BRACHIOPOD SPECIES OF SPIRIFERIDINA FROM THE PERMIAN FAUNAS OF EAST AUSTRALIA AND NEW ZEALAND

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List of families, genera and species New taxa in bold

Biozone	**North Bowen Basin** Formation	**Cracow, SE Bowen Basin** Formation	**Springsure, SW Bowen Basin** Formation	**North Sydney Basin** Formation	**New Zealand** Formation
Echinalosia conata	?Wall Sandstone*		Aldebaran* Definitely younger in part	Greta Coal Measures*	McLean Peaks Heartbreak
Spinomartinia adentata	unconformity	unconformity	unconformity		Chimney Peaks
Ingelarella plana	Upper Tiverton	Roses Pride	Sirius Mudstone Member	?	Brunel
Notostrophia zealandicus					
Taeniothaerus subquadratus	Middle Tiverton	Pindari	Staircase Moorooloo Riverstone	Upper Farley?	Gondor
Magniplicatina undulata	Middle Tiverton	Elvinia	Reid Dome Beds* [control poor]	Farley	(Dunton Range)
Notostrophia bifurcata	Lower Tiverton	Dresden		? Basal Farley	?Longwood Group, without described fossils
Echinalosia curtosa		Fairyland		Rutherford	
Bandoproductus macrospina	basal Tiverton?	Camboon VolcanicGroup (no fossils at Cracow)			
Crassispinosella subcircularis	Lizzie Creek Volcanic Group			Allandale	
Strophalosiaria concentrica				Lochinvar	

Table 4. Occurrence of marine faunal biozones in Early Permian formations as named in important sequences the Bowen and Sydney Basins of Queensland and in New Zealand. Grey panels signify the absence or scarcity of marine faunas, and asterisks signify mostly or entirely non-marine conditions, with poor macro-faunal control. The Staircase and Moorooloo sandstone units between the Sirius and Riverstone fossiliferous bands in the southwest Bowen Basin imply a possible faunal gap, but the western Bowen basin faunas need to be systematically examined in modern terms. The upper Aldebaran Formation of the Springsure region contains late Early Permian brachiopods (Waterhouse 2001, Earthwise 3, p. 74), but older Aldebaran beds are not dated by brachiopods. 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 for the volcanics. 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.

REPOSITORIES

Fossils described throughout this report from the University of Queensland, Department of Mineralogy & Geology, are housed in the Bulk Storage of the Queensland Museum and Science Annex, Hendra, Brisbane, and are registered individually by number with the prefix **UQF**. They come from localities numbered with the prefix **UQL**. Fossils from **GSQ**, Geological Survey of Queensland, and **QMF**, Queensland Museum, are also stored at Hendra, Brisbane. In New South Wales, the repository includes **AMF** for Australian Museum, Sydney; with **ANU,** Australia National University, and **CPC** – now **AGSO**, former Bureau of Mineral Resources – at Canberra ACT. For Victoria, **NMVP**, Museum of Victoria, Melbourne and **MUGD**, Department of Geology, University of Melbourne. In Tasmania, **GST**, Geological Survey of Tasmania, Hobart, and for Western Australia, **GSWA**, Geological Survey of Western Australia, Perth. For New Zealand, repositories involve **BR**, for brachiopods kept at the Institute of Nuclear and Geological Sciences, Lower Hutt, **OU**, Department of Geology, Otago University, Dunedin; and **V**, Department of Geology, Victoria University, Wellington. From further afield, in England, **BMNH** and **BB** refer to collections at the Museum of Natural History, London and **S.M.E**. Sedgwick Museum, Cambridge; **CCGBH**, Changchun College of Geology, Jilin, China; **CASG** to the Department of Geology at Chandigarh, Punjab and **GSI**, Geological Survey of India, Kolkata (Calcutta); India; **GSC**, Geological Survey of Canada, Ottawa, **U.C**. University of Calgary (according to the publication, not UC = Field Museum of Natural History, Chicago), with specimens stated to be on loan to the Geological Survey of Canada; and **USNM**, United States National Museum, Washington D. C., USA.

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SPIRIFERIFORM BRACHIOPODS IN THE PERMIAN OF EAST AUSTRALIA AND NEW ZEALAND

Abstract

Spiriferiform brachiopods, in which are included mostly transverse shells with plicae, fascicles and ribs, and internal spiralia, are moderately common in the Permian sediments of east Australia and New Zealand, as species which appear to have been relatively short-ranging, without the exuberant evolution and often localized development exhibited by many members of Productida.

INTRODUCTION

In this study, the nature and distribution of individual species of spiriferiform brachiopods are recorded from Permian sediments of east Australia and New Zealand, to complete the record of Spiriferida, for which Martinidina have been outlined in Earthwise 25 (Waterhouse 2024a). Punctate spiriferiiforms, including Spiriferinida. follow in Earthwise 27 (Waterhouse 2024b). Not all are covered: some of the small or fragmentary specimens that cannot be specifically identified are set aside, and there may have been inadvertent omissions. The species within each section are ordered by age, and the order and generic content of each section for this volume of Earthwise, no. 26 is as follows :

HYPORDERS IN SUBORDER SPIRIFERIDA WAAGEN, 1883

Abstract

Hyporders are recognized for superfamilies within the brachiopod suborder Spiriferidina Waagen, 1883.

INTRODUCTION

The section of the *Revised Brachiopod Treatise* that dealt with Spiriferida Waagen by Carter & Gourvennec (2006a) presented a huge improvement over previous classifications. This summary on Spiriferida extends that classification, by discussing several hyporders, by grouping superfamilies that share critical features and are differentiated by those features from allied hyporders. It is believed that a hyporder is equivalent to an infrasuborder, and names for infrasuborders that have already been recognized are transferred into hyporders. Hyporders are the preferred term, because they have been extensively recognized in Class Bivalvia by Carter et al. (2011), and it is believed that classificatory terminology should be as uniform as possible across phyla.

Order **SPIRIFERIDA** Waagen, 1883

Suborder **MARTINIIDINA** Waterhouse, 2010

[Martiniidina Waterhouse, 2010, p. 13].

Distinguished from Spiriferidina by the presence of tabellae, called in some studies dorsal adminicula, which support the crural plates in the dorsal valve. Some constituents have secondarily lost the tabellae.

Hyporder Cyrtiidei Waterhouse, 2016

[Nom. transl. hic ex Cyrtiimorphi Waterhouse, 2016, p. 33].

Cyrtiidei embraces three superfamilies, Cyrtioidea Fredericks, 1924 of late Upper Ordovician to Lower Devonian age, Adolfioidea Sartenauer, 1966 of Silurian (Wenlock) and Devonian age, and Ambocoelioidea George, 1931, which ranged from Silurian (Wenlock) into Lower Triassic, and possibly as high as Upper Triassic. All three superfamilies as classified in the *Revised Brachiopod Treatise* vary considerably in their internal morphologies.

Cyrtioidea have sulcus and fold, may display costae or plicae, and varied micro-ornament of capillae and growth increments. The delthyrium may be open in Cyrtiidae, or occupied by cover plate or deltidial plates, and no genus clearly shows a subdelthyrial connector plate, to judge from figures in the *Revised Brachiopod Treatise*. The internal mould for *Hedeinopsis* Gourvennec for example does not show any connector plate. In many genera, dental supporting plates are linear and so could be a single plate, or two plates well aligned, a question requiring resolution. In other genera, such as *Macropleura* Boucot and *Espella* Nilova, adminicular and dental plates lie at different angles. Crural plates and tabellae may be present, but a cardinal process is absent from early forms. Adolfioidea display comparable dental supports, including possible adminicula, and developed a ctenophorium, and the delthyrium is open. In many genera there are no readily observable tabellae, but conspicuous tabellae are found in *Eurekaspirifer* Johnson, and suggestions of short tabellae occur in *Indospirifer* Grabau and *Howittia* Talent. The descriptions in the *Revised Brachiopod Treatise* as summarized by Johnson (2006a) and Johnson & Hou (2006) should be expanded to more closely elucidate these features.

Ambocoelioidea are also small shells, and may be biconvex though tending towards planoconvexity. In 2016, p. 360, Waterhouse regarded the group as constituting a separate infrasuborder on the basis that many component genera lacked adminicula and dental plates and tabellae, but it is now considered that the group should be incorporated within Cyrtiidei. The ornament is varied but most often spinose or pustulose, arranged in commarginal rows. Internal plates are highly varied, and may involve linear dental plates without obvious adminicula, though many genera lack dental plates and adminicula. Several genera in Superfamily Ambocoelioidea appear to display tabellae, although in other forms the morphology of the crura and its supporting plates is obscure, and crura appear to extend from the crural plates to the floor of the valve, but could prove to involve low tabellae. In the ambocoelioid group Rhynchospiriferidae Paulus, elevated here from subfamily status, the dorsal valve displays well-developed crural plates in a cruralium supported by a septum, conceivably a septum duplex made up of two tabellae. A simple bulbous cardinal process is present in many genera, although some genera display a ctenophoridium. Radial ornament is comparatively rare. No subdelthyrial connector plate as far as known, though the figure of *Diazoma* Dürkoop of mid-Devonian age in the *Revised Brachiopod Treatise* (Johnson & Hou 2006, Fig. 1142.5f, p. 1741) suggests the need for checking.

Hyporder Martiniidei Waterhouse, 2010

[Nom. transl. Waterhouse 2024a, p. 5 ex Martiniiformii Waterhouse 2010, pp. 13, 63].

The time range is from Silurian (upper Wenlock) to Late Permian. Ingelarelloidea Cambell has well-developed adminicula and tabellae. Elythyniidae Gourvennec ranges from Early to Middle Devonian and is close to Ingelarelloidea, with adminicula and tabellae, whereas Tenellodermidae (Silurian to Middle Devonian) lacks tabellae and has adminicula. Brachythyroidea Fredericks is close in internal plates to Martinioidea Waagen (see Waterhouse 2024a, p. 17) and both superfamilies have lost the adminicula and tabellae, but in other respects, involving shape, musculature and micro-ornament, are close to Ingelarelloidea. There is no subdelthyrial connector plate in any known member genus.

Hyporder Choristitidei Waterhouse, 2016

[Nom. transl. hic ex Choristitimorphi Waterhouse 2016, p. 112}.

Both member superfamilies have tabellae, and lack a connector plate. Theodossioidea Ivanova, 1959 of Lower to Upper Devonian age has capillate or costate or plicate ornament and short tabellae. Constituents within Choristitoidea Waterhouse (Upper Devonian to Middle Permian) are distinguished by their long tabellae, and ornament of strong costae. This group is rearranged from the interpretation in the *Revised Brachiopod Treatise*, as summarized in Waterhouse (2016, pp. 112-138), with the gathering together of a number of families scattered throughout the Spiriferoidea section of the *Revised Brachiopod Treatise*. Angiospiriferinae Legrand-Blain 1985, is excluded. This group was classed within Choristitidae by Carter (2006a, p. 1780), following Carter et al. (1994), but belongs rather as a full family in Trigonotretoidea.

Suborder **SPIRIFERIDINA** Waagen, 1883

[Nom. correct. Pitrat 1965, p. 668 pro suborder Spiriferacea Waagen, 1883, p. 447].

No tabellae present, the crural plates being unsupported. A subdelthyrial connector plate is developed under the umbo in the ventral valve.

Spiriferidei Waagen, 1883

[Nom. transl. hic ex Spiriferida Waagen, 1883, nom. correct. Moore, 1952, p. 221, pro order Spiriferacea Kuhn, 1949, p. 104, nom. transl. ex suborder Spiriferacea Waagen, 1883, p. 447].

This hyporder is discriminated for shells that are mostly transverse and ornamented by costae, which lie over plicae and may be arranged in fascicles, sulcus and fold with wide often alate hinge, delthyrium often partly closed by stegidia. Internal plates include adminicula, dental and crural plates and ctenophoridium, but never tabellae, and a subdelthyial connector plate is the rule. Range Upper Devonian (Famennian) to Late Permian (Changhsingian). Superfamilies include Spiriferoidea King and Spiriferelloidea Waterhouse, as discussed in the following text. Cyrtospiriferoidea Termier & Termier, 1949 of Devonian age is also included, and was ancestral to the punctate Syringothyroidea, as discussed below.

Trigonotretidei new

Large plicate shells, may be costate, with internal plates largely like those of Spiriferidei, but lacking a connector plate, although a thickened shelf bearing a swollen callosity is often present. Superfamilies include Trigonotretoidea Schuchert, 1893 and Neospiriferoidea Waterhouse, 1968, the latter distinguished by the presence of deltidial plates or cover plate, and transverse rather than anterior-posterior longitudinally oriented spiralia, and often lacking callosity and shelf. Possibly the Pterospiriferinae Waterhouse, and possibly much or all of Paeckelmannelloidea belong here as there is no connector plate. Genera assigned to Paeckelmannelloidea, Subfamily Pterospiriferinae, in Carter 2006b such as *Celsifornix* Carter and also *Johncarteria* Waterhouse do have a connector plate and fit much better with Sergospiriferinae Carter in Carter et al., a spiriferoid assemblage.

As discussed in an Appendix, a group of Arctic spiriferiforms externally like Spiriferidae and Neospiriferidae require closer attention, because many individual ventral valves have a thickened subdelthyrial structure, like a connector plate in that it forms shelf between the dental plates and adminicula, but thicker, and often bearing a small umbonal callosity, leaving uncertainty as to whether the specimens are spiriferoid or trigonotretoid. See p. 167ff.

Syringothyridei Grunt, 2006

[Nom. transl. hic ex Syringothyridina Grunt, 2006, p. 158].

Syringothyrids were treated as a major component of punctate spiriferids and referred to Spiriferinida Ivanova by Carter & Gourvennec (2006b), but here they are regarded as having evolved out of the impunctate Superfamily Cyrtospiriferoidea Termier & Termier, 1949 through the introduction of punctation independently from Spiriferinidina. Cyrtospiriferoidea thus straddles two hyporders, Spiriferidei and Syringothyridei. It ranged from Lower Devonian (Emsian) to Upper Devonian (upper Famennian) in age, with typical transverse shape, well-formed sulcus and fold that may be smooth or costate, and numerous narrow plicae or strong costae over the lateral slopes, generally with capillate or pustulose micro-ornament. The hinge is generally wide with subalate to alate cardinal extremities, and the interarea may be high or low. A subdelthyrial plate is present, as well as adminicula, often well-formed dorsal myophragm or septum, ctenophoridium, but never tabellae, apart from *Subcuspidella* Mittmeyer, 1965 which is said by Johnson (2006b, p. 1725) to display dorsal adminicula, that is tabellae, inviting further enquiry. Early members of Syringothyroidea Fredericks, 1926 developed punctation. They have a syrinx, which could be interpreted as a modification of a connector plate. Later components lost the syrinx, and retained the punctation. They are discussed further in the next volume of Earthwise (vol. 27) with note made on the development of punctation in different streams of Brachiopoda.

Suborder **DELTHYRIDINA** Ivanova, 1972

[Delthyridina Ivanova, 1972, p. 41]

Delthyridina Ivanova, 1972 is well summarized in the *Revised Brachiopod Treatise* by Johnson, Hou, Carter & Gourvennec (2006), with two superfamilies Delthyroidea Phillips, ranging from Silurian (upper Llandovery) into Lower Carboniferous (Visean), and Reticularioidea Waagen, ranging from Silurian ((upper Llandovery) into Late Permian (Changhsingian), united by the fine spinose style of ornament, and including adminicula and in some components tabellae. Only a very few possible examples are known in the Permian of New Zealand, and none so far in east Australia.

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_____ 2024b: Punctate spiriferiform brachiopods from the Permian faunas of east Australia and New Zealand. Earthwise 27: 1-60.

AMBOCOELIOIDEA IN THE PERMIAN OF EAST AUSTRALIA AND NEW ZEALAND

Abstract

The section records species of Ambocoeliodea George, 1931 that have been described from the Permian of east Australia and New Zealand. All belong to the subfamily Attenuocurviinae Waterhouse, 2010, with fine spines, raised and elongate median ridge for the ventral muscles, and truncated spire. A new member genus *Gilcurriella* is proposed for a species from northern New South Wales.

SYSTEMATIC SUMMARY

Superfamily **AMBOCOELIOIDEA** George, 1931

[Nom. promoveo Johnson & Carter *in* Carter et al. 1994, p. 336 ex Ambocoeliinae George, 1931, p. 42].

Diagnosis: Small plano-convex to biconvex shells lacking deep sulcus and high fold, often without costae or plicae, micro-ornament varied, usually dominated by fine spines or pustules in commarginal rows. No members showing fimbriate or frilled ornament, but the rows of fine uniramous and usually homogeneous spines approach the pattern seen in some Delthyridiina. A form of delthyrial cover is present in some genera, apparently absent from others, and as far as can be discerned, derived as a rule from stegidial plates. In the Devonian genus *Ladjia*, well described by Veevers (1959, p. 128ff) from the Fitzroy Basin of Western Australia, the teeth leave tracks that converge under the ventral umbo, and Veevers described a pedicle collar in his species *Emmanuella torrida*. *Echinocoelia* Cooper & Williams has a well-developed cover plate (Johnson 1966). Adminicula and dental plates are missing from most Ambocoeliidae, which has crural plates, often supported by what appear to be tabellae, though they might instead be large high crural bases, and certainly one genus *Paracrurithyris* Liao, 1981 that was assigned to Ambocoeliinae by Carter *in* Johnson et al. (2006, p. 1736) has well-developed tabellae. A spondylium and/or cruralium are developed in other groups, the associated subfamily

Rhynchospiriferinae Paulus or as here preferred, Rhynchospiriferidae, being typified by a cruralium (see Johnson et al. 2006, p. 1739), and one constituent genus *Diazoma* Dürkoop, 1970 having adminicula as well. The cardinal process is knob-like, tubercular or with few lamellae, and the brachia simple or spiriferiform.

Discussion: Genera of this superfamily show a limited range in micro-ornament, but vary in the nature of internal plates. The oldest constituent genera are very slightly younger than some genera within Cyrtioidea. No connector plate is present in most if not all genera. Dorsal muscle scars often form an anterior and posterior pair, or inner and outer pair, not the same as those of Productida, but approaching them, because in both groups the dorsal valve is often almost flat, and gently concave or convex. The lack of adminicula and widespread absence of dental plates from many genera may reflect the overall build of the shell, in which the dorsal valve is often almost flat and much lighter than the highly convex ventral valve, so that little physical stress was placed on the teeth, with no need for reinforcement or support.

Contrary to the understanding of their evolution expressed in a diagram by Carter & Gourvennec (2006, Fig. 1104, p. 1693), ambocoelioids did not necessarily lose their crural plates as a rule, though the presence or absence of tabellae for some genera remains moot, as to whether they are sturdy bases of the crura, or discrete although small tabellae.

There are numerous permutations displayed by genera, involving ornament, presence or absence and nature of dorsal plates, shape and disposition of muscle impressions, and presence or absence of a delthyrial cover. Classification is considerably hindered by the failure to determine all features relevant to each genus for some genera, but the implication remains that various features could vary within subfamilial or tribal clusters.

Possibly the superfamily developed directly from Cyrtioidea. The cyrtiid genus *Dongbeiispirifer* Liu in Liu & Huang (1977, p. 58) was stated to have only short adminicula, and one of the features of early ambocoeliids is the absence of adminicula. This Chinese genus is poorly known, planoconvex, with ill-defined fold. It was classed as Cyrtiinae Fredericks by Johnson & Hou (2006) and is of Ludlow (Silurian) age. No group amongst Cyrtioidea or Adolfioidea seems to lack adminicula, and their loss or reduction in a majority of genera marked a major change for the development of Ambocoeliodea. The cyrtioid genus *Espella* Nilova of middle Llandovery-Wenlock (Silurian) age is smooth like ambocoeliids, and has adminicula and cruralium, like various members of Rhynchospiriferinae according to the *Revised Brachiopod Treatise*, which are no older than Lower Devonian (Emsian). In terms of time range, members of Ambocoelioidea were amongst the few to survive the extinction shock at the end of the Permian Period (Chen et al. 2005), though reliable records suggest they did not irrefutably persist long into the Triassic Period.

Ambocoelioidea and Delthyroidea underwent somewhat comparable evolutionary trajectories, differing to some extent in micro-ornament, musculature, spiralia and internal plates, and a few Devonian ambocoelioid genera such as *Emanuella* are almost delthyridin in attributes of micro-ornament, though as a rule less transverse and less plicate.

Family **AMBOCOELIIDAE** George, 1931

[Nom. promoveo Ivanova 1959, p. 56 ex Ambocoeliinae George, 1931, p. 42].

Diagnosis: Ventri-biconvex shells, smooth with varied micro-ornament, involving spines, growth lamellae and fine capillae, as a rule without adminicula, dental plates small or lacking as a rule, but with exceptions. Crura supported by sturdy plates as a rule, tabellae stubby or may be absent. Silurian (Wenlock) to at least basal Triassic (Scythian).

Subfamily **ATTENUOCURVINAE** Waterhouse, 2010

[Subfamily Attenuocurvinae Waterhouse, 2010, p. 64].

Diagnosis: Ventral valve highly convex, elongate to subelongate, ventral umbo prominent to attenuate, delthyrium as a rule closed by flat deltidial plates each side of a median arch. Dorsal valve gently convex to almost flat or weakly concave. Micro-ornament of crowded minute spines, uniform or varying in diameter. Dorsal costae present in some species. Dental supports rare apart from one genus, in which they form apparently single plates between teeth and floor of valve. Ventral adductor and diductor scars placed on long high ridge, dorsal muscle scars as in *Crurithyris* George, more or less laterally arranged. Cardinal process sessile, small, tuberculate or feebly lamellate. Crural and socket plates stubby and sessile, tabellae well developed in two genera, otherwise slender and low if present, but the reality of their presence remains uncertain; spiralia truncated to one coil. Lower Permian (Asselian) to Upper Permian (Changhsingian).

Genera: *Attenuacurvus* Waterhouse*, Attenuatella* Stehli, *Biconvexiella* Waterhouse, *Gilcurriella* n. gen..

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, 2010, p. 68 have inner and outer dorsal muscle scars as in Attenuocurvinae, but mostly lack the prominent ventral muscle ridge, and the cardinal process is raised above the floor of the valve, with a small notothyrial cavity. *Ogilviecoelia* Shi & Waterhouse does have a ventral internal ridge, but lacks spines and has crurithyrid spiralia (Waterhouse 2018, pp. 380-389). The spire is known to be truncated in both *Biconvexiella* Waterhouse, 1983 and *Attenuocurvus* Waterhouse, 2010, and probably *Attenuatella*, whereas several coils are present in *Crurithyris* and allies.

The delthyrium is partly covered under the ventral umbo in *Attenuocurvus* by two small lateral plates that merge medianly in an arch. *Biconvexiella* is like *Attenuocurvus* in its truncated spire, but has different dorsal adductor scars, a slender posterior pair, and larger outer overlapping pair. Microspines are differentiated in *Biconvexiella* and *Attenuatella*, as in *Crurithyris* (Brunton 1984), but are uniform in *Attenuocurvus* and *Gilcurriella. Gilcurriella* apparently has simple plates supporting the teeth from the floor of the valve, and short well-formed tabellae.

Genus ***Attenuocurvus*** Waterhouse, 2010

Diagnosis: Small, slightly to moderately elongate, ventral valve inflated with incurved ventral umbo and high interarea divided by partly covered delthyrium, shallow sulcus. Dorsal valve gently concave as a rule, may be gently convex posteriorly. Both valves ornamented by dense array of small erect spines of uniform diameter. Teeth not supported by plates. High ventral adductor platform with anterior ridge extending to anterior third of shell; socket plates, crural plates sessile or possibly supported by very low tabellae. Spiralia truncated to part of a coil on each side.

Type species: *Attenuatella attenuata* Waterhouse, 1964, p. 108 from a Tertiary boulder derived from Upper Permian sediment, Takitimu Mountains, New Zealand, OD.

Attenuocurvus australis **(**Armstrong & Brown, 1968)

Fig.1, 2

1968 *Attenuatella australis* Armstrong & Brown, p. 60, pl. 8, fig. 1-16, text-fig. 1.
2010 *Attenuocurvus australis* – Waterhouse, p. 67, Fig. 30.
2015b ?*A. australis* – Waterhouse, p. 55, Fig. 17G.

Diagnosis: Ventral valve elongate with median channel well-defined posteriorly, dorsal valve almost flat with swollen posterior. Spines homogenous over both valves, fine and crowded in commarginal rows.

Holotype: UQF 52677 figured by Armstrong & Brown (1968, pl. 1, fig. 9) from Kolbar Formation, southeast Queensland, OD.

Fig. 1. *Attenuocurvus australis* (Armstrong & Brown). A, interior of dorsal valve, UQF 46647, x4. B, dorsal aspect of holotype UQF 52677 x4. C, ventral aspect UQF 52679, x4. Although not stated in the caption, these are presumably latex casts. Kolbar Formation, Gympie, southeast Queensland. (Armstrong & Brown, 1968).

Morphology: Specimens of *australis* at the Queensland Museum and Science Annex at Hendra, Brisbane, show that the posterior delthyrium is closed by two slender plates, separated by a median plate ridged posteriorly and grooved in front, and are crossed by growth striae and rugae concave forwards in outline. A few specimens show short grooves behind some spines, as noted by Armstrong & Brown (1968).

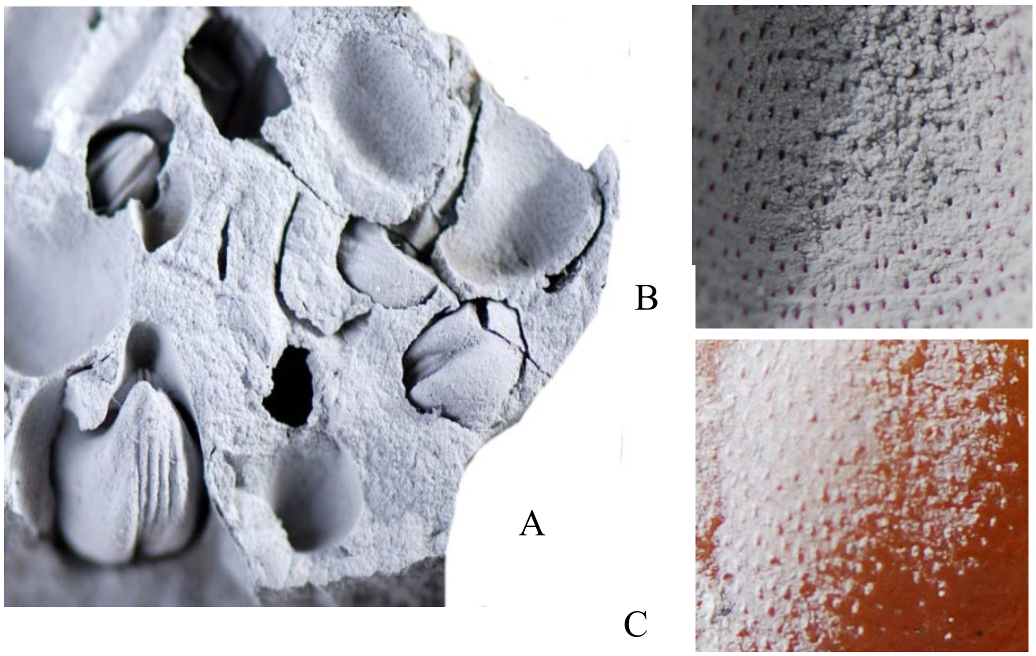


Fig. 2. *Attenuocurvus australis* (Armstrong & Brown). A, crowded ventral valves including UQF 81603 at lower left, showing delthyrium and cover, x3.5. B, C, external mould and latex cast of ventral valve UQF 81397 showing spinules, x10. Kolbar Formation, near Gympie. (Waterhouse 2015b).

Stratigraphy: This species is found 600ft below the Gigoomgan Limestone inland from Gympie in southeast Queensland, and is accompanied by *Protoanidanthus pokolbinensis* Briggs (1998). *Attenuocurvus australis* probably belongs to the *Bandoproductus macrospina* Zone, deemed to be of late Asselian age.

?***Attenuocurvus*** sp.

Fig. 3

1987 ?*Attenuatella* sp. Waterhouse, p. 5, pl. 1, fig. 8, 9.

A ventral valve from the Dresden Limestone of the southeast Bowen Basin of Queensland. The sulcus is very shallow, and the delthyrium is bordered by narrow dental ridges. No dorsal valve is known.

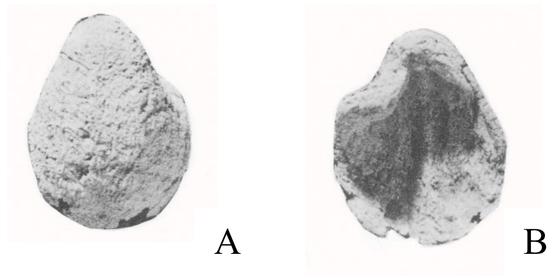


Fig. 3. ?*Attenuocurvus* sp. A, B, external and internal aspects of ventral valve UQF 74120, x6. Dresden Limestone, southeast Bowen Basin, Queensland. (Waterhouse 1987).

Attenuocurvus altilis (Waterhouse, 1968)

Fig. 4

1968 *Attenuatella* Landis & Waterhouse, p. 144, pl. 1, fig. 1-5.
1968 *A. altilis* Waterhouse, p. 16, pl. 2, fig. 2-12, 15, pl. 16, fig. 5, text-fig. 2B, 3-5.
2002 *A. altilis* – Waterhouse, p. 23.

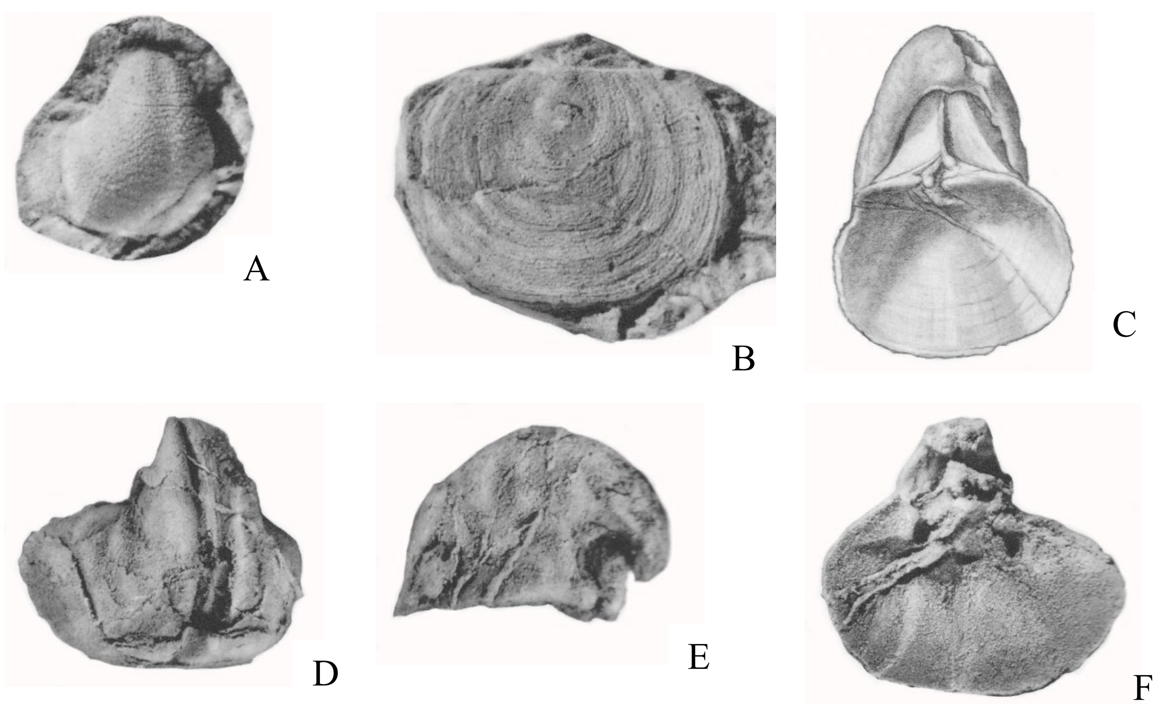


Fig. 4. *Attenuocurvus altilis* (Waterhouse). A-C, Wesney Siltstone. A, latex cast of ventral valve OU 2447. B, latex cast of dorsal exterior, OU 2448. C, latex cast of holotype, BR 1295, dorsal aspect. D-F, upper Takitimu Group. Ventral, lateral and dorsal aspects of internal mould BR 1294. Specimens x4. (Waterhouse 1968).

Diagnosis: Spines slightly less dense than in *Attenuatella incurvata*, low fold and costae on a number of dorsal valves, Dorsal median septum apparently absent, alveolus deep.

Holotype: BR 1295 from upper Takitimu Group, figured in Waterhouse (1968, pl. 2, fig. 11, 15, pl. 16, fig. 5) and herein as Fig. 4C, OD.

Morphology: Numerous specimens are available. Many specimens are comparatively broad, and the ventral posterior walls are concave in outline as a rule. The delthyrium has a narrow convex cover plate, which is bordered each side by a broad flat deltidial plate.

Stratigraphy: The species is found in the Wesney Siltstone of the Eglinton Valley and Elbow Creek Formation of the upper Takitimu Group, Takitimu Range, south New Zealand, judged to be of upper Artinskian (=Baigendzinian) age.

Attenuocurvus sp. or spp.

Fig. 5, 6

1968 *Attenuatella* sp. cf. *incurvata* [not Waterhouse] – Armstrong, p. 791, pl. 142, fig. 13-18.
1968 *Attenuatella* sp. Armstrong, p. 791, pl. 142, fig. 24-26.

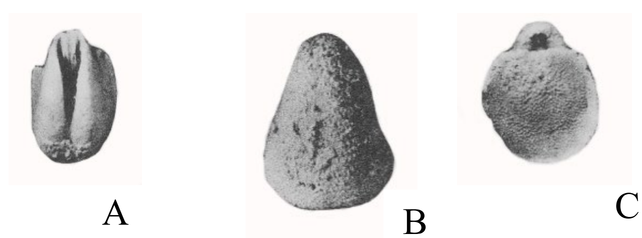


Fig. 5. *Attenuocurvus* sp., ventral internal mould CPC 9019. B, ventral latex cast CPC 9021. C, dorsal aspect of conjoined specimen, latex cast, CPC 9022. Specimens x 4 from Barfield Formation, figured as cf. *incurvatus*. (Armstrong 1968, pl. 142, fig. 13, 16, 17).

A few individual specimens have been described by Armstrong (1968) from the Barfield and overlying Flat Top Formations of the southeast Bowen Basin in Queensland. More material is needed to determine whether or not the specimens from the Barfield Formation are conspecific with the Flat Top specimens as figured below. This does seem likely, given the elongated ventral valve, although the Flat Top ventral valve has a more channelled ventral valve (Fig. 6A). With his conviction that New Zealand Permian faunas were merely a pale shadow of vastly superior faunas found and incontrovertibly elucidated in east Australia, Armstrong declared that the Queensland Barfield specimens matched those of the New Zealand Arthurton Group, called *A. incurvatus*, but they have a much more elongate shape with very long posterior lateral walls. The long ventral posterior walls suggest an approach to *Gilcurriella multispinosa* (Waterhouse), but Barfield and Flat Top specimens show no sign of the dental support plates typical of that species, nor of the dorsal costae.

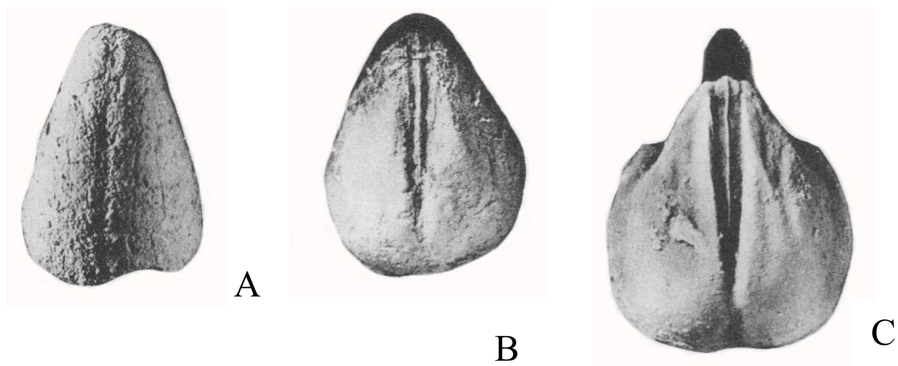


Fig. 6. *Attenuocurvus* sp. A, B, external latex cast and internal mould of ventral valve CPC 9028 x4, from near Bundaleer Homestead, central Queensland, with no stratigraphic information provided, but presumably Flat Top beds. C, ventral internal mould, GSQF 3459 x4 from Flat Top Formation. (Armstrong 1968, pl. 142, fig. 24, 25, 26).

Attenuocurvus incurvatus (Waterhouse, 1964)

Fig. 7 - 10

1925 Gasteropoda sp. Marwick, p. 362.
1964 *Attenuatella incurvata* Waterhouse, p. 108, pl. 20, fig. 1-12, pl. 21, fig. 1-9, text-fig. 47-52.
?1968 *Attenuatella* sp. cf. *convexa* [not Armstrong] – Armstrong, p. 788, pl. 142, fig. 19.
1969 *Attenuatella* sp. Runnegar & Ferguson, p. 254, pl. 3, fig. 5.
2010 *Attenuocurvus incurvatus* – Waterhouse, p. 64, Fig. 29A-G.
2015b *A. incurvatus* – Waterhouse, p. 92, Fig. 29.
2016 *A. incurvatus* – Waterhouse, Fig. 486.

Diagnosis: Small with ornament of dense uniform spines, rarely with low fold over concave dorsal valve.

Holotype: BR 905 from Permian limestone block in Tertiary,sediment, figured by Waterhouse (1964, pl. 20, fig. 3, 6, 11, pl. 21, fig. 1, 5) and herein as Fig. 7C, D, Fig. 9B, OD.

Morphology: Ventral valve small, subelongate, strongly inflated. Umbo broad, massive, incurved over the ventral interarea. Dorsal valve semicircular in outline, gently convex posteriorly, planar in front. Cardinal extremities rounded, maximum width near mid-valve. Ventral interarea apsacline, high, dorsal area anacline, low. Ventral valve has shallow sulcus and fine radial capillae.

A question surrounds the material recorded by Armstrong (1968, p. 789) from the Gympie district. He considered that the material possibly approached what is now called *Biconvexiella convexa* Armstrong (1968), and provided an inadequate stratigraphic summary. But the locality was included in the South Curra Limestone in Waterhouse (2015b, p. 123) and Armstrong's illustrated specimen refigured as *Attenuocurvus incurvata* (Waterhouse 2015b, Fig. 29A), though the figure is not particularly diagnostic.

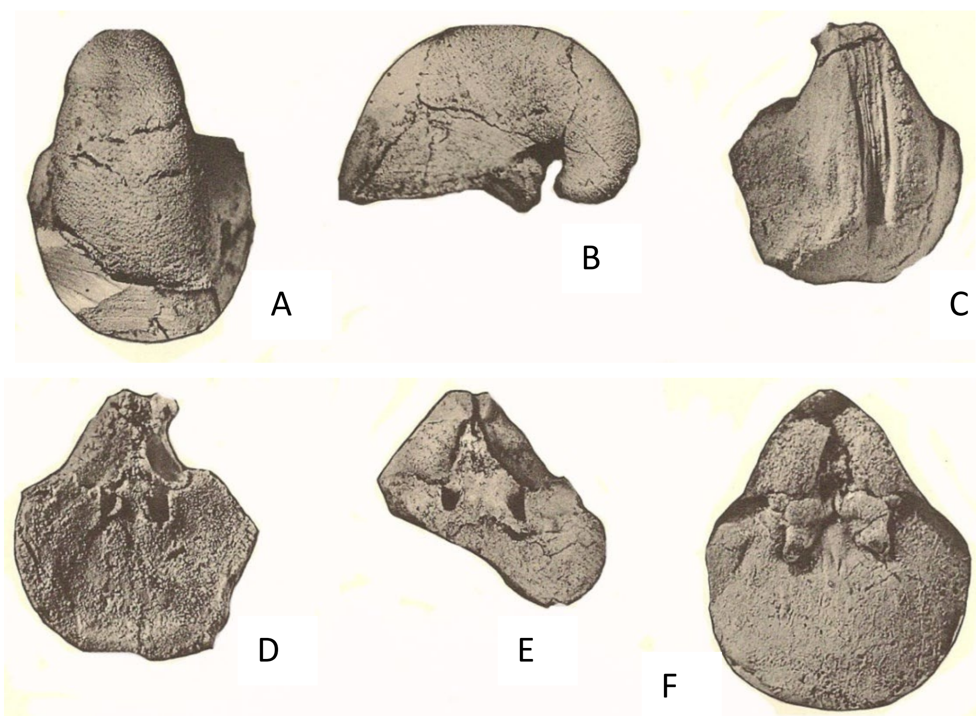


Fig. 7. *Attenuocurvus incurvatus* (Waterhouse). A, B, ventral and lateral aspects of PVC cast, BR 697, x5. C, D, ventral and dorsal aspects of internal mould, BR 905, holotype. E, dorsal aspect of internal mould, OU 2203, x2.5. F, PVC cast showing dorsal interior and part of posterior ventral valve, BBR 688. Specimens x5 approx., from Tertiary boulder derived from Hilton Limestone or equivalent in south New Zealand. (Waterhouse 1964).

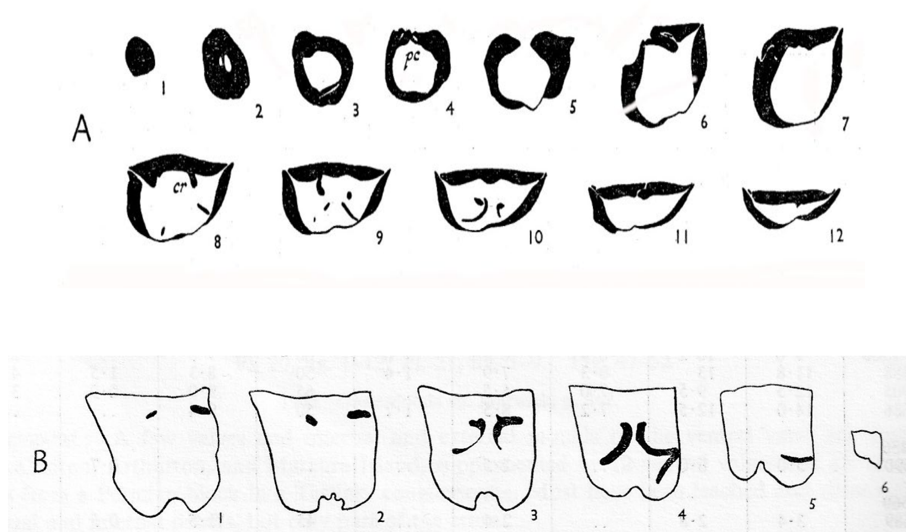
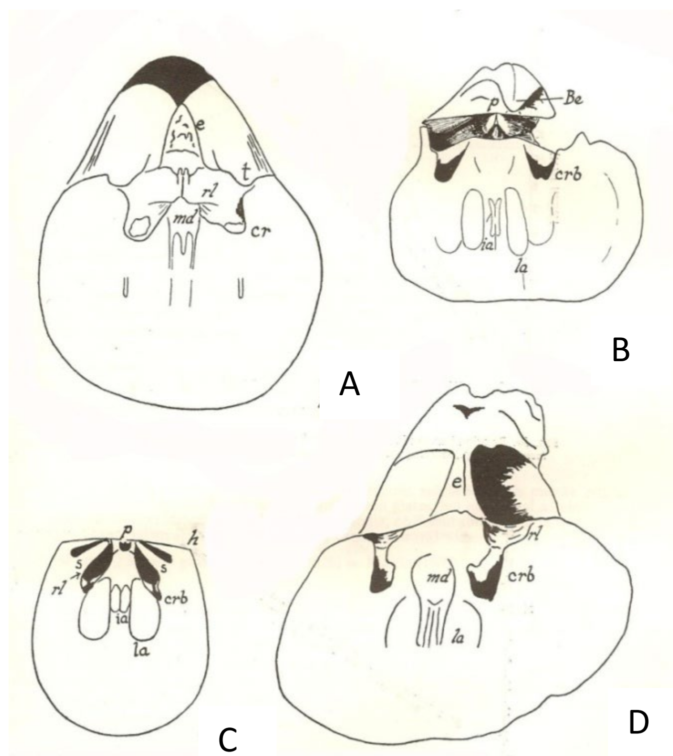


Fig. 8. Serial sections of *Attenuocurvus incurvatus* (Waterhouse). Specimens at 0.5mm intervals, x3. A, specimen with shell preserved from Trig DD Formation. B, internal mould from Tertiary boulder, commencing 5mm from umbonal tip. cr = crus, pc = pedicle collar. (Waterhouse 1964).

Fig. 9. *Attenuocurvus incurvatus* (Waterhouse), dorsal aspects of internal moulds, x3 approx. A, BR 688. B, BR 905, holotype. C, BR 929. D, BR 686, C from Kildonan Member, others from Tertiary boulder. Be – ventral beak; cr – crus; crb – mould of base of crus; e – delthyrium; h – hinge; ia – inner pair of dorsal adductors; la – lateral adductors; md – median mound; p – cardinal process; rl – crural plate; s – dental socket; t – tooth. From Late Permian of New Zealand. (Waterhouse 1964).



Tabellae, if present, are difficult to separate from the crural bases in this material, and further study is required to be sure that they are present.

Stratigraphy: The species is found primarily in the Kildonan Member of the Bagrie Formation and in the overlying Trig DD Formation of the Arthurton Group of the north limb of the Southland Geosyncline in south Otago, New Zealand. Along the southern limb, the species is found in the Hilton Limestone (Waterhouse 2002, p. 75), and represented in a Tertiary boulder on the western flanks of the Taktimu Range. Near Gympie in southeast Queensland, the same species is represented in the lower fauna of the South Curra Limestone.

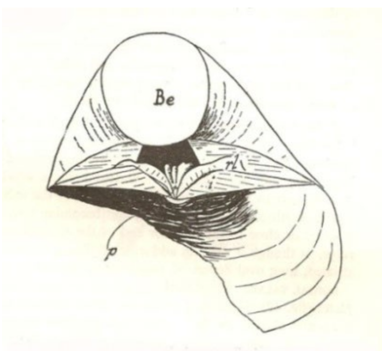


Fig. 10. *Attenuocurvus incurvatus* (Waterhouse), dorsal aspect of OU 2203 x4 showing ventral beak (be), sectioned, above an open delthyrium (the deltidium having been lost), and dorsal valve with crural plate (rl), cardinal process (p) and dorsal interarea (i). A small deltidial plate is normally present over at least the upper delthyrium in *Attenuocurvus*. Tertiary boulder of New Zealand. (Waterhouse 1964).

Genus ***Biconvexiella*** Waterhouse, 1983

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 shallow median channel 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 extending to anterior third of shell; dorsal crural plates, supported by short tabellae. Spiralia truncated to part of a coil.

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

Discussion: This genus is very close to *Attenuatella* Stehli, 1954 in ornament, but is distinguished by its moderately convex comparatively broad ventral valve with only moderately extended and incurved ventral umbo. 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. Johnson et al. (2006) stated that the ornament in *Attenuatella* was like that of *Crurithyris* George, 1931, in which there are two very distinct orders of spines (see Brunton 1984 and Johnson 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. 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 has been 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 1968, pl. 142, fig. 11). The cardinal process is tubercular in *Biconvexiella* (Armstrong 1968, pl. 142, fig. 12), whereas it is lamellate in *Attenuatella attenuata* (Cloud) (Cooper & Grant 1976a, p. 2132, pl. 590, fig. 34) and crural bases in this species are large like those of *Attenuocurvus*, without clearly distinguishable tabellae.

Unlike *Biconvexiella, Attenuocurvus* Waterhouse, 2010, type species *Attenuatella incurvata* Waterhouse, 1964, 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 so that tabellae if present must be very low, and poorly distinguished from the base of the crura. The spire is truncated in both genera, as shown for *Biconvexiella* by Armstrong (1968, text-fig. 2) and for *Attenuocurvus* by Waterhouse (1964, Fig. 48A, B).

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.

Biconvexiella convexa (Armstrong, 1968)

Fig. 11, 12

1968 *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, Briggs & Parfrey, p. 134.
1983 *Biconvexiella convexa* – Waterhouse, p. 154.
2006 *B. convexa* – Johnson et al., p. 1733, Fig. 1138a-e.
2010 *B. convexa* – Waterhouse, p. 65, Fig. 28.
2015a *B. convexa* – Waterhouse, p. 148, Fig. 101.
2016 *B. convexa* – Waterhouse, p. 366.

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 channel, as a rule limited to anterior shell.

Holotype: UQF 53036 from the *Capillonia armstrongi* band, Tiverton Formation, figured by Armstrong (1968, pl. 142, fig. 7, 9, 10) and herein as Fig. 11D, OD.

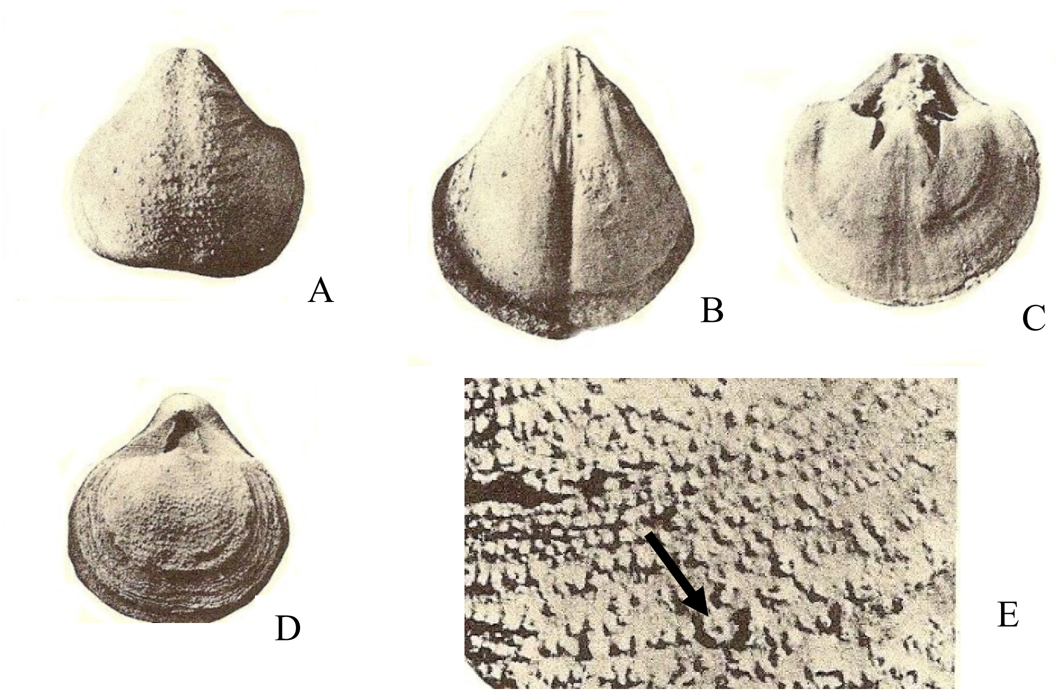


Fig. 11. *Biconvexiella convexa* (Armstrong). A, latex cast of ventral exterior, UQF 53033. B, internal mould of ventral valve UQF 53029. C, dorsal aspect of internal mould UQF 53030. D, dorsal aspect of latex cast of exterior UQF 53037, holotype. Specimens x4. E, detail of spines on UQF 53038 (ventral valve), x22. Arrow points to large spine. From the *Capillonia armstrongi* band, Tiverton Formation, north Bowen Basin. (Armstrong 1968).

Morphology: Armstrong recorded his species as coming from UQL 3127, but this is a generalized locality for all of the Tiverton Formation near Homevale Station, and Waterhouse (2015a; 2023, p. 45) found that the species was limited to the lower part of the *Capillonia armstrongi* band in the middle Tiverton Formation. Armstrong (1968, p. 789) suggested that an unfigured ventral valve from sandstone below the “Upper Limestone” (now Gigoomgan Limestone) near Gympie was conspecific, but this may well belong to *Attenuocurvus incurvata* (Waterhouse).

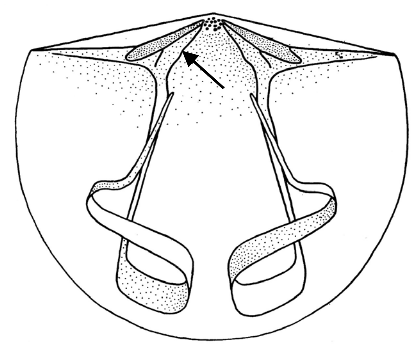


Fig. 12. *Biconvexiella convexa* (Armstrong). Reconstruction of spiralia. The arrow points to a very low tabellum, supporting the base of the crus. From the *Capillonia armstrongi* Subzone, Tiverton Formation. (Armstrong 1968).

Under the ventral umbo, the delthyrial cover plate forms a very narrow median ridge with concave strip each side. Both valves are covered by 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 on the ventral valve were figured by Armstrong (1968, 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 1968, pl. 142, fig. 7, 9). The ventral muscle platform is long and raised, and the crural plates supported by tabellae which are unusually well-developed for the subfamily. The cardinal process is small and tuberculate, and the abbreviated and simple brachidia are figured by Armstrong (1968, text-fig. 1, 2).

Material that was referred to *convexa* by Armstrong & Telford (1970, p. 115, pl. 10, fig. 3-9) and herein as Fig. 13 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 cover like that of type *convexa* is developed on UQF 54456. Spines appear to be comparatively uniform, and lie in short commarginal rows, but there appear to be a few thicker spines on the two valves (Fig. 13A, B) and thinner spines in bands. Whether these specimens really belong to *convexa* requires first hand inspection. They have a weak ventral sulcus and very shallow if any median dorsal channel, and the dorsal valve appears to be less convex than type *convexa*.

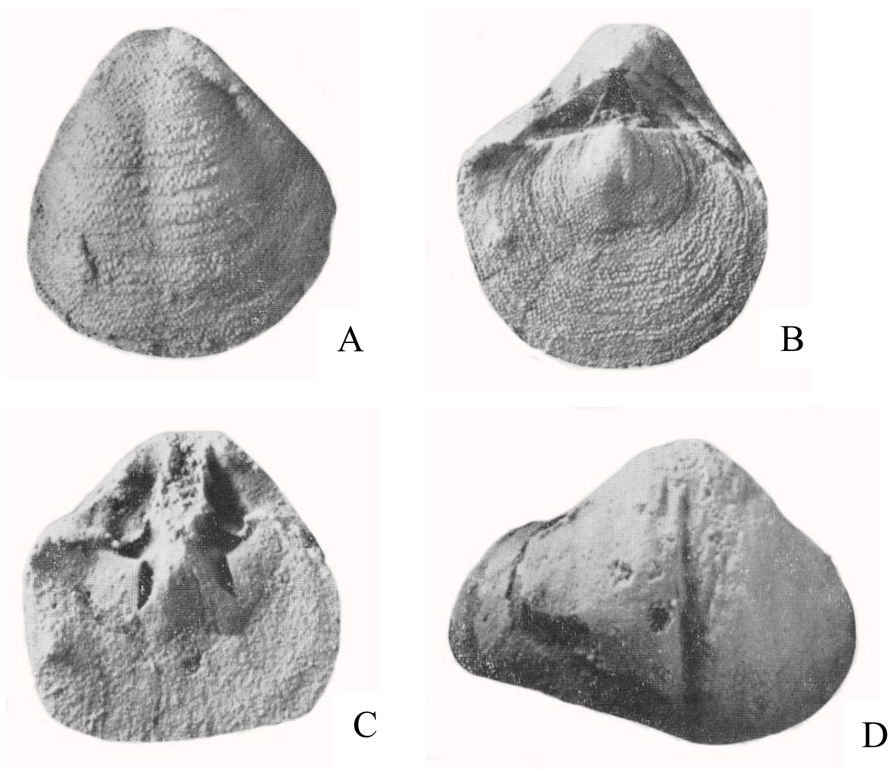


Fig. 13. *Biconvexiella convexa* (Armstrong)?. A, B, C, latex cast of ventral valve, dorsal aspect of external latex cast and internal mould of conjoined specimen, UQF 54457. D, ventral internal mould UQF 54452. Specimens x5, from Farley Formation, New South Wales. (Armstrong & Telford 1970).

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, and show short tabellae, but it is not clear from the figures whether the dorsal valve is gently convex or weakly concave.

Stratigraphy: In east Australia the species is found in the upper middle Tiverton Formation of the north Bowen Basin, and allied shells come from the Farley Formation of the north Sydney Basin.

Genus ***Gilcurriella*** n. gen.

Diagnosis: Distinguished by the presence of dental support plates and distinct dorsal tabellae. Ventral valve highly convex with incurved ventral umbo, dorsal valve gently concave as a whole, convex posteriorly. Ornament of uniform fine spines over both valves, dorsal valve may have a few well-developed ribs. Ventral valve with long median ridge bearing muscle scars; dorsal valve with small inner and large outer adductor scars.

Type species: *Attenuatella multispinosa* Waterhouse, 1967 from near Drake, northern New South Wales, here designated.

Discussion: The teeth are supported each by a slender plate that extends to the floor of the valve. Each looks like a single plate without any change in angle, though closer examination is needed to determine whether the adminicula are present but lying in the same plane as the dental plates of other Spiriferida. Tabellae are clearly formed. In these respects, the genus differs from *Attenuatella* and *Attenuocurvus,* but approaches *Biconvexiella* which has tabellae. *Gilcurriella* is like *Attenuocurvus* in shape, micro-ornament, musculature and cardinal process. The genus is close to forms recorded by Kletz (2005, pl. 21) as *Attenuatella majaensis* Kletz and A. *omolonensis* Zavodowsky from northeast Russia, for these species also have dental supporting plates and tabellae, but the dental plates are long, and shell less elongate than *Gilcurriella*.

Gilcurriella multispinosa (Waterhouse, 1967)

Fig. 13. 14

1967 *Attenuatella multispinosa* Waterhouse, p. 168, pl. 24, fig. 1-7, text-fig. 1-3.
1970 *A. incurvata* [not Waterhouse] – Armstrong & Telford, p. 113, pl. 10, fig. 10-17.
1987 *A. multispinosa* – Waterhouse, p. 5.

Diagnosis: Elongate moderately incurved shells with very long ventral posterior walls, slight or no ventral sulcus, spines fourteen to sixteen per mm as a rule. Ribs lie over the dorsal valve.

Holotype: AMF 42104 from Gilgurry Mudstone, northern New South Wales, figured by Waterhouse (1967, pl. 24, fig. 5, 6), OD.

Morphology: It will be noted that some of the figured ventral valves from the Gilgurry beds are elongate like at least some specimens from the Barfield and Flat Top Formations. But these latter specimens do not appear to show adminicula or tabellae, and none show dorsal ribs, which become more conspicuous in more mature examples of *multispinosa*.

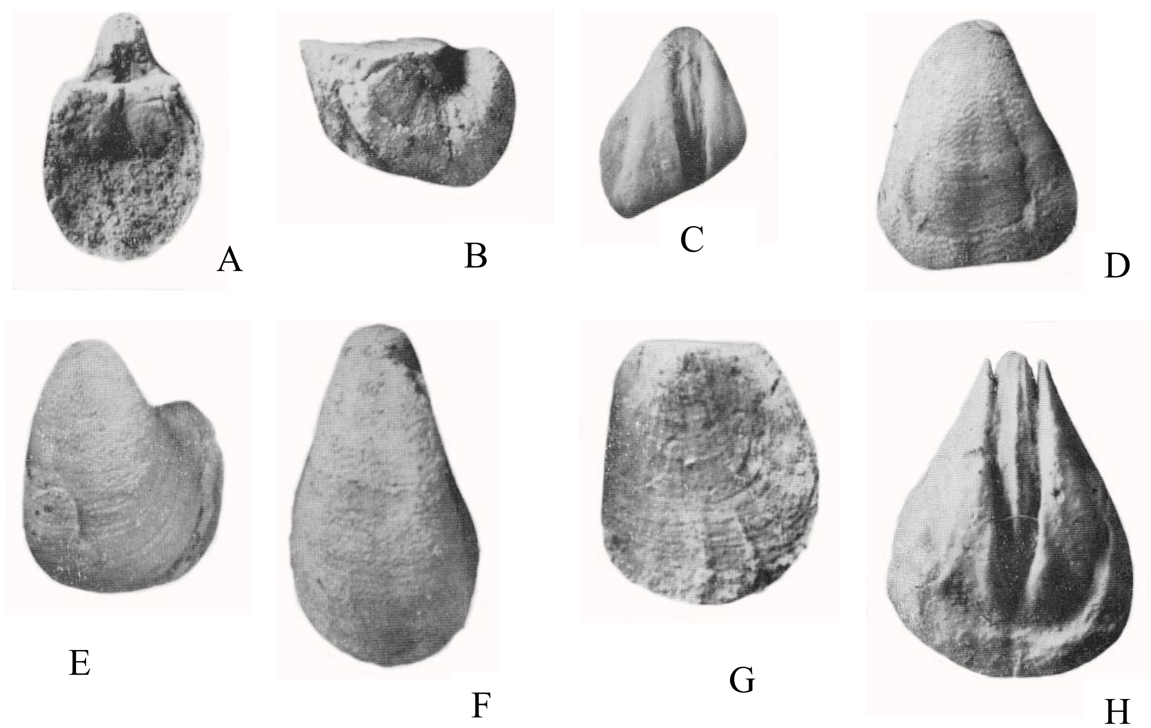


Fig. 13. *Gilcurriella multispinosa* (Waterhouse). A, dorsal aspect of latex cast, conjoined valves, UQF 54441. B, lateral view of latex cast UQF 54423. C, ventral internal mould, UQF 54434. D, latex cast of ventral exterior, UQF 54419. E, latex cast of ventral exterior, UQF 54437. F, latex cast of ventral exterior, UQF 54428. G, latex cast of dorsal exterior UQF 54417. H, ventral internal mould, AMF 42105. Specimens x6 from Gilgurry Mudstone, New South Wales. (Armstrong & Telford 1970).

Stratigraphy: The Gilgurry Mudstone is poorly dated as yet, but has been considered to be possibly as young as early Wuchiapingian in age. It is true that specimens show the long posterior walls as in ventral valves from the Barfield and Flat Top Formations of the southeast Bowen Basin, which may signify that the Gigurry beds are of similar age, at Wordian (mid-Guadalupian) rather than Lopingian in age. But the Gilcurry species seems distinct though its internal plates, and may well prove to be of Wuchiapingian age.

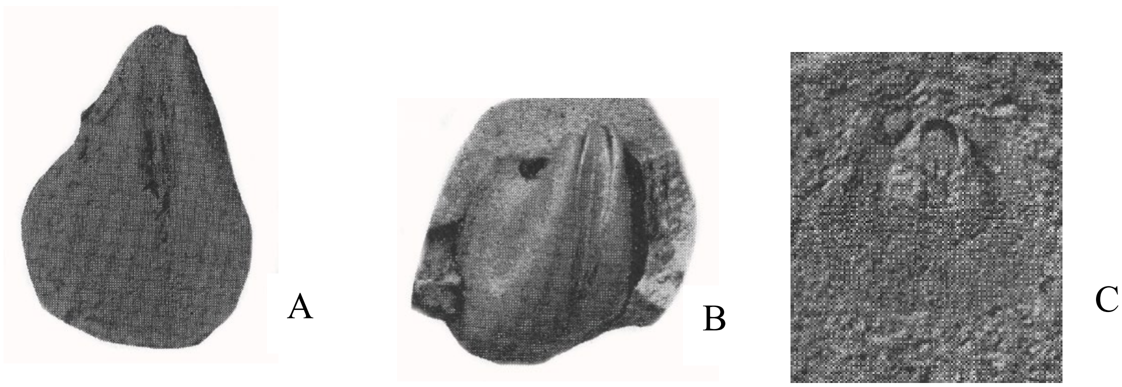


Fig. 14. *Gilcurriella multispinosa* (Waterhouse). A, ventral internal mould, AMF 42102, x4. B, posterior ventral internal mould AMF 51523, x4, showing adminicula. C, dorsal internal mould, AMF 51524, with short tabellae, x 8. Gilgurry Mudstone, northern New South Wales. (Waterhouse 1967).

Ambocoeliid, gen. & sp. indet.

Fig. 15

1968 Crurithyrid? Waterhouse, p. 13, pl. 2, fig. 1, text-fig. 2E.

Fig. 15. Ambocoeliid gen. & sp. indet., dorsal interior of BR 1414, x4. Trig DD Formation, New Zealand. (Waterhouse 1968).

A brachiopod from the Trig DD Formation of south Otago, New Zealand, preserves no ventral valve or external ornament, but the short strong posterior gaps in the mould strongly suggest possibly low sturdy tabellae, such as seen in *Biconvexiella* and *Gilcurriella*. Possibly the gentle convexity favours the former genus, but this remains uncertain.

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SPIRIFEROID BRACHIOPODS IN THE PERMIAN OF EAST AUSTRALIA AND NEW ZEALAND

Abstract

A few spiriferoid species are found in the Permian deposits of east Australia and New Zealand. They are distinguished by their subdelthyrial construct which involves the presence of a connector plate.

SYSTEMATIC AND STRATIGRAPHIC SUMMARY

Order **SPIRIFERIDA** Waagen, 1883

Suborder **SPIRIFERIDINA** Waagen, 1883

Hyporder **SPIRIFERIDEI** Waagen, 1883

Shells with subdelthyrial connector plate in the ventral valve. The plate is slender and not thickened and does not bear any callosity, Spiralia transverse.

Superfamily **SPIRIFEROIDEA** King, 1846

Shells generally costate and transverse, rarely plicate, but often fasciculate.

Family **SPIRIFERIDAE** King, 1846

Subfamily **SPIRIFERALARIINAE** Waterhouse, 2016, p. 186

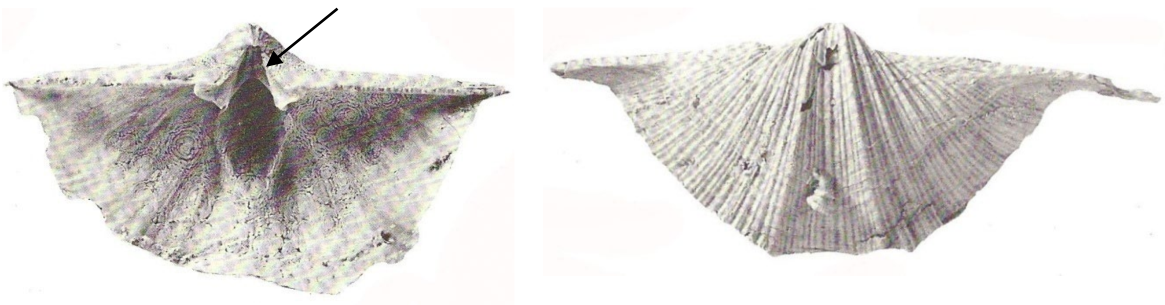

Fig. 1. *Spiriferalaria thesculus* (Cooper & Grant). A, ventral interior, x7, showing the subdelthyrial connector plate as arrowed, formed by projections from the junction between dental and adminicular plates that fuse medianly to form a single plate. B, *Spiriferalaria bakeri bakeri* (King), ventral view, x1. From Road Canyon Formation (Roadian), Texas, USA. (Cooper & Grant 1976).

Members of Spiriferalariinae belong to Spiriferidae King. The name genus *Spiriferalaria* Waterhouse is found in the Permian of west Texas, with type species *Neospirifer thesculus* Cooper & Grant, 1976, p. 2189 from the Road Canyon Formation, and species are distinguished from other Spiriferidae by the ornament of costate plicae, so as to look like Neospiriferidae. But they differ from Neospiriferidae through possessing a subdelthyrial connector plate that spans the subdelthyrial gap between the junctions of the adminicula with the dental plates in the ventral valve.

Genera: *Spiriferalaria* Waterhouse, *Gibbospirifer* Waterhouse, *Koenigoria* Waterhouse (see p, 130), *Simplicisulcus* Waterhouse, *Tegulispirifer* Poletaev.

Discussion: The plate below the delthyrium that passes across the delthyrial gap between the dental plates and adminicula is here term a subdelthyrial connector plate, following Waterhouse (2016) and other studies. It was not specifically described in any meaningful or recognizable way by Williams & Brunton (1997, pp. 428, 431) in their presentation of morphological and anatomical terms for the *Revised Brachiopod Treatise*, nor adequately addressed in the well-illustrated article in the same work on morphology by Williams et al. (1997). But Carter (2006) did record a delthyrial plate in Spiriferoidea for the same work, without detailed definition or description.

Genus ***Simplicisulcus*** Waterhouse, 2002

Diagnosis: Small shells with well-formed plicae, sulcus deep without subplicae and critically, not entered by lateral plicae, fold low, not joined by innermost pair of plicae. External delthyrium covered partly or entirely by a single arched plate called a neodeltidium.

Type species: *Neospirifer arthurtonensis* Waterhouse, 1968, p. 28 from Arthurton Group, New Zealand, OD (Waterhouse 2002, p. 231).

Discussion: A neodeltidium appears to be a single plate, differing in that regard from a deltidium which is formed by convergence of two lateral plates (ie. stegidia).

Simplicisulcus concentricus (Waterhouse, 1987)

Fig. 2

1987 *Neospirifer concentricus* Waterhouse, p. 21, pl. 4, fig. 7-13.
2016 *Simplicisulcus concentricus* – Waterhouse, p. 188, Fig. 228.

Diagnosis: Small little inflated shells with low persistent plicae, costae low with rounded crests, commarginal and radial ornament well-developed, secondary thickening slight.

Holotype: UQF 70100 figured in Waterhouse (1987, pl. 4, fig. 14) and Fig. 2A herein, from Brae Formation, southeast Bowen Basin, OD.

Stratigraphy: This species is found only in the Brae Formation, Bowen Basin, Queensland.

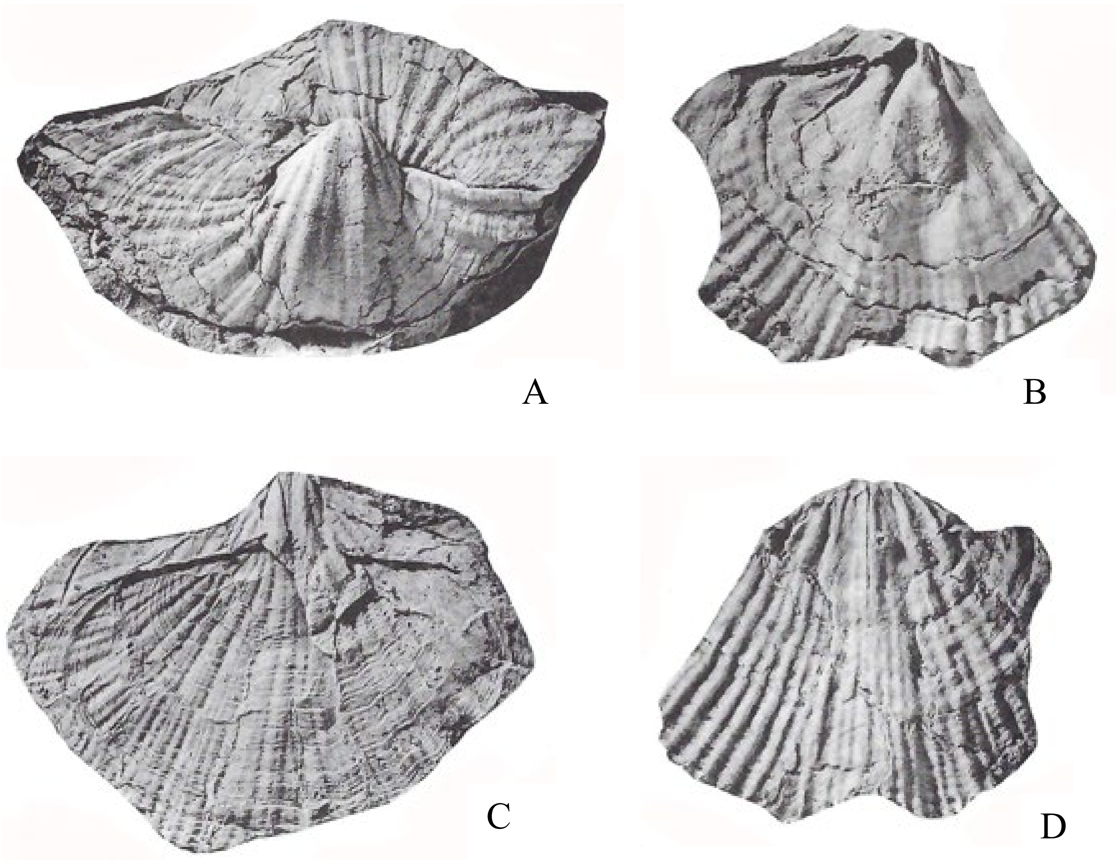

Fig. 2. *Simplicisulcus concentricus* (Waterhouse). A, posterior view of holotype, valves conjoined and ventral valve below, UQF 70100, x1.5. B, D, ventral and dorsal aspects of internal mould UQF 70105, x2. C, dorsal external mould with ventral umbonal region attached, UQF 74145, x2. From Brae Formation, southeast Bowen Basin. (Waterhouse 1987).

Simplicisulcus arthurtonensis (Waterhouse, 1968)

Fig. 3, 4A-E, 5

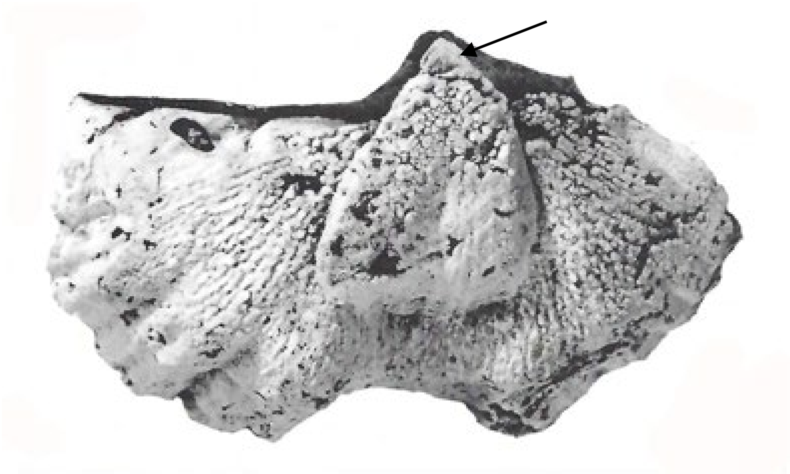

Fig. 3. *Simplicisulcus arthurtonensis* (Waterhouse), holotype BR 521 showing subdelthyrial connector plate as arrowed, x2, from Earnvale Member, New Zealand. (Waterhouse 1968).

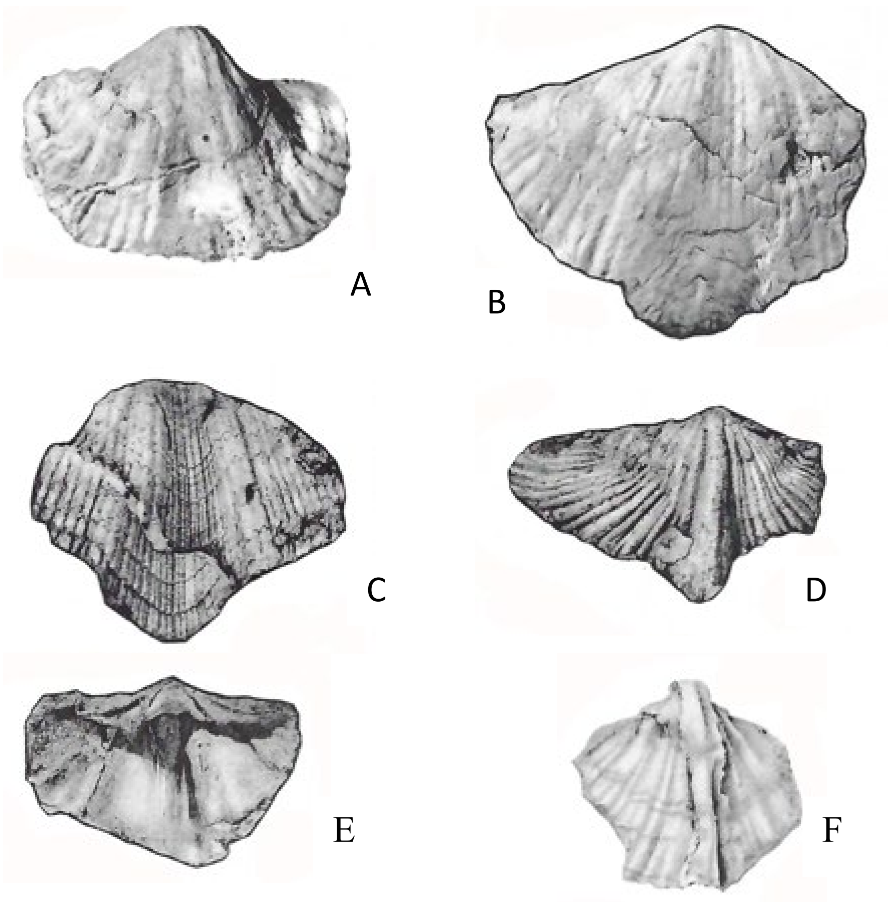

Fig. 4. A-E, *Simplicisulcus arthurtonensis* (Waterhouse). A, decorticated ventral valve BR 519, x1. B, decorticated ventral valve, BR 517 x1. C, PVC cast of ventral valve BR 523 x1. D, PVC cast of dorsal exterior, BR 524 x1. E, PVC cast of dorsal interior, BR 525, x1. From Earnvale Member, Bagrie Formation, New Zealand. F, *Neilotreta gigoomganensis* (Waterhouse). dorsal aspect of internal mould of specimen with valves conjoined, BR 1317, x2, from Kildonan Member, Bagrie Formation. See p. 129**.** (Waterhouse 1968).

1968 *Neospirifer arthurtonensis* Waterhouse, p. 28, pl. 2, fig. 14, 16, pl. 3, fig. 1-3, 5, 7-9, pl. 17, fig. 1, 3, text-fig. 7C, D, 9A, 10-13 (part, not pl. 3, fig. 4, 6 = *Neilotreta gigoomganensis*).
2001 *Simplicisulcus arthurtonensis* – Waterhouse, p. 191.
2002 *S. arthurtonensis* – Waterhouse, p. 231.
2016 *S. arthurtonensis* – Waterhouse, p. 188, Fig. 227, 229.

Diagnosis: Small with persistent plicae in some four pairs and stout costae.

Holotype: BR 521 figured in Waterhouse (1968, pl. 3, fig. 1) and Fig. 3 herein from the Earnvale Member in the Bagrie Formation, Arthurton Group of north Otago, OD.

Stratigraphy: This species is represented by material in the Earnvale Member of the Bagrie Formation of South Otago, New Zealand. Material from the overlying Kildonan Member is represented only by small and incomplete specimens, regarded by Waterhouse (1968, p. 34, pl. 3, fig. 4, 6) as of uncertain identity (see Fig. 4F), and because there is no clearly discernible subdelthyrial plate, they appear to belong to *Neilotreta gigoomganensis* Waterhouse, 2015b (see p. 129).

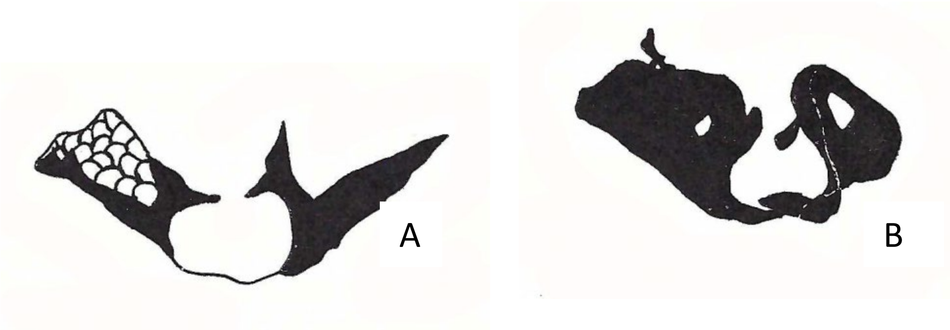

Fig. 5. *Simplicisulcus arthurtonensis* (Waterhouse), transverse sections across ventral umbonal region, showing presence of connector plate formed by inward extensions from the junction between each adminiculum and dental plate. A, BR 1426 at 7mm from umbonal tip. B, BR 1323 at 6.5mm from umbonal tip. Sections x2, from Earnvale Member, New Zealand. (Waterhouse 1968).

Spiriferalarian gen. & sp. indet.

Fig. 6, 7

?1964 *Neospirifer* sp. A Hill & Woods, pl. P8, fig. 2-4.
?1972 *Aperispirifer wairakiensis* [not Waterhouse]- Hill et al., pl. P8, fig.2-4 (part, not fig. 5 = *A. hillae*).
2022 Spiriferalarian gen. & sp. indet. Waterhouse, p. 83, Fig. 14-16.

Diagnosis: Large transverse shells with subrectangular outline and wide hinge, ventral umbo moderately prominent, sulcus well-defined, ventral plicae raised and persistent, inner pair of plicae incorporated in the sulcus anteriorly, costae moderately high. Ventral muscle field large and elongately oval, dental plates and adminicula short, joined by subdelthyrial connector plate.

Morphology: The ventral valve with its sharp-crested plicae differs from other related spiriferalarians found in the region.

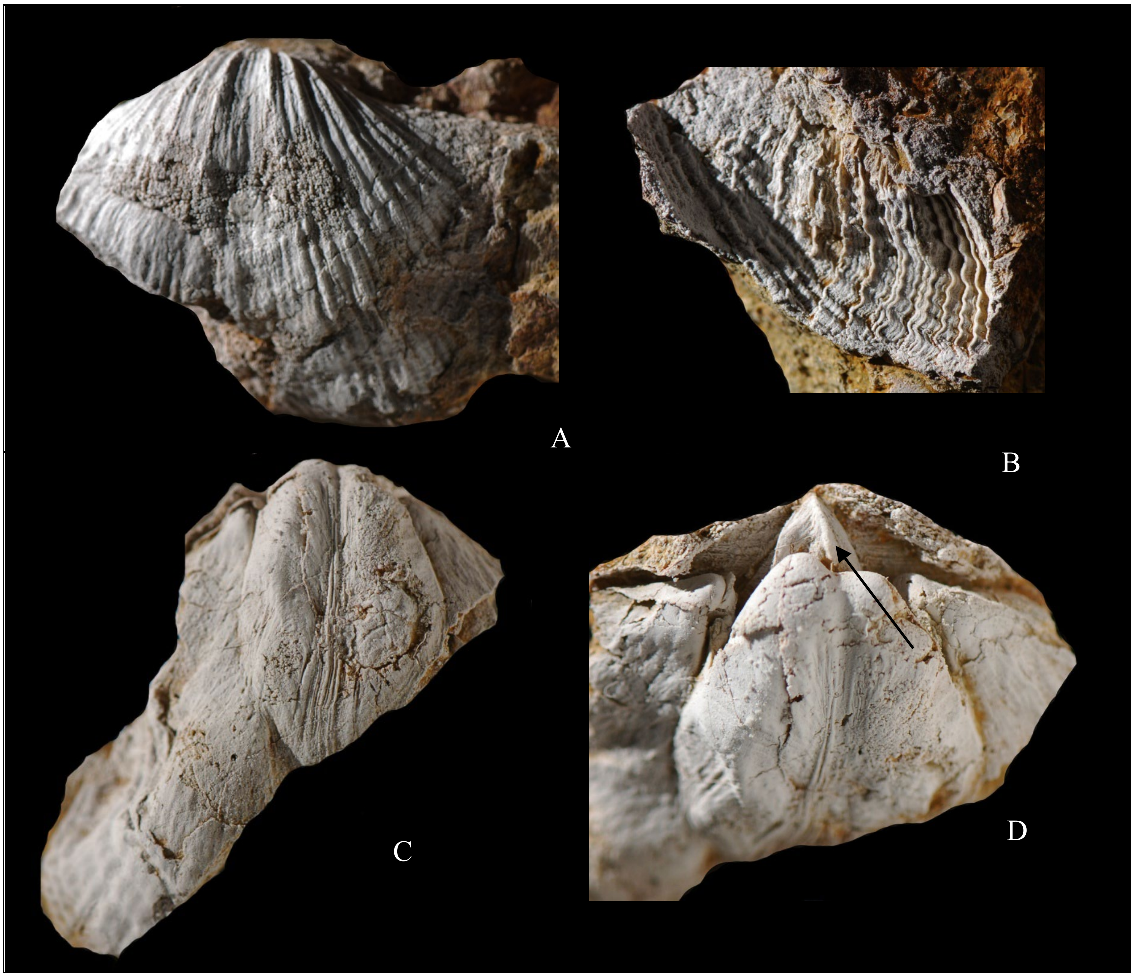

Fig. 6. Spiriferalarian sp. A, B, ventral valve UQF 69654, x1. A, external aspect, B, fragment of external mould. C, D, broken ventral internal mould UQF 82787, after leaching in acid, showing detail of delthyrial area and connector plate. C, ventral aspect, x1.5. D, part of specimen x2, tilted posteriorly to show subdelthyrial connector plate, as arrowed. Mantuan Member, southwest Bowen Basin. (Waterhouse 2022).

Stratigraphy: This species is found in the Mantuan Member of the southwest Bowen Basin. Whether this form is characteristic of the Mantuan level remains to be determined.

Fig. 7. Spiriferalarian sp., latex cast of delthyrial area with subdelthyrial connector plate, as arrowed, UQF 82787, x3. Mantuan Member, southwest Bowen Basin. (Waterhouse 2022).

Subfamily **GYPOSPIRIFERINAE** Waterhouse, 2004

Diagnosis: Spiriferiform genera characterized by low costae with steep flanks and rounded crests, may be organized in a number of low and narrow fascicles, which are generally restricted to the posterior shell. Delthyrium may appear open, or bear stegidial plates. Possibly equipped with subdelthyrial connector plate and obliquely to laterally directed spiralia, but these facets require consolidation from closer examination of the type material.

Name genus: *Gypospirifer* Cooper & Grant, 1976, p. 2210 from Permian of Glass Mountains, Texas.

Gypospirifer Cooper & Grant, 1976

The Glass Mountains material is very well-preserved, but deficiencies in the illustrations and descriptions failed to cover adequately the ventral interior, and have left ambiguities over its internal construct. Provisionally, these deficiencies are remedied by referring to occurrences further afield, but the interpretation needs to be consolidated through a more thorough enquiry into type material from the type material in Texas, and placement as Spiriferidei remains insecure until this is accomplished. Cooper & Grant (1976, p. 2211) considered that the species *condor* d'Orbigny as in Kozlowski, 1914 belonged to *Gypospirifer*. The Kozlowski figure of pl. 1, fig. 1, pl. 7, fig. 10-12, Fig. 16 shows the delthyrium to be closed by a succession of transverse platelets, and Samtleben (1971, pl. 11, fig. 1a, b, 2, 3) figured oblique but essentially laterally directed spiralia for the species, which appears to accord with a figure for *G. anancites* Cooper & Grant (1976, pl. 593, fig. 21), although Cooper & Grant asserted that the spiralia were posteriorly directed (p. 2210) or oblique (p. 2211). Clearly it would be desirable to clarify this matter. Legrand-Blain (1986, Fig. 2, 4) has shown a connector plate for *G. quelmounensis* from Algeria, that shares the same sort of delthyrial cover figured by Kozlowski (1914), as well as the distinctive ribbing of *Gypospirifer*. On the other hand, the figure of her *Gypospirifer* (see pl. 2, fig. 10) from Algeria does not show any clear sign of a connector plate.

***Gypospirifer*? sp.**

Fig. 8

1995 Brachiopod (*Neospirifer*?) Hada & Landis, Fig. 3, p. 353.

Hada & Landis (1985) reported this specimen from limestone near Benmore Dam in South Canterbury, New Zealand, whereas most brachiopods in the New Zealand record are limited to Northwest Nelson, in a crustal fragment that sourced from the New England Orogen of east Australia, and oceanwards, a volcanic arc and sediments that originally lay off-shore from the New England Orogen, and through tectogenesis came to be split apart, leaving after

Fig. 8. *Gypospirifer*? sp. ventral valve from near Lake Benmore, New Zealand. (Hada & Landis 1995).

the opening of the Tasman Sea one segment represented in the Gympie province of southeast Queensland, and another segment forming a belt best exposed in east Nelson and in Southland and south and west Otago. *Martiniopsis woodi* has also been found in North Auckland, above volcanic rocks that appear to represent seaward representatives of the volcanic arc (Waterhouse 2024, p. 70), together with rocks and faunas of New Caledonia. The present specimen occurs beyond these geographic and geological entities, from what appears to be close to the margin of a Pahau Basin or trough, oceanward of the Gympie volcanic arc and a Rakaia Basin (Waterhouse 2015a, p. 125). It is found in Canterbury, New Zealand, with fusulines and ammonoids in a limestone block of the Akatarawa Melange, and judged to be of Kungurian age, thanks to the identification by Hada of *Parafusulina japonica* (Gumbel), a fossil also found to the north at Glenfalloch Stream in New Zealand.

The specimen never received a published registration number, and it does not appear to be at Otago University, and nor has it been established that it is kept with Dr. Hada in Japan. It is judged to be possible *Gypospirifer* from the nature of the ribs.

Subfamily **FUSISPIRIFERINAE** Waterhouse, 2004

Fig. 9, 10

[Fusispiriferinae Waterhouse, 2004, p. 143].

Diagnosis: Markedly transverse with slightly variable costation and plication in different genera. Connector plate.

Genera: *Fusispirifer* Waterhouse, *Cracowspira* Waterhouse, *Cratispirifer* Archbold & Thomas, *Transversaria* Waterhouse & Gupta. Lower Permian (Sakmarian) to Upper Permian (Changhsingian).

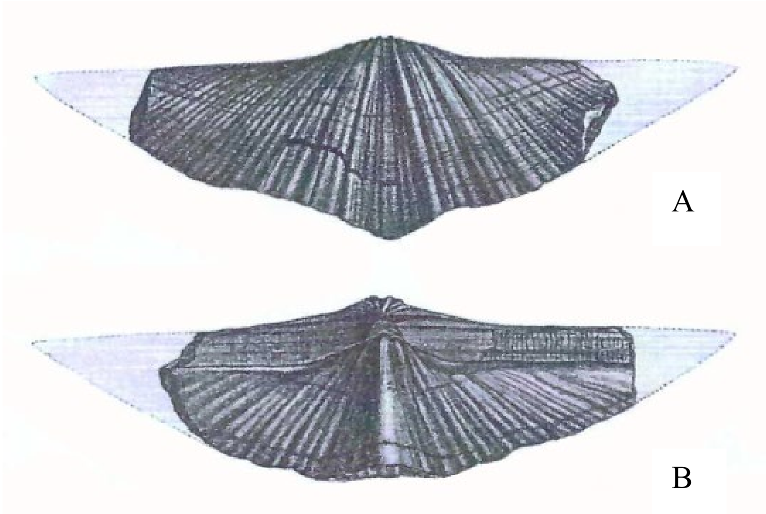

Fig. 9. *Fusispirifer nitiensis* (Diener). A, B, ventral and dorsal aspects of lectotype x1 from Productus Shales of Spiti, northwest Himalaya. (Diener 1897).

Discussion: This is a very distinctive group, involving highly transverse and plicate shells principally found in southern temperate paleolatitudes of the Permian Period in the Himalaya, Timor and Western Australia, expanding rarely into eastern Australia, New Zealand and northeast Russia. *Cracowspira* of east Australia is characterized by weakly defined fascicles on the dorsal valve, and virtually imperceptible fascicles on the ventral valve, in contrast to the strong plication in *Fusispirifer*. The costation differs in the two genera. In *Fusispirifer*, the costae are varied, being especially strong along the crests of fascicles, and fine within the sulcus and over the fold, and laterally towards the cardinal extremities. In *Cracowspira,* the ribs are largely subuniform with wide rounded crests and only feeble bundling. Another genus that demonstrates the range of morphology achievable within the subfamily is *Transversaria marcouiformis* (Jin, 1976). It has fine costae and subdued fascicles, and is characterized principally by the unusually wide anterior fold and sulcus (Waterhouse 2004, pp. 148-150). *Cratispirifer* Archbold & Thomas, 1985 named for a west Australian species, might belong to Fusispiriferinae, but the nature of its reported "massive delthyrial plate" was not analyzed in detail. The delthyrial apparatus appears to be spiriferoid: but the descriptions of species in Western Australia are too generalized to tell, and no figure is informative. Moreover serial sections were never prepared, the authors of *Cratispirifer* relying on external appearance, and failing to adequately analyze the evidence provided by the delthyrial construct. What is not clear for Fusispiriferinae is the nature of the mantle canal system: the canals are slender and crowded in *Fusispirifer,* but otherwise not known.

Fig. 10. *Fusispirifer nitiensis* (Diener), BR 3216, plaster duplicate of ventral internal mould showing large connector plate, as arrowed, x1, and fine mantle canals. From Lopingian of western Nepal. Original kept at Geologisches Bundesanstalt in Vienna, Austria. (Waterhouse 2016).

For many parts of Gondwana, especially the Himalaya and east Australia, the specimens of Fusispiriferinae come from clastic sediments that do not favour the preservation of any delthyrial cover plate or stegidia. But a broad subdelthyrial connector plate is developed in a specimen figured by Waterhouse (1966, pl. 11, fig. 1), identified as *Fusispirifer nitiensis* (Diener), and now kept at the Geologisches Bundesanstalt in Vienna (see Fig. 10). The plate is gently concave dorsally, and the plate anteriorly can be seen to lie between the dental plates and the adminicula. By apparent contrast, a specimen from the Shyok Valley of the western Himalaya, identified as *Occidalia plicatus* (Waterhouse 2004, pl. 5, fig. 7) and kept at the Geological Survey of India in Kolkata (Calcutta), registered as GSI 13199, shows a small convex possible umbonal callosity below the ventral beak, more suggestive of Neospiriferidae, and type *Occidalia* as extensively figured by Archbold (1997) does not indicate any connector plate, even though *Occidalia* is very transverse. In short, Fusispiriferinae is not, as supposed in the *Revised Brachiopod Treatise* (Carter 2006), close to Neospiriferidae, but more likely to be related to Spiriferidae, as a group evolved probably from Spiriferalariinae, given the predominant ornament.

Fusispiriferinae gen. & spp. indet.

Fusispiriferin fragments, too incomplete to allow generic assignment, have been reported from the Elvinia Formation of the southeast Bowen Basin by Waterhouse (1987, p. 22) and from the Hilton limestone of Wairaki Downs in New Zealand by Waterhouse (2001, p. 90, pl. 6, fig. 8, 9).

Genus ***Cracowspira*** Waterhouse, 2004

Diagnosis: Transverse with alate cardinal extremities, low ventral interarea, three pairs of scarcely visible weak plicae, costae slightly finer within sulcus, sturdy with rounded crests, bifurcating rarely.

Type species: *Fusispirifer laminatus* Waterhouse, 1987, p. 23, OD.

Cracowspira laminatus (Waterhouse, 1987)

Fig. 11

1987 *Fusispirifer laminatus* Waterhouse, p. 23, pl. 5, fig. 11-14, pl. 6, fig. 1-4 (part, not pl. 6, fig. 5-7 = *Aperisprifer parfreyi acuta*).
2004 *Cracowspira laminatus* – Waterhouse, p. 151, Fig. 26.3-5.
2007 *F. laminatus* Gourvennec *in* Gourvennec & Carter, p. 2781.
2016 *C. laminatus* – Waterhouse, p. 193, Fig. 236C-E.

Diagnosis: As for genus.

Holotype: UQF 74179 from Roses Pride Formation, southeast Bowen Basin, figured by Waterhouse (1987, pl. 5, fig. 11-14), repeated by other references as in the synonymy, and

Fig. 11A-C herein, OD.

Morphology: In *Cracowspira*, the costae include fine ribs in the sulcus and over the fold, but costae are uniformly coarse over the fascicles and laterally. Further differences from *Fusispirifer* are enumerated in Waterhouse (2004, pp. 151-153). Although Gourvennec *in* Gourvennec & Carter (2007, p. 2781) with advice from L. Angiolini synonymized *Cracowspira* with *Fusispirifer*, that view is rejected. It has been demonstrated that one of the short-comings of the studies in the last century, as summarized and to some extent enshrined by some of the authors in the *Revised Brachiopod Treatise* of 2006 and 2007, has been inadequate attention to details of ornament, as emphasized by Ma & Day (2007) and Schemm-Gregory (2011). There are several species of *Fusispirifer*, all consistent in costation and fasciculation, including for example *F. nitiensis* (Diener), *F. semiplicata* Jin, and *F. jini* Waterhouse. They all differ consistently in ornament from *Cracowspira*. To recognize two genera is the best initial way of demonstrating similarities and differences, although certainly an argument could be sustained for subgeneric rather than full generic distinction.

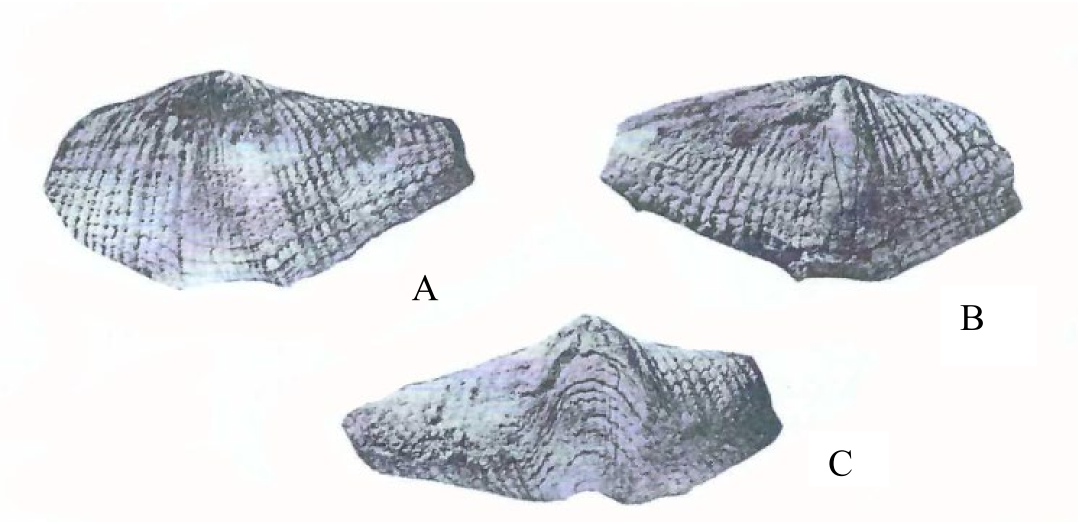

Fig. 11. *Cracowspira laminatus* (Waterhouse), ventral, dorsal and anterior views, x1. From Roses Pride Formation (Artinksian), Queensland. (Waterhouse 1987).

Stratigraphy: The genus has been found so far only in the Roses Pride Formation, deemed to be of lower Artinskian (Aktastinian) age.

Genus ***Transversaria*** Waterhouse & Gupta, 1983

Fig. 12

Diagnosis: Large transverse shells with weak bundling of two or three ribs limited to umbonal shell, well-developed sulcus and fold, both of which widen and become broad anteriorly. Ventral shell may be very thick posteriorly.

Type species: *Fusispirifer marcouiformis* Jin, 1976, p. 209 from Late Permian near Mt Qomolangma, south Tibet, OD.

Discussion: Writers have gone to some length to discredit the validity of *Transversaria*, in order to synonymize it with *Fusispirifer*, asserting for instance that the genus was based on internal moulds and that the genus had been founded on the basis that plicae were lacking from the internal mould. These assertions are not true, and can only be justified by a supposed need to defend the validity of *Latispirifer* Archbold & Thomas, 1985. It was claimed by Archbold & Thomas that the lectotype of *marcouiformis* was an internal mould which failed to show anything of external ornament or plicae, yet mysteriously was able to be identified by them as *Fusispirifer.* In fact, part of the ventral exterior is preserved, and it lacks plicae. Shen et al. (2003) retained the type species of *Transversaria* as being *Fusispirifer*, but figured external shells to make it clear that the species is not *Fusispirifer* (see Fig. 12 herein). The specimens lack fasciculae and plicae, just like the best-preserved specimens of the original suite (Zhang & Jin 1976, pl. 12, fig. 1, 2, 10, 11), which I had examined in 1980. The specimens show the exterior and the dorsal fold is massive, unlike that of any species of *Fusispirifer*. One specimen (Shen et al. 2003, pl. 14, fig. 5) shows a delthyrial cover in the form of a neodeltidium.

The genus *Latispirifer* Archbold & Thomas, 1985 shows comparable weak bundling over the umbonal region and so is threatened by being possibly a junior synonym. It was perhaps this aspect that bothered Archbold & Thomas (1985, p. 270; 1987, p. 177) for they declared that whereas the type specimen of *marcouiformis* was *Fusispirifer*, a topotype was indeed *Latispirifer*! But to me, the fears of synonymy were groundless: the sulcus and fold are far more conspicuous in *Transversaria* than in *Latispirifer*. The two authors took a somewhat casual approach to spiriferidin genera, unlike the earlier more thorough work by G. A. Thomas (1971), who prepared serial sections. Instead, Archbold & Thomas evaluated

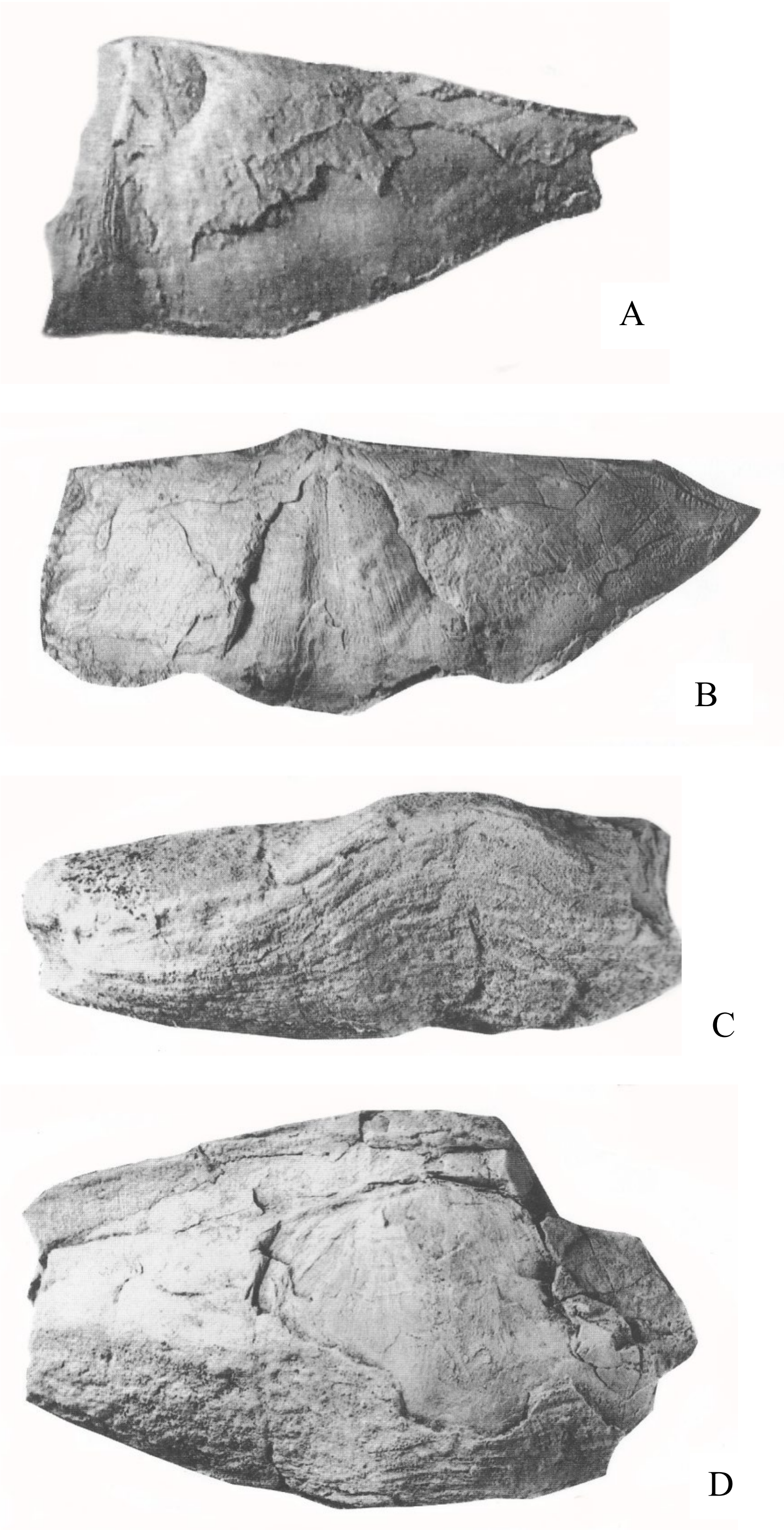

Fig. 12. *Transversaria marcouiformis* (Jin) from the lower Qubuerga Formation, south Tibet, x1. A, Unregistered ventral valve, supplied by Prof. Shuzhong Shen. B, NMVP 306029. C, D, anterior and dorsal aspects of NMVP 306031. (Shen et al. 2003).

genera solely from external appearance, and spiriferids were supposedly non-plicate, unlike neospiriferids which were deemed plicate, and both were regarded as costate. They failed to detect the presence of a subdelthyrial plate in one suite, and not in the other, because they failed to prepare their well-preserved material. Productida were much more amenable to external analysis, and so Archbold's work on that group has proved much more satisfactory, whereas his spiriferid studies require closer scrutiny and often need further elucidation of internal morphology.

Transversaria pauciplicus (Waterhouse, 1987)

Fig. 13, 14

1987 *Fusispirifer pauciplicus* Waterhouse, p. 23, pl. 5, fig. 15, pl. 6, fig. 1-4, text-fig. 4 (part, not fig. 5-7 = *Aperispirifer parfreyi acuta*).
2004 *Transversaria pauciplicus* – Waterhouse, p. 150, text-fig. 28.
2016 *T. pauciplicus* – Waterhouse, Fig. 237.

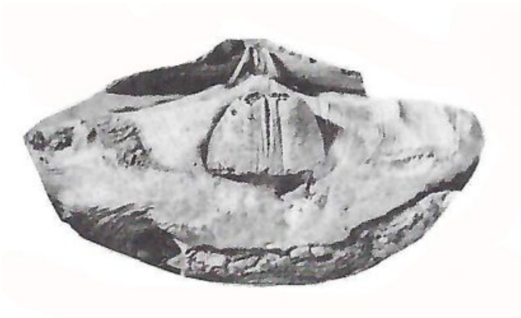

Fig. 13. *Transversaria pauciplicus* (Waterhouse), partly leached ventral interior, UQF 42216 x1.5, from Barfield Formation of southeast Bowen Basin, Queensland. (Waterhouse 1987).

Diagnosis: Relatively small with low broad fold and shallow anterior sulcus. Costae fine with minor bundling.

Holotype: UQF 42221 from Barfield Formation, southeast Bowen Basin, figured in Waterhouse (1987, pl. 6, fig. 1, 2, 4; 2004, text-fig. 28.1, 2, 4; 2016, Fig. 237A, B, D), and Fig. 13A,C, D herein, OD.

Morphology: The specimen figured in Waterhouse (1987, pl. 5, fig. 15) is a ventral valve leached in acid, and shows a moderately broad adductor platform, and closed delthyrium, as reproduced herein as Fig. 13.

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

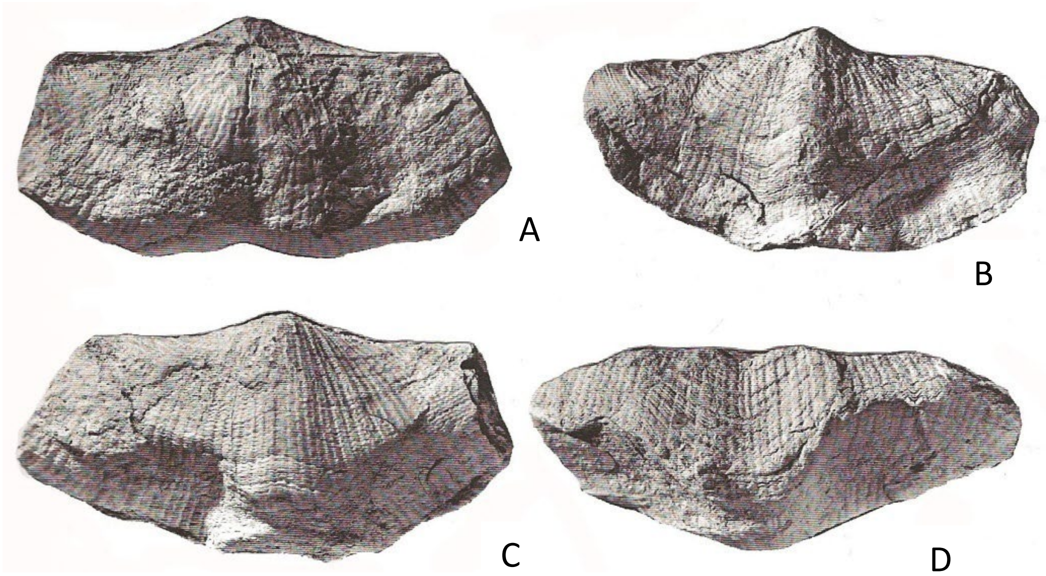

Fig. 14. *Transversaria pauciplicus* (Waterhouse). A, C, D, ventral, dorsal and anterior aspects, of holotype, UQF 42221, x1. B, dorsal valve UQF 42220, x1. From Barfield Formation (Wordian) of southeast Bowen Basin, Queensland. (Waterhouse 1987).

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SPIRIFERELLOID BRACHIOPODS IN THE PERMIAN OF NEW ZEALAND

Abstract

Occurrences of the brachiopod Superfamily Spiriferelloidea are summarized for the Permian deposits of New Zealand. There are no known occurrences of the superfamily in the Permian of east Australia.

SYSTEMATIC AND STRATIGRAPHIC SUMMMARY

Superfamily **SPIRIFERELLOIDEA** Waterhouse, 1968

[Nom. transl. Waterhouse 2016, p. 212 ex Spiriferellinae Waterhouse, 1968, p. 10].

Diagnosis: Medium-sized shells with distinctive subelongate, subpentagonal or subtriangular shape, normally plicate, sulcate, may be costate, with micro-ornament of commarginal and radial capillae, often pustulose. Umbonal callosity or delthyrial cover plate and connector plate. Adminicula, dental plates, crural plates, no tabellae. Ventral valve often secondarily thickened.

Discussion: Spiriferelloidea ranged in time from middle Carboniferous (?Bashkirian or Moscovian) to Upper Permian (Changhsingian). They constitute a highly distinctive but not very large group, standing apart in being subequilateral in shape, less transverse than most Spiriferoidea, with thickened ventral valve and distinctively pustulose micro-ornament. On the other hand, denticulate hinge and internal plates are shared with members of other superfamilies in the Spiriferidina. In a few species such as *Canalisella leviplica* (Waterhouse & Waddington), spiralia are posteriorly directed (Waterhouse & Waddington 1982, Waterhouse 2020, Fig. 280B, p. 326), with Lee *in* Lee et al. (2019) also recording posteriorly directed spiralia for Svalbard material. The implications for classification are still to be elucidated. The mantle canal system seems special to Spiriferelloidea, and shows a pattern moderately like that of spiriferids, but coarser in depth and spacing of pits, and some specimens indicate a closely spaced anastomosing radiating pattern as illustrated in Waterhouse (2016, Fig. 263-265), differing from the standard spiriferid pattern, but not forming an open subrectangular network as in choristitids and various trigonotretids. There appears to be variation in the development of a delthyrial cover plate, and presence or absence of a prominent umbonal callosity. *Spiriferella* and its allies may exhibit one or other, or both. A discrete connector plate is frequently visible, unless it has been buried in secondary callus. One of the special features of many species in Spiriferellidae is the substantial secondary thickening in the ventral valve. One publication attempted to merge spiriferellids with spiriferids, but such an effort was based on embarrassingly oversimplified cladistical studies which left out and failed to evaluate various prime characteristics of both groups.

Family **SPIRIFERELLIDAE** Waterhouse, 1968

[Nom. transl. Waterhouse 2016 ex Spiriferellinae Waterhouse, 1968, p. 9. Proposed de novo as full family by Termier et al., 1974, p. 136, with no reference to Spiriferellinae Waterhouse, 1968].

Diagnosis: Externally distinctive, with plicae rounded in section and separated by narrow interspaces, exterior may be smooth or costate, micro-ornament cancellate with pustules, developed as a rule along commarginal growth laminae. Adminicula short, may be largely buried in secondary thickening, subdelthyrial connector plate, dental plates and adminicula, ctenophoridium and crural plates, no tabellae. Posterior ventral valve heavily thickened as a rule.

Discussion: This is a highly distinctive family, and with its sister group Elivinidae Waterhouse, 2004, which has reduced secondary thickening and has secondarily lost the micro-ornament of pustules, stands apart from members of Spiriferoidea, as distinct as any superfamily, and showing considerable variation. For example. the micro-ornament may be pustulose or cancellate, the plicae may be costate or smooth, the fold varies considerably in prominence and transverse profile, and the delthyrium may be open with umbonal callus, or closed by a delthyrial cover plate as noted by Shen et al. (2001, pp. 165, 167). A connector plate is visible for example in *Bamberina* (see Waterhouse 2016, Fig. 272, p. 218), and the suite ascribed to *Spiriferella* and allied species from the Glass Mountains of Texas, with favorable preservation of the ventral umbonal shell, establishes that a connector plate was developed, at least in many species, and that it was often buried in secondary shell. Secondary thickening in the ventral valve may be great, much more than in other members of Spiriferidina, and together with extensive pustulation, helps define a highly distinctive group.

Subfamily **SPIRIFERELLINAE** Waterhouse, 1968

[Spiriferellinae Waterhouse, 1968, p. 10. Syn. Hunzininae Angiolini, 2001, p. 332].

Diagnosis: Moderate to well-developed dorsal fold, traversed by median groove. Shape subpentagonal, weakly transverse to subelongate.

Genera: *Spiriferella C*hernyshev, *Alispiriferella* Waterhouse & Waddington, *Bamberina* Waterhouse, *Canalisella* Waterhouse, *Eliva* Fredericks, *Eridmatus* Branson, *Hunzina* Angiolini, *Nakimusiella* Shen et al., ?*Spiriferellaoides* Lee, Gu, & Li (syn. *Spiriferelloides* Li, Gu & Li, nom. nud.),and *Tintoriella* Angiolini, its validity disputed by Shen, Shi & Archbold (2003), but accepted by Waterhouse (2020). Upper Carboniferous (Kasimovian) to Upper Permian (Changhsingian).

Genus ***Nakimusiella*** Shen, Archbold, Shi & Chen, 2001

Diagnosis: Variably elongate shells with obsolete sulcus and simple costae which may bifurcate anteriorly. Dorsal fold with anterior median groove in New Zealand species.

Type species: *Nakimusiella selongensis* Shen et al., 2001 from Qubuerga Formation, south Tibet, OD.

Discussion: The type material for genus *Nakimusiella* Shen et al. (2001, p. 173) lacked any dorsal valve. The genus was left out of the *Revised Brachiopod Treatise* by Carter (2006) and Gourvennec & Carter (2007), but was recorded in Waterhouse (2016, p. 218, Fig. 273).

Nakimusiella oweni Waterhouse, 1999

Fig. 1

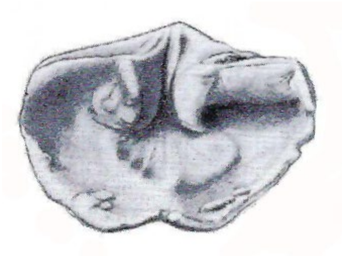
1878 *Spirifer glaber* [not Sowerby] – Hector, p. xii.
1967 *Spiriferella* n. sp. Waterhouse, p. 92, text-fig. 5G, 32.
1999 *Nakimusiella oweni* Waterhouse, p. 20.
2001 *N. oweni* – Waterhouse, p. 96.

Diagnosis: Small well-inflated shells with plicae reduced to one anterior pair, costae low, sulcus narrow, V-shaped in section, fold low with median anterior groove.

Holotype: BR 654 figured by Waterhouse (1967, Fig. 5G, 32) and herein as Fig. 1 from Pig Valley Limestone, Nelson, New Zealand.

Morphology: The species is highly distinctive, but more figures are needed to bolster the textual description.

Fig. 1. *Nakimusiella oweni* Waterhouse, view of ventral interior, BR 654 x1, from Pig Valley Limestone, Nelson, New Zealand. (Waterhouse 1967).



Stratigraphy: The Pig Valley Limestone (Waterhouse 1987; 2002, p. 137) is regarded as very late Permian, close to the age of the type species of *Nakimusiella* as described from late Changhsingian fauna at the hill of Selong in south Tibet.

Genus ***Spiriferella*** Tschernyschew, 1902

Diagnosis: Subequilateral shells with sulcus and fold bearing distinct and narrow median channel, plicae variably costate, delthyrium open or closed by cover plate.

Type species: *Spirifer saranae* Verneuil, 1845 from Artinskian of Russia, OD.

Discussion: It should be noted that in the *Revised Brachiopod Treatise*, Carter (2006, Fig. 1198.1) figured as type species for *Spiriferella saranae* (Verneuil) material illustrated by Tschernyschew (1902) from the Schwagerinakalk of Sula River. That particular material has been named *Spiriferella barchatovae* by Waterhouse & Waddington (1982), and is now evaluated as a species of *Arcullina* Waterhouse, 1986 (see Waterhouse 2016, Fig. 266). Type *saranae* comes from younger beds of Artinskian age, as figured by Tschernyshew (1902, text-fig. 41-46) and has a narrowly channelled fold, unlike *barchatovae*.

Spiriferella supplanta Waterhouse, 1964

Fig. 2

1964a *Spiriferella* n. sp. Waterhouse, p. 72.
1964b *Spiriferella supplanta* Waterhouse, p. 141, pl. 27, fig. 3, 4, 6, pl. 28, fig.1-6, pl. 29, fig. 1-7, text-fig. 67A, B, D, E, 68, 69A, B.
2002 *S. supplanta* – Waterhouse, p. 34.

Diagnosis: Subrounded pentagonal in outline, varying from slightly elongate to weakly transverse. Two or three costae as a rule in the sulcus, with median costa missing from some specimens, no more than five costae over each plication, plicae in three major pairs with additional fine ribs laterally. Dorsal fold groove clearly defined. Dental plates short.

Holotype: BR 558 from middle Letham Formation, Wairaki Downs, New Zealand, figured in Waterhouse (1964b, pl. 28, fig. 1, pl. 29, fig. 3, 5-7, text-fig. 67A, 69A, B), OD.

Stratigraphy: The species is known only from the middle Letham Formation, with the strophalosiidin species *Wyndhamia, typica* and is regarded as being of middle Kungurian age.

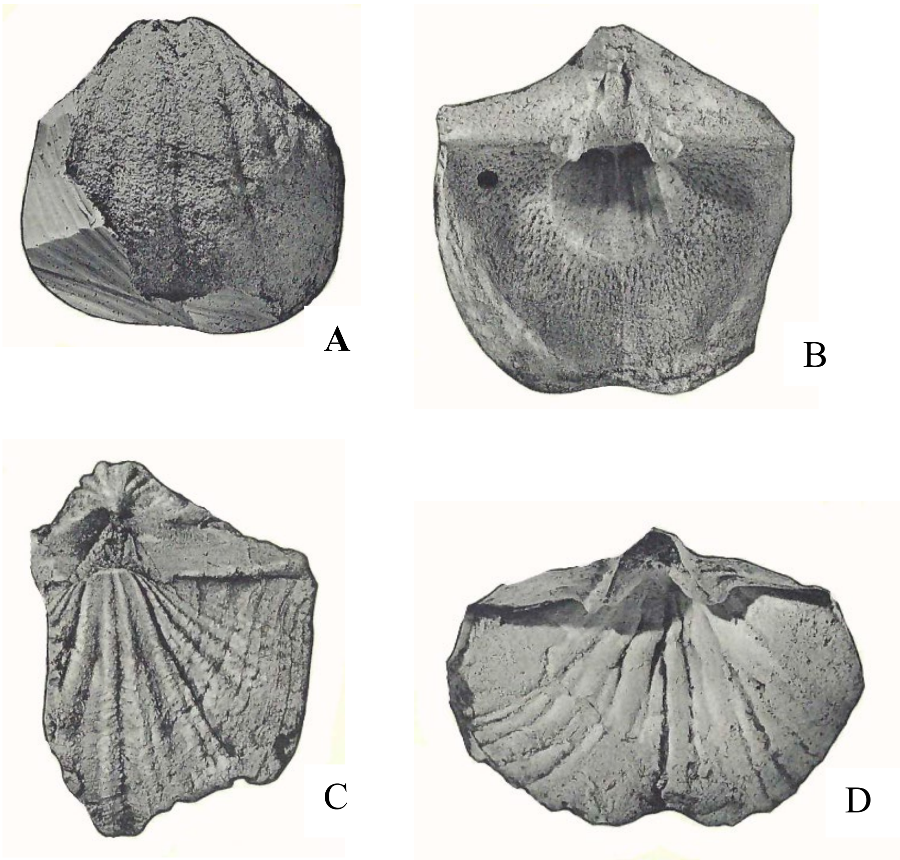


Fig. 2. *Spiriferella supplanta* Waterhouse. A, PVC cast of exterior, BR 559. B, PVC cast of internal ventral valve, showing interior, BR 826. C, dorsal view of PVC cast of exterior, BR 562. D, PVC cast showing dorsal interior and part of ventral interior, BR 562. Specimens x1.5 from middle Letham Formation, Wairaki Downs, New Zealand. (Waterhouse 1964b).

***Spiriferella*? sp. A**

Fig. 3

1968 *Spiriferella* sp. Waterhouse, p. 50.
1982 *Spiriferella* sp. Waterhouse, p. 54.

1999 *Spiriferella* sp. Waterhouse, p. 19.
2001 *Spiriferella* sp. B, Waterhouse, p. 95, pl. 6, fig. 11, 16.
2002 *Spiriferella* sp. Waterhouse, p. 65.

Worn ventral valves come from the Glendale Limestone at Wairaki Downs in New Zealand. No dorsal valves are available.

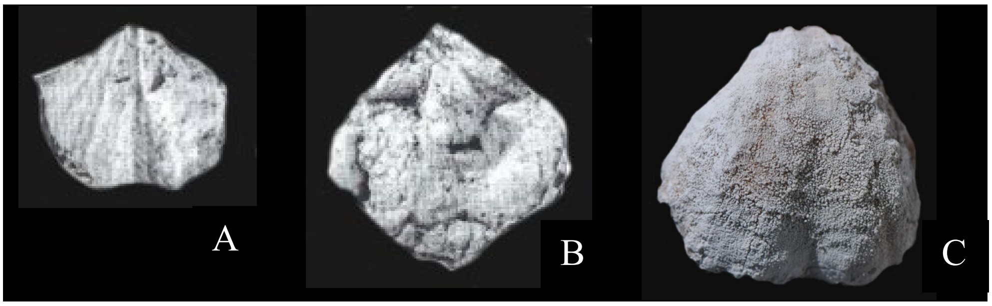


Fig. 3. *Spiriferella*? sp. A. A, ventral valve OU 2462. B, internal mould of leached ventral valve OU 2463. C, unregistered OU ventral valve. Specimens x1 from Glendale limestone, Wairaki Downs, New Zealand. (Waterhouse 2001 and new).

***Spiriferella*?** sp. B

2001 *Spiriferella* sp. A Waterhouse, p. 95, pl. 6, fig. 13.

The fragment of a ventral valve OU 18285 from Hilton Limestone, Wairaki Downs, New Zealand.

Subfamily **TIMANIELLINAE** Waterhouse, 2016,

[Timaniellinae Waterhouse, 2016, p. 220].

Diagnosis: Dorsal channel along crest of dorsal fold exceptionally wide.

Name genus: *Timaniella* Barchatova, 1968 from Timan Peninsula, Russia, OD.

Genera: *Timaniella* Barchatova, *Alispiriferella* Waterhouse & Waddington, *Undulatina* Waterhouse.

Discussion: *Undulatina* Waterhouse, 2020, p. 334 was classed as Arcullinae, but this is surely an error, because its dorsal fold is very like that of *Timaniella*, and the shell shape is close to that of *Alispiriferella*, the difference being that more plicae are present. A particularly fine array of species for these two genera has been described by Kletz (2005) from northeast Siberia, and a number of his *Plicatospiriferella* species are deemed to belong to *Undulatina*.

Genus ***Alispiriferella*** Waterhouse & Waddington, 1982

Diagnosis: Medium to large, transverse with alate cardinal extremities and wide median channel along dorsal fold.

Type species: *Spirifer* (*Spiriferella*) *keilhavii ordinaria* Einor, 1939, p. 140 from Novaya Zemlya, OD.

Discussion: The broad channel along the dorsal fold is a critical feature of the genus. The original figure of Salter *in* Salter & Blanford, 1865 for *Spiriferella rajah* as reproduced in Waterhouse (2016, Fig. 269) shows only a narrow median groove along the dorsal fold, with five or six pairs of plicae over the lateral slopes. Carter *in* Gourvennec & Carter (2007, p. 2786, Fig. 3a) replicated an unattributed figure from Davidson (1866, pl. 2, fig. 3) which shows a rounded fold, but the Davidson rendition is inaccurate, and Angiolini (2001, pl. 4, fig. 8) showed the nature of the fold to be in accord with that of the Salter figure.

The relatively wide channel along the fold is developed widely amongst spiriferellid species, in specimens assigned for instance to *Spiriferella rajah* of Shen et al. (2001, Fig. 7)

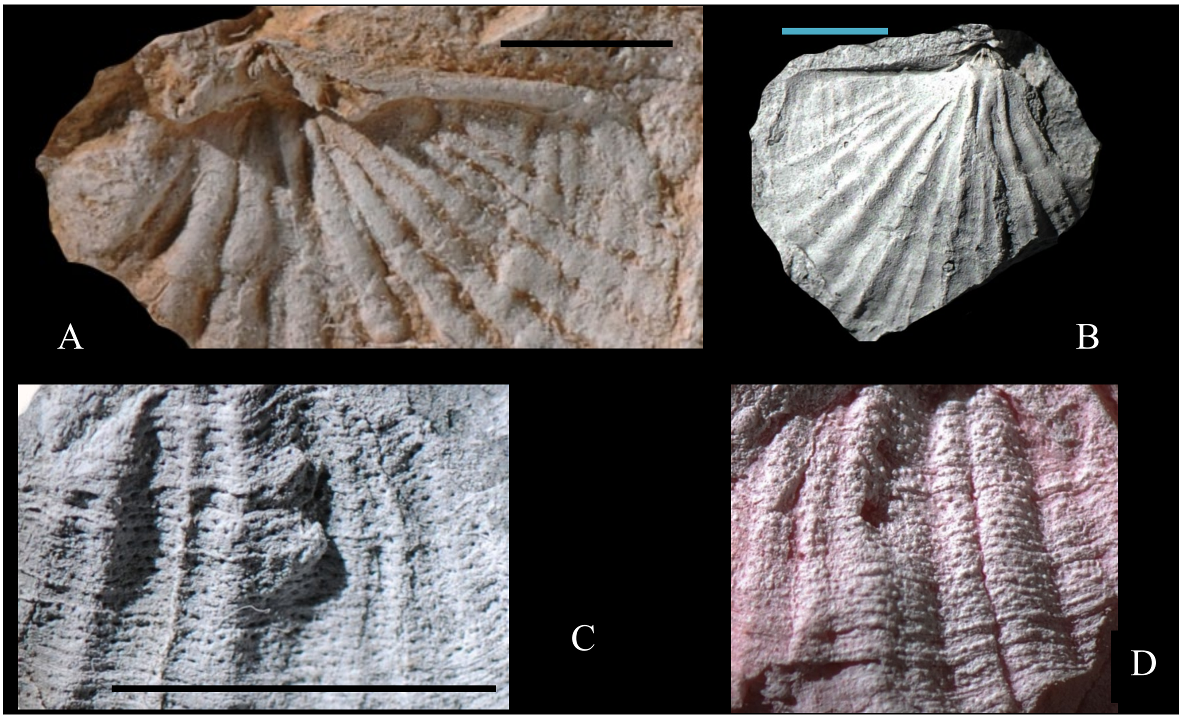


Fig. 4. *Alispiriferella turnbulli* Waterhouse & Campbell. A, B, latex cast and internal mould of dorsal valve BR 2449. C, D, external mould and latex cast of dorsal exterior near fold, BR 2455, showing minute spinules, sharing space bar. Space bar 10mm long. From Eglinton Subgroup, Dunton Range, New Zealand. (Waterhouse & Campbell 2021).

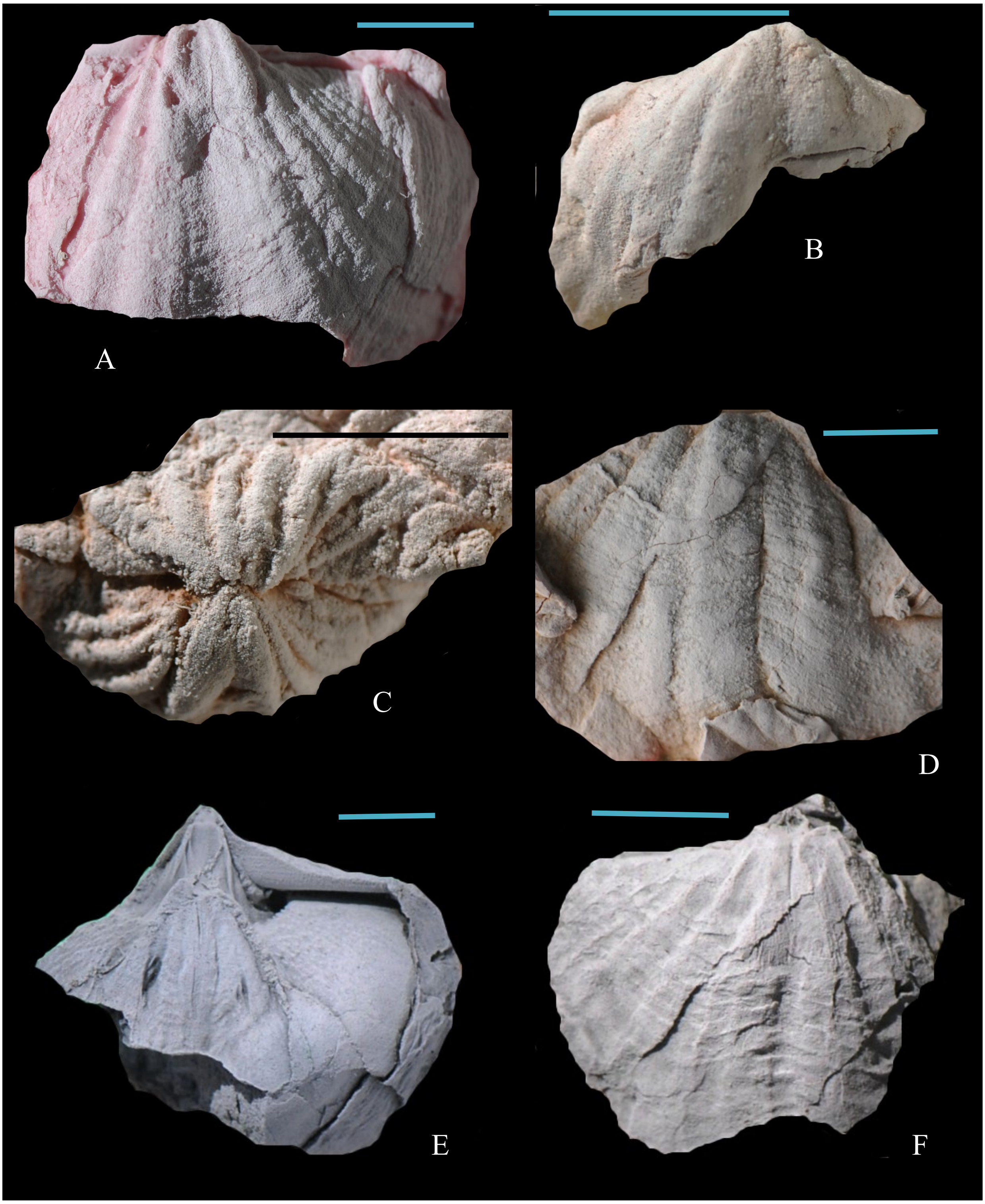


Fig. 5. *Alispiriferella turnbulli* Waterhouse & Campbell. A, D-F, BR 2468, holotype. A, latex cast, showing much of ventral valve. D, latex cast of dorsal external mould of the same specimen. E, F, ventral and dorsal aspects of internal mould. B, latex cast of small ventral valve, ventral exterior, BR 2480. C, latex cast of specimen with valves conjoined, BR 2469, dorsal valve on top. Space bar 10mm long. From Eglinton Subgroup, Dunton Range, New Zealand. (Waterhouse & Campbell 2021).

has a dorsal fold like that of *Alispiriferella*, as in so-called *Tintoriella laticostata* Waterhouse (2020, p. 341, Fig. 289). from east Greenland, and is close to the fold of *Timaniella* Barchatova, 1968, so that *laticostata* should be reassigned to *Alispiriferella*.

Alispiriferella turnbulli Waterhouse & Campbell, 2021

Fig. 4, 5

2021 *Alispiriferella turnbulli* Waterhouse & Campbell, p. 36, Fig. 11, 12.

Diagnosis: Shell of medium size, weakly subalate cardinal extremities, three to four pair of plicae with a few anterior costae, postero-lateral shell costate.

Holotype: BR 2468 figured by Waterhouse & Campbell (2021, Fig. 11A, D-F) and herein as Fig. 5A,D-F, OD.

Stratigraphy: This species is found in the Eglinton Subgroup of west Otago, on the Pacific side of the Brook Street Volcanic Arc, and is of Sakmarian age.

Alispiriferella sp.

Fig. 6

1968 *Spiriferella* sp. Waterhouse, p. 50.
1982 *Spiriferella* sp. Waterhouse, p. 54.
1999 *Alispiriferella* n. sp. Waterhouse, p. 21.
2001 *Alispiriferella* n. sp. Waterhouse, p. 97, pl. 7, fig. 1-3, text-fig. 7c.

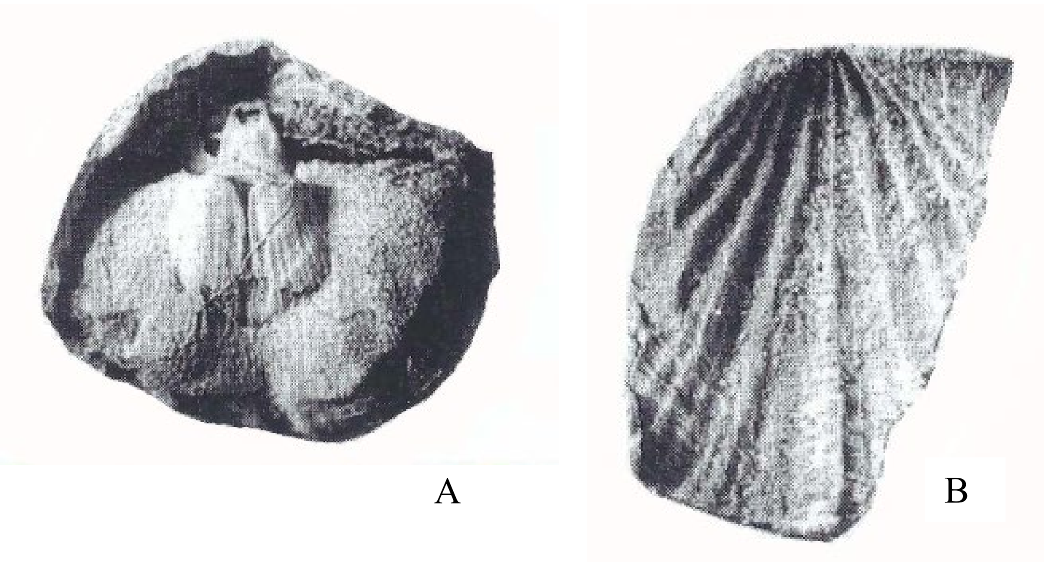


Fig. 6. *Alispiriferella* sp. A, internal mould of ventral valve OU 18286. B, part of dorsal external mould OU 18287. Specimens x2 from lower Glendale Formation, Wairaki Downs, New Zealand. (Waterhouse 2001).

Morphology: Specimens are weakly transverse with extended cardinal extremities, moderately inflated ventral valve and little inflated dorsal valve, five pairs of plicae, weak costae, well-defined sulcus and low broad dorsal fold with wide channel.

Stratigraphy: This species is found in the clastic beds of the lower Glendale Formation, below *Spiriferella* sp. A reported previously on p. 59. The age is likely to be early Changhsingian, found in the faunal zone that includes *Capillonia brevisulcus* (see Waterhouse 2001, p. 15).

Subfamily **ARCULLININAE** Waterhouse, 2016

[Nom. correct. hic ex Arcullinae Waterhouse, p. 220].

Diagnosis: Dorsal fold high with narrow crest and no sign of median groove. Cisuralian to Guadalupian of Urals and Arctic. Upper Pennsylvanian (Kasimovian) to Upper Permian (Changhsingian).

Name genus: *Arcullina* Waterhouse, 1986, p. 4 from Guadalupian of the Arctic, OD.

Discussion: Arcullininae Waterhouse, 2016, p. 220 is based on *Spiriferina polaris* Wiman, 1914, p. 39, and like ally *Plicatospiriferella* Waterhouse & Waddington, 1982, has a distinctive high dorsal fold which lacks the median groove or channel that characterizes most of the other genera assigned to Spiriferellidae. The genus is represented by a number of species in the Arctic, especially well illustrated by Grunt (2006), and several species are found in the Late Permian of the southern paleohemisphere in the Himalaya and Timor (Waterhouse 2004, p. 211ff). Unlike species of *Arcullina*, the type species of *Spiriferella, saranae* of Verneuil, has a fold with a narrow median groove, as indicated in the original figure of a broken posterior dorsal valve (Verneuil 1845, pl. 6, fig. 156), and specimens from the same horizon as examined at the Tschernyschew Museum of St Petersburg, Russia, have a dorsal fold with a shallow median groove. According to Waterhouse & Waddington (1982, p. 19) and Waterhouse (2016, p. 214, Fig. 266), the fold has a rounded crest in Tschernyschew's so-called *saranae*, and they proposed the name *barchatovae*, with the specimen figured by Tschernyschew (1902, pl. 12, fig. 4) designated as holotype, and now to be placed in *Arcullina*.

Genus ***Arcullina*** Waterhouse, 1986

Diagnosis: Fold simple with rounded crest and no median channel. Plicae well developed, not costate as a rule, sulcus generally costate.

Type species: *Spiriferella polaris* Wiman, 1914 from the Spirifer Limestone and lower Brachiopod Chert of Spitzbergen, OD.

Arcullina humilis Waterhouse, 2001

Fig. 7

2001 *Arcullina humilis* Waterhouse, p. 97, pl. 6, fig. 12, 14, 15, 17-21, text-fig. 7d, e.

Diagnosis: Small size, heavy ventral internal thickening, low narrow sparsely costate plicae, very high ventral interarea.

Holotype: OU 18766 figured in Waterhouse (2001, pl. 5, fig. 14) possibly from McLean Peaks Formation, Wilanda Downs, New Zealand, OD.

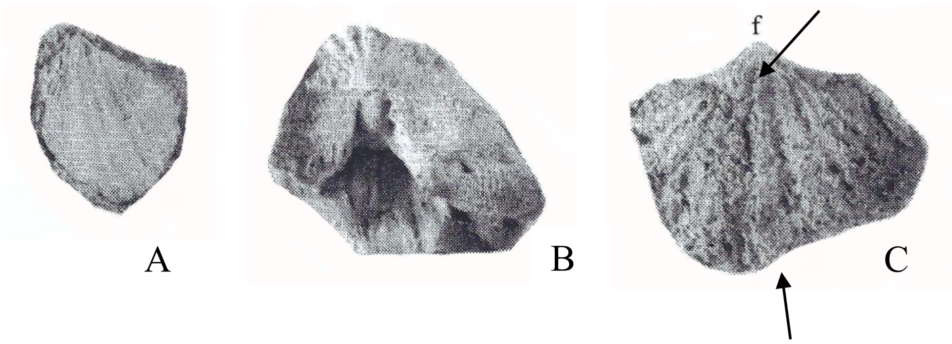


Fig. 7. *Arcullina humilis* Waterhouse. A, ventral valve OU 18764. B, latex cast showing ventral interior, OU 18765. C, latex cast of dorsal exterior OU 18787. The dorsal fold lies between the arrows in Fig. 7C. Specimens x1.5 from McLean Peaks Formation?, upper Takitimu Group (*Echinalosia conata* Zone). (Waterhouse 2001).

Stratigraphy: The species is found in the upper middle Takitimu Group of New Zealand, probably in the McLean Peaks Formation.

CONCLUSIONS

A number of spiriferelloid species are found in New Zealand, all within a central band of sediments containing fossils otherwise close to those of east Australia, where faunas are abundant, but lack members of the superfamily. The New Zealand region with faunas more exactly like those of east Australia lies to the west, in northwest Nelson, and regions to east in the main (curving southwards from a north-south direction into an east-west orientation for the Southland Syncline) have conodonts and fusulines, also missing from east Australia. Through the presence of Spiriferelloidea, the central band exposed in the Takitimu Mountains and at Wairaki Downs and east Nelson in New Zealand comes close in some aspects of the make-up of its fossil faunas to those of the Arctic regions found in northern Canada and northeast Russia in the northern hemisphere, and Western Australia and the Himalayas of the southern hemisphere, though unlike some of these regions there are no conodonts or fusulines in this particular part of New Zealand. Members of the other spiriferelloid family Elivellidae Waterhouse, 2004, distinguished by the less thickened shell and absence of pustules, are restricted to more warm-water faunas, and are not known in New Zealand or in Western Australia.

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TRIGONOTRET0ID BRACHIOPODS FROM EAST AUSTRALIA AND NEW ZEALAND

Abstract

Fossil species belonging to Trigonotretoidea Schuchert, 1913 and Neospiriferoidea Waterhouse, 1968, both grouped as Trigonotretidei, that are found in marine sediments of east Australia and New Zealand are summarized, with illustrations.

INTRODUCTION

Permian spiriferiform genera of east Australia and New Zealand fall into two major categories. One group possesses a subdelthyrial connector plate that passes under the delthyrium and connects the dental and adminicular plates where they join each side of the delthyrium. This group, which includes Spiriferoidea and Spiriferelloidea, is referred to Hyporder Spiriferidei King. and is closely allied to Cyrtospiriferoidea that gave rise to punctate shells grouped as Syringothyroidea. The other group lacks the subdelthyrial connector plate, and is referred to Trigonotretidei Schuchert. Within this hyporder, there are two major subdivisions, between species which have or are believed to have posteriorly directed spiralia, called Trigonotretoidea Schuchert, and a second group with laterally directed spiralia, called Neospiriferoidea Waterhouse.

Many Trigonotretidei appear to have been relatively short-ranging, without the exuberant evolution and often localized development exhibited by many members of Productida. They thus offer high potential for east Australian and New Zealand Permian correlations, though this potential is weakened by the failure to describe and illustrate extensive faunas in modern terms rather than merely list fossils from some of the Permian sequences in Tasmania and parts of the Sydney Basin of New South Wales and southwest Bowen Basin, as well as update the faunal descriptions for the Yarrol Basin in Queensland. There are disadvantages offered by the shells of large spiriferiforms, because the interior of the shell has to be determined, or identification can only be provisional, and the shells are large and so more easily broken. Present indications are that evolution of species was far less exuberant at given intervals, compared with productiform and even some ingelarelloid groups, which in some instances were geographically more limited, to the extent that different but related species of the same genus inhabited coeval sediments even within the one basin, thereby complicating the task of achieving correlation across extensive areas.

SYSTEMATIC AND STRATIGRAPHIC SUMMARIES

Phylum Brachiopoda Duméril, 1806

Order SPIRIFERIDA Waagen, 1883

Suborder SPIRIFERIDINA Waagen, 1883

Hyporder TRIGONOTRETIDEI new

Diagnosis: Transverse as a rule, plicate and may be costate shells with interareas and delthyrium. Adminicula, dental plates, crural plates. No tabellae or subdelthyrial connector plate, but a thickened shelf or pleromal build-up may be present, with often large callosity.

Discussion: Two superfamilies are allocated to the hyporder, Trigonotretoidea and Neospiriferoidea, distinguished by the direction of the spiralia, which are posteriorly directed in the first superfamily and laterally directed in Neospiriferoidea. Theoretically, it seems possible that some groups included in Neospiriferoidea arose independently from Trigonotretoidea rather than from Neospiriferoidea, such as Family Georginakingiidae, a matter requiring further study.

Superfamily **TRIGONOTRETOIDEA** Schuchert, 1893

[Nom. transl. hic ex Trigonotretinae Schuchert, 1893, p. 156] et seq.

Diagnosis: Large plicate shells with costae to varying degree, stegidia and modifications apparently absent**.** Adminicula, dental plates, and crural plates, no tabellae, no subdelthyrial plate but may be pleromal build-up forming a shelf, bearing massive callosity. Spiralia posteriorly directed where known; mantle canals well-spaced, at least in Australian examples.

Name genus: *Trigonotreta* Koenig, 1825, p. 3 from Early Permian of Tasmania, OD.

Discussion: Further study is required on this group, to clarify whether some of the attributes found in *Trigonotreta* pertain to allies beyond the particular domain of the genus in the very cold Permian waters of east Australia. Such uncertainties involve for instance the spacing and development of mantle canals and the substantial development of an umbonal callosity in the ventral valve.

Family **TRIGONOTRETIDAE** Schuchert, 1893

Diagnosis: Shells without delthyrial cover plate or stegidia, spiralia believed to be posteriorly directed, mantle canal system may be closely or well-spaced. Ornament dominated by plicae, which are costate to varying degree, costae often robust and may be differentiated.

Genera include *Trigonotreta* Koenig and subgenus *Grantonia* Brown, *Adminiculoria* Waterhouse, *Alispirifer* Campbell, *Brachythyrinella* Waterhouse & Gupta (syn. *Pericospirifer* Cisterna & Archbold), *Costuloplica* Waterhouse and *Maxwellispirifer* Waterhouse.

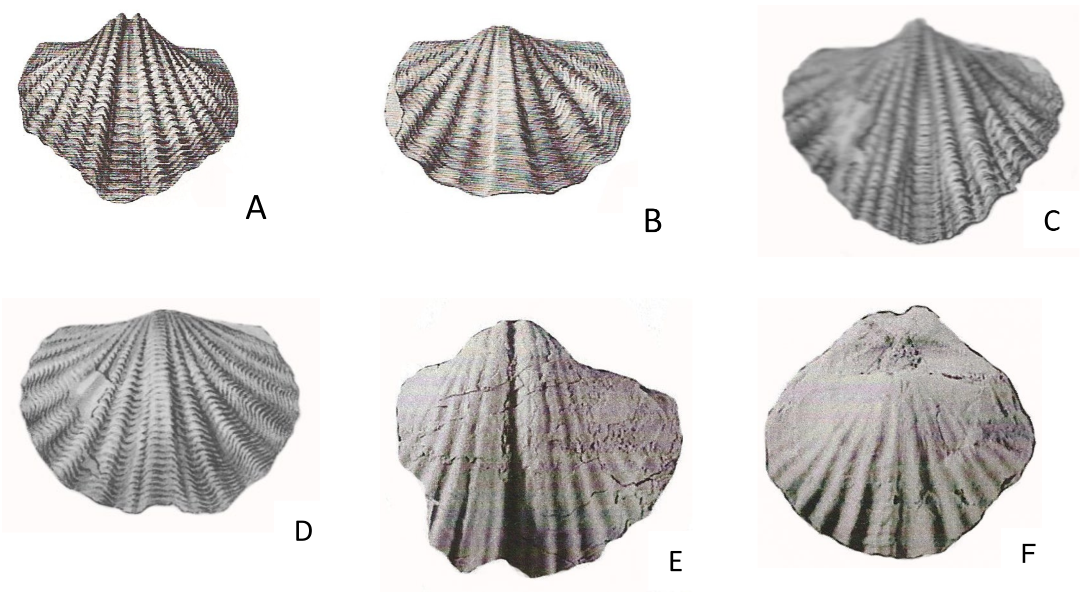


Fig. 1. A-D. *Brachythyrinella narsahensis* (Reed), x1.5. A, B, ventral and dorsal views. C, ventral valve. D, dorsal valve. Lower Permian (Sakmarian) of India. (Reed 1928). Regarded as senior synonym for E, F, *Pericospira sanjuanensis* (Lech & Acenolaza), x1. E, ventral view. F, dorsal view. Argentina (mid- to upper Pennsylvanian). (Cisterna & Archbold 2007).

Few of these genera have had their spiralia revealed, apart from species assigned to *Grantonia,* a deficiency that renders any attempt at classification no better than provisional. But most do show the large umbonal callus of the ventral valve, and often coarse network of vascular canals, which strongly point to a trigonotretid alliance, without being able to rule out an approach to the genus *Aperispirifer*, which has transverse spiralia. The genera are for the most part discussed and figured in Waterhouse (2016, pp. 227-237), and are principally of

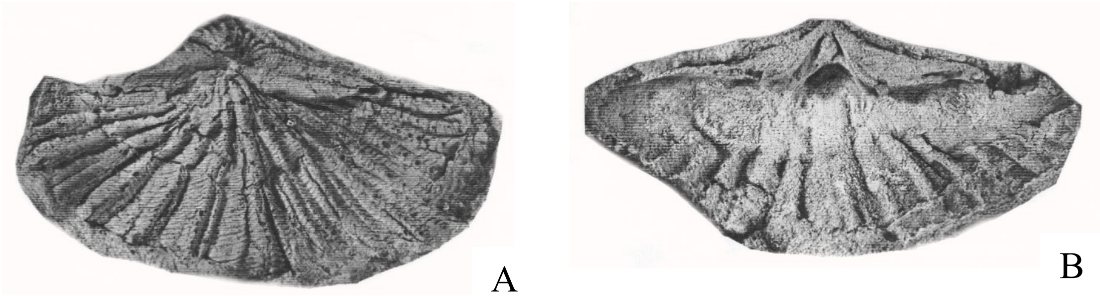


Fig. 2. A , B, *Varuna varuna* (Diener), x0.8. A, dorsal aspect, latex cast, GSI 11104, lectotype. B, latex cast of ventral interior, unregistered, showing pleromal shelf and callus (also seen in *Adminiculoria*). Fenestella Shale, Kashmir. (Waterhouse 2016).

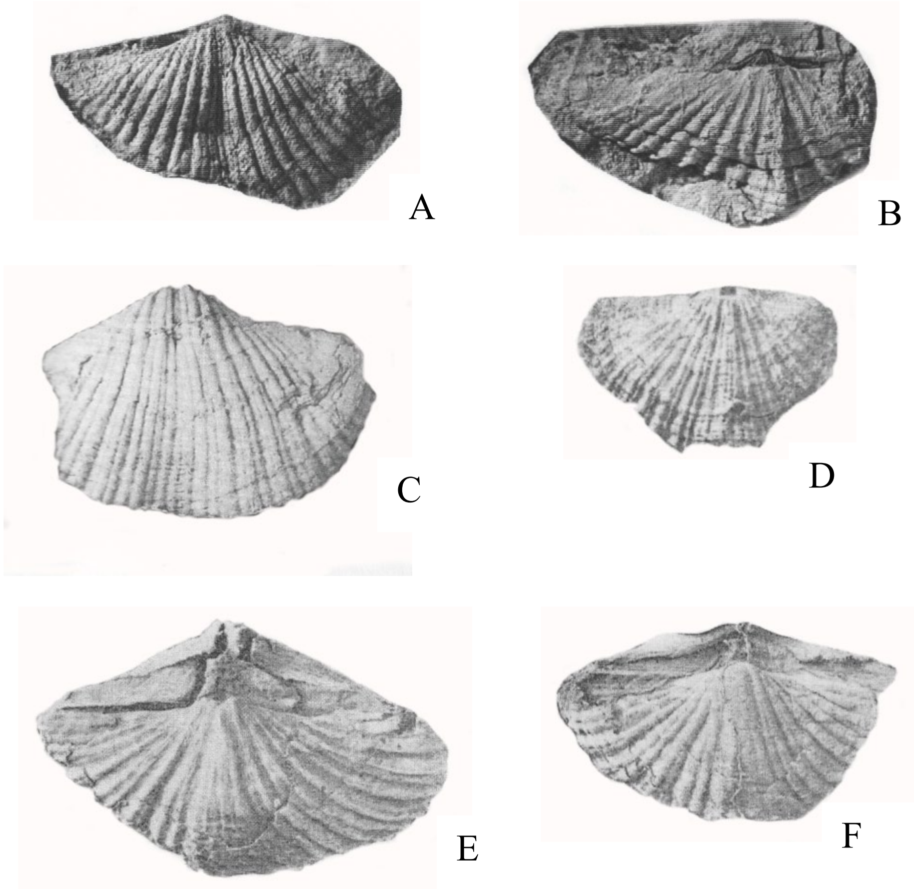


Fig. 3. A , B, *Adminiculoria middlemissi* (Diener), x1. A, latex cast, ventral exterior, CASG 519. B, dorsal internal mould, CASG 520. From Fenestella Shale, Kashmir. (Waterhouse & Gupta 1979). C, *Costuloplica senilis* (Maxwell), x1, latex cast of ventral exterior, AMF 57783. D, *C. campbelli* (Maxwell), dorsal internal mould, UQF 46473. Both species were named by Maxwell, 1964. (Roberts et al., 1976; Hill & Woods 1964a). E, F, *Maxwellispirifer exora* (McKellar), x1.5. Dorsal aspect of internal mould and latex external cast of internal mould with valves conjoined, GSQF 9023. Branch Creek Formation, Yarrol Basin. (McKellar 1965).

Gondwanan distribution and of late Early Upper Carboniferous to Early Permian in age. They were arranged by Waterhouse (2016) in subfamilies for the most part, and Trigonotretinae is now thought to include *Trigonotreta* and *Grantonia*, as well as genus *Brachythyrinella,* regarded as senior synonym for *Pericospirifer*. Subfamily Costuloplicinae Waterhouse, 2004, p. 187 is based on the presence of numerous fine ribs in genera *Costuloplica* and *Maxwellispirifer.* The plicae number some seven pairs, as is also found in species of *Trigonotreta.* Varuninae Waterhouse, 2016, p. 247 embraces genera *Varuna* and *Adminiculoria*, based on species described by Diener (1915) from the late Early Carboniferous faunas of the Fenestella Shales in Kashmir. Carter (2006b, p. 1875) referred *Adminiculoria* to Bashkiriinae Nalivkin, but the genus appears trigonotretid rather than paekelmannelloid. The genera are somewhat triangular in shape with angular plicae and strong costae in the case of *Varuna*, and numerous plicae in the case of *Adminiculoria.* These two genera appear to be allied to *Alispirifer* Campbell, 1961 from the late Early Carboniferous *Marginirugus barringtonensis* Zone and Branch Creek Formation and comparable levels in east Australia. Their relationship to *Trigonotreta* depends on the as yet unknown nature of the spiralia (Waterhouse 2016, pp. 229-234), but *Varuna* and allies are not represented by any conjoined specimens, other than external moulds, so that the nature of the spiralia cannot be determined. Their well-spaced mantle canals and strong umbonal callosity and open delthyrium strongly suggest a general relationship to Trigonotretidae, and it is an unanswered question whether they could possibly have given rise to the Permian family Georginakingiidae, given the approach in shape and plication. This family has laterally oriented spiralia. Some genera analyzed in Waterhouse 2016 may need to be shifted after ongoing study recognizes different allegiances, though of course this is an ongoing matter. Trigonotretidae was centred in east Australia, with relatives also recognized in South America and Himalayas.

Shells classed as Angiospiriferidae Legrand-Blain, 1985 are very close to *Trigonotreta*, with similar internal plates, and similar mantle canal system, but do not display costae. The spiralia are posteriorly directed. Members were classed as Choristitidae by Carter (2006a) in the *Revised Brachiopod Treatise*, following Carter et al. 1994, but choristitids differ in their long close-set adminicula and tabellae, and in their predominantly costate ornament.

For this section, the sequence of each genus is changed from the normal treatment, with *Trigonotreta* as the leading genus summarized first and then followed by *Grantonia* and *Brachythyrinella.*

Genus ***Trigonotreta*** Koenig, 1825

Diagnosis: Medium-sized shells with more or less costate plicae, well-defined sulcus, fold of moderate strength, not sharply separated from lateral shell. Short adminicula and dental plates which diverge forward, and may be extended along their inner edge by pleromal ridges. Secondary thickening is developed as a pleromium under the umbo, much thicker than a connector plate and restricted to lying just under the umbo. It often supports a high umbonal callosity. Dorsal socket and crural plates, no tabellae, no subdelthyrial or connector plate. Delthyrium open, well-spaced mantle canal system. Spiralia posteriorly or postero-laterally directed as far as known, though this is yet to be firmly established for some species, including the type species *Trigonotreta stokesi*. But closely allied species assigned herein to subgenus *Grantonia* Brown are known to have posteriorly directed spiralia, as does the probable ancestral group Angiospiriferidae Legrand-Blain.

Discussion: As discussed in Waterhouse (2021b, p. 9ff), *Trigonotreta* in east Australia is reliably limited to the basal Permian, and is found in Tasmania, Victoria and New South Wales, and one possible and slightly younger species is found in the uppermost Asselian with the productid *Bandoproductus* Jin & Sun, 1981 in the Gympie region of Queensland. No species have yet been found in New Zealand, where no brachiopods are to be found in deposits of likely Asselian age, although bivalves and rare gastropods are present.

Uncertainty remains over the limits of the genus. The most important concern centres on the orientation of the spiralia in *Trigonotreta*, whether they are laterally or more posteriorly directed. Recent students of the type species, such as Armstrong (1968) and Cisterna & Shi (2014) have not determined the orientation of the spiralia, even though suitable material was available to them. Species assigned to subgenus *Grantonia* Brown, 1953 are better known, Brown taking the trouble to elucidate the nature of the spire, which she found to be posteriorly directed. But as pointed out by Armstrong (1968), this taxon is very close to *Trigonotreta*. There appears to be only one noticeable and consistent difference between the two taxa, in the number of plicae pairs. They number some seven well-developed pairs in type *Trigonotreta*, and three to five well-developed pairs as a rule in *Grantonia* Brown. Not a great difference, with the difference weakened by a degree of uncertainty, especially as type *Grantonia* has low and poorly defined fascicles laterally. But provisionally, in the hope of providing credibility to Brown's proposed generic name, a subgeneric division is drawn between *Trigonotreta* with some seven pairs of plicae, and *Grantonia*, three or four pairs and less commonly up to five or six pairs of plicae.

Subgenus ***Trigonotreta*** Koenig, 1825

Diagnosis. Seven pairs of plicae as a rule, and variably developed costae.

Type species: *Trigonotreta stokesii* Koenig, 1825, p. 3 from Swifts Jetty Sandstone, Tasmania (fide Clarke 1979, p. 199), SD Buckman 1908, p. 30.

Trigonotreta (***Trigonotreta***) ***stokesi*** Koenig, 1825

Fig. 4, 5

1825 *Trigonotreta stokesi* Koenig, p. 3, pl. 6, fig. 70.
1965 *T. stokesi* – Pitrat, p. 706, Fig. 574.1a, (part, not Fig. 574.1b, c, d = *Tasmanospirifer tasmaniensis*).
cf. 1969 *Neospirifer* sp. nov. Runnegar, p. 293, pl. 20, fig. 17, 18, 19? (part, not fig. 16 = *Grantonia*?). See p. 81 herein.
1979 *T. stokesi* – Clarke, p. 199, pl. 1, fig. 1-9, pl. 2, fig. 1-9.
1990 *T. stokesi* – Clarke, p. 62, pl. 7A-H.
1992 *T. stokesi* – Clarke, p. 18, pl. 7A-H.
2006a *T. stokesi* – Carter, p. 1801, Fig. 1195.2a-c.
2014 *T. stokesi* – Cisterna & Shi, p. 540, Fig. 8.1-8.16.
2016 *T. stokesi* – Waterhouse, p. 297, Fig. 287A-D.
2021b *T. stokesi* – Waterhouse, p. 15, Fig. 6A-D.

Diagnosis: Large, transverse and plicate shells with six to usually seven plicae pairs and strong slightly differentiated costae, though these are fine on some specimens, large bulbous callosity at apex of delthyrium. Ventral muscle platform long and narrow.

Lectotype: Sole specimen BM (NH) B 4798, figured by Koenig (1825), Clarke (1979, pl. 1, fig. 3, 4), Carter (2006a, Fig. 195b) and Waterhouse (2016, Fig. 287B), SD Clarke (1979, p. 199).

Morphology: This species is large and transverse. Costation varies in strength, as illustrated in material figured by Cisterna & Shi (2014), as in Fig. 5 herein. In some specimens from the

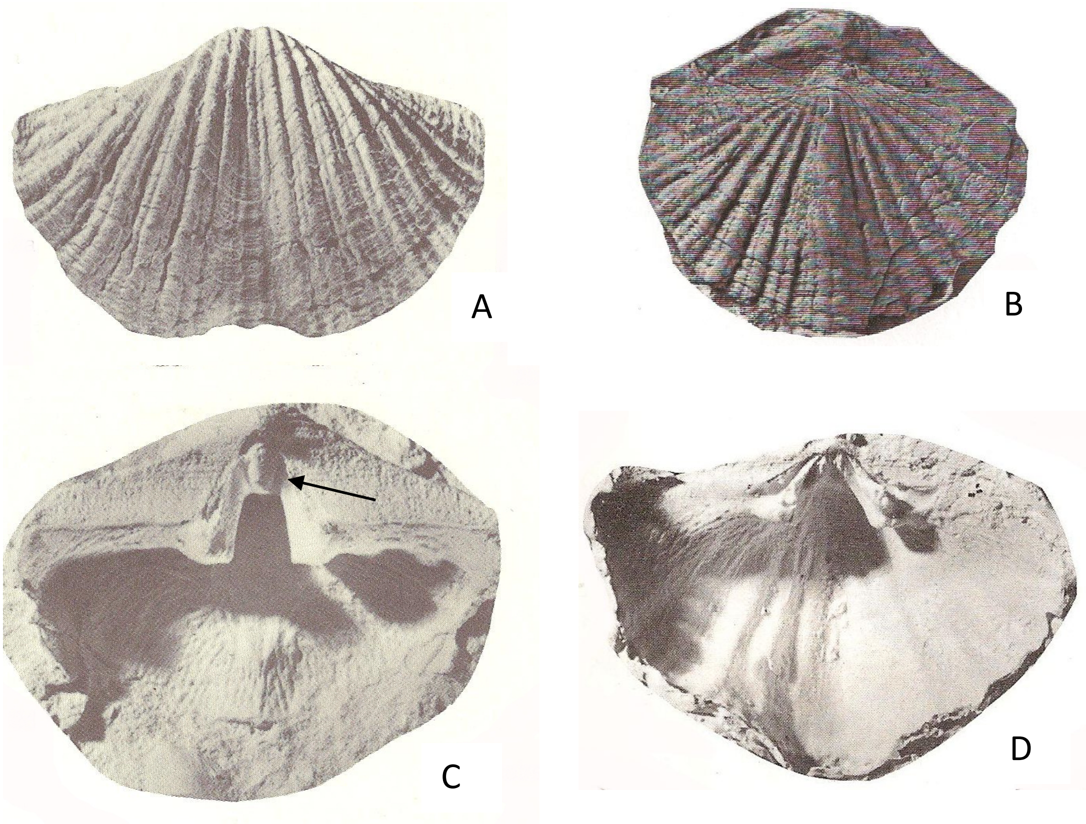


Fig. 4. *Trigonotreta stokesi* Koenig. A, ventral valve TMF 368401. B, lectotype BM (NH) B 4798, dorsal aspect. Note the subsidiary plication attached to the anterior dorsal fold and inner sulcal subplicae. C, fibreglass cast of ventral interior TMF 368405. D, fibreglass cast of dorsal interior, TMF 361094. The large umbonal callosity rests on a thick shelf formed by pleromal tissue (arrowed) which is connected to the lower dental plates. Specimens A-C, x1 and D, x1.2. From Lower Permian (Asselian) of Tasmania. (Clarke 1979).

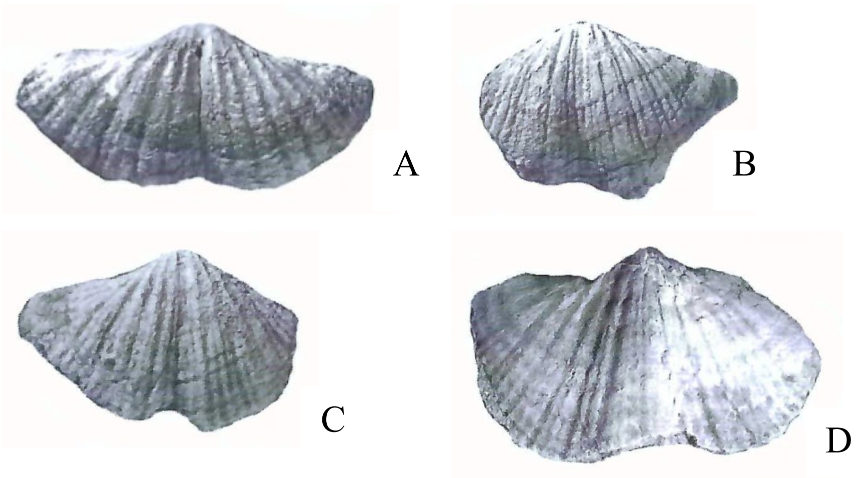


Fig. 5. *Trigonotreta stokesi* Koenig. A, ventral valve NMVP 309950. B, ventral valve NMVP 309954 with fine costae. C, NMVP 309945. D, dorsal valve NMVP 309958. From upper Wasp Head Formation, south Sydney Basin, x1 approx. (Cisterna & Shi 2014).

upper Wasp Head beds, the ribs may be a little finer than those of type *stokesi*, so that it is suggested that width and shape of the shell rather than rib strength may provide the prime distinction. Critically the direction of the spiralia for *stokesi* remains to be determined, with none of the prime authors in the synonymy attempting to determine the nature and direction of the spires. A pleromium is developed in some specimens, thicker than the connector plate of spiriferids, and bearing a massive umbonal callosity.

Stratigraphy: The species comes from several formations in Tasmania in the upper Golden Valley Group, and is rated as upper middle Asselian in the international time scale. There have been a number of other reports, some far from reliable, but Cisterna & Shi (2014) illustrated a number of specimens from the Wasp Head Formation and so extended the geographic range of the species into New South Wales.

Trigonotreta*? *murrayi (Waterhouse, 2015b)

Fig. 6

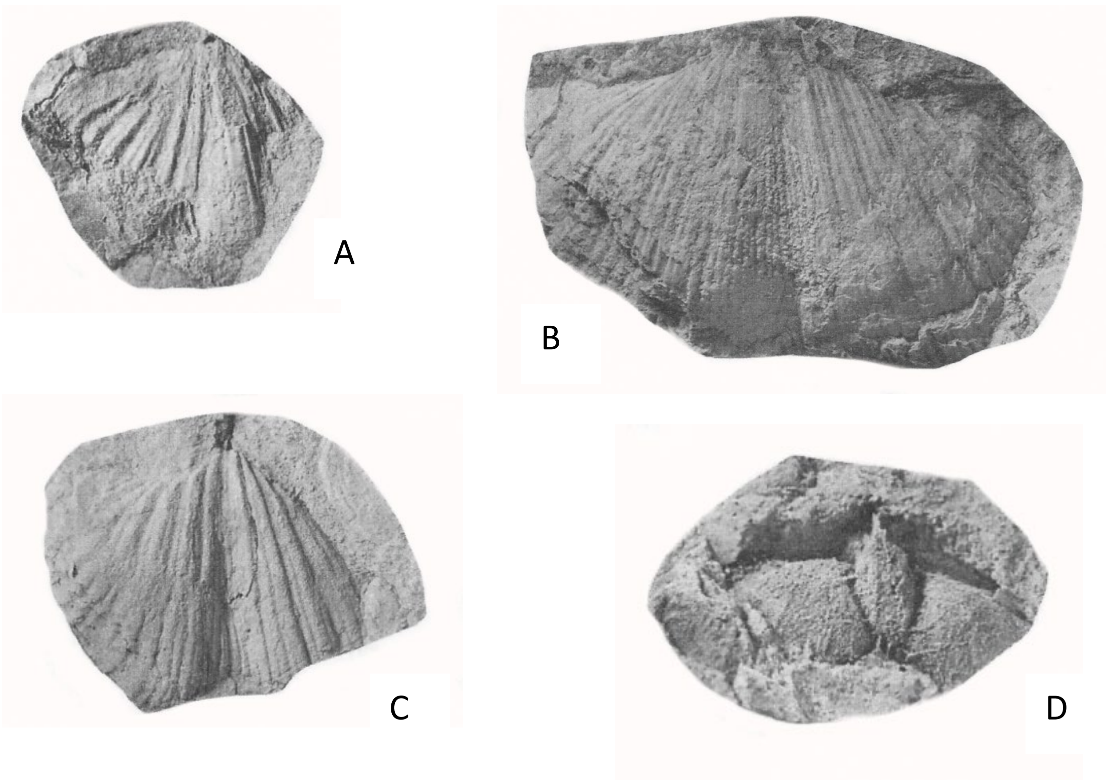


Fig. 6. *Trigonotreta*? *murrayi* (Waterhouse). A, dorsal valve QMF 14399, x1. B, large ventral valve, GSQF 13168, x0.8. C, latex cast of ventral valve QMF 17762, holotype x1. D. internal mould of ventral valve GSQF 13198, x1 from uncertain locality. From upper Rammutt Formation, Gympie. (Waterhouse 2015b).

2015b *Grantonia murrayi* Waterhouse, p. 59, Fig. 19.
2021b *Trigonotreta*? *murrayi* – Waterhouse, p. 16.

Diagnosis: Large transverse shells with some seven pairs of plicae, relatively broad costae, ventral muscle field narrow, well-developed umbonal callosity.

Holotype: QMF 17762 from upper Rammutt Formation, Gympie, southeast Queensland, figured in Waterhouse (2015b, Fig. 19E) and Fig. 6C herein, OD.

Morphology: This species is incompletely known, with the orientation of the spiralia needing to be determined, which may be difficult because of the lack of specimens with valves conjoined. The fold is narrower and costae are broader and slightly lower than in *stokesi,* and of subeven strength, whereas the muscle field is similar. It is the high number of plicae and narrow fold that point to *Trigonotreta*: *Grantonia* and *Aperispirifer* have fewer plicae, and *Neilotreta* has a much broader dorsal fold.

Stratigraphy: The species is found only in the upper Rammutt Formation of the Gympie district in southeast Queensland, in the *Bandoproductus macrospina* Zone, of upper Asselian age.

Subgenus ***Grantonia*** Brown, 1953

Diagnosis: Transverse shells with strong persistent plicae, as a rule numbering three pairs, extending to five pairs, with minor additional fascicles laterally in a few specimens, costae variable in development and may be well-differentiated, with primary costae predominant in some species, open delthyrium, large umbonal callosity in some species. Spiralia posteriorly oriented.

Type species: *Grantonia hobartensis* Brown, 1953, p. 61 from Berriedale Limestone, Tasmania, OD.

Discussion: Type *Grantonia* is distinguished from type *Trigonotreta* by having fewer plicae, chiefly in three pairs. That is not a substantial difference, and was understandably regarded by Armstrong (1968) followed by Carter (2006a) as not warranting generic distinction, so that they synonymized *Grantonia* with *Trigonotreta*. Trigonotretid species with fewer pairs of plicae, like type *Grantonia*, are found in beds just as old, or even older, than the beds with *Trigonotreta*. It is possible that *Grantonia* arose from such a genus as *Maxwellispirifer* of Pennsylvanian age (see Fig. 3E, F), which has three to four plicae pairs and may display differentiated costae. That could imply that the genus should be placed in Costuloplicinae Waterhouse, 2004, though *Costuloplica* itself has seven or more plicae pairs. So much more needs to studied regarding Upper Carboniferous faunas.

Waterhouse (2016) separated *Grantonia* as Grantoniinae, but this subfamily is now regarded as redundant.

Trigonotreta* (*Grantonia*) *victoriae (Archbold, 1991)

Fig. 7, 8

1991 *Trigonotreta victoriae* sp. nov. Archbold, p. 323, Fig. 2A-X.
1997 *T. victoriae* – Archbold et al., p. 2, Fig. 3A-J.
1998 *T. victoriae* – Archbold, Fig. 3A-J.
2021b *T. victoriae* – Waterhouse, p. 10, Fig. 1-5.
For fuller synonymy, see Archbold (1991) and Waterhouse (2021b).

Diagnosis: Shell weakly transverse to subelongate, characterized by fine ribs covering both valves, three or four pairs of plicae are prominent, with lateral fascicles in up to three pairs in some specimens, fold low and anteriorly broad, weakly distinguished from lateral shell, tends to possess a weak lateral pair of subplicae as in *Trigonotreta* (*Trigonotreta*) *stokesi*. Umbonal callosity low or absent. Spiralia posteriorly oriented.

Holotype: NMVP 120316 figured by Archbold (1991, Fig. 2A-C) and Archbold et al. (1997, Fig. 3A-C) from the west side of Coimadai Creek (now submerged by Lake Merrimu), Bacchus Marsh, Victoria, OD.

Morphology: Costae may be finer or as fine as ribs in some specimens of *Trigonotreta* (*Trigonotreta*) *stokesi,* though the type of the latter form has coarser ribs. Internally the umbonal callosity is less well developed, and the muscle field shorter and wider, and the shell is less transverse. Cisterna & Shi (2014, p. 542) considered that *Trigonotreta victoriae* was likely to be synonymous with *Trigonotreta stokesi* Koenig and *T. tangorini,* the latter classed herein as a separate genus *Neilotreta* in the trigonotretoid family Georginakingiidae (see p. 123). Their description of *T. stokesi* is inadequate, making it doubtful whether they were justified in deprecating the studies by other authors, including N. W. Archbold.

Stratigraphy: This species is found in the basal Permian rocks of Victoria and New South Wales. Material from Tasmania that shows comparably fine costation is enumerated in Waterhouse (2021b), some from below *Trigonotreta stokesi*, some specimens from apparently with *stokesi,* and first-hand and expert appraisal is required to ascertain whether

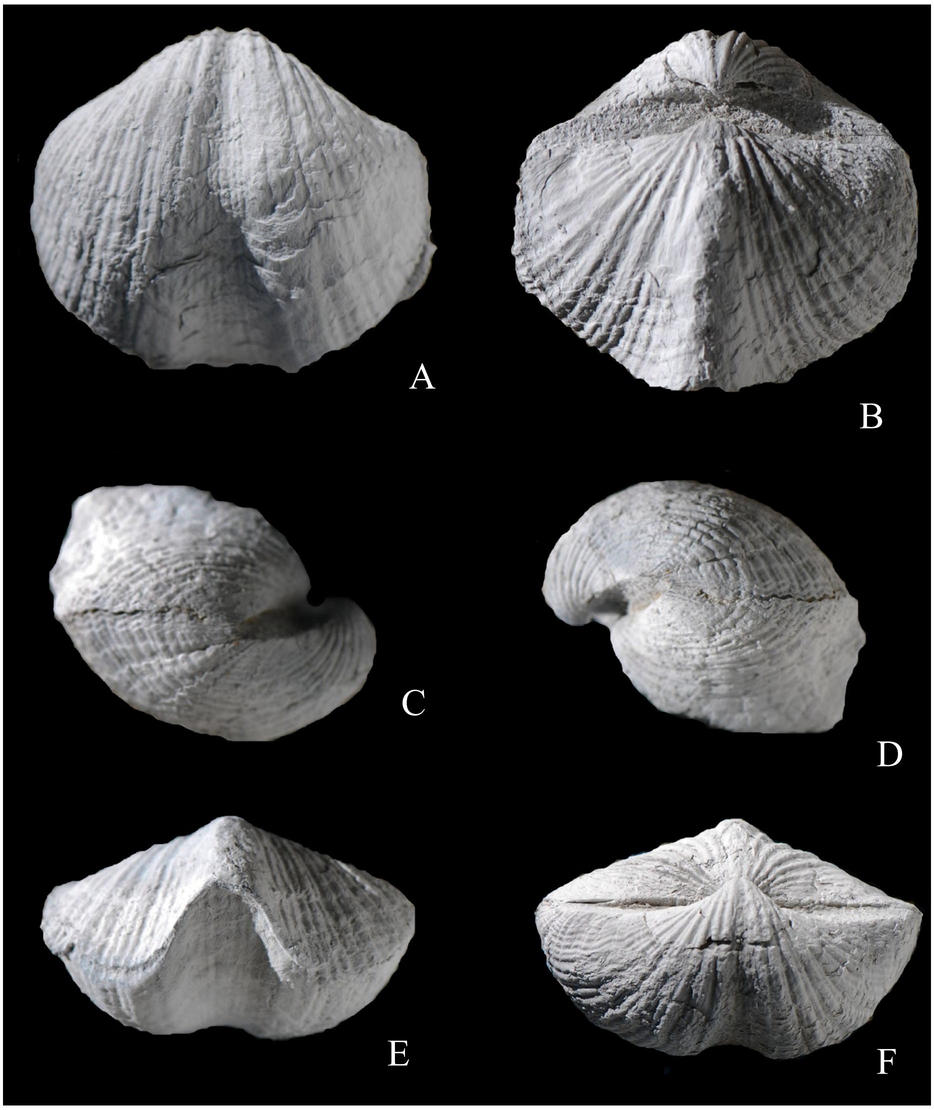


Fig. 7. *Trigonotreta* (*Grantonia*) *victoriae* Archbold. A-F, ventral, dorsal, lateral (dorsal valve on top in C and below in D), anterior and posterior (ventral valve below) aspects of UQF 82616 from Lochinvar Formation, New South Wales, x1. (Waterhouse 2021b).

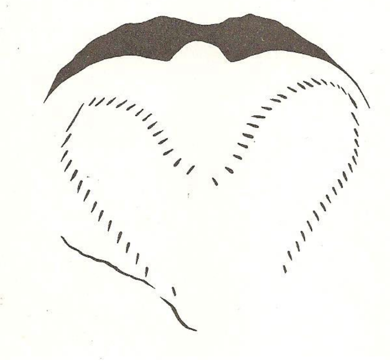


Fig. 8 *Trigonotreta* (*Grantonia*) *victoriae* Archbold, section through both valves, with ventral valve on top, showing dorsally convergent spiralia. From Lochinvar Formation, New South Wales, x1. (Waterhouse 2021b).

the species entirely preceeded the range of *stokesi*, or overlapped in range.

McClung (1980, pl. 19.1, fig. 12) figured a ventral valve as *Trigonotreta* sp. A from the Tamby Creek Formation which is low in the Permian sequence at Cranky Corner, New South Wales. He listed his *Trigonotreta* sp. A from the Lochinvar, Allandale and Wasp Head Formations. Uncertainty over age and distribution will remain until further documentation is provided for Early Permian trigonotretids.

Trigonotreta (***Grantonia***) aff. ***victoriae*** Archbold, 1991

Fig. 9

1969 *Neospirifer* sp. nov. Runnegar, p. 293, pl. 20, fig. 16 (part, not fig. 17, 18, 19? = *stokesi*).

Diagnosis: Subequidimensional with three pairs of well-rounded costate plicae.

Fig. 9. *Trigonotreta* (*Grantonia*)? sp., ventral valve UQF 49144 from Darlington Limestone, Tasmania, x1. (Runnegar 1969).

Dr

Morphology: Only the one distinctive specimen is known. It shows only three pairs of plicae in contrast to the much greater number of plicae in *Trigonotreta*, and the costae are broad and low with rounded crests, and plicae with crests broader and more rounded in section than those of *victoriae*, though the sulcus is similarly narrow. The specimen recalls the general appearance of *Spiriferella*, with some suggestion that the median rib is broader than the costae to each side over each plication, and needs to be examined at first hand to confirm that it is trigonotretid. It looks spiriferelloid, a superfamily not known elsewhere is east Australia.

Stratigraphy: The specimen comes from the Darlington Limestone of Tasmania.

Trigonotreta* (*Grantonia*) *cracovensis Wass, 1966

Fig. 10, 11, 13B, D, F?

1964b *Grantonia* cf. *hobartensis* [not Brown] – Hill & Woods, pl. P8, fig. 6, 7.
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*).
1986 *T. cracovensis* – Parfrey, p. 60, Fig. 2.4a-d.
1987 *T. cracovensis* – Waterhouse, p. 16, pl. 3, fig. 6-13, ?15-?17.
1989 *T. cracovensis* – Waterhouse, pl. 1r.
2015a *G. cracovensis* – Waterhouse, p. 193, Fig. 143B, D, F, 145C, 146B.

Diagnosis: Subelongate or weakly transverse, plicae include pair within sulcus and three lateral pair with weak outer pair in ventral valve, interspaces narrow, dorsal plicae high and persistent, interplical spaces narrow, primary costa prominent posteriorly along crest of plicae.

Holotype: UQF 43392 from Fairyland Formation, southeast Bowen Basin, figured by Wass (1966, pl. 3, fig. 7) and Fig. 10B herein, OD.

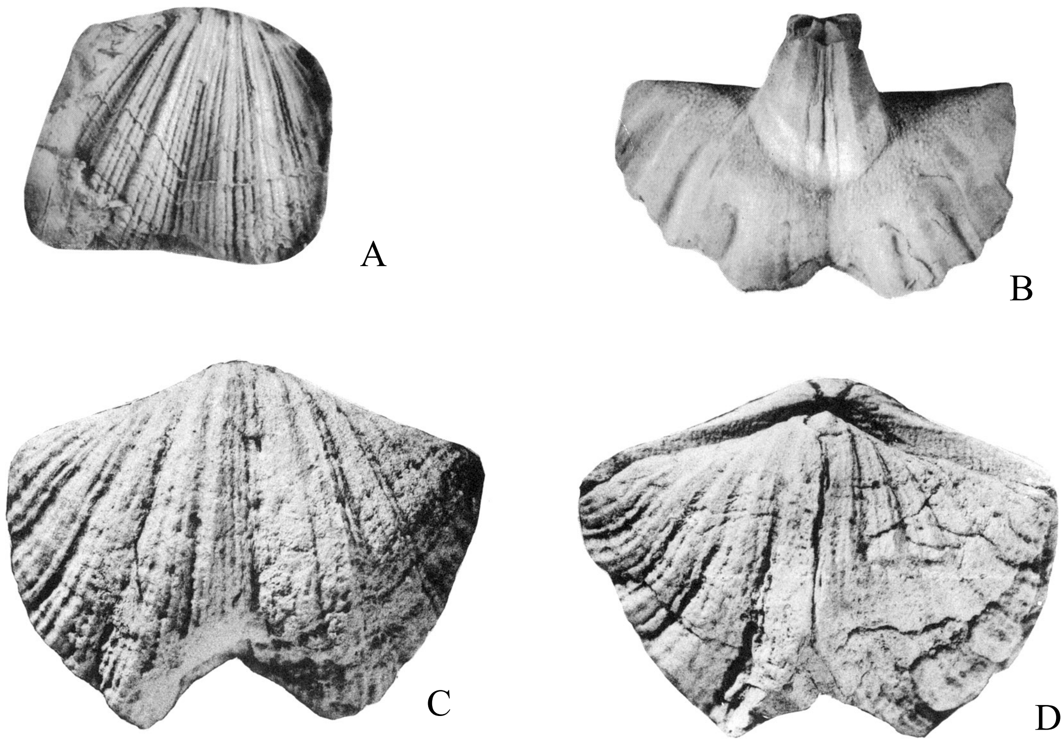


Fig. 10. *Trigonotreta* (*Grantonia*) *cracovensis* Wass. A, ventral valve UQF 43396. B, ventral internal mould UQF 43392, holotype. C, D, ventral and dorsal aspects of UQF 74155. Specimens x1 from Fairyland Formation, southeast Bowen Basin. (A, B – Wass 1966, C, D – Waterhouse 1987).

Morphology: The question that pertains to this species centres on its generic affiliations. *Grantonia* differs from *Trigonotreta* in the number of its plicae pairs, with only three pairs and intrasulcal pair prominent in the type species, compared with six to usually seven pairs that grade laterally in strength in type *Trigonotreta*. The species *cracovensis* Wass was assigned by its author to *Grantonia*, and well-preserved topotype specimens from the Fairyland Formation in the southeast Bowen Basin, as figured in Waterhouse (1987), have four pairs of plicae and moderately developed fifth pair.

Specimens figured in Waterhouse (1987, pl. 3, fig. 15-17) from the Dresden Limestone in the southwest Bowen Basin look to be close to *G. cracovensis*, but well-preserved specimens are not available.

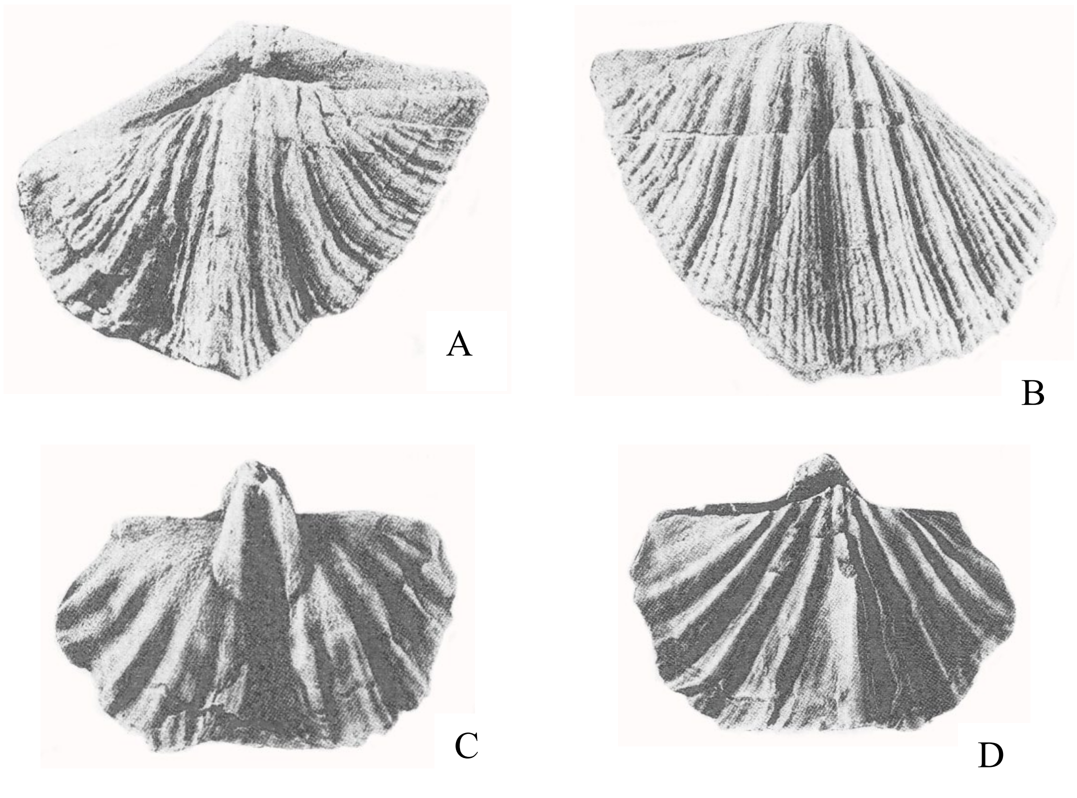


Fig. 11. *Trigonotreta* (*Grantonia*) *cracovensis* Wass. A, B, dorsal and ventral aspects of latex cast, GSQF 12958. C, ventral and dorsal aspects of internal mould GSQF 12959. Camboon Volcanics. (Parfrey 1986).

Stratigraphy: This species is found in the Fairyland Formation and Camboon Volcanics of the southeast Bowen Basin, and possibly in the Dresden Formation, and in the lowermost

Tiverton Formation of the north Bowen Basin (Waterhouse 2015a. p. 193). The Camboon Andesite fauna described by Parfrey (1986) was shown to be correlative with that of the Fairyland Formation by Waterhouse (2024b, pp. 188, 189). McCarthy et al. (1974) reported the species from the Emu Creek beds in northern New South Wales, but the material appears to belong to *Trigonotreta australis*, given its transverse outline. The Emu Creek specimens are accompanied by *Taeniothaerus subquadratus*.

Trigonotreta (***Grantonia***) ***australis*** (Bion, 1928)

Fig. 12, 13A, C, E

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* [new name, not Foord] Bion, p. 30.
1964b *Grantonia* sp. Hill & Woods, pl. P8, fig. 8.
1968 *Trigonotreta stokesi* [not Koenig] – Armstrong, p. 83, pl. 6, fig. 1-3, 5 (part, not fig. 4 = *stokesi*).
1970 *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* [not Wass]– McCarthy et al., Fig. 4F.
1983 *Aperispirifer* or *Neospirifer* sp. Waterhouse, Campbell & Williams, p. 303, Fig. 2.
1987 *T. australis* – Waterhouse, p. 17, pl. 3, fig. 14?, 18-20, pl. 4, fig. 1-3, ?4, 5, 6.
2004 *G. australis* [Bion, not Foord] – Waterhouse, p. 170.
2015a *G. australis* – Waterhouse, p. 136, Fig. 143A, C, E, 144, 145A, B, D, 147, 148A, B, 149A, ?B, 150, ?151 (Fig.149, 151B also like *G. hobartensis*).
2016 *G. australis* – Waterhouse, p. 235, Fig. 301.

Fig. 12. *Trigonotreta* (*Grantonia*) *australis* (Bion), latex cast showing ventral interior, x2, from middle Tiverton Formation of north Bowen Basin, Queensland, Australia. (Waterhouse 2015a).

Diagnosis: Transverse shells with pair of sulcal plicae and three or four well-formed lateral plicae with intrasulcal pair, bearing high and often broad primary costae, well-defined growth lamellae, fold high with narrow crest, adminicula short and well-spaced.

Holotype: For *australis* Bion, 1928 [not Foord 1890], GSQF 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.

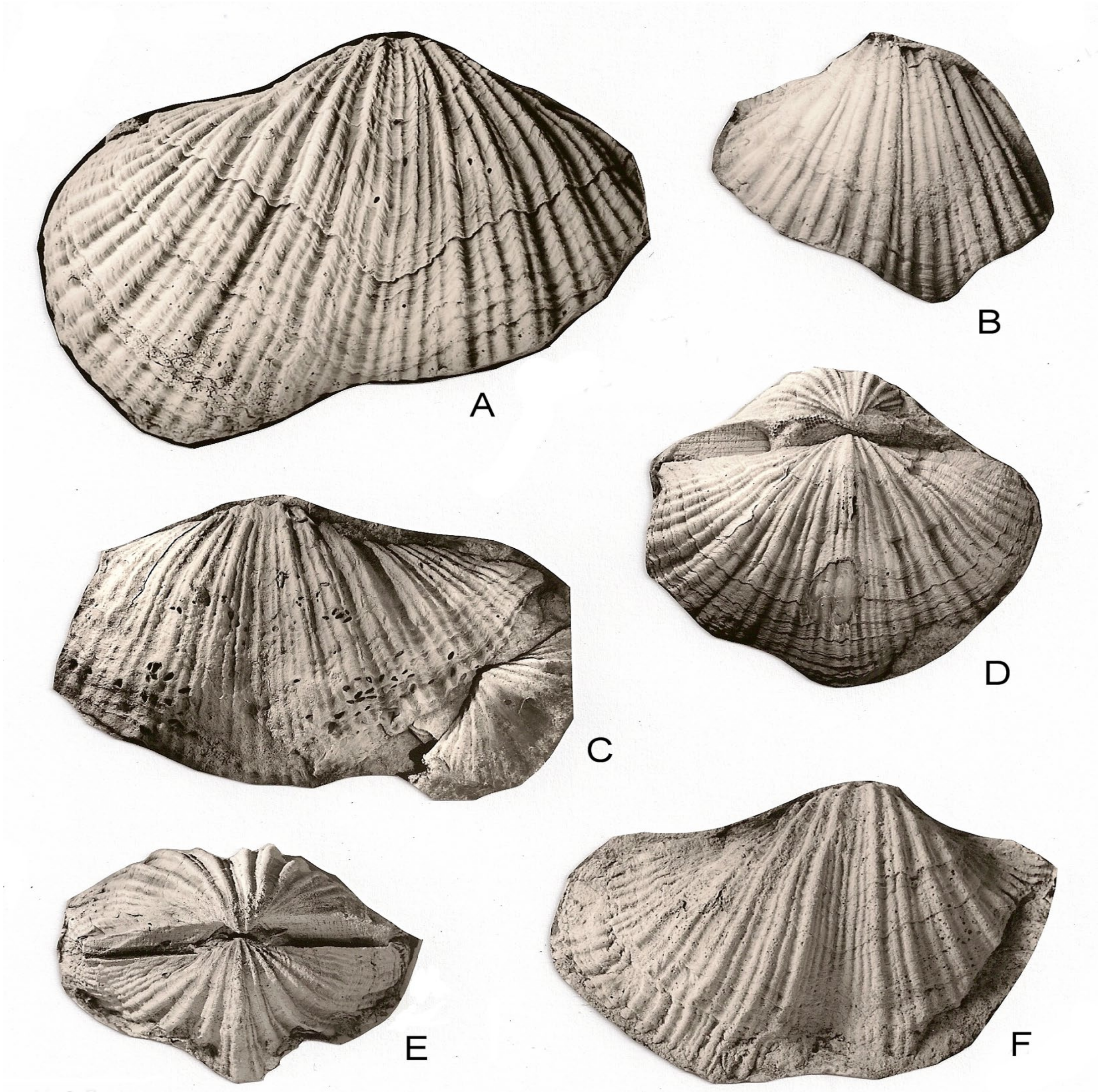


Fig. 13. A, C, E, *Trigonotreta* (*Grantonia*) *australis* (Bion). A, latex cast of ventral valve UQF 20998, x2. C, latex cast of ventral valves including UQF 81360, x2. E, dorsal aspect of latex cast of UQF 81366 with valves conjoined, x0.66. B, D, F?, *Trigonotreta* (*Grantonia*) *cracovensis* Wass. B, latex cast of ventral valve UQF 81359, x2. D, dorsal aspect of latex cast of specimen with valves conjoined UQF 81363, x1. F, latex cast of ventral valve UQF 81362, x1, associated with *cracovensis* but as transverse as *australis*. From middle Tiverton Formation, north Bowen Basin. (Waterhouse 2015a).

Morphology: Shells are more transverse than in *cracovensis* and have a similar number of plicae, that are lower and less prominent than in *cracovensis*. The spiralia are posteriorly orientated in a few specimens, with no known examples of transverse spiralia.

Stratigraphy: The species is found in the *Magniplicatina undulata* and lower *Taeniothaerus subquadratus* Zones of the middle Tiverton Formation in the north Bowen Basin.

Taxonomy: Archbold & Thomas (1986) considered that Foord (1890) used the name *australis* in a varietal sense for his species *hardmani,* which means that his name does not formally pre-empt Bion's use of the same word to name a species. Bion also ascribed varietal status to his Australian form, but as principal first revisor, Waterhouse (1987) upgraded the name to subspecies and full species status. The full range and validity of the two suites here assigned to *australis* and *hobartensis* require clarification over morphological variation and stratigraphic distribution. It still needs to be established if the differences in costation and shape are typifying separate species, or just individuals within one species.

Collections made near Homevale Station by J. D. Armstrong through the Tiverton Formation that were examined by Waterhouse (2015a) had been lumped by Armstrong into one registered collection, not according to stratigraphic distribution, to confuse the distribution of the two morphological suites. There thus remains uncertainty over the naming and distribution of taxa here called *australis* and *hobartensis*, exacerbated by the repetition of the name *australis* by Bion (1928), well after prior use of the name *australis* by Foord (1890). Should it be decided that Foord's name does hold validity, because assessments are always open to revision, then *hobartensis* may be substituted for *australis* Bion, or Bion's taxon receive a new name. There is an additional complication concerning *hobartensis*, as discussed below, because *hobartensis* appears to be characterized in particular by the high median rib over plicae, and where this development first occurred requires clarification.

McClung (1980, Fig.19.2) referred to *Trigonotreta australis*, with no author, in a crowded table in which the information is obscured by the smallness of the scale. Whether he intended to refer to *australis* Bion, implying that he may have uncovered the use of this name for himself, or learned about it from me, or even intended *australis* Foord is not clear, but the last option seems most likely. No author in Australia appears to have come across the Bion proposal until 1987.

Trigonotreta (***Grantonia***) ***hobartensis*** Brown, 1953

Fig. 14, 15

1953 *Grantonia hobartensis* Brown, p. 61, pl. 6, fig. 1-9.
1979 *G. hobartensis* – Clarke, p. 200, pl. 3, fig. 1-9.
2015a *G. australis* [not Bion?] – Waterhouse, Fig. 149, 150D, 151.
2016 *G. hobartensis* – Waterhouse, p. 234, Fig. 299.

Diagnosis: Transverse shells with pair of sulcal plicae and three to five (mostly four) well-formed lateral plicae which bear high and often broad primary costae, moderately prominent growth lamellae, fold high with narrow crest, adminicula short and well-spaced.

Holotype: AMF 44666 from Berriedale Limestone of southern Tasmania, figured by Brown (1953, pl. 6, fig. 1a, b), Clarke (1979, pl. 3, fig. 1), Waterhouse (2016, Fig. 299), and Fig. 14B herein, OD.

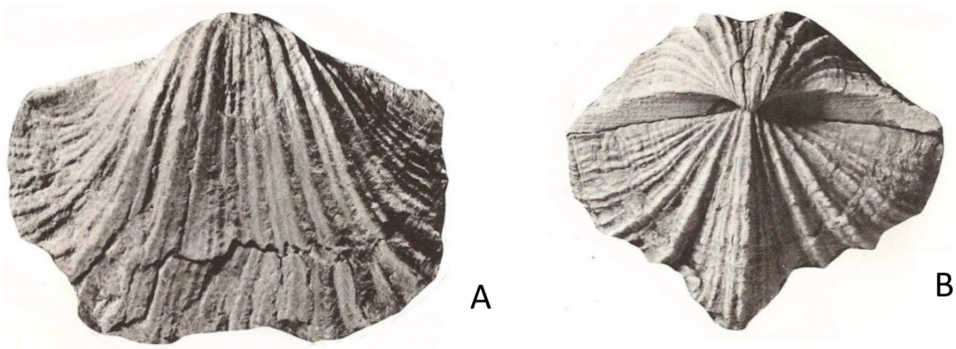


Fig. 14. *Trigonotreta* (*Grantonia*) *hobartensis* Brown. A, ventral view of TMF 368408. B, dorsal view of holotype, AMF 44666. Specimens x1, from Berriedale Limestone of Tasmania. (Clarke 1979).

Morphology: The primary costa is typically higher than bordering costae. The full range and validity of the two suites here assigned to *australis* and *hobartensis* require clarification over variation and stratigraphic distribution. For morphology, it needs to be determined if the differences in costation and the strength of the primary costa in inner plicae, especially over the dorsal valve, is consistently different in specimens assigned to the two species.

Stratigraphy: Brown (1953) described her species from the Berriedale Limestone, of Aktastinian age, and whether her species is to be found in the Tiverton Formation below beds correlative with the Berriedale Limestone and with *Taeniothaerus subquadratus* is not certain.

A number of specimens from the lower middle Tiverton Formation below *T. subquadratus* have the high median costa over plicae that appears to typify *Grantonia hobartensis.*

Fig. 15. Possible *Trigonotreta* (*Grantonia*) *hobartensis* Brown, latex cast of dorsal valve UQF 81617 x2 from either the lower or upper middle Tiverton Formation, showing the high and broad primary costae that are considered to typify the species. (Waterhouse 2015a).

Genus ***Brachthyrinella*** Waterhouse & Gupta, 1978

Diagnosis: Small transverse shells with five to seven pairs of plicae as a rule, costae few, developed anteriorly over lateral shell and within sulcus, fold with channel. Adminicula short, delthyrium open with small to well-formed umbonal callosity.

Type species: *Spirifer narsahensis* Reed, 1928, p. 379 from Umaria beds of India, OD.

Discussion: The claim by Waterhouse & Gupta (1978) that adminicula were absent went against the assessment by Thomas (1971, pl. 19, fig. 8) and was corrected by Waterhouse (1983c, p. 158) and Archbold & Thomas (1984).

Brachythyrinella simplicitas n. sp.

Fig. 16

aff. 1969 *Trigonotreta* sp. Runnegar, pl. 20, fig. 15.
2003 *Trigonotreta* sp. nov. Archbold, p. 164, Fig. 4: 15-18.

Diagnosis: Transverse shells with five to eight pairs of plicae, median sulcal rib, fold with shallow median depression, plicae may bear minor signs of costation or splitting.

Holotype: CPC 35330 figured by Archbold (2003, Fig. 4.11, 12) and herein as Fig. 16C, from Beckers Formation, Cranky Corner, New South Wales, OD.

Morphology: Several broken specimens were reported and figured from the lowest beds of the Beckers Formation at Cranky Corner, New South Wales, and one is nominated as holotype. Archbold (2003) compared the material with *Spirifer* [now *Brachythyrinella*] *hesdoensis* Sahni & Dutt, 1959 (see also Archbold et al. 1996) from Manendragarh, India, and Sahni & Dutt had noted the close of their species to the Reed species from Umaria, which is now the type of *Brachythyrinella*. A similar looking and more complete ventral valve was recorded by Runnegar (1969) from the Wasp Head Formation in the south Sydney Basin and it resembles the Cranky Corner material in its median sulcal rib, but has a few more plicae laterally (Fig. 16D).

Stratigraphy: The species is found in the Beckers Formation at Cranky Corner, New South Wales, and an allied specimen is found in the upper Wasp Head Formation of the south Sydney Basin.

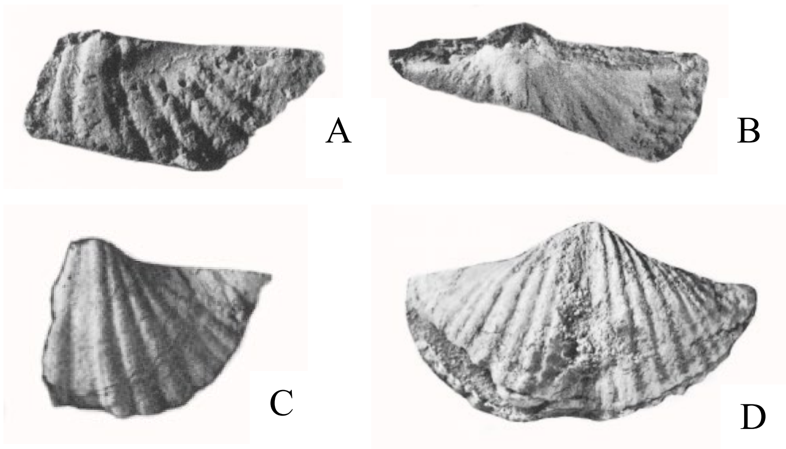


Fig. 16. *Brachythyrinella simplicitas* n. sp. A, B, latex cast x3 and internal mould x 1.8 of dorsal valve CPC 35332. C, ventral valve CPC 35330, holotype x 1.6. From Beckers Formation, Cranky Corner, New South Wales. (Archbold 2003). D, *B*. aff. *simplicitas*, ventral valve ANU 17776 x1, Wasp Head Formation, south Sydney Basin. (Runnegar 1969).

Superfamily NEOSPIRIFEROIDEA Waterhouse, 1968

[Nom. transl. hic ex Neospiriferinae Waterhouse, 1968, p. 9] et seq.

Diagnosis: Distinguished from Trigonotretoidea by the spiralia, which are laterally rather than posteriorly or postero-laterally directed. Neodeltidium or single plate may cover the delthyrium, but there are no stegidia, and there is no subdelthyrial connector plate. Umbonal callosity normally small or often absent, but not in all genera, especially species found in Gondwana or peripheral Gondwana, but genera do not display the thick shelf seen in species ascribed to Trigonotretidae, though a platform may be developed. Dental and adminicular plates, socket and crural plates, as in Trigonotretoidea, no tabellae.

Discussion: In terms of missing connector plate and lack of stegidia, this superfamily comes close to Trigonotretidae, but differs in the orientation of its spiralia. The group appears to be in part a warm-water and certainly more widely distributed relative of Trigonotretidae, although it could be argued that the group represents divergence from Spiriferoidea, by involving more changes in the morphological attributes. The neospiriferids appear to have commenced in Early Carboniferous time (Waterhouse 2016, pp. 197-201) with the Visean genus *Frechella* Legrand-Blain, 1986b. This genus as described and figured by Legrand-Blain has finely plicate costae, alate cardinal extremities, a largely open delthyrium with arched posterior delthyrial cover, and no subdelthyrial connector plate (Legrand-Blain 1986b, p. 33, pl. 2, fig. 1, 6, 8).

Family **NEOSPIRIFERIDAE** Waterhouse, 1968

[Nom. transl. Waterhouse 2016, p. 197 ex Neospiriferinae Waterhouse 1968, p. 9].

Subfamily **NEOSPIRIFERINAE** Waterhouse, 1968

Diagnosis: Transverse as a rule with plicae and costae, sulcus and fold. Delthyrium covered by a single cover plate, called neodeltidium, unlike the stegidia comprised as a rule of at least two plates in many Spiriferidae, but the cover plate is readily lost and may never have been present in some genera. No subdelthyrial connector plate, nor distinctive shelf as in Trigonotretidae, short dental plates and adminicula, crural plates, no tabellae, umbonal callosity varies in strength and presence, often absent. Spiralia laterally extended.

Genera: *Neospirifer* Fredericks, *Aperispirifer* Waterhouse, *Betaneospirifer* Gatinaud, *Forticosta* Waterhouse, *Frechella* Legrand-Blain, *Kaninospirifer* Stepanov & Kulikov, *Lutuginia* Poletaev, ?*Occidalia* Archbold, *Ovispirifer* Waterhouse, *Pondospirifer* Waterhouse, *Quadrospira* Archbold, *Tibetospirifer* Liu & Wang, *Trigorhium* Waterhouse, *Wadispirifer* Waterhouse.

Discussion: There is the potential for tribal strands to be recognized amongst genera assigned to this subfamily, and several subdivisions for this family are outlined in Waterhouse (2016, p. 197ff), including Septospiriferinae, recognized for allies with a distinct low ventral median septum, and allied Alphaneospiriferidae, based on a genus that lacks adminicula and has a cruralium or sessalium. Some genera need more clarification over their morphology, especially internal features. Particular uncertainty centres over the contents and limits of Kaninospiriferinae Kalashnikov, 1996, as discussed by Waterhouse (2020, p. 300ff), based on *Kaninospirifer* Kulikov & Stepanov *in* Stepanov et al. 1975 from Middle Permian of Kanin Peninsula, Russia. This genus involves transverse costate and plicate shells with delthyrium open as far as known. The dental plates may be low, but not in all specimens, and adminicular and crural plates are normal, spiralia are transverse, and the development of umbonal callosity limited and mostly lacking. There appears to be no subdelthyrial plate or shelf. Such features appear to be neospiriferin and especially close to *Aperispirifer* Waterhouse. Granted that *Kaninospirifer* apparently lacks a delthyrial cover plate or neodeltidium found in *Neospirifer*, the feature may be viewed as less than reliable, because such a plate is all too readily lost from buried shells, though further study over this feature may prove it amounts to a significant difference, but not necessarily of subfamilial import. Other features seem of dubious value: that *Kaninospirifer.* unlike *Neospirifer*, may have plicae that fade anteriorly (Grunt 2006), a feature also found in *Aperispirifer*, and may have low dental plates (Waterhouse 2004, p. 129; 2020, p. 300), such as displayed in the original study by Stepanov et al. 1975. Other specimens are more normal in displaying more persistent plicae and moderately high dental plates. Shi et al. (2002) claimed that there no adminicula in this genus, as was mistakenly accepted by Carter (2006a, p. 1789). Lee et al. (2016, Fig. 3) provided a figure to show that "*Kaninospirifer kaninensis*" had high dental plates and exceptionally low adminicula. But the so-called *kaninensis* came from China, not the type region of Russia: the claim that *Kaninospirifer kaninensis* had no adminicula, or very low adminicula, must be set aside as erroneous, as shown by Kalashnikov (1998, *in* Molin et al. 1983). Evidence is not conclusive over the standing and validity of Kaninospiriferinae.

Perhaps a tribal standing will prove feasible, once full understanding of the genus is achieved, but so far, available evidence suggests that there is no subfamilial difference between *Kaninospirifer* and members of the Neospiriferinae.

Gourvennec *in* Gourvennec & Carter 2007, p. 2781) claimed that *Kaninospirifer* was senior synonym to *Fasciculatia* Waterhouse, ignoring the observation that *Fasciculatia* differs in its plicae and fascicles, and delthyrial construct.

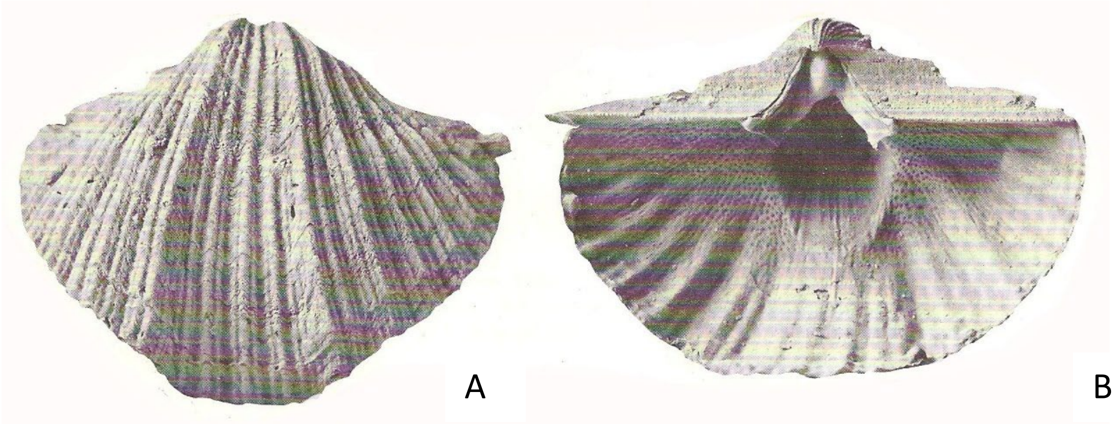
Genus ***Aperispirifer*** Waterhouse, 1968

Diagnosis: Shell transverse, fold high to broad with rounded crest, plicae may either fade anteriorly or extend to anterior margin, vary from three to five or less commonly six prominent pairs, first and often second inner pair of plicae incorporated within sulcus as a rule, costae numerous and may be moderately differentiated, micro-ornament of radial and commarginal capillae. Delthyrium open without stegidia or cover plate, large umbonal callosity, no subdelthyrial connector plate, short but consistently high dental and adminicular plates, no tabellae, scapular-shaped crural plates. Low dorsal septal ridge as a rule. Well-spaced mantle canal impressions, spiralia laterally directed.

Type species: *Neospirifer wairakiensis* Waterhouse, 1964, p. 127 from Letham Burn Member, Wairaki Downs, New Zealand, OD.

Discussion: This genus displays trigonotretid attributes such as well-spaced mantle canal system, open delthyrium and large umbonal callosity apparently caused by the habitation in cold or cool temperate climes approaching those conditions at least episodically which prevailed during the life-time of *Trigonotreta* and *Grantonia*. But *Aperispirifer* differs from these genera, proven in the case of *Grantonia,* in the direction of the spiralia. In this regard *Aperispirifer* is like *Neospirifer* and allies, but differs in lacking a delthyrial cover plate, implying that the generic morphology had been influenced by climate. Or did the genus did evolve from Trigonotretidae from a form such as *Grantonia* with its three strong pairs of plicae, and mimic some aspects of Neospiriferinae? To rely purely on morphology, it would appear on present knowledge that the genus is best treated as a member of Neospiriferinae.

One genus is found in the middle Permian of United States, with laterally directed spiralia (Cooper & Grant 1976, pl. 592, fig. 11), called *Trighorium* Waterhouse, 2001, with type species *Neospirifer amphigyus* Cooper & Grant, 1976. (See Fig. 17). This raises the question: does the presence of such a genus in Texas signify the presence of a brief cold climatic interval, or invasion by a robust cool to cold-water species?



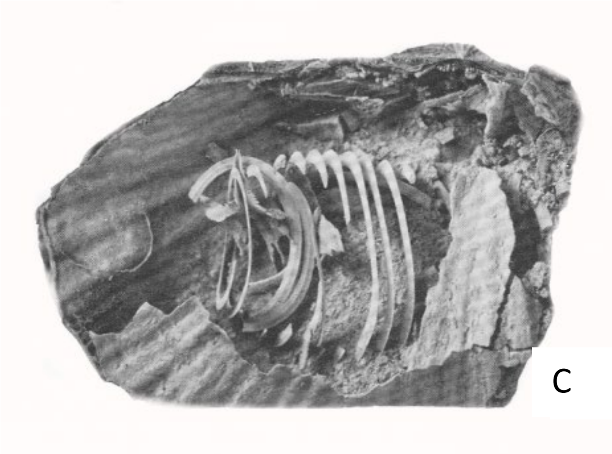


Fig. 17. *Trigorhium amphigyus* (Cooper & Grant), ventral valve exterior (A) and interior (B), showing characteristic three subplicae in the sulcus, and the strong umbonal callosity, and C, transverse spiralia, x1.2. From Word Formation (Wordian), Texas. (Cooper & Grant 1976).

Aperispirifer initialis n. sp.

Fig. 18

1968 *Aperispirifer* A Waterhouse, p. 36, pl. 3, fig. 11 (part, not text-fig. 6C = sp. and gen. indet.).
1983a *A. crassicostatus* [not Waterhouse] – Waterhouse, p. 158, pl. 1, fig. 5, 7-10, pl. 2, fig. 1, 4.
1991 *A. crassicostatus*? [not Waterhouse] – Begg & Ballard, p. 147, Fig. 7.

Diagnosis: Costae fine with narrow crests, in three pairs of principal plicae over ventral valve, with strong subsidiary pair in sulcus, outer ribs in less well-defined fascicles, sulcus narrow and bordered by angular-crested plicae.

Holotype: BR 1422 from upper Brunel Formation, *Notostrophia homeri* Zone, New Zealand, figured in Waterhouse (1968, pl. 3, fig. 11) and herein as Fig. 18A, here designated.

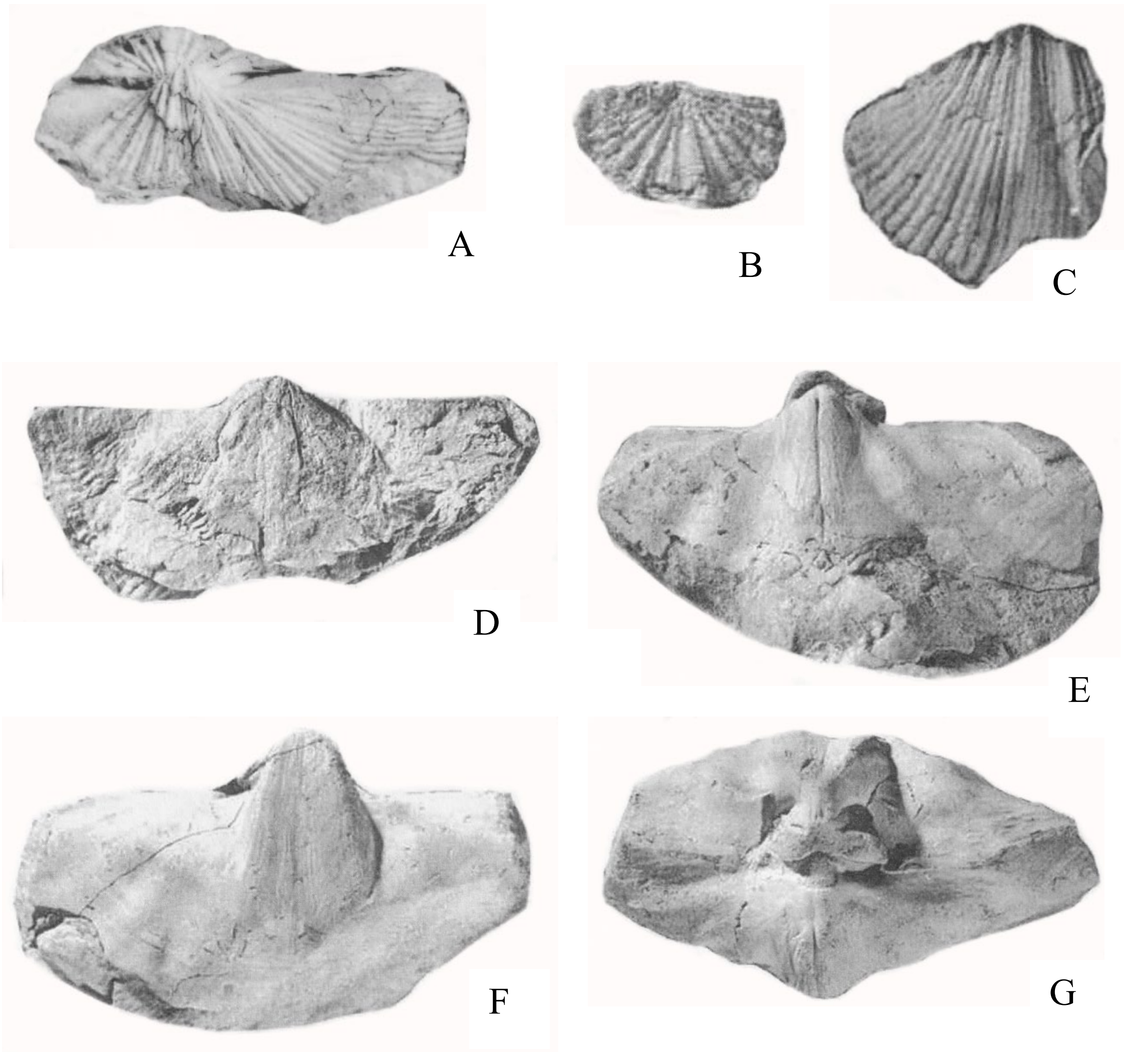


Fig. 18. *Aperispirifer initialis* n. sp. A, ventral aspect of latex cast of BR 1422, holotype, x1 from Brunel Formation, New Zealand. (Waterhouse 1968). B-F, from upper Tiverton Formation, north Bowen Basin, Queensland. B, latex cast of dorsal exterior of juvenile specimen, UQF 70041, x2. C, latex cast of ventral exterior, UQF 70043, x1. D, worn ventral valve UQF 70044, x0. 5. E - G, internal mould, dorsal, ventral and posterior aspects of UQF 70042, x0.5, ventral valve on top in G. (Waterhouse 1983a).

Morphology: This species is distinguished by its narrow sulcus and fold, and fine angular-crested costae. There is adequate material in both the upper Brunel Formation of New Zealand and the upper Tiverton Formation of the north Bowen Basin in Queensland (Waterhouse 1983a) to round out the circumscription fo the species and its variations.

Stratigraphy: The species has been described from the *Notospirifer homeri* Zone of the Brunel

Formation in the Takitimu Group, as well as the Mantle Volcanics in the Skipper Range in southern New Zealand, and from the *Echinalosia preovalis* - *Ingelarella plica* Zone of the upper Tiverton Formation in the north Bowen Basin, equivalent to the *Notostrophia homeri* Zone of the upper Brunel Formation (Waterhouse 1983a).

Aperispirifer archboldi Waterhouse, 1999

Fig. 19, 20

1964 *Neospirifer wairakiensis* [not Waterhouse] – Waterhouse, p. 127, pl. 23, fig. 5, 7-10, pl. 24, fig. 1-3, pl. 25, fig. 2-4, 6, 7, text-fig. 61A, 62, 63 (part, not pl. 23, fig. 4, 6, pl. 24, fig. 1, 5, pl. 25, fig. 1, 5, Fig. 56-60, 61A = *wairakiensis*).
1968 *Aperispirifer wairakiensis* – Waterhouse, p. 35.
1978 *N. wairakiensis* [not Waterhouse] – Suggate et al., text-fig. 4.5, fig. 10, 13.
1981 *A. wairakiensis* [not Waterhouse] – Speden & Keyes, pl. 5, fig. 10, 13.
1982 *A. wairakiensis* [not Waterhouse] – Waterhouse, p. 54, pl. 15, fig. a.
1999 *A. archboldi* Waterhouse, p. 12.
2001 *A. archboldi* – Waterhouse, p. 92, pl. 6, fig. 10.
2002 *A. archboldi* – Waterhouse, p. 34.
2006a *A. wairakiensis* [not Waterhouse] – Carter, p. 1802, Fig. 1196b-e (part, not 1196a = *wairakiensis*).
2016 *A. archboldi* – Waterhouse, Fig. 300.
2016 *A. wairakiensis* [not Waterhouse] – Waterhouse, Fig. 302B (part, not Fig. 02A = *wairakiensis*).

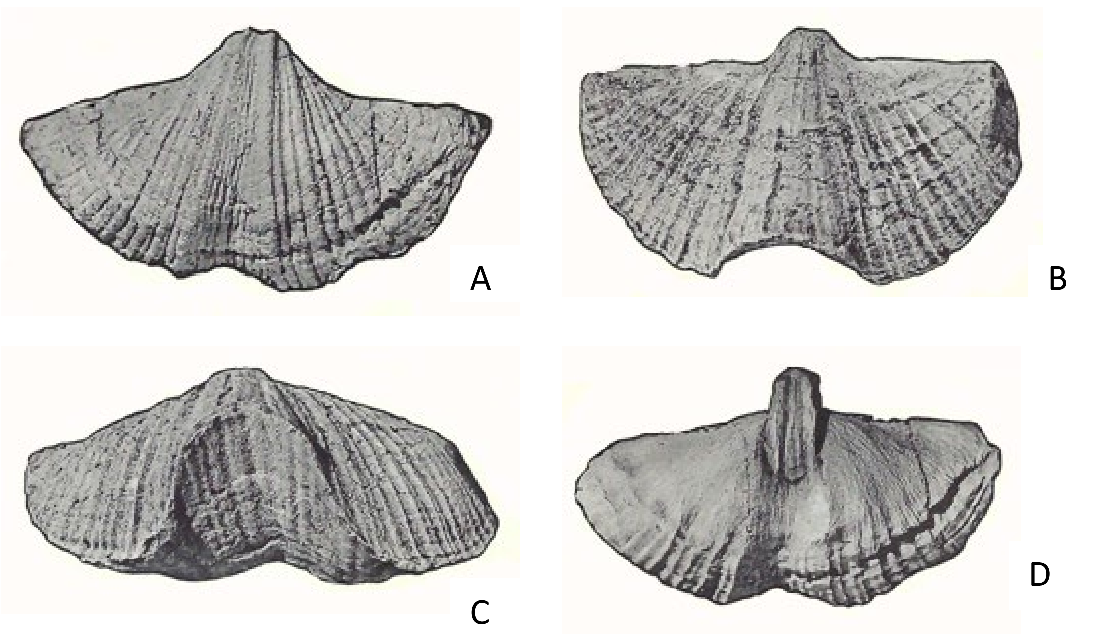


Fig. 19. *Aperispirifer archboldi* Waterhouse. A, D, PVC cast of ventral valve and ventral internal mould, holotype BR 814, x1. B, C, dorsal and anterior aspect of internal mould of specimen with valves conjoined, BR 468, x0.8. Specimens from middle Letham Formation, Wairaki Downs, New Zealand. (Waterhouse 1964).

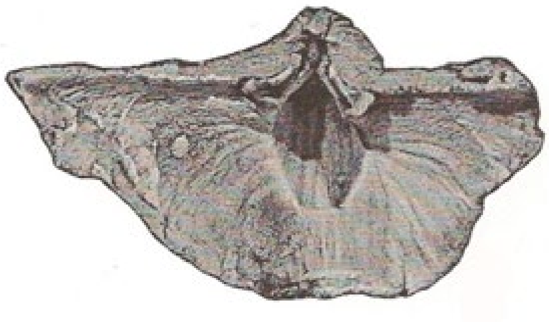


Fig. 20. *Aperispirifer archboldi* Waterhouse, latex cast showing interior of ventral valve, BR 467 x1, from middle Letham Formation, Wairaki Downs, New Zealand. (Waterhouse 1964).

Diagnosis: Moderately large transverse specimens with heavy secondary callus, plicae moderately persistent, ribs coarse with rounded crests, sulcus broad anteriorly.

Holotype: BR 814 figured by Waterhouse (1964, pl. 23, fig. 4; 1982, pl. 15, fig. 1), Suggate et al. (1978, text-fig. 4.5, fig. 10), Speden & Keyes (1981, pl. 5, fig. 10) and Fig. 19A, D herein, from middle Letham Formation, OD.

Stratigraphy: This distinctive species occurs in the middle Letham Formation of Wairaki Downs in south New Zealand. It appears also to be found in the Freitag Formation of the southwest Bowen Basin, though poor preservation would allow the material to be *lethamensis* instead. The species has also been provisionally recognized, pending full systematic study, in the Elderslie Formation of the north Sydney Basin (Waterhouse 2001, p. 93; 2002).

Aperispirifer lethamensis Waterhouse, 1968

Fig. 21

1968 *Aperispirifer lethamensis* Waterhouse, p. 38, pl. 3, fig. 13, pl. 4, fig. 1-7, pl. 5, fig. 2, 3, 4, 6, 7, pl. 6, fig. 3, text-fig. 11-14 (part, not pl. 5, fig. 1, 5, pl. 6, fig. 2, text-fig. 15 = *A. parfreyi* Waterhouse).
1978 *Asperispirifer* (sic) *lethamensis* – Suggate et al. text-fig. 4.6, fig. 10-12.
1981 *A. lethamensis* – Speden & Keyes, pl. 6, fig. 10-12.
1982 *A. lethamensis* – Waterhouse, p. 91, text-fig. 29c.
aff. 1983 *Trigonotreta* sp. C McClung, p. 68, Fig. 9.5, 6.
1984 A. cf. *nelsonensis* [not Waterhouse] – H. J. Campbell et al., Fig. 6.1, 2.
1999 *A. lethamensis* – Waterhouse, p. 13.
2001 *A. lethamensis* – Waterhouse, p. 93.
2002 *A. lethamensis* – Waterhouse, p. 36, Tables 5, 6
2021a *A. lethamensis* – Waterhouse, p. 93.
2023 *Simplicisulcus* sp. Lee *in* Lee et al., p. 25, Fig. 12AA-AH, 13.

Diagnosis: Large transverse specimens with high interarea, numerous moderately persistent plicae pairs, costae broad, low over ventral umbo.

Holotype: BR 1314 figured by Waterhouse (1968, pl. 4, fig. 1-4) and Fig. 21A-D herein, from upper Letham Formation, New Zealand.

Morphology: The ribs are not as strong as those in *archboldi*, and the fold is narrow and high. The sulcal plication is more conspicuous in this species, compared with that of *archboldi.*

Stratigraphy: The scope of this species was later restricted by the proposal of a further species, *parfreyi*, and the stratigraphic succession corrected from the depiction in Mutch (1972), to show that the species was older, not younger, than *Aperispirifer wairakiensis.* This correction was set aside by Briggs (1998), conveniently ignoring the fact that it was I who discovered and collected the locality, and knew more about the stratigraphy of the fossil localities than did A. R. Mutch. But Mutch's view suited Briggs in his misrepresentation of the stratigraphy and a somewhat erratic identification of strophalosioid species, which, although endorsed by some Australian paleontologists, lacks stratigraphic integrity with his identifications of some species also highly questionable (Waterhouse 2024a, pp. 199ff).

Material described by McClung (1983) from level E in the Eddystone core is overall like *lethamensis* in ornament and shape, though its shape is also like that of *parfreyi*. More

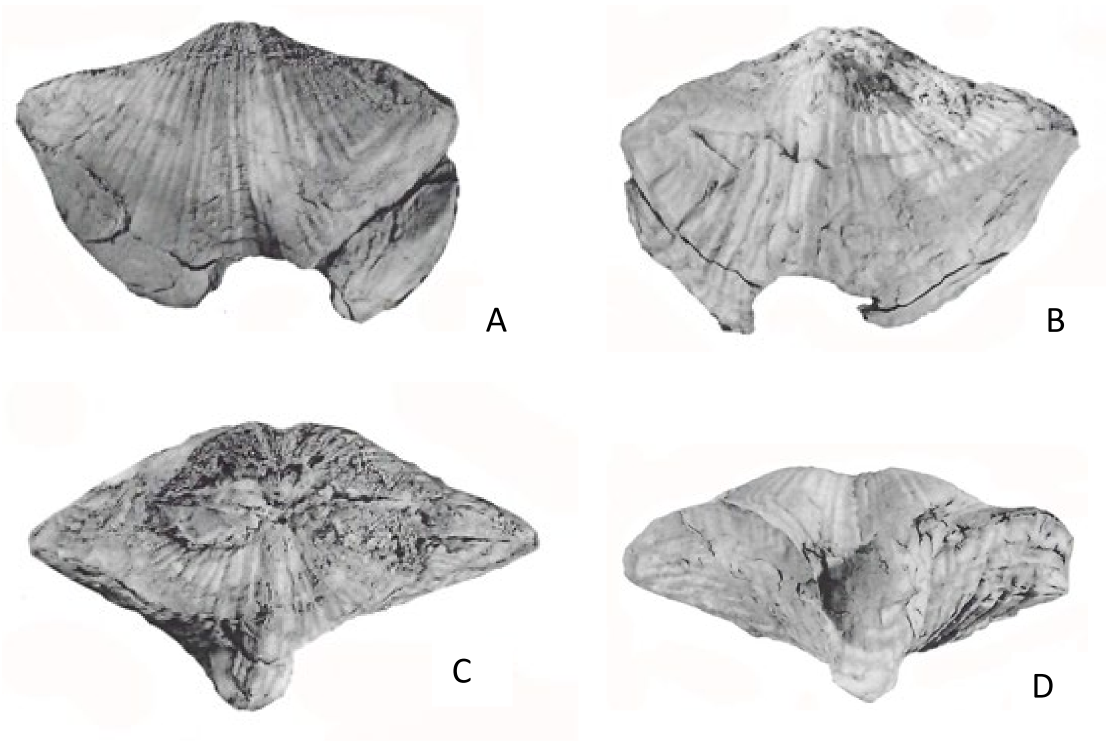


Fig. 21. *Aperispirifer lethamensis* Waterhouse. A-D, ventral, dorsal, posterior and anterior aspects (ventral valve on top) for holotype, BR 1314, x0.8. (Waterhouse 1968).

material would allow a more reliable identification.

The species has been provisionally reported from the Fenestella Shale in Waterhouse (2002, p. 178), but this needs confirmation. The species is close to *archboldi* but has more plicae pairs, finer costae and narrower dorsal fold, with prominent lateral plication.

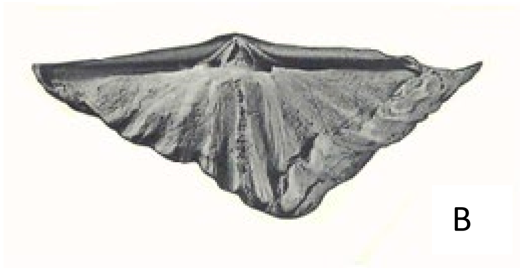
Aperispirifer wairakiensis (Waterhouse, 1964)

Fig. 22

1964 *Neospirifer wairakiensis* Waterhouse, p. 127, pl. 23, fig. 4, 6, pl. 24, fig. 1, 5, pl. 25, fig. 1, 5, Fig. 56-60, 61B (part, not pl. 23, fig. 5, 7-10, pl. 24, fig. 1-3, pl. 25, fig. 2-4, 6, 7, Fig. 61A, 62, 63 = *archboldi*).
1968 *Aperispirifer wairakiensis* – Waterhouse, p. 35.
1999 *A. wairakiensis* – Waterhouse, p. 14.
2001 *A. wairakiensis* – Waterhouse, p. 93.
2002 *A. wairakiensis* – Waterhouse, Table 8, p. 48.
2006a *A. wairakiensis* – Carter, p. 1802, Fig. 1196a (part, not b-e = *archboldi*).
2016 *A. wairakiensis* – Waterhouse, Fig. 302A (part, not 302B = *archboldi*).

Diagnosis: Transverse with three or four pairs of strong plicae fading anteriorly, and firm though slender costae, crests angular posteriorly. Inner plicae pair broad and incorporated anteriorly in the sulcus.

Holotype: BR 482, figured by Waterhouse (1964, pl. 23, fig. 4), Carter (2006a, Fig. 1196a) and Fig. 22A herein from Letham Burn Member, Mangarewa Formation, Wairaki Downs, New Zealand, OD.



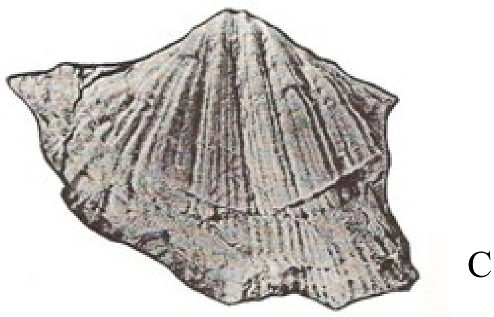


Fig. 22. *Aperispirifer wairakiensis* (Waterhouse). A, ventral interior, PVC cast BR 489, x1. B, dorsal internal mould, BR 486 x1.2. C, ventral exterior BR 482, holotype, x1. Letham Burn Member, New Zealand. (Waterhouse 1964).

Stratigraphy: The species is found in the Letham Burn Member at the base of the Mangarewa Formation at Wairaki Downs, New Zealand, and has been tentatively reported from the Sydney Basin in the mid-Belford Formation (with *Echinalosia maxwelli robusta*) by Waterhouse (2002, p. 179) and also in the faunas of the upper Wandrawandian Formation, reports that need verification.

Aperispirifer hillae Waterhouse, 1999

Fig. 23

1953 *Neospirifer* sp. Campbell, p. 9, pl. 2, fig. 1-8.
1964b *Neospirifer* sp. B – Hill & Woods, pl. P8, fig. 5.
1972 *N. wairakiensis* – Hill et al. pl. P8, fig. 5 (part, not P8, fig. 2-4 = *parfreyi*).
1999 *Aperispirifer wairakiensis hillae* Waterhouse, p. 14.
2001 *A. wairakiensis hillae* – Waterhouse, p. 93.

Diagnosis: Rhomboidal shape much as in *Aperispirifer wairakiensis*, plicae more persistent than in *wairakiensis*, lateral fascicles well developed, sulcus broad and deep anteriorly.

Holotype: UQF 14316 figured by Campbell (1953, pl. 2, fig. 1), Hill & Woods (1964b, pl. P8, fig. 5), Hill et al. (1972, pl. P8, fig. 5) and Fig. 23A, B herein, from near Dry Creek, southwest Bowen Basin.

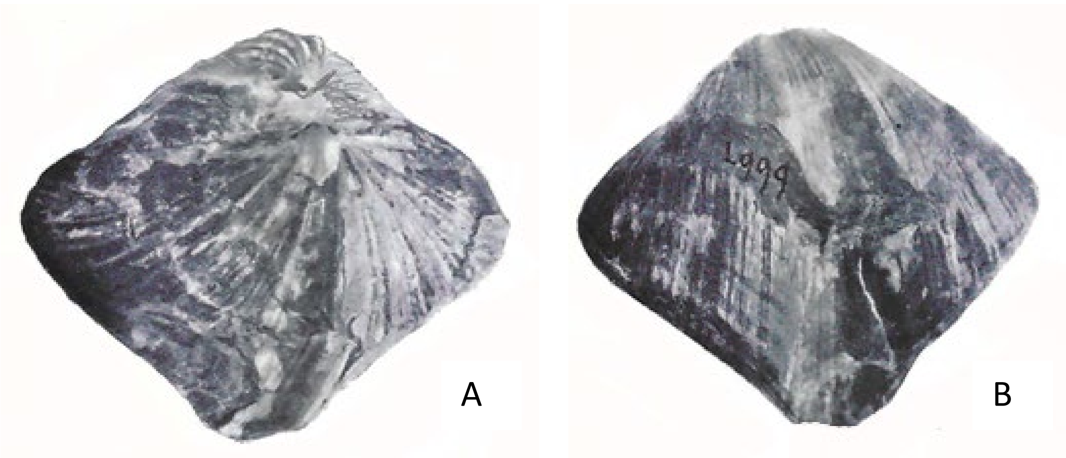


Fig. 23. *Aperispirifer hillae* Waterhouse,. A, B, dorsal and ventral aspects of holotype, UQF 14316, from shale near Dry Creek, southwest Bowen Basin, x1. (Campbell 1953).

Morphology: This taxon is now ranked as a full species, given its more persistent plicae, and given the presence of firm lateral fascicles, but remains poorly known.

Stratigraphy: Campbell (1953) stated that his material came from near Dry Creek. Hill & Woods (1964b) indicated a source from shale, which suggests lower Peawaddy Formation, and Parfrey (1988, p. 32, text-fig. 10) stated that the specimens entered the succession above the Ingelara Formation, and were present in the Catherine Sandstone and what is now regarded to be lower Peawaddy Formation. Like these units, the Ingelara Sandstone contains *Pseudostrophalosia ingelarensis,* and so would appear to be younger than *Echinalosia maxwelli* and the Letham Burn Formation of New Zealand. In New Zealand, *Ps. ingelarensis* occurs above the Letham Burn Member, but there is no accompanying *hillae* as far as is known.

Aperispirifer parfreyi Waterhouse, 1999

Fig. 24

1952 *Spirifer* aff. *tasmaniensis* [not Morris] – Fletcher, p. 15, pl. 1, fig. 2.
1959 *Spirifer* aff. *tasmaniensis* [not Morris] – Speden *in* Grindley et al. pl. 1, fig. 1.
1964 *Neospirifer* sp. A Waterhouse, p. 134, pl. 26, fig. 1.
1964b *Neospirifer* sp. A Hill & Woods, pl. P8, fig. 2-4.
1968 *Aperispirifer lethamensis* [not Waterhouse] – Waterhouse, p. 38, pl. 3, fig. 15, pl. 5, fig. 1, 5, 8, pl. 6, fig. 2, text-fig. 11-13, 14D, 15 (part, not pl. 3, fig. 13, pl. 4, fig. 1-7, pl. 5, fig. 2-4, 6, 7, pl. 6, fig. 3, text-fig. 11-13, 14A-C = *A. lethamensis*).
1972 *Neospirifer wairakiensis* [not Waterhouse] – Hill et al., pl. P8, fig. 2-4 (part not fig. 5 = *A. hillae*).
1983 *Aperispirifer* sp. Waterhouse & Jell, p. 245, pl. 2, fig. 4, 5.
1983 *Trigonotreta* sp. D McClung, Fig. 8.1, 2?, 3, 4, 7.
1987 *A. lethamensis* [not Waterhouse] – Waterhouse, p. 21, pl. 5, fig. 1-3, 5-8, 10.
1988 *A. wairakiensis* [not Waterhouse] – Parfrey, p. 17, pl. 3, fig. 14, 18, 20, 21, 23-25, pl. 4, fig. 1.
1999 *A. parfreyi* Waterhouse, p. 15.
2001 *A. parfreyi* – Waterhouse, p. 94.
2002 *A. parfreyi* – Waterhouse, Tables 10-12, text-fig. 2.6A.
2008 *A. parfreyi* – Waterhouse, p. 366, Fig. 7H.

Diagnosis: Large shells typically with four or five pairs and up to six pairs of strong persistent plicae and firm costae, as a rule transverse with well-rounded anterior lateral margins, subplicae pair incorporated within sulcus, fold high and narrow.

Holotype: UQF 69977 figured in Waterhouse (1987, pl. 5, fig. 1, 3) and Fig. 24A, B herein, from Barfield Formation, southeast Bowen Basin, OD.

Morphology: This a distinctive species, compared extensively with other species in Waterhouse (1999), and varying amongst individuals to a minor extent. The synonymy includes various immature specimens and unusual variants from the stratigraphic equivalents.

McClung's (1983) material includes worn material and an exceptionally narrow ventral valve (Fig. 9.2) and two well preserved small valves with typical plicae.

Stratigraphy: The species is prominent in the Barfield and lower Flat Top faunas, and also the

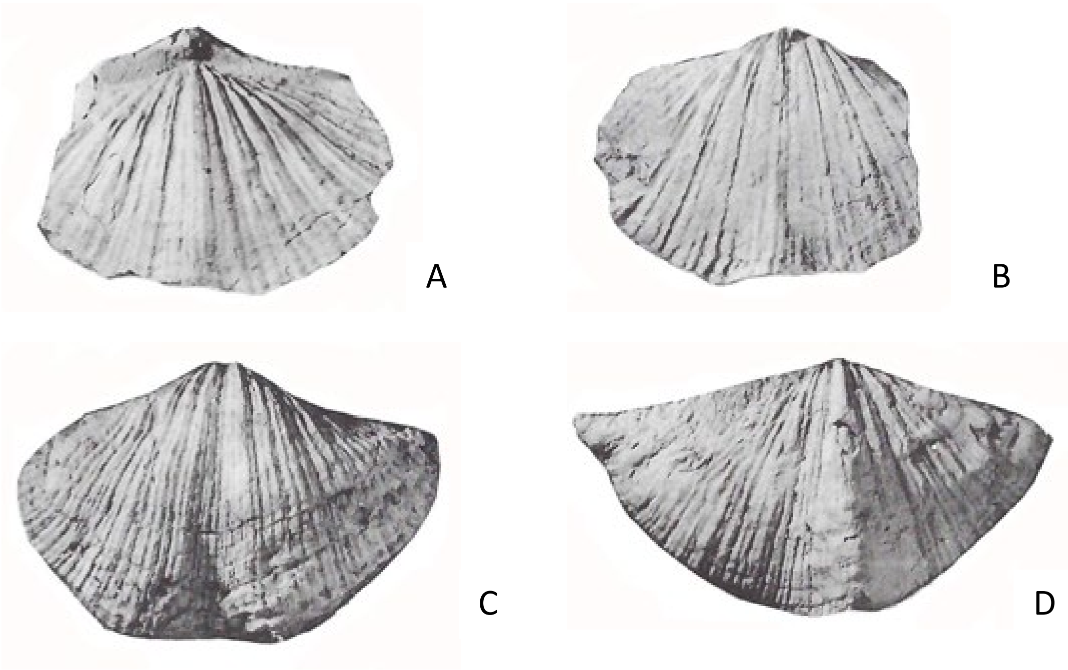


Fig. 24. *Aperispirifer parfreyi* Waterhouse. A, B, dorsal and ventral aspects of holotype, UQF 69977 from Barfield Formation. C, ventral aspect of UQF 74174 from Flat Top Formation. D, dorsal valve UQF 74176. Specimens x1, from southeast Bowen Basin. (Waterhouse 1987).

Peawaddy Formation and Mantuan Member of the southwest Bowen Basin, and lower Blenheim Formation of the north Bowen Basin. The specimens figured by McClung (1983, Fig. 9.1, 3, 4, 7) came from LD 96, regarded as transitional between Ingelara and Catherine Sandstone (McClung 1983, p. 62). In the north Sydney Basin, the species was provisionally identified in the Muree Formation, and in the Nowra and Berry Formations of the south Sydney Basin by Waterhouse (2002, p. 179). In New Zealand, the species comes from units 6 and 7 of the Mangarewa Formation at Wairaki Downs.

Aperispirifer parfreyi acuta (Waterhouse, 1987)

Fig. 25

1987 *Fusispirifer* sp. B Waterhouse, p. 23, pl. 5, fig. 16, 17.
1987 *Fusispirifer pauciplicus* [not Waterhouse] – Waterhouse, p. 23, pl. 6, fig. 5-7 (part, not pl.

5, fig. 15, pl. 6, fig. 1-4, text-fig. 4 = *Cracowspira laminatus*).
2004 *Crassispirifer acuta* Waterhouse, p. 158.

Diagnosis: Transverse with acute cardinal extremities, wide but shallow sulcus, low fold, four pairs of low plicae with sulcal pair, costae comparatively fine.

Holotype: UQF 74182 from Flat Top Formation, southeast Bowen Basin, figured in Waterhouse (1987, pl. 6, fig. 5) and herein as Fig. 25A, OD.

Morphology: This taxon was treated in Waterhouse (2004) as a species of *Crassispirifer* Archbold & Thomas (1985) first described from Western Australia, but although there are similarities, the Flat Top material does not have the hunched appearance of that genus, with its low and incurved inconspicuous ventral umbo. It is now suggested that the material is much more closely related to *Aperispirifer parfreyi*, having a similar transverse subpentagonal outline and fine costae, and distinguished by its very low plicae, as illustrated in Fig. 25A. The specimens of McClung (1983, Fig. 9.5, 6) from level E in the Eddystone 1 core show subdued plicae but the anterior lateral margins are more rounded than in type *acuta*.

Fig. 25. *Aperispirifer parfreyi acuta* (Waterhouse). A, ventral valve holotype UQF 74182 x1. B, ventral internal mould, UQF 74175. C, dorsal aspect of UQF 74183. Specimens x1 from Flat Top Formation, southeast Bowen Basin. (Waterhouse 1987).

Stratigraphy: The specimens come from the Flat Top Formation, and are now regarded as a minor and contemporaneous subspecies – or even variant – of *Aperispirifer parfreyi*. A possible occurrence in the underlying Oxtrack Formation of the southeast Bowen Basin was indicated by Waterhouse (1987, p. 23).

Aperispirifer demulceatus Waterhouse, 2022b

Fig. 26

2022b *Aperispirifer demulceatus* Waterhouse, p. 173, Fig. 35-37.

Diagnosis: Shells with three inner pairs of costate plicae, and two up to six lateral pairs of slender plicae and fascicles laterally. Sulcus well-defined, fold with rounded low crest. Size small, despite maturity of shell.

Holotype: UQF 65486 from lower *Echinalosia* (*Unicusia*) *minima* Zone above Scottville Member in north Bowen Basin, figured in Waterhouse (2022b, Fig. 36), OD.

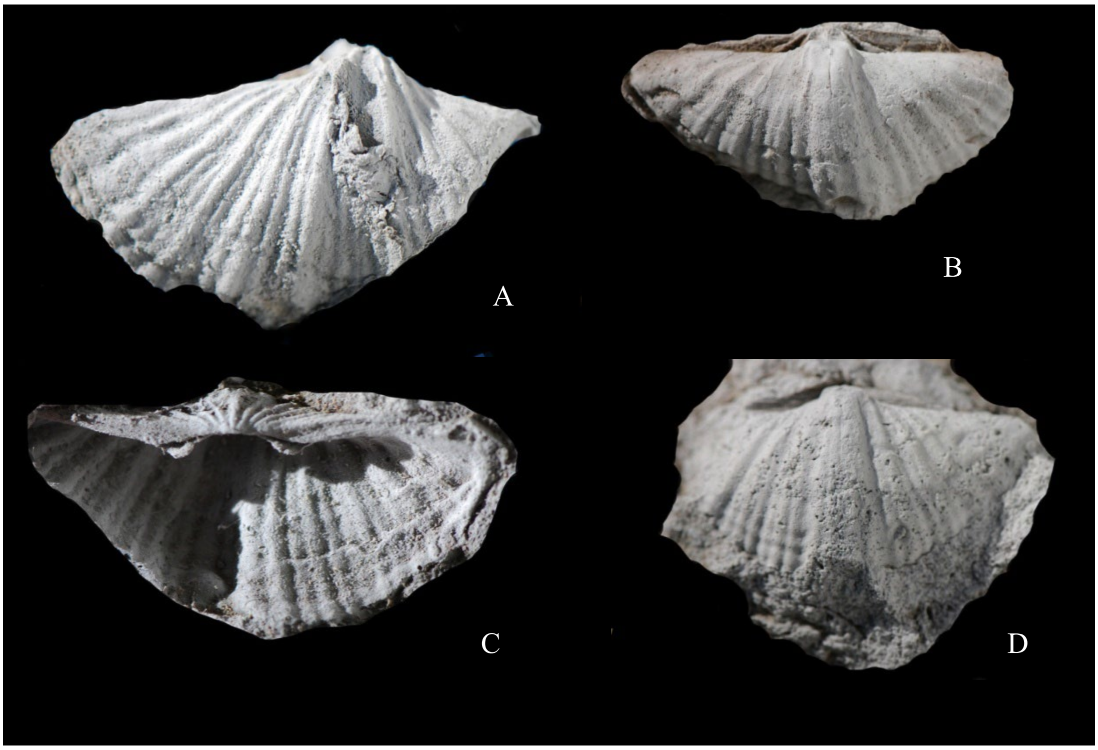


Fig. 26. *Aperispirifer demulceatus* Waterhouse. A, small ventral valve, latex cast, UQF 82698, x2. B, C, dorsal internal mould and latex cast, UQF 82699, x1.5. D, dorsal internal mould, x 1.5, UQF 82701. From base of *Echinalosia* (*Unicusia*) *minima* Zone, north Bowen Basin. (Waterhouse 2022b).

Morphology: *Aperispirifer parfreyi* (Waterhouse, 1999) is much larger than *A. demulceatus*, with moderately well-defined and similarly persistent plicae and similar sulcus and fold. One marked difference from *demulceatus* is that the specimens of *parfreyi* are more costate, with more costae over the fold and sulcus, and the lateral extremities are costate, though shells of both taxa have four or five up to six pairs of persistent plicae. As well the ventral umbo of *demulceatus* is slightly broader, and the dorsal fold more elevated medianly. These differences are only in part due to the smaller size, but no lesser maturity of the present specimens, aspects which suggest specimens of *parfreyi* which had persisted but had to adapt to less favourable conditions. The species has more numerous and persistent plicae and fascicles than seen in the type species of *Aperispirifer, A. wairakiensis,* but shares the same basic ornament, delthyrial construct, and shape. Material from the Mantuan Member have a quite different morphology internally, as reported in Waterhouse (2022b, p. 83, Fig. 14-16) and discussed herein on pp.43 and 44.

Stratigraphy: This species has been found only in the earliest beds of the *Echinalosia* (*Unicusia*) *minima* Zone, just above the Scottville Member of the upper Blenheim Formation.

Aperispirifer sp. A

1964 *Neospirifer* n. sp. A Waterhouse, p. 134 (part, not pl. 20, fig. 1 = *parfreyi*).
1999 *Aperispirifer parfreyi* [not Waterhouse] –- Waterhouse, pp. 15, 16 only (remainder = *parfreyi*).
2002 *Aperispirifer* sp. Waterhouse, Table 18, p. 57.

Material including BR 465 from the *Ingelarella costata* Zone in New Zealand is like *Aperispirifer parfreyi* in details of plicae and sulcal subplicae, but has very fine costae, and is small. It is mentioned briefly by Waterhouse as in the synonymy.

Aperispirifer nelsonensis (Waterhouse,1964)

Fig. 27, 28

1917 *Spirifer* cf. *bisulcatus* [not Sowerby] – Trechmann, p. 60, pl. 5, fig. 1, 2.
1964 *Neospirifer nelsonensis* Waterhouse, p. 135, pl. 26, fig. 2-8, pl. 27, fig. 2, 5, text-fig. 56-58, 59B, 64-66.
1968 *Aperispirifer nelsonensis* – Waterhouse, p. 35.
1978 *Neospirifer nelsonensis* – Suggate et al., Fig. 4.7.12.
1982 *A. nelsonensis* – Waterhouse, p. 55, pl. 14h.
2010 *A. nelsonensis* – Shi et al., Fig. 9G, I, J.

Diagnosis: Large and transversely subrectangular or subelongate shells with sulcus shallow, V-shaped posteriorly in profile, entered anteriorly by innermost plicae pair, plicae low, fading over posterior third of valve, costae broad and few in number.

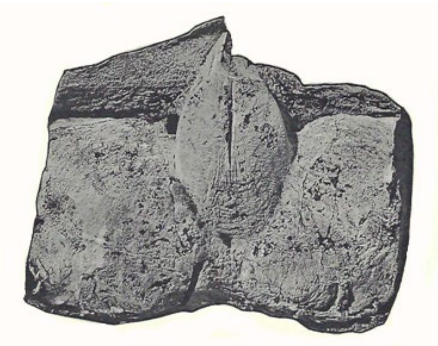


Fig. 27. *Aperispirifer nelsonensis* (Waterhouse), ventral internal mould, BR 496, x1. Pig Valley Limestone, Nelson, New Zealand. (Waterhouse 1964).

Holotype: BR 500 figured by Waterhouse (1964, pl. 26, fig. 3) and Fig. 28A herein from Pig Valley Limestone, Nelson, New Zealand, OD.

Morphology: The species is represented by a substantial number of large specimens. The indication of a high myoseptum in Fig. 27 is exceptional for the species.

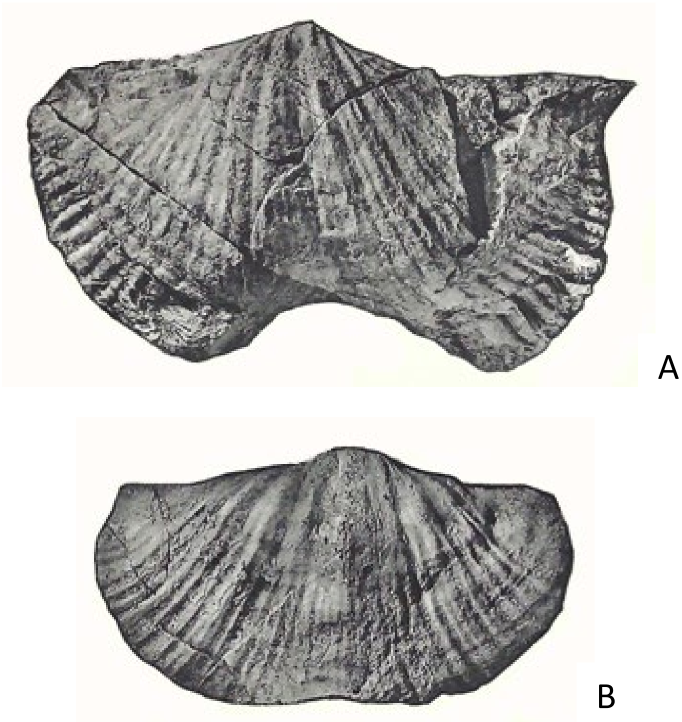


Fig. 28. *Aperispirifer nelsonensis* (Waterhouse). A, ventral valve, BR 500, holotype. B, dorsal valve, BR 388. Specimens x1. Pig Valley Limestone, Nelson, New Zealand. (Waterhouse 1964).

Stratigraphy: The species is found in the Pig Valley limestone lenses of east Nelson, New Zealand, and is considered to be of late Changhsingian age. Somewhat incomplete specimens were compared with this species by H. J. Campbell in Campbell et al. (1984, Fig.

6.1, 2) from Stephens Island, New Zealand, but those specimens look much more like *Aperi-spirifer lethamensis*, consonant with the age of the fossils preferred by Briggs & Campbell (1993) and Waterhouse (2021a) rather than the Late Permian age promulgated by Campbell et al. (1984). Hyden et al. (1982) identified the species from Late Permian rocks near Mossburn, but the ornament is very different from that of *nelsonensis*. (See *Betaneospirifer*? *mossburnensis*, below).

Genus ***Betaneospirifer*** Gatinaud, 1949

Diagnosis: Transverse as a rule, with wide hinge, and well-formed plicae and costae, delthyrium overlain by a cover plate or neodeltidium, apparently derived from a single stegidium, and readily lost. No connector plate nor shelf, short dental plates and adminicula, low crural plates, no tabellae, spiralia laterally directed. The mantle canal network is finely spaced.

Type species: *Spirifera moosakhailensis* Davidson, 1862 from Wargal Formation, Salt Range, Pakistan, OD.

Discussion: The hinge is much wider than in *Neospirifer* Fredericks, 1926.

Betaneospirifer*? *dubius (Etheridge Snr, 1872)

Fig. 28

1872 *Spirifera dubia* Etheridge Snr, p. 330, pl. 16, fig. 6.
1892 *S. dubia* – Etheridge Jnr, p. 231, pl. 10, fig. 14.
1948 *Neospirifer dubius* – Branson, 1948, p. 426.
1969 *Trigonotreta? dubia* – Runnegar & Ferguson, p. 251.
1987 *N. dubius* – Waterhouse & Balfe, p. 30, pl. 1, fig. 5.
2008 *N. dubius* – Waterhouse, p. 354, Fig. 3B, C.
2015b *Betaneospirifer*? *dubius* – Waterhouse, p. 22, Fig. 6A-F.

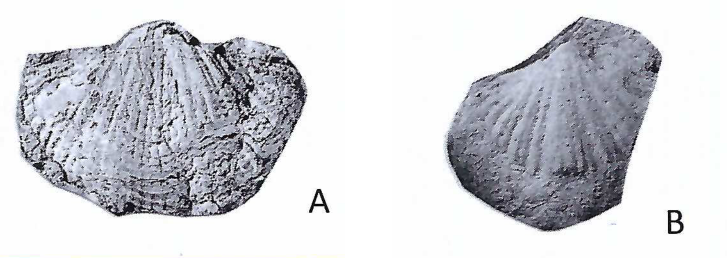


Fig. 28. *Betaneospirifer*? *dubius* (Etheridge Snr). A, neotype GSQF 13152. B, dorsal valve QMF 14408. Specimens x1 from Rammutt Formation, Gympie, Queensland. (Waterhouse 2015b).

Diagnosis: Shell small as preserved, distinguished by shallow broad ventral sulcus, and low dorsal fold. Well-defined plicae, with low moderately numerous branching costae, crossed by prominent growth lamellae, cardinal extremities angular. Interior poorly known.

Neotype: Specimen GSQF 13152 from Rammutt Formation (Asselian), Gympie, figured by Waterhouse & Balfe (1987, pl. 1, fig. 5), Waterhouse (2015b, Fig. 6A) and Fig. 28A herein, SD Waterhouse 2015b, p. 154.

Morphology: Specimens figured as *Trigonotreta stokesi* by Cisterna & Shi from the upper Wasp Head Formation of the south Sydney Basin are more transverse with more plicae and large pleromium with umbonal callosity (Cisterna & Shi, 2014, Fig. 8.3).

Stratigraphy: The species has so far been found only in the volcanic green sandstone of the Rammutt Formation of the Gympie area in southeast Queensland.

Betaneospirifer? **_mossburnensis_** (Waterhouse, 1999)

Fig. 29, 30?, 31?,aff. 32

aff. 1964 *Neospirifer* cf. *nelsonensis* [not Waterhouse] – Waterhouse, p. 140, pl. 27, fig. 1.
1967 *Neospirifer* sp. Waterhouse, p. 91, text-fig. 28.
1982*Trigonotreta nelsonensis* [not Waterhouse] – Hyden et al., p. 104, Fig. 2a-d, ?5a, b.
?1982 *Aperispirifer* or *Neospirifer* sp. Waterhouse, p. 55, Fig. 17P.
1999 *N. mossburnensis* Waterhouse, p. 11.
?2002 *Neospirifer*? Waterhouse, p. 65.

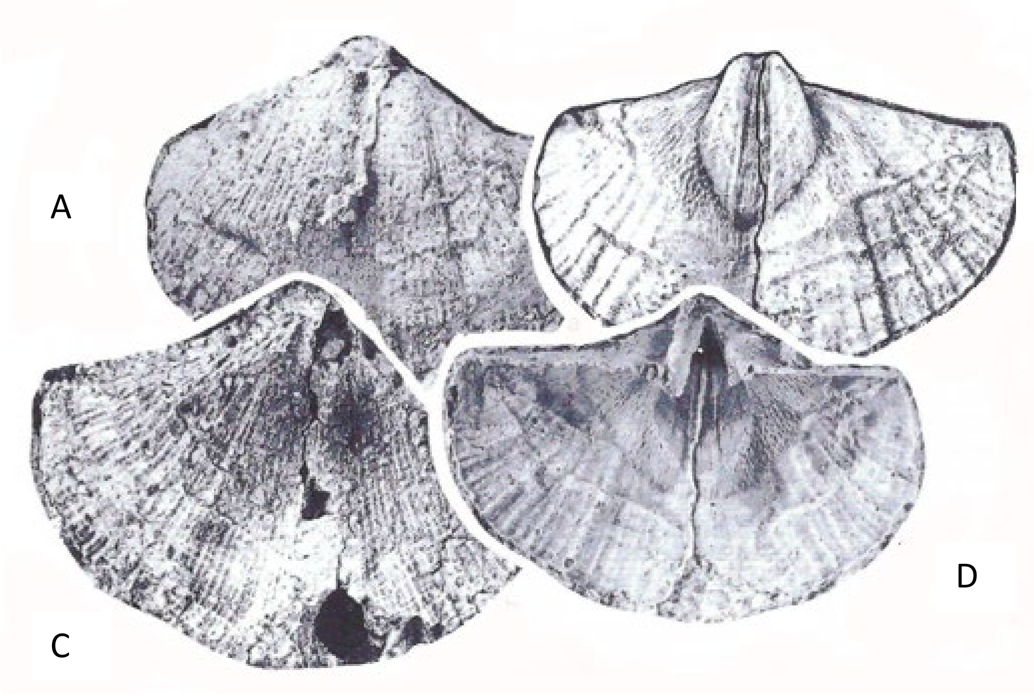


Fig. 29. *Betaneospirifer*? *mossburnensis* (Waterhouse). A, C, latex cast and external mould of ventral valve, holotype OU 2590, x2. B, D, internal mould and latex cast of same specimen, x2. From Countess Formation, Mossburn, New Zealand. (Hyden et al. 1982).

Diagnosis: Weakly transverse shells at maturity with inner two pairs of plicae broad and low, costae externally fine: internally the costae are stronger and the plicae arranged in some five or six pairs. Dorsal fold narrow, hinge moderately wide.

Holotype: OU 2590 figured by Hyden et al. (1982, text-fig. 2a-d) and Fig. 29A, C herein from Countess Formation at Mossburn, New Zealand, OD.

Morphology: The illustration in Hyden et al. (1982) indicates an open delthyrium with no subdelthyrial plate, so that a position within *Aperispirifer* or *Neospirifer* - *Betaneospirifer* appears likely, and the latter is preferred because there is no sign of a pleromal shelf or the

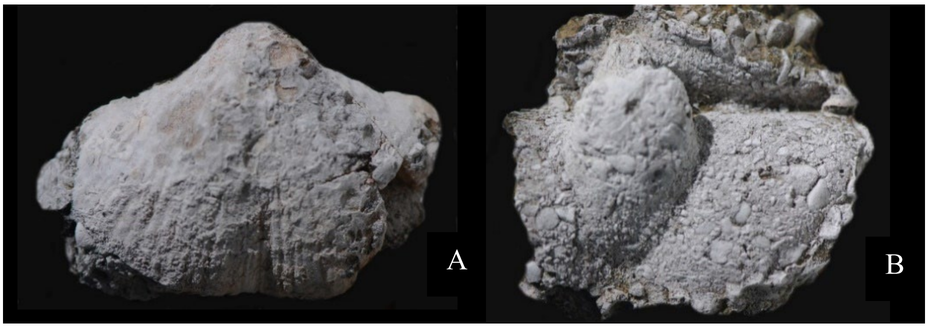


Fig. 30. ?*Betaneospirifer mossburnensis* (Waterhouse). A, ventral exterior, OU 2463. B, leached ventral internal mould from same locality. Specimens x1 from Glendale Limestone, Wairaki Downs, New Zealand. (New).

umbonal callosity which typifies *Aperispirifer*. Nor is there any resemblance externally to *Trigonotreta*, despite the assignment of the specimens to that genus by Hyden et al. (1982), because the plicae are low and broad, and costae are fine.

Fig. 31. ?*Betaneospirifer mossburnensis* (Waterhouse), x1.5, latex cast of cardinal area of the specimen in Fig. 13B. (New).

Stratigraphy: The species is represented in what was called the Countess Formation at Mossburn by Hyden et al. (1982). Later, the Countess rocks further north in the Countess

Range were subdivided into several formations by Aitchison, Landis & Turnbull (1988), but no firm match could be suggested for the Mossburn rocks. According to Waterhouse (2002, pp. 117, 118) the brachiopods figured in Hyden et al. (1982) suggested an array of ages, as if at least some, and possibly all, had been derived. This is supported by the similarity of *Betaneo-spirifer*? *mossburnensis* to specimens (Fig. 30, 31) found in a conglomerate lens in the limestone of the Glendale Formation (Waterhouse 2002, p. 65) at a stratigraphic level some-what older than any of the Countess or Stephens rocks. These show apparently comparable ornament with few broad and low plicae, low anteriorly, and broad and low costae. The umbonal callosity is low and broad with median groove, and there is no subdelthyrial connector plate. The Glendale specimens are signified in the preceeding synonymy with question marks.

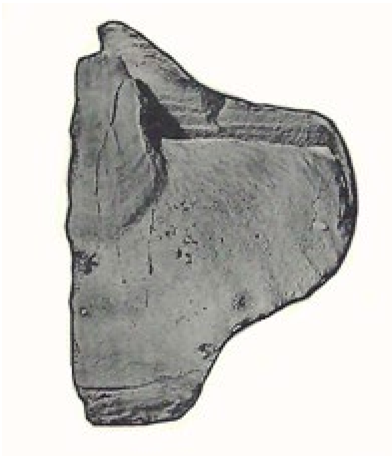


Fig. 32. aff. *Betaneospirifer mossburnensis* (Waterhouse), ventral internal mould BR 818 x1 from Wairaki Breccia, Wairaki Downs, New Zealand. (Waterhouse 1964).

On the other hand, a possibly allied ventral internal mould comes from the Wairaki Formation at Wairaki Downs (Fig. 32). This is moderately close in shape, but does not show ornament well, so that identity is conjectural.

Genus ***Forticosta*** Waterhouse, 2018

Diagnosis: Transverse shells with weakly defined sulcus and low fold, costae moderately strong with a number of bifurcations. Delthyrium covered by a single plate, unlike the stegidia comprised as a rule of two plates in many Spiriferidae, no connector plate.

Type species: *Forticosta transversa* Waterhouse, 2018, p. 348 from basal Jungle Creek Formation, Yukon Territory, Canada, OD.

Discussion: This genus is characterized by its strong branching costae, but as a recently introduced form, so far is not widely known, with the type species joined by an Early Permian species described by Hu (1983, pl. 14, fig. 7-12, text-fig. 7, 8) from the Zhanjin Formation in the Duomo Rutog region of Xizang (Tibet). The present species, found in Early Permian of New Zealand, appears to be close. The development or otherwise of a ventral umbonal callosity is not established for either the Canadian form or the possible New Zealand material, but it seems unlikely.

Family relationships: Where the genus is to be placed remains uncertain, but a delthyrial cover plate is present in the type species, suggesting the genus may be treated as a member of Neospiriferidae. But uncertainty remains over the relationship to *Gypospirifer*, which has similar strong ribs, but might and only might have a connector plate, as discussed on p. 45.

Forticosta*? *inexpectans (Waterhouse & Campbell, 2021)

Fig. 33

2021 *Gypospirifer*? *inexpectans* Waterhouse & Campbell, p. 42, Fig. 13, 14.

Diagnosis: Transverse shells with well-defined fold and ill-defined sulcus, plicae developed on only a few specimens, costae dominant with steep flanks and rounded crests, arising by both intercalation and especially by bifurcation, crossed by fine commarginal growth increments. Delthyrium apparently open, no visible umbonal callus or pleromium, short dental plates and adminicula, no connector plate, crural plates present, spiralia laterally directed.

Holotype: BR 2458 from the Eglinton Subgroup in the Dunton Range, west Otago, New Zealand, figured by Waterhouse & Campbell (2021, Fig. 13A) and Fig. 33B herein, OD.

Morphology: Though assigned to *Gypospirifer*? by Waterhouse & Campbell (2021), this position seems contentious, because the species lacks a connector plate of the sort figured by Legrand-Blain (1986a). The costal ornament is certainly close to that of *Gypospirifer*, especially in the rounded crests and steep flanks of the costae and their narrow interspaces. There is a strong approach by the New Zealand species to *Forticosta transversa* Waterhouse (2018) from Arctic northwest Canada. This genus is transverse with strong round-crested branching costae in weakly defined posterior fascicles, with faint suggestion of posterior plicae in some specimens. There is no subdelthyrial plate in this species, but a cover plate is preserved, whereas no cover plate is preserved for the New Zealand species. Both species have transverse spiralia,

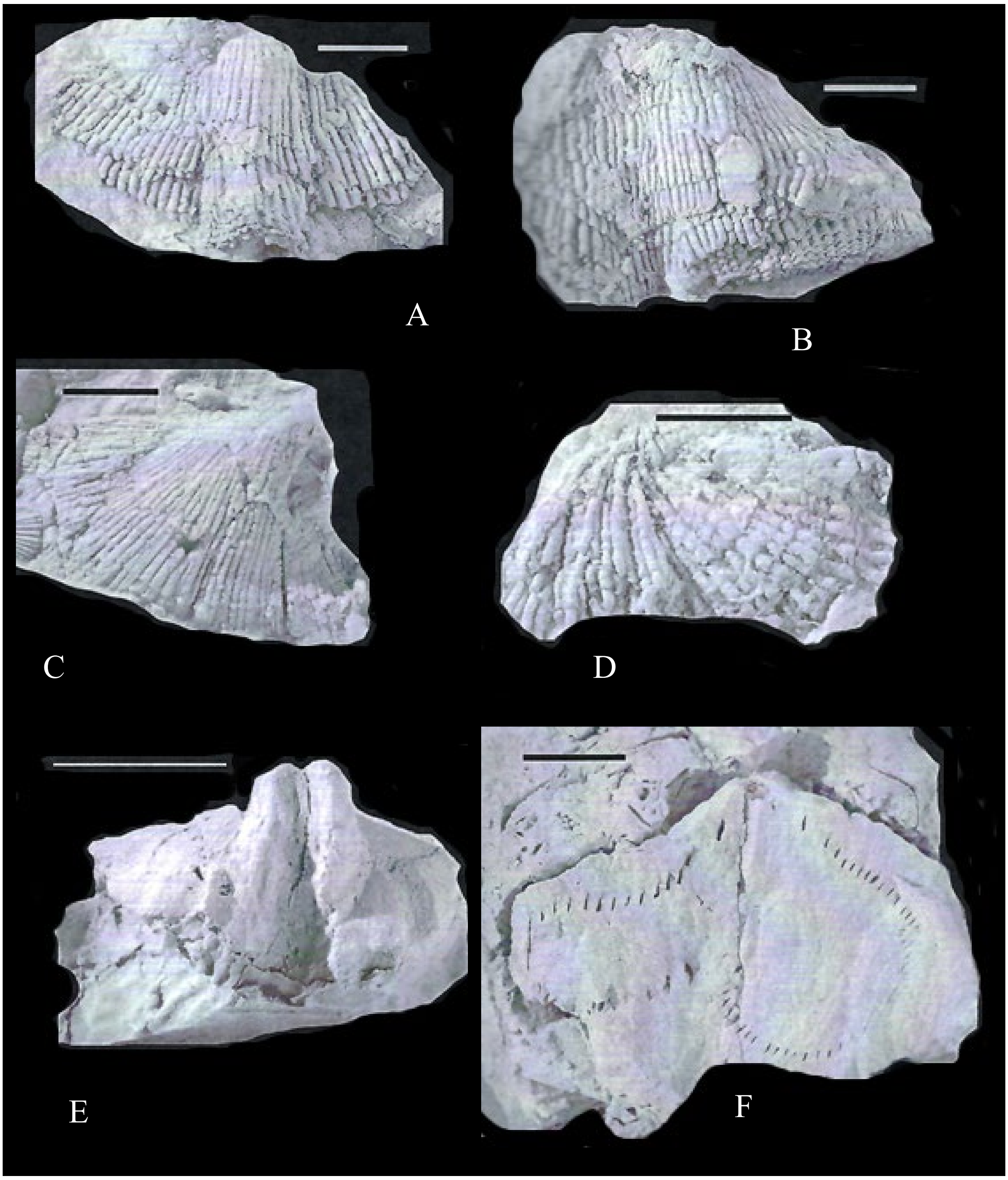


Fig. 33. *Forticosta*? *inexpectans* (Waterhouse & Campbell). A, latex cast of dorsal exterior, BR 2462. B, latex cast of ventral exterior, BR 2458, holotype. C, latex cast of ventral exterior BR 2431. D, latex cast of small ventral valve with unusually well-defined plicae, BR 2451. E, internal mould of ventral valve BR 2471. F, section through specimen with both valves conjoined, showing laterally directed spiralia. Space bar 5mm long. From Eglinton Subgroup, Dunton Range, west Otago, New Zealand. (Waterhouse & Campbell 2021).

but unlike the Canadian species, the ventral muscle field of the New Zealand form is not exceptionally broad.

Stratigraphy: The species is found with *Echinalosia curvata* Waterhouse in the Eglinton Subgroup of the Dunton Range, New Zealand, and is deemed to be of Sakmarian age.

Discussion: At present, the study of such spiriferids with strong costae and feeble plication is at an early phase. No species from east Australia is known to be comparable.

Genus ***Wadispirifer*** Waterhouse, 2004

Diagnosis: Large subrectangular to quadrate shells with wide hinge and subalate cardinal extremities, three or four plicae pairs limited to posterior shell, costae coarse, deep broad sulcus, fold broad with gently rounded crest. No connector plate. No delthyrial cover preserved, but possibly lost.

Type species: *Neospirifer grandis* Archbold & Thomas 1986, p. 143 from Hardman Formation of Canning Basin, Western Australia, OD.

Discussion: The type species is close in shape and most attributes to *Neospirifer* (*Quadrospira*) Archbold, 1997, p. 214, named for fossils from Western Australia, Arabia, Afghanistan, Pakistan, Timor, and other south Asia countries, but is distinguished by the feeble plicae, in contrast to the strong and persistent plicae of *Quadrospira*, which has a higher and narrower dorsal fold, and somewhat comparable rectangular shape. The subgenus *Quadrospira* is regarded as a full genus, as in the *Revised Brachiopod Treatise* (Gourvennec & Carter 2007, p. 2784). Other species described from Western Australia by Archbold & Thomas (1986) are like *grandis* in size, and have a similar massive innermost plicae pair bordering the sulcus, but are more subtriangular in shape, such as some mature *amplus* (Archbold & Thomas 1986, Fig. 9A, C, D), and indeed *Q. hardmani* and *Q. plicatus* in their early growth stages are triangular in outline. [*For amplus*, Fig. 9, the labelling is badly confused and cites a different holotype from that in Fig. 8. The text confirms the citation in Fig. 8]. They have comparable ornament and often display a small umbonal callosity in the upper delthyrium, as in some specimens of *Quadrospira hardmani* (see Archbold & Thomas 1986, Fig. 2I).

The adminicula of *grandis* were stated to be minute in juveniles (Archbold & Thomas 1986, p. 147, Fig. 11F), but they are high and strong in mature specimens (eg. their Fig. 12B).

In one article, Waterhouse (2010) referred the New Zealand species *crassicostatus* to *Kaninospirifer* Kulikov & Stepanov *in* Stepanov et al. 1975, because the dental plates though inadequately exposed appear to be low as in many individuals of *Kaninospirifer.* But the shape of *Kaninospirifer* is more typically that of *Aperispirifer* and *Betaneospirifer*. *Wadispirifer* Waterhouse, 2004, from Western Australia and Nepal offers a better comparison with the east Australian and New Zealand taxa, and shares a profound and broad ventral sulcus and very large bordering plicae pair.

Wadispirifer crassicostatus (Waterhouse, 1983a)

Fig. 34

1964 *Neospirifer hardmani*? [not Foord] – Waterhouse, p. 122, pl. 22, fig. 4-8, pl. 23, fig. 1-3, text-fig. 55-58.
2004 *Kaninospirifer crassicostatus* – Waterhouse, p. 131 (part only, includes *initialis* as well).
2010 *K. crassicostatus* – Waterhouse, p. 76, Fig. 33.

Diagnosis: Large subrectangular shells with minutely alate cardinal extremities and long lateral margins. Sulcus broad and deep anteriorly. Costae coarse, plicae subdued and extending

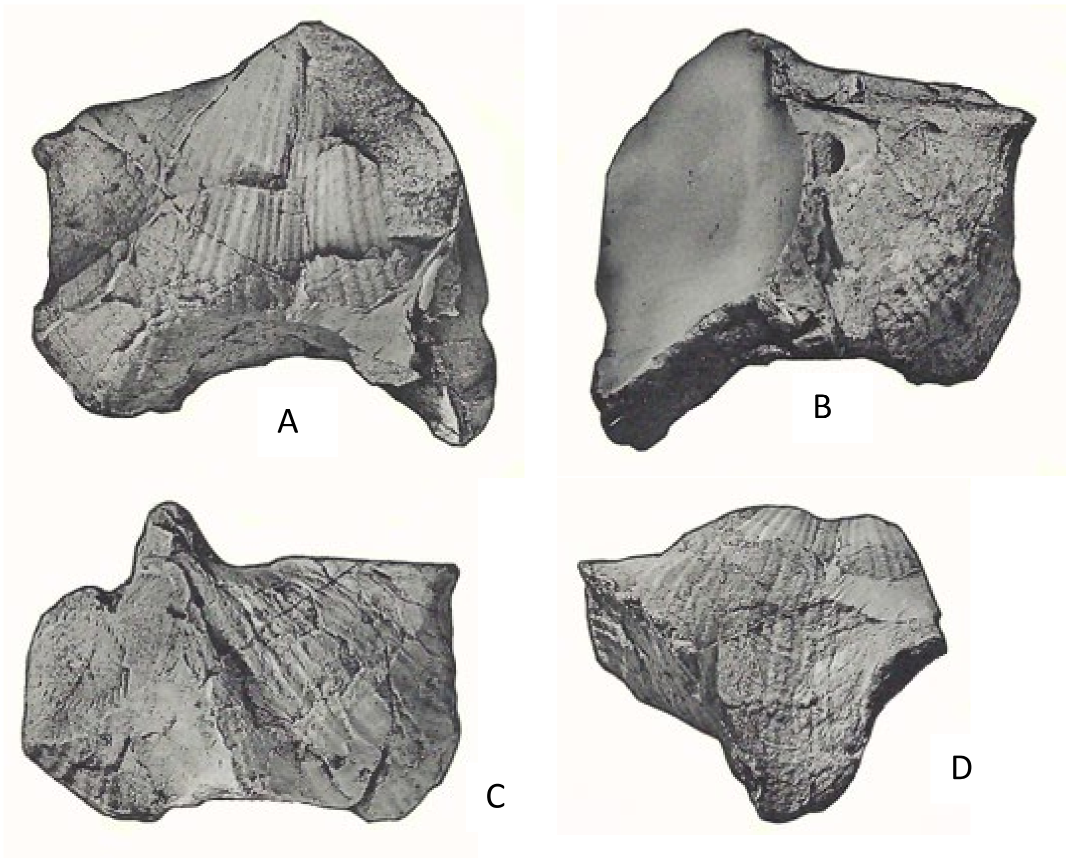


Fig. 34. *Wadispirifer crassicostatus* (Waterhouse), . A, B, D, PVC cast, ventral, dorsal, and anterior aspects. C, internal mould, dorsal aspect, holotype BR 546 from Brunel Formation, Takitimu Mountains, New Zealand, x1. (Waterhouse 1964).

little beyond the umbonal region. Sulcus wide and deep, fold with narrow crest. Dental plates apparently low.

Holotype: BR 546 from the *Notostrophia zealandicus* Zone, Brunel Formation, figured by Waterhouse (1964, pl. 22, fig. 4-8, pl. 23, fig. 1-3; 2010, Fig. 33A-E) and Fig. 34A-D herein, OD.

Morphology: There is no known delthyrial cover, nor umbonal callosity, nor subdelthyrial plate. The mantle canal system does not appear to be well-spaced (Waterhouse 1964, pl. 22, fig. 8), but is deeply impressed in Waterhouse (1964, pl. 23, fig. 3). Possibly the dental plates are low, without being entirely clear (see Waterhouse 1964, pl. 23, fig. 3).

Stratigraphy: The species has been described from the *Notostrophia zealandicus* Zone of the Brunel Formation in the Takitimu Group in southern New Zealand, below the zone of *Notostrophia homeri* which matches the uppermost Tiverton Formation in the north Bowen Basin..

Family **GEORGINAKINGIIDAE** Waterhouse, 2004

[Nom. transl. Waterhouse 2016, p. 249 ex Georginakingiini Waterhouse, 2004, p. 184].

Diagnosis: Transverse shells with variable number of strong plicae, usually rounded in section, may bear few to several costae arising posteriorly or well in front of umbones. Commarginal lamellae and fine capillae developed. Umbonal shelf or platform and callosity common, denticulate hinge, complexly ramose vascular impressions. Dental plates, adminicula, crural plates, no tabellae, no connector plate. Lower to Upper Permian (Asselian - Changhsingian).

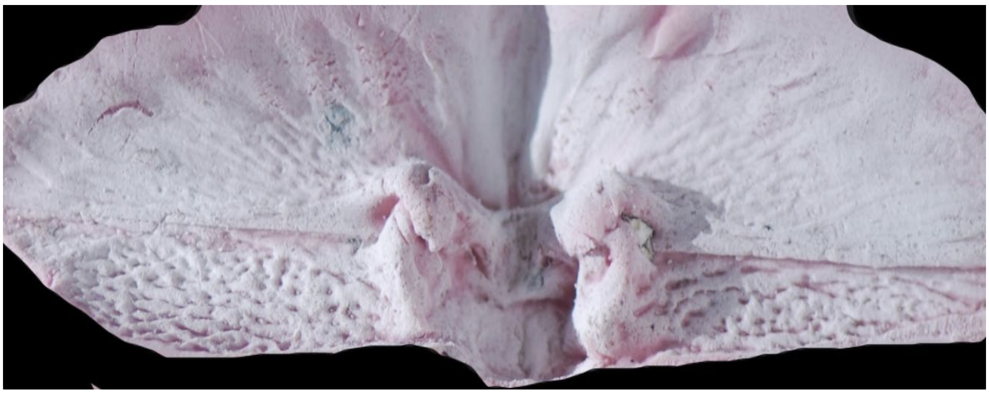


Fig. 35. *Georginakingia aviculiformis* Waterhouse. Posterior part of cast BR 3216 with dorsal valve on top, prepared from internal mould supplied by Natural History Museum, London, figured as *Spirifer avicula* Sowerby by Morris (1845, pl. 17, fig. 6), x1.7, from the Malbina Formation at Eaglehawk Neck, Tasmania. (Waterhouse 2016).

Genera: *Georginakingia* Waterhouse, *Angulispirifer* Waterhouse, *Neilotreta* Waterhouse, *Sulciplica* Waterhouse, *Tasmanospirifer* Waterhouse, *Unicostatina* Waterhouse.

Discussion: Georginakingiidae were discriminated for shells that are mostly dominated by an ornament of simple plicae, and so approach the older trigonotretoid group Angiospiriferidae Legrand-Blain, 1985, but where known, have transverse spiralia (*Neilotreta, Cancellospirifer*). The family is possibly descendent from *Adminiculoria* Waterhouse, 2016 of late Early Carboniferous age. *Georginakingia* is a genus of large shells of Guadalupian (Wordian) age in eastern Australia. The genus is ornamented by numerous pairs of strong costate plicae, with sulcal and fold costae, and subcancellate micro-ornament. It shows only a superficial similiarity to *Fusispirifer,* an identification which was proposed by Clarke (1973, 1987) and endorsed by Archbold & Thomas (1987) and Gourvennec *in* Gourvennec & Carter (2007, p. 2781). *Georginakingia* is like *Fusispirifer* in being large and transverse and plicate, but the two genera differ in costation, plication (plicae are much more numerous), mantle canal system and delthyrial appurtenances, involving a delthyrial connector plate in *Fusispirifer* that is absent from *Georginakingia*. The afore-mentioned authors paid limited attention to internal structures, other than G. A. Thomas in his earlier work, and the delthyrial construct of varous species referred to *Fusispirifer* from Western Australia by Archbold & Thomas (1987) needs to be clarified. Externally, a number of species show the high number of plicae, suggestive of *Georginakingia*.

Lee *in* Lee et al. (2023, p. 26) regarded Georginakingiidae as Trigonotretidae and Trigonotretinae. He either ignored or downplayed the critical and consistent difference in the orientation of the spiralia. However the family ranking cannot be regarded as final, given the need for more morphogical assessments of various genera, and eventually subfamily level may be deemed more appropriate.

Some species of genera belonging to Georginakingiidae have no costae, but younger species in the same genus tend to be more costate.

Genus ***Angulispirifer*** Waterhouse, 2016

Diagnosis: Transverse with extended cardinal extremities, ornamented by numerous plicae with angular crests and interspaces, prominent commarginal growth laminae. Sulcus narrow with median central rib, and fold with median channel. Prominent ventral umbonal callosity.

Type species: *Spirifer phalaena* Dana, 1849, p. 485 from Guadalupian of Tasmania, here designated.

Discussion: Specimens from east Australia approaching this genus have been referred to *Spirifer vespertilio* Sowerby, 1844, but this taxon is now not represented by Sowerby's material in any known museum collection, and there has never been good information about the stratigraphic source, so that the name must be abandoned.

This genus is distinguished from *Unicostatina* by having more and angular plicae and wide cardinal extremities, and is less transverse than *Sulciplica* or *Georginakingia*, which have more rounded plicae. Lee *in* Lee et al. (2023) considered that the fold in *Angulospirifer* was essentially the same as that of *Sulciplica*, but students will readily be able to distinguish an otherwise smooth fold bearing a single well-defined median channel from folds with channel and accompanying plicae, subplicae or costae, and will note that within species from controlled and restricted stratigraphic units, the difference is consistent. *Tasmanospirifer* has a narrower hinge with less extended cardinal extremities and more plicae over the sulcus and fold.

Angulospirifer jervisbayensis (Waterhouse & Lee) *in* Lee et al., 2023

Fig. 36 - 38

2023 *Tasmanospirifer jervisbayensis* Waterhouse & Lee *in* Lee et al., p. 26, Fig. 13, 14, 15A-Q.
2023 *Sulciplica transversa* [not Waterhouse] – Lee *in* Lee et al., p. 30, Fig. 15AD, AE, AF, AG, 16A-I (part, not 15R-V?, W-Z, AA?, AB, AC, AH = *Sulciplica pauciplicus* – see p. 135).

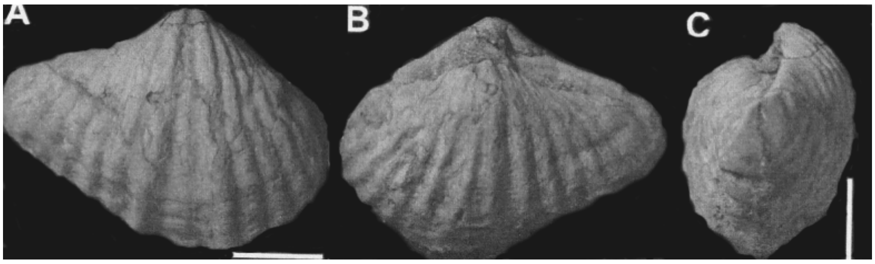


Fig. 36. *Angulospirifer jervisbayensis* (Waterhouse & Lee). A, B, C, ventral, dorsal and lateral aspects of the holotype CPC 44474 from Snapper Point Formation, x1 approx. (Space bar 10mm). (Lee et al. 2023).

Diagnosis: Small weakly transverse shells with five to seven pairs of subangular to round-crested plicae. Sulcus narrow with median plication, fold bearing longitudinal median channel, lateral plicae rarely bifurcate, no apical callus.

Fig. 37. *Angulospirifer jervisbayensis* (Waterhouse & Lee), dorsal aspect of AMF 159066, scale bar 10mm, from Snapper Point Formation. This and several other specimens were identified with *Sulciplica transversa* by Lee. (Lee et al. 2023).

Holotype: CPC 44474 from Snapper Point Formation, figured in Lee et al. (2023, Fig. 14A-E) and herein as Fig. 36A-C, OD.

Morphology: The species belongs to *Angulospirifer*, which is characterized by having a dorsal fold bearing a median channel. *Tasmanospirifer* to which Lee had referred the species has several pairs of plicae over its fold. A low short median septum or ridge was reported for the dorsal valve, and it was noted that commarginal laminae became prominent anteriorly. The antero-lateral shell margins are more rounded in outline than those of *Angulospirifer phalaena* and the shell is triangular in outline. The synonymy has some uncertain aspects: paint was applied to a critical part of the morphology in Fig. 15U, and some specimens are not well preserved. Although my name was added out of generosity on the part of Sangmin Lee, it was

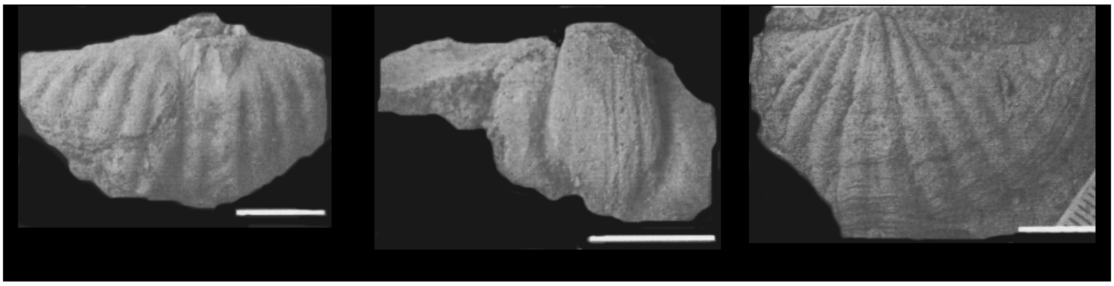


Fig. 38. *Angulospirifer jervisbayensis* (Waterhouse & Lee). A, ventral internal mould CPC 44490. B, posterior part of ventral valve CPC 44489, showing ventral muscle field. C, latex cast of dorsal valve AMF 159080. Scale bar 10mm. Snapper Point Formation. (Lee et al. 2023).

he who identified and described the species, making an invaluable contribution to the scope and geologic occurrences of the genus. It may yet be established that the specimens assigned in error to *Sulciplica transversa* are larger and more transverse than *jervisbayensis*. Whatever, it is clear that thanks to collections made by G. R. Shi and systematic study by Lee (*in* Lee et al. 2023), the species is now better known than *phalaena*, the type species of the genus, and better lighting for illustrations will massively contribute to understanding the species.

Stratigraphy: The species is so far limited to the Snapper Point Formation of the south Sydney Basin.

Angulospirifer phalaena (Dana, 1849)

Fig. 39

1845 *Spirifer vespertilio* [nomen nudum] – Morris, p. 283, pl. 17, fig. 3.
1849 *S. phalaena* Dana, p. 685, pl. 2, fig. 4.
1877 *S. vespertilio* – Koninck, p. 189, pl. 13, fig. 4, 4a, pl. 14, fig.3 9 (part, not pl. 13, fig. 4b, c).
?1888 *Spirifera vespertlio* – Johnston, pl. 11, fig. 7 (part, not fig. 8).
1892 *S. stutchburii* [not Etheridge] – Etheridge p. 232 (part, not pl. 38, fig. 4-6 = *Unicostatina stutchburii* – see p. 143).
?1901 *Spirifera vespertilio* – Frech, pl. 57C, fig. 31 and unnumbered figures on following page.
?1907 *Spirifera tasmaniensis* [not Morris] – David, pl. 38, fig. 2.
1965 *S. phalaena* – Waterhouse & Vella, p. 67, pl. 3, fig. 6.
2016 *Angulospirifer phalaena* – Waterhouse, p. 255, Fig. 328.
2023 *Sulciplica phalaena* Lee *in* Lee et al., p. 32, Fig. 16J-L.

Diagnosis: Transverse with alate cardinal extremities, fold with well-defined median channel, lateral shell with high number of simple plicae.

Holotype: Specimen figured by Morris (1845, pl. 17, fig. 3) and herein as Fig. 39 from Malbina beds at Eagle Hawk Neck, Tasmania, SD Waterhouse & Vella (1965, p. 67).

Fig. 39. *Angulispirifer phalaena* (Dana), external cast BR 3219 of dorsal valve, prepared from mould of the holotype x1 approx., kept at Natural History Museum, London. From the Malbina Formation at Eaglehawk Neck, Tasmania. (Waterhouse 2016).

Morphology: Lee *in* Lee et al. (2023) depicted a few specimens from the Snapper Point Formation as belonging to this species, and like the Tasmanian original, they have a very well-defined dorsal channel and rather narrow-crested plicae, compared with the predominant species in the formation, called *jervisbayensis*.

Stratigraphy: The species is of mid-Guadalupian age, in Tasmania and is found in the Snapper Point Formation of the south Sydney Basin.

Genus ***Cancellospirifer*** Campbell, 1953

Diagnosis: Small subequilateral shells with some five pairs of simple costae-like plicae. Low short dental plates, adminicula and crural plates, no tabellae, spiralia transverse.

Type species: *Cancellospirifer maxwelli* Campbell (1953) from the lower Peawaddy Formation (former upper Ingelara shale), southwest Bowen Basin.

Discussion: This genus has slender ribs that may be regarded as plicae by some authorities, and as costae by others. But a few fine ribs occur on the flanks of the larger ribs, suggesting that the larger ribs are plicae. There are similarities in shape to *Tasmanospirifer*, but the fold and sulcus carry fewer ribs.

Cancellospirifer maxwelli Campbell, 1953

Fig. 40, 41

1953 *Cancellospirifer maxwelli* Campbell, p. 11, pl. 3, fig. 1-10, text-fig. 2.
1968 *C. maxwelli* – Waterhouse, text-fig. 17, p. 48.
2006a *C. maxwelli* – Carter, p. 1779, Fig. 1172.6a-c.
2016 *C. maxwelli* – Waterhouse, p. 228, Fig. 288-290.

Diagnosis: Small subequilateral shells with some five pairs of simple costae-like plicae. Low short dental plates, adminicula and crural plates, no tabellae, spiralia transverse. The species is reliably known only from the type locality.

Holotype: UQF 14242 from Ingelara shale (ie. lower Peawaddy Formation), figured by Campbell (1953, pl. 3, fig. 4-6) and Fig. 40A herein, OD.

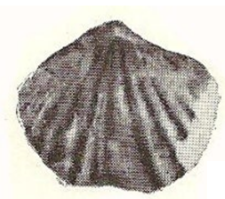
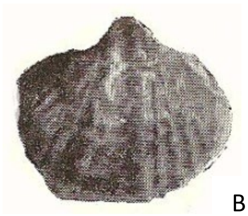

A

Fig. 40. *Cancellospirifer maxwelli* Campell, x1.5. A, dorsal valve UQF 14242, holotype. B, ventral valve UQF 14247. From Ingelara Formation. Queensland. (Campbell 1953).


B

Morphology: This genus is so small that it would seem possible that the form was a juvenile rendition of *Aperispirifer.* But *Cancellospirifer* Campbell has only simple plicae and cancellate micro-ornament, and only a few signs of costae in some specimens. There is a suggestion of subdued ribs on the sulcal and fold side of the innermost plication in Fig. 4OA, B, not mentioned by Campbell (1953), but implying that *Cancellospirifer* did bear incipient costation, and perhaps was based on immature specimens. The genus was judged by Carter (2006a, p. 1779) to belong to Sergospiriferinae Carter, and there are similarities to *Sergospirifer* and to members of Angiospiriferinae, both of Early Carboniferous age, but *Cancellospirifer* is closer in outline and ornament to other members of Trigonotretoidea such as *Brachythyrinella, Tasmanospirifer* and *Neilotreta*, and is of mid-Permian age. There are more plicae than in species of *Aperispirifer* found in the same general region in beds of the same general age, so the specimens are not juveniles of that genus. Transverse sections of the type species provided by Campbell (1953) and Waterhouse (1968) reveal well-developed dental plates and adminicula, and there was definitely no connector plate even in small specimens. Spiralia are transverse.

Stratigraphy: The specimen was described from shale originally assigned to the Ingelara Formation, and later treated as the lower part of the Peawaddy Formation by the Geological Survey of Queensland.

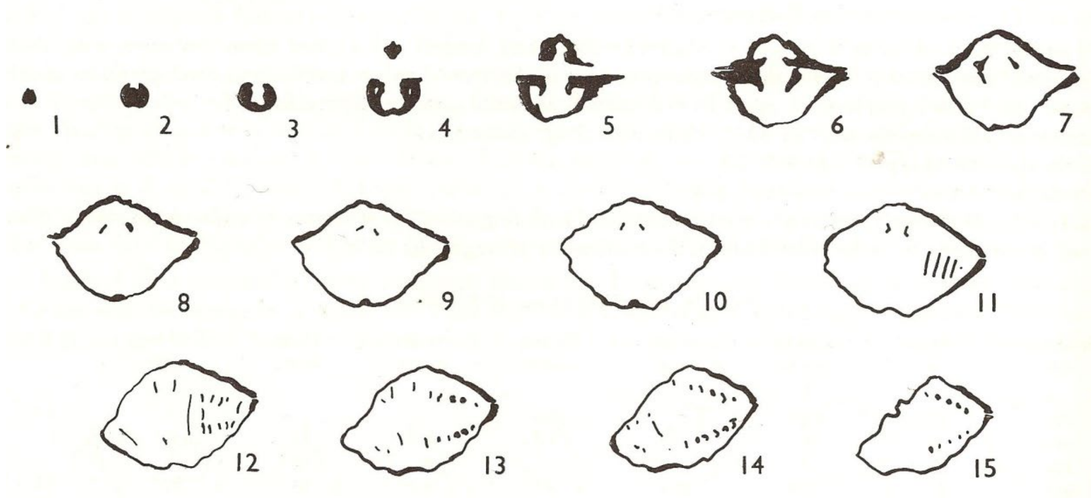


Fig. 41. *Cancellospirifer maxwelli* Campbell, serial sections of the type species, from the lower Peawaddy Formation of Queensland, east Australia, at intervals of 0.5mm, x2. (Waterhouse 1968).

Genus ***Georginakingia*** Waterhouse, 2004

Diagnosis: Equilateral to highly transverse shells, dominated in ornament by numerous simple plicae, which may be costate in some specimens. Internal plates like those of Trigonotretidae, with umbonal callosity, open delthyrium, short high dental plates, adminicular and crural plates, no tabellae. Spiralia transverse.

Type species: *Spirifera avicula* Morris (1845, p. 282, pl. 17, fig. 6), from Eagle Hawk Neck, Tasmania, of Middle Permian age, renamed *aviculiformis* Waterhouse (2016, p. 253), designated by Waterhouse (2004, p. 184).

Discussion: The name *avicula* as applied by Morris (1845) has been used for many years, but is technically inappropriate, because Morris based his identification on a species named by Sowerby (1844), which was never described nor illustrated, and the original material cannot be found, or replenished by further collections with certainty over coming from the same source as the type material. No appeal has ever been addressed to the International Commission on Zoological Nomenclature to justify (ie. overrule the rules) and validate Morris' material as the type. Therefore the Morris material has been renamed.

Georginakingia is characterized by its costate plicae, and in other respects is very close to *Sulciplica* (see p. 133). The difference between the genera is not so great, and it would be feasible to regard *Georginakingia* as a subgenus or even an exceptional species within the genus *Sulciplica,* because at least until the present, only the one species of *Georginakingia* has been recognized in east Australia. But the genus may be well represented by many species named by Archbold & Thomas (1987) in Western Australia, and and referred to *Fusispirifer*. If so then the type species is a rare extension of the genus into east Australia from the west.

Georginakingia aviculiformis Waterhouse, 2016

Fig. 42

?1844 *Spirifer avicula* G. B. Sowerby, p. 160, nomen nudum.
1845 *Spirifer avicula* [not G. B. Sowerby] – Morris, p. 282, pl. 17, fig. 6.
1973 *Fusispirifer avicula* – Clarke, pp. 50, 59.
1987 *F. avicula* – Archbold & Thomas, p. 196, Fig. 12A-D, 13A-G, 14A-C.
1987 *F. avicula* – Clarke, p. 267, Fig. 5A-E.
2004 *Georginakingia avicula* – Waterhouse, p. 184, text-fig. 34.
2016 *G. aviculiformis* Waterhouse, p. 253, Fig. 321, 322.
2023 *Fusispirifer avicula* – Lee *in* Lee et al., p. 32.

Diagnosis: Transverse with numerous plicae bearing fine costae, as a rule anteriorly. Closely spaced growth laminae.

Holotype: GST 887, figured by Clarke (1987, Fig. 5A) from Malbina Formation, Tasmania, OD.

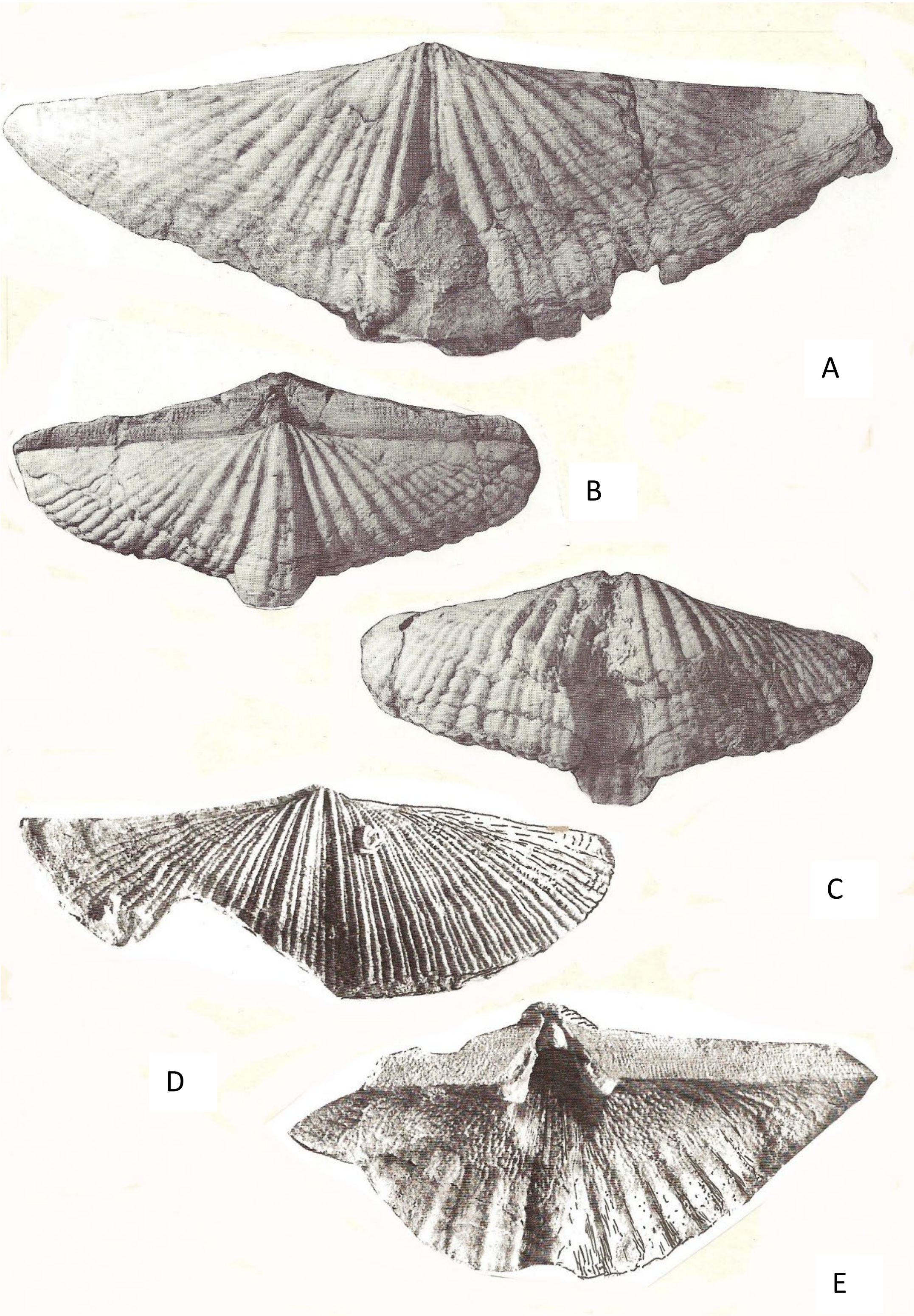


Fig. 42. *Georginakingia aviculiformis* Waterhouse. A, large ventral valve. B, C, dorsal and ventral aspects of another specimen. D, finely costate ventral valve. E, ventral valve interior, showing bulbous umbonal callosity on thick posterior shell. Specimens x1, from Malbina Formation of Tasmania, Australia. (Clarke 1987).

In proposing a new species for the material, Waterhouse (2016) endeavoured to clear up the position under which authors were referring the species to a form named by G. B. Sowerby, 1844, for which no description or figures were ever published. The subsequent nomination in Waterhouse (2016) provided description and figures for the type material, and for the benefit of Australian paleontologists, placed the type at an accessible place in east Australia instead of England.

Morphology: This species is transverse with numerous plicae and so approaches *Sulciplica transversa* Waterhouse, 1968, p. 27 in most respects, apart from the presence of costae.

Clarke (1987), Archbold & Thomas (1987), Gourvennec *in* Gourvennec & Carter (2007, p. 2781) and Lee *in* Lee et al. (2023) regarded what has been called *avicula* Morris as a member of *Fusispirifer,* but *Fusispirifer* has a subdelthyrial connector plate that is certainly absent from *Georginakingia* or *Sulciplica*. The relevant aurhors in the *Revised Brachiopod Treatise* persistently ignored or glossed over the nature and presence or absence and differences between internal structures in Spiriferida, in contrast to their individual and high-quality studies on Brachiopoda from somewhat constrained regions of limited age in their scientific articles. One of the difficulties involved in any study of Spiriferida that aspires to reflect interrelationships and possible course of evolution is that more than just the external appearance of the shell has to be evaluated.

Stratigraphy: The species at present is known from Eaglehawk Neck in the Malbina Formation of east Tasmania, with a small sample ascribed to the Tasmanian form by Archbold & Thomas (1987, Fig. 14A-C) from the Budgong Sandstone, equivalent to the Broughton Formation, of the Sydney Basin.

Genus ***Neilotreta*** Waterhouse, 2008

Diagnosis: Small shells distinguished by wide dorsal fold with rounded cross-profile. Plicae number as a rule five to seven pairs, may be non-costate or closely costate, hinge may be at maximum width and shells tend to be subequilateral. Spiralia laterally directed.

Holotype: *Trigonotreta narsahensis occidentalis* Thomas, 1971, p. 108 from upper Lyons Group, Early Permian, of Western Australia.

Discussion: Archbold (2003) and Cisterna & Shi (2014) referred species of this genus to

Trigonotreta, but these authors never took account of the spiralia, and consistently failed to prepare specimens in order to discover the orientation of the spires. The present genus has laterally directed spiralia, as shown for the type species by Thomas (1971), and also a very broad dorsal fold. Older species tend to be exclusively or predominantly plicate, and lateral costae appear in younger forms.

Neilotreta tangorini (Archbold, 2003)

Fig. 43

2003 *Trigonotreta tangorini* Archbold, p. 162, Fig. 4.1-14.
2014 *T. stokesi* [not Koenig] – Cisterna & Shi, p. 542.
2021b *Neilotreta tangorini* – Waterhouse, p. 36.

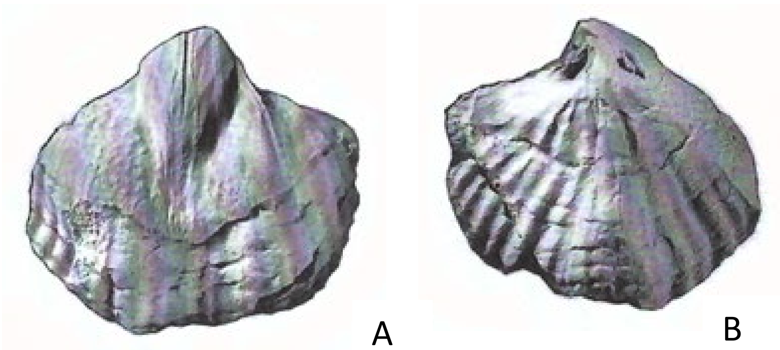


Fig. 43. *Neilolotreta tangorini* (Archbold). A, B, ventral and dorsal aspects of holotype, CPC 35327, x1.6, from Beckers Formation, Cranky Corner Basin, New South Wales. (Archbold 2003).

Diagnosis: Small subequilateral shells with up to seven pairs of plicae, inner plicae may subdivide, sulcus well-defined and fold broad and rounded in cross-profile, both sulcus and fold closely costate. Ventral muscle field broad.

Holotype: CPC 35327 figured by Archbold (2003, Fig. 4.1-7) and Fig. 43A, B herein from Beckers Formation, Cranky Corner Basin, New South Wales, OD.

Morphology: This species is close in appearance to the type species as described by Thomas (1971).

Stratigraphy: The species is known only from the Beckers Formation at Cranky Corner, New South Wales, believed to be of early Asselian age.

Neilotreta lakeensis Waterhouse, 2021c

Fig. 37, 38

2021c *Neilotreta lakeensis* Waterhouse, p. 135, Fig. 22-30.

Diagnosis: Transverse with hinge normally at maximum width of shell, and alate, six to seven pairs of plicae that bear costae over inner pairs, fold well-rounded in profile and sulcus somewhat V-shaped in profile.

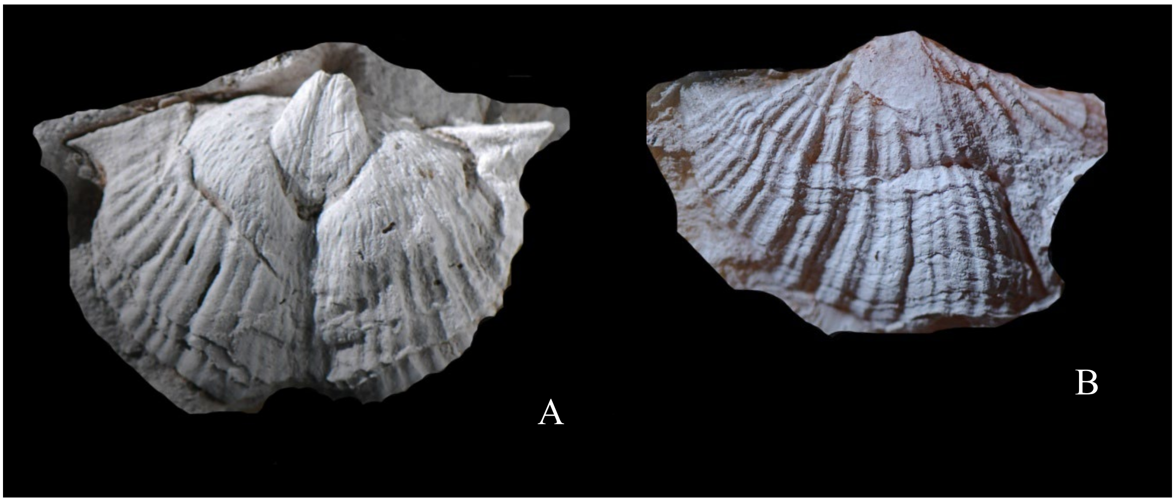


Fig. 37. *Neilotreta lakeensis* Waterhouse. A, ventral valve holotype, UQF 13554 x2. B, latex cast of UQF 13564, x1.5. Lakes Creek Formation. (Waterhouse 2021b).

Holotype: UQF 13554 figured by Waterhouse (2021c, Fig. 22A, 26E, F) and Fig. 37A herein from Lakes Creek Formation, east Queensland, OD.

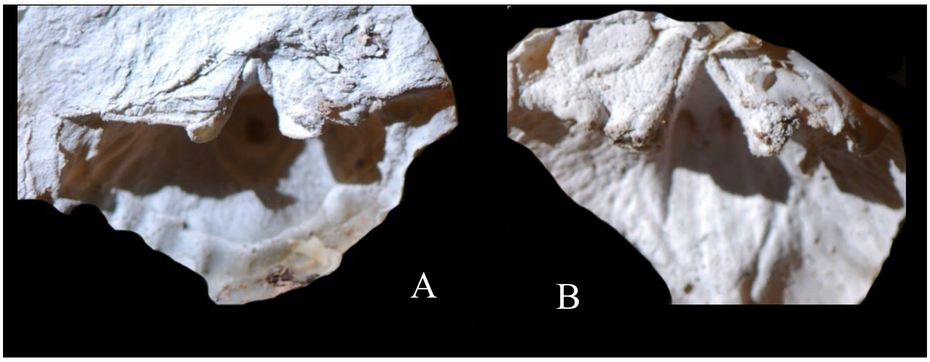


Fig. 45. *Neilotreta lakeensis* Waterhouse. Latex casts of ventral valve showing the outer edge of plates, or the previous position of the teeth, in the delthyrium. A, UQF 156**3**9, x3. B, UQF 13557, x2.5. Lakes Creek Formation. (Waterhouse 2021c).

Morphology: The species demonstrates the evolution of the genus into species that are more costate than older species, with increased width of the hinge. The dental plates are high and form prominent ridges bordering the delthyrium.

Stratigraphy: The species is known only from the Lakes Creek Formation, developed with the New England Orogen, and correlated with the *Taeniothaerus subquadratus* Zone of late Sakmarian age.

Neilotreta ovalis (Waterhouse, 1987)

Fig. 46

1987 *Aperispirifer ovalis* Waterhouse, p. 18, pl. 4, fig. 14-20, pl. 5, fig. 4.
2008 *A. ovalis* – Waterhouse, p. 363, Fig. 7C.

Diagnosis: Small subrounded to elongate shells with six to eight narrow subdued plicae on each valve, plicae each bearing only two or three narrow costae. Cardinal extremities broadly alate or obtuse, fold broad and low with rounded crest. Dental tracks prominent.

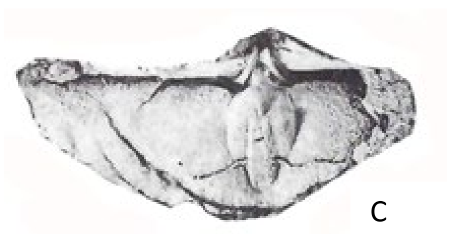
Holotype: UQF 59270 figured in Waterhouse (1987, pl. 4, fig. 14) and Fig. 46A herein, from Oxtrack Formation, southeast Bowen Basin, OD.

Morphology: This distinctive species should be classified as *Neilotreta*, given the nature of the dorsal fold.

Stratigraphy: The species is limited as far as known to the Oxtrack Formation in the south-east

A

B



C

Fig. 46. *Neilotreta ovalis* (Waterhouse). A, ventral valve holotype UQF 59270. B, dorsal valve UQF 70613. C, ventral internal mould UQF 70576. Specimens x1 from Oxtrack Formation, southeast Bowen Basin. (Waterhouse 1987).

Bowen Basin. It was listed from a member in the Flowers Formation by H. J. Campbell from Northwest Nelson, New Zealand, but the identification needs to be confirmed, as the Nelson material comes from a fauna somewhat younger than the Oxtrack Formation.

Neilotreta gigoomganensis (Waterhouse, 2015b)

Fig. 47, 48

1976 *Neospirifer arthurtonensis* [not Waterhouse] – Waterhouse, p. 244, Fig. 6.5, 7.7.
2001 *N. arthurtonensis* [not Waterhouse], p. 91, pl. 6, fig. 5-7.
2015b *Betaneospirifer gigoomganensis* Waterhouse, p. 154, Fig. 75.

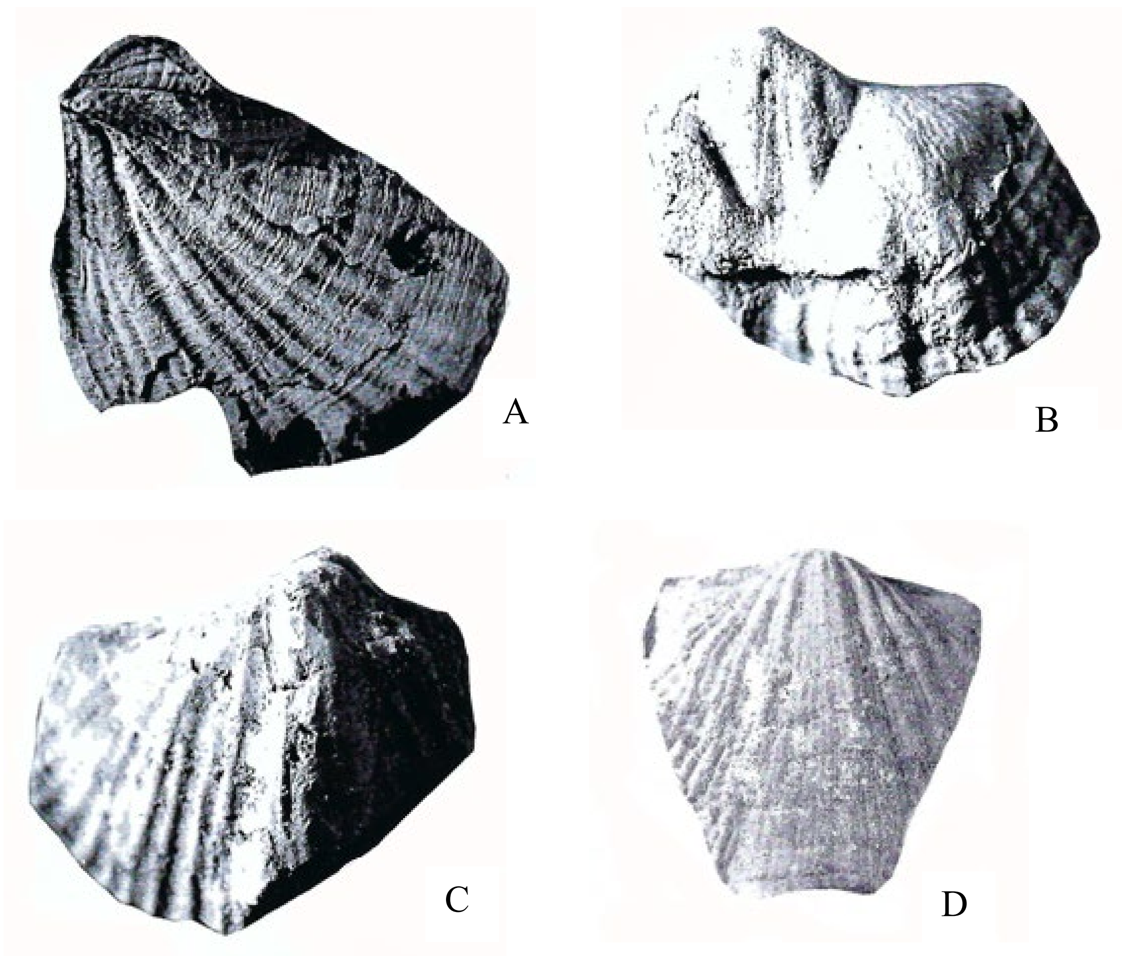


Fig. 47. *Neilotreta gigoomganensis* (Waterhouse). A, dorsal internal mould of OU 18282 from clastics of lower Glendale Formation, Wairaki Downs, Southland, New Zealand, x2. (Waterhouse 2001). B, dorsal valve BR 1764, x2 from Kildonan Member, Bagrie Formation, north Otago, New Zealand. C, dorsal internal mould of OU 18282 from clastics of lower Glendale Formation, Wairaki Downs, x2. (Waterhouse 2001). D, dorsal valve BR 1764, x2 from Kildonan Member, north Otago. (Waterhouse 1976).

Diagnosis: Hinge at maximum width and dorsal fold very broad, with rounded cross-profile. Seven pairs of plicae, inner four pairs costate.

Holotype: UQF 46697 figured in Waterhouse (2015b, Fig. 75) and Fig. 48A, B herein from Gigoomgan Limestone near Gympie, southeast Queensland.

Stratigraphy: The species is found in the Gigoomgan Limestone and in the Teebar Conglomerate northwest of Gympie in Queensland, and in New Zealand in the Kildonan Member of the Bagrie Formation from the Clinton-Waipahi region along the northern limb of the Southland Synclinorium and in the clastic part of the Glendale Formation at Wairaki Downs. These latter faunas, like those from near Gympie, are of Changhsingian age, and faunas include *Capillonia brevisulcus, Paucispinauria verecunda* and *Neilotreta gigoomganensis* (Waterhouse 2002, p. 65).

Fig. 48. *Neilotreta gigoomganensis* (Waterhouse). A, B, dorsal and ventral aspects of UQF 46697, holotype, x2. Gigoomgan Limestone, near Gympie, southeast Queensland. (Waterhouse 2015b).

***Neilotreta*? *browni* (**Waterhouse, 2015b)

Fig. 49

cf. 1978 ?*Neospirifer* sp. Waterhouse & Mutch, p. 521, Fig. 10, 11.
2015b *Koenigoria browni* Waterhouse, p. 144, Fig. 62-64.

Diagnosis: Small transverse shells with acute cardinal extremities, four pairs of plicae, relatively strong costae, primary costae remaining high especially on dorsal valve, ventral muscle field of moderate width, heavy posterior thickening.

Holotype: UQF 46673 figured by Waterhouse (2015b, Fig. 64A, B) and Fig. 49A, B herein, from the Gundiah Bridge Greywacke in the unpublished thesis by C. D. Brown (1964) in the Gigoomgan area near Gympie.

Morphology: This species does not have a subdelthyrial connector plate, and so belongs with Trigonotretoidea. Any umbonal callosity is inconspicuous. The plicae are well-defined, more than usual for other species of *Neilotreta*, although approaching those of *N. gigoomanensis* (see above) and the shell shape is distinctive with wide hinge and lateral slopes converging

Fig. 49. *Neilotreta*? *browni* (Waterhouse). A, B, holotype, dorsal and ventral aspects of UQF 46673, x 1. C, D, ventral and dorsal aspect of internal mould, UQF 46672, x1. Gundiah Bridge Greywacke near Gympie, southeast Queensland. (Waterhouse 2015b).

forwards more than usual. The reason for assigning the species tentatively to *Neilotreta* lies in the broad anterior and multicostate well-rounded dorsal fold, but exceptionality is marked by the narrowness of the fold posteriorly in some specimens, such as that figured in Fig. 49D. The New Zealand material agrees in general shape and well-defined plicae, but adds no significant detail.

As discussed below, this species was originally assigned to *Koenigoria* from Western Australia, but the type species *Neospirifer neoaustralis* Archbold & Thomas, 1986 appears to contain specimens of two different species, and the type specimen appears to be spiriferoid rather than trigonotretoid, as discussed below.

Stratigraphy: The informal unit called Gundiah Bridge Greywacke is correlative with the South Curra Limestone of Gympie, regarded as lower Changhsingian in age (Waterhouse 2015b). Poorly preserved but likely allied specimens BR 2226 and 2227 were reported from the Nemo Formation of Mutch (1972), correlative with the Hilton Limestone in the Wairaki Downs area of southern New Zealand.

The question of *Koenigoria*

Genus ***Koenigoria*** Waterhouse, 2004

Fig. 50 - 52

Diagnosis: Transverse shells markedly triangular outline, thanks to a very wide hinge, very deep anterior sulcus, three to five well developed plicae pairs, costate, fold wide anteriorly. Detail of the delthyrium in the type species appears to differ in different specimens, as discussed below,

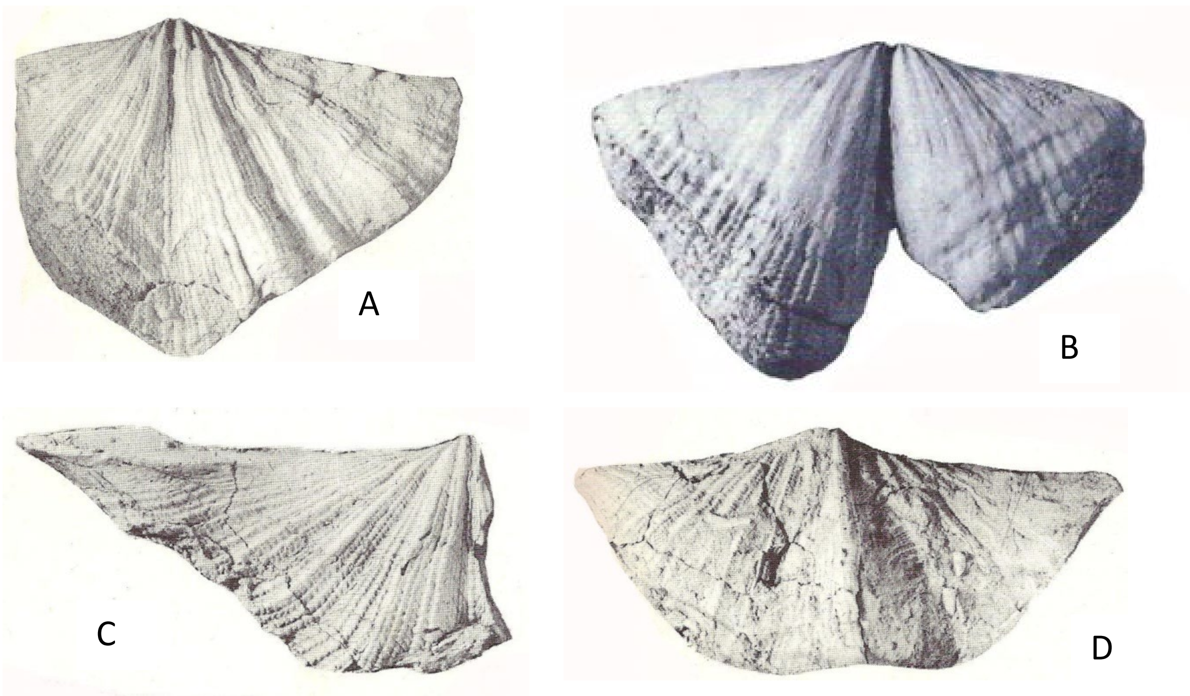


Fig. 50. *Koenigoria neoaustralis* (Archbold & Thomas). A, ventral view MUGDF 6575, x1, B, decorticated ventral valve GSWAF 11205 from Fossil Cliff Member, Perth Basin. See also Fig. 51B herein, x1. C, ventral valve, MUGDF 6573 x1. D, dorsal view, MUGDF 6572, x0.9. Specimens x1, from Callytharra Formation (Sakmarian), Western Australia. (Archbold & Thomas 1986).

leaving uncertainty about the affiliations of the type species, but suggests that two taxa were included in the original description of the type species.

Type species: *Trigonotreta neoaustralis* Archbold & Thomas, 1986, p. 152 from Callytharra Formation, Carnarvon Basin, Western Australia, OD.

Discussion: The genus ranged through much of the Permian Period in Western Australia.

In Archbold & Thomas (1986, Fig. 17B), as reproduced herein as Fig. 51B, a small arched plate lies across the upper delthyrium. Is this a neospiriferin cover plate? Or is it an arched subdelthyrial connector plate? Another specimen as figured by Archbold & Thomas (1986, Fig. 17L), reproduced in Fig. 51A, is surely a subdelthyrial connector plate. Yet two other specimens figured by Archbold & Thomas (1986, Fig. 16E, G), as reproduced in Fig. 51C, D,

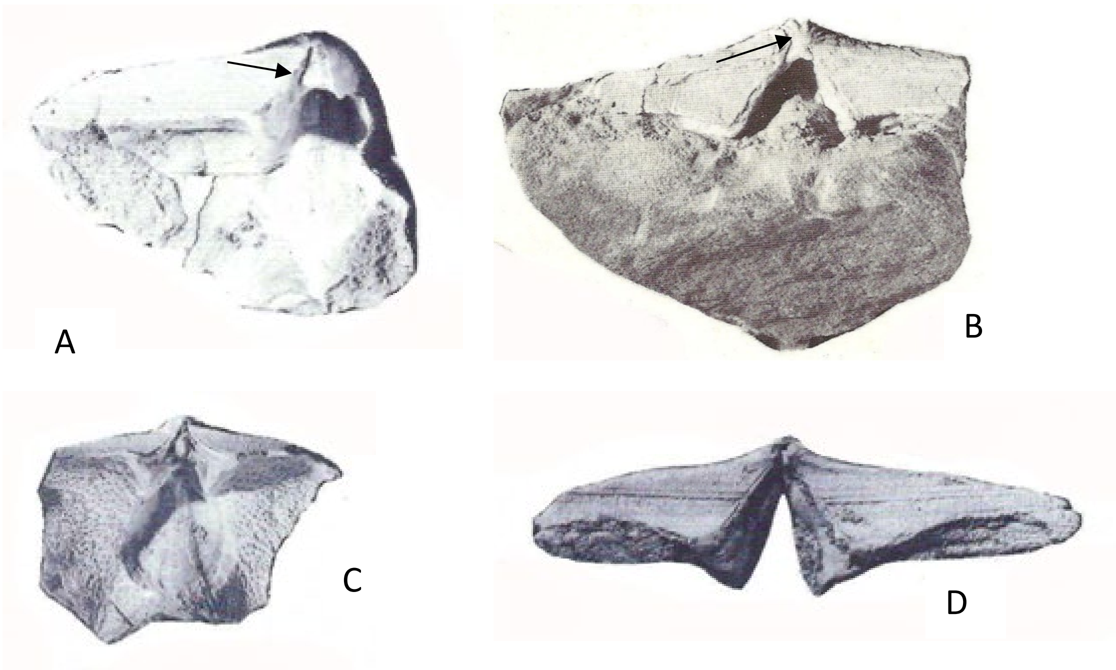


Fig. 51. *Trigonotreta neoaustralis* Archbold & Thomas. A, inner view of mature ventral valve MUGDF 6576 from Callytharra Formation with apparent subdelthyrial plate arrowed, as in Spiriferidae. B, posterior view of ventral valve MUGDF 6575 showing apparent arched delthyrial plate, arrowed. C, D, shells with umbonal callosity, as is common amongst Trigonotretoidea. C, inner view of ventral valve MUGDF 6568 from Callytharra Formation. D, inner view of ventral valve GSWAF 11205 from Fossil Cliff Formation. See Fig. 50B. Specimens x1 from Western Australia. (Archbold & Thomas 1986).

show an *Aperispirifer*-like delthyrium, with pleromal infilling and a modest umbonal callosity. This has implications, of which the major ones appear to be that on the one hand, two species were incorporated as *neoaustralis*, one spiriferin with connector plate and several well-defined plicae and the other with no connector plate, a small umbonal callosity, and large swollen inner pair of plicae, and less widely alate cardinal extremities, probably trigonotretid as signified by the Archbold & Thomas assignment of the species to *Trigonotreta*. Such a view is supported by what appears to be a strongly consistent difference in the delthyrial structures throughout world faunas between Trigonotretoidei and Spiriferidei. On the other hand, the differences may justify questions about the consistency and validity of delthyrial differences. In that case, *Koenigoria* may stand unchallenged, characterized by shape, and even by its variable delthyrium.

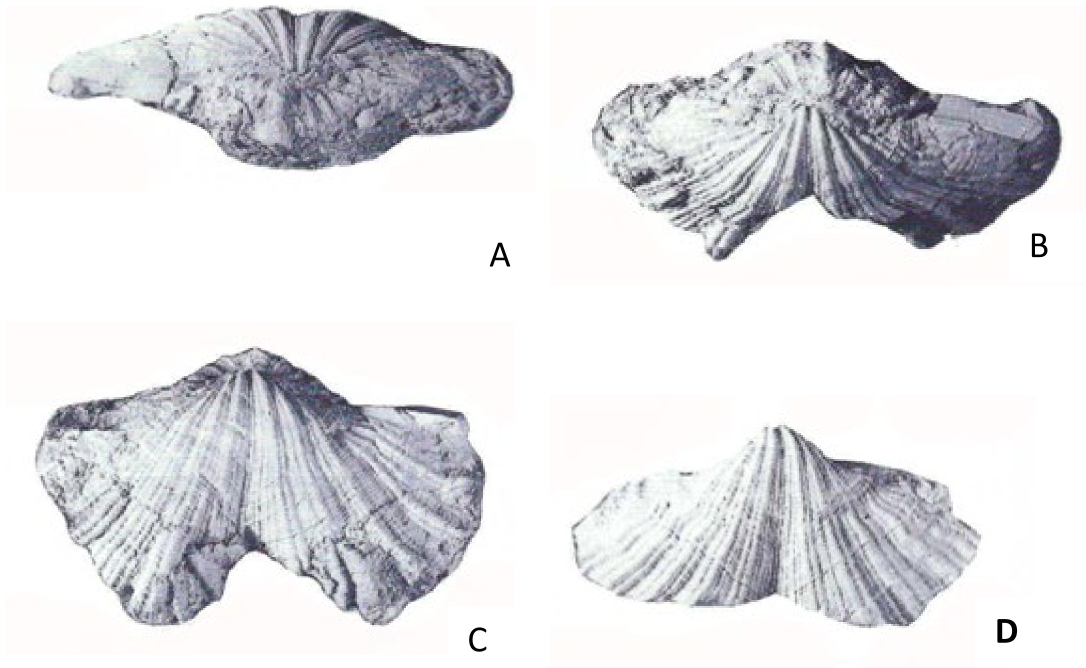


Fig. 52. *Koenigoria neoaustralis* (Archbold & Thomas). A, B, C, posterior and ventral aspects of holotype, GSWAF 1/4963a. D, crushed ventral ventral valve GSWAF 1/4963b. Specimens x1 from Callytharra Formation, Western Australia. (Archbold & Thomas 1986).

Most of the specimens show a consistent shape, and have a sulcal pair of plicae along the outer sulcus (Fig. 52A, B). The holotype itself has slightly rounded and only slightly protruding anterior lateral margins, but the growth lines indicate rather transverse and triangular shapes for the earlier growth stages. There is some difference from shells that bear a small umbonal callosity under the ventral umbo. These have slightly less sharply defined plicae, and the edges of the sulcus are defined by larger and wider swellings to form the innermost plicae with subsidiary subplicae.

Genus ***Sulciplica*** Waterhouse, 1968

Diagnosis: Transverse shells with numerous fine round-crested plicae over both valves, bearing several subplicae over sulcus and fold, cardinal extremities acute, micro-ornament cancellate, may suggest tiny pustules. Umbonal callus.

Type species: *Sulciplica transversa* Waterhouse, 1968 from mid-Permian of east Australia.

Sulciplica pauciplicus n. sp.

Fig. 53

2023 *Sulciplica transversa* [not Waterhouse] – Lee *in* Lee et al., p. 30, Fig. 13, 15R-V?, W-Z, AB, AH (part, not? 15AA?, AD-AG, Fig, 16A-I = *Angulispirifer jervisbayensis*?).

Diagnosis: Shaped like *Sulciplica transversa* but smaller and with fewer strong non-costate plicae in as few as six pairs, with much finer ribs laterally. Sulcal ribs much as in *transversa,* but less robust, fold ribs comparable to much fewer in number.

Holotype: AMF 159065 from Snapper Point Formation, figured in Lee et al. (2023, Fig. 15W, X) and herein as Fig. 53A, B. here designated.

Morphology: There are similarities in shape, ornament and interior to *Sulciplica transversa*, but the details of plicae differ, subtly perhaps, but nonethess in actualily. Lee *in* Lee et al.

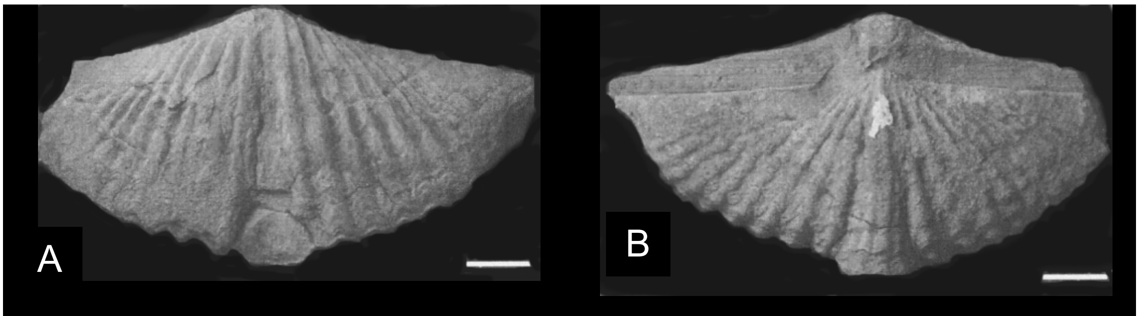


Fig. 53. *Sulciplica pauciplicus* n. sp. A, B, ventral and dorsal aspects of AMF 159065, holotype. C, dorsal aspect of AMF 159067. Snapper Point Formation. (Lee et al. 2023).

(2023) noted that the cancellate ornament was not visible, but as he cautioned, this might well be because of preservation.

Stratigraphy: The species is distinctly older than Tasmanian and other New South Wales occurrences of *Sulciplica*, but comes close in age to the occurrences of that species as recorded in the Moonlight Sandstone of the north Bowen Basin as described by Waterhouse & Jell (1983). The material figured by Waterhouse & Jell is close to typical *transversa,* but more specimens are needed to compare with the excellent figures of specimens provided by Clarke (1987).

Sulciplica? sp.

Fig. 54

1984 *Notospirifer* sp. H. J. Campbell et al., Fig. 6.7.

A small ventral valve shows fine plicae and two slender ribs within the sulcus. It is not particularly transverse, but arguably suggests an early form of *Sulciplica*, far from fully developed, and at an early growth stage. It comes from a boulder at Stephens Island that appears to have been derived from early Middle Permian deposits of the Brook Street Volcanic Arc in New Zealand, as discussed by Waterhouse (2021a). If that is correct, the appearance of a possible septum in the figure must be misleading.

Fig. 54. *Sulciplica*? sp., immature ventral valve BR 1637, x5, from Brook Street boulder at Stephens Island. (Campbell et al. 1984).

Sulciplica transversa Waterhouse, 1968

Fig. 55

1845 *Spirifer vespertilio* Sowerby – Morris, p. 282, pl. 17, fig. 1, 2 (part, not fig. 3 = *Angulispirifer phalaena*).
1849 *S. vespertilio* – Dana, p. 685, pl. 2, fig. 3a-c.
1877 *S. convolutus* [not Phillips] – Koninck, p. 187, pl. 12, fig. 2, pl. 13, fig. 3, a, ?b-c.
1888 *Spirifera convolutus* [not Phillips] – Johnston, pl. 12, fig. 1.
1968 *Sulciplica transversa* Waterhouse, p. 27 (part, not pl. 16, fig. 1, 4 = *Sulciplica vellai*).
1970 *Sulciplica transversa* – Armstrong, pl. 15, fig. 2.
?1983 *Sulciplica transversa* – Waterhouse & Jell, p. 243, pl. 2, fig. 2, 3.
1987 *Sulciplica transversa* – Clarke, p. 269, Fig. 6A-D, 7A-E, 8A-F.
2016 *Sulciplica transversa* – Waterhouse, Fig. 323A, B, ?C.

Diagnosis: Widely transverse with several strong subplicae over sulcus and fold, with or without median sulcal rib.

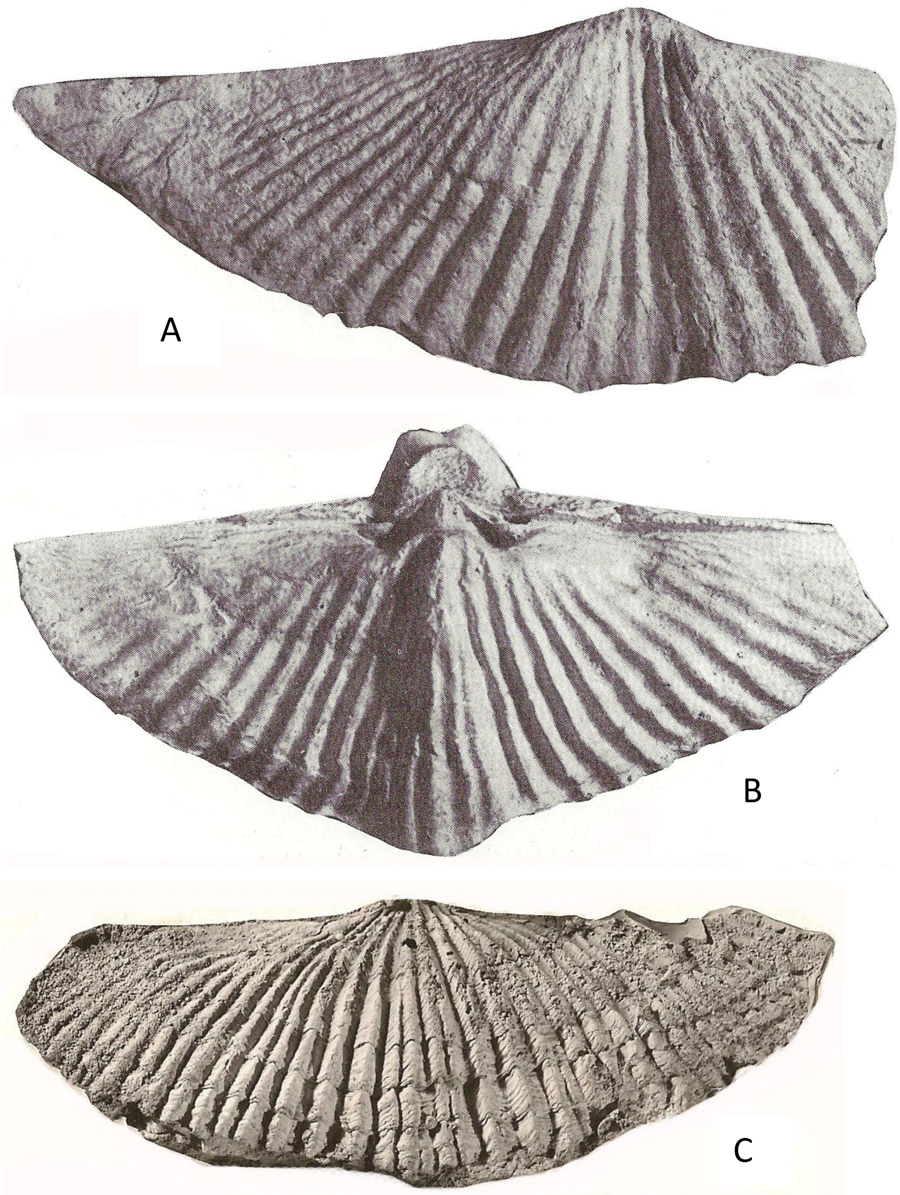


Fig. 55. *Sulciplica transversa* Waterhouse. A, ventral valve exterior, x1. B, dorsal interior, x1. From mid-Guadalupian of Eagle Hawk Neck, Tasmania. (Clarke 1987). C, dorsal exterior, x1.3. From Moonlight Sandstone, Blenheim Group, Queensland. (Waterhouse & Jell 1983).

Holotype: USNM 3596 figured by Dana (1849, pl. 2, fig. 3a, b) from Gerringong Volcanics at Black Head, south Sydney Basin, OD.

Morphology: Minor variations in morphology have been addressed by Clarke (1987) and Waterhouse (1968). The number of plicae in Tasmanian specimens of *transversa* is given as twenty four to thirty six by Clarke (1987).

Stratigraphy: The Gerringong Volcanics are more or less mid-Guadalupian in age, approximately Wordian, and Clarke (1987) has reported the species in the middle and late Lymingtonian faunas of Tasmania. Slightly older specimens close to *transversa* are recorded from the Moonlight Sandstone of the north Bowen Basin in Waterhouse & Jell (1983), but more specimens would be desirable for a confident identification.

Sulciplica vellai Waterhouse, 1999

Fig. 56

1965 "*Spirifer*" aff. *vespertilio* Dana not Sowerby – Waterhouse & Vella, p. 66, pl. 3, fig. 1, 2, 3,5.
1968 *Sulciplica transversa* [not Waterhouse] – Waterhouse, p. 25, pl. 16, fig. 8, 10.
1998 *S. transversa* [not Waterhouse] – H. J. Campbell et al., p. 292.
1999 *Sulciplica vellai* Waterhouse, p. 17.

Diagnosis: Large transverse shells with close to twenty pairs or more of relatively fine plicae, crests rounded. Sulcal subplicae strong, numbering up to three pairs.

Holotype: Specimen (without published registration number and kept at Victoria University Department of Geology, with registration number prefixed by V) as figured in Waterhouse & Vella (1965, pl. 3, fig. 4) and Fig. 56A herein from Flowers Formation, west Nelson, New Zealand, OD.

Morphology: As noted by Archbold (1995), the plicae are finer with more rounded crests than in *Sulciplica transversa*.

H. J. Campbell in Campbell et al. (1998) identified specimens from northwest Nelson from the same beds, and these have yet to be described. He also listed material as *Fusispirifer* that might prove to belong to the same species, but these have yet to be described or adequately documented.

Stratigraphy: The species comes from the *Echinalosia* (*Unicusia*) *minima* Zone, deemed to be of Capitanian age (Waterhouse 2022b).

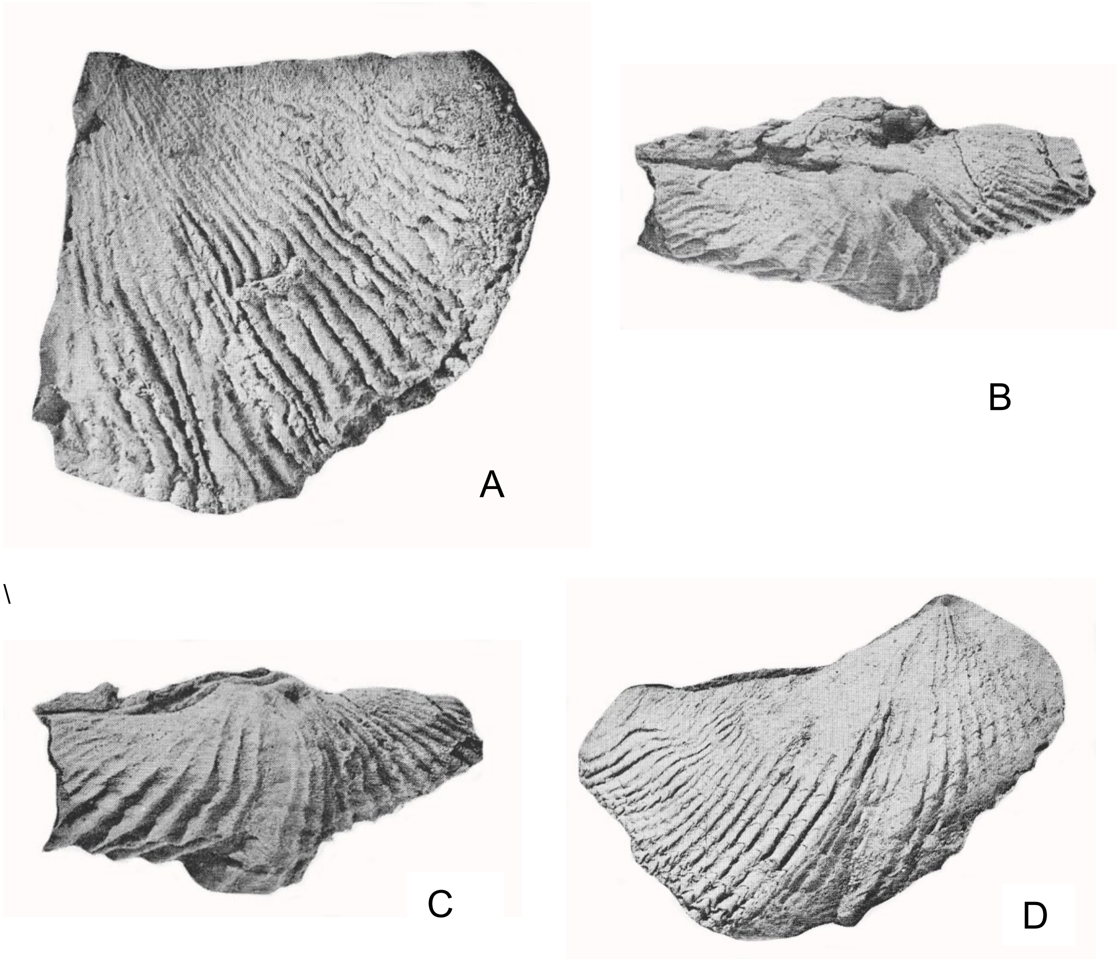


Fig. 56. *Sulciplica vellai* Waterhouse. A, ventral valve, holotype. B, dorsal internal mould of dorsal valve. C, dorsal internal mould. D, ventral valve. Specimens x1 from Flowers Formation, Nelson, kept at Department of Geology, Victoria University, Wellington. (Waterhouse & Vella 1965).

Genus ***Tasmanospirifer*** Waterhouse, 2016

Diagnosis: Weakly transverse with rounded cardinal extremities, and eight to ten pairs of plicae, bearing subangular to rounded crests, fold and sulcus moderately defined, with a few pairs of subplicae, micro-ornament cancellate. Open delthyrium, umbonal callosity which lie on shelf, dental plates, short adminicula; ctenophoridium, crural plates, no tabellae. Spiralia transverse, reticulate mantle canal system.

Type species: *Tasmanospirifer clarkei* Waterhouse, 2016 from Berriedale Limestone (Aktastinian) of Tasmania, here designated.

Discussion: This genus has more and finer plicae than those of *Unicostatina* from east Australia, and has fewer plicae and is much less transverse than Guadalupian genera *Angulispirifer*, *Georginakingia* and *Sulciplica*. Of the genera now placed in Georginakingiidae, *Tasmanospirifer* comes close to *Cancellospirifer* Campbell, which is known as a single species in the western Bowen Basin (see p. 121), and the possible relationship needs to be more closely assessed. But the fold and sulcus of *Tasmanospirifer* has more subplicae than in *Cancellospirifer.*

Tasmanospirifer clarkei Waterhouse, 2016

Fig. 57, 58

1968 ''*Spirifer*'' *tasmaniensis* [not Morris] – Armstrong, pl. 6, fig. 8-12 (part, not fig. 7 = *tasmaniensis* Morris).
1979 *S. tasmaniensis* – Clarke, p. 206, pl. 4, fig. 1-4, 9 (part, not fig. 5-8 = *tasmaniensis* Morris).
2016 *Tasmanospirifer clarkei* Waterhouse, p. 254, Fig. 326.

Diagnosis: Weakly transverse with subangular plicae and rare additional costae.

Holotype: TMF 36817, figured by Clarke (1979, pl. 4, fig. 2) and herein Fig. 57A, from the Berriedale Limestone at Granton's Quarry, Tasmania, OD.

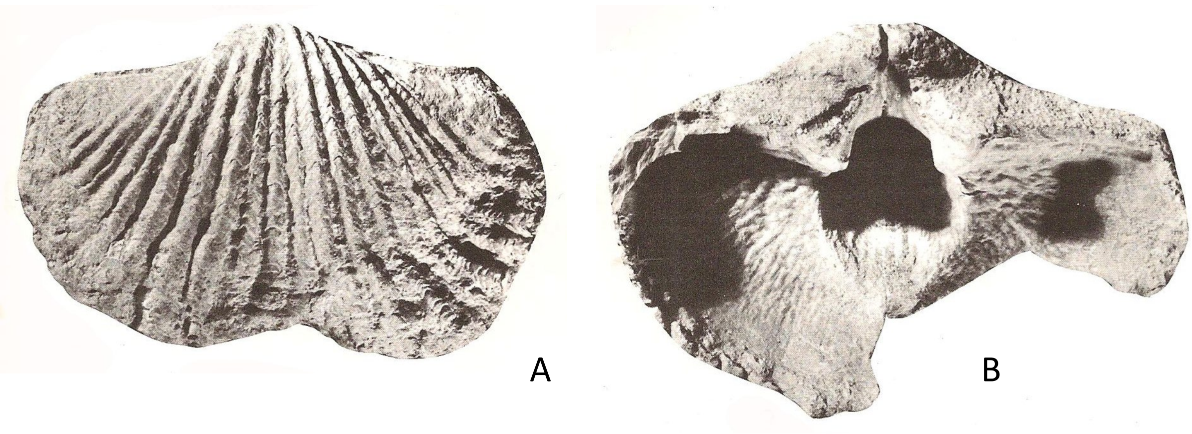


Fig. 57. *Tasmanospirifer clarkei* Waterhouse. A, ventral valve holotype TMF 36817. B, interior view of ventral valve, with delthyrial shelf and low callosity. Specimens x1, from Berriedale Limestone, Tasmania, Australia. (Clarke 1979).

Morphology: This species has been described, chiefly by Clarke (1987), together with *tasmaniensis*, and is distinguished by its larger size, and subangular plicae, whereas the plicae of *tasmaniensis* Morris (1845, p. 280, pl. 15, fig. 3) have more rounded crests, and also tend to have fewer sharply defined adventitious costae. The species *tasmaniensis* comes from beds younger than the Berriedale Limestone, in an unnamed limestone at Eastern Marshes, rated by Clarke (1979) as mid-Lymingtonian Stage in his local stage scheme for Tasmanian Permian, as compared with his Bernacchian Stage for the Berriedale Limestone. The comparative ages are early Artinskian for *clarkei,* and either Kungurian or Roadian for *tasmaniensis*.

Stratigraphy: This species typifies the Berriedale Limestone of Tasmania.

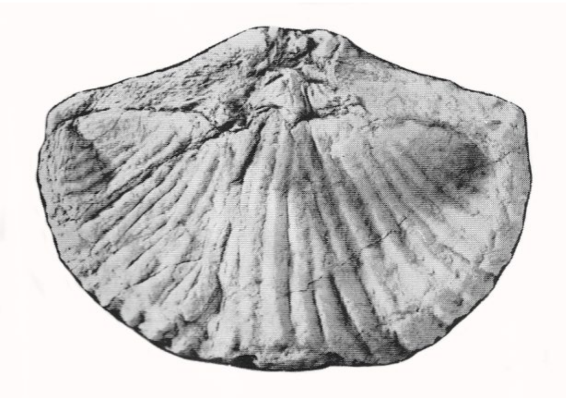


Fig. 58. *Tasmanospirifer clarkei* Waterhouse, dorsal aspect of UQF 29926 x1 from Berriedale Limestone. (Armstrong 1968).

Tasmanospirifer tasmaniensis (Morris, 1845)

Fig. 59

1845 *Spirifer tasmaniensis* Morris, p. 280, pl. 15, fig. 3.
1953 *Trigonotreta stokesi* [not Koenig] – Brown, pl. 5, fig. 5 (part, not fig. 1-4 = *stokesi*).
1968 *S. tasmaniensis* – Armstrong, p. 84, pl. 6, fig. 7 (part, not fig. 8-12 = *clarkei*).
1979 *Sulciplica tasmaniensis* – Clarke, p. 206, pl. 4, fig. 5-8 (part, not fig. 1-4, 9 = *T. clarkei*).
2016 *Tasmanospirifer tasmaniensis* – Waterhouse, p. 253, Fig. 327.

Diagnosis: Medium-sized shells, plicae numerous, with crests a little more rounded than in *clarkei.*

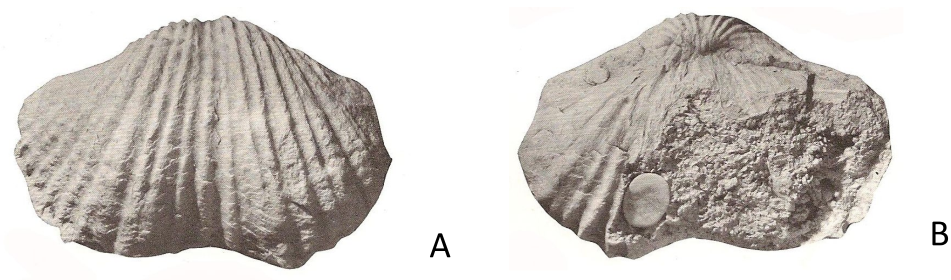


Fig. 59. *Tasmanospirifer tasmaniensis* (Morris), lectotype BB 6246, x1. A, ventral view. B, dorsal view. From unnamed limestone at Eastern Marshes, Tasmania, Australia. (Clarke 1979).

Lectotype: BB 4794, figured by Morris (1845, pl. 15, fig. 3), Brown (1953, pl. 5, fig. 1), Armstrong (1968, pl. 6, fig. 7), Clarke (1979, pl. 4, fig. 5-8) and herein (Fig. 59), from mid-Lymington Stage of Clarke (see 1979), SD Etheridge 1902, p. 66).

Morphology: The species is compared with *clarkei* in the preceeding text

Stratigraphy: The species occurs in what Clarke (1979) called mid-Lymingtonian Stage, approximately Roadian and perhaps lower Wordian in age in Tasmania.

Genus ***Unicostatina*** Waterhouse, 2004

Diagnosis: Moderately large transverse shells with well-rounded cardinal extremities, few strong plicae and a mid-sulcal costa as a rule, may be joined by further costae within the sulcus and over the fold. Interior as in other genera of Georginakingiidae. Umbonal callosity may be massive.

Type species: *Sulciplica subglobosa* Clarke, 1990, p. 64 from “Spirifer Zone” (Asselian), Darlington, Maria Island, Tasmania, OD Waterhouse, 2004, p. 184.

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 rib. 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 Georginakingiidae, and secondary thickening is heavy posteriorly in the ventral valve. Member species are much larger than those of *Cancellospirifer* and have a somewhat thickened ventral valve and more transverse and alate outline and fewer plicae pairs. *Brachythyrinella* (see p. 90) has a distinct fold channel, and *Neilotreta* has a much wider and more costate dorsal fold (see p. 125).

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 Trigonotretidei, whereas choristitids normally have conspicuous adminicula and tabellae, and differ in plication-costation, micro-ornament and delthyrium.

Unicostatina crassa (Clarke, 1990)

Fig. 60

1990 *Sulciplica crassa* Clarke, p. 64, Fig. 8A-N.
1992 *S. crassa* – Clarke, p. 19, Fig. 8A-N.
2004 *Unicostatina crassa* – Waterhouse, p. 184.
2015a *U. crassa* – Waterhouse, p. 204.

Diagnosis: Weakly transverse shells with six to seven plicae pairs, median sulcal rib well developed, with a few additional ribs in some specimens, fold ribbing not recorded. Growth laminae and radial fine ribs, posterior lateral shell heavily thickened, apex of delthyrium with bulbous callist.

Holotype: GST 14127 from Early Permian "Spirifer Zone" at Maria Island, Tasmania, figured by Clarke (1990, Fig. 9G; 1992, Fig. 9G), OD.

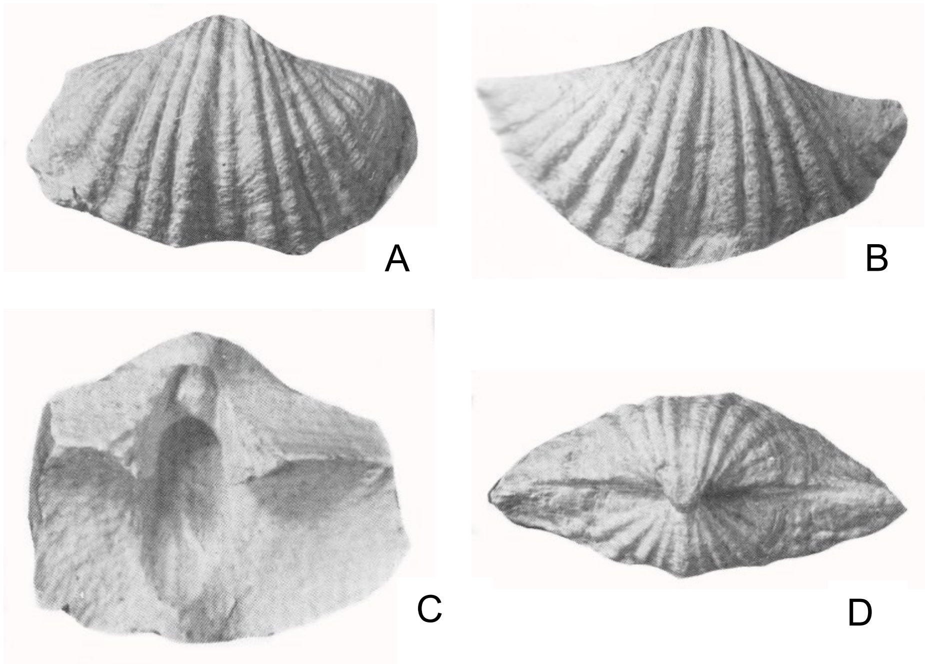


Fig. 60. *Unicostatina crassa* (Clarke). A, ventral valve GST 14124, B, ventral valve GST 14123. C, ventral valve interior, GST 14136. D, posterior view of GST 14134. Specimens x1 from "Spirifer Zone", Maria Island, Tasmania. (Clarke 1990).

Morphology: Archbold (2003) reported the species from the Cranky Corner Sandstone at Cranky Corner in New South Wales, as figured in Fig. 65. He showed more completely preserved dorsal valves, which features a rounded fold as in Clarke's species. But the ventral sulcus of Clarke's material has traces of an inner rib along the inner side of the bordering plication, not seen in Cranky Corner specimens, and a strong central rib, although a fine rib is visible that is a little offset from the mid-line in specimens from Cranky Corner. The significance of these differences is not securely established, but it does seem likely that Archbold's specimens should be re-identified with *Unicostatina stutchburii*, because it also has fine costae over the sulcus and fold of at least some specimens. Archbold took no account of Etheridge's species. See p. 145. Although Lee *in* Lee et al. (2023, p. 32) referred the type species *subglobosa* to *Tasmanospirifer*, this latter genus has more and finer plicae and a much less conspicuous dorsal fold, and lacks the prominent mid-sulcal rib.

Stratigraphy: The species is recorded from the "Spirifer Zone" of Maria Island and Swifts Jetty Sandstone, upper Bundella Mudstone and other localities of similar age in Tasmania, as specified by Clarke (1990, 1992).

Unicostatina subglobosa (Clarke, 1990)

Fig. 61

1990 *Sulciplica subglobosa* Clarke, p. 64, Fig. 9A-M.
1992 *S. subglobosa* – Clarke, p. 21, Fig. 9A-M.
2004 *Unicostatina subglobosa* – Waterhouse, p. 184.
2023 *Tasmanospirifer subglobosa* Lee *in* Lee et al., p. 32.

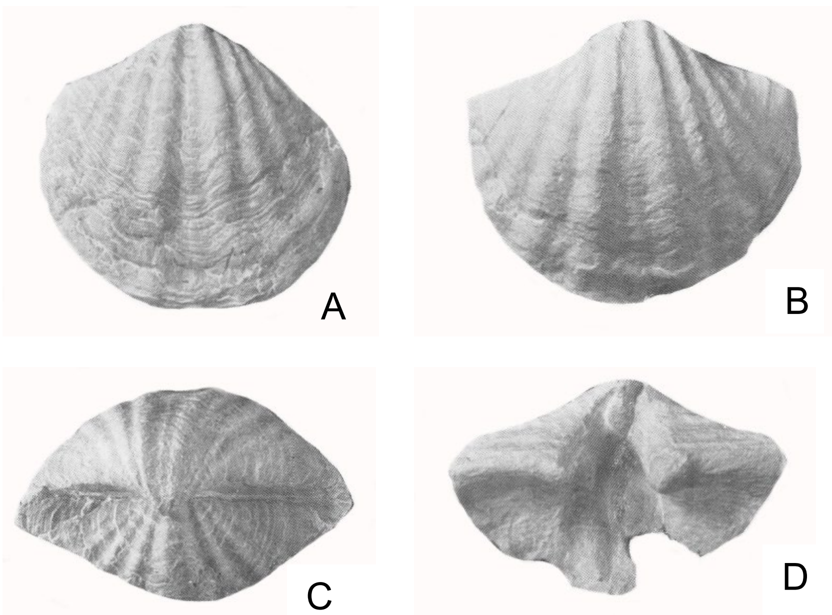


Fig. 61. *Unicostatina subglobosa* (Clarke, 1990). A, ventral valve GST 14138. B, ventral valve GST 14139. C, posterior view of 14146. D, posterior aspect of ventral interior, GST 14148. Specimens x1 from "Spirifer Zone", Maria Island. (Clarke 1990).

Diagnosis: Small to medium size, four or five plicae pairs, sulcus with weak median rib, fold without any rib or plication. Radial capillae said to be lacking.

Holotype: GST 14137 from "Spirifer Zone" at Maria Island, figured in Clarke (1990, Fig. 9L; 1992, Fig. 9L) from the "Spirifer Zone", Maria Island, Tasmania.

Stratigraphy: The species is found only at the one locality.

Unicostatina stutchburii (Etheridge, 1892)

Fig. 62, 63, 64?

1892 *Spirifera stutchburii* Etheridge, p. 232, pl. 38, fig. 4-6.
1968 *Sulciplica stutchburii* – Waterhouse, p. 24.
1970 *Sulciplica stutchburii* – Armstrong, p. 205, pl. 15, fig. 1.
2004 *S. stutchburii* or *Unicostatina*? – Waterhouse, pp. 183, 184.
2015a *Unicostatina stutchburii* – Waterhouse, p. 201, Fig. 152-158.
2015b *U. stutchburii* Waterhouse & Balfe *in* Waterhouse, p. 103. p. 64, Fig. 8A-N;

Diagnosis: Comparatively small transverse shells with six to eight pairs of plicae, tending to

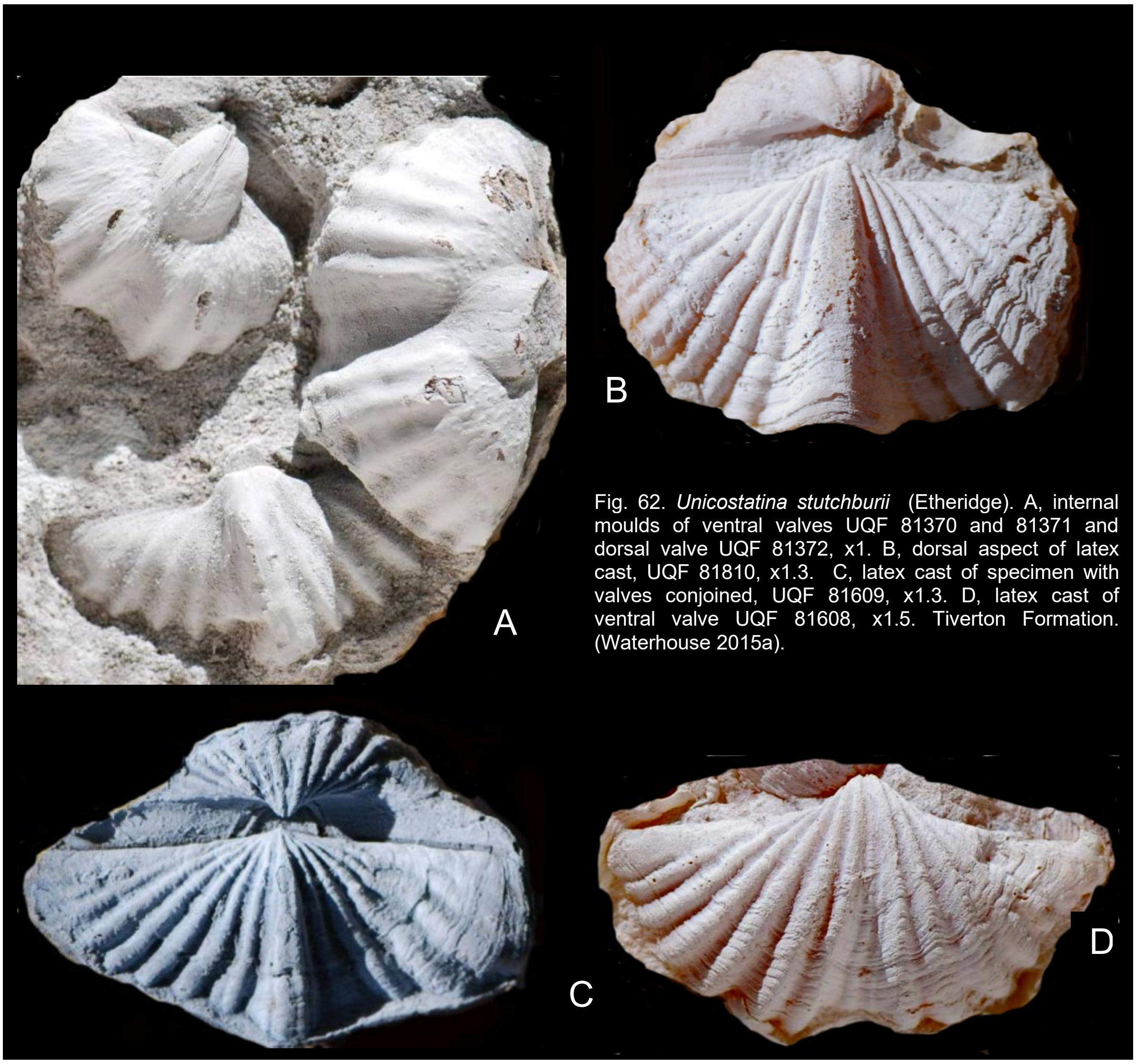


Fig. 62. *Unicostatina stutchburii* (Etheridge). A, internal moulds of ventral valves UQF 81370 and 81371 and dorsal valve UQF 81372, x1. B, dorsal aspect of latex cast, UQF 81810, x1.3. C, latex cast of specimen with valves conjoined, UQF 81609, x1.3. D, latex cast of ventral valve UQF 81608, x1.5. Tiverton Formation. (Waterhouse 2015a).

have subrounded crests, deep sulcus with central rib and in some shells, two faint lateral costae; fold may also show faint costae.

Fig. 63. *Unicostatina stutchburii* (Etheridge). A-C, dorsal, lateral and ventral aspects of internal mould of conjoined specimen, holotype. Mt Britton Gold Field, Tiverton Formation, north Bowen Basin. (Etheridge 1892).

Holotype: Sole specimen figured by Etheridge (1892, pl. 38, fig. 4-6) and herein as Fig. 63A-C from Tiverton Formation, SD Waterhouse (1968, p. 24). Kept at Queensland Museum, Brisbane.

Morphology: The Tiverton specimens are slightly younger, Sakmarian, rather than the Asselian species named by Clarke (1990, 1992). Shape is more transverse. The fold of the dorsal valve of the Tasmanian species is poorly known, and the fold for Cranky Corner

Fig. 64. *Unicostatina* from the Cranky Corner Sandstone. A, CPC 35342 x1.5, ventral valve. B, C, latex cast and dorsal internal mould, CPC 35341, x1.5. These were identified with *crassa*, but there are traces of costae in the sulcus and fold, as in the species *stutchburii.* Cranky Corner Sandstone. (Archbold 2003).

specimens, identified by Archbold (2003) with *crassa*, is well-rounded, and signs of fine costae are visible over sulcus and fold (Archbold 2003, Fig. 5.15, 16, 18), reminiscent of the sulcus and fold of many specimens of *stutchburii*.

Stratigraphy: The species is found in the middle Tiverton Formation of the north Bowen Basin, and it would seem possible, the Cranky Corner Formation at Cranky Corner, New South Wales**.** Cranky Corner individuals are transverse with comparable number of plicae, approaching *stutchburii,* and like these have one or two fine costae over the sulcus and fold of some specimens.

Unicostatina chatsworthensis (Balfe & Waterhouse *in* Waterhouse, 2004)

Fig. 65

1969 "*Spirifer*" cf. *stutchburii* [not Etheridge Jnr] – Runnegar & Ferguson, pl. 3, fig. 1-4.
1987 *Sulciplica* n. sp. Waterhouse & Balfe, p. 32, pl. 2, fig. 7-11.
2004 *Sulciplica chatsworthensis* Balfe & Waterhouse *in* Waterhouse 2004, p. 182.
2015b *Unicostatina chatsworthensis* – Waterhouse, p. 100, Fig. 32, 33.

Diagnosis: Three sulcal costae of moderate strength, may subdivide, three to five pairs of lateral plicae in ventral valve, with two or three further pairs laterally. Pair of subplicae on outer flanks of sulcus and fold; wide sulcus.

Holotype: UQF 454266 from South Curra Limestone, Gympie, figured by Runnegar & Ferguson (1969, pl. 3, fig. 2), OD.

Morphology: Shells transverse, length-width ratio about 0.5, but variable. Shell biconvex, dorsal valve less inflated than ventral valve. Ventral umbo slightly incurved, innermost pair of ventral plicae lies within sulcus as a rule, and plicae are high with narrow subangular crests, unlike the more rounded crests of older species. The dorsal fold is high and narrow, and may bear a crestal furrow. A subsidiary pair of plicae lies on fold, and usually three to five pairs of plicae lie over dorsal flanks. Ribs are strong in the sulcus and fold, and the sulcal bordering plication may also be ribbed. Micro-ornament is of radial and commarginal threads, with intersections raised in small knob-like protuberances.

Compared with *Unicostatina stutchburii* (Etheridge), *chatsworthensis* has a broader ventral sulcus with different sulcal costation. In *stutchburii* the median rib is stronger than in the new species, lateral sulcal plicae are much less strongly developed, and subsidiary costae arising from lateral sulcal plicae are more strongly developed in *chatsworthensis*.

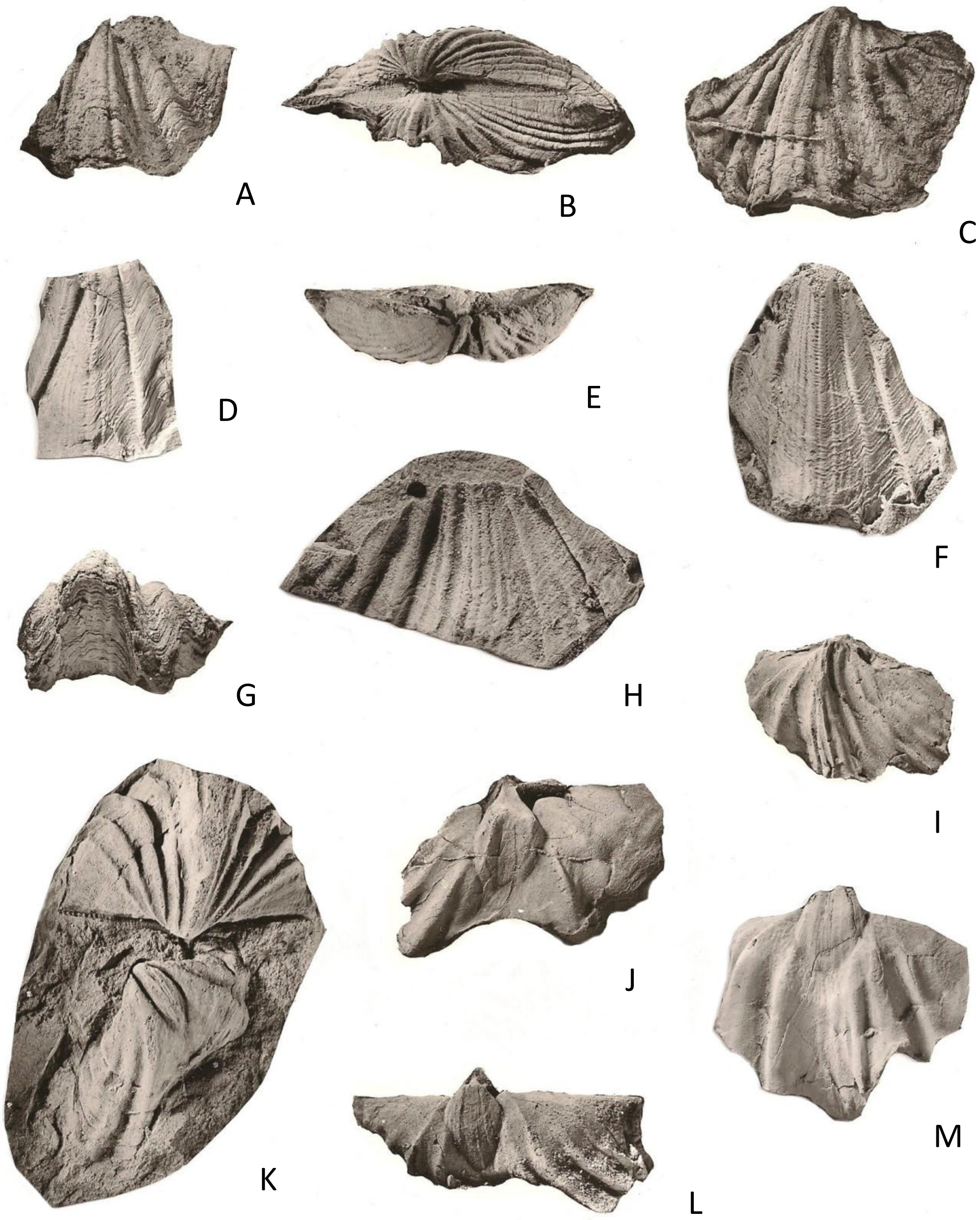


Fig. 66. *Unicostatina chatsworthensis* (Balfe & Waterhouse). A, latex cast of dorsal valve UQF 69262. B, posterior view of latex cast of specimen with valves conjoined, UQF 69281. C, latex cast of dorsal valve UQF 69301. D, ventral external mould of anterior sulcus, UQF 45428. E, posterior view of latex cast of ventral valve UQF 69188. F, anterior ventral mould UQF 45576. G, anterior view of latex cast of both valves UQF 69262, dorsal valve on top. H, ventral anterior external mould UQF 76951. I, dorsal internal mould UQF 69265. J, ventral internal mould UQF 69281. K, ventral internal mould UQF 45378 and dorsal internal mould UQF 59591. L, ventral internal mould UQF 45577. M, ventral internal mould UQF 69279. Specimens x0.9. South Curra Limestone. (Waterhouse 2015b).

Lateral plicae are lower. Over the ventral interarea, cardinal lineations produce a scalloped effect in *chatsworthensis*, but in *stutchburii* lineations on the interarea are quite straight.

Stratigraphy: The species is found in the South Curra Limestone near Gympie, southeast Queensland, of early mid-Changhsingian age.

?Superfamily **PAECKELMANNELLOIDEA** Ivanova, 1972

[Nom. correct. Waterhouse 2004, p. 227 ex Paeckelmanelloidea Carter *in* Carter et al. 1994, p. 347 pro Paeckelmannellacea Ivanova 1981, p. 22 nom. transl. ex Paeckelmannellidae Ivanova, 1972, p. 401]. Paeckelmannelloidea was named after W. Paeckelmann, but the family group name was mis-spelled by Carter (2006b, pp. 1812, 1818, and *in* Carter et al. 1994), by not following Licharew (1934, p. 212).

Poletaev (2001, p. 42) has revised the nature of Strophopleuridae, as reviewed in Waterhouse (2016, p. 151 ff.), in reporting that adminicula were missing from *Strophopleura*. This is not a massive change, because the adminicula are very short or have not been found in a number of other genera assigned to the superfamily in the *Revised Brachiopod Treatise* by Carter (2006b).

The placement of Pterospiriferinae Waterhouse, 1975 appears more contentious. Whereas *Paeckelmannella* has a median ventral septum and often a median prominent sulcal rib and high narrow dorsal fold, these features are absent from *Pterospirifer* and allies. Certainly the shell is highly transverse like *Paeckelmannella*, but so are some members of Georginakingiidae. The adminicula are short, but not unduely so. The interior of Pterospiriferinae is essentially the same as that of Neospiriferoidea, and the shell shape with its sulcus, fold, plicae, costae and micro-ornament and internal plates are neospiriferid. The question is then whether Pterospiriferinae should be regarded as a transverse development within that superfamily, rather than a member of Paeckelmannelloidea. There is no connector plate in either Pterospiriferinae or in Paeckelmannelloidea, signifying a relationship to Neospiriferoidea rather than Spiriferoidea.

Family **PTEROSPIRIFERIDAE** Waterhouse, 1975

[Nom. transl. hic ex Pterospiriferinae Waterhouse, 1975, p. 15].

Pterospiriferinae was included as a subfamily within Strophopleuridae by Carter (2006b), but may also be regarded as a transverse suite within Neospiriferidae.

Genus ***Pteroplecta*** Waterhouse, 1978

Diagnosis: Transverse multiplicate shells with sulcus, fold and plicae developing costae as a rule, prominent commarginal laminae. Adminicula, dental plates, no subdelthyrial connector plate or median septum; socket and crural plates, no tabellae or median septum.

Type species: *Pteroplecta laminatus* Waterhouse, 1978, p. 86 from Nisal Member, Senja Formation (Changhsingian) of west Nepal, OD.

Discussion: *Pterospirifer* Dunbar, 1955, p. 129, based on *Spirifer alatus* Schlotheim, 1816 from the Zechstein of Europe, has a broad sulcus bearing only a slender central rib, and plicae have no costae, unlike the ornament in *Pteroplecta*. *Pterospirifer terechovi* (Zavodowsky, 1968) has three faint sulcal costae, but the plicae are simple as in *alatus*. Neither of these genera bear a subdelthyrial connector plate, as far as can be determined, whereas genus *Johncarteria* Waterhouse, 2004, p. 230 displays a well-developed subdelthyrial connector plate, clearly shown for the type species by Cooper & Grant (1976, pl. 625, fig. 24, 27, 28), and therefore unlikely to belong to Pterospiriferinae, with similarities to that subfamily due to convergence from a spiriferoid source, such as Sergospiriferinae Carter in Carter et al. (1994). *Celsifornix* Carter, classed in the Pterospiriferinae by Carter (2006b), also should be shifted to Sergospiriferinae.

Pteroplecta blakei Waterhouse, 2021c

Fig. 67, 68

2021c *Pteroplecta blakei* Waterhouse, p. 131, Fig. 19 -21.

Diagnosis: Transverse shells with well-formed numerous plicae becoming costate anteriorly, sulcus and fold costate for much of the length. Commarginal laminae well-developed. Ventral muscle field broad.

Holotype: UQF 13580 from Lakes Creek Formation, east Queensland, figured by Waterhouse (2021c, Fig. 19C-F, 21A-C) and herein as Fig. 67C-F, 68B, C, OD.

Morphology: This species is close to *Pteroplecta laminatus* Waterhouse (1978, p. 86, pl. 13, fig. 9-16) [fig. 8 belongs to *Sulcispiriferina plicata* Waterhouse & Gupta, 1981] from the Changhsingian Nisal Formation of west Dolpo, western Nepal, but has a greater number of plicae pairs. The fold in the Dolpo specimens is narrow and high, except for that of pl. 13, fig. 9, whereas it is broad and close to that of the present material in specimens recorded from the Galte Member of Changhsingian age in north-central Nepal in Waterhouse & Chen (2007, pl. 8, fig. 4-7). *Pteroplecta joharensis* (Diener, 1897, pl. 4, fig. 3) from the Productus Shale of Wuchiapingian age in the Lissar Valley in the Indian Himalaya is more costate with better-defined sulcus and fold.

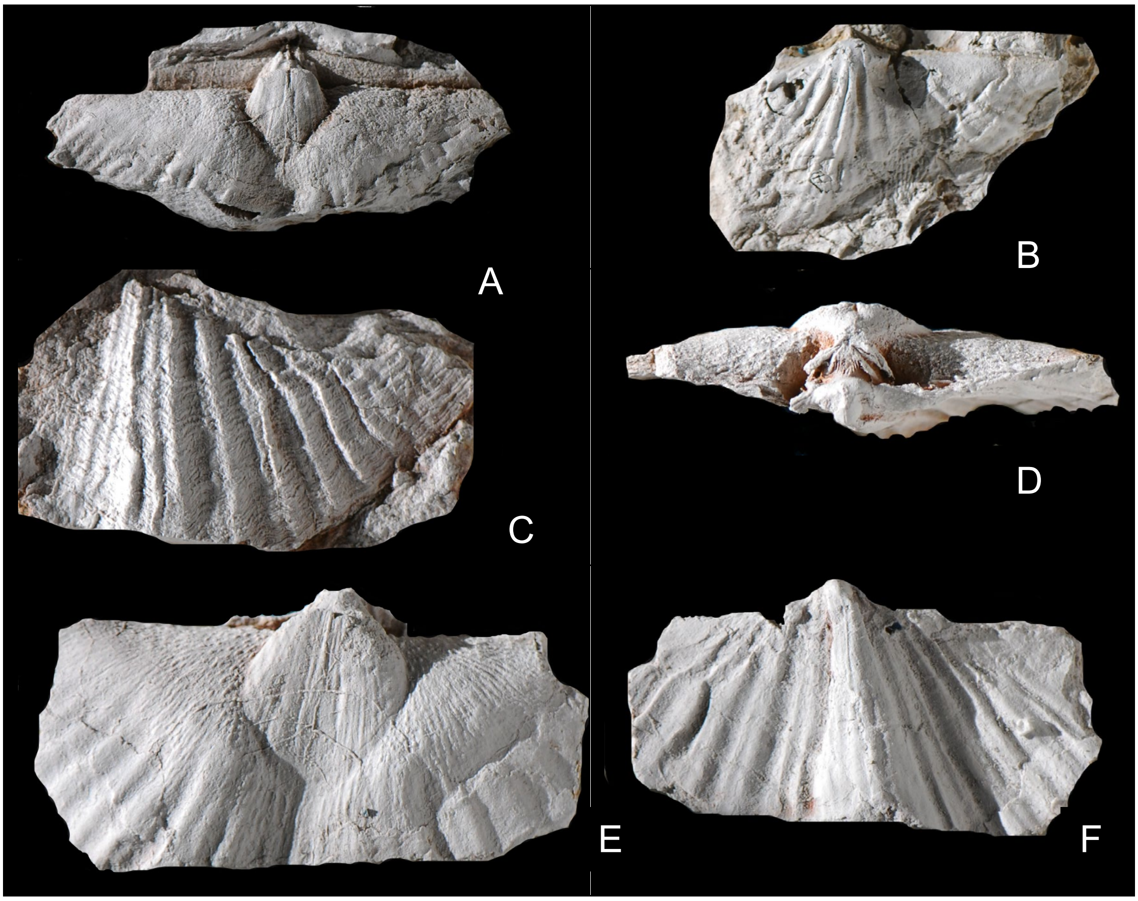


Fig. 67. *Pteroplecta blakei* Waterhouse. A, ventral internal mould UQF 13589. x1. B, dorsal valve UQF 82610, x1.5. C-F, holotype UQF 13580, x1.5. C, external mould of dorsal valve, the fold lying to extreme left. D-F, posterior (ventral valve on top), ventral and dorsal aspects, x1.5. Lakes Creek Formation. (Waterhouse 2021c).

Another Late Permian species slightly older than the type, *P. sulcata* Waterhouse (1983b, p. 132, pl. 5, fig. 8-18, pl. 6, fig. 1-4) from the Pija Member of north-central Nepal, and mislabelled *laminatus* in Waterhouse (2016), shows a distinctly narrower sulcus and narrow fold, broader than that of *laminatus*, and plicae are as numerous, but narrower than in the present form.

Fig. 68. *Pteroplecta blakei* Waterhouse. A, latex cast of external mould for dorsal valve (see Fig. 67B), x2. B, C, ventral external mould and cast. Holotype UQF 13580, x1.5. Lakes Creek Formation. (Waterhouse 2021c).

Stratigraphy: This species of *Pteroplecta* comes from the Lakes Creek Formation of eastern Queensland and is judged to belong to the *Taeniothaerus subquadratus* Zone, of upper Sakmarian age. It is much older than previously known species of the genus, Sakmarian as against Lopingian, and as an isolated and rare form, suggests that much of the history of the genus remains hidden. Two other members of Pterospiriferinae are of Early Permian age, named *Spiriferinaella* Fredericks, 1926 with rather high borders to the sulcus, and

Haplospirifer Li & Gu, 1976 with costate as well as plicate flanks and smooth sulcus and fold (see Carter 2006b).

?Suborder **DELTHYRIDINA** Ivanova, 1972

Fig. 69

There are no definite occurrences of brachiopods belonging to this suborder in the Permian faunas from east Australia and New Zealand, but a very few specimens from New Zealand show approaches, and need to be reinspected. The internal mould of a dorsal valve was assigned to ?Elythidae by Waterhouse (1968, p. 52. It shows a wide hinge, rounded cardinal extremities, large ctenophoridium and two pair of muscle impressions, and no tabellae. It comes from the middle Letham Formation, with *Wyndhamia typica typica* (see Waterhouse 2024a, p. 103) and *Spiriferella supplanta* (see p. 60 herein).

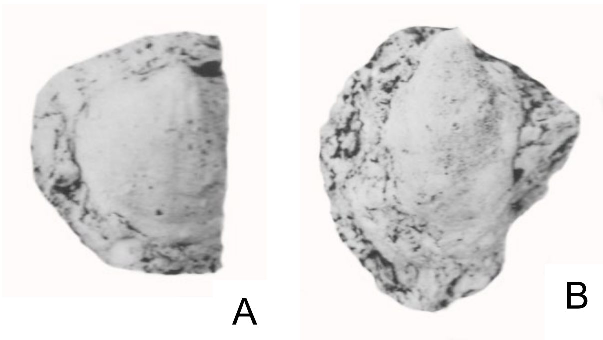


Fig. 69. Possible delthyridin specimens. A, dorsal internal mould, BR 1239, x2. B, ventral internal mould, BR 1424. Kildonan Member, Bagrie Formation, New Zealand. (Waterhouse 1968).

The internal mould and part of the external mould of a dorsal valve comes from the Kildonan Member of the upper Bagrie Formation in the Arthurton Group of north Otago, New Zealand. It is described in Waterhouse (1968, p. 81, pl. 15, fig. 4) as gen. & sp. indet C, and needs to be re-inspected (Fig. 69A). The most important aspect centres on the possible presence of slender single-barrelled spines, two or three per millimetre, suggesting Reticulariidae, A ventral valve from the same locality, recorded as gen. & sp. indet. D by

Waterhouse (1968, p. 81, pl. 15, fig. 5) is illustrated as a small swollen shell (Fig. 69B). The text refers to possible punctae, but perhaps these are deep internal pits rather than punctae.

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