EARLY PERMIAN CONULARIIDA, BRACHIOPODA AND MOLLUSCA FROM HOMEVALE, CENTRAL QUEENSLAND

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This monograph describes most of the brachiopods and molluscs that are found in the richly fossiliferous Permian outcrops of the Tiverton Formation near Homevale Station, inland from Mackay in north central Queensland, Australia. The fossils were collected by staff and students and colleagues at the Department of Geology and Mineralogy at the University of Queensland from outcrops that are now part of Homevale National Park, and the material is kept at the Queensland Museum and Science Centre Annex at Hendra in Brisbane.

The study is dedicated to the memory of Professor Dorothy Hill, who did so much to foster paleontological studies, and in honour of two of her post-war students, G. R. Maxwell and K. S. W. Campbell who initiated the detailed post-World War II studies on the paleontological record at Homevale.

SUMMARY

More than 90 species of Brachiopoda and Mollusca are described from one of the richest macro-fossil locations known amongst Permian outcrops in east Australia, in the Tiverton Formation at Homevale, north Bowen Basin, Queensland. Faunas are arranged in successive assemblages, commencing with a band of rock bearing only two Early Permian brachiopod species, followed by representatives of the *Bookeria pollex* Zone, then the *Bookeria geniculata* Zone with the *Svalbardia armstrongi* Subzone at the top, and *Taeniothaerus subquadratus* Zone. These zones reflect the evolution of marine invertebrates in response to episodic climate change during the Permian Period. Based on brachiopod, bivalve and gastropod correlations with Western Australia, and widely through Gondwana, the zones are deemed to be of Sakmarian age. The Early Permian (Cisuralian) biozones for macro-fauna in Australia are reviewed and shown to fall close in number to the conodont zones based on Permian outcrops of eastern Europe and fore-Urals in Russia. Macro-faunal correlations with the zonal succession in Western Australia indicate that trans-Australian palynomorph biozones vary in sequence and duration either side of the continent, although more in phase with each other across Australia during early Cisuralian and Guadalupian (Early and Middle Permian) time. In particular, it appears that the *Pseudoreticulatispora pseudoreticula* Zone appeared later in Western Australia than in east Australia.

New genera are proposed, brachiopods *Bookeria*, type species *Bookeria sparsispinosa* n. sp. (Family Paucispinauriidae), and *Validifera*, type species *Ingelarella valida* Campbell, 1961 (Family Ingelarellidae Campbell), bivalves *Zigzagia,* type species *Glyptoleda buarabae* Campbell, 1951 (Family Polidevciidae Kumpera, Prantl & Ružička) and *Protraxia*, type species *Cardiomorpha gryphoides* de Koninck (Family Pachydomidae), and gastropod *Globosospirina,* type species *G. mcclungi* n. gen., n. sp. (Family Phymatopleuridae). Additional newly proposed species and subspecies are *Svalbardia armstrongi* n. sp., *S. saeptata* n. sp., *Echinalosia cenula* n. sp., *Maxwellosia bryani* n. sp., *Lakismatia sulcata* n. sp., *Bookeria drysdalei* n. sp., *Notostrophia laticostata* n. sp., *Plekonella whitehousei* n. sp., *Notospirifer triplicata* n. sp., *Papulinella wilsoni* n. sp. , *Fletcherithyris burdenae* n. sp., *Maorielasma balfei* n. sp., *Eremithyris*? *longinquincus* n. sp., *Yanceyopsis alleni* n. sp., *Pseudomyalina perquiritus* n. sp., *Merismopteria cona* n. sp., *Orbiculopecten cokeri* n. sp. , *Eurydesma glaebula* n. sp., *Etheripecten playfordi* n. sp., *Primaspina banksi* n. sp., *Stutchburia laminata* n. sp. and *Astartella heideckeri* n. sp.

A new tribe of Gastropoda, Walnichollsiini is erected, based on *Walnichollsia* Fletcher, 1958, within Family Phymatopleuridae.

Copies of this monograph may be purchased from

The author at 25 Avon Street, Oamaru 9400, New Zealand.

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	Attenuocurvus beds		
Artinskian	*Echinalosia conata*		Wall Sandstone
	Spinomartinia adentata		?
	Ingelarella plica	Tiverton Formation	upper beds
Sakmarian	***Taeniothaerus subquadratus***		middle beds
	Bookeria geniculata		
	Bookeria pollex		lower beds
Asselian	*Bandoproductus macrospina*		basal beds
	Crassispinosella subcircularis	Lizzie Creek Volcanic Group	
	Strophalosiaria concentrica		

Table 1. International stages matched with marine invertebrate biozones in east Australasia, set against the marine succession for formations and members in the north Bowen Basin, Queensland, with the Wall Sandstone which may be terrestrial. The principal Tiverton biozones discussed in this study are shown in bold font. Gaps in the sequence within the formation are ignored. The Wuchiapingian Stage is oversimplied, and is briefly outlined further in the Appendix , p. 348.

INTRODUCTION

Homevale is the name of a farming station north of the settlement of Nebo, central Queensland, and the name Homevale has been extended by geologists to a highly fossiliferous low ridge (Fig. 1) located within the western end of the Homevale National Park, just east of the homestead. The fossils were first collected in the late nineteenth century, with several described in Jack & Etheridge (1892). More intensive stratigraphic and paleontological study commenced in the 1950's, especially under the aegis of the Department of Geology & Mineralogy, University of Queensland, Brisbane, by graduate students, some of whom later took employment at the University of New England at Armidale, Australian National University, Canberra, and Sydney University. The focus on Late Paleozoic stratigraphy and faunas was undertaken as a deliberate policy on the part of Professor Dorothy Hill, as she explained in a history of the first fifty years of the department (Hill 1981, p. 13). Hill (1950) and Maxwell (1954, 1964) made initial studies of some Productida, and Campbell (1959, 1960, 1961a, 1965), who started at the University of Queensland and later moved to the University of New England, Armidale, and then Australian National University, Canberra, provided leading studies in brachiopod monographs on Ingelarelloidea and Terebratulida. Isbell (1955) offered an extensive geological map that included Homevale, and noted aspects of the stratigraphy. Later Armstrong (1968–1970) closely studied a number of Homevale brachiopod species, and Runnegar (1965, 1966, 1967) helped initiate studies of pholadomyan bivalves, and the two combined with another university graduate to study ammonoid specimens (Armstrong, Dear & Runnegar 1967). As well, Wass (1968) listed and described several bryozoan species when he moved to the University of Sydney. In the meantime, the region was mapped geologically by the then Bureau of Mineral Resources (now Geoscience Australia), Canberra, in co-operation with the Geological Survey of Queensland (Malone et al. 1966), and Dickins (1961a, 1963), who worked in the Bureau of Mineral Resources and completed a Ph. D. study at the University of Queensland, made some reference to Homevale bivalves. In 1976 Runnegar, then based at the University of New England, cooperated with Pojeta from the United States Geological Survey in a comprehensive study on Rostroconchia, and described a new genus and species from Homevale. From the University of Queensland and later conducting post-doctoral study at Deakin University and then University of New South Wales, Briggs (1998, in Waterhouse et al. 1983) studied several Productida. Archbold (1983b) from Melbourne University wrote on a chonetid brachiopod, and Clarke (1970), Geological Survey of Tasmania, named a new strophalosiid. These studies have imparted considerable significance to the Homevale beds, by erecting no less than seven new genera based on material from the outcrops. The various studies, mostly in short and scattered articles published in a variety of Australian, German and American journals, together with the few accounts by the present author, covered about a third of the macro-fossil species to be found at Homevale. The aim of this study is to review and where necessary update descriptions and identifications, describe the various species and genera not so far recorded, and provide comprehensive illustrations, and discuss the question of correlation. The focus is on Brachiopoda and Mollusca apart from Orthoceratida. Species of bryozoa and crinoids and microfauna are not studied, and corals appear to be absent. Particular attention is paid to species lineages within Strophalosioidea, Aulostegoidea, Linoproductidina, Ingelarelloidea and Pectinida, groups abundantly represented in east Australia. On the basis of faunal descriptions and revisions, the problem of trans-Australian correlations is addressed and some adjustment made to the biozonal succession for macro-faunas. Evidence suggests that palynomorph biozones are not identical in sequence and duration either side of the continent.

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PART 1

OVERVIEW OF STRATIGRAPHY AND FOSSILS

1. Tiverton Formation

The fossiliferous beds at Homevale (Fig. 1) have long been collected for their abundant macro-invertebrate faunas, and have been discussed by Jack & Etheridge (1892), Whitehouse (1928), Reid (1929), Isbell (1955) and Campbell & Tweedale (1960). The rocks are now placed in the Tiverton Formation, proposed by Malone et al. (1966) for the lower subdivision of the Back Creek Group in the northern part of the Taroom Trough in the Bowen Basin, Queensland (Fig. 2, 3), where the formation crops out along a narrow strip trending north and northwest from near Mt Landsborough in the MACKAY 1:250 000 sheet to 8.5km northwest of Emu Plains homestead in the BOWEN 1:250 000 sheet. The formation lies above the Lizzie Creek Volcanic Group, and below the Gebbie and Blenheim Formations. The type section for the Tiverton Formation (Malone et al. 1966, p. 29) was located in a small creek 3.5km NNW of Blenheim homestead with grid references cited as 6518 3669 (top) to 6521 3672 (base) in the MT COOLON 1: 250 000 sheet area. Tiverton beds extend as a narrow band NNE across Tiverton holding east of Blenheim homestead, and the base is well exposed in Hazelwood Creek. The Homevale site has been mapped in a generalized way by Isbell (1955), Malone et al. (1964), Jensen et al. (1966), and Runnegar & McClung (1973). Later, a different application was proposed for the Tiverton Formation by Dickins & Malone (1973, p. 36), as a unit that extended throughout the basin, incorporating a variety of lithologies and correlated through faunal content and aspects of gross lithology, but this has not been accepted by Koppe (1978) or McClung (1981) or in the overview of the Bowen Basin by Draper (2013). Draper (2013) dated the faunas as Artinskian, but failed to note any of the paleontological studies of the 21st century, and furthermore regarded the Tiverton Formation as passing northwards into the Collinsville Coal Measures. But the Tiverton Formation is older.

The Tiverton beds at Homevale strike at 80° E, almost at right angles to the regional strike, and the beds are surrounded on three sides by alluvium. The Lizzie Creek Volcanic Group underlies the formation to the northeast, and includes shales which have yielded leaves of the Late Paleozoic plant *Glossopteris* and a small macro-invertebrate fauna, summarized by Runnegar (1968b, p. 15), and still not completely described, but containing brachiopod *Permasyrinx erecta* Waterhouse and bivalves *Protraxia gryphoides* (de Koninck) and *Pyramus laevis* Dana, which point to an Asselian age, correlative with the Allandale Formation of New South Wales, middle Rammutt Group of Gympie, and *Crassispinosella subcircularis* Zone of Tasmania. The Tiverton Formation is marine and made up of fine to medium-grained quartz sandstones and siltstones, with carbonaceous sheets and laminae, and some calcareous beds, as summarized by Campbell & Tweedale (1960, p. 200) and Malone et al. (1966, p. 30). The basal Tiverton Formation at Homevale (Table 2) crops out next to Tertiary rhyolite as a thin bed at UQL 4505 which contains the brachiopods *Validifera prima* n. sp., and *Ambikella,* closest to an Early Permian species named *elongata* McClung & Armstrong. It lies below beds without fossils, in turn followed by beds of the lower Tiverton Formation and a distinctive faunal assemblage, collected for fossils at localities UQL 4506-4508, and referred to the *Bookeria pollex* Zone. Some 122m of barren sandstones follow, overlain by 45m of fossiliferous strata (UQL 4509-4515) in the lower middle Tiverton Formation, belonging to the *Bookeria geniculata* Zone. Outcrop is not continuous: low ridges packed with fossils persist along strike for up to 300 metres, and are separated by intervals of weathered rock and soil, often rich in fossil moulds. The upper middle Tiverton Formation is somewhat similar with numerous fossils at UQL 4516-4525, in the *Taeniothaerus subquadratus* Zone. Some distance beyond alluvium, younger Permian beds from 10-30m thick and with more siltstone and shale, are found at Oaky Creek, containing fossils of a distinctly younger *Ingelarella plica* biozone, and these beds are called the upper Tiverton Formation. In earlier studies such as in Malone et al. (1966), the upper Tiverton beds were assigned to the lower Gebbie Formation, but the beds in question have igneous pebbles like those in the underlying Tiverton beds, and Waterhouse & Jell (1983) transferred the Gebbie – Tiverton boundary upwards

Fig. 1. The south side of "Fossil Ridge" near Homevale Station, from edge of track, showing the molasses tank (arrowed), used as a centre for collections by F. W. Whitehouse, and standing in the midst of the *Taeniothaerus subquadratus* Zone, in the Tiverton Formation. Photo G. R. Shi.

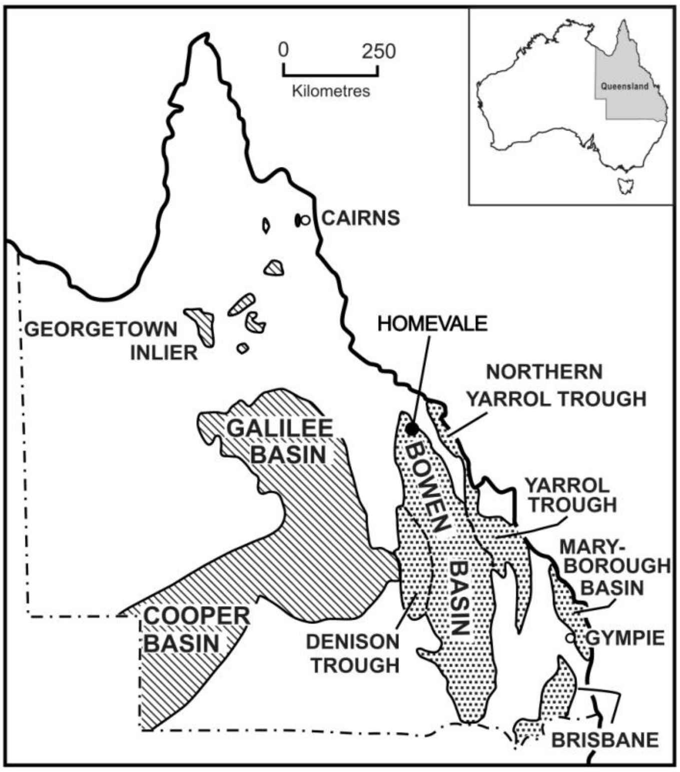


Fig. 2. Generalized location of Bowen Basin, Yarrol Basin and Gympie and other areas of Permian sedimentation in Queensland, east Australia.

to the base of massive white quartzite 61m thick, called the Wall Sandstone Member. That change provides a readily mapped boundary on the basis of lithology and geochemistry and has been accepted by Briggs (1998), as further discussed by Waterhouse (2002a, p. 240), and the change marks the inception of non-marine sedimentation.

2. Faunal succession in eastern Australia

Summary of previous work

Early and Middle Permian rocks are widespread in eastern Australia and there have been many paleontological studies over the past 150 years. Those of value are confined to published and illustrated systematic descriptions. The numerous faunal lists that have been compiled are set aside, because the accuracy is uncheckable: it would be necessary to re-examine the faunas for confirmation, and unless the faunas are then described, they will remain of uncertain character. Although gaps remain, sufficient is known of the east Australian faunas to be able to place the Homevale faunas within a zonal scheme for east Australia, and in this first section, before the systematic descriptions, questions are addressed on how Homevale faunas relate to marine faunas of Western Australia and to palynomorph biozones, and to the rest of marine Gondwana. Finally, available evidence on world correlations is discussed.

HOMEVALE		**CRACOW**	
Tiverton UQL localities	**Biozone**	**Formation**	**Biozones, subzones (S)**
3725	*Ingelarella plica*	Rose's Pride	*Ingelarella plica*
4516-4524	*Taeniothaerus subquadratus*		
4513-4515	*Svalbardia armstrongi* (S)		
4509-4512	*Bookeria drysdalei*	Elvinia	*B. geniculata*
4506-4508	*Bookeria pollex*	Dresden, Fairyland	*Bookeria pollex* (S) *Acanthalosia domina* (S) *Azygidium mitis* (S)
4505	*Validifera prima* *Ambikella* cf. *elongata*		

Table 2. The faunal zones and subzones (S) in the Tiverton Formation of the north Bowen Basin and correlative formations of the southeast Bowen Basin at Cracow.

With the addition of this current study, the bulk, but not quite all, of the Permian macro-invertebrate conulariid, brachiopod and molluscan faunas of the northern Bowen Basin will have been described (Armstrong 1968a, 1970a, 1970c, Campbell 1960, 1961a, 1965, Pojeta & Runnegar 1976, Runnegar 1970, Waterhouse 1983d, 2008a, 2010a, Waterhouse & Jell 1983). One of the few east Australian Permian sequences to have had the bulk of the macro-invertebrate faunas systematically examined is in the southeast Bowen Basin, more than 500km south of Homevale, near the gold-mining settlement of Cracow (Parfrey 1986, 1988; Waterhouse 1986a, 1987a, b). Impressive sequences are found in the southwest Bowen Basin, but these require faunal revision and synthesis. The Late Carboniferous and Early Permian rocks and faunas of the Yarrol region in central Queensland have been extensively summarized by Maxwell (1964), with some difficulty caused by the brief descriptions and poor reproduction of figures. This region has been regarded as a separate basin since Maxwell (eg. 1964), and although Fielding et al. (2001, 2008) proposed to treat the area as part of the Bowen Basin, the Yarrol Basin was retained as a distinct entity in the text on Queensland geology edited by Jell (2013). The region is separated from the Bowen Basin to the west, as near Cracow, by the Auburn Arch and Camboon volcanics, on to which the Bowen Permian sediments lap unconformably. The Permian succession in the Gympie Basin, southeast Queensland, offers a faunal succession assessed in Waterhouse (2015), building on studies by Etheridge Snr (1872), Etheridge (1892), Runnegar & Ferguson (1969) and Waterhouse & Balfe (1987), and relevant assessments of the faunas are incorporated in this study.

More scattered sequences in the Sydney Basin, best known for the Hunter Valley, northern New South Wales, are well understood stratigraphically (McClung 1980), and have had most of the critical species covered, in many papers and monographs. The southern Sydney Basin is well exposed along the southern coast of New South Wales, but has received only partial attention. In Tasmania a number of studies especially on Brachiopoda by Clarke (eg. 1969, 1987, 1992a) have established excellent but incomplete coverage of Early and Middle Permian faunal sequences.

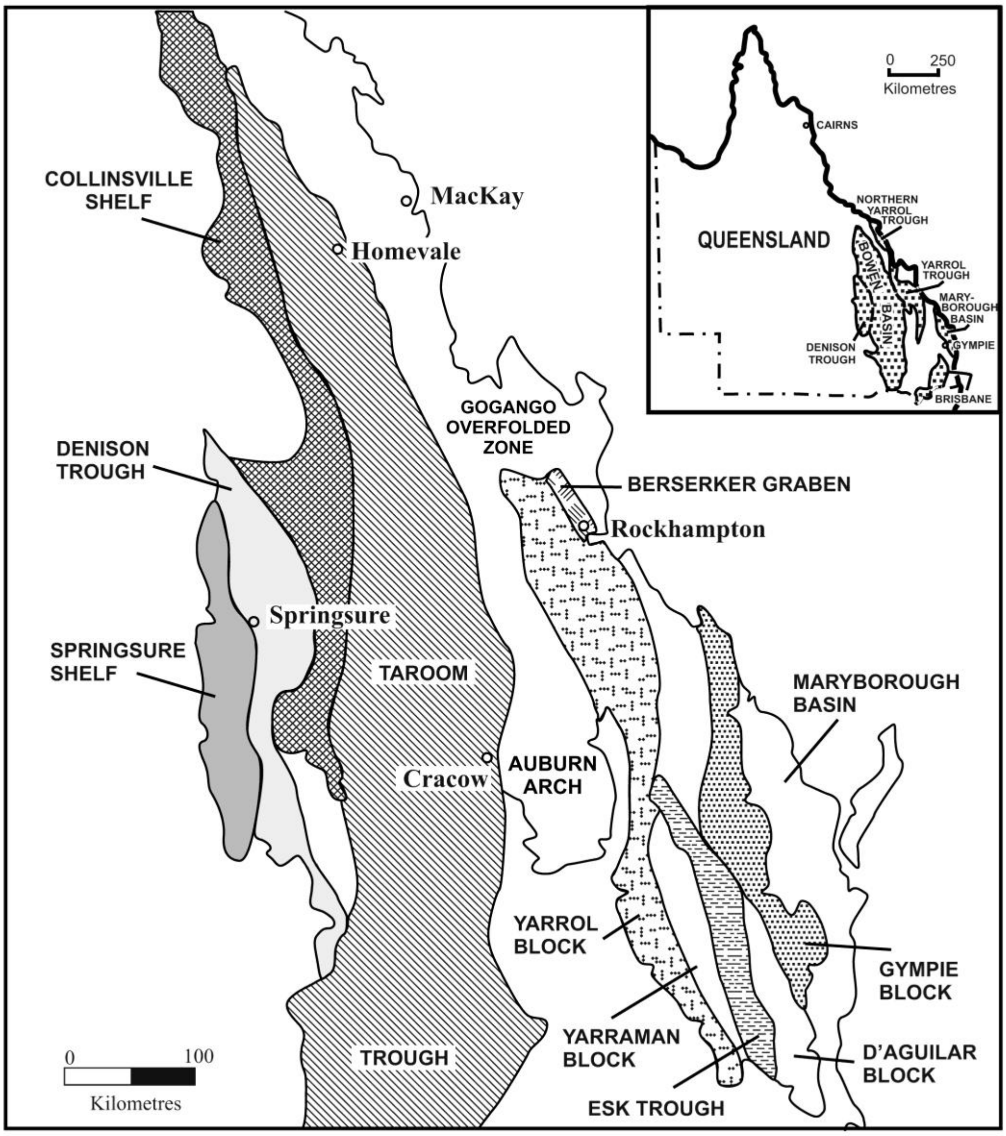


Fig. 3. Major marine Permian sedimentary areas of Queensland, generalized from Balfe et al. (1988) and Murray et al. (1987), to show place-names and geologic entities mentioned in the text. The Esk Trough is largely Triassic.

The best-known rocks and faunas of Queensland and New South Wales (Table 3) show stratigraphic and faunal gaps, so that faunas well developed in one area are feebly developed or absent from other sequences. The same arrangement pertains widely over eastern Australia, where packets of often fossiliferous Permian sediment are separated by chronologic and faunal gaps undetectable, or at least immeasurable in terms of duration, except through fossil correlation. The gaps are not visible in the field – they have to be detected through close study of the fossils. That is why problems arise from efforts to correlate rocks only on the basis of sequence stratigraphy and tectonostratigraphic and sedimentary models: these lack essential time control, whether through radiometry or fossils, and express only one unproven possibility amongst several alternatives. The staggered nature of the marine fossil record may be calibrated against the more continuously marine sequences of New Zealand (Waterhouse 2002a), which at intervals shared faunas with the Bowen Basin (Waterhouse & Sivell 1987). The lower Early Permian of east Australia may be buttressed through consideration of faunal sequences in Western Australia and south and southeast Asia.

Biozone	**North Bowen Basin** Formation	**Cracow, south Bowen Basin** Formation	**Springsure, w Bowen Basin** Formation	**North Sydney Basin** Formation	**New Zealand** Formation
Echinalosia conata	?Wall Sandstone*	unconformity	Aldebaran?* Definitely younger in part	Greta Coal Measures*	McLean Peaks Heartbreak
Spinomartinia adentata	unconformity		unconformity		Chimney Peaks
Ingelarella plica	Upper Tiverton	Rose's Pride	Sirius Mudstone Member	?	Brunel
Taeniothaerus subquadratus	Middle Tiverton	Pindari	Staircase Moorooloo Riverstone	Upper Farley?	Gondor
Bookeria geniculata	Middle Tiverton	Elvinia	Reids Dome Beds* [control poor]	Farley	Dunton Volcanics
Bookeria pollex	Lower Tiverton	Dresden Fairyland		Basal Farley Rutherford	?Longwood Group
Bandoproductus macrospina	basal Tiverton?	Camboon Volcanic Group			
Crassispinosella subcircularis	?Lizzie Creek Volcanic Group			Allandale	
Strophalosiaria concentrica				Lochinvar	

Table 3. Occurrence of marine faunal biozones in Early Permian formations as named in important sequences in the Bowen and Sydney Basins and New Zealand. Grey panels for the Bowen Basin signify the absence or scarcity of marine faunas, and asterisks signify mostly or entirely non-marine, with poor macro-faunal control. The Staircase and Moorooloo sandstone units between the Sirius and Riverstone fossiliferous bands imply a possible faunal gap, but few of the western Bowen basin faunas have been systematically examined in modern terms. The Aldebaran Formation of the Springsure region contains late Early Permian brachiopods (Waterhouse 2001, p. 74), but may range into older Permian. The age spread of the Camboon Volcanics is considerable. In the southeast Bowen Basin near Cracow the Fairyland Formation overlies the volcanics, to imply an Asselian age, but Parfrey (1986) has described Sakmarian brachiopods from further north. In New Zealand, the Longwood Group is poorly dated, and might well prove to be close in age to the Rammutt Formation or even the older Highbury volcanics of Gympie in southeast Queensland.

b. Distribution of major Permian marine sequences in east Australia

An overview of rocks and faunas in east Australia from the Sydney and Bowen Basins and Tasmania provides a framework for the application of macro-faunal biozones and a background for the correlation of the Tiverton Formation at Homevale. The diverse array of more scattered faunas and rocks throughout the New England Orogen, to the east of the Sydney and Bowen Basins, is summarized and discussed by Briggs (1998).

Southeast Bowen Basin

The rocks and faunas of the southeast Bowen Basin near Cracow are complex, and cannot be resolved without careful attention to controlled collection and analysis of the invertebrate fossils. The formations accumulated off-shore from a

Species	Cracow				Homevale		
	Fairyland	Dresden 1	Dresden 2	Elvinia	T1	T2	T3
Capillonia cracowensis	x						
Lipanteris cracowensis	x						
L. sparsispinosus	x	x					
Costatumulus prolongata	x	x			x	aff.	
Bookeria pollex	x	x	?		aff.		
Protoanidanthus compactus	x	x			x		
Echinalosia curtosa		x			aff.		
Azygidium mitis		x					
Echinalosia dejecta		x					
Lakismatia lakismatos			x				
Acanthalosia domina			x		x		
Anidanthia paucicostata				x		x	x
Costatumulus farleyensis				x			
Bookeria geniculata				x		x	x
Magniplicatina undulata				x		x	
Echinalosia curvata				x			x

Table 4. Lists for Productiformii from formations in the southeast Bowen Basin, near Cracow, and occurrences in the lower Tiverton Formation, *Bookeria pollex* Zone (T1), middle Tiverton Formation, *Bookeria geniculata* Zone (T2), and upper middle Tiverton Formation, *Taeniothaerus subquadratus* Zone (T3) at Homevale.

pile of Camboon andesitic volcanics, and changed laterally according to distance and depth offshore (Fig. 4, p. 21). The formations share many species with the Tiverton Formation (Tables 4, 5), and the Fairyland and Dresden Formations have been proposed as offering a type section for the closely studied *Bookeria pollex* Zone, equivalent to the lower Tiverton Formation (Waterhouse 2008b). Because of the complexity of the area, and significance of the fossil faunas, it is deemed necessary to set aside the conservative proposal by Draper et al. (1990a, b) that the various units be treated as a homogeneous Buffel Formation: that reflects too generalized a mapping approach for adequate analysis of the sedimentary regime and faunal distribution and evolution. Lithological divisions exist, detailed mapping has been published, and the subdivisions are no finer than those established for the Permian in New South Wales, Tasmania or Western Australia. The Queensland Permian is basically no different and certainly not simple. The following summary comes from Waterhouse (1986a, 1987a, b).

Species	**Cracow**				**Homevale**		
	Fairyland	Dresden 1	Dresden 2	Elvinia	T1	T2	T3
Grantonia cracovensis	x	?			x		
Grantonia australis			x			x	x
Ambikella regina	x				x		
Tabellina denmeadi	x						
Geothomasia cracowensis	x						
Notospirifer paraextensus	x						
Permasyrinx procera	x				x		
Spiriferellina ? *disparata*	x						
Attenuocurvus ? sp.		x					
Geothomasia postglabra		x	?				
Permasyrinx subelongata		x	?				
Sulcicosta costata		x					
Spiriferellina anguliplicata		x					
Punctospiriferina sp.			x				
Unicostatina stutchburii			x			x	x
Fusispirifer ? sp.				x			
Ambikella ovata			?	x		x	x
Geothomasia valida				x		x	x
Geothomasia profunda				x		x	x
Papulinella hillae				x		x	x
Papulinella wilsoni						x	x
Cyrtella subparallela			x				
Permasyrinx elongata				?		x	x
Pustulospiriferina lirata			x				
P. etheridgei				x		x	x

Table 5. Occurrences of Spiriferiformii in southeast Bowen Basin at Cracow and in Tiverton Formation (T1 – 3) at Homevale, north Bowen Basin. T1 = *Bookeria pollex* Zone; T2 = *Bookeria geniculata* Zone; T3 = *Taeniothaerus subquadratus* Zone.

The basal Fairyland Formation of marine volcaniclastic fine sandstone and mudstone has yielded some 35 species, many distinctive, including brachiopods *Bookeria pollex* (Hill) and other species summarized in the following section on biozones. The Dresden Limestone overlies the Fairyland Formation, and is composed of laminated calcilutites with poorly washed biosparite and packed biomicrite, bearing fossils in bands. To the south the limestone becomes darker and more marly, and interbedded with thick-bedded calcarenite and calcrudite. From its type section on

Buffel Hill, the limestone increases to the west at the expense of the overlying Elvinia Formation, with limestone resting directly on Camboon Volcanics over the Pindari Hills. To the north the limestone is reduced to lenses. Along Buffel Hill, limestone replaces lower Elvinia Formation to the north. A basal fossil assemblage contains *Lipanteris cracowensis* (Hill) and *Eurydesma ovale truncatum* Waterhouse, and is faunally close to fossils from the Fairyland Formation. Above, an *Azygidium mitis* fossil community is well developed, with further species listed in the section on biozones. Higher, vestiges of a community dominated by *Lakismatia lakismatos* (Briggs) are found, and this is followed by a distinctive *Acanthalosia domina* community, sharing many of the species found in older beds. The *domina* suite is found in a distinctive Boughyard Member, which is a shell bank on Buffel Hill that passes laterally into limestone. Red limestone at the top contains *Squamuliferipecten latispatia* Waterhouse, and passes laterally into basal Elvinia Formation.

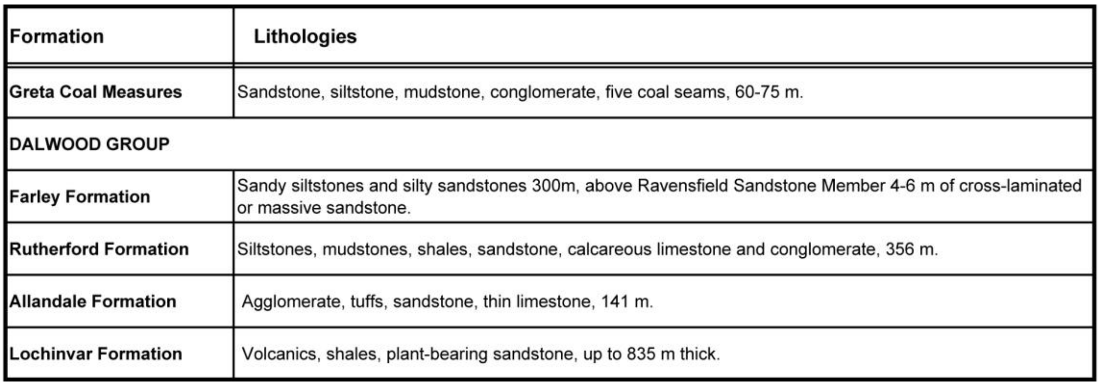
This complex of Fairyland and Dresden faunas is significant for overall Late Paleozoic faunal correlation in east Australia. Several shared species are found at the base of the Tiverton Formation at Homevale, and in the lower *Eurydesma* beds of the Wallaby rocks near Warwick, southeast Queensland (Richards & Bryan 1924), but they are not represented throughout the bulk of the beds at Homevale, contrary to claims by Briggs (1998). His assertions are carefully examined in this study, and cannot be supported by detailed examination of the particular Linoproductidina and Strophalosiidina he discussed, nor by the accompanying Brachiopoda and Mollusca which he did not consider. There is even less paleontological or detailed mapping support for the interpretation offered by Dickins in Archbold & Dickins (1991, p. 8) that the Dresden Limestone was the same as the Oxtrack Formation, which is younger and contains a very different faunal assemblage, belonging to the *Echinalosia maxwelli* Zone (see Waterhouse 2002a, p. 239). James et al. (2009, Fig. 6) made the same error. They assigned the Dresden Limestone near the base of the Geological Survey of Queensland Munduberra 10 core to Oxtrack limestone, despite GSQ reports and paleontological and detailed mapping surveys by Holcombe & Jell (1983), Briggs (1998) and Waterhouse (1986a). On that basis James et al. misrepresented faunal content and climatic implications.

The Elvinia Formation is about 55m thick and is composed of shelly sandstones, calcareous sandstone and siltstones, with over 30 fossil species. Above the basal band the faunas belong to a *Bookeria geniculata* Zone, further documented in the biozonal section (pp. 22-24), and equivalent to the lower middle Tiverton faunas. The Elvinia Formation is overlain by Pindari beds, largely barren of marine macro-fossils except for some conulariids. Some 13km north of Cracow and 20km north of Buffel Hill is the Rose's Pride Formation, composed of shallow-water marine volcaniclastic and quartzose sandstones and conglomerate of andesitic pebbles, suggestive of high-stand sea-level insofar as it transgresses onto Camboon volcanics. The faunas are distinctive, with some 25 species known. *Ingelarella plica* Campbell is shared with the upper Tiverton beds of Homevale, and *Acanthalosia mysteriosa* Waterhouse is shared with the Cattle Creek Formation of the southwest Bowen Basin. Additional species include *Notostrophia bifurcata* Waterhouse, *Anidanthus springsurensis* Booker, and *Maorielasma inflata* Waterhouse.

Rocks above the Elvinia, Rose's Pride and Pindari Formations are of Middle Permian age, including the Brae Formation (*Echinalosia discinia* Zone, of upper Kungurian age) and Oxtrack Formation with the *Echinalosia maxwelli* Zone, followed by the Barfield Formation with the *Pseudostrophalosia blakei* Zone, both of Roadian age. A faunal break is indicated between Rose's Pride and Brae formations, with a gap in the succession (Waterhouse 2008b).

New South Wales (Table 6)

Ingelarellid species have been used to zone the Early Permian formations in the Hunter Valley by McClung (1978). The basal Lochinvar Formation is characterized (with appropriate generic adjustments) by reported but unconfirmed *Ambikella elongata*, the Allandale Formation by *Monklandia konincki*, the Rutherford Formation by *Geothomasia branxtonensis*, which persists into the Farley Formation, and *Ambikella ovata*, found in the upper Farley Formation. Many bivalves found at Homevale were first described from the Allandale Formation by Dana (1847, 1849), Morris (1845) and M'Coy (1847) and further elaborated in studies such as those by Etheridge & Dun (1906, 1910) and Fletcher (1929a, b, 1932). A number of the bivalves range from Lochinvar to Farley Formations. More precise correlations are indicated by several Productida, as summarized from Briggs (1998). *Bandoproductus walkomi* Briggs is found in the Rutherford Formation and widely elsewhere. *Costatumulus farleyensis* (Etheridge & Dun), an ally of *C. tumida* at Homevale, and *Bookeria geniculata* Waterhouse range through the Farley Formation. *Svalbardia* is found in the middle of both the Farley and Tiverton Formations, and Farley *Biconvexiella* is close to the Tiverton species *B. convexa* (Armstrong). The Farley Formation at the top of the Dalwood Group is overlain by the Greta Coal Measures, which at least partly matches the stratigraphic gap between the Rose's Pride and Brae Formations in the southeast Bowen Basin. The Greta Coal Measures are in turn overlain by the Elderslie Formation at the base of the Maitland Group. Only some of the fossils have been described from the Elderslie Formation, including a number of ingelarellids (McClung 1978), here assigned to *Tumulosulcus undulosa* (Campbell) (syn. *Ingelarella cessnockensis* McClung), *Oviformia magna* (Campbell) and *Johndearia brevis* (Campbell), as summarized by Waterhouse (1998, 2002a, p. 178, 2014, p. 171). Several of these species are also found in Queensland, in the lower Blenheim Group well above the *Ingelarella plica* Zone at the top of the Tiverton Formation. That correlation conflicts with the view of Dickins (1968), Archbold & Dickins (1991) and Briggs (1998) who matched Elderslie with the upper Tiverton Formation and "upper" *Echinalosia preovalis* Zone. The evidence for correlation provided by the ingelarellids is confirmed by other brachiopods, *Echinalosia floodi* Waterhouse, *Wyndhamia typica* (Booker), *Anidanthus perdosus* Waterhouse, *Paucispinauria paucispinosa wardenensis* Waterhouse, and *Aperispirifer archboldi* Waterhouse (Waterhouse 2001, 2002a, p. 178, 2013).



Formation	**Lithologies**
Greta Coal Measures	Sandstone, siltstone, mudstone, conglomerate, five coal seams, 60-75 m.
DALWOOD GROUP	
Farley Formation	Sandy siltstones and silty sandstones 300m, above Ravensfield Sandstone Member 4-6 m of cross-laminated or massive sandstone.
Rutherford Formation	Siltstones, mudstones, shales, sandstone, calcareous limestone and conglomerate, 356 m.
Allandale Formation	Agglomerate, tuffs, sandstone, thin limestone, 141 m.
Lochinvar Formation	Volcanics, shales, plant-bearing sandstone, up to 835 m thick.

Table 6. Early Permian (Asselian to upper Artinskian) formations and lithologies of the north Sydney Basin in the Hunter Valley, New South Wales.

Gympie

In southeast Queensland the Rammutt Formation of the Gympie area has yielded a suite of early Permian fossils related to those of the Allandale Formation in the Sydney Basin, followed by a *Bandoproductus* fauna, related to that of the lower Rutherford Formation in the Sydney Basin. A Teebar fauna from nearby Gigoomgan, with geology described by Cranfield (1989), has strong links to the *Taeniothaerus subquadratus* Zone of Tasmania and Tiverton Formation of Queensland. The younger deposits, belonging to the South Curra Limestone, Tamaree Formation, Gundiah Bridge Formation (Brown 1964) and Gigoomgan Limestone, are younger than other faunas found in east Australia, and match those of the lower Changhsingian in New Zealand (Waterhouse 2015).

Tasmania

In Tasmania, the well preserved macro-faunas have been arranged in stages by Clarke & Farmer (1976), as reproduced in Waterhouse (2015, p. 4). At the base is the Hellyerian Stage, of possibly Late Carboniferous age, with no marine fossils, followed by the Tamarian Stage, with three zones numbered as Faunizones 1-3, involving *Eurydesma*, and two strophalosiid brachiopod zones, for which the key species and generic positions have been revised in Waterhouse (2013, pp. 218 - 220) as *Strophalosiaria concentrica* (Clarke) followed by *Crassispinosella subcircularis* (Clarke). Clarke (1992a) also recognized a *Unicostatina crassa* Zone (3), difficult to distinguish beyond Tasmania, sharing *C. subcircularis*, but possibly equivalent to the *Bandoproductus macrospina* Zone elsewhere. The Bernacchian Stage commences with "Stage 3 microflora" in non-marine beds, followed by two marine faunas called Faunizones 4 and 5, with reported *Ambikella ovata*, *Grantonia hobartensis, Costatumulus farleyensis* and *Taeniothaerus subquadratus*. This stage is represented in the upper middle Tiverton Formation of Queensland, but the basal Tiverton and Fairyland-Dresden faunas of Homevale and Cracow do not appear to be present in Tasmania. The Lymington Stage at the top of the Tasmanian Permian stage sequence is subdivided into five zones, with Middle Permian species such as

Paucispinauria concava and *Johndearia brevis,* seemingly not as complete or as diverse as the sequences of New South Wales, Queensland or New Zealand. The report of the species *plana* suggests that possibly the basal zone matches the topmost *Ingelarella plica* Zone of the Tiverton Formation, but this has not been verified through description. The Tasmanian sequences are significant, and overall confirm the pattern adduced for Queensland successions, and have been enhanced through the study of micro-floras. Unfortunately a number of the faunas have not been described, leaving the overall faunal progression overdependent on faunal lists that still have not been verified by published systematic study. Their reliability can only be judged through reference to more completely described sequences.

EARLY PERMIAN ZONES IN EASTERN AUSTRALIA (Table 1, 7, 8)

Introduction

Macro-invertebrate zones for the Early Permian of eastern Australia are based principally on productidin and ingelarellid brachiopods, and have been proposed in studies by Clarke (1992a), Briggs (1998) and Waterhouse (1987b). Earlier, a succession of 13 zones was recognized by Campbell (1961a) at Homevale, as shown in Fig. 5, p. 26, based on incomings and outgoings of six species of ingelarellid and notospiriferid species. My closely spaced collections through a broad section do not confirm some of the incomings and outgoings, or species ranges, so that although the zones were maintained as reference points by Briggs (1998), it seems more objective as well as practical to set them aside and use a simpler scheme that is more widely applicable in eastern Australia (Tables 1, 3). The International Stratigraphic Guide (Salvador 1994, p. 65) counselled against using "esoteric zonal criteria", and logically, it is here postulated, esoteric criteria include gaps or supposed gaps in the range of a species, which had been used by Campbell to construct some of his "zones". The Campbell scheme for the Tiverton Formation was also modified for more general applicability to the Permian of east Australia by Runnegar & McClung (1975) and McClung (1978). Waterhouse, Briggs & Parfrey (1983) sought to establish a more robust zonation at Homevale in the sense of seeking wider application, based principally on Productida, and reinforced by Spiriferida. Not at variance with previous work, they established the presence of two distinctive and easily recognizable major biozones in the middle Tiverton Formation, a lower zone based on such species as (names now updated) as *Svalbardia armstrongi, Costatumulus tumida, Bookeria drysdalei, B. geniculata*, and *Biconvexiella convexa*, followed by an overlying zone dominated by large species of *Lipanteris* and *Taeniothaerus* with *Pseudostrophalosia brittoni*. The zones are recognizable not only over east Australia, but may be traced further afield into the subcontinent of India and South America, with vestiges recognizable in the northern paleohemisphere, as in Arctic Canada. Below these zones, Waterhouse in Waterhouse et al. (1983) suggested the possible presence of two meagre but older faunas. That view has been modified though sustained to a degree by Foraminifera (Palmieri 1990) and the present study.

A historical summary has been provided by Briggs (1998), to give a readily available entry into the literature. Based on key strophalosiid species, Briggs (1998) proposed 25 brachiopod zones. Archbold (1999, p. 65), whilst endeavouring to use that scheme, noted that not all of the zones are "in objective stratigraphical successions". This is confirmed in monographs by Waterhouse (2001, 2002a), which demonstrated that some key species had been misidentified, and that some zones are shown in wrong stratigraphic order for late Early and Middle Permian. In addition, some strophalosioid and linoproductinidin taxa are restricted only to one basin or part of a basin, and of very brief time range, so that there is little prospect of being able to trace them throughout the Permian of eastern Australia. These short-lived species are better regarded as opportunistic and/or local community dominants within a larger more extensive zone. Amongst further reservations, it may be noted that Briggs' zones in eastern Australia were not delineated to modern standards, and lacked defined FAD (First Appearance Datum) of key species. This need has now been partly addressed in Waterhouse (2008b). The reader is referred to that article for preliminary designation of measured type sections and fossil localities throughout eastern Australia and New Zealand, and the relationship to preceeding and succeeding zonal key species in the same sequence.

Mutiple First Appearence Data (MFAD)

In the establishment of international world standard stages and zones, emphasis has been placed on recording first appearances of species judged critical, and treating the interval between that first appearance and the first appearance of the next key or index fossil (FAD) as the zone, with the name based on the index species which signals the FAD. A problem that besets the procedure of basing zones on first appearance of a designated species or form species arises when the key species ranges well beyond the FAD of the succeeding species. It becomes no more than an assumption difficult to prove objectively that the true FAD will always be found, and will always be precisely synchronous. If the key species is not preserved, or did not exist due to ecological factors in that region, or if it was misidentified, overlooked or not extracted, miscorrelation will be facilitated by relying on false FAD. The proposal of successive zones based on PFAD or PFOD (Provisional first occurrence datum) of species or form taxa that persist through culminative PFAD's can be no more than a proposition to be tested through the full examination of accompanying species, preferably within more than one phylum.

The world standard divisions of the marine fossil zones are based on conodonts, as summarized shortly on pp. 43-44. Permian sequences of east Australia, like those for more than half of the globe, cannot be zoned satisfactorily by conodonts, for such are too spasmodic or too rare except in tropical and some temperate paleolatitudes – and indeed to this day, no conodonts have been found in east Australia, and are scarce in Western Australia and New Zealand. The most common of marine fossils in Australia are shelly benthic invertebrates, particularly brachiopods and in some successions bivalves. These are less amenable to the kind of FAD treatment applied to conodont zonation. Based on widespread experience based on observation of brachiopod and molluscan incomings in the Permian of east Australia, New Zealand, Thailand, Canada and the Himalayas, I have observed that a single macro-invertebrate species may enter along strike at different intervals measured from section to section, and even along strike of a single prominent and thin rock band, using such controls as a bedding plane, a lithological feature or horizon, and entry of other species. In detailed studies on Early Triassic faunas of the Himalaya, presented in Waterhouse (2000, 2002c), it was found that even critical ammonoids and the bivalve *Claraia* and allies, although astonishingly abundant, did not enter a distinct member or formation at precisely the same level, within sections along strike and measured to centimetres. The same has been found to be true of various brachiopod species found in the prominent bands of limestone which make up the Oxtrack Formation in the southeast Bowen Basin in Queensland. Emphasis on a single key brachiopod species and its FAD would be potentially misleading and inaccurate. Instead of first appearances of successive single species, emphasis is here placed on fossil assemblages and multiple first appearances (MFAD), with evaluation of macro-fauna involving chiefly Brachiopoda, Bivalvia and Gastropoda for the Australian Permian: bryozoans and corals would offer valuable additions, but more study is needed on the former, and the latter are surprisingly rare. Echinoderms have scarcely been studied, Cephalopoda are rare, and fusulines absent. The first appearance of any one of a number of species is regarded as establishing the commencement of a zone. This fulfils the proposal that FAD-based zones need to be reinforced by enough data to underpin nominated index species with a range of other taxa that show related or identical ranges, and therefore buttress nominate species against possibilities of erratic preservation or discovery.

Titular names for biozones

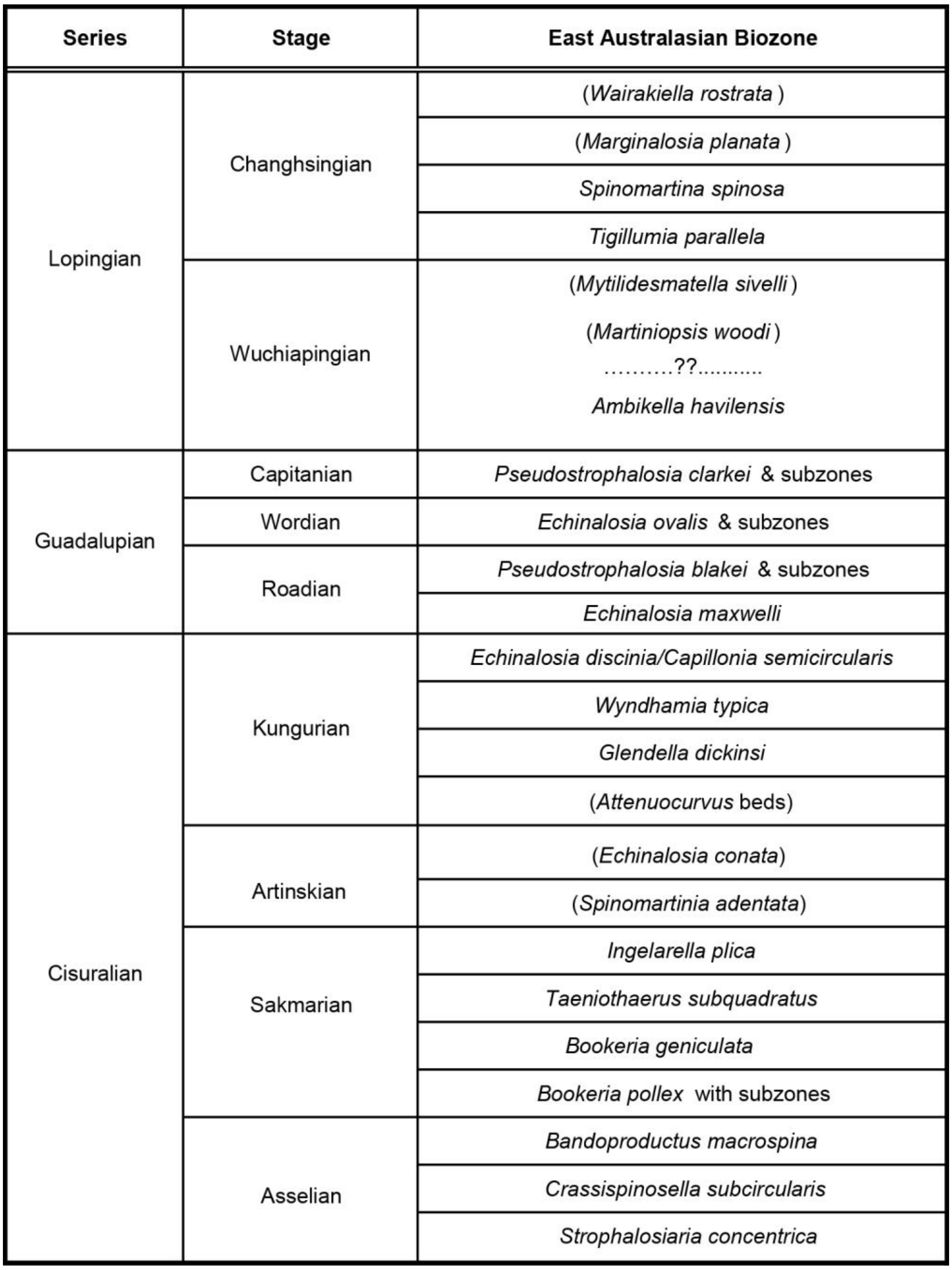
Given that the biozones in east Australia are based on a number of associated species, it will be realized that the selection of one of those associated species in any one biozone becomes somewhat arbitrary, and subject to revision from ongoing work. Several of the name-giving species for zones do not occur throughout east Australia, but are related to other close allies, or are absent. Runnegar & McClung (1975) based their zones on Ingelarellidae, and Briggs (1998) on Productida, and both groups have much to commend them, but a broader base of species is here preferred. With ongoing study after Briggs (1998), it appears that many Productida were evolving so rapidly that contemporaneous sediments even in a single basin contained slightly different species, reflecting different environments and different spatial colonization in different parts of a basin. And the morphological and temporal limits of species, whilst undergoing ongoing improvement, cannot be deemed to be secure without much further study.

Subgenera – simplification

Throughout the discussion of biozones and correlation, the distinctions of genera from subgenera are set aside, with reference only to the genus or subgenus name. In analyzing the development and evolution of taxa, the recognition of interrelations is enhanced through recognition of subgenera, but that tends to clutter a study which is aimed principally at biostratigraphic correlation. The same may be said of subspecies, and it seems likely that species recognized amongst Productida could be downgraded to subspecies.

3. Early Permian macro-faunal zones in east Australia (Tables 2, 7)

The following summary, made partly on the basis of previous studies by Clarke (1992a) and Briggs (1998), incorporates



Series	Stage	East Australasian Biozone
Lopingian	Changhsingian	(*Wairakiella rostrata*)
		(*Marginalosia planata*)
		Spinomartina spinosa
		Tigillumia parallela
	Wuchiapingian	(*Mytilidesmatella sivelli*) (*Martiniopsis woodi*) ……….??.......... *Ambikella havilensis*
Guadalupian	Capitanian	*Pseudostrophalosia clarkei* & subzones
	Wordian	*Echinalosia ovalis* & subzones
	Roadian	*Pseudostrophalosia blakei* & subzones
		Echinalosia maxwelli
Cisuralian	Kungurian	*Echinalosia discinia/Capillonia semicircularis*
		Wyndhamia typica
		Glendella dickinsi
		(*Attenuocurvus* beds)
	Artinskian	(*Echinalosia conata*)
		(*Spinomartinia adentata*)
	Sakmarian	*Ingelarella plica*
		Taeniothaerus subquadratus
		Bookeria geniculata
		Bookeria pollex with subzones
	Asselian	*Bandoproductus macrospina*
		Crassispinosella subcircularis
		Strophalosiaria concentrica

Table 7. Sequence of marine macro-invertebrate biozones in the Permian rocks of east Australia and New Zealand, elaborated from Waterhouse (2008b). A poorly defined zone (*Attenuatella, Trabeculatia*) lies between the *conata* and *dickinsi* zones, and another, possibly above *Martiniopsis woodi*, based on *Mytilidesmatella sivelli* (Waterhouse 2002a, p. 234). The Wuchiapingian Stage is further discussed on p. 348. Bracketted biozones are not found in east Australia.

the new data on the Tiverton Formation at Homevale, as well as fossil sequences near Gympie in southeast Queensland (Waterhouse 2015). Proposed stratotypes and detailed FAD are discussed in Waterhouse (2008b).

The *Nambuccalinus bourkei* fauna – basal Permian?

In a wide-ranging synthesis of mostly invertebrate fossils belonging to Productidina and Strophalosiidina in east Australia, Briggs (1998) proposed that the oldest known Permian zone should be based on *Lyonia bourkei* Briggs. The genus is much more spinose than *Lyonia*, and is now the type species of *Nambuccalinus* Waterhouse, 2001, p. 33, characterized by its multiple rows of large spines along the hinge, numerous well formed ventral spines and numerous dorsal spines, as endorsed by Angiolinii et al. (2005) and Brunton (2007), and the fauna is restricted to the northern part of New South Wales. Briggs (1998, pp. 23-26) has carefully discussed the available evidence for its stratigraphic position, and noted there was no known stratigraphic or even tectonic relationship to any underlying or overlying different zone. There are only three adequately described species, *Nambuccalinus,* and two species of *Briggsia* Waterhouse, 2014*,* with undescribed *Trigonotreta* and *Deltopecten*, species that might also be useful in assessing the possible correlation and age of the fauna. Although the zone may prove to be a local variant or older phase of the *Bandoproductus macrospina* Zone, the distinct nature of the three lyoniin species support the Briggs contention that the fauna is of an age different from any other known biozone in the Permian of east Australia. Unfortunately not enough is known about its stratigraphic position and too few elements of its fauna have been described to justify proposal of a zone, or allow certainty of its stratigraphic position. Instead, the *Nambuccalinus bourkei* assemblage should remain as a "fauna", with content, stratigraphic position and significance yet to be established (Waterhouse 2008b). Briggs (1998) argued that it was older than other known Permian faunas in east Australia.

Basal Cisuralian Series

Strophalosiaria concentrica Zone

The *Strophalosiaria concentrica* Zone is based on outcrops and faunas in Tasmania, studied in detail by Clarke (1990, 1992a). The nominate species, revised in Waterhouse (2013, p. 218), is found in the Quamby and Woody Island Formations, and first appears in the uppermost Wynyard Tillite and correlative levels. Accompanying species include *Arctitreta costellata* (Clarke), *Trigonotreta stokesii* Koenig, *Etheripecten tenuicollis* (Dana), *Eurydesma konincki* Johnston, reported *E*. *burnettensis* Waterhouse, *Protraxia gryphoides* (de Koninck), *Pyramus laevis* (Sowerby), *Schizodus australis* Runnegar and *Keeneia twelvetreesi* Dun. Allied faunas are found in the lower Wasp Head Formation of the south Sydney Basin and Lochinvar Formation of the north Sydney Basin, and parts of northern New South Wales in the Tamworth Block, Peel Fault Zone, and Texas block (Briggs 1998).

Crassispinosella subcircularis Zone

This zone is found above the *Strophalosiaria concentrica* Zone, appearing in the lower Bundella Formation, Golden Valley Group, Darlington Limestone and correlatives in Tasmania. Accompanying species include *Monklandia konincki* (Etheridge) and many species that persist from the underlying zone. The possibly correlative faunas in the upper Wasp Head Formation (see Briggs 1998, text-fig. 16, p. 29) include some of the species described by Runnegar (1969), which he called *Neospirifer* and *Pseudosyrinx* in bed 5.2.32 at Wasp Head. *Pseudosyrinx* is like the Allandale species *Permasyrinx allandalensis* (Armstrong, 1970a), which Clarke (1992a, p. 25) also recorded from the Swifts Jetty Sandstone, Masseys Creek Group and Kansas Creek Formation and Darlington Limestone in Tasmania. The *Neospirifer* approaches *Simplicisulcus dubius* (Etheridge) from the middle Rammutt Formation at Gympie, Queensland. Briggs (1998) reported *subcircularis* in the Kensington Formation near the Peel Fault of northern New South Wales, and below the top of the faulted Alum Rock beds in the Texas Block, together with other possible occurrences, which still await full systematic substantiation. Briggs (1998) deprecated the stratigraphic value of the species *Ambikella elongata* and *Monklandia konincki*, which were supposed to co-exist in turn with *concentrica* and *subcircularis*. Archbold (2003) dismissed the claim, but his strictures require further evaluation, the species identified with *elongata* in Tasmania belonging to a separate species *bundellaensis* Waterhouse, 2014.

In the middle of the Rammutt Formation (Jell & Cranfield 2013), the "green fossiliferous sandstone", a unit some 10m thick and moderately rich in fossils in the Gympie succession in southeast Queensland above the Highbury volcanics is correlative (Waterhouse 2014). The fauna includes bivalves *Megadesmus* and *Pyramus* belonging to well known species named by Dana (1847, 1849) from the Allandale Formation, together with *Monklandia gympiensis* Waterhouse, 1998, *Permasyrinx*? *acuta* (Etheridge Snr, 1872), and *Simplicisulcus dubius* (Etheridge Snr, 1872), which may be matched with *Neospirifer* described from Wasp Head by Runnegar (1969). The Productida reported by Runnegar & Ferguson (1969, p. 251) as coming from the Rammutt Formation were misidentified with younger forms.

Unicostatina crassa Subzone

In Tasmania, Clarke (1992a) recognized a *Unicostatina crassa* Zone, which may be defined by the first entry of the nominate species, accompanied by *U. subglobosa* Clarke, *Geothomasia branxtonensis* (Etheridge), *Myonia* sp. (*elongata* not Dana of Clarke 1992a), *Rhabdocantha intermedia* Clarke and *Tabellina* (syn. *Kelsovia*) *superba* (Clarke) [identifications modified]. A number of species, including *Crassispinosella subcircularis*, persist from the underlying zone. Clarke (1992a) reported the presence of the zone at several areas of Tasmania, including the Snug-Margate area of Maydena, in the Bundella Formation of Forestier Peninsula, the Billpo Sandstone in the upper Golden Valley Group in the Poatina-Golden Valley area, and the Swifts Jetty Sandstone in the Beaconsfield-Frankford area. Recognition of the zone elsewhere has not been certain, but it appears possible that the fauna could match the *Bandoproductus macrospina* Zone of east Australia in New South Wales and Queensland, unless it is the top of the *subcircularis* Zone.

Bandoproductus macrospina Zone

The *Bandoproductus macrospina* Zone marks a significant faunal interval. It was recognized by Briggs (1998) as the *B. walkomi* Zone, and *walkomi* appears to be a species contemporaneous with and indeed sometimes cohabiting with *macrospina*. The species are found in the Burnett Formation above the *Eurydesma burnettensis* fauna in the Yarrol Basin, and as *walkomi* in the lower Rutherford Formation of the Hunter Valley, together with a report in the Silver Spur outlier of Goondiwindi, south Queensland. The genus is not known in either Tasmania or the Bowen Basin of Queensland. The fullest description of the *Bandoproductus* fauna so far is provided by Waterhouse (2015) in recording species from the upper Rammutt Formation of Gympie, southeast Queensland, and includes *Protoanidanthus pokolbinensis* Briggs, *Magniplicatina dunstani* Waterhouse, *Attenuocurvus australis* (Armstrong & Brown), *Ambikella* cf. *elongata* (McClung & Armstrong), *Oviformia sweeti* Waterhouse, and *Neilotreta* sp., as well as a stenoscismatid and martiniid, and further species. *Neilotreta* is an unusual genus, known elsewhere in east Australia as *N. tangorini* (Archbold) in the Beckers Formation and rarely in the Cranky Corner Corner Formation of the Cranky Corner Basin in New South Wales. The same level in the basin also yields type *Ambikella elongata* (McClung & Armstrong), which may prove to be restricted to this level, though this remains provisional.

Palynomorph zones

Palynomorphs have been widely studied in Australia, and Price (1983) formalized subdivisions of the east Australian Permian, building on earlier work by Evans (eg. 1967), and recognizing palynostratigraphic units, with stages numbered from 1 to 5, and subdivided by letter, a, b etc. The code was changed both in letter and number by Price (1985, in Price et al. 1985) to a series of designations PP1 – PP6, with subdivisions, further amended by Price (1997). The units were delineated by the incoming of a key species, and closed by the incoming of the next key species, a procedure also applied for conodont subdivisions of the world Permian. The zones were established with no standard sections, or measured data on first appearances, and therefore are to some extent conceptualizations still being tested, which of course is true of all fossil biozones. The studies are still ongoing, with refinement and even replacement of some key species, and have the advantage of application to marine and non-marine deposits.

Palynomorph unit APP 1 is based on glacigene palynofloras of east Australia, discriminated by the introduction of taeniate bisaccate pollen, especially *Protohaploxypinus* and including *Potonieisporites*, subordinate to monosaccate forms, with trilete spores also present. Bisaccate taeniate pollen resembling *Protohaploxypinus* is found in Westphalian C of western Europe, the Russian Moscovian Stage, late Bashkirian to early Moscovian in the Angara Basin of north China, and later – diachronously – in south China (Balme & Foster 2003, p. 129). Views over the age differ. Jones & Truswell (1992) favoured a Westphalian D to early Asselian correlation, and Jones (1996) preferred a correlation no younger than Westphalian C. Balme & Foster (2003, p. 130) were relunctant to accept so great an age, on the understanding that the overlying *Pseudoreticulatispora confluens* Zone APP 122 was Sakmarian, as explained shortly. Palynomorph stage 3 (APP 21) has a higher proportion of taeniate disaccate pollen and is signalled by the first appearance of *Pseudoreticulatispora pseudoreticulata.* Powis (1984) judged unit 3a to be Gzhelian (Late Carboniferous), and Foster (1983) showed Unit 3 as basal Permian, following Kemp et al. (1977). *Ps. pseudoreticulata* is found in the Allandale fauna of New South Wales, and is well represented with macro-faunas in the upper Quamby-Woody Island lithological association according to Briggs (1998), above supposed *Eurydesma burnettensis* (probably *E. konincki*) and below the youngest occurrences of *Strophalosiaria concentrica* in the Bundella-Golden Valley beds of Tasmania. Archbold (2001a, b) correlated the *Ps. pseudoreticulata* Zone with the *Crassispinosella subcircularis* Zone, and Allandale Formation, lower Pebbley Beach Formation, Bundella Formation and Golden Valley Group. Calver, Clarke & Truswell (1984, text-fig. 3) showed *pseudoreticulata* as present through palynozone 3a (ie. “ *konincki* Zone”), and *Microbaculispora tentula* in palynozone 2 (ie. *concentrica* Zone?). They reported palynomorph zone 3b or APP 22 established for the entry of *Microbaculispora trisina* at the topmost so-called *konincki* Zone (= *Crassispinosella subcircularis*), but the integration with faunizones is obscure in their article. Evans (1991) reported a *trisina* flora or its equivalent in the basal Pebbley Beach Formation of the south Sydney Basin, but there is no satisfactory faunal control at present to indicate macro-faunal zonal correlation for the Pebbly Beach beds.

Briggs (1998) argued that the *Microbaculispora trisina* Zone incorporated most of the *Bandoproductus macrospina* (= *walkomi*) Zone, and also the "*Tomiopsis strzeleckii*" Zone. There seems to be no direct evidence for this proposal, but it nonetheless appears to be at least partially correct, because *trisina* is found in the upper Cranky Corner Formation of the Cranky Corner Basin (Balme & Foster 2003, pp. 130, 131), with *Neilotreta* and *Ambikella elongata*, two species that are also found in the underlying Beckers Formation with *Pseudoreticulatispora pseudoreticulata*, and which have close affinities to specimens from the upper Rammutt Formation with *Bandoproductus*, and with cf. *elongata* at the base of the Tiverton Formation. A different version was offered by Archbold (2001b, table 5), who showed that this *Bandoproductus* Zone was to be matched with a *Striatopodocarpites fusus* Zone, followed by the *Microbaculispora trisina* Zone commencing high in the *Bandoproductus* Zone.

Middle Cisuralian Series

Bookeria pollex Zone

This zone was proposed on the basis of outcrops and described macro-invertebrate faunas near Cracow (Fig. 4) in the southeast Bowen Basin (Waterhouse 2008b). It is highly characteristic, and some of the key species are listed in Tables 4 and 5. The nominate species *Bookeria pollex* Hill first enters at the base of the Fairyland Formation, and persists through the overlying Dresden Formation into the base of the Elvinia Formation, to be followed by key index fossils of the next zone. Other species that are persistent include *Notostrophia bifurcata* Waterhouse, *Protoanidanthus compactus* Waterhouse and *Grantonia australis* (Bion). The zone is regarded as younger than the *Bandoproductus* Zone, because of field relationships in the Hunter Valley, New South Wales (Briggs 1998), and Yarrol Basin, Queensland (Maxwell 1964), and in the north Bowen Basin is represented above meagre faunas apparently correlative with the *Bandoproductus macrospina* Zone. Three subzones are well developed the Cracow area, as follows:

Echinalosia curtosa Subzone

The zone proposed by Waterhouse (1987b) and endorsed by Briggs (1998) is here relegated to subzonal status, because the aim of the zonal scheme for east Australia is to have robust and widely recognizable units, whereas subzones are localized. The subzone is typically exemplified in the Fairyland Formation of southeast Bowen Basin. Species limited to the zone include *Svalbardia cracowensis* (Etheridge)*, Echinalosia curtosa* Waterhouse*, Lipanteris cracowensis* (Hill)*, L. sparsispinosus* Briggs*, Costatumulus prolongata* Waterhouse*, Ambikella regina* (Waterhouse)*, Geothomasia cracowensis* (Waterhouse), *Tabellina denmeadi* (Campbell)*, Notospirifer paraextensus* Waterhouse*, Grantonia cracovensis* Wass, *Spiriferellina disparata* Waterhouse and *Marinurnula prima* Waterhouse. Mollusca include species like those of Early Permian faunas, together with *Eurydesma ovale truncatum* Waterhouse and *Concentiolineatus biornatus* (Waterhouse), *Pleurocinctosa promenata* Waterhouse and other distinctive forms. *Ambikella regina* is found in the lower Tiverton Formation at Homevale, with *Bookeria pollex*, *Grantonia cracovensis* and *Concentiolineatus biornata*. According to Briggs (1998), *Echinalosia curtosa* is found in the lower Farley Formation of the north Sydney Basin, above the Rutherford Formation with *Bandoproductus*.

Azygidium mitis Subzone

The *Azygidium mitis* Subzone is found in the lower Dresden Limestone of the southeast Bowen Basin. *Azygidium* is an unusual marginiferid brachiopod that lacks a zygidium, which is a small projection at the hinge immediately in front of the basal part of the cardinal process. Briggs (1998, text-fig. 72A) misunderstood the morphology, and figured a broken hinge to one side of the cardinal process as representing a zygidium, and referred the genus to synonymy of *Anemonaria*. The species *mitis* is certainly not *Anemonaria*, which belongs to a different subfamily and has large strut spines, whereas strut spines are completely absent from *Azygidium*. The subzone has several distinctive critical and short-lived species, including *Echinalosia dejecta* Waterhouse, *Plekonina spissatella* Waterhouse and *Spiriferellina anguliplica* Waterhouse. Some additional species appeared and persisted into the next zone, such as *Notostrophia bifurcata* Waterhouse, *Geothomasia postglabra* (Waterhouse), *Permasyrinx subelongata* Waterhouse, *Spiraculinella radiata* Waterhouse and *Pleurocinctosa fletcheri* Waterhouse. A number of critical species are shared with the *Echinalosia curtosa* Subzone, including *Bookeria pollex*, *Protoanidanthus compactus*, and doubtful *Grantonia cracovensis*, as well as some bivalves and gastropods, to imply a close relationship. *Geothomasia branxtonensis* (Etheridge) is found in the Rutherford Formation and lower Farley Formation, and also in the lower Tiverton Formation, but also reported, dubiously, from the *Unicostatina crassa* Zone of Tasmania by Clarke (1992a). Few of the restricted species are known elsewhere, except in the Yarrol limestone of the Yarrol Basin, with *Echinalosia dejecta,* described

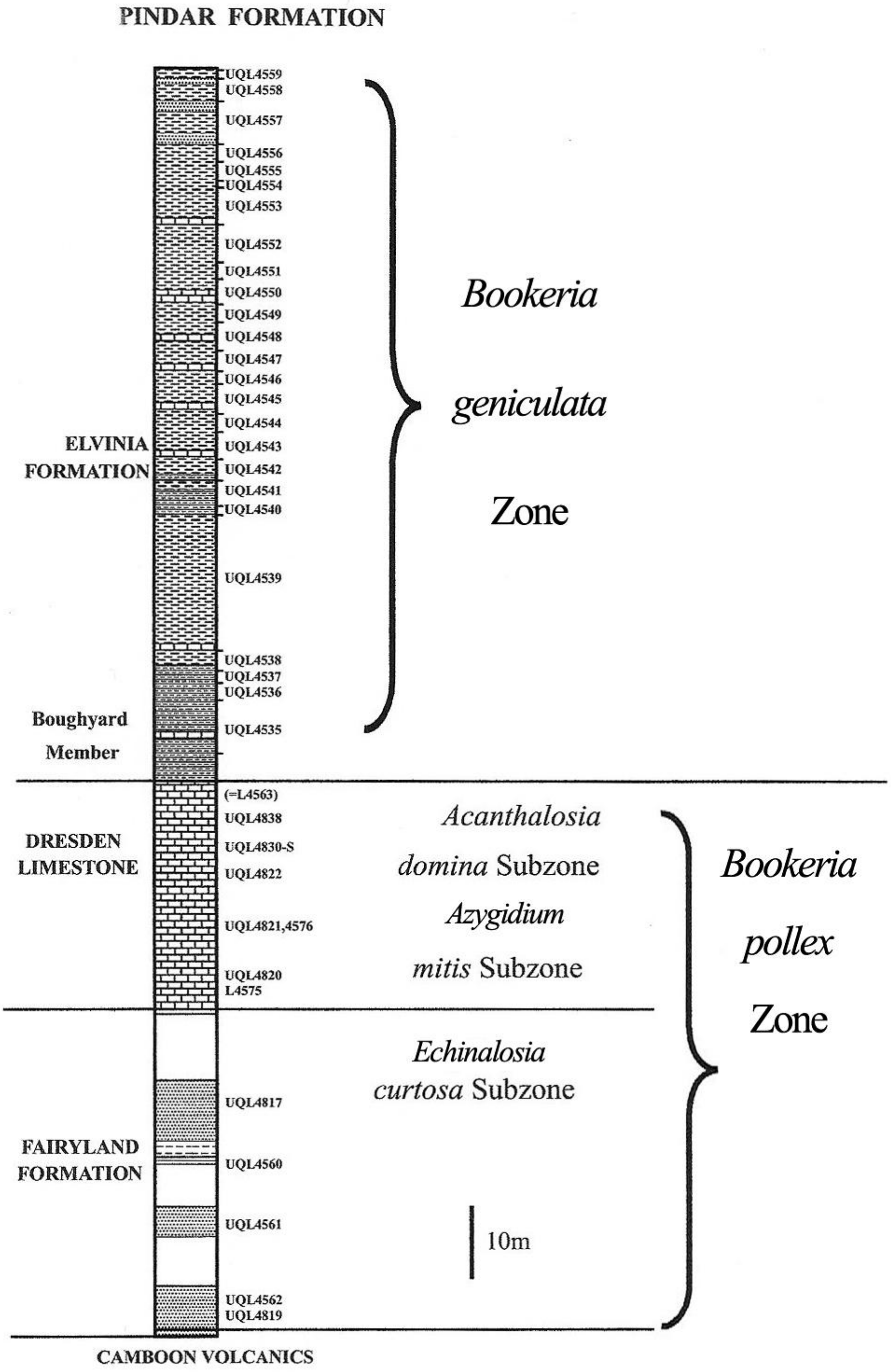


Fig. 4. Stratigraphic column for middle Early Permian formations of southeast Bowen Basin near Cracow, synthesized from Briggs (1998) and Waterhouse (1986a): minor gaps and volcanics are omitted as they infilled by beds and faunas exposed along strike. The Boughyard Member has *Echinalosia curvata* and *Costatumulus farleyensis*, and *Bookeria geniculata* enters in the overlying UQL 4836.

described as *Strophalosia preovalis* by Maxwell (1964).

***Acanthalosia domina* Subzone**

In the upper Dresden Formation, *Azygidium* disappears, and *Acanthalosia domina* Waterhouse and *Lakismatia lakismatos* (Briggs) enter as characteristic species. Many of the accompanying species or closely allied forms persist from the *Azygidium mitis* level, including *Notostrophia bifurcata*, *Bookeria pollex*, *Permasyrinx subelongata* and *Geothomasia postglabra* or close allies.

Acanthalosia domina is present near the base of the Tiverton Formation (Table 9), together with possible *Bookeria pollex* and *Ambikella regina*, implying that these subzones were present but only thinly represented. The bivalve *Eurydesma glaebula* is common at this level in the Tiverton Formation, and is also found in the *Eurydesma* beds of the Wallaby Formation in the Stanthorpe Road Block, south Queensland (Richards & Bryan 1924), together with *Capillaria warwicki* (Maxwell). The *Bookeria pollex* Zone is also reported further north from the type area near Mt Breast (GSQ D38), but the subzone is not certain.

There is a report of *Echinalosia warwicki* in the Nassau Siltstone of Tasmania, but faunas at this level in Tasmania have not been monographed. Otherwise it seems that the *Bookeria pollex* Zone is not represented by marine faunas in Tasmania, appearing as the “Freshwater beds” in cliff and quarry sections near Darlington, Maria Island, and the zone has not been definitely identified in New Zealand, or further afield in India or South America.

Biozone and Subzone	Queensland	New South Wales	New Zealand
Echinalosia conata			*Echinalosia conata*
Spinomartinia adentata			*Spinomartinia adentata*
Ingelarella plica	*Ingelarella plica*		*Notostrophia homeri* *N. zealandicus*
Taeniothaerus subquadratus	*T. subquadratus*	*T. subquadratus*	*T. subquadratus*
Bookeria geniculata	*B. geniculata*	*B. geniculata*	= *B. geniculata*
Bookeria pollex	*B. pollex*	*B. pollex*	
Bandoproductus macrospina	*Ba. macrospina*	*Ba. macrospina*	
Crassispinosella subcircularis		*C. subcircularis*	
Strophalosiaria concentrica	*Eurydesma burnettensis*	*S. concentrica*	

Table 8. Occurrence of Permian macro-invertebrate biozones in Asselian to Artinskian faunas in east Australia and New Zealand. It appears likely that *drysdalei* is present in New Zealand, correlative with *geniculata*.

***Bookeria geniculata* Zone** (Table 10)

This zone is typified by a plethora of species, some of which are listed in Tables 3 and 4 for the Elvinia and lower middle Tiverton Formation. There is a documented transition in the southeast Bowen Basin (Waterhouse 1987b, table 9, p. 205) faunally and lithologically from the *Acanthalosia domina* Subzone, with residual species from the *Bookeria pollex* Zone joined by incoming **Echinalosia curvata* Waterhouse, **Anidanthia paucicostata* (Waterhouse), **Magniplicatina undulata* Waterhouse, *Bookeria geniculata* (Waterhouse), *Costatumulus farleyensis* (Etheridge & Dun), *Coledium elvinia* Waterhouse, *Cyrtella subparallela* Waterhouse, **Permasyrinx elongata* (Armstrong), **Unicostatina stutchburii* (Etheridge), **Grantonia australis* (Bion), **Ambikella ovata* (Campbell), **Validifera valida* (Campbell), **Papulinella hillae* Campbell, *Pustulospiriferina lirata* Waterhouse, **Etheripecten tenuicollis* (Dana), **Concentiolineatus homevalensis* (Waterhouse) and **Stutchburia farleyensis* Etheridge. Asterisked species are shared with or are very close to species in the lower middle Tiverton Formation (UQL 4509-4515), which provides the best exemplar for the zone (Fig. 5) and was

BRACHIOPODA
Echinalosia curtosa sulcata n. subsp.
+*Acanthalosia* cf. *domina* Waterhouse
+*Protoanidanthus compactus* Waterhouse
+ *Bookeria* cf. *pollex* Hill
+*Costatumulus* aff. *prolongata* Waterhouse 2?
Ambikella regina (Waterhouse)
Geothomasla branxtonensis (Etheridge)
Notospirifer triplicata n. sp.
Grantonia cracovensis Wass 3, 4
+*Fletcherithyris* sp.

BIVALVIA
Merismopteria banksi n. sp.
Squamuliferipecten mitchelli (Etheridge & Dun) 2, ?4
Concentiolineatus biornatus (Waterhouse)
Eurydesma glaebula n. sp. 3+
Stutchburia laminata n. sp. 4+
Pachymyonia morrisii (Etheridge) 3
+*Myomedia davidis* (Dun) 3
GASTROPODA
Globosospirina mcclungi n. sp. 3, 4

Table 9. Species in the *Bookeria pollex* Zone of lower Tiverton Formation. Species that range higher indicated by 2 – *Bookeria geniculata* Zone, 3 – *Svalbardia armstrongi* Subzone. 4 – *Taeniothaerus subquadratus* Zone. Common to dominant species in bold. Rare species +.

BRACHIOPODA
Svalbardia armstrongi n. sp. 3*
Echinalosia cenula n. sp. 2, 3, 4
+*Pseudostrophalosia brittoni* (Maxwell) 3#, 4
Maxwellosia bryani n. sp. 4
Lipanpteris anotos (Briggs) 4
Taeniothaerus sp. indet. 3+
Anidanthia paucicostata (Waterhouse) 2, 3, 4
Bookeria sparsispinosa n. sp. 2, 3, 4
Bookeria drysdalei n. sp. 3, 4
+*Magniplicatina undulata* Waterhouse
Costatumulus tumida (Waterhouse) 2, 3, 4
+*C.* aff. *prolongata* Waterhouse 1
Biconvexiella convexa (Armstrong) 3
Ambikella ovata (Campbell) 4
Geothomasia symmetrica (Campbell) 4
G. profunda (Campbell) 4
Validifera valida (Campbell) 3, 4
Tweedaleia tweedalei Waterhouse 3, 4
+*Ingelarella* sp. 3
Papulinella hillae (Campbell) 4
*_P. wilsoni_ n. sp. 4
Tabellina undulata (Parfrey) 2
Grantonia australis (Bion) 2, 4#
Unicostatina stutchburii (Etheridge) 2, 4

Permosyrinx elongata (Armstrong) 4
P. granulata (Armstrong) 2, 4
Pustulospiriferina etheridgei (Armstrong) 3, 4
Fletcherithyris farleyensis faba Campbell 4?
F. burdenae n. sp. 2, 3, 4
Gilledia homevalensis Campbell 2, 4#
BIVALVIA
Promytilus homevalensis Waterhouse 3, 4
Squamuliferipecten mitchelli (Etheridge & Dun) 1, 2, 4
S. squamuliferus (Morris)
Elviniaria limitans (Waterhouse) 3, 4
Orbiculopecten cokeri n. sp. 2, 4
Eurydesma glaebula n. sp. 1, 3#
Etheripecten playfordi n. sp. 2, 4
Astartella heidemckeri n. sp. 2, 4#
Mellicusia jelli Waterhouse 2, 4
Pachymyonia morrisii (Etheridge) 1, 3
+*Myomedia davidi* (Dun) 1, 3
Protraxia gryphoides (de Koninck) 2, 4
GASTROPODA
Globosospirina mcclungi n. sp. 1?, 3, 4
Pleurocinctosa cf. *allandalensis* Fletcher 3, 4
Spirovallum sp. 4
CEPHALOPODA
Gobioceras cancellatum (Dear) 3

Table 10. Fossil species of the *Bookeria geniculata* Zone in lower middle Tiverton Formation, pre- *Svalbardia armstrongi* Subzone – 2; species found in the *armstrongi* subzone indicated by 3. 1 – also in *Bookeria pollex* Zone. 4 – also in *Taeniothaerus subquadratus* Zone. Common to dominant species in bold, rare species signified by +, and # present but rare.

nominated as biostratotype in Waterhouse (2008b). Here the fauna is joined by *Echinalosia cenula* n. sp. and *Maxwellosia bryani* n. sp. Several critical species are replaced by closely related forms, interpreted as local variants, *Bookeria sparsispinosa* n. sp. in place of *B. geniculata*, and *Costatumulus tumida* (Waterhouse) in place of *C. farleyensis,* and *Bookeria drysdalei* n. sp. appears. *Svalbardia armstrongi* is abundant in bands near the middle of the Tiverton Formation, with brachiopod *Biconvexiella convexa* (Armstrong) and the ammonoid *Gobioceras cancellatum* (Dear)? Most of the species found with *Svalbardia* are found in underlying rocks, and many persist higher in the formation. A number of the species are also found in the Yarrol Formation of the Yarrol Basin (Maxwell 1964). Other faunas include those of the upper Wallaby rocks above the lower *Eurydesma* beds in the Stanthorpe Road block (Richards & Bryan 1924). The zone is represented in the Farley Formation of the Hunter Valley through *Svalbardia saeptata* n. sp., *Anidanthia paucicostata* (Waterhouse), *Costatumulus farleyensis* (Etheridge & Dun), *Biconvexiella,* rare *Geothomasia profunda* (Campbell) and *Ambikella ovata* (Campbell) with abundant *Geothomasia branxtonensis* (Etheridge). Lists indicate that the zone is developed in Faunizones 4 and 5 of Clarke & Farmer (1976) with *Costatumulus farleyensis, Grantonia hobartensis*, *Ambikella ovata, Geothomasia profunda* and *Validifera valida,* but the occurrences have not been systematically described.

***Svalbardia armstrongi* Subzone**

This species is present in great numbers at UQL 4512 to 4515 in the middle Tiverton Formation. Species of Productida and Spiriferida are found in abundance in the subzone, and are found in underlying localities as well. An allied species *Svalbardia saeptata* occurs in the middle of the Farley Formation in the north Sydney Basin (see Waterhouse et al. 1983, text-fig. 2). Whether or not the band is present in Tasmania is not known.

***Taeniothaerus subquadratus* Zone** (Table 11)

This zone immediately overlies the *Bookeria geniculata* Zone (Fig. 5, p. 26), and typical species include *Taeniothaerus subquadratus* (Morris), *T. homevalensis* Briggs, *Lipanteris anotos* (Briggs), *Pseudostrophalosia brittoni* (Maxwell) and *Notostrophia laticostata* n. sp. The zone, incorporating UQL 4516-4525 at Homevale, is the same as that named previously *Pseudostrophalosia brittoni* Zone (Waterhouse 1987b), but *Taeniothaerus subquadatus* is more widespread, and has a more restricted time range, and *Ps. brittoni* has now been found to first appear in the *Svalbardia armstrongi* band. The *Taeniothaerus subquadratus* Zone immediately succeeds the preceeding *Bookeria geniculata* Zone, and is distinguished by the influx of taeniothaerid species and genera. Species of *Echinalosia*, *Acanthalosia*, *Anidanthia*, *Bookeria, Grantonia, Ambikella*, *Geothomasia, Papulinella*, *Unicostatina, Permasyrinx, Pustulospiriferina, Fletcherithyris* and *Gilledia* persist from the underlying zone, so that the two zones share many genera and species, and are chiefly distinguished by the abundance of taeniothaerins. Bivalves and gastropods are particularly diverse. Elements of this fauna are developed in the Riverstone Sandstone Member of the Cattle Creek Formation in southwest Bowen Basin, though Briggs (1998, Fig. 23, cs. pp. 37, 39) tabulated species for the Riverstone Member which differ from his textual summary. *Taeniothaerus farleyensis* Briggs, from a single station, position unstated, in the Farley Formation in Hunter Valley, is close to *homevalensis,* and is well represented in the Lakes Creek beds near Rockhampton, east Queensland (Waterhouse 2013, p. 277). Scattered faunas are to be found in New England. The zone is well developed in the Berriedale Limestone of Tasmania, with *Taeniothaerus subquadratus* and *Grantonia hobartensis* Brown in place of *G. australis* (Bion), and is represented in the Gondor Formation of Eglinton Valley, New Zealand (Waterhouse, Williams & Campbell 1983). The ammonoid *Gobioceras lobulatum* (Armstrong et al.) is found in the *Taeniothaerus subquadratus* Zone at Homevale.

***Ingelarella plica* Zone**

The highest beds of the Tiverton Formation at UQL 3725, not far from Homevale, have yielded a moderately large and characteristic fauna, monographed by Waterhouse (1983d), and characterized by *Echinalosia preovalis* (Maxwell), *Anidanthus springsurensis* Booker, *Terrakea dickinsi* Dear, *Kaninospirifer crassicostatus* (Waterhouse), *Ingelarella plana* Campbell, *I. plica* Campbell and *Glyptoleda javesi* Waterhouse. This zone is the same as the *Echinalosia preovalis – Tomiopsis plica* Zone of Waterhouse (1987b, p. 212), and *E. preovalis* Zone remains an appropriate name-giver, but *plica* is preferred because the range of *preovalis* was extended well beyond its natural limits by Briggs (1998) and Archbold (2000). The zone is also recognized in the Rose's Pride Formation of southeast Bowen Basin. In the upper Cattle Creek Formation at Reids Dome, southeast Bowen Basin, a more diverse fauna contains some typical species, a number still to be described. Faunas in two subzones are found in the Brunel Formation of New Zealand, which has over 30 species of brachiopods and mollusks (Waterhouse 1964a, 2002a). This zone is of limited distribution, not known in New South Wales and yet to be established in Tasmania through systematic description of any of the key species. Ammonoid *Neocrimites* (or *Aricoceras*) is found in the standard section.

BRACHIOPODA

Echinalosia cenula n. sp. 2, 3
E. (*Echinalosia*) *curvata* Waterhouse
Pseudostrophalosia brittoni (Maxwell) 3
Maxwellosia bryani n. sp. 2, 3
Lipanteris anotos (Briggs)
Taeniothaerus subquadratus (Morris)
T. homevalensis Briggs
Taeniothaerus sp.
Lipanteris anotos (Briggs) 3
Taeniothaerus sp. indet. 3
Anidanthia paucicostata (Waterhouse) 2, 3
Bookeria sparsispinosa n. sp. 2, 3
B. drysdalei n. sp. 2, 3
Costatumulus tumida (Waterhouse) 2, 3
Notostrophia laticostata n. sp.
Plekonella whitehousei n. sp.
Ambikella ovata (Campbell) 2, 3
Validifera valida (Campbell) 3
Geothomasia symmetrica (Campbell) 2, 3
G.. profunda (Campbell) 2
Tweedaleia tweedalei Waterhouse 3
Papulinella hillae (Campbell) 2
P. wilsoni n. sp. 3
Tabellina armstrongi Waterhouse
Grantonia australis (Bion) 2
Unicostatina stutchburii (Etheridge) 2
Permosyrinx elongata (Armstrong) 2
P. granulata (Armstrong) 2
+*P. archboldi* n. sp.
Pustulospiriferina etheridgei (Armstrong) 3
?*Fletcherithyris farleyensis faba* Campbell 2, 3?
F. burdenae n. sp. 2, 3
Maorielasma balfei n. sp.
Gilledia homevalensis Campbell 2
Eremithyris? longinquincus n. sp.

BIVALVIA

+*Palaeoneilo* ? sp.
+*Yanceyopsis alleni* n. sp.
Zigzagia stevensi n. gen., n. sp.
Promytilus homevalensis Waterhouse 3
Pseudomyalina perquiritus n. sp.
+*Squamuliferipecten mitchelli* (Etheridge & Dun) 1, 2
+*S. squamuliferus* (Morris) 2
+*Elviniaria limitans* (Waterhouse) 3
Concentiolineatus homevalensis (Waterhouse)
Orbiculopecten cokeri n. sp. 2
?*Furcatia petulantis* (Waterhouse)
Eurydesma sp.
Etheripecten tenuicollis (Dana)
E. playfordi n. sp. 2
Primaspina vagrans n. sp.
Hillaepecten queenslandica Waterhouse
Stutchburia laminata n. sp. 1
Astartella heideckeri n. sp. 2
Melicusia jelli Waterhouse 2
Protraxia gryphoides (de Koninck) 2
P. nobilissimus (de Koninck)
+*Australomya* cf. *hillae* (Runnegar)

GASTROPODA

+*Paraplatyschisma rotunda* (Etheridge)
+*Planikeeneia* sp.
Globosospirina mcclungi n. sp. 1, 3
Pleurocinctosa cf. *allandalensis* Fletcher 3
+*Glyptotomaria*? sp.
+*Austroscalata*? sp.

CEPHALOPODA

Gobioceras lobulatum (Armstrong et al.)
G. whitehousei (Armstrong et al.)

CONOCARDIIDA

Bransonia wilsoni Pojeta & Runnegar

Table 11. Fossils of the *Taeniothaerus subquadratus* Zone at Homevale. Species that range further in the Tiverton Formation indicated by 1 – also in *Bookeria pollex* Zone, 2 – also in *Bookeria geniculata* Zone, 3 – also in *Svalbardia armstrongi* Subzone. Common to dominant species shown in bold, rare species +. Species of unknown zonal occurrence involve *Undosusia tivertonensis* (Waterhouse), *Astartila* sp., *Vacunella waterhousei* (Dun) and *Warthia* sp.

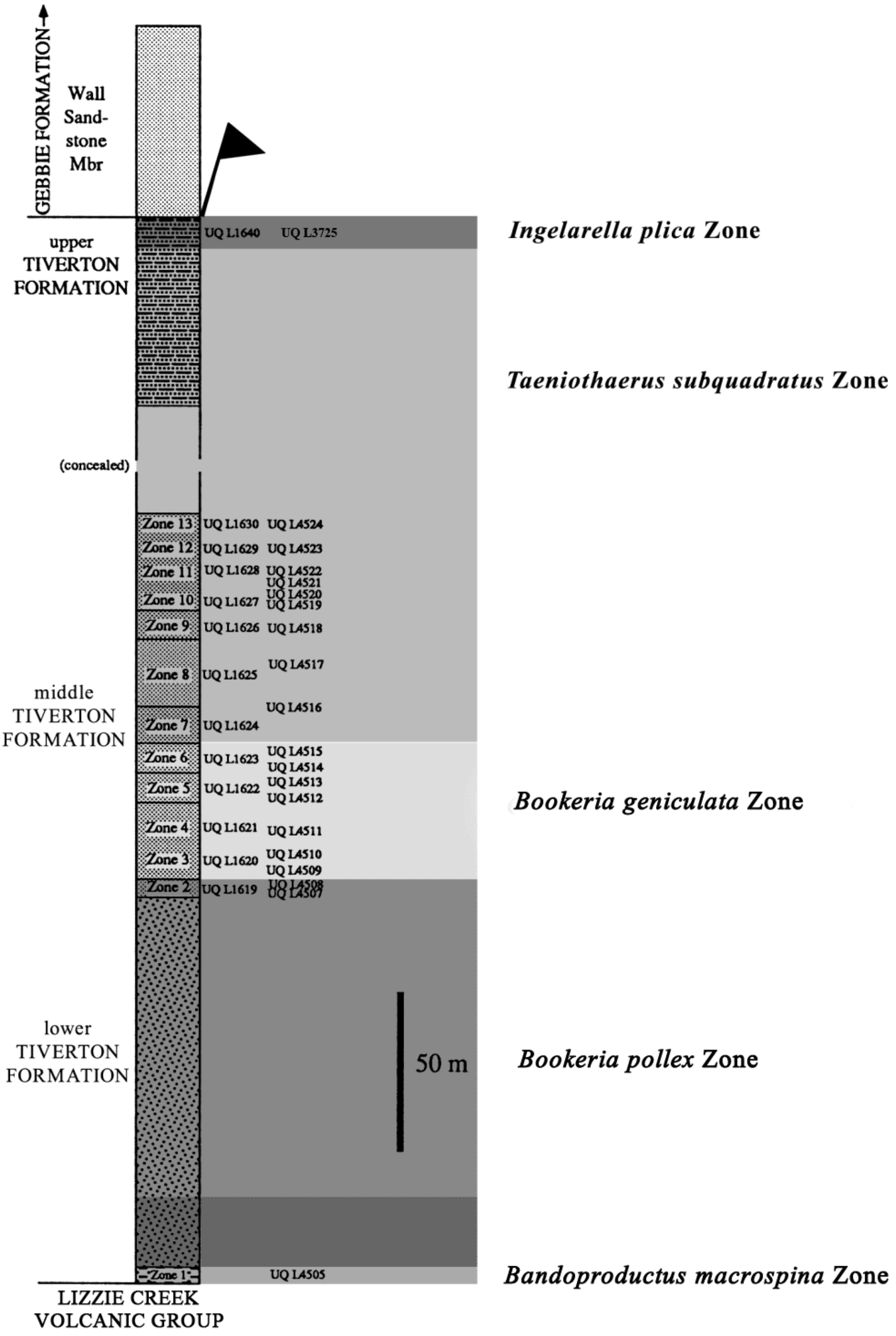


Fig. 5. Zonal sequence with critical fossil localities in the Tiverton Formation at Homevale. The Black Flag symbolizes the start of an interval without marine biozones (see Waterhouse 2008b). The column of numbered zones and UQL localities 1619 to 1630 are based on Campbell (1961a), and the column of UQL numbers from 4505 to UQL 4525 and 3725 is from fieldwork by the author. The presence of the *Bandoproductus macrospina* Zone is no more than provisional.

Palynomorph evidence

Palynomorph zones are not securely tied to the macrofaunal biozones between *Bookeria pollex* and *Ingelarella plica*. Briggs (1998, p. 60, Fig. 5) showed the marine biozones or their equivalents as approximately matching palynomorph Stage 4 (APP 31), characterized by the entry of *Phaselisporites cicatricosus*, succeeded by *Praecolpatites sinuosus* (4a), then *Acanthotriletes villosus* (4b). Balme & Foster (2003) reported the *Phaselisporites cicatricosus* APP 31 Zone but no *Praecolpatites sinuosus* zone in the Greta Coal Measures of the DM Tangorin DDH1 core at Cranky Corner, and noted the common concurrence of *Camptotriletes biornatus* Balme & Hennelly, first described from the Greta Coal Measures of the Sydney Basin. *Phaselisporites cicatricosus* as an index for APP 31 is found in the upper Reids Dome beds, not dated adequately by marine fossils, and in the overlying Cattle Creek Formation (Rigby & Heckel 1977), with beds supposed to contain *Capillaria warwicki.* Although the macro-fossil identifications shown in Briggs (1998, text-fig. 23) have yet to be verified through systematic description, it is possible (but speculative) that equivalents of the *Bookeria geniculata* or perhaps *Taeniothaerus subquadratus* faunas are involved. APP 3 floras appear at the base of faunizone 4 in Tasmania (Calver et al. 1984), with the entry of reported brachiopod species *Ambikella ovata* and *Geothomasia profunda*, but the faunas have not yet been described. *P. cicatricosus* enters higher. “Stage 3 or younger” microfloras appear in a core in non-marine strata, below Fairyland Formation in the southeast Bowen Basin, according to Wood (1984). Briggs (1998, Fig. 35) indicated incoming but unconfirmed *Phaselisporites cicatricosus* (APP 31).

Bowen Basin, Queensland		**New Zealand**	
Formation	**Zone**	**Zone**	**Formation**
Freitag*	*Wyndhamia typica*	*Wyndhamia typica*	lower Letham
Glendoo	*Glendella dickinsi*	scattered fossils	lower Letham
---	no fauna described	*Attenuocurvus* fauna	Elbow Creek
Aldebaran*	no fauna described	*Echinalosia conata*	McLean Peaks
Aldebaran*	no fauna described	*Spinomartinia adentata*	Chimney Peaks
Top Tiverton	*Ingelarella plica*	*Ingelarella plica*	Brunel
MiddleTiverton	*Taeniothaerus subquadratus*	*T. subquadratus*	Gondor
MiddleTiverton	*Bookeria geniculata*	*B. drysdalei*	(Dunton Range)
Dresden-Fairyland	*Bookeria pollex*		-no fauna?

Table 12. Intercorrelations between Bowen Basin and New Zealand, documented in detail in Waterhouse (2001, 2002a). * Freitag and Aldebaran Formations interpolated from southwest Bowen Basin, where they lie above the Sirius Shale which contains *Ingelarella plica* Zone.

Archbold (2001b) correlated the *Striatopodocarpites fusus* Zone with the Rutherford Formation, Faulkner and Liffey Groups, and upper Pebbley Beach Formation, based not on palynomorphs in those formations, nor on brachiopods but stratigraphic position, perhaps simply by extrapolation from Western Australia. No explanation was provided. The full *Microbaculispora trisina* Zone, which extended into the lower *Bandoproductus* Zone according to Briggs (1998), was not shown by Archbold (2001b), but by implication, would have involved the Farley Formation, and if so, the correlative Elvinia and middle Tiverton Formations of the Bowen Basin, involving the *Bookeria pollex, B. geniculata* and *Taeniothaerus subquadratus* Zones. Archbold (2003, text-fig. 2) showed *Didecitriletes byroensis* Zone, top APP 21, as occurring in east Australia. Just where it actually occurs in east Australia was not documented by Archbold: it is a zone of Western Australia, found above *fusus* in the upper Callytharra Formation, and it seems likely that Archbold intended to indicate correlation with rather than presence in eastern Australia.

Praecolpatites sinuosus marking the start of APP 32 is found in the upper Cattle Creek Formation with *Echinalosia preovalis* s.s. and equivalent to the *Ingelarella plica* Zone, and *Praecolpatites sinuosus* is also found in the Staircase Sandstone. Foster (1979) concluded that the upper Cattle Creek and lower Aldebaran beds could be correlated through palynofloras with the Blair Athol Coal Measures, with rare *Praecolpatites sinuosus*, and even *Microbaculispora tentula* persisting from very Early Permian. The palynomorphs appear to reinforce the Dickins and Briggs view that the *Echinalosia preovalis* Zone, or what is now called *Ingelarella plica* Zone, postdated the Greta Coal Measures, a view that runs counter to faunal analysis of critical brachiopods (Waterhouse 2001, 2002a). However Rigby & Heckel (1977) and Foster (1977) recorded *P. sinuosus* well below these levels in the Reids Dome beds and below the incoming of *Phaselisporites cicatricosus*, and Calver et al. (1984, Fig. 3) reported a comparable distribution in Tasmania, entering above Stage 3 ("APP 32") at the start of "stage 4" and well below *Phaselisporites cicatricosus*. It is inferred from such records that in some places, *Phaselisporites cicatricosus* possibly appeared well before *sinuosus*, and in other places, even within one basin, *Praecolpatites sinuosus* appeared before *Phaselisporites cicatricosus*, to imply that the two indices are not time-constant, and if so cannot be trusted for precise correlation.

Microbaculispora villosa is key for the base of APP 33 (upper stage 4b) and appears to be well constrained only for the Denison Trough, in the upper Cattle Creek Formation (Heywood 1977). Helby (1970) recorded *M. villosa* in the upper Belford Formation of the Sydney Basin, and Briggs (1998, p. 60) extrapolated the range downwards to the base of his "*Echinalosia maxwelli*" – in fact *Echinalosia discinia* – Zone, but the relationship between palynomorphs and brachiopod zones remains conjectural.

Review of previous work on the *Bookeria pollex* to *Ingelarella plica* Zones

Briggs (1998) proposed a somewhat different zonal scheme for the east Australian Permian. He recognized four zones for the same part of the stratigraphic column that covered the *Bookeria pollex* to *Ingelarella plica* Zones. His first and basal zone, supposed to follow that of *Bandoproductus*, was named "*Tomiopsis strzeleckii"* (now corrected to *Monklandia gympiensis*), based on the fauna from the "green fossiliferous sandstone" in the Rammutt Formation at Gympie. In fact *gympiensis* preceeds, not follows *Bandoproductus* (Waterhouse 2015). Not a single species of Productida could be enumerated by Briggs (1998, p. 32), and the only other occurrence of "*strzeleckii"* was supposed to be in the upper Rutherford Formation in the Hunter Valley. It is true that Rutherford material is generically close to *strzeleckii*, and these specimens are now referred to *Monklandia mcclungi* Waterhouse, 2015, p. 171, Fig. 80. They are distinguished by having fewer plicae than in *gympiensis*. The Briggs interpretation was based a zone found at only two localities, miscorrelated, and reliant on a single described species. It was shown in Waterhouse (2015) that the so-called *strzeleckii* Zone sensu Briggs in the middle Rammutt Formation at Gympie is correlative with the Allandale fauna, and not a unique faunal level.

The second zone of Briggs (1998, p. 33) is the *Echinalosia curtosa* Zone of Waterhouse (1987b), downscaled herein to a subzone. Briggs (1998) misrepresented several of the affinities and generic positions and correlations, as documented herein in the section on systematics, but did point to the occurrence of *curtosa* in the lower Farley Formation in the north Sydney Basin. Briggs (1998, p. 35) speculated that the Hickman Formation in Tasmania was correlative but the fauna has not been described or figured.

The third zone recognized by Briggs (1998, p. 35) was the *Echinalosia* (now *Capillaria*) *warwicki* Zone, with a type area for which the faunal descriptions of most of the taxa have not been published. Briggs (1998) stated that *warwicki* could be confused with *preovalis*, and stated that "*Tivertonia yarrolensis"* and *Magniplicatina transversa* Briggs were also significant. These species have been reassessed in the systematic section. Briggs argued that *warwicki* was widely known in the lower middle Tiverton Formation, but this is not confirmed by systematic study. Various other reported occurrences were not substantiated by description or figures, including supposed occurrences in the Yarrol Formation of Queensland, not that description failure denies the accuracy of the report, but it remains to be confirmed. The species was said to range through the Farley Formation of the north Sydney Basin, and in the Nassau Siltstone of Tasmania, with no figures or detailed description provided. It would seem advisable to designate a more reliable nominate species, buttressed if possible by additional species sufficient to make up an assemblage zone.

A fourth zone was recognized by Briggs (1998) as the *Echinalosia preovalis* Zone, extended far beyond the stratigraphic range of *preovalis* sensu stricto. According to Briggs (1998), the lower *Echinalosia preovalis* Zone was typified by Campbell's (1961a) zones 8-13 of the Tiverton Formation at Homevale. The zone is called the *Taeniothaerus subquadratus* Zone herein. The upper *preovalis* zone, which corresponds closely with the restricted *E. preovalis* Zone as delimited by Waterhouse (1987b), was typified by upper Tiverton Formation, with the fauna described by Waterhouse (1983d). Briggs (1998) matched the fauna with those of the Dresden and Elvinia Formations of southeast Bowen Basin, the lower Elderslie Formation in the south Sydney Basin (upper *preovalis*), and noted – as long reported by Waterhouse (1964a, 1982a) – the similarity to faunas in the lower Takitimu Group of New Zealand. Briggs also included the faunas of the overlying *Spinomartinia adentata* and *Echinalosia conata* Zones of the Takitimu Group in New Zealand. The zone was considered to be followed by the *Echinalosia maxwelli* Zone and then *E. davidi* Zone. There are many anomalies. The Tiverton "zones 8-13" of Campbell (1960), supposedly typifying the lower *Echinalosia preovalis* Zone, do not contain *Echinalosia preovalis*, and another of Briggs supposedly significant species allied to what he called *Acanthalosia* "*domina*" enters the succession well below "zone 8". The lists of Productida and Spiriferida provided herein as Tables 2 and 3 show that the Dresden faunas have little in common with the "zones 8-13" of Homevale, but have meagre ties with basal Tiverton faunas – ie "zones 1 and 2" of Campbell (1961a). The Elvinia faunas are like those of "zones 3-6" at Homevale – certainly not the uppermost Tiverton faunas with *Terrakea dickinsi*, *Ingelarella plica* and *I. plana*. The lower Elderslie Formation does not have *Echinalosia preovalis* but a younger species, called *E. floodi* Waterhouse (2001, p. 59, pl. 4, fig. 1-5, cf. pl. 5, fig. 17), which differs in shape and inflation, and appears to be a descendent from *E. preovalis*. In the southern Sydney Basin, what may well be the same species *floodi* comes from the Snapper Point Formation and is found with *Wyndhamia typica*. The *Spinomartinia adentata* and *Echinalosia conata* Zones of the Takitimu Group in New Zealand that Briggs (1998) asserted matched those of the upper *preovalis* Zone include these fossils: *Echinalosia conata, Wyndhamia* sp., "*Taeniothaerus*" aff. *ingens, Protoanidanthus, Attenuocurvus altilis, Arcullina humilis, Spinomartinia adentata, Aphanaia glabra, A. otamaensis, Coronopsis vagrans, Platyteichum spirolaxum, Spirovallum fasciatum, Spironemella dignitas* and other species, all of them illustrated and systematically described (Waterhouse 1963a, 1964a, 1982a, 2001 etc.). Not a single species found in these rocks and faunas is known from any of the Australian faunas referred by Briggs (1998) to his "upper *preovalis* Zone". Instead they belong to two zones nowhere found in eastern Australia, and represented instead by barren beds, coal measures and unconformity (Waterhouse 2008b). The *Spinomartinia adentata* and *Echinalosia conata* Zones have no species in common with east Australia, but do show links with the lower Byro faunas of Western Australia, within the biozones (or fossil communities) named after *Echinalosia prideri* to *Fusispirifer byroensis* by Archbold (1993b).

Late Cisuralian Zones in east Australasia

Above the *Ingelarella plica* Zone found in the neighborhood of Exmoor Station and Bowen River comes the Wall Sandstone, a white quartzite without known marine fossils. Given the lack of marine fossils, the age is not clear, and the stratigraphic position indicates that it may equate to the *Spinomartinia adentata* Zone, or the *Echinalosia conata* Zone in New Zealand (see Table 12, p. 27), or perhaps both, and may, as seems quite likely in the field, overlie the upper Tiverton Formation with a degree of paraconformity. It is this band that appears to pass northwards into the Collinsville Coal Measures. The *Glendella dickinsi* Zone is developed in the Glendoo Sandstone Member of the Gebbie Formation above the Wall Sandstone, and is characterized by a few bivalve species and brachiopod *Notospirifer gentilis* (Waterhouse & Jell, 1983, Waterhouse 2002a, p. 173). The fauna is judged to be Kungurian (Filippovian). The *Wyndhamia typica* Zone follows, characterized by such species as *Paucispinauria paucispinosa wardenensis* Waterhouse, *Echinalosia floodi* Waterhouse, *Aperispirifer archboldi* Waterhouse and *Tumulosulcus undulosa* (Campbell). The zone is well represented in the Bowen Basin near Homevale in the upper Gebbie Formation, and in the southwest of the basin in the Freitag Formation (Waterhouse 2002a, p. 173), as well as Sydney Basin, Tasmania and New Zealand. This zone is overlain by the *Echinalosia discinia* Zone, well developed in the southeast Bowen Basin as well as Sydney Basin and New Zealand.

The sequence at Cranky Corner, New South Wales

A core through the rocks of the Cranky Corner Basin, northern New South Wales (Table 13) was examined in detail by Balme & Foster (2003). The lower Seaham Formation contained what was identified as palynomorph unit APP1, although it lacked *Protohaploxpinus*, and indeed the guide for APP12, *Microbaculispora tentula,* appears. However

Balme & Foster (2003) suggested the identity was possibly suspect, although whether this was because of dissonance with favoured succession or palynomorph morphology was not explained.

Supposedly Permian brachiopods and bivalves have been reported in the younger Seaham Formation. Briggs (1998, text-fig. 14) listed *Eurydesma burnettensis* Waterhouse, a species which is found in the Early Permian Burnett Formation of the Yarrol Basin. Briggs (1998, p. 59) asserted that this species belonged to the APP 12 zone, whereas Balme & Foster preferred an APP 1 correlation for the upper Seaham Formation. It is not clear whether Briggs' *burnettensis* is the same as a fragmentary right valve supposedly from the Seaham beds and figured as *Eurydesma* sp. by Runnegar (1970, pl. 16, fig. 1) and further *Eurydesma* reported in Runnegar (1979). The figure shows what appears to be a discrete bulbous tooth. Another Seaham Formation specimen was recorded as *Posidonia* by Campbell (1961b), and this may belong to an ambonychioid *Amosius* Gonzalez & Waterhouse, 2004, described from the Las Salinas Formation in the Argentine, belonging to the *Levipustula levis* Zone of "mid-Carboniferous" age. Briggs (1998) also recorded from the Seaham Formation possible "*Tomiopsis konincki*", and so-called "*Trigonotreta campbelli*" of McClung, 1975, not Maxwell, 1964. Type *campbelli* comes from the Branch Creek Formation, and belongs to *Costuloplica* Waterhouse (2004a, p. 188), a genus represented widely in Late Carboniferous faunas of eastern Australia and Argentine. Roberts et al. (1976, p. 222) pointed out various differences between type ''*Trigonotreta*" *campbelli* and the Seaham material, but so far the Seaham material does not appear to have been even figured. Archbold (2003) described macro-invertebrate fossils from the Cranky Corner Basin, but did not mention the Runnegar or Briggs material, so it remains unclear whether his species *Neilotreta tangorini* (Archbold) is what has been confused with "*Trigonotreta*" *campbelli* by McClung (1975), or whether two separate species are involved: nor is it clear how his specimens of *elongata* compare with the ingelarellid material identified by Briggs (1998) as "*konincki*", and supposedly from the Seaham Formation.

Above the Seaham Formation at Cranky Corner, the Tamby Creek Formation has not yielded palynomorphs, but radiometric ages bracket 300-303Ma (Claoué-Long & Korsch 2003). Such ages suggest that Briggs' alleged *Eurydesma burnettensis* and "*Trigonotreta campbelli*" in the Seaham Formation, if correctly located, are Late Carboniferous. They contradict the Briggs (1998, p. 28) correlation with the *Strophalosiaria concentrica* Zone, or indicate that the *concentrica* Zone is Carboniferous, or suggest that there has been confusion in Runnegar (eg. 1972, p. 310) and Briggs (1998) over the stratigraphy and source of the fossils. Presumably the latter option is the most likely, given that names have been under revision, and that the memoir on Cranky Corner geology had substantial input from a stratigraphic core not available to earlier authorities.

Balme & Foster (2003) described *Pseudoreticulatispora confluens*, the index to Stage 2 (APP 122), from the lower Beckers Formation at Cranky Corner, noting gross differences from the APP 1 flora in the Seaham beds, and a diminution in cryptogram spores. Although Briggs (1998, p. 59) criticized the Confluens Zone and concept, this flora is particularly widespread, having been reported from South America, Yunnan, Antarctica and Oman. Balme & Foster (2003) assigned a Sakmarian age, but allowed that the zone might extend into the Asselian. Supposed *Trigonotreta* was figured by Archbold (2003, text-fig. 4.15-18), not well preserved, and requiring more material to be identified and compared, but apparently close to *Spirifer hesdoensis* Sahni & Dutt of the Manendragarh fauna in the Early Permian of India, and constituting an early member of *Neilotreta* or even a distinct genus. Archbold (2001b, table 5) showed the *Pseudoreticulatispora confluens* Zone as incorporating the *Strophalosiaria concentrica* Zone, as also evaluated by Foster & Waterhouse (1988). It is represented in or correlative with the Lochinvar Formation, Wasp Head Formation, New South Wales, and Woody Island Formation, Tasmanites Shale and Quamby Formation of Tasmania.

Balme & Foster (2003) reported the *Pseudoreticulatispora pseudoreticulata* Zone in the upper Beckers Formation and lower Cranky Corner Sandstone, and noted that it is represented in the Fossil Cliff Formation of the Perth Basin, considered to be of upper Sakmarian age from ammonoid evidence, and asserted that it possibly extends into the Artinskian Stage. From the Beckers Formation at Cranky Corner, Archbold (2003) listed undescribed and unfigured bivalve *Eurydesma cordatum* Morris, together with described *Pyramus* and *Keeneia*, above described brachiopods *Neilotreta tangorini* (Archbold) and *Ambikella elongata* (McClung & Armstrong). These two brachiopod species display links with the upper Rammutt Formation at Gympie, southeast Queensland, where allied forms are found with *Bandoproductus,* and possible *elongata* occurs in the basal Tiverton Formation of the north Bowen Basin.

Palynomorph Stage 3b or APP 22 was established for the entry of *Microbaculispora trisina*, which has been found in the upper Cranky Corner Formation and in the Billy Brook Formation by Balme & Foster (2003) at Cranky Corner. Whether *Neilotreta tangorini* and *Ambikella elongata* are found in the upper Cranky Corner Formation is not clear. A match with Faunizone 2 of Tasmania and the upper Callytharra Formation and Wooramel Group was proposed, and Sterlitamakian to Baigendzinian age suggested. Marine faunas were stated by Balme & Foster (2003, p. 132) to include *Eurydesma cordatum*, said to point to an Allandale correlation (cs. Archbold 2003, text-fig. 2), but the specimens have not been described or figured, so the species identification, *cordatum,* or *glaebula* perhaps, remains unverifiable.

Biostratigraphic age	**Formation**	**Palyno-stratigraphic Unit**	**Invertebrate fauna**	**Radiometric age (Ma)**
Baigendzinian	Greta Coal Measures	APP 31 (*Phaselisporites cicatricosus*)		
Aktasktinian	Billy Brook	APP 22 (*Microbaculispora trisina*)		285. 8 285.4
Sterlitamakian	Cranky Corner		*Pyramus laevis, Eurydesma cordatum,* *Keeneia platyschismoides,* *Unicostatina crassa, Neilotreta tangorini,* *Ambikella elongata*	
		APP 21 (*Pseudoreticulatispora pseudoreticulata*)	*Neilotreta tangorini, Ambikella elongata, Stutchburia randsi*	284.1
	Beckers			287.1
Tastubian		APP 122 (*Pseudoreticulatispora confluens*)	*"Trigonotreta"* n. sp.	
Asselian				
Stephanian	Tamby Creek	no data		300.13 303.3 302.4 303.7
Westphalian	Seaham	APP 1 (*Microbaculispora tentula*)		306.5

Table 13. Stratigraphic column for Cranky Corner, New South Wales, after Balme & Foster (2003). Brachiopod names adjusted from Archbold (2003). *Microbaculispora tentula* was only tentatively identified by Balme & Foster (2003). The molluscan determinations, taken from Archbold (2003), are open to further study, as are some of the biostratigraphic and radiometric ages.

The Cranky Corner and Beckers faunas described by Archbold (2003) show no significant difference between those of the APP 21 *Pseudoreticulatispora pseudoreticulata* Zone and those of the APP 22 *Microbaculispora trisina* Zone. Both APP 21 and APP 22 included *Ambikella elongata*, and Archbold (2003, text-fig. 2) matched the Cranky Corner *Ambikella elongata* fauna with the *Strophalosiaria concentrica* and upper *Nambuccalinus bourkei* faunas. Briggs

(1998) deprecated the stratigraphic value of the species *Ambikella elongata* and *Monklandia konincki*, which were supposed to co-exist in turn with *concentrica* and *subcircularis*. Archbold (2003) dismissed the claim, but his strictures require further evaluation, and available evidence suggests that Briggs (1998) was correct at that time, and his reservations may now be consolidated. The report by Clarke (1990, 1992a) that *elongata* occurred with *Strophalosiaria concentrica* in Tasmania has now been reassessed, and his specimens assigned to a different, older species, *Ambikella bundellaensis,* and specimens from the Hunter Valley sequence that were deemed to belong to *konincki* have been renamed *Monklania mcclungi* (see Waterhouse 2015). *Eurydesma, Pyramus, Myonia* and *Keeneia*, none of them satisfactorily identified, were shown by Archbold (2003) as occurring in the upper Cranky Corner Sandstone, and equivalent to the *Crassispinosella subcircularis - konincki* Zone, and lower *Pseudoreticulatispora pseudoreticulata* Zone APP 21, not the *Microbaculispora trisina* Zone as favoured by Balme & Foster (2003). *Unicostatina crassa* (Clarke) figured by Archbold (2003) from the Beckers and Cranky Corner beds was supposed to be post-*elongata* by Clarke (1992a) and conceivably matches specimens in the *Bandoproductus* faunas in New South Wales and Queensland. The Cranky Corner specimens of *Unicostatina* have a distinctly rounded median dorsal fold, whereas type *crassa* has fold neither illustrated nor described, so that identification is yet to be confirmed (see p. 203). The presence of *Neilotreta*, described as *Trigonotreta tangorini* by Archbold (2003), suggests a tie with the *Neilotreta occidentalis* Zone of Western Australia (also within the *Pseudoreticulatispora confluens* palynomorph zone), and a possible link exists between *Ambikella elongata* (Armstrong & McClung) from the Cranky Corner faunas and the basal Tiverton Formation with *A.* cf. *elongata.* These links would be more consistent with the rather fragile radiometric value of 285Ma (Table 13). Possibly the *Neilotreta* horizon represents a brief or cryptic fauna in east Australia, too small to be delineated as a zone, that followed the *Bandoproductus* Zone, but it seems more likely that it overlapped with *Bandoproductus*, as indicated in the upper Rammutt Formation of Gympie in southeast Queensland (Waterhouse 2015). Significantly, the Cranky Corner sequence lacks any macrofossils, according to Archbold's account, of the *Bandoproductus macrospina, Bookeria pollex, B. geniculata, Taeniothaerus subquadratus* and *Ingelarella plica* Zones. The first three of these zones are developed in the Hunter Valley below the Greta Coal Measures, with meagre possible representatives of the *subquadratus* Zone, and definitely no *Ingelarella plica* Zone. Yet the palynomorphs provide, as so far interpreted, no indication that these faunal zones are missing at Cranky Corner, and the range of the *pseudoreticulata* Zone at Cranky Corner seems slightly out of phase with the brachiopod and palynomorph zones in Tasmania and Western Australia.

Part B. CORRELATION

PERMIAN OF WESTERN AUSTRALIA (Table 14)

Marine faunas

There are four major divisions for the Permian faunas of Western Australia. The early zones are somewhat depauperate and of "Gondwanan" appearance thanks to the presence of various bivalves such as *Eurydesma* and *Deltopecten*, and strophalosiid brachiopods as well as *Costatumulus*, *Lyonia, Ambikella* and *Neilotreta*. The diverse faunas of the *Coronalosia irwinensis* Zone in the Callytharra and correlative formations retained Gondwanan influence, and after a faunal decline in the High Cliff and Wooramel beds, a second major association of faunas became varied and diversified with subtropical (southeast Asian) affinities throughout much of the Byro Group and correlative levels, up to the Nalbia Sandstone, when faunas again became somewhat depauperate and Gondwanan, to typify a third faunal association. Late Permian faunas reverted to forms common in high temperate to subtropical paleolatitudes. This pattern is much like that of eastern Australia and New Zealand (Waterhouse 1982a, Waterhouse & Shi 2010).

Brachiopods from the Permian sedimentary basins of Western Australia have been comprehensively described by N. W. Archbold, partly in collaboration with G. A. Thomas, and many of the bivalves and gastropods by J. M. Dickins. The faunas have been arranged in zones (Archbold 1993b), named after leading or key species, and even though the generic names have had to be amended in some cases, the Archbold work greatly facilitates understanding by briefly encapsulating the results of numerous and detailed systematic studies. However there is little or no documentation over FAD and measured entry data or relationship to formations and members, and many of the zones are based on very few localities, collected generally from a stratigraphic unit. That reflects on the very large and relatively inaccessible geographic area involved. In 1993b Archbold showed each zone as restricted roughly to its fossil locality or localities, with parts of the formations not placed in any zone, but later (eg. Archbold 2000), the gaps were omitted, and zones treated as forming a continuous succession. Thanks particularly to the studies by Archbold, we have a general and initial approximation for the geographically extensive and diverse Permian faunas of Western Australia.

According to present assessments, one of the oldest Permian faunas from Western Australia come from the Grant Group, involving the Calytrix Formation of Barbwire Terrace in the Canning Basin, as described by Foster & Waterhouse (1988). The Calytrix assemblage, informally named *Crassispinosella calytrixi* fauna, is characterized by *Crassispinosella calytrixi* (Archbold) and *Calytrixia capillata* (Waterhouse), with *Sommeriella obrieni* Archbold, *Brachythyrinella* ["*Trigonotreta*" of Archbold – see Waterhouse 2004a] and "*Martinia*", representing a family not otherwise found in Western Australia. *Crassispinosella* is also found in the *Crassispinosella subcircularis* Zone of Tasmania. Critically, the palynoflora was found to belong to the *Pseudoreticulatispora confluens* Zone, APP 12, which also occurs in the *Strophalosiaria concentrica* Zone of Tasmania.

Western species	Stratigraphic unit	Eastern allied species	Stratigraphic unit
Crassispinosella calytrixi	Calytrix	*C. subcircularis*	Lower Bundella
Carilya baracoodensis	Callytharra	*"Taeniothaerus subquadratus"*	Yarrol
Costatumulus irwinensis	Callytharra, Fossil Cliff	*Costatumulus farleyensis*	Elvinia, Farley
Costatumulus occidentalis	High Cliff	*Costatumulus farleyensis*	Elvinia, Farley
Quadrospira hardmani	Callytharra	*Kaninospirifer crassicostata*	upper Tiverton
Neilotreta occidentalis	Lyons	*Neilotreta tangorini*	Beckett (NSW)
Fusispirifer carnavonensis	Callytharra	*Cracowspira pauciplicus*	Rose's Pride
Tomiopsis woodwardi	Callytharra	*Ambikella ovata*	Tiverton, Elvinia, Farley
Tomiopsis woodwardi	Nura Nura	*Geothomasia branxtonensis*	Tiverton, Elvinia, Farley
Gilledia inornata	Wandagee	*Gilledia homevalensis*	Tiverton
"Polidevcia darwini"	Lyons, Carrandibby, Nura Nura	*Polidevcia darwini*	Branxton Subgroup
"Modiolus" koneckii	Fossil Cliff, Callytharra	*Promytilus homevalensis*	Tiverton
Pseudomyalina sp.	Fossil Cliff, Nura Nura	*Pseudomyalina perquiriitus*	Tiverton
Etheripecten tenuicollis	Callytharra, Fossil Cliff, High Cliff	*E. tenuicollis*	Tiverton, Elvinia, Allandale
Stutchburia hoskingae	Fossil Cliff	*Stutchburia laminosa*	Tiverton
Stutchburia variabilis	Lyons	*Stutchburia farleyensis*	Farley, Tiverton
"Astartila" obscura	Fossil Cliff, Callytharra, Cuncudgerie	*Protraxia gryphoides*	Tiverton, Farley
"Astartila" tumida	Fossil Cliff	*Protraxia nobilissimus*	Farley
"Keeneia" carnarvonensis	Lyons	*Paraplatyschisma rotunda*	Tiverton, Elvinia
Mourlonia (Mourlonia) sp.	Callytharra	*Globosospirina mcclungi*	Tiverton, Wasp Head
"Peruvispira" cf. *umariensis*	Fossil Cliff	*Pleurocinctosa allandalensis*	Allandale, Tiverton

Table 14. Permian fossils showing linkage between east and west Australia. Column on left indicates the species as described, or amended as to genus, and major stratigraphic sources within Western Australia. Two columns to right indicate species and amended genus, and stratigraphic unit in eastern Australia. Inverted commas indicate initial generic identification, corrected in the column to the right. Nura Nura *woodwardi* differs from the Callytharra material.

The Calytrix Formation is one of three formations recognized by Redfern (1991) in the upper Grant Group, and it has been correlated with the Wye Worry Member, a subdivision containing tillite below the uppermost Millajiddee Member of the Carolyn Formation in the Grant Group by Jones & Young (1993). *Etherilosia carolyni* Archbold, 1995 from the Wye Worry Member is now assigned to *Fimbrinialosia* (see Waterhouse 2013, p. 216), based on a genus from the early Permian of Rajasthan, India, and with *Pseudoreticulatispora confluens* palynomorphs. That means that two significant Early Permian strophalosiids, *Fimbrinialosia* and *Crassispinosella*, are found in the Grant Formation. A small bivalve-dominated fauna was described by Dickins et al. (1978) from the Wye Worry Member, a subdivision of the upper sandstone unit, containing tillite, below the topmost Millajiddee Member of sandstone, but evidence for matching Calytrix beds with Wye Worry beds is thin, and probably the two were of slightly different age, as suggested in Table 15. Archbold (1995) added the brachiopod *Sommeriella obrieni*. [*Sommeriella* was recognized as a subgenus of *Neochonetes* Muir-Wood by Archbold (1981b, 1982), but lacks the pair of strong median vascular trunks in the ventral interior (Waterhouse 2001, p. 14) and so is judged to be a full genus]. Archbold considered that the faunas were younger than those of the *Lyonia lyoni* Zone, but from brachiopod evidence they appear to be older.

The *Lyonia lyoni* Zone, as outlined by Archbold (1993b), is found in the lower and middle Lyons Group, with *Rhynchopora australasica* Archbold, *Arcullina* ["*Spiriferella*" of Archbold 1995a], *Ambikella notoplicatus* (Archbold & Thomas) and "*Trigonotreta" lyonsensis* Archbold & Thomas. [The species *lyonsensis* Archbold & Thomas (1986a) is a very transverse species with four or five pair of plicae and weakly predominant primary costae, as in *Koenigoria* Waterhouse. It is not typical *Trigonotreta*, nor is it represented as claimed in Pakistan (see Waterhouse 2004a, pp. 174-175)]. The *Lyonia lyoni* Zone contains the palynomorph *Pseudoreticulatispora confluens* and is correlated as a rule with the lower Holmwood Shale in the Perth Basin of Western Australia, involving the Beckett Member which contains *Juresania jacksoni* (Etheridge) of either late Asselian or basal Sakmarian age (Glenister et al. 1993, p. 55; Archbold 1993b). Though the Beckett Member is regarded as correlative with the middle Lyons Group, it could be slightly younger.

The overlying zone above the *lyoni* faunas is constructed from various scattered and meagre faunas, assigned to the *Neilotreta occidentalis* Zone, and marked by the incoming of this species and *Eurydesma playfordi* Dickins. *Neilotreta*, a very distinctive genus (Waterhouse 2008b, p. 269), is also found at Cranky Corner in New South Wales and in the upper Rammutt Formation at Gympie in southeast Queensland (Waterhouse 2015). Significant species such as *Lyonia lyoni* persisted from the underlying zone, and *Costatumulus* entered the fauna. The zone is represented in the upper Lyons Group, and also in the basal conglomerate of the Callytharra Formation of the Carnarvon Basin. The species *Sommeriella obrieni* and *Ambikella notoplicatus* also are found in the Carrandibby Formation of the Byro Sub-basin. *Juresanites jacksoni* occurs in the Woolaga Limestone, middle member of the Holmwood Shale, Perth Basin, with another ammonoid *Uraloceras irwinensis* Teichert & Glenister (which has been identified as *Svetlanoceras* by some authorities, an identification rejected by Leonova 1998). Archbold (1993b) included the Calytrix floral and faunal assemblage of the Canning Basin in the *Neilotreta occidentalis* Zone, but it differs considerably, and seems likely to lie below these faunas. Only *Sommeriella obrieni* is shared between the two, and chonetids are not always restricted in time range (Waterhouse 2001, p. 14). Palynomorphs in all three zones form part of the *Pseudoreticulatisporites confluens* assemblage (Mory & Backhouse 1997), so that from palynomorph evidence the Calytrix fauna could slightly older than the *lyoni* assemblage, or slightly younger than the *Neilotreta occidentalis* Zone, or equivalent to either of them: in the absence of stratigraphic sequence, the succession must be determined from the affinities of the macrofaunas. A pre-*Lyonia* position is favoured, based on faunal sequences in Afghanistan and east Australia.

The overlying *Coronalosia irwinensis* Zone is very well represented in Western Australia and of critical significance for Gondwana and Australian Permian correlations. The brachiopod component is very large, and includes *Neochonetes pratti* (Davidson), *Comuquia australis* Archbold, *Archboldina micracantha* (Hosking), *Wooramella senticosa* (Hosking), *Carilya* (?) *baracoodensis* (Etheridge)*, Taeniothaerus quadratiformis* Archbold, *Callytharrella callytharrensis* (Prendergast), *Cimmeriella foordi* (Etheridge), *Latispirifer callytharrensis* Archbold & Thomas, *Koenigoria neoaustralis* (Archbold & Thomas), *Lamnaespina papilionata* (Hosking) and many other species. Many bivalves were described by Dickins (1963). Ammonoids described by Glenister et al. (1990, 1993) and Glenister & Furnish (1961) come from the Callytharra Formation and Fossil Cliff Member and slightly younger forms from the Nura Nura Member.

Metalogoceras kayi Glenister et al. (1973) and *Propopanoceras* were deemed to favour a Sterlitamakian age by Glenister et al. (1993, p. 56). Nicholl & Metcalfe (1998, Fig. 2) assigned the zone to upper Sterlitamakian and lower Aktastinian, and reported a few cold-water conodonts, involving *Mesogondolella bisselli* and *Sweetognathus pequopensis*, also found in Timor with Sakmarian ammonoids (van den Boogard 1987). According to Kozur (1998, Fig. 3), *bisselli* entered the succession in the late Sakmarian, and was joined by *pequopensis* in the mid-Artinskian. On present information, therefore, there are slightly different possibilities over age for the Callytharra Formation, between Sakmarian and lower Artinskian.

The Callytharra Formation has been re-examined, remapped and subdivided by Mory (1996) and Mory & Backhouse (1997), with the recognition of a Ballythanna Sandstone towards the top, overlain by the upper Callytharra Formation and Jimba Jimba unit. Some fossil species have been described from these refined subdivisions (Hogeboom & Archbold 1999, Archbold & Hogeboom 2000), but the full fauna needs revision. In examining borehole cores, Archbold & Hogeboom (2000) found that *Cimmeriella foordi* (Etheridge) occurred in the lower formation below the Winnema Sandstone Member, and *C. flexuosa* (Waterhouse) was found in beds above the Winnema Sandstone Member. It was shown that the zone incorporates no less than three palynomorph zones, but so far, no clear concomitant change in macrofauna has been recorded.

The *Sommeriella magnus* Zone in the High Cliff Sandstone of the Perth Basin and *Coronalosia jimbaensis* Zone of the Wooramel Group in the Carnarvon Basin are represented by small and restricted faunas, with a few non-diagnostic conodonts (Nicholl & Metcalfe 1998), although those authors did not tabulate the Wooramel Group. Younger faunas of Artinskian age in Western Australia are exceptionally well developed by Gondwanan standards. The Byro Group in the Carnarvon Basin is made up of a succession of formations, each with its own zone, or what might prove to be fossil community, named after *Echinalosia prideri, Mingenewia anomala, Pseudostrophalosia colemani, Fusispirifer byroensis, Tornquistia magna, Fusispirifer cundlegoensis, F. wandageensis, Sommeriella nalbiaensis*, and *Svalbardia thomasi* by Archbold (1993b). *Neogondolella idahoensis* and *Vjalovognathus shindyensis* were reported by Nicholl & Metcalfe (1998) from the Coyrie Formation in the Carnarvon Basin and middle Nooncanbah Formation of the Canning Basin, which were considered to indicate an early Kungurian age. But they noted problems over the identification of *shindyensis* in the literature, and allowed that *idahoensis* was considered to be a late Artinskian (Leonardian) species in North America, and earliest Chihsian in China. Moreover Foster & Archbold (2001, p. 184) stated that the supposed Nooncanbah occurrence came in fact from Triassic beds, and indicated that the alleged Coyrie occurrence was in fact from the younger Cundlego Formation, not Coyrie Formation.

The overlying Kennedy Group commences with the Coolkilya Sandstone and *Sommeriella afanasyevae* Zone. Archbold (eg. 2002, table 1) put the top of the Artinskian in the middle of the *Fusispirifer byroensis* Zone of the Madeline Formation, extending into the Mallens and Bogadi Sandstones, and classed the *Tornquistia magna* to *Svalbardia thomasi* Zones as Kungurian. Artinskian – mostly Baigendzinian – ammonoids have been described from the Wooramel and Byro Groups of the Carnarvon Basin, involving *Neocrimites, Pseudoschistoceras* and *Bamyaniceras*.

Palynomorph zones in Western Australia (Table 15)

The *Pseudoreticulatispora confluens* Zone is reported from the lower section of the Holmwood Shale in the Perth Basin (Backhouse 1993), and Mory & Backhouse (1997, p. 5) described Permian palynomorph Stage 2 (= *Lyonia lyoni* brachiopod Zone) in the lower Lyons Group and in the upper Lyons Group (= *Neilotreta occidentalis* brachiopod Zone). Studies on the palynomorphs of the Callytharra Formation of Western Australia indicate that the Callytharra Formation containing the *Coronalosia irwinensis* brachiopod Zone has a succession of index species (Mory & Backhouse 1997, Archbold & Hogeboom 2000). The *Pseudoreticulatispora pseudoreticulata* Zone APP 21 is found in the lower Callytharra Formation, above *P. confluens* of the upper Lyons Group, and is followed by *Striatopodocarpites fusus* in the Ballythanna Sandstone Member, and then *Didecitriletes byroensis* in the upper part of this member. As far as can be determined, these latter two zones, notwithstanding claims by Archbold (eg. 2001b, table 6), are not found in east Australia. *Microbaculispora trisina* appeared in the uppermost Callytharra Formation and in the Irwin River Coal Measures of the Perth Basin, shown by Archbold & Hogeboom (2000, text-fig. 13) as involving the *Sommeriella magna* and *Coronalosia jimbaensis* Zones, above the *Coronalosia irwinensis* Zone in Western Australia. Incomings and outgoings vary somewhat in different cores, reflecting the varying development of the members, to the extent that *trisina* and *byroensis* are also found above the Callytharra Formation, in the Cordalia Formation, as in core Burna 1. The

<table>
<tr><th colspan="2">Western Australia</th><th colspan="2">East Australasia</th></tr>
<tr><th>Brachiopod zone</th><th>Palynomorph zone</th><th>Palynomorph zone</th><th>Brachiopod-mollusc zone</th></tr>
<tr><td><i>Sulciplica occidentalis</i></td><td><i>Didecitriletes ericianus</i></td><td><i>Didecitriletes ericianus</i></td><td rowspan="3"><i>Echinalosia ovalis</i></td></tr>
<tr><td rowspan="2"><i>Fusispirifer coolkilyaensis</i></td><td><i>Dulhuntysporites granulata</i></td><td rowspan="7"><i>D. granulata</i> and <i>Dulhuntysporites dulhuntyi</i> Zones
?</td></tr>
<tr><td rowspan="2"><i>Microbaculispora villosa</i></td></tr>
<tr><td rowspan="2"><i>Sommeriella afanasyevae</i></td><td><i>Pseudostrophalosia blakei</i></td></tr>
<tr><td rowspan="11"><i>Praecolpatites sinuosus</i></td><td rowspan="2"><i>Echinalosia maxwelli</i></td></tr>
<tr><td><i>Svalbardia thomasi</i></td></tr>
<tr><td>(gap?)</td><td><i>Echinalosia discinia</i></td></tr>
<tr><td><i>Sommeriella nalbiaensis</i></td><td><i>Wyndhamia typica</i></td></tr>
<tr><td>(gap?)</td><td rowspan="8"><i>Microbacullipora villosa</i></td><td><i>Glendella dickinsi</i></td></tr>
<tr><td><i>Fusispirifer wandageensis</i></td><td>(<i>Attenuocurvus</i> fauna)</td></tr>
<tr><td><i>Fusispirifer cundlegoensis</i></td><td rowspan="6">(<i>Echinalosia conata</i>)
?</td></tr>
<tr><td><i>Tornquistia magna</i></td></tr>
<tr><td><i>Fusispirifer byroensis</i></td></tr>
<tr><td><i>Pseudostrophalosia colemani</i></td></tr>
<tr><td rowspan="2"><i>Echinalosia prideri</i>
<i>Mingenewia anomala</i></td></tr>
<tr><td rowspan="4"><i>Microbaculispora trisina</i></td></tr>
<tr><td><i>Sommeriella magnus</i></td><td rowspan="4"><i>Phaselisporites cicatricosus</i> and/or <i>Praecolpaptites sinuosus</i>?</td><td rowspan="2">(<i>Spinomartinia adentata</i>)</td></tr>
<tr><td rowspan="2"><i>Coronalosia jimbaensis</i></td></tr>
<tr><td rowspan="2"><i>Ingelarella plica</i></td></tr>
<tr><td rowspan="5"><i>Coronalosia irwinensis</i></td><td><i>Didecitriletes byroensis</i></td></tr>
<tr><td><i>Striatopodocarpites fusus</i></td><td rowspan="5"><i>Microbaculispora trisina?</i>
?</td><td rowspan="2"><i>Taeniothaerus subquadratus</i></td></tr>
<tr><td rowspan="3"><i>Pseudoreticulatispora pseudoreticulata</i></td></tr>
<tr><td><i>Bookeria geniculata</i></td></tr>
<tr><td><i>Bookeria pollex</i></td></tr>
<tr><td><i>Neilotreta occidentalis</i></td><td rowspan="4"><i>Pseudoreticulatispora confluens</i></td><td rowspan="2"><i>Bandoproductus macrospina</i></td></tr>
<tr><td><i>Lyonia lyoni</i></td><td><i>Pseudoreticulatispora pseudoreticulata</i></td></tr>
<tr><td><i>Crassispinosella calytrixi</i></td><td rowspan="2"><i>Pseudoreticulatispora confluens</i></td><td><i>Crassispinosella subcircularis</i></td></tr>
<tr><td><i>Fimbrinialosia carolyni</i></td><td><i>Strophalosiaria concentrica</i></td></tr>
</table>

Table 15. The brachiopod zones of Western and eastern Australia shown as correlative, with their attendant and partly disparate palynomorph zones, as itemized by Archbold. Note that palynomorph evidence for the *carolyni* fauna is only presumed, and the palynomorph zones for the eastern upper brachiopod zones are conjectural to a degree. Gray panels lack palynomorph data. The purported position of *Fimbrinialosia carolyni* is suppositious only. Bracketted zones only in New Zealand. The highly disparate ranges for *sinuosus* and *cicatricosus*, as set out on p. 27, lack firm verification.

Microbaculispora trisina Zone is followed by the *Praecolpatites sinuosus* Zone ranging through much of the Byro Group, as far as the *Svalbardia thomasi* Zone. In east Australia the Sinuosus Zone has been said to commence in the “upper *Echinalosia preovalis* Zone” of Briggs (1998), which is in fact the *E*. *preovalis* Zone sensu stricto that is now called *Ingelarella plica* Zone to avoid ambiguity, but information on palynomorph-brachiopod assemblages regarding *sinuosus* and the brachiopod zones of *pollex-geniculata-subquadratus-plica* is meagre. The *Praecolpatites sinuosus* Zone is chiefly of Baigendzinian and Kungurian age in Western Australia. It could be of similar age, or in part older in east Australia. Reinforcing the difference between east and west is the fact the *Phaeselisporites cicatricosus* Zone, well represented in east Australia, is missing from Western Australia, and replaced by zones named after *Didecitriletes byroensis* and *Microbaculispora trisina*.

Match between Western and eastern Australia

At first sight, the westerly sequences broadly match those of eastern Australia. The Calytrix Formation of the Grant Group in the Canning Basin has *Crassispinosella calytrixi* (Archbold) and the *Pseudoreticulatispora confluens* palynological Zone (Foster & Waterhouse 1988), pointing to correlation with the *C. subcircularis* Zone of east Australia. The *Lyonia lyoni* Zone might match the either the *Nambuccalinus bourkei* fauna, or *Bandoproductus macrospina* Zone, probably the latter. The *Neilotreta occidentalis* Zone, although characterized by faunas somewhat different from those of eastern Australia, includes reported but possibly suspect *Arctitreta costellata* (Clarke) found in the *Strophalosiaria concentrica* Zone of Tasmania and south Sydney Basin, and the nominate species comes close to *Neilotreta tangorini* (Archbold) from the Beckers Formation and Cranky Corner Formation at Cranky Corner, north of the Hunter Valley, New South Wales. The basal Callytharra Formation possibly has a discrete or separable fauna, and closer examination is required.

The *Coronalosia irwinensis* Zone in the Callytharra Formation, with its ammonoids described as Sterlitamakian, also contains prominent taeniothaerin and rhamnariid species. In east Australia, taeniothaerins and rhamnariids enter the Fairyland Formation (*Echinalosia curtosa* Subzone), and persisted and increased through the *Bookeria geniculata* Zone and especially *Taeniothaerus subquadratus* Zone. The *Coronalosia jimbaensis* Zone of the Wooramel Group, Carnarvon Basin, could equate with the *Ingelarella plica* Zone of the topmost Tiverton Formation (Waterhouse 1976a, p. 95), in so far as it stratigraphically overlies the *Coronalosia irwinensis* Zone and contains the palynomorph *sinuosus*. Ammonoid *Neocrimites fredericksi* (Emeliancev) was reported in the *Ingelarella plica* Zone at the top of the Tiverton Formation and in the Coyrie Formation, below the Madeline Formation of Western Australia.

These potential faunal correlations were not accepted by Archbold (2000). He matched the *Neilotreta occidentalis* Zone with the *Strophalosiaria concentrica* Zone of Tasmania. The Callytharra *Coronalosia irwinensis* Zone (*irwinensis* being initially identified as *Strophalosia* by Archbold 1986a) was matched by Archbold (2000) with the *Crassispinosella subcircularis* Zone of eastern Australia – with no species in common, and setting aside many of the species links between Callytharra and Tiverton faunas (Table 8). Given that miscorrelation, remaining east Australian zones have had to be shifted upwards, and it is probably this miscorrelation that has resulted in the age data conveyed by ammonoid and other fossils and radiometric data being ignored by Briggs (1998) and Archbold (2000) for Permian correlations in eastern Australia. The *Bandoproductus macrospina* Zone was matched with the *Coronalosia jimbaensis* Zone (“Aktastinian”) of the Wooramel Group, even though *Bandoproductus* is absent, and none of the species found with *Bandoproductus* in eastern Australia approach Wooramel species. The “*Tomiopsis strzeleckii* Zone” was correlated with the *Echinalosia prideri* to *Sommeriella magna* zones, and the rest of the Briggs’ 1998 biozones for eastern Australia were tabulated in Archbold (2000 etc.) by succession, regardless of affinities, and not dependent on any species or even genus distribution – the correlations are independent of the faunas. Briggs (1998, text-fig. 3-5), followed with emendations by Archbold (eg. 2000, 2001a, b), based east Australian Permian stratigraphy and brachiopod zones on palynomorph correlations, and disregarded the brachiopod and molluscan evidence, even though Foster & Archbold (2001, pp. 176, 187) noted the need for caution over palynomorph zones, and pointed out that various key micro-fossils were yet to be illustrated. It seems advisable to assess the brachiopod-bivalve zones independently for their age implications, irrespective of other evidence, and then test them against the evidence from palynomorphs. If they disagree, so be it – one or other set of zones should not be suppressed. Both Briggs and Archbold appear to have believed that the Permian palynomorph zones extended synchronously across the continent. But there are some clear differences in those palynomorph zones which are found between the *Pseudoreticulatispora confluens* APP 12 and

Dalhuntysporites granulata APP 41 zones in east and Western Australia. (See Waterhouse 2010b, p. 210, Table 2). The palynomorph succession of key species in east Australia, ideally, runs *confluens*, *pseudoreticulata, trisina, cicatricosus* and *sinuosus*, with, as discussed below, uncertainties and variations involved for *trisina, cicatricosus* and *sinuosus* and further subdivisions based on *indica, baculata* and *villosus*. In Western Australia there is no *cicatricosus*, and the sequence runs *confluens*, *pseudoreticulata, fusus*, *byroensis, trisina, sinuosus, villosus*. The palynomorph zones across the country from east to west are not identical. It seems clear that *confluens* lasted through two or three brachiopod zones in Western Australia, whereas it persisted for only part of one or two brachiopod zones in east Australia. The Pseudoreticulata Zone may also have ranged differently each side of the continent. Moreover as shown by Archbold (2002, tables 1, 2, 4), the extent and nature of the palynomorph zones for other segments of Gondwana, in Africa and India, differ substantially from the sequences in Western and eastern Australia. Thus over the supercontinent of Gondwana, during Permian time, plant assemblages developed regional signatures, and it appears that different floral provinces and palynomorph zones developed over east and west Australia during at least some intervals of Permian time, whereas somewhat similar brachiopod and bivalve marine assemblages developed widely in Australia, India, Himalaya, Afghanistan, Tibet and Oman, as elaborated shortly.

The divergence of macro-faunal and palynomorph evidence

Pseudoreticulatispora pseudoreticulata signals the point of greatest divergence between brachiopod-bivalve zones and palynomorph zones of eastern and Western Australia. The content and nature of the brachiopod zones associated with palynomorph Pseudoreticulata Zone APP 21 is far from the same on either side of the continent. In eastern Australia, the zone takes in the upper part of a limited *Strophalosiaria concentrica* Zone and, according to Briggs (1998) and Archbold (1999, 2001, Table 6), much or all of the *Crassispinosella subcircularis* Zone, whereas Calver et al. 1984 reported *trisina* in the upper *Strophalosiaria concentrica* Zone, below the *Crassispinosella subcircularis* Zone. Clarke (1992a) stated that the *Pseudoreticulatispora pseudoreticulata* Zone also encompassed the *Unicostatina crassa* Zone of Tasmania. But in Western Australia what is supposed to be the same palynomorph *Ps. pseudoreticulata* APP 21 Zone incorporates much of the Callytharra and Fossil Cliff Formations and *Coronalosia irwinensis* Zone, bearing faunas quite different from those of the *Crassispinosella subcircularis* Zone, and like the faunas of the *Bookeria pollex, B. geniculata* and *Taeniothaerus subquadratus* Zones above the Concentrica-Subcircularis Zones in east Australia. It is my contention that the brachiopods, bivalves and gastropods of the *Coronalosia irwinensis* Zone support correlation with the *Bookeria pollex* and *Bookeria geniculata* Zones, and especially the *Taeniothaerus subquadratus* Zone in east Australia. The present *Taeniothaerus subquadratus* Zone was shown as lower *Echinalosia preovalis* Zone and equivalent to the APP 31 *Phaselisporites cicatricosus* Zone by Briggs (1998, text-fig. 10), together with the *Bookeria pollex* and *Bookeria geniculata* Zones, but was represented by Archbold (2000) as largely matching the *Praecolpatites sinuosus* Zone, together with the rest of the *Echinalosia preovalis* Zone. Interpretation of the palynomorphs conflicts with the interpretation of the macrofossils, and the palynomorph zones themselves are out of phase across the continent.

There are possible solutions, but all require further information. It appears that various key species ranged higher in the sequences, and thus overlap much younger key species – examples involving *pseudoreticulata, trisinus, sinuosus* and *cicatricosus*. If the key species is absent, through facies, oversight, local conditions or other causes, a wrong age will be determined. Normally, this will not increase the downward age. But *sinuosus* has been recorded at levels much lower than its expected position (Rigby & Heckel 1977, Foster 1977) in the Cattle Creek Formation, to interfer in turn with the time span for *cicatricosus*. Apart from these uncertainties, it appears likely that the differences in ranges on the two sides of the continents were caused by different climatic regimes, in which there was a drag effect on either terrestrial or marine life, during a time when life in one kingdom (floral or faunal) persisted, whilst life of the other (in my view, animal) kingdom evolved. The evidence from marine fossil faunas is followed for correlation, because the international standard is based on marine faunas, and because somewhat related faunas occur in sequence throughout south Asia, as summarized shortly. It is suggested that the disparity was caused by climatic conditions becoming more disparate across the Australian continent, remaining cooler to the east than to the west, and affecting plant life more profoundly than marine habitats.

Foraminiferal evidence for trans-Australian Lower Permian

Foraminiferal correlations have been provided for especially the Bowen Basin Permian by Palmieri (1990, 1998, in

Draper et al. 1990a), and Briggs (1998, p. 63) inserted foraminiferal occurrences into his proposed brachiopod zones. One of the correlations urged by Briggs (1998) showed that the *Echinalosia curtosa* Zone [now treated as a Subzone] was represented in the Farley Formation in the Hunter Valley, whereas Foraminifera favoured an older match with the upper Lochinvar Formation, according to the Palmieri study, an unlikely suggestion. The occurrences of Foraminifera in Western Australia provided by Palmieri (1993) were based largely on earlier studies culminating in the work by Crespin (1958), and Palmieri underlined the need for much better stratigraphic control. Putative matches were suggested between Holmwood – Callytharra faunules and those of the Pokolbin limestone of Hunter River and Mostyndale Member of the Cattle Creek Formation, which agrees by and large with present brachiopod correlations rather than palynomorph studies. A comparison was made by Palmieri between the Byro and Nooncanbah beds of Western Australia with possible equivalents in the Branxton Formation and Wandrawandian Siltstone of the Sydney Basin and Moorooloo Mudstone to the Sirius Mudstone of the Cattle Creek Formation in southeast Bowen Basin. Conceivably the similarities reflected climate change, and probably sediment type and water depth rather than temporal control, although ages are indeed close. Briggs (1998, Fig. 12) used the incoming of *Howchinella rigida* as a marker for Carnarvon Basin in the Wooramel Group, and lowest *H. woodwardi* for the Holmwood Shale (Perth Basin) and Callytharra Formation (Carnarvon Basin), as well as Fairyland Formation (Bowen Basin) – which agrees with brachiopod evidence. *Ammodiscus oonahensis* was treated as useful for linking the lower Holmwood Shale of the Perth Basin with the Carrandibby Formation of the Carnarvon Basin and middle member of the Grant Formation in the Canning Basin. *Howchinella rigida* was reported by Palmieri from the uppermost Fairyland Formation, as well as Farley Formation and Berriedale Formation. On the whole, reported occurrences do not seem to follow any consistent pattern.

Bryozoan evidence for trans-Australian Lower Permian correlation

Bryozoa are scarce as fossils in the Tiverton Formation, and Wass (1968) in his study of species from the Bowen Basin illustrated only two species. Engel & Phillips Ross (1993) called Bryozoa “useful if somewhat neglected”, and commented on their “undoubted stratigraphic potential”. Crockford (1957) had noted that the Nooncanbah and Callytharra faunules differed considerably, despite their being usually correlated. Engel & Phillips Ross (1993) stated that Nooncanbah species compared with those of Byro and Kennedy Groups, and faunally approached those of equivalent strata in Timor, Urals, some North America faunas, and even Middle Productus Limestone of “India” (sic – Pakistan). That is surprising, because the upper Middle Productus Limestone is of Late Permian (Wuchiapingian) age. Engel & Phillips Ross (1993) concluded that there were significant differences in Bryozoa from the two sides of the continent.

GONDWANAN AND ARCTIC CORRELATIONS

Thailand, Malaysia

Bandoproductus monticulus occurs in a fauna of the Phuket Group at Ko Muk, Thailand, in a fauna found immediately above diamictites, and judged to be late Asselian by Waterhouse (1982c, p. 350), with *Sulciplica thailandica* (Hamada), a chonetid genus *Komukia*, and the terebratulid genus *Elasmata*, which is also represented in the Bap fauna of Rajasthan in west India (see below). A younger species, as yet unnamed, of *Bandoproductus* has been described from the nearby upper Singa Formation of Langkawi Island, northwest Peninsula Malaysia by Shi et al. (1997), accompanied by various species which mostly typify the *Spinomartinia prolifica* faunal assemblage, found also in Thailand in the Ko Yao Noi Formation above the Phuket Group. The ammonoid *Metalegoceras* has been reported from the same fauna by Leonova et al. (1999), pointing to a Sterlitamakian or upper Sakmarian correlation. The faunas are close enough to each other geographically, to indicate that there were two *Bandoproductus* horizons, one in late glacial sediment, and the other in non-glacigene sediment. Asselian and Sakmarian ages respectively have been assigned. A younger brachiopod *Masitoshia perplexa* (Sone & Leman) from a Middle Permian (Wordian) fauna of Malaysia is close to *Bandoproductus*, but has finer ventral spines and better developed commarginal rugae (Waterhouse 2013, p. 446).

Indian Subcontinent, Tibet, Yunnan

In a general way, the Early Permian faunas of India follow the same pattern as those of eastern Australia (Waterhouse 1976a). In the Nagmarg or “Chumik” Formation of Kashmir, a fauna dominated by the bivalve *Eurydesma* is followed by a more diverse fauna with taeniothaerids (Waterhouse 1970a, Waterhouse & Chen 2007). In the Siang District of the eastern Himalaya, *Eurydesma* beds in the Rangit Formation are overlain by the Garu Formation with species of

Costatumulus, Koenigoria and *Ambikella,* similar to faunas of the *Bookeria geniculata* Zone in the lower middle Tiverton Formation. The fauna includes ammonoid *Uraloceras* cf. *irwinensis* Teichert & Glenister, which is *Svetlanoceras* according to Glenister et al. (1993) but doubted by Leonova (1998), and allied to the West Australian species found in the Woolaga Limestone Member and Callytharra Formation. Singh & Archbold (1993) argued for a Sterlitamakian age, though nothing appears to rule out a slightly older correlation. A richer fauna is found in the Bijni tectonic unit in the western Himalaya near Jogira and Doggada (= Duggada) in the Pauri Garwhal, described as Sakmarian by Waterhouse & Gupta (1978, 1979). *Svalbardia* and *Costatumulus* are found with *Anidanthia, Coronalosia*, *Neilotreta thomasi* (Waterhouse), and two bivalves approaching east Australian forms, *Etheripecten* aff. *tenuicollis* (Dana) and *Squamuliferipecten* (Waterhouse & Gupta 1978). Archbold & Singh (1993) verified the occurrences, which had been disputed by some authorities who claimed that no fossils acquired by V. J. Gupta had really come from the Himalaya, and Archbold & Singh (1993) postulated a Tastubian age. The fauna is clearly older than the taeniothaerin fauna of Kashmir, and approaches the Garu fauna of the east Himalaya and the lower middle Tiverton *Bookeria geniculata* faunas at Homevale. *Brachythyrinella* is found in a small fauna at Umaria, central India, together with *Umaria umariensis* (Reed) [see Waterhouse 2013], *Ambikella barakensis* (Reed) and *Pleurocinctosa umariensis* (Reed). The *umariensis* fauna was deemed to be slightly younger than a chiefly bivalve fauna with *Neilotreta hesdoensis* (Sahni & Dutt) found at Manendragarh in central India by Sahni & Dutt (1959). The oldest of known Permian marine faunas in Peninsula India comes from the Bap Formation, Rajasthan, described by Waterhouse & Ranga Rao (1989), with *Fimbrinialosia perfecta* (Waterhouse) and *Lamniplica punctata* Waterhouse, accompanied by the key palynomorph *Pseudoreticulatispora confluens*. *Fimbrinialosia* is represented by *F. carolyni* (Archbold) in the Carolyn Formation of the basal Permian in the Canning Basin, Western Australia.

In the Jilong Formation of Tingri County, south Tibet, a *Bandoproductus* assemblage was described as *B. hemiglobus* Jin & Sun, in addition to *Cimmeriella flexuosa* (Waterhouse), *Stepanoviella gracilis* Jin, *Brachythyrinella* and reported *Attenuatella convexa* Armstrong (now *Biconvexiella*). The fauna shows similarities to various Early Permian faunas of east and Western Australia, and the presence of *Bandoproductus* and the accompanying species may be taken to indicate ties with the *Bandoproductus macrospina* Zone of eastern Australia. In the Pondo Group of Lhünzhub County, south Tibet, *Cimmeriella flexuosa* is found above *Bandoproductus*, which in turn occurs above diamictites (Jin 1985, p. 29). Jin (1985) and Jin & Sun (1981) matched the *Bandoproductus* fauna with *Pseudoschwagerina* faunas of Asselian age. *Bandoproductus qingshuigouensis* Shen, Shi & Zhu from the Dingjiazhai Formation of western Yunnan was also rated as likely to be of late Asselian age (Shen, Shi & Zhu 2000).

Pakistan

Assemblage 1 of Angiolini (1995) in the lower Gircha, Lupghar and Lashkargaz Formations of the Karakorum Range include *Bandoproductus*, *Rhynchopora*, a highly transverse "*Trigonotreta*" (see Waterhouse 2004a, p. 175), with reported *Etheripecten, Deltopecten* and *Eurydesma*, close to the Lyons fauna of Western Australia. Angiolini et al. (2005) argued for an upper Asselian age. The second assemblage in the faunas of the Karakorum Range includes *Umaria* cf. *rossiae* (Fantini Sestini), *Costatumulus irwinensis* Archbold, and *Grantonia paucicostulata* (Reed), judged to be late Sakmarian or early Artinskian, correlative with the *Bookeria geniculata* Zone of Homevale and east Australia.

Afghanistan

Many Permian faunas in south Asia are so scattered that there must be an element of uncertainty in allocating the relative age. In central Afghanistan, there is a much clearer sequence (Termier et al. 1974). An "*Asyrinxia*" assemblage at the base with *Squamuliferipecten* in tillite was assigned to Gzhelian (Late Carboniferous), followed by an Asselian (?) Bokan Series with the Asselian-Sakmarian ammonoid *Eoasianites modestus*, found with fossils identified as west Australian species [generic names amended] *Lyonia lyoni* (Prendergast) and *Cimmeriella flexuosa* (Waterhouse) by Lapparent et al. (1971). These identifications need to be verified by published systematic description. This level was matched with beds in Wardak that have a *Eurydesma* faunal assemblage, including *Cyrtella, Ambikella, Gilledia, Oriocrassatella*, possible *Australomya* [called *Parallelodon* by Termier et al. 1974, pl. 8, fig. 1], and *Keeneia* ["*Euconospira*" of Termier et al. 1974, pl. 8, fig. 4, 5]. This is followed reportedly by an *Umaria umariensis* fauna in the Bini Darzak level, allied to that of Umaria, central India, with *Cancrinella* and *Deltopecten*, assigned by Termier et al. (1974) to the Tastubian Substage, overlain by so-called *Reedoconcha permixtus* (but see Waterhouse 2013, p. 281) in the Doni Yarchi Series, assigned to the Sterlitamakian Substage. Again, the shells identified with *umariensis* have not been illustrated or described. But whilst there may be uncertainties over identifications and ages, and whilst the material ascribed to *lyoni* and *umariensis* has not been figured, these studies help interpret the scattered Indian faunas, and reinforce the thesis that *Eurydesma* so common in early Permian faunas of Gondwana is followed by possible *Bandoproductus*, and affirm that the *Taeniothaerus-Reedoconcha* assemblage is younger still.

Oman

Angiolini et al. (1997) updated the brachiopod faunas from southeast Oman, including *Reedoconcha permixtus* Reed, (though her material seems to be *Taeniothaerus* – Waterhouse 2013, p. 281) in the Saiwan Formation, with ammonoids deemed to be of late Sakmarian age. This fauna is presumably close to the *Taeniothaerus subquadratus* fauna of east Australia, but is more diverse, and shows no further similarities.

Summary of Permian marine faunas in south Asia

The sequence over the Indian Subcontinent and south Asia may be summarized as follows:

4. Taeniothaerin faunas of west India, Oman and Afghanistan, deemed to be Sterlitamakian (Termier et al. 1974, Angiolini et al. 1997) and broadly matching taeniothaerin-rhamnariin faunas of the Callytharra Formation in Western Australia and *Taeniothaerus subquadratus* Zone of east Australia. Given ammonoid evidence in Western Australia, the faunas may be Sterlitamakian or arguably lower Artinskian (Aktastinian).

3. *Svalbardia, Costatumulus, Coronalosia, Neilotreta, Brachythyrinella*, in Bijni tectonic unit and Garu Formation of India with *Uraloceras,* and allied to *Neilotreta*, *Coronalosia* and *Costatumulus* faunas from east and west Australia. Also with *Cimmeriella* in Tibet and Afghanistan, and *Umaria*, *Costatumulus* and *Trigonotreta* in Karakorum Range, Pakistan. Equivalent to *Bookeria pollex* and *Bookeria geniculata* Zones of east Australia. These faunas are judged to be of Sakmarian age, a Tastubian age being favoured by Termier et al., Angiolini et al. and Singh & Archbold.

2. *Bandoproductus* has been found in the upper Phuket Group of Thailand, below the *Spinomartinia prolifica* fauna, and in the Bokhan Series of Afghanistan below reported but unconfirmed *Umaria umariensis*. These have been dated as Asselian, together with other occurrences of *Bandoproductus* in south Tibet (Jin & Sun 1981), and in the Gircha Formation of the Karakorum Range (Angiolini et al. 2005), and in Yunnan (Shen et al. 2000).

1. *Fimbrinialosia* fauna at Bap, India, with *Pseudoreticulatispora confluens* microflora, closely tied to a fauna of the Carolyn fauna of the Grant Group, Western Australia, and considered to be probably Asselian.

One apparent anomaly is offered by *Bandoproductus* faunas in Langkawi Island, Malayasia Peninsula, with the Sakmarian ammonoid *Metalogecoceras*. The accompanying *Spinomartinia prolifica* fauna is considered to be of Sakmarian age (Waterhouse 1981), distinctly younger than the *Bandoproductus* of the underlying Pukhet Group, and the occurrence appears to be exceptional. Another unusual occurrence of *Bandoproductus* is suggested for material in the *Ingelarella plica* Zone of the Brunel Formation in New Zealand (Waterhouse 2001, p. 32).

Argentine

In the Río del Peñón Formation of the Rio Blanco Basin of La Roja Province, Argentina, Archbold, Cisterna & Simanauskas (2004) have reported three zones of presumed basal Permian age, below the *Pseudoreticulatispora confluens* Zone. The oldest, considered to be of early Asselian age, includes *Streptorhynchus, Etherilosia, Costatumulus* and *Trigonotreta*, followed by a middle assemblage with “*Tivertonia*”, *Costatumulus*, *Kochiproductus*, and *Trigonotreta*. An upper assemblage contains *Rhynchopora*. According to this interpretation, *Costatumulus* entered the Argentine successions apparently before entry into Australia. Stratigraphy and faunas are further clarified in studies by Cisterna (2010), Pagani & Taboada (2010) and Taboada (2010). In a fauna of the Rio del Peñón Formation at the top of the *Nothorhacopteris argentinica* megafloristic Zone, Cisterna (2010, Fig. 4) listed *Kochiproductus, Etherilosia, Costatumulus* and *Pericospira,* the latter genus very close to *Trigonotreta* s.s. These genera are best known in the Permian, but there seems no clear reason why they should not be late Carboniferous, as indicated by floral evidence. The overlying faunal level, the so-called *Tivertonia* (sic) *jachalensis* Zone, includes *Kochiproductus* and *Pericospira riojanensis* (Lech & Aceñolaza), with *Costatumulus* and supposed *Streptorhynchus*, and is followed by a faunule with *Septosyringothyris, Costatumulus* and *Neochonetes*. Cisterna (2010, p. 93) recorded *jachalensis* with *Costatumulus*, above *P. riojanensis* and *Saltospirifer guevarii* (Cisterna & Archbold) in the Del Salto Formation of the Calingasta-Uspallata Basin. The *Costatumulus amosi* Zone is subject to some difference of opinion: Cisterna (2010) regarding it as much the same as the *Tivertonia jachalensis- Streptorhynchus inaequiornatus* Zone, Taboada (2006, 2010) considering it to be younger. The fauna includes *Coolkilella keideli* Taboada, a genus of Western Australia and south Asia

(Waterhouse & Chen 2007), and Pagani & Taboada (2010, Fig. 5) indicated that in the Tepuel – Genoa Basin of Patagonia, the zone could be subdivided, with successive faunas typified by *Cimmeriella willi, Jakutoproductus sabattiniae*, and *J. australis*, the latter two judged to be Artinskian, the *Cimmeriella* fauna Sakmarian, and a basal Asselian zone typified by *Verchojania archboldi* (Taboada & Pagani 2010).

The three zones based on *Kochiproductus, Tivertonia* and and *Septosyringothyris* were considered by these authors to constitute well defined levels of basal Permian age, older than any well defined zone in Australia, and through their character, indicating that even the oldest of Australian Permian zones would be post-Asselian (Cisterna, Simanauskas & Archbold 2002, Archbold et al. 2004). But the model requires revision. The so-called *Tivertonia jachalensis* – *Streptorhynchus inaequiornatus* Zone (both genera in need of reassessment) in the San Juan Province, regarded as being of basal Permian age (Asselian) age by Taboada (2010, pp. 167, 168), is of Moscovian (Upper Carboniferous) age according to radiometric values (Césari et al. 2011), and the species lie well below the first entry of the palynomorph *Converrucosporites* (also referred to *Pseudoreticulatispora)*) *confluens* (Archangelsky & Gamerro), which is largely Asselian in age and entered successions in very late Carboniferous (Stephenson 2009). Various genera supposed to be of Permian age require closer study. The so-called *Tivertonia* is not *Tivertonia* Archbold (see pp. 60ff). *Kochiproductus* lacks the commarginal rib-like rugae typical of the genus. *Costatumulus amosi* Taboada, 1998 from the Agua del Jaguel Formation has numerous ventral ear spines, pointing to *Auriculispina* Waterhouse, based on *Cancrinella levis* Maxwell of late Carboniferous age in the Yarrol Basin, Queensland. The radiometric evidence and reassessment of fossils implies that the Argentine zones are of Late Carboniferous age, and allows the Australian zones centred on *Strophalosiaria, Crassispinosella* and *Bandoproductus* to be older than Sakmarian. The *Auriculispina levis* Zone of the Yarrol Basin may prove to be closely related, and is regarded as likely to be of Gzhelian (topmost Carboniferous) age.

Canada

The preceeding sequences for Gondwanan Early Permian faunas follow a pattern of changing diversities and faunal affinities, paleotemperate faunas alternating with low diversity faunas dominated by *Eurydesma* and *Squamuliferipecten* (Waterhouse 1963c), the interpretation reinforced through widespread statistical analysis by Waterhouse & Bonham-Carter (1972, 1975). Climatic changes are well demonstrated in extensive Late Carboniferous and Early Permian sequences in the Ogilvie Mountains of northern Yukon Territory, Canada, dated through comparisons with faunas of northern and northeast Russia, as summarized by Bamber & Waterhouse (1971) and Shi & Waterhouse (1996), with further study now in progress (Waterhouse 2013, in prep). Three Asselian zones are represented in the lower Jungle Creek Formation by the *Kochiproductus* and sparse *Ogilviecoelia* faunas, followed by dolomitic sandstones with *Uraloproductus*, and an *Ogilviecoelia*-dominated diverse fauna.

The overlying bracket of zones in Arctic Canada is strongly reminiscent of the Gondwanan sequences in the Tiverton Formation. The Ey *Muirwoodia transversa* Zone of the Ogilvie Mountains has an abundance of Productida, and includes *Protoanidanthus* and *Terrakea*, typical of Australian faunas. Specimens ascribed to *Tomiopsis ovulum* Waterhouse by Shi & Waterhouse (1996, pl. 28, fig. 6-8) come very close to *Geothomasia postglabra* (Waterhouse, 1987a, pl. 7, fig. 16, 17, 19), found in the Dresden Formation near Cracow. Both sets of specimens are distinctive amongst Ingelarellidae, with shallow or no sulcus posteriorly, well spaced short tabellae, and moderately short well-spaced adminicula. *Tomiopsis ovulum* Waterhouse (1971b, p. 15, fig. 1-15, pl. 16, fig. 1-15, pl. 17, fig. 3, 6, 8, 11, 12, text-fig. 3-7) from the Kindle Formation of western Canada belongs to *Ambikella*, and is moderately close to though less plicate than *A. notoplicatus* (Archbold & Thomas, 1986b, p. 586, text-fig. 3.1-11) from the upper Lyons Group and basal Callytharra Formation in Western Australia. The ammonoid *Tabantalites bifurcatus* (Ruzencev, 1952) was described by Shi & Waterhouse (1996) from the Ey and Eog zones of the Jungle Creek Formation in the Ogilvie Mountains (lower and middle Sakmarian) and ranges from upper Asselian to Tastubian in Russia. Nassichuk et al. (1966) also recorded *Metalegoceras crenulatum*, resembling species from Sakmarian and Aktastinian faunas of Russia (Ruzencev 1952).

The younger zones in the Yukon Territory of Canada are less diverse faunally, and are divided into the *Ogilviecoelia inflata* Zone (Eog), *Tornquistia* Subzone (Et), and *Jakutoproductus verchoyanicus* Zone (Ej). Similarities to the Tiverton faunas are slightly reduced. *Cimmeriella* is found in the Eog fauna. Ammonoid species of *Prothalassocceras, Properrinites, Tantabilites, Eoasianites* and *Somoholites* have been described from beds above the Ey zone, within the Eog or Et faunas and include the Australian species *Uraloceras* cf. *irwinensis* Glenister & Furnish, as documented by Nassichuk (1971). Bamber & Waterhouse (1971), followed by Furnish (1973), preferred a Sterlitamakian age, but Nassichuk (1971) assigned them to Tastubian. In Western Australia, the species *U. irwinensis* has been described from both the *Coronalosia irwinensis* and the *Neilotreta occidentalis* Zones. Significantly, the ammonoid occurs in Canada above faunas that show ties with the *Bookeria pollex* and *Bookeria geniculata* Zones of east Australia, and so suggests equivalence with the *Taeniothaerus subquadratus* Zone. The Ej Yukon fauna contains fusulines, such as *Eoparafusulina yukonensis* (Skinner & Wilde) and *Schwagerina*. Although a Tastubian age was favoured by Ross (1967), *Eoparafusulina* is especially common in Aktastinian faunas of Russia, and Shi & Waterhouse (1996, p. 25) considered that the evidence favoured an Aktastinian age. This is reinforced by Artinskian fusulines and by ammonoids *Neoshumardites* and *Uraloceras* found in south Ellesmere Island in the Canadian Arctic Archipelago, assigned by Nassichuk et al. (1966) to late Sakmarian (Sterlitamakian) or Aktastinian.

Such sequences are widespread throughout the Arctic, and exemplify an overall faunal development of zones very close to those observed in Western Australia, and especially eastern Australia. Younger faunas in the Ogilvie Mountains have incoming brachiopods of warmer-water affinities, indicative of a Baigendzinian age.

THE RUSSIAN AND INTERNATIONAL STANDARD

World Standard Cisuralian Series (Table 16)

The international Early Permian Cisuralian Series was named and proposed by Waterhouse (1983b) and internationally endorsed in Jin (1996) and Jin et al. (1997). The Cisuralian standards are exemplified in Kazakhstan and Russia, and faunally based on conodont zones, which appear long-lasting – rather more so than the high number of apparently short-lived conodont zones proposed for the Late Permian Lopingian Series. The base of the Cisuralian Series is classed as the Asselian Stage, and the type section is found in the Aidaralash Creek section at Aktöbe (formerly Aktyxbinsk) of Kazakhstan, with a supplementary section at Usolka (Davydov & Wardlaw 2005), signified by the first appearance of the conodont *Streptognathodus isolatus* (Davydov et al. 1998). Three successive conodont zones are developed according to Kozur (1998), and six according to Davydov & Wardlaw (2005), fusulines are abundant, and brachiopods extremely numerous and well preserved. The stage closes with the disappearance of the fusuline *Sphaeroschwagerina*, within the Kurmain Formation. Kurmaian Substage has long been applied to the topmost zone of the stage (Licharew 1966, Waterhouse 1976a), but topmost Kurmaian has post-Asselian faunas (Wardlaw, Leven et al. 1999). V. Davydov suggests the unit be renamed Shikhanian, as adopted by Archbold (2000), but in fact the faunal content for Shikhanian remains to be explored (V. Davydov, pers. comm.). Customary procedure in consolidating Permian stage units has been to retain the name and alter the boundaries and content – as for the Asselian, Artinskian and Kungurian Stages, and the Roadian-Capitanian in the Guadalupian Series, so that use of the Kurmaian Substage would follow this procedure. However it may be premature to apply substages while the attributes of each stage are being analysed. When stages are fully established, some workers may desire to allocate zones each to a substage.

The world stratotype for the Sakmarian Stage is at Kondarovska, in the Orenburg Province of Russia, marked by the entry of the conodont *Streptognathodus merrilli* and first appearance of the fusuline *Schwagerina moelleri* (Chuvashov et al. 2002b). Two Sakmarian substages were formally recognized by Waterhouse (1976a) on the basis of Russian work, Tastubian and Sterlitamakian, and just two conodont and ammonoid zones are delineated. However at least three conodont zones can be discriminated in deep-water facies of the Urals (Davydov in Waterhouse 2002a, p. 188). Even within the Russian world standard sequences, there are very substantial gaps in the ammonoid record (Ruzencev 1952, 1956), and at some levels, Permian ammonoids are not particularly diagnostic. The lower Tastubian Substage has few ammonoids, of Asselian appearance. The upper Tastubian Substage has a number of distinctive ammonoid genera and species, constituting a much more convincing assemblage. Although brachiopods are very numerous and well preserved, it is many years since they were comprehensively studied. Fusulines have retained high importance. The Sakmarian Stage is now known to have been of moderate duration, 6 Ma according to Menning & Hendrich (2012), and this must influence any interpretation of the Sakmarian in Australia. The Artinskian Stage has at least three major conodont zones, one in the Aktastinian or Burtsevian Substage, and two or three in the overlying and classic Arti sequence of the standard Baigendzinian Substage, containing the Irginian and Sarginian levels, and lasting for only 4.5 Ma. At the top, the classical Artinskian (Licharew 1966) has been truncated by moving the Saranin level into the Kungurian Stage at the top of the Early Permian Series, not because of faunal affinities, but because of the distribution of conodonts that are needed for drawing a firmly controlled boundary. Davydov & Wardlaw (2005) have provided a detailed account of the history, stratigraphy and palaeoenvironments relevant to the stage. They suggested that the best section is at Dal'ny Tulkas, with a chronomorphocline from *Sweetognathodus binodosus* to the FAD of *S. whitei*. The Saranin level, now treated as basal Kungurian, shares many links with the underlying Sarga (Sarginian) faunas, including the key fusuline *Parafusulina solidissima* (see Waterhouse 1976a, p. 96). Younger Kungurian faunas are much more closely related to those of Middle rather than Early Permian age, when the faunas "were renewed" and showed substantial change (Stepanov 1973). Were faunal links to be based on fusulines, brachiopods and molluscs, Kungurian would be grouped with Middle Permian, and Saranin placed at the top of the Early Permian. The world stratotype for classic Kungurian of the Urals etc. could be shifted to the Guadalupe Basin and Glass Mountains successions of Texas, United States, below the Roadian Stage. Here the Cathedral Mountain and Bone Spring faunas are treated as upper Kungurian, and Skinner Ranch as lower Kungurian. But aspects of historical understanding, geopolitical considerations, and focus on conodonts, have helped to shape the international standard for Permian time, with natural steps in faunal development and world-wide environmental change seemingly of secondary consideration. Yet these may prove to be world-wide, and offer strong prospects of event-corerelation.

GLOBAL STAGE	**RUSSIAN COMPOSITE STRATIGRAPHIC UNIT**	**KEY CONODONTS**	**EAST AUSTRALIAN BRACHIOPOD ZONES**
Kungurian	Irenian Filippovian Saranian	***Neostreptognathodus pnevi***	*Echinalosia discinia* *Wyndhamia typica* *Glendella dickinsi* *Attenuocurvus altilis* fauna
Artinskian	Sarginian Irginian Burtsevian	***Neostreptognathodus pequopensis*** ***Neostreptognathous clarki,*** ***N. ruzhenzevi*** ***Sweetognathodus whitei***	*Echinalosia conata* *Spinomartinia adentata* *Ingelarella plica*
Sakmarian	Sterlitamakian Tastubian	***Sweetognathodus primus*** ***Sweetognathodus anceps*** ***Sweetognathodus merrilli*** ***Diplognathodus aff. stevensi*** ***Sweet. aff. merrilli*** and ***Mesogondolella uralensis***	*Taeniothaerus subquadratus* *Bookeria geniculata* *Bookeria pollex* (*Acanthalosia domina*) (*Azygidium mitis*) (*Echinalosia curtosa)*
Asselian	Shikhanian Kholodnologian [Uskalykian] [Syurenan]	***St. barskovi – St. postfusus*** ***Streptognathodus constrictus*** ***St. cristellaris – St. sigmoidalis*** ***Streptognathodus glenisteri*** ***Strpeptoganthodus isolatus***	*Bandoproductus macrospina* *Crassispinosella subcircularis* *Strophalosiaria concentrica*

Table 16. Correlations between the international Cisuralian Series based on the sequences in the east European Platform and Pre-Uralian foredeep, from Menning et al. (2006, Fig. 5) and the brachiopod zonal sequence for east Australia and New Zealand (Waterhouse 2008b, 2013), with subzones of *Bookeria pollex* Zone in brackets. Russian units in square brackets are introduced for the middle and lower Asselian from the pre-Urals fore-deep, following Licharew (1966) and Waterhouse (1976a, p. 53). Note the dismal conodont record for the Filippovian, which has been used to justify moving the Saranin from classic Artinskian into Kungurian, and retaining the Kungurian in the Cisuralian, whereas true Kungurian would be better treated as start for the Middle Permian Guadalupian Series (Waterhouse 1983b).

The base of the Sarana Horizon is exemplified by the Sylva Formation of reefal limestone, laterally equivalent to Shurtan Formation of marls and clayey limestone, and overlain by the Filippovsk (classic base for the Kungurian Stage) and Irenian Horizons. The Kamai Formation below the Sarana Horizon has few fossils, so that ties to the Sarga (top Artinskian) Horizon are not firm. The Shurtan Horizon has the *Neostreptognathodus pnevi* conodont Zone. A better section at Mechetlino settlement at the Yuryuzan River has the *N. pnevi* Zone in Beds 19-20, and Filippovian conodonts in Beds 21-22, according to Davydov & Wardlaw (2005). *N. pnevi* is shallow water, and *Vjalovognathodus shindyensis* is pelagic.

Australian correlations – the basic assumptions

Over the last few decades there have been several models for correlating Australian Permian with the international standard, and of course the change in the international standard from one based solely on Russian sequences has meant additional difficulties for Australia. The original proposals by Waterhouse (1983b) that the Early Permian should be called the Cisuralian Series, and that Middle and Late Permian should be recognized not from Russian outcrops but from standard sequences in United States and China was eventually accepted by the International Subcommission for the Permian Period (Jin et al. 1994, Jin 1996; Jin et al. 1997), but that has disadvantaged efforts at international correlation for Australian Permian, because Australian mid-Permian has more in common with Russia than with the United States.

Australian Permian correlation as proposed herein is premised on these assumptions: 1, that brachiopod-mollusc zones are largely isometric with international conodont zones, and with zones elsewhere in Gondwana. 2, that the correlations should be close at least to those suggested by ammonoid, conodont and radiometric evidence where available. 3, that gaps in the sedimentary record cannot be easily detected in the absence of outside faunal evidence. The preferred conclusions are that 1, that in Australia Permian marine sedimentation with faunas commenced in the Asselian Stage. 2, that the *Crassispinosella calytrixi* fauna probably lies below the *Lyonia lyoni* Zone. 3, there is a faunal gap of Baigendzinian age in eastern Australia, between the *Ingelarella plica* and *Wyndhamia typica* Zones. 4, that palynomorph zones were by and large synchronous in the Asselian-early Sakmarian and Kungurian across Australia, but diverged in Sakmarian – Artinskian.

Radiometric ages

According to Ramezani et al. (2007), the best currently available means for obtaining radiometric values for Permian rocks is the ID-TIMS U-Pb zircon method and Tempora standard. Ramezani et al. (2007) reported a value of 298.90 Ma and an additional very small uncertainty factor, with what is virtually a return to placing the Carboniferous–Permian boundary at just under 300 Ma, much as in Waterhouse (1978b), who calculated values from faunal studies and an attempted solar chronology, interpreted through faunal diversity signatures. Mostly SHRIMP techniques have been applied to Permian rocks in eastern Australia, not the Tempora standard, and not adjusted for subtle intergrain and intergrain heterogeneities in zircons, including inheritance and lead-loss effects, explained by Metcalfe et al. (2001, p. 242). It is therefore difficult to regard the radiometric values in east Australia as reliable, as also forcefully argued by Korte et al. (2008, p. 5), reinforced by Foster & Archbold (2001), with Draper & Fielding (1997) highlighting the purported estimation for the Black Alley Shale as being particularly unacceptable (cf. Roberts et al. 1997). SHRIMP-based radiometric ages for east Australian Permian have had a mixed reception, with a number of results being contradicted by subsequent study. Thus values in Roberts et al. (1991) were changed by Roberts et al. (1995). Improved results were provided by Chuvashov et al. (1996) and Roberts et al. (1996), which included a SHRIMP value for 290.5+/-2.8 Ma and another at 293.7+/-3.4 Ma for Alum rocks, said to be just below the *Crassispinosella subcircularis* Zone, and near a locality with 3a palynomorphs. These values indicate Asselian Stage, in close agreement with Balme's (1980) preferred age for the spores.

The radiometric values for the Cranky Corner succession hold more challenges, especially for the Permian measurements. Readers will notice the upward increase in age (see Table 13). Claoué-Long & Korsch (2003) gave an age of 287 Ma by SHRIMP dating for the Beckers Formation, which contains species of the *Ambikella elongata* fauna, according to Archbold (2003), a value equivalent to mid-Sakmarian in Menning et al. (2006), followed by 284 Ma for the Cranky Corner beds. The reliability of the data may be challengeable – there are two major populations, and it seems difficult to rule out Pb loss for the 287 Ma value. Moreover the macrofaunal identifications carry uncertainty. *Unicostatina crassa* is not securely the same as the Tasmanian types, and *Neilotreta* points to a match with the *Neilotreta occidentalis* Zone of Western Australia, and *Stutchburia* to Fossil Cliff and Callytharra specimens of the *Coronalosia irwinensis* Zone in Western Australia. *Ambikella elongata* has been reported from the *Strophalosiaria concentrica* Zone in Tasmania, but the Tasmanian material differs in several respects (see p. 155), and may be present in the *Bandoproductus* fauna of Gympie with *Neilotreta*: the age hovers close to the Asselian–Sakmarian boundary, perhaps slightly greater than the 287 Ma value.

For the Branxton Formation 12m above the Greta Coal Measures, Chuvashov et al. (1996) and Roberts et al. (1996) provided a value of 272.2+/-3.2 Ma. Korsch et al. (2009) re-evaluated the age as 275 Ma, which corresponds with the age now favoured for the base of the Kungurian Stage, although Korte et al. (2008, Fig. 2) preferred a value of 279.5 Ma. From the stand-point of faunal affinities, the early Branxton faunas, with the *Wyndhamia typica* Zone, are strong in cold-water affinities and suggestive of a Filippovian (lower mid-Kungurian) age (Waterhouse 2001, 2002a) and the Branxton faunas are like those of younger (Guadalupian) faunas of east Australia. In Russia, basal Kungurian (Saranin) faunas are like those of the Artinskian, and differ strongly from those of mid-Kungurian (ie. Filippovian) and Guadalupian age. In short, the uncorrected age in Roberts et al. (1996) would seem in better accord with the faunas, and is close to the age of 270-272 Ma suggested by Waterhouse (1978b). But it is clear that further clarification is required. Estimates of 277 Ma, 274-275 Ma, and 272.5 Ma have been given for the Kungurian base respectively in Menning (1995), Wardlaw (1999), and Menning et al. (2006), with no information provided for the start of the critical Filippovian faunas. The allocation of a mere 5 million years duration to the Kungurian Stage in Menning et al. (2006) seems too short, and the age in Korte et al. (2008) and Korsch et al. (2009), regardless of the Australian value, seems much more reasonable, with a duration of 7 Ma years conceded in Menning & Hendrich (2012).

The radiometric value for the Mulbring Formation appears to agree with the brachiopod age, Chuvashov et al. (1996) citing 264.1+2.2 Ma, compared with an upper Wordian age preferred by Waterhouse (1976a, 2002a), leaving a discrepancy of some 2 Ma apart from the uncertainty factor: Menning et al. (2006) cited 266-265 Ma. Korte et al. (2008) provided a different set of interpretations, but depended on an outdated and less than correct biozonation and correlation schemes offered by Briggs (1998) and Archbold (eg. 2000), as analyzed in Waterhouse (2001, 2008b).

Natural divisions of the marine Permian invertebrate biozones in Australia

The marine Permian biozones of Australia and New Zealand fall naturally into a succession of several major associations:

1. (basal). The zones based on *Strophalosiaria, Crassispinosella* and *Bandoproductus-Lyonia-Neilotreta* in east and Western Australia.
2. Zones based on *Bookeria pollex, Bookeria geniculata, Taeniothaerus subquadratus* and *Ingelarella plica* Zones in east Australia and New Zealand, and chiefly the *Coronalosia irwinensis* Zone and possibly the *Sommeriella magna* and *Coronalosia jimbaensis* Zones in Western Australia.
3. A number of zones (or faunal communities) recognized in Western Australia by Archbold (1993b), including those based on *Echinalosia prideri* and *Fusispirifer byroensis* , and the *Spinomartinia adentata* and *Echinalosia conata* Zones of New Zealand. Conditions in eastern Australia were non-marine.
4. A full succession of zones in east Australia, commencing with *Glendella dickinsi*, and based on species of *Wyndhamia, Echinalosia, Pseudostrophalosia, Paucispinauria and Terrakea*, shared with New Zealand, and equivalent to the possibly less complete succession of zones commencing with *Sommeriella magna* and closing with *Fusispirifer coolkilyaensis* and *Georginakingia occidentalis* in Western Australia.
5. Zones commencing with *Martiniopsis woodi*, followed by *Tigillumia parallela* and *Spinomartinia spinosa* in the Gympie Basin of Queensland and in New Zealand, matched with the *Liveringa magnifica* and *Wimanoconcha imperfecta* Zones of Western Australia, that equate to the lower part of the east Australasian succession.
6. The *Marginalosia planata* and *Wairakiella rostrata* Zones of late Lopingian age in New Zealand.

Summary of correlation data

To match the Australian Permian marine faunas with the world standard is no easy task. Permian fusulines are entirely lacking from Australia, unlike nearby New Zealand, and Permian conodonts are very few, limited to Western Australia and New Zealand, with none in eastern Australia. Ammonoids are found at a few limited horizons, chiefly in Western Australia, far from the more fully studied ammonoid sequences of Russia and United States, and in a different hemisphere. As Glenister et al. (1993) noted, Early Permian ammonoid faunules are strikingly provincial, adding further uncertainty. Reliance therefore must be based on stratigraphic sequence and overall nature and affinities of faunas, with support from radiometric dating and rare conodonts, where available. Plant spores are widespread, but of course suffer the same disadvantage as the macro-invertebrates, in showing few links with the Russian world standard. It does not appear possible at present to achieve finality. Australian workers suffer great difficulties because of the lack of attention to macro-invertebrate fossil faunas in even the world standard sequences, especially Cisuralian. Cisuralian brachiopods and molluscs were studied mostly in pre-war times, and no comprehensive and detailed study linked to conodonts has been available. For Australia, to some extent, there must be reliance on ammonoid occurrences which give somewhat inconsistent ages, as is clear from the summary of Canadian data (pp. 42, 43). The best to be done is assemble Australian faunas into controlled biozones, and note the correlations with related faunas elsewhere. Resolution of some of the ambiguous or conflicting data with regard to faunal interpretation may have to await either an extensive review and integration of world standard invertebrate faunas, or the development of a sophisticated analysis of climate sequencing through changes in faunal affinities, or wide-ranging application of the TIMS radiometric technique. In such regards, Australian Permian studies are in the same position as those of much of the rest of the world, outside of the Permian paleotropical marine sequences. Thus it is considered that a prime focus of the present study is delineation of species, genera and biozones: international correlation retains uncertainties that cannot be resolved at present.

Basal or pre-Asselian Stage

The *Nambuccalinus* fauna of northern New South Wales may be the oldest marine Permian in Australia, apart from a few mostly bivalve faunas under poor age control. The youngest of Carboniferous zones in east Australia is based on *Auriculispina levis* (Maxwell), in the Yarrol Basin, Queensland, but as yet a Carboniferous age cannot be ruled out for the *Nambuccalinus* fauna.

Asselian Stage

The *Strophalosiaria concentrica* and *Crassispinosella subcircularis* Zones are found in reliable stratigraphic succession in Tasmania. They might prove to be younger than the *Nambuccalinus* fauna, and are matched to a degree with the *Crassispinosella calytrixi* and *Fimbrinialosia carolyni* faunas in the Grant Group of the Canning Basin in Western Australia. These faunas all share the palynomorph *Pseudoreticulatispora confluens*. There is no known ammonoid, conodont or fusuline evidence for correlation with the world standard, so that the age must depend on interpreted stratigraphic position, and correlation with a *Fimbrinialosia perfecta* fauna of Asselian age in India. A radiometric value for Alum rocks just below the *Crassispinosella subcircularis* fauna in New South Wales supports an Asselian age.

The *Bandoproductus macrospina* Zone is developed in the Burnett Formation of the Yarrol Basin, lying above *Eurydesma burnettensis* and below Yarrol faunas equivalent to the *Bookeria pollex* Zone followed by the *Bookeria geniculata* Zone, and matched by *B. walkomi* Briggs (1998) in the lower Rutherford Formation of the Hunter Valley, below the *Bookeria pollex* and *B. geniculata* Zones of the Farley Formation. A diverse fauna described in Waterhouse (2015) occurs at Gympie, southeast Queensland. The *Lyonia lyoni* Zone in the Lyons Group in the Carnarvon Basin of Western Australia is likely to be correlative. So far no close systematic evaluation of *Lyonia* from the different faunal levels has been published, and there are certainly differences in the faunas of the lower and middle Lyons Group, even from the summary presented by Archbold (1993b, p. 314). According to his account, *Rhynchopora, Kiangsiella* and *Deltopecten* are found in the lower beds, and *Cyrtella, Grumantia, Ambikella* and “*Trigonotreta*” in the middle beds. No palynomorphs have been described from the *Bandoproductus macrospina* Zone in east Australia, at least where *Bandoproductus* is present, but it is possible that equivalents are represented by *Ambikella elongata* (Armstrong & McClung) and *Neilotreta tangorini* (Archbold) in the Cranky Corner sequence (see pp. 29-32). Briggs (1998) suggested that *Microbaculispora trisina* would typify the zone, whereas Archbold (2001, table 5) tabulated palynomorph *Striatopodocarpites fusus* for most of the zone, followed by *Microbaculispora trisina*. At Cranky Corner, *Neilotreta tangorini* is found in the palynomorph zone APP 21 with *Pseudoreticulatispora pseudoreticulata*, and in APP 22 characterized by *M. trisina*, as endorsed by Foster & Archbold (2001).

The *Neilotreta occidentalis* Zone of the Carnarvon Basin, embracing the upper Lyons Group and lower Callytharra Formation, may be in part correlative, to imply a much more substantial and diverse role for *Lyonia-Neilotreta* in Western Australia, compared with *Bandoproductus-Neilotreta* in eastern Australia. Ammonoids *Juresanites jacksoni* and *Uraloceras* (or *Svetlanoceras*) *irwinense* are found in the Woolaga Limestone Member of the Holmwood Shale in the Perth Basin, correlated with either upper Tastubian or Sterlitamakian, though provisionally regarded as Sterlitamakian (Glenister et al. 1993). In Western Australia, *Ps. pseudoreticulata* is found in the lower Callytharra Formation of the Carnarvon Basin, and *trisina* in the uppermost Callytharra, above two further discriminated palynomorph zones. That seems to accord well on both sides of the continent. But *Ps. pseudoreticulata* is also characteristic, and indeed regarded as most characteristic, of the Allandale and other faunas with *Eurydesma* in New South Wales (Archbold 1999, 2002), largely matching the *Crassispinosella subcircularis* Zone of Tasmania.

Sakmarian Stage

Tastubian

The *Bookeria pollex* Zone is assigned to this level, a diverse faunal assemblage, especially well developed in the Bowen and Sydney Basins, and with brachiopod links to faunas of south Asia and Canada. Three well defined subzones are recognized, named after *Echinalosia curtosa, Azygidium mitis* and *Acanthalosia domina* (pp. 20ff).

Sterlitamakian

Faunas of the *Bookeria geniculata* Zone, well developed in the Yarrol, Bowen and Sydney Basins and probably Tasmania, share a number of species with the underlying zone. A single ammonoid in the Farley Formation of New South Wales, *Uraloceras pokolbinense* Teichert & Fletcher, 1943, is not particularly informative with regard to age, and *Gobioceras cancellatum* (Dear) in the Yarrol Basin and Bowen Basin indicates no more than a general Sakmarian to Kungurian age. Overall the zones indicate a Sakmarian age, with somewhat related faunas in India (Singh 1978a) and Canada (Nassichuk 1970) yielding ammonoids considered to be Tastubian on the whole, but with some younger elements, and open for more refined study. Thus the age is only provisional, offered to allow consistency with the *Neocrimites* (or *Aricoceras*) in younger faunas. The *Svalbardia armstrongi* Subzone at the top of the *Bookeria geniculata* Zone has a number of distinct taxa. APP 3 floras are found with *ovata* and *profunda* in Tasmania, involving Stage 4 palynomorphs, *Phaselisporites cicatricosus*, followed by *Praecolpatites sinuosus* (4a) then *Acanthotriletes villosus* (4b).

The overlying *Taeniothaerus subquadratus* Zone of the upper middle Tiverton Formation at Homevale is comparatively rich in species, and has a ready match in the Berriedale Formation of Tasmania. Ammonoid *Gobioceras lobulatum* is found near the base, but is difficult to date precisely. Faunas are close to those of the Callytharra Formation in Western Australia, and are allied to *Taeniothaerus or Reedoconcha* faunas of south Asia, in Kashmir, Pakistan and Oman (Reed 1932, Angiolini et al. 1997). Amongst ammonoids described by Glenister et al. (1990, 1993) and Glenister & Furnish (1961) from the Callytharra Formation and Fossil Cliff Member and slightly younger forms from the Nura Nura Member, *Metalegoceras kayi* Glenister et al. (1973) and *Propopanoceras* favour a Sterlitamakian age, as elaborated by Glenister et al. (1993, p. 56), and the correlative *Taeniothaerus* faunas of south Asia have been assigned a similar age. On the other hand supposed *Neocrimites* (now *Aricoceras*) *meridionalis* Teichert & Fletcher of younger Cisuralian age has been recorded, by Armstrong et al. 1967 from the Lakes Creek beds with *Taeniothaerus farleyensis* (see Waterhouse 2013, p. 277) near Rockhampton. The identification of the ammonoid material requires confirmation. Evidence for the Sterlitamakian age seems good, but raises a difficulty with the presence of *Aricoceras* or *Neocrimites* of Baigenzinian age in overlying faunas. One possibility is that the two were separated by unconformity, as favoured by Glenister et al. (1993). Another is that the Sterlitamakian ammonoids have been misdated and are slightly younger, at Aktastinian – or that the brachiopod faunas of the *Taeniothaerus subquadratus* Zone in east Australia are slightly younger than those of the Callytharra Formation and the faunas of Oman. The present solution is overall the simplest, but the need for further study must be underlined.

Artinskian Stage

Aktastinian

The *Ingelarella plica* Zone is restricted in distribution to the Bowen Basin and New Zealand. Although limited in extent, the zone has two faunas, a comparatively diverse fauna, overlain by an impoverished fauna in the Brunel Formation of New Zealand (see p. 346), and less diverse fauna in the Bowen Basin of Australia, with the Cattle Creek faunas still to be fully described. It has been deemed to be of Aktastinian age, because its brachiopod faunas are close to those of Sakmarian age, and it is understood that Aktastinian fusulines and brachiopods are close to those of type Sakmarian age (Waterhouse 1976a, 2002a). Ammonoids in the Aktastinian of Russia are few. What challenges this putative correlation is the occurrence of supposed *Neocrimites fredericksi* (Emeliantsev) from the upper Tiverton Formation, northern Bowen Basin, and originally reported from the lower Baigendzinian of the Aktyubin District in the Urals: the full time range might be slightly greater, but the genus is typical of Baigendzinian (Leonova & Dmitriev 1989, p. 163), at least in the northern paleohemisphere. The Tiverton specimen was identified by B. F. Glenister and W. M. Furnish in Armstrong et al. (1967, p. 95), and also was compared with *Neocrimites* sp. from the Coyrie Formation of the Carnarvon Basin in Western Australia, above the *Coronalosia irwinensis* Zone*. Neocrimites* also occurs in the Cordalia Sandstone near the base of the underlying Wooramel Group, as affirmed by Glenister et al. (1993). Glenister et al. (1993)

considered that the Wooramel beds were therefore likely to be Baigendzinian, but they noted that Aktastinian faunas (meaning ammonoids, though unstated) were difficult to recognize beyond the Urals. Leonova (1998) and Leonova & Bogoslovkaya (1990) have re-assessed Australian species of so-called *Neocrimites* as coming much closer to *Aricoceras*, close to Yaktashian (Artinskian) and Bolorian (lower Kungurian) of the Tethys and Donets (see Menning et al. 2006, Fig. 4, p. 334), especially suggestive because those outcrops also include *Bamyaniceras* as in Western Australia. Leonova (1998) suggested that the age was likely to be late Artinskian or Kungurian, but the age remains open for further assessment, with an Akastinian age not to be entirely ruled out. Archbold (2000, table 2), followed by Korte et al. (2008), treated *Neocrimites fredericksi* as Filippovian in age, which does not accord with the Coyrie correlation favoured by B. F. Glenister and W. M. Furnish in Armstrong et al. (1967). There is thus some disagreement between interpretations of the brachiopods and of the ammonoid, and any decision is provisional, for it may be overturned by further study. The faunas are placed provisionally as Aktastinian, likely to be close in age to the Cordalia Sandstone at the base of the Wooramel Group, which has been in part assigned to the Aktastinian by Archbold (1993b, table 1). Such a correlation suggests that the ammonoid entered Australian faunas a zone earlier than in the Urals. The *Coronalosia jimbaensis* Zone is allied to the underlying *Coronalosia irwinensis* Zone in Western Australia. Palynomorph *Praecolpatites sinuosus* (4a) is found in the upper Cattle Creek beds (*Ingelarella plica* Zone) of the western Bowen Basin. This is much earlier than its appearance in the *nalbianesis* fauna of Carnarvon Basin, Western Australia, and *Praecolpatites sinuosus* is reported in older beds of the southeast Bowen Basin.

Baigendizinian

Baigendzinian faunas are well developed in Western Australia, with distinctive brachiopods and ammonoids nowhere found in eastern Australia. It is deemed that deposition in eastern Australia was non-marine, involving coal measures such as the Greta Coal Measures, Collinsville Coal Measures and Blair Athol Coal Measures. This unconformity may have commenced during deposition of the *Ingelarella plica* Zone, which is limited to the Bowen Basin in eastern Queensland, and in Western Australia, the Wooramel Group of the Carnarvon Basin is matched with the Irwin River Coal Measures of the Perth Basin. Palynomorph *Striatopodocarpus fusus* followed by *Didecitriletes byroensis* are found at this level in Western Australia.

This correlation is further supported by the sequences above the *Ingelarella plica* Zone in New Zealand. These sequences lack coal measures and contain two equivalent marine biozones (Table 13), named after *Spinomartinia adentata* followed by *Echinalosia conata* in beds that are extraordinarily thick, having accumulated as a detrital fan on the flanks of volcanic outpourings. The two zones lie in clear succession immediately above the *Ingelarella plica* Zone, and below the *Wyndhamia typica* Zone and meagre faunas equivalent to the *Glendella dickinsi* Zone. The New Zealand faunas include *Echinalosia conata* Waterhouse, allied to *E. prideri* Coleman from the eponymous zone of the lower Madeline Formation in Western Australia, and “*Aulosteges” ingens* Hosking, also found in the *Pseudostrophalosia colemani* Zone in the upper part of the Madeline Formation, as well as an allied and unusual spiriferellin genus called *Arcullina*, found in both New Zealand and correlative faunas of Western Australia.

Kungurian Stage

The “*Attenuocurvus altilis* fauna” lies above the *Echinalosia conata* Zone, and is correlated with the fauna in the Upukerora Formation with taeniothaerid, martiniid, *Trabeculatia marwicki* (Waterhouse, 1958) and other species (Waterhouse 2002a, p. 116) at Gyzeh Peak, east of West Dome, Mossburn. The fauna is deemed correlative with the Saranian level at the base of the Kungurian Stage.

The Filippovian, classic base of the former Kungurian Stage, is represented in east Australia by a cold-water fauna of low diversity referred to the *Glendella dickinsi* Zone, developed in the Gebbie Formation of the Bowen Basin (Waterhouse & Jell 1983, Waterhouse 2008b), and represented by a meagre fauna in New Zealand in the basal Letham Formation of Wairaki Downs (Waterhouse 2002a). A more extensive *Wyndhamia typica* Zone, represented in the Bowen and Sydney Basins and in New Zealand includes the ammonoid *Aricoceras meridionalis* (Teichert & Fletcher) from the lower Elderslie Formation in the Branxton Subgroup of the Hunter Valley, and radiometric data supports a Kungurian age. Four brachiopod zones in east Australia (Waterhouse 2002a) have been assigned to the Kungurian Stage, which is close to the five conodont zones recognized for the world standard (Kozur 1998). Amongst the few and scattered conodonts, *Vjalovognathodus shindyensis* and *Mesogondolella idahoensis* from the Cundlego Formation of Western

Australia indicate an early Kungurian correlation (Nicoll & Metcalfe 1998). Archbold (1998, p. 92) disputed the Kungurian age assigned to *V. shindyensis* from the Coyrie Formation and argued that the conodont ranged from late Artinskian into early Kungurian, whilst later articles by Archbold did not mention the occurrence of the species. But the Bulgadoo Shale, Cundlego and Wandagee Formations appear likely to be Kungurian, with the ammonoid *Bamyaniceras*.

Roadian Stage

The *Echinalosia maxwelli* and *Pseudostrophalosia blakei* Zones of the Bowen and Sydney Basins and New Zealand are assigned to the Roadian Stage at the base of the Middle Permian or Guadalupian Series (Waterhouse 2002a, 2008b). In Western Australia the ammonoid *Daubichites* appeared in the *Svalbardia thomasi* Zone of the Baker Sandstone to signify a Roadian age. The *Sommeriella* sp. nov. B Zone of Archbold (1993b) in the underlying Nalbia Sandstone is very close to, and hardly defensible as a zone separate from the *Svalbardia thomasi* Zone. However Archbold (1999, p. 62) found it necessary to challenge assumptions about *Daubichites*, and to postulate that from the evidence of associated fauna, *Daubichites* appeared earlier in Australia than in various northern faunas. That provides a warning – especially when the earlier Permian ages of Australia are based on evolutionary assumptions without specific identification to northern hemisphere forms, and when genera that ranged through several stages are used to correlate at substage or conodont zone level. The west Australian Permian faunas assigned by Archbold (1993b) to the international Roadian Stage have two or three zones, a substantial gap, and the beginning of a further zone, although it may be necessary to reassess whether the units should rate as full zones. World-wide, one conodont and ammonoid zone is recognized in shallow water deposits, but there are two pelagic zones, *Mesogondolella siciliensis - M. phosphorensis*, above *M. gracilis - M. saraciniensis*, according to Kozur (1998), and two brachiopod-bivalve zones in New Zealand and eastern Australia.

Summary of conclusions

Brachiopod – mollusc zones almost isometric with conodonts, independent of palynomorphs: marine independent of non-marine.

The zones in east Australia (and New Zealand) fall approximately in line with world standard conodont zones in duration and number, but exact matches remain frustrated by the paucity of conodonts, fusulines and ammonoids in Gondwanan successions, and the inattention to other marine invertebrate constituents of world standard Cisuralian biostratotypes. In Australia, the *Nambuccalinus* fauna is apparently younger than three Late Carboniferous zones recorded in the Argentine, and the *Strophalosiaria concentrica* and *Crassispinosella subcircularis* Zones are tentatively regarded as Asselian. The *Bandoproductus macrospina* Zone is likely to be late Asselian, assuming it matches the south Asian level. The overlying *Bookeria pollex, Bookeria geniculata* and *Taeniothaerus subquadratus* Zones extended throughout the Sakmarian Stage, followed by the *Ingelarella plica* Zone, for which an Aktastinian age is preferred as against the Baigendzinian age supposedly favoured by the ammonoid *Neocrimites* (or *Aricoceras*). Widespread non-marine deposition followed in east Australia, with marine equivalents in Western Australia (Wooramel Group) and also in New Zealand, where represented by the *Spinomartinia adentata* and *Echinalosia conata* Zones as Artinskian, and small faunas as early Kungurian (Saranin). The *Glendella dickinsi* Zone, then *Wyndhamia typica* and *Echinalosia discinia* Zones are of younger Kungurian age. The *Echinalosia maxwelli* and *Pseudostrophalosia blakei* Zones (Roadian), *E. ovalis* Zone (Wordian) and *P. clarkei* Zone (Capitanian) make up the Guadalupian Series. Within these major units are lesser more geographically restricted intervals of subzonal status, and finer very short-lived intervals or horizons. This largely conforms with ammonoid evidence and several radiometric ages in Roberts et al. (1996) as discussed by Waterhouse (2002a, pp. 226-228). According to this scheme, the Asselian was a time of extensive glaciation interspersed with some warmer intervals. Faunas accumulated in marine conditions under crust-bending weight of ice, and faunas were of meagre diversity. The Sakmarian was a time of recovery, characterized by several major faunas and faunal levels dominated by various short-lived species, under fluctuating conditions. The late Artinskian and basal Kungurian was a climatic optimum, with extensive coal accumulation (especially under isostatic crustal rebound after deglaciation and extensive swamp development caused by rising sea-level), and warm-water marine faunas (Loughnan 1973, 1975, Waterhouse 1963c, pp. 217-221, 1976b, Fig. 3, p. 255). Cool or cold conditions returned in the Filippovian (early Kungurian), and ameliorated and deteriorated under fluctuating conditions throughout the Guadalupian Series

(Waterhouse 2002a, p. 198). For Late Permian of Australasia, the marine record is best preserved in New Zealand, with limited application in east Australia, apart from the Gympie region (Shi et al. 2010, Waterhouse 2015).

The scheme has the advantages of conforming in a general way with the conodont record, and with the biostratigraphic records in south Asia (eg. Afghanistan, India, Nepal, Tibet, Pakistan, Oman, Thailand) and New Zealand, and north polar regions (eg. Arctic Canada). But the brachiopod and mollusc-based zones do not conform with palynomorph zones across Australia. The palynomorph zones above the *Strophalosiaria* and *Crassispinosella* zones of Asselian age and below the zones of Kungurian age seem to be off-set, as if they were consistently younger in Western Australia, and of great duration in some instances. Moreover within this interval of time, the *cicatricosus* Zone is absent from Western Australia, and the *fusus* and *byroensis* Zones are absent from east Australia. Even despite uncertainty and a measure of disagreement about the exact interrelationship of successive incoming key forms of palynomorphs and brachiopods, there appear to be major discrepancies, and it is postulated that the changes to plant-life producing the palynomorphs, and to the marine fossils, were not time-concordant across the continent. The most likely explanation appears to be that the climate ameliorated more rapidly in the marine basins of Western Australia than to the east, as affirmed by the diversity and paleogeographic affinities of brachiopods and molluscs, and supported by divergence of the floras. Significantly, the marine faunas known from the now scattered segments of Gondwana share a number of distinctive genera and show roughly concomitant changes in fauna through time. But the same Gondwanan segments differ to some extent in the palynomorph record, as summarized for example by Archbold (2001, tables 1, 2, 4). It is thus acceptable to consider that east and Western Australia also had different plant successions.

PALEOECOLOGY AND PALEOGEOGRAPHY

The biozones as here assembled are constituted of various communities: these will not be set forth because they are relatively simple, and can be gleaned from the tabulation of species (Tables 8-10). Attention is here focused on a broad overview of the macro-faunas, in relation to a world setting.

Paleoclimate

It has long been established that east Australia lay close to the Permian south geographic and magnetic poles. The comparatively high latitudes with cool temperatures led to the widespread accumulation of cool and cold-water rocks such as diamictites, varves and drop-stones, developed from scattered upland glacial ice-sheets (eg. Dickins 1985). Although some American authors claimed that the Permian of eastern Australia witnessed one long-lived and severe glaciation, it has been recognized that there were rather a succession of glacial advances and retreats, as expressed by Waterhouse (1964b, 1969b, p. 13, 1976a, b, 1977, 1978b; Waterhouse & Bonham-Carter 1972, 1975, 1976), starting with three advances in the Early Permian, followed by two or three lesser advances in the Kungurian and Guadalupian. Fielding et al. (2008) acknowledged four glacial episodes, each with many minor phases, and provided a tabulation of Permian formations and major phases for the Sydney and Bowen Basins. They did not discuss either of the two best dated and most closely studied faunal successions (southeast and north Bowen Basin), but showed what may be deemed as correlative Yarrol Formation and Farley and part of the Rutherford Formations as belonging to a post-glacial (P2) warm phase. The authors incorrectly claimed they were first to depict the Permian glaciations as mutiple, and there are errors of correlation. For example the *Echinalosia discinia* Zone is claimed to follow the *E. maxwelli* Zone. That is undoubtedly wrong, as shown in the type area for the species concerned and detailed published map at 1: 12 000 (Waterhouse 2002a). On the other hand it is pleasing to see allowance made for isostatic adjustments in sedimentation, and the realization that the Greta Coal Measures accumulated during a warm climatic regime, as argued by Waterhouse (1964b, 1976a) and subsequent articles.

The south geographic pole was probably sited near, perhaps south of, Tasmania, and this is confirmed in a very approximate way from wandering paths of the Permian paleomagnetic pole. Queensland lay further north, in lower paleolatitudes than New South Wales, which in turn lay further north than Tasmania. The differences in paleolatiitude are reflected by the nature of the marine faunas. Those of higher paleolatitude are less diverse in number of species and genera, and contain fewer taxa that are typical of very low paleolatitudes (Waterhouse 1969c). Such are generalizations. It is not difficult for diversity to be affected by incomplete sampling or preservation, and to overcome such bias, a formula may be applied following Waterhouse & Bonham-Carter (1975), a more qualitative approach than that based on the rarefaction formula of Sanders (1968) and Miller & Foote (1996). From faunal diversity and intrinsic diversity standpoints, the *Bookeria pollex* Zone involved a cool climatic phase (*Echinalosia curtosa* Subzone), warm phase (*Azygidium mitis* Subzone) and cool phase (*Acanthalosia domina* Subzone). The overlying *Bookeria geniculata* Zone was cool but more stable, with a flourishing of species and genera that culminated in the *Svalbardia armstrongi* Subzone: conditions were neither as cold as the *Echinalosia curtosa* and *Acanthalosia domina* Subzones, nor as warm as the *Azygidium mitis* Subzone. The following *Taeniothaerus subquadratus* Zone marked a steady warming, reinforced by bottom conditions that often favoured the entry of bivalves, with a return to cooler conditions in the overlying *Ingelarella plica* Zone at the top of the Tiverton Formation. These varying conditions were homogenized and disregarded in the study by Fielding et al. (2008). This theme is elaborated in studies on temperature and diversity fluctuations for southern Gondwana (Waterhouse 2010b, Waterhouse & Shi 2010, Shi & Waterhouse, 2010). It should be recalled that as shown by Waterhouse & Bonham-Carter (1975), the climatic shifts and faunal responses were world-wide, and so enable widespread intercontinental correlation and a calibration of evolutionary development. Further discussion is provided in the Conclusions on pp. 343-348.

Clapham & James (2008) provided an overview of fossil occurrences in part from new collections, that was substantially out of date from the time of its publication. No allowance was made for the systematic studies and taxonomies provided in the international Treatise series of Invertebrate Paleontology on Brachiopoda, such as Brunton et al. (2000), Brunton (2007), Carter (2006a, b) and various other articles, nor to various monographs and revisions to the faunas in Waterhouse (2001, 2002a, b, 2004a, b, 2008a, b). The correlations in Clapham & James were simplistic, and identifications redolent of mid twentieth century. More recent studies by Shi, Waterhouse & McLoughlin (2010) and Waterhouse & Shi (2010) have traced the changes in faunal content and source by evolution and immigration, and responses to climatic change of east Australian Permian invertebrate fossils, with an overview summarized in Fig. 278, p. 346.

PART 2

SYSTEMATIC STUDIES

INTRODUCTION

Collections

This study is based on assemblages of collections made by students and staff from the Department of Geology and Mineralogy, University of Queensland, between the years of approximately 1925 and 1985. Most of the collections were allocated a serial number with prefix UQL, but some collections were limited to a stratigraphic bed or brief interval, whereas others more wide-ranging. Localities such as UQL 3127 covered a range of beds, under a strategy that prevailed during the 1960's under which specimens were sought and aggregated from an entire formation, so that good specimens are available, from a mix of *Svalbardia armstrongi* Subzone and *Taeniothaerus subquadratus* Zone, or ranging from the base through the middle of the formation. The collections most reliably located in a stratigraphic sense are the suites collected by K. S. W. Campbell and G. Tweedale (UQL 1619-1630) and the suite collected by the present writer (UQL 4505-4525). Substantial collections that bracket UQL 2620 to 2631 were also made systematically from the Tiverton Formation by F. W. Whitehouse, but their stratigraphic position is slightly less reliable, with no measurements made from a base-line or top now available in the records. But UQL 2621, 2625, 2626, 2627?, 2628, 2629 came from the *Svalbardia armstrongi* Subzone and UQL 2620, 2630, 2631 came from the *Taeniothaerus subquadratus* Zone. A number of collections were assigned UQF numbers, with limited locality data and no locality number. These are tabulated in the appendix from the records kept at the Queensland Museum and Science Centre Annex at Hendra in Brisbane, where possible: files for the remainder are kept at the museum. Some collections from Homevale, such as LT3 and Cutler Collection, seem to come from several levels. The details for these have not been recorded, although in some instances it is possible to deduce the biozone from the nature of the fossils. Most specimens are preserved as natural internal and external moulds, and the external moulds are readily broken during extraction. Some paleontological studies have focused on internal moulds, but it is believed that the external mould is significant for shape, ornament and dimensions, and it is these that are measured, unless otherwise stated.

Repositories

The collections, including the types, are now housed at the Queensland Museum and Science Centre Annex at Hendra, Brisbane. They are registered serially by number with prefix **UQL**, and many are assigned an **UQF** number. Other Homevale fossils are also stored at the museum, collected for the Geological Survey of Queensland (prefix **GSQ**) and Queensland Museum (prefix **QM**), with prefix F followed by a registration number. A valuable catalogue for Geological Survey of Queensland fossils has been published by Parfrey (1996). Further collections relevant to this study are held in geological museums or repositories at Australia Geoscience, Canberra, and are registered by number **AGSO** or **CPC**, the Australian Museum, Sydney (**AM** – see Fletcher 1971), the Australian National University (**ANU**), the crown research institute GNS at Lower Hutt, New Zealand (prefixes **BR, TM**), Department of Geology, University of Newcastle (**NUF**), since transferred to the Australian Museum, Tasmanian Museum, Hobart (**TMB** – see Crespin 1964a) and **GST**, University of New England (prefix **UNE**), now rehoused mostly at the Australian National University (**ANU**) or Australian Museum, and University of Western Australia (prefix **UWAF**) (see Crespin 1964b). Collections formerly at the Mining Museum, Sydney (**MMF**) and **SUP** (Department of Geology, Sydney University), have been mostly transferred to the Australian Museum. Further afield, specimens with prefix **NHM** refers to specimens kept at the Natural History Museum, London, **CASM E** Sedgwick Museum, Cambridge, England, **PIN**, Paleontological Institute, Moscow, and **USNM** refers to Smithsonian Institution, Washington D.C. Other specimens and localities are explained in the text.

A particular problem centres on the material recorded in the monograph by Briggs (1998). Many University of Queensland specimens were improperly allocated an AMF number, implying that they are now housed at the Australian Museum, Sydney. But that is not the case: they were said to have been left at the University of New South Wales. The same treatment has been meted out to genuine AM material, which also has not been returned. By great good fortune, Dr Peter Jell retrieved some of the material from Briggs for the Queensland Museum. The remainder has not been accessible, and I am informed that it is definitely not in the Department of Geology at the University of New South

Wales, and its whereabouts is a matter for conjecture. Fortunately in most cases topotypes have been available in various collections, especially at Queensland Museum and Australian Museum, and the type material of species not erected by Briggs (1998) remains intact.

Morphological terms

In describing aspects of micro-ornament, use is made of terms newly or recently proposed. These are as follows for BRACHIOPODA:

Barchan spines: small low spines formed by a ramp that increases anteriorly in height, raised at anterior terminus and stopping abruptly at posterior end of groove or globon (qv). The anterior face is extended laterally each side of the globon or surface groove as a low ridge, so that overall the spine is shaped like a barchan. Barchans are isolated mounds of sand forming dunes of crescentic form, and the horns of the crescent extend forward in advance of the main body (Cotton 1945, p. 269). Found in Notospiriferidae.

Connector plate: a plate that lies between the dental plates and adminicula in Syringothyridina, rather than between the dental tracks rimming the delthyrium, spanning the delthyrial gap and placed ventral to delthyrial cover.

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

Mesopunctae: hollow pores in the middle of the shell in some Notospiriferidae, extending to surface.

Myosepta: a pair of low septa in the posterior of the ventral valve, dividing adductor from diductor impressions. Found in *Syrella* Archbold (Waterhouse & Chen 2007).

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

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

Syrellum: a calcite rod at the posterior end of the ventral adductor platform, developed in some Syringothyridina, and described by Archbold (1996).

Tabellae: (plural) – name for the plates supporting crural plates in the dorsal valve. Also called dorsal adminicula or crural plates (inaccurately) through parts of the Treatise on Invertebrate Paleontology.

BIVALVIA: See Waterhouse (2001, p. 115, text-fig. 9; 2008a, pp. 9, 10, text-fig. 2).

Auricle: the anterior extension of the valve like a wing, above a byssal notch, and containing the ligament on the inner side, in pteriomorph bivalves.

Canalivincular ligament: ligament long and narrow, as in *Mytilus*.

Ear: the slender anterior portion of shell above a byssal notch, without ligament on inner side.

Lativincular ligament: a ligament with very broad resilifer.

Lineavincular ligament: ligament slender or broad, and long, may have grooves and ridges, no resilifer.

Platyvincular ligament: a ligament that is planar and broad, without perceptible resilifer, as in *Maitaia*.

Pseudotrabeculae: ridges of shell material forming an inverted V with crest below the umbo in shell that bears ligament as in some Deltopectinidae and Cyrtorostridae. Possibly developed within a flat broad resilifer.

Replivincular ligament: A ligament area with mutiple small resilifers vertical to commissure, as in *Inoceramus* or some *Claraia*.

Truncavincular ligament: found rarely in Monotidina such as *Eurydesma*, where the resilifer lies at the anterior end of the ligament. See Runnegar (1970, pl. 13, fig. 1).

Wing: the slender and often differently ornamented portion of shell along the hinge posterior to the umbo in pteriomorph bivalves, usually bearing ligament on inner side.

Abbreviations

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

In the synonymy: use of square brackets [….] enclose the conclusion that the attribution of species and author was incorrect.

Species variation

The species described in this study show considerable variation, more than appears to be the case for species described by Cooper and Grant in their great series on Permian brachiopods from west Texas, at least to judge from their text and illustrations (see Cooper & Grant 1972-1976b herein). The detail of this variation is presented in the description of Homevale species, with special attention to variation in shape, and in plication and other details of ornament. On available evidence, the variation is infrasubspecific, and implies that biota in high southerly latitudes of the Permian world were more variable than in the paleotropics (see Waterhouse 2010b).

Ordinal classification

In this study, the author of each ordinal category is deemed to be the first author who validly proposed an ordinal category at any rank, the system following that applied to family group names. The principles are discussed in Waterhouse (2010a, p. 6, 2013). Brachiopod orders are allocated to superorders, following the natural affiliations within the phylum, as discussed in Waterhouse (2010a, 2013). Productida were the subject of a monograph by Waterhouse (2013) in which all known genera were classified and many illustrated and discussed, and Spiriferida are to be monographed by Waterhouse (in prep.), these two studies building on the lengthy and detailed treatment provided in the international Treatise on Invertebrate Palaontology.

SYSTEMATIC DESCRIPTIONS

Phylum COELENTERATA Frey & Lenckart, 1847

Class SCYPHOZOA Gotte, 1887

Subclass CONULATA Moore & Harrington, 1956

Order CONULARIIDA Miller & Gurley, 1896

Superfamily **CONULARIOIDEA** Walcott, 1886

Family **CONULARIIDAE** Walcott, 1886

Conulariid gen. & sp. indet.

Fig. 6

Material: A fragment from UQL 2626. *Svalbardia armstrongi* Subzone.

Description: The fragment represents the face of a conulariid, 20mm wide and crossed by fine ribs, 10-12 in 5mm, with broad crests, steep sides and almost flat-floored slightly narrower interspaces. The ribs are slightly irregular, with intercalated ribs especially on the outer edge of one side, and at the centre on the other, and the face is divided by a vertical somewhat irregular depression with median angular groove. A row of small tubercles lies over each costa.

Fig. 6. Conulariid, external fragment of face of UQF 81850 from UQL 2626, x4.

Resemblances: The lack of any information about the corner grooves prevents even generic determination. The ribbing is finer than on many of the species described from the Permian of east Australia by Thomas (1969) and New Zealand by Waterhouse (1979b), or the southeast Bowen Basin by Waterhouse (1986a), and the only form with comparably fine ribs amongst the species described from Tasmania by Parfrey (1982) is an Ordovician genus *Tasmanoconularia* Parfrey, with a single row of tubercles along each rib. A specimen described as *Conularia crenulata* Fletcher (1938, p. 252, pl. 26, fig. 15) from the “Lower Marine” rocks or Dalwood Group of the Sydney Basin has moderately fine ribs, 14 in 10mm, and described by Fletcher as crenulate, referring to weak angular arches or zig-zags in the course of the ribs. Such crenulations are not visible in the Tiverton species. Fine tubercles are developed over the ribs, but are coarser than seen on the Tiverton fragment. Some Triassic forms from New Zealand do have fine ribs, but they have narrower faces and lack tubercles.

Phylum BRACHIOPODA Duméril, 1806

Classification: The Treatise series of six volumes has established a detailed and comprehensive classification of the phylum Brachiopod that offered no assessment of a different classification, with recognition of several subclasses within Articulata Huxley by Afanasieva & Dagys (1989) and Grunt (2006a). In Waterhouse (2010a, 2013, in prep.), certain orders are assembled into superorders, and some Productida and Spiriferida are divided into infrasuborders.

Subphyllum RHYNCHONELLIFORMEA Williams et al. 1996

Class STROPHOMENATA Williams et al. 1996

Superorder STROPHOMENIFORMII Őpik, 1934

This superorder (nom. transl. Waterhouse 2010a, p. 8 ex suborder Strophomenoidea Őpik, 1934, p. 75) includes Strophomenida and Triplesiida, for which nomenclatural background and critical aspects of morphology were discussed in the 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 Treatise volumes of 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. 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 (2010a, p. 9).

Suborder ORTHOTETIDINA Cooper & Grant, 1974

Williams & Brunton (2000, p. 644) referred to Order Orthotetida Waagen, 1884, but Waagen neither proposed 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.

Superfamily **ORTHOTETOIDEA** Waagen, 1884

Family **SCHUCHERTELLIDAE** Williams, 1953

Subfamily **STREPTORHYNCHINAE** 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.

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.

The 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, but nevertheless their version must be judged as far better than others available in western studies. 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, but 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. That is not always done for morphologies of other phyla.

Genus ***Notostrophia*** Waterhouse, 1973

Type species*: Notostrophia homeri* Waterhouse, 1973, p. 36 from Brunel Formation, Takitimu Group (Artinskian), New Zealand, OD.

Diagnosis: Non-plicate non-auriculate shells with ventral costae finer as a rule than those of dorsal valve, ventral valve may be reflexed anteriorly. Node each side of cardinal process formed by low ridge continuing across outer face of process from brachial ridge.

Notostrophia laticostata n. sp.

Fig. 7 - 9

Derivation: lati – broad; costa – rib, Lat.

Holotype: Specimen UQF 54551 from UQL 1352, Tiverton Formation, figured herein as Fig. 8C, here designated.

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

Material: Specimens from UQL 1352, 1625, 1626, 2628, 3127, 4514, 4518 and 4519; UQF 21375. *Taeniothaerus subquadratus* Zone.

Dimensions in mm: ventral valve

UQF	UQL	Width	Length	Height
81299	4518	37	35.5	?14
Dorsal valve				
81301	4519	32	20	8
21375	1626	40	32	11

Fig. 7. *Notostrophia laticostata* n. sp. latex cast of ventral valve UQF 81448 from UQL 3127, x1.5.

Description: 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, perideltidium broad, flat or gently convex, separated by groove from pseudodeltidium which is also broad and convex, both share low growth steps parallel to commissure and fine impersistent vertical striae. Ventral valve gently and broadly convex, lacking sulcus, fold or plicae, surface marked by fine low close-set costae, 13-14 in 5mm at 35mm from umbo; anterior two thirds of shell bears some seven low commarginal wrinkles and growth pauses. Dorsal valve convex with shallow anterior sulcus, up

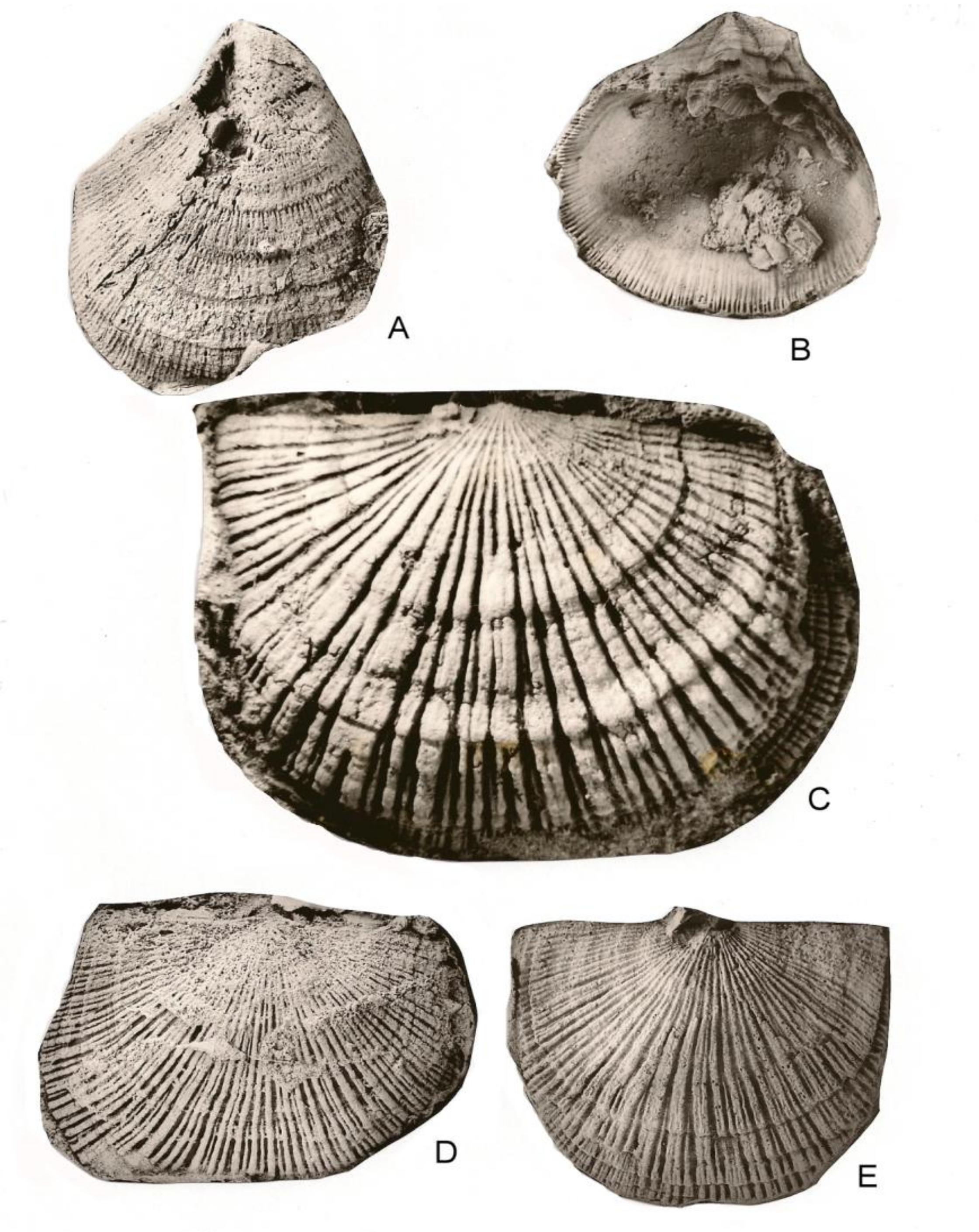


Fig. 8. *Notostrophia laticosta* n. sp. A, latex cast of ventral valve UQF 21057 from UQL 1625, x1.5. B, aspect of latex cast of ventral valve UQF 81299 from UQL 4118, x2. C, holotype, latex cast of dorsal exterior, UQF 54551 from UQL 1352, x2.5. D. latex cast of dorsal exterior UQF 21076 from UQL 1626, x2. E, latex cast of dorsal exterior UQF 43478 from UQL 4514, x1.5.

to third of width of shell, hinge wide and cardinal extremities measuring 100-115°, bluntly angular or gently rounded, interarea low and vertical to commissure, notothyrium obscure. 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.

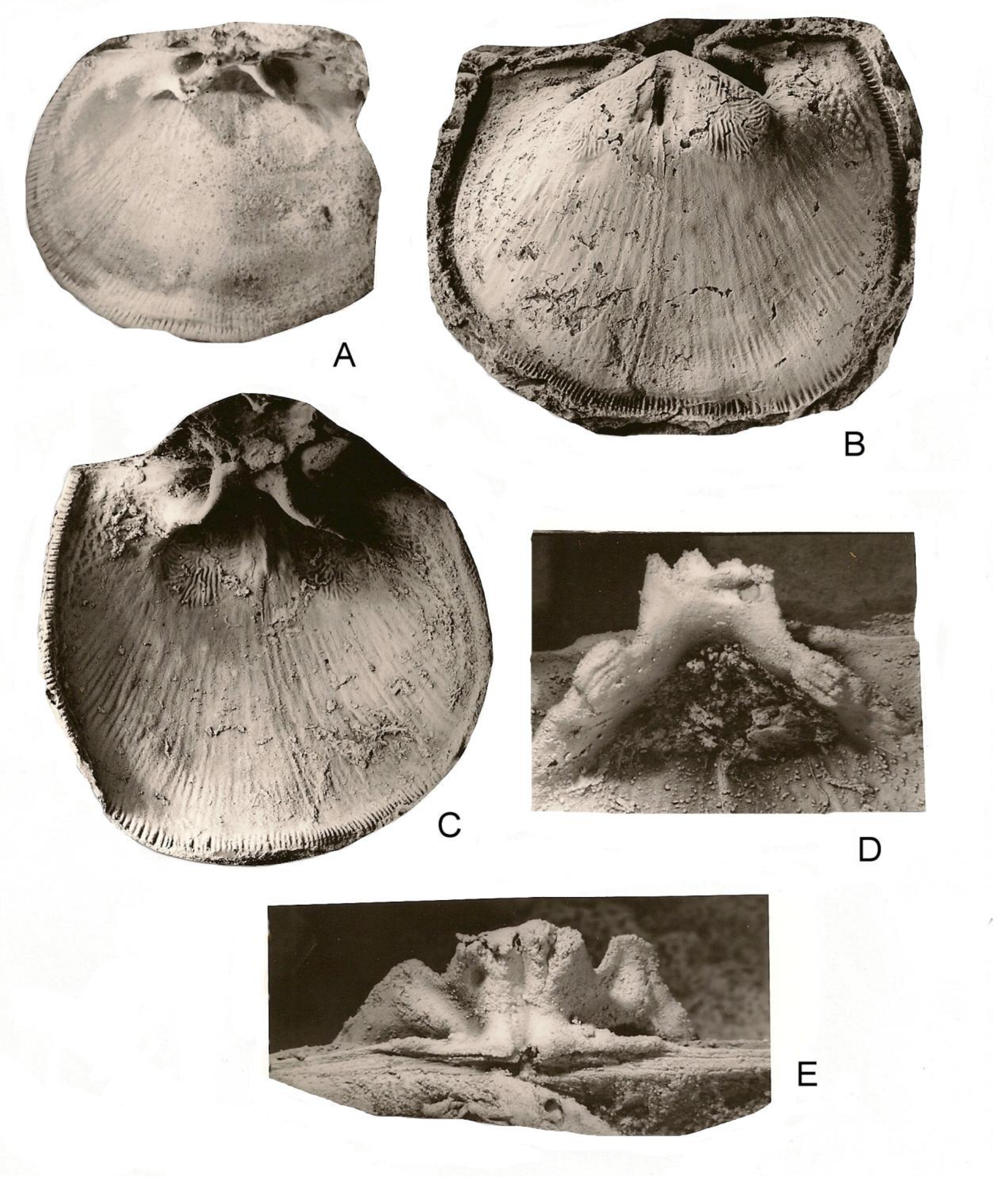


Fig. 9. *Notostrophia laticostata* n. sp. A, latex cast of dorsal interior UQF 81301 from UQL 4519, x2. D, E, detail of cardinal process, internal (ventral) and dorsal aspects, same specimen, x5. B, C, dorsal internal mould and latex cast of UQF 21375, x2.

Ventral interior without dental supports, and 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) but unlike the socket plates of various brachiopods, extend well in front of the dental sockets, and constituted 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), and in their appearance and function, justify the Cooper-Grant name of erismata. Low anterior nodes lie at base of exterior process. 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**.**

Resemblances: This species is characterized by its broad dorsal ribs that may be clustered into mutiples and by lack of reflexed ventral anterior. *Notostrophia bifurcata* Waterhouse (1986a, p. 20, pl. 2, fig. 9-19) from the Fairyland and Dresden Formations of the southeast Bowen Basin is a smaller more elongate species with very fine ventral ribs and dorsal ribs that are broad-crested, but not as broad or as differentiated as those of the new species, to which it was probably ancestral. *N. alta* Waterhouse (1986a, p. 20, pl. 2, fig. 20-24) from Rose's Pride Formation of the southeast Bowen Basin is a very elongate shell with high ventral interarea and very fine ventral ribs and strong dorsal ribs, not as broad as those of the new species, and likely to have been a contemporary of the two New Zealand species *zealandicus* and *homeri*. *N. zealandicus* Waterhouse (1982a) from the Brunel Formation, Takitimu Group, of south New Zealand, has a more inflated and transverse dorsal valve with higher and narrower costae, and the slightly younger species *N. homeri* Waterhouse (1973, 1982a) from overlying beds and also recorded from the Mantle Volcanics by Begg & Ballard (1991) has a less inflated dorsal valve, with strong narrow costae: internal details are close to those of the present species. The two New Zealand species come from the *Ingelarella plica* Zone, and are younger than the Tiverton species (Waterhouse 2002a, p. 193).

Following a number of species in the *Ingelarella plica* Zone, the genus seems to have disappeared from the fossil record in both east Australia and New Zealand.

Superorder PRODUCTIFORMII Waagen, 1883

In this category are grouped spinose (or secondarily non-spinose) strophomenatans Chonetida and Productida, sub-divided into Productidina, Strophalosiidina, Linoproductidina and Oldhaminidina (= Lyttoniidina), as explained by Waterhouse (2010a, p. 9; 2013).

Order CHONETIDA Muir-Wood, 1962

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

Suborder CHONETIDINA Muir-Wood, 1962

Superfamily **CHONETOIDEA** Bronn, 1862

Family **RUGOSOCHONETIDAE** Muir-Wood, 1962

Subfamily **SVALBARDIINAE** Archbold, 1982b

Genus ***Svalbardia*** Barchatova, 1970

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

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 scars 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.

Discussion: A chonetid common at one stratigraphic level in the Tiverton Formation has been identified with *Lissochonetes yarrolensis* Maxwell, 1964, p. 35 from the Yarrol Basin in central Queensland. Maxwell's species was made type of the genus *Tivertonia* Archbold (1983b, p. 71), and the definition and description of *Tivertonia* was based substantially on the Tiverton Formation material, rather than the types from the Yarrol Basin. Analysis of the genus by Rachebouef (2000, p. 420) does not provide categoric differences between *Tivertonia* and several allied genera of seniority, and incorrectly stated that the maximum width lay in front of the hinge in immature individuals of *Tivertonia*. This is denied by his own figure (Racheboeuf 2000, Fig. 275.1a) which clearly shows a specimen at an early growth stage with maximum width at the hinge. Shi & Waterhouse (1991) were not able to find quantitative differences from three other genera (*Lissochonetes, Komiella* and *Leurosina*), but they stressed that this underlined the need for further characters in *Tivertonia* to be evaluated. N. W. Archbold elaborated his diagnosis in Waterhouse (1986a, p. 22), to note differences from *Leurosina* Cooper & Grant, 1975. Later it was pointed out that *Tivertonia* approached *Capillonia* Waterhouse, 1973 in general shape and internal attributes (Waterhouse 2001, p. 14). This suggestion is reinforced to some extent by re-examination of the types of *yarrolensis*. Most of the figured type specimens (Maxwell 1964, pl. 6, fig. 9, 11, 13, 14), including the holotype of *yarrolensis*, belong to Rugosochonetidae Muir-Wood, 1962. Two of the ventral valves in this suite (Maxwell 1964, pl. 6, fig. 13, 14) show a well formed ventral sulcus, deeper than seen in Tiverton material, or in the specimen shown in Maxwell (1964, pl. 6, fig. 11), and Yarrol material kept at the Queensland Museum confirms that a well formed sulcus is typical of the species. The holotype is a dorsal valve, which appears to have a low narrow fold. Internally, the dorsal septum, although described as short, is long (Maxwell 1964, pl. 6, fig. 9), and the ventral median septum is short, somewhat as in *Capillonia* Waterhouse. One figured ventral valve shows a ring of strong pustules close to the shell margin. In several respects, the species *yarrolensis* appears close to *Capillonia*, although certainty is lacking because of incomplete preservation, which obscures true shape and aspects of the interior, and does not show the exterior in fine detail, leaving the nature of the micro-ornament obscure. The type species of *Capillonia, Lissochonetes brevisulcus* Waterhouse, 1964a*,* is widest at the hinge in a half-moon shape with concave dorsal valve, and was said to be distinguished by its apparent very faint dorsal capillae, as well as aspects of internal septa and pustules, including a band of strong pustules in the anterior ventral valve. The external preservation of *yarrolensis* is too poor to show if capillae were present, but other features come close to those of *Capillonia*, and on available evidence, *Tivertonia* is possibly a junior synonym of *Capillonia,* although the ventral median septum is a little longer*. Lissochonetes semicircularis* Campbell, 1953, and *L. semicircularis solida* Dear, 1971 from mid-Permian of the Bowen Basin in Queensland are also regarded as belonging to *Capillonia*, following Parfrey (1988) and Waterhouse (1986a, 2001), and have a short ventral septum and similar shape, but the ventral band of pustules is diffuse and close to that of the Tiverton species.

Other specimens assigned to *yarrolensis* by Maxwell (1964, pl. 6, fig. 10, 12) have a highly arched non-sulcate ventral valve, and external ornament of fine ribs. They are deemed to belong to the Anopliidae Muir-Wood, 1962, but require further material for generic identification.

The large suite of Homevale material differs internally from *Capillonia* in that the ventral median septum is generally long, the two parallel vascular trunk ridges are longer and less well defined, and the anterior band of papillae over the floor of the ventral valve is more diffuse, succeeded laterally and anteriorly by a band of fine pustules. The dorsal valve of the Tiverton species is less concave and internally the anderidia between the adductor scars of the Homevale material are more prominent and may be prolonged into the brachial shields. The dorsal median septum is longer, and the pustules between the brachial shields more distinctive than in *Capillonia*.

The genus that the Homevale material most closely approaches is *Svalbardia* Barchatova, 1970, named for *Chonetes capitolinus* Toula, 1875 from the Spirifer Limestone and Brachiopod Chert of Spitsbergen. The Spirifer Limestone is now termed the Vøringen Member and judged to be late Artinskian on conodont evidence (Shen et al. 2005). The overlying Brachiopod Chert, now the Svenskegga Member followed by Hovtinden Member, has been variously dated as early Guadalupian to Lopingian in age, as summarized by Shen et al. (2005). The lectotype of *Svalbardia*, with source beds still not exactly known, was nominated by Gobbett (1964, p. 121) as that figured by Toula (1875, pl. 8, fig. 9a), kept at the Naturhistorisches Museum, Vienna, and refigured by Gobbett (1964, pl. 15, fig. 11) – not pl. 27 as stated in his text. This species has a smooth shell, just as in Homevale specimens and is of subrectangular shape. The dorsal valve tends to be flat, or weakly geniculate anteriorly, as in only some of the Queensland specimens, and the maximum width tends to lie near mid-length, as in specimens of so-called *yarrolensis* described from the Farley Formation by Archbold (1986b). The type material of *Svalbardia* examined in Toula (1875) requires clarification of internal detail, and is to a general and generic degree close to the Homevale material, and the specimen shown by Gobbett (1964, pl. 15, fig. 13) shows only a short dorsal septum and short diverging anderidia. The ventral septum was not figured by Gobbett (1964). But Ifanova (1972, pl. 2, fig. 33-35) illustrated a long median septum in each valve for shells of similar shape and ornament from the Petchora Basin, northwest Russia, in the Talatin and Yarchyargin Suites. There is no ventral marginal ring of strong pustules, but an anterior row of sturdy pustules is developed in the dorsal valve, together with a long septum. No significant difference of generic rank can be discerned between shells ascribed to *Svalbardia capitolinus* and the specimens from the Tiverton Formation. Archbold (1981a, p. 3) restricted *Svalbardia* to species with recurved anterior portion of the brachial ridges being raised in mature individuals, a feature also displayed by Farley and Tiverton chonetid specimens.

Svalbardia armstrongi n. sp

Fig. 10 - 18

1892 *Chonetes* sp. ind. (d) Etheridge, p. 264, pl. 37, fig. 19.

1964b *Lissochonetes* sp. Hill & Woods, p. 8, pl. 4, fig. 4.

1972 *L. australis* Maxwell – Hill, Playford & Woods, p. 8, pl. 4, fig. 4.

1983 *L. yarrolensis* [not Maxwell] – Waterhouse, Briggs & Parfrey, p. 126, pl. 1, fig. 1-3.

1983b *Tivertonia yarrolensis* – Archbold, p. 71, pl. 2, fig. A-P.

Derivation: Named for J. D. Armstrong.

Holotype: UQF 81627 from UQL 4515, figured herein as Fig. 12A, B, Fig. 14A from Tiverton Formation, here designated.

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.

Material: Many specimens available as ventral and dorsal valves and specimens with valves conjoined, from localities UQL 1347, 1415, 1622, 1623, 1624, 2623, 2625, 2626, 2628, 2629, 3127, 4512-4515 and LT3. *Svalbardia armstrongi* Subzone.

Fig. 10. *Svalbardia armstrongi* n. sp. UQF 81379 from UQL 4515, x6.

Description: The species has been described chiefly by Archbold (1983b). 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 (1986b) claimed that the hinge spines were short, but a specimen at early maturity has spines 8mm long, which is not unduely short. One ventral valve shows taleolae or possible spine bases regularly disposed over the worn surface. 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 from UQL 2626 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. The adductor scars vary from subquadrate to elongate in shape, and pustules are numerous and fine with an anterior band of more prominent pustules. 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 anderidia are well developed in mature specimens, and may pass forward into broad ridges leading into the brachial shields, but are short in most specimens and diverge in some, as figured by Archbold (1983b, Fig. 2E cs. 2D, F). Pustules and patterns vary throughout ontogenetic development, and are fine and crowded, forming a band near the anterior margin.

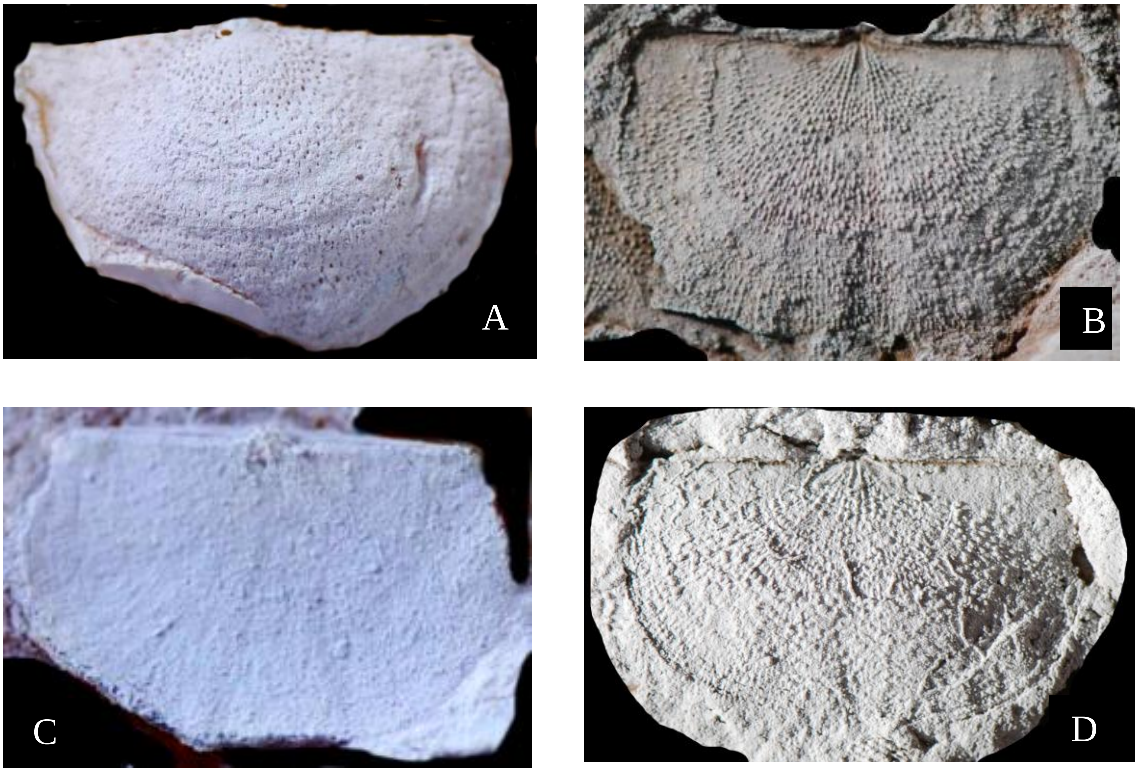


Fig. 11. *Svalbardia armstrongi* n. sp. A, latex cast of ventral exterior, UQF 20881 from UQL 1622, x3.5. B, dorsal external mould, anterior tilted view UQF 81626 from UQL 4514, x4. C, latex cast of dorsal exterior UQF 81279 from UQL 4515, x5. D, dorsal external mould UQF 81812 from UQL 4514, x 3.5.

Resemblances: The species characterizes a particular level 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 deeper ventral sulcus, short ventral septum and different vascular pustules, possibly but not certainly belonging to *Capillonia* Waterhouse, rather than *Svalbardia*. Etheridge (1892) figured a ventral valve UQF 1486 from the Tiverton Formation of the Mt Britton Goldfield: another Tiverton taxon *Bookeria drysdalei* n. sp. is present on the same rock sample (p. 126).

Occurrences were also noted in the Sydney Basin by Waterhouse (1970b, p. 389) and Waterhouse et al. (1983), as confirmed and illustrated by Archbold (1986b). 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 1986b, Fig. 1L), and long but variable ventral median septum and long dorsal median septum, and because of these differences, the Farley material is herein separated as a different species (see below).

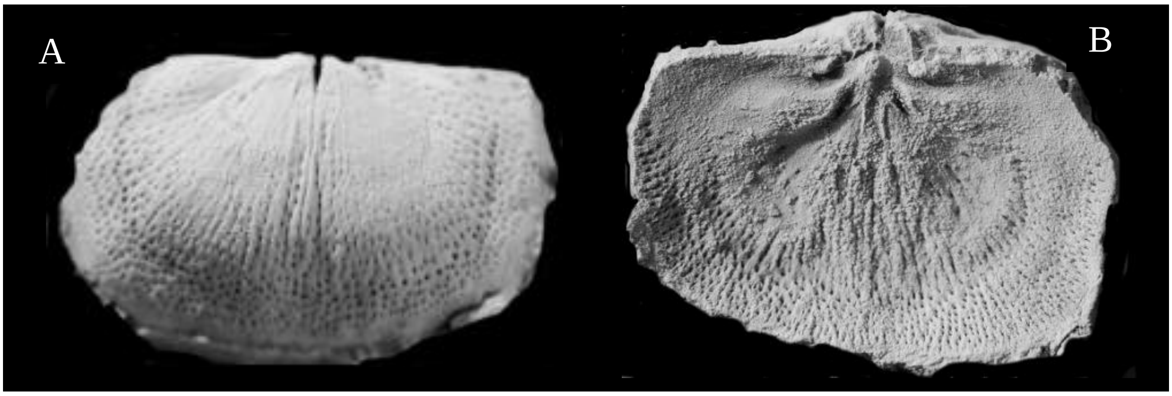


Fig. 12. *Svalbardia armstrongi* n. sp., holotype, ventral and dorsal views of internal mould UQF 81627 from UQL 4515, x3.5. See also Fig. 14A.

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 are now identified as *Capillonia brevisulcus* (Waterhouse) in Waterhouse (2014). Begg & Ballard (1991, p. 146, Fig. 4) compared specimens from the Mantle Volcanics of the Skippers Range, New Zealand, to *yarrolensis* Maxwell, but their figured dorsal valve shows a short dorsal septum, unlike that of *yarrolensis,* and the comparison must be set aside.

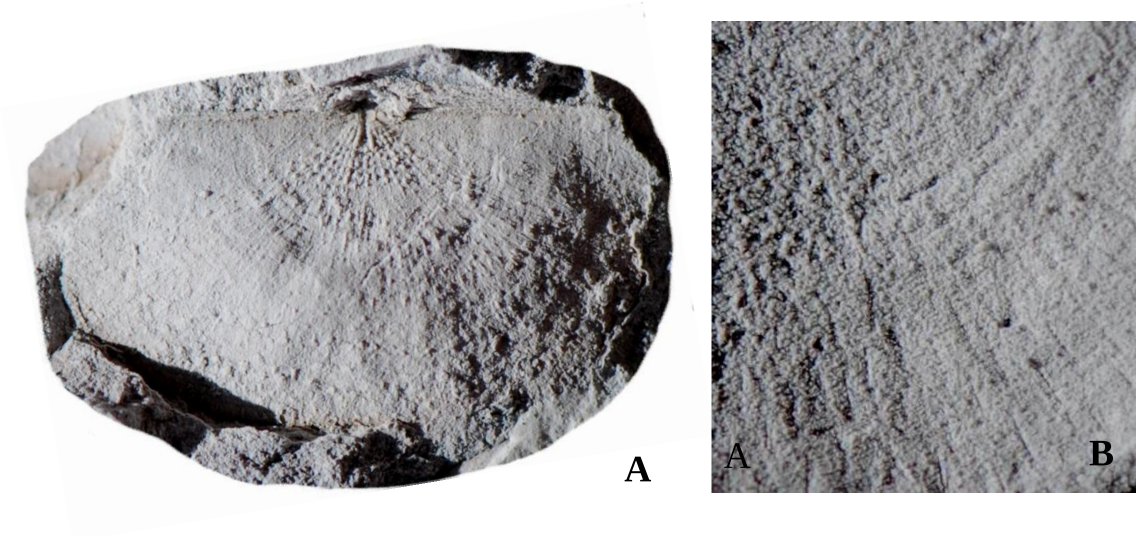


Fig. 13. *Svalbardia armstrongi* n. sp. A, external mould of principally dorsal valve, partly worn, but suggesting smooth surface without ribs posteriorly, UQF 81187 from UQL 4515, x3. B, external mould of ventral valve UQF 81408 from UQL 4514, showing matrix cores to top left, as possible hollowed out cores of taleolae, and to lower right, slender longitudinal depressions possibly representing low ridges formed by spines. The surface in this area is also crossed by fine commarginal growth-lines, suggesting true exterior is preserved. Specimen x 10.

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*.

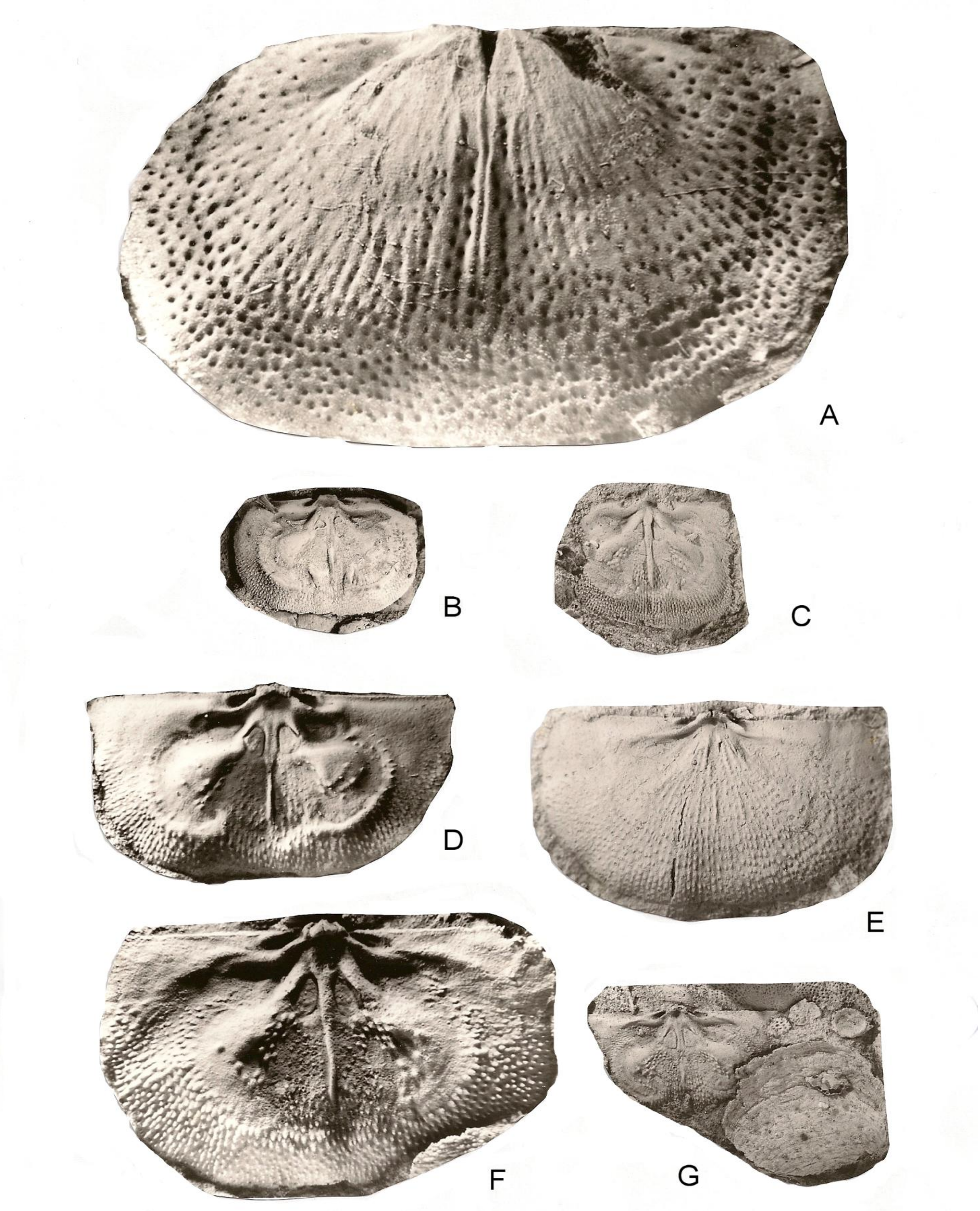


Fig. 14. *Svalbardia armstrongi* n. sp. A, holotype, ventral internal mould UQF 81627 from UQL 4515, x6. B, latex cast of dorsal interior, near UQF 20871 from UQL 1622, x1.6. C, latex dorsal internal mould UQF 81181 from UQL 3127, x1.5. D, latex cast of dorsal interior, UQF 21000 from UQL 1624, x3. E, latex cast of immature dorsal interior, UQF 81183 from UQL 4514, x3. F, latex cast of dorsal interior, UQF 20913 from UQL 1622, x3. G, latex dorsal internal cast UQF 81182 from UQL 3127 with part of dorsal cast of *Echinalosia cenula* n. sp., x1.5.

Moderately well preserved shells described as *Svalbardia thomasi* Archbold, 1981a from the Nalbia and Baker Formations of the Carnarvon Basin, Western Australia, are particularly close to the Homevale form, and have lamellar growth lamellae and maximum width at mid-length. The ventral hinge spines were described as only 1mm long, but it is not clear if the full length has been preserved. The ventral septum is long, the dorsal septum slightly shorter and dorsal pustules fine. The dorsal lateral ridges pass into the cardinal process, but are shorter than in some of the Queensland specimens. A very shallow alveolus may be developed. The species is like *Svalbardia* in shape, but lacks strong anterior dorsal pustules. Apparent spines lie in quincunx over one figured ventral valve, marking an unusual development which requires further assessment.

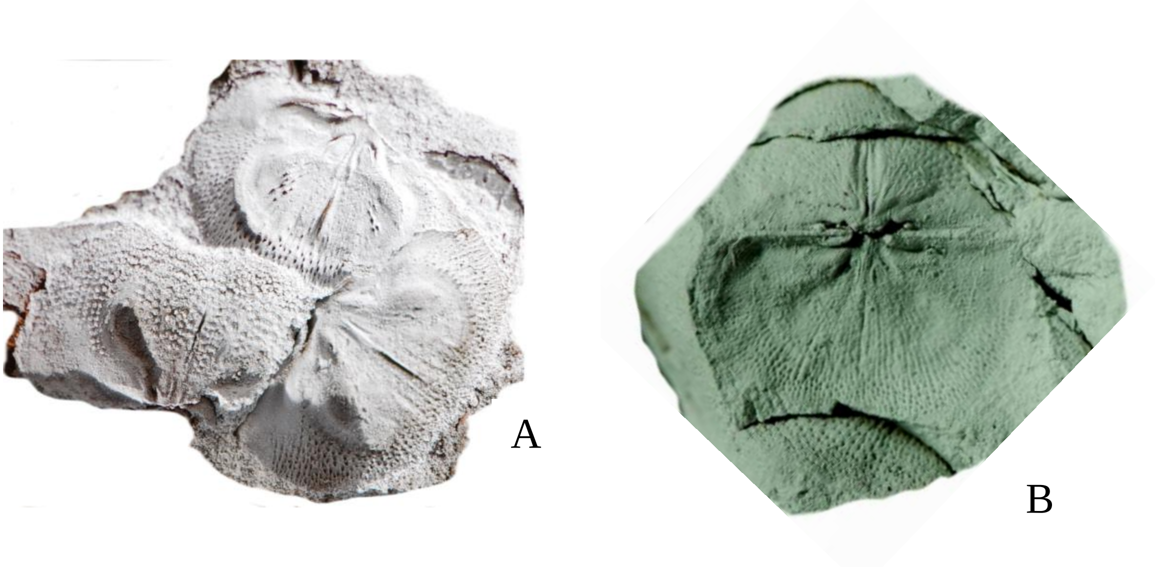


Fig. 15. *Svalbardia armstrongi* n. sp. A, internal moulds of dorsal valves UQF 81376 and UQF 81377 from UQL 4515, x3. B, internal mould of dorsal and ventral valve UQF 81184 from UQL 4515, x3.

From the Fairyland Formation of the southeast Bowen Basin, *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 *armstrongi* and the dorsal septum is only moderately long, and strong pustules lie between the brachial shields. Maximum width varies from hinge to mid-length. Type *Capillonia* is also close but has shorter ventral septum and more concave dorsal valve.

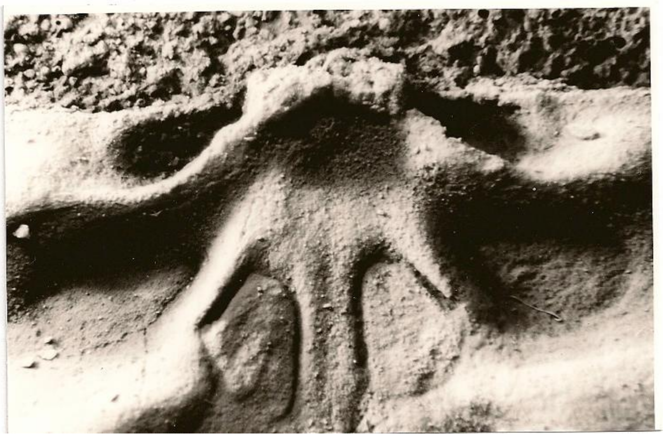


Fig. 16. *Svalbardia armstrongi* n. sp. Dorsal interior of UQF 21000 from UQL 1624, showing anderidia in fully mature specimen, x12.

Chonetes pillahuincensis Harrington (1955) from the lower Bonete Formation of Argentina was reidentified as *Tivertonia* by Pagani (1998, Fig. 2b, c, d), but unlike *Tivertonia* has a well-formed single median ridge along the ventral interior. The species *Lissochonetes jachalensis* Amos, 1961 from the Tupe Formation, San Juan Province, Argentine, was assigned to *Tivertonia* by Cisterna et al. (2002, p. 186), and is generically similar to *armstrongi* rather than *Tivertonia yarrolensis*, belonging to *Svalbardia*. Various other chonetid species, as summarized by Cisterna et al. (2002, p. 189), need to be reassigned – if generically identical with *armstrongi*, they will have to be reallocated to *Svalbardia*. *Tivertonia tatamariensis* Singh & Archbold (1993, p. 58) from the Garu Formation of the eastern Himalaya in the Himalayan foothills differs from *armstrongi* in that the anderidia are not fully developed, at least as far as illustrated, and there is a broad sulcus and fold, suggestive of *Leurosina* Cooper & Grant, 1975. Unlike *Leurosina*, the median septum is short in each valve (Singh & Archbold 1993, Fig. 2C, E, J, L; Singh 1978b, pl. 1, fig. 1).

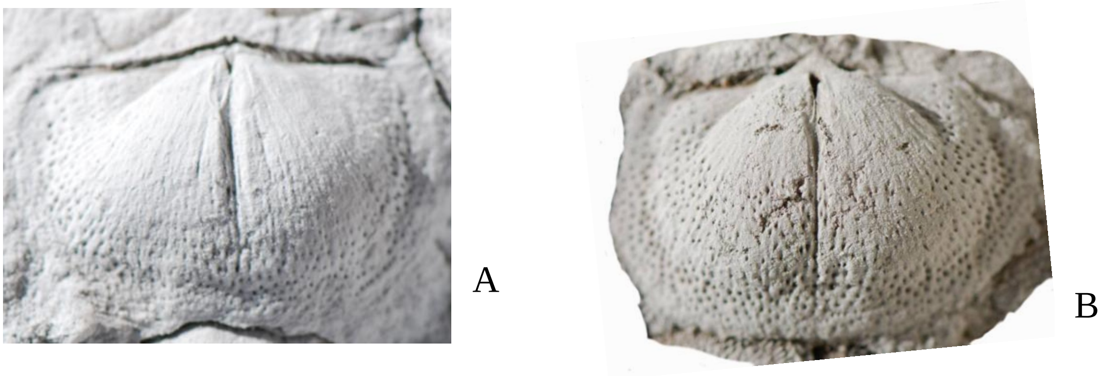


Fig. 17. *Svalbardia armstrongi* n. sp. A, ventral internal mould UQF 81186 from UQL 4515, x3. B, ventral internal mould UQF 20868 from UQL 1622, x4.

Fig. 18. *Svalbardia armstrongi* n. sp., latex preparation from the bedding plane of a slab from UQL 3127, showing dorsal interiors UQF 81181 and 81182, x1.3.

Taxonomy: Hill et al. (1972) referred to *Lissochonetes australis* Maxwell, a mistake as 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.

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

Svalbardia saeptata n. sp.

1986b *Tivertonia yarrolensis* [not Maxwell] – Archbold, p. 413, Fig. 1A-N.

Derivation: saepta – wall, fence, Lat.

Holotype: Specimen MMF 2386A from Farley Formation, New South Wales, figured by Archbold (1986b, Fig. 1F), here designated.

Diagnosis: Median septum of each valve very long, especially that of the dorsal valve.

Description: The material has been described and illustrated by Archbold (1986b).

Discussion: This species is recognized for material from the Farley Formation of the Sydney Basin, because the dorsal septum is especially long, and the septa in both valves are longer than in the Tiverton material. In addition, the maximum width is placed often near mid-length rather than along the hinge, some specimens are sulcate, and there may be fewer spines along the ventral hinge row, although this varies. These differences are substantial enough to suggest specific discrimination from the Tiverton material called *Svalbardia armstrongi* n. sp.

Genus ***Tivertonia*** Archbold, 1983b

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

Diagnosis: Transverse shells, maximum width as rule at hinge, sulcus broad and shallow but well formed, narrow dorsal fold, surface uncertain, appears to be essentially smooth. Ventral median septum high posteriorly, short, 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.

Discussion: This taxon differs from the Tiverton chonetid previously assigned to the species and now described as *Svalbardia armstrongi* through the smaller size, deeper and wider ventral sulcus, and short ventral septum, judged from examination of topotypes UQF 43036-43041, 43158, 68017, 68018, 68020 and other specimens. 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, and includes the species *semicircularis* Campbell and *brevisulcus* Waterhouse. 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.

In summary, available topotype material of *Tivertonia* seems too sparse to rule out synonymy with *Capillonia*.

Order PRODUCTIDA Waagen, 1883

Suborder STROPHALOSIIDINA Waterhouse 1975, 1978a

Discussion: Brunton et al. 1995, p. 931 attributed Strophalosiidina to Waagen (1883, p. 613), an error because Waagen had classed *Strophalosia* as a member genus of Chonetinae. Later Brunton in Brunton et al. (2000, p. 565) claimed that Strophalosiidina was “nom. transl. Brunton, Lazarev & Grant 1995, p. 931 ex Strophalosiinae Schuchert, 1913a, p. 391”. This statement was clearly incorrect, but was made probably in response to it being pointed out to Howard Brunton (J. B. W. in litt.) that Waagen had not even allocated family rank to *Strophalosia* and allies, and that Waterhouse had named the suborder. Schuchert (1893, 1913) proposed Strophalosiinae as a subfamily, placed within Family Product-

-idae. He took good care to arrange his groupings in family and ordinal groups, and the claim that he nominated an ordinal group for strophalosiids is a misrepresentation at best, if not patronising. In the last volume of the brachiopod Treatise series, Brunton (2007) corrected a number of the errors in Brunton et al. (2000), but made no further contribution to the authorship of Strophalosiidina. By contrast, Archbold & Simanuskas (2001, p. 29), Shen et al. (2003, p. 67) and Grunt (2006a, p. 132) have not accepted Schuchert as author. The most serious implication of the stance by Brunton et al. (2000) is that it threatens to destabilise ordinal nomenclature and authorship. If authors feel at liberty to set aside a rule-conforming proposal in favour of an author who earlier had named a family-group member in the same ordinal grouping, and subsequently insist with all the power of an principal author and editor on that step, taxonomy at ordinal level will never become consolidated and will always under threat of change.

Superfamily **STROPHALOSIOIDEA** Schuchert, 1913

Family **DASYALOSIIDAE** Brunton, 1966

Subfamily **ECHINALOSIINAE** Waterhouse, 2001

Diagnosis: Genera distinguished by having spines of one series on dorsal valve. Ventral valve usually has spines of one or two series, generally one erect and the other recumbent. Fine commarginal lamellae developed on dorsal valve, radial capillae generally faint or usually absent. Ventral attachment scar, teeth and sockets, interareas, dorsal median septum and muscle scars as in the family.

Tribe **ECHINALOSIINI** Waterhouse, 2001

Diagnosis: Ventral spines of two series. Dorsal valve not thickened anteriorly.

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

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

Diagnosis: Spines of two series interspersed over ventral valve, simple, not normally sinuous or arranged in special rows or aggregated to form lateral brush, usually present but may be few or missing over ventral ears; spine cores over middle valve may extend well forward from spine base. Dorsal spines fine and erect. Capillae present or absent, commarginal ornament subdued or absent.

Discussion: *Echinalosia* is one of the more important genera used to arrange the Permian faunas of east Australia into biozones, a concept initiated through a pioneering study by Maxwell (1954), and first enunciated as a table by Runnegar & McClung (1975). A number of species have been recognized, particularly by Briggs (1998).

Three subgenera were recognized in Waterhouse (2010a), but some reservations apply to the practise, because on the whole, the Treatise on Brachiopoda acknowledged few subgenera, and in their great survey of Permian Brachiopoda from the Glass Mountains of Texas, Cooper & Grant (1969-1976b) recognized none. This is understandable: apart from the uncertainty that must pertain to subgeneric as opposed to generic standing, the usage of generic and subgeneric categories is not convenient for discussion of faunas and biostratigraphy. On the other hand, subgenera may express views on interrelationships between species and clusters of species. Mention will be made of close alliances, but few are relevant to the present study. *Glabauria* Waterhouse*,* type species *Echinalosia runnegari* Briggs, 1998, is characterized by having ears largely to entirely devoid of spines on the ventral valve (Waterhouse 2010a). *Capillaria* Waterhouse, 2001, type species *Strophalosia preovalis* var. *warwicki* Maxwell, 1954, p. 543 from Wallaby Formation (Sakmarian), south Queensland, is also close to *Echinalosia* (Waterhouse 2010a). *Echinalosia* has less developed row of hinge spines, rarely has strong postero-lateral spines, and the dorsal valve is feebly capillate or not capillate. The type species of *Capillaria* has a ventral spine pattern which differs from that of type *Echinalosia*, in so far as spines are somewhat irregularly distributed over the mature shell, and are dominated by sturdy suberect spines, with few prostrate spines. By contrast, the ventral valve of species in *Echinalosia* sensu stricto displays an ornament in which prostrate and variously recumbent to more rarely erect strong spines are distributed fairly evenly across the valve, rarely with strong postero-lateral spines, and no clearly developed hinge row as a rule. The dorsal valve of type *Echinalosia* is dominated by fine erect spines and somewhat ragged growth laminae, with few if any dimples, before becoming rather smooth through wear later in ontogeny. Several species previously assigned to *Echinalosia* show a pattern of ventral spines similar to that of *warwicki*, though without a prominent hinge row, and differ in that regard from the more regular spine array of semirecumbent spines and scattered prostrate spines in type *Echinalosia*. The dorsal valve in these species has fine growth laminae, generally few erect spines though such may rarely be numerous, and regularly dispersed dimples, approaching those of type *Capillaria*, but they show only faint or discontinuous dorsal capillae. Provisionally, these species are allocated to *Echinalosia*. The species include those described as *Echinalosia curtosa* Waterhouse, and *E. dejecta* Waterhouse, together with a new species *E*. *cenula*. Most are of Sakmarian – early Artinskian age. Species with capillate dorsal valve are so far limited to forms in the upper Wallaby rocks near Warwick and the Farley Formation of north Sydney Basin (UQF 75202), with an occurrence in the Macleay Series of northern New South Wales. Other occurrences were reported by Briggs (1998) and have yet to be verified: a few have had to be discounted (Waterhouse 2001).

One aspect that requires further study is the nature and length of the spine cores in front of the spine base over the middle ventral valve. These are shown to be very long in the type species of *Echinalosia*, as illustrated in Waterhouse (2010a, Fig. 17, 18). Spine cores are not so well preserved or obvious in some other species, and are short in a few ventral valves of *Echinalosia cenula* n. sp., which may prove to indicate a significant difference.

Echinalosia curtosa sulcata n. subsp.

Fig. 19 – 21

1983 *Strophalosia* cf. *subcircularis* [not Clarke] – Waterhouse et al., p. 126, pl. 1, fig. 4, 5.

Holotype: UQF 81260 from UQL 4508 from Tiverton Formation, figured herein Fig. 19A, B, 21A-D, here designated.

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

Material: Specimens from UQL 1619, 1622, 2622, 4508, LT3, T3 and TK1/2. *Bookeria pollex* Zone and possibly younger (T3 uncertain).

Dimensions in mm:

UQF	UQL	Valve	Width	Length	Height	Hinge
81256	4508	ventral	27	25.5	11.5	17
81255	TK1/2	ventral	19	18	10.5	13
81260	4508	both	37	27	17	21

Description: Ventral valve evenly rounded in outline and cross-profile, steep posterior wall, sulcus or rarely median flattening, umbonal angle 90°, no umbonal cicatrix, rounded cardinal extremities, ventral interarea low, at right angle to commissure, concave. Dorsal valve from UQL 4508 moderately to deeply concave, rarely with fold, no geniculation, very low interarea in plane of commissure or at right angles to commissure. Ventral spines 0.3 and 0.4-0.5mm up to 0.8-0.9mm in diameter, reaching up to 1mm laterally in material from T3, anteriorly spaced 1.5 to 3mm apart along slightly irregular commarginal rows, varying in position and diameter, with examples of a fine spine 0.3mm in diameter placed close to a spine 0.6mm in diameter, both erect. Posterior lateral extremities have one or more sturdy spines 0.7-0.8mm or more in diameter. Recumbent spines rare, 0.3-0.5mm in diameter, not present in all specimens. Fine but worn commarginal growth increments, a few ragged growth steps, and low radial rugae present. One dorsal exterior shows low growth increments, and sturdy erect spines anteriorly, and another from UQL 4508 shows scattered erect spines over the anterior disc and possibly trail. There are traces of fine radial capillae over parts of the disc and trail, five or six in 1mm. UQF 73313 (Waterhouse et al. 1983, pl. 1, fig. 5) shows short discontinuous radial threads.

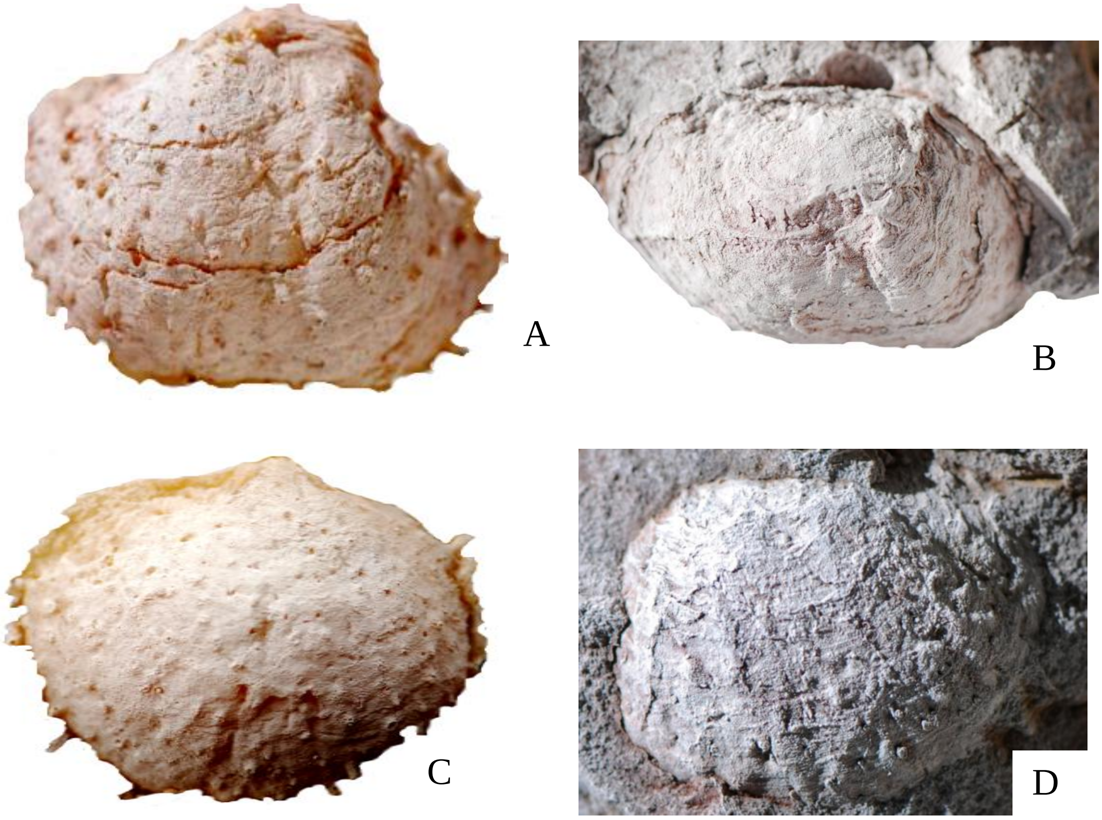


Fig. 19. *Echinalosia curtosa sulcata* n. subsp. A, B, holotype, latex cast of ventral valve UQF 81260 from UQL 4508, and dorsal external mould, x2. C, latex cast of ventral valve UQF 81303 from TK1/2 (= UQL 4508), x2.5. D, dorsal external mould UQF 81373 from T3, x2.

Ventral adductor platform from TK1/2 long and triangular, short in T3 specimen, faintly impressed anteriorly placed diductors and some spine bases opening into the interior, no elongate channels. Teeth small. The holotype is a large mature specimen which has smooth elongate adductor scars, divided by myophragm for most of length, and large but not deeply impressed diductor scars. Cardinal process narrow, dorsal adductors with long posterior subrectangular pair and inner oval anterior pair. Septum extends for only half length of valve, brachial impressions weak or absent.

Resemblances: This subspecies is distinguished by its large size, deeply concave dorsal valve and usually sulcate ventral valve, erect and scattered ventral spines, and occasional presence of capillae on the dorsal valve. The types of *Echinalosia curtosa* Waterhouse (1986a, p. 24, pl. 3, fig. 5-14, pl. 15, fig. 9; Briggs 1998, p. 72, Fig. 38A-H) from the Fairyland Formation of the southeast Bowen Basin are smaller, elongate and arched, with deeply concave dorsal valve and high ventral valve, weakly sulcate in some instances. Ventral spines are more sturdy but less erect, and the ventral muscle field is similar. The subspecies is moderately close to *Strophalosia preovalis* var. *warwicki* Maxwell, 1954, p. 543, pl. 54, fig. 16-19; refigured as *Echinalosia preovalis* (not Maxwell) by McClung (1980, pl. 19.1, fig. 1) and *E. warwicki* by Briggs (1998, p. 73, Fig. 39A-H). This is now the type species for *Capillaria* Waterhouse, 2001, p. 67; Brunton 2007). The species is smaller than the present subspecies with less concave dorsal valve and less arched ventral valve, and is characterized by a row of hinge spines, large posterior lateral ventral spines, and dorsal capillae. But some *warwicki* come close to the present form. Collections of *warwicki* from the type area in the lower or *Eurydesma* beds of the Stanthorpe

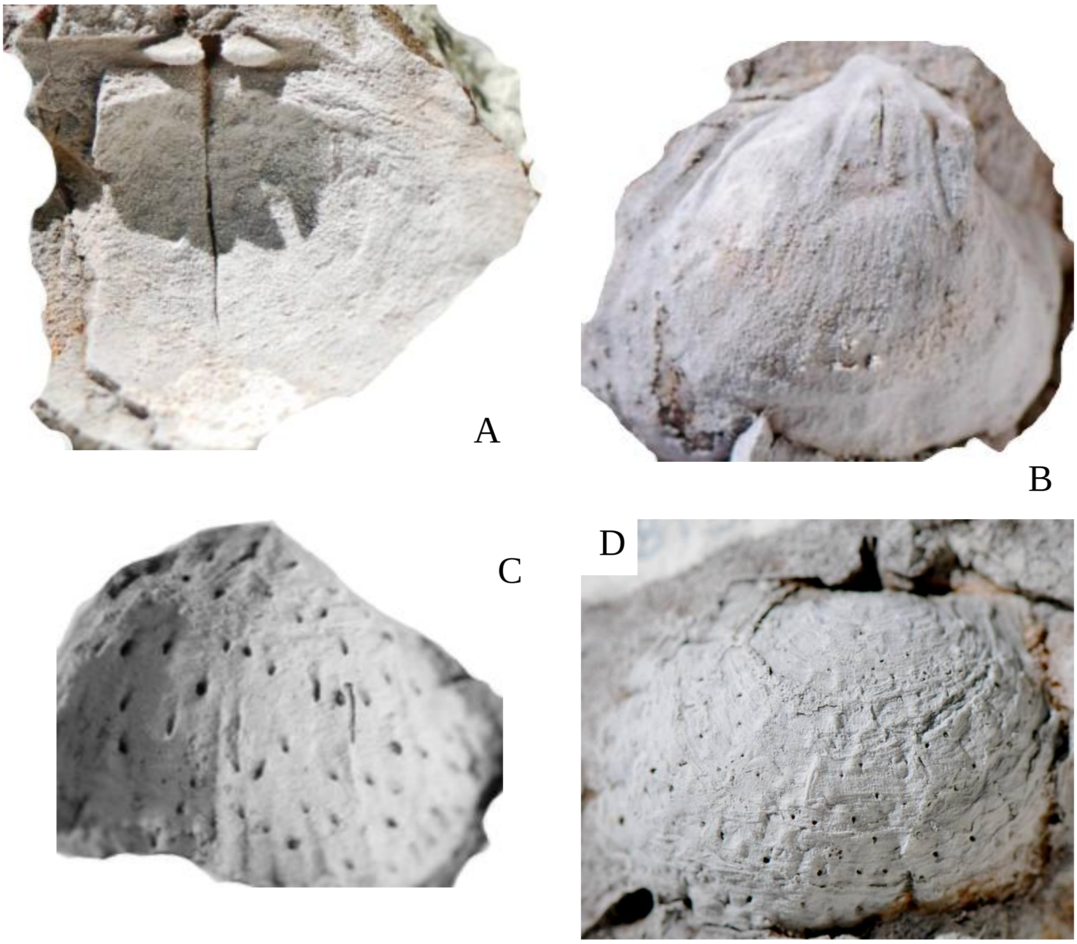


Fig. 20. *Echinalosia curtosa sulcata* n. subsp. A, dorsal internal mould UQF 81259 and part of external ventral mould UQF 81256 from UQL 4508, x3. B, internal mould, ventral valve UQF 81445 from UQL 4508, x2.5. C, external mould of ventral valve, UQF 81258 from UQL 4508, x2. D, dorsal external mould UQF 81450 from LT3, x3.

road block are kept at the Queensland Museum and Science Annex at Hendra in Brisbane. They show considerable variation. On the whole, ventral valves are convex with steep posterior walls, and scattered erect or suberect to less commonly semirecumbent spines. In the ventral valve, large spines lie in a row along the hinge (UQF 15627), with two or three additional spines. Some lateral spines are semi-recumbent, but most spines are erect in commarginal rows (eg. UQF 15626), up to 1mm in diameter. Commarginal growth laminae are well developed on ventral valve UQF 15626. Briggs (1998) emphasized the length of the ventral adductors. The dorsal valve is concave, moderately to weakly laminate, with dimples and often rare spines. Amongst the type specimens of Maxwell (1954) is a dorsal valve with rare spines and faint radial capillae, and few dimples and pustules. From UQL 140, dorsal valve UQF 8633 has spines over the anterior disc and all of the large trail, but dimples, pustules and commarginal laminae are missing. UQF 8588 from the same locality is a gently concave dorsal valve with very close-set spines. Dorsal valve UQF 75206 from UQL 5190 has well developed capillae, few dimples and few commarginals, and dorsal valve UQF 75202 from UQL 5114 has rare well spaced dorsal spines, close commarginals, a few dimples, and short capillae. Two relatively well preserved dorsal valves from UQL 622, including UQF 15268, have commarginals, dimples and pustules, and no visible spines, whereas another otherwise similar dorsal valve from the same collection has erect fine spines over the anterior disc and trail. One well preserved dorsal valve from UQL 140 is gently concave with wide hinge and erect spines

0.2-0.3mm in diameter over the anterior disc and all of the trail: the same block has more concave dorsal valves with fewer spines and more dimples.

Material is scarce other than in the Stanthorpe road block. Part of the Briggs' synonymy is emended, because a ventral interior figured by Hill & Woods (1964b, pl. P4, fig. 9) and Hill, Playford & Woods (1972) is deemed to belong to *Acanthalosia*, with its thick posterior shell, emphasized muscle scars, and strong spine bases on the ears. The specimen figured as *preovalis* by Clarke (1969, p. 47, pl. 6, fig. 7) was transferred to *warwicki* by Briggs (1998, p. 73), yet it was indicated as a topotype specimen of *preovalis* by Clarke (1969). The source for Clarke's other figured specimen (Clarke 1969, pl. 6, fig. 8) was not provided, and is poorly known, being an internal mould, but has muscle scars like those typical of *preovalis*.

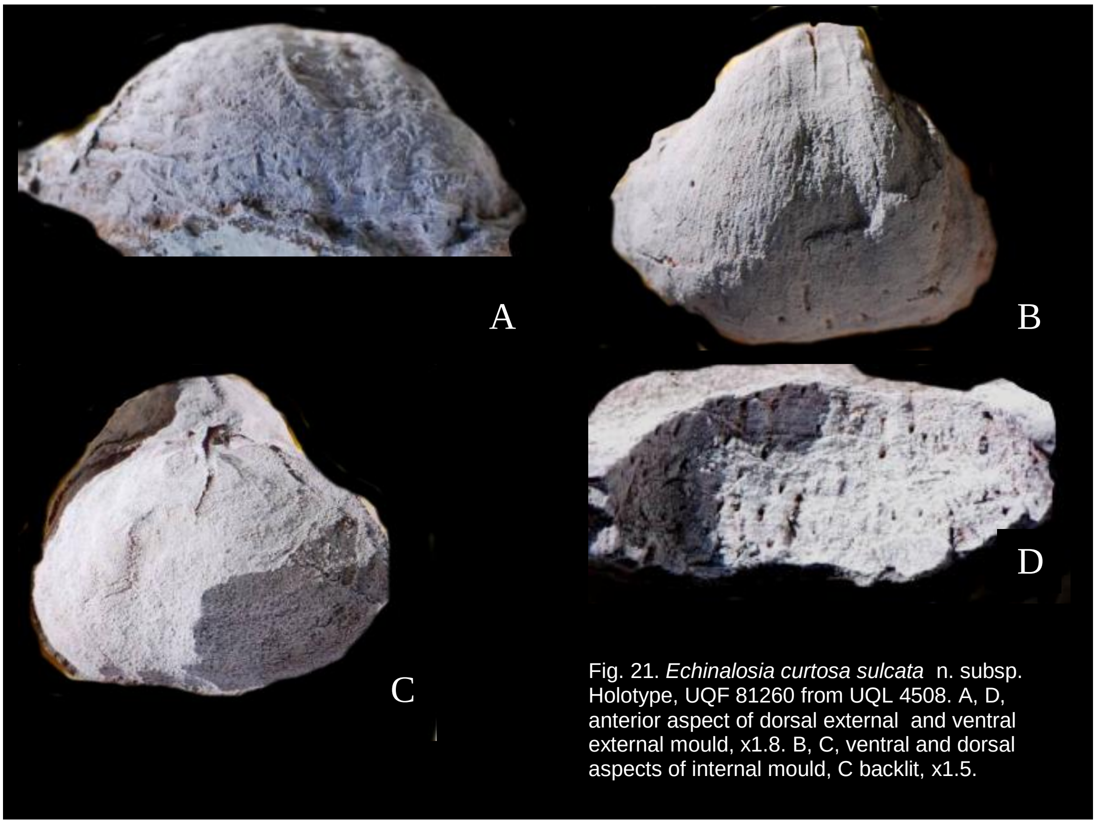


Fig. 21. *Echinalosia curtosa sulcata* n. subsp. Holotype, UQF 81260 from UQL 4508. A, D, anterior aspect of dorsal external and ventral external mould, x1.8. B, C, ventral and dorsal aspects of internal mould, C backlit, x1.5.

Homevale material at GSQL 778 and UQL 1619-1624, 4507, 4513, 4514 and 4515 was referred by Briggs (1998, p. 73, Fig. 39) to the species *warwicki*, but the specimens available from most of these collections differ from *warwicki* in ornament and internal musculature. Briggs reported the occurrence of *warwicki* at UQL 4507, which would accord with the present assessment of the range of the species, but he extended its range to include what is here called the *Svalbardia armstrongi* Subzone. This was a critical factor in his understanding of the *warwicki* Zone, which was deemed to range from above the *Echinalosia curtosa* Zone up to the lower *Echinalosia preovalis* Zone. This is at variance with present understanding, because *warwicki* is deemed closest in time range to the *E*. *curtosa* Subzone, which is represented in the lower middle Tiverton Formation, as at UQL 4507, and is not deemed to be not younger than *curtosa*. Shells identical with the Tiverton specimens he referred to *warwicki* are found to range throughout the faunas he matched with his "lower *preovalis* Zone", to compromise his proposed limits and contents of the *warwicki* and *preovalis* Zones. According to Briggs (1998, p. 76), the species *warwicki* is represented in the Colraine Mudstone in the Hastings Manning Block of New South Wales. Large collections by A. H. Voisey from the "*Strophalosia Linoproductus*" Horizon in the "MacLeay Series" at Kimbriki are kept at the Australian Museum. The material belongs to *Echinalosia curvata* Waterhouse, agreeing in size and shape, and ornamented much as in the Elvinia Formation types of this species, and the dorsal valve lacks radial capillae or prominent commarginal laminae, and generally shows inconspicuous dimples and pustules. However dorsal valve AMF 42062 in a different matrix of more sandy and green siltstone matrix in the same general area has moderate commarginal laminae and anterior faint radial capillae, with spines over the anterior half, as in *warwicki*. The ventral interarea is moderately high. This is supposed to be from the same beds, but clearly comes from different rock.

Runnegar & Ferguson (1969, pl. 2, fig. 10-14) identified *Wyndhamia preovalis* var. *warwicki* from the lower South Curra Limestone of Gympie, and this was changed to *preovalis* by Briggs (1998). Specimens are well represented in the South Curra Limestone and Gundiah Bridge beds and Gigoomgan Limestone to the northwest in the Gympie area, and have been described as a new species *E. denmeadi* Waterhouse & Balfe of Waterhouse, 2015. The hinge is narrower than in *warwicki*, and the shells more oval in shape and less concavo-convex, with less developed hinge row of spines, and ventral muscle field is less elongate: certainly it is closer to *preovalis* than *warwicki*, but has slightly finer more numerous and uniformly dispersed spines. The material recorded as *warwicki* by Briggs (1998, p. 76) from the Rammutt Formation at Gympie has not been relocated.

Taxonomy: In 1961 the International Subcommission for Zoological Nomenclature declared that varieties of species named by previous workers had no valid standing, being of infrasubspecific rank, as rule 45e (Stoll, 1961). It was left to "principal revisors" to decide whether the varietal name should be validated, or replaced, or synonymized. Under that rule, variety *warwicki* Maxwell was renamed *warwickensis* by Waterhouse (1986a, p. 24, 1986b, p. 1). But the procedure was rescinded in 1985, and varieties proposed before were declared to be valid taxonomic entities, to be transferred to specific or subspecific standing, thereby retrospectively negating taxa proposed by workers who had followed the Code of 1961.

Echinalosia cenula n. sp.

Fig. 22 – 29

1954 *Strophalosia preovalis* [not Maxwell] – Maxwell, p. 542, pl. 54, fig. 4, 5 (part, not fig. 1-3, 6-11 = *preovalis*).
1981 *Echinalosia preovalis* – Dickins, pl. 4, fig. 3 (part, not fig. 1, 2, 4, 5 = *discinia* Waterhouse).
1998 *E. warwicki* [not Maxwell] – Briggs, p. 76 (part not p. 77, Fig. 39 = *warwicki*).
Derivation: cenula – little dinner, Lat.

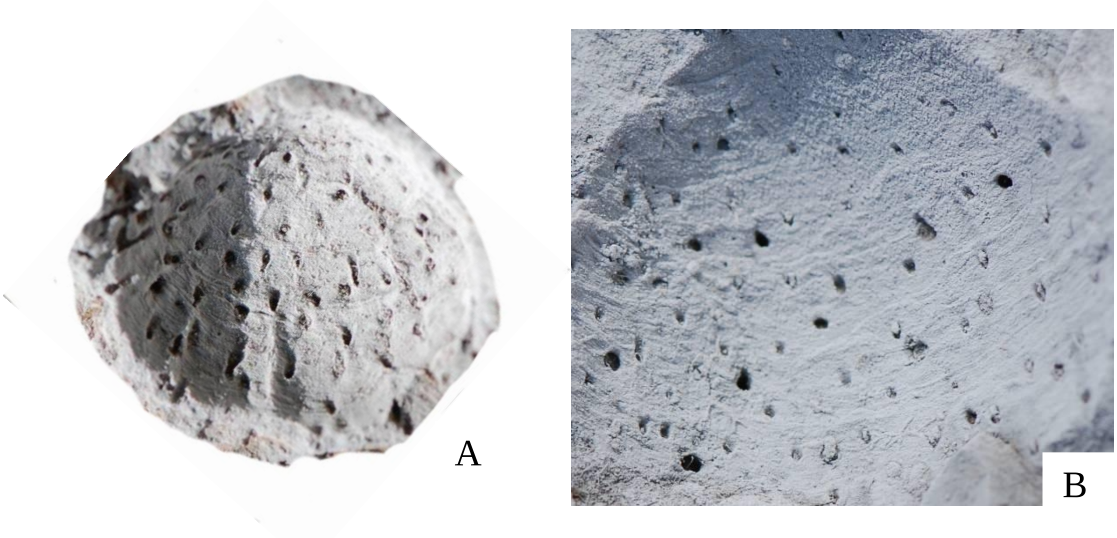


Fig. 22. *Echinalosia cenula* n. sp. A, external mould of ventral valve UQF 81262 from UQL 2622, x3. B, external mould of ventral spine bases, UQF 81437 from UQL 1630, x 3.

Holotype: Specimen UQF 81820 from UQL 2625, Tiverton Formation, figured herein as Fig. 26A, here designated.

Diagnosis: Small highly convex ventral valve, deeply concave dorsal valve, not showing clear geniculation, ventral valve coarse series of spines 0.3 to 0.6mm in diameter, and some spines up to 1mm in diameter, recumbent series 0.3-0.4mm in diameter, dorsal spines rare, 0.2 to 0.4mm usually in diameter over a band close to start of trail, dorsal dimples and commarginal laminae prominent, no capillae.

Material: Abundant specimens are found at UQL 1382, 1621, 1622, 1623, 1626, 1630, 1632, 2584, 2622 - 2629, 3127, 4510 - 4519, 4524 and 4525. This species is found especially in the Tiverton equivalents of the *Bookeria geniculata* Zone and less commonly in the *Taeniothaerus subquadratus* Zone. Apparently the species is limited to the northern Bowen Basin.

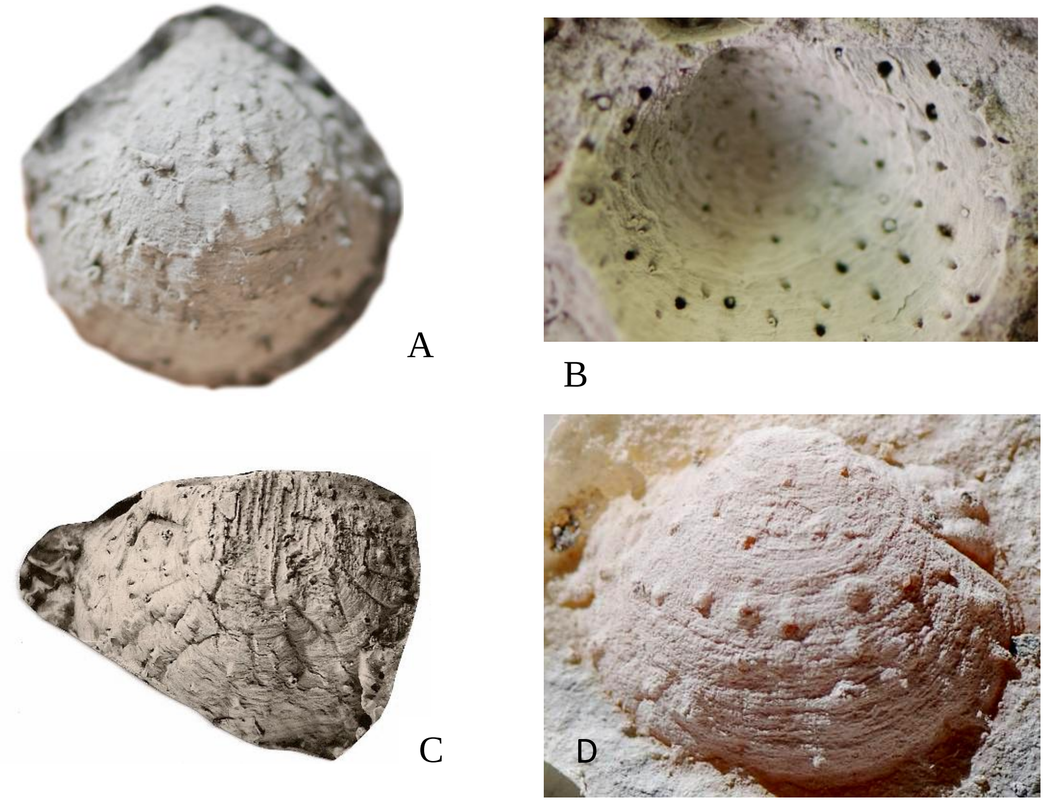


Fig. 23. *Echinalosia cenula* n. sp. A, latex exterior of ventral valve UQF 81302, found on a block with UQF 20175, x2. B, external mould of ventral valve UQF 81264 from UQL 2628, x2.5. C, latex cast of ventral exterior showing cicatrix, UQF 81814 from UQL 2625, x3. D, latex cast of ventral valve UQF 81434 from UQL 4511, x 4.

Description: Mean size average from mature specimens, excluding juveniles, and from several collections is width 23.5mm, length 26mm and height 16.5mm (n = 25). The shape varies: a number of specimens are equilateral or rarely weakly transverse, and maximum width lies near mid-length. The ventral valve is highly convex without median flattening or sulcus, and the umbo is incurved. Specimens are transverse, or highly convex and elongate in outline. The dorsal valve is deeply concave, helping to enclose a slender visceral cavity 4mm thick in a specimen 24mm wide, and the trail curves smoothly on from the disc. The hinge is of moderate width, and the ventral interarea low to moderate in height, with slender pseudodeltidium, and lies in the plane of the commissure, whereas the low dorsal interarea lies at a high angle to the commissure. Ventral spines are mostly suberect at an angle often 50^o from the shell surface in front, and the spines are generally 2-3mm apart, especially over the first-formed part of the valve, and on some shells moderately regular in spacing, but often irregular, in short commarginal rows, or well spaced and subquincunxial. Some spines lie close to the hinge and on the ears, but there is no well-formed hinge row, although a few strong spines lie at the cardinal extremities.

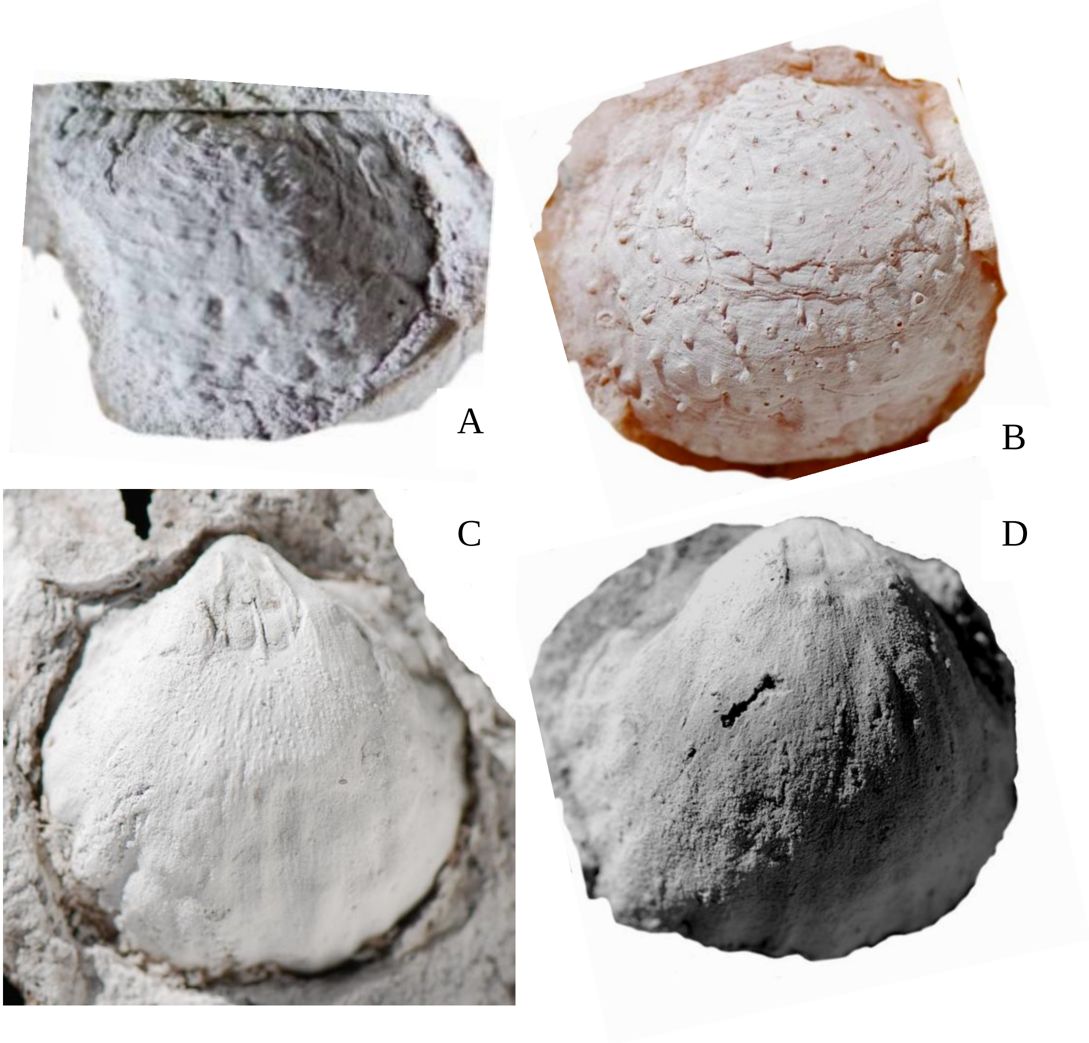


Fig. 24. *Echinalosia cenula* n. sp. A, dorsal external mould UQF 81263 from UQL 4514, x 3. B, latex cast of ventral exterior, UQF 20960 from UQL 1623, x 3. C, ventral internal mould UQF 81827 from UQL 4512, x3. D, ventral internal mould UQF 81265 from UQL 2625, x3.

Spines tend to vary as a rule between 0.4 to 0.6mm in diameter, and may be up 0.8mm in diameter. There are a few adpressed spines, some fine, others no different from the erect spines in diameter, often 0.4-0.6mm, and there may be short grooves up to 1mm wide, with no visible spine – possibly formed by a spine from another specimen, because the species was gregarious. A few specimens have well dispersed spines, fewer than usual, and up to 0.9 to 1mm in diameter, especially postero-laterally, as in specimens from UQL 2626 and 2628. In some specimens finer and thicker spines are interspersed, in others there are rows of four to six fine spines and rows of four to six coarser spines, but often the spines are uniform and close to 0.6mm. In a mature specimen from UQL 3127 some 23mm wide, anterior spines 0.6mm in diameter are aligned, three or four in 5mm, both in single rows and in bands of two or three close-set commarginal rows, separated by interspaces 3-4mm wide. Often spines arise from short bases, and may be interspersed with short radial rugae or channels. It appears that spine bases or cores in front of the spine base are comparatively short. Commarginal laminae are conspicuous, generally seven per mm. A juvenile ventral valve 7mm long has fine well spaced spines, 0.3mm in diameter, most erect, some inclined 60° from the surface, with commarginal laminae and no radial filae. Dorsal spines are arrayed in close quincunx over the anterior disc and start of the trail in two to four rows as a rule, with spines 1.5 to 2mm apart along and between rows, but spines may be rare, and are entirely missing from some specimens. Dorsal spines generally between 0.2 -0.4mm, with a few 0.1mm in diameter, rarely 0.4 up to 0.6mm in diameter near the anterior margin, and on some specimens, spines have a short posteriorly prolonged base, and very rarely are prostrate. Despite this substantial variation in size, with some anterior spines 0.3 and 0.6mm across being in proximity, the spines appear to form one erect series of variable diameter, and the thick spines are rare. Spines are rare over the disc, often 3 to 5 up to 8mm apart and are missing from the concave, flat or usually convex nepionic area, which varies from 1-7mm, generally 2mm, in width. As well there are dense and well developed low commarginal lamellae over the dorsal valve, and conspicuous well spaced dimples and mounds, which are usually round, but may be slightly elongate, especially anteriorly. There may be short channels for a few mm, up to 1mm wide, probably caused by spine tunnels extending forward from the base of spines. The anterior shell of both valves may carry low radial rugae, 12-20mm long, and the anterior shell of the dorsal valve may be undulose, with anterior spines semi-recumbent, inclined only 20-30° from the disc.

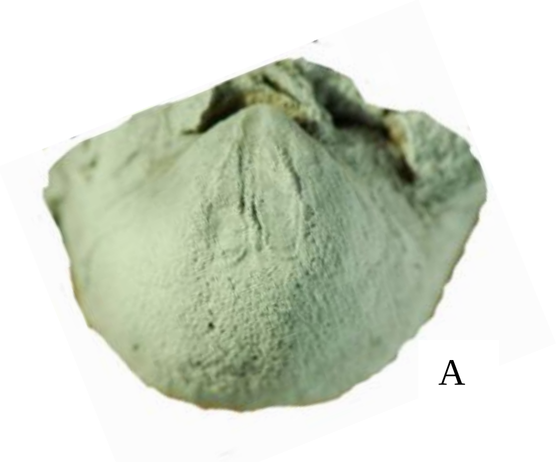


Fig. 25. *Echinalosia cenula* n. sp., ventral internal moulds. A, UQF 81266 from UQL 2626, x2.5. B, external mould of ventral valve UQF 81253 from UQL 3127, x3.

Ventral adductors are small, low, clearly defined, posteriorly to very posteriorly placed, with flanks widening forward and weakly subtriangular in shape, rarely with a more oval outline, and in some shells very short and small, even in large specimens. They are smooth and in some specimens are divided by a median groove and very low ridge, overlapped for a third to almost half their length by small diductor scars very faintly impressed as a rule, even in relatively large specimens up to 27mm across. Teeth are small in size, except for a few specimens, close-set and elongated along the hinge. In a very few specimens at a gerontic growth phase, a low ridge extends in front of the hinge behind the muscle field and trends across the posterior lateral extremities, and pustules develop in front of the muscle field. Internal short spine channels 2mm to rarely 3mm long are present anteriorly in some specimens, and in others anterior spines open into the interior.

The dorsal valve has a short cardinal process, and a septum which is broadest immediately in front of the cardinal process and extends for about half the length of the valve. Adductor scars are small, slightly raised, smooth, and subdivided into transverse posterior lateral and subrounded inner anterior scars. Brachial ridges are weakly if at all defined, and a low ridge develops in larger specimens across the posterior lateral shell.

Resemblances: The present suite approaches *Echinalosia curtosa* Waterhouse, 1986a from the Fairyland Formation of the southeast Bowen Basin in its highly convex ventral valve and deeply concave dorsal valve, and in umbones and aspects of the hinge and cardinal areas, and in the nature of the ventral spines. Specific differences are that many specimens of *E. cenula* are less elongate in shape, and *curtosa* specimens have a generally different dorsal ornament in the lack of strong commarginal laminae and dimples, presence of faint radial capillae (UQF 73945) and more numerous dorsal spines as a rule, especially anteriorly, although some *E. cenula* agree in spine distribution. Ventral spines of *E. curtosa* are more sturdy and more clumped and more prominent along the lateral flanks. Internally, the ventral adductors of *E. cenula* are usually shallower and often shorter, but again there is a degree of overlap. The considerable similarity between the two populations would allow *cenula* to be either a geographic sibling, separated geographically, or a slightly younger descendent, and the latter is favoured by the known age ranges and affinities of accompanying fossils.

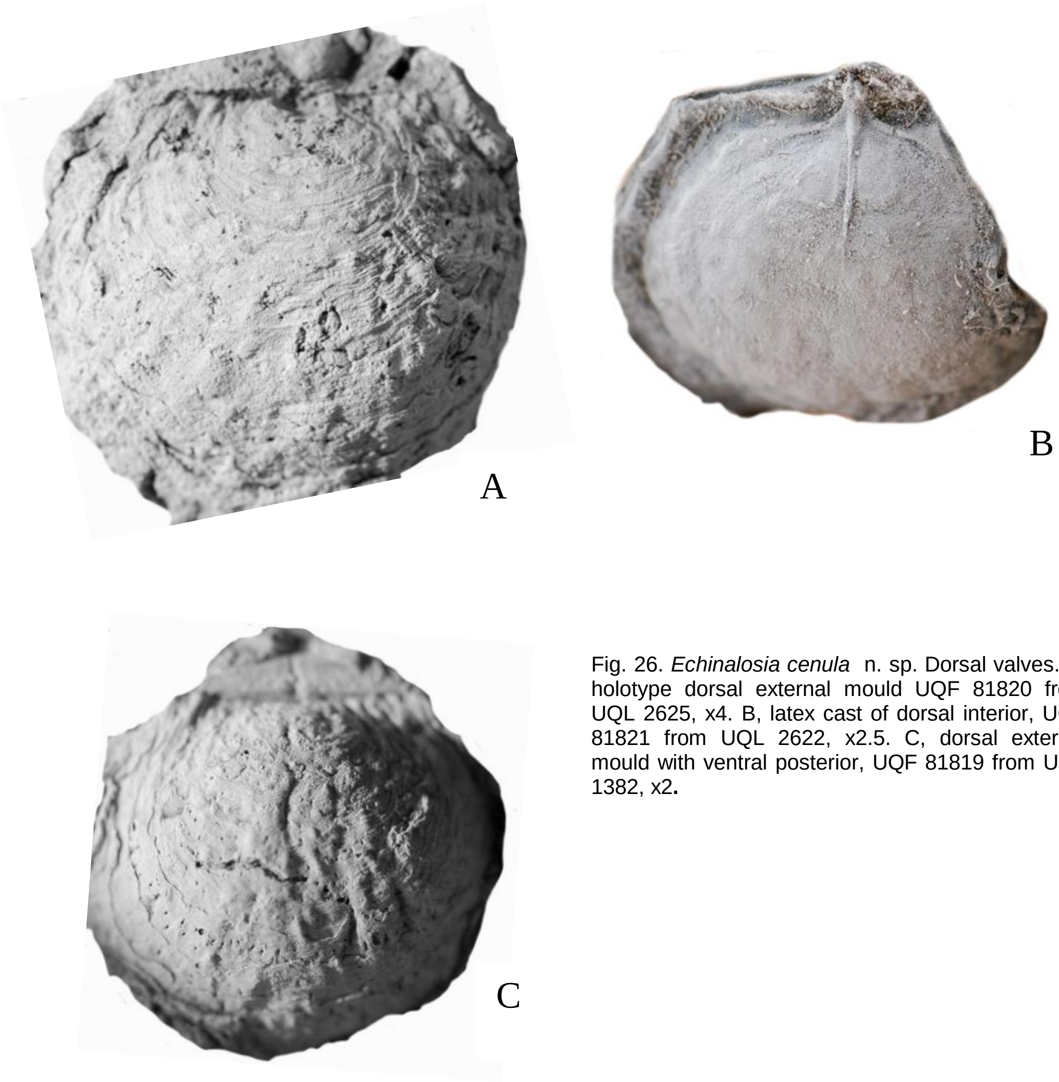


Fig. 26. *Echinalosia cenula* n. sp. Dorsal valves. A, holotype dorsal external mould UQF 81820 from UQL 2625, x4. B, latex cast of dorsal interior, UQF 81821 from UQL 2622, x2.5. C, dorsal external mould with ventral posterior, UQF 81819 from UQL 1382, x2**.**

Briggs (1998) synonymized the species *Echinalosia dejecta* Waterhouse (1986a, pl. 3, fig. 15-24) from the Dresden Limestone, southeast Bowen Basin, with *E. preovalis*, but *dejecta* has sturdy ventral spines, 0.8mm in diameter, some thick recumbent and slightly rhizoid (see Waterhouse 1986a, pl. 3, fig. 15, anterior shell), and numerous erect dorsal spines 0.3mm in diameter. In addition, the ventral muscle scars are more anteriorly placed, and the dorsal median septum much longer than in *Echinalosia preovalis* or *curvata* – and there are various other differences. Ventral interiors figured as *preovalis* by Maxwell (1964, pl. 7, fig. 11, 12) from calc-rich beds of the Yarrol Formation, Yarrol Basin, probably belong to *dejecta,* because an unfigured ventral exterior from the same locality and kept at the Queensland Museum shows similar rhizoid sturdy recumbent spines. Briggs (1998) referred the Yarrol material to *Echinalosia warwicki*, but this identification seems to be wrong, in view of the nature of the ventral spines, shape and ventral muscle field. It appears that *dejecta* colonized calcareous substrate, being found in limestone both in the southeast Bowen Basin and in the Yarrol Basin. The dorsal valve is not known for the Yarrol material. At least some of the Homevale material at GSQL 778 and UQL 1619-1624, 4507, 4513, 4514 and 4515, chiefly the *Svalbardia* band, was referred by

Briggs (1998, p. 73, Fig. 39) to *Echinalosia warwicki* (Maxwell). This species is based on material from the so-called upper Wallaby beds in the Wildash Group of southern Queensland, in part of the New England Orogen, and is now referred to *Capillaria* Waterhouse (2001, p. 67), as in Brunton (2007, p. 2665, Fig. 1773a-e). The

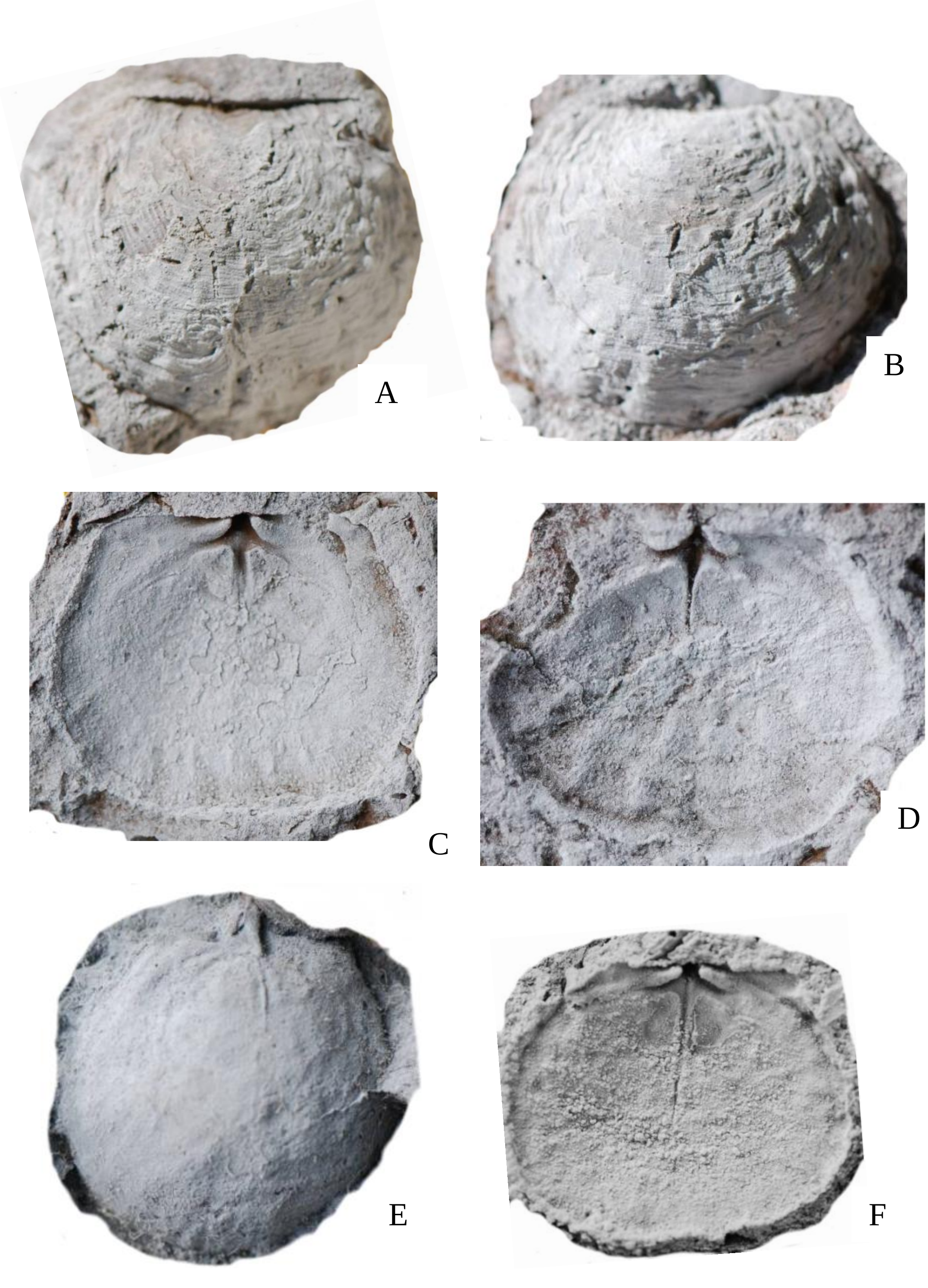


Fig. 27. *Echinalosia cenula* n. sp. Dorsal valves. A, external mould UQF 81822 from UQL 2623, x3. B, external mould UQF 81261 from UQL 2622, x3. C, internal mould UQF 81823 from UQL 4519, x3. D, internal mould UQF 81827 from UQL 4518, x2. E, latex internal mould UQF 81824 from UQL 2622, x2. F, dorsal internal mould UQF 81292 from UQL 4518, x4. Note that Fig. 27D and F in coming from UQL 4518 might prove to be specimens of *Echinalosia curvata* Waterhouse, which is also found at the same locality: the two species are discriminated on external ornament, and share similar dorsal interiors.

species incorporates shells with often narrow hinge, poorly formed or no ears, distinguished by presence of moderately well developed radial capillae on the dorsal valve. Specimens of *warwicki* include some that are larger, more transverse, and have slightly flatter dorsal disc, compared with *Echinalosia cenula*. Two or three additional large spines are present postero-laterally, as in *Echinalosia cenula*. Ventral body spines of two orders in *warwicki* were described by Briggs (1998) as shallow embedded and 0.3mm in diameter and erect at 0.5mm diameter. Thick erect spines 0.6-1mm diameter tend to be developed laterally. Dorsal spines are erect and as a rule few, 0.1mm diameter, and rarely form a band like that of *Echinalosia cenula* near the start of the trail (Briggs 1998, Fig. 39D). The dorsal exterior shows a few dimples, fewer than in *cenula*, and commarginal ornament is present but less conspicuous compared with *Echinalosia cenula*. In the Warwick species, the posterior wall is more massive and high, the ventral muscle field is as a rule much longer, and dorsal capillae are strongly developed, without prominent commarginal laminae. Thus there are a number of external similarities in overall size, spine size, spine opening and aspects of spine distribution, and presence of dorsal dimples, but the Warwick form marks a highly distinctive species. Material from the Gympie faunas in the so-called “Lower Brachiopod fauna” near the base of the South Curra Limestone, was described by Runnegar & Ferguson (1969, pl. 2, fig. 10-14) as *Wyndhamia preovalis* var. *warwicki* (Maxwell), and the material does display fine capillae over parts of some dorsal valves. But the spines are finer and appear to be much more regularly distributed over the ventral valve (Runnegar & Ferguson 1969, pl. 2, fig. 10) and on the dorsal valve (Runnegar & Ferguson 1969, pl. 2, fig. 14) spines are fine and more numerous and more regularly distributed than is normal for topotype material of *warwicki* from south Queensland. The Gympie species (except for pl. 2, fig. 13) is treated as a full species of *Echinalosia*, named *E. denmeadi* Waterhouse & Balfe in Waterhouse (2015).

Echinalosia mcclungi Briggs (1998, p. 79, Fig. 41A-H) from the Pebbley Beach Formation, south Sydney Basin, has strong spines postero-laterally on the ventral valve, thicker than those of *E. cenula*, and the ventral adductors are elongate. The hinge is short, the ventral spines moderately scattered and variable in diameter, with fine apparently recumbent spines and thicker suberect spines, and the dorsal valve is only gently concave, and is slightly thickened. The dorsal exterior, shallowly concave, was reported to have a few erect and possibly interspersed finer spines, which might imply a relationship to *Acanthalosia* Waterhouse, and with no report of laminae or dimples or capillae. The brachial ridges are well developed. The species has been dated as equivalent to upper Cattle Creek Formation by Briggs (1998). Briggs (1998) also asserted that similar material was to found in the Rose’s Pride and basal Elvinia Formations of the southeast Bowen Basin, but did not figure or cite any of the identified material from the southeast Bowen Basin, so that it is not possible to verify his observation, and I have failed to find any *mcclungi*-like specimens in those formations. *Acanthalosia mysteriosa* Waterhouse 2010a is found in these units, bearing much more numerous spines than illustrated for *mcclungi.* The species and age are further discussed by Waterhouse (2001, p. 59), in discounting Briggs’ assertion of similarity to a New Zealand species now named *Echinalosia conata* Waterhouse, 2001, a species found throughout a thick succession of volcanic detritus in the Takitimu Group of southern New Zealand.

In many respects *Echinalosia cenula* is close to *E. curvata* Waterhouse (1986a, p. 26, pl. 3, fig. 25-29, pl. 4, fig. 1-5) in size, concave dorsal valve, and various internal features, apart from having slightly less prominent ventral muscle field. But the ventral spines of *E. cenula* are of very different appearance, with fewer and somewhat coarser scattered erect spines and few prostrate spines compared with *E. curvata*. As well there are more large spines on the ventral ears of *E. curvata*. The dorsal disc of *E. cenula* has fewer spines as a rule and is ornamented by well developed commarginal growth laminae and dimples. In these respects the species *E. curvata* is closer to *E. maxwelli* (Waterhouse).

Briggs (1998, p. 78) recorded material as *Echinalosia preovalis* (Maxwell, 1954) from UQL 1630, 4517 (cf.), 4523 and 4525, but the specimens so identified at least from 4523 and 4525 probably belong to *Pseudostrophalosia brittoni* (Maxwell) or *Maxwellosia bryani* n. sp., to judge from their morphology. Type material for *Echinalosia preovalis* (Maxwell) shows dense and fine dorsal spines, and subdued commarginals and few or certainly inconspicuous and rare dimples. Ventral spines differ in spine diameter, spine uniformity and distribution.

Fossils figured as *preovalis* from the Eight Mile and Tunnel blocks of south Queensland by Dickins

(1981) belong to *Echinalosia discinia* Waterhouse, and are associated with *Tumulosulcus undulosa* (Campbell) and the bivalve *Undopecten* Waterhouse.

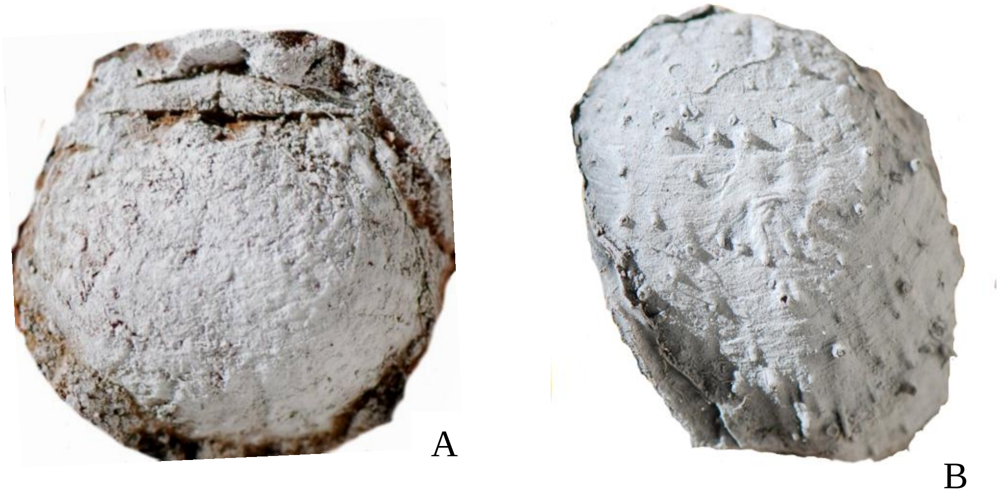


Fig. 28. *Echinalosia cenula* n. sp. A, external mould of dorsal valve and ventral posterior, UQF 81406 from UQL 3127, x3. B, latex cast of ventral exterior, UQF 81445 from UQL 2622, x2.

Fig. 29. *Echinalosia cenula* n. sp., dorsal internal mould UQF 81825 from UQL 4514, x5.

However there is a more apposite question, concerning the relationship of various echinalosiin species to *Strophalosia preovalis pristina* Maxwell, 1954 from the lower Cattle Creek Formation at Riverstone Gorge, southwest Bowen Basin, placed in the *Taeniothaerus subquadratus* Zone. The holotype is GSQF 2093, figured by Maxwell (1954, pl. 54, fig. 12), and, compared with *preovalis*, was regarded as smaller, less transverse, with wider hinge, higher interarea and more primitive teeth. Such features do not suggest *cenula* or *curvata,* but the material is very poorly preserved, and the spine detail and exterior not described and scarcely preserved. From what can be ascertained, there are few spines and no dorsal capillae. The specimens are small, and several other similar dorsal valves are preserved on the slab. The taxon may well prove to be senior synonym of *warwicki*, *curvata* or *cenula*, or even *brittoni*, *bryani* or *concava*, given that it apparently comes from approximately correlative or slightly younger beds (Waterhouse 2002a, p. 189). The slab that holds the specimen figured as *Terrakea pollex* Hill (1950, pl. 9, fig. 9) also comes from the Riverstone Gorge Creek, and has two ventral valves that closely approach *Echinalosia cenula* as far as they are preserved. But these ventral valves do not show the ornament in detail, and the dorsal ornament remains unknown. Furthermore there is uncertainty about the exact source of the Riverstone Gorge specimens described by Hill (1950) and Maxwell (1954), because GSQ collections from the same area made by P. Balfe and G. McClung and now housed at the Queensland Museum show much coarser matrix, with no material approaching that of the earlier collections. Given such uncertainty, the taxon is set aside until full examination can determine the nature of *pristina.* In the meantime, it is regarded as conforming with the diagnosis and description by Maxwell (1954), and as having small size and wide hinge. Waterhouse (1986a) treated *pristina* as a variety, of no taxonomic standing, following the International Code of Zoological Nomenclature (Stoll 1961). This provision was rescinded in 1985, article 45g, as endorsed in 1999. In that regard, it might have been preferable to retain the earlier practice, at least as an option, which allowed discretion, as that would have enabled unsuitable and poorly based taxa to be removed from the corpus of zoological taxa. The now current procedure will continue to destabilize nomenclature, if, eventually, topotypes are recovered and proved to be senior synonym of one or other of the contemporaneous species. But on the other hand there should be no wish to suspend all systematic description and taxonomic study until the matter can be resolved, though that may prove difficult, especially because the Geological Survey of Queensland have made substantial collections from the Riverstone Gorge, but failed to find any rock or fossils of similar appearance. Referring back to the specimen figured by Hill (1950, pl. 9, fig. 9) as *Terrakea pollex* from the same locality as type *pristina,* it is so obscure that it could even be a decorticated strophalosiid. It adds little to the circumscription of the species.

Amongst the many strophalosioid species recorded from the Permian of Western Australia, only *Echinalosia simpsoni* Archbold (1996, p. 22, Fig. 3A-V) from the Mingenew Formation (Baigendzinian) of the Perth Basin shows any approach to *E. cenula*, and it is readily distinguished by the elongate outline and sulcate ventral valve, and numerous fine dorsal spines. The ventral spines include many fine spines which appear to be high-angle recumbent, interspersed with a few fine prostrate spines.

Another strophalosiid genus that is found in the Tiverton Formation at Homevale is *Pseudostrophalosia brittoni* (Maxwell), and this is readily distinguished as a much larger form with robust shell, large spines especially postero-laterally, internal marginal ridge around the ventral valve (see Briggs 1998, Fig. 40D) and large strongly developed internal features positioned differently. The dorsal valve is only gently concave, and is moderately to strongly thickened. *Maxwellosia* in the same beds is another allied shell, large in size with varied erect and recumbent, often dense spines on both valves and concave dorsal valve, whereas the otherwise similar genus *Acanthalosia* has almost flat dorsal valve.

Echinalosia curvata Waterhouse, 1986a

Fig. 30 – 33

1986a *Echinalosia preovalis curvata* Waterhouse, p. 26, pl. 3, fig. 25-29, pl. 4, fig. 1-5.

? 1986a *Echinalosia curtosa* [not Waterhouse] – Waterhouse, pl. 3, fig. 8.

Holotype: UQF 73959 from UQL 4553, Elvinia Formation, southeast Bowen Basin, figured in Waterhouse (1986a, pl. 4, fig. 2, 5), OD.

Diagnosis: Shells usually transverse, moderately concavo-convex and moderately large for the genus. Numerous spines on both valves, many sturdy.

Material: A number of ventral and dorsal valves from UQL 1332, 4516 and 4518. *Taeniothaerus subquadratus* Zone.

Dimensions in mm:

UQF	UQL	Width ventral	Length ventral	Length dorsal	Height	Hinge
81828	4518	25		21	?3.5	?14
81829	4518	21	19		6.5	

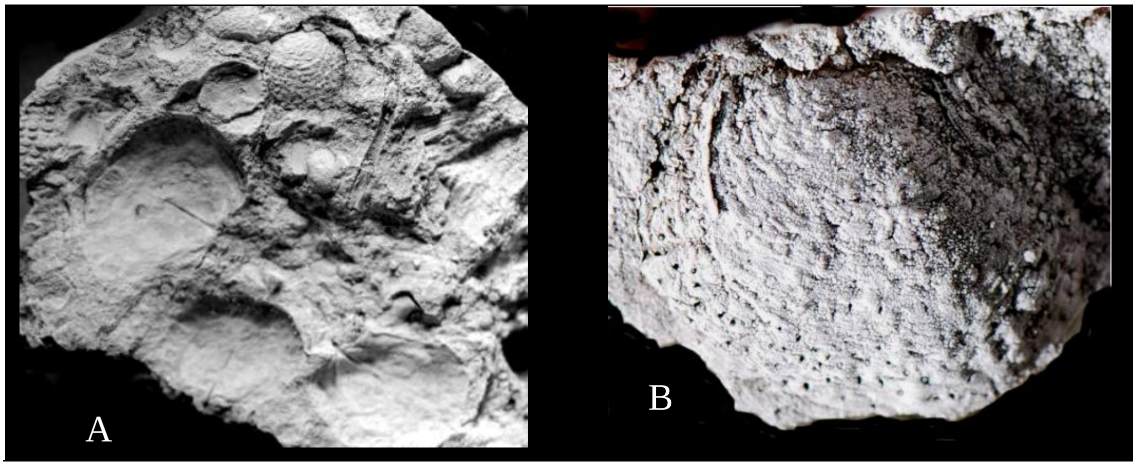


Fig. 30. *Echinalosia curvata* Waterhouse. A, internal moulds of dorsal valves UQF 81250-81252 and external mould UQF 81826, x1. B, dorsal external mould, UQF 81433. Shells from UQL 4518, x3.

Description: Shells concavo-convex, dorsal valve gently and subevenly concave, low semigeniculate trail, ventral interarea moderate in height, in plane of commissure, weakly concave with well defined pseudodeltidium, dorsal interarea plane, at high angle to commissure. Ventral valve has protruding umbo and rounded posterior lateral extremities; fine and coarse high-angle spines in quincunx, or clustered often postero-laterally, 0.3mm up to 0.8mm in diameter, very rare recumbent spines 0.2-0.3mm in diameter. Spines on a mature ventral valve are up to 1mm thick, with prostrate spines 0.4mm thick. Dorsal exterior with fine commarginals and sublamellae at intervals and low short rugae; posterior third of valve may be without spines; spines numerous and crowded over most to all of the valve, up to 2mm apart, erect, and 0.1 to 0.2mm in diameter. Cardinal process slender, median septum extends variably from less than mid-length up to mid-length, dental sockets small, adductor scars faintly raised, low posterior hinge ridge and faint ridge around the start of the trail in some specimens.

Fig. 31. *Echinalosia curvata* Waterhouse, UQF 81828, latex cast showing dorsal valve from UQL 4518, x2.

Resemblances: These specimens are like *Echinalosia curvata* Waterhouse in shape and size as moderately transverse and not highly inflated. What distinguishes the specimens is the nature of the dorsal ornament, in which the shell is covered by closely spaced fine erect spines, whereas the dorsal valve of *Echinalosia cenula* is dominated by lamellae and tubercles. Without the exterior, it is difficult to distinguish dorsal internal moulds, and some dorsal interiors assigned to *E. cenula* n. sp. in Fig. 27D, F herein could belong to either species. Ventral spines are highly variable in diameter and mostly suberect, and comparatively crowded, whereas in *cenula* they are more scattered and irregularly distributed in mature specimens. One of the present suite (Fig. 31) has the posterior dorsal valve free of spines. A dorsal valve figured as *Echinalosia curtosa* by Waterhouse (1986a, pl. 3, fig. 8) is of similar appearance, with a large posterior part of the venter devoid of spines, and feebly marked by fine short radial flutings: anterior spines are numerous. Whether this represents the present form or an unusual development is not certain, because only the one valve is known. The specimen lacks a median fold. The specimen comes from the *Echinalosia curtosa* Subzone of the Fairyland Formation, southeast Bowen Basin. As well a dorsal valve assigned to *Pseudostrophalosia brittoni* by Briggs (1998, Fig. 60B) is comparable. In these two instances, the exceptional specimens come from the type locality of the species concerned.

Fig. 32. *Echinalosia curvata* Waterhouse, slab of specimens including dorsal valve UQF 81828, and ventral external moulds UQF 81829, 81830 and UQF 81831 from UQL 4518, x2.

Evidently the species *curvata* made a brief foray into the upper middle Tiverton Formation. The specimens are younger than those of the type area, which are found in the *Bookeria geniculata* Zone, and also younger than material found in the same zone in the “MacLeay Series” of New South Wales. The precise age of the species in the Farley Formation of New South Wales is not fully clear, but seems likely to match the *Bookeria geniculata* Zone. The species is found in the Dunton Range in New Zealand.

Echinalosia preovalis (Maxwell, 1954), as further revised by Briggs (1998, p. 76, Fig. 40A-M), with reliable topotypes figured in A, C, D, E, G, K, L, M and supposedly conspecific specimens from the Drake Syncline near Warwick, south Queensland (Briggs 1998, Fig. 40H, 1, J and Rokeby F) is close in shape and in musculature to *E. curvata* from the Elvinia Formation of the southeast Bowen Basin. The fact that several of Briggs’ figured specimens are more transverse than *curvata* and show few or no radial ridges, and differ somewhat in ventral muscle field and clarity of brachial ridges may have little significance. It is the spines that appear to differ slightly, but significantly from the Elvinia specimens. The diameter in the upper Cattle Creek material is given as 0.2-0.3mm for recumbent and up to 0.5mm for the ventral valve erect series, and the dorsal spine diameter was given as 0.1 to 0.2mm. Material figured as *Echinalosia preovalis* by Briggs (1998, Fig. 40B) from the Warbro “Stage”, Willi Willi, New South Wales, has well spaced spines, up to 0.5mm thick: the identity requires confirmation. For type *curvata*, Waterhouse (1986a) measured erect ventral spines as 0.6mm in diameter, and noted some as coarse as 1mm. Within type *preovalis*, there is a low ridge or smooth area slightly raised in both valves, as in part noted by Waterhouse (1986a). Briggs (1998) suggested that this applied (in the case of the dorsal valve) to *Acanthalosia*, not *Echinalosia*, but a similar ridge is visible in his illustrated material for *preovalis* (Briggs 1998, Fig. 40D, L?, M). Although Briggs (1998) elected to synonymize *curvata* with *preovalis*, the two may be separated by taking care. Some poorly located material labelled as *preovalis* from the Cattle Creek Formation does have dorsal dimples and few posterior spines, much as in *cenula*, and whether these represent variants or *cenula* requires further material for closer examination.

Fig. 33. *Echinalosia curvata* Waterhouse. Latex cast of ventral valves UQF 81829, 81830 and 81831 from UQL 4518, x5.

Tribe **WYNDHAMIINI** Waterhouse, 2010a

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

Discussion: This group associates *Wyndhamia* and *Pseudostrophalosia.* The two genera are close to Arcticalosiini, but have some fine ventral prostrate spines, which are missing from *Arcticalosia* Waterhouse, *Orthothrix* Geinitz and *Marginalosia* Waterhouse: these genera have only one order of spine on each valve. That contrasts with the ventral spines of Wyndhamiini, which may be varied in diameter, and include very sturdy spines either over the ventral disc or postero-laterally. *Notolosia* Archbold is judged to be a synonym of *Pseudostrophalosia*, displaying a comparable burst of ear spines (see Waterhouse 2013, p. 230).

Genus ***Pseudostrophalosia*** Clarke, 1970

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

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

Discussion: The source of the genus is not clear: it obviously arose from stock different from that *of preovalis* and *curvata*, and perhaps, if it arose from within Australian faunas, ancestry lies with the species described as *Echinalosia curtosa* Waterhouse, 1986a from the Fairyland Formation, for this species is highly convex with strong spines, and has strongly impressed muscle scars. Until clarified by Briggs (1998), species of *Pseudostrophalosia* were mistakenly assigned to *Wyndhamia* Booker, 1929, a genus which lacks the cluster of ventral ear-spines. *Pseudostrophalosia* appears to be senior synonym of *Notolosia* Archbold, 1986a, type species *N. dickinsi* Archbold, 1986a from the Hardman Member of the Canning Basin, Western Australia, with similar burst of ventral ear spines and wedge-shaped dorsal valve. *Notolosia* was proposed as a subgenus of *Echinalosia*, and was treated as a full genus by Brunton et al. (2000, p. 574).

Pseudostrophalosia brittoni (Maxwell, 1954)

Fig. 34-40

1954 *Strophalosia brittoni* Maxwell, p. 543, pl. 54, fig. 20-22, pl. 55, fig. 1-3.
1964b *Strophalosia* sp. Hill & Woods, pl. P4, fig. 10.
1970 *Pseudostrophalosia brittoni* – Clarke, p. 987.
1970 *Wyndhamia enorme* Clarke, p. 987.
1972 *W. enorme* – Hill, Playford & Woods, pl. P4, fig. 10.
1998 *P. brittoni* – Briggs, p. 113, Fig. 60A-F.

Holotype: UQF 15657 from Tiverton Formation, 6.4km SW of Eungella Station, figured by Maxwell (1954, pl. 54, fig. 20-22), OD. Holotype for *enorme*, specimen UQF 16258 from Tiverton Formation at Homevale, figured by Maxwell (1954, pl. 55, fig. 1, 2), OD.

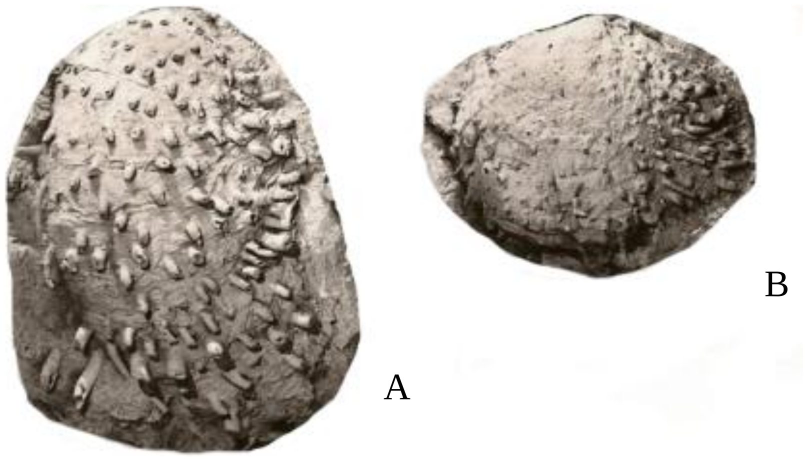


Fig. 34. *Pseudostrophalosia brittoni* (Maxwell). A, latex cast of ventral valve UQF 81295 from UQL 4519, x2. B, latex cast of ventral valve 81296 from UQL 2628, x1.5

Diagnosis: Moderately large and inflated shells with weakly concave dorsal valve which may bear low median fold, moderately wide hinge, ventral spines close-set, of two series, usually in commarginal rows, low angle recumbents about 0.2m in diameter and much more common semi-recumbent spines some 0.6mm in diameter, coarse over ears and forming brush. Dorsal spines closely spaced, 0.2mm in diameter, prominent commarginal lamellae and crowded small dimples. Posterior ventral valve heavily thickened, elongate adductor scars, buttressed large teeth, rare or no internal tunnels. Dorsal valve with raised brachial ridges, thickened anteriorly.

Material: UQL 1626, 1629, 1630, 2584?, 2619, 2620, 2625?, 2626, 2628, 2631, 2629, 2628, 3127, 4515 - 4520.

Taeniothaerus subquadratus Zone, rare in *Svalbardia armstrongi* Subzone. Briggs (1998) recognized the species only at UQL 1629.

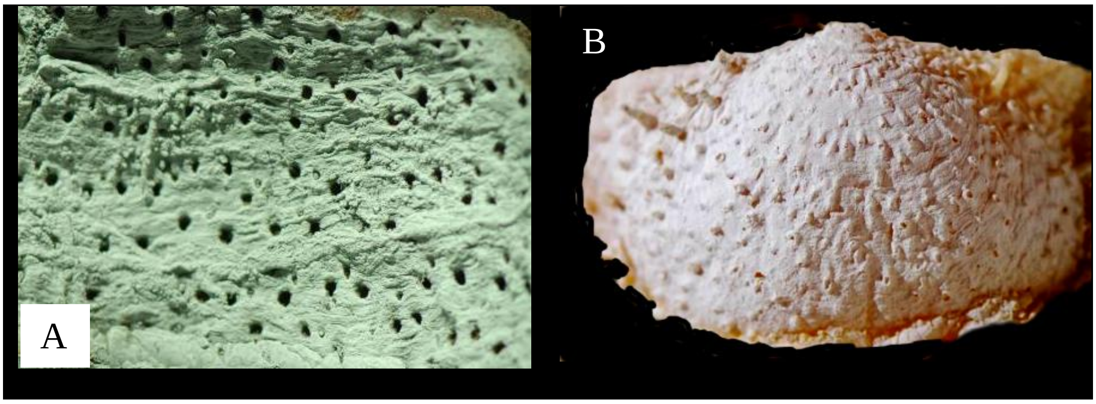


Fig. 35. *Pseudostrophalosia brittoni* (Maxwell). A, detail of anterior ventral external mould, UQF 81280 from UQL 2619, x3.5**.** B, latex cast of ventral valve UQF 81282 from UQL 2625, x2.

Description: Shells large for family, up to 45mm wide, gently arched ventrally, flat medianly, only moderately concavo-convex, and show a dorsal fold. The ventral valve is gently inflated with moderately wide hinge. Ventral ornament involves recumbent spines 0.2mm in diameter and medium-angle recumbent (30^o) spines 0.6mm and up to 1mm in diameter, coarse and close-set over the ears, over 0.7mm in diameter, forming an erect brush (UQL 4518), an important diagnostic feature for the genus first pointed out by Waterhouse (1986a, p. 28). Often ventral spines are arrayed in commarginal rows somewhat approaching those illustrated by Briggs (1998, Fig. 60A – UQF 21206). UQF 21207 shows a few semi-recumbent spines. Ventral spines open into the ears and anterior trail, but spine tunnels are seen over the disc only in immature specimens, except for one mature specimen from UQL 2629 in which there are short channels about 2mm long. Lack of spine tunnels and evidence for spine-openings into the disc implies that spines were isolated from the growing mantle at the circumference of the shell. The dorsal valve is gently to moderately concave with low anterior fold, and displays fine spines, small pits and on some specimens, fine capillae.

Fig. 36. *Pseudostrophalosia brittoni* (Maxwell). A, latex cast of ventral valve UQF 81615 from UQL 4520, x2. B, latex cast of ventral valve UQF 81605 from UQL 2626, x2.

The ventral interior has a heavy posterior umbonal ridge, high and long ventral adductor platform, deeply impressed wide diductor scars, and large teeth. The adductor platform is posteriorly placed and not very long in immature specimens, but becomes long and high with advanced maturity, and diductor scars are placed well forward. The immature dorsal valve has median septum extending to mid-length, broad posteriorly, well defined brachial ridges, firmly impressed elongate inner adductor scars and long ovally triangular posterior lateral adductor scars, comparatively large cardinal process and dental sockets, and well defined brachial ridges. The mature dorsal valve is almost flat internally and somewhat thickened, and curves abruptly into the trail.

A few specimens are found in the *Svalbardia armstrongi* Subzone. A large unusually elongate ventral internal mould from UQL 3127 belongs to the species, with high adductor platform, very large diductor scars, high posterior marginal ridge and comparatively close-set teeth, without buttresses. No spine tunnels are present. The specimen is found with *Svalbardia*. As well, two ventral internal moulds from UQL 4515 of more oval shape belong to the genus and species, showing open spine bases in commarginal rows and no spine tunnels, and closely pitted valve floor.

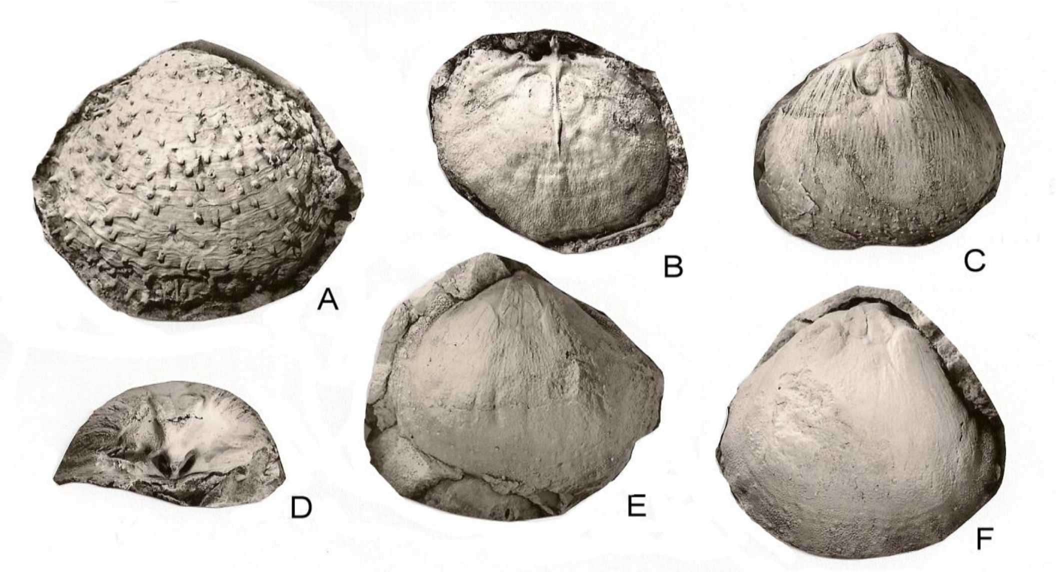


Fig. 37. *Pseudostrophalosia brittoni* (Maxwell). A, latex cast of ventral exterior, UQF 81281 from UQL 1626, x2. B, latex cast of dorsal interior, UQF 81847 from UQL 4518, x 1. C, D, ventral internal mould UQF 81283 from UQL 4519 x1, ventral and posterior aspects. E, ventral internal mould UQF 81284 from UQL 4515, x1. F, ventral internal mould UQF 81616 from UQL 4515, x1.

Resemblances*:* *Pseudostrophalosia brittoni* (Maxwell) is best represented in the Tiverton Formation by large and well preserved ventral valve interiors. The species is not very common. It is found with another large strophalosiid, *Maxwellosia*, which may be distinguished by its denser array of recumbent slender and sturdy erect spines on both valves, fewer spines on the ventral ears, internal spine tunnels, greater convexity-concavity and shorter hinge. Briggs (1998) was first to observe that there are two large strophalosiid species in the Tiverton Formation, whereas the previous survey by Maxwell (1954), as accepted by Waterhouse (1964, p. 32), wrongly mixed the two species. The Briggs clarification also lends considerable weight to the analysis that younger species (*blakei, clarkei*) fall within the same genus *Pseudostrophalosia* (Waterhouse 2001). Because Maxwell figured no exteriors, assessment of the type material depends almost solely on the curvature and inflation of the valves. Three ventral valves were figured by Maxwell and a number of ventral valves from the Tiverton Formation at Homevale agree in profile with that figured by Maxwell (1954, pl. 55, fig. 3).

So-called *Wyndhamia colemani* Archbold, 1987 from the upper part of the Coyrie Formation, Carnar-

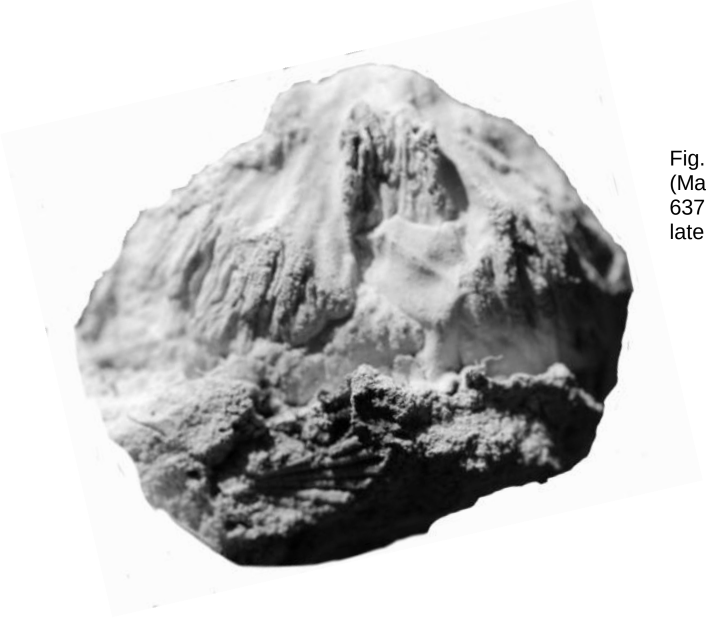


Fig. 38. *Pseudostrophalosia brittoni* (Maxwell), dorsal internal mould of UQF 63768, specimen with valves conjoined at late maturity, x1.5.

von Basin, Western Australia, is a close ally, but is a little less inflated. It belongs to *Pseudostrophalosia*. *Echinalosia (Echinalosia) cenula* is smaller, with more uneven spine array, less developed ear spines, fewer dorsal spines and more dimples and more prominent commarginal laminae. This species is more arched with more concave dorsal valve, smaller ventral muscle field and smaller teeth and other differences.

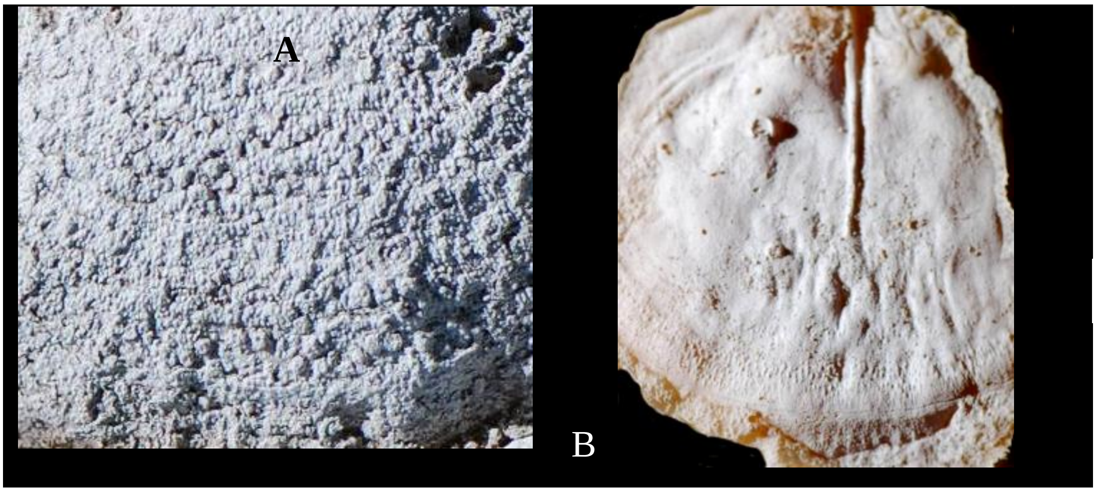


Fig. 39. *Pseudostrophalosia brittoni* (Maxwell), A, external mould of dorsal valve UQF 81344 from UQL 2620, x4. B, latex cast of interior of dorsal valve UQF 81832, from UQL 4518, x2.2, showing anterior pattern of pustules, specimen at early maturity.

Subfamily **DAYSALOSIINAE** Brunton, 1966

Diagnosis: Two series of generally crowded spines on each valve.

Discussion: Only a few genera are known for this subfamily: *Dasyalosia* Muir-Wood & Cooper, *Maxwellosia* Waterhouse and *Acanthalosia* Waterhouse, ranging from Lower Permian into Middle Permian (Waterhouse 2013, p. 225).

Genus ***Acanthalosia*** Waterhouse, 1986a

Type species: *Acanthalosia domina* Waterhouse, 1986a, p. 32 from Dresden Formation (Sakmarian), southeast Bowen Basin, Queensland, OD.

Fig. 40. *Pseudostrophalosia brittoni* (Maxwell), dorsal internal mould of UQF 63768, with valves conjoined, at late maturity, x3. See Fig. 38.

Diagnosis: Moderately to weakly concavo-convex medium-sized to large shells with numerous spines in two orders on ventral valve, prostrate spines thin to almost as strong as erect or suberect series, dorsal spines also crowded, with a number of recumbent as well as erect spines.

Acanthalosia* cf. *domina Waterhouse, 1986a

Fig. 41

cf. 1986a *Acanthalosia domina* Waterhouse, p. 32, pl. 5, fig. 9-18, pl. 15, fig. 8.

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

Diagnosis: Transverse shells with gentle curvature medianly, prominent ventral umbo, dense erect and fine recumbent ventral spines.

Material: Fragments of the ventral exterior from UQL 4506, *Bookeria pollex* Zone.

Dimensions in mm: estimated, from UQL 4506

UQF	Width	Length	Height	Hinge length	
81286	27	?23	7	22	
81287	22	25		17	
81288	13	16.5	7		specimen deformed

Description: Ventral valve of moderate size, weakly transverse, prominent ventral umbo having an umbonal angle of 80°, projecting well beyond hinge, without visible cicatrix, hinge wide, cardinal extremities subangular, moderately high interarea inclined steeply from commissure and bearing high pseudodeltidium. Shell only gently convex with broad umbo and may show wide shallow anterior sulcus. Another specimen has a broad umbo. The ornament is comprised of crowded erect or semirecumbent spines, 0.5mm in diameter posteriorly and 0.8 to 0.9mm anteriorly, spaced often only 1mm apart along rows 1mm apart, and interspersed with fewer low angle

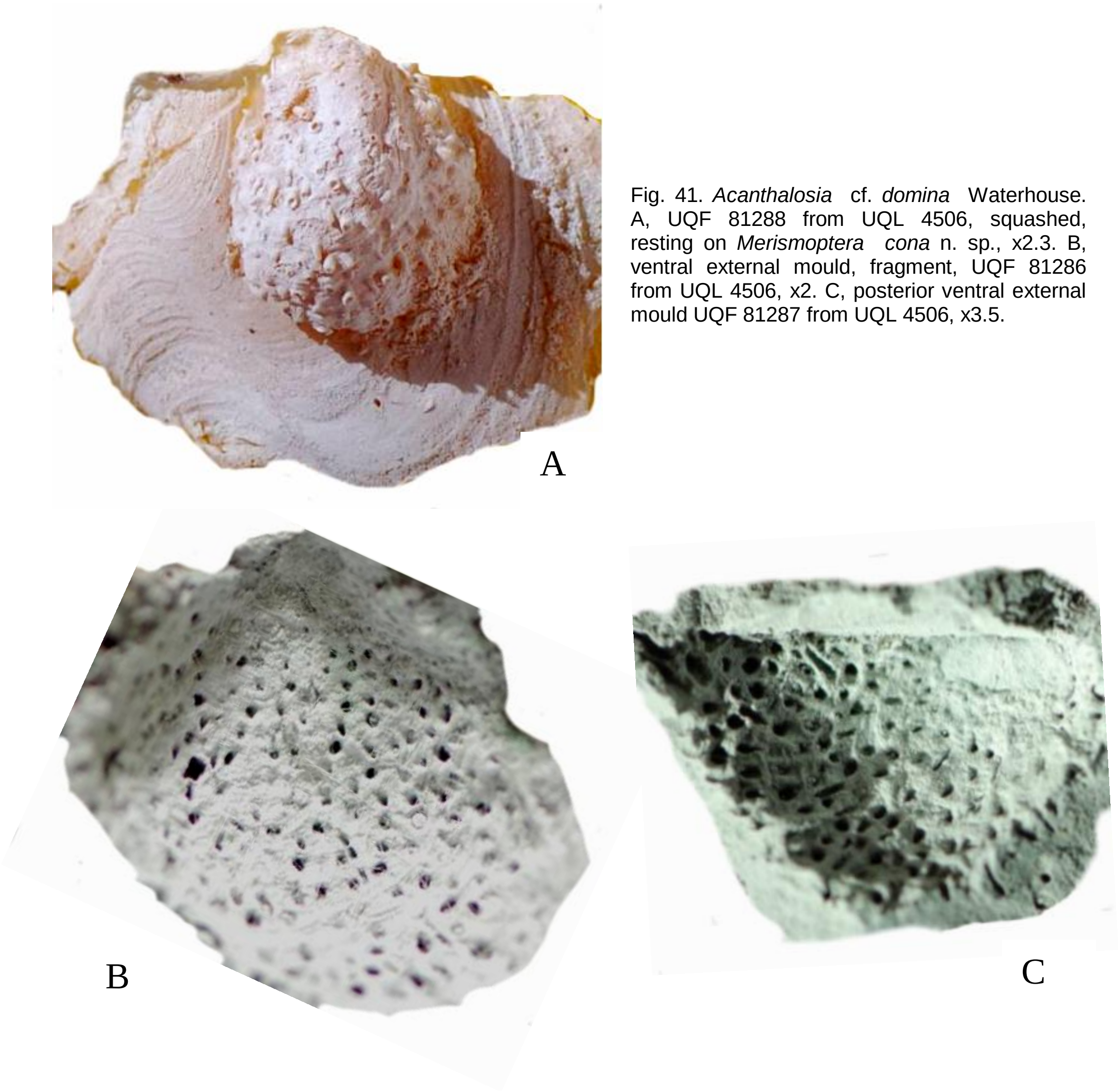


Fig. 41. *Acanthalosia* cf. *domina* Waterhouse. A, UQF 81288 from UQL 4506, squashed, resting on *Merismoptera cona* n. sp., x2.3. B, ventral external mould, fragment, UQF 81286 from UQL 4506, x2. C, posterior ventral external mould UQF 81287 from UQL 4506, x3.5.

recumbent to prostrate fine spines, 0.3-0.4mm in diameter. Growth increments are well developed but low, about six per mm anteriorly.

Resemblances: The wide hinge and dense spines of these specimens point to *Acanthalosia domina* from the Dresden Limestone and Boughyard Member of the southeast Bowen Basin, as figured by Waterhouse (1986a, pl. 5, fig. 9-18, pl. 15, fig. 8), although the spacing of prostrate spines is slightly closer in the present specimens – and the diameter for recumbent spines on *domina* was not provided by either Waterhouse (1986a) or Briggs (1998, p. 108). The Dresden specimens were recorded as showing a median flattening of the convexity, but no sulcation. However the dorsal valve in Waterhouse (1986a, pl. 15, fig. 8) shows the presence of a low fold, and a shallow sulcus would be expected at least in this specimen. Other aspects cannot be adequately compared. There is also considerable approach to *Maxwellosia concava* (Maxwell, 1954) from the upper Wallaby Beds near Warwick (see Briggs 1998, Fig. 57; Waterhouse 2010a, Fig. 23), a species with narrower hinge. Unfortunately the present specimens are too fragmentary to compare adequately, because the dorsal valve and ventral interior, both critical for species delineation, are not preserved. The specimens differ from *Maxwellosia bryani* n. sp. found in higher Tiverton beds, in having denser ornament and in some being transverse with sulcus, and having wide hinge. *Acanthalosia mysteriosa* Waterhouse, 2010a from the Rose's Pride Formation of the southeast Bowen Basin and Cattle Creek Formation of the southwest Bowen Basin has crowded spines, which are much finer (0.3mm) than in the present material, and the venter is gently convex and the overall shape equidimensional.

Genus ***Maxwellosia*** Waterhouse, 2013

Type species: *Strophalosia jukesi concava* Maxwell (1954, p. 551) from Wallaby rocks (Sakmarian), southeast Queensland, OD.

Diagnosis: Moderately large with deeply concave dorsal valve bearing spines of two orders.

Discussion: This genus is distinguished from *Acanthalosia* by the more deeply concave dorsal valve. *Acanthalosia domina, A. mysteriosa* and *A. deari* all have a comparatively flat dorsal valve, more as in *Dasyalosia*.

Maxwellosia bryani n. sp.

Fig. 42 - 49

1964b *Strophalosia preovalis* [not Maxwell] – Hill & Woods, pl. P4, fig. 9 (part, not fig. 6-8 = *preovalis*).

?1964b *S. jukesi concava* [not Maxwell] – Hill & Woods, pl. P4, fig. 15.

1972 *Echinalosia preovalis* – Hill, Playford & Woods, pl. P4, fig. 9 (part, not fig. 6-8 = *preovalis*).

?1972 *Wyndhamia jukesi* – Hill, Playford & Woods, pl. P4, fig. 15.

2013 *Maxwellosia* n. sp. Waterhouse, Fig. 7.17, 7.18.

Derivation: Named for W. H. Bryan.

Fig. 42. *Maxwellosia bryani* Waterhouse, latex cast of ventral exterior UQF 81804 from UQL 1627, x3 .

Holotype: UQF 81269 from UQL 2629, Tiverton Formation, figured herein as Fig. 43, here designated.

Diagnosis: Oval shells with highly convex ventral valve and moderately concave dorsal valve with concave dorsal disc, ventral valve ornamented by coarse spines 0.8 to 1.5mm in diameter, and moderate number of recumbent spines 0.4-0.8mm in diameter. Dorsal spines in two series, erect spines 0.4-0.5mm in diameter, crowded, and rare to moderately numerous low angle recumbent spines of similar diameter. Ventral adductor platform elongate and raised, not posteriorly placed, strong ventral teeth.

Material: Specimens from UQL 1626, 1627, 1630, 1631, 2619, 2620, 2623, 2625, 2626, 2628, 2629, 2631, 3127, 4510 - 4512, 4513?, 4515 - 4520, TK1/2 and T3. *Bookeria geniculata* and *Taeniothaerus subquadratus* Zones.

Dimensions in mm:

UQL	Valve	Width	Length	Height
2629	both	41	37	24
2629	ventral	41	35	16.5

UQL	Width	Length ventral	Length dorsal	Height dorsal	Hinge length
1332	28	27	23.5	9.5	17
4518	18.5		14	5.5	?12

Description: Shells large, the largest specimen 45mm wide, transverse, subequidimensional or elongate, hinge just over half to rarely nearly two thirds of width, maximum width placed near mid-length. Some specimens are transverse and others elongate, rarely with shallow sulcus or low dorsal fold. Cardinal extremities may be acute and produced, venter gently to moderately convex, posterior walls steep. Several specimens have the dorsal interarea in the plane of the commissure with the ventral interarea at a high angle; in other specimens the ventral interarea lies close to the commissural plane with dorsal interarea inclined at a high angle. Ventral spines in two series, erect spines usually from 0.4 to 0.8 and up to 1.5mm in diameter, more or less in rows 2-3.5mm apart with 1-3mm between spines, clustered postero-laterally, low angle recumbent to prostrate spines 0.4-0.5mm in diameter, rarely up to 0.8mm in diameter, less regularly arranged, extended for 3-5mm over shell. Specimens from higher in the Tiverton Formation have finer spines. Irregular strong radial rugae over especially anterior shell. Dorsal valve moderately concave, without fold, tiny convexo-concave nepionic area, which is lamellose with no definite spines, remainder of valve covered by dense mostly erect spines varying from 0.2-0.3mm to 0.4-0.5m in diameter, with scattered comparatively rare prostrate spines of similar diameter, scattered small dimples, close-set low commarginal lamellae, slightly irregular, two up to four or five in 1mm, no radial capillae, rugae rare. Trail short, not geniculate, marked by pits.

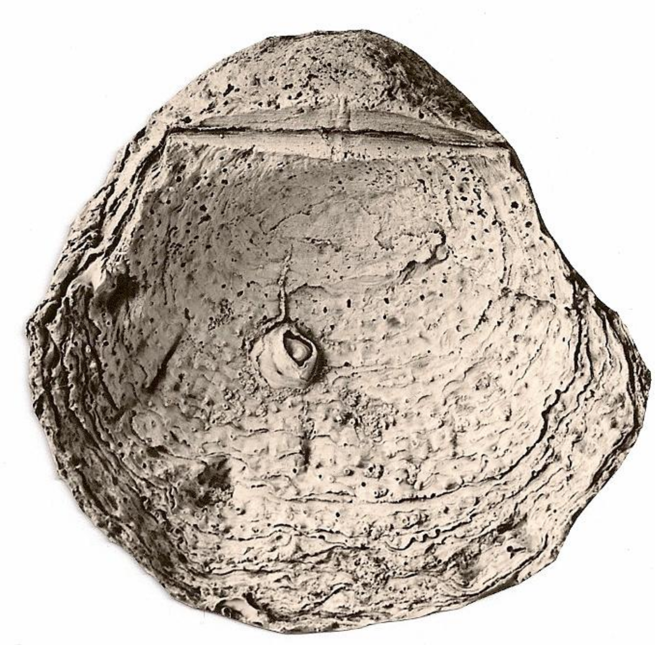


Fig. 43. *Maxwellosia bryani* n. sp., holotype, dorsal view of latex cast of UQF 81269 from UQL 2629, x2.

Ventral interior with sturdy teeth supported by buttresses (UQL 4515, UQF 21080-1) which may reach the floor of the valve (Fig. 45D). Adductor platform very long and raised, usually 13-15mm long in shells about 40mm long, may be marked by one or two longitudinal ridges, and often by growth ridges parallel to anterior margin, placed close to the posterior wall except in one specimen (Fig. 46A). Diductor scars heavily impressed,

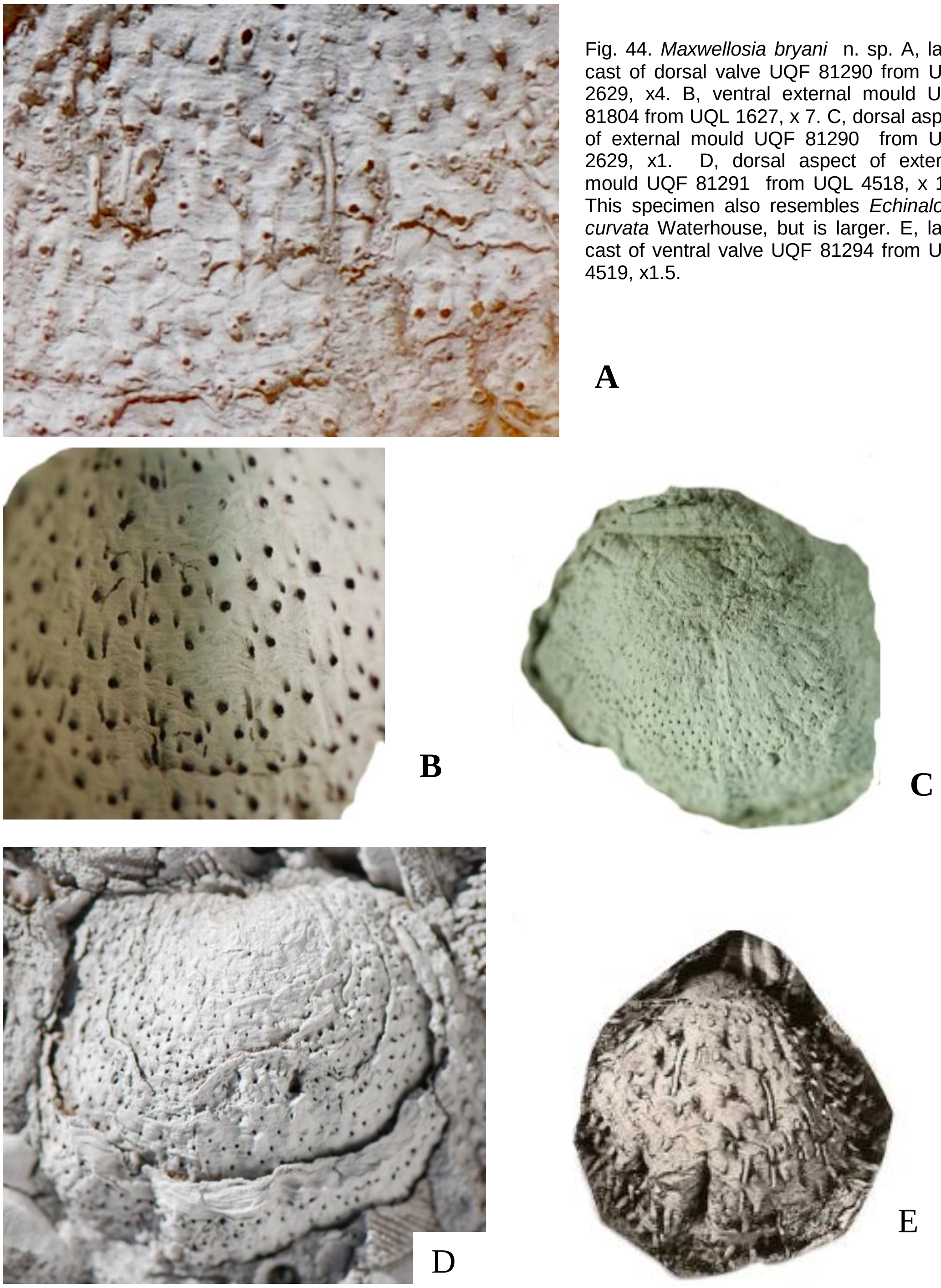


Fig. 44. *Maxwellosia bryani* n. sp. A, latex cast of dorsal valve UQF 81290 from UQL 2629, x4. B, ventral external mould UQF 81804 from UQL 1627, x 7. C, dorsal aspect of external mould UQF 81290 from UQL 2629, x1. D, dorsal aspect of external mould UQF 81291 from UQL 4518, x 1.5. This specimen also resembles *Echinalosia curvata* Waterhouse, but is larger. E, latex cast of ventral valve UQF 81294 from UQL 4519, x1.5.

scored by grooves, placed a little in front of adductors (UQF 21080). Posterior walls thick, and covered by pustules, anterior floor bearing faint grooves and pustules, spines open into the anterior valve. Submarginal ridge may extend around posterior and postero-lateral edge of disc. A number of specimens are marked by long spine tunnels extending through the shell in front of the spine base in a median strip, in front of the muscle field and behind the anterior shell in which spines open directly into the interior.

Dorsal interiors rare, with thick median septum extending just past mid-length, large cardinal process, broad low ridge each side behind adductor scars, posterior lateral scars either triangular and slender or more subrectangular in outline, anterior scars triangular and may be large, both sets smooth until late ontogeny, then becoming dendritic. Brachial ridges clearly defined only in late maturity, low posterior marginal ridge, no conspicuous pustules. The dorsal shell appears not to be thickened into an anterior wedge (UQL 4518, 4519) until maturity, and then becomes thick.

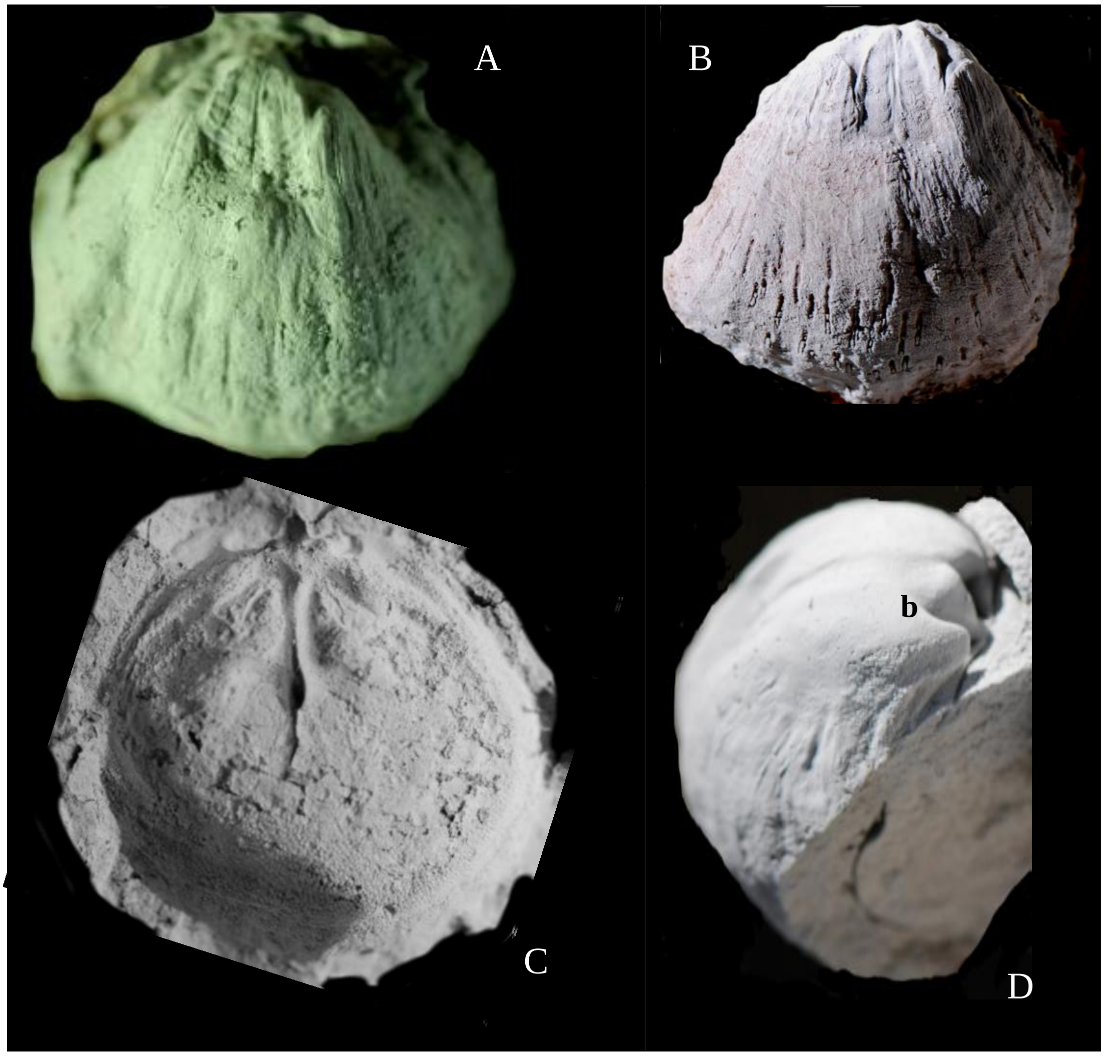


Fig. 45. *Maxwellosia bryani* n. sp. A, ventral internal mould UQF 81297 from UQL 4517, x2. B, ventral internal mould UQF 21080, x2. C, dorsal internal mould UQF 81298 from UQL 2619, x2. D, internal mould of ventral valve oriented vertically, to show large dental buttresses (b), UQF 81806 from UQL 2631, x2.3.

Resemblances: The shells are large like those of *Pseudostrophalosia brittoni* (Maxwell) in the same beds, and have rather similar interior as far as large teeth and marginal ridges are concerned, but spine tunnels are present in many of the ventral interiors. The species is distinguished by its considerable height, and more dense and diverse spines on both valves. Briggs (1998) assigned some of the specimens from UQL1625-1627 to *Acanthalosia domina* Waterhouse, but specimens of this species are slightly smaller, with more arched ventral umbo, wider hinge, much less concave dorsal valve, finer prostrate ventral spines only 0.2mm in diameter, erect spines less organized in commarginal rows, denser and finer ventral spines, and especially dense dorsal spines with more recumbent spines 0.2 and 0.4-0.5mm in diameter, and less elongate ventral adductor scars. The species *domina* comes from the Dresden Limestone and Boughyard Member in the southeast Bowen Basin, and from the basal Tiverton Formation at Homevale. The dorsal spines of *bryani* are not as tangled nor as clearly biserial as in the type species of *Acanthalosia, A. domina*, or *Maxwellosia concava*, and some of the dorsal exteriors, such as those figured in Fig. 46C and 50C, D, look close to those of *Echinalosia curvata*

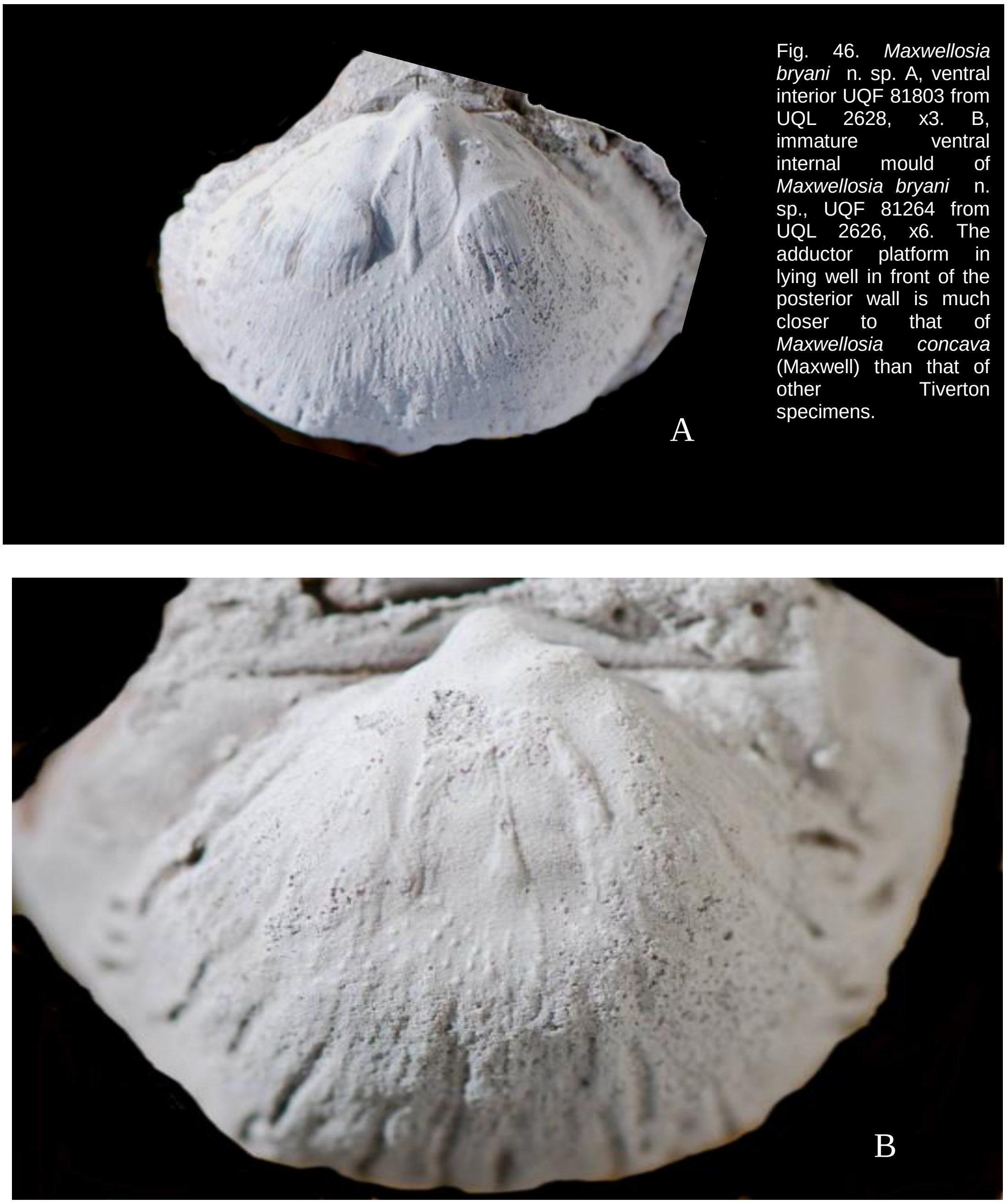


Fig. 46. *Maxwellosia bryani* n. sp. A, ventral interior UQF 81803 from UQL 2628, x3. B, immature ventral internal mould of *Maxwellosia bryani* n. sp., UQF 81264 from UQL 2626, x6. The adductor platform in lying well in front of the posterior wall is much closer to that of *Maxwellosia concava* (Maxwell) than that of other Tiverton specimens.

Waterhouse. The specimens are however larger than specimens of *Echinalosia curvata*, and display internal ventral spine tunnels, so they are allocated to *Maxwellosia bryani*, and this appears to be reinforced by external casts of the specimens which suggest prostrate and erect spines.

Briggs (1998) identified somewhat similar material from the “upper Wallaby beds” of the Wildash Group at Rokeby, south Queensland, with *Strophalosia jukesi concava* Maxwell), assigning them to *Acanthalosia concava*. The type material of *concava* that was described and figured by Maxwell (1954, pl. 57, fig. 1-3), including the holotype (fig. 2, 3), involves small ventral valves with high muscle field standing above the posterior wall, and extending well behind the diductor scars. As well the hinge is short and posterior shell constricted. UQF 15637 has a strong sulcus and short hinge, and the holotype UQF 15638 is also small with small dental buttresses and low ventral adductor platform and internal spine channels. The unfigured fragment of an external ventral valve on the same block as UQF 15637 shows scattered erect spines and rare spine tunnels but no prostrate spines. An unfigured dorsal valve on the same rock sample UQF 15638 has erect spines, and no apparent capillae. These specimens are poorly preserved, and appear to lack the numerous prostrate spines found on both valves of this genus, but this could be due to either poor preservation or to small size. Briggs (1998) allocated them to *Acanthalosia*, because larger specimens from the same collection clearly belong to *concava*, with prostrate ventral spines and mixed prostrate and erect dorsal spines. A large ventral valve (Briggs 1998, Fig. 57H) also shows the adductor.platform standing above the floor of the valve and projecting posteriorly. That the large Wallaby specimens are the same as the small figured types has an element of uncertainty which cannot be gainsaid, but judged from the nature of the muscle scars, the Briggs interpretation is favoured. As a rule, the Tiverton material does not possess similar adductors in either small or large specimens, in which the adductors are less extended behind the diductors and less deeply impressed into the posterior wall, except in UQF 81264 as figured in Fig. 46B. As well the dorsal valve of the Tiverton form is less concave with more flattened disc, and the ventral valve more convex, so that the visceral cavity of these specimens is more inflated than that of *curvata*. The similarities, apart from differences in concavity and size, are deemed to reflect convergence from different stock.

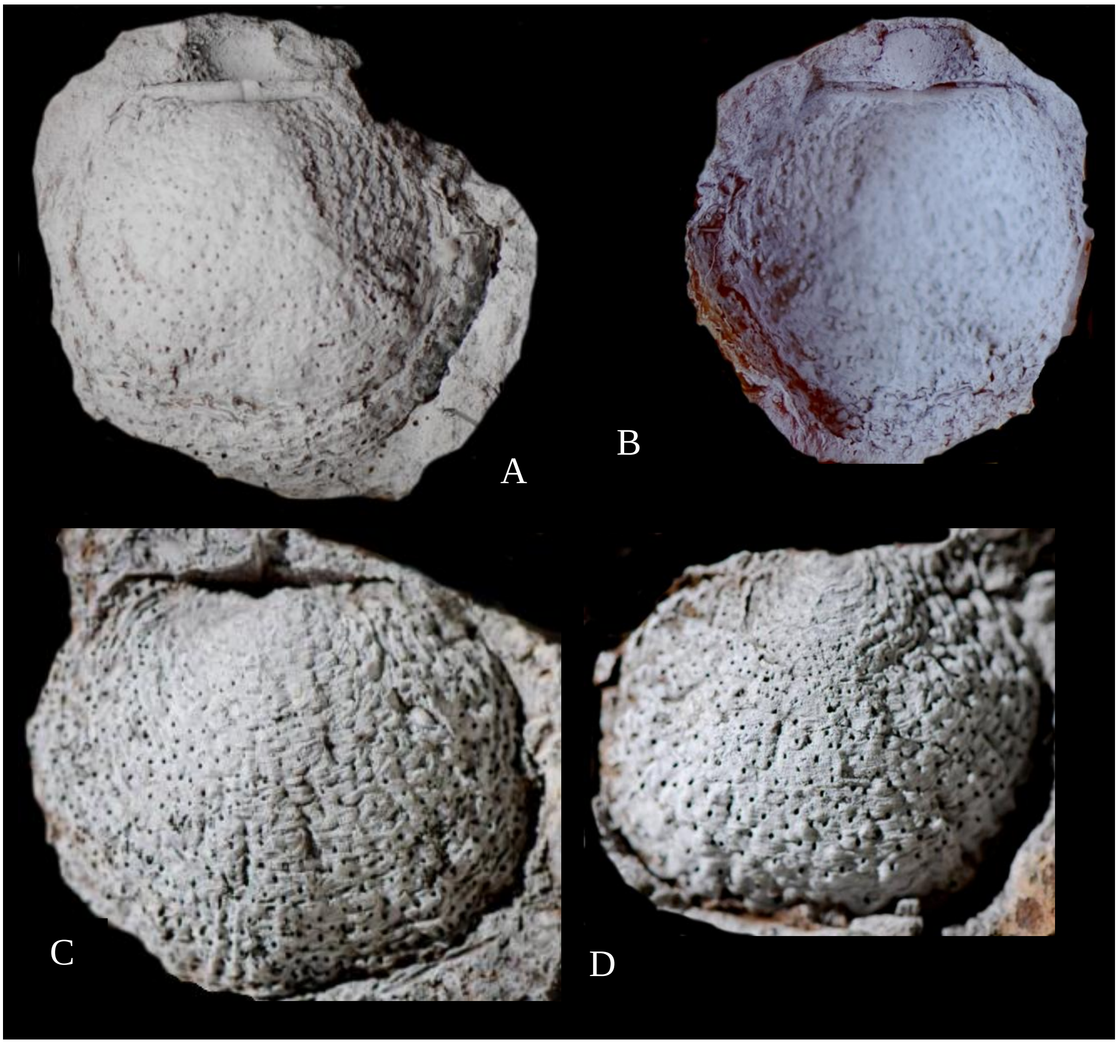


Fig. 47. *Maxwellosia bryani* n. sp. A, B, dorsal external mould and latex cast of UQF 81802 from UQL 2631, x2. C, dorsal external mould of UQF 81293 from UQL 4516, x2. D, dorsal external mould of UQF 81849 from UQL 1626, x2. The identity of C and D is not certain, and show some approach to *Echinalosia* (*Echinalosia*) *curvata* Waterhouse, but are larger and the external casts suggest *Maxwellosia*.

Fig. 48. *Maxwellosia bryani* n. sp. UQF 81804 from UQL 4519, x 2.

Topotype specimens of *concava* so far described are slightly smaller, and the spines are finer, from 0.4 to 0.8mm in diameter for the erect ventral spines (compare 0.4-1.5mm for Tiverton material), and recumbent spines are 0.3 up to 0.5mm (compare 0.4-0.8mm for Tiverton shells), but some spines shown in figures by Briggs (1998) appear to be coarser than the measurements he gave for *concava* topotypes. Dorsal spines are fine, at 0.1 to 0.2mm, from measurements provided by Briggs (1998), compared to 0.2-0.3mm for Tiverton shells. Dorsal recumbent spines are more numerous in Wallaby specimens. Topotype *concava* has been extensively figured in Briggs (1998) and Waterhouse (2010a, Fig. 23). Further specimens were figured by

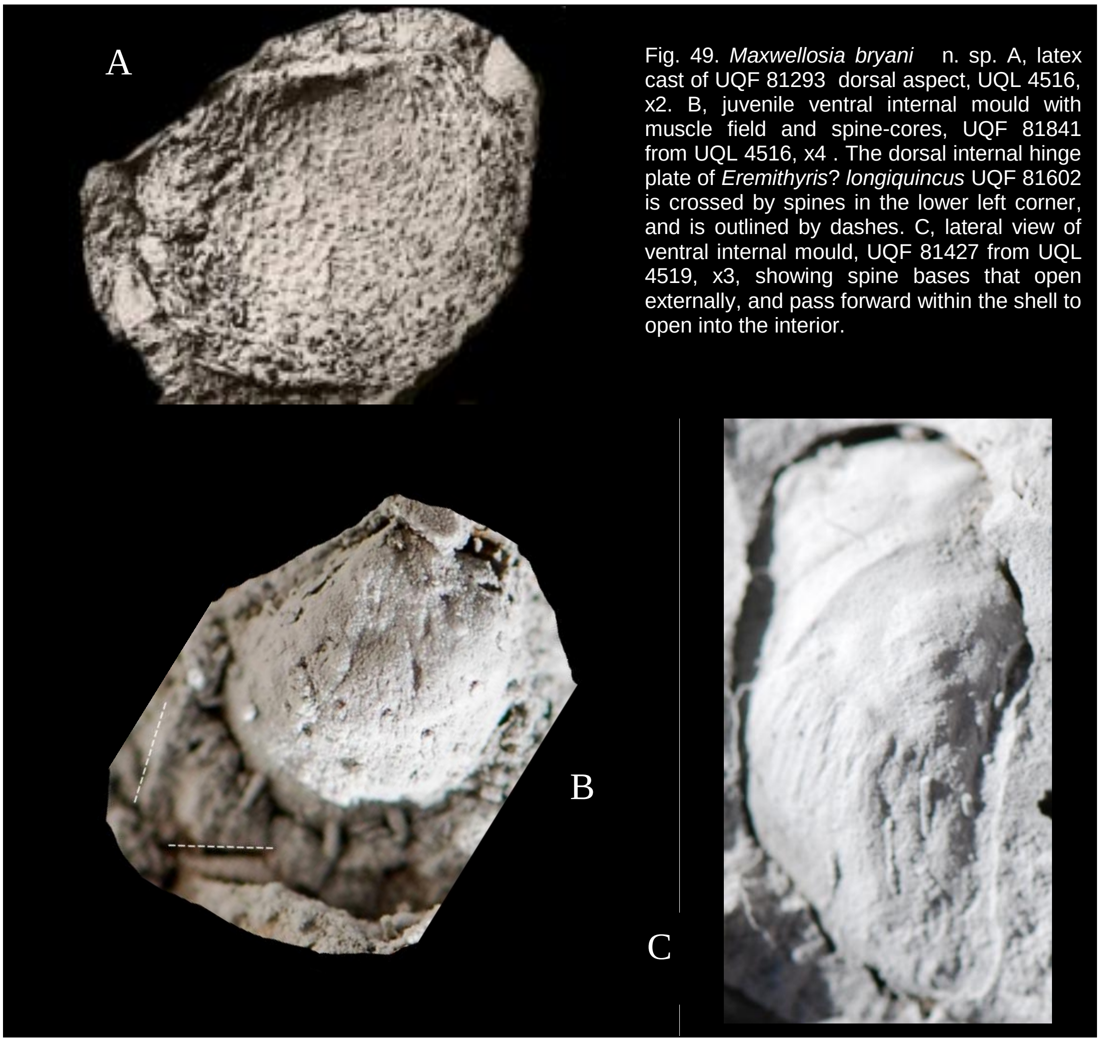


Fig. 49. *Maxwellosia bryani* n. sp. A, latex cast of UQF 81293 dorsal aspect, UQL 4516, x2. B, juvenile ventral internal mould with muscle field and spine-cores, UQF 81841 from UQL 4516, x4 . The dorsal internal hinge plate of *Eremithyris*? *longiquincus* UQF 81602 is crossed by spines in the lower left corner, and is outlined by dashes. C, lateral view of ventral internal mould, UQF 81427 from UQL 4519, x3, showing spine bases that open externally, and pass forward within the shell to open into the interior.

Richards & Bryan (1924) as *Strophalosia jukesi* [not Etheridge], including a dorsal interior (pl. 20, fig. 4). The specimens on a block figured by Richards & Bryan (1924, pl. 20, fig. 3) are more difficult to interpret from the figure, but show elongate ventral adductor muscle field placed well in front of the posterior walls (UQF 40182). They were not included in *Acanthalosia concava* by Briggs (1998), but appear to belong to that species. *Acanthalosia mysteriosa* Waterhouse (2010a, Fig. 24) is based on material from the Rose's Pride and upper Cattle Creek Formations, and shows a marked change in the genus to finer and more numerous ventral spines. Material from the southwest Bowen Basin is particularly abundant, judged from Geological Survey of Queensland collections (eg. D80) at the Queensland Museum. *A*. *deari* (Briggs, 1998), based on UQF 73991 figured by Waterhouse (1986a, pl. 5, fig. 24, 29) from the Flat Top Formation of the southeast Bowen Basin also has fine and numerous spines, and the specimens are small with flattish dorsal valve and more numerous ventral recumbent spines 0.1-0.2mm in diameter, and no hinge row of spines.

Echinalosia ardua Waterhouse, 1982a, p. 30, with holotype BR 1476 from the Brunel Formation, New Zealand, is more transverse, and is sulcate, with few internal spine tunnels, and more posteriorly placed and short ventral adductor scars. The recumbent to prostrate spines on the dorsal valve are thicker than the erect dorsal spines, as discussed in Waterhouse (2001, p. 83). The species is highly distinctive, notwithstanding claims by Briggs (1998) that it is the same as *concava*, but generic aspects do indicate that the species is likely to belong to *Maxwellosia*.

Infrasuborder AULOSTEGIMORPHII Waterhouse, 2010a

This infrasuborder is derived from within Strophalosioidea, and involves superfamily Aulostegoidea, and its derivative superfamily Richthofenioidea. In Aulostegoidea, members are united by spine-dominated ornament, tendency to develop low ventral interareas, and small scars of attachment, with dendritic muscle scars and no teeth. Shells are particularly diverse in shape and ornament, and possess a large cardinal process of unusual nature, involving two large lateral sheaves, and unusual posterior elevator muscle scars on the ventral valve. Ventral spines may be prolonged anteriorly in spine tunnels.

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

Discussion: The general relationships of Aulostegoidea are summarized by Waterhouse (2013, Fig. 10.1). Many authorities have preferred an alliance with *Strophalosia* (Strophalosiidina), as in Muir-Wood & Cooper (1960) and Brunton et al. (2000), following the pioneering studies of the nineteenth century, whereas Coleman (1957, p. 34), Waterhouse (1983b, 2001), Brunton & Mundy (1988) and Briggs (1998) have placed the superfamily with Productidina. In particular the nature of the brachial ridges is productin (Waterhouse 1983b, p. 192), as is the nature of the cardinal supports and the dorsal adductor scars, with further similarities, well documented by Briggs (1998). But as shown in Waterhouse (2013), Aulostegoidea were derived from Strophalosioidea, Subfamily Rhytialosiinae Lazarev, and must be classed in the same suborder, even though members developed a productiform morphology.

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

Subfamily **TAENIOTHAERINAE** Waterhouse, 2002b

Diagnosis: Large shells with erect and/or prostrate spines on both valves, not rhizoid on dorsal valve, spine bases variable and patterns vary. Interior with large ventral muscle scars that often include small ancillary scars lateral to the adductors.

Discussion: This subfamily differs from Aulosteginae in the lack of rhizoid spines. Genera include *Taeniothaerus* Whitehouse, *Carilya* Archbold, *Lakismatia* Waterhouse, *Lipanteris* Briggs and *Wyatkina* Fredericks. The subfamily flourished in Australia during Permian time.

Genus ***Taeniothaerus*** Whitehouse, 1928

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

Diagnosis: Shells distinguished from allied genera by wide hinge, low to moderately high ventral interarea, spines numerous on venter, arise from short to long spine tubercles or ridges, spine cores extended anteriorly from base within shell over median part of valve, spines crowded on posterior flanks and form halteroid brushes. Dorsal valve with regular closely spaced elongate dimples and tubercles, spines comparatively uniform, erect or semi-recumbent, arising from pustules, may be finer and arranged in rows anteriorly. Cardinal process not deeply embayed or strongly incurved.

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

Briggs (1998) failed to acknowledge the revision of *Taeniothaerus subquadratus* by Parfrey (1983), based on material from the Berriedale Limestone, Tasmania. Parfrey (1983, Fig. 3B) noted fine and coarse spines interspersed near the ventral anterior margin, whereas coarse and fine spines are interspersed over the entire valve in *Saeptathaerus* Waterhouse.

Taeniothaerus subquadratus (Morris, 1845)

Fig. 50 - 53

1845 *Productus subquadratus* Morris, p. 284.

1892 *Productus subquadratus* – Etheridge, p. 252, pl. 37, fig. 18, pl. 38, fig. 7-10, pl. 40, fig. 5?

1909 *Productus* (?) *subquadratus* – Etheridge & Dun, p. 300, pl. 16, fig. 1 (part, not fig. 2 - 5 = *homevalensis* Briggs).

1950 *Aulosteges* (*Taeniothaerus*) *subquadratus* – Hill, p. 6, pl. 1, fig. 1 (part, not pl. 5, fig. 1, 2 = *homevalensis*; pl. 6, fig. 4 = *farleyensis* Briggs).

1957 *Taeniothaerus subquadratus* – Coleman, p. 87, pl. 15, fig. 1-7.

1983 *T. subquadratus* – Waterhouse et al., p. 126, pl. 1, fig. 11.

1983 *T. subquadratus* – Parfrey, p. 291, Fig. 2-4.

1998 *T. subquadratus* – Briggs, p. 139.

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

Diagnosis: Large elongately oval shells with sulcate venter, low dorsal fold, moderately wide hinge, spines coarse for genus, up to 1.5mm in diameter anteriorly, well developed halteroid brush, coarse elongate spine ridges, dorsal spines 0.2-0.7mm in diameter anteriorly, reaching 1mm, dimples closely spaced, interspersed with some fine spines at start of trail at least in Tasmanian specimens (Parfrey 1983, Fig. 2C).

Material: Specimens from the Tiverton Formation are found at UQL 1383, 1627, 1630, 2619, 2620, 2631, 3127, 3129, 4516, 4517, 4518, 4519, 4520, 4524, 4525 and T3. *Taeniothaerus subquadratus* Zone.

Description: Mature specimens large, with inflated ventral valve bearing a broad and enrolled umbo, above a narrow and low interarea, and as a rule, a ventral sulcus. The dorsal valve is convex near the hinge, then becomes concave, and turns sharply into the trail. The hinge is wide, and ears not prominent. The species is characterized by its large and well spaced posteriorly elongated spine bases over both valves, as well illustrated by Hill (1950), Coleman (1957) and Parfrey (1983). The spines themselves may be large, often exceeding 1mm in diameter on both valves, and reaching 1.5mm on the ventral valve, and over the middle shell are extended in front of the base through the shell as tunnels. Dorsal spines as a rule 0.3-0.5mm in diameter. As shown in Fig. 50C and 51B, the posterior ventral adductors lie within a pair of additional muscle scars, subdendritic and extended postero-laterally. The dorsal interior of mature shells is enclosed by a high marginal ridge posteriorly.

The distribution through the Tiverton Formation is expanded from that presented by Briggs in Waterhouse et

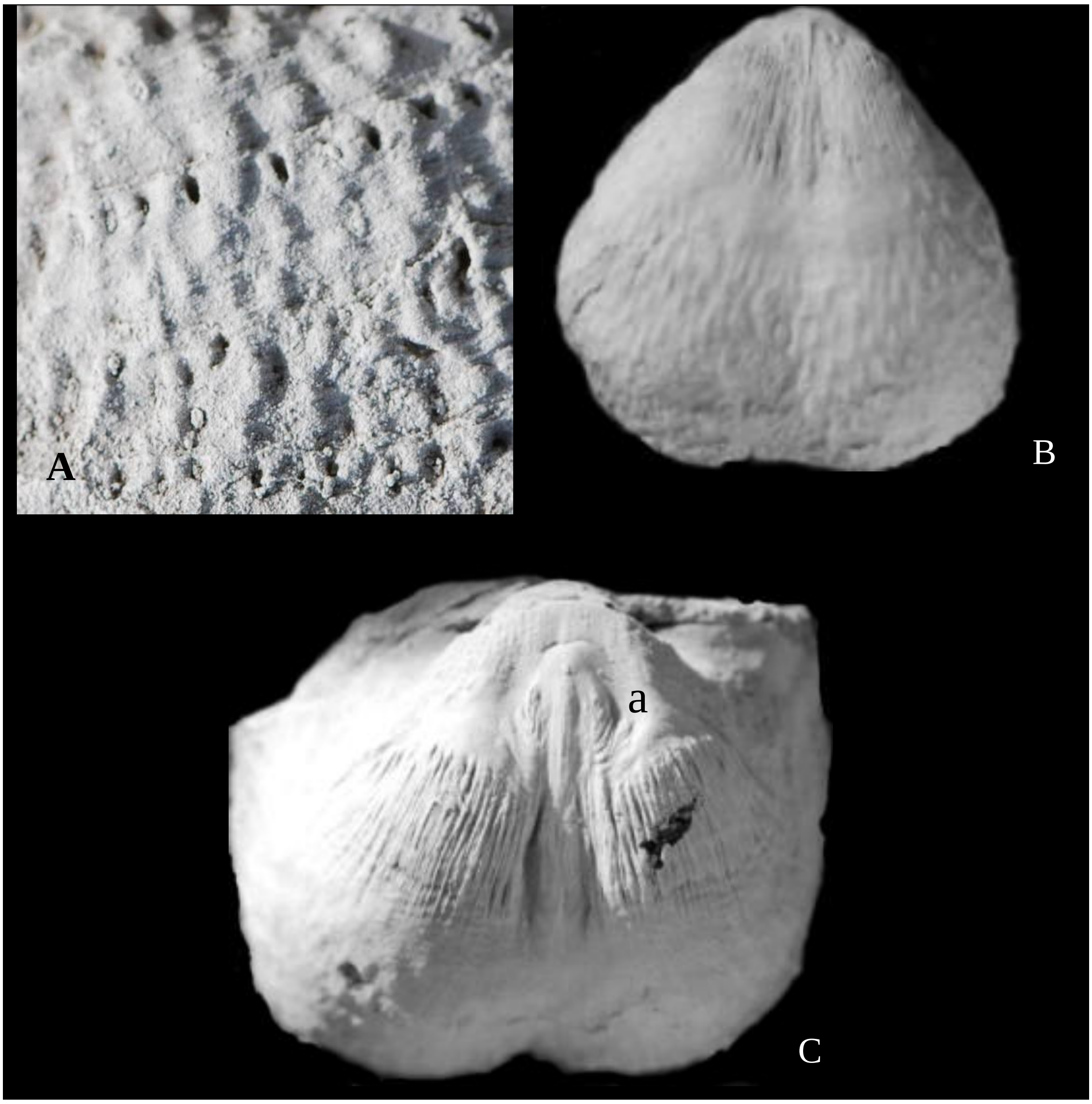


Fig. 50. *Taeniothaerus subquadratus* (Morris). A, detail on external mould of dorsal valve UQF 81195 from UQL 4519, x4. B, ventral aspect of internal mould UQF 81189 from UQL 2620, x1. C, ventral internal mould UQF 81188 from UQL 2620, x1.5. Note ancillary scars (a) each side of the posterior adductors in C.

al. (1983) and Briggs (1998). Briggs in Waterhouse et al. (1983) limited *subquadratu*s to the upper middle Tiverton Formation localities UQL 4521- 4524, but dorsal valves from UQL 4520 have comparable spines 0.6-0.8mm in diameter, and a ventral valve from UQL 4517 has ventral spines 1.2mm in diameter. Briggs (1998) recorded few specimens from Homevale (UQL 1630, 2620 and 4519), but many more specimens from additional localities belong to the species. A fragment from UQL 4525, not included in previous studies, has spines 1.2 to 1.4mm in diameter on the lateral slopes, and another from the same locality has spines 1.5mm wide. A fragment from UQL 3127 has spines 1.5mm wide, and another fragment from UQL 3127 has anterior lateral spines 1.2mm in diameter. Ventral body spines on a small specimen from UQL 4517 are 1mm in diameter. Several dorsal and ventral valves have very large and well spaced spine bases, such as those from UQL 1383 and 2619, like some of the specimens that come from UQL 4519. Thus the species would, if they are interpreted from the criteria adduced by Briggs (1998), appear to be more common than previously recognized, and moreover, it overlaps with *homevalensis* Briggs, being found in some of the same localities.

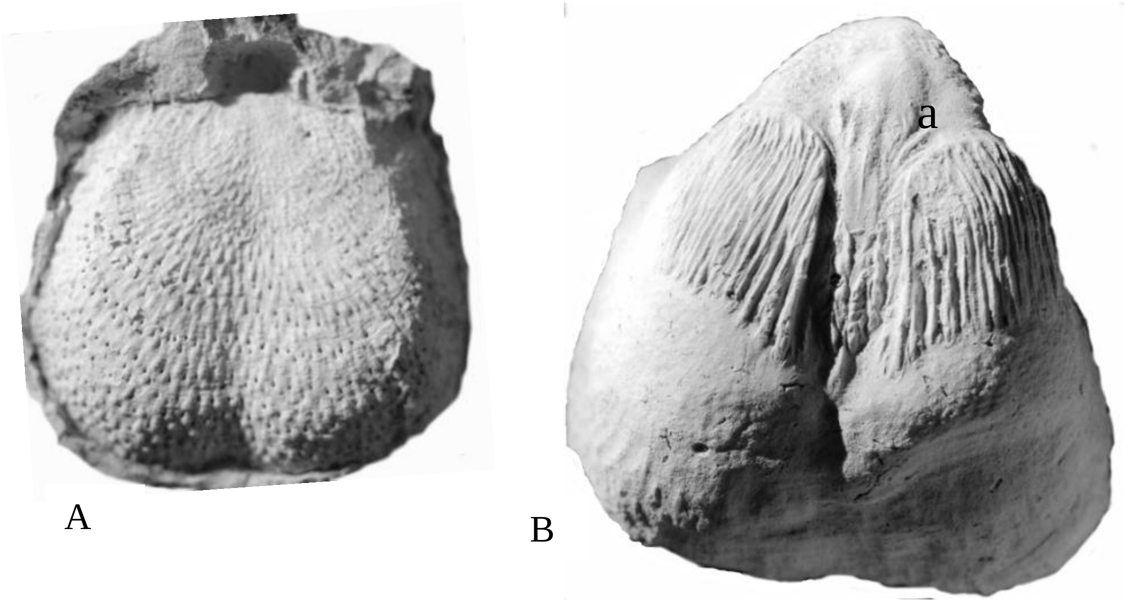


Fig. 51. *Taeniothaerus subquadratus* (Morris). A, dorsal external mould of UQF 81276 from UQL 4519, x1. B, ventral internal mould UQF 81191 from UQL 3127, x1.5. Note ancillary muscle scars (a) each side of posterior adductors.

The ventral valve has long narrow adductor impressions, a long inner pair with faint grooves and a outer pair of ancillary scars with dendritic or postero-laterally inclined moderately deep grooves. Dorsal adductors include a small inner anterior pair, with irregular ridges and large posterior lateral scars marked by dendritic ridges. Pustules are prominent over the anterior inner shell.

Fig. 52. *Taeniothaerus subquadratus* (Morris), A, B, detail of dorsal external mould near start of trail, showing spine bases as black circles, UQF 81426 from UQL 2631, x6.

Resemblances: The Tiverton material is identified with *Taeniothaerus subquadratus* from the Berriedale Limestone of Tasmania, although aspects of the Tasmanian material remain uncertain, and in a number of Tasmanian specimens the ventral spine bases are shorter and spaced further apart. A specimen AMF 11571 as figured by Coleman (1957, pl. 15, fig. 7) has ventral spines 1.5mm in diameter, that appear to be spaced a little further apart than in present material. Material close to *subquadratus* is kept at the National Museum of Victoria, collected by G. A. Thomas from the Callytharra Formation in the K52 Range, north of the main road, at Middalya Station, Carnarvon Basin. There are sturdy thick ventral spines with short bases up to 2mm wide, and fine radial threads over parts of the shell, and dorsal dimples. Coleman (1957, pl. 15, fig. 8-12) reported somewhat similar material from the Fossil Cliff Formation of Western Australia.

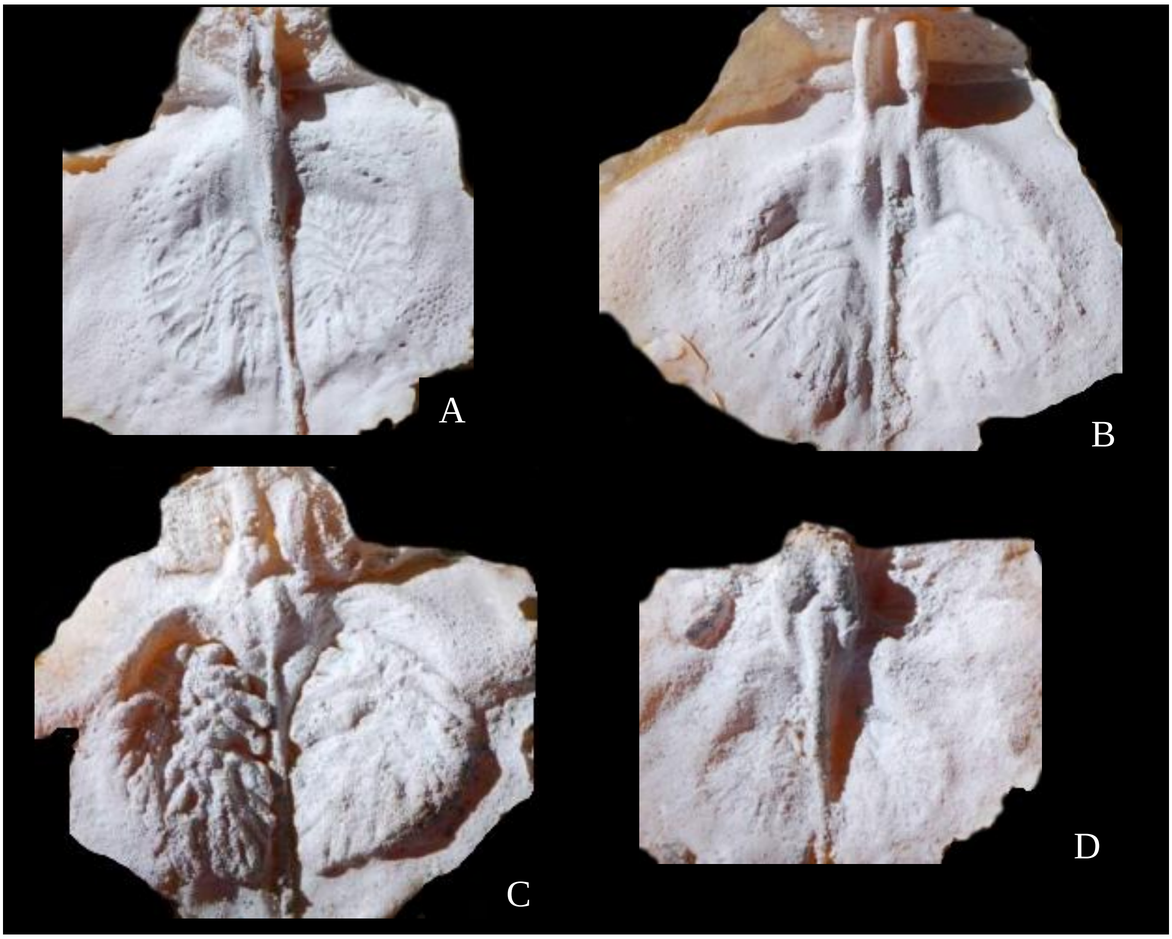


Fig. 53. *Taeniothaerus subquadratus* (Morris), latex casts of cardinalia of dorsal valve. A, UQF 81189 from UQL 2620, x1.5. B, UQF 81211 from UQL 2620, x1.5. C, UQF 81190 from UQL 4517, x2. D, UQF 81193 from UQL 4518, x1.5.

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

Note on *acanthophorus* (Fletcher, 1945b)

1945b *Aulosteges acanthophorus* Fletcher, p. 314, pl. 23, fig. 1-3.

1950 *Aulosteges* (*Taeniothaerus*) *subquadratus* var*. acanthophorus* – Hill, p. 7, pl. 2, fig. 3-4, ?5, ?6.

1964b *T. subquadratus* var. *acanthophorus* – Hill & Woods, pl. 5, fig. 3 (part, not fig. 4 = ?*homevalensis*).

1972 *T. subquadratus* [not Morris] – Hill, Playford & Woods, pl. 5, fig. 3 (part, not fig. 4 = ?*homevalensis*).

1998 *T. subquadratus* – Briggs, pp. 139, 140 (part).

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

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

Discussion: Briggs (1998) synonymized the taxon *acanthophorus* Fletcher, 1945b from the lower Cattle Creek Formation with *Taeniothaerus subquadratus*. The two certainly look similar, and the spacing of the ventral spines is close to that of Berriedale specimens of *subquadratus*. The type specimen of *acanthophorus* and UQF 1994 (Hill 1950, pl. 2, fig. 4) have spine-bases 5mm long that swell to a width of 1.5mm and comparably coarse semi-recumbent ventral spines, which appear to be less regularly disposed over the venter than in Tiverton *subquadratus.* The type specimen of *acanthophorus* is not perfectly preserved. The spines making up the lateral brush are fewer than in typical *subquadratus*, but are close-set (Fletcher 1945b, pl. 23, fig. 1-3; Hill 1950, pl. 2, fig. 3-6; Hill & Wood 1964b, pl. P5, fig. 3; Hill, Playford & Wood 1972, pl. P5, fig. 3). Ventral anterior spines are very coarse. Spine bases are coarse and elongate (often 5mm), less regularly in quincunx than in *subquadratus*, and erect anteriorly, and they are mixed with more slender and subprostrate spines. The dorsal exterior of *acanthophorus* is poorly preserved and dorsal spines appear to involve sets of erect and semi-recumbent spines, whereas dorsal spines are uniform and erect or high-angle recumbent on *T. subquadratus* from Homevale. It is not clear that regular dorsal tubercles are developed as in *subquadratus*. The dorsal interior figured by Fletcher (1945b, pl. 23, fig. 2) suggests the presence of lateral buttress plates, a feature completely absent from *Taeniothaerus*, but present in *Colemanosteges* Waterhouse and *Saeptasteges* Waterhouse, prominent in Permian faunas of Western Australia (Waterhouse 2002a, p. 230; 2002b, p. 49). The species *acanthophorus* appears closest to *Colemanosteges,* given the similarity in spines and the presence of lateral buttress plates. *Colemanosteges* is classed as Rhamnariinae Muir-Wood & Cooper, within Rhamnariidae, Superfamily Sccachinelloidea Licharew (see Waterhouse 2013, p. 249). Fragments figured by Hill (1950, pl. 2, fig. 5, 6) are too small to be identified with confidence, and need not belong to *acanthophorus*. On one, there are buttress supports which converge anteriorly as in *Taeniothaerus*. Despite various collecting expeditions by members of the Geological Survey of Queensland, no further material appears to have been found.

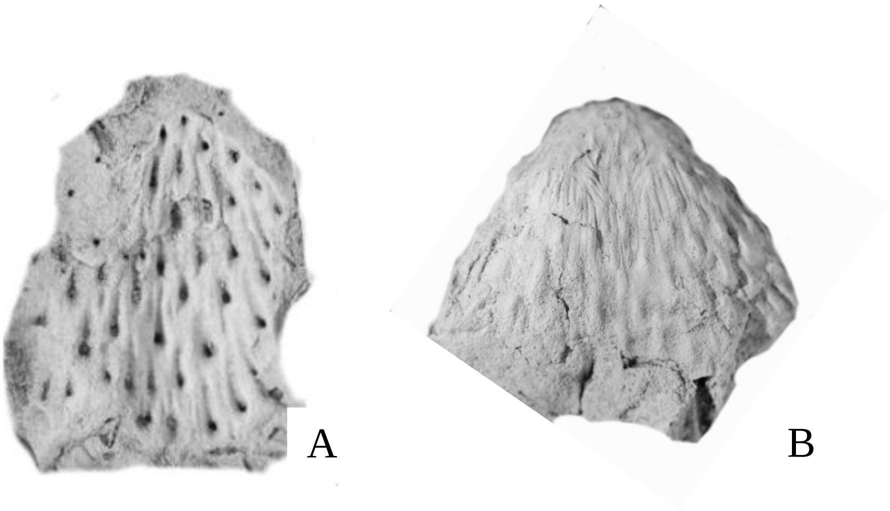
Material from the Yarrol Basin includes specimens UQF 12413-4 labelled *Aulosteges* (*Taeniothaerus*) *subquadratus* var. *acanthophorus* (Fletcher) as identified by Fletcher (1945b, p. 315) from UQL 591 at Yarrol Station above the Burnett River bank west of the homestead. A ventral fragment shows evenly spaced semi-recumbent to erect spines 0.7 to 1.2mm in diameter, with small or no posterior bases, and more close-set anteriorly. The dorsal valve has dense fine spines 0.2-0.4mm in diameter, most prostrate but a number erect. A high blade is suggested in the dorsal shell structure, and appears to be a medium septum. These specimens somewhat resemble the Cracow species named *Taeniothaerus lakismakos* by Briggs (in Waterhouse 1986a), now the type species of *Lakismatia* Waterhouse, 2010a, p. 18.

Taeniothaerus sp.

Fig. 54

A fragment of an exterior of a ventral valve from UQL 4518 has exceptionally coarse spine bases, nearly 2mm wide, and tapering posteriorly for more than 10mm, and 4mm apart. The spines are close to 1mm in diameter. There is a shallow sulcus, but nothing is known of the interior or ears, or dorsal valve, so that the material may be no more than a variant of *subquadratus*. A fragment from UQL 1630 shows a spine apparently 2.5mm wide. A few other specimens, as from UQL 1383, 4517 and 4519 come close to this individual, but have smaller slightly more closely spaced spine-bases, approaching those of *Taeniothaerus subquadratus*.

Fig. 54.



Taeniothaerus sp. A, external mould of ventral valve from UQF 81194 from UQL 4518, x1. B, small ventral internal mould UQF 81192 from UQL 4519, x2.

Taeniothaerus homevalensis Briggs, 1983

Fig. 55, 56

1909 *Productus subquadratus* [not Morris] – Etheridge & Dun, p. 300, pl. 41, fig. 2-5 (part, not fig. 1 = *subquadratus*).

1950 *Aulosteges (Taeniothaerus) subquadratus* – Hill, p. 6, pl. 5, fig. 1, 2 (part, not pl. 1, fig. 1 = *subquadratus*; not pl. 6, fig. 4 = *farleyensis* Briggs).

1964b *T. subquadratus* – Hill & Woods, p. 10, pl. P5, fig. 5, 6.

1964b *T. subquadratus* var. *acanthophorus* [not Fletcher] – Hill & Woods, pl. P. 5, fig. ?4 (part, not fig. 3 = *acanthophorus*).

1972 *T. subquadratus* – Hill, Playford & Woods, p. 10, pl. P5, fig. ?4, 5, 6 (part, not fig. 3 = *acanthophorus*).

1974 *T. subquadratus* – McCarthy et al., Fig. 4c.

1983 *T. homevalensis* Briggs in Waterhouse et al., p. 127, pl. 2, fig. 1-7.

1986 *T. homevalensis* – Parfrey, p. 59, Fig. 2.1a, b.

1998 *T. homevalensis* – Briggs, p. 137, Fig. 67A, B.

2015 *T. homevalensis* – Waterhouse, p. 131, Fig. 49, 50A, ?B, C, D.

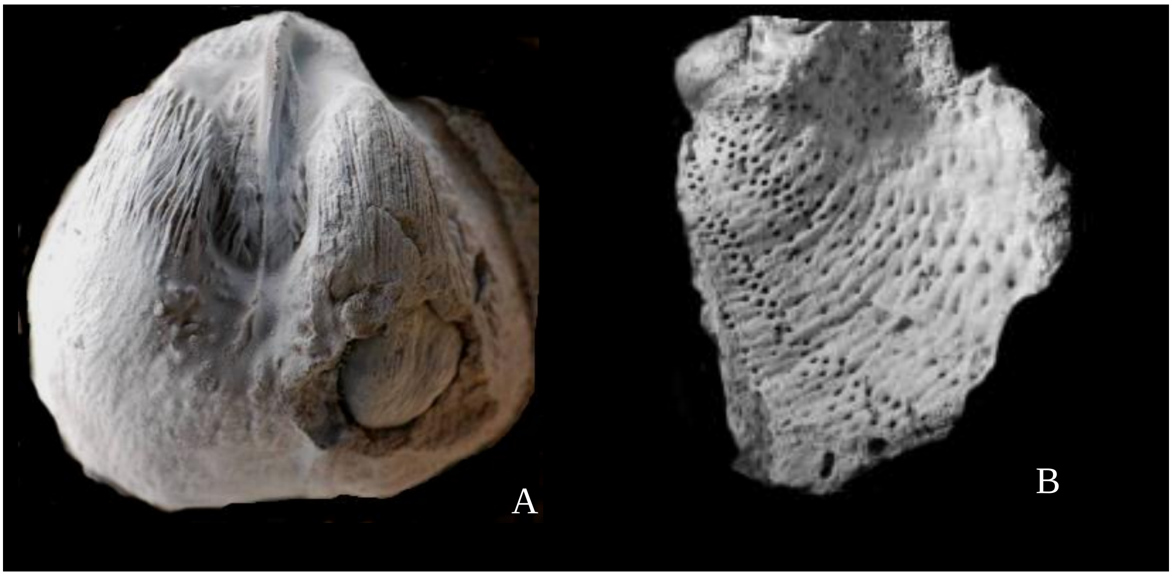


Fig. 55.*Taeniothaerus homevalensis* Briggs. A, ventral internal mould, UQF 81196 from UQL 4519, x1. B, part of ventral external mould UQF 81197 from UQL 4519, x1.

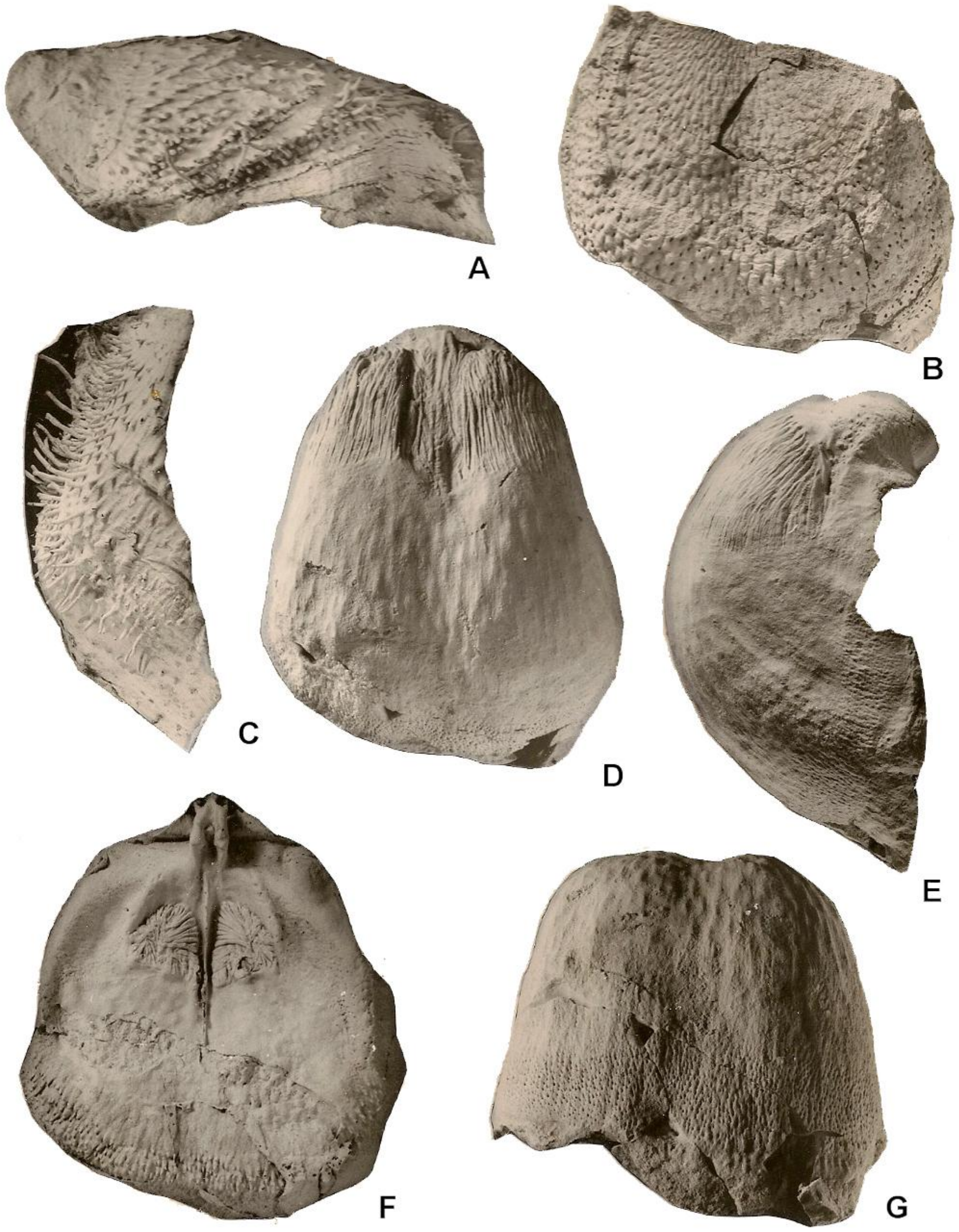


Fig. 56. *Taeniothaerus homevalensis* Briggs. Holotype UQF 72738 from UQL 2584, x1. A, C, lateral and ventral view of ventral exterior. B, dorsal external mould. D, E, G, ventral, lateral and anterior aspects of ventral internal mould. F, latex cast of dorsal interior. From Waterhouse et al. (1983, pl. 3, fig. 1-7).

Holotype: UQF 72738 from UQL 2584, Tiverton Formation, figured in Waterhouse et al. (1983, pl. 2, fig. 1-7) and Fig. 56 herein, OD.

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

Material: Specimens from UQL 1626-1630, 2584, 2620, 2631, 3128, 3129?, 3780, 4517-4520. *Taeniothaerus subquadratus* Zone.

Description: This species is close in overall shape to *Taeniothaerus subquadratus*, and was distinguished primarily through its ventral spines that are rarely up to 0.8mm in diameter, according to Briggs, as compared with coarser spines up to 1.4mm in diameter over the disc anteriorly and in the lateral halteroid brushes of *subquadratus*. Dorsal spines are 0.4-0.5mm in diameter, thinner than in *subquadratus,* vary in spacing and distribution over different specimens, and may cover all of the valve, or be concentrated over the anterior disc and trail, often in commarginal rows, erect or high-angle recumbent. Spines may be thick or thin in the halteroid brush, and the spine bases are more crowded, lower and thinner than in specimens assigned to *Taeniothaerus subquadratus*. Based on spine diameter, collections from UQL 4517-4520, as well as 1630 and 2631, include individuals of both *subquadratus* and *homevalensis*, and whether there are really two distinctive assemblages of *Taeniothaerus* is not fully clear. One of the difficulties in assessing specific limits for the specimens in the present collections is that most are incomplete, and many are internal moulds, obscuring the spine dimensions, so that there is uncertainty over some collections. Briggs (1998) limited the species to UQL 4517-4519, but such limitations do not reflect the nature of the material. Present collections, although imperfect, show some range in density and diameter of spines and in density, width and length of spine bases. They suggest that the species *homevalensis* is not very different from *subquadratus*.

Resemblances: A ventral valve from Cessnock, New South Wales, figured as *Reedoconcha* sp. by Briggs (1998, Fig. 68) is badly preserved and poorly known. It might be allied to *Taeniothaerus homevalensis*, but has very long spines bases stated to exceed 15mm in length, suggestive of an approach to *Taeniothaerus farleyensis* Briggs. *Reedoconcha* Kotlyar is distinguished by the lack of a ventral interarea (Waterhouse 2013, p. 281).

Taeniothaerus homevalensis is represented by large specimens (UQF 46685, 46713, 46714, 46716, 46717) with well formed ventral sulcus and comparatively coarse spines in the Teebar Formation of Cranfield (1989) near Gigoomgan north of Gympie at Teebar Creek, recorded as being "on the north bank of Ten Chain Road", and another as "half a mile north of Glenbar Station" as elaborated in Waterhouse (2015).

Taxonomy: The specimen figured by Hill (1950, pl. 6, fig. 4) from Lakes Creek, Rockhampton, was referred by Briggs (1998, pp. 136, 137) to both *Taeniothaerus farleyensis* and to *T. homevalensis*. The specimen belongs to *farleyensis*.

Genus ***Lakismatia*** Waterhouse, 2010a

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

Diagnosis: Elongate with high ventral interarea, ventral and dorsal spines each in two orders, fine tending to be prostrate, coarse spines variably inclined, spine bases comparatively short. Halteroid brush over posterior flanks.

Discussion: This form is very close to *Taeniothaerus*, but is regarded as of generic rank, given the difference in spines: spines in *Taeniothaerus* belong mostly if not entirely to one series, and spine bases are long. In addition, the shell is subsymmetrical with extended ventral umbo.

Lakismatia sulcata n. sp.

Fig. 57

?1983 *Megasteges* cf. *randsi* Briggs in Waterhouse et al., p. 131, pl. 3, fig. 1.

Derivation: sulcus – furrow, Lat.

Holotype: UQF 81205 from UQL 1380, Tiverton Formation, figured as Fig. 57A, here designated.

Diagnosis: Ventral umbo elongate and distorted, ventral interarea high, ventral sulcus well developed.

Material: Ventral valves from UQL 1380, 1623 cf, 1630, 1631, 2622, 2623, 2584, 4517 and 4519. *Svalbardia armstrongi* Subzone and *Taeniothaerus subquadratus* Zone.

Dimensions in mm: ventral valve

UQF	UQL	Width	Length	Height
81205	1380	51	51	26
81204	2623	55	62	28

Description: Specimens with elongate outline, extended and distorted bluntly terminated ventral umbo, high ventral interarea above a wide hinge, bearing deltidium with arched base, and narrow-floored ventral sulcus. The internal mould is ornamented by short swollen spine bases over most of the valve, and most spines are coarse, but there are scattered fine prostrate spines. There are elongate ventral spine bases over the exterior, and ventral spines 0.4mm and 0.7mm in diameter, with possibly other spines as well. The dorsal valve has spines of two orders according to Briggs (1986a, p. 40). The dorsal spines were described as coarse, erect and recumbent, and spine bases appear to be long (Waterhouse 1986a, pl. 8, fig. 8), but are somewhat obscure. Internally, the ventral adductors are elongate and dendritic, and the diductor scars heavily scored by grooves.

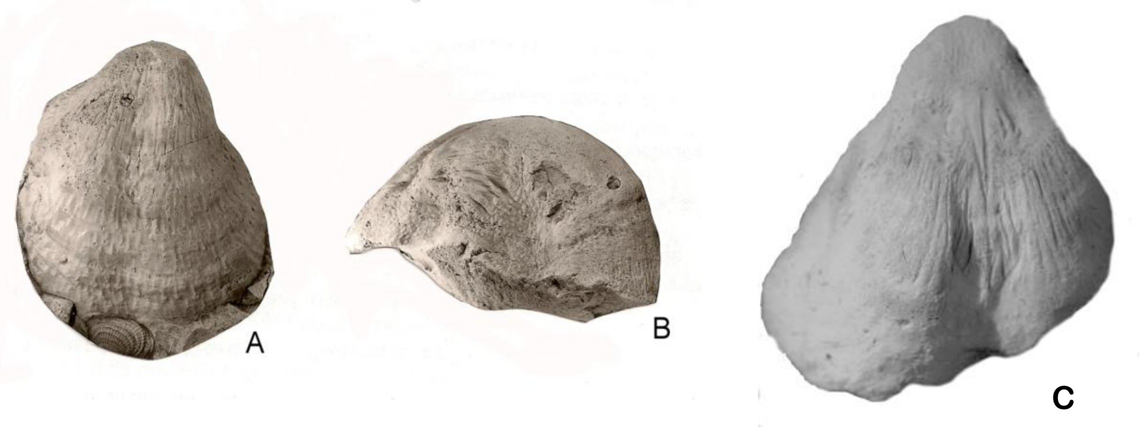


Fig. 57. *Lakismatia sulcata* n. sp. A, ventral valve holotype UQF 81205 from UQL 1380, x0.66. B, C, lateral and ventral aspects of ventral valve UQF 81204 from UQL 2623 x0.66.

Resemblances: Specimens of this form are not well preserved, but in shape and high ventral interarea clearly come close to the distinctly elongate species with distorted ventral umbo and high interarea, called *Lakismatia lakimatos* (Briggs) from the basal Elvinia Formation, also reported from the Camboon Volcanics in southeast Bowen Basin. The spine pattern as far as preserved confirms the generic position. What distinguishes the present form is its more highly distorted ventral umbo, higher ventral interarea, and clearly developed irregular ventral sulcus. Material from the Rose's Pride Formation (Fig. 58) looks similar in shape, but has short ventral spine bases.

The specimens are large, though smaller than *Taeniothaerus subquadratus* or *T. homevalensis,* and have an ovally subpentagonal shape, with posteriorly extended ventral umbo that is generally somewhat distorted, high ventral interarea, and convexo-concave dorsal valve with geniculate trail. The species occurs in the Tiverton Formation, and superficially similar specimens have been recorded from the Rose's Pride Formation in the south Bowen Basin in Waterhouse (1986a). The Tiverton and Rose's Pride material was regarded by Briggs in Waterhouse et al. (1983) and Briggs (1998) as comparable to *Megasteges* (now *Austrothaerus*) *randsi* (Hill, 1950, pl. 6, fig. 1a-d), but this is in error, because Tiverton ventral valves have elongate swollen spine bases, not observed in Hill's species. The Tiverton ventral valves resemble *randsi* in characteristic features of overall shape, large size, distorted umbonal region, well developed ventral sulcus and high interarea, but differ in the nature of the spines and their bases. The ornament is moderately close to that of *Taeniothaerus,* but the present specimens are more irregular in shape with high ventral interareas. Briggs (1986) did not include in his synonymy for "*randsi*" the material he had compared to that species in Waterhouse et al. (1983) from the Tiverton Formation, from UQL 2622, 2623, 2584, and 4513. His figured specimen shows a well formed sulcus and cluster of posterior lateral spines, and spines in two orders, but is less deformed than present material. Amongst material from the Rose's Pride Formation that was compared to *randsi* by Briggs (1986), two specimens (pl. 8, fig. 9, 10) are refigured as Fig. 58. The figures are not entirely clear over the nature of posterior lateral spines, but they appear to have been erect, without the prolonged bases typical of *Lakismatia sulcata*, and so, even though they display something of a ventral sulcus, and share elongate ventral beak and high interarea with *sulcata*, may well prove to belong to *Austrothaerus*. Another specimen from the Rose's Pride Formation (Briggs in Waterhouse 1986a, pl. 8, fig. 6) is broad and sulcate and somewhat deformed, and its generic position uncertain, but perhaps it is *Austrothaerus. Austrothaerus* Waterhouse, 2010a, p. 15, based on type species *Aulosteges* (*Taeniothaerus*) *randsi* Hill, 1950, is distinguished from *Megasteges* by the uniform erect ventral spines and development of an ear brush, whereas *Megasteges* has erect ventral spines of varied diameter and lacks an ear-brush.

Several species from Western Australia are also asymmetric in shape with extended or distorted ventral umbones. *Aulosteges lyndonensis* Coleman, 1957, p. 46 from the base of the Bulgadoo Shale (upper Sarginian?), Carnarvon Basin, involves large asymmetric shells with high ventral interarea and distorted ventral umbo. The ventral spines display only slightly prolonged bases over disc and trail, more erect laterally, and spines are in two series. A posterior lateral brush is not strongly developed. Dorsal spines are slender and recumbent, and varied in diameter. The species is taeniothaerin in general morphology. Coleman (1957, pl. 4, fig. 1-10) drew attention to the elongate spine bases bearing erect spines, interspersed haphazardly with non-elongate bases bearing erect spines, and made note of fine spine-bases over the top of the pseudodeltidium. Coleman (1957, p. 47) reported that dorsal spines were finer than on the ventral valve, erect or suberect, especially fine over the first formed part of the shell and around the margins, and coarse over the disc. He considered that *Aulosteges baracoodensis* Etheridge was a close ally, but it has finer spines and is symmetrical in shape, and the interior is not known. *Aulosteges ingens* Hosking (1931, pl. 5, fig. 1, pl. 6, fig. 2) from the lower Byro Group of Western Australia is another large and asymmetric species with coarse elongate ventral spine bases and spines that may be of a single order, and fine more erect dorsal spines. Unfortunately the dorsal interior is not entirely clear. Coleman (1957, pl. 3, fig. 5) figured one specimen with lateral buttress plates, and another seemingly without (Coleman 1957, pl. 3, fig. 7). Neither of the dorsal valves are topotypes, and the specimen with buttress plates is closer in shape to type *ingens*.

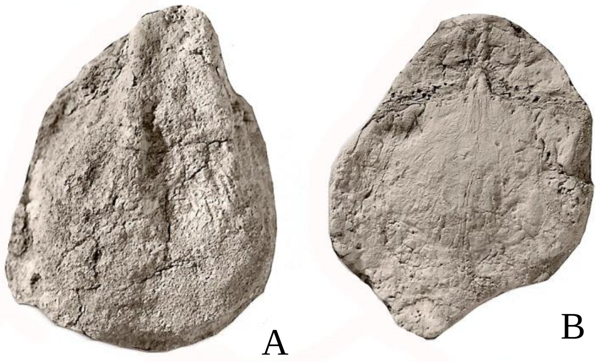


Fig. 58. Possible *Austrothaerus* cf. *randsi* (Hill). A, worn ventral valve UQF 73752. B, dorsal aspect UQF 73751 with valves conjoined. Specimens x1, from UQL 4671, Rose’s Pride Formation, southeast Bowen Basin.

Genus ***Lipanteris*** Briggs, 1986

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

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

Discussion: The lack of ventral lateral spine brushes is a prime feature.

Lipanteris anotos (Briggs, 1983)

Fig. 59 - 61

1983 *Taeniothaerus anotos* Briggs in Waterhouse et al., p. 130, pl. 1, fig. 6-10.

?1986a *Megasteges* cf. *randsi* [not Hill] – Briggs in Waterhouse 1986a, p. 39, pl. 8, fig. 6, 9, 10 (part, not fig. 7, 8 = *Austrothaerus*? cf. *randsi*).

1998 *Lipanteris anotos* – Briggs, p. 135.

Holotype: UQF 72790 from UQL 4519, Tiverton Formation, figured in Waterhouse et al. (1983, pl. 1, fig. 6, 7) and Fig. 59A, B herein, OD.

Diagnosis: Large elongate shells with umbones less enrolled than in other species, sulcus broad and shallow, ears small, spines mostly high angle and moderately coarse 0.8-1mm in diameter, interspersed with finer recumbent spines (diameter 0.3-0.4mm) on ventral flanks. Spine ridges coarse on disc, passing into long discontinuous spine ridges on the trail, fine flank costae and no halteroid brush. Dorsal spines recumbent, 0.15 to 0.6mm thick, anterior spines erect and fine. Ventral valve heavily thickened internally, diductor scars commence just in front of hinge almost as far back as the adductor scars. The anterior muscle field is gently folded into median projection.

Material: Specimens from UQL at UQL 1380, 1623, 1626, 1630, 1631, 2622, 2623, 2628 - 2630, 2584, 4513, 4514, 4515, 4517, 4519, 4525 and LT3. *Svalbardia armstrongi* Subzone and *Taeniothaerus subquadratus* Zone.

Dimensions in mm: ventral valve

UQF	UQL	Width	Length	Height
81202	4515	44	49	21

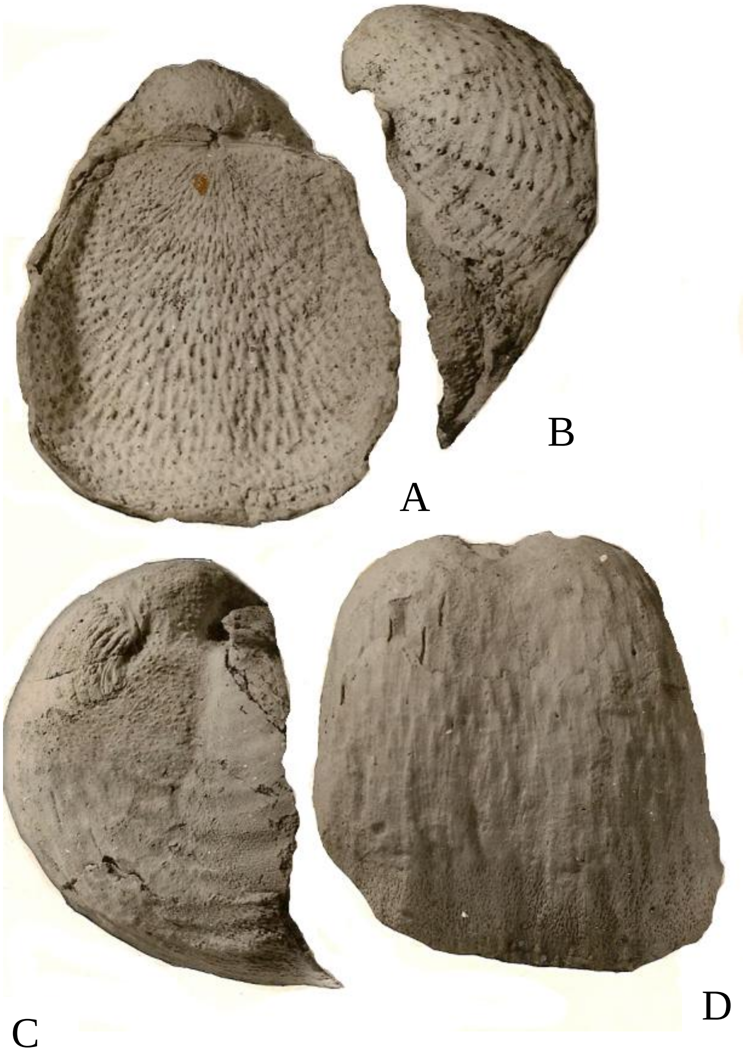


Fig. 59. *Lipanteris anotos* (Briggs). A, B, dorsal and lateral views of holotype UQF 72790 from UQL 4519, x1. C, D, lateral and ventral aspects of internal mould UQF 72787 from UQL 2630, x 1. From Waterhouse et al. (1983, pl. 1, fig. 6-9).

Description: Specimens symmetrical with elongate outline, weakly extended and undistorted ventral umbo with angle of 120-150^{o}, moderately high ventral interarea above a wide hinge, bearing deltidium with arched base, and narrow-floored ventral sulcus. The cardinal extremities are angular at 110^{o}, without ears. The dorsal disc is almost flat, with no visible interarea, low and semigeniculate trail and low median fold. The ventral valve is ornamented by swollen spine bases 4-5mm long over most of the valve, interspersed with a few slender spines 0.6mm in diameter without swollen

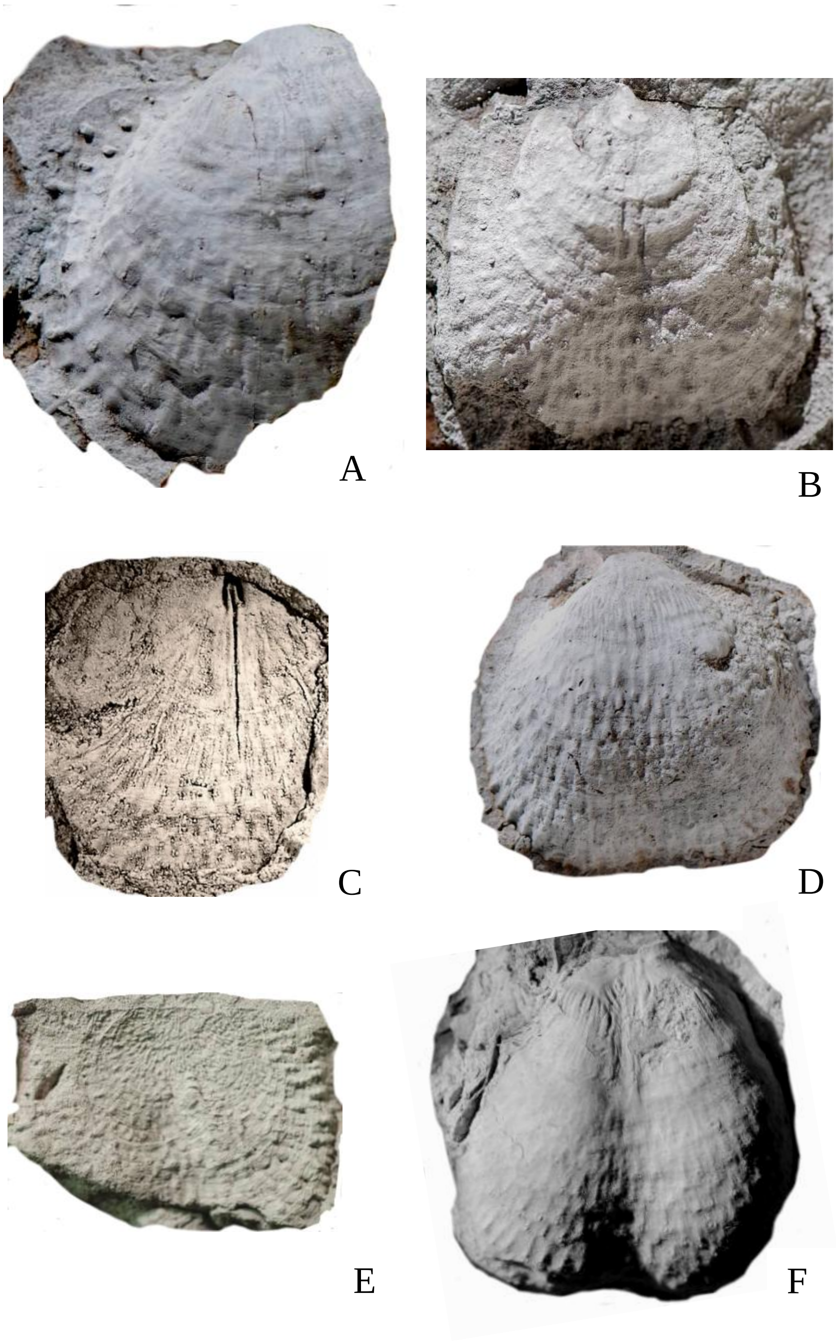


Fig. 60. *Lipanteris anotos* (Briggs). A, ventral valve UQF 81199 from UQL 4515, x1.5. B, ventral valve UQF 81198 from UQL 4513, x2. C, dorsal valve internal mould UQF 81201 from UQL 4514, x2. D, ventral valve UQF 81200 from UQL 4525, x1. E, external mould of ventral valve UQF 81203 from UQL 1630, x1. F, ventral internal mould UQF 81202 from UQL 4515, x1.

Fig. 61. *Lipanteris anotos* Briggs. A, fragment of lateral external mould of ventral valve UQF 81584 from UQL 4515, x1.5. B, detail of external mould of ventral valve UQF 81805 from same block, showing spine cores extending anteriorly from spine bases, x4.

bases, spines erect laterally; no strong ear-burst. There are strong commarginal growth rugae, numbering at least eleven over the valve. The dorsal valve has swollen elongate spine bases, dimples, and slender recumbent spines varying in diameter between 0.2 and 0.6mm, with few or none prostrate. The ventral adductors are elongate and dendritic, the diductor scars heavily scored by grooves. A well preserved small dorsal valve from UQL 4514 is 20mm long and 25mm wide, almost flat apart from median arching, with spines measuring 0.1-0.2mm and 0.4mm in diameter, median septum more than half as long as the valve, two short cardinal support plates, and muscle field of small lateral posterior scars and long inner anterior adductor scars.

Discussion: The material appears to be immature, judged from size, shell thickness and nature of the internal morphology. It is close in shape to mature *Lipanteris anotos* as described by Briggs in Waterhouse et al. (1983), and represents less mature specimens of that species. *L. anotos* is distinguished from two other east Australian species, described as *Lipanteris cracowensis* (Hill, 1950) and *L. sparsispinosus* Briggs, in Waterhouse 1986a, both from the Fairyland Formation of the southeast Bowen Basin. Whereas spines are fine anteriorly on the dorsal trail of *anotos*, they are coarse on the dorsal trail of *cracowensis* according to Briggs (1998, p. 37), but no figures were provided. No adequate illustration of the dorsal exterior has been provided for species of *Lipanteris*, other than for *L. anotos*.

Suborder LINOPRODUCTIDINA Waterhouse, 2013

Members of this suborder evolved from a ribbed chonetid, as opposed to Productida and Strophalosiidina which evolved from a smooth chonetid without ribs (Waterhouse 2013). Three superfamilies are known, each derived from a separate subfamily within Devonoproductidae Muir-Wood & Cooper, 1960, and these devonoproductinid subfamilies were close to their ribbed chonetid ancestors in having interareas and teeth and sockets.

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

This superfamily embraces three families, Anidanthidae, Paucispiniferidae and Yakovleviidae, each of which arose from Devonoproductinae Muir-Wood & Cooper (see Waterhouse 2013, p. 311).

Family **ANIDANTHIDAE** Waterhouse, 1968

Discussion: Proposed as a subfamily and member of Linoproductidae Stehli and retained as such by Brunton et al. (2000), this group was elevated to family rank by Sarytcheva (1977). It is unusual in several respects. Its ventral adductor scars are exceptional in being smooth, and the dorsal valve carries prominent commarginal lamellae as a rule. Internally, and unlike most Linoproductoidea, there may be a low but distinct marginal ridge, high posteriorly, in each valve. In these respects, Anidanthidae Waterhouse approaches Devonoproductinae Muir-Wood & Cooper, especially *Devonoproductus* Stainbrook, sharing a row of ventral hinge spines and an internal marginal ridge in each valve and similar muscle scars, but differing in the lack of interareas, teeth and sockets.

Subfamily **ANIDANTHINAE** Waterhouse, 1968b

Diagnosis: Well defined costellae increasing mostly by intercalation, hinge spines moderately developed, visceral disc and trail spines inconspicuous as a rule, no dorsal spines. Dorsal valve lamellate to varying degree.

Discussion: Lirariinae Waterhouse, 2013 lacks dorsal lamellae, and Lamiproductinae Liang, 1990 differs further in the presence of strongly branching ribs.

Fig. 62. Ventral adductor impressions typical of Devonoproductidae and Anidanthidae, displayed by *Anidanthia paucicostata* (Waterhouse), UQF 81273 from UQL 4511, x3.

Genus ***Anidanthia*** Waterhouse, 2013

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

Diagnosis: Moderately large shells with prominent radial ornament, spines limited to ventral valve, forming well defined hinge row, scattered or rare over disc and trail. Dorsal ears laterally extended, not twisted, trail long, geniculate, not thickened.

Discussion: *Anidanthia* includes the species described as *Megousia solita* Waterhouse from the lower Wandrawandian Formation of the south Sydney Basin, as further illustrated by Briggs (1998, Fig. 98A – E). The younger species *Anidanthia crenulata* (Briggs, 1998) is found in higher beds of the Wandrawandian Formation, and *A. aplini* Waterhouse & Balfe occurs in the South Curra Limestone at Gympie (Waterhouse 2015).

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 nature of the dorsal ears, which extend laterally, and rarely forwards in *Anidanthia*, and are largely smooth externally. In *Megousia*, the ears show a forward twist, as displayed in the Glass Mountains species described by Cooper & Grant (1975) as *auriculata, definita, flexuosa*, and *mucronata*. The generic position of species *girtyi* (King) is uncertain due to incomplete preservation, unless it is belongs to *Protoanidanthus,* and *waagenianus* Girty from the Capitanian looks close to *Fusiproductus* Waterhouse. An additional distinction for *Megousia*, pointed out by Brunton et al. (2000, p. 532), is that the dorsal ears bear ribs which curve anterodorsally, whereas the external ears in *Anidanthia* tend to be smooth.

Anidanthus is a very distinctive form, characterized by extended dorsal ears, 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 by Waterhouse (1986a, pl. 14, fig. 13, 16-18) for material described, wrongly, as a separate species and genus. A further species *Anidanthus perdosus* Waterhouse, 2013 with a wedge-like dorsal valve is represented in the Branxton Subgroup (Waterhouse 2013, Fig. 15.20).

Anidanthia paucicostata (Waterhouse, 1986a)

Fig. 62 - 65

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* [not Booker] – 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.

1964b *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*).

1968c *Megousia* sp. Waterhouse, p. 1174, pl. 154, fig. 7, 12, 13.

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.

1986a *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).

2013 *Anidanthia paucicostata* – Waterhouse, p. 330, Fig. 15.21 - 15.22.

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

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

Material. Specimens from UQL 1380, 1620, 1621, 1624, 1630, 2524, 2584, 2620, 2622, 2623-2626, 2628, 3127, 3129, 4509, 4510, 4511- 4519. *Bookeria pollex*, *Bookeria geniculata* and *Taeniothaerus subquadratus* Zone. Briggs (1998) cited specimens from UQL 1620, 1621, 1624, 4507, 4509, 4513, 4515-4517 and 4519 as *cessnockensis*, and referred material from BMR M12, M412b and UQL 1630 to *springsurensis*.

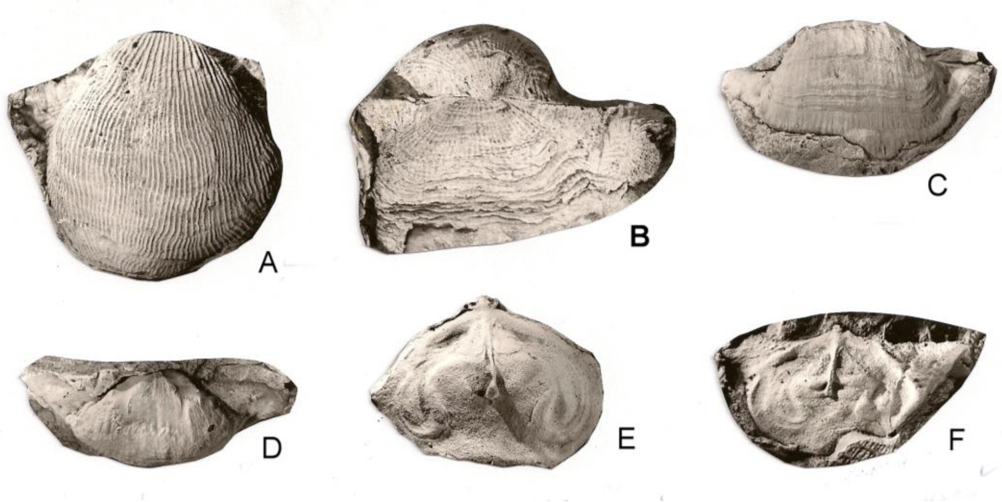


Fig. 63. *Anidanthia paucicostata* (Waterhouse). A, latex cast of ventral valve UQF 81206 from UQL 4511, x1.2. B, dorsal aspect of UQF 81207 from UQL 4511, x1.1. C, D, anterior ventral and posterior ventral aspect of ventral internal mould UQF 81208 from UQL 3127, x1. E, latex cast of dorsal interior UQF 81271 from UQL 4510, x1.5. F, latex cast of dorsal interior UQF 81210 from UQL 4509, x1.5.

Description: Although specimens are not numerous, they display a considerable range of features. The ventral valve tends to have a subelongate to equilateral swollen visceral disc, with large ears, very shallow sulcus and low fold, costae generally numbering seven to nine in 5mm, some splitting or with very slender threads, and as coarse as six in 5mm in material from UQL 2628. Small specimens from UQL 4510, lower *Bookeria geniculata* Zone, have exceptionally fine costae, 12 in 5mm and may represent either a variant or different taxon. The dorsal valve is transverse, and ornament variable, with 8.5 ribs counted in 5mm on a dorsal valve from UQL 1380. Commarginal lamellae are moderately strong, but may be missing often from the posterior disc, and also on some specimens from the anterior trail. (Briggs 1998, p. 202 did not accept this observation, asserting that part of the ventral valve overlay the dorsal valve, but this is not correct). The ribs increase sometimes by branching, and mostly by intercalation on the ventral valve, even though Briggs (1998) claimed that the ribs only divided. Internal detail has been described in various articles. Internally, a ridge lies across the posteral lateral slopes, and one to four ridges around the start of the trail, related to the commarginal lamellae. Not all specimens show the alar dorsal extensions of the ears, and so approach the genus *Protoanidanthus*. But the costae and lamellae on these specimens are like those of alar *paucispinosa*, with 30-34 costae as a rule, and so it is deemed that the specimens are all conspecific, with the extended ears broken off some specimens.

Resemblances: This species is more elongate than *Anidanthus springsurensis* Booker, and normally is not sulcate, and there are many intercalate ribs. The total number of ventral and dorsal ribs over the anterior disc of *springsurensis* is close to 40, compared with 30-34 primary ribs in Tiverton specimens of *paucicostata*, and anteriorly the *paucicostata* ribs may become more numerous, because of splitting into very fine ribs. Rib counts for the ventral valves of the types of *springsurensis,* which come from the upper Cattle Creek Formation or Sirius Shale in the southwest Bowen Basin, suggest that 8-10 ribs in 5mm are normal for specimens figured by Booker (1932), 11-13 in Briggs (1998) and 8-9 in Hill & Woods (1964b) and 8-9 in Hill (1950, pl. 7, fig. 2), on the assumption that the scale of the figures is accurate. More reliably, Hill (1950) reported 18 in 10mm, but this applies to *paucicostata* as well as *springsurensis*. The counts for type *paucicostata* from the Elvinia Formation are 8, 8, 9-10, 7, 8-9, 5, and 7-8 in 5mm. For specimens from the Tiverton Formation, they are mostly 7 to 8, but range from 6 to 10, and from the Farley Formation, they range from 6 to 10. Thus there is a difference in ribbing between *springsurensis* and *paucicostata*,

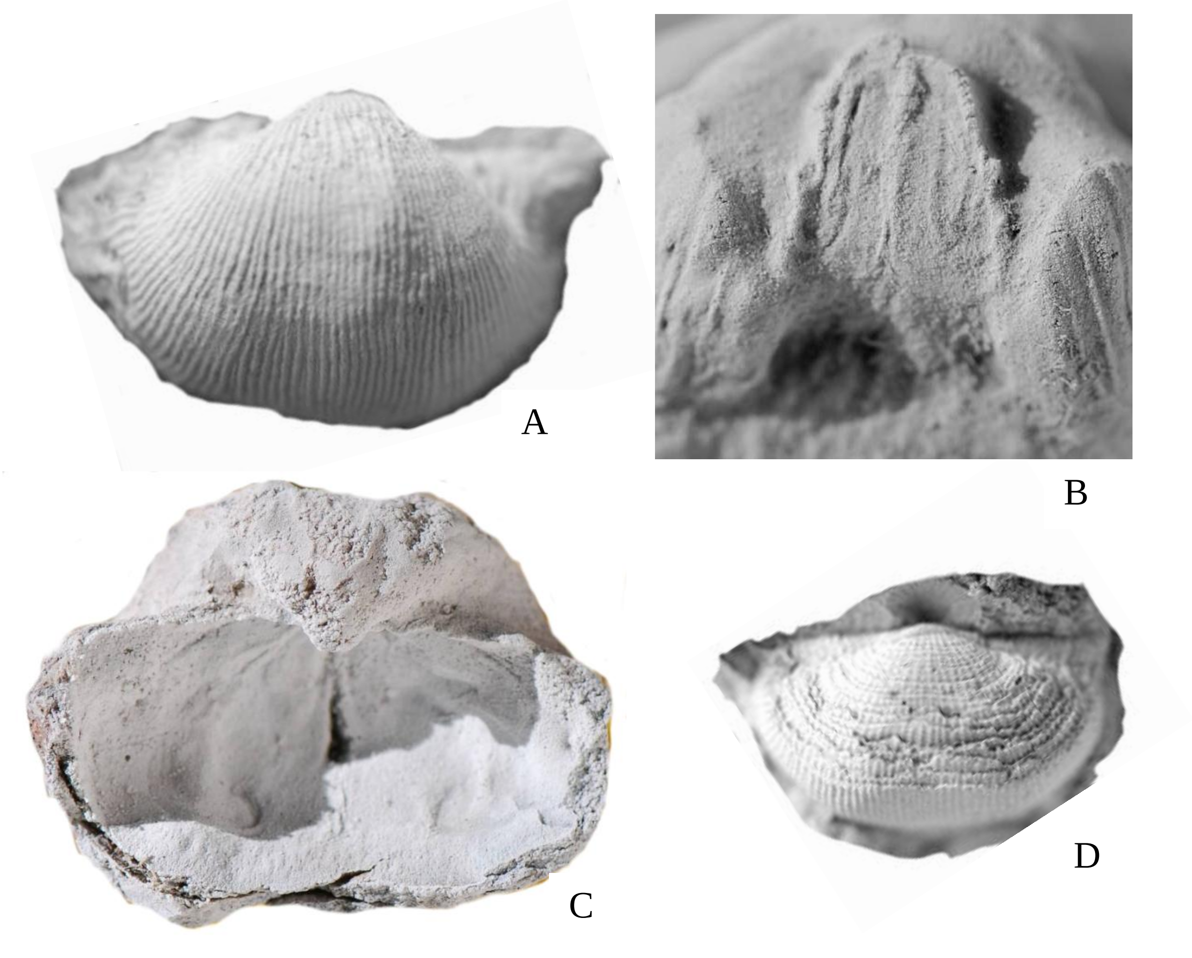


Fig. 64. *Anidanthia paucicostata* (Waterhouse). A, latex cast of ventral exterior UQF 81212 from UQL 4509, x3. B, ventral aspect of internal mould UQF 81271 from UQL 4510, x6. C, dorsal aspect of internal mould UQF 81209 from UQL 2620, x3. D, dorsal valve exterior UQF 81270 from UQL 4510, x2.

but not consistently so, and the mean between the two is 8.5 (n = 10) for *springsurensis*, and 7 (n = 40) for *paucicostata.* In addition, the secondary costae are intercalated and may remain fine for longer in *paucicostata* than in *springsurensis.* The dorsal valve figured as *springsurensis* by Hill (1950, pl. 7, fig. 6 – UQF 10764) has some 10 ribs in 5mm. This was stated to come from near Cracow homestead, above limestone, presumably Elvinia Formation and is probably *paucicostata*. Briggs (1998) doubted the significance of the difference in costal counts, and pointed to a suite from a locality UQL 1123, a locality in an unnamed unit near Warwick, southeast Queensland, that varied considerably in its density of costation. Whilst this is an obviously unsatisfactory reference sample because of the lack of reliable information over the age and associated fauna, counts do vary, and the difference of costae is a difference between means and averages, and not an infallible guide. It appears that the variation is mostly displayed by *paucicostata*: the ornament in *springsurensis* appears to be consistently fine; that of *paucicostata* is generally coarser, but includes specimens with more numerous 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, is larger and more transverse and sulcate in *springsurensis* than in *paucicostata*.

Specimens figured in McCarthy et al. (1974) from the Emu Creek beds north of Drake, New South Wales, have 7-8 costae in 5mm anteriorly on the dorsal valve, and appear to belong to the species *paucicostata*, but no description and few figures were provided. The specimens figured from the Camboon Andesite near Biloela, south Bowen Basin, by Parfrey (1986) as *Anidanthus springsurensis* look like *Protoanidanthus*. From the Lakes Creek Group near Rockhampton, east Queensland, a slab figured by Hill (1950, pl. 7, fig. 1) shows a dorsal valve with some 9 ribs in 5mm (UQF 2004), the same as in a Cattle Creek specimen of Hill (1950, pl. 7, fig. 2 – UQF 2003). From the lower South Curra Limestone of Gympie, southeast Queensland, so-called *Anidanthus* figured by Runnegar & Ferguson (1969, pl. 2, fig. 15-17) has relatively fine costae, 10-11 in 5mm, and coarse and crowded growth lamellae on the dorsal valve. It was described as a distinct species *Anidanthia aplini* Waterhouse & Balfe (2015).

Fig. 65. *Anidanthia paucicostata* (Waterhouse), dorsal aspect of latex cast, UQF 81272 from UQL 4511, x4. The long ear on the right side is bent towards the observer.

Briggs (1998) recognized a separate species *cessnockensis* from the Farley Formation at Singleton, Hunter Valley, in the northern Sydney Basin that overlaps *paucicostata* in range. Two species were lumped in his description, and one suite of specimens is reallocated to *Protoanidanthus compactus* Waterhouse, as detailed below. Judged from published figures, costae number 6-8 in 5mm on the ventral valve of type *cessnockensis*, but in the text were counted at 8-11 in 5mm anteriorly. The species was said to be distinguished by its prominent sublamellate commarginal wrinkles with higher wider crest, and flatter dorsal valve of 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 of why the synonymy for the species in 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. Unfortunately it is not possible to adequately compare the nature and strength of dorsal commarginal ornament on *springsurensis* types, for few examples have been illustrated, with only the interior so far figured, and it has not been possible to find the types: they do not appear to be kept at either the Australian Museum or Queensland Museum.

A suite of specimens was described from the Rose's Pride Formation of the southeast Bowen Basin near Cracow, as *Nothokuvelousia aurifera* Waterhouse, 1986a. The Rose's Pride faunas are equivalent to those of the *Ingelarella plica* Zone of the Tiverton Formation, and *aurifera* is synonymized with *Anidanthus springsurensis*. Other specimens from the Rose's Pride Formation were figured as *A. springsurensis* by Hill (1950, pl. 6, fig. 4, 5 – UQF 10768, 10760).

Genus ***Protoanidanthus*** Waterhouse, 1986a

Type species: *Protoanidanthus compactus* Waterhouse, 1986a, p. 60 from Dresden Formation (Sakmarian), southeast Bowen Basin, Queensland, OD.

Diagnosis: Small shells with reduced dorsal ears lacking alar extensions, and comparable ventral ears; ornament much as in *Anidanthus*.

Discussion: This genus was relegated to synonymy of *Anidanthus* Booker by Brunton (2007, p. 2652), but *Protoanidanthus* does not have a wedge-shaped dorsal valve, and the dorsal ears are much smaller than in *Anidanthus, Anidanthia* or *Megousia*. No systematic study has been published to justify or provide even meagre support for the claim by Brunton (2007) that the size of the ears was an intrageneric character, and in other summaries of genera, Brunton (2007), rightly it would seem, granted substantial importance to the large size of the ears for *Labaella* (p. 2644) and *Auriolinoproductus* (p. 2652). It thus appears that size of ears is a feature used by various authors, including Brunton (2007). That is not to argue that the ear-size is an infallible guide – to that extent, the exploration of morphological variation and relationship to taxonomy remains a frontier science, and all classification is provisional to a degree. But it is believed that final or better answers will arise from careful segregation rather than lumping on an ad hoc and inconsistent basis.

Protoanidanthus compactus Waterhouse, 1986a

Fig. 66

1960 *Anidanthus* sp. Muir-Wood & Cooper, p. 299, pl. 112, fig. 14-20.

1986a *Protoanidanthus compactus* Waterhouse, p. 61, pl. 13, fig. 19-22, pl. 15, fig. 16-18.

1986 *Anidanthus springsurensis* [not Booker] – Parfrey, p. 59, Fig. 2.2.

1998 *P. compactus* – Briggs, p. 201, Fig. 95P.

1998 *A. cessnockensis* [not Briggs] – Briggs, p. 201, Fig. 96D-F, H, I (part, not Fig. 96A- C, G = *cessnockensis* syn. *paucicostata*).

Holotype: UQF 74080 from UQL 4820, Dresden Limestone, southeast Bowen Basin, figured by Waterhouse (1986a, pl. 13, fig. 22), OD.

Diagnosis: Dorsal ears wide and ventral ears large, 8-10 ribs in 5mm, hinge row of spines well developed, and ventral exterior bears moderately numerous spines, dorsal laminae fine in small specimens, becoming slightly thickened at maturity.

Material: Block with various specimens from UQL 4508. *Bookeria pollex* Zone.

Description. This species is found in the Colraine Mudstone at the "Linoproductus Horizon" of the Macleay Series at Colraine, Kimbriki, exposed on the bank of the Macleay River, New South Wales. Material from Kimbriki was also figured by Muir-Wood & Cooper (1960, p. 299, pl. 112), and further specimens recorded as *cessnockensis* by Briggs (1998, Fig. 96 E, F). They carry a large number of suberect body spines over the venter. Specimens as preserved on blocks AMF 37965 and 42054 confirm the spine pattern and show sharply defined dorsal lamellae and comparatively large convex ventral ears (Briggs (1998, Fig. 96F). Similar specimens come from the Berseker beds near

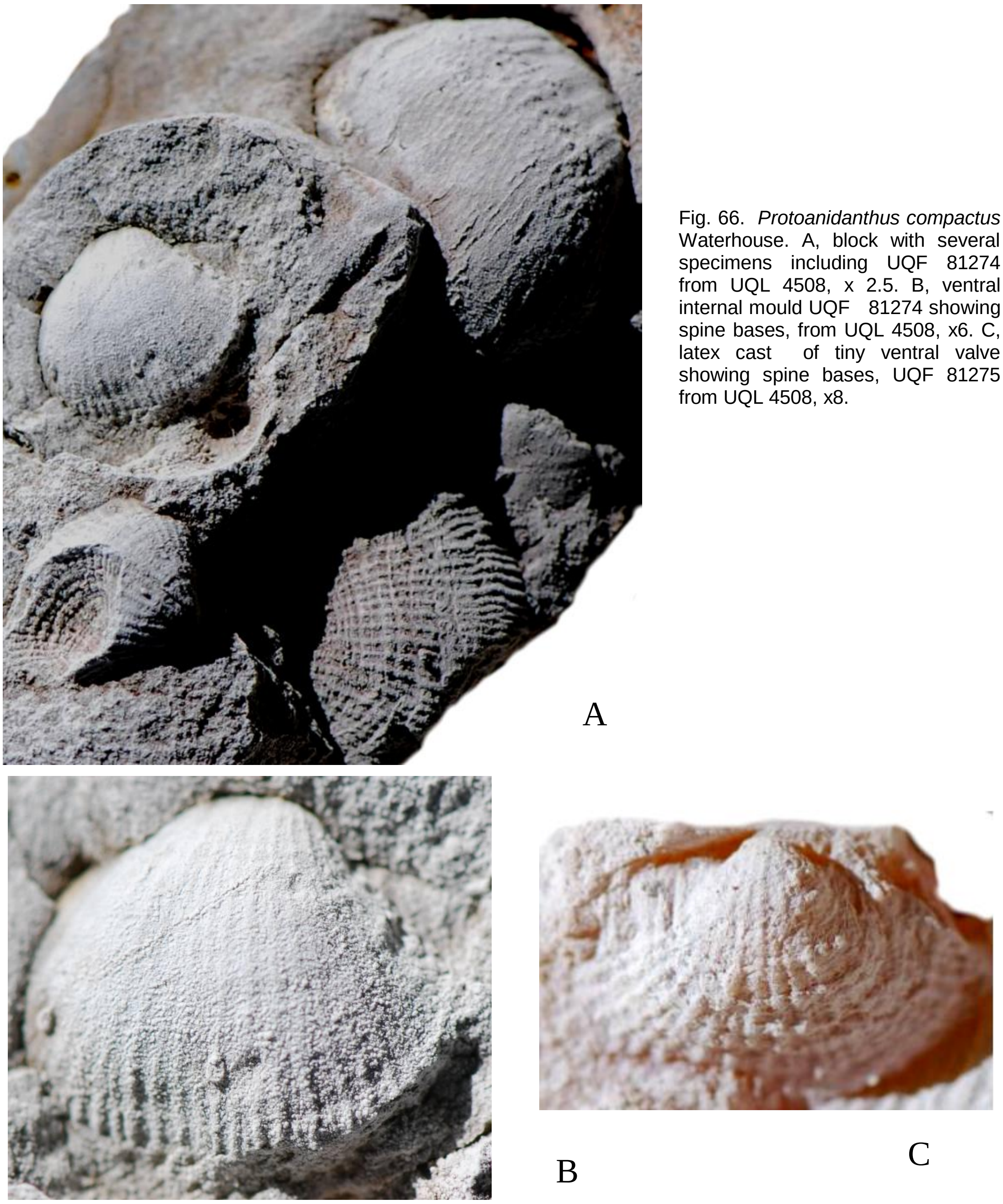


Fig. 66. *Protoanidanthus compactus* Waterhouse. A, block with several specimens including UQF 81274 from UQL 4508, x 2.5. B, ventral internal mould UQF 81274 showing spine bases, from UQL 4508, x6. C, latex cast of tiny ventral valve showing spine bases, UQF 81275 from UQL 4508, x8.

Rockhampton (UQF 13528). The ventral spines are more numerous than in *paucicostata* and *springsurensis. Anidanthus springsurensis* of Parfrey (1986, p. 59, Fig. 2.2a-c) from the Camboon Andesite of Queensland appears to be *Protoanidanthus compactus*, with coarser ribs, 8 in 10mm.

None of the other specimens placed in synonymy with *cessnockensis* by Briggs (1998) confirm the presence of many ventral spines But the two additional species of *Protoanidanthus* described by Briggs (1998) as *gosforthensis* from the Lochinvar Formation, New South Wales and *pokolbinensis* from the Texas area of south Queensland have more spines over the ventral disc than displayed by *Anidanthus* or *Anidanthia*, presumably to compensate for the shorter ears. The species *pokolbinensis* is well represented in the upper Rammutt Formation at Gympie and Kolbar Formation nearby at Gigoomgan (Waterhouse 2015) in southeast Queensland.

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

Diagnosis: Some to many ventral spines, emerging anteriorly over disc from a slight to considerable swelling, through which the hollow spine base is prolonged. One, two or rarely three costae or ribs may pass forward into the swollen spine base, and no more than one rib, and often none, may continue forward from the swelling. Erect spines may be numerous over ventral ears. Commarginal wrinkles often developed.

Discussion: This superfamily evolved from members of the Devonian subfamily Plicoproductinae Waterhouse, which shares elongate ventral spine bases, and is distinguished by interarea, teeth and sockets (Waterhouse 2013).

Family **PAUCISPINAURIIDAE** Waterhouse, 1986b

Diagnosis: Ventral spines with elongate bases arranged in regular quincunx over disc, crowded or rare over ears and outer umbonal slopes, dorsal spines crowded as a rule, erect, may be large. Radial ribs and weak to strong commarginal rugae. Body corpus moderately thick, ventral adductor scars dendritic. Cardinal process trilobed. Trail well developed and single, not elongated into a proboscidellin tube.

Discussion: Members of the Family Auriculispinidae Waterhouse are close and distinguished by thin body corpus, less regular and generally fewer and often thinner ventral spines, and more slender spine bases, and dorsal spines much less commonly developed. The ventral adductor impressions of *Auriculispina* tend to be striate rather than dendritic until late in ontogeny. Proboscidellidae is of Lower Carboniferous age, with no dorsal spines and with bilobed cardinal process.

Subfamily **PAUCISPINAURIINAE** Waterhouse, 1986b

Diagnosis: Ventral spines with elongate bases arranged in regular quincunx over disc, crowded or rare over ears, tend to be large over inner ears, dorsal spines crowded, may be of varied diameter. Radial ribs as a rule and weak or no commarginal rugae. Body corpus moderately thick.

Tribe **PAUCISPINAURIINI** Waterhouse, 1986a

Diagnosis: Weakly transverse shells with thick visceral corpus. Ventral spines uniform over disc, ribbing present.

Discussion: Holotricharinini Waterhouse is an exceptional tribe which has lost the ribbing and developed thin as well as thick ventral disc spines, and low regular rugae over both valves.

Genus ***Bookeria*** new genus

Derivation: Named for F. W. Booker.

Type species*:* *Bookeria sparsispinosa* new species from middle Tiverton Formation (Sakmarian), here designated.

Diagnosis: Shells with variable number of moderately large spines along ventral inner ears, disc with a few equally large spines on lateral slopes, other disc and trail spines of modest to low diameter. Dorsal spines numerous but slender on the whole, lacking strong anterior spines.

Diagnosis: Members of this genus are very close to other genera found in east Australia and New Zealand, called *Paucispinauria* Waterhouse and *Terrakea* Booker. *Paucispinauria* Waterhouse, 1986a, type species *Terrakea concava* Waterhouse, 1964a, p. 67 from Letham Burn Formation (Roadian), New Zealand, is characterized by having few ventral ear spines, and dorsal anterior spines tend to be large. Genus *Terrakea* Booker, 1930, type species *Productus brachythaerus* Morris, 1845, p. 284 from the Broughton Formation (Wordian), south Sydney Basin, New South Wales is distinguished by having a brush of sturdy spines over the ventral ears. Dorsal anterior spines also tend to be thick. The present genus is interpreted as progenital to both *Paucispinauria* and *Terrakea*. Two species, *sparsispinosa* and *geniculata*, have few ventral ear spines, and are believed to have developed into *Paucispinauria*: *Bookeria* is of lower and upper Sakmarian age, and the oldest species of *Paucispinauria* known so far is *Paucispinauria concava wardenensis* from the Wandrawandian Formation at Warden Head, south Sydney Basin, and in the lower Letham Formation, of Filippovian age in New Zealand (Waterhouse 2001, p. 35). *Paucispinauria* retained the sparsity of ventral ear spines, and developed sturdy anterior dorsal spines.

Terrakea differs from *Bookeria* in developing strong anterior dorsal spines and consistently numerous thick spines over the inner ventral ears and lower posterior umbonal slopes. The oldest species of *Terrakea* is found at the top of the Tiverton Formation, as *Terrakea dickinsi* Dear, of Aktastinian age (Dear 1971). It is here suggested that over this interval through the Tiverton Formation, and in the species assigned to *Bookeria*, we are seeing the apodicty – the cusp or peak flush – of evolution for two new genera, *Paucispinauria* and *Terrakea.* From this time onward, two distinct stocks existed with consistently different species, each with their own evolutionary trajectories. In the case of *Paucispinauria, Bookeria sparsispinosa* and *B*. *geniculata* evolved into *Paucispinauria paucispinosa* and

P. paucispinosa wardenensis (Waterhouse 1986a, 2001), followed by *P. concava*, *P. solida*, and *P. verecunda. Bookeria pollex* and *B*. *drysdalei* evolved into *Terrakea dickinsi* Dear, followed by *T. exmoorensis* Dear, *T. brachythaera* (Morris) and *T. elongata* (Etheridge & Dun). Younger species are much larger than their forebears in both lineages, and throughout the Permian stratigraphic succession above the Tiverton Formation, species of each genus alternated in succession through the zones.

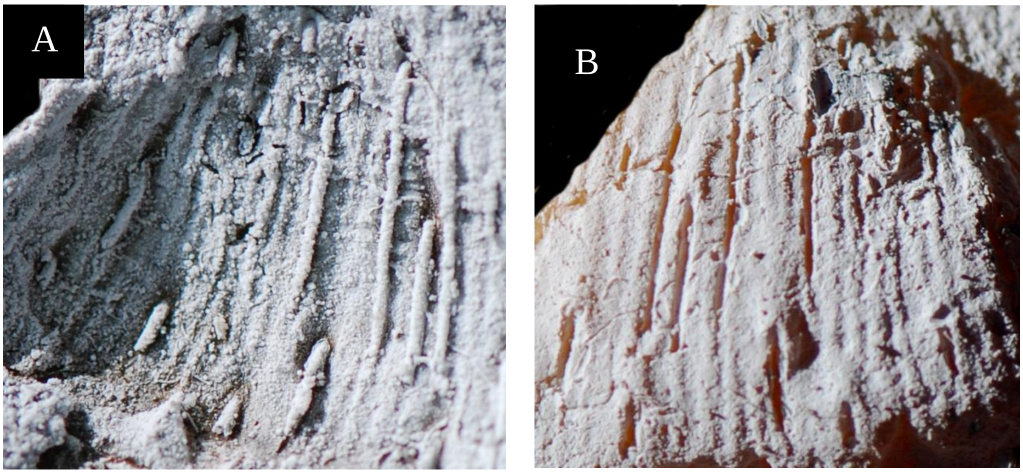


Fig. 67*.* *Bookeria sparsispinosa* new species, external mould (A) and latex cast of ventral anterior shell (B), showing spine bases that are extended forward each by a hollow tunnel that presumably connected the spine with the growing mantle. UQF 81813, x6. In B, the anterior spine channels have been worn out to leave open gutters.

Bookeria sparsispinosa n. sp.

Fig. 67 – 76

1950 *Terrakea pollex* [not Hill] – Hill, pl. 9, fig. 9?, 10? (part not pl. 9, fig. 6-8, 11, 12 = *pollex*).

?1964b *T. pollex* [not Hill] – Hill & Woods pl. P5, fig. 7, 8.

?1972 *T. pollex* – Hill, Playford & Woods pl. P5, fig. 7, 8.

Derivation: spargo – scatter, spinosus – thorny, Lat.

Holotype: UQF 81232 from UQL 4515, Tiverton Formation, figured as Fig. 75, here designated.

Diagnosis: Small tumid to transverse shells with close-set costellae, moderately short spine bases on ventral valve with long anterior tunnels, dorsal spines fine posteriorly and may be stronger in front, dorsal valve geniculate, ventral ears with few (five or six and very rarely one or two more or less) erect spines.

Fig. 68. *Bookeria sparsispinosa* n. sp., external mould of ventral valve UQF 81233 from UQL 4510, x2.

Material: Specimens with typical ear spines come from UQL 1621, 1623?, 2584, 2621, 2623, 2626, 2629, 2631, 3127, 4509, 4510, 4514, 4515, 4518 and 4519. Several specimens, mostly ventral valves and specimens with valves conjoined, from UQL 1630, 1380, 1624, 1626, 2626, 2628, 4509, 4511, 4516- 4518 and 4524 seem likely to belong to the species but ear spines are obscure. *Bookeria geniculata* and *Taeniothaerus subquadratus* Zones.

Dimensions in mm: means, n = 20.

Width	Length	Height
23	22	13

Description: Shells small, dorsal valve deeply concave, ears comparatively small, capillae fine and persistent over both valves. The largest specimen was measured at 26mm in width, 23mm in length and 15mm in height. The Tiverton and Elvinia specimens share much the same spine pattern, having few spines over the ears and suberect ventral spines over the disc, with spine bases usually 3.5mm up to 5mm long, but with some bases short and thick, varying on different specimens. Hinge row of spines not clearly defined. The spines do not conform to one pattern, but are erratic in distribution, and are very few over the ears and adjoining umbonal slopes. On material from UQL 4510, spine bases are 2.5mm long, and 0.6-0.7mm wide. Within the shell the spine tunnels are 8mm long. A number of shells have very small ears, with few spines. Costellae number 10-12 in 5mm anteriorly. The dorsal valve is geniculate and has erect fine spines 0.1mm in diameter, and a number of small dimples especially anteriorly, as well as over the ears. Scattered anterior dorsal spines are thick at 0.5mm and rarely 0.6mm in diameter on specimens from UQL 4519. Dorsal commarginal wrinkles are more prominent than on the ventral valve, numbering six in 5mm postero-laterally, and fine growth increments number 8 in 1mm anteriorly.

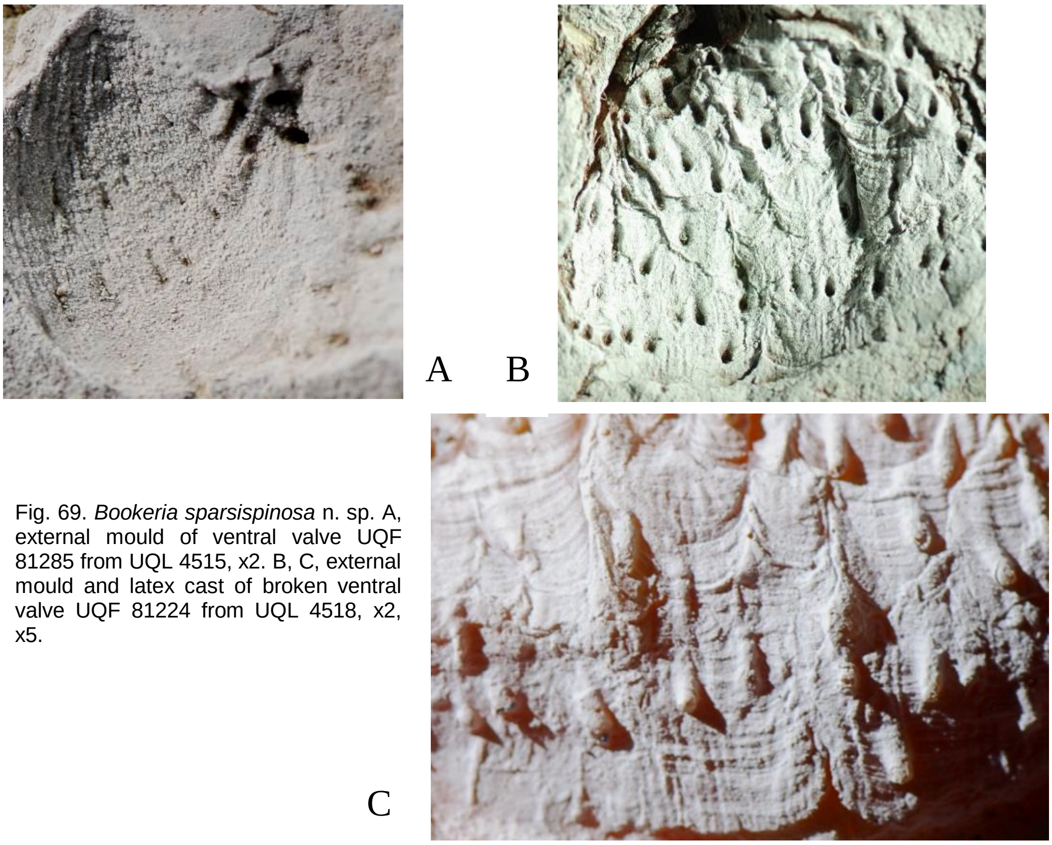


Fig. 69. *Bookeria sparsispinosa* n. sp. A, external mould of ventral valve UQF 81285 from UQL 4515, x2. B, C, external mould and latex cast of broken ventral valve UQF 81224 from UQL 4518, x2, x5.

Ventral adductor scars not strongly impressed, weakly dendritic, may be divided by slender anterior myophragm, diductor impressions faint with radial grooves. The posterior walls slightly thickened. Dorsal median septum extends a little past mid-length, cardinal process low, adductor scars not deeply impressed, bordered posteriorly by low ridge extending from base of cardinal process. Posterior dorsal adductors vary from smooth to moderately dendritic, almost smooth anterior adductors; median septum broad posteriorly and divided by shallow groove. Low pustules developed at edge of disc near start of trail.

Resemblances: The presence of this species in the Tiverton Formation was recorded by Waterhouse (2001, p. 42). Compared with material described as *Paucispinauria geniculata* by Waterhouse (1986a, p. 51, pl. 12, fig. 4-11 and including pl. 15, fig. 13) from the Elvinia Formation of the southeast Bowen Basin, the Tiverton material involves

Fig. 70. *Bookeria sparsispinosa* n. sp., dorsal aspect of latex cast UQF 81225 from UQL 4515, x4.

specimens that may be slightly larger, and less commonly sulcate, and shows slightly less numerous spines along the inner ears and lower umbonal slopes (see Waterhouse 1986a, pl. 12, fig. 7) and slightly broader spines over the anterior dorsal valve (see Waterhouse 1986a, pl. 12, fig. 11). The Tiverton specimens were identified with *Terrakea pollex* Hill, 1950 by Briggs (1998), but are distinguished by the sparsity of spines over the ventral ears, and also by the smaller size, and less elongate outline, slightly thicker spines over the trail, and higher angle of ventral spine emergence from the ventral disc. Specimens of *Bookeria geniculata* from the Elvinia Formation are close in spine detail and in size, but include sulcate and also more transverse specimens, as well as other specimens that are weakly or non-sulcate. Few Tiverton specimens are sulcate: most resemble the Elvinia specimens figured in Waterhouse (1986a, pl. 12, fig. 9-11). The species *geniculata* was also reported from the Chalmers Formation, central Queensland coast near Rockhampton, by Crouch & Parfrey (1998, p. 20).

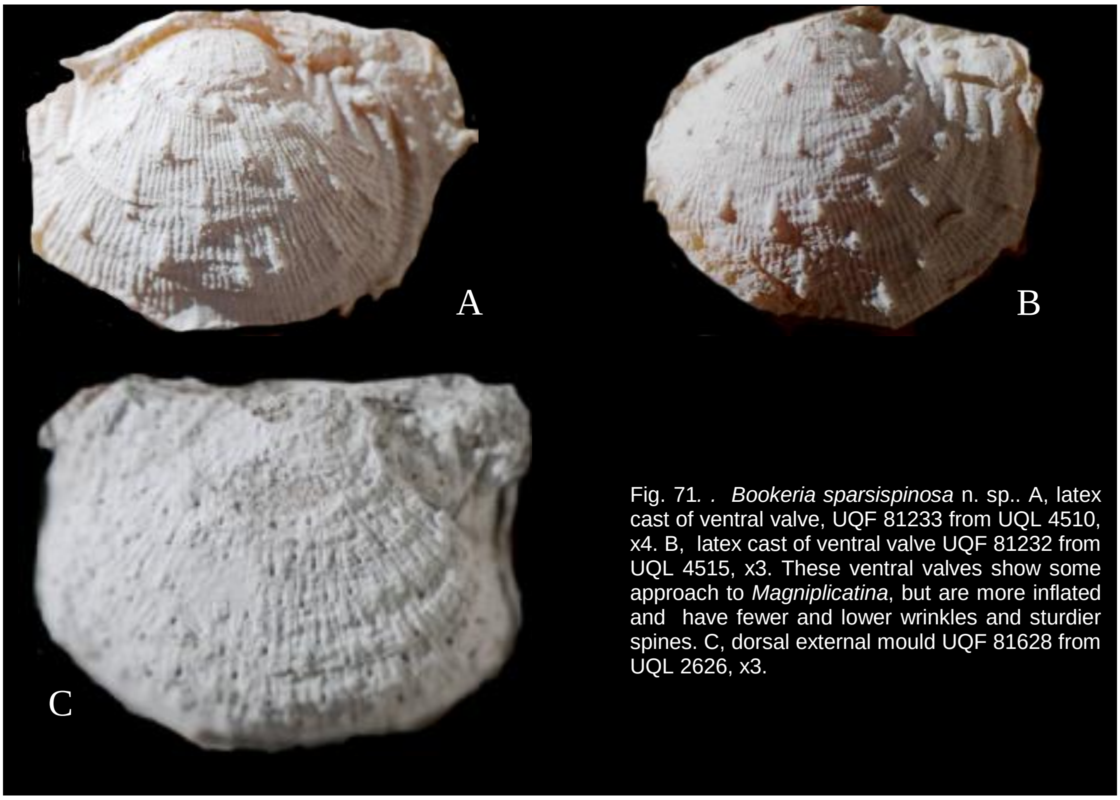


Fig. 71. . *Bookeria sparsispinosa* n. sp.. A, latex cast of ventral valve, UQF 81233 from UQL 4510, x4. B, latex cast of ventral valve UQF 81232 from UQL 4515, x3. These ventral valves show some approach to *Magniplicatina*, but are more inflated and have fewer and lower wrinkles and sturdier spines. C, dorsal external mould UQF 81628 from UQL 2626, x3.

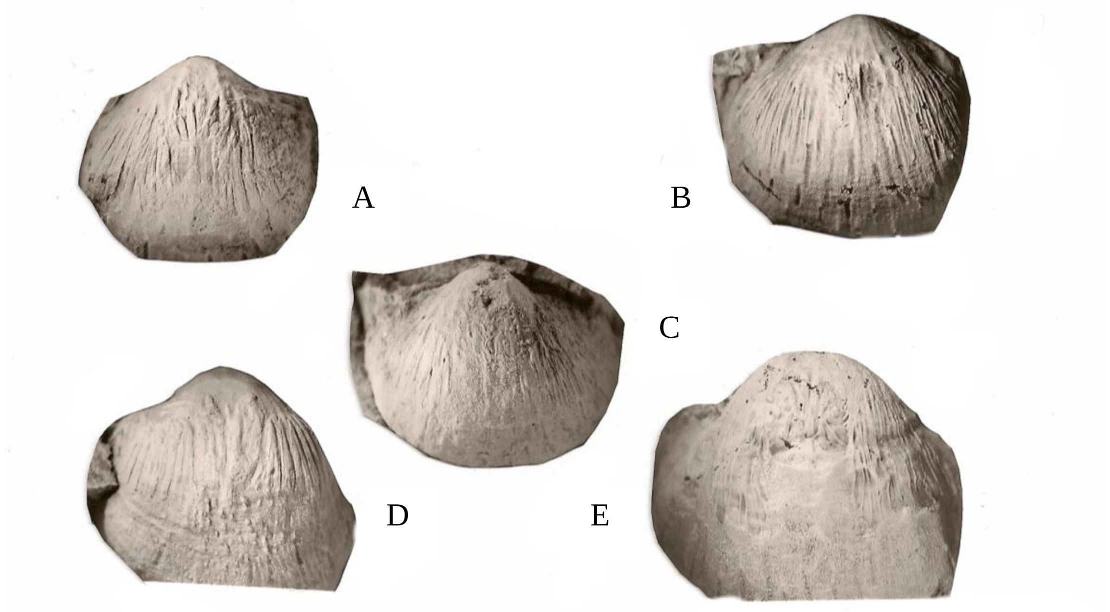


Fig. 72. *Bookeria sparsispinosa* n. sp. A, internal mould of ventral valve UQF 81225 from UQL 3127, x 1.5. B, ventral internal mould UQF 81228 (trimmed on right side) from UQL 3127, x1.5. C, internal mould of ventral valve UQF 81229 from UQL 4515, x2. D, internal mould of ventral valve UQF 81227 from UQL 3127, x1.5. E, internal mould of ventral valve UQF 81230 from UQL 3127, x2 .

Material identified as *Terrakea pollex* from the Cattle Creek Formation at Little Gorge Creek, west Queensland, by Hill & Woods (1964b) and Hill et al. (1972) might belong to the species, or to *Bookeria drysdalei*. The specimen of Hill (1950, pl. 9, fig. 9) has prominent dorsal commarginal ornament and the genus is not clear from the figure. Another specimen (Hill 1950, pl. 9, fig. 12) was stated to have come from Cracow, but changed to Little Gorge Creek in Hill et al. (1972, pl. P5, fig. 8) and could belong to either species. The other specimen of Hill & Woods (1964b)

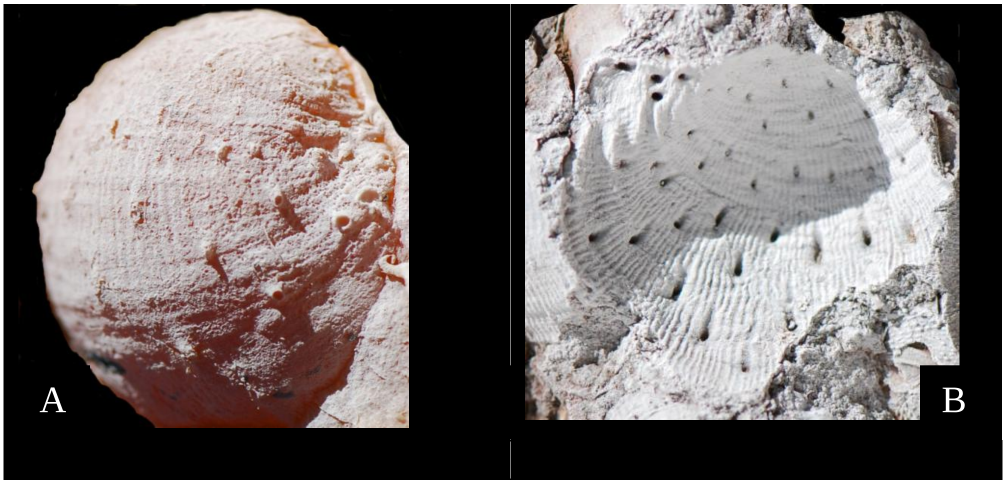


Fig. 73. *Bookeria sparsispinosa* n. sp. A, tilted lateral aspect of latex cast of ventral valve UQF 81231 from UQL 4515, x2.5. B, ventral external mould UQF 81232 from UQL 4510, x2.

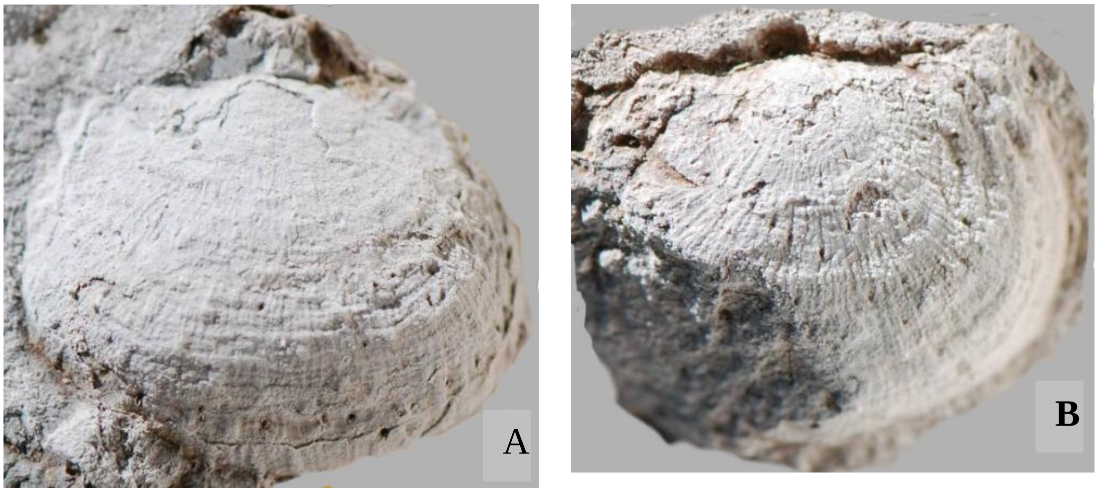


Fig. 74. *Bookeria sparsispinosa* n. sp. A, dorsal external mould UQF 81800 from UQL 2621, x3. B, dorsal external mould UQF 81801 from UQL 4515, x3.

Fig. 75. . *Bookeria sparsispinosa* n. sp., specimens on block, including ventral external mould holotype UQF 81232 from UQL 4515, x2.5.

and also figured by Hill et al. (1972, pl. P5, fig. 7) is an obscure ventral valve, which possibly belongs to *Bookeria sparsispinosa* new species because there appear to be few ear spines, but preservation is poor, and the identification uncertain.

Fig. 76. *Bookeria sparsispinosa* n. sp. external mould of dorsal valve UQF 81234 from UQL 4519, x3.

Bookeria cf. ***pollex*** **(**Hill, 1950)

Fig. 77

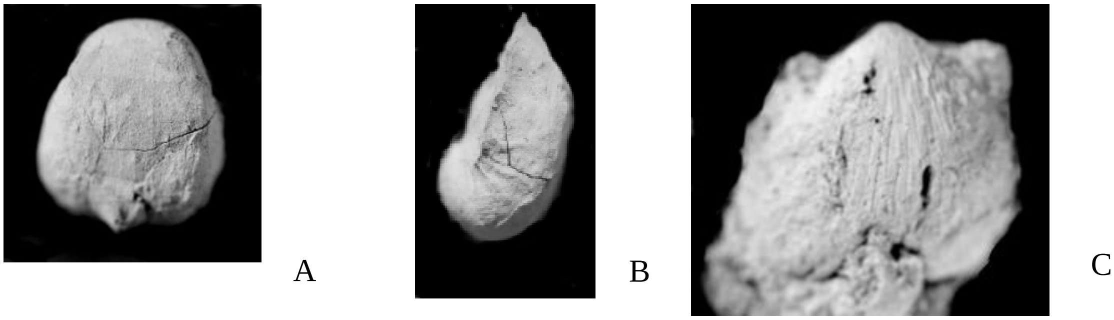
cf. 1950 *Terrakea pollex* Hill, p. 20, pl. 9, fig. 6-8, 11, 12 (part, not fig. 9, ?10 = *Bookeria geniculata*).

cf. 1986a *T. pollex* – Waterhouse, p. 49, pl. 11, fig. 19, 21-23, 25-27 (part, not fig. 20, 24 = *Bookeria drysdalei* n. sp.).

cf. 1998 *T. pollex* – Briggs, p. 163, Fig. 81D, F (part, not A-C, E, G = *drysdalei*).

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

Diagnosis: Shells of small to intermediate size, ventral ears convex and not strongly differentiated, numerous ear spines,



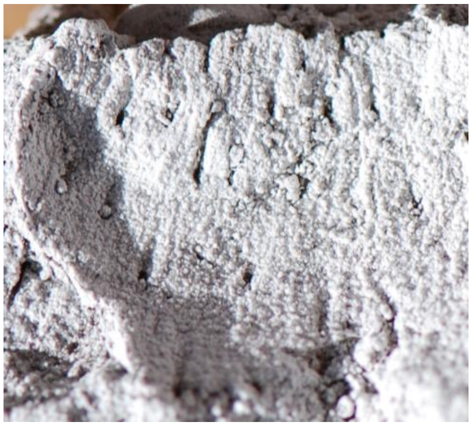


Fig. 77. *Bookeria* cf. *pollex* (Hill). A, B, ventral and lateral aspects of worn ventral valve UQF 81236 from UQL 4506, x1. C, ventral internal mould UQF 81237 from UQL 4506, x 2. D, external mould of anterior ventral valve, UQF 81835 from TK1= UQL 4506, x3.

short spine bases over the venter.

Material: Two fragmentary ventral valves from TK1/2, and dorsal valve from UQL 4506. *Bookeria pollex* Zone.

Description: One ventral valve shows the external and internal mould of the posterior shell, and is approximately 15mm wide, 17mm long and 7mm high, with incurved umbo, no ventral sulcus and well formed convex ears bearing erect crowded spines 0.5mm in diameter. The venter has fine close-set costae and short spine bases, less than 2mm long and 0.2mm wide. The interior has many long spine tunnels, and muscle impressions are faint and immature. An external mould of a ventral valve over 25mm wide lacks a sulcus and has fine costae, about 16 in 5mm, and spines 0.4 to 0.6mm in diameter with short bases generally close to 0.75mm wide and only 1.5mm long, although a few are just over 2mm long. The dorsal valve is small with fine costae and large ears bearing dimples opposing the ventral ear spines.

Resemblances: The material is incomplete, but the narrow thumb-like appearance and fineness of ribs and shortness of the spine-bases are features of *Terrakea* (now *Bookeria*) *pollex*, as illustrated by Hill (1950). The specimen UQF 43046 recorded as *T. pollex* by Maxwell (1964, p. 44) from the Yarrol Basin is shaped like *pollex* but ornament is obscure and the specific position uncertain. The specimens figured from Little Gorge Creek near Springsure, southwest Bowen Basin, by Hill (1950, pl. 9, fig. 9, 10) may belong to *Bookeria sparsispinosa* or *geniculata*, because the dorsal valve shows few dimples on the ears, which suggests few spines on the ventral ears.

Briggs (1998, p. 165) referred specimens from the Camboon Volcanics, Prospect Creek, southeast Bowen Basin, that had been referred by Parfrey (1986, Fig. 2.3a-d) to *Terrakea pollex*. Parfrey had considered that the specimens were too large to belong to *pollex*, and this was rejected by Briggs (1998). The Parfrey specimens are transverse and possibly sulcate, close to the specimen figured by Hill (1950, pl. 9, fig. 8a) and have moderately long crowded ventral spine-bases, 1.5 to 2mm long, arising from costellae that number about five or six in 5mm anteriorly, though these estimates are based only on figures. But the critical ears and ear spines are not displayed on these specimens.

Bookeria drysdalei n. sp.

Fig. 78 – 83

1986a *Terrakea pollex* – 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. 81 D, F = *pollex*).

Derivation: Named for John Drysdale.

Holotype: Specimen UQF 81242 from UQL 2631, Tiverton Formation, figured herein as Fig. 80C and 83A, here designated.

Diagnosis: Small subequilateral shells with weakly convex transverse venter, moderately large ears clearly separated from umbonal walls, numerous ventral ear spines, ventral spines emerge at high angle with broad comparatively short bases, dorsal spines erect.

Material: Specimens from UQL 2584, 2629, 2630, 2631, 4512, 4515 – 4519 and LT3. *Svalbardia armstrongi* Subzone and *Taeniothaerus subquadratus* Zone. As noted for *Bookeria sparsispinosa*, specimens from a number of localities are not readily identifiable to species or genus because ventral ears are poorly preserved, and may belong to either *sparsispinosa* or *drysdalei*.

Dimensions in mm: means

n	Width	Length	Height
10	21	18	9.5

Description: Shells small, weakly transverse or seldom elongate, with well developed ears, rounded venter and geniculate trail. Ventral umbo broad with angle of 90-100^o, incurved, umbonal walls steep and high, ears large and moderately long as a rule, maximum width of shell either at hinge or close to mid-length. Dorsal valve with concave disc, large ears and moderate to high trail curving gradually from the visceral disc. Ventral costellae fine, 14-16 in 5mm anteriorly, including trail. Ventral spines over disc sturdy, generally 0.8-0.9mm wide at base, inclined at high angle from shell, with short bases often 1 or 2mm long, rarely up to 3.5mm long, pass forward from two costellae as a rule. Spines numerous, erect and close-set over ventral ears, numbering 12-14. Dorsal ears with corresponding dimples. Dorsal spines erect, 0.2-0.3

mm in diameter posteriorly, close to 0.5mm in diameter anteriorly. Dorsal costellae fine, faint, up to 18 in 5mm anteriorly, especially faint where trail commences (UQL 4516), compared with 14 in 5mm in a specimen from UQL 4519, in which the costellae are disrupted by hollows. Elongate dimples developed near commencement of trail, and low anterior radial folds present. Commarginal wrinkles low and close-set over dorsal valve, most noticeable at start of trail, very faint over ventral valve.

Ventral adductor scars not strongly impressed, weakly dendritic, may be divided by slender anterior myophragm, diductor impressions faint with radial grooves, posterior walls slightly thickened. Dorsal median septum extends a little past mid-length, cardinal process low, adductor scars not deeply impressed, bordered posteriorly by low ridge extending from base of cardinal process. Posterior adductors weakly dendritic, almost smooth anterior adductors; median septum broad posteriorly and divided by shallow groove. Low pustules developed at edge of disc near start of trail.

Resemblances: This species is close to *Bookeria geniculata* (Waterhouse, 1986a) and *B. sparsispinosa* n. sp. in size, shape and general appearance, but has a dense array of spines over the ventral ears. Other differences may not be fully consistent*:* the ears tend to be large, and the trail less geniculate and dorsal disc slightly more concave, compared with *geniculata*. Ventral spines appear to be slightly more inclined from the shell surface, but only on some specimens, and the spine bases tend to be shorter and broader. Dorsal spines are like those of *Bookeria sparsispinosa*, but may be more numerous, and finer anteriorly. The two forms *Bookeria drysdalei* and *B. sparsispinosa* are found together in some collections (UQL 2584, 2629, 2631, 4515) and whilst collections were not made layer by layer, it seems possible that the two species did co-exist.

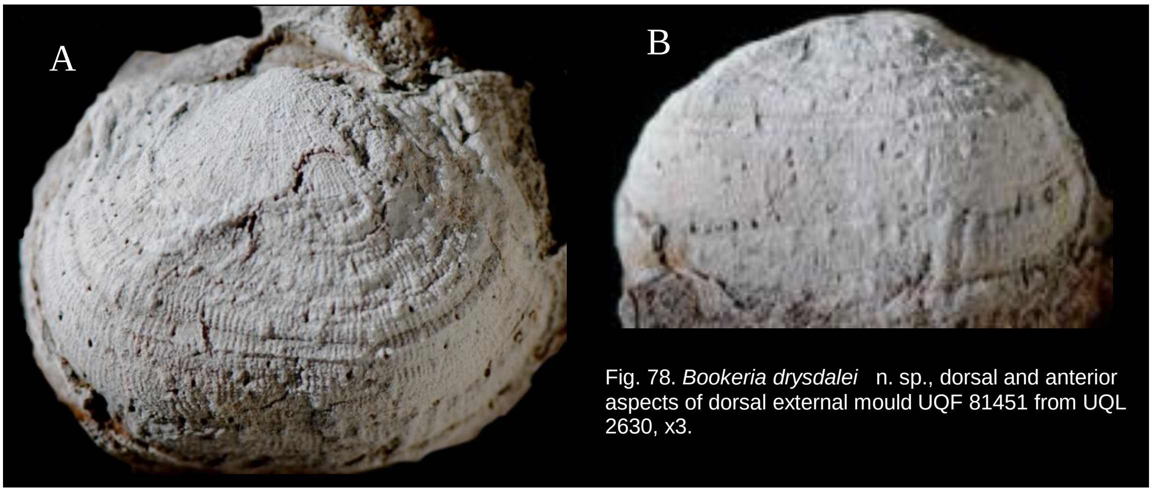


Fig. 78. *Bookeria drysdalei* n. sp., dorsal and anterior aspects of dorsal external mould UQF 81451 from UQL 2630, x3.

Bookeria pollex (Hill, 1950, pl. 9, fig. 6-8, 11, 12) from the Fairyland Formation of the southeast Bowen Basin is very close, and *drysdalei* is treated as a related species, of younger age, but perhaps should be a subspecies. The species of *Terrakea* in east Australia, *dickinsi, exmoorensis, brachythaera* and *elongata*, are all larger and much closer to each other than to *pollex* or *drysdalei*. Differences between *drysdalei* and type *pollex* involve the larger size of the ears, especially on the dorsal valve, and, with some reservation, a more consistently transverse rather than elongate shape. Curiously, most of the topotype material figured for *pollex* by Hill (1950) is elongate and thumb-shaped like those from the lower Tiverton Formation, with specimens up to 30mm wide and 35-40mm long, whereas most of the specimens figured from the same formation by Waterhouse (1986a) and Briggs (1998) are more transverse, suggesting that they came from slightly different populations. Only one of Hill's specimens (1950, pl. 9, fig. 8) is transverse and sulcate. Ornament is scarcely shown on Hill's specimens, and is better preserved in the material described by Briggs (1998) and by Waterhouse (1986a). These indicate that ear spines form a denser cluster, persisting further forward and comparatively uniform over *drysdalei* as compared with *pollex* (see Briggs 1998, Fig. 81A, B and Waterhouse 1986a, pl. 11, fig. 19, 20, 24). Such implies that *drysdalei* marked a younger form, progressing towards *Terrakea*.

Fig. 79. *Bookeria drysdalei* n. sp. A, dorsal external mould UQF 81431 from LT3, x4. The black tubes on the left side are hollows in the matrix, left by the dissolving of halteroid ventral ear spines.

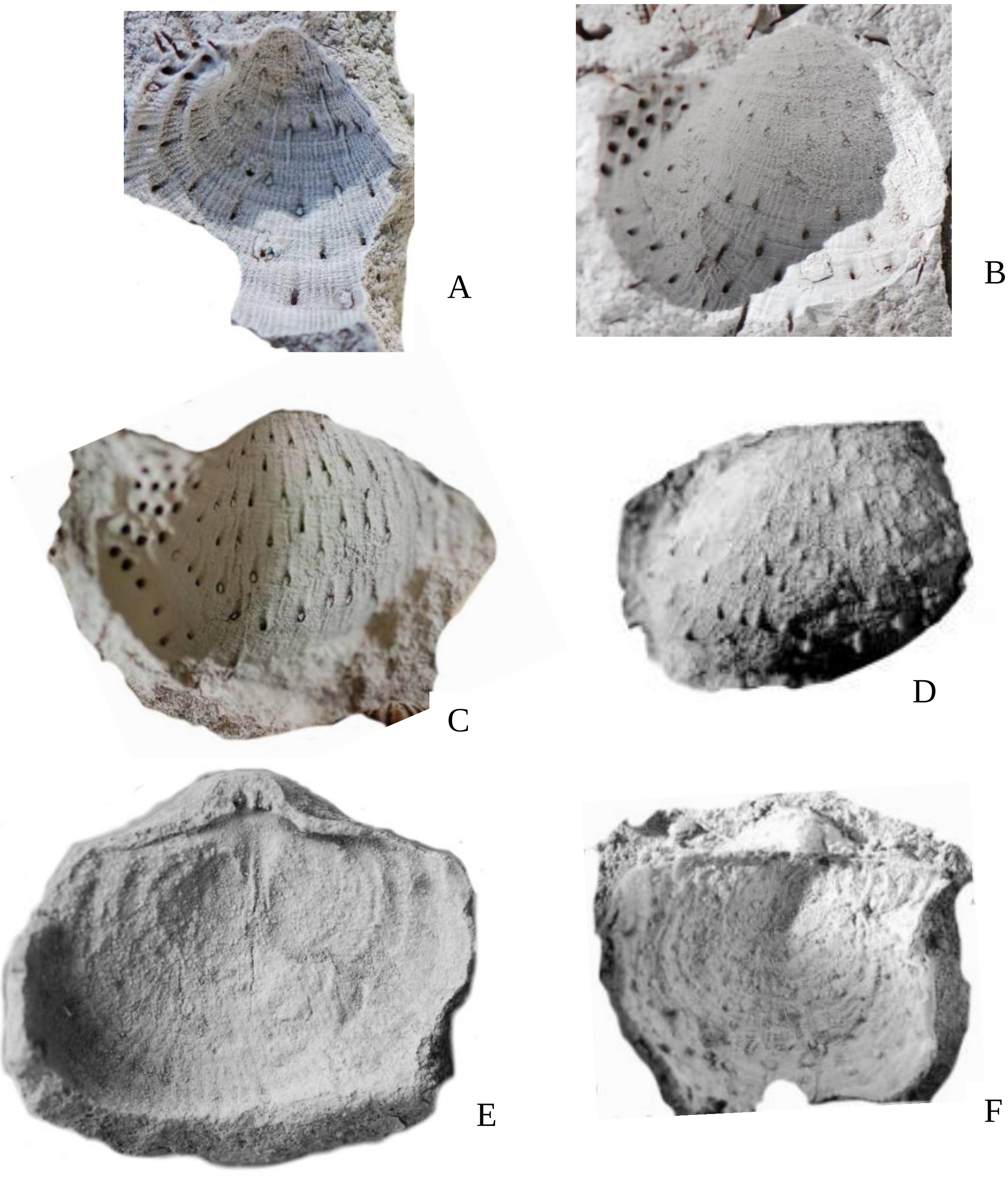


Fig. 80. *Bookeria drysdalei* n. sp. A, ventral external mould UQF 81807 from UQL 4519, x4. B, ventral external mould UQF 81241 from UQL 4519, x2. C, holotype ventral external mould UQF 81242 from UQL 2631, x2. D, latex external cast of ventral valve UQF 81243 from UQL 4519, x2.5. E, dorsal aspect of internal mould UQF 81247 from UQL 4517, x4. F, latex cast of external mould, dorsal aspect of UQF 81244 from UQL 4519, x3.

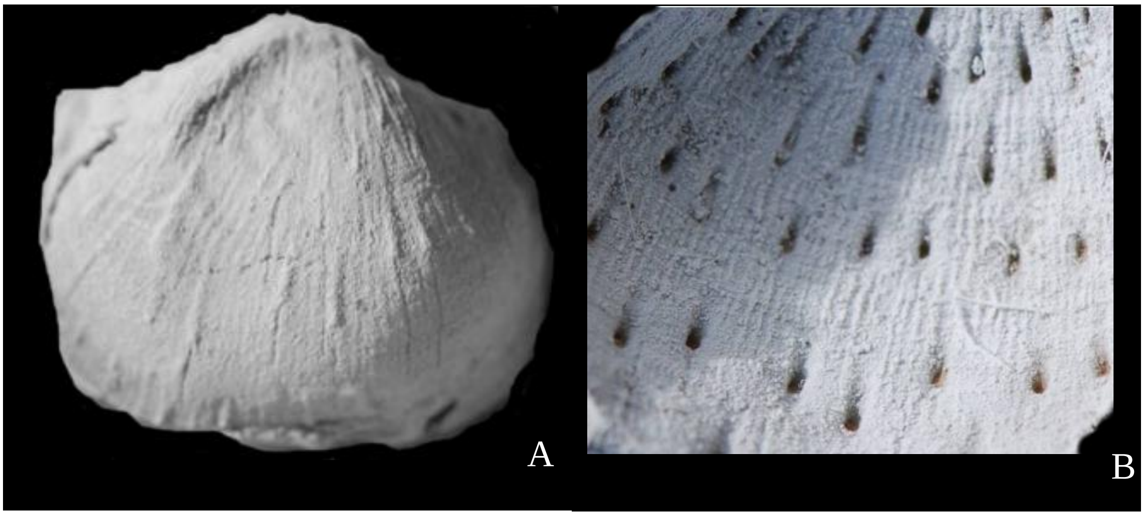


Fig. 81. *Bookeria drysdalei* n. sp. A, ventral aspect of internal mould UQF 81239 from UQL 4519, x3. B, ventral external mould UQF 81430 from LT3, x3.

Waterhouse (2001, p. 42) noted that the Tiverton "*Terrakea"* showed slightly fewer ear spines as compared with *pollex*, which seems correct if all are counted, and thick spines are fewer, and ventral spine bases longer. It was also noted that geniculation commenced at a slightly greater size. The costae are slightly stronger and the ears on both valves not as large as in the new species, nor as clearly separated from the umbonal slopes. Internally the ventral muscle scars of *pollex* are larger, more anteriorly placed, more strongly impressed, with more dendritic adductors and more impressed and striate diductors. But these differences are not great, and not fully consistent. Specimens figured as *pollex* by Waterhouse (1986a, pl. 11, fig. 20, 24) from the basal Elvinia Formation of southeast Bowen Basin are like the species *drysdalei* in the size of the ventral ears, though they are less strongly demarcated from the disc. Subspecific ranking might be more appropriate for this taxon.

Fig. 82. *Bookeria drysdalei* n. sp., latex cast of dorsal interior UQF 81239 from UQL 4519, x4.

Briggs (1998) identified *Terrakea pollex* in both Farley and Tiverton Formations, but Farley material requires further documentation. Specimens from the lower Cattle Creek Formation of southwest Bowen Basin that

Hill (1950, pl. 9, fig. 10) had referred to *pollex* come from the Riverstone Sandstone Member near Springsure. The specimens figured by Hill (1950, pl. 9. fig. 9-12) were rejected from synonymy by Briggs (1998), without suggesting any specific identification. This is justified, as the material is poorly preserved, and shows little of no ornament. They are found at the same biostratigraphic level as *drysdalei* and *geniculata*. The specimen UQF 2001 figured by Hill (1950, pl. 9, fig. 9) has strong commarginal ornament, and is difficult to identify from the figure (and see p. 120), but the specimen figured by Hill (1950, pl. 9, fig. 11) from Cracow is shaped like Hill's *pollex*: unfortunately no ornament is preserved, so that its identity remains insecure.

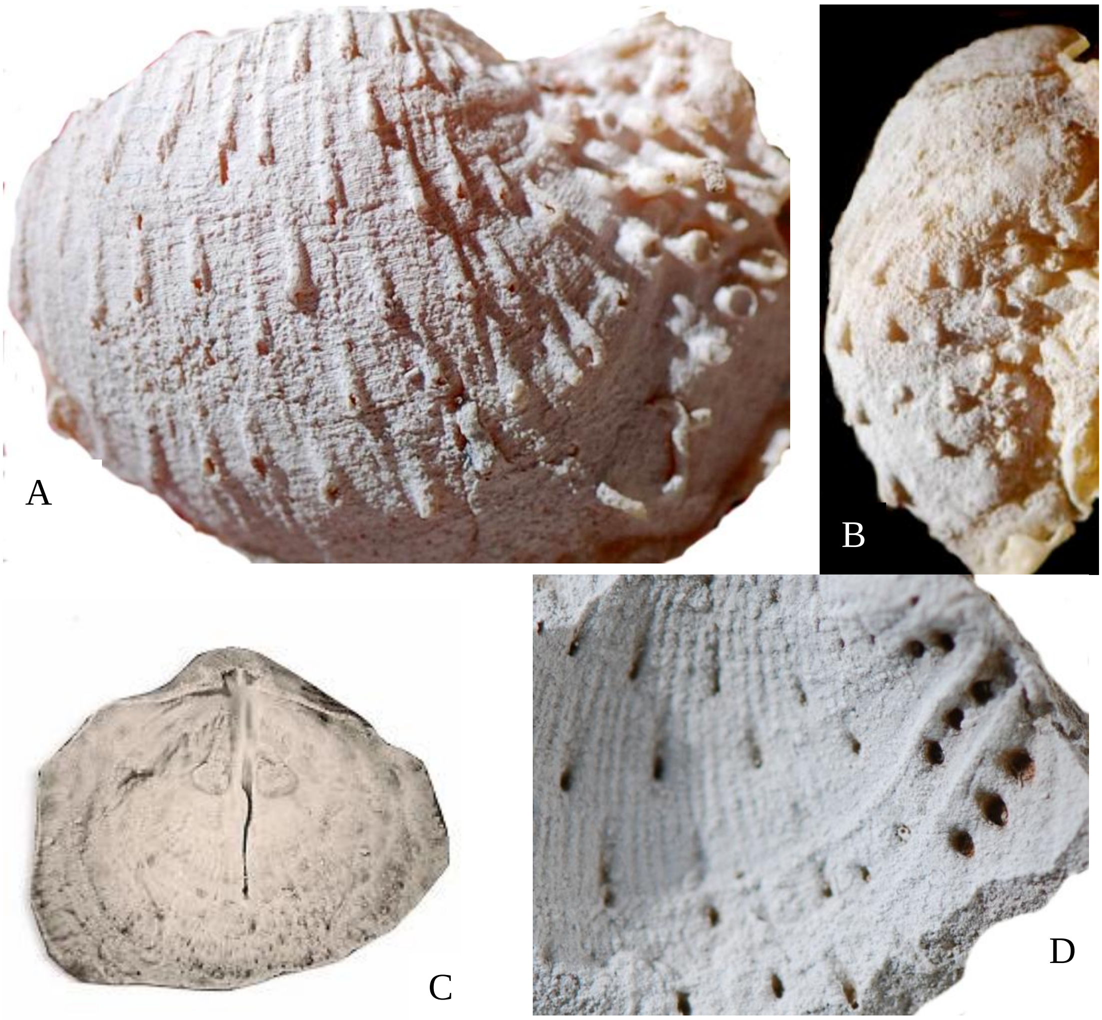


Fig. 83. *Bookeria drysdalei* n. sp. A, holotype, latex cast of ventral exterior UQF 81242 from UQL 2631, x4. B, latex cast of ventral valve UQF 81433 from UQL 4516, x3, showing umbonal slope rows of spines. C, dorsal aspect of internal mould, UQF 81238 from UQL 4519, x3. D, external mould of UQF 81629 from UQL 4515, x5, showing large closely spaced ear spines over anterior umbonal slopes.

Terrakea dickinsi Dear (1971, pl. 4, fig. 2-9), from the upper Tiverton Formation near Homevale, is twice as large as *Bookeria drysdalei*, showing a marked increase in size, and the species displays high posterior walls, long spine tunnels and many ear spines and elongate geniculate dorsal trail with thick anterior spines and deep visceral cavity, and strongly impressed muscle scars.

Subfamily **MAGNIPLICATINAE** Waterhouse, 2001

Diagnosis: Shells with thin body cavity and strong commarginal wrinkles, costate, spines little differentiated, hinge spines usually in two or three rows, body spines semi-recumbent with prolonged bases, dorsal spines present or absent. Ventral adductors faintly impressed, dendritic.

Tribe **MAGNIPLICATININI** Waterhouse, 2001

Diagnosis: Pronounced commarginal rugae, ventral spines in rows along hinge, body spines in regular quincunx.

Discussion: An allied tribe Engellinini is of Lower Carboniferous age and has numerous ventral ear spines and disc spines may be scattered, in regular quincunx, or rare. The valves are less rugose.

Subtribe **MAGNIPLICATININAI** Waterhouse, 2001

Diagnosis: Commarginal rugae over both valves.

Discussion: Subtribe Cancrinellinai has rugae mostly over the dorsal valve, with rugae absent from the ventral disc.

Genus ***Magniplicatina*** Waterhouse, 1983c

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

Diagnosis: Closely costate shells with ventral spines in one, two to three 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.

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).

Magniplicatina undulata Waterhouse, 1986a

Fig. 84, 85

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 tumida*).

1964b *C. farleyensis* – Hill & Woods, pl. P6, fig. 12 (part, not 13-16 = *C. tumida*).

1964a *C.* aff. *farleyensis* – Waterhouse, p. 61, pl. 9, fig. 3.

1972 *C. farleyensis* – Hill, Playford & Woods, pl. P6, fig. 12 (part, not 13-16 = *tumida*).

1986a *Magniplicatina undulata* Waterhouse, p. 45, pl. 9, fig. 17-20.

1986a *Magniplicatina transversa* Briggs, p. 187, Fig. 91B-J (part, not 91A = *Platycancrinella* n. sp.).

1998 *M. undulata* – Briggs, p. 188, Fig. 92A-J.

Holotype: For *undulata* – UQF 74019 from Elvinia Formation, southeast Bowen Basin, figured by Waterhouse (1986a, 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.

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

Material: Specimens from UQL 4510 and 4512. Reported from UQL 1621 by Briggs (1998, p. 188). *Bookeria geniculata* Zone. Also Lakes Creek Group, Berseker Formation, UQL 29.

Dimensions in mm:

UQF	UQL	Width	Length	Height
81249	4512	14	13.5	3.5

Description: Ventral valve small, umbonal angle 100°, ears small with obtuse cardinal extremities, hinge with row of spines and some extra spines, spines in regular quincunx over venter, with elongate bases nearly 2mm long anteriorly; in front on worn shell a channel or rib extends forward. Ribs fine, four per mm anteriorly; shell crossed by rugae, steadily increasing forwards in strength and spacing, steep and more crowded laterally. Muscle scars weakly defined.

Discussion: *Magniplicatina* is rare in the present collections from the Tiverton Formation, but Briggs (1998) reported material belonging to *transversa* at UQL 1621. The species *transversa* has not been adequately established, and some specimens look like *Magniplicatina undulata* Waterhouse (1986a, 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 (1986a, 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. As noted by Waterhouse (2010a, p. 43), a specimen assigned to *transversa* by Briggs (1998) from Rockhampton belongs to a different genus, *Platycancrinella* Waterhouse, 1983a, because it displays numerous ventral ear spines.

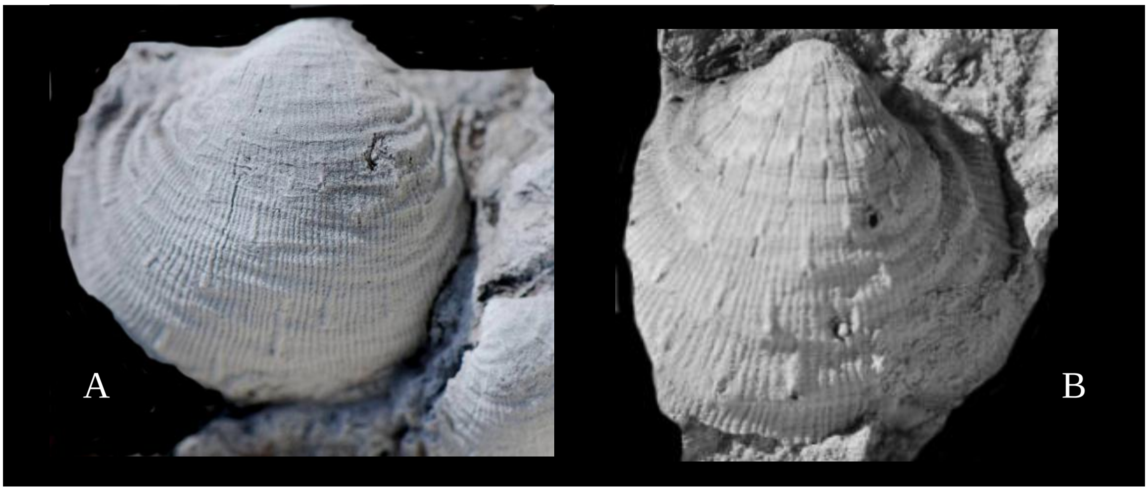


Fig. 84. *Magniplicatina undulata* Waterhouse. A, ventral valve UQF 81248 near small specimen to lower right, from UQL 4510, x3. B, small ventral valve UQF 81249 from UQL 4512, x4.

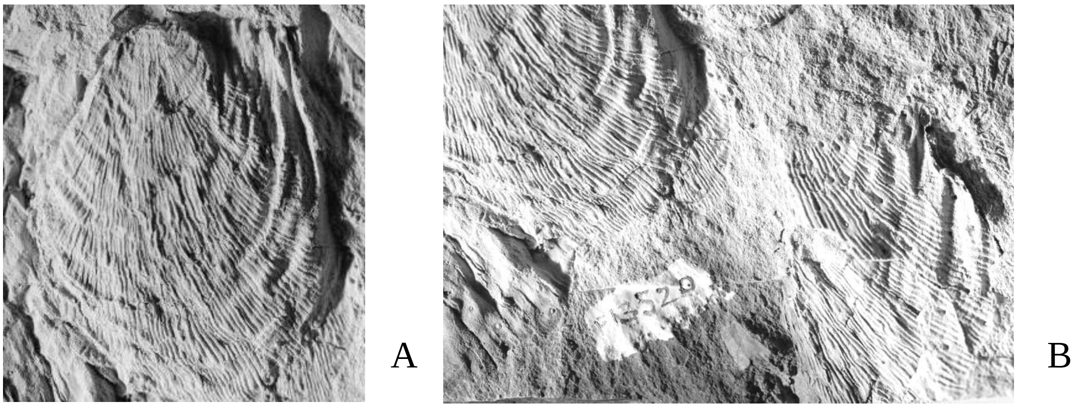


Fig. 85. *Magniplicatina undulata* Waterhouse. A, ventral internal mould UQF13520. B, UQF 13520A, showing external mould with spine bases and spines represented in reverse. From UQL 29, Lakes Creek Group, x2.

The dorsal valves of these specimens are not known, so that identity is based principally on low inflation. The small size means that they are close to *Costatumulus*, but they seem to have dendritic adductors, and they have slightly stronger wrinkles than in *Costatumulus* or *Paucispinauria*. If the identity is correct, larger specimens will show stronger wrinkles, and the dorsal valve will lack spines.

Magniplicatina dunstani Waterhouse, 2015 from the upper Rammutt Formation of Gympie, southeast Queensland, is close, but has finer and more closely spaced rugae, and wider hinge.

Family **AURICULISPINIDAE** Waterhouse, 1986a

Diagnosis: Both valves ornamented by slightly irregular ribs, ventral spines arranged along hinge in one to four rows, and arranged in quincunx over the ventral disc, with elongate bases, spines 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 subfamilies are known, Auriculispininae as described shortly, Lyoniinae Waterhouse which includes *Bandoproductus* and is widely developed in especially early Permian deposits of Gondwana, and Filiconchinae Waterhouse, found especially in Middle Permian of east Australia and Arctic faunas, 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, 1986a

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.

Discussion: The prime features are the slender disc, slender and elongate ventral spine bases, and striate nature of the ventral adductors. Contents of this important 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 is 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 by Brunton et al. (2000, p. 537), but was regarded as a valid family group within Linoproductoidea by Waterhouse (2013), on the basis of the nature of the ornament and the muscle impressions.

Genus ***Costatumulus*** Waterhouse, 1986b

Type species: *Auriculispina tumida* Waterhouse in Waterhouse et al. (1983, p. 133) from Tiverton Formation (Sakmarian), Bowen Basin, OD.

Diagnosis: Transverse to 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, weakly to well defined. Dorsal adductor scars becoming dendritic, platform developed in front of cardinal process, joined by two diverging ridges parallel to hinge.

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 1993a), India (Singh & Archbold 1993), China (Chen & Shi 2006), northern Russia (Waterhouse 2013), Canada, Svalbard and New Zealand (Waterhouse 2001, pl. 1, fig. 10; 2013).

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, but 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 tumida (Waterhouse, 1983)

Fig. 86 - 93

1950 *Cancrinella farleyensis* – Hill, p. 14, pl. 8, fig. 1, 4-6 (part, not pl. 7, fig. 7, pl. 8, fig. 2, 3 = *Magniplicatina undulata* Waterhouse).

1964 *C. farleyensis* – Maxwell, p. 43, pl. 7, fig. 21, 22.

1964b *C. farleyensis* – Hill & Woods, pl. P6, fig. 13-16 (part, not pl. P6, fig. 12 = *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.

1983c *Costatumulus tumida* – Waterhouse, p. 44.

2000 *C. tumida* – Brunton et al., p. 538, Fig. 376.2a-d.

2007 *C. tumida* – Waterhouse & Chen, text-fig. 1D.

Holotype: UQF 73302 from UQL 4515, Tiverton Formation, figured by Waterhouse et al. (1983, pl. 3, fig. 2), OD.

Diagnosis: Large shells of generally transverse outline, venter often tumid, moderately large ears, low commarginal wrinkles, and moderate density of ventral spines over disc and trail.

Material: Specimens from UQL 29, 1383, 1385, 1621, 1622, 1625, 1626, 1630, 2584, 2619, 2622 - 2626, 2628, 2629, 3127, 4509 - 4515, 4519, 4524 and LT3; UQF 20956, 20957, 20958. *Bookeria geniculata* and *Taeniothaerus subquadratus* Zones.

Dimensions in mm:

	Width	Length	Height	
Transverse and subequilateral shells, mean = 15				
	41	28.5	18	(maximum width 49)
Subelongate shells with tumid anterior, mean = 10				
	36	38	24	(maximum width 44)

Fig. 86. *Costatumulus tumida* (Waterhouse), latex mould of ventral valve UQF 81449 from UQL 4519, x2.

Description: *Costatumulus* 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 different morphologies in the present assemblage – transverse and little inflated specimens with gently concave ventral anterior, 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. The ears are generally short, but several specimens from UQL 4515 have larger, slightly longer ears that tend to be slightly flatter than usual. Dorsal valves are well represented, and the trail is subgeniculate. Costellae are fine and vary between 12 and 17 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 in two rows along the hinge, with one to three additional spines laterally, but spines lie in a single row in some shells. Body spines are disposed in quincunx, and are generally nearly twice as wide as costellae, but wider in specimens from UQL 4511. 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 are variations, with ribs sometimes disappearing beside the spine, and then resuming or replaced a little in front. Lazarev (2003, 2004) made much of the relationship between spine bases and rib numbers in a few linoproductoid species and genera, but in *Costatumulus* there is a degree of variation which discourages any simplistic generalization. Commarginal rugae are developed over the posterior walls and in some specimens the ears, and are more prominent on the dorsal valve. Micro-ornament is not very well preserved, but some specimens (eg. UQF 20957) indicate that about 13-15 growth increments occur over each wrinkle, suggestive of a fortnightly control, presumably tidal under the influence of the moon, and 18-25 wrinkles can be counted from the edge of the nepionic shell to the trail, with possibly two to four wrinkles lost. This implies, at face value, a life span of a month or two longer than a year, but there is a speculative element, because the growth increments cannot be observed for the entire shell, having to be extrapolated from the number of wrinkles.

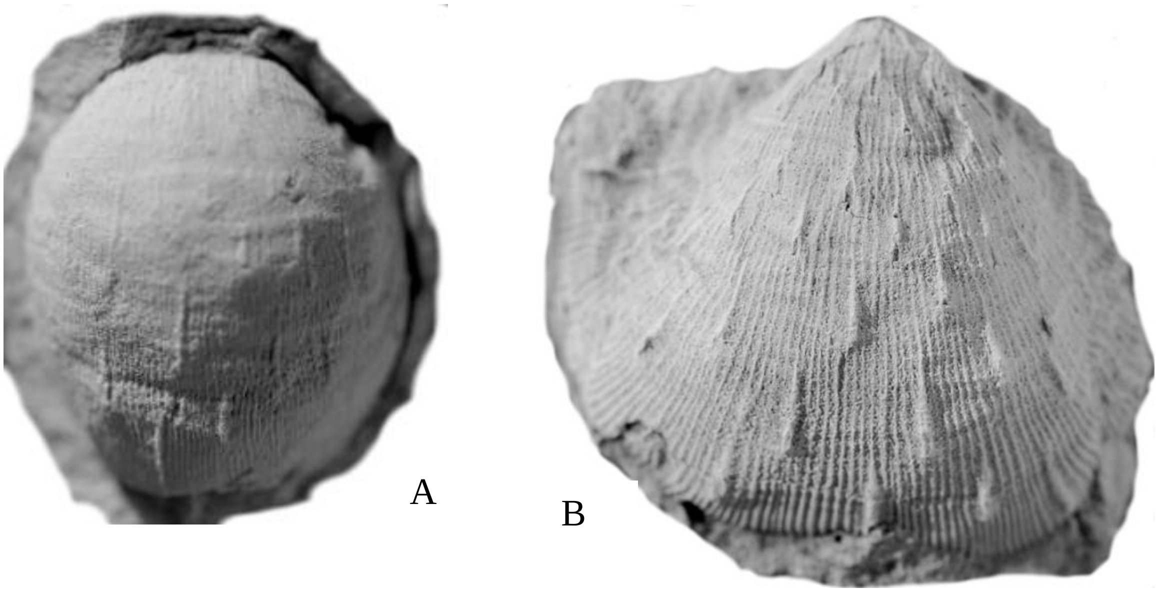


Fig. 87. *Costatumulus tumida* (Waterhouse). A, ventral internal mould UQF 81213 from UQL 4510, x2. B, ventral valve UQF 81428 from UQL 4509, x3.

The ventral interior is significant because of the nature of the adductor scars. These are elongate and divided in many but not all specimens posteriorly by a myophragm. The surface is comparatively smooth until maturity, when fine striae appear over the anterior adductors, and scallops develop laterally at the outer edge of the posterior adductors such as shown in Fig. 92 (p. 138), and during ongoing maturity scallops extend obliquely inwards, and muscle scars become high and more dendritic. Even in late maturity, the adductor scars are distinctive, very posteriorly placed, with heavy shell thickening to the sides so that the scars are impressed. Briggs (1998, Fig. 73) clearly illustrated the differences in position and ridging found in *Costatumulus* as compared with *Magniplicatina* and *Terrakea*. The anterior adductors remain finely and weakly striate with ridges less convoluted than in paucispinaurian genera such as *Terrakea*, and their ontogeny indicates a significant apomorphy.

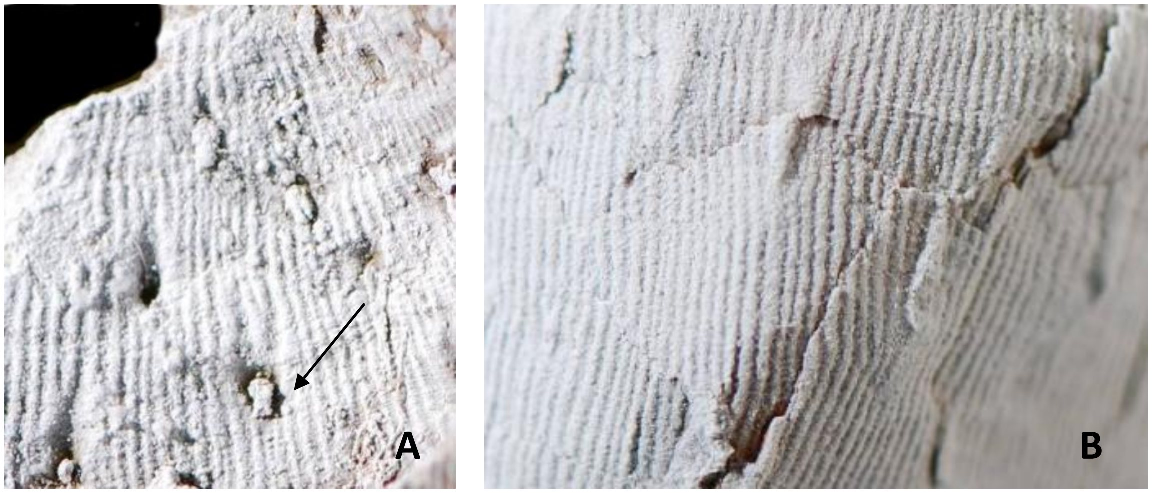


Fig. 88. *Costatumulus tumida* (Waterhouse). A, detail of ornament on anterior ventral valve external mould, showing posteriorly prolonged spine bases which have been broken short, and anteriorly prolonged spine cores (arrowed). UQF 81269 from UQL 1383, x4. B, detail on ventral trail of UQF 81214 from UQL 4510, x4.

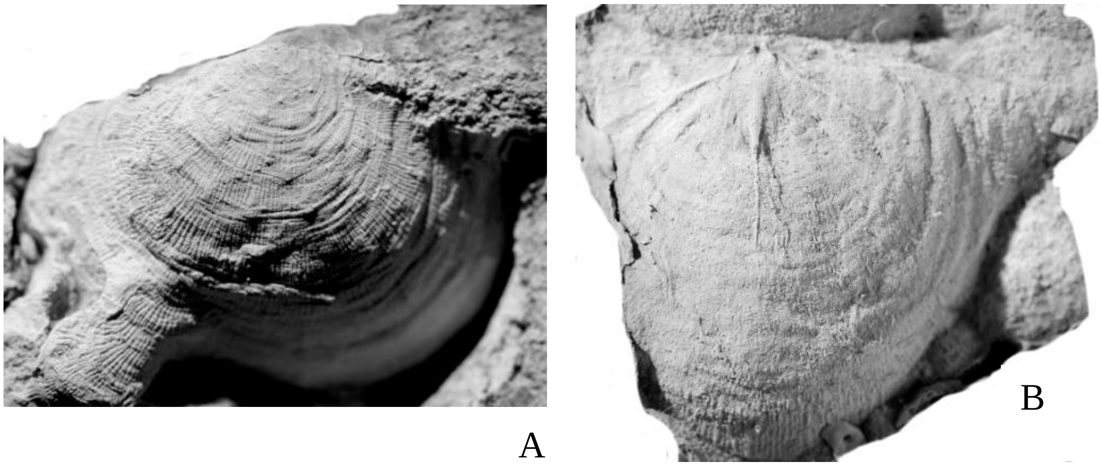


Fig. 89. *Costatumulus tumida* (Waterhouse). A, dorsal valve showing irregular and quite exceptional extension of the trail, UQF 81220 from UQL 2623, x1.5. B, latex cast of dorsal interior, UQF 81221 from UQL 4515, x1.5.

The dorsal median septum is less than half of the length of the valve, and is broad and low posteriorly, joined each side by a lateral ridge inclined obliquely forward in front of the hinge and behind the posterior adductors. The posterior and anterior adductors are smooth until well into maturity, and then become dendritic. Brachial ridges are faintly if at all impressed. The visceral cavity is 5mm deep in a shell 33mm long, 7mm deep in a specimen 35mm long (UQF 20956), and nearly 8mm thick in an elongate specimen 50mm long, and nearly 9mm thick in a specimen 35mm long.

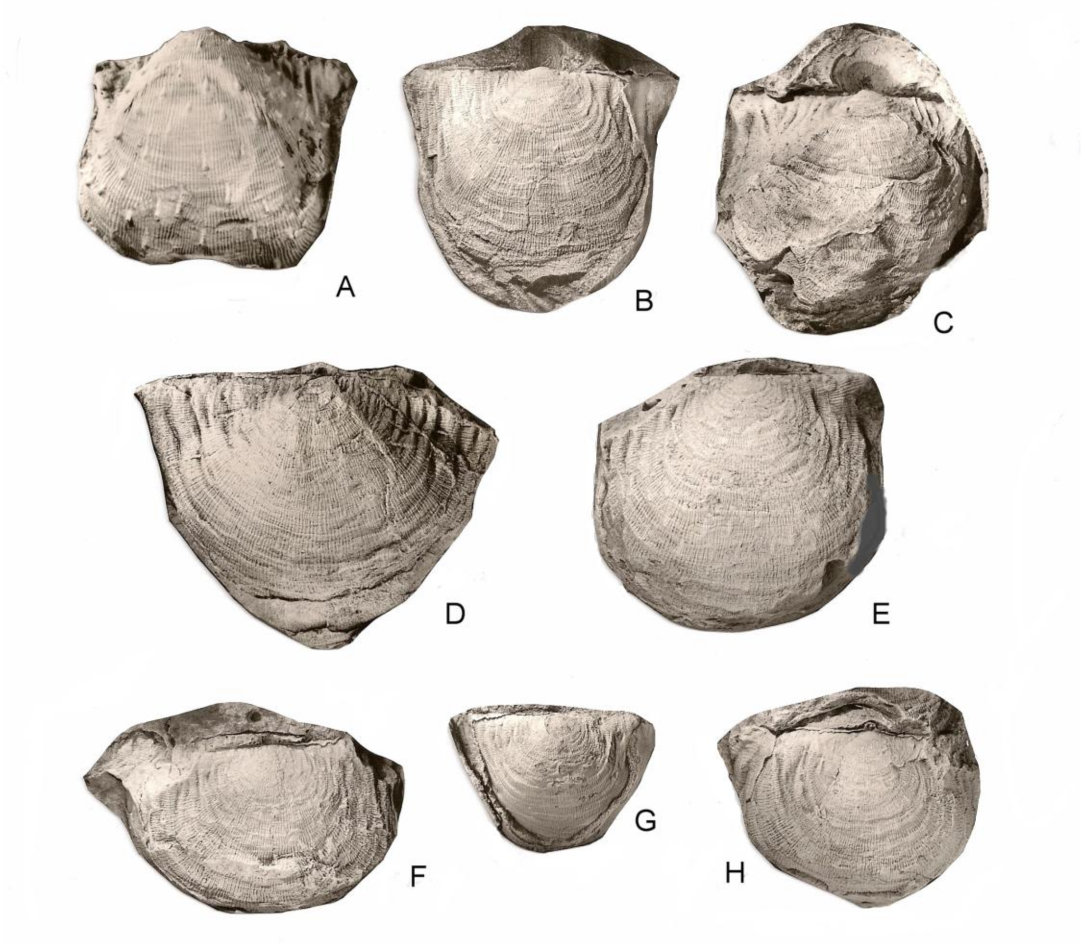


Fig. 90. *Costatumulus tumida* (Waterhouse). A, latex exterior (slightly flawed) of ventral valve UQF 81216 from UQL 4511, x1. B, dorsal external mould and ventral umbo, UQF 81217 from UQL 4514, x1. C, deformed dorsal external mould and ventral umbo, UQF 81268 from UQL 4519, x1. D, dorsal external mould UQF 81600 from UQL 3127, x1. E, dorsal external mould UQF 81218 from UQL 2625, x1. F, dorsal external mould UQF 20957, x1. G, dorsal external mould UQF 81219 from UQL 4515, x0.75. H, dorsal external mould UQF 20958, x1.

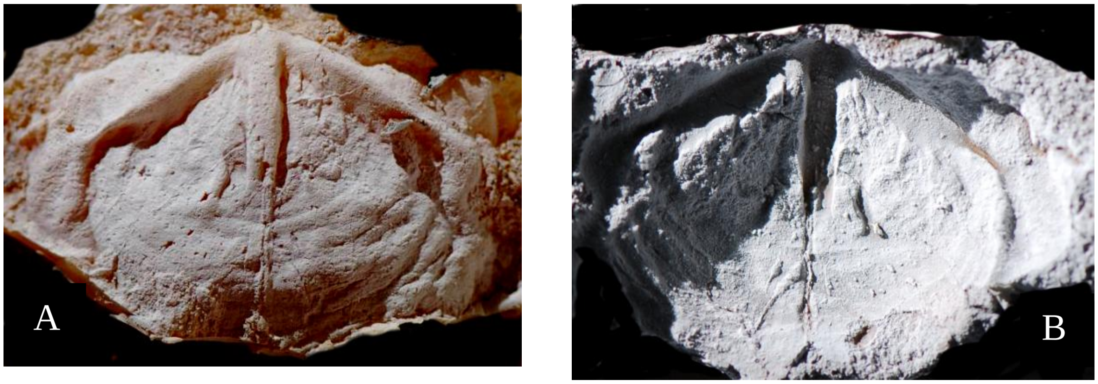


Fig. 91. *Costatumulus tumida* (Waterhouse), dorsal latex cast and external mould UQF 81267 from UQL 2622, x2.5.

Resemblances: The Tiverton material is close to *Costatumulus farleyensis*, described as *Productus cora* var. *farleyensis* by Etheridge & Dun (1909, p. 302, pl. 42, fig. 9, 11 – part, not fig. 10 = *Magniplicatina undulata* Waterhouse) from the Farley Formation of New South Wales, and further described by Briggs (1998, p. 157, Fig. 73A-B, 79A-I). The Farley specimens are weakly transverse, and often weakly sulcate without a tumid anterior, and with costellae numbering only 10-12 in 5mm over the anterior half (Briggs 1998, p. 159), and with spine bases 1.5 to 2mm long, as in the original types AMF 35480 and 35485. The tumid shape of many of the Tiverton specimens suggests discrimination, and the difference in strength and number of ribs suggests that all should be discriminated. 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 10-14 costellae in 5mm as in type *farleyensis*, spine bases are 1.5 - 3mm long, and the specimens lack a tumid anterior.

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 11 ribs in 5mm, and UQF 43045 is tumid and has 11-12 ribs in 5mm. A specimen described by Etheridge (1892, p. 255, pl. 13, fig. 6) as *Productus* sp. indet. (a) from near Yarrol Station in the Burnett district appears to belong to *Bandoproductus* Jin & Sun (Waterhouse 2014).

A few other species of *Costatumulus* are found in the Late Paleozoic faunas of east Australia. *C. prolongata* Waterhouse (1986a, pl. 9, fig. 10-16) comes from the older Fairyland Formation of the southeast Bowen Basin, and is distinguished by its small size and elongate shape. Costellae number 12-13 near mid-length and 9-11 anteriorly in 5mm on the ventral valve, with ventral spine bases less elongate than in *C. tumida*. Briggs (1998) suggested that these features vary in Tiverton and Farley collections of *Costatumulus*, but elongate specimens of *tumida* from the Tiverton Formation are much larger, less elongate and more incurved than *prolongata*, and more commonly have a tumid anterior. The bases of the ventral body spines in *prolongata* are up to 3.5mm in length and slender (0.6mm wide), but anteriorly become short and broad. Briggs suppressed the species, but the shape and aspects of ornament are distinctive, and indeed the external moulds figured in Waterhouse (1986a, 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, and the costellae number some 13-14 in 5mm, 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.

Fig. 92. *Costatumulus tumida* (Waterhouse), late mature ventral internal mould UQF 44027 from UQL 2625, x3.

Costatumulus meritus Waterhouse (1986a, pl. 9, fig. 5-10) from the Cattle Creek Formation, also figured by Briggs (1998, Fig. 80A-H), is large with 10-12 costellae in 5mm, and very fine growth increments (18-20 in 1mm), and coarser spine ridges and stronger cardinal spines in a wide band along the hinge, with other differences. An Elvinia specimen figured by Waterhouse (1986a, 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*. The textual captions in Waterhouse (1986a) err: they refer to 11, 12, instead of 12, 13. The specimen in Waterhouse (1986a, 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 (2015), 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.

Hill (1950, p. 15), Runnegar & Ferguson (1969, p. 251) and Briggs (1998, p. 157) assigned to *farleyensis* the 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 *Bandoproductus* (see Waterhouse 2015).

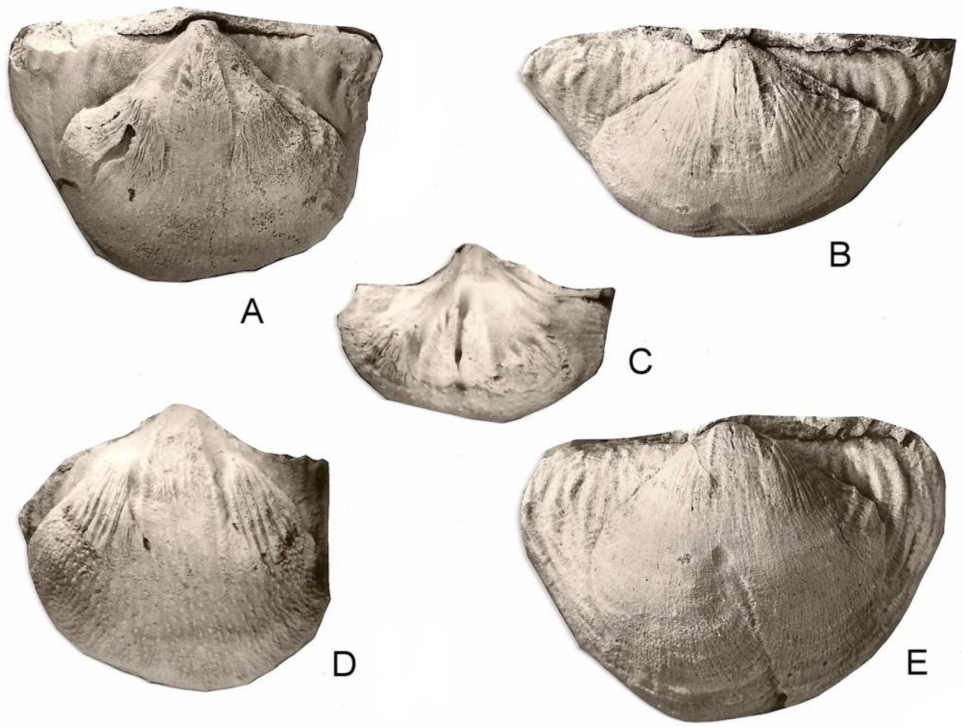


Fig. 93. *Costatumulus tumida* (Waterhouse). A, ventral internal mould, UQF 20827 from UQL 1622, x1.25. B, E, posterior and ventral aspects of internal mould UQF 81222 from UQL 3127, x1.25. C, posterior view of internal mould UQF 44027 from UQL 2625, x1. D, ventral internal mould UQF 81223 from UQL 4512, x 1.25.

As Briggs (1998) noted, *Cancrinella irwinensis* Archbold, 1983a from the Fossil Cliff Formation or Member in the Perth Basin, Callytharra Formation, Carnarvon Basin, and Cuncudgerie Sandstone, Canning Basin, Western Australia, is close to *Costatumulus farleyensis,* but the Western Australian form is more elongate with more sharply defined rugae. *Costatumulus occidentalis* Archbold (1993a, Fig. 9A-1; 1997, Fig. 8A-L) from the High Cliff Sandstone is closer to *farleyensis* and *tumida* in general appearance, and has a more evenly arched venter, neither tumid nor transverse or sulcate. It has 10 costellae in 5mm a little in front of the umbo and 8 in 5mm anteriorly on the ventral valve. Dorsal dimples and ventral spine bases are similar in those of east Australian species. The examples figured by Archbold (1993a) appear to have thin shell and less developed muscle field, but in shape and ornament fall close to some of the range of *tumida* specimens found in the Tiverton Formation, and come close to *farleyensis*.

Costatumulus sahnii Singh & Archbold (1993, p. 62, Fig. 4A-P, Fig. 5 A-P) from the Sakmarian Garu Formation of the eastern Himalaya, India, is comparatively close, similar in shape, with two rows of spines along the ventral hinge, and slightly finer ventral disc spines and slightly more convex ventral valve, and dorsal pits.

***Costatumulus* aff. *prolongata* Waterhouse, 1986a**

Fig. 94

aff. 1986a *Costatumulus prolongata* Waterhouse, p. 58, pl. 9, fig. 11-16.

Holotype: UQL 74015 from UQL 4560, Fairyland Formation, southeast Bowen Basin, figured by Waterhouse (1986a, pl. 9, fig. 13-15), OD.

Diagnosis: Elongate comparatively small shells, costellae 12-13 in 5mm over mid-length, 9-11 in 5mm anteriorly, ventral spine bases 3-5mm long and 0.6mm wide.

Material: Specimens from UQL 4507 and 4508. *Bookeria pollex* Zone. Allied material in UQL 4509, two ventral valves and two specimens with valves conjoined from UQL 4510, basal *Bookeria geniculata* Zone.

Dimensions in mm:

UQL	Width	Length	Height	
4508	23	17.5	8	ventral valve
4510	25	30	14	ventral valve
4510	31	50	23	internal mould

Description: Two ventral valves from UQL 4507, immature specimen with 20 costellae in 5mm, and spine bases that are 1.5mm wide and 3.5-4mm long; the other with 13-14 costellae in 5mm and spine bases slender and 3.5 to 4mm long. Specimen from UQL 4508 is transverse with 14-15 ribs in 5mm and short narrow spine bases less than 2mm long.

Fig. 94. *Costatumulus* aff. *prolongata* Waterhouse, dorsal external mould UQF 81429 from UQL 4508, x5.

A specimen from UQL 4509 is highly vaulted and narrow, and has 9-10 costellae in 5mm anteriorly on the dorsal valve, with spine bases over 4mm long. Specimens from the overlying locality UQL 4510 also include several elongate specimens, in which costae may be as numerous as 13 in 5mm, and spine bases are up to 6mm long in the measured specimens and usually 3-5mm long.

Resemblances: *Costatumulus prolongata* is characterized by its small size, narrow shape with arched venter, and ventral spine bases that are short anteriorly. Costellae number 12-13 in 5mm at mid-length on the ventral valve, and 9-11 anteriorly, whereas *tumida* has 12-14 in 5mm anteriorly and more in some specimens. *C. tumida* and *C. farleyensis* are broader less vaulted and larger shells, with longer spine bases anteriorly, and *C. meritus* is closer to *prolongata* in shape, but much larger with almost comparable fine radial ribbing. Some specimens from UQL 4509 and 4510 approach *C. 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 a 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. A very few specimens from younger localities (UQL 1621, 2621, 2622 and 2628) show some similarity in being subelongate, but are tumid.

Class RHYNCHONELLATA Williams et al., 1996

Williams et al. (1996) proposed Rhynchonellata as a class within Subphylum Rhynchonelliformea, but there are uncertainities over aspects of their classification, with Bassett et al. (2010) indicating a possible close link between Subphyllum Craniiformea and Class Strophomenata, on the basis of ongoing DNA studies.

Superorder RHYNCHONELLIFORMII Kuhn, 1949

Waterhouse (2010a, p. 12) suggested that the Rhynchonellida could be attributed to Schuchert (1913) on the basis that Schuchert clearly applied his new suborder Rostracea only to Family Rhynchonellidae, and included a second family Eichwaldiidae with reservations and query. Rostracea was included by Schuchert (1913) as a suborder of Order Orthacea Beecher & Schuchert. Thus the concept as an ordinal group was enunciated by Schuchert (1913), and his proposed name may be corrected to one with generic stem. But such a proposal requires further consideration, and it was Kuhn (1949, p. 104) who was first to apply the name Rhynchonellida to an ordinal assemblage. The present grouping is close to Subclass Rhynchonellata Grunt, 2006b. The non-strophic hinge and peduncular attachment and crura grading into spiralia are shared together with various internal structures by Orders Rhynchonellida, Atrypida and Athyrida. Members of Pentamerida Schuchert & Cooper, 1932 display many features in common with Rhynchonellida, but lack a pedicle and may show in later forms only simple crura. They were classed with Subclass Orthata by Afanasieva & Dagys (1989) together with Orthida. The interrelationships remain open for further analysis, and much more study is required to reconcile or finally disprove one or others of the present alternative schemes.

Order RHYNCHONELLIDA Kuhn, 1949

Two suborders are recognized, Rhynchonellidina and Stenoscismatidina Waterhouse, 1981 (Sapelnikov & Mizens 1985, Waterhouse 2001).

Suborder RHYNCHONELLIDINA Kuhn, 1949

Rhynchonellidina are comparatively rare in the Permian of Australia. This stands in contrast with the abundance of genera – some 29 – in west Texas, according to Cooper & Grant (1976a). Most east Australian species of Permian age belong to the one genus, *Plekonella* Campbell, and there is a second genus *Plekonina* Waterhouse (1986a, 2010a) in the Dresden Limestone of southeast Bowen Basin. Late Permian genera *Aphaurorhynchia* Waterhouse and *Wairakiella* Waterhouse in Wellerellinae and Allorhynchidae respectively (Waterhouse 2010a) and an Early Permian *Pugnoides* Weller (Petasmariidae) are represented in New Zealand.

Superfamily **WELLERELLOIDEA** Licharew, 1956

Family **WELLERELLIDAE** Licharew, 1956

Subfamily **WELLERELLINAE** Licharew, 1956

Subfamily **PLEKONELLINAE** Waterhouse, 2010a

Diagnosis: Small, both valves ornamented from near umbonal tip by angular-crested costae and fine radial lirae; deltidial plates well developed, dental plates short, hinge plate entire with sturdy median ridge, supported by strong short dorsal septum, socket plates may be crenulate. Crura oval in section, curve towards ventral valve.

Discussion: *Plekonella* has been referred to Wellerellinae by Savage (2002, pp. 1256-8), but costae cover or almost cover both valves, so that the genus externally approaches Strigirhynchiinae Cooper & Grant (1976a, p. 1196), based on a few species found in the late mid-Permian (Capitanian) of west Texas, United States. *Strigirhynchia* is like *Plekonella* in having angular-crested costae, sulcus and fold and high dorsal septum supporting an undivided hinge plate. Differences are that in Strigorhynchinae deltidial plates tend to be reduced or absent, and the hinge plate carries a median swelling, and no median ridge, and sockets are not crenulate. The other member of Strigirhynchiinae is *Chaeniorhynchus* Cooper & Grant from the Cathedral Mountain Formation (Kungurian) of west Texas, with open delthyrium, no deltidial plates, long median septum and uncorrugated sockets. These genera, especially *Strigirhynchia*, are moderately close to *Plekonella* and it might be argued that the differences are of no more than generic significance. However the hinge plate in *Strigirhynchia* is like that of many other wellerellid genera recognized by Cooper & Grant (1976a), divided from the sockets by a groove, or sharp change in angle, and bearing a broad median swelling. Such is never seen in various species of *Plekonella* – the hinge plate merges imperceptibly with the socket plates, and never carries a median arch, but is divided by a narrow strong ridge. Because the Texan species and genera share their particular style of hinge plate, it seems likely that they are more closely related to each other than to the genus found in east Australia and New Zealand. The similarity in internal morphology amongst so many Glass Mountains Rhynchonellida indicates a rapid proliferation of genera and species from a very limited root-stock.

Lissella Campbell, 1961b, p. 452 from the Upper Carboniferous Booral Formation of New South Wales also has a flat dorsal hinge plate with median ridge and belongs to the same subfamily Plekonellinae. The dorsal septum is strong, and costae are few and anteriorly placed. *Plekonina* Waterhouse from the Dresden Limestone of the southeast Bowen Basin is allied, with anterior costae only and no socket corrugations (Waterhouse 1986a; 2010a, p. 61).

Genus ***Plekonella*** Campbell, 1953

Type species: *Plekonella acuta* Campbell, 1953, p. 18 from Ingelara Shale (Wordian), southwest Bowen Basin, Queensland, OD.

Diagnosis: Moderately well developed sulcus and fold, costae covering both valves, dental plates present and dorsal septalium bearing prominent median ridge, dental sockets crenulate, median dorsal septum long and sturdy.

Discussion: *Plekonella* is the most common member of Rhynchonellida found in the Permian of east Australia and New Zealand, ranging throughout the Permian Period, and reported from Late Carboniferous of New South Wales.

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Fig. 95. *Plekonella* sp. , internal ventral mould UQF 81304 from UQL 4508, x3.

Plekonella sp.

Fig. 95

A single specimen with valves conjoined is found at UQL 4508, lower Tiverton Formation. It is very like *Plekonella acuta* Campbell, 1953 in being triangular in shape with long posterior walls and two costae in the sulcus, with four costae each side.

Plekonella whitehousei n. sp.

Fig. 96 - 98

Derivation: Named for F. W. Whitehouse.

Holotype: UQF 81306 from UQL 1620, Tiverton Formation, figured herein as Fig. 98A, here designated.

Diagnosis: Subtriangular inflated shells with well defined sulcus and fold, sulcal and fold costae somewhat variable in number and arrangement, one to three costae on floor of sulcus, some four pairs of costae laterally, dorsal fold smooth posteriorly as a rule, three to five costae in front, dorsal septum well developed and median ridge divides the septalium.

Material: Specimens from UQL 1620, 1626, 1630, 2619, 2620, 3127, 4512, 4518 and 4519. Rare in *Svalbardia armstrongi* Subzone, more common in *Taeniothaerus subquadratus* Zone.

Description: Dorsal valve from UQL 1630 6.5mm wide and nearly 6mm long. Ventral valve with sulcus, dorsal fold commences in front of umbo and growth lamellae crowded over anterior fold. One or three or rarely two ribs lie along the middle of the sulcus, dorsal valve smooth in front of umbo, and smooth lateral posterior shell in one specimen, and one or three and rarely five costae traverse the fold, with usually three pair of lateral costae, but four costae on one side of fold and two on other in one specimen. Micro-ornament of fine disrupted capillae. Short dental plates and teeth in ventral valve. Dorsal median septum extends for more than a third of length of shell, high median ridge conspicuous on septalium, dental sockets closely crenulate (UQL 4519).

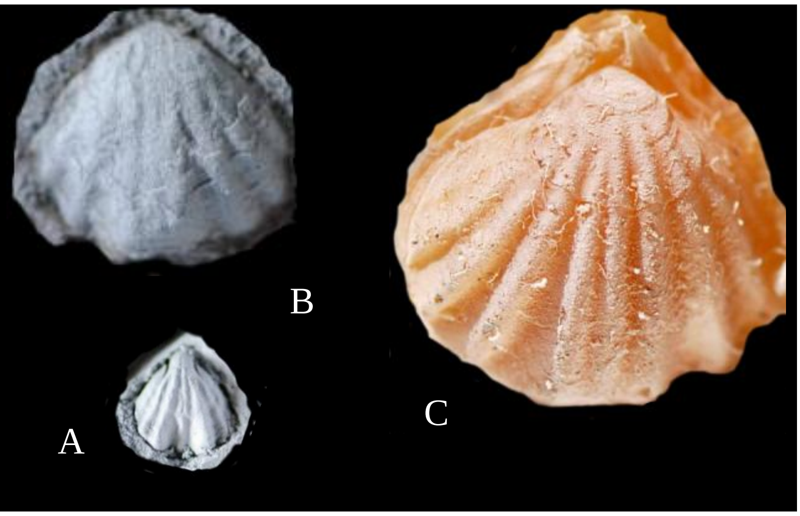


Fig. 96. *Plekonella whitehousei* n. sp. A, immature ventral valve UQF 81305 from UQL 2620, x3. B, dorsal valve UQF 81614 from UQL 4519, x5. C, dorsal aspect of latex cast, UQF 81441 from UQL 3127, x5.

Resemblances: The presence of three costae on the fold on some specimens suggests possible identification with *Plekonella acuta* Campbell, 1953 from the Middle Permian Ingelara, Flat Top and Barfield Formations of the southwest and southeast Bowen Basin and Middle and Upper Permian Mangarewa and Pig Valley Formations in New Zealand. This species has consistently long ventral posterior walls and only two costae in the sulcus and three on the fold, whereas the present species is more bulky in shape, tending to have shorter ventral posterior walls, and a somewhat variable number of moderately broad and not very high costae over the sulcus and fold.

Two other species are close in the bulky shape and comparatively short posterior lateral walls and sturdy costae. *Plekonella rara* Waterhouse (1986a, p. 64, pl. 14, fig. 22-25) from the Rose’s Pride Formation, southeast Bowen Basin, has two costae along the sulcus with another entering the sulcus from each side anteriorly, and three to five costae on the fold. The costae arise close to the dorsal umbo. *Plekonella campbelli* Waterhouse (1964a, pl. 16, fig. 2-12) from the Brunel Formation of the Takitimu Group in New Zealand is also a robust inflated shell with moderately long posterior walls that are convex in outline, and strong regularly arranged costae, including three in the sulcus and four on the fold which commence close to the umbones. The dorsal septum is short. Inspection suggests that the costae next to the ventral sulcus also branch into two, so that *campbelli* is close to *rara*, although having more regular costae, with usually four rather than three or five costae over the fold. Costae in both species arise close to the umbonal tip.

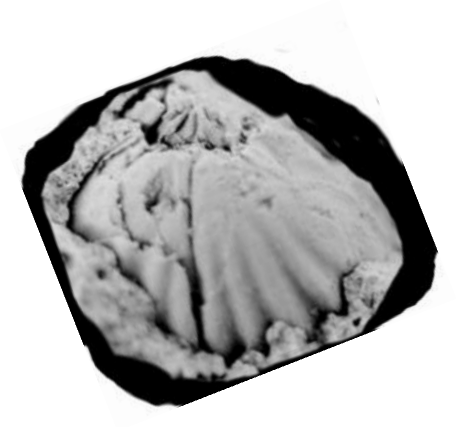


Fig. 97. *Plekonella whitehousei* n. sp. dorsal internal mould UQF 81587 from UQL 4519, x3.

Plekonella acuta Campbell, *P. campbelli* Waterhouse and to lesser degree *P. southlandensis* (Fletcher) are all consistent in the number of sulcal and fold costae. The present species *P. whitehousei* is an exception. New Zealand specimens of *Plekonella* from the *Echinalosia discinia* Zone (Kungurian) in the upper Letham Formation and from the *Wyndhamia typica* Zone in the lower Letham Formation also vary in the number of sulcal and fold costae, and include forms in which costae branch. This suite has individuals like *P. acuta*, others like *P. southlandensis*, and others different from any described species. McClung (1983, Fig. 10) figured variable specimens from GSQ locality 96 in the Denison Trough of the Bowen Basin, from beds equivalent to the Catherine Sandstone above the Ingelara Shale and approximately equivalent to the *Pseudostrophalosia blakei* Zone. These examples show that at intervals the morphology of *Plekonella* became destabilized, although in the case of the New Zealand example, it is not clear whether one species was involved, or an assortment of species, including *acuta, southlandensis*, and at least one distinct species, not as yet named. Another species *Plekonella multicostata* Waterhouse has a number of costae within the sulcus and over the fold, and is well represented at Gympie in the upper South Curra Limestone and in the Gigoomgan Limestone, of Changshingian age (Waterhouse 2015).

Fig. 98. *Plekonella whitehousei* n. sp. A, holotype, dorsal internal mould of UQF 81306 from UQL 1620, x4.5. B, dorsal valve internal mould UQF 81307 from UQL 4519, x4.

Suborder STENOSCISMIDINA Waterhouse, 1981

Superfamily STENOSCISMOIDEA Oehlert, 1887

Family STENOSCISMIDAE Oehlert, 1887

Subfamily STENOSCISMINAE Oehlert, 1887

Genus ***Coledium*** Grant, 1965

Type species: *Coledium erugatum* Grant, 1965 from Moorefield Formation (Visean), Oklahoma, United States, OD.

Diagnosis: Small as a rule with few anterior costae or often none, narrow or no stolidium, deltidial plates small or absent, spondylium on low median septum duplex and may be sessile posteriorly, intercamarophorial plate strong and thick. Stolidium small or absent.

Discussion: Members of this group are rare in the Sakmarian and Artinskian of eastern Australia, and only one species *Coledium elvinia* Waterhouse has been described from the Elvinia Formation of the southeast Bowen Basin. An indeterminate stenoscismatid is found in the upper Rammutt Formation, and possible *Stenoscisma papilio* Waterhouse in the Gigoomgan Limestone, both in the Gympie region. Even New Zealand has several more species and genera, although they are not particularly common.

Coledium ? sp.

Fig. 99

Material: A specimen from UQL 4519, middle Tiverton Formation. *Taeniothaerus subquadratus* Zone.

Description: Specimen with valves conjoined, small, 10.5mm wide, 9.3mm long and about 5.5mm high, ventral valve damaged with beak destroyed, largely smooth, short anterior groove with broad floor and short median costa. Dorsal valve with low fold over anterior third of shell length, bearing shallow median sulcus, no sign of stolidium. Ventral interior somewhat destroyed, preserves part of spondylium and median septum. Dorsal valve with large laminate cardinal process, short high medium septum about one quarter of length of valve, narrow camarophorium and high sturdy intercamarophorial ridge, but the hinge plate and further detail obscure.

Fig. 99. *Coledium* ? sp. dorsal aspect of UQF 81378 from UQL 4519, x4.

Resemblances: What is known of this specimen agrees with features of *Coledium* Grant, but preservation is far from complete, and the generic position is not secure. The material described as *Coledium elvinia* Waterhouse (1986a, pl. 14, fig. 30-34) is more costate anteriorly, with more elongate outline and probably a narrower ventral umbo. Carlson & Grant (2002, p. 1220) without explanation claimed that some uncertainty had to be attached to the generic position of *elvinia* Waterhouse. On the other hand, no stolidium is preserved, pointing to *Coledium* rather than *Stenoscisma*, and the close relationship of various Himalayan and Timor species to *Coledium crassa* (Hamlet, 1928) as identified by Grant (1965, p. 97) and the Timor record of *C. nuculum* Schellwien in Hamlet (1928) suggests that the genus was widespread in Permian faunas of at least peripheral Gondwana (Waterhouse 2004a, pp. 76-82). Therefore the presence in the Early Permian of the Bowen Basin, which occupied paleolatitudes somewhat lower than those of the Sydney Basin and Tasmania, is not anomalous, but clearly better material is required to consolidate the generic identification and distribution.

Order ATHYRIDA Boucot, Johnston & Staton, 1964

Suborder ATHYRIDINA Boucot, Johnston & Staton, 1964

Superfamily **ATHYROIDEA** Davidson, 1881

Family **ATHYRIDAE** Davidson, 1881

Diagnosis: Dental plates present as a rule, but absent from some late forms, cardinal plate apically perforate, entire or not developed.

Subfamily **CLEIOTHYRIDININAE** Alvarez, Rong & Boucot, 1998

Diagnosis: Shell medium to small in size, numerous commarginal lamellae bearing flat spines, dental plates low and short, hinge plates well developed as a rule, inner hinge plates subtrapezoidal, wide, sited dorsal to outer hinge plates, cardinal plate subtriangular, may be absent, pierced by foramen or entire, jugum much as in *Athyris* with longer jugal accessory lamellae usually terminating in front of lateral branches.

Discussion: Some aspects of the constitution, diagnoses and differentiation for genera proferred for members of Cleiothyridininae by Alvarez & Rong (2002) do not withstand close analysis, and several genera (eg. *Carteridina* Alvarez, Rong & Boucot, *Deltachania* Waterhouse, *Himathyris* Waterhouse and *Rawdonia* Peou) were so misrepresented as to require considerable revision. Reassessments and further information on constituent genera have been provided by Waterhouse & Chen (2007).

Genus ***Cleiothyridina*** Buckman, 1906

Type species: *Atrypa pectinifera* J. de C. Sowerby, 1840, p. 14 from Magnesian Limestone (Wuchiapingian), England, OD.

Diagnosis: Transverse to subequidimensional ovate shells with dental plates, perforated hinge plate and long distinct dorsal medium septum.

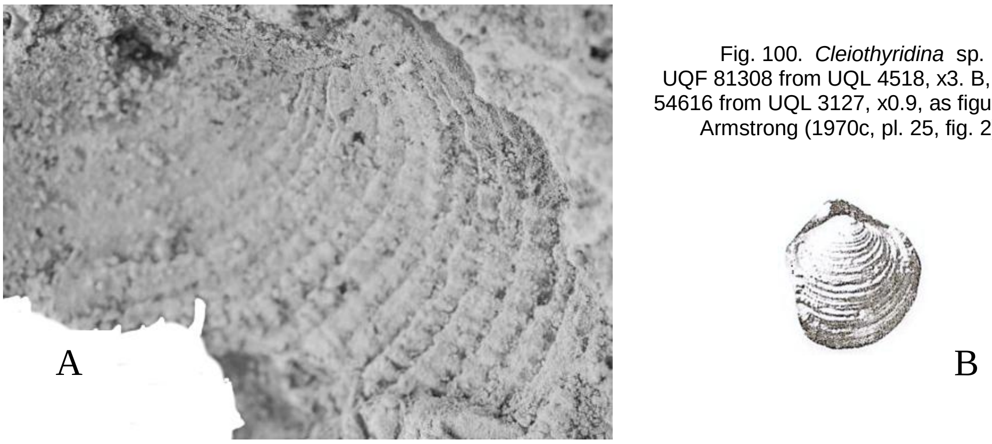


Fig. 100. *Cleiothyridina* sp.
UQF 81308 from UQL 4518, x3. B, UQF 54616 from UQL 3127, x0.9, as figured by Armstrong (1970c, pl. 25, fig. 2).

Cleiothyridina sp.

Fig. 100

1970c *Cleiothyridina* sp. Armstrong, p. 319, pl. 25, fig. 2.

Material, Description: A single dorsal valve with part of a ventral valve UQF 54456 was reported from UQL 3127, Tiverton Formation, by Armstrong (1970c). This specimen occurs on a block that contains *Svalbardia armstrongi*. A fragment of another specimen UQF 81308 has been found at UQL 4518, *Taeniothaerus subquadratus* Zone, more than 20mm across and little inflated, with strong lamellae bearing flattened spines.

Superorder SPIRIFERIFORMII Waagen, 1883

The superorder incorporates mostly punctate shells (Spiriferinida) and impunctate shells (Spiriferida) with laterally directed spiralia and shared internal plates. This is the same as Subclass Spiriferata Afanasieva & Dagys, 1989.

Order SPIRIFERIDA Waagen, 1883

A three-fold subdivision of Order Spiriferida is recognized, based on major clades traced through most of the Palaeozoic Era. These are Spiriferidina Waagen, Martiniidina Waterhouse and Delthyridina Ivanova.

Suborder MARTINIIDINA Waterhouse, 2010a

This group includes the superfamilies Ambocoeloidea George, 1931, Martinioidea Waagen, 1883, and Ingelarelloidea Campbell, 1959, as well as others discussed in Waterhouse (in prep.). The group is typified by essentially smooth or coarsely plicate shells, often with elaborate and low micro-ornament. Early members display simple crura and few internal plates. Aspects of the evolution are traced by Johnston et al. (2006), Carter & Gouvennec (2006a, b) and Waterhouse (1998, 2004a, 2010a, in prep.). The shape of members of the suborder is somewhat like that of members of Suborder Delthyridina, which associates Delthyridoidea Phillips, 1841 and Reticularioidea Waagen, 1883 by means of ctenophoridium and fimbriate and commarginal micro-ornament that became increasingly elaborate. In this suborder the shell changed from plicate to non-plicate, whereas early members of Martiniidina were non-plicate, and some evolved into plicate forms. Spiriferidina are distinguished by prominent ornament of ribs, micro-ornament of radial and commarginal filae as a rule, and ventral adminicula but no tabellae.

Superfamily **AMBOCOELIOIDEA** George, 1931

Diagnosis: Small shells lacking deep ventral sulcus and high dorsal fold, varied micro-ornament, cardinal process often simple and knob-like, outer hinge plates present, spire may be simple.

Family **AMBOCOELIIDAE** George, 1931

Diagnosis: Comparatively smooth or rarely plicate shells with variable micro-ornament, involving spines, growth lamellae and fine capillae, dental plates small or lacking, crura supported by sturdy plates as a rule.

Subfamily **ATTENUOCURVINAE** Waterhouse, 2010a

Diagnosis: Elongate to subelongate, dorsal valve gently convex to weakly concave, ventral umbo prominent to attenuate. Micro-ornament where well known of minute spines, uniform or varying in diameter. Ventral adductor and diductor scars sited on long prominent ridge. Dorsal muscle scars in inner and outer pair. Cardinal process sessile, socket plates supported by crural plates extending along the floor of the valve, tabellae if present very low, no notothyrial cavity. Spire truncated where known, with only part of one coil.

Discussion: This subfamily is distinguished by the prominent median ventral ridge that bears the adductor and diductor scars. *Ambocoelia* and other members of Ambocoeliinae lack such a ridge, and are further distinguished by the dorsal muscle scars which are arranged in posterior and anterior pairs. Members of Crurithyrinae Waterhouse have inner and outer dorsal muscle scars, as in Attenuocurvinae, but lack the prominent ventral muscle ridge, and the cardinal process is raised above the floor of the valve, with a small notothyrial cavity. The spire is truncated in both *Biconvexiella* (Armstrong 1968c) and *Attenuocurvus* (Waterhouse 1964a), whereas several coils are present in *Crurithyris* and allies.

Genus ***Biconvexiella*** Waterhouse, 1983c

Type species: *Attenuatella convexa* Armstrong, 1968c, p. 788 from Tiverton Formation (Sakmarian), Bowen Basin, Queensland, OD.

Diagnosis: Small, slightly to moderately elongate, ventral valve moderately inflated with weakly to moderately incurved ventral umbo and high interarea divided by partly closed delthyrium, shallow sulcus. Dorsal valve gently convex with median sulcus in type species, may be convexo-concave. Both valves ornamented by dense array of small erect spines in a range of diameters, interspersed with rare large spines at least three times greater in diameter than finer spines. High ventral adductor platform with anterior ridge or tigillum extending to anterior third of shell; dorsal crural plates support socket plates. Spiralia truncated to part of a coil.

Discussion: This genus is very close to *Attenuatella* Stehli, 1954 in ornament, internal plates and cruralium, but is distinguished by its gently convex comparatively broad ventral valve with only moderately extended and incurved ventral umbo, and also by its non-prostrate spines. In the type species of *Attenuatella*, *A. texana* Stehli, the ventral valve is narrow with strongly incurved umbo and the dorsal valve is weakly convex. Johnston et al. (2006) stated that the ornament was like that of *Crurithyris* George, 1931, in which there are two very distinct orders of spines (see Brunton 1984 and Johnston et al. 2006, Fig. 1138.4d). Some thick and mostly thin spines, erect and recumbent, are figured for *A. texana* Stehli by Cooper & Grant (1976b, pl. 745, fig. 64-68), and the dorsal valve is gently convex, as confirmed by inspection of the types at Smithsonian Institution, Washington, D. C., United States. The specimens of *texana* are tiny, the ventral valve measuring no more than 9mm in length, and the ventral valve is slender and incurved. It is assumed that spiralia are missing from *Attenuatella*, with only the brachidia developed, but in fact this has not been ascertained for type or other species of the genus, although it seems highly likely (Cooper & Grant 1976a, p. 2132). Spines in *Biconvexiella* are also of varied diameter, some three times larger than others, and all are erect (Armstrong 1968c, pl. 142, fig. 11). The cardinal process is tubercular in *Biconvexiella* (Armstrong 1968c, pl. 142, fig. 12), whereas it is lamellate in *Attenuatella texana* (Cooper & Grant 1976a, p. 2132, pl. 590, fig. 34).

Unlike *Biconvexiella, Attenuocurvus* Waterhouse, 2010a, type species *Attenuatella incurvata* Waterhouse, 1964a, is more incurved with narrower more arched ventral valve, and dorsal valve that is usually concave. The spines are uniform in bands, with no interspersed coarser spines. The cardinal process is tubercular, the crural plates often appear to be sessile and poorly distinguished from the base of the crura, with the presence of tabellae not clear, and if present they must be very low. The spire is truncated in both genera, as shown for *Biconvexiella* by Armstrong (1968c, text-fig. 2).

The type species of *Biconvexiella* is found in the Tiverton Formation. Specimens described from the Farley Formation of the north Sydney Basin have similar shape, but less convex dorsal valve, and the same is true of material from south Tibet, described by Jin & Sun (1981).

Biconvexiella convexa (Armstrong, 1968c)

Fig. 101

1968c *Attenuatella convexa* Armstrong, p. 788, pl. 142, fig. 1-12, 19, text-fig. 1, 2, 4.
1970 *A. convexa* – Armstrong & Telford, p. 115, pl. 10, fig. 3-9.
1983 *A. convexa* – Waterhouse et al., p. 134, text-fig. 2.
1983c *Biconvexiella convexa* – Waterhouse, p. 154.
2006 *B. convexa* – Johnson et al., p. 1733, Fig. 1138a-e.
2010a *B. convexa* – Waterhouse, p. 65, Fig. 28.

Holotype: UQF 53036 from UQL 3127, Tiverton Formation, figured by Armstrong (1968c, pl. 142, fig. 7, 9, 10) and herein as Fig. 101C, OD.

Diagnosis: Shells with weakly elongate outline, shallow ventral sulcus may be restricted to middle third of valve length, gently convex dorsal valve with slender median groove.

Material: The species is clustered at a few stations only, and most material comes from UQL 3127. *Svalbardia armstrongi* Subzone.

Description: This species has a moderately extended ventral umbo and rounded lateral and anterior outline, with wide hinge, high ventral interarea, narrow ventral sulcus, and dorsal valve that is narrowly sulcate medianly. Under the ventral umbo the apical plate forms a very narrow median ridge with concave strip each side (UQF 55029, 47526). Both valves are covered in commarginal rows of erect slender hollow spines, of unknown length and varying in diameter, most fine, a few three times as wide. The different spine diameters were figured by Armstrong on two specimens (pl. 142, fig. 5, 11). Over the dorsal valve of UQF 53036 and 53037 larger spines are developed medianly, surrounded by finer spines, as shown in the illustrations (Armstrong 1968c, pl. 142, fig. 7, 9). The ventral muscle platform is long and raised, the crural plates sessile, the cardinal process small and tuberculate. The abbreviated and simple brachidia are figured by Armstrong (1968c, text-fig. 1, 2).

Discussion: This species is restricted to the lower part of the *Svalbardia armstrongi* band in the middle Tiverton Formation. Armstrong (1968c, p. 789) suggested that an unfigured ventral valve from sandstone below the

"Upper Limestone" (now Gigoomgan Limestone) near Gympie was conspecific, but this belongs to *Attenuocurvus incurvata* (Waterhouse). Material that was referred to *convexa* by Armstrong & Telford (1970, p. 115, pl. 10, fig. 3-9) from the Farley Formation of New South Wales is close in outline, and the dorsal valve was described as gently convex, except in a distorted specimen. A delthyrial plate like that of type *convexa* is developed on UQF 54456. Spines appear comparatively uniform, and lie in short commarginal rows. Specimens from the Jilong Formation near Mt Everest in south Tibet that were referred to *Attenuatella convexa* by Jin, Liang & Wen (1977, pl. 2, fig. 6-10) are close in detail of the ventral valve, but it is not clear from the figures whether the dorsal valve is gently convex or weakly concave.

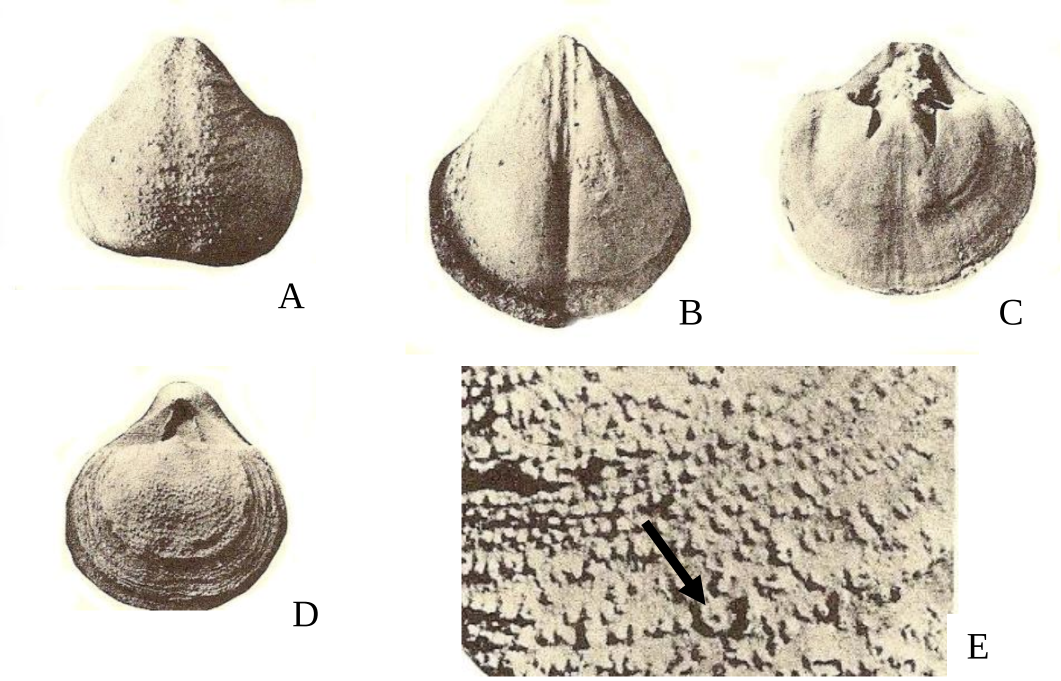


Fig. 101. *Biconvexiella convexa* (Armstrong). A, latex cast of ventral exterior, UQF 53033. B, internal mould of ventral valve UQF 53029. C, dorsal aspect of internal mould UQF 53030. D, dorsal aspect of latex cast of exterior UQF 53037, holotype. Specimens x4. E, detail of spines on UQF 53038 (ventral valve), x22. Arrow points to large spine. From Armstrong (1968c, pl. 142), collected from UQL 3127 in the *Svalbardia armstrongi* Subzone, Tiverton Formation.

Superfamily **INGELARELLOIDEA** Campbell, 1959

Diagnosis: Shells usually with sulcus and fold, simple or no plicae, variably developed micro-ornament, involving small spines, grooves, or/and exopunctae. Ventral interior with usually well developed dental plates and adminicula, dorsal valve with socket and crural plates and varied development of tabellae.

Discussion: One of the outstanding genera amongst Ingelarelloidea is *Rorespirifer* Waterhouse & Piyasin, 1970, with tiny but well formed spines over both valves: this was treated as sole member of a distinct Subfamily Rorespiriferinae Waterhouse, 1998. Carter (2006a, p. 1758) placed *Rorespirifer* in Family Crassumbidae Carter, 2006, together with Early and Late Carboniferous genera, *Crassumbo* Carter, *Arktikina* Grunt, and *Nodea* Tachibina. All are subglobose and non-plicate and ornamented by very fine spinules, or in other genera, comparatively large spines. It is here proposed that they be treated as a group allied to Ingelarellidae, with Rorespiriferidae, given its seniority, upgraded from subfamily to family, and embracing two subfamilies, Crassumbinae Carter (from Crassumbidae Carter, 2006a, p. 1758), distinguished by the fine capillae, and Rorespiriferinae Waterhouse, lacking capillae. Members of Rorespiriferidae are limited in distribution to paleotropical and northerly faunas of basal Carboniferous to Middle Permian age, and are not known in any part of the Gondwanan realm.

Family **INGELARELLIDAE** Campbell, 1959

Diagnosis: Smooth or plicate shells, fold crest rounded or channeled, sulcus with subplicae, costa, or smooth, fine surface ornament of dense grooves, rarely with sliver-spines, internal plates as a rule including well developed tabellae, ventral myophragm low or absent.

The shell in *Ingelarella* and allies is largely composed of fibres steeply inclined forward from the outer surface at which the structure may be complex, and the shell contains taleolae, solid rods of shell first reported by Campbell (1959, p. 335, pl. 56, fig. 14) in *Ingelarella*, the shell apparently arching upwards towards the surface, and also found by Waterhouse (1964a, p. 149, pl. 37, fig. 2, 3) in a New Zealand species of *Martiniopsis* Waagen.

Superfamily INGELLARELLOIDEA Campbell, 1959

Family Ingelarellidae Campbell, 1959

Family Notospiriferidae Archbold & Thomas, 1986b
    Subfamily Notospiriferinae Archbold & Thomas, 1986b
    Subfamily Glendoniinae Clarke, 1992b
    Subfamily Mesopunctiinae Waterhouse, 1998
Family Rorespiriferidae Waterhouse, 1998
    Subfamily Rorespiriferinae Waterhouse, 1998
    Subfamily Crassumbinae Carter, 2006a

Table 17. Classification of Ingelarelloidea Campbell

Discussion: This family is abundantly represented by numerous species in Australia and New Zealand. It ranges over marine faunas of the world, but is especially characteristic of high paleolatitudes. Genera and subgenera include *Ingelarella* Campbell, *Tomiopsis* Benedictova, *Ambikella* Sahni & Srivastava, *Martiniopsis* Waagen, *Johndearia* Waterhouse, *Geothomasia* Waterhouse, *Tweedaleia* Waterhouse, *Tumulosulcus* Waterhouse, *Oviformia* Waterhouse and *Tigillumia* Waterhouse (Table 18). *Tomiopsis* Benedictova, 1956 is the oldest of these genera, at lower Carboniferous, based on type species *Tomiopsis kumpani* (Yanischevsky, 1935). The genus is small with six or more pair of plicae and well developed sulcal subplicae, and channel developed in the fold. Adminicula are of moderate length and spacing, diverging a little forwards, and tabellae are short, diverging into the interspace between the two inner pairs of plicae. Micro-ornament is characteristic, with strong commarginal growth increments, rugae and growth steps, and short elongate grooves in quincunx. There are a number of other species from the Upper Carboniferous and Permian in Russia and Kazakhstan which have been referred to *Tomiopsis*, with different shape, plication and micro-ornament, quite probably belonging to some of the different generic strands that have been recognized in Australia.

Ambikella, first named for an Indian species, is particularly diverse in Australia. A form that internally comes close to *Ambikella* was named *Homevalaria* Waterhouse, type species *Ingelarella ovata* Campbell. This differs from type *Ambikella* by displaying distinctive and tiny sliver-spines, each of which is developed as a blade along a growth-line at the posterior end of a groove, well figured by Campbell (1961a) and Armstrong (1970d). But this feature is not observed on many shells otherwise like the species *ovata*, and so is now believed to be a weathering phenomenon, or a rare exception. Such sliver spines are also visible in specimens assigned by Armstrong (1970d) to *profunda* Campbell, a species identified principally by its well developed plicae. Yet type and other *profunda* examined in this study never show such spines. I therefore consider that sliver spines are not taxonomically significant, and the proposed subgenus *Homevalaria* is abandoned. *Ambikella* is represented in early Permian faunas of Canada, as *ovulum* Waterhouse, 1971, and is known in early Permian faunas of Kashmir (Bion 1928) and eastern Himalaya (Singh & Archbold 1993). In eastern Australia the genus is well represented in the Asselian faunas of east Australia as *elongata* Armstrong & McClung and *bundellaensis* Waterhouse, and in the Sakmarian faunas of the Fairyland, Dresden, Elvinia and Tiverton Formations of the Bowen Basin, as well as Sakmarian faunas of Western Australia, and although no species have been firmly recognized in the Middle Permian of Australia or New Zealand, a very late Permian species was described as *A. furca* Waterhouse, 1967, p. 96 in the Pig Valley Member of the Waiiti Formation in east Nelson, New Zealand.

Validifera is named for a small group of Early Permian (Sakmarian) species, limited to east Australia as far as known, with widely spaced adminicula diverging forward, and otherwise close to *Ambikella.* Only two species have been named, in the basal and middle Tiverton Formation. A slightly younger genus *Johndearia* may have evolved from *Validifera*, and developed very large little or non-plicate shells with channeled fold, heavy posterior thickening and short widely spaced adminicula and tabellae. Surface grooves were developed, often closely spaced. The genus was restricted to east Australia and, rarely, New Zealand, chiefly of Middle Permian age, extending into Late Permian.

The first named member of the family is *Martiniopsis* Waagen, 1883, based on Middle and Late Permian species in the Salt Range of Pakistan. Unlike most genera, there is virtually no ventral sulcus or dorsal fold, and no plicae, but micro-ornament and internal plates are like those of *Ambikella*, even though referred to a different family Martiniopsidae Kotlyar & Popeko, 1967 by Carter et al. (1994, p. 340). Several species of early Permian age were referred to *Martiniopsis* by Tschernyschew (1902), whereas the genus in the strict sense is almost unknown in east Australia, apart from a possible occurrence in the upper Rammutt Formation of Gympie in southeast Queensland (Waterhouse 2015). But two species are represented in the Late Permian of New Zealand, *M*. *woodi* Waterhouse of Wuchiapingian age, and *M. patella* Waterhouse in the very latest Permian, assigned to the *Wairakiella rostrata* Zone.

A likely descendent from *Martiniopsis* is *Tigillumia* Waterhouse, characterized by long adminicula and tabellae. The earliest known species, *T. adminiculata* (Waterhouse) is close to *Martiniopsis* in shape and sulcation, but plicae and deeper sulcus developed in younger species, which include *T. biparallela* in the Brae Formation of mid-Permian (Roadian) age in the southeast Bowen Basin, and two Late Permian species of early Changhsingian age shared between Gympie and New Zealand, *subparallela* and *mintyi* as named by Waterhouse (1968a, 1999).

The genus *Ingelarella* Campbell appeared in the later Cisuralian, as a species in the *Svalbardia armstrongi* Subzone (mid-Sakmarian), followed by *Ingelarella plica* (Aktastinian), and became a prominent genus during Middle Permian time in east Australia and New Zealand. The genus persisted as *I. havilensis* Campbell in the basal Wuchiapingian (Late Permian) of Queensland, and continued into the late Changhsingian as *I. antesulcata* (Waterhouse) in the Pig Valley Member of Nelson, New Zealand. Later incomplete specimens are known from the *Wairakiella rostrata* Zone of New Zealand, probably belonging to *Ingelarella* or *Ambikella*. The genus is very close to *Ambikella* in micro-ornament and plates, but is distinguished by having a channeled fold and a tigillum, which is a median ventral thickening.

In Western Australia, a number of species named by Archbold & Thomas (1986b) are rather similar to each other, but differ slightly from type and allied *Ambikella*. The shell is thin, and the sulcus either grooved or rarely with subplicae, and the fold round-crested. Adminicula are of moderate length and close-set, and the tabellae are short and diverge widely, although some individuals differ as a matter of infrasubspecific variation. Surface grooves are long and well spaced like those of *Ambikella*. They are classed as *Geothomasia* Waterhouse, 1998, p. 23, and were possibly derived from late Carboniferous species of northeast Russia (see p. 170). In east Australia the species of *Geothomasia* are larger with thicker shell compared with species in Western Australia.

A rare form appeared in the Tiverton Formation, as *Tweedalia* Waterhouse, distinguished by the absence of tabellae: it is likely to have evolved from *Geothomasia*.

Tumulosulcus Waterhouse is characterized by its anterior vental fold in the sulcus and channeled dorsal fold. Adminicula are short to moderate in length and tabellae short to moderate, leaving uncertainty as to whether the genus arose from *Geothomasia or Ingelarella.* Species are chiefly Middle Permian in age, restricted to east Australia. *Oviformia* Waterhouse is somewhat similar, with channeled fold, commencing in the Asselian, and ranging into Middle Permian. Upper Carboniferous species from east Russia that may have given rise to *Geothomasia* vary somewhat in the channeling along the dorsal fold, and *Tomiopis convexa* Kotlyar has comparable internal plates.

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

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

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

Oviformia – moderate to low plicae, fold sulcate, sulcus with median fold, adminicula and tabellae moderately long.

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

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

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

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

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

Tumulosulcus – plicae low or absent, sulcus with anterior median swelling or fold, fold crest rounded, not sulcate. Adminicula and tabellae moderately long.

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

Table 18. Genera of Ingelarellidae.

Genus ***Ingelarella*** Campbell, 1959

Type species: *Ingelarella angulata* Campbell, 1959, p. 340 from Ingelara Formation (Wordian), southeast Bowen Basin, OD.

Diagnosis: Medium to large plicate shells with sulcus usually subplicate and fold bearing distinct sulcus, adminicula and tabellae well developed, moderately spaced, tigillum lies along anterior mid-line of ventral valve.

Ingelarella sp.

Fig. 102

Material: An internal mould with valves conjoined from UQL 2624, and dorsal valves from UQL 1622 and 4515. *Svalbardia armstrongi* Subzone.

Dimensions in mm: internal mould

UQF	UQL	Width	Length	Height	
81342	2624	63	48	36	both valves
20906	1622	47	30	8	dorsal valve

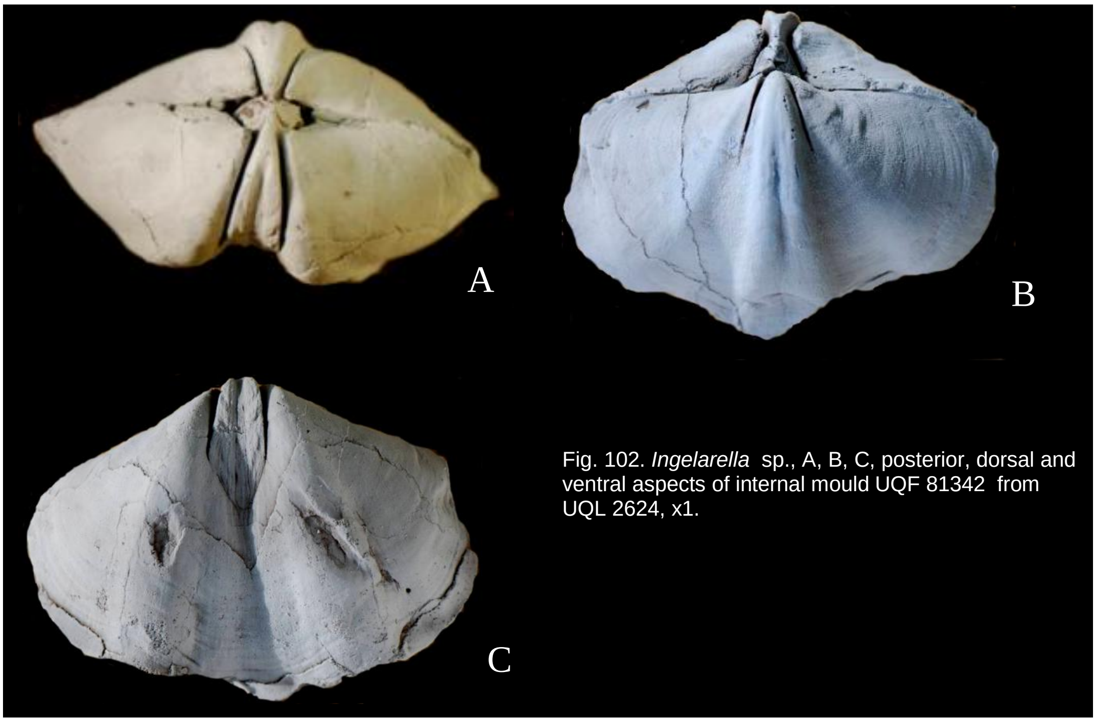


Fig. 102. *Ingelarella* sp., A, B, C, posterior, dorsal and ventral aspects of internal mould UQF 81342 from UQL 2624, x1.

Description: Specimen from UQL 2624 transverse, ventral valve well inflated with incurved umbo and well developed sulcus, widening at 35° and bearing two low subplicae, bordered by slightly raised pair of plicae, with faint second pair laterally. Dorsal fold divided by shallow median channel, one lateral pair of widely diverging plicae. Micro-ornament not known. Hinge wide, delthyrium with angle of 70°, high dental plates and high adminicula, diverging to the floor of the valve, and subparallel in length, extending for nearly one fourth of the length of the valve, enclosing muscle field, tigillum subdued. Dorsal interior with ctenophoridium, dental sockets, diverging tabellae extending for more than a fourth of the length of the valve, lightly impressed adductor scars and no well developed median septum. Dorsal valve UQF 20906 with well developed fold bearing narrow channel, three pair of low plicae, with only the inner pair moderately developed, micro-ornament of crowded short grooves, without spines.

Resemblances: Unlike other ingelarellids from the lower and middle Tiverton Formation, this species has a channeled dorsal fold, and so suggests *Ingelarella*: it appears to be the oldest representative so far known in Australia*.* A slightly younger species is *Ingelarella plica* Campbell (1960, pl. 136, fig. 8-13) from the zone of that name in the upper Tiverton Formation, and from the upper Cattle Creek Formation of southeast Bowen Basin, with similar plates, shorter tabellae, and slightly stronger plicae. Campbell (1960) recorded a channeled fold, well seen in his fig. 12, although not apparent in his fig. 13. Further specimens were figured from the *plica* Zone by Waterhouse (1983d, pl. 2, fig. 2, 3, 5-9), the specimens having a channeled fold, but having three rather than four pair of plicae. Allied material was described from the Rose's Pride Formation of the southeast Bowen Basin by Waterhouse (1987a), and from the Brunel Formation of New Zealand (Waterhouse 1968a, pl. 8, fig. 1-6, 8), with channeled fold. Some shells from the *Notostrophia homeri* Zone in New Zealand have four pair of plicae and some have longer tabellae than usual (Waterhouse 1968a, pl. 10, fig. 1-6, 8). *Ingelarella sulcata* Waterhouse (1964a) from the Brunel Formation in New Zealand involves shells that are less plicate than *plica*, with higher fold more deeply channeled posteriorly, and adminicula and tabellae spaced further apart.

The presence of only one pair of emphasized lateral plicae on the specimen from UQL 2624 suggests an approach to *Geothomasia symmetrica* (Campbell, 1961a), as described below, but this species and genus has a round-crested fold, shorter more close-set adminicula spaced further apart, and shorter tabellae. Given the nature of the internal plates, it is much more likely that the genus *Ingelarella* evolved from *Ambikella*. First known appearance of the genus is in the upper Sakmarian Tiverton Formation.

Genus ***Ambikella*** Sahni & Srivastava, 1956

Type species: *Ambikella fructiformis* Sahni & Srivastava, 1956, p. 207 from Early Permian (?Sakmarian) of Sikkhim, Himalaya, OD.

Diagnosis: Shells with broad sulcus and fold, sulcus may be subplicate, fold without median channel, lateral shell with or without lateral plicae, adminicula and tabellae moderately to well developed, surface ornament of elongate grooves more or less in quincunx.

Discussion: The genus was first described under the mistaken impression that the deformed ventral valve was the dorsal valve. This was corrected by Waterhouse (1965b) from examination of the types. Subsequent studies (Singh 1978b, Waterhouse 1978a) were able to establish that *Ambikella* was a long-ranging and widely distributed genus, and could be discriminated from *Tomiopsis* Benedictova by having fewer if any plicae, finer micro-ornament, and longer tabellae. It was further established that in these aspects, the genus was identical with *Ingelarella* Campbell, 1959, proposed for an Australian species shortly after publication of the Indian genus. Although Singh (1978b) had defended the validity of *Ambikella* and the interpretation by Waterhouse on the basis of further material, Singh & Archbold (1993) discredited *Ambikella*, and further claimed that the type and other species of *Ingelarella* could be distinguished by having small c-shaped spines behind the surface grooves. That argument is substantially undercut by careful elucidation of the micro-ornament of the type species of *Ingelarella*, which shows that no spines were developed (Waterhouse 1998, p. 4). Furthermore, a species closely allied to and, to judge from age and morphology, probably synonymous with the type species of *Ambikella*, was described as *Tomiopsis siangensis* Singh & Archbold (1993). This species clearly belongs to *Ambikella*. It is concluded that *Ambikella* is a valid and widespread genus, found in the Himalaya, and common in Australia during especially Early Permian time. *Ingelarella* is very close, but is distinguished on the basis of having shell thickening along the median ventral valve in front of the ventral muscle field, and in having a channel along the crest of the dorsal fold.

Ambikella cf. ***elongata*** (McClung & Armstrong, 1975)

Fig. 103

cf. 1975 *Martiniopsis elongata* McClung & Armstrong, p. 231, fig. 1a-j.
cf. *M. elongata* – Runnegar & McClng, pl. 31.1, Fig. 1, 2.
cf. 1978 *Ingelarella elongata* – McClung, p. 46, pl. 2, fig. 1-2, pl. 3, fig. 7-11.
1983 *Tomiopsis elongata* – Waterhouse et al., p. 134, pl. 3, fig. 8 (part, not fig. 5 = *Validifera prima* n. sp.; fig. 9, 10, 13 = *branxtonensis* (Etheridge)).
cf. 2003 *T. elongata* – Archbold, p. 162, Fig. 3.1-23.
cf. 2004 *T. elongata* – Archbold et al. Fig. 2A-F.
aff. 2015 *Ambikella* aff. *elongata* – Waterhouse, p. 57, Fig. 18.

Holotype: UNEF 13017, figured by McClung & Armstrong (1975, fig. 1) and McClung (1978, pl. 3, fig. 7, 8) from

Beckers Formation (Asselian), north Sydney Basin, OD.

Diagnosis: Small, transverse with high rounded fold and deep sulcus, no plicae as a rule, adminicula of moderate length, subparallel, tabellae long to medium in length, subparallel, heavy secondary posterior thickening.

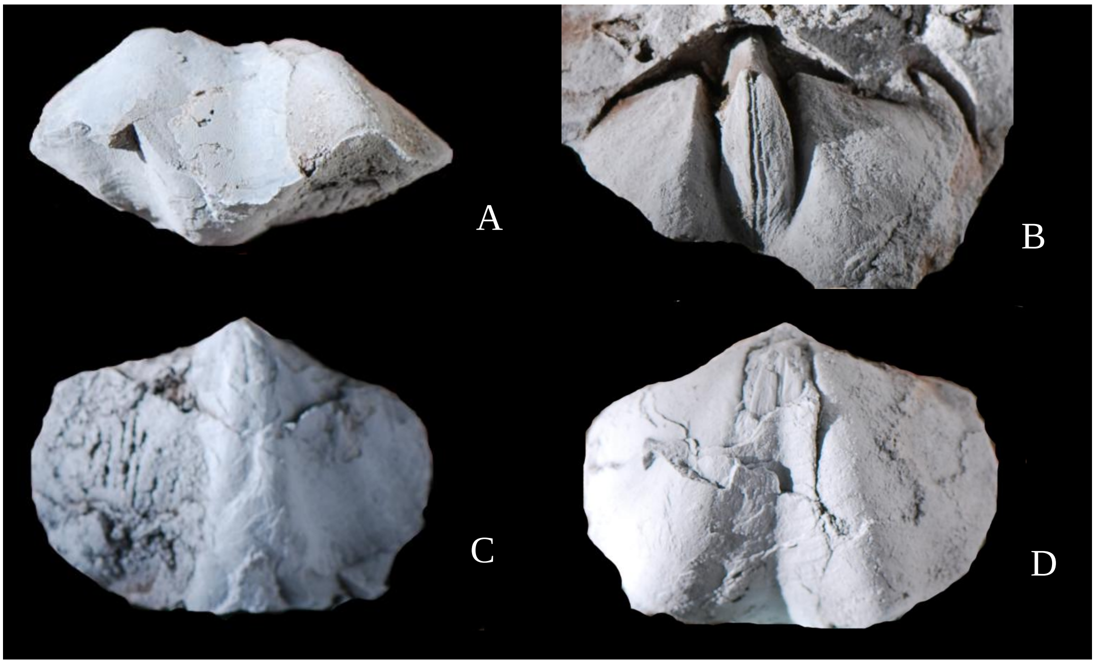


Fig. 103. *Ambikella* cf. *elongata* (McClung & Armstrong), from UQL 4505. A, C, D, anterior, dorsal, and ventral aspects of partly shelly specimen, showing dorsal spire on left in C, UQF 81683, x2. Ventral valve on top in A. B, ventral internal mould UQF 81680, x1.5.

Material: Specimens from UQL 4505. Possibly *Bandoproductus macrospina* Zone.

Description in mm: internal mould

Width	Length	Height	
48	34	13	ventral valve
40	32	30	both valves

Description: A number of slightly distorted mostly internal moulds are characterized by transverse outline, well rounded cardinal extremities, deep sulcus with angle close to 30^o and no subplicae, high fold with rounded crest, most specimens without plicae but some shells with two or three lateral pair of plicae on each valve, the innermost pair especially well developed on the dorsal valve. Micro-ornament obscure, suggesting fine dimples, perhaps signifying the ends of prisms in the shell.

Adminicula long and subparallel to parallel, vary in spacing, may be weakly bowed in outline and subvertical, extend between half and a third of the length of the ventral internal mould, converge weakly on large dental plates which diverge towards the hinge. Ventral adductors sited on high narrow ridge, diductor scars broad, considerable secondary thickening. Heavy secondary thickening along the hinge. Tabellae 0.2 to 0.35 length of valve, diverge widely from posterior wall within first pair of interspaces next to fold, then curve to lie parallel. Very small ctenophoridium, dorsal median septum long and in some shells high, pair of elongate muscle impressions, little secondary thickening.

Resemblances: These specimens are close to typical *Ambikella elongata* (McClung & Armstrong), described from the Beckers Formation at Cranky Corner and later recorded from the Tamby Creek Formation by McClung (1978, pl. 3, fig. 10, 11), although according to Stevenson (2003) and Balme & Foster (2003) there are no marine fossils in this formation. The species was also recorded, but not figured and therefore uncheckable, from the west limb of the Lochinvar Anticline in the Hunter Valley, New South Wales by McClung (1978). The present specimens agree in shape and size and sulcus and fold, but some specimens are weakly plicate, a difference not considered to be specifically discriminant. The holotype and figured paratype (McClung 1978, pl. 3, fig. 9) have comparably long adminicula and long tabellae, up to almost half of the length of the internal mould. Yet various dorsal valves figured by Archbold (2003, pl. 3.2, 11, 17, 19) from the upper Beckers Formation have tabellae only half as long. A very few specimens from the upper Rammutt Formation of Gympie are moderately close, and could well prove conspecific. *Bandoproductus* occurs in the same faunal level at Gympie, and is provisionally interpreted as a potentially co-occuring genus at this particular biostratigraphic level.

The Tasmanian suite from the basal Bundella Formation and Inglis Formation figured as *elongata* by Clarke (1990, p. 64, Fig. 10A-L; 1992a, p. 22, Fig. 10A-L) is similar to *elongata* in many respects, with shells laterally smooth or plicate and suggestions of two low subplicae in the sulcus and rounded dorsal fold. There are differences from type *elongata,* and the specimens have been assigned to *Ambikella bundellaensis* Waterhouse, 2015, as a species related, perhaps as a precursor, to *elongata*, but distinguishable through shape and tabellae. The outline of the Tasmanian specimens is distinctly less transverse than type *elongata*, with posterior walls diverging less, and the sulcus is often narrower. The adminicula are short to moderately long and subparallel anteriorly – indeed they may appear to converge anteriorly to a slight degree. Some of the Tasmanian specimens (eg. Clarke 1990, text-fig. 10A, C, I) suggest the presence of a low and narrow tigillum, but closer inspection is required. The specimens figured by Clarke (1992a, Fig. 10B, D, F) have tabellae extending for about a fifth to a third of the length of the valve, and they diverge widely immediately in front of the hinge, unlike those of restricted and type *elongata*, in which the tabellae diverge at a gentle angle. Adminicula extend for a quarter up to half of the length of the valve and are subparallel to parallel, moderately close to those of typical *elongata*.

According to Briggs (1998, p. 31), the species *elongata* ranges as high as “Faunizone 3” on Maria Island at the top of the *Strophalosia* (now *Crassispinosella*) *subcircularis* Zone, and his figured specimens are elongate with weakly defined sulcus, long extended ventral umbones, and narrowly diverging posterior walls, close to *bundellaensis*. There is no information in Briggs (1998) on the dorsal valve or internal plates. Archbold (2003, p. 162) rejected Briggs’ interpretation. Nonetheless, there is a degree of variation in suites of ingelarellid species that underlines the need for careful evaluation. Available data does not fully agree with Briggs (1998, Fig. 14), who claimed that the Cranky Corner Sandstone was equivalent to Allandale Formation and contained *Tomiopsis konincki* in place of *elongata*. Archbold (2003, Fig. 3) did not confirm the occurrence of *konincki* at Cranky Corner, but figured only material from the upper Beckers Formation, so that further checks are needed.

Various specimens from the Tiverton Formation were identified by Waterhouse in Waterhouse et al. (1983) with *elongata*, an identification rejected by Clarke (1992a), Briggs (1998) and Archbold (2003). These authors were understandably confused by the gathering of three species as one form. The specimens came from two different levels, and now only some of the UQL 4505 material is assigned, provisionally, to *elongata.* Briggs (1998) referred all the specimens to *regina* Waterhouse, but this species has a very different appearance, with more elongate, more rounded outline, subdued inconspicuous sulcus, well rounded dorsal fold and longer adminicula. Clarke (1992a, p. 23) identified some of these specimens as *Tomiopsis branxtonensis* (Etheridge), which applies to the material from the younger locality at UQL 4506. Compared with present material from UQL 4505, the species *branxtonensis* has usually more plicae, a similar though lower broader fold, and shallower sulcus with less parallel adminicula, and tendency to have sulcal subplicae, especially in Tasmanian specimens. Internal plates are not particularly close, insofar as the tabellae of *branxtonensis* are much shorter and more divergent, and secondary thickening is much greater.

Ambikella regina (Waterhouse, 1987a)

Fig. 104 – 106A

1987a *Tomiopsis regina* Waterhouse, p. 28, pl. 7, fig. 3-6, 8-10.

Holotype: UQF 21499 from Fairyland Formation, southeast Bowen Basin, figured by Waterhouse (1987a, pl. 7, fig. 3, 4), OD.

Diagnosis: Medium-sized shells with well formed sulcus that becomes broad anteriorly, lacking subplicae, low well formed fold, lateral plicae low with innermost pair emphasized or the only pair developed, most shells without plicae, little shell thickening, adminicula moderately long, subparallel or weakly divergent, close-set, tabellae diverge then lie parallel, of moderate length. Surface grooves dense.

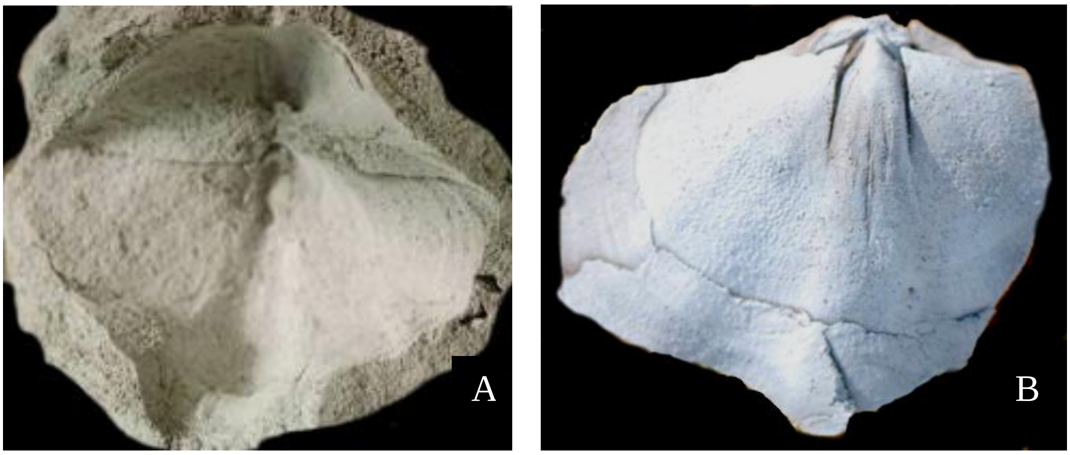


Fig. 104. *Ambikella regina* (Waterhouse). A, external mould of dorsal valve with ventral umbonal region, UQF 81319 from UQL 4508, x1. B, dorsal aspect of UQF 81321 from UQL 4508, x2.

Material: Specimens from UQL 1385, 1619, 3127, 4507, 4508 and LT3. *Bookeria pollex* Zone.

Dimensions in mm: entire shell

UQL	Width	Length	Height		
4508	44	38	18	internal mould	
4508	58	39	32	both valves	26.5 height ventral valve
1619	52	45	28	both valves exterior	
4508	41	31.5	25.5	both valves	

Description: Specimens of moderate size with well-formed sulcus, sulcal angle 35-40^{o}, no subplicae, usually no plicae over most ventral valves, though one specimen has two lateral pair. Dorsal fold with gently rounded crest and gently sloping flanks, or with steeper sides, and one valve with three pair of well defined but low plicae, other specimens without plicae. Surface grooves are 1-1.5mm long, and very shallow and weakly defined. The delthyrial angle is 50-60^{o} and the notothyrial angle 115^{o}.

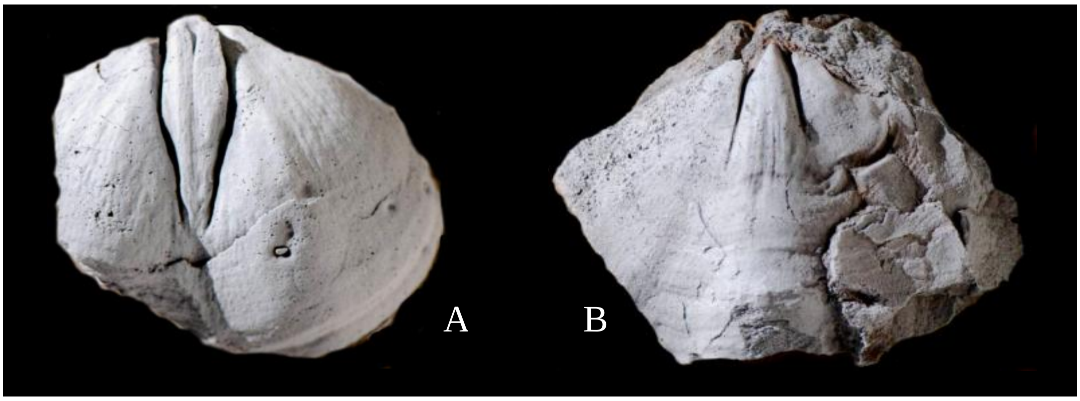


Fig. 105. *Ambikella regina* (Waterhouse). A, ventral internal mould UQF 81619 from UQL 4507, x1.1. B, dorsal view of internal mould of both valves, UQF 81611 from UQL 4508, x1.3.

Dental plates are high and converge at 45° to meet subvertical to vertical adminicula which are long and subparallel, without a tigillum. There is a short myophragm in some specimens. Posterior thickening slight in both valves, dimples lie over the posterior floor, median dorsal septum may be strong. Tabellae divergent and moderately close-set, a fifth of the length of the valve in small specimens, a fourth of length and comparatively widely spaced in larger specimens, remaining weakly divergent. They support low scapular-shaped crural plates, diverging forwards, and inwards at 100-110°, bearing a slender ridge next to the tabellae. Elongate and striate adductor scars extend in front beyond the tabellae. Spiralia have 14-15 coils in UQF 81320.

Resemblances: These specimens are identical with *Ambikella regina* (Waterhouse), first described from the Fairyland Formation of the southeast Bowen Basin, and stand apart from the suite of species that include *branxtonensis* and *elongata*, in being larger, with fewer plicae and broader sulcus. The species was a contemporary of *branxtonensis,* but has longer internal plates, and so may have diverged from *elongata* stock, or have been of independent origin. The species *regina* was identified in the basal Tiverton Formation by Briggs (1998, Fig. 22), as occurring at UQL 4505. Those particular specimens are not *regina*, and are described herein as *Ambikella* cf. *elongata* (McClung & Armstrong) and *Validifera prima* n. sp. The present specimens from the lower Tiverton Formation were identified as the species *Ingelarella ovata* in Campbell (1961a, table 1) and Waterhouse et al. (1983, text-fig. 1). They share with that species somewhat similar but usually shorter and more widely spaced ventral plates and dorsal fold. Similar specimens have been observed in the *Eurydesma* beds of the Wallaby rocks near Warwick, southeast Queensland, collected by E. Gill, and kept at the National Museum of Victoria, Melbourne.

The Tiverton suite assigned to *Ambikella regina* differs from *elongata* in having slightly longer and less widely spaced adminicula, and the tabellae are proportionately shorter as a rule, though the tabellae in a few specimens approximate those of the New South Wales species. As well the dorsal fold is wider, and the sulcus slightly better defined in the Queensland specimens.

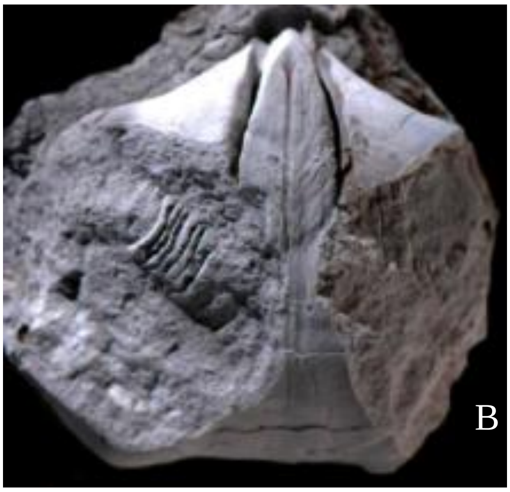


Fig. 106. *Ambikella regina* (Waterhouse). A, posterior view of internal mould UQF 81321, dorsal valve on top, from UQL 4508, x 2.
B, *Ambikella ovata* (Campbell) ventral aspect of UQF 81326 from UQL 3127, x1, showing spire.

The suite of ingelarellid species from overlying localities in the Tiverton Formation at Homevale are larger with more thickening, less defined sulcus and fold, and less elongate subparallel tabellae, but the species *ovata* is close overall and could have evolved from *regina*. *Geothomasia symmetrica* (Campbell) has more emphasized lateral plicae and more posterior thickening, with shorter more widely spaced tabellae as in juvenile *regina*, but micro-ornament grooves may be similarly dense.

With its long and closely spaced adminicula, this species approaches genus *Tigillumia* Waterhouse, characterized by very long and closely spaced adminicula that lie beside and in front of heavy thickening, forming a tigillum along the base of the narrow sulcus, but early species of *Tigillumia* are generally weakly or non plicate with comparatively shallow sulcus, so that they more likely arose from *Martiniopsis* Waagen.

Ambikella ovata (Campbell, 1961a)

Fig. 106B, 107 – 110

1961a *Ingelarella ovata* Campbell, p. 177, pl. 24, fig. 3-9.

1964 *I. ovata* – Maxwell, p. 47, pl. 9, fig. 29, 30.

1964b *I. ovata* – Hill & Woods, pl. P9, fig. 10-12.

1970b *I. ovata* – Armstrong, p. 204, pl. 14, fig. 4 (part, not fig. 5, 6 = *Geothomasia profunda*).

1972 *I. ovata* – Hill, Playford & Woods, pl. P9, fig. 10-12.

1975 *Martiniopsis ovata* – Runnegar & McClung, pl. 31.1, fig. 6, 8, 9, 24 (part, not fig. 7 = *symmetrica*).

1978 *I. ovata* – McClung, p. 47, pl. 2, fig. 7, pl. 4, fig. 14, 15, 18, 19, pl. 5, fig. 1 (part, not pl. 2, fig. 8, pl. 4, fig. 16, 17, 20 = *Geothomasia symmetrica* (Campbell)).

1983 *Ambikella ovata* – Waterhouse, Williams & Campbell, p. 303, text-fig. 3, 4.

1983 *Ambikella* sp. Waterhouse, Williams & Campbell, p. 303, text-fig. 5.

1986c *Homevalaria ovata* – Waterhouse, p. 110.

1987a *Tomiopsis ovata* – Waterhouse, p. 29, pl. 7, fig. 7, 15, 18, 20-21, 22, pl. 8, fig. 1, 2, 3-6?

2006b *H. ovata* – Carter & Gouvennec, p. 1763, Fig. 1160.2a-e.

2015 *Ambikella ovata* – Waterhouse, p. 133, Fig. 51.

Holotype: UNEF 3182 from “zone 13” of Tiverton Formation, Homevale, figured by Campbell (1961a, pl. 24, fig. 4a-c), Hill & Woods (1964b, pl. P9, fig. 10, 11), Hill, Playford et al. (1972), and Carter & Gouvennec (2006b, Fig. 1160.2a-c), OD.

Diagnosis: Weakly transverse and inflated large shells with broad ventral sulcus bearing faint signs of two subplicae in some specimens, lateral shell generally smooth or may be weakly plicate, adminicula long and subparallel, tabellae of moderate length and angle of divergence.

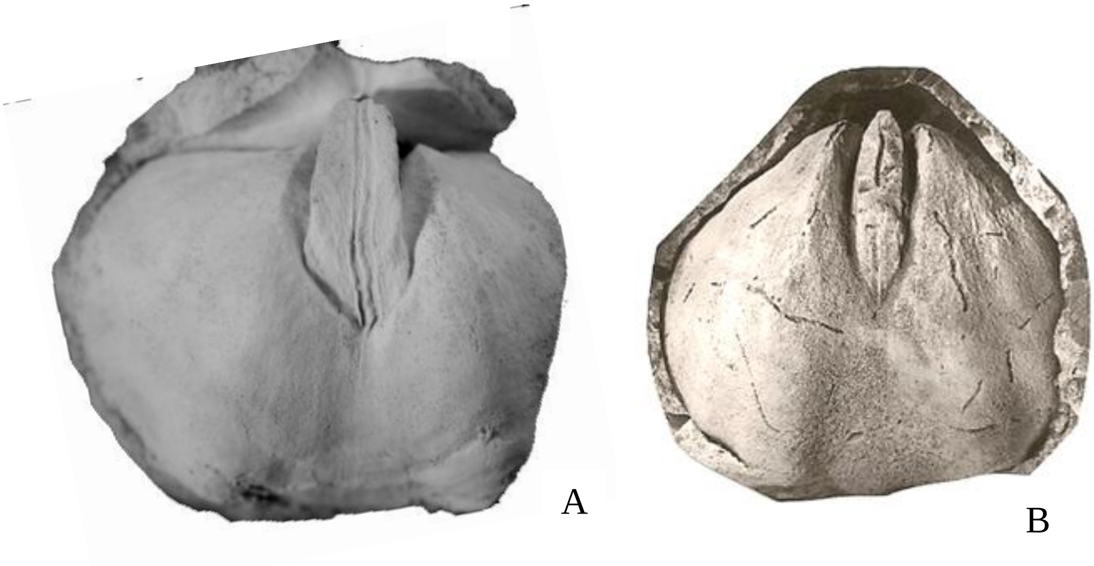


Fig. 107. A, B, *Ambikella ovata* (Campbell). A, ventral internal mould UQF 81325 from UQL 2630, x1. B, dorsal aspect of UQF 81310 from UQL 2619, x1.5.

Material: Specimens come from UQL 1380, 1621, 1622, 1626, 1627, 1630, 2023, 2526, 2584, 2610, 2619, ?2622, 2624 - 2626, 2628 - 2631, 2635, 3127, 4509, 4510, 4511, 4513 - 4516, 4518, 4519, 4521, 4523, 4525 and 4566. The species ranges through the middle Tiverton Formation. Campbell (1961a, table 1, p. 169) recognized gaps for zone 6 (ie. UQL 4514-6) and zone 7 (ie. UQL 4523-4), but specimens of *Ambikella ovata* have been collected from within these intervals. *Bookeria geniculata* and *Taeniothaerus subquadratus* Zones.

Description: This species is moderately abundant, the largest specimen measuring 84mm in width. The species was well described by Campbell (1961a) and numerous figures have been provided. It is characterized by its parasulcate commissure with broad sulcus, in some shells carrying the suggestion of two subdued broad subplicae, and others bearing the faint suggestion of a plication at the sulcal margin. The fold is entire, and some specimens have a single pair or two pairs of faint lateral plicae. Some specimens from UQL 2619 have a low pair of dorsal plicae. A few specimens from UQL 2622 and 3127 are close to *ovata*, but most from these collections are plicate and belong to *Geothomasia.* Large specimens from UQL 4510 have internal plates as in *ovata*, but have three pair of low dorsal plicae and four pair of low ventral plicae. The specimens are identified by shape and plates, and few show micro-ornament. Adminicula are moderately long and parallel or subparallel, and variable in length, tending to be relatively shorter in small specimens. Specimens from UQL 4519 have very long and close-set adminicula. The posterior ventral valve is thickened, up to 12mm. Tabellae are of moderate length: they may be bowed in outline and thick posteriorly, thin in front. The dorsal adductor scars form two elongately oval pair of impressions, the outer pair commencing well before the inner pair, and obliquely striate. Adductor muscle scars are dendritic over the inner pair in a specimen from UQL 2619.

Fig. 108. *Ambikella ovata* (Campbell) dorsal aspect of internal mould UQF 81323 from UQL 3127, x1.5.

Dimensions in mm: ventral valve (external)

UQL	Width	Length	Height	Height both valves
2628	42	38	?16	
2630	76	64		?30
2619	69	59		44
4510	63	57		

Resemblances: McClung (1978) figured specimens of *ovata* from the Farley Formation of the Hunter Valley, and reported specimens from the Pebbley Beach Formation of the south Sydney Basin, but the nature of the micro-ornament was not determined. This is also true of specimens described from the Yarrol Formation, Yarrol Basin, by Maxwell (1964) and the Elvinia Formation and Boughyard Member or basal Elvinia Formation of the southeast Bowen Basin by Waterhouse (1987a). Specimens reported by Waterhouse (1987a, pl. 7, fig. 7, 15, pl. 8, fig. 3-6) from the Rose's Pride Formation, southeast Bowen Basin, are close in general appearance but have a less well developed sulcus and lower fold and worn exterior. The species is represented by poorly preserved material in the Gondor Formation of southwest New Zealand, but the report by Waterhouse (1964a, p. 152) of *ovata* in the Brunel Formation, Takitimu Group of New Zealand may be discounted, the specimens belonging to the slightly younger species *Ingelarella sulcata* Waterhouse, a species with narrower more grooved ventral sulcus and channeled fold.

Discussion: *Homevalaria* Waterhouse (1986c, p. 110) was distinguished primarily by its tiny sliver-spines, developed at the end of linear surface grooves, with type species *Ingelarella ovata* Campbell, 1961a, p. 177 from middle Tiverton Formation (Sakmarian), Bowen Basin, Queensland. The distinctive micro-ornament was well figured by Campbell (1961a, pl. 24, fig. 9), Hill & Woods (1964b, pl. P9, fig. 12), Hill, Woods & Playford (1972, pl. P9, fig. 12) and Armstrong (1970d) for the species *ovata*, and also figured by Armstrong (1970d,

Fig. 1E, I) for what was identified as *profunda,* although identification requires verification. Archbold & Thomas (1986b), supported by Singh & Archbold (1993, p. 66), maintained that *Ingelarella* could be distinguished from *Ambikella* by having low "c-shaped" protuberances at the posterior end of the grooves. Even though Waterhouse (1987a) had reported that *Ingelarella angulata* Campbell lacks c-spines (or what was called sliver spines by Waterhouse 1998), Singh & Archbold (1993) refused to accept the observation, claiming that Archbold had found the types of *angulata* to be worn. This is not true of all topotype material, and the matrix surrounding some topotype material has been carefully etched to reveal a complete absence of spines (Waterhouse 1998, p. 4) and presence of elongate shallow grooves. A number of species ascribable to *Ambikella* by their rounded dorsal fold and moderately long tabellae, together with other distinctive external and internal features, have similar *Ingelarella*-like grooved micro-ornament, even though denied by Singh & Archbold. No other genus, *Tomiopsis, Ambikella* or *Ingelarella*, shows the sliver spines stressed by Armstrong (1970d) and Waterhouse (1986c). Clarke (1992a, p. 22) expressed the view that the spines were of no significance, and this view is supported by close survey of the voluminous material from the Tiverton Formation that belongs to various species of Ingelarellidae. Clarke described the spines as a ramp gradually increasing in height behind a groove. In other instances, as appears to apply to the case for the surface of rare specimens of *ovata* that were photographed by Campbell (1961a) and Armstrong (1970d), and repeated in Hill & Woods (1964b) and Hill et al. (1972), the so-called sliver-spine is very slender and transverse, and steep-sided on the posterior as well as anterior face; the slivers may be straight or curved. Clarke quoted the mistaken opinion of Archbold & Thomas (1986b) that *I. angulata* had "c-shaped spines", and asserted that the long and closely spaced grooves of *ovata-plana-profunda* simulated microspines. This is not entirely correct – only rare specimens of *ovata*, and according to Armstrong (1970d, text-fig. 1E, I), rare *profunda*, have spines: *plana* does not. Nor is it acceptable to assert that *Ingelarella-Ambikella* are the same as *Tomiopsis*, Clarke even basing his interpretation of *Tomiopsis* micro-ornament from the Tasmanian shells that he had identified as *Tomiopsis*. *Tomiopsis* must be interpreted from the type species, not from Tasmanian specimens thought to be *Tomiopsis*. The micro-ornament for *Ingelarella* and *Ambikella* does not show the somewhat ragged, uneven and variable micro-ornament of *Tomiopsis*, which has been illustrated by Benedictova (1956), as confirmed from examination of the type and other species at the Paleontological Institute in Moscow, Russia, by the writer. *Tomiopsis* s. s. differs from the other known Australian genera in plication, sulcation, size, shell thickness, tabellae, and micro-ornament. There is certainly a range of possibilites with regard to the micro-ornament on *ovata*. Is it possible that sliver-spines have not been preserved on various specimens from various collections? Were they a minor variant that arose in a few

Fig. 109. *Ambikella ovata* (Campbell). A, ventral internal mould UQF 81312 from UQL 2631, at full maturity, x0.75. B, ventral internal mould UQF 81316 from UQL 4513, x1.

specimens only, and if so, should they be regarded as signifying a minor detail, or a specific criterion, or the beginning of a potential genus that failed to survive? The genus *Homevalaria* was proposed in good faith, under the conviction that micro-ornament would provide a significant guide to interrelationships, a procedure also espoused by Clarke (1990) in his studies on Notospiriferidae and reinforced by further study (Waterhouse 1998). Now evidence suggests that the development within Ingelarellidae was less simple, with greater potential for alternative paths. Not all of the alternatives can be resolved, and some options have to remain open, pending further study. Although the taxon was recognized as having full taxonomic standing by Carter (2006a), it is now believed that the name should be abandoned, from even the subgeneric status allocated by Waterhouse (1998). Now evidence indicates that sliver-spines were a minor and short-lived phenomenon, at least in some examples caused by slight wear of the true surface, and to judge from the present study, were formed, or at least preserved, in few specimens. They appear to signify a morphological detail of questionable reality, or if real, a phenomenon that was soon aborted, and therefore, arguably, of no taxonomic value, or at best, no more than ephemeral significance.

Fig. 110. *Ambikella ovata* (Campbell) ventral aspect of internal mould UQF 81323 from UQL 3127, x2.

Genus ***Geothomasia*** Waterhouse, 1998

Type species: *Tomiopsis teicherti* Archbold & Thomas, 1986b, p. 593 from the Wandagee Formation (Baigendzinian) of Carnarvon Basin, Western Australia, OD.

Diagnosis: Large shells with well formed sulcus, fold without channel, often few very strong plicae, fine surface grooves. Adminicula of moderate length and moderately well spaced, tabellae short, diverge widely as a rule.

Discussion: *Geothomasia* was proposed initially as a subgenus of *Tomiopsis* Benediktova, for a group of species rather similar to each other, and confined to Permian deposits of late Cisuralian to Lopingian age in Western Australia. A closely related group with similar short widely diverging tabellae is developed in east Australia, especially in Early Permian faunas. In Western Australia, adminicula of *Geothomasia* are well spaced and tend to be short and widely divergent, and the secondary thickening much less compared with east Australian material. Externally, no specimens of *Geothomasia* from Western Australia show the strong pair of plicae that is developed in many individuals from east Australia, apart from one dorsal valve in the type species *G. teicherti* which has a moderately strong inner pair of plicae as figured by Archbold & Thomas

Ambikella

elongata – small shells with sulcus and round-crested fold, no subplicae, lateral plicae rare and low, moderately long adminicula and tabellae.

regina – inflated shells, sulcus and round-crested fold, subplicae rare, lateral shell may be weakly plicate, moderately long adminicula and tabellae. Micro-grooves in quincunx.

ovata – broad deep sulcus, no plicae or subplicae except in a few specimens, moderately long adminicula and medium-length tabellae, varying a little in length and spacing. Sliver spines rarely observed, as a rule micro-ornament of shallow elongate grooves in quincunx.

Geothomasia

branxtonensis – sulcus sometimes without subplicae, surface ornament grooves ill-defined, adminicula moderately spaced to close-set, tabellae well spaced, moderately short. Micro-grooves in quincunx, but worn material suggests uneven texture with elevations.

symmetrica – strong pair of lateral plicae on dorsal valve and strong edges to ventral sulcus, may be faint additional plicae. Adminicula short and widely spaced, tabellae short and well spaced. Micro-grooves with no sliver-spines.

profunda – laterally plicate, short tabellae and surface grooves.

Validifera

valida – widely spaced adminicula, parallel or diverging tabellae of moderate length, plicate, often with strong inner pair of plicae. Micro-grooves in quincunx.

prima – wide spaced adminicula, relatively long tabellae, two or three pair of plicae.

Tweedaleia

tweedalei – heavy posterior shell thickening, rare or no plicae, crural plates rest on posterior walls, no distinct tabellae.

Ingelarella

sp. – ventral subplicae and channeled dorsal fold. Micro-grooves in quincunx. Moderately long adminicula and tabellae, tigillum.

Table 19. Ingelarellid species and subspecies in the lower and middle Tiverton Formation at Homevale.

(1986b, Fig. 6.4). Sulcal subplicae appear in a number of specimens in various species of *Geothomasia*, and the flanks of the fold are steep and well defined. *Geothomasia* includes the west Australian species *teicherti, hardmani, balgoensis, globosus* and *pauciplicatus*, all named as species of *Tomiopsis* by Archbold & Thomas (1986b), and of Baigendzinian (late middle Early Permian) to Wuchiapingian (Late Permian) age. A late Permian ally is present in the Himalaya as "*Tomiopsis*" *himalayicum* Waterhouse, 1978a, p. 58, named for a species described by Diener (1903, pl. 9, fig. 2-4). Older species in Western Australia, including type *woodwardi* and *notoplicatus*, and perhaps *rarus*, belong to *Ambikella*. *Geothomasia* appeared in Asselian (early Cisuralian), and ranged no higher than Aktastinian (mid-Cisuralian) in east Australia. Somewhat similar forms are found in mid-Carboniferous faunas of northern Russia (see p. 171), described by several authors, and varying a little in the nature of the fold, so that it would appear that evolution

Zone (Subzone)	species
plica	*Ingelarella plica* Campbell, *Ambikella plana* (Campbell)
subquadratus	*Ambikella ovata* (Campbell), *Geothomasia symmetrica* (Campbell), *G. profunda* (Campbell), *Validifera valida* (Campbell), *Tweedaleia tweedalei* Waterhouse
(***armstrongi***)	*Ambikella ovata* (Campbell), *Tweedalia tweedalei* Waterhouse, *Ingelarella* sp.
geniculata	*Ambikella ovata* (Campbell), *Geothomasia symmetrica* (Campbell), G. *profunda* (Campbell)
pollex	*Ambikella regina* Waterhouse, *Geothomasia branxtonensis* (Etheridge)
	no fauna
	Ambikella cf. *elongata* (McClung & Armstrong), *Validifera prima* n. sp.

Table 20. Sequence of species of Ingelarellidae in the Tiverton Formation, Homevale.

possibly involved migration from Carboniferous stock into the Early Permian of east Australia, and into Western Australia in later Cisuralian time.

Micro-ornament consists of short radially elongated grooves generally in quincunx over the shell surface. Over the surface of some specimens the intervening ridges are slightly raised, and appear to terminate abruptly at the commencement of a groove, much as described by Clarke (1992a). But this is deemed to be due to slight weathering of the surface, or arguably to vagaries of shell structure, with possible influence from taleolae, although it must be allowed that closer study is required of the subtle variations in surface shell texture.

Geothomasia symmetrica is found with *Ambikella ovata* (Campbell), and is distinguished by well spaced shorter adminicula and very short tabellae. In some specimens there are low ridges along the valve floor, which are not connected to the small and short tabellae attached to the crural plates. *Ambikella* differs in its internal plates, with longer less divergent tabellae and slightly longer and more close-set adminicula, and no species of *Ambikella* shows the emphasized inner pair of plicae found in some *Geothomasia.* The oldest known species of *Geothomasia* in east Australia is probably a form identified as *konincki* [not *Monklandia konincki* (Etheridge) which has a low broad steep-sided and channeled fold], as figured by McClung (1978, pl. 3, fig. 2 – AMF 77781 (formerly UNE 12243) from the Wasp Head Formation, also identified as *Martiniopsis konincki* [not Etheridge] by Runnegar & McClung (1975, Pl. 31.3). The dorsal fold in McClung's material is moderately high with well rounded crest, unlike that of *konincki*, and tabellae are short and divergent. It has been named *Geothomasia simplicitas* Waterhouse (2015).

Geothomasia perished in the early Permian. Two further genera might, but only might, prove to have been descendents. One is *Validifera* n. gen., based *Ingelarella valida* Campbell, 1961a, p. 181, and of much the same age, with well formed sulcus and rounded dorsal fold, and tabellae of moderate to length. The other genus is *Johndearia* Waterhouse, erected as a subgenus of *Tomiopsis*, but so distinctive that it may be upgraded to full generic rank, as in Gouvennec & Carter (2007, p. 2778). It is of late Early Permian (*isbelli, brevis*) and Middle Permian age (*pelicanensis*), and rare in the Late Permian (*isbelliformis*). Member species are large shells with shallow ventral sulcus and broadly channeled fold as a rule, no plicae or subplicae, adminicula short and well spaced, tabellae short to moderately short and well spaced. But the short and highly divergent tabellae in *Geothomasia* would seem to rule out any ancestral status.

Geothomasia branxtonensis (Etheridge, 1919)

Fig. 111 - 114

1919 *Martiniopsis subradiata* var. *branxtonensis* Etheridge, p. 185, pl. 28, fig. 5-6, pl. 29, fig. 1, 2.

1975 *M. branxtonensis* – Runnegar & McClung, pl. 31.1. fig. 4, 5.

1978 *Ingelarella branxtonensis* – McClung, p. 45, pl. 2, fig. 5, 6, pl. 3, fig. 12-19, pl. 4, fig. 1-5, ?11, ?cf. 12 (part, not pl. 4, fig. 6-10 = *Monklandia mcclungi*).

1983 *Tomiopsis* cf*. elongata* [not McClung & Armstrong] – Waterhouse et al., p. 134, pl. 3, fig. 9, 10, 13 (part, not fig. 5 = *Validifera prima* n. sp., not fig. 8 = *Ambikella* cf. *elongata* (McClung & Armstrong).

Lectotype: AMF 22 figured by Etheridge 1919, pl. 29, fig. 1) and McClung (1978, pl. 3, fig. 16, 17) from Farley Formation, SD Waterhouse (1964a, p. 165).

Diagnosis: Transverse with high rounded fold and well formed sulcus that may bear low subplicae, lateral plicae low, number three to five pair in types, adminicula of moderate length and close-set, tabellae short, close to quarter length of valve and diverge slightly.

Material: Specimens from UQL 1385, 4506 and LT3. *Bookeria pollex* Zone.

Dimensions in mm: from UQL 4506

Width	Length	Height	
44	36	24.5	both valves
43	32	24	both valves
40.5	31	21	both valves
49	34	15	ventral valve

Fig. 111. *Geothomasia branxtonensis* (Etheridge) detail of slightly worn shell structure on UQF 81311 from UQL 4506, x3.

Description: Shells mostly small for genus, one broken internal mould of a large specimen with valves conjoined 64mm wide and 34mm thick, weakly transverse in outline, inconspicuous incurved ventral umbo, walls diverging at 100° and gently concave in outline, dorsal umbo inconspicuous, hinge wide, cardinal area moderately high and concave, delthyrial angle close to 75°, dorsal interarea concave with broad notothyrium widening towards the commissure at 90° with concave margins, cardinal extremities well rounded. Ventral sulcus moderately well developed, commencing at umbonal tip, widening at angle varying from 30-35°, may flare more widely in front, may be well defined by bordering plication, with faint suggestions of two subplicae in some specimens. Dorsal fold of moderate height, bearing flatly rounded or weakly convex crest with steep flanks. Lateral plicae weakly developed in one, two or three pairs on some specimens.

Shell structure and micro-ornament are complex and require further study. The inner shell surface of both valves shows fine linear striae, 10 in 5mm anteriorly, reflecting a shell structure of elongate and aligned fibres. Anteriorly on the external surface of the shell are fine elongate grooves, like those of *Ambikella* and *Ingelarella*, as many as five in 5mm, and these are crossed by growth rugae, 10-12 in 5mm, and fine daily increments, approximately 25 per mm, indicating a life-span of more than two years for individuals. The grooves are interspersed with a few broader grooves as wide as three to five fine grooves. Further from the anterior margin such grooves cover the shell surface and may be elongate, but often broaden anteriorly and stop abruptly, often at a growth rugation. Over parts of the shell each groove commences in front of a small spine-like elevation with edges curving forward each side of the groove, like the barchan spines of some notospiriferid genera, including *Papulinella* – see pp. 184, 188. Certainly the apparent spines differ from the sliver spines of some *Ambikella ovata* from the middle Tiverton Formation. But it is far from clear that the ornament is truly external – it might be subsurface, and possibly affected by the taleolae observed in ingelarellids by Campbell (1959). The apparent structure underlines the need to further examine various species ascribed to *Ambikella* and *Ingelarella*.

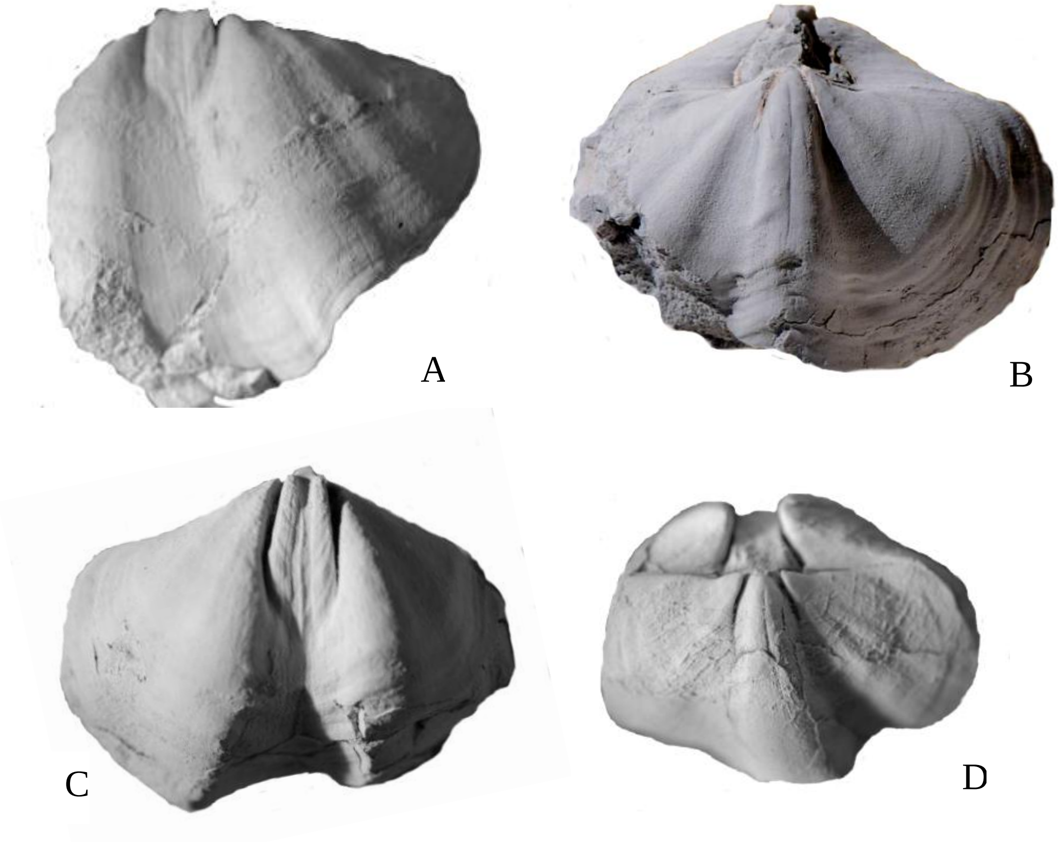


Fig. 112. *Geothomasia branxtonensis* (Etheridge). A, ventral aspect UQF 81313 from UQL 4506, x1. B, C, dorsal and ventral views, UQF 81314 from UQL 4506, x 1.5. D, dorsal aspect of internal mould with valves conjoined, UQF 81315 from UQL 4506, x1.

Ventral adminicula extend for just over 0.25 to 0.33 of the valve length, weakly diverging or almost parallel, moderately well separated and almost vertical, supporting scapular-shaped dental plates that diverge and are just as high. Adductor scars lie on a narrow platform which may be bordered by ridge each side, subdivided only in few specimens by short high posterior myophragm and anterior ridge, flanked each side by broad diductor scars each as wide as the entire adductor field, with longitudinal ridges and oblique ridges parallel to anterior diductor margin. Shell surface marked by light rays, and in maturity by dimples over posterior floor and in front of muscle field. Very low ridge may lie medianly in front of the adductor scars.

In the dorsal valve, teeth enclosed by socket plates and crural plates sloping inwards from the hinge, supported by subvertical tabellae which diverge widely from the umbo and in some shells curve to lie almost subparallel in front, extending for 0.12 rarely up to 0.25 of the length of the valve. In small specimens the tabellae are short and widely diverging as low ridges. Slender median septum extends for half of the valve length, dividing inner pair of adductors from outer more posteriorly extended adductor muscle impressions. Ctenophoridium well developed but small. UQF 81618 shows the spire in section, with 12 coils each side and the inner coil of each spire in close proximity to the other.

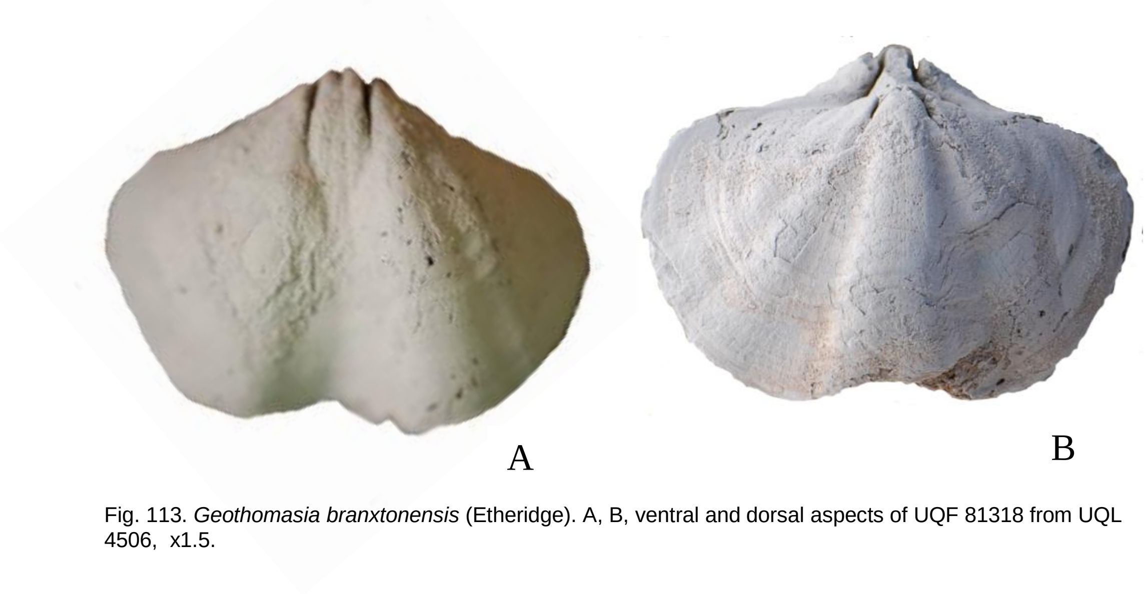


Fig. 113. *Geothomasia branxtonensis* (Etheridge). A, B, ventral and dorsal aspects of UQF 81318 from UQL 4506, x1.5.

Resemblances: The present suite in general appearance comes close in many respects to shells described as *Martiniopsis branxtonensis* Etheridge, 1919 from the Farley Formation, north Sydney Basin. The Sydney Basin species has similar fold and sulcus, and shows four or sometimes five pair of low plicae as a rule, whereas two or three plicae are common in the Tiverton suite, like the Farley specimen figured by McClung (1978, pl. 3, fig. 14, 19), and McClung (1978) stated that in his view the permissible range in the number of plicae was three to five. Adminicula are variably spaced and weakly divergent and moderately long, allowing for the secondary thickening, though not as long as in Tiverton specimens, and tabellae may be bowed and become subparallel or straight and divergent. The tabellae in the mature shell are spaced further apart and diverge more than those in the Tiverton species, and often are short. The species *Martiniopsis konincki* Etheridge, 1892 from the Allandale Formation of the north Sydney Basin, as further figured by McClung (1978, pl. 3, fig. 1-6) with neotype figured by Waterhouse et al. (1983, pl. 3, fig. 11), is moderately similar in the nature of its internal plates but the species has broader usually channeled fold and and sulcal subplicae as a rule, and more plicae.

Some of the specimens figured as *branxtonensis* by McClung (1978, pl. 4, fig. 6-10) are notospiriferid in the shortness of the tabellae, channeled fold and subplicate sulcus and are judged to be a new species of *Monklandia*, *M. mcclungi* Waterhouse, 2015, allied to *M. gympiensis* Waterhouse, 1998 from the Rammutt Formation at Gympie (Waterhouse 2010a, p. 74).

Clarke (1990, Fig. 12A-K; 1992a, Fig. 12A-L) described material comparable to the present suite as aff. *branxtonensis* from “Zone 3” of the Tamarian Stage in Tasmania, and they are close to Etheridge’s species apart from a tendency to have wider sulcus with subplicae in some specimens, and stronger plicae and bowed tabellae. Even small specimens have subparallel rather than divergent tabellae (Clarke 1992a, Fig. 12E).

Nura Nura specimens assigned to *Tomiopsis woodwardi* Archbold & Thomas (1986b) from Western Australia approach *branxtonensis* Etheridge, and are weakly plicate. The adminicula are close but long and subparallel, and tabellae arch somewhat as in *branxtonensis,* and are moderately long in mature shells, but short and widely divergent or parallel in small specimens. The species has micro-ornament of elongate shallow grooves.

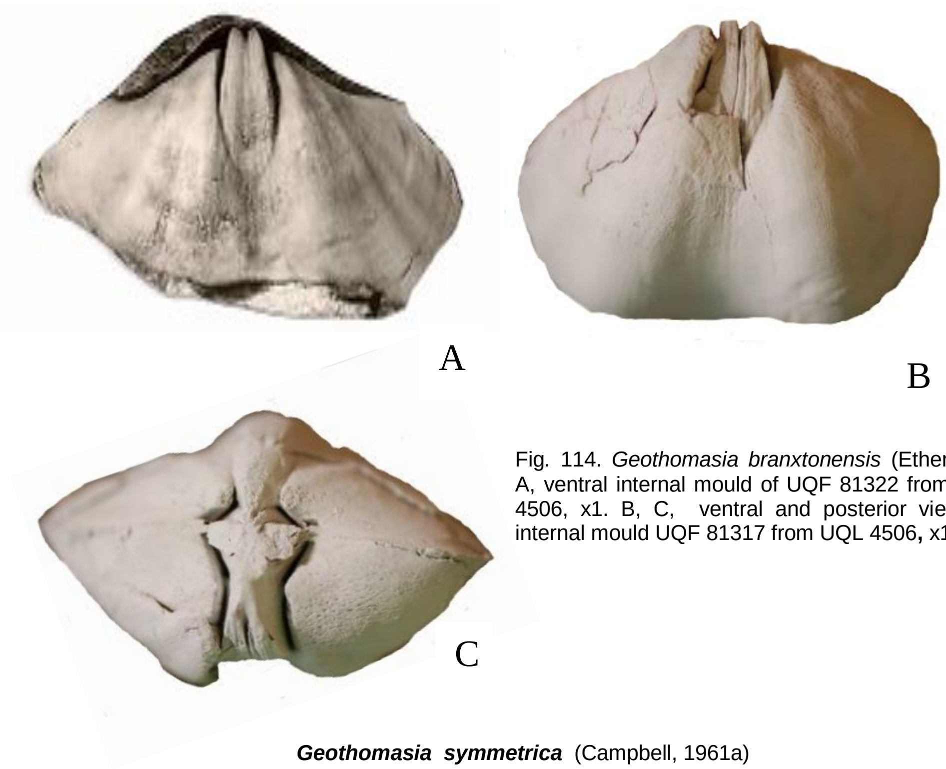


Fig. 114. *Geothomasia branxtonensis* (Etheridge). A, ventral internal mould of UQF 81322 from UQL 4506, x1. B, C, ventral and posterior views of internal mould UQF 81317 from UQL 4506**,** x1.5.

Geothomasia symmetrica (Campbell, 1961a)

Fig. 115 - 121

1961a *Ingelarella symmetrica* Campbell, p. 179, pl. 23, fig. 1-6.

1970b *I. ovata* [not Campbell – Armstrong, pl. 14, fig. 14, fig. 4 (part, not fig. 5, 6 = ?*profunda*). See Waterhouse (2015, p. 134).

1974 *Martiniopsis ovata* – McCarthy et al., Fig. 4D.

1975 *M. ovata* [not Campbell] – Runnegar & McClung, pl. 31.7 (part, not fig. 6, 8, 9, 24 = *ovata*).

1978 *Ingelarella ovata*– McClung, p. 47, pl. 2, fig. 8, pl. 4, fig. 16, 17, 20 (part, not pl. 2, fig. 7, pl. 4, fig. 14, 15, 18, 19, pl. 5, fig. 1 = *ovata*).

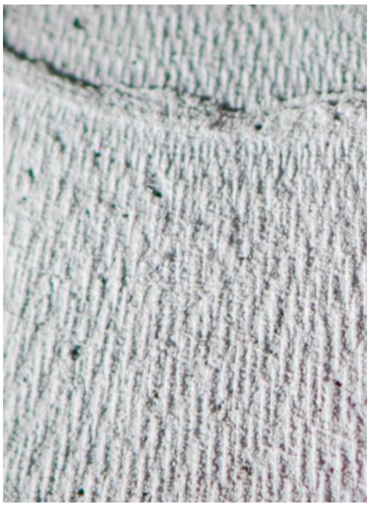


Fig. 115. *Geothomasia symmetrica* (Campbell), fragment of ventral valve UQF 81459 from UQL 2619, detail of micro-ornament, x 10. Note fine commarginal growth-lines. The fragment is an external mould, and the raised slender ridges are infillings of surface grooves.

Holotype: UNEF 5851 from Tiverton Formation at Homevale, figured by Campbell (1961a, pl. 23, fig. 1), OD.

Diagnosis: Shells with prominent pair of plicae on dorsal valve near fold as a rule, borders of sulcus may also be elevated. Adminicula moderately well spaced and short, tabellae short and divergent.

Material: Specimens from UQL 1619, 1622, 1623, 1624, 1626, 1630, 2524, 2584, 2615, 2619, 2622, 2628, 2584, 2625, 2626, 2628, 3127, 4510, 4512-4516 and 4519. Campbell (1961a) restricted the species only to "zone 7", at UQL 1624, equivalent to UQL 4515 and possibly 4516. The typical adminicula and tabellae are well shown in specimens from UQL 4515, 2615, 2622, 2628 and 3127. *Bookeria geniculata* and *Taeniothaerus subquadratus* Zones.

Dimensions in mm: ventral valves, exterior

UQL	Width	Length	Height
4515	59	?46	?22
?2628	54	48	+19
4519	51.5	47	+31

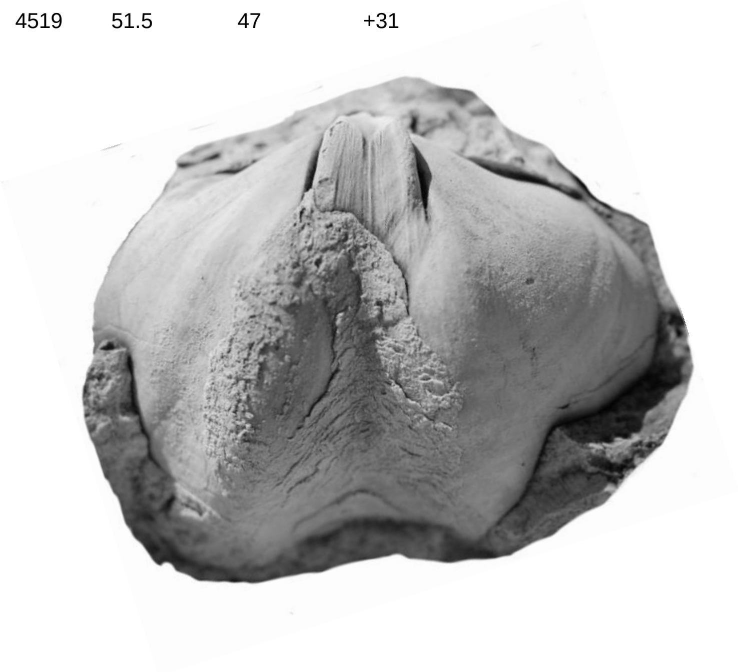


Fig. 116. *Geothomasia symmetrica* (Campbell), ventral valve UQF 81333 from UQL 4512, x1.

Description: Compared with *Ambikella ovata* and *Geothomasia profunda*, the specimens are characterized, according to Campbell (1961a) and McClung (1978, p. 46), by less transverse outline, uniplicate rather than parasulcate commissure, slightly greater umbonal thickening, lower tabellae and a single distinct lateral plication. As McClung (1978) noted, specimens from the northern Sydney Basin approach *symmetrica* in having a commissure less strongly parasulcate than typical *ovata*, and with up to two weak plicae on the flanks of several individuals. He concluded that *ovata* and *symmetrica* were closely related, but did not ob-

Fig. 117. A, *Geothomasia symmetrica* (Campbell), ventral internal mould UQF 81328 from UQL 4519, x1.

Fig. 118. *Geothomasia symmetrica* (Campbell), dorsal aspect UQF 81442 from UQL 2628, x1.5, showing thick secondary tissue in ventral umbonal region. Dendritic adductor scars clearly marked.

serve the nature of the internal plates or the micro-ornament, so that his identifications remain unconfirmed, and it is not advisable to rely solely on external appearance of worn shells. The figure of an external mould of *symmetrica* in Campbell (1961a, pl. 23, fig. 6b) does not clearly show tiny sliver-spines, and the micro-ornament was described by Campbell (1961a) as being the same as that for *ovata*. Although poor preserv-

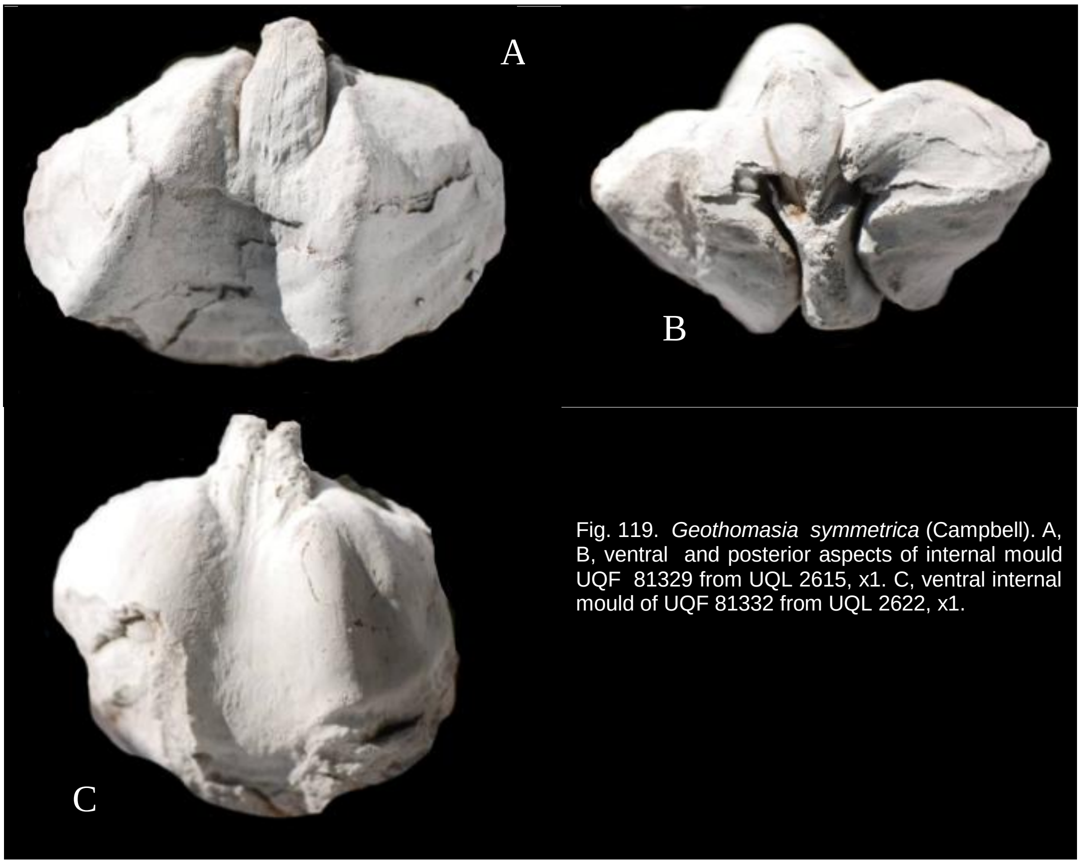


Fig. 119. *Geothomasia symmetrica* (Campbell). A, B, ventral and posterior aspects of internal mould UQF 81329 from UQL 2615, x1. C, ventral internal mould of UQF 81332 from UQL 2622, x1.

ation or variation was possibly involved, no specimens have been found to show sliver-spines. Indeed Campbell (1961a, p. 177) did not explicitly record sliver-spines for *ovata* from the Tiverton collections at Homevale, merely stating that the grooves were rounded in outline posteriorly, and tapered anteriorly.

Resemblances: *Geothomasia cracowensis* (Waterhouse, 1987a, p. 27, pl. 7, fig. 11-14) from the Fairyland Formation, southeast Bowen Basin, has a higher narrower fold and even shorter tabellae, but longer and more closely spaced adminicula, compared with *Geothomasia symmetrica* (Campbell). One specimen of *cracowensis* as figured by Waterhouse (1987a, pl. 7, fig. 14) has a weak groove due to wear along the fold. The specimens are further distinguished by having a very high pair of narrow inner plicae next to the sulcus and the fold on most of the two valves, so that it is readily distinguished from any of the Homevale species.

There is considerable approach to *Tomiopsis larini* Abramov (1970, p. 155, pl. 17, fig. 15, 16) from the middle and late Carboniferous of Verchoyan. These specimens are transverse with wide sulcus, fold, and sulcal subplicae (Abramov & Grigorieva 1983, pl. 31, fig. 4-9) and tabellae are short, but longer and and not so divergent as in *symmetrica*, and adminicula are subparallel. Baikal material was reported by Kotlyar & Popeko (1967, pl. 52, fig. 1-3). *T. tricosta* Kotlyar in Kotlyar & Popeko (1967) from the mid-Carboniferous Harashibir Suite at Lake Baikal has widely spaced adminicula along the second lateral pair of interspaces from the sulcus, and short tabellae. The fold is high and channeled.

Tomiopsis postglabra Waterhouse (1987a, p. 28, pl. 7, fig. 16, 17, 19, text-fig. 5) from the Dresden Formation, southeast Bowen Basin, has the sulcus commencing a little in front of the umbonal tip, low or no plicae, and moderately developed rounded fold commencing in front of the hinge. Adminicula are moderately close-set and short and the tabellae comparatively short and well spaced, as in *Geothomasia*. No Early Permian *Ambikella* or allies are particularly close. The presence of rounded fold and well spaced tabellae and parallel adminicula also recall features of *Geothomasia* from Western Australia, but the tabellae are spaced further apart and are subparallel.

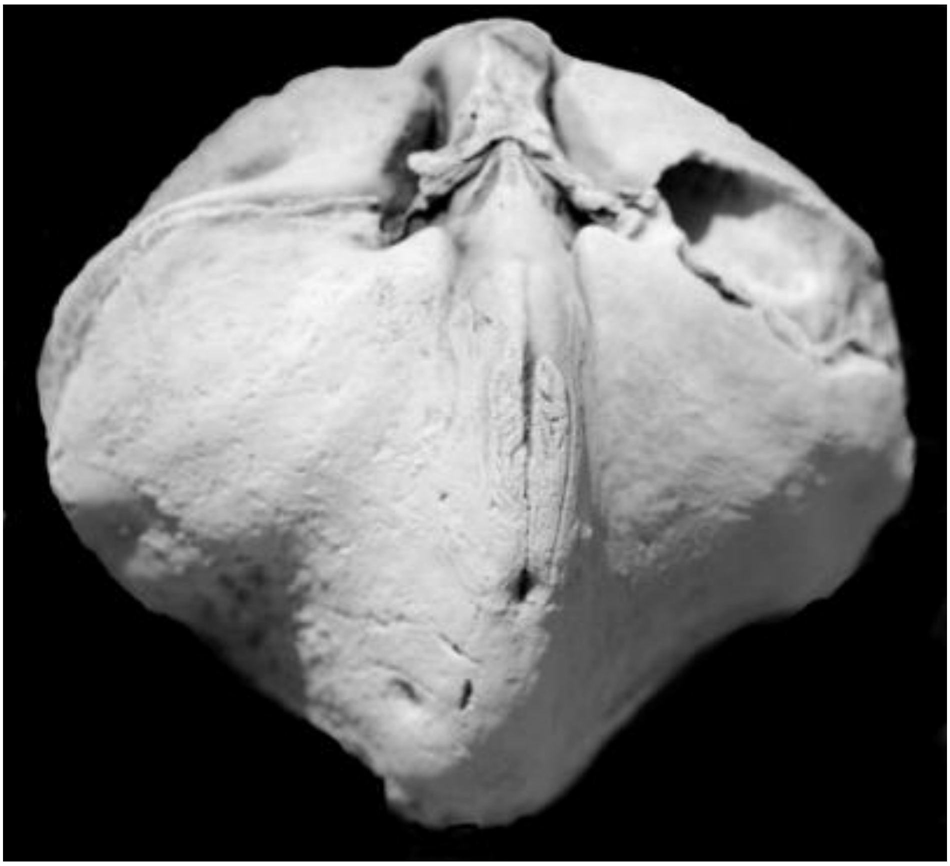


Fig. 120. *Geothomasia symmetrica* (Campbell). Dorsal aspect of internal mould UQF 81443 from UQL 4515, x2. Dendritic adductor scars clearly marked.

Fig. 121. *Geothomasia symmetrica* (Campbell), dorsal aspect of internal mould UQF 81328 from UQL 2619, x1.5.

Geothomasia profunda (Campbell, 1961a)

Fig. 122, 123, 138G

1892 *Martiniopsis darwinii* [not Morris] – Etheridge, p. 240, pl. 39, fig. 5-7 (part, not pl. 9, fig. 13, 14 = aff. *Notospirifer*).

1961a *Ingelarella profunda* Campbell, p. 174, pl. 24, fig. 10-14?, pl. 28, fig. 9-13.

1964b *I. profunda* – Hill & Woods, pl. P9, fig. 15-16.

1964 *I. profunda* – Maxwell, p. 47, pl. 9, fig. 26-28.

1970b *I. profunda* – Armstrong, p. 204, pl. 13, fig. 8-10.

?1970b *I. ovata* [not Campbell] – Armstrong, p. 204, pl. 14, fig. 5, 6 (part, not fig. 4 = *symmetrica*?). See Waterhouse 2015, p. 135.

1970d *I. profunda* – Armstrong, p. 294, Text-fig. 1E, I.

1972 *I. profunda* – Hill, Playford & Woods, pl. P9, fig. 15-16.

1975 *M. profunda* – Runnegar & McClung, pl. 13.1, fig. 17-18.

1978 *I. profunda* – McClung, p. 46, pl. 2, fig. 9, pl. 4, fig. 13?

2015 *Geothomasia profunda* – Waterhouse, p. 135, Fig. 52.

Holotype: UQF 21922 (Campbell (1961a, pl. 28, fig. 11), from upper middle Tiverton Formation, OD.

Diagnosis: Shells with moderately well developed sulcus and fold and usually three pair of plicae.

Material: Specimens from UQL 1621, 1622, 1623?, 1625, 2619, 2622, 2624, 2626, 2628, 2635, 3127, 3250 (or 3750), 3730, 4509, 4510, 4511, 4514, 4515, 4518, 4519, F3 and LT3. *Bookeria geniculata* and *Taeniothaerus subquadratus* Zones.

Dimensions in mm: external shell

UQL	Width	Length	Height both valves	Height dorsal valve
4510	70	54	53	
4510	75	56		24

Description: The Homevale species *symmetrica* and *profunda* recognized by Campbell (1961a) differ from each other in the degree of plication. Collections from localities such as UQL 2622 low in the Tiverton Formation ("zone 5") show a degree of convergence between *symmetrica* and *profunda*. They have a prominent pair of dorsal plicae, and two further subdued pair of plicae. The ventral exterior is closer to that of *Ambikella ovata*, apart from lateral plicae, but the external differences from *ovata*, also mentioned by previous authors, appear to be of neglible significance for species discrimination. Fine growth increments are developed on external moulds, 12-15 per mm, and a large specimen from UQL 4510 is 70 mm wide, 54mm long and 53mm high (both valves). Adminicula vary in length and spacing: they are of mod-

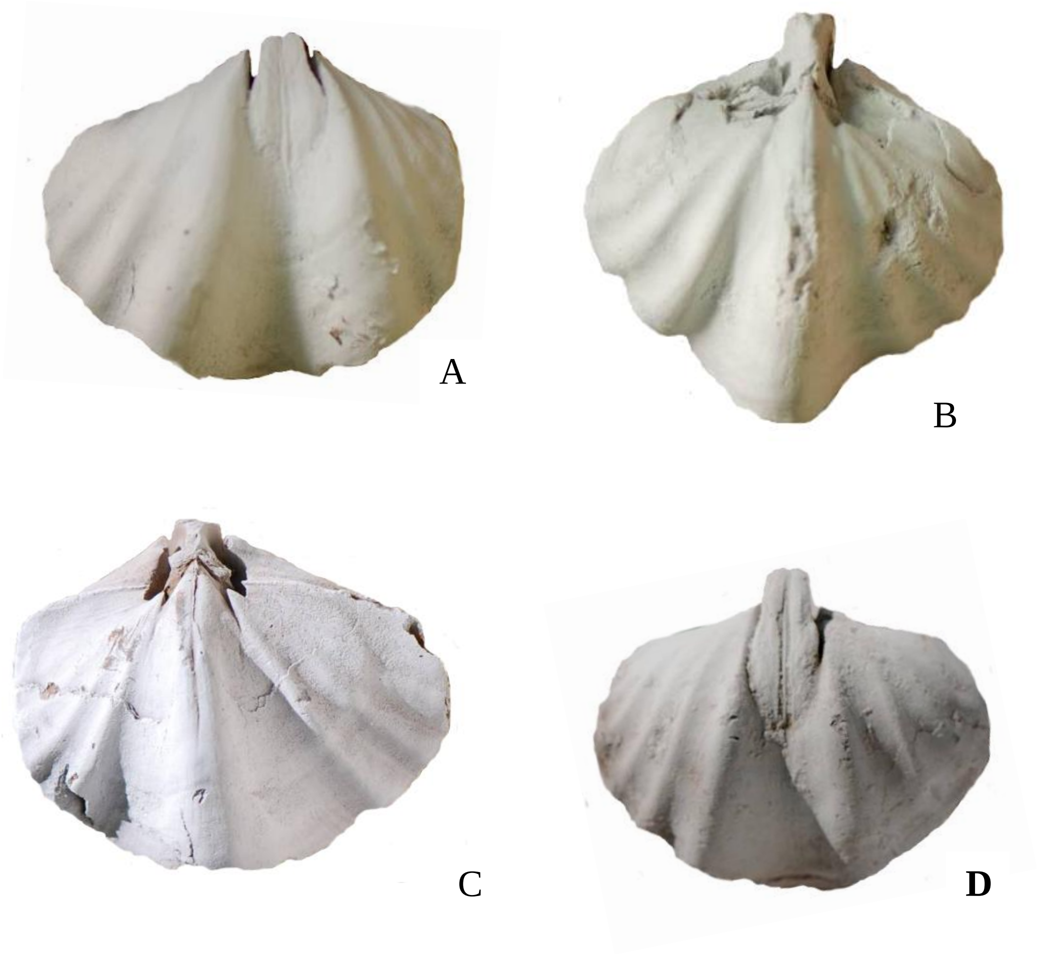


Fig. 122. *Geothomasia profunda* (Campbell). A, C, ventral and dorsal aspects of internal mould with valves conjoined, UQF 81334 from UQL 2628, x1.5. B, D, dorsal and ventral aspects of UQF 81335 from UQL 2628, x1.5.

erate length and often parallel. Tabellae are short and lie parallel or diverge, pointing to a relationship with *Geothomasia symmetrica*. Specimens from UQL 3127 with short tabellae are close to *symmetrica* in sulcus and fold, but some have a pair of dorsal plicae, and some specimens have subdued further dorsal plicae, and suggestions of a ventral pair of plicae, and so are mostly placed in *profunda*. Adminicula may be widely spaced and some diverge, suggestive of an approach to *valida* Campbell. One specimen from UQL 2622 has the outer dorsal adductor scars only faintly impressed, and in a shell from UQL 3217, the adductor scars are deeply dendritic. The median septum develops anteriorly, and extends from the posterior wall well forward in mature specimens. Specimens from UQL 4515 are scored externally by long radial grooves (Fig. 123) for the length of the shell, and these are an artifact of weathering.

Resemblances: Specimens figured by Etheridge (1892) from the Mt Britton Goldfield of the north Bowen Basin are large and fully mature specimens with comparatively well developed tabellae. The material from the lower South Curra Limestone at Gympie that was figured as *Ambikella profunda* by Runnegar & Ferguson (1969, pl. 4, fig. 1, 2), has two subplicae in the sulcus, a channeled dorsal fold, and long tabellae, and is assigned to a distinctive Late Permian species *Ingelarella alteplicata* Waterhouse & Balfe (2015, p. 94, Fig. 30; see also Waterhouse & Balfe 1987, pl. 2, fig. 12).

Tomiopsis notoplicatus Archbold & Thomas, 1986b from the Callytharra Formation of the Carnarvon Basin, Western Australia, is somewhat similar in outline and plication, with smaller size and sharper ventral umbo compared to the species *profunda.* Internally the species is distinguished by its moderately long and subparallel adminicula and tabellae, as in *Ambikella*.

It appears that the presence or absence of plicae is of low value for discriminating species, and there is scope for merging the specimens into broader and more natural populations, with Campbell's type specimen of *profunda* apparently falling within the *symmetrica* association, and perhaps better treated as a subspecies, or even infrasubspecific variant of *symmetrica*.

Fig. 123. *Geothomasia profunda* (Campbell), micro-ornament on slightly worn dorsal exterior, UQF 81327 from UQL 4515, indicating ridges, due to wear and not original, x2.

Genus ***Validifera*** new genus

Derivation: Named from species name, valida, validus – strong, powerful, Lat.

Type species*:* *Ingelarella valida* Campbell, 1961a, p. 177 from Tiverton Formation (Sakmarian), here designated.

Diagnosis: Plicate shells with adminicula that are placed well apart and diverge widely. Tabellae moderately well developed, subparallel.

Discussion: The well spaced adminicula and consequently broad ventral adductor scars are an unusual attribute amongst Ingelarellidae, and material has been described from Permian faunas in Queensland and New South Wales, and reported from Tasmania by Clarke & Farmer (1976).

Validifera valida (Campbell, 1961a)

Fig. 124 - 127

1961a *Ingelarella profunda valida* Campbell, p. 177, pl. 28, fig. 14, 15.

1987a *Tomiopsis profunda valida* – Waterhouse, p. 30, pl. 8, fig. 10, 11.

Holotype: UQF 21918 from Tiverton Formation, figured by Campbell (1961a, pl. 28, fig. 14), OD.

Diagnosis: Large shells with well spaced adminicula, sulcus and low lateral plicae.

Material: Specimens from UQL 1380, 1626, 1628, 2619, 2620, 2624, 2625, 2628, 3127, 3780, 4515 and 4521. Campbell (1961a, Table 1, p. 169) reported the taxon from "zones 4 to 10" (his text, p. 177, says 4 -11). *Svalbardia armstrongi* Subzone and *Taeniothaerus subquadratus* Zone.

Fig. 124. *Validifera valida* (Campbell), dorsal aspect of internal mould UQF 81444 from UQL 2624, x2.

Dimensions in mm: ventral internal mould

UQF	UQL	Width	Length	Height
81594	2619	71	54	23
81809	2620	68	59	30

Fig. 125. *Validifera valida* (Campbell) internal mould of ventral mould UQF 81594 from UQL 2619, x1.

Description: Ventral valves few, large with broad deep sulcus, none or two or three pair of lateral plicae, substantial secondary posterior thickening and well spaced adminicula diverging anteriorly each side of a very large muscle field. A few specimens such as those from UQL 2628 have similar adminicula and very wide muscle field, and lack plicae, being externally close to *Ambikella ovata,* but differing in internal plates. Tabellae well formed, about 0.2 of shell length, parallel. One ventral valve from UQL 2620 has well defined growth wrinkles in front of the muscle field as far as the anterior margin, and a sturdy myophore extends for half the length of the muscle field in some specimens, including individuals from UQL 2628.

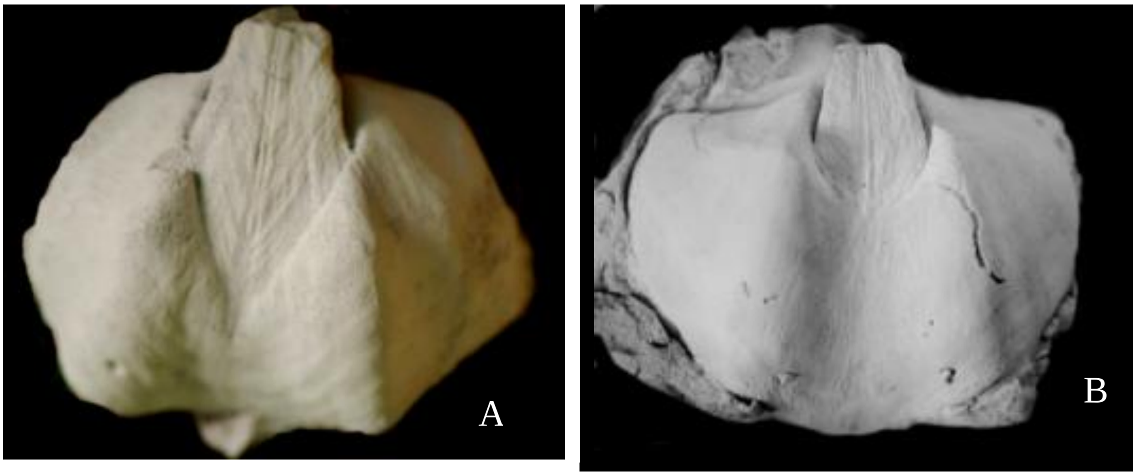


Fig. 126. *Validifera valida* (Campbell). A, internal mould of ventral valve UQF 81337 from UQL 2620, x1. B, ventral internal mould UQF 81809 from UQL 2628, x1.

Resemblances: The present material shows the same widely separated adminicula that characterize the types of *valida*. Similar material was also recorded from Rose's Pride Formation, southeast Bowen Basin, equivalent to upper Tiverton beds of the *Ingelarella plica* Zone, with deep sulcus, high fold, plicae and widely spaced not very long adminicula (Waterhouse 1987a). A Canning Basin specimen from the Nura Nura beds (Western Australia) that was assigned to *Tomiopsis woodwardi* by Archbold & Thomas (1986b, Fig. 3.21, 22) has comparable well spaced internal plates and wide muscle field, but its tabellae are short and widely divergent, somewhat as in *Johndearia*. A specimen labelled *branxtonensis* (not Etheridge) by McClung (1978, pl. 3, fig. 13) from the Farley Formation of New

South Wales is congeneric, probably conspecific. Otherwise the form is virtually unknown in Late Palaeozoic faunas, with none known in New Zealand, and as far as is known in other segments of Gondwana or northern palaeolatitudes. *Johndearia brevis* (McClung & Armstrong) and allies do display short and well spaced often divergent adminicula and somewhat comparable tabellae. They differ externally in that species are large and bear sulcal subplicae, and often channeled fold (Waterhouse 1998). *Johndearia* is not known in its typical form in faunas older than the Kungurian *Wyndhamia typica* Zone and correlative faunas, but the nature of the internal plates suggest that its forebears were to be found in late Sakmarian and Aktastinian faunas of east Australia as *Validifera*, if stress is to be laid on the internal plates. On the other hand the sulcus in the dorsal fold is shared with *Ingelarella*, but there is no tigillum. The widely spaced adminicula and short widely spaced tabellae of *Tomiopsis larini* and *T. tricosta* Kotlyar from Lake Baikal, with channeled fold, suggest an alternative but less likely source. (See Kotlyar & Popeko, 1967).

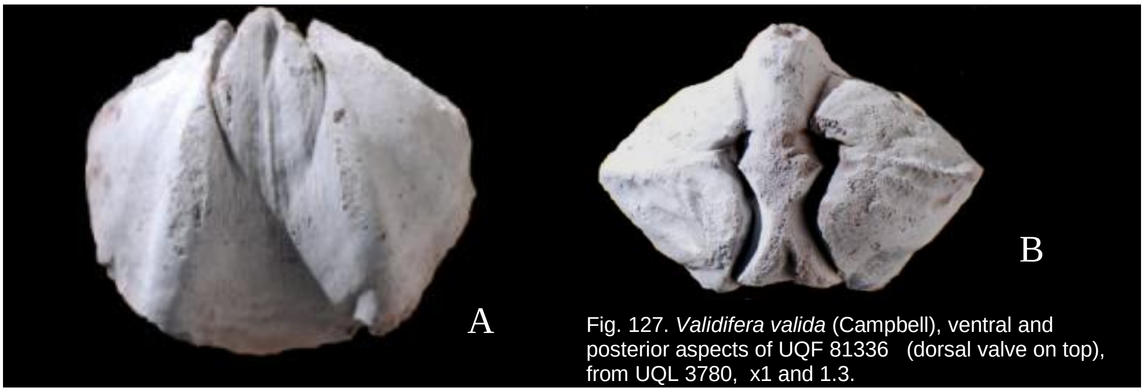


Fig. 127. *Validifera valida* (Campbell), ventral and posterior aspects of UQF 81336 (dorsal valve on top), from UQL 3780, x1 and 1.3.

Validifera prima new species

Fig. 128, 129

1983 *Tomiopsis elongata* – Waterhouse et al., p. 134, pl. 3, fig. 5, 8 (part, not fig. 9, 10, 13 = *branxtonensis* (Etheridge)).

Derivation: primo – at first, in the beginning, Lat.

Holotype: UQF 81309 from UQL 4505, lower Tiverton Formation (Fig. 128), here designated.

Diagnosis: Small, transverse with high rounded fold and deep sulcus, three to five pair of plicae, adminicula of moderate length, somewhat divergent and well spaced, tabellae medium length to long, subparallel, heavy secondary posterior thickening.

Material: Specimens from UQL 4505. Possibly *Bandoproductus macrospina* Zone.

Dimensions in mm: internal mould

Width	Length	Height	
48	34	13	ventral valve
40	32	30	both valves

Description: A number of slightly distorted mostly internal moulds are characterized by well rounded cardinal extremities, deep sulcus with angle close to 30° and no subplicae, and high fold with rounded crest. Specimens have two or three weak to moderate lateral pair of plicae on each valve, the innermost pair especially well developed on the dorsal valve, rare specimens non-plicate. Micro-ornament obscure, suggesting fine dimples, perhaps signifying the ends of prisms in the shell.

Adminicula moderately long and well spaced and diverging forward, may be weakly bowed in outline and subvertical, extend for a third or fourth of the length of the ventral internal mould, converge weakly on large dental plates which diverge towards the hinge. Ventral adductors sited on high narrow ridge, diductor scars broad, considerable secondary thickening. Heavy secondary thickening along the hinge. Tabellae 0.25 to 0.3 length of valve, diverge widely from posterior wall within first pair of interspaces next to fold, then curve to lie parallel. Very small ctenophoridium, dorsal median septum long and in some shells high, pair of elongate muscle impressions, little secondary thickening.

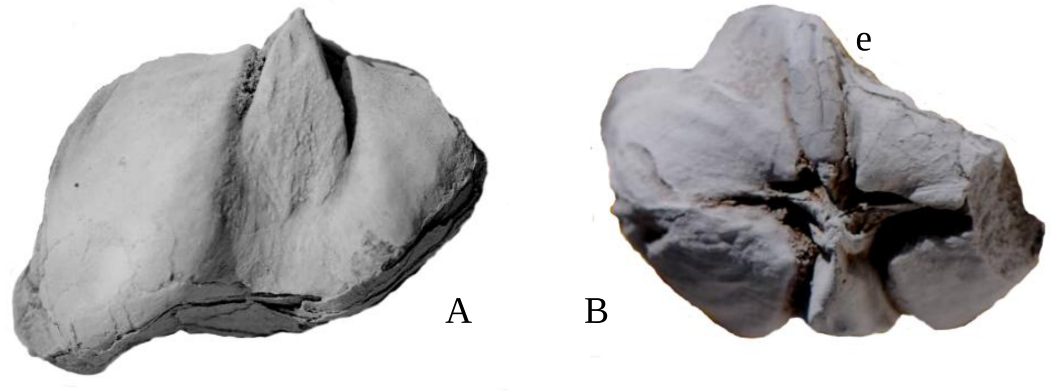
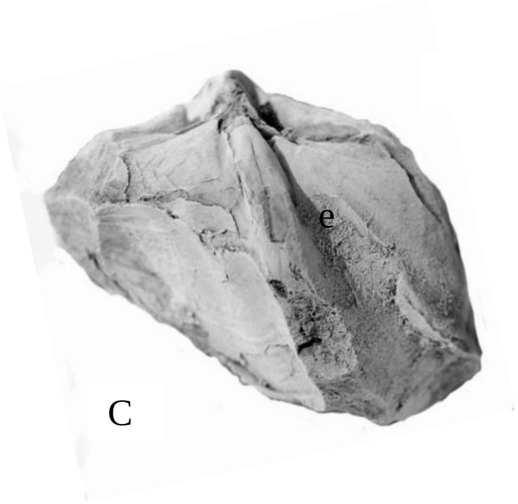


Fig. 128. *Validifera prima* n. sp. A, B, C, holotype, ventral, posterior, and dorsal views of internal mould UQF 81309, dorsal valve on top. Specimen from UQL 4505, x1.5. The letter e marks the anterior end of the tabella.



Resemblances: This species is slightly older than *Validifera valida* (Campbell), and is smaller, often with slightly more prominent plicae, and smaller ventral adductors with adminicula not as strongly divergent or as well spaced.

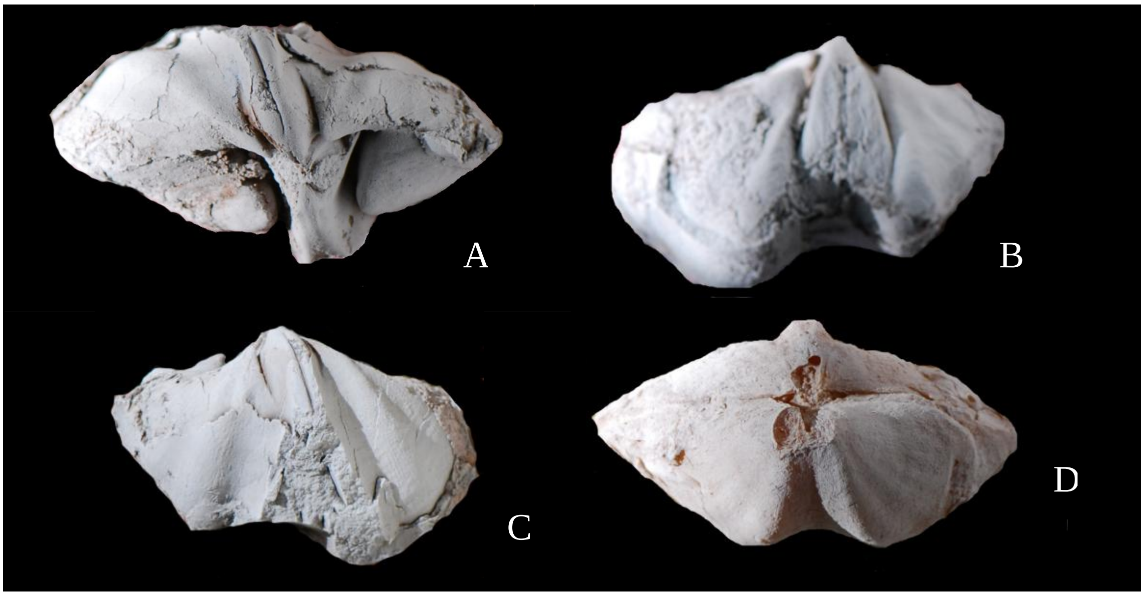


Fig. 129. *Validifera prima* n. sp. from UQL 4505. A, B, C, posterior (dorsal valve on top), ventral and dorsal aspects of internal mould UQF 81681, x1.5 . D, latex external mould, posterior aspect, dorsal valve on top, UQF 81682, x1.5.

Genus ***Tweedaleia*** Waterhouse, 2010a

Type species: *Tweedaleia tweedalei* Waterhouse, 2010a, p. 71 from Tiverton Formation (Sakmarian), Queensland, OD.

Diagnosis: Distinguished by lack of tabellae from dorsal interior.

Discussion: *Tweedaleia* is an outstanding genus amongst Ingelarellidae, because tabellae are lacking. In other respects, from shape, micro-ornament and ventral interior, the genus has evolved from east Australian species allocated to *Geothomasia*. The large size and lack of plicae help indicate that the genus is not notospiriferid.

Tweedaleia tweedalei Waterhouse, 2010a

Fig. 130, 131

aff. 1978 *Ingelarella ovata* [not Campbell] – McClung, pl. 4, fig. 16, 17.

2010a *Tweedaleia tweedalei* Waterhouse, p. 60, Fig. 25, 26.

Holotype: Specimen UQF 81340 from UQL 3127, Tiverton Formation, figured in Waterhouse (2010a, Fig. 25 C, D, F, 26A), and herein as Fig. 130A, 131C, D, F, OD.

Diagnosis: Specimens with reduced tabellae and unusually high fold.

Material: Specimens from UQL 2619, 2622, 2628, 3127 and 4513. *Svalbardia armstrongi* Subzone and *Taeniothaerus subquadratus* Zone.

Dimensions in mm: both valves, internal mould

UQF	UQL	Width	Length	Height
81340	3127	53.5	50	36

Description: Shells subequidimensional, with wide hinge, broad moderately well defined sulcus without subplicae and broad moderately high fold with rounded crest. The holotype from UQL 3127 has a sulcus with angle of 30°, no plicae, two long subparallel subvertical dental plates converging at only 50° on high adminicula that extend for over a quarter of the length of the valve but are largely buried in secondary thickening. The adductor and diductor impressions are narrow and striate. The dorsal valve has well developed fold, and faint suggestion of a low plicae pair laterally. Socket plates lie each side of short vertical crural plates and the medium septum extends well forward, between elongate and striate adductor scars, with the outer adductors clearly defined and commencing well behind the inner adductors. The inner pair of dorsal plicae is moderately well defined, and very low plicae lie outside the sulcal boundaries. A dorsal valve from UQL 2628 has a pair of low lateral plicae pair, and no well-formed tabellae, but a very low ridge less than 1mm high lies each side of the muscle field. Another specimen with valves conjoined from UQL 2628 has exceptionally thick dorsal septum and low ridges in the position of tabellae in other genera, but the ridges are low and not connected to crural plates. A small internal mould from UQL 3127 has thick posterior walls and dorsal muscle field bordered by a low ridge each side, extending for more than a quarter of the length of the shell, and almost parallel anteriorly.

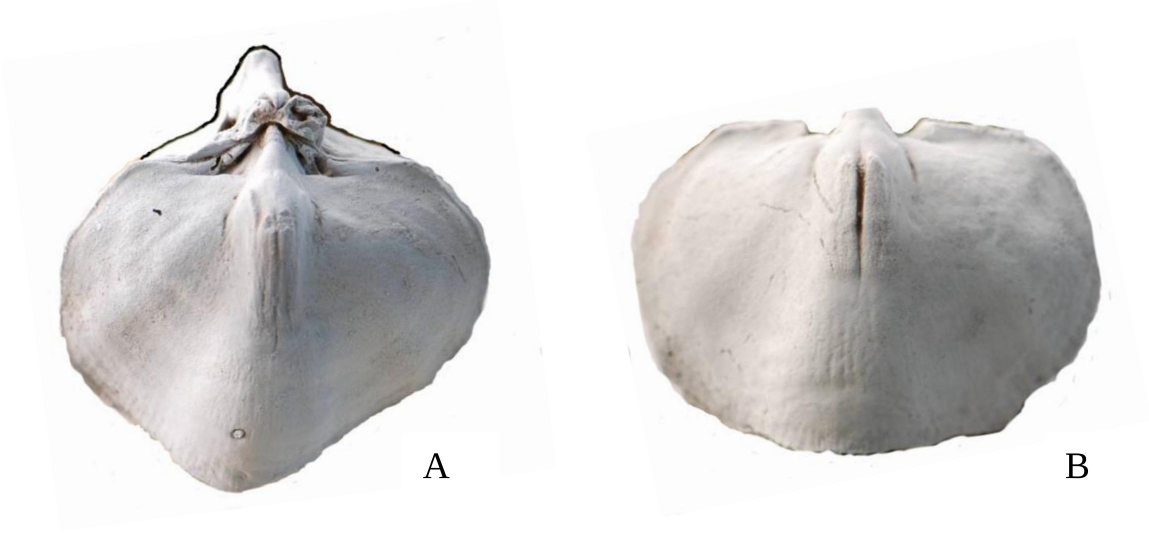


Fig. 130. *Tweedaleia tweedalei* Waterhouse. A, dorsal aspect of holotype UQF 81340 from UQL 3127, x1. B, dorsal valve UQF 81341 from UQL 2622, x1.5.

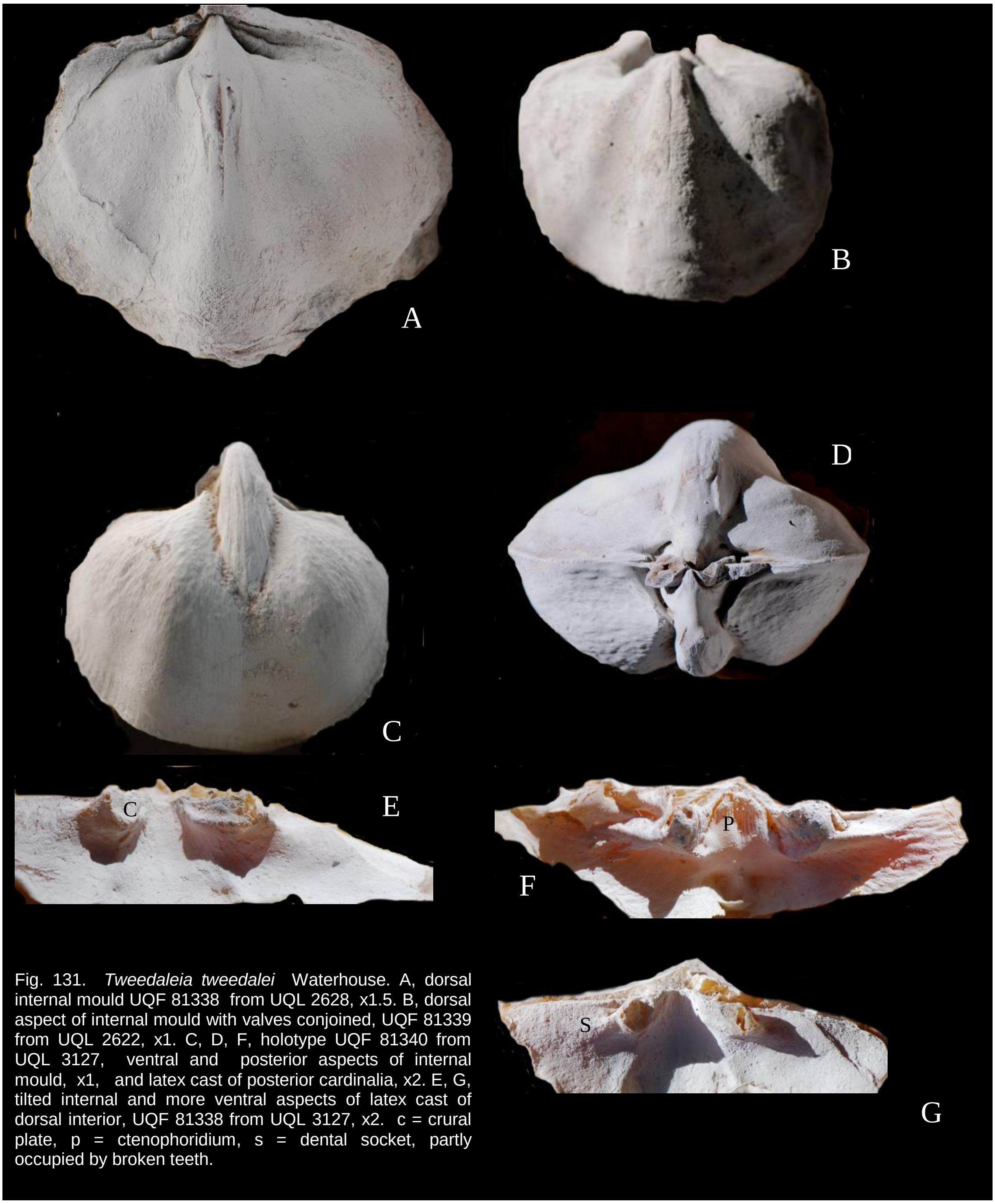


Fig. 131. *Tweedaleia tweedalei* Waterhouse. A, dorsal internal mould UQF 81338 from UQL 2628, x1.5. B, dorsal aspect of internal mould with valves conjoined, UQF 81339 from UQL 2622, x1. C, D, F, holotype UQF 81340 from UQL 3127, ventral and posterior aspects of internal mould, x1, and latex cast of posterior cardinalia, x2. E, G, tilted internal and more ventral aspects of latex cast of dorsal interior, UQF 81338 from UQL 3127, x2. c = crural plate, p = ctenophoridium, s = dental socket, partly occupied by broken teeth.

Resemblances: An internal mould from the Farley Formation, New South Wales, figured by McClung (1978, pl. 4, fig. 16, 17) might be conspecific. The reduced tabellae and well developed sulcus and fold, and remnant plicae point to derivation from *Geothomasia* stock, from species such as *Ingelarella symmetrica* Campbell and *I. profunda* Campbell which are found in slightly older beds of eastern Australia. Approaches to the genus *Johndearia* Waterhouse, 1998 are suggested by the wide hinge, low if any plicae, very substantial thickening over the hinge region, and especially, by the moderately short adminicula. *Johndearia brevis* (McClung & Armstrong) from the Elderslie and Snapper Point Formations of the Sydney Basin is a broader shell with wider and sulcate lower fold and shallow sulcus, and strong posterior thickening, widely spaced adminicula and well spaced short tabellae. *Tumulosulcus undulosa* (Campbell, 1961a, pl. 26, fig. 4-9) from beds 5km from Homevale, and equivalent to the *Glendella dickinsi* faunal assemblage of the Glendoo Sandstone Member (McClung 1981, Waterhouse & Jell 1983), also has moderately well developed and non-channeled higher fold and shallower sulcus, and is as long as wide, with well formed tabellae, and stronger plication. McClung (1978, pl. 8, fig. 1-3, 7) described comparable material with wider hinge from the Elderslie Formation of the north Sydney Basin, and *T*. *undulosa* is also found in the *Wyndhamia typica* Zone of the Freitag Formation, southwest Bowen Basin (Waterhouse 2001, p. 100).

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

Diagnosis: Small to medium-sized plicate shells with diverse micro-ornament, involving varying development of small spines or protuberances, and shallow grooves, globons, or mesopunctae. Tabellae as a rule very short or not developed.

Discussion: This family is distinguished from Ingelarellidae by its more complex surface structure and ornament, and by the lack or poor development of tabellae, although crural plates are fully developed. Shells are invariably plicate, whereas Ingelarellidae includes species that are smooth or simply sulcate. The family flourished in east Australia and New Zealand, and appears to have been limited otherwise to comparatively few species over Gondwana, with no certain occurrences in the northern hemisphere.

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

Diagnosis: Surface ornament of globons, which are small globose hollows in the surface of the shell, small barchan spines or protuberances may lie behind globons, and flanks of globons may be ridged, so that the shell surface is made up of pits surrounded by a network of shell.

Discussion: Two further subfamilies have been discriminated. Glendoniinae Clarke, 1992b has a micro-ornament of shallow elongate grooves terminated posteriorly by low transverse spinules, and Mesopunctiinae Waterhouse, 1998 has deep punctae called mesopunctae which penetrate the middle of the shell, and varied development of spinules and grooves.

Genus ***Notospirifer*** Harrington, 1955

Type species: *Spirifer darwini* Morris, 1845, p. 279 from Elderslie Formation (Roadian), north Sydney Basin, New South Wales, OD.

Diagnosis: Plicate shells bearing two prominent subplicae within sulcus as a rule, low dorsal fold normally channeled, micro-ornament of globons, short adminicula and reduced or no tabellae.

Discussion: The amount of variation displayed in micro-ornament by *Notospirifer*-like shells was not fully realized for many years, having been hampered by poor preservation of the type material of Harrington's genus. The micro-ornament of *Notospirifer* has been figured to show a closely spaced array of globons (Armstrong 1968a, pl. 2, fig. 9), but was reported by Armstrong (1970d) as consisting of small blunt spines and shallow grooves, although this is not shown in his figure. Clarke (1992a, p. 73), apparently quoting Armstrong (1970d) rather than adding new observations, stated that *Notospirifer* had small upright microspines behind short grooves leading anteriorly into deep globose and elongated pits. But it is not certain that grooves lie in front of spines. Campbell (1960, 1961a) recorded only "deep closely packed subcircular or slightly elongate pits" and made no reference to spines of any sort. Thus, regrettably, the exact nature of the micro-ornament in the type species remains to be verified. External features involving the shape, number and nature of plicae, and nature of sulcus and fold also help provide key attributes. There may be a degree of variation, but the type and other species are little inflated with shallow low plicae and shallow sulcus bearing as a rule two subplicae, and low fold as a rule bearing a median channel.

Several other morphotypes in the past have been referred to *Ingelarella*, but appear to belong to Notospiriferidae, from aspects of shape and micro-ornament. So-called *Ingelarella strzeleckii* (not de Koninck) of McClung (1978) differs substantially in having wide subplicate sulcus and channeled broad fold, with a number of narrow plicae, surface ornament allied to that of *Notospirifer* and short tabellae, so that the species, now named *gympiensis*, is referred to a separate genus *Monklandia* Waterhouse, 1998, within Notospiriferidae. Shells referred to *Ingelarella konincki* (Etheridge) are externally very close, and will be referred to *Monklandia*, because the neotype suggests, with some uncertainty, an array of short ridges, raised anteriorly, and shallow grooves. Another supposed *Ingelarella* named *I. denmeadi* Campbell has a high wide simple fold and sulcus and many fine plicae, and a somewhat similar species *Notospirifer undulatus* Parfrey has notospiriferid micro-ornament. The species are referred to *Tabellina* Waterhouse, which appears to be senior synonym of *Kelsovia* Clarke, 1990.

Notospirifer triplicata n. sp.

Fig. 132 - 136

1983 *Tomiopsis konincki* [not Etheridge] – Waterhouse et al., p. 135, pl. 3, fig. 15 (part, not fig. 11, 12, 14 = *konincki*).

Derivation: tri – three; plica – fold, Lat.

Holotype: Specimen UQF 81343 from UQL 4508, lower Tiverton Formation, figured in Fig. 133, 134A, 135, here designated.

Fig. 132. *Notospiirfer triplicata* n. sp. , ventral aspect of internal mould UQF 81853 from UQL 4508, x4.

Diagnosis: Medium-sized moderately inflated shells with three or five pair of low ventral plicae, usually three pair of dorsal plicae, sulcus generally with two low subplicae, rarely may be smooth, fold smoothly rounded or with median groove, micro-ornament of shallow dense globons and small barchan spines.

Fig. 133. *Notospirifer triplicata* n. sp. dorsal aspect of internal mould of holotype UQF 81343 from UQL 4508, x2.5.

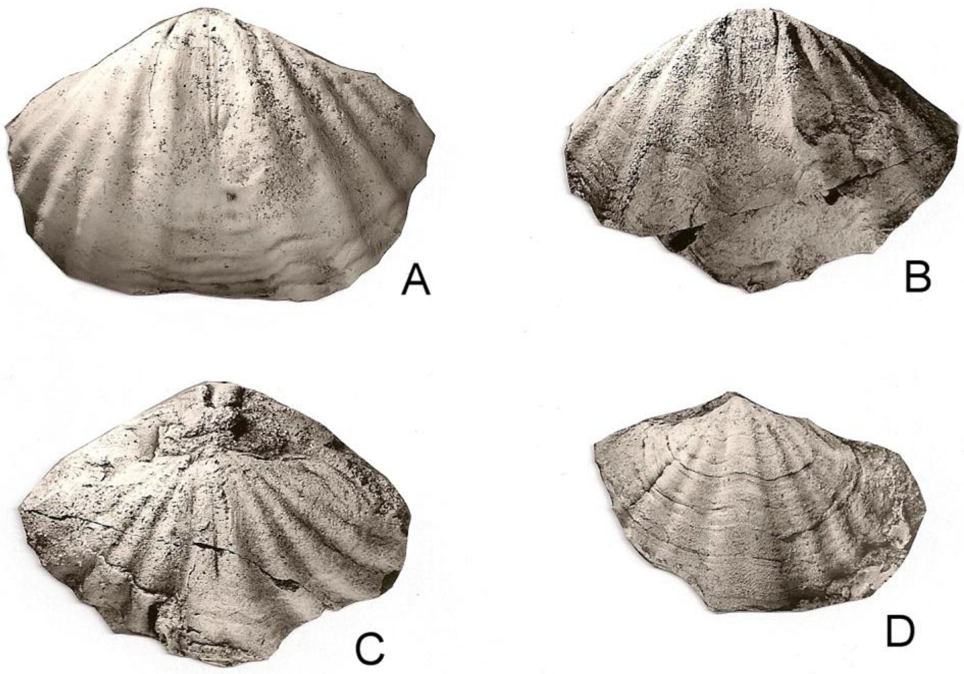


Fig. 134. *Notospirifer triplicata* n. sp. A, ventral aspect of specimen with valves conjoined, holotype UQF 81343 from UQL 4508. B, C, ventral and dorsal aspects of internal mould with valves conjoined, UQF 81344 from UQL 4508. D, latex cast of dorsal valve UQF 81345 from UQL 4508. Specimens x1.

Material: Specimens from UQL 4506, 4507, 4508, TK1 and TK1/2. *Bookeria pollex* Zone.

Dimensions in mm:

UQF	UQL	Width	Length	Height ventral	Height dorsal	Height both valves
81344	TL1	50	27		10	
81343	4508	52	38	15	13	21 holotype

Description: Shells of moderate size, transverse, hinge about two thirds of shell width, ventral interarea high and gently concave, dorsal interarea very low, cardinal extremities obtuse. Sulcus commences at umbo and widens at an angle close to 25°, with anterior tongue, usually bears two very low subplicae, dorsal fold low with steep low walls, and broad crest, smooth, or with very shallow median groove. Three pairs of plicae on each valve with signs of fourth or fifth pair in some specimens. Micro-ornament of small barchan spines each with short swollen pit in front, crowded, about four in 1mm across the shell, and two per mm longitudinally. Some growth lamellae well developed.

Adminicula high, about 0.25 of shell length, curve outward from umbo and lie subparallel for most of length as a rule. Adductor scars on ridges occupy half the width of muscle field, diductor scars narrow, no tigillum, secondary thickening slight. Dorsal valve with very short tabellae extending along second pair of interspaces from fold, cardinal process not visible, median septum extending almost two thirds length of valve, dorsal adductors not clearly impressed.

Resemblances: This species is referred to *Notospirifer* because of its low inflation, shallow sulcus and low fold. Some specimens agree with the type of the genus in the presence of sulcal subplicae and median groove in the fold, but there is variation, suggesting the need for tolerance of morphological constraints. The micro-ornament shows, rarely, small barchan spines, the presence of which has not yet been established as present on the type species of *Notospirifer*.

Notospirifer darwini (Morris, 1845), type species of the genus, has very subdued plicae, shallow sulcus with sulcal subplicae, and low fold bearing channel. The adminicula are short and widely divergent, and tabellae are tiny and lie in the first pair of interspaces next to the fold. *N. gentilis* Waterhouse in Waterhouse & Jell (1983, pl. 3, fig. 1-5) from the Glendoo Sandstone Member above the Tiverton Formation in the north Bowen Basin has three pair of plicae, two sulcal subplicae and comparatively narrow low round-crested fold, broadening anteriorly. The adminicula are shorter and more widely diverging and the tabellae are slightly longer than in the present species. *N. paraextensus* Waterhouse (1987a, p. 38, pl. 9, fig. 2, pl. 10, fig. 15, pl. 11, fig. 4) from the Fairyland Formation of southeast Bowen Basin has four to five pairs of plicae, no sulcal subplicae, very low dorsal fold without channel, deep globons, and widely spaced short adminicula, with no tabellae. *N. extensus* Campbell (1961a, pl. 28, fig. 1-4) from the Stanleigh Shale, southwest Bowen Basin, has sulcal subplicae in a comparatively wide sulcus, flattened crest to dorsal fold, and as a rule two or three pair of ventral plicae, and is close in shape to the new form. It is distinguished by its widely divergent short adminicula. The holotype UQF 21959 (Campbell 1961a, pl. 28, fig. 1a-c) has a mid-sulcal rib, but this is worn and weak in UQF 21953. Such a rib suggests an approach to *Glendonia* McClung & Armstrong, 1978 or *Farmerella* Clarke, 1992b. Armstrong (1970d, p. 291, Fig. 21) showed that *extensus* has internal pits or mesopunctae, and though referred to *Mesopunctia* by Waterhouse (1998, p. 41), belongs to *Farmerella*, characterized by mesopunctae and sulcal rib.

Fig. 135. *Notospirifer triplicata* n. sp. posterior view (dorsal valve on top) of holotype UQF 81343 from UQL 4508, x2.

The present species is smaller than *Tabellina denmeadi* (Campbell, 1961a) from the Fairyland Formation of southeast Bowen Basin, and has comparably high ventral interarea, fewer plicae, lower narrower dorsal fold, comparable adminicula and tabellae and longer dorsal median septum. *Tabellina undulata* (Parfrey, 1986) from Camboon Andesite near Biloela, southeast Bowen Basin, differs in much the same way, as far as known, with prominent fold and moderately deep sulcus. The Tasmanian species described as *Kelsovia superba* Clarke (1990, Fig. 13A-N; 1992a, Fig. 13A-N) from the Swifts Jetty Sandstone, Massey Creek Group and Fossil Cliffs, Darlington, Maria Island, is close to *denmeadi* in general appearance, with four to five pairs of slender plicae, more rounded and more prominent wider dorsal fold, and comparatively well spaced spinules and grooves. Compared with the present form, the Tasmanian species has a wide and high fold and slightly narrower sulcus, long dorsal septum and slightly longer tabellae that curve into the first lateral interspace each side of the fold. *Kelsovia* was synonymized with *Tabellina* Waterhouse, 1987a by Waterhouse (1998).

Monklandia gympiensis Waterhouse, 1998 from the Early Permian Monkland beds of Gympie has less emphasized sulcus with stronger subplicae, more plicae pairs and slightly more raised dorsal fold with flat or sulcate crest. The species *glendonensis* Waterhouse, 1998 from the Muree Formation, north Sydney Basin, is closer in appearance, with similar tabellae, but the plicae are raised and narrower, and there is a deep dorsal channel along the fold, and surface grooves are more elongate. Compared with *triplicata*, the specimens have more sulcate fold, sulcus with well defined subplication as in *Glendonia* and comparably short tabellae. The neotype of *konincki*, UQF 73296 (Waterhouse et al. 1983, pl. 3, fig. 14), shows short elongate ridges, tending to widen forward, and shallow grooves, apparently notospiriferid and approaching the micro-ornament of *M. gympiensis*. The grooves are not sunken into pits. Apart from the micro-ornament, *konincki* differs from the present species in developing more robust and longer adminicula, and lower ventral interarea. The tabellae lie closer to the fold and are longer, at least in the Tasmanian material, but in Wasp Head *Geothomasia simplicitas* Waterhouse, figured as *konincki* by McClung (1978, pl. 3, fig. 1, 2), the tabellae are short and widely divergent.

Fig. 136. *Notospirifer triplicata* n. sp., detail of latex cast of ventral valve UQF 81348 from UQL 4508, x7.

Genus ***Papulinella*** Waterhouse, 1998

Type species: *Notospirifer hillae* Campbell, 1961a, p. 185 from Tiverton Formation (Sakmarian) of Bowen Basin, Queensland, OD.

Diagnosis: Shells large for the family, plicae are high with narrow crests and broad interspaces, sulcus may lack subplicae, fold high with or without median groove, micro-ornament varied, dominated by globons, often with short posterior protuberances or blunt or crescentic barchan spinules passing anteriorly into ridge each side of globon, or globon may be encircled by ridge, or replaced by shallow groove.

Discussion: This genus is distinguished by the high dorsal fold and strong plicae from *Notospirifer* Harrington, 1955. The plicae are high and have narrow rounded crests, narrower and less rounded than in *Notospirifer*. Small spines are definitely present, as show in figures of the micro-ornament provided for *hillae* by Armstrong (1970d, Fig. 1B, G, H). *Notospirifer* has swollen exopunctae (ie. globons) and small posterior knobs, according to Armstrong (1968a, pp. 198, 199), but no figure has been published, and initial appraisals of the micro-ornament by Campbell (1959, 1960, 1961a) and Waterhouse (1998) suggested that no spines were present, the globons entering the shell without the shell surface being raised behind each globon, though this must be qualified, as shown in Fig. 136. Given the uncertainty over whether *Notospirifer* really lacks spines, *Papulinella* could be provisionally treated as a subgenus of *Notospirifer*, distinguished by the large size, strong plicae, high dorsal fold, lack of subplicae from the sulcus in some material, and possibly, but only possibly, by the presence of barchan spines, but the difference in fold and nature of the plicae suffices to distinguish two generic strands. In *Papulinella*, tabellae are generally lacking but rare specimens suggest short tabellae entering the first pair and in other specimens the second pair of interspaces next to the sulcus and fold. *Notospirifer* has no tabellae or tiny tabellae entering the innermost pair of interspaces and adminicula cut across the second lateral pair of interspaces to lie in the first pair of interspaces: there is little difference in tabellae between the two, and indeed the tabellae where present are so short that relating them to interspaces is difficult. *Farmerella* Clarke, 1992b has mesopunctae and tiny blunt barchan spines, and is further distinguished by the presence of a median rib along the sulcus.

Papulinella hillae (Campbell, 1961a)

Fig. 137, 138A-F, 139

1961a *Notospirifer hillae* Campbell, p. 185, pl. 25, fig. 6, pl. 27, fig. 1-6, 11.

1961a *N. hillae plicata* Campbell, p. 187, pl. 27, fig. 7-10.

1964b *N. hillae* – Hill & Woods, pl. P9, fig. 7-9.

1970b *N. hillae* – Armstrong, p. 204, pl. 14, fig. 7, 8.

1970d *N. hillae* – Armstrong, p. 208, Fig. 1B, G, H.

1972 *N. hillae* – Hill, Playford & Woods, pl. P9, fig. 7-9.

1998 *Papulinella hillae* – Waterhouse, p. 34.

2007 *Papulinella hillae* – Carter, p. 2779, Fig. 1860.1a-c.

Holotype: UNEF 3007 from Tiverton Formation, Bowen Basin, figured by Campbell (1961a, pl. 27, fig. 3), OD. Holotype of *plicata*, UNEF 3043, Tiverton Formation, figured by Campbell (1961a, pl. 27, fig. 10a-c), OD.

Diagnosis: Comparatively large shells with three to six pair of strong plicae, sulcus rarely with faint subplicae, fold may be grooved as a rule, short well spaced adminicula, no tabellae as a rule.

Material: Specimens from UQL 1127, 1621, 1622, 1625, 1626, 1628, 2620 - 2622, 2628, 2629, 2684, 2631, 3127, 3780, 4510, 4511, 4514, 4515, 4517, 4519, 4521 and 4566. *Bookeria geniculata* and *Taeniothaerus subquadratus* Zones.

Fig. 137. *Papulinella hillae* (Campbell), dorsal internal mould of small specimen UQF 81347 from UQL 4521, x4.

Description: Specimens variable, especially from UQL 3127, have a channel as a rule along the dorsal fold, but the sulcus lacks subplicae. Adminicula are short and usually well spaced, lying in the first or second pair of interspaces from the sulcus (first pair in the holotype), or starting over the innermost pair of plicae. Tabellae are absent from most specimens, but a few specimens have very short tabellae lying in either the first or second pair of interspaces from the fold: a specimen from UQL 3127 shows five pair of plicae, rounded fold and short well developed tabellae extending along the innermost pair of interspaces. Other specimens, such as those from UQL 2631, have tabellae in the second pair of interspaces, others have a channeled fold. The micro-ornament consists of close-set globons, for which figures were provided by Campbell (1961a, pl. 27, fig. 2a) and Armstrong (1970d, Fig. 1B, G. H). The globons are round to slightly elongate and vary in shape over different parts of the shell. Some lie in front of a stubby posterior elevation, prolonged as a ridge like barchan horns each side of the globon. In front the globon is bordered by the posterior terminus of the ridge commencing the next barchan. In other specimens, or over parts of the surface, the globons lie in quincunx, with each lateral ridge passing forward into the spine behind a globon: in other parts, the posterior ridge is not elevated, and the surface ornament looks like a meshwork of ridges with hollows in between. Spines are rarely seen, and then only over parts of the shell and in specimens with sulcate fold.

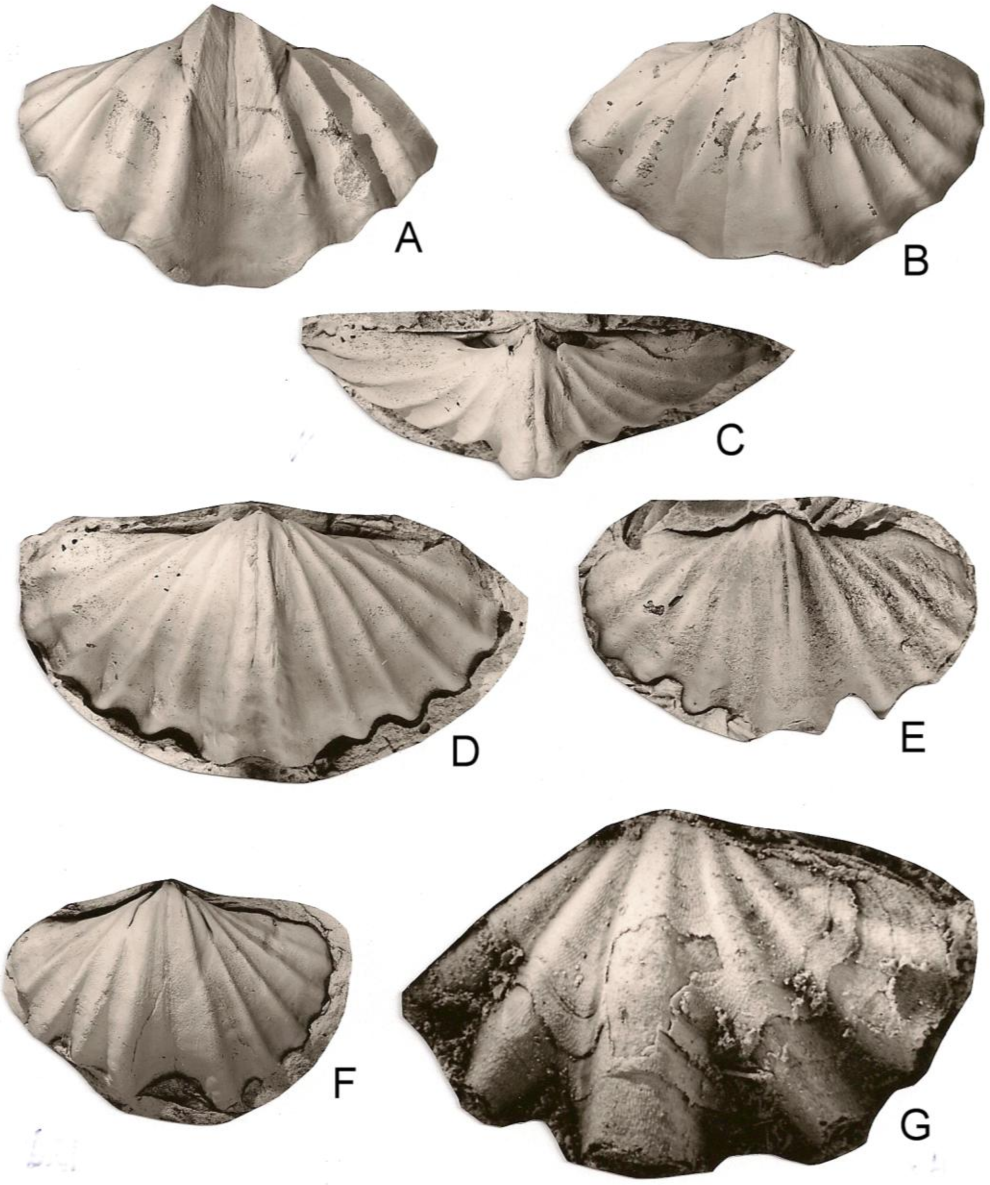


Fig. 138. A-F. *Papulinella hillae* (Campbell). A, B, ventral and dorsal aspects of internal mould with valves conjoined, UQF 81349 from UQL 3127, x1. C, D, posterior and dorsal aspects of internal dorsal mould UQF 81350 from UQL 2631, x1. E, dorsal internal mould UQF 81351 from UQL 4510, x 0.8. F, ventral internal mould UQF 81352 from UQL 2621, x1. G, *Geothomasia profunda* (Campbell), latex cast of small dorsal valve UQF 81353 from UQL 4518, x4.

Campbell (1961a) discriminated a subspecies *plicata* for shells from his “zones 4 -10” of the Tiverton Formation, for shells which tended to be more plicate, as compared with *hillae hillae*, found in his “zones 11 – 13”. Campbell (1961a, table 3) was able to show a distinct decrease by one pair of plicae in specimens from above his “zone 10” and a increase in number of specimens with four pair of plicae and diminution of specimens having six pairs of plicae, but discrimination according to such criteria has not been found to be practical from present material. His holotype for *plicata* has no sulcal subplicae, a dorsal channel along the fold, adminicula possibly in the second lateral pair of interspaces, and no tabellae. The specimen has five pair of plicae. The holotype of *hillae hillae* has no sulcal subplicae, adminicula in the second interspace, and again, five pair of plicae, the fifth pair inconspicuous. The dorsal valve is not preserved. Specimens from UQL 2684, 3127, and 2619 have six plicae pairs, specimens from UQL 3127 and 2631 have five pair, and specimens from UQL 2622 and two specimens from UQL 3127 have four pair. The proposal by Campbell (1961a) that two subspecies were involved, *hillae* with a limited range in number of plicae, and *plicata* with a range encompassing greater number of plicae, is not established. That two variable subspecies were involved is one of several possibilities. It could well be that there were several persistent subspecies (or species), each characterized by a set number of plicae. Even within the parameters proposed by Campbell (1961a), two subspecies could have co-existed.

Resemblances: Specimens of *Papulinella hillae* (Campbell) have been reported from the Rose's Pride Formation and lower Elvinia Formation of the southeast Bowen Basin by Waterhouse (1987a, p. 39, pl. 10, fig. 10?, 14). The Rose's Pride specimens have four pair of plicae, approaching those from the upper middle Tiverton Formation at Homevale. The sulcus of specimens from the Elvinia Formation was recorded as grooved, which is not the case for most Tiverton specimens. *Notospirifer* sp. aff. *hillae* Campbell described by Waterhouse (1968a, p. 74) from the Brunel Formation of southern New Zealand has micro-ornament of spines and anterior grooves, suggestive of Glendoniinae. Compared with *Notospirifer triplicata* n. sp. which has three or four pair of plicae, the *hillae* specimens are larger, with higher and narrowly crested fold, channeled in some specimens, not in others, higher plicae, more abruptly rounded cardinal extremities, and adminicula spaced further apart.

Fig. 139. *Papulinella hillae* (Campbell). A, external mould of dorsal valve UQF 81811 from UQL 2620, x9. B, a fragment of the true exterior of ventral valve UQF 81854 from UQL 4515, x7.

Papulinella wilsoni n. sp.

Fig. 140

Derivation: Named for A. F. Wilson.

Holotype: UQF 81355 from UQL 2619, Tiverton Formation, figured as Fig. 141B, here designated.

Diagnosis: Medium to large for genus, with three or less commonly four pairs of narrow high plicae and wide interspaces, dorsal fold high.

Material: Shells from UQL 1622, 2619, 3127, 4517 and 4521. Rare in *Bookeria geniculata* Zone, chiefly *Taeniothaerus subquadratus* Zone.

Dimensions in mm: specimens with three pair of plicae.

UQF	UQL	Width	Length	Length	Height	Height
			dorsal	ventral	dorsal	ventral
81355	2619	56	38		15	
81354	4521	52		32		14

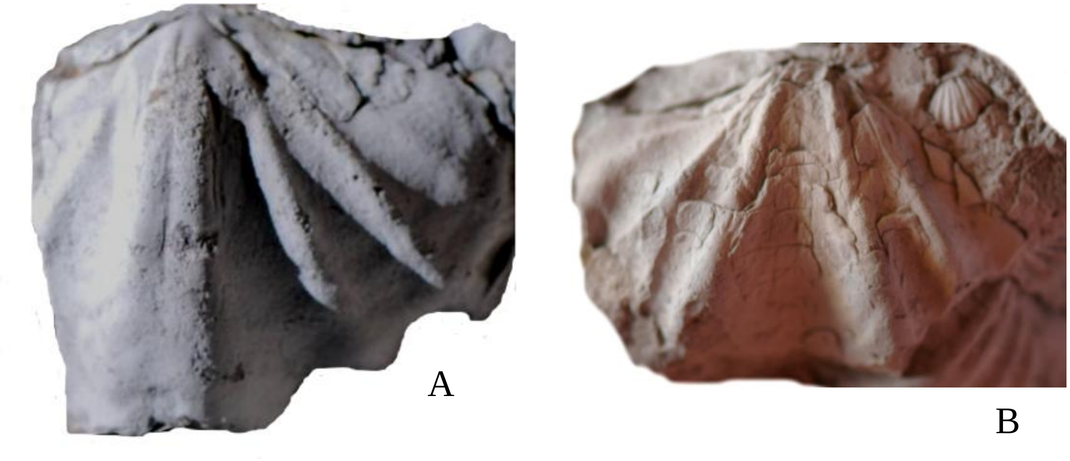


Fig. 140. *Papulinella wilsoni* n. sp. Specimens with few plicae. A, dorsal internal mould UQF 81354 from UQL 4521, x2. B, holotype, partly decorticated ventral valve UQF 81355 from UQL 2619, x1.

Description: Most specimens have only three pairs of plicae, and occasionally a fourth pair. The shells are large, transverse, with umbo incurved, having an angle of 110^{o}, hinge wide, cardinal extremities obtuse, ventral interarea moderately high, concave and bearing open delthyrium with angle of 80^{o}, dorsal interarea low. Ventral sulcus broad and bordered by plicae diverging forward at 40^{o}, without subplicae, rib or groove, dorsal fold upstanding and medianly flattened or usually channeled. Ventral plicae lie in three pair, with fourth subdued outer pair on some specimens, dorsal plicae similar, crests on both valves narrow, interspaces broad. Micro-ornament of globons surrounded by ridges, close-set, in quincunx, blunt short barchan spinules, and irregular and few commarginal laminae.

Teeth born on scapular-shaped dental plates which diverge to floor of valve at 100^{o}, supported by slightly lower and short adminicula which diverge widely forward along the second pair of interspaces from the sulcus. Ventral adductor scars narrow, diductor scars broad. Dental sockets are contained within horizontal outer hinge plates and inwardly inclined crural plates, supported by very short tabellae in some specimens which are vertical and cut across the innermost plicae pair to lie in the interspaces next to the fold; tabellae usually absent. Ctenophoridium small, median septum extends for half the length of the shell, adductor scars weakly impressed.

Resemblances: The specimens are distinguished by having only three pair – or rarely four pair – of plicae, and the plicae are high and narrow and the interspaces very wide. They differ strongly from *Notospirifer triplicata*, with three pair of plicae, and much lower fold.

Subfamily **GLENDONIINAE** Clarke, 1992b

Diagnosis: Distinguished by micro-ornament of low ramped spines behind long shallow grooves, tabellae short or absent.

Discussion: This subfamily is close to Notospiriferinae, but surface grooves are shallower and longer than the globons characteristic of Notospiriferinae.

Genus ***Tabellina*** Waterhouse, 1987a

Type species: *Ingelarella denmeadi* Campbell, 1961a, p. 171 from Fairyland Formation (Sakmarian), southeast Bowen Basin, Queensland, OD.

Diagnosis: Large for family with strong high and broad dorsal fold bearing rounded crest, moderately well defined to deep ventral sulcus, which may bear two subplicae, lateral plicae well defined, may be numerous, micro-ornament of low ramped spines behind elongate not very deep grooves. Adminicula moderately developed, tabellae short or absent, long low dorsal septum.

Discussion: *Kelsovia* Clarke, 1990, p. 70, type species *K. superba* Clarke, 1990 from the early Permian of Tasmania is a subjective synonym, agreeing in ornament and internal plates, as discussed by Waterhouse (1998). Clarke (1990, 1992a) and Carter (2006a) placed *Tabellina* in Family Ingelarellidae, but the genus belongs with *Kelsovia* in the notospiriferid subfamily Glendoniinae, being similar in micro-ornament and internal plates. The micro-ornament typical of the genus is well figured by Clarke (1992a, Fig. 13K).

Tabellina undulata (Parfrey, 1986)

Fig. 141A-C

1986 *Notospirifer undulatus* Parfrey, p. 62, Fig. 2.5, 3.1.

Holotype: GSQ F 12936 from Camboon Andesite (?Sakmarian), figured by Parfrey (1986, Fig. 3.1b), OD.

Diagnosis: Large with several pairs of plicae, two sulcal subplicae, medianly flattened dorsal fold, reduced tabellae.

Material: Specimen from UQL 2622. *Bookeria geniculata* Zone.

Dimensions in mm: internal mould, UQF 81358

Width	Length	Length dorsal	Height both	Height ventral	Height dorsal
56	48	43	33	23	18

Description: Shell transverse, moderately inflated, wide hinge with obtuse cardinal extremities, ventral interarea moderately high and gently concave, posteriorly inclined, delthyrium with angle of 80°, dorsal valve with low interarea in plane of commissure, interrupted by broad notothyrium with angle of 120°. Ventral sulcus shallow, widening at angle of 27°, bearing two broad subplicae, lateral shell with six pair of plicae plus an outermost inconspicuous pair; dorsal fold low posteriorly, prominent anteriorly, with crest very gently convex, seven or eight pair of dorsal plicae.

Teeth supported by very high scapular-shaped dental plates, marked by low growth rugae, inclined inwards at 130°, supported by lower adminicula that diverge outwards and weakly forwards, aligned with the second lateral pair of interspaces from sulcus. Ventral muscle field very large, extending half the length of the valve, with broad adductor ridges and only moderately wide diductor scars with posterior oblique markings, and radial lineations over most of the surface. Low striae lie behind the muscle scars. In dorsal valve ctenophoridium small, dental sockets slender, contained partly by thick horizontal outer hinge plates and crural plates inclined inwards towards floor of valve, and extending along the floor of the second lateral pair of interspaces from the sulcus, but not resting on tabellae, which are reduced to short nicks in the internal mould. Crural bases pass along the inner edge of the crural plates. A long median septum extends well forward beyond mid-length, and adductor impressions form two narrow pair.

Resemblances: Although the external micro-ornament is not preserved, the material is judged to belong to *Tabellina* on the basis of overall shape, prominent fold and sulcus with two subplicae, and numerous plicae. *T. undulata* (Parfrey, 1986) from Camboon Andesite near Biloela, southeast Bowen Basin, is somewhat similar, with broad fold with rounded crest and five to six pair of strong lateral plicae, and thus close in overall shape and number of plicae and nature of fold. The appearance of the present specimen is slightly different, because it is an internal mould, whereas the Camboon specimens are well preserved with shell intact. None of the Camboon specimens appear to have sulcal subplicae externally, unlike the suggestion of such in the Tiverton specimen, but the internal mould figured by Parfrey (1986, Fig.

2.5d) shows sulcal subplicae. Micro-ornament consists of closely spaced shallow linear pits widening posteriorly and possible crescentic – ie. barchan – spines. The specimen is close to *T. denmeadi* (Campbell, 1961a) – see Waterhouse (1987a, p. 26) from the Fairyland Formation near Cracow, southeast Bowen Basin, in the number of plicae, but the fold is slightly lower, and the adminicula slightly more divergent and shorter. Only one of various figured specimens of *denmeadi* has sulcal subplicae (Campbell 1961a, pl. 23, fig. 12). The species described as *Kelsovia superba* Clarke, 1990 from the Swifts Jetty Sandstone and “Spirifer” Zone of Fossil Cliffs, Darlington, Maria Island, Tasmania, has very prominent dorsal fold, and only three to four pair of plicae, and tabellae are slightly longer than in *T. denmeadi*. Subplicae are variably developed in two of the three figured ventral valves, the adminicula are more subparallel but short, the dorsal septum is long, and surface grooves long and shallow.

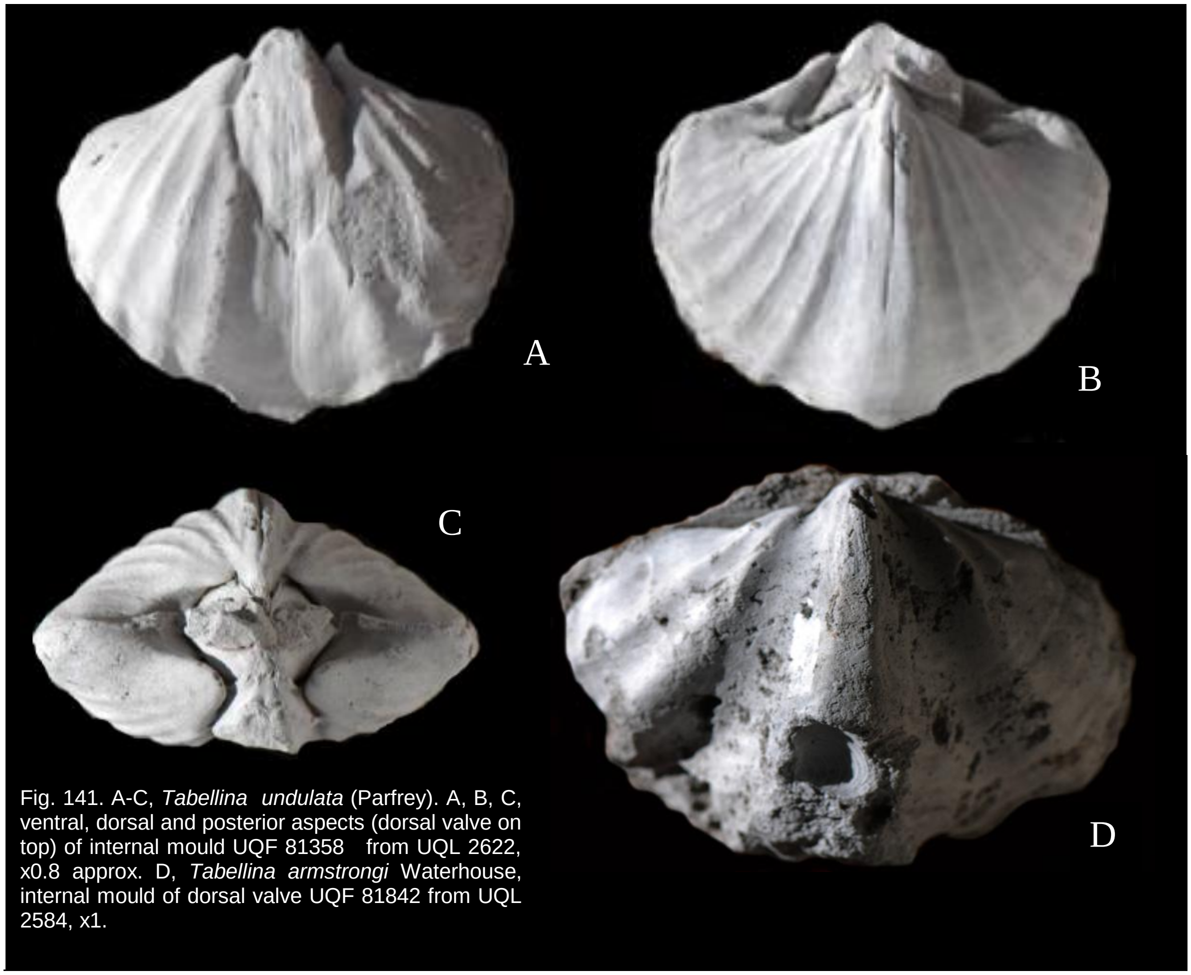


Fig. 141. A-C, *Tabellina undulata* (Parfrey). A, B, C, ventral, dorsal and posterior aspects (dorsal valve on top) of internal mould UQF 81358 from UQL 2622, x0.8 approx. D, *Tabellina armstrongi* Waterhouse, internal mould of dorsal valve UQF 81842 from UQL 2584, x1.

Tabellina cracowensis Waterhouse (1987a, pl. 7, fig. 11-14) from the Fairyland Formation of the southeast Bowen Basin has high dorsal fold and high inner pair of plicae on each valve, especially the dorsal valve. It is a very distinctive species, now referred to *Geothomasia*. *T. armstrongi* Waterhouse, 1998, p. 36, based on specimens figured as *Notospirifer*? n. sp. by McClung & Armstrong (1978, pl. 2, fig. 21-25), has lower and fewer plicae. The species comes from the Cattle Creek Formation of southwest Bowen Basin.

Tabellina armstrongi Waterhouse, 1998

Fig. 141D, 142

1978 *Notospirifer*? n. sp. McClung & Armstrong, p. 4, pl. 2, fig. 21-25.

1990 *Kelsovia* sp. Clarke, p. 72.

1998 *Tabellina armstrongi* Waterhouse, p. 36.

Holotype: GSQF 12287 from Cattle Creek Shale (Aktastinian), figured by McClung & Armstrong (1975, pl. 2, fig. 24, 25), OD.

Diagnosis: Well developed ventral sulcus, three pair of plicae.

Material: A dorsal internal mould from UQL 2584 and external mould from UQL 4518. *Taeniothaerus subquadratus* Zone.

Description: Ventral valve with well formed sulcus three pair of plicae and glendoniin micro-ornament. A large dorsal valve 74mm wide, 57mm long and 28mm high is characterized by having a very high fold bearing gently rounded crest, and three pairs of lateral plicae, the inner pair of plicae strong, the second pair rather weakly defined and third pair very faint. The interarea is moderately high and the notothyrium broadens at an angle of nearly 70^{o}. Small cardinal process, socket plates and crural plates, tabellae very short.

Resemblances: This species is characterized by its very high fold and very short tabellae, and micro-ornament of elongate grooves in front of barchan spines.

Fig. 142. *Tabellina armstrongi* Waterhouse, latex cast of ventral valve UQF 81356 from UQL 4518, x4.

Suborder SPIRIFERIDINA Waagen, 1883

This suborder includes a large group of superfamilies, including the root-stock of Spiriferidina, Cyrtioidea Fredericks, followed by Adolfioidea Sartenauer, a branch Cyrtospiriferoidea Termier & Termier, Paeckelmannoidea Ivanova, and Spiriferoidea King. The group is primarily and overall characterized by lack of tabellae and by ribbing, with little in the way of specialized micro-ornament compared with Delthyridina or Martiniidina. Changes through time were substantial, so that generalizations need to be qualified, but the succession of changes are traced in the Paleontological brachiopod Treatise volume 5 by Carter & Gouvennec (2006a). Martiniidina began with smaller shells with less macro-ornament and less developed plates, and Delthyrididina with plicate shells and fimbriate and commarginal micro-ornament.

A study of Spiriferidina by Waterhouse (2004a) published before the summary of classification by Carter & Gouvennec (2006a) proposed an elaboration and adjustment of classification from Carter et al. (1994) that met with some reservation in turn from Gouvennec & Carter (2007, p. 2779). At least some of their arguments are difficult to follow: they claimed to “correct” Waterhouse by asserting that Neospiriferinae and Kaninospiriferinae ought to be associated - yet that is what was done in the Waterhouse study (Waterhouse 2004a, pp. 8, 104, 129). One remains mystified by the assertion by Gouvennec & Carter (2007) that the Waterhouse arrangement ignored the presence/absence of the delthyrial plate. It was Carter (2006a) who ignored the presence/absence, even referring Neospiriferinae to Trigonotretidae. But these are matters that can be resolved through further study, and to some extent are addressed in a monograph on Spiriferida by Waterhouse (in prep.).

Superfamily **TRIGONOTRETOIDEA** Schuchert, 1893

Discussion: Shells are plicate and costate as a rule, with cancellate micro-ornament of fine radial and commarginal lirae. Dental plates supported by adminicula, median septum rarely present, crural plates developed, and no tabellae. The group arose from Pinguispiriferinae.

Family **TRIGONOTRETIDAE** Schuchert, 1893

Diagnosis: Small to large shells with denticulate hinge, plicae pairs moderate to numerous, costae rare to well developed, umbonal callosity developed in most forms. Vascular impressions laterally ramiform.

Discussion: Family group relationships for Trigonotretidae were discussed in Waterhouse (2004a, pp. 161-191). From analysis of ornament, including plication, costation and micro-ornament, delthyrial apparatus and interior including plates and vascular patterns, it was considered that the Trigonotretidae were to be distinguished from Neospiriferidae Waterhouse, whereas Carter (2006a, in Carter et al. 1994) had treated Neospiriferinae as a subfamily of Trigonotretidae. The revision of the spiriferids (s.l.) in the Treatise on Invertebrate Paleontology by Gouvennec & Carter (2007) focused on genera, and with the retirement of Carter, had little scope for consideration of new proposals, not to mention the inherent difficulty of coping with Gondwana genera without first hand examination.

Subfamily **TRIGONOTRETINAE** Schuchert, 1893

Diagnosis: This subfamily is distinguished from other member subfamilies by the better developed costae, which may, however, be limited to the anterior shell, or to the sulcus and fold.

Genus ***Grantonia*** Brown, 1953

Type species: *Grantonia hobartensis* Brown, 1953, p. 61 from Berriedale Limestone (Sakmarian), Tasmania, OD.

Diagnosis: Large transverse shells with strong persistent plicae, as a rule in three to five prominent pair, and minor additional plicae, costae variable in development, primary costae generally predominant, open delthyrium and large umbonal callosity.

Discussion: The genus *Grantonia* is found mostly in east Australia in beds of Early Permian age, and, as noted by Waterhouse (2004a, p. 171), material from the Early Permian of India appears to be congeneric. The genus has been synonymized with *Trigonotreta* Koenig since a study by Armstrong (1968b), as accepted by Carter (2006a, p. 1801). However *Grantonia* has a wider hinge with weakly alate extremities, better developed costae posteriorly, with higher primary costae, and fewer plicae pairs. Costae are much better developed and more numerous, whereas ventral plicae of *Trigonotreta* may be non-costate. The fold and sulcus of this genus contain one to three costae, compared with 10 or 12 in many *Grantonia*. The differences are clearly shown in a study by Clarke (1979) of the type species of *Trigonotreta* and *Grantonia*. The type species *Trigonotreta stokesii* has seven or commonly eight pairs of plicae, including two pair within the sulcus, and strong high few costae, and indeed in many aspects approaches *Unicostatina* and some species assigned to *Sulciplica*. *Grantonia hobartensis* has three to five pair of plicae, including one or rarely two pair in the sulcus and more costae, and approaches *Neospirifer* or *Betaneospirifer* in external appearance.

Allied genera are more distinctive. *Aperispirifer* Waterhouse, 1968a, p. 35 is a genus related to *Grantonia* and common in especially Middle Permian faunas of east Australia and New Zealand. It is distinguished from *Grantonia* by its fewer plicae, which fade anteriorly, and finer costae of which the primaries are inconspicuous. *Koenigoria* Waterhouse, 2004a, p. 173, type species *Neospirifer neoaustralis* Archbold & Thomas, 1986a is found in the Early Permian of Western Australia, and is characterized by its subtriangular shell with long and alate hinge, and deep ventral sulcus, bearing sulcal plicae that fade anteriorly, four lateral pair of plicae and strong primary costae. Like *Aperispirifer* it may have many costae, but is distinguished from that genus by the triangular shape and strong plicae. It is close to *Grantonia* apart from the triangular shape and deep sulcus. Another ally is *Trigorhium* Waterhouse, 2001, p. 92, a striking genus based on *Neospirifer amphigyus* Cooper & Grant (1976a, p. 2175, pl. 592, fig. 11, pl. 593, fig. 1-15, pl. 594, fig. 1-11), with very strongly alate and extended cardinal extremities and four to six pair of plicae, as well as three plicae within the sulcus in mature shells and deep split along crest of the dorsal fold. Costal crests are rounded. It is found in Middle Permian faunas of United States, and appears to have evolved as a geographic variant from *Koenigoria* (Waterhouse 2004a, p. 173).

The genus *Saltospirifer* Cisterna & Archbold, 2007, type species *S. guevarii* Cisterna & Archbold from the lower Del Salto Formation of Argentina was regarded as trigonotretid by its authors, but the very broad fold, overall shape, and aspects of costation and delthyrium suggest a likely relationship to *Cartorhium* Cooper & Grant, 1976a from the Glass Mountains, Texas, and also the allied genus *Ovispirifer* Waterhouse, 2004a, p. 99 from the Salt Range, Pakistan. Both are neospiriferid rather than trigonotretid.

Grantonia cracovensis Wass, 1966

Fig. 143B, D, F, 145C, 146B

1964b *Grantonia* cf. *hobartensis* [not Browne] – Hill & Woods, pl. P8, fig. 6, 7 (part, not fig. 8 = *australis* (Bion).

1966 *G. cracovensis* Wass, p. 98, pl. 3, fig. 6-11.

1972 *Trigonotetra stokesi* [not Koenig] – Hill, Playford & Woods, pl. P8, fig. 6, 7 (part, not fig. 8 = *australis* (Bion)).

1986 *T. cracovensis* – Parfrey, p. 60, Fig. 2.4a-d.

1987a *T. cracovensis* – Waterhouse, p. 16, pl. 3, fig. 6-13, ?15-?17.

Holotype: UQF 43392 from Fairyland Formation (Sakmarian), Cracow, figured by Wass (1966, pl. 3, fig. 7), OD.

Diagnosis: Subelongate as a rule, plicae include pair within sulcus and three lateral pair with weak outer pair in ventral valve, interspaces narrow, dorsal plicae high and persistent and interspaces moderately developed, primary costa prominent along crest of plicae.

Material: A few Tiverton specimens from LT3 (that part equivalent to UQL 4508?) and UQL 4508; UQF 66018. *Bookeria pollex* Zone and possibly younger, LT3 being of uncertain position.

Dimensions in mm:

UQL	Width	Length	Length dorsal	Height dorsal
LT3	61	52	42	18

Description: Shells not fully mature, most weakly transverse, apart from one transverse specimen (Fig. 143F), having incurved ventral umbo with angle of more 100°, and well formed interarea largely in plane of commissure, incurved under beak, with broad open delthyrium with angle of 80-90°; ventral interarea at high angle to dorsal interarea, which has broad notothyrium. Cardinal extremities alate where well preserved, but usually appear obtuse because of wear. Ventral sulcus broad, overall concave floor, widening forwards at 30° but without the anterior flare that characterizes the sulcus of many spiriferidins, probably because the specimens are not fully mature. The dorsal fold is moderately high with sharply rounded crest. There are three pair of ventral plicae, together with a narrower pair incorporated within the sulcus, and a very weak outermost plication in the transverse specimen. In the dorsal valve there are three pair of plicae, and an innermost pair sited close to or on the flanks of the dorsal fold. Costae cover both valves, with primary costae especially broad and passing along the crest of the plicae. Further costae arise on the flanks, with three costae over much of the length of the plicae, and the median costae splitting near the anterior margin. The lateral flanks bear costae that branch rarely. Commarginal growth increments are well developed, numbering two to three in 1mm, and fine radial filae are present.

Internal detail is unexceptional, with moderately developed dental plates, very short adminicula largely buried in secondary shell, adductor and diductor scars. The dorsal valve has socket and crural plates and low median septum, and small laminate ctenophoridium.

Resemblances: In many respects *Grantonia cracovensis* is close to *G. australis* (Bion) and *G. hobartensis* (Brown). Differences are that the present specimens assigned to *G. cracovensis* tend to be more elongate with less alate cardinal extremities, although transverse specimen are occasionally found in association (see Fig. 143F). The dorsal plicae especially tend to have narrower interspaces, and the primary costae tend to be slightly lower. The Tiverton specimens come close to the type material from the Fairyland Formation of the southeast Bowen Basin in shape and sulcus, but the outermost plication is better developed, perhaps because of greater maturity, and costae appear to be finer, but only at a larger size. Internally the ventral muscle field is not so wide, or the flanks diverge more anteriorly from a narrow posterior end in *cracovensis* as compared with *australis*. None of these differences are very substantial, and further enquiry on the validity of *cracovensis* is needed. The specimens described by Waterhouse (1987a, pl. 3, fig. 15-17) from the Dresden Formation, southeast Bowen Basin, are too small to allow certain identification, so that it is not certain whether the species ranged above the *Echinalosia curtosa* Subzone and Fairyland Formation.

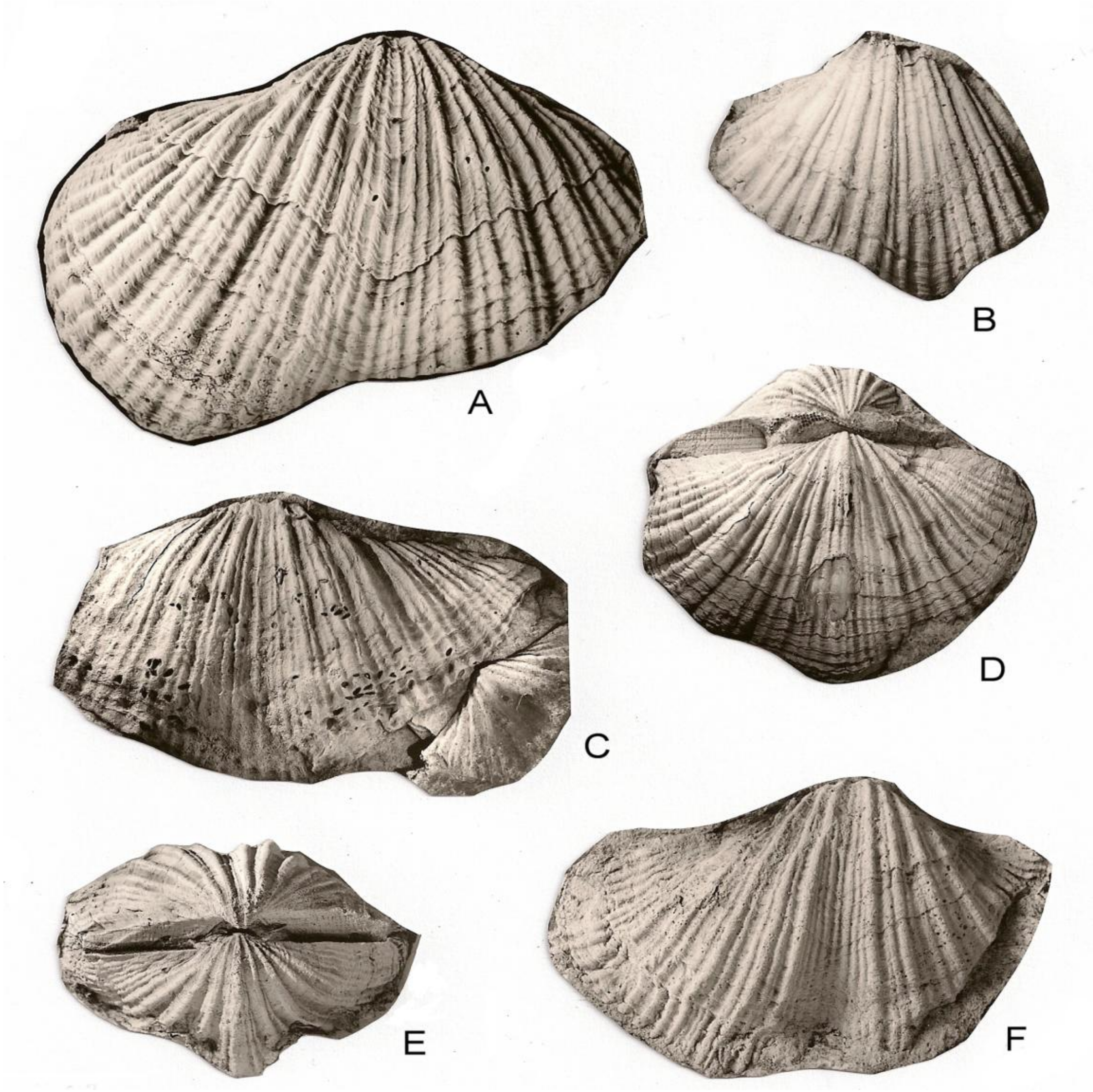


Fig. 143. A, C, E, *Grantonia australis* (Bion). A, latex cast of ventral valve UQF 20998 from UQL 1623, x2. C, latex cast of ventral valves including UQF 81360 from UQL 1628, x2**.** E, dorsal aspect of latex cast of UQF 81366 with valves conjoined, from UQL 1622, x0.66. B, D, F, *Grantonia cracovensis* Wass. B, latex cast of ventral valve UQF 81359 from LT3, x2. D, dorsal aspect of latex cast of specimen with valves conjoined UQF 81363 from LT3, x1. F, latex cast of ventral valve UQF 81362 from LT3, x1, associated with *cracovensis* but as transverse as *australis*, found in younger beds.

Grantonia australis (Bion, 1928)

Fig. 143A, C, E, 144, 145 A, B, D, 146A, 147 - 151

1892 *Spirifer stokesii* [not Koenig] – Etheridge, p. 232, pl. 10, fig. 2, 3, pl. 39, fig. 2-4 (part, not pl. 10, fig. 4 = indet.).

1928 *S. stokesii* var. *australis* Bion, p. 30.

1964b *Grantonia* sp. Hill & Woods, pl. P8, fig. 8.

1968b *Trigonotreta stokesi* [not Koenig] – Armstrong, p. 83, pl. 6, fig. 1-3, 5 (part, not fig. 4 = *stokesii*).

1970b *Trigonotreta stokesi* – Armstrong, p. 205, pl. 15, fig. 3, 5, 6, 7, 8.

1972 *T. stokesi* – Hill, Playford & Woods, pl. P8, fig. 8 (part, not fig. 6, 7 = *cracovensis*).

1974 *T. cracovensis* – McCarthy et al. Fig. 4F.

1987a *T. australis* – Waterhouse, p. 17, pl. 3, fig. 14?, 18-20, pl. 4, fig. 1-3, ?4, 5, 6.

2004a *G. australis* – Waterhouse, p. 170.

2015 *G. australis* – Waterhouse, p. 136, Fig. 53, 54.

Holotype: For *australis* Bion not Foord: GSQ F 1480 figured by Etheridge (1892, pl. 39, fig. 2-4), Hill & Woods (1964b, pl. P8, fig. 8) and Hill, Playford & Woods (1972, pl. P8, fig. 8) from Tiverton Formation, Homevale, Queensland, OD.

Diagnosis: Transverse shells with pair of sulcal plicae and three to five well formed lateral plicae bearing high and often broad primary costae, well defined growth lamellae, fold high with narrow crest, adminicula short and well spaced.

Material: Specimens from UQL 1383, 1621, 1622-1626, 1628, 1634?, 2584, 2626, 2628, 2631, 2635, 3127, 4510 – 4519; UQF 66020 and possibly 66921. *Bookeria geniculata* and lower *Taeniothaerus subquadratus* Zones.

Dimensions in mm: means, n = 10, ventral valve.

Width	Length	Height
54	42	30

Fig. 144. *Grantonia australis* (Bion), dorsal internal mould UQF 81445 from UQL 3127, x2, tilted posteriorly to show cardinalia.

Description: Shells large, cardinal extremities rounded or weakly alate, ventral umbo incurved, angle close to 100°, ventral interarea moderately high, curving from approximate right angle to commissure to lie almost within the plane of the commissure, marked by low horizontal striae and usually weak subvertical striae, hinge weakly denticulate (see Armstrong 1970b, pl. 15, fig. 6), delthyrium obscure and apparently open, with broad umbonal callosity, angle 90-100°, bordered by ridges formed by tooth tracks, the delthyrial edges may be disrupted by shallow indentations and bulges, which are growth irregularities that may reflect vicissitudes of attachment. In UQF 66020 there seems to be a narrow plate below the delthyrial edge on each side, forming an double elongate narrow triangle. Some specimens weakly alate, others with rounded cardinal extremities. Dorsal valve moderately inflated, interarea low, at right angles to commissure, planar in small specimens, becomes concave and curves to lie subparallel to commissure in large specimens, subvertical striae may be strong, notothyrium broad and low with angle of 100-110°. Ventral sulcus commences at beak, angle about 35°, no specimens preserved that show wide anterior flaring, as possibly no specimens were collected that had reached late maturity, floor narrow with median rib as a rule. Ventral plicae form four or usually five prominent pair, arising at umbo

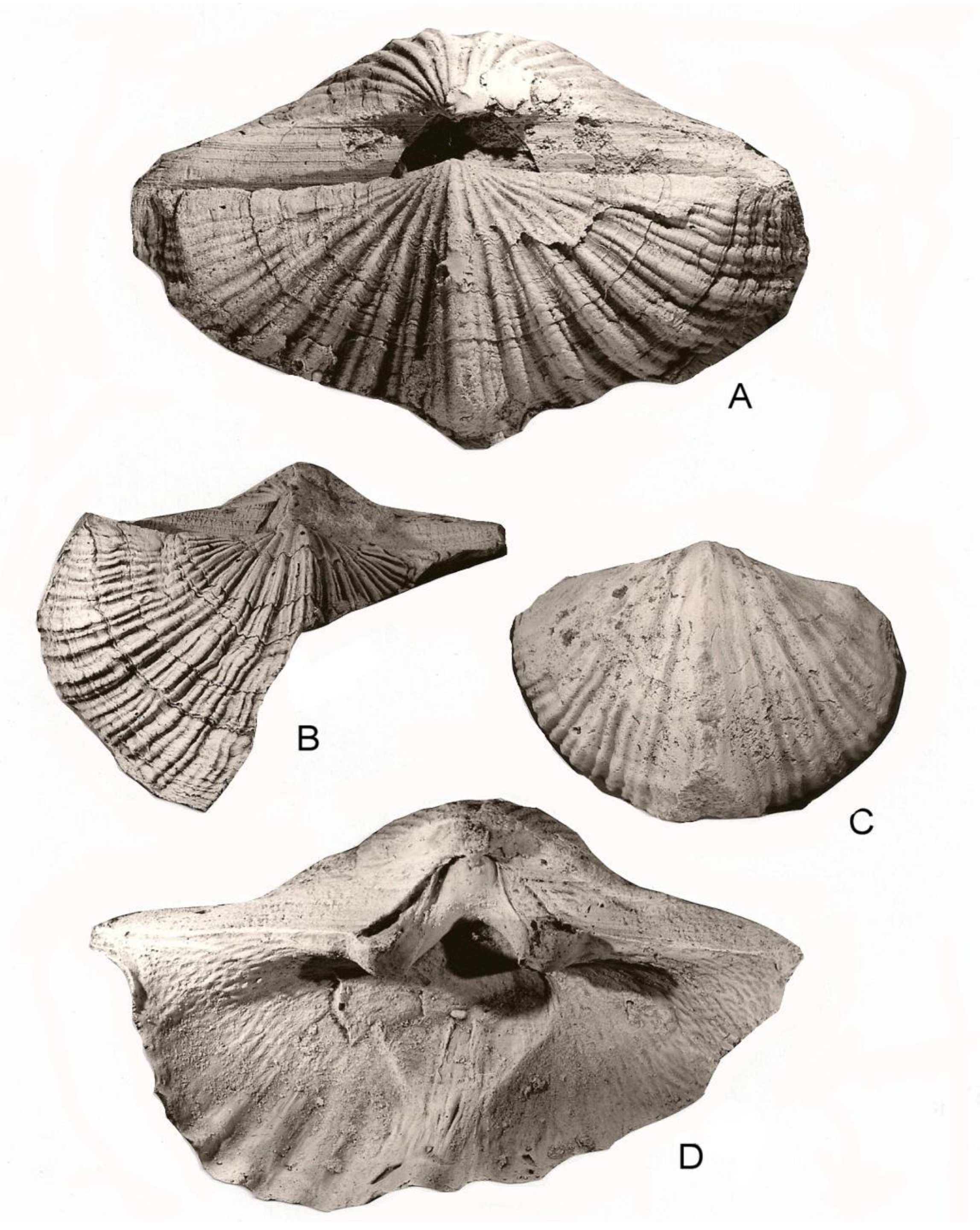


Fig. 145. A, B, D, *Grantonia australis* (Bion). A, dorsal aspect of latex cast of UQF 21107 from L 1626, valves conjoined, x2. B, dorsal aspect of latex cast of UQF 21070 with valves conjoined from UQL 1626, x1. D, latex cast of ventral interior, UQF 81367 from UQL 3127, x2. C, *Grantonia cracovensis* Wass, dorsal aspect of internal mould, UQF 66018 (see p. 350), x1.

and persisting to the anterior margin. The innermost pair is narrower than the second pair, and as a rule becomes incorporated within the sulcus, diverging at 20^o. The next three pair are well developed, and an outermost pair is subdued to scarcely differentiated. Rare specimens, less than 5% of the samples, have a weak sixth plication, including a dorsal valve from UQL 3127, and a ventral valve from UQL 2622. Costae are well developed, and the primary costa, coinciding with the crest of the plication posteriorly, remains high and broad for most or all of the length of the shell. Secondary costae arise at 10 up to 30mm from the umbo, and become more numerous and prominent on the inner rather than the outer side of plicae. Crests are rounded and flanks high and steep. Three to five costae lie within the sulcus between the innermost plicae, and a very few costae lie laterally beyond the plicae. On the dorsal valve the innermost plicae pair remains narrow and placed close to the fold, and may be incorporated in the fold anteriorly, or may remain discrete. Lateral plicae are prominent, usually in four pair, often in three pair, rarely five pair, and tend to be more symmetrical than on the ventral valve, with primary costa remaining conspicuous; outer costa well developed, may split more than inner costae (UQF 66020), though this varies. Commarginal laminae are well developed, as well as fine radial capillae, poorly preserved, but apparently six to eight in 1mm anteriorly.

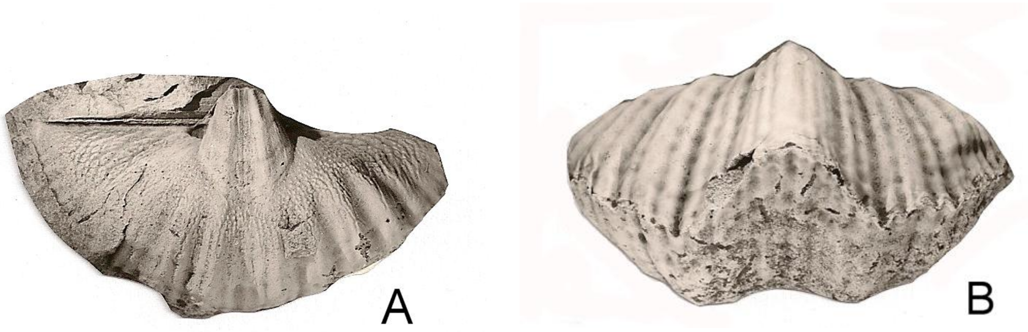


Fig. 146. A, *Grantonia australis* (Bion), ventral internal mould UQF 81365 from UQL 3127, x1.1. B, *G. cracovensis* (Wass), anterior view of internal mould with valves conjoined, dorsal valve on top, UQF 81364 from LT3, x1.

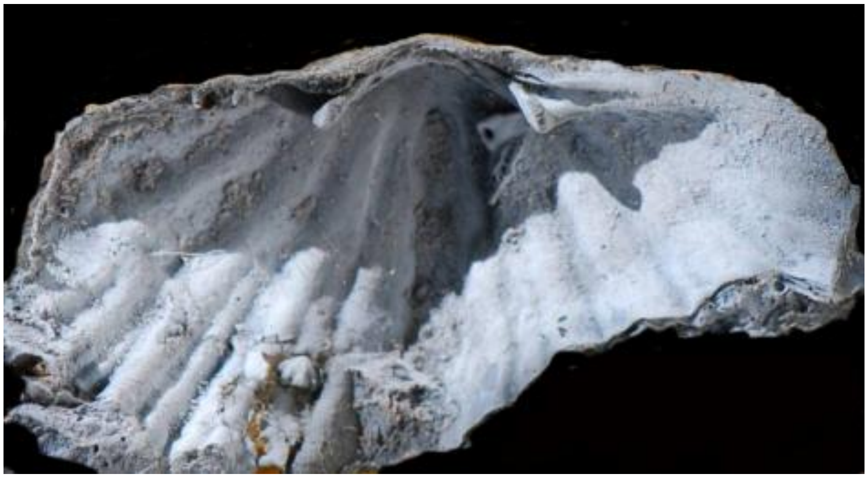


Fig. 147. *Grantonia australis* (Bion), latex cast of dorsal interior, UQF 81848 from UQL 1626, x2.

Teeth supported by scapular-shaped dental plates which diverge at 70°, and are supported by weakly diverging short adminicula, which become buried in secondary shell. Muscle field moderately broad but elongate in some large specimens, adductor scars poorly differentiated, elongate, generally two ridges with weakly concave or convex surface, smooth or linearly striate, no well developed myophragm, diductor scars broad, with growth undulations parallel to anterior margin, and faint longitudinal and rarely more complex grooves and ridges. Posterior shell thick and floor marked by pits,

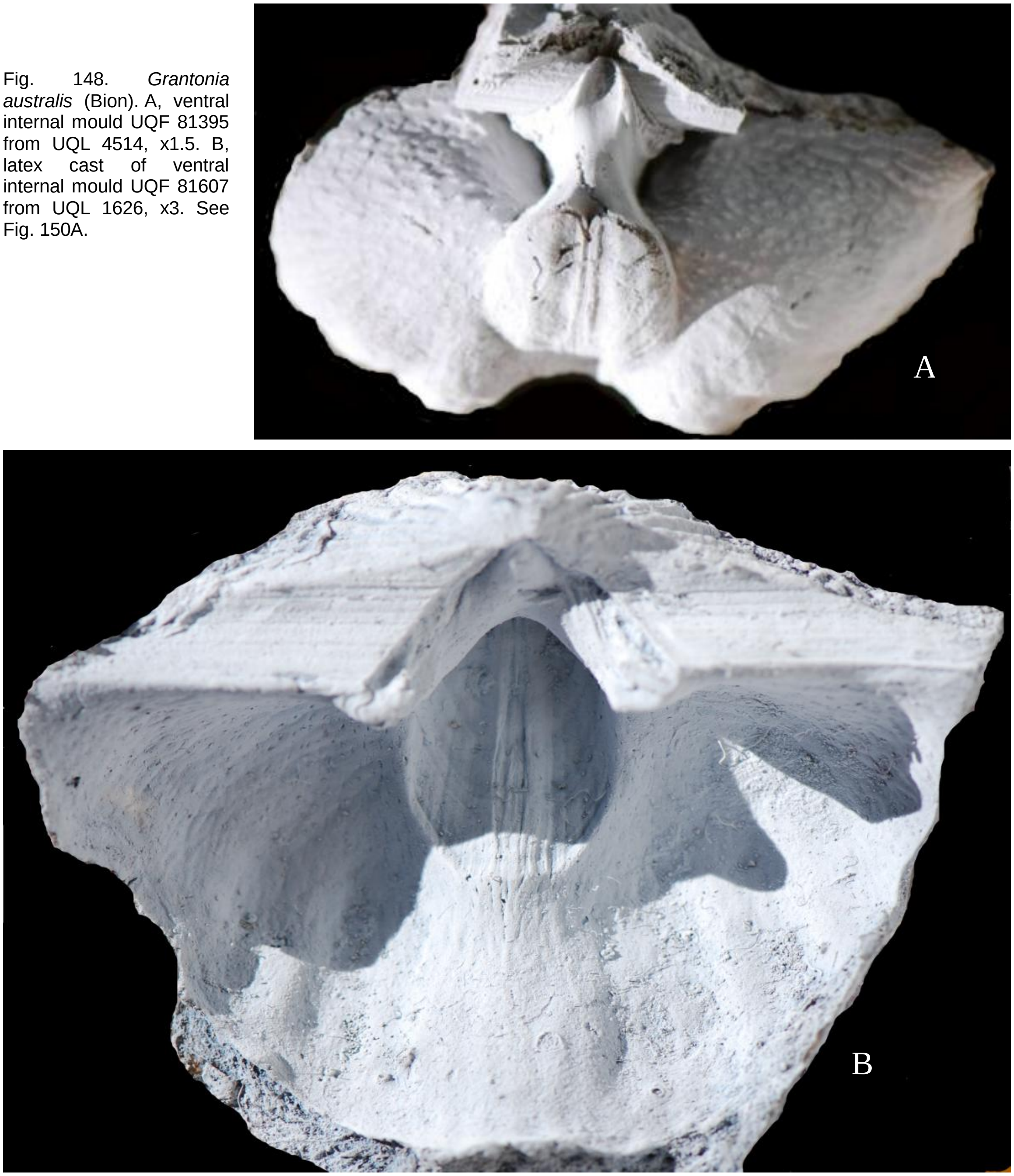


Fig. 148. *Grantonia australis* (Bion). A, ventral internal mould UQF 81395 from UQL 4514, x1.5. B, latex cast of ventral internal mould UQF 81607 from UQL 1626, x3. See Fig. 150A.

but ramiform vascular impressions present in only a few specimens, and rarely preserved. In dorsal valve, ctenophorium large and well developed, dental sockets enclosed between horizontal plates and vertical or subvertical crural plates which diverge forward at 90^{o}, crura pass along lower edge of plates, spire not revealed. Median septum only one fourth to one fifth of shell length, slender, adductor scars weakly impressed, finely striate, poorly delineated. Shell floor without conspicuous pits or markings.

Resemblances: This description is the first available for the Homevale taxon named *australis* by Bion (1928), apart from some features particularized by Armstrong (1970b) for specimens misidentified as *Trigonotreta stokesii*. Material from the Elvinia Formation of the southeast Bowen Basin was described by Waterhouse (1987a), but it is not well preserved.

Specimens from the Rose's Pride Formation that were included do not appear close, especially the finely ribbed and lamellate ventral valve figured in Waterhouse (1987a, pl. 3, fig. 14, pl. 4, fig. 4), and these may belong to *Kaninospirifer.* The Tiverton specimens are similar in essential detail to *Grantonia hobartensis* as figured from the Berriedale Limestone of Tasmania by Brown (1953, p. 61, pl. 6, fig. 1-9), Spry & Quilty (1963, Fig. 1) and Clarke (1979, p. 200, pl. 3, fig. 1-9). Additional material was figured and described as *stokesi* by Armstrong (1968b, p. 83, pl. 6, fig. 1-3, 5 (part, not fig. 4 = *stokesii*) and 1970b, p. 205, pl. 15, fig. 3, 5-8 (part, not pl. 15, fig. 6 = *stokesii*). Compared with *hobartensis*, the Queensland shells are transverse and may have an additional or better developed pair of plicae laterally. The ventral muscle field is broad in the specimens of *hobartensis* figured by Clarke (1979), with subparallel flanks, and the same is true of only some of the fully mature specimens of *australis* from the Tiverton Formation. The two taxa are kept separate, but only provisionally, given the uncertainty over variation for topotype Tasmanian *hobartensis.*

Grantonia cracovensis Wass, 1966 from the Fairyland Formation and Camboon Andesite (Parfrey 1986) of southeast Bowen Basin has strong high close-set plicae and usually more elongate outline. The species was kept separate from *australis* Bion by Parfrey (1986) and Waterhouse (1987a, pp. 16-18) but criteria considered significant for discrimination are not fully invariant. An internal mould from the Emu Creek beds near Drake, New South Wales, that was ascribed to *cracovensis* by McCarthy et al. (1974, Fig. 4F) appears to be identical with *australis*.

Maxwell (1964, pl. 8, fig. 19-22, pl. 9, fig. 18-25) compared specimens from the Yarrol Formation of the Yarrol Basin to *hobartensis*, *Trigonotreta* sp, and *stokesii*, but the specimens are difficult to evaluate from figures, being small and somewhat incomplete, and they include *Unicostatina* or ally. The species *australis* is found in the Teebar unit of Brown (1964) and Cranfield (1989) in the Gigoomgan area of the Gympie Province in southeast Queensland, but not in the Rammutt Formation, which has no faunas that match the middle and upper Tiverton faunas.

Fig. 149. *Grantonia australis* (Bion). A, internal mould of broken dorsal valve UQF 81369 from UQL 3127, x3. B, external mould of dorsal valve UQF 81617 from UQL 3127, x3.

Taxonomy: In a monograph of Permian fossils from Kashmir of India, Bion (1928, p. 30) proposed a subspecies *Spirifer stokesii* var. *australis* for a species illustrated by Etheridge (1892) from the Tiverton Formation at Homevale, as also noted by Hosking (1931) and Reed (1944), and then forgotten until pointed out by Waterhouse (1987a). Bion's varietal name *australis* was the same as that applied by Foord (1890, p. 147, pl. 7, fig. 2) for *Spirifera musakheylensis* Davidson var. *australis* var. nov. As the name was applied to a different species, *stokesii* not *musakheylensis*, it appears that both names potentially have validity if elevated to species rank and especially if belonging to different genera, as is the case. As regards *musakheylensis australis*, the name has been allowed to lapse, Archbold & Thomas (1986a, p. 128) referring Foord's taxon to synonymy of *Neospirifer hardmani* (Foord, 1890), later repositioned as *Quadrospira*. Bion's name, applied to a different species and genus, still retained potential validity, when applied by Waterhouse (1987a) to a full species.

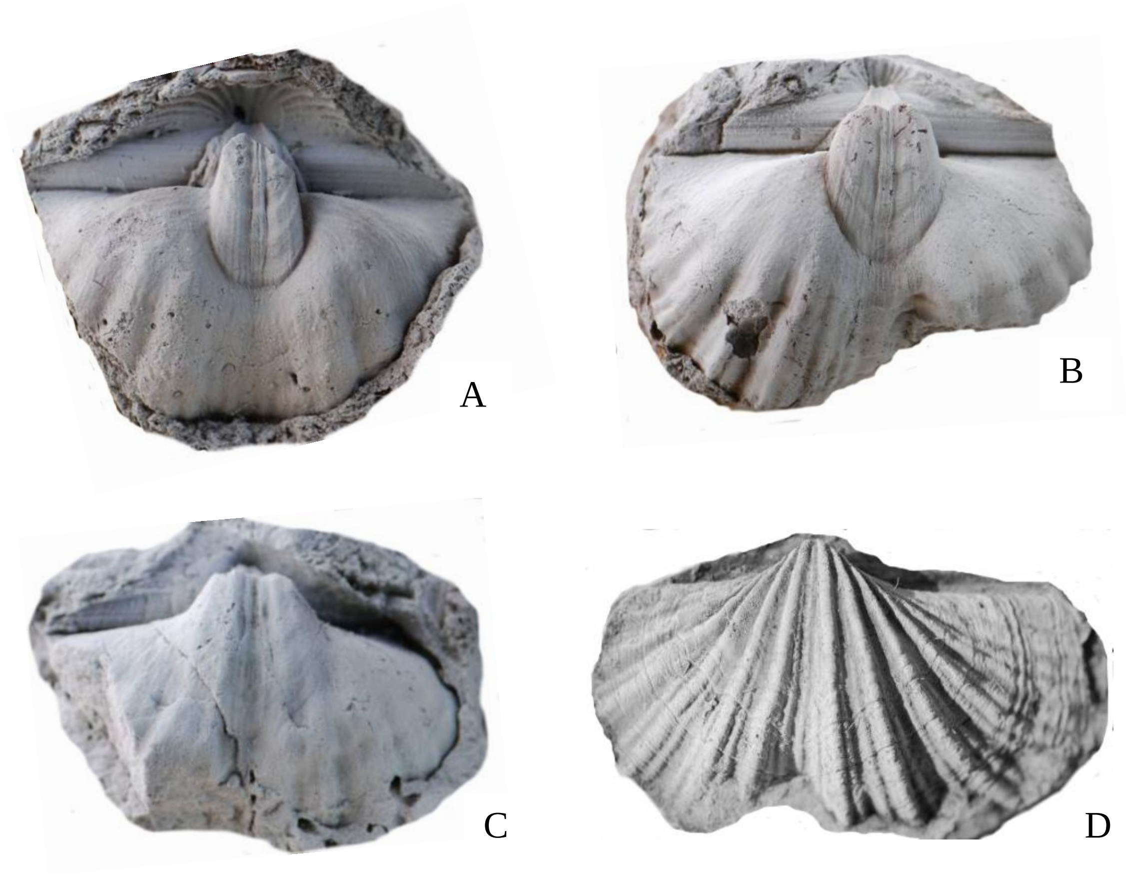


Fig. 150. *Grantonia australis* (Bion), A – C, ventral internal moulds. A, UQF 81607 from UQL 1626, x1.1. B, UQF 81367 from UQL 3127, x1. C, UQF 81368 from UQL 1626, x1. D, latex cast of ventral exterior UQF 81446 from UQL 1621, x1.5.

Fig. 151. *Grantonia australis* (Bion), latex cast of dorsal valve UQF 81617 from UQL 3127, x4.

Subfamily **ANGIOSPIRIFERINAE** Legrand-Blain, 1985

Diagnosis: Shells transverse, plicae numerous, simple or subcostate, sulcus and fold plain or costate, micro-ornament of radial lirae and commarginal laminae. Delthyrium open with large callosity, reduced or no delthyrial plate, dental plates supported by short adminicula, crural plates and sockets moderately developed, no tabellae. Vascular impressions ramiform or weakly to moderately reticulate.

Discussion: This subfamily appears to be very close to Trigonotretinae Schuchert, 1893, but its shells are less costate. The two subfamilies were extensively discussed by Waterhouse (2004a) and it is here suggested that *Brachythyrinella* Waterhouse & Gupta should be transferred to Angiospiriferinae from Trigonotretinae. Costuloplicinae Waterhouse, 2004a, p. 187 involves plicate shells with very low costae, and a delthyrium blocked by low umbonal callosity passing into low pleromal plates or ridges. Sergospiriferinae Carter in Carter et al. (1994) is difficult to distinguish from Angiospiriferinae, even though Carter (2006a) placed Sergospiriferinae in Spiriferidae, and Angiospiriferinae in Choristitidae. Ramiform vascular tracks, short adminicula, and lack of tabellae do not typify Choristitidae, but do conform with Trigonotretidae.

Tribe **ANGIOSPIRIFERINI** Legrand-Blain, 1985

Diagnosis: Transverse shells with round-crested plicae bearing no costae, sulcus and fold smooth or costate.

Discussion: This group is distinguished from Georginakingiini Waterhouse 2004a, p. 184, which incorporates transverse shells with somewhat fastigate plicae bearing a few costae arising well in front of the umbones.

Genus ***Unicostatina*** Waterhouse, 2004a

Type species: *Sulciplica subglobosa* Clarke, 1990, p. 64 from “Spirifer Zone” (Asselian), Darlington, Maria Island, Tasmania, OD.

Diagnosis: Moderately large transverse shells with well rounded cardinal extremities, few strong plicae and one sulcal costa, may be joined by feeble further costae within the sulcus and over the fold.

Discussion: Compared with *Sulciplica* Waterhouse, *Unicostatina* encompasses smaller less transverse shells with narrower hinge, obtuse to weakly alate cardinal extremities, several strong non-costate plicae pairs and sulcus bearing one major costa. The micro-ornament on both genera is comprised of radial lirae and commarginal growth increments and laminae, which rarely appear pustulose. Internal plates are as in most other Spiriferoidea, and secondary thickening is heavy posteriorly in the ventral valve.

This genus was placed in Family Choristitidae by Gouvennec & Carter (2007, p. 2781). But it displays delthyrial apparatus, vascular markings, and costation detail as in Trigonotretidae, whereas choristitids lack vascular markings and may have tabellae and differ in plication-costation, micro-ornament and delthyrium, aspects which strongly suggest membership of a different superfamily (see Waterhouse in prep.).

Unicostatina stutchburii (Etheridge, 1892)

Fig. 152 – 158

1892 *Spirifera stutchburii* Etheridge, p. 232, pl. 38, fig. 4-6.
1968a *Sulciplica stutchburii* – Waterhouse, p. 24.
1970b *S. stutchburii* – Armstrong, p. 205, pl. 15, fig. 1.
2004a *S. stutchburii* – Waterhouse, p. 183.
2015 *Unicostatina stutchburii* Waterhouse & Balfe, p. 103.

Holotype: Sole specimen figured by Etheridge (1892) from Tiverton Formation, SD Waterhouse (1968a, p. 24). Kept at Queensland Museum, Brisbane.

Diagnosis: Comparatively small transverse shells with six to eight pair of plicae, tending to have subrounded crests, deep sulcus with central rib and in some shells, two faint lateral costae.

Material: Specimens from UQL 1383, 1622, 1626, 1628, 1630, ?2127, 2584, 2619, 2622, 2623, 2625, 2631, 2884, 3127, 3129, 3720, 4510 - 4515, 4518 - 4521 and LT3 and UQF 55884. The species is found chiefly in the *Bookeria geniculata* Zone and rarely in the *Taeniothaerus subquadratus* Zone.

Dimensions in mm: ventral valves, means, n = 10

Width	Length	Height
43	29	16
	Dorsal valves, n = 7	
26	14	4

Fig. 152. *Unicostatina stutchburii* (Etheridge), latex cast, dorsal aspect of UQF 81610 from UQL 4512, x3.

Description: Shells of moderate size for genus, transverse with moderately incurved ventral umbo and posterior walls diverging at 100-110°, concave posteriorly in outline, cardinal extremities obtuse, ventral interarea concave under umbo, largely in plane of commissure, interrupted by delthyrium bordered by delthyrial rims and opening at angle of 60-70°. Dorsal interarea low, inclined posteriorly from commissure, notothyrium opening at 150°. Sulcus commences at umbonal tip and widens at angle of 25-30°, with broadly concave floor bearing single costa that commences posteriorly, two low costae commencing anteriorly on the flanks in some specimens. Dorsal fold upstanding, groove developed along the crest of many but not all specimens, and two costae lie each side, one along the crest and one below, or more rarely, two or three costae only. Plicae on both valves generally number six pair, up to seven or eight, covering all but lateral posterior

Fig. 153. *Unicostatina stutchburii* (Etheridge) latex cast of ventral valve with denticulate hinge, UQF 81456 from UQL 1383, x3. See Fig. 156A.

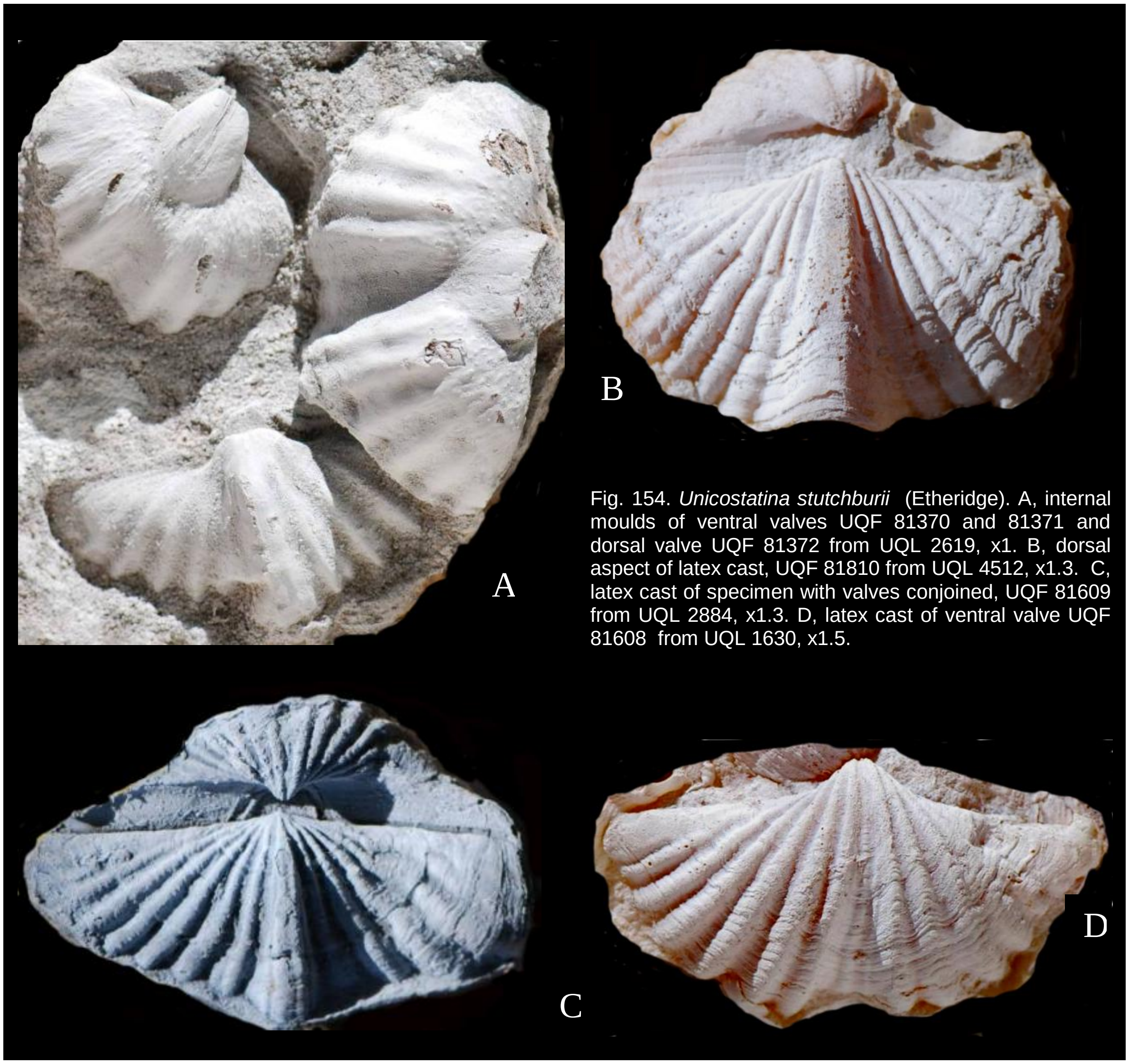


Fig. 154. *Unicostatina stutchburii* (Etheridge). A, internal moulds of ventral valves UQF 81370 and 81371 and dorsal valve UQF 81372 from UQL 2619, x1. B, dorsal aspect of latex cast, UQF 81810 from UQL 4512, x1.3. C, latex cast of specimen with valves conjoined, UQF 81609 from UQL 2884, x1.3. D, latex cast of ventral valve UQF 81608 from UQL 1630, x1.5.

shell, with rounded crests and outward sloping flanks, and concave interspaces. Rarely a costation appears along the anterior part of a plication. Micro-ornament of fine radial capillae, 12 per mm posteriorly, and fine growth increments, 10-12 per mm, within 10mm of dorsal umbo, crossed by prominent commarginal lamellae, which appear to be developed at six or seven increments per lamellum, but some lamellae spaced further apart. The arrangement suggests that shells reached 10mm length in six months, maturity in a year, and continued growth for at least three more months, assuming that the increments appeared on a daily basis. Compared with Productida, growth in size appears to have been much more rapid.

Delthyrium closed under umbo by two pleromal thickenings passing along the dental plates and fusing under the umbo. Dental plates scapular-shaped, supported by short adminicula buried in secondary shell which is very thick posteriorly. Muscle field narrow, ill-defined adductor scars and diductor impressions, posterior floor pitted, no specimens showing vascular impressions. The posterior shell is substantially thickened, up to 5mm posteriorly, compared with anterior shell 1mm thick, in a specimen 40mm wide.

Ctenophoridium broad and laminate, dental sockets slender, horizontal outer socket plates, inclined crural plates and long low median septum. Inner anterior adductor scars subquadrate, striate, posterior outer pair obscure.

Fig. 155. *Unicostatina stutchburii* (Etheridge) latex cast of dorsal valve UQF 43442 from UQL 2584, x2.

A few ventral valves, including specimens from UQL 1627, 2619 and 4515 and UQF 20812 from L 1622, have five or six pair of plicae and a single costa along the sulcus. The fold in these specimens, only preserved posteriorly, has no costae. The specimens do not vary noticeably in other respects from *Unicostatina stutchburii*, and are interpreted as variants, but might prove to be a separate subspecies or species, characterized by having one or two pair of plicae fewer than typical of the species. They resemble *Unicostatina* as described by Archbold (2003) from Cranky Corner, New South Wales, and so might represent hold-overs of that species, or variants of *stutchburii*.

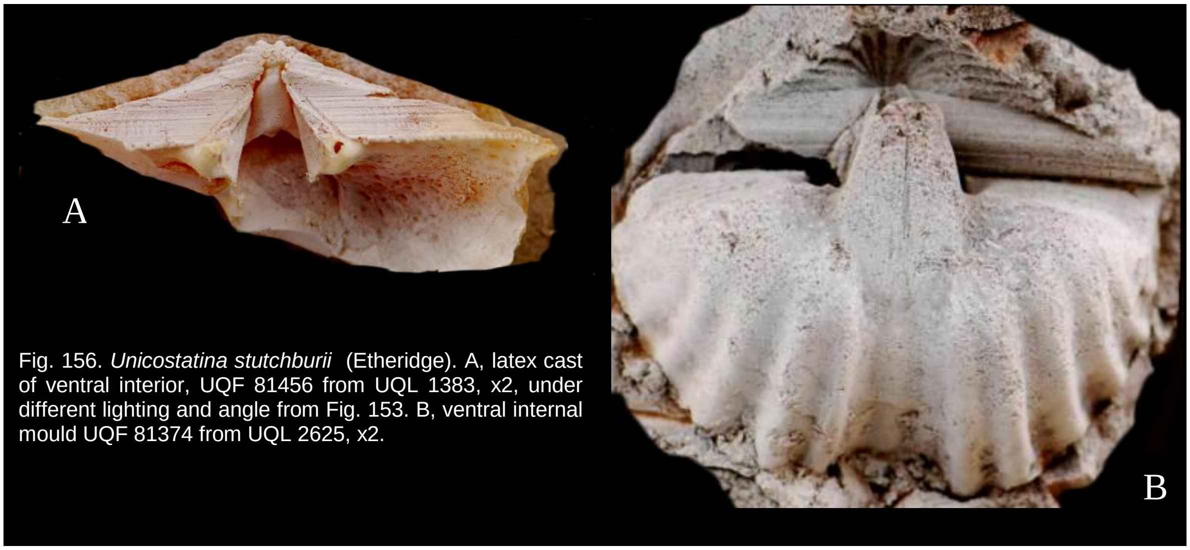
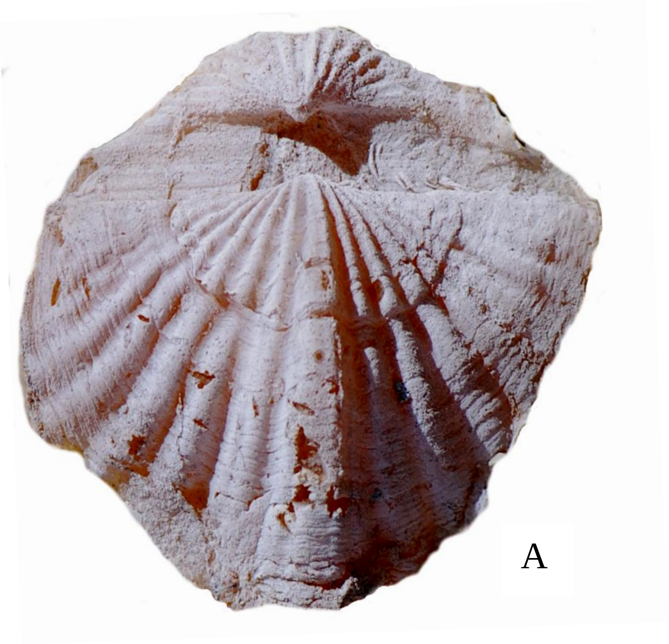


Fig. 156. *Unicostatina stutchburii* (Etheridge). A, latex cast of ventral interior, UQF 81456 from UQL 1383, x2, under different lighting and angle from Fig. 153. B, ventral internal mould UQF 81374 from UQL 2625, x2.

Resemblances: This species is scarcely distinguishable from *Unicostatina crassa* (Clarke, 1990, p. 64, Fig. 8A-N; 1992a, p. 19, Fig. 8) as far as that species is known. The Tiverton specimens are slightly younger, Sakmarian rather than late Asselian. Shape is similar, and there are much the same number of plicae. The fold of the dorsal valve of the Tasmanian species is not known, and the fold for Cranky Corner specimens, identified by Archbold (2003) with *crassa*, is well rounded with no sign of costae, unlike that on many specimens of *stutchburii*.

Unicostatina chatsworthensis (Balfe & Waterhouse, 2004) from the Late Permian South Curra Limestone of Gympie is more costate, and further comparisons are provided in Waterhouse & Balfe (2015).

Fig. 157. *Unicostatina stutchburii* (Etheridge). A, dorsal aspect of internal mould with valves conjoined, UQF 81375 from UQL 3127, x3. B, latex cast of ventral posterior, UQF 81432 from LT3, x 2. C, detail of micro-ornament in ventral valve UQF 81624 from UQL 4519, x7.



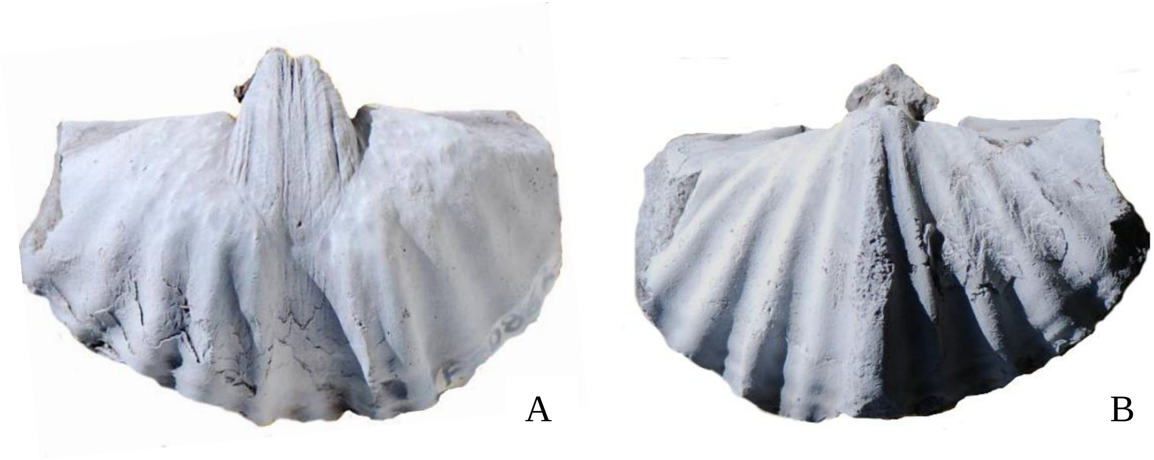


Fig. 158. *Unicostatina stutchburii* (Etheridge), ventral and dorsal views of internal mould UQF 20862 from UQL 1622, x1.75.

Order SPIRIFERINIDA Ivanova, 1972

Ivanova (1972, p. 41) proposed suborder Spiriferinidina, and excluded Syringothyroidea (Syringothyridoidea) and included Cyrtinoidea. Cooper & Grant (1976b, p. 2666) recognized Order Spiriferinida, and included only Retziidina and Spiriferinidina, the latter mistakenly thought to be a new proposal, and made no mention of syringothyrids or cyrtinoids. The presently accepted order was in fact established by Carter & Johnson in Carter et al. (1994), consolidated by Carter (2006b), and elaborated by Carter & Gouvennec (2006c).

Suborder SYRINGOTHYRIDINA Grunt, 2006b

Diagnosis: Large narrowly plicate spiriferiform shells with well developed interareas, often high in ventral valve, and may display perideltidial areas, micro-ornament of fine short radial striae and elongate pustules or spinules, dental plates and adminicula well developed, no tabellae, median ventral septum rare, syrinx may be developed, punctae generally fine if present.

Discussion: The proposal by Grunt (2006b, p. 158) to separate Superfamily Syringothyroidea from Spiriferinidina Ivanova, 1972 is accepted. The latter suborder involves genera of Pennospiriferinoidea and Spiriferinoidea that as a rule are smaller, with fewer plicae or no plicae, median septum, no syrinx, no perideltidial areas, and with punctae that are more varied in size, and micro-ornament much more diverse in character, including development of strong commarginal lamellation. Spiriferinidina ranged from Upper Devonian to Lower Jurassic, whereas Syringothyridina ranged from Upper Devonian to Permian. The other suborder, Cyrtinidina Carter & Johnson, 1994 is of varied appearance, smooth or plicate lateral slopes, subconical or hemipyramidal in early forms, variable in younger, with delthyrium generally covered in early genera, more variable in younger forms, and elevated adductor attachment structures in the ventral interior. It ranged from Lower Devonian to Lower Jurassic. The interrelationships between the three suborders are well shown by Carter & Gouvennec (2006c, Fig. 1251) and of the three groups, the Syringothyridina, classed by them as Syringothyridoidea, is the most compact and least diverse.

Licharewia and allies, classed in Licharewiidae Slusareva, 1958, were treated as a family within Syringothyridoidea by Carter (2006b, p. 1906), and were promoted to a superfamily by Grunt (2006b), correctly in my opinion, because the shell is impunctate, unlike syringothyrids. Indeed Waterhouse & Waddington (1982, p. 11) considered that licharewiids were close to spiriferellids in many respects, although the prevailing view is that this is due to convergence from different stock. Gourvennec & Carter (2007, p. 2796) considered that the difference between Licharewioidea and Syringothyroidea centred on the presence of a perideltidial area, but this seems dubious.

Superfamily **SYRINGOTHYROIDEA** Fredericks, 1926

Family **SYRINGOTHYRIDAE** Fredericks, 1926

Diagnosis: Transverse finely punctate shells with high ventral valve, low dorsal valve, high ventral interarea with perideltidial area as a rule, fold and sulcus smooth or costate, plicae fine and numerous, adminicula present.

Discussion: Carter (2006b) followed by Gouvennec & Carter (2007) stressed the presence of perideltidial areas as a prime distinction from Licharewiidae Slusareva, but dense punctation is a more amenable criterion. It is not clear that all densely punctate species and genera now associated with Syringothyrididae, and especially within Permasyrinxinae, have perideltidial areas.

Taxonomy: Ivanova (1959, p. 55) promoted Syringothyrinae Fredericks to Family Syringothyridae, which was amended to Syringothyrididae by Pitrat (1965, p. 691). The “id” nowadays seems redundant. The ICZN (1999) proposes to allow omission of the id for taxa proposed after 1999, but this will encourage a medley of names, including introduced and omitted “id”. In my view, the simpler, the better. It does seem that the arcane if splendid rules of nomenclature, where centred on Latin grammar, are of a past age, no longer enforceable, and no longer desirable.

Subfamily **PERMASYRINXINAE** Waterhouse, 1986b

Diagnosis: Syrinx absent, perideltidial areas variably defined or not developed.

Discussion: This subfamily lacks the syrinx found in Syringothyrinae, and lacks the high median septum and syrinx found in the ventral valve of Septosyringothyrinae. According to Carter et al. (1994, p. 366), most genera of the family fall within this subfamily, which is widespread, and ranged from Early Carboniferous to Late Permian in age, but there is a division between genera with a calcite rod or syrellum, and those without. The perideltidial area is well developed in *Syringothyris*, but appears to be lacking from some species of *Permasyrinx*. A connector plate lies across the delthyrium, extending between the junctions of the adminicula and dental plates.

Genus ***Permasyrinx*** Waterhouse, 1986b

Type species: *Subansiria procera* Armstrong, 1970a, p. 149 from Fairyland Formation (Sakmarian), southeast Bowen Basin, Queensland, OD.

Diagnosis: Large transverse shells with high ventral interarea, delthyrium closed by connector plate, sulcus well defined, smooth, fold high and smooth, plicae numerous, micro-ornament of shallow linear grooves extending in front of tiny spinules, shell densely punctate. Dental plates high, adminicula high and short, without syrinx, muscle field short with syrellum or calcite rod posteriorly, myosepta may be developed within posterior adductor scars. Dorsal ctenophoridium, short subhorizontal socket plates, crural plates, low median ridge.

Discussion: There is no syrinx, but a syrellum or rod of calcite is developed as a cylindrical callus between the posterior adductor scars (see Waterhouse 1987a, pl. 2, fig. 21), as illustrated herein for *Permasyrinx elongata* (Armstrong) and Fig. 163C, E herein. As well, myosepta may be developed, one each side. Archbold (1996) stressed the presence of these features as characterizing his genus *Syrella*, but there is some variation in their development and preservation, and *Syrella* is regarded as a genus to be distinguished from *Permasyrinx* by its channeled dorsal fold, whereas the fold in *Permasyrinx* is rounded in cross-profile. *Primorewia* Licharew & Kotlyar, 1978 from Kungurian to Roadian of northeast Russia also has a syrellum. Shell structure of *Permasyrinx* has been described by Armstrong (1968d).

Permasyrinx is very close in many aspects to the Early Permian genus *Subansiria* Sahni & Srivastava, 1956, also discussed with further references by Singh & Archbold (1993). In erecting *Permasyrinx* it was noted that *Subansiria* lacked surface pustules or tiny spines, but it should be allowed that preservation of the Himalayan material is not good. Angiolini in Angiolini et al. (1997, p. 393, Fig. 11.7-9) reported elongate pustules in her diagnosis of *Subansiria*, and added that dental plates and adminicula were long, and that a deeply sunken delthyrial plate (that is, a connector plate) and a cylindrical callus were present above the floor of the valve. Compared with *Permasyrinx*, species ascribed to *Subansiria* in the Himalaya have more numerous and narrower plicae and a well developed highly convex connector plate in the upper delthyrium, and narrow fold and sulcus. They look externally like at least some species ascribed to *Permasyrinx*, and closer scrutiny of further material is required to determine its morphological attributes. Carter (2006b) regarded the genus as being close to *Cyrtella* Fredericks, apart from having the connector plate, which he called delthyrial plate, close to the inner valve surface. Potentially one additional difference may lie in the nature of the ventral interarea. Amongst well preserved Syringothyridae, the interarea each side of the delthyrium is subdivided, but this is not always clearly the case for *Permasyrinx*. Sahni & Srivastava (1956), followed by Singh (1978c, p. 162) described a ventral interarea for *Subansiria* that "is divided into a median and two lateral portions", possibly like that normal for syringothyrid genera, but there is ambiguity, because they might have been referring only to the delthyrium with interarea each side. Singh (1973, 1978c) recorded commarginal growth lines, but did not observe any spinules in a new but clearly related species, which shows a large convex plate under the posterior delthyrium, not particularly close to the floor of the ventral valve. Somewhat similar material recorded as *Subansiria* sp. by Singh & Archbold (1993, Fig. E-H) displays a strong median dorsal septum, more developed than in any known specimen of *Permasyrinx*.

Sulcicosta Waterhouse, 1983c, type species *Subansiria plicata* Armstrong, 1970a, pl. 2, fig. 6-11, is distinguished by the presence of costae over the sulcus and fold. There is no syrellum or myosepta in the ventral valve, as far as can be determined. Several species are found in east Australia, and *Subansiria ananti* Singh & Archbold (1993) from the Early Permian of the Himalaya is congeneric.

Permasyrinx procera (Armstrong, 1970a)

Fig. 159

1970a *Subansiria procera* Armstrong, p. 149, pl. 2, fig. 12-15 (part, not pl. 2, fig. 16-18, pl. 3, fig. 14 = various spp.).

1987a *Permasyrinx procera* – Waterhouse, p. 7, pl. 1, fig. 10-12, 19.

Holotype: UQF 12607 figured by Armstrong (1970, pl. 2, fig. 12-15) from Fairyland Formation, southeast Bowen Basin, OD.

Diagnosis: Smooth well formed sulcus and fold, six to eight pair of narrow plicae, high gently curved ventral interarea.

Material: A specimen with valves conjoined from UQL 4508, Tiverton Formation. *Bookeria pollex* Zone.

Dimensions in mm: internal mould UQF 81384

Width	Length	Height	Height ventral
30	19	14	9.5

Description: Shell transverse with narrow cardinal extremities and high gently concave ventral interarea divided by triangular delthyrium, nature of cover obscure, each side of interarea marked by strong horizontal growth grooves and weak vertical striae, best preserved near inner hinge, weakly defining perideltidial areas. Sulcus deep and narrowly concave, fold high and narrow-crested, slightly crushed. Plicae narrow with slightly subangular crests and interspaces, numbering six well formed pair and two faint pair laterally, micro-ornament of fine numerous spines in single rows between well formed growth laminae. Dental plates high and resting on high adminicula, remnants of transverse plate at junction; muscle scars weakly impressed. Dorsal ctenophoridium with short vertical laminae, vertical small crural plates and small horizontal dental socket plates.

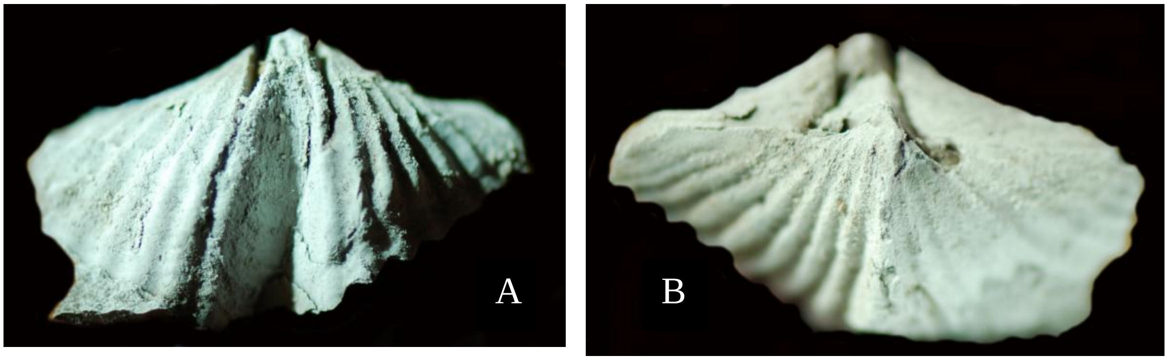


Fig. 159. *Permasyrinx procera* (Armstrong), ventral and dorsal aspects in internal mould of specimen with valves conjoined, UQF 81384 from UQL 4508, x1.5.

Resemblances: In shape and ornament this specimen is like *Permasyrinx procera* (Armstrong) from the Fairyland Formation of southeast Bowen Basin, and shows the same micro-ornament as figured by Waterhouse (1987a, pl. 1, fig. 19). As a rule this species has six pair of plicae, but in the present specimen two additional but very fine ribs are visible laterally, whereas the corresponding shell in type *procera* is smooth – as far as it is preserved. The plicae are much narrower and more sharply crested than in *P. elongata* (Armstrong, 1970a), which also has six or seven pair of plicae, and the plicae are fewer than in *P. granulata* (Armstrong), which is transverse like *procera* but has more and broader plicae.

Permasyrinx elongata (Armstrong, 1970a)

Fig. 160 – 163A - E

1964 *Spirifer* cf. *tasmaniensis* [not Morris] – Maxwell, pl. 8, fig. 13.

1964b *Pseudosyrinx* sp. Hill & Woods, pl. P7, fig. 14, 15.

1970a *Subansiria elongata* Armstrong, p. 151, pl. 2, fig. 1-5, text-fig. 4.

1970a *S. procera* [not Armstrong] – Armstrong, p. 149, pl. 2, fig. 16 (part, not pl. 2, fig. 12-15 = *procera*, not pl. 2, fig. 17, 18, pl. 3, fig. 14 = spp. indet.).

1972 *S. procera* – Hill, Playford & Woods, pl. P7, fig. 14, 15.

1987a *Permasyrinx elongata* – Waterhouse, p. 9, pl. 2, fig. 1-4.

Holotype: UQF 52857 from UQL 3127, Tiverton Formation, figured by Armstrong (1970b, pl. 2, fig. 2), OD.

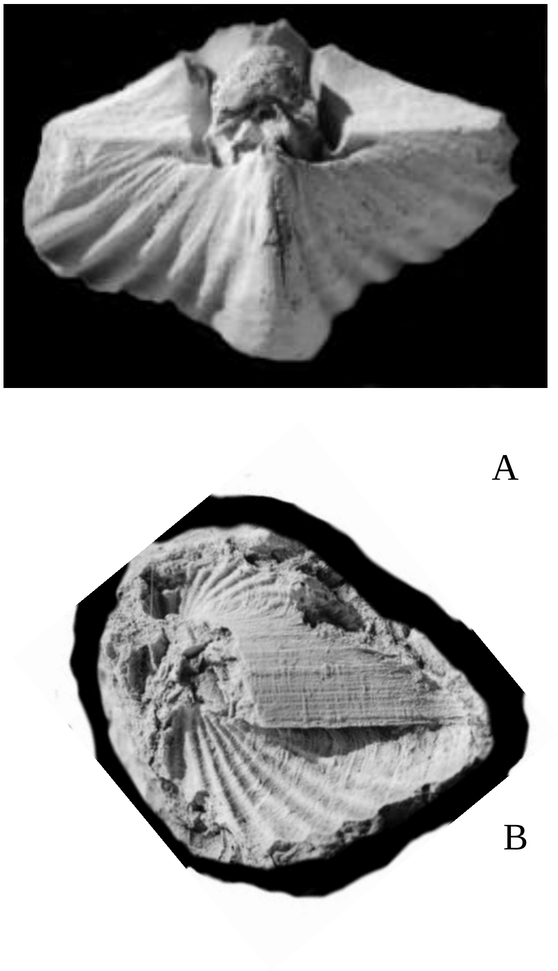


Fig. 160. *Permasyrinx elongata* (Armstrong). A, dorsal aspect of internal mould, UQF 81385 from UQL 4518, x2. B, dorsal aspect of broken external mould, showing high ventral interarea with ill-defined perideltidial area marked by vertical striae, UQF 81393 from UQL 2619, x1.

Diagnosis: Somewhat elongate shells with apsacline ventral interarea, about six to seven pair of narrow plicae, adminicula short and subparallel.

Material: Specimens from UQL 2619, 2622, 2631, 2633, 2625, 3127, 3780, 4511, 4512, 4514, 4515, 4518, 4523 and LT3. Poorly preserved specimens from UQL 1630, 2526, 2623, 2626 and 3780 might belong to this species or to *granulata* Armstrong. *Bookeria geniculata* and *Taeniothaerus subquadratus* Zones.

Dimensions in mm: ventral valves, exterior

UQF	UQL	Width	Length	Height
81388	2625	54	42	22
81392	3127	43	35	15

Description: Specimens moderately large, weakly transverse, hinge very wide, posterior walls diverging at close to 150°, ventral interarea high and subplanar, divided by delthyrium widening at angle of 40°, bordered by delthyrial rims and apically closed by arcuate delthyrial plate outside the connector plate. Dorsal valve less inflated than ventral valve, bearing low interarea in plane of commissure and broad notothyrium with angle of 100-110°. Ventral sulcus widens at angle close to 25°, without median rib or subplicae, but incorporating innermost pair of plicae anteriorly as a rule, plicae narrow and close-set, numbering some six or rarely seven pair. Dorsal fold narrow, moderately high, round-crested, innermost pair of plicae at lateral edge of fold; lateral extremities in both valves may be smooth or carry subdued plicae. Shell surface marked by very fine pores, tiny spines and close-set grooves, 0.5-0.7mm long, some four to six in 1mm, low growth lamellae and growth increments, six to nine per mm, irregular in width and course. In the ventral valve, dental tracks border the sides of the delthyrium and may show pits and irregular mounds.

Fig. 161. *Permasyrinx elongata* (Armstrong) latex cast of dorsal interior, UQF 81390 from UQL 4511, x5. Base of the crura rest within crural plates.

Dental plates high and scapular-shaped, diverging weakly forward towards dorsal valve, supported by high adminicula which are thickened posteriorly on the inner side, so that outer edge is straight, but inner edges diverge forward posteriorly and lie parallel in front. Myophragm moderately developed posteriorly and may form low short septum, narrow adductor scars divided by groove, marked by fine longitudinal striae, wide diductors separated from adductors by ridges that fade anteriorly, marked by low longitudinal striae and growth lines parallel to anterior margin. Two tiny possible peduncular muscle impressions are visible on inner flank of dental plates just above adminicula in front of delthyrium in some specimens. Posterior shell up to 9mm thick, bearing pits on the floor.

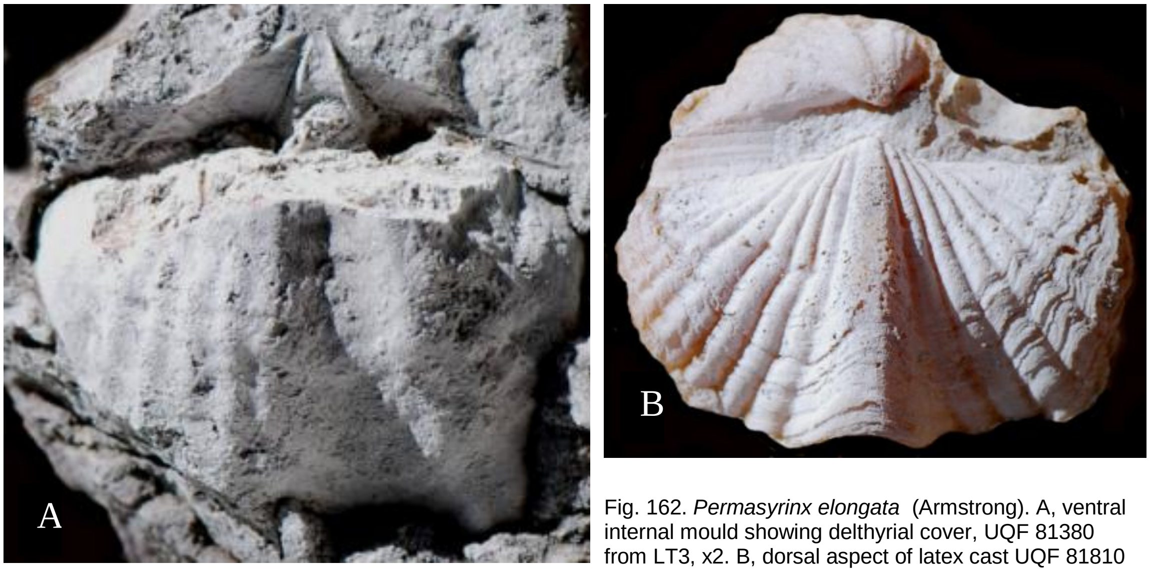


Fig. 162. *Permasyrinx elongata* (Armstrong). A, ventral internal mould showing delthyrial cover, UQF 81380 from LT3, x2. B, dorsal aspect of latex cast UQF 81810 from UQL 4512, x1.3.

In dorsal valve, ctenophoridium small, blades vertical or concave inwards towards the mid-line, dental sockets with weak growth rugae, curved parallel to anterior edge, sockets contained between sturdy horizontal outer hinge plates and inner vertical crural plates concave inwards, containing crural bases; median septum extends for more than half the length of the valve, adductor scars faintly impressed. Shell closely punctate, five or six pores per square mm.

Resemblances: This distinctive species is less transverse with lower ventral interarea and fewer plicae than in *Permasyrinx procera* (Armstrong) from the Fairyland Formation, southeast Bowen Basin. *P. subelongata* Waterhouse

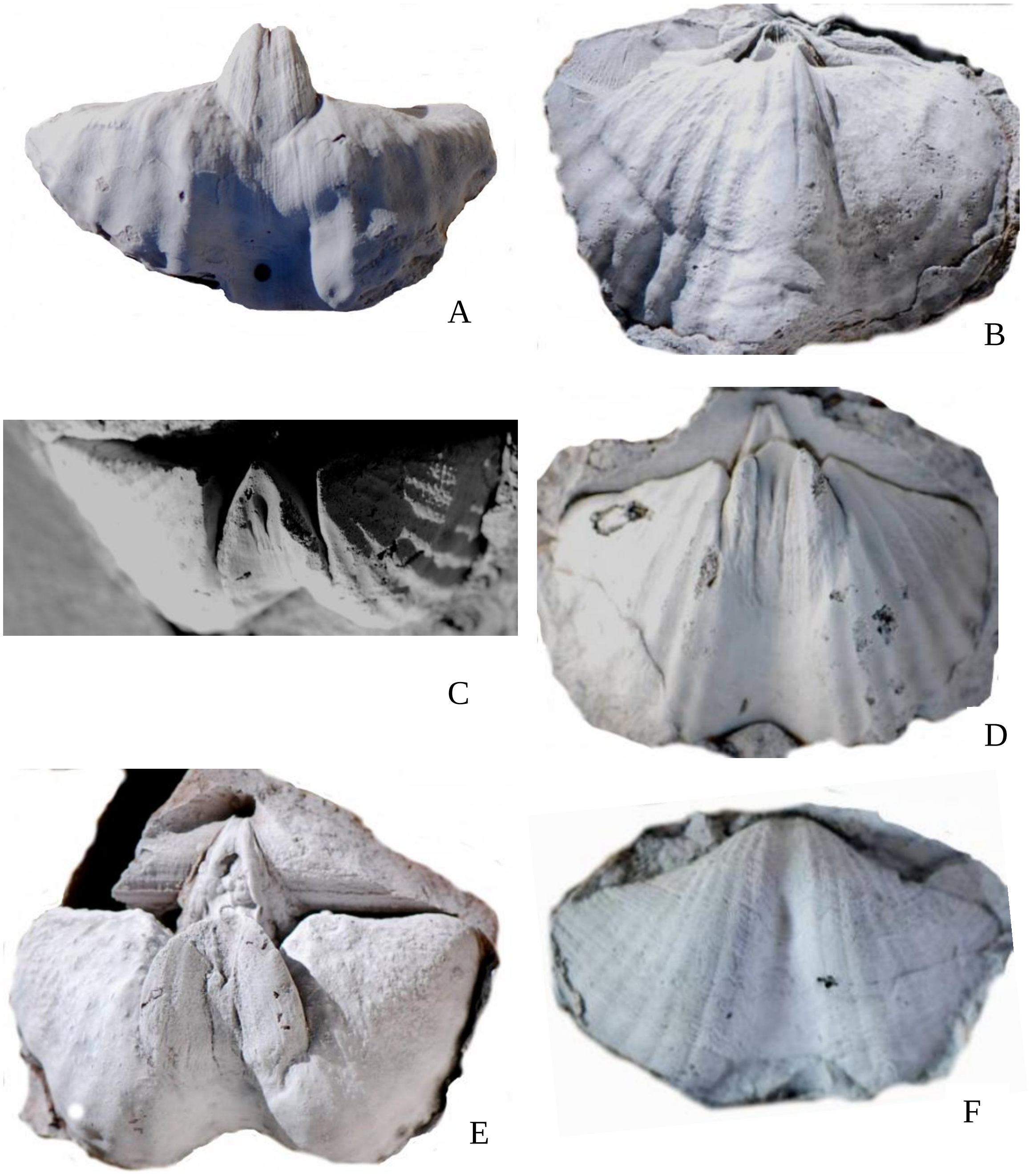


Fig. 163. A-E, *Permasyrinx elongata* (Armstrong). A , ventral aspect of internal mould UQF 81389 from UQL 3780, x2. B, dorsal internal mould UQF 81390 from UQL 4511, x1. C, posterior aspect of ventral interior, UQF 81833 from UQL 2631, x1.1, showing syrellum at posterior end of adductor scars. D, ventral internal mould UQF 81392 from UQL 3127, x1. E, ventral internal mould UQF 81388 from UQL 2625, x 2. F, *P. granulata* (Armstrong) latex cast of ventral valve UQF 81391 from UQL 2622, x1.

(1987a, p. 8, pl. 1, fig. 13-18, 20?) from the Dresden Formation of the same area is very close in number of plicae and other detail, but has more concave less widely diverging posterior walls, imparting a different outline, and the sulcus is shallower and the ventral interarea more curved. *P. transversa* (Armstrong, 1970a, pl. 4, fig. 2-4) from the Rose's Pride Formation of the southeast Bowen Basin is more transverse with low ventral area.

Perhaps overlooking the fact that *Permasyrinx* was proposed before *Syrella*, Archbold (1996, p. 34), as accepted by Waterhouse & Chen (2007, p. 57), indicated that the species *elongata* might belong to *Syrella* Archbold, because figures appeared to suggest the presence of two myosepta (see p. 204). But examination of the Tiverton material shows that the figures were exaggerated by shadows caused by relief and height differences between the muscle scars.

Permasyrinx granulata (Armstrong, 1970a)

Fig. 163F, 164 - 169

1964b *Spirifer* sp. Hill & Woods, pl. P8, fig. 1.

1970a *Subansiria granulata* Armstrong, p. 153, pl. 3, fig. 1-4, 5?, 6-12, pl. 4, fig. 1, pl. 5, fig. 11-12, pl. 6, fig. 3, 5, 6, text-fig. 5 (part, not pl. 3, fig. 13 = cf. *procera* (Armstrong), not pl. 5, fig. 13, 14 = sp. indet.).

1972 *S. granulata* – Hill, Playford & Woods, pl. P8, fig. 1.

Holotype: UQF 52862 from UQL 3127, Tiverton Formation, figured by Armstrong (1970a, pl. 3, fig. 1, 2), OD.

Diagnosis: Transverse shells with wide hinge and subtriangular outline, some nine to eleven pair of plicae.

Fig. 164. *Permasyrinx granulata* (Armstrong), latex cast of ventral valve aspect, UQF 81387 from UQL 3127, x2.

Fig. 165. *Permasyrinx granulata* (Armstrong), dorsal aspect of latex cast, UQF 81387 from UQL 3127, x2.5.

Fig. 166. *Permasyrinx granulata* (Armstrong), ventral internal mould UQF 81850 from UQL 4514, x2.

Material: Specimens from UQL 1383?, 2619, 2622, 2628, 3127, 3720, 4511, 4514, 4515, 4517 and T3. *Bookeria geniculata* and *Taeniothaerus subquadratus* Zones.

Dimensions in mm: ventral valves, exterior, means, n = 7

Width	Length	Height
46	32	14

Fig. 167. *Permasyrinx granulata* (Armstrong), internal mould of ventral valve UQF 81386 from UQL 2622, x2. Note small scars (a).

Description: This species is not as common in the Tiverton Formation as *Permasyrinx elongata*, and is distinguished by its transverse outline and more pair of plicae, usually nine and up to eleven pair. The species may be found in the same band as *elongata*, and rarely, on the same block. The two taxa are very similar to each other, and arguably both could be placed in the one species: *elongata* has page priority and has featured more in the literature. Several specimens of *granulata* suggest the presence of spinules, three to four per mm in commarginal rows (UQL 2628).

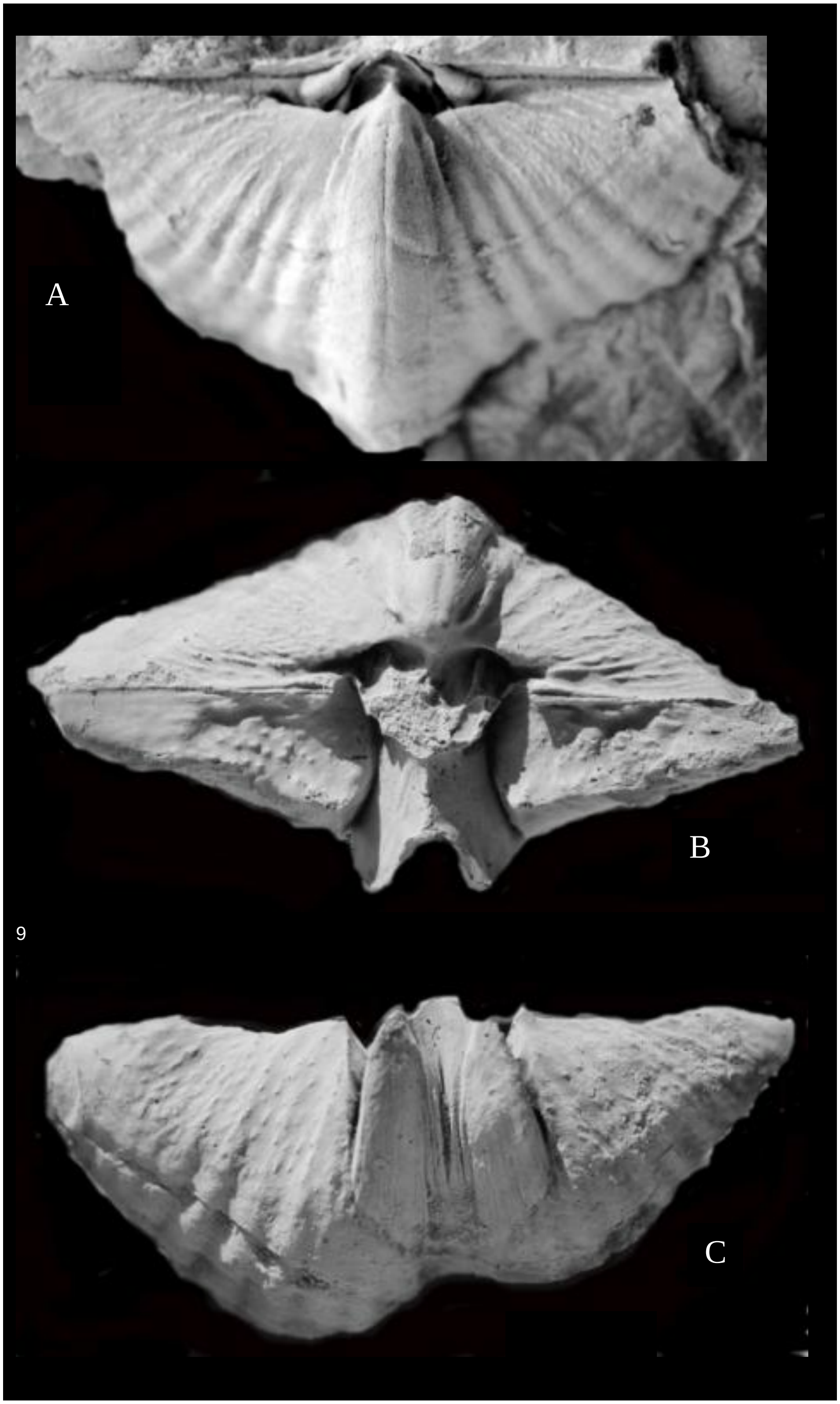


Fig. 168. *Permasyrinx granulata* (Armstrong). A, internal mould of dorsal valve UQF 81447 from UQL 4515, x2. B, C, UQF 81839 from UQL 3720, internal mould of specimen with valves conjoined. B, posterior aspect, dorsal valve on top, x2. C, ventral aspect, x2.

Resemblances: Armstrong (1970a) recorded and figured material from the Berriedale Limestone of Tasmania. He also incorporated specimens from the Sirius Shale of the Cattle Creek Formation from the southeast Bowen Basin, but the dorsal fold of these specimens has a well defined channel. Although Armstrong stated that the fold in *granulata* was “with

Fig. 169. *Permasyrinx granulata* (Armstrong), latex cast of posterior internal shell, ventral valve on top, UQF 81839 from UQL 3720, x2. The cracks are in the latex mould, not the original.

or without a gentle median furrow", none of the suites of either *elongata* or *granulata* in present collections shows a dorsal fold channel, and no channel is found in type *procera*. The specimen figured and compared to the species from Wallaby rocks in the fault blocks south of Warwick (Armstrong 1970a, pl. 3, fig. 13) is close but appears to have plicae more closely spaced than in the Tiverton specimens, and is elongate like *procera* from the Fairyland Formation of the southeast Bowen Basin.

Discussion: One ventral valve of the present suite (Fig. 164) shows a split in the plication outside the one bordering the sulcus. A specimen figured from the same locality as the holotype (Armstrong 1970a, pl. 3, fig. 8, 12) shows a number of plical splits on each valve. This would appear to be an intrasubspecific variation. Archbold (1996, p. 30) noted the same phenomenon in a west Australian form, which he distinguished as a new genus, *Cundaria*, as also noted by Etheridge (1915, p. 29). That provided the distinction from *Cyrtella* Fredericks, 1924, but the distinction may not be of generic significance, given the presence of such subplication in a few other forms as allowed by Archbold (1996), and not all specimens of *Cundaria aquilaformis* Archbold show such plical splitting.

Permasyrinx archboldi n. sp.

Fig. 170

aff. 1970a *Pseudosyrinx allandalensis* [not Armstrong] – Armstrong, p. 140, pl. 1, fig. 4, 7 (part, not pl. 1, fig. 1-3, 5, ?6 = *allandalensis*).

1987a *Cyrtella erecta* [not Waterhouse] – Waterhouse, p. 12, pl. 2, fig. 15, 17 (part, not fig. 14, 21 = *erecta*).

Holotype: UQF 81396 from UQL 4519, Tiverton Formation, figured in Fig. 170A, here designated.

Diagnosis: High ventral interarea, pointed ventral umbo, well defined ventral sulcus and 8-13 pair of narrow plicae.

Material: Single ventral valves from UQL 4517, 4519, 4520 and LT3. *Taeniothaerus subquadratus* Zone, LT3 uncertain.

Description: Specimens preserved as mostly internal moulds, that from UQL 4517 measuring approximately 46mm wide, 33mm long and 11mm high, with extended umbo having umbonal angle of 90-100°, subpentagonal outline, and well formed sulcus with angle of 25°. The interarea is high and not strongly incurved, the delthyrium narrow with angle of 35°, closed by plate with arched growth-lines. Plicae form nine pairs in two of the specimens and 13 pairs in the shell from UQL 4520, low and close-set, with interspaces as wide as plicae; micro-ornament poorly preserved, with vestiges of small pustules and pores. Adminicula high, diverge forwards at angle of 45°, diverge slightly to floor of valve, supporting dental plates which diverge at low angle to teeth. Specimen from UQL 4519 shows small convex plate under umbo, in addition to the connector plate, and has a rod of shell over the posterior muscle field. This is not a syrinx, but matches the calcite rod recorded by Archbold (1996) for *Syrella occidenta*. Adductor scars narrow, bordered each side by low ridge, called myoseptum by Waterhouse & Chen (2007, p. 57), and divided by low ridge extending almost to half length; diductors wide, marked by growth-lines parallel to curved anterior margin. The specimen from LT3 has a well defined cardinal interarea with no perideltial areas, and a convex connector plate covering the delthyrium.

Resemblances: Ventral valves like those of present material have been described and figured by Armstrong (1970a) from the Tiverton Formation, though the exact level was not provided. Similar material was illustrated by Waterhouse (1987a) from the Rose's Pride Formation in the *Ingelarella plica* Zone of the southeast Bowen Basin, and the dorsal valve (pl. 2, fig. 17) has a rounded crest without a median channel, although there is a faint suggestion of a discontinuous median slit.

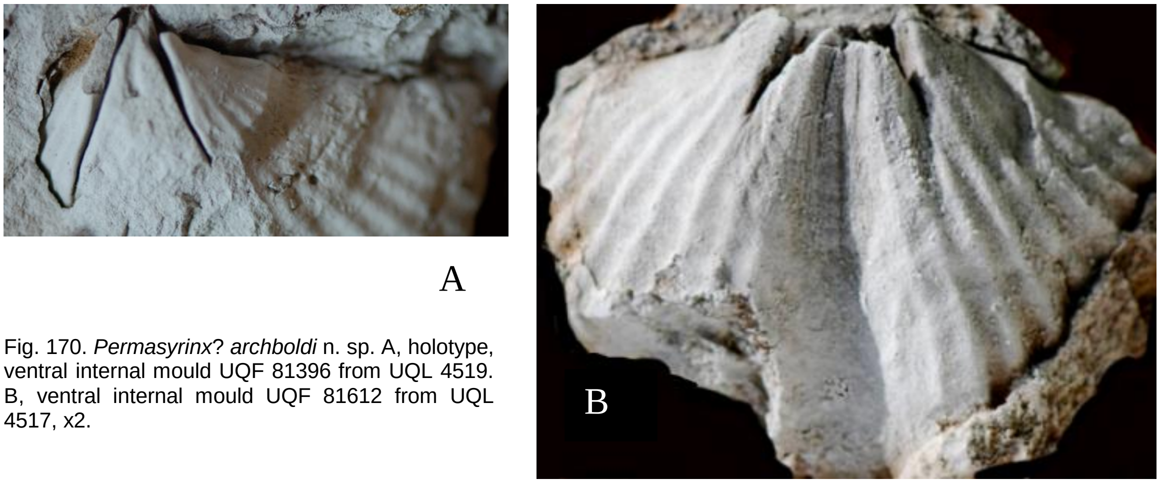


Fig. 170. *Permasyrinx*? *archboldi* n. sp. A, holotype, ventral internal mould UQF 81396 from UQL 4519. B, ventral internal mould UQF 81612 from UQL 4517, x2.

Syrella Archbold 1996, based on type species *Syrella occidenta* Archbold, 1996, p. 32 from the Mingenew Formation of Artinskian age in Western Australia. is judged to be very close to *Permasyrinx* Waterhouse, and is distinguished from that genus by the presence of a narrow sulcus along the crest of the dorsal fold. The genus probably includes various species from east Australian Permian that were referred to *Cyrtella* Fredericks, 1924, although this is not certain for all species, where the nature of the inner ventral shell is poorly known. The presence of the calcite rod at the posterior end of the ventral adductor scars in mature specimens, stressed as a prime discriminant for the genus by Archbold (1996), is also developed in *Permasyrinx*, and the two genera are close in most respects, although there must remain some reservation about the nature and length of the connector plate between the junction of the dental plates and adminicula in type *Syrella*, because this was not described as such by Archbold. He did record a "delthyrial plate" at the level of the delthyrial grooves, but its nature is not clear. His illustration in Fig. 8L suggests the likelihood of a connector plate normal for the subfamily.

The present species is characterized by its high number of narrow plicae, and its extended and pointed ventral umbo. In that regard it comes close to the species called *Spirifera bisulcata* Sowerby var. *acuta* Etheridge Snr (1872, p. 329, pl. 16, fig. 1) from the middle Rammutt Formation of Gympie, southeast Queensland. Etheridge's species has many fine plicae and extended ventral umbo. It is finely punctate, and was referred to *Permasyrinx* by Waterhouse & Balfe (1987, pl. 1, fig. 3), and although various details remain obscure, the similarity in shape suggests that the species might closely allied to the present form (Waterhouse 2015), though the fold of *acuta* is poorly known and, unlike the present form, there is no definite syrellum, a matter obscured by the mode of preservation. The material described as *Cyrtella erecta* Waterhouse, 1987a comes from the Early Permian volcanics at Collaroy, and is moderately close to *Permasyrinx allandalensis*, as a narrower form with fewer pairs of plicae (eight, and possibly one or two lateral pair not shown), and a well defined channel at the crest of the dorsal fold, at least anteriorly. The species *P. allandalensis* (Armstrong) comes from the Lizzie Creek Volanic Group and has a high number of plicae that tend to be well rounded, and the umbo is broad.

A specimen somewhat similar in outline was described as *Subansiria pelicanensis* by Armstrong (1970a, pl. 4, fig. 11, 12) from the Middle Permian (late Capitanian) *pelicanensis* beds in the north Bowen Basin. This species has weak sulcal costae and apparently non-costate dorsal fold, so that it appears to belong to *Verkhotomia* Sokolskaya, 1963. The type species *Verkhotomia plenoides* Sokolskaya, 1963 from the Visean of the Kuznets Basin of Russia was named for medium-sized to large shells with moderately low ventral interarea, numerous simple plicae, sulcus with few ribs on sides and smooth or weakly ribbed dorsal fold. The adminicula, delthyrial plate and median septum are all long. The genus is close to *Sulcicosta* Waterhouse, 1987a, but is more elongately subpentagonal in shape, and has a much less costate fold, and somewhat less costate sulcus. As well ribs are finer, at least in the type species. *Subansiria* sp. cf. *campbelli* Armstrong (1970a, pl. 4, fig. 10) from the early Middle Permian Oxtrack Formation of the southeast Bowen Basin is also similar in outline, and differs from *campbelli* and from the Tiverton specimens in having very fine plicae.

So-called *Subansiria* sp. nov. of Runnegar & Ferguson (1969, pl. 3, fig. 6, 7) and reidentified as *S. procera* by Armstrong (1970a, pl. 2, fig. 18) belongs to *Cyrtella* Fredericks. It was described as *Cyrtella papula* from the lower South Curra Limestone of Gympie, and has a strong ventral median septum and high interarea, and papillose micro-ornament (Waterhouse & Balfe 2015).

Suborder SPIRIFERINIDINA Ivanova, 1972

Superfamily **PENNOSPIRIFERINOIDEA** Dagys, 1972

Family **PUNCTOSPIRIFERIDAE** Waterhouse, 1975

Diagnosis: Normally transverse shells with narrow sulcus, fold and plicae, short adminicula, long median septum, micro-ornament of radial capillae and transverse growth lamellae.

Genus ***Pustulospiriferina*** Waterhouse, 1983e

Type species: *Punctospirifer etheridgei* Armstrong, 1970c, p. 317 from Tiverton Formation (Aktastinian), north Bowen Basin, Queensland, OD.

Diagnosis: Small shells with narrow sulcus and fold, slender plicae, characterized by having fine spines as well as radial capillae and commarginal growth lamellae.

Pustulospiriferina etheridgei (Armstrong, 1970c)

Fig. 171 - 173

1970c *Punctospirifer etheridgei* Armstrong, p. 317, pl. 25, fig, 6-10, 12-19, 21, 22.

1983e *Pustulospiriferina etheridgei* – Waterhouse, p. 303.

2006b *Pustulospiriferina etheridgei* – Carter, p. 1912, Fig. 1272a-c.

Holotype: UQF 54612 from UQL 3127, Tiverton Formation, figured by Armstrong (1970c, pl. 25, fig. 19) and Carter (2006b, Fig. 1272a), OD.

Diagnosis: Shells with narrow fold and sulcus, usually five pair of plicae, varying between four and six pairs.

Material: Specimens from UQL 2622, 2623, 2626, 2629, 2631, 2127?, 3127, 3780, 4511, 4512, 4515, 4517 - 4519, 4524 and LT3. *Svalbardia armstrongi* Subzone and *Taeniothaerus subquadratus* Zone. LT3 uncertain.

Dimensions in mm:

UQF	UQL	Valve	Width	Length	Height ventral	Height both
81401	4512	ventral	18.5	9.5	2.5	
81400	4512	both	17	13	5.5	10

Description: This species has been described by Armstrong (1970c) and the present suite of collections includes specimens from the type locality. Some of the available specimens are a little larger than those figured by Armstrong (1970c). They are weakly transverse with obtuse cardinal extremities, and have a high ventral interarea with narrow delthyrium of angle 25-30°. Some internal moulds of specimens with valves conjoined suggest that the delthyrium was open, but large ventral valves have an weakly convex plate, arched towards the umbo, with two growth rugae, closing the delthyrium and bearing a median recession. At the umbonal end of several ventral valves lies a small outwardly convex plate that tapers forward each side into a low ridge placed close to mid-height of the dental supports (adminicula and dental plates), at the umbonal end of the median septum. Sulcus and fold narrow, as a rule five pair of subangular

Fig. 171. *Punctospiriferina etheridgei* (Armstrong), internal mould of ventral valve UQF 81405 from UQL 4512, x5.

plicae and interspaces, and micro-ornament of radial capillae, about 15 per mm, and fine growth increments, five or six per mm, as well as commarginal lamellae, generally with six to eight increments between each lamellum. Tiny spines, four to six per mm, are found over the shell, each above a pore that opens into the interior: on some specimens the anterior surface lacks spines.

Ventral median septum strong and extending for half length of valve, adminicula vertical, not half as long as the median septum, very high dental plates, ventral muscle field lies between the adminicula and extends to the anterior end

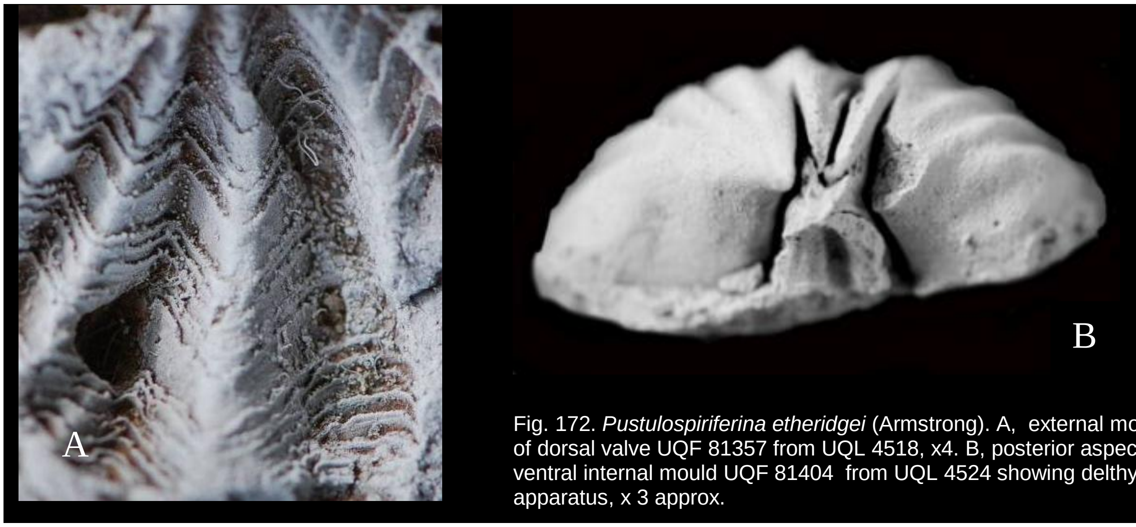


Fig. 172. *Pustulospiriferina etheridgei* (Armstrong). A, external mould of dorsal valve UQF 81357 from UQL 4518, x4. B, posterior aspect of ventral internal mould UQF 81404 from UQL 4524 showing delthyrial apparatus, x 3 approx.

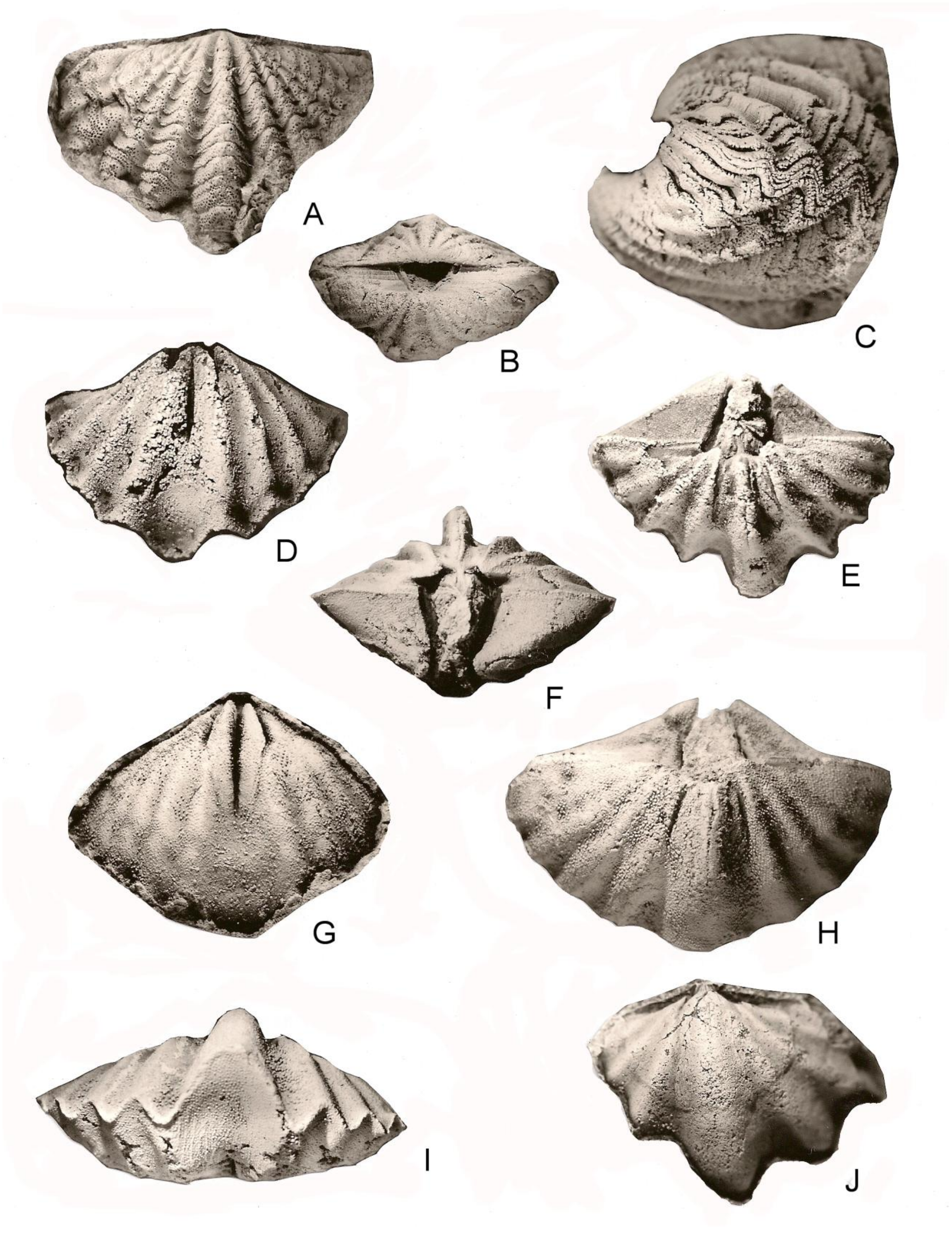


Fig. 173. *Pustulospiriferina etheridgei* (Armstrong). A, latex cast of dorsal exterior, UQF 81398 from UQL 4515, x 2. B, C, posterior and lateral aspects of specimen with valves conjoined, dorsal valve on top, UQF 81399 from UQL 4517, x2, x3**.** D, E, F, ventral, dorsal and posterior aspects of internal mould with valves conjoined, dorsal valve on top, UQF 81400 from UQL 4512 x 3.5. G, ventral internal mould UQF 81401 from UQL 4512, x2. H, I, dorsal and anterior aspects of internal mould with valves conjoined UQF 81402 (dorsal valve on top) from UQL 4512, x3. J, dorsal internal mould UQF 81403 from UQL 3780, x3.5.

of the median septum. Adductor scars narrow each side of the septum, marked by ridges and grooves. Diductors are much wider than adductors and marked by pits and growth-lines curving parallel to the posterior and anterior margins.

Dorsal median septum low, extending for over half the length of the valve, ctenophoridium small, elongate and lamellate, with crura commencing in front at the base, dental sockets slender, narrow socket plates, comparatively large crural or hinge plates converge inwards at 100^o, straight or weakly concave inwards, adductor scars faintly impressed, with open pores as for the ventral muscle scars, may be demarcated laterally by slightly higher growth-lines to leave a slender ridge along the lower flanks of the innermost pair of plicae.

Resemblances: The species is distinguished from *Pustulospiriferina? lirata* Waterhouse (1987a, pl. 13, fig. 3-10) from the Elvinia and Rose's Pride Formations of the southeast Bowen Basin by having more plicae pairs, and denser pustules. These specimens show a high ridge bordering the outer edge of the dorsal muscle field (Waterhouse 1987a, pl. 13, fig. 10). From the lower Elvinia Formation or Boughyard Member in the same region, poorly preserved specimens show some approach to *etheridgei* (Waterhouse 1987a, p. 45, pl. 12, fig. 26-28) but a specimen from the Rose's Pride Formation has fewer plicae (Waterhouse 1987a, pl. 12, fig. 29), although the plicae are high like those of *etheridgei*.

Taxonomy: Armstrong spelled the species name *etheridgi* in the heading for the description, but this is believed to be a lapse or printing error, because in the text and plate caption, the name was rendered *etheridgei*, so that is how it was spelled in Waterhouse (1987a).

Superorder TEREBRATULIFORMII Waagen, 1883
Order TEREBRATULIDA Waagen, 1883
Suborder TEREBRATULIDINA Waagen, 1883

Gray (1848) was first to recognise terebratulids as belong to a distinct order, which he called Ancyclobrachia, a name retained – with altered content – until Waagen (1883) introduced Terebratulida as an alternative.

Superfamily **DIELASMOIDEA** Schuchert, 1913
Family **DIELASMIDAE** Schuchert, 1913

Superfamily Dielasmoidea Schuchert, 1913

- **Family Dielasmidae Schuchert, 1913**
  - Subfamily Dielasminae Schuchert, 1913
    - Tribe Dielasmini Schuchert, 1913
    - Tribe Plectelasmini Waterhouse, 2010a
    - Tribe Fletcherithyrini Waterhouse, 2010a
    - Tribe Hoskingini Waterhouse, 2010a
  - Subfamily Centronelloideinae Stehli, 1965
  - Subfamily Nucleatulinae Muir-Wood, 1965
- **Family Heterelasminidae Licharew, 1956**
  - Family Heterelasminidae Licharew, 1956
  - Family Pseudodielasmidae Cooper & Grant, 1976b
- **Family Gilledidae Campbell, 1965**
  - Subfamily Gilledinae Campbell, 1965
  - Subfamily Hemiptychininae Campbell, 1965
  - Subfamily Maorielasminae Waterhouse & Piyasin, 1970
- **Family Beecheridae Smirnova, 2004**

Table 21. Classification of Dielasmoidea Schuchert.

Diagnosis: Genera as a rule small in size, with variably flexed anterior commissure, foramen generally permesothyrid and labiate, collar well developed, dental plates developed as a rule but may be reduced, septalium well developed, may be sessile or supported on high septum, loop acuminate in juvenile form, deltiform at maturity, may develop anterior vertical blade medianly.

Subfamily **DIELASMINAE** Schuchert, 1913

Diagnosis: Dental plates well developed, septalium of inner and outer hinge plates, may be divided, sessile or raised on low to high septum, loop deltiform.

Tribe **FLETCHERITHYRIN**I Waterhouse, 2010a

Name genus: *Fletcherithyris* Campbell, 1965, p. 24 from Broughton Formation (Wordian), south Sydney Basin.

Diagnosis: Septalium supported on high dorsal septum. Commissure rectimarginate to sulciplicate.

Discussion: This tribe was discussed by Waterhouse (2010a, p. 82). In *Fletcherithyris* the septalium is supported by a high septum, as in *Campbellelasma* Smirnova and *Sokelasma* Smirnova, and in Late Triassic genera, including *Adygella* Dagys, ?*Coenothyri*s Douvillé, ?*Paradygella* Liao & Sun, *Pirethyris* Sun & Ye and *Tunethyris* Calzada Badia et al. These latter genera may have arisen de novo during Triassic time, but do resemble Permian *Fletcherithyris* in overall shape and other attributes. Girtyellinae Stehli are a small group of Carboniferous and Permian genera also characterized in part by high dorsal septum, but are cryptonelliform. Some other genera developed a dorsal septum but the loop passed through an acuminate and possibly haploid growth stages, and the genera are referred to Angustothyrididae Dagys, for which *Praeangustothyris* Koczyrkevicz is of Middle Permian age, and other genera are Triassic.

The genus *Sokelasma* Smirnova, 2004, type species *S. guttiformis* Smirnova (2004) has internal plates, including dental plates, close to those of *Fletcherithyris* (Smirnova 2004, text-fig. 1). It is not like *Beecheria*, though referred to Beecheridae by Lee et al. (2007, p. 2801), and no clear difference from *Fletcherithyris* Campbell has been established. *Beecheria* lacks dental plates and the inner and outer hinge plates form a double tented structure (Waterhouse 2010a).

Genus ***Fletcherithyris*** Campbell, 1965

Type species: *Terebratula amygdala* Dana, 1847, p. 142 [not *T. amygdala* Catullo 1846] from Broughton Formation (Wordian), south Sydney Basin, OD, replaced by *Atrypa biundata* M'Coy, 1847, p. 231.

Diagnosis: Anterior commissure broadly sinuate or weakly sulciplicate, septalium raised on high median septum, crural points high.

Discussion: The anterior septalium is carried high on the dorsal median septum. Despite extensive examination of numerous specimens of *Fletcherithyris*, it has not been possible to confirm the claim by Jin et al. (2006), taken uncritically from Campbell (1965, p. 25), that the inner hinge plates may unite on the floor of the valve.

The genus has been reported from Pennsylvanian faunas of Nevada by Perez-Huerta (2004, p. 1507), but his material differs substantially, lacking a median dorsal septum, and displaying a different, more elaborate loop.

Taxonomy: *Fletcherithyris* was proposed as nom. nov. for *Fletcherina* Stehli, 1961 not *Fletcherina* Lang, Smith & Thomas.

Fletcherithyris farleyensis Campbell, 1965

1965 *Fletcherithyris farleyensis* Campbell, p. 33, pl. 6, fig. 1-10.

Holotype: ANU 14092 from Farley Formation, Sydney Basin, figured by Campbell (1965, pl. 6, fig. 7, 8), OD.

Diagnosis: Shaped like *Fletcherithyris amygdala* (Dana), septalium V-shaped in section, strong crural bases.

Discussion: Campbell (1965, p. 34) reported this species at GSQ localities at Homevale.

Fletcherithyris farleyensis faba Campbell, 1965

Fig. 174, 175B, C, 188B

1965 *Fletcherithyris farleyensis faba* Campbell, p. 34, pl. 2, fig. 45-59, text-fig. 11.

Holotype: CPC 5319 from 2km southeast of Lizzie Creek, Tiverton Formation, north Bowen Basin, OD.

Diagnosis: Small shells very close to *farleyensis*, slightly narrower and smaller, sinuate at moderately early growth stage, stronger anterior socket ridges than in *farleyensis*.

Material: Specimens from UQL 3127, 4509 - 4511. *Bookeria geniculata* Zone and uncertain.

Fig. 174. *Fletcherithyris fareyensis faba* Campbell, latex cast of block with numerous specimens, including UQF 81406 and 81407 from UQL 3127, x2. The cracks developed in the latex, and are not present in the original material.

Description, Resemblances: Campbell (1965) allocated specimens from the Tiverton Formation to a subspecies of *Fletcherithyris farleyensis* Campbell (1965, p. 33, pl. 6, fig. 1-10) from the Farley Formation, Sydney Basin. He noted that unlike *farleyensis* the specimens were not only small, but showed a flattening of the ventral valve some 8-12mm from the umbonal tip, especially on Homevale material. As topotype specimens of *faba* from Tiverton beds only 32km north of Homevale varied in the degree of flattening, the variation was deemed by Campbell (1965) to indicate that only a subspecific difference was involved. A number of specimens in present collections are shaped like *farleyensis* and *faba*, and at least some (Fig. 175B) display a median flattening closer to the ventral umbo than developed in *farleyensis*. It is difficult to assess the comparative nature of the socket plates, even though moderately well preserved. Campbell (1965, text-fig. 11) illustrated serial sections which show a very low broad median dorsal

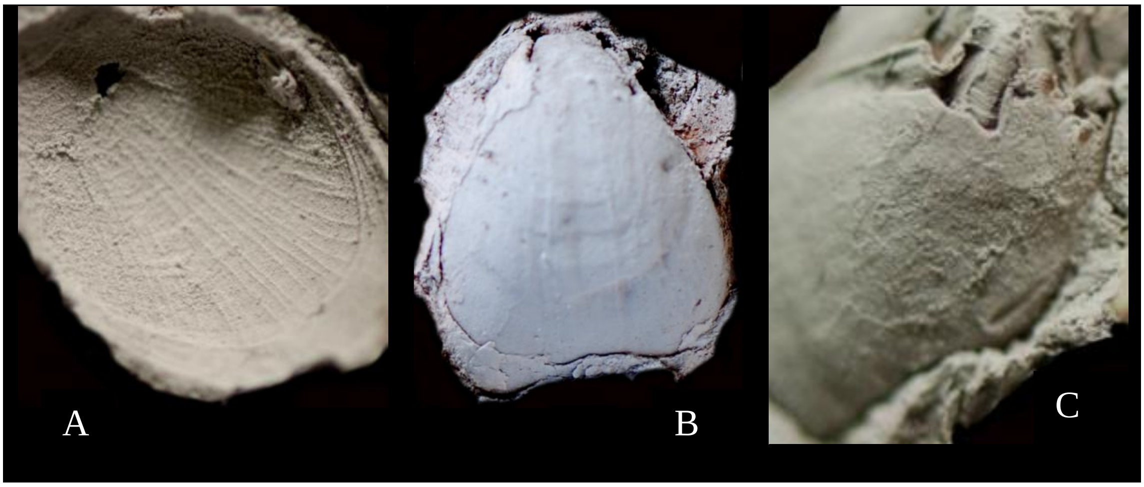


Fig. 175. A, *Fletcherithyris burdenae* n. sp. A, ventral valve external mould UQF 81413 from UQL 2626, x4. B, C, *Fletcherithyris farleyensis faba* Campbell. B, decorticated ventral valve UQF 81436 from UQL 4511, x4. C, dorsal view of internal mould UQF 81412 from UQL 4511, x6.

septum, but illustrated material in Campbell (1965, pl. 2) show that other specimens have a high median septum.

Fletcherithyris burdenae n. sp.

Fig. 175A, 176, 177

Derivation: Named for Elvira Burden.

Holotype: UQF 81419 from Tiverton Formation, figured as Fig. 176B, C, E, here designated.

Diagnosis: Small and elongate shells usually with fine radial threads over the shell surface.

Material: Specimens from UQL 1383, 1385, 1628, 2619, 2626, 3127, 4513 - 4515, 4518, and 4519. *Bookeria pollex* Zone, *Bookeria geniculata* Zone, *Svalbardia armstrongi* Subzone and *Taeniothaerus subquadratus* Zone.

Dimensions in mm: both valves

UQF	UQL	Width	Length	Height
81408	4515	9	11	3.3
81419	4514	19	12	9

Description: Shells are small and elongate. The umbonal foramen is large, up to 1.7mm across, and posterior walls diverge at 65-70°, and are almond-shaped, with maximum width placed near the anterior third of the length. The ventral valve is moderately inflated, the dorsal valve gently convex, the anterior commissure rectimarginate or weakly uniplicate, the shell finely and evenly punctate. Both valves are ornamented by shallow radial grooves separated by broad ribs 0.6-0.8mm apart as figured in Fig. 175A, arising near mid-length of both valves, or closer to the hinge on some specimens, and persisting to the anterior margin, or fading anteriorly. Crura arise close to the posterior wall in UQF 81625 from UQL 4519.

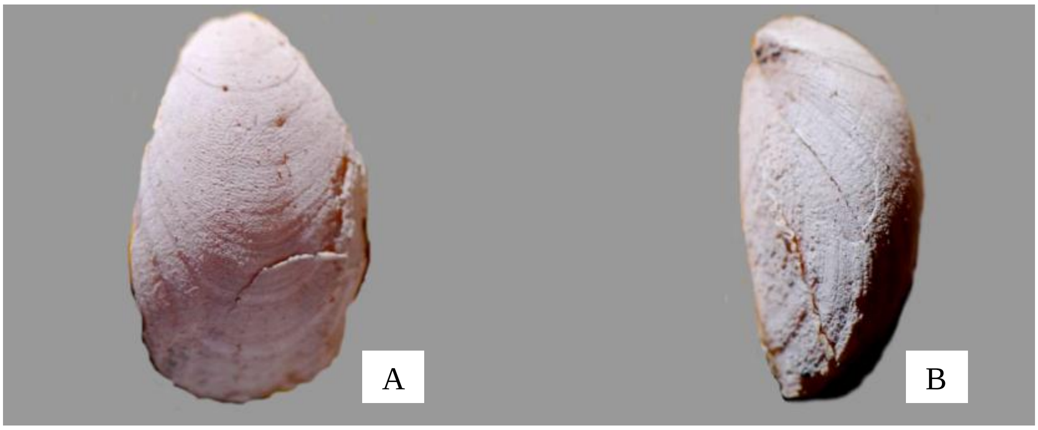


Fig. 176. *Fletcherithyris burdenae* n. sp. , ventral and lateral aspects of latex cast of UQF 81419 from UQL 4514, x3.

Resemblances: The predominant form of *Fletcherithyris* recorded by Campbell (1965) at Homevale belonged to *F. farleyensis faba* Cambell, and this is found according to present collections especially in the *Bookeria geniculata* Zone. The present species is more widespread, and is distinguished by its more elongate shape, with a length width ratio of 0.55 to 0.66, compared with ratios often of 0.7 to 0.8 from measurements provided by Campbell (1965) for *faba*. In addition, the present species bears fine radial grooves and ribs over both valves. No such ornament was recorded in the original description of *faba.* A few ventral valves, including specimens from UQL 1627, 2619 and 4515, and UQF 20812 have up to five or six ribs per mm – indeed Campbell (1965) provided no data on the exterior ornament of the subspecies or the species. However Campbell (1965) did state that *farleyensis* was externally identical with *amygdala* Dana, which has faint signs of radial threads figured in Campbell (1965, pl. 3, fig. 6), so that it is not completely certain that *faba* or *farleyensis* lack such radial ribs. *Fletcherithyris runnegari* Waterhouse & Balfe (2015) from the Late Permian South Curra Limestone of the Gympie district in southeast Queensland is larger, with maximum width placed well forward, and comparatively strong radial markings. Cooper & Grant (1976b) recorded radial markings in some of the large number of species of *Dielasma* described from the Glass Mountains Permian faunas in Texas, but the radial markings are colour bands, rather than grooves or ribs.

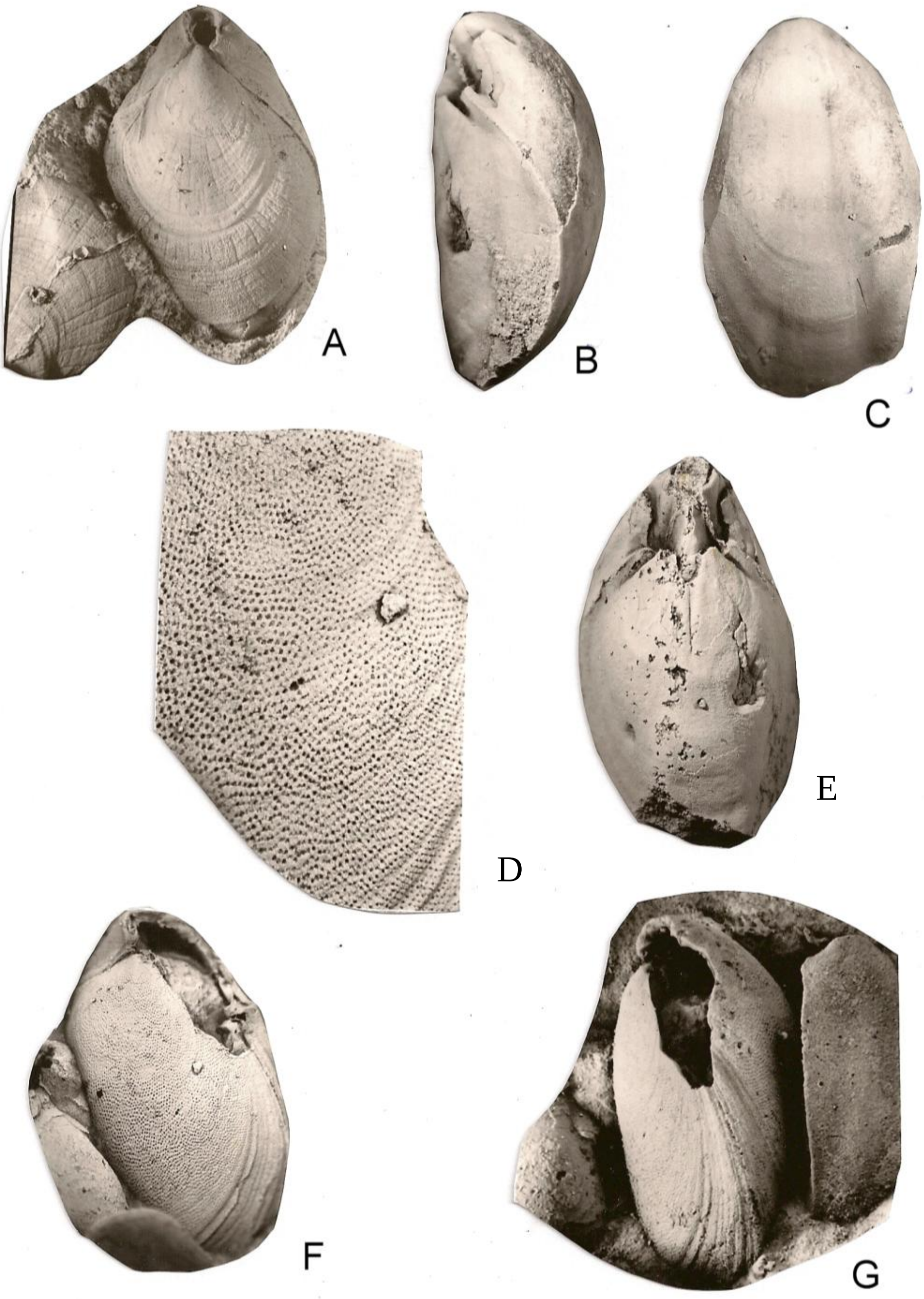


Fig. 177. *Fletcherithyris burdenae* n. sp. A, dorsal aspect of latex casts of two specimens UQF 81438 and 81439 (to left) from UQL 3127, x5. B, C, E, holotype, lateral, ventral and dorsal aspects of internal mould UQF 81419 from UQL 4514, x3. D, F, G, detail of surface, x10 and dorsal and lateral aspects of latex cast, x2.5, for UQF 81409 from UQL 1383. UQF 81410 lies to the right in G.

Fletcherithyris **sp.**

Fig. 178

A specimen from UQL 4606, *Bookeria pollex* Zone, with valves conjoined has dental plates and septalium raised on a median septum. It is slightly larger and distinctly more transverse and oval in shape than the other *Fletcherithyris* from the lower and middle Tiverton Formation.

Fig. 178. *Fletcherithyris* sp. , dorsal aspect of internal mould UQF 81411 from UQL 4506, x3.

Family **GILLEDIIDAE** Campbell, 1965

Diagnosis: No dental plates, crura arising directly from crural plates sited on floor of valve or uniting to form cruralium.

Subfamily **GILLEDINAE** Campbell, 1965

Diagnosis: Shells smooth or simply plicate, shoulders of ventral valve with thick callus deposits. No dental plates, inner hinge plates rarely united, usually sessile or lost, no median septum.

Discussion: There is some similarity to Heterelasminidae Licharew, 1956, as assessed in Waterhouse (1987a). The type species *Heterelasmina* Licharew, 1939, *Hemiptychina dieneri* Gemmellaro, 1899 from Sicily, lacks dental plates, and has crura arising from a slender subvertical plate from the floor of the valve, between the dental sockets. There is no sign of an “inner hinge plate perforate apically, free of valve floor and supported by crural plates” that was alleged to be diagnostic for the family (yet not the genus) by Jin et al. (2006, p. 2038). This diagnosis may have been repeated from Stehli (1965, p. 760): there seems to have been an interpretation that the interior had been modified from a cryptonelloid interior, in which a cardinal plate lies between the dental sockets. No evidence for such a view was offered by Stehli (1962, 1965). Nor do the other genera assigned to the Heterelasminidae show a perforated cardinal plate. Stehli (1965, pp. 760-762) discussed the family, and referred *Heterelasmina* to synonymy of *Jisuina* Grabau.

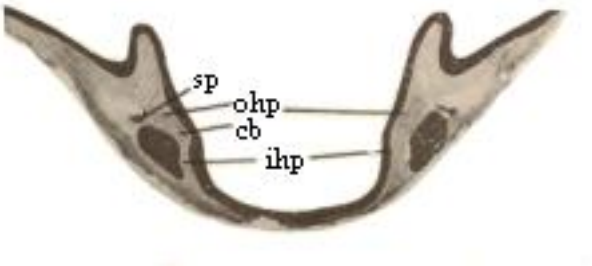


Fig. 179. *Gilledia culburrensis* Campbell, section of dorsal valve showing dental sockets and inner and outer hinge plates, from Campbell (1965, pl. 17, fig. 4), x8 approx. cb - crural base; ihp – inner hinge plate; ohp – outer hinge plate; sp – indicates an unusual cavity and apparent additional plates, not normal for the genus. See Waterhouse (2010a, p. 84, Fig. 35).

The general diagnosis for Gillediidae provided by Jin et al. (2006) stated that outer hinge plates were attached to socket ridges, or directly to the floor of the valve, and that inner hinge plates were absent or small and joined to the floor of the valve along their inner edges, or broad and uniting to form a sessile septalium. But

Waterhouse (2010a) demonstrated that for *Gilledia* Stehli, type species *Terebratula cymbaeformis* Morris, 1845, the outer hinge plates were attached to the socket plates, and joined by low inner hinge plates resting on the floor of the valve, and bearing the crural bases. The relationship is especially well illustrated for *G. culburrensis* by Campbell (1965, pl. 17, fig. 3-5) as reproduced in Fig. 179. The dorsal interior thus approaches that of Tribe Plectelasmini Waterhouse, 2010a, based on Permian genera in west Texas, and the genus is distinguished by the lack of dental plates from the ventral valve, and also by the larger size. Other genera that show essentially similar interior include *Lowenstamia* Stehli, *Pyandzhelasma* Smirnova & Grunt, and *Tacinia* Glushenko. *Aneuthelasma* Cooper & Grant, although included in Gillediidae by its authors as accepted uncritically by Jin et al. (2006, p. 2041, pl. 762, fig. 26-61), lacks outer hinge plates, and may belong within Heterelasminidae. *Camerelasma* Cooper & Grant (1976b, pl. 745, fig. 57, pl. 763, fig. 36-51, pl. 764, fig. 1-20) may be similar: figures are obscure and the text not clear, but it seems likely that the genus is close to *Aneuthelasma*.

Genus ***Gilledia*** Stehli, 1961

Type species: *Terebratula cymbaeformis* Morris, 1845, p. 278 from upper Elderslie Formation (Roadian), north Sydney Basin, New South Wales, OD.

Diagnosis: Small to large shells with short terebratuliform loop, transverse band often incomplete.

Discussion: This genus was discussed in Waterhouse (2010a, pp. 83, 84), in showing that the outer hinge plates were normally if not always attached to the socket plates, and did not connect with the floor of the valve to form a tented structure, unlike the arrangement in *Beecheria* Hall & Clarke*.* Whether the presence of the inner hinge plates is as variable as stated in Jin et al. (2006, p. 2041) seems open to question.

Gilledia homevalensis Campbell, 1965

Fig. 180 - 182

1964b *Gilledia* sp. Hill & Woods, pl. P7, fig. 1-4.

1965 *Gilledia homevalensis* Campbell, p. 74, pl. 1, fig. 1-27, pl. 9, fig. 33-41, text-fig. 27-29.

1972 *G. homevalensis* – Hill, Playford & Woods, pl. P7, fig. 1-4.

Holotype: UQF 20825 from unstated level in Tiverton Formation, Homevale, figured by Campbell (1965, pl. 1, fig. 15-19), OD.

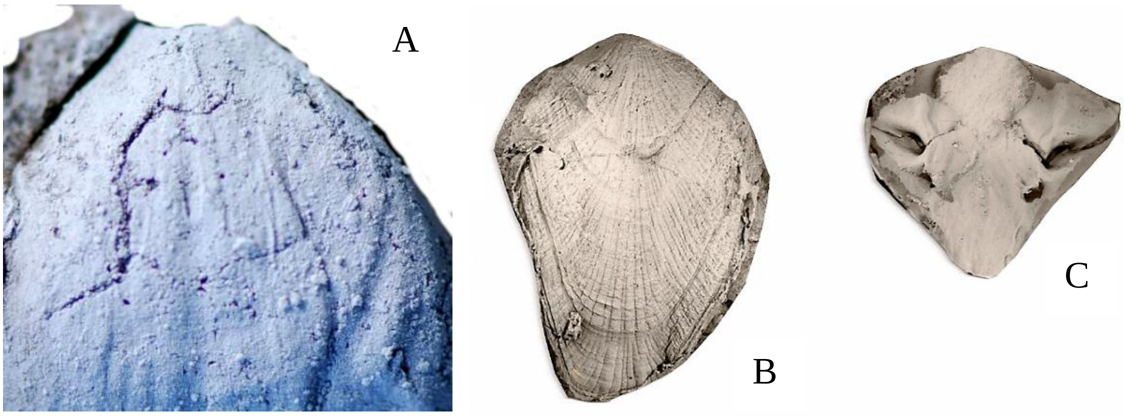


Fig. 180. *Gilledia homevalensis* Campbell. A, posterior ventral internal mould showing floor markings, UQF 81439 from UQL 4510, x2. B, latex cast of ventral valve UQF 81415 from UQL 4511, x1. C, latex cast of cardinalia, ventral valve on top, UQF 81416 from UQL 2622, x1.5.

Diagnosis: Moderately large shells with broad anterior flattening of sulcus ventrally, dorsal valve well inflated, surface marked by divaricating ribs, foramen strongly labiate, inner and outer hinge plates very narrow, dorsal pedicle adjustor scars short.

Material: Specimens from UQL 1383, 1619, 2622, 2626, 2628, 3127, 4510-4512, 4514 and 4519. *Bookeria geniculata* Zone, rare in *Taeniothaerus subquadratus* Zone.

Dimensions in mm: both valves, internal moulds

UQF	UQL	Width	Length	Height
81418	1383	19	30	13
81417	4511	22.5	35+	19.5
81416	2622	27	40+	20

Description: A specimen from UQL 4610 is over 38mm long and 27mm wide. Broken external moulds are available, showing the characteristic large size and fine surface ribs. Grooves radiate from the middle of the shell, aligned longitudinally along the center, and to each side curve towards the anterior lateral margin.

Fig. 181. *Gilledia homevalensis* Campbell, dorsal aspect of internal mould UQF 81418 from UQL 1383, x 2.

Aspects of the interior are well displayed, to show that no dental plates are developed, and preserving muscle impressions over the posterior ventral valve. The crural plates arise from the floor of the valve, and extend laterally to join the socket plates. There is no median septum.

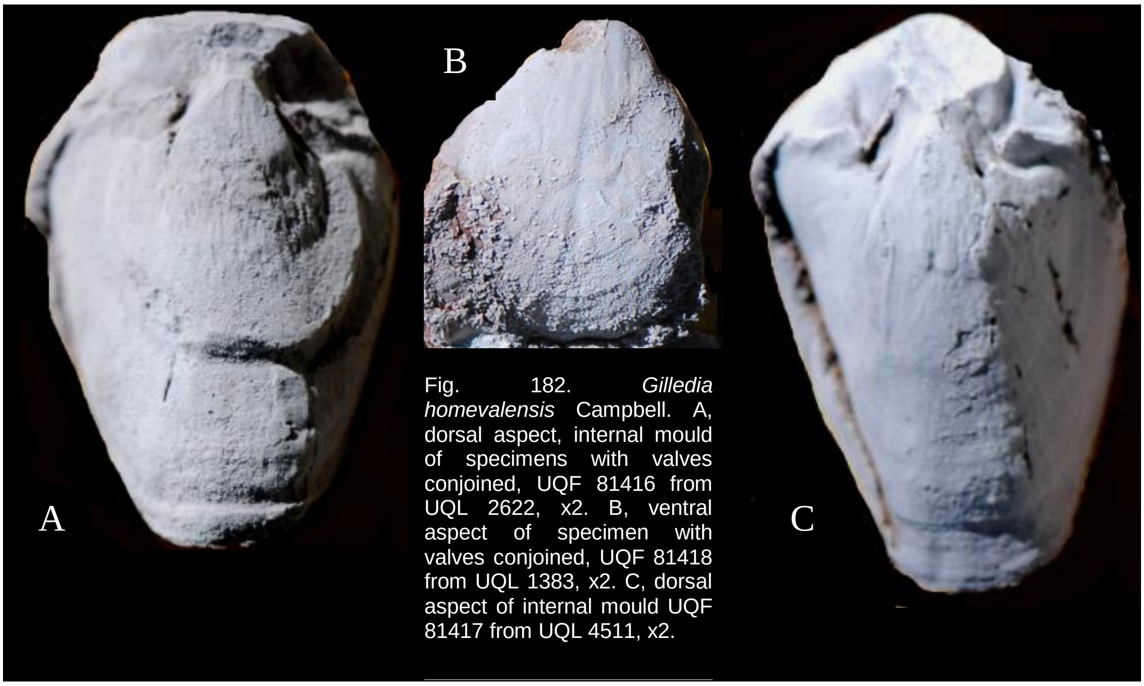


Fig. 182. *Gilledia homevalensis* Campbell. A, dorsal aspect, internal mould of specimens with valves conjoined, UQF 81416 from UQL 2622, x2. B, ventral aspect of specimen with valves conjoined, UQF 81418 from UQL 1383, x2. C, dorsal aspect of internal mould UQF 81417 from UQL 4511, x2.

Resemblances: This species was described by Campbell (1965) from the Tiverton Formation at Homevale, as well as from the Dilly beds (now Riverstone Sandstone Member) of the southeast Bowen Basin, and from the Farley Formation of the north Sydney Basin in New South Wales. The latter specimens were compared, but seem identical. The material identified as *Gilledia homevalensis* by Runnegar & Ferguson (1969, pl. 2, fig. 21, 22) from the lower South Curra Limestone of Gympie has somewhat similar ornament of low radial ribs. But the interior is that of *Fletcherithyris* Campbell, with high dorsal median septum supporting a septalium, as shown by Waterhouse & Balfe (1987, pl. 2, fig. 13-15). The radials are strong and separated by narrow grooves, much as in *Gilledia*, and not like the radials of *Fletcherithyris farleyensis faba*. A somewhat similar specimen has been reported by J. Begg and H. Campbell, GNS, Lower Hutt, New Zealand, in the *Echinalosia conata* Zone of the upper Takitimu Group in New Zealand, but the two are not conspecific, the New Zealand species being distinguished by a deep sulcus bordered by carina in the ventral valve, and a median fold in the dorsal valve.

Subfamily **MAORIELASMINAE** Waterhouse & Piyasin, 1970

Diagnosis: Large shells without dental lamellae, large and well formed septalium.

Discussion: *Maorielasma* Waterhouse, 1964a is widespread in eastern Australia (Campbell 1965), and is based on *M. imperatum* Waterhouse from the Mangarewa Formation (Capitanian) of New Zealand. It differs from *Hoskingia* Campbell in lacking dental plates, and is placed in Maorielasminae Waterhouse & Piyasin, 1970. Because of the absence of dental plates, and commissural plication, the genus was treated as a member of Gillediidae by Campbell (1965) and Jin et al. (2006). The nature of the cardinalia strongly suggests a position within Dielasmidae, as concluded in Waterhouse (2010a, p. 82), but on the other hand the large size points to Gillediidae, so that *Maorielasma* could be regarded as a relative, distinguished by the large and well formed septalium adpressed against the floor of the valve. *Hoskingia* Campbell is a large dielasmatid with adpressed large septalium and with dental plates, and arguably *Maorielasma* is more closely related to that genus than to *Gilledia*. The Early Carboniferous genus *Balanoconcha* Campbell, 1957 is also large without dental plates, and has a large septalium, attached laterally to socket plates, and said to be sessile anteriorly, although not all detail is clear.

Genus ***Maorielasma*** Waterhouse, 1964a

Type species: *Maorielasma imperatum* Waterhouse, 1964a, p. 175 from upper Mangarewa Formation (Capitanian) of New Zealand, OD.

Diagnosis: Medium to large, ornamented only by growth lines and rugae, no dental plates, large sessile septalium. No radials.

Maorielasma balfei n. sp.

Fig. 183

Derivation: Named for Paul Balfe.

Holotype: UQF 81414 from UQL 4511, Tiverton Formation, figured as Fig. 183A, here designated.

Diagnosis: Medium size for genus, long weakly concave or concavo-convex posterior walls in ventral valve, maximum width placed well forward, ventral valve with narrow sulcus posteriorly and broad anterior sulcus that may bear median swelling.

Material: Single ventral valves from UQL 4510, 4511 and 4513. *Bookeria geniculata* Zone. A possible dorsal valve from UQL 4519. *Taeniothaerus subquadratus* Zone.

Dimensions in mm:

UQF	UQL	Width	Length	Height	Valve
81414	4511	22	31	10	ventral
81613	4519	12.5	15	3.5	dorsal

Description: Shell elongate, maximum width just in front of mid-length, broad and shallow anterior sulcus, large permesothyrid foramen with well formed labrum, no radial ornament, no dental plates. The dorsal valve has septalium, dental sockets that are broad, and sturdy median septum, lower than in *Fletcherithyris farleyensis faba* Campbell.

Resemblances: The ventral valves are shaped and ornamented differently from Tiverton *Gilledia*, and belong to *Maorielasma*. No species so far described from east Australia or New Zealand comes close in shape. The species *Maorielasma inflata* Waterhouse (1987a, pl. 13, fig. 17-19) from the Rose's Pride Formation, southeast Bowen Basin, is closest in age, but is much more swollen. Two further species from the Middle Permian of east Australia, *M. callosum* Campbell (1965, p. 96, pl. 4, fig. 20-25, pl. 14, fig. 1-8; Waterhouse 1987a, p. 48, pl. 13, fig. 23) from the Ingelara Shale, Barfield Formation and Flat Top Formation in the Bowen Basin, and *M. globosum* Campbell (1965, p. 97, pl. 4, fig. 1-19, pl. 14, fig. 9-16, text-fig. 40) from the Mantuan shell bed in the Peawaddy Formation (north Bowen Basin) are larger with posterior ventral walls more rounded in outline, and no ventral groove or anterior sulcus. This latter species appears to be conspecific with the type species *M. imperatum* Waterhouse (1964a, p. 175, pl. 34, fig. 3-

5) from the Mangarewa Formation of Wairaki Downs, south New Zealand (see also Waterhouse 1982a, p. 65, pl. 18, fig. a, f, g) and from the Flat Top Formation of the southeast Bowen Basin. The present species is the oldest known, and readily distinguished.

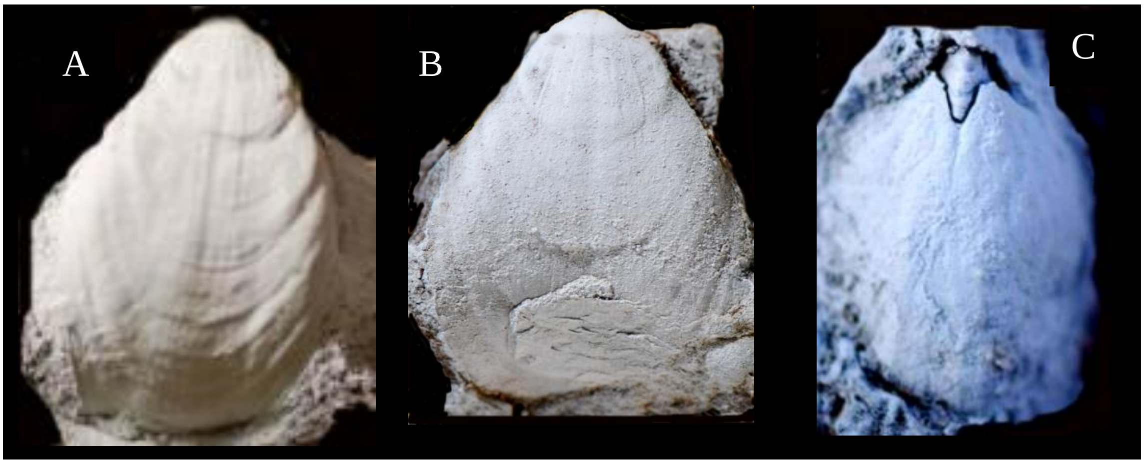


Fig. 183. *Maorielasma balfei* n. sp. A, holotype, ventral valve UQF 81414 from UQL 4511, x2. B, ventral valve UQF 81435 from UQL 4513, x2. C, dorsal internal mould UQF 81613 from UQL 4519, x1.5.

Superfamily **CRYPTONELLOIDEA** Thomson, 1926

Family **CRANAENIDAE** Cloud, 1942

Subfamily **GIRTYELLINAE** Stehli, 1965

Genus ***Eremithyris*** Bruegge, 1973

Type species: *Eremithyris muhlbergensis* Bruegge, 1973, p. 199 from Zechstein (Wuchiapingian), Germany, OD.

Diagnosis: Small to small medium broadly subpentagonal shells, widest near mid-length, with rectimarginate or uniplicate anterior margin, dental plates, imperforate hinge plate supported by median septum, loop deltiform.

Discussion: The Permian Terebratulida of eastern and Western Australia are dominated by Dielasmoidea in a few widespread genera represented by a number of species, as shown by Campbell (1965) in his extensive study of the group. Two exceptional and rare genera, represented by a few specimens, were found by Campbell (1965) in the Middle Permian of the Bowen Basin, and identified as ?*Pseudodielasm*a Brill and ?*Glossothyropsis* Girty. ?*Pseudodielasma* sp. was reported from the Flat Top Formation and “Big Strophalosia Zone” of the southeast and northern Basin Basin, and lacked dental plates and showed narrow outer hinge plates attached to the inner socket ridges. ?*Glossothyropsis* came from the Ingelara Shale of the southwest Bowen Basin, and is closer to the present material. It has a sulcate anterior commissure, dental plates, and shallow septalium supported by a sturdy dorsal median septum. No further examples of these genera have been found. In this study, another rare genus is added, represented by a few well preserved specimens in the upper middle Tiverton Group. The generic position is uncertain. The form is assigned to *Eremithyris* Bruegge, described from the Zechstein (Lopingian) of Germany, but the loop remains undetermined. The species is named in view of its implications in regard to distribution of both the genus and superfamily.

Eremithyris? longiquincus n. sp.

Fig. 49B, 184 - 186

Derivation: longinquincus – remote, distant, Lat.

Holotype: UQF 81420 from UQL 4518, Tiverton Formation, figured as Fig. 185A, here designated.

Diagnosis: Small and relatively transverse in shape, rectimarginate or weakly uniplicate, permesothyrid foramen, dental plates well formed and divergent, hinge plate entire without foramen, deeply concave in section, supported posteriorly by short thick septum.

Material: Two dorsal valves from UQL 4518, one from UQL 4516 and ventral valve from UQL 2626, several specimens from UQL 4519. *Taeniothaerus subquadratus* Zone.

Fig. 184. *Eremithyris? longiquincus* n. sp. Specimens including UQF 81422 and UQF 81423 scattered over small slab from UQL 4519 with dorsal valve of *Costatumulus tumida* UQF 81424, *Orbiculipecten* and *Ambikella* (lower right), x2 approximately.

Dimensions in mm:

UQF	UQL	Width	Length	Height	Valve
81421	2626	7.5	8.5	3.5	ventral
81420	4518	10.5	9.5	4	dorsal

Description: Specimens small, ventral valve elongately ovoid, foramen large, permesothyrid, posterior walls diverging at 63^o, maximum width placed near anterior third, shallow short groove in front of foramen, anterior commissure rectimarginate or transverse, hinge moderately wide, weak anterior growth wrinkles over shell anteriorly, anterior margin weakly uniplicate, anterior shell curves abruptly at right angle to commissure in one specimen. Dental plates divergent and short, posterior floor of ventral valve marked by light radial striae, and median pair of light adductor impressions, within small pair of posterior-lateral closely striated pedicle adjustor impressions. Dorsal valve with widely divergent well formed non-crenulate sockets, joined by inner hinge plates that form V-shaped shelf, not perforated, and less than 1.5mm long, supported by very short high septum 1.5mm long, and extended to mid-length as a very low slender ridge in the holotype. A second specimen UQF 81602 from UQL 4516 shows tiny and apparently tubercular cardinal “process”, bordered anteriorly by low rim arching posteriorly, and non-crenulate sockets. In this specimen, the hinge plate is broad, deeply concave and marked by growth-lines: it is less deeply V-shaped than in the holotype but is damaged, and partly masked in one specimen by spines from a strophalosiid (Fig. 49B, p. 98). Muscle impressions in two pair, a tiny elongately oval posterior pair, and anterior larger ovally elongate pair, floor in front marked by shallow radial grooves. Fine punctae, 80-100 per square millimetre.

Resemblances: The family alliances of these specimens are somewhat obscure, because of the lack of knowledge about the loop. The overall shape and dorsal morphology are consistent with Cryptonelloidea, but unlike most genera of this superfamily, the inner hinge plate forms a concave septalium, whereas in some cryptonellids the plates may fuse with the floor. Moreover the hinge plate is imperforate, unlike the majority of cryptonelloids. Furthermore the rectimarginate to uniplicate anterior commisssure, and lack of dorsal or ventral median sulcus are not common features in the family or superfamily, although typical of several genera. There is some approach in shape to *Eremithyris*, especially in shape. Some aspects also suggest the Mississippian genus *Girtyella* Weller, 1911, but this genus is more elongate with maximum width anteriorly placed. ?*Glossothyropsis* Girty, 1934 was reported by Campbell (1965, p. 107, text-fig. 43, 44) from the Ingelara Shale of the southwest Bowen Basin, as another small cryptonelloid, with dorsal sulcus and long median septum in the dorsal valve. It differs substantially in external

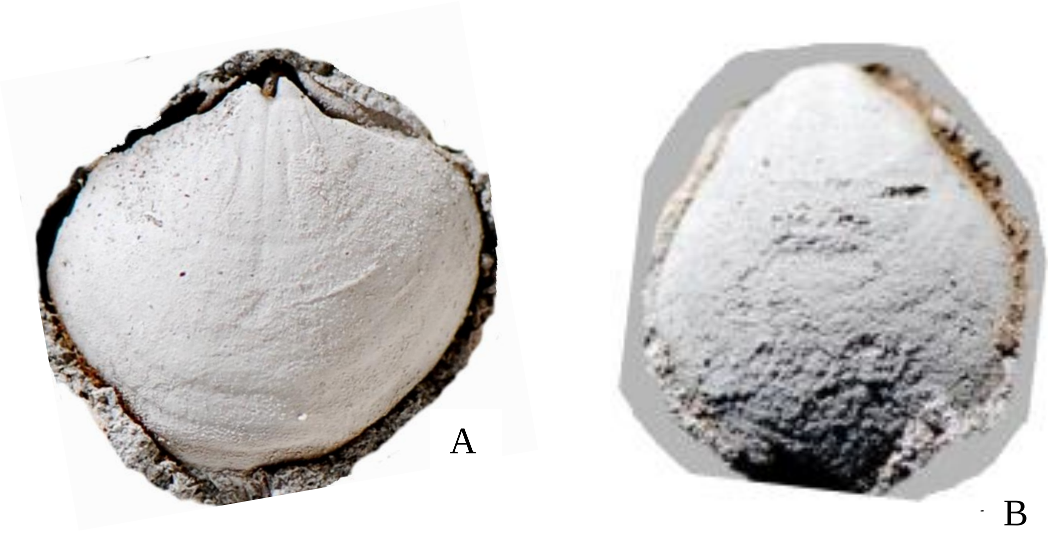


Fig. 185. *Eremithyris*? *longiquincus* n. sp. A, holotype dorsal internal mould UQF 81420 from UQL 4518, x7. B, ventral valve UQF 81421 from UQL 2626, x 6.

appearance, and it is not clear whether or not the septalium was perforate. The Tiverton species must await the discovery of further material for clarification of generic and family relationships.

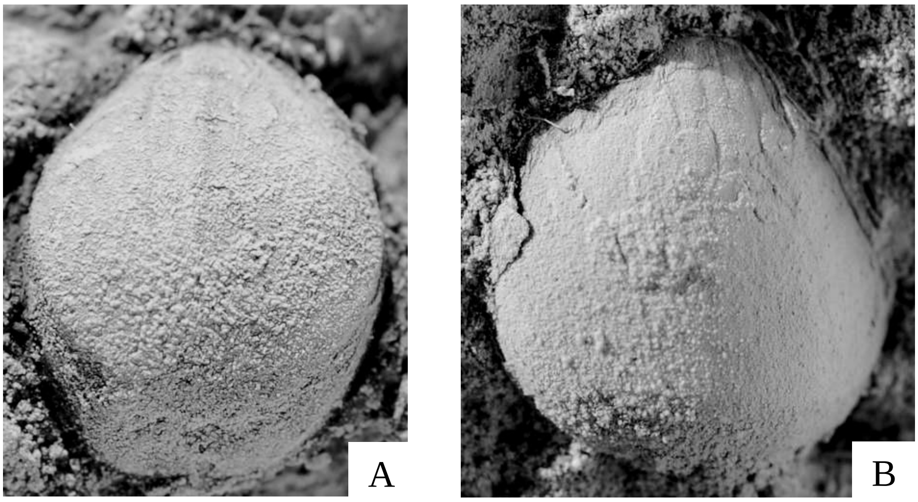


Fig. 186. *Eremithyris*? *longiquincus* n. sp. A, ventral internal mould UQF 81440 from UQL 4518, x5. B, ventral internal mould UQF 81602 from UQL 4516, x6.

Phylum MOLLUSCA Cuvier, 1797

Class BIVALVIA Linnaeus, 1758

Classification largely follows that summarized by Carter et al. (2011).

Clade EUBIVALVIA J. G. Carter in Carter et al. 2011

Infraclass PROTOBRANCHIATA Pelseneer, 1859

Subclass PALAEOTAXODONTA Korobkov, 1954

Superorder NUCULIFORMII Dall, 1889

Order NUCULIDA Dall, 1889

Superfamily **NUCULOIDEA** Gray, 1824

Family **NUCULIDAE** Gray, 1824

Subfamily **PALAEONUCULINAE** Carter, 2001

Genus ***Yanceyopsis*** Waterhouse, 2010a

Type species: *Quadratonucula stella* Yancey, 1978, p. 320 from Riepetown Formation (Cisuralian), Nevada, OD.

Diagnosis: Umbones broad, sited near mid-length, anterior shell higher than posterior shell, surface marked by low commarginal growth-lines, teeth similar in number in front of and behind the resilifer, three small pedal scars.

Discussion: This genus differs in several respects from *Quadratonucula* Dickins, 1963 to which Yancey (1978) had referred his species. The posterior shell is not as slender as in *Quadratonucula*, although otherwise moderately close in shape. A resilifer is absent from *Quadratonucula*, and the shell surface bears low commarginal ribs, slightly weaker than in the new form. Unlike *Yanceyopsis*, *Quadratonucula* has twice as many posterior teeth as anterior teeth. Although *Quadratonucula* has been reported widely, it so far is reliably found only in Western Australia and New Zealand (Dickins 1963, Waterhouse 1965a), with occurrences to be expected in east Australia, but not as yet confirmed. Several species have been described from Argentina, and are related as members of Malletiidae, but differ considerably in shape and arrangement of teeth: they are now placed in *Obliquomallus* Waterhouse, 2010a, p. 86). *Nuculopsis* Girty differs considerably in shape, with anterior shell not as developed as posterior shell. *Anthraconeilopsis* Tasch, 1953, p. 391, type species *A. kansana* Tasch, 1953, p. 392 from the Dry Shale of Late Carboniferous age in Kansas shows some approach, but is very small, with exterior unknown, and apparently no resilifer (Waterhouse 2010a, p. 85).

Yanceyopsis alleni n. sp.

Fig. 188B, 189A, H

Derivation: Named for R. Allen.

Holotype: UQF 81453 from UQL 1383, Tiverton Formation, figured herein as Fig. 188B, 189A, H, here designated.

Diagnosis: Umbones placed close to anterior margin which is steeply inclined from the dorsal margin, commarginal ornament of fine ribs, anterior and posterior teeth about the same in number.

Material: A few valves from UQL 1383. *Taeniothaerus subquadratus* Zone.

Dimensions in mm: right valve

Length	Height	Width
8	8	2.3

Description: Shells small with umbones placed very close to anterior margin, outline subquadrate except for extended ventral posterior, no pronounced umbonal ridge, ornament of light close-set commarginal lirae. Hinge taxodont, six anterior teeth, eight posterior teeth, curved towards the umbo, resilifer shallow, widening at just over 90°. Anterior and posterior adductor scars prominent, with tiny retractor scar above posterior adductor, together with one well defined and two further pedal umbonal pits below umbo, pallial line entire, anterior inner margin smooth.

Resemblances: This species is close to *Yanceyopsis stella* (Yancey, 1978), but has more anterior umbones.

Superorder NUCULANIFORMII Carter, Campbell & Campbell, 2000

Order NUCULANIDA Carter, Campbell & Campbell, 2000

Superfamily **MALLETIOIDEA** H. Adams & A. Adams, 1858 (d' Orbigny 1846)

Family **MALLETIIDAE** H. Adams & A. Adams, 1858

Subfamily **PALAEONEILINAE** Babin, 1966

Genus ***Palaeoneilo*** Hall & Whitfield, 1869

Type species: *Nuculites constricta* Conrad, 1842, p. 249 from Upper Devonian of New York, SD Hall (1885, p. xxvii).

Diagnosis: Faint posterior groove and no internal septum, ornament commarginal.

Discussion: There is a regrettable history of ill-advised but not entirely uncommon manipulation of nomenclature and authorship for this genus, briefly summarized by McAlester (1968, p. 16).

Palaeoneilo? sp. or spp.

Fig. 187A

Material: An internal mould of a specimen with valves conjoined from UQL 1383, *Taeniothaerus subquadratus* Zone, and an internal mould from UQL 4506. *Bookeria pollex* Zone, Tiverton Formation.

Description: Specimen from UQL 1383 is 8mm long, 5.3mm wide (both valves), with umbones sited 3.5mm from anterior, broad and procrescent, anterior dorsal margin concave in outline, escutcheon well formed; eight to ten anterior chevron teeth and twelve or more posterior teeth, no resilifer. Further detail not exposed. The specimen from UQL 4506 is similar in shape but has more anteriorly placed umbones, 2mm from the anterior in the specimen 10mm long. The hinge shows some 12 anterior and 16 posterior teeth. No resilifer can be discerned, but preservation is not good.

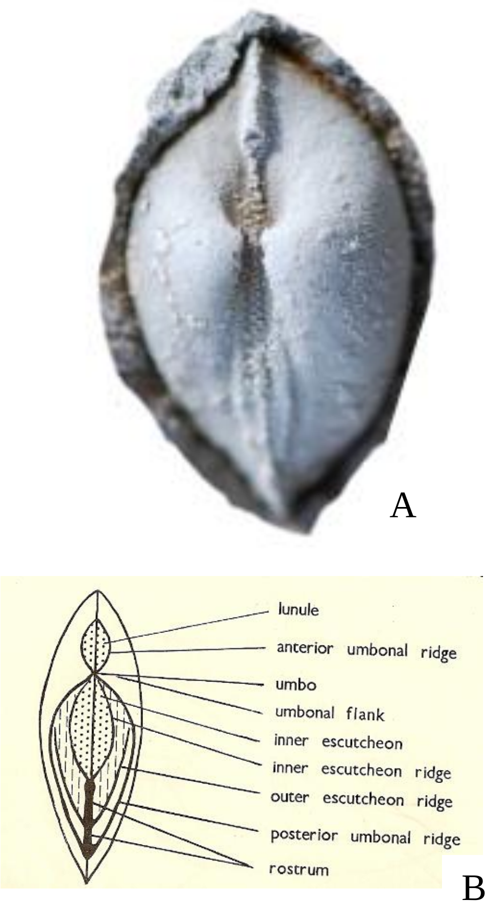


Fig. 187. A, *Palaeoneilo*? sp. dorsal aspect of UQF 81452 from UQL 1383, x6. B, *Glyptoleda*, dorsal view showing exterior along hinge. *Zigzagia stevensi* has a weakly developed or no outer escutcheon ridge.

Resemblances: The Tiverton specimens are close only in a general way to *Palaeoneilo*: they differ externally in lacking strong radial posterior ribbing, but their generic affinities are uncertain.

Superfamily **NUCULANOIDEA** H. Adams & A. Adams, 1858

Family **POLIDEVCIIDAE** Kumpera, Prantl & Ružička, 1960

Discussion: Gonzalez (2006) reviewed the family.

Genus ***Zigzagia*** new genus

Type species:*Glyptoleda buarabae* Campbell, 1951, p. 30 from Buaraba Creek (Wordian), Esk, Queensland, here designated.

Derivation: From the word zigzag.

Diagnosis: Costae form an upright V, axis generally behind the beaks, and additional small V's. Outer escutcheon ridges feebly developed or absent.

Discussion: Unlike *Glyptoleda*, outer escutcheon ridges are weakly developed. Puri (1969) considered that *Glyptoleda* was a subgenus of *Veteranella* Patte, 1926, and this was followed by Li Xiaochi & Grant-Mackie (1994, p. 267), whereas Hill, Playford & Woods (1972) synonymized the two. But *Veteranella* has fine ribs forming an inverted V with apex in front of the umbo. The nature of the lunule, escutcheon and interior are not known for *Veteranella*. *V. (Ledoides) langonensis* Wen Lan (1976, p. 29, pl. 19, fig. 48-52) is readily distinguished, with commarginal ribs over the first formed part of the shell, succeeded by radial ribs crossing the commarginals over the rest of the shell. It was described from the mid-Triassic of China.

Glyptoleda used to be regarded as characteristic of Middle Permian faunas in east Australia, but a distinct species is found in the late Early Permian *Ingelarella plica*

Zone of the upper Tiverton Formation, called *G. javesi* Waterhouse, 1983d, of Artinskian age. Here a species is described from the Tiverton Formation that differs from *Glyptoleda* in the lack or poor development of an outer escutcheon ridge, agreeing in that respect with a species described by Campbell (1951) from beds of likely Middle Permian age in the Esk trough north of Brisbane in southeast Queensland.

Zigzagia stevensi n. sp.

Fig. 188A-C, 189B-G

Derivation: Named for Neville S. Stevens.

Holotype: UQF 81454 from UQL 1383, Tiverton Formation, figured herein as Fig. 189B, here designated.

Diagnosis: Small shells with simple open V formed by ribs which later revert to commarginal, outer escutcheon ridge very weak or not developed.

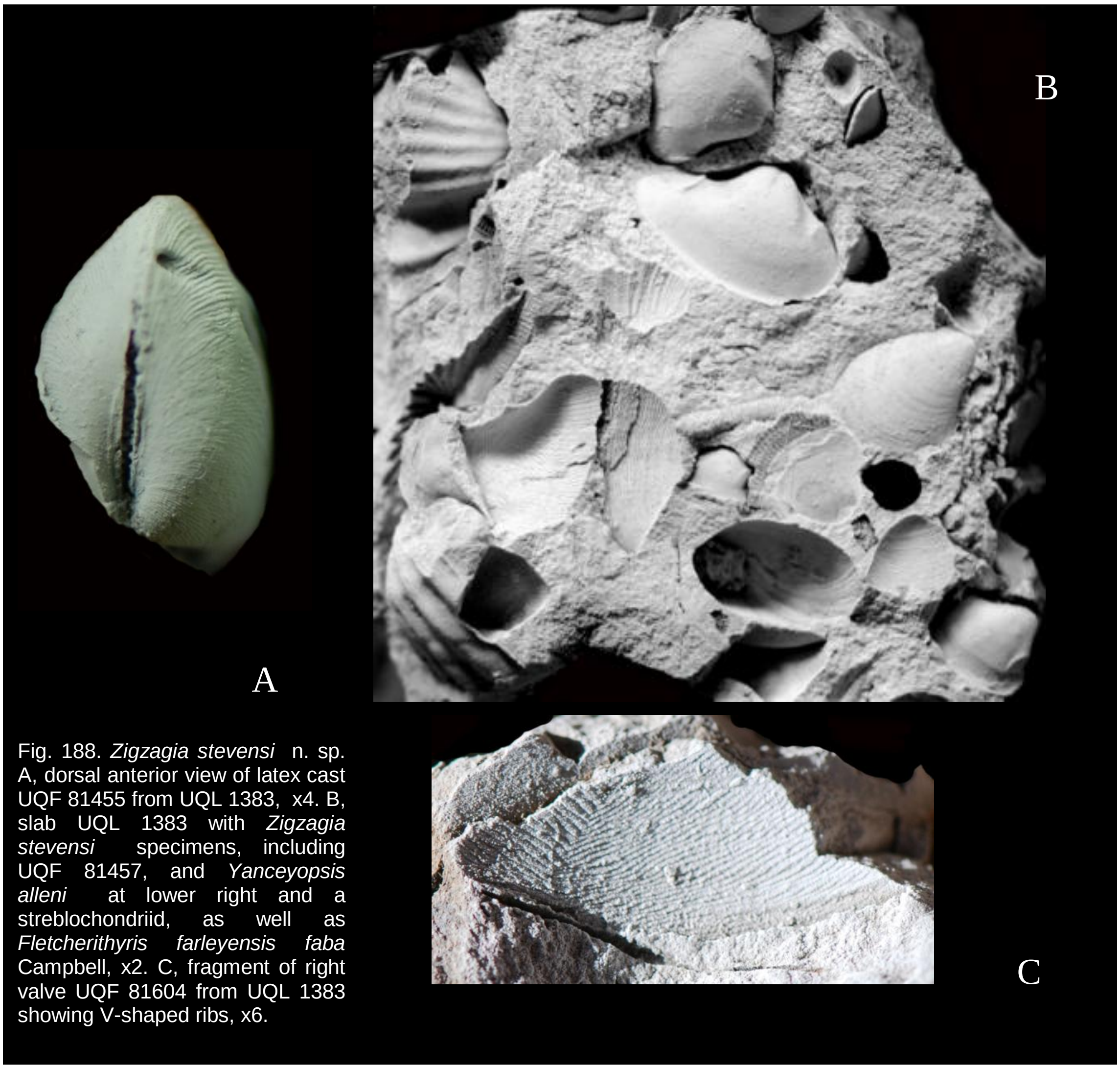


Fig. 188. *Zigzagia stevensi* n. sp. A, dorsal anterior view of latex cast UQF 81455 from UQL 1383, x4. B, slab UQL 1383 with *Zigzagia stevensi* specimens, including UQF 81457, and *Yanceyopsis alleni* at lower right and a streblochondriid, as well as *Fletcherithyris farleyensis faba* Campbell, x2. C, fragment of right valve UQF 81604 from UQL 1383 showing V-shaped ribs, x6.

Material: Some six specimens with valves conjoined and a number of single valves from UQL 1383. *Taeniothaerus subquadratus* Zone.

Dimensions in mm:

UQF	UQL	Length	Height	Width	Valve
81457	1383	19	13	9.5	both
81454	1383	13.5	9.4	2.3	left

Description: Shells small, equivalve, elongate, umbones sited in front of mid-length, orthogyrous with angle of 110-115^{o}, anterior shell high, posterior shell tapered, anterior hinge as long as posterior hinge. Lunule slender and weakly defined by low ridge, escutcheon also weakly defined, inner ridge feeble, lacking the outer escutcheon ridge seen in type *Glyptoleda*, but with parallel depression on outer shell. Ribs fine, three or four in 1mm, cover entire valve including lunule and escutcheon, form open ill-defined V below umbones, the pattern differing in each specimen. In one specimen, a shallow V lies below and in front of the umbones. In another, ribs curve parallel to the anterior margin and intersect at an angle with ribs parallel to the ventral margin, and these ribs divert ventrally behind the umbo and intersect another set of ribs parallel to the ventral margin. In a third specimen, an open V is developed behind the umbones after an interval of conformably commarginal ribs. Low and small v's or undulations lie along some rib-bands.

Some eight teeth lie along each anterior hinge, but otherwise dentition and resilifer are obscured. Anterior and posterior adductor scars well impressed, pallial line not clearly defined. Ridge lies below umbo, with large and small pedal scars, varying in size and position on different specimens.

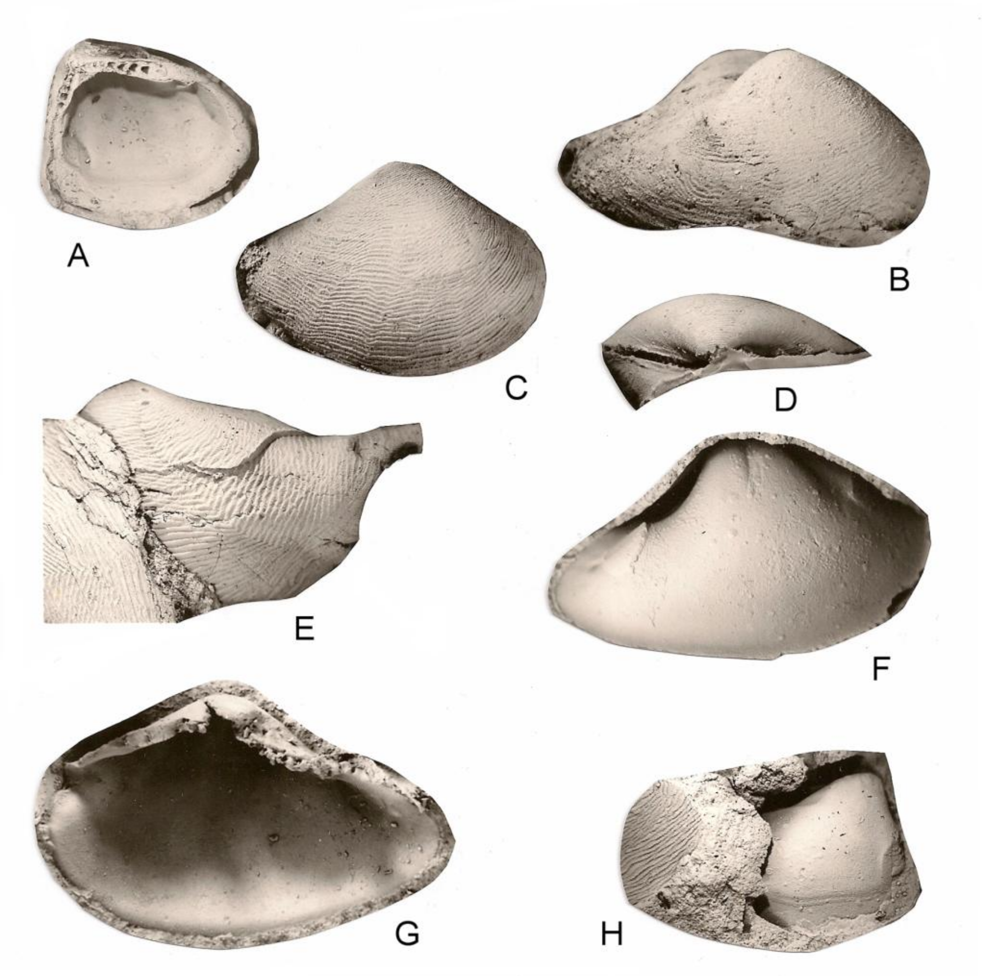


Fig. 189. A, H, *Yanceyopsis alleni* n. sp. , holotype UQF 81453 from UQL 1383, x4, latex cast and internal mould. B – G, *Zigzagia stevensi* n. sp. B, holotype, latex cast of specimen with valves conjoined, UQF 81454 from UQL 1383, x3. C, D, lateral and dorsal views of latex cast of specimen with valves conjoined, UQF 81455 from UQL 1363, x3. E, latex cast of UQF 81458 from UQL 1383, x3. F, G, internal mould and latex cast of UQF 81457 from UQL 1383, x4.

Resemblances: This species is readily distinguished by its ornament and the feebly delimited lunule and escutcheon, and apparently was a forebear of but not the same as younger species typical of *Glyptoleda*. *Glyptoleda javesi* Waterhouse, 1983d from the upper Tiverton Formation in the north Bowen Basin, slightly younger than the present form, is moderately close, but has better defined V-ornament and better defined wide escutcheon with inner and outer bordering ridges. Younger species retained the well developed outer escutcheon ridge and the ribbing developed a still deeper V, as in *G. glomerata* Fletcher, 1945a from the Ingelara Shale and Peawaddy Formation of the Bowen Basin (Roadian, Wordian) and Letham Burn Formation (Roadian) of New Zealand (Wordian). Later species (Capitanian) that are found especially in the *Pseudostrophalosia clarkei* Zone of the upper Mangarewa Formation at Wairaki Downs, New Zealand, such as *G. flexuosa* Waterhouse*, G. intricata* Waterhouse and *G. simplicata* Waterhouse, display as a rule more elaborate V-shaped ornament (Waterhouse 1965a).

From the Buaraba beds of Brisbane valley, southeast Queensland, *Zigzagia buarabae* (Campbell, 1951, pl. 1, fig. 8-12) has more simple ribbing in a slightly erratic wavy pattern, and poorly distinguished outer escutcheon ridges. The ribs are parallel to the ventral margin posteriorly (UQF 12014).

Muromseva (1984, p. 34) reported species of *Glyptoleda* from northeast Russia, and *G. borealis* Biakov (1998, p. 131, fig. 3) is moderately close to the present form in the nature of the open and simple nature of the V-ribs, with a few chevrons, and has 10-14 large anterior teeth and 16 slightly finer posterior teeth. It is much younger than the present form, coming from the ?Capitanian Gijigin beds of northwest Siberia.

Subclass AUTOBRANCHIATA Grobben, 1894

Infraclass PTERIOMORPHIA Beurlen, 1944

Cohort MYTILOMORPHI Férussac, 1822

Order MYTILIDA Férussac, 1822

Superfamily **MYTILOIDEA** Rafinesque, 1815

Family **MYTILIDAE** Rafinesque, 1815

Subfamily **MODIOLINAE** G. Termier & H. Termier, 1950

Diagnosis: Modioliform shells with beak slightly behind anterior margin in most genera, hinge margin smooth or marked by fine vertical striae, radial ornament usually absent or minor, periostracum fibrous hairy as a rule.

Genus ***Promytilus*** Newell, 1942

Type species: *Promytilus annosus annosus* Newell, 1942, p. 38 from Kansas City and Langsing Groups (upper Missourian), Kansas, OD.

Diagnosis: Shell thin, beaks subterminal to terminal, anterior lobe small and set off from rest of shell by broad sulcus extending from beaks to ventral marginal sinuosity, umbonal ridge rounded and curved in outline, hinge line smooth.

Discussion: A summary of some recent views on *Promytilus* is provided in Waterhouse (2008a, pp. 14, 15).

Promytilus homevalensis Waterhouse, 2008a

Fig. 190, 191

1986 *Promytilus* sp. Parfrey, p. 63, Fig. 3.3.

2008a *Promytilus homevalensis* Waterhouse, p. 15, text-fig. 4.

Holotype: Specimen UQF 21190 from Tiverton Formation, figured by Waterhouse (2008a, text-fig. 4) and herein as Fig. 190A, OD.

Diagnosis: Small shells with pronounced sulcus and well curved posterior ridge, umbones subterminal, commarginal growth lines and ridges crossed by irregular fine radial ridges and filae.

Material: Specimens from UQL 1383, 1626, 1628, 3127, 4512, 4519 and 4523. *Svalbardia armstrongi* Subzone and *Taeniothaerus subquadratus* Zone.

Dimensions in mm:

UQF	UQL	Length	Height	Width	valve
81462	4519	40	27	9	left
21901	1620	39	28	8	right

Description: Shells of moderate size, equivalve, with subterminal umbones, umbonal ridge extending at 25-30° from the hinge and curving to lie approximately 50° from the hinge ventrally, anterior shell extends in front of umbones, and broad sulcus extends from under umbo to posterior ventral margin. Hinge just over half of valve length, ligament inconspicuous, posterior margin rounded and extended. Commarginal increments cover shell, about 12 per mm posteriorly, with growth steps and laminae up to 20-22 increments apart, crossed by subfusc slightly erratic and impersistent radial ridges, increasing by intercalation.

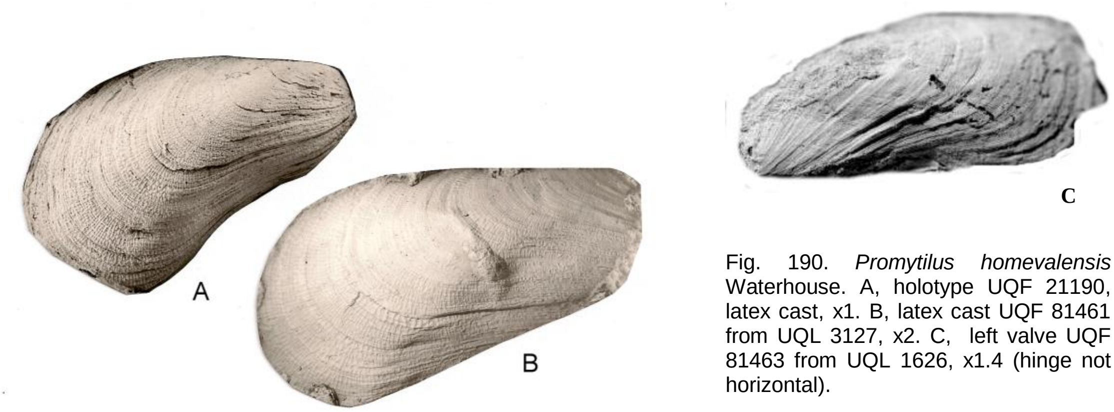


Fig. 190. *Promytilus homevalensis* Waterhouse. A, holotype UQF 21190, latex cast, x1. B, latex cast UQF 81461 from UQL 3127, x2. C, left valve UQF 81463 from UQL 1626, x1.4 (hinge not horizontal).

Resemblances: The specimens described as *Promytilus cancellatus* by Maxwell (1964, pl. 3, fig. 4-6), also figured in Hill & Woods (1964b, pl. P11, fig. 10) and Hill, Playford & Woods (1972, pl. P11, fig. 10), have somewhat similar ornament and subterminal umbones, but lack the curved posterior umbonal ridge and the prominent sulcus, thus approaching *Volsellina* Newell. The species was referred to that genus by Waterhouse (1987b, p. 137) in describing Maxwell's species from the Dresden Formation and lower Elvinia Formation in the southeast Bowen Basin. Maxwell's types come from the Burnett Formation of the Yarrol Basin. Clarke (1992a, p. 34, Fig. 24G-I) reported Maxwell's species as *Promytilus* from the basal Bundella Formation and Tasmanites Shale of Tasmania, but his specimens are very high, with umbones placed far from the anterior and no indication of radial threads. They belong to *Promytilus*, not to Maxwell's species *Volsellina cancellata*.

Fig. 191. *Promytilus homevalensis* Waterhouse, lateral and dorsal aspects of latex cast UQF 81462 from UQL 4519, x3, x2.

Modiolus mytiliformis Etheridge, 1892 from the Middle Permian Flat Top or Barfield Formation of the southeast Bowen Basin is larger with less marked sulcus, stronger umbonal ridge, and less conspicuous radials, compared with the present species. The species was redescribed by Waterhouse (1980, p. 106), in reporting the species as *Promytilus* from the *Pseudostrophalosia clarkei* Zone (Capitanian) of the Mangarewa Formation in New Zealand. The Tasmanian species *Modiomorpha*? *ornatissima* Johnston (1888, pl. 15, fig. 15) from Porter's Hill, Hobart, has a long hinge and less curved outline, as in *Volsellina*.

Promytilus sp. described by Parfrey (1986) from the Camboon Andesite near Biloela, southeast Bowen Basin, is moderately close to Tiverton specimens, especially those figured herein as Fig. 190B, C. The present species is moderately like *Modiolus koneckii* Dickins (1963, pl. 8, fig. 6-11, text-fig. 9) from the Callytharra Formation, Fossil Cliff Formation and base of the Poole Sandstone in Western Australia and differs mainly in the presence of fine ribs. Dickins (1963) discussed the question of whether *Promytilus* should be distinguished from the living genus *Modiolus* Lamarck, and concluded that there appeared little difference, except for a better developed anterior lobe in *Modiolus*. That of the Tiverton species is not quite so prominent, and otherwise is close to *koneckii*, but it is here preferred to use the name *Promytilus.*

Cohort OSTREOMORPHI Férussac, 1822
Subcohort ARCIONI GRAY, 1854
Order ARCIDA Gray, 1854
Superfamily **ARCOIDEA** Lamarck, 1809
Family **PARALLELODONTIDAE** Dall, 1898
Subfamily **PARALLELODONTINAE** Dall, 1898
Genus ***Parallelodon*** Meek & Worthen, 1866

Parallelodon? sp. indet.
Fig. 192

A fragment from the Tiverton Formation at UQL 2628 is allied to this genus and family. It is close to 17mm long and 13mm high, and ornamented by close-set ribs crossed by a few growth lamellae and growth steps. This genus has been recently discussed by Amler (1989).

Fig. 192. *Parallelodon*? sp., external mould of right valve UQF 81460 from UQL 2628, x5.

Subcohort OSTREIONI Férussac, 1822
Megaorder MYALINATA H. Paul, 1936
Order MYALINIDA H. Paul, 1936
Superfamily **AMBONYCHIOIDEA** Miller, 1877
Family **MYALINIDAE** Frech, 1891
Genus ***Pseudomyalina*** Dickins, 1956

Type species*: Pseudomyalina obliqua* Dickins, 1956, p. 26 from Coolkilya Formation (Roadian), Carnarvon Basin, Western Australia, OD.

Diagnosis: Large subtriangular shells with radial ornament and no umbonal plate.

Discussion: *Pseudomyalina* was recognized for a species of Middle Permian (Roadian) age in the Coolkilya Formation of the Carnarvon Basin, Western Australia. In distribution, the genus is restricted to Australia. Dickins (1956, p. 23) emphasized the inequivalved nature, the large size of the prisms making up the shell, and the anterior position of the umbones, but the significance of these factors is discounted, because many species of *Myalina* de Koninck, 1842, as described by Newell (1942), are inequivalve and have anteriorly placed umbones and have large prisms. The Australian genus is particularly close to *Myalina* (*Myalinella*) Newell, 1942, type species *Myalina meeki* Dunbar, 1924, from Desmoinesian to Permian faunas of the United States, but none of the American species developed radial ornament.

Pseudomyalina perquiritus n. sp.

Fig. 193 - 195

1961a *Pseudomyalina* sp. Dickins, p. 124, pl. 16, fig. 11, 12.

1964b *Pseudomyalina* sp. Hill & Woods, pl. P11, fig. 8.

1972 *P.* cf. *mingenewensis* [not Etheridge] – Hill, Playford & Woods, pl. P11, fig. 8.

Derivation: perquiro – ask diligently after, Lat.

Holotype: Specimen UQF 81464 from UQL 3127, Tiverton Formation, figured herein as Fig. 194A, B, 195B, here designated.

Diagnosis: Large triangular shells with low umbones, small anterior wing, radial ribs.

Material: Specimens from UQL 1626, 3127, 4511, 4518, 4519 and 4523. *Taeniothaerus subquadratus* Zone.

Dimensions in mm:

UQF	UQL	Length	Height	Width both	Width left valve	Width right valve	
81464	3127	+89	72	25	17	9.5	holotype
81466	3127	46	47	15	11	5	

Description: Shells triangular-cuneiform in shape, with subdued pointed umbones, umbonal angle of 60° in left valve, and 55° for right valve, shell extended as small anterior lobe, now partly lost. Left valve more inflated than right valve, both valves have steep anterior walls and maximum width lying close to anterior ventral wall. Ornament consists of a number of low round-crested ribs separated by slightly wider interspaces, covering the entire valve. Posterior wing weakly differentiated on left valve, with acute cardinal extremity and concave posterior margin, wing lost from right valves of available material.

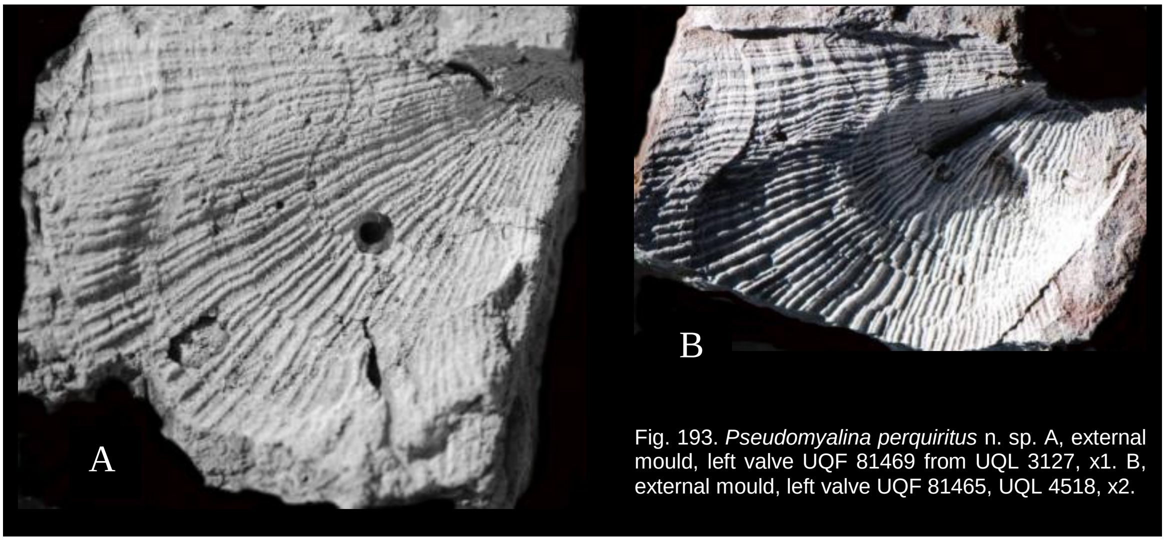


Fig. 193. *Pseudomyalina perquiritus* n. sp. A, external mould, left valve UQF 81469 from UQL 3127, x1. B, external mould, left valve UQF 81465, UQL 4518, x2.

The ligament area is 3.5 to 4mm high, with longitudinal grooves, and there is no umbonal plate. A line of small muscle pits passes posteriorly from the umbones close to the hinge in each valve, and two larger scars are present close to the hinge near the umbo of the right valve. On the left valve a scar of similar size is more ventrally placed. No clearly defined posterior adductor scar is visible on any of the specimens. The shell is prismatic in some specimens, and 3.5mm thick anteriorly, and 1.5mm thick elsewhere. A right valve from UQL 4519 has an outer prismatic layer 0.8mm thick and inner homogeneous layer just as thick. In one specimen the shell is not prismatic, 0.8mm thick anteriorly and 0.4mm thick over most of the right valve, but its structure is not known.

Resemblances: The species is close in size, shape and ornament to *Pseudomyalina obliqua* Dickins from the Coolkilya Formation, Carnarvon Basin, Western Australia, but has more pointed and less prominent umbo. *P. mingenewensis* (Etheridge, 1907, p. 24, pl. 5, fig. 4, pl. 6, fig. 3, 4) from Irwin River, Western Australia, has blunter umbones and possibly larger posterior wings. Figured specimens include only left valve internal moulds and do not show the fluctuating radii mentioned in the text as being preserved on an external mould. The right valve was described as comparatively flat, less inflated than the left valve. Hill, Playford & Woods (1972) compared Tiverton specimens of the present species to Etheridge's form, but the two may be readily distinguished. Dickins (1961a) figured one specimen UQF 21006 from the Tiverton Formation, and another from the Dilly beds, southwest Bowen Basin, deemed to have come from the lower Staircase Sandstone, later revised to Riverstone Sandstone Member.

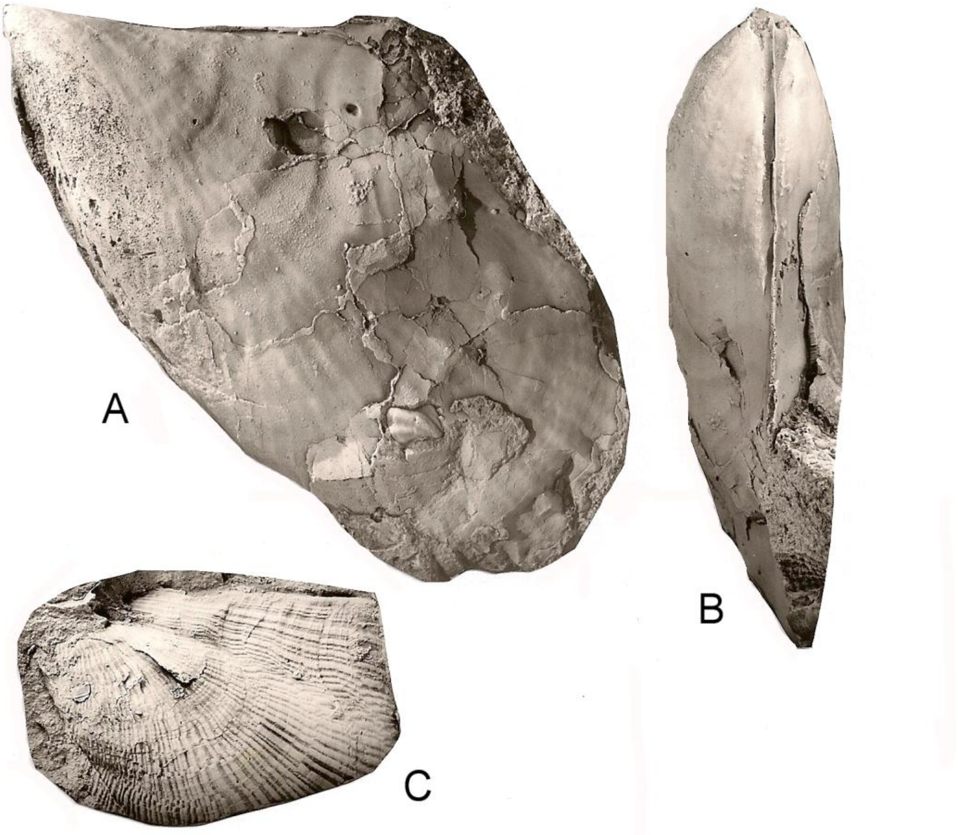


Fig. 194. *Pseudomyalina perquiritus* n. sp. A, B. left lateral and dorsal aspects of holotype with valves conjoined, UQF 81464 from UQL 3127, x1. C, latex cast of left valve UQF 81465 from UQL 4511, x1.

Pseudomyalina sp. A of Dickins (1963, pl. 10, fig. 10-15) is close to the Tiverton species in shape, with reduced anterior lobe, but its costae are separated by wider interspaces. Dickins' material comes from the Fossil Cliff Formation, base of the Poole Sandstone and limestones of the Nura Nura Member in Western Australia.

Superfamily **INOCERAMOIDEA** Giebel, 1852

Family **ATOMODESMIDAE** Waterhouse, 1976c

Diagnosis: Medium to large shells, inequivalve to equivalve, inequilateral, umbones anteriorly placed, byssal notch may be in both valves, ligament lineavincular, posterior adductor scar large, pallial line discontinuous, pitted, shell prismatic.

Discussion: Kolymiidae Kuznetsov, 1973 is close in size, shape and prismatic shell, but a small anterior wing is developed in each valve and a prominent byssal gape may be enclosed by the anterior wings of the two valves, whereas in atomodesmids, the anterior commissure is more adpressed. The muscle field differs considerably in the two families, and the ligament is developed above the inner shell lamellar layer in Kolymiidae, whereas that of Atomodesminae is, at least as a rule, placed above the prismatic layer. Most atomodesmids have an umbonal septum, never found in *Kolymia* or allies. Therefore the claim by some Russian authorities such as Biakov (2008) and Nevesskaya (2009) that atomodesmids belong to Kolymiidae is rejected (Waterhouse 2008a), even though the ligament of the two is regarded as identical (Biakov 1993). It appears that Kolymiidae are like Retroceramidae Pergament in Koschelkina, which is shown to be close in the development of its ligament to the pterioid Isognomonidae (Crampton 1988) and the family overall looks pteriiform, whereas some aspects of morphology in Atomodesmidae point to an ambonychiid alliance. The array of morphologies is diverse and complex. *Permoceramus* Waterhouse, for instance, shares shape and muscle field with *Aphanaia* de Koninck, yet has a ligament like that of *Inoceramus*, with ligament attached to lamellar shell, not prismatic shell (A. Biakov, pers. comm.).

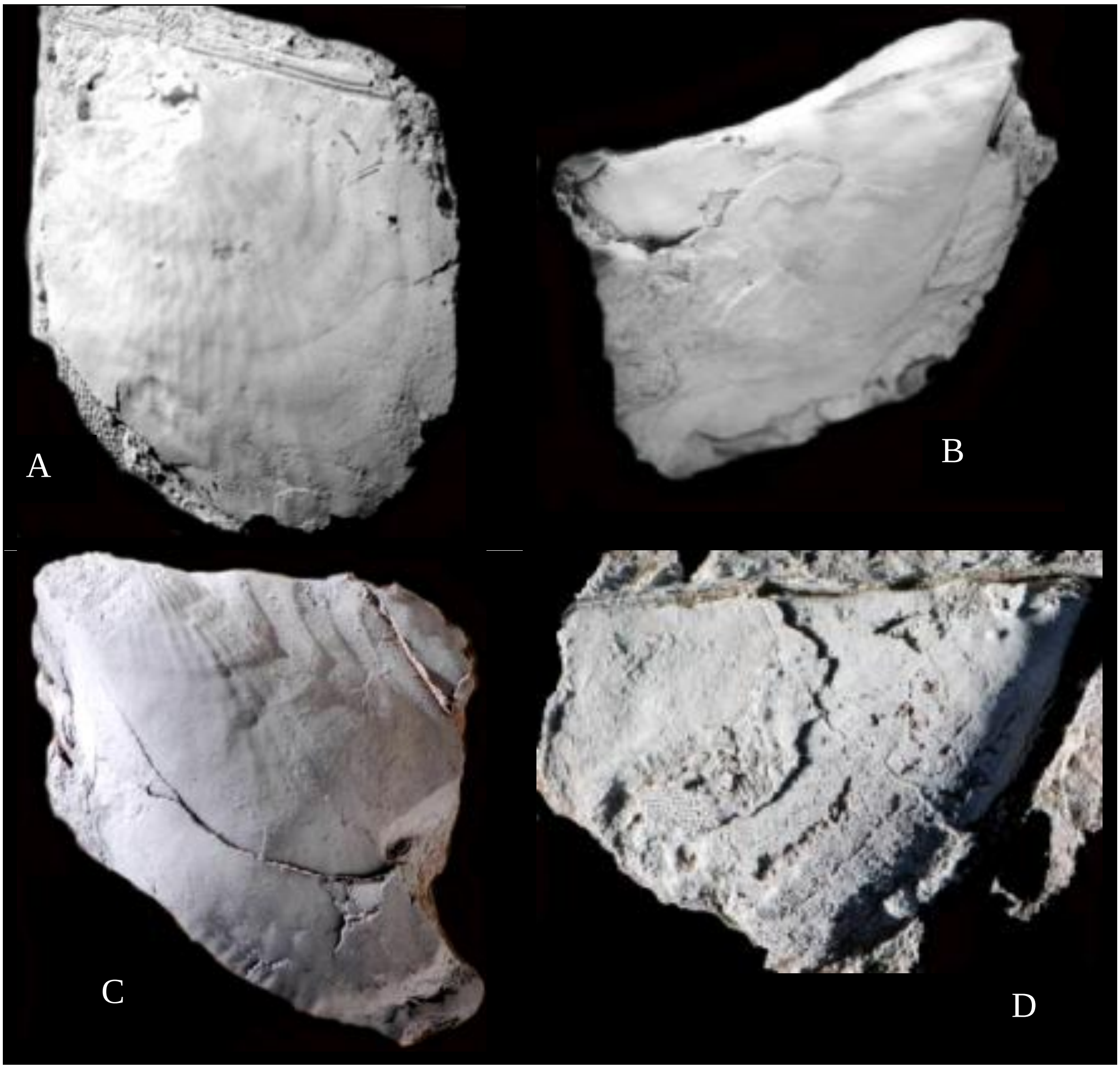


Fig. 195. *Pseudomyalina perquiritus* n. sp. x1. A, internal left valve mould UQF 81466 from UQL 3127, x1. B, right lateral aspect of holotype UQF 81464 from UQL 3127, x1. C, left lateral aspect of specimen with valves conjoined UQF 81467 from UQL 3127, x1.5. D, right valve internal mould UQF 81468 from UQL 4519, x1. A and B are oriented with hinge not horizontal.

Subfamily **ATOMODESMINAE** Waterhouse, 1976c

Diagnosis: Umbonal deck developed below under ligament.

Discussion: Subfamily Malmanininae Waterhouse, 2001, p. 112 lacks the umbonal deck. Members of Atomodesminae are most prominent in Permian temperate paleolatitudes, particularly in Siberia and New Zealand,

and extend widely over Gondwana and into North America.

Nomenclature: The proposal of Atomodesminae by Waterhouse (1976c) was changed by Johnston & Stevens (1985) to Atomodesmatidae. The Greek stem is believed to be desm by some workers, including Sowerby (1838) and Reed (1932), which would mean that Atomodesminae would have been correct according to the arcane rules of zoological nomenclature. Others interpret the stem as desma. Even so, the requirement to derive the stem by deleting the case ending of the appropriate genitive singular (ICZN 1999, Article 29.3) is abandoned for names proposed after 1999 (Article 29.4). In future the time-line, given its arbitrary nature, seems likely to be set aside, and the proposed insertion of "at" may be set aside as overpedantic and without perceptible use or relevance. Whether or not consistency is a virtue, it may be advisable to simplify procedure and get rid of the intrusive "id" and "at".

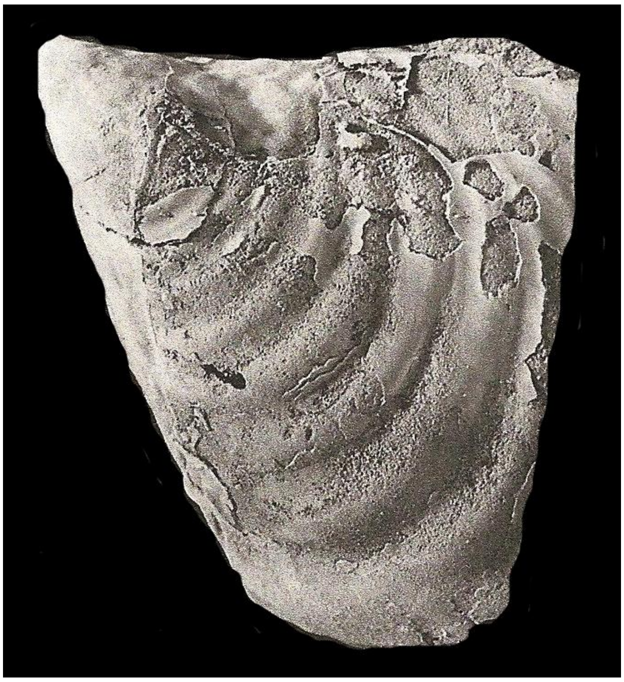


Fig. 196. *Undosusia tivertonensis* (Waterhouse), left valve holotype UQF 54214 from UQL 3127, Tiverton Formation, x1.5. This is based on a specimen collected by B. Runnegar, without detailed stratigraphic information.

Genus ***Undosusia*** Waterhouse, 2008a

Type species: *Aphanaia tivertonensis* Waterhouse, 1979a, p. 4 from Tiverton Formation (Sakmarian), Bowen Basin, Queensland.

Diagnosis: Left valve more inflated than right valve, growth stops moderate on right valve, ornament of persistent regular undulations over entire shell.

Discussion: In studies of Kolymiidae and Atomodesmidae from Permian faunas of northeast Russia, Biakov, 2008 has placed considerable importance on the nature of the ornament, mostly involving commarginal rugae and growth steps. Extending his observations to genera found in Australia and New Zealand, it may be noted that *Maitaia* has low closely spaced commarginal wrinkles, whereas *Mytilidesmatella*, with its characteristic very large umbonal septum, has growth steps and few wrinkles on both valves. *Trabeculatia* Waterhouse shows commarginal rugae on both valves, weaker and less regular than in *Undosusia*, and no growth steps. Both valves are identical in these three genera. Thus *Maitaia, Mytilidesmatella* and *Trabeculatia* probably rested on the anterior face, rather than on the right valve, much as in *Atomodesma* Beyrich (Waterhouse & Chen 2006). They were likely to have been attached by byssal threads, which have left little or no trace in the shell, without the development of a byssal gape.

Forms close to *Undosusia* are *Costatoaphanaia ganelini* Biakov, 2008 from the Kungurian lower Dzhigdali (Djigdali) Formation in the Omolon Massif, northeast Russia, together with *C. popowi* (Muromseva & Guskov) in Muromseva, 1984 from the Kungurian lower Tumara Subformation of west Verchoyan, but in both the rugae are less regular.

In the past, Dickins (1956) and Kaufmann & Runnegar (1975) placed forms allied to but not the same as

Atomodesma in subgenera, but the diversity and number of species is such that full generic standing is indicated, as verified by the studies on Siberian occurrences by Muromseva (1984), Astafieva (1993) and Biakov (eg. 2007, 2008).

Undosusia tivertonensis (Waterhouse, 1979a)

Fig. 196

1975 *Atomodesma (Aphanaia)* sp. Kauffman & Runnegar, p. 31, pl. 2, fig. 1-7, pl. 3, fig. 2, 4-6, text-fig. 1A, C-E.
1979a *Aphanaia tivertonensis* Waterhouse, p. 4, pl. 1, fig. 3, 6, 7, pl. 2, fig. 3.
cf. 1983 *A*. cf. *tivertonensis* – Waterhouse et al., p. 304, Fig. 9-11.
2008a *Undosusia tivertonensis* Waterhouse, p. 31, text-fig. 15.

Holotype: UQF 54214 from Tiverton Formation, Homevale, figured by Kauffman & Runnegar (1975, pl. 2, fig. 2, 3, 6, 7, pl. 3, fig. 2) and Waterhouse (1979a, pl. 1, fig. 3, 6, 7), and herein (Fig. 196), OD.

Diagnosis: Moderately large shells with prosogyrous narrow and extended umbones, high and steep rounded anterior face, moderately large posterior wing, ornament of commarginal wrinkles, broad umbonal septum with straight anterior margin.

Material: Five specimens from UQL 3127 were described by Waterhouse (1979a), and no further specimens have come to hand. The collection was made with no stratigraphic control, and the zone is not known.

Description: A large specimen measured about 60mm in length and 85mm in height, with estimated width of 30mm.

Megaorder OSTREATA Férussac, 1822
Superorder OSTREIFORMII Férussac, 1822
Order OSTREIDA Férussac, 1822
Suborder MALLEIDINA Gray, 1854

Family **PTERINEIDAE** Meek, 1864

Diagnosis: Inequivalve, left valve more inflated than right valve, orbicular to strongly prosocline, with small or obsolescent anterior wings, largely opisthodetic duplivincular ligament, muscles heteromyarian or monomyarian, anterior muscle scar reinforced by buttress in some genera, dentition absent or strong, actinodont or parallelodont, with variable number of small cardinals and commonly posterior laterals diverging from near umbones.

Discussion: In Carter et al. (2011, p. 8), the family was regarded as a paraplesion in the suborder.

Genus ***Merismopteria*** Etheridge, 1892

Type species: *Pterinea macroptera* Morris, 1845, p. 276 from Spring Hill (?Guadalupian), Tasmania, OD.

Diagnosis: Shells procrescent with anteriorly placed umbones, well formed posterior wings, anterior ventral extension, no anterior wing, left valve more inflated than right, commarginal ribs. Myophoric buttress, anterior and posterior adductor scars, pedal retractor pits, anterior pallial line usually discontinuous, exceptionally entire.

Discussion: Newell & LaRoque (1969, p. 301) stated that the pallial line in *Merismopteria* is discontinuous anteriorly, and this is confirmed by Dickins (1960, text-fig. 1.1) for the type species. But the present species includes specimens which have a pallial line that is either entire or crinkled but virtually continuous, as well as others with discontinuous pallial line. In other respects, the species conforms to the diagnosis standard for *Merismopteria*.

Merismopteria cona n. sp.

Fig. 41A, 197

Derivation: Named from Mt Cona, near Homevale Station.

Holotype: UQF 81470 figured herein as Fig. 197A, F, from UQL 4506, Tiverton Formation, here designated.

Diagnosis: Prosocline small shells with moderate anterior lobe, defined commarginal ribs, pallial line entire as a rule.

Material: Specimens from UQL 4505 and 4506. *Bookeria pollex* Zone.

Dimensions in mm:

UQF	UQL	Length	Height	Width both	
81470	4506	45	28	14.5	holotype
81471	4506	48	32	25	

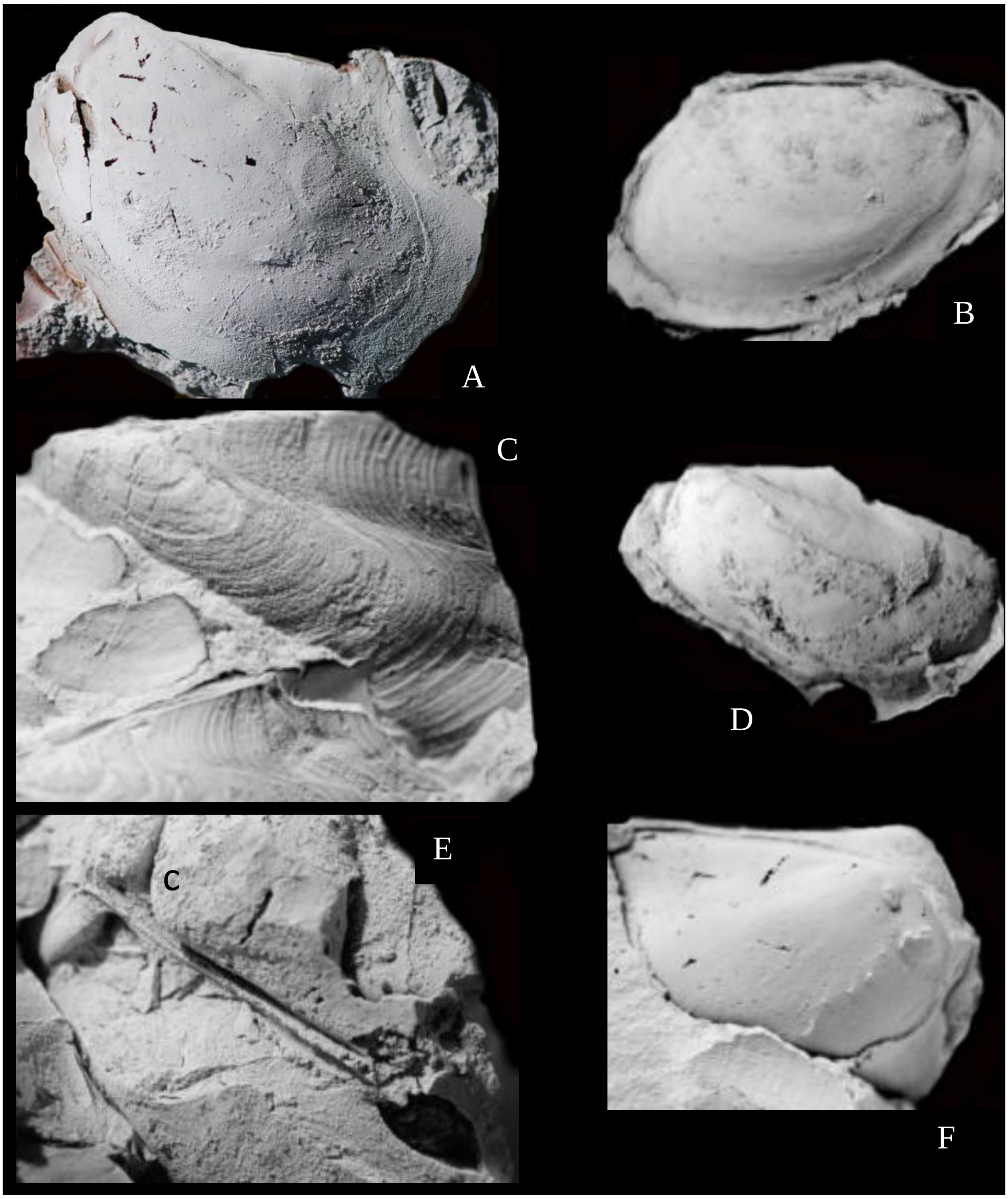


Fig. 197. *Merismopteria cona* n. sp. from UQL 4506. A, F, holotype, internal mould, left valve aspect of UQF 81470, x1.6, and anterior of right valve, x2. B, left aspect of internal mould UQF 81595, x1.5. C external mould and specimen showing posterior dorsal shell on two specimens, UQF 81473 and UQF 81474, x 3. D, internal mould of left valve UQF 81471, x1. E, dorsal aspect of internal mould with valves conjoined showing hinge and clavicle c, UQF 81472, x2. Hinge not horizontal for A and E.

Description: Shells strongly prosocline, inequivalve, the left valve more inflated than the right, with anteriorly placed umbones, for which the angle measures 95°, and conspicuous posterior umbonal ridge. A small anterior bulge extends in front of the umbo, and a long slender posterior wing is developed in each valve, with acute posterior cardinal extremity, the angle varying from 50-110°, not extending as far back as the body of the shell, posterior margin concave in outline. Ornament of close-set growth lirae, five to six in 5mm, becoming better spaced ventrally and over much of the posterior wing. Internally, the myophoral ridge or clavicle low to moderately developed. The ligament area is internal, slender and linear behind the beaks, bearing two grooves and ridges, and long blade-like tooth at the posterior end. The right valve shows an anterior tooth in front of the clavicle, and two dental sockets. Two deep pedal retractor muscle scars lie over each umbo behind the clavicle, and a small anterior adductor scar is sited low on the valve and is attached dorsally to a retractor pedal scar. Small mantle insertion pits lie over the dorsal shell, especially in the umbonal cavity. Posterior adductor scar large and high, placed over umbonal ridge (Fig. 197A); pallial line entire anteriorly in most specimens and passes well below the anterior adductor scar, unlike the arrangement shown for *Merismopteria carrandibbensis* (Dickins 1957, text-fig. 1) in which the pallial pits are aligned with the base of the adductor scar.

Resemblances: This species is moderately close in size and shape to the material at Harper's Hill in the Allandale Formation, Hunter Valley, New South Wales, described as *Modiolopsis imbricata* Dana (1847, p. 159), and figured as *Cypricardia* by Dana (1849, pl. 8, fig. 5, 6, 7) and refigured as *Merismopteria imbricata* by Waterhouse (1988, pl. 1, fig. 4, 6, 7, 11). The lectotype, designated by Waterhouse (1988, p. 170), is USNM 3461 (Dana 1849, pl. 8, fig. 5; Waterhouse 1988, pl. 1, fig. 4). This specimen is more elongate than the Tiverton shells, and its growth-lines are moderately thick, not fine or lamellar, with six in 5mm dorsally and five in 5mm anteriorly, each 0.5mm thick, and separated by interspaces of comparable width. Another species from the same station was described as *Modiolopsis arcoides* Dana (1847, 1849, pl. 8, fig. 8a, b, ?9), the holotype by monotypy being USNM 3646. [The specimen shown by Dana (1849, pl. 8, fig. 9) was not referred to in the text, unless misrepresented as pl. 9, fig. 8, which is in error (Waterhouse 1988, p. 171)]. The type specimen is smaller than *imbricata*, with possibly less anterior sulcus, and distinctly higher shape. Being decorticated, the ornament is not clear. The specimen CASM E10748 figured as *Modiola crassissima* by M'Coy (1847, pl. 15, fig. 2) from Harper's Hill, selected as lectotype by Waterhouse (1988, p. 171), approaches the lectotype of *imbricata* Dana. A second figured specimen from Harper's Hill, *Modiola crassissima* M'Coy (1847, pl. 15, fig. 3), is large with conspicuous anterior bulge, deep sulcus and long hinge, and presumably represents the mature *imbricata*. The species *arcoides* and *imbricata* were referred to *Merismopteria* by Etheridge (1919, p. 192), and refigured and synonymized by Waterhouse (1988, p. 170, pl. 1, fig. 4, 6-9, 11), together with *crassissima*, although such a synonymy is based on very few specimens and it would be desirable to have a much larger collection of specimens for assessment. The specimens overall have a conspicuous anterior ventral bulge, and slightly longer posterior wing and lower ornament than in *Merismopteria cona*. Dickins (1981, p. 28, pl. 2, fig. 14, 15) described small and somewhat squashed specimens from the Warwick area, south Queensland, as *Merismoptera* cf. *imbricata*, but they are not very close to Dana's type or to present material.

Merismoptera macroptera (Morris, 1845, pl. 13, fig. 2, 3), also figured by Dana (1849, pl. 8, fig. 4a, b), Waterhouse & Jell (1983, pl. 3, fig. 25, 28) and aff. Dickins (1981, pl. 2, fig. 16) is close, as a larger shell with higher anterior lobe compared with the new species. *Pterinea sublunulata* de Koninck (1877, pl. 26, fig. 4) is probably conspecific. Tasmanian specimens attributed to *macroptera* from the Abels Bay Formation by Clarke (1992a, Fig. 18E, F, H, I) and from the Tasmanites Shale (Fig. 18C, D) and from Bundella Formations (Fig. 22A-F), with outlines provided in Clarke (1992a, Fig. 23), have a particularly large and high anterior lobe and slightly less prosocline outline and deep sinus. They fall close to the specimen assigned to *crassissima* by M'Coy (1847, pl. 15, fig. 3), but are less elongate, and are close to the Morris species.

Leiopteria? carrandibbiensis Dickins (1957, p. 30, pl. 4, fig. 13-17) from the upper Lyons Group, Western Australia, is deemed to belong to *Merismopteria*. It is close to the present species in ornament and shape, with slightly shorter posterior wings and much smaller size.

Order PECTINIDA Gray, 1854

Members of Order Pectinida have an extended anterior shell, and an alivincular ligament as a rule, with well formed resilifer, although initial family groups display a duplivincular ligament which evolved or retromorphed into a replivincular or canalivincular form in later families. Members include free-swimming forms, a marked change from other members of Class Bivalvia. There is a variety of shell composition, calcitic and/or aragonitic, but thick prismatic shell is reduced to outer layers, and internally musculature is normally monomyarian, having changed from the anisomyarian musculature normal for Pteriida.

The classification of fossil Pectinida owes much to the study of the group by Newell & Boyd (1995). They recognized a number of new families that were based on only one genus, which hardly is customary procedure, and must be considered a bold step. Yet their recognition has proved to be justified, for in a further overview of the group by Waterhouse (2008a), it was found possible to reinforce monogeneric families with a number of additional genera, and in some cases, recognize constituent subfamilies.

Suborder ANOMIIDINA Gray, 1854

Hyporder AVICULOPECTINOIDEI Starobogatov, 1992

Diagnosis: Both valves subequally convex or planoconvex, comparably or differently ornamented, shape normally upright, ligament amphidetic.

Discussion: Limidina Waller is distinguished by the generally procrescent outline and modestly developed right anterior auricle and left anterior wing. Shell composition and structure, muscle scars and foot differ considerably in living limids, but Paleozoic limids more closely approach aviculopectens. Heteropectinoidea are distinguished by the unequal valves with different profile and ornament on each, and Monotoidei Waterhouse has opisthodetic or almost opisthodetic ligament, with severely reduced anterior shell and anterior right valve ear which does not contain the ligament (Waterhouse 2008a).

Taxonomy: Nevesskaya (2009, p. 6) ascribed Suborder Aviculopectinidina to Waterhouse (2001), whereas Waterhouse (2008a, p. 70) considered the author of the suborder to be Starobogatov, 1992, whilst substantially modifying the definition and content.

Superfamily **AVICULOPECTINOIDEA** Meek & Hayden, 1865

Diagnosis: Shells biconvex with similar ornament as a rule on each valve, right valve may be slightly less inflated, posterior wings large and well defined or small, umbonal slope steep, large right anterior auricle, deep byssal notch as a rule, may have well developed left anterior auricular sinus, ligament external and amphidetic, alivincular to platyvincular, hinge teeth generally absent, minor if present.

Family **DELTOPECTINIDAE** Dickins, 1957

Diagnosis: Large, biconvex, ornament of radial plicae or subplicae, plain or variably costate, costae may be intercalate or increase by branching on right valve. Large right anterior auricle with deep byssal notch, large left anterior wing, posterior wings small. Ligament normally platyvincular, may be broadly concave, or bear a shallow median depression suggestive of a small resilifer.

Discussion: Externally, members of Deltopectinidae approach those of Aviculopectinidae in that both valves are convex to varying degree, and both valves are ornamented subequally. A notable difference is that the posterior wings of each valve are much larger in Aviculopectinidae. As well, the hinge is less regularly alivincular in Deltopectinidae. In *Deltopecten* itself, where known, the ligament occuped a shallow broad concavity extending for the full length of the hinge, and *Confundopecten* Waterhouse has a shallow depression or shallow resilifer below the umbones, whereas the ligament area is flat in *Squamuliferipecten* and *Corrugopecten*. However the hinge for *Deltopecten* is not known for the type species, and generic limits remain poorly defined: neither constancy nor variation in morphology can yet be ascertained. Studies by Dickins incorporated species which vary considerably from proven *Deltopecten*, perhaps in the belief that until generic limits could be established, variations should be incorporated. Waterhouse (2008a) restricted the genus to species of demonstrable similarity in morphology, in the belief that such an approach would reveal the limits of variation and demand careful attention to the actual morphology.

Subfamily **SQUAMULIFERIPECTININAE** Waterhouse, 2008a

Diagnosis: Small to large biconvex shells with well developed simple plicae, varying to complexly costate, growth laminae strongly developed, hinge usually platyvincular to lativincular, and often bears well developed pseudotrabeculae, or displays a shallow resilifer under umbones.

Discussion: The subfamily includes *Corrugopecten* Waterhouse, 1982b, *Burnettilina* Waterhouse, 2008a and *Confundopecten* Waterhouse, 2008a. *Deltopecten* lacks strong commarginal laminae, and in the few examples known, costation is minor or absent, and the hinge lacks pseudotrabeculae. But known specimens are so few that the nature and limits of the genus remain open to speculation. At present, various genera ascribed to Squamuliferipectininae are better known than the types of *Deltopecten*, but validity requires substantiation.

Genus ***Squamuliferipecten*** Waterhouse, 1986b

Type species: *Aviculopecten extensus* Fletcher, 1929b, p. 6 from Kungurian of south Sydney Basin, OD. This appears to be a junior subjective synonym of *Aviculopecten media* Laseron, 1910.

Diagnosis: Large shells, biconvex with right valve less inflated than left, well developed right anterior auricle with byssal notch, well formed small posterior wings. Ornament of interlocking or opposed numerous subangular to rounded plicae on both valves, with a varying number of secondary ribs or costae, crossed by well formed close-set growth lamellae. Ligament platyvincular, may bear pseudotrabeculae.

Discussion: In this genus, the right valve is convex but less inflated than the left valve. Both valves are plicate, the plicae being much coarser than the fine and usually much more differentiated ribs characteristic of Etheripectinae.

Deltopecten Etheridge Jnr, 1892, type species *Pecten illawarrensis* Morris, 1845, p. 277, involves large biconvex shells ornamented by simple plicae and lativincular or scoop-like ligament not as planar as in *Squamuliferipecten*. No specimens have been described that show pseudotrabeculae, but few specimens are known that show the hinge. Although many species have been referred to *Deltopecten*, shells conforming in morphology to the type species are rare. The type species, as well figured by Newell (1938, pl. 8, fig. 6a-d), differs from *Squamuliferipecten* in having strong plicae with steep or vertical sides, flattened or convex crests, flat-floored interspaces, and weak commarginal ornament. In *Squamuliferipecten*, the plicae are more rounded over the crests, and have sloping sides, interspaces are concave, and plicae and interspaces are crossed by strong commarginal laminae. Most species referred to *Deltopecten* belong in fact to *Squamuliferipecten*, having a different kind of plication, and having regular and well developed commarginal laminae over both valves. Two species that show typically deltopectin ornament have been described as *D. lyonsensis* Dickins, 1957 from the Lyons Group, and *D. waterfordi* Dickins, 1963 (see also Newell & Boyd 1995, Fig. 35.1a, b, 2) from the Callytharra Formation in the Carnarvon Basin, Western Australia, and Briggs (1998, p. 23) reported a specimen like *D. lyonsensis* from the *Nambuccalinus bourkei* fauna in the New England Orogen of northern New South Wales. Further afield, *Aviculopecten* cf. *mitchelli* of Reed (1932, p. 45, pl. 12, fig. 1, 1a) from the Agglomeratic Slate of Kashmir is apparently congeneric, whereas other *Deltopecten* reported from India belong to *Squamuliferipecten*.

Genus *Corrugopecten* Waterhouse, 1982b, type species *C. multicostatus* Waterhouse, 1982b, displays very complex ornament on both valves, but is like *Squamuliferipecten* in hinge and inflation, and is chiefly of Middle Permian age in east Australia and New Zealand. *Squamuliferipecten* is mostly of Early Permian age, and the late Early Permian type species is comparatively small.

Squamuliferipecten mitchelli (Etheridge & Dun, 1906)

Fig. 198A, B, 199A, 200, 201, 202B, C

1849 *Pecten illawarrensis* [not Morris] – Dana, p. 705, pl. 9, fig. 9, 9a.

?1877 *Aviculopecten illawarrensis* – de Koninck, p. 163, pl. 22, fig. 1.

1892 *Deltopecten illawarrensis* – Etheridge, p. 269, pl. 41, fig. 3 (part, not pl. 43, fig. 2 = *Etheripecten playfordi*).

1906 *A. mitchelli* Etheridge & Dun, p. 11, pl. 1, fig. 1-3, pl. 2, fig. 1, pl. 10, fig. 5, pl. 12, fig. 5, pl. 13, fig. 3, pl. 14, fig. 2, 3.

1924 *A. mitchelli* – Richards & Bryan, pl. 20, fig. 2.

1928 *A. mitchelli* – Whitehouse, p. 282.

1929b *A. mitchelli* – Fletcher, p. 15.

1953 *“A.” mitchelli* – Kegel, p. 1, Fig. 1-3.

1957 *Deltopecten mitchelli* – Dickins, p. 40, pl. 7, fig. 8, pl. 8, fig. 10, text-fig. 8.

cf. 1959 *A. mitchelli* – Sahni & Dutt, p. 659, pl. 24, fig. 3.

1963 *D. limaeformis* [not Morris] – Dickins, pl. 12, fig. 1, 2, ?3.

1977 *D. illawarensis* – Webb, pl. 2, fig. 4.

cf. 1978d *D. mitchelli* – Singh, p. 300, pl. 5, fig. 1-3.

1987b *D. illawarrensis* – Waterhouse, p. 154, pl. 6, fig. 9 (part, not fig. 6 = *squamuliferus* (Morris).

cf. 1992a *D. illawarrensis* – Clarke, p. 41, Fig. 25A-I, 26A-F.

2008a *Squamuliferipecten mitchelli* – Waterhouse, p. 85, text-fig. 41A-C.

2015 *S. mitchelli* – Waterhouse, p. 139, Fig. 56.

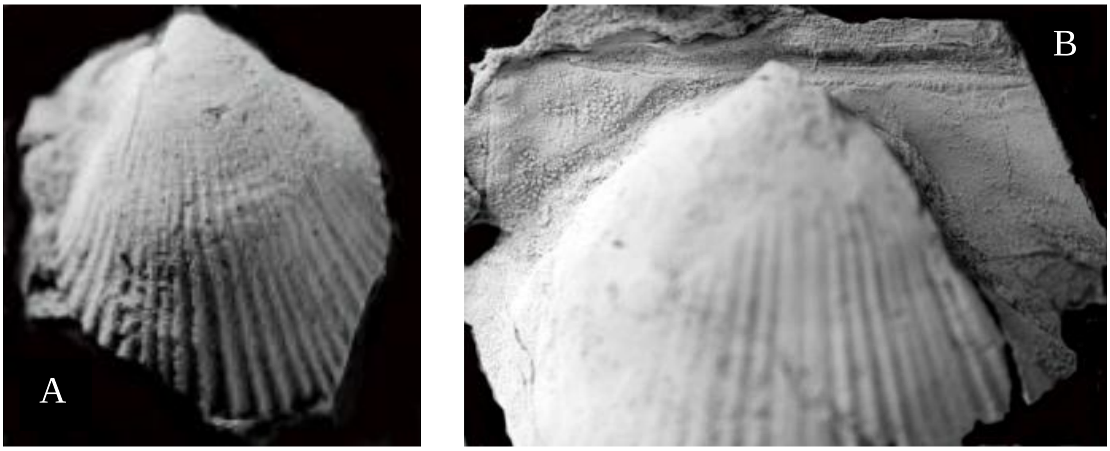


Fig. 198. A, B, *Squamuliferipecten mitchelli* (Etheridge & Dun). A, internal mould of small left valve UQF 81477 from UQL 1626, x1. B, internal mould of right valve with a ligament area that appears to be doubled, UQF 81478 from UQL 3127, x1.5. C. *Squamuliferipecten squamuliferus* (Morris), external mould of left valve UQF 21183 from L 1628, x1.

Lectotype: AMF 35304 figured by Etheridge & Dun (1906, pl. 1, fig. 1, 2) from Allandale Formation, north Sydney Basin, SD Waterhouse (2008a, p. 88).

Diagnosis: Biconvex shells with some 20 to 27 coarse ribs that may carry median groove, and rare secondary ribs. Commarginal lamellae well developed and well spaced on both valves.

Material. Right and left valves from Tiverton Formation at UQL 1621, 1622, 1625, 1626, 1628, 2622, 2623, 2625, 2626, 3127, 4505, 4510, 4512, and 4515. *Bookeria pollex* and *Bookeria geniculata* Zones, and less reliably *Taeniothaerus subquadratus* Zone.

Description: Specimens large, most incomplete, the largest left valve from UQL 1627 measuring 107mm in width, ?90mm in height and 22mm in width, whereas a right valve measures 90mm in length, 94mm in height and 13mm in width. There is a moderate number of strong primary ribs numbering as a rule close to 25, and seldom exceeding 27. Rarely the ribs divide close to the hinge, and a few carry a median groove. Commarginal laminae and growth lines cover both valves, but are subdued. The posterior wings are smaller than the anterior left wing and long anterior right auricle, which is convex and extends above a byssal notch. The hinge is platyvincular, with no sign of resilifer, and pseudotrabeculae are developed weakly in some of the present specimens. One left valve from UQL 3127 is unusual in having a double ligament (Fig. 198B), in which a posterior ligament, lying parallel to and separately from a more anterior ligament placed nearer the right valve, perhaps reflecting an adjustment in position of the shell. A small cluster of pedal retractor scars lies under the anterior left valve umbo, but the major muscle complex is not shown in available material.

Resemblances: This material is identified with *Deltopecten mitchelli* (Etheridge & Dun), originally described from the Allandale Formation of New South Wales. The number of ribs on the suite described by Etheridge & Dun (1906) varies between 22 and 26. This species has not been reported widely, but appears to include the specimens figured as *D. illawarrensis* (Morris) from the Fairyland and Rose’s Pride Formations of the southeast Bowen Basin

(Waterhouse 1987b). Dickins (1957, 1963) regarded the species *mitchelli* as probably conspecific with *Deltopecten illawarrensis* (Morris, 1845, p. 277, pl. 14, fig. 3), with further material figured from Allandale by Etheridge & Dun (1906, p. 24, pl. 2, fig. 2, 3). But the Etheridge & Dun specimens from the Allandale Formation also appear to belong to *mitchelli*, judged from the number and nature of ribs. The specimen figured by de Koninck (1878, pl. 22, fig. 1, 1a) from Harper's Hill, New South Wales, might belong to the species, but the illustration is not completely clear over the nature of the plicae. Several specimens at the Museum of Natural History, London, include PL 4088, identified correctly as *mitchelli*, showing platyvincular ligament with pseudotrabeculae, said to be from "Maitland, Hunter Valley", New South Wales, and PL 566 from Blenheim Station, probably the Tiverton Formation.

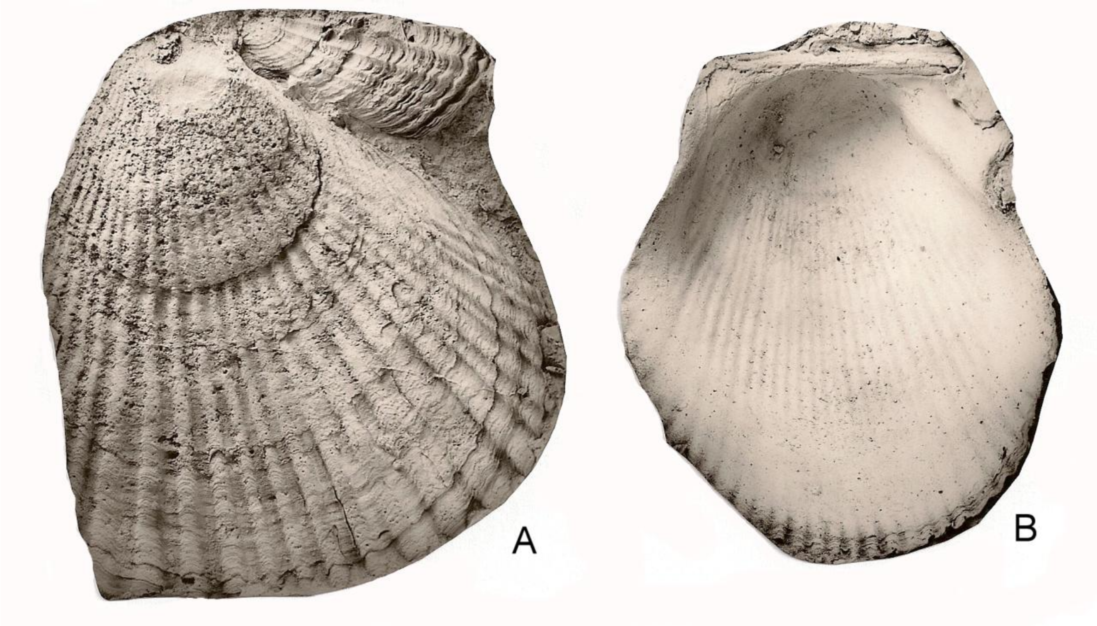


Fig. 199. A, *Squamuliferipecten mitchelli* (Etheridge & Dun). A, latex cast of incomplete right valve UQF 81476 from UQL 1625, x0.8. B, *Squamuliferipecten squamuliferus* (Morris), latex cast, interior of left valve supplied with photograph x1 from Tiverton Formation by D. J. C. Briggs. This shows well the playvincular ligament, but the specimen from which the cast was prepared was not provided and its whereabouts unknown.

Internal views of two left valves were figured as *Deltopecten* cf. *illawarrensis* [not Morris] by Newell & Boyd (1995, Fig. 35. 3, 4), and without the exterior are not easy to identify. They appear to have more plicae than *illawarrensis*, and possibly more than *mitchelli*. Newell & Boyd (1995, Fig. 21.1) figured a large left valve from the Marlborough Group, Tasmania, as *Heteropecten* cf. *Aviculopecten mitchelli*, as an interior, that shows a deep and well-formed resilifer, which is not seen in *mitchelli*. The specimen is difficult to identify because of the failure to illustrate or describe the external ornament and wings, but the strength and number of the plicae and the well formed resilifer strongly point to *Confundopecten limaeformis* (Morris).

A left valve figured as *Aviculopecten mitchelli* from Early Permian of Manendragarh, India, by Sahni & Dutt (1959, p. 659, pl. 24, fig. 3) has comparable ribbing and shape, and appears moderately close to this species, and Singh (1978d, pl. 5, fig. 1-3) illustrated allied material from the Bomte Shale of the Garu Formation in the eastern Himalaya. *Aviculopecten* cf. *mitchelli* figured by Reed (1932, pl. 12, fig. 1, 1a) from Kashmir has plicae like those of *Deltopecten*, not *Squamuliferipecten*. Termier et al. (1974, pl. 2, fig. 6) figured a left valve from a Gzhelian fauna of Wardak, Afghanistan, as *Deltopecten mitchelli*, but the plicae appear to be finer. A somewhat similar valve from the Asselian of the same area was ascribed to *Heteropecten* cf. *exemplarius* (Newell), figured in Termier et al. (1974, pl. 5, fig. 4).

Deltopecten harringtoni Rocha-Campos & Carvalho (1975, p. 187, pl. 1, fig. 1-6) from the lower Bonete Formation, Sierra de Pillahuinco, east Argentina, is moderately close in plication, with prominent right anterior auricle, and small size.

Squamuliferipecten angulatus Waterhouse (1987b, pl. 4, fig. 14, pl. 14, fig. 1) is only moderately close to *S. mitchelli*. The holotype AMF 30052 from the Lochinvar Formation, north Sydney Basin, is very well preserved, and has strong plicae, but there are also a number of firm costae posteriorly, the ribs totalling 30-40 or so, and some splitting. The left valve (pl. 14, fig. 1) from the ?Lochinvar Formation has only 33-35 radial ribs. Such rib counts bring the specimens close to *Confundopecten limaeformis* (Morris), which has 34-40 ribs (Waterhouse 2008a, p. 93), though the overall appearance of type *angulata* is very different with less inflated left valve, narrower right valve, and stronger and more costate plicae. The ligament of *angulata* is not known, and comparison with the collections at the Natural History Museum, London, is required before its validity can be secure, but rib counts suggest *limaeformis*.

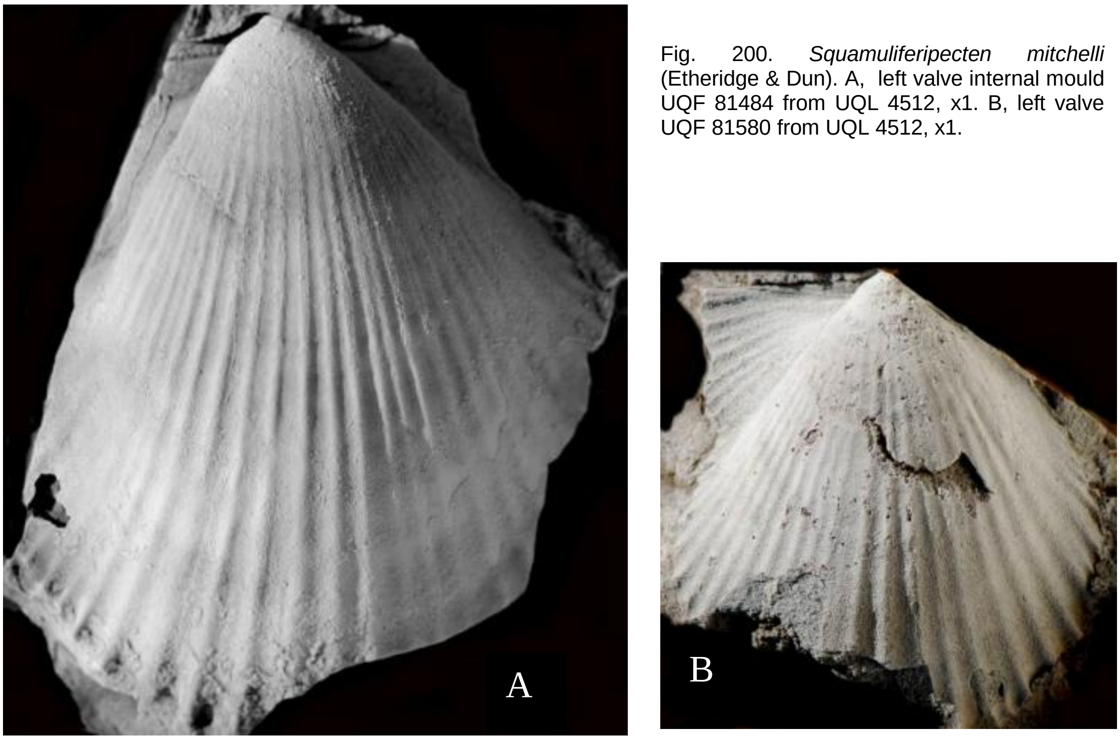


Fig. 200. *Squamuliferipecten mitchelli* (Etheridge & Dun). A, left valve internal mould UQF 81484 from UQL 4512, x1. B, left valve UQF 81580 from UQL 4512, x1.

Deltopecten illawarrensis, as illustrated by Morris (1845) and especially by Newell (1938, p. 63, pl. 8, fig. 6a-d) has distinctly fewer and very simple ribs with wide interspaces, judged from the lectotype and paratype, the number making up as few as 15, up to 20, judged from the incomplete fragments. The crests of the ribs are almost flat, whereas those of *mitchelli* are gently rounded, and the sides of the ribs are steep, less concave, and curving more abruptly into the interspaces than in *mitchelli*. Growth laminae are low, close-spaced, and subdued, quite unlike those of *mitchelli*. The *illawarrensis* specimens appear to have been weakly transverse, and the matrix was described as reddish-brown to grey granular limestone (Bairstow in Newell 1938, p. 64). According to Morris (1845), the types came supposedly from Illawarra, a most unlikely source, because Illawarra rocks are of Middle Permian age. Dickins (1963) considered that the specimens came from Harper's Hill, but the matrix is not the same as that found with *D. mitchelli*. No more material has been discovered in the well-collected Allandale Formation. Runnegar (1968b, pl. 1, fig. 13) figured a specimen of *Deltopecten* UQF 49037 from the upper Quamby beds of lower Golden Valley Group at Western Creek, Quamby Bluff, north Tasmania, which has some 18 plicae, each with steep flanks and gently convex crest to the plicae and subdued commarginal growth laminae, and general size and nature of the ribbing raise the question if this could have been the true source for Morris' species. The ribbing of *illawarrensis* closely approaches that of two Early Permian species from Western Australia, *D. waterfordi* Dickins (1963, pl. 12, fig. 5-11) from chiefly the Callytharra Formation and *D. lyonsensis* Dickins (1957, pl. 7, fig. 1-5, pl. 8, fig. 11-13, pl. 9, fig. 12, pl. 10, fig. 3, 4, text-fig. 9) from chiefly the Lyons Group in the Carnarvon Basin. This material from Western Australia substantially clarifies the nature of *Deltopecten*. Newell & Boyd (1995) synonymized the three taxa, whereas Dickins (1963) pointed to various differences between the taxa. Left valves AMF 35373 and 32911 from Kempsey and Maria Island, Tasmania, are like *Deltopecten* in their ribbing, with some 30 ribs. They are labelled *Deltopecten macleayi* de Koninck.

Fig. 201. *Squamuliferus mitchelli* (Etheridge & Dun), internal mould of right valve UQF 81479 from UQL 4510, x1.

Uncertainty also pertains to a taxon named *Aviculopecten diemenensis* Johnston, 1887, p. 9, never figured. This came from the Darlington Limestone of Maria Island, Tasmania. Johnston (1887) recorded about 22 simple raised ribs separated by narrow interspaces, and “sharp concentric lines of growth”, separated by numerous microscopic wavy commarginal striae. Such a description suggests *mitchelli*. Specimens from the Early Permian of Tasmania, including Darlington Limestone, Maria Island, that were figured as *Deltopecten illawarrensis* by Clarke (1992a, Fig. 25A-I, Fig. 26A-F) tend to have less than 20 ribs, but two or three specimens have up to 28 or so, judged from figures. The interspaces appear to be more concave and narrower than in type *illawarrensis*, and so approach *mitchelli,* apart from having smooth or closely ribbed lateral extremities, and not showing much sign of ribs with median grooves. The hinge appears to be platyvincular in several specimens (Clarke 1992a, Fig. 25G, 26A, B). Whether Clarke’s specimens were the same as those identified as *diemenensis* is not certain, and although they appear to have come from the same beds, the nature of Johnston’s taxon is arguably too uncertain to be revived. Available evidence suggests that the Clarke material may be treated as a subspecies of Allandale *mitchelli*. An internal mould from Maria Island that was figured as *D. limaeformis* (Morris) by Etheridge & Dun (1906, pl. 11, fig. 1, 2) is superficially close to *mitchelli*, but is worn and obscure, and examination of the specimen shows it belongs to *Corrugopecten*. *Corrugopecten* Waterhouse, 1982b was confused with *Heteropecten* Kegel by Newell & Boyd (1995), but is biconvex with moderately inflated valves, platyvincular ligament and elaborate ornament on each valve.

Squamuliferipecten squamuliferus (Morris, 1845)

Fig. 198C, 199B, 202A, D

1845 *Pecten squamuliferus* Morris, p. 278, pl. 14, fig. 1.
1872 *Aviculopecten multiradiatus* Etheridge Snr, p. 327, pl. 13, fig. 1.
1906 *A. squamuliferus* – Etheridge & Dun, p. 8, pl. 1, fig. 4, pl. 8, fig. 4 (part, not pl. 2, fig. 4, 5 = n. sp. or var.).
1906 *A. profundus* [not de Koninck] – Etheridge & Dun, p. 9, pl. 11, fig. 4, 5.
1929b ?*A. squamuliferus* – Fletcher, p. 4.
1959 *A. squamuliferus* – Sahni & Dutt, p. 658, pl. 24, fig. 1, 2.
1964b *Deltopecten limaeformis* [not Morris] – Hill & Woods, pl. P11, fig. 11, 12.
1972 *D. limaeformis* – Hill, Playford & Woods, pl. P11, fig. 11, 12.
1982b ?*Corrugopecten squamuliferus* – Waterhouse, pl. 24, fig. e.
1987b *D. limaeformis* – Waterhouse, p. 153, pl. 6, fig. 1 (part, not pl. 5, fig. 12 = *latispatia*).
1987b *D. illawarrensis* [not Morris] – Waterhouse, p. 154, pl. 6, fig. 6 (part, not fig. 9 = *mitchelli*).
1987b *Squamuliferipecten illawarrensis* – Waterhouse, p. 154, pl. 6, fig. 6 (part, not fig. 9 = *mitchelli*).
1987b *S. squamuliferus* – Waterhouse, p. 157, pl. 7, fig. 1, pl. 8, fig. 10.
1987b *Squamuliferipecten* sp. Waterhouse, p. 155, pl. 6, fig. 2, 4.
?1987b *S. latispatia* Waterhouse, p. 156, pl. 7, fig. 11.

1987 *D. limaeformis* –- Waterhouse & Balfe, p. 30, pl. 1, fig. 10, 11.

2008a *S. squamuliferus* – Waterhouse, p. 88, text-fig. 42.

2015 *S. squamuliferus* – Waterhouse, p. 30, Fig. 8A-D.

Lectotype: NHM PL 3685 from Mount Wellington, Tasmania, probably Cascades Group, figured by Morris (1845, pl. 4, fig. 1) and Waterhouse (1982b, pl. 24, fig. e), SD Waterhouse (1982b, caption pl. 24, fig. e). The probable locality exposes undifferentiated Cascades Group, which crops out on Huon Road, just past Turnip Fields Road in the Hobart suburb of Lenah Valley (M. R. Banks, pers. comm. to B. Runnegar). Holotype for *multiradiatus*, QM F 17760 (17/1208) from the Rammutt Formation, Gympie, southeast Queensland, figured by Etheridge Snr (1872), Waterhouse & Balfe (1987, pl. 1, fig. 10) and Waterhouse (2015, Fig. 8A, C), by monotypy.

Diagnosis: Large shells, right valve a little less inflated than left valve, right anterior auricle very large, ornament of 37-50 round-crested plicae and secondary costae which are moderately numerous, commarginal lamellae prominent.

Material: Right valves from Tiverton Formation at UQL 1621, 1622, 1628 and T3, and left valves from UQL 1627, 1628, 2626, 4512 and 4519. *Bookeria geniculata* Zone, rare in *Taeniothaerus subquadratus* Zone.

Dimensions in mm:

UQF	UQL	Length	Height	Width	Valve
21183	1628	?75	?75	11	right
81483	4512	67	82	27	left

Description: Shells large, left valve almost twice as wide as right valve, right anterior auricle very large with long deep byssal notch, left anterior wing moderately large with anterior margin convex in outline, posterior wings of both valves small, with generally sinuous posterior margin and rounded posterior cardinal extremity. Plicae number just under 40 up to 50, crests round, interspaces evenly concave, growth lamellae strongly developed, four to six in 5mm, weakly arched across interspaces and plicae. Interspaces may carry median ribs and plicae may have two costae ventrally, with interspaces narrower on right valve and wider on the left valve for some specimens. Five or six ribs on right anterior auricle, and the wings are firmly ribbed, with close-set growth lines. No internal detail preserved.

Resemblances: These specimens are larger than the type specimens from Tasmania, but have similar anterior right valve auricle and posterior wing, low inflation and a comparable number of similar plicae. An allied specimen has been figured from the Farley Formation of the Sydney Basin in the Hunter Valley by Etheridge & Dun (1906, pl. 1, fig. 4), but another Farley specimen and a Ravensfield specimen (Etheridge & Dun 1906, pl. 2, fig. 4, 5) are small and have much finer costae, numbering close to 60, and the latter specimen AMF 35298 from Ravensfield has a platyvincular hinge. They appear comparable with the holotype of *angulata*, as discussed on p. 250, with more plical splits. Fletcher (1929b, p. 5) referred the specimen figured by Etheridge & Dun (1906, pl. 1, fig. 4) “to my species *A. largis*”, but no description of this species appears to have been provided. Specimens from the Elvinia and Rose’s Pride Formations of southeast Bowen Basin were described by Waterhouse (1987b), with a report of doubtful material from the Boughyard Member in that area. From the Manendragarh fauna of Peninsula India, Sahni & Dutt (1959) reported specimens which are moderately close, with 45 ribs in the right valve.

Etheridge & Dun (1906) and Fletcher (1929b) considered that *Aviculopecten multiradiatus* Etheridge Snr (1872, pl. 13, fig. 1) from the Gympie area, southeast Queensland, also figured by Waterhouse & Balfe (1987, pl. 1, fig. 10), should be synonymized with *squamuliferus*. The genus is probably *Squamuliferipecten*, and the number of plicae is close to 50, consonant with or slightly more than the number in *squamuliferus*. But many details are not known for the Gympie material.

Squamuliferipecten squamuliferus has broader outline, less convex left valve and many more ribs than *Pecten* (now *Confundopecten*) *limaeformis* Morris. Type *squamuliferus* has some 48 ribs, whereas the holotype of *limaeformis* has 36 ribs, as counted by Morris (1845) and verified from the figure, and other *limaeformis* have 35-40 ribs and shallow resilifer (Waterhouse 2008a).

The original specimen figured by de Koninck (1877, p. 161 (236), pl. 22, fig. 3) as *Aviculopecten profundus* n. sp. from Harper’s Hill, Hunter Valley, has been destroyed by fire. The specimen was a right valve, and was described as having 30-40 slightly angular folds separated by shallow furrows grooved at the base, and smooth posterior wing. The figure shows a decorticated specimen, with traces of the plicae as described, and superimposed are fine costae, about 10 over each fold, so that the specimen clearly belongs to *Undopecten* Waterhouse, 1982b, for which the type species is *Pecten fittoni* Morris, 1845. The material figured as *A. limaeformis* [not Morris] by de

Koninck (1877, pl. 22, fig. 4, 4a) from Harper's Hill, New South Wales, also belongs to *Undopecten*, to judge from the illustrations, and also has been destroyed by fire.

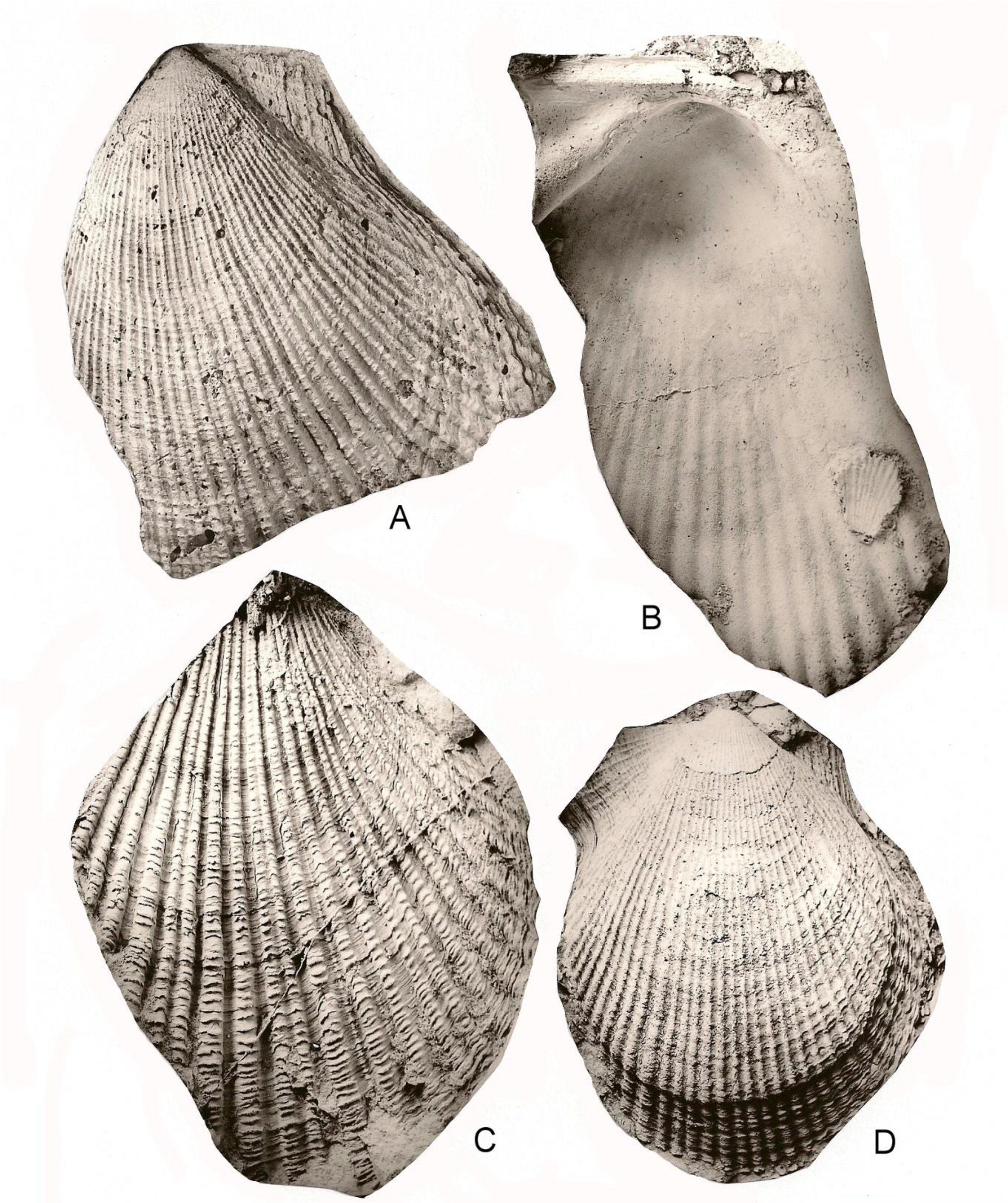


Fig. 202. A, D, *Squamuliferipecten squamuliferus* (Morris). A, latex cast of left valve UQF 81480 from UQL 4519, x1. D, latex cast of left valve UQF 41483 from UQL 4512, x1. B, C, *Squamuliferipecten mitchelli* (Etheridge & Dun). B, latex cast of internal right valve UQF 81481 from UQL 2623, x1. C, latex cast of right valve UQF 81482 from UQL 1622, x1.

Two specimens were provisionally assigned to *Aviculopecten profundus* de Koninck by Etheridge & Dun (1906, p. 9, pl. 11, fig. 4, 5) from the Farley Formation (s.l.) at Ravensfield and Rutherford, Hunter Valley. The specimen AMF 35307 (pl. 11, fig. 5) lacks a resilifer, and both appear to belong to *Squamuliferipecten*, and are characterized by 40 to 50 primary or primary and secondary ribs, much as found in *squamuliferus*, and approaching the number counted in *S. multiradiatus* (Etheridge Snr, 1872, pl. 13, fig. 1) from Gympie. The byssal notch is supposed to be undeveloped in the Etheridge & Dun material, but their right valve (pl. 11, fig. 4) looks more like a left valve than a right valve. *D. limaeformis* [not Morris] of Etheridge & Dun (1906, pl. 10, fig. 4) from Ravensfield probably belongs to the same species. The specimens are very close to *squamuliferus* and *multiradiatus*, and the ribs are not quite as fine as those of the Farley specimens assigned, dubiously, to *squamuliferus* by Etheridge & Dun (1906, pl. 2, fig. 4, 5).

Of other species, *Aviculopecten extensus* Fletcher (1929b), the designated type species of *Squamuliferipecten*, is smaller, with 33-40 ribs and small posterior wings, with only moderately developed growth lamellae. The species has been discussed by Waterhouse (2008a, p. 90), and shown to be the same as *Aviculopecten media* Laseron (1910) from the "Wandrawandian Suite" at Burrier, south New South Wales.

Squamuliferipecten latispatia Waterhouse (1987b, pl. 7, fig. 11) from the Dresden Formation of southeast Bowen Basin has widely spaced strong plicae numbering 35 primaries with additional fine costae, and is large and not strongly inflated. It has fewer ribs than found on *squamuliferus*, but is otherwise close in shape and inflation, but may prove conspecific or related to *limaeformis*. A specimen from the Fairyland Formation in the same area, figured as *Deltopecten limaeformis* by Waterhouse (1987b, pl. 5, fig. 12), possibly belongs to the same species: it has coarse well-spaced plicae, but is not well preserved, and is indeed moderately close to the Morris species. The species *mitchelli* is narrower and slightly more inflated with fewer ribs, and the ribs of *limaeformis* are close in number at 34-40 to those of *latispatia* but more closely spaced, and the left valve more inflated. *S. angulatus* Waterhouse, 1987b from the Allandale and possibly Lochinvar Formations of the Hunter Valley, New South Wales, has about 40 round-crested plicae with angular interspaces. Both species have strongly developed commarginal lamellae.

Aviculopecten ponderosus Etheridge & Dun (1906, pl, 5, pl. 12, fig. 4) from the Maitland Group of the northern Sydney Basin looks from the figures to be a member of *Squamuliferipecten*, with some 35 primary ribs, and platyvincular hinge. But parts of the shell preserve a little of the original ornament to show secondary and tertiary costae, as in the genus *Corrugopecten* Waterhouse, 1982b.

Family **CYRTOROSTRIDAE** Newell & Boyd, 1995

Diagnosis: Biconvex with alivincular to lativincular ligament, ornament on each valve of high costae flanked by lower finer costae which bear large spines. Posterior wings reduced in size.

Discussion: *Cyrtorostra* is like *Streblochondria* in its distinctive shape, but two considerations are believed to favour a closer association with deltopectinids, the lack of any known streblochondroid with plicae, and the lack of any streblochondroid with pseudotrabeculae, so-named for shell ridges crossing the ligament area obliquely (Waterhouse 2001, p. 115, text-fig. 9e) in the hinge. *Cyrtorostra,* type species *C. varicostata* Branson*,* is biconvex, and has an alivincular or lativincular ligament, and a small knob-like tooth is developed anteriorly in each valve (Newell & Boyd 1995, p. 62). Newell & Boyd (1995) evidently regarded the genus as allied to Aviculopectinidae, and Waterhouse (2001) noted the presence of pseudotrabeculae within the broad resilifer, as in deltopectinids. Shell structure is unusual, the fibres arching a long way ventrally from the interspaces in both valves to form the plicae (Fig. 204A). There is also some approach to Late Paleozoic Limidae in some aspects of shape, but not in ornament or byssal notch. Although classed as a subfamily within Deltopectinidae by Waterhouse (2008a), the recognition of Squamuliferipectininae as a much closer ally of *Deltopecten*, and the nature of the shell structure, suggest that *Cyrtorostra* belongs to a separate family.

Genus ***Elviniaria*** Waterhouse, 2008a

Type species: *Cyrtorostra limitans* Waterhouse, 1987b, p. 158 from Elvinia Formation (Sakmarian), southeast Bowen Basin, Queensland, OD.

Diagnosis: Subequally biconvex upright shells with well developed spinose ribs between gentle to strong primary plicae, right anterior auricle smooth, ligament platyvincular or modified lativincular, no tooth in either valve. No pseudotrabeculae.

Discussion: *Elviniaria limitans* (Waterhouse, 1987b, p. 158) from the Elvinia Formation of the southeast Bowen Basin of Queensland has three, sometimes four, costae in the interspaces, although the central interspatial ribs remain prominent, as in *Cyrtorostra varicostata* Branson, 1930 from the early Middle Permian of mid-United States (Ciriacks 1963, Newell & Boyd 1995). The valves are not strongly prosogyrous, and the right valve more inflated than in *Cyrtorostra* and unlike *Cyrtorostra*, the hinge of *Elviniaria* lacks a tooth from each valve and shows no clear indication of pseudotrabeculae.

Elviniaria limitans (Waterhouse, 1987b)

Fig. 203 - 205

1987b *Cyrtorostra limitans* Waterhouse, p. 158, pl. 9, fig. 3-8, 10.

2008a *Elviniaria limitans* – Waterhouse, p. 95, text-fig. 46A-C.

Holotype: UQF 74358 from UQL 4823, Elvinia Formation, figured by Waterhouse (1987b, pl. 9, fig. 3), OD.

Diagnosis: Subequally biconvex, orthogyrous, right anterior auricle without costae, primary costae not high, convex interspaces with well defined ribs crossed by low commarginal laminae, ligament platyvincular.

Material: Right or left vaves valves from UQL 1367, 3127, 4511 and 4515, left valves from UQL 1630, and fragments from UQL 1383 and 4517. *Svalbardia armstrongi* Subzone and *Taeniothaerus subquadratus* Zone.

Fig. 203. *Elviniaria limitans* (Waterhouse), left valve and anterior aspect for UQF 51928 from UQF 3127, collected by B. Runnegar from unspecified level in Tiverton Formation, Homevale, x1.5.

Discussion: A single specimen with valves conjoined UQF 51928 was collected and identified as *Cyrtorostra* by B. Runnegar, and figured as *C. limitans* by Waterhouse (1987b, pl. 9, fig. 6-8). The specimen from UQL 1367 measures 13.5mm in length, 16mm high and 5mm wide, with moderately narrow umbo, small posterior wing moderately high but short anterior auricle and high byssal notch. Ribs subdued in the interspaces and the specimens narrower than specimens of *Elviniaria limitans* from the Elvinia Formation of the southeast Bowen Basin. Fragments from UQL 1383 show primary ribs, and spines, and aspects of shell structure. The right valve from UQL 4515 is 14mm long, 15mm high and 7mm wide, with some 12 primary costae of which some are spinose around the periphery, and interspaces bearing at least two ribs. The anterior auricle is large, above a high short byssal notch, and the posterior wing is small. The ligament is linear and lativincular with narrow bourrelets behind, very faintly discriminated, and no anterior bourrelet, and no teeth.

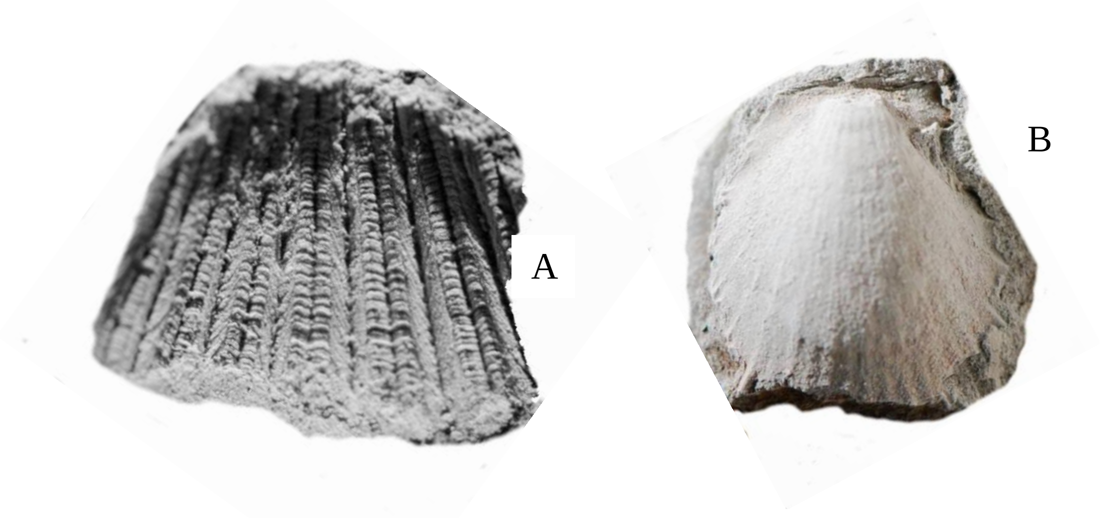


Fig. 204. *Elviniaria limitans* (Waterhouse). A, detail of exterior on left valve UQF 81487 from UQL 1367, x5. B, right valve UQF 81486 from UQL 4515, x5, showing lativincular ligament area.

Fig. 205. *Elviniaria limitans*, ventral anterior of left valve UQF 81489 showing spines arising from ribs between broad plicae, from UQL 1367, x5.

Superfamily **CHAENOCARDIOIDEA** Miller, 1889

Diagnosis: Shell biconvex, equivalve to subequivalve with relatively small posterior wings in each valve. Right anterior auricle and byssal notch well developed. Ornament varies, coarse to fine but no genera known to be strongly plicate, costae tend to increase by branching but implantation is also common, growth lines often arch ventrally in interspaces and hingewards over costae. Ligament external and amphidetic, alivincular, lativincular or platyvincular, some genera with few simple teeth.

Discussion: This is a superfamily of wide diversity, some members close to Aviculopectinidae in alivincular hinge and close to Deltopectinidae in having small posterior wings, but overall small and somewhat rounded in shape, with not very large anterior wing or auricle as a rule. The source of the group is yet to be clarified. There has been no discussion of the origins prior to the study by Waterhouse (2008a), which suggested, provisionally, that the superfamily might be a sister group with Aviculopectinoidea, being similarly subequivalve with ornament the same on each valve, and with usually alivincular hinge. The origins for Aviculopectinoidea lay within Pseudaviculopectininae Waterhouse of Superfamily Pterinopectinoidea Newell, and the lack of plicae in most Chaenocardioidea suggest the possibility of a separate pterinopectiniform source.

Family **STREBLOCHONDRIIDAE** Newell, 1938

Diagnosis: Shells biconvex, almost equivalve to inequivalve, upright to slightly procrescent, well defined umbonal slopes, posterior wings small, ornament variable. Short amphidetic alivincular ligament as a rule with small resilifer extended slightly outward. Teeth rarely developed.

Discussion: Members of the family are distinguished from members of Chaenocardiidae Miller by having a more symmetrically alivincular ligament.

Subfamily **ORBICULOPECTININAE** Waterhouse, 2001

Diagnosis: Hinge lativincular to platyvincular, edentulous.

Genus ***Orbiculipecten*** Gonzalez, 1978

Type species: *Orbiculipecten parma* Gonzalez, 1978, p. 1091 from upper beds of Lower Tepuel Group, (Bashkirian?), Chubut Province, Argentina, OD.

Diagnosis: Small upright to weakly opisthocline shells with left valve more inflated, right anterior auricle costate, fine ribs on left anterior wing, both valves ornamented by very fine radial filae, which may branch, and fine commarginal growth threads. Ligament lativincular.

Discussion: *Orbiculopecten* and *Striochondria* both display radial filae (Waterhouse 1982b, pl. 13, fig. c, pl. 14, fig. c, pl. 21, fig. e) far finer than those of *Streblochondria*, and moreover increase by branching on the right valve, at least in *Striochondria*. Whereas the latter genus has a small deep resilifer, the hinge of *Orbiculopecten* is lativincular to platyvincular. Newell & Boyd (1995) erred in claiming that *Striochondria* was poorly known.

Orbiculipecten cokeri n. sp.

Fig. 206 – 208

Derivation: Named for John Coker.

Holotype: UQF 81499 from UQL 3127, Tiverton Formation, figured herein as Fig. 207D, here designated.

Diagnosis: Shape usually upright, right anterior auricle with one strong costae near ventral margin, may be absent, no left anterior wing costa, ornament of fine radial filae on both valves, ligament lativincular.

Material: Specimens from UQL 1269, 1383, 2155, 2619, 2622 3127, 3129 and 4519. *Bookeria geniculata* and *Taeniothaerus subquadratus* Zones.

Dimensions in mm: means, n = 9, left valve

Length	Height	Width
26	27.5	7

Description: Specimens moderately large and inflated, upright in shape, with prominent posteriorly placed incurved umbones, umbonal angle close to 85°, long anterior umbonal slope gently concave in outline for right valve and tending to be straight for left valve, steep, extending to maximum length close to mid-height, posterior slope short. Right valve may be slightly thinner, but not consistently, a specimen UQF 81503 from UQL 3129 measuring 25.5mm in length, 28.5mm in height, and 10.5mm in width. Right anterior auricle large and convex, extending for little more than half of the length of the anterior umbonal slope, above a long byssal gutter, leading to a narrow comparatively short and high byssal notch: the ventral or inner edge of the auricle is as a rule raised into a sturdy rib, although rare specimens lack a rib (UQF 81506). Left anterior wing gently convex, smooth, with obtuse extremity, anterior margin slightly recessed next to umbonal slope, no visible rib. Posterior wing in each valve small, short, gently convex, obtuse, and slightly recessed ventrally. Exterior seldom well preserved, but several fragments indicate fine radial filae and low commarginal wrinkles. The ligament area in right valves from UQL 3127 and 4519 is traversed by two or three ridges and grooves which increase in height and depth under the umbonal region, and left valve UQF 81493 has a broad lativincular resilifer. A shallow broad lativincular double depression is preserved in left valve UQF 81495. Muscle scars not clearly defined, posterior adductor impression comparatively large and posteriorly placed. Shell is 1.8mm thick in a right valve from UQL 3129, and composed of prisms, but in a large right valve from UQL 3127 the shell is less than 0.5mm thick, and of indiscernible structure at low magnification, without prismatic layer.

Resemblances: This species is characterized by the radial filae over most of the shell, and by the strong costa along the lower margin of the right anterior auricle as a rule, although some specimens appear to have no rib. The type species of the genus is readily distinguished by the lack of a right auricular rib, and is an upright larger shell.

The auricular rib suggests the species *Aviculopecten englehardti* Etheridge & Dun, recorded from the Early and Middle Permian in New South Wales, and described (Etheridge & Dun 1906, pp. 17, 18) as having a rib close to the ventral edge of the right anterior auricle according to the figure, but no longer clear on the specimen. A poorly preserved rib is present in the internal mould AMF 35301 (Etheridge & Dun 1906, pl. 9, fig. 6) from Shoalhaven, south Sydney Basin, and there are traces of some three additional ribs. The similarities to the Tiverton form are clear. There is a right valve auricle with strong rib, and Etheridge & Dun (1906, p. 17, 18) recorded very fine "radii", and this is clearly shown on the lectotype designated by Campbell (1952, p. 21) as the right valve figured by Etheridge & Dun (1906, pl. 9, fig. 9 – AMF 35302). The right anterior auricle of the lectotype is damaged and does not show any strong rib, but a rib is clearly visible on the right anterior auricle of specimen AMF 35297 (Etheridge & Dun 1906, pl. 9, fig. 8) from Cabbage Tree Point. No radials are shown now, though there is a possible suggestion of such in the figure. Other specimens figured as *englehardti* by Etheridge & Dun (1906) are not well preserved, and include a strong rib on the anterior right valve auricle and left valve wing, according to Etheridge & Dun (1906). AMF 35292 (Etheridge & Dun 1906, pl. 9, fig. 7) from the older Permian beds at Parish Heddon of New South Wales is a well inflated shell with fine radial ribs, and a well defined rib close to the ventral margin of the right anterior auricle according to the figure, but no longer clear on the specimen. One specimen (Etheridge & Dun 1906, pl. 9, fig. 8) has some 20 or more low ribs coarser than in present material and so suggestive of *Streblochondria*, though the ribs are not clearly shown in the figure. According to Etheridge & Dun (1906) a rib is also present on the left valve anterior wing. This is not true of the Tiverton material, and no rib is illustrated in any of the Etheridge & Dun figures. The ligament for the Tiverton material is lativincular, but is not known for any of the types kept at the Australian Museum. The specimens figured as *englehardti* have the umbones posteriorly placed especially in the right valves from the

Maitland Group (ie. Upper Marine Series) of Middle Permian age. Most Tiverton specimens are more upright with umbones medianly placed, but this is not invariant. In summary, the types of *englehardti* are not well preserved: none show the ligament, and the anterior auricle is often lost, and the ornament obscure. The Etheridge and Dun species is younger than the Tiverton material, but is not well enough preserved to be fully matched or contrasted, to make the recognition of any species a very uncertain matter. Moreover, specimens somewhat similar to *englehardti* and of comparable age definitely have a resilifer, rather than platyvicular ligament, and are referred to *Striochondria* Waterhouse, 1983c, type species *Streblochondria auriocosta* Waterhouse from the Letham Burn Member (Roadian), of Wairaki Downs, New Zealand.

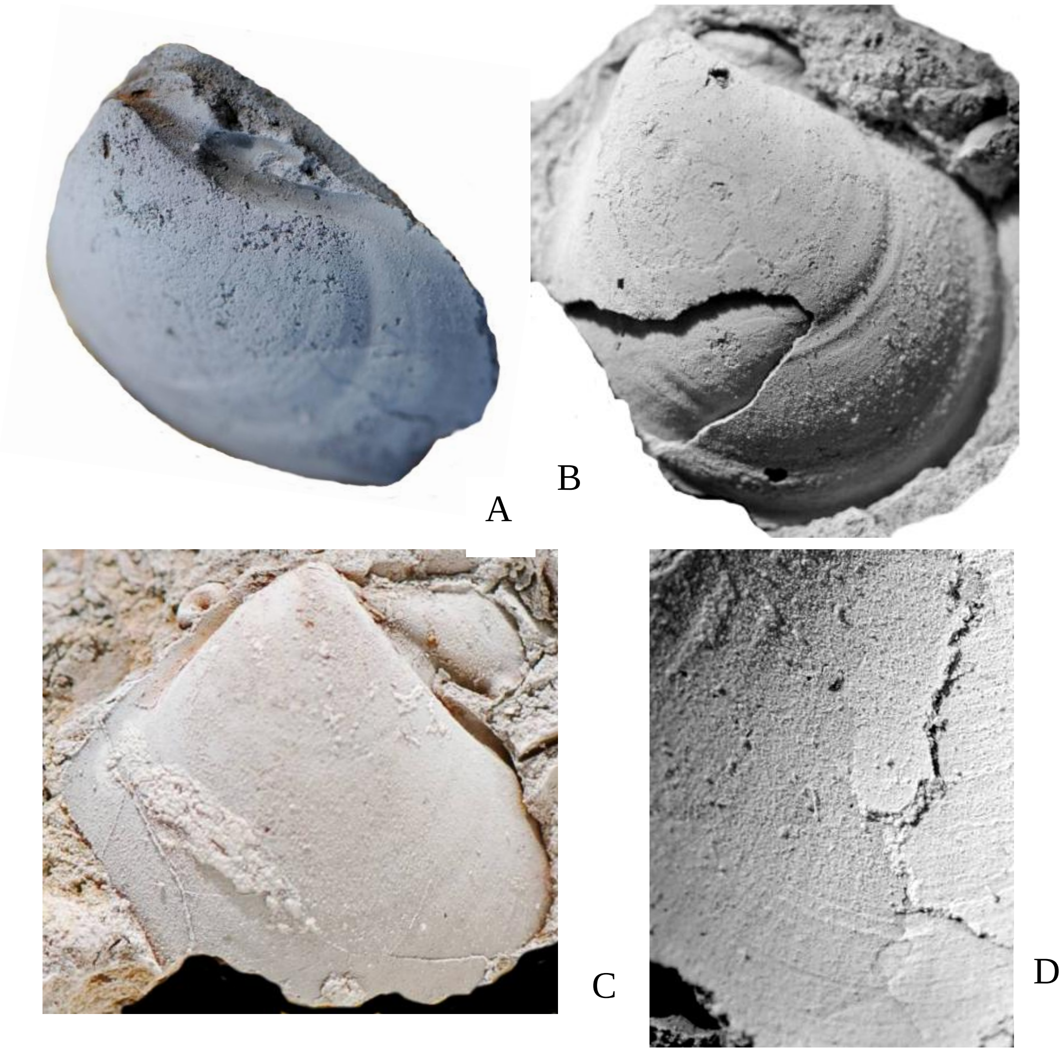


Fig. 206. *Orbiculipecten cokeri* n. sp. A, oblique anterior view showing right anterior auricle and byssal notch, UQF 81497 from UQL 3127, x3. B, right valve internal mould UQF 81503 from UQL 3129, x2. The underlying valve shows radial markings. C, small decorticated right valve UQF 81597 from UQL 4519, x4. D, external mould of right valve UQF 41502 from UQL 3127, x5. The external radials are finer than suggested on some internal moulds.

Specimens from the Early Permian Dalwood Group of New South Wales that were ascribed to *englehardti* by Etheridge & Dun (1906, pl. 9, fig. 10, 11, 12, pl. 14, fig. 6-8) are upright like most Tiverton specimens and possibly both sets make up a species different from type *englehardti*. Given a degree of variation, and uncertainty over the nature of the left anterior wing and ligament, it is at present difficult to fully delineate the Dalwood specimens, and they can only be provisionally compared with the Tiverton species.

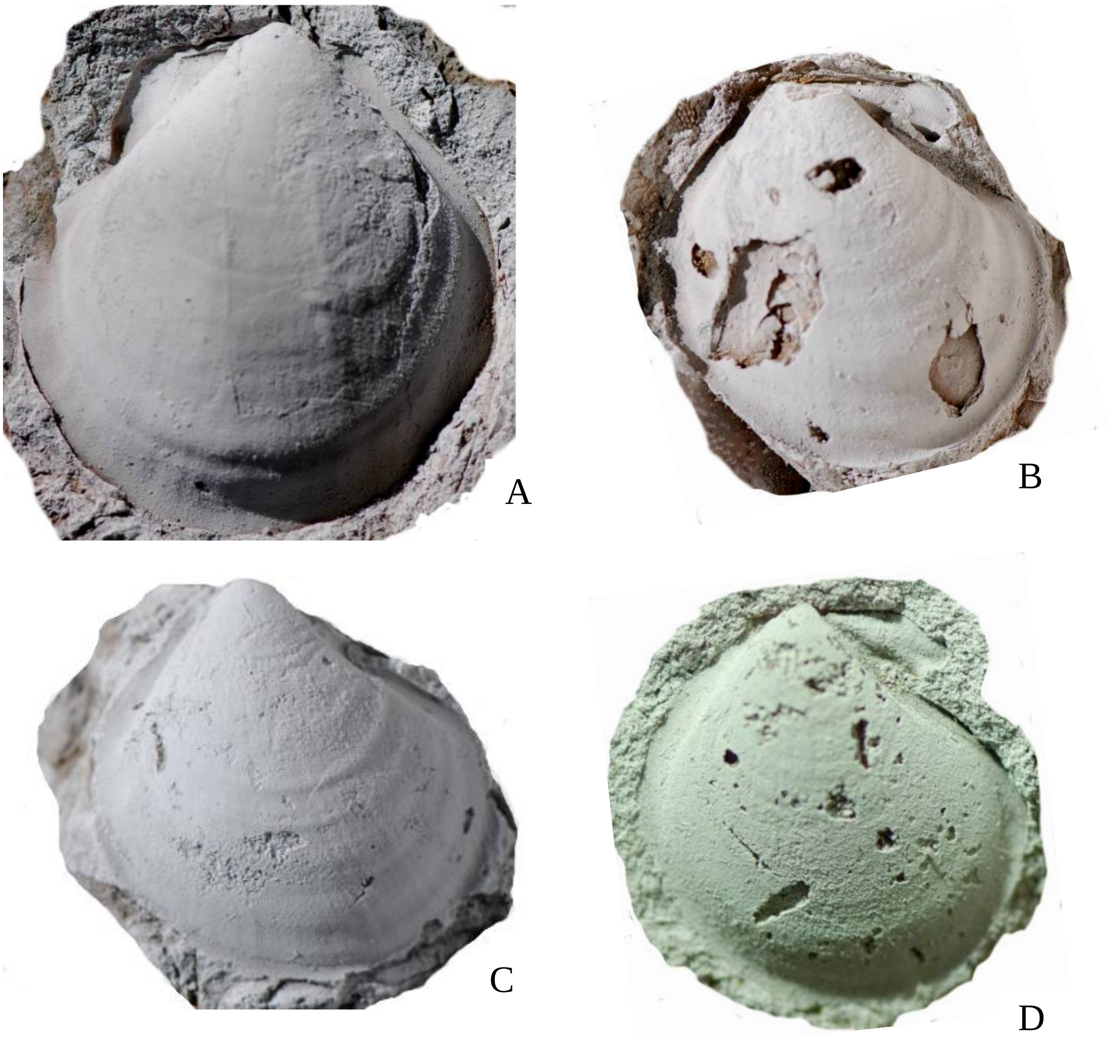


Fig. 207. *Orbiculipecten cokeri* n. sp. A, left valve UQF 81493 from UQL 3127, x2. B, right valve showing hinge, UQF 81495 from UQL 3127, x2. C, internal mould of right valve UQF 81498 from UQL 2619, x3. D, holotype, internal mould of right valve UQF 81499 from UQL 3127, x2.5.

A number of Sydney Basin specimens were referred to *Aviculopecten parkesi* Fletcher (1929b, p. 13) Two different holotypes were cited by Fletcher, one on p. 14, pl. 5, fig. 1 – AMF 19472, and the other on p. 13, pl. 5, fig. 2, AMF 19494. Pl. 5, fig. 1 shows the better preserved of the two specimens, and this is consolidated as holotype. AMF 19472 has two auricular ribs, and the specimen of pl. 5, fig. 2 has radial ribs. The specimen of pl. 5, fig. 3 is a poorly preserved left valve with radials apparently stronger than in *englehardti.* AMF 35292 figured by Etheridge & Dun (1906, pl. 14, fig. 6, 7, 8) from Parish Heddon has weak radials that are stronger than in *englehardti*, and possibly no auricular ribs. The material described as *parkesi* by Fletcher (1929b) comes from "Upper Marine" or Maitland beds of the south Sydney Basin, and was characterized by its inflation and long anterior slope (p. 14). But the shape of the holotype is upright, and the extended anterior mentioned by Fletcher is often seen in *englehardti*. A number of specimens at the Australian Museum that are ascribed to *englehardti* by Etheridge & Dun (1906) have been relabelled as *parkesi* by H. O. Fletcher, and his assessments according to the labels were that specimens figured by Etheridge & Dun (1906, pl. 9, fig. 10, 11, pl. 14, fig. ?6-?9) belong to *parkesi* Fletcher. But Fletcher (1929b) did not published his identifications.

Waterhouse (1982b, p. 31) also recorded the species *parkesi* from the Letham and Mangarewa Formations of Wairaki Downs, New Zealand, and stated that the right anterior auricle was ornamented by up to two costae in some specimens, and mostly by no costae, in collections from both the Sydney Basin and New Zealand. In that study it was considered that shape and inflation did help to distinguish two groups. It is now proposed that examination of better preserved collections with larger number of individual specimens is required to consolidate the validity and limits of the taxa, but it may be noted that there appears to have been some deterioration in the preservation of the collected material, perhaps a slight and slow crumbling of slightly weathered surfaces. The species *parkesi* has delicate fine radial filae over most of the shell (Fletcher 1929b, Waterhouse 1982b; 2001, p. 127) and belongs to *Striochondria* or to *Orbiculopecten*, depending on the nature of the ligament. No specimens of *parkesi* or *englehardti* as described by Etheridge & Dun (1906) and Fletcher (1929b) were found that revealed the hinge, and the validity of *parkesi* remains open to question. Two New Zealand species distinguished by their consistent and distinctive shape and ascribed to *Striochondria erecta* (Waterhouse) and *S. orbiculata* (Waterhouse) both have a variable number of right anterior auricular ribs, as well as moderately developed resilifer. The type species *auriocosta* has numerous anterior auricular costae like *erecta* and *orbiculata*, and has a deep small resilifer (Waterhouse 1982b, p. 32).

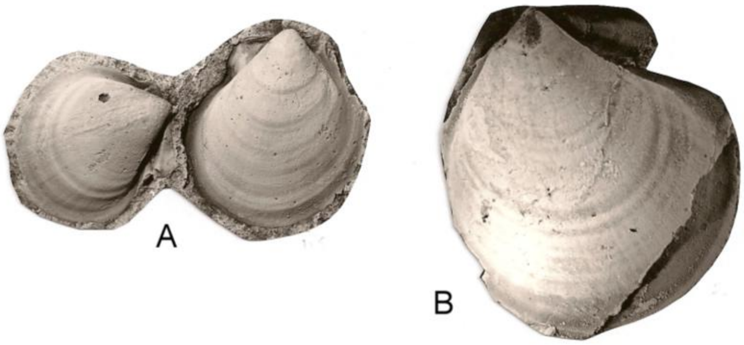


Fig. 208. *Orbiculipecten cokeri* n. sp. A, right and left valve internal moulds UQF 81504 and UQF 81505 (left) from UQL 4519, x1. B, internal mould of right valve UQF 81506 from UQL 3127, x1.5.

Striochondria is most common in the Kungurian and younger faunas of east Australia and New Zealand. Although the genus may have evolved from *Streblochondria*, the fine radial ornament resembles that displayed by a species called *Streblochondria histion* Campbell (1962, p. 49, pl. 12, fig. 11-16) from the Upper Carboniferous *Levipustula levis* Zone of northeast New South Wales. Ribs are developed on the right anterior auricle, and the ligament is lativincular, so that the species is placed in *Orbiculopecten*.

Taxonomy: Etheridge & Dun (1906, pl. 14, 19) spelled their species *englehardti* as followed by other authors such as Fletcher (1929b) and Campbell (1951). But Etheridge & Dun (1906, p. 17) also rendered the name *engelhardti*. I have not been able to find out the spelling of the person after whom the species was named, and therefore retain the spelling more commonly used by Etheridge & Dun (1906).

Subfamily **SATURNOPECTININAE** D. Campbell in J. G. Carter et al., 2011

Diagnosis: Radial ribs absent from valves except over wings and auricle.

Discussion: This subfamily was proposed to replace Saturnellinae Astafieva, 1993, based on *Saturnella* Astafieva not Hedinger, 1993.

Genus ***Concentiolineatus*** Waterhouse, 2008a

Type species: *Streblopteria homevalensis* Waterhouse, 1986b, p. 5 from Tiverton Formation (Sakmarian), Bowen Basin, Queensland, OD.

Diagnosis: Upright to slightly opisthocline, anterior wing and auricle longer than or equal in length to posterior ears, both valves with commarginal ornament, right anterior auricle ribbed. Hinge platyvincular.

Discussion: The nominated type species of this genus was originally referred to *Streblopteria* M'Coy, 1844, because, like this genus, radial ornament is lacking, other than from the right anterior auricle. *Streblopteria* is based on *Meleagrina laevigata* M'Coy, 1851, p. 170, pl. 12, fig. 5, SD Meek & Worthen, 1866, p. 333. It is assumed that the ligament has a resilifer, as evaluated by Newell (1938, p. 88) and accepted by Amler (1994) and Waterhouse (1982b, 2001, p. 126). M'Coy (1851) recorded a tooth in the hinge, but no such tooth was illustrated, and the reality of its presence was dismissed by Wilson (1962, p. 70). The present species *homevalensis* has no hinge teeth, and is like *laevigata* in showing fine but distinct commarginal growth laminae over both valves, but differs in having a very much smaller and more clearly differentiated posterior wing, in contrast to the left valve holotype of *laevigata*. (See also Hind 1903, pl. 11, fig. 1-7, the type refigured in fig. 3). The large wing is a very distinctive feature of *Streblopteria*, and it appears, from examination of world-wide collections and literature, that the feature marks an unusual genus of limited geographic extent and of Carboniferous age (Waterhouse 2008a).

The scope of *Concentiolineatus* must be modified from that envisaged by Waterhouse (2008a), because it has been discovered that the hinge is platyvincular as a rule. That implies a close approach to *Montorbicula* Waterhouse, 2008a from South America. Moreover it suggests that externally similar Carboniferous species in Europe might not be congeneric, insofar as they might have a resiifer, though this is yet to be ascertained.

Fig. 209. *Concentiolineatus homevalensis* (Waterhouse), right valve, latex cast, UQF 81489 from LT3, x4. Hinge inclined posteriorly from horizontal.

Concentiolineatus homevalensis (Waterhouse, 1986b)

Fig. 209 - 213

1964b *Streblopteria engelhardti* [not Etheridge & Dun, 1906] – Hill & Woods, pl. P11, fig. 18.

1972 *Streblopteria* cf. *parkesi* [not Fletcher] – Hill, Playford & Woods, pl. P11, fig. 18.

1982b *Streblochondria* sp. Waterhouse, pl. 13, fig. e.

1986b *Streblopteria homevalensis* Waterhouse, p. 5.

1987b *S. homevalensis* – Waterhouse, p. 150, pl. 6, fig. 7, pl. 7, fig. 3-5 (part, not pl. 4, fig. 3 = *Montorbicula* sp.).

2008a *Concentiolineatus homevalensis* Waterhouse, p. 100, text-fig. 49.

Holotype: CPC 5177, from Tiverton Formation, figured by Waterhouse (1982b, pl. 13, fig. e) and Waterhouse (2008a, text-fig. 49), OD.

Diagnosis: Large suboval little inflated shells with long right anterior auricle bearing three to nine fine ribs, small posterior auricle, left anterior auricle bearing slender ribs, commarginal lirae over remainder of shell.

Material: Specimens from UQL 1620, 2155, 2619, 2620, 2622, 3127, 3129, 4511, 4517, 4519, 4521, T3 and LT3. *Bookeria geniculata* and *Taeniothaerus subquadratus* Zone.

Dimensions in mm: n = 5

Valve	Length	Height	Width
right	29	32	10
left	31	33	9.5

Fig. 210. *Concentiolineatus homevalensis* (Waterhouse), detail of micro-ornament on left valve UQF 81507 from UQL 2620, x7.
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Description: Specimens moderately large and inflated, upright in shape, with prominent posteriorly placed incurved umbones, long anterior umbonal slope and shorter posterior slope. The right anterior auricle is large and convex, and extends for little more than half of the length of the adjoining anterior umbonal slope, above a deep slender byssal notch. The anterior auricle has three to rarely nine fine ribs, best developed towards the lower margin. The lower posterior wing carries three or four fine ribs and is gently convex with rounded posterior margin. The left anterior wing is separated from the anterior slope by a groove, and one or two fine ribs lie each side of the groove. The left valve posterior wing is small, gently concave, with light commarginal growth lines and no ribs. The surface of the body of the shell is covered by commarginal growth increments, close to 10 in 1mm, which may be arranged in shallow undulations, with growth steps and laminae. In the left valve from T3 the hinge is straight, and the right hinge weakly bowed. Muscle scars are not clearly defined. Shell of right valve thin, entirely prismatic.

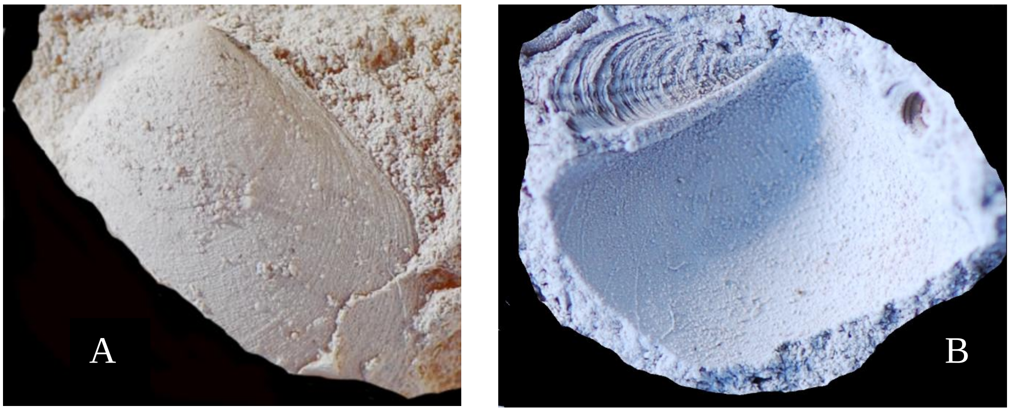


Fig. 211. *Concentiolineatus homevalensis* (Waterhouse). A, latex cast of left valve UQF 43223 from UQL 2619, x4. B, right valve UQF 81620 from UQL 4519, x5, with external mould of *Pleurocinctosa allandalensis* Fletcher to upper right.

Resemblances: These specimens agree with the holotype of *Concentiolineatus homevalensis* in shape and in shell ornament and wing-auricle size. Specimens described from the Elvinia Formation of the southeast Bowen Basin are like the type in having fine ribs on the right anterior auricle and left anterior wing (Waterhouse 1987b, pl. 6, fig. 7, pl. 7, fig. 3-5).

Fig. 212. *Concentiolineatus homevalensis* (Waterhouse). A, right valve UQF 81490 from UQL 3127, x1.5. The granular surface is assumed to be due to matrix. B, anterior aspect showing gape formed by right anterior auricle and left anterior wing, UQF 81851 from UQL 3127, x3. C, right aspect of latex cast of UQF 81491 with valves conjoined, from T3, x4. See Fig. 213C.

Other east Australian species differ in shape. *Streblopteria* (now *Concentiolineatus*) *biornata* Waterhouse (1987b, pl. 6, fig. 3, 5, 8, pl. 14, fig. 2, 3) from the Fairyland Formation of the southeast Bowen Basin has very fine auricular ribs, and is upright but longer and inflated and more rugose. C. *minauris* (Waterhouse, 1987b, pl. 7, fig. 2, 6-10, pl. 8, fig. 1, 3) from the Brae Formation of the southeast Bowen Basin is somewhat rounded in outline and lacks auricular ribs and resilifer. *Streblochondria regularis* Feng (1988, pl. 2, fig. 14-19, 21) from the mid to late Carboniferous Shiqiantan Formation of the Junggar Basin, China, is close but is more extended anteriorly, and its ligament is not known.

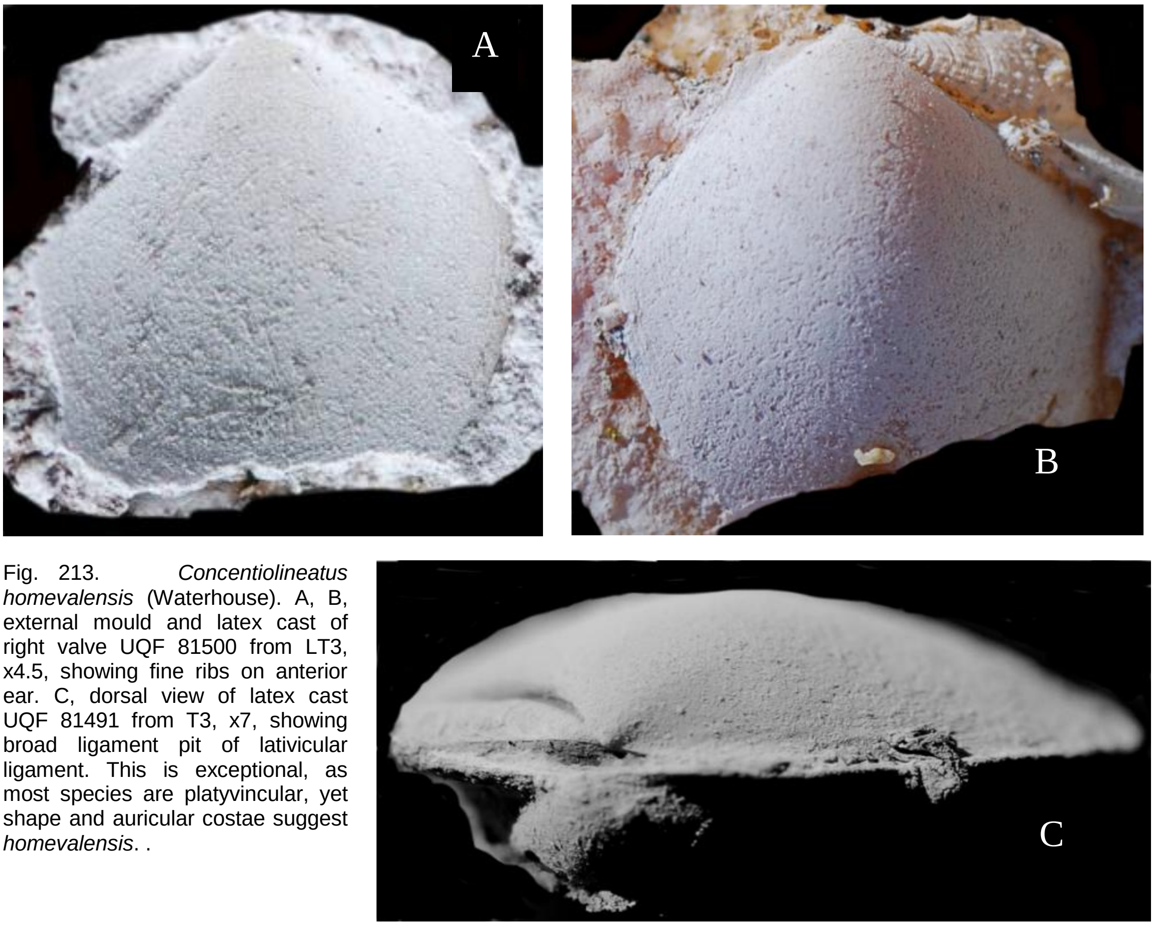


Fig. 213. *Concentiolineatus homevalensis* (Waterhouse). A, B, external mould and latex cast of right valve UQF 81500 from LT3, x4.5, showing fine ribs on anterior ear. C, dorsal view of latex cast UQF 81491 from T3, x7, showing broad ligament pit of laticivular ligament. This is exceptional, as most species are platyvincular, yet shape and auricular costae suggest *homevalensis*. .

Concentiolineatus biornata (Waterhouse, 1987b)

Fig. 214, 215

1987b *Streblopteria biornata* Waterhouse, p. 149, pl. 6, fig. 3, 5, 8, pl. 14, fig. 2, 3.

Holotype: UQF 74344 figured by Waterhouse (1987b, pl. 6, fig. 8) from Fairyland Formation, southeast Bowen Basin, OD.

Diagnosis: Moderately large erect and subrounded shells with fine ribs on the right valve anterior auricle, ornament of commarginal threads and low rugae.

Material: Tiverton specimens from UQL 4506, 4507 and 4508. *Bookeria pollex* Zone.

Dimensions in mm: From UQL 4508.

UQF	Length	Height	Width	Valve
81494	28	31	8	left
81496	30?	33	8.5	right

Description: Shell moderately large, close in shape and appearance to *homevalensis* with slightly greater inflation and more medianly placed umbones, larger posterior wing, and smaller anterior auricle with shallow moderately high byssal notch in specimens from UQL 4508, notch long and narrow in material from UQL 4506. Ornament of commarginal threads and subevenly spaced commarginal rugae. The right anterior auricle has fine ribs, and lies above a narrow byssal notch. The hinge, visible in several specimens, is platyvincular. Shell very thin, apparently recrystallized, but surface of both valves finely and densely pitted, suggestive of prismatic structure.

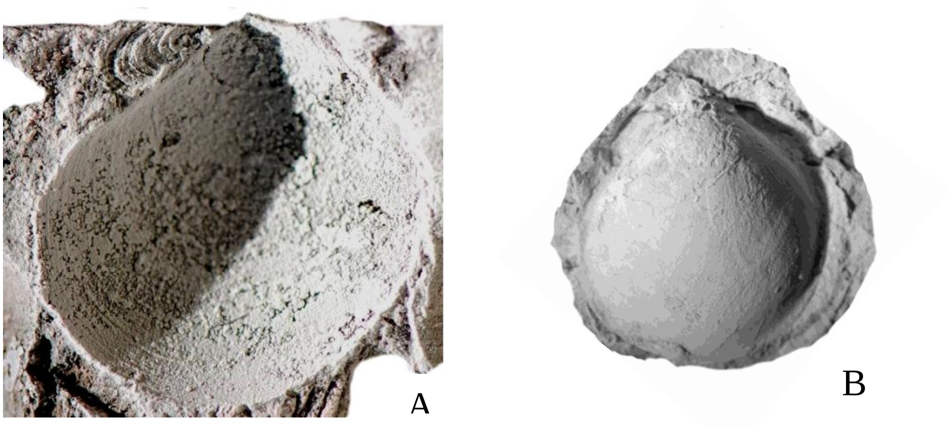


Fig. 214. *Concentiolineatus biornata* (Waterhouse). A, external mould of right valve UQF 81502 from UQL 4506, x4. B, left valve internal mould of UQF 81494 with valves conjoined, from UQL 4506, x1.2.

Resemblances: The species described as *Streblopteria biornata* by Waterhouse (1987b, pl. 6, fig. 3, 5, 8, pl. 14, fig. 2, 3) from the Fairyland Formation of the southeast Bowen Basin is close in shape and appearance, and has commarginal rugae and fine ribs over the right anterior auricle. The left anterior wing was described as finely costate by Waterhouse (1987b). In addition the byssal notch was reported as deep and narrow, which is true of material from the fine matrix of UQL 4506, but not true of the specimens in the coarse sandy matrix of UQL 4508. Given the variability in Middle Permian auricular costation reported by Waterhouse (1982b) for *Striochondria*, as based on east Australian and New Zealand material of mostly Middle Permian age, the significance of the difference is uncertain, and the similarity in shape and nature of commarginal rugae are here treated as more important.

The specimens are also very close to *Concentiolineatus homevalensis* from slightly younger beds, apart from being slightly more rounded in shape and in being more rugose.

The shape, hinge area and rugae approach features of *Montorbicula* Waterhouse, 2008a, p. 105, text-fig. 53, based on *Streblopteria montgomeryi* Gonzalez, 2006, p. 140, Fig. 8 from Early Permian of Patagonia. This species was described as smooth apart from growth wrinkles, but there are a very few commarginal narrow rugae around the ventral margin. Wrinkles are well developed in *C. biornatus*, not quite as regular or prominent near the umbones as in *M. montgomeryi*, but close, and the species differs from the Patagonian form in the presence of fine costae on the anterior auricle and left valve wing. The basal Elvinia Formation specimen from the southeast Bowen Basin figured as *Streblopteria homevalensis* by Waterhouse (1987b, pl. 4, fig. 3) has several strong wrinkles as in *Montorbicula*, and the right anterior auricle lacks costae.

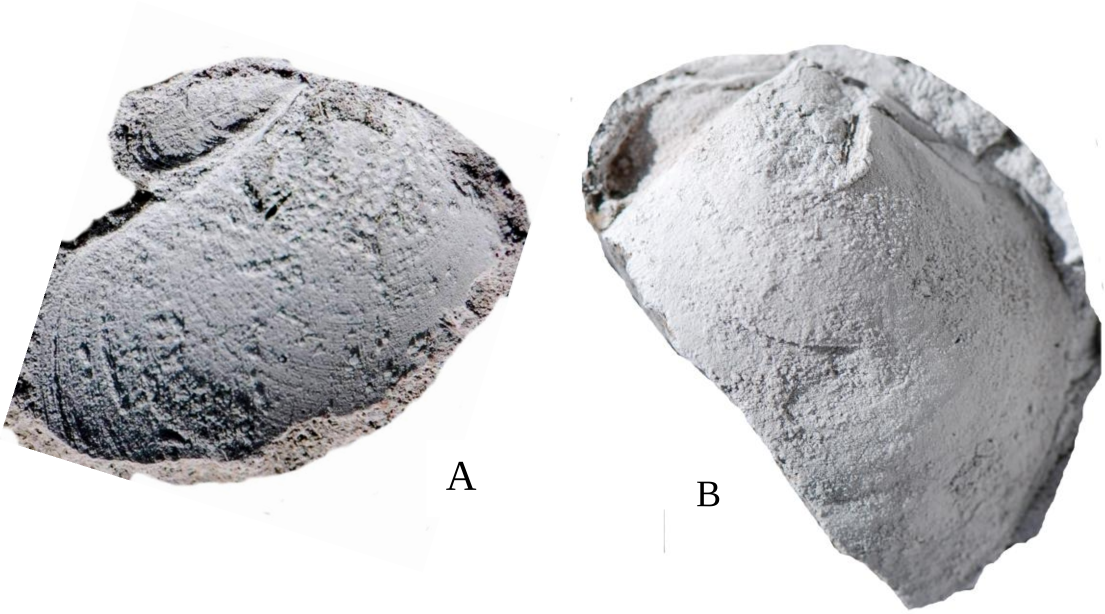


Fig. 215. *Concentiolineatus biornatus* (Waterhouse). A, external mould of broken right valve UQF 81852 from UQL 4507, x8. B, left internal mould UQF 81496 from UQL 4508, x2.

Superfamily **HETEROPECTINOIDEA** Beurlen, 1954

Diagnosis: Anterior shell extended with well developed anterior left valve wing and anterior right valve auricle, attached by byssus as a rule, growth symmetrical, umbonal slopes well defined in left valve.

Discussion: Members of Pseudomonotoidea Newell, 1938 are moderately close, but tend to be attached, and rarely show anterior sinus. The Mesozoic Superfamily Oxytomoidea Ichikawa, 1958 has very gentle left valve umbonal slopes and the anterior shell is considerably reduced, although a right anterior auricle remains and the ligament is alivincular: the left valve anterior wing and in many genera posterior wings may disappear. In Aulacomyellidae Ichikawa, another mostly Mesozoic group, the right anterior auricle is lost, and the ligament becomes largely or entirely opisthodetic. This group is placed in Posidonioidea.

The source of the superfamily has been traced to an early Devonian Family Natalissimidae Waterhouse, 2008a, in which two genera, *Natalissima* Waterhouse and *Yassapecten* Waterhouse differ from other Pterinopectinoidea having an almost flat right valve with ornament differing from that of the left valve: most pterinopectins are subequivalve biconvex with ornament much the same on each valve. It appears that Natalissimidae gave rise to a group of shells also typified by having the right valve much less inflated than the left valve, and by having the ornament of the right valve different from that of the left valve. Other differences were also entailed: the ligament developed a subumbonal resilifer or ligament pit, like that found in a number of Chaenocardioidea.

Family **HETEROPECTINIDAE** Beurlen, 1954

Diagnosis: Shells inequivalve, right valve comparatively flat, anterior and posterior wings large, umbonal slopes well defined, ornament primarily costate, not plicate, increase mostly by intercalation rather than branching on left valve and by intercalation or by branching on right valve, growth-lines swing hingewards in interspaces. Hinge alivincular, no hinge teeth.

Subfamily **HETEROPECTININAE** Beurlen, 1954

Diagnosis: Left valve ornamented by subplicae or prominent costae, increase by intercalation, right valve ribs increase by branching. Pallial line open dorsally.

Discussion: This subfamily has been recently reviewed and expanded in Waterhouse (2008a). Members are close in many respects to genera within Etheripectininae, but are discriminated by the branching ribs on the right valve.

Genus ***Hillaepecten*** Waterhouse, 2010a

Type species: *Hillaepecten queenslandica* Waterhouse, 2010a, p. 87 from Tiverton Formation (Sakmarian) of north Bowen Basin, Queensland, OD.

Diagnosis: Left valve ornamented by several orders of costae, primary costae bearing small spines as a rule; right valve ornamented by ribs that increase by branching, and tend to be bundled. Ligament platyvincular or lativincular.

Discussion: This genus is distinguished from other members of Heteropectininae by the scaly lamellae over the left valve which produce small and close-set open spines over the costae. The genus is apparently close to *Vorkutopecten*, but interpretation of this genus causes difficulty, because the type species *Aviculopecten* (*Deltopecten*) *giganteus* Chao var. *talis* Lyutkevich & Lobanova (1960, pl. 16, fig. 10, pl. 17, fig. 1), as nominated by Guskov (in Muromseva 1984, p. 73), is very incomplete, and based principally on a right valve from east Taimyr, of Roadian age. The holotype right valve does clearly show branching ribs and large anterior auricle, suggestive of Heteropectininae. All of the specimens ascribed to *talis* by Guskov in Muromseva (1984, pl. 21, fig. 4, 6, 7, pl. 27, fig. 14, pl. 29, fig. 7, 12, pl. 53, fig. 6) are consistent in generic character, and a left valve (pl. 29, fig. 7) suggests that spines are larger and spaced further apart compared with those of *Hillaepecten.* Guskov included *Aviculopecten subclathratus* Licharew, 1927 in *Vorkutopecten*, and this as figured in Muromseva (1984, pl. 25, fig. 15, 16, pl. 27, fig. 9, pl. 29, fig. 3, 6, 11, 14, pl. 31, fig. 8, 11-13) carries some suggestion of small spines (pl. 29, fig. 3, 11, pl. 31, fig. 13) which are larger and spaced further apart than those of *Hillaepecten*. Costae are less simple than in *Hillaepecten*, especially on the right valve. Preservation is not good, and the nature of the ornament not entirely clear.

Heteropecten Kegel & Costa, 1951 is readily distinguished: the left valve has subplicae and costae, the right valve has bundled ribs that increase by branching, and no spines are developed on either valve (Reed 1930, Kegel & Costa 1951, Rocha-Campos 1970, Waterhouse 2008a, Text-fig. 84-87).

Astafieva (1997) included Licharew's species *subclathratus* in her genus *Neptunella*, type species *N. sulciconcentrica* Astafieva, from Late Permian of Mongolia. The name *Neptunella* was not available, having been first proposed by Gray (1854) for a different genus and species. The left valve has up to four orders of ribs increasing by intercalation, with spines over the first and often second order ribs, and spines prominent at the anterior margin. The right valve is moderately convex with ribs described as intercalated, but definitely branching as well as shown on the figure provided by Astafieva (1997, pl. 3, fig. 5b). The primary ribs show a few long spines. Astafieva (1997) dismissed *Vorkutopecten* with the claim that numerous specimens with different characteristics had been ascribed to *V. talis* in Muromseva. That may be so, but does not adequately defend her *Neptunella* against the possibility that it is a junior synonym (Astafieva 1997, pl. 29, fig. 12). Subject to the unsatisfactory nature of the holotype for *talis*, it appears that *Neptunella* sensu Astafieva is a synonym of *Vorkutopecten*. but the Russian material tends to be decorticated, and although none appears to show the true ornament of the left valve very clearly, they appear to have large spines on the left valve costae.

Other genera show some approach and belong to the same subfamily. *Nodulipecten* Waterhouse (2008a, p. 149, pl. 1, fig. 3), type species *N. hoskingi* Waterhouse from the Madeline Formation of Western Australia, has several orders of ribs increasing by intercalation on the left valve, and the primary ribs bear subdued spines. The right valve ribs are paired through branching, and are ornamented by well developed nodes. *Vanvleetia* Waterhouse, 2001 is represented by a number of species in the especially Pennsylvanian faunas of the United States, with ribs that are branching and bundled on the right valve, and strong primary ribs or subplicae on the left valve, bearing large hollow spines, and with fine ribs in the broad interspaces. *Inaequalitaria* Waterhouse, 2008a, p. 147, type species *Aviculopecten subquadratus* Bell, 1929 from the Carboniferous Horton-Windsor Group of Nova Scotia is very like *Hillaepecten* in overall shape and comparatively simple ribbing, but lacks spines. Apart from the nature of right valve ribs, the small and numerous spines of the left valve of the present species indicate a clear difference from the coarse and well spaced left valve spines of *Vanvleetia* and *Primaspina* (see p. 278), and probably *Vorkutopecten*.

Hillaepecten queenslandica Waterhouse, 2010a

Fig. 216 - 218

2010a *Hillaepecten queenslandica* Waterhouse, p. 89, Fig. 36-38.

Holotype: UQF 81517 from UQL 1630, Tiverton Formation, figured by Waterhouse (2010a, Fig. 36B, 38C) and herein as Fig. 216B, 217C, OD.

Diagnosis: Small shells, left valve gently convex with several orders of closely spaced ribs crossed by commarginal spiny laminae, right valve convex but less inflated than left, with comparatively broad branching non-spinose ribs. Ligament lacks a resilifer.

Material: Specimens from UQL 1383, 1630, 3127, 3780, 4518 and 4519. Possible specimens from UQL 1622, 1630, 2619, 3780 and LT3. *Bookeria geniculata* and *Taeniothaerus subquadratus* Zones.

Dimensions in mm: left valves

UQF	UQL	Length	Height	Width
81622	3780	17.5	17	5
81520	3127	19	15	3
81518	3127	24	22.5	3.5

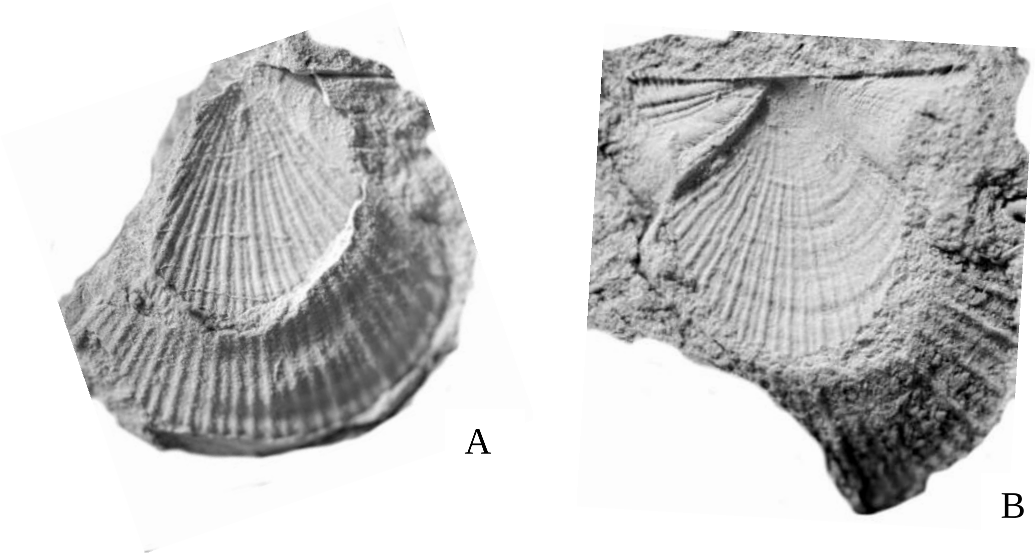


Fig. 216. *Hillaepecten queenslandica* Waterhouse. A, internal and external moulds of UQF 81518 from UQL 3127, x2. B, internal and external mould of holotype UQF 81517 from UQL 1630, x2.

Description: Shells small, left valve gently convex, hinge slightly less than maximum width of shell, anterior wing convex and slightly longer than more gently convex posterior wing; umbonal angle varies between 80° and 95°, anterior slope steep and gently concave in outline, posterior slope straight in outline. Right valve moderately convex, anterior umbonal slope gently concave in outline and posterior umbonal slope almost straight in outline and gently convex in profile. Anterior auricle long with ctenolium, gently convex below hinge, becoming concave above long narrow byssal slit. Posterior wing convex next to hinge and mostly concave with high moderately deep sinus. Left valve ornamented by ribs increasing through intercalation in three orders, some ten or eleven primary ribs commencing at umbo; ribs closely spaced with rounded crests and bear small scaly spines at intersections with commarginal laminae. Growth lines low, close-set, may arch weakly hingewards over costal crests. Anterior wing ornamented by six or seven costae and posterior wing ornamented by more numerous finer ribs. Right valve ornamented by branching ribs with low crests slightly broader than interspaces. Anterior auricle carries three strong ribs near middle, and posterior wing marked by some nine or more fine ribs over the sinused sector. At the cardinal extremity the margin curves obtusely forward over a short distance. Growth lines on the right valve increase in height next to the hinge, and project slightly from the anterior auricle. The ligament area is concave and low on the left valve, and marked by fine horizontal striae: there is no resilifer below the beak. The ligament area of the right valve is very low, with one or two horizontal striae, but is not preserved below the beak. Muscle scars not visible.

Resemblances: *Aviculopecten sprenti* Johnstone (1887, p. 9; 1888, p. 127, pl. 14, fig. 11 (fig. 8 in error) was described from Early Permian at One Tree Point, Tasmania, but the only figured specimen has been lost. The figure shows a small specimen with detail of micro-ornament. Further material was described from Farley and Harper's Hill in the Hunter Valley by Etheridge & Dun (1906, p. 15, pl. 2, fig. 6, 7, pl. 13, fig. 9, pl. 16, fig. 5, 6). The left valve AMF 35327 as figured from Lochinvar by Etheridge & Dun (1906, pl. 2, fig. 7) and Waterhouse (1982b, pl. 2, fig. a, d) shows episodic high growth lamellae arching hingewards over the ribs, and more closely spaced than in the present species, at three in 5mm, and much more closely spaced and smaller than in *Primaspina* (see p. 278). The internal mould of left valve AMF 35326 (Etheridge & Dun 1906, pl. 2, fig. 6) from Farley is very similar and suggests nodes on the ribs. The other specimens figured by Etheridge & Dun (1906) could not be found at the Australian Museum, but may well be allied. Dun (1912) noted the recurved anterior and posterior outline and referred to decussations on the primary and secondary costae. *Hillaepecten sprenti* differs from the Tiverton species in having more and finer left valve costae and more closely spaced spines especially over the first formed part of the shell. No right valves are known. The Lochinvar right valve called *Aviculopecten* sp. by Etheridge & Dun (1906, pl. 12, fig. 1) and compared to *sprenti* might be conspecific, but is moderately inflated, with low even ribs, suggestive of *Deltopecten* or

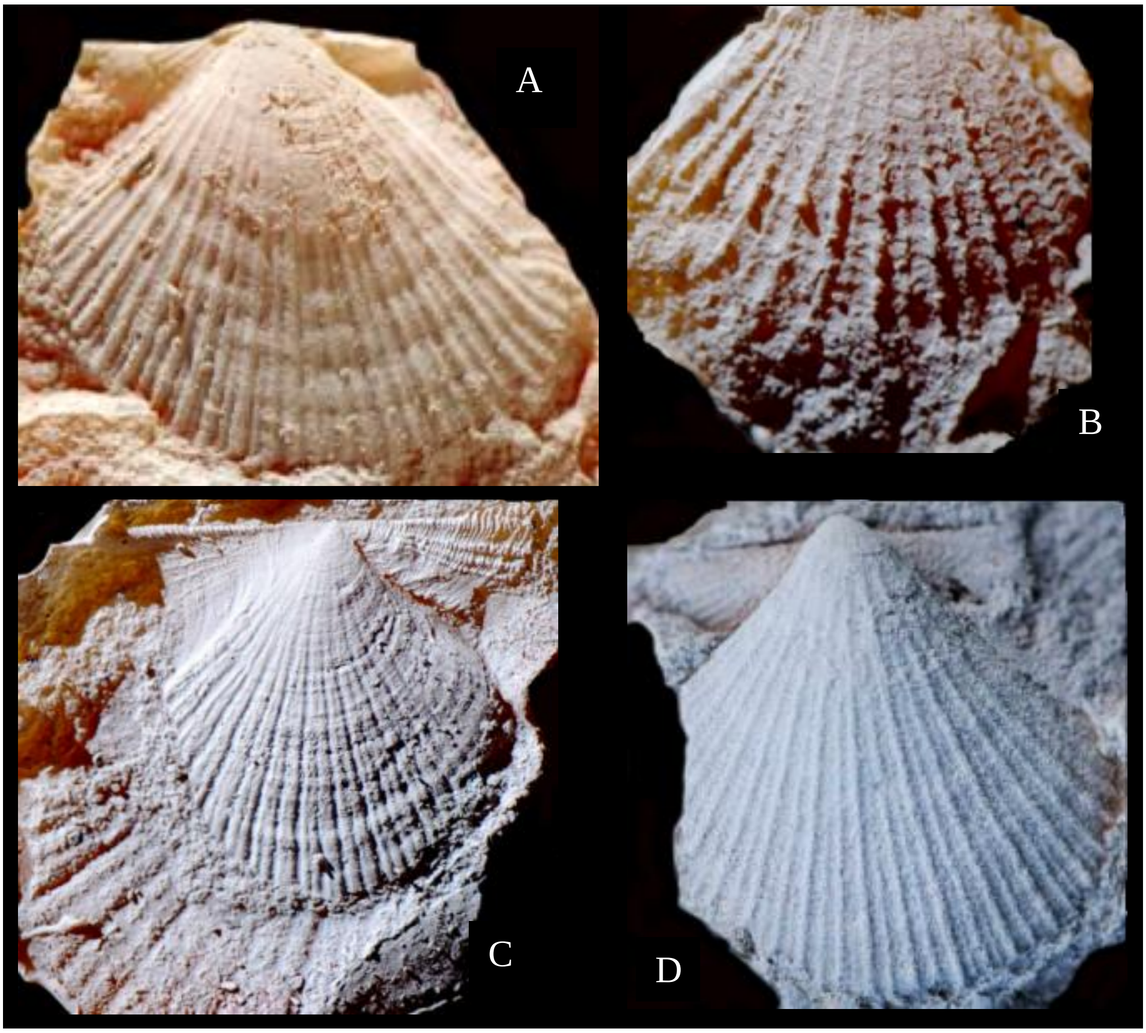


Fig. 217. *Hillaepecten queenslandica* Waterhouse. A, latex cast of worn ventral valve UQF 81520 from UQL 3127, x4. B, latex cast of ventral exterior, UQF 81589 from UQL 1383, x 3.5. C, latex cast of holotype UQF 81517 from UQL 1630, showing right valve resting on left valve, x 4. D, left valve UQF 81622 from UQL 3780, x3.

Squamuliferipecten. Dickins (1957, 1963) considered that *Aviculopecten sprenti* Johnston was probably conspecific with Dana's species *tenuicollis*, as reviewed in Waterhouse (1982b, p. 17), but first-hand inspection of material shows that Etheridge & Dun (1906) were correct in their discrimination of *sprenti* as a separate species. Etheridge & Dun (1906, p. 16) had borrowed material from Tasmania, and were satisfied that *sprenti* was different from *tenuicollis*. Various Middle Permian specimens assigned to *Aviculopecten sprenti* by Fletcher (1929b) from the south Sydney Basin do not appear to belong to *Hillaepecten.*

Etheridge (1907, p. 32, pl. 7, fig. 5, 6) identified *Aviculopecten sprenti* from Irwin River, Western Australia, on the basis of vestiges of an originally ornate ornament. There are sufficient differences between the Irwin River material and *sprenti* to suggest a separate species.

Aviculopecten jemsensis Peou & Engel (1979, Fig. 7F, 8.A1-7) from the late Visean or early Namurian Faulkland Formation of northern New South Wales is allied, with small left valve spines, long right valve anterior auricle and branching right valve ribs. Fine lirae were reported over the costae and interspaces. Primary ribs are prominent over the left valve, and the right valve byssal sinus is high and deep.

The species differs from *Vorkutopecten* Guskov in the nature of left valve spines which are small and numerous. Unfortunately the ligament area of *Vorkutopecten* and its various species is not known, and the exterior appears to be often decorticated. It may prove to have a resilifer in the ligament area, and left valve spines appear to be rare, and comparatively large. Externally there is considerable approach of the present species to *Aviculopecten mutabilis* Licharew, 1927 from the Early Permian of the Urals and Russian Platform. This species has intercalated left valve ribs of several orders, and branching right valve ribs, and although the ribbing is more differentiated on the left valve and right valve ribs are broader, the general similarity is very strong. As noted in Muromseva (1984), *Aviculopecten guadalupensis* Girty (1909a, pl. 16, fig. 20, 20a) is also close, but the figured material was sparse and did not show surface detail, according to Girty (1909a). Nakazawa (1999, Fig. 5.6-10) described *Vorkutopecten svalbardensis* from the Hovtinden Member of Spitsbergen for which the illustrations agree with the presentation herein, but he described the right valve ribs as intercalated, which they do not seem to be. Right valve ribs have low spines formed by close-set growth laminae. The posterior wings are comparatively large.

Fig. 218. *Hillaepecten queenslandica* Waterhouse. A, latex cast of right valve UQF 81518 from UQL 3127, x 4. B, detail of left valve ornament on external mould, UQF 81475 from UQL 4519, x 8.

Subfamily **ETHERIPECTININAE** Waterhouse, 1982b

Diagnosis: Ornament of intercalate costae on left and right valve, branching exceptional, costae variably spinose.

Genus ***Etheripecten*** Waterhouse, 1963b

Type species: *Etheripecten striatura* Waterhouse, 1963b, p. 195 from Kildonan Member (Changhsingian), New Zealand, OD.

Diagnosis: Left valve bears costae in several orders as a rule, arising by intercalation, primary costae generally remaining prominent. Right valve costae simpler and more uniform. Growth lines arch dorsally in interspaces. Shell aragonitic or calcitic.

Discussion: This genus, named for the distinguished paleontologist R. Etheridge Jnr, is represented by numerous species in east Australia, and has been widely recognized, for example by Nakazawa (1999) and Dickins (1981). Fang & Morris (1999) dismissed the claim by Newell & Boyd (1995) that the genus was synonymous with *Heteropecten* Kegel & Costa, 1951. The primary ribs in the left valve of *Heteropecten* are broad like narrow plicae, whereas the primary ribs in *Etheripecten* are solid costae, and the interspaces are much wider in *Etheripecten* than the narrow interspaces characteristic of *Heteropecten*. In the right valve, as stressed by Nakazawa (1999), the ribs are broad and bifurcated in *Heteropecten*, and narrow and intercalated in *Etheripecten*, a difference also underlined as significant by Fang & Morris (1999).

Etheripecten is particular common in the Permian of east Australia, and many of the species have been described by Dana (1849), M'Coy (1847), Etheridge & Dun (1906) and Fletcher (1929b), with some refigured by Waterhouse (1982b).

The question of shell composition requires consolidation. Aragonite is typically involved in the make-up, but Waterhouse (1982b, pp. 10-13) noted evidence for a purely calcitic composition in New Zealand pectiniforms, and pointed to Dodd (1964) and Lowenstam (1954a, b, 1963, 1964) who claimed that the percentage of calcite in shell varied inversely with temperature. The New Zealand evidence seems hard to gainsay, and of course it is difficult for scholars working on northerly paleotropical faunas to accrue evidence to the contrary. Clearly a field for further study.

Etheripecten tenuicollis (Dana, 1847)

Fig. 219, 220

1847 *Pecten tenuicollis* Dana, p. 160.
1847 *Pecten sub-5-lineatus* M'Coy, p. 298, pl. 17, fig. 1.
1849 *P. tenuicollis* – Dana, p. 705, pl. 9, fig. 7, 7a.
1906 *Aviculopecten tenuicollis* – Etheridge & Dun, p. 13, pl. 13, fig. 10-12, pl. 14, fig. 5.
1957 *A. tenuicollis* – Dickins, p. 45, pl. 6, fig. 7, 8 (part, not 9 = *Fletcheripecten*).
1963 *A. tenuicollis* – Dickins, p. 82, pl. 11, fig. 5, pl. 13, fig. 12-16, 17, pl. 14, fig. 1.
1982b *Etheripecten tenuicollis* – Waterhouse, p. 161, pl. 1, fig. g, pl. 2, fig. a-g, pl. 3 fig. a, d.
1983d *E. tenuicollis* – Waterhouse, p. 163, pl. 4, fig. 7, fig. 11, 12.
1986 *E. tenuicollis* – Parfrey, p. 63, Fig. 4a-c.
1987b *E. tenuicollis* – Waterhouse, p. 146, pl. 4, fig. 2, 6, 7, 13.
1988 *E. tenuicollis* – Waterhouse, p. 173, pl. 2, fig. 5.
1992a *E. tenuicollis* – Clarke, p. 40, Fig. 24A-F.

Holotype: USNM 3658 from Allandale Formation, Harper's Hill, Hunter Valley, New South Wales, figured by Dana (1849, pl. 9, fig. 7, 7a), Dickins (1963, pl. 14, fig. 1) and Waterhouse (1982b, pl. 3, fig. d; 1988, pl. 2, fig. 5), by monotypy. Type for *subquinquelineatus*, CASM E 10720, figured by M'Coy (1847), by monotypy.

Diagnosis: Medium-sized shells with only moderately inflated left valve, anterior umbonal slope inclined from hinge at 30-40°, left valve ornament of radial ribs well differentiated in three or four orders, primary and then secondary costae remaining distinct, higher than costae arising later, narrow.

Material: Small specimens, mostly left valves, from UQL 1383, 1620, 1630, 2618, 2619, 3127, 3780, 4514, 4518, T3 and LT3. *Bookeria pollex*, *Bookeria geniculata* and *Taeniothaerus subquadratus* Zones.

Description: Specimens up to 70mm long and high, with close-set ribs in three orders, the primary ribs remaining prominent but slender, and secondary ribs increasing in strength.

Resemblances: The specimens as far as they are preserved appear to be identical with *Etheripecten tenuicollis* (Dana). This species is very widespread, allowing for the qualifications noted by Waterhouse (1982b, 1987b), and occurs in Early Permian throughout east Australia including Tasmania, and extends into the Callytharra and Fossil Cliff Formations of the Carnarvon Basin and Fossil Cliff Formation and High Cliff Sandstone, Perth Basin, and Nura Nura Member of the Poole Sandstone, Canning Basin, Western Australia, and Brunel Formation, *Ingelarella plica*

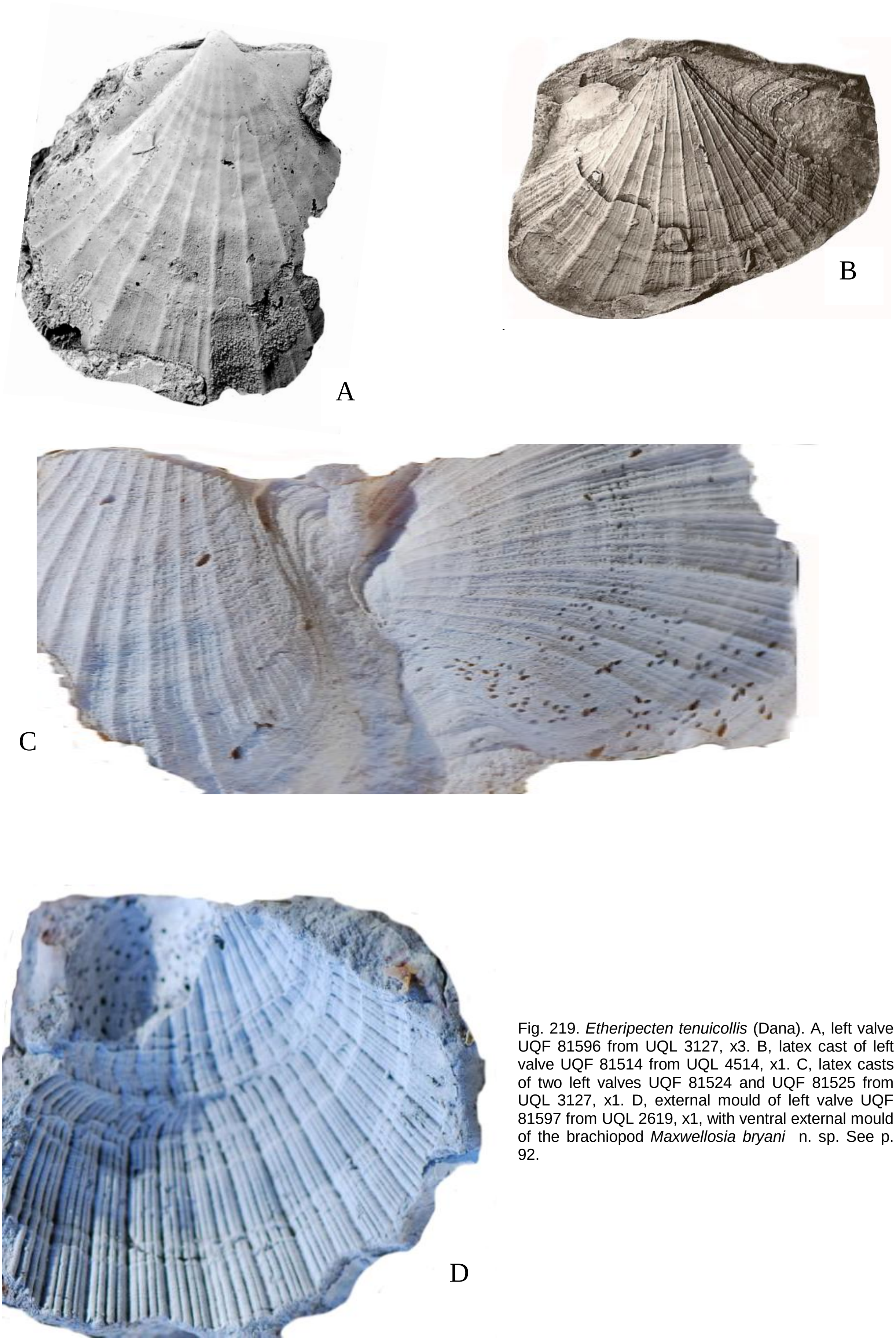


Fig. 219. *Etheripecten tenuicollis* (Dana). A, left valve UQF 81596 from UQL 3127, x3. B, latex cast of left valve UQF 81514 from UQL 4514, x1. C, latex casts of two left valves UQF 81524 and UQF 81525 from UQL 3127, x1. D, external mould of left valve UQF 81597 from UQL 2619, x1, with ventral external mould of the brachiopod *Maxwellosia bryani* n. sp. See p. 92.

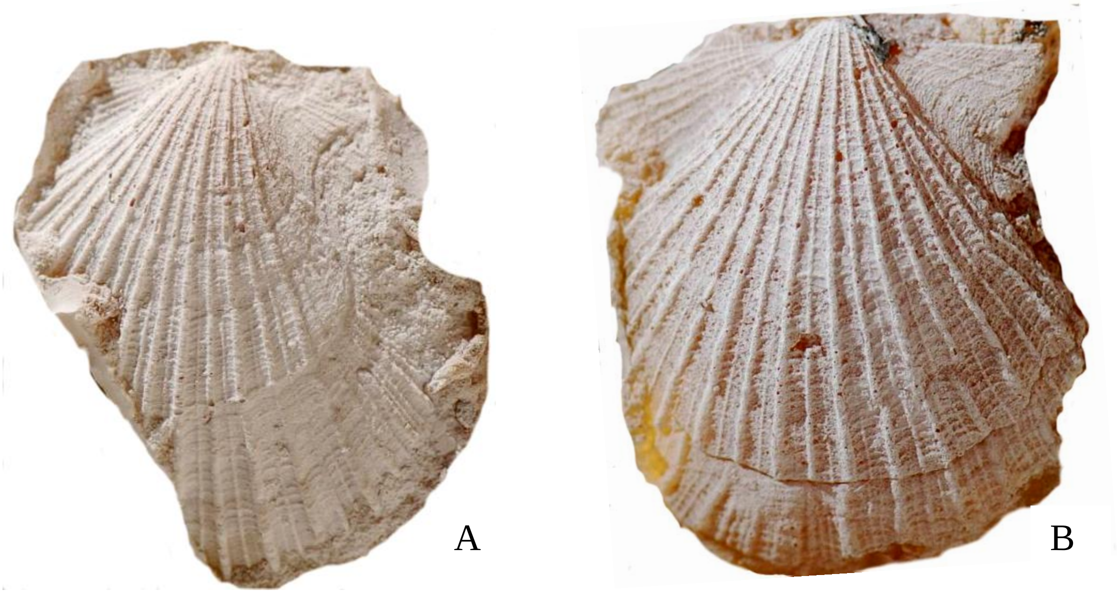


Fig. 220. *Etheripecten tenuicollis* (Dana). A, latex cast, left valve UQF 81526 from UQL 2619, x2.5. B, latex cast of UQF 81529 from LT3, x3. Commarginal laminae are unusually well preserved.

Zone of New Zealand (Waterhouse 1987b, p. 147). *Pecten subquinquelineatus* M'Coy (1847, pl. 17, fig. 1) is very close to and probably the same species as *tenuicollis* (Waterhouse 1987b, p. 146). The type specimen comes from the Allandale Formation at Harper's Hill, New South Wales, and has slightly broader left valve and fine costae.

Etheripecten playfordi n. sp.

Fig. 221 - 227

1892 *Deltopecten illawarrensis* [not Morris] – Etheridge, pl. 43, fig. 2.

1963 *Aviculopecten* sp. nov. Dickins, pp. 78, 81, pl. 11, fig. 1?, 2, 3.

1964b *Aviculopecten* sp. Hill & Woods, pl. P11, fig. 13a, b.

1964b *Aviculopecten* cf. *subquinquelineatus* (M'Coy) – Hill & Woods, pl. P11, fig. 14, 15 (part, not fig. 16 = *Primaspina dawsonensis* (Runnegar & Ferguson)).

1972 *Aviculopecten* sp. nov. Hill, Playford & Woods, pl. P11, fig. 13, 14.

1972 *A. tenuicollis*? Dana – Hill, Playford & Woods, pl. P11, fig. 15.

1982b *Etheripecten*? sp. Waterhouse, pl. 3, fig. i.

Derivation: Named for Geoffrey Playford.

Holotype: Specimen UQF 81590 from UQL 4520, Tiverton Formation, figured herein as Fig. 223A, here designated.

Diagnosis: Large shells with moderately inflated left valve, large posterior wing, ornamented by prominent primary costae bearing fine ribs and several additional orders. Right valve convex, with broad low close-set ribs.

Material: Specimens from UQL 1621, 1622, 1625, 1626, 1627, 1628, 1629, 2619, 2622, 2628, 2629, 3127, 3129, 4509, 4514-4519, 4521 and LT3. *Bookeria geniculata* and *Taeniothaerus subquadratus* Zones.

Dimensions in mm: left valves

UQF	UQL	Length	Height	Width
81515	4521	76	77	15
81590	4520	48	44	9.5

Description: Shells large, left valve convex, largest specimens over 90mm in length with one from UQL 3127 measuring 115mm in length, 120mm in height and 29mm in width, umbo subcentrally placed with angle of 70-80^{o}, umbonal walls moderately high and convex, anterior wall steeper than posterior wall, left anterior wing concave, with

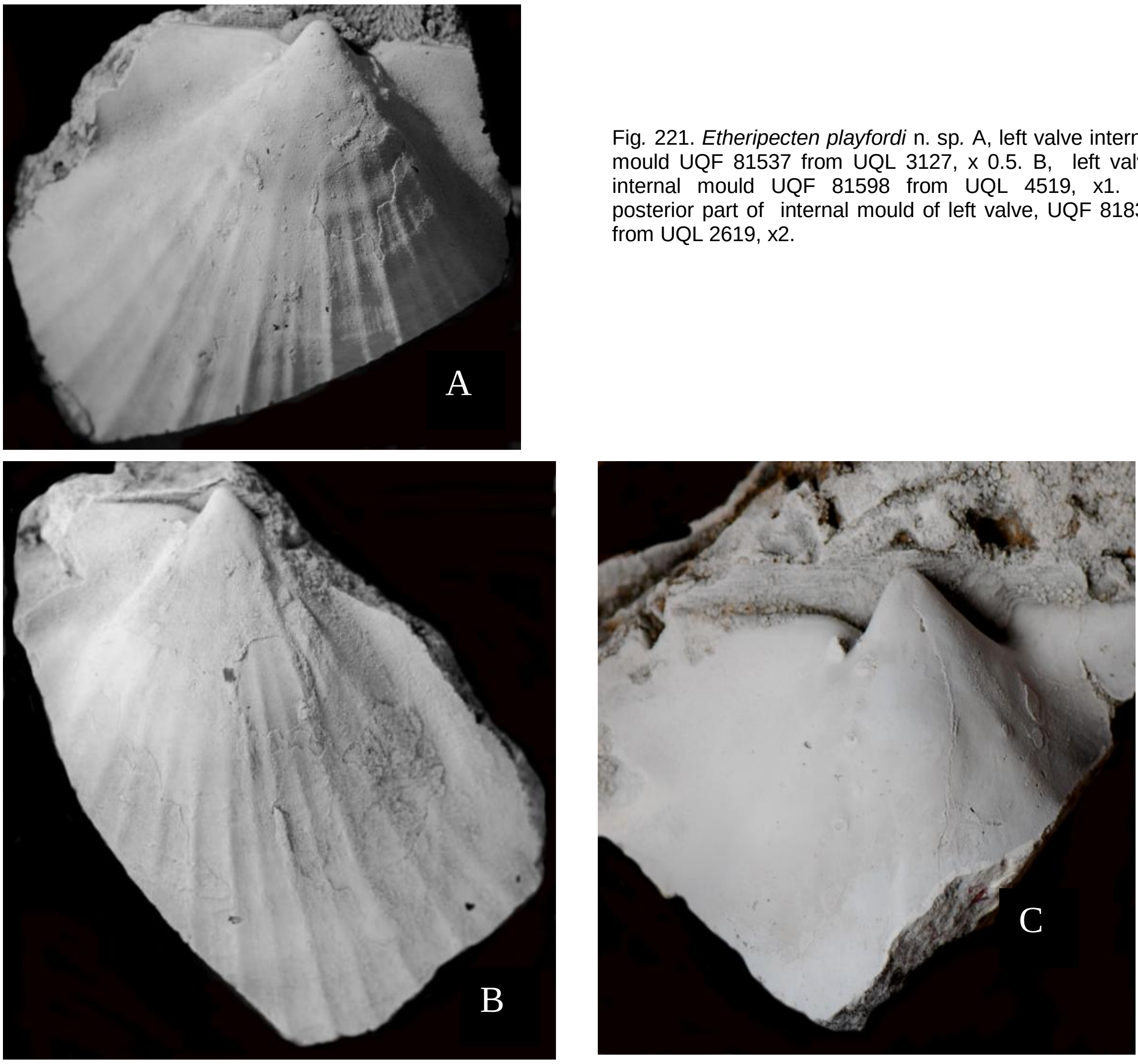


Fig. 221. *Etheripecten playfordi* n. sp. A, left valve internal mould UQF 81537 from UQL 3127, x 0.5. B, left valve internal mould UQF 81598 from UQL 4519, x1. C, posterior part of internal mould of left valve, UQF 81838 from UQL 2619, x2.

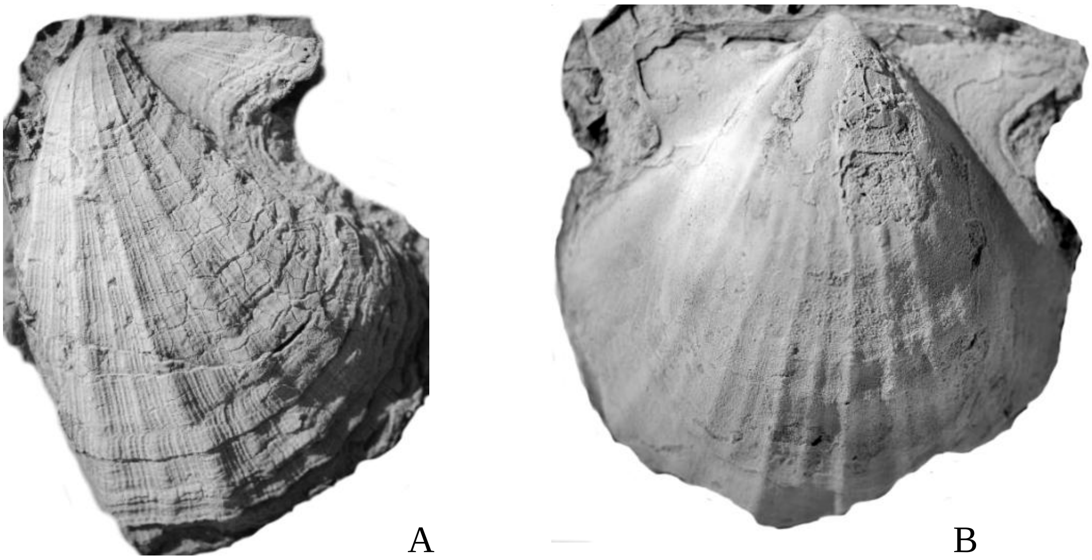
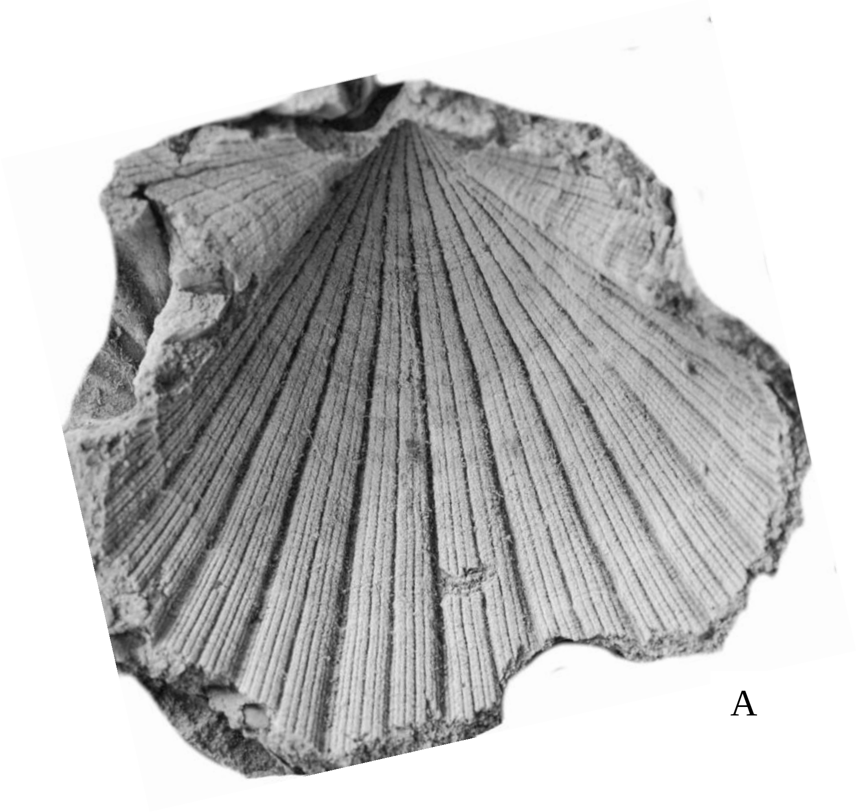


Fig. 222. *Etheripecten playfordi* n. sp. A, latex cast left valve UQF 20810 from L 1622, x1. B, internal mould of left valve UQF 81515 from UQL 4521, x1.



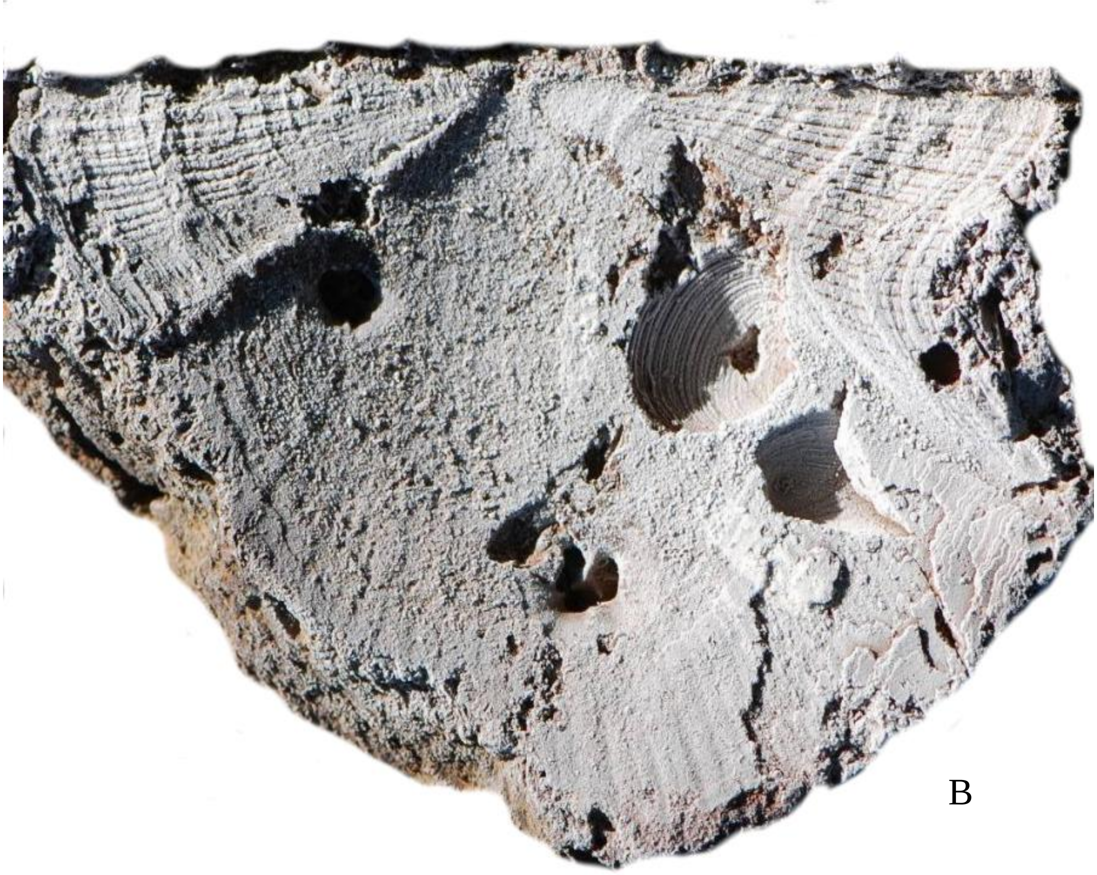


Fig. 223. *Etheripecten playfordi* n. sp. A, holotype, external mould of left valve UQF 81590 from UQL 4520, x2. B, external mould of right valve UQF 21067, x1.6, with attached bivalves, including *Astartella heideckeri* n. sp., UQF 81549. See Fig. 240A, C, D.

Fig. 224. *Etheripecten playfordi* n. sp., external mould of left valve UQF 81591 from UQL 1627, x 1.5.

posterior margin concave in outline and acute cardinal extremity, becoming more rounded in outline and obtuse in larger specimens, wing large with small if any byssal sinus, weakly convex with obtuse cardinal extremity, posterior wing large. Right valve gently convex with low steep posterior and anterior walls, right anterior auricle large, flat, with long narrow byssal notch widening anteriorly in a valve 57mm long, but shallower in a larger specimen; posterior wing large, gently concave, posterior outline concave or convex. Primary ribs of left valve prominent, numbering 11-12, rarely fewer at 8-9, develop ventrally into narrow or gentle plicae, rib remains prominent at crest and broader than secondary and subsequent ribbing, flanks of primary ribs low and rounded, crests develop one to five or more fine micro-ribs ventrally some 20mm from umbo, slightly finer than in interspaces. Ribs of three further orders arise by intercalation within interspaces, and only secondary ribs become prominent, the interspaces remaining concave, and the growth lines and laminae arching hingewards. Four or five growth steps and growth increments cover the valve, two or three per mm ventrally, arch hingewards between primary costae. Anterior and posterior wings of left valve marked by close-set differentiated ribs of mostly two orders. Right valve with broad-crested very low fine and numerous ribs increasing by intercalation and shallow flat wider interspaces, posterior wing covered by up to 24 fine differentiated ribs, anterior auricle with fewer but well defined ribs, numbering 14 in one specimen, and not developed near the inner ear, which is marked only by growth laminae, anterior auricle and posterior wing both crossed by fine growth increments. Hinge alivincular, marked by fine striae parallel to hinge and by well formed resilifer, pedal scar and several retractor scars in curved line under left valve umbo; large adductor complex visible on right valve from LT3, pits between dorsal ends of pallial line. Pallial line outlined by pits in UQF 81838, open dorsally and with deep small adductor scar anteriorly.

Resemblances: Dickins (1963, p. 78) first drew attention to this species as likely to be new. A specimen figured as *Aviculopecten tenuicollis*? [not Dana] by Hill & Woods (1964b, pl. 11, fig. 15), repeated in Hill, Playford & Woods (1972) from the Tiverton Formation, appears to have more prominent primaries than in the present species, but might be a variant. Small left valves of the present form are close to specimens of Early Permian age, mostly from the Lochinvar and Allandale Formations of the Hunter Valley, Sydney Basin, that have been assigned to *Etheripecten* *tenuicollis* (Dana 1847, 1849). The species *tenuicollis* has close-set and similarly differentiated ribs and the left valve primary ribs show no sign of broadening, unlike those of *playfordi*. A left valve AMF 35288 from the Lochinvar Formation, Hunter Valley, identified as *subquinquelineatus* M'Coy by Etheridge & Dun (1906, pl. 3, fig. 2), has coarse primary ribs, but is an internal mould, so that the presence or absence of fine supracostal micro-ribs cannot be ascertained.

Fletcheripecten Waterhouse from Permian faunas of east Australia and New Zealand is very close, and characterized by narrow plicae in place of left valve primary ribs. A fine example is offered by *F. laticostatus* Waterhouse, renamed for *Pecten comptus* Dana not M'Coy. Some plicae in the type species, *F. heterosus* Waterhouse, may carry two or three ribs, but as a rule the ribs are smooth without subsidiary micro-ribs or riblets. There is a degree of secondary convergence between *Etheripecten* and *Fletcheripecten*.

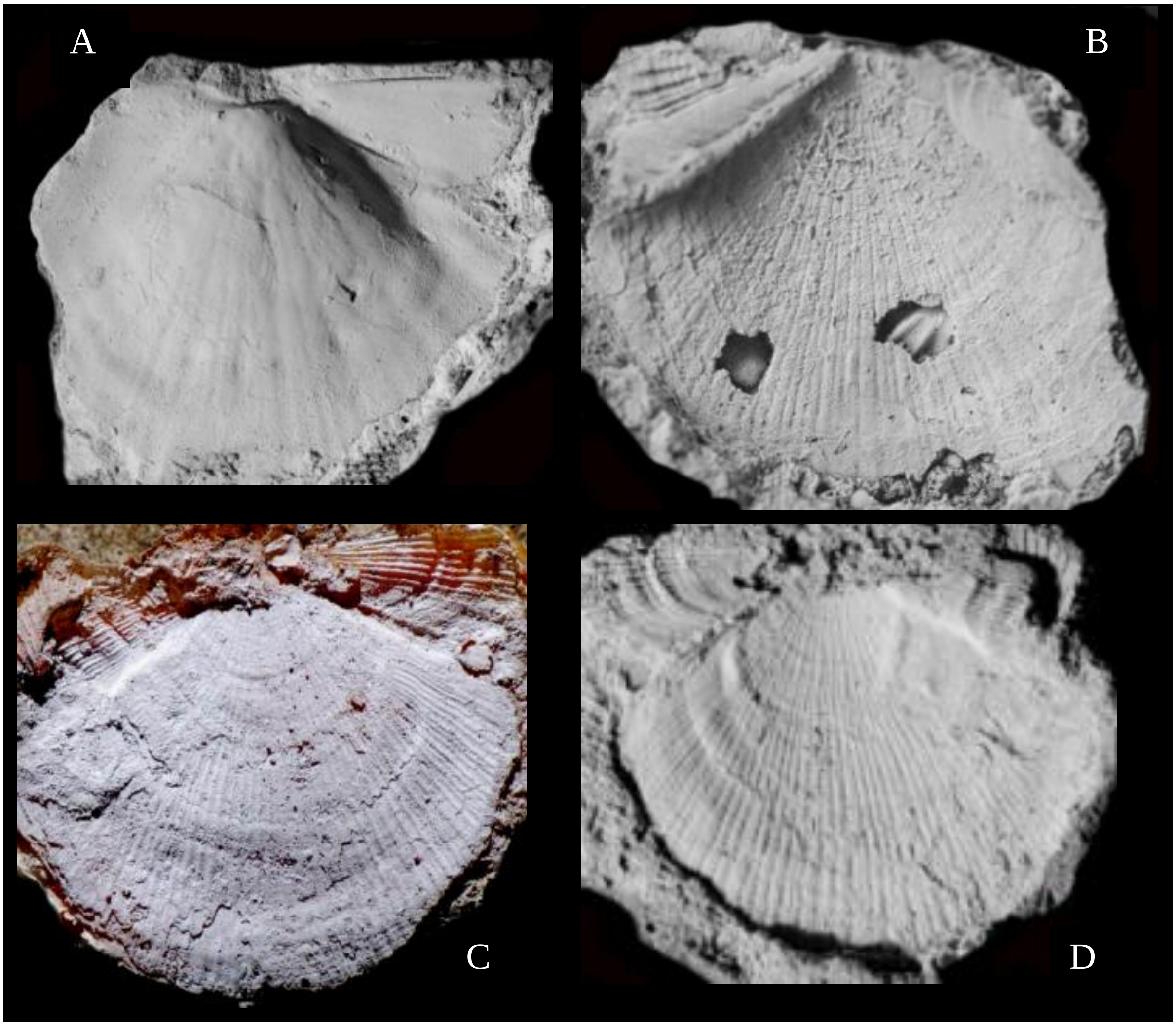


Fig. 225. *Etheripecten playfordi* n. sp., right valves. A, internal mould UQF 81527 from UQL 4518, x1. B, external mould UQF 81523 from UQL 3127, x1.5. C, D, latex cast and external mould UQF 81528 from UQL 4518, x1.

Younger species of *Etheripecten* described from east Australia and New Zealand by Fletcher (1929b) and Waterhouse (1982b) differ from the present form in having slightly narrower but often higher primary costae without fine ribs over the crest ventrally and no plicae. However the type species of the genus, *Etheripecten striatura*, does have fine ribs along some of the primaries, and conceivably this species together with *playfordi* should be placed in *Etheripecten* (*Etheripecten*) and separated from species characterized by high narrow primary costae without micro-ribbing. The holotype of *Etheripecten striatura* was misrepresented as being a juvenile left valve of Lower Permian age by Newell & Boyd (1995, p. 34). The valve is at early towards full maturity, judged by muscle impressions and

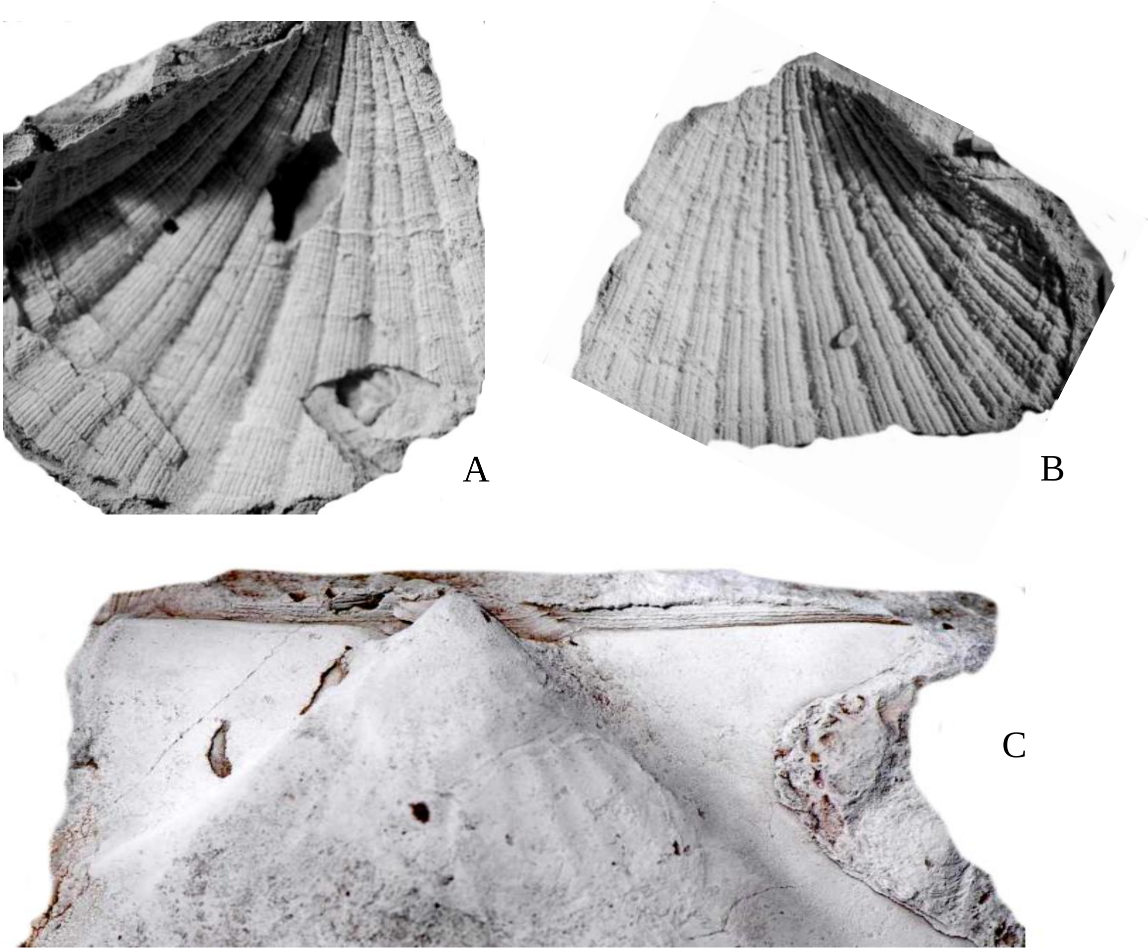


Fig. 226. *Etheripecten playfordi* n. sp. A, external mould of left valve UQF 20767, x1. B, external mould of left valve UQF 81523 from UQL 3127, x 1. C, internal mould of left valve showing hinge**,** UQF 81516 from UQL 4518, x1.

Fig. 227. *Etheripecten playfordi* n. sp. detail of micro-ornament on external mould of left valve UQF 81621 from UQL 3127, x6.

other attributes of it and associated specimens, and the type material comes from the *Paucispinauria verecunda*

Zone, now called *Tigillumia parallela* Zone in the Arthurton Group and in the South Curra Limestone at Gympie, southeast Queensland (Waterhouse & Balfe 2015), of Changhsingian (Late Permian) age.

The present species is moderately close in general appearance to genus *Etheriplica* Waterhouse, 2008a, type species *Etheripecten plicatus* Waterhouse in Waterhouse & Jell (1983, p. 248) from the Moonlight Sandstone Member, north Bowen Basin, Queensland, of Middle Permian age. These are large shells in which the left valve is convex with costae in several orders, increasing by intercalation, and plicae develop in the interspaces between primary costae over the lower half to two thirds of the left valve. The right valve is almost flat, covered by close-set branching costae, without plicae, and two or three pits lie between dorsal ends of pallial line, as in the present form.

Genus **Primaspina** Waterhouse, 2008a

Type species: *Aviculopecten dawsonensis* Runnegar & Ferguson, 1969, p. 262 from Flat Top Formation (Wordian), southeast Bowen Basin, Queensland, OD.

Diagnosis: Primary ribs of left valve high, secondary ribs also prominent, crests elevated at regular commarginal intervals into c-shaped lamellar spines that arch towards the hinge, additional fine ribs. Right valve nearly flat with intercalated costae, no right valve spines.

Discussion: The development of left valve spines is somewhat reminiscent of *Neptunella* Astafieva, 1997 not Gray, 1854 (the latter a synonym of *Cabestana* Röding, 1798) from Upper Carboniferous and Permian faunas, but the right valve of this genus is more inflated, and bears more complex ornament of ribs in bundles.

Primaspina banksi n. sp.

Fig. 228 - 231

Derivation: Named for Rodney Banks.

Holotype: UQF 81531 from UQL 2622, Tiverton Formation, figured herein as Fig. 230, here designated.

Diagnosis: Large for genus, with ribbed primaries and numerous fine ribs over interspaces, spines subdued.

Material: Specimens as left valves from UQL 1626, 1630, 2622, 2623, 2625, 2631?, 3127, 3129, 4514, 4518, LT3 and T3. *Taeniothaerus subquadratus* Zone.

Dimensions in mm: left valves

UQF	UQL	Length	Height	Width	
81531	2622	30.5	26.5	5.5	holotype
81521	3127	67	54	11.5	
81533	4514	50	39+	8	

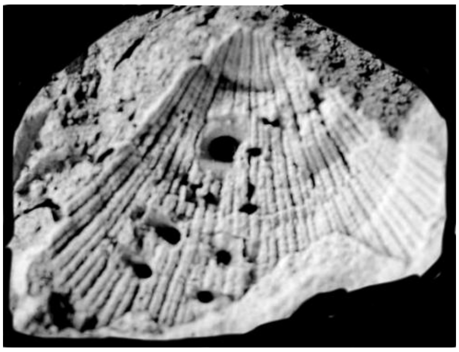


Fig. 228. *Primaspina banski* n. sp., external mould of right valve UQF 81834 from LT3, x1.5.

Description: Left valve gently inflated, up to 70mm long, anterior wing with obtuse cardinal extremity gently concavo-convex in outline, anterior wall steep, posterior wing long and high, gently concave with acute cardinal extremity and concave posterior margin, separated from body of shell by low but sharply defined umbonal slope. Some six primary ribs high with broad crests and steep flanks, secondary ribs remain differentiated for 30-40mm before becoming as strong as the primaries, tertiaries fine. Interspaces traversed by fine ribs, five or six at some 25mm from beak and up to 12 at anterior margin of largest specimens, often with median rib more prominent. The primary and secondary ribs carry spines formed by elevated growth lines arching dorsally towards the hinge. Ventrally the primary ribs swell and carry fine ribs for intervals. Interspaces crossed by close-set growth increments and growth lamellae that arch dorsally. Both wings marked by close-set growth lines and four or five sharply defined slightly differentiated ribs. Right valves few and rather like those of *playfordi*, apart from smaller size, with close-set ribs that increase by intercalation. Ligament alivincular, resilifer shallow, moderately large, extended posteriorly. Small pedal scars lie over the umbo, and part of a large adductor complex lies near the ventral margin.

Resemblances: Compared with *Etheripecten playfordi* n. sp. from the same beds, this species is smaller, with stronger and spinose primary and secondary ribs, relatively smaller posterior wings and lower inflation.

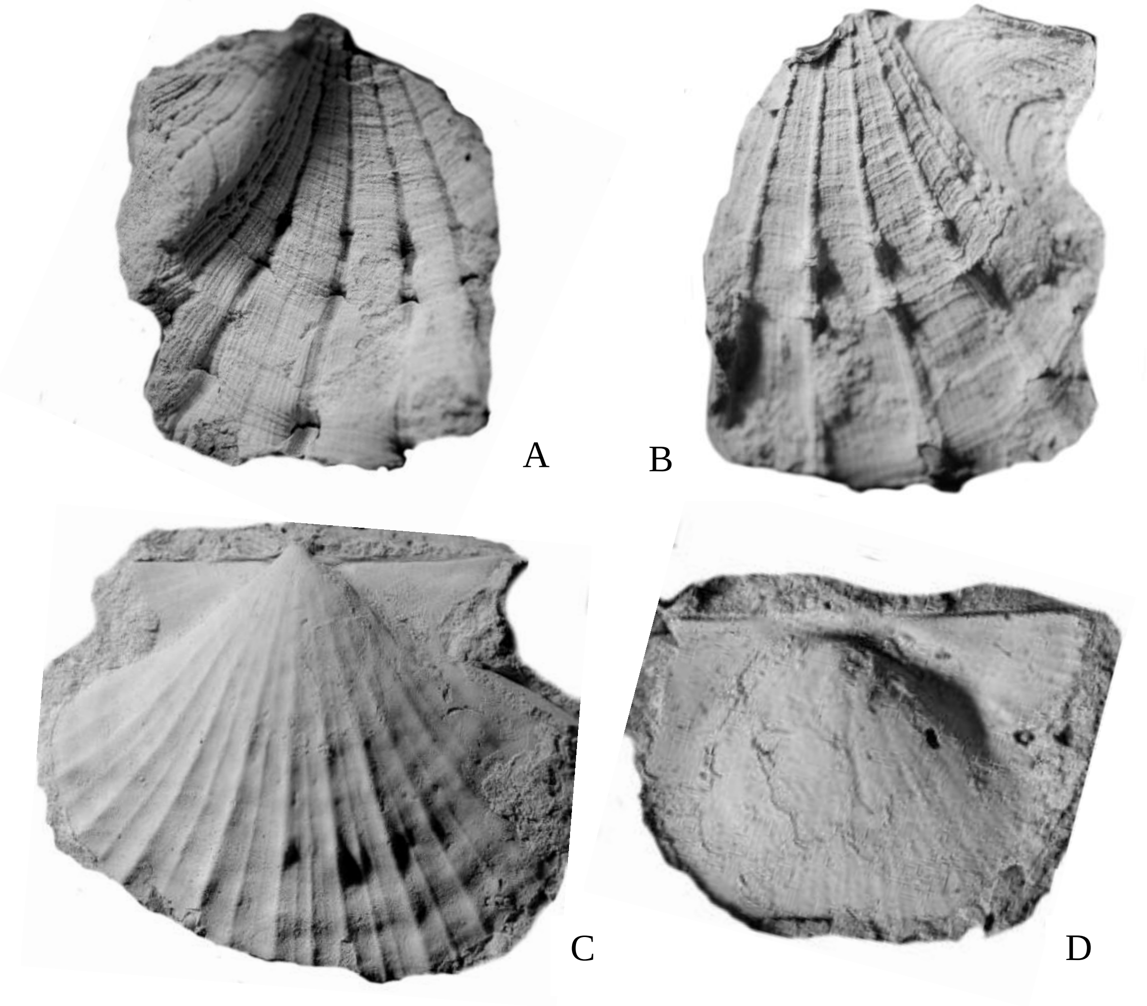


Fig. 229. *Primaspina banksi* n. sp. A, B, external mould and latex cast of left valve UQF 81519 from UQL 2625, x2. C, left valve internal mould UQF 81521 from UQL 3127, x1. D, right valve internal mould UQF 81542 from LT3, x2.

Primaspina dawsonensis (Runnegar & Ferguson, 1969, pl. 5, fig. 14-15, 17-19, not 16) from the Flat Top Formation of southeast Bowen Basin, also figured by Waterhouse (1987b, pl. 5, fig. 4, 5, 7-10, 13; 2008a, text-fig. 83), has slightly lower primary ribs and smaller spines, and is larger in size. The specimen from the *Ingelarella plica* Zone in the upper Tiverton Formation figured as *Etheripecten* sp. by Waterhouse (1983d, pl. 4, fig. 8) might belong to the genus, as it has strong primary ribs, but no lamellar spines are preserved. *Etheripecten tenuicollis* (Dana) is definitely present in this collection.

This species is distinguished from *Vanvleetia vanvleeti* (Beede, 1903; Newell & Boyd, 1995) by its larger size and slightly lower spines on the left valve. Right valve ribs of *Vanvleetia* split in two and are associated in bundles of up to eight ribs. The type species comes from “Leonardian” and lower Guadalupian faunas of Texas, and is reported without full documentation from the Late Permian Whitehorse Sandstone and Dozier Dolomite of Oklahoma. “*Aviculopecten*” *girtyi* Newell from Utah shows right valve costae splitting in pairs and associated in bundles. *Vorkutopecten* Guskov in Muromseva (1984) and *Neptunella* Astafieva, 1997 not Gray are also close as discussed in Waterhouse (2008a, p. 148, 149). In view of the nature of the right valve ornament with its split and bundled ribs, *Vanvleetia* and *Vorkutopecten* are classed in Heteropectininae Beurlen, 1954 rather than Etheripectininae, which has intercalated right valve ribbing.

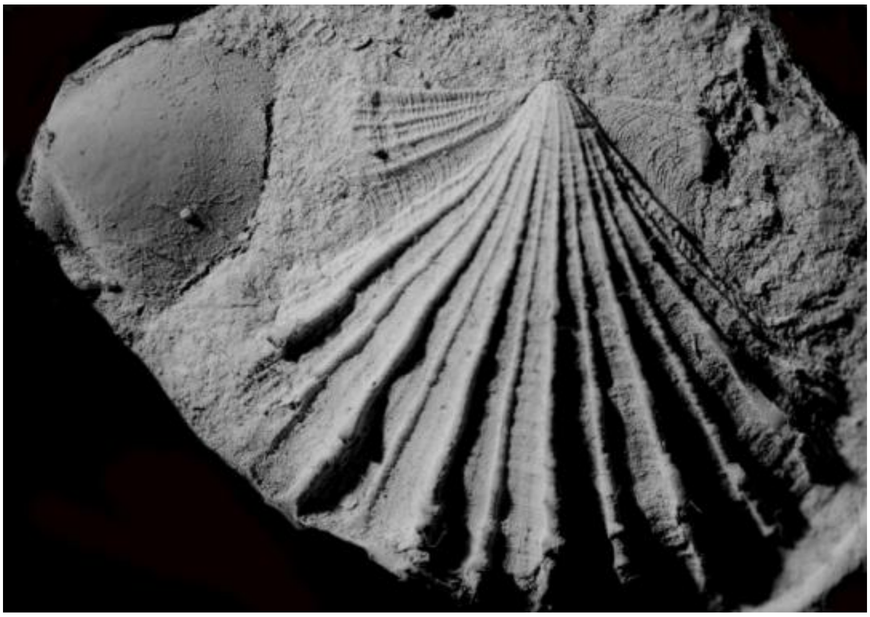


Fig. 230. *Primaspina banksi* n. sp. Latex cast of left valve holotype UQF 81531 with *Concentiolineatus homevalensis* (Waterhouse) left valve UQF 81530 to left. From UQL 2622, x2.

Fig. 231. *Primaspina banksi* n. sp. external mould of left valve UQF 81533 from UQL 4514, x2.

Aviculopecten mutabilis Licharew of Astafieva-Urbaitis & Ramovs (1978, pl. 1, fig. 7-9) of Gzhelian age in Slovenia has broad primary ribs on the left valve, with spines at intervals. *A. hatai* Murata (1964, pl. 34, fig. 10a-d) from the Kanokura Formation of Japan has more prosocline and elongate shell. But given the absence of the right valve, the species could be either etheripectinin (*Primaspina*) or heteropectinin (*Vorkutopecten, Vanvleetia*).

Family **HUNANOPECTINIDAE** Yin, 1985

Subfamily **FURCATIINAE** Waterhouse, 2001

[Nom. transl. hic ex Furcatiini Waterhouse 2001, p. 133].

Diagnosis: Distinguished from Hunanopectininae by its costate right valve and lack of teeth from the hinge.

Genus ***Furcatia*** Waterhouse, 2001

Type species: *Etheripecten petulantis* Waterhouse, 1987b, p. 146 from Elvinia Formation (Sakmarian) of southeast Bowen Basin, Queensland, OD.

Diagnosis: Inequivalve, both valves ornamented by strong costae which increase by branching as a rule in both valves, although some arise by intercalation, crossed by weaker but regularly spaced commarginal ribs. Anterior right auricle and left valve wing costate, deep byssal notch and deep anterior left valve sinus. Hinge with resilifer, no teeth.

Discussion: This genus was assigned to Hunanopectininae Yin, 1985 of Family Pseudomonotidae on the basis of its inequivalve character, large anterior left valve wing and right anterior auricle by Waterhouse (2001, p. 133), and although Waterhouse (2008a, p. 181) reassessed the position as more likely to be streblochondroid, the overall shape is not typically streblochondroid, especially in the symmetry of the left valve and its large anterior wing, though the position is not completely secure.

Furcatia petulantis (Waterhouse, 1987b)?

Fig. 232

1987b *Etheripecten petulantis* Waterhouse, p. 146, pl. 4, fig. 5, 8-12.

2001 *Furcatia petulantis* – Waterhouse, p. 133.

2008a *F. petulantis* – Waterhouse, p. 181.

Holotype: UQF 74336 figured by Waterhouse (1987, pl. 4, fig. 9, 11) from basal Elvinia Formation, Queensland, OD.

Diagnosis: Small subequivalve with long right anterior auricle and large extended right posterior wing. Ornament on both valves of firm ribs increasing mostly by branching, some by intercalation, crossed by finer commarginal ribs.

Material: A fragment from Tiverton Formation at UQL 4514. *Svalbardia armstrongi* Subzone.

Description: The fragment shows strong radial ribs crossed by evenly spaced slightly ragged commarginal ribs slightly less robust than the costae. The fragment includes part of a large left valve posterior wing.

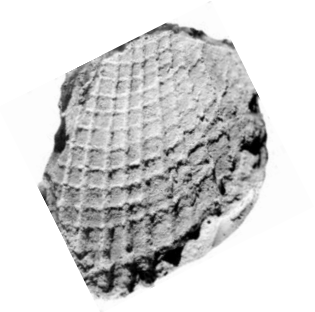


Fig. 232. *Furcatia petulantis* (Waterhouse)?, latex cast of left valve external fragment UQF 81508 from UQL 4514, x1.5.

Resemblances: The identification of this fragment is far from secure. It is based on a degree of similarity in ornament to that observed on parts of *Furcatia petulantis* from the Elvinia Formation of the southeast Bowen Basin, although it may be noted that the commarginals in the Elvinia material tend to arch hingewards in interspaces, whereas growth laminae form only slight deflections in the present fragment, and the ribs are coarser and spaced a little further apart. There is no confirmation of the similarity from branched ribs, or detail of hinge and anterior shell etc. The one redeeming facet apart from a similarity in ornament is that the age would be overall much the same.

There is another Permian genus with similar ornament over the entire shell, and without branching or intercalate ribs, and that is the genus *Tesseratia* Waterhouse, 2008a, p. 49, based on *Pterinopecten serbodowae* Fredericks, 1915 from Early Permian of Urals and Timan. This form displays strong radial costae crossed by well spaced growth laminae on both valves, and its hinge is pterinopectiniform. Several species are represented in the Early Carboniferous of Europe. The tesselate ornament also approaches that of the streblochondriid genus *Tesselarulina* Waterhouse, 2008a, p. 106, a genus apparently restricted to the Carboniferous. Tesselate ornament is also displayed by meagre Lower Carboniferous material described by de Koninck (1877, p. 160, pl. 22, fig. 11) and Etheridge & Dun (1906, p. 21, pl. 15, fig. 8, 9) from northern New South Wales as *Aviculopecten tesselatus*. Originally described as *Avicula tessellata* Phillips, 1836, pl. 6, fig. 6 from the Lower Carboniferous near Cork, Ireland, this species is now referred to *Tesseratia* Waterhouse (2008a, p. 49, text-fig. 24). Whether the New South Wales specimens are pterinopectiniform or not is unknown.

Hyporder MONOTOIDEI Waterhouse, 2001

Diagnosis: Pectinidan shells with opisthodetic ligament, anteriorly placed umbones and procrescent symmetry. Valves often inequivalved, may have little or no radial ornament, monomyarian. Right anterior ear with no internal ligament, poorly to generally well developed.

Discussion: The opisthodetic as opposed to amphidetic nature of the ligament for Monotidei is not in complete harmony with other characteristics of gross morphology that help distinguish the hyporder, and there is considerable difference between eurydesmoid shells in which the ligament traverses the inner side of short if any anterior projection and shells in which the anterior wing or ear lies in front of the ligament as in Monotoidea. There are essentially two arrangements between the anterior ear and anterior ligament. In *Eurydesma, Glendella, Krumbeckiella*, *Frigidusia*, and probably *Mysidiella*, which are classed as Eurydesmidae, the ligament stops virtually under the umbo, and lies in turn above a small to large internal shelf, sited below the commissure and below the ligament. There is little in the way of auricular development in any of these genera, but there may be a small anterior projection bordered by an ear ledge beyond the byssal channel, and this projection contains the internal shelf, and it may contain the short anterior end of the ligament. Such is best displayed in the late Triassic genus *Krumbeckiella* (see Waterhouse 2008a, text-fig. 64), whereas in the other genera the ligament commences under the umbo, where it is compressed. In Late Triassic *Monotis* (Monotidae) and in Late Mesozoic *Buchia* (Buchiidae), the anterior right ear is more distinctive, and it lies entirely in front of the ligament and involves the equivalent of the internal shelf. This is especially well displayed in the Triassic genus *Hokonuia* Trechmann, in which the large right anterior ear projects in front of the body cavity and below the anterior end of the ligament, as figured by Waterhouse (1960, Fig. 25, text-fig. 2; repeated by Cox 1969, Fig. C96. 4c,d and Waterhouse 2008a, text-fig. 67).

The muscle scars are not entirely like those of Aviculopectinoidei, and in Monotidae form a small postero-ventrally placed subrounded scar (Grant-Mackie 1978a, b, Waterhouse 2008a, text-fig. 58). But in *Eurydesma*, the adductor complex is large and subcentral, close to that of Aviculopectinoidea and Heteropectinoidea. These differences give me some misgivings about their being associated, but habitats were very different. Eurydesmidae arose, it is believed, from Chaneocardiidae (see p. 283), whereas the source for Monotoidea requires further analysis, possibly from Streblochondriidae (Waterhouse 2008, Text-fig. 109, p. 188).

Superfamily **EURYDESMOIDEA** Reed, 1932

[Nom. transl. Waterhouse (2008a, p. 114 ex Eurydesmidae Reed, 1932, p. 50].

Diagnosis: Inequivalve to equivalve, inequilateral, ligament opisthodetic, external, canalivincular or with resilifer, right anterior ear if present small or modified in a partly articulatory structure as an ear-ledge, independent of ligament, hinge may have simple large teeth and broad sockets, ornament reduced, generally no posterior wing.

Discussion: Members of this superfamily are readily distinguished from Superfamily Monotoidea Fischer, 1887, which are subequivalved shells with well developed right anterior ear, ornament of close-set radials in two or three orders in many shells, and external canalivincular ligament without resilifer.

Family **EURYDESMIDAE** Reed, 1932

[Nom. just. et defendo Waterhouse 2008a, p. 114 ex heading Eurydesmidae Reed, 1932, p. 50].

Diagnosis: Often large inequilateral, usually subequivalve shells with extremely reduced and modified anterior projection, byssal channel in each valve, ligament external, opisthodetic or largely opisthodetic, may be truncavincular, heavily thickened hinge with one or two large dental bosses and shallow sockets, smooth exterior.

Discussion: The morphology and variation together with a brief summary of various suggestions on family alliances are discussed in Waterhouse (2008a), in which it was shown that the most likely ancestral stock lies close to *Chaenocardia* Miller, 1877, with shortened anterior and asymmetric ligament, a suggestion anticipated by Newell & Boyd (1995). *Chaenocardia* is mostly of Pennsylvanian age. The oldest *Eurydesma* are regarded as being of Early Permian age, unknown below the *Strophalosiaria concentric*a Zone in east Australia (Clarke & Farmer 1976).

Eurydesma shell has a calcitic lamellar outer shell layer, a thick inner endostracum layer, believed to be calcitic, and middle "hypostracum" (Dickins 1957). The muscle impressions in *Eurydesma* have been analyzed by Runnegar (1970, pp. 90, 91) and Waterhouse (2008a, p. 120, text-fig. 61) and compared and contrasted to those of Aviculopectinidae, and the unusual hinge approaches that displayed by the Cretaceous oxytomoid bivalve *Maccoyella* Etheridge. Some writers would prefer an alliance with Ambonychiidae, as strongly suggested by shape and aspects of hinge and shell structure, but the nature of the pallial impressions, adductor muscle field and similarity of the hinge to that of *Maccoyella* strongly suggest pectiniform affinities (Waterhouse 2008a).

Taxonomy: Reed (1932) proposed the family name as a heading, without any diagnosis or discussion. The diagnosis was first provided by Waterhouse (2008a) and credited to Reed (1932).

Nomenclature: Reed (1932) preferred the ending Eurydesmidae.

Genus ***Eurydesma*** Morris, 1845

Type species: *Eurydesma cordatum* Morris, 1845, p. 276 from Allandale Formation (Asselian), north Sydney Basin, New South Wales (Dickins 1961b, p. 143), OD.

Diagnosis: Large equivalve or subequivalve shells with anteriorly placed umbones, byssal notch below small right anterior ear-ledge, right anterior ear-ledge may jut into left valve hinge, left valve anterior ear-ledge may lie parallel to hinge or jut across commissure, ligament opisthodetic, hinge somewhat variable, right valve may have broad shallow socket, or one or two low dental bosses, left valve may have one large or less commonly two dental bosses and may have intervening socket, posterior adductor muscle scar large, faintly impressed, subcentrally placed, pallial line continuous ventrally, pitted dorsally, possibly closed beneath umbo.

Discussion: Species were named for *Eurydesma* by Dana (1849), followed by Johnston (1887, 1888) and de Koninck (1877), that encompass most of the major forms of *Eurydesma* in east Australia. They belong to three associations if based on shape, one centred on *Eurydesma cordatum* and also including *E. konincki, E. burnettensis, E. sacculum* and *E. glaebula*, another based on *E. ovale* with *E. hobartensis* and subspecies, and a third involving *E. protrudus* and *E. alisulcatum.* These will be treated mostly as full species. Although it seems likely that some should be downscaled to subspecies, aspects for especially the hinge and dentition need to be determined for several of these taxa before it will be possible to refine the interrelationships. Re-examination of the collections studied by Etheridge & Dun (1910) and kept at the Australian Museum, Sydney, suggests that understanding of species limits may be expanded from Etheridge & Dun (1910) and Runnegar (1970), and parameters of shape, involving shell inflation, shell outline, position of the umbones, outline of the anterior dorsal margin and development or absence of wing-like posterior, are much more constant with regard to stratigraphic and geographic position than asserted by Runnegar (1970). These aspects are outlined in the discussion of the new species from the Tiverton Formation.

Many species were named for *Eurydesma* from the Salt Range, Pakistan, by Reed (1936). Fossa Mancini (1944, p. 91) and Harrington (1955, p. 122) deprecated the validity of these fourteen forms, and suggested they were individual variations of a polymorphous species. Their attitude reflected the then-current understanding that far too many species had been named in the past, and the number would have to be reduced, just as Professor Ernst Mayr had drastically reduced the number of "valid" names for living bird species. It was further understood in those days that it was exceptional for two species to co-exist, given what were understood to be genetic controls. This in turn helped to justify what now seems to be very low estimates of species numbers. Taking a similar approach, Boss (1971) estimated there were about only 6000 living species for Bivalvia, and Raup (1976, p. 289) reported only about 190,000 named fossil invertebrate species, with, of course, due reservations. Several following articles were based on the estimates, making major conclusions. Such counts in my opinion hugely understate the number of living and fossil species, and the conclusions therefore are far from substantiated. For example, Raup (1976, p. 284) reported

893 species of Brachiopoda for the Permian Period. Cooper & Grant in their series published during the 1970's on Permian brachiopods from west Texas, United States, described about 1000 species, most of them new. In New Zealand alone, which is no more than a tiny fragment of the earth's crust and surrounding ocean, a single worker P. Maxwell found some 3000 species (microforms) yet to be described amongst Tertiary fossils (Beu et al. 2008). Bouchet et al. (2002) stated that "earlier studies in the tropical Indo-Pacific have grossly underestimated the richness of macro-faunal species". In New Caledonia, a small team recorded 278 marine molluscan species in a mere 400 "man-days" , far greater than recorded in the literature from any comparable area elsewhere. DNA studies on birds have proved that early workers were often correct, and that Mayr, for all the forceful influence exerted on taxonomy and understanding of species, was not infallible and was partly wrong. A degree of consolidation for the Salt Range *Eurydesma* taxa has been suggested on the basis of shape by Waterhouse & Gupta (1982) and Waterhouse & Ranga Rao (1989, p. 35), but their comments on relations to east Australian *Eurydesma* in those studies were compromised by accepting proposals from Runnegar (1970, 1979), that now require a degree of reassessment. The Salt Range forms should be re-assessed first hand, to compensate for the limited information conveyed by text and figures. Some additional species were named for specimens from the eastern Himalaya by Sahni & Srivastava (1956), poorly figured, and in need of assessment. Clarke (1992a, p. 38) claimed that dozens of species [of *Eurydesma*] had been named, but this appears to be an exaggeration – there may have been some 25 taxa, and the lack of attention to internal morphology and variation in hinge detail should require a degree of caution before lumping various proposed species. Clarke (1992a) did not provide any analysis of the various named taxa, and accepted Runnegar's merging of *ovale* Etheridge & Dun with *konincki*, and did not notice the outstanding characteristics of either *alisulcatum* or new species *glaebula*.

Taxonomy: *Leiomyalina* Frech, 1891 is a synonym of *Eurydesma*, being based on *L. antarctica* Frech, which is here shown to be a close ally of *Eurydesma hobartensis* Johnston and especially *E. cordatum ovale* Etheridge & Dun.

Eurydesma glaebula n. sp.

Fig. 233 - 236, 237 part, 238A

1924 *Eurydesma cordatum* [not Morris] – Richards & Bryan, pl. 19, fig. 7.
1928 *E. cordatum* – Whitehouse, p. 282.
1970 *E. hobartense konincki* [not Johnston] – Runnegar, pl. 13, fig. 11.
1987b *Eurydesma* sp. Waterhouse, p. 140, pl. 3, fig. 4.
2008a *Eurydesma* n. sp. Waterhouse, text-fig. 61B.

Derivation: glaebula – a piece of earth, Lat.

Holotype: Specimen UQF 81512 from UQL 4508, Tiverton Formation, Fig. 234A, B, C, here designated.

Diagnosis: Shells close to *Eurydesma* de Koninck in prominence of umbones, close to *cordatum* in position of umbones and concave anterior margin, moderately to very well inflated, generally no posterior sulcus, and more elongate or subequidimensional than high.

Material: Specimens from UQL 1619, 1622, 2584, 2622, 3127, 4505-4509, 4514 and TK. Mostly *Bookeria pollex* Zone, rare in *Svalbardia armstrongi* Subzone.

Dimensions in mm:

UQF	UQL	Length	Height	Width	Valve
81511	2622	67	76	48	both, external
81509	1619	80	85	52	both, largely internal mould

Description: Shells large and well inflated, and equivalve or almost equivalve, a specimen with valves splayed from UQL 4509 having left valve more inflated than right valve. Umbones sited well back from anterior margin, anterior dorsal margin concave, ventral anterior, ventral and posterior margins well rounded, not slender posteriorly. Valves globose without sulcus, surface with low growth increments and wrinkles. Hinge of moderate length, opisthodetic, ligament area large and concave, with longitudinal ridges and grooves, no sign of resilifer in either valve. Shell thickened into a shelf below and in front of the ligament. Anterior commissure slightly sinuous, with slender anterior gape, no projecting ear, but left valve may exhibit slender bulge. The right valve has a very low ear ledge with strong growth laminae externally, above a short V-shaped byssal notch, marked by strong growth steps; the ledge may project forwards or across the left valve commissure into the interior of the left valve, as in specimens from UQL 1619 and 4514. A tiny right valve 6mm long has small thin anterior ear ledge projecting in front of the umbo, and a small swollen posterior bulge. In the left valve, a short ledge of varying length and bearing growth laminae may project forwards parallel to the commissure, or rarely into the right valve, and is usually smaller than the right anterior ear ledge, next to byssal channel. As a rule, the left valve has a prominent linear dental boss, fitting into right valve socket, without a left valve socket. Adductor scar very large and faintly impressed, posteriorly placed behind a faint and shallow internal sulcus; small deep pits lie under the umbo, the pattern varying in each specimen. These might represent the dorsal end of the pallial line, but were called retractor pits by Reed (1932, p. 52) and Sahni & Svristava (1956). A byssal scar and possible gill suspensory retractor scar are present above the adductor complex. The shell is as thick as 14mm posteriorly, and only 1mm thick ventrally, and right valve UQF 43449 has shell 21mm thick posteriorly.

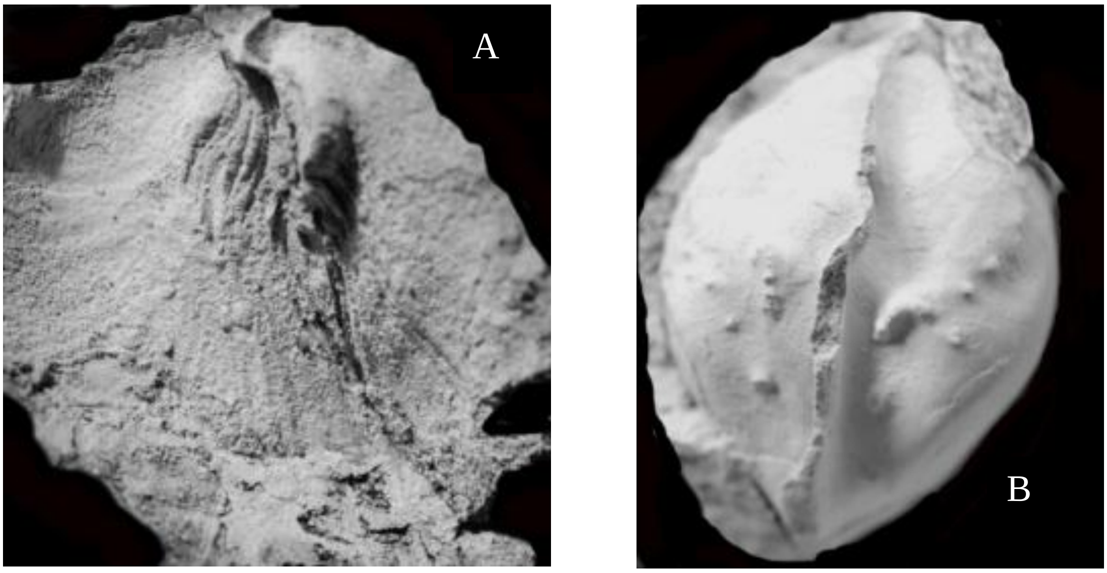


Fig. 233. *Eurydesma glaebula* n. sp. A, external mould of specimen with valves conjoined, anterior view, UQF 81511 from UQL 2622, x2. B, dorsal view of internal mould of specimen with valves conjoined UQF 81510 from UQL 4508, x1.

Resemblances: These specimens come from the Tiverton Formation, and are also represented in the *Eurydesma* beds (lower Wallaby beds) near Warwick (Richards & Bryan 1924), and basal Elvinia Formation of Cracow (Waterhouse 1987b). They are characterized by their large size, relatively posterior position for the umbones, concave anterior dorsal margin, and usual lack of both lateral sulcus and slender posterior portion. In some of these attributes, the specimens are close to *Eurydesma cordatum* Morris (see Fig. 237, p. 291). The lectotype for this species, as designated by Etheridge & Dun (1910, p. 72) and reaffirmed by Dickins (1961b, p. 143), came from Harper's Hill, Allandale Formation, north Sydney Basin, to judge from the matrix, and specimens that were initially described as *E. globosum* Dana, and *E. ellipticum* Dana, as figured by Dana (1849) and refigured by Waterhouse (1988), came from the same rocks. The second specimen figured by Morris (1845) has a matrix of black limestone, suggestive of the limestones on Maria Island, Tasmania, and has been identified as *konincki* by Runnegar (1970, p. 97), and as *E. protrudus* Waterhouse (2008a, p. 121). A particularly large suite of *cordatum* was figured from the Allandale Formation by Etheridge & Dun (1910), and is kept at the Australian Museum, Sydney, and similar specimens from the same locality have been figured by Runnegar (1970, pl. 13, fig. 2-7, 9, pl. 14, fig. 3-6, pl. 16, fig. 4?, 8). They are well inflated as a rule, and have a hinge that is generally of moderate length, but the hinge is short in specimens figured by Etheridge & Dun (1910, pl. 17, fig. 1, 2, pl. 18, fig. 1) and registered as AMF 6837 and 7247 respectively. Both these specimens were inadvertently cited as holotype by of *E. cordatum inflatum* Waterhouse (1987b), and the matter is here clarified with the selection of holotype AMF 7247. Distinctions from typical *cordatum* are minor, and may constitute a subspecific difference, but more likely are infra-subspecific, because many specimens, including the holotype and AMF 10129 (Etheridge & Dun 1910, pl. 21, fig. 1) have a short hinge. A few specimens are little inflated, such as AMF 26592 (Runnegar 1970, pl. 16, fig. 8). The Allandale specimen figured by Runnegar (1970, pl. 13, fig. 7) is shown as having a very anteriorly placed umbo (UQF 36624), but possibly the figure has been tilted. Most Allandale specimens have a posterior lateral sulcus, as suggested in the lectotype, and the sulcus is shallow in a few specimens such as AMF 35423 (Etheridge & Dun 1910, pl. 23, fig. 1). This is cited as coming from Maria Island, Tasmania, but has matrix apparently like that of the Allandale Formation, and its umbones are like those of *konincki*.

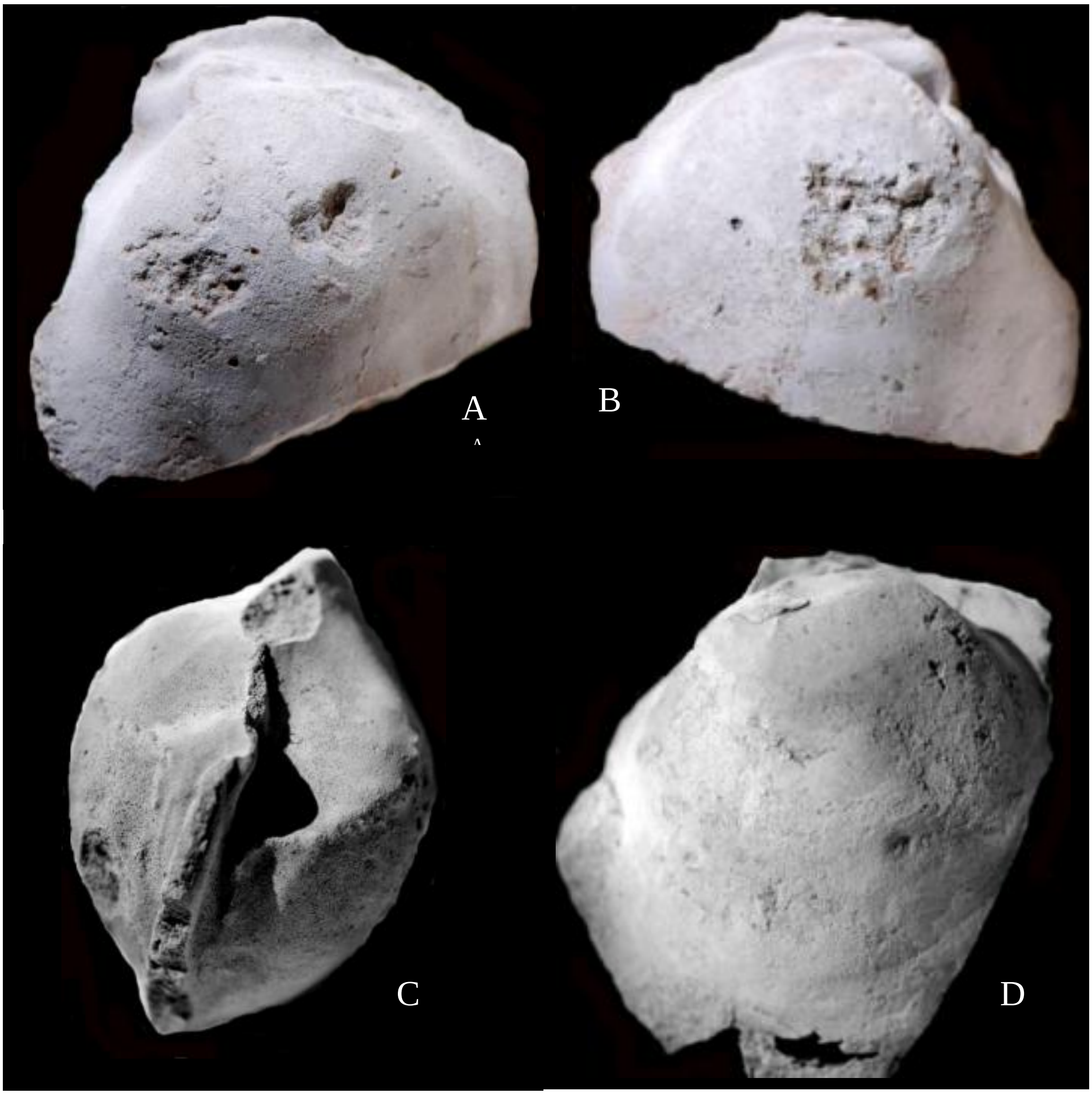


Fig. 234. *Eurydesma glaebula* n. sp. A, B, C, holotype, left, right and dorsal views of internal mould UQF 81512 from UQL 4508, x1. D, left valve UQF 81513 from UQL 1619, x1.

There is virtually no sulcus in the specimen figured as *cordatum* by Dana (1849, pl. 8, fig. 1, 1a), but it is unusual in that regard. *E. cordatum sacculum* not M'Coy of Etheridge & Dun (1910, pl. 20, fig. 1 - AMF 7242) is exceptionally large, and proportionately much higher than smaller specimens. Growth-lines show that the shell at earlier growth-stages was like that of typical *cordatum*. It has a short hinge and well formed posterior-lateral sulcus. Other specimens treated as *sacculum* by Etheridge & Dun (1910, pl. 19, fig. 1, 2 – AMF 6877, and pl. 24, fig. 1, 2 – AMF 7249) are like mature *cordatum*. The Tiverton specimens are similar to Allandale specimens of *E*. *cordatum* in size, inflation and position of umbones and concave anterior-dorsal margin, and dissimilar in being smaller and slightly more elongate and in having lower umbones and usually lacking a lateral sulcus. *E. cordatum* has been described principally from faunas equivalent to the *Crassispinosella subcircularis* Zone, significantly older than the *Bookeria pollex* Zone with *E. glaebula*. From Tasmania, Clarke (1992a, p. 38) considered that *cordatum* was restricted to rocks of middle Tamarian age.

Fig. 235. *Eurydesma glaebula* n. sp., dorsal view of internal mould of specimen with valves conjoined, UQF 81599 from UQL 1619, x1. Anterior to top of figure.

A somewhat similar species from the Burnett Formation, Yarrol Basin, Queensland, has been identified as *Eurydesma burnettensis* Waterhouse, 1987b and figured by Maxwell (1964, pl. 11, fig. 8-14), Runnegar (1970, pl. 14, fig. 7-15) and Webb (1977, pl. 2, fig. 1-3). Compared with *cordatum* and *glaebula*, this species (see Fig. 237, p. 291), also has subcentral to more anteriorly placed umbones, slightly to usually moderately longer hinge, and as a rule concave and moderately steeply inclined anterior dorsal margin, and no posterior-lateral sulcus. In shape the specimens approach the lectotype of *E. elliptica* Dana, from the Allandale Formation. This also lacks a sulcus and has more centrally placed umbo and shorter different hinge, and appears to be an immature specimen of *cordatum.* Dentition in *burnettensis* is somewhat unusual, especially in small specimens, with large right valve tooth-like projection formed by and below the “ear-ledge” in front of a very small depression equivalent to the large socket of other species, and the left valve has a very small tooth and large socket in front to receive the right valve tooth. There is a left valve socket rather than large dental boss below the anterior ligament, the reverse or at least substantial modification of the dentition in *cordatum*, *glaebula* and *konincki* (Waterhouse 2008a). The specimens are close to *E. konincki* (Johnston) in lacking a sulcus, and are similarly inflated with umbones more anteriorly placed.

Briggs (1998) compared Tasmanian specimens figured by Runnegar (1970, pl. 15, fig. 4) and Clarke (1992a, fig. 20G) from the *Strophalosiaria concentrica* and *Crassispinosella subcircularis* Zones to *burnettensis*, but they are probably immature specimens of *konincki*. Specimens figured by Runnegar (1970, pl. 17, fig. 1-4) as cf. *cordatum* from the Gosforth Shales of Hunter Valley (equivalent to Lochinvar Formation), New South Wales, come close to *burnettensis*, given the anteriorly placed umbones and steep anterior margin. In addition, specimens figured from the Wasp Head Formation by Runnegar (1969, pl. 19, fig. 5-7; 1970, pl. 14, fig. 2, pl. 16, fig. 7) as *E. cordatum* are somewhat similar to *burnettensis*, apart from being slightly larger, and more inflated, especially anteriorly, with slightly better defined sulcus. They have anteriorly placed umbones and steeper longer anterior margin. They thus differ to some degree from typical *burnettensis*, but are closer to this species than to *cordatum.* However it is not yet established that their dentition is like that of *burnettensis*. The zonation is not certain: the Wasp Head specimens likely came from the younger beds above *Strophalosiaria concentrica*. Briggs (1998, pp. 23-26) considered that the species *burnettensis* characterized an Early Permian zone above the *Auriculispina levis* Zone, and that it was correlative with what is now called *Strophalosiaria concentrica* Zone. The New South Wales material may be provisionally identified as *burnettensis*, subject to the nature of the hinge in small specimens. Runnegar (1970) had assigned the type Burnett specimens to *Eurydesma playfordi* Dickins (1957) described from the upper Lyons Group of the Callytharra Basin, Western Australia. The Western Australian shells differ from *burnettensis* in being slender small shells with anterior umbones, high straight or only gently concave anterior dorsal margin, and somewhat similar hinge with large right valve tooth formed by the anterior margin of the ear ledge in front of a shallow socket: this projects into the left valve cavity below the ligament (Dickins 1957, p. 33). There is said to be no socket in the left valve, but according to Dickins " a smaller dental process" fits over the sinus of the right valve.

Fig. 236. *Eurydesma glaebula* n. sp., latex cast of right valve hinge, UQF 81532 from UQL 1622, x5. The right valve "tooth" shown as "t" , and ear flange to the left is not as large as that of *burnettensis*.

In size, shape and lack of lateral sulcus, *burnettensis* is close to specimens from the Speckled Sandstone form called *E. hobartense bigener* Reed (1936, p. 19, pl. 1, fig. 1-3), though it is difficult to fully compare internal moulds with external shell. Notably the pitted pallial line or row of retractor pits is linear in *bigener*, not recurved as in east Australian forms. *E. hobartense rotundata* Reed (1936, p. 20, pl. 1, fig. 4-7b, pl. 2, fig. 5, 5a) from the same beds is close, and also like *burnettensis*, but with less anteriorly placed umbones. Singh (1978d) assigned specimens from the Bomte Shale in the Garu Formation of the eastern Himalaya to *Eurydesma cordatum* [not Morris] and they like the present material lack a lateral sulcus, but the umbones are twisted forward.

The species *Eurydesma cordatum* was an approximate contemporary of *E. konincki* Johnston (1887, 1888, pl. 18, fig. 2, 3) found in the Darlington Limestone of Maria Island, Tasmania. The lectotype for this species was cited by Runnegar (1970, p. 97) as the specimen figured by Johnston (1888, pl. 18, fig. 2). This specimen is now lost. It was figured in side-view, and appears, perhaps deceptively, to have been slender, with moderately extended anterior and concave anterior dorsal margin, and slender posterior dorsal margin. The neotype cited as UQF 51940 by Runnegar (1970, pl. 16, fig. 2, 3) is a well inflated specimen, approaching mature *burnettensis* in inflation but with less anterior beaks, no posterior wing and different hinge. A strong tooth lies in the left valve below the anterior ligament and well behind the anterior ear-ledge. There may be some misgivings about the choice for neotype, but there is no certain evidence that the neotype belongs to a different taxon, especially given the fact that the lectotype was immature, and that the reader must rely on a drawing, and growth-lines on the neotype suggest an outline moderately close although not identical to that of the original figured specimen. The species as interpreted from the neotype comes from the Darlington Limestone of Maria Island, Tasmania, and was described by Clarke (1992a, p. 38) as being medium-sized to very large, strongly inflated shells with generally weak if any lateral sulcus and evenly rounded posterior margin and expanded anterior margin, imparting a well rounded shape. The umbones are less prominent than is usually the case for *cordatum,* but in most respects the species is close to *cordatum,* and arguably no more than a subspecies of that taxon. Specimens that belong to *E. konincki* include *E. cordatum* of Etheridge & Dun (1910, pl. 18, fig. 1, 2, pl. 23, fig. 1, 2) with anteriorly placed umbones, *E. hobartense konincki* of Clarke (1992a, Fig. 20C, 21B), and *E. hobartense konincki* of Runnegar (1970, pl. 16, fig. 2, 3). Shells identified as *cordatum* from Maria Island, Tasmania, by Runnegar (1970, pl. 13, fig. 1, 8, pl. 14, fig. 1) also belong to *konincki*, because they appear to have umbones less prominent than those typical of *cordatum*. Various other specimens were assigned to *konincki* by Runnegar, including fragments that convey insufficient data to allow identification. Others display an array of morphological features not consonant with the neotype or allied material found in the Darlington Limestone and allied horizons of Tasmania. Some are reassigned to *glaebula* n. sp. (Runnegar 1970, pl. 13, fig. 11, pl. 17, fig. 10, 11), others are identical with *E*. *ovale* Etheridge & Dun, 1910 (eg. Runnegar 1970, pl. 16, fig. 9) and aff. *ovale* or *antarctica* (Runnegar 1970, pl. 17, fig. 9, 13), and others belong to *sulcatum* Waterhouse (Runnegar 1970, pl. 15, fig. 5, pl. 17, fig. 7, 8). The specimen of Runnegar (1970, pl. 16, fig. 6) is now placed as *E. alisulcatum* Waterhouse. These reassignments, based on morphological analyses, result in a restricted time range for *konincki*, which evidently typified Early Permian, especially for Tasmania, and, counter to Runnegar (1970), did not range into the middle or late Early Permian of New South Wales. But relationships remain obscured by the lack of data on dentition.

There are a number of other species in the Australian Permian, distinguished by different position of the umbones, the presence of slender and extended posterior segment approaching a posterior wing, and development of a lateral sulcus. The youngest species is *Eurydesma alisulcatum* Waterhouse (1987b, pl. 1, fig. 27, pl. 3, fig. 8, pl. 4, fig. 1) from the Ulladulla Formation of the south Sydney Basin, of upper Kungurian age, and characterized by its long hinge, concave anterior dorsal margin, lateral sulcus, and slender shell posteriorly. It was figured as *E. hobartense konincki* by Runnegar (1970, pl. 16, fig. 6) but differs in shape, inflation, and sulcation from that species. Additional specimens were figured as *Eurydesma* sp. from the lower Snapper Point Formation, south Sydney Basin, by Shi & Weldon (2002, pl. 8, fig. 1, 3, 4).

Material described as Eurydesmidae gen. & sp. in the *Ingelarella plica* Zone of the Mantle Volcanic Formation in the Skippers Range, New Zealand, by Begg & Ballard (1991, Fig. 12, 13) displays a well developed posterior wing in each valve, and was stated to have an anterior right valve wing (or at least very slender anterior, judged from the illustration, assuming that the valve is a right valve). The material might represent a new species, with apparently well defined posterior wing and weak if any lateral sulcus, and unusual anterior. At present, the material has not yet been lodged in any accessible repository, nor available for inspection.

The species *Eurydesma hobartense* (Johnston, 1887, 1888, pl. 16, fig. 2) is based on a slender and probably immature specimen from Tasmania. The lectotype is left valve TMB 736, refigured by Runnegar (1970, pl. 15, fig. 3), SD Crespin (1964, p. 16). The species *hobartensis* has an almost circular outline, with anteriorly placed inconspicuous umbones, moderately long hinge, and gently concave steep anterior dorsal margin, and no lateral sulcus. A narrow ridge lies behind a large shallow socket. The lectotype comes from the Deep Bay Formation, and is apparently of late Early Permian or possibly very early Middle Permian age. No further topotype material has been figured, and clearly the age and the immaturity of the lectotype call for caution in assessing the characteristics of the species. Examples figured by Clarke (1992a, Fig. 20G, 21C) come from the much older Tasmanites Shale and from the Glencoe Formation, and come close to the lectotype in shape, although not age. Dun (1912, pl. 1) illustrated a large rounded specimen from the Tasmanites Shale beds of the Mersey River, Tasmania. Runnegar (1970, pl. 15, fig. 3, 4, 6, 7, 9) figured similar specimens from or below the Tasmanites Shale and Bundella Mudstone, and added possible Berriedale ("Berridale" in his terminology) Limestone specimens (Runnegar 1970, pl. 15, fig. 1, 2). A Berriedale specimen identified as *konincki* by Runnegar (1970, pl. 15, fig. 10, 11) is slender like *hobartense*, but also approaches *ovale* Etheridge & Dun. Thus the specific limits defining *hobartensis* call for further enquiry. According to Clarke (1992a), *hobartensis* has a lengthy time range, but this needs to be substantiated with the description of much more material. Attributes such as a somewhat rounded outline, moderately anterior umbones, no sulcus or posterior wing and low inflation may suffice to delimit the species, but possibly will incorporate only juvenile and immature specimens of various species. Restricted *hobartensis* may be descendent from *burnettensis*.

The Indian specimen from Manendragarh that was identified as *E. hobartense* by Sahni & Dutt (1959, p. 659, pl. 25, fig. 5, 6) is moderately close to *hobartense*, but seems more likely to be conspecific with shells identified by Sahni & Dutt (1959, pl. 26, fig. 2, 6, 6a) with *E. playfordi* Dickins, and probably the other specimens named as new species *manendragarhensis* (Sahni & Dutt, 1959, pl. 25, fig. 3, 3a) and *hesdoensis* (Sahni & Dutt, 1959, pl. 25, fig. 2, 2a). These in turn are close perhaps to *E. subobliquum* Reed and *rotundata* Reed from the Salt Range, Pakistan. The two named Manendragarh species are similar to each other in shape and have high attenuated umbones, not like Australian species in shape.

Eurydesma cordatum ovale Etheridge & Dun (1910, p. 94, pl. 21, fig. 45, pl. 25, fig. 1, 2) appears to be a full species, subject to its possible synonymy with *antarctica* Frech. It comes from the Ravensfield Sandstone at the base of the Farley Formation in the Sydney Basin, with AMF 35690 of Etheridge & Dun (1910, pl. 25, fig. 1) nominated as lectotype by Runnegar (1970, p. 98). It is a high subrectangular to subquadrate shell with anteriorly placed inconspicuous umbo, lateral sulcus, moderately long hinge and no posterior "wing". It is higher and more upright than *E. hobartense*, but close in being slender with low umbones. Reference to *hobartense konincki* as in Runnegar (1970, pl. 16, fig. 9) is rejected, because *konincki* is more inflated and tends to have more centrally placed and inconspicuous umbones and more concave anterior dorsal profile. Two further forms may be closely related, to judge from the subrectangular shape and anterior umbones. *E. cordatum truncatum* Waterhouse (1987b, pl. 2, fig. 1, 6, pl. 3, fig. 2, 3) is now regarded as a possible ally of *ovale*, and comes from the Fairyland and especially Dresden Formations of southeast Bowen Basin, with holotype UQF 43410 (Waterhouse 1987b, pl. 2, fig. 1, 6). Further material of this taxon has been figured as *E*. *hobartense* by Hill & Woods (1964b, pl. 11, fig. 1, 2) and Hill, Playford & Woods (1972, pl. 11, fig. 1, 2) from the same rocks, and as *konincki* by Runnegar (1970, pl. 15, fig. 5). The umbonal fragments figured by Hill & Woods (1964b) show a large buttress at the anterior end of the ligament, grading into growth-lined ear ledge and shallow byssal channel in the left valve, and a concave inner shelf to receive this boss, below the anterior ligament and growth-striated ear ledge of the right valve. Runnegar (1970, pl. 17, fig. 7, 8) figured as *konincki* a somewhat similar-looking but much smaller specimen UQF 51942 from the general "Buffel Formation", which encompasses a range of zones and rock units, so that the locality and stratigraphic control are unfortunately in need of more precision. The subspecies *truncatum* is very large, with very anteriorly placed umbones and very high steep anterior dorsal profile, higher than in *ovale* or *hobartense*, shallow posterior lateral sulcus and considerable inflation. A right valve ear-ledge passing ventrally into a tooth is present (Waterhouse 1987b, pl. 2, fig. 1, pl. 3, fig. 2), allied to that seen in *burnettensis* and *hobartensis*, but developed more below the commissure.

Eurydesma sulcatum Waterhouse (1987b, p. 141, pl. 2, fig. 7, 9, pl. 3, fig. 9) from Rose's Pride Formation is inflated, with well formed posterior-lateral sulcus, and anteriorly placed umbones, close to *truncatum*, but also allied to *ovale,* and now treated as a subspecies within the *ovale* complex. The Berriedale Limestone specimens figured as *hobartense* and *konincki* by Runnegar (1970, pl. 15, fig. 1, 2, 10, 11) somewhat approach *hobartense*, but also show signs of a lateral sulcus and steep anterior dorsal margin suggestive of an approach to *sulcatum*, although the specimens are not as high. It would be desirable to examine fully mature *Eurydesma* from the Berriedale Limestone.

?*Myalina (Leiomyalina) antarctica* Frech (1891) is similar to *Eurydesma ovale* and the associated subspecies in outline, and lacks a sulcus. Uncertainty over provenance and inaccessibility if not loss of the type material led Waterhouse (1987b) to set the taxon aside, but further collecting may yield enough material to determine without question its provenance and allow citation of a neotype. According to Runnegar (1970), Frech's species may have come from the Conjola Formation (which included Wasp Head Formation), south Sydney Basin. The type is distinguishable through its substantial height from Wasp Head specimens that approach *burnettensis*. The original figure was reproduced by Runnegar (1970, pl. 17, fig. 5, 6), and the shape is particularly close to *E. ovale* Etheridge & Dun, other than in lacking a sulcus. Runnegar (1970) referred *antarctica* to the synonymy of *konincki*, in spite of the differences in shape and inflation. Specimens from the Sirius Mudstone Member, Cattle Creek Formation, southwest Bowen Basin, have a long hinge and steep anterior dorsal outline, and might be related, but identification is hindered by the fact that only part of the specimens were figured by Runnegar (1970, pl. 17, fig. 9, 13). The left valve hinge shows a very reduced dental boss close to the start of the ligament, and a left valve tooth is also present in a

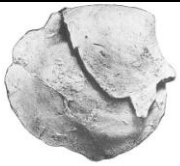
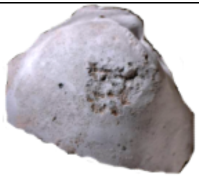
Echinalosia discinia		 alisulcatum		
dalwoodensis				
Glendella dickinsi	 hobartensis			
Attenuocurvus				
conata				
adentata				
plica				
Taeniothaerus subquadratus		 ovale sulcatum		
geniculata				
Bookeria pollex	 glaebula	 ovale	 ovale truncatum	 ovale truncatum
macrospina				
Crassispinosella subcircularis	 konincki	 cordatum	 sacculum	
Strophalosaria concentrica	 protrudus		 burnettensis	 burnettensis

Fig. 237. Species of *Eurydesma* in the Early and early Middle Permian of eastern Australia. Most are restricted to one zone (left-hand column), and a few range a little above or below. The unusual dentition for *burnettensis* shows the large right tooth projection, allied to the dentition of *truncatum* and *hobartensis*, whereas other species have a prominent left valve projection. *Glendella* is eurydesmid, characteristic of a cold-water fauna of low diversity. Figures taken from Etheridge & Dun (1910), Maxwell (1964), M'Coy (1847), Runnegar (1970) and Waterhouse (1987b).

Conjola specimen (Runnegar 1970, pl. 17, fig. 12). Externally these look like *ovale* Etheridge & Dun, yet differ in dentition from *truncatum* with its right valve tooth-like boss. More information is needed to show the significance – and consistency – of the dentition in these forms of *Eurydesma*, and to test if transposition occurred.

Amongst species and subspecies described from Kashmir and the Salt Range, *E. cordatum mytiloides* Reed (1932, p. 50, pl. 11, fig. 1-3b; 1936, pl. 3, fig. 1, 2) is a high shell with steep anterior margin as in the *ovale* complex, and *E*. cf. *globosum* [not Dana] of Reed (1932, p. 53, pl. 10, fig. 5, 5a and less pl. 11, fig. 4) is apparently similar.

Yet another form is represented by *Eurydesma sacculum* (M'Coy, 1847, p. 301, pl. 14, fig. 5) from the Allandale Formation at Harper's Hill, Sydney Basin, with large size, subcentral umbones, thin posterior and well formed posterior sulcus. The holotype is CASM E 10759 by monotypy. *Eurydesma sacculum* Dana (1849, p. 700, pl. 7, fig. 8a, b), refigured by Waterhouse (1988, p. 176, pl. 4, fig. 5) from the same beds differs in lacking the posterior "wing", possibly through breakage. A broken specimen figured from the Bundella Formation of Tasmania as *E. cordatum* by Clarke (1992a, p. 34, text-fig. 21A) might be allied, but is very incomplete. The species *sacculum* has generally been referred to *E. cordatum* (eg. Runnegar 1970, p. 92), but *cordatum* has a shallower more posteriorly located sulcus and lacks the posterior "wing". Examples of *sacculum* are so rare that they might merely be unusual variants of *cordatum* – but they also might well be a very different species. Waterhouse & Gupta (1982) pointed out a strong approach to *Notomya gouldi* Johnston (1888, pl. 17, fig. 1) from marine mudstones at Bridgewater, Tasmania. Johnston's figure shows a well preserved specimen with deep ventral sulcus and apparently lacking a posterior "wing".

Eurydesma protrudus Waterhouse (2008a, p. 121, text-fig. 62) from Darlington Limestone, Maria Island, figured extensively by Etheridge & Dun (1910), is characterized by low inflation, long hinge, strongly curved anterior dorsal margin, extended anterior, generally subcentral umbones, and often no lateral sulcus. The left valve prominent ear ledge projects like a tooth, and may have a slender ridge below the ligament. The species is represented by a number of described and well figured specimens in the Australian Museum, Sydney. The right valve (Etheridge & Dun 1910, pl. 20, fig. 6) has a large shallow socket. Left valve AMF 14778 of Etheridge & Dun (1910, pl. 25, fig. 4, 5) shows a swollen ear ledge marked by growth-lines, behind a byssal depression, and in front of the ligament. There is no tooth-like boss in this specimen. Further Tasmanian specimens of *protrudus* were identified with *E. hobartense konincki* Johnston by Runnegar (1970, p. 97), and are much less inflated and shaped very differently from *konincki*, with extended anterior and other differences. The species to judge from shape gave rise to *E. alisulcatum* Waterhouse, found in the late Early Permian Ulladulla Formation, and distinguished by a weakly defined posterior wing and a lateral sulcus, and by having a left valve tooth.

Eurydesma cordatum var. *compressa* Reed (1932, pl. 10, fig. 7, 8, pl. 11, fig. 5) from the Agglomeratic Slate of Kashmir is very like *E. protrudus* in shape, and *E. cordatum quadrata* Reed (1932, p. 52, pl. 10, fig. 6) from the same beds is similar. It also compares with so-called *E. ellipticum* Dana of Waagen (1891, p. 141, pl. 6, fig. 5, 6, pl. 7, fig. 1, pl. 8, fig. 1, 2) from the Salt Range, Pakistan. Thus the form is apparently more common in the Indian subcontinent than in east Australia.

Eurydesma sp.

Fig. 238B - D

Diagnosis: High subrectangular shells with high anterior dorsal margin sloping moderately well forward from anteriorly placed umbo, hinge long without posterior wing, lateral sulcus moderately developed. Right valve socket.

Material: Tiverton specimens from UQL 1626 and 1627. *Taeniothaerus subquadratus* Zone.

Description: A large left valve UQF 21075 from UQL 1626 is 101mm long, 112mm high and 45mm wide, with steep and high anterior wall, steep anterior dorsal margin that slopes forward at 50° from hinge, anteriorly placed not incurved umbo, and well formed lateral sulcus behind the umbo; internally the pallial pits are as figured, but the large muscle scar complex is vaguely impressed. There is a large anterior buttress, and the ligament carries distinct longitudinal striae. The other valve is a large right valve UQF 21157 from UQL 1627 with the long hinge and ligament area preserved, and an anterior inner shelf, which is concave and probably received the tooth from the left valve. This is bordered by the ear-ledge in front.

Resemblances: These specimens differ from the species of *Eurydesma* that are most common at and near this level

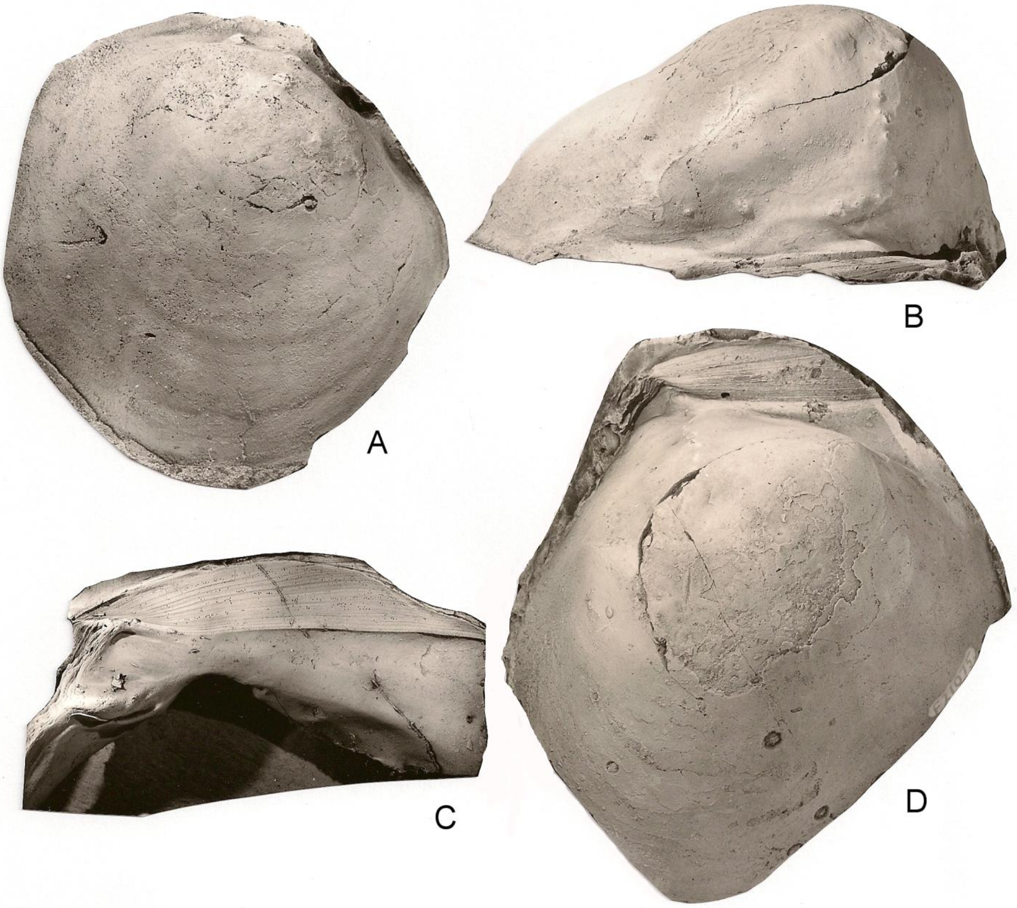


Fig. 238. A, *Eurydesma glaebula* n. sp., right valve of specimen with valves conjoined, UQF 81509 from UQL 1619, x1. B-D*, Eurydesma* sp. B, D, left valve internal mould, UQF 21075, dorsal view and lateral view, x0.66 and 0.75. C, latex cast of hinge, right valve UQF 21157, x0.8.

in east Australia. Such form a plexus centred on *E. ovale* Etheridge & Dun (1910) – and perhaps *E. antarctica* (Frech) – with moderate inflation, low umbones and subrectangular shape involving anteriorly placed umbones and steep anterior margin virtually at right angles to the hinge. The form closest in shape to present material is *E. ovale sulcatum* Waterhouse, with a comparable well defined posterior-lateral sulcus from the Rose's Pride Formation of the southeast Bowen Basin, a subspecies slightly younger than the present specimens. The dentition is not known for this subspecies. But an apparently close ally, *E. ovale truncatum* Waterhouse from the Fairyland and Dresden Formations of the southeast Bowen Basin has right valve tooth rather than socket as in the present form. If the dentition is consistent rather than occasionally transposed, then the present material belongs to a different complex. On the other hand Cattle Creek *Eurydesma* have a left valve tooth, implying a right valve socket. There is some similarity externally to *E. alisulcatum* Waterhouse, and a left valve of this species that was figured as *E. hobartensis konincki* [not Johnston] by Runnegar (1970, pl. 17, fig. 12) has a large tooth. A right valve interior of *E. alisulcatum* that was figured by Waterhouse (1987b, pl. 1, fig. 27) is more difficult to interpret, but possibly shows a tooth and hollow below, somewhat like that of the Tiverton right valve.

Infraclass HETEROCONCHIA Hertwig, 1895

Cohort CARDIOMORPHI Férussac, 1822

Subcohort CARDITIONI Dall, 1889

Order CARDITIDA Dall, 1885

Superfamily **CRASSATELLOIDEA** Férussac, 1822

Family **ASTARTIDAE** d'Orbigny, 1844

Subfamily **ASTARTELLINAE** Boyd & Newell, 1968

Diagnosis: Extinct members of the family, characterized by having only two cardinal teeth in each valve, the one in the left valve lying in front of that in the right valve.

Genus ***Astartella*** Hall, 1858

Type species: *Astartella vera* Hall, 1858, p. 715 from Pennsylvanian of Illinois and Indiana, United States, OD.

Diagnosis: Small oval to rhomboidal shells ornamented by commarginal furrows and well spaced laminae, cordiform lunule. Valve margins may be crenulate. Right valve with narrow trigonal 3b, oblique 5b and marginal laterals, left valve 2 partly fused as hook with raised A11 lunular margin, 4b strong, broad and oblique, and P11 small. Muscle scars small.

Discussion: The diagnosis is taken from Chavan (1969). Boyd & Newell (1968, 1969) have provided a clear account of the dentition and features of the genus.

Astartella heideckeri n. sp.

Fig. 223B, 239 – 241, 244H

1964b *Astartella* sp. Hill & Woods, pl. P12, fig. 8.

1972 *Astartella* sp. Hill, Playford & Woods, pl. P12, fig. 8.

Derivation: Named for Eric Heidecker.

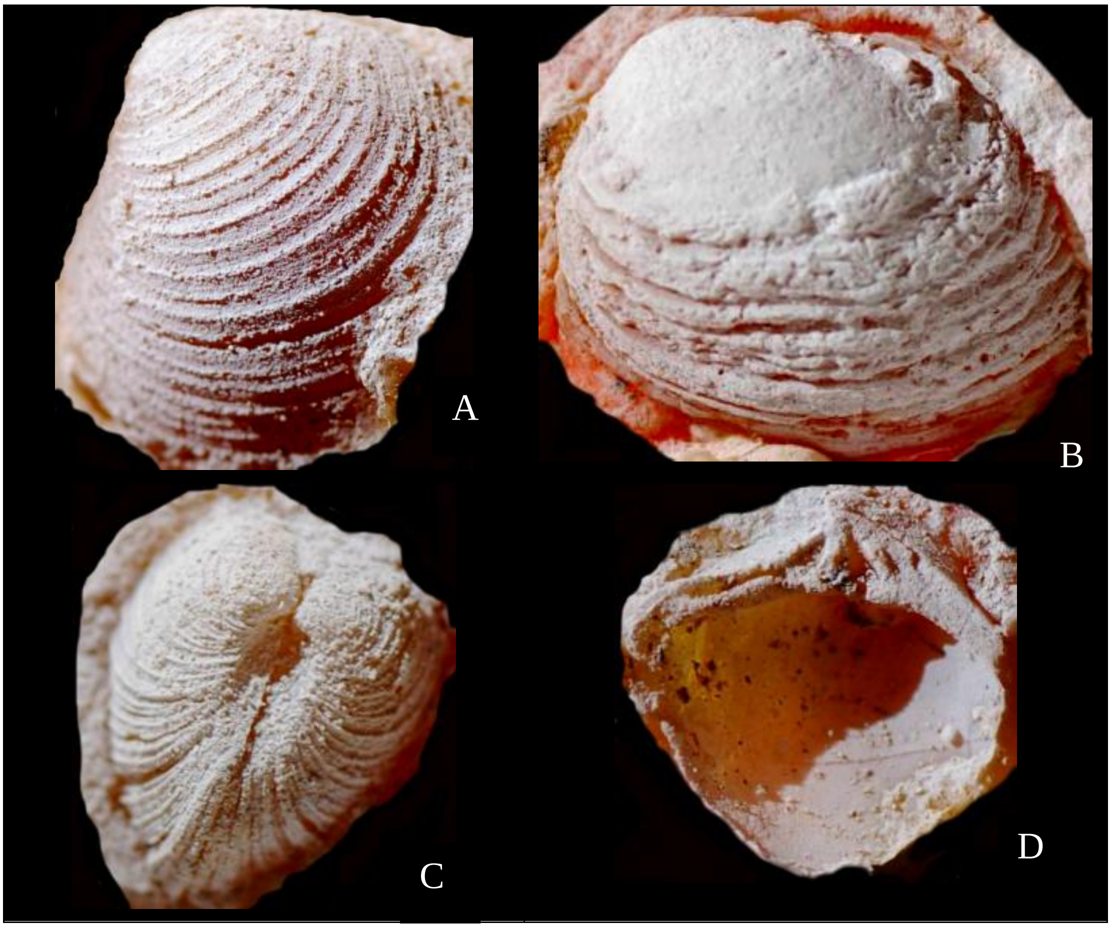


Fig. 239. *Astartella heideckeri* n. sp. A, left valve latex cast UQF 81546 from UQL 2584, x4. B, holotype, latex cast of left valve, UQF 81549 from UQL 4519, x3, shell at late maturity judged by sturdy and worn ornament. C, cast of external mould of UQF 81593 from LT3, x5, tilted, dorsal anterior aspect showing weakly circumscribed lunule. D, latex cast of right valve interior, UQF 81545 from UQL 4515, x6.

Holotype: UQL 81549 from UQL 4519, Tiverton Formation, figured herein as Fig. 223B, 240A, C, D, here designated.

Diagnosis: Small inflated shells with broad lunule, very narrow escutcheon, ornament of ragged growth steps.

Material: Conjoined external moulds from UQL 1625, 1626, 2584, 3127, 4511, 4515, 4519 and LT3. *Bookeria geniculata* Zone, less common to rare in *Taeniothaerus subquadratus* Zone.

Description: Specimens small, one measuring 10mm long and 7.5mm wide, and a left valve UQF 21068 from UQL 1626 measures 14.5mm long, 13mm high, 4mm thick, with umbo sited 6mm from anterior margin. Shells equivalve, well inflated, umbones inconspicuous and prosogyrous, placed near anterior third of shell length, umbonal angle of about 100°, broad short deep lunule not bordered by ridge, narrow long escutcheon. Ornament of ragged growth-rugae and steps, 10-12 in 5mm, composed of ragged projecting laminae separated by concave interspaces bearing up to 15 growth increments. Shell margin weakly crenulate.

Interior shown on right valve from UQL 4515, prominent and thickly trigonal 3b and longer robust 5b, behind the sockets for left valve teeth; a slender posterior lateral tooth, sited on sturdy hinge plate. Anterior adductor small, placed well forward. An internal mould shows the two cardinal teeth interlocking along the anterior hinge, left tooth in front, and comparatively well defined rounded anterior adductor impression. No pallial line or posterior adductor is visible.

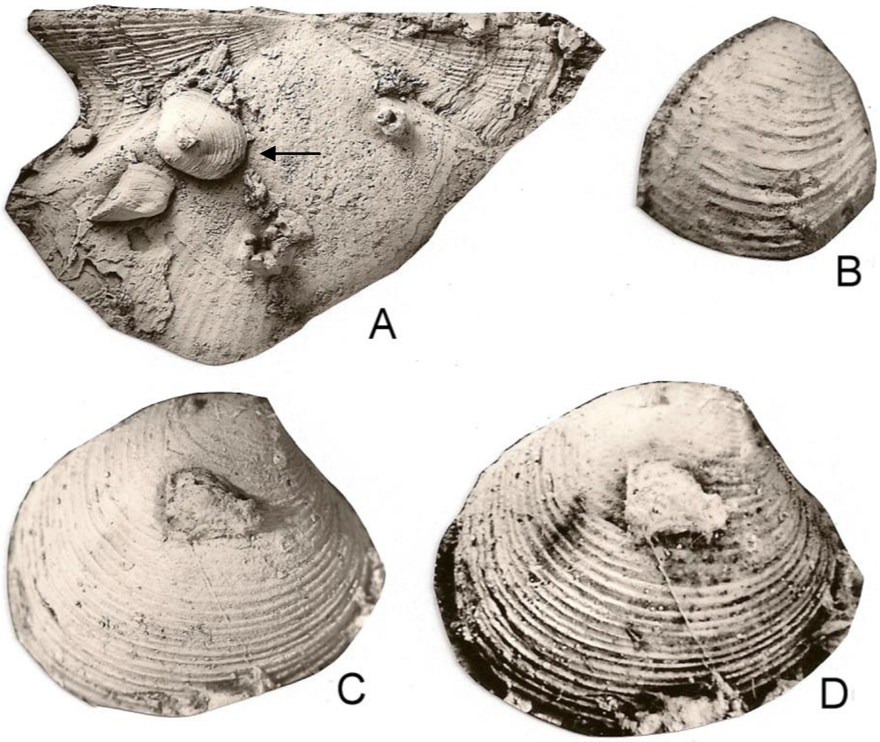


Fig. 240. *Astartella heideckeri* n. sp. A, latex cast of right valve UQF 21068 (arrowed) from L 1626 and resting on a right valve of *Etheripecten playfordi* n. sp. UQF 21067, x1. C, D, latex cast of the same right valve UQF 21068, x 3.5 and x4, under different lighting. B, latex cast of right valve UQF 81592 from LT3, x4. See also Fig. 223B.

Resemblances: *Astartella rhomboidea* Etheridge (1892, pl. 14, fig. 15) from Gympie, southeast Queensland, with no further locality detail, has anteriorly placed umbones and well defined commarginal lamellae. Its interior is not known, and the species requires further study, but the umbo is more anteriorly placed than in the Tiverton species. *Astartella obliqua* Dickins (1963, p. 104, pl. 16, fig. 2-9, text-fig. 13) was described from the Callytharra Formation, Nura Nura Sandstone and Cuncudgerie Sandstone of Western Australia. Chavan (1969) was doubtful about the generic position, and Dickins (1963) stated that the species lacked the distinctive lamellate ornament, yet such is shown in Dickins (1963, pl. 16, fig. 5). The present species is of similar age. The Queensland species is larger and more inflated, with more oval outline and short more concave anterior umbonal slope, wider lunule, stronger ornament, and stronger teeth. Dickins (1981, p. 29, pl. 2, fig. 1-4) also compared material from the Eight Mile and Tunnel Blocks in south Queensland near Warwick to *obliqua*: the specimens differ a little in shape from *A. heideckeri,* but closer inspection is required to assess their specific affinities. *Astartella* sp. figured by Hill & Woods (1964a, pl. C13, fig. 11-13) from the Yarrol Basin Carboniferous, further detail not provided, is moderately close to the present species. The specimens are registered as UQF 46466-46468.

Astartella toyomensis Nakazawa & Newell (1968, p. 98, pl. 10, fig. 3-5; Murata 1969, p. 19, pl. 4, fig. 9-17) from the lower and especially middle Toyoma Formation, and also the upper Kowaragi Formation of Japan is moderately close in shape and ornament, with thinner commarginal lamellae, and more medianly placed umbones. From the Late Permian Oudjah el Rhar Group of Djebel Tebaga, Tunisia, *A. gemmifera* Termier & Termier (1959, text-fig. 2, fig. 10, 13, 14; Termier et al. 1977, pl. 17, fig. 5-9, text-fig. 43) has more medianly placed umbones and strong teeth in the left valve.

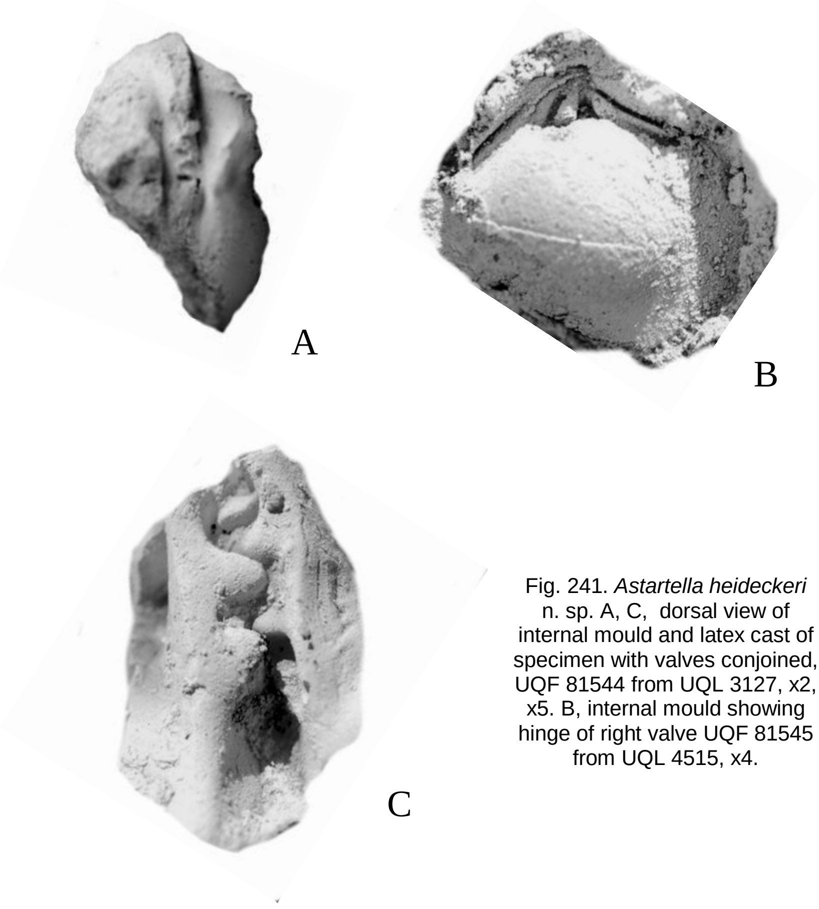


Fig. 241. *Astartella heideckeri* n. sp. A, C, dorsal view of internal mould and latex cast of specimen with valves conjoined, UQF 81544 from UQL 3127, x2, x5. B, internal mould showing hinge of right valve UQF 81545 from UQL 4515, x4.

The type species of the genus, *Astartella vera* Hall from Pennsylvanian faunas of United States, is more trigonal in shape. *A. aueri* Boyd & Newell (1968, text-fig. 7D-G, 8C-J, 10, 22-24) from the Grandeur Member of the Phosphoria Formation in Wyoming, and other mid-west formations, including Road Canyon Formation of the Glass Mountains, Texas, is also slightly more trigonal in outline, with less widely diverging anterior and posterior slopes, wider escutcheon, and slightly different teeth. One figured specimen (Boyd & Newell 1968, Fig. 10C) shows dark radial lines, not visible on the exterior as a rule, but visible in transmitted light. The outline of the present species is much closer to that of *A. subquadrata* Girty (1909b, pl. 10, fig. 10-13), and the possibly synonymous *A. nasuta* Girty. The external ornament of the Queensland species is more regularly arranged and more closely spaced, and the posterior less elongate and subquadrate in outline, although overall proportions and inflation and cordiform lunule are similar. Girty's species has been found in the Road Canyon Formation of Texas, upper Kaibab Formation of Arizona, Grandeur Member of Idaho, and other stratigraphic units in western United States. Species of somewhat similar shape have been described as *A. tunstallensis* (King, 1850, pl. 16, fig. 2) from the Magnesian Limestone of England, and *A. vallisneriana* (King) from the same beds has a more elongate outline (see Logan 1967). Newell (1955) and

Ciriacks (1963) have commented that the similarity of such small representatives of the genus in the so-called late (meaning Middle and Late) Permian was "cosmopolitan" (meaning, in their understanding, North Atlantic, United States and European Russia), and, age apart, the term is now reinforced by the Queensland species.

Subcohort CARDIONI Férussac, 1822
Megaorder CARDIATA Férussac, 1822
Superorder CARDIIFORMII Férussac, 1822
Order MODIOMORPHIDA Newell, 1969
Superfamily **MODIOMORPHOIDEA** Miller, 1877
Family **CYPRICARDINIIDAE** Ulrich in Ulrich & Scofield, 1894

The family definition and position are discussed by Pojeta (1969, p. 20), Morris (1978) and Johnston (1993, p. 86).

Fig. 242. *Melicusia jelli* Waterhouse. A, latex cast of umbonal hinge in left valve UQF 81536 from UQL 4518, x 6. B, latex cast of dentition below umbo in right valve UQF 81535 from UQL 3127, x4.

Genus ***Melicusia*** Waterhouse, 2010a

Type species: *Melicusia jelli* Waterhouse, 2010a, p. 100 from Tiverton Formation (Sakmarian) of Queensland, OD.

Diagnosis: Equivalve, low prosogyrous umbones, ornament of commarginal laminae with discontinuous radial threads especially on first formed part of shell, simple opisthodetic ligament that is entirely or largely internal, no defined lunule and often no escutcheon; cardinal teeth involve three major teeth below commissure, slender postero-lateral teeth.

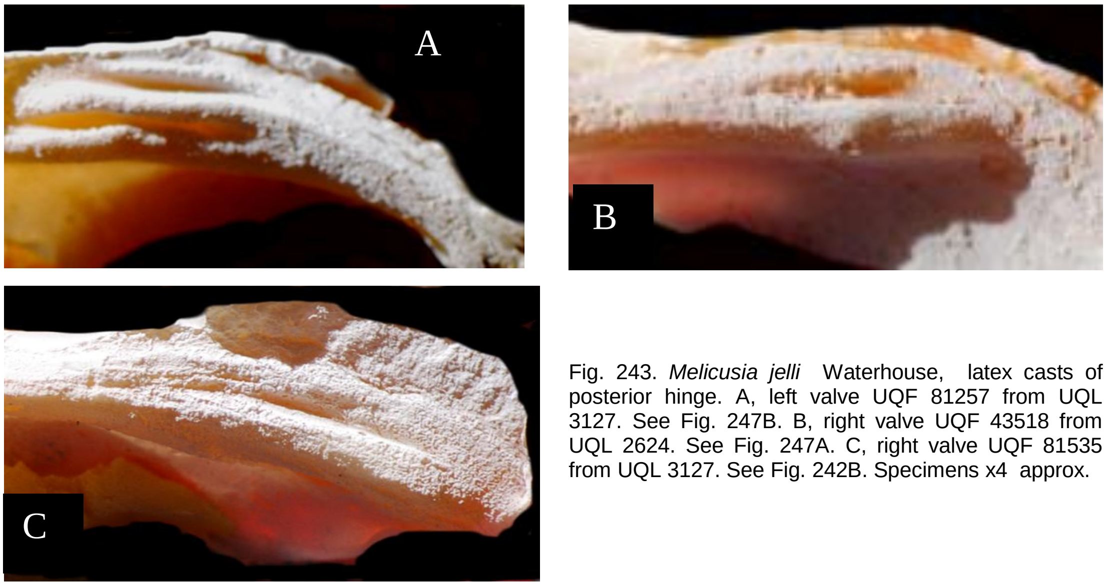


Fig. 243. *Melicusia jelli* Waterhouse, latex casts of posterior hinge. A, left valve UQF 81257 from UQL 3127. See Fig. 247B. B, right valve UQF 43518 from UQL 2624. See Fig. 247A. C, right valve UQF 81535 from UQL 3127. See Fig. 242B. Specimens x4 approx.

Discussion: *Melicusia* is based on *M. jelli* Waterhouse from the Tiverton Formation, Bowen Basin, and possibly includes *Cypricardinia*? *elegantula* Dickins (1963) from the Fossil Cliff Formation, Callytharra Formation and other formations in Western Australia, and *Pleurophorus gregarius* Etheridge, 1900 from the Sydney Basin. The species are close to *Cypricardinia* Hall, 1859, type species *C. lamellosa* Hall, 1859 from the Devonian of New York, in overall shape and size, the presence of radial flutings (only on the right valve in some species of *Cyrpicardinia*), the lack of a clearly defined lunule and presence of only an ill-defined escutcheon. Three cardinal teeth and sockets are present in the right valve and three in the left valve of the type species *Melicusia jelli*, whereas the right and left valves in *Cypricardinia* have one prominent cardinal tooth, with a slender posterior cardinal tooth in the right valve. A ridge below the anterior dorsal margin is counted as a tooth in the left valve, and a slender right valve tooth may lie below the posterior ligament groove. The detail is discussed and well illustrated in a number of studies on Devonian studies on Devonian species, including Beushausen (1895), Haffer (1959) and Johnston (1993). Posteriorly, *Cypricardinia* usually displays two posterior lateral teeth in the right valve and a single posterior lateral. Pojeta (1969, p. 20) preferred placement in Cypricardiidae, and this was accepted with discussion by Johnston (1993, p. 86), and the family was placed in Superfamily Modiomorphoidea Miller with a query, as followed by Bradshaw (1999).

The present species is like Devonian species of *Cypricardinia*, particularly in the lack of lunule and

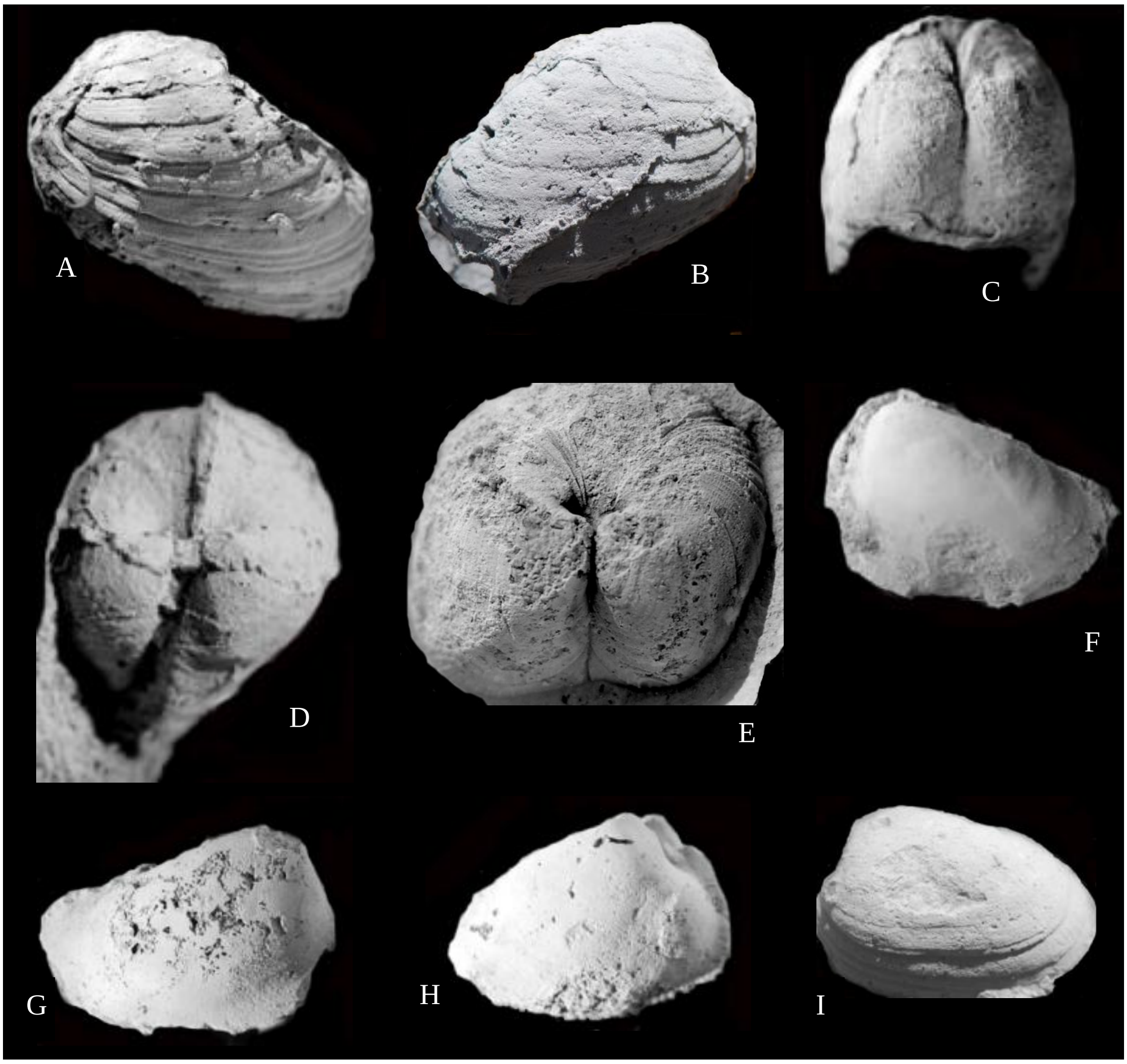


Fig. 244 A – G, I, *Melicusia jelli* Waterhouse. A, B, right and left valve aspects of latex cast, holotype UQF 81547 from UQL 4519, x1.5. C, E, tilted antero-dorsal view of same specimen, x2. D, latex cast of both valves conjoined, anterior dorsal aspect, UQF 81543, x2. F, G, left and right valve aspects of internal mould UQF 81548 from UQL 4511, x1.5. I, latex cast of left valve UQF 81586 from UQL 4518, x1.5. H, *Astartella heideckeri* n. sp. right valve

aspect of UQF 81544 from UQL 4515, x1.5.

escutcheon and presence of well spaced commarginal laminae. Devonian species are laterally sulcate, whereas the present form lacks such a sulcus, and Devonian specimens may be inequivalved, whereas the present species is equivalve. Light radial ribs appear in some Devonian species, as in the present suite.

Neocypricardinia Liu, 1976, type species *Cypricardinia sinensis* Chao from the Late Carboniferous of China, is close to *Cypricardinia* and shows little approach to the present form. The lateral tooth is subdivided into two or three parts posteriorly.

Melicusia jelli Waterhouse, 2010a

Fig. 242, 243, 244A-G, I, 245, 246C, D, 247

2010a *Melicusia jelli* Waterhouse, p. 102, Fig. 42-47.

Holotype: Specimen UQF 81547 from UQL 4519, Tiverton Formation, figured in Waterhouse (2010a, Fig. 44A, B, C, E, 46C, D, 47C, D) and herein as Fig. 244A-C, E, 246C, D, 247C, D, OD.

Diagnosis: Inflated, equivalve, elongate, with anteriorly placed umbones, well spaced commarginal lamellae, faint radial lirae on at least some specimens. Left valve with three principal cardinal teeth, right valve with three cardinal teeth, two well developed.

Material: Specimens with valves conjoined from UQL 1623, 1628, 1630, 2619, 2624, 3127, 3180, 4511, 4514, 4518 and 4519. *Bookeria geniculata* and *Taeniothaerus subquadratus* Zones.

Dimensions in mm:

Left valves		Length	Height	Width (both valves)
mean = 7		27	17	7.5
UQF	UQL	largest right valve		
46518	2624	37.5	22.5	10

Fig. 245. *Melicusia jelli* Waterhouse. latex cast of left valve showing ornament at early maturity. UQF 81585 from UQL 4514, x7.

Description: Specimens suboval, equivalve, gently rounded ventral margin, weakly diverging posteriorly from dorsal margin, anterior margin concave in front of umbo with lower anterior margin bulging forward, umbones anteriorly placed, incurved and twisted anteriorly, no lunule or escutcheon, no lateral sulcus, surface ornamented with low growth laminae spaced 2.5mm apart ventrally. Fine radial grooves and ribs lie over each step, especially well developed on a small specimen at an early stage of growth. Anterior adductor impressions lie close to margin, with small attached retractor scar; posterior scar also well defined with small dorsally attached scar; pallial line not impressed but defined by change in pits over shell surface, without pallial sinus. Left valve with three cardinal teeth under the umbo, the middle one most prominent, the anterior tooth swollen, and posterior tooth elongate. A slender ridge lies behind just below the anterior ligament. The right valve has two well developed teeth below the umbo, fitting behind the anterior left valve tooth and low posterior cardinal tooth. Posterior lateral teeth involve usually two in the right valve, one or sometimes two in the left valve: further detail is provided in the discussion of the genus. The ligament is opisthodetic and elongate, and largely if not entirely internal. Shell recrystalized, 1.5 to 2mm thick at ventral margin, so that interior of shell is comparatively smooth, showing little or nothing of the external growth steps.

Resemblances: *Cypricardinia? elegantula* Dickins (1963, p. 98, pl. 16, fig. 10-19) from the Fossil Cliff Formation and possibly Callytharra Formation and other levels of Western Australia is only moderately similar, with less twisted umbones, higher posterior shell, lower inflation and less regular commarginal growth laminae. It is not clear that the left valve has three prominent cardinal teeth, and Dickins (1963) recorded two or three posterior lateral teeth below the ligament. It seems possible that the species belongs to the new genus, but uncertainties remain over the dentition.

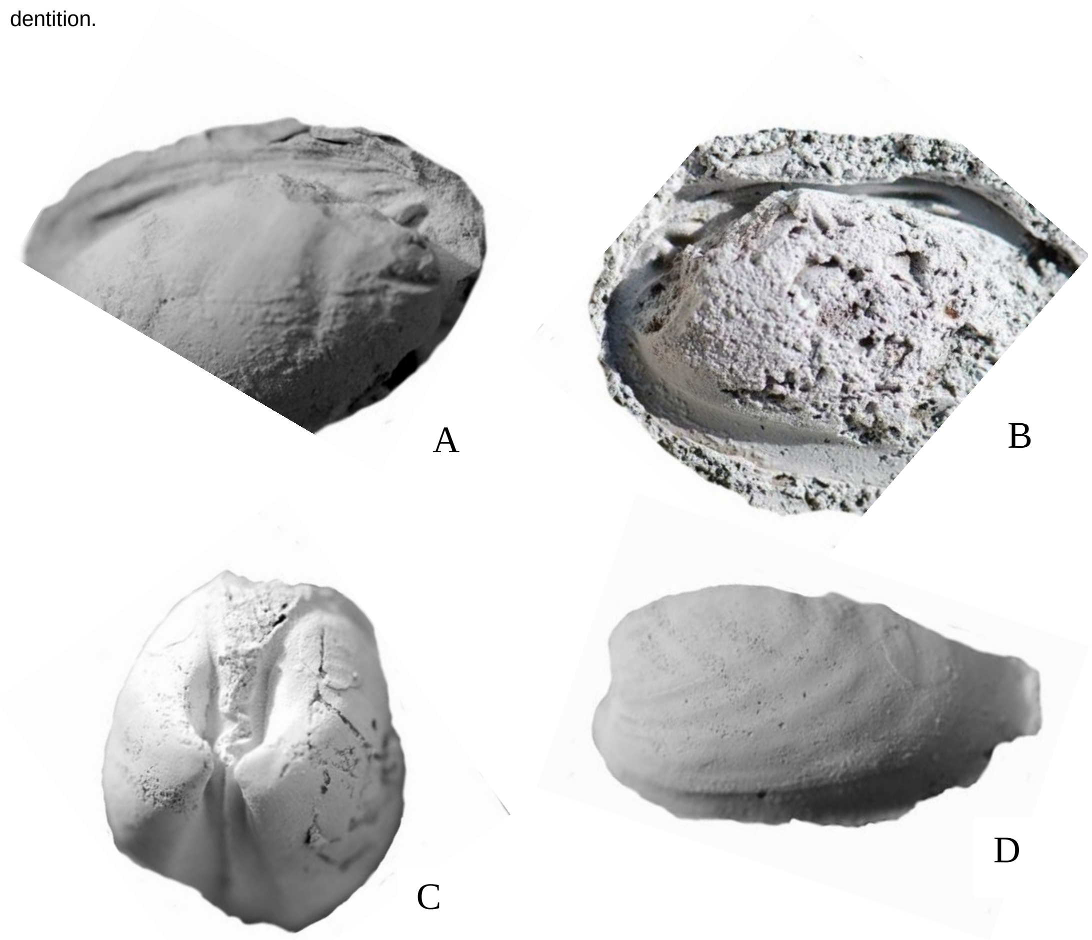


Fig. 246. *Melicusia jelli* Waterhouse. A, right valve internal mould showing dentition, UQF 81535 from UQL 3127, x2. B, damaged internal mould of left valve UQF 81536 from UQL 4518, x3. C, D, tilted anterior aspect showing dentition and left valve aspect of internal mould with valves conjoined, holotype UQF 81547 from UQL 4519, x2.

Permophorus gregarius (Etheridge, 1900, p. 185, pl. 33, fig. 2-5) from the Farley Formation of the north Sydney Basin also has a feeble if any myophoric buttress, despite the figure implying otherwise, and the posterior part of the anterior adductor scar is impressed deeply into the shell. The lectotype is here designated as AMF 14236 (formerly AMF 29507), figured by Etheridge (1900, pl. 33, fig. 2-4). It measures 42mm long, 19mm high and the valves are together 18.5mm wide. Etheridge reported a long escutcheon and shallow cordiform lunule. Overall the shape of *gregarius* differs slightly from that of the Queensland species, tending to have dorsal and ventral margins parallel, with ventral margin straight and long rather than gently rounded in outline, and the inflation is lower. There is no sign of radial flutings, but ribs were apparently observed by Etheridge (1900) on a specimen from Wollongong, of much younger age and probably not conspecific. The hinge was shown as having two right cardinal teeth and a prominent left tooth (4b) and low anterior tooth (2). Unfortunately the lectotype has now lost much of its dentition, and in the right valve there is one tooth and signs of a second in front: in the left valve a low tooth lies in front of the right valve tooth, looking like that of the Queensland material, and two posterior lateral sockets in the left valve (Etheridge 1900, pl. 33, fig. 4). Dickins (1963, pl. 16, fig. 20, 21), hopefully without destroying the dentition, prepared and figured latex casts of what is now the lectotype (formerly AMF 29507), and the figures show clearly two left valve teeth with a possible thin posterior tooth or ridge in the left valve and two lateral teeth, and what appears to be a large anterior right valve tooth with smaller tooth behind with well rounded anterior socket. Possibly what appears in the figure to be a long right anterior tooth is really a socket surrounded by a ridge. Whatever the interpretation, the left valve is like that of Queensland specimens, but the right valve dentition is not fully clear. Dickins (1963) referred Etheridge's species to *Cypricardinia* Hall on the basis of dentition, shape and ornament. As allowed by Dickins (1963, p. 98), *Cypricardinia* lacks a lunule and escutcheon, whereas such were described by Etheridge (1900), though they may not in fact be present.

Pleurophorus gregarius inflata Laseron (1910, p. 215, pl. 19, fig. 2-6) from Wandrawandian Siltstone of the Burrier district of south New South Wales is larger than *gregarius* or the Queensland material, with a moderate ridge behind the anterior adductor, ragged thick shell and no hinge data. The lectotype is here designated as AMF 20172 (Laseron 1910, pl. 19, fig. 6), and the taxon is upgraded to a full species, but the genus is uncertain, and as it has a myophore ridge, it does not belong to *Melicusia*. *Cypricardinia* species have been reported from the Late Carboniferous of Argentina (Gonzalez 2002), but do not show dentition or radial fluting.

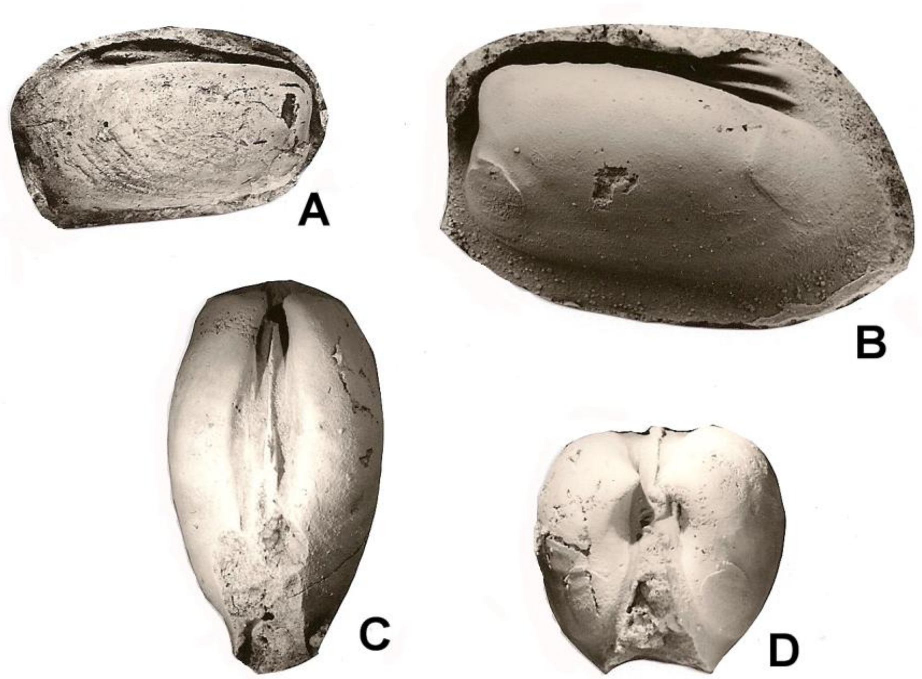


Fig. 247. *Melicusia jelli* Waterhouse. A, right valve internal mould UQF 43518 from UQL 2624, x1. B, left valve internal mould UQF 81257 from UQL 3127, x2. C, D, dorsal and anterior aspects of specimen with valves conjoined UQF 81547 from UQL 4519, x1.5.

Order CARDIIDA Férussac, 1822

Superfamily **KALENTEROIDEA** Marwick, 1953

Family **KALENTERIDAE** Marwick, 1953

Diagnosis: Medium-sized trapezoidal to modioliform inequilateral shells, radial ribs may be present, tend to be obsolete or absent anteriorly, internal margin smooth, marginal ligament and long nymph. Cardinals partly obsolete, tuberculiform or elongate, 5b and laterals lacking in most shells, posterior lateral placed well back, that of left valve usually stronger, anterior and pedal scars, generally thickened anterior buttress, small anterior pedal scar prominent.
Discussion: This family has been discussed by Waterhouse (2010a, pp. 96, 97). Carter et al. (2011) rightly granted standing to Kalenteridae Marwick, though denied by Chavan (1969, p. 543).

Genus ***Stutchburia*** Etheridge, 1900

Type species: *Orthonota*? *costata* Morris, 1845, p. 274 from Broughton Formation (Wordian), south Sydney Basin, New South Wales, OD.

Diagnosis: Elongate equivalve or subequivalve shells, umbones small and anteriorly placed, lunule and deep escutcheon present, commarginal ornament traversed by costae radiating from umbo in some species. Cardinals 2 and 3b obsolescent, P1 and P111 also obsolete and P11 well defined. Anterior adductor scar large, adjoining low myophore buttress posteriorly, posterior adductor scar large, less impressed.

Discussion: Chavan (1969, p. 547) referred the genus *Stutchburia* Etheridge to Subfamily Myoconchinae Newell, 1957. But the genus is very close to *Permophorus* (see Logan 1964), and subfamilial separation from that genus is not warranted by any apparent morphological feature. Chavan placed *Netschajewia* Yakovlev, 1928 in Permophorinae, although Newell (1957, p. 8) treated it as a subgenus of *Stutchburia*. Chavan (1969) explained that the lack of a lunule (and, it might be added, an escutcheon) from *Netschajewia* justified separation between the two genera. But in that case, it is hard to understand why Chavan placed *Netschajewia*, without a lunule, in Permophorinae together with *Permophorus*, which has a lunule, and placed *Stutchburia*, which has a lunule, in Myoconchinae.

Stutchburia laminata n. sp.

Fig. 248 - 250

Holotype: Specimen UQF 81538 from Tiverton Formation, figured as Fig. 248, 249B herein, here designated.

Diagnosis: Large elongate shells, comparatively well inflated, with subterminal umbones and six to eight costae behind umbones; commarginal laminae strongly developed.

Material: Specimens from UQL 1623?, 1625, 1627, 2584, 2619, 2622, 3127, 4505, 4506, 4508, 4517, 4518, TK and LT3. The species is most common in the *Bookeria pollex* Zone, and is found rarely in the *Taeniothaerus subquadratus* Zone.

Dimensions in mm:

UQF	UQL	Valve	Length	Height	Width	
43498	2619	right	70	25.5	8.3	
43447	2622	right	65	27.5	9.5	
81539	1627	right	74	32	10	internal mould
81540	4508	left	65	29	6.5	

Description: Specimens comparatively large with anteriorly placed small umbones and long parallel dorsal and ventral margins, lunule short and moderately wide, escutcheon long, narrow and shallow. Valves moderately inflated for genus: in the holotype, the right valve internal mould is 8mm wide, compared with a width of 10mm for the left valve. Internally a gentle sulcus slopes back from the anterior umbo, but this is less obvious externally. Costae extend from behind the umbones posteriorly to the posterior margin, number six to eight, with very narrow crests and broad interspaces. The entire shell is also covered by thin upstanding growth laminae, 9-14 in 5mm, and these arch gently towards the hinge in the interspaces between costae in well preserved external moulds. Little of the hinge and dentition is preserved. The anterior adductor scar is deeply impressed and located in the anterior ventral bulge of shell below the umbo, in front of a modestly developed myophore ridge. A conspicuous pedal retractor scar lies closer to the hinge and behind the adductor scar, and a small scar is present or suggested at the umbonal tip, especially on the right valve. The pallial line is continuous and without a sinus, and the posterior adductor scar is deeply impressed and located close to the dorsal margin, and may adjoin three small pits at the dorsal margin.

The specimen from UQL 4517 has seven ribs but the posterior shell is lost and the full number not clear.

Resemblances: *Stutchburia farleyensis* Etheridge (1900, p. 182, pl. 32, fig. 3-6) from the Farley Formation of the north Sydney Basin, with material also figured by Dickins (1981, pl. 3, fig. 1-11), is distinctly less elongate and higher than the present species. The species *farleyensis* is not well known, being based on two internal moulds, whereas the lower Tiverton specimens from the *Bookeria pollex* Zone are moderately well preserved externally, and show commarginal laminae, and have costae that cannot be exactly matched with those of the poorly preserved types of *farleyensis*. The moulds of type *farleyensis* have a deep muscle impression above and separate from the anterior adductor scar, and the posterior adductor scar is placed close to the hinge, with small anterior projection. The myophoric buttress is moderately strong. Etheridge (1900, p. 183) reported faint indications of posterior radiating costae, and considered that Wollongong material was of similar shape. The species was reported from the Elvinia

Formation, southeast Bowen Basin, by Waterhouse (1987b, p. 164). Clarke (1992a, p. 43, Fig. 16F – L) illustrated similar specimens as *farleyensis* from somewhat older beds of the Swifts Jetty Sandstone in Tasmania. These have only five faintly developed posterior ribs and display a well developed lateral sulcus on some specimens.

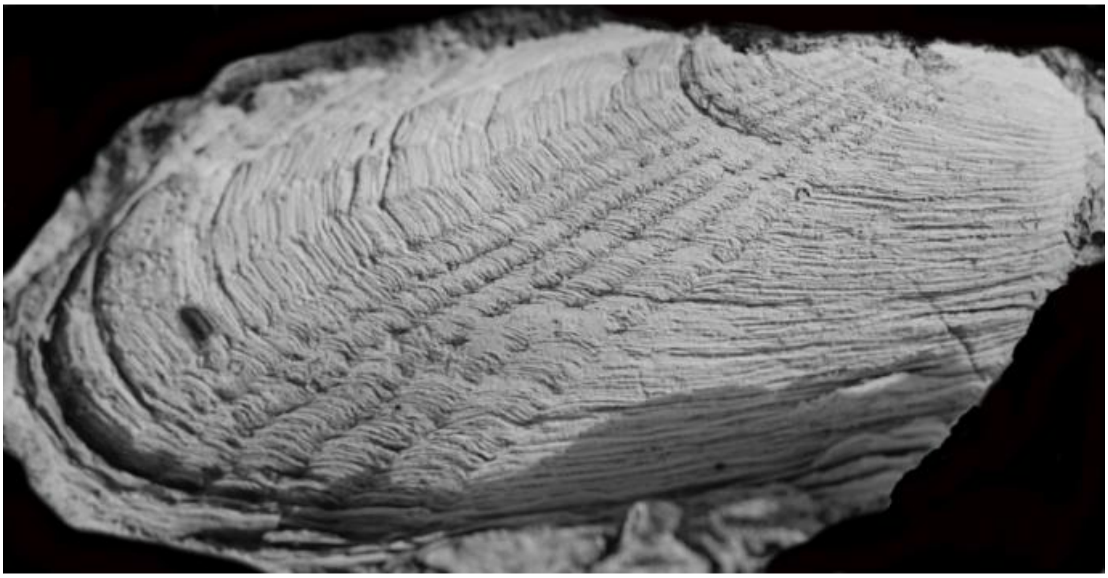


Fig. 248. *Stutchburia laminata* n. sp., holotype, external mould of left valve UQF 81538 from LT3, x1.9.

The present specimens are close to *Stutchburia costata* (Morris, 1845), a species widespread in Guadalupian beds of eastern Australia and New Zealand, as summarized by Waterhouse (1980, p. 113; 1987b, p. 166). The Tiverton shells are distinguished from *S. costata* through their moderate number of costae, fewer than on the types of *costata*, the slightly smaller size and tendency to slightly greater inflation, the lack of well formed external sulcus below the umbones, and on well preserved specimens, the stronger commarginal laminae. However it must be allowed that the Middle Permian material varies somewhat in shape and in costation, inviting closer study of the *costata* assemblage. At present, the Tiverton assemblage appears to belong to a fairly consistent morphotype, not exactly matched by any of the younger specimens so far documented, although it yet may prove that it continued into younger sediments.

There are similarities in shape to a smaller species with fewer costae, described as *Pleurophorus randsi* Etheridge (1892, pl. 14, fig. 14), reported from the Burnett district of central Queensland, although not endorsed by Maxwell (1964) in his study of faunas from the Yarrol Basin. Dickins (1963, pl. 15, fig. 14, 15) refigured the type specimen GSQF 943 (by monotypy), and figured material from the Eight Mile and Tunnel Blocks near Warwick, southeast Queensland (Dickins 1981, p. 29, pl. 3, fig. 12-16). Apart from being slightly less elongate, the species *randsi* looks very close to *S. obliqua* Etheridge (1900, pl. 31, fig. 3 – AMF 41680), recorded as coming from the Shoalhaven district and Farley Formation of the Sydney Basin. Archbold (2003, p. 166, Fig. 5.1, 2, 4) figured material from the Beckers Formation of Cranky Corner, northern New South Wales, which he ascribed to *S. variabilis* Dickins (1957, pl. 2, fig. 7-14; 1963, pl. 15, fig. 24) from the Callytharra and Fossil Cliff Formations of Western Australia, according to Dickins (1963), and from top of the Lyons Group in his 1957 study. Growth laminae are well and closely developed in the Cranky Corner specimens, as in only one of figured *variabilis* (Dickins 1957, pl. 2, fig. 14) and costae are firmly developed, again as only in Dickins (1957, pl. 2, fig. 14). Dickins (1957, p. 22) stressed that *variabilis* was distinguished from *randsi* by its well spaced ribs, distinct posterior umbonal ridge, and maximum inflation near the posterior end. The Cranky Corner material does not clearly agree with *variabilis* in these attributes, and ribs and shape suggest a likely approach to *S. randsi* (Etheridge). The present Tiverton specimens lack a distinct posterior umbonal ridge and are most inflated anteriorly, so they clearly differ from *variabilis*.

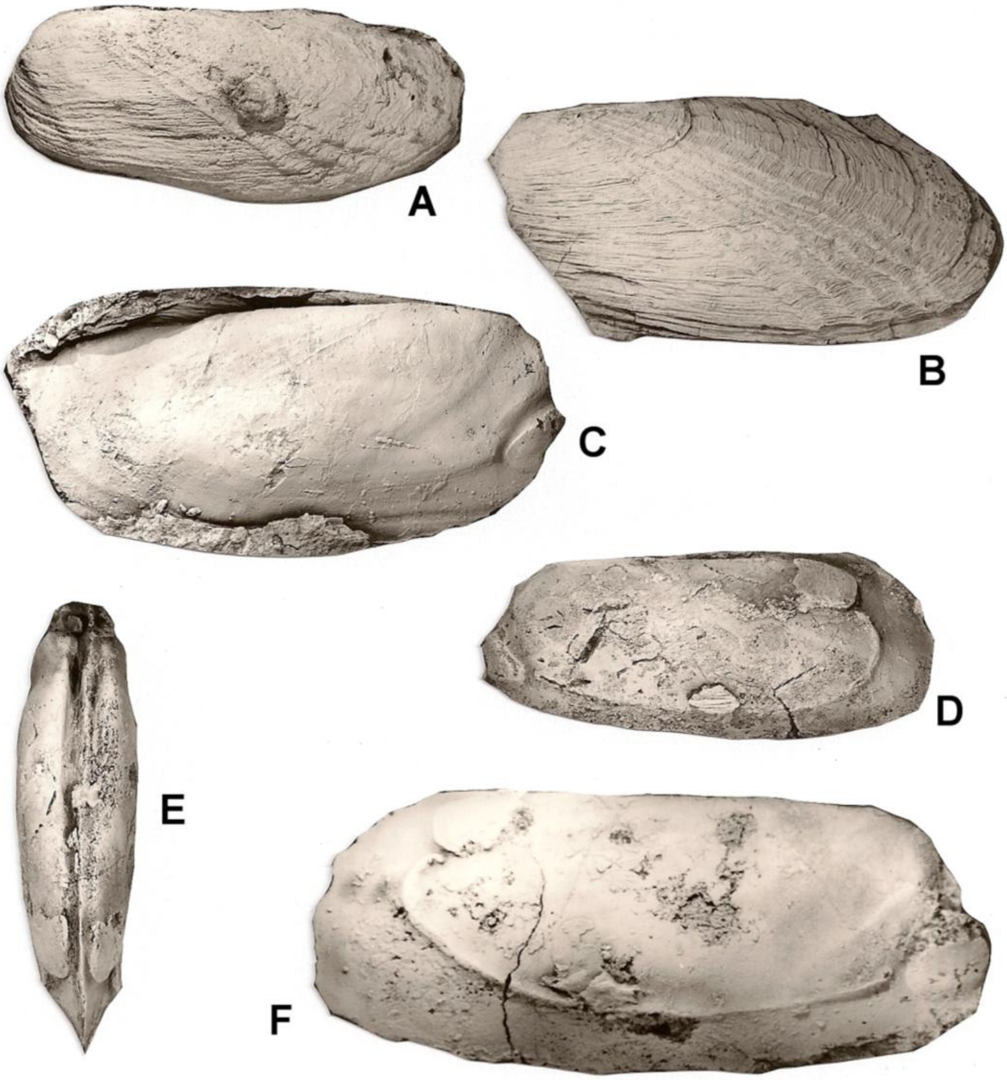


Fig. 249. *Stutchburia laminata* n. sp. A, latex cast, left valve UQF 81540 from UQL 4508, x1. B, holotype, latex cast of incomplete left valve UQF 81538 from LT3 (= UQL 4508), x 1. C, internal mould of right valve UQF 81539 from UQL 1627, x1. D, E, F, internal mould of both valves conjoined, D, E, left valve and dorsal view, x1. F, right valve, UQF 43447 from UQL 2622, x1.5.

Stutchburia compressa (Morris, 1845) described by Maxwell (1964, pl. 10, fig. 11-15 – eg. UQF 43145) from the Yarrol Formation of the Yarrol Basin, together with further material (UQF 68012) lacks ribs, and is short and tapers posteriorly, suggesting a different species, somewhat reminiscent of *randsi* and especially *farleyensis*. It was noted by Waterhouse (1980, p. 117) that the Yarrol specimens were not conspecific with *compressa*, because the agreement in shape is not complete, and the pedal scars are well developed above the anterior adductor scars. The left valve UQF 43145 is 50mm long, 24mm high and 7mm wide, with the umbo anteriorly placed at 8mm from the anterior margin. *Stutchburia hoskingae* Dickins (1963, pl. 15, fig. 16-23) from the Fossil Cliff Formation of the Perth Basin shows ribs somewhat similar to those of the present species, and higher posterior and smaller size. Another species with somewhat similar shape was described as *Stutchburia muderongensis* by Dickins (1956) from the Coolkilya Greywacke, Carnarvon Basin, Western Australia. Similar material was reported from the Mangarewa Formation of New Zealand by Waterhouse (1980).

Taxonomy: *Clidophorus pallasi obliquus* Gowlinsky, 1869 has been referred to *Stutchburia*, and Muromseva (1984, p. 85) placed *pallasi* in *Stutchburia*. If correct, *Stutchburia obliqua* Etheridge (1900) would appear to be a junior homonym, and so was renamed *S. etheridgei* by Waterhouse (1987b).

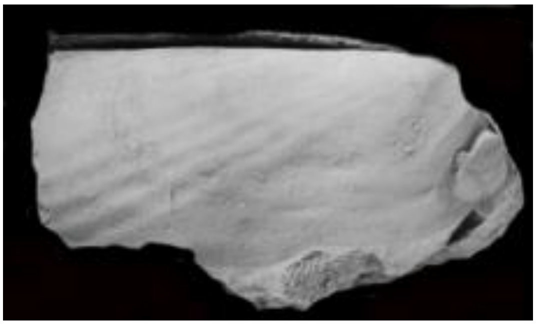


Fig. 250. *Stutchburia laminata* n. sp. A, right valve internal mould UQF 81541 from UQL 3127, x1. B, latex cast of right valve UQF 43498 from UQL 2619, x2.

Superorder PHOLADIFORMII Gray, 1854

Order PHOLADIDA Gray, 1854

Superfamily **PLEUROMYOIDEA** Zittel, 1895

Family **VACUNELLIDAE** Astafieva-Urbaitis, 1973

Genus ***Vacunella*** Waterhouse, 1965c

Type species: *Allorisma curvatum* Morris, 1845, p. 270 from “Illawarra”, Broughton Formation (Wordian), south Sydney Basin, New South Wales.

Diagnosis: Medium-sized to large shells with moderate to substantial posterior gape, pedal gape often present, no posterior carination, umbones placed well forward, pallial sinus, anterior retractor scar connected by isthmus to anterior adductor scar.

Discussion: The concept that *Vacunella* evolved from *Myonia* which was championed by Runnegar (1967) and opposed by Waterhouse (1969b, 2001) may now be set aside, with the demonstration that *Vacunella* not only differs morphologically from *Myonia* but is represented in Carboniferous glacial deposits (Gonzalez 2002) in western Argentina, much older than the genus *Myonia* from which it supposedly evolved. There are close allies of *Vacunella* in the Carboniferous of northern Russia, called *Praemyonia* Astafieva-Urbaitis, 1988 and *Cuvavella* Astafieva-Urbaitis, 1990 (see Waterhouse 2001, pp. 149, 150). The recent taxonomic history of *Vacunella* and its classificatory position has been overviewed by Gonzalez (2006, pp. 142, 143), summarising the different approaches by Runnegar (1974), Runnegar & Newell (1974), Astafieva-Urbaitis (1973) and Morris et al. (1991). Gonzalez (2006) concluded that *Vacunella* and allies should be classed with Pholadomyidae, because of the lack of a lunule and close approach to Mesozoic members of the family, as proposed by Waterhouse (1966b, 1969b, 2001, pp. 148ff).

Oblicarina Waterhouse, 1967b, type species *Chaenomya? carinata* Etheridge, 1892, p. 279 from the Flat Top Formation (Wordian), southeast Bowen Basin, was named for markedly procrescent shells with carinate posterior umbonal ridge, regular commarginal rugae over lateral and anterior shell and not over posterior shell, and posterior gape. The anterior adductor and protractor scars are much as in *Vacunella*, but the isthmus between the two is very short. The hinge is edentulous. The genus is distinguished from *Vacunella* principally through its carinate posterior umbonal ridge and regular commarginal rugae over the lateral and anterior shell. The genus is found in Queensland and in the Indian subcontinent (Waterhouse 1969b, p. 40; 1987b, p. 175; 2001, p. 149). The regularity of the commarginal wrinkles approaches that displayed by the sanguinolitid genus *Sueroa* Gonzalez (2006, p. 147) from Carboniferous to Early Permian beds of Patagonia. This genus shows distinct lateral and posterior grooves, and somewhat resembles *Myofossa* Waterhouse of Carboniferous and Early Permian age (Morris et al. 1991), as noted by Gonzalez (2006, p. 147).

Vacunella waterhousei (Dun, 1932)

Fig. 262C

1932 *Myonia waterhousei* Dun, p. 412, pl. 52, fig. 2, 3.

1965b *M. waterhousei* – Waterhouse, p. 850.

1966 *Vacunella* cf. *waterhousei* – Runnegar, text-fig. 1c.

1967 *V?. waterhousei* – Runnegar, p. 69, pl. 10, fig. 1.

1967 *V*. cf. *waterhousei* – Runnegar, p. 70, pl. 10, fig. 2-13.

1967 *Myonia? sulcata* Runnegar, p. 59, pl. 7, fig. 1-5, 10-14 (part, not fig. 6 = *Dundulomya parallela* (Dun)).

1969 *Australomya sulcata* – Runnegar, p. 285.

1969 *A*. cf. *waterhousei* – Runnegar, p. 288.

2001 *Vacunella sulcata* – Waterhouse, p. 150.

cf. 2003 *Myonia* sp. Archbold, Fig. 5.5.

Holotype: For *waterhousei* – AMF 6589 figured by Dun (1932, pl. 52, fig. 3) and Runnegar (1967, pl. 10, fig. 1) from Farley Formation, SD Waterhouse (1965b, p. 850). For *sulcata* – CPC 7509 from upper part of Lizzie Creek Volcanics, Mt Coolon, figured by Runnegar (1967, pl. 7, fig. 1, 14), OD.

Diagnosis: Inflated shells with deep lateral sulcus, no posterior carina.

Material: A broken small right valve (see Fig. 262C, p. 322) from UQL 3127, Tiverton Formation, zone not known.

Description: The specimen is small with the posterior broken away. It has an inconspicuous incurved umbo, moderately extended anterior, and shallow sulcus commencing below and behind the beak. The hinge is edentulous.

Resemblances: Runnegar (1969) included material identified as cf. *waterhousei* in his genus *Australomya*, but inexplicably made no mention of *waterhousei*. Remarkably, he included a figure of the lectotype (Runnegar 1967, pl. 10, fig. 1) in his synonymy as cf. *waterhousei*, which apparently meant that Runnegar considered that the lectotype could be compared to but was not identical with the species for which it was standard bearer. The suites of *sulcata* and *waterhousei* are very similar to each other, with moderately to well developed lateral sulcus, as in the holotype of *waterhousei* and paratype AMF 31084 of Dun (1932). Most specimens are elongate, but several specimens of cf. *waterhousei* in Runnegar (1967, pl. 10, fig. 3, 12-13, and less fig. 4, 5, 10, 11) have a higher shell, concave posterior dorsal margin and shallow if any sulcus. The specimen AMF 51058 from the Ravensfield Sandstone Member (Runnegar 1967, pl. 10, fig. 3) is especially high, showing an approach towards the Middle Permian species *curvata* Morris and *etheridgei* de Koninck.

The Tiverton fragment matches the anterior part of shells figured as *Myonia? sulcata* by Runnegar (1967), from the “Lower Bowen Volcanics”, Tiverton Formation, Allandale Formation, and *Eurydesma* beds near Rokeby, south of Warwick (eg. UQF 6622 with *Capillaria warwicki*). No material was reported by Runnegar (1967) at Homevale. Runnegar (1967) was doubtful about the generic position of the species, because it lacked a posterior carina, but of course *Myonia* also lacks a posterior umbonal carina. The type species *Myonia elongata* Dana (SD Fletcher 1932, p. 398) has a well rounded posterior umbonal slope, as figured by Dana (1849, pl. 5, fig. 4, 4a, b), Fletcher (1932, pl. 48, fig. 2), and Waterhouse (1988, pl. 8, fig. 1, 2, pl. 9, fig. 1). Species with a subdued posterior carina, such as *Pachydomus carinatus* Morris, 1845, that were confused with *elongata* by Runnegar (1967, pl. 5, fig. 12, 18), are now referred to *Myomedia* Waterhouse, 1969b. But Runnegar (1967) was also able to point out that specimens of *sulcata*, and it may be added, *waterhousei*, displayed a slight posterior gape, indicating *Vacunella* rather than *Myonia*. He therefore later referred the species to *Australomya* Runnegar, 1969, p. 285, a genus that is very close to *Vacunella*, but may be distinguished by the slender shell and gently rounded posterior umbonal ridge.

Vacunella waterhousei (syn. *sulcata*) is also close in most attributes involving shape and sulcus to *V.*

etheridgei (de Koninck, 1877, pl. 17, fig. 2), a species extensively discussed and illustrated by Runnegar (1967, p. 67). De Koninck's species is found in the Gebbie Subgroup and Ingelara Formation in Queensland and Branxton Subgroup of New South Wales, of mid-Permian age, younger than the Early Permian mid-Artinskian age assigned by Runnegar (1967). Runnegar (1967) has provided a number of figures that illustrate well some of the variation seen within both taxa, and *etheridgei* exhibits slightly more inflated shell and upturned shape, with concave dorsal outline.

The incomplete specimen figured as *Myonia* sp. from the Cranky Corner Sandstone in northern New South Wales by Archbold (2003, text-fig. 5.5) is clearly *Vacunella*, but has more upright stance and shallower lateral sulcus than usual for *sulcata* or *etheridgei*. It falls within the ambit of *Vacunella waterhousei* (Dun, 1932).

Genus ***Australomya*** Runnegar, 1969

Type species: *Australomya hillae* Runnegar, 1969, p. 287 from Wasp Head Formation (Asselian), south Sydney Basin, New South Wales.

Diagnosis: Slender shell without well defined posterior umbonal ridge, and very shallow if any pallial sinus and pallial gape.

Discussion: *Vacunella* is possibly senior synonym of *Australomya* Runnegar, 1969. The type species of *Australomya* is poorly known with regard to musculature and dentition, but is very like *Vacunella* in its banana-like upwardly curved shape and in having a posterior gape, slender because the species is slender, and therefore naturally with shallow pallial sinus. The change in outline of the posterior umbonal slope is more gentle than in other species now referred to *Vacunella*. Other species associated with *Australomya* by Runnegar (1969) appear to belong to *Vacunella* in all known aspects, including shape, posterior gape, pallial sinus and musculature (Waterhouse 2001, p. 150), involving *Vacunella? dawsonensis* of Runnegar (1967, pl. 11, fig. 1-8) and *V*. cf. *waterhousei* of Runnegar (1966, 1967, pl. 10, fig. 2-13), which belongs to *V. waterhousei* (Dun) together with *Myonia? sulcata* Runnegar. *Chaenomya* sp. of Dickins (1963, pl. 8, fig. 12-16) from the Fossil Cliff, Callytharra Formations and Nura Nura Member of Western Australia was included in *Australomya* by Runnegar (1969, p. 285), but is well inflated with substantial posterior gape, and approaches *Vacunella* sp. A of Runnegar (1967, pl. 11, fig. 9-11) from the Lizzie Creek Volcanic Group of the north Bowen Basin. Runnegar (1969, p. 285) also suggested that ?*Sanguinolites amatopensis* Thomas from Peru belonged to *Australomya*, a suggestion dismissed by Morris et al. (1991, p. 66), who referred the species to *Myofossa* Waterhouse, subgenus *Ragozinia.* Morris et al. (1991, p. 61) also disputed the claim by Runnegar (1974, p. 932) that *Australomya* approached the Carboniferous bivalve *Sedgwickia*. They showed that Runnegar had misinterpreted *Sedgwickia* and had confused with that genus specimens of *Myofossa* Waterhouse.

Runnegar (1969, p. 287) classed *Australomya* as Pachydominae in Family Pholadomyidae. The genus, if valid, is a close ally of *Vacunella*, and is not pachydomid. Runnegar & Newell (1974, Fig. 10) figured a "rare megadesmid" (sic) from a "Bone Springs Limestone" of the Guadalupe Mountains, New Mexico, United States, as *Australomya* new species, with no further description.

Australomya cf. ***hillae*** Runnegar, 1969

Fig. 251

cf. 1969 *Australomya hillae* Runnegar, p. 287, pl. 18, fig. 7, 8, 10-12, pl. 20, fig. 12, text-fig. 53Aa.

Holotype: ANU 17773 from Wasp Head Formation, south Sydney Basin, figured by Runnegar (1969, pl. 18, fig. 11), OD.

Diagnosis: Slender and elongate shells with very slight posterior gape and no well developed pallial sinus.

Material: A left valve from Tiverton Formation at UQL 3127. *Taeniothaerus subquadratus* Zone.

Dimensions in mm:

Length	Height	Width
47	22	9

Description: Valve elongate, slender for the genus, with orthocresent umbo placed at anterior third of shell length, no lateral sulcus, posterior umbonal ridge very weakly concave in outline, very slight posterior gape, adductor scars very faintly impressed, retractor scars and pallial line not clearly outlined.

Resemblances: This specimen appears to be an immature representative of *Australomya hillae* Runnegar, described from Early Permian (Asselian) beds at Wasp Head, south Sydney Basin. It agrees well with the specimen figured by

Fig. 251. *Australomya* cf. *hillae* Runnegar, left valve UQF 81563 from UQL 3127, x1.2.

Runnegar (1969, pl. 18, fig. 8). As shells of *Australomya* grew, the dorsal outline became upwardly concave like typical *Vacunella*, and the posterior gape became wider (see Runnegar 1969, pl. 18, fig. 10). Runnegar (1969, p. 287) described a well defined lateral sulcus in the diagnosis, but modified this by mentioning only an indistinct sulcus in the description. This might constitute a significant difference between the New South Wales material and the present specimen, which is not sulcate, but no sulcus is visible in the Harper's Hill specimen from the Allandale Formation, north Sydney Basin, figured by Runnegar (1969, pl. 20, fig. 12), and any sulcus is so shallow and faint that it is not shown in any of his other figures. This feature is therefore judged to be of either little significance, or at least permissibly variable in delineating the species. The one specimen included in his synonymy of *hillae* that clearly shows a sulcus was originally figured as *Myonia? sulcata* Runnegar (1967, pl. 7, fig. 10) from the Allandale Formation at Harper's Hill and transferred to *hillae* by Runnegar (1969). This specimen is clearly closer to *Vacunella waterhousei* than to *hillae*.

Vacunella? dawsonensis Runnegar, 1967 from the Flat Top Formation of the southeast Bowen Basin is somewhat similar to *hillae* in aspects of shape, but is more inflated with posterior gape and pallial sinus, and belongs to *Vacunella* ss.

Megaorder SOLENATA Dall, 1889

Order HIATELLIDA J. Carter in Carter et al. 2011

Superfamily **EDMONDIOIDEA** King, 1850

Family **PACHYDOMIDAE** Fischer, 1887

Diagnosis: Shell equivalve, inequilateral, ligament internal, tooth in right valve, minor or no posterior gape, small or no pallial sinus.

Discussion: Whereas Runnegar (1967) dissociated Pachydominae from Edmondiidae, Morris et al. (1991) and Waterhouse (1966b, 2001) linked the two, as in de Koninck (1877-78).

Taxonomy: Megadesmatidae Vokes, 1968 was proposed as a replacement for Pachydomidae Fischer, and did not mark any conceptual advance. Vokes merely made a name substitution, with no diagnosis or comparison: he accepted the validity of the concept family Pachydomidae, and "corrected" the name. The name change was made on the basis that Pachydomidae had been based on the genus *Pachydomus* Morris, 1845, which was shown to be an unnecessary substitute name for *Megadesmus* Sowerby, 1838, not *Megadesma* Bowdich. Extraordinarily, Vokes (1980, p. xxiv) admitted that Article 40 of the ICZN nomenclatural regulations stated "When, after 1960, a nominal type-genus is rejected as a junior synonym (objective or subjective), a family-group name based on it is *not* [italics here added] to be changed, but continues to be the valid name of the family-group taxon that contains both the senior and junior synonyms". Thus the proposal of Megadesmatidae knowingly defied the rules, presumably to express disagreement with the rule. ICZN (1999, p. 46) consolidated its earlier ruling, Article 40.1 stating that "When the name of a type genus of a nominal family-group taxon is considered to be a junior synonym of the name of another nominal genus, the family-group name is not to be replaced on that account alone". Article 40.2 allows an exemption for names proposed before 1961, but that does not apply in this case. It is therefore considered that Newell (1969) should not have consolidated the substitution by Vokes (1968, 1980), and that subsequent authors were misled in following Newell's lead. Claims of "preponderance of use" or "stability of nomenclature" do not have any merit in this case. Indeed, most articles since 1960 to 2008 have used Pachydomidae. The rules are clear, the proposal was made deliberately against the rules, and a mere thirty years of usage, by relatively few studies (perhaps a dozen or so, including some by the present author), should not provide a basis for upsetting the rules.

Vokes proposed the family as Megadesmatidae, which was emended to Megadesmidae by Newell (1969,

p. 823). Newell as followed by many authors cited Vokes 1967, but the correct date of publication was 1968, according to Vokes (1980, page opposite p. iii).

Subfamily **PACHYDOMINAE** Fischer, 1889

Diagnosis: Moderately large to small shells with small posterior gape and shallow pallial sinus, small to strong tooth in right valve, elongate shells, and characteristic pedal muscle scars.

Genus ***Protraxia*** new genus

Derivation: protraho – bring forward, drag out, Lat.

Type species: *Megadesmus gryphoides* (de Koninck, 1877, p. 210) from Farley Formation (Sakmarian) of Sydney Basin, here designated.

Diagnosis: Large shells with low to moderately high and enrolled anteriorly placed umbones, shell thin, right tooth variable, may become obsolete, posterior gape slight, anterior adductor scar connected to anterior retractor scar by isthmus.

Discussion: This new genus is very close in most attributes to the genus *Megadesmus* Sowerby, 1838, based on type species *Megadesmus globosus* Sowerby, 1838 from the Allandale Formation (Asselian), Sydney Basin, SD Woodward (1856, p. 302). The genus *Cleobis* Dana, 1847, type species *Cleobis grandis* Dana, 1847, p. 154 from "Illawarra", Broughton Formation (Wordian), south Sydney Basin, New South Wales, SD Newell 1956, p. 10, is synonymized with *Megadesmus*, although Runnegar (1967), Waterhouse (1969b) and Waterhouse & Jell (1983) treated *Cleobis* as a subgenus of *Megadesmus*. There are differences between the two type species, notably the comparatively thin shell, lack of coarse rugged growth-lines and usually weaker dentition found in *Cleobis grandis* as compared with *Megadesmus globosus*, which helps explain why Newell (1956) defended the validity of the genus, but the overall shape is very close. The accessory anterior muscle scars are significant in pointing to interrelationships between species and genera. In the species assigned to the new genus, such as *nobilissimus* and *gryphoides*, the anterior adductor is joined posteriorly to the anterior retractor scar by an isthmus (see Fig. 252A herein, and Runnegar 1965, Fig. 1d, e, pl. 14, fig. 7; Waterhouse 1969b, text-fig. 7A, 17). In distinction, in *Cleobis grandis* (Runnegar 1965, Fig. 1a) and so-called *Globicarina grossula* Waterhouse, a synonym (Waterhouse 1969b, p. 53, text-fig. 7, 29), a small subrounded anterior pedal retractor scar is attached to the upper posterior edge of the anterior adductor scar, and is separated by a small gap from the small anterior retractor impression: there is no isthmus. The anterior muscle impressions of type *Megadesmus* are seldom displayed, except for one specimen, illustrated by Runnegar (1965, Fig. 1f), to show an attached pedal protractor scar separated from the anterior pedal retractor, and so like the musculature of type *Cleobis*. There is thus a morphological distinction between the species *nobilissimus* and *gryphoides* from the type species of *Megadesmus* and *Cleobis*. *Cleobis robusta* Laseron (1910, pl. 16, fig. 1) from Burrier in the south Sydney Basin has an obscure isthmus in the holotype, according to Waterhouse (1969b, p. 47) and *Megadesmus* (*Cleobis*) *deflatus* Waterhouse in Waterhouse & Jell (1983, p. 250, pl. 5, fig. 1, 6) from the Glendoo Sandstone Member of the north Bowen Basin also has a pedal isthmus, as in the new genus. Species referred to *Astartila*? by Dickins (1957, 1963) conform closely in shape and ornament to the limits displayed by east Australian species of the new genus.

A further question remains, concerning the relationship to *Vacunella* Waterhouse, which has a similar anterior isthmus, but has posterior sinus and gape, and apparently developed independently (Gonzalez 2006).

Protraxia gryphoides (de Koninck, 1877)

Fig. 252 – 254A, B, C

1877 *Cardiomorpha gryphoides* de Koninck, p. 210, pl. 18, fig. 4.
1888 *C. gryphoides* – Johnston, pl. 15, fig. 1.
1907 *C. gryphoides* – David, pl. 35, fig. 3.
1924 *C.* cf. *gryphoides* – Richards & Bryan, pl. 19, fig. 6.
?1957 *Astartila*? *obscura* Dickins, p. 25, pl. 3, fig. 1-6.
1964b *Astartila* ? cf. *gryphoides* – Dickins in Hill & Woods, pl. P10, fig. 6a, b.
1965 *Megadesmus (Megadesmus) gryphoides* – Runnegar, p. 239, pl. 13, fig. 1-10, 12, 13.

1967 *M. (Megadesmus) gryphoides* – Runnegar, pl. 3, fig. 14, 15.

1969b *M. gryphoides* – Waterhouse, p. 44, pl. 9, fig. 1, 2, text-fig. 19B, C.

1969b *Globicarina* sp. nov. Waterhouse, pl. 13, fig. 1, 4.

1972 *M. gryphoides* – Hill, Playford & Woods, pl. P10, fig. 6a, b.

1972 *M. pristinus* Runnegar, p. 310, pl. 1, fig. 1-6.

1974 *M. gryphoides* – Runnegar & Newell, Fig. 11E.

1977 *M. pristinus* – Webb, p. 56, pl. 2, fig. 5, 6.

1986 *Megadesmus* sp. Parfrey, p. 64, Fig. 3.5a, b.

1988 *M. gryphoides* – Waterhouse, pl. 20, fig. 2.

1992a *M. pristinus* – Clarke, p. 27, Fig. 15A-F.

?1993 *Astartila*? *obscura* – Dickins & Skwarko, pl. 48, fig. 27.

Neotype: AMF 44021 from upper part of Farley Formation (Sterlitamakian), Hunter Valley, selected by Runnegar (1965, p. 239). Holotype for *pristinus* – UNEF 12533, now AMF 77641, from "top of Seaham Formation", Cranky Corner, (but probably younger – ?Asselian rather than restricted Seaham Formation, as discussed on p. 30), figured by Runnegar (1972, pl. 1, fig. 5, 6), OD. Holotype for *Astartila*? *obscura* – CPC 2215, top Lyons Group (late Asselian), Carnarvon Basin, figured by Dickins (1957, pl. 3, fig. 2-5) and Dickins & Skwarko (1993, pl. 48, fig. 27), OD.

Diagnosis: Umbones highly enrolled, with or without a weak posterior ridge.

Material: Tiverton specimens from UQL 1622, 1624, 2622, 3127, T3 and LT3. *Bookeria geniculata* and *Taeniothaerus subquadratus* Zones.

Dimensions in mm: right valves

UQF	Length	Height	Width
20899	63	63	30
20900	60	60	22.5

Description: Shells equivalve, umbones prominent and highly enrolled, placed near mid-length, and procresent to orthocresent, shallow depression anteriorly near the ventral margin in about half the specimens, weak posterior umbonal ridge in several specimens, and ornament of commarginal growth ribs, about five per 5mm, as well as low undulations spaced further apart. Very slight posterior gape present in at least some specimens. Hinge obscured, most specimens not showing muscle scars, but two specimens including UQF 20900 have anterior adductor scar and large elongate posterior scar. Another specimen shows the adductor scar joined anteriorly by a short isthmus, as in *Protraxia nobilissimus* (see Waterhouse 1969b, text-fig. 7A), and a pedal scar sited dorsally, suggestive of the arrangement in *Megadesmus* (formerly *Cleobis*) *grandis* (see Waterhouse 1969b, text-fig. 7E). Pallial line faintly impressed, with a very shallow sinus; well spaced mantle pits also visible. The shell is at least 2mm thick.

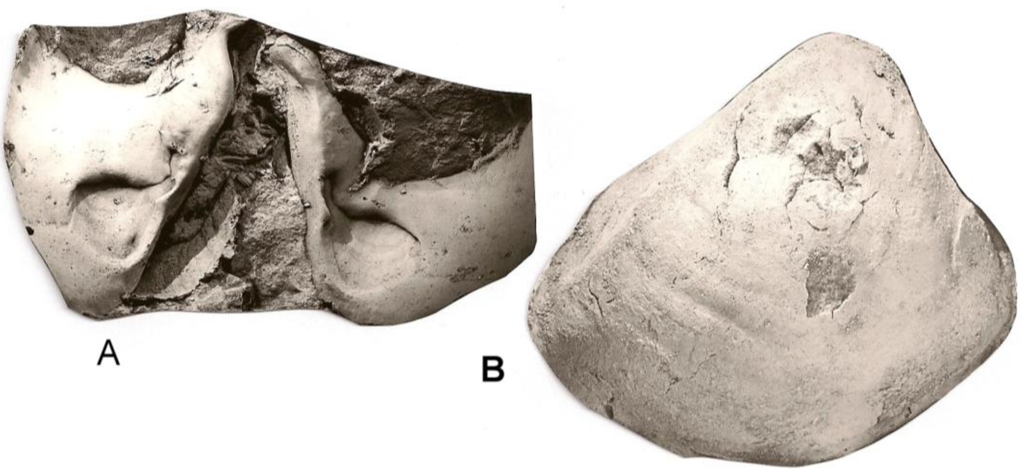


Fig. 252. *Protraxia gryphoides* (de Koninck). A, latex cast of anterior valves, showing deep adductor impressions and pedal scars attached by an isthmus projecting from the adductor scar, UQF 81558 from UQL 3127, x1.5. B, right valve internal mould UQF 81559 from UQL 1624, x1.

Resemblances: These specimens are close in size and shape to *Protraxia gryphoides* (de Koninck) from the Ravensfield Sandstone Member of the north Sydney Basin, and reported also from the Marine Mudstone of Latrobe, Tasmania. According to Waterhouse (1969b, p. 45), the New South Wales shells lack a posterior umbonal ridge, apart from a specimen figured by David (1907) from the Farley Formation, though one is clearly developed in a Ravensfield specimen figured by Waterhouse (1969b, pl. 13, fig. 1). A number of Tiverton specimens have a subdued posterior umbonal ridge and the posterior face may be weakly flattened, or gently convex. The presence of such a ridge was thought by Waterhouse (1969b) to characterize a separate cluster of species as "*Globicarina*", but this is now discounted. The species *gryphoides* is close in outline and inflation to the taxon named *Megadesmus pristinus* Runnegar (1972, pl. 1, fig. 1-6) and the original figures include specimens closely approaching de Koninck's species (cf. Runnegar 1972, pl. 1, fig. 3-5). The only difference claimed to distinguish the two taxa was the stated presence of "an obvious concavity near the ventral margin" in *pristinus*, but the figures, reproduced at x0.8 rather than x1 as stated in the text, show no such obvious concavity, and the material described by Runnegar (1972), now kept at the Australian Museum, Sydney, show only a very shallow if any depression anteriorly. A shallow depression is also to be seen in Ravensfield *P. gryphoides* (see Waterhouse 1969b, pl. 13, fig. 4, and possibly pl. 9, fig. 1). The species *pristinus* was initially described from the "upper Seaham Formation" of Cranky Corner, northern New South Wales, but data provided by Stevenson (2003) and Balme & Foster (2003) indicates that Runnegar's interpretation of stratigraphy at Cranky Corner requires elaboration. Runnegar recorded various "Permian key fossils" from what is established as Late Carboniferous on the basis of radiometric dating (Claoué-Long & Korsch 2003). The taxon *pristinus* was also reported from the Youlambie Conglomerate in the Yarrol Basin (Webb 1977), and figured from the Tasmanites Shale, Spreyton Formation, Swifts Jetty Sandstone etc. in Tasmania by Clarke (1992a, Fig. 15A-F). *Megadesmus* sp. figured by Parfrey (1986, Fig. 5a, b) from the Camboon Andesite near Biloela, southeast Bowen Basin, is possibly related. Given the degree of variability shown by suites of *gryphoides* from the Ravensfield Sandstone Member, it is judged that *pristinus* and *gryphoides* belonged to one long-lived species.

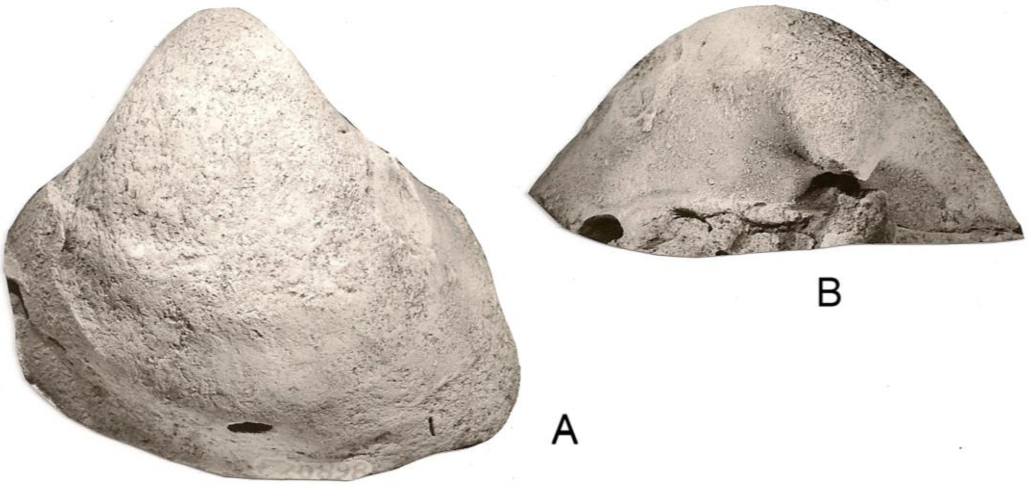


Fig. 253. *Protraxia gryphoides* (de Koninck). A, B, left valve, lateral and dorsal aspects, UQF 20898 from UQL 1622, x1.

There is considerable similarity between the species *gryphoides* and *Astartila? obscura* Dickins (1957, pl. 3, fig. 1-6) from the top of the Lyons Group in the Callytharra Basin, Western Australia, also figured in Dickins & Skwarko (1993, pl. 48, fig. 27). Dickins' species is a very high shell with prominent umbo and attenuated posterior. The various species assigned to *Astartila* by Dickins (1956, 1957, 1963, Dickins & Skwarko 1993), including *fletcheri* Dickins, 1956, *condoni* Dickins, 1957, *blatchfordi* Hosking, 1931 and *tumida* Dickins, 1963, all appear to belong to *Protraxia* or *Megadesmus*, and there is no evidence to support placement with *Astartila*, which differs considerably in shape, ornament, nature of escutcheon and lunule, and aspects of hinge or musculature. But the detailed nature of the anterior musculature is not known for the west Australian species.

Protraxia nobilissimus (de Koninck, 1876)

Fig. 254D

1876-7 *Edmondia nobilissimus* de Koninck, p. 269, pl. 20, fig. 2, 2a.

1876-7 *E. intermedia* [not de Koninck] – de Koninck, p. 270, pl. 20, fig. 4.

1907 *Edmondia*? *nobilissima* – David, pl. 35, fig. 2.

1965 *Megadesmus* (*Megadesmus*) *nobilissimus* – Runnegar, p. 237, pl. 13, fig. 14, 16-18, pl. 14, fig. 1, 2, 5, 7, 13 (part, not pl. 13, fig. 11, 15, pl. 14, fig. 3, 4, 6, 8-12, 15 = *Megadesmus ponderosus* Waterhouse, 2010a).

1969b *M. nobilissimus* – Waterhouse, p. 43, pl. 6, fig. 2, 5, 6, pl. 7, fig. 1, 3 (not 2 as in caption), text-fig. 7A, 8A, 17, 19A (part, not pl. 10, fig. 3, pl. 22, fig. 3, pl. 23, fig. 1-3, text-fig. 18 = *ponderosus* Waterhouse).

Neotype: AMF 39557 from Ravensfield Sandstone, Farley Formation, Sydney Basin, figured by Waterhouse (1969b, pl. 6, fig. 5), SD Waterhouse (1965b, p. 850).

Diagnosis: Elongate with subdued umbones, low ornament.

Material: A Tiverton left valve from UQL 4514. *Svalbardia armstrongi* Subzone.

Description: Specimen small, subelongate with anteriorly placed inconspicuous umbo, and low commarginal ribs separated by broad interspaces, shell thin and no sulcus.

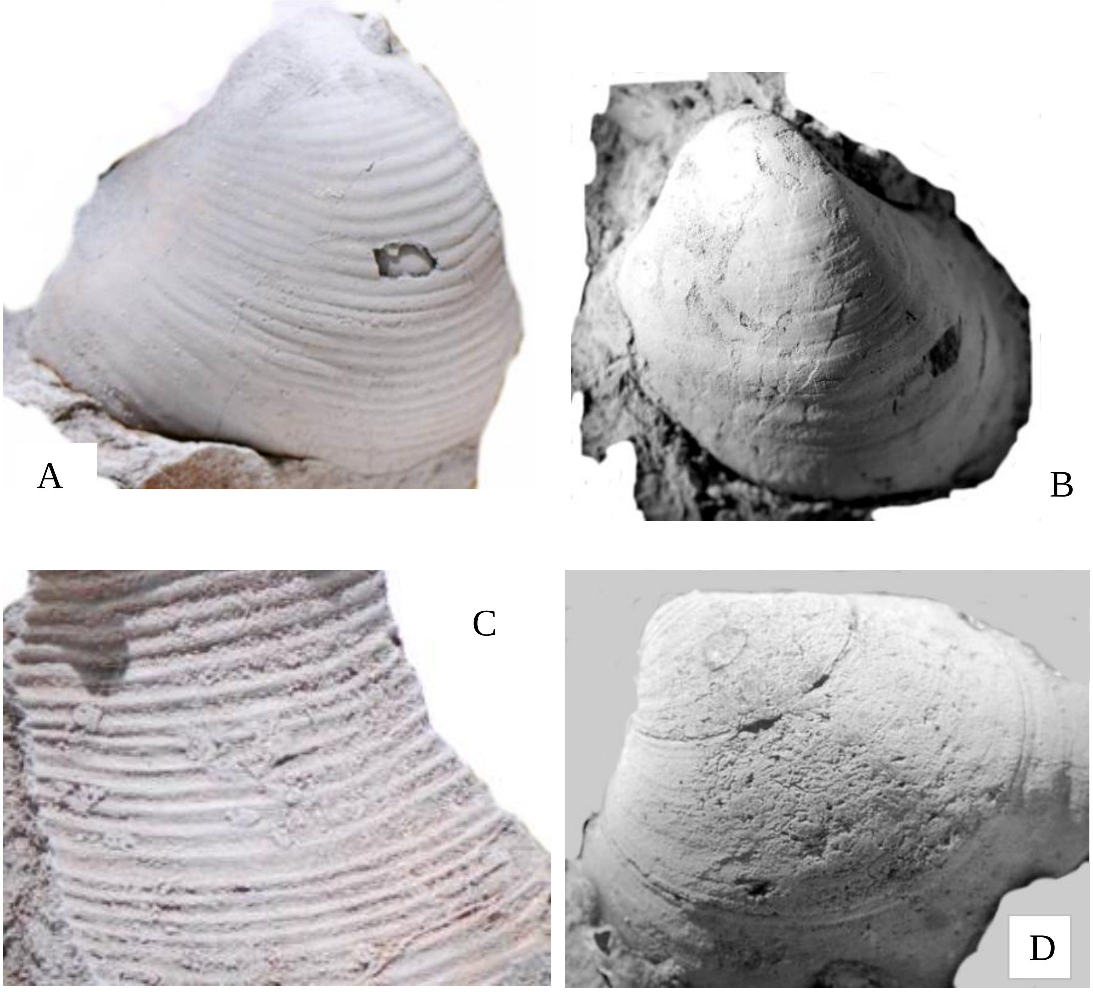


Fig. 254. A – C, *Protraxia gryphoides* (de Koninck). A, left valve UQF 81570 from UQL 3127, x2. B, left valve UQF 81560 from UQL 3127, x1. C, detail of ornament on small specimen UQF 81572 from UQL 3127, x1.5. D, *Protraxia nobilissimus* (de Koninck), latex cast of left valve UQF 81568 from UQL 4514, x1.5.

Resemblances: The specimen is identical in shape and ornament with *Protraxia nobilissimus* (de Koninck), best known from the Farley Formation and Ravensfield Sandstone Member of the Sydney Basin. The specimen described as *Astartila cytherea* by Etheridge (1892, pl. 14, fig. 3, 4) from the Bowen River Coal Field might be allied, but has a more prominent umbo: its stratigraphic position is not certain. A number of specimens from the “basal mollusc fauna” of the South Curra Limestone at Chatsworth, Gympie, had been assigned to the species by Runnegar (1965) as accepted by Waterhouse (1969b) but the umbones are slightly more extended, and differences suggest the need for reappraisal, Waterhouse & Balfe (1987, pl. 2, fig. 1, 2) assigning the specimens to *Megadesmus* sp., redescribed as *Megadesmus ponderosus* Waterhouse (2010a, p. 108, Fig. 48, 49), with many additional figures provided as *Megadesmus nobilissimus* not de Koninck by Runnegar (1965, 1968) and Runnegar & Ferguson (1969, pl. 1, fig. 1-3). The species comes from the basal South Curra Limestone of lower Changhsingian age at Gympie, southeast Queensland, and is only moderately close to the present form, being well inflated with thick shell and swollen umbones and massive tooth in the right valve, aspects shared with some *Megadesmus*.

Notomya trigonalis Johnston (1887, p. 14; 1888, pl. 19, fig. 2) is also comparable, as noted by Runnegar (1965), although the type specimen, refigured in Waterhouse (1969b, pl. 7, fig. 2, 4), has slightly different umbo and anterior. Some of the topotype specimens assigned to *nobilissimus* are less elongate than the holotype or present Tiverton specimen, as figured in Waterhouse (1969b, pl. 6, fig. 6, pl. 7, fig. 1) and thus come closer in that regard to *gryphoides*, but are less inflated with less incurved umbones; whether they represent a separate taxon is yet to be clarified. A closely allied species was described as *Astartila*? *tumida* Dickins (1963, pl. 4, fig. 4-10; Dickins & Skwarko 1993, pl. 48, fig. 28) from the Fossil Cliff Formation of the Irwin River area, Perth Basin, Western Australia. It differs slightly in having more elevated umbones.

Subfamily **ASTARTILINAE** Waterhouse, 1969b

Diagnosis: Variable in shape and carination, lunule or escutcheon poorly defined or absent, no pedal or posterior gape or pallial sinus, no accessory a and b scars.

Discussion: *Astartila* Dana and allies of Subfamily Astartilinae are closely related to Plesiocyprinellinae Simoes, Marques, Cruz de Mello & Anelli, 1997. This subfamily, better treated as a tribe within Astartilinae, involves shells with a triangular outline with posterior carina, large right tooth and left valve boss “raised to function as a second tooth” (Runnegar & Newell 1971, p. 35) in *Casterella* and *Terrazia*. There is typically no lunule or escutcheon and no accessory a and b scars, and therefore the members of the group come close to Astartilinae rather than Pachydominae, being distinguished principally by the more carinate shell and prominent umbones. The group is restricted to South America (Mello & Simoes 1996, Waterhouse 2001, p. 147).

Tribe **ASTARTILINI** Waterhouse, 1969b

[Nom. transl. hic ex Astartilinae Waterhouse, p. 55]

Diagnosis: Small subrounded shells with subdued umbones, no posterior carina, right tooth and often left valve tooth-like prominence, or with denticulate margins, pallial line entire, distinctive accessory muscle scars. Escutcheon may be weakly defined, and lunule weak or absent.

Discussion: Astartilini Waterhouse, 1969b incorporates genera with subrounded outline, which may have left as well as right tooth in the hinge (Waterhouse 2001, p. 146), entire pallial line, and characterized by distinctive anterior accessory musculature. There is no separate anterior protractor, although the anterior adductor may show a posterior division, and there are small separate anterior and umbonal retractor scars. The protractor-retractor complex which forms an isthmus in *Protraxia* extending from the posterior dorsal margin of the anterior adductor scar is absent from *Astartila*. There is no pedal or posterior gape, and no tiny muscle insertion points over the interior, unlike *Megadesmus* or *Pyramus* of Pachydomidae.

Pleurikodonta Runnegar from the Permian of Australia and New Zealand belongs to the same tribe.

Genus ***Astartila*** Dana, 1847

Type species: *Astartila intrepida* Dana, 1847, p. 155 from “Illawarra”, Broughton Formation (Wordian), south Sydney Basin, New South Wales, SD Stolickza (1871, p. xix).

Diagnosis: Small shells with procresecent umbones and no posterior ridge, weakly developed escutcheon, weak if any lunule. Right cardinal tooth well developed, often left valve tooth or margin to right tooth also prominent, at least in Middle Permian species (Waterhouse 1988, 2001). Anterior pedal retractor separate from adductor scar, anterior protractor apparently conjoined with anterior adductor, posterior adductor scar, pallial line entire.

***Astartila*? sp.**

Fig. 255

Material: Two Tiverton specimens with valves conjoined preserved as internal and external moulds, from L. G. Cutler collection, “locality C”, at Queensland Museum. *Taeniothaerus subquadratus* Zone.

Dimensions in mm: valves conjoined

Length	Height	Width	
13.8	12	6.6	internal mould
15	12.5	8	external mould

Description: Small equivalve, umbonal angle 85°, procresent, slightly tapered posteriorly, no posterior umbonal ridge nor sulcus, deep escutcheon-like depression on internal mould, anterior umbonal ridge and very narrow depression close to hinge, suggestive of possible shallow lunule, low ragged growth increments. Ventral margin not crenulate. Right valve tooth, left valve hinge elevated each side to form socket with slight indentation of right valve hinge. Anterior adductor scar suboval, impressed, anterior retractor scar elongate, slender, sited close to hinge, small umbonal pedal scar. No distinct protractor scar or division of anterior adductor. Posterior adductor scar elongately oval, placed close to commissure, almost in touch with posterior retractor. Pallial line entire. One of the specimens is on the same block as “*Anidanthus springurensis*” (now *Anidanthia paucicostata*) figured by Waterhouse (1968b, pl. fig. 1, 4, 6). It is 13.5mm long and shows the anterior adductor and umbonal retractor scar with small scar in front.

Resemblances: *Astartila* comes from faunas of mostly Middle Permian age (Fletcher 1929a), so that these Tiverton specimens are exceptional in age. They are close to type *Astartila* in shape, and differ from Middle Permian species in having a more prominent right valve tooth and lacking a prominent left valve tooth in front of the right tooth. There are also subtle differences in muscle impressions, the anterior retractor being more slender and elongate, and the posterior retractor is separate and not attached to the posterior adductor. No anterior protractor is differentiated. The separate posterior pedal retractor is moderately like that of *Notomya* M'Coy (see Waterhouse 1969b, text-fig. 24) and *Pyramus* Dana (Waterhouse 1969b, text-fig. 22, 23), *Myonia* Dana (Waterhouse 1969b, text-fig. 10) and *Megadesmus* Sowerby = *Cleobis* Dana (Waterhouse 1969b, text-fig. 7G). The anterior pedal scar is unique, but very close to that of type *Astartila*, and moderately close to the pedal scar in *Pyramus* and *Notomya* (the two regarded as synonymous). The material lacks the isthmus between the anterior pedal scar and anterior adductor scar of species that are ascribed to *Protraxia*.

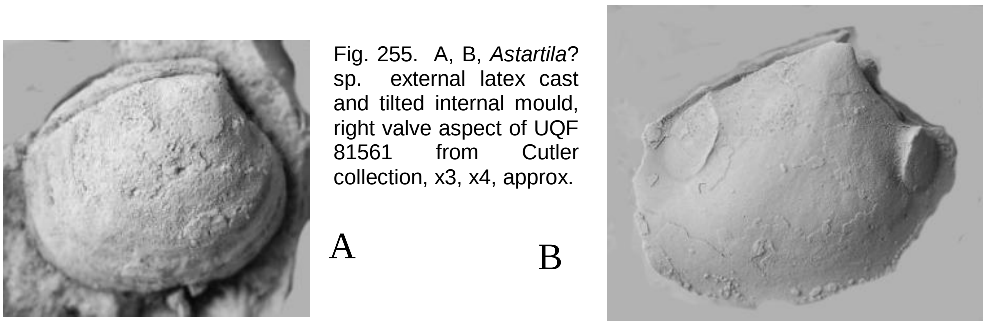


Fig. 255. A, B, *Astartila*? sp. external latex cast and tilted internal mould, right valve aspect of UQF 81561 from Cutler collection, x3, x4, approx.

Wass (1972) presented an account of the musculature in a possible Early Permian *Astartila* in which it was claimed that musculature varied and signified little, in accord with Runnegar (1965, 1966), although neither provided any documentary proof of variability in the form of detailed and specific description, citation of specimens, or photographs. Wass (1972) described a Farley specimen SUP 11608 that was said to show a pedal retractor and pedal protractor, but these scars were not labelled, so that his interpretation cannot be verified from his illustration. Wass (1972) remained uncertain whether his specimen belonged to *Astartila* or *Megadesmus*, and examination of the shell shape, carination, posterior musculature and nature of the pallial line is needed to resolve such questions. Although fossil collections of Sydney University have been deposited at the Australian Museum, the Wass material is not kept at the museum, and its whereabouts are not known.

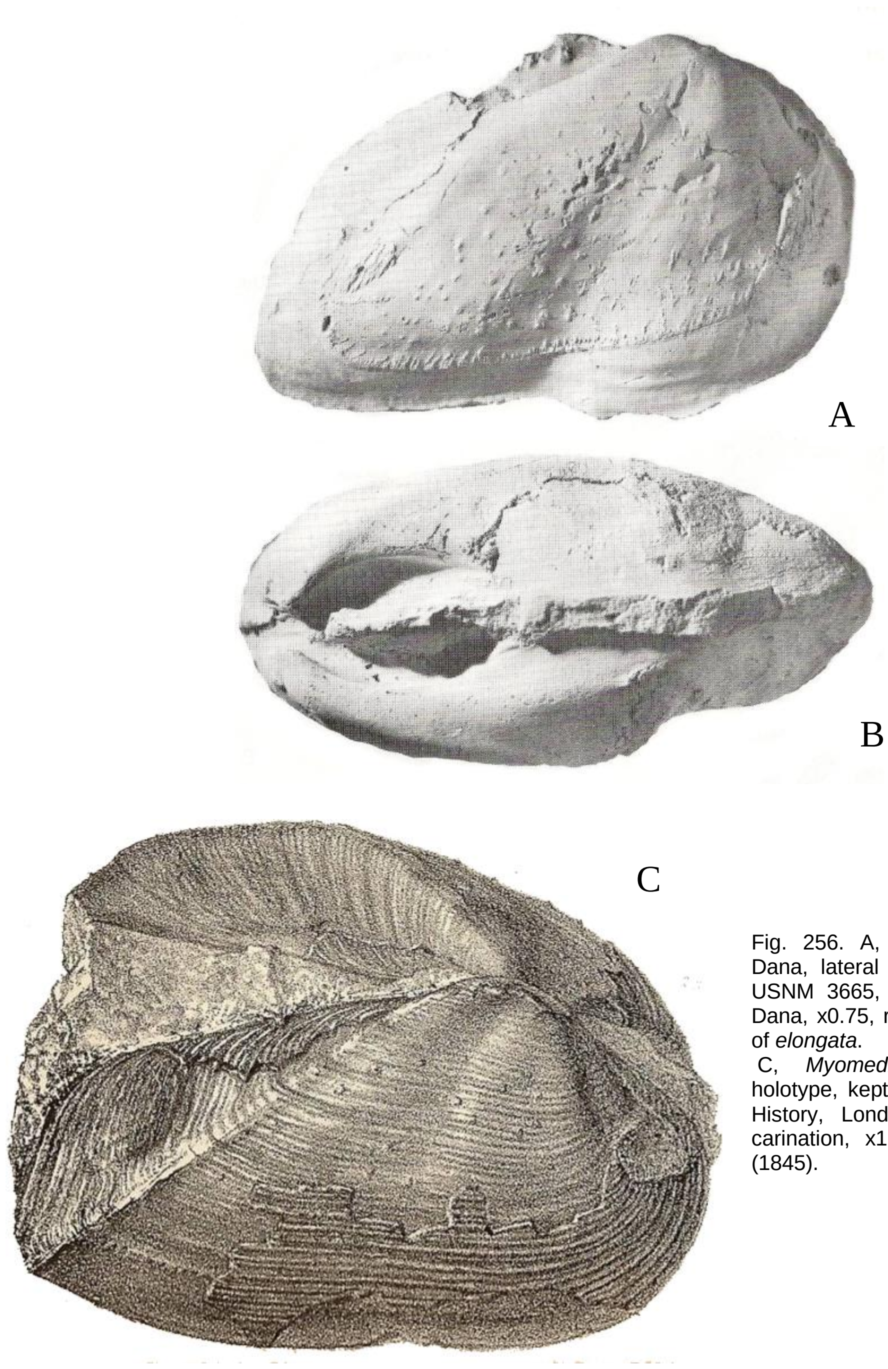


Fig. 256. A, B, *Myonia elongata* Dana, lateral and dorsal aspects of USNM 3665, lectotype of *M. valida* Dana, x0.75, regarded as a synonym of *elongata*.
C, *Myomedia carinata* (Morris), holotype, kept at Museum of Natural History, London, showing posterior carination, x1 approx. From Morris (1845).

Family **EDMONDIIDAE** King, 1850

Diagnosis: Pholadomyid shells with no posterior gape, no hinge teeth, hinge plate or septum present or poorly developed.

Subfamily **MYONIINAE** Waterhouse (1969b), 1987b, 2001

Diagnosis: Large upright shells without internal plate other than vestigal, accessory muscle scars more numerous than in Edmondiinae.

Discussion: In proposing the family group based on *Myonia*, as a tribe Myoniides, Waterhouse (1969b, p. 28) provided a diagnosis and extensive overview of various genera, but also expressed a tentativeness that goes against the ICZN code of 1999. His definition was "*Myonia* and allies……….… belong to a distinct tribe [within Edmondiinae], distinguished from *Edmondia* by the large size, heavy nymphs, presence of an escutcheon, consistent ornament of granular costae and feeble development of the inner ligament pit, and absence of a ridge behind the adductor…. The anterior musculature …differ [s] in the two tribes.” Waterhouse (1969b, table 2, pp. 26, 27) tabulated the differences between various genera in Myoniides, Pachydominae and Astartilinae, illustrated the material with photographs and comparative diagrams, and pp. 24, 25 discussed and compared various genera within Edmondiinae, and Table 1 (p. 21) provided an evolutionary table, showing two tribes as Edmondiides and Myoniides. However Waterhouse (1969b) also allowed a degree of tentativeness – *Myonia* and allies may possibly belong to a distinct tribe, and stated that more information is needed. Whilst of course there is always justification for scientific caution, the analysis lacked the certainty deemed necessary for a proper proposal (ICZN 1999, Article 15.1). Campbell (1965) in proposing the genus *Hoskingia* made the same mis-step, as discussed in Waterhouse (2010a, p. 81).

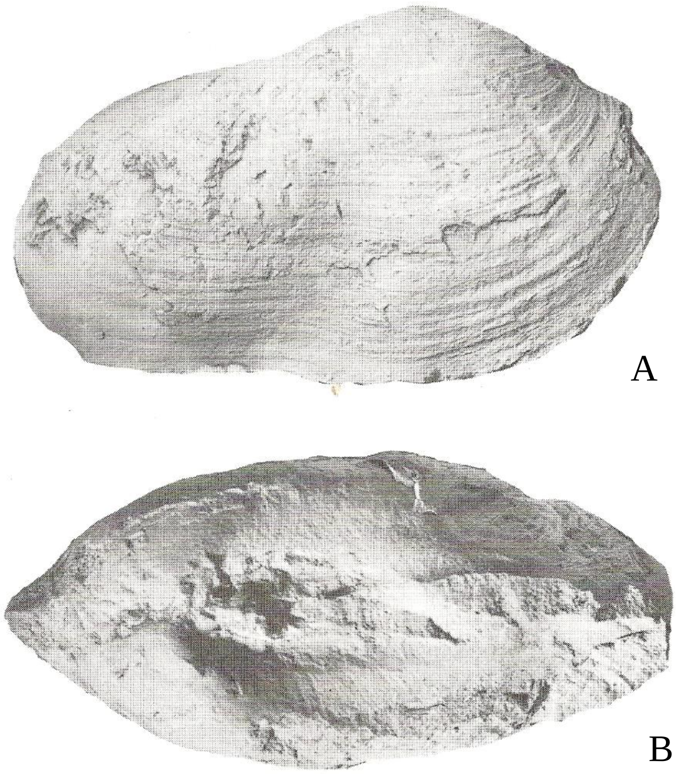


Fig. 257. *Myonia elongata* Dana. A, B, lateral and dorsal views of lectotype USNM 3584 x 0.7, from Black Head, south Sydney Basin. Note the lack of a carinate posterior umbonal ridge, the presence of which was deemed crucial for recognition of the genus by (Runnegar (1967) and for recognition of the family Myoniidae by Skarlato & Starobogatov (1979).

Nonetheless, application of the ICZN rule requires a degree of discernment to determine if it is indeed applicable on any other than an entirely superficial level. Arguably, although Waterhouse noted a degree of uncertainty, he nonetheless proceeded to set aside that caution and virtually overrule his caution, in providing such a detailed analysis, documentation, and illustration. That may be contrasted with a Russian study, that indicated no uncertainty whatsoever, nor discussion, nor illustrations, ignored most of the literature, and offered a false diagnosis of the same group, which failed to offer any specific discrimination for the group.

With no reference to the studies by Waterhouse (1965c, d, 1966b, 1969a, b), Skarlato & Starobogatov (1979) proposed Family Myoniidae, in an extensive but extremely porous review of bivalves. On p. 22, Myoniidae was placed as a member of Edmondioidea, and on p. 32, they explained the proposal: “ About this genus *Myonia* Dana, 1847 (and subgenus *Pachymyonia* Dun, 1932), they are sharply distinguished from Megadesmatidae [ie. Pachydomidae – inserted – see Waterhouse 2010a, pp. 106, 107] – and should be separated independently as

Family Myoniidae as a link between Megadesmatidae and Edmondiidae. The diagnosis for Myoniidae is: shell elongate, low orthogyrous umbones, moderate anterior. Posterior margin obliquely truncated, with weak sulcus in front, carina crest developed, strongly developed deep pits by which the growing mantle penetrates the thickness of the valves, ligament channel appears degenerate, ligament external, pallial mantle". (See also Boss & Johnston 1985, p. 51). No differences between Myoniidae and Edmondiidae or "Megadesmatidae" were specified, and nor was it specified why the group was intermediate between Edmondiidae and Megadesmidae. The definition would remove *Myonia* from Myoniidae. The account shows considerable unawareness of the studies by Dana (1847, 1849), Dun (1932), Fletcher (1932) or Waterhouse (1969b), leading to a misunderstanding of the nature of *Myonia*, passing in turn to a misrepresentation of Myoniidae, and no discrimination from Edmondiidae or Pachydomidae, meaning the differences between the three were not provided, nor could be correctly inferred. There are possible but spurious distinctions for Myoniidae contained in their diagnosis. They concern the carinal crest, allegedly present in *Myonia*, following Runnegar (1967), but in fact absent, and absent from *Edmondia* or *Megadesmus*. And there is the possibility of deep pits in the shell. But such pits are also present in Pachydomidae, and other groups (see Runnegar 1966 Fig. 1A, E, G, H), relevant to *Vacunella, Chaenomya, Myonia* and *Protraxia*. There are several errors in the so-called diagnosis by Skarlato & Starobogatov. Even in their brief discussion, it is clear that they were unfamiliar with the actual fossils, so that they misconceived the group. They were unable to differentiate the group from either Edmondiidae or Pachydomidae, and did not specify the differences that justified the family. As the 1999 Code, Recommendation 13A specifies, there should be "a summary of the characters that differentiate the new nominal taxon from related or similar taxa." The prime difficulty with the Russian proposal is that whereas that of Waterhouse (1969b) indicated a need for further study, which was surely realistic from a scientific standpoint, but otherwise provided a succinct and accurate diagnosis and elaborated differences by which the group could be distinguished from Edmondiidae and Pachydomidae, the Skarlato-Starobogatov proposal failed to provide any distinctions from Edmondiidae or Pachydomidae. The fact that their diagnosis was flawed is of less significance, because distinctions should become more refined and often corrected through time. It would have sufficed to justify Myoniidae Skarlato-Starobogatov by simply resurrecting and validating the Waterhouse diagnosis. Instead, and unaware of that study and all the preceeding works other than the misrepresentation of *Myonia* by Runnegar, they concocted a diagnosis – and concocted is appropriate – and did not show how to distinguish the family group. Such a difficulty need not in all cases rest on word-specific failure, because studies may involve a broad overview in which distinctions, though not explicitly stated, are implicit in the overview. But that defence cannot be sustained in this example. No impressive overview was provided, and the explicit diagnosis related only vaguely and imperfectly to the taxa in question. Thus the proposals by both sets of authors failed to fully meet the requirements stipulated for adequate proposal of a new family group name, and of the two, that of Skarlato & Starobogatov (1979) must be deemed useless and at least arguably invalid, whereas the discussion by Waterhouse (1969b) was useful, but invalid.

To retrieve the situation, it seems advisable to enquire the nature of subsequent usage, because ICZN (1999, Article 15.1) included the phrase, " is not thereby made available". So what does make the name available? Presumably a firm proposal, and recognisably accurate diagnosis and specified distinctions. Neither Skarlato nor Starobogatov have added any further information or clarification, to amend their diagnosis and render it applicable. On the other hand several publications have removed the uncertainty expressed in the original Waterhouse discussion. Waterhouse (1987b, p. 170) used the heading Myoniinae new subfamily, building on Waterhouse (1969b), sweeping away the uncertainty, and in 1988, p. 180 referred to Myoniinae Waterhouse, 1987. In 2001 Waterhouse (p. 143) offered a succinct diagnosis and comparison, justifiably incomplete because it built on earlier explicit work. The genera within the Myoniinae involve large upright subrectangular shells, close to Edmondiinae in shape and escutcheon, but larger, with allied hinge lacking teeth. There is no large internal plate, unlike many but not all *Edmondia*, and accessory muscles are more numerous than any known for any Edmondiinae. Pachydomidae (as Megadesmidae) were discussed and compared further on p. 144. The wide-ranging discussion on the morphologies, historical summary, and provision of numerous references with illustrations allow the compass of the subfamily to be comprehended, without the uncertainty that clouded the initial proposal of a family-group name, and with the provision of adequate morphological attributes, and distinctions from closely related family groups. To that extent, the family group has (at last!) been defined and discussed in a manner meeting requirements of the International Code of Zoological Nomenclature.

There are, to my mind, further considerations over the authorship of family groups, and indeed taxonomy for genera which are not fully codified, and therefore depend on the discretion of the subsequent or “principal revisor”. There is room in taxonomy for courtesy, which may involve a degree of flexibility over application of rules, in order to ensure that priority is where possible given credit. This has the merit of putting a stop to “claim-jumping”, in other words using regulations to supplant the originator’s name with one’s own name. I have often sought to apply this principal. (See Eurydesmidae herein). Of course Skarlato and Starobogotov were certainly not claim-jumping, and although their approach may be interpreted by some as cavalier and far from thorough, I would have attributed the name to them had there been no prior claim, even though their proposal did not conform with the requisite need to discriminate the newly proposed groups from other family groups. But it would have been by courtesy.

Genus ***Pachymyonia*** Dun, 1932

Type species: *Maeonia morrisii* Etheridge, 1919, p. 186 from Allandale Formation (Asselian), north Sydney Basin, New South Wales, OD.

Diagnosis: Moderately large shells with very strong posterior umbonal ridge.

Discussion: This genus has been recognized as valid by Dickins (1963) and Muromseva (1984) but denied by Runnegar (eg. 1974). Runnegar (1967) misinterpreted *Myonia*, claiming that it was carinate, which in turn justified synonymizing *Pachymyonia* with *Myonia*. The type species of *Myonia, M. elongata* Dana, 1847 lacks a posterior carina, as demonstrated by the type and allied specimens, which have been figured by Dana (1849) and refigured by Waterhouse (1988), and further figured herein (Fig. 256A, B). Runnegar (1967) had confused a weakly carinate species called *M. carinata* Morris with *elongata* (Runnegar 1967, pl. 5, fig. 12-15, 18), as reinforced in his other articles, including Runnegar (1974, pl. 1, fig. 8). This error was compounded by Skarlato & Starobogatov (1979) with their possible but not specified reliance on the carination, non-existent in *Myonia*, to justify separation of Myoniidae as a distinct family. Were Myoniidae to be carinate, the nominate genus *Myonia* would have to be excluded from Myoniidae. Morris et al. (1991) sharply disagreed over the lumping of *Pachymyonia* with *Myonia*, and recognized both genera. They suggested that *Pachymyonia* might best fit within Sanguinolitidae, and it is very close externally. However the pedal and retractor scars of *Pachymyonia* are like those of *Myonia* (Waterhouse 1969b).

Pachymyonia morrisii (Etheridge, 1919)

Fig. 258 - 260

1919 *Maeonia morrisii* Etheridge, p. 186, pl. 28, fig. 7, 8.
1919 *M. morrisii* var. (?) Etheridge, p. 187, pl. 30, fig. 1, 2.
1932 *Pachymyonia morrisii* – Dun, p. 412. pl. 51, fig. 1.
1932 *Pachymyonia etheridgei* Dun, p. 412, pl. 51, fig. 2, 3 (part, not pl. 52, fig. 6 = *Myomedia davidis* Dun).
1957 *P. morrisii* – Dickins, p. 27.
1964b *Myonia* cf. *davidis* – Hill & Woods, pl. P10, fig. 8.
1965c *Pachymyonia morrisii* – Waterhouse, p. 376, text-fig. 3g.
1967 *M. morrisi* – Runnegar, pl. 20, fig. 11.
1967 *M. morrisi* – Runnegar, p. 53, pl. 4, fig. 3-5, pl. 5, fig. 1-11, 16, 17, pl. 12, fig. 4.
1969b *P. morrisi* – Waterhouse, p. 32, pl. 2. fig. 1-4, text-fig. 7H, 8G, 11, 12.
1972 *M. morrisi* – Hill, Playford & Woods, pl. P10, fig. 8.
1972 *M. morrisi* – Runnegar, pl. 1, fig. 1, 2.
1992a *Myonia (Pachymyonia) morrisi* – Clarke, p. 30, Fig. 16A-D.
2015 *P. morrisii* – Waterhouse, p. 128, Fig. 47.

Holotype: AMF 16978 from Allandale Formation, Harper’s Hill, Hunter Valley, figured by Etheridge (1919, pl. 28, fig. 7, 8), refigured by Runnegar (1967, pl. 5, fig. 15, 16), by monotypy. Lectotype for *etheridgei*, AMF 31083 from same locality, figured by Dun (1932, pl. 51, fig. 2, 3), SD Waterhouse (1965d, p. 850).

Diagnosis: Strongly inflated shells with anteriorly placed umbones, and very high posterior umbonal carina, behind deep lateral sulcus.

Material: Specimens from Tiverton Formation at UQL 1621, 1622, 2584, 2619, 2625, 2626, 2631, 2584, 3127, 4505, 4507, 4514, 4517, 4520 and TK1/2. *Bookeria pollex* Zone and *Svalbardia armstrongi* Subzone. Rare in

Taeniothaerus subquadratus Zone.

Dimensions in mm:

UQF	UQL	Length	Height	Width	Valve
81553	1622	69	54	21	right
81550	3127	104	77	49	left
81836	4520	107	77	38	left

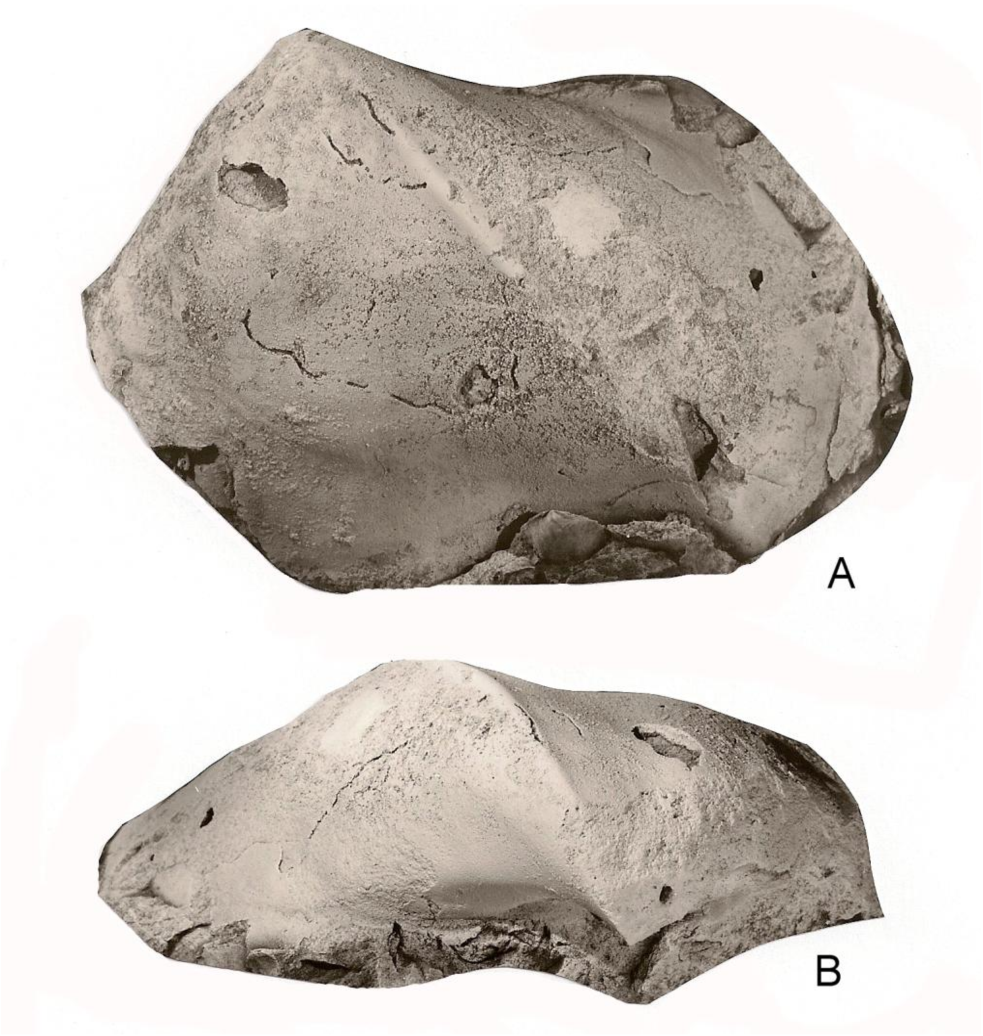


Fig. 258. *Pachymyonia morrisii* Dun, left valve UQF 81836 from lateral and dorsal aspects, from UQL 4520, x1. Although internal moulds, the carina remains highy visible, providing ready distinction from internal moulds of *Myonia*.

Description: Shell equivalve with anteriorly placed forward pointing umbones, hinge moderately long as a rule, deep lateral sulcus sloping back from the umbo, and very high keel along the posterior umbonal slope, posterior-dorsal face broad and convex. The maximum width of the shell lies at the posterior keel. Shell covered by ragged commarginal ribs, 8-9 in 10mm ventrally, increasing by intercalation posteriorly, with rounded crests. Hinge edentulous, adductor scars, protractor and pedal retractor scars present, pallial line entire. Shell massive without visible structure, 2mm thick at umbo. A small specimen 9.5mm long from UQL 4517 is deemed to belong to the species. Like juvenile valves of *morrisii*, it shows that the carina developed after a phase with gently rounded posterior umbonal slope.

Resemblances: These specimens are typical of *Pachymyonia morrisii* (Etheridge), even though the types come from the Allandale Formation, which is older than the Tiverton Formation. The species has been described by Etheridge (1919), Dun (1932), Runnegar (1967), Clarke (1992a) and Waterhouse (1969b). A specimen AMF 5734 referred to *Pachymyonia etheridgei* by Dun (1932) that had been figured as *morrisii* by Etheridge (1919, pl. 30, fig. 1, 2) from Lochinvar, Hunter Valley, New South Wales, is squashed, but is probably *morrisii*, as also noted by Runnegar (1967, p. 53). A fragment identified with *morrisii* by Runnegar & Ferguson (1969, pl. 1, fig. 4) from the basal South Curra Limestone at Gympie, southeast Queensland, lacks the deep lateral sulcus, has a lower posterior carina, and is not conspecific, but a specimen is found in the Kolbar Formation from Gigoomgan area, southeast Queensland (Waterhouse 2015).

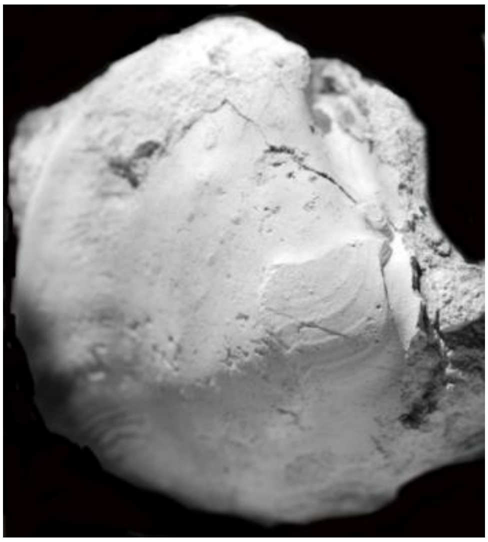


Fig. 259. *Pachymyonia morrisii* Dun, anterior part of right valve internal mould UQF 81554 from UQL 3127, x1.

The species *Pachymyonia etheridgei* Dun (1932, pl. 51, fig. 2, 3), with AMF 31083 selected as lectotype by Waterhouse (1965d, p. 850), also comes from Harper's Hill of the north Sydney Basin. It is figured to suggest a longer hinge, but is similarly inflated posteriorly. Runnegar (1967, p. 53) referred the type specimen to *morrisii,* as did Waterhouse (1969b, p. 70). The type could not be found at the Australian Museum (in December 2006), which hinders full assessment: to judge from the figures it looks close to *morrisii*. The other specimen AMF 59, figured by Dun (1932, pl. 52, fig. 6) from the Farley Formation, has weaker growth lines, thinner shell and lower posterior carina than in *morrisii*, and was referred by Runnegar (1967, p. 59) to *Myonia sulcata* Runnegar, a species shown herein to be synonymous with *Vacunella waterhousei* (Dun). *P. morrisii* is well represented in the Lizzie Creek volcanics, according to Runnegar (1967).

There is some approach to *Myonia farleyensis* Dun, 1932 from the Farley Formation. These specimens are coloured brown with matrix differing from that of *etheridgei*. The lectotype of *farleyensis* AMF 51786 (Dun 1932, pl. 51, fig. 6), cited by Waterhouse (1965d, p. 850), has been partly squashed, and has a carina on one side (right valve) and abruptly rounded posterior umbonal ridge on the other less distorted and figured left valve. There is slight or no sulcus. As the valve shares the same prominent commarginal growth wrinkles and general proportions with the other type *farleyensis* material, it seems likely that the right valve has been squashed to exaggerate the angularity of the posterior umbonal ridge, and Waterhouse (1969b, p. 34) noted that some unfigured Farley specimens in collections at the Australian Museum had a rounded posterior ridge. Thus the species belongs to *Myonia* Dana, though it was synonymized with "*Myonia morrisi*" by Runnegar (1967, p. 53). Because of the crushing, some specimens of *farleyensis* do look like *Pachymyonia*, but are less inflated, less carinate and differently ornamented from *Pachymyonia morrisii.*

The species *Pachymyonia morrisii* is readily distinguished from *P. triangulata* Waterhouse (1969b) from the Flat Top and Blenheim Formations of the Bowen Basin and Mangarewa Formation of New Zealand, by the height of the posterior carina, depth of lateral sulcus, and more elongate shell. *Pachymyonia corrugata* (Fletcher, 1932, pl. 50, fig. 2, 3) from the Sydney and Bowen Basins is moderately close, larger in size, with thick shell and coarse growth striae. It is little inflated, and very elongate.

Small elongate specimens with posterior carina from the Early Permian of Argentina were referred to *Pachymyonia* by Gonzalez (2006, p. 146, Fig. 11B, C) and compared to *Myonia parallela* Dun (1932) from the Allandale Formation at Harper's Hill, north Sydney Basin. Dun's species, with holotype AMF 51787 indicated by monotypy as the sole figured specimen, has a less well marked and rounded posterior umbonal ridge, and with its weak posterior gape, belongs to a sanguinolitid genus, *Dundulomya* Waterhouse, 2010a, p. 112, not *Myonia* or *Pachymyonia*, unlike the Argentinian material.

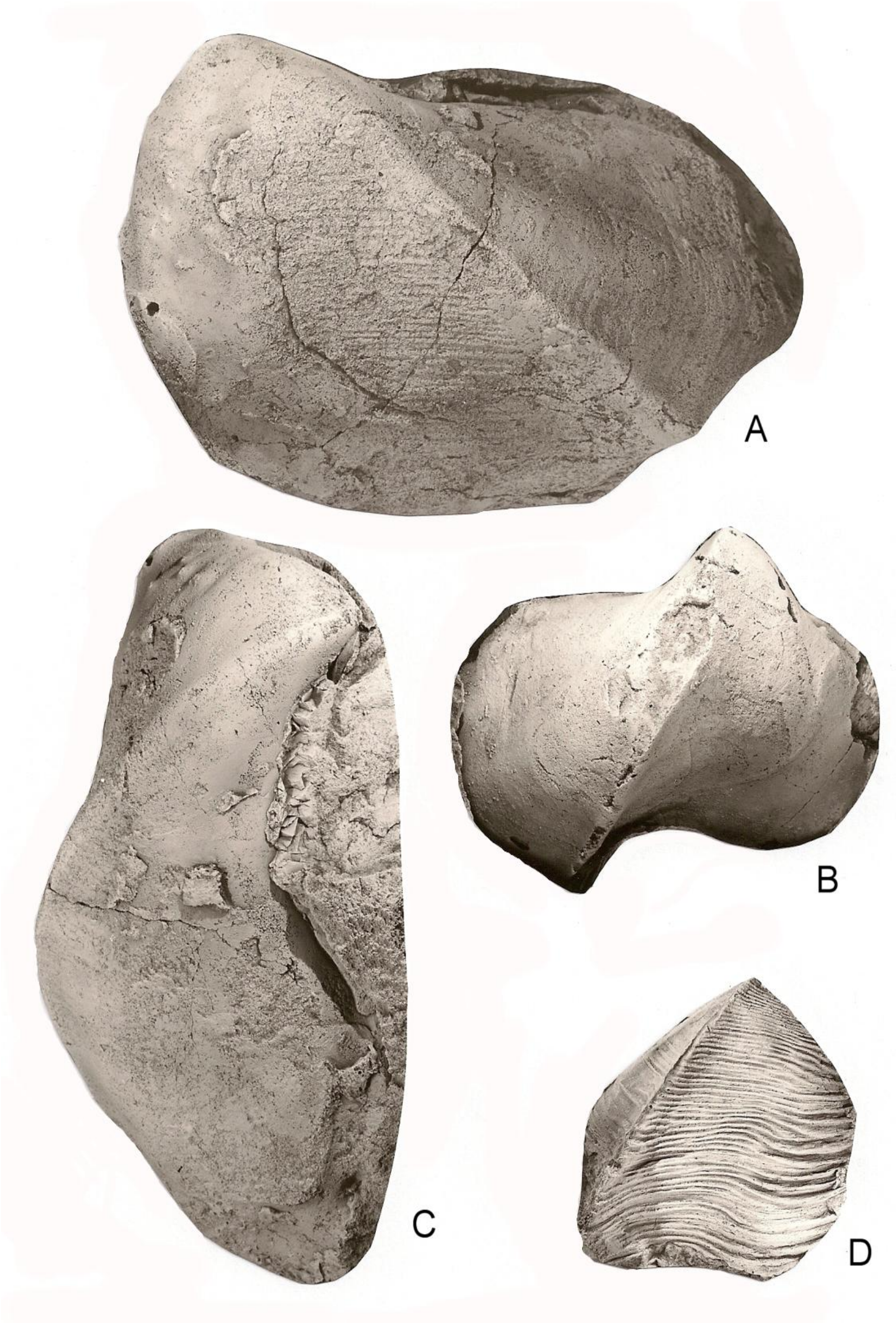


Fig. 260. *Pachymyonia morrisii* Etheridge & Dun. A, C, lateral and dorsal aspects of left valve UQF 81550 from UQL 3127, x1. B, right valve UQF 81551 from UQL 1622, x1. D, latex cast showing well preserved exterior of right valve UQF 81552 from UQL 3127, x1.

Genus ***Myomedia*** Waterhouse, 1969b

Type species: *Pachydomus carinatus* Morris, 1845, p. 273 from “Illawarra” (?Broughton Formation, Wordian), south Sydney Basin, New South Wales.

Diagnosis: Generally elongate shells with moderately carinate posterior umbonal ridge, posterior dorsal face almost flat or concave, escutcheon moderately well developed.

Discussion: This genus is intermediate between *Myonia* Dana, which has a well rounded posterior umbonal ridge, and *Pachymyonia* Dun, which is more inflated with very high and strongly carinate posterior umbonal ridge. Details of hinge and musculature and shell structure are similar in all three genera. In that the carination is less pronounced than in *Pachymyonia*, but clearly developed as opposed to the arrangement in *Myonia, Myomedia* appears to fall closer to *Pachymyonia*.

Myomedia davidis (Dun, 1932)

Fig. 261, 262 A, B, D

1932 *Myonia davidis* Dun, p. 413, pl. 51, fig. 4, pl. 52, fig. 4.

1932 *Pachymyonia etheridgei* Dun, p. 412, pl. 52, fig. 6 (part, not pl. 51, fig. 2, 3 = *etheridgei,* syn. *morrisii*).

?1964 *Myonia parallela* [not Dun] – Maxwell, pl. 10, fig. 17.

Lectotype: AMF 30060 from Ravensfield Sandstone Member of Farley Formation, figured by Dun (1932, pl. 52, fig. 4), SD Waterhouse (1965d, p. 850, AMF 30600 cited in error).

Material: Two Tiverton specimens with valves conjoined from UQL 4506 and a specimen with both valves conjoined and left valve from UQL 3127. *Bookeria pollex* Zone and *Svalbardia armstrongi* Subzone.

Dimensions in mm:

UQF	UQL	Length	Height	Width left valve	Width both valves
81556	4506	39	25	13	
81555	3127	25	15	6.5	12.5
81557	3127	48.5	27.5	13	

Description: Specimens small and immature, umbones placed behind mid-length. Lateral sulcus shallow, extends steeply below the umbones, posterior carina sharply defined and raised, a second gentle depression lies just in front. Posterior face gently convex.

Fig. 261. *Myomedia davidis* (Dun), left valve UQF 81557 from UQL 3127, x2.

Resemblances: These specimens are identified with *Myomedia davidis* (Dun), which has the umbo well back from the anterior margin and a comparable posterior umbonal ridge and posterior face. Growth-lines are fine, and sulcus broad but shallow. The species *davidis* was tentatively assigned to *Myomedia* by Waterhouse (1969b, p. 30), and this may be confirmed, as the original material shows a distinct but low posterior carina and low inflation, approaching features of *Pachydomus carinatus* Morris, 1845, the type species of *Myomedia* Waterhouse. The species *Myonia farleyensis* Dun is more inflated, with strong commarginal growth-wrinkles, and the lectotype has a rounded umbonal ridge on the uncrushed left valve, as in *Myonia*. Although Waterhouse (1969b) considered that *davidis* belonged to *Myomedia*, stating it agreed in shape, he also noted that *davidis* was possibly allied or conspecific (p. 34) with *farleyensis*, a view now set aside.

Even small specimens of *Pachymyonia morrisii* have umbones that are anteriorly placed and so are not to be confused with that species. The umbones of a small specimen of *morrisii* 25mm long from UQL 3127 for example lie 9.5mm from the anterior, compared with a UQL 4605 specimen of *davidis* 39mm long, with umbo placed 23mm from the anterior margin. The umbones of *morrisii* are high and narrow, and the umbonal walls diverge at 70°, as compared with 110° (UQL 3127) and 130° (UQL 4506) for the Tiverton specimens assigned to *davidis*. The species *davidis* and *farleyensis* were synonymized with *morrisii* by Runnegar (1967, p. 53), but *morrisii* has much stronger posterior umbonal keel, broader posterior shell, deeper lateral sulcus and more anteriorly placed and more prosogyrous umbones.

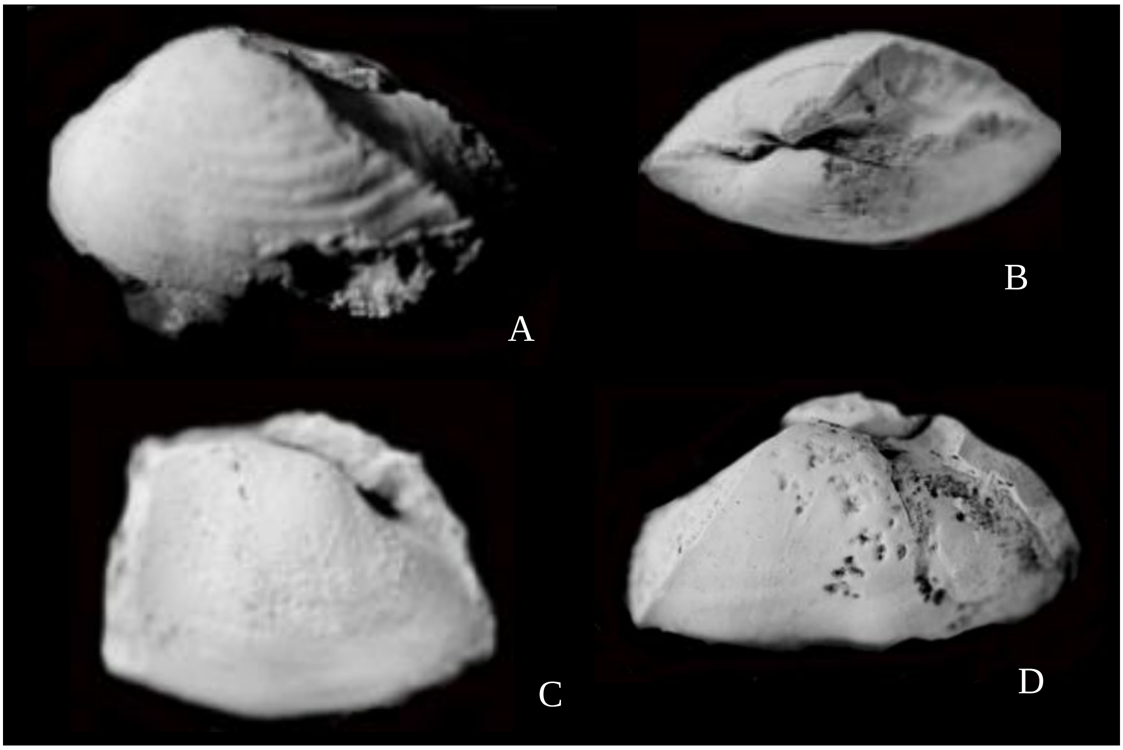


Fig. 262. A, B, D, *Myomedia davidis* (Dun). A, B, lateral and dorsal aspects of UQF 81555 from UQL 3127, x3, x2.5. D, incomplete right valve UQF 81556 from UQL 4506, x2. C, *Vacunella waterhousei* (Dun), anterior of right valve UQF 81562 from UQL 3127, x2.

Myomedia pollocki (Maxwell, 1964, p. 17, pl. 3, fig. 12-17) from the Upper Carboniferous Rands Formation of the Yarrol Basin is close, but has incurved to procrescent umbones placed at about the anterior third of the shell length, and a carinate posterior umbonal ridge with broad posterior – it seems to involve decorticated specimens and is less inflated than *Pachymyonia*. Maxwell (1964, pl. 10, fig. 17) also described a specimen from the Burnett Formation of the Yarrol Basin, Queensland, as *Myonia parallela* Dun, but the specimen is carinate with medianly placed umbones, and seems very close to *Myomedia davidis* (Dun).

Class GASTROPODA Cuvier, 1797

Subclass STREPTONEURA Spengel, 1881

Superorder EUOMPHALINIFORMII de Koninck, 1881

[Nom. transl. hic ex Eomphalina de Koninck, 1881].

Order BELLEROPHONTIDA Ulrich & Scofield, 1897

Superfamily **BELLEROPHONTOIDEA** M'Coy, 1861

Family **EUPHEMITIDAE** Knight, 1956

Genus ***Warthia*** Waagen, 1880

Type species: *Warthia brevisinuata* Waagen, 1880, p. 131 from Amb Formation? (late Cisuralian), Salt Range, Pakistan. SD de Koninck (1882, p. 81).

Diagnosis: Involute symmetrically coiled smooth shells with apertural sinus but selenizone obscured by perinductural layer.

Warthia sp.

Fig. 267A

Material: Specimen from Tiverton Formation at UQL 4519. *Taeniothaerus subquadratus* Zone.

Description: Specimen 17mm across at maximum diameter and 11mm wide, with shell-filled umbilicus and a small apertural notch, indicated by a growth-line.

Resemblances: *Warthia* is represented by three species in the Guadalupian of east Australia, named *micromphala* (Morris), *stricta* (Dana) and *perspecta* Fletcher, as reviewed by Fletcher (1958) and Waterhouse (1963a). The present specimen falls close to *micromphala*. Fletcher (1958, p. 147) recorded mostly more inflated specimens from the Ravensfield Sandstone Member of the Farley Formation of the Sydney Basin. From the Early Permian Wasp Head Formation at Durras, south Sydney Basin, Runnegar (1969, pl. 20, fig. 7-11) described specimens of *Warthia* sp. that are close to the Tiverton specimen in degree of inflation, but they have a broader apertural notch. There appear to be Early Permian species in east Australia yet to be named.

Suborder MACLURITIDINA Cox & Knight, 1960

Superfamily **EUOMPHALOIDEA** de Koninck, 1881

Family **EUOMPHALIDAE** de Koninck, 1881

Genus ***Paromphalus*** Grabau, 1936

Type species: *Paromphalus mapingensis* Grabau, 1936, p. 302 from Maping Limestone (Asselian), Kweichow, China, OD.

Diagnosis: Subcircular whorls with subdued ornament, no spiral keels and no well-formed apertural sinus; loosely coiled.

Paromphalus? sp. indet. A

Fig. 263A

Material: UQF 81565 from Tiverton Formation at UQL 3127. Zone not known.

Description: Coils loose in conispiral with wide deep umbílicus, outer whorl 14.5mm high and 11.5mm wide. Little of earlier whorls is preserved apart from the umbilical flank of the penultimate whorl. The outer whorl bears strong growth increments, crossed on the inner side of the whorl by spiral ribs, 8-9 in 5mm. The upper whorl is preserved only as an outer fragment, sloping back strongly from the suture. The penultimate whorl is crossed by growth striae, curving back to meet the striae at the periphery and forming a scarcely perceptible and very shallow sinus, with inner striae vertical: the inner face is ornamented by low collabral and spiral ribs.

Resemblances: The present specimen is too incomplete to allow generic determination, and the generic position is not clear. It is in a general way close to *Paromphalus,* as represented by the type species. There is some similarity to what was recorded as *Straparollus ammonitiformis* Etheridge, 1902, pl. 33, fig. 1, 2, which was reassigned to *Paromphalus* by Fletcher (1958, p. 146, pl. 21, fig. 1-5), but the spire is much higher in the present form: nonetheless the whorl in section is comparatively close. The Etheridge species comes from the Allandale Formation of the Sydney Basin. As discussed by Waterhouse (2010a, p. 115), *Fletcherispira rotundatum* (Morris) has higher whorls, though as in the present form the whorl is comparatively rounded, with no keel or strong spiral ornament and no coarse collabral ribs.

Paromphalus? sp. indet. B

Fig. 263B

Material: Tiverton specimen UQF 20983 from UQL 1622. *Bookeria geniculata* Zone.

Description: Coils loose in conispiral with wide deep umblicus, outer whorl 9.5mm wide and high. Little of earlier whorls is preserved. The inner whorl is ornamented by low collabral ribs, three in 5mm, with finer ribs numbering three in 1mm, and the lower outer whorl is covered by fine spiral ribs, three in 1mm; the upper outer whorl and most of the earlier whorls are destroyed.

Resemblances: Only a fragment is known, differing considerably in its fine spiral ribs and coarser collabral ribs from the other Tiverton specimen. *Straparollus ammonitiformis* Etheridge, 1902, pl. 33, fig. 1-2 from the Allandale Formation is more planospirally coiled, with only collabral ornament.

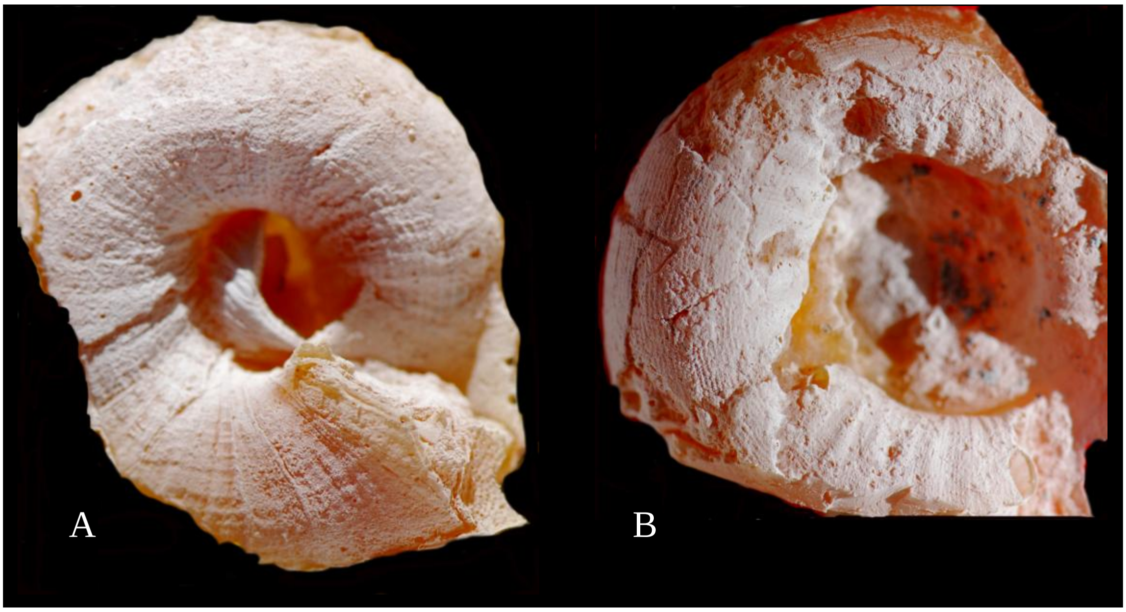


Fig. 263. A, *Straparollus*? sp., basal view of UQF 81565, latex cast from UQL 3127, x3. B, *Straparollus* sp. B, UQF 20983, UQL 1622, basal view of latex cast, x3.

Order PATELLIDA Rafinesque, 1815

Suborder VETIGASTROPODINA Salvini-Plawen, 1980

Superfamily **PLEUROTOMARIOIDEA** Swainson, 1840

Family **SINUOPEIDAE** Wenz, 1938

Subfamily **TURBONELLINAE** Knight, 1956

Genus ***Planikeeneia*** Fletcher, 1958

Type species: *Planikeeneia minor* Fletcher, 1958, p. 135 from Allandale Formation (Asselian), north Sydney Basin, New South Wales, OD.

Diagnosis: Medium-sized to large low-spired shells with four or five whorls, narrow sinus in outer lip, occasionally leaving a selenizone. Ornament of crowded sharply defined collabral lirae.

Planikeeneia sp.

Fig. 264

Material: Fragment of spire from Tiverton locality UQL 4515. *Taeniothaerus subquadratus* Zone.

Description: Spire low, gently convex upper whorl, no selenizone or pseudoselenizone in spire, ornament of fine sharply defined lirae curving convex forward backward from suture, about 10 per mm on third whorl, but faint on next whorl.

Resemblances: The fragment is closest to *Planikeeneia insculpta* Fletcher (1958, p. 138, pl. 17, fig. 3-5) from the Allandale Formation, north Sydney Basin, but is smaller with finer radial ribs. Hitherto the genus has been reported only from the Sydney Basin in New South Wales, with Fletcher (1958) describing species mostly from the Allandale Formation, and one from the Elderslie Formation.

Fig. 264. *Planikeeneia* sp., external mould of spire, UQF 81583 from UQL 4515, x3. The faint spirals have been lost from the figure.

Genus ***Paraplatyschisma*** Waterhouse, 1983c

Type species: *Platyschisma branxtonensis* Fletcher, 1958, p. 146 from Elderslie Formation (Roadian), north Sydney Basin, New South Wales, OD.

Diagnosis: Whorls inflated and subrounded, broad shoulder, widely phaneromphalous base, in some shells closed by plug, notch in aperture well below mid-height, spire large, ornament of collabral growth-lines and low spiral ribs.

Discussion: In this genus the notch is placed lower on the aperture than in the Carboniferous genus *Platyschisma* M'Coy, which has the notch above mid-whorl, as well as a smaller spire and minutely phaneromphalous base. *Keeneia* Etheridge, 1902, type species *K. platyschismoides* Etheridge, 1902, and *Planikeeneia* Fletcher, 1958, type species *P. minor* Fletcher, 1958, are Permian genera of east Australia which come close to *Paraplatyschisma*, but have a more flattened upper body whorl, distinct sinal notch which may form a keel at least in some species, and little or no spiral ornament. Further differences are enumerated in Waterhouse (1987b, p. 176).

Paraplatyschisma rotunda (Etheridge Snr, 1872)

Fig. 265

1872 *Pleurotomaria rotunda* Etheridge Snr. p. 336, pl. 18, fig. 3.

1892 *Platyschisma rotunda* – Etheridge, p. 286, pl. 15, fig. 6.

1987b *Paraplatyschisma rotunda* – Waterhouse, p. 177, pl. 11, fig. 9-11, 15, 16.

Holotype: Sole specimen figured by Etheridge Snr (1872) from Fairyland Formation (Sakmarian), southeast Bowen Basin.

Material: Single specimens from UQL 1622 and 4515. *Svalbardia armstrongi* Subzone, *Taeniothaerus subquadratus* Zone.

Diagnosis: Moderately large, high swollen spire and well developed spiral ribs.

Description: Specimen UQF 81566 from UQL 4515 seen mostly in section, 32mm across, 28mm high, body whorl 13mm wide and 18mm high, broad shoulder, outward sloping upper face, apertural sinus placed below mid-height of whorl, base gently rounded, widely phaneromphalous, shell thick, ornament of spiral ribs, two to three in 1mm, visible on poorly exposed external mould.

Resemblances: The specimen is poorly preserved, but appears to belong to *Paraplatyschisma rotunda*, first described from the Fairyland Formation near Cracow, southeast Bowen Basin, and mentioned as occurring in the Rose's Pride Formation in the same area by Waterhouse (1987b). The type species of *Paraplatyschisma*, *P. branxtonensis* (Fletcher 1958, pl. 16, fig. 1-3) from the Elderslie Formation of the north Sydney Basin has more rounded whorls and lower spire. *P. etheridgei* Waterhouse (1987b, pl. 12, fig. 1-3, 6 – not fig. 5 as in text) from the Elvinia and Rose's Pride Formations of the southeast Bowen Basin is distinguished by its high spire, inflated whorls and well defined spiral ornament. *Keeneia carnarvonensis* Dickins (1957, pl. 9, fig. 9-11) from the upper Lyons Group of the Carnarvon Basin, Western Australia, also belongs to *Paraplatyschisma*, and is very close to *P. rotunda* (Etheridge), having fine spiral ribs, and differs in its slightly more extended upper face and better defined collabral growth increments.

Keeneia afflicta was described by Wass (1967, text-fig. 2) from the Buffel Group of the southeast Bowen

Basin, which includes the Fairyland Formation, and no spiral ornament was figured or described. The species was also illustrated as *Keeneia* sp. by Hill & Woods (1964b, pl. P12, fig. 14) and as *K. afflicta* by Hill, Playford & Woods (1972, pl. P12, fig. 14). The whorl profile of *afflicta* is moderately close to that of *rotunda* in the Wass illustration, but the upper whorl profile is flatter in the Hill & Woods figure, and closer to that typical of *Keeneia*. Decortication means that ornament is not well preserved.

Fig. 265. *Paraplatyschisma rotunda* (Etheridge), mould of UQF 81566 from UQL 4515, with specimens of *Pleurocinctosa allandalensis* Fletcher, x2. The ribs on the external mould are faintly visible to the right side of the specimen, though not shown in this figure.

Family **EOTOMARIIDAE** Wenz, 1938

Subfamily **PTYCHOMPHALINAE** Wenz, 1938

Tribe **WALNICHOLLSIINI** new tribe

Name genus: *Walnichollsia* Fletcher, 1958, p. 143 from Broughton Formation (Wordian), Sydney Basin, here designated.

Diagnosis: Turbiniform small to large shells with slit and selenizone placed just above mid-height on whorls, slit generally 0.25 to 0.33 of circumference, whorls globular, variously ornamented with growth lines, collabral ribs, and/or spiral ribs. Base anomphalous, cryptomphalous or phaneromphalous.

Discussion: The tribe differs from Ptychomphalini in having more globular whorls with slit placed high on the whorl. The tribe includes *Walnichollsia* Fletcher, *Mourlonopsis* Fletcher and *Globosospirina* n. gen., and appears to have been limited in distribution to Australia and New Zealand.

Genus ***Globosospirina*** n. gen.

Derivation: globoso – rounded, swollen; spira – coil, Lat.

Type species: *Globosospirina mcclungi* n. sp. from Tiverton Formation, here designated.

Diagnosis: High-spired shells with selenizone moderately high on the whorl, placed slightly above mid-height to upper third, bordered by high keel above and below, slit no more than 0.25 of circumference, whorls globose to subglobose, with well formed shoulder, no gutter below selenizone, selenizone exposed in the spire, base rounded, anomphalous in type species, ornament collabral and spiral.

Discussion: This genus is close in many respects to the Lower Carboniferous genus *Mourlonia* de Koninck, 1883, type species *M. carinata* (J. Sowerby, 1812, p. 34), with somewhat comparable spire, swollen whorls and selenizone bordered by ribs and placed near the periphery of the whorl. Dickins (1976) suggested that an umbilicus was present in some specimens of *carinata*, not in others, as discussed by Batten (1967). There is no gutter below the selenizone and the selenizone is gently concave. Ornament consists of fine spiral and stronger collabral ribs. *Mourlonia* differs from the new genus in having a less swollen upper whorl and in having a less conspicuous shoulder below the suture, and the selenizone may lie just above the periphery or maximum circumference of the whorl close to the lower third of the whorl height. *Ptychomphalina* Fischer, 1887, type species *P. striata* (J. Sowerby, 1817, p. 159, pl. 171, fig. 1) differs only slightly from *Mourlonia*, consistently lacking an umbilicus, and in having the selenizone lie between a narrow groove above, and broader groove below, as elaborated by Dickins (1976, p. 46, pl. 2, fig. 1-6).

There are several genera from the Permian of Australia which come close to the new genus. Somewhat similar ornament is displayed by *Walnichollsia* Fletcher, 1958, type species *Pleurotomaria subcancellata* Morris (1845, p. 288, pl. 18, fig. 6) from Middle Permian beds at Illawarra, south Sydney Basin, also figured by de Koninck (1877, pl. 23, fig. 15), Fletcher (1958, pl. 13, fig. 1-6) and Waterhouse (1963a, Fig. 2B; 1987b, pl. 12, fig. 18). Other species include *W. pygmaea* Fletcher (1958, pl. 12, fig. 4-8) from the Gerringong Volcanics (Wordian) of south Sydney Basin, *W. minuta* Waterhouse (1963a, Fig. 24, 25, 27, 28) from the Takitimu Group (upper Sakmarian) of New Zealand, and *W. erecta* Waterhouse (1963a, Fig. 23, 26, 29-32) from the Mangarewa Formation, New Zealand (Capitanian). The whorls are swollen with prominent upper shoulders slightly more exaggerated than in the present species, and the inner whorl next to the suture is almost flat. The type species has a low broad spire and flatter upper whorl with somewhat similar selenizone placed just above mid-height and below the upper third of the whorl, and the selenizone is like that of *Ptychomphalina* in lying between two depressed strips, notably in the body whorl, though this could be due to decortication and related to two thickened strips of shell one each of the selenizone. The slit is more than a quarter of the length of the circumference. The base is phaneromphalous, the aperture has a shallow basal sinus and the ornament is more regular and cancellate than in *Globosospirina*.

Platyteichum Campbell, 1953 is a gastropod common in especially Middle Permian faunas of the Bowen Basin, and material has been figured by Waterhouse (1987b, pl. 12, fig. 13-16) as *coniforme* Etheridge, and pl. 12, fig. 4, 17 as *loratum* Waterhouse, and as misidentified *Mourlonia* (*Mourlonia*) *strzeleckiana* [not Morris] by Dickins (1989, pl. 2, fig. 13-18). *P. loratum* is abundant in New Zealand, as figured in Waterhouse (1963a, part 2, Fig. 4. 37-50). Ornament and position of the selenizone and spire angle are much the same in species referred to *Platyteichum* as in the Tiverton material, apart from the tendency of some of the *Platyteichum* material to have a higher spire and lower spiral angle, but *Platyteichum* species have a flatter upper body whorl and often penultimate whorl, whereas early whorls are swollen like those of *Globosospirina*. The whorl below the selenizone in *Platyteichum* is swollen and shouldered above the base, whereas the whorl below the selenizone in the Tiverton material rounds more gently onto the base. *Platyteichum* is not close to *Walnichollsia* or its allies, in having the selenizone placed above a poorly to well defined often concave or flat band in the outer whorl, approaching that in *Eirlysia* Batten, *Glabrocingulum* Thomas and *Ananias* Knight.

Mourlonopsis Fletcher, 1958, type species *Pleurotomaria strzeleckiana* Morris (1845, p. 287, pl. 18, fig. 5) from Middle Permian faunas of east Australia and New Zealand, is close to *Walnichollsia* in the nature of its selenizone, which is placed at the upper third of the whorl height, higher than in *Globosospirina*. The type species is large, higher-spired, and loosely coiled with the outer whorl slightly more shouldered above the base, with upper whorls more fully shouldered and phaneromphalous, bearing little ornament other than coarse spirals on some specimens, and subdued collabral ornament, very faint on most specimens (see Fletcher 1958, pl. 9, fig. 9-11; Waterhouse 1963a, Fig. 2a, 21, 22; 1987b, pl. 12, fig. 11, 12; 2001, pl. 10, fig. 1-4) and specimens identified as *Walnichollsia subcancellata* in Shi & Weldon (2002, pl. 11, fig. 5). The slit is less than a quarter of the circumference in the holotype (Waterhouse 1963a, p. 123), but may be slightly longer in other specimens, and the sinus is deeper than in *Walnichollsia* (Waterhouse 1963a, Fig. 2). So far only the one species of *Mourlonopsis* has been identified, limited to faunas of Middle Permian age in east Australia and New Zealand. Of the three genera, *Platyteichum, Walnichollsia* and *Mourlonopsis*, it is the latter which appears to come closest to the Tiverton material in terms of whorl profile, though not in the nature of the base, spiral angle, ornament or position of the selenizone.

Neoplatyteichum Maxwell, 1964, type species *N. dickinsi* Maxwell, 1964, p. 20 from the Late Carboniferous Rands Formation of the Yarrol Basin, Queensland, is especially well figured in Hill & Woods (1964a; 1973, pl. C14, fig. 1a, b, 2). Maxwell's species is very close in general appearance to *Globosospirina*, and has collabral and stronger spiral ornament, swollen whorls, sutural shoulder and anomphalous base. Maxwell (1964) stressed the weak development of the selenizone, and although this was considered variable by Waterhouse (2001), it is now believed to imply a critical difference, and as well, the selenizone where visible is placed slightly higher on the whorl than in *mcclungi*. *Neoplatyteichum* is represented in the Kolbar Formation near Gympie (Waterhouse 2015).

Globosospirina mcclungi n. sp.

Fig. 266, 267B - E

Derivation: Named for G. McClung.

Holotype: UQF 81567 from UQL 4506, Tiverton Formation, figured as Fig. 267B, C, here designated.

Material: Single Tiverton specimens from UQL 1630, 2619, 2620, 2628, 3127, 4506, 4508, 4514, 4519, 4521, LT3 and TK3. *Bookeria pollex* Zone, *Svalbardia armstrongi* Subzone and *Taeniothaerus subquadratus* Zone.

Diagnosis: Medium small with swollen whorls, clearly defined selenizone, ornament of fine spiral ribs crossed especially in the spire by moderately prominent collabral filae.

Dimensions in mm:

UQF	UQL	Width	Height	Height of Body chamber	Spire angle
	TK3	9	8.3	5.5	75°
	2619	16.5	18		70°
	4521	?10	12.5?	6.8	70°
81567	4506	12	12.5	7	70°
81571	2619	16	18	?	70°

Description: The specimens are small with high spire having an apical angle of 70-75°, whorls turbinate, body chamber appears slightly more globose than whorls in spire, in which the upper whorl may be slightly less shouldered, selenizone sited just below the upper third of whorl height (example whorl height 6.7mm, top of selenizone 2.3mm below suture, selenizone 1mm high: comparable dimensions for penultimate whorl of another specimen are 3.5mm, 1.2mm, 0.7m, and 6.5mm and 2.5mm for another specimen. Upper whorl rounded with shoulder below the seam and tight suture, more emphasized in the spire, where the suture may be channeled, selenizone well exposed in spire. Coiling overlap for whorl 4.5mm high is 2mm. Base gently rounded, anomphalous, columella only slightly thickened and reflected back onto preceeding whorl, slit no more than 0.25 of circumference. Ornament distinctive, upper whorl bearing fine collabral ribs slightly convex forward and inclined at 40-45° from suture, four to five per mm on penultimate whorl, fade just above selenizone; growth lines slightly raised on lower whorl and outer base, curving forward slightly below the selenizone, and then gently back, leaving very shallow broad sinus. On the body whorl the ribs are less regular and sometimes are aggregated or bundled. Spiral threads about six to eight in 5mm over body whorl, lower whorl bears spiral ribs. There is some variation, in that a specimen from UQL 4508 has comparatively faint spiral ribbing. The selenizone is narrow and concave with crowded fine lunulae, and bordered above and below by a sturdy spiral rib. The slit in a specimen from UQL 3127 for which the body whorl is 8mm high and 13.5mm in diameter is 3.3mm deep. In another specimen, from UQL 1383, the slit is 2.8mm deep in a specimen 9.3mm in diameter.

Fig. 266. *Globospirina mcclungi* n. sp. tilted lateral aspect of latex cast, UQF 81571 from LT3, x7.

Resemblances: No gastropod so far described from Australia appears to be exactly the same. *Neoplatyteichum dickinsi* Maxwell, 1964 from the Late Carboniferous Rands Formation and older beds of the Yarrol Basin, Queensland, is moderately similar in general appearance, but is larger in size with broader spire, and more cancellate ornament, lacking the emphasized collabral ribs on the upper whorl, and with selenizone obscure and placed high on the whorl. From the Wasp Head Formation of south Sydney Basin, *Mourlonia* (*Mourlonia*) sp. of

Runnegar (1969, p. 292, pl. 18, fig. 15) shows some similarities, especially in the position of the selenizone and swollen upper whorl, but the spire is much broader and although the ornament shows spirals and collabrals, it differs in having weaker radials over the upper whorl.

The Wasp Head specimen shows some approach to *Mourlonia*? *impressa* Waterhouse, 1966a from the Croisilles ultramafic complex of New Zealand (see Waterhouse 2001, p. 152), and this species also lacks the relatively conspicuous upper whorl radials displayed by *Globosospirina mcclungi*. The species *impressa* is widely phaneromphalous, and so, given its high spire, could be an early *Mourlonopsis* with moderately well formed sinus, but the selenizone is placed near mid-height, whereas it lies on the upper third of the whorl in *Mourlonopsis* (see Waterhouse 2001, pl. 10, fig. 1-4), and as well the body whorl is slightly more globose than the whorls in the spire, which are like those of the present species. The species *impressa* comes closer to *Globosospirina* than to other named genera.

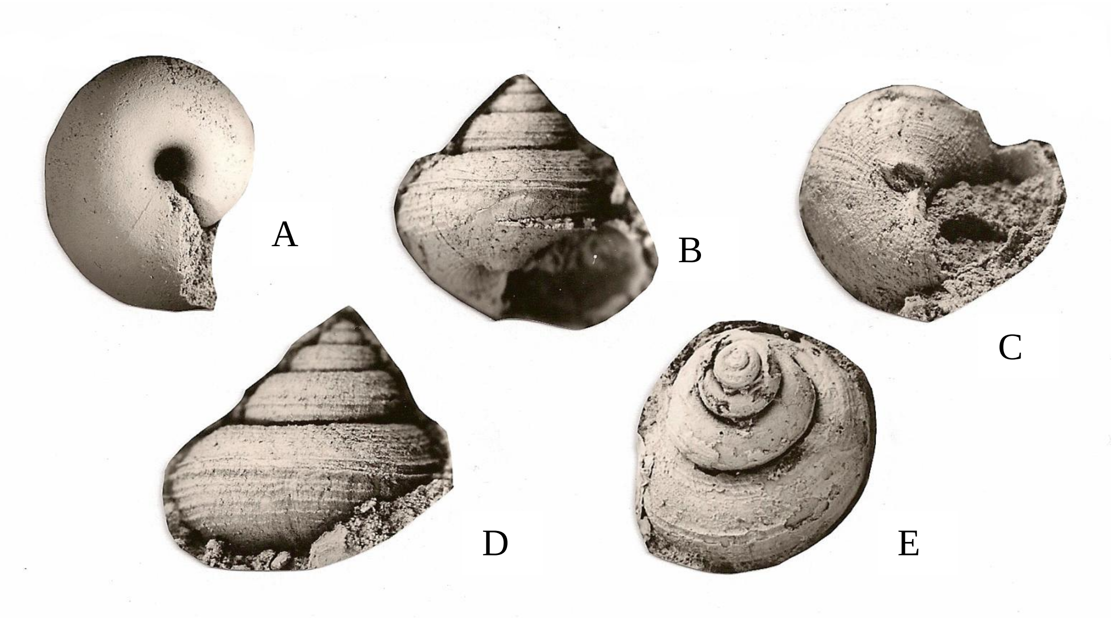


Fig. 267. A, *Warthia* sp, UQF 81564 from UQL 4519, x2. B-E, *Globosospirina mcclungi* n. gen., n. sp. B, C, latex cast of holotype UQF 81567 from UQL 4506, lateral and basal views, x4. D, E, latex cast of UQF 43224 from UQL 2619, lateral and tilted lateral aspects, x3.

The gastropod named *Walnichollsia minuta* Waterhouse, 1963a from the Brunel Formation, Takitimu Group, New Zealand, probably equivalent to the *Taeniothaerus subquadratus* beds of Homevale, shows similarities in whorl profile and position of selenizone. The shoulders are more emphasized than in the present species, and whorls are transverse with flatter upper whorl, so that the shells are less turbinate, and the base is phaneromphalous, as in *Walnichollsia*. The shell is small, with predominant collabral ribs above and especially below the narrow selenizone. The Guadalupian species *Walnichollsia subcancellata* (Morris, 1845) of east Australia is much larger, with ornament like that of *Neoplatyteichum*, and less turbinate broader spire. The selenizone lies between two ribs on the upper half of the whorl, and whorls are swollen and the base phaneromphalous. *W. erecta* Waterhouse (1986b, p. 6) from the *Pseudostrophalosia clarkei* Zone in the Mangarewa Formation of New Zealand, as figured by Waterhouse (1963a, Fig. 23, 26, 29-32) is smaller than *W. subcancellata*, and has higher whorls and higher spire, but the shape differs from that of *Globosospirina mcclungi* in that the body whorl is much larger and higher relative to the spire.

The solitary specimen called *Mourlonia* (*Mourlonia*) sp. by Dickins (1963, p. 119, pl. 23, fig. 18-21) from the Callytharra Formation in the Carnarvon Basin, Western Australia, is moderately close in ornament and selenizone, but has less swollen upper whorl, and more regular collabral ribs and cancellate ornament. A sinus is developed much as in *Mourlonopsis,* and appears to lie slightly lower on the whorl, though this is not fully clear because the lower part of the last whorl is lost. The nature of the umbilicus was not determined by Dickins (1963), but subject to the nature of this attribute, the species may be close to *Globosospirina*. From the Aifat Formation of west

Irian Jaya, *Mourlonia aifamensis* Dickins & Skwarko (1981, pl. 6, fig. 10, 11, 14, 15) is moderately close, but is larger with more conspicuous shoulder, and less rounded upper whorl, and selenizone placed high on the whorl, as in *Mourlonopsis*. The nature of the base was not determined.

Platyteichum Campbell shows considerable approach in size and overall ornament and position of selenizone. Although the upper whorl of outer whorls is flattened, a few show swollen convex whorls approaching that of the present genus, especially amongst specimens of *P. loratum* Waterhouse, 1963a.

Subfamily **NEILSONIINAE** Knight, 1956

Tribe **NEILSONIINI** Knight, 1956

Diagnosis: Small anomphalous high-spired shells with collabral ornament, selenizone prominent, well developed carina may lie above and/or below bordering carina of selenizone.

Genus ***Pleurocinctosa*** Fletcher, 1958

Type species: *Pleurotomaria trifilata* Dana, 1847, p. 150, from Westley Park Tuff (Wordian), south Sydney Basin, New South Wales, OD.

Diagnosis: Small shells with prominent collabral ornament, upper whorl gently convex above concave channel dorsal to selenizone, carina above selenizone subdued and often absent, carina below selenizone moderately developed to rarely subdued.

Discussion: Fletcher's genus is very close to *Peruvispira* Chronic, 1949, type species *P. delicatula* Chronic, 1949, and it fell into disuse for some years, until revived in Waterhouse & Jell (1983, p. 253). *Peruvispira* is distinguished by its concave upper whorl, which generally lacks a carina above the selenizone-bounding ridge, and has a strong peribasal carina below the lower edge of the selenizone. *Pleurocinctosa* is found widely in the Permian of Australia, and includes the following Early Permian species: *allandalensis* Fletcher, *promenata* Waterhouse, *umariensis* (Reed), ? *nuda* (Dana), *fletcheri* Waterhouse, and the Middle Permian species *trifilata* Dana (syn. *morrisiana* M'Coy). The very Late Permian species *volupta* Waterhouse, 1963a is an outstanding form, allied to *Pleurocinctosa*, with sinusoidal upper whorl and strong radial ribs that fade towards the selenizone. *Peruvispira* is represented in the Early and especially Middle Permian of east Australia and New Zealand by species which include *elegans* Fletcher, and species *lochinvarensis, imbricata, robusta*, *modesta*, and *carinata* named by Waterhouse (1963a, 1987b). A few fine spirals are present on the upper whorl of various species, especially in east Australia.

Fig. 268. *Pleurocinctosa allandalensis* Fletcher, latex casts. A, UQF 81575 from UQL 4515, worn but showing upper whorl convexity well, x8. B, UQF 81623 from UQL 4519, x7.5.

Pagodina Wanner, 1942, p. 166, type species *P. typus* Wanner, from the Basleo beds (early Late Permian) of Timor has turreted spire and selenizone, and is distinguished by the presence of one to three strong spiral ribs above the selenizone, with a carina below the selenizone and base of the selenizone projecting to form the periphery. *P. rugosa* Wanner from the same beds has stronger collabral ornament over the upper whorl and finer spiral ornament. The upper whorl is convex. *Bicarinella* Waterhouse, 1965e is a rare genus which has no carina below the selenizone, and the upper whorl is deeply concave and ornamented by collabral ribs. It is found in New Zealand, Australia and possibly Japan. The type species, *Carinella bicarinata* Waterhouse, 1963a, p. 603 from

Kildonan Member (Changhsingian), New Zealand, displays a high spired shell with anomphalous base, concave upper whorl like that of *Peruvispira*, concave selenizone bordered by prominent ribs, and ornament of distinct radial threads. The genus name was amended by Waterhouse (1965e, p. 1227) because *Carinella* had been pre-empted as a generic name. The species described as *Peruvispira kuttungensis* Campbell (1961b, pl. 56, fig. 10-17) from the *Levipustula levis* Zone in the Late Carboniferous Booral Formation of northern New South Wales belongs to *Bicarinella*, with sharply defined collabral ribs, high spire, anomphalous base, and slightly more sinusoidal upper whorl: it is a good example of the genus, being much better preserved than the type species. However the material ascribed to *Peruvispira kempseyensis* by Campbell (1962, p. 48, pl. 12, fig. 1-4) from the *Levipustula levis* Zone of the "Kullatine Series" in northeast New South Wales shows little resemblance to *Peruvispira* or *Pleurocinctosa*, and is close to *Baylea* de Koninck or *Ananias* Knight in the position of the selenizone and whorl profile.

Pleurocinctosa allandalensis Fletcher, 1958

Fig. 268 - 270

1849 *Pleurotomaria morrisiana* [not M'Coy] – Dana, p. 706, pl. 9, fig. 16 (part, not fig. 15, 15a = *trifilata* Dana).

1958 *Pleurocinctosa allandalensis* Fletcher, p. 141, pl. 11, fig. 7-9, pl. 12, fig. 2.

Holotype: Specimen figured by Dana (1849, pl. 9, fig. 16) from Allandale Formation, Harper's Hill, New South Wales, OD.

Diagnosis: Small shells with gently convex upper whorl, peribasal rib usually well defined but rarely subdued, fine collabral ornament, 12-18 in 1mm.

Material: Tiverton specimens from UQL 2631, 3127, 4514, 4515, 4518, 4519, 4566 and LT3. *Svalbardia armstrongi* Subzone and *Taeniothaerus subquadratus* Zone.

Fig. 269. Slab from UQL 4514 with specimens of *Pleurocinctosa allandalensis* Fletcher, including UQF 81574, preserved mostly as internal moulds, x3.

Description: Specimens small, that from LT3 measuring just over 6mm high and 6mm wide, with spiral angle of 50°, selenizone bordered by prominent keel above and below, above a slender and shallow concave band and strong peribasal carina. The upper whorl is gently convex overall, and concave just above the selenizone, and the base is anomphalous. Well defined and slender collabral ribs, 12-18 in 1mm, cross the upper whorl, and are faint over the base. A specimen from UQL 4515 has a low discontinuous rib high on the upper whorl just below the suture, possibly caused by an overlap and distortion through compression. A peribasal carina is not developed in some specimens from UQL 4518, but it is present as a rule.

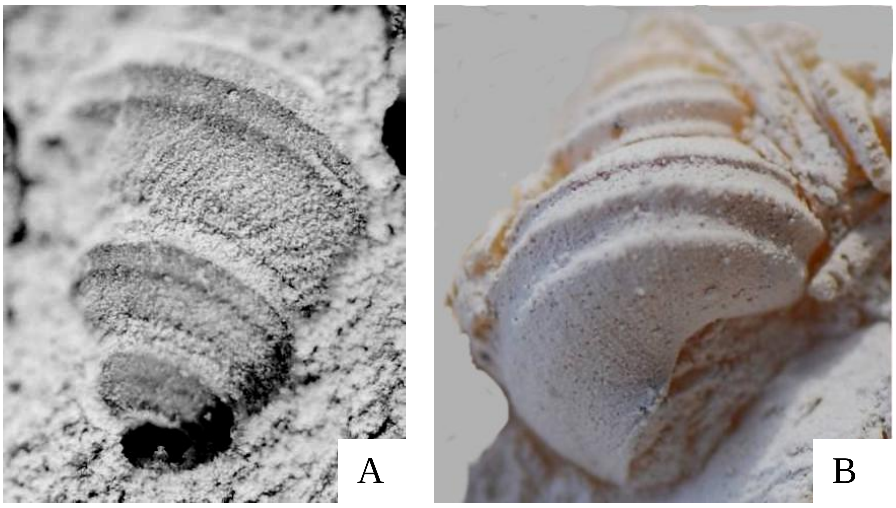


Fig. 270. *Pleurocinctosa allandalensis* Fletcher. A, UQF 81575 from UQL 4515 x 10, inverted to suggest shape, from external mould. B, latex cast of UQF 81582 from LT3, tilted to show base, x10.

Resemblances: *Pleurocinctosa allandalensis* Fletcher, 1958 from the Allandale Formation in the Hunter Valley, New South Wales, is close in size and overall appearance, and has very fine collabral ribs, up to 18 in 1mm, and two to four spirals over the upper whorl. *P. promenata* Waterhouse (1987b, pl. 13, fig. 2-5) from the Fairyland Formation of southeast Bowen Basin has only five or six ribs per mm, and *P. fletcheri* Waterhouse (1987b, pl. 13, fig. 7, 10, 11) from the Dresden Formation of southeast Bowen Basin has 10 ribs per mm, and fine spiral threads. *Peruvispira lochinvarensis* Waterhouse, 1987b, as figured by Fletcher (1958, pl. 12, fig. 3) has 18 fine collabral ribs in 1mm. It comes from the Lochinvar Formation, Hunter Valley, and is a larger shell with concave upper whorl profile bearing a few fine spiral threads, and weakly defined carina below the selenizone.

This species is also similar to *Pleurocinctosa umariensis* (Reed, 1928, pl. 34, fig. 12, 13, pl. 35, fig. 11-13) from the Umaria beds of Sakmarian age in central India, and recorded as *Ptychomphalina* from the upper Lyons Group of likely Asselian age in the Carnarvon Basin of Western Australia by Dickins (1957, pl. 9, fig. 1-5), but has a slightly higher spire. The material recorded as *Peruvispira* cf. *umariensis* by Dickins (1963, pl. 24, fig. 7, 8) from the Sakmarian Fossil Cliff Formation in the Perth Basin of Western Australia is also close, with a somewhat more subdued carina below the selenizone. The species belongs to *Pleurocinctosa* and has strong well spaced collabral ribs at only three costae per mm over the upper whorl.

Tribe **SPIROVALLINI** Waterhouse, 2001

Diagnosis: Selenizone placed on prominent peripheral flange, slit short, ornament simple and collabral with simple or bundled radial lirae. Base anomphalous.

Discussion: This tribe is close to Neilsoniini and differs in that genera lack the spiral carina above and below the selenizone, and involves shells larger than members of Neilsoniini, with more turretted whorls and less deeply concave selenizone.

Genus ***Spirovallum*** Waterhouse, 1963a

Type species: *Spirovallum liratum* Waterhouse, 1963a, p. 607 from a Tertiary boulder derived from Hilton Limestone (Changhsingian), south New Zealand, OD.

Diagnosis: Medium-size with flat or concave upper whorl ornamented by collabral threads, selenizone at periphery with strong bordering keels, base anomphalous.

Spirovallum sp.

Fig. 271

Fig. 271. *Spirovallum* sp., latex cast of UQF 81573 from UQL 4513, x3.

Material: A specimen from Tiverton Formation at UQL 4513. *Svalbardia armstrongi* Subzone.

Description: Specimen fragmentary, showing parts of two whorls, nearly 16mm wide, with estimated spiral angle close to 60°, upper whorl almost flat, but may be very gently convex, and for part of whorl, upper whorl below suture raised in low rampart. Selenizone placed at periphery, elevated, concave, bordered below and above by firm keels. Collabral ribs number some 9 in 5mm on larger whorl, curve weakly forward from the suture then sweep back at angle of 50° to the upper keel, concave over the selenizone. Further morphology not clear or destroyed.

Resemblances: The specimen is distinguished by the upper ramp and weakly convex upper whorl from *Spirovallum liratum* Waterhouse. A few specimens with weakly convex upper whorl were noted by Waterhouse (2001, p. 156) that lack the upper ramp. Specimens were also reported from a slightly older faunal zone which show weak spiral as well as radial ribs. *S. fasciatum* Waterhouse, 1963a from the *Echinalosia conata* Zone of New Zealand is distinguished by its bundled ribs.

Family **PHYMATOPLEURIIDAE** Batten, 1956

Diagnosis: Discoidal to moderately high-spired pleurotomarioids with selenizone well defined, bordered by rims, located at or near periphery, on comparatively narrow usually vertical outer face, ornament variable, base anomphalous to widely phaneromphalous.

Discussion: The diagnosis is amended from that provided by Knight in Knight et al. (1960, p. 214), because the selenizone is not always low on the whorl (see *Borestus* Thomas), and not all genera are highly ornamented, nor the slit always very deep.

Genus ***Glyptotomaria*** Knight, 1945

Type species: *Glyptotomaria apiarium* Knight, 1945, p. 577, from Mississippian of United States, OD.

Diagnosis: Low- to high-spired with concave to convex upper whorl profile, flat to deeply invaginated base, flat concave selenizone depressed below surface of subvertical outer whorl, sinus moderately deep, a further sinus on base, columellar lip reflexed and straight.

Discussion: A full diagnosis is provided by Batten (1958, p. 210). The present specimens are very incomplete, and lack the base and aperture which are crucial for genus determination.

Glyptotomaria? sp.

Fig. 272, 273

Material: Two Tiverton specimens from UQL 4518. *Taeniothaerus subquadratus* Zone.

Description: One specimen just over 8mm in diameter and estimated to be 4mm high, with three or four whorls visible but protoconch damaged and base destroyed. Upper whorl concave, almost horizontal, ornamented by collabral threads, three or four per mm on body whorl and penultimate whorl, arching forward, meeting high rim at outer edge, outer whorl subvertical, very weakly convex but almost flat, bearing selenizone at mid-height, defined above and below by strong bordering ribs, with fine almost straight lunulae, selenizone exposed on lower outer face in the spire. Outer face has very fine collabral threads, 9-12 in 1mm on penultimate whorl, and body whorl outer face has two spiral ribs.

Fig. 272.*Glyptotomaria?* sp. fragment UQF 81576 from UQL 4518, external mould, x8.

The other fragment is larger at 11.5mm in diameter, and displays an additional whorl. Both this and the penultimate whorl differ from those of the other specimen in that the concave upper whorl is like a broad gutter with the outer edge elevated abaxially into a broad shoulder that rounds onto the outer face. Earlier whorls are just like those of the smaller specimen. The outer face is flat, slightly inclined outward basally, and the base is not exposed. Spiral ribs lie in the gutter, and one is elevated on the inner shoulder into a row of tubercles; spiral ribs persist onto the outer shoulder, not present on the outer face in the spire, but present on the body whorl (or at least the last whorl preserved) above the selenizone. Selenizone 1.5mm high, comparatively flat, and bordered by a subdued rib above and below. Ornament is obscured below the selenizone.

Fig. 273. *Glyptotomaria*? sp. tilted lateral aspect of latex cast of UQF 81850 from UQL 4518, x8.

Resemblances: The lack of information about the base of the specimens prevents any firm identification. There is some approach to *Glyptotomaria* (*Glyptotomaria*) *pistra* Batten, 1958, pl. 37, fig. 5-8 from the Leonardian to Middle Guadalupian of southwest United States. This identification is strongly reinforced by the second and larger specimen, which shows that the shell architecture changed with increase in size. The presence of the rounded shoulder between the broad concave sutural gutter and the weakly convex subvertical outer face, and the presence of spiral ornament strongly suggest *Glyptotomaria* (*Glyptotomaria*). In visible aspects the smaller specimen is also close to the subgenus *Discotomaria*, recorded by Batten (1956) from Upper Pennsylvanian through middle Guadalupian of United States. Compared with the Tiverton specimens, the species described by Batten (1958) have stronger collabral ribbing and more ornate rim bordering the upper whorl, and they lack spiral ribs from the outer face.

Genus ***Austroscalata*** Waterhouse, 1987b

Type species:. *Austroscalata marina* Waterhouse, 1987b, p. 181 from Flat Top Formation (Wordian), southeast Bowen Basin, Queensland, OD.

Diagnosis: Medium to large gradate turbiniform widely phaneromphalous shells, thin shelled, whorls transverse and rounded with emphasized gutter at suture and gently convex outer face, bearing well defined selenizone bordered by carinae, sinus narrow, slit of moderate depth up to a third of whorl circumference. Ornament of fine collabral and spiral costae. Outer face bordered above by strong keel, and upper whorl subhorizontal and gently convex.

Discussion: This genus was compared with *Borestus* Thomas by Waterhouse, 1987b, and also comes close to the more ornamented *Dictyotomaria* Knight and *Callitomaria* Batten from North America. However the present specimen lacks the upper body whorl and entire spire, so that its identity is far from secure. It is older than the two Middle Permian species so far ascribed to *Austroscalata*.

Austroscalata? sp.

Fig. 274

Material: Part of body whorl from Tiverton Formation at LT3. Zone uncertain.

Description: The fragment is almost 20mm across, with gently convex outer face, shouldering abruptly onto the well rounded base, which circumscribes a wide umbilicus. Ornament consists of fine spiral threads, 10-12 in 5mm, crossed by finer and more closely spaced collabral striae, about 5 in 1mm. The selenizone lies at mid-height of the outer whorl face and is well defined, 1mm high, bordered by carinae, and crossed by fine lunules.

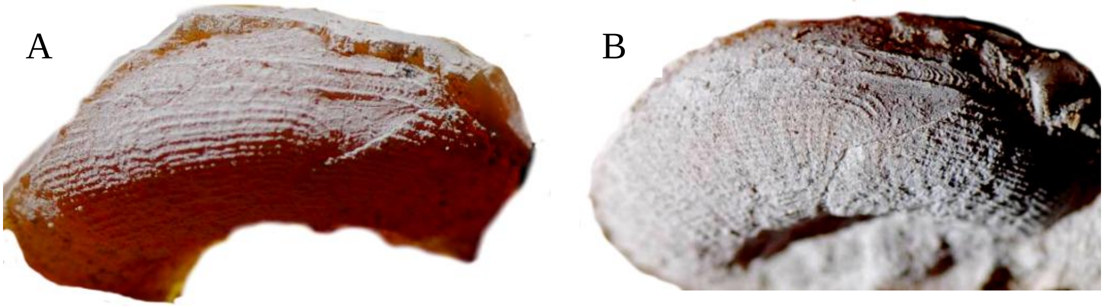


Fig. 274. *Austroscalata*? sp. latex cast of UQF 81569 from LT3, showing lateral and tilted basal aspects, under different lighting, x3.

Resemblances: This fragment is close in whorl profile and base as far as it is preserved to *Austroscalata marina* Waterhouse (1987b, p. 181, pl. 12, fig. 19-21, 23) from the Flat Top Formation, southeast Bowen Basin and has comparably placed and otherwise similar selenizone and comparable collabral ornament, but the spiral threads are stronger. *A. branxtonensis* Waterhouse (1987b, p. 181, pl. 12, fig. 22, 24) from the Branxton Formation of the north Sydney Basin is also close, but has no spiral ornament as far as can be seen. The upper whorl and spire of the present specimen are lost, hindering full comparison. Possibly the fragment represents a new species, distinguished by its stronger spiral ornament, but that can only be ascertained through the discovery of further material which confirms the generic position.

In ornament of fine spirals and weak collabral ornament, the fragment comes close to *Walnichollsia* Fletcher, 1958, although the outer face is more convex and less flatly convex. Certainly none of the species described are exactly the same in ornament, and all differ in whorl profile. *Neoplatyteichum* Maxwell, 1964, type species *N. dickinsi* Maxwell, 1964 from the Late Carboniferous Rands Formation of the Yarrol Basin, Queensland, may display a shouldered and usually well rounded outer whorl and comparable ornament, but its selenizone is scarcely defined and the base appears to be anomphalous.

Class CEPHALOPODA Cuvier, 1797

Subclass AMMONOIDEA Zittel, 1884

Order CLYMENIIDA Hyatt, 1884

Superfamily **GONIATITOIDEA** de Haan, 1825

Family **SPIROLEGOCERATIDAE** Nassichuk, 1970

Subfamily **SPIROLEGOCERATINAE** Nassichuk, 1970

Diagnosis: Subdiscoidal conch with reticulate ornament, umbilicus narrow to wide, suture characterized by broad ventral lobe with wide subdivisions, and subdivision of umbilical lobe.

Discussion: This subfamily is based on the assessments by Nassichuk (1970) and Bogoslovskaya & Pavlova (1988). It was initially proposed as a subfamily of Metalegoceratidae Plummer & Scott, as interpreted by Miller et al. (1957), who provided an extremely conservative analysis in which genera and families were reduced to a minimum. Nassichuk (1970) included the genera *Spirolegoceras* and *Sverdrupites* in his subfamily, and later *Epijuresanites* was added. Bogoslovskaya & Pavlova (1988) extended the subfamily to include a new genus *Gobioceras* and reinterpreted the group and its evolution, though readers will note the number of unproven postulations, and a measure of uncertainty over the exact sequence and timing.

Genus ***Gobioceras*** Bogoslovskaya, 1988

Type species: *Gobioceras elenae* Bogovslovskaya in Bogoslovskaya & Pavlova 1988, p. 106 from Kungurian of Outer Mongolia, OD.

Diagnosis: Weakly involute to subevolute shells with moderately wide umbilicus, ornament of reticulate lirae and radial tubercles over umbilical walls of some to all of the whorls. Collabral striae project ventrally. Ventral lobe wide, each division wider than first lateral lobe, floor of lobes prolonged as well defined recessed notch, saddles somewhat swollen. Umbilical lobe comparatively narrow, with rudimentary three-part division.

Discussion: In describing *Gobioceras* from beds of likely Kungurian age in Mongolia, Bogoslovskaya (1988) included *Uraloceras lobulatum* Armstrong et al. from the Tiverton beds of Queensland, and the Australian species agrees with the type species in ornament and nature of coiling and whorl section, and in the outer suture. The inner suture for *G. elenae* was not shown, which leaves the identification incomplete. Both species are notably more evolute with wider umbilicus than in *Spirolegoceras* and *Sverdrupites*. In her reconstruction of the course of evolution, Bogoslovskaya assumed that *Uraloceras* evolved into *Gobioceras*, but her evidence for timing is not well grounded, because it was asserted that Canadian occurrences of *Uraloceras* were Artinskian. On available evidence, they are Sakmarian.

Morphology: The present description is based on morphological interpretation of Triassic ammonoids, and differs a little from the account in Bogoslovskaya (1988), in which for example the notch in the suture is called a tooth, and the degree of coiling described as involute.

Gobioceras cancellatum*?* (Dear, 1966)

Fig. 275A, B, D

?1966 *Uraloceras cancellatum* Dear, p. 200, pl. 25, fig. 1-4.

Holotype: GSQF 9060 from Yarrol Formation, Yarrol Basin, figured by Dear (1966, pl. 25, fig. 1-4), OD.

Diagnosis: Spirally coiled subevolute shells with well rounded venter and wide umbilicus, whorls equidimensional or subequidimensional, ornament cancellate of collabral and spiral fine ribs, subdued coarser ribs may be present over the lateral wall of early coils. Suture forms eight lobes, constricted at apex, saddles swollen above basal constriction.

Material: Tiverton fragments from UQL 3128, 4512, 4514 and 4515; UQF 51680. *Bookeria geniculata* Zone, *Svalbardia armstrongi* Subzone.

Description: Shells widely umbilicate, whorls weakly transverse in section, almost equidimensional, venter well rounded, lateral walls steep, gently convex and diverging ventrally, umbilical walls steep and low. Ornament of spiral threads, about 10 in 5mm over penultimate whorl, most pronounced over venter and outer walls, crossed by fine growth increments and low wrinkles, weak radial rises on the lateral flanks of early whorls on some specimens, missing from others. The full length of the body chamber is not known: it extends for at least half a whorl. The aperture is not preserved.

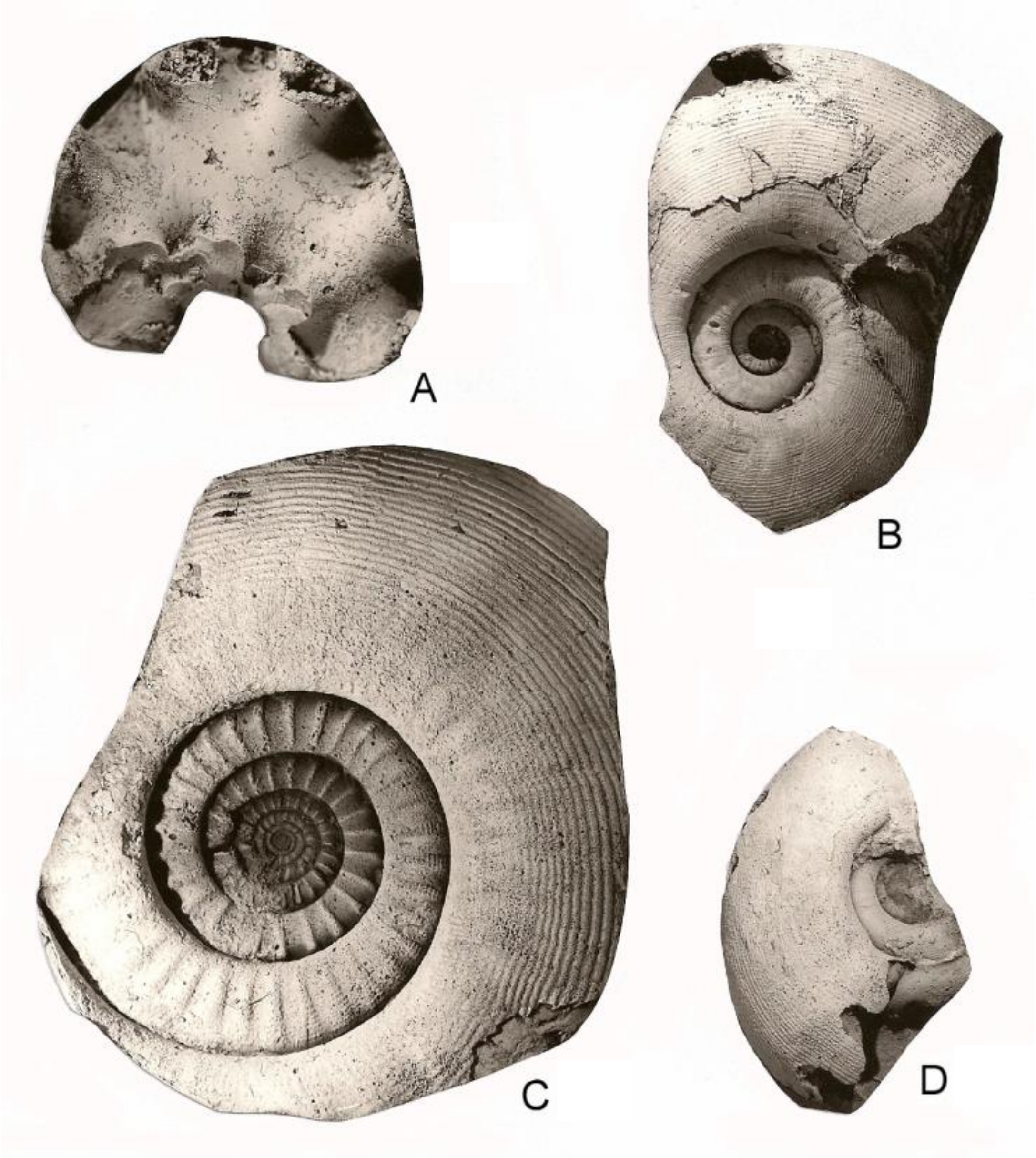


Fig. 275. A, B, D, *Gobioceras cancellatum* (Dear). A, whorl section, latex cast UQF 51680 from UQL 3128, x2. B, latex cast of UQF 81577 from UQL 4514, x1. D, latex cast of UQF 81578 from UQL 4512, x1. C, *Gobioceras lobulatum* (Armstrong et al.), latex cast UQF 81579 from UQL 4519, x2.

Discussion: These specimens are tentatively assigned to *Gobioceras cancellatum* (Dear), but the holotype as sole known topotype of this species lacks inner whorls, and is too poorly known to ascertain specific limits, so that it is not established whether it shows similar ornament to present material. That is assumed on the basis that Dear's species comes from faunas correlative with present material, and the identification clearly needs to be reinforced by discovery of further topotype specimens which show the inner whorls.

Gobioceras lobulatum (Armstrong, Dear & Runnegar, 1967)

Fig. 275C

1967 *Uraloceras lobulatum* Armstrong, Dear & Runnegar, p. 91, pl. 5, fig. 1-13, text-fig. 2A-C.

Holotype: GSQF 10556 from middle Tiverton Formation, figured by Armstrong et al. (1967, pl. 5, fig. 1, 2, text-fig. 2B), OD.

Diagnosis: Spirally coiled evolute shells with well rounded venter and wide umbilicus, whorls equidimensional or sub-equidimensional, ornament cancellate of collabral and spiral fine ribs, sturdy collabral coarse ribs present over the lateral wall of early coils, and umbilical wall of a later whorl, later whorl or whorls may display or lack such strong ribs. Suture forms eight lobes, constricted at apex, saddles swollen above basal constriction.

Material: Broken Tiverton specimens from UQL 3128 and 4519. *Svalbardia armstrongi* Subzone and chiefly *Taeniothaerus subquadratus* Zone.

Description: The species has been well described, and present material adds little, except to pose questions over the synonymy and variability in shape, whorl dimensions, and ornament. Shells widely umbilicate, the umbilicus about 40% of width, reducing to 32% in largest specimen recorded by Armstrong et al. (1967), whorls weakly transverse in section, almost equidimensional and have a Height/Width ratio of 0.9, venter well rounded. The ornament also varies in the presence of the sturdy radial ribs, which lie over the first six whorls of one specimen, five whorls in another specimen, four whorls in two specimens, and only three in another.

Discussion: The specimens from the *Taeniothaerus subquadratus* Zone have heavily ribbed whorls, and agree with *lobulatum* as described by Armstrong et al. (1967). Nassichuk (1970) regarded *Uraloceras cancellatum* Dear (1966) as conspecific with *U. lobulatum* Armstrong et al. (1967), but no reasons were provided – the suggestion may well prove correct, but it is preferred to draw attention to the difference in ornament between specimens from the different zones, until the species and morphological limits can be clarified. Armstrong et al. (1967) compared *lobulatum* to *Uraloceras complanatum* (Voinova) from Aktastinian beds of the Urals, and this species shows some approach in ornament and swollen saddles, but the mature whorl is more tapered ventrally, the coarse ornament on the umbilical walls tends to be subtubercular, and the umbilicus narrow and shell a little more involute (Ruzencev 1956, pl. 25, fig. 2-6). In all *Uraloceras*, growth-lines are protractive, not biconvex as in the Australian species, and the suture of *Uraloceras* (Ruzencev 1956, text-fig. 62c, d) differs: any approximation is therefore apparently coincidental. It may be noted that the swollen saddles are not restricted to that species of *Uraloceras*, but are found in various Early Permian genera.

Gobioceras whitehousei (Armstrong, Dear & Runnegar, 1967)

Fig. 276

1966 Paragastrioceratidae gen. & sp. Dickins in Malone et al.: 74.

1967 *Uraloceras whitehousei* Armstrong et al. , p. 93, pl. 6, fig. 1-4, text-fig. 2D.

Holotype: GSQF 10555 from middle Tiverton Formation, figured by Armstrong et al. (1967, pl. 6, fig. 1-3, text-fig. 2D), OD.

Diagnosis: Distinguished by slightly lower whorls with heavy lateral costae.

Material: Tiverton specimens GSQF 10551, 10578, UQF 64143, 64145. *Taeniothaerus subquadratus* Zone.

Discussion: In many respects this species is close to *Gobioceras lobulatus*, but the whorls are slightly lower and lateral ornament is more prominent and covers more whorls. The species comes from the same locality as *lobulatus*, and was distinguished by its umbilical ribs which remain prominent thoughout growth. Armstrong et al. (1967) considered that the growth-lines on *lobulatus* indicated an aperture slightly different from that of *whitehousei*, protractive with a broad rounded salient at all growth-stages in *whitehousei* and with broad shallow sinus in the salient in mature whorls of *lobulatus*. The sample size was not clear in the Armstrong et al. account, and Nassichuk (1970) did not appear to regard the observation as important. There are minor differences in the suture of *whitehousei*, elaborated by Armstrong et al. (1967), but arguably of no more than individual significance. Given the variation displayed by specimens, it seems possible that *whitehousei* and *lobulatus* are conspecific.

Taxonomy: As pointed out by Waterhouse et al. (1983, p. 136), the Zoological Records for 1968 (vol. 105, pt A, p. 161) assigned *Uraloceras whitehousei* Armstrong et al. (1967) to *Queenslandoceras* Mikesh, 1968, but this genus was only proposed in a thesis, and was never formally published.

Fig. 276. *Gobioceras whitehousei* (Armstrong et al.), holotype, GSQF 10555, as figured by Armstrong et al. (1967, pl. 6, fig. 3), from Tiverton Formation, x1.

Summary of stratigraphic distribution:

Archbold (2000, table 2) misrepresented the stratigraphic occurrence of *Gobioceras* in Queensland. He showed the species *Gobioceras lobulatus* as occurring in the *Echinalosia curtosa* Zone, as defined by Waterhouse (1987b) and Briggs (1998), together with what he called *Uraloceras whitehousei*, which has identical suture and rather similar ornament. The two species do not occur in the *curtosa* Zone, but in the *Taeniothaerus subquadratus* Zone, which is equivalent to part of what Archbold treated as *Echinalosia preovalis* Zone. Archbold (2000) placed *U. cancellatum* as older, which is shown to be correct. But it was assigned to the "*Tomiopsis strzeleckii*" Zone, which to present knowledge is not known in the Yarrol Basin, even in the sense used by Briggs and Archbold. The ammonoids were correlated with lower to middle Baigendzinian, but no analysis or justification has been published. Available evidence is that the ammonoids occur in the middle of the middle part of the Tiverton Formation. Armstrong et al. (1967, p. 92) stated that the holotype of *lobulatum* was found with the chonetid now referred to *Svalbardia* and *Taeniothaerus* in "zone 6" of Campbell (1961a). These two brachiopod genera seldom occur together in east Australia, and at Homevale *Taeniothaerus* enters the sequence above "zone 6". The collections made by Armstrong and his colleagues were not under tight stratigraphic control, but focused more on finding specimens. However the present author has collected the species both from the *Svalbardia armstrongi* Subzone, and from the *Taeniothaerus subquadratus* Zone (UQL 4519).

Class ROSTROCONCHIA Pojeta, Runnegar, Morris & Newell, 1972

Discussion: The validity of this class has been challenged by Starobogatov (1992), with the claim that the group constituted a superorder within Class Bivalvia. Nevesskaya (2009) placed with a query the Order Conocardiida in Superorder Septibranchia Pelsenner. Starobogatov (1992) asserted that the Cambrian rostroconch genus *Fordilla* Pojeta showed links with bivalve order Pholadomyida Newell, and added other facets deemed to support a bivalve relationship. He complained that the analysis of the group by Pojeta & Runnegar (1976) had failed to address Russian analyses, and ignored Russian taxonomic units, even though validly proposed. Starobogatov further pointed to what were interpreted as well developed adductor scars in *Eopteria* – which would have closed valves, unnecessary if the shell was univalved. Starobogatov (1992, p. 5) considered that the shell of rostroconchs did not grow as a solid single shell, but in a logarhythmic spiral which reflected gradual divergence of the two sides (ie. separate valves). This certainly seems to be the case, judged from my limited knowledge of the group. Pojeta and Runnegar considered that was achieved by periodic breakage along the hinge, which seems remarkable. Pojeta & Runnegar (1976, p. 13) argued that the dorsal shell was rigid, and “energy was needed to separate the valves so that new increments could be added to the commissure. The energy sufficed to rupture parts of the dorsal valve margin in almost all rostroconchs”. There is thus some similarity to the expansion of tree trunks – but for trees, the bark shows the expansion; and I am not sure that the dorsal shell of rostroconchs records such rupture, although Fig. 227C shows the dorsal view and indicates some irregularity of ribbing.

The material in the Tiverton Formation is too fragmentary to justify assessment of the rival claims, but the Pojeta-Runnegar scheme is accepted, because, whatever the failings with regard to adequate attention to prior classifications, their study was very thorough and wide-ranging, beyond the level attained by Russian experts, as far as can be judged.

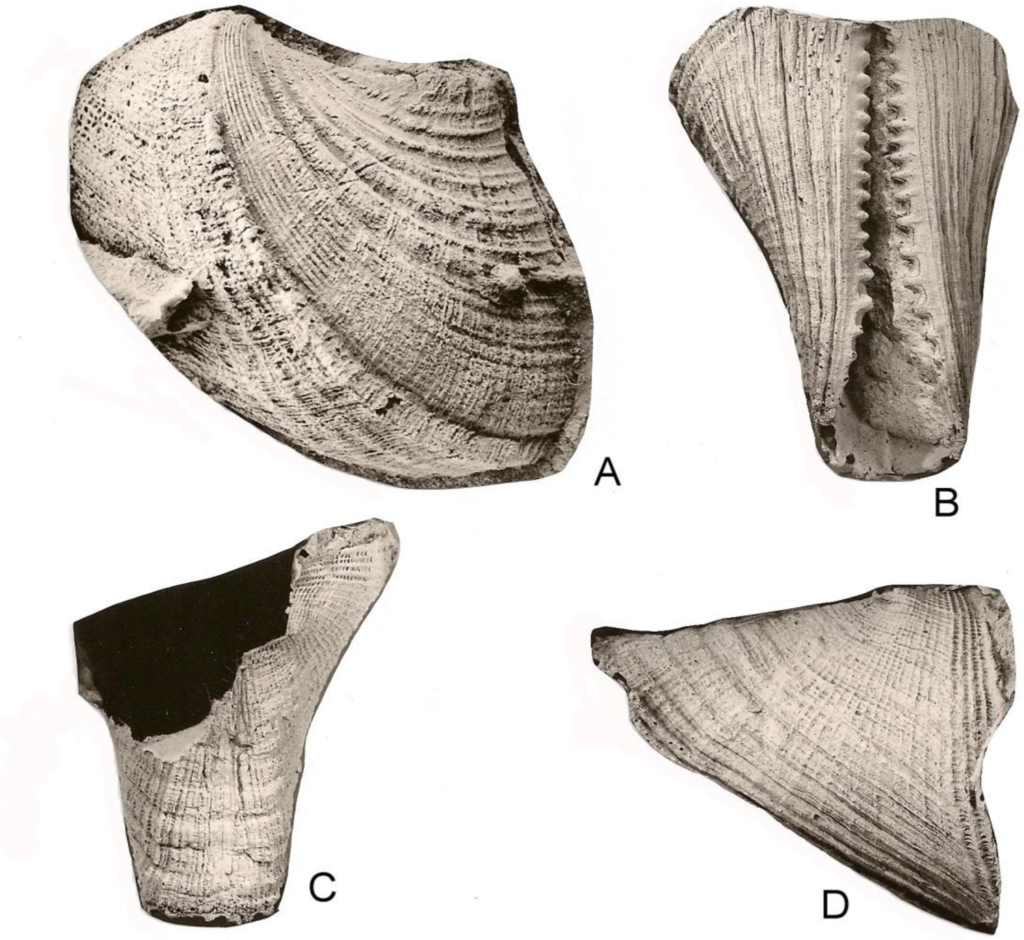


Fig. 277. *Bransonia wilsoni* Pojeta & Runnegar, latex casts. A, UQF 6231, x2. B, C, D, rostrum, dorsal and lateral aspect of UQF 81581 from UQL 3127, x 2.

Order CONOCARDIIDA Neumayr, 1891

Suborder CONOCARDIIDINA Neumayr, 1891

Superfamily **CONOCARDIOIDEA** Miller, 1889

Family **BRANSONIIDAE** Pojeta & Runnegar, 1976

Genus ***Bransonia*** Pojeta & Runnegar, 1976

Type species: *Bransonia wilsoni* Pojeta & Runnegar, 1976, p. 71 from Tiverton Formation (Sakmarian), Bowen Basin, Queensland, OD.

Diagnosis: Shells with reduced anterior gape limited to dorsal part of anterior face, or in some specimens extended ventrally as narrow slit. Ribs finer over posterior shell than on anterior face and snout. As far as can be discerned, the specimens are univalved.

Bransonia wilsoni Pojeta & Runnegar, 1976

Fig. 277

1976 *Bransonia wilsoni* Pojeta & Runnegar, p. 72, pl. 51, fig. 1-10, 17, pl. 52, fig. 1-5, 9.

Holotype: UNEF 14789 from middle Tiverton Formation, figured by Pojeta & Runnegar (1976, pl. 51, fig. 1-6), OD.

Diagnosis: Large, prominent snout and rostrum shorter than snout, body of shell carinate posteriorly, rostrum and hinge not co-linear, rostral clefts prominent, ventral aperture present.

Material: Tiverton specimens from UQL 3127, 3129, 4518 and LT3; UQF 6231. *Taeniothaerus subquadratus* Zone.

Description: A few fragments of this distinctive form are available, showing the gaping and extended snout, curved keel and posterior, and interlocking ribs along the ventral margin.

Stratigraphy: Pojeta & Runnegar (1976) gave a “Middle Permian” age to *Bransonia wilsoni*, without explanation. There is no evidence that the species is younger than Early Permian, and a late Sakmarian age is preferred.

CONCLUSIONS

PALEOECOLOGY, PALEOGEOGRAPHY, PALEOECOLOGY

1. Faunal diversity.

Newly evolved genera within the *Bookeria pollex*, *B. geniculata* and *Taeniothaerus subquadratus* Zones in the Permian of eastern Australasia, were made up of local forms that diverged from local ancestral stock, or diverged in the course of migration to the region, included these genera: *Notostrophia, Azygidium, Costatumulus, Bookeria, Pseudostrophalosia, Acanthalosia, Plekonella, Plekonina, Tweedaleia, Grantonia, Pustulospiriferina* and possibly *Maorielasma* and *Gilledia*. *Fletcherithyris* may have evolved locally, but has been reported (?wrongly) from the Pennsylvanian of Nevada (Perez-Huerta 2004, p. 47), and the source(s) of *Notospirifer* and *Tabellina* are not certain, but may prove to have been of local or other high southerly latitudes such as South America. Genera with strong northerly links, and possibly derived from such immigrants, include *Svalbardia, Anidanthia, Protoanidanthus, Terrakea, Magniplicatina, Echinalosia, Ambikella* and possibly *Geothomasia*, *Permasyrinx,* and *Cyrtella*. Tiverton *Eremithyris* is very much older than the type species of the genus, but is a cryptonelloid, more typical of paleotropical waters. The sources of *Taeniothaerus* and *Lipanteris* are uncertain, but given their preponderance in Gondwana faunas, they may have been of local origin.

Amongst Bivalvia, *Glyptoleda, Pseudomyalina, Squamuliferipecten, Elviniaria, Furcatia*, perhaps *Melicusia*, are of local origin. *Concentiolineatus* and *Orbiculopecten*, and perhaps *Eurydesma* have strong affinities with Patagonia, *Primaspina* appears to have descended from *Etheripecten*, itself a genus found in Early Carboniferous of Europe, whereas *Hillaepecten* has a number of Carboniferous and Permian links, through *Heteropecten, Inaequalitaria, Nodulipecten, Vanvleetia* and *Vorkutopecten*. The genera *Myonia, Vacunella* and allies have local sources that show strong links with northeast Asia and Patagonia, and *Megadesmus*, *Protraxia* and *Astartila* may have evolved locally. Many bivalves are more wide ranging, examples including *Palaeoneilo*, *Yanceopsis, Promytilus, Stutchburia* and *Astartella*. Within Gastropoda, most have persisted from older local faunas: *Warthia, Paraplatyschisma, Planikeeneia, Bicarinella* and *Pleurocinctosa* have local sources from earlier Permian faunas: *Austroscalata* is confined to east Australia, and *Glyptotomaria*? (*Glyptotomaria*) an import from paleotropical waters. *Globosospirina* possibly has older allies in the early Permian of east Australia and New Zealand.

The total number of Permian macro-invertebrate species and genera peaked for the *Bookeria pollex, B. geniculata* and *Taeniothaerus subquadratus* Zones in east Australia, with maximum number of new genera, locally evolved and immigrant, in the Pollex-Geniculata Zones, and maximum number of species in the Subquadratus Zone. The number then fell sharply, commencing in the *Ingelarella plica* Zone, and continuing through the upper Cisuralian Series. There was some recovery during Guadalupian and uneven progression through the Lopingian Series (Waterhouse 2010b), but numbers never reclaimed their peak through the remainder of the era. Such a trend is also repeated in the Permian macro-faunas of Western Australia, Thailand, Canada and the Urals. The faunal collapse in diversity was second only to the end-Permian extinction in a number of stations around the world (Waterhouse 2010b). That may seem to be denied in a study by Clapham et al. (2009), but in that study data was smoothed by analysing faunas at the crude level of stages, and so-called “singletons” – that is genera which lasted only for a stage or less, were deleted. Such techniques skew the data and delete inhomogeneities, thereby ensuring a smooth progression, and so cannot be considered objective. The assertion that singletons do not represent reality is an incomplete truth even if the singletons are only part of the data preserved. But there have to be instances where singletons represent the full record, most obviously where the course of evolution is disrupted by a life crisis. In such cases – and notably at the end of the Permian Period, ignoring Late Permian singletons is to seriously distort the record. Ruling out singletons, and yet taking into account crude and exaggerated time ranges, such as for *Martinia* M’Coy or *Linoproductus* Chao (see Waterhouse 2013, p. 357 ff) will distort conclusions irreparably.

2. Source of the faunas.

It is clear from the foregoing review that most of the species and genera found in the Tiverton Formation had either evolved locally in east Australia, or were sourced from other high latitude faunas, mostly Patagonia, or northern Russia and Canada. That is analyzed further by Shi & Waterhouse (2010), Waterhouse (1976b, 1977, 2010b), and Waterhouse & Shi (2010), and is consistent with the model that the hinterland of east Australia was glaciated during Early Permian time, as has been well established at least since David (1907), and written about earlier (see quote from Rands (1889) in Waterhouse 2015, p. 45), yet has been repeated as a new discovery ever since into present day studies, usually by geologists from North America and the United Kingdom. There is no support from the faunas for the so-called "tropical pump" thesis that life evolved in tropical or paleotropical regions, and was driven into progressively higher latitudes by further tropical evolution (Briggs 1987). At least during Permian time in east Australia, marine invertebrates such as brachiopods and bivalves evolved locally, and immigrant stock sourced mostly – not entirely – from other high latitude regions. There thus might appear to be support for the thesis advocated by Powell (2005, 2007), that Late Carboniferous and Early Permian glaciation had destroyed paleotropical life, so that marine paleotropics of younger age became stocked from high latitudes by long-lived widely distributed genera. That is denied by the character and distribution of Permian brachiopods in particular: the Tiverton faunas show a limited number of commonalities with the paleotropical faunas of west Texas, as monographed by Cooper & Grant (1974, 1975, 1976a, b) and of the Pamirs by Grunt & Dmitriev (1973). The high latitude faunas lack for example the richthofeniids, lyttoniids, and wellerellids which commenced in paleotropics of Early Carboniferous, and flourished in the Early Permian paleotropics. According to the Powell thesis, such forms should not have survived after the Early Carboniferous. Lyttoniids and richthofeniids, together with many other paleotropical forms, including conodonts and fusulines, are completely unknown in east Australia. To judge from the present study, neither the "tropical pump" thesis nor the "polar pump" thesis were applicable to Early Permian marine faunas. Both propositions have never been any more than conjecture, based on theory and a lack of familiarity with actual world-wide faunas. Rather, evolution was widely dispersed, proceeding in polar, temperate and tropical regions, and further affected by distribution and redistribution. A critical facet of faunal analyses requires avoidance of distinguishing between only polar and tropical – temperate regimes were just as distinctive, and temperate faunas just as important and as different as polar or tropical faunas.

3. Nature of the faunas.

It was claimed by Stehli (1970) and Stehli & Grant (1971) that Permian faunas became progressively less diverse from the paleotropics towards the paleopoles. This appears to be largely true as far as brachiopods and gastropods are concerned: it is not quite so clear with regard to bivalves, because these have not been comprehensively monographed for instance in the paleotropical faunas of west Texas, but will possibly prove correct. On that basis Stehli (1970) deduced that there was a diminution in the number of families – or genera – from paleotropics to paleopoles. But this assumption proves to be oversimplistic. Rather, high latitude faunas developed a distinctive assemblage or series of assemblages, less diverse than those of the paleotropics, but with genera and even subfamilies not found in the paleotropics. For example, Anidanthinae, Paucispinauriinae, Wyndhaminii, Rhamnariinae, Plekonellinae, Fletcherithyrini, Maorielasminae and Gillediinae are present in the lower Early Permian of east Australia, and absent from the correlative paleotropical faunas of west Texas and Asia. (Elements of some of these families did later penetrate west Texas in the late Kungurian and Guadalupian, clearly sourced from high latitudes – Waterhouse 2010b). Amongst Bivalvia, Eurydesmidae, Myoniinae and Astartilinae are widespread in east Australia, and absent from west Texas and central Asia. And on the other hand, numerous families, subfamilies and genera are present in paleotropical faunas that are completely missing from east Australia. In short, the high paleolatitude Permian marine faunas of east Australia were distinctive – not just a fading and diminished relict of paleotropical faunas, but made up to varying degree of distinctive and evolving genera, and subfamilies. The Tiverton faunas exemplify this very well. They are closely and well sampled, and include a sprinkling of rare forms with paleotropical sources – such as possible *Eremithyris* and *Glyptotomaria* (*Glyptotomaria*). But the faunas are dominated by genera never found in correlative paleotropical faunas – such as *Costatumulus*, *Paucispinauria, Pseudostrophalosia, Acanthalosia, Unicostatina, Gilledia* and many others.

4. Comparison with other east Australasian faunas.

The middle and upper Tiverton faunas belong to distinctive assemblages which differ substantially from older and younger faunas. Older faunas, best exemplified in Tasmania (Clarke 1992a), share some of the brachiopod and molluscan genera, but are characterized by strophalosiids (*Strophalosiaria, Crassispinosella*) and *Trigonotreta*, and lack anidanthins, paucispinaurians, Echinalosiinae, and various Rhynchonelliformii and Spiriferiformii, including ambocoeliids, and terebratulids. The *Bandoproductus macrospina* Zone has a very distinctive assemblage, sharing few genera with older or younger faunas. The younger Kungurian and Guadalupian faunas of east Australia are well developed and widely distributed, and studies summarized in Waterhouse (2001, 2002a) as well as Briggs (1998) demonstrate the disappearance of such genera as *Notostrophia, Svalbardia, Taeniothaerus, Lipanteris, Protoanidanthus, Azygidium, Biconvexiella, Geothomasia, Tweedaleia* and *Pustulospirina*, the last flicker in the mid-Kungurian of bivalves *Eurydesma* and *Squamuliferipecten*, not to mention the disappearance of a number of rarer genera such as brachiopods *Platycancrinella*, *Plekonina*, *Coledium* and *Eremithyris*?, and bivalves *Pseudomyalina, Hillaepecten, Melicusia* and *Astartella.* Persistent genera include *Echinalosia, Wyndhamia, Pseudostrophalosia, Acanthalosia, Anidanthia, Paucispinauria, Terrakea, Magniplicatina, Plekonella, Ambikella, Ingelarella, Martiniopsis, Notospirifer, Simplicisulcus, Permasyrinx*, *Sulcicosta*, *Fletcherithyris, Gilledia, Maorielasma* and *Marinurnula*, and bivalves *Polidevcia*, *Glyptoleda, Parallelodon, Promytilus, Merismopteria, Etheripecten, Stutchburia, Myonia, Pachymyonia, Myomedia, Protraxia, Astartila* and *Vacunella*. New entries include *Neochonetes, Lethamia, Johndearia, Mesopunctia, Aperispirifer,* and bivalves *Nuculopsis, Quadratonucula, Nucundata, Elimata* and *Palaeosolen,* as reviewed by Waterhouse (2002a), in which tables 6 – 18 summarize the zonal distributions of Guadalupian and middle to late Kungurian species described in systematic studies.

There are a number of other genera as well: they all heighten the differences between Early and Middle Permian, and there is much more to be added about further faunas and zones of eastern Australasia. But the nature of the Tiverton faunas, and the similarities and contrasts from immediately underlying and from overlying especially Guadalupian faunas, begs the question – are the differences real, or due to collection and description failure, or ecological parameters? Ecological parameters are of prime importance, and involve substrate, preservation and taphomical considerations, association with or repellance from other biota, global location, climate and other controls. At a practical and hands-on level, based on careful field-work, close inspection of available collections in institutions, and up-to-date systematic study, the adequacy of collection may be judged from assessment of density or spacing of collection stations, the length of time spent in collecting, and the area and nature of outcrop. Description coverage may be assessed critically from publications on systematic studies – because lists not based on published systematic description are of very low value, not only because they cannot be checked without further inspection of the collections, but because the identifier has not established through descriptions and illustrations the accuracy of his or her identifications. Indeed even lists sometimes betray a degree of unreliability – as for instance in Clapham & James (2009), who recorded an attempt to assess faunal distributions based on a brief field trip to east Australia, and published faunal lists that lumped genera and species into taxa superseded and refined by the international Treatise on Invertebrate Paleontology, as if such coarse and outdated systematics could convey the subtleties and ecologic and temporal implications of the actual fossil record.

Statistical evaluations

Parameters that influenced faunal development have been completely ignored in recent attempts to simplify faunal analysis by relying on mere diversity or presence-absence of genera according to one template, in which it is claimed that the absence of species and genera reflect undersampling. The techniques have mostly been extended from industrial testing, devised to assess variation and constancy of single manufactured items, for which time is a constant, and morphological range miniscule, and one kind of sample tested. Such simple techniques cope poorly with the much greater variability and complexity of biota through time and space. Stehli (1970) and Stehli & Grant (1971) applied a concept and formula of "cosmopolitan dominance" without ever establishing that the families cited were truly cosmopolitan. Nonetheless, that approach did acknowledge the need to test if samples were fully or less than fully sampled – or fully preserved: the principle was sound, but it proved too complex to resolve through any formulaic approach. In recent years, "rarefaction" has been applied to large numbers of fossil brachiopod collections, including lists, with no preceeding test for undersampling. Rarefaction was first applied by Sanders (1968) to the distribution of echinoderms in present seas, developing a formula that fitted numbers of taxa belonging to a single biotic group and constant with regards to time – the present – to a normal frequency curve. The outline of the curve depended on establishing the full number of species: a lesser number, deemed undersampled, could be fitted to the curve with predictability provided by the full number. But many assumptions have to be made that the lesser number is indeed related to the "full" number. Raup (1976) in trying to adapt that principle to fossil faunas, warned that there were a range of normal frequencies. Clearly substrate, and other geological parameters of time and space affect the numbers and kinds of species. Studies will fail if they do not provide any test or even assessment of undersampling, with no allowance for substrate, no close time control, and no adjustment for constraints due to paleolatitude and various environmental parameters, including ocean currents, water depth, and temperature. They may rely on the initial number to both prove undersampling and provide the final assessment of "real" potential peak number, but such studies ignore the reality of faunal distributions through time and space. In reality, faunas from any east Australian Permian station differ so much from west Texas faunas that they have to be assessed separately to test for undersampling and for the maximal number of species present. The same applies through time: analysis must be zone by zone if not community by community, and certainly not lumped in 5 Ma bands.

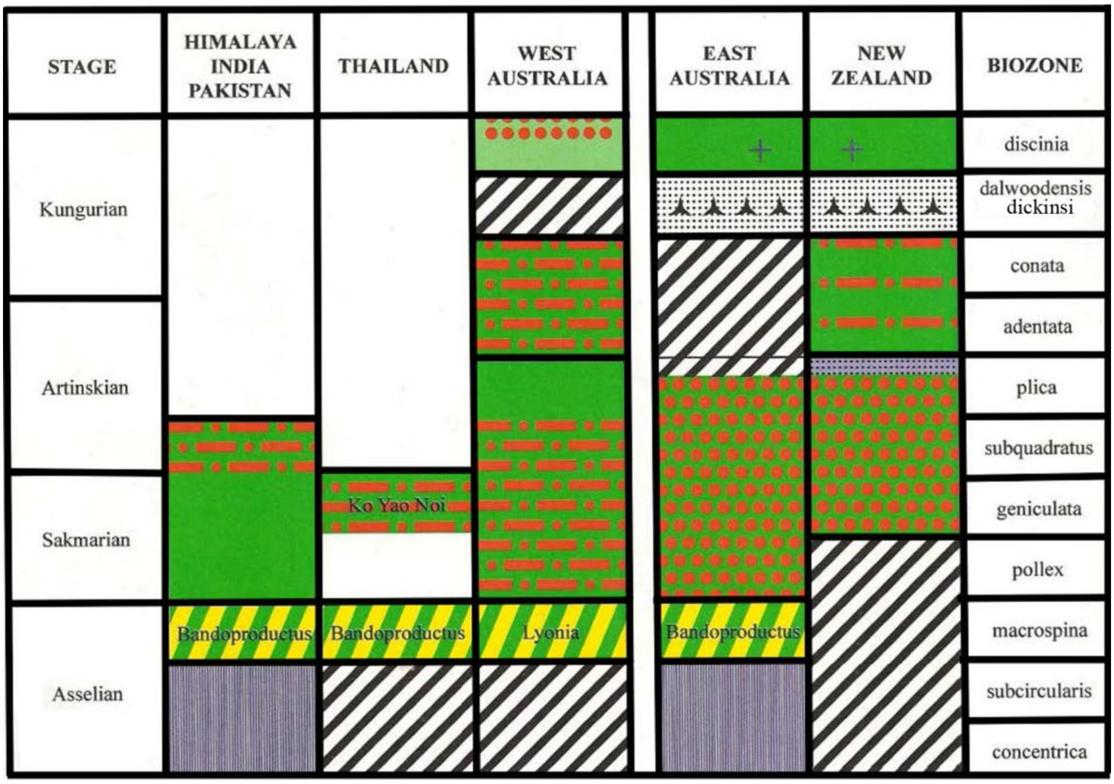


Fig. 278. Major faunal assemblages, or faunal provinces, distinguished by pattern, as based on Brachiopoda and Mollusca, for parts of the southern paleohemisphere. 1, Strophalosiid brachiopod zones *concentrica* and *subcircularis* with *Eurydesma* and *Deltopecten* , and cold-water lithosubstrates. 2, *Bandoproductus macrospina* and other moderately temperate to warm-water indices. 3, The zones named *pollex* to *plica* comprised of dasyalosiids (ie. *Echinalosia*, *Capillaria, Pseudostrophalosia, Acanthalosia*) with *Bookeria*, ingelarellids and bivalve *Squamuliferipecten* in east Australia, some genera extending into warmer water faunas of peripheral Gondwana. Brief cold episode indicated for top of *Ingelarella plica* Zone in New Zealand. 4, *adentata* and *conata*, warm-water faunas with rhamnariids and other Productida in New Zealand and Western Australia, coal measures in east Australia. The *Echinalosia conata* Zone is followed by an unshown *Trabeculatia marwicki* assemblage, also termed *Attenuocurvus* beds in Tables 1 and 7, with paleotemperate shell fish, of early Kungurian age. 5, *Glendella dickinsi* Zone with few and cold-water indices, including *Glendella* as a eurydesmid bivalve below *Wyndhamia dalwoodensis*, cold water indices numerous; and 6, *Echinalosia discinia* Zone and overlying Middle Permian faunas, involving genera and species of *Etheripecten, Fletcherithyris*, etc. and without earlier Permian genera such as *Deltopecten, Bookeria, Grantonia* etc. (See Waterhouse 2008b, 2010a, Waterhouse & Shi 2010). Cross hatching signifies rocks with few or no marine fossils.

Miller & Foote (1996) used rarefaction analysis to modify and try to correct the implications of raw diversity trends of marine invertebrates through the Ordovician Period. Their approach cannot however be applied without substantial modification to changing diversities of Permian invertebrate taxa in east Australia: they measured diversity only at series level in a stratigraphic sense – the series being of very unequal length, which they were attempting to adjust. They rarified the taxa of one series to the series of the next (Miller & Foote 1996, p. 307). The smoothing of data, the assumption that stations with few genera are undersampled compared with stations with numerous genera, the assumption that a zone and its fauna can be adjusted to conform with an overlying or underlying zone, are all questionable, and the techniques applied by Miller & Foote (1996) in a search for the world diversity changes seem inapplicable to the quest for calibrating changes in taxonomic diversity through the stratigraphic column, at least in Permian of Gondwana. Even simple raw data provide critical information that should not be lost, and commercial sample formulae are misapplied if they smooth out, or disguise and conceal, meaningful fluctuations – such techniques too easily ensure that the medium becomes the message. The vast ability of computers nowadays enables the application of complex techniques to replace of the simplistic modes of analyses currently favoured, and it has to be questioned why so many studies in paleontology avoid the use of sophisticated computer-aided mathematics, and rely on simplistic overgeneralized application of formulae devised for much more circumscribed problems. If that cannot be done, studies would be more fruitfully devoted to systematically analyzing more faunas. One important prerequisite is the need to analyse zones, not stages or series, or arbitrary 5Ma bands of time, divorced from biological reality. Another is the assessment of sampling reliability from the range and number of stations sampled. Clearly one sample for one lithology must be inadequate, and unfortunately, rarefaction of a few stations from each different lithologies has to be questionable. But data based on many samples, from a range of lithologies, and a range of geological settings, is going to be of high value. Nevertheless, in some settings, even samples from limited lithology that have few species can prove highly instructive – because the very paucity of taxa, if not due to tectonic or other such geologic processes, is pointing to environmental constraints that must have influenced the evolution and abundance of biota.

So how does the sampling rate for the succession of Tiverton faunas? Clearly the basal ingelarellid fauna is undersampled: just two species in closely allied genera. Potentially correlative with faunas described from Cranky Corner by Archbold (2003) and upper Rammutt fauna of Gympie (Waterhouse 2014), it provides no more than a datum point, and to estimate the full diversity of any contemporaneous fauna from the northern Bowen Basin would require extrapolation of diversity trajectories calculated from analysis of better known and more widespread faunas. The next faunal interval shares a number of species with the *Bookeria pollex* Zone of the southeast Bowen Basin, and is clearly undersampled, in the sense of actual impoverishment as opposed to inadequate collecting, and even suggests some faunal mixing. The following two zones, named after *Bookeria geniculata* and *Taeniothaerus subquadratus* appear to be adequately sampled. The *Bookeria geniculata* Zone is more diverse than the zone in the Elvinia Formation and Riverstone Sandstone Member of the southeast and southwest Bowen Basin, and correlative faunas of the Sydney Basin. But the slight differences appear to be real, rather than due to undersampling. There were differences across the Bowen Basin in the presence/absence of some species and genera, just as there are in present seas and embayments. The full diversity for a geological zone is readily and realistically obtained by amalgamating the different faunal assemblages. These combine the species distribution in a number of lithofacies and substrates and water-depths, volcanic breccia, conglomerate, a range of sandstones, mudstones and siltstones, and limestones, though coral and bryozoan bioherms are lacking. Much the same applies to the *Taeniothaerus subquadratus* Zone, obtained from a greater diversity of carbonates as well as clastic sediments. There would seem to be no point in applying the Stehli formula, or rarefaction analysis, because the zones are not undersampled, and any further collecting or search through repositories seems unlikely to add more than a handful of brachiopod or mollusc species and genera.

More of a challenge centres on the *Ingelarella plica* Zone at the top of the Tiverton Formation. The Tiverton fauna is not large, and therefore open to caution. But shared and short-ranged species are shared with the Cattle Creek Formation, in a finer lithofacies, and with the Rose’s Pride Formation, in a shallower-water facies of coarse quartzitic sandstone and conglomerate, that expand the number of species and genera. Further afield, the Brunel Formation (Waterhouse 1982a) and Skippers Volcanics (Begg & Ballard 1991) of New Zealand has the same key species and still more genera, found in volcanigenic breccia, sandstone and tuffaceous siltstone and argillite. Thus five different stations have each contributed samples from different fossil communities, and must come close to presenting a reasonable if not full record of the genera and species then inhabiting rocks and sea-floor during the time of the *Ingelarella plica* Zone.

Peculiarities of the *Ingelarella plica* Zone

There is an interesting and significant additional aspect to the nature of the *Ingelarella plica* Zone. In New Zealand, the upper part of the zone in the Brunel Formation is severely depleted in numbers of species: key species persist – but many others are lacking. The remaining species are especially typical of east Australasia: *Notostrophia, Terrakea, Ingelarella,* and bivalves *Squamuliferipecten* and *Etheripecten*. Missing are such genera as *Rhipidomella, Capillonia, Acanthalosia, Pugnoides, Plekonella, Psilocamara, Tigillumia, Kaninospirifer* and other genera, and bivalves *Striochondria*, *Corrugopecten* and *Fletcheripecten,* which are found in underlying beds. Yet the substrate is very similar for both faunas. A comparable fauna with the same key species *Notostrophia homeri* Waterhouse is found in the Mantle Volcanics of the Skippers Range, southern New Zealand, together with the psychrophilic genus *Eurydesma* (Begg & Ballard 1991; Waterhouse 2002a, p. 194), and yet another possible exemplar in the Grampian Formation of Nelson (Bruce 1962, Waterhouse 2002a, p. 195). This suggests that another factor became important: one that left no visible trace in the sediment, yet helped remove a number of the species and genera that are less widespread in east Australian faunas of this approximate age, and more typical of lower latitude faunas (*Rhipidomella, Pugnoides, Psilocamara, Kaninospirifer*), indeed leaving not a single species with traits of lower latitudes. Therefore it is hypothesized that the fauna reflects a short-lived cold episode, to be tolerated only by typical east Australia genera inured to cold conditions. To treat the fauna as "undersampled" is unrealistic. To amalgamate the two *plica* faunas, or intergrate them as treated in some rarefaction studies, would be both inaccurate and destructive of information concerning the palaeoecology and palaeoclimatic record. Moreover, in other parts of east Australia, there is no sign of such a fauna. This is because there are gaps in the record. No applications of the rarefaction treatment or Stehli formula will ever detect such gaps: they are more likely to pretend that they did not exist. But a gap, or a "non-existence", has reality.

APPENDIX

THE WUCHIAPINGIAN STAGE IN EAST AUSTRALIA AND NEW ZEALAND

Marine representation of the Wuchiapingian Stage, basal unit of the Lopingian Series, and an important stage with more conodont zones than any other Permian stage, would appear to be limited, to judge form the local biozones as summarized in Table 1, p. 4 of this monograph. This is partly a reflection of the need to conduct more studies on rocks and faunas of the stage in both east Australia and New Zealand, and partly because comparatively thick rocks occupying a stratigraphic position below Changhsingian faunas and above Capitanian faunas have few fossils. A basal Wuchiapingian biozone is represented by *Ingelarella havilensis* Campbell, 1960 at the top of the marine sequence in the northern Bowen Basin, called the Havilah fauna by Dear (1972). This found in the upper part of the Blenheim Formation and in the MacMillan Formation and Black Alley Shale, as elaborated by Dickins (1983, 1989), and lies above a transitional fauna exemplified by what Dear (1972) called the Pelican Creek fauna, which shares a number of species with the underlying Scottville fauna with *Pseudostrophalosia clarkei* (Etheridge Snr) and *Terrakea elongata* (Etheridge & Dun), dated as Capitanian of the Middle Permian Guadalupian Series. All three faunas as they were termed by Dear need amplification, and only the *Pseudostrophalosia clarkei* Zone with elements of the Pelican Creek fauna are represented at Wairaki Downs in New Zealand (Waterhouse 1998a, 2001, 2002a).

The topmost zone for the Wuchiapingian Stage in east Australia – New Zealand is represented by the *Martiniopsis woodi* Zone. This has been correlated through *Martiniopsis woodi* and *Simplicisulcus arthurtonensis* and other species with the lower Chhidru Formation, Kufri Member, of the Salt Range, Pakistan (Waterhouse 2002a, pp. 212-213), and the lower Chhidru beds have Wuchiapingian conodonts (Wardlaw 1997, Wardlaw & Mei 1999, Shen et al. 2003). The zone is best represented as the Earnvale Member at Arthurton, and further study is required of possible passage beds or prolonged fossil ranges in the area of Wairaki Downs (Waterhouse 2001, 2002a).

In New Zealand, thick limestone and minor sandstones of the Wooded Peak Subgroup lie below the *Martiniopsis woodi* Zone and above the *Pseudostrophalosia clarkei* Zone, and probably represent the bulk of the Wuchiapingian Stage. There are only scattered and often solitary fossils as a rule, involving the brachiopod *Capillonia*, rare *Paucispinauria*, and a lens at Wairaki Downs that contains distinctive species of *Neospirifer* sensu lato and *Spiriferella* sensu lato (Waterhouse 2002a, p. 65). The bivalve *Mytilidesmatella woodi* (Waterhouse) is found in two carbonate units of the Wooded Peak Group, in the Otaria Formation at Arthurton (Waterhouse 2002a, p. 99) and in the Waimahaka Limestone near Kuriwao (Waterhouse 2002a, p. 94). A related species *M. sivelli* Waterhouse is found in an overlying sandstone unit, Barrington Sandstone (Waterhouse 2002a, p. 233).

It is clear that further study is required to clarify the relationships and nature of fossils in the Capitanian and early Wuchiapingian of east Australia, and possibly the Wuchiapingian-Changhsingian interface in New Zealand, and bring together the information provided by various fossils from intervening beds. Until this is done, the Wuchiapingian is not accurately or fully represented in correlation charts or proposed correlations.

DETAIL OF UQL COLLECTIONS

VARIOUS LOCALITIES IN EAST AUSTRALIA

UQL	Description
29	Berseker beds, Berseker Graben, Lakes Creek Quarry, Rockhampton.
140	Wallaby beds, Stanthorpe Road block. Wallaby Rocks, Silverwood, Warwick.
622	*Eurydesma* beds, Stanthorpe Road block. Low divide between *Cardiomorpha* and *Eurydesma* gullies. Parish Wildash, Warwick.
1347	Neerkol, Isolate Creek. Coll. W. G. H. Maxwell.
4836	Elvinia Formation, near Cracow, near base. Bush-covered spur north of Buffel Hill, top of eastern face. Near Cracow homestead. Mundubbera map sheet.
5114	Farley Formation, Lochinvar Anticline. Track south of Mount View, from richly fossiliferous sandstone overlying band with abundant chonetoids. Singleton. Coll. D. J. C. Briggs.

COLLECTIONS FROM TIVERTON FORMATION

Collections by W. G. H. Maxwell, 3/1952

UQL	Description
1382	Homevale Station, at base of ridge that bears molasses tank.
1383	Homevale Station, 50 yards SW of UQL 1382, near fence which crosses Homevale-Nebo Road.
1385	Ridge south of Homevale – Elphinstone Road (Mt Coolon Map), at Bull Creek crossing.

Collections by K. S. W. Campbell and G. W. Tweedale, in 1956 from Tiverton Formation at Homevale. See Fig. 5, p. 26. Note that the “beds” are bands, some with several beds.

UQL	Description
1619	Homevale Bed No. 2.
1620	Homevale Bed No. 3.
1621	Homevale Bed No. 4.
1622	Homevale Bed No. 5.
1623	Homevale Bed No. 6.
1624	Homevale Bed No. 7.
1625	Homevale Bed No. 8.
1626	Homevale Bed No. 9.
1627	Homevale Bed No. 10.
1628	Homevale Bed No. 11.
1629	Homevale Bed No. 12.
1630	Homevale Bed No. 13.

Collections by F. W. Whitehouse, 8/1962, grid reference, McKay 4-mile map, 21°26”14’ S; 145° 32”10’.

UQL	Description
2584	Homevale Station.
2619	Homevale Beds. Bed 12. On the NE flank of the most southwesterly of three ridges. Eastern edge.
2620	Homevale Beds. Bed 11. Upper part of middle of three ridges, extending down on its SW flank to the benched track at the molasses tank.
2621	Homevale Beds. Bed 1. Thin limestone bed in the NE portion of the northeasterly of two depressions.
2622	Homevale Bed 1. Lowest fossiliferous limestone and talus extending down about 10 feet of lower slope.
2623	Homevale. Bed 2. About 5 inches of shales capped by limestone bed in middle of the NE of three ridges.
2624	Homevale Bed 3. From the limestone beds to about 8 feet below the topmost point of the NE of three ridges at the molasses tank.
2625	Homevale Bed 4. The top 8 feet of the NE of three ridges at the molasses tank.
2626	Homevale Bed 5. The limestone bed fringing the SW capping of NE portion of northeasterly of three ridges.
2627	Homevale Bed 7. The upper of two limestone beds in the NE portion of the three ridges.

2628	Homevale Bed 8. Immediately on the NE side of the gutter draining the more northeasterly of the three ridges.
2629	Homevale Bed 9. Immediately SW of the gutter draining the more northeasterly of two depressions.
2630	Homevale Bed 10. About halfway up the NE slope of the middle of three ridges at the molasses tank.
2631	Homevale Bed 11. Upper part of middle of three ridges, extending down its SW flank, to the bench.

Collections by J. D. Armstrong and B. Runnegar, 10/1966.

UQL	**Description**
3127	General collections near Homevale Station, through middle Tiverton Formation.
3128	Ammonoids near Homevale Station, erosion gully cut across track which comes in from track from homestead to Collinsville – Nebo Road. Grid reference 21^{o} 26.5'S, 148^{o} 32' E.
3780	Homevale.

Collection by J. S.Jell and J. B. Waterhouse

3725	About 5.5km SE of Exmoor Homestead, near boundary fence between Exmoor and Blenheim stations. Stratigraphically 40m below base of Wall Sandstone. Urannah 1: 100 000 topo series PC 8556, grid. reference 2147 8002. Bowen.

Collections by J. B. Waterhouse with P. Balfe and D. J. C. Briggs, 1/7/1979 and 2/7/1979. Grid reference MCKAY Sheet 584 281. See Fig. 5, p. 26.

UQL	**Description**
4505	160m from UQL 4507 NE on flat. Base of Tiverton Formation.
4506	40m distance and ?10m stratigraphic thickness above 4505.
4507	Largely barren sandstone, 2m richly fossiliferous along base of hill.
4508	*Eurydesma* band along base of hill, persisting to saddle.
4509	NE flank to hill NE of molasses tank.
4510	Hill crest, calcareous band beyond gulch and molasses tank.
4511	Band 4m thick up hillside NE of molasses tank and gulch.
4512	2m calcareous bed up hillside NE of molasses tank and gulch.
4513	Conspicuous 0.7m calcareous band NE of gulch.
4514	2-3m stratigraphic thickness and 20m distance up slope to NE from gulch. Chonetid common.
4515	2m stratigraphic thickness at gulch NE of molasses tank. Chonetid abundant.
4516	5-7m on NE slope of hill away from molasses tank. Rare *Taeniothaerus*.
4517	Road leading to molasses tank on Homevale fossil hill.
4518	3m including 0.7m calcareous bed below road leading to molasses tank.
4519	5-6m stratigraphic thickness up the hill bearing the molasses tank.
4520	Base of the hill bearing the molasses tank.
4521	Gully in the fossil hill between the molasses tank and road to Mt Britton, 2-4m thick.
4522	NE bank of hill (down sequence) of Mt Britton Road, 3-4m in stratigraphic thickness.
4523	Highly fossiliferous band on NE side of road leading to Mt BrItton in upper part of sequence.
4524	SW side of road to Mt Britton, top of Homevale sequence at the Homevale fossiliferous hill.
4525	160m NE from UQL 4524.

UQF LOCALITY DATA. No UQL number allocated.

UQF 6231	Mt Britton ridge near Nine Mile Creek, Mt Britton.
UQF 21901	Homevale Zone 3, Mt Britton.
UQF 20956	Homevale beds, Bowen Basin. Coll. G. W. Tweedale.
UQF 20957	As above.
UQF 20958	As above.
UQF 64143	*Uraloceras whitehousei*, E of Homevale Homestead, 20 miles NW of Nebo.
UQF 64145	Same as preceeding.
UQF 66018	0.4km E of Homevale Station. GR 21^{o}26' S, 148^{o} 32' E. Coll. P. McInnes.
UQF 66020	0.4km E of Homevale Station, GR 21^{o} 26.5' S, 148^{o} 32' E. Coll. P. McInnes.
UQF 66021	0.4km E of Homevale, GR 21^{o} 26.5' S, 148^{o} 32' E. Coll. P. McInnes.

GSQ data. Data is on file at Queensland Museum Science Annex at Hendra, and see Briggs (1998).

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INDEX

Index to fossil genera and species mentioned in the text. Names in bold signify genera in Tiverton Formation. Figures in bold script indicate description of the taxon