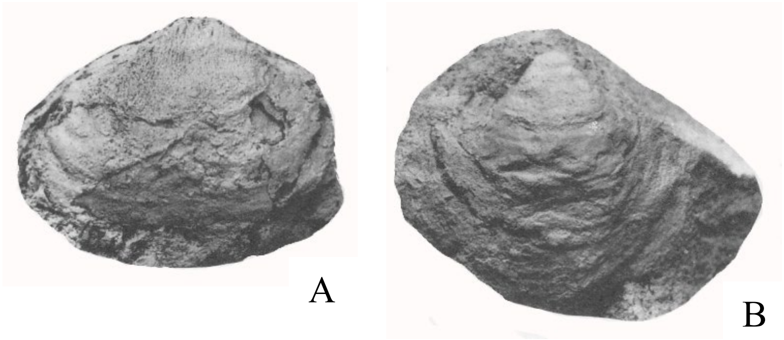

Fig. 9. *Lethamia collina* Waterhouse. A, internal mould of small ventral valve, BR 1182, x2. B, decorticated immature ventral valve BR 49, x2. Kildonan Member, Bagrie Formation, New Zealand. (Waterhouse 1982).

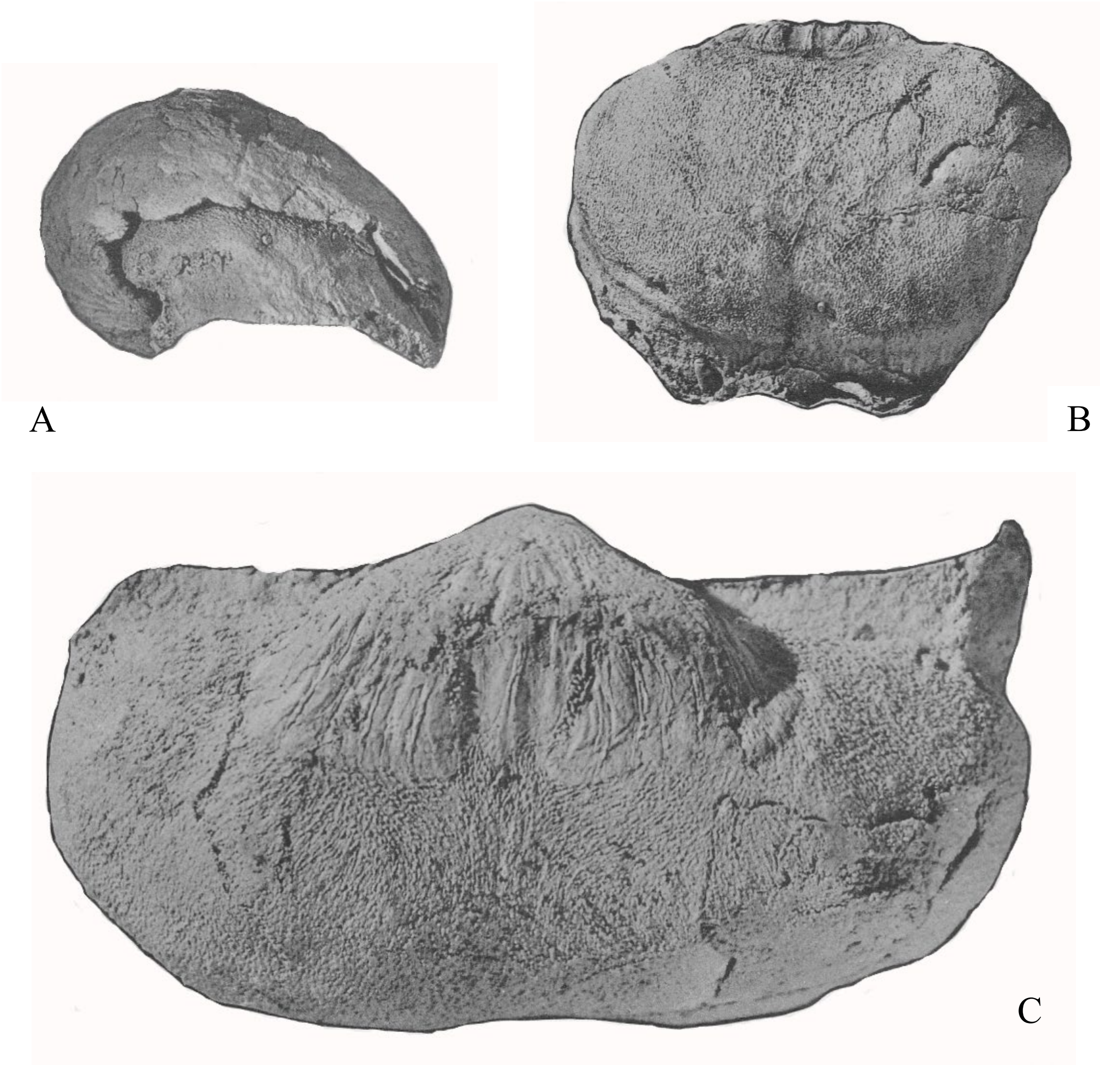

Fig. 10. *Lethamia collina* Waterhouse. A-C, lateral aspect x2, anteroventral aspect, x2 and postero-ventral view x4 of holotype, BR 51. Kildonan Member, Bagrie Formation, New Zealand. (Waterhouse 1964b).

Morphology: The hunched appearance of the mature shell is very distinctive.

Stratigraphy: *Lethamia collina* is found in the Kildonan Member and overlying Trig D Formation in New Zealand.

?***Lethamia*** sp.

Fig. 11

1982 *Sowerbina* sp. Waterhouse, p. 44, pl. 10c, d.

A small and worn ventral valve from the Pig Valley Limestone at Nelson, New Zealand, could possibly belong to *Lethamia* as noted by Waterhouse (1982), though this is not established. The specimen shows small pustules over the shell surface, which were taken to suggest horridoniid affinities.

Fig. 11. ?*Lethamia* sp. Worn ventral valve BR 1493, x3. Pig Valley Limestone, Nelson. (Waterhouse 1982).

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

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

Tribe **WIMANOCONCHINI** Waterhouse, 2013

[Wimanoconchini Waterhouse, 2013, p. 198].

Diagnosis: Large shells with flat to very gently concave dorsal valve, with no externally visible trail or geniculation.

Type species: *Ruthenia wimani* Fredericks, 1934 from Middle Permian of Spitzbergen.

Genera: *Wimanoconcha* Waterhouse, *Patellamia* Waterhouse, *Quenstedtia* Waterhouse, *Villaconcha* Waterhouse. Middle to Upper Permian (Roadian to Wuchiapingian).

Genus ***Wimanoconcha*** Waterhouse, 1983

Diagnosis: Large shells with flat to very gently concave dorsal valve, thickened into a wedge.

Type species: *Ruthenia wimani* Fredericks, 1934 from Spitsbergen, OD.

Discussion: Brunton et al. (2000, p. 517) synonymized *Wimanoconcha* with *Waagenoconcha*, claiming that Archbold (1993) had done that. Not so. The claim was a falsehood. Archbold (1993, p. 20) wrote that “*Waagenoconcha imperfecta* Prendergast is assigned to *Wimanoconcha*.”

?***Wimanoconcha*** aff*.* ***imperfecta*** Prendergast, 1943

Fig. 12

1982 *Waagenoconcha* cf. *imperfecta* – Waterhouse, p. 41, pl. 8a.

A single ventral valve from New Zealand shows some similarity in shape with the species described by Prendergast (1935, Pl. 11, fig. 1-3; 1943, pl. 3, 6, 9) and Coleman (1957, pl. 10, fig. 8-14, pl. 11, fig. 1-6) from the Hardman Member and Lightjack Member of the Liveringa Formation of Western Australia. This species is also close to *Productus waageni* Rothpletz (1892, pl. 10, fig. 19a, b) from Ajer Mati and similar specimens recorded by Broili (1916, pl. 118, fig. 1-5), as noted by Muir-Wood & Cooper (1960, p. 253). Fragments of external shell found with the New Zealand specimen show an ornament of long and narrow spines, crowded together over the posterior region of the specimen with even finer more erect spines 1mm in diameter anteriorly.

Fig. 12. *Wimanoconcha* aff. *imperfecta* (Prendergast), lateral tilted aspect of leached ventral valve, BR 739, x2. From Earnvale Member, Bagrie Formation, New Zealand. (Waterhouse 1982).

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SUBORDER LINOPRODUCTIDINA WATERHOUSE.

A SUMMARY OF SPECIES FOUND IN THE PERMIAN MARINE FAUNAS OF EAST AUSTRALIA AND NEW ZEALAND.

ANIDANTHIDAE

Abstract

There are numerous species of Anidanthidae in the marine Permian of east Australia and New Zealand, and these are recorded with synonymies, typology, brief diagnosis and record of stratigraphic occurrences, together with illustrations. A list of species is provided near the start of this monograph, starting on p. 4.

SYSTEMATIC SUMMARY

Suborder LINOPRODUCTIDINA Waterhouse, 2013

This group has been proposed for three superfamilies Paucispiniferoidea Muir-Wood & Cooper, Linoproductoidea Stehli and Proboscidelloidea Muir-Wood & Cooper, symplesiomorphic superfamilies that arose from the strophalosiiform Family Devonoproductidae. They share predominantly radial costation but differ in details of spination and interior. Origins appear, from the fossil record, to have stemmed from a costellate chonetid, at least generically different from the smooth-shelled ancestors of Productidina and Strophalosiidina.

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

Family **ANIDANTHIDAE** Waterhouse, 1968a

[Nom. transl. Kotlyar in Sarytcheva, 1977, p. 53 ex Anidanthinae Waterhouse, 1968a, p. 1172] et seq.

Subfamily **ANIDANTHINAE** Waterhouse, 1968a

[Anidanthinae Waterhouse, 1968a, p. 1172]

Diagnosis : Well-defined costellae, hinge spines moderately developed, visceral and trail spines inconspicuous as a rule, no dorsal spines, apart from the exceptional genus *Mongolosia* Manankov, derived from *Protoanidanthus*. Dorsal valve lamellate to varying degree. Upper Carboniferous (?Moscovian or younger) to Upper Permian (Changhsingian).

- **Family Paucispiniferidae Muir-Wood & Cooper, 1960**
  - Subfamily Paucispiniferinae Muir-Wood & Cooper, 1960
    - Tribe Paucispiniferini Muir-Wood & Cooper, 1960
    - Tribe Retimarginiferini Shi & Waterhouse, 1996
    - Tribe Probolioniini Muir-Wood & Cooper, 1960
      - Subtribe Probolioniinai Muir-Wood & Cooper, 1960
      - Subtribe Kozlowskiinai Brunton, Lazarev & Grant, 1995
  - Subfamily Productininae Muir-Wood & Cooper, 1960
  - Subfamily Bibatiolinae Waterhouse, 2002b
  - Subfamily Chonetellinae Licharew, 1960
    - Tribe Chonetellini Licharew, 1960
    - Tribe Odonovaniini Waterhouse, 2013
- **Family Anidanthidae Waterhouse, 1968a**
  - Subfamily Anidanthinae Waterhouse, 1968a
    - Tribe Anidanthini Waterhouse, 1968a
    - Tribe Megousiini Waterhouse, 2013
  - Subfamily Lirariinae Waterhouse, 2013
  - Subfamily Lamiproductinae Liang, 1990
- **Family Yakovleviidae Waterhouse, 1975**
  - Subfamily Yakovleviinae Waterhouse, 1975
  - Subfamily Muirwoodiinae Waterhouse, 2013
  - Subfamily Paramarginiferinae Lazarev, 1990

Table 1. Superfamily Paucispiniferoidea Muir-Wood & Cooper, 1960.

Discussion: Brunton et al. (2000, p. 531) also recognized *Protanidanthus* Liao, 1979 and *Zia* Sutherland & Harlow, 1973 as members of Anidanthinae, but *Zia* shows little similarity to the subfamily, belonging to Reticulatiinae (Waterhouse 2013, p. 130), and *Protanidanthus* Liao lacks dorsal lamellae and so is deemed to belong to Lirariinae (Waterhouse 2013, p. 332). As well, *Protoanidanthus* Waterhouse, 1986 was overlooked by Brunton et al. (2000), and in 2007 Brunton endeavoured to retrieve the lapse by denying validity to the proposal. But *Protoanidanthus* appears to be a valid genus and is widespread in high paleolatitudes of both hemispheres (Briggs 1998). It differs from *Anidanthus* in having an unthickened dorsal valve, and in lacking the extended alar ears of *Anidanthus*, *Megousia*, *Kuvelousia, Ogamousia* and *Anidanthia*. Two Siberian species ascribed to *Anidanthus* by Klets (2005, pl. 9, fig. 1-11), *A. boikowi* (Stepanov) and *A. megensis* Solomina, are of interest in that the high quality illustrations suggest that the dorsal valve was not thickened (eg. Klets 2005, pl. 9, fig. 1b), and indicate that the dorsal ears were not large and laterally twisted, nor are they bifid (Klets 2005, pl. 9, fig. 4, 8, 9, 10). The ventral ears are relatively large, but otherwise appear close to *Protoanidanthus*. The genus *Anidanthus* shares significant attributes with its ancestral stock centred in *Devonoproductus* Muir-Wood & Cooper, 1960, which had ventral radial ribs and dorsal commarginal laminae, but lacks the teeth and sockets found in *Devonoproductus*.

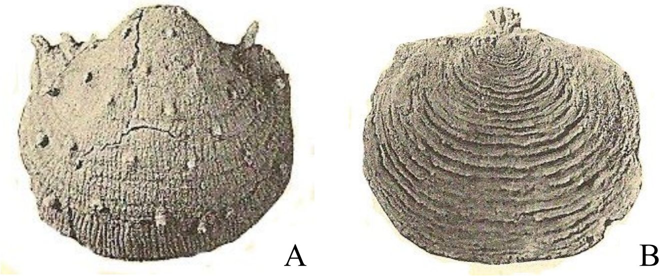

Fig. 1. *Devonoproductus walcotti* (Fenton & Fenton). A, ventral valve USNM 123923d, x3. B, dorsal valve USNM 123923e, x3. Hackberry Cerro Gordo Member (Upper Devonian), Iowa, United States. See Muir-Wood & Cooper (1960, pl. 45, fig. 6, 10).

Tribe **ANIDANTHINI** Waterhouse, 1968a

Australian members of Anidanthinae all belong to the Tribe Anidanthini, lacking the denticulate hinge of Megousiini Waterhouse, 2013 which is discussed further in the Appendix 2, starting on p. . Further differences involve the often bifid dorsal ears. and their often twisted and differently oriented nature.

Genera: *Anidanthus* Whitehouse (syn. *Nothokuvelousia* Waterhouse), *Akatchania* Klets, *Anidanthia* Waterhouse, *Fusiproductus* Waterhouse*, Mongousia* Manankov, *Protoanidanthus* Waterhouse, ?*Pseudomarginifera* Stepanov. Genera within Megousiini are discussed starting on p. 237.

Genus ***Anidanthus*** Whitehouse, 1928

Diagnosis: Small shells, spines only on ventral valve, along hinge row and scattered over disc and trail, ribs over both valves, dorsal valve lamellate and wedge-shaped without discrete trail, and with large laterally extended ears.

Type species: *Linoproductus springsurensis* Booker, 1932, p. 67 from Cattle Creek Formation (lower Artinskian, ie. Aktastinian) of Bowen Basin, Queensland, Australia.

Discussion: Controversy over the authorship of *Anidanthus* has been discussed by Waterhouse & Chen (2007, p. 16). Those authors, together with Briggs (1998), preferred to ascribe the authorship to Whitehouse (1928), whereas Brunton et al. (2000) granted the authorship to Hill (1950), yet placed *Pseudomarginifera* Stepanov, 1934 in synonymy. Hill

(1950) was first to describe the genus as *Anidanthus* according to the rules of the International Subcommission of Zoological Nomenclature (1999), but such rules did not apply when Whitehouse (1928) first proposed the genus, and certainly in practise, genera proposed before 1931 were deemed acceptable despite failure to use binomial nomenclature (see ICZN 1999, p. 67. article 67.2.2). "Although making no description or diagnosis, Whitehouse indicated specimens typical of his genus which had been previously described (and figured), and one of these at least was subsequently placed in a well-defined species, which may therefore be taken as type species, following normal procedure with "genus caelebs"" (Waterhouse 1966, p. 20). Melville (1984) in scrutinizing just a few aspects of *Anidanthus*, ignored that discussion. But Waterhouse & Chen (2007) argued that tolerance should be allowed for a genus proposed before the rules became established, and considered Whitehouse (1928) to be the author. Dorothy Hill would be the last person to have stooped to name-claiming.

Anidanthus springsurensis Booker, 1932

Fig. 2 - 4

1928 *Anidanthus* Whitehouse, p. 285.
1932 *Linoproductus springsurensis* Booker, p. 67, pl. 3, fig. 1-6, pl. 4, fig. 1-4 (part, not fig. 5-7 = *Anidanthia paucicostatus*)
1950 *Anidanthus springsurensis* – Hill, p. 10, pl. 7, fig. 2a, b, ?6, 7 (part, not fig. 1, 3-5 = *paucicostatus*).
1964 *A. springsurensis* – Hill & Woods, pl. P6, fig. 9 (part, not fig. 8, 10, 11 = *paucicostatus*).
1968b *A. springsurensis* – Waterhouse, p. 236, Fig. 2C, 3, pl. 1, fig. 2, 3 (part, not Fig. 2A, B, D, pl. 1, fig. 1, 4-6 = *paucicostatus*).
1972 *A. springsurensis* – Hill et al., pl. P6, fig. 9 (part, not fig. 8, 10, 11 = *paucicostatus*).
1986 *Nothokuvelousia aurifera* Waterhouse, p. 63, pl. 14, fig. 3, 10-19.
1998 *A. springsurensis* – Briggs, p. 204, Fig. 97I-K (part, not A-H = *paucicostatus*).

Diagnosis: Small transverse shells with extended ventral ears and wedge-shaped dorsal valve.

Holotype: For *springsurensis*, QMF 2545 from upper Cattle Creek Formation, figured by Booker (1932, pl. 3, fig. 1, 2), and Fig. 4A, B herein, OD. For *aurifera*, UQF 74096 from Roses Pride Formation, figured by Waterhouse (1986, pl. 14, fig. 13, 18) and herein Fig. 3A, B, OD.

Morphology: The species has been widely confused with *Anidanthia paucicostatus* (Waterhouse), a species readily distinguished by its larger size and much more concave

Fig. 2. *Anidanthus springsurensis* (Booker). A, decorticated interior of topotype dorsal valve GSQF 2541 figured by Booker (1932, pl. 4, fig. 4). B, decorticated dorsal interior of paratopotype GSQF 2543. Specimens x1.5, from Cattle Creek, Springsure, Bowen Basin. (Waterhouse 1968a).

dorsal valve. *Nothokuvelousia aurifera* was distinguished by its wedge-shaped dorsal valve, and it was later realized that *Anidanthus* was the same. Briggs (1998, p. 207) confused the taxon with *Megousia solita*, which belongs to the same genus but a different species, and consequently gave a wrong age to the Roses Pride Formation.

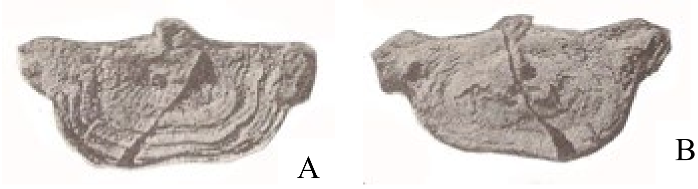

Fig. 3. *Anidanthus springsurensis* (Booker), external and internal aspects of dorsal mould UQFv 74096, holotype of *Nothokuvelousia aurifera* Waterhouse, showing dorsal laminae and wedge-shape and short trail, x1. From Roses Pride Formation, Queensland. (Waterhouse 1986).

Anidanthus is a very distinctive form, characterized by extended dorsal ears which are smooth externally, and by an anteriorly thickened dorsal valve in which mutiple trails are fused into a wedge, unlike the trail of other forms in which the trail is comprised of separate sheets of shell or a single thin structure. The wedge-shaped dorsal valve is clearly figured in the illustrations in Booker (1932, pl. 4, fig. 1, 2, 3), and also by Waterhouse (1986, pl. 14, fig. 13, 16-18) for material described, wrongly, as a separate species and genus. Briggs (1998, Fig. 97I, J, K) figured few and uninformative specimens from the Cattle Creek Formation, and lumped in other material of uncertain age. None of the *Revised Brachiopod Treatise* studies, or the overview by Muir-Wood & Cooper (1960), provided any figures or analysis of genuine *Anidanthus*.

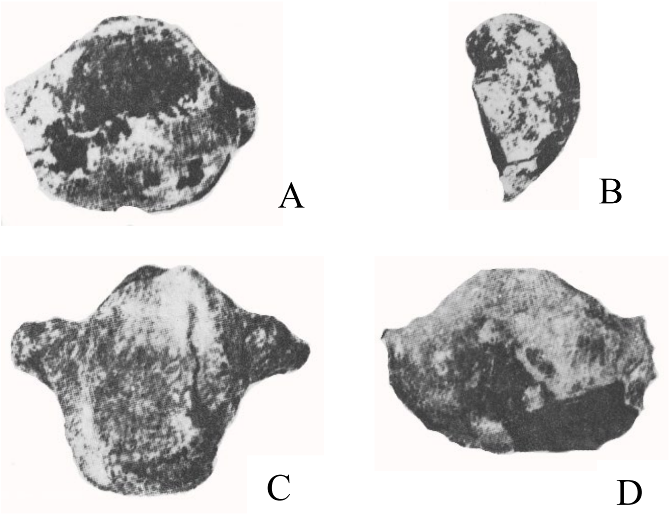

Fig. 4. *Anidanthus springsurensis* (Booker). A, B, ventral and lateral aspects of holotype, QMF 2545. C, ventral valve. D, ventral valve. Specimens x1. Upper Cattle Creek Formation. (Booker 1932).

Stratigraphy: The species is limited to faunas of the *Echinalosia preovalis* Zone, in the upper Cattle Creek Formation of the southwest Bowen Basin, and in the Roses Pride Formation of the southeast Bowen Basin, Queensland.

Anidanthus solitus (Waterhouse, 1968a)

Fig. 5 - 7

1968a *Megousia solitus* Waterhouse, p. 1172, pl. 154, fig. 1-6, 8-10
1984 *Anidanthus* sp. Campbell et al., fig. 6. 11-13.
1993 *Megousia solita* – Briggs & Campbell, p. 326, fig. 3.1-10.
1993 Anidanthid cf. *Megousia solita* – Briggs & Campbell, p. 32, fig. 3.11, 12.
1998 *M. solita* – Briggs, p. 207, Fig. 98A- I.
2001 Anidanthin gen. & sp. indet. Waterhouse, pp. 26, 44.
2002a Anidanthin gen. & sp. indet. Waterhouse, p. 27.
2013 *Anidanthus perdosus* Waterhouse, p. 328, Fig. 15.20.
2021 *A. solitus* – Waterhouse, p. 85, Fig. 7-10.

Diagnosis: Transverse shells, dorsal ears large and extend forward close to the visceral disc, dorsal valve wedge-shaped, without extended dorsal trail.

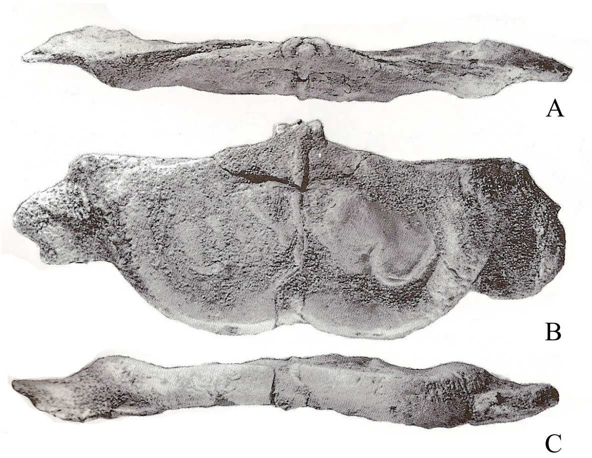

Fig. 5. *Anidanthus solitus* (Waterhouse), posterior, ventral and anterior aspects of dorsal valve UQF 75365, holotype of *perdosus* an unnecessary name, from Branxton Subgroup, north Sydney Basin, New South Wales, Australia, x1.5. (Briggs 1998).

Holotype: For *solitus*, ANU 17752b figured by Waterhouse (1968a, pl. 154, fig. 1; 2013, Fig. 15.20) and Fig. 7A, B herein from lower Wandrawandian Formation, south Sydney Basin, OD. For *perdosus*, UQF 75365 figured by Briggs (1998, Fig. F-H), Waterhouse (2013, Fig. 15. 20A-C; 2021, Fig. 7) and herein Fig. 5, from Branxton Subgroup, OD.

Morphology: The material in the synonymy is characterized by a wedge-shaped dorsal valve. As well, the lateral ears are moderately large and extend laterally with a forward anterior bulge, though they are not as extended nor as wide as in *Anidanthia paucicostatus* (Waterhouse). Both ventral and dorsal valves are wider than in *springsurensis* Booker (1932, pl. 3, fig. 1-6, pl. 4, fig. 1-7), as confirmed for specimens from Roses Pride Formation (Waterhouse 1986, pl. 14, fig. 3, 10-19), and shape provides the most ready distinction between the two species. Details are described in the studies mentioned in the synonymy.

Fig. 6. *Anidanthus solitus* (Waterhouse). A, dorsal external mould, BR 2316. B, dorsal external mould BR 2315 from Stephens Island, New Zealand, x1.5. (Briggs & Campbell 1993).

The original reference to *Megousia* Muir-Wood & Cooper is now regarded as having been error. *Megousia* was first named for shells from the Glass Mountains of Texas and has large alar extensions in the dorsal valve that extend forward, and may twist, whereas the alar extensions of *Anidanthus* extend laterally, as do those of *Anidanthia*. Furthermore the ears of *Megousia* are bifid as a rule, carrying a small posterior extension, never seen in *Anidanthus* or *Anidanthia*, and the hinge is denticulate. Therefore *Megousia* is separated as a tribe Megousiini Waterhouse, 2018, p. 225, with further discussion in Appendix 2, p. 237ff.

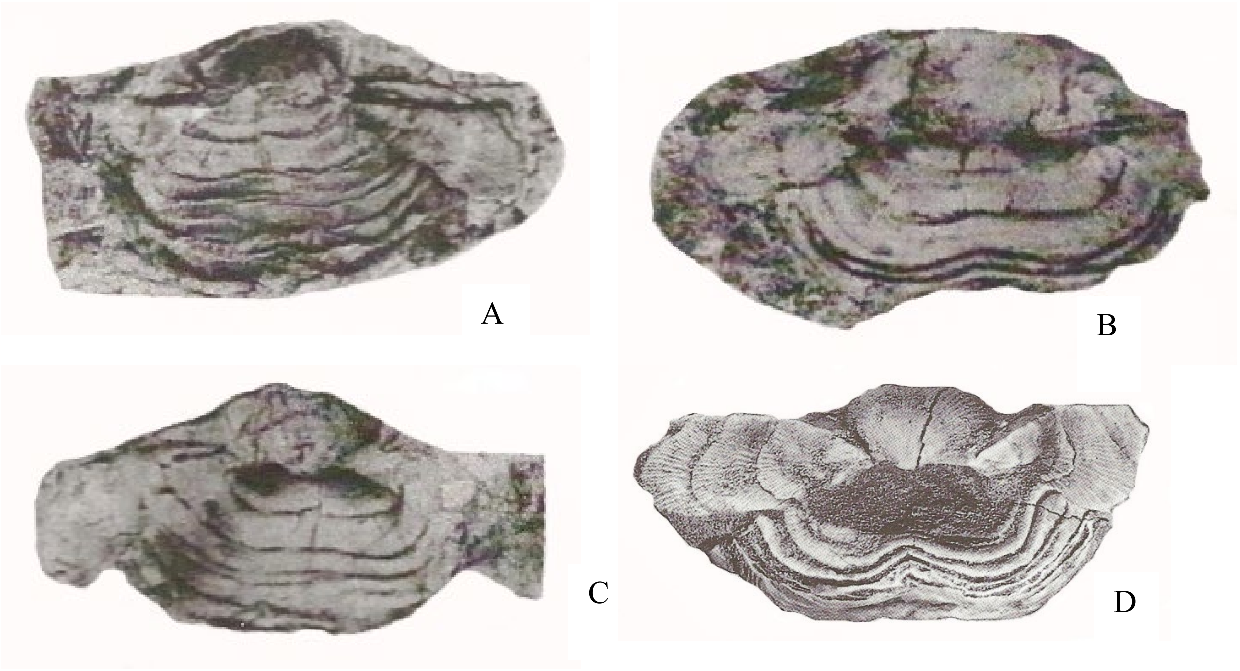

Fig. 7. *Anidanthus solitus* (Waterhouse). A, B, dorsal aspect of external mould and latex cast, holotype ANU 17752, x 1.5. C, dorsal aspect AMF 23986, latex cast of external cast. Specimens from Berrara, New South Wales. (Waterhouse 1968b). D, latex cast of specimen from Belford Dome, x 1.5. (Briggs 1998). The quality of these figures A – C reproduced from the Journal of Paleontology reflects the somewhat flawed copying process.

Stratigraphy: The type material of *Anidanthus solitus* comes from the Branxton Subgroup in the Sydney Basin in New South Wales. From New Zealand, comparable material has been found in the Queens Beach Formation on Stephens Island, northern South Island (Campbell et al. 1984), but the formation is of Triassic age, and the material reworked from older but unknown deposits (Waterhouse 2002a, p. 142). Elsewhere similar specimens are found in the Caravan Formation of Wairaki Downs, southern New Zealand, of early middle Kungurian (Filippovian) age (Briggs & Campbell 1993, Waterhouse 2002a, p. 27). Briggs (1998) reported the species from the Eight Mile Block at Warwick and stations in the Sydney Basin from the Fenestella Shale and Wandrawandian beds, and these need closer scrutiny. The range of the species is not clear, pending clarification of Wandrawandian faunas.

Genus ***Anidanthia*** Waterhouse, 2013

Diagnosis: Shells moderately large for the subfamily, with prominent radial ornament, spines limited to ventral valve, forming a prominent hinge row, scattered and rare over disc and trail. Dorsal ears laterally extended, not twisted, trail long, geniculate, not thickened. Hinge not denticulate.

Type species: *Anidanthus paucicostatus* Waterhouse, 1986, p. 62 from Elvinia Formation (Sakmarian) of southeast Bowen Basin, north Queensland, OD.

Discussion: Examination of anidanthin genera in east Australia shows that the group has been misrepresented to some extent. *Anidanthus springsurensis* (Booker, 1932, p. 67), the type species of *Anidanthus*, was interpreted substantially on the basis of material from Homevale, north Bowen Basin, Queensland, rather than the type locality in the Cattle Creek Formation of the southwest Bowen Basin, examples being provided by Hill (1950), Waterhouse (1968b), Briggs (1998), Brunton et al. (2000) and Brunton (2007). Muir-Wood & Cooper (1960) based their interpretation of *Anidanthus* partly on Homevale material, and treated anidanthids from Kimbriki, New South Wales, as typical for illustrating the genus. The Kimbriki shells have reduced dorsal ears, and are referable to *Protoanidanthus compactus* Waterhouse, 1986. Waterhouse (1986) established that Homevale and Elvinia material differed at least specifically from type *springsurensis*, and, as well, a separate genus *Nothokuvelousia* was discriminated in the Rose's Pride Formation of southeast Bowen Basin, distinguished from Homevale and Elvinia material by its wedge-like dorsal valve. Briggs (1998) synonymized *Nothokuvelousia* with *Anidanthus*, and was right to do so, because it is now realized that type *Anidanthus* also has a wedge-like dorsal valve. By contrast, the Elvinia and Tiverton anidanthids have a non-thickened dorsal valve with separate mutiple trails, just as in *Protoanidanthus*, but differ from *Protoanidanthus* in having extended dorsal ears.

Anidanthia is like *Megousia* Muir-Wood & Cooper, 1960 in having laterally extended dorsal ears and a moderately long slender trail. It differs from *Megousia* in the non-denticulate hinge and the nature of the dorsal ears, which extend laterally, and rarely forwards in *Anidanthia* (see Appendix 2, p. 237 herein) and are not bifid. An additional distinction for *Megousia*, pointed out by Brunton et al. (2000, p. 532), is that the dorsal ears bear ribs which curve antero-dorsally, whereas the external ears in what is now *Anidanthia* are smooth, or more accurately, smoother, for there is some variation. In *Megousia*, the ears show a forward twist, as displayed in the Glass Mountains species described by Cooper & Grant (1975) from Texas as *auriculata, definita, flexuosa*, and *mucronata*. The generic position of species *girtyi* (King, 1931) is uncertain due to incomplete preservation, unless it belongs to *Protoanidanthus.* The species *waagenianus* Girty, 1909 from the Capitanian looks close to *Fusiproductus* Waterhouse, 1966.

It seems that various authors have treated the nature of the dorsal trail as variable and of no taxonomic significance. So far, it has been found that collections from single stations are consistent in that aspect of their morphology, and it is judged advisable to treat generic and specific names as reflective of morphology, with the limits circumscribed through extensive observation. Whilst it may be deemed to be “only” an ecologic factor, this is not established for productid dorsal valves, and the feature is a significant morphological feature of various strophalosiid genera such as *Wyndhamia* and *Arcticalosia*, a yakovleviid called *Archboldevia*, and a waagenoconchid genus called *Wimanoconcha*: it is an objective morphological feature. The trail in species with wedge-like dorsal valve is short and often not externally geniculate or semi-geniculate. Not a single specimen of the anidanthid specimens from the lower and middle Tiverton Formation and partly correlative Elvinia Formation of the Bowen Basin in Queensland, shows a wedge-shaped dorsal valve, whereas at a younger level dorsal valves from the upper Cattle Creek Formation and correlative Roses Pride Formation in the Bowen Basin are all wedge-shaped in section.

Anidanthia paucicostata (Waterhouse, 1986)

Fig. 8, 9

1892 *Productus* sp. indet. Etheridge, pl. 12, fig. 17.
1932 *Linoproductus springsurensis* [not Booker] – Booker, p. 67, pl. 4, fig. 5-7? (part, not pl.

3, fig. 1-6, pl. 4, fig. 1-4 = *springsurensis*).
1950 *Anidanthus springsurensis* – Hill, pl. 7, fig. 1, 3, 4 (part, not fig. 2, 5, 6 = *springsurensis*).
1964 *A. springsurensis* – Maxwell, p. 44, pl. 7, fig. 13-16.
1964 *A. springsurensis* – Hill & Woods, pl. P6, fig. 8, 10, 11 (part, not fig. 9 = *springsurensis*).
1968b *A. springsurensis* – Waterhouse, p. 236, pl. 1, fig. 1, 4, 5, 6, text-fig. 2A, B, D (part, not pl. 1, fig. 2, 3, text-fig. 2C, 3 = *springsurensis*).
1972 *A. springsurensis* – Hill, Playford & Woods, pl. P6, fig. 8, 10, 11 (part, not fig. 9 = *springsurensis*).
1974 *A. springsurensis* – McCarthy et al., Fig. 4J.
1980 *A. springsurensis* – McClung, pl. 19.1, fig. 6.
1986 *A. paucicostatus* Waterhouse, p. 62, pl. 13, fig. 23-27, pl. 14, fig. 1, 2, 4-9.
1998 *A. springsurensis* – Briggs, p. 204, Fig. 97A-F, G?, H? (part, not Fig. 97I-K = *springsurensis*).
1998 *A. cessnockensis* Briggs, p. 201, Fig. 96A, C, G (part, not B, D, E, F, H, I = *Protoanidanthus compactus* Waterhouse).

Diagnosis: Shells moderately elongate as a rule with arched venter, moderately coarse costae, often with fine intercalated costellae.

Holotype: For *paucicostata*, UQF 74083 from Elvinia Formation, southeast Bowen Basin, figured by Waterhouse (1986, pl. 13, fig. 25), OD. For *cessnockensis*, UQF 75357 from Farley Formation, figured by Briggs (1998, Fig. 96A, C), OD.

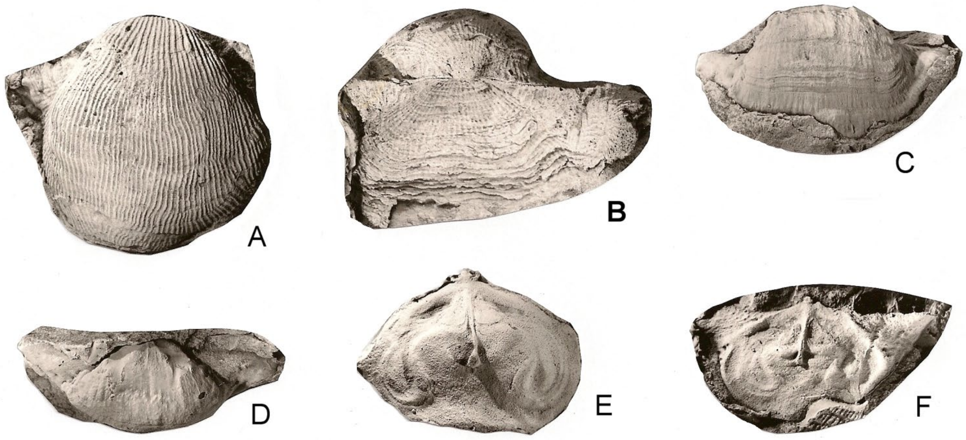

Fig. 8. *Anidanthia paucicostata* (Waterhouse). A, latex cast of ventral valve UQF 81206, x1.2. B, dorsal aspect of latex cast UQF 81207, x1.1. C, D, anterior ventral and posterior ventral aspect of ventral internal mould UQF 81208, x1. E, latex cast of dorsal interior UQF 81271, x1.5. F, latex cast of dorsal interior UQF 81210, x1.5. Tiverton Formation, north Bowen Basin, Queensland. (Waterhouse 2013).

Morphology: This species is normally not sulcate, and there are many intercalate ribs. It appears that rib variation is mostly displayed by *paucicostata* rather than *springsurensis*: the ornament in *springsurensis* appears to be consistently fine; that of *paucicostata* is generally coarser, but includes specimens with more numerous and more differentiated costae, partly because of rib splitting and intercalation. The species *paucicostata* is slightly but distinctly older than *springsurensis*, and differs strongly in the nature of the dorsal valve and trail. Another difference lies in the nature of the visceral disc, which, in undistorted specimens, may be larger and more transverse and sulcate in many *springsurensis* than in most *paucicostata*.

Briggs (1998) recognized a separate Australian species *cessnockensis* from the Farley Formation of the northern Sydney Basin at Singleton, Hunter Valley, New South Wales. The species overlaps *paucicostata* in range. Two species were lumped in his description, and one suite of specimens is reallocated to *Protoanidanthus compactus* Waterhouse. Judged from published figures, costae number six to eight in 5mm on the ventral valve of type *cessnockensis*, and in the text were counted at eight to eleven in 5mm anteriorly. The species was said by Briggs to be distinguished by its prominent sublamellate “concentric” (ie. commarginal) wrinkles with higher wider crests, and flatter dorsal valve for which the anterior margin is placed well behind that of the ventral valve. But the strength and nature of the commarginal dorsal wrinkles appears variable on populations, with no consistent stratigraphic record, and no explanation was provided why the synonymy for the species in Briggs (1998)

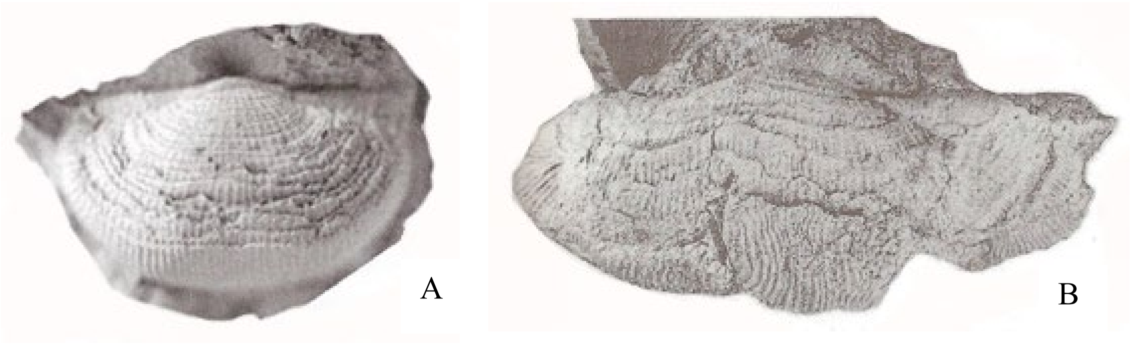

Fig. 9. A, *Anidanthia paucicostata* (Waterhouse), dorsal external mould of immature specimen from lower Tiverton Formation, Queensland, x2. (Waterhouse 2015a). B, *A. cessnockensis* (Briggs), dorsal external mould x2. Both figured dorsal valves show long trails and the dorsal valve is not thickened and wedge-shaped. (Briggs 1998).

includes occasional individuals referable to *springsurensis* and *paucicostata,* even under the criteria adduced by Briggs (1998). Close examination of the Tiverton suites shows no consistent pattern, and the dorsal lamellae of the Tiverton and Elvinia specimens are as slender as in the holotype of *cessnockensis* (Briggs 1998, Fig. 96C) from the Farley Formation at Singleton, Hunter Valley, and the dorsal anterior margin lies close to the ventral anterior margin, as far as they are preserved.

Anidanthia crenulata (Briggs, 1998)

Fig. 10

1998 *Megousia crenulata* Briggs, p. 209, Fig. 99A-H.

Diagnosis: Small transverse shells with fine ribs, numbering nine to thirteen in 5mm, spines rare. Ventral ears laterally extended, without bulging forward, dorsal valve not thickened.

Holotype: AMF 92693 from Wandrawandian Formation, figured by Briggs (1998, Fig. 99A, D, G), OD. This has been lost for over twenty years at time of writing, and it is proposed to replace the specimen with a neotype from the same locality, UQF 75366, as figured by Briggs (1998, Fig. 99B and herein as Fig. 10B.

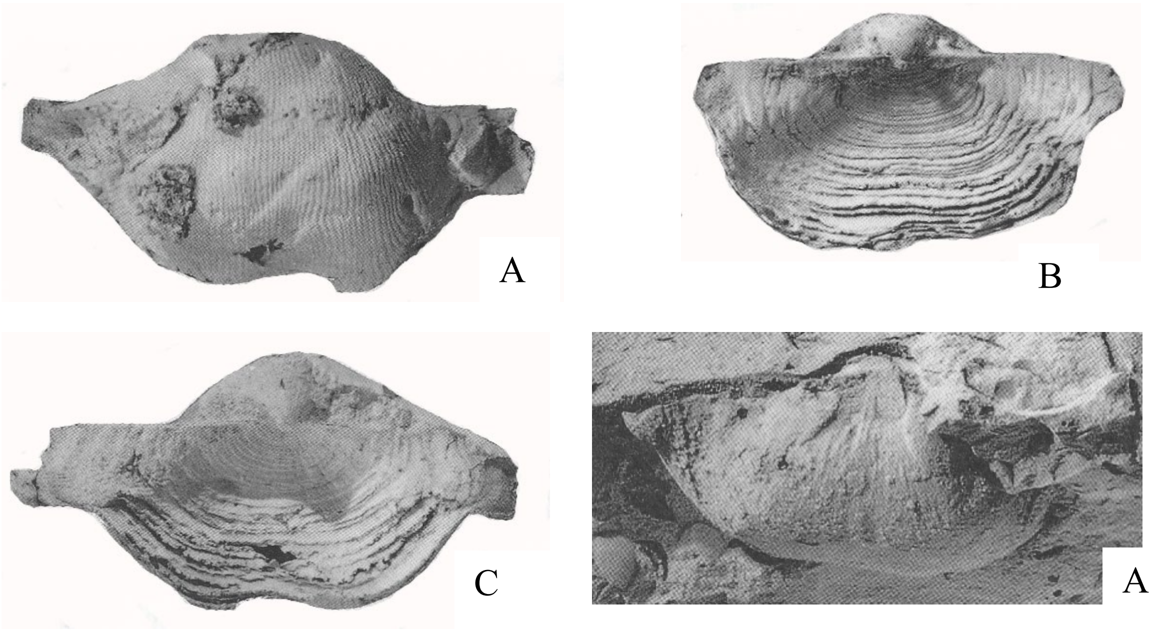

Fig. 10. *Anidanthia crenulata* (Briggs). A, C, ventral valve and dorsal aspect of latex cast AMF 96293, holotype, now lost. B, latex cast of specimen with valves conjoined, UQF 75366, designated neotype. D, posterior view of ventral internal mould, AMF 96295. Specimens x2 except D x0.9, from Wandrawandian Formation. (Briggs 1998).

Stratigraphy: The species is distinctive. It comes from the lower *Echinalosia discinia* Zone in what Briggs termed the middle Wandrawandian Formation.

Anidanthia aplini Waterhouse, 2015b

Fig. 11

1969 *Anidanthus springsurensis* [not Booker] – Runnegar & Ferguson, pl. 2, fig. 15-17.
2015b *Anidanthia aplini* Waterhouse, p. 86, Fig. 26.

Diagnosis: Moderately transverse shells with strong moderately close-spaced ribs, dorsal ears usually ribbed, dorsal lamellae moderately developed.

Holotype: UQF 69231, South Curra Limestone (Changhsingian), illustrated in Waterhouse (2015b, Fig. 26C) and Fig. 11C herein, OD.

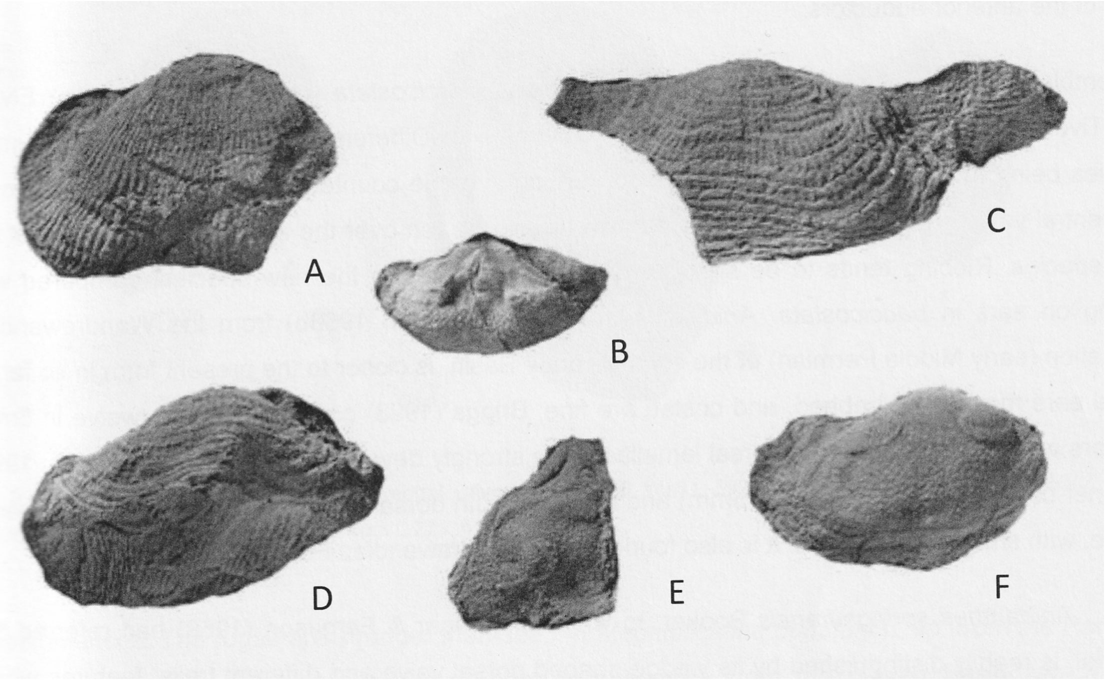

Fig. 11. *Anidanthia aplini* Waterhouse. A, ventral valve UQF 69237, x2. B, posterior aspect of ventral internal mould UQF 69242, x2. C, dorsal valve holotype UQF 69221, x2. D, anterior dorsal valve and trail, UQF 69226, x2. E, dorsal interior of same specimen, x2. F, ventral internal mould UQF 69234, x1.5. From South Curra Limestone, Gympie, southeast Queensland. (Waterhouse 2015b).

Morphology: The shell is transverse as a rule, trail long and geniculate, weak dorsal fold present anteriorly. Ventral exterior covered by radial costellae, twenty to twenty one in 10mm at 10mm from umbo, increase mostly by intercalation, but in the sulcal region increase appears to have been by bifurcation, with newly formed costellae showing sharp angular divergence from parent rib, crests round, as wide as interspaces. Ventral spines sparsely distributed, emerging at high angle from the costae which may diverge and reunite around the spine base.

This species looks close to *Anidanthia paucicostata* (Waterhouse) from the Elvinia and Tiverton Formations of the Bowen Basin, Queensland. Differences involve shape, the Gympie species being more transverse. Ribs on average number seven to nine in 5mm on the ventral valve in *paucicostata*, compared with nine to eleven over the anterior ventral valve of *aplini*. *A. crenulata* (Briggs, 1998) has finer costae (nine to thirteen in 5mm) and rather smooth dorsal ears, but is close in its transverse outline, with smaller dorsal ears.

Stratigraphy: The species is found in the South Curra Limestone and Gundiah Bridge Greywacke of Queensland.

Genus ***Protoanidanthus*** Waterhouse, 1986

Diagnosis: Small shells with dorsal ears much smaller than the auricular extensions of related genera, dorsal valve concave and not wedge-like.

Type species: *Protoanidanthus compactus* Waterhouse, 1986 from Dresden Formation, southeast Bowen Basin, Queensland, OD.

Discussion: Brunton (2007) refused to accept the validity of this genus, and Briggs (1998) in accepting the genus claimed to have revised the diagnosis, as if Waterhouse had not recognized the difference between the ears in *Protoanidanthus* and *Anidanthus*, but Briggs failed to adequately compare the genus with *Anidanthus*, because he either overlooked or underrated the significance of the concavity of the dorsal valve, and failed to assess the non-denticulate nature of the hinge.

Protoanidanthus gosforthensis Briggs, 1998

Fig. 12

1998 *Protoanidanthus gosforthensis* Briggs, p. 198, Fig. 95A-D.

Diagnosis: Small shells with sturdy ventral costae, eleven to fifteen in 5mm over mid-disc.

Holotype: UQF 75347 from Lochinvar Formation, figured by Briggs (1998, Fig. 95A-D) and herein Fig. 12A, B, OD.

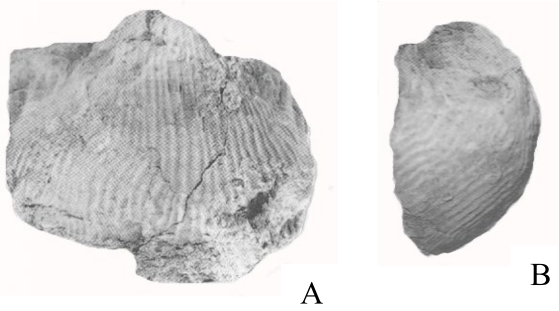

Fig. 12. *Protoanidanthus gosforthensis* Briggs. A, B, ventral and lateral aspects of holotype, UQF 75347, x2. Lochinvar Formation, Sydney Basin. (Briggs 1998).

Morphology: Briggs offered comparisons with material from northeast Russia.

Stratigraphy: The species is found in the Lochinvar Formation of the north Sydney Basin.

Protoanidanthus polkibinensis Briggs, 1998

Fig. 13

1987 *Protoanidanthus* n. sp. 2 Briggs, p. 137.
1998 *Protoanidanthus polkibinensis* Briggs, p. 199, Fig. 95E-0.

Diagnosis: Transverse subrectangular shells with wide hinge and relatively large ears for the genus, strong commarginal laminae over dorsal valve.

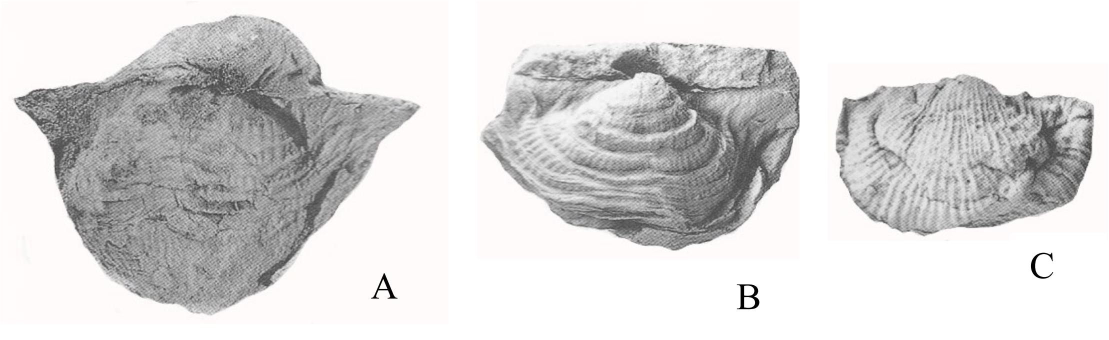

Fig. 14. *Protoanidanthus polkibinensis* Briggs. A, latex cast of holotype, UQF 75348. B, external mould showing dorsal valve and ventral umbo, UQF 75356. C, latex cast of ventral valve UQF 75349. Specimens x2, from Silver Spur beds. (Briggs 1998).

Holotype: UQF 75348 from grey silty sandstone of Silver Spur beds, Goondiwindi, Texas area in south Queensland near the southern border, figured by Briggs (1998, Fig. 95J, K) and herein as Fig. 14A, OD.

Stratigraphy: The species comes from the same faunal zone as *Bandoproductus macrospina walkomi* in the Silver Spur outlier, and is also reported from the Rutherford Formation in the north Sydney Basin.

Protoanidanthus compactus Waterhouse, 1986

Fig. 15

?1960 *Anidanthus springsurensis* [not Booker] – Muir-Wood & Cooper, p. 209, pl. 112, Fig. 14-20.
1986 *Protoanidanthus compactus* Waterhouse, p. 61, pl. 13, fig. 19-22, pl. 15, fig. 16-18.
1991 *P. compactus* – Waterhouse, pl. 1, fig. I, j.
?1998 *P. compactus* – Briggs, p. 201, Fig. 95P.
1998 *A. cessnockensis* Briggs, p. 201, Fig. 96B, D, E, F, H, I (part, not Fig. 96A, C, G = *cessnockensis* = *paucicostata*).

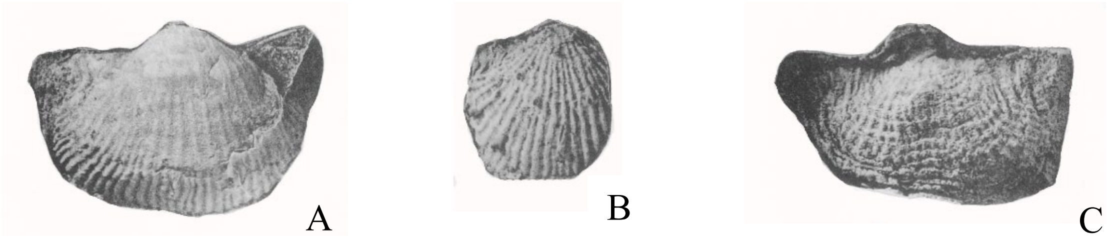

Fig. 15. *Protoanidanthus compactus* Waterhouse. A, ventral latex cast UQF 74439. B, ventral latex cast UQF 74440. C, dorsal external mould UQF 74437. Specimens x2. Fairyland Formation. (Waterhouse 1986).

Diagnosis: Small ovally subrectangular shells with firm costae over both valves, numbering nine to eleven in 5mm, ventral disc spines moderately conspicuous, ventral hinge row of spines up to 0.8mm in diameter.

Holotype: UQF 74080 from Dresden Formation, figured by Waterhouse (1986, pl. 13, fig. 22), OD.

Stratigraphy: The species is found in the Fairyland Formation (*Maxwellosia curtosa* Zone) and Dresden Formation of the southeast Bowen Basin, Queensland, and apparently at

Kimbriki in the north Sydney Basin. Briggs (1998) figured a dorsal valve from the "Buffel Formation", which is of group status, but better stratigraphic control is desirable.

Protoanidanthus costatus Waterhouse, 2021

Fig. 16 - 19

?1968a *Megousia* sp. Waterhouse, p. 1174, pl. 154, fig. 7, 12, 13.
2021 *Protoanidanthus costata* Waterhouse, p. 115, Fig. 7-10.

Diagnosis: Elongate with sturdy costae.

Holotype: Specimen UQF 13528, Fig. 7, 8, specimen b, and Fig. 19b herein, OD.

Morphology: The ventral valves are elongate with relatively strong ribs,at five in 5mm, which bear scattered and slender spines 0.3-0.5mm in diameter arising from the crest, and narrower than the crest. A row of much stronger spines 1mm in diameter extends along the inner ears.

This species is characterized by its elongate shape and strong costae. In the Lakes Creek beds it is found in finer sediment than is the norm for other species of *Protoanidanthus* in east Australia, and is slightly younger than other occurrences in Queensland, but appears to have been contemporaneous with possible occurrence of *P. compactus* in Tasmania.

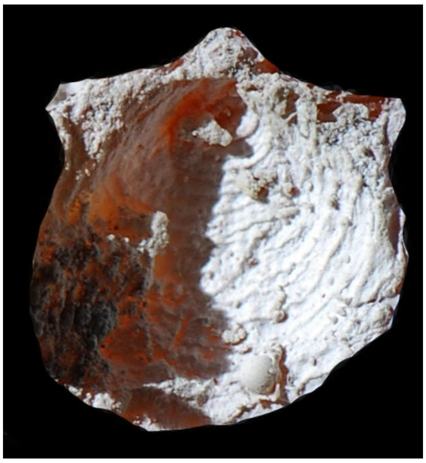

Fig. 16. *Protoanidanthus costatus* Waterhouse, latex cast of dorsal valve UQF 82608, x4 approx. Lakes Creek Formation, Queensland. (Waterhouse 2021).

Protoanidanthus umbonatus Shi & Waterhouse (1996, p. 101, pl. 18, fig. 1-16; Waterhouse 2018, p. 224, Fig. 191) is the closest of species so far known from the northern hemisphere, with comparatively strong ribs counted at six to seven in 5mm. Specimens are more transverse than the present species, and come from the *Yakovlevia transversa*,

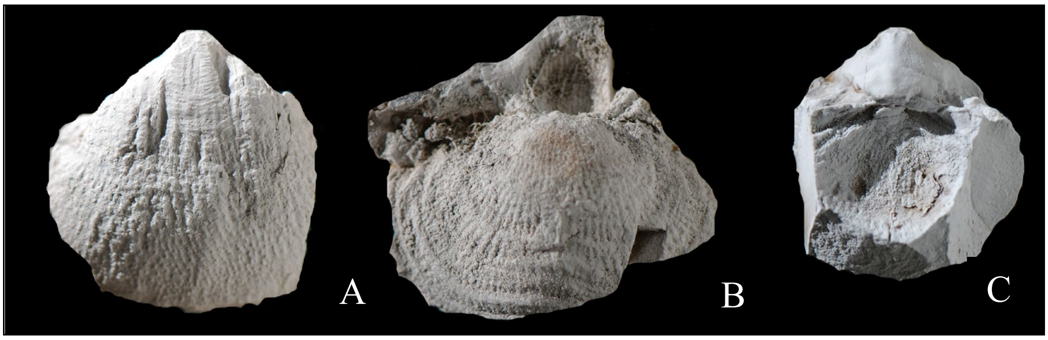

Fig. 17. *Protoanidanthus costatus* Waterhouse. A, C, ventral and dorsal aspects of internal mould. B, dorsal aspect of external mould, showing dorsal valve and part of ventral valve. Specimen UQF 82609, x2. Lakes Creek Formation, Queensland. (Waterhouse 2021).

Rugivestis commarginalis and *Ogilviecoelia shii* Zones, of broadly Sakmarian age, in the upper Jungle Creek Formation in the Yukon Territory of Canada. In east Australia, specimens (Fig. 18) were reported from the Berriedale Limestone of Tasmania that may prove to belong to this species, because they agree in shape with moderately prominent ears and with comparable costation (Waterhouse 1968), estimated at being close to seven or eight ribs in 5mm, though allowance must be made for a degree of obscurity in the figures. The dorsal ears within these specimens as in the types lack the large extensions of *Anidanthus*.

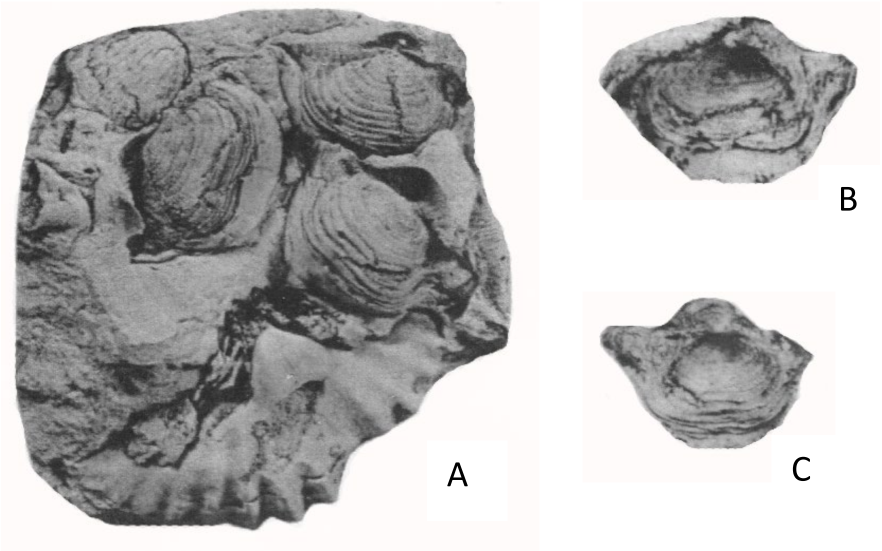

Fig. 18. *Protoanidanthus costatus* Waterhouse?. A, block x1, Pratt Collection, BMNH B 19313. B, C, latex casts x1 from the block, dorsal aspect of specimens with valves conjoined, unregistered individually. From Berriedale Limestone at Ben Lomond, Tasmania. (Waterhouse 1968a).

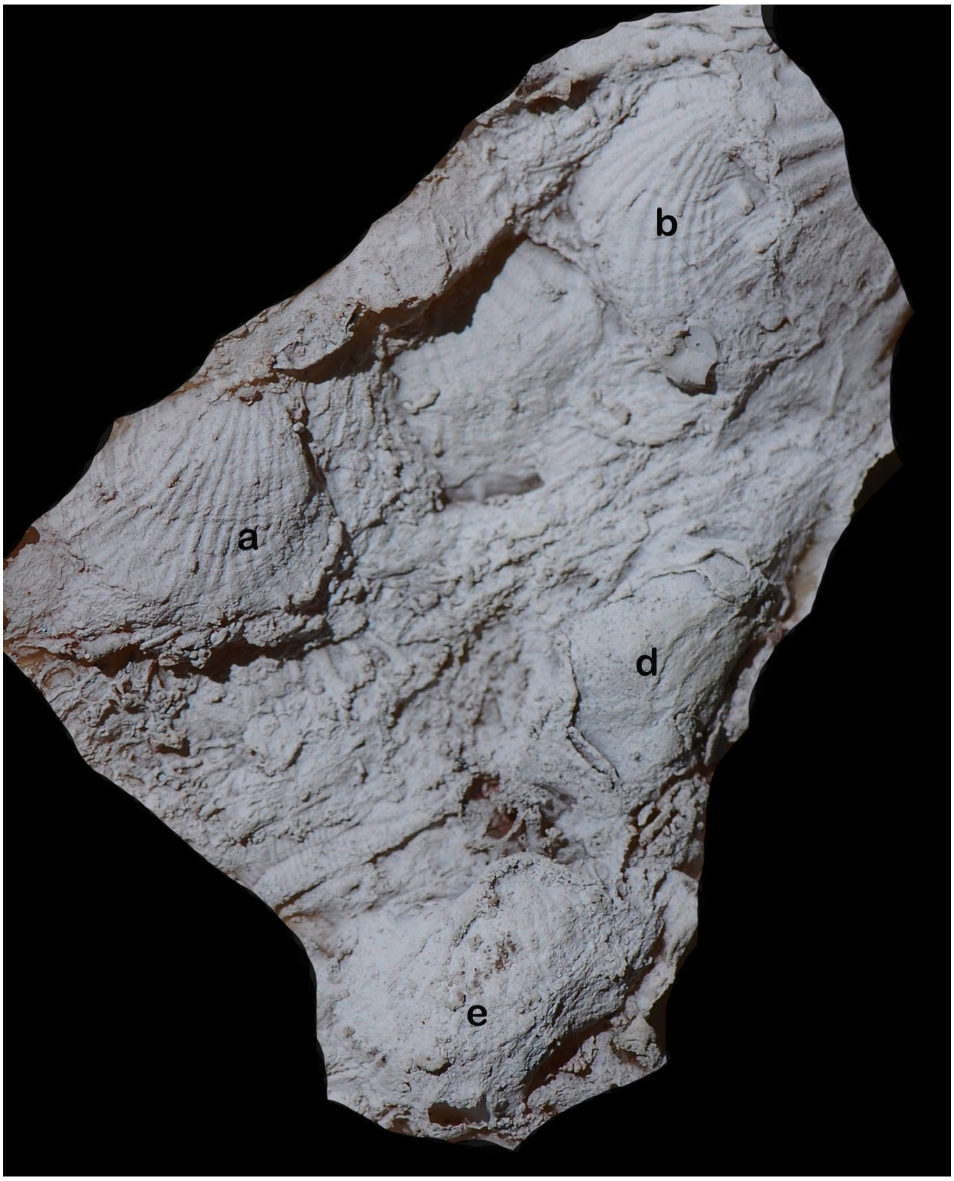

Fig. 19. *Protoanidanthus costatus* Waterhouse, latex cast x3 showing scattered and broken specimens, preserved as moulds, mostly as ventral external moulds, and (d) as a worn dorsal internal mould. Holotype = b, UQF 13528. Other specimens include a = UQF 82607, d = UQF 82607, e = UQF 82734. Lakes Creek Formation, Queensland. (Waterhouse 2021).

Subfamily **LIRARIINAE** Waterhouse, 2013, p. 332

Diagnosis: Both valves costellate, spines inconspicuous, limited to ventral valve, forming row along or close to hinge, may be scattered and erect over ventral valve. Dorsal valve not lamellate or spinose. Ventral adductors smooth or deeply scored by longitudinal grooves. Lower Permian (Asselian) to Middle Permian (Wordian).

Genera: *Liraria* Cooper & Grant, *Calandisa* Waterhouse & Campbell, *Cimmeriella* Archbold, *Globiella* Muir-Wood & Cooper, *Protanidanthus* Liao.

Genus ***Calandisa*** Waterhouse & Campbell, 2013

Diagnosis: Small highly arched shells with costellae over both valves, spines in hinge row, rare body spines, and one to five strong spines on each outer ear, additional to hinge row spines.

Type species: *Calandisa solitarius* Waterhouse & Campbell in Waterhouse 2013 from Takitimu Group (upper Sakmarian), Dunton Range, New Zealand, OD.

Discussion: The distinctive feature of this species, as for the genus, lies in the presence of the large erect spine or spines on each ventral ear. Otherwise the genus and species is moderately close to *Liraria* Cooper & Grant, 1975 and *Cimmeriella* Archbold & Hogeboom, 2000.

Calandisa solitarius Waterhouse & Campbell, 2013

Fig. 20

2013 *Calandisa solitarius* Waterhouse & Campbell in Waterhouse, p. 332, Fig. 15.25.
2021 *C. solitarius* – Waterhouse & Campbell, p. 17, Fig. 5.

Diagnosis: Transverse to elongate shells with rare ventral spines, and one or more large spines on outer ventral ear.

Holotype: BR 2400 from Eglinton Volcanics, Dunton Range, New Zealand, figured by Waterhouse & Campbell (2013, Fig. 15.25B; 2021, Fig. 5B) and herein Fig. 20B, OD.

Morphology: Shells weakly transverse, the ventral valve highly convex, umbo incurved with wide angle of 95-100°, and moderately large convex ears and obtuse cardinal extremities. There is no sulcus, and the anterior commissure varies from slightly receeded or produced. The dorsal valve is concave and the trail subgeniculate and moderately long. Both valves are crossed by fine radial ribs, eight in 5mm at mid-length on the ventral valve, and covering the ears. The ventral valve is also covered over disc and trail by low to very low rugae, numbering at least thirteen on the largest specimen. The dorsal valve bears very low growth rugae and pauses, but no laminae. A single row of spines lies along the ventral hinge, the outermost spine 1mm wide, and strong erect spines varying between one and five lie on each outer ear; erect spines 0.2 and 0.3mm across lie over the anterior disc and start of trail, arising from the crest of a costa, which passes through otherwise undisturbed.

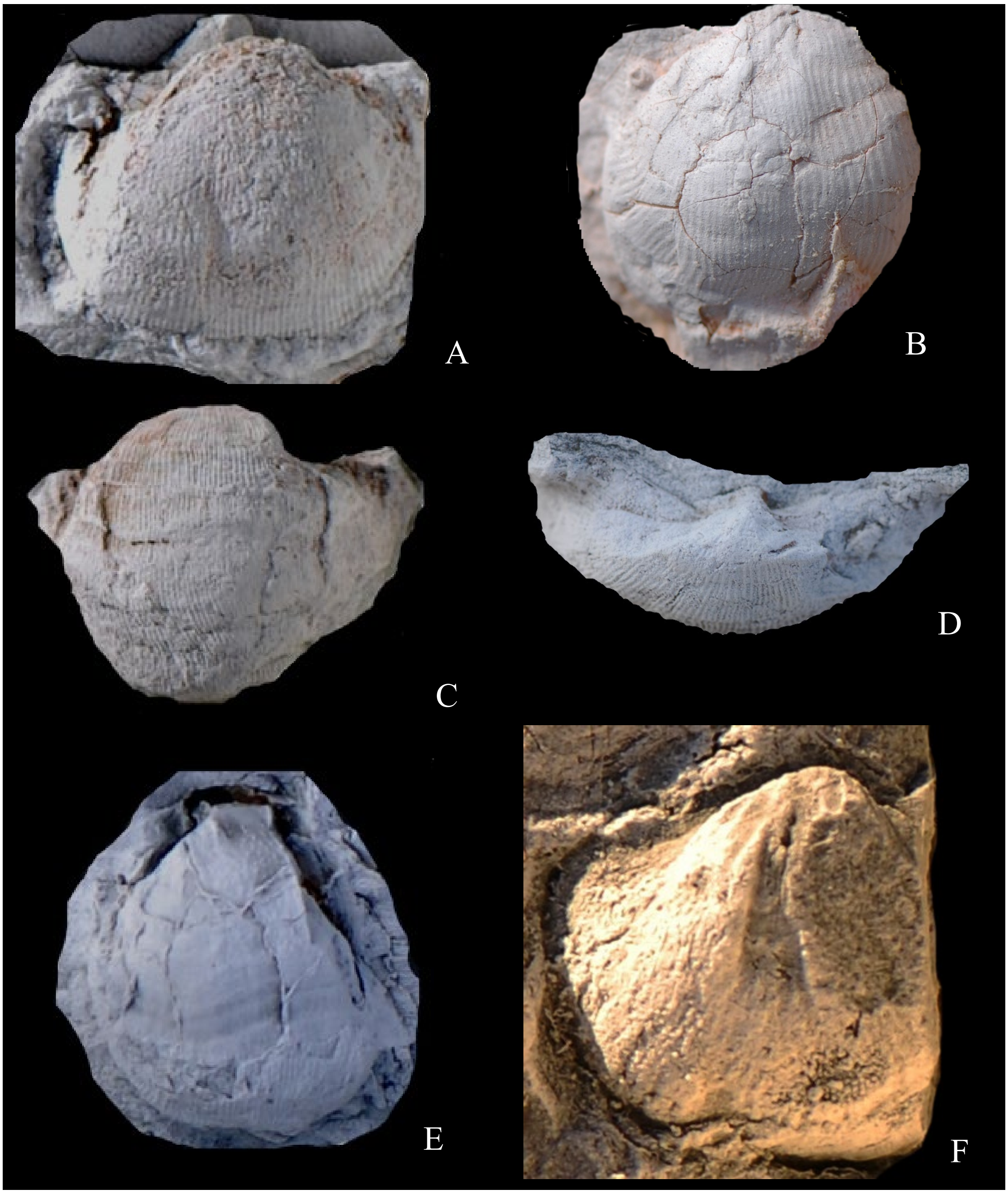

Fig. 20. *Calandisa solitarius* Waterhouse & Campbell. A, ventral internal mould BR 3065, x3. B, latex cast of ventral valve holotype, BR 2400, x3. C, D, ventral and posterior aspects of ventral valve BR 3091, x2. E, internal mould, ventral valve BR 2486, x2.5. F, internal mould of ventral valve BR 2402, x3.5. From Eglinton Volcanics, New Zealand. (Waterhouse 2013).

Stratigraphy: The species is found in the Eglinton Volcanics of New Zealand, with the accompanying fauna described by Waterhouse & Campbell (2021) and judged to be of middle Sakmarian age, in the *Echinalosia curvata* Zone.

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PERMIAN PAUCISPINAURIIDAE (BRACHIOPODA, SUBORDER LINOPRODUCTIDINA) IN EAST AUSTRALIA AND NEW ZEALAND, WITH MENTION OF ALLIES FURTHER AFIELD

Abstract

Species are described from the Permian of east Australia and New Zealand as members of four genera in Paucispinauriinae Waterhouse, a subfamily of the Paucispinauriidae Waterhouse, 1986a which belongs to Proboscidelloidea Muir-Wood & Cooper. Comparisons are made with Permian paucispinaurians reported from the northern paleohemisphere, chiefly the United States, and similarities are briefly evaluated for species described from northeast Russia, Mongolia and Japan. Related genera classed in Tribe Magniplicatini and in Family Auriculispinidae with genera belonging to Tribes Auriculispinini, Filiconchini and Lyoniini are also recorded from east Australia and New Zealand. The earliest known species entered Australian faunas during Sakmarian time and the time of greatest diversification in east Australia was during the Guadalupian Series (Middle Permian), with related species persisting in the region until very Late Permian.

INTRODUCTION

It was Booker (1930) who first applied a new generic name to a member of what came to be called Paucispinauriidae in east Australia. The genus *Terrakea* Booker was over the years recognized as a prominent and common brachiopod found widely in the marine Permian sediments of east Australia, and with allied genera now classed in Paucispinauriinae Waterhouse, has high potential for purposes of correlation. Members of the family are absent from the earliest known marine sediments of east Australia, and entered the succession during the somewhat warmer Sakmarian times, and persisted throughout much of the remaining period in marine sediments. Briggs (1998) and Brunton (2007) followed by Tazawa (2008a) demurred at the recognition of genera other than *Terrakea*, but Briggs (1998, p. 161) inconsistently allowed that subgenera could be defined, Brunton et al. (2000, pp. 533) recognized *Paucispinauria,* and Brunton (2007, p. 2653) recognized an allied genus *Spargospinosa*, as well as *Pinegeria*, now classed in an allied group.

Members of a closely allied tribe Magniplicatininae are recorded as *Magniplicatina* from much the same faunas in east Australia and New Zealand: the genus is also well represented in the Permian faunas of the Glass Mountains, west Texas, as described by Cooper & Grant (1975). Further genera *Filiconcha* Dear and *Costatumulus* Waterhouse, are classed in Auriculispinidae Waterhouse, together with a small cluster of genera in Lyoniinae, well represented in the lower Early Permian of east Australia. (See Table 1)

Family Proboscidellidae Muir-Wood & Cooper, 1960

- Subfamily Proboscidellinae Muir-Wood & Cooper, 1960
- Subfamily Undariinae Waterhouse, 2001
- Subfamily Fluctuariinae Nalivkin, 1979
- Subfamily Dawesioniinae Waterhouse, 2013

Family Paucispinauriidae Waterhouse, 1986a

- Subfamily Paucispinauriinae Waterhouse, 1986a
    - Tribe Paucispinauriini Waterhouse, 1986a
    - Tribe Holotricharinini Waterhouse, 2013
- Subfamily Magniplicatininae Waterhouse, 2001
    - Tribe Magniplicatinini Waterhouse,2001
        - Subtribe Magniplicatininai Waterhouse, 2001
        - Subtribe Cancrinellinai Waterhouse, 2013
    - Tribe Engellinini Waterhouse, 2013
- Subfamily Coolkilellinae Waterhouse, 2001

Family Auriculispinidae Waterhouse, 1986b

- Subfamily Auriculispininae Waterhouse, 1986b
    - Tribe Auriculispinini Waterhouse, 1986b
    - Tribe Filiconchini Waterhouse, 2001
- Subfamily Lyoniinae Waterhouse, 2001
- Subfamily Siphonosiinae Lazarev, 1990

Family Stepanoviellidae Waterhouse, 1975

Table 1. Classification of Proboscidelloidea Muir-Wood & Cooper, 1960, amended slightly from Waterhouse (2013).

SYSTEMATIC DESCRIPTIONS

Order PRODUCTIDA Waagen, 1883

Suborder LINOPRODUCTIDINA Waterhouse, 2013

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

[Nom. transl. Waterhouse 2013, p. 404 ex Proboscidellinae Muir-Wood & Cooper, 1960, p. 325].

Diagnosis: Both valves costate unless ribbing secondarily lost; ventral spines over disc with elongate bases.

Discussion: In Linoproductoidea the ventral disc spines are erect as a rule without posteriorly or anteriorly prolonged bases. In Proboscidelloidea, spine-bases are prolonged posteriorly over the outer surface, and, in at least Permian and late Carboniferous members of the group, are prolonged forwards within the shell from the spine base, as if keeping contact with the mantle edge (Waterhouse 2010, 2013. p. 404). Possibly this explains the considerable degree of variability in the ribbing on the ventral valve, in contrast to the consistent pattern of ribs for members of Superfamily Linoproductoidea. In addition, commarginal rugae are widely present in Proboscidelloidea, much more organized than in Linoproductoidea. The fossil record indicates that the two superfamilies arose each from within a different subfamily of Family Devonoproductidae, Superfamily Proboscidelloidea from Subfamily Plicoproductinae, and Superfamily Linoproductoidea from Subfamily Eoproductellinae. *Stepanoviella* Zavodowsky, 1960 was classed in a separate allied group as Stepanoviellinae Waterhouse 1975, p. 12. This subfamily was synonymized with Linoproductinae by Brunton in Brunton et al. (2000), yet the genus was classed not in Linoproductinae but in Grandaurispininae Lazarev, 1986 (sic) by Lazarev *in* Brunton et al. (2000, p. 533). The muddles in view of such a bewildering array of genera and family groups are understandable, and there still remains the need for complete clarity over the presence of proboscidelloid spine cores in the shell of *Stepanoviella*, to distinguish the group from Anidanthidae, although the genera *Bocharella* and *Kolymaella* erected by Ganelin & Lazarev (1999, 2000) appear to be proboscidelloid.

Family **PAUCISPINAURIIDAE** Waterhouse, 1986a

[Nom. transl. Waterhouse 2013, p. 416 ex Paucispinauriinae Waterhouse, 1986a, p. 2. Syn. Grandaurispininae Lazarev, 1990, p. 130].

Taxonomy: Paucispinauriinae was proposed by Waterhouse (1986a, June, p. 2) at the same time as Grandaurispininae Lazarev (1986, June, p. 32) was listed, but not proposed or discussed. Brunton et al. (2000, p. 533) wrongly claimed that Paucispinauriinae had not been proposed until September, 1986 (Waterhouse 1986b, p. 37), and did not acknowledge that the Lazarev proposal was in a list, with no diagnosis or explanation. Lazarev (1986) did not provide a description or definition that stated in words characters which purported to differentiate the taxon, as stipulated by the International Commission for Zoological Nomenclature (1999, article 13.1, p. 17). Waterhouse (1986a) did provide a brief explanation with diagnoses, and indicated both the name genus and allied genera. The proposal was reinforced shortly afterwards by Waterhouse (1986b). Not until 1990 did Lazarev (1990, p. 130) provide validation, and its validity dates from 1990. Prior mentions, even though promoted by Brunton et al. (2000), carry no standing, according to the rules of zoological nomenclature. This was eventually accepted without acknowledging any correction by Brunton (2007, p. 2652).

Diagnosis: Shells small to medium in size, ventral spines generally with elongate bases in regular quincunx over disc, crowded or rare over ears and in row or rows along hinge, dorsal spines usually present, crowded, erect, may be differentiated and may be unusually large for Productida. Radial ribs and weak to strong commarginal rugae. Body corpus usually moderately thick and trail extended, often geniculate. Cardinal process trilobed, dorsal medium septum single or with shallow slit near the adductors, forming double ridge in some genera, but less markedly than in many Auriculispinidae.

Family relationships: Members of Paucispinauriidae differ from Linoproductidae in having less well-defined radial ribs that may be spaced further apart, and in ventral disc spines having prolonged bases which may leave spine tunnels within the shell. Various paucispinauriid species have a thick body cavity as in Linoproductidae, but this is regarded as of lesser importance, because ontogenetic studies show that species and genera which are thin-disced at maturity could become thick-disced at a gerontic stage of development. Some paucispinaurian genera carry thin and even thick spines also on the dorsal valve, and several otherwise similar genera differ only in the presence or absence of coarse dorsal spines. Species within Auriculispinidae are close to those of Paucispinauriidae in some respects, but members have persistently thin body corpus, less regular ventral spines, more transverse shape as a rule, and generally shorter and thinner ventral spine bases, and often no dorsal spines, which are thin where present. The ventral adductor scars of Auriculispinidae are striate until late maturity, and generally sited on a platform which is raised anteriorly and set into the posterior wall posteriorly, whereas the ventral adductor scars of Paucispinauriidae are dendritic, and less impressed into the shell. The median septum in Auriculispinidae is often doubled, much more strongly than in Paucispinauriidae.

Origins for the family are not entirely clear. The oldest member appears to be Magniplicatininae, which is represented by at least one genus *Globicorrugata* Waterhouse (2013, p. 424) in Visean faunas, and by genera of Engellinini Waterhouse, 2013. Paucispinauriidae apparently arose from Magniplicatinae through diminution of the commarginal rugae and development of longer and thicker spines over the ventral ears and umbonal slopes and presence of fine erect dorsal spines. *Proboscidella* Muir-Wood & Cooper, 1960 of Lower Carboniferous age and with bifid rather than trifid cardinal process may display somewhat paucispinaurian dendritic adductor scars, not to mention a very long trail.

Subfamily **PAUCISPINAURIINAE** Waterhouse, 1986a

[Paucispinauriinae Waterhouse, 1986a, p. 2].

Diagnosis: Spines crowded over both valves. Dendritic adductor scars, body corpus often thick.

Tribe **PAUCISPINAURIINI** Waterhouse, 1986a

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

Diagnosis: Spines with elongate bases over visceral disc, dorsal spines present and may be differentiated. Permian (Sakmarian - Changhsingian).

Genera: *Paucispinauria* Waterhouse, *Appelinaria* Waterhouse, *Bellaspinosina* Waterhouse, *Bookeria* Waterhouse, *Grandaurispina* Muir-Wood & Cooper, *Saetosina* Waterhouse, *Spargospinosa* Waterhouse, *Terrakea* Booker, ?*Vagarea* Waterhouse.

Discussion: The evolution is summarized in Waterhouse (2013, pp. 459-464) as offering an example of development within a tribe. Genera are distinguished by spine pattern, including the distribution of thick and thin spines over both valves, as shown by Waterhouse (1986a, b). The other tribe is called Holotricharinini, based on *Holotricharina* Cooper & Grant, as discussed on p. 170 herein.

Genus ***Paucispinauria*** Waterhouse, 1983b

Diagnosis: Distinguished from *Terrakea* by paucity of sturdy erect spines from the ventral ears and lateral slopes, distinguished from *Bookeria* by presence of sturdy erect spines over the anterior dorsal valve.

Type species: *Terrakea concava* Waterhouse, 1964b, p. 67 from Letham Burn Member, Wairaki Downs, New Zealand, by original designation in Waterhouse (1983b, p. 130).

Paucispinauria paucispinosa Waterhouse 1986b

Fig. 1, 2

?1952 *Terrakea fragilis* [not Dana] – Fletcher, p. 12 (not pl. 1, fig. 3-6 = *Terrakea elongata crassiconcha*).
aff. 1982 *Terrakea concava* [not Waterhouse] – Waterhouse. p. 49. pl. 10k.
1986b *Paucispinauria paucispinosa* Waterhouse, p. 52, pl. 12, fig. 12-16.
1988 *Terrakea* sp. McLoughlin, pl. 1, fig. 2, 3.
1998 *Terrakea paucispinosa* – Briggs, p. 172, Fig. 85A, B?.
cf. 2001 *Paucispinauria paucispinosa wardenensis* [not Waterhouse] - Waterhouse, p. 35, pl. 1, fig. 18-21, text-fig. 5d. (Species acceptable, not the subspecies).

Diagnosis: Ventral disc spines in quincunx, approximately ten to twelve along a commarginal row in the holotype and another figured specimen, spines few over ventral ears, which in the type and figured topotype are poorly separated from body of shell. No burst of erect spines along the posterior lateral slopes.

Holotype: UQF 70137 from Brae Formation, southeast Bowen Basin, figured by Waterhouse (1986b, pl. 12, fig. 12, 14), OD.

Morphology. The dorsal interior was figured in Waterhouse (1986b), with the dorsal exterior poorly shown. In pl. 13, fig. 16, the dorsal ears are moderately extended from the disc. Briggs (1998, pp. 172, 173, Fig. 85) assigned Oxtrack specimens to *paucispinosa*, but his figured ventral valve shows more ventral disc spines along a commarginal row, numbering up to twenty at mid-length. Briggs (1998, p. 180) suggested that *paucispinosa* was allied in some respects to New Zealand specimens identified as *Terrakea elongata*, now discriminated as *elongata crassicostata* (see p. 160), but allowed that the elongate shape and enrolled form of the shell and long dorsal trail did distinguished the New Zealand form. He ignored the differences in spinose ornament.

The specimens figured by Briggs (1998, p. 172, Fig. 85) from the Drake volcanics could well belong to the species. On the other hand his claim that a specimen figured by Waterhouse

(1986b, pl. 12, fig. 17) from the Oxtrack Formation of southeast Bowen Basin is rejected. Specimens from the Freitag Formation of the southwest Bowen Basin (Waterhouse 2001) have reduced ears just like the Brae specimens and spine distribution appears largely comparable, though more needs to be known about the arrangement of dorsal spines for Brae material. A specimen assigned to *Terrakea concavum* by Waterhouse (1982, pl. 10k) from the *Wyndhamia typica* fauna in New Zealand is a ventral valve with crowded and numerous spines, and could even be *Terrakea rylstonensis* Briggs. Such is the preservation that the specimen cannot be clearly differentiated from *Terrakea* or *Paucispinauria*, but is provisionally assigned to *paucispinosa*.

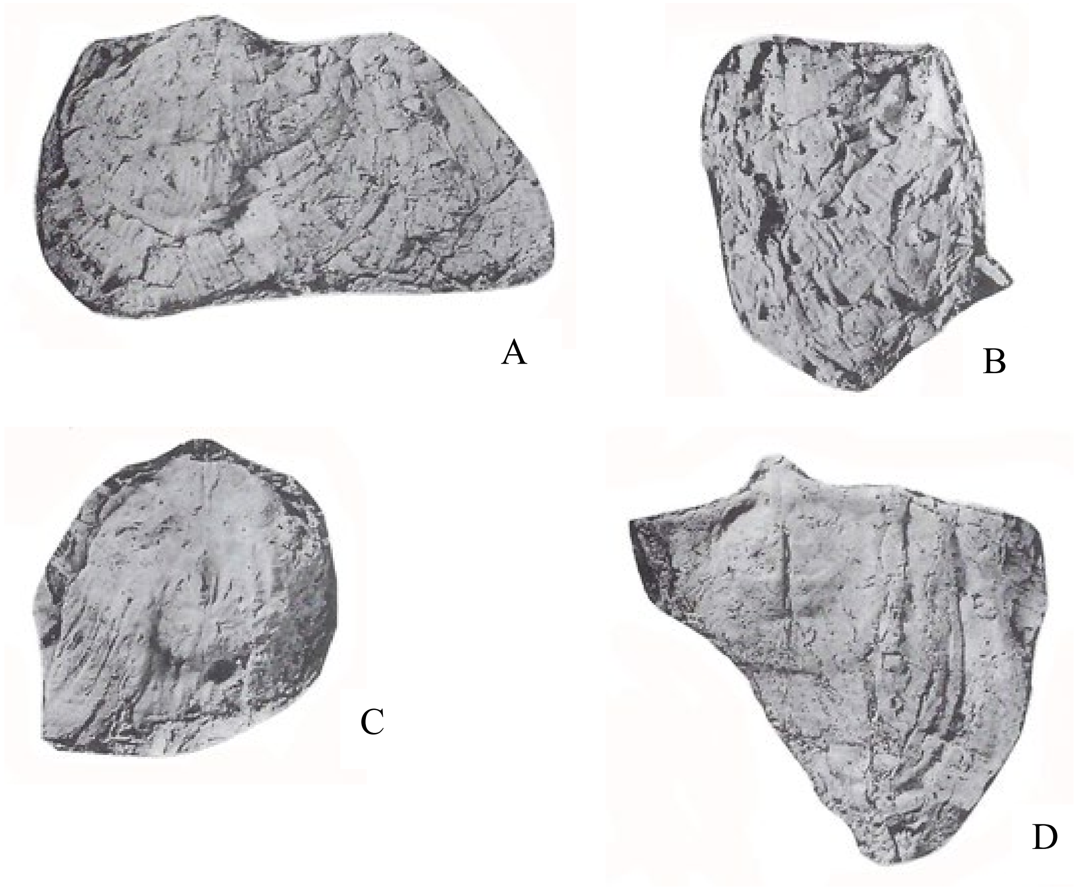


Fig. 1. *Paucispinauria paucispinosa* Waterhouse. A, latex cast of ventral valve UQF 70137. B, latex cast of ventral valve UQF 70319. C, posterior ventral internal mould UQF 70117. D, dorsal interior, UQF 74067. Specimens x2, from Brae Formation. (Waterhouse 1986b).

Stratigraphy: This species is found chiefly in the southeast Bowen Basin in the Brae Formation, and appears to be moderately close to material from the Freitag Formation, a similarity consistent with other fossils in the formation. The New Zealand material mentioned by Fletcher

(1952) and Waterhouse (1982) comes from the broadly correlative Letham Formation of Wairaki Downs, but is not well known, and identification uncertain.

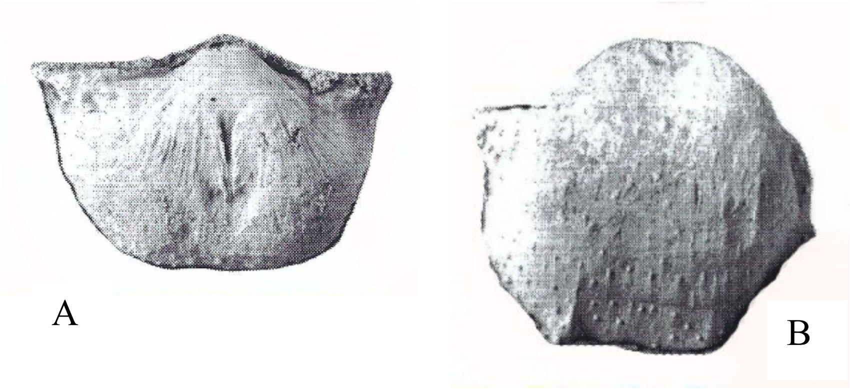


Fig. 2. *Paucispinauria* cf. *paucispinosa* Waterhouse. A, B, internal mould of ventral valve UQF 65423, x2, from Freitag Formation, southwest Bowen Basin. (Waterhouse 2001).

Paucispinauria concava concava (Waterhouse, 1964a)

Fig. 3

1964a *Terrakea concava* Waterhouse, p. 67, pl. 10, fig. 6-10, pl. 11, fig. 1-10, pl. 35, fig. 1, text-fig. 23B, 24B, C, 25-30.
1971 *T. concava* – Waterhouse, p. 349, text-fig. 1.
1983b *Paucispinauria concava* – Waterhouse, p. 130.
2000 *P. concava* – Brunton et al., p. 533, Fig. 371.2a-e.
2013 *P. concava* – Waterhouse, p. 460, Fig. 21.2, 21.4.

Diagnosis: Transverse little inflated shells with wide auriculate hinge, ventral spines of regular size evenly disposed in quincunx, ear spines comparatively few and erect like those of trail, no development of posterior lateral or lateral thick and erect spines. Dorsal spines fine and erect over dorsal disc, not dense but subevenly spaced and much the same in number along commarginal rows as those of the ventral disc, thick, erect and well-spaced in one or two rows over the trail. Muscle scars clearly defined, dorsal median septum extends from half to three quarters of length of dorsal valve.

Holotype: BR 200 from Letham Burn Formation, figured in Waterhouse (1964a, pl. 10, fig. 9, 11, pl. 11, fig. 4, 5, 9, pl. 35, fig. 1), Waterhouse (2013, Fig. 21.2C) and Fig. 4C, F herein, OD.

Morphology: This species is represented by numerous well-preserved specimens from several localities in the Letham Burn Formation. Aspects of the Briggs synonymy are uncertain: he included an Etheridge & Dun (1909, pl. 43, fig. 6) specimen from the Nowra Sandstone that is highly inflated with strong costae and no spines preserved, only possibly belonging to *concava,* as it shows a dorsal interior that might well be *brachythaera* and Briggs also included

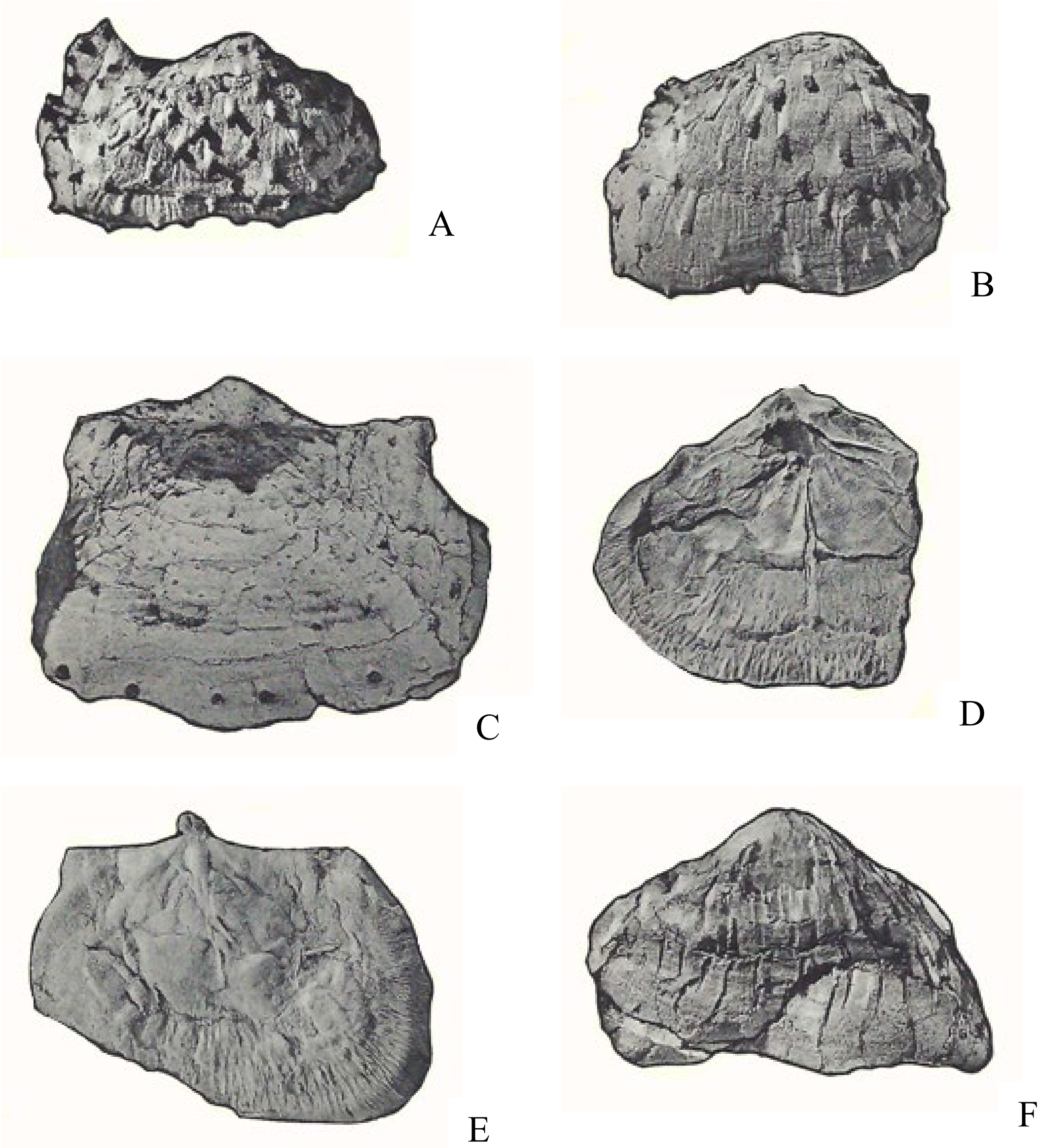


Fig. 4. *Paucispinauria concava concava* (Waterhouse). A, B, ventral posterior and ventral aspects of PVC cast of ventral valve BR 207. C, F, dorsal aspect of specimen with valves conjoined and ventral aspect of internal mould, PVC cast, BR 200, holotype. D, dorsal aspect of internal mould with valves conjoined, BR 842. E, PVC cast of dorsal interior, BR 788. Specimens x 2, from Letham Burn Member, Wairaki Downs, New Zealand. (Waterhouse 1964a).

as *concava* the ventral internal moulds figured as *Terrakea* cf. *dickinsi* Dear by Dickins (1981, pl. 4, fig. 6, 7, 8-10), which are less transverse and more highly arched than *concava*, and have no ears preserved.

Stratigraphy: The species is reliably found in the Letham Burn Formation of New Zealand. Waterhouse (2002a, p. 179) reported the species in the Wollong Member of the Belford Formation of the north Sydney Basin and upper Wandrawandian beds of the south Sydney Basin, but they have yet to be described and illustrated.

As is the case for all too many of the productiform species in east Australia and New Zealand, Briggs (1998) has presented a misleading account of the actual occurrences of *Terrakea* (now *Paucispinauria*) *concava* in its type localities. He has shown (1998, Fig. 11) its position as lying below that of *Echinalosia discinia* – it lies above, in the lower Mangarewa Formation, not in the Letham Formation. And it occurs with, not above *Echinalosia maxwelli*.

Paucispinauria concava multispina n. subsp.

Fig. 4, 5

1986b *Paucispinauria concavum* – Waterhouse, p. 53, pl. 12, fig. 17, pl. 13, fig. 1-5, pl. 15, fig. 15 (part, not pl. 12, fig. 18 = *Magniplicatina perflecta* as in Briggs 1998).
2008 *P. concava* – Waterhouse, p. 363, Fig. 7D.

Derivation: multi – many, spina – thorn (Lat.).

Diagnosis: Ventral spines numerous over the disc, numbering twenty or more along a single commarginal row. Inflation low, ears often reduced in size. Trail low.

Holotype: UQF 70691 from Oxtrack Formation, figured in Waterhouse (1986b, pl. 13, fig. 1), refigured herein as Fig. 5B, here designated.

Fig. 4. *Paucispinauria concava multispina* n. subsp., worn ventral valve UQF 70562, x3. From Oxtrack Formation. (Waterhouse 1986b).

Morphology: The taxonomic position of this suite is somewhat contentious. The shells are distinguished by the greater number of disc spines over both valves, and most specimens share the reduced ears, close to those of *concava*, and not as severely reduced as in some *Paucispinaria paucispinosa,* in which ears may fail to project beyond the lateral margin, though similarity is close. Inflation is low, close to that of *concava*. The spines number about

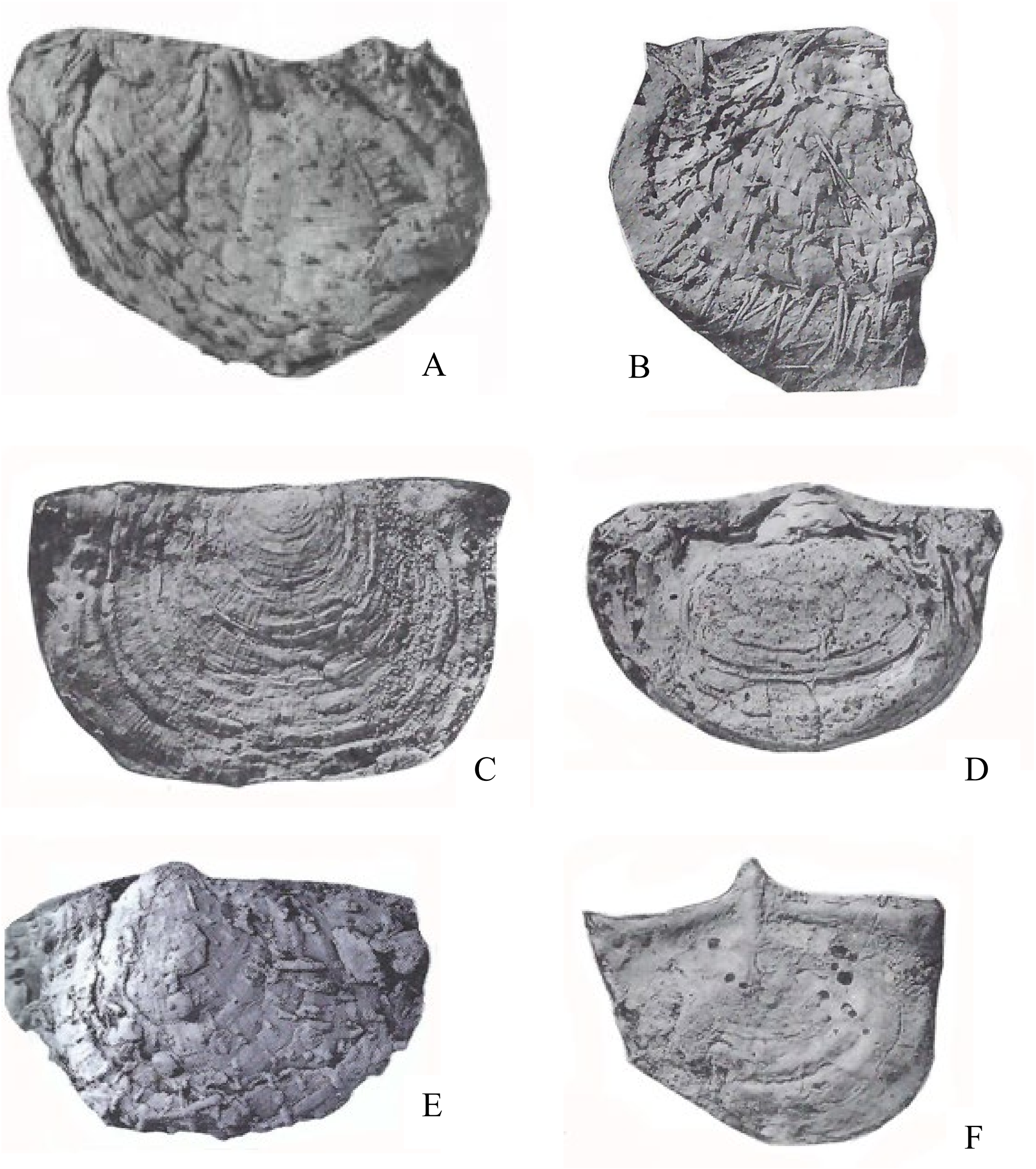


Fig. 5. *Paucispinauria concava multispina* n. subsp. A, latex cast of ventral valve UQF 70740, x2. B, latex cast of ventral exterior, UQF 70691, holotype, x1. C, dorsal external mould, UQF 70554, x2. D, dorsal external mould with ventral umbonal region, UQF 70570, x1. E, ventral valve latex cast, AMF 96264, x1.5. F, worn dorsal interior, UQF 70570, x1. Specimens from Oxtrack Formation, southeast Bowen Basin. (A-D, F, Waterhouse 1986b; E, Briggs 1998).

twenty along a commarginal row, a few more than in *concava concava*, which mostly has spines of twelve to sixteen, usually about fourteen in a transverse row. An Oxtrack specimen figured by Waterhouse (1986b, pl. 12, fig. 17) appears to be *Magniplicatina perflecta,* as also concluded by Briggs (1998), though the figure does not show strong rugae.

Stratigraphy: The subspecies is found in the Oxtrack Formation.

Paucispinauria concava wardenensis Waterhouse, 2001

Fig. 6

1909 *Productus brachythaerus* [not Morris] – Etheridge & Dun, p. 5, pl. 43, fig. 6 (part, remainder = *brachythaera*).
1930 *Terrakea leve* Booker, pp. 70, 71, AMF 1158.
1998 *T. concava* – Briggs, p. 170, Fig. 84A-I.

Diagnosis: Very close to *Paucispinauria concava*, a little more inflated and ears better developed in some but not all specimens. Spines evenly arranged in quincunx, slightly coarser than in types, and more numerous over the trail.

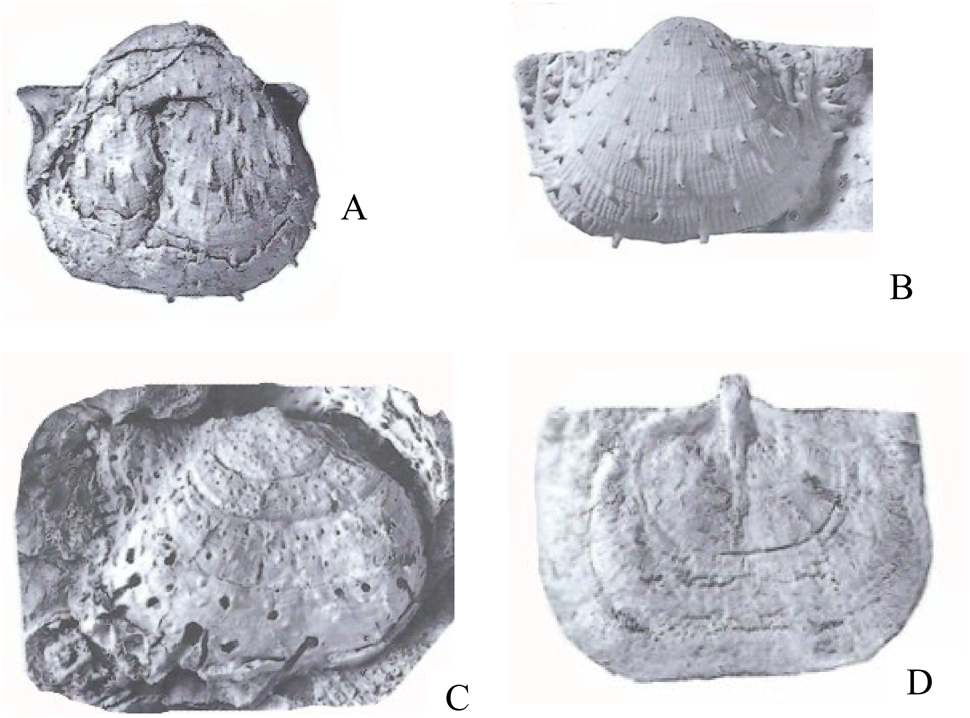


Fig. 6. *Paucispinauria concava wardenensis* Waterhouse. A, latex cast, ventral valve UQF 75323, x1.5. B, latex cast, ventral valve UQF 75333, holotype, x1.5. C, dorsal aspect of external mould of specimen with valves conjoined, UQF 75331, x1. D, latex cast, dorsal interior, UQF

75325, x1.5. Specimens x1.5, figured in A, C, D from Fenestella Shale, south Sydney Basin. B from Wandrawandian Formation, near Montagu Point. (Briggs 1998).

Holotype: UQF 75333 from the upper Wandrawandian Formation, Sydney Basin, figured by Briggs (1998, Fig. 84G) and Fig. 6B herein, OD.

Morphology: From Warden's Head in the Wandrawandian Formation of the south Sydney Basin, a ventral valve figured by Waterhouse (2001, pl. 1, fig. 21) shows a ventral valve with most spines conforming with the requisite pattern, but two anterior rows have more numerous spines.

Stratigraphy: This subspecies is found chiefly in the south Sydney Basin in the upper Wandrawandian Formation.

Paucispinauria solida (Etheridge & Dun, 1909)

Fig. 7

1892 *Productus brachythaerus* [not Morris] – Etheridge, p. 252, pl. 44, fig. 14.
1909 *Productus*? *solida* Etheridge & Dun, p. 303, pl. 43, fig. 1-4.
1964 *Terrakea solida* – Hill & Woods, pl. P6, fig. 3-7.
1971 *T. solida* – Dear, p. 19, pl. 5, fig. 6, 7, pl. 6, fig. 1-7.
1972 *T. solida* – Hill et al., pl. P6, fig. 3-7.
1989 *T solida* – Dickins, p. 75, Fig. 4A-H.
1998 *T. solida* – Briggs, p. 183, Fig. 90A-C, H (part, Fig. 90D-G uncertain).
2001 *Paucispinauria solida* – Waterhouse, p. 38, pl. 1, fig. 22-27, pl. 3, fig. 1, 3-5 (part not fig. 2, 6 = *elongata crassiconcha*).

Diagnosis: Body corpus thick, ventral valve vaulted, ears moderately developed, trail of moderate height, ventral spines moderately spaced and sturdy, few over the ventral ears, with a very few just in front. Dorsal spines poorly known, doubtfully a little more closely spaced than on ventral valve, but this requires confirmation. Muscle scars clearly defined, dorsal median septum extends to mid-length or further forward.

Lectotype: AMF 35478 from Mantuan Formation, southwest Bowen Basin, figured by Etheridge & Dun (1909, pl. 43, fig. 1, 2) and Dickins (1989, text-fig. 4A-D), SD Dear (1971).

Morphology: This is an outstanding species and differs from other species assigned to *Paucispinauria* in its greater inflation and better developed ears, but agrees with *Paucispinauria* in its ventral ornament by and large, and length of dorsal septum. Knowledge of the dorsal ornament is poor, and the most informative figures provided by Briggs (1998, Fig. 90D-F) show irregularly spaced slender anterior spines in two or three rows, but the source of the material is not adequately explained in either geographic or stratigraphic terms, so that specific identity still needs to be established. If correctly identified, the dorsal trail spines appear to be unusually slender, though the degree of maturity needs to be established. Specimens assigned to *solida* by Waterhouse (2001) that had been described originally as *Terrakea elongata* [not Etheridge & Dun] in Waterhouse (1964a, p. 81, pl. 15, fig. 1-6, pl. 16, fig. 1, 7, text-fig. 26-30) and as *T. brachythaera* [not Morris] in Waterhouse & Jell (1983, p. 242, pl. 1, fig. 14, 16-18, pl. 2, fig. 1) are left out of synonymy because they have crowded strong erect spines over the inner ventral ears and posterior lateral slopes, as in *Terrakea*.

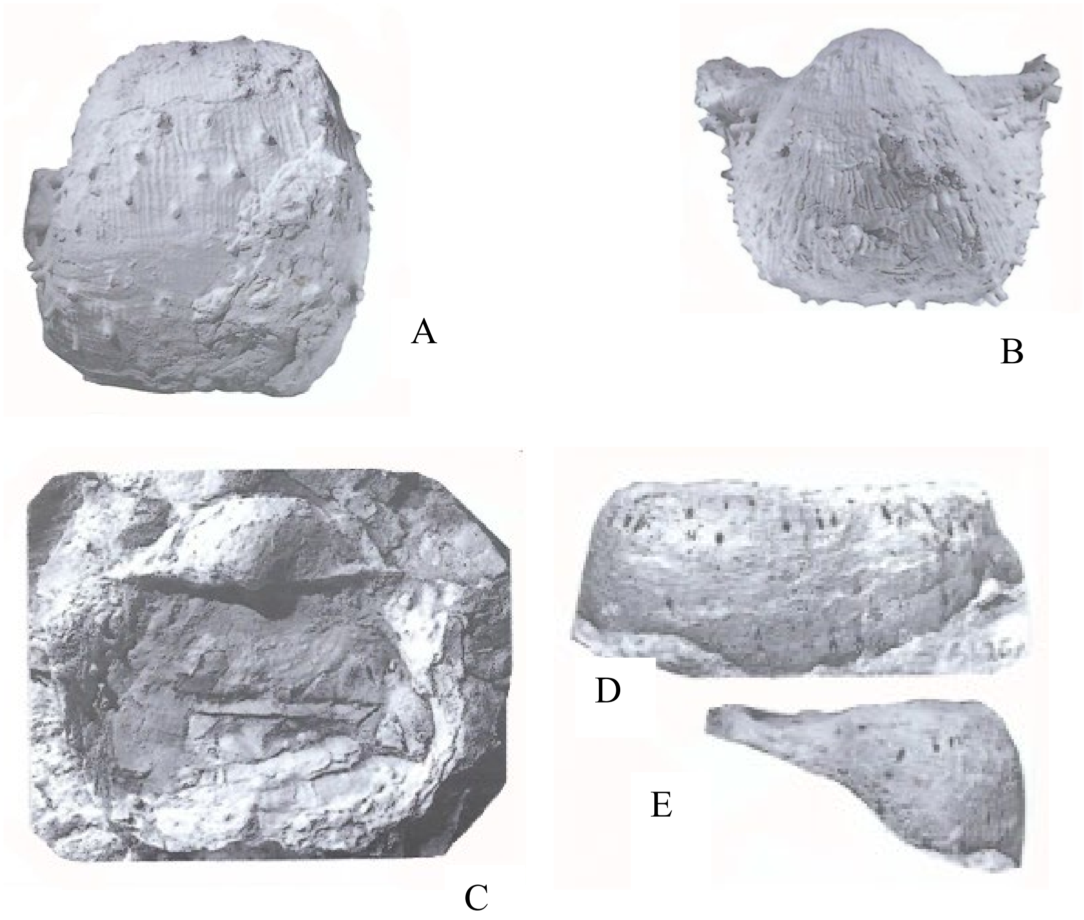


Fig. 7. *Paucispinauria solida* (Etheridge & Dun). A, B, anterior and posterior aspects of ventral valve CPC 31690, x1. C, dorsal aspect of specimen with valves conjoined, UQF 60737, x1. D, E, anterior and lateral aspects of dorsal external mould, showing spines over trail, UQF 62543, x1. A-C from Mantuan Formation, D, E from “Warwick Military Map”, stratigraphic information not provided. (Briggs 1998).

Stratigraphy: The species is typical of the Mantuan Member in the southwest Bowen Basin. Briggs (1998, p. 187) reported but did not figure *solida* from one locality in the Flat Top Formation of the southeast Bowen Basin, and listed material from the Condamine block, also unfigured. He did provide figures for specimens from the Warwick map sheet with UQF numbers, but no UQL locality detail, and no stratigraphic information. These have only comparatively fine spines over the dorsal trail, yet to be established as typical of the species. The species appears to be present also in the Mangarewa Formation (Waterhouse 2001), but figures of the ventral spines for the New Zealand material are required.

Paucispinauria verecunda (Waterhouse, 1982)

Fig. 8, 9

1969 *Terrakea* cf. *solida* [not Etheridge & Dun] – Runnegar & Ferguson, pl. 5, fig. 1-4.
1971 *Terrakea* n. sp. Waterhouse, p. 348, text-fig. 1.
1982 *T. verecundum* Waterhouse, p. 50, pl. 12b-e, g, i, k, text-fig. 17L, M (not *multispinosa* Dear as in plate caption, an editorial error).
2001 *Paucispinauria verecunda* – Waterhouse, p. 41.
2002a *P. verecunda* – Waterhouse, p. 65.
2008 *P. verecunda*– Waterhouse, p. 368, Fig. 8J.
2015b *P. verecunda* – Waterhouse, pp. 109, 149, Fig. 37A, 68.

Diagnosis: Small weakly transverse shells with rather large ears, and ventral disc medianly flattened to weakly sulcate. Ventral spines coarse and well-spaced, a few spines only over ventral ears, and a very few over posterior lateral slopes, trail spines not clear. Dorsal spines fine and erect, more numerous than those of the ventral valve, in few rows over low trail, and fine. Muscle scars lightly impressed, dorsal median septum extends only to mid-length.

Holotype: BR 1181 from Kildonan Member of Bagrie Formation, Arthurton Group, New Zealand, figured by Waterhouse (1982, pl. 12b, c, g, i, k) and Fig. 8B-D herein, OD.

Morphology: This is a distinctive species with broad and often medianly sulcate or gently convex ventral disc, and like other members of the genus in having strong well-spaced ventral disc spines, with few over the ears and posterior lateral slopes in front of the large ears. Yet the dorsal valve repeats attributes of *Terrakea* and even *Bookeria*, in having more numerous disc spines, and in having only fine spines over the trail.

Stratigraphy: The species is found in younger deposits of the South Curra Limestone of Gympie and Gigoomgan Limestone of the nearby Gigoomgan areas in southeast Queensland

(Waterhouse 2015b), and in the Glendale clastics and overlying (fault-separated?) Glendale limestone of Wairaki Downs, New Zealand (Waterhouse 2002a, p. 65) as well as the type area in the Arthurton Group of New Zealand (Waterhouse 1982).

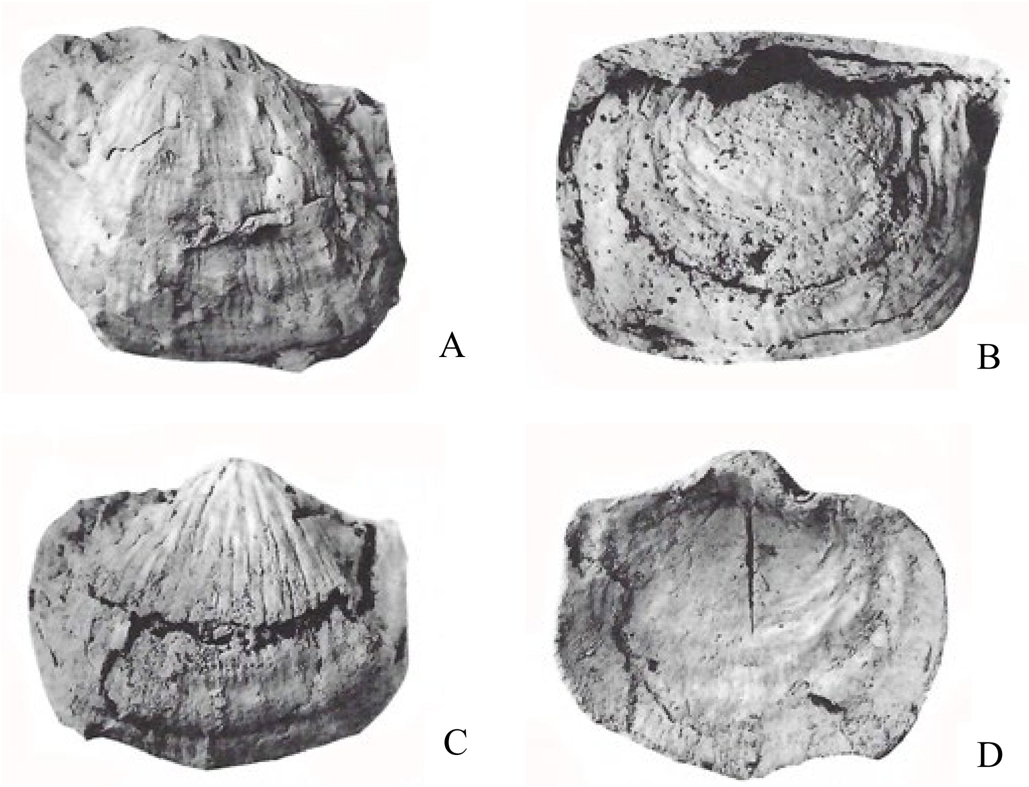


Fig. 8. *Paucispinauria verecunda* (Waterhouse). A, ventral exterior BR 1496. B-D, holotype BR 1181, B, dorsal external mould, C, D, ventral and dorsal aspects of internal mould. From Kildonan Member, Bagrie Formation, New Zealand, x2. (Waterhouse 1982).

Fig. 9. *Paucispinauria verecunda* (Waterhouse), external mould UQF 46698, x3. From Gigoomgan Limestone, near Gympie, southeast Queensland. (Waterhouse 2015b).

Genus **Bookeria** Waterhouse, 2015a

Diagnosis: Small to medium-sized subequilateral shells with ears projecting little if at all beyond lateral margins, which are low to medium in height. Ventral spines arranged in quincunx, may only number about ten along commarginal row of disc, dorsal disc spines more crowded, up to twice as numerous. Ventral spines numerous, thick and varying in number over ventral ears, may be crowded and strong over posterior lateral slopes. Dorsal spines over posterior lateral slopes may be slightly thicker than dorsal disc spines, but are never thick over the trail. Muscle scars vary in strength.

Type species: *Bookeria sparsispinosa* Waterhouse, 2015a from middle Tiverton Formation, north Bowen Basin, Queensland, OD.

Discussion: This genus embraces Early Permian paucispinaurians which are similar to each other in lacking strong spines over the dorsal trail. Given the variable features that characterize species through the Permian in east Australia, there are several ways of associating species in lineages, and the chosen associations show varying links with other lineages: chiefly in the nature of the spines over the ventral ears and the posterior lateral slopes, so that relying on that facet alone, the number of genera could be reduced, and species assigned to *Bookeria* divided between the genera *Terrakea* and *Paucispinauria*. In Waterhouse (2015a), it was preferred to regarded *Bookeria* as a single genus that contain different species which later gave rise to these two genera, but there are alternative interpretations.

Bookeria pollex (Hill, 1950)

Fig. 10, 11

1950 *Terrakea pollex* Hill, p. 20, pl. 9, fig. 6-8, 11, 12 (part, not fig. 9? = n. det., ?10 = *B. geniculata* or *sparsispinosa* Waterhouse).
1986b *T. pollex* – Waterhouse, p. 49, pl. 11, fig. 19, 21-23, 25-27 (part, not fig. 20, 24 = *Bookeria drysdalei* Waterhouse).
1989 *T. pollex* – Waterhouse, pl. 1, fig. g, h.
1998 *T. pollex* – Briggs, p. 163, Fig. 81D, F (part, not fig. 81A-C, E, G = *B. drysdalei*).
2008 *T. pollex* – Waterhouse, p. 354, Fig. 7E.
2013 *T. pollex* – Waterhouse, p. 459.
cf. 2015a *Bookeria* cf. *pollex* – Waterhouse, p. 125, Fig. 77A-D.

Diagnosis: Shells small to intermediate in size, overall thumb-like in shape with incurved ventral umbo, ventral ears weakly differentiated, numerous comparatively strong ear spines on both valves, ventral disc spines low in number (ca. ten to twelve along a row) with bases short.

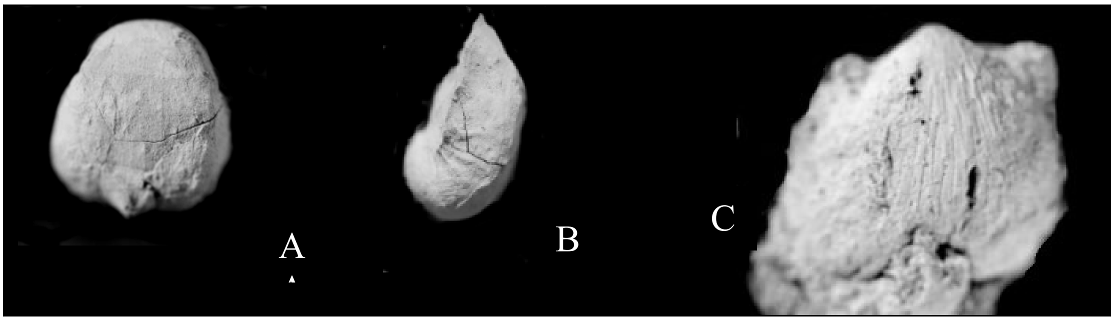
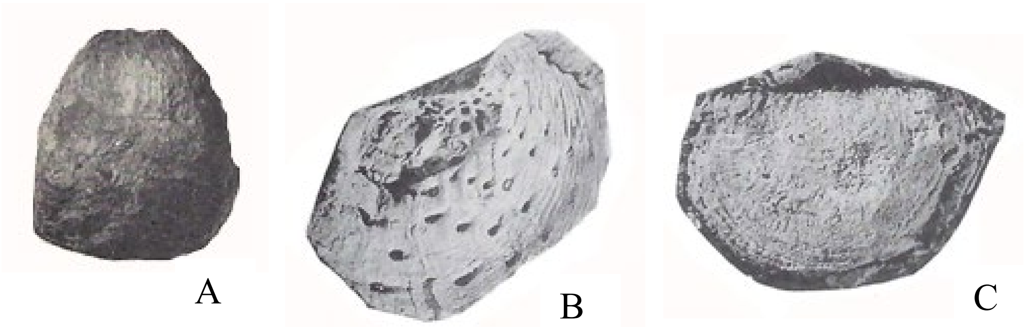


Fig. 10. *Bookeria pollex* (Hill). A, B, ventral and lateral aspects of worn ventral valve UQF 81236, x1. C, ventral internal mould UQF 81237, x 2. From basal Tiverton Formation, x3. (Waterhouse 2015a).

Dorsal trail high for the genus, with relatively fine spines in three or four rows, well-spaced.

Holotype: UQF 10758 from Fairyland Formation, southeast Bowen Basin, figured by Hill (1950, pl. 9, fig. 6a, b) and Fig. 11A herein, OD.



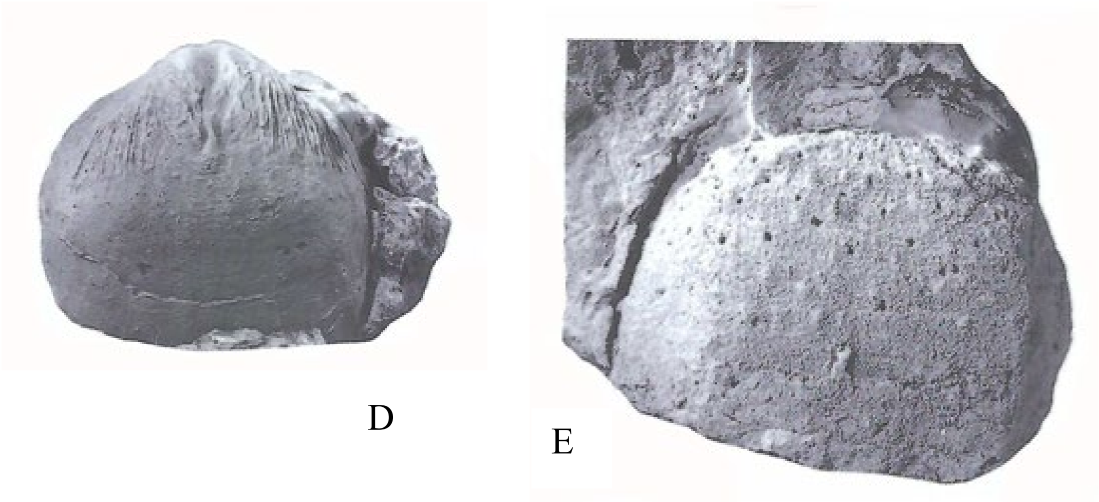


Fig. 11. *Bookeria pollex* (Hill). A, holotype, ventral valve, UQF 10758, x1. B, detail of ventral external mould UQF 74043, x2. C, posterior dorsal external mould UQF 74045, x2. D, ventral internal mould UQF 96262, x2. E, dorsal external mould UQF 96263, x2. From Fairyland Formation. (A - Hill 1950; B, C - Waterhouse 1986b; D, E - Briggs 1998).

Morphology: The figures in Hill (1950) show the shape well, and figures in Waterhouse (1986b) and Briggs (1998, Fig. 81D, F) show more of the ornament. The dorsal valve shown in Hill (1950, pl. 9, fig. 9) has very strong commarginal rugae, stronger than any other known *Bookeria*, and so seems unlikely to belong to the genus. The internal mould figured by Hill (1950, pl. 9, fig. 10) from the Dilly beds near Springsure could belong to one of several species of *Bookeria*, including *drysdalei* or *sparsipinosa.*

Stratigraphy: The species is found in the Fairyland Formation of the southeast Bowen Basin, and is probably present in the lower Tiverton Formation of the northern Bowen Basin.

Bookeria geniculata (Waterhouse, 1986a)

Fig. 12

1986a *Paucispinauria geniculata* Waterhouse, p. 3.
1986b *P. geniculata* Waterhouse, p. 51, pl. 12, fig. 4-11.
1998 *Terrakea geniculata* – Briggs, p. 165.
1998 *T. geniculata* – Crouch & Parfrey, p. 20.
2015a *Bookeria geniculata* – Waterhouse, p. 122.

Diagnosis: Small usually transverse shells with ears less than maximum width which lies in front of mid-length, ventral valve often weakly sulcate. Ventral disc spines have short bases and lie up to twenty in a commarginal row, short bases. Spines numerous and erect over ears, stronger than those over the disc, with a few strong posterior lateral spines in front of the ears.

Dorsal disc spines erect, a little more numerous than those of the ventral disc, ear spines fine. Ventral trail spines only slightly stronger than those of anterior disc, up to 0.7mm in diameter and up to 1mm in diameter compared with diameter of 0.4mm over mid-disc, may be slightly fewer in number than in comparable area over anterior disc. Dorsal trail spines only a little thicker and approximately as crowded as spines over the dorsal disc.

Holotype: UQF 74065 from Elvinia Formation, southeast Bowen Basin, figured by Waterhouse (1986b, pl. 12, fig. 10), OD.

Morphology: The figures in Waterhouse (1986b) show well the shape and spine detail.

Stratigraphy: Reliable accounts of the species are limited to the Elvinia Formation of the southeast Bowen Basin, but Briggs (1998, p. 166) reported occurrences in the Eight Mile Tunnel Block of the Warwick area, without description or illustration. He also considered that *Terrakea aurispina* Waterhouse, 1982, p. 47, pl. 11, fig. 11a-d, f – i) from New Zealand closely resembled *geniculata*, but he left out the earlier reference to the same New Zealand taxon in Waterhouse (1964a, p. 64, pl. 10, fig. 1-5). Compared with *geniculata*, the New Zealand specimens have much stronger and fewer spines over the much higher trail, and stronger and more numerous

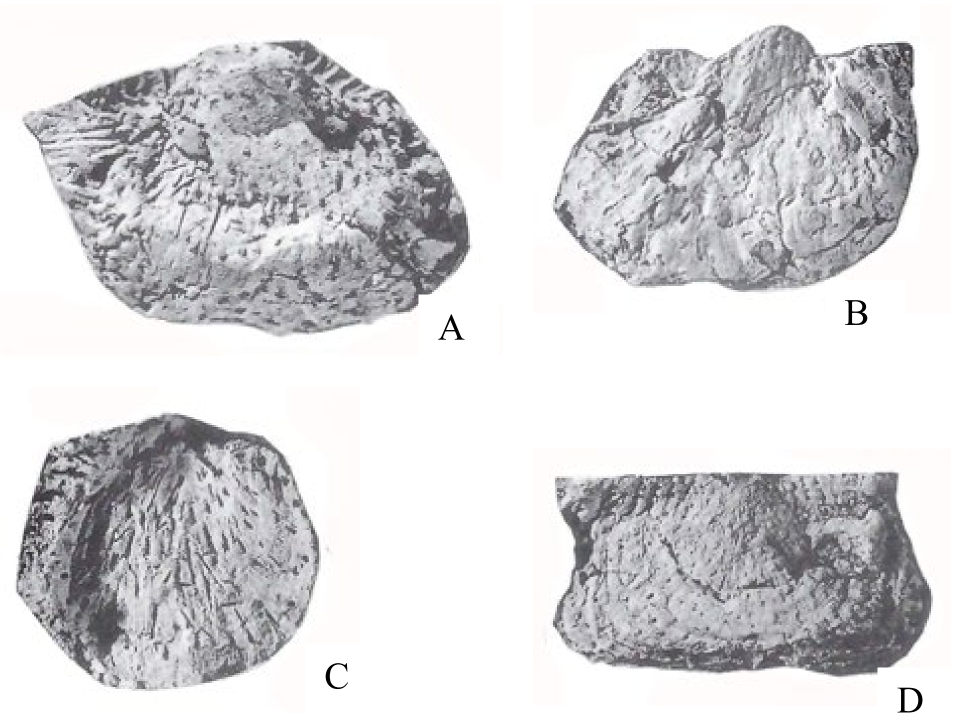


Fig. 12. .*Bookeria geniculata* (Waterhouse. A, latex cast of ventral valve UQF 74060, x2. B, ventral valve UQF 76041, x1. C, ventral external mould UQF 74062. D, dorsal external mould UQF 74063. Specimens from Elvinia Formation, southeast Bowen Basin. (Waterhouse 1986b).

spines over the ears. The New Zealand specimens are called *aurispina* and are regarded as most closely allied to *Terrakea dickinsi* Dear. (See Fig**.** 20 herein). They are certainly not *geniculata*.

The species was reported from the Chalmers Formation near Rockhampton, central Queensland, by Crough & Parfrey (1998).

Bookeria drysdalei Waterhouse, 2015a

Fig. 13

1986b *Terrakea pollex* [not Hill] – Waterhouse, p. 49, pl. 11, fig. 20, 24 (part, not fig. 19, 21-23, 25-27 = *pollex*).
1998 *T. pollex* [not Hill] – Briggs, p. 163, Fig. 81A-C, E, G (part, not Fig. 81D, F = *pollex*).
2015a *Bookeria drysdalei* Waterhouse, p. 126, Fig. 78-83.
2021 *B. drysdalei* – Waterhouse & Campbell, p. 22, Fig. 6A-**I**.

Diagnosis: Small subequilateral shells with weakly convex venter, moderately large ears clearly separated from the disc, numerous thick and erect spines over the ventral ears and in front over the posterior lateral slopes, not extending on to the low trail, disc spines moderately strong, steeply semi-recumbent with very short bases, numbering about ten to sixteen along a commarginal row. Dorsal disc spines fine and erect, about twice as numerous as those of ventral valve, along commarginal rows, becoming slightly stronger anteriorly and over the trail, without becoming very thick or reducing in number. Muscle scars subdued, median septum extends to mid-length or a little beyond.

Holotype: UQF 81242 from upper middle Tiverton Formation, figured in Waterhouse (2015a, Fig. 80C, 83A) and Fig. 13B herein, OD.

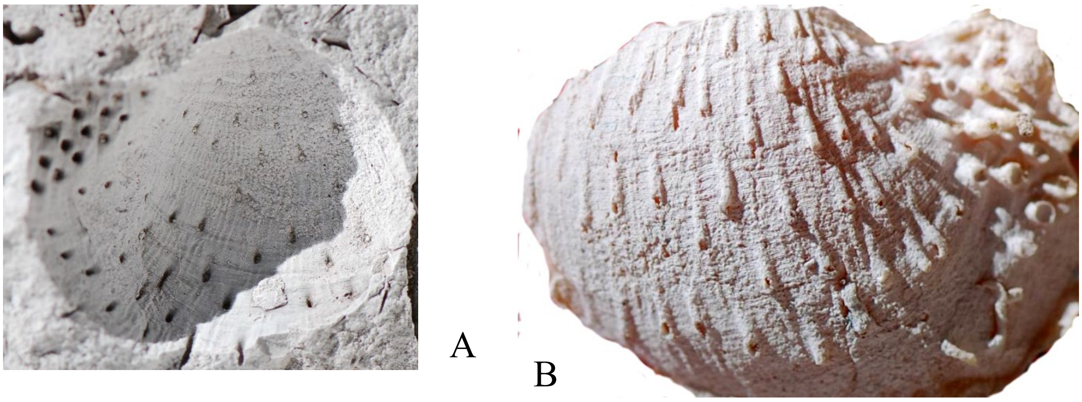


Fig. 13. *Bookeria drysdalei* Waterhouse. A, ventral external mould UQF 81241, x2. B, holotype, latex cast of ventral exterior UQF 81242, x3. C, latex cast of external mould, dorsal aspect of UQF 81244, x3. D, anterior aspect of dorsal external mould UQF 81451, x3. From Tiverton Formation, north Bowen Basin. (Waterhouse 2015a).

Morphology, Stratigraphy: This species is very close to *Bookeria geniculata* from the Elvinia Formation, and arguably should be treated as a subspecies of that taxon. Prime distinction lies in the non-sulcate venter of *drysdalei.* The species is slightly younger than *B. geniculata*, coming from the band with the chonetid *Svalbardia armstrongi*, and from the *Taeniothaerus subquadratus* Zone. There is also considerable similarity to a number of specimens from the Fairyland Formation, called *B. pollex* (Hill), as discussed by Waterhouse (2015a, p. 127). *B. drysdalei* was also recorded from the Eglinton Subgroup in the Dunton Range of New Zealand (Waterhouse & Campbell 2021), in deposits believed to be slightly older than the s*ubquadratus* Zone and equivalent to the *Magniplicatina undulata* of east Australia, which is represented in the Elvinia Formation together with *B. geniculata*.

Bookeria sparsispinosa Waterhouse, 2015a

Fig. 14

1964 *Terrakea pollex* [not Hill] – Hill & Woods, pl. P5, fig. 7, 8.
1972 *T. pollex* [not Hill] – Hill et al., pl. P5, fig. 7, 8.
2015a *Bookeria sparsispinosa* Waterhouse, p. 120, Fig. 67-76.

Diagnosis: Small tumid to transverse closely ribbed shells, small ears, hinge often at maximum width, trail short and as a rule dorsally subgeniculate. Ventral ears with a few strong and erect spines, generally two to five in number, concentrated near the umbo, and along the hinge, disc spines semi-recumbent and in quincunx, about eight to ten along a commarginal row, more erect and no more numerous over the short trail. Dorsal disc spines erect and up to twice as numerous compared with ventral disc spines, arranged along commarginal rows, and somewhat less regular in distribution, gradually increase in strength and spacing over the trail, without becoming very thick, reaching 0.6mm in diameter in some specimens. Muscle scars well-defined on ventral valve, anterior dorsal adductors smooth, posterior adductor scars smooth or moderately dendritic, median dorsal septum extends to about mid-length.

Holotype: UQF 81232 from Tiverton Formation, figured in Waterhouse (2015a, Fig. 73B, 75), and Fig. 14E herein, OD.

Morphology: Many more details and individual variations with illustrations are provided in Waterhouse (2015a).

Stratigraphy: The species is found in the *Magniplicatina undulata* Zone and overlying *Taeniothaerus subquadratus* Zone in the Tiverton Formation. The *undulata* zone used to be called the *Terrakea* (now *Bookeria*) *geniculata* Zone of the Elvinia Formation, and is preferred as nominate species for the zone as it is more widespread. A ventral exterior

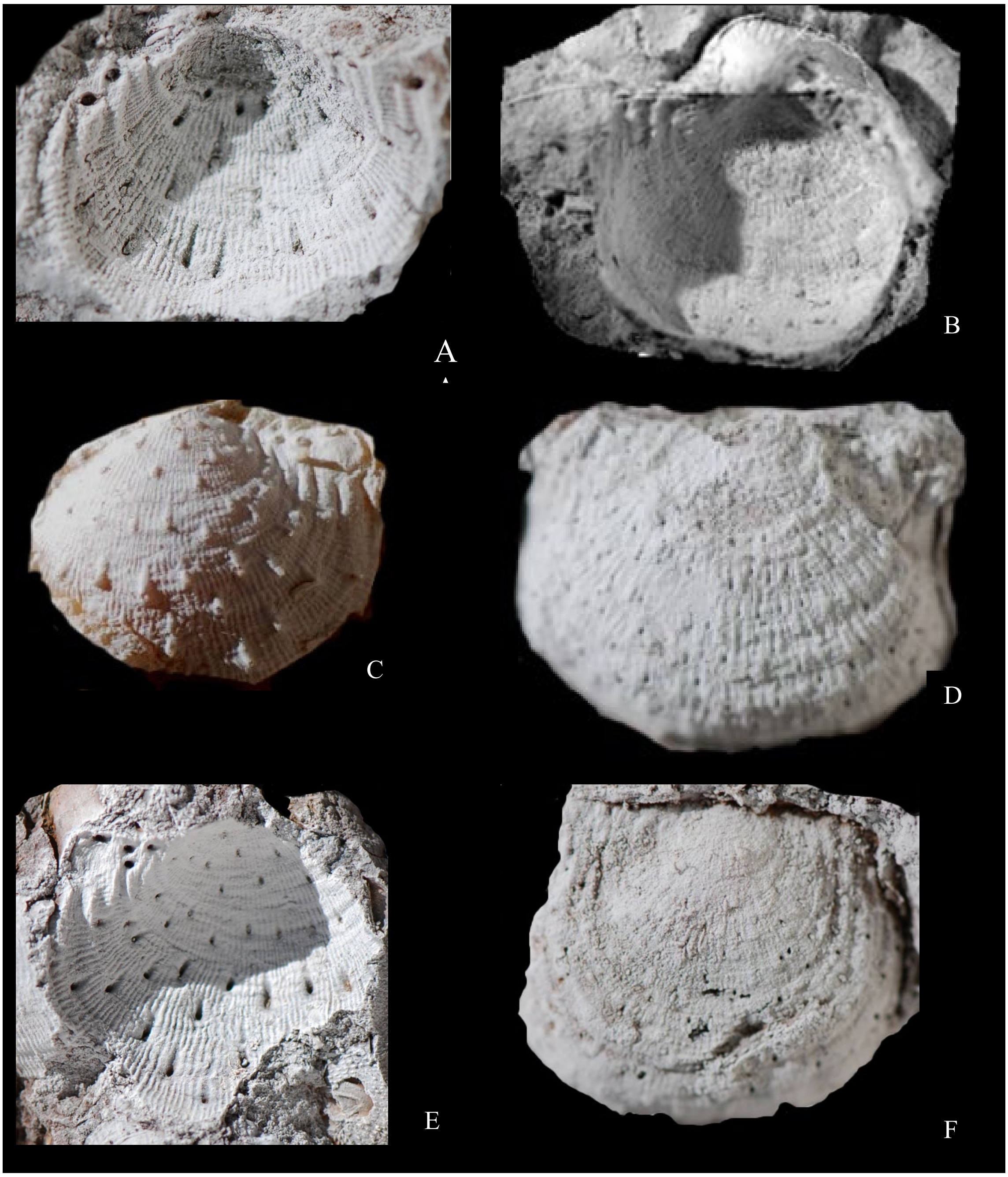


Fig. 14. *Bookeria sparsispinosa* Waterhouse. A, mould of ventral valve UQF 81233, x2. B, dorsal aspect of latex cast UQF 81225, x4. C, latex cast of ventral valve UQF 81232, x3. D, dorsal external mould UQF 81628, x3. E, ventral external mould UQF 81232, holotype x2. F, external mould of dorsal valve UQF 81234, x2. From middle Tiverton Formation, north Bowen Basin. (Waterhouse 2015a).

and lateral view showing the specimen in section figured in Hill & Woods (1964, pl. P5, fig. 7, 8) and Hill et al. (1972) suggests few spines and so appears to be *sparsispinosa*.

Genus ***Saetosina*** Waterhouse, 1986b

Diagnosis: Medium size with only moderately developed ears and low to medium-length trail, characterized by exceptionally fine spines and ribs over ventral valve, and fine closely spaced spines over the dorsal valve. Fine and numerous ventral ear spines are present and no prominent thick erect spines over ventral ears or posterior lateral slopes, or over trail of both valves. Muscle scars well-defined, median dorsal septum extends to mid-length.

Type species: *Terrakea multispinosa* Dear, 1971, p. 18 from Flat Top Formation of southeast Bowen Basin, OD.

Discussion: Parfrey (1988), Briggs (1998) and Brunton et al. (2000, p. 534) refused to recognize any generic distinction from *Terrakea,* but the lack of strong erect spines from the ears, posterior lateral slopes and trail as well as fine numerous spines and fine costellae offer clear distinctions. *Saetosina* is close to *Paucispinauria*, but this genus has well-spaced and strong spines over the ventral disc, and as a rule, strong trail spines, and often smaller ears. There is some similarity in the relative shortness of the dorsal median septum, but spines are much more numerous and radial capillae are much finer in *Saetosina*.

Saetosina dawsonensis Waterhouse, 2001

Fig. 15, 16

1986b *Terrakea multispinosa* [not Dear] – Waterhouse, p. 54, pl. 13, fig. 6, 7 (part, not fig. 8-11 = *multispinosa*).
1988 *T. multispinosa* [not Dear] – Parfrey, p. 14, pl. 2, fig. 22, pl. 3, fig. 6-10.
1998 *T. multispinosa* [not Dear] – Briggs, p. 181 (part, not Fig. 88 = *multispinosa*).
2001 *Saetosina dawsonensis* Waterhouse, p. 48.

Diagnosis: Large and transverse shells with costellae numbering six to seven and rarely up toeight or even ten in 5mm at start of dorsal trail, ventral spines fine with short prolonged bases, about 0.3 to 0.5mm in diameter.

Holotype: GSQF 12991 from Barfield Formation, southeast Bowen Basin, figured by Parfrey (1988, pl. 3, fig. 9) and Fig. 15A herein, OD.

Morphology: This species is more transverse than *Saetosina multispinosa*, and has fewer ribs on both valves, and spines are less crowded and slightly thicker. The ventral valve has some

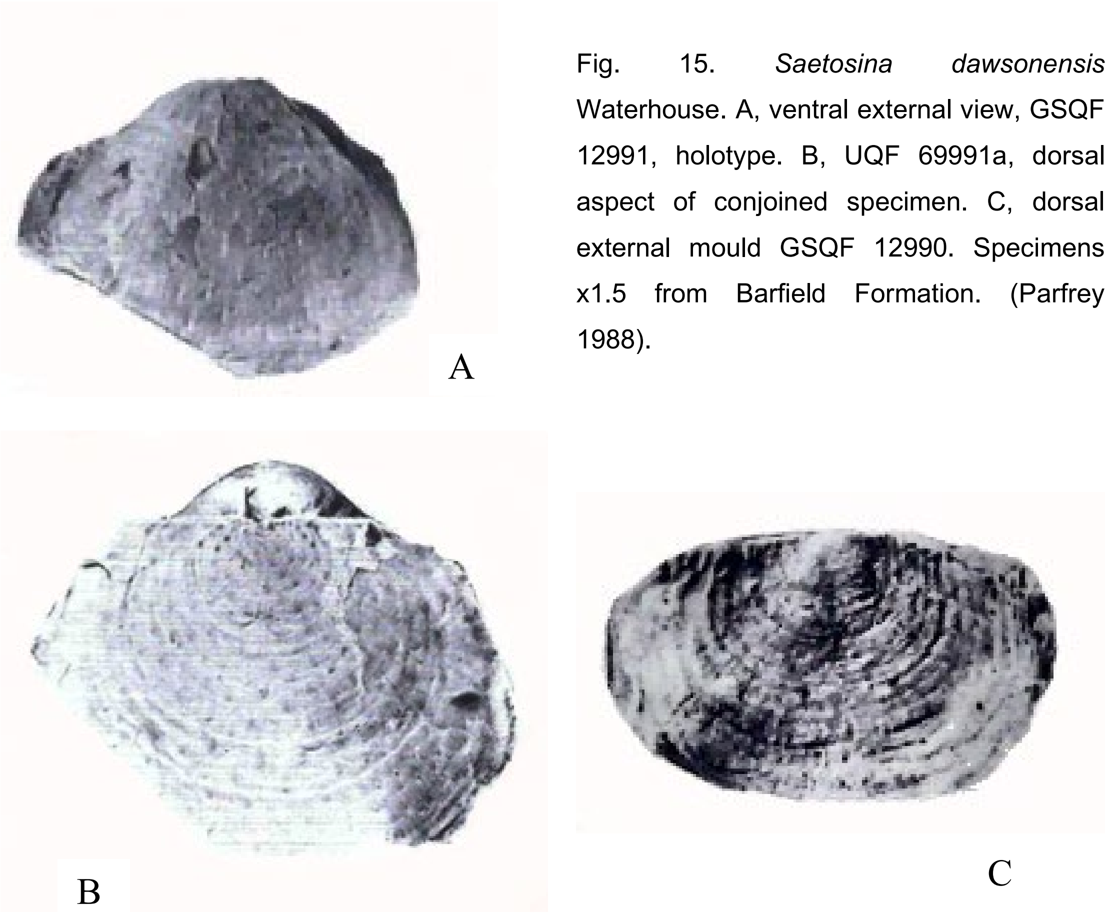


Fig. 15. *Saetosina dawsonensis* Waterhouse. A, ventral external view, GSQF 12991, holotype. B, UQF 69991a, dorsal aspect of conjoined specimen. C, dorsal external mould GSQF 12990. Specimens x1.5 from Barfield Formation. (Parfrey 1988).

three to four spines in 5mm at 5mm from the beak, and up to two spines in 5mm at 20mm from the beak, with three in 5mm posteriorly, compared with commonly two up to four spines in 5mm at 20mm from the dorsal umbo. The ventral valve has five or six ribs in 5mm posteriorly and seven to eight in 5mm anteriorly, and the dorsal valve has four to five ribs, often six to seven ribs in 5mm at 20mm from the dorsal umbo. The diameters of the spines are 0.3-0.5mm in *dawsonensis*, compared with 0.2-0.3 mm for *multispinosa*.

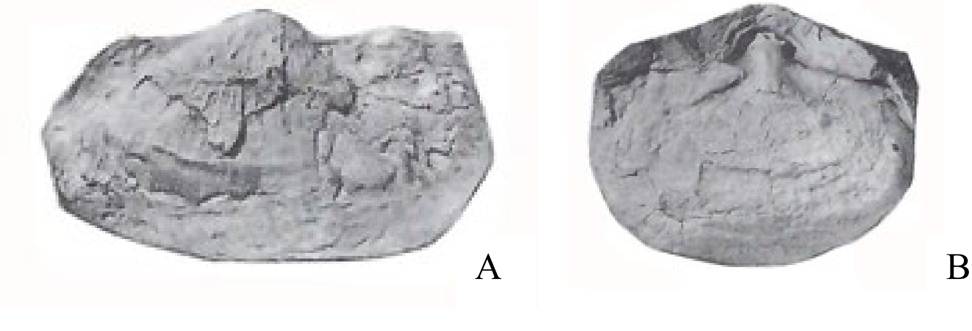


Fig. 16. *Saetosina dawsonensis* Waterhouse. A, ventral external view, UQF 70762, x1.5. B, dorsal interior, UQF 69991, x1. Specimens from Barfield Formation. (Waterhouse 1986b).

There is scope for further analysis of the variation within populations and at stratigraphic intervals. It appears that *dawsonensis* occurs only in part of the Barfield Formation and that *multispinosa* was developed elsewhere, if reliance for species discrimination is placed on the density of ribbing.

Stratigraphy: As far as is known, the species is reliably limited to part of the Barfield Formation.

Saetosina multispinosa (Dear, 1971)

Fig. 17, 18

1971 *Terrakea multispinosa* Dear, p. 18, pl. 7, fig. 1-11.
1986b *Saetosina multispinosa* – Waterhouse, p. 54, pl. 13, fig. 8-11 (part, not fig. 6, 7 = *dawsonensis*.
1998 *T. multispinosa* – Briggs, p. 180, Fig. 88A-E.
1998 *T. quadrata* [not Briggs] – Briggs, p. 180, synonymy. See p. 155 herein.
2013 *S. multispinosa* – Waterhouse, p. 420, Fig. 21.6.

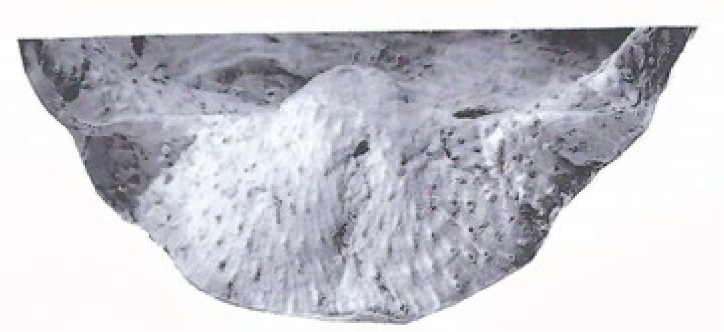


Fig. 17. *Saetosina multispinosa* (Dear), posterior aspect of latex cast AM 96266, x2, lower middle Flat Top Formation. Specimen now lost. (Briggs 1998).

Diagnosis: Characterized by very fine numerous ribs and numerous fine spines over both valves. Shells subelongate as a rule, trail low, median dorsal septum extends to mid-length. Ears moderately well developed.

Holotype: GSQF 11889 from Flat Top Formation, figured by Dear (1971, pl. 7, fig. 1), OD.

Morphology: Ventral ribs number mostly twelve to seventeen in 5mm at 20mm from the ventral umbo, and eleven to eighteen in 5mm for the dorsal valve, almost twice as numerous as ribs in *dawsonensis.* Dear (1971 reported fifteen to sixteen ribs in 5mm for the dorsal valve, Briggs (1998) fifteen to eighteen ribs in 5mm, and Waterhouse eleven to eighteen ribs in 5mm for the dorsal valve, though the numbers vary: with twenty ribs in 5mm at 10mm from the dorsal beak and twenty spines in 5mm at 17mm from the dorsal umbo, and nine to sixteen spines in 5mm at 10 mm from the dorsal umbo.

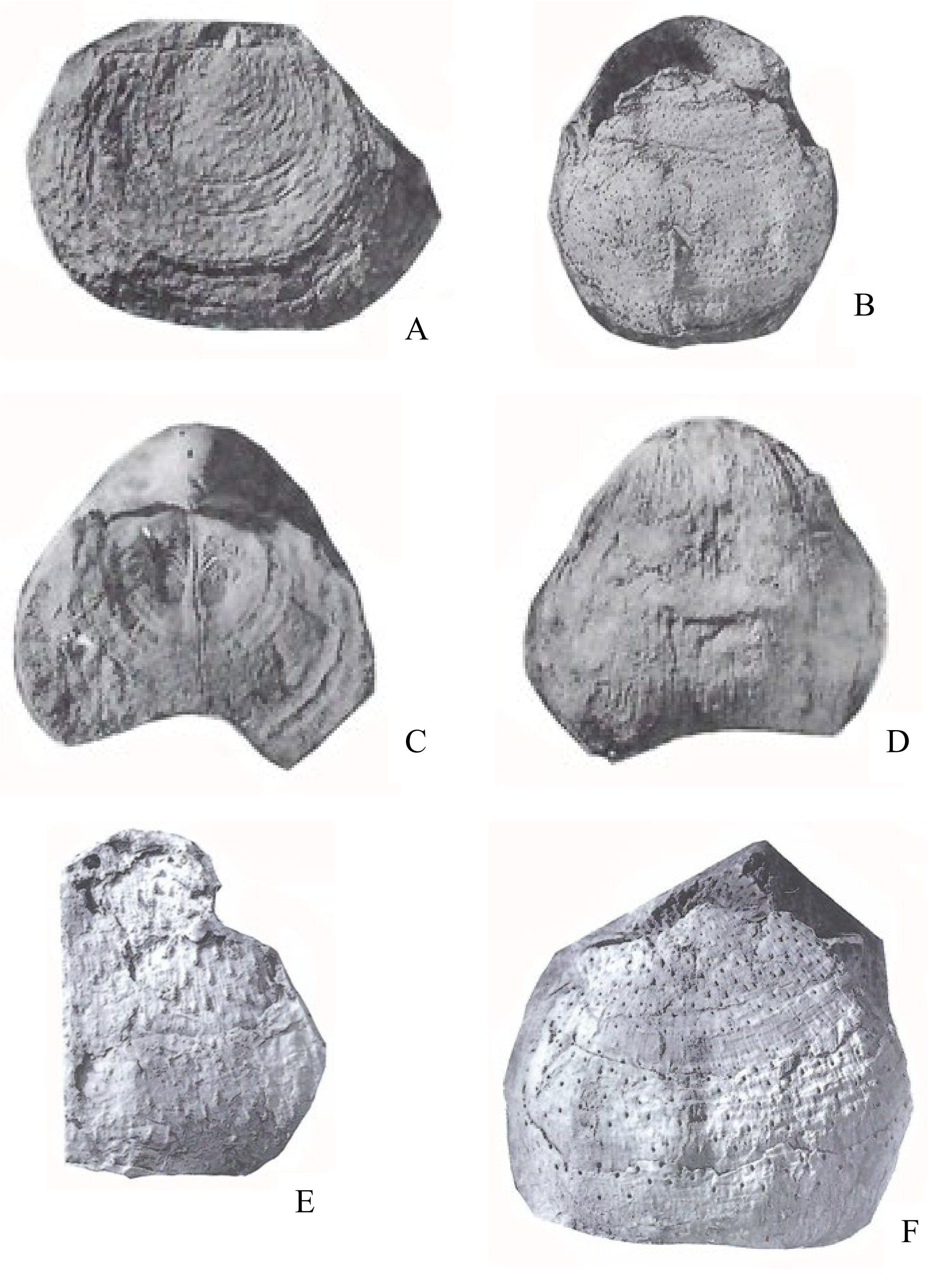


Fig. 18. *Saetosina multispinosa* (Dear). A, dorsal disc of conjoined specimen, UQF 74070, x1.5. B, dorsal aspect of external mould of conjoined specimen with conjoined valves, UQF 74071, x1. C, D, dorsal and ventral aspects of internal mould with valves conjoined, UQF 74073, x1.5. E, latex cast of ventral exterior, AMF 96267, x1.5. F, dorsal aspect of external mould with valves conjoined, AMF 96268, x1.5. The AM specimens were taken from the Queensland Museum, and are now disappeared. Fig. A, B, Barfield Formation, C-F from lower middle Flat Top Formation. (Fig. A-D Waterhouse 1986b; Fig. E, F Briggs 1998).

Ventral spine numbers are fewer, at three to four in 5mm at 5 mm from the beak and two to three at 20mm from the beak. Spines are usually 0.2 to 0.3mm in diameter, close to those of *dawsonensis* and up to thirty lie along a commarginal row over much of the shell, more numerous than in *dawsonensis*. Spines fine over ventral ears, numerous or patchy. Over the trail, the ribbing may coarsen, but spines remain thin and not in many rows. with little change in spacing. There is no development of strong spines over the ears or posterior lateral slopes. But specimens do show a range in the number of capillae and density of spines. Dear (1971, p. 77, Fig. 19.1-3) showed on average some four to five spines in 5mm for the ventral valve and three to five spines in 5mm for the dorsal valve, whereas from coarser sandstone at localities to the north close to the highway from Dawson, Waterhouse (1986b) showed there could be up to six spines in 5mm on the ventral valve and six to eight dorsal spines in 5mm, but in other specimens spine densities are closer to those of Dear (1971), at three to four ventral spines in 5mm and four to five dorsal spines in 5mm. In specimens figured by Briggs (1998B, C) from the lower middle Flat Top Formation, there are on average some four spines in 5mm over both ventral and dorsal valves, and the number of ribs in 5mm are about ten for the ventral valve and twelve for the dorsal valve, near mid-length of the figures. A well-preserved dorsal valve from the Barfield Formation (Waterhouse 1986b, pl. 13, fig. 9) shows some ten to eleven ribs in 5mm and four or five spines in 5mm near mid-length. Whether these differences are consistent enough to justify subspecific or specific separation requires further study: they may prove to be minor variations with no perceptible stratigraphic consistency.

Stratigraphy: The species is found principally in the lower middle Flat Top Formation, and appears also to be present in the Barfield Formation.

Genus ***Terrakea*** Booker, 1930

Diagnosis: Medium-sized to large costellate shells with numerous erect and strong spines over the ventral ears and posterior lateral slopes, extending as a rule along lateral margins and on to the trail. Dorsal spines slender and erect over the disc, crowded as rule over the posterior lateral slopes and possibly ears, typically thick over trail.

Type species: *Terrakea brachythaera* (Morris, 1845) from middle Permian of Tasmania, SD Maxwell 1956. (ICZN opinion 486, 1957).

Terrakea dickinsi dickinsi Dear, 1971

Fig. 19

1971 *Terrakea dickinsi* Dear, p. 15, pl. 4, fig. 2-9.
1983c *T. dickinsi* – Waterhouse, p. 157, pl. 1, fig. 3.
1986b *T.* cf. *dickinsi* – Waterhouse, p. 50, pl. 11, fig. 28-32, pl. 15, fig. 14.
1998 *T. dickinsi* – Briggs, p. 166, Fig. 82A-F.

Diagnosis: Roundly subrectangular and weakly transverse, dorsal disc shallowly concave and curving sharply into a geniculate trail, ventral umbonal shoulders low and gently rounded. Few large spines over anterior trail.

Holotype: GSQF 11710 from upper Tiverton Formation, north Bowen Basin, figured by Dear (1971, pl. 4, fig. 2), OD.

Morphology: This marks the first appearance in the stratigraphic record in east Australia of a paucispinaurian with thick lateral and anterior spines, especially over the dorsal valve, combined with numerous ventral ear spines.

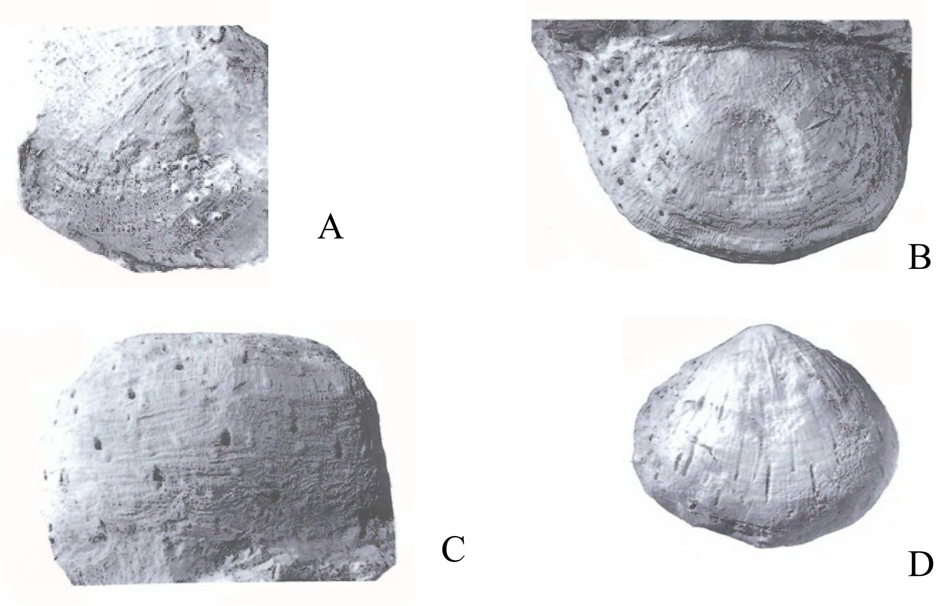


Fig. 19. *Terrakea dickinsi dickinsi* Dear. A, posterior lateral latex cast of ventral valve GSQF 13482. B, C, views of disc and trail of dorsal external mould, GSQF 13484. D, ventral internal mould of GSQF 36170. Specimens from uppermost Tiverton Formation, Bowen Basin, x1.5. (Briggs 1998).

Stratigraphy: The species is found principally in the upper Tiverton Formation, upper Cattle Creek Shale and Roses Pride Formation, in faunas deemed to be of early Artinskian (ie

Aktastinian) age. Briggs reported other occurrences of *dickinsi* in the Yarrol block and Drake Syncline and Hastings block, without providing descriptions or illustrations or stratigraphic data.

Terrakea dickinsi aurispina Waterhouse, 1982

Fig. 20

1964a *Terrakea* n. sp. aff. *pollex* Waterhouse, p. 64, pl. 10, fig. 1-5, text-fig. 23A, 24A.
1971 *Terrakea pollex* n. subsp. Waterhouse, pl. 2, fig. 16.
1982 *T. pollex aurispina* Waterhouse, p. 47, pl. 11a-c, f – i (part, not pl. 11d = *verecunda*), text-fig. 17H, J. K.
2001 *T. dickinsi* – Waterhouse, p. 42.
2008 *T. dickinsi* – Waterhouse, p. 359, Fig. 6B.

Diagnosis: Close to *Terrakea dickinsi*, distinguished by coarser spines and stronger costae.

Holotype: BR 217, figured in Waterhouse (1964a, pl. 10, fig. 1-3, text-fig. 23A, 24A) and Fig. 20C herein from Brunel Formation, Takitimu Range, New Zealand, OD.

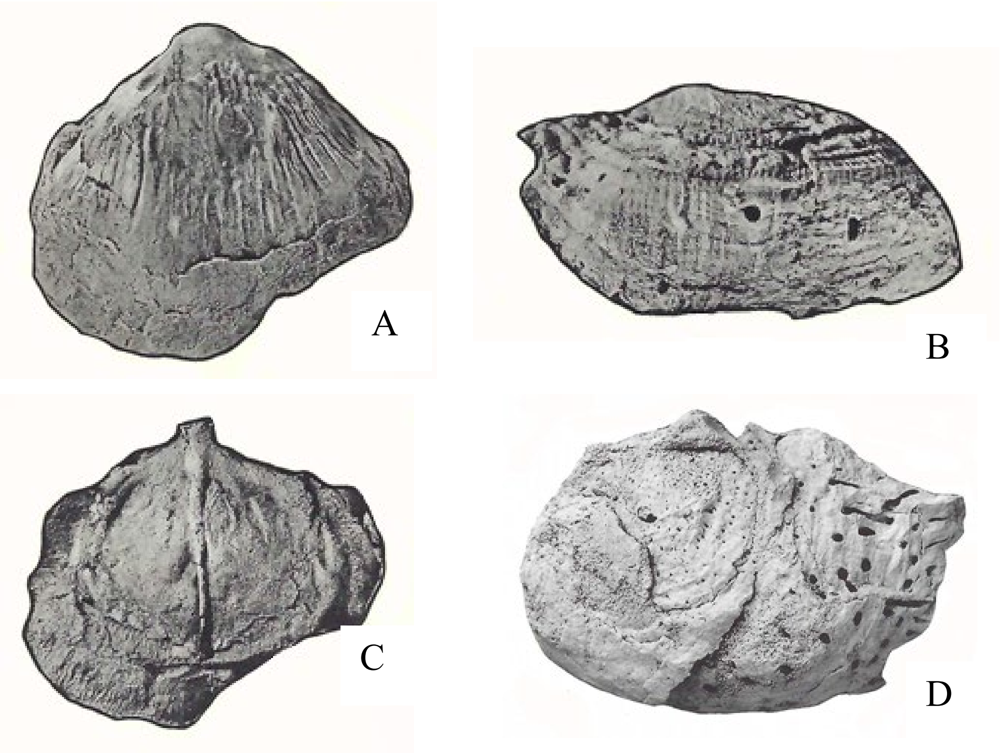


Fig. 20. *Terrakea dickinsi aurispina* Waterhouse. A, ventral internal mould, BR 217, x2. B, anterior view showing trail of dorsal external mould, BR 218, x2. C, PVC cast of dorsal interior, BR 217 holotype, x2. D, external mould of dorsal valve, BR 1487, x1.5. Specimens x2, from Brunel Formation of Takitimu Mountains, New Zealand. (Waterhouse 1964a, 1982).

Stratigraphy: The subspecies is found in the Brunel Formation of New Zealand. Its first appearance is in the *Notostrophia zealandicus* Zone, and the species persisted into the overlying *N. homeri* Zone, which is correlative with the *Echinalosia preovalis - Ingelarella plica* Zone of the upper Tiverton Formation and correlative formations in Queensland. The New Zealand specimens definitely do not occur as shown by Briggs (1998, Fig. 11) in a higher band called the Caravan Formation. *T. dickinsi dickinsi* is distinctly older than the Caravan Formation, separated by several units, including the biozones of *Capillaria conata* and *Spinomartinia*? *adentata.* The *Terrakea* from the Caravan Formation differs from *dickinsi,* though now we are forced to rely on published descriptions and figures, because Briggs borrowed the material, and never returned it. It is now lost.

Terrakea rylstonensis Briggs, 1998

Fig. 21 - 23

1905 *Productus* sp. Etheridge, p. 67, pl. 18, fig. 4, 5 (fide Briggs 1998).
?1980 *Terrakea dickinsi* [not Dear] – McClung, p. 369, pl. 19.1.4, 5.
?1982 *Terrakea* sp. Waterhouse, p. 48, pl. 10h, j.
cf.1993 ?*Terrakea* sp. Briggs & Campbell, p. 328, Fig. 3.11, 12.
cf. 1993 *Terrakea* sp. Briggs & Campbell, p. 328, Fig. 3.13-19.
1998 *Terrakea rylstonensis* Briggs, p. 168, Fig. 83A-H.
?2001 *T. exmoorensis* – Waterhouse, p. 42, pl. 1, fig. 16, 17, text-fig. 5c.
2002a *T. exmoorensis* – Waterhouse, pp. 35, 37.
?2021a *T. exmoorensis* (including *rylstonensis*) – Waterhouse, Fig. 11.

Diagnosis: Small equidimensional shells with ears at maximum width along the hinge, roundly geniculate, trail short, ribbing fine, at ten to thirteen in 5mm over ventral valve and thirteen to fifteen in 5mm over dorsal valve. Ventral spines with somewhat prolonged bases over the disc, varying from eight to over sixteen or more along a commarginal row, fine at 0.4mm diameter, erect and crowded over ears (though not completely known) and posterior lateral slopes, up to 0.5mm in diameter; dispersed and in up to four rows of comparatively fine diameter over trail on now-vanished type material. Dorsal disc spines not described by Briggs, but spines fine and scattered in some four rows over the trail. Muscle scars moderately impressed, dorsal median septum extends for over three quarters of the length of the disc.

Holotype: AMF 45480, Snapper Point correlative, figured by Briggs (1998, Fig. 83C), OD. This specimen appears to have been “lost”, in other words, never deposited with the Australian

Museum, just like the rest of the specimens figured as this species by Briggs and taken from the Queensland Museum, and published as registered with the Australian Museum.

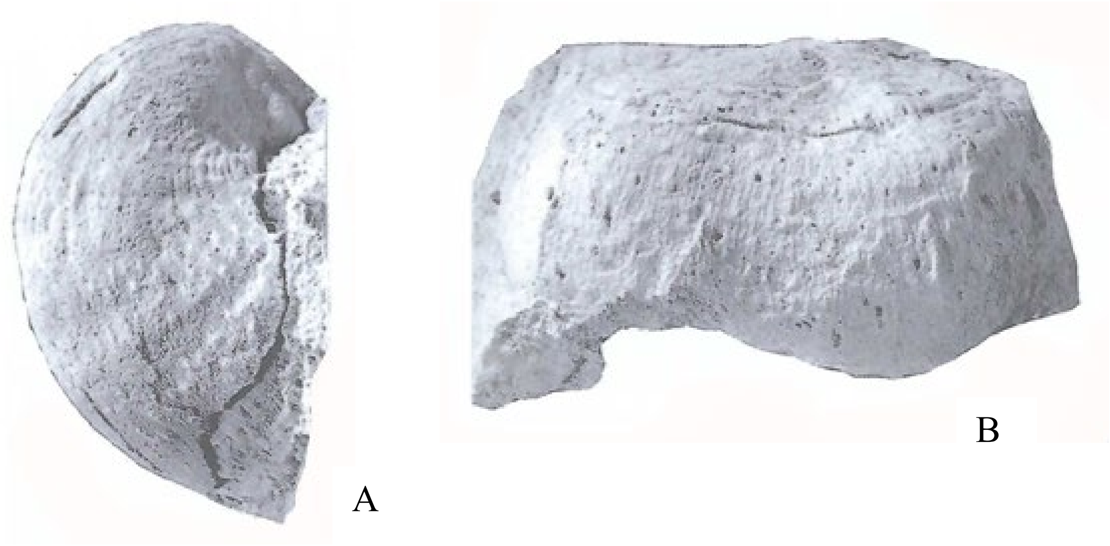


Fig. 21. *Terrakea rylstonensis* Briggs. A, lateral aspect of the Briggs holotype, ventral internal mould AMF 45480. B, anterior aspect of dorsal mould AMF 45475. From no registered locality, in rocks correlative of Snapper Point Formation, x2. The specimens apparently not at and never were at the Australian Museum and so need to be replaced. (Briggs 1998).

Discussion: This species is in limbo. The holotype and syntypes figured by Briggs (1998) cannot be found. They were never deposited at the Australian Museum, where they according to the publication were registered, even though the material belonged to the Queensland Museum. Furthermore, no species distinction for *rylstonensis* was offered by Briggs (1998), and from the inadequate figures offered by Briggs (1998, Fig. 83), no ready distinction from *Terrakea exmoorensis* Dear is apparent (Waterhouse 2001). Of course someone may be able to improve on this assessment, but it would be preferable, if not mandatory, to obtain more material that can be assigned to *rylstonensis*. No figure in Briggs (1998) shows the full ventral ears, nor the dorsal disc, so that the nature of spines for these significant parts of the shell remains not known, as far as the original type material is concerned. As noted by Waterhouse (2001, 2021a), the species comes from a critical part of the east Australian succession, and it would be highly desirable to have the Rylstone and lower Elderslie rocks and probably Snapper Point rocks or their correlatives characterized by a unique species. But at present, it is not possible to confidently distinguish the species from *T. exmoorensis* Dear, though this latter species appears to have somewhat coarser spines over the dorsal trail, and numerous spines over the ventral posterior lateral slopes.

Other specimens come from much the same or slightly older stratigraphic level, but as a rule are also poorly known. They include the material figured as *Terrakea dickinsi* from the lower Gebbie Formation by McClung (1980, p. 369, pl. 19.1.4, 5) which shows little of value. The caption in McClung (1980) noted the similarity to Branxton and Snapper Point material. The figured ventral valve is less informative, showing an internal mould. The specimens figured as *Terrakea* sp. by Waterhouse (1982, p. 48, pl. 10h, j) and Briggs & Campbell (1993, Fig. 3.20) from the Caravan Formation at Wairaki Downs, New Zealand, show close-set ventral disc spines and crowded erect spines over the ventral ears, impinging onto the umbonal slopes, closely spaced dorsal disc spines, and fine dorsal trail spines, and ventral interior – more critical detail than is displayed for figured *rylstonensis* by Briggs (1998). The material could be conspecific, even though it comes from beds likely to be slightly older than those which yielded type *rylstonensis*. These specimens were taken by Briggs, and have disappeared. They will be hard to replace. Another suite was described from a boulder found in the lower Queens Beach Formation at Stephens Island, New Zealand (Campbell et al., 1984, Fig. 6.3, 4; Briggs & Campbell 1993, Fig. 3.13-19; Waterhouse 2021a, Fig. 11). These show many of the attributes essential for determining a species, and so might seem to offer an escape from the impasse contrived by Briggs. But once again – the specimens were removed by Briggs, with the connivance of one GNS staff member, who showed no qualms about sending overseas material that had already been figured, when plaster casts and the available figures would have sufficed. The specimens were never returned – they are presumed lost. They show closely spaced ventral ear spines, with few impinging on the umbonal slopes, closely spaced ventral spines, somewhat obscure dorsal disc spines apparently with spacing and number much the same as for the ventral disc, and a short subgeniculate trail. Unlike the trail spines figured for *rylstonensis* by Briggs (1998, Fig. 83D), the trail spines, though moderately numerous, are comparatively robust, and so possibly a little closer to those of type *exmoorensis* (see Dear 1971), arguably supporting the suggestion by Waterhouse (2021a, p. 90) that the specimens belong to *exmoorensis*, but possibly indicating that trail spines thickened with age. The trail spines thus differ from the relatively thin trail spines figured by

Briggs for *rylstonensis*. It seems that only by revisiting and recollecting the fossil localities in the Rylstone rocks, Elderslie Formation and the Queens Beach Formation on Stephens Island will unravel the nature and validity or otherwise of *rylstonensis*.

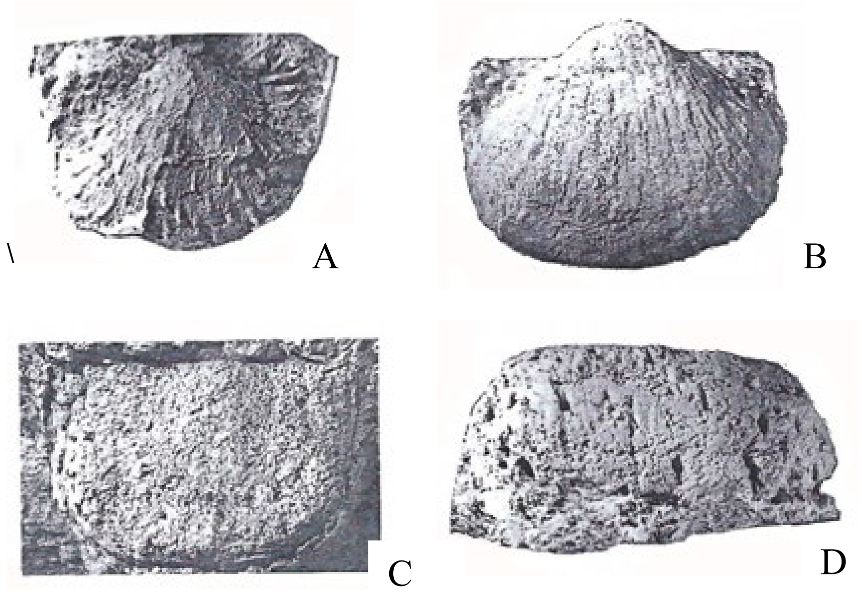


Fig. 23. *Terrakea* cf. *rylstonensis* Briggs?. A, latex cast of ventral valve. B, internal mould of ventral valve. C, D, dorsal and anterior aspects of dorsal valve. Specimens x1.5, from Queens Beach Formation, Stephens Island, New Zealand. BR numbers were applied, but specimens have now disappeared as part of the Briggs imboglio. Dorsal spines are thicker than shown for *rylstonensis* figured in Briggs (1998). (Briggs & Campbell 1993).

Terrakea exmoorensis Dear, 1971

Fig. 24, 25

?1964 *Terrakea* cf. *fragilis* [not Dana] – Hill & Woods, pl. P5, fig. 9a, b, 10a-c.
1971 *T. elongata exmoorensis* Dear, p. 18, pl. 5, fig. 3-5.
?1972 *T. exmoorensis* Hill et al. pl. P5, fig. 9, 10a-c.
1983 *T. elongata exmoorensis* – Waterhouse & Jell, p. 242, pl. 1, fig. 10.
1983 *T. brachythaera* [not Morris] – Waterhouse & Jell, p. 242, pl. 1, fig. 9, 11 -13, 15 (part, not fig. 14, 16-18, pl. 2, fig. 1 = *brachythaera).*
1998 *T. exmoorensis* – Briggs, p. 179.
2001 *T. cf. exmoorensis* – Waterhouse, p. 42, pl. 1, fig. 14, 15.
2002a *T. exmoorensis* – Waterhouse, p, 49.
2021a *T. exmoorensis* – Waterhouse, p. 89, Fig. 11 [or *rylstonensis*] (part, not Fig. 12 and the following figure, mislabelled 12 instead of 13 = *brachythaera).*

Diagnosis: Subelongate to subquadrate or moderately transverse shells with gently convex venter and moderate to long curved or subgeniculate trail, numerous erect spines of moderately thick spines over inner ears, umbonal slopes and posterior lateral slopes, many fine body spines with short to more rarely long bases over ventral valve. Dorsal valve may be dimpled, many erect spines over posterior lateral slopes, not as coarse as in younger species, and dorsal disc spines seem more closely spaced than those over the ventral valve and over the moderately long dorsal trail (Dear 1971, pl. 5, fig. 5b).

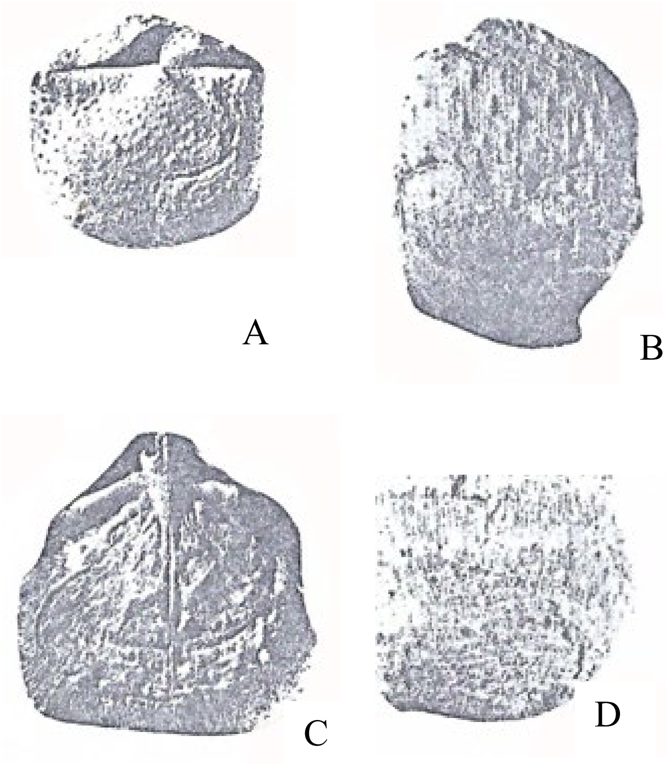


Fig. 24. *Terrakea exmoorensis* Dear. A, dorsal aspect of internal mould of conjoined specimen, GSQF 5537, x1.5. B, anterior aspect of ventral valve GSQF 11856, x1. C, latex cast of dorsal interior of GSQF 5537, x1.5 (see A). D, anterior aspect of dorsal mould, GSQF 11856, x1 (see B). The reproduction is poor, but does show the relative size of the dorsal trail spines, each of which may span some three capillae. From lower Blenheim Formation, now revised to Moonlight Formation. (Dear 1971).

Holotype: GSQF 5537 from lower Blenheim Formation, reinterpreted as Moonlight Formation, north Bowen Basin, figured by Dear (1971, pl. 5, fig. 3a, c), OD.

Morphology: The trail spines are not as thick as those of *Terrakea dickinsi*, nor those of *elongata* and or *brachythaera*, and are stronger than those of type *rylstonensis* figured in Briggs (1998). Spines over both valves are numerous. There is scope for further clarification of this species: large collections from levels in the Bowen Basin show that the shape varies somewhat, as well as degree of geniculation, but spines are numerous, and none as thick as those of *macrospina* or *elongata.*

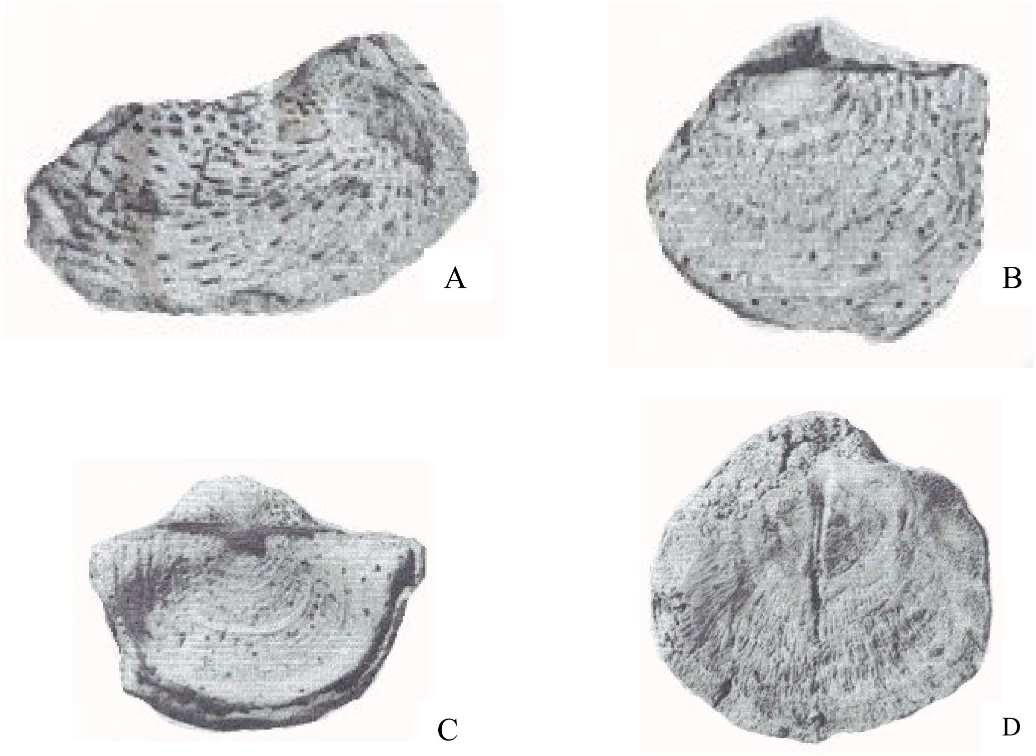


Fig. 25. *Terrakea exmoorensis* Dear. A, part of external mould of ventral valve UQF 73209, x1.5. B, D, dorsal aspect of external mould and interior, UQF 73203, x1.5. C, dorsal aspect of latex cast of specimen with valves conjoined, UQF 73204, x1. From upper Moonlight Sandstone (Waterhouse & Jell, 1983).

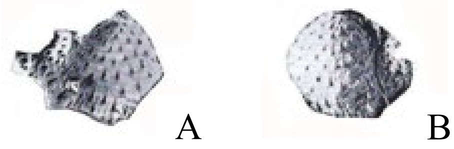


Fig. 22. *Terrakea exmoorensis* Dear?, or the poorly known *rylstonensis* Briggs, ventral external mould and latex cast, x1, GSQF 5537. Stated to be from the Gebbie Formation, which implies *rylstonensis.* Or could it be Moonlight, with *exmoorensis*?, north Bowen Basin. (Hill et al. 1972).

Stratigraphy: The species was first named for material from the "basal Blenheim Formation" according to Dear (1971) and is found in the Moonlight Sandstone at the base of this formation as understood herein. McClung (1983, Fig. 19) described internal moulds as *Terrakea solida* from the Catherine Sandstone at LD96. These possibly belong to *Terrakea exmoorensis*, to judge from shape and strong ventral muscle impressions. Parfrey (1988) reported the species from the Ingelara Formation, Catherine Formation and Peawaddy Formation. Whether the species is found in the Sydney Basin is uncertain. It seems possible that specimens of ex*moorensis* have been confused with *brachythaera*, but this requires verification. In New Zealand, the species was listed from a number of zones in the *Echinalosia discinia* Zone by Waterhouse (2002, tables 5, 6, pp. 35, 37), including the *Lethamia ligurritus* Subzone, in the upper Letham Formation (unit 3), though these specimens may well prove to be *rylstonensis* if the standing of this taxon can be consolidated. The species *exmoorensis* is present in the *Pseudostrophalosia blakei* Zone of the lower Mangarewa Formation (unit 5), as figured in Waterhouse (2001, pl. 1, fig. 14, 15) with localities listed and mapped in Waterhouse (2002a, p. 49), whereas the listed occurrences of *Terrakea* ascribed to *exmoorensis* in Waterhouse (2001, pl. 1, fig. 16, 17; 2002a, Tables 5, 6, pp. 35, 37 [f126 should read f326] may prove to be *rylstonensis*, a matter requiring clarification and justification of the *rylstonensis* name.

Terrakea etheridgei Briggs, 1998

Fig. 26, 27

cf. 1909 *Terrakea brachythaera* var. *elongatus* Etheridge & Dun, p. 7, pl. 42, fig. 2, 3, 7 (part, not pl. 43, fig. 5, 7 = *elongata*).
1969 *Terrakea* sp. Wass & Gould, p. 226, pl. 14, fig. 19.
1969 *T. solida* [not Etheridge & Dun] – Wass & Gould, p. 215.
1998 *T. etheridgei* Briggs, p. 173, Fig. 86A-F. Briggs also referred to Fig. 72D, which is labelled as *Anemonaria mitis* (Hill). But his Fig. 73D shows part of a ventral topotype of *etheridgei.*

Diagnosis: Moderately large subequidimensional shells, venter with gently convex crest and steep high sides, moderately thick spines over the posterior lateral slopes of both valves, long thick erect spines over ventral ears, dorsal spines finer and more numerous over the disc compared with the number over the trail in the holotype (which is the only figured dorsal exterior). The ventral disc and lateral and trail spines are of moderate to considerable strength, and of a density comparable to that of the dorsal trail. Trail steeply rounded without being angularly geniculate. Muscle scars well-defined especially on ventral valve. Dorsal medium septum long.

Holotype: SUP 25553 from Permian outlier near South Marulan, New South Wales, figured by Briggs (1998, Fig. 86A) and Fig. 26B herein, OD. No repository for locality SUP was provided by Briggs, but it may be a registered specimen from Sydney University. Wass & Gould (1969) assigned registration numbers to their specimens, but provided no information on where the material was stored.

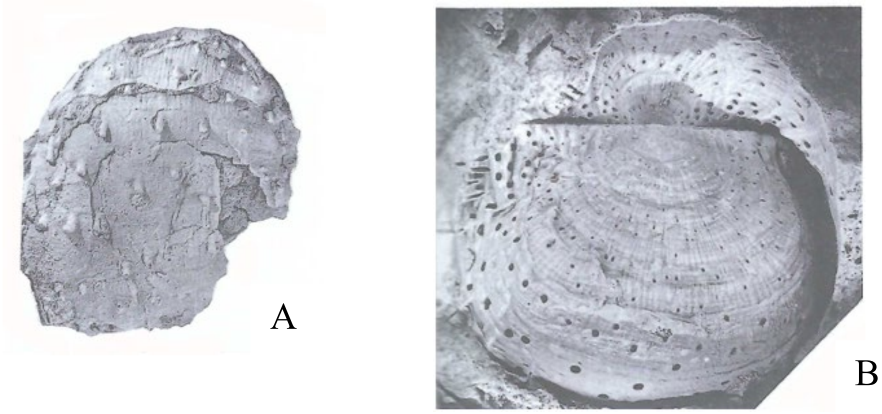


Fig. 26. *Terrakea etheridgei* Briggs. A, anterior part of flattened ventral valve, UQF 75332 from Muree Formation, x1. B, external mould showing dorsal valve and part of ventral valve, holotype, SUP 25553, x1.5, from South Marulan. New South Wales. (Briggs 1998).

Morphology: Briggs (1998) included in his synonymy material figured as *brachythaerus* and *brachythaerus* var. *elongatus* from Nowra by Etheridge & Dun (1909, pl. 42, fig. 2, 3, 6, 7) and specimens recorded as *Terrakea fragile* and *T. elongata* by Booker (1930, pl. 1, fig. 1-5, pl. 2, fig. 1, pl. 3) and *elongata* (Booker 1930, pl. 1, fig. 6). The figures are internal moulds that provide only limited information about spine detail. The specimens of Etheridge & Dun and Booker show highly arched ventral valves, with a profile approaching that of *brachythaera* as figured by Muir-Wood & Cooper (1960), and not the same as that of the South Marulan specimens figured in Briggs (1998). Booker had emphasized that his *fragile* were sharply geniculate, whereas the curve between disc and trail in the dorsal valve of the *etheridgei* holotype is more rounded. Dana (1849, p. 686, pl. 2, fig. 7) in his original description and figure for *fragile* was not particularly informative. It is possible that various specimens as originally named *fragile* by Dana (1847, 1849) and later referred to that taxon by various authors are truly *brachythaera*, as concluded by Waterhouse (1964a). They could be the same as *etheridgei* Briggs, which may be either a valid species, or identical with *brachythaera*. The question requires further study. In the meantime, *etheridgei* not only remains insecure because of its possible relationship to *brachythaera*, but under threat of being a junior synonym to *fragile*. The ventral spines for *etheridgei* from South Marulan are strong, well-spaced and regular over the disc as shown herein in Fig. 26A. Possibly therefore *etheridgei* is not quite the same as *brachythaera* though anticipating various aspects of that species, but discrimination between the two is not easy.

The Tasmanian material figured by Clarke (1987, Fig. 3A-P, not Q) from Malbina E Formation and referred to *etheridgei* by Briggs (1998) shows moderately steep and high ventral lateral walls and closely spaced dorsal disc spines somewhat as in the *etheridgei* holotype, but the disc is broader and the steep walls lower than in type *etheridgei*. Ventral disc and trail spines appear to be well-spaced. But whether the ventral ear spines are as long and as strong as for *etheridgei* on the Tasmanian shells is doubtful, and the spines seem to be significantly finer than those of the specimen recorded allegedly from the Oxtrack Formation by Briggs (1998), as refigured in Fig. 27. Much of the understanding of *etheridgei* is provided by this ventral valve figured by Briggs (1998), which shows numerous coarse posterior lateral spines over the ears and posterior lateral margins. This specimen has disc spines distinctly finer than those shown on the South Marulan venter (compare Fig. 26A). The specimen of Fig. 27 herein was stated to have come from the Oxtrack Formation, yet no other comparable material has been described or figured from the Oxtrack Formation, so that its source must be questioned. It came from an early UQ locality, possibly when the Oxtrack Formation was regarded as occurring much more widely than now recognized (Waterhouse 2000a, p. 241), and it is therefore dubious whether it should be regarded as a reliable indicator of morphology typifying *etheridgei*. What Briggs has definitely shown is that South Marulan specimens have numerous dorsal ear spines, and have well-spaced sturdy spines over the venter. Its relationship to *brachythaera* remains an open question.

Material from northwest Nelson of New Zealand was regarded as allied by Briggs (1998).

Fig. 27. *Terrakea etheridgei* Briggs. A, latex cast of flattened shell showing ventral spines, UQF 36181, x1.25. (Briggs 1998). This specimen supposedly came from the Oxtrack Formation of the southeast Bowen Basin, but is like no other specimen described and illustrated from this formation. Could it be close to *Bookeria. drysdalei*, found also in the Tiverton Formation and to be expected in the Dresden Formation in the southeast Bowen Basin? Some studies have incorrectly extended the Oxtrack Formation to incorporate Dresden and even Elvinia beds of the Buffel Group. (See Waterhouse 2001, p. 241).

Ventral lateral slope and ear spines are dense, the ventral valve highly arched (Waterhouse & Vella 1965, pl. 3, fig. 3), and the ventral disc and dorsal trail spines well spaced. But the dorsal disc spines are not clearly figured and the dorsal septum is not long. The ventral ear spines are finer than indicated for type *etheridgei*, apparently contradicting the Briggs assessment. Overall the sparsity of figured type material of *etheridgei* (Briggs 1998, Fig. 86A, C only) hampers assignment of other collections to the proposed taxon, and does not allow confident separation from *brachythaera*. It should be understood in fairness to Briggs, that he was apparently limited – whether by his choice or not we do not know – to providing no more than one plate, on a rather small page, for each taxon, and this is far from adequate for highly variable species, especially when specimens are reproduced at twice natural size, as is desirable.

Stratigraphy: Briggs (1998, p. 174) placed the species in the *Echinalosia hanloni* Zone, referring to a species which is reliably represented in the Nowra and Muree beds of the south and north Sydney Basin, ie. pre-*runnegari* and post-*discinia*. The South Marulan fauna as partly described by Wass & Gould (1969) would allow such an age. The species *hanloni* occurs within the range of *T. brachythaera.*

Terrakea macrospina Waterhouse, 2022a

Fig. 28

2022a *Terrakea macrospina* Waterhouse, p. 51, Fig. 6-11.

Diagnosis: Subequilateral shells with steep but not high lateral ventral flanks. Ribs fine, spines distinctive: ventral disc spines more numerous than usual, with short bases, and lateral and trail spines extremely thick over both valves, well-spaced. Muscle scars clearly defined, dorsal median septum long, as in other contemporaneous and younger forms.

Holotype: UQF 82770 from lower Mantuan Member, figured by Waterhouse (2022a, Fig. 10D, 11) and Fig. 28A herein, OD.

Fig. 28. *Terrakea macrospina* Waterhouse. A, lateral aspect of dorsal internal mould, UQF 82770 x 2, holotype. B, posterior ventral aspect of ventral valve UQF 69656, x1. (Waterhouse 2022).

Morphology: The species is readily distinguished by its unusually strong spines, and by the numerous ventral disc spines and fine ribbing. It is likely to have been a forebear for *Terrakea elongata* (Etheridge & Dun) and presumably developed from stock allied to *T exmoorensis*, or may have been a variant of *brachythaera*.

Stratigraphy: The species was collected by L. G. Elliott, from rocks he assigned to the Mantuan level. No other material is known that compares with these specimens, and it would be interesting to determine just where the species occurs in the Mantuan Formation. Briggs (1998, p. 185) reported important observations by G. McClung (as pers. comm.) that much of the Mantuan succession through a measured section contained a new finely costate species of *Terrakea*, below the coarsely costate species *Paucispinauria solida* (Etheridge & Dun). This then-unnamed species appears to be *macrospina*, because it is finely costate just as reported for McClung's distinct species. Associated species, as described in Waterhouse (2022a) are largely but not entirely typical of the *Maxwellosia ovalis* Zone and fauna. Unfortunately, according to the account in Briggs, McClung provided no information about the spines in his new form. The exact relationship to *Terrakea brachythaera* remains an unanswered question: it might be slightly older, or slightly younger, or most likely equivalent to part of the range of that species.

Terrakea brachythaera brachythaera (Morris, 1845)

Fig. 29 - 31

1845 *Productus brachythaerus* Morris, p. 284, pl. 14, fig. 4 only.
1847 *P. fragilis* Dana, p. 153.
1849 *P. fragilis* Dana, p. 686, pl. 2, fig. 7.
1877 *P. brachythaerus* – Koninck, p. 198, pl. 10, fig. 4, 4a, pl. 11, fig. 1.
1902 *Productus brachythaerus* [not Morris or Sowerby] – Frech, p. 578, pl. 57d, fig. 1a, b.
1909 *P. brachythaerus* – Etheridge & Dun, p. 5, pl. 42, fig. 1, 4, 8, pl. 43, fig. 6, 8-11, (part, not fig. 5 = *Magniplicatina*)
?1909 *P. brachythaerus* var. *elongatus* [not Etheridge & Dun] – Etheridge & Dun, p. 7, pl. 42, fig. 2, 3, 7 or possibly *etheridgei* if valid. (Part, not pl. 43, fig. 5, 7 = *elongata*).
1930 *Terrakea fragile* [not Dana] – Booker, p. 71, pl. 1, fig. 1-5, pl. 2, fig. 1, pl. 3.
1930 *T. elongata* [not Etheridge & Dun] – Booker, p. 74, pl. 1, fig. 6.
1930 *P. brachythaerus* – Booker, p. 70, fig. 1, fig. 2, 5.
1930 *P. leve* Booker, p. 70, pl. 2, fig. 3, 4.
1950 *P. brachythaera* – Hill, p. 18, pl. 2, fig. 1.
1960 *P. brachythaerum* – Muir-Wood & Cooper, p. 315, pl. 119, fig. 14-17, 21, 22.
1960 *T. fragile* – Muir-Wood & Cooper, p. 315, pl. 119, fig. 13, 18-20, 23.
1965 *T. brachythaerum* – Muir-Wood, p. 503, Fig. 375.2a-d.
1965 *T. fragile* Muir-Wood, p. 503, Fig. 375.2e, f.
1983 *T. brachythaera* – Waterhouse & Jell, p. 242, pl. 1, fig. 14, 16-18, pl. 2, fig. 1 (part, not pl. 1, fig. 9, 11-13, 15 = *exmoorensis*).
1987 *T. brachythaera* [not Morris] – Clarke, p. 266, Fig. 3A-P, Q?.
1998 *T. brachythaera* – Briggs, p. 176, Fig. 87A-I.
2008 *T. exmoorensis* [not Dear] – Waterhouse, Fig. 7J.
2013 *T. brachythaera* – Waterhouse, p. 459 (part, not Fig. 21.3, 21.5 = *densispinosa*).
2021a *T. exmoorensis* [not Dear] – Waterhouse, p. 89, Fig. 12, 12 (mistake, should be 13) (part, not Fig. 11 = cf. *rylstonensis*?).

Diagnosis: Shells vary in shape from equilateral to transverse or elongate, shell moderately inflated, with steep but not very high ventral lateral slopes, spines much as in other species close in age, and spines finer and more numerous over dorsal disc than over dorsal trail, which in spacing are like those over the ventral disc and trail. Spines crowded and of moderate strength along ventral posterior umbonal slopes, ears and trail, and similarly placed on dorsal valve. Trail sharply curved or geniculate, muscle scars distinct, dorsal median septum long.

Lectotype: BB 9466 from Illawarra, probably Broughton Formation, south Sydney Basin, figured by Morris (1845, pl. 14, fig. 4c) and Hill (1950, pl. 2, fig. 1) and herein Fig. 29, SD Maxwell 1956, ICZN Opinion 486.

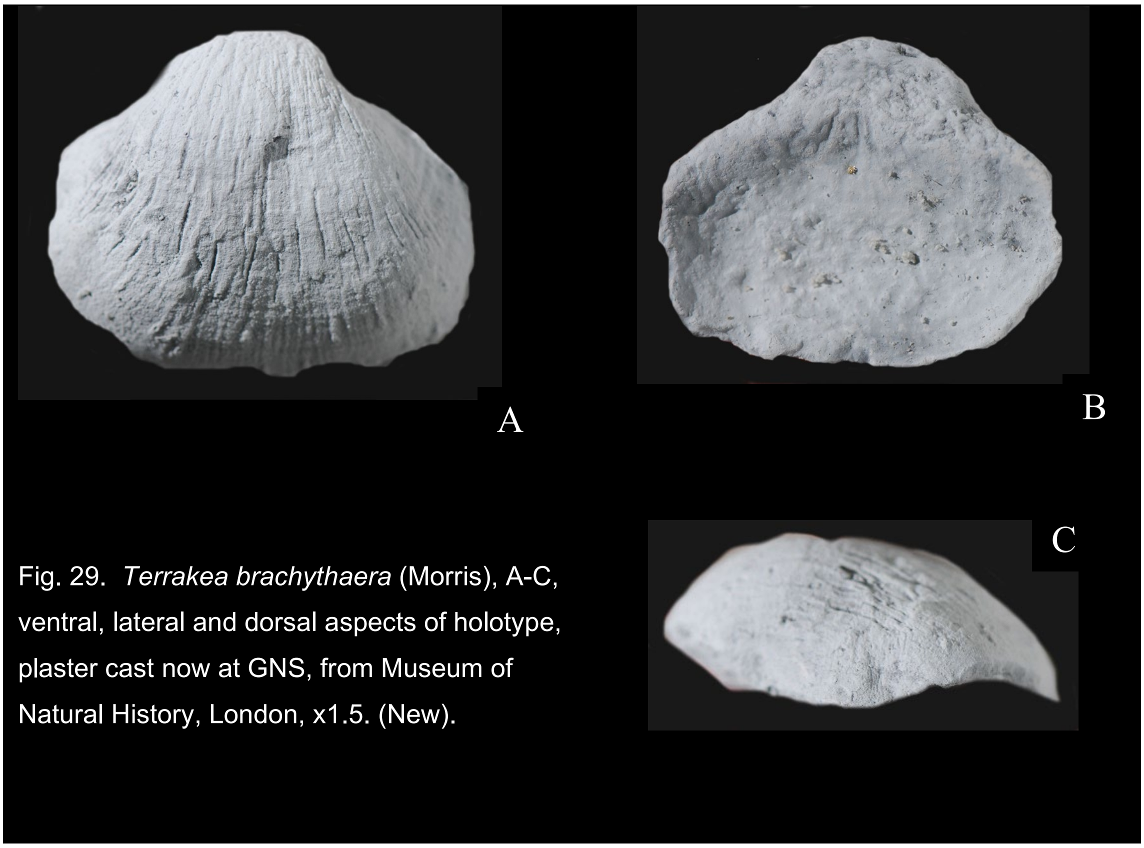


Fig. 29. *Terrakea brachythaera* (Morris), A-C, ventral, lateral and dorsal aspects of holotype, plaster cast now at GNS, from Museum of Natural History, London, x1.5. (New).

Morphology: Weight is given to the figuring by Briggs (1998) of a number of specimens from the Broughton Formation, regarded as source of the species as analyzed in Briggs (1998). This agrees with the earlier assessments by Hill (1950, p. 19) and Waterhouse (1964a), but Clarke (1987) later forcefully attacked Waterhouse (not Hill) for this assessment, asserting that the type specimen came from the Muree Sandstone, probably at Raymond Terrace in the north Sydney Basin. The matter is further discussed in Waterhouse (2001, p. 45).

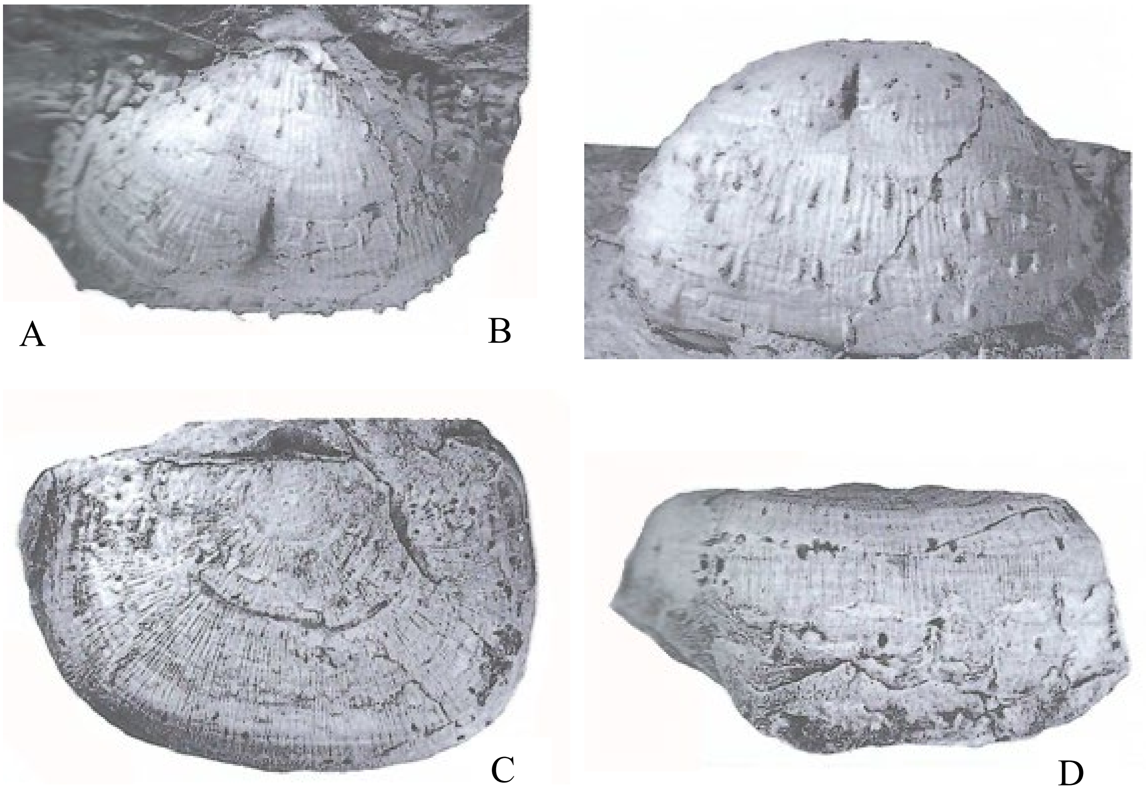


Fig. 30. *Terrakea brachythaera* (Morris). A, B, anteroventral and and posteroventral aspects of latex cast of ventral valve, UQF 75339. C, D, disc and trail of dorsal external mould UQF 75340. Specimens x1.5 from Kiama Sandstone Member, Broughton Formation, south Sydney Basin. (Briggs 1998).

However, Briggs (1998) surely erred in regarding his figured specimens as typifying the species, because they were comparatively transverse, whereas the designated type of *brachythaera*, as figured by Morris (1845) and refigured herein as Fig. 29 is more elongate. That does not mean the transverse specimens must be excluded – the species *brachytharea* was variable in shape, judged from the range of shapes to be found at highly fossiliferous stations. For that reason, the synonymy does not entirely follow Briggs, and the morphology is reinterpreted with closer attention to spinosity and shape. and variability, though accepting much of the synonymy in Briggs, which largely follows that provided by Waterhouse (1964a) in allowing variability in shape and thereby synonymizing *fragile* and *leve,* not only the original material, but Muir-Wood & Cooper specimens, excluded by Briggs (1998). It seems probable that the Briggs synonymy must be expanded, to include for example the Tasmanian material figured by Clarke (1987), rather than referring it to *etheridgei* as in Briggs (1998), because of the strength of spines. The inclusion of the Muir-Wood & Cooper material is important, because they provided lateral aspects for the ventral valve, though Briggs did give average proportions, and the shape of their specimens is more normal than that of the unusually transverse specimens emphasized by Briggs (1998).

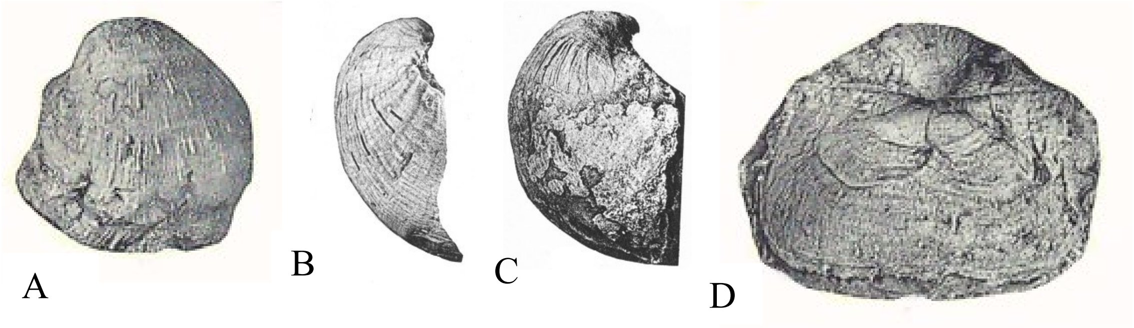


Fig. 32. *Terrakea brachythaera* (Morris). A, ventral valve, USNM 3633f . B, lateral aspect of specimen USNM 112149a. C, lateral aspect of USNM 3633b, called *fragile* in Dana (1847, 1849). A and C were called *fragile* by Dana. D, dorsal aspect of specimen with valves conjoined USNM 124094a, latex cast. Specimens x1 from Wollongong, south Sydney Basin, kept at Smithsonian Institute. (Muir-Wood & Cooper 1960).

Briggs (1998, p. 173) stated that *etheridgei* was less transverse than *brachythaera* with an evenly arched ventral valve with finer costae and shallower sulcus. His interpretation of *brachythaera* was shaped by his preference for figuring transverse and relatively short specimens for *brachythaera*. These are like the Booker specimen (1930, pl. 2, fig. 2) assigned to *brachythaerum*. But the type specimen for the species, as figured herein, is less transverse and more elongate than the Morris original. Briggs included comparatively high and narrow specimens figured by Booker (1930, pl. 1, fig. 1) as typifying *etheridgei,* but many *brachythaera* are of the same shape, including the shells figured as *fragile* by Muir-Wood & Cooper (1960, pl. 119, fig. 13, 18-20, 23). These have spines close to those of *etheridgei*. The form named *etheridgei* appears to come very close to *brachythaera*, except for its slightly coarser spines over the venter, and it may prove preferable to treat *etheridgei* as simply a contemporaneous subspecies or even variant of *brachythaera*.

There are various other references to *brachythaera* in the scientific literature, but these need to be further explored. For example the report by Etheridge Jnr (1892, p. 108, pl. 12, fig. 10-13) shows somewhat similar specimens, but need to be examined at first hand to determine distinctions from *elongata*. Similarly *Productus* sp. indet. of Etheridge in Jack & Etheridge (1892, pl. 13, fig. 3) needs inspection: it looks close to *elongata*.

Stratigraphy: This species characterizes the younger sediments of the Sydney Basin, especially the south, and is found in the upper Nowra beds according to Briggs (1998, p. 178) but he exaggerated the range of the species, claiming it occurred in the Oxtrack Formation and Moonlight Sandstone in the Bowen Basin, putative occurrences which are rejected herein. The species is found in the lower Blenheim Formation below the Scottville Member, though the density of dorsal trail spines could be a little greater than usual (Waterhouse & Jell 1983, pl. 2, fig. 1), and in the Malbina E fauna described by Clarke (1987).

Terrakea brachythaera quadrata Briggs, 1998

Fig. 33, 34

1964 *Terrakea* cf. *brachythaera* – Hill & Woods, pl. P6, fig. 1?, 2.
1972 *T. multispinosa* [not Dear] – Hill et al., pl. P6, fig. 1?, 2.
1986b *T. brachythaera* – Waterhouse, p. 50, pl. 12, fig. 1-3.
1998 *T. quadrata* Briggs, p. 181, Fig. 89A-G.

Diagnosis: Very close to *Terrakea brachythaera*, distinguished by slightly coarser spines over disc of both valves.

Neotype: The specimen UQF 74059 figured in Waterhouse (1986b, pl. 12, fig. 3) and herein as Fig. 33B, here designated. This specimen was cited in his synonymy by Briggs (1998) from the Flat Top Formation, southeast Bowen Basin. The nominated holotype AMF 96272 from lower middle Flat Top Formation, figured by Briggs (1998, Fig. 89C, D, E), is or was a specimen that belonged to the Queensland Museum, and has “disappeared”, along with so many other specimens figured by Briggs (1998) and so needs to be replaced by a neotype, unless the Briggs taxa are to be abandoned as nomen nuda.

Morphology: Briggs (1998, p. 183) allowed that this form “did show a partial return to the morphology of the early late Permian species *Terrakea brachythaera*, particularly in the proportions of the shell and the density of the posterior group of ventral spines”. That is correct – except it was hardly a return, but a local and geographically distinguished variation

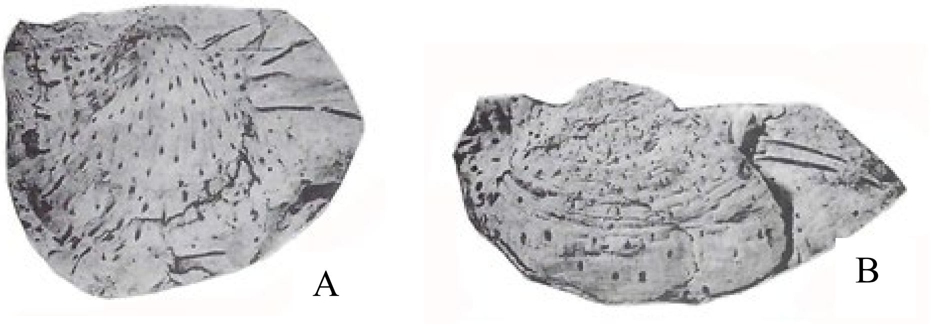


Fig. 33. *Terrakea brachythaera quadrata* Briggs. A, external mould, ventral valve UQF 74056. B, dorsal external mould UQF 74059, proposed as neotype. Specimens x2 from lower Middle Flat Top Formation. (Waterhouse 1986b).

with largely identical time-range. Only flexible tolerance grants validity to this taxon. He emphasized heavy internal thickening for internal features. The disc spines are similar in number to those of *brachythaera*, but a little thicker, and dorsal trail spines are more numerous, to suggest possible subspecific discrimination, but overall pattern as well as shape are similar. The emphasis on thickening is hardly consistent, given the fact that he allowed New Zealand specimens with very heavily reinforced features to belong to *brachythaera*, as well as other material with slender internal features. Such differences suggest a degree of variation that reflected substrate and the amount of activity in the form of wave and ocean current motion on the sea-floor, and availability of shell-building material.

Briggs (1998) referred one of the Dear specimens (1971, p. 18, pl. 7, fig. 10) figured as *multispinosa* to *Terrakea quadrata* Briggs but the figure shows fine ear spines and probably belongs to *multispinosa*.

The specimen of Hill & Woods (1964, pl. P6, fig. 1?) and Hill et al. (1972) was put in *multispinosa* Dear by Briggs (1998, p. 180-181) and separated from Hill & Woods (1964, pl. 6, fig. 2), which is not mentioned as far as I can discover in Briggs (1998), nor was it included in *multispinosa*. Both specimens, of comparable size and shape, are provisionally regarded as belonging to *quadrata* herein.

Stratigraphy: Briggs (1998) allocated *quadrata* to the *Echinalosia deari* Zone. His text appears

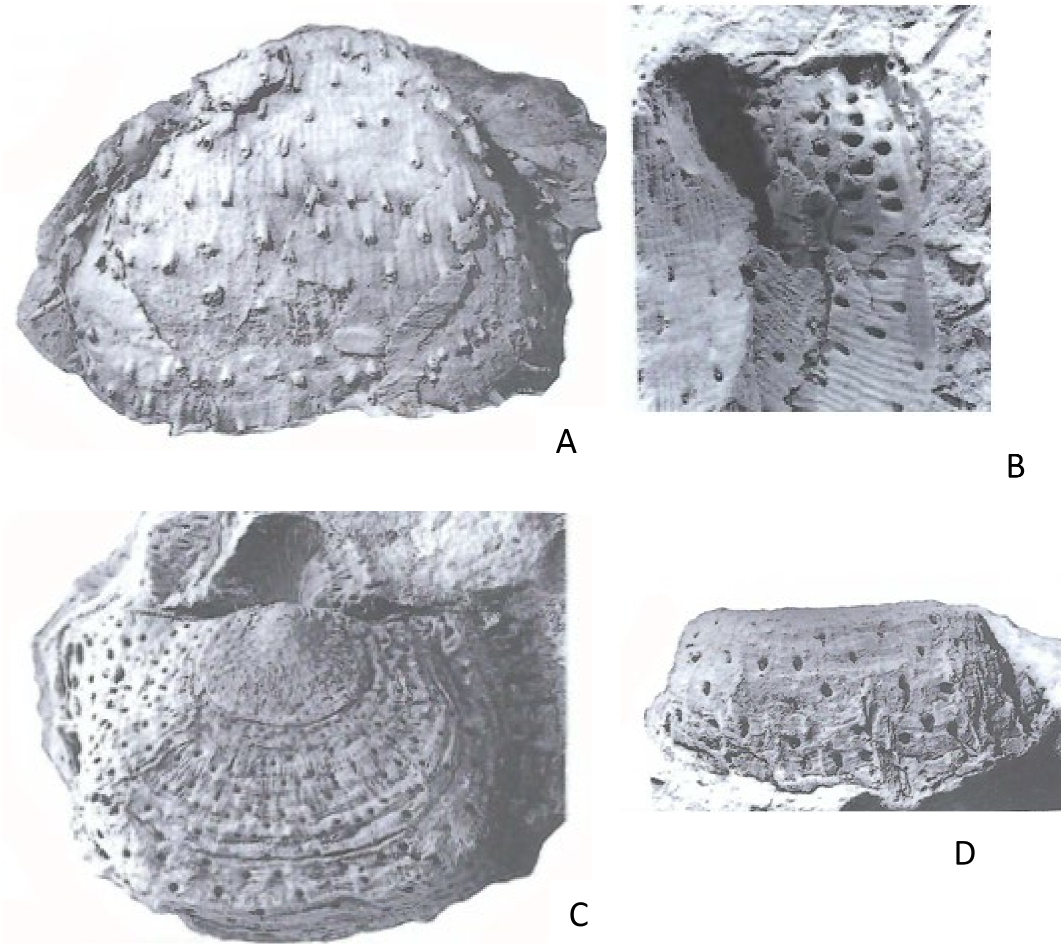


Fig. 34. *Terrakea brachythaera quadrata* Briggs. A, latex cast of ventral valve, AMF 96270, x1.5. B, part of ventral external mould, AMF 96271, x2. C, D, dorsal disc and anterior aspect of external mould of specimen with valves conjoined, holotype AMF 96272, x1.5. From Flat Top Formation. These were Queensland Museum specimens improperly registered as belonging to the Australian Museum, since "lost". (Briggs 1998).

to be riddled with inconsistencies and identification-errors over this placement. He claimed that *deari* occurred above the localities with *quadrata* in the Flat Top outcrops examined by Waterhouse (1986b), and that *quadrata* marked a "return" in morphology to *brachythaera* found in the supposedly much older Broughton beds of the Sydney Basin. The Briggs' so-called *deari* in his synonymy of Waterhouse (1986a, pl. 5, fig. 6, 7) has ventral spine tunnels and a more concave dorsal valve than restricted *deari,* which belongs to *Acanthalosia*, not *Echinalosia*, and his alleged *deari* from the lower middle Flat Top beds apparently belongs to the dominant *Echinalosia* in the Flat Top beds (= *glabra*), unless it turns out to be *Maxwellosia* *ovalis*. The accompanying fauna differs substantially from that found with true *deari*, as shown in the descriptions, figures and summary tables in Waterhouse (1986b, 1987a, b). The claim that *quadrata* was younger than *T. elongata* is denied by various lines of evidence, including the fact that he allowed that *brachythaera* was present as reported by Waterhouse & Jell (1983) in the north Bowen Basin. This occurrence underlies *elongata* in the Scottville Member. There seems little point in documenting the further inconsistencies and misidentifications. In brief, the lower middle Flat Top faunas, of which *quadrata* is part, shares a number of species that are also found with *brachythaera* in Tasmania, New South Wales, and Queensland, and the zone to which it belongs is part of the *Maxwellosia ovalis* Superzone, with *Terrakea brachythaera* an important constituent. The differences displayed by *quadrata* from *brachythaera* are minor, reflective of bottom conditions, not age.

Terrakea elongata elongata (Etheridge & Dun, 1909)

Fig. 35

1909 *Productus brachythaerus* var. *elongatus* Etheridge & Dun, p.7 in separate paper, p. 299 in volume, pl. 43, fig. 5, 7 (part, not pl. 42, fig. 2, 3, 7 = *etheridgei* or *brachythaera*).
1930 *Terrakea elongata* – Booker, p. 74.
1971 *T. elongata* – Dear, p. 16, pl. 4, fig. 10-12, pl. 5, fig. 1, 2. (This species was ascribed wrongly to Booker).
1982 *T. elongatum* – Waterhouse, pl. 12a.
1998 *T. elongata* – Briggs, p. 179.
2001 *T. elongata* – Waterhouse, p. 47 (part).
2022b *T. elongata elongata* – Waterhouse, p. 106, Fig. 8.

Diagnosis: Readily distinguished by the long trail and high lateral ventral flanks, dorsal disc gently concave. Spines thick over ears, posterior lateral flanks of ventral valve, and lateral shell and trail of dorsal valve, dorsal disc spines apparently more closely spaced than over the ventral valve, as in *brachythaera* and other species. Muscle scars clearly developed, dorsal median septum moderately long. Ventral disc spines mostly with long spine tunnels, whereas ventral anterior disc and trail spines are erect with short rounded non-prolonged entry points through the shell.

Holotype: AMF 35475 (originally F 2374) from Scottville Member, north Bowen Basin, figured by Etheridge & Dun (1909, pl. 43, fig. 5), SD Waterhouse (1964a, p. 82).

Morphology: This species is distinctive, and has not been reliably found elsewhere in Australia. Three subspecies may be recognized. As well as *Terrakea elongata elongata*, a subspecies with flatter disc has been discriminated as *T. elongata planidisca* Waterhouse, 2022b. The subspecies is found in rocks immediately above the Scottville Member with *T. elongata elongata*. The third subspecies as described below in found in the upper carbonates of the Mangarewa Formation, above faunas containing *Paucispinauria solida* (Etheridge & Dun). It has coarser costae and fewer spines than in *T. elongata elongata*, but has the same long trail, and is like *elongata elongata* in having a concave dorsal disc.

Fig. 35. *Terrakea elongata elongata* (Etheridge & Dun), anterior aspect of external mould of specimen x1.5 with valves conjoined. From Scottville Member near Clermont. (Waterhouse 1982).

Terrakea etheridgei Briggs appears to be slightly older than *T. elongata*, but shares a somewhat similar shape, and aspects of spine ornament, opening the possibility that *elongata* evolved from *etheridgei* rather than from *brachythaera*. But *etheridgei* is too poorly known to allow certainty. Various internal moulds identified as *elongata* by Etheridge & Dun (1909, pl. 42, fig. 2, 3, 7) and referred to *etheridgei* by Briggs (1998) are older than *elongata*, and could belong to *T. brachythaera*, but, allowing for the seriously deficient description of *etheridgei*, also fall close to *etheridgei,* as far as one can judge from internal moulds.

Stratigraphy: The species and subspecies *elongata elongata* is so far only found definitely in the Scottville Member of the north Bowen Basin. There have been other reports, but mainly on the basis of broken valves that fail to show the extended trail typical of the species and subspecies, so these reports are set aside as unreliable.

Terrakea elongata planidisca Waterhouse, 2022c

Fig. 36

2022c *T. elongata planidisca* Waterhouse, p. 152, Fig. 20-25.

Diagnosis: Dorsal disc large, wide and almost flat, trail geniculate.

Holotype: UQF 82758 from UQL 3515, Blenheim Formation, just above Scottville Member, figured by Waterhouse (2022c, Fig. 25D), and Fig. 36D herein, OD.

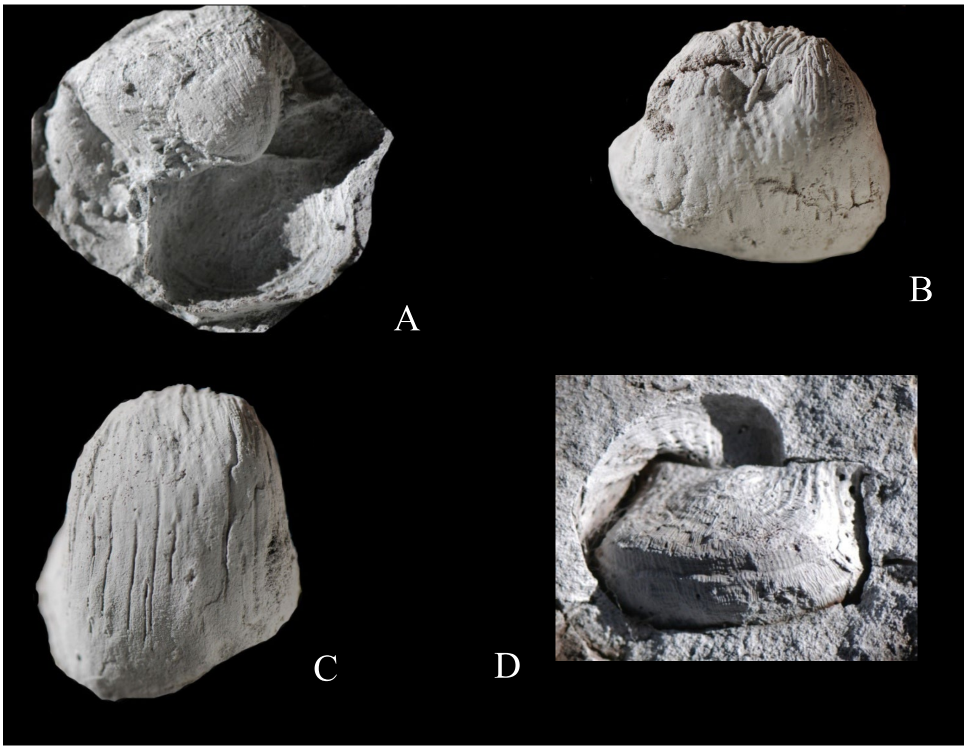


Fig. 36. *Terrakea elongata planidisca* Waterhouse. A, latex cast of posterior ventral and dorsal valve, UQF 82670. B, posterior aspect of ventral internal mould, UQF 82675. C, anterior aspect of internal mould of ventral valve, UQF 82676. D, oblique anterior aspect of specimen with valves conjoined, preserved as external mould and showing typically flat dorsal disc, holotype UQF 82758. Specimens x1 from immediately above the Scottville Member, north Bowen Basin. (Waterhouse 2022c).

Morphology: This species is close to *Terrakea elongata elongata*, and has flatter dorsal disc.

Stratigraphy: The subspecies is found in a layer overlying the Scottville Member, and belongs to an early level in the *Echinalosia* (*Unicusia*) *minima* Zone.

Terrakea elongata crassicosta n. subsp.

Fig. 37

1952 *Terrakea fragilis* [not Dana] – Fletcher, p. 12, fig. 1-3.
1952 *T. brachythaera* [not Morris] – Fletcher, p. 13.
1964a *T. elongata* – Waterhouse, p. 81, pl. 15, fig. 1-6, pl. 16, fig. 1, 7.
2002a *T. elongata* – Waterhouse, Table 17, p. 56.

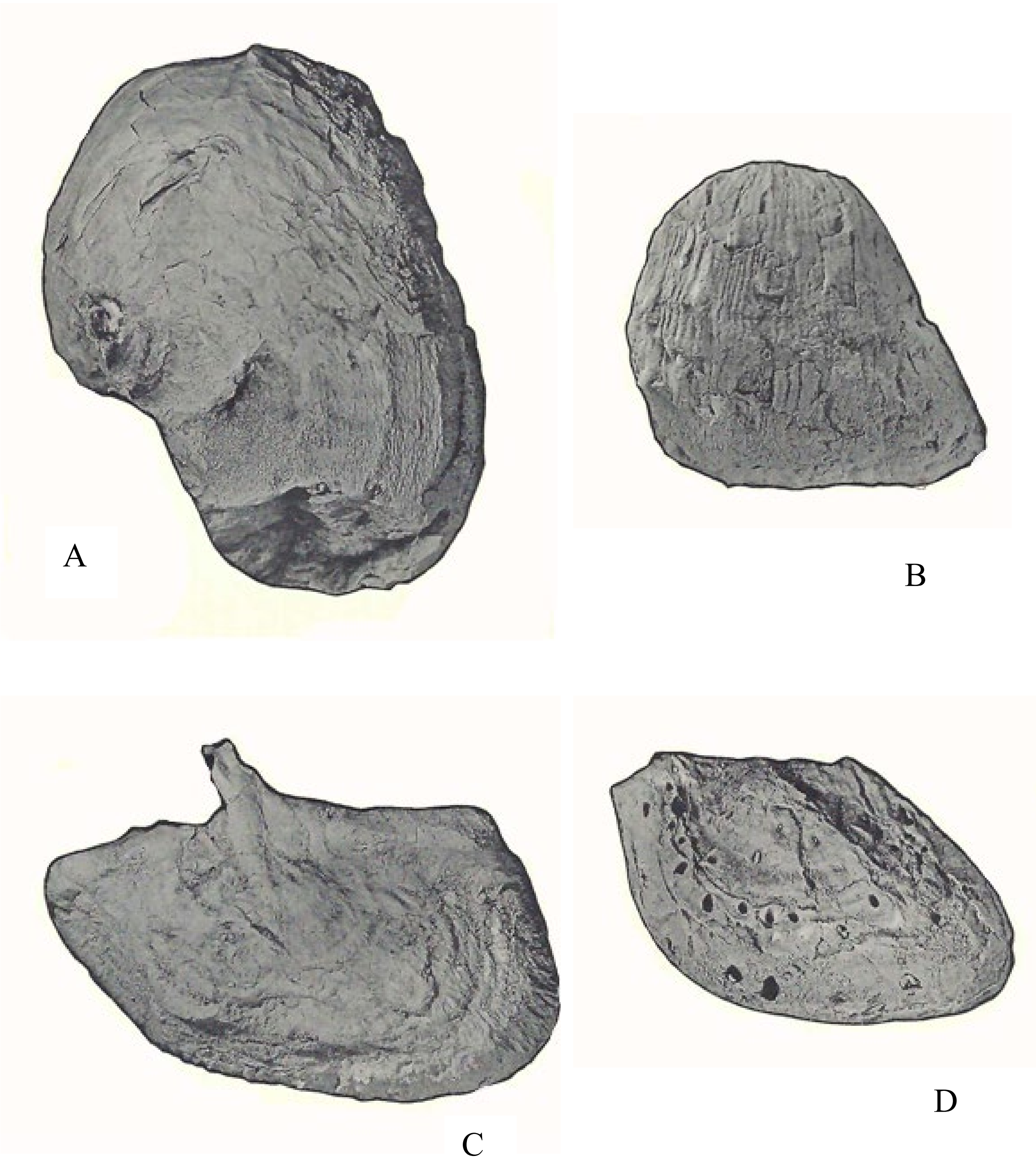


Fig. 37. *Terrakea elongata crassicosta* n. subsp. A , lateral view of decorticated ventral valve, BR 183, holotype. B, exterior of broken ventral valve BR 183. C, interior of dorsal valve BR 193. D, external mould of dorsal valve BR 749. From Mangarewa Formation, x1. (Waterhouse 1964a; Fig. 19A, B also figured by Fletcher 1952).

Diagnosis: Large shells with long trail and steep lateral ventral flanks, coarse costae measuring about four in 5mm, few well-spaced ventral disc spines and unusually few dorsal disc spines, dorsal trail spines as numerous as in type *elongata*. Muscle scars clearly defined and dorsal median septum moderately long.

Holotype: BR 183 figured by Fletcher (1952, pl. 1, fig. 3), Waterhouse (1964a, pl. 15, fig. 2, 3) and Fig. 37A herein, from the younger Mangarewa Formation, Wairaki Downs, New Zealand, here designated.

Stratigraphy: Extensive fossil collections were referred to a GS locality 3616, and the exact level is not certain, but was rated as coming from part of Mangarewa unit 8 towards the top of the formation, and above the level with *Paucispinauria solida*.

Terrakea densispinosa Waterhouse, 2021b

Fig. 38

1964a *Terrakea brachythaera* [not Morris] – Waterhouse, p. 73, pl. 12, fig. 1-8, pl. 13, fig. 1-12, pl. 14, fig. 1-13, pl. 37, fig. 1. Text-fig. 23c, 24D, E, 26-31.
1978 *T. brachythaera* – Suggate et al., text-fig. 4.5.4, 5, 11.
1981 *T. brachythaerum* – Speden & Keyes, pl. 5, fig. 4, 5, 11.
cf. 1989 *Echinalosia* cf. *minima* [not Maxwell] – Dickins, p. 75, pl. 3, fig. 1, 6 (part, not fig. 2-5, 11 = *Pseudostrophalosia cryptica* Waterhouse (not pl. 3, fig. 10, 12-21 = *Nonauria commarginalis*).
2001 *T. elongata* – Waterhouse, p. 47 (part).
2013 *T. brachythaera* [not Morris] – Waterhouse, Fig. 21.3 - 21.5.
2021b *Terrakea densispinosa* Waterhouse, p. 131, Fig. 6-9.
2022d *T. densispinosa* – Waterhouse, p. 275, Fig. 3, 4.

Diagnosis: Medium-sized subequilateral to elongate or transverse in outline, high and steep lateral ventral walls, ventral disc gently convex as a rule, rarely may be sulcate, dorsal disc gently concave to flat, trail long but not very long. Ears large, with numerous crowded erect and sturdy spines, with further spines emerging from the outer lateral shell. Ventral spines more numerous than usual, more than twenty five along a commarginal row; appear to be of much the same density over the posterior trail, not well known for anterior trail. Dorsal spines just as numerous over the disc as in other species such as *brachythaera* and *elongata*, and also numerous over the short trail. Muscle scars well defined, median dorsal septum broad posteriorly, long.

Holotype: BR 66 from uppermost Mangarewa Formation, Wairaki Downs, New Zealand, as figured by Waterhouse (1964a, pl. 13, fig. 12; 2013, Fig. 21.3B; 2021b, Fig. 6B), and Fig. 38B herein, OD.

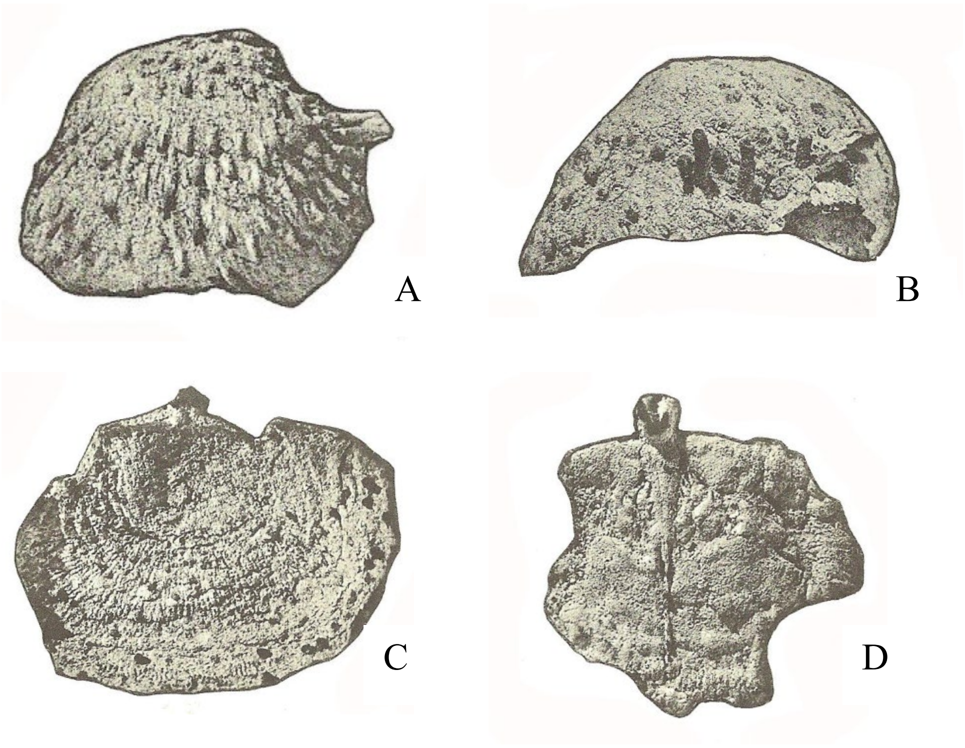


Fig. 38. *Terrakea densispinosa* Waterhouse. A, PVC external cast of immature specimen BR 80, x3. B, holotype, lateral aspect of PVC cast of ventral valve, BR 66, showing bases of crowded ear spines, x2. C, PVC cast of dorsal external mould BR 146, x2. D, PVC cast of dorsal interior, BR 923, x2. Specimens from uppermost Mangarewa Formation, Wairaki Downs, New Zealand, x2. (Waterhouse 1964a).

Morphology: The species has been illustrated and described by Waterhouse (1964a), with summary in Waterhouse (2021b). It may be interpreted as a descendent of the subspecies of *elongata* found in underlying beds, with abbreviated trail, and spines close in spacing and density, except for the greater number of spines along a reduced number of commarginal rows for the dorsal trail. Dorsal internal detail is similar.

Stratigraphy: This is the youngest of well-preserved *Terrakea* and is found not only in the late Capitanian upper Mangarewa Formation of New Zealand, but in the correlative *Ingelarella costata* Zone of the northern and southwestern Bowen Basin (Waterhouse 2022d). The associated fauna in clastics at the very top of the Mangarewa Formation in New Zealand includes *Johndearia* aff. *isbelliformis*, *Ingelarella costata*, *I. havilensis* (not figured), *Maorielasma imperatum* and several palaeotaxodont bivalves. These are classed as belonging to the *Ingelarella costata* Zone (Waterhouse 2021b).

Paucispinaurian gen. & sp. indet. A

Fig. 39A-C

1967 *Terrakea* sp. Waterhouse, p. 80, Fig. 5A, B, C.

Three specimens were described from the Pig Valley Limestone in the Nelson district of New Zealand, apparently belonging to the *brachythaera* complex, but some critical aspects are not preserved.

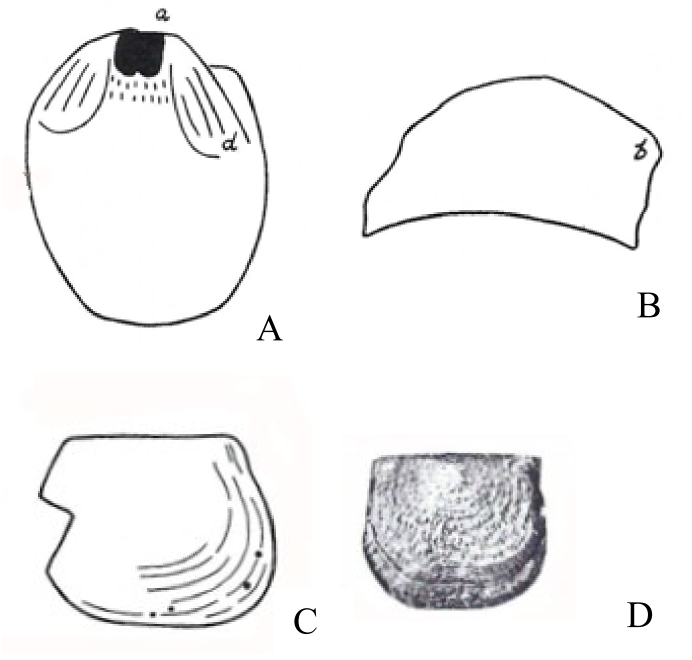


Fig. 39. Late Permian paucispinaurians from New Zealand. A-C, Paucispinaurian gen. & sp. indet. A from Pig Valley Limestone, x1.5. A, ventral valve BR 216, a = adductor scars, d = diductor scar. B, lateral aspect of same specimen, b at umbo. C, external mould of dorsal valve BR 123. (Waterhouse 1967). D, Paucispinaurian gen. & sp. indet. B, OU 2602 dorsal external mould x1 from Wairaki Breccia equivalents near Mossburn. (Hyden et al. 1982).

Paucispinaurian gen.& sp. B

Fig. 38D

A dorsal valve from what was called the Countess Formation was figured from near Mossburn, and putatively correlated with the Wairaki Breccia of Wairaki Downs, further to the south. The valve is geniculate with many fine disc spines and a short geniculate trail, and could represent the youngest form of *Terrakea*, unless it has been derived. With only a dorsal valve figured, its generic position is insecure, and the species indeterminable. The stratigraphic position is further discussed in the section of *Betaneospirifer*, in a forthcoming study. This though found in the same Countess beds at Mossburn appears to have been possibly derived, because it appears to be identical with material found in the somewhat older Glendale Limestone.

PAUCISPINAURIANS AND ALLIES FROM THE NORTHERN HEMISPHERE

NORTH AMERICA

UNITED STATES

Various occurrences in the United States are reviewed in Waterhouse (2013, pp. 461, 462).

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

Fig. 40, 41

Diagnosis: Characterized by presence of very large spines over the inner ventral ears, extending onto posterior lateral slopes. Dorsal spines uniformly fine and trail spines of both valves fine. Dorsal dimples conspicuous.

Type species: *Grandaurispina kingorum* Muir-Wood & Cooper, 1960, p. 305 from Word Formation of Glass Mountains, Texas, OD.

Fig. 40. *Grandaurispina kingorum* Muir-Wood & Cooper, oblique view of silicified ventral valve and ear. Very large spines arise from the concavity between ears and umbonal slopes, and may show fine projections, with one arrowed in this figure. Silicified specimen BR 3052, x2. from Appel Ranch Member (Capitanian), west Texas, United States. (Waterhouse 2013).

Other species include *Grandaurispina elongata* Cooper & Grant and *G. gibbosa* Cooper & Grant (which also approaches *Terrakea*).

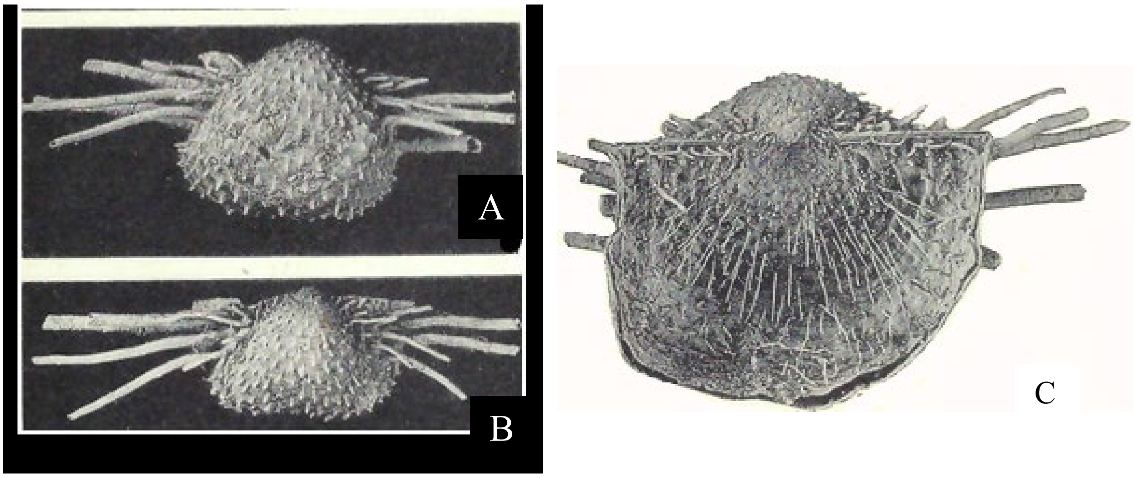


Fig. 41. *Grandaurispina kingorum* Muir-Wood & Cooper. A, B, ventral and posterior aspects of silicified ventral valve USNM 123455c, x0.9. C, dorsal view of silicified specimen with valves conjoined, USNM 123454, holotype, x2. From Word Limestone no. 3, Texas. (Muir-Wood & Cooper 1960).

It was claimed by Waterhouse (1971) that forms closely allied to *Terrakea* had been allocated to a different genus *Grandaurispina* Muir-Wood & Cooper, 1960 recognized in the late Early Permian and Middle Permian of United States. Cooper & Grant (1975, p. 1162) tried to refute the alliance, and in turn, Briggs (1998, p. 163) was dismissive of their objections. Some of their analyses relied on an inadequate understanding of the morphology and variation displayed by *Terrakea* and east Australian allies, concerning the cardinal process and dorsal median septum. Some species described as *Grandaurispina* appear to lack radial ornament, but this is clearly developed in other Texan species, such as *G. crassa* as illustrated in Cooper & Grant (1975, pl. 438). But Cooper & Grant (1975) raised two aspects which require further consideration. According to Cooper & Grant (1975), *Grandaurispina* differed from *Terrakea* in displaying dimples in front of ventral and dorsal spines. Yet none of their numerous figures of ventral valves for *Grandaurispina* show such dimples, and dimples are not visible in the few specimens which I collected in the Glass Mountains of Texas, nor are dimples present over the ventral valve of *Terrakea*. That objection is therefore set aside. There are dorsal dimples over Australasian *Terrakea* and United States *Grandaurispina*. A second difference lay in the nature of spine bases within the ventral shell, and this objection carries more weight. The spine bases form long spine tunnels in *Terrakea*, which were said to be absent from *Grandaurispina*. This would surely constitute a significant difference. As far as I can see, the observation by Cooper & Grant (1975) was correct: ventral spines in *Grandaurispina* appear to pass directly into the lumen of the visceral disc. Moreover the ventral disc spines have slightly elongate and rather swollen bases on some specimens, somewhat overtonioid in appearance. Yet the cardinal process and various internal details involving dorsal septum and papillation are comparable between suites of United States *Grandaurispina* and Australian *Terrakea*, and external appearance is close. What cannot be adequately compared is the nature of muscle scars, very poorly known for the American species. At present, the two suites are regarded as cotribal, as also concluded by Briggs (1998) and Brunton et al. (2000). But that admittedly downplays the significance of the ventral spine bases. Whether that reflects an evolutionary difference or an ecological one requires further study. Should the difference prove valid in an evolutionary sense, Grandaurispininae Lazarev, 1990 would embrace the genera from United States, as distinct from the Australian genera, and familial position would require further consideration**.** It was allowed by Muir-Wood & Cooper (1960) and Cooper & Grant (1975) that ventral muscle scars were poorly preserved, often the adductors being faint and seldom dendritic, and virtually nothing being ascertainable of diductor scars: the same is true of material from west Texas that I collected. This either is signifying a significant difference from Australian paucispinaurians, or as one possible alternative, implies that the inner shell of the ventral valve has been lost from specimens of Texas, and not replaced properly by silica. In that case, spine tunnels would be also lost, together with much of the muscle scars and papillation. Provisionally, this explanation is adopted. The matter might be most easily resolved by preparing Glass Mountains material that has come from clastic sediment, and has not been silicified.

Genus ***Appelinaria*** Waterhouse, 2013

Fig. 42

Diagnosis: Ventral ear spines and those of posterior lateral slopes strong as in *Terrakea* and spines of posterior-lateral shell on dorsal valve strong. Trail spines of each valve less robust. Dorsal dimples conspicuous.

Type species: *Grandaurispina crassa* Cooper & Grant, 1975, p. 1164 from Word and Appel Ranch Members, Glass Mountains, Texas, OD.

Other species: Possibly *Grandaurispina undulata* Cooper & Grant and *G. rudis* Cooper & Grant. The dorsal valve is not well known for some of these species, but they lack very large ear spines and large trail spines, as far as can be seen.

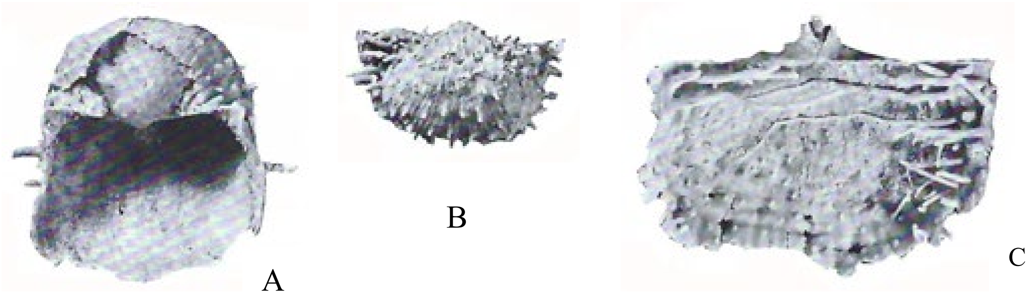


Fig. 42. *Appelinaria crassa* (Cooper & Grant). A, posterior internal view of silicified ventral valve USNM 150018k x1. B, posterior view of silicified ventral valve USNM 150018c, holotype, x1. C, dorsal aspect of silicified dorsal valve USNM 150018q, x2. From Appel Ranch Member. (Cooper & Grant 1975).

Discussion: These species come close to *Terrakea,* and differ only to a minor extent from that genus. The designated type species differs from *Grandaurispina* Muir-Wood & Cooper, 1960 in many respects. The ventral ear brush of spines is less developed, with thinner and fewer spines, and ventral body spines are comparatively thick. In the dorsal valve, the posterior lateral spines are much thicker than the fine spines over the rest of the valve, and approach in thickness those of the ventral ears and ventral lateral slopes, whereas dorsal spines in *Grandaurispina* are all slender. The dorsal posterior lateral spines are directed inwards across the dorsal disc, whereas comparably placed spines in *Terrakea* and allies appear to be directed dorsally. The shell is highly vaulted, with steep ventral lateral walls, ribbing is well defined, and the cardinal process very sturdy.

No Australian genus is exactly comparable, and all species lack the sturdy postero-lateral spines of the dorsal valve. *Terrakea* Booker, 1930 has a strong burst of spines over the ventral ears and lateral slopes, and dorsal spines are stronger over the anterior trail, whereas they are only moderately thick over the trail in the American species. *Paucispinauria* Waterhouse, 1983b differs in the same way, and its postero-lateral ventral spines are thick but few in number, approaching those of *Appelinaria*. Ventral body spines are thick and ribs strong in *Paucispinauria,* but shells are more transverse with thinner visceral disc and the cardinal process less sturdy. The dorsal interior of *Appelinaria* has a long dorsal septum, but muscle scars and brachial shields are not well preserved.

Genus ***Bellaspinosina*** Waterhouse, 2013

Fig. 43

Diagnosis: Spines fine over both valves and subuniform, short elongate bases over ventral disc, otherwise erect. Spines over posterior lateral slopes inside the ventral ears moderately strong and evenly spaced. Ears small, disc elongate, ventral valve strongly arched.

Type species: *Grandaurispina bella* Cooper & Grant, 1975, p. 1162 from Willis Ranch and Appel Ranch Members of Word Formation, Glass Mountains, Texas, OD.

Other species: *Grandaurispina rara* Cooper & Grant, 1975, p. 1169 from the Appel Ranch Member is congeneric, and ?*G. belliformis* Cooper & Grant, 1975 is probably related.

Discussion: This genus is distinguished from other Texan paucispinaurians by the uniform to subuniform nature of the crowded and numerous spines over both valves. *Bellaspinosina* is characterized by its almost uniformly fine spines over both valves. It is thus readily distinguished from *Grandaurispina* Muir-Wood & Cooper, which has prominent and thick halteroid spines along the umbonal slopes of the ventral valve, and differs from *Appelinaria* which has thicker ventral spines, stronger radial ribs and spines of two different diameters over the dorsal valve. In the nature of the spines, the genus comes closest to *Saetosina* Waterhouse, 1986b, based on *Terrakea multispinosa* Dear, 1971 from the Flat Top Formation of the southern Bowen Basin, Queensland, Australia, with species of Wordian and Capitanian age. *Saetosina* shows similarly dense but finer spines over both valves, and although the ventral spines tend to be slightly more prostrate over the ventral disc, and the body shape is more transverse with larger ears and thinner visceral disc, such differences need not be of generic significance, allowing the possibility that either both arose from common stock, or that either species evolved from the other. But there are further, if slight, differences. The spines on the American form are more regularly disposed over disc and trail, whereas those of the Australian species of *Saetosina* tend to show banding, with slight differences in diameter and even bands with few or no spines (see Dear 1971, pl. 7, fig. 2b; Waterhouse 1986b, pl. 13, fig. 9), and the dorsal valve of *Saetosina* bears less conspicuous dimples and pustules. In addition, the dorsal interior of *Bellaspinosina* is close in some aspects to that of North American *Grandaurispina*, suggesting that the genus may have arisen from that genus, rather than by migration. It displays slightly more emphasized posterior dorsal hinge ridges and postero-lateral ridge, more elongate tubercles over the dorsal anterior and less emphasized adductor scars (perhaps affected by incomplete silicification), compared with *Saetosina*.

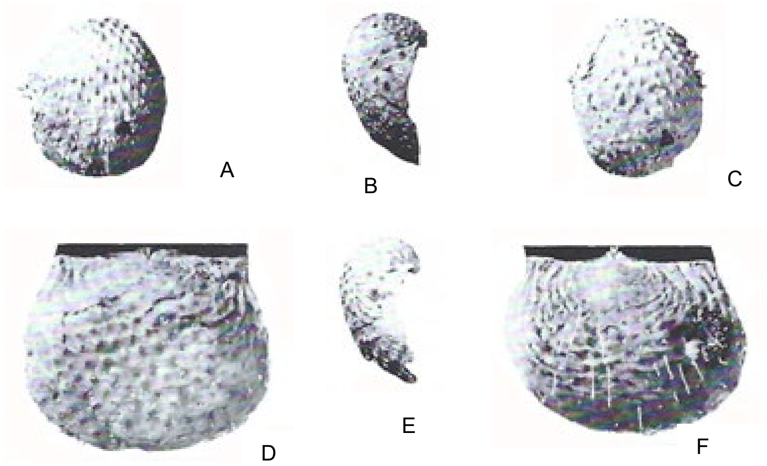


Fig. 43. *Bellaspinosina bella* (Cooper & Grant). A, B, ventral and lateral aspects of silicified ventral valve USNM 149988p, x1, holotype. C, E, ventral and lateral aspects of silicified ventral valve USNM 149988b, x1. D, silicified dorsal valve USNM 149988i, x2. F, silicified dorsal valve USNM 149988g, x2. From Willis Ranch Member, Word Formation. (Cooper & Grant 1975).

The genus *Vagarea* Waterhouse, 2013, p. 420 was proposed for *Grandaurispina*? *vaga* Cooper & Grant, 1975, p. 1172 from the Cathedral Mountain Formation of the Glass

Mountains, older than other paucispinaurians from the Glass Mountains, and differing from them in the lack of fine radial ornament. With numerous erect spines over both valves, especially fine and hair-like over the dorsal valve, they appear to be overtonioid or marginiferid, but on the other hand could prove to be allied to *Holotricharina* Cooper & Grant, which has only very fine capillae, as seems to have been the conclusion of Cooper & Grant (1975). Although the numerous and closely spaced spines over both valves of *Holotricharina*, and the nature of the posterior dorsal hinge ridges and strong anterior papillae suggest a position within Overtonioidea Muir-Wood & Cooper, Cooper & Grant stressed the close relationship of *Holotricharina* to *Grandaurispina* Muir-Wood & Cooper, 1960, as indicated by the linoproductiform cardinal process, and fine capillae.

CANADA

A possible *Terrakea* was recorded by Shi & Waterhouse (1996, pl. 17, fig. 21, 22, 24) from Sakmarian faunas of the Jungle Creek Formation of Yukon Territory, but ventral ornament is too poorly known to allow any closer generic determination. *Terrakea arctica* Waterhouse, 1971 was reassigned to *Cancrinella* in Waterhouse (2020, p. 210).

RUSSIA

Fig. 44, 45

Genus ***Pinegeria*** Waterhouse, 2001

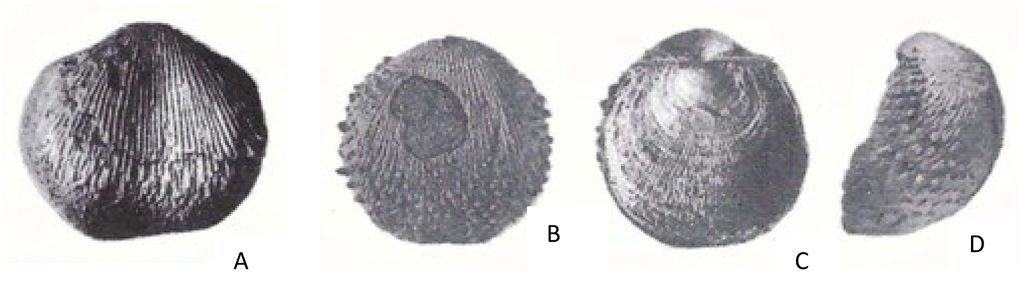


Fig. 44. *Pinegeria pinegensis* (Grigorieva). A, ventral valve PIN 1120/643. B-D, ventral, dorsal and lateral aspects of PIN 1120/771, holotype. Specimens x1, from Kazanian Stage, Russia. (Sarytcheva 1977).

Six species from Russia, including two with a query, were assigned to *Terrakea* Booker in Sarytcheva (1977), and discussed in Waterhouse (2013, p. 463). Of these species, *Terrakea*? *hemisphaeroidali*s (Netschajew 1894), would appear to be closer to *Globiella* Muir-Wood & Cooper, and the firmly costate and densely spinose *T.*? *pingenensis* Grigorieva (see Sarytcheva 1977, p. 144, pl. 21, fig. 10, pl. 22, fig. 1-4), the type species of *Pinegeria* Waterhouse (2001, p. 49) as shown in Fig. 44, is close in some respects, and should be classed as Lirariinae Waterhouse (2013, p. 332). This in turn was placed in Anidanthidae Waterhouse, but I have reservations about this position, noting a close approach of its constituent genera to genera classed as Engellini Waterhouse, 2013, p. 431, placed in Paucispinauriidae Waterhouse. The other species are described and illustrated in Sarytcheva (1977), but the descriptions do not contain references to some morphological detail now deemed critical for generic placement, and the photographs were not reproduced to modern standards. They therefore invite closer inspection. The one exception is provided by *Terrakea belokhini* Ganelin, referred to a separate genus*, Spargospinosa*.

Genus ***Spargospinosa*** Waterhouse, 2001

Fig. 45

Diagnosis: Characterized by distinct row of spines along the ventral hinge, otherwise few over ears and lateral slopes, spines in quincunx over ventral disc and trail, of moderate strength with long spine tunnels. Dorsal spines well developed over posterior lateral slopes and trail, finer over disc. Trail geniculate, median septum long.

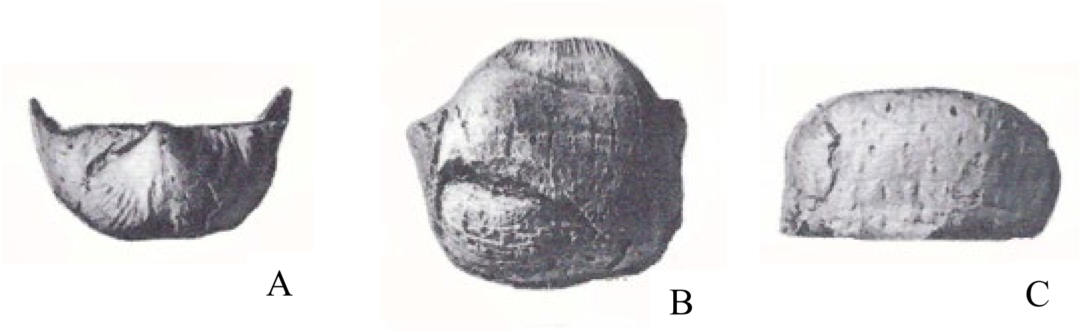


Fig. 45. *Spargospinosa belokhini* (Ganelin). A, posterior aspect of ventral valve PIN 2834/339, showing hinge spines. B, ventral aspect PIN 2834/349, holotype. C, dorsal trail, PIN 2834/ 332. Specimens x1 from Omolon beds of northeast Russia. (Sarytcheva 1977).

Type species: *Terrakea belokhini* Ganelin in Sarytcheva (1977, p. 141, pl. 21, fig. 1-3, Fig. 80) from Omolon level, Kolyma-Omolon of northeast Russia, OD.

MONGOLIA

Fig. 46

Further species were assigned to *Terrakea* by Manankov (1992), but as assessed in Waterhouse (2013, pp. 462, 463) may not be that close to that genus, other than possibly *T. echinata* Manankov (1992, p. 72, pl. 16, fig. 9-13), from the middle Permian Uldzinsk Suite of northwest Mongolia. This has a number of ear spines, and a mix of coarse and fine spines over both valves, and there is some approach to *Grandaurispina.*

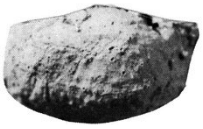


Fig. 46. *Terrakea echinata* Manankov, ventral valve, from Tsaganui, southeast Mongolia. (Manankov 1992).

JAPAN

Fig. 47

Of the species reported as *Terrakea* from Japan by Tazawa (2008a, b, 2012), few can be securely referred to *Terrakea* or allies. *Terrakea japonica* Tazawa 2008b has strong radial ribs, and numerous erect ventral spines without elongate bases, crowded over the ears, and so appears to be related to Lamiproductinae Liang, 1990, as discussed in Waterhouse (2013, p. 335) and further discussed in Appendix 1 (p. 229).

Terrakea yanagidai Tazawa (2008c) is moderately close to Paucispinauriinae, displaying fine distinct ribs, ventral spines with elongate bases and spine tunnels, and erect

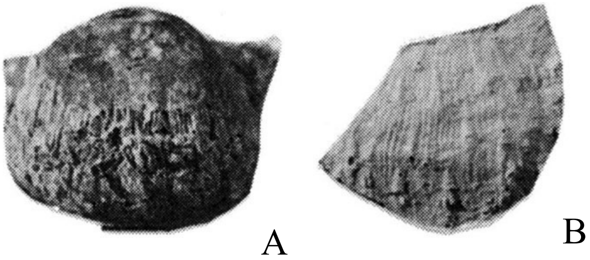


Fig. 47. *Terrakea yanagidai* Tazawa . A, ventral valve. B, ornament over ventral disc. Specimens x2 from Mizukoshi area of Hida Gaien Belt, Japan. (Tazawa 2008c).

dorsal spines. Spines were reported as being numerous over the ears, though not evident in provided figures, suggesting they were few, as in *Paucispinauria*. Other material allocated to *Terrakea* from Japan is briefly discussed in Waterhouse (2013, p. 463).

Subfamily **MAGNIPLICATININAE** Waterhouse, 2001

Tribe **MAGNIPLICATININI** Waterhouse, 2001

[Magniplicatinini Waterhouse, 2001, p. 49].

Diagnosis: Commarginal rugae moderately to strongly developed, otherwise close to Paucispinauriini in costation. Spines not differentiated to same extent as in Paucispinauriini, but interior much the same.

Discussion: Compared with Auriculispinidae Waterhouse, 1986b, disc spine bases are generally more elongate and transverse rugae are stronger. Ventral adductors are striate and especially dendritic throughout ontogeny (Shi & Waterhouse 1996, p. 96), at least in Permian members, and are not posteriorly impressed into the posterior wall, whereas ventral adductor scars are striate and subelongate rather than dendritic at early into full maturity in several Auriculispinidae, and are impressed into the posterior wall. In a number of instances, the adductor scars being scarcely if at all perceptible in paucispinaurians, especially in Tribe Magniplicatinini, because they tend to be masked by costae and rugae from the exterior, whereas auriculispinids developed a palpably visible adductor platform. Brunton et al. (2000, pp. 533, 543) assigned *Cancrinella* to Grandaurispininae (ie. Paucispinauriinae), presumably because it had dorsal spines, and *Magniplicatina* to Auriculispininae, presumably because it has no dorsal spines, but the two genera are so close that the difference in dorsal spinosity would seem to be of generic importance only. *Magniplicatina* is now known to be widespread in the northern hemisphere, including the Glass Mountains of Texas, United States. Such species were assigned to *Cancrinella* by Cooper & Grant (1975), until reassessed by Brunton et al. (2000, p. 544). To judge from the fossil record, *Magniplicatina*, which includes various species previously referred to *Cancrinella*, is more widespread and more numerous than other genera of Paucispinauriinae during Permian time.

Subtribe **MAGNIPLICATININAI** Waterhouse, 2001

[Nom. transl. Waterhouse 2013, p. 423 ex Magniplicatinini Waterhouse, 2001, p. 49].

Diagnosis: Commarginal wrinkles equally developed on both valves. Lower Carboniferous (Visean) to Upper Permian (Changhsingian).

Genera: *Magniplicatina* Waterhouse (syn. *Helenaeproductus* Lazarev fide Brunton et al. 2000), *Auritusinia* Waterhouse, *Commarginalia* Waterhouse, *Globicorrugata* Waterhouse, *Rugania* Waterhouse, ?*Teleoproductus* Li Li.

Discussion: Subtribe Cancrinellinai has rugae mostly over the dorsal valve, with rugae absent from the ventral disc. An allied tribe Engellinini is of Lower Carboniferous age and has numerous ventral ear spines and disc spines may be in regular quincunx, or rare and scattered. The valves are less rugose.

Genus ***Magniplicatina*** Waterhouse, 1983b

Diagnosis: Closely costate shells with ventral spines in one, two to three, rarely four rows close to hinge, arranged in quincunx over venter with posteriorly prolonged bases, may be erect over trail, dorsal valve without spines, both valves covered by rugae. Muscle scars dendritic from early ontogeny.

Type species: *Cancrinella magniplica* Campbell (1953, p. 7) from Ingelara Shale (Roadian), southwest Bowen Basin, OD.

Discussion: *Magniplicatina* is a very widespread genus, and apparently long-lived. Previously many species had been identified with *Cancrinella* Fredericks, 1928, but this genus has dorsal spines and lacks ventral disc rugae (Waterhouse 2013). Species allied to *Magniplicatina* in the Early Carboniferous, especially Visean, called *Globicorrugata*, have thicker visceral disc and bilobed rather than trilobed cardinal process (Waterhouse 2013, p. 424).

Magniplicatina dunstani Waterhouse, 2015b

Fig. 48, 49

1872 *Productus cora* [not d'Orbigny] – Etheridge Snr, p. 328, pl. 15, fig. 1, 2.

1872 *Strophomena rhomboidalis* var. *analoga* [not Phillips] – Etheridge Snr, p. 331, pl. 15, fig. 3, pl. 16, fig. 7, pl. 18, fig. 1? (part, not pl. 15, fig. 5 = *Protoanidanthus pokolbinensis*).

1892 *S. rhomboidalis* var.*analoga* Etheridge Jnr, p. 245, pl. 12, fig. 9 (part, not pl. 8, fig. 8 as reapeated from Etheridge 1872, pl. 18 (not pl. 8), pl. 40, fig. 6 = indet.)

1892 *P. cora* – Etheridge Jnr, p. 248, pl. 12, fig. 14 (part, not pl. 13, fig. 1, pl. 38, fig. 11 = *Costatumulus farleyensis*).
2015b *Magniplicatina dunstani* Waterhouse, pp. 49, 68, Fig. 14A, B, Fig. 15A, B.

Diagnosis: Small little inflated shells, with small ears, close-set fine wrinkles and fine capillae, ventral spines emerging from short and slender bases over body of shell. No spines seen on dorsal valve.

Holotype: QMF 14433, upper Rammutt Formation (Asselian), Gympie, figured in Waterhouse (2015b, Fig. 15A) and herein as Fig. 49A, OD.

Fig. 48. A, rock slab with dorsal valve of *Protoanidanthus pokolbinensis* Briggs (UQF 46607) (see herein p. 96), and *Magniplicatina dunstani* Waterhouse (UQF 46606, x2), including a ventral valve external mould with row of prominent hinge spines. Rammutt Formation, Gympie. (Waterhouse 2015b).

Morphology: Ventral valve gently convex with no sulcus or median flattening, ventral umbo broad with angle of 110-120° and extended little beyond hinge, ventral umbonal slopes low, gently convex, cardinal extremities subangularly obtuse at 110°, but acute with angle of 50-60° in some specimens, ears gently convex, maximum width of shell placed near mid-length. Dorsal valve gently concave with concave ears, short semi-geniculate trail. Both valves covered by fine even capillae, numbering twenty two to twenty eight in 10 mm anteriorly; increase on ventral valve by intercalation, crossed by nineteen to twenty fine wrinkles on both valves, with rounded crests and evenly concave interspaces, covering entire dorsal valve and most of ventral valve, but absent from anterior ventral valve and trail. Ventral spines fine, cover entire valve, erect in two irregular rows over posterior ears; some erect over visceral disc and trail, most body spines emerge from slender slightly raised spine bases extended posteriorly for some 2-3mm. Dorsal valve bearing large pits along hinge, and lacking spines. Visceral disc less than 1mm thick in mature specimens, possibly a little compressed.

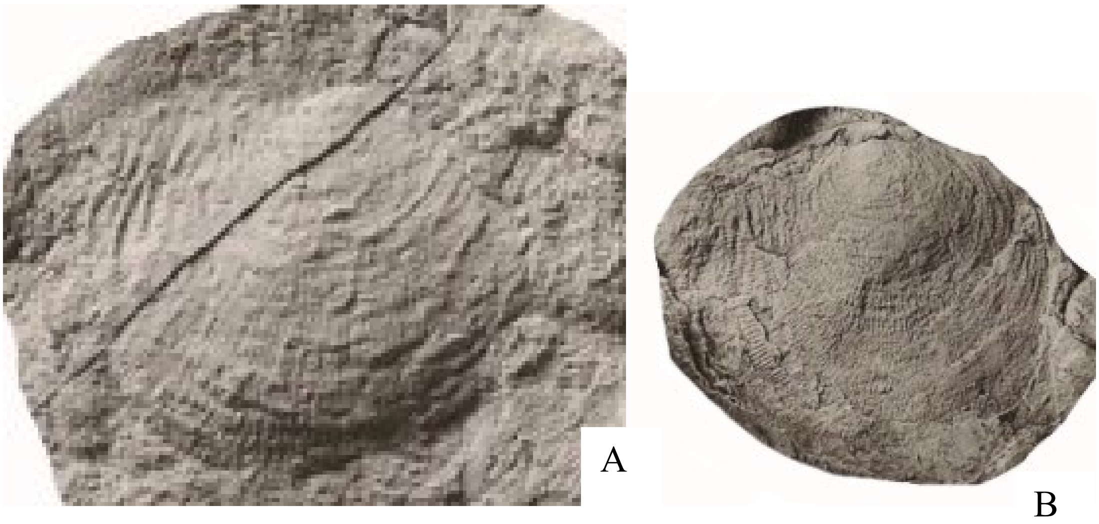


Fig. 49. *Magniplicatina dunstani* n. sp. A, ventral valve QMF 14433, holotype, x.2.5. B, dorsal external mould QMF 17761, x3. From Rammutt Formation (Monkland beds), Gympie. (Waterhouse 2015b).

Several species of *Magniplicatina* from Permian faunas in east Australia and New Zealand are close in overall size, shape and ornament, but are distinguished by having much stronger and in some cases fewer commarginal wrinkles.

Stratigraphy: This is a common species in the Monkland beds near Gympie in southeast Queensland.

Magniplicatina undulata Waterhouse, 1986b

Fig. 50, 51

1950 *Cancrinella farleyensis* [not Etheridge & Dun] – Hill, p. 14, pl. 7, fig. 7a, b, pl. 8, fig. 2a, b, 3a, b, ?5 (part, not fig. 1, 4a, b, 6a, b = *Costatumulus farleyensis*).
1964 *C. farleyensis* – Hill & Woods, pl. P6, fig. 12-16.
1964a *C.* aff. *farleyensis* – Waterhouse, p. 61, pl. 9, fig. 3.
1972 *C. farleyensis* – Hill, Playford & Woods, pl. P6, fig. 12-16.
1986b *Magniplicatina undulata* Waterhouse, p. 45, pl. 9, fig. 17-20.
1998 *Magniplicatina transversa* Briggs, p. 187, Fig. 91D-F (part, not Fig. 91A, B, C, G-J = *Platycancrinella lata* see p. 188).
1998 *M. undulata* – Briggs, p. 188, Fig. 92A-J.
2001 *M. undulata* – Waterhouse, p. 50.
2013 *M. undulata* – Waterhouse, p. 131, Fig. 84, 85.

Diagnosis: Small weakly transverse shells with rugae comparatively low and closely spaced over the venter, prominent row of ventral hinge spines and a few additional spines.

Holotype: For *undulata* – UQF 74019 from Elvinia Formation, southeast Bowen Basin, figured by Waterhouse (1986b, pl. 9, fig. 19), OD. For *transversa* – AMF 38076 from Colraine Mudstone, Kimbriki, Manning Block, northern New South Wales, figured by Briggs (1998, Fig. 91D, E, F), OD.

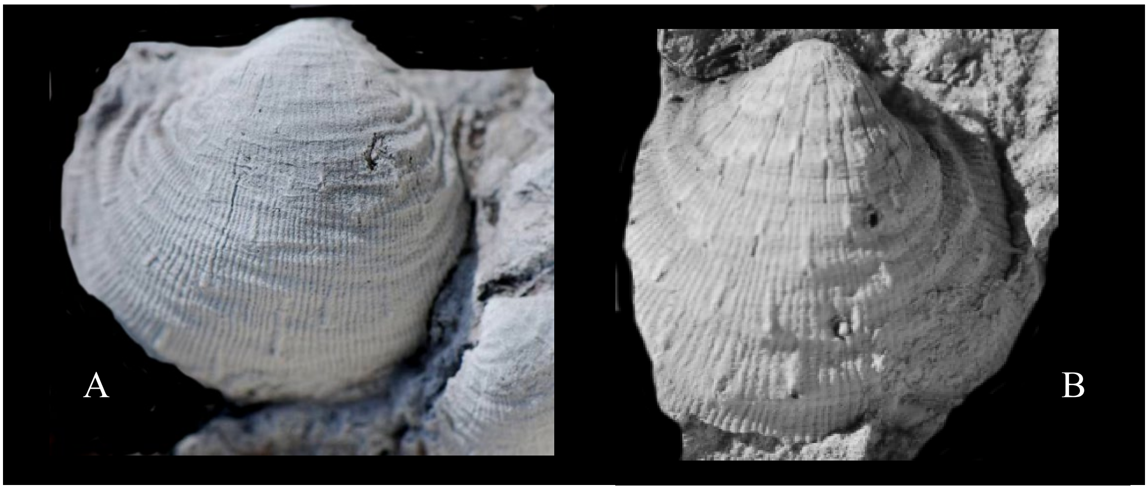


Fig. 50. *Magniplicatina undulata* Waterhouse. A, ventral valve UQF 81248, x3. B, small ventral valve UQF 81249, x4. From middle Tiverton Formation, north Bowen Basin. (Waterhouse 2015a).

Stratigraphy: The species is found in the Elvinia Formation of the southeast Bowen Basin, and more rarely in the middle Tiverton Formation of the north Bowen Basin and lower Cattle Creek beds of the southwest Bowen Basin, as well as the Colraine beds of New South Wales, in the Manning Block. Other material was figured by Briggs (1998) from the Wabro beds near Kempsey, New South Wales. Waterhouse (2015a) also reported the species in the Lakes

Creek beds near Rockhampton in the New England Orogen. A specimen figured as aff. *farleyensis* by Waterhouse (1964a, pl. 9, fig. 3) from the Brunel Formation of the Takitimu Mountains in New Zealand could be allied but further specimens are required to ensure specific relationships. Some Cattle Creek material (eg. Briggs 1998, Fig. 92C, G. H) looks close, and more stratigraphic information would be useful. Briggs (1998) reported the species from various other localities in Queensland and New South Wales: feasible, though further documentation would be desirable. Briggs (1998, p. 190) claimed that the species came from the Buffel Formation, a woefully inadequate interpretation of the stratigraphic position, and claimed that it was to be found in the *Echinalosia preovalis* Zone and correlatives. Not so. The types came from the Elvinia Formation, older than the *preovalis* Zone, and roughly if not exactly equivalent to the "*Echinalosia*" (now *Capillaria*) *warwicki* Zone. His stratigraphy, biostratigraphy, and generic determinations were all suspect.

It appears that two genera were described in the Briggs (1998) analysis of a supposedly new taxon, recorded as *Magniplicatina transversa*. The nominated holotype of *transversa* is subequidimensional and shows ventral spines arranged in one or two rows along the hinge. It came from the Colraine Mudstone at Kimbriki in New South Wales. The other figured specimens came from Silver Spur in New South Wales, and one clearly shows a different arrangement of ventral spines close to the hinge, for they are crowded over the ears. These are therefore discriminated and referred to a different taxon, *Platycancrinella lata* n. sp. (See p. 188).

Some of the specimens assigned to *transversa* look like *Magniplicatina undulata* Waterhouse (1986b, pl. 9, fig. 17-20), also figured by Briggs (1998, Fig. 92A-I). The species *transversa* was said to be characterized by several features that are qualified or even contradicted by figures of the actual material. Stress was laid on the transverse outline and especially on having comparatively low wrinkles over the venter. That is true of the types of *transversa*, but it is also true of a number of *undulata*, including those figured by Waterhouse (1986b, pl. 9, fig. 17, 20) and Briggs (1998, Fig. 92A, B, G): the strength of wrinkles does vary. Briggs (1998) also stressed that spine bases were short and alleged that prolonged spine ridges were absent from *transversa*, but spine ridges of *transversa* figured in Briggs

(1998, Fig. 91B,G, J) are as long as in *undulata* figured by Briggs (1998, Fig. 92C, F, G, H), and it is concluded that spine channels may be equally long in both sets of shells.

Stratigraphy: Briggs (1998) stated that his species *transversa* came from the zonal range of *Echinalosia* (now *Capillaria*) *warwicki.*

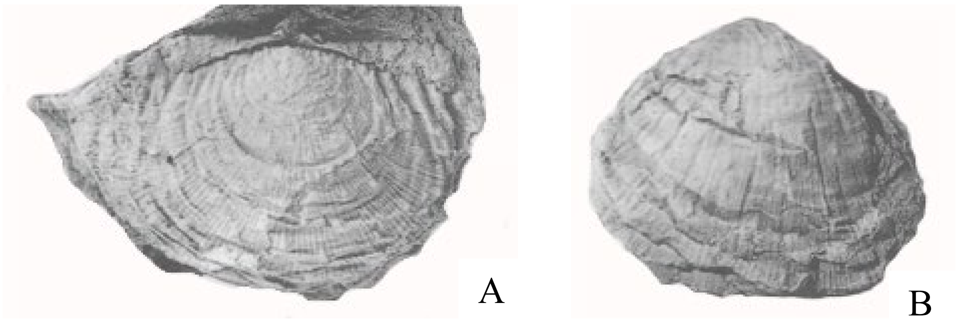


Fig. 51. *Magniplicatina transversa* Briggs = *undulata* Waterhouse. A, B, holotype AMF 38076 from "Kimbriki" New South Wales. (Briggs 1998).

Magniplicatina halli (Waterhouse, 1982)

Fig. 52 - 56

1964a *Cancrinella magniplica* [not Campbell] – Waterhouse, p. 62, pl. 9, fig. 4-8
1982 *Cancrinella halli* Waterhouse, p. 45, pl. 10e-g, i. pl. 23g, h.
1986b *Magniplicatina superba* Waterhouse, p. 45, pl. 9, fig. 21-27, pl. 10, fig. 1-4, text-fig. 9.
cf. 1998 *M. perflecta* [not Waterhouse] – Briggs, p. 190, Fig. 93C, D, G (part, not Fig. 93A, B, E, F, H = *perflecta* Waterhouse).
1998 *M. superba* – Briggs, p. 194.
2000 *M. halli* – Brunton et al. p. 543, text-fig. 378.2a-c.
2001 *M. halli* – Waterhouse, p. 50, pl. 3, fig. 7, 8.
2013 *M. superba* – Waterhouse, Fig. 17.18, p. 422.

Fig. 52. *Magniplicatina halli,* originally named *superba* Waterhouse, latex cast of ventral valve UQF 70093, x3. Brae Formation Queensland, (Waterhouse 1986b).

Diagnosis: Little inflated weakly transverse shells with moderately strong close-set rugae, two rows of ventral hinge spines and fine costellae, twenty or more in 5mm over ventral valve.

Holotypes: For *halli,* BR 950 figured in Waterhouse (1982, pl. 10 fig. e, pl. 23, fig. h) and herein Fig. 53B, D from *Echinalosia discinia* Zone, Letham Formation, Wairaki Downs, New Zealand. For *superba*, UQF 70078 figured by Waterhouse (1986b, pl. 10, fig. 2-4) and Fig. 55B herein, from same zone, in Brae Formation, southeast Bowen Basin, OD.

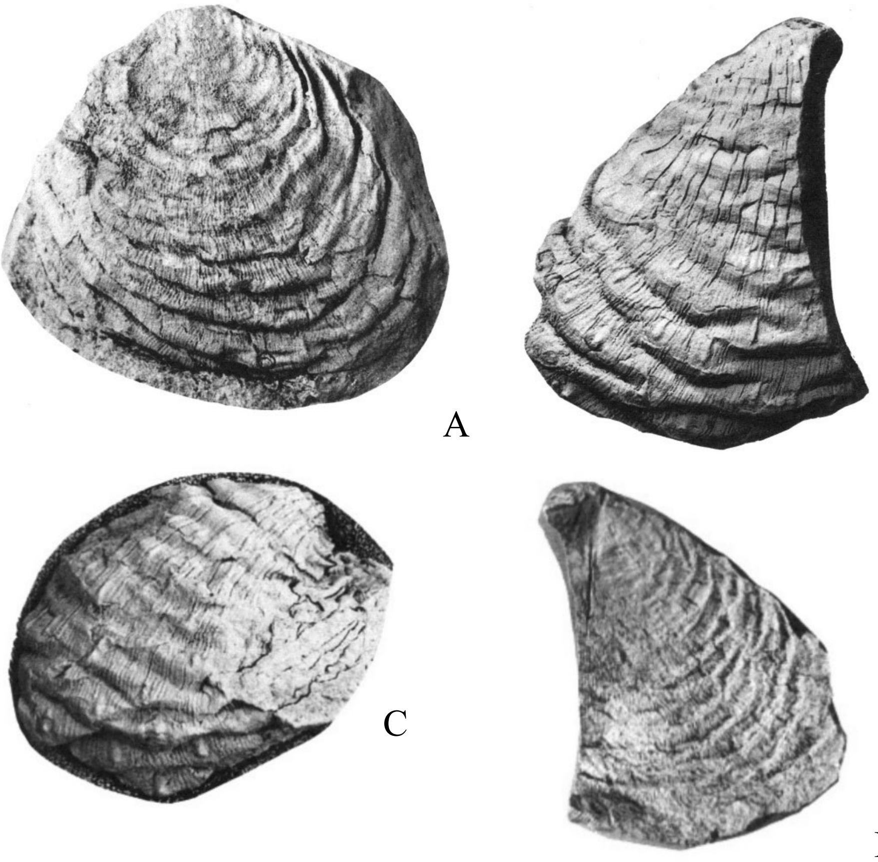


Fig. 53. *Magniplicatina halli* (Waterhouse). A, ventral internal mould BR 950, x2. B, D, ventral and dorsal aspects of BR 951, holotype, x2, x1.5. C, lateral view of ventral internal mould BR 1171, x2. Upper Letham Formation, New Zealand. (Waterhouse 1982).

Morphology: The species *Magniplicatina superba* was assessed as being essentially identical with *M. halli* by Waterhouse (2001, p. 50), after further preparation of Brae material to reveal the double row of spines along the ventral hinge. Both suites have identical fine ribbing, and the style and number of wrinkles is much the same, and there is sufficient variation in Brae specimens to accommodate the inflation of type *halli* as compared with the low inflation of the ventral valve such as figured originally as *superba* and shown herein as Fig. 55B.

Some specimens assigned to *perflecta* by Briggs (1998) from the Ulladulla region and Fenestella Shale appear to be close to *halli*, to suggest the two species are closely allied and need further comparative scrutiny.

Fig. 54. *Magniplicatina halli,* originally named *superba* Waterhouse. Latex cast of ventral anterior shell, UQF 70095 from Brae Formation, x2. (Waterhouse 1986b).

Stratigraphy: The species is found in the middle and upper Letham Formation of New Zealand, and in the Brae Formation of southeast Bowen Basin, in the *Echinalosia discinia* Zone. Possible *halli* was also recorded from the lower Wandrawandian Formation in the south Sydney Basin by Waterhouse (2002a, p. 178). As far as can be resolved, the specimens originally assigned to a separate species, *superba*, from the Brae Formation of the southeast Bowen Basin, are conspecific. This species has some twenty four to twenty five

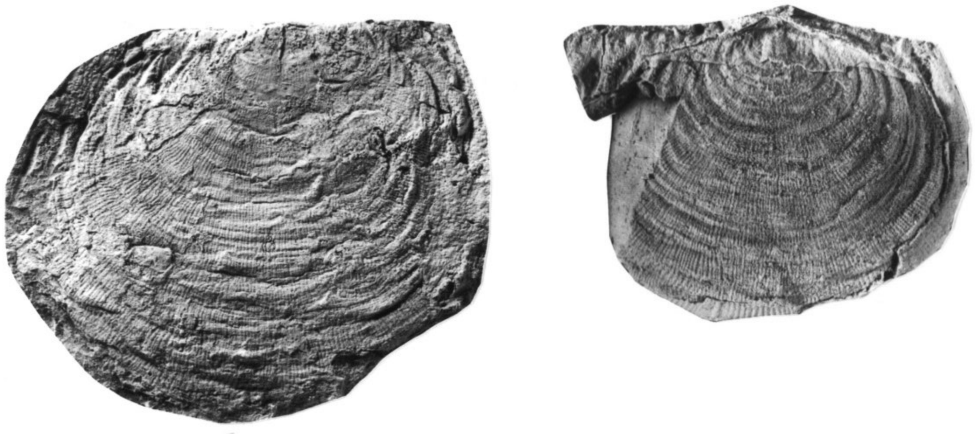


Fig. 55. *Magniplicatina halli,* originally named *superba* Waterhouse. A, dorsal ventral external mould, UQF 70565. B, internal mould of dorsal valve, UQF 70078, holotype for *superba*. Specimens x 2, from Brae Formation. (Waterhouse 1986b).

Fig. 56. *Magniplicatina halli* Waterhouse. A, D, ventral and dorsal aspects of internal mould, BR 848. B, anterior view of ventral PVC cast, BR 737. C, dorsal external mould of BR 848, as figured in A, C. From middle Letham Formation (Kungurian), Wairaki Downs, New Zealand, x2. (Waterhouse 1964a).

ribs in 5mm posteriorly, eighteen to twenty one ribs in 5mm anteriorly and twenty to twenty five ribs at the start of the trail, compared with twenty ribs in 5mm at 10mm from the ventral beak and nineteen at the anterior margin in *halli.* The dorsal valve has some twenty five ribs in 5mm at the anterior margin. So rib counts are moderately close for each taxon and not so different as claimed in Waterhouse (1986b). There are fine rugae posteriorly over the ventral valve of specimens figured in Waterhouse (1964a) from the middle Letham Formation of New Zealand. Some twenty spines along a commarginal row, and anteriorly there are at most seven spines along a commarginal row in the Letham form,

Magniplicatina perflecta Waterhouse, 1986b

Fig. 57

1909 *Productus farleyensis* [not Etheridge & Dun] Etheridge & Dun, pl. 42, fig. 10, 11 (part not fig. 9 = *farleyensis*).
1971 *Cancrinella gyrandensis* [not Dear} – Dear, p. 15.
1986b *Magniplicatina perflecta* Waterhouse, p. 47, pl. 10, fig. 6-11.
1986b *Paucispinauria concava* [not Waterhouse] – Waterhouse, pl. 12, fig. 18 (part, not pl. 12, fig. 17, pl. 13, fig. 1-5, pl. 15, fig. 15 = *P. concava multispina*).
1998 *M. perflecta* – Briggs, p. 190, Fig. 93A, B, E, F, H (part, not Fig. 93C, D, G = allied but uncertain and also aff. *M. halli,* especially C, D).

Diagnosis: Medium size little inflated shells with firm ribbing that numbers fourteen in 5mm over anterior ventral disc and twelve to thirteen in 5mm on ventral trail.

Holotype: UQF 70565 figured by Waterhouse (1986b, pl. 10, fig. 6) from Oxtrack Formation.

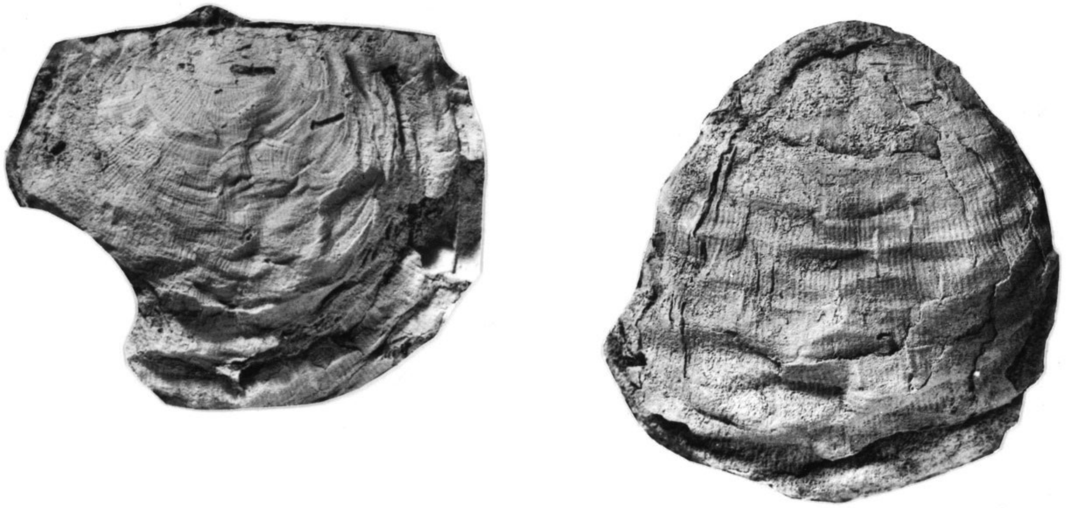


Fig. 57. *Magniplicatina perflecta* Waterhouse. A, dorsal external mould UQF 70566. B, ventral internal mould UQF 70565, holotype. Specimens x 2 from Oxtrack Formation. (Waterhouse 1986).

Morphology: This form is close to *Magniplicatina halli* from the slightly older beds of the upper Letham Formation in New Zealand, but the ventral valve of the Queensland species is less arched, and has slightly more rugae, and slightly coarser ribs. Two of the specimens figured in Waterhouse (1986b, pl. 10, fig. 10, 11) have finer ribs than is the norm. Ventral spine bases are very short anteriorly over the ventral valve, but this appears to be a feature of the genus. Allied material was figured by Briggs (1998, Fig. 93A, E) from Copper Point, New South Wales, as well as material from beds equivalent to Nowra Sandstone (Briggs 1998, Fig. 93B, H) and a specimen in Briggs (1998, Fig. 93 F) with three hinge rows of spines, all identifiable with *perflecta*. Specimens figured by Briggs (1998, Fig. 93C, D) have fine ribs, and come from Ulladulla, a rather broad location, and the specimen from the Fenestella Shale called aff. *perflecta* by Briggs (1998, Fig. 93G) has fine ribs and numerous spines: to suggest the need for closer and extensive reassessment for the range of morphotypes. In some respects, they look closer to *M. superba* = *halli*, though Fig. 93H was agreeably rated as aff. *perflecta* by Briggs.

Briggs (1998, p. 191-192) referred the specimen figured by Etheridge & Dun (1909, pl. 42, fig. 10) to *Magniplicatina perflecta*. This specimen had previously been referred to *farleyensis* by Etheridge & Dun, supposedly from locality F260, described as a road cutting in the Farley Formation in the Hunter Valley. Etheridge & Dun (1909, pl. 42, fig. 11) provided what purported to be a full ventral view of the same specimen, yet this was excluded by Briggs. See Fig. 66, p. 196 herein for replication of the specimen.

Stratigraphy: The species is found in the Oxtrack Formation, and in the Nowra equivalents of the Sydney Basin, and material from the upper Wandrwandian beds and Fenestella Shale need to be assessed.

Magniplicatina magniplica (Campbell, 1953

Fig. 58, 59

1953 *Cancrinella magniplica* Campbell, p. 7, pl. 1, fig. 1-5.
1953 *C.* cf. *magniplica* Campbell, pl. 1, fig. 6-8.
1953 *Cancrinella* sp. Campbell, pl. 1, fig. 9.
1964 *C.* cf *magniplica* – Hill & Woods, pl. P6, fig. 17a, b.
1966 *C. gyrandensis* Wass, p. 97, pl. 3, fig. 1-5.
1971 *C. magniplica* – Dear, p. 13, p. 14.
1972 *C. gyrandensis* – Hill et al., pl. P6, fig. 17a, b.
?1983 *C. magniplica* – McClung, p. 75, Fig. 16. 1, 2.
1983b *Magniplicatina magniplica* – Waterhouse, p. 130.
1986b *M. magniplica* – Waterhouse, p. 48, pl. 10, fig. 5.
1988 *M. magniplica* – Parfrey, p. 13, pl. 2, fig. 9, 20, 21.
?1998 *M. magniplica* – Briggs, p. 194, Fig. 73C, 94A-F.

Diagnosis: Large for genus, strong rugae, deep visceral cavity in maturity, some fourteen to twenty ribs in 5mm, ventral spines few and large.

Holotype: UQF 14214 figured by Campbell (1953, pl. 1, fig. 1, 2) from the lower Peawaddy Formation, southwest Bowen Basin, OD. For *gyrandensis*, UQF 43422 from Barfield Formation, southeast Bowen Basin, figured by Wass (1966, pl. 3, fig. 1-3).

Morphology: Campbell (1953) indicated a density of thirty five to forty ribs in 10mm on his type material of *magniplica*, and I counted twenty six ribs in 10mm at 15mm from the beak on one topotype specimen, and thirty in 10mm on UQF 14273, another topotype. Briggs (1998) counted fourteen to twenty ribs in 5mm for his specimens assigned to *magniplica*: but most of his specimens come from Drake rather than the type area, so that his identification lacks certainty. The material from Interval E in the Eddystone core is incomplete (McClung 1983) and needs more material for confirm the specific affinities.

Stratigraphy: The species is found in the Ingelara Formation, Catherine Sandstone, lower Peawaddy Formation of the southwest Bowen Basin, and upper Barfield and Flat Top Formations of the southeast Bowen Basin. Briggs (1998) figured several specimens from Drake near the southern Queensland border. The range of these specimens involves the *Echinalosia blakei* and *Maxwellosia mantuanensis wassi* Zones. But disconcertingly, in New Zealand specimens that look to be close to *Magniplicatina magniplica* come from a somewhat older zone, equivalent to the *Wyndhamia typica* Zone (Fig. 56, p. 182). They have similar strong rugae and ribbing, shape and spines appear much the same though posteriorly the spines along rows are as many as twenty per row, almost twice the number seen in the one

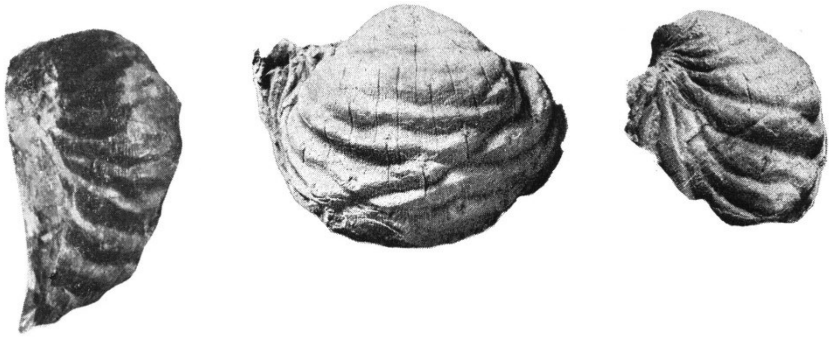


Fig. 58. *Magniplicatina magniplica* (Campbell). A, lateral aspect of ventral valve UQF 14274 x1 from lower Peawaddy Formation, southwest Bowen Basin. (Campbell 1953). B, C, ventral and dorsal aspects of UQF 14273 x1, from Barfield Formation, southeast Bowen Basin. (Hill et al. 1972).

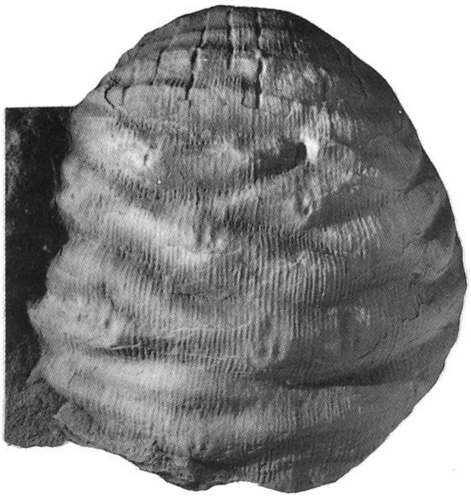


Fig. 59. *Magniplicatina magniplica* (Campbell), ventral valve UQF 69980 x2 from Barfield Formation, southeast Bowen Basin. (Briggs 1998).

specimen figured by Briggs that shows a comparable part of the shell, and are now referred to *Magniplicatina halli*.

Magniplicatina heywoodi Waterhouse, 2001

Fig. 60

1986b *Magniplicatina halli* [not Waterhouse] – Waterhouse, p. 48, pl. 10, fig. 12-14.
?1998 *M. magniplica* [not Campbell] – Briggs, p. 195 (part, not Fig. 72C, 94A-F = *magniplica*).
2001 *M. heywoodi* Waterhouse, p. 52.

Diagnosis: Moderately inflated somewhat compressed shells with closely spaced low rugae bearing somewhat angular crests posteriorly, rugae becoming higher and spaced further apart anteriorly, interspaces tend to be subangular. Two to usually three or four rows of spines along the ventral hinge, ventral body spines arise mostly in front of two costellae, bases 2-5mm long, costellae fine, more than twenty in 5mm anteriorly.

Holotype: UQF 74025 figured by Waterhouse (1986b, pl. 10, fig. 14) and herein as Fig. 60A, from Flat Top Formation, southeast Bowen Basin, OD.

Morphology: The material resembles *Magniplicatina halli* in several respects, but the shells are more arched, and rugae and interspaces are more angular in profile, and finer and more numerous posteriorly, becoming larger in front. There are usually three or four rows of ventral hinge spines, whereas *halli* has two rows, and further differences are discussed by Waterhouse (2001, p. 52). Briggs (1998, p. 195) referred the type material to *M. magniplica*, and the specimens are close to this species in shape and inflation, but the Flat Top shells have lower more numerous rugae posteriorly, and finer costellae, with differences in spines.

Stratigraphy: The species is found in the lower middle Flat Top Formation, southeast Bowen Basin, and possibly in the correlative part of the Mangarewa Formation of Wairaki Downs,

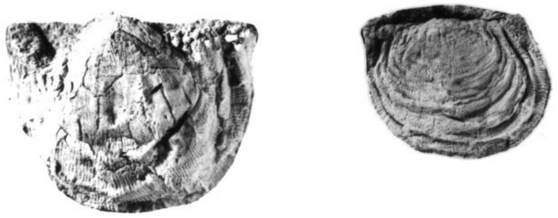


Fig. 60. *Magniplicatina heywoodi* Waterhouse. A, posterior ventral internal mould UQF 74025, holotype. B, dorsal external mould UQF 74023. Specimens x1 from Flat Top Formation. (Waterhouse 1986b).

New Zealand. Specimens recorded as *heywoodi* from four localities in what is now recognized as the *Maxwellosia ovalis wassi* faunas of the upper Mangarewa Formation in Waterhouse (2001, p. 52) are similar in shape and rugae but the nature of the hinge spines is not secure.

Magniplicatina cranfieldi Waterhouse & Balfe, 2015b

Fig. 61

1969 *Cancrinella farleyensis* [not (Etheridge & Dun)] – Runnegar & Ferguson, pl. 2, fig. 18 (part, not ?19, ?20 = *Costatumulus randsi*?).
2015b *Magniplicatina cranfieldi* Waterhouse & Balfe in Waterhouse, p. 88, Fig. 27 (part, not p. 141, Fig. 58 = *Platycancrinella* sp.).

Diagnosis: Small transverse shells with rugae comparatively low and closely spaced over the venter, prominent row of ventral hinge spines and a number of additional spines.

Holotype: UQF 45383 from lower South Curra Limestone (Changhsingian), Gympie, figured by Runnegar & Ferguson (1969, pl. 2, fig. 18), OD.

Fig. 61. *Magniplicatina cranfieldi* Waterhouse. A, ventral valve UQF 69198, x1. B, ventral valve UQF 45383, x2. C, ventral valve UQF 69190, x1. From South Curra Limestone, Gympie. (Waterhouse 2015b).

Morphology: Specimens of moderate size, with large ears and wide hinge, usually at maximum width, and broad ventral umbo. Ribs are fine and sharply raised posteriorly and broad but low anteriorly, numbering eighteen to twenty two in 10mm. Persistent low and narrow commarginal rugae cover both valves. A well-formed row of spines with other posterior spines close by is developed along the hinge, and a few further ear spines are comparatively well-developed; spines in quincunx over the venter, with slender elongate bases, up to 4mm long. The dorsal valve lacks spines, but may display slender and short dimples. Internal detail is not well preserved, the muscle scars being feebly impressed, without prominent ventral adductor platform, implying they could have been dendritic.

A specimen reported by Waterhouse (1982) from the correlative Kildonan Member of the Arthurton Group in New Zealand differs in so far as rugae are not developed over the posterior disc, thereby coming close to *Cancrinella* Fredericks of Subtribe Cancrinellinai, as elaborated in Waterhouse (2013, p. 430). The text and caption in Waterhouse (1982, p. 46, pl. 11f) referred to this specimen as ?*Cancrinella* sp., but it was not figured, having been inexplicably replaced by a fragment of the external mould of *Terrakea pollex aurispina*.

Stratigraphy: The species is limited to the South Curra Limestone of southeast Queensland.

Genus ***Platycancrinella*** Waterhouse, 1983b

Diagnosis: Closely rugose shells with firm fine ribs, spines limited to ventral valve, numerous over comparatively large ears.

Type species: *Platycancrinella grandauris* Waterhouse, 1983b, p. 126 from Pija Shale of Changhsingian age in Nepal.

Discussion: *Platycancrinella* is distinguished from *Magniplicatina* by the large and more spinose ventral ears. *Magniplicatina* has ventral spines in one to three rows along the hinge, rarely with a few additional spines, whereas spines lie in five to six rows over the ears of *Platycancrinella. Platycancrinella* was confused with *Cancrinella* by Brunton et al. (2000, p. 533) but *Cancrinella* has dorsal spines, not found in *Platycancrinella* and ear spines are limited to one or two rows.

Platycancrinella lata n. sp

Fig. 62

1998 *Magniplicatina transversa* [not Briggs] – Briggs, p. 187, Fig. 91A, B, C, G-J (part, not D-F = *M. transversa* Briggs = *undulata*).
2010 *Platycancrinella* sp. – Waterhouse, p. 43, Fig. 13.

Derivation: lata – broad (Lat.).

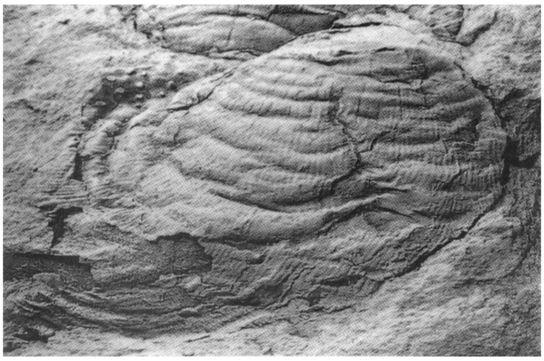
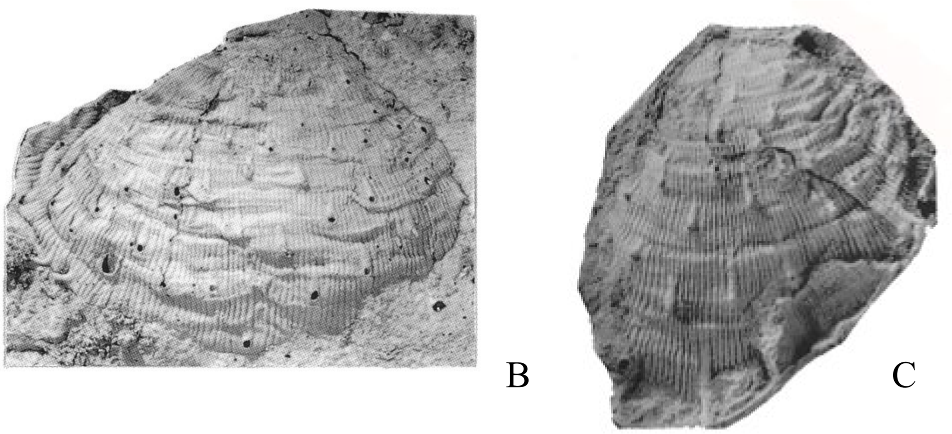


Fig. 62. *Platycancrinella* lata n. sp. A, ventral internal mould AMF 96275 x2, holotype. B, latex cast showing ventral exterior, AMF 96276, x2. C, latex cast of ventral exterior, AMF 96280. Specimens x2 from Silver Spur. (Briggs 1998).



Diagnosis: Weakly transverse to subelongate shells with moderately strong rugae; numerous erect spines over ventral ears.

Holotype: AMF 96275 from Silver Spur, figured by Briggs (1998, Fig. 91A), here designated. That of course awaits the discovery of the Briggs material. Otherwise the locality should be recollected for a neotype.

Morphology: Material from at Silver Spur, as shown in Fig. 62, shows the ventral ear bearing crowded erect spines as helps typify *Platycancrinella* as distinct from *Magniplicatina*, which has one to two, rarely more rows of hinge spines which cross the ears. The cited holotype for *transversa* to which Briggs had referred the material has fewer ear spines, and with spines aligned along the hinge, belongs to *Magniplicatina*.

Stratigraphy: Briggs (1998) assigned the Silver Spur beds to the *Echinalosia* (now *Capillaria*) *warwicki* Zone, largely equivalent to the *Magniplicatina undulata* Zone.

Platycancrinella sp.

Fig. 63

2015b *Magniplicatina cranfieldi* [not Waterhouse & Balfe] – Waterhouse & Balfe in Waterhouse, p. 141, Fig. 58 (part, not p. 88, Fig. 27 = *cranfieldi*).

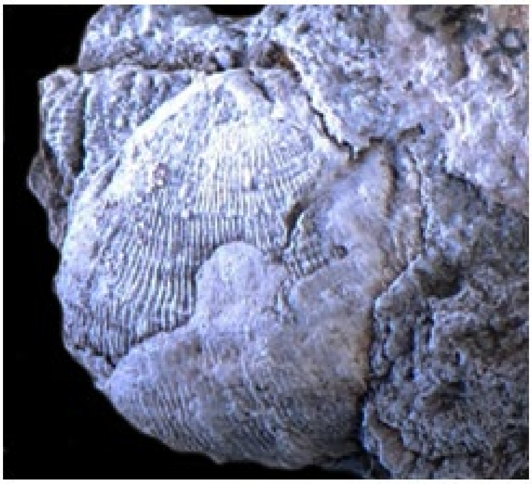


Fig. 63. *Platycancrinella* sp., ventral valve UQF 50265, x2. From Gundiah Bridge Greywacke, Gympie region. (Waterhouse 2015b).

A specimen from the Gundiah Bridge Greywacke of Brown (1964) as figured herein (Fig. 63) has large ears with suggestions of many spines, and a number of the spines over the venter appear to be erect, whereas other spines have prolonged bases as in type *cranfieldi.* Ribs are present at fifteen to sixteen in 5mm.

Family **AURICULISPINIDAE** Waterhouse, 1986b

[Nom. transl. Waterhouse 2013, p. 440 ex Auriculispininae Waterhouse 1986b, p. 57] et seq.

Diagnosis: Both valves ornamented by slightly irregular ribs, ventral spines lie along hinge in one to four rows, and arranged in quincunx over the ventral disc, with elongate bases, spine cores further prolonged anteriorly within the shell, spines erect over trail. Dorsal spines usually absent, if present erect and undifferentiated. Commarginal rugae often prominent. Ventral adductor scars usually striate and sited on platform set deeply into posterior shell, becoming dendritic in later growth stages. Dorsal median septum often doubled. Visceral disc slender as a rule, cardinal process trilobed.

Discussion: Several groups of genera are known: Auriculispinini as described shortly, found widely also in south and east Asia, and Filiconchini Waterhouse, found especially in Middle Permian of east Australia and Arctic faunas, Lyoniinae Waterhouse which includes *Bandoproductus* and is widely developed in especially early Permian deposits of Gondwana, whereas Siphonosiinae Lazarev is confined to paleotropical faunas of United States.

With its trilobed cardinal process, members of this family are moderately close to members of Paucispinauriidae, but usually lack dorsal spines and usually have a more slender visceral disc and different ventral adductor scars.

Subfamily **AURICULISPININAE** Waterhouse, 1986b

Diagnosis: Ventral spines with elongate bases arranged in regular quincunx over disc, may be crowded over ears and in row or rows along hinge, dorsal spines absent. Radial ribs and weak to strong commarginal rugae. Body corpus usually thin, ventral adductor scars posteriorly placed, elongate and striate until late in ontogeny when simple dendritic patterns appear. Trail short and not elongated into a proboscidellin tube.

Tribe **AURICULISPININI** Waterhouse, 1986b

Diagnosis: Shells large for the group, tend to be elongately oval in shape and often tumid, ribbing may be strong. Ventral spine bases may be long.

Discussion: The prime features are the slender disc, elongate ventral spine bases, and striate nature of the ventral adductors. Contents of this subfamily are considerably altered from the scheme proferred by Brunton et al. (2000) and sustained without published analysis or discussion by Brunton (2007), in which genera displaying such features were scattered through different subfamilies. A classification more consistent with a wide range of morphological features was attempted in Waterhouse (2002b, 2013). Ovatiinae Lazarev, 1990, p. 121, based on the Early Carboniferous and reportedly Devonian genus *Ovatia* Muir-Wood & Cooper, 1960, was synonymized with Auriculispininae in Brunton et al. (2000, p. 537), but was regarded as a valid family group within Linoproductoidea by Waterhouse (2013, p. 372), on the basis of the nature of the ornament and the muscle impressions.

Genus ***Costatumulus*** Waterhouse, 1983a

Diagnosis: Transverse often tumid shells with radial ribs, low commarginal wrinkles often only on lateral shell, spines over ventral valve with moderately narrow short to long spine bases, spines erect over ears in one to three rows along hinge, dorsal valve without spines, visceral disc moderately thin. Ventral posterior walls relatively thick, adductor platform impressed and posteriorly placed, smooth to finely striate until advanced maturity, then becoming subdendritic to dendritic, posteriorly placed, diductor scars large, weak to clearly defined. Dorsal adductor scars becoming dendritic, platform developed in front of cardinal process, joined each side by ridge parallel to hinge.

Type species: *Auriculispina tumida* Waterhouse in Waterhouse et al. (1983, p. 133) from Tiverton Formation (Sakmarian), Bowen Basin, OD, now synonymized with *farleyensis* Etheridge & Dun, 1909.

Discussion: *Costatumulus*, recognized first in the Late Paleozoic faunas of east Australia, has proved to be widespread amongst especially the Early Permian faunas of Gondwana, including Western Australia (eg. Archbold 1993), India (Singh & Archbold 1993), China (Chen & Shi 2006), northern Russia (Waterhouse 2013), Canada, Svalbard and New Zealand (Waterhouse 2001, 2013, p. 448ff).

Brunton (2007, p. 2655) wished to expand the scope of the genus by including *Costatumulus tazawai* Shen et al. (2000) from the Late Permian of south Tibet, but this species has very large ears (cropped out of the illustration of the holotype as figured by Shen et al. 2000, Fig. 12.2, though complete in Shen et al. 2000, fig. 12.12), strong commarginal rugae, and dendritic ventral adductors as far as they can be discerned. The species belongs to a distinct cancrinelliform rather than auriculispiniform genus called *Auritusinia* Waterhouse, 2002b, within the Paucispinauriinae Waterhouse (see Waterhouse 2013, Fig. 17.25, p. 429).

Costatumulus prolongata Waterhouse, 1986b

Fig. 64, cf. Fig. 65

1986b *Costatumulus prolongata* Waterhouse, p. 58, pl. 9, fig. 11-16.
1998 *C. farleyensis* [not Etheridge & Dun] – Briggs, p. 157.
cf. 2015a *C.* aff. *prolongata* – Waterhouse, p. 140, Fig. 94.

Diagnosis: Small elongate shells characterized by ribs of moderate strength and short ventral spine bases.

Holotype: UQF 74015 figured by Waterhouse (1986b, pl. 9, fig. 13-15) and Fig. 64B herein from Fairyland Formation, southeast Bowen Basin, OD.

Morphology: *Costatumulus prolongata* is characterized by its small size, narrow shape with arched venter, and ventral spine bases that are short anteriorly. Costellae number twelve to thirteen in 5mm at mid-length on the ventral valve, and nine to eleven anteriorly, and *farleyensis-tumida* has similar ribs numbering twelve to fourteen in 5mm anteriorly and more in some specimens. Spines in quincunx lie over ventral valve, many erect, some with elongate bases up to 3.5mm long and 0.6mm wide, low numerous wrinkles and shallow depressions and swellings cover both valves. The bases of the ventral body spines in *prolongata* are up to 3.5 mm in length and slender (0.6mm wide), but anteriorly become short and broad. The body cavity is slender.

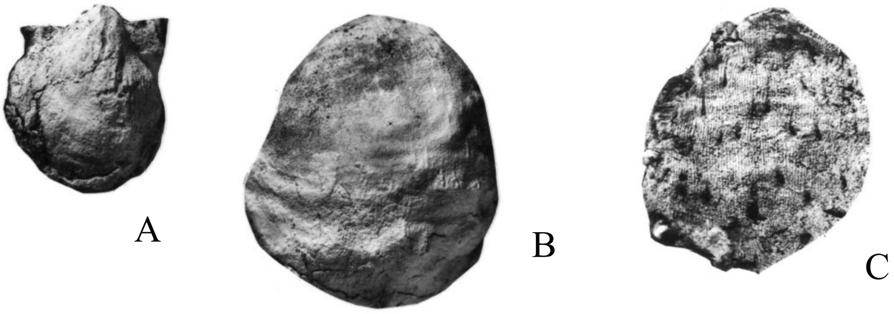


Fig. 64. *Costatumulus prolongata* Waterhouse. A, ventral internal mould UQF 74012. B, anterior aspect ventral internal mould UQF 74015, holotype. C, part of external mould of same specimen. Specimens x1 from Fairyland Formation. (Waterhouse 1986b).

Briggs (1998) suggested that the diagnostic features of *prolongata* varied in Tiverton and Farley collections of *Costatumulus*, but elongate specimens of *farleyensis-tumida* from the Tiverton Formation that are shaped like *prolongata* are much larger, less elongate and more incurved, and more commonly have a tumid anterior. Briggs suppressed the species, but the shape is distinctive, and indeed the external moulds figured in Waterhouse (1986b, pl. 9, fig. 15, 16) differ markedly from any ventral exteriors known for *tumida* or *farleyensis*. For “proof” of his assertion, Briggs (1998, Fig. 79D) referred to his figure of a Farley specimen of *farleyensis* as being like *prolongata*. The figure shows the middle part of a broad and only moderately inflated ventral valve, not like *prolongata* in shape or size, though the costellae are similar in density, and the spine bases vary in length from 2mm to 3mm long, as measured from the figure – the exact limits of the spine bases are difficult to ascertain. But although this specimen was chosen in the hope of proving that *prolongata* was the same as *farleyensis*, it has to be said that the claim is not convincing. Moreover Sydney Basin material is yet to be examined thoroughly, to determine if *prolongata* is represented in the lower Farley beds or underlying Rutherford Formation.

Elongate and comparatively small shells, with twelve to thirteen ribs in 5mm over mid-length, and numbering nine to eleven in 5mm anteriorly come from the lower Tiverton Formation, as described in Waterhouse (2015a). The ventral spine bases are 3-5mm long and 0.6mm wide. They are moderately close to *Costatumulus prolongata*. One specimen is highly vaulted and narrow, and has nine to ten costellae in 5mm anteriorly on the dorsal valve, with spine bases over 4mm long. Specimens from the overlying locality also include several elongate specimens, in which costae may be as numerous as thirteen in 5mm, approaching *farleyensis*, and spine bases are up to 6mm long in the measured specimens and usually 3-5mm long. Other specimens are shaped like *farleyensis*.

Fig. 65. *Costatumulus* cf. *prolongata* Waterhouse?, dorsal external mould UQF 81429 from lower Tiverton Formation, x5. (Waterhouse 2015a).

Stratigraphy: The species is known only from the Fairyland Formation of the southeast Bowen Basin, and allied material comes from the basal Tiverton Formation in the northern Bowen Basin. Some specimens a little above the base of the Tiverton Formation approach *Costatumulus prolongata* in shape and fineness of costae, although some *tumida* have just as many or more costellae, but have longer spine bases. There is thus a degree of overlap between the two species and suggestion of gradation. The specimens from UQL 4507 in the *Bookeria pollex* Zone are like type *prolongata*, in being small, so that the short spine bases of the anterior mature ventral valve are not shown, and the specimens from the overlying zone could represent surviving stock. The development in the genus is not simple: other specimens from locality UQL 4509 are closer to typical *tumida*, and various specimens from UQL 4510 are transverse and less inflated, with locality detail provided in Waterhouse (2015a, p. 350). A very few specimens from younger localities as elaborated in Waterhouse (2015a) show some similarity in being subelongate to *prolongata*, but are much more tumid.

Costatumulus farleyensis (Etheridge & Dun, 1909)

Fig. 66A, 67 - 72

1892 *Productus* sp. indet. (a) Etheridge, p. 255, pl. 13, fig. 6.
1909 *Productus cora farleyensis* Etheridge & Dun, p. 302, pl. 42, fig. 9 (part, not fig. 10,11 = *Magniplicatina perflecta* fide Briggs).
1950 *Cancrinella farleyensis* – Hill, p. 14, pl. 8, fig. 1, 4-6 (part, not pl. 7, fig. 7a, b, pl. 8, fig. 2, 3 = *Magniplicatina undulata* Waterhouse).
1964 *C. farleyensis* – Maxwell, p. 43, pl. 7, fig. 21, 22.
1964 *C. farleyensis* – Hill & Woods, pl. P6, fig. 13-16 (part, not pl. P6, fig. 12 = *Magniplicatina undulata*).
1972 *C. farleyensis* – Hill, Playford & Woods, pl. P6, fig. 13-16 (part, not pl. P6, fig. 12 = *undulata*).
1980 *C. farleyensis* – McClung, pl. 19.1, fig. 7.
1983 *Auriculispina tumida* Waterhouse in Waterhouse et al., p. 133, pl. 3, fig. 2-4, 6-7.
1983a *Costatumulus tumida* – Waterhouse, p. 44.
1986b *Cancrinella farleyensis* – Waterhouse, p. 44.
1986b *C. tumida* – Waterhouse, p. 59, pl. 11, fig. 1-9, pl. 15, fig. 12, 13.
1998 *C. farleyensis* – Briggs, p. 157, Fig. 79A-H.
1998 *C. meritus* [not Waterhouse] – Briggs, p. 160 (part, most = *meritus*).
2000 *C. tumida* – Brunton et al., p. 538, Fig. 376.2a-d.
2007 *C. tumida* – Waterhouse & Chen, text-fig. 1D.
2015a *C. tumida* – Waterhouse, p. 134, Fig. 86, 87, 88-93.

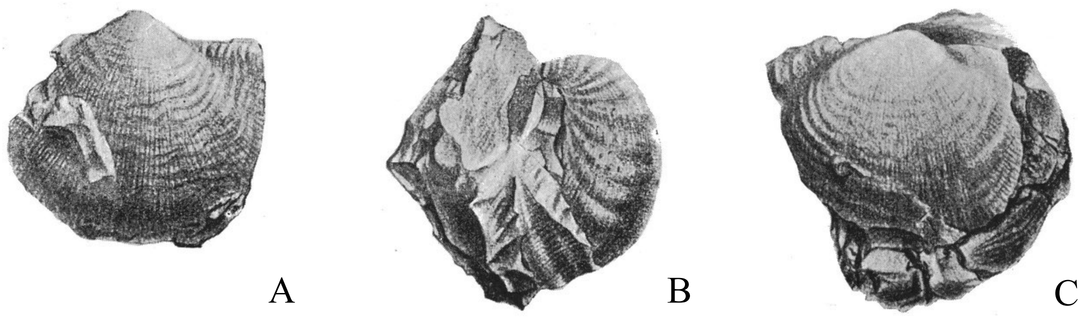


Fig. 66. A, *Costatumulus farleyensis* (Etheridge & Dun), ventral valve, AMF 35480, lectotype, x1, from Farley Formation. B, C, lateral and ventral aspects of ventral valve, AMF 260, x1, figured as *farleyensis* by Etheridge & Dun (1909, pl. 42, fig. 10, 11) and reassigned to *Magniplicatina perflecta* (Waterhouse) by Briggs (1998, p. 159). Though noted by Briggs as coming from the Shoalhaven Group according to the label this term was not used in the days of Etheridge & Dun, so probably was applied later, anomalously, and presumably accurately. The strong rugae in Fig. 66B strongly suggest *Magniplicatina.*

Diagnosis: Large shells of generally transverse but often elongate outline, venter as a rule transverse, often tumid with incurved ventral umbo and comparatively steep ventral posterior walls, moderately large ears, low commarginal wrinkles, and moderate density of ventral spines over disc and trail.

Holotypes: For *farleyensis*, AMF 35480 figured by Etheridge & Dun, 1909, pl. 42, fig. 9) and Fig. 66A herein from Farley Formation, Sydney Basin, designated by Hill (1950). For *tumida*, UQF 73302 from UQL 4515, Tiverton Formation, figured in Waterhouse et al. (1983, pl. 3, fig. 2), OD.

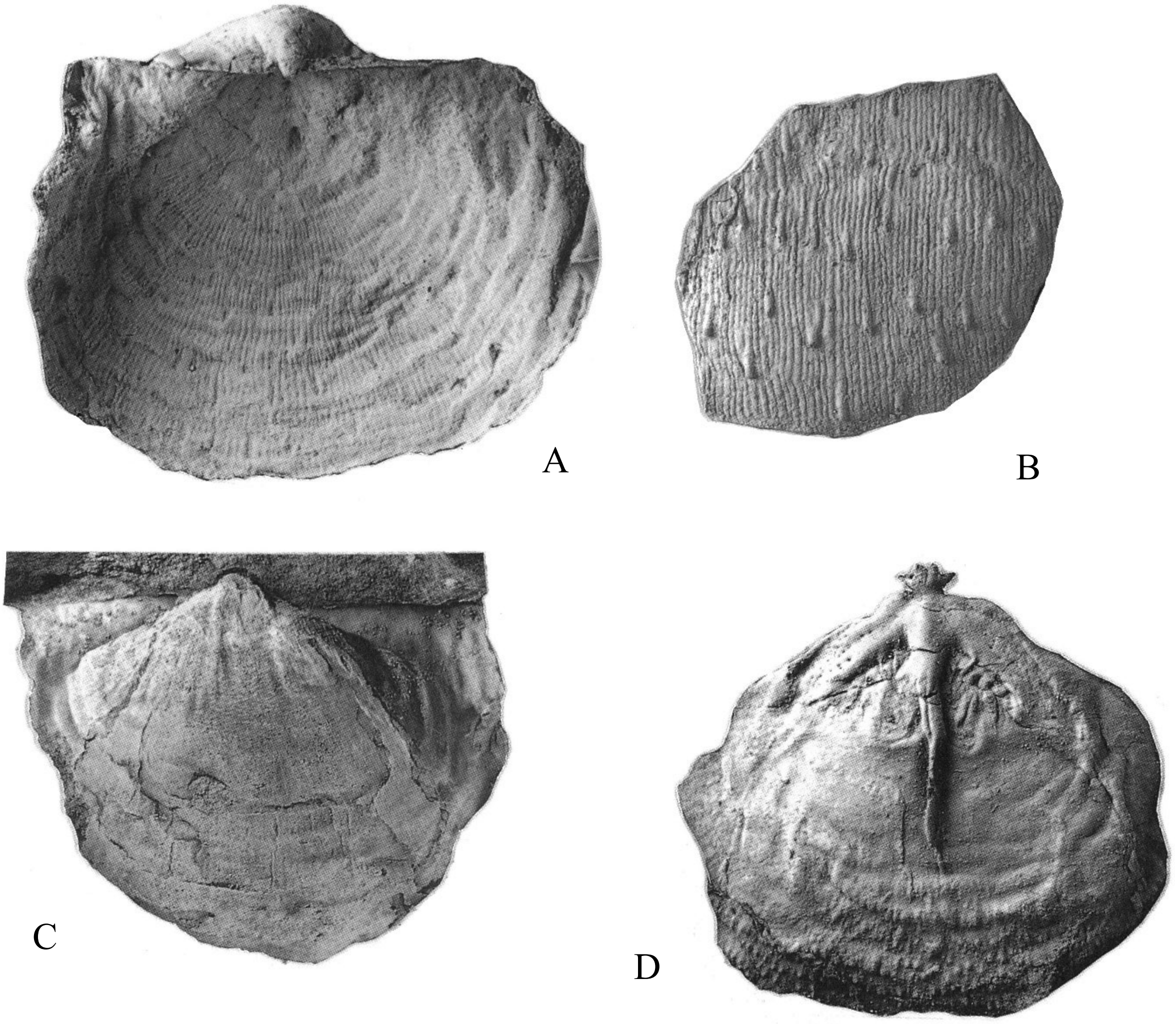


Fig. 67. *Costatumulus farleyensis* (Etheridge & Dun). A, D, latex cast of dorsal exterior and ventral umbo, and of dorsal interior, UQF 15310, x1.5. B, latex cast of ventral exterior, UQF 75311. C, internal mould of ventral valve UQF 75313, x1.5. From Farley Formation, north Sydney Basin. (Briggs 1998).

Morphology: Briggs (1998) determined that the species *farleyensis* did not belong to *Cancrinella* or its related genus *Magniplicatina*, but to *Costatumulus*. This is far from evident according the earlier studies. The figure of the type of *farleyensis* shows no elongate spine bases, Waterhouse (1986b, p. 44) recording only short spine bases 2mm long with twelve costellae in 5mm, and about twenty commarginal rugae in AMF 35480, the type specimen, the rugae of spacing similar to those of *Costatumulus tumida*, but more strongly defined. Briggs presumably clarified generic allegiances through re-examining the type material at the Australian Museum. Accepting his claims, it must be concluded that *Costatumulus farleyensis* (Etheridge & Dun) is one of the more abundant and well-preserved fossils to be found in the middle Tiverton Formation at Homevale. It ranges throughout most of the outcrops, and is large for a proboscidelloid. Most of the specimens are mature. There are two morphologies in the Tiverton assemblage – transverse and little inflated specimens with gently concave ventral anterior sulcus or flattening, and more elongate and inflated specimens with tumid ventral anterior. There is no clear stratigraphic difference between the two, apart from a tendency for the transverse shells to come from younger sediments, and details of ornament seem to be same in both groups. As well, there are a number of shells of intermediate shape. Costellae are fine and vary between twelve and seventeen in 5mm over the mature anterior valve. The dorsal exterior has a corresponding array of slender pits in quincunx, less conspicuous, finer and shorter than the spine-bases, and corresponding in position, having been formed concurrently at the growing edge of the mantle. Both valves are also ornamented by commarginal wrinkles, rather subdued over the ventral disc. Spines generally lie in two rows along the hinge, with one to three additional spines laterally,

Fig. 68. *Costatumulus farleyensis* (Etheridge & Dun), latex mould of ventral valve UQF 81449 from upper middle Tiverton Formation, x2. (Waterhouse 2015a).

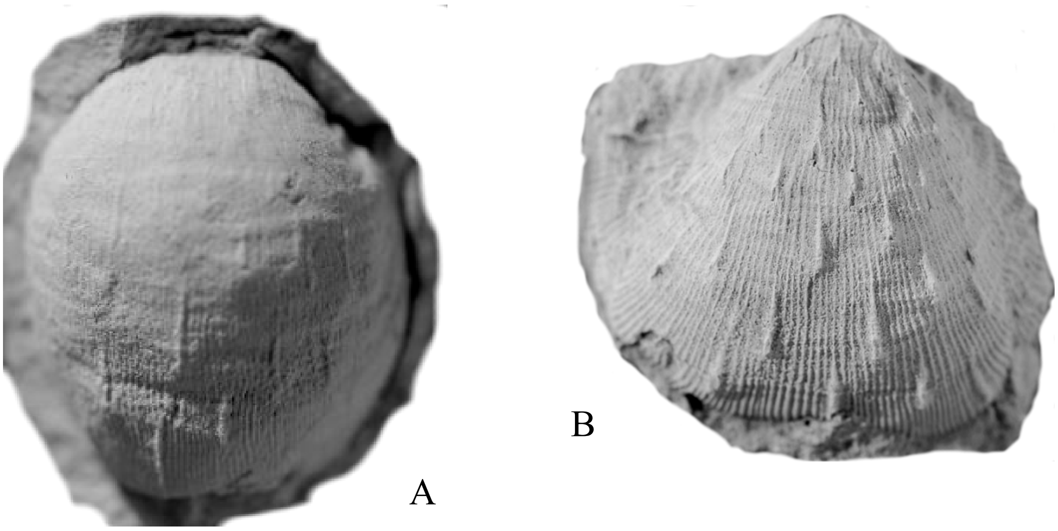


Fig. 69. A, *Costatumulus farleyensis* (Etheridge & Dun), ventral internal mould UQF 81213, x2. B, ventral valve UQF 81428, x3. From middle Tiverton Formation. (Waterhouse 2015a).

But spines form a single row in some shells. Body spines are disposed in quincunx, and are generally nearly twice as wide as the costellae, but rarely are wider. The spine bases are consistent in length on many individuals, and usually close to 3mm long, but may be as short as just over 1mm, or as long as more than 4mm. As a rule spines emerge from a single rib, but on rare specimens a spine may emerge from the junction of two ribs, and occasionally, even three or four ribs. Ribs resume at about the same number in front of the spine, but there

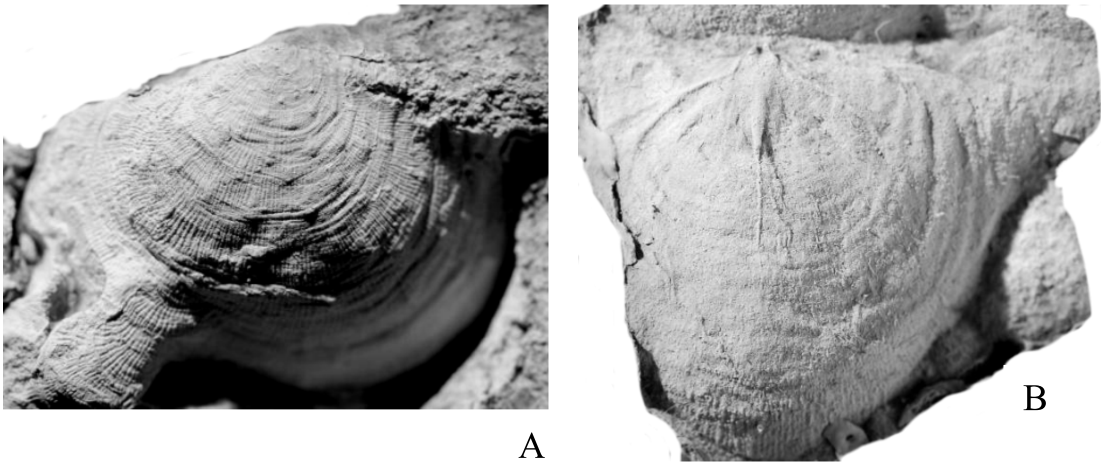


Fig. 70. *Costatumulus farleyensis* (Etheridge & Dun). A, dorsal valve showing irregular and exceptional extension of the trail, UQF 81220, x1.5. B, latex cast of dorsal interior, UQF 81221, x1.5. From Tiverton Formation. (Waterhouse 2015a).

are variations, with ribs sometimes disappearing beside the spine, and then resuming or replaced a little in front. Commarginal rugae are developed over the posterior walls and in some specimens the ears, and are more prominent on the dorsal valve.

The Farley specimens described and illustrated as *Costatumulus farleyensis* by Briggs (1998) are weakly transverse, not elongate, and without any strongly incurved ventral umbo. They have costellae numbering only ten to twelve in 5mm over the anterior half (Briggs 1998, p. 159), and spine bases 1.5 to 2mm long, as in the original types. The Elvinia material described from the southeast Bowen Basin by Waterhouse (1986a, p. 59, pl. 11, fig. 1-9, pl. 15, fig. 12, part, not fig. 13 = sp. indet.) have ten to fourteen costellae in 5mm as in type *farleyensis*, spine bases are 1.5 - 3mm long, and the specimens lack a tumid anterior.

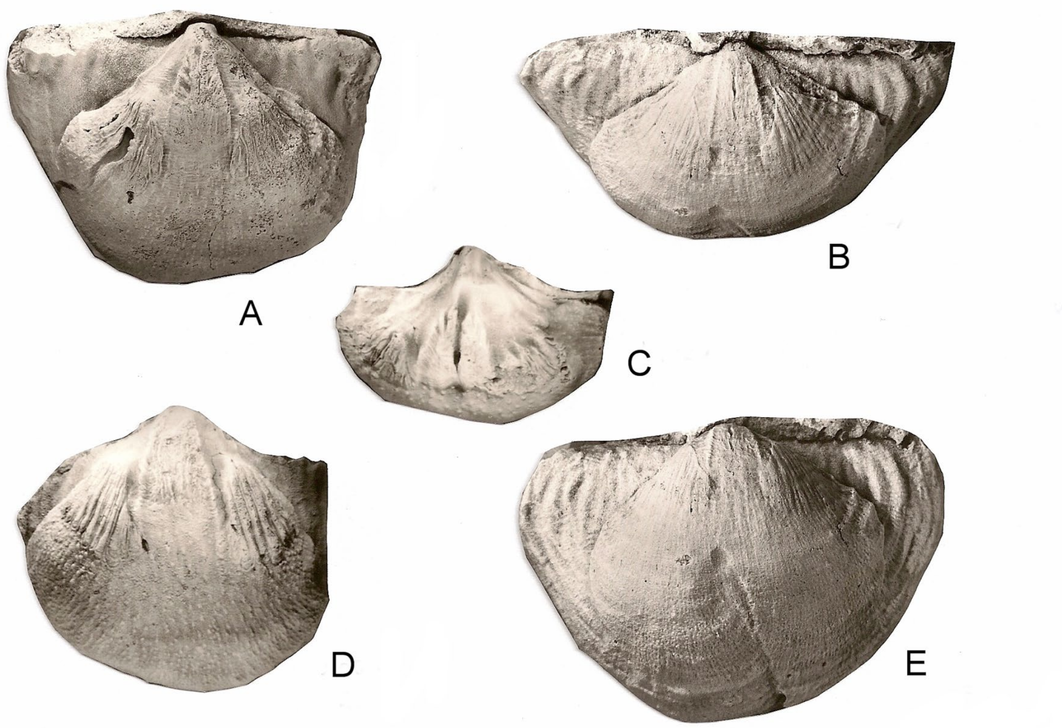


Fig. 71. *Costatumulus farleyensis* (Etheridge & Dun). A, ventral internal mould, UQF 20827, x1.25. B, E, posterior and ventral aspects of internal mould UQF 81222, x1.25. C, posterior view of internal mould UQF 44027, x1. D, ventral internal mould UQF 81223, x 1.25. From Tiverton Formation. (Waterhouse 2015a).

Stratigraphy: The types were reported from the Farley Formation, stratigraphic position not known, and the species is common in the middle Tiverton Formation of the north Bowen Basin. Hill (1950, p. 15), Runnegar & Ferguson (1969, p. 251) and Briggs (1998, p. 157) assigned to *farleyensis* specimens from the New Caledonian reef at Gympie, and so likely to be from the upper Rammutt Formation, that were figured as *Productus cora* D'Orbigny by Etheridge Snr (1872, p. 328, pl. 15, fig. 1, 2) as repeated by Etheridge (1892, pl. 12, fig. 14). These specimens belong to *Magniplicatina cranfieldi* (see p. 187 herein).

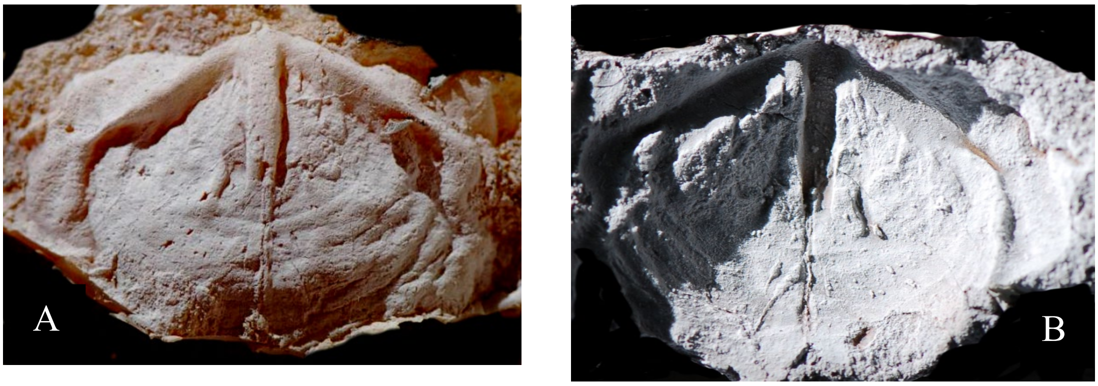


Fig. 72. *Costatumulus farleyensis* (Etheridge & Dun), dorsal latex cast and external mould UQF 81267, x2.5. From Tiverton Formation. (Waterhouse 2015a).

The Yarrol Formation specimens ascribed by Maxwell (1964, pl. 7, fig. 20, 21) to *Cancrinella farleyensis* are poorly preserved but possibly belong to the species. UQF 43201 has some eleven ribs in 5mm, and UQF 43045 is tumid and has eleven to twelve ribs in 5mm. A specimen recorded by Etheridge (1892, p. 255, pl. 13, fig. 6) as *Productus* sp. indet. (a) from near Yarrol Station in the Burnett district was assigned to *C. farleyensis* by Briggs (1998, p. 157).

Fig. 73. *Costatumulus farleyensis* (Etheridge & Dun), late mature ventral internal mould UQF 44027 from UQL 2625, x2. From Tiverton Formation. (Waterhouse 2015a).

Costatumulus meritus Waterhouse, 1986b

Fig. 74

1986b *Costatumulus meritus* Waterhouse, p. 59, pl. 9, fig. 5-10.
1998 *C. meritus* – Briggs, p. 161, Fig. 80A-H.

Diagnosis: Large elongate shells with prolonged trail and fine ribs.

Holotype: UQF 74009 figured by Waterhouse (1986b, pl. 9, fig. 8) from Cattle Creek Formation, southwest Bowen Basin, OD.

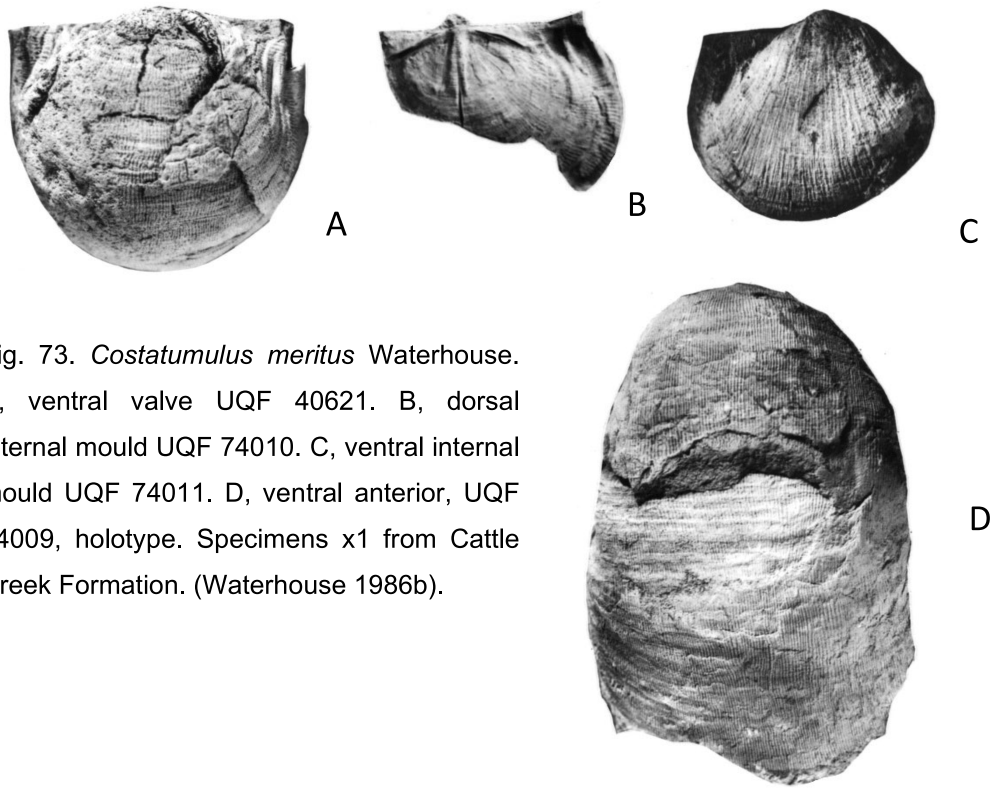


Fig. 73. *Costatumulus meritus* Waterhouse. A, ventral valve UQF 40621. B, dorsal internal mould UQF 74010. C, ventral internal mould UQF 74011. D, ventral anterior, UQF 74009, holotype. Specimens x1 from Cattle Creek Formation. (Waterhouse 1986b).

Morphology: Specimens may be over 50mm long and more than 40mm wide. The ventral valve lacks any sulcus or flattening and the dorsal valve shows no fold or geniculation. Costellae number ten in 5mm at mid-length and twelve in 5mm anteriorly, crossed by low rugae, numbering about thirty. Spines are limited the ventral valve and form a double row near the hinge, and show prolonged bases up to 4mm long along single ribs.

Stratigraphy: The species is limited to the upper Cattle Creek Formation in the southwest Bowen Basin, in the *Echinalosia preovalis* Zone.

An Elvinia specimen figured by Waterhouse (1986b, pl. 15, fig. 12) was referred to *meritus* by

Briggs (1998, p. 160), but his identification is dubious: it is mostly an internal ventral mould, and is shaped like *farleyensis* and *tumida*. The textual captions in Waterhouse (1986b) err: they refer to 11, 12, instead of 12, 13. The specimen in Waterhouse (1986b, pl. 15, fig. 13) seems most unlike *Costatumulus*: and Briggs (1998, p. 165) correctly referred it to *Terrakea* – now *Bookeria – geniculata.*

Briggs (1998, p. 161) thought that *Costatumulus meritus* was represented by specimens figured as *Costatumulus* sp. by Waterhouse & Balfe (1987, pl. 2, fig. 6) and as *Cancrinella farleyensis* by Runnegar & Ferguson (1969, pl. 2, fig. 18-20) from the South Curra Limestone of the Gympie district, southeast Queensland. The ribs are slightly coarser and ears wider than in *meritus*, and the specimen of Runnegar & Ferguson (1969, pl. 2, fig. 18) is ascribed to *Magniplicatina cranfieldi* by Waterhouse & Balfe in Waterhouse (2015b), and the other figured specimens appear to be *Costatumulus randsi* Balfe & Waterhouse, 2010. The Gympie specimens tend to be consistently more transverse and less tumid than typical *meritus*, and have a thinner and non tumid visceral disc. Ventral spines are generally only 0.4mm in diameter, increasing to 0.75mm on the ears.

Costatumulus randsi Balfe & Waterhouse, 2010

Fig. 74

1950 *Cancrinella farleyensis* [not Etheridge & Dun] – Hill, p. 15, pl. 8, fig. 1, 4, ?5, ?6 (part, not pl. 7, fig. 7, pl. 8, fig. 2, 3 = *Magniplicatina undulata* Waterhouse).
?1969 *C. farleyensis* – Runnegar & Ferguson, p. 254, pl. 2, fig. 19, 20 (part, not fig. 18 = *Magniplicatina cranfieldi*).
1987 *Costatumulus* n. sp. Waterhouse & Balfe, p. 32, pl. 2, fig. 6.
1998 *C. meritus* [not Waterhouse] – Briggs, p. 160.
2010 *C. randsi* Balfe & Waterhouse in Waterhouse, p. 34, Fig. 9A-O.
2013 *C. randsi* – Waterhouse, p. 458, Fig. 21.1B-D.
2015b *C. randsi* – Waterhouse, p. 90, Fig. 28.

Diagnosis: Concavo-convex geniculate shells, transverse as a rule, with narrow commarginal rugae which are strongest on ears and flanks, weak over disc, venter and trail. Ventral spines fine, emerging from raised somewhat broadened bases, short as a rule. Dorsal ornament without conspicuous radial pits or closely branching costellae.

Holotype: UQF 69212 from lower South Curra Limestone (Changhsingian), Gympie, figured by Balfe & Waterhouse in Waterhouse (2010, Fig. 9A) and herein as Fig. 74A, OD.

Morphology: Shells transverse or rarely subelongate, ventral ornament of fine radial costellae numbering twenty four to thirty in 10mm at 10mm from the umbo, increasing anteriorly by intercalation rather than bifurcation; low close-set commarginal wrinkles, most strongly developed on ears and flanks, continuous though faint across venter, about 1.5mm apart. Ventral spines fine and relatively few, arise from slight swellings of costellae, 1 to 2mm apart, 0.4mm in diameter, some bases extended for more than 10mm in length, spines more or less quincunxially arranged, coarser on ears (ca. 0.75mm in diameter), closely spaced hinge spines, numbering six to eight, erect and in a single row near umbo, increasing to two to three rows laterally. No dorsal spines, linear depressions rare, present as sparsely distributed elongate pits.

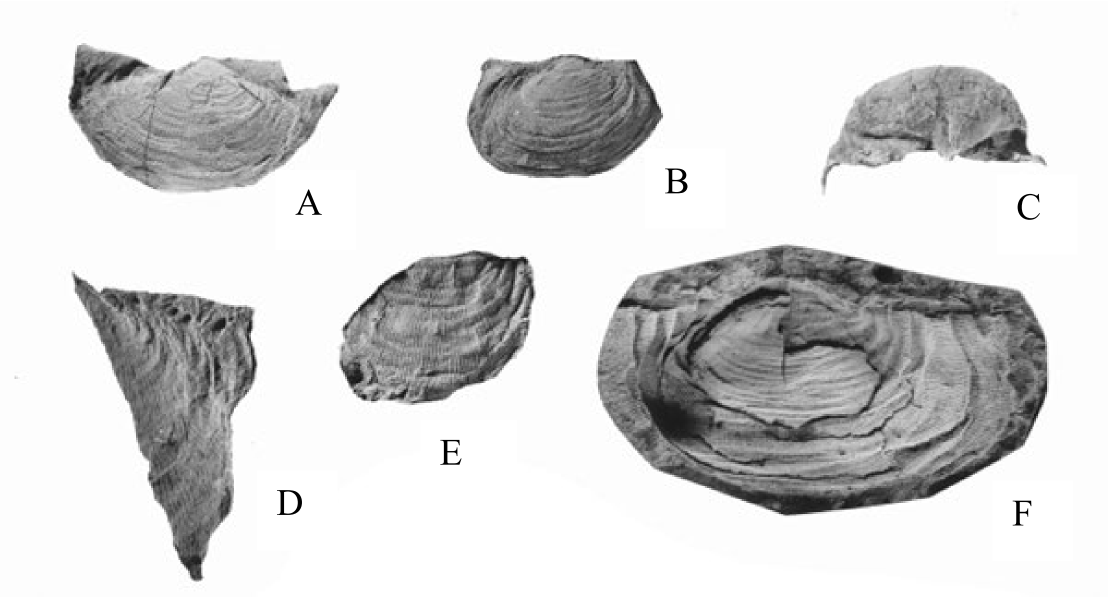


Fig. 74. *Costatumulus randsi* Balfe & Waterhouse. Specimens x1 unless otherwise indicated. A, holotype, ventral valve UQF 69212. B, ventral valve UQF 69214. C, posterior view of ventral valve UQF 69196. D, external mould of ventral valve showing hinge spine bases, UQF 69161, x2. E, fragment of external mould, ventral valve UQF 69215, x1.5. F, ventral internal mould resting on dorsal external mould, UQF 69121. South Curra Limestone, Gympie. (Waterhouse & Balfe in Waterhouse 2015b).

Stratigraphy: *Costatumulus randsi* is represented by mostly small typically transverse specimens, with shallow visceral cavity, numerous fine commarginal wrinkles, and comparatively few major spines along the ventral hinge. The species is less tumid and as a rule less elongate than other species of *Costatumulus* from east Australia, with finer ventral spines and more weakly defined ventral adductor platform, differences that may reflect ongoing development within the genus. The species is limited to the lower South Curra Limestone near Gympie, southeast Queensland, of Changhsingian age.

Tribe **FILICONCHINI** Waterhouse, 2001

[Filiconchini Waterhouse, 2001, p. 33].

Diagnosis: Shell weakly transverse as a rule, with ventral disc usually of low convexity, subrectangular outline and subgeniculate trail. Ventral body spines numerous with elongate bases, spines few and organized in row or rows close to hinge. Dorsal valve with or without spines, trail subgeniculate, interior distinguished by development of a double ridge posteriorly, may replace the dorsal median septum. Lower Permian (Kungurian) to Upper Permian (lower Changhsingian).

Genera: *Filiconcha* Dear, *Cameronovia* Waterhouse, *Kolymaella* Ganelin & Lazarev, *Omolonia* Ganelin, 1990 not Alexseeva, 1967, *Spitzbergenia* Kotlyar.

Discussion: Although this tribe was ignored by Brunton (2007), it is very distinctive, with its roundly subquadrate shape, and small size, with shell build of Type 6 (see Waterhouse 2013, p. 24), the visceral disc shallow and becoming higher anteriorly, but not tumid. There are regular ventral spines with elongate bases in quincunx which dominate the ventral ornament, fine to extremely fine costellae, or no costellae. Members tend to have posterior dorsal ridges which slope obliquely forward laterally, and in some specimens, what appears to be lateral buttress plates are developed, as in *Spitzbergenia loveni* (Wiman 1914, pl. 17, fig. 18; Kotlyar in Sarytcheva 1977, Fig. 87). Apart from shape, most detail is close to that of Auriculispininae, and the dorsal interior is particularly close to that of *Auriculispina* and *Costatulumus*.

Genus ***Filiconcha*** Dear, 1969

Diagnosis: Roundly subrectangular in outline with wide hinge, moderately developed row of hinge spines (see Dear 1969, pl. 21, fig. 10) and numerous spines with elongate bases over the visceral disc, and fine erect dorsal spines. The ventral adductor scars are impressed and posteriorly placed, with subrectangular outline, bearing striae until late in ontogeny, when oblique grooves develop. The dorsal adductors include a small rounded and smooth anterior pair. The cardinal process is trilobate from an inner or ventral aspect, with small alveolus, and two median ridges pass forward from a broad median ridge: in some specimens a median septum lies in front. As well, there are support ridges that angle laterally from in front of the cardinal process. In short, the shape and interior of the dorsal valve are very distinctive. The type species of *Filiconcha* is found in the Wordian faunas of the Flat Top Formation in the Bowen Basin, Queensland, and another species is found in the Changhsingian Trig D Formation of New Zealand (Waterhouse 1976, p. 238; 2002a, p. 33).

Filiconcha hillae Dear, 1969

Fig. 75, 76

1969 *Filiconcha hillae* Dear, p. 303, pl. 21, fig. 1-8.
1986b *F. hillae* – Waterhouse, p. 56, pl. 11, fig. 10-18.
1998 *F. hillae* – Briggs, p. 197.
2013 *F. hillae* – Waterhouse, Fig. 17.49.

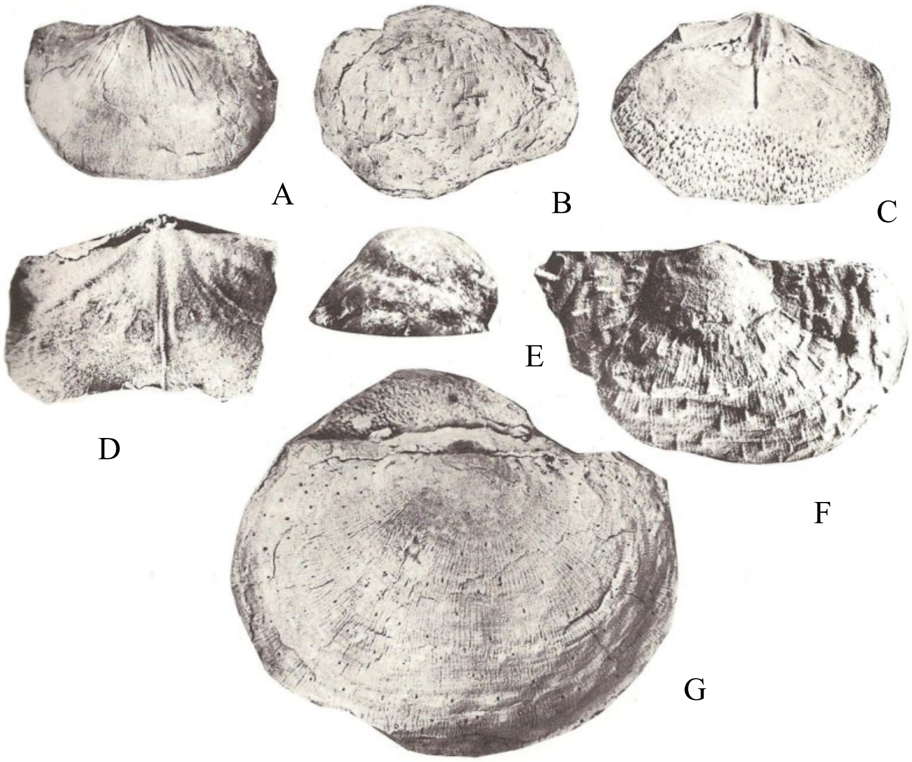


Fig. 75. *Filiconcha hillae* Dear. A, internal mould of ventral valve GSQF 9832, x1. B, latex cast of ventral exterior, GSQF 9472a, x1. C, dorsal internal mould GSQF 9870, x1. D, latex cast of dorsal interior, GSQF 10883, x3. E, lateral aspect of ventral internal mould, GSQF 9843, x1. F, latex cast of ventral exterior, GSQF 10922a, x2. G, external mould of dorsal valve, GSQF 9829, x2. Flat Top Formation, Queensland. (Dear (1969).

Diagnosis: Transverse somewhat oval to subrectangular shells with fine ribs and fine spines arranged in quincunx over both valves, with elongate bases in ventral valve. Dorsal valve geniculate or subgeniculate. Adductor platform impressed posteriorly, somewhat subrectangular in shape, dorsal septum bifid posteriorly.

Holotype: UQF 10996a figured by Dear (1969, p. 21, fig. 1, 2) from Flat Top Formation, southeast Bowen Basin, OD.

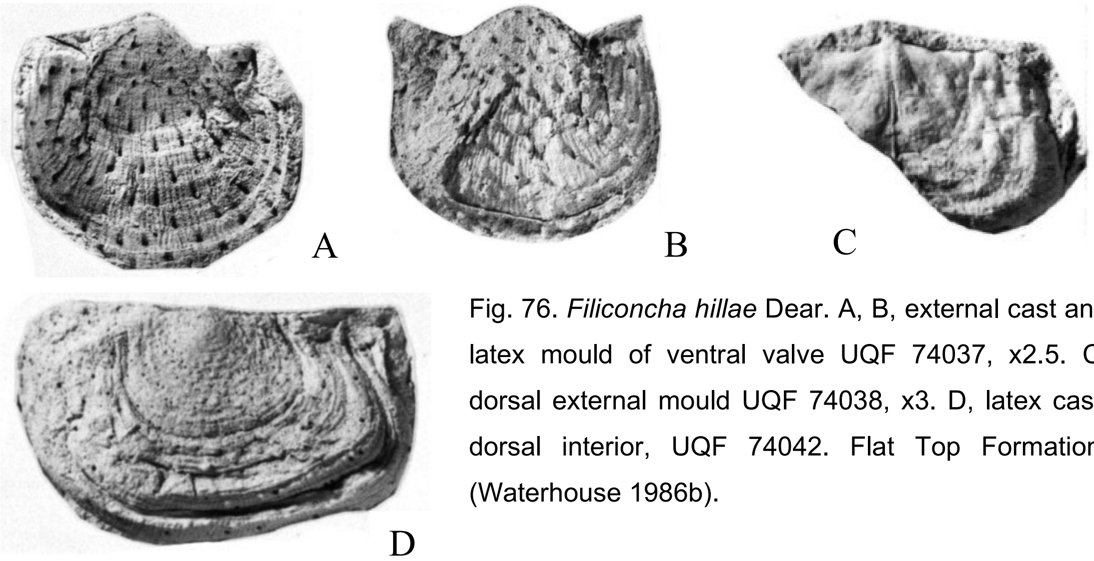


Fig. 76. *Filiconcha hillae* Dear. A, B, external cast and latex mould of ventral valve UQF 74037, x2.5. C, dorsal external mould UQF 74038, x3. D, latex cast, dorsal interior, UQF 74042. Flat Top Formation. (Waterhouse 1986b).

Morphology. Briggs (1998) claimed that some of the specimens (none actually specified) figured as this species by Waterhouse (1986b) were in fact like *Terrakea*. He did not identify the species, but argued that the subquadrate shape and geniculate trail indicated *Terrakea*. To me, the specimens look like *Filiconcha*, and they lack the stout erect spines typical or so many paucispinaurians, coming closest in this regard to *Saetosina*, which has different ventral adductors and different dorsal septum, and less developed rugae, elongate shape, more spines and other differences. Some of the specimens are refigured herein as Fig. 76. Briggs also referred Gympie material figured by Runnegar & Ferguson (1969, pl. 5, fig. 5-7) to the species, but they are now placed in *Costatumulus* (see p. 202). On the other hand he rightly corrected the attribution by Waterhouse (1986b) of a dorsal valve in Hill & Woods (1964, pl. P6, fig. 2) from *Filiconcha* to *Terrakea*, even though his reasons were challengeable, such as subquadrate shape and geniculate trail, which in fact feature in many *Filiconcha*.

Combined with faint if any radial ornament, the shape suggests affinity with the ventral internal mould figured by Hill & Woods (1964, pl. P6, fig. 1), given its *Terrakea-like* rather than filiconchid ventral adductor platform.

Stratigraphy: The species is found in the lower middle Flat Top Formation of the southeast Bowen Basin.

Filiconcha sp.

Fig. 77

1956 *Terrakea* sp. A Marwick in Wood, p. 46.
1964b *Anidanthus* n. sp. Waterhouse, p. 215.
1969 Marginiferid Waterhouse, text-fig. 42.
1976 *Filiconcha* sp. Waterhouse, p. 238, Fig. 4.2.
1982 *Filiconcha* sp. Waterhouse, p. 51, pl. 12j.
1998 *Lethamia collina* [not Waterhouse] – Briggs, p. 197.

Two specimens were described as *Filiconcha* sp. from the Earnvale Member at the base of the Bagrie Formation in Waterhouse 1976, and another added by Waterhouse (1982). They were distinguished from *F. auricula* of the overlying fauna zone and beds by their larger size, smaller ears, flatter visceral disc and faint if any radial ornament. However material is too sparse to be confident of definite separation as a distinct taxon, though it was noted that *Filiconcha hillae* has a less flattened disc and longer sulcus and fold. The geniculate nature of the dorsal valve is like that of *Filiconcha*.

Fig. 77. *Filiconcha* sp., internal mould of ventral valve BR 1269 x2 from Earnvale Member, Bagrie Formation, New Zealand. (Waterhouse 1982).

Briggs (1998, p. 197) asserted that the specimen might be overtoniid, but its ventral muscle scars are not at all overtoniid, and the ventral valve is much less arched and tumid than *Lethamia collina* Waterhouse, despite the appraisal by Briggs.

Filiconcha auricula Waterhouse, 1976

Fig. 78, 79

1969 *Filiconcha hillae* [not Dear] – Runnegar & Ferguson, pp. 268-269, pl. 5, fig. 5-7.
1976 *F. auricula* Waterhouse, p. 238, Fig. 4.3-14.
1987 *F. hillae* [not Dear] – Waterhouse & Balfe, p. 26.

Diagnosis: Transverse shells with flat disc, some specimens sulcate, dorsal valve may bear fold, but not in all specimens, ears large and sharply obtuse. Trail geniculate. Dorsal valve with two posterior brevisepta. Ears better defined and capillae much fainter than in *Filiconcha hillae*.

Fig. 78. *Filiconcha auricula* Waterhouse, showing double posterior median septum in latex cast of dorsal valve, BR 1709, x3. From boulder derived from Kildonan Member, Bagrie Formation, New Zealand. Waterhouse (1976).

Holotype: BR 1703 figured by Waterhouse (1976, Fig. 4.4) from Kildonan Member, Arthurton Group, New Zealand, OD.

Morphology: The species is described in Waterhouse (1976). The most obvious difference from *Filiconcha hillae* is provided by the weakness of the radial ornament.

Stratigraphy: The species is restricted to the Kildonan Member of the Bagrie Formation in the Arthurton Group of New Zealand and South Curra Limestone at Gympie, Queensland.

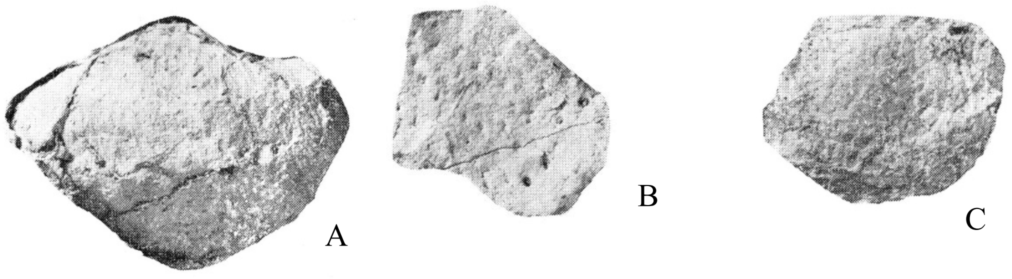


Fig. 79. *Filiconcha auricula* Waterhouse. A, ventral internal mould BR 1721, x1. B, detail of ventral external mould BR 1706 x2. C, dorsal exterior BR 1708 x2. From Kildonan Member, Bagrie Formation, New Zealand. (Waterhouse 1976).

Subfamily **LYONIINAE** Waterhouse, 2001

[Nom. transl. Waterhouse 2013, p. 445 ex Lyoniini Waterhouse, 2001, p. 32].

Diagnosis: Transverse shells with wide hinge and broad visceral disc, gently convex ventral valve, slender body corpus, both valves costellate. Spines usually only on ventral valve, forming well-defined row close to the hinge, and arranged in quincunx with elongate bases over the visceral disc. Some genera have more numerous spines over the ventral ears, and have dorsal spines. Ventral adductor scars lightly to moderately defined, lightly striate and not strongly dendritic. Lower Permian (Asselian) to Upper Permian (Changhsingian).

Genera: *Lyonia* Archbold, *Ainimia* Waterhouse, *Bandoproductus* Jin & Sun (mis-spelled *Pondoproductus* by Jin, 1985, pl. 1, fig. 19, 20), subgenus *Briggsia* Waterhouse, *Masitoshia* Waterhouse, *Nambuccalinus* Waterhouse, *Nambdoania* Waterhouse, *Nikitinia* Kotlyar, Zakharov & Polubotko.

Discussion: The tribe was recognized as valid by Brunton (2007), and includes the genera *Lyonia* Archbold and *Nambuccalinus* Waterhouse, both with dorsal spines, whereas other genera have only ventral spines. *Lyonia* is particularly close in shape to *Bandoproductus*, but has dorsal spines, to suggest that presence or absence of dorsal spines in some stock may not be significant to other than generic, subtribal, or tribal level.

Genus ***Bandoproductus*** Jin & Sun, 1981

Diagnosis: Medium size, wide hinge, row of stout spines along hinge, spines numerous over venter with prolonged and swollen bases emerging from costae. Ventral adductor scars subrectangular.

Type species: *Bandoproductus hemiglobica* Jin & Sun, 1981, p. 138 from Bando Group (Asselian), Tibet, OD.

Discussion: A subgenus is now recognized within *Bandoproductus*.

Bandoproductus (***Bandoproductus***) ***macrospina macrospina*** Waterhouse, 1986b

Fig. 80 - 82

?1892 *Productus* sp. ind. (a) Etheridge Jnr, p. 255, pl. 13, fig. 6.
1964 *Linoproductus* cf. *lyoni* (not Prendergast) – Maxwell, p. 43, pl. 7, fig. 28-31.
1976 *Linoproductus* cf. *lyoni* – Roberts et al., fig. 6.

1986b *Cancrinelloides* (*Bandoproductus*) *macrospina* Waterhouse, p. 57, pl. 13, fig. 13, 14, 17, 18 (part, not fig. 15, 16 = *walkomi* fide Briggs.
1987 *Cancrinelloides* or related genus Waterhouse & Balfe, pl. 1, fig. 14-16.
1998 *Bandoproductus macrospina* – Briggs, p. 155, Fig. 78A-D.
1998 *Costatumulus farleyensis* [not Etheridge & Dun] – Briggs, p. 157 in synonymy. See p. 211 herein.
2008 *B. macrospina* – Waterhouse, p. 353, Fig. 3D.
2015b *B. macrospina* – Waterhouse, p. 51, Fig. 15C-E, Fig. 16.

Diagnosis: Large highly convexo-concave shells distinguished by moderately coarse costellae (ca. eleven to sixteen in 10mm anteriorly), spines in row along hinge with a few additional spines, narrow spine bases in ventral valve, both valves bearing well-defined commarginal wrinkles.

Fig.80. A, B, *Bandoproductus* (*Bandoproductus*) *macrospina macrospina* Waterhouse. A, ventral internal mould, x1. B, ventral external mould, x1. (Waterhouse 2015b, Waterhouse & Balfe 1987).

Holotype: UQF 43142 from Burnett Formation (Asselian), Yarrol Basin, Queensland, figured by Maxwell (1964, pl. 7, fig. 29) and Waterhouse (1986b, pl. 13, fig. 17) and Fig. 82C herein.

Morphology: Both valves ornamented by costellae, sixteen to eighteen in 10mm at 10mm from ventral umbo, and eleven to thirteen in 10mm anteriorly and over much of the shell, increasing by intercalation, with broadly convex crests and narrow V-shaped interspaces. Both valves also covered by fine wrinkles, highest postero-laterally, and faint on ears, numbering just over thirty on large specimens, and not completely regular in course, may fade laterally. Fine growth-lines also developed, two to four per mm. Single row of hinge spines well-developed, may diverge laterally from hinge, spines erect and 1.5mm in diameter, rarely a few additional spines present. Fine spines scattered over the remainder of the valve, emerging from crest of costellae, some erect, especially laterally, others emerging from gradually widening spine-bases, 3-5mm long, diameter up to 0.8mm, usually 0.6mm. No dorsal spines.

Briggs (1998, p. 157) referred specimens figured by Waterhouse & Balfe (1987, pl. 1, fig. 14-16 – not fig. 13-15 as in the caption) to *Costatumulus farleyensis*, but they are better placed in *Bandoproductus* (*Bandoproductus*) *macrospina macrospina*.

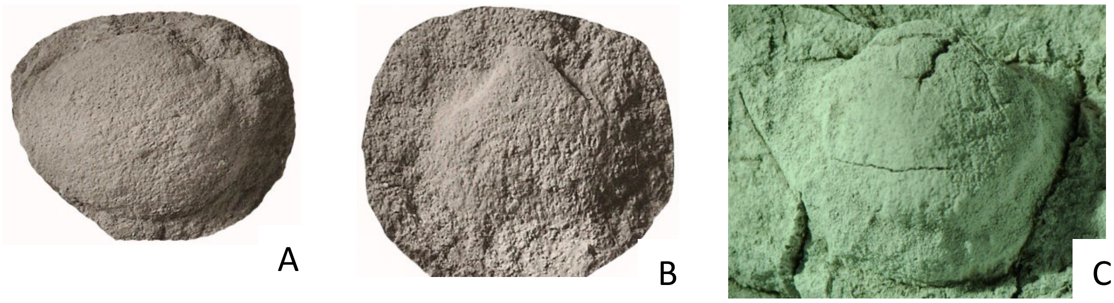


Fig. 81 .*Bandoproductus* (*Bandoproductus*) *macrospina macrospina* Waterhouse. A, ventral valve GSQF 13187, x1. B, ventral valve GSQF 13186, x2. C, UQF 61932 from upper Burnett Formation, Yarrol Basin, x1. (Waterhouse 1986b).

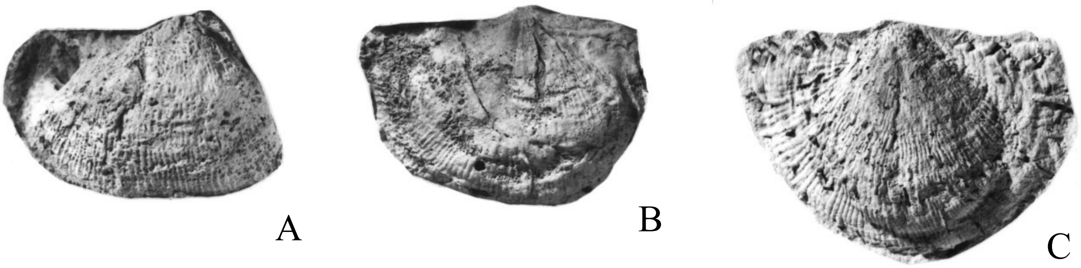


Fig. 82. *Bandoproductus* (*Bandoproductus*) *macrospina macrospina* Waterhouse. A, ventral valve UQF 43140. B, ventral internal mould, UQF 43141. C, latex external mould of ventral valve, UQF 43142 holotype. Specimens x1 from upper Burnett Formation, Yarrol Basin. (Waterhouse 1986b).

Stratigraphy: Type *Bandoproductus macrospina* (Waterhouse, 1986b) comes from the upper Burnett Formation of the Yarrol Basin (Maxwell, 1964) and is likely to be of late Asselian age, as discussed by Waterhouse (2015a, pp. 19, 39, 40), and the ventral valve figured by

Etheridge Jnr (1892, pl. 13, fig. 6) from the Burnett district of central Queensland appears to be conspecific. The species is abundantly represented in the Rammutt Formation of the Gympie region in southeast Queensland, and, as summarized below, *Bandoproductus walkomi* Briggs from the lower Rutherford Formation of the north Sydney Basin is possibly a subspecies, but is essentially conspecific. The species therefore is a useful marker as a zonal key. Given the limited validity of subspecies *walkomi,* any zone is better named after *macrospina* rather than *walkomi*, though Briggs preferred *walkomi* .

Bandoproductus **(*Bandoproductus*)** ***macrospina walkomi*** Briggs, 1998

Fig. 83

1986b *Cancrinelloides* (*Bandoproductus*) *macrospina* [not Waterhouse] – Waterhouse, p. 57, pl. 13, fig. 15, 16 [fide Briggs 1998] (part, not pl. 13, fig. 13, 14, 17, 18 = *macrospina*).
1998 *Bandoproductus walkomi* Briggs, p. 153, Fig. 77A-J.

Diagnosis: Close to *Bandoproductus* (*Briggsia*) *macrospina*, distinguished by finer ventral hinge species and variable presence of low commarginal rugae.

Holotype: UQF 75301 from lower Rutherford Formation, figured in Briggs (1998, Fig. 77C, D), OD.

Morphology: Ventral valves display a row of hinge spines and moderately numerous spines over the venter, with slightly swollen and prolonged spine bases. The ribs are strong, numbering nine to thirteen in 5mm anteriorly according to Briggs (1998, p. 153). According to Briggs, *walkomi* differs from *macrospina* in having weaker ventral hinge spines and in displaying on some specimens fine irregular rugae. Figures would suggest that the latter feature is not demonstrated in many specimens assigned to *walkomi* by Briggs, and that hinge spines in both suites vary a little in diameter and are not markedly or consistently different.

Stratigraphy: Briggs (1998) recognized co-occurrences of *walkomi* with *macrospina* amongst the type collections described by Waterhouse (1986b), and at Gympie both morphotypes are to be found. At least some Gympie specimens are less rugose than the types. The form *walkomi* was stated to occur in the Burnett Formation in the Yarrol trough and Silver Spur outlier, as well as Rutherford Formation and Rammutt Formation. Briggs (1998, p. 153) included in his synonymy reference to *Cancrinella levis* (Maxwell, 1964, p. 8, fig. 8e), and this seems to refer to a record, not an illustration, in the right-hand column of Maxwell's chart.

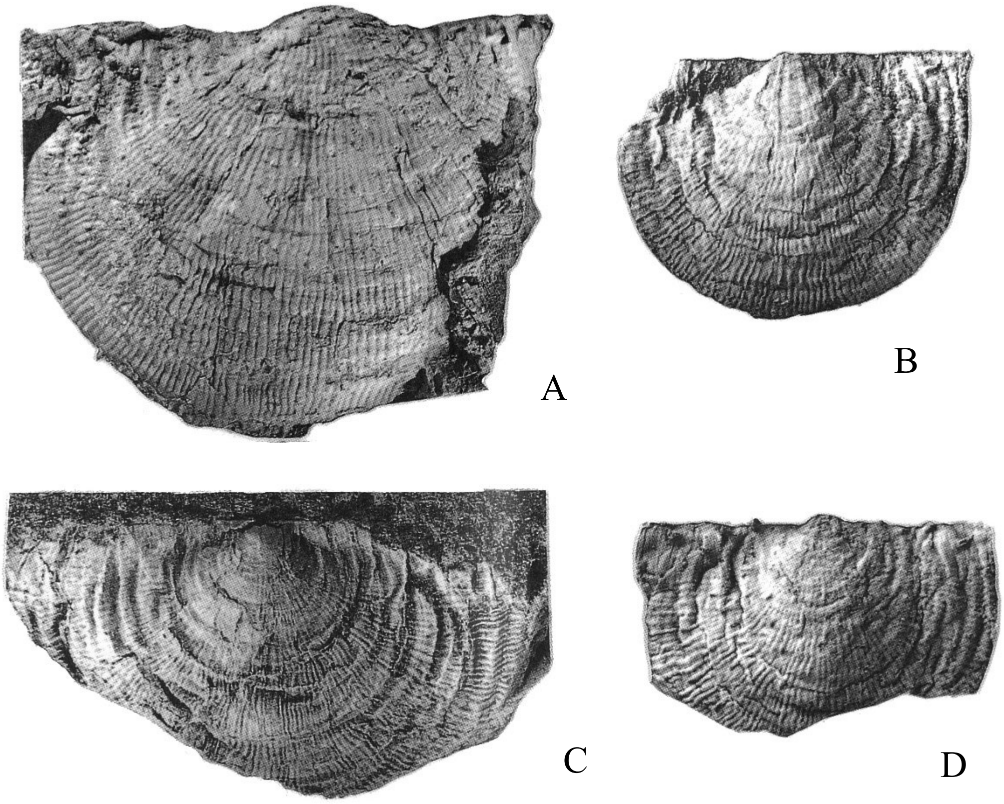


Fig. 83. *Bandoproductus* (*Bandoproductus*) *macrospina walkomi* Briggs. A, latex cast of ventral exterior, UQF 75300, x2. B, D, ventral internal mould and external latex cast of UQF 75302, x2. C, dorsal external mould UQF 75304, x2. From Silver Spur beds. (Briggs 1998).

Subgenus ***Briggsia*** Waterhouse, 2015b

Diagnosis: Shells moderately large for subfamily, ventral spines comparatively fine over venter and trail, each spine base not swelling and little if at all prolonged, hinge spines coarse and in a row along hinge. Posterior thickening substantial and ventral adductor scars very long.

Type species: *Bandoproductus* (*Briggsia*) *hastingsensis* Briggs, 1998, p. 149 from "Giro beds" of New South Wales, OD.

Discussion: The New South Wales species described as *Bandoproductus hastingsensis* and *B*. *youdalensis* by Briggs (1998) are outstanding in the nature of their costae which are little disrupted by the ventral spines, whereas the ventral body spines on type and other species typical of *Bandoproductus* have bases that are swollen and affect the costae strongly. *Lyonia* Archbold, 1983, p. 244 and *Nambuccalinus* Waterhouse, 2001, p. 33 are distinguished by the presence of dorsal spines, and *Ainimia* Waterhouse, 2013, p. 447 has a wide hinge, and body spines with swollen prolonged bases. *Nambdoania* Waterhouse, 2002b, p. 52 has comparatively narrow hinge and numerous body spines with swollen but short spine bases, and less prominent row of ventral hinge spines, whereas *Nikitinia* Kotlyar, Zakharov & Polubotko, 2004, p. 521 has prominent commarginal rugae and elongate ventral spine bases. The genus *Masitoshia* Waterhouse, 2013, p. 446 also has prominent commarginal rugae. Its hinge spines are fine and body spines few without prominent bases. The genera are reviewed by Brunton (2007, pp. 2656 ff) and Waterhouse (2013, p. 445 ff).

Bandoproductus* (*Briggsia*) *hastingsensis (Briggs, 1998)

Fig. 84

1998 *Bandoproductus hastingsensis* Briggs, p. 149, Fig. 75A-G.

Diagnosis: Large weakly transverse shells with fine costellae numbering seven to ten per 5mm, hinge spines strong and spaced far apart, spines fine over disc and trail, 0.3mm in diameter, arise from ribs without swollen bases, dorsal costellae six to eight in 5mm.

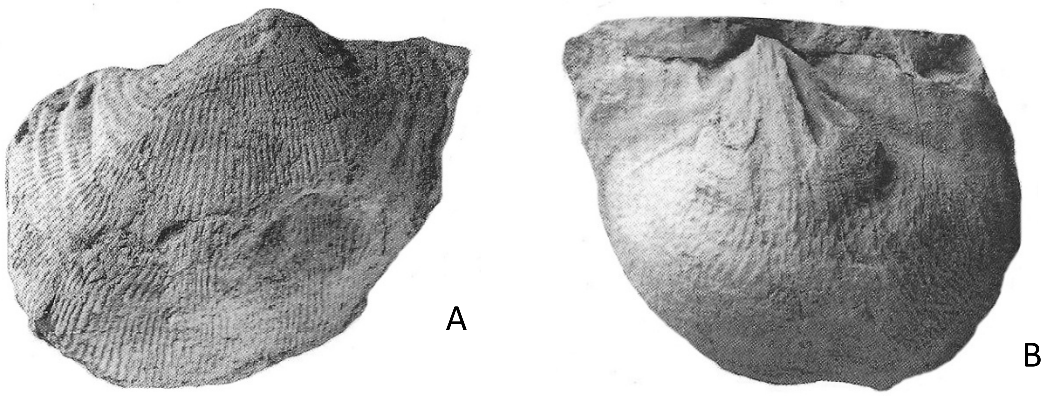


Fig. 84. *Bandoproductus* (*Briggsia*) *hastingsensis* (Briggs). A, latex cast of ventral exterior, holotype, UQF 75296, x2. B, internal mould of ventral valve, showing long embedded adductor scars, UQF 75297, x2. From Giro beds, New South Wales. (Briggs 1998).

Holotype: UQF 75296 figured by Briggs (1998, Fig. 75A, B) and Fig. 84A herein from Giro beds, New South Wales, OD.

Stratigraphy: The species is limited to the "Giro beds" in the Hastings Block in New South Wales, deemed to be of late Asselian age.

***Bandoproductus* (*Briggsia*) *youdalensis* (Briggs, 1998)**

Fig. 85

1998 *Bandoproductus youdalensis* Briggs, p. 152, Fig. 76A-E.

Diagnosis: Equidimensional to slightly elongate shells, with ventral valve somewhat arched and with prominent umbo, ventral costellae number six to eight in 5mm and strong. Dorsal costellae also broad, six to seven in 5mm. Ventral umbonal region strongly thickened.

Holotype: UNEF 12509 figured by Briggs (1998, Fig. 76A, C, E) and Fig. 85A herein from "Mooraback beds" of Hastings Block, OD.

Morphology: Variation is poorly known for this species.

Stratigraphy: The species is found in the "Mooraback beds" of the Hastings Block, and unnamed metasediments at Styx River in the Nambucca Block, deemed to be of upper Asselian age.

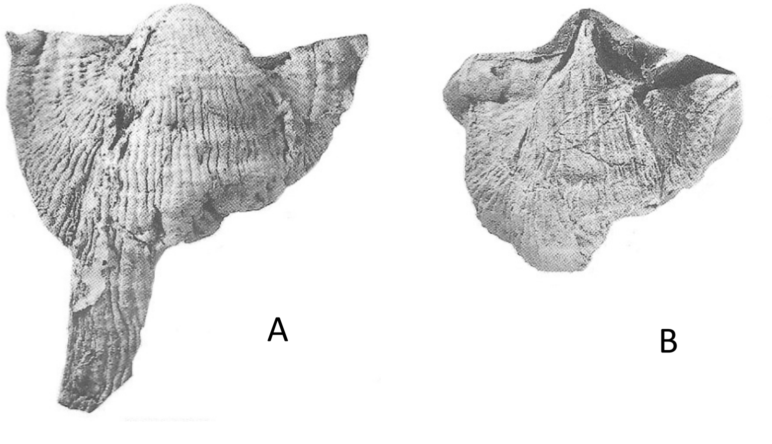


Fig. 85. *Bandoproductus* (*Briggsia*) *youdalensis* (Briggs). A, latex cast of external ventral valve holotype AMF 96252. B, ventral internal mould of same specimen. Specimens x1.5, from Hastings block, New South Wales. (Briggs 1998).

Genus **Nambuccalinus** Waterhouse, 2001

Diagnosis: Large transverse shallow-bodied shells, widest at hinge, large ears, acute cardinal extremities, two to three rows of long erect and sturdy spines along ventral hinge, scattered subprostrate ventral spines over ventral disc, with short extended bases, dorsal valve with numerous fine erect spines, absent from ears, no dimples.

Type species: *Nambuccalinus bourkei* Briggs, 1998, p. 147 from "Giro beds" of Hastings block, New South Wales.

Discussion: This genus is distinguished by the presence of dorsal spines, and development of more than one row of cardinal spines. Brunton (2007) suggested that the fact the interior of *Nambuccalinus* was like that of *Lyonia* may indicate that the two genera were synonymous, but students of Brachiopoda have long known that the dorsal internal features are usually more conservative than overall shape and ornament.

Nambuccalinus bourkei (Briggs, 1998)

Fig. 86

1955 *Linoproductus cora* var. *farleyensis* [not Etheridge & Dun] – Fletcher, p. 92.
1970 "*Linoproductus*" sp. nov. Runnegar, p. 709.
1979 *Cancrinella* cf. *lyoni* [not Prendergast] – Degeling & Runnegar, p. 11.
1987 ?*Lyonia* sp. Briggs, p. 135.
1998 *Lyonia bourkei* Briggs, p. 147, Fig. 74A-G.
2001 *Nambuccalinus bourkei* – Waterhouse, p. 33.
2007 *N. bourkei* – Brunton, p. 2656, Fig. 1776a-d.

Diagnosis: As for genus, repeating the diagnosis: Large transverse shallow-bodied shells, widest at hinge, large ears, acute cardinal extremities, two to three rows of long erect and sturdy spines along ventral hinge, scattered subprostrate ventral spines over ventral disc, with short extended bases, dorsal valve with numerous fine erect spines, absent from ears, no dimples.

Holotype: UQF 75314 figured by Briggs (1998, Fig. 74A) and Fig. 86A herein from "Giro beds" of Manning block, New South Wales, OD.

Stratigraphy: The species was described from the Nambucca Block at the Styx River and Halls Peak volcanics, and from the "Giro beds" of the Hastings Block. The age requires further study: the generic affinities point to an Asselian age, as accepted by Briggs (1998), whereas radiometric SHRIMP data suggests a Late Carboniferous age (Waterhouse 2000).

But admittedly the accuracy of SHRIMP evaluations, prior to manipulation, is far from reassuring.

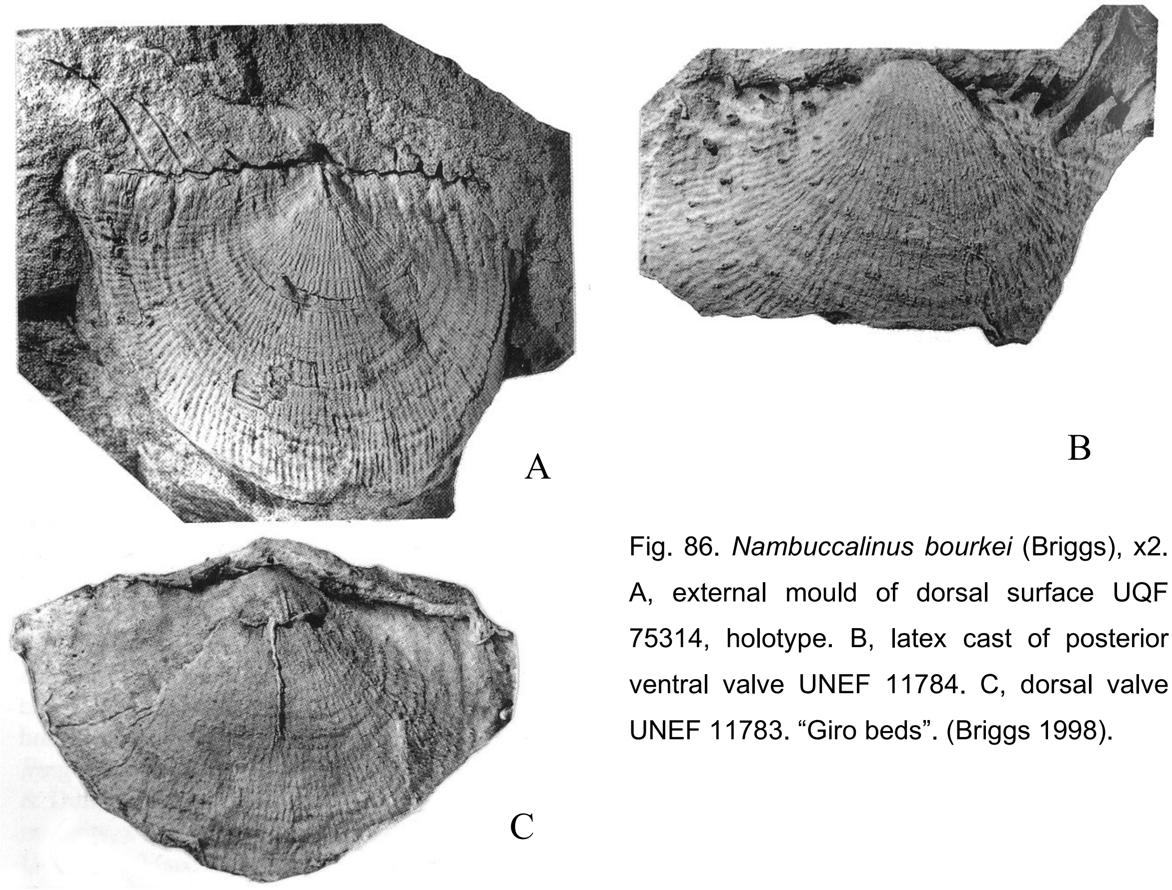


Fig. 86. *Nambuccalinus bourkei* (Briggs), x2. A, external mould of dorsal surface UQF 75314, holotype. B, latex cast of posterior ventral valve UNEF 11784. C, dorsal valve UNEF 11783. “Giro beds”. (Briggs 1998).

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APPENDIX 1

A NEW PAUCISPINIFEROID BRACHIOPOD GENUS FROM THE PERMIAN OF JAPAN

by

J. Tazawa & J. B. Waterhouse

Abstract

A new genus, *Hiranesania*, is proposed for *Terrakea japonica* Tazawa, 2008b, p. 316, found in the lower Kanokura Formation in the southern Kitakami Mountains of northeast Japan. The genus is a member of Subfamily Lamiproductinae Liang, Family Anidanthidae Waterhouse, and is distinguished by its numerous ventral spines.

INTRODUCTION

The present genus was collected by J. Tazawa and Y. Ibaraki in 2000 from shelly fine sandstone beds of the upper lower Kanokura Formation in the southern Kitakami Mountains (southern Kitakami Belt) in northeast Japan. The fossil locality KF217 is a road cutting along the Ishikagorisawa, a small tributary of Imosawa, Imo, Yahagi-cho, Rikuzentakata City, Iwate Prefecture. The age is considered to be Wordian Stage, Guadalupian Series (Middle Permian), based on ammonoid data (Misaki & Ehiro 2004; Ehiro & Misaki 2005). The specimens described in this study are registered and housed in the Department of Geology, Faculty of Science, Niigata University.

SYSTEMATIC DESCRIPTION

Order PRODUCTIDA Waagen, 1883

Suborder LINOPRODUCTIDINA Waterhouse, 2013

This group incorporates three superfamilies Paucispiniferoidea Muir-Wood & Cooper, Linoproductoidea Stehli and Proboscidelloidea Muir-Wood & Cooper, symplesiomorphic superfamilies that arose from the strophalosiiform Family Devonoproductidae. They share predominantly radial ornament but differ in details of spination and interior. Origins appear, from the fossil record, to have stemmed from a costellate chonetid, at least generically different from the smooth ancestors of various Productidina and Strophalosiidina.

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

[Nom. transl. Waterhouse 2013, p. 310 ex Paucispiniferinae Muir-Wood & Cooper, 1960, p. 319].

Diagnosis: Characterized by ventral strut spines in a number of genera. Shells small to medium in size, radial ornament usually prominent, no dorsal spines as a rule, interior may be close to that of marginiferoids in usually displaying prominent marginal ridges. Dorsal trails simple or mutiple.

Discussion: The superfamily is united by ancestry, available evidence for two of the families pointing to a source from the strophalosiiform Devonoproductinae. Some groups share strut spines, which are long and sturdy erect spines, evenly distributed over the ventral valve in some groups, in pairs, or along the median line, and early component members display lamellate dorsal valve..

Family **ANIDANTHIDAE** Waterhouse, 1968

Family Anidanthidae is of Carboniferous and Permian age, and its main subfamily constituent, Anidanthinae Waterhouse, 1968, is very like the progenital group Devonoproductinae in ornament and musculature, but differs in lacking teeth, sockets, interareas and large brachial shields. Ribs are well developed on both valves, and spines are erect, without prolonged bases, and never in the form of strut spines. The subfamily Anidanthinae was regarded as a member of Linoproductidae Stehli by Brunton et al. (2000, p. 530), but as shown by Waterhouse (2013), Linoproductidae descended from the Lower to Middle Devonian Subfamily Eoproductellinae Lazarev, 1987, a different group which lacks lamellae from the dorsal valve. Anidanthidae shares linoproductoid features with Linoproductidae, but the family groups evolved each from different though related ancestors. See Table 1, p. 82.

Subfamily **LAMIPRODUCTINAE** Liang, 1990

[Nom. transl. Waterhouse 2013, p. 335 ex Lamiproductidae Liang, 1990, pp. 204, 466].

The dorsal valve is not lamellate, and spines are found only on the ventral valve, and are erect, without prolonged bases. Costae branch strongly over the ventral valve, and are intercalated on the dorsal valve. Members so far are found only in the Middle and Upper Permian (Roadian to Wuchiapingian Stages), in Pakistan, Thailand, Timor and China, and now in Japan.

Name genus: *Lamiproductus typica* Liang, 1990, p. 205 from Middle Permian of China, OD.

Genus ***Hiranesania*** new genus

Derivation: Named from Mt Hiranesan, to the north of the fossil locality.

Diagnosis: Of medium size for subfamily, both valves strongly costate, spines erect and numerous over inner ears and umbonal slopes, arising from costal crests over visceral disc and trail. No strong posterior hinge ridge in dorsal interior.

Type species: *Terrakea japonica* Tazawa, 2008b, p. 336 from lower Kanokura Formation (Wordian) of southern Kitakami Mountains, southeast Japan, here designated.

Discussion: In many respects, the genus *Asperlinus* Waterhouse & Piyasin 1970, p. 132 comes closest to the new genus, at least with respect to its ornament of ribs and spines, because ventral spines are comparatively numerous, although not as dense as those of *Hiranesania*. *Asperlinus* is based on *Productus asperulus* Waagen, 1884, p. 693 from the lower part or Kufri Member of the Chhidru Formation (formerly Upper Productus Limestone) of the Salt Range, Pakistan (Waterhouse 2010). Occurrences of *Asperlinus* are also known in the Wuchiapingian faunas of Timor, and in the early Middle Permian of Thailand. *Asperlinus* has moderately strong ribs, not quite as strong as those of the new genus. Close-set erect spines lie over the ventral disc and trail, and spines are few over the umbonal slopes and inner ears, with signs that a row of spines is developed along the hinge (Waagen 1884, pl. 79, fig. 3a, b). Liang (1990, p. 204 [p. 466]) referred two species of similar appearance to his new genus *Lamiproductus* Liang from a Capitanian fauna in Zhejiang, China. Spine detail is not entirely clear for *Lamiproductus typica*, and is better revealed in the figure for *L. usualis* Liang (1990, p. 207, pl. 35, fig. 13), but overall it appears that the two forms are very close, and *Lamiproductus* seems likely to prove to be a junior synonym of *Asperlinus*. The type species of both *Asperlinus* and *Lamiproductus* display internal well-formed posterior dorsal ridges that slope obliquely forward from the hinge (Liang 1990, text-fig. 26), whereas such ridges are not known for the species *japonica* from Japan. Liang (1990) referred *Lamiproductus* to a new family Lamiproductidae, which was treated as a tribe within Anidanthidae by Waterhouse (2013). The proposal by Brunton et al. (2000, p. 544) that *Lamiproductus* was a synonym of *Pseudohaydenella* Liang, 1990 and not close or identical to *Asperlinus* must be set aside. Although *Pseudohaydenella* is poorly known in some respects, it clearly differs in shape and ornament from *Asperlinus*. The genus may be close to *Chianella* Waterhouse, 1975 as suggested by Brunton et al. (2000), or otherwise related to Chonetellinae Licharew.

In summary, the new genus is distinguished by its strong ribs and by the crowded and erect ventral spines. The small and posteriorly placed muscle scars are features shared with *Stepanoviella* and *Liraria*. Internally, the new genus lacks the strong posterior dorsal ridges that typify *Asperlinus* and its possible junior synonym, *Lamiproductus*.

Hiranesania japonica (Tazawa, 2008b)

Fig. 1, 2

2008a *Terrakea* sp. A Tazawa, p. 63, Fig. 2A-L.
2008b *Terrakea japonica* Tazawa, p. 336, Fig. 3A-L.

Diagnosis: Average size for subfamily, shells slightly transverse to elongate, generally with median ventral sulcus, may be slightly nasute anteriorly, ventral spines particularly numerous, and some open into interior.

Holotype: NU-B702, figured by Tazawa (2008b, Fig. 3A-C) from locality KF217, lower Kanokura Formation, Japan, OD.

Material: Topotype material as elaborated by Tazawa (2008b) includes specimens NU-B702 to 708, plus NU-B710 and three small fragmentary ventral valves, not registered. (Specimen NU-B709 is judged to be a specimen with valves conjoined, of a different genus and species). Material is preserved as natural external and internal moulds, with no shell remaining.

Dimensions in mm: specimens incomplete, partly deformed.

Specimen NUB	Width	Length	Height	
704	23	28	9.5	dorsal valve and internal mould
705	19.5	24	11	internal mould
703	27.5	19.5	9.5	ventral external mould
707	26	27	9	ventral internal mould
702	32.5	28	8	internal mould and dorsal external mould

Description: Specimens of size normal for members of the subfamily, vary from weakly transverse to slightly elongate, hinge wide and at or close to maximum width, which lies in some specimens near anterior third of shell length. Ears small but well-formed, the ventral ears convex, the dorsal ears concave. Ventral umbonal slopes moderately steep but low, and umbo projects a little beyond hinge, with angle of 90° to 110° affected by distortion. A shallow sulcus with angle close to 20° and corresponding dorsal fold commence close to the dorsal beak in half of the specimens, whereas other ventral valves are medianly convex, and dorsal valves concave, without fold. The trail is slender and up to a third of the length of the shell, and non-geniculate, except where specimens have been slightly crushed and distorted.

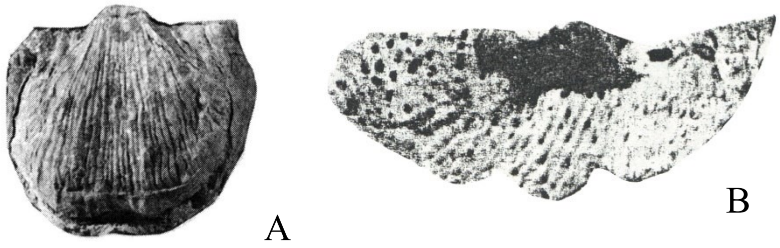

Fig. 1. *Hiranesania japonica* (Tazawa). A, ventral external mould, x1. B, external mould of ventral valve, x2 approx. Lower Kanokura Formation, South Kitakami belt, Japan. (Tazawa 2008b).

In some specimens the sulcus and fold if present disappear anteriorly and the anterior margin becomes weakly nasute. Both valves are ornamented by strong costae, six in 5mm anteriorly, the ventral ribs branching, and dorsal ribs increasing by intercalation. Ribbing is fainter over the umbonal slopes, and absent from the ears. Low commarginal rugae lie over the posterior dorsal valve, and scattered irregular growth stops and laminae are present on both valves, especially the posterior trail, but growth increments are not preserved. Spines are limited to the ventral valve and are erect without prolonged bases. They are crowded over the inner ears and umbonal slopes, with five in 5mm, and are missing from the outer ears near the hinge in NU-B703, but appearing to extend as far as the hinge in a small unregistered specimen. There is no special row of spines along the hinge or umbonal slopes. Finer spines arise along the ribs, two to three in 5mm. Internal moulds show that a few spines open into the interior over the anterior disc and trail.

The ventral interior is dominated by the imprint of costae from the exterior. Adductor scars are only faintly recognizable and placed close to the posterior wall, with shallow anterior diductor impressions, posteriorly impressed in NU-B710. In this specimen which is comparatively mature, the posterior wall is smooth, and fine sharp pustules may be discerned over much of the valve amongst the irregular rugations from the external costae. The cardinal process appears to have a high shaft, but is somewhat obscure. The median septum is clearly defined and extends for approximately a third of the length of the valve and may end in a terminal pillar. Adductor scars are posteriorly placed, and tend to be smooth and subtriangular in shape, but not clearly divided into anterior and posterior pairs, perhaps obscured by poor preservation and the imprint of external costation. Brachial shields are small and laterally placed, the septum terminating about half way along their length. There is no strong marginal ridge sloping forward obliquely from the hinge, but the brachial shields are linked to a moderately strong ridge. The floor of the valve bears numerous moderately large pustules, close in spacing to that of the spines of the ventral exterior.

Fig. 2. *Hiranesania japonica* (Tazawa). Ventral internal mould NU-B708, x5 approx., from a small tributary of Imosawa, Imo, Iwate Prefecture, Japan, showing smooth adductor scars between arrows. (Waterhouse 2013).

Discussion: We have been unable to find any other material that is comparable in morphology, but several species come moderately close. *Productus asperulus* Waagen (1884, p. 693, pl. 79, fig. 3-6) from the “Cephalopod bed” of Jabbi and Chhidru and upper

Wargal Limestone at Kafirkot in the Salt Range, Pakistan, is of smaller size, and although spines are moderately numerous over the venter, there is no array of posterior lateral spines as in *japonica*. This species is now the type species of *Asperlinus* Waterhouse & Piyasin (1970, p. 132), and is of Wuchiapingian (lower Upper Permian) age (Shen et al. 2003), not upper Lower Permian and Upper Permian (Capitanian) as claimed by Brunton et al. (2000, p. 537). (It should be noted that Capitanian is Middle Permian, as shown by Jin et al. 1997, rather than Upper Permian as claimed by Brunton et al. 2000). Rothpletz (1892, p. 76, pl. 10, fig. 14) and Hamlet (1928, p. 27, pl. 5, fig. 2, 4, 5) reported the species *asperulus* from Ajer Mati, Basleo and other Wuchiapingian localities in Timor, and the specimens are moderately close, but require first hand examination: the spines are not clearly illustrated. Frech (1911, p. 162) referred one of Waagen's specimens (pl. 79, fig. 3f-h) to *Productus sino-indicus* Frech (1911, pl. 22, fig. 1a, b, c, 2). Frech's species is dictyoclostid, together with a Salt Range specimen that he figured, wrongly, as *asperulus* (Frech, 1911, pl. 22, fig. 1d, e), but true *asperulus* is not dictyoclostid, so that Hayasaka (1922) and Reed (1931, p. 2) refused to accept Frech's claim.

Specimens initially allocated to species *asperulus* by Waterhouse & Piyasin (1970) from the lower Ratburi Limestone at Khao Phrik, southern Thailand, of Roadian (Middle Permian) age, have coarser costae and slightly more numerous spines, with none over the ears or umbonal slopes, compared with *asperulus*. These specimens are now referred to *Asperulus yanagida* Waterhouse, 2004, p. 38, distinguished by more elongate outline, sturdier costae and more numerous ventral spines. Yanagida (1970, p. 15, fig. 15a-d) figured a ventral valve from the same locality as *Cancrinella* sp. indet. that shows numerous spines, including an apparent hinge row and a few over the umbonal slopes, and of two ventral valves figured by Waterhouse & Piyasin (1970), one has some spines close to the hinge, and the other seems to lack such spines.

The Chinese material described as *Lamiproductus typica* Liang (1990, p. 205, pl. 35, fig. 1-12, 14-8, text-fig. 26) from the Lengwu Formation (Capitanian) of Zhejiang Province, China, is moderately close, with more branching ribs, and apparently fewer spines. Internally the dorsal valve displays oblique posterior ridges as in the Salt Range material, and it appears that the species are congeneric with *Asperlinus*. *L. usualis* Liang (1990, pl. 35, fig. 13) is more transverse, but lacks a sulcus, and looks to be close to the other species.

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APPENDIX 2

TRIBE MEGOUSIINI IN NORTH AMERICA

Abstract

Species and genera from United States and Canada that belong to Tribe Megousiini are reviewed.

INTRODUCTION

Tribe **MEGOUSIINI** Waterhouse, 2018

[Megousiini Waterhouse, 2018, p. 225].

Diagnosis: Distinguished from Anidanthini by having a denticulate hinge, and strong tendency for ventral ears to be bifid.

Discussion: Members of the tribe are distinguished from the southern counterparts of the Permian world, chiefly in east Australia, by the denticulate hinge. Another difference that pertains to many species, but not all, is the presence of bifid dorsal ears, as illustrated herein in Fig. 1 and 2. Bifid ears are displayed principally by species belonging to the genus *Megousia* Muir-Wood & Cooper, 1960, with a number of species described from the Permian beds of the Glass Mountains in Texas by Cooper & Grant (1975). Such features are never seen in Anidanthini.

Genus ***Megousia*** (***Megousia***) Muir-Wood & Cooper, 1960

The bifid appearance of the dorsal ears is caused by a small lateral projection along the hinge, and a much larger extension in front of the main ear, which in many specimens may be

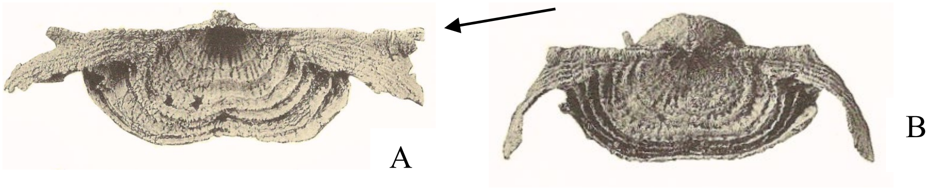

Fig. 1. *Megousia* (*Megousia*) *auriculata* Muir-Wood & Cooper. A, dorsal aspect of small paratype USNM 124108d, x2, with arrow pointing to small posterior ear, giving a bifid appearance. B, dorsal aspect of mature specimen, USNM 104108b, holotype, showing slender trail, x2. Wordian of Texas. (Muir-Wood & Cooper 1960).

twisted. The posterior extension along the hinge matches the extension along the hinge of the ventral ears, and the ventral valve shows no larger anterior extension to match that of the dorsal valve (Fig. 2A, B).

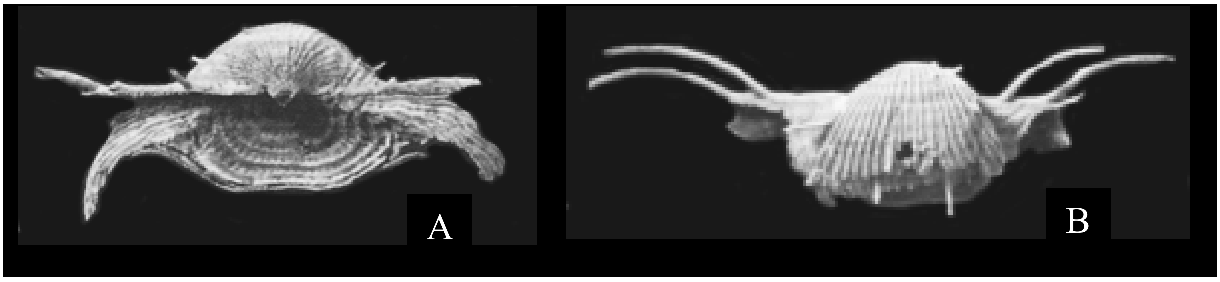

Fig. 2. A, B, *Megousia* (*Megousia*) *auriculata* Muir-Wood & Cooper. A,, dorsal aspect of conjoined specimen, showing bifid dorsal ears, USNM 149940u, x2. B, ventral aspect of USNM 149936, x1.9. From Road Canyon Formation, Texas. (Cooper & Grant 1975).

Other species assigned to *Megousia* from the Glass Mountains by Cooper & Grant (1975) show a similar arrangement, including the species they described as *flexuosa* and *mucronata*. For the species *umbonata*, a particularly swollen species, most examples have bifid ears, but a few are monifid, or almost monifid, and the species *M. definita* Cooper & Grant (1975, pl. 449) from the Willis Ranch Member in the Glass Mountains has a very reduced or non-bifid appearance, though the ventral ears are moderately extended. The anterior lateral extensions of the dorsal ears are also less than in other species.

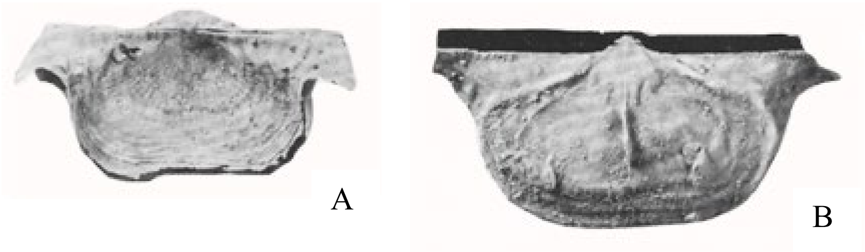

Fig. 3. *Megousia* (*Megousia*) *definita* Cooper & Grant. A, dorsal view of holotype, USNM 149953a, x2. B, dorsal interior, USNM 149953h, x2. From Willis Ranch Member, Word Formation. (Cooper & Grant 1975).

Of other species assigned to *Megousia* by Cooper & Grant 1975, *M*? *girtyi* (King, 1931, p. 76, pl. 17, fig. 3, 5a, b, not 4) and refigured by Cooper & Grant (1975, pl. 452, fig. 1-5) is too incomplete to be recognized, with only small and apparently earless ventral valves illustrated. It could even belong to *Protoanidanthus*, if it is anidanthid. The shells assigned to *Megousia*? *waageniana* (Girty, 1909, pl. 12, fig. 6, a-c, 7, 7a} by Cooper & Grant (1975) from the Capitanian looks like *Fusiproductus* Waterhouse, 1966.

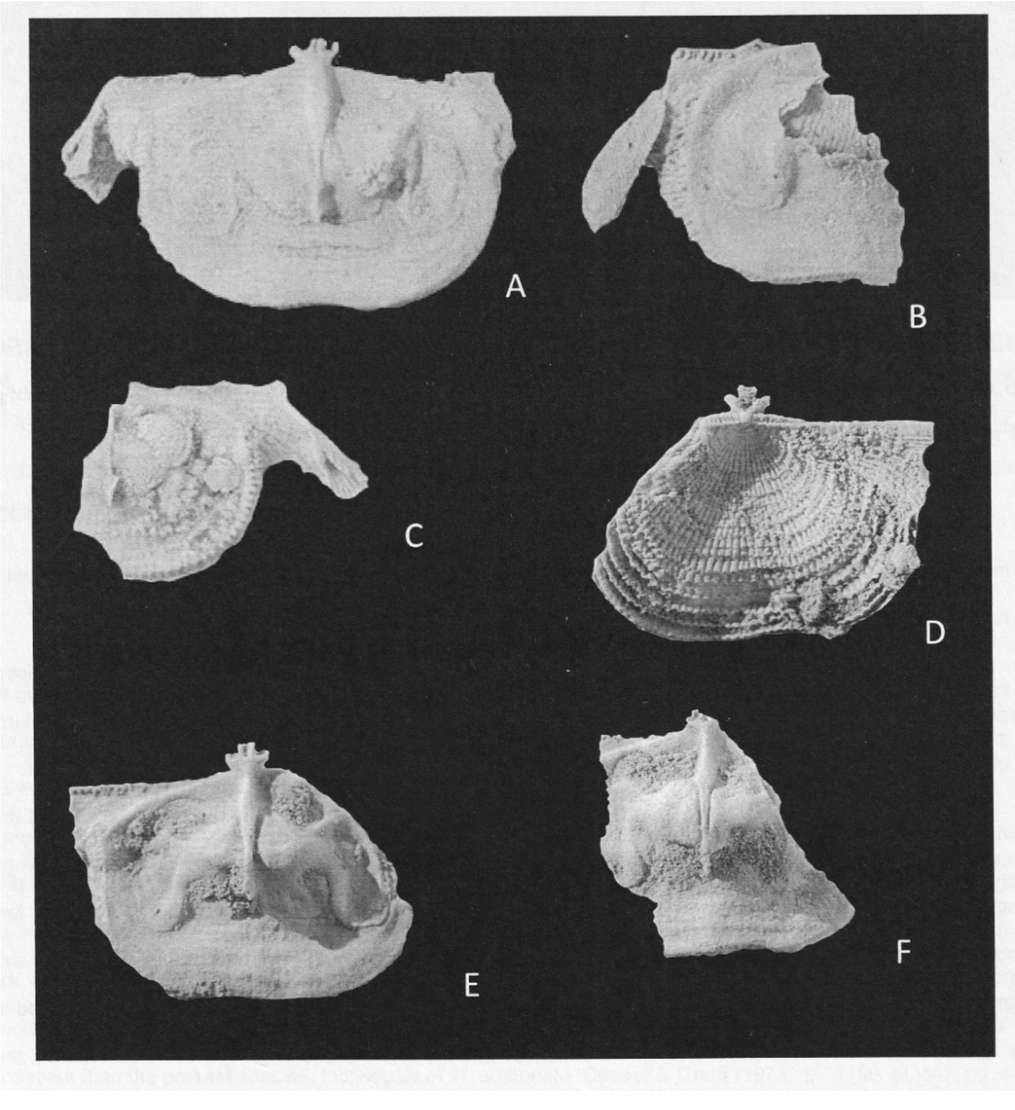

Fig. 4. *Megousia* (*Megousia*) *tortus* Waterhouse. A, dorsal internal mould GSC 140811. B, dorsal internal mould GSC 140812. C, dorsal internal mould GSC 140813. D, E, external and internal aspects of GSC 140814. F, dorsal interior GSC 140815. Specimens x2, from unnamed sandstone in Richardson Mountains, Yukon Territory. (Waterhouse 2020).

Megousia tortus Waterhouse, 2020 from Canada approaches *M. definita*, and lacks well developed bifid ears, but shows feeble development of bifid ears, and the anterior long extension is twisted, or partly twisted, like those of the Texan species.

Fig. 5. *Megousia* (*Megousia*) *tortus* Waterhouse, GSC 27030, x2, holotype, dorsal interior, showing twisted dorsal ear, from Permian sandstone unit, Yukon Territory, Canada. (Waterhouse 2013).

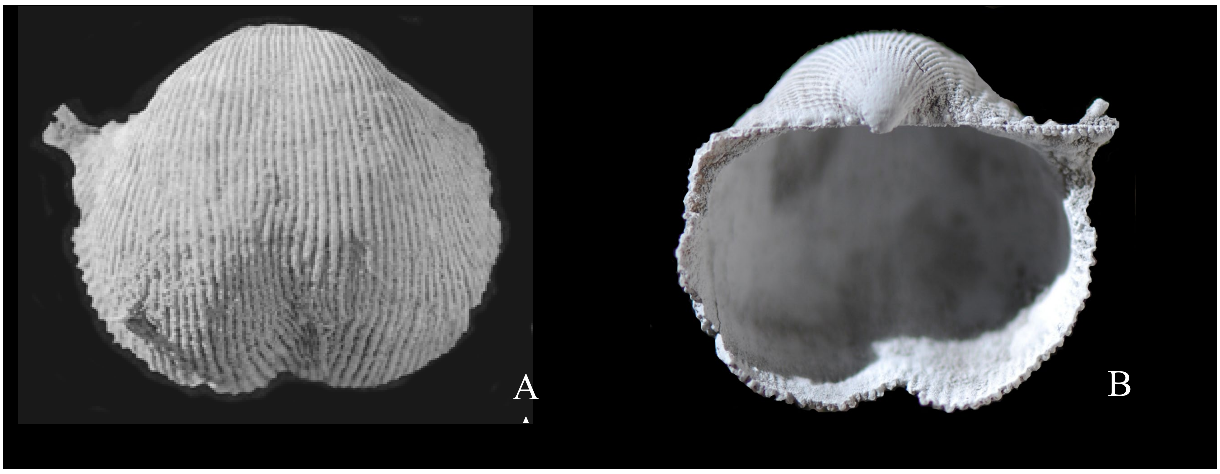

Fig. 6. *Megousia* (*Megousia*) *tortus* Waterhouse. A, B, ventral exterior and internal aspects, GSC 140804, x2. From unnamed sandstone McDougal Pass, Richardson Mountains, Yukon Territory. (Waterhouse 2020).

Subgenus ***Ogamousia*** n. subgen.

Derivation: ogam, mode of Arctic script.

Diagnosis: Medium to large anidanthids with strong radial costae, spines limited to row close to ventral hinge and over the ventral disc, dorsal valve thickened into wedge, and only gently concave with short trail, dorsal ears large and extended, bifid, with no sign of twist. Hinge with coarse denticles.

Type species: *Kuvelousia leptosa* Waterhouse, 1968, p. 1181 from Canyon Butte Formation, Cornucopia Quadrangle, Oregon, OD.

Discussion: A new subgeneric name is introduced for the species described as *Kuvelousia leptosa* Waterhouse, 1968. Originally the species was considered to belong to the genus *Kuvelousia* Waterhouse, 1968, because it shared a wedge-shaped dorsal valve, but the relationships are reassessed, because the species *leptosa* has extended dorsal ears that are bifid, with a small ear projecting laterally along the hinge, behind a much large extension that reached laterally and forwards. In this detail, *leptosa* is like *Megousia* Muir-Wood & Cooper, 1960. But although *leptosa* shares bifid dorsal ears with *Megousia*, it may be readily distinguished by its wedge-shaped greatly thickened dorsal valve, and as well the dorsal ears show no sign of a lateral twist. Denticles are present along the hinge, as in *Megousia*, but more strongly developed.

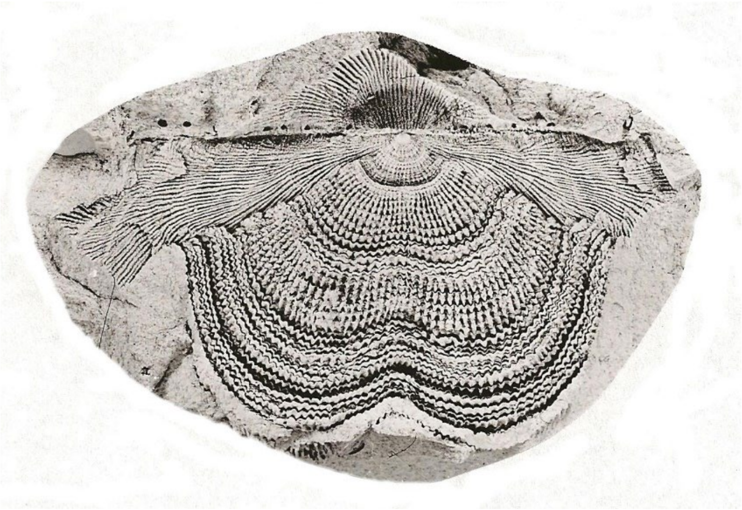

Fig. 7. *Megousia* (*Ogamousia*) *leptosa* (Waterhouse), dorsal external mould and posterior part of ventral valve with row of hinge spines, left as holes. USNM 151591j, holotype, x2. From Canyon Butte Formation (Sakmarian), Oregon, United States. (Waterhouse 1968).

Megousia (***Ogamousia***) ***leptosa*** (Waterhouse, 1968)

Fig. 7, 8F

1968 *Kuvelousia leptosa* Waterhouse, p. 1181, pl. 156, fig. 1-16.
2013 *K. leptosa* – Waterhouse, Fig. 15.18, p. 327,
2021 “*K*”. *leptosa* – Waterhouse, p. 84, Fig. 6.

Holotype: USNM 151591j, figured in Waterhouse (1968, pl. 156, fig. 4, 9, 11, 12, 14, 15) from Canyon Butte Formation, Oregon, OD.

Resemblances: In many respects this species approaches *Kuvelousia sphiva* Waterhouse 1968 from the Canadian Arctic, in size, shape, ornament, denticulate hinge and wedge-like dorsal valve, but is like *Megousia* in its bifid dorsal ears, though wedge-like dorsal valves are not known in *Megousia* ss.

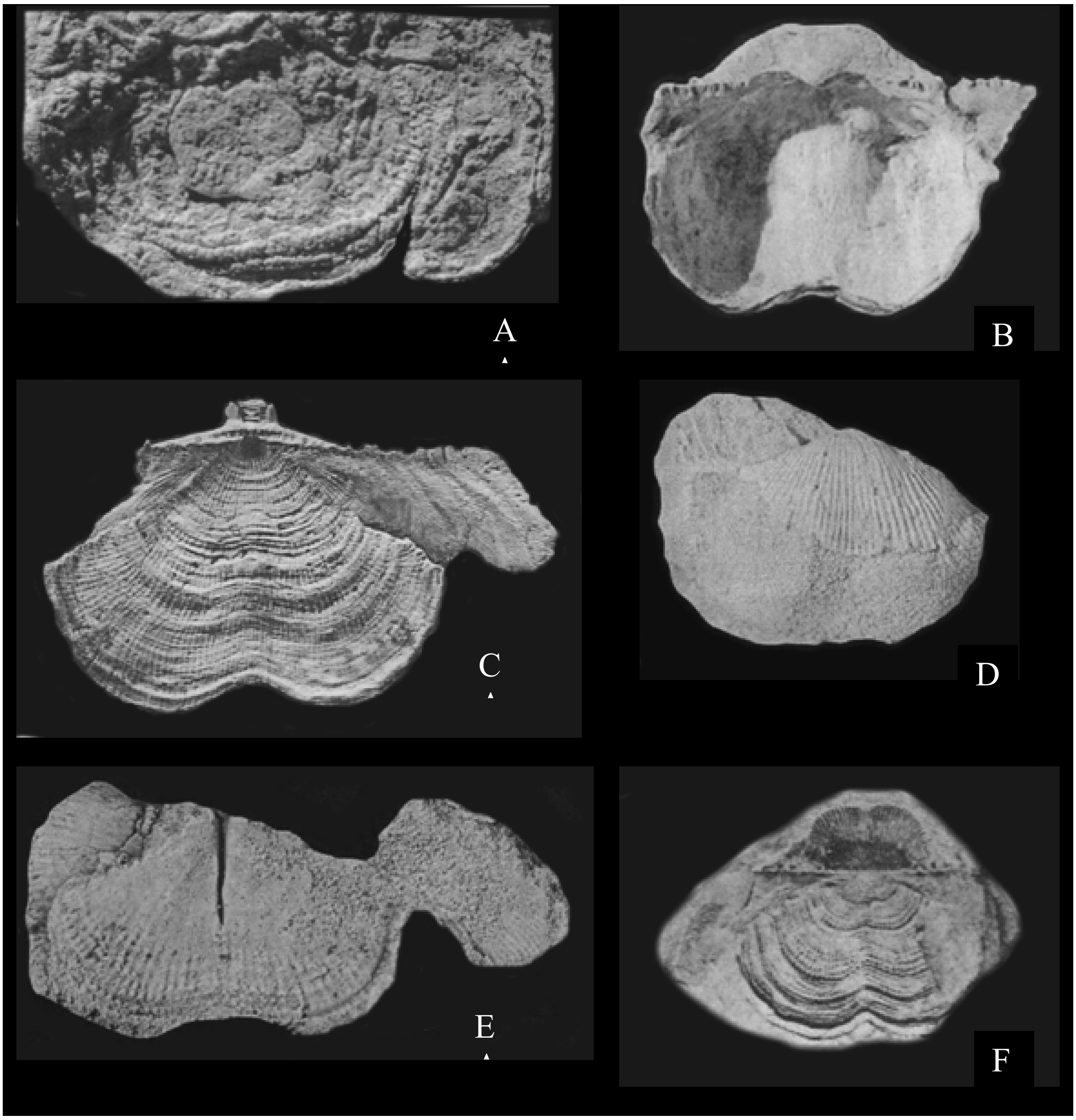

Fig. 8. A, *Kuvelousia* sp. dorsal aspect showing large auricle on right side, x2. From Late Carboniferous Member A, Jungle Creek Formation, Yukon Territory. (Waterhouse 2018). B, C, *Kuvelousia sphiva* Waterhouse. B, ventral interior, C, dorsal exterior, unregistered specimens at Geological Survey of Canada, Ottawa, x2, From Cameron Island, Canadian Arctic. (Waterhouse 2013). D, E, *K. perpusillus* Waterhouse. D, ventral exterior GSC 140827 holotype. E, dorsal internal mould GSC 140833, x2. From Degerböls Formation?, Ellesmere Island. (Waterhouse 2020). F, *Megousia* (*Ogamousia*) *leptosa* Waterhouse, dorsal view external mould, USNM 151591a, x1.5. From Canyon Butte Formation, Oregon. (Waterhouse 1968, 2020).

Genus ***Kuvelousia*** Waterhouse, 1968

Fig. 8A-E

Several species of *Kuvelousia* are found in northern Canada. The genus is distinguished by its thickened dorsal valve, which retains the denticulate hinge of *Megousia,* but shows no sign of bifid dorsal ears. In the earliest known species (Waterhouse 2018), the dorsal ear extends forward from the hinge (Fig. 8A). It comes from the *Septospirifer tatondukensis* Zone in the lowest unit, Member A, of the Jungle Creek Formation, deemed to be of Late Carboniferous age. *Kuvelousia sphiva* Waterhouse, 1968 comes from the Trold Fiord, Degerböls and Assistance Formations of the Canadian Arctic, and is distinguished by the deep ventral sulcus, with dorsal ears extending laterally along the hinge, and *K. perpusillus* Waterhouse, 2020 is a more transverse shell with shallow ventral sulcus, from the Degerböls and Assistance Formations, and possibly the Tahkhandit Formation of Yukon Territory on mainland Canada. The dorsal ears are widely splayed.

A summary of some of the other occurrences of *Kuvelousia* especially from Spitsbergen, and also Russia, is provided in Waterhouse (2020, pp. 160, 161).

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

_____ 2021: A fossiliferous block from Stephens Island. Earthwise 18: 79-122.

INDEX

Selective index to species and subspecies, with information on taxa assigned previously to different genera