

**MACRO-FAUNAL BIOZONES FROM THE EARLY
MARINE PERMIAN OF EAST AUSTRALIA
AND NEW ZEALAND,
WITH DESCRIPTION OF SOME AUSTRALIAN FAUNAS**

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PREFACE

This volume contains information on aspects of the Early Permian macro-faunas from east Australia. In the first article, a brachiopod species is assigned to *Trigonotreta victoriae* Archbold from the Lochinvar Formation of Early Permian age in New South Wales, and the Australian Late Paleozoic spiriferiforms overviewed, with figures provided for *Costuloplica* from the Carboniferous of Queensland. Particular attention is paid to the spiralia and the delthyrial construct in these and allied genera, with comparison to an Arctic Permian genus *Fasciculatia*. A question arises over what is meant by crural plates amongst Brachiopoda

(Article 2). For Spiriferida, crura arise from the outer hinge plates, and so may be termed crural plates. But amongst rhynchonellides and terebratulides, and by implication all brachiopods, the crura were considered to arise from the inner hinge plates in the *Revised Brachiopod Treatise*, and it is these that have been termed crural plates. East Australian species assigned to *Eurydesma* Morris are revised in the third paper, and appear to have had limited time ranges. The species *sacculum* M'Coy, 1847 seems to have been sourced from the Snapper Point or lower Wandrawandrian Formation of the south Sydney Basin, close to the source originally quoted by M'Coy, rather than the much older Allandale Formation as commonly understood. A new subspecies is described from the Pebbley Beach, Snapper Point and Wandrawandrian Formations of the south Sydney Basin, and, reinforced by a few brachiopods, helps to show that at least part of the Pebbley Beach Formation is younger than supposed in a number of recent articles. Brachiopods are described in the fourth paper largely for the first time from the Lakes Creek Formation of east Queensland, of Sakmarian age. They include well preserved spiriferiform genera, including the genus *Pteroplecta*, not previously known in Australia. Bivalves *Intomodesma* sp. and *Oblicarina* sp. are reported from the Freitag Formation of the Bowen Basin in Queensland (Article 5).

These studies help provide the basis for an examination of the macro-faunal biozones in east Australia and comparable sequences in New Zealand. In an introductory paper the strengths of radiometric and biological dating are discussed, leading to a seventh article on the biozones for the Early Permian of eastern Australia and part of New Zealand, elaborated from Waterhouse (2008, 2011), with the incorporation of the additional information from the descriptions in the present report, as well as data recently published about the Permian macro-faunas from the Gympie region in southeast Queensland and allied macro-faunas found in New Zealand. Recent interpretations on palynomorph zones and radiometric values are assessed, but differences remain, at least for the present.

The macro-faunal zones were strongly influenced by climate, and help provide a record of glaciation (last paper), commencing with profound glaciation during the Asselian Stage, followed by ameliorated conditions during the Sakmarian Stage, when evolution proceeded rapidly, and succeeded by colder times during the Kungurian Stage.

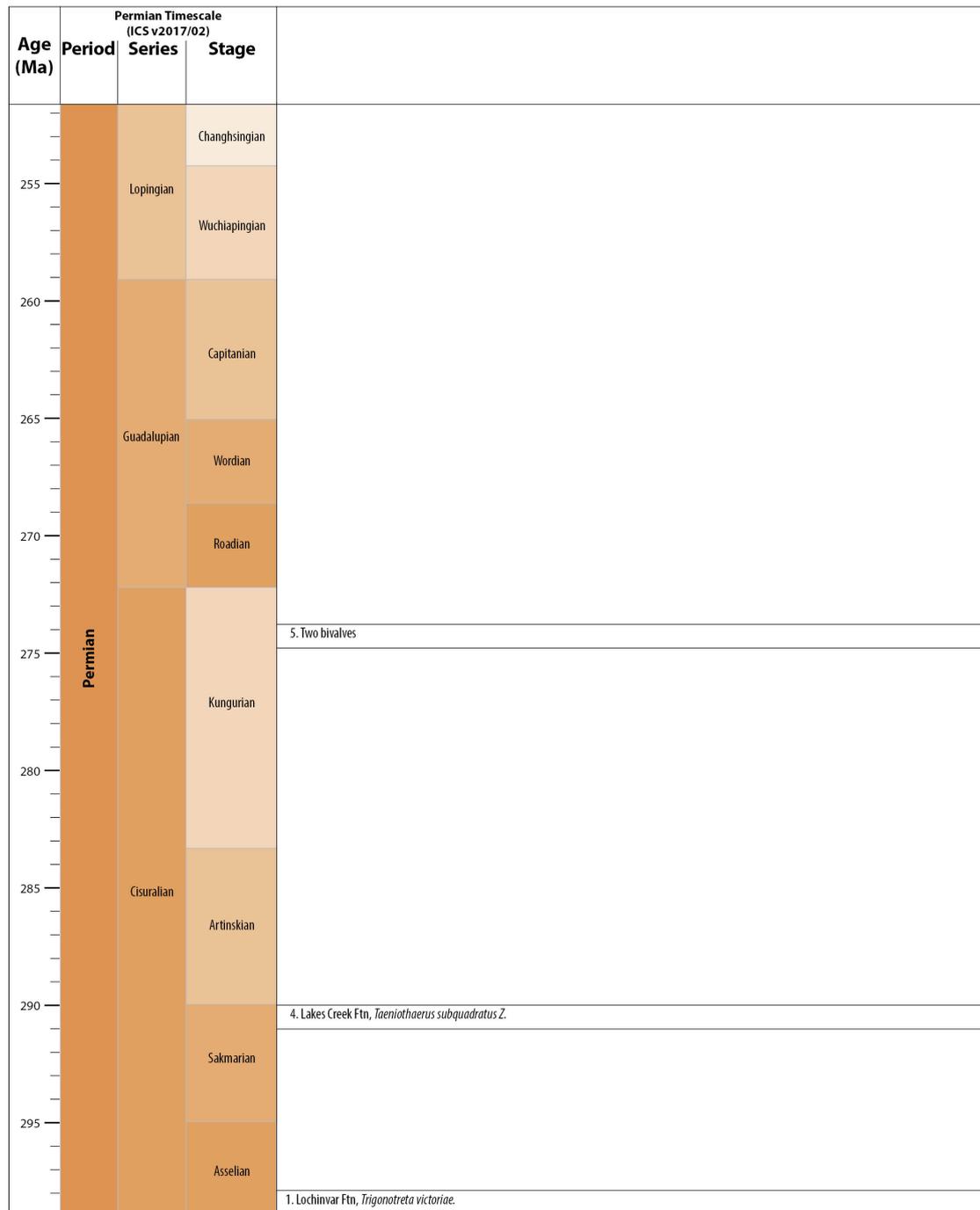


Fig. 1. Permian timescale for the Permian Period, with approximate correlations for the accompanying articles. *Eurydesma* ranges from Asselian into Kungurian. Time chart adapted from Smith et al. (2017).

Episodes of alternating warm and cool to cold conditions are traced throughout the Cisuralian Series (Lower Permian Period), based partly on successive changes in faunal links throughout the globe.

THE IMPACT OF GLACIATION ON AUSTRALIAN PERMIAN FAUNAS

The Permian geology of east Australia has long been known for its glacial sediments, and the development of unusual macro-faunas adapted to glacial conditions. The situation was very different from present-day conditions, in which shell fish at high latitudes and in cold conditions find difficulty in extracting calcium carbonate from the environment to build up the shell (Clarke 1990, 1993), because CaCO_3 is more soluble in colder waters. The build-up of massive carbonates was summarized for the Permian of east Australia by James et al. (2009), but their purported correlations were unexplained and in woeful need of correction. Macro-fossil shells from high latitudes of the present day are thin (Nicol 1967). As asserted by Kirk (1928) and Murphy (1928), organisms secreting large amounts of limestone are most abundant in the tropical seas, and rare in cold waters. But that was not the case for the Permian macro-faunas from glacial terranes, for these as a rule have thick shells – much thicker than those from the paleotropics, as represented for the Permian Period in the Glass Mountains of Texas, as well as Caucasus, China and Fergana-Caucasus. Carey & Ahmad (1961, p. 889) suggested that deposition in east Australian Permian was affected by sub-zero dry-base glaciation. To them “ A wet-base glacier causes dilation of the sea by large volumes of fresh water. A dry-base glacier, by contrast, causes saturation of actual precipitation of lime along bottom zones in the path of outward salinity currents. This may affect shell thickness in three ways: (a) the physiology of some organisms may be such that they precipitate more CaCO_3 into their shells in waters in which those ions are most concentrated; (b) any organisms selectively adapted to high CaCO_3 may multiply at the expense of others which can dominate them in less saline waters; and (c) the lime saturation of the bottom water inhibits resolution of shells and produces a limestone”. Carey & Ahmad (1961) proceeded to interpret the coquina limestones with glacial erratics and named the Darlington and Berriedale limestones in Tasmania as examples of deposition offshore from dry glaciers. But there is more to be explained. The Carey-Ahmad explanation would seem to apply best to advancing glaciation. What about receding glaciation, when “wet-base” glaciers would be expected in east Australia? That might imply thinner shell, but there seems to be no strong evidence that this may have been the case for any Australian faunas, even though it appears that Sakmarian faunas were more diverse than those of Asselian or Guadalupian age. On the

other hand, shells from the off-shore volcanic arc and its sediments that lay off-shore from what then constituted east Australia and now found in Queensland and New Zealand do appear to be thinner, and perhaps this was because the volcanic arc sustained less vigorous if any glaciation. This remains a subject inviting further exploration.

In some groups, ornament is more strongly developed in shells from high latitudes. Excellent substantiation is found amongst the Ingelarelloidea, which in low paleolatitudes and even temperate paleolatitudes, tend to be smooth apart from very fine micro-ornament of short surface grooves in quincunx. Allied members in high paleolatitudes are strongly plicate. The simplicity or elaboration of micro-ornament is less consistent. In Spiriferelloidea, growth pustules are larger in high paleolatitudes than in members of the same genera from lower paleolatitudes (Waterhouse & Waddington 1982). But amongst Ambocoeloidea (Delthyridina), the micro-ornament for example from *Attenuatella* Stehli, 1954 and *Heella* Waterhouse, 2016 from the paleotropics is more elaborate than in the otherwise similar *Attenuocurvus* Waterhouse, 2010. Yet *Biconvexiella* Waterhouse, 1983 from east Australia has micro-ornament close to that of *Attenuatella*. Campbell (1965) suggested that terebratulid genera from warm waters had more punctae per mm² than those from cold waters, and Foster (1974) found that species of living genera in Antarctic waters varied in a similar fashion, and also reported a decrease in density with greater depths. Wu et al. (2019) showed that the display of more elaborate ornament increased in lower paleolatitudes of the Changhsingian Stage at the end of the Permian Period, as compared with high paleolatitudes. Of course, this is reinforced by the fact that paleotropical genera were far more diverse and numerous than genera from polar and subpolar regions. It would instructive to confirm this trend, preferably from specifically located and well dated older faunas, when climatic gradients were more emphasized, and to my mind, preferably when all faunas had been described in modern terms, a prospect still seemingly remote thanks to present-day focus on short papers and avoidance of extensive and comprehensive systematic studies on fossil groups. It is clear from examining actual material (as opposed to examining just publications) that brachiopod genera and families varied in these respects, and the same is true amongst Bivalvia, keeping in mind the highly developed ornament on some high

paleolatitude Nuculanidae and various but far from all pteriomorphs. Indeed Vörös (2010, 2014) found that ornament became more elaborate towards the poles in Jurassic biota.

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1. *Trigonotreta victoriae* ARCHBOLD FROM THE LOCHINVAR FORMATION, NEW SOUTH WALES, AND THE TRIGONOTRETOIDEA SCHUCHERT

Abstract

Trigonotreta victoriae Archbold is described from the basal Lochinvar Formation of early Asselian age in the north Sydney Basin. Relationships are described for *Trigonotreta* and its subfamily Trigonotretinae Schuchert, 1913 to spiriferiform genera such as *Angiospirifer*, *Varuna* and *Brachythyrina*, of Early Carboniferous age, *Costuliplica* and *Maxwellispirifer*, of Upper Carboniferous age, and Permian genera such as *Cancellospirifer*, *Grantonia*, *Aperispirifer*, *Neilotreta*, *Trighorium* and *Koenigoria*. Some of these genera have postero-laterally directed spiralia as in Trigonotretidae, but others have laterally directed spiralia, and so approach Neospiriferidae. *Neospirifer* and allies resemble *Trigonotreta* in lacking a subdelthyrial plate, but have a delthyrial cover plate, like early *Angiospirifer*, and whether they evolved from Trigonotretoidea or Spiriferoidea is a matter for contention. *Gypospirifer* Cooper & Grant is probably not related. Questions remain. For instance, the Arctic genus *Fasciculatia* has fasciculate costae and plicae suggestive of Spiriferoidea. It lacks a free-standing subdelthyrial connector plate, but may display heavy delthyrial callus, arranged as though it were filling the delthyrial space between a connector plate and the wall of the valve, to suggest a modification from a spiriferoid construct.

New taxon: Subfamily Aperispiriferinae.

New morphological term: pleromium, infilling of delthyrium under ventral umbo of pleromal ridges over inner edges of dental plates and umbonal callosity. From Greek, "I fill".

SYSTEMATIC DESCRIPTION

Phylum Brachiopoda Duméril, 1806

Order SPIRIFERIDA Waagen, 1883

Suborder SPIRIFERIDINA Waagen, 1883

Superfamily TRIGONOTRETOIDEA Schuchert, 1913

Family TRIGONOTRETIDAE Schuchert, 1913

Subfamily **TRIGONOTRETINAE** Schuchert, 1913Genus ***Trigonotreta*** Koenig, 1825

Diagnosis: Medium-sized shell with five to seven pairs of plicae as a rule, and variably developed costae. Well defined sulcus, fold of moderate strength, not sharply separated from lateral shell. Short adminicula and dental plates converge posteriorly, and may be extended along their inner edge by pleromal ridges. Underlying secondary thickening is developed under the umbo, here called a pleromium, and as a rule supports a high umbonal callosity. Dorsal socket and crural plates, no tabellae, no subdelthyrial plate. Delthyrium open, well spaced mantle canal system. Spiralia posteriorly or postero-laterally directed, as far as known.

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

Discussion: *Trigonotreta victoriae* as described below is more costate than the type species of *Trigonotreta*, and more elongate in shape. The spiralia are orientated posterolaterally, rather than laterally, but there appears to have been no record of the orientation for spiralia in type *Trigonotreta*, a matter for enquiry, because *Grantonia* Brown also has postero-laterally directed spiralia, whereas Permian genera from east Australia such as *Neilotreta* Waterhouse and *Aperispirifer* Waterhouse have laterally directed spiralia.

Trigonotreta victoriae Archbold, 1991

Fig. 1 – 5

1969 *Trigonotreta* sp. nov. Garratt, p. 108.

1969 *Trigonotreta* Thomas, p. 1284.

1975 *T. cf. narsahensis occidentalis* [not Thomas] – McClung, p. 387.

1976 *Trigonotreta stokesi* [not Koenig] – Roberts et al. Fig. 17A?, B-E.

1976 *T. cf. narsahensis occidentalis* [not Thomas] – Bowen & Thomas, pp. 131, 141.

1980 *Trigonotreta* sp. nov. A McClung, photo 19.2.12.

1988 *T. cf. narsahensis occidentalis* [not Thomas] – Bowen & Thomas, pp. 202, 211.

1988 *Brachythyrinella* sp. Vanderberg, p. 38, pl. 3, fig. 4a-c.

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.

Diagnosis: Shell weakly transverse to subelongate, characterized by fine ribs covering both valves in up to seven narrow plicae, fold low and anteriorly broad, weakly distinguished from lateral shell, tends to support a weak lateral pair of subplicae. Umbonal callosity low or absent. Spiralia posteriorly oriented.

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

Material: Five specimens with valves conjoined, four ventral valves and a dorsal valve from UQL 4851, collected by D. J. C. Briggs from the basal Lochinvar Formation, Hunter Valley, New South Wales. (No further details were supplied).

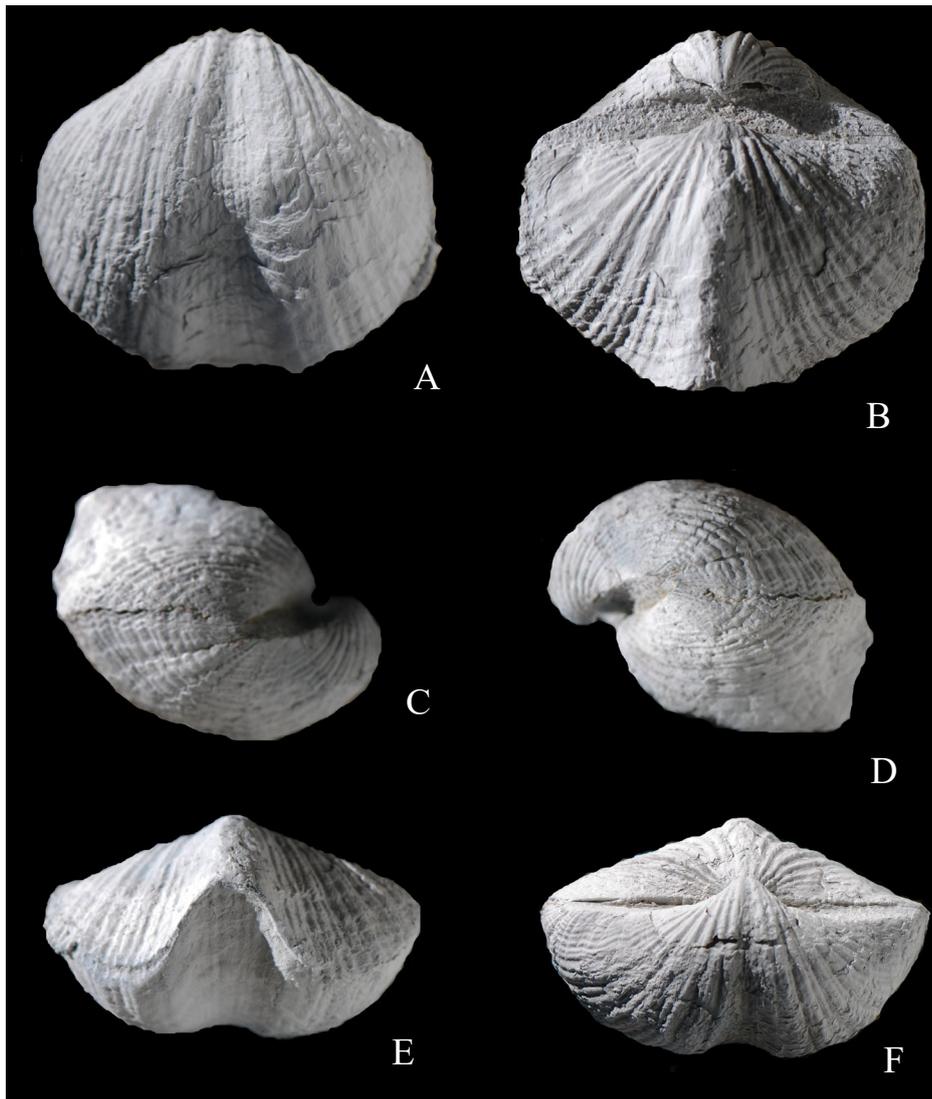


Fig. 1. *Trigonotreta victoriae* Archbold. A-D, ventral, dorsal, lateral (dorsal valve on top and below), anterior and posterior (ventral valve below) aspects of UQF 82616 from UQL 4851, Lochinvar Formation, x1.

Dimensions in mm:

Width	Length	Height	
52.5	46	34	both valves, holotype
44	34.5	22	both valves
42	32	14	dorsal valve
50	49	27	ventral valve

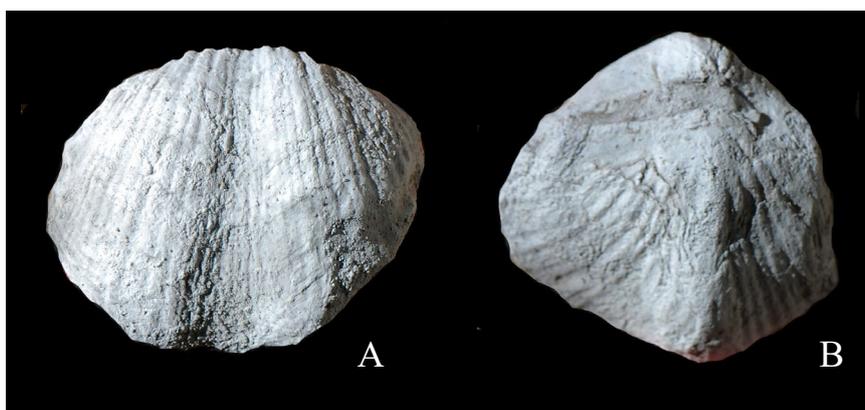


Fig. 2. *Trigonotreta victoriae* Archbold. A, ventral aspect, UQF 82617, x1. B, dorsal aspect, UQF 82618, x1. From UQL 4851, Lochinvar Formation, x1.

Description: Shells of medium size, weakly transverse with obtuse cardinal extremities throughout all growth stages as indicated by growth lines, maximum width lying near mid-length, ventral umbo incurved, with angle of just over 90°, ventral interarea high, concave, largely in the plane of the commissure with open delthyrium having an angle of 85°. Dorsal interarea low, flat, inclined at high angle posteriorly from commissure. The sulcus commences at the umbonal tip and widens at an angle close to 25°, extending anteriorly as a short tongue. The fold is less well defined, having a rounded crest and broad sloping sides that merge gradually with the lateral margins. Seven pairs of narrow plicae lie over the ventral valve and seven pairs on the dorsal valve, becoming finer laterally, succeeded by ribs near the cardinal extremities. The plicae commence at or close to the hinge and persist to the anterior margin. The innermost pair of ventral plicae is narrow, lying posteriorly at the edge of the sulcus and entering the sulcus close to the posterior third of the shell length. On the dorsal valve the innermost plicae pair is close posteriorly to the fold and may form part of the fold on its lateral flanks, and anteriorly merges with the lateral slopes of the fold. Adjoining

plicae gradually reduce in height and width laterally. Both valves are covered by fine slender costae (or costellae), at least nine in the sulcus, and comparable number over the fold, although comparatively weak over the anterior fold. The strongest plicae are ornamented by three costellae, three in four mm. Six to eight ribs lie laterally beyond the outermost plication. Traces of fine radial capillae are preserved on external moulds, and low growth laminae are visible postero-laterally near the hinge. Anteriorly, growth lamellae and growth steps are developed.

The slightly calcareous nature of the matrix hinders satisfactory leaching of the shell material because it dissolves along with the shell. Allowing for imperfect preservation, adminicula and dental plates are like those typical of *Trigonotreta* and allied genera, being short and high, the dental plates diverging laterally and anteriorly, and the adminicula more steeply inclined. There is definitely no subdelthyrial plate, and the high umbonal callosity typical of *Trigonotreta stokesi* is less developed (Archbold 1991, Fig. 2N), possibly because of imperfect preservation or a degree of immaturity. Nor does available material show substantial secondary shell in the umbonal region of the ventral valve, possibly for the same reasons. The ventral muscle field lies between the adminicula and is subrectangular and not particularly long. In the dorsal valve a sectioned specimen showed spiralia sublongitudinally oriented, diverging ventrally (Fig. 5), rather than laterally directed.

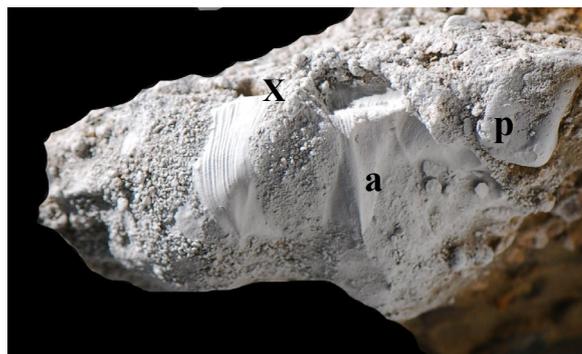


Fig. 3. *Trigonotreta victoriae* Archbold, posterior aspect of ventral valve, x1.5, which has been leached in dilute HCl, to show (a) adminicula, and (x), where a connector plate would be if present, as *Spirifer* and allies, but absent from Trigonotretoidea. Pebbles (p) are present in the matrix. UQF 82619 from UQL 4851.

Resemblances: The material is identified with *Trigonotreta victoriae* as described by Archbold (1991) from the Early Permian at Bacchus Marsh, Victoria. This species is elongate

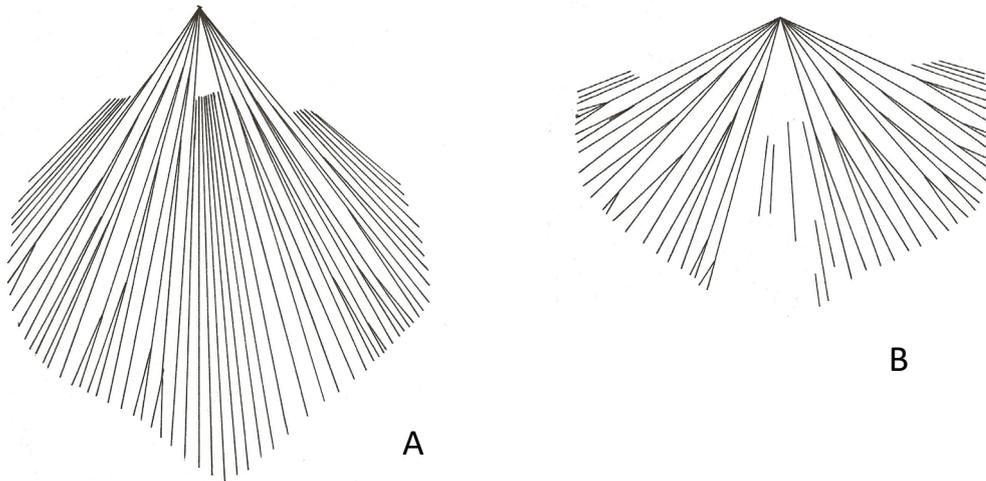


Fig. 4. *Trigonotreta victoriae* Archbold, costal diagrams for A, ventral valve, and B, dorsal valve of UQF 82616 (see Fig. 1) from UQL 4851, x1.

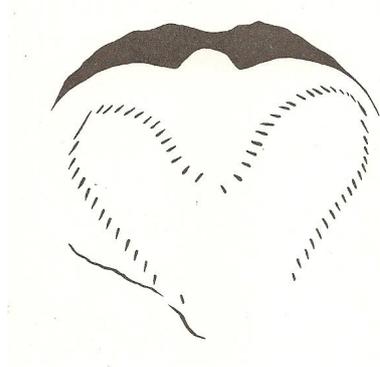


Fig. 5. *Trigonotreta victoriae* Archbold, section through both valves, with ventral valve on top, showing dorsally convergent spiralia. From UQL 4851, Lochinvar Formation, x1. Record of further sections are kept at the Queensland Museum.

like the present specimens, with only a small or no umbonal callosity. Archbold (1991, Fig. 2D-G, T, U, V) included some specimens that have less costate plicae, but figures suggest they are decorticated, as they do not appear to show commarginal growth increments; on the other hand they may prove to belong to a different taxon. Internal moulds are better preserved than in present material, but Archbold did not describe the nature of the spiralia. Archbold provided a lengthy synonymy, shortened herein, because of its limited relevance

and lack of figures. The Bacchus Marsh specimens came from low in the sequence, with meagre palynological evidence pointing to “Stage 2” according to Douglas (1969), which equates approximately to Faunizone 1 in Tasmania (Calver et al. 1984), though data is sparse and in need of updating. That would suggest an age close to that of the New South Wales specimens which come from the base of the Lochinvar Formation.

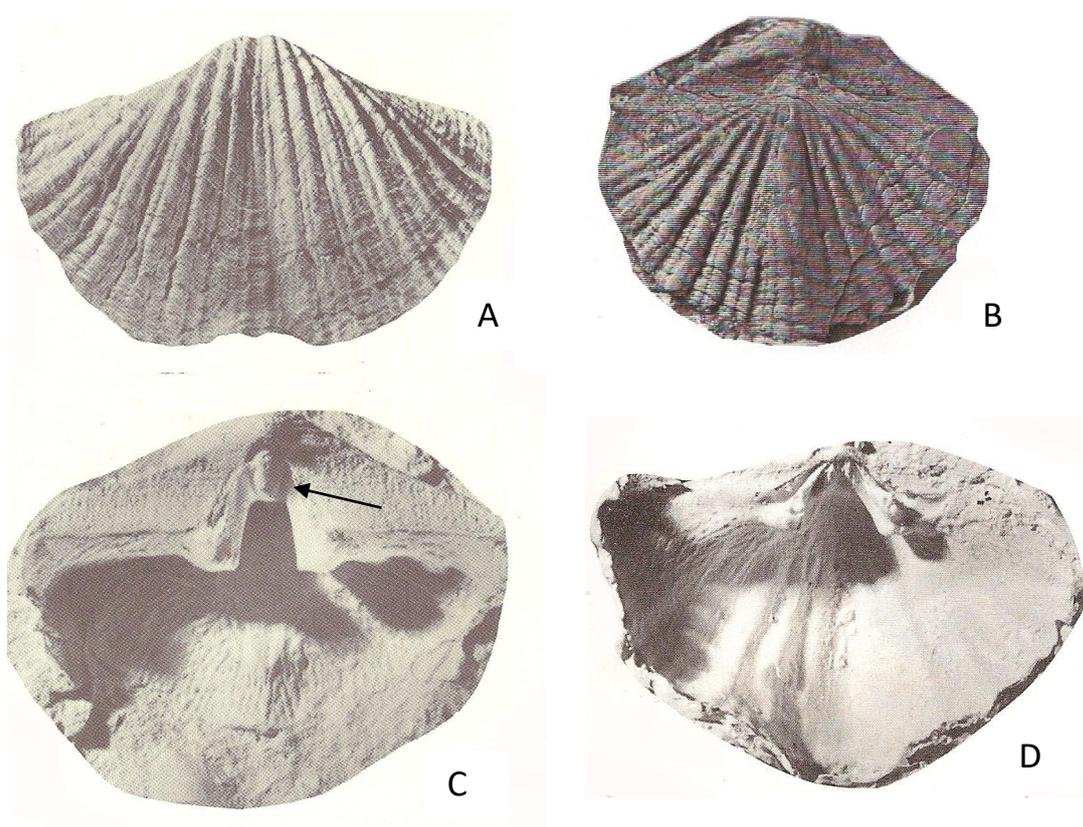


Fig. 6. *Trigonotreta stokesi* Koenig. A, ventral valve. B, lectotype, dorsal aspect. C, ventral interior. D, dorsal interior. Note the subsidiary plication attached to the anterior dorsal fold and inner sulcal subplicae. The large umbonal callosity rests on a shelf connected to the inner dental plates with pleromal reinforcement (arrowed). Specimens x1 and 1.2 (D only). From Lower Permian (Asselian) of Tasmania. (Clarke 1979).

This species is more costate and less transverse than *Trigonotreta stokesi* (Fig. 6) and has a smaller umbonal callosity. Indeed none is shown in the figure of Archbold (1991, Fig. 2I, J), and only a small callosity appears in Archbold (1991, Fig. 2N). Possibly this reflects the degree of maturity. A comparable finely ribbed specimen was recorded from the

Wasp Head Formation in the South Sydney Basin by Runnegar (1969, pl. 20, fig. 17), but the shell appears to be more transverse. A moderately costate specimen from the upper Wasp Head beds was figured by Cisterna & Shi (2014, Fig. 8.17), with no description, and identified as a trigonotretid, and the specimen appears to be more transverse than *victoriae*. Possibly a ventral valve figured by McClung (1980, Fig. 19.2.12) from an unspecified locality somewhere within the upper Lochinvar, Rutherford or Farley Formation is identical, agreeing largely in shape and ornament. Roberts et al. (1976) figured specimens from the basal Bundella Formation that could prove to be a late lingering member of *victoriae*, although their Fig. 17A is more transverse, and has a low umbonal callosity, apparently better developed than in Fig. 17B, C. Specimens from the Glencoe Formation of the Golden Valley Group (Clarke 1992, Fig. 7A, B) and “Spirifer Zone” (Clarke 1992, Fig. 7C) of Fossil Cliffs in the Darlington Limestone in Tasmania display fine costation, but the Glencoe specimens are transverse, whereas the full shape of the “Spirifer Zone” specimen is uncertain. Clarke (1992) maintained that the specimens were conspecific with *Trigonotreta stokesi* Koenig.

From present information, shells like *Trigonotreta victoriae* appeared earlier in the succession, having finer costae and a shorter ventral muscle field, to be succeeded by the more transverse and larger species *T. stokesi*. As well figured by Clarke (1979, 1990, 1992), the delthyrium in *stokesi* is partly closed by a large callosity resting on secondary umbonal thickening (Fig. 6C). There is no published information on the orientation of spiralia in *stokesi*.

A further species of *Trigonotreta* is likely to be so-called *Grantonia murrayi* Waterhouse (2015b, p. 59, Fig. 19A-E) from the upper Rammutt Formation of the Gympie Province in southeast Queensland. The spiralia are not known, but the mature shell is moderately large and has up to seven pairs of persistent plicae, and well developed costae. The fauna from the upper Rammutt Formation belongs to the *Bandoproductus macrospina* Zone of late Asselian age (Waterhouse 2015b, and see p. 201 herein).

Yet another species is described as *Neilotreta lakeensis* n. sp. from the Lake Creek Formation of east Queensland, from a fauna belonging to the *Taeniothaerus subquadratus* Zone (see herein, p. 105ff). Specimens show well the delthyrial structure, which is consistent with the morphology of *Neilotreta*, and there are six to seven plicae pairs. But the direction of spiralia needs to be determined to rule out *Trigonotreta*.

RELATIONSHIPS

In the nature of its costate plicae, open delthyrium and lack of a subdelthyrial connector plate between the junctions of the adminicula and dental plates, *Trigonotreta* is allied to a number of spiriferiform genera of late Paleozoic age. Within these genera, one critical aspect remains known for only some taxa – namely the direction of the spiralia. In non-type *T. victoriae*, as shown above, the spiralia are posteriorly or postero-laterally directed, and the same orientation has been reported for *Grantonia* by Brown (1953). By contrast, spiralia are laterally directed in *Cancellospirifer* Campbell, 1953 as shown by Waterhouse (1968), *Aperispirifer* Waterhouse, 1968, as confirmed in that study and in Waterhouse (1964), and in *Neilotreta* Waterhouse 2008, as demonstrated by Thomas (1971). The spire forms a significant part of brachiopod morphology, and has been regarded as critical for classification amongst Rhynchonellida and Terebratulida. For *Angiospirifer* Legrand-Blain, 1985, Davidson (1858) figured a specimen with posteriorly directed spiralia like those of *Trigonotreta victoriae*. Spiralia do not appear to be known for various Upper Carboniferous genera from east Australia, or various possible trigonotretoids from India, Western Australia and elsewhere, so there has to be assumptions in any attempt to establish classification substantially on spiralia. Carter (2006) in the *Revised Brachiopod Treatise* left the nature of spiralia entirely out of consideration, and Waterhouse (2016) placed emphasis on the shell form and nature of the ornament, but did provide information on spiralia. The classification therefore has been pragmatically based and follows the scheme proposed in Waterhouse (2016), but cannot be regarded as fully satisfactory, given the degree of ignorance about the spiralia for some significant groups. That points to the need for a significant undertaking to discover much more about the orientation of spiralia in various genera and species.

COMPARISONS WITH OTHER SPIFERIFORMS IN THE LATE PALEOZOIC OF AUSTRALIA

A. SUBFAMILY TRIGONOTRETINAE SCHUCHERT, 1913

Fig. 7

Grantonia Brown, 1953

In the type species of *Grantonia*, Brown (1953, p. 60) recorded that the spiralia were oriented postero-laterally in the type species, which agrees with the arrangement for *Trigonotreta*

victoriae from the Lochinvar Formation. In *Grantonia* Brown, 1953, the inner plicae are strengthened, and the number of plicae commonly reduced to three or four pairs from six or seven pairs in *Trigonotreta*. The dorsal fold is narrow and higher, and costae, especially the median costa over a plication, are high as rule, at least in the type species. The outstanding specimen figured by Runnegar (1969, pl. 20, fig. 16) from the Wasp Head Formation may belong to this genus, signifying an early appearance. Several specimens of *Grantonia* from the upper Sakmarian Berriedale Limestone were misidentified as *Trigonotreta stokesi* by Armstrong (1968, p. 83, pl. 6, fig. 1, 2, 3, ?5), and the dorsal valves are less regularly plicate than the ventral valves. Another species of *Grantonia*, called *G. australis* (Bion, 1928), is of middle Sakmarian age. *G. cracovensis* Wass, 1966 from the Fairyland Formation of basal Sakmarian age shows affinities with both *Grantonia* and *Trigonotreta*, as reviewed in Waterhouse (1987, p. 17), and all three species are found in Sakmarian faunas of east Australia. The pleromium is well displayed in specimens figured by Waterhouse (2015a, Fig. 145D, 148B). On the basis of having fewer plicae, Waterhouse (2016) discriminated a new subfamily Grantoniinae, but this is now regarded as of lesser rank, no more than infrasubfamilial rank, if not superfluous.



Fig. 7. *Grantonia australis* (Bion), UQF 74165 from Elvinia Formation, southeast Bowen Basin, showing posteriorly directed spiralia under ventral valve, x1. (Waterhouse 1987).

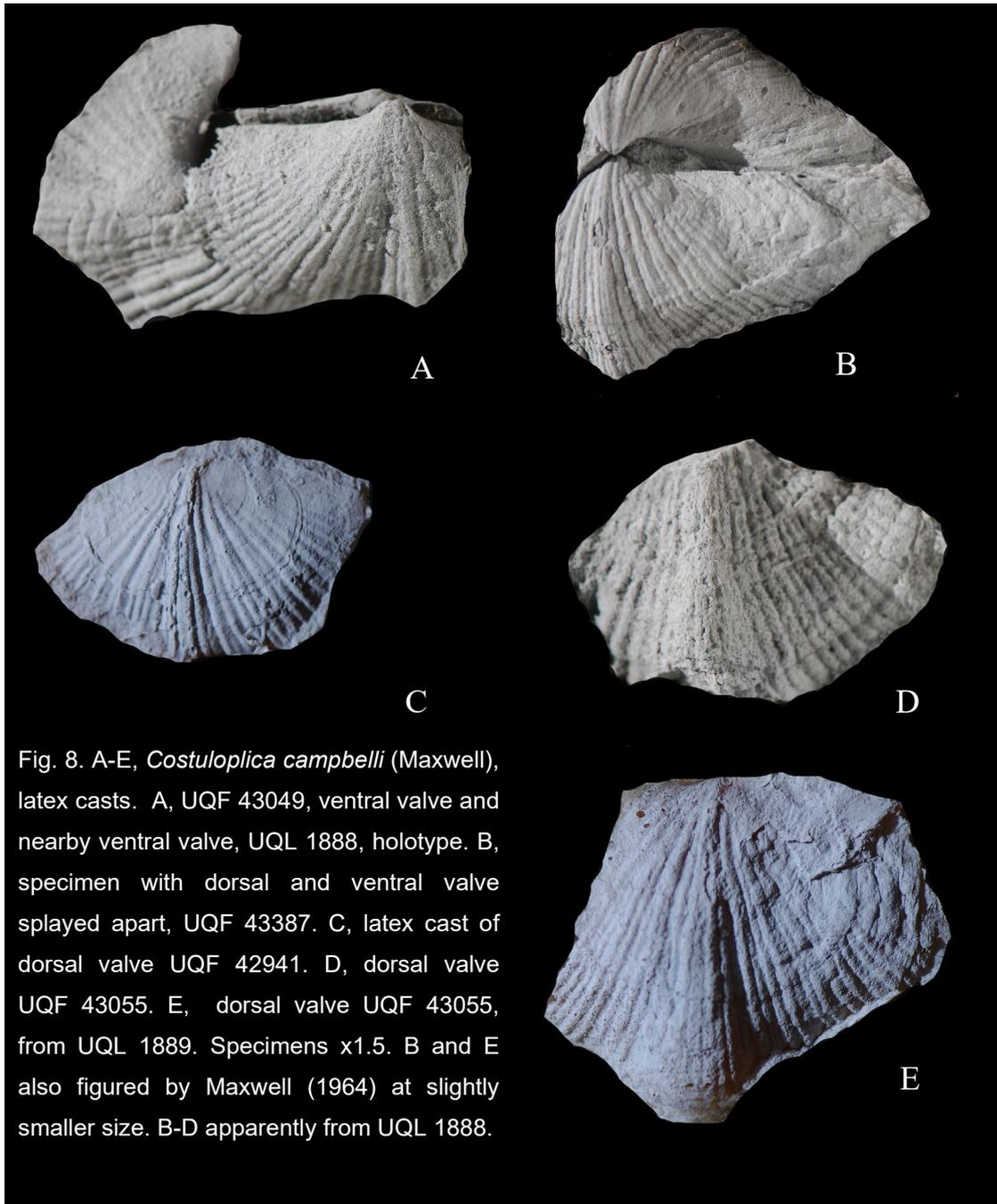
B. SUBFAMILY COSTULOPLICINAE WATERHOUSE, 2004

Fig. 8 – 13

Costuloplica Waterhouse, 2004

Placement of this family group without knowledge of the spiralia is a challenge. The preservation of most of the material is such that no spiralia can be revealed, and the deficiency offers a major hurdle in understanding the relationships and developments with Trigonotretoidea, and also the relationship to Aperispiriferinae n. subfam., which is moderately like *Costuloplica*, and has transversely directed spiralia. It was originally

evaluated as a possible descendent from Angiospiriferinae and precursor to Trigonotretinae, but given the lack of knowledge about the spiralia, a relationship to Neospiriferidae cannot be ruled out, especially in view of the delthyrial construct in *Costuloplica*, which lacks a prominent umbonal callosity, with little or no pleromium.



The type species, *Neospirifer campbelli* Maxwell, 1964 from the Branch Creek Formation of the Yarrol Basin of Queensland, and rated as Namurian (= Bashkirian), differs

from *Trigonotreta victoriae*, although there are a number of basic similarities. The type species of *campbelli* (Fig. 8) was described by Maxwell (1964, p. 31, pl. 6, fig. 19-25); Hill & Woods (1964, pl. 11, fig. 13-15); McKellar (1965, pl. 4, fig. 9); Hill, Playford & Woods (1972, pl. 11, fig. 13-15); Roberts et al. (1976, p. 221, Fig. 15A-E) and Waterhouse (2016, Fig. 292A

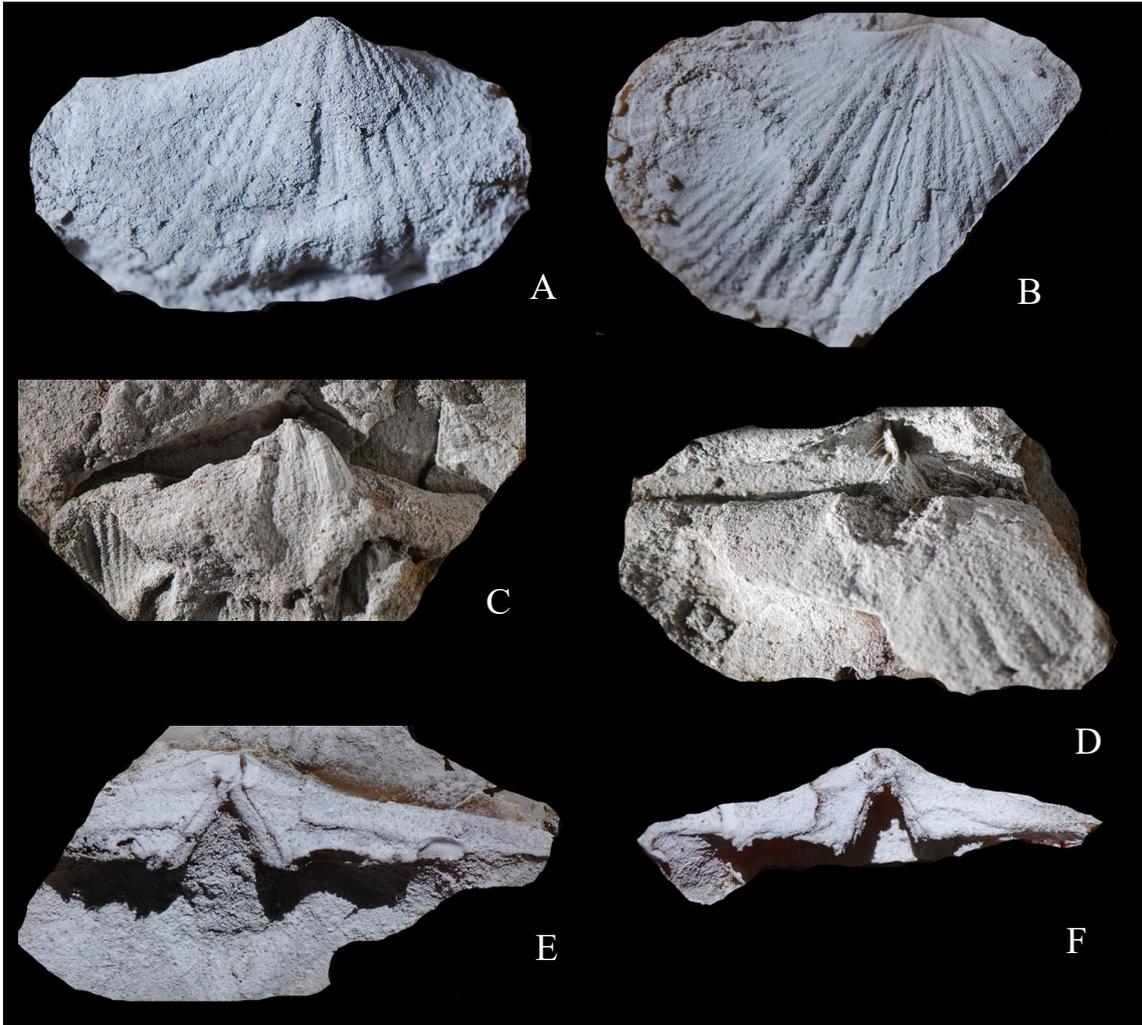


Fig. 9. *Costuloplica senilis* (Maxwell). A, latex cast of ventral valve, UQF 82622. B, latex cast of dorsal valve, UQF 82623. C, F, internal mould with ventral area and latex cast of UQF 82621. D, E, internal mould and latex cast of UQF 82620. The prominent ridge each side of the delthyrium is formed by the edge of the dental plate, and terminates in the tooth, with a narrow gap to the edge of the interarea. Specimens are topotypes, x1, from UQL 1923, Branch Creek Formation. Located as 4n in map of Maxwell 1964, Fig. 1, collected by W. G. H. Maxwell. Note the lack of pleromium and umbonal callosity.

A-C, 293C, 294A, B). A second species was originally treated as var. *senilis* (Maxwell 1964, p. 31, pl. 6, fig. 26- 33) and was elevated to species rank by Roberts et al. (1976, p. 222, Fig. 16A-D; Waterhouse 2016, Fig. 293A, B, 294C, D). It is figured herein as Fig. 9-11. Both species are transverse with six to nine slender plicae pairs, of which some three pairs lie within the sulcus, many lateral ribs, and fine costellae. The species are placed in genus *Costuloplica* Waterhouse, 2004 in a separate subfamily Costuloplicinae Waterhouse, and further occurrences in Argentina and Lake Baikal region are summarized from Roberts et al. (1976) by Waterhouse (2004, p. 188). Costae are fine, numerous and low, and the umbonal callosity is small, unlike the prominent umbonal callosity of most Trigonotretinae. There is no pleromium or subdelthyrial plate, the ventral muscle field is broad as a rule, and the mantle canal system is finer than in Trigonotretinae. So far the nature of the spiralia remains unknown, because many of the specimens are preserved as single valves.

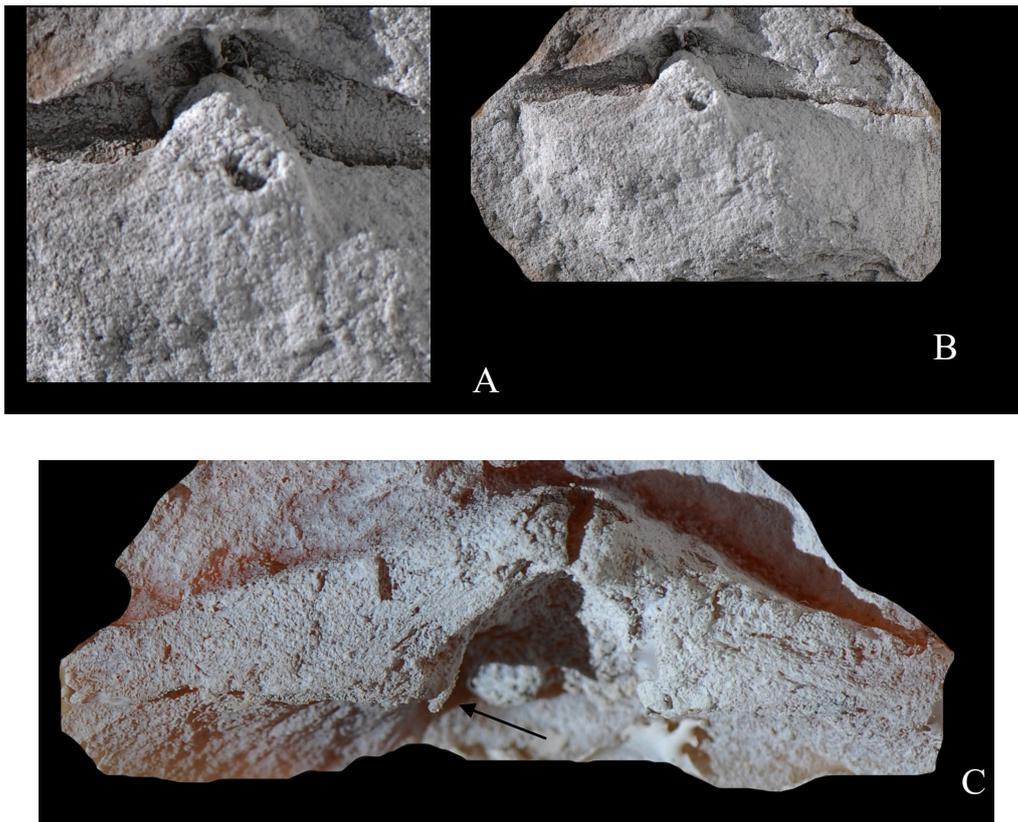


Fig. 10. *Costuloplica senilis* (Maxwell), A, B, internal mould of ventral valve UQF 82624, x1, x 2, from the type locality, UQL 1923, Branch Creek Formation, x2, x1. C, latex cast, x3. An arrow points to the inner upturned edge of the dental plate.

It would be interesting to compare *Trigonotreta victoriae* with specimens discussed but not figured or described as *Trigonotreta campbelli* Maxwell by Runnegar & McClung (1975). The form was noted as occurring with the first appearance of *Eurydesma* in east

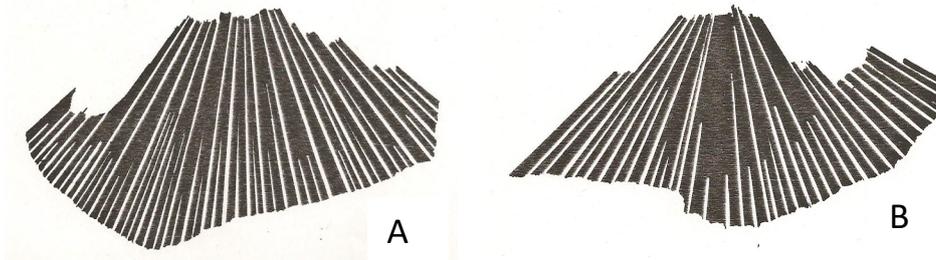


Fig. 11. *Costuloplica senilis* (Maxwell), costal diagrams. A, UQF 42987, ventral valve of Maxwell (1964, pl. 6, fig. 29). B, UQF 43384 dorsal valve of Maxwell (1964, pl. 6, fig. 30). Specimens x 1 from type locality, UQL 1923, Branch Creek Formation, Queensland.

Australia and found in the uppermost Seaham Formation in the Cranky Corner Basin, Mindaribba Syncline of New South Wales and at Alum Rock, Queensland. Roberts et al. (1976, p. 222) dismissed the alleged similarity to type *campbelli*, and Briggs (1998, p. 28) reported that the so-called *campbelli* occurred at Alum Rock with early Permian fossils. Interpreting these particular specimens is hampered by the lack of description and illustrations.

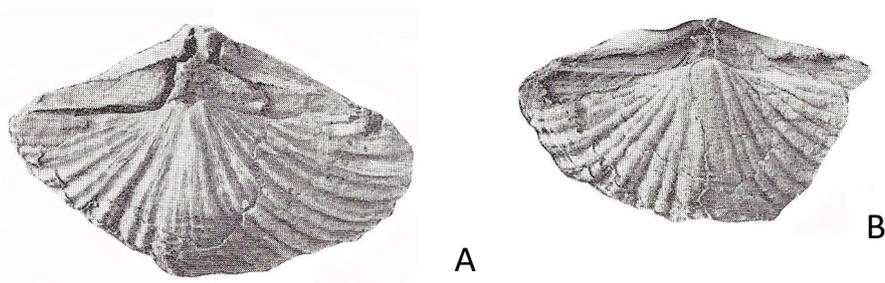


Fig. 12. *Maxwellispirifer exora* (McKellar), dorsal views of internal mould and latex cast, GSQ 9023, x1.5. Specimens from Branch Creek Formation, Middle Carboniferous of Queensland. (McKellar 1965). The genus differs strongly in ornament from *Costuloplica*, but whether it is allied to *Neospirifer* or *Trigonotreta* is uncertain.

Maxwellispirifer Waterhouse, 2004

Maxwellispirifer Waterhouse, based on *Neospirifer campbelli exora* McKellar (1965, p. 10, pl. 4, fig. 1-6; Waterhouse 2016, Fig. 295A-C) is less transverse than *Costuloplica*, with fewer but more clearly defined plicae and coarser costae (Fig. 12). Both *Costuloplica* and *Maxwellispirifer* come from the Bashkirian to Moscovian Branch Creek Formation of the Yarrol Basin in Queensland. But figures for the type species of *Maxwellispirifer* do not show certain critical aspects of the delthyrium or spiralia, though there are specimens with conjoined valves, offering the opportunity to discover the nature of the spiralia.

A possible species of *Maxwellispirifer* has been reported by Waterhouse (2016, p. 232, Fig. 297A-D, Fig. 298A, B), and see Fig. 13, 14, with similar distinctive ribbing and plication (see Waterhouse 2016, Fig. 297B). In 2016, Queensland Museum stated the material came from the Riversleigh beds in the Munduberrah district of Queensland, with later confirmation by e-mail stating that the fossils came from what was then Latza's farm, and had been collected by F. W. Whitehouse in 1951. The Riversleigh term is now applied to Precambrian deposits in the text of Queensland geology, edited by Jell (2013). Latex casts prepared from ventral valves show variation, one (Fig. 13A) displaying little umbonal

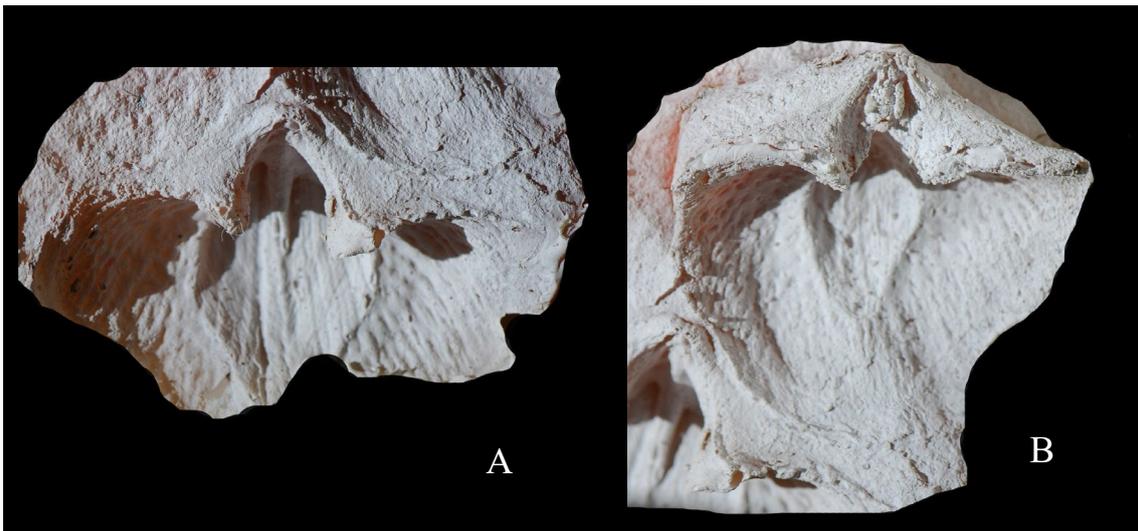


Fig. 13. *Maxwellispirifer* sp. A, latex cast showing interior of ventral valve UQF 12850, x2 from UQL 1286, near Munduberra, Queensland. B, latex cast of ventral valve from same locality, x2, showing well-developed pleromium without of without an umbonal callosity. (See Waterhouse 2016, Fig. 297, 298).

build-up, the other showing massive umbonal secondary tissue, overlain by a massive umbonal callosity (Fig. 13B). In this specimen the muscle field is smaller than that of the other specimen. A dorsal valve (Fig. 14) displays broad fold grading into the lateral shell and only ill-defined plicae, with numerous costae, weaker than in another dorsal valve figured in Waterhouse (2016, Fig. 297B). These Munduberra specimens are significant, insofar as they show that shells with trigonotretoid morphology were already to be found in east Australia, well before Permian time. It seems likely that the specimens are *Maxwellispirifer*, but whether they should be grouped with *Costuloplica* seems doubtful, given the differences in delthyrial construct.

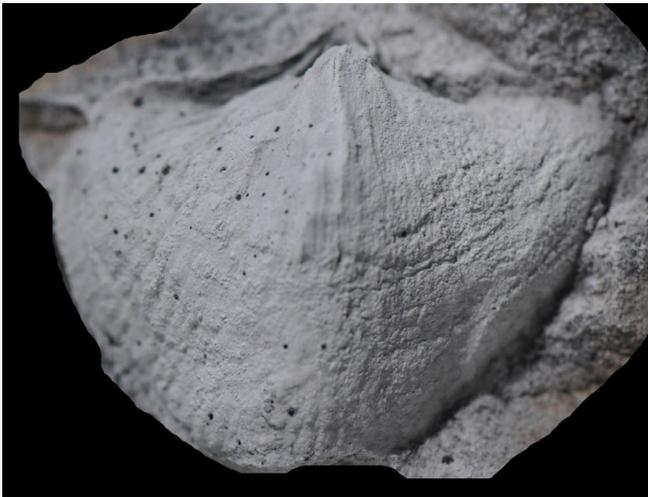


Fig. 14. "*Maxwellispirifer*" sp., dorsal internal mould, UQF 12849 x1.5, from UQL 1286.

SUBFAMILY APERISPIRIFERINAE N. SUBFAM.

Fig. 15, 16

Diagnosis: Medium to large generally transverse shells with three to six pairs of plicae as a rule, closely costate, sulcus and fold well developed, delthyrium open without stegidia or cover plate or subdelthyrial connector plate, may display pleromium; dental plates, adminicula, crural and socket plates present, without tabellae, no well formed median dorsal septum. Mantle canals may be well spaced. Spiralia laterally directed.

Name genus: *Aperispirifer* Waterhouse 1968, p. 35, here designated.

Discussion: Several genera previously referred to Trigonotretinae Schuchert, 1913 or Grantoniinae Waterhouse, 2016 differ in having spiralia that are laterally rather than postero-laterally directed. These include a suite of genera found mostly in Australia, namely *Aperispirifer* and *Koenigoria* and the comparatively similar genus *Trighorium* from the United States, recognized by Waterhouse (1968, 2004, 2016). Possibly some or all of the chiefly west Australian genera named by Archbold & Thomas (1986), including *Costatispirifer*, *?Crassispirifer*, *Imperiospirifer*, as well as *Quadrospira* Archbold, 1997 and *Wadispirifer* Waterhouse, 2004 belong to the group, but these as a rule have very low dental plates and so were referred in Waterhouse (2016) to Kaninospiriferinae Kalashnikov, 1996. *Kaninospirifer* remains an inadequately known genus (see Waterhouse 2020), but *Kaninospirifer* and *Quadrospira* are known to have laterally directed spiralia.

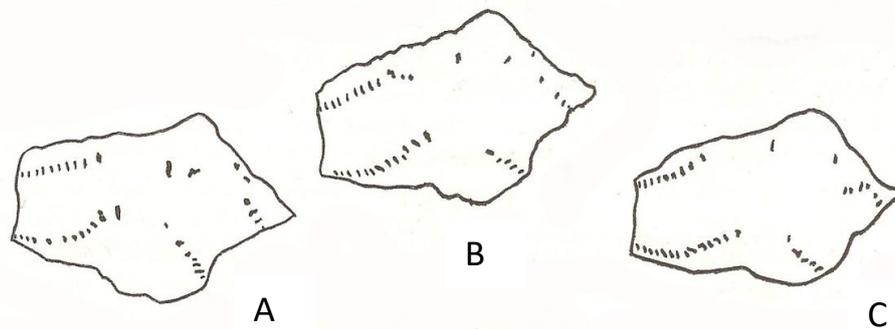


Fig. 15. *Aperispirifer archboldi* Waterhouse. A-C, serial sections of internal mould at 14mm, 16mm and 18mm from the umbo. (Waterhouse 1964).

It is difficult to trace the geological origins for Aperispiriferinae, because so many authors have paid little attention to distinguishing adminicula from dental plates, and have disregarded the nature of the spiralia and delthyrial construct. Although *Costuloplica* of Bashkirian and younger age of east Australia has somewhat similar ornament, the delthyrial construct differs, with less developed pleromium and umbonal callosity. The nature of the spiralia is not known for *Costuloplica*. The genus *Aperispirifer* and its allies have hitherto been interpreted as large and closely costate allies of Trigonotretinae, with similar delthyrial construct (see Waterhouse 1964, pl. 25, fig. 2) and moderately strong and well spaced

mantle canals. On the other hand, Neospiriferinae Waterhouse are close externally and internally in many details, although lacking the large umbonal callosity of some Aperispiriferinae, and having more closely spaced mantle canals, and having a neodeltidium, which is formed by a single plate across the delthyrium, (Waterhouse 2016, p.

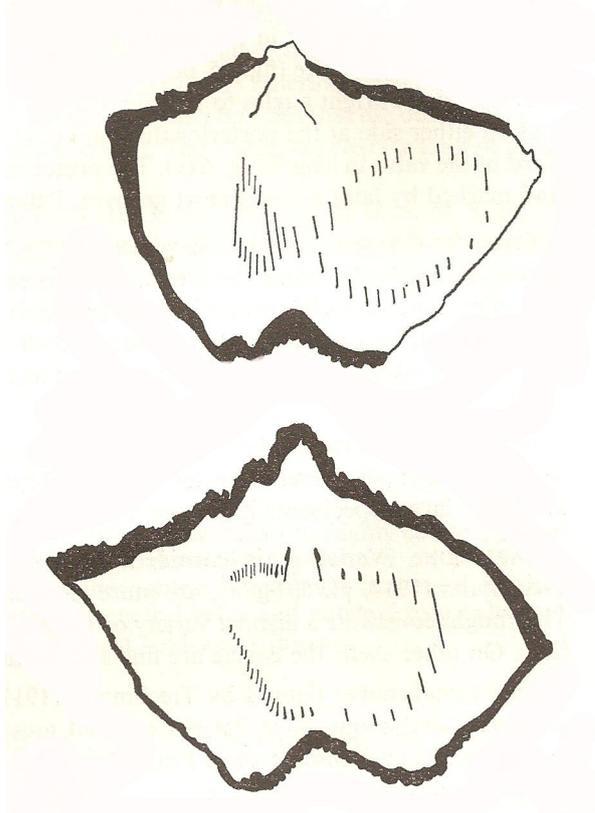


Fig. 16. *Aperispirifer nelsonensis* (Waterhouse) from Late Permian of New Zealand, showing laterally directed spiralia. From Waterhouse (1964, Fig. 66), x1.

197), whereas a deltidium is formed by two plates, which may fuse medianly, growing from the sides of the delthyrium. Unlike known members of Trigonotretinae, members of Neospiriferinae do share with Aperispiriferinae transversely directed spiralia. It is therefore possible that Aperispiriferinae arose during Permian times from neospiriferid stock, directly or indirectly, through change in these particular morphological attributes remains a matter that requires further assessment.

In summary, the particular source for Aperispiriferinae may have been either Neospiriferinae, well represented in south Asia, or as close allies in Western Australia amongst genera referred provisionally to Kaninospiriferinae Kalashnikov, 1996, though this subfamily still requires consolidation, as discussed in Waterhouse (2020, pp. 300-304). As one alternative, the group arose from within Georinakingiidae, as outlined below. *Georinakingia* itself is plicate and costate, and has a prominent umbonal callosity as well as

other morphological features shared with *Aperispiriferinae*, although it is readily distinguished by its extremely transverse outline, and most members of the family have fewer costae and more numerous plicae. *Georginakingia* entered the Permian faunas of east Australia at roughly the same time as *Aperispirifer*, and a much less transverse and simply plicate genus *Unicostatina* entered in the Asselian. *Koenigoria* commenced in the earlier Permian of Western Australia, and so might have provided a more likely ancestral stock, given its shape and ornament. The delthyrial construct in *Koenigoria* appears from figures to have an umbonal callosity (Archbold & Thomas (1986, Fig. 16E, G, ?Fig. 17B), their text (p. 154) stating that some specimens had a flattened apical callosity, whereas other specimens had a bulbous apical callosity. This genus is regarded as the most likely progenitor for *Aperispiriferinae*. The group could have sourced from within *Neospiriferidae*, although the relationships and origins still need further enquiry, and arguably would have involved more change than an origin from within *Trigonotretidae* or *Georginakingiidae*.

***Aperispirifer* Waterhouse, 1968**

In *Aperispirifer* Waterhouse, plicae in several species, including the type, are reduced in number, and as a rule they fade anteriorly, though there are exceptions. Costae are low and numerous, and cardinal extremities are often alate, much as in *Koenigoria*. The spire in a series of thin sections illustrated by Waterhouse (1964, Fig. 60) for the type species suggest that spiralia could have been broken but indicative of a lateral orientation, and other species show laterally directed spiralia (Waterhouse 1964, Fig. 63, 65, 66), slightly differing in detail (Fig. 15, 16). Serial sections of *Betaneospirifer* Gatinaud, 1949 from the Salt Range, Pakistan, show laterally directed spiralia that remain distinct even anteriorly (Waterhouse 1968, text-fig. 8). This genus belongs to *Neospiriferidae*, distinct from *Trigonotretidae*, because the delthyrium has a cover plate (= neodeltidium) and the spiralia are not postero-laterally directed, although like *Trigonotreta* and *Aperispirifer*, there is no subdelthyrial connector plate (Waterhouse 1968, 2016). Nor is there a pleromium typical of *Trigonotretidae*.

***Koenigoria* Waterhouse, 2004**

A number of species mainly from Western Australia and also the Gympie Province of Queensland and distinguished as *Koenigoria* Waterhouse, 2004, have alate hinge, triangular shape, four pairs of costae and strong persistent plicae. The orientation of spiralia is not

known, but there are many specimens available with valves conjoined, so this should not be difficult to determine.

Trigorhium Waterhouse, 2004

A striking invasion of the middle Permian paleotropical faunas of Texas is shown by the genus *Trigorhium* Waterhouse. This has the same delthyrial apparatus as *Trigonotreta*, in contrast to that of *Neospirifer*, and is distinguished by tending to have three pairs of narrow plicae within the sulcus (Fig. 17), recalling the numerous sulcal plicae in *Costuloplica*. Otherwise the genus is apparently a descendent from *Koenigoria* Waterhouse. It has up to six pairs of lateral plicae, and is close to type *Trigonotreta* with its large umbonal callosity. The full form of the spiralia is not preserved, but is laterally directed (Cooper & Grant 1976, pl. 591, fig. 11). No other species from the Glass Mountains in Texas appears to be congeneric, although interpretation of the numerous and well-preserved species referred to *Neospirifer* by Cooper & Grant (1976) is difficult, because of the failure to discriminate adminicula from dental plates, and lack of full description of the delthyrial construct.

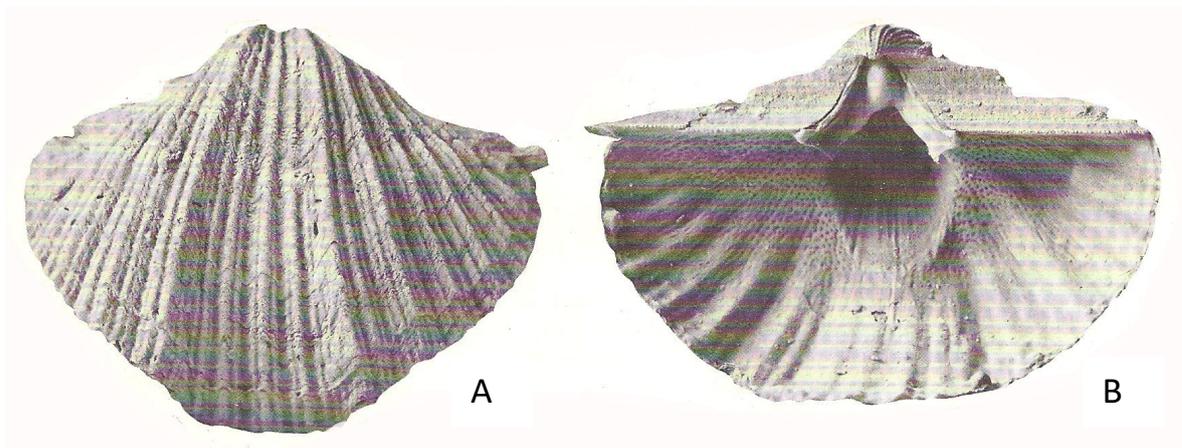


Fig. 17. *Trigorhium amphigyus* (Cooper & Grant), ventral valve exterior (A) and interior (B), showing characteristic three subplicae in the sulcus, and the strong trigonotretid pleromium with umbonal callosity, x1.2. From Word Formation (Wordian), Texas. (Cooper & Grant 1976).

A number of the illustrations for Glass Mountains species assigned to *Neospirifer* strongly suggest that a subdelthyrial connector plate is well developed in several species and Waterhouse (2016) suggested that these were descendent not from *Neospirifer* or *Betaneospirifer*, which lack a connector plate, but from Spiriferidae, which does have a well

developed subdelthyrial connector plate. They were distinguished as a distinct subfamily Spiriferalariinae Waterhouse, 2016. There is no umbonal callosity over the connector plate, and the shells from Texas are characterized by extremely alate cardinal extremities. There is one exception. Specimens ascribed to *Neospirifer notialis* Cooper & Grant (1976, pl. 608, fig. 12, 13) suggest posteriorly fused dental plates with no callosity or shelf, or subdelthyrial connector plate. Costae are numerous and the fold displays a broad well rounded crest whereas plicae are subdued and fascicles developed. Closer study of this species would be of interest. It comes from the Taylor Ranch Member of the Hess Formation, of Sakmarian age, and implies the possible presence of an aperispiriferin species, to underline the desirability of further examination of northern hemisphere spiriferiforms.

C. FAMILY ANGIOSPIFERIDAE LEGRAND-BLAIN, 1985, THE PRECURSOR FAMILY

SUBFAMILY ANGIOSPIRIFERINAE LEGRAND-BLAIN, 1985

Fig. 18, 19

Angiospirifer Legrand-Blain

Angiospirifer Legrand-Blain, 1985 has simple plicae, a coarse mantle canal system, a mostly open delthyrium, and large umbonal callosity, all features shared with *Trigonotreta*, and distinguished by its simple plicae, according to Waterhouse (2016, p. 240). Being of Early Carboniferous age, and found especially in Europe, it is deemed to have been ancestral to Trigonotretinae. The arrangement of the spiralia is indicated by Davidson (1858, pl. 6, fig. 17)

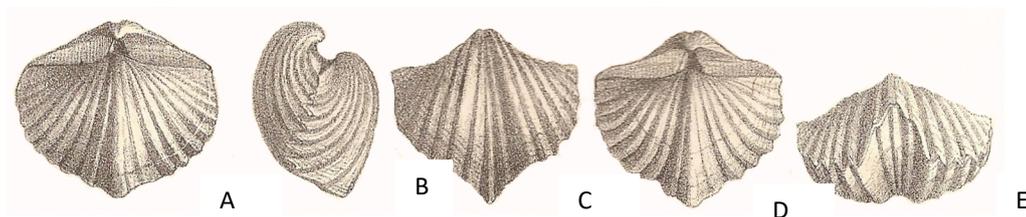


Fig. 18. *Angiospirifer trigonalis* (Martin, 1809), the type species of *Angiospirifer* as figured from the Lower Carboniferous of England and Scotland, x1. (Davidson 1858).

as being postero-laterally directed, though serial sections were prepared by Angiolini et al. (2011) failed to show any spiralia. The nature of the spiralia supports the relationship to

Trigonotretinae proposed in Waterhouse (2016, whereas figures of some material ascribed to *trigonalis* by Sowerby are less convincing (see Fig. 19C, D).

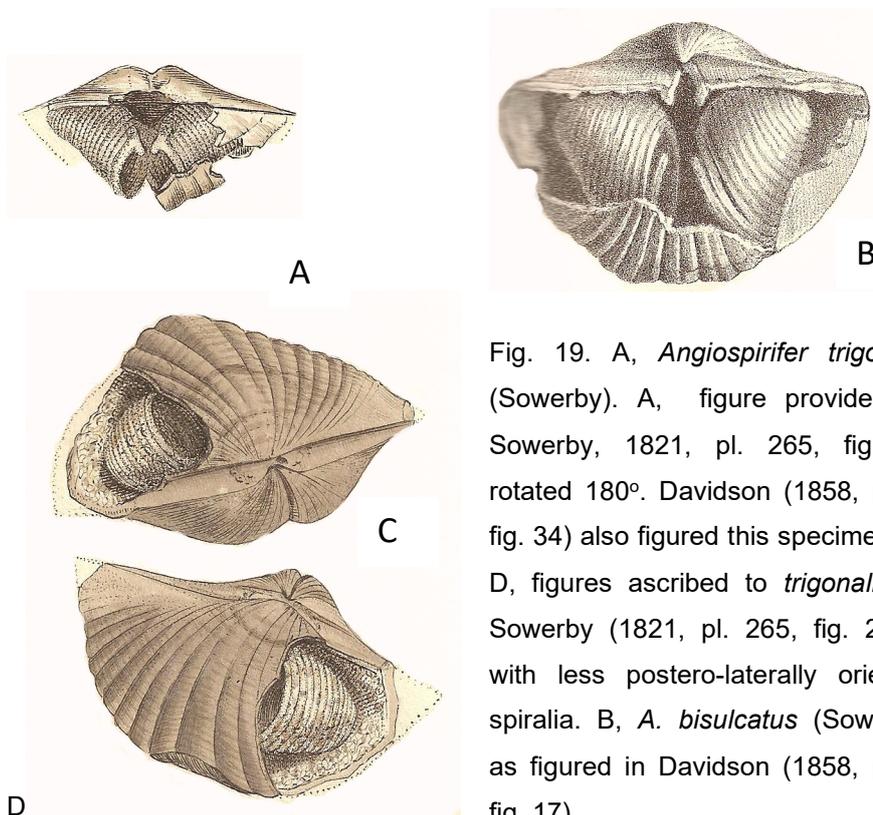


Fig. 19. A, *Angiospirifer trigonalis* (Sowerby). A, figure provided by Sowerby, 1821, pl. 265, fig. 1), rotated 180°. Davidson (1858, pl. 5, fig. 34) also figured this specimen. C, D, figures ascribed to *trigonalis* by Sowerby (1821, pl. 265, fig. 2, 3), with less postero-laterally oriented spiralia. B, *A. bisulcatus* (Sowerby) as figured in Davidson (1858, pl. 6, fig. 17).

SUBFAMILY VARUNINAE WATERHOUSE, 2016

Fig. 20

Varuna Waterhouse, 2004, *Adminiculoria* Waterhouse & Gupta, 1979 and *Alispirifer* Campbell, 1961 are small in size with highly transverse shape and acute cardinal extremities. A few costae are developed, and the delthyrial construct, internal plates, and umbonal callosity are features typical of the superfamily. The first mentioned genera come from the Early Carboniferous of Kashmir, India. *Alispirifer* Campbell, 1961 comes from the Visean to Moscovian of east Australia, and was placed in Pterospiriferinae by Carter (2006, p. 1815). It has simple plicae and open delthyrium, and placement as an ally of Angiospiriferinae would seem to be more in keeping with its age and distribution. As shown in Fig. 20D, a pleromium with large umbonal callosity is developed as in many Trigonotretoidea.

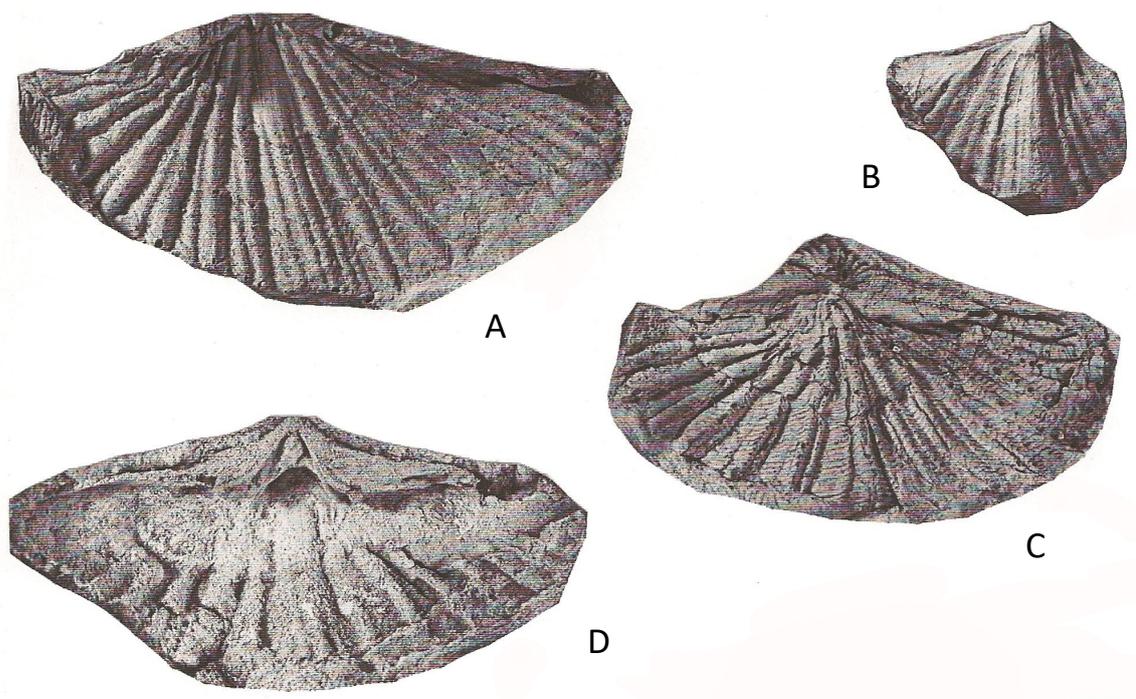


Fig. 20. *Varuna varuna* (Diener), A, latex cast of dorsal valve. B, dorsal internal mould. C, latex cast of dorsal exterior (lectotype). D, latex cast of ventral valve, showing umbonal callosity and pleural ridges, forming a large apparent pleuralium rather than subdelthyrial connector plate. Specimens x2. From Fenestella Shale (Visean-Serpukhovian) of Kashmir. (Waterhouse 2004). Although reported as Moscovian by some authorities, the so-called Fenestella Shales of the northwest Himalaya in Kashmir and correlative beds in Nepal contain large Rugosochonetidae of mostly Visean extending into Serpukhovian age, as confirmed by G. Termier, pers. comm.

FAMILY GEORGINAKINGIIDAE WATERHOUSE, 2004

Fig. 21 – 28

***Georginakingia* Waterhouse**

Type *Georginakingia* Waterhouse and *Sulciplica* Waterhouse are highly transverse and closely plicate forms, with trigonotretoid plates and delthyrium. *G. aviculiformis* Waterhouse has been referred to *Fusispirifer* Waterhouse by Clarke (1987) as endorsed by Gourvenec in Gourvenec & Carter (2007, p. 2781) and Archbold & Thomas (1987), but the genus lacks the subdelthyrial connector plate which is well developed in *Fusispirifer* (see Waterhouse 2016, Fig. 240, p. 196) and has the delthyrial construct typical of Trigonotretoidea. The genus

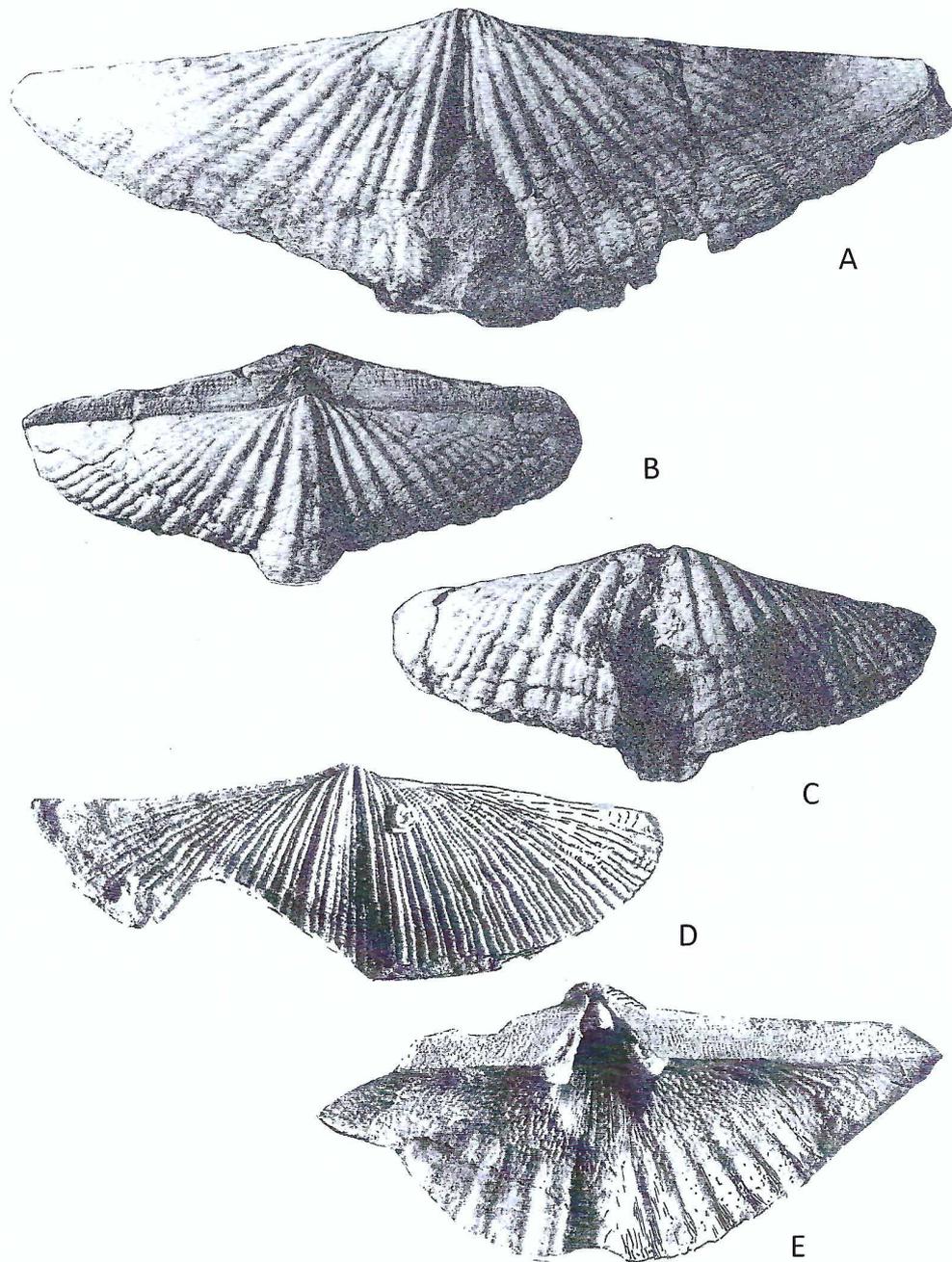


Fig. 21. *Georinakingia aviculiformis* Waterhouse. A, large ventral valve. B, C, dorsal and ventral aspects of another specimen. D, finely costate ventral valve. E, ventral valve interior, showing bulbous umbonal callosity. Specimens x1, from Guadalupian beds of Tasmania, Australia. (Clarke 1987; Archbold & Thomas 1987).

certainly looks like *Fusispirifer*, having closely costate plicae (Fig. 21D). In *Sulciplica transversa* on the other hand, costae are largely limited to the sulcus and fold

(Fig. 21). Specimens referred to *Trigonotreta* by Archbold (2003, Fig. 4.15-18) from the Beckers Formation at Cranky Corner, New South Wales, show a very few sulcal ribs and moderately prominent fold that carries suggestions of either a median channel or traces of subdued ribs. Transverse in outline, they might mark an early appearance of *Sulcipleca* or close ally. A genus common in the Early Permian of east Australia is *Unicostatina* Waterhouse, with few or only one to three sulcal ribs (Fig. 23). This is a subelongate genus, so determination of the orientation of the spiralia would be interesting.



Fig. 22. *Sulcipleca transversa* Waterhouse, ventral valve exterior, x1. From mid-Guadalupian of Eagle Hawk Neck, Tasmania. (Clarke 1987).

***Tasmanospirifer* Waterhouse, *Angulispirifer* Waterhouse**

Another genus from east Australia, *Tasmanospirifer* Waterhouse, 2016 (Fig. 24A), has only a moderate number of costae, with rounded cardinal extremities: it possibly evolved from *Unicostatina*. *Angulispirifer* Waterhouse, 2016, p. 266 (Fig. 23D) is characterized by plicae with angular crests, wide hinge, alate cardinal extremities and channelled fold without costae. It is probably a member of Georinakingiidae, though its angular plicae are reminiscent of the Early Carboniferous genus *Varuna* Waterhouse, 2004 (Fig. 20C). The course of spiralia has not been determined for any of the constituents, but *Sulcipleca* and *Georinakingia* are so transverse that it would seem most unlikely that their spiralia were anything other than laterally directed.

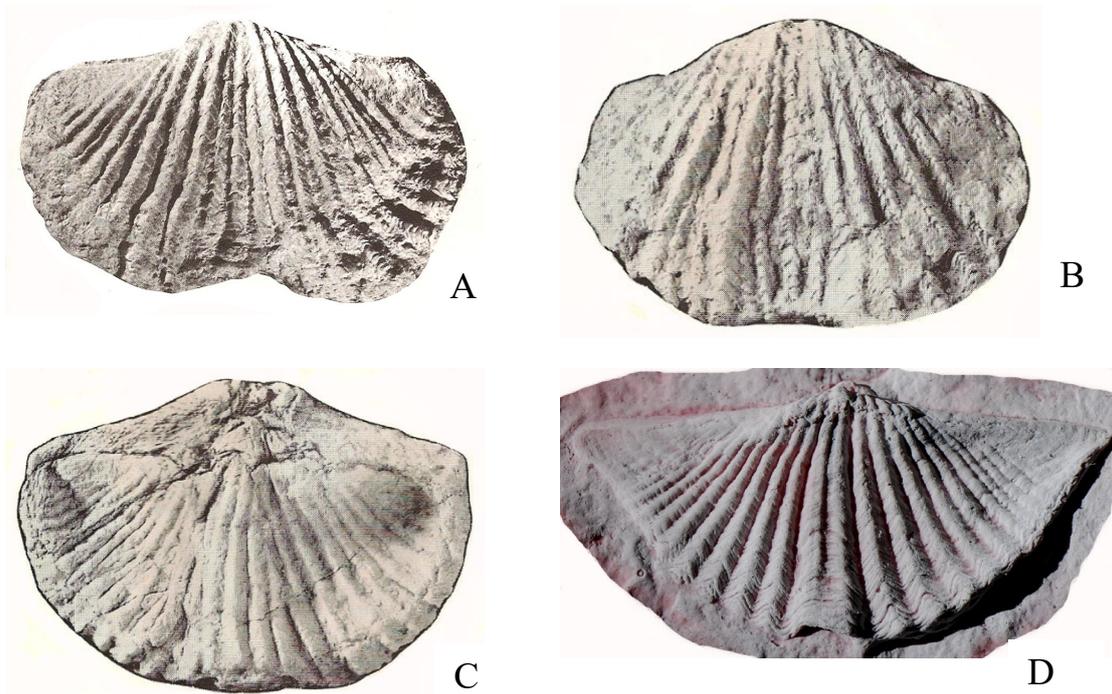
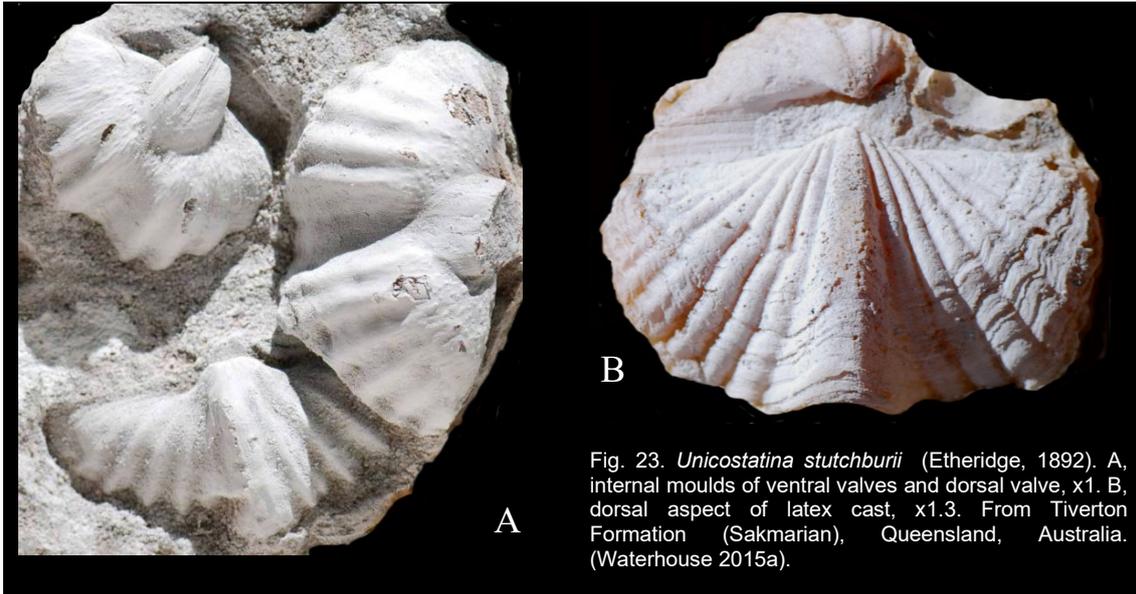


Fig. 24. A-C, *Tasmanospirifer clarkei* Waterhouse, 2016 from Berriedale Limestone (upper Sakmarian), Tasmania, Australia. A, ventral valve holotype TMF 36817, x1. (Clarke 1979). B, C, ventral and dorsal valves (Armstrong 1968). D, *Angulispirifer phalaena* (Dana, 1849), external mould BM (NH) BR 3219 of dorsal valve, holotype x1, kept at Museum of Natural History, London. From Eaglehawk Neck, Tasmania, Australia (upper-Guadalupian). (Morris 1845).

Cancellospirifer Campbell

Cancellospirifer Campbell, 1953 of Middle Permian age is much smaller than other members of Trigonotretoidea, with obtuse cardinal extremities and simple plicae (Fig. 25). The sulcus is simple and the fold entire. There must be questions over the maturity of the shell, given

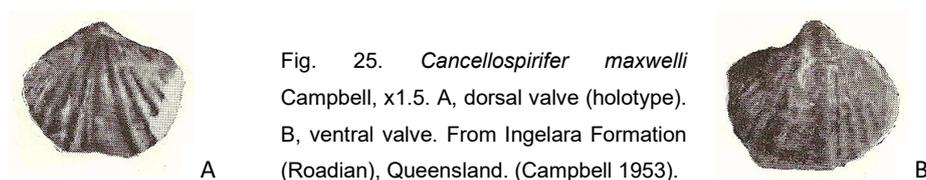


Fig. 25. *Cancellospirifer maxwelli* Campbell, x1.5. A, dorsal valve (holotype). B, ventral valve. From Ingelara Formation (Roadian), Queensland. (Campbell 1953).

its small size, but provisionally the type species is regarded as fully grown, implying descent by pedomorphosis. Serial sections of a toptype suggest laterally directed spiralia, but the anterior parts are obscure (Waterhouse 1968, text-fig. 17A). The nature of the spiralia suggest that it descended from *Aperispirifer* or ally, rather than from *Trigonotreta* or *Grantonia*, and given its shape and the nature of the ornament, ancestral stock was provided by *Neilotreta*, as described below.

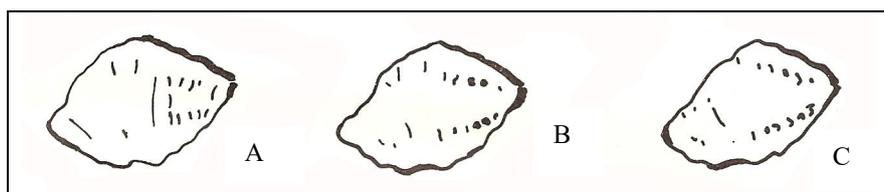


Fig. 26. *Cancellospirifer maxwelli* Campbell, x1.5, serial sections through a toptype specimen from Ingelara Formation (Roadian), Queensland. (Waterhouse 1968).

Neilotreta Waterhouse

Neilotreta Waterhouse, 2008 was proposed for *Trigonotreta occidentalis* Thomas, 1971, small shells (Fig. 27) with numerous simple to weakly costate plicae, the costation varying between species and outstandingly broad costate fold and sulcus. The spiralia are laterally directed (Thomas 1971, Text-fig. 40). Cisterna & Shi (2014) could not distinguish *Neilotreta* from *Trigonotreta*, but comparison between type *Trigonotreta* and type *Neilotreta* shows that *Neilotreta* possesses a very broad and closely costate dorsal fold with well rounded crest and no subsidiary subplicae, and, for the type species, comparatively simple plicae with few

costae, with no pleromium, whereas the dorsal fold in *Trigonotreta* has a narrow but rounded crest and is slightly higher, with a subsidiary subplication along the flanks, and fewer costae, and plicae tend to be more costate than most species assignable to *Neilotreta*. A pleromium is well developed as a rule. Some specimens ascribed to *Trigonotreta* are obviously less

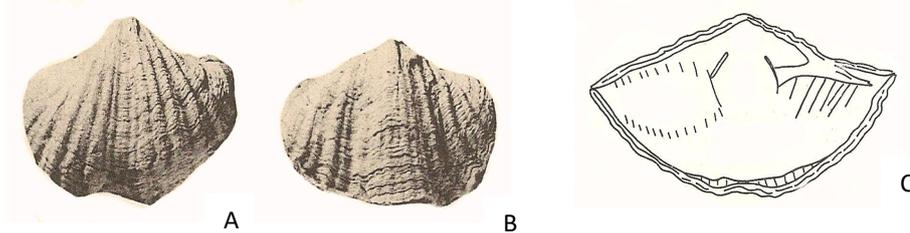


Fig. 26. *Neilotreta occidentalis* (Thomas). A, B, ventral and dorsal aspects of holotype, x1. C, section showing interior with laterally directed spiralia, x1. From upper Lyons Group (Asselian) of Western Australia. (Thomas 1971).

less costate so as to approach *Neilotreta*, but lack growth increments, so that they provide dubious information on the nature of the external ornament. Furthermore, the spiralia in *Neilotreta* are laterally directed. My initial diagnosis for *Neilotreta* failed to draw out the distinctions adequately, but competent paleontologists are well aware of the limitations of diagnoses and prefer to look at the type specimens, or their illustrations, and centre their understanding on the material rather than human interpretations. Other species appear to be allied with *Neilotreta*. *T. tangorini* Archbold (2003, Fig. 4) from the Beckers Formation and doubtfully Cranky Corner Formation of the Cranky Corner Basin in New South Wales is similar, and another species, *N. thomasi* (Waterhouse, 2004, pl. 7, fig. 6-9) comes from a Sakmarian fauna of the Bijni tectonic unit in the Garwhal Himalaya of India and has more costae, approaching the even more costate species *N. lakeensis*. Spiralia are not known for the latter three species. These species are similar to each other, specifically distinguishable, and form a lineage recognizable through their broad dorsal fold and overall size and shape. Cisterna & Shi (2014) argued that *Neilotreta* was a synonym of *Trigonotreta*, but this is contradicted by the nature of the spiralia, as well as details of fold, plicae and costae and aspects of the delthyrial construct.

***Brachythyridella* Waterhouse & Gupta, *Pericospirifer* Cisterna & Archbold**

Brachythyridella Waterhouse & Gupta (Fig. 28A, B) displays a number of comparatively simple plicae that developed anterior costae, such as also appeared in the sulcus and over the fold. The fold may be channelled and is not costate. There appears to be no well-developed pleromium. These descriptors apply to the mature shell. Species of the genus are

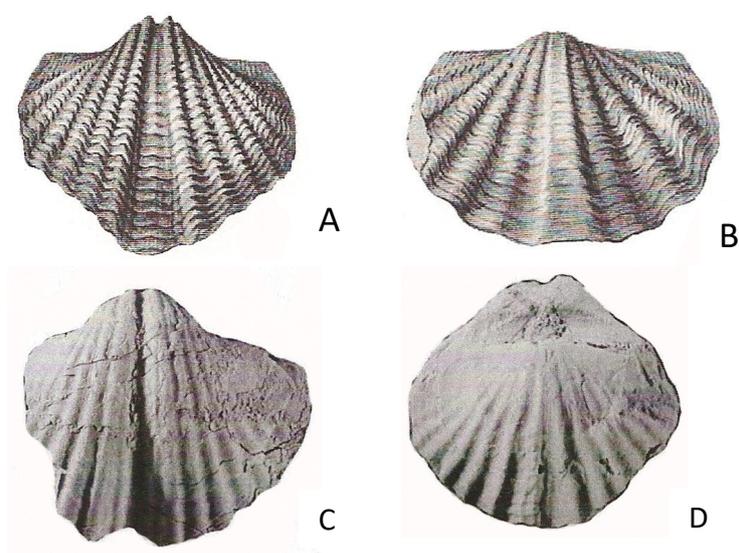


Fig. 28. A, B, *Brachythyridella narsahensis* (Reed), ventral and dorsal views, x2. From Lower Permian (Sakmarian) of India (Reed 1928). Note the presence of growth increments, which ensure that the material is not decorticated. C, D, *Pericospira sanjuanensis* (Lech & Acenolaza, 1987). C, ventral view. D, dorsal view. Specimens x1, decorticated, from mid- to upper Pennsylvanian of Argentina. (Cisterna & Archbold 2007).

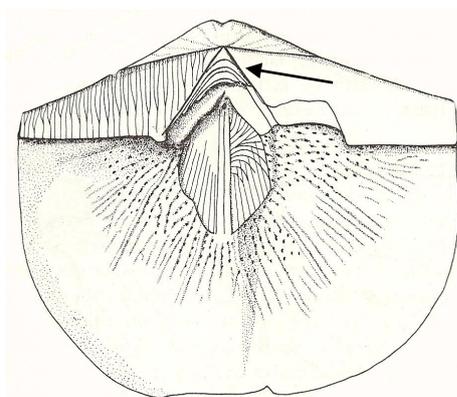
found in India as well as Australia. Ignoring the difference in fold profile, Clarke (1990) dismissed the genus on the basis that immature *Trigonotreta* were similar, and that view was endorsed by Archbold (1991), as if ontogeny did not matter and involved no potential change from immaturity into maturity, and the nature of the fold were unimportant. Ironically, the Argentinian genus *Pericospirifer* Cisterna & Archbold, 2007 (Fig. 27C, D) from the Del Salto Formation also has simple plicae on the whole, with anterior costae and channelled dorsal fold, and pleromium with apical callus. That this genus is a junior synonym of *Brachythyridella* seems highly possible, if it can be proven that the difference in development of a pleromium is unimportant. Orientation of spiralia has not been determined

for either taxon, and it should not be concluded that Archbold was the only paleontologist to neglect this important feature. These latter genera, *Cancellospirifer*, *Brachythyrius*, *Brachythyrinella* and if valid *Pericospirifer* are all rather similar in shape and size, and arguably merit tribal distinction.

THE RELATIONSHIP TO NEOSPIRIFERIDAE Waterhouse, 1968

Frechella Legrand-Blain, *Neospirifer* Fredericks

Fig. 28. *Frechella gynneriformis* (Legrand-Blain), ventral valve showing neodeltidium, as arrowed. From Early Carboniferous of Algeria. (Legrand-Blain 1971).



Like members of the Trigonotretoidea, genera within Neospiriferidae lack a subdelthyrial connector plate, and strong plication and fine and numerous costae suggest a possible relationship to *Aperispirifer* and to *Georginakingia*. *Neospirifer* and allies are in part characterized as a rule by the possession of a delthyrial cover plate or neodeltidium (Poletaev 1997; Waterhouse 1968, 2016, Fig. 243), which covered the delthyrium at roughly the level of the adjoining interareas to each side, extending from the outer level of the dental plates, in contrast to the subdelthyrial connector plate, which lay at the level of the inner edge of the dental plates. It would seem likely that the neodeltidium arose from a single stegidial plate, unlike the deltidium, which has formed from two plates. Of course it can be lost from specimens, and in addition, it appears likely that in some branches of Neospiriferidae, such as Septospiriferinae, the neodeltidium did not develop. The genus *Spirifer striatus fascicostatus* Menchikoff, 1930 and *Neospirifer fascicostatus gywinneriformis* Legrand-Blain, 1971, later called *Frechella* Legrand-Blain, 1986, from the upper Visean of Algeria, has fine costae, strong plicae, and posterior delthyrial cover plate (Waterhouse 2016, Fig. 244, 246), as shown herein as Fig. 28 and interpreted by Waterhouse (2016) as close to *Neospirifer* and

Betaneospirifer, signifying development well before the appearance of *Trigonotreta* and *Grantonia* in the Early Permian of Australia. On the other hand, *Costuloplica* of Pennsylvanian age has fine costae and numerous plicae, but this genus lacks a neodeltidium, and from external appearance and many internal features, could have arisen from either trigonotretid or neospiriferid stock, a matter that will be further clarified when the orientation of the spiralia is resolved. But the nature of the delthyrium is close to that of Neospiriferidae.

The position of Gypospiriferinae Waterhouse, 2004

Gypospiriferinae are a group of closely ribbed and moderately plicate transverse spiriferiform genera, *Gypospirifer* centred in Texas, United States, with many species described by Cooper & Grant (1976). Most of their figures show that the delthyrium is closed by stegidial plates, and otherwise was open with no sign of a subdelthyrial connector plate, though a low umbonal callosity was developed in some specimens. In *G. condor* (d'Orbigny) from Bolivia, regarded as typical of *Gypospirifer* by Cooper & Grant (1976), a connector plate was shown in section by Legrand-Blain (1986), and Samtleben (1971, pl. 11, fig. 1a, b, 2, 3) figured postero-laterally directed spiralia, to strongly suggest that Gypospiriferinae are an unusual group, provided that these features were invariant. The placement of *Gypospirifer* in Neospiriferidae by Poletaev (1997), Carter (2006a) and, Angiolini & Long (2008) and in Neospiriferinae with severe reservations by Waterhouse & Campbell (2021, p. 41) seems most unlikely.

RELATIONSHIPS TO OTHER SPIRIFERIFORM GENERA

ALLEGIANCE UNCERTAIN

Genus *Fasciculatia* Waterhouse, 2004

Fig. 30 - 32

Some genera may prove to belong to either Trigonotretoidea or Spiriferoidea, an adherence not always easy to resolve, given a certain lack of attention to morphological detail other than general shape and ornament, and further hindered by poor preservation. The genus *Fasciculatia* Waterhouse, 2004, based on *F. greenlandicus* Waterhouse, 2004 from Wuchiapingian beds of Greenland, offers some intriguing challenges through examination of a related and slightly older (Roadian-Wordian) species called *Spirifer striatoparadoxus* Toula, 1873, and revised by Lee et al. (2016) and Waterhouse (2020) from specimens found in

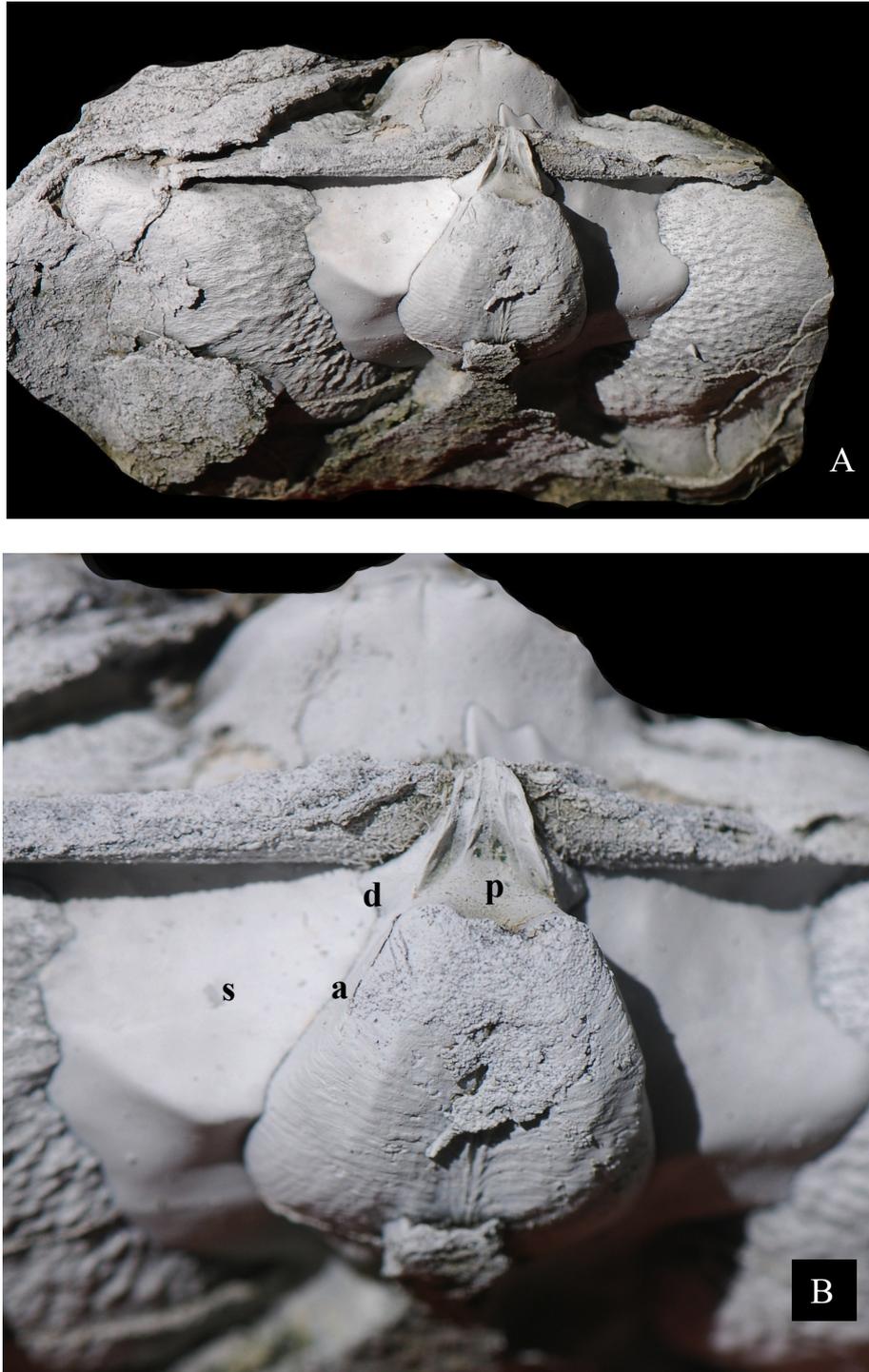


Fig. 30. *Fasciculatia striatoparadoxus* (Toula), internal mould of ventral valve, featuring the interarea and outer surface of subdelthyrial thickening behind the muscle field, x1.5 and x3. Specimen GSC 142469 From Trolld Fiord Formation (Wordian), Canadian Arctic Archipelago. The dorsal surface of the umbonal callosity coincides with the junction between dental plates and adminicula, and carries scars suggestive of pedicle muscles. a = adminiculum; d = dental plate; p = position of umbonal callosity; s = undissolved shell.



Fig. 31. *Fasciculatia striatoparadoxus* (Toula), internal mould of ventral valve GSC 142470, featuring the interarea and outer surface of subdelthyrial thickening behind the muscle field, x2. Troid Fiord Formation (Wordian), Canadian Arctic Archipelago.

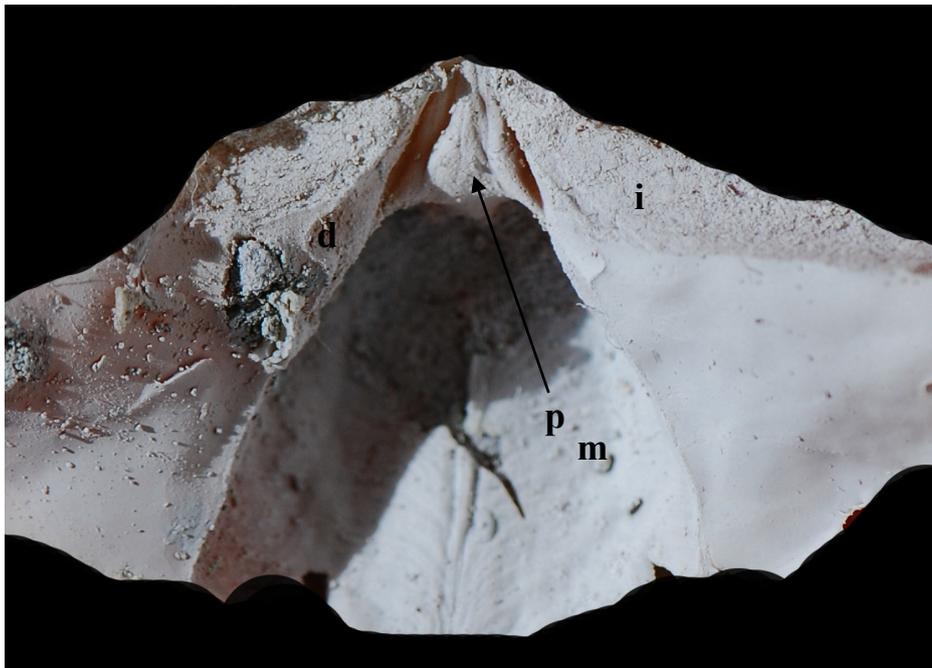


Fig. 32. *Fasciculatia striatoparadoxus* (Toula), latex cast of delthyrial region in ventral valve GSC 142469, featuring the interarea (i) and outer surface of subdelthyrial thickening behind the muscle field (p), the muscle field (m), d = dental plate, x4. See Fig. 30. Troid Fiord Formation (Wordian), Canadian Arctic Archipelago.

Spitsbergen and the Canadian Arctic Archipelago. The species are large and subrectangular in shape, with feebly developed plicae and numerous fasciculate costae, externally close to *Spirifer* Sowerby, 1814. But unlike *Spirifer*, no specimens have clearly demonstrated the presence of a free-standing subdelthyrial connector plate, and instead show a massive umbonal build-up of secondary callus. What is intriguing is that in Canadian specimens assigned to *striatoparadoxus*, the shell thickening appears to occupy what would have been the umbonal space beneath a subdelthyrial connector plate and its outer or dorsal surface is positioned just the same as the subdelthyrial plate, lying between the dental plates and adminicula. The illustration of Fig. 32 strongly suggests that a connector plate was present. The surface lacks any suggestion of a swollen callosity as in the pleromium that is developed in many Trigonotretoidea. Perhaps the thickening under the plate was necessary because of the stress placed on the plate by being the seat of muscle scars. The space found in normal Spiriferidae is infilled by callus in this instance. The dorsal surface of the callus is very gently concave, and varies from smooth to a surface clearly marked by ridges and depressions, possibly suggestive of the attachment bases for scars for the pedicle.

So does this mean that *Fasciculatia* was an exceptional spiriferid, or an unusual trigonotretoid? Some caution is required in assessing any possibility of a trigonotretoid relationship, because early and even immature growth stages have not yet been determined for *Fasciculatia*, leaving unresolved the possibility that a subdelthyrial plate in early growth stages was present in the Canadian specimens, or *Fasciculatia* in general. Perhaps a subdelthyrial plate in early growth stages was later infilled from below by secondary callus. Moreover externally similar specimens referred to *striatoparadoxus* by Lee et al. (2016, Fig. 3D, 6-10) differ internally to a minor extent, pointing to intrasubspecific variation if not the merging of two different taxa, and possibly casting a cloud over the identification of the Canadian specimens. Serial sections in their Fig. 7A-C show umbonal thickening but little more. Their Fig. 10E suggests a possible subdelthyrial plate, but Fig. 10G suggests possibly no delthyrial or umbonal thickening. Their text on p. 124 mentioned that a delthyrial plate was absent or weakly developed, with a small apical callus (Fig. 10G?), without providing explicit description of what was meant by delthyrial plate

Suborder **MARTINIIDINA** Waterhouse, 2010

Infrasuborder **MARTINIIMORPHI** Waterhouse, 2010

Superfamily **MARTINIOIDEA** Waagen, 1883

Family **BRACHYTHYRIDAE** Fredericks, 1924

Subfamily **BRACHYTHYRININAE** Waterhouse, 2004

Fig. 33

***Brachthyrina* Fredericks, *Vasculumia* Waterhouse**

Brachythyrininae Waterhouse, 2004, p. 236 includes *Brachthyrina* and other members of the group, initially placed with Brachythyridinae (Brachythyridinae). But Carter (2006a) referred *Brachthyrina* to Angiospiriferinae Legrand-Blain, so Waterhouse (2016) shifted the subfamily to follow the treatment in the *Revised Brachiopod Treatise*. This was a mistake. Objections to the proposal of the subfamily Brachythyrininae by Gourvennec in Carter & Gourvennec (2007, p. 2789) were addressed by Waterhouse (2016, p. 245). The delthyrial construct was misrepresented to a degree by Waterhouse (2016, p. 243): it involves dental plates which fuse posteriorly and may form a large umbonal callosity in some species and genera, as exemplified by *Vasculumia* (Fig. 31). An association with martinioid genera is favoured by the nature of the internal plates. A number of genera are characterized by wide hinge, simple plicae, sulcal subplicae and no adminicula or tabellae, so as to suggest a possible martinioid

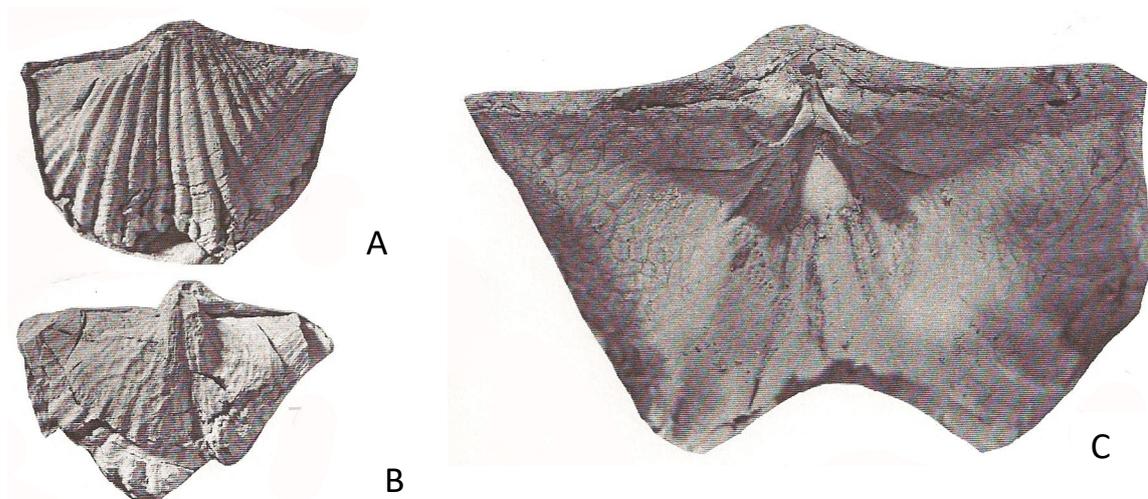


Fig. 31. *Vasculumia boonlomi* (Waterhouse). A, latex cast of ventral valve, holotype, x1. B, ventral internal mould, x1, showing well spaced mantle canal system. C, ventral internal mould, with dental plates but no adminicula, x2. From Ko Yao Noi Formation (Sakmarian) of southern Thailand. (Waterhouse 1981).

origin, whereas some attributes, such as the umbonal callosity and well spaced mantle canal system of some forms are reminiscent of features in Trigonotrotoidea. On the other hand, the very wide hinge suggests the *Revised Brachiopod Treatise* interpretation of Paeckelmannelloidea Ivanova, 1972, in so far as as one member family Strophopleuridae Carter, 1974 has wide hinge, simple plicae as in Brachythyrininae and allies. *Strophopleura* lacks adminicula according to Poletaev (2001), to strongly suggest a martinioid rather than paeckelmannelloid alliance. Most of the constituent genera in Strophopleuridae are of Upper Devonian and Lower Carboniferous age, and *Xizispirifer* Liang, 1990 of Upper Permian age probably belongs with Brachythyrininae, though classed as Pterospiriferinae Waterhouse, 1975 by Carter (2006b, p. 1818). It may well prove that Brachythyrininae is a junior synonym of Strophopleuridae, and that genera assigned to Strophopleuridae are in fact members of Martiniioidea.

THE SIGNIFICANCE OF A PLEROMIUM, CONNECTOR PLATE, AND ORIENTATION OF SPIRALIA

The differences in delthyrial construct and orientation of spiralia between various genera deserve to be noted in any description that purports to be objective, but the consistency and significance remain to be established. The chief indications of generic distinction have rightly centred on external criteria of major shell construct, shape and ornament, and internal plates have played an increasingly important role in helping to distinguish different evolutionary streams. Muscle scars and mantle canal systems and even spiralia have been regarded with a degree of indifference by many authors, aided by the current preference for silicified material, which does not display muscle impressions or mantle canals as well as internal moulds. But the features of the delthyrium surely require further study. Stegidial or neostegidial plates are readily lost, and the subdelthyrial connector plate or the pleromium are concealed features, and require preparation of fossil material. Even so, the delthyrial structures have been ignored in many otherwise notable studies. The development of a pleromium is strongly influenced by the ontogenetic development of an individual shell, and so the apparent variation may reflect the degree of maturity. But knowledge of its presence and form and consistency requires extensive study of populations preferably from different

paleolatitudes. As for the orientation of spiralia, the general acceptance that it was insignificant – or so one would gather from how frequently the orientation has been so widely ignored, even by such authorities as Carter and Archbold, – seems to reflect deplorable habit, challenged by the significance attached to the brachidium by students of Rhynchonellida and Terebratulida. That in the meantime has left the significance uncertain, because orientation is known for so few species, to leave the present classification in a precarious state of validity. One can only hope that more effort will be directed to discovering the orientation of spiralia and its consistency in Spiriferida. In the meantime, the fact that the delthyrial construct has been determined for more readily for a number of Spiriferida means that that has played a greater role in interpreting relationships.

REPOSITORIES

BM (NH): The Natural History Museum, London; **GSQ:** Geological Survey of Queensland, Brisbane; **MVP:** Museum of Victoria, Melbourne; **TM:** Tasmania Museum, Hobart; **UQF:** Queensland Museum, bulk storage depot, Hendra, Brisbane; **UQL:** fossil locality collected by Department of Geology, University of Queensland, Kept at Hendra, Brisbane.

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CRURAL PLATES IN BRACHIOPODS

Abstract

It is pointed out that plates which support the crura in various spiriferiform species are those also called the outer hinge plates, whereas according to the *Revised Brachiopod Treatise*, it is stated without any qualification that it is the inner hinge plates which support crural bases.

A QUESTION

Spiriferiform genera make up a substantial part of the corpus of Brachiopoda, and members of Spiriferidina are characterized in part by the absence of tabellae, also called inner hinge plates, or by some “dorsal adminicula”, a term I find long, clumsy, and repetitive. The outer hinge plates give rise to crural bases which lead to large spiralia, as emphasized by Campbell (1965). In other spiriferiform groups, such as Martiniidina, especially Ingelarelloidea, the outer hinge plates are supported by inner hinge plates, or tabellae. But Williams & Brunton (1996, p. 428) defined the crural plate as a “plate extending from the inner edge of the outer hinge plate or crural base to (the) floor of (the) dorsal valve”, which implies that it is the inner plate which supports the crura. To them therefore, the crural plates are the inner plates, placed inside and in many genera supported by the outer plates. Williams et al. (2000, pp. 371, 372) in a discussion of rhynchonellides and terebratulides asserted it was the inner plates that supported the crura and so were crural plates. A number of sketched examples (Fig. 329, 330) showed the brachiophores as lying between the two sets of plates, so it is not clear from the sketches which set of plates is actually supporting them, and in some sketches, the designations seem open for further examination. One of the co-authors, Brunton (1984), in his major study of Carboniferous brachiopods from Ireland, did not clearly differentiate hinge plates or crural plates, and therefore may not have been particularly concerned over this aspect of nomenclature and construct. For many of the Terebratulida illustrated by Cooper (1983), it is the outer plates that bear the crura, not the inner plates. The variation may be real, between different brachiopod groups, or have changed during the progress of time, or may be more apparent in some groups, or have been misinterpreted, a matter than would appear to require closer examination and exploration of shell structure. Johnson (2006, p. 1725) is somewhat uninformative but

possibly treated the inner hinge plates as crural plates. In Carter & Gourvenec (2006a, Fig. 1103, p. 1692), the unnamed plate forming the inner flank of the dorsal socket and essentially equivalent to an outer hinge plate or what I would call crural plate was shown as supporting the crural base (Fig. 1). There are no tabella or dorsal adminiculum. Carter in Carter & Gourvenec (2006b, p. 1748) wrote of “dorsal adminicula or crural plates”, as if dorsal adminicula correspond with the outer hinge plates, but they don’t – they correspond with inner hinge plates, and it is the crural plates which match the outer hinge plates. Elsewhere Carter did write of “dorsal adminicula” without any reference to crural plates. Campbell (1965, pp. 10-12) provided a summary of the variation displayed even within genera for various family groups, and it is clear from both his overview and the analysis in Cooper (1983) that the nature of crura in various brachiopods that the *Revised Brachiopod Treatise* was far too simplistic and at least partly inconsistent if not entirely inaccurate in its definition of crural plates. Is it even possible that the crura were attached to the inner hinge plates, and that these became severely reduced in size in spiriferids and terebratulids but remained otherwise intact, and still attached to the outer hinge plates? Study of shell structure might help resolve such a possibility.

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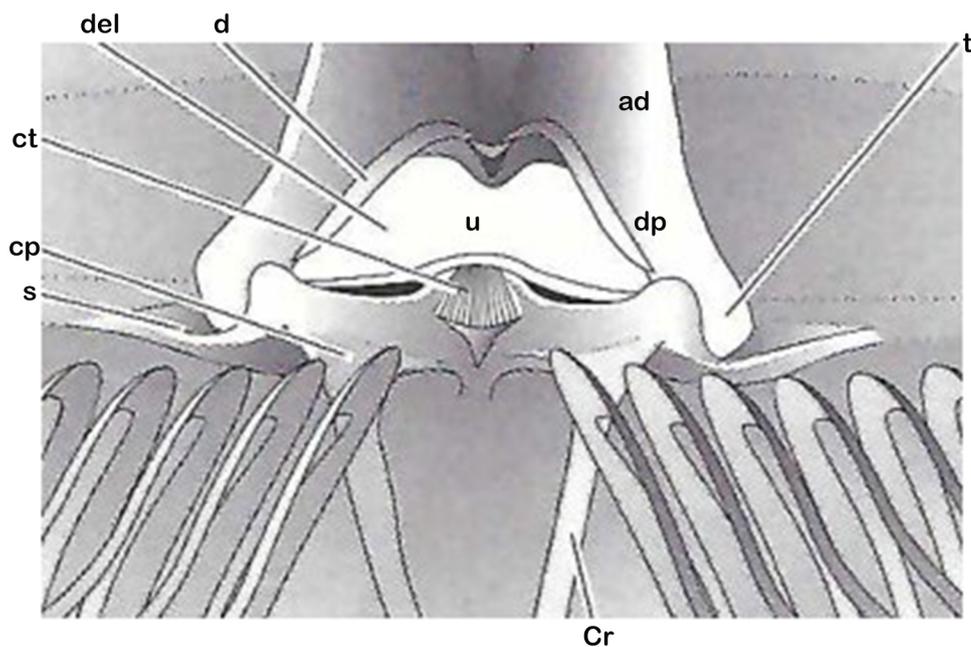


Fig. 1. The interior of a spiriferid (s. l.), as presented by Carter & Gourvenec (2006), with parts relabelled. ad – adminiculum; cp – crural plate; cr – crus leading to the spire; ct – ctenophoridium; d – dental track (“deltidial ridge”); del – delthyrium; dp – dental plate; s – socket; t – tooth; u – position of ventral umbo.

3. SPECIES OF THE BIVALVE *Eurydesma* MORRIS IN EAST AUSTRALIA

Abstract

Diagnoses and illustrations are provided for the species and subspecies ascribed to the bivalve *Eurydesma* Morris in the Permian of east Australia. Each taxon appears to have had a moderately limited range through time, just like most of the brachiopod and many but far from all the bivalves known from east Australia. *Eurydesma sacculus* (M'Coy) is judged to be a valid species, characterized by an extended anterior shell. It is judged likely to have been sourced from the latest Early Permian and early Middle Permian of the south Sydney Basin, as stated by M'Coy (1847), rather than the Allandale Formation of the north Sydney Basin. A new subspecies of this species is described from the upper Pebbley Beach, Snapper Point and Wandrawandian Formations of the south Sydney Basin. The range of these latter taxa reinforces a few brachiopods found in the upper Pebbley Beach Formation in pointing to correlation with part of the Gebbie Formation in the northern Bowen Basin, of likely Kungurian age, and this in turn reflects on the age and nature of the glacial conditions when the Pebbley Beach Formation was formed. There are conflicting ages provided for these formations by radiometry, and the present fossil evidence appears to support the Kungurian rather than Wordian value for the Snapper Point and Wandrawandian Formations.

New taxon: *Eurydesma sacculum snapperensis* n. subsp.

INTRODUCTION

Eurydesma cordatum was proposed by Morris (1845, p. 276, pl. 2, fig. 1, 2) for a Permian genus and species from east Australia, and is the type species of a genus found widely throughout the Early Permian of Gondwana. It seems that two species were inadvertently included by Morris (1845) in his proposed species, and one specimen has been designated lectotype by Dickins (1961), to incorporate inflated shells with steep anterior margin and umbones subanteriorly placed as a rule. One of the features of the other specimen figured by Morris (1845) as *cordatum* is that the umbones lie well behind the anterior margin, differing from the position of the umbo in the lectotype. This opens up the question of source for the

Morris specimens. It has been assumed for many years that Morris (1845) erred in stating that his material came from Illawarra, on the south coast of the Sydney Basin. Certainly, the conclusions of Dana (1849) and Etheridge & Dun (1910) were that the lectotype came from what is now known to be the Early Permian of the Hunter Valley in the north Sydney Basin, rather than the somewhat younger Permian of the Illawarra region in the south Sydney Basin, and this finds support in the nature of the matrix, as quoted by Dickins (1961).

There is less clarity over the source of the specimen with elongate anterior shell. Few *Eurydesma* in eastern Australia are presently known to have such a prominent anterior shell, but one suite of specimens is found sparsely in the Darlington Limestone of Maria Island, Tasmania, as shown by Clarke (1992), and the other is found in the general Illawarra region, where Runnegar (1979a) and Shi & McLoughlin (1997, Fig. 15) drew attention to two beds crammed with *Eurydesma*, near the base of the Snapper Point Formation and top of the underlying Pebbley Beach Formation. Specimens of *Eurydesma* found in these rocks show a bulging anterior somewhat like that of the original Morris non-lectotype specimen. For example, from the Wandrawandian Formation, Runnegar (1970, pl. 16, fig. 6) figured a comparatively complete specimen from North Head near Ulladulla, Waterhouse (1987b, pl. 3, fig. 8) figured a similar specimen from Point Upright, near Ulladulla, and Shi & McLoughlin (1997, pl. 8, fig. 1) illustrated another such specimen from near Clear Point in the Snapper Point Formation.

Comparison with the lectotype of *Eurydesma cordatum* Morris

Specimens were assigned to *Eurydesma cordatum* by Dana (1849, eg. pl. 8, fig. 1, 1a) from Harpers Hill, "Illawarra" (really Hunter Valley), New South Wales, and in a major overview of the genus in east Australia, Etheridge & Dun (1910) recorded specimens of *cordatum* from Allandale, near west Maitland in the Hunter Valley of the northern Sydney Basin, and from Maria Island, Tasmania. Runnegar (1969) added newly found occurrences from the "lower sandy unit of the Conjola Formation," now Wasp Head Formation, of the south Sydney Basin. In a substantial review, Runnegar (1970) confirmed occurrences of the species *cordatum* in the Darlington Limestone of Maria Island and Allandale Formation at Harpers Hill, Hunter Valley, and Clarke (1992, Fig. 20C, F, E) illustrated specimens of *cordatum* from Maria Island.

The approach of the Morris non-lectotype *Eurydesma* to *E. konincki* Johnston

The taxon *Eurydesma konincki* (Johnston, 1888, p. 121) is close to the non-type specimen assigned to *cordatum* by Morris (1845, pl. 15 lower figure). The species *konincki* has a prominent anterior shell extending well in front of the umbones, and is very like material figured as *E. hobartense* from Maria Island of Tasmania by Etheridge & Dun (1910, pl. 20, fig. 6, pl. 21, fig. 3, pl. 22, fig. 1, 2, pl. 23, fig. 5, pl. 24, fig. 3?, pl. 25, fig. 4, 5) and later named *protrudus* by Waterhouse (2008a), though this name is now deemed redundant. A fine specimen was figured as *hobartense konincki* by Clarke (1992, p. 38, fig. 20C, together with fragments figured in Fig. 20F and 20E) from the "Spirifer zone" of the Darlington Limestone on Maria Island. (See Fig. 8B herein). These are moderately inflated shells with low umbones. The Tasmanian species is like south Sydney Basin *Eurydesma* figured by Runnegar (1970, pl. 16, fig. 6), Waterhouse (1987b, pl. 3, fig. 8) and Shi & McLoughlin (1997, fig. 1, 2) in having a prominent anterior shell, but differs in its lesser inflation and less prominent umbones, and the anterior curvature of the shell in the Morris figure suggests a specimen that is lower than in *konincki* or the specimens from the south Sydney Basin figured by Runnegar (1970) and others, though there are no published additional views of the Morris material, so that the degree of inflation and presence or absence of lateral sulcus are not certain. The south Sydney Basin specimens figured in Shi & McLoughlin (1997) and others appear to be more inflated than *E. konincki*, and a lateral sulcus is developed, with a better defined posterior wing, unlike the arrangement in *konincki*. At present, the Morris non-lectotype material cannot be confidently assigned to any species, but according to Dickins (1961), S. Ware at the Natural History Museum in London indicated that the matrix appeared to resemble that of material from Maria Island (Dickins 1961), to suggest possible identification with *E. konincki*, with differences between specimens to be ascribed to infrasubspecific variation.

The relationship to *Eurydesma hobartense* Johnston, 1887

Pachydomus hobartensis Johnston (1887, p. 16; 1888, pl. 16, fig. 2) was named for a small slender shell from Tasmania, refigured by Runnegar (1970, p. 95, pl. 15, fig. 3). The species was interpreted by Runnegar as being a medium-sized to large little inflated shell with inconspicuous umbones, a shallow lateral sulcus and almost circular outline, and specimens

were figured from the Berriedale Limestone (Runnegar 1970, pl. 15, fig. 1, 2) and much older specimens from the Tasmanites bed and Quamby and Bundella Mudstones in Tasmania. The trouble is that the lectotype designated by Runnegar is so small that it is surely juvenile, and therefore of uncertain relevance to the classification of adult shells. Bundella and Quamby Mudstone specimens figured by Runnegar (1970, pl. 15, fig. 6-11) have especially low umbones, and the shape is not in full agreement with that of the lectotype. *Eurydesma* from the base of the “upper sandy unit of the Conjola Formation”, now Snapper Point Formation, was assigned to *E. hobartense* by Dickins et al. (1969, p. 219) and Runnegar (1970, p. 97), but this identification was not reinforced by any figures. A striking unpublished photograph of the *Eurydesma* shell bed in the upper Pebbley Beach Formation by Prof. B. Runnegar which was kindly provided to Prof. G. R. Shi and passed on to me shows a number of small specimens shaped like the Tasmanian lectotype of *hobartense*, except for their slightly blunter umbones, together with a mature specimen, shaped like the Wandrawandian specimens with extended anterior shell. The photograph suggests the small *hobartense*-like specimens grew into shells with extended anterior, like the specimens from Snapper Point and Wandrawandian Formations. Runnegar (1979a, pp. 276-277, Fig. 14) provided details on *Eurydesma* occurrences in the upper Pebbley Beach and lower Snapper Point Formations.

The close association between upper Pebbley Beach and lower Snapper Point beds is strengthened by the true stratigraphic position of *hobartense*. Runnegar was informed that the likely source of *hobartense* was the Berriedale Limestone, but this has been adjusted to the somewhat younger Deep Bay Formation of Tasmania (Clarke 1992; *in* Farmer 1985, pp. 35-37). Accompanying fossils include *Ingelarella* (now *Tumulosulcus*) *undulosa* Campbell, 1961, first described from the Kungurian upper Gebbie Formation of the Bowen Basin, and close to *T. cessnockensis* (McClung, 1978) from the Wandrawandian Formation, together with *Wyndhamia dalwoodensis* [= *typica*] (Booker), found in the Snapper Point Formation. Clarke & Banks (1975) and Clarke & Farmer (1976) classed the Deep Bay Formation as belonging to faunizones 6 – 8, or lower to middle Lynington Stage of Clarke & Farmer (1976), and many of the listed fossils suggest an age within the Kungurian Stage *sensu* Waterhouse (2008b), as elaborated on p. 228. The Tasmanian *Wyndhamia* has a high number of slender prostrate spines anteriorly over the ventral valve, unlike the arrangement

in *W. typica* Booker, as figured by various authors, including Muir-Wood & Cooper (1960, pl. 5, fig. 7, 9, 10) and Brunton et al. (2000, text-fig. 405.3a-c), and was named *W. clarkeina* Waterhouse (2001, p. 75), though a subspecific designation would be more appropriate. The overall fossil lists strongly suggest a broad Snapper Point or less likely lower Wandrawandian correlation for the Deep Bay Formation. It seems highly likely that type *Eurydesma hobartense* was at least partly coeval.

The relationship of the Morris non-lectotype to *alisulcatum* Waterhouse, 1987b

Eurydesma alisulcatum was proposed for specimens from the Wandrawandian Formation, the holotype AMF 46915 coming from near Ulladulla. At first sight, the type specimen differs substantially from the Morris lower figure in being much more upright and well inflated, with less extended anterior. On the other hand, the growth lines show that there was an anterior ventral bulge, approaching that of Wandrawandian, Snapper Point and Pebbley Beach specimens with extended anterior shell.

The relationship of *alisulcatum* to *Eurydesma sacculum* (M'Coy)

Eurydesma sacculum (M'Coy) is based on a large specimen with valves conjoined, bearing an extended anterior shell, low posterior wing, and lateral sulcus. It is more inflated and higher in outline than *E. konincki* (Johnson). Various articles have synonymized the species with *E. cordatum*, in the belief that the type came from the Allandale Formation of the north Sydney Basin, but *sacculum* does not agree in shape, having a protruding lower ventral margin extending well in front of the umbones, a well-defined lateral sulcus, and slender low posterior wings. It closely agrees in these aspects with the holotype of *E. alisulcatum* Waterhouse (Fig. 15A), and is close in several respects to *Eurydesma* specimens that are well inflated, but of lesser height from the Pebbley Beach, Snapper Point and Wandrawandian Formations. According to M'Coy (1847), *sacculum* came from Black Head (Geroa) or Wollongong, indicative of an origin from the south Sydney Basin along the South Coast of New South Wales. Outcrops near Black Head and Wollongong are a little younger than those of the Snapper Point and Wandrawandian Formations, and have not yielded any known specimens of *Eurydesma*. It appears possible and indeed likely that the M'Coy locality was described in terms generalized enough to include the outcrops then without named

settlements near Snapper Point. These beds are all much younger than the Allandale outcrops with *cordatum* in the north Sydney Basin.

The sedimentological record for the Pebbley Beach Formation

Fielding et al. (2008a) offered a fine analysis for the lower Pebbley Beach exposures along the coast. They recognized a lower unit of short-lived stratal units, 23 according to Fielding et al. (2008a) and 22 according to Fielding et al. (2008b), each unit made up of diamictite grading up into fine mudstone. The need for caution remains, because there is little information over specific locations, and no photographs provided, but more information especially on older sediments is provided in Tye et al. (1996), and Runnegar (1979b) stated that the Clyde Coal Measures are developed nearby in the core DM Callala DDH1 between the basal Pebbley Beach Formation and underlying Wasp Head Formation. The diamictites were believed to reflect retreating glaciation followed by eustatic sea-level rise, though other interpretations are of course possible, such as advancing glacial surges providing abundant sediment, followed by a pause in which erosion slowed, or even fluctuations reflecting short-lived seasonal changes in sediment, due to temperature change. The younger Pebbley Beach sediments were interpreted as representing an interval of waning or at least retreating glaciation, followed by a final episode of estuarine and tidal flat deposits, as expounded in Fielding et al. (2006), still under the influence of cold climate, when glendonites formed. The entire formation was said to be only 75m thick, half that estimated by Gostin & Herbert (1973). To Fielding et al. (2008b), the formation offered the best example of the second major glaciation recognized by those authors in the Permian of east Australia, as developing during Sakmarian and Artinskian time.

Age of the lower and middle Pebbley Beach Formation

The age of the Pebbley Beach Formation still needs to be substantiated. Fielding et al. (2008b) asserted that the Pebbley Beach Formation had yielded a "rich marine invertebrate fauna". That is a substantial misrepresentation. Trace fossils are present: certainly ecologically significant, but with age implications poorly understood. Gostin & Herbert (1973, Fig. 2) matched the beds with Rutherford and Farley Formations of the north Sydney Basin,

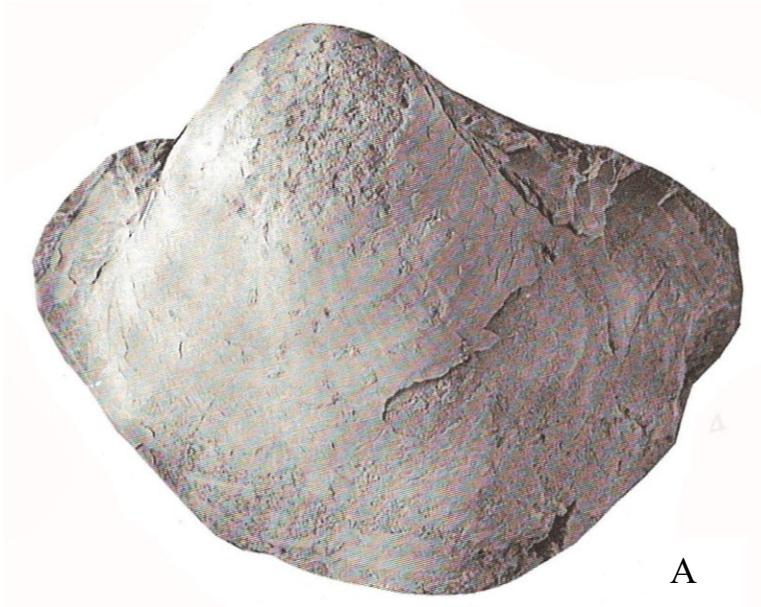


Fig. 1. A, bivalve figured as *Eurydesma* sp. by Shi & McLoughlin (1997, pl. 8, fig. 4), NMV P1456828, National Museum of Victoria, Melbourne, slightly reoriented. This approaches *Megadesmus* in appearance, and comes from the Snapper Point Formation. What is the real identity of the shell? Have similar shells from underlying beds been identified with *Megadesmus*? Has it been decorticated? B, holotype of *Megadesmus globosus* Sowerby, plaster cast, not retouched, from Museum of Natural History, London, L 61043, from the Allandale Formation. Specimens at natural size, that of *Megadesmus* with a much better preserved exterior.

citing *Megadesmus nobilissimus*. But it seems possible, as illustrated in Fig. 1, that *Megadesmus* or its close ally *Protraxia* persisted as high as the overlying Snapper Point Formation, so that such shells ranged in age well beyond that of the Farley Formation. The lower and middle beds, making up most of the Pebbley Beach Formation, could prove to be Sakmarian or lower Artinskian, judged by foraminiferal reports by Scheibnerova (1982) and Stutchbury (1989), which are somewhat confusing given that completely different taxa were identified in the two studies, and focused on faunas of limited time range, the two studies not providing any comparative assessment with foraminifera from Aktastinian deposits, as represented in the Sirius Shale and upper Cattle Creek beds of the Bowen Basin. Dickins & Runnegar in Dickins et al. (1969, p. 218) listed impoverished faunas from the so-called upper Conjola beds, later named Pebbley Beach deposits, mentioning only five macrofaunal species, none described, illustrated or validated. A study by Shi et al. (2020) after additional collecting were able to find only scattered and rare brachiopod species, together with a few undescribed bivalves. The reliance for age on “a rich marine invertebrate fauna” by Fielding et al. (2008b) remains misplaced, and their statement contradicted by Gostin & Herbert (1973), and by the published record on paleontological studies for the formation. Only one adequate macrofossil, possibly – conjecturally even – from the lower or middle beds, has ever been figured, and that has long been lost (see p. 89, Fig. 12), with its geographic and stratigraphic source highly uncertain. The fossil does suggest highly probable affinities with *Eurydesma ovale* Etheridge & Dun from the Ravensfield Formation of the north Sydney Basin, of likely Sakmarian age, and related subspecies from Sakmarian and Aktastinian (lower Artinskian) faunas in Queensland, but such similarities can be regarded as no better than provisional, given that the specimen is lost, and its source never better than speculative. Fossil localities have been collected from the basal beds of the Pebbley Beach Formation, recorded as 1275, 1276, and 1277 in the core of D. M. Callala D.D.H. 1 by Runnegar (1979b, Fig. 3) on the north side of Jervis Bay, but no fossil list has been published. There has been an identification of the ingelarellid species *ovata* Campbell by McClung (1978) which is predominantly of Sakmarian age, but no locality was provided, and no description or figure given in substantiation: perhaps it came from the core samples quoted above, but that is speculation. However, as a speculation, it is one or more of those

collections that yielded the *Ingelarella ovata* specimens reported by McClung (1978). The middle and lower parts of the Pebbley Beach Formation therefore remain poorly dated. Macro-fossils in the form of incomplete *Eurydesma* hinges are found in the middle of these beds, but no macro-fauna is reliably known from older beds. The report (in a poster) of palynomorph *trisina* by Evans (1991), with meagre published documentation, might suggest that the lower Pebbley Beach beds are of Sakmarian age, and Smith et al. (2017) tabulated correlation of the entire Pebbley Beach Formation with the *Pseudoreticulatispora pseudoreticulata* APP2.1 and *Microbaculispora trisina* APP2.2 palynomorph zones, though giving no specific references. These palynomorph first-entry zones are accompanied in marine deposits of east Australia by cool rather than cold water macro-faunas, as elaborated in Parts 7 and 8 of this monograph, and therefore seem out of phase with the cold-water deposits described by Fielding et al. (2008a, b). Indeed both key palynomorphs ranged into beds of much younger Permian age, so there may not be any firm guarantee that the occurrences of *trisina* or *pseudoreticulata* were first appearances. In that respect, the presence or absence of accompanying macrofossils would be useful for helping to indicate whether a palynomorph was “first entry” or a survivor. Herein, the close lithological comparison proposed by Fielding et al. with the upper Cattle Creek and Sirius Shale of the Bowen Basin is assessed as having considerable value, which would suggest an Aktastinian age, and the underlying Yarunga Coal Measures and Tallong and Yadbora clastics could match, loosely, part of the Rutherford and Farley Formations of the north Sydney Basin. There is some support from the nature of the *Eurydesma* species described by Frech (1891), because his species is close to *E. ovale sulcatum* Waterhouse, 1987b from the Roses Pride Formation of the southeast Bowen Basin, which is correlative with the Sirius Shale. These *Eurydesma* share anteriorly placed umbones, and steeply inclined anterior shell with Frech’s figure of *antarctica*, although Frech’s shell is somewhat higher. Moreover the hinge as figured for *antarctica* by Frech (1891) is very close to that of a Sirius Shale specimen figured by Runnegar (1970, pl. 17, fig. 9). This matter is further discussed on p. 90, and palynomorph assessments are further discussed on p. 69ff.

Age of the upper Pebbley Beach Formation

The age of the upper Pebbley Beach Formation is more secure. These beds were treated as

a separate unit by Stutchbury (1989), and they appear to be of early Kungurian age, on the basis of *Eurydesma*, shared with the overlying Snapper Point Formation.

In terms of macro-fauna from the upper Pebbley Beach Formation, brachiopod *Notospirifer gentilis* Waterhouse suggests an early Kungurian age through correlation with the Gebbie fauna of the northern Bowen Basin (Waterhouse & Jell 1983; Waterhouse 2008b), and accompanying brachiopods mostly conform with or permit a Kungurian age (Shi et al. 2020). The brachiopods do not signify a Sakmarian-Artinskian age, but point to an age little greater than that of the *Wyndhamia typica* (Booker) biozone found in the overlying Snapper Point Formation. *Eurydesma* found near the top of the Pebbley Beach Formation also helps to associate the beds with the Snapper Point and Wandrawandian Formations, reinforcing the age implications from the brachiopods. Any assertion that the Pebbley Beach Formation is separated by a major disconformity from the overlying Snapper Point Formation as in Smith et al. (2017) is certainly not supported by either the sediments and what is exposed of their stratigraphic relationships, nor by the macrofossils. There was a change in type of sediment, and that was all – no great faunal change, and bedding remained conformable (Runnegar 1979a). From available evidence, the upper Pebbley Beach Formation belongs not with glacial phase 2 of Fielding et al. (2008a, b), but with their glacial phase 3. Any correlation between upper Pebbley Beach and upper Cattle Creek beds (Fielding et al. 2008a, p. 136; 2008b, p. 121) is wrong. Both have marine faunas, which belong to two different faunal zones, separated by rocks and faunas of the Baigendzinian Substage, which is the upper part of the international Artinskian Stage. The Cattle Creek Formation marks the genuine end of the so-called “glacial phase 2”, such as it was. Distinguished by fossils of the *Echinalosia preoivalis* - *Ingelarella plica* Zone, it was at least two macrofaunal zones older than the upper Pebbley Beach faunas, lower Artinskian in age as compared with lower Kungurian. The age of the middle and lower Pebbley Beach Formation is uncertain: the beds may have been Kungurian, closely associated with the upper Pebbley Beach sediments, or Aktastinian as favoured by the sedimentological analysis in Fielding et al., or Sakmarian as may be inferred from palynomorph and foraminiferal lists.

Implications from the age of the Pebley Beach Formation

The presence of *Eurydesma* with extended anterior near the top of the Pebley Beach Formation, implies that the upper Pebley Beach Formation was little older than the Snapper Point Formation. The lower Snapper Point Formation is intruded by monzonite, and zircons from that intrusion have been dated as early Kungurian through SHRIMP analysis by A. Nutman, as recorded by Shi et al. (2020). The age of the intrusion implies that the intruded formation cannot be younger than early Kungurian, and given the overall geological context, likely to have been slightly older, possibly no more than early Kungurian in age. Given the age of *Notospirifer gentilis* and the presence of the particular kind of *Eurydesma*, the age of the upper Pebley Beach Formation is deemed to be early Kungurian – equivalent to Saraninian or early Filippovian in the Urals of Russia, in sediments treated as international world stratotype, though not as fossiliferous as correlative beds in the United States.

Such an age conflicts with ages preferred for the Pebley Beach Formation over several decades, but is closer to what was understood of the stratigraphic succession during the last decades of the nineteenth century and early twentieth century. In those days, it was thought by Laseron (1910) that the entire succession of the south Sydney Basin matched only what was called the Upper Marine Series, later to be called the Maitland Group, of the north Sydney Basin, in the Hunter Valley. There was deemed to have been a substantial gap below, with the entire Dalwood Group missing. Then very early Permian was found at the base of the succession by V. Gostin, and the basal faunas were matched with those of Allandale Formation of the Hunter Valley, through the studies by Runnegar (1969), Dickins et al. (1969), Gray (1969) and Gostin & Herbert (1973). The beds were named Wasp Head Formation, and faunas assigned to what are now the *Crassispinosella subcircularis* and *Strophalosia concentrica* Zones (Nillsen 1982; Briggs 1998; Cisterna & Shi 2014; Waterhouse 2013, 2015a, herein, pp. 194-198). The Pebley Beach Formation in various articles was stated to be Sakmarian-Artinskian, partly on the basis of reported *Eurydesma hobartensis* as in Runnegar (1970), for which the age had been misinterpreted as equivalent to Berriedale Formation (of upper Sakmarian age) and undescribed but listed *Megadesmus nobilissimus* de Koninck, originally found in the Farley Formation, of Sakmarian age. The report of *Notospirifer gentilis* and revision of *Eurydesma* means that at least the upper part of

the Pebbley Beach Formation is little older than the Snapper Point Formation, and that much of the Sakmarian and Artinskian, equivalent to the Rutherford and at least lower Farley Formations in the north Sydney Basin is represented in the underlying coal measures and clastics of the Tallong and Yadboro conglomerates, or, as implied by palynomorphs, restricted to the lower Pebbley Beach Formation.

One possibility is that Stutchbury (1989) was correct in suggesting that the upper Pebbley Beach beds were distinguishable, and it may well be time for this aspect to be reassessed. The base of the formation rests on Wasp Head Formation, which is of Asselian age and in part correlated with the Allandale Formation. There are no outcrops of the Clyde Coal Measures (Tye et al. 1996) found further north and best developed inland and west of Ulladulla, but whether the Clyde Coal beds overlay the Wasp Head Formation or passed laterally into them is a matter for dispute, and although various studies have correlated the two units, the bore D. M. Callala D.D.H.1 shows the Pebbley Beach beds as overlying the Clyde Coal Measures (Runnegar 1979b, Fig. 3). The Clyde Coal Measures were lumped with the (in reality, possibly overlying) Yarrunga Coal Measures and (in reality, probably underlying) Wasp Head Formations in Smith et al. (2017) within one *Pseudoreticulatispora pseudoreticulata* APP2.1 palynomorph zone. Yet the Wasp Head Formation contains two macrofossil zones, named after strophalosiid species and demonstrably of Asselian age, older than the APP2.1 zone (see pp. 195-196). Surface outcrop of the type Yarrunga Coal Measures of Gray (1969) in the upper Shoalhaven River valley has since been drowned. Herbert (1972) showed the Yarrunga beds as overlying Tallong Formation in one sequence, matched with Clyde Coal Measures lying over the same formation in other sections, and Gostin & Herbert (1973, Fig. 2, 3) pictured the Clyde Coal Measures as ranging from lower Rutherford to much of the Greta Coal Measures, shown as time-transgressive and fringing a time-transgressive Pebbley Beach and Snapper Point Formations, but these assessments seem likely to have been in error. Bore-holes indicate that the Yarrunga beds are overlain by and were interpreted as passing laterally into Snapper Point Formation (Tye et al. 1996). Shi & Weldon (2002, p. 16) suggested the Yarrunga beds might have been stratigraphically equivalent to the Pebbley Beach and even part of the overlying Snapper Point Formation, and Mantle et al. (2010) and Smith et al. (2017) showed the Yarrunga Coal Measures as

passing laterally into the lower Pebley Beach Formation. Why the coal measures could not have been separate entities in time is far from clear, but much more study would seem to be needed, with tightly controlled geological mapping and extensive and detailed paleontological study based chiefly on palynomorphs to clarify what is after all a structurally comparatively simple if sedimentologically complex region. Certainly any sharing of the long-ranging key palynomorph *Pseudoreticulatispora pseudoreticulata* would not establish any detailed correlation in itself: it has to be part of a proven sequence of palynomorph form taxa. Accepting the premise that the Yarrunga Coal Measures underlay at least part of the Pebley Beach Formation, the question arises afresh about its age, though correlations in Smith et al. (2017) appear to rule out correlation with the Greta Coal Measures.

There is still very poor age control over the ages of the Clyde and Yarrunga Coal Measures, and the question of whether they passed laterally into marine sediments with faunas is still contentious.

The report of the palynomorph *Protohaploxypinus trisina* by Evans (1991) suggests that the lower Pebley Beach Formation could be more or less upper Sakmarian age, to follow the correlation scheme outlined in Part 7 of this report. Assuming of course that the *trisina* palynomorph did mark a first incoming and not persistence of the form, or much less likely, an example like that of *Protohaploxypinus trisina* reported by Calver et al. (1984) in the *Crassispinosella subcircularis* Zone of Tasmania, presumably based on a misidentification. The palynomorph summaries suggest the need to recognize two gaps, one gap above the Wasp Head Formation, for which the upper beds belong to the *Crassispinosella subcircularis* Zone, equivalent to the *Pseudoreticulatispora confluens* palynomorph APP1.22 zone, and one gap below the upper Pebley Beach Formation. But the lack of systematic documentation, and keeping in mind the possibility of reworking and derivation through glacial outwash, implies that the occurrence of *trisina* requires considerable elaboration and refinement.

In Nicoll et al. (2017) and Smith et al. (2017, Fig. 7), the Pebley Beach Formation is placed in the lower *Protohaploxypinus trisina* and upper *Pseudoreticulatispora pseudoreticulata* palynomorph zones, separated by a substantial sedimentological and time

gap from the Snapper Point Formation. The *Phaselisporites cicatricosus*, *Praecolpatites sinuosus* and *Microbaculisporites villosa* palynomorph zones were considered to be missing.

The conflict

The conclusions of this study reinforce the SHRIMP radiometric age determination for monzonite in the lower Snapper Point Formation by A. Nutman as reported in Shi et al. (2020), and raise questions about recent evaluations of the south Sydney Basin Permian in Metcalfe et al. (2015), Nicoll et al. (2015; 2017) and Smith et al. (2017). These authorities assigned the upper Pebbley Beach Formation to the *trisina* APP2.2 palynomorph zone, allegedly mostly upper Artinskian and basal Kungurian in age, though as judged from wide-ranging macro-faunal data the first entry occurrences for *trisina* were probably older, and its nominate zone is in no way Kungurian judged through macrofaunal evidence with radiometric support (Waterhouse 2015a, and see pp. 207, 220 herein). The Pebbley Beach Formation was shown by Smith et al. (2017) as separated by a long time-gap from the overlying Snapper Point Formation, which was allocated to the mid-Wordian in the International time scale, and assigned to the *Didecitriletes ericianus* palynomorph zone APP4.2. That long pause in deposition between the two formations, lasting for most of the Kungurian Stage, all of the Roadian Stage, and the lower Wordian Stage is not supported by macro-faunal and some radiometric data. The radiometric value for monzonite in the Snapper Point beds challenges the correlations summarized in Smith et al. (2017), being of lower Kungurian in age. Admittedly radiometric procedures have been subject to much review over recent years, and clearly the SHRIMP method has yielded some highly aberrant results, but it will be assumed until judicious adjustments (if any are necessary) are achieved that the results are close to being approximately correct. The monzonite could not have been intruded during Kungurian time into beds as young as mid-Wordian. Moreover the brachiopod and bivalve fossils support a close relationship between Snapper Point and underlying Pebbley Beach faunas, just as implied by the stratigraphic relationships between the two formations. They indicate that the upper Pebbley Beach rocks are little older than Snapper Point faunas. The *Eurydesma* bed and the overall nature of the fauna indicate an early Kungurian age, consonant with faunas in Queensland, Tasmania, Western Australia and New Zealand, where, for the two latter regions, it has been possible to some extent to strengthen

provisional age determinations through fusulines, ammonoids and conodonts, as expounded in Part 7. Recent evaluations of the east Australian Permian based on radiometric values and adjustments to the palynomorph zones have dismissed macro-faunal determinations as being without value, but the world stratotypes and biochronological successions are based on marine fossils, not on radiometric values, nor on palynology. Whilst species described by Shi et al. (2020) and herein are not numerous, all of the available fossils are consistent in their implications for age. None suggest a greater age for the upper Pebley Beach Formation. The Farley-Rutherford correlation proposed by Dickins et al. (1969) is challenged by numerous brachiopod and mollusc studies from faunas in the southeast Bowen Basin (Waterhouse 1986a, 1987a, b), northern Bowen Basin (Waterhouse 2015a) and Gympie Province (Waterhouse 2015b). The upper Pebley Beach fossils do not match the pre-Kungurian fossils from these regions, any more than they match the fossils from the Farley and Rutherford beds, or correlative faunas of Western Australia or New Zealand.

Radiometric determinations

Several critical age evaluations were made for the Sydney Basin Permian by Metcalfe et al. (2015). In the south Sydney Basin, the upper Broughton Formation at the top of the Shoalhaven Group was evaluated through CA-IDTIMS as 263.51 +/- 0.05 Ma, to indicate a mid-Capitanian age, perfectly in concert with the brachiopods and molluscs, which have been assessed as belonging to the *Echinalosia ovalis* Superzone, containing many typical fossils, such as *Terrakea brachythaera* and *Ingelarella mantuanensis* of mid-Capitanian age. But in the north Sydney Basin, the Rowan Formation at the top of the Greta Coal Measures was dated through CA-IDTIMS by Metcalfe et al. (2015) as 271.60 +/- 0.08 Ma of lower Roadian age. The stratigraphic source of the material used for radiometric evaluations is somewhat confused in Metcalfe et al. (2015, Table 1, p. 65, Table 2, p. 73 and Fig. 14, p. 75), because the sample was claimed to have come from both the Newcastle Coal Measures and the somewhat older Greta Coal Measures. The latter level is presumably correct, because the locality was also cited as involving the Rowan Formation, which is considered to lie within the Greta Coal Measures. Laurie et al. (2016, p. 12) essentially verified the Metcalfe et al. date for the Rowan Formation at 16.8m below the Branxton Formation, using zircons from Roberts et al. (1996, p. 411), to provide an age of 271.89 +/-0.14 Ma. Roberts et al. (1996, p. 411)

had provided an even younger SHRIMP age of 268.9 +/- 2.0 Ma at 11m below the Branxton Formation, recalculated and essentially verified by Laurie et al. (2016, p. 12) to be 268.9 +/- 3.1 Ma, though there are clearly risks and unadmitted uncertainties involved in such "recalculations". The Rowan Formation underlies the *Wyndhamia typica* macrofaunal Zone in the Branxton Formation, and this macrofaunal zone is also developed in the Snapper Point Formation, with Nutman's radiometric age determination of 281 Ma, equivalent to lower Kungurian. The two radiometric ages conflict, and both cannot be right. It may be objected that one should not select preferred radiometric ages and dismiss others, but it is the radiometric ages that are in conflict with each other, not the macro-faunal zonation, and a choice must be made.

Metcalf et al. (2015, Table 2) noted that whereas seven samples centred around their preferred age of 271Ma, one sampled zircon was distinctly older at 274.33+/-90 Ma. That greater age comes closer to the Nutman radiometric value and the paleontological data, to imply that the younger values could have been affected if not entirely controlled by metamorphic crystallization some time after emplacement, as an alternative to the possibility that the older zircon had been picked up during emplacement. A value of 274 Ma according to the charts in Smith et al. (2017) suggests a Kungurian age, and placement in the *sinuosus* APP3.2 palynomorph Zone, an age approaching that favoured by macro-faunal evidence, and less out of phase with Nutman's radiometric determination. The very stratigraphic column presented by Metcalfe et al. (2015, Fig. 17) raises questions. It showed for the south Sydney Basin highly compressed Snapper Point to Broughton Formations, and an extremely long-lasting Pebbley Beach Formation, at odds with even the interpretation in Fielding et al. (2008a).

SUMMARY OF SPECIES OF *EURYDESMA* FROM EAST AUSTRALIA

Eurydesma is a Permian bivalve first described from east Australia, and reported widely from the early Permian of Gondwana. Its classification is summarized in Carter et al. (2011, p. 11), shown as a constituent of the superfamily Eurydesmatoidea Reed, 1932 in the Hyporder Monotoidei Waterhouse, 2001, p. 134.

Genus *Eurydesma* Morris, 1845

Type species: *Eurydesma cordatum* Morris, 1845.

Lectotype: A critical aspect of the genus *Eurydesma* concerns the source and nature of the lectotype, as selected formally by Dickins (1961, p. 143). Morris (1845) had provided two figures, neither specifically designated by letter or figure. The figure at the top of the page shows the inner view of an incomplete right valve, and below, two valves, matching right and left, presumably of one specimen that is more complete. Dickins chose the small fragment as lectotype, rather than the better-preserved material. This choice conformed with the judgement by Etheridge & Dun (1910, p. 72) who featured a large number of *Eurydesma* to indicate that the upper figure in Morris conformed with their interpretation of *cordatum*. Morris had stated that both of his specimens came from Illawarra on the coast south of Sydney, exposing mostly Middle Permian rocks of the south Sydney Basin, but Etheridge & Dun (1910) assigned material to *cordatum* not from Illawarra but from older faunas at Harpers Hill and Allandale in the Hunter Valley, north Sydney Basin, and from the Darlington Limestone at Maria Island, Tasmania. Consulting Stan Ware at the Museum of Natural History in London, Dickins learned that the upper specimen, now the lectotype, was enclosed by matrix like that of material from Harpers Hill.

It has to be admitted that the hinge illustrated for the lectotype does not exactly conform with that depicted for Allandale or Maria Island specimens by Etheridge & Dun (1910) or Runnegar (1970), because the byssal notch and anterior boss slope backwards. And of course the overall shape is not revealed. But little can be done to remove uncertainties, and it is clear that a highly distinctive *Eurydesma* is well represented especially in the Allandale Formation of the Hunter Valley, Wasp Head Formation of the south Sydney Basin and Darlington Limestone of Maria Island. Should in future there be found cause to challenge the source and attributes of *E. cordatum* as now understood, then *E. ellipticum* Dana, 1847 is of secure source and description, and may replace the name *cordatum*.

Morphology

Morphology for *Eurydesma* has been discussed by many authors, notably Runnegar (1970), with contributions in Etheridge & Dun (1910), Waterhouse (1987b, 2008a) and Waterhouse & Gupta (1979).

***Eurydesma cordatum* Morris, 1845**

Fig. 2 - 5

- 1838 *Isocardia?* sp. Sowerby, p. 15, pl. 2, fig. [fide Runnegar 1970].
 1845 *Eurydesma cordatum* Morris, p. 276, pl. 12, fig. 1 (part, not fig. 2, 3).
 1847 *E. elliptica* Dana, p. 158.
 1847 *Eurydesma globosa* Dana, p. 158.
 ?1847 *E. cordatum* [not Morris] – M'Coy, p. 299.
 1849 *E. elliptica* – Dana, p. 700, pl. 7, fig. 6a-d.
 1849 *E. globosa* – Dana, p. 700, pl. 7, fig. 7, 7a.
 1849 *E. sacculus* [not M'Coy] – Dana, p. 700, pl. 8, 8a.
 1904 *E. globosum* – Koken, p. 97, text-fig. 1-3.
 1910 *E. cordatum* – Etheridge & Dun, p. 71, pl. 17, fig. 1, 2, pl. 18, fig. 1, pl. 19, fig. 3-5, pl. 20, fig. 2-5, pl. 21, fig. 1, pl. 22, fig. 3-5.
 1910 *E. cordatum* var. *sacculum* [not M'Coy] – Etheridge & Dun, p. 74, pl. 19, fig. 1, 2, pl. 20, fig. 1, pl. 24, fig. 1, 2.
 1910 *E. hobartense* [not Johnston] – Etheridge & Dun, p. 75, pl. 18, fig. 2, 3, pl. 20, fig. 6, pl. 23, fig. 1-4, pl. 21, fig. 2, 3.
 1969 *E. cordatum* – Runnegar, p. 279, pl. 18, fig. 9, pl. 19, fig. 5-7.
 1970 *E. cordatum* – Runnegar, p. 92, pl. 13, fig. 1-11, pl. 14, fig. 1-6, pl. 16, fig. 7, 8 (part, not pl. 16, fig. 9 = *glaebula*).
 1970 *E. hobartensis konincki* [not Johnston] – Runnegar, p. 97, pl. 15, fig. 7, 8?
 1987b *E. cordatum inflatum* Waterhouse, p. 140.
 1988 *E. cordatum* – Waterhouse, p. 176, pl. 4, fig. 1-4, pl. 5, fig. 1.
 1992 *E. cordatum* – Clarke, p. 34, Fig. 19A, B, 20D.
 cf. 2015b *Eurydesma* sp. Waterhouse, p. 34, Fig. 10D-F.

Diagnosis: Medium to large subelongate and moderately to highly inflated shells with steeply inclined anterior portion and umbones placed well forward as a rule. Dental boss where known large and closing anterior end of ligament

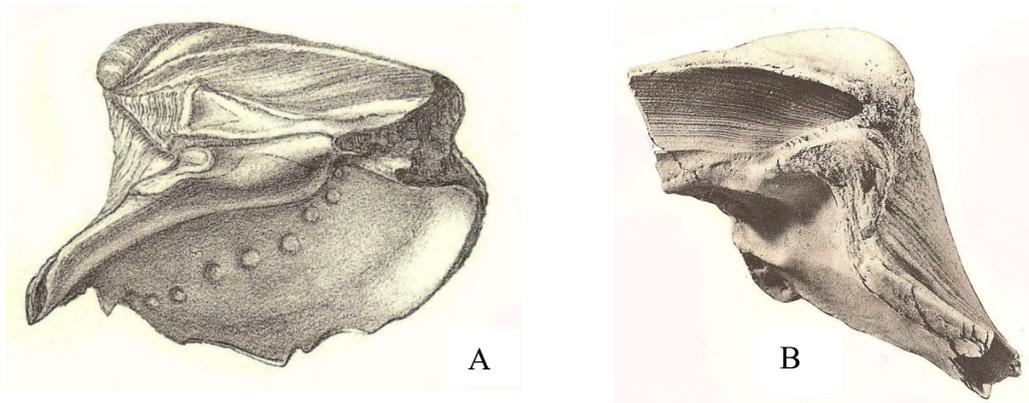


Fig. 2. *Eurydesma cordatum* Morris. A, internal aspect of lectotype BM (NH) PL 3267 (x1) as figured by Morris (1845, pl. 12), but tilted down to the right, also figured by Runnegar (1970, pl. 13, fig. 5), presumed to be from the Allandale Formation, Hunter Valley. The dorsal external view is also provided by Runnegar (1970, pl. 13, fig. 6). B, hinge of left valve UQF 50405 from Allandale Formation, Hunter Valley, as figured by Runnegar (1970, pl. 13, fig. 3), x1.

Lectotype: For *cordatum*, BM(NH) PL 3267, figured by Morris (1845, upper figure), designated by Dickins (1961, p. 143). Refigured by Runnegar (1970, pl. 13, fig. 5, 6) and herein as Fig. 2A. For *elliptica*: USNM 3601, figured as above by Dana (1849) and Waterhouse (1988, p. 4, fig. 4, pl. 5, fig. 1) and herein as Fig. 4, SD Runnegar (1970, p. 92). For *globosa*: USNM 3600, figured as above by Dana (1849) and Waterhouse (1988, pl. 4, fig. 3), SD Runnegar (1970, p. 92). The taxon *elliptica* came from the Allandale Formation at Harper's Hill, and *globosa* supposedly from Harpers Hill, "Illawarra district". The two original specimens of *globosa* as figured in Waterhouse (1988, pl. 4, fig. 2, 3) are small, and need to be oriented with hinge horizontally placed. For *E. cordatum inflatum* holotype, specimen figured by Etheridge & Dun (1910, pl. 17, fig. 1, 2, pl. 18, fig. 1), OD.

Age: Middle Asselian.

Discussion: The synonymy embraces many of the shells referred to *cordatum*. They come from beds of Early Permian age, principally the Allandale Formation of Hunter Valley, north Sydney Basin, Wasp Head Formation of south Sydney Basin and Darlington Limestone of Tasmania. Small shells from the Rammutt Formation of Gympie might be conspecific (Waterhouse 2015b). The shell is of highly characteristic shape, as diagnosed, although a little uncertainty remains, given the fragmentary nature of the lectotype and the implied



Fig. 3. *Eurydesma cordatum* Morris. A, left valve UQF 49081, x1, Darlington Limestone, Tasmania. B, UQF 36624 x1 as figured by Runnegar (1970, pl. 13, fig. 7) from Allandale Formation, Hunter valley, north Sydney Basin. (Runnegar (1970).

outline of the anterior shell, which seems more prominent than in most specimens from the Allandale Formation. Dana (1847, 1849) had proposed a so-called variety *elliptica* for material from the Allandale Formation, and the type, nominated by Runnegar (1970) and refigured in Waterhouse (1988) and herein as Fig. 4, may assume naming rights for the taxon, should it ultimately prove that the designated lectotype for *cordatum* belonged to a different taxon, and the Allandale shells become bereft of a specific name. *Eurydesma globosa* involves small specimens with short hinge, apparently long anterior which is reduced when the hinge is oriented horizontally, and short posterior shell, too small and from too insecure a source locality to warrant closer attention. *E. cordatum inflatum* Waterhouse has a long hinge and anteriorly placed umbones with reduced anterior. It is certainly distinguished from the lectotype of *cordatum*, but is herein regarded as a variation of *E. cordatum*, in conformity with the current interpretation of that species. As discussed later, *Eurydesma sacculus* (M'Coy) is regarded as discrete from *E. cordatum*, but specimens assigned to M'Coy's species by Dana (1849) and Etheridge & Dun (1910) from Harpers Hill cannot be distinguished from Harpers Hill specimens assigned to *cordatum* by the same authors.

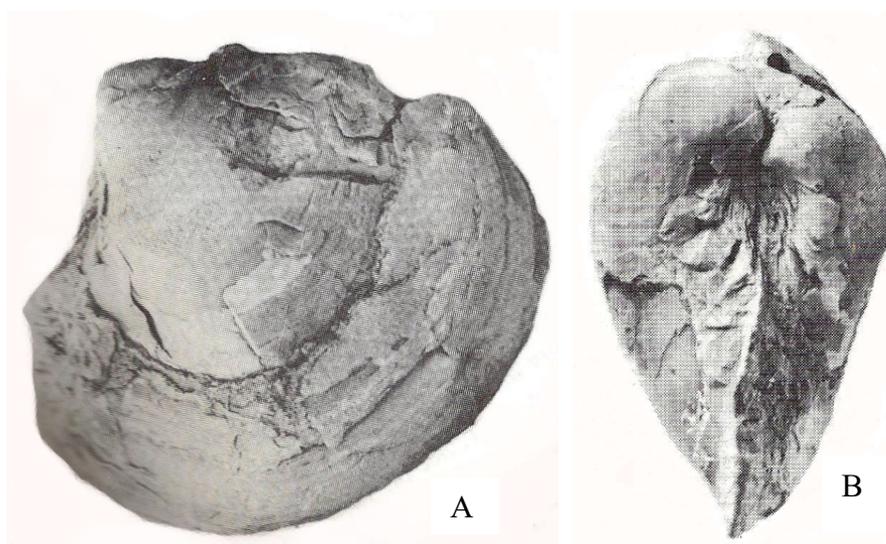


Fig. 4. *Eurydesma cordatum* Morris. A, B, left lateral and dorsal aspects of the type of *E. elliptica* Dana, USNM 3601 from Allandale Formation, Harper's Hill, Hunter Valley, x1. This is the senior name for material that reliably comes from Hunters Hill. (Waterhouse 1988).

Eurydesma burnettensis Waterhouse, 1986b

Fig. 5A, B

- 1924 *Eurydesma hobartensis* [not Johnston] – Browne & Dun, p. 199.
 1964 *E. hobartensis* [not Johnston] – Maxwell, p. 50. pl. 11, fig. 8-14.
 1970 *E. playfordi* [not Dickins] – Runnegar, p. 98, pl. 14, fig. 7-15.
 1970 *E. hobartense konincki* – Runnegar, p. 97 (part, pl. 15, fig. 9?).
 1970 *Eurydesma* sp. Runnegar, pl. 16, fig. 1.
 1970 *Eurydesma* cf. *cordatum* [not Morris] – Runnegar, pl. 17, fig. 1-4.
 1977 *E. playfordi* [not Dickins] – Webb, p. 56, pl. 2, fig. 1-3.
 1986b *E. burnettensis* Waterhouse, p. 4.
 1987b *E. burnettensis* – Waterhouse, p. 140.
 1998 *E. burnettensis* – Briggs, p. 28.
 2015a *E. burnettensis* – Waterhouse, p. 287, Fig. 237 lower right.

Diagnosis: Small inflated shells with long posterior hinge, poorly discriminated or no posterior wing or lateral sulcus, large right valve tooth-like projection formed by and below the ear-ledge and smaller left valve tooth and large socket in immature shells. There is a left valve socket rather than large dental boss below the anterior ligament.

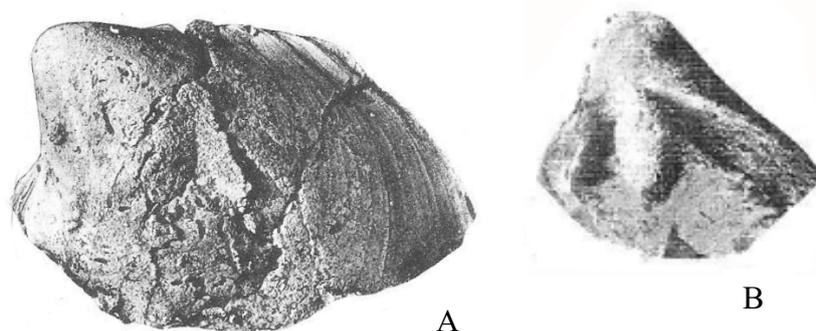


Fig. 5. *Eurydesma burnettensis* Waterhouse. A, left valve latex cast of UQF 51936, figured by Runnegar (1970). B, right valve interior UQF 43139, figured by Maxwell (1964). Specimens x1 from Burnett Formation, Yarrol Basin.

Holotype: UQ F 43148 figured by Maxwell (1964, pl. 11, fig. 13) and Runnegar (1970, pl. 14, fig. 12) from Burnett Formation, Queensland, OD.

Age: Chiefly or entirely Early Asselian, seemingly correlative with what is now called the *Strophalosia concentrica* Zone.

Resemblances: Briggs (1998, p. 28) considered that this species was represented widely in the earliest Permian of east Australia, including the basal Lochinvar Formation, the Gosforth

Shale of Browne & Dun (1924), and the Tasmanites bed at the base of the Quamby lithological assemblage in Tasmania. Shells from the Gosforth Shale (Fig. 6) at the base of the Lochinvar Formation in the Hunter Valley (Browne & Dun 1924) were figured by Runnegar (1970, pl. 17, fig. 1-4), and although compared to *cordatum*, have a unique shape, and long posterior hinge. A slender shell with long hinge and small pointed anterior umbones from the Quamby Shale (Runnegar 1970, pl. 15, fig. 9) was assigned to *E. hobartense konincki*, but somewhat approaches the Gosforth shells. The sharp umbo and shape certainly suggests such a possibility.

Discussion: The dentition in small shells of *Eurydesma burnettensis* is the reverse of the arrangement in *cordatum* and *ellipticum*. With increase in size, the depth of the byssal notch in *burnettensis* decreases, and the right valve tooth diminishes in size (Webb 1977). *E. playfordi* Dickins from the upper Lyons Group of Western Australia shows somewhat similar dentition in the right valve but lacks the deep left valve socket, and differs in shape, with less rounded outline, more linear anterior margin, and as a rule more anteriorly placed umbones. The species is somewhat younger than the present form. A swollen right tooth is present in a specimen from supposed Seaham beds of Hunter Valley according to Runnegar (1970, pl. 16, fig. 1), but the full shape of this specimen is not known.

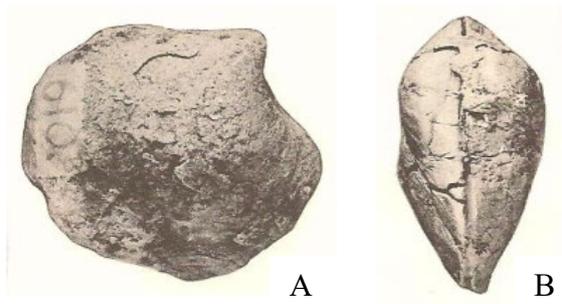


Fig. 6. *Eurydesma burnettensis* Waterhouse from Gosforth Shale, Hunter Valley, lateral and dorsal aspects, US 610B, x1. (Runnegar 1970). Repository not provided, presumably either Australian Museum or Geological Survey of New South Wales.

***Eurydesma konincki* (Johnston, 1887)**

Fig. 7 - 9

?1845 *Eurydesma cordatum* Morris, p. 276, pl. 12, lower figure.

1887 *Pachydomus konincki* Johnston, p. 15.

1888 *P. konincki* – Johnston, pl. 18, fig. 2, 3?

1888 *Pachydomus globosus* [Sowerby, invalid species] – Johnston, pl. 18, fig. 1, a, b.

1910 *Eurydesma hobartense* [not Johnston] – Etheridge & Dun, p. 75, pl. 20, fig. 6, pl. 21, fig. 3, pl. 22, fig. 1, 2, pl. 23, fig. 5, pl. 24, fig. 3?, pl. 25, fig. 4, 5.

1970 *E. hobartense konincki* – Runnegar, p. 97, pl. 15, fig. 6, 7, 8 (part, not fig. 5 = indet., fig. 9 = *burnettensis?*, fig. 10, 11 = cf. *ovale sulcatum*), pl. 16, fig. 2, 3 (part, not fig. 4 = n. det., fig. 5 = cf. *ovale sulcatum*, fig. 6 = *snapperensis*, fig. 9 = *ovale ovale*, pl. 17, fig. 10, 11 (part, not fig. 5, 6 = *antarctica* = aff. *ovale*, fig. 7-9, 12, 13 = aff. *ovale sulcatum*).

1992 *E. hobartense konincki* – Clarke, p. 38, Fig. 20C, ?E, ?F.

2008a *E. protrudus* Waterhouse, p. 121, text-fig. 62.

2015a *E. protrudus* – Waterhouse, p. 292, Fig. 237.

Type: For *Pachydomus konincki*: neotype UQF 51940 from Darlington Limestone, Fossil Cliff, Maria Island, Tasmania, Fig. 7 herein, designated by Runnegar (1970, p. 97). For *protrudus*, holotype AMF 14656 figured by Etheridge & Dun (1910, pl. 23, fig. 5) and Waterhouse (2008a, text-fig. 62), Fig. 8 herein, from Darlington Limestone, Maria Island, OD.

Diagnosis: Comparatively large and moderately inflated shells with lengthy anterior portion and subdued umbones.

Age: Upper middle Asselian.

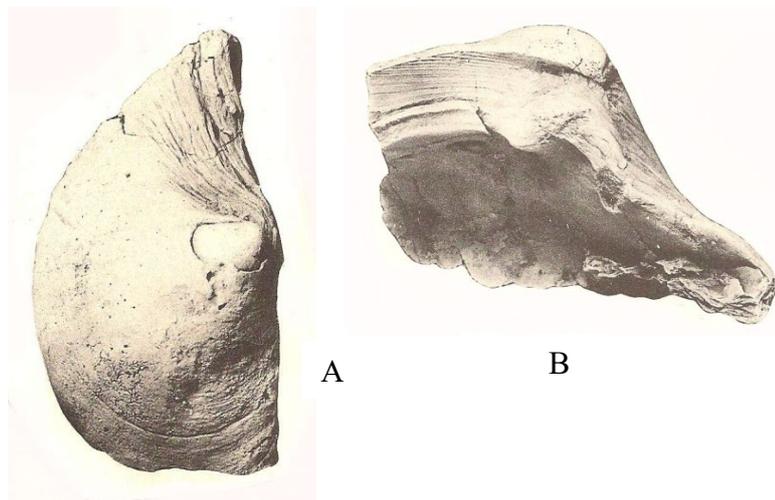


Fig. 7. *Eurydesma konincki* (Johnston). Neotype UQF 51940 left valve. A, dorsal aspect, x0.75. B, hinge, stated to be x0.75. Considered to be from Darlington Limestone, Maria Island, Tasmania. (Runnegar 1970).

Discussion: This is a minor morphotype, best known from Tasmania and ranging as far as Queensland. *Eurydesma cordatum* is more inflated and has a less extended anterior, with a different ontogeny as traced by growth-lines. The dental boss is positioned much the same in the two taxa, across the anterior end of the ligament. The species is possibly represented by one of the original drawings presented in Morris (1845), as shown in Fig. 9, although the umbones seem a little higher than in type *protrudus* and the well preserved

specimen shown in Clarke's figure (Fig. 8B), but closer to those of the *konincki* neotype. The matrix is said to agree with that of the Darlington Limestone. The difference in umbonal prominence may suggest a significant distinction between *konincki* and *protrudus*, but is set aside as a morphological variation.



Fig. 8. *Eurydesma konincki* (Johnston). A, holotype for *protrudus* Waterhouse from Allandale Formation, AMF 14656 figured by Etheridge & Dun (1910), x0.5. B, a fine specimen figured by Clarke (1992, Fig. 20C) from "Spirifer Zone", Maria Island, Tasmania. Specimens x 0.5.

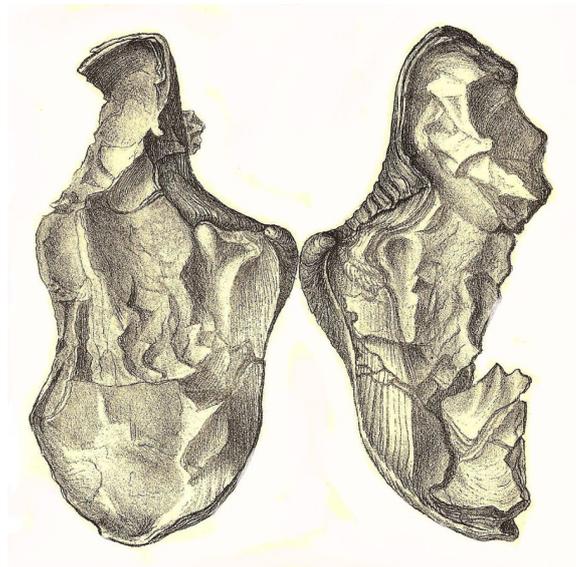


Fig. 9. *Eurydesma konincki* (Johnston), figured as *Eurydesma cordatum* by Morris (1845, lower figure), x0.6. The source is uncertain, but the matrix suggests Darlington Limestone of Tasmania, according to S. Ware, Natural History Museum, London.

Specimens from the Lizzie Creek Volcanics of the northern Bowen Basin (Runnegar 1970, pl. 17, fig. 10, 11) suggest an extended anterior. Although the specimens are small, they do suggest a strong approach to *konincki*.

Johnston (1888, pl. 18, fig. 1, a, b) figured as *Pachydomus globosus* Sowerby a large and swollen specimen with both valves intact, from Maria Island, which provided the source for *konincki*. The shell is close in shape to that of *sacculum* M'Coy, but lacks the lateral sulcus.

A small collection of distinctive *Eurydesma* was reported from the basal Elvinia Formation in the southeast Bowen Basin by Waterhouse (1987b, p. 140, pl. 3, fig. 4) with swollen anterior shell. It is stratigraphically younger than *E. konincki*, but perhaps lies in the lineage represented by *E. konincki* and *E. sacculum*.

***Eurydesma glaebulum* Waterhouse, 2015a**

Fig. 10, 14A

- 1924 *Eurydesma cordatum* [not Morris] – Richards & Bryan, pl. 19, fig. 7.
 1928 *E. cordatum* – Whitehouse, p. 282.
 1970 *E. cordatum* – Runnegar, p. 279, p. 16, fig. 9 (part).
 1970 *E. hobartense konincki* [not Johnston] – Runnegar, pl. 13, fig. 11 (part only).
 1979 *Eurydesma* sp. indet. Murray et al., p. 75, Fig. 4.
 2008a *Eurydesma* n. sp. Waterhouse, text-fig. 61B.
 2015a *E. glaebula* Waterhouse, p. 284, Fig. 233-236, 237 part, 238A.

Holotype: UQF 81512 figured in Waterhouse (2015a, Fig. 234A-C) from lower Tiverton Formation, north Bowen Basin, Queensland, OD.

Diagnosis: Swollen shells with anterior margin slanting steeply forward to anterior ventral margin, umbones subcentral and low, lateral shell as a rule without lateral sulcus.

Age: Lower and middle Sakmarian.

Discussion: This taxon appears to have developed from *Eurydesma cordatum* through steepening of the anterior margin and increased inflation, eventually progressing into the development of shells of the *E. ovale* Etheridge & Dun complex. It appears to be present in the Ravensfield Sandstone of the north Sydney Basin.

A right valve GSQ F 12804 figured in Murray et al. (1979) from the Amamoor beds in the New England Orogen northwest of Maleny, southeast Queensland, appears to be conspecific, given the swollen nature of the shell.

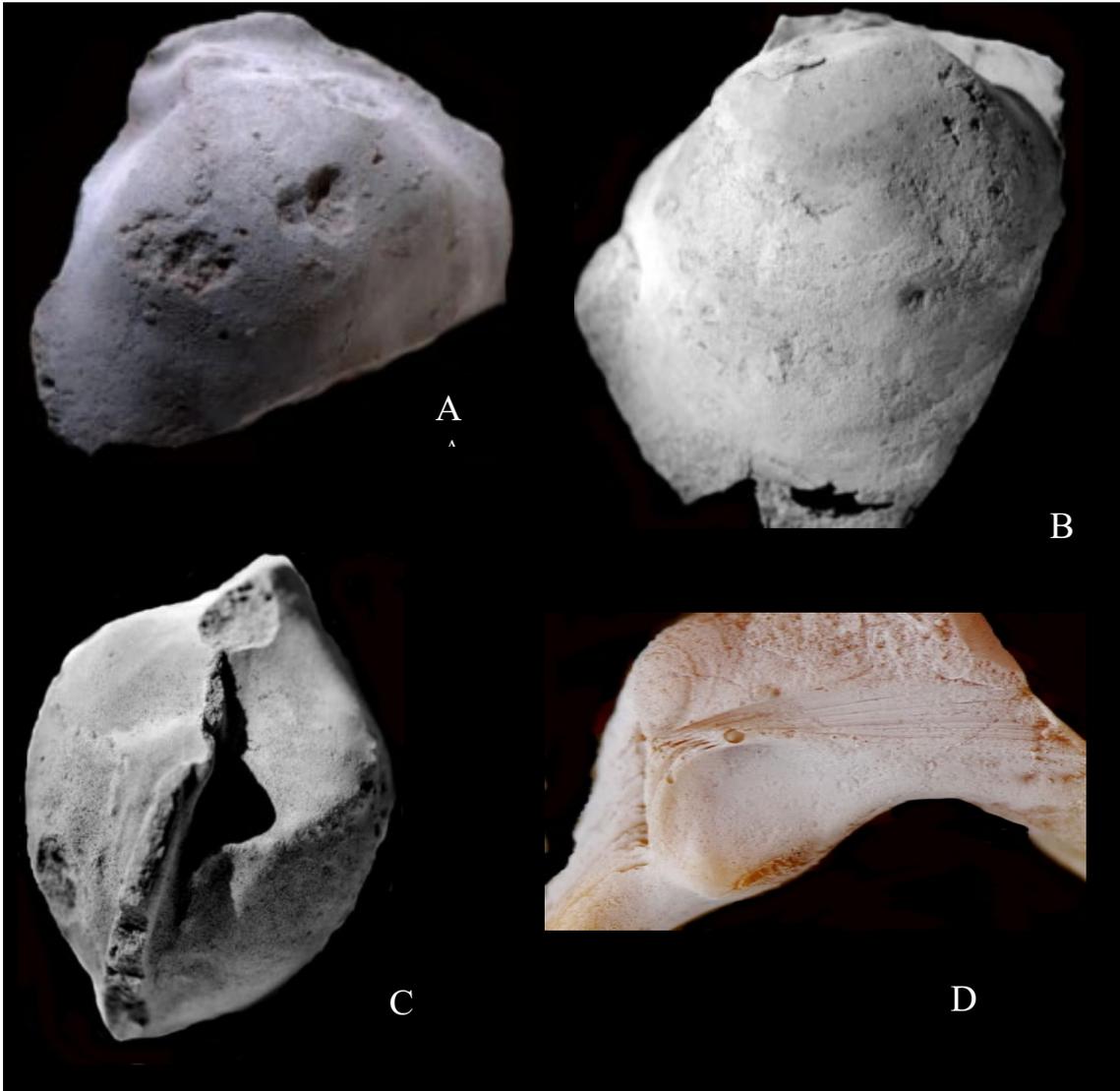


Fig. 10. *Eurydesma glaebulum* Waterhouse. A, C, holotype, left, and dorsal views of internal mould UQF 81512 from UQL 4508, x1. B, left valve UQF 81513 from UQL 1619, x1. D, latex cast of right valve hinge, UQF 81532 from UQL 1622, x3. Lower Tiverton Formation. (Waterhouse 2015a).

***Eurydesma ovale ovale* Etheridge & Dun, 1910**

Fig. 12A

1910 *Eurydesma cordatum* var. *ovale* Etheridge & Dun, p. 74, pl. 21, fig. 4, 5, pl. 25, fig. 1, 2.
 1970 *E. cordatum* [not Morris] – Runnegar, pl. 16, fig. 9? (part).
 ?1987b *Eurydesma cordatum truncatum* Waterhouse p. 139 (part), pl. 3, fig. 3 only.
 2015a *E. ovale* – Waterhouse, p. 290, Fig. 237.

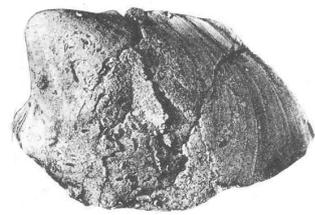
<p><i>Magniplicatina</i> <i>undulata</i> Zone</p>	 ovale	
<p><i>Bookeria pollex</i> Superzone</p>	 glaebulum	 truncatum ovale
<p><i>Bandoproductus</i> <i>macrospina</i> Zone</p>		
<p><i>Crassispinosella</i> <i>subcircularis</i> Zone</p>	 konincki	 cordatum
<p><i>Strophalosaria</i> <i>concentrica</i> Zone</p>	 burnettensis	 burnettensis

Fig. 11. Species of *Eurydesma* in the Asselian Stage and much of the Sakmarian Stage in the Early Permian of eastern Australia. Most are restricted to one zone (left-hand column), and a few range a little above or below. The unusual dentition for *burnettensis* shows the large right tooth projection. Figures taken from Etheridge & Dun (1910), Maxwell (1964), and Waterhouse (1987b, 2015a). Note the absence of *Eurydesma* from the *Bandoproductus macrospina* Zone: was this because waters were then too warm?

Diagnosis: Large oval little inflated shells with anterior placed umbones, steeply inclined anterior margin, and long hinge with no posterior wing or lateral sulcus.

Lectotype: AMF 35690 figured by Etheridge & Dun (1910, pl. 25, fig. 1) from Ravensfield Sandstone Member, Farley Formation, Hunter Valley, SD Runnegar (1970, p. 98). Fig. 12A herein.

Age: Sakmarian.

Discussion: Although submerged within *Eurydesma hobartense konincki* by Runnegar (1970), *E. ovale ovale* is readily distinguished by its higher shape and more anteriorly placed umbones. The species came from the Ravensfield Quarry which would appear to be of low or middle Sakmarian age, and approximately equivalent to the *Bookeria pollex* Zone or more likely *Magniplicatina undulata* Zone as discussed later in this monograph, starting on p. 209: age control is not as good as it should be, given the need for up-to-date appraisal of the faunas from the north Sydney Basin. It is clear that the species is distinctly younger than constituents of the *cordatum* plexus, and partly overlaps and is partly younger than *E. glaebulum*. It helps to characterize an array of morphotypes from the Sakmarian-lower Artinskian stages, rather than Asselian Stage.

A small specimen figured in Waterhouse (1987b, pl. 3, fig. 3) as referenced in the synonymy appears to belong to the species: its source is uncertain, but is thought to have come from the Dresden or basal Elvinia Formation in the southeast Bowen Basin.

Several allied taxa were named by Waterhouse (1987b) from the Bowen Basin, chiefly in the southeast, and are related in so far as the umbones are anteriorly placed and the anterior margin steep. It appears likely that shells from the Berriedale Limestone of upper Sakmarian age in Tasmania form part of the *ovale* complex (see Fig. 11), with specimens that are close to *sulcatum*.

***Eurydesma ovale truncatum* Waterhouse, 1987b**

Fig. 12B, C

1964 *Eurydesma hobartense* [not Johnston] – Hill & Woods, pl. P11, fig. 1, 2.

1972 *E. hobartense* – Hill et al., pl. P11, fig. 1, 2.

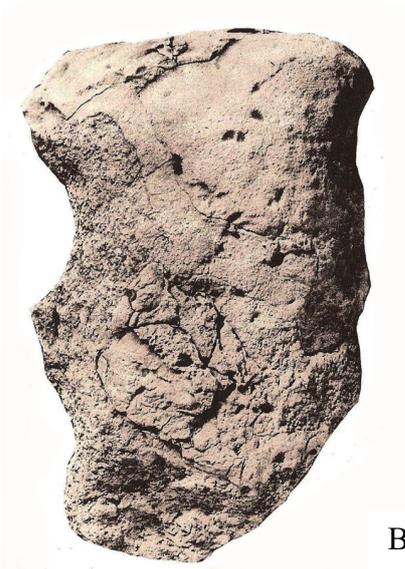
1987b *E. cordatum truncatum* Waterhouse, p. 139, pl. 2, fig. 1, 6, pl. 3, fig. 2, 3.

2015a *E. ovale truncatum* – Waterhouse, p. 290, Fig. 237.



A

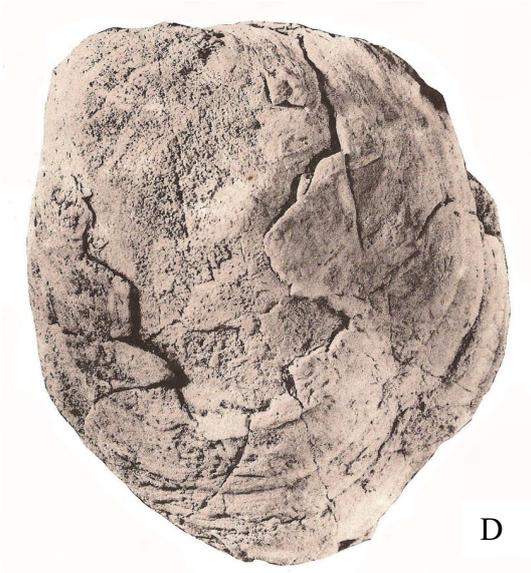
Fig. 12. A, *Eurydesma ovale* Etheridge & Dun, lectotype AMF 35690 figured by Etheridge & Dun (1910) from Ravensfield Sandstone at the base of the Farley Formation, Hunter Valley. B, C, *E. ovale truncatum* Waterhouse, external and internal aspects of right valve holotype, UQF 43410 from Dresden Limestone, Bowen Basin, x0.75. D, E, *E. ovale sulcatum* Waterhouse, lateral and anterior aspects of holotype, UQF 74317 from Roses Pride Formation, Bowen Basin, x0.6.



B



C



D



E

Diagnosis: Large upright subrectangular shells with anteriorly projecting umbones and large boss in the right valve.

Holotype: UQF 43410 figured in Waterhouse (1987b, pl. 2, fig. 1, 6) from Dresden Formation, southeast Bowen Basin, Queensland, OD. See also Fig. 12B, C.

Age: Lower and middle Sakmarian.

Discussion: This subspecies is close to *Eurydesma ovale ovale*, full comparison being limited by the availability of material and the need for more extensive collections with full appraisal of the morphologies and variations within the two subspecies.

***Eurydesma ovale sulcatum* Waterhouse, 1987b**

Fig. 12D, E, cf. Fig. 13, cf. Fig. 14B-D

cf. 1970 *Eurydesma hobartense hobartense* [not Johnston] – Runnegar, pl. 15, fig. 1, 2, possibly fig. 5 or indet., (part), pl. 17, fig. 7, 8 (part).

1970 *Eurydesma hobartense konincki* [not Johnston] – Runnegar, p. 97, pl. 15, fig. 10, 11 (part), pl. 16, fig. 5? (part), pl. 17, fig. 7-9, 12, 13 (part).

1987b *E. sulcatum* Waterhouse, p. 141, pl. 2, fig. 7, 9, pl. 3, fig. 9.

2015a *E. ovale sulcatum* – Waterhouse, p. 289, Fig. 237.

Diagnosis: Large subquadrate to subrectangular shells with broad inconspicuous umbones and shallow posterior sulcus, moderately inflated, long posterior hinge but no defined posterior wing.

Holotype: UQF 74317 figured by Waterhouse (1987b, pl. 2, fig. 1, 6) from Roses Pride Formation, southeast Bowen Basin, Queensland, OD. See Fig. 12D, E.



Fig. 13. *Eurydesma* sp., left valve UQF 29950 x1 approx. from the Berriedale Limestone, as figured by Runnegar (1970, pl. 15, fig. 10). This is possibly *E. ovale sulcatum*, assuming that larger shells increased in height.

Age: Aktastinian, and possibly also within the *Taeniothaerus subquadratus* Zone of likely upper Sakmarian age in the Tiverton and Berriedale Formations. A specimen figured by Runnegar (1970) comes from a vaguely defined level as “Buffel Formation” involving Sakmarian beds.

Discussion: This subspecies differs from *Eurydesma ovale ovale* and *E. ovale truncatum* in being well inflated, with lateral sulcus as a rule, and in having umbones that project less forward. The type material comes from beds with *Echinalosia preovalis* and *Anidanthus springsurensis* beds of Aktastinian age, regarded as closer to the Sakmarian Stage than upper Artinskian or Baigendzinian Substage (Waterhouse 2015a, Fig. 237). The type

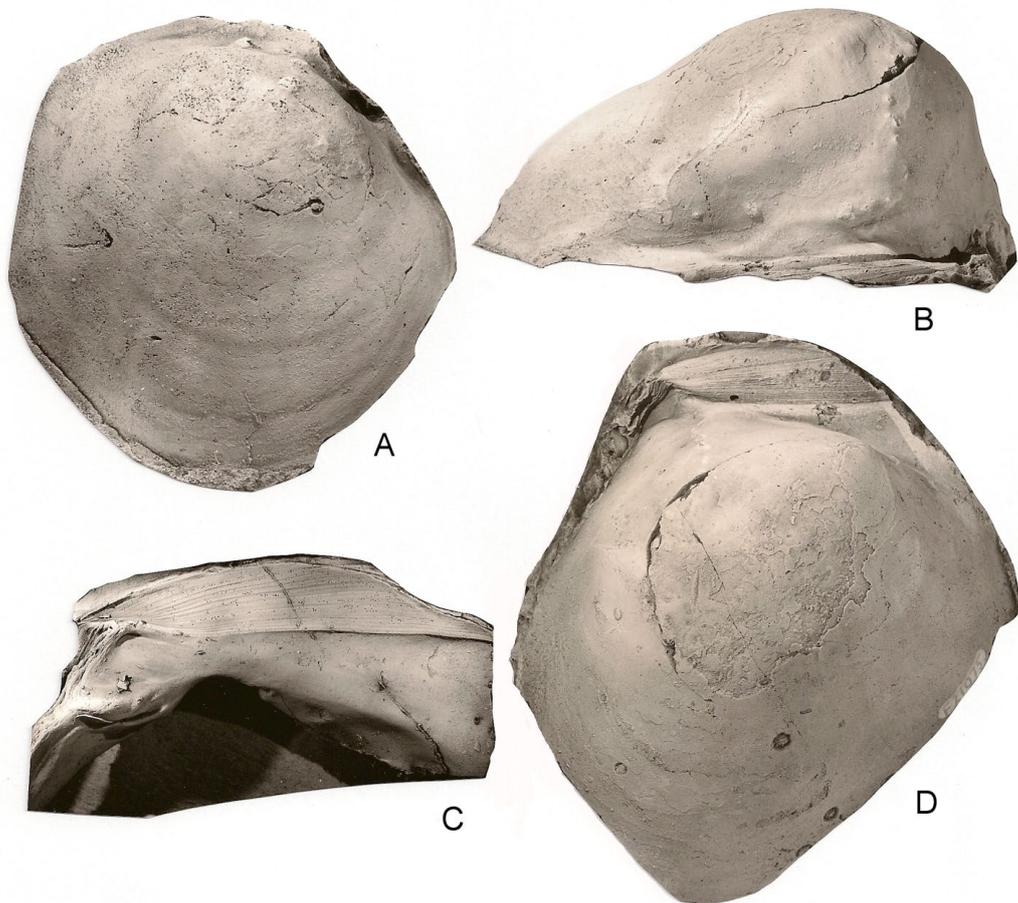


Fig. 14. A, *Eurydesma glaebulum* Waterhouse, right valve of specimen with valves conjoined, UQF 81509 from UQL 1619, lower Tiverton Formation, x1. B-D, *Eurydesma* sp. B, D, left valve internal mould, UQF 21075, dorsal view and lateral view, x0.66 and 0.75. C, latex cast of hinge, right valve UQF 21157, *Taeniothaerus subquadratus* Zone, upper middle Tiverton Formation, x0.8. In shape these specimens are close to *E. ovale sulcatum*. (Waterhouse 2015a)

specimen is close to that figured as type *E. antarctica* (Frech), but is not as high a shell. Early growth lines and small specimens of *sulcatum* indicate that the height increases substantially with increasing maturity of the shell, and a similar change in shape with increased maturity is indicated for Frech's taxon. *Eurydesma* sp. from the Berriedale Formation of possible upper Sakmarian age is a potential ally (Fig. 13). It comes from the *Taeniothaerus subquadratus* Zone (Waterhouse 2008b), and shows some approach to *E. ovale sulcatum*. The right valve hinge for a Berriedale specimen was figured by Runnegar (1970, pl. 15, fig. 2), but hinge detail and variation in shape for *Eurydesma* from the Berriedale Limestone is still to be clarified by published description. From the *Taeniothaerus subquadratus* Zone in the upper middle Tiverton Formation, *Eurydesma* as figured in Fig. 14C-D shows considerable approach to *sulcatum*, with the hinge very like that figured by Runnegar (1970, pl. 15, fig. 2). A Roses Pride specimen figured by Waterhouse (1987b, pl. 3, fig. 9) is close to the Berriedale specimen. These specimens are all close to type *sulcatum* in shape, and several show the lateral sulcus. There is thus the strong implication that *Eurydesma* from the Roses Pride Formation is close to the species from the underlying *Taeniothaerus subquadratus* Zone, though it is not clear that the older shells increased so much in height with increase in size.

***Eurydesma antarctica* (Frech, 1891)**

Fig. 15

1891 ?*Myalina* (*Leiomyalina*) *antarctica* Frech p. 201, text-fig. 21, 22.

1970 *Eurydesma hobartense konincki* [not Johnston] – Runnegar, p. 97, pl. 17, fig. 5, 6.

Diagnosis: Upright subrectangular shells with anteriorly placed umbones, steep anterior outline, hinge long but without defined posterior wing. Ligament area low and left valve boss moderately well developed below ligament area.

Holotype: Sole figured specimen of Frech (1891), now lost and of uncertain source.

Age: Uncertain, conjecturally upper Sakmarian or lower Artinskian.

Discussion: This taxon is known only from the original figures provided by Frech (1891). It came from an uncertain source, named as Kilama, New South Wales. This was interpreted by Runnegar to represent the Conjola Formation, now divided into the Wasp Head and Pebbly Beach Formations, which crop out south of Kiama in the south Sydney Basin, and

Frech's material differs strongly from Wasp Head material assigned to *Eurydesma cordatum*. The Frech material is now lost. Were further material of comparable preservation to be discovered, predictably from the lower or middle Pebbley Beach Formation, the taxon could potentially assume naming rights for all the taxa and subspecies here grouped as species *ovale* Etheridge & Dun, because Frech's name has priority. Certainly the figure suggests a species moderately close to *ovale* itself, and even closer to *ovale truncatum*, a mid- and upper Sakmarian subspecies, and *E. ovale sulcatum*, an Aktastinian species.

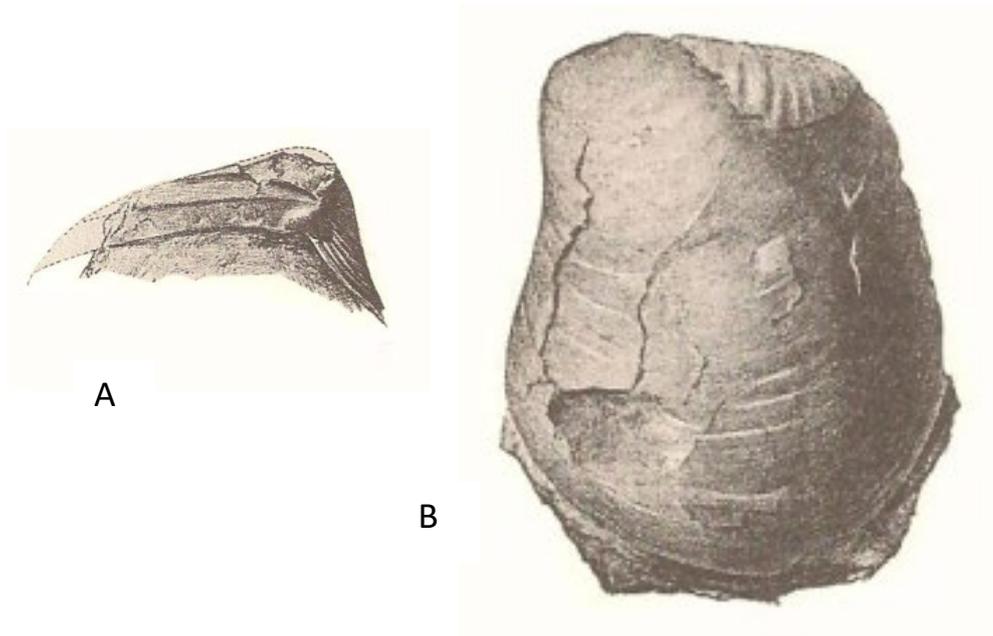


Fig. 15. *Eurydesma antarctica* (Frech, 1891) as figured and now lost. Locality not established, x1 approx.

Two figures of fragmentary specimens representing the hinge suggest a reasonable match with Frech (1891) species, although the full shape is not known, and the incomplete preservation would allow identification with other species. These incomplete specimens involve AMF 21952, figured by Runnegar (1970, pl. 17, fig. 12 (see Fig. 18B) and AMF 21953, figured by Waterhouse (1987b, pl. 1, fig. 27), both from Point Upright, which lies roughly near the middle of the Pebbley Beach Formation. A further indication that the species *antarctica* sourced from these rocks is suggested by a figure in Runnegar (1970, pl. 17, fig. 8)

of a hinge of a specimen CPC 8177 of *Eurydesma* from the Sirius Mudstone, which is moderately close to that of *antarctica*. The Sirius Mudstone was judged to be correlative with the Pebble Beach Formation by Fielding et al. (2008a).

But given the threat to the status of *Eurydesma ovale ovale* Etheridge & Dun, caution is warranted, and only the designation, description and illustration of a neotype that is stratigraphically and reliably located can retrieve the situation.

***Eurydesma sacculum* (M'Coy, 1847)**

Fig. 16, 18A, 19

1847 *Pachydomus sacculus* M'Coy, p. 301, pl. 14, fig. 5.

1987b *E. alisulcatum* Waterhouse, p. 142, pl. 4, fig. 1 (part, not pl. 1, fig. 2?? = uncertain, not pl. 3, fig. 2 = *sacculum snapperensis*).

Diagnosis: Large upright and inflated shells with extended anterior shell, small extended posterior wing and prominent lateral sulcus.

Holotype (by monotypy): Sedgwick Museum SM E 10759 as figured by M'Coy (1847) and herein, Fig. 16A, B, said to come from Black Head (Geroa) or Wollongong. Assessed by various authors as coming from Allandale Formation, probably Harper's Hill, north Sydney Basin, but no Allandale specimens look particularly like *sacculus*, whereas specimens from the Wandrawandian Formation, not far from Black Head or Wollongong, although from slightly older sediments, strongly approach *sacculus* in hinge, posterior wing, protruding outline of the anterior shell, and lateral sulcus. Holotype for *alisulcatum*: AMF 46915 figured by Waterhouse (1987b, pl. 4, fig. 1) and herein Fig. 18A, from Wandrawandian Formation, OD.

Age: Kungurian.

Discussion: M'Coy (1847) stated that the inflation was considerable, with width measuring two thirds of the length, and shell very thick. Waterhouse & Gupta (1982) noted an approach to *Pachydomus gouldi* Johnston (1888, pl. 17, fig. 2) from marine mudstones at Bridgewater in Tasmania.

Compared with *Eurydesma cordatum*, to which this taxon has been assigned in recent studies, the holotype differs in outline. The specimens examined by Etheridge & Dun



Fig. 16. *Eurydesma cordatum sacculum* (M'Coy), A, B, holotype SM E 10759, right valve and posterior aspect, x1. Possibly from Snapper Point or Wandrawandian Formation, south Sydney Basin. Photographed from left side and posterior aspect, from plaster cast, x1. The crack in the mould is an artifact.



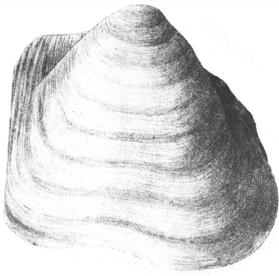
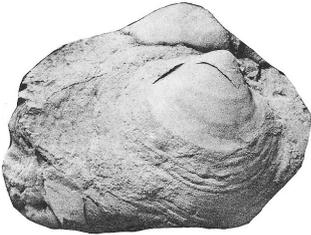
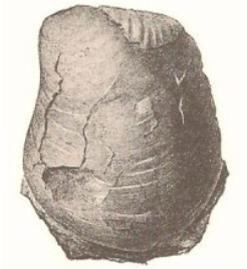
<i>Echinalosia discinia</i> Zone		 sacculum
<i>Wyndhamia typica</i> Zone	snapperensis	?sacculum
<i>Glendella dickinsi</i> Zone	 snapperensis	<i>Glendella dickinsi</i>
<i>Ech. conata</i> Zone		
<i>Spino. adentata</i> Zone		
<i>Ingelarella plica</i> Zone	 antarctica (lost, uncertain locality)	 ovale sulcatum
<i>Taeniothaerus subquadratus</i> Zone		?probable ovale sulcatum

Fig. 17. Species of *Eurydesma* in the late Early and early Middle Permian of eastern Australia. Most are restricted to one zone as shown in the left-hand column, and a few range a little above or below. *Glendella* is eurydesmid, characteristic of a cold-water fauna of low diversity. Figures taken from Frech (1891), M'Coy (1847), and Waterhouse (1987b).

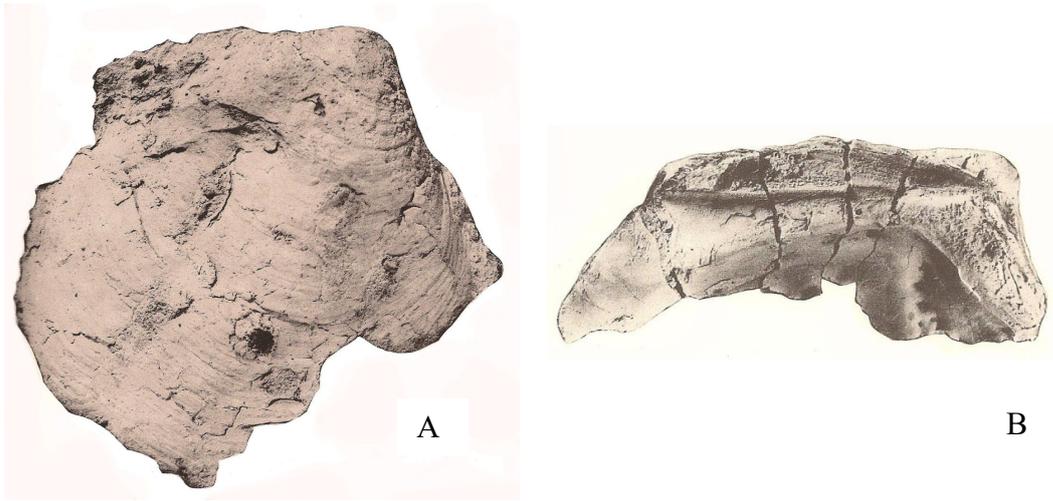


Fig. 18. A, *Eurydesma sacculum* (M'Coy), the holotype of *E. alisulcatum* Waterhouse. UQF 46915 from Wandrawandian Formation, x0.5. (Waterhouse 1987b). B, hinge region in fragment from Point Upright, Pebbley Beach Formation (Runnegar 1970). This specimen is too incomplete to allow confident identification, and could prove to be allied to *E. sacculum*, *E. sacculum snapperensis* n. subsp., or, as favoured, *Leiomyalina antarctica* (Frech).

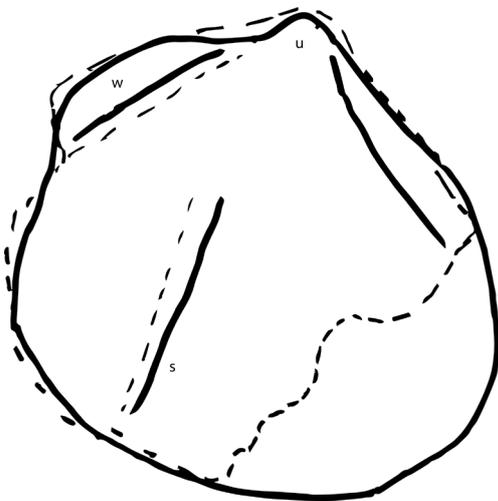


Fig. 19. *Eurydesma sacculum* (in bold line, from Fig. 16A) overlain by outline of *E. alisulcatum* (dashed, from Fig. 18A), x0.5 approx. s = sulcus, u = umbo, w = posterior wing.

(1910) do show the lateral sulcus found in *sacculum*, but their shells are otherwise closer to *cordatum* in shape, as discussed by Waterhouse (2015a, p. 286). The holotype itself as figured by M'Coy (1847) has a slender posterior wing, and somewhat extended lower anterior margin. The outline is close to that of a group distinguished as *Eurydesma alisulcatum* Waterhouse, 1987b from the Wandrawandian Formation, with somewhat similar posterior

wing, low broad umbo, protruding anterior, comparable high inflation and lateral sulcus. When the outline of the holotype of *sacculum* is laid over the figure of type *alisulcatum* (Waterhouse 1987b, pl. 4, fig. 1), the agreement is very close, apart from a slightly more posterior position for the lateral sulcus in *alisulcatum* (Fig. 19). Therefore the two are regarded as synonymous, and the stratigraphic significance of *sacculum* revised, to come much closer to that published in the original description. Fragments of *Eurydesma* (see Fig. 18B) that show the hinge which were figured by Runnegar (1970, pl. 17, fig. 12) and Waterhouse (1987b, pl. 1, fig. 27) from Point Upright, comparatively low in the Pebbly Beach Formation, might prove to be conspecific, but would seem more likely to belong to *E. antarctica* (Frech).

***Eurydesma sacculum snapperensis* n. subsp.**

Fig. 20B

1970 *E. hobartense konincki* [not Johnston] – Runnegar, pl. 16, fig. 6 only.

1987b *E. alisulcatum* – Waterhouse, pl. 3, fig. 8 (part).

1997 *Eurydesma* sp. Shi & McLoughlin, pl. 8, fig. 1, 2 (?not fig. 3 = *Megadesmus* or *Protraxia* sp.)

2002 *Eurydesma* sp. Shi & Weldon, pl. 8, fig. 1, 3 (?part, not fig. 4 = *Megadesmus* or *Protraxia?* sp.?)

2010 *Eurydesma* sp. Shi, Weldon & Pierson, pl. 8, fig. 1, 3 (?part, not fig. 4 = *Megadesmus* or *Protraxia* sp.?)

Derivation: Named for Snapper Point.



Fig. 20. A, *Eurydesma hobartense* (Johnston), lectotype TM B736, from Deep Bay Formation, Tasmania (Johnston 1888). B, *E. hobartense snapperensis* n. subsp., holotype AMF 21945 from North Head, near Ulladulla, Wandrawandian Formation (Waterhouse 1987b). Specimens x1.

Diagnosis: Medium to large subelongate and moderately inflated shells with extended anterior portion and umbones placed near anterior third of shell length. Dental boss large, closing anterior end of ligament.

Holotype: AM F 21945 figured by Runnegar (1970, Pl. 16, fig. 1) and Waterhouse (1987b, pl. 3, fig. 8) and herein as Fig. 20B from Wandrawandian Formation at Point Upright, south Sydney Basin, here designated.

Age: Kungurian.

Discussion: In naming this form as a new subspecies, it is wished to be able to designate a morphotype without undue conjecture over stratigraphic position. The shell is swollen with extended anterior shell and growth lines suggest that it is closely related to *sacculum* (= *alisulcatum*), which assumed a more upright stance with less inflated and less protruding anterior.

Eurydesma hobartense (Johnston, 1887)

Fig. 20

1887 *Pachydomus hobartensis* Johnston, p. 16.

1888 *P. hobartensis* – Johnston, pl. 16, fig. 2.

1970 *E. hobartense* [not Johnston] – Runnegar, p. 85, pl. 15, fig. 3 (part).

Lectotype: TM B736 figured Johnston (1888) and Runnegar (1970) from Deep Bay Formation, Tasmania, SD Runnegar (1970, p. 95).

Diagnosis: Known only from immature specimen, little inflated, with subrounded outline, anteriorly placed umbo.

Age: Kungurian.

Discussion: Uncertainty surrounds *Eurydesma hobartense* (Johnston, 1887, 1888), named for an immature valve found in the Deep Bay Formation of Tasmania, which is significantly younger than the Berriedale Limestone, mistakenly indicated as the source for the species by Runnegar (1970). Species cannot be reliably delineated solely on the basis of immature specimens as a rule, and the identification of specimens by Runnegar (1970) from various parts of the stratigraphic column with *hobartensis* carries no conviction. The species *hobartense* must be interpreted from mature specimens, but figures or description of mature specimens from the Deep Bay Formation have never been provided. There are a number of

immature *Eurydesma* in the two shelly bands near the base of the Snapper Point Formation and top of the Pebbly Beach Formation, and they look moderately close to *hobartense*, apart from blunter and more massive umbones. Perhaps they developed into the form here called *snapperensis* (Fig. 20B). But pending further information, the taxon *hobartense* is regarded as a likely junior synonym of *sacculum*, at least in the broad sense.

Amosius Gonzalez & Waterhouse, 2004

Gonzalez & Waterhouse (2004) described a eurydesmid genus *Amosius*, type species *Eurydesma harringtoni* Gonzalez, 1972, from the lower *Levipustula levis* Zone of the Las Salinas Formation, central Patagonia, and noted possible occurrences in east Australia, described as *Posidonia* sp. by Campbell (1961), and a possible specimen from the Ridgeland area in Queensland, collected by Prof. J. Roberts. The genus has a channel-form (ie. canaliform) ligament with a tooth at the anterior end in each valve, as described and illustrated in Gonzalez & Waterhouse (2004).

REPOSITORIES

AMF: Australian Museum, Sydney; **BM(NH):** Museum of Natural History, London; **NVM:** National Museum of Victoria, Melbourne; **SME:** Sedgwick Museum, Cambridge; **TM:** Tasmania Museum, Hobart; **UQF:** University of Queensland, collections now housed in the Queensland Museum bulk storage at Hendra; **USNM:** United States National Museum, Washington D. C.

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E. G. Brighton, Sedgwick Museum, Cambridge, kindly provided a mould of *Eurydesma sacculum* (M'Coy); J. Pojeta, U. S. Geological Survey arranged the loan of Dana's *Eurydesma*, and H. O. Fletcher organized the viewing of material kept at the Australian Museum. As noted in the text, a photograph by Bruce Runnegar proved most useful.

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4. PERMIAN BRACHIOPODS AND BIVALVES FROM THE LAKES CREEK FORMATION, QUEENSLAND

Abstract

Early Permian brachiopods are described from the Lakes Creek Formation in the New England Orogen of eastern Queensland, and are shown to belong to the *Taeniothaerus subquadratus* Zone of upper Sakmarian age. Two spiriferiform species are exceptional, one judged to belong to *Neilotreta*, and showing critical features of the delthyrium, the other a member of *Pteroplecta*, typical of the Late Permian in the Himalayas, and not known previously in east Australia. A few bivalves are also described.

New taxa: *Protoanidanthus costata* n. sp., *Ingelarella intrudus* n. sp., *Pteroplecta blakei* n. sp., *Neilotreta lakensis* n. sp.

INTRODUCTION

The Lakes Creek Formation is found in the Berserker Subprovince near Rockhampton in eastern Queensland, as summarized by Blake & Withnall (2013, p. 350), building on overviews by Crouch & Parfrey (1998) and Murray et al. (2012). The formation includes thin to medium-bedded siltstone and fine to medium-grained lithofeldspathic to quartzofeldspathic sandstone, with fossiliferous calcareous sandstone varying to limestone limited to the quarry. The specimens are labelled as coming from UQL 29, Nerimbera Quarry, Lakes Creek, Rockhampton, changed later to read Berseker beds, Lakes Creek Quarry. The fossils were first discovered by Whitehouse (1928), but have never been systematically described, other than having one species recorded as *Anidanthus springsurensis* (Booker) by Hill (1950), and another species illustrated as *Taeniothaerus farleyensis* Briggs in Waterhouse (2013).

SYSTEMATIC DESCRIPTIONS

Phylum Brachiopoda Duméril, 1806

Superorder PRODUCTIFORMII Waagen, 1883

Order CHONETIDA Muir-Wood, 1962

Superfamily **CHONETOIDEA** Bronn, 1862

Family RUGOSOCHONETIDAE Muir-Wood, 1962

Rugosochonetid gen. & sp. indet.

Fig. 1

Material: An external mould of a dorsal valve UQF 26435 with part of the ventral interior.

Description: The dorsal external mould is 21.5mm wide and 11mm long, with vestiges of the cardinal area, obtuse cardinal extremities, and fine growth increments, but without ribbing or fold. The fragment of the ventral internal mould shows fine radial capillae.



Fig. 1. Rugosochonetid, dorsal external mould with part of internal ventral valve to left, UQF 26435, x2.

Resemblances: Too little of this specimen is preserved to allow identification. In its transverse outline, the specimen shows some approach to *Gympietes aseptus* Waterhouse, 2015b, p. 14 from the Rammutt Formation of Asselian age in the Gympie Province, southeast Queensland, but there seems to be little significance in this apparent similarity.

Order PRODUCTIDA Waagen, 1883

Suborder STROPHALOSIIDINA Waterhouse, 1975

Infrasuborder STROPHALOSIMORPHI Waterhouse, 1975

Superfamily **STROPHALOSIOIDEA** Schuchert, 1913

Family **DASYALOSIIDAE** Brunton, 1966

Subfamily **ECHINALOSIINAE** Waterhouse, 2001

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

Tribe **ECHINALOSIINI** Waterhouse, 2001

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

Genus ***Echinalosia*** Waterhouse, 1967

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

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

Echinalosia curvata Waterhouse, 1986a

Fig. 2 - 4

- 1986a *Echinalosia preoivalis curvata* Waterhouse, p. 26, pl. 3, fig. 25-29, pl. 4, fig. 1-5.
 1986a *Echinalosia curtosa* [not Waterhouse] – Waterhouse, pl. 3, fig. 8 (part, not pl. 3, fig. 5-7, 9-14, pl. 15, fig. 9 = *curtosa*).
 1998 *E. preoivalis* [not Maxwell] – Briggs, p. 76 (part).
 2015a *E. curvata* – Waterhouse, p. 82, Fig. 30-33.
 2021 *E. curvata* – Waterhouse & Campbell, p. 10, Fig. 2-4.

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

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

Material: Thirteen ventral valves, some preserved as external moulds, others as internal moulds, and two dorsal external moulds.

Description: The largest specimen is 31mm wide, 24mm long and 11mm high, with no median sulcus or fold, maximum width placed near mid-length. Most ventral valves are smaller, and are little inflated. Dorsal valves are moderately concave, with well developed interarea. Ventral spines lie mostly in regular quincunx and vary in different specimens, some being erect, in other specimens being recumbent or semirecumbent as in types, mostly

uniform in diameter. Dorsal spines are very fine and erect, moderately crowded but with irregular distribution.

The ventral adductor platform is posteriorly placed as a rule, bears a few transverse ridges and grooves, and varies in shape and markings from specimen to specimen. Diductor scars overlap for approximately half their length. Teeth are of moderate size, without supporting buttresses. Some irregularities lie over the inner surface of the shell, but there are only a few spine tunnels. Dorsal interior not exposed.

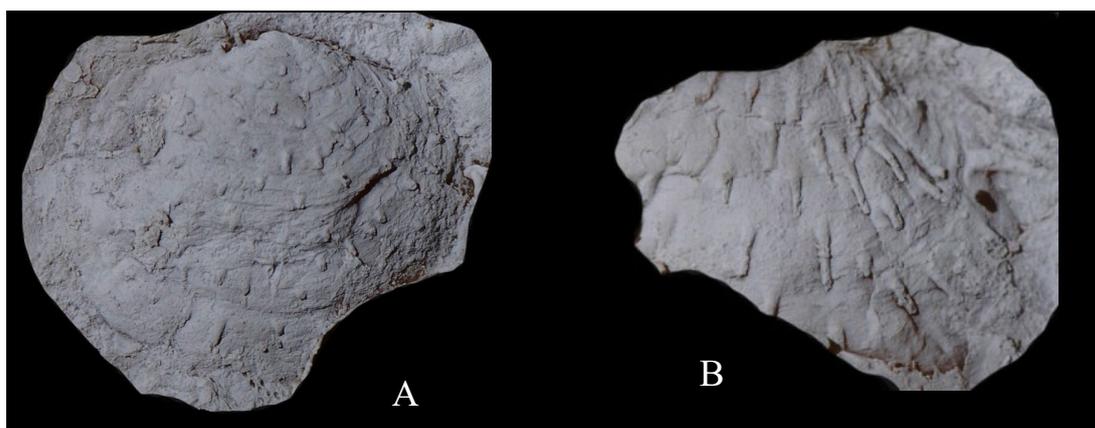


Fig. 2. *Echinalosia curvata* Waterhouse, latex casts of ventral exterior, x3. A, UQF 140. B, UQF 139.

Resemblances: The specimens are referred to *Echinalosia curvata* because of shape and the comparatively strong spines, and the ventral muscle scars which agree with those of *curvata*. Fine recumbent ventral spines are very few, as in the types.

The species *curvata* has been described from the *Magniplicatina undulata* Zone of the Elvinia Formation of the southeast Bowen Basin and the *Taeniothaerus subquadratus* Zone in the upper Tiverton Formation of the north Bowen Basin in Queensland, and from the *Magniplicatina undulata* Zone in the Dunton Range, New Zealand.

Discussion: Briggs (1998) referred *Echinalosia curvata* to *E. preovalis* (Maxwell, 1954), but *preovalis* involves smaller specimens with finer ventral spines at full maturity, and more concave dorsal valve and highly arched ventral valve, and smaller ventral adductor platform. The species *preovalis* is limited to the Sirius Shale and upper Cattle Creek Formation and correlative levels, including the topmost Tiverton Formation, whereas *curvata* is distinctly

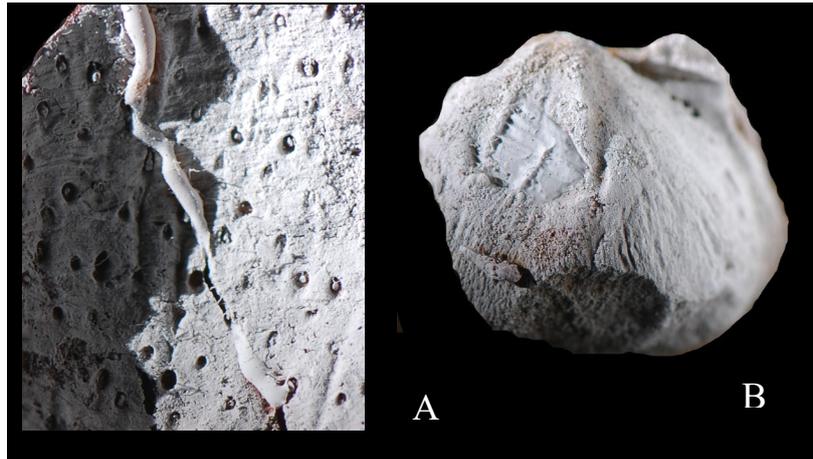


Fig. 3. *Echinalosia curvata* Waterhouse. A, panel showing external mould of ventral valve with strong erect spines, UQF 82604, x2.5, contrasting with the recumbent spines shown in Fig. 2, but of similar diameter. B, internal mould of incomplete ventral valve, with shell infilling part of the adductor field, and showing part of the ventral interarea, UQF 82605, x2.

older, coming from the Elvinia and middle Tiverton Formations. The species *preovalis* is not present in the Elderslie Formation of the Sydney Basin as claimed by Briggs (1998, p. 79), who mistook the species *E. floodi* Waterhouse (2001, p. 60, pl. 4, fig. 1-5, pl. 5, fig. 17) for *preovalis*. The species *preovalis* also seems unlikely to be in the Pebbley Beach Formation (= *floodi*?), where it was reported, but without figures, and the material now apparently lost.

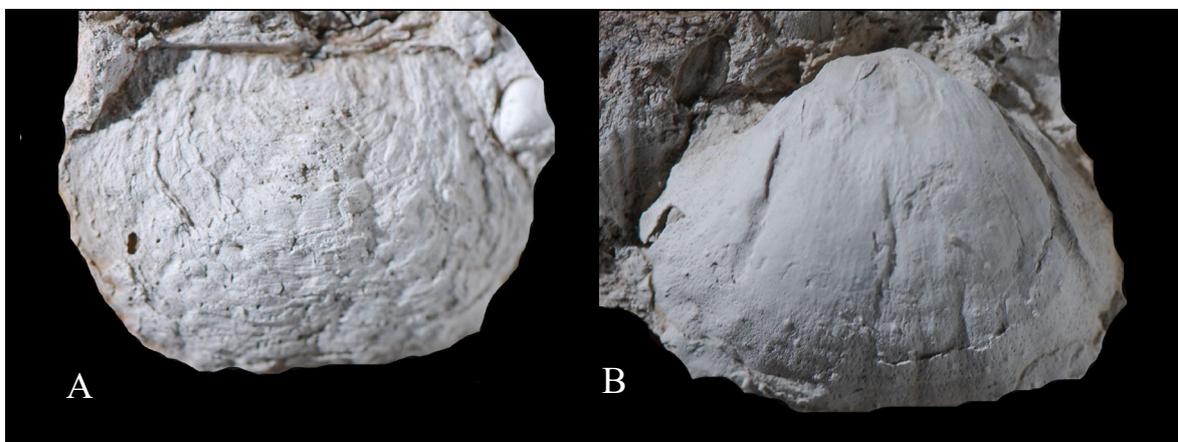


Fig. 4. *Echinalosia curvata* Waterhouse. A, dorsal external mould UQF 143, x2. B, ventral internal mould, UQF 147, x2.

Infrasuborder AULOSTEGIMORPHI Waterhouse, 2010

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

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

Subfamily **TAENIOTHAERINAE** Waterhouse, 2002

Genus ***Taeniothaerus*** Whitehouse, 1928

Diagnosis: Large with thick body corpus, ventral interarea, spines on each valve of mostly one size, in quincunx over both valves and with elongate bases. Cardinal process large with supporting buttress plates.

Type species: *Productus subquadratus* Morris, 1845, p. 248 from Berriedale Limestone (upper Sakmarian) of Tasmania, Australia.

Discussion: This genus is characteristic of somewhat warmer water faunas in east Australia and New Zealand, and is found also in Irian Jaya, Western Australia, the Indian subcontinent, Tibet, Pamirs, and possibly Afghanistan and Oman. In east Australia it culminated in late Sakmarian time, as discussed on p. 213 ff.

Taeniothaerus farleyensis Briggs, 1998

Fig. 5, 6

1909 *Productus subquadratus* [not Morris] – Etheridge & Dun, p. 9 (part).

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

1998 *Taeniothaerus farleyensis* Briggs, p. 136, Fig. 69A-F.

1998 *T. homevalensis* [not Briggs] – Briggs, p. 137 [the specimen of Hill 1950, pl. 6, fig. 4 as referred to *homevalensis*].

1998 *Reedoconcha* sp. Briggs, p. 133, Fig. 68A-C.

2013 *T. farleyensis* – Waterhouse, p. 277, Fig. 10.5-10.7.

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

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

Material: Two ventral valves, five dorsal valves and a number of broken and crushed fragments.

Description: Ventral valve large with incurved umbo, umbonal angle measures 100° , not deformed, low concave interarea strongly marked by horizontal growth lines and weak vertical striae, divided by pseudodeltidium under umbo, arched at hinge to leave a gap where the

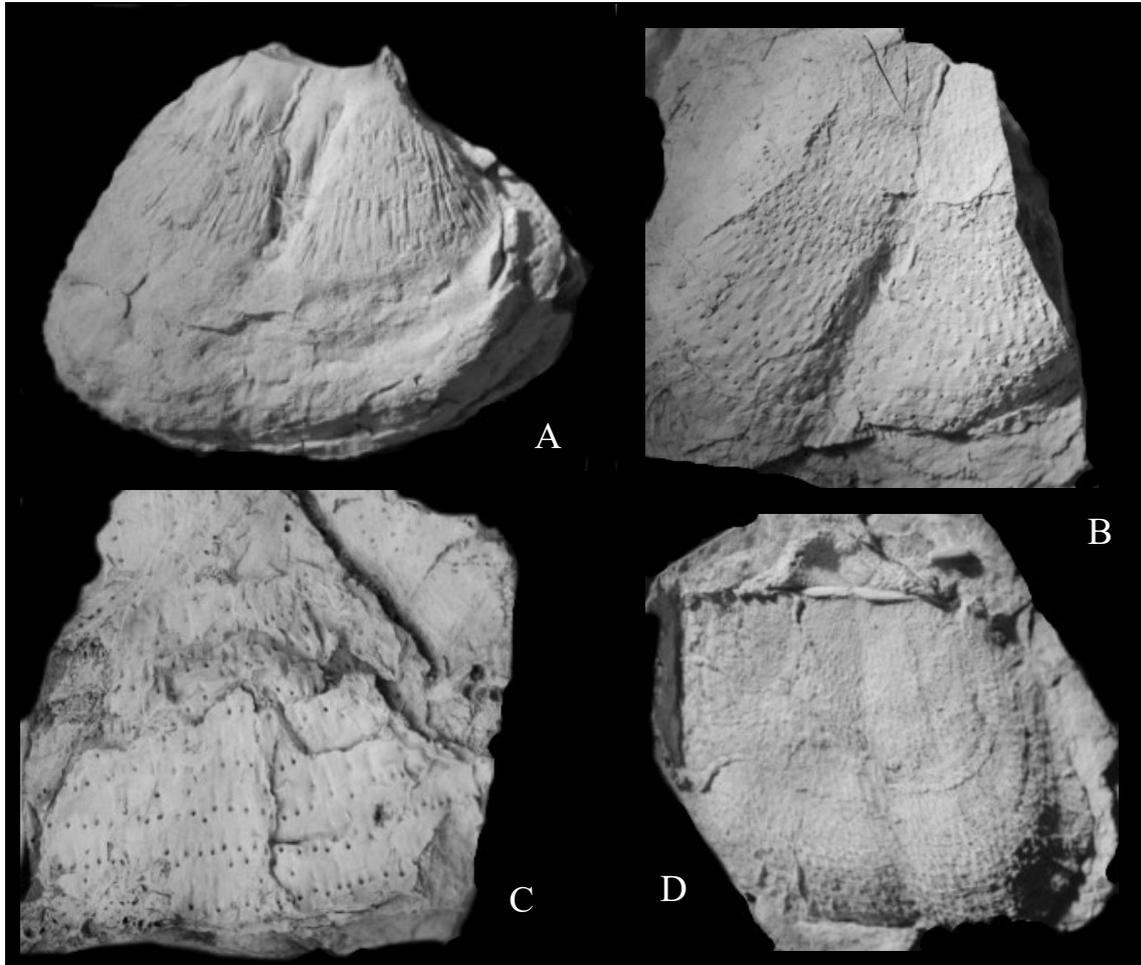


Fig. 5. *Taeniothaerus farleyensis* Briggs. A, ventral internal mould UQF 13540, x0.66. B, dorsal external mould UQF 26439, x0.66. C, external mould of ventral valve UQF 26440, x0.75. [registration number corrected from Waterhouse 2013]. D, dorsal external mould with ventral umbo, UQF 13535, x0.6. (Waterhouse 2013).

outer side of the cardinal process impacted (UQF 26440). The ventral valve is traversed by a moderately well formed shallow and narrow sulcus. Cardinal extremities are abruptly obtuse, with angle of $100-110^\circ$. The dorsal disc is gently concave and curves gradually into a low trail. A narrow fold commences close to the dorsal hinge, which carries a low flat interarea steeply inclined forward from the disc. Ventral ornament over the umbo consists of fine erect spines 0.4-0.5mm in diameter, and anteriorly erect spines lie up to 2-3mm apart along commarginal

rows up to 7mm apart, spines reaching a diameter of 0.8mm, but usually slightly less. Very low spine ridges extend posteriorly towards the preceding spine row, 3mm up to 7mm long: they gradually increase forward in height and width to terminate anteriorly at the spine base. Some ridges are present without spines. Growth-increments number up to thirty five in 5mm anteriorly, to suggest a life-span for the shells of close to a year or slightly more, and implying rapid growth, given the size of the shell. Dorsal spines anteriorly become as coarse as those of the ventral valve, up to 2-2.5mm apart along rows 2-4mm apart. Spine-bases are less conspicuous than in the ventral valve, but intervening dimples are well formed and elongate. In most specimens the dorsal spines are erect, but anteriorly over the trail of a few specimens some (UQF 13535) to many spines (UQF 13542) are prostrate and the dimples are subrounded rather than elongate.

Ventral adductors sited on two broad ridges, between strongly grooved diductor impressions. The shell, not preserved, appears to have been thin in one specimen, because the external ornament is preserved on the interior, with no other internal markings, but was thicker in other specimens, which have smooth internal surface, and the inner shell surface bears fine pustules anteriorly.



Fig. 6. *Taeniothaerus farleyensis* Briggs. A, dorsal internal mould UQF 13534, x1. B, external mould of dorsal valve and ventral beak UQF 13543, x0.9. From Lakes Creek Formation. (Waterhouse 2013).

Cardinal process long and narrow, with deep trough in one specimen, bearing a median slender median ridge on the inner face in the other (UQF 13534). The median septum extends from in front of the process for up to 0.75 of the length of the valve. Adductor scars are large and dendritic, without obvious subdivision into pairs, and a low platform extends forward from the anterior shaft of the cardinal process. The posterior floor is smooth and the anterior floor in front of the adductor scars and especially over the anterior disc and trail bears deep pits which, it may be speculated, extended into the spines.

Resemblances: *Taeniothaerus farleyensis* Briggs has a strongly arched ventral valve, and although Briggs (1998) stressed that the hinge of *farleyensis* was short, this is not confirmed from the figure of the holotype (Briggs 1998, Fig. 69B) as being very much shorter than in other species of *Taeniothaerus*. According to the Briggs' text, ventral spines in *farleyensis* are usually 0.6mm in diameter and dorsal spines are 0.3-0.4mm in diameter, compared with up to 0.8mm in the ventral valve and 0.4-0.5mm in the dorsal valve of *T. homevalensis* Briggs in Waterhouse et al. 1983, but spines are up to 1mm in diameter with bases 3-5mm long in the *farleyensis* topotype UQF 75290, judged from Briggs (1998, Fig. 69F). Over the ventral ears, spine bases are 0.6mm thick in UQF 75289, and form rows of closely spaced spines in curtains, but another external mould has more numerous spines, and the ears of UQF 75292 have many fine spines in clumps. The spine-bases as figured for *farleyensis* are not as coarse as those over the venter of *homevalensis*, but are just as numerous. On the other hand, dorsal spines are finer and spaced further apart in *farleyensis*, and the dorsal valve is less dimpled, and the ventral muscle field smaller, in comparison with *homevalensis*. Adequate information on the stratigraphic position of type *farleyensis* was not provided by Briggs and so presumably was not available, probably a reflection of the nature of the outcrops..

Briggs (1998) referred a Yarrol specimen of Maxwell (1964, pl. 7, fig. 35) to the same species, but it has much finer and denser spines.

Suborder LINOPRODUCTIDINA Waterhouse, 2013

Members of this suborder evolved from a ribbed chonetid, as opposed to Productida and Strophalosiidina which evolved from a smooth chonetid without ribs (Waterhouse 2013).

Three superfamilies are known, each derived from a separate subfamily within Devonoproducidae Muir-Wood & Cooper, 1960, and these devonoproducina subfamilies were close to their ribbed chonetid ancestors in having interareas, teeth and sockets.

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

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

Family **ANIDANTHIDAE** Waterhouse, 1968a

Subfamily **ANIDANTHINAE** Waterhouse, 1968a

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

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

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

Diagnosis: Small shells with dorsal ears smaller than in allied genera; ornament much as in *Anidanthus*.

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

Discussion: This genus was relegated to synonymy of *Anidanthus* Booker by Brunton (2007, p. 2652), but *Protoanidanthus* does not have a wedge-shaped dorsal valve, unlike *Anidanthus*, and the dorsal ears are much smaller than in *Anidanthus*, *Anidanthia* or *Megousia*. No systematic study has been published to justify or provide even meagre support for the claim by Brunton (2007) that the size of the ears was an intrageneric character, and in other summaries of genera, Brunton (2007) granted substantial importance to the large size of the ears, as for *Labaelia* (p. 2644) and *Auriolinoproductus* (p. 2652). That is not to argue that the ear-size is an infallible guide – to that extent, the exploration of morphological

variation and relationship to taxonomy remains a frontier science, and all classification is provisional to a degree. But it is believed that uncertainties over classification stand a better chance of resolution through careful but provisional segregation rather than lumping on an ad hoc and inconsistent basis.



Fig. 7. *Protoanidanthus costata* n. sp., block showing scattered and broken specimens, preserved as moulds, x3 approx. a, ventral external mould UQF 82606, b the designated holotype UQF 13528. c, ventral external mould UQF 82730. d, dorsal internal mould UQF 82607. e, ventral external mould UQF 82734.

***Protoanidanthus costata* n. sp.**

Fig. 7 – 10

Derivation: costa – rib, Lat.

Dagnosis: Elongate with sturdy costae.

Holotype: Specimen UQF 13528, Fig. 7, 8, specimen b, here designated.

Material: Two specimens with valves conjoined, eight broken ventral valves and two dorsal valves.

Description: The ventral valves are broken and crowded together. They are elongate with relatively strong ribs, at five in 5mm, which bear scattered and slender spines 0.3-0.5mm in diameter arising from the crest, and narrower than the crest. A row of much stronger spines 1mm in diameter extends along the inner ears. The dorsal valve is deeply concave, and one specimen, 13mm wide and long, suggests that ears were small with acute cardinal extremities, and slightly less than the maximum width of the shell. In other specimens the ears seem similar but are not well preserved. Costae are coarse, crossed by a number of commarginal laminae.

The internal mould of the visceral disc bears a septum that arises well in front of the hinge and extends to mid-length, and very low adductor scars.

Resemblances: This species is characterized by its elongate shape and strong costae. It is found in finer sediment than is the norm for other species of *Protoanidanthus* in east Australia, and is slightly younger than other occurrences in east Australia.

Protoanidanthus compactus Waterhouse (1986a, p. 61, pl. 13, fig. 19-22, pl. 15, fig. 16-18; 2015a, p. 117, Fig. 66) from the Fairyland, Dresden and lower Tiverton Formation (*Bookeria pollex* Superzone) is more transverse with much finer costae at nine to eleven in 5mm. Various other specimens from east Australia belong to the same species, including some specimens assigned to *Anidanthus cessnockensis* not Briggs (1998, Fig. 96D-F, H, I) and material figured as *Anidanthus* sp. by Muir-Wood & Cooper (1960, pl. 112, fig. 14-26) from the Colrairie Mudstone of the Macleay "Series" at Kimbriki, New South Wales.

Protoanidanthus pokolbinensis Briggs (1998, Fig. 95E-O) from Silver Spur beds in the Texas area of Queensland also has seven to ten costae in 5mm over transverse shells. Its ears are moderately large for the genus. From the Lochinvar Formation of New South Wales, *P. gosforthensis* Briggs (1998, p. 198, Fig. 95A-D) has finer ribs, counted at thirteen to fifteen in 5mm, and is weakly transverse. These specimens bear UQF registration numbers and so are presumably extant, unlike the Briggs AMF specimens which have disappeared.

From the lower South Curra Limestone of Gympie, southeast Queensland, so-called *Anidanthus springsurensis* [not (Booker)] of Runnegar & Ferguson (1969, pl. 2, fig. 15-17) has relatively fine costae, ten to eleven in 5mm, and coarse and crowded growth lamellae on the dorsal valve. It was described as a distinct species *Anidanthia aplini* Waterhouse & Balfe in Waterhouse (2015b).



Fig. 8. *Protoanidanthus costata* n. sp., latex cast x3 approx. showing scattered and broken specimens, preserved as moulds, mostly as ventral external moulds, and (d) as a worn dorsal internal mould. Holotype = b, UQF 13528. a = UQF 82607, d = UQF 82607, e, UQF 82734, as in Fig. 7.

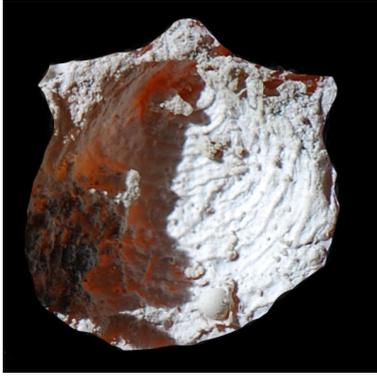


Fig. 9. *Protoanidanthus costata* n. sp., latex cast of dorsal valve UQF 82608, x3 approx.

Protoanidanthus umbonatus Shi & Waterhouse (1996, p. 101, pl. 18, fig. 1-16; Waterhouse 2018, p. 224, Fig. 191) is the closest of species so far known from the northern hemisphere, with comparatively strong ribs counted at six to seven in 5mm. Specimens are more transverse than the present species, and comes from the *Yakovlevia transversa*, *Rugivestis commarginalis* and *Ogilviecoelia shii* Zones, of broadly Sakmarian age, in the upper Jungle Creek Formation in the Yukon Territory of Canada.



Fig. 10. *Protoanidanthus costata* n. sp. A, C, ventral and dorsal aspects of internal mould. B, dorsal aspect of external mould, showing dorsal valve and part of ventral valve. Specimen UQF 82609, x2.

Genus *Anidanthia* Waterhouse, 2013

Diagnosis: Shells with moderate to large dorsal ears, and smaller ventral ears; ornament much as in *Anidanthus*. Dorsal valve not wedge-shaped, trail long.

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

Discussion: This genus is close to *Anidanthus* Booker, 1932, but lacks the wedge-shaped and almost flat dorsal valve of that genus, the dorsal valve being concave and not thickened, and possessing a long trail. *Nothokuvelousia* Waterhouse, 1986a from the Roses Pride Formation of the southeast Bowen Basin is synonymous with *Anidanthus*.

Anidanthia paucicostata (Waterhouse, 1986a)

Fig. 11 – 13

- 1892 *Productus* sp. indet. Etheridge, pl. 12, fig. 17.
 1932 *Linoproductus springsurensis* [not Booker] – Booker, p. 67, pl. 4, fig. 5-7? (part, not pl. 3, fig. 1-6, pl. 4, fig. 1-4 = *springsurensis*).
 1950 *Anidanthus springsurensis* [not Booker] – Hill, pl. 7, fig. 1, 3, 4 (part, not fig. 2, 5, 6 = *springsurensis*).
 1964 *A. springsurensis* – Maxwell, p. 44, pl. 7, fig. 13-16.
 1964 *A. springsurensis* – Hill & Woods, pl. P6, fig. 8, 10, 11 (part, not fig. 9 = *springsurensis*).
 1968b *A. springsurensis* – Waterhouse, p. 236, pl. 1, fig. 1, 4, 5, 6, text-fig. 2A, B, D (part, not pl. 1, fig. 2, 3, text-fig. 2C, 3 = *springsurensis*).
 1968c *Megousia* sp. Waterhouse, p. 1174, pl. 154, fig. 7, 12, 13.
 1972 *A. springsurensis* – Hill, Playford & Woods, pl. P6, fig. 8, 10, 11 (part, not fig. 9 = *springsurensis*).
 1974 *A. springsurensis* – McCarthy et al., Fig. 4J.
 1980 *A. springsurensis* – McClung, pl. 19.1, fig. 6.
 1986a *A. paucicostatus* Waterhouse, p. 62, pl. 13, fig. 23-27, pl. 14, fig. 1, 2, 4-9.
 1998 *A. springsurensis* – Briggs, p. 204, Fig. 97A-F, G?, H? (part, not Fig. 97I - K = *springsurensis*).
 1998 *A. cessnockensis* Briggs, p. 201, Fig. 96A, C, G (part, not D, E, F, H, I = *Protoanidanthus compactus* Waterhouse).
 ?2013 *Anidanthia paucicostata* – Waterhouse, p. 330, Fig. 15.21 - 15.22.
 2021 *A. paucicostata* – Waterhouse, Fig. 2A.

Diagnosis: Shells moderately transverse with wide venter, moderately coarse costae, often with fine intercalated costae, dorsal valve with sharply raised commarginal ribs.

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

Material: Three ventral valves and five dorsal valves and two broken specimens with valves conjoined.

Description: The ventral valve is vaulted and transverse, with broad incurved umbo measuring 110° to 120°, and without a sulcus. The dorsal valve has a broad only gently concave disc. Ventral cardinal extremities are obscure, and the dorsal ears are not laterally extended very far in three specimens, probably because they are poorly preserved, but two dorsal valves UQF 13530 and UQF 82731 have extended ears: reconstructing UQF 13530, the overall

width is 32mm, and the width of the disc 15mm. The dorsal valve is not thickened. Costellae number six to seven in 5mm at the anterior margin of the ventral valve, with interspaces as wide as the ribs. The dorsal ornament is more striking, with six to eight ribs in 5mm anteriorly and the visceral disc is crossed in five of the six specimens by well formed commarginal ribs of regular spacing and strength, numbering about five in 5mm. In some specimens these ribs are upstanding, in others, each rib is bordered posteriorly by a sharply defined cincture, so that they are each formed from a lamellum. The inner ears are ornamented by these commarginal ribs, like the inner ears of the ventral valve. Low commarginal growth steps also lie close to the anterior margin of the dorsal valve. Fine erect spines are scattered over the posterior disc and anterior ventral valve, arising from the crest of ribs, but preservation does not show if a hinge row is present, and there are no dorsal spines.

The ventral adductor scars are impressed posteriorly into a secondarily thickened posterior shell, and are subrectangular and slightly elongate in outline. To each side subrounded triangular diductor impressions overlap the adductors for more than half of their length. In front the floor of the valve is marked by elongate pits, the pits gradually reducing in size and becoming less elongate anteriorly.

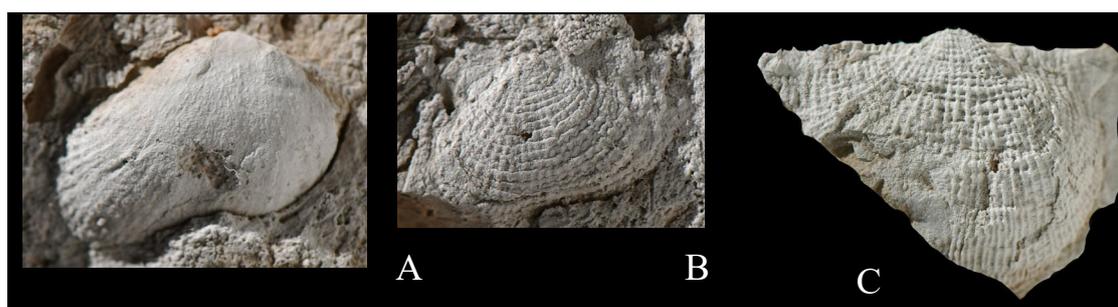


Fig. 11. *Anidanthia paucicostata* (Waterhouse). A, ventral internal mould UQF 13527, x1.5. B, dorsal external mould UQF 13526, x2. C, dorsal external mould UQF 13529, x1.5.

Resemblances: These specimens are of the same size with similar strong costae as in *Anidanthia paucispinosa*. The emphasized commarginal growth ridges approach those of the type suite figured by Waterhouse (1986a), although more defined and less overlapping. On the other hand, a smaller dorsal valve UQF 13526 has overlapping lamellae, and the material figured by Hill (1950, pl. 7, fig. 1) from the same quarry suggests a strong approach to *pauci-*



Fig. 12. *Anidanthia paucicostata* (Waterhouse). A, dorsal valve UQF 13530 x4. Arrow points to large dorsal ear preserved on right side. B, dorsal valve UQF 13531, x5.

costata. A dorsal valve has some eight to nine ribs in 5mm (GSQF 2004), the density comparable to that of ribs on a Cattle Creek specimen of Hill (1950, pl. 7, fig. 2 – GSQ F 2003), but the specimens appear to be closer in size and other attributes to the material recorded herein as *Anidanthia paucicostata*. The difference invites further comparison, limited in this study by the paucity of available specimens, but provisionally the upstanding commarginal ribs are regarded as a variation from the normal development of lamellae. Briggs (1998, p. 204) referred *paucicostata* to synonymy of *springsurensis*, and ignored or overlooked the different nature of the dorsal valve in the two species.



Fig. 13. *Anidanthia paucicostata* (Waterhouse), dorsal valve UQF 82731.

Order SPIRIFERIDA Waagen, 1883

Suborder MARTINIIDINA Waterhouse, 2016

Superfamily **INGELARELLOIDEA** Campbell, 1959

Family **INGELARELLIDAE** Campbell, 1959

Genus ***Ingelarella*** Campbell, 1959

Diagnosis: Medium to large plicate shells with ventral sulcus usually subplicate and dorsal fold channelled by a narrow sulcus, adminicula and tabellae well developed, moderately spaced, tigillum may lie along anterior mid-line of ventral valve.

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

Ingelarella intrudus n. sp.

Fig. 14, 15

2011 *Ingelarella* sp. Waterhouse, Fig. 2J.

2015a *Ingelarella* sp. Waterhouse, p. 153, Fig. 102A-C.

2016 *Ingelarella* sp. Waterhouse, Fig. 68.

Derivation: intrudus – force in, Lat.

Diagnosis: Moderately large with sulcal subplicae and channelled fold, low, faint or no lateral plicae, adminicula moderately close-set and a quarter to a third of the length of the shell, tabellae weakly diverging, short.

Holotype: UQF 81342 from Tiverton Formation, figured by Waterhouse 2015a, Fig. 102A-C, here designated.

Material: Three ventral valves, a dorsal valve and two specimens with valves conjoined.

Dimensions in mm: ventral valve, distorted

Width	Length	Height
46	34	8

Description: Specimens preserved as internal moulds, transverse, sulcus well formed with two prominent subplicae, two or three low lateral plicae on the ventral valve. Dorsal plicae on conjoined specimen number two on one side and none on the other. Fold well defined with steep lateral sides and broad crest bearing weak suggestions of a channel. Ventral interarea comparatively flat and high, with open delthyrium for which the angle measures 25° , dental plates high, adminicula high and steeply inclined, diverging weakly forward for slightly less than a third of the length of the valve. Muscle field lies between the adminicula, adductor scars raised, with two linear ridges forming bases for the adductor scars, weakly rounded in section, divided by low ridge. Diductor scars wider, with low ridges and grooves sloping postero-laterally. Posterior floor with shallow small pits. Dorsal valve with tiny medianly recessed ctenophoridium, very short median septum, and divergent tabellae extending over posterior fourth of shell length. An ovally subrectangular impressed area lies in front of the

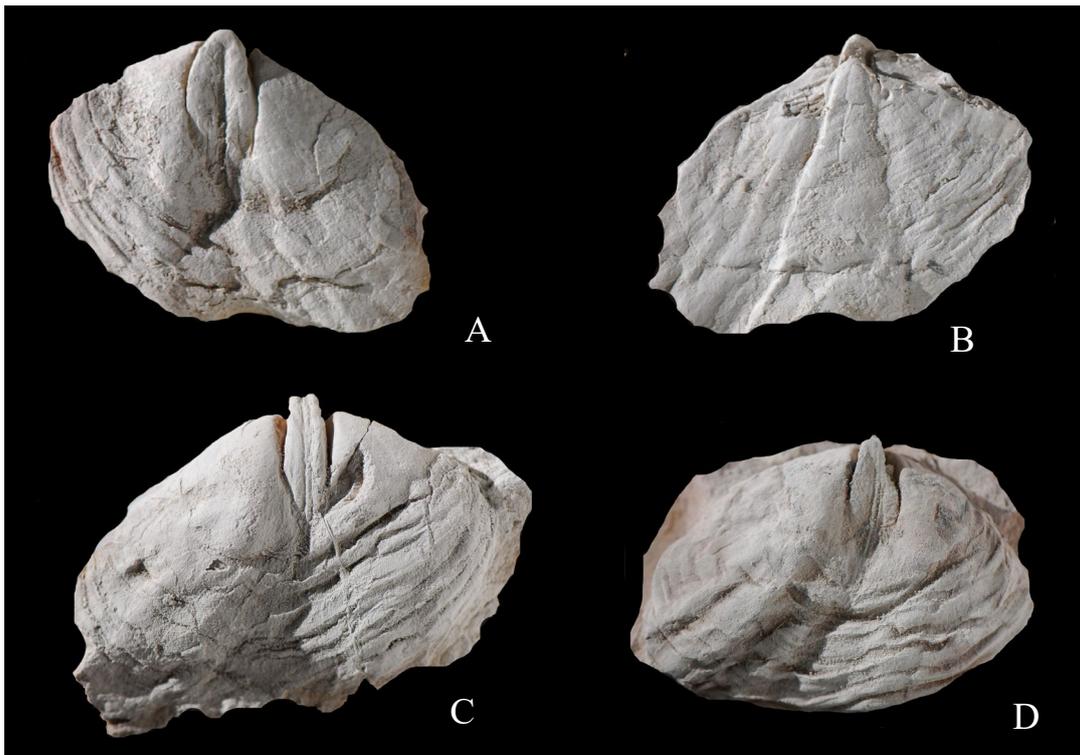


Fig. 14. *Ingelarella intrudus* n. sp. A, B, ventral and dorsal aspects of internal mould UQF 13511, x1. C, ventral internal mould UQF 13505 x1. D, ventral internal mould UQF 13509, x1.

septum, possibly representing dorsal adductor scars. Very fine pits lie over this area and laterally over the posterior floor of the valve.

Resemblances: *Ingelarella* sp. of Waterhouse (2015a; 2016) from the *Svalbardia armstrongi* band at the top of the *Magniplicatina undulata* Zone and start of the *Taeniothaerus subquadratus* Zone in the upper middle Tiverton Formation shows similarities in plication, and has sulcal subplicae and channelled dorsal fold. These are now assigned to the species *intrudus*, and are deemed identical with present material. Adminicula and tabellae are moderately similar and are anteriorly parallel or subparallel. A dorsal valve figured by McCarthy et al. (1974, Fig. 4D) and called *Martiniopsis ovata* (Campbell) from the Emu Creek beds near Drake might prove to be related, but the information about the ventral valve would be desirable. Closest of other species of *Ingelarella* is the slightly younger *I. plica* Campbell, 1960, which comes from the top of the Tiverton Formation and also from equivalent beds of the Brunel Formation in the Takitimu Group of New Zealand (Waterhouse 1964). Compared with *intrudus*, this species has stronger plicae, shorter tabellae, and similar adminicula.



Fig. 15. *Ingelarella intrudus* n. sp. A, C, ventral and dorsal aspects of internal mould UQF 13507 x1. B, dorsal internal mould UQF 46638, x1.

The specimens are larger and less inflated than species of *Geothomasia* described from Western Australia, which have the fold consistently low and broad and sulcus wide and shallow. In eastern Australia, species of *Geothomasia* are larger than those of Western Australia and may have more prominent plicae, sulcus and fold, such as *Geothomasia profunda* (Campbell, 1961), extensively illustrated in Waterhouse (2015a) from the Tiverton

Formation of the Bowen Basin. The dorsal fold is consistently high with rounded crest in Tiverton specimens, and plicae are strong. Comparable ventral valves have also been reported from the Teebar Formation, near Gympie in southeast Queensland (Waterhouse 2015b, p. 135, Fig. 52).

Genus *Ambikella* Sahni & Srivastava, 1956

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

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

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

ventral valve in front of the ventral muscle field, and more importantly, in having a channel along the crest of the dorsal fold, a facet ignored by Singh & Archbold (1993).

Some specimens of *ovata* from the type area near Homevale in the north Bowen Basin do have small c-shaped or sliver spines (Campbell 1961, pl. 24, fig. 9), leading to the proposal of a distinct genus *Homevalaria* by Waterhouse (1986b, p. 110), but it has been found that specimens assigned to *ovata* from this region vary – a few have c-spines, but most do not, leading to the conclusion that the phenomenon was purely an intrasubspecific variation (Waterhouse 2015a, pp. 160-162), limited to a few individual specimens.

Ambikella ovata (Campbell, 1961)

Fig. 16, 17

- 1961 *Ingelarella ovata* Campbell, p. 177, pl. 24, fig. 3-9.
 1964 *I. ovata* – Maxwell, p. 47, pl. 9, fig. 29, 30.
 1964 *I. ovata* – Hill & Woods, pl. P9, fig. 10-12.
 1970 *I. ovata* – Armstrong, p. 204, pl. 14, fig. 4 (part, not fig. 5, 6 = *Geothomasia profunda*).
 1972 *I. ovata* – Hill, Playford & Woods, pl. P9, fig. 10-12.
 1975 *Martiniopsis ovata* – Runnegar & McClung, pl. 31.1, fig. 6, 8, 9, 24 (part, not fig. 7 = *symmetrica*).
 1978 *I. ovata* – McClung, p. 47, pl. 2, fig. 7, pl. 4, fig. 14, 15, 18, 19, pl. 5, fig. 1 (part, not pl. 2, fig. 8, pl. 4, fig. 16, 17, 20 = *Geothomasia symmetrica* (Campbell)).
 1983 *Ambikella ovata* – Waterhouse, Campbell & Williams, p. 303, text-fig. 3, 4.
 1983 *Ambikella* sp. Waterhouse, Williams & Campbell, p. 303, text-fig. 5.
 1986b *Homevalaria ovata* – Waterhouse, p. 110.
 1987a *Tomioopsis ovata* – Waterhouse, p. 29, pl. 7, fig. 18, 20-21, 22, pl. 8, fig. 1, 2 (part, not pl. 7, fig. 7, 15, pl. 8, fig. 3-6 = n. sp.?)
 2006 *H. ovata* – Carter & Gouvenec, p. 1763, Fig. 1160.2a-e.
 2015a *Ambikella ovata* – Waterhouse, p. 159, Fig. 106B, 107-110.
 2015b *A. ovata* – Waterhouse, p. 133, Fig. 51.
 2016 *A. ovata* – Waterhouse, Fig. 69.

Diagnosis: Weakly transverse and inflated large shells with broad ventral sulcus bearing faint signs of two subplicae in some specimens, fold high without channel, lateral shell generally smooth but may be weakly plicate, adminicula long and subparallel, tabellae of moderate length.

Holotype: UNEF 3182 from “zone 13” of Tiverton Formation, Homevale, figured by Campbell (1961, pl. 24, fig. 4a-c), Hill & Woods (1964, pl. P9, fig. 10, 11), Hill, Playford et al. (1972), and Carter & Gouvenec (2006, Fig. 1160.2a-c), OD.

Material: Eighteen ventral valves, a dorsal valve and four specimens with valves conjoined, some distorted and most collected as internal moulds.

Description: As is clear from the synonymy, this species has been described in a number of publications, and the present collection adds little to any circumscription of the species. One specimen has three ventral plicae pairs and two dorsal plicae pairs, but some other specimens have non-plicate flanks. The sulcus generally lacks any subplicae, but may show a narrow central groove that commences at or front of the beak, and the fold has a rounded crest. Dental plates are high and scapular-shaped, the adminicula are high, moderately long and spaced well apart, the adductor scars placed on two narrow ridges, and diductor scars are wider with a few longitudinal grooves and ridges. In the dorsal valve the tabellae are short to moderate in length and border the fold.

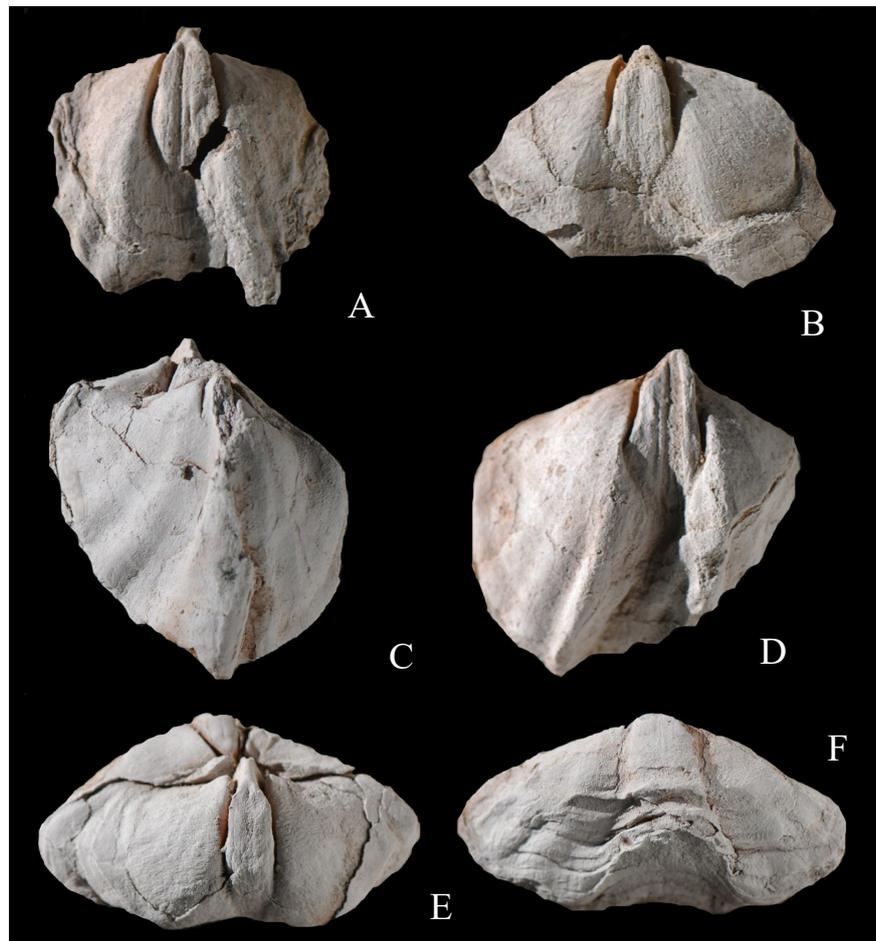


Fig. 16. *Ambikella ovata* (Campbell). A, ventral internal mould UQF 13501, x1. B, ventral internal mould UQF 13502. C, D, ventral and dorsal aspects of internal mould of specimen with valves conjoined, UQF 13500, x1. E, F, posterior and anterior aspect of distorted specimen UQF 13506, x1, dorsal valve on top.

Resemblances: The species is found in the *Magniplicatina undulata* and *Taeniothaerus subquadratus* Zones of the Tiverton Formation in the north Bowen Basin. McClung (1978, p. 46) figured specimens of *ovata* from the Farley Formation of the Hunter Valley, and reported specimens from the Pebbley Beach Formation of the south Sydney Basin, not stratigraphically located in terms of position within the formation, nor specified as to locality, but possibly from supposed basal beds that might match an older level..



Fig. 17. *Ambikella ovata* (Campbell). A, posterior aspect of internal mould of specimen with valves conjoined, UQF 13500, x1.5. See also Fig. 16C, D. B, posterior aspect of internal mould of specimen with valves conjoined, UQF 13508, x1.25.

Specimens were also described from the Yarrol Formation, Yarrol Basin, by Maxwell (1964) and from the Elvinia Formation and Boughyard Member of the southeast Bowen Basin by Waterhouse (1987a), and the Teebar Formation near Gympie (Waterhouse 2015b). Specimens reported by Waterhouse (1987a, pl. 7, fig. 7, 15, pl. 8, fig. 3-6) from the Roses Pride Formation, southeast Bowen Basin, are close in general appearance but have a less well-developed sulcus and lower fold, and may well prove to belong to a separate species. Adminicula appear to be short and closely spaced in these specimens (Waterhouse 1987a, pl. 8, fig. 4) but the nature of tabellae is obscure. The species *ovata* is represented by poorly preserved material in the Gondor Formation of southwest New Zealand. The report by Waterhouse (1964a, p. 91; 1964b, p. 152) of *ovata* in the Brunel Formation, Takitimu Group of New Zealand may be discounted, the specimens belonging to the slightly younger species

Ingelarella sulcata Waterhouse, a species with narrower more grooved ventral sulcus and channelled fold. Compared with *Ingelarella intrudus* n. sp. from the Lakes Creek Formation, the fold is high with rounded crest, and the sulcus concave. Adminicula are spaced a little further apart.

Genus ***Tigillumia*** Waterhouse, 1998

Diagnosis: Sulcus may be very shallow, especially in older species, fold varies from low to high, with rounded crest and no channel, micro-ornament of shallow elongate grooves arranged in quincunx. Adminicula and tabellae long and close-set, tigillum or median thickening generally present along anterior mid-line of ventral valve.

Type species: *Martiniopsis biparallela* Waterhouse, 1987a from the Brae Formation (Kungurian), southeast Bowen Basin, Queensland, OD.

Tigillumia adminiculata Waterhouse, 1982?

Fig. 18

?1964b *Martiniopsis* n. sp. Waterhouse, p. 147, pl. 30, fig. 1, 2, text-fig. 70.

?1982a *M. adminiculata* n. sp. Waterhouse, p. 56.

?1998 *Tigillumia adminiculata* – Waterhouse, p. 27.

2021 *T. adminiculata?* – Waterhouse & Campbell, p. 31, Fig. 9.

Diagnosis: Subglobular broadly sinuate shell with well inflated dorsal valve, no plicae, low fold, adminicula long and close-set, tabellae long and well spaced.

Holotype: BR 603 from Brunel Formation, Takitimu Group, figured in Waterhouse (1964b), OD.

Material, Description, Resemblances: A ventral valve UQF 13512 with narrow sulcus and no plicae has long close-set adminicula, narrow adductor scars sited in a single groove and narrow diductor scars with oblique growth lines directed postero-laterally. A similar ventral valve was figured from the Eglinton Subgroup in the Dunton Range of New Zealand, from slightly older beds of the *Magniplicatina undulata* Zone, by Waterhouse & Campbell (2021).

The adminicula resemble those of *Tigillumia* Waterhouse, which also has long closely spaced tabellae, but no dorsal valve is preserved for the present form. McClung (1978) regarded such specimens as belonging to *Ingelarella* – but he treated all members of the family in east Australia as belonging to a single genus *Ingelarella*, and did not provide any scrupulous assessment of morphological features. A very few east Australian and New Zealand species

have been placed in *Tigillumia*, but a scattering of specimens from other levels approach *Tigillumia*, and it is far from clear whether these are members of the *Tigillumia* lineage, or convergent developments within other lineages.



Fig. 18. *Tigillumia adminiculata* (Waterhouse)?, ventral internal mould, UQF 13512, x1.

Suborder SPIRIFERIDINA Waagen, 1883

Superfamily **PAECKELMANNELLOIDEA** Ivanova, 1972

The classification of Paeckelmannelloidea apparently needs to be modified from the arrangement offered in the *Revised Brachiopod Treatise* by Carter (2006), because Poletaev (2001, p. 42) has substantially revised the nature of Strophopleuridae, as reviewed in Waterhouse (2016, p. 151 ff.). The Poletaev revision raises the question of whether the Strophopleuridae would be better regarded as martinoid rather than packelmannelloid, give the stated lack of adminicula.

Family **PTEROSPIRIFERIDAE** Waterhouse, 1975

Subfamily **PTEROSPIRIFERINAE** Waterhouse, 1975

Genus ***Pteroplecta*** Waterhouse, 1978

Diagnosis: Transverse multiplicate shells with sulcus, fold and plicae developing costae as a rule, well developed 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 (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*. These genera do not 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 non-paeckelmannelloid entity.

***Pteroplecta blakei* n. sp.**

Fig. 19 - 21

Derivation: Named for Paul Blake.

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: UQ F 13580, Fig. 19C-F, 21A-C, here designated.

Material: A ventral valve and two small dorsal valves, and specimen with valves conjoined, as well as fragments.

Dimensions in mm:

Width	Length	Height	
+58	+30	13	holotype, both valves, UQF 13580
56	27	9.5	ventral valve internal mould, UQF 13589
25	13.5	5	dorsal valve UQF 26428

Description: Shells transverse with broad ventral umbo displaying an angle estimated to be close to 120°, and subulate cardinal extremities, not unduly prolonged. Ventral interarea of moderately height, only gently concave, weakly inclined ventrally from the commissure, bearing traces of subvertical striae but not well preserved, interrupted by delthyrium which has an angle of 70° and is rimmed by lateral dental flanges. Dorsal interarea low, almost flat, inclined posterodorsally from commissure at 45° approximately, notothyrial angle of 115°. The sulcus widens at an angle of 35°, with a concave floor rounding gently on to the lateral flanks, and the fold is well defined, with angle of 30° and rounded crest. There are eight pairs of plicae on each valve, and anteriorly two or rarely three costae develop over inner plicae, more

conspicuously on the dorsal valve. Costae extend along the sulcus and fold, three costae close to mid-length and five anteriorly. Fine commarginal laminae cross each valve, some six to seven in 5mm over the median valve.

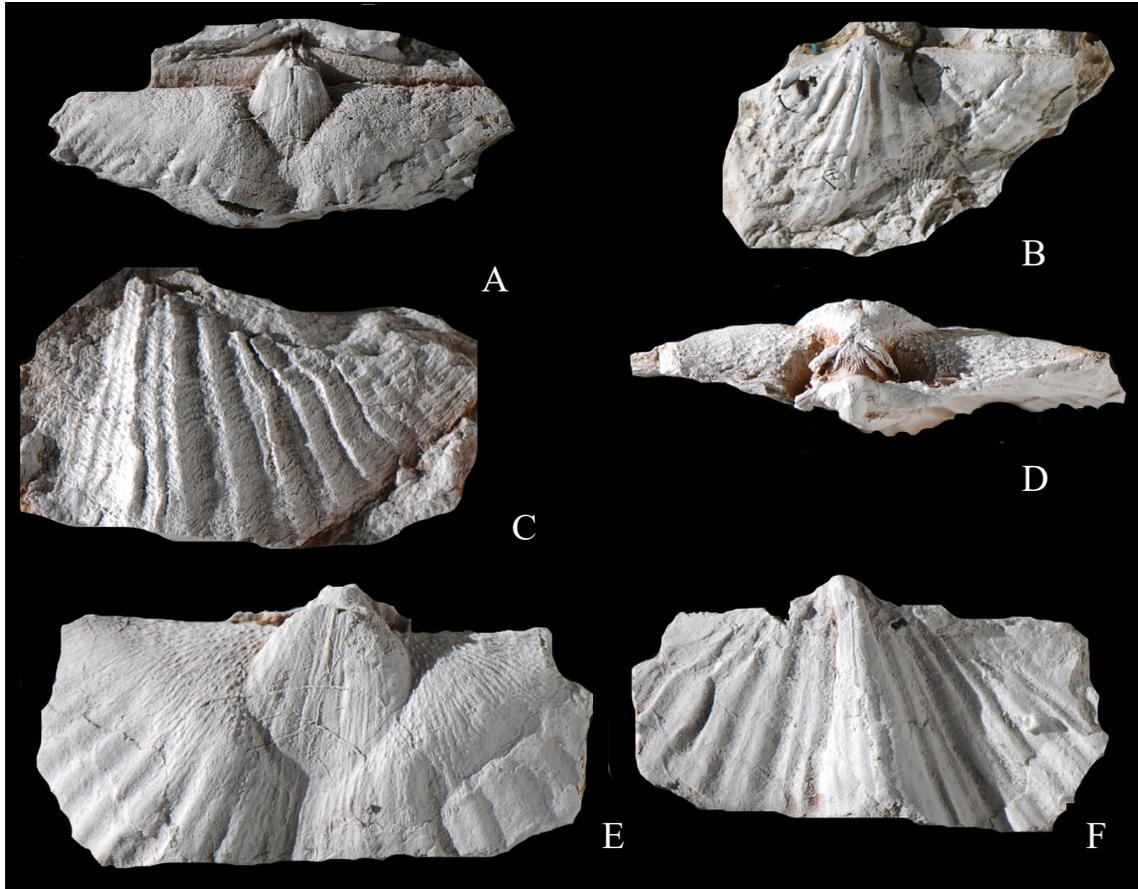


Fig. 19. *Pteroplecta blakei* n. sp. A, ventral internal mould UQF 13589. x1. B, dorsal valve UQF 82610, x1.5. C-F, holotype UQF 13580, x1.5. C, external mould of dorsal valve, the fold lying to extreme left. D-F, posterior (ventral valve on top), ventral and dorsal aspects, x1.5.

Teeth supported by short but high dental plates and short high adminicula which are largely buried in secondary shell. These diverge forward each side of a broad and short ventral muscle field, divided posteriorly by a short myophragm. There is no subdelthyrial connector plate. Adductor scars not clearly differentiated, bearing impersistent radial grooves and ridges; diductor scars broad with more persistent longitudinal grooves and ridges.

Secondary thickening considerable, floor covered by shallow pits, anterior shell almost smooth.

Broad triangular ctenophoridium bearing a number of vertical laminae, recessed medianly, between narrow dental sockets. Low median septum extends past mid-length, between faintly impressed elongate weakly pitted adductor scars. Spiralia concealed by matrix.

Fig. 20. *Pteroplecta blakei* n. sp., dorsal internal mould UQF 26428, x5.



Resemblances: This species is close to *Pteroplecta laminatus* Waterhouse (1978, p. 86, pl. 13, fig. 9-16) [not fig. 8 = *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 broader 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.

Another Late Permian species slightly older than the type, *P. sulcata* Waterhouse (1983a, 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. 21. *Pteroplecta blakei* n. sp., A, latex cast of external mould for dorsal valve (see Fig. 19C), x2. B, C, ventral external mould and cast. Holotype UQF 13580, x1.5.

Discussion: This species of *Pteroplecta* 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 2006).

Superfamily **TRIGONOTRETOIDEA** Schuchert, 1893

Family **GEORGINAKINGIIDAE** Waterhouse, 2004

Genus *Neilotreta* Waterhouse, 2008a

Diagnosis: Medium-sized shells with five to seven pairs of persistent plicae, and varyingly developed costae. Clearly defined sulcus, fold prominent and broadly rounded. Short adminicula, short dental plates which meet posteriorly and may support a modest umbonal callosity in late maturity, socket and crural plates, no tabellae, no subdelthyrial plate. Delthyrium open, and well spaced mantle canal system. Spiralia laterally directed in type species.

Type species: *Trigonotreta narsahensis occidentalis* Thomas 1971, p. 108 from upper Lyons Group, Western Australia, OD.

Discussion: The present species is close to *Neilotreta* in size and shape and broad and closely costate dorsal fold (fastigium), and is exceptional in being more costate than other species assigned to the genus. There are also similarities to *Trigonotreta* Koenig, 1825 rather than *Grantonia* Brown, 1953 in having some five to seven pairs of well developed costate and persistent plicae, whereas the inner three to four pairs of plicae are more strongly developed in *Grantonia*, and costae may be more differentiated..

***Neilotreta lakeensis* n. sp.**

Fig. 22 - 30

Derivation: Named from Lakes Creek Formation.

Diagnosis: Transverse, may be subalate, with numerous costae, six to seven pairs of plicae.

Holotype: UQF 13554, illustrated as Fig. 22A, 26E, F, here designated.

Material: Thirteen ventral valves as well as eight broken external moulds, and four dorsal valves and three external moulds, and a specimen with valves conjoined.

Dimensions in mm:

UQF	Width	Length	Height	
13554	46	26.5	7	ventral valve
13557	53.5	23	8	ventral valve
13556	35	20	13.5	both valves
13561	39	23.5	8	dorsal valve
13582	55	27	10.5	ventral valve

Description: Specimens are small and weakly transverse, with gently incurved ventral umbo bearing umbonal angle of 100°, and hinge at maximum width, as a rule with small alate extremities. The ventral interarea is of modest height and gently concave, lying in the plane of

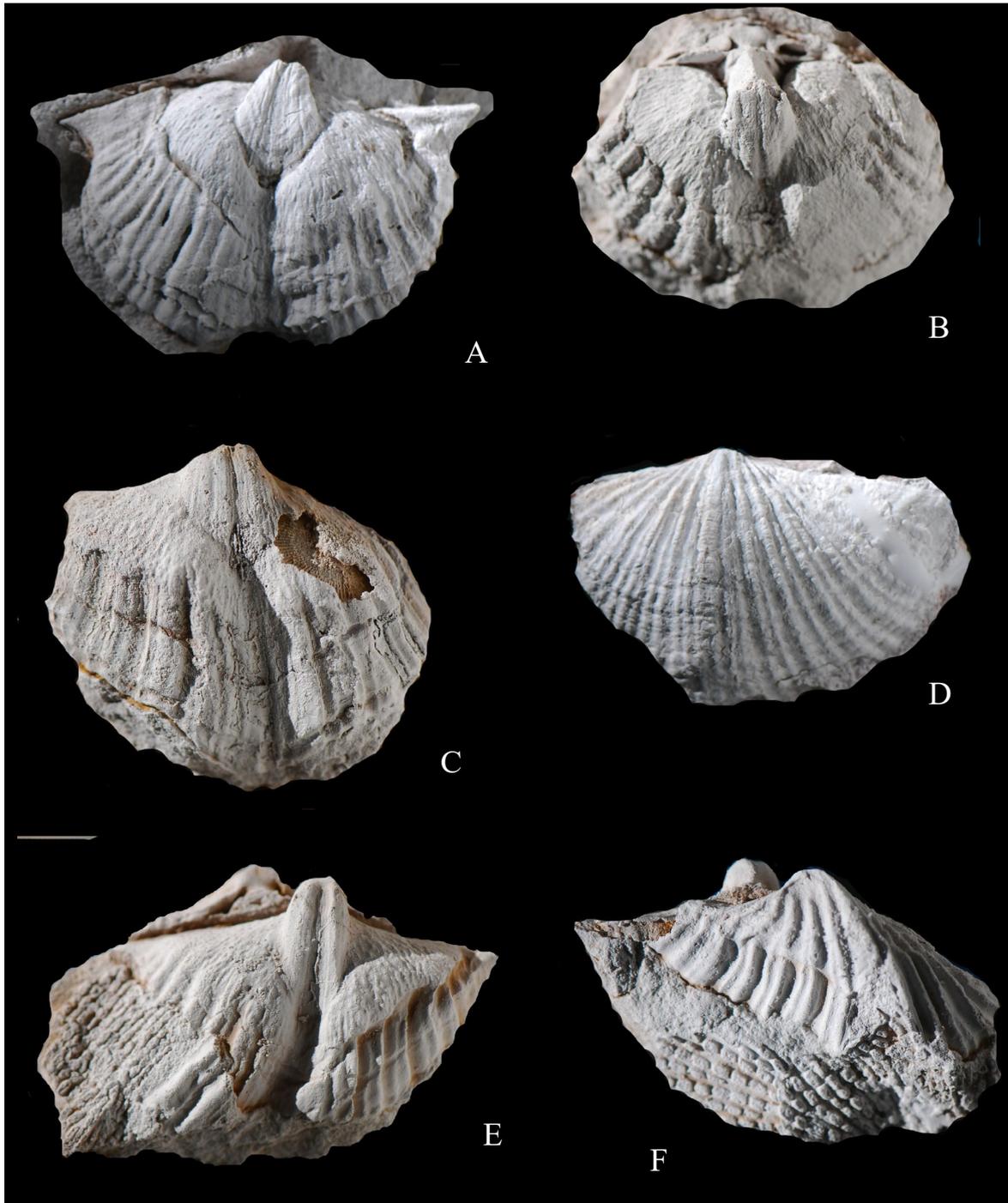


Fig. 22. *Neilotreta lakeensis* n. sp. A, ventral valve holotype, UQF 13554 x2. See Fig. 27E, F. B, posterior aspect of ventral valve, UQF 13358 x2. C, ventral valve UQF 13385 x2. D, dorsal exterior, UQF 82611, x2. E, F, ventral and dorsal aspects of internal mould with valves conjoined, UQF 13554, x2. This specimen was ground down in the vain effort to see the spire.

the commissure, and marked by horizontal grooves. There is a narrow delthyrium with angle close to 25°, closed under the umbo by the posterior outer ends of the dental plates which

extend along the sides of the delthyrium. The dorsal interarea is low. It becomes more concave with advanced ontogeny, starting at a low angle from the commissure but arching to be inclined at a steep angle from the commissure.

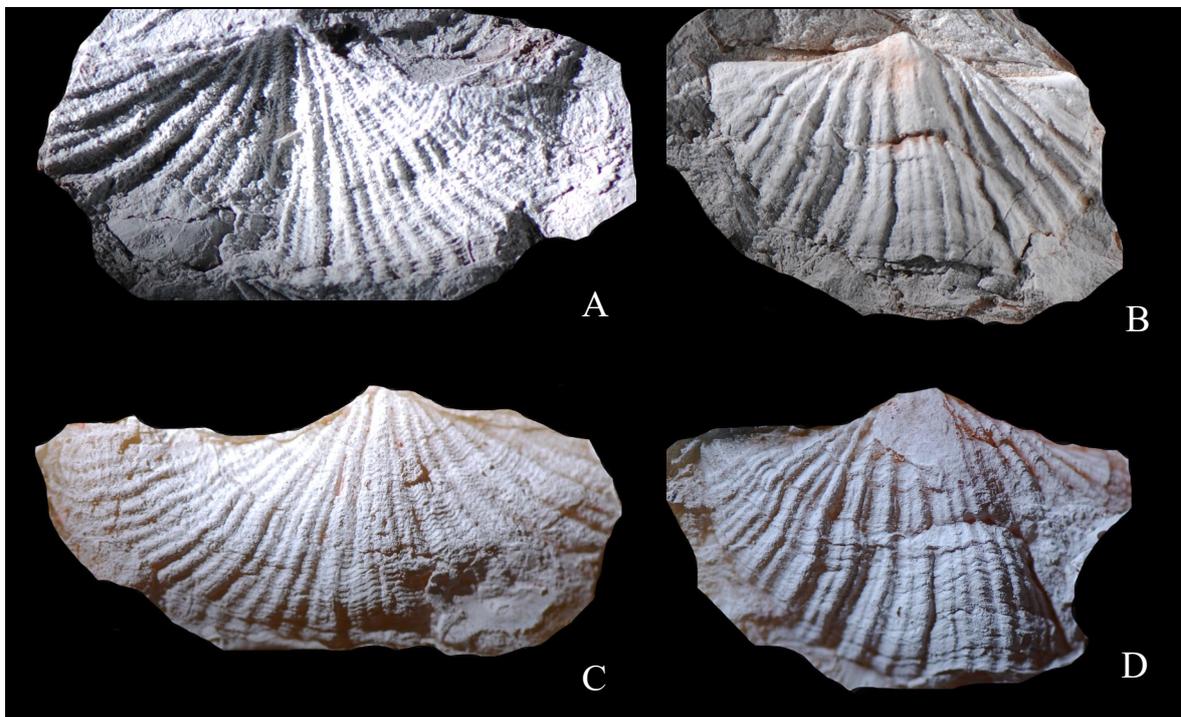


Fig. 23. *Neilotreta lakeensis* n. sp., dorsal valves. A, C, dorsal external mould and latex cast of UQF 13584 x1.5. B, dorsal internal mould UQF 13561, x1.5. D, latex cast of UQF 13564, x1.5.

The sulcus commences at the beak, and widens at a low angle close to 25° , narrower posteriorly, and anteriorly the sulcus widens more at a sulcal angle of 30° to incorporate the innermost pair of plicae. The U-shaped cross-profile has a gently concave median portion and diverging sides. The dorsal fold is distinct, with well rounded and broad crest, and a subsidiary pair of plicae extends along its flanks. Six or seven pairs of narrow plicae characterize the ventral valve, arising close to the hinge, and narrowly arched in section with narrow interspaces, varying to being mirror images of the interspaces. Dorsal plicae number six pair, and the innermost pair is distinct from the fold throughout its length, but may lie on the outer flanks of the fold. Costellae cover both valves, eight in the anterior sulcus and six to eight over the anterior fold. The inner plicae bear two ribs, with three ribs over the third

and fourth plication from the midline. Additional ribs arise anteriorly through intercalation. There are traces of very fine radial fila, and commarginal growth increments are pronounced, from ten to twelve in 5mm.

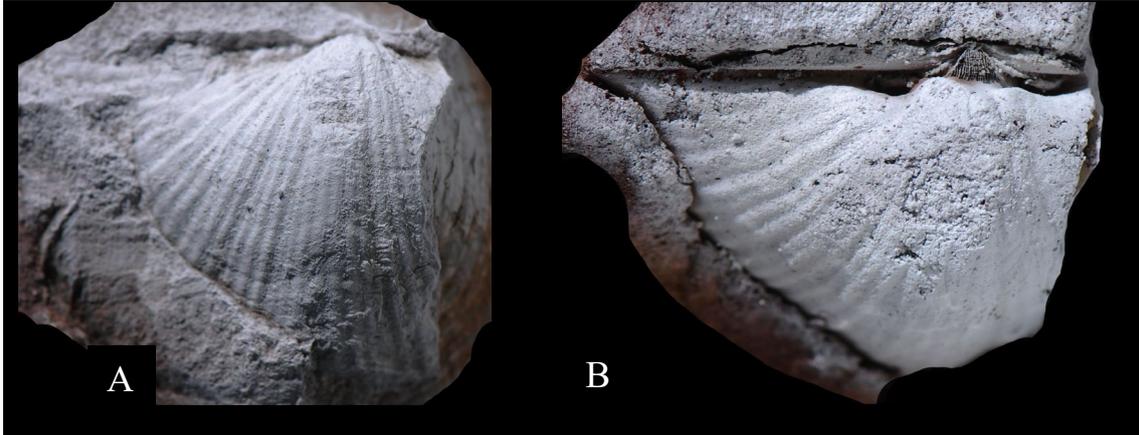


Fig. 25. . *Neilotreta lakensis* n. sp. A, dorsal valve, UQF 82612, x2. B, posterior aspect of the same specimen after leaching in dilute HCl, x2.

High dental plates diverge forward and outward to small teeth lying inside the groove bordering the delthyrium, and they are supported by subvertical short adminicula, which become largely buried in secondary thickening. Posteriorly, the dental plates are often reinforced by pleromal ridges along the inner edge, which unite posteriorly (Fig. 26, 27), and at late maturity, bears a slender umbonal callosity, as illustrated in Fig. 28. The posterior junction of the dental plates rarely bears a swelling, but usually a groove, and some specimens show two growth ridges each side of a median groove. The ventral muscle field is elongate and either subrectangular or trapezoidal, with narrow adductor platform, varying in definition for different specimens, and divided by a short blunt myophragm posteriorly. Diductor scars are broad with a number of longitudinal grooves and ridges. The mantle canals form a closely spaced network of grooves over substantial posterior thickening.

In the dorsal valve, a small ctenophoridium lies between dental socket plates, which are not supported by tabellae. In a larger specimen the ctenophorium is broadly triangular with many vertical laminae. A low erratic median septum extends over the posterior third of the shell length, but there are no clear signs of muscle scars.

Resemblances: This species is more costate than other known species, and is of interest in displaying well the delthyrial construct of the ventral valve, which lacks the broad infilling and large umbonal callosity typical of *Trigonotreta*. The broadly rounded and closely costate fold is typical of *Neilotreta*.

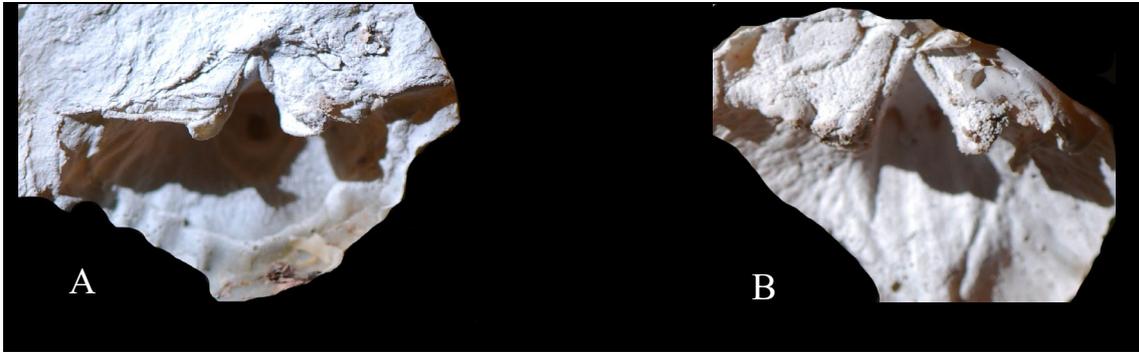


Fig. 26. *Neilotreta lakeensis* n. sp. Latex cast of ventral valve showing the outer edge of the delthyrial plates. A, UQF 15639, x3. See Fig. 27C, D. B, UQF 13557, x2.5. See Fig. 27A.

The type species of *Neilotreta*, *Trigonotreta narsahensis occidentalis* Thomas (1971, p. 108, pl. 19, fig. 1-6, 9-13, Text-fig. 38-40) from the upper Lyons Group in Western Australia, is less transverse and more inflated than the present species, and the plicae are strongly developed, but costae much less evident. Spiralia are laterally directed in the type species. What is needed is a Lakes Creek specimen with well preserved spiralia, to determine the generic position of the species, whether with *Trigonotreta*, or *Neilotreta*, and the present form is exceptional for either genus. *Trigonotreta tangorini* Archbold (2003, p. 162, text-fig. 4.1-14) from the Beckers Formation of the Cranky Corner Basin is moderately close in shape, but is much less costate, and referable to *Neilotreta*. Internal detail is poorly displayed in the material described. *N. thomasi* Waterhouse (2004, p. 166, pl. 7, fig. 6-9) from the Bijni tectonic unit in the Garwhal Himalaya of India is less elongate with simpler plicae, compared with the present species, but approaches the present form in having more costae than the afore-mentioned species. Detail of the delthyium in these species is not quite so clearly displayed as in the present species, but Thomas (1971, pl. 19, fig. 6b) clearly illustrated the delthyrial plates in one specimen of *occidentalis*, although they are not so well shown in a second specimen, perhaps because of the way lighting was arranged. The transverse sections show clearly a projecting edge, as in the present material.

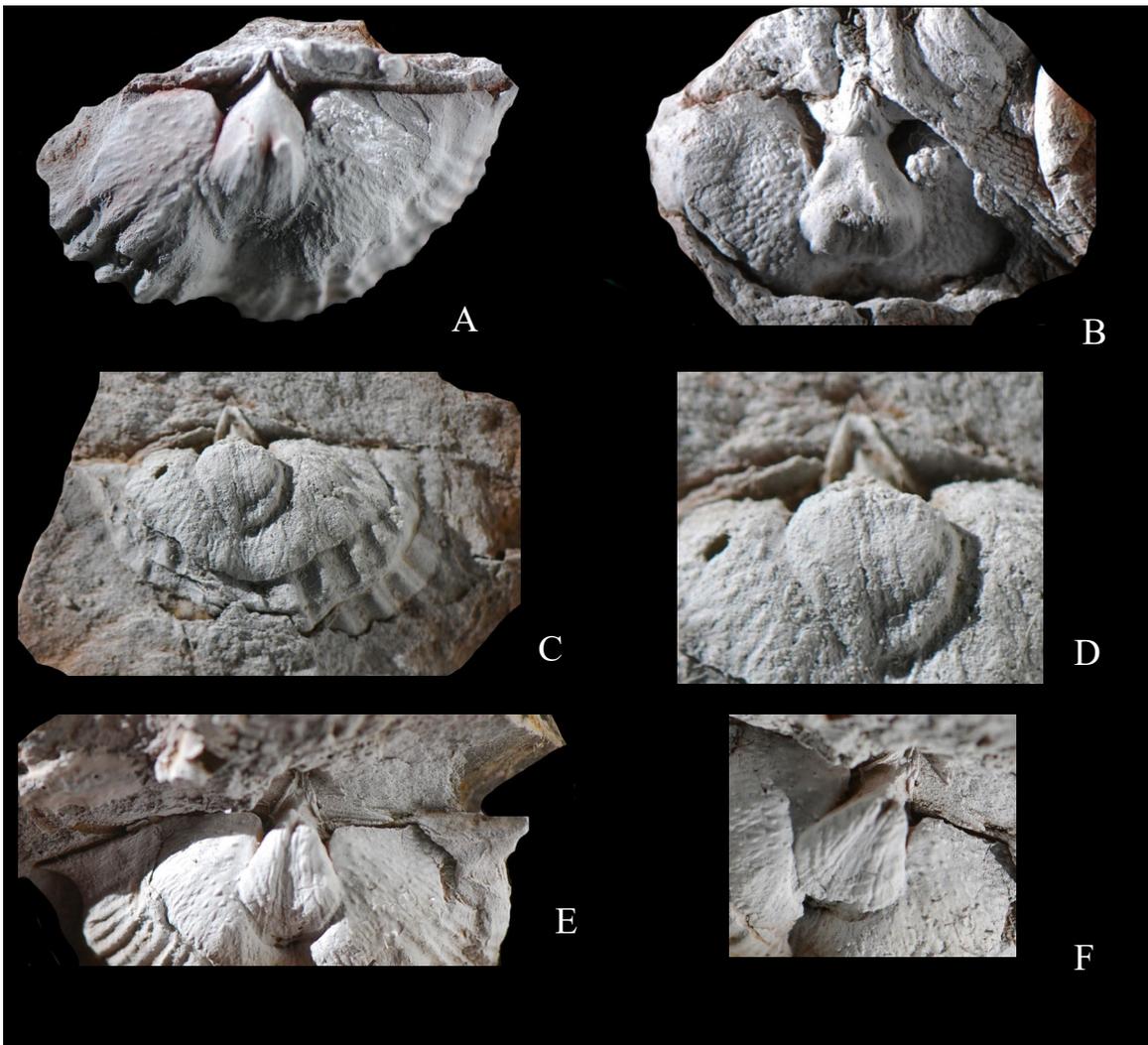


Fig. 27. *Neilotreta lakeensis* n. sp. A, ventral internal mould UQF 13557, x3. See Fig. 26B, D. B, mature ventral internal mould, UQF 82614, x3. C, D, ventral internal mould UQF 15604 and detail of delthyrium, x 2, x4.5. E, F, hinge area and detail of delthyrial area and ventral muscle field for holotype, UQF 13554, x 1.5, x3. See Fig. 22A.

This species is much smaller than *Trigonotreta stokesi* Koenig, 1825, and as a rule the cardinal extremities are more alate, and the dorsal fold broader. *T. victoriae* Archbold, 1991 is less transverse, and no specimen appears to have been alate. *Grantonia murrayi* Waterhouse (2015b, p. 59, Fig. 19A-D) from the *Bandoproductus macrospina* Zone of the upper Rammutt Formation appears to belong to *Trigonotreta*, having six pairs of well formed persistent plicae and well formed arched dorsal fold sharply separated from the lateral shell, with innermost plicae pair separated from the fold, and the inner pair of ventral plicae entering

the sulcus early. All three of these species are judged to be of Asselian age, whereas the east Australian trigonotretid genus most widely represented in faunas close to age to the present form belongs to *Grantonia* Brown. The three known species, *G. hobartensis* Brown, 1953, *G. australis* (Bion, 1928), and *G. cracovensis* (Wass, 1966) are all larger, with the inner plicae pairs much more prominent, as reviewed in Waterhouse (2015a).



Fig. 28. *Neilotreta lakensis* n. sp. Posterior aspect of latex cast and internal mould cast, showing delthyrial region for UQF 13582, at full maturity, x3.

Phylum Mollusca Linneus, 1758

Subclass Autobranchiata Grobben, 1894

Infraclass Pteriomorphia Beurlen, 1954

Megaorder OSTREATA Férussac, 1822

Superorder OSTREIFORMII Férussac, 1822

Order PECTENIDA Gray, 1854

Suborder ANOMIIDINA Gray, 1854

Hyporder AVICULOPECTENOIDEI Starobogatov, 1992

Superfamily **CHAENOCARDIOIDEA** Miller, 1889

Family **STREBLOCHONDRIIDAE** Newell, 1938

Subfamily **STREBLOCHONDRIINAE** Newell, 1938

Genus ***Streblopteria*** M'Coy, 1851

Diagnosis: Small acline to slightly opisthocline shells, right valve gently convex, left valve slightly more inflated. Right anterior auricle bearing a few to numerous costae, finer ribs on left anterior wing. Both valves ornamented by commarginal lirae. Resilifer assumed to be present, but the hinge for the type species requires clarification.

Type species: *Meleagrinnella laevigata* M'Coy, 1844 of Early Carboniferous age, from Ireland, OD.

Discussion: I deplore the custom of changing the spelling of taxonomic names to conform with arcane rules manufactured for Latin by medieval and modern scholars: so the "e" of pecten names is retained herein for family and ordinal group names, instead of being replaced by the letter "i". The essential need is for simplicity and consistency, achievable by adding the agreed family-group ending to the name of the genus, which should be left unaltered in its spelling.

Streblopteria homevalensis Waterhouse, 1986

Fig. 29

1964 *Streblopteria engelhardti* [not Etheridge & Dun] – Hill & Wood, pl. 11, fig. 18.

1972 *Streblopteria* cf. *parkesi* [not Fletcher] – Hill, Playford & Woods, pl. 11, fig. 18.

1982b *Streblopteria* sp. Waterhouse, pl. 11.3c.

1986 *S. homevalensis* Waterhouse, p. 5.

Diagnosis: Suboval little inflated shells with right anterior auricle bearing nine to eleven fine ribs, small posterior auricle, left valve auricles small, anterior bearing several fine ribs; remainder of shell ornamented by fine commarginal lirae and rugae.

Holotype: CPC 5177, as figured in Hill & Woods (1964) and Hill et al. (1972), from Tiverton Formation, north Bowen Basin, OD. Kept at AGSO, Canberra.

Material: Four right valves and specimen with valves conjoined.

Description: The specimens are small and no exterior is preserved apart from part of an anterior auricle near the umbo. The best preserved specimen UQF 26441 is 18.5mm long, 17.5mm high and 5mm high, with subrounded outline. Another specimen is more upright and narrower, and two other specimens more elongate. The right valve umbonal angle varies from 75° to 105°, and is inwardly curved, and the anterior umbonal ridge is straight to gently concave in outline. The anterior auricle is convex and extends from the umbo halfway to the anterior margin, lying above a deep byssal notch. A fragment of external shell bears well defined growth increments parallel to the anterior auricular margin. The posterior wing is short with angularly obtuse cardinal extremity. A small deep resilifer is preserved under the umbo, disrupting a long ligament area with horizontal striae.

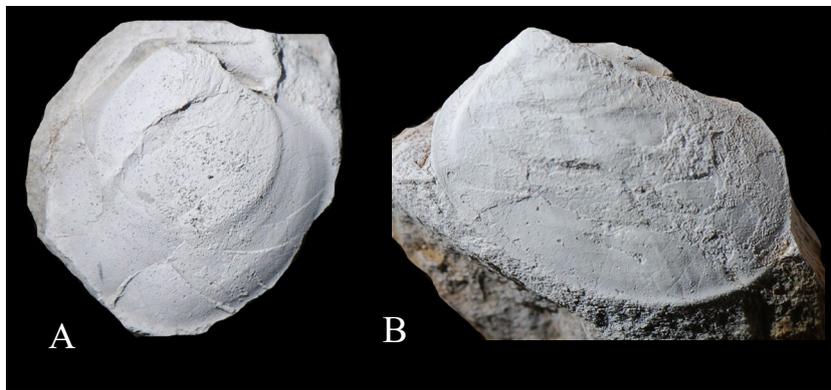


Fig. 29. *Streblopteria homevalensis* Waterhouse, internal moulds of right valves, x2. A, UQF 26441. B, UQF 26443.

Resemblances: These specimens appear to be identical with *Streblopteria homevalensis* from the Tiverton Formation, and also the Elvinia Formation, of the Bowen Basin, and apparently found also in slightly younger sediments of the Brunel Formation in New Zealand. Various streblochondriid species from the Early Permian of east Australia have been allocated to the genera *Orbiculopecten* Gonzalez, 1978 and *Concentiolineatus* Waterhouse, 2008b, both readily distinguished from the present form by their platyvincular ligament, with no resilifer. There is no sign of the fine radials that typify *Striochondria* Waterhouse, 1982b, and the

presence of commarginal lirae are deemed to typify *Streblopteria*, though detail of its hinge needs to be determined.

Superfamily **HETEROPECTENOIDEA** Beurlen, 1954

Family **HETEROPECTENIDAE** Beurlen, 1954

Subfamily **ETHERIPECTENINAE** Waterhouse, 1982b

Diagnosis: Ornament of intercalate costae on left and right valve, branching exceptional.

Genus ***Primaspina*** Waterhouse, 2008b

Diagnosis: *Etheripecten*-like shells distinguished by presence of arcuate spines along the crest of primary ribs.

Type species: *Aviculopecten dawsonensis* Runnegar & Ferguson, 1969, p. 262 from Flat Top Formation, Bowen Basin, OD.

Primaspina banksi Waterhouse, 2015a

Fig. 30, 31

2015a *Primaspina banksi* Waterhouse, p. 278, Fig. 228-231.

Diagnosis: Well spaced moderately prominent primary ribs bearing low c-shaped lamellar spines, arching ventrally, secondary ribs moderately prominent, may be spinose, many finer ribs.

Holotype: UQF 81531 illustrated in Waterhouse (2015a, Fig. 230) from *Taeniothaerus subquadratus* Zone of Tiverton Formation, Bowen Basin, OD.

Material: Four left valves.

Description: UQF 13465 is 32.5mm long, 23mm high and approximately 4mm wide with large anterior and posterior wings, the hinge being somewhat shorter than the maximum length.

There are some twelve spinose primary ribs in this specimen, but apparently only ten in another specimen. Spinose secondary ribs, withless or non-spinose tertiary and quaternary ribs are well developed. A number of fine apparently non-spinose ribs lie over the anterior wing, whereas the posterior wing bears only growth increments but this may reflect preservation, and there are signs of fine ribs. Growth increments are strong over the shell.

Resemblances: These specimens are provisionally identified with *Primaspina banksi* Waterhouse, coming from beds of much the same age as the types, and with primary costae more numerous than those of *Primaspina dawsonensis* (Runnegar & Ferguson) from the Flat Top and Blenheim Formations in the Bowen Basin. The primary costae are even more numerous in one specimen from the Lakes Creek Formation, and this is possibly a variation. Fragments figured by Runnegar & Ferguson (1969, pl. 5, fig. 16, 17) from the Peawaddy Formation of southwest Bowen Basin and South Curra Limestone of Gympie have more and finer ribs, but are too incomplete to assess.

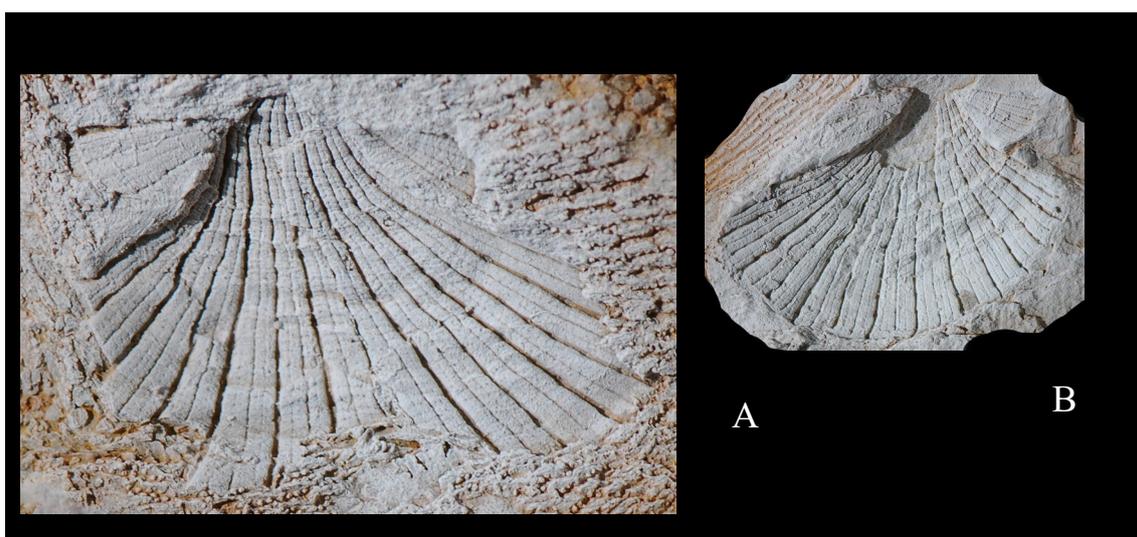


Fig. 30. *Primaspina banksi* Waterhouse, external moulds of left valves, x2. A, UQF 13455. B, UQF 13516.

Adequate comparison with *Primaspina sprengi* (Johnston, 1887, 1888, pl. 14, fig. 11) is frustrated by the uncertain reliability of the drawn figures provided for the type material from One Tree Point, Tasmania, by Johnston (1888) and Etheridge & Dun (1906, p. 15, pl. 16, fig. 5, 6). Their specimens are now lost. In *P. banksi* from the Tiverton Formation of the north Bowen Basin there are six or eight to ten strong primary ribs on the left valve, and secondary ribs bring the number of prominent ribs up to twenty or so, with the secondary ribs remaining weaker to the ventral margin. The figures for *sprengi* specimens from One Tree Point imply either approximately twenty primary ribs, or more likely twenty subequal primary and secondary ribs. I retain reservations over the validity of *banksi* as opposed to *sprengi*, but in

proposing *banksi*, believed there was value in at least having types and illustrations that could be available as a standard. At present, there seems to be no published material suitable



Fig. 31. *Primaspina banksi* Waterhouse, latex casts of left valve. A, UQF 13455, x3. B, UQF 13516, x4.

for nomination as neotype of *sprenti*, but surely more material must be available from One Tree Point. The Pokolbin specimen of Etheridge & Dun (1906, pl. 13, fig. 1) has more diverse

costae, and their Farley specimen (fig. 9) is obscure. The best preserved specimen assigned to *sprenti* in the literature, as figured in Etheridge & Dun, 1906, pl. 2, fig. 6, 7, and refigured in Waterhouse (1982b, pl. 2, fig. a, d) comes from the basal Lochinvar Formation, and has ornament close to that of *banksi*, but suggests that there is less difference between primary and secondary ribs than displayed by *banksi*, so it is arguably closer to Johnston's *sprenti*. It has ribs over both the anterior and posterior wings of the left valve. Fletcher (1929, p. 9, pl. 3, and Fig. 1) ascribed a number of specimens to *sprenti*, but they came from the younger marine Permian, and appear to be more costate. Dickins (1957, 1963) considered that the species *sprenti* was probably conspecific with Dana's species *Etheripecten tenuicollis*, as reviewed in Waterhouse (1982b, p. 17), but inspection of material shows that Etheridge & Dun (1906) were correct to assess the two species as separate (Waterhouse 2010, p. 92).

Hyporder LIMOIDEI Moore *in* Moore, Lalicker & Fischer, 1952

Superfamily **LIMOIDEA** Rafinesque, 1815

Family **LIMIDAE** Rafinesque, 1815

Subfamily **LIMATULININAE** Waterhouse, 2001

Carter et al. (2011, p. 11) attributed Limatuliniinae to Kasum-Zade, 2003, but the family group was first proposed as a subfamily in Waterhouse (2001, p. 128).

Tribe **CALCICANICULARIINI** Waterhouse, 2008b

Genus ***Calcicanicularia*** Waterhouse, 1983c

Diagnosis: Small limid shells with smooth or costate exterior and simple channel-form ligament lacking a chondrophore.

Type species: *Calcicanicularia glabra* Waterhouse, 1983c from upper Tiverton Formation, OD.

Calcicanicularia? sp.

Fig. 32

Description: Small asymmetrical left valve UQF 26448 more than 12mm long and 13mm high, with numerous fine ribs, twelve in 5mm, displaying narrow crests and broad U-shaped interspaces.

Fig. 32. *Calcicanicularia?* sp., cast of left valve UQF 26448, x5.



Resemblances: The type species which comes from the upper Tiverton Formation has a smooth shell without costae and so is readily distinguished, and *Calcicanicularia* sp. from the Brae Formation of southeast Bowen Basin has a smooth umbonal portion and only a few ribs below (Waterhouse 1987b, p. 161, pl. 10, fig. 9). *C. antesulcata* Waterhouse (1987b, p. 162, pl. 10, fig. 5-8) from the Flat Top Formation of the southeast Bowen Basin is more costate, approaching the present form more closely, but anterior costae are stronger than those over the posterior shell, a trend suggested in the present specimen, but less marked.

The present specimen approaches shells assigned to *Plagiostoma?* sp. by Dickins (1963, p. 93, pl. 15, fig. 1-5) from the Callytharra Formation and Fossil Cliff Formation of Western Australia, shells which are close in age to that of Lakes Creek beds. One of the Dickins specimens shows a ligament pit, to suggest that it is not *Calcicanicularia*. But the placement of the west Australian material remains uncertain, and identification with *Palaeolima* Hind, 1903 would appear from the information provided to remain a possibility. This genus is based on *Pecten simplex* Phillips, 1836, p. 212, SD Cox 1952, p. 48. As far as the Lakes Creek specimen is concerned, it may or may not prove to be more closely allied to other limid species found in the Bowen Basin.

Order CARDIIDA Férussac, 1822

Superfamily **KALENTEROIDEA** Marwick, 1953

Family **KALENTERIDAE** Marwick, 1953

Genus ***Stutchburia*** Etheridge Jnr, 1900

Diagnosis: Elongate equivalve or subequivalve shells, umbones small and anteriorly placed, lunule and deep escutcheon present, commarginal ornament traversed by costae radiating from umbo in some species. Cardinals 2 and 3b obsolescent, P1 and P111 also obsolete and P11 well defined. Anterior adductor scar large, adjoining low myophore buttress posteriorly, posterior adductor scar large, less impressed into shell.

Type species: *Orthonota? costata* Morris, 1845, p. 274 from Broughton Formation (Wordian), south Sydney Basin, New South Wales, OD.

Stutchburia randsi (Etheridge Jnr, 1892)

Fig. 33

1892 *Pleurophorus randsi* Etheridge Jnr, p. 275, pl. 14, fig. 14.

1963 *Stutchburia randsi* – Dickins, p. 97, pl. 15, fig. 14, 15.

?1969 *S. costata* [not Morris] – Wass & Gold, p. 219, pl. 14, fig. 1-5.

1981 *S. randsi* – Dickins, p. 29. pl. 3, fig. 12-16.

Diagnosis: Small shells with four ribs over median shell sloping from umbo to ventral margin.

Holotype: Specimen GSQ F 943 figured by Etheridge Jnr (1892, pl. 14, fig. 14; Dickins 1963, pl. 15, fig. 14, 15) from Burnett district, by monotypy.

Material: A left valve, preserved as incomplete external mould.

Fig. 35. *Stutchburia randsi* (Etheridge), latex cast of left valve UQF 141, x4.



Description: The left valve is 23mm long, 11mm high and 5mm wide, with umbo placed well in front, although its exact position is not clear. Dorsal and ventral margins are subparallel and anterior and posterior margins well rounded. The valve is covered by sharply defined commarginal growth increments, and there are four low costae sloping posteriorly from the umbo over the median shell to reach the posterior ventral margin. A slender escutcheon appears to be developed.

Resemblances: The specimen is identified with *Stutchburia randsi* (Etheridge), a poorly known species bearing four posterior costae and small in size. It comes from a stratigraphic level somewhat older than that of the present specimen, W. G. H. Maxwell considering that the type came from below the Yarrol Limestone with the *Taeniothaerus subquadratus* fauna and close to the level with *Eurydesma hobartensis* Johnston [now *E. burnettensis*], as quoted by Dickins (1963, p. 98). Dickins (1963) refigured the type specimen, and reported a somewhat similar specimen from the Warwick district of southeast Queensland (Dickins 1981). He distinguished the species from *Stutchburia farleyensis* Etheridge (1900, p. 183, pl. 32, fig. 3-6; Dickins 1981, pl. 3, fig. 1-11) of the Farley Formation in the Sydney Basin, noting that the shell was wider along the posterior umbonal ridge, with a sulcus in front in *farleyensis*, and reporting a few radiating posterior ribs in some specimens.

Specimens ascribed to *Stutchburia costata* (Morris) by Wass & Gould (1969, p. 219, pl. 14, fig. 1-5) are small with only a few posterior costae, approaching in shape and costation *S. randsi*. They come from South Marulan in New South Wales, in a fauna judged to be of upper Guadalupian age, which suggests that *randsi* possibly had a long time range, to underline the need for revision of the genus in east Australia.

Megaorder SOLENATA Dall, 1889

Order HIATELLIDA J. Carter in Carter et al. 2011

Superfamily **EDMONDIOIDEA** King, 1850

Family **EDMONDIIDAE** King, 1850

Diagnosis: Pholadomyid shells with no posterior gape, no hinge teeth, hinge plate or septum present or poorly developed.

Subfamily **MYONIINAE** Waterhouse (1969b), 1987b, 2001

Diagnosis: Large upright shells with no internal plate other than vestigial, accessory muscle scars more numerous than in Edmondiinae.

Discussion: In proposing the family group based on *Myonia*, as a tribe Myoniides, Waterhouse (1969b, p. 28) provided a diagnosis and extensive overview of various genera, but also expressed a tentativeness that now goes against the ICZN code of 1999. With no reference to the studies by Waterhouse (1965b, c, 1966, 1969a, b), Skarlato & Starobogatov (1979) proposed Family Myoniidae. No differences between Myoniidae and Edmondiidae or "Megadesmatidae" were specified. Nor was it stated why the group was intermediate as claimed between Edmondiidae and Megadesmidae (sic = Pachydomidae). The definition, which focused on the alleged presence of a carinate posterior ridge in their proposed family, would remove *Myonia* from Myoniidae. Only possible but spurious distinctions for Myoniidae were contained in their diagnosis, given their emphasis on a carinal crest, which in fact is absent from *Myonia*. Mention was also made of deep pits in the shell, but these are also present in Pachydomidae. As the 1999 Code, Recommendation 13A specifies, there should be "a summary of the characters that differentiate the new nominal taxon from related or similar taxa," and such characters were not provided. The Skarlato-Starobogatov proposal failed to provide any distinctions from Edmondiidae or Pachydomidae. Thus the proposals by both Waterhouse and Skarlato & Starobogatov failed to fully meet the requirements stipulated for adequate proposal of a new family group name, and of the two, that of Skarlato & Starobogatov (1979) must be deemed useless and at least arguably invalid, whereas the discussion by Waterhouse (1969b) was useful, but invalid. Both these judgements are admittedly based on standards elevated after the names were proposed, but the standards are fully justifiable.

Later, Waterhouse (1987b, p. 170) used the heading Myoniinae new subfamily, building on Waterhouse (1969b), sweeping away the uncertainty, and in 1988, p. 180 referred to Myoniinae Waterhouse, 1987b. In 2001 Waterhouse (p. 143) offered a succinct diagnosis and comparison, justifiably incomplete because it built on earlier explicit work. To that extent, the family group has (at last!) been defined and discussed in a manner which met requirements of the International Code of Zoological Nomenclature.

Genus *Myomedia* Waterhouse, 1969b

Diagnosis: Shells with weakly carinate posterior umbonal ridge, elongate and moderately inflated to slender.

Type species: *Pachydomus carinatus* Morris (1845, p. 273) from "Illawarra, New South Wales", OD.

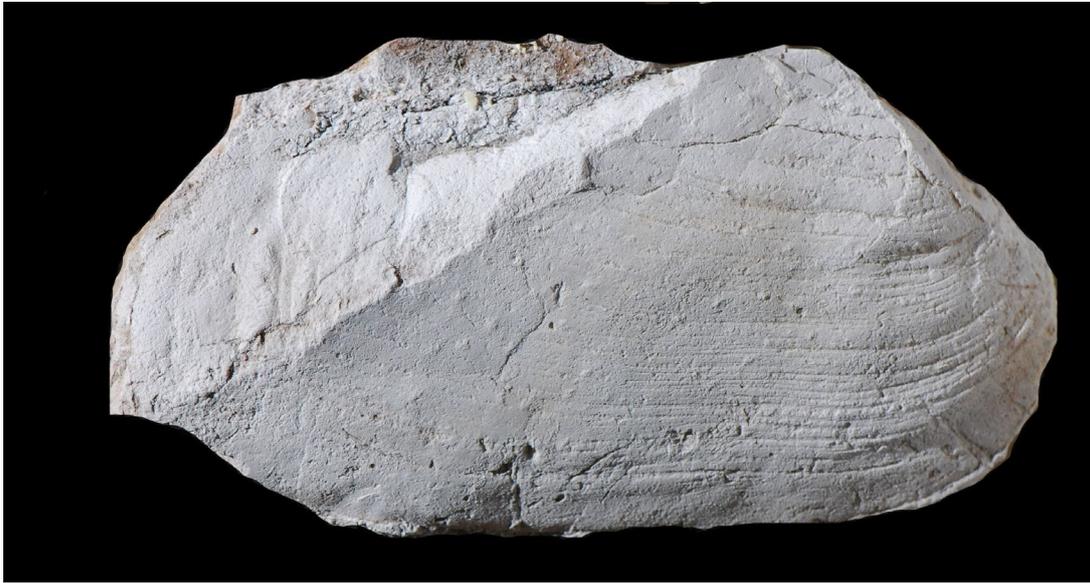


Fig. 34. *Myomedia carinata* (Morris), right valve UQF 82615, x1.5.

Myomedia carinata (Morris, 1845)

Fig. 34

- 1845 *Pachydomus carinatus* Morris, p. 273, pl. 11, fig. 3 (part, not fig. 4 = *Myonia elongata*).
 1847 *P. carinatus* – M'Coy, p. 301.
 1849 *Maeonia? carinata* – Dana, p. 696, pl. 6, fig. 1.
 1849 *M. fragilis* Dana, p. 696, pl. 6, fig. 2, 3.
 1880 *Pachydomus? carinatus* – Etheridge Jnr, p. 300, pl. 16, fig. 53.
 1887 *Notomya (Maeonia) elongata* [not Dana] – Ratte p. 139, pl. 3.
 1888 *Pachydomus carinatus* – Johnston, pl. 11, fig. 15, 15a?
 1932 *Myonia carinata* – Fletcher, p. 401, pl. 49, fig. 1-3.
 1932 *M. carinata etheridgei* [not de Koninck] - Fletcher, p. 407.
 1950 *M. carinata* – David, pl. 36, fig. d.
 1964 *M. carinata* – Hill & Woods, pl. P10, fig. 9, 10.
 1965 *M. carinata* - Waterhouse & Vella, p. 77, pl. 5, fig. 11.
 1967 *M. carinata* – Runnegar, p. 50, pl. 4, fig. ?8, 9 (part not pl. 4, fig. 11-13 = *Pachymyonia?*), pl. 5, fig. 20, pl. 12, fig. 7, 14.
 1967 *M. elongata* [not Dana] – Runnegar, pl. 5, fig. 12-15, 18, 19.
 1969b *M. (Myomedia) carinata* – Waterhouse, p. 67, pl. 1, fig. 2.
 1972 *M. carinata* – Hill et al. , pl. P10, fig. 9, 10.

- 1983 *M. (Myomedia) carinata* – Waterhouse & Jell, p. 251, pl. 5, fig. 7, pl. 6, fig. 14.
 1987b *M. (Myomedia) carinata* – Waterhouse, p. 171, pl. 10, fig. 24.
 1988 *M. (Myomedia) carinata* – Waterhouse, p. 183, pl. 7, fig. 3, pl. 15, fig. 6.
 2010 *M. (Myomedia) carinata?* – Shi et al., pl. 11, fig. 18, 19.

Diagnosis: Elongate shells with subdued posterior carina and convex posterior lateral shell.

Lectotype: BM (NH) L 6155 figured by Morris (1845, pl. 11, fig. 3), SD Waterhouse & Vella (1965, p. 77).

Material: A right valve.

Description, Resemblances: The specimen is decorticated and slightly crushed, and now measures 102mm long, 53mm high and 13mm wide. The posterior shoulder bears a low but distinct carina, and low narrow rugae and growth increments cover the exterior. The species is typical of Middle Permian faunas in east Australia and New Zealand.

SUMMARY

The following species are described from the Lakes Creek Formation. Brachiopods involve *Echinalosia curvata* Waterhouse, *Protoanidanthus costata* n. sp., *Anidanthia paucicostata* (Waterhouse), *Taeniothaerus farleyensis* Briggs, *Ingelarella intrudus* n. sp., *Ambikella ovata* (Campbell), *Tigillumia adminiculata* (Waterhouse)?, *Pteroplecta blakei* n. sp., and *Neilotreta lakeensis* n. sp. Bivalves include *Streblopteria homevalensis* Waterhouse, *Primaspinga banksi* Waterhouse, *Calcicanicularia?* sp., *Stutchburia randsi* (Etheridge) and *Myomedia carinata* (Morris). The fauna belongs to the *Taeniothaerus subquadratus* Zone, well developed throughout much of east Australia and present in New Zealand, as summarized in Waterhouse (2008a, 2011, 2015a), and elaborated within this publication starting on p. 181. One species that appears to conflict with this correlation is *Stutchburia randsi*, originally described from an older level in the Burnett district, possibly matching the level which also contains the very early Permian species *Eurydesma burnettensis* (see p. 76ff). But the species apparently ranged into younger faunas. Dickins (1981) reported the species from Warwick, in a fauna he matched with that of *Echinalosia preovalidis* (Maxwell), although several of the accompanying species suggest a younger age, and somewhat similar specimens have been described from South Marulan by Wass & Gould (1969). *Myomedia carinata* is known chiefly as a Middle Permian species, so that the present occurrence is exceptional, and more

material would be desirable. Elements of the fauna are possibly present in the upper beds of the Emu Creek beds northeast of Drake (McCarthy et al. 1974), but first hand examination of the fossils is required.

REPOSITORIES

AGSO: Australian Geological Services, Canberra; **AMF:** Australian Museum, Sydney; **BR:** brachiopod registry, Institute of Geological and Nuclear Sciences, Lower Hutt; **UQF:** University of Queensland, collections now housed in the Queensland Museum bulk storage at Hendra; **UNE:** University of New England, Armidale, now transferred to Australian Museum, Sydney.

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5. BIVALVES FROM THE FREITAG FORMATION, SOUTH-WEST BOWEN BASIN

Abstract

Intomodesma sp. and *Oblicarina* sp. are described from in the upper Freitag Formation in the southwest Bowen Basin.

INTRODUCTION

Two bivalve specimens are described from rocks that have not yielded many described macrofossils.

SYSTEMATIC DESCRIPTIONS

Subcohort OSTREIONI Férussac, 1822

Megaorder MYALINATA H. Paul, 1939

Order MYALINIDA H. Paul, 1939

Superfamily **INOCERAMOIDEA** Giebel, 1852

Family **ATOMODESMIDAE** Waterhouse, 1976

Diagnosis: Medium to large shells, inequivalve to equivalve, inequilateral, umbones anteriorly placed, byssal notch may be present in each valve, ligament lineavincular, posterior adductor scar large, pallial line discontinuous, pitted, shell prismatic.

Genus *Intomodesma* Popov, 1958

Diagnosis: Equivalve to inequivalve shells with strong commarginal rugae, steeper on the ventral face.

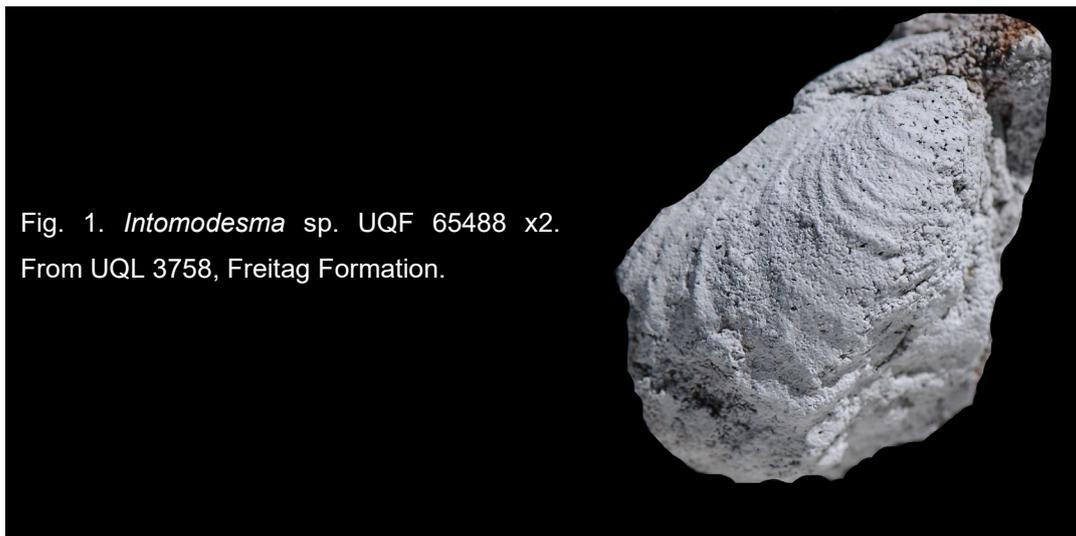
Type species: *Intomodesma costata* Popov, 1958, p. 48 from Late Permian of northeast Russia.

Intomodesma sp.

Fig. 1

Description, Resemblances: A small right valve 25mm long (UQF 65488) from UQL 3158, Freitag Formation, is covered by strong commarginal rugae, steeper on the lower or anterior face, as in *Intomodesma* from Arctic Russia. This genus is also represented in the

Echinalosia discinia Zone of the Brae Formation in the southeast Bowen Basin by *Intomodesma minusculus* Waterhouse, 2008, p. 30, but rugae in the present specimen are less regular and not visibly separated by finer growth ribs, unlike the arrangement in the Brae species. *Undosusia* Waterhouse, 2008, p. 31, type species *Aphanaia tivertonensis* Waterhouse, 1979, p. 4, from the Sakmarian Tiverton Formation is allied, but distinguished by the undulations being symmetrical in cross-section.



Superorder PHOLADIFORMII Gray, 1854

Order PHOLADIDA Gray, 1854

Superfamily **PLEUROMYOIDEA** Zittel, 1895

Family **VACUNELLIDAE** Astafieva-Urbaitis, 1973

Genus ***Oblicarina*** Waterhouse, 1967

Diagnosis: Strongly prosocline moderately to well inflated specimens with incurved umbones and pronounced posterior umbonal shoulder, posterior dorsal face concave or flat. Posterior dorsal gape narrow. Shallow sulcus on the flank of the shell. Ornament of commarginal rugae and low ribs and fine pustules. Hinge edentulous and thickened. Anterior adductor impression subquadrate, sited at anterior ventral extremity, joined by short protractor to small rounded anterior retractor scar. Posterior adductor impression large, other scars not known, pallial

sinus apparently shallow. Ligament partly external and opisthodetic, supported by nymphs, partly internal.

Type species: *Chaenomya? carinata* Etheridge, 1892, p. 279 from Flat Top Formation, southeast Bowen Basin, OD.

***Oblicarina* sp.**

Fig. 2

Diagnosis: High shells, somewhat prosocline with anteriorly placed umbones and well-formed sulcus.

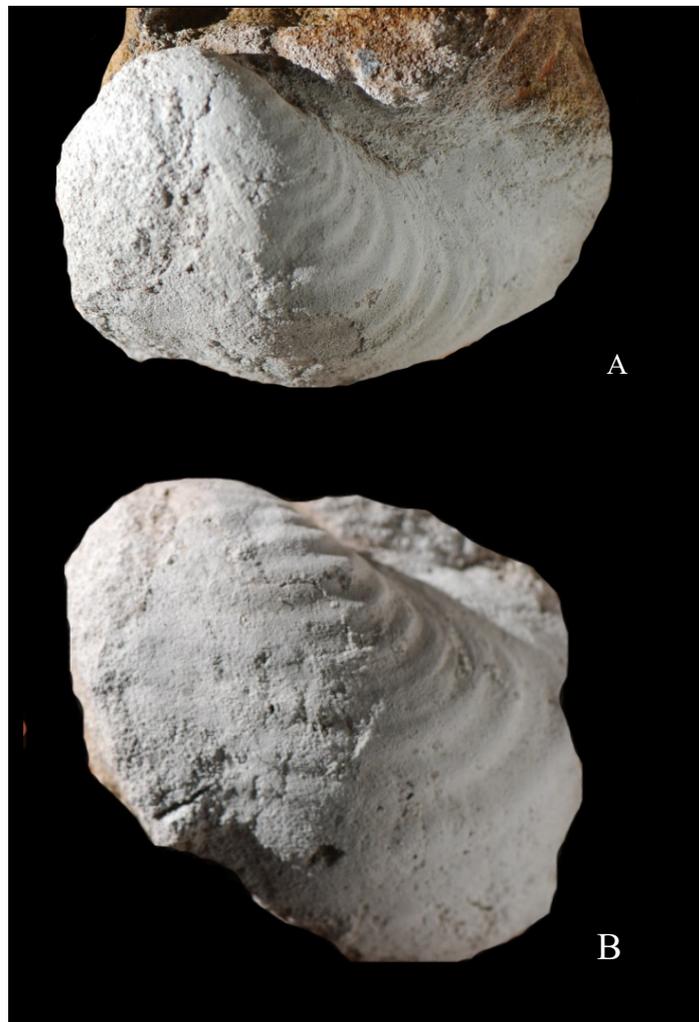


Fig. 2. *Oblicarina* sp. A, B, posterior and lateral aspects of broken left valve UQF 65484 from UQL 3758, Freitag Formation, x1.

Material: A large but broken left valve UQF 65484 from UQL 3758, Freitag Formation.

Description: The specimen is large, high and prosocline with moderately well formed sulcus, but very incomplete. Commarginal plicae are well developed, and fade posteriorly towards the hinge.

Resemblances: This specimen shows the outline and strong posterior umbonal ridge typical of *Chaenomya ? carinata* Etheridge (1892, p. 279, pl. 43, fig. 5, 6; Waterhouse, 1967, p. 56, pl. 1, fig. 2, 3, text-fig. 2E) and Fig. 5 herein. Stated to be from Banana Creek, the holotype appears to have come from the Flat Top Formation in the southeast Bowen Basin. Another specimen from this formation was figured by Waterhouse (1987, p. 173, pl. 11, fig. 8) and identified as *Oblicarina etheridgei* (de Koninck). But the similarity is at generic level, because the present form compared with Etheridge's species is markedly less prosocline and has a posterior umbonal ridge that is more gently rounded in profile.

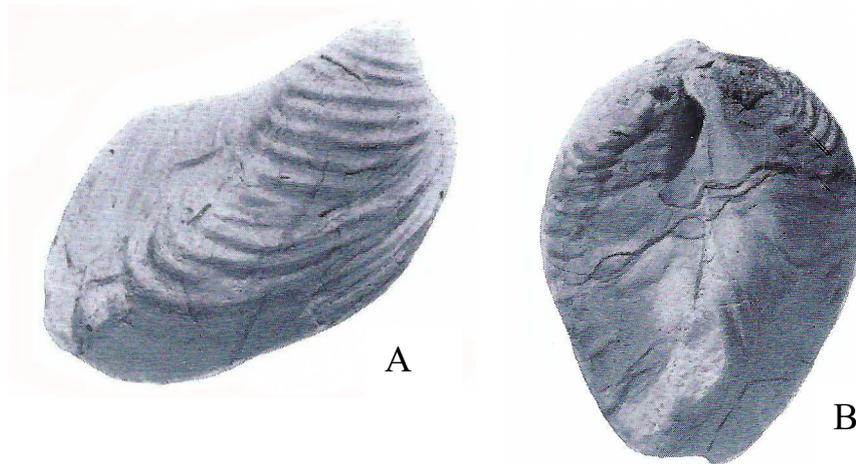


Fig.3. *Oblicarina carinata* (Etheridge), lateral (A) and dorsal (B) aspects of the holotype F 1218, Queensland Museum, x1. (Waterhouse 1967).

Another species of *Oblicarina* includes a well dated specimen from the Ingelara Formation of the southwest Bowen Basin (Runnegar 1967, pl. 9, fig. 1). This is much more elongate than *carinata* and bears a well defined lateral sulcus. Runnegar identified the specimen with *Vacunella etheridgei* (de Koninck) and figured a number of specimens (1967, pl. 9, fig. 2-14), not all well located. The original material of *Sanguinolites etheridgei* de Koninck, 1877, p. 262, pl. 17, fig. 2, part, not pl. 16, fig. 2) had been destroyed by fire, and no

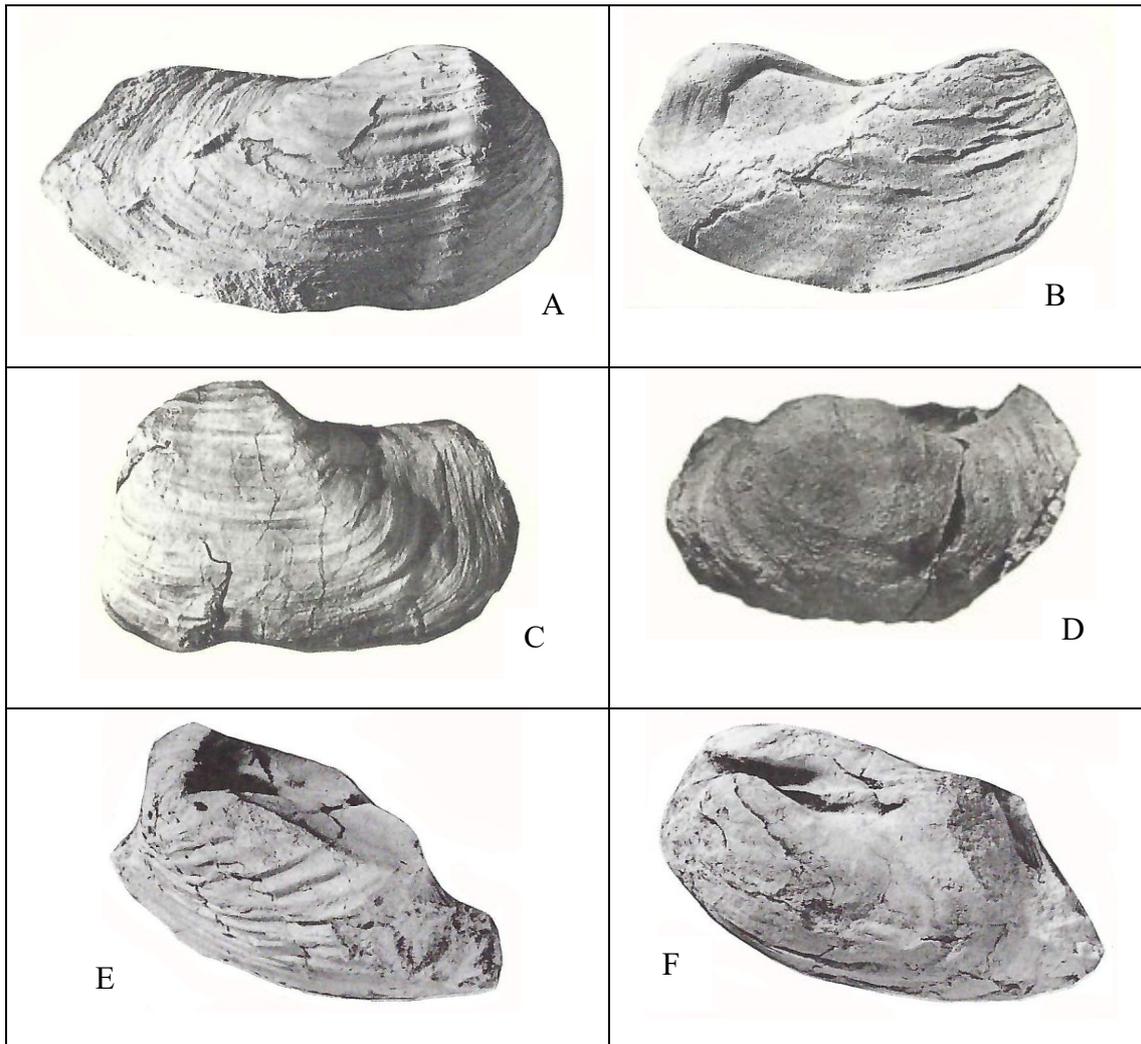


Fig. 4. A, B, *Oblicarina* identified as *Vacunella etheridgei* (de Koninck) from Ingelara Formation and Branxton Subgroup (Runnegar 1967). C, *Oblicarina oblonga* (Waterhouse) from upper Mangarewa Formation. D, *Vacunella* sp. from topmost Mangarewa Formation. (Waterhouse 1969). E, F, possible *Oblicarina* specimens from Flat Top Formation. (Waterhouse 1987).

replacement has been selected, because no available material is known to have come from the same source as de Koninck's original, as explained by Runnegar (1967, p. 68). It may be time to move on and simply look for similar material from a different locality, because *etheridgei* as interpreted by Runnegar (1967) certainly defines a different and distinctive species, and the material is much closer to the present form than to *carinata* in its shape and profile of the posterior umbonal ridge. Other material has been ascribed to the species by

Etheridge Jnr (1894, p. 532, pl. 40, fig. 5). From the lower Mangarewa Formation of New Zealand, *Vacunella oblonga* Waterhouse (1969, p. 74, pl. 19, fig. 3, 5-7) is close in many details, but has a larger anterior shell and so is less prosocline in outline.

Fossil locality:

UQL 3758, fence 8km SW of 'Springwood', 60km S of Springsure, Qld. Springsure 1:250,000 (grid ref. 9393 6556). Lower Permian, 10m below top of Freitag Formation.

This locality was recorded in an honours thesis at the Department of Geology & Mineralogy of the University of Queensland, by L.G. Elliott.

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6. PERMIAN CORRELATION - THROUGH USE OF BIOZONES, FIRST APPEARANCES OR RADIOMETRIC VALUES?

Abstract

Methods of correlation of geological rocks are discussed. A few pages are taken to reflect on the advantages and hindrances arising from current procedures.

OVERVIEW

The geological record that established systems and periods was based in part on the predominant nature of sedimentary rock – as indicated in the names Carboniferous, Triassic, Cretaceous – and on their constituent macro-invertebrate faunas. The divisions of each period into series and stages reflect rather crudely the same concepts, but much more refined subdivisions are as a rule deemed preferable, at least by experts in the field, and these more closely reflect the biological changes evident under close analysis. Such divisions set aside the lithological variations which record many of the prevailing environmental parameters and rely on evolution of biota, so that they aim at establishing a biochronology, rather than biostratigraphy and chronostratigraphy. At present, two different methodologies are favoured, not necessarily inimical to each other, but with somewhat different outcomes and implications. The concept of successive biozones is in many ways an inheritance from the division of world geological history into periods, and has changed enormously by coming to value more and more the huge diversity of life forms and the intricate changes recorded by fossils. Perhaps the biggest change over the years came to be the appreciation of micro-invertebrates, micro-remains and often only partial remains of vertebrates, and pollen and palynomorphs as parts of plants. There are severe disadvantages to the use of biozones, because the process is far from simple, and requires increasing specialization in unravelling significant and consistent – or even inconsistent – biological change, which means that results have to be simplified for general communication even amongst paleontologists, let alone geologists. In some local attempts, the leading authors, though seldom as expert as they may themselves believe, just give up, and either ignore more complex and therefore realistic versions, or feebly suggest that readers may pursue for themselves other interpretations. Paleontology is so complex, that many experts resort to publishing brief

articles, often scattered amongst different publications, whereas the most significant and enduring of contributions have mostly come from monographs which are long enough to embrace significant time spans. It is the major works by Sowerby, Davidson, Waagen, Diener, Tschernyschew and an array of more recent works by Chao, Cooper, Grabau, Grant, Grunt, Hind, Licharew, Stepanov and others, not to mention the Treatise series on Invertebrate Paleontology, that continue to hold value, whereas short articles all too often disappear into the morass of time. There are exceptions of course, where the author has been careful to devote articles to a common theme, such as N. W. Archbold on the Permian brachiopods from Western Australia, or S. S. Lazarev on Late Paleozoic Productida from Russia. But on the whole, short papers have a short life, unless rescued by more advanced paleontological studies – led by the Treatise series – and fitted into overall schemes. Granted that publication of short articles is more convenient, and suits a short attention span imposed all too frequently by the inordinate demands on authors who have so many different responsibilities, but the advantages are short-term, and in some ways, have been captured and even strongly influenced to suit major and highly profitable publishers.

The complexity of biota, and the differing rates of evolution and survival amongst different life-forms ensure that it is increasingly difficult for experts in one field to know about advances in another field remains. For the Permian Period, huge advances have been made by students of conodonts, but articles on conodonts – and they are almost totally articles rather than monographs – ignore other life-forms, which means they remain content with very specialized studies that ignore other specialized studies, and deal with only a fraction of biotic realities, and therefore environmental realities that are fundamental to earth history. This is at least partly caused by the focus on establishing an essentially simple biochronology from the very best – or at least best-known – successions wherever they are to be found. Alleged exceptions to the biochronology are regarded as due to error in identification or confusion over stratigraphic succession, which might lead cynics to ask if the biochronology was more ideal than real. But these are early days, and the approach may change when a reasonable range of conodonts are covered for the entire globe, and allow conodont specialists to broaden their approach.

Biozones are used for correlation. That depends at its simplest to have understanding and control of the stratigraphic succession, because to earth scientists time is all important. It took much exploration

International & Himalayan			New Zealand	
Period	Stage	No. of zones	Key fossils, local stages (bold)	
TRIASSIC	(Middle)	Illyrian	3	4. <i>Beaumontites bartrumi</i> 3. <i>Mellarium mutchi</i> “Etalian” 2. <i>Durvilleoceras woodmani</i> “Nelsonian”
		Pelsonian	1	(gap)
		Bithynian	3	<i>Ussurites arthaberi</i> = 1. “<i>Owenites koeneni</i>” “Malakovian”
		Aegean	3	<i>Stenopopanoceras mirabilis</i>
		Manasluan	2	(gap)
	(Early)	Mesokantoan	4	<i>Pseudoflemingites</i>
		Gangapurnan	2	<i>Flemingites</i>
		Annapurnan	4	<i>Paranorites</i>
		Gangetian	2	(gap)
		Changhsingian	5-8	5. <i>Wairakiella rostrata</i>

Table 1. The Triassic succession of faunas, principally ammonoids, in the Himalayas and in New Zealand. Columns to the left show the succession of Middle and Early Triassic zones and stages in the Himalaya, similar to those of Canada but with more diverse faunas (Waterhouse 2002b). The column to the right under the heading “New Zealand” shows the likely succession of New Zealand ammonoid assemblages, some called local stages, and in the correct stratigraphic and temporal order. But some New Zealand geologists regarded stage 1 based on “*Owenites koeneni*” as younger than stage 2 based on *Durvilleoceras woodmani*. The Himalayan stages listed as Gangetian, Annapurnan, Gangapurnan, Mesokantoan (Tozer 1994) match the international stages Gangetian, Dienerian, Smithian and Spathian, and Manasluan of the Himalayas is part Aegean. The Himalayan rocks and faunas are named after geographic features rather than contrived names, though that does not discredit the ingenious and praiseworthy Canadian names. They are, unlike the International stages, exposed in sequence over a tiny area of north-central Nepal, not widely scattered, and are much more fossiliferous, with more zones than in the International Standard provided by Canada. In the New Zealand scheme for local stages, the “Nelsonian Stage” when published was regarded as older than the “Malakovian Stage” – but its nominated type section and type fossil are both younger than Malakovian, and close in age to the New Zealand “Etalian Stage”. Yet the “Nelsonian Stage” was also visualized as including ammonoids of the international Dienerian and Smithian Stages. One of the sobering aspects of geology is the way in which some geologists set themselves up as knowledgeable and justified in ignoring expert opinion.

and analysis to achieve an understanding of succession, depending basically on the sequence of beds and formations, especially where the original sedimentary regime has been complicated by

tectonic disturbance. Understanding the original sequence may seem a simple matter, yet even in recent times, New Zealand geologists managed to invert part of the sequence, and proposed a so-called Nelsonian Stage as being older than a so-called Malakovian Stage, whereas in fact the Nelsonian unit is the younger of the two. How did this arise? By assuming that a stratigraphic sequence younged progressively in one direction, making some unwarranted assumptions about the age of the fossils on the basis of that younging, as well as ill-supported correlations, and ignoring evidence published to the contrary. So what was the contrary view based on? By the examination and publishing of seven monographs on the sequence of ammonoid species and genera in the magnificently exposed sequences of the Himalayas (admittedly exposed at high altitudes between 15 000 ft and 20 000 ft, and so only checkable under arduous conditions) and comparison of those ammonoids with the ammonoids found in New Zealand. (See Waterhouse 1999, 2002a, b, 2021, pp. 106-112). The error in interpreting succession reflects mainly on the willingness to set aside the published views of experts in favour of local opinion based on limited experience and research. The lack of any specialist paleontologist devoted to particular parts of the geological column in many countries is an all-too-frequent problem in geological surveys, at least in east Australia and New Zealand.

First Appearance Data

For a lengthy time, oil companies used fossils chiefly as time indices, and fastened on a very few fossils that reliably appeared to enter a succession with time consistence, to provide a time-line. This was adapted by McLaren (1970) for the academic and scientific communities, with the construction of an FAD scheme of successive first appearances. The methodology still involves a great deal of expert study, to select the most wide-ranging markers with, as far as can be discerned, consistent first appearances, and the emphasis and goal centre on correlation: once a satisfactory scheme is achieved, other biota are ignored (or as in some egregious examples, scorned). This methodology, if properly applied, does achieve correlation much more rapidly and simply than the biozonal approach. On the other hand, its aims are much more narrow. In itself, the FAD method provides a very limited understanding of earth history, for which it is necessary to greatly expand coverage after establishing the fundamentals of time control. For east Australia, it was realized that "form-taxa" as palynomorphs used to establish FAD range far beyond their first appearance, and may endure through a succession of FAD-based zones. Therefore, at least

ideally, additional proof for first appearance should be supplied, from accompanying palynomorphs or from macro-fossils with shorter time ranges. For the Permian conodont FAD-based zones, many key species also typify limited range zones, which sounds ideal. It is quite amazing that vertebrate species ranged so widely in so many different kinds of facies and lived for such short intervals, and we may look forward to further underpinning or amplification and even modification of this understanding, when there is a thorough and fully published account of conodonts in region by region, facies by facies, with full documentation of their consistent appearance and disappearance or replacement across the globe. And when the numerous and apparently disparate occurrences are rationalized and explained by careful scrutiny. Their physiology must have been outstandingly versatile and adaptable.

Radiometry

It is not entirely an accident of history that earth history came to be interpreted by sedimentary and biological change. Had modern methods of age-dating through radiometry been available, we may have had earth history divided into 100 million year intervals, and, in my opinion at least, what a loss that would have been. Figures gain all the more meaning when they can be attached to independent facets of what happened. But the current methodology centred around the CA-TIMS procedure for interpreting zircons offers an outstandingly refined calibration. Some may accept the values uncritically, having become dissatisfied at the difficulties and uncertainties arising from older methodologies: other experts may be a little more cautious, in remembering the ephemeral accuracy of those past measurements. Until very recently, the history of age-dating through chemistry has been erratic and unreliable, and in east Australia, for instance, several articles by a substantial team of experts, headed by J. Roberts using the SHRIMP method, provided values of mixed reliability, encouraging a degree of scepticism, made worse by the limited understanding of the stratigraphy and faunas involved in the sampling. Yet criticism should not be unreserved. Thanks to C. Foster, the article by Roberts, Clauqué-Long & Foster (1996) provided much more biostratigraphic and geologic context for the radiometric values than has become the norm. Their age for the Black Alley Shale of 250 Ma close to the Boundary Clay of China was criticised by Draper & Fielding (1997), and lowered a little in Metcalfe et al. (2013), yet essentially accepted by Smith et al. (2017). Possibly that means we are still playing catch-up, depending on the latest assessment, which implies it is only a matter of time before the last-published value is overturned, once again. Over

this particular question, the precise correlation for the fossils from the Black Alley Shale, or at least the study of fossils, are a let-down, and each group clearly needs further study before they can offer more conclusive evidence for correlation. There is a swarm of acritarchs (Price 1983), for which no satisfactory world correlation has been achieved, although in other parts of the globe, acritarchs are highly regarded for international correlation. Foraminifera suggested ties with the Mantuan Member of the upper Peawaddy Formation according to Palmieri et al. (1994), to imply a late Guadalupian age. Palynomorphs indicate *Dulhuntysporites parvihola* APP5 zone (Wood 1984). This seems to be of limited use, because the form has been found throughout most of the Guadalupian and Lopingian beds of the Bowen Basin in Queensland, in sediments with Guadalupian faunas dated through numerous matches with overseas including world stratotype faunas and overlain by coal beds. The form taxon *parvithola* has been reported from or above beds assigned to or equivalent to the *typica*, *discinia*, *maxwelli*, *blakei*, *deari*, *ovalis*, *clarkei*, *perplexa*, *costata*, and in the marine equivalents of the Bowen and Sydney Basin coal measures, found in Gympie and New Zealand: *woodi*, *denmeadi*, *spinosa*, *planata* and probably *rostrata* macro-faunal zones. Such a *parvithola* zone is ridiculously long-ranging as far as any hopes of correlation are concerned.

There must be every support and hope that CA-TIMS and perhaps successor methods will provide at last reliable and indeed immutable ages. And that the geological and paleontological interpretations will, eventually, prove to have been infallible. Not yet, I fear, without a great deal more study.

CONCLUSIONS

All three methods, and their numerous deviations and complexities, provide invaluable information on earth history. For all, there is a struggle to gain enough resources, and avoid entrapment by certain publishers, in order to unravel and understand more the huge and challenging complexity of earth history.

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7. MACRO-FAUNAL CORRELATIONS FOR THE EARLY PERMIAN (ASSELIAN – KUNGURIAN) MARINE BEDS IN EAST AUSTRALIA AND NEW ZEALAND

Abstract

Fifteen macro-faunal zones and additional subzones are discussed for the marine Early Permian of east Australia and New Zealand. The base of the Permian remains obscure, but otherwise the faunal assemblages represent a fairly complete record, characterized by a number of faunal assemblages that were strongly influenced by very cold conditions for a number of biozones. The correlations based on macro-fauna are compared with the palynomorph zones favoured currently for east Australia, and some discrepancies are noted. Few of these can be resolved without further study, but it has to be remarked that many of the palynomorph zones are of considerable duration, and therefore do not resolve some of the questions of stratigraphic succession, because rocks have been finely divided according to their lithologies, so that the stratigraphic units are closer to the macro-fossil zones. It is shown that the correlations based on macro-fauna appear to agree moderately well with those of the international standard sequences in Russia-Kazakhstan for the Cisuralian Series, with linking faunas provided in southeast Asia and Arctic.

INTRODUCTION

This study builds on the outline proposed for east Australian Permian stages in Waterhouse (1987b, 2008b) and further consolidated in Waterhouse (2011). Because of the importance of the Gympie district in southeast Queensland, which includes rocks and faunas of Asselian and younger age, the relevant rocks of New Zealand are also included, as zoned in Waterhouse (1982a, 1998, 2002). Together Gympie and more or less central New Zealand particularly in the South Island were part of a long volcanic arc, with shelf and later fore-deep, that extended offshore to the present east of the Australian mainland and lay a little further from the ice that accumulated over east Australia.

What biotic elements?

The focus for this article is on macro-faunas. The implications for palynomorphs are discussed in footnotes and discussion over radiometric values are provided in earlier articles in this monograph, especially in article 3 (pp. 71, 72). There are a number of discrepancies between the macro-faunal correlations and those adduced from palynomorphs. These questions are discussed as problems for discussion and in need of clarification.

Prime stress for this study is based on brachiopods, which are numerous and diverse. Foremost are members of the Productida, which are often numerous, and given their highly varied ornament, are amenable to close scrutiny and comparison. Yet there were times when evolution seemed to become exuberantly rapid, with the appearance of short-lived and little dispersed species that inhibit the recognition of wide-ranging range zones and so complicate the task of correlation. Members of other major groups, especially amongst Spiriferida, may have been slightly slower to evolve in some instances, but as a rule became widely distributed, and so provide a useful check on productid changes, and they were reinforced by other brachiopods, especially amongst Orthisidina, Rhynchonellida and Terebratulida. Considerable weight is also assigned to bivalves and gastropods. Some molluscan groups such as the Paleotaxodonta are found only irregularly, but members of Pteriomorpha are as useful as Productida, including members of Atomodesmidae, Chaenocardioidea, Etheripecteninae, whereas large-shelled species especially amongst Deltopectenidae, and many Edmondiidae and Pachydomidae seem to have evolved more slowly so that species persisted for several zones. Gastropoda can be highly amenable to zonation, especially amongst the genera *Peruvispira* and *Pleurocinctosa*, but they do tend to be irregular in their appearance in faunas. The differing length of time ranges for these species within long-lived genera, just as displayed for other fossil taxa such as conodonts as summarized in Henderson (2018), challenges the assumptions of steady mathematically predictable change favoured by some geneticists, and the implication from the fossil record is surely that biota and their genes were responding to varying regimes imposed by climate and numerous other environmental as well as biotic factors. Foraminifera are still poorly known and require comprehensive and expert study, but clearly show promise (Sheibnerova 1982, Stutchbury 1989, Palmieri 1998). It is believed that bryozoans are of high potential, but they have been neglected apart from a few narrowly focused studies and certainly there has

been no systematic study and published description of species with tight stratigraphic occurrences throughout east Australia. There are few conulariids (Thomas 1969, Waterhouse 1979, 1986), not common enough to be of importance for correlation, and members of other major groups have seldom been described. There are no conodonts or fusulines in east Australia, and ammonoids, invaluable for correlation, are rare.

Significant sequences

A number of areas are critical for the macro-faunal zonation of the Early Permian Period in east Australia and New Zealand. Tasmania has yielded fine and well preserved faunas, described principally by Clarke (1990, 1992), but post-war systematic descriptions of less than half of the faunal sequence from Tasmania have been published overall. There has been limited recent study of the south Sydney Basin apart from attention by Campbell (1960, 1961, 1965), McClung (1978) and Briggs (1998) to particular fossil groups amongst some brachiopods, and some molluscs as in Fletcher (1929a, b, 1932) and Runnegar (1965, 1967, 1970). The gap is currently being remedied by Prof. G. R. Shi and colleagues, but has a long way to go. By contrast, the north Sydney Basin has long been the focus of studies since the mid-nineteenth century, enabling a general understanding, though the occurrences of many fossils are now in need of stratigraphic clarification and substantial systematic revision. To the north in Queensland, the large Bowen Basin falls into three major regions, the southeast, comprehensively studied by Waterhouse (1986, 1987a, b), the north by Waterhouse & Jell (1983) and Waterhouse (1983c, 2015a), and the southwest Bowen Basin, with no comprehensive overview, and only some circumscribed studies (eg. Hill 1950, Maxwell 1954, Campbell 1959), so that it remains a significant lacuna in various aspects important for correlation. The faunas of the Yarrol Basin to the east were studied in pioneering work by Maxwell (1964), but updating is clearly required.

The present overview touches only lightly on a huge area of rocks and faunas assigned to the New England orogen, with rocks and on the whole poorly known faunas, though Briggs (1998) has provided some useful assessments, and a fauna from the Lake Creek Formation near Rockhampton has been described herein (Article 4). Other regions have been examined on in student theses, unpublished and inaccessible.

Up until recently, one particular part of the east Australian record has been severely misrepresented. This is the Gympie Province of southeast Queensland, and its continuation preserved especially in New Zealand, and to less extent in New Caledonia. These regions formed a highly active volcanic arc with narrow to broad offshore shelf, and later-developed fore-deep. The significance of this part of east Australasia is that the rocks and faunas not only show close links with the Bowen, Yarrol and Sydney Basins of Queensland and New South Wales (Waterhouse 2015b), but provide fossiliferous marine equivalents of coal measures found in east Australia. New Zealand is a complex array of terranes and ocean floor sediments and volcanics, and a substantial basin now to the east. Many rocks and faunas are of limited relevance for east Australia, even though they have yielded fusulines and conodonts regarded as highly useful for international correlation, because of limited and extremely generalized mapping and the scarcity of co-existing brachiopods and molluscs. The fossiliferous sequence extends from early Sakmarian to latest Permian in the provinces of Marlborough, Nelson, Otago and Southland.

In short, for the Permian macro-faunas of east Australia, sufficient is known to allow a comprehensive overview, but there remain significant gaps.

What kind of zone?

The zones applied herein are mostly assemblage and shared range zones. They are based on an association of short-lived brachiopod species with largely concurrent ranges, and reinforced by mollusc species, some of which were short-lived, although others lasted much longer. These zones, assemblage and shared range, monitor changes through time, but have some disadvantages, because they demand systematic assessments for many species, and an acknowledgement of those analyses. The end result provides substantial information on evolution and possible causes behind evolution, and on environment, pointing to an association between the macro-faunal zone and climatic change, and the recognition of such zones enables correlation and distinctions between relatively finely discriminated stratigraphic units. In addition to macrofaunal zones, subzones are nominated. One kind of subzone simply records the addition of one or more species to an established assemblage, with little overall change. Another and more significant kind records the drastic change to the fauna, with the addition of many species to a few key species, or vice versa, though to my mind, this demands zonal rather than subzonal discrimination. These changes are noted and deemed to be indices for correlation and climatic change. Because

biological development is so complex, there has to be a judicious measure of compromise and simplification, difficulties met to some extent by the recognition of subzones as well as full zones. Indeed there is scope for also delineating at least some superzones, which include several zones, united by the sharing of a prominent species or closely related species. Overall, the aim is to recognize robust biozones that are distinguished by a range of different species, and are geographically extensive enough to show that they are not merely localized developments. That in turn entails problems caused by geographic differentiation, related particularly to differences in paleolatitude, posing questions for which final solutions are yet to be achieved, but are at least recognized as requiring further study. Throughout this overview, there is little attention to “first appearances” because it is faunal assemblages which receive principal focus rather than a lineage of separate and single species. Information on FAD first appearance data for east Australia was summarized in Waterhouse (2008b) and is available for closely collected sequences tabulated for the southeast and northern Bowen Basin, part of the Gympie Basin and New Zealand, but is difficult to assess from collections made long ago. Briggs (1998) in seeking to delineate a succession of significant and short-lived strophalosiid species provided limited FAD information, with the appearance of a few species deemed critical found in very few localities and shown in idealized sections rather than properly located on geological maps, and therefore not easily refindable.

Type sections for zones

The practise of recognizing zones at large, with no designated type section, is set aside: it may have been endorsed in publications with international imprimature, but there is great advantage in being able to retest published interpretations, and the procedure is flexible enough to allow replacement of a type section, should it have been later destroyed or rendered inaccessible, or deemed unsatisfactory. The citation of data from cores is of more dubious value, because of the limited range of recollection points. This also relates to the desirability of providing geological maps that show the collection localities, because maps will provide independent line of checking faunal succession, and facilitate recollection of localities. The practise of condensing fossil occurrences throughout a formation by compacting the data into a single section may be instructive, but may err in its presentation, with no way of checking the accuracy. The reliance on maps at a scale of 1: 250 000 cannot adequately establish the position of fossil localities and their interrelationships: such a scale is understandable, given the size of east Australia, but

should be reinforced by more detailed maps of smaller regions deemed critical for fossil occurrences. Detailed collecting and mapping of areas previously covered by 1: 250 000 maps has revealed numerous additional fossil localities with significant faunas in the south-east and north Bowen Basin, and has shown that there can be little certainty as to the exact location of the original collection, use of GPS notwithstanding.

Genera and species

There is no satisfactory way of escaping the formidable nomenclature and complexity of brachiopod and molluscan systematics, so that names cited for zonal content are, without any intention to confound, bewildering in their inaccessibility and ultraspecialization. Some paleontologists, and more understandably, some non-specialists, have been content to use the comparatively simplistic terminology of many decades ago, such as summarized in the first editions of the *Treatises* on Invertebrate Paleontology. For brachiopods that involved the series published in 1965, with 927pp., rather than the more recent edition, from 1997-2006, with 3226pp. Even the *Revised Brachiopod Treatise* appeared years ago, and is now seriously out-of-date, just as the first edition soon lost its lustre. For example, the studies on Productida by S. S. Lazarev in a series of articles in the *Paleontological Zhurnal* that appeared during the first few years of this century overthrew or greatly elaborated the classifications offered by Brunton et al. (2000) and Brunton (2007) for some fossil groups in the *Revised Brachiopod Treatise*. There may be complaints about the complexity – and to non-specialists, impenetrability of the fossil names, but we need to do our best to conform to nature, rather than reshape nature to our desires, or pretend that simplistic statistics gives an accurate portrayal of nature. In this study, names are used to the best of my understanding, with genera updated as far as possible. Some of the names receive explanatory footnotes herein. Many have been discussed and explained in the *Brachiopod Treatise* series, and in the *Earthwise* series. These are well illustrated publications, and should not be ignored just because they are complex, or not held in the nearby library which has not bothered or could not afford to acquire them, often because certain notorious international publishers had enforced compulsory acquisitions at inflated prices. But whatever, authorities who have not seen the publications have no right to proceed as though they do not count, and even regard their failure to examine the publications as a good reason for ignoring them.

Alternate zonal schemes

The assemblage range zones as used herein differ from the zonal constructs used for the palynomorph zones of east Australia. These palynomorph zones are based on first entry data of palynomorphs and stand supreme in the way they can unite non-marine with marine sediments, though that huge advantage is challenged by their delicacy, because palynomorphs are destroyed by low grade metamorphism caused by overburden or tectonic stress. They are summarized by Smith et al. (2017), building on numerous studies, notably including those in Queensland by Price (eg. 1985, 1997). At present, there is poor correspondence between these zones and the macro-faunal zones in marine deposits of east Australia. There are two major differences. The palynomorph zones are based on the first appearance of single "species" – ie. palynomorphs, and close at the appearance of the next designated "species". Each zone is not based on the full range of the nominate "species" – which as a rule extends far beyond its entry time and is found in succeeding zones. Sadly, the palynomorph is seldom tied to an actual species though a generic tie may be indicated, and the nature of the parent plants and associated plant species are not considered in articles on the palynomorph zones. The second difference from the present macro-faunal scheme is that the palynomorph zones are much longer than the macro-faunal zones. The use of very lengthy palynomorph zones for which one lasted from mid-Wuchiapingian right through the Changhsingian (in their understanding for correlation), another from mid-Wordian into lower Wuchiapingian and so on, has disadvantages for detailed correlation and understanding of stratigraphic succession. Such zones are long indeed. This leads to considerable uncertainty within each palynomorph zone, because formations can in some instances be regarded as contemporaneous only at a very broad scale, unless there is additional stratigraphic information. There is far greater potential in Permian palynomorphs beyond distinguishing large blocks of rock. More refined correlation, as offered by marine fossils and potentially by palynomorphs, will help solve relations and sequences of different rocks (sometimes including coal beds) at present lumped together in one unit. According to Smith et al. (2017), their zonation potentially provides valuable information on the development of hydrocarbons – oil and gas – where they were referring to the long sustained but poorly rewarded search for commercial oil deposits in Queensland, with currently what would appear to be dismal

prospects for ever being able to exploit them even if they were present. The recently proposed zonation of marine macro-faunas carries no such intent, and is devoted purely to aspirations of correlation, with significant implications for climate analysis and evolution.

Some advocates complain that there is no agreed consistency for macro-faunal zones. That is explicable partly because the aims are much more ambitious, and also because of the peculiar contribution from D. J. C. Briggs¹ on Permian zonation, with some ill-judged interpretations that conflict with available evidence, as in Draper et al (1990). But basically all science keeps on changing as knowledge expands, and expansion is inevitable until research becomes complacent and unwilling to change. Currently a favoured objection against macro-faunal zones, as expressed in Draper (2013) and Laurie et al. (2016), is founded on the desire to have nature conform with what their understanding, rather than the other way round. There is a problem in communication, but that is no excuse for blaming the problem on the specialist, nor for giving up any aspiration of achieving refined correlation.

The international standard for correlation in the Permian Period is based on marine fossils – not on palynology nor on radiometric values. The most widely used fossils are conodonts, and are interpreted from first appearances, just as for the east Australian palynomorphs. Like many macro-invertebrate fossils, they have limitations: none are terrestrial. Importantly, there so far has been little effort to integrate their studies with other fossil studies, whether macro-faunal or palynological. The conodont zones in current studies are three times as refined in length as the east Australian palynomorph zones, and many are also range zones, which goes far beyond the template for palynomorph zones as interpreted in east Australia. Regrettably the conodont zones cannot be applied to east Australia, because the Permian sediments contain no conodonts. It is true that some macro-fossils extend beyond east Australia, at intervals, especially for the Lower Permian, into conodont-bearing rocks, but there are limits to the extent that east Australian faunas can be matched with macro-faunas of the world standard sequences. Even the conodont identifications for Permian in Western Australia by Nicoll & Metcalfe (1998) do not “make sense” according to Foster & Archbold (2001). The identification of conodonts in a New Zealand study by Ford et al. (1999) showed conodont genera and species as being at a single locality, yet the identified taxa were not supposed to overlap, according to a world-wide review of Permian conodont

zones in Henderson (2018). We are left, obviously, with the possibility that the material was misidentified. But the fact is also incontrovertible that conodonts from the deep south are poorly known, which means that the specific limits and the time ranges remain open to consolidation.

Reservations

The present summary of macro-faunal zones outlined for the Permian marine deposits of east Australia is intended as a simplified overview, based primarily on brachiopods, with substantial input from molluscs. Molluscs are not chosen as the prime source, because many species and genera tended to live longer, and subdivision would lead to a coarser framework, though much finer than that proposed by Dickins (1964) or Runnegar (1969c). Cocks (2011) has shown that brachiopods tended to be more short-lived than more favoured fossil subdivisions in the Cambrian to Devonian Periods, which may invite caution over the use of brachiopods for Permian zonation, though the preference for longer-lived forms may suggest a resort to convenience and simplicity in preference over a more difficult but more informative group of fossils. But regardless, the Permian Period is primarily subdivided and correlated through conodont fossils, and where explored in at least some parts of the world, such as the Permian of Canada, there is moderately close agreement between conodont and brachiopod zones (Waterhouse 2020). In this study, there is considerable simplification, for the purpose of conveying an overall model, so that complexities resulting from different fossil communities in different sedimentary settings are not so much glossed over as accommodated in a flexible model. The presentation of biologic realities presented by McGowran (1986) are applicable to Permian faunas in east Australia, but would demand too much space and would complicate an already complicated model. However it is impossible to avoid the importance of coeval latitudinal changes to fossils throughout one time zone, and these are addressed, briefly and imperfectly, but certainly are far from ignored. The unacknowledged setting aside of such changes can only result in a scheme seriously devoid of biological reality. Today, as we know, land-based plants and off-shore marine life change from north to south, from northern Queensland to Tasmania, and the same happened during Permian time, when climatic differentiation under a regime of glaciation was even more pronounced.

Radiometry

The application of radiometry to the Permian in east Australia has had a long, but checkered history. The use of SHRIMP and the Temora standard to replace earlier somewhat erratic values premised on potassium-argon and rubidium-strontium and other methodologies was claimed in Fielding et al. (2008a) to have at last achieved a way of subdividing Late Paleozoic in Australia, to thereby enable “the comprehensive re-evaluation of the glacial record in eastern Australia”. But this claim was unrealistically hopeful. The SHRIMP results, as authored by J. Roberts and colleagues, fell into considerable disrepute, because of uneven and unreliable results exposed by Ramezi et al. (2007) and specifically for east Australia by Korte et al. (2007) and Metcalfe et al. (2015). It has been necessary to revise and modify those SHRIMP estimates, and the favoured methodology is now CA IDTIMS, similarly centred on crystals of zircon much more carefully prepared: indeed prepared to a degree that allows the analysis of a now no longer natural mineral, reconstituted in the laboratory. That may still warrant a level of caution, when considering the past history of radiometric determinations. One way of consolidating the value of radiometry would be to see what substantial number of analyses prepared from several laboratories along strike of outcrop for a considerable distance achieved genuine statistical reliability, as against a handful of values, and compare the results against well defined and persistent zones or subzones to establish that there is concurrence between chemical and biochemical-biological evidence. That will also help decipher the extent to which the radiometric values are reflecting instantaneous emplacement times as against metamorphic times, something that any petrologist would welcome, given that zircon crystals are so obviously metamorphic, and clearly grew after the emplacement and consolidation of the ground mass. It would be reassuring if zircons from different matrices could be tested to see if the radiometric values remained consistent, and rule out the possibility that the timing of crystallization that formed virtually perfect cubes in a matrix of previously crystallized igneous rock has been influenced by the chemical status of the surrounding matrix.

At the time of writing, correlations for the Permian of east Australia are dominated at least in some circles by a scheme based on palynomorphs, modified by several radiometric values achieved through CA IDTIMS, as summarized by Smith et al. (2017). Contradictory

radiometric values have been expressed for roughly the middle part of the column in east Australia, where beds regarded as correlative with those giving a CA IDTIMS age of Roadian age (basal Middle Permian age) are overlain by beds with a SHRIMP radiometric age of Kungurian age (late Early Permian age). Only one of the ages can be right. But it was noted on p. 72 that the CA IDTIMS results included one value amongst a number of zircon dates as closer to the Kungurian result.

There are further difficulties, apart from my short-comings, that mitigate against careful and scientific scrutiny of the marine macro-fossil zonation of the Permian in east Australia. As coal geologists, Mallett et al. (1995, p. 302) complained about “the lack of consistency in fossil description and erection of zones, endemism of the macrofaunas and methodological differences between lithostratigraphy and biostratigraphy”, and these complaints were endorsed by Draper (2013) in his summary of Bowen Basin geology. Not for them the wise cautions issued by Foster (1983, p. 107). What should one say? How about “Welcome to the real world”. It will be many years before fossil descriptions and erection of zones become standardized and, as Mallett and colleagues would apparently wish, become immutable and regarded as Holy Writ. We are still learning, and if there is to be improvement, change is inevitable. And yes, the faunas are endemic. Most faunas (and floras) over the globe, of any age – arguably all - are endemic. That is no reason for ignoring them. It may be a pity that they are endemic, but nature rules, not the coal geologist. And of course there are differences between lithostratigraphy and biostratigraphy: that is why there are different terms and different procedures. It may too difficult for some, but world-wide, scientists have coped. Dr Mallett was entitled to feel that lithological classification had far outpaced biostratigraphic categorization. There may be excuses, but it is undoubtedly true, and Australia has not been well served by paleontological studies for several decades.

Part 1. A SUMMARY OF MACRO-FAUNAL ZONES FOR EAST

AUSTRALIA AND NEW ZEALAND

BASAL PERMIAN OR LATE CARBONIFEROUS?

***Nambuccalinus bourkei* fauna**

In a wide-ranging synthesis of mostly brachiopods belonging to Productidina and Strophalosiidina in east Australia, Briggs (1998) proposed that the oldest known Permian zone should be based on *Lyonia bourkei* Briggs. The genus is much more spinose than *Lyonia*, and is now the type species of *Nambuccalinus* Waterhouse, 2001, p. 33, characterized by its multiple rows of large spines along the hinge, numerous well formed ventral spines and numerous dorsal spines, as endorsed by Angiolini et al. (2005) and Brunton (2007). The genus is possibly Asselian in age (Briggs 1998), though dated as Late Carboniferous on unadjusted SHRIMP data as reported by Waterhouse (2000), and the fauna is restricted to the northern part of New South Wales. Briggs (1998, pp. 23-26) has carefully discussed the available evidence for its stratigraphic position, and noted that there was no known stratigraphic or even tectonic relationship to any underlying or overlying different zone. There are only three adequately described species, *Nambuccalinus*, and two species of *Briggsia* Waterhouse, 2015b, with reported *Trigonotreta* and *Deltopecten*, species that might also be useful in assessing the possible correlation and age of the fauna, but have yet to be described. The zone may yet prove to be a local variant or older phase of the *Bandoproductus macrospina* Zone, of much the same age as *Lyonia* in Western Australia. Unfortunately not enough is known about its stratigraphic position and too few elements of its fauna have been described to justify proposal of a zone, or allow certainty of its stratigraphic position. Instead, the *Nambuccalinus bourkei* assemblage should be treated as a "fauna", with content, stratigraphic position and significance yet to be established (Waterhouse 2008b).

Further uncertainty surrounds the age and nature of beds and fauna below the first well defined brachiopod zone, recognized in this study and named after *Strophalosiaria concentrica* (Clarke). In Tasmania as summarized by Clarke (1992) and Clarke & Banks (1975), the early and middle Wynyard Tillite contains *Eurydesma* and *Deltopecten*, belonging to species yet to be carefully scrutinized, and possibly only the upper part is associated with the *concentrica* Zone. Views on the age of these glacials in Australia have varied: from Westphalian D to early Asselian on the basis of palynomorphs approaching *Protohaploxylinus* and *Potonieiosporites* in palynomorph zone APP1.1 in the early Wynyard tillites. *Auriculispina levis* (Maxwell) in the lower Burnett Formation and underlying Neerkol

Formation was recognized as Late Carboniferous by Engel (1975) and Waterhouse (1976, p. 238). This *levis* Zone has been featured as the youngest known Carboniferous index fossil for east Australia, and the same genus appears to be present in Late Carboniferous of Argentina (Waterhouse 2015a, p. 42), based on reinterpretation of *Costatumulus amosi* Taboada, 1998. It is suggestive that Late Carboniferous (Gzhelian) rocks in northern Canada form a number of cyclothems (Waterhouse 2018), suggestive of waxing and waning glaciation elsewhere, presumably in Gondwana, including Australia. In South Africa, Stephenson (2009) asserted that *Pseudoreticulatispora confluens*, regarded as key to the Permian APP 1.22 in east Australia, was of Late Carboniferous age, based on radiometric dating. Could it be speculated that *Eurydesma* and *Deltopecten* in these tillites below the palynomorph *Microbaculispora tentula* zone APP1.21 typified Gzhelian deposits in east Australia, and the *Auriculispina levis* Zone signalled the Kasimovian Stage? Unfortunately the Upper Carboniferous of east Australia is poorly understood as far as marine macro-fauna is concerned, with reluctance as expressed in Fielding et al. (2008a) to compare the Australian sequences with those of international stratotypes in Russia (see Davydov et al. 2004) and a preference underlined for relying on the faunas and stratigraphy of Western Europe. The Russian sequences are the agreed world international stratotypes, and its marine faunas are far superior to those of western Europe. Extensive Yarrol Basin collections made by the Geological Survey of Queensland would be invaluable for clarifying the Late Carboniferous of east Australia, but although extensively recollected by the Geological Survey of Queensland, they have yet to be examined properly, and the Carboniferous-Permian interface remains obscure.

CISURALIAN SERIES

International standards for the Cisuralian Series are found in the Urals and Kazakhstan, and currently defined on the basis of conodonts, with substantial fusuline, ammonoid and brachiopod components. But east Australia lacks fusulines and conodonts, and its brachiopods, like its palynomorphs, differ generically and specifically from those of the world standard sequences. The hope for correlation therefore depends on three lines of evidence, namely the occasional foraminifer and ammonoid found in local successions, the faunal link

through mainly brachiopods and molluscs with other Gondwanan sequences that are better dated through ammonoids, fusulines or conodonts, and the climatic similarity to these and other sequences signalled by biotic diversity and sedimentary studies, world-wide.

ASSELIAN STAGE

Strophalosiaria concentrica Zone

The *Strophalosiaria concentrica* Zone is based on outcrops and faunas in Tasmania, studied in detail by Clarke (1990, 1992), and buttressed by adequate geological maps and locality data. The nominate species, revised in Waterhouse (2013, p. 218), is found in the Quamby and Woody Island Formations and Tasmanites Shale, and first appears in the uppermost Wynyard Tillite and correlative levels. Accompanying species include *Notostrophia costellata* (Clarke), which in Tasmania was found to be missing from the next zone, *Etheripecten* sp.,

Series	Stage	East Australasian Biozone
Cisuralian	Kungurian	<i>Echinalosia discinia</i>
		<i>Wyndhamia typica</i>
		<i>Glendella dickinsi</i>
		(<i>Attenuocurvus</i> beds)
	Artinskian	(<i>Echinalosia conata</i>)
		(<i>Spinomartinia adentata</i>)
		<i>Ingelarella plica</i>
		<i>Notostrophia zealandicus</i>
	Sakmarian	<i>Taeniothaerus subquadratus</i>
		<i>Magniplicatina undulata</i>
		<i>Notostrophia bifurcata</i>
		<i>Echinalosia curtosa</i>
	Asselian	<i>Bandoproductus macrospina</i>
		<i>Unicoſtatina crassa</i> subzone
		<i>Crassispinosella subcircularis</i>
		<i>Strophalosiaria concentrica</i>

Table 1. Sequence of marine macro-invertebrate biozones in the Early Permian rocks of east Australia and New Zealand, elaborated from Waterhouse (2008b). Bracketted biozones are found in New Zealand and mostly are represented in east Australia by coal measures.

Protraxia gryphoides (de Koninck), *Pyramus laevis* (Sowerby), *Neoschizodus australis* Runnegar and *Keeneia twelvetreesi* Dun.

Strophalosiaria concentrica is also found in the lower Wasp Head Formation⁴ of the south Sydney Basin. Other brachiopod species identified in the assemblage included are “*Arctitreta*”? sp. [not adequately preserved for generic placement], and *Geothomasia simplicitas*⁵ Waterhouse (2015b, p. 169). A large suite of specimens assigned to this species under the title *Tomiospis konincki* by Cisterna & Shi (2014) appear to involve several morphologies, including shells with two sulcal subplicae, and others with a central sulcal swelling, as well as at least some specimens with widely diverging tabellae. Such different morphologies are consistent attributes of separate lineages of species in younger Ingelarellidae, and close analysis of the Wasp Head material should tease out the different strands. Supposed *Pseudosyrinx*? sp. was also recorded by Cisterna & Shi (2014) as ranging throughout the formation. This genus is not known elsewhere in the east Australian Permian, and the species in question seems likely to belong to *Permasyrinx*, but needs adequate description.

In the north Sydney Basin, the Lochinvar Formation has long yielded numerous bivalves and some brachiopods to signify an Early Permian age. *Trigonotreta victoriae* Archbold is found in the basal Lochinvar Formation (see p. 10), and is probably belongs to the *concentrica* Zone. It contains the *Microbaculispora tentula* palynomorph zone APP1.21, which is assigned to much of the Asselian Stage and to at least upper Gzhelian Stage at the top of the Carboniferous in Smith et al. (2017)². Note the small case use of “z” consistently for palynomorph zones by palynomorph specialists, in contrast to the capital letter Z for macro-invertebrate zones. Briggs (1998) suggested that *Eurydesma burnettensis* Waterhouse helped to typify macrofaunas accompanying the palynomorph *Microbaculispora tentula* zone APP1.21. *E. burnettensis* is discussed on p. 76ff. The species is found in the lower third of the Burnett Formation of the Yarrol Basin (Maxwell 1964), below *E. cordatum* Morris, just as in the Youlambie Conglomerate in the Spring Creek Syncline of the same basin (Dear 1968). Briggs (1998, p. 28) identified *E. burnettensis* in the Quamby Formation low in the *concentricus* Zone in Tasmania, and in the basal Lochinvar Formation (Gosforth Shale of Browne & Dun 1924 – see Runnegar 1970, p. 94, pl. 17, fig. 1-4, and herein on p. 77), but the

nature of the hinge needs to be determined in order to fully validate the specific identification for these specimens.

***Crassispinosella subcircularis* Zone**

This zone is found above the *Strophalosiaria concentrica* Zone, appearing in the lower Bundella Formation, Golden Valley Group, Darlington Limestone and correlatives of Tasmania (Clarke 1990, 1992; Briggs 1998, p. 67). Accompanying species include *Ambikella konincki* (Etheridge) and other species that persist from the underlying zone. *Ambikella bundellaensis* Waterhouse³ comes from the basal Bundella Formation in Tasmania, being distinguished from *Ambikella elongata* by its less transverse shape and short subparallel tabellae. *Eurydesma konincki* (Johnston) is found in the Darlington Limestone of Tasmania.

The diagnostic brachiopod *Crassispinosella subcircularis* is present in the middle and upper parts of the Wasp Head Formation at Turrise Point and Emily Miller Beach localities (see Briggs 1998, text-fig. 16, p. 29). Amongst the species described by Runnegar (1969a), *Trigonotreta stokesi* Koenig was figured, and his so-called *Pseudosyrinx* is like the Allandale species *Permasyrinx allandalensis* (Armstrong, 1970), which Clarke (1992, p. 25) also recorded from the Swifts Jetty Sandstone, Masseys Creek Group and Kansas Creek Formation and Darlington Limestone in Tasmania. One specimen identified as *Neospirifer* by Runnegar (1969a, pl. 20, fig. 16) has only a few strong plicae and so resembles *Grantonia* Brown, 1953, a genus better known in younger Early Permian deposits (see Waterhouse 2011, Fig. 5). These species are associated with a bivalve-dominated assemblage, which includes *Eurydesma cordatum*, *Neoschizodus australis* Runnegar, *Megadesmus globosus* Sowerby, *Pyramus laevis* (Sowerby), *Australomya hillae* Runnegar, *Warthia*, and *Keeneia ocula* (Sowerby). *Mourlonia?* cf. *impressa* Waterhouse, was described as *Mourlonia* (*Mourlonia*) sp. by Runnegar (1969a) and compared to an Early Permian New Zealand species (Waterhouse 1966, 2001, p. 152) from a mid-ocean spreading ridge making up part of the Croisilles Volcanics, found above atomodesmid bivalves in northwest Marlborough, as summarized in Waterhouse & Sivell (1987b).

An uppermost Wasp Head fossil assemblage includes *Trigonotreta stokesi* Koenig and a species described as *Tomiopsis piersoni* Cisterna & Shi (2014). The holotype of *piersoni* belongs to *Geothomasia*, as it lacks a dorsal fold channel and has short widely

diverging tabellae. The upper Wasp Head beds are not easy to assign to a zone on macro-faunal evidence: they might belong to the *subcircularis* Zone or be slightly younger.

The Allandale Formation in the north Sydney Basin is especially rich in bivalves as described by Dana (1847, 1849), to characterize the “Allandale fauna” of Runnegar (1969a). Strophalosiids were recorded from the uppermost Allandale beds by David (1932), but Briggs could find no such specimens in institutions, and both Lochinvar and Allandale formations are overdue for renewed attention to their fossil content and sequence. Briggs (1998) reported *subcircularis* in the Kensington Formation near the Peel Fault of northern New South Wales, and below the top of the faulted Alum Rock beds in the Texas Block of the New England Orogen, together with other possible occurrences, which still await full systematic substantiation. He deprecated the stratigraphic value attached to the species *Ambikella elongata* and *Ambikella konincki*⁵, which were supposed to co-exist in turn with *concentrica* and *subcircularis* (Briggs 1998, p. 31, Fig. 18). Archbold (2003) dismissed the claim, but the Briggs’ strictures may require further evaluation, the species identified as *Ambikella elongata* in Tasmania belonging to a separate species *bundellaensis* Waterhouse (2015b, p. 168), because it possesses much shorter tabellae in most dorsal valves. *Ambikella elongata* McClung & Armstrong is found in higher beds of the Lochinvar Formation, but stratigraphic information about the species is limited. Type *Ambikella elongata* McClung & Armstrong, 1975 came from the Beckers Formation at Cranky Corner, New South Wales, with specimens also figured by McClung (1978, pl. 2, fig. 1, 2, pl. 3, fig. 7-11) and Archbold (2003, pl. 3, fig. 1-23), although further evaluation is required. Supposed but poorly preserved *Trigonotreta* was figured by Archbold (2003, text-fig. 4.15-18), clearly in need of critical scrutiny, and possibly belonging to an early form of *Sulcifica*, given its simple and numerous plicae. Balme & Foster (2003) described *Pseudoreticulatispora confluens*, the index to zone APP1.22, from the lower Beckers Formation, noting gross differences from the flora in the Seaham beds of Carboniferous age, and a diminution in cryptogram spores. Although Briggs (1998, p. 59) criticized the *confluens* zone and concept, this flora is particularly widespread, having been reported from South America, Yunnan, Antarctica and Oman. Balme & Foster (2003) assigned a Sakmarian age, but allowed that the zone might extend into the Asselian. An

Asselian age is preferred herein, certainly not Sakmarian, but questions remain over the possible permutations for a Late Carboniferous age (Stephenson 2009).

The Gympie succession in southeast Queensland preserves a volcanic arc and apron of sediments that lay offshore from mainland Australia (Waterhouse & Sivell 1987a; Waterhouse 2015b). Above the Highbury volcanics and in the middle of the Rammutt Formation (Jell & Cranfield 2013), the “green fossiliferous sandstone”, a unit some 10m thick and moderately rich in fossils is correlative with the *Crassispinosella subcircularis* Zone (Waterhouse 2015b). Species included streptorhynchin, *Gympietes aseptus* Waterhouse, *Monklandia gympiensis* Waterhouse, *Betaneospirifer (?) dubius* (Etheridge Snr), *Permasyrinx allandalensis* (Armstrong), *P? acuta* (Etheridge Snr), *Undopecten fimbriatus* (Etheridge Snr), and *Pyramus concentricus* (Etheridge Snr), as well as species of *Ambikella*, *Martiniopsis*, *Notospirifer* and *Sulcicosta*. Several of the species from the Rammutt fossiliferous green sandstone indicate correlation with the Allandale Formation of the north Sydney Basin, and the middle Wasp Head Formation of the south Sydney Basin. A specimen close to *Permasyrinx allandalensis* (Armstrong) is shared between these formations and also reported from the Lower Bowen Volcanics (= Lizzie Creek Volcanic Group) of the north Bowen Basin, which as well appears to have *Eurydesma konincki* as in Tasmania (see p. 78). Amongst the bivalves from the Rammutt beds, *Pyramus laevis* (Sowerby) is present, characteristic of the Allandale Formation, and reported from the Wasp Head Formation of the south Sydney Basin. *Eurydesma* is probably juvenile *E. cordatum* Morris, which is especially typical of the Allandale and correlative beds (see p. 74) and *Stutchburia simplex* (Dana) has been reported elsewhere only from the Allandale fauna. *Squamuliferipecten squamuliferus* (Morris) is also found at this level, but ranges into younger Permian beds. Some of these species are also reported in early Permian faunas of Tasmania by Clarke & Banks (1975, p. 456), with systematic descriptions provided by Clarke (1990, 1992).

***Unicostatina crassa* Subzone**

In Tasmania, Clarke (1992) recognized a *Unicostatina crassa* Zone, which may be defined by the first entry of the nominate species, accompanied by *U. subglobosa* (Clarke), *Geothomasia branxtonensis* (Etheridge), “*Myonia* sp. *elongata*” [not Dana] of Clarke 1992 which is a species allied to *Vacunella*, given the substantial posterior gape illustrated in Clarke’s figure,

Rhabdocantha intermedia Clarke and *Tabellina* [syn. *Kelsovia*] *superba* (Clarke). A number of species, including *Crassispinosella subcircularis*, persist from the underlying zone, so that the unit is provisionally reduced in status to that of a subzone. Clarke (1992, Fig. 12 I-K) reported the presence of the fauna at several areas of Tasmania. The species *Geothomasia branxtonensis* was originally described from the Farley Formation of Sakmarian age, as figured by Etheridge (1919, pl. 28, fig. 5, 6, pl. 29, fig. 1, 2) and McClung (1978, pl. 2, fig. 5, 6, pl. 3, fig. 7-9, pl. 4, fig. 1-5, 12-19), and the somewhat older specimens from the *crassa* Subzone of Tasmania that were compared with *branxtonensis* by Clarke (1992a) to the species show minor differences from the types, as noted by Waterhouse (2015a, p. 167).

In the Cranky Corner Formation⁶ at Cranky Corner, New South Wales, Archbold (2003) reported (with updating of the names) *Unicostatina crassa*, together with *Neilotreta tangorini* (Archbold), *Ambikella elongata*, and *Keeneia platyschismoides*. A possible link exists between *Ambikella elongata* (Armstrong & McClung) from the Cranky Corner faunas and allied specimens of *elongata* found in the basal Tiverton Formation of the north Bowen Basin (Waterhouse 2015a, p. 154, Fig. 103) in beds which underlie the *Bookeria pollex* Zone, and so may, uncertainly, belong to the *crassa* Subzone, or to the *Bandospina macrospina* Zone. Archbold (2003) listed but did not describe or figure the bivalve *Eurydesma cordatum* Morris from high in the Cranky Corner Sandstone. *Pyramus laevis* Dana at the top of the Cranky Corner Formation as reported by Archbold (2003) from above *Eurydesma* also needs further evaluation, because the material is very poorly preserved, and not very like *P. laevis*. There must be reservations over purported correlations for the Beckers and Cranky Corner Formations, because palynomorph determinations, summarized in Footnote 5, show *trisina* APP2.2 in the Cranky Corner Formation, correlative with the younger Rutherford Formation and lower Farley Formation in the Hunter Valley of New South Wales (Smith et al. 2017), to suggest the need for fuller documentation and revision of the Cranky Corner faunas. Judged from the illustrated macro-faunas and palynomorph data, at least some of the Archbold identifications and correlation seem dubious.

Asselian in Western Australia

According to present assessments, one of the oldest Permian faunas from Western Australia comes from the Grant Group, involving the Calytrix Formation of Barbwire Terrace in the

Canning Basin, as described by Foster & Waterhouse (1988) and assessed in Waterhouse (2015a). The Calytrix assemblage, informally named *Crassispinosella calytrixi* fauna, is characterized by *Crassispinosella calytrixi* (Archbold) and *Calytrixia capillata* (Waterhouse), with *Sommeriella obrieni* Archbold, *Brachythyrinella* [*Trigonotreta*] of Archbold – see Waterhouse 2004 and herein, p. 37] and shells identified as *Martinia*, which represents a family not otherwise reported as yet from Western Australia. *Crassispinosella* is also found in the *Crassispinosella subcircularis* Zone of Tasmania. Critically, the palynoflora was found to belong to the *Pseudoreticulatispora confluens* zone APP1.22 (Mory & Backhouse 1997), which also occurs in the *Strophalosiaria subcircularis* Zone of Tasmania. The Calytrix Formation is one of three formations recognized by Redfern (1991) in the upper Grant Group, and it has been correlated with the Wye Worry Member, a subdivision containing tillite below the uppermost Millajiddee Member of the Carolyn Formation in the Grant Group by Jones & Young (1993). Unlike the type species of *Etherilosia* Archbold, 1993a, named for *Strophalosia etheridgei* Prendergast, 1943, *Etherilosia carolyni* Archbold, 1995 from the Wye Worry Member displays pronounced dorsal capillae, and so is assigned to *Fimbrinialosia* (see Waterhouse 2013, p. 216), based on a genus which occurs from the early Permian of Rajasthan, India (Waterhouse & Ranga Rao 1989) where it is accompanied by *Pseudoreticulatispora confluens*. This means that two significant Early Permian strophalosiids, *Fimbrinialosia* and *Crassispinosella*, are found in the Grant Formation to signify an Asselian age and strong links with Tasmania. A small bivalve-dominated fauna was described by Dickins et al. (1978) from the Wye Worry Member. Archbold (1993b) included the Calytrix floral and faunal assemblage of the Canning Basin in the *Neilotreta* [originally *Trigonotreta*] *occidentalis* Zone, but the Calytrix biota differ considerably, and are judged to be older. Only *Sommeriella obrieni* is shared between the two, and chonetids like palynomorphs are not always restricted in time range (Waterhouse 2001, p. 14).

***Bandoproductus macrospina* Zone**

The *Bandoproductus macrospina* Zone marks a significant faunal interval. It was recognized by Briggs (1998) as the *B. walkomi* Zone, and *walkomi* appears to be a species contemporaneous with and indeed sometimes cohabiting with *macrospina*. Differences between the two species are precariously based, and *macrospina* is preferred as name-giver

to the zone, given the contentious validity of *walkomi*, which could prove to be a junior synonym. Both nominate forms are found in the Burnett Formation above the *Eurydesma burnettensis* fauna in the Yarrol Basin, and *walkomi* is present in the lower Rutherford Formation of the Hunter Valley (Briggs 1998), but it is not clear if the zone involved all of the Rutherford Formation, which contains all of the *Pseudoreticulatispora pseudoreticulata* APP2.1 palynomorph zone, and much of the *Microbaculispora trisina* APP2.2 palynomorph zone, according to Smith et al. (2017). *Bandoproductus* is not known in either Tasmania or the Bowen Basin of Queensland. The fullest description of the *Bandoproductus* fauna so far is provided by Waterhouse (2015b) in recording species from the upper Rammutt Formation of Gympie, southeast Queensland. The fauna includes *Protoanidanthus pokolbinensis* Briggs, *Magniplicatina dunstani* Waterhouse, *Bandoproductus macrospina* Waterhouse, *B. walkomi* Briggs, *Attenuocurvus australis* (Armstrong & Brown), *Ambikella* cf. *elongata* (McClung & Armstrong), *Oviformia sweeti* Waterhouse [which is might prove to be allied to one upper Wasp Head specimen figured as “*Tomiopsis*” *piersoni* Cisterna & Shi (2014, Fig. 7.29)], *Trigonotreta murrayi* (Waterhouse) and *Hoskingia glabra* Waterhouse as well as a stenoscismatid and martiniid and the bivalve *Squamulifera squamuliferus* (Morris). In the nearby Gigoomgan area of the Gympie Province, an allied fauna with *Protoanidanthus pokolbinensis* and *Attenuocurvus australis* and other species are found in the Kolbar Formation (Waterhouse 2015b, p. 125ff). *Protoanidanthus pokolbinensis* Briggs is also found with *Bandoproductus walkomi* in the Silver Spur beds of south Queensland.

Upper Asselian in Western Australia

Bandoproductus is not known in Western Australia, but the genus is close in many respects to *Lyonia lyoni* Archbold, 1993a, found in the middle Lyons Group with *Rhynchopora australasica* Archbold, *Arcullina* [= “*Spiriferella*” of Archbold 1995], *Ambikella notoplicatus* (Archbold & Thomas) and *Koenigoria lyonsensis* (Archbold & Thomas)⁷. *Lyonia* is characterized by its dorsal spines, and is allied to a genus *Nambuccalinus* Waterhouse, 2001, p. 33 from Nambucca, New South Wales. The *Lyonia lyoni* Zone contains further occurrences of the palynomorph *Pseudoreticulatispora confluens* and has been correlated as a rule with the lower Holmwood Shale in the Perth Basin of Western Australia, involving the Beckett Member which contains *Juresanites jacksoni* (Etheridge) of either late Asselian or basal

Sakmarian age (Glenister et al. 1993, p. 55; Archbold 1993b). Leonova (2016) regarded *Juresanites* as present in Asselian as well as Sakmarian deposits, and cautioned that the lower age limit proffered on the basis of ammonoids in Glenister et al. (1993) and Archbold & Dickins (1991) was unproven. That is sustained by the present work, as in Waterhouse (2015a). Moreover, although the Beckett Member has been regarded as correlative with the middle Lyons Group, it could be slightly younger.

The zone above the *Lyonia lyoni* Zone is constructed from various scattered and meagre faunas, and assigned to the (now) *Neilotreta occidentalis* Zone by Archbold (1993b), marked by the incoming of this species and *Eurydesma playfordi* Dickins. The *Neilotreta occidentalis* Zone is represented in the upper Lyons Group and in the basal conglomerate of the Callytharra Formation of the Carnarvon Basin. *Neilotreta*, a distinctive genus (Waterhouse 2008b, p. 269; herein, p. 35), is also found at Cranky Corner in New South Wales, as well as India in the Bijni tectonic unit of the Garwhal Himalaya (see p. 36). Significant species such as *Lyonia lyoni* persisted from the underlying zone, and *Costatumulus* entered the fauna. The species *Sommeriella obrieni* and *Ambikella notoplicatus* also are found in the Carrandibby Formation of the Byro Sub-basin. *Juresanites jacksoni* occurs in the Woolaga Limestone, middle member of the Holmwood Shale, Perth Basin, with another ammonoid *Uraloceras irwinensis* Teichert & Glenister, which has been identified as *Svetlanoceras* by some authorities, an identification rejected by Leonova (1998). Palynomorphs in all three zones form part of the *Pseudoreticulatispora confluens* assemblage (Mory & Backhouse 1997).

International Correlation

The *concentrica* and *subcircularis* Zones of eastern Australia must be deemed to be no younger than Asselian because they underlie *Bandoproductus*. As summarized on p. 221, *Bandoproductus* is found widely through south and east Asia, largely though not entirely limited to faunas of upper Asselian age according to various authors. Many years ago the classic Asselian was subdivided into three, the Kurmaian, Uskalik and Surenan, and now there are several conodont zones recognized, four short lived forms, followed by three longer lasting taxa, called lineage interval partial range zones by Henderson (2018). Whilst it would seem reasonable to suppose that the development and evolution of conodonts were under the same marine influences as brachiopods and molluscs, the brevity of the lower conodont

zones, on average 0.56 Ma, seems exceptional, and perhaps overall there were four zonal shifts, unless the brachiopod-molluscan components changed so subtly that the changes have yet to be discerned, or evolution proceeded at completely different rates in different biota, in spite of being under similar environmental influences. It is also clear that whereas short-lived climatic changes may have influenced paleotemperature zones, such changes would have been less evident close to the ice-sheets, and close to the paleotropics. The four-fold macrofaunal subdivision in east Australia comes close to the arrangement in the Yukon Territory (Waterhouse (2018)). There are three zones and one proposed subzone in east Australia, approaching the arrangement in northern Canada, which developed in paleolatitudes more temperate than polar. Both of these climatic belts are lumped as antitropical in some studies, but it is preferred to recognize their separation, just as in present-day studies.

MIDDLE CISURALIAN SERIES

SAKMARIAN AND LOWER ARTINSKIAN (AKTASTINIAN) STAGES

Sakmarian marine macrofaunas are well developed throughout the Bowen Basin and Gympie Province of Queensland, the north Sydney Basin and New England complex of New South Wales and Queensland, including the Yarrol Basin, and in Tasmania. But only some of the faunas have been comprehensively described, and notably those of Tasmania and west Bowen Basin have been merely listed, apart from a meagre scattering of systematic studies. In the north Sydney Basin, the Rutherford Formation is followed by the Farley Formation with many Sakmarian fossils, which need to be comprehensively revised, apart from Productiformi by Briggs (1998), Ingelarellidae by McClung (1978) and Terebratulida by Campbell (1965), and many bivalves that have received attention from H. O. Fletcher and B. Runnegar. In the Yarrol Basin, *Bandoproductus* in the Burnett Formation is followed by the Yarrol Formation with many Sakmarian fossils. But the best currently known macrofaunal developments are now in the southeast and northern Bowen Basin, and these serve as exemplars for the stage.

***Bookeria pollex* Superzone**

This superzone was initially proposed as a zone on the basis of outcrops and described

macro-invertebrate faunas near Cracow in the southeast Bowen Basin (Waterhouse 1987b, 2008b). The nominate species *Bookeria pollex* (Hill)⁸ first enters at the base of the Fairyland Formation, and persists through the overlying Dresden Formation into the base of the Elvinia Formation, to be followed by key index fossils of the next zone. Other persistent species include *Notostrophia bifurcata* Waterhouse, *Protoanidanthus compactus* Waterhouse and

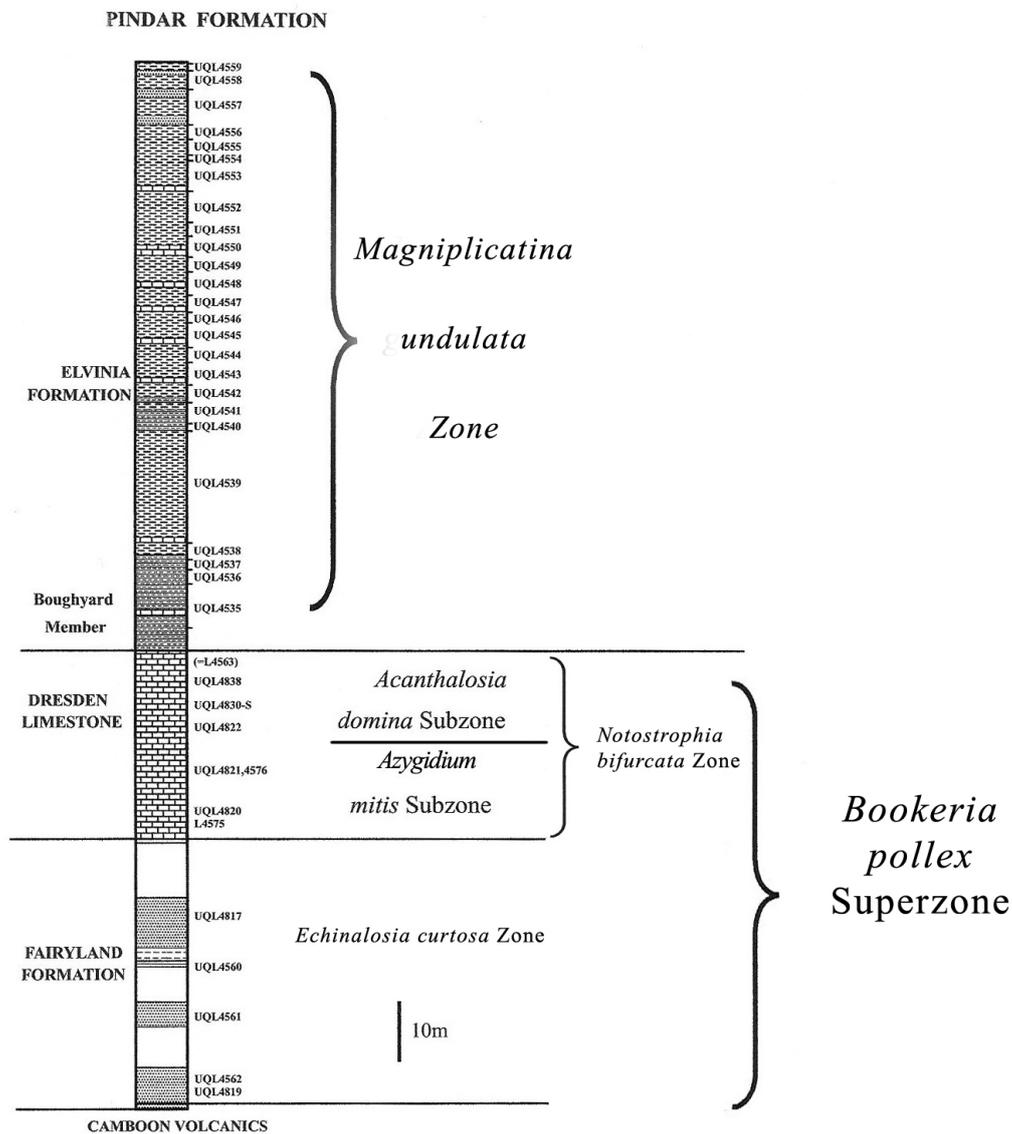


Fig. 1. Stratigraphic column for middle Early Permian formations of the southeast Bowen Basin near Cracow, synthesized from Briggs (1998) and Waterhouse (1986): minor gaps and volcanics are infilled by beds and faunas exposed along strike. The Boughyard Member has *Echinalosia curvata* and *Costatumulus farleyensis*, and *Bookeria geniculata* enters in the overlying locality UQL 4536. These levels are part of the biozone named after *Magniplicatina undulata*.

Grantonia australis (Bion). The superzone is regarded as younger than the *Bandoproductus* Zone, because of field relationships in the Hunter Valley, New South Wales (Briggs 1998), and Yarrol Basin, Queensland (Maxwell 1964). In the north Bowen Basin, meagre faunas at the base of the Tiverton Formation are possibly correlative with either the *Unicostatina crassa* Subzone or the *Bandoproductus macrospina* Zone, but faunas lack either of the nominate species (Waterhouse 2015a, pp. 156, 176). The basal beds are followed by condensed faunas of the *Bookeria pollex* Superzone.

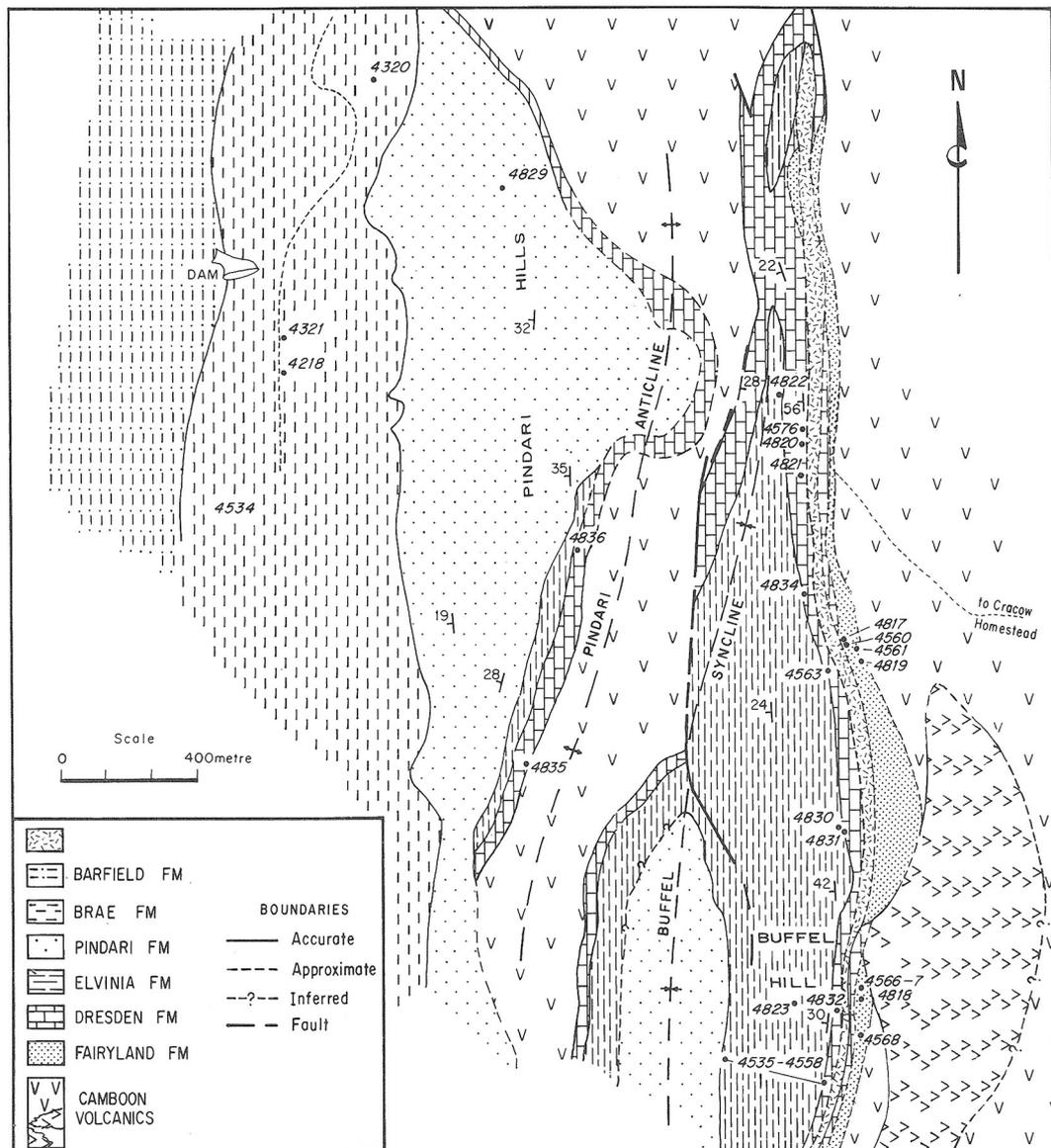


Fig. 2. Geological map of the Cracow area, showing the Camboon Volcanics and overlying Permian formations, with fossil localities bearing fossils, as monographed by Waterhouse (1986, 1987a, b). The very thin Otrack Formation lies between the Brae and Barfield Formations (See Fig. 3). (Waterhouse 1986).

In the southeast Bowen Basin, the superzone has been divided into two zones, and the younger zone divided in turn into two subzones. These subzones probably merit full zonal status, but are difficult to recognize in Tasmania, north Sydney Basin and Yarrol Basin,

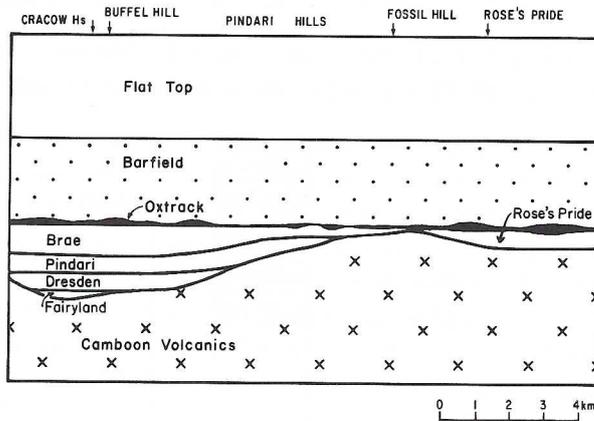


Fig. 3. Formations of Back Creek Group from Cracow homestead north towards Theodore, showing approximate changes in thickness and relationships along strike. Vertical scale exaggerated, 1mm = approx. 30m. (Waterhouse 1986).

possibly because of the lack of comprehensive systematic study, updated to at least conform with but preferably build on the classifications of the revised *Treatises* on Brachiopoda and Bivalvia. It means that new data may well qualify the present analysis, a qualification caused by the failure to fully describe faunas from Tasmania, New South Wales and southwest Bowen Basin. The *Bookeria pollex* Zone is not known to be represented by marine faunas in Tasmania, and the zone has not been definitely identified in Gympie or New Zealand, or further afield in India or South America. Concentrating on what is known, the faunas are best developed in the Cracow area.

***Echinalosia curtosa* Zone**

The zone proposed by Waterhouse (1987b) and endorsed by Briggs (1998) is typically exemplified in the Fairyland Formation of southeast Bowen Basin (Waterhouse 1986, 1987a, b). Species limited to the zone include *Svalbardia cracowensis* (Etheridge), *Echinalosia curtosa* Waterhouse, *Lipanteris cracowensis* (Hill), *L. sparsispinosus* Briggs, *Costatumulus prolongata* Waterhouse, *Ambikella regina* (Waterhouse), *Geothomasia cracowensis* (Waterhouse), *Tabellina denmeadi* (Campbell), *Notospirifer paraextensus* Waterhouse, *Grantonia cracowensis* Wass, *Spiriferellina disparata* Waterhouse and *Marinurnula prima*

Waterhouse. Mollusca include species like those of Early Permian faunas, together with *Eurydesma ovale truncatum* Waterhouse and *Concentiolineatus biornatus* (Waterhouse), as well as *Deltopecten* and *Squamuliferipecten*. Gastropods include *Pleurocinctosa promenata* Waterhouse and other distinctive forms. *Ambikella regina* is found in the lower Tiverton Formation at Homevale, with *Bookeria pollex*, *Grantonia cracovensis* and *Concentiolineatus biornatus*. According to Briggs (1998), *Echinalosia curtosa* is found in the lower Farley Formation of the north Sydney Basin, above the Rutherford Formation with *Bandoproductus* and presumably within the *Microbaculisporites trisina* APP2.2 palynomorph zone.

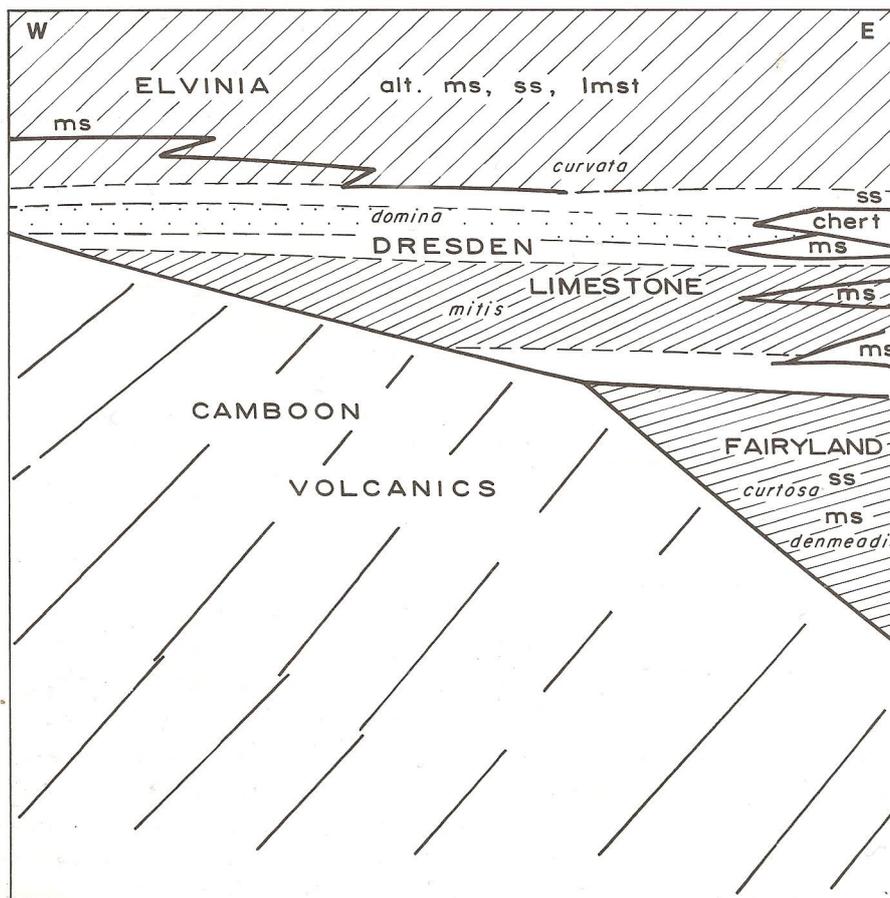


Fig. 4. Diagrammatic cross-section for the Permian formations and biozones at Cracow, southeast Bowen Basin. (Waterhouse 1986). The species *denmeadi* belongs to *Tabellina* Waterhouse. The species *mitis* belongs to *Azygidium*, *domina* to *Acanthalosia*, and *curvata* and *curtosa* to *Echinalosia*. lmst = limestone, ms = mudstone, ss = sandstone.

***Notostrophia bifurcata* - *Geothomasia postglabra* Zone**

This zone amalgamates two distinctive subzones, united by the presence of *Bookeria pollex*,

Notostrophia bifurcata, *Geothomasia postglabra* and other species, and not clearly developed beyond the Bowen Basin. Each subzone is arguably a full zone, but is known only over a limited geographic area, possibly reflecting the lack of descriptions for so many faunas in Tasmania, New South Wales and west Bowen Basin.

***Azygidium mitis* Subzone**

The *Azygidium mitis*⁹ Subzone is found in the lower Dresden Limestone¹⁰ (Holcombe & Jell 1983; Waterhouse 1983a, 1986) of the southeast Bowen Basin. The subzone has several distinctive species, including *Echinalosia dejecta* Waterhouse, *Plekonina spissatella* Waterhouse and *Spiriferellina anguliplica* Waterhouse. Some additional species appeared and persisted into the next zone, such as *Notostrophia bifurcata* Waterhouse, *Geothomasia postglabra* (Waterhouse), *Permasyrinx subelongata* Waterhouse, and gastropods *Spiraculinella radiata* Waterhouse and *Pleurocinctosa fletcheri* Waterhouse. A number of critical species are shared with the underlying *Echinalosia curtosa* Zone, including *Bookeria pollex*, *Protoanidanthus compactus*, and doubtful *Grantonia cracovensis*, as well as some bivalves, including *Eurydesma ovale truncatum* Waterhouse and gastropods. *Geothomasia branxtonensis* (Etheridge) is found in the Rutherford Formation (level not certain) and lower Farley Formation, and also in the lower Tiverton Formation, but has been also reported from the *Unicostatina crassa* Subzone of Tasmania by Clarke (1992). Few of the restricted species are known elsewhere. The only pteriomorph bivalve is the long-lived *Deltopecten illawarraensis* (Morris).

***Acanthalosia domina* Subzone**

In the upper Dresden Formation, *Azygidium* disappears, and *Acanthalosia domina* Waterhouse and *Lakismatia lakismatos* (Briggs) enter as characteristic species. Many of the accompanying species or closely allied forms persist from the *Azygidium mitis* level, including *Notostrophia bifurcata*, *Bookeria pollex*, *Permasyrinx subelongata* and *Geothomasia postglabra* or close allies. In the northern part of the basin, *Acanthalosia domina* is present near the base of the Tiverton Formation (Fig. 5, Table 2), together with possible *Bookeria pollex* and *Ambikella regina*, implying that these faunas were present but only thinly represented, apparently condensed. Several pteriomorphs are present, including *Eurydesma glaebula* Waterhouse, *Merismoptera banksi* Waterhouse, *Squamuliferipecten mitchelli*

(Etheridge & Dun) and *Concentiolineatus biornatus* (Waterhouse). *Deltopecten illawarrensensis* from the underlying beds is joined by *Etheripecten* and *Streblopteria*. The bivalve *Eurydesma glaebuga* is also found in the *Eurydesma* beds of the Wallaby Formation in the Stanthorpe Road Block, south Queensland (Richards & Bryan 1924), and might be correlative, or match slightly younger faunas – not enough is known about the faunas.

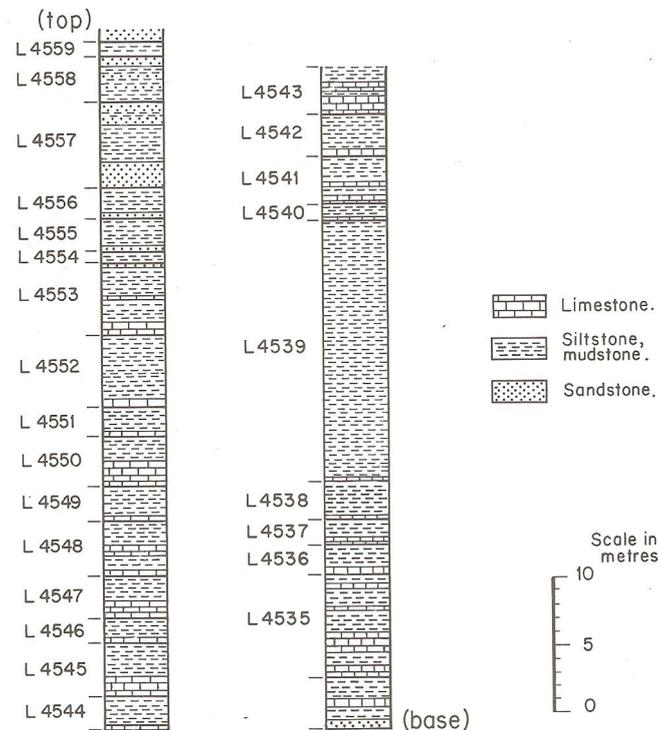


Fig. 5. Close sampling through the Elvinia Formation in the southeast Bowen Basin, setting a standard not always reached elsewhere, but highly desirable. (Waterhouse 1987b).

***Magniplicatina undulata* Zone**

This zone is typified by a plethora of species, some of which are listed for the Elvinia and lower middle Tiverton Formation in Waterhouse (2015a, Tables 3, 4). Some of the more conspicuous species vary a little in their ranges and distribution, leading to an arbitrary choice for nominate species, and the nominate species is selected from a member of Productida that

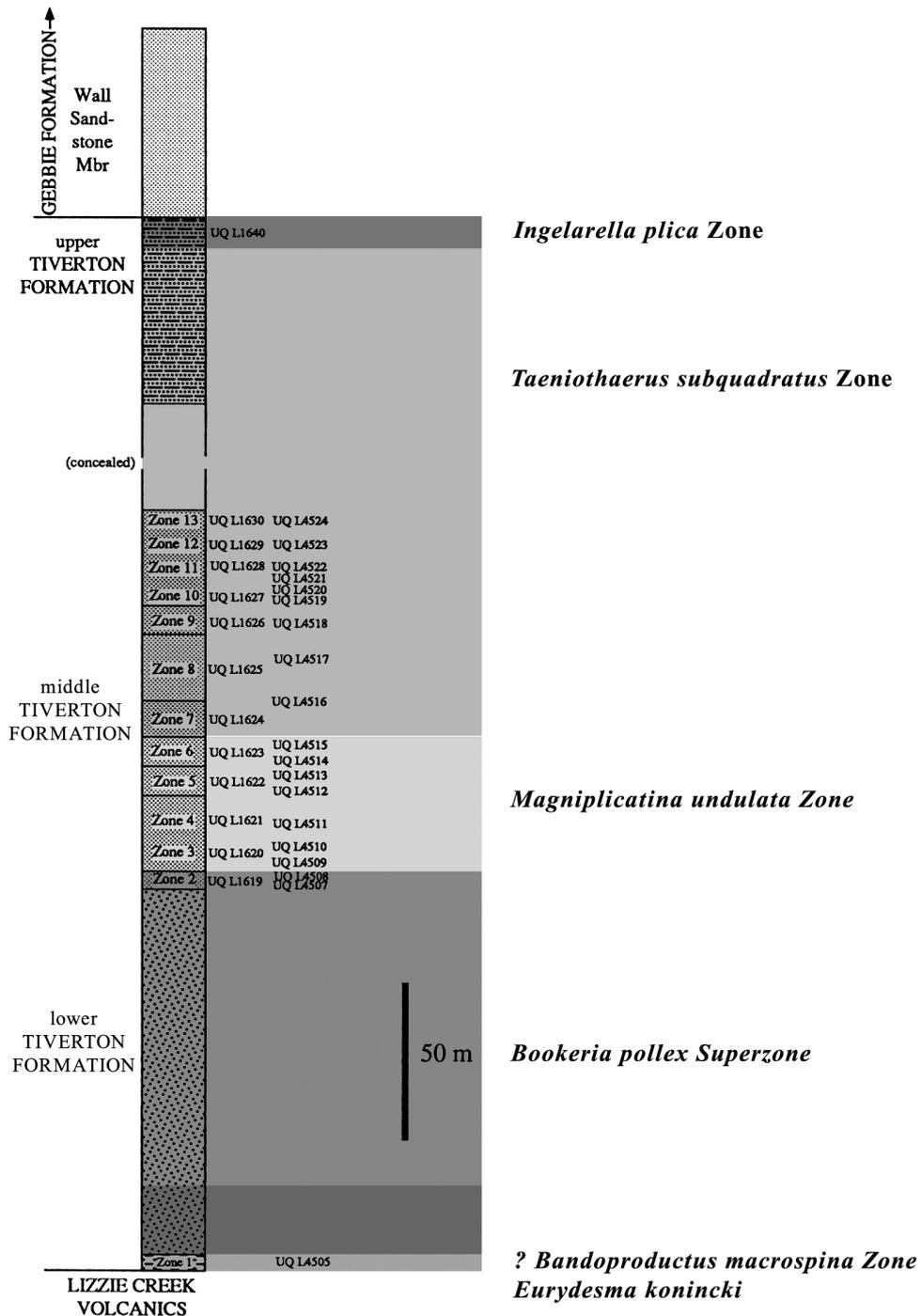


Fig. 6. Zonal sequence with critical fossil localities in the Tiverton Formation at Homevale. The column of numbered so-called zones and UQL 1619 to 1630 are based on Campbell (1961), and the column of UQL numbers from UQL 4505 to UQL 4525 and 3725 is from fieldwork by the author (Waterhouse 2015a). The presence of the *Bandoproductus macrospina* Zone is no more than provisional, and *Eurydesma konincki* is shared with the *Crassispinosella subcircularis* Zone in Tasmania.

is shared between the Elvinia and middle Tiverton Formations. Some of the other restricted species are found in one or other formation, and a number of the middle Tiverton forms persist into the overlying *Taeniothaerus subquadratus* Zone. There is a documented transition in the southeast Bowen Basin (Waterhouse 1987b, table 9, p. 205) faunally and lithologically from the *Acanthalosia domina* Subzone, in passing from the upper Dresden Formation into the Elvinia Formation, with residual species from the *Bookeria pollex* Superzone joined by incoming **Echinalosia curvata* Waterhouse, **Anidanthia paucicostata* (Waterhouse), **Magniplicatina undulata* Waterhouse, *Bookeria geniculata* (Waterhouse), *Costatumulus farleyensis* (Etheridge & Dun), *Coledium elvinia* Waterhouse, *Cyrtella subparallela* Waterhouse, **Permasyrinx elongata* (Armstrong), **Unicostatina stutchburii* (Etheridge), **Grantonia australis* (Bion), **Ambikella ovata* (Campbell), **Validifera valida* (Campbell), **Papulinella hillae* Campbell, *Pustulospiriferina lirata* Waterhouse. Bivalves include **Concentiolineatus homevalensis* (Waterhouse) and **Stutchburia farleyensis* Etheridge. In the basal Elvinia Formation pteriomorphs become numerous, including *Eurydesma* sp., *+Deltopecten illawarrensensis* (Morris), *+Squamuliferipecten squamuliferus* (Morris), **Streblopteria homevalensis* Waterhouse, *+Etheripecten tenuicollis* (Dana) and *Furcatia petulantis* (Waterhouse), the +forms being long-lived. *+Confundopecten limaeformis* (Morris) entered higher. Asterisked species are shared with or are very close to species in the lower middle Tiverton Formation, which provides the best exemplar for the zone and was nominated as biostratotype in Waterhouse (2008b). Here the fauna is joined by *Echinalosia cenula* Waterhouse and *Maxwellosia bryani* Waterhouse. Several critical species are replaced by closely related forms, interpreted as local variants, *Bookeria sparsispinosa* Waterhouse in place of *B. geniculata*, and *Costatumulus tumida* (Waterhouse) in place of *C. farleyensis* of the Farley Formation, joined by *Bookeria drysdalei* Waterhouse. Pteriomorphs are numerous, including *Squamuliferipecten mitchelli* (Etheridge & Dun), *S. squamuliferus* (Morris), *Elvinaria limitans* Waterhouse, *Orbiculopecten cokeri* Waterhouse, a few *Eurydesma glaeubula* Waterhouse and *Etheripecten playfordi* Waterhouse. Related faunas are found in the upper Wallaby rocks above the lower *Eurydesma* beds in the Stanthorpe Road block (Richards & Bryan 1924), but more needs to be known about the fossils to be confident of their correlation and nature.

The zone is represented in the Farley Formation of the Hunter Valley by *Anidanthia paucicostata* (Waterhouse) [described as *Anidanthus cessnockensis* Briggs, 1998], *Costatumulus farleyensis* (Etheridge & Dun), *Biconvexiella*, rare *Geothomasia profunda* (Campbell) and *Ambikella ovata* (Campbell) with abundant *Geothomasia branxtonensis* (Etheridge). Fossil lists indicate that the zone is developed in Faunizones 4 and 5 of Clarke & Farmer (1976) with *Costatumulus farleyensis*, *Grantonia hobartensis*, *Ambikella ovata*, *Geothomasia profunda* and *Validifera valida*, but the occurrences have not been systematically described, and require verification.

N BOWEN BASIN		SE BOWEN BASIN	
Tiverton UQL localities	Biozone	Formation	Biozones, subzones (S)
3725	<i>Ingelarella plica</i>	Rose's Pride	<i>Ingelarella plica</i>
4516-4524	<i>Taeniothaerus subquadratus</i>	-	-
4513-4515	<i>Svalbardia armstrongi</i> (S)	-	-
4509-4512	<i>Magniplicatina undulata</i>	Elvinia	<i>M. undulata</i>
4506-4508	<i>Bookeria pollex</i> Superzone	Dresden	<i>Acanthalosia domina</i> (S) <i>Azygidium mitis</i> (S)
		Fairyland	<i>Echinalosia curtosa</i>
4505	<i>Validifera prima</i> <i>Ambikella cf. elongata</i>		

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

Capillaria warwicki (Maxwell) as interpreted by Briggs (1998, p. 73) and Waterhouse (2001, p. 67) potentially offers a means of consolidating this zone as a wide-ranging and distinctive, being present in the Farley Formation and New England Orogen. It was widely reported by Briggs (1998), but his reports need first to be substantiated by examination of the external ornament, rather than relying on size and internal moulds. Some specimens described as *warwicki* by Briggs (1998) do not show the *warwicki* external ornament (Waterhouse 2015a) and should not be referred to that species without additional support. The first essential required to commence a proper appraisal of zonal value would be to

publish the full species descriptions of taxa accompanying type *warwicki*, to clarify whether *warwicki* is limited to the *Magniplicatina undulata* Zone, or if it entered earlier. There is a report of *Capillaria warwicki* in the Nassau Siltstone of Tasmania, but faunas at this level in Tasmania have not been monographed.

New Zealand

In New Zealand, this zone is represented in the Eglinton Subgroup of the Brook Street Volcanic Group of the Dunton Range, where *Calandisa solitarius* Waterhouse & Campbell in Waterhouse (2013) represents an unusual genus, accompanied by *Echinalosia curvata* Waterhouse and *Bookeria drysdalei* Waterhouse, two species typical of the Tiverton and Elvinia Formations in the Bowen Basin, as well as comparatively exceptional species named *Duntonia duntonensis*, *Pustuloplica*, *Alispiriferella turnbulli* and *Gypospirifer* (?) *inexpectans* to indicate a basic diversity greater than that of the east Australian counterparts (Waterhouse & Campbell 2021a).

***Taeniothaerus subquadratus* Zone**

This zone immediately overlies the *Magniplicatina undulata* Zone (Waterhouse 2015a, Fig. 5, p. 26), and typical species include *Taeniothaerus subquadratus* (Morris), *T. homevalensis* Briggs, *Lipantheris anotos* (Briggs), *Pseudostrophalosia brittoni* (Maxwell) and *Notostrophia laticostata* Waterhouse, developed in the upper middle Tiverton Formation of the northern Bowen Basin, and in the upper Elvinia Formation of the southeast Bowen Basin. *Taeniothaerus subquadratus* is widespread, and has a restricted time range. *Lakismatia lakismatos* (Briggs) and *L. sulcata* Waterhouse [also in the *Svalbardia armstrongi* band, as described below] are striking species in the Tiverton Formation. Species of *Echinalosia*, *Acanthalosia*, *Anidanthia*, *Bookeria*, *Grantonia*, *Ambikella*, *Geothomasia*, *Papulinella*, *Unicostatina*, *Permasyrinx*, *Pustulospiriferina*, *Fletcherithyris* and *Gilledia* persist from the underlying zone, together with many of the same pteriomorphs, joined by possible *Furcatia petulantis* Waterhouse, *Primaspinga vagrans* Waterhouse and *Hillaepecten queenslandica* Waterhouse. Bivalves and gastropods are particularly diverse.

Elements of this fauna appear to be developed in the Riverstone Sandstone Member of the Cattle Creek Formation in southwest Bowen Basin, although confirmation is badly needed. *Taeniothaerus farleyensis* Briggs, recorded from a single station, position unstated,

in the Farley Formation in Hunter Valley, is close to *homevalensis* from the Tiverton Formation and is well represented in the Lakes Creek beds near Rockhampton, east Queensland (Waterhouse 2013, p. 277; herein, p. 110). Scattered faunas are to be found in New England. In the Yarrol Basin of Queensland, *Taeniothaerus subquadratus* is found in the upper Yarrol Formation with a fauna otherwise much the same as that of the Tiverton Formation, but including shells close to *Echinalosia dejecta* Waterhouse of the Dresden Formation of the southeast Bowen Basin [identified as *Strophalosia preovalis* by Maxwell 1964]. There are a few underlying bivalves, from either this or an older zone, and underlying beds of the Yarrol Formation are apparently barren. The faunas have to be interpreted from collections made and identified long ago and published later by Maxwell (1964), so that further study is needed to update understanding of the formation. The *Taeniothaerus subquadratus* Zone is well developed in the Berriedale Limestone of Tasmania (Parfrey 1983), with *Wyndhamia jukesi* (Etheridge), as well as *Grantonia hobartensis* Brown in place of *G. australis* (Bion).

Biozone	Queensland	New South Wales	New Zealand
<i>Echinalosia conata</i>			<i>Echinalosia conata</i>
<i>Spinomartinia adentata</i>			<i>Spinomartinia adentata</i>
<i>Ingelarella plica</i>	<i>Ingelarella plica</i>		= <i>Notostrophia homeri</i> <i>N. zealandicus</i>
<i>Taeniothaerus subquadratus</i>	<i>T. subquadratus</i>	<i>T. subquadratus</i>	<i>T. subquadratus</i>
<i>Magniplicatina undulata</i>	<i>M. undulata</i>	<i>M. undulata</i>	= <i>Bookeria drysdalei</i>
<i>Bookeria pollex</i> Superzone	<i>B. pollex</i>	<i>B. pollex</i>	
<i>Bandoproductus macrospina</i>	<i>Ba. macrospina</i>	<i>Ba. macrospina</i>	
<i>Crassispinosella subcircularis</i>		<i>C. subcircularis</i>	
<i>Strophalosiaria concentrica</i>	= <i>Eurydesma</i> <i>burnettensis</i>	<i>S. concentrica</i>	

Table 3. Occurrence of Permian macro-invertebrate biozones in Asselian to Artinskian faunas in east Australia and New Zealand. *Bookeria drysdalei* in New Zealand is also in the *Magniplicatina undulata* Zone of Australia. Subzone *Unicostatina crassa*, and the subzones and zone within the *Terrakea pollex* Zone, namely *Echinalosia curtosa*, *Azygidium mitis* and *Acanthalosia domina* are omitted.

From the Gigoomgan area near Gympie in southeast Queensland, the Teebar Formation has yielded *Taeniothaerus homevalensis* Briggs, *Ambikella ovata* (Campbell), *Geothomasia profunda* (Campbell), *Grantonia australis* (Bion) and *Squamuliferipecten mitchelli* (Etheridge & Dun), as monographed in Waterhouse (2015b, p. 130ff). Jell & Cranfield (2013) erred in claiming that the formation matched the Tamaree Formation near Gympie, which is of Late Permian age (Waterhouse 2015b). The zone is also represented by a few critical species in the Gondor Formation of Eglinton Valley, New Zealand (Waterhouse, Campbell & Williams 1983).

***Svalbardia armstrongi* band**

The species *Svalbardia armstrongi* Waterhouse, 2015a is present in great numbers in the middle Tiverton Formation, in a band recognized as acme for the species, with *Biconvexiella convexa* (Armstrong, 1968) and the ammonoid *Gobioceras cancellatum* (Dear, 1966), and possibly *Gobioceras lobulatum* (Armstrong et al., 1967), though provided locality details were vague, and species could have come from just below.

Species of Productida and Spiriferida are found in abundance in the band, and are found in underlying localities as well. An allied species *Svalbardia saeptata*¹¹ occurs in profusion in the middle of the Farley Formation in the north Sydney Basin. Whether or not the band is present in Tasmania is not known.

***Echinalosia preovalis* - *Ingelarella plica* Zone**

The highest beds of the Tiverton Formation at UQL 3725, not far from the older Permian faunal sequences near Homevale, have yielded a moderately large and characteristic fauna, described in Waterhouse (1983d), and characterized by *Echinalosia preovalis* (Maxwell), *Anidanthia springsurensis* Booker, *Terrakea dickinsi* Dear, *Quadrospira*¹² *crassicostatus* (Waterhouse), *Ingelarella plana* Campbell and *I. plica* Campbell, together with bivalves *Glyptoleda javesi* Waterhouse and *Calcicanicularia glabra* Waterhouse as well as a few other pteriomorph species, not specifically named. This zone is the same as the *Echinalosia preovalis* - *Tomioopsis* [ie. *Ingelarella*] *plica* Zone of Waterhouse (1987b, p. 212), and *E. preovalis* Zone remains an appropriate name-giver, although the name was compromised by being applied well below its natural limits by Briggs (1998) and Archbold (2000). Examination of the so-called pre-type *preovalis* identified by Briggs (1998) shows that specimens were

misidentified, and differ from *preoivalis* (Waterhouse 2001, 2015a) in being larger with different shell profile and different spines. The zone is also recognized in the Roses Pride Formation of southeast Bowen Basin. Here brachiopods include several of the key species, as well as *Cracowspira laminatus* (Waterhouse)¹³. Pteriomorphs include *Eurydesma ovale sulcatum* Waterhouse, as well as species from other faunas, including long-lived *Etheripecten tenuicollis* (Dana), *Confundopecten limaeformis* (Morris), *Deltopecten illawarrensensis* (Morris) and *Squamuliferipecten squamuliferus* (Morris), with *Aphanaia* or *Maitaia*. In the upper Cattle Creek Formation at Reids Dome, southeast Bowen Basin, a diverse fauna contains some typical species¹⁴, a number still to be described, including several listed by Briggs (1998, Fig. 23). It should be noted that *Taeniothaerus subquadratus* is found below the upper Cattle Creek faunas. The *Echinalosia preoivalis* - *Ingelarella plica* Zone is of limited distribution, not known in New South Wales and yet to be established in Tasmania through systematic description of any of the key species.

Complications in New Zealand

***Notostrophia zealandicus* Zone**

A zone named for rocks and faunas in the Brunel Formation of New Zealand has over thirty species of brachiopods and molluscs (Waterhouse 1964b, 1982a, b, 2002). This has been found only in a section that exposes rocks some 70m thick along the Wairaki River. It contains *Terrakea dickinsi* Dear, *Quadrospira crassicostratus* (Waterhouse), and *Ingelarella plica* Campbell as in the standard *Echinalosia preoivalis* - *Ingelarella plica* Zone of east Australia, but also includes a number of genera not found in east Australia, such as *Rhipidomella*, possible *Bandoproductus* (Waterhouse 2001, p. 32), *Pugnoides* and *Psilocamara*, as well as unusual genera found rarely elsewhere, such as *Tigillumia* and *Pustuloplica*. The fauna arguably could be treated as part of the same entity as the overlying zone, as a matter for discussion and resolution, and here the preference is to treat it as a separate zone, mainly in order to keep the overlying fauna separable as a full zone that extends through both New Zealand and Queensland. The climatic implications of the fauna are discussed further on pp. 282-283.

It does seem possible that the nature of the fauna could have owed much to a local warm ocean current, which created exceptional conditions in the off-shore volcanic arc, so

Biozone	North Bowen Basin Formation	Cracow, SE Bowen Basin Formation	Springsure, SW Bowen Basin Formation	North Sydney Basin Formation	New Zealand Formation	
<i>Echinalosia conata</i>	?Wall Sandstone*	unconformity	Aldebaran?*	Greta Coal Measures*	McLean Peaks Heartbreak	
<i>Spinomartinia adentata</i>	unconformity		unconformity		Chimney Peaks	
<i>Ingelarella plica</i>	Upper Tiverton	Roses Pride	Sirius Mudstone Member	?	Brunel	
<i>Notostrophia zealandicus</i>						
<i>Taeniothaerus subquadratus</i>	Middle Tiverton	Pindari	Staircase Moorooloo Riverstone	Upper Farley?	Gondor	
<i>Magniplicatina undulata</i>	Middle Tiverton	Elvinia	Reid Dome Beds* [control poor]	Farley	(Dunton Range)	
<i>Notostrophia bifurcata</i>	Lower Tiverton	Dresden		?	Basal Farley	?Longwood Group (no fossils)
<i>Echinalosia curtosa</i>		Fairyland				
<i>Bandoproductus macrospina</i>		basal Tiverton?		Camboon Volcanic Group (no fossils)		
<i>Crassispinosella subcircularis</i>	Lizzie Creek Volcanic Group	Camboon Volcanic Group (no fossils)		Allandale		
<i>Strophalosia concentrica</i>				Lochinvar		

Table 4. Occurrence of marine faunal biozones in Early Permian formations as named in important sequences in the Bowen and Sydney Basins and New Zealand. Grey panels signify the absence or scarcity of marine faunas, and asterisks signify mostly or entirely non-marine, with poor macro-faunal control. The Staircase and Moorooloo sandstone units between the Sirius and Riverstone fossiliferous bands imply a possible faunal gap, but few of the western Bowen basin faunas have been systematically examined in modern terms. The upper Aldebaran Formation of the Springsure region contains late Early Permian brachiopods (Waterhouse 2001, p. 74), but older 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, but Parfrey (1986) has described Sakmarian brachiopods from further north. In New Zealand, the Longwood Group is poorly dated, and might well prove to be close in age to the Rammutt Formation or even the older Highbury volcanics of Gympie in southeast Queensland.

that questions remain over the significance and implications of this unusual fauna. On the other hand, some studies in Russia have indicated the presence of more than one fauna in the Aktastinian Substage (Licharew 1966, p. 218; Grunt & Dmitriev 1973), opening the possibility that the single conodont zone recognized for Aktastinian as in Henderson (2018) or

single ammonoid zone recognized by Leonova (2016) was matched by at least two faunas amongst fusulines and brachiopods in at least some parts of the world, including east Australasia. The question may further arise about the international correlation for the *Taeniothaerus subquadratus* Zone, and whether it could possibly prove to be of lower Aktastinian age, but the zone appears distinct from the *Notostrophia zealandicus* Zone.

***Notostrophia homeri* Zone**

Faunas from the Brunel rocks immediately above the *Notostrophia zealandicus* Zone in the Takitimu Mountains are severely depauperate, and contain a very few genera, including *Quadrospira crassicosatus* (Waterhouse), and *Ingelarella plica* Campbell. Similar species occur in the Skippers Range further west (Begg & Ballard 1991). Most of the species are shared with the zone in east Australia in the upper Tiverton Formation, Sirius Shale and upper Cattle Creek beds, and Roses Pride Formation.

Sakmarian – lower Artinskian in Western Australia

In Western Australia, the *Coronalia irwinensis* Zone lies above the *Lyonia* faunas and *Pseudoreticulatisporites confluens* palynomorph zone of the Lyons Formation and basal Callytharra Formation, with the significant entry of Aulostegoidea, just as in the *Bookeria pollex* Superzone of east Australia. The brachiopod component is very large, and includes *Neochonetes pratti* (Davidson), *Comuquia australis* Archbold, *Archboldina micracantha* (Hosking), *Wooramella senticosa* (Hosking), *Carilya* (?) *baracoodensis* (Etheridge), *Taeniothaerus quadratiformis* Archbold, *Callytharella callytharrens* (Prendergast), *Cimmeriella foordi* (Etheridge), *Latispirifer callytharrens* Archbold & Thomas, *Koenigoria neoaustralis* (Archbold & Thomas), *Lamnaespina papilionata* (Hosking) and many other species. Many bivalves were described by Dickins (1963). Ammonoids recorded by Glenister et al. (1990, 1993) and Glenister & Furnish (1961) come from the Callytharra Formation and Fossil Cliff Member and slightly younger forms from the Nura Nura Member. *Metalogoceras kayi* Glenister et al. (1973) and *Propopanoceras* were deemed to favour a Sterlitamakian age by Glenister et al. (1993, p. 56). Nicoll & Metcalfe (1998, Fig. 2) assigned the *Coronalia irwinensis* Zone to upper Sterlitamakian and lower Aktastinian, and reported a few cold-water conodonts, involving *Mesogondolella bisselli* and *Sweetognathus pequopensis*, also found in Timor with Sakmarian ammonoids (van den Boogard 1987).

According to Kozur (1998, Fig. 3), *bisselli* entered the succession in the late Sakmarian, and was joined by *pequopensis* in the mid-Artinskian. Henderson (2018) showed these two conodonts as mostly lower Artinskian and upper Artinskian respectively, so ages and identifications of the conodonts recorded by Nicoll & Metcalfe require consolidation. It is clear from the Henderson overview that conodont age assessments made a few years previously need to be updated, or set aside, or used to modify the international scheme. Nor indeed is it entirely clear that conodonts are in some circumstances more reliable as age determinants than ammonoids. On present information, there are slightly different possibilities over age for the Callytharra Formation, between Sakmarian and lower Artinskian. The Callytharra Formation has been re-examined, remapped and subdivided by Mory (1996) and Mory & Backhouse (1997), with the recognition of a Ballythanna Sandstone towards the top, overlain by the upper Callytharra Formation and Jimba Jimba unit. Some fossil species have been described from these refined subdivisions (Hogeboom & Archbold 1999; Archbold & Hogeboom 2000), but the full fauna needs revision. It was shown by those authors that the zone incorporates no less than three palynomorph zones, but so far, no clear concomitant change in macrofauna has been recorded. That implies the need for further evaluation of the *irwinensis* faunas, which had been commenced by Dr Z-Q. Chen, but never was completed. In Western Australia, *Taeniothaerus* and allied genera are common in the Callytharra Formation, and extend into the High Cliff Sandstone (Archbold 1997).

Match between Western and eastern Australia

At first sight, the westerly sequences broadly match those of eastern Australia. The *Coronalia irwinensis* Zone in the Callytharra Formation contains prominent taeniothaerin and rhamnariid species. In east Australia, taeniothaerins and rhamnariids enter the Fairyland Formation (*Echinalosia curtosa* Zone), and increased through the *Magniplicatina undulata* Zone into the *Taeniothaerus subquadratus* Zone, and they are present but greatly diminished in the *Echinalosia preovalis* Zone. The *Coronalia jimbaensis* Zone of the Wooramel Group, Carnarvon Basin, could equate with the *Echinalosia preovalis* - *Ingelarella plica* Zone of the topmost Tiverton Formation (Waterhouse 1976, p. 95), in so far as it stratigraphically overlies the *Coronalia irwinensis* Zone. The ammonoid *Neocrimites fredericki* (Emeliancev) was reported in the *Echinalosia preovalis* - *Ingelarella plica* Zone at the top of the Tiverton

Formation and in the Coyrie Formation of Western Australia, just above the Wooramel Formation and below the Madeline Formation, though this match may well require further scrutiny. The correlations, which seem obvious, were not countenanced by Archbold (2000)¹⁵. He based his correlations for brachiopods solely on evidence from palynomorphs. It seems advisable to assess the brachiopod-bivalve zones independently for their age implications, irrespective of other evidence, and then test them against the evidence from palynomorphs. If they disagree, so be it – one or other set of zones should not be suppressed, and if reconciliation is uncertain or impossible, again, so be it. Maybe plants evolved at a different rate from marine fossils (which themselves varied). But marine fossils were part of the marine environment, and palynomorphs were not, any more than marine fossils were part of the dry land. Radiometric values could apply to both settings, but it has long been decided that mere numbers could not suffice for understanding sediments, even though geochemists and physicists may not agree.

Summary of Permian marine faunas in south Asia

Many rich Permian faunas in south Asia have been described, in numerous monographs, not to mention short and therefore poorly integrated articles. The sequence over the Indian Subcontinent and south Asia may be summarized as follows:

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

3. *Svalbardia*, *Costatumulus*, *Coronalosia*, *Neilotreta*, *Brachythyrinella*, found in the Bijni tectonic unit¹⁶ and Garu Formation of India with *Uraloceras*, and allied to *Neilotreta*, *Coronalosia* and *Costatumulus* faunas from east and west Australia (Waterhouse & Gupta 1978, 1979). Allied correlative beds also contain *Cimmeriella* Archbold in Archbold & Hogeboom 2000, originally described in Western Australia, and found in Tibet and Afghanistan, and *Umaria*, *Costatumulus* and *Trigonotreta* in the Karakorum Range of Pakistan. Equivalent to *Bookeria pollex* and *Magniplicatina undulata* Zones of east Australia,

these faunas are judged to be of Sakmarian age, a Tastubian age being favoured by Termier et al. (1974), Angiolini et al. (1997) and Singh & Archbold (1993).

2. *Bandoproductus* has been found in the upper Phuket Group of Thailand (Waterhouse 1982c), below the *Spinomartinia prolifica* fauna (Waterhouse et al. 1981), and in the Bokhan Series of Afghanistan below reported but unconfirmed *Umaria umariensis* (Termier et al. 1974). These have all been dated as Asselian, together with other occurrences of *Bandoproductus* in south Tibet (Jin & Sun 1981), and in the Gircha Formation of the Karakorum Range (Angiolini et al. 2005), and in Yunnan (Shen, Shi & Zhu 2000). Asselian fusulines were reported with the Tibet occurrence by Jin & Sun (1981).

1. *Fimbrinialosia* fauna at Bap, India, with *Pseudoreticulatispora confluens* microflora, closely tied to a fauna of the Carolyn fauna of the Grant Group, Western Australia, and considered to be probably Asselian (Waterhouse & Ranga Rao 1989).

Northern hemisphere temperate paleolatitudes

Overall Sakmarian and lower Artinskian macrofaunas from paleotemperate latitudes of the northern hemisphere show a general similarity to the succession of east Australian faunas¹⁷, sharing some genera, and still closer to those of Western Australia. The correlative faunas of northern Canada in the Yukon Territory have been monographed and discussed in Shi & Waterhouse (1996) and Waterhouse (2018, 2020). Although now found in high latitudes, they were during Permian time much more palaeotemperate – not paleotropical, important distinctions masked by use of the term antitropical.

Palynomorph evidence

Palynomorph zones are summarized for east¹⁸ and Western Australia¹⁹ in footnotes. The palynomorph zones incorporate large units, embracing terrestrial and marine sediments, and so are more simple and thus more accessible for non-specialists, and facilitated by the use of a sequentially numbered and lettered scheme. Over the years, there have been continued to be changes and improvements, and the recent work as summarized in Smith et al. (2017) have smoothed out differences between east and west, and provided a zonation for the entire continent, without deviation or any hint of ecological or environmental differences throughout, a remarkable achievement.

BAIGENDZINIAN SUBSTAGE, UPPER ARTINSKIAN STAGE

No marine faunas are found for this substage in east Australia, but one SHRIMP age for a detrital zircon was determined as close to 276 Ma, near the 275 Ma age assigned to the Kungurian - Artinskian boundary, in Korsch et al. 2009²⁰.

In New Zealand two marine biozones are developed in the thick and rapidly accumulated Takitimu Group²¹, with marine fossil shell fish nowhere found in contemporaneous deposits of east Australia, although faunas of other ages from the two regions share many species in common. The older New Zealand faunas belong to the *Spinomartinia adentata* Zone, immediately above the *Notostrophia homeri* Zone (see p. 218), which is equivalent to the *Echinalosia preovalidis* - *Ingelarella plica* Zone (Waterhouse 1982a, pp. 81-84). Other species in the *Spinomartinia adentata* Zone include ?*Wyndhamia*

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

Table 5. Early Permian (Asselian to upper Artinskian) formations and lithologies of the north Sydney Basin in the Hunter Valley, New South Wales.

sp., *Taeniothaerus*, *Protoanidanthus*, *Psilocamara* and *Attenuocurvus altilis* (Waterhouse) with gastropods prominent, including *Coronopsis regularis* Waterhouse, *Platyteichum spiroloxum* Waterhouse and *Spironemella dignitas* Waterhouse, suggestive of a rocky shoreline. Some of these gastropod species are found with *Trabeculatia marwicki* Waterhouse in the Upukerora Breccia of Cawood (1986) at Gyzeh Peak, a species misidentified with *T. trabeculum* Waterhouse by Cawood, but decidedly older. Bivalve *Aphanaia glabra* Waterhouse is accompanied by conodonts to the north at Meyers Pass, and include forms identified in Ford et al. (1999) as *Mesogondolella bisselli* (Clark & Behnken) and *M.*

idahoensis (Youngquist, Hawley & Miller) which are both supposedly found in Baigendzinian of North America. However, in Henderson (2018), *bisselli* was shown as mostly lower Artinskian and *idahoensis* as upper Kungurian. As the specimens came from one locality, that helps underline some of the difficulties in interpreting microfossils from moderate to high southerly paleolatitudes. [Not that the paleolatitudes were that high for this region in New Zealand. New Zealand is a highly complex region of disparate terranes melded together, and the Pahau terrane, source of the Meyers Pass conodonts and also yielding scattered fusulines, developed far from the Brook Street volcanic arc and bordering sediments (Waterhouse 2015c, Fig. 8.1)]. *Aphanaia glabra* is found in the *Spinomartinia adentata* Zone of the Takitimu Group, and with the conodonts at Meyers Pass, and in the Kaka Volcanics of the Owhai Group in the Brook Street volcanic arc of northeast Nelson (Waterhouse 2001, pp. 109, 110). Atomodesmid taxa are highly useful for refined correlation in New Zealand, as in northeast Russia (Biakov et al. 2021).

The overlying *Echinalosia conata* Zone (Waterhouse 1982a, pp. 83, 84) includes *Taeniothaerus* cf. *ingens* (Hosking), originally described from the *Pseudostrothalosia colemani* beds of Western Australia, *Attenuocurvus altilis* Waterhouse, *Arcullina humilis* Waterhouse, *Grebneffia plicata* Waterhouse & Campbell (see Waterhouse & Campbell 2021b), *Deltopecten* and gastropod *Spirovallum fasciatum* Waterhouse. *Aphanaia otamaensis* Waterhouse is found in this zone in the Takitimu Mountains, as well as the Waipahi Group of south Otago and Rai Group of east Nelson (Waterhouse 1982c). Atomodesmid species are in the New Zealand setting more widespread than other macrofossils and thus offer evidence for correlation, but have been misinterpreted by various geologists, misrepresented as long-ranging and of low value in some cases, and flagrantly misidentified in other brief articles that sought to justify mistaken preconceptions over age and correlation (Waterhouse 2021, pp. 103-104).

Further afield in the Carnarvon Basin of Western Australia²², the Madeline Formation, Mallens Sandstone and Bulgadoo Shale are approximately correlative, with brachiopods of the *Sommeriella magnus*, *Echinalosia prideri*, *Mingenewia anomala*, *Pseudostrothalosia colemani*, *Fusispirifer byroensis*, *Tornquistia magna* and *Fusispirifer cundlegoensis* Zones recognized by Archold (1993b), who also named most of the species. The macro-

faunal zones seem excessively short-lived and localized and might better be regarded as fossil communities. The Irwin River Coal Measures of the Perth Basin in Western Australia may equate with the lower Greta Coal Measures, and the overlying marine beds and faunas as well as those of the Carnarvon Basin are regarded as approximately equivalent to the Greta Coal Measures²³ of the Sydney Basin, and Collinsville Coal Measures and Blair Athol Coal Measures, as well as upper Reid's Dome beds (Rigby 1983) of the Bowen Basin. But whether the Greta Coal Measures are represented in the south Sydney Basin is uncertain, and on current information, seems unlikely²⁴. The zonation offered for macro-faunas from the western Bowen Basin is not in harmony with the zonation proffered from palynomorphs, with particular discord involving the correlations and age of the *Echinalosia preovalidis* - *Ingelarella plica* Zone²⁵, and overlying beds assigned to the *Glendella dickinsi* and *Wyndhamia typica* (s. l.) Zones.

THE TOP OF THE CISURALIAN SERIES,

LATE EARLY PERMIAN

Kungurian Stage

The Kungurian Stage is well represented in Russia, and is dominated by macro-fauna that as shown by Stepanov (1973) record a sharp change on the whole from underlying Cisuralian (Early Permian), with loss of fossils regarded as indices for warm waters, such as fusulines. The change offers a marker event that helps to compensate for limited conodont faunules, which are more abundant in the United States. In making the original proposal of the Cisuralian Series, Waterhouse (1983b) wished to transfer the standard beds and faunas equivalent to the Kungurian Stage to the United States where fossils were more abundant and included many conodonts, as marking the start of the Guadalupian Series. Geopolitics and a strong sense of history – human rather than fossil - prevailed rather than the faunas, and the stratotype Kungurian was largely retained (somewhat nominally) in Russia. The faunas are divided in Russia into the Saranin, with vestigial faunas of the underlying Baigendzinian Stage, the Filippovian, marking the sharp change in fauna (Stepanov 1973), and Irenian with richer faunas. An Elkin fauna is recognized at the top (Waterhouse 1976), impoverished in Russia, though not necessarily elsewhere.

Glendella dickinsi Zone

The oldest fauna of Kungurian age in east Australia is the *Glendella dickinsi* Zone, with a smattering of other macro-fossils, including *Kaibabella boydi* Waterhouse, *K. ovata* Waterhouse and *Megadesmus deflatus* Waterhouse in the Glendoo marine incursion of the Collinsville Coal Measures (Dear 1972, McClung 1983) in the north Bowen Basin

Bowen Basin, Queensland		New Zealand	
Formation	Zone	Zone	Formation
Freitag*	<i>Wyndhamia typica</i> subsp.	<i>Wyndhamia typica</i>	lower Letham
Glendoo	<i>Glendella dickinsi</i>	scattered fossils	lower Letham
---	no fauna known	<i>Attenuocurvus</i> fauna	Elbow Creek
---	no fauna known	<i>Echinalosia conata</i>	McLean Peaks
---	no fauna known	<i>Spinomartinia adentata</i>	Chimney Peaks
Top Tiverton	<i>Ingelarella plica</i>	<i>Notostrophia homeri</i>	Brunel
	no fauna known	<i>N. zealandicus</i>	“ “
MiddleTiverton	<i>Taeniothaerus subquadratus</i>	<i>T. subquadratus</i>	Gondor
MiddleTiverton	<i>Bookeria drysdalei</i> <i>Magniplicatina undulata</i>	<i>B. drysdalei</i>	(Dunton Range)
Dresden-Fairyland	<i>Bookeria pollex</i>		-no fauna?

Table 6. Intercorrelations between Bowen Basin and New Zealand, documented in detail in Waterhouse (2001, 2002) and Waterhouse & Campbell (2021a). * Freitag Formation interpolated from southwest Bowen Basin, where it and the Aldebaran Formation lie above the Sirius Shale which contains *Ingelarella plica* Zone. But Freitag could be slightly younger, as possibly suggested by *Tumulosulcus undulatus* (Campbell).

(Waterhouse & Jell 1983). *Glendella* is a characteristic bivalve, derived from *Eurydesma* (Runnegar 1970). It has also been found and illustrated from GSQ Eddystone 1 core (McClung 1983). McClung reported *Glendella* from beds in the top of the Staircase Sandstone in southwest Bowen Basin, but as the Staircase beds underlie the Sirius Shale, the report would indicate an exceptionally old occurrence, and as it remains unverified by any formal description let alone illustration, has to be regarded with caution. The upper Pebbley

Beach Formation²⁶ of the south Sydney Basin contains one of the brachiopod species accompanying *Glendella*, called *Notospirifer gentilis* Waterhouse, as well as *Tabellina laseroni* Waterhouse, and *Paragilledia kioloaensis* Waterhouse, species showing similarities to Kungurian and Middle rather than Early Permian species (Shi et al. 2020). Briggs (1998) reported but did not figure supposed *Echinalosia preovalis*, and it seems likely that the form in fact belonged to *E. floodi* Waterhouse, 2001, which is common in overlying beds and in the Branxton Formation of the north Sydney Basin. Another unusual brachiopod was described as *E. mcclungi* Briggs, with two series of dorsal spines, suggestive of *Acanthalosia*, but with the types now apparently lost. The most prominent fossil in the uppermost Pebbly Beach Formation is *Eurydesma sacculum snapperensis* Waterhouse (see p. 94), shared with the overlying Snapper Point and Wandrawandian Formations, as explained on pp. 94, 95. *Glendella*, *Eurydesma*, and the general impoverished nature of the faunas as a whole point to very cold conditions, and correlation with the Filippovian fauna of the Russian Kungurian, which saw a huge decline in fusulines and conodonts, biota that required warm conditions.

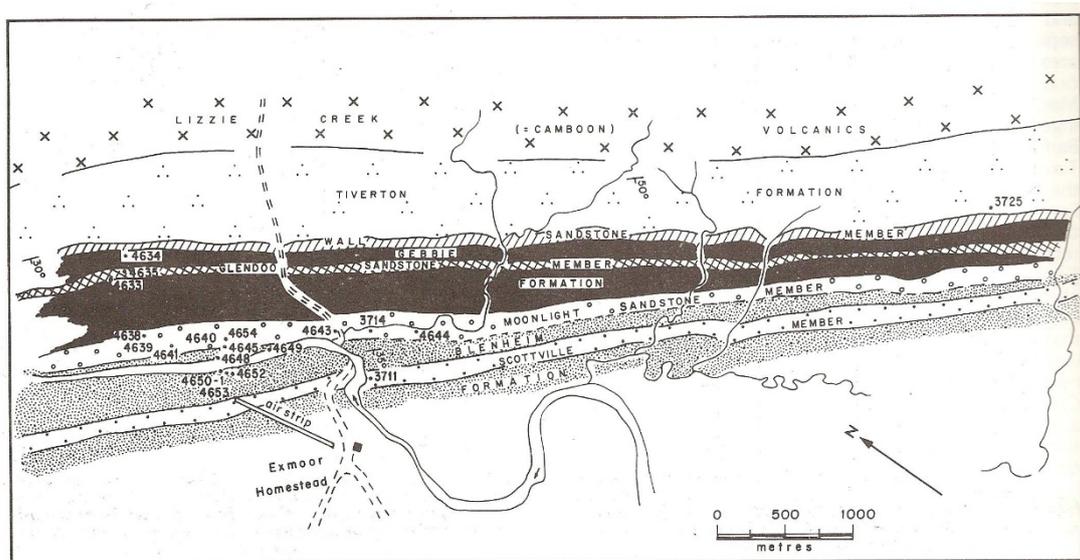


Fig. 7. Early and Middle Permian formations with fossil localities near the Bowen River in the north Bowen Basin. (Waterhouse & Jell 1983). In this map the Lizzie Creek Volcanics are broadly correlated with the Camboon Volcanics.

Contemporaneous faunal sequences are developed at Wairaki Downs of New Zealand, where, for the numerous formations and zones discussed in this text, a detailed

paucispinaurian species (Briggs & Campbell 1993; Waterhouse 1982a, p. 84; 2001, pp. 26, 44; 2002, p. 27; 2021). Scattered molluscs are also found higher in the basal Letham Formation (Waterhouse 2002, p. 27). The general poverty of the faunas and their overall context and content invite comparison with the *Glendella dickinsi* Zone.

***Wyndhamia typica* Zone**

The *Wyndhamia typica* Zone in the Branxton Formation of the north Sydney Basin and Snapper Point Formation²⁸ of the south Sydney Basin (Waterhouse 2002, p. 178) includes *Echinalosia floodi* Waterhouse, *Paucispinuria paucispinosa wardenensis* Waterhouse, *Terrakea rhyllstonensis* Briggs [or *exmoorensis* Dear²⁹], *Johndearia brevis* McClung & Armstrong), and *Aperispirifer archboldi* Waterhouse, described and figured in Briggs (1998), McClung & Armstrong (1975), and Waterhouse (1999, 2001). These faunas are much more diversified than those of the *Glendella dickinsi* Zone, and they are putatively correlated with the Irenian faunas of Russia. An ammonoid from the Branxton beds recorded by Teichert & Fletcher (1943) has been identified with *Aricoceras* by Leonova (1998, p. 159) and assigned a Kungurian age. It seems that the *Wyndhamia typica* Zone is to be found in the Bowen Basin only in the upper Aldebaran and in the Freitag Formations³⁰, though the presence of *Tumulosulcus undulosa* might be indicating a slightly younger age. Although it may be moot whether the zone is developed in Tasmania, because the faunal lists provided are not supported by systematic description, one taxon, recorded as *Wyndhamia clarkeina* Waterhouse, 2001, p. 75 from the Grange Mudstone, and Malbina A and B of Tasmania appears to be a likely geographic development or variant of *W. typica*, and points to the *Wyndhamia typica* Zone. Other well preserved faunas of this interval in Tasmania remain to be described.

An exemplar of the *Wyndhamia typica* Zone is found above the depauperate faunas of the basal Letham Formation. Briggs (1998) criticised the identification of *typica*, but his remarks are inaccurate, and as a concession, “possible” *W. typica* is found with *Paucispinuria paucispinosa* Waterhouse, possible *Ingelarella cessnockensis* McClung³¹, and *Aperispirifer archboldi* Waterhouse (Waterhouse 2001, 2002, p. 178), all typical of the *Wyndhamia typica* Zone in east Australia, as well as a number of other species, including *Spiriferella supplanta* Waterhouse, 1964b, member of a genus not found anywhere in east

Australia, and a few pteriomorphs, such as *Etheripecten latus* (Fletcher) and *Striochondria auriocosta* Waterhouse.

***Echinalosia discinia* Zone**

The best exemplar of the *Echinalosia discinia* Zone is offered by the Brae Formation of the southeast Bowen Basin (see Fig. 2), where a rich and fully described macro-fauna (Waterhouse 1986, 1987a, b) includes twenty seven macro-faunal species in 7 localities, including *Echinalosia discinia* Waterhouse, *Lethamia hillae* Waterhouse, *Magniplicatina superba* Waterhouse, *Paucispinauria paucispinosa* Waterhouse, *Spinomartinia queenslandica* Waterhouse and a number of molluscs, named in Waterhouse (1987b), including *Streblopteria minauris*, *Echinorbis papillosa*, *Elimata symmetrica*, and *Calicanicularia* sp. Genera unusual for east Australia include *Simplicisulcus concentricus* (Waterhouse), *Sedecularia glabra* (Waterhouse), *Tigillumia biparallela* (Waterhouse)³² and *Pustuloplica papillosa* Waterhouse. This formation lies above the Pindari Formation with only rare conulariids, and commences with conulariids at the base, so that the zone commences above these, within the lower but not basal beds of the formation (Waterhouse 1986). Superior outcrops are developed above the *Wyndhamia typica* Zone in the lower Wandrawandian Formation of the south Sydney Basin, which offers a much fuller and more clearly developed sequence, and the faunas and distribution details are now being studied (Prof. G. R. Shi, pers. comm.). Pending that study, *E. discinia*, *Paucispinauria paucispinosa wardenensis*, *Magniplicatina halli*, possible *Terrakea exmoorensis* and *Simplicisulcus concentricus* were provisionally reported by Waterhouse (2001), correlative with the Fenestella Shale above the Branxton Formation in the north Sydney Basin, which contains *Echinalosia discinia*, *Anidanthus solitus*, *Paucispinauria paucispinosa wardenensis*, *Ingelarella subplicata* and *Aperispirifer lethamensis*. Some species persist into the overlying Belford Formation. Several productid species have been described in Briggs (1998) and revised in Waterhouse (2001, 2002, pp. 179-180). Possible *Tumulosulcus undulosus* was reported in the middle Wandrawandian Formation by McClung (1978, p. 47, pl. 8, fig. 1-3, 7), the sulcus having a median swelling as in type *Tumulosulcus undulosus*, originally described from the upper Gebbie Formation of the north Bowen Basin.

The species *undulosus* is also found in the Freitag Formation of the southwest Bowen Basin (McLoughlin 1988), together with *Wyndhamia typica crassispina* Waterhouse, 2001, suggesting correlation with either the *Wyndhamia typica* or *Echinalosia discinia* Zone.

This zone is well represented in the upper Letham Formation of New Zealand, immediately above the *Wyndhamia typica* Zone at Wairaki Downs. The zone includes such species as *Echinalosia discinia*, *Paucispinauria paucispinosa wardenensis*, *Magniplicatina halli*, *Terrakea exmoorensis* Dear, *Ingelarella subplicata* and *Aperispirifer lethamensis*. Diverse bivalves include *Streblopteria minauris* and *Elimata symmetrica* as in the Brae Formation, as well as *Streblochondria flexuosa* Waterhouse, *Striochondria auricosta* (Waterhouse), and *Etheripecten chandleri* Waterhouse, with gastropods.

A boulder in the lower Queens Beach Member of Campbell et al. (1984) on Stephens Island contains a number of species found in the *Echinalosia discinia* Zone (Briggs & Campbell 1993, Waterhouse 2021), including the Wandrawandian *Anidanthus solita* (Waterhouse, 1968), found in a boulder sourced from the Brook Street volcanic arc.

***Echinalosia denisoni* Subzone**

Echinalosia denisoni Archbold, 1987 [syn. *E. bookeri* Briggs] is found at the top of the Fenestella Shale, and also occurs in Queensland in the upper Brae Formation, and at level C of the Eddystone 1 core, as figured in McClung (1983). It is also represented at a comparable level in Zealand (Waterhouse 2001, p. 63), below the *Lethamia ligguritus* Subzone (see below). The species appears to have been very short-lived, in a style comparable to that treated as a "horizon" in Russian and other literature, though the concept was disfavoured by Salvador (1989).

***Lethamia hillae* – *L. ligguritus* Subzone**

The upper Brae Formation, with detail on thickness and localities provided in Waterhouse (1987b, pp. 213, 214,) is typified by the zonal fossil species, joined by *Lethamia hillae* and *Stenoscisma glabra*. *L. hillae* was also reported from the Drake Volcanics at Warwick, southern Queensland, by Briggs (1998, p. 129). This level is matched in New Zealand by the upper Letham Formation, where *Echinalosia discinia* is joined by *Lethamia ligguritus* Waterhouse, with forty species in 17 localities, especially rich in bivalves (Waterhouse 2002, Table 6, p. 37), including a number of restricted species.

The subzone does not appear to be represented in the Sydney Basin, presumably under the influence of colder climate and higher paleolatitudes, so that *Lethamia* was excluded.

2. INTERNATIONAL CORRELATIONS

Correlations for the east Australian Permian zones may be provisionally made with the world international standards, as represented by the Cisuralian Series of Russia, the Guadalupian Series of United States, and Lopingian series of China, a scheme first suggested by Waterhouse (1983b) in proposing the Cisuralian Series and a three-fold arrangement for the Permian Period, as later endorsed by Jin (1996; Jin et al. 1997), with elaboration of the Lopingian Series in Jin et al. (1996), so that the divisions are now the International Standard. Three different modes of correlation are considered. The prime method of calibrating Permian fossil faunas in terms of the International Standard is based on conodont zones. But conodonts are missing from the entire marine Permian of eastern Australia, and therefore recourse is made to brachiopods, bivalves and gastropods primarily, with reference to occasional other molluscs such as ammonoids, though these are too rare to allow widespread correlation in east Australia. As for Foraminifera and Bryozoa, no study has adequately resolved any satisfactory and comprehensive zonation for the marine faunas of east Australia, reflecting the need for much more study. The correlation potential for these fossils is surely high. There are some 18 conodont zones for the Early Permian Period, compared with 15 brachiopod-mollusc zones plus several subzones, some of which may deserve to be elevated in status in the Permian of the east Australia and New Zealand. This difference is not great, and may be due partly to the incomplete fossil record for east Australia. The conodont zones are based on first entry data, and are based on the best available sequences around the globe, mainly Russia-Kazakhstan, United States, and China, whereas the present region available for analysis is much more circumscribed, and limited not only by the failure to describe many faunas, but uncertainty over where the Permian Period started. For the conodont zones, a number of range zones are based on single "species", irrespective of accompanying fauna. The east Australian zones are based on whole fauna analysis for brachiopods and molluscs, to construct assemblage and range zones. Herein, preference is for the assemblage zones rather than first entry zones, because

these convey much more information on biotal succession, evolution and environmental parameters. An independent approach, based on palynology, is also based on first entry data, and has the great advantage of incorporating non-marine sediment, though the palynomorphs are even less related to international stratotype data than the brachiopods and molluscs, because international subdivisions for the Permian Period are based on marine faunas, not palynomorphs. International correlation for palynomorph zones in Australia now depends on independent radiometric assessments rather than floral relationships to world stratotypes. A further severe disadvantage prevails for Australian palynomorph zones. Currently only seven zones are recognized for the early Permian, less than twice the number of Permian stages, and only a third of the number of conodont zones, and much less than half the number of brachiopod-mollusc zones. This has severe ramifications for correlation, because the palynomorph zones fail to distinguish various formations in stratigraphic order in several instances, and are less useful for detecting gaps in the fossil and stratigraphic record. A number of the zones are by no means range zones, because their nominate form ranges far beyond the designated limits of the zone, which always opens up the possibility of failure to find the next FAD at exactly the same place as elsewhere. I believe it must be possible to greatly expand the resolution and correlatability of palynomorphs, as has long been achieved for other parts of the column world-wide.

Asselian Stage

The prime key for delineating the Asselian Stage in east Australia is provided by *Bandoproductus*, found widely in Gondwana in beds of upper Asselian age, with no known older occurrences, and widespread agreement on the correlation for earliest appearance of the genus through south Asia. This date places the upper Rammutt Formation of Gympie and basal Rutherford Formation of the northern Sydney Basin. The underlying faunas, with *Eurydesma* prominent in the Lochinvar and Allandale and numerous other faunas, are deemed to be Asselian, just as in other parts of Gondwana. But the boundary between the Carboniferous and Permian Periods remains in need of elucidation.

In east Australia, three major zones are recognized, and one subzone. More faunal entities might be developed in earlier beds, but fossils are few and where the Carboniferous Period ends and the Permian Period starts is not clear. For conodonts, seven zones are

recognized, four of which are very short-lived and minor for the early Asselian (Henderson 2018). For palynomorphs, two zones, the older one partly Carboniferous, called *confluens* and *tentula* are recognized (Smith et al. 2017, Fig. 12), with Lochinvar assigned to *tentula* and Allandale to *confluens*. These involve the marine *concentrica* and *subcircularis* Zones and *crassa* Subzone. It is difficult to obtain firm data on the nature of the palynomorphs in the *Bandoproductus macrospina* Zone, and it possibly fits within the *pseudoreticulata* APP2.1 zone.

Sakmarian Stage, Aktastinian Substage

As summarized on p. 218ff, there is general similarity of the Productiformi including *Taeniothaerus* of this age to faunas in Western Australia, and extending through southeast and south Asia into the Middle East. Some of these faunas have ammonoids related closely to the international standard successions of Russia and Kazakhstan.

The east Australian marine Sakmarian is divided into three zones, and includes two further subzones, each substantial enough to be considered as full zones, making up four zones, compared with a possible four conodont zones. The Aktastinian division of the Artinskian Stage is allocated to one conodont zone, compared with one macro-faunal zone in Australia, and one additional and local fauna is restricted to New Zealand, treated herein as also being Aktastinian.

Baigendzinian Stage

There is no known marine fauna of this age in east Australia, but marine faunas are present in Western Australia and New Zealand, those of Western Australia accompanied by Baigendzinian ammonoids, and those of New Zealand related, less securely, to conodonts dated as Baigendzinian, though in my opinion of low reliability because of problems of identification, and possible constraints imposed by moderately high latitude and southerly distribution. The Greta Coal Measures accumulated in the north Sydney Basin during this time, which world-wide was a time of increased planetary warmth, as reflected in the marine fossils, and when, according to Loughnan (1973, 1975), the soils and plants of the Greta Coal Measures indicated subtropical conditions.

There are two conodont zones world-wide, and two brachiopod-mollusc zones in New Zealand.

Kungurian Stage

The Kungurian Stage in east Australia and New Zealand indicates a sharp return to cold conditions with glaciation, recalling conditions that prevailed during parts of the Asselian Stage. This corresponds with a drastic change in faunas world-wide, especially in the northern hemisphere and Russia in particular. A New South Wales ammonoid *Aricoceras* has been assigned a Kungurian age by Leonova (1998). *Terrakea ? vaga* Cooper & Grant (1975) from the Cathedral Mountain Formation of Kungurian age is like what Briggs (1998) called *Terrakea rhyllstonensis* [Kungurian herein] from east Australia. In east Australia, the presumed Kungurian has three zones, *Glendella dickinsi*, *Wyndhamia typica* and *Echinalosia discinia* Zones, with an underlying New Zealand fauna not formally placed, and these levels are putatively matched with Saranian, Filippovian, Irenian and Elkin in Russia. According to Henderson (2018), the Kungurian conodont zones number four, with four local zones. But the actual macrofaunal correlation for the *Echinalosia discinia* Zone is not tight, and a Roadian match cannot be ruled out.

3. FOOTNOTES

1. In this study, the succession of brachiopod species proclaimed in a major study by Briggs (1998) is deemed to be, in parts, open to question. Difficulties have been further compounded by his failure to return type and other material, so that his proposed species potentially remain in a vacuum, with no supporting and accessible type material available for inspection. In this and earlier Earthwise publications, attempts have been made to underpin, validate and justify taxa proposed by Briggs, even the absence of type material, but for at least some taxa, his taxa will require steps to be taken to either find the material or nominate neotypes. Perhaps the best solution would be to involve the Association of Australasian Palaeontologists, which published the Briggs work, but did not verify his claim in the text that types had been lodged in the museum, even though validation should always be stipulated as a requirement for publication. The study by Briggs (1998) was a major work, in which some 75 productid species were described from eastern Australia, of which twenty eight species were new, and three had previously been named by him. The other forty one species had been previously named by various authors. Emphasis was on species: Briggs had only ever

erected one new genus, but he did provide means of validating and distinguishing between the genera *Wyndhamia* Booker and *Pseudostrophalosia* Clarke, and had endorsed and expanded the species content of several genera proposed by Waterhouse, such as *Echinalosia*, *Acanthalosia*, *Megasteges*, *Costatumulus*, *Magniplicatina*, *Protoanidanthus* and *Lethamia*. But taxonomically, it cannot be said that he ever came close to matching the contribution by N. W. Archbold, who described many species, and recognized new genera and new family groups and studied Permian successions in various parts of the world. It is thus in the field of biostratigraphy for one period in east Australia, and only in that field, that Briggs made a substantial mark. He took great trouble to reassess previous studies of Productida, travelling extensively in the field and to various institutions, to present a zonal interpretation through often idealized stratigraphic columns, in a fashion that enabled application of his zonal scheme to the marine Permian of east Australia. Was his scheme largely correct? That is a difficult question. Briggs failed to understand and deal with the role and significance of the major coal measures in east Australia. The Greta Coal Measures were assumed to have no disruptive significance to any sequence of productid species. Part of his problem was adoption, with no supporting proof, of the contention by various paleontologists such as Armstrong, Dickins, McClung and Runnegar that the New Zealand Permian sequence was a version, inferior but otherwise identical with that of east Australia. Therefore two major zones in New Zealand were obliterated, whereas in fact they match the Greta Coal Measures. To Briggs (1998, Fig. 35), the *Echinalosia preovalis* Zone was immediately followed by the *Echinalosia maxwelli* Zone. The *Spinomartinia adentata*, *Echinalosia conata* and *Wyndhamia typica* Zones were swept away in defiance of field evidence, partly because of his lamentably circumscribed experience, restricted to parts of east Australia. And in the same way the Byro Group with marine faunas were mismatched and misinterpreted in any consideration of east Australian faunas.

These large errors were associated with smaller scale reversals of stratigraphic order throughout much of the column, errors resulting partly from misidentification, and also from a focus on museum collections and core data, rather than careful and detailed geological mapping.

2. Many conodont and brachiopod taxa and species did not persist from the Carboniferous Period into the Permian Period, and it has seldom been deemed desirable to have a zone spilling over from one period to the next, because it simply implies uncertainty over the nature and correlation of the zone, rather than reality. Did this palynomorph zone APP1.21 really spill over? Or are bets being hedged, so as to be at least partly right (good?), and as a consequence, partly wrong (less than good?).

3. *Tomioopsis elongata* reported from Tasmania by Clarke (1990, Fig. 10A-L; 1992a, p. 22, Fig. 101-L) differs from *elongata* McClung & Armstrong in shape and detail of the internal plates. It was separated as *Ambikella bundellaensis* by Waterhouse (2015b, p. 168), but differences are overall slight, and arguably of subspecific status only.

4. For the south Sydney Basin, Nicholl et al. (2017) and Smith et al. (2017, Fig. 17) placed the Wasp Head Formation in the *Pseudoreticulatispora pseudoreticulata* APP2.1 palynomorph zone (found also in the lower Rutherford Formation of the north Sydney Basin), and placed the Allandale Formation in the *Ps. confluens* APP1.22 palynomorph zone. Macro-fossils strongly suggest that the middle and apparently the upper Wasp Head Formation is correlative with the Allandale Formation (Runnegar 1969a). The lower Wasp Head Formation shares fossil species with the *Strophalosiaria concentrica* Zone in Tasmania, elsewhere placed in the *tentula* APP1.21 palynomorph zone.

In palynomorph studies, the Wasp Head Formation was shown as the lateral equivalent of the Clyde Coal Measures. Just because two formations share the key palynomorph, that is no evidence for precise correlation rather than a sequential relationship. As macro-fossils show that the Wasp Head beds are correlative with faunas associated with the *confluens* zone, the Clyde Coal Measures may well signify a significantly warm climatic interval, after the cold interval when the Wasp Head beds and cold-water marine fossils accumulated, and conceivably the Clyde Coal Measures could have matched the warm *Bandoproductus macrospina* Zone. Indeed Fielding et al. (2008a, p. 136) argued that the Wasp Head Formation pointed to waning glaciation, and correlated the beds with the Clyde Coal Measures, though they provided no clear stratigraphic or paleontological evidence. Sedimentation is highly complex, highly dependent on local rather than temporal controls, especially over supply and accommodation, and cannot always be used as a reliable

substitute for biota or radiometry in correlation. The difficulty experienced by some sedimentologists in relating sediment to ecological conditions is indicated by the highly selective references in Fielding et al. (2008a, Fig. 2) to other studies on Permian glaciation in east Australia, which claimed that only one major glaciation occurred in east Australia. In fact other studies on sediments and fossils showed that the claim by Fielding et al. to be first in recognizing multiple glaciations was incorrect (cs. Waterhouse 1963, 1964a, c, 1976, Fig. 3, p. 255; etc.).

5. A species *Geothomasia simplicitas* Waterhouse, 2015b, p. 169 has been confused with *Ingelarella konincki* (not Etheridge) by McClung (1978, pl. 2, fig. 3, 4, pl. 3, fig. 1, 2) and *Tomioopsis konincki* by Cisterna & Shi (2014). The original material for *konincki* de Koninck (1877, pl. 10, fig. 11, 11a) was destroyed, and the neotype, UQF 73296, not cited by Cisterna & Shi (2014), is figured in Waterhouse, Briggs & Parfrey (1983, pl. 3, fig. 14) together with further material from the Allandale Formation, as in McClung (1978, pl. 3, fig. 4-6). It has a broad weakly channelled fold and stronger plicae than in *simplicitas*. Sulcal subplicae are well developed, and adminicula of moderate length and weakly divergent.

6. The lower Cranky Corner Sandstone belongs to the *Pseudoreticulatispora pseudoreticulata* palynomorph APP2.1 zone and the upper Cranky Corner Formation is accompanied by APP2.2 key palynomorph *Microbaculispora trisina*, according to Balme & Foster (2003, p. 131). Archbold (2003, p. 157) stated that the upper Cranky Corner faunas, with abundant *Eurydesma cordatum*, was equivalent to the *subcircularis* Zone of Clarke (1992) and equated with the Allandale Formation. That appears to indicate a major contradiction, for the Allandale beds are not regarded as typified by *trisina*, which is found in the upper Rutherford and lower Farley beds. Analysis is frustrated at least in part by the failure to illustrate and describe any of the Cranky Corner specimens assigned by Archbold to *E. cordatum*, and the specimens could even prove to belong to a somewhat younger species, such as *ovale* or *glabula*. (See p. 199).

In his article on the Cranky Corner faunas, Archbold (2003) made much of the blunders by Waterhouse (1987b, p. 199) in referring some undoubted Permian faunas to Carboniferous. Mea culpa. I was totally wrong – well, reservations were offered, but wrong I was. However Archbold overlooked or ignored the correction in several following articles,

principally Waterhouse (2001, p. 11 etc.; 2002, pp. 189, 223), well before 2003, leading to the question: why did he bother? The mistake had already corrected by its author.

7. The species *Trigonotreta lyonsensis* Archbold & Thomas (1986a) is a markedly transverse species with four or five pairs of plicae and weakly prominent primary costae, as in *Koenigoria* Waterhouse, 2004, which is based on *Neospirifer neoaustralis* Archbold & Thomas, 1986a. The species *lyonsensis* is not typical *Trigonotreta*, having fewer pairs of plicae, nor is it represented as claimed in Pakistan (see Waterhouse 2004, pp. 174-175). It seems likely that the spiralia were transverse rather than postero-laterally oriented, a matter requiring confirmation.

8. *Bookeria* is an interesting genus, well represented in the Tiverton Formation of the north Bowen Basin in Queensland. It displays the features of other genera of Paucispinaurini in east Australia, but has only fine spines over the dorsal valve, whereas allied genera *Terrakea* Booker and *Paucispinauria* Waterhouse both have coarse as well as fine dorsal spines (Waterhouse 2015a, p. 119).

9. *Azygidium* Waterhouse, 1986 is an unusual marginiferid brachiopod that lacks a zygidium, which is a small projection at the hinge immediately in front of the basal part of the cardinal process. Briggs (1998, text-fig. 72A) misunderstood the morphology, and figured what seems to be a broken hinge to one side of the cardinal process as representing a zygidium, and referred the genus to synonymy of the paucispinaurian genus *Anemonaria* Cooper & Grant, 1975. The species *mitis* is certainly not *Anemonaria*, which belongs to a different subfamily and has large strut spines. Strut spines are completely absent from *Azygidium*, which is marginiferid rather than paucispinaurian.

10. The Dresden Limestone lies immediately above the Fairyland Formation with the *Echinalosia curtosa* Zone, and apparently followed it with minimal loss of time, and was followed in turn by the Elvinia Formation. These two latter formations were lumped by Fielding, Stephens & Holcombe (1997, Fig. 2) as the Buffel Formation of Wass (1965), though that was proposed for a massive unit which incorporated the Fairyland beds and overlying beds of the Pindari Formation, left out of the amended Buffel unit by Fielding et al. So their move defied recommendations of the International Code of Stratigraphic Nomenclature that it is better to rename units rather than drastically emend them (Salvador

1989). Critically, the amended Buffel Formation was shown by Fielding, Stephens & Holcombe (1997) as separated from the Fairyland beds by a gap in time and sediments, but that time-gap is against available evidence, and was not supported by any documentation. These authors claimed to be first to dismiss the reality of a proposed Grantleigh Trough, without acknowledging that Flood (1983) had already argued that the concept was in error.

11. Specimens from the Farley Formation that were described as *Tivertonia yarrolensis* [not Maxwell] by Archbold (1986a, p. 413) have been renamed *Svalbardia saeptata* by Waterhouse. The original material treated as type had been ascribed to *Lissochonetes yarrolensis* Maxwell, 1964, p. 35 from the Yarrol Formation of the Yarrol Basin. It includes some specimens that appear to be anoplid, and others, including the designated holotype, that could prove to belong to *Capillonia* Waterhouse, 1973, although preservation is not the best, and specimens are few in number (Waterhouse 2001, p. 14; 2015a, pp. 60, 61). Archbold (1986a) made Maxwell's species the type of a new genus *Tivertonia*, but it needs further study and demonstrable differences from *Capillonia* to be validated.

12. *Quadrospira* Archbold, 1997 was proposed for type species *Neospirifer plicatus* Archbold & Thomas, and includes several species such as *N. postplicatus* Archbold & Thomas, *Quadrospira woolagensis* Archbold and *Spirifer hardmani* Foord from Western Australia, with several species from further afield. *Aperispirifer crassicostatus* Waterhouse, 1983c from the uppermost Tiverton Formation of Queensland and *Notospirifer zealandicus* Zone of New Zealand is close in general shape (see Waterhouse 1964b, pl. 22, fig. 4-8), especially to *Q. foordi*, even though the species does have broader fold, weaker fewer plicae that fade anteriorly, and coarser costae. Posterior internal thickening is greater in the species from east Australasia than in species from Western Australia.

13. The interior of *Cracowspira* is not known and the genus might belong to either Fusispiriferidae or Georinakingiidae. The delthyrium in another transverse species, recorded as *Fusispirifer* B in Waterhouse (1987a, pl. 5, fig. 16, 17) from the Oxtrack Formation, has dental plates which join under the umbo, pointing to Georinakingiidae. The delthyrium in *Fusispirifer pauciplicus* Waterhouse, 1987a, later reidentified as *Transversaria* in Waterhouse (2004), is not fully open as in members of Georinakingiidae but closed (Waterhouse 1987a, pl. 5, fig. 15), possibly suggestive of a deeply placed and concave subdelthyrial plate (Waterhouse 2004, pp. 150, 151), as in Fusispiriferinae Waterhouse,

2004, though this needs to be checked by first-hand examination. This species comes from the Barfield and lower Flat Top Formations. *Fusispiriferinae* is a member of Spiriferidae, because it has a subdelthyrial connector plate (Waterhouse 2016), whereas *Georginakingia* lacks such a plate.

14. After articles by Hill (1950) and Maxwell (1954) that examined a few fossils from the Cattle Creek faunas, the Geological Survey of Queensland has made detailed field studies and fossil collections in the southwest Bowen Basin. But no updated macro-faunal studies have been published. Briggs (1998, p. 140) recorded, without providing photographic evidence, *Taeniothaerus subquadratus* (Morris) together with reported *Echinalosia preovalis* from the Cattle Creek Formation at GSQ Taroom core, and *Taeniothaerus* is found with *preovalis* in the upper Tiverton Formation, though the specific affinities need to be determined. Predominant *T. subquadratus* normally occurs at a level below that of *preovalis*. At Planet Warrinilla no 1 core, *Taeniothaerus subquadratus* was reported by Briggs (1998) with what he identified as *Acanthalosia domina* (probably *Maxwellosia*) in the mid-Cattle Creek Formation, which accords with what is known of the distribution elsewhere, especially in the Tiverton Formation.

15. Archbold (2000) matched the *Neilotreta occidentalis* Zone of Western Australia with the *Strophalosiaria concentrica* Zone of Tasmania. The Callytharra *Coronalosia irwinensis* Zone (*irwinensis* being initially identified as *Strophalosia* by Archbold 1986b) was matched by Archbold (2000) with the *Crassispinosella subcircularis* Zone of eastern Australia – with no species in common, and setting aside many of the species links between Callytharra and Tiverton faunas (Waterhouse 2015a, Table 8). Given that miscorrelation, remaining east Australian zones had to be shifted, and it is probably this miscorrelation that has resulted in the age data conveyed by ammonoid and other fossils and radiometric data being ignored by Briggs (1998) and Archbold (2000) for Permian correlations in eastern Australia. The *Bandoproductus macrospina* Zone was matched with the *Coronalosia jimbaensis* Zone (Aktastinian) of the Wooramel Group, even though *Bandoproductus* is absent, and none of the species found with *Bandoproductus* in eastern Australia approach Wooramel species. The “*Tomioptis strzeleckii* Zone” of eastern Australia was correlated with the *Echinalosia prideri* to *Sommeriella magna* Zones in Western Australia, and the rest of the Briggs’ 1998 biozones for eastern Australia were tabulated in Archbold (2000) by succession, regardless of affinities, and not dependent on any species or even genus distribution – the correlations are independent of the faunas. Briggs (1998, text-fig. 3-5), followed with

emendations by Archbold (eg. 2000, 2001a, b), based east Australian Permian stratigraphy and brachiopod zones on what was then understood for palynomorph correlations, and disregarded the brachiopod and molluscan evidence, even though Foster & Archbold (2001, pp. 176, 187) noted the need for caution over palynomorph zones. It seems advisable to assess the brachiopod-bivalve zones independently for their age implications, irrespective of other evidence, and then test them against the evidence from palynomorphs – one or other set of zones should not be suppressed. Respect should be applied – both ways. Briggs and Archbold seem to have believed that the Permian palynomorph zones extended synchronously across the continent. But at that time, there appeared to be some clear differences in those palynomorph zones which are found between the zones of *Pseudoreticulatispora confluens* APP1.22 and *Dulhuntysporites granulata* APP4.1 in east and Western Australia. The palynomorph succession of key species in east Australia, ideally, runs *confluens*, *pseudoreticulata*, *trisina*, *cicatricosus* and *sinuosus*, with further subdivisions based on *indica*, *baculata* and *villosus*. In Western Australia, when Briggs and Archbold were writing, there was deemed to be no *cicatricosus*, and the sequence was believed to run *confluens*, *pseudoreticulata*, *fusus*, *byroensis*, *trisina*, *sinuosus*, *villosus*. The palynomorph zones across the country from east to west, at least in those days, did not seem to be identical. It now seems clear that *confluens* lasted through two or three brachiopod zones in Western Australia, whereas in those days it was thought to have persisted for only part of one or two brachiopod zones in east Australia. This understanding has now changed, and palynomorphs now match the marine biozones more closely. The *Pseudoreticulatispora pseudoreticulata* Zone now is accepted, it appears, as concurrent across the continent: in those days it seemed to have ranged differently each side of the continent, according to macrofaunal evidence. Moreover, as shown by Archbold (2002, tables 1, 2, 4), the extent and nature of the palynomorph zones for other segments of Gondwana, in Africa and India, differed substantially from the sequences in Western and eastern Australia. Thus over the supercontinent of Gondwana, during Permian time, plant assemblages developed regional signatures, and it seemed that different floral provinces and palynomorph zones developed over east and west Australia during at least some intervals of Permian time, whereas somewhat similar brachiopod and bivalve marine assemblages developed widely in Australia, India, Himalaya, Afghanistan, Tibet and Oman. But whilst Archbold's correlations across Australia seem questionable, his suggested international

correlations for the sequences in Western Australia (Archbold 2000, Fig. 3) are close to those preferred in the present account.

16. A rich macrofauna is found in the Bijni tectonic unit in the western Himalaya near Jogira and Daggada (= Duggada) in the Pauri Garwhal, and described as Sakmarian by Waterhouse & Gupta (1978, 1979). *Svalbardia* and *Costatumulus* are found with *Anidanthia*, *Coronalosia* and *Neilotreta thomasi* (Waterhouse). *Costatumulus* is a highly characteristic productid, first described from east Australia, and widely found in east and south Asia. Two bivalves approach east Australian forms, *Etheripecten* aff. *tenuicollis* (Dana) and *Squamuliferipecten* (Waterhouse & Gupta 1978). Archbold & Singh (1993) verified the occurrences, which had been disputed by one would-be “authority” who claimed that no fossils acquired by V. J. Gupta had really come from the Himalaya. [That authority had never published descriptions of any Late Paleozoic fossils, other than *Linoproductus*, which Indian geologists have asserted (perhaps mischievously?) is a striated pebble, not a fossil brachiopod]. Archbold & Singh (1993) postulated a Tastubian (lower Sakmarian) age. The fauna is clearly older than the taeniothaerin fauna of Kashmir, and approaches the Garu fauna of the east Himalaya and the lower middle Tiverton *Magniplicatina undulata* faunas in the Tiverton Formation of the north Bowen Basin.

17. Specimens ascribed to *Tomioopsis ovulum* Waterhouse by Shi & Waterhouse (1996, pl. 28, fig. 6-8) come close to *Geothomasia postglabra* (Waterhouse, 1987a, pl. 7, fig. 16, 17, 19), found in the Dresden Formation near Cracow, southeast Bowen Basin. Both sets of specimens are distinctive amongst Ingelarellidae, with shallow or no sulcus posteriorly, well spaced short tabellae, and moderately short well-spaced adminicula. Type material of *Tomioopsis ovulum* Waterhouse (1971, p. 15, fig. 1-15, pl. 16, fig. 1-15, pl. 17, fig. 3, 6, 8, 11, 12, text-fig. 3-7) from the Kindle Formation of western Canada belongs to *Ambikella*, and is moderately close to though less plicate than *A. notoplicatus* (Archbold & Thomas, 1986b, p. 586, text-fig. 3.1-11) from the upper Lyons Group and basal Callytharra Formation in Western Australia.

18. In east Australia, palynomorph zones relate only broadly to the macro-faunal zones. None are securely tied to the macrofaunal biozones between and including those named after *Bookeria pollex* and *Ingelarella plica*. *Pseudoreticulatispora pseudoreticulata* is now regarded as characterizing the lower Rutherford Formation as APP2.1, and *Microbaculispora trisina* (APP2.2) embraces the rest of the

Rutherford Formation and lower Farley Formation, with the upper Farley beds, overlying Neath Sandstone and lower Greta Coal Measures typified by *Phaselisporites cicatricosus* (APP3.1) according to Smith et al. (2017, Fig. 12).

19. In Western Australia, the *Pseudoreticulatispora confluens* Zone APP1.22 is reported from the lower section of the Holmwood Shale in the Perth Basin (Backhouse 1993), and Mory & Backhouse (1997, p. 5) described Permian palynomorph Stage 2 in the lower Lyons Group (= *Lyonia lyoni* macrofaunal Zone) and in the upper Lyons Group (= *Neilotreta occidentalis* Zone). Studies indicate that the Callytharra Formation containing the *Coronalosia irwinensis* macrofaunal Zone has a succession of index palynomorphs (Mory & Backhouse 1997, Archbold & Hogeboom 2000). The *Pseudoreticulatispora pseudoreticulata* zone APP2.1 is found in the lower Callytharra Formation, above *P. confluens* of the upper Lyons Group, and is followed by the *Striatopodocarpites fusus* zone in the Ballythanna Sandstone Member, and then *Didecitriletes byroensis* zone in the upper part of this member.

The *Microbaculispora trisina* APP2.2 zone of the upper Rutherford and Farley Formations in the north Sydney Basin appeared in the uppermost Callytharra Formation and in the Irwin River Coal Measures of the Perth Basin, shown by Archbold & Hogeboom (2000, text-fig. 13) as involving the macrofaunal zones of *Sommeriella magna* and *Coronalosia jimbaensis*, above the *Coronalosia irwinensis* Zone in Western Australia. The Wooramel beds of the Carnarvon Basin and the Irwin River Coal Measures of the Perth Basin were shown in Smith et al. (2017) as belonging to the *Microbaculispora trisina* zone. Incomings and outgoings vary somewhat in different cores, reflecting the varying development of the members, to the extent that *trisina* and *byroensis* are also found above the Callytharra Formation, in the Cordalia Formation, as in core Burna 1 (Archbold & Hogeboom 2000), but occurrences were smoothed out in the reconstruction presented in Smith et al. (2017).

20. In Korsch et al. (2009), the SHRIMP radiometric sample was stated to have come from Pengelly Sandstone, a name applied to shelly sandstone at the base of the South Curra Limestone of Gympie, for which the fossils have been described by Waterhouse (2015b, p. 76ff). Earlier publications indicate that the sample for radiometric analysis came from older beds, within the upper Rammutt Formation (Sivell & Arnold 1999; Sivell & McCulloch 2001, p. 379), and more definitively, Mortimer (2007) stated that the sample came from the upper Nash level, still further below the South Curra Limestone. On that basis,

considerable doubt must be attached to the proposition that the radiometric sample came from what was treated as basal South Curra limestone by Runnegar & Ferguson (1969). It might even seem that the locality detail was shifted to accord with what was thought to be likely Kungurian rocks. But macro-fossils are few (Waterhouse 2015b), and so clarification of the actual locality would be desirable.

21. Mutch (1972, p. 39, Fig. 24) evaluated the thickness of the Takitimu Group as being well over 10,000m, made up of sediment, sills, lava flows and minor intrusives and dikes. An Australian authority declared such a thickness to be impossible. Not according to Mutch, who actually mapped the rocks.

22. According to Hogeboom, the *Microbaculispora trisina* palynomorph zone in Western Australia is followed by the *Praecolpatites sinuosus* zone, ranging through much of the Byro Group, as far as the *Svalbardia thomasi* macrofaunal Zone. The *Praecolpatites sinuosus* palynomorph zone is chiefly of Baigendzinian and Kungurian age in Western Australia. It could be of similar age, or in part older in east Australia. In accounts from late in the twentieth century, the *Phaeselisorites cicatricosus* zone, well represented in east Australia, was thought to be missing from Western Australia, and replaced by zones named after *Didecitriletes byroensis* and *Microbaculispora trisina* (Mory & Backhouse 1997, Archbold & Hogeboom 2000) but in Smith et al. (2017) the Byro Group was referred to the *Phaeselisorites cicatricosus* and *P. sinuosus* Zones of APP3.1 and 3.2.

23. The Greta Coal Measures display the entire *Praecolpatites sinuosus* APP3.2 zone, and the lower coal measures overlap with the upper *Phaeselisorites cicatricosus* (APP3.1) zone and uppermost Farley Formation in the Hunter Valley (Smith et al. 2017). At Cranky Corner, Balme & Foster (2003) reported the *Phaeselisorites cicatricosus* APP3.1 zone but no *Praecolpatites sinuosus* (APP3.2) zone in the Greta Coal Measures of the DM Tangorin DDH1 core through the Cranky Corner Basin, and noted the common concurrence of *Camptotriletes biornatus* Balme & Hennelly, first described from the Greta Coal Measures of the Sydney Basin.

24. It would be interesting to learn the exact age of the Yarunga Coal Measures from refined palynology. Although it may seem that they could be as young as Greta Coal Measures, Herbert (1972, Fig. 2) showed the Yarrunga Coal Measures lying below the Pebbley Beach Formation, and above the Tallong conglomerate, developed also below the Clyde Coal Measures, as at least partly confirmed in NSW core D.M. Callala D. D. H. 1, according to Runnegar (1979b). The Yarunga beds were shown in Smith et al.

(2017) as overlying the Wasp Head Formation and Clyde Coal Measures, within the *Pseudoreticulatispora pseudoreticulata* APP 2.1 palynomorph zone.

25. In the southwest Bowen Basin, beds of Reid's Dome have been assigned to *Microbaculispora trisina* APP2.2 and the upper beds together with most of the Cattle Creek Formation were assigned to the *Praecolpatites sinuosus* APP3.2 zone in the Sirius Mudstone, and in the Staircase Sandstone and the Collinsville Coal Measures of the north Bowen Basin (Smith et al. 2017). The Sirius Shale shares brachiopods of the *Echinalosia preovalis* - *Ingelarella plica* Zone with the upper Cattle Creek Formation, as well as upper Tiverton Formation in the north Bowen Basin. The *Microbaculispora villosa* APP3.3 zone is found in the lower Aldebaran Formation. Foster (1979) concluded that the upper Cattle Creek and lower Aldebaran beds could be correlated through palynofloras with the Blair Athol Coal Measures, which shared rare *Praecolpatites sinuosus* APP3.2 palynomorphs and even *Microbaculispora tentula*, which clearly persisted from very Early Permian. He corrected earlier reports in Rigby & Heckel (1977) and Foster (1977) of *P. sinuosus* well below these levels in the beds of Reids Dome and below the incoming of *Phaselisporites cicatricosus*, and challenged the report in Calver et al. (1984, Fig. 3) of a comparable distribution in Tasmania, entering above what was called Stage 3 ("APP 3.2") at the start of "stage 4" and well below *Phaselisporites cicatricosus*.

In the northern Bowen Basin, the Collinsville Coal Measures overlies the Lizzie Creek Volcanic Group, as shown in Smith et al. (2017), but the column in Smith et al. (2017) omits the Tiverton Formation, which is much thicker at 700m (Draper 2013, p. 378) than many of the slender formations carefully portrayed in their same table. Was it a lapse, or because of a failure to find, or examine the palynofloras? There may be parts of the stratigraphic column in which Collinsville Coal Measures appears to overlie Lizzie Creek Volcanic Group, but that is far from being the prevalent style of geological relationship. The Lizzie Creek Volcanic Group was shown in Smith et al. (2017) to involve lower *cicatricosus* APP3.1 at its top, whereas macrofaunas and stratigraphic position for the Lizzie Creek volcanics below the Tiverton Formation suggest a likely *confluens* APP1.22 or at most *pseudoreticulata* APP2.1 zone, at least in terms of the arrangement in New South Wales.

The positive aspects for the interval during which Greta Coal Measures accumulated involve the complete absence in east Australian macro-faunas so far as they are known of faunas developed in New

Zealand, with links to possible Baigendzinian conodonts, and also developed in Western Australia, where upper Artinskian (Baigendzinian) ammonoids are found. The identification of palynomorph zones APP3.2 (*sinuosus*) and APP 3.1 (*cicatricosus*) in the Greta Coal Measures helps explain the absence of these palynomorph zones from the south Sydney Basin, where there is no secure equivalent of the Greta Coal Measures, and also their absence from the southeast Bowen Basin, where the likely Greta equivalent is the largely non-marine Pindari Formation. It is a major failing of the study by Briggs (1998, Fig. 35) that his study failed to recognize this critical and undoubted gap in the succession of brachiopod faunas that corresponded with the Greta Coal Measures. In Western Australia, palynomorph zones APP3.2 and APP3.1 are present in the marine beds of the Byro Group. As well, the lower Byro Group is considered to incorporate the upper APP2.2 *Microbaculispora trisina* zone, according to Smith et al. (2017), in discord with the macro-faunal succession in the Sydney Basin, unless latitudinal and longitudinal parameters or inconsistent temporal controls are invoked.

The Byro Group is overlain by the Coolkilya and Mungadan beds with the *Microbaculispora villosa* APP3.3 zone according to Smith et al. (2017), as far as I can follow their table. The Coolkilya macrofauna indicates an age distinctly younger than that of the *Echinalosia preovalis* - *Ingelarella plica* Zone in Queensland and New Zealand, perhaps Kungurian and more likely Roadian, as against Aktastinian. The same *villosa* Zone APP3.3 is shown as incorporating the lower Aldebaran Sandstone and upper Collinsville Coal Measures in the Bowen Basin. And in the Sydney Basin, the *villosa* Zone incorporates the Snapper Point and Branxton Formations. On macro-faunal assessments, the east Australian faunas are slightly older than Coolkilya, as Kungurian rather than Roadian, and perhaps this is in error, or there has been time displacement across the continent. Disconcertingly out of phase with macro-faunal evidence, the Freitag Formation from the north Bowen Basin, which shares brachiopods with the Snapper Point, Wandrawandian and Branxton Formations, is shown in Smith et al. (2017) as belonging to a much younger *Dulhuntyispora parvithola* APP5 Zone. Which suggests that latitudinal control over floras and faunas should not be ignored.

26. The Pebley Beach Formation of the south Sydney Basin lies immediately below the Snapper Point Formation. It is shown in the palynological charts of Smith et al. (2017) as belonging to the *trisina* (APP2.2) and *pseudoreticulata* (APP2.1) zones, and separated by a substantial sedimentary gap from the

overlying Snapper Point Formation of the *Didecitriletes ericianus* APP 4.2 Zone, allocated in Smith et al. (2017) to the Wordian Stage. Yet macro-fossils show that the uppermost Pebbley Beach Formation is little older than the Snapper Point Formation. More information is needed about the age-data for the middle and lower Pebbley Beach Formation. Incomplete macrofossil data suggest that the middle part of the formation either belongs with the upper part (see pp. 64, 65), or was somewhat older, the uncertainty arising out of the fragmentary nature of the only available macro-fossils, which, to judge from the few *Eurydesma* fragments and possibly a more complete but now lost and unreliably sourced specimen, could well confirm the assessment in Fielding et al. (2008a, b) that the beds were correlative with the Sirius Mudstone Shale, within palynomorph *sinuosus* zone APP3.2. It remains uncertain whether the Pebbley Beach Formation is a single sedimentary unit as named, in which case it could all be as young as Kungurian, or whether there were substantial sedimentary breaks. I am not sure where the palynomorphs indicating *pseudoreticulata* APP 2.1 came from, and how they were related to the *trisina* palynomorphs, stated by Evans (1991) to have come from basal Pebbley Beach beds. Is there any possibility that *pseudoreticulata*, and even *trisina* were post-first entry data? After all, both forms persisted well beyond their first appearances and subsequent first appearances of later key forms, so that their occurrence does not necessarily pin down a zone or age, unless it is proven that they were first occurrences. The true age of the Pebbley Beach Formation thus remains a major unknown. The fossil localities at the base of the Pebbley Beach Formation in core D. M. Callala D. D. H. 1 may well have been the source of the ingelarellid species identified as *ovata* by McClung (1978). This species occurs in the *Magniplicatina undulata* and *Taeniothaerus subquadratus* Zones in the Bowen Basin, and is accompanied by *trisina* in the Sydney Basin But McClung gave no detail, so that the locality and identification remain unverified. But if it came from the base of what was called Pebbley Beach Formation in Runnegar (1979b), it suggests a possible – only possible - equivalence to the Tallong or Yadboro clastics.

27. D. J. C. Briggs borrowed the New Zealand material and has never returned it, which is particularly regrettable, because the specimens took a long time to find and collect. They represent the only fossil locality known for the Caravan Formation. The Briggs (1998, p. 207) treatment of the anidanthid is challenging. He lumped as one species specimens from the Roses Pride Formation (southeast Bowen

Basin) with “*Megousia*” *solita* from the Wandrawandian Formation (south Sydney Basin), specimens from the Queens Beach Member, Stephens Island, New Zealand, and specimens from the Caravan Formation of New Zealand. These localities involve specimens from the *Echinalosia preovalis* - *Ingelarella plica*, *Glendella dickinsi* and *Echinalosia discinia* Zones. Closer inspection shows significant differences between specimens from the various collections, as summarized in Waterhouse (2001, pp. 26, 27).

28. The Snapper Point Formation is assigned in articles on palynology to the Wordian Stage, and separated by a substantial pause in sedimentation from the Pebble Beach Formation (Smith et al. 2017). But the Snapper Point beds are intruded by monzonite, which has been dated as lower Kungurian in age by A. Nutman, as quoted in Shi et al. (2020). Kungurian rocks cannot intrude Wordian rocks. Therefore, if Nutman’s radiometric age is right, and it agrees with the macro-fossil interpretation, the international correlation shown in Smith et al. (2017) is wrong. An approximately correlative ammonoid was dated as Kungurian by Leonova (1998).

29. *Terrakea exmoorensis* was named and described by Dear (1971, p. 18, pl. 5, fig. 3-5) from the Moonlight beds, in the *Pseudostrothalosia blakei* Zone, of north Bowen Basin, with further less than informative material illustrated by Hill & Woods (1964) and Hill et al. (1972, pl. 5, fig. 9, 10). Specimens misidentified as *Terrakea brachythaera* [not Morris] in Waterhouse & Jell (1983, pl. 1, fig. 9, 11-18, pl. 2, fig. 1) from the same beds give a much better appreciation of the species. Clearly *Terrakea exmoorensis* precursed *Terrakea brachythaera-elongata-macrospina*, and was not a subspecies of *elongata* as supposed by Dear (1971) followed by Waterhouse & Jell (1983, pl. 1, fig. 10). *T. rhyllstonensis* was named and erected by Briggs (1998, p. 168, Fig. 83) from slightly older levels in the Elderslie and Snapper Point Formations. It would be most useful to be able to distinguish two species from these successive stratigraphic levels, but no clear means of distinction was provided by Briggs (1998) and he did not figure any *exmoorensis*. Therefore, since the two cannot be distinguished from the available description and figures, *rhyllstonensis* is regrettably treated as a junior synonym, as in Waterhouse (2001, p. 42). It is to be hoped that closer examination of *rhyllstonensis* will enable distinction, but this is not possible at present.

30. From a small Freitag fauna, Waterhouse (2001) reported, described and figured *Wyndhamia typica crassispina*, *Paucispinauria paucispinosa wardenensis*, *Tumulosulcus undulosus* (Campbell), and poorly

preserved and so provisional *Aperispirifer archboldi* Waterhouse. Bivalves *Intomodesma* and *Oblicarina* are recorded in this monograph (pp. 165-170). The species *undulosus* was first described from the lowermost Blenheim Formation (sensu McClung 1981) or upper Gebbie Formation of the northern Bowen Basin. The species also occurs in the lower Wandrawandian Formation of the south Sydney Basin. The material is not perfectly preserved, and also approaches a species of *Tumulosulcus* Waterhouse, described as *Ingelarella cessnockensis* McClung (1978, p. 49, pl. 10, fig. 4-15, 18, 19) from the Elderslie Formation of the north Sydney Basin. The Freitag Formation has yielded the widespread and long-lived palynomorph *Dulhuntyispora parvithola*, as well as a diverse ichthnofauna. The beds lie above upper Aldebaran with *parvithola* and below Ingelara Formation and are close in appearance to strata of the lower Pebbley Beach Formation in the south Sydney Basin according to Fielding et al. (2006, 2008b). In short, the macro-fauna pinpoints an age close to the one of the relatively early occurrences of the long-ranging *parvithola* in Queensland but pre- *parvithola* in New South Wales, just as also argued by Dickens (1989, p. 65).

31. *Ingelarella cessnockensis* McClung, 1978 from the Elderslie Formation of the north Sydney Basin is close in shape to *I. undulosa* Campbell from the basal Blenheim Formation or topmost Gebbie Formation in the north Bowen Basin. Shape and internal plates are much the same, but understanding of *cessnockensis* is incomplete, because only internal moulds were figured. These suggest a dorsal fold without median channel, and possibly a weak anterior median sulcal channel (McClung 1978, pl. 10, fig. 13), though this is not apparent in other figured specimens. In the original description of *I. undulosa* Campbell, 1961, a median sulcal swelling is strongly suggested, as in *Tumulosulcus* Waterhouse, 2015b, p. 170, but again, no external ventral valve was figured for *undulosa*. *Tumulosulcus*, based on type species *Ingelarella magna* Campbell, 1960, has a swelling rather than two subplicae within the sulcus, and the fold lacks a well formed channel. It is otherwise close to *Oviformia* Waterhouse, 2015b, type species *Spirifera (Brachythyris) oviformis* M'Coy, 1847, which has broad sulcus with anterior median swelling or even rib with two lateral ribs, but differs in the nature of its dorsal fold, which is deeply channelled. Elderslie specimens figured as *undulosa* by McClung (1978, pl. 8, fig. 1-3, 7) show the rounded dorsal fold and anterior sulcal swelling like that of *Tumulosulcus*, as in the original material. These taxa delineate lineages within a large number of short-lived and wide-ranging species of

Ingelarellidae, formerly lumped under the mantle of *Ingelarella* or even the early Carboniferous genus *Tomioopsis* Benediktova.

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8. THE IMPACT OF GLACIATION ON THE EARLY PERMIAN MACRO-FAUNAS FROM EAST AUSTRALASIA

Abstract

This article reviews the impact of climatic changes on marine macrofaunas during the Early Permian Period in east Australia. The first major interval of glaciation lasted for much of the Asselian Stage, and the second extended throughout the Kungurian to Capitanian Stages. The Lower Permian Sakmarian Stage was much warmer on the whole, apart from a brief cool episode at the start of the stage, whereas the basal Artinskian was warm, and was followed by more pervasive evidence for a cold episode of upper Lower Artinskian (Aktastinian) age. The overlying upper Artinskian (Baigendzinian) Substage was decidedly warm, estimated to have been subtropical by Loughnan (1973). Several major glacial episodes followed in the Middle Permian, starting during the Kungurian Stage at the top of the Early Permian.

INTRODUCTION

It is well established that marine biota reflect ecological conditions of their surrounds, involving not only salinity and availability of food, and substrate, ocean currents and wave action, but temperature, which in turn reflects paleolatitude, duration of sunlight, and gain or loss from solar radiation and other influences, that at times may have led to glaciation, and was a critical factor affecting food supply and the nature of the substrate. It was not that paleolatitudes changed under rapid and oscillating continental displacement, but that temperatures changed, under oscillating climate and ultimately reflective of the energy provided by the sun (Shi & Waterhouse 2010). Climate played a vital role in the distribution and succession of faunas (Spjeldnaes 1961, Williams 1969, Krassilov 1974), with a number of additional references summarized in Clapham & James (2008). These latter authors attempted to analyse the response of Permian brachiopods in east Australia to climatic change, based mainly on collections during a field trip, but their analysis largely though not entirely depended on faunal identifications barely up to the standard set by the first edition of the *Brachiopod Treatise* which appeared in 1965 (Moore, 1965), and confused the Early

Permian Dresden Formation with the Middle Permian Oxtrack Formation, so their analyses were somewhat astray. Stehli & Grant (1971) drew attention to the potential interplay between faunal diversity and paleolatitude for Permian faunas, and Waterhouse & Bonham-Carter (1972, 1975) analyzed the world-wide and time-controlled distribution of all then-known brachiopods at family level, to demonstrate the strong relationship between brachiopod faunas and their geographic location in the Permian Period, which in turn reflected a degree of temperature control. Some biota are obviously controlled in their distribution by paleolatitude and temperature, and are never found at high paleolatitudes, which strongly implies they could not tolerate low temperatures. Unfortunately for students of the Permian biota in east Australia, this has had a negative impact for faunal diversity in east Australia, such that conodonts and fusulines are completely absent – clearly because the sea was too cold for such life forms. On the other hand, many brachiopods as well as molluscs apart from ammonoids and nautiloids became well adapted to cool or even cold conditions, and diversified in their morphologies, so that shell-fish in the Early Permian of east Australia developed specialized adaptations to cold conditions and thereby helped signal the peculiar conditions which prevailed in east Australia. There have been conjectures from United States authorities that Australia like the rest of Gondwana became simply a haven for inferior species that had been driven into high paleolatitudes by burgeoning evolution of new and superior species in low latitudes, notably present in the United States. Those conjectures were somewhat ill-founded, to be heavily qualified by the realities of taxonomic studies, which show that certain groups flourished and expanded in high paleolatitudes, and even invaded the paleotropics during world-wide intervals of cooler climate. The focus of this article is to provide a simple and preliminary analysis of the evidence provided by marine faunas for temperature change throughout the early Permian rocks of east Australia. There are of course many different ways of searching for climate change and temperature shifts, as summarized in Shi & Waterhouse (2010), with greater focus on faunas in east Australia in Waterhouse & Shi (2010), but this article has a narrow focus devoted to a fresh approach on the problem.

METHODOLOGIES

Palynology

In focusing on the potential for interpreting environmental parameters from fossil brachiopods and molluscs, it is by no means intended to discount the value of other biota, and the relevance of sedimentology. Plants that inhabited the drylands endured great ranges in temperature, to which species and genera become well adapted and diversified, to the extent that, living or dead, they convey an enormous amount of data about their environment, including climate and temperature and rainfall. For biota that developed under shallow seas, conditions were more equable, and therefore reflective only of more marked and sustained changes in temperature, with much less impact from weather. A leading field for study on Permian of east Australia concerns palynomorphs, derived from plants, and therefore potentially indicative of climate and climate change, in the way achieved by Cenozoic and Pleistocene-Anthropocene palynologists. At present, palynomorph studies in east Australia have concentrated on erecting a scheme for correlation of relatively long-lasting intervals of rock throughout east Australia. But that does not fully reflect on the potential value of palynomorphs. Resolution of the relationship between palynomorphs and their parental plants, akin to the understanding achieved extensively for the Cenozoic-Tertiary and Pleistocene would help solve relations and sequences of different rocks (especially including coal beds) at present lumped together in one unit, and would help enormously in the clarification of sequential changes to climate.

Sedimentology

Fielding et al. (2008a, b) offered a model of climatic change based on the nature of rocks, an entirely commendable and practical approach, although there appears to have been some misinformation over correlation in some instances. But the overviews in Fielding et al. (2008a, b) provide very few observations or detail on rock type, other than for the Pebley Beach Formation of the south Sydney Basin and Cattle Creek and Freitag beds in the southwest Bowen Basin. In the present survey, the likely changes in temperature are traced for the entire stratigraphic column throughout the Early Permian of eastern Australia by analysing the changes in diversity of faunas. The fossil record has some advantages in signalling climatic change, because the marine fossils are preserved in sediments deposited some distance

from shore, whereas palpably glacial rock such as tillite tends to be best developed in terrestrial and near-shore marine conditions, where it was highly vulnerable to later erosion. The sedimentological signals for climate interference were diminished in deeper waters, though more likely to be preserved, and contemporaneous biota are much more likely to be well preserved. However, knowledge of the macro-fossil record is not ideal for the Permian of east Australia, partly because of gaps in the record, and more pervasively, gaps in the study of macrofauna (see herein, pp. 183, 184). In that regard, palynomorphs have the advantage, but their delicacy ensures a loss of preservation in coarse or even lightly metamorphosed rocks.

Macro-fossils

It is suggested, following Krassilov (1974, 1975) and Waterhouse (eg. 1964a, 1979) that the diversity changes and the very nature of the fossil faunas reflect climatic change that may have been world-wide, just as Pleistocene changes to climate were world-wide, not to mention current climate change. If these changes can be firmly associated with the faunal successions in world stratotypes for Permian chronology, then geologists of east Australia need not rue the absence of direct fossil links with world stratotypes. That remains a project for the future, with the possibility of expanding the techniques elaborated in Waterhouse & Bonham-Carter (1975) for world-wide and sequential analysis of faunal content. Mere counting of species and genera will not suffice, any more than the application of oversimplistic metrics devised for industrial purposes: the nature and affinities of each genus matters, and there are taxa which even as solitary forms, such as the brachiopod *Lyttonia* or bivalve *Eurydesma*, convey powerful information on climate and distribution. Surveys as in Clapham et al. (2008) that have attempted to elucidate diversity records by deleting stations that yield only one or two occurrences (so-called singletons) are revealing a preference for oversimplifying the complexity of biological realities.

Data for macro-fossils from the Cisuralian of the east Australian Permian is of uneven merit, and there is little point in analysing mere fossil lists, which unfortunately have been treated by some as substitutes for full systematic description. Illustrations and descriptions are necessary to allow verification, and permit updating of generic and specific assignments, short of re-examining specimens in institutions, which will only result in yet

another list, unless there is published systematic documentation. One of the revealing aspects pertinent to east Australian Permian studies is to see how accurate fossil lists have been when the author ventures into an occasional description of species and genera. Publication is a major reason to take away the need for first hand examination, and even so, the reported fossils may require further scrutiny, especially since systematic classification and morphological descriptions are becoming increasingly refined. Because only some of the fossils have ever been described, and updated, present classification must be incomplete and amenable to improvement, and therefore open to change, provided advances are still being made.

A simple method of calibrating the influence of temperature

From the fossil collections of east Australia, as substantiated by systematic descriptions, illustrations and publications, it is evident that a basic faunal range is displayed at most stations, involving species and genera classed as Streptorhynchinae, Rugosochonetidae (*Svalbardia*, *Capillonia*), Taeniothaerinae, Echinalosiidae, Paucispinauriidae, Plekonellinae, Ingelarellidae, Notospiriferidae, Trigonotretidae, Georinakingiidae, Pennospiriferidae, Permasyrinxinae, Dielasmidae and Gillediidae in fourteen family groups that are widely pervasive and often dominant in Permian faunas of east Australia. [I retain reservations about *Capillonia*, which tends to faunas of somewhat higher diversity, and at best lies very close to being set aside]. They are grouped under the heading EAD, standing for east Australian dominants. It needs to be understood that these family groups are not necessarily confined to east Australia. Some genera are more typical of east Australia, whereas other genera in one family group ranged widely over the globe – such as *Magniplicatina* in Paucispinauriidae, for instance. Stress on subfamilies and families recognizes that genera and generic strands were evolving locally in east Australia, and that mere number of genera does not suffice on its own to signal climatic change, given the likelihood of other ecological parameters, and evaluation is best reinforced by having a number of collections from various lithologies. Stations and biozones that display genera limited to this narrow range of EAD family groups are considered to have signified cool to cold-water, well adapted to living in high paleolatitudes typical of the east Australian Permian. Zones that have yielded only some EAD genera, and have no non-EAD genera are open to at least two different interpretations. They might be

considered to indicate insufficient sampling, an approach favoured by Stehli & Grant (1971), who purported to construct world-relevance from only one sampled station in the Canadian Arctic. Many of the east Australasian zones are represented by twenty, thirty and even more stations for only one of the several to many sections. Insufficient sampling applies still to some zones, unavoidably, but not in most cases. Even for some of the well sampled zones, for one reason or another, the range of genera was truly limited, either by substrate, or temperature, or other factors. The Oxtrack Formation in the southeast Bowen Basin has few EAD and almost no exceptional genera. I sampled many stations along its outcrop, and found nothing untoward – the fossils throughout were always the same. Fossil localities and biozones that have additional genera, not normally found in east Australia, are likely to be signifying conditions closer to those prevailing in nearby lower paleolatitudes, such as in Western Australia, Timor and south Asia, where those same genera are found. As well, some genera in parts of the Bowen Basin were remarkably persistent, as if reflecting elements within a population that survived, or flourished locally, despite vicissitudes of climate, substrate and competition. In addition, a few genera were particularly characteristic of east Australia, but appeared only at intervals. *Costatumulus* is a good example, belonging to Auriculispinae, and *Biconvexiella* and *Attenuocurvus* of Attenuocurviniae made rare entries in faunas of somewhat higher diversity. These are not assessed as EAD constituents.

In tables accompanying this text, the number of family groups counted as East Australian Dominants (EAD) is divided into the number of genera present that do not fall within the EAD category, and therefore indicate exceptional conditions, involving invasion by genera normally found at lower paleolatitudes. That assumption provides a first approximation to conditions prevailing during the accumulation of a particular zone. An overall chart (Fig. 1) is constructed from the values estimated for the type sections of each macrofaunal biozone, and a further diagram is constructed to suggest the shifting growth and decline of climatic zones across a hemisphere (Fig. 2), which is based on an interpretation of Fig. 1. For some zones, especially those rated as very cold – glacial – the values are the same whether measured for the Bowen Basin (Glendoo Member) or Sydney Basin (upper Pebbley Beach Formation). For other zones, the Bowen Basin tends to have more diverse faunas than those of the Sydney Basin. And the Gympie-New Zealand Highbury and Brook Street volcanic

arc yields higher diversity again, reflective of its offshore position and probably greater accessibility to faunas migrating from further afield.

EARLIEST PERMIAN OR LATEST CARBONIFEROUS

In Tasmania, Clarke (1992, p. 5) has described a Hellyeran Stage, characterized by the Stage 1 *Potonieisporites* microflora of Truswell (1978) as found in glaciomixite widely developed in the Wynyard Formation and other Tasmanian units. This corresponds with the *Protohaploxipinus* spp. palynomorph zone APP1.1 shown in Smith et al. (2017). No macrofauna has been described. Overlying massive diamictites and various glaciogene sediments with palynomorphs belonging to *Pseudoreticulatispora tentula* APP1.21 zone also point to widespread glaciation (Dickins 1996), as described for the Youlambie Conglomerate of the Cania area in southeast Queensland by Dear et al. (1971) and the Hastings Block of New South Wales by Roberts et al. (1991), also recorded as Youdale B in Fielding et al. (2008b, p. 135). These are treated as basal Permian. According to Fielding et al. (2008b, Fig. 1), there is a conspicuous lack of palynomorph data for Carboniferous rocks, but they depicted the Late Carboniferous, from Moscovian to Gzhelian, as non-glacial, apparently at odds with the Tasmanian record, and partly at odds with Late Carboniferous (Gzhelian) rocks in northern Canada which form a number of cyclothems (Waterhouse 2018), suggestive of glaciation elsewhere, presumably in Gondwana, including Australia. In South Africa, Stephenson (2009) asserted that *Pseudoreticulatispora confluens* was of Late Carboniferous age, based on radiometric dating, and this palynomorph is widely found in sediments of east Australia. The same form has been identified in Argentina with Late Carboniferous brachiopods (Waterhouse 2015a, p. 42), which are a little older than *concentrica*. Uncertainty stems from the failure to provide as yet adequate studies of the Pennsylvanian macro-faunas of east Australia, and from the setting aside of any attempt to relate those faunas to the world standard in Russia, as summarized for instance in Davydov et al. (2004): astonishingly the view has been expressed that preference would lie for correlations with western Europe (see Fielding et al. 2008b, p. 132; Draper 2013). That may be understandable for palynomorph studies, but has failed for macrofaunas, and reflects on the inability to cope with improvements to the world international system, and specifically the emphasis on studies in

the Russian language, demanding a degree of familiarity with that language, which appears to have been a factor behind attempts to deprecate the relevance of the International Standard to Australian faunas.. Substantial faunas collected from the Yarrol Basin by the Geological Survey of Queensland offer good prospects, but have still not been assessed in modern terms.

CISURALIAN SERIES

International standards for the Cisuralian Series are found in the Urals and Kazakhstan, and currently defined on the basis of conodonts, with substantial input from fusulines, ammonoids and brachiopods. But east Australia lacks fusulines and conodonts, and its brachiopods and palynomorphs differ generically and specifically from most of those in world stratotypes. The aspirations for correlation through use of macro-fossils therefore depends on three lines of evidence, the occasional ammonoid found in local successions, the faunal link through mainly brachiopods and molluscs with other Gondwanan sequences that are better dated through the presence of ammonoids, fusulines or conodonts, and the climatic similarity to these and other sequences signalled by diversity and sedimentary studies, world-wide.

ASSELIAN STAGE

***Strophalosiaria concentrica* Zone, *Crassispinosella subcircularis* Zone, *Unicostatina crassa* Subzone**

These zones are described on pp. 194-199. Sediments deposited during this interval in east Australia have long been recognized as betokening glacial conditions. The zones of *concentrica* (= APP2.1) and *subcircularis* (=APP2.2) each have a miserable handful of brachiopod species, classed as Strophalosiidae, Ingelarellidae, Notospiriferidae, Trigonotretidae, Georinakingiidae and Syringothyridae (Permasyrinxinae). The overlying *crassa* Subzone sees these few taxa joined by *Unicostatina*, also classed in Trigonotretoidea. In the DM Tangorin DDH1 core in the Cranky Corner Basin, Archbold (2003, p. 157) recorded brachiopods now recognized as *Ambikella elongata* (McClung & Armstrong) and *Neilotreta tangorini* (Archbold) only in the Beckers Formation, joined by *Unicostatina crassa* in the Cranky Corner Formation. Conditions were very cold, as shown by the nature of the rocks, and reinforced by the nature of the fossils, and were only replicated later throughout the

Permian Period in the early Kungurian Stage. A few more bivalves, dominated by *Eurydesma* and with common *Pyramus* and *Megadesmus*, as well as gastropods were present in the faunas of Cranky Corner, apparently more at home. But Archbold's correlations seem questionable, to judge from the palynomorph record (p. 199) and several questionable bivalve identifications.

A greater diversity of macro-fossils is found at Gympie, on the off-shore volcanic arc, which was further from the ice-sheets, and enjoyed better access to world-faunas, being part of the volcanic arc complex that extended from the Tethys through Indonesia and New Caledonia (Waterhouse 1987b). Given that such conditions prevailed widely across Gondwana, with faunas closely related to those of east Australia, it is clear that massive ice-sheets were developed during the Asselian Stage at the base of the Permian Period.

Macrofaunal zone	Number of non EAD genera A	Number of EAD groups B	Ratio A/B
<i>macrospina</i>	5	6	0.8
<i>crassa</i> subzone	0	6	0
<i>subcircularis</i>	0	5	0
<i>concentrica</i>	0	5	0

Table 1. Changes in brachiopod diversity for the Asselian Stage. Prime values from the Tasmania and Gympie.

A warm and interglacial phase: the *Bandoproductus macrospina* Zone of upper Asselian age

A marked increase in faunal diversity occurred with the onset of the *Bandoproductus macrospina* Zone in east Australia, to signal considerable warming during in the late Asselian Stage. *Bandoproductus* is found in the north Sydney Basin (Hunter Valley) and scattered over

New England, with occurrences also in the Yarrol Basin and at Gympie, where faunas are well represented. In the upper Rammutt Formation of the Gympie region, thirteen brachiopod species and genera are found, well in excess of the number found in the underlying zones, although it is true that the region was likely to have been further from the ice-sheets. The fossils involved six genera in families common to the biome that occupied east Australia, but also included genera regarded from their world-wide distribution to have been comparatively warm-water, of temperate rather than high paleolatitudes as a rule, such as *Bandoproductus*, *Stenosisma*, *Attenuocurvus* and *Martinia*, with *Hoskingia* normally found in Western Australia and southeast Asia, rather than eastern Australia.

Bandoproductus is widely represented further afield over Gondwana, in the last phases of major glaciation, and was a close ally of *Lyonia* in Western Australia. The age implied by Smith et al. (2017) appears to be mid-Artinskian, but the genus is found most widely and consistently in faunas independently dated as upper Asselian in age by various authorities beyond the Australian hegemony. *Bandoproductus* is not known in Tasmania,

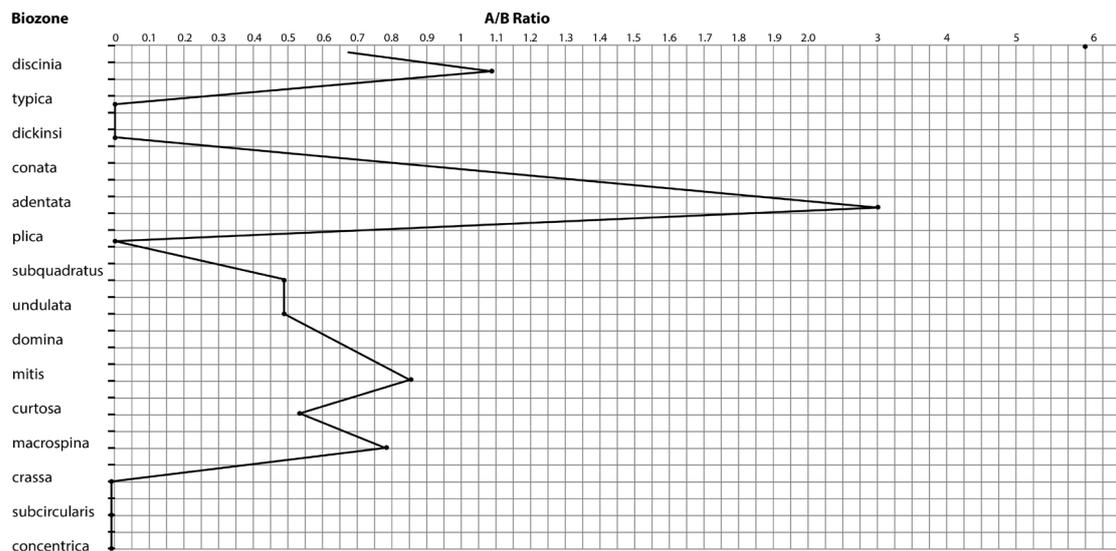


Fig. 1. Line graph plotting the changes in A/B ratios (standing for number of non-EAD family groups divided by the number of EAD family groups) through the successive biozones of the marine Permian of east Australia. The lowest score lies to the left, and progressive increases in the A/B ratio to the right are assumed to indicate increasingly warm temperatures. Biozones are listed in the left-hand column.

perhaps because the sea-floor had risen under isostatic adjustment due to loss of ice, leading to the deposition of the “Freshwater series” and Faulkner Group. Nor has the genus been found in the Wasp Head Formation of the south Sydney Basin, where the Clyde Coal Measures may have followed the Wasp Head

Bandoproductus is not known in Tasmania, perhaps because the sea-floor had risen under isostatic adjustment due to loss of ice, leading to the deposition of the “Freshwater series” and Faulkner Group. Nor has the genus been found in the Wasp Head Formation of the south Sydney Basin, where the Clyde Coal Measures may have followed the Wasp Head Formation, as discussed further on pp. 68, 69, and may have formed in a warm climatic interval, quite possibly contemporaneous with the *Bandoproductus* marine beds. The Clyde Coal Measures were evaluated as representing an interglacial phase by Fielding et al. (2008b), but those authors also included the upper Wasp Head beds, which seems unlikely because they contain fossils allied to those of the *Strophalosiaria subcircularis* Zone, best represented in Tasmania.

MIDDLE CISURALIAN SERIES

SAKMARIAN AND LOWER ARTINSKIAN (AKTASTINIAN) STAGES

Echinalosia curtosa Zone, *Notostrophia costellata* Zone with *Azygidium mitis* and

Acanthalosia domina Subzones, *Magniplicatina undulata*, *Taeniothaerus*

subquadratus and *Echinalosia preovalis* - *Ingelarella plica* Zones

Throughout Sakmarian time, faunas of the east Australian Permian were far more diverse and therefore different from those of the Asselian Stage, as argued also by Dickins (1985), basically building on the level of diversity established during the *Bandoproductus macrospina* Zone. If as claimed by Fielding et al. (2008a, b), ice sheets prevailed during that time, they were far less aggressive, and climate less severe compared with early Permian conditions. To be cynical, one might as well believe in warm ice, but realistically, perhaps it was wet ice, that is melting ice. Tillite, glendonite, and rafted clasts are much less evident than in underlying sediments. On the whole, the Sakmarian and Aktastinian brachiopods and molluscs from east Australia and New Zealand indicate cool rather than cold conditions, not nearly as severe as those prevailing during all but late Asselian time, because the faunal

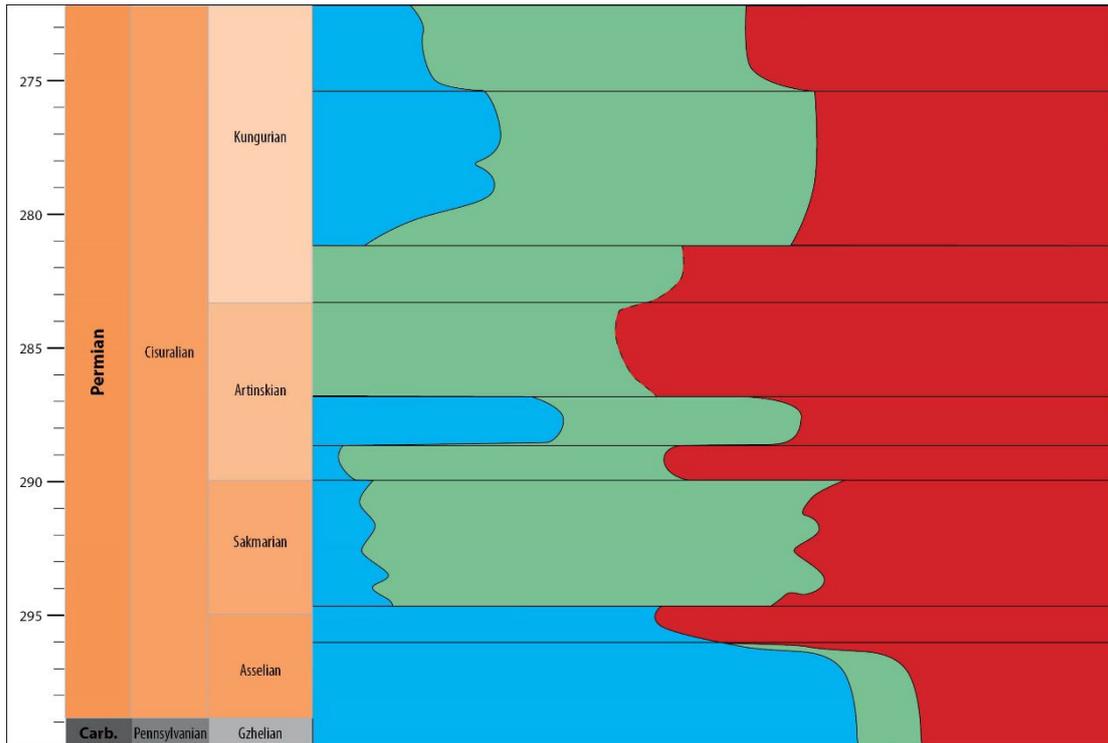


Fig. 2. Interpretation of climatic change based on shifts in faunal distributions of tropical, temperate and glacial climatic attributes, judged principally from evidence for macro-faunal changes throughout the southern hemisphere for the Early Permian Cisuralian Series, blue equivalent to conditions of severe cold, the red to tropical and subtropical conditions, with intervening paleotemperate (green) realm and biome. For simplicity Tasmania has been placed at the extreme left, perhaps at 60° S, perhaps further south, whilst the extreme right represents tropical latitudes. Time control centres chiefly on the biozonation for east Australia, reinforced by the New Zealand record, with considerable input from the rest of Gondwana.

diversity increased, especially amongst brachiopods, although it was still cool enough to allow the presence of *Eurydesma*, one of the most reliable of indices for low temperatures. A number of new genera entered the succession, including *Pseudostrothalosia* and *Acanthalosia*, as well as large aulostegids, and linoproductoids such as *Terrakea* and allies such as *Bookeria*, and *Magniplicatina*. *Trigonotreta* was joined by species of the allied genus *Grantonia* and reinforced by aperispiriferin genera *Aperispirifer* and *Koenigoria*, genera provisionally though questionably counted as Trigonoretidae (see pp. 25, 26). Georinakingiid genera *Sulcipleca* and *Unicostatina* flourished. The similarity to Gondwana faunas from further afield diminished, indicating warmer temperatures and shrinkage of ice

sheets from much of Gondwana. That the “Glacial phase 2” of Fielding et al. (2008a, b) should be regarded as marking an interval of extensive ice-sheets like those of the Asselian is regarded as incorrect. There was only a moderately cool episode at the start (*Echinalosia curtosa* Zone) and a colder one at the end (*Echinalosia preovalis* - *Ingelarella plica* Zone). For the rest of the time, conditions were stable and cool, but warmer than the *Echinalosia curtosa* Zone, and the one cold episode was short-lived.

Zonal succession

Proceeding up the column from the *Bandoproductus macrospina* Zone, the faunas from the *Echinalosia curtosa* Zone at the base of the *Bookeria pollex* Superzone in the southeast Bowen Basin are of modest diversity. The locally predominant family groups are well represented with nine EAD. There are six non-EAD genera, including ?*Notostrophia*, *Svalbardia*, *Lipanteris*, *Schuchertella*, *Cleiothyridina* and *Linoproductus*. The northern Bowen Basin was even more markedly east Australian, with only *Costatumulus* of Auriculispiniinae outstanding – and that as a genus prominent in faunas of this age in east Australia. Faunas of this biozone were less diverse than those of the underlying *Bandoproductus* zone, without being as reduced as those of earlier Asselian faunozones, nor as reduced in some of the following zones. In the southeast Bowen Basin, the *Azygidium mitis* Subzone of the lower Dresden Formation was moderately rich in basic predominants, with a reduced number of east Australian dominants (eight out of fourteen), but saw the entry of *Azygidium*, with links to paleotropical Marginiferidae. *Plekonina*, which is an unusual local evolute, and *Cleiothyridina*, with a possible but rare and indeterminate member of Attenuocurvinae, strongly indicate warmer waters through greater diversity. The overlying *Acanthalosia domina* Subzone was relatively cooler, because it displayed a substantially east Australian assemblage (nine of fourteen EAD family groups), with an unfigured and exceptional shell described as overtoniid, perhaps implying the Australia genus *Lethamia*, but poorly preserved. Diversity increased markedly during the *Magniplicatina undulata* Zone. In addition to all of the basic east Australian members, *Costatumulus*, *Biconvexiella* and *Pustulospirifer* appeared in the northern Bowen Basin, genera not unknown in other Australian faunas, but relatively rare. This zone in the Elvinia Formation of the southeast Bowen Basin was even more diverse, with *Orbiculoidea*, ?*Arctitreta*, *Costatumulus*, *Coledium* and *Composita*, and a slight fall-off in

local dominants (nine of fourteen EAD), so that the ratio is somewhat higher at 1.0 than the underlying *Acanthalosia domina* Subzone, and arguably preferable because it is in the same southeast Bowen Basin. For the *Taeniothaerus subquadratus* Zone, all the usual EAD dominants were present in the north Bowen Basin, including *Notostrophia*, *Taeniothaeris*, *Lipanteris*, and *Pustulospiriferina*, and an unusual entry from the paleotropics in *Eremithyris*, as well as *Costatumulus*. The ratio is the same as that for the underlying zone in the northern Bowen Basin, and less than that of the southeast Bowen Basin, reflecting local conditions and local species distribution. Both zones show a flourishing fauna with various communities dominated variously by different Productida and Spiriferida.

Macrofaunal zone	Number of non EAD genera A	Number of EAD groups B	Ratio A/B
<i>conata</i> ⁺	5	3	1.7
<i>adentata</i> ⁺	3	1	3
<i>preovalis-plica</i> [*]	3	10	0.3
<i>preovalis-plica</i>	0	9	0
<i>subquadratus</i>	6	11	0.5
<i>undulata</i>	6	13	0.5
<i>undulata</i> [*]	9	9	1.0
<i>domina</i> [*]	4	6	0.66
<i>mitis</i> [*]	6	7	0.87
<i>curtosa</i> [*]	6	9	0.55

Table 2. Changes in brachiopod diversity for the Sakmarian and Artinskian Stages. Prime values from the northern Bowen Basin, southeast Bowen Basin (asterisked) and New Zealand⁺.

In summary, this interval of Sakmarian age witnessed the development of comparatively prolific faunas, having adapted to post-glacial and warmer conditions that were probably cool but far from severe, and to limited extent shared with other regions of

Gondwana, notably Western Australia and south Asia, where faunas were more diverse. Then a sharp reversion occurred back to somewhat cold conditions, in the *Echinalosia preovalidis* - *Ingelarella plica* Zone, which apparently coincides with the cold-water sediments of the Cattle Creek and possibly lower Pebbly Beach rocks (Fielding et al. 2006), though the age of the latter is still in need of consolidation. In the north Bowen Basin, the fauna was overwhelmingly cold, with predominants only, and no genus in any way exceptional. In the better sampled Roses Pride Formation of the southeast Bowen Basin, predominants make up most of the faunas, but include *Megasteges* and an exceptional genus *Cracowspira*, a genus that requires further clarification, because it is related either to Fusingiriferinae so prominent in Western Australia and South Asia, or as would seem more likely, Georinakingiidae, an east Australian family linked to Trigonotretoidea, as a member of the EAD family groups.

But it is the off-shore volcanic arc that is most interesting, to underline the potential for exceptionality, and the need for close and careful collecting. There are two distinct faunas. The lower *Notostrophia zealandicus* Zone in southern New Zealand shares species with the *Ingelarella plica* Zone of east Australia, numbering only six EAD, but has several exceptional species and genera, including *Rhipidomella*, linoproductoid (possibly *Bandoproductus*), *Pugnoides* and *Psilocamara*, not found anywhere in east Australia, though found in subtropical or paleotropical faunas of lower paleolatitudes. In addition, a chonetid, *?Bandoproductus*, *Martinia* and *Pustuloplica* were present as in only some east Australian biozones which displayed warmer-water affinities. This fauna is highly unusual, unmatched elsewhere in New Zealand or anywhere in east Australia, and continued the upward diversity trend from that of the *Taeniothaerus subquadratus* Zone. Whether it signified a world-wide warming, or the result of local warming due an ocean current, remains uncertain (see pp. 216-218). Above lies what one expect from the Australian record, as a well exposed, but extremely depauperate zone, the *Notostrophia homeri* Zone, with all members typical of the east Australian realm, indicative of very low temperatures, and shared with the *Echinalosia preovalidis* - *Ingelarella plica* Zone in Queensland. The *homeri* faunas are found in the Takitimu Mountains (Waterhouse 1964b, 1982) and the Skippers Range (Begg & Ballard 1991) of New Zealand. The latter area includes *Eurydesma*, the only occurrence known in

New Zealand, and the *homeri* fauna clearly indicates a cold spasm, in no way caused by substrate which is identical with that of the underlying subzone.

For these two zones, it is to be wished that successions in New South Wales and Tasmania could be examined more closely, and described, in order to see if there is any suggestion of such a fauna below the *Echinalosia preovalis* fauna.

Did this Sakmarian-Aktastinian association of rocks and faunas represent a separate and full-blown glacial phase? The claim by Fielding et al. (2008a) that the Pebbley Beach Formation of the south Sydney Basin constituted a separate phase, belonging to Glacial episode 2 requires some adjustment. The uppermost part of the Pebbley Beach Formation is Kungurian and belongs with the overlying major glacial interval (see pp. 60, 66). The underlying glacial beds are of uncertain age, and have yielded very few macro-fossils, belonging mostly to *Eurydesma*, and offering some but uncertain support for the claim by Fielding et al. (2008a, b) that the beds matched those of the upper Cattle Creek Formation in southwest Queensland, as discussed on p. 66. The assurance conveyed by Fielding et al. (2008a, b) that fossils were numerous and well known is grossly incorrect. The upper Cattle Creek faunas belong to the *Echinalosia preovalis* - *Ingelarella plica* Zone, as in the Sirius Shale of the Springsure shelf, so that the observation in Fielding et al. (2008b) would fit very well with the cold climate indicated by fossils of the *Echinalosia preovalis* - *Ingelarella plica* Zone in the Bowen Basin and correlative *Notostrophia homeri* Zone (which also has *plica*) of New Zealand. The faunas are considered to be of Aktastinian (lower Artinskian) age. They certainly do not betoken an entire Sakmarian Stage, but appear to indicate a comparatively short-lived glacial phase, much shorter than that which prevailed throughout much of the late Carboniferous and early to middle Asselian Stage. The lower and middle Pebbley Beach beds did not constitute a long lasting major glacial event comparable to that of the lower and middle Asselian Stage.

BAIGENDZINIAN SUBSTAGE, UPPER ARTINSKIAN STAGE

***Spinomartinia adentata* and *Echinalosia conata* Zones**

No marine faunas are found for this substage in east Australia, but two marine biozones are developed in New Zealand, and these are matched with the Greta Coal Measures of the

north Sydney Basin. The assessment by Loughnan (1973) that the Greta Coal Measures were formed during a subtropical climate has never been refuted, and the marine faunas of Western Australia and New Zealand that accumulated at the same time support his thesis. The sedimentary conditions for the New Zealand faunas were unusual, because the beds were unusually thick, accumulated as fore-set beds on the flank of an active volcanic arc, so that sea-floor conditions for habitation were far from suitable, and rather few specimens have been collected. Nonetheless, the specimens that have been found strongly indicate that they were exceptional for an east Australasian setting, and include a number of genera more characteristic of lower paleolatitudes. From the *Spinomartinia adentata* Zone in New Zealand, only four genera are known, a poorly preserved shell deemed, perhaps unreliably, to be trigonotretid, typical of east Australian conditions (ie. one EAD) and three less usual genera, *Psilocamara*, aulostegid and *Spinomartinia*, as immigrants from warmer waters. From the overlying *Echinalosia conata* Zone, only eight brachiopod genera are known. Three point to normal east Australian conditions (*Echinalosia*, *Aperispirifer* and *Notospirifer*, making up three EAD), and others are exceptional, involving an aulostegid, *Taeniothaerus*, *Martinia*, *Attenuocurvus* and *Grebneffia*. *Taeniothaerus* is of special interest – the genus was well distributed through Sakmarian faunas and diminished in early Artinskian, and which witnessed its last appearance in east Australia. But it is present in New Zealand in the upper Artinskian, as in the Byro Group of Western Australia. *Echinalosia*, aulostegid and *Taeniothaerus* resemble species from Western Australia, and *Attenuocurvus* is found only in relatively warm waters with comparatively high diversity, as a rule. *Grebneffia* belongs to Tribe Dielasmini typical of tropical, subtropical and warm temperate regions rather than the Tribe Fletcherithrini common in east Australia and New Zealand.

The lower Aldebaran Sandstone above the Sirius Shale is non-marine, or largely non-marine, and in sedimentological terms, could be equivalent to the *Echinalosia preovalis* - *Ingelarella plica* Zone of the north and southeast Bowen Basin or be slightly younger and correlative with the Collinsville Coal Measures, and the Greta Coal Measures of the north Sydney Basin: the beds have been placed in the *Microbaculispora villosa* APP3.3 zone. The clearest sign of an interglacial episode is provided by the Blair Athol Coal Measures, west of the Bowen Basin (Foster 1975), through the presence of luxuriant coal measures. Of course,

terrestrial sediment could still have formed in a warm climatic interval, but currently palynomorph experts have not differentiated between warm and cold climatic episodes.

The brachiopods from correlative levels in Western Australia, as extensively monographed by N. W. Archbold, and summarized in Archbold (1993), are of high diversity, with few ties to east Australia, and approach faunas from southeast and south Asia.

THE TOP OF THE CISURALIAN SERIES

Glendella dickinsi, *Wyndhamia typica*, *Echinalosia discinia* Zones

Overall, the Kungurian to Capitanian Stages, or more precisely for east Australia, the *Glendella dickinsi* to *Ingelarella costata* Zones, are judged to represent cool to cold conditions, interspersed with warmer episodes. Apart from the early Kungurian Stage, conditions for biota appear to have been more favourable for marine life than in the earliest Permian, as represented by the *Strophalosiaria concentrica* and *Crassispinosella subcircularis* Zones of Tasmania and Sydney Basin, but for the most part were not as favourable as for faunas that accumulated in Sakmarian time, when faunal diversity was distinctly higher for Brachiopoda and Mollusca. One striking difference between the Asselian to Aktastinian faunas and the Kungurian to Capitanian faunas is the complete absence of the cold-water bivalve *Eurydesma* and its descendent *Glendella* after Kungurian time. But Mesozoic descendents appear to be represented in the form of *Krumbeckiella* Ichikawa, 1958 and *Frigidusia* Waterhouse, 2008a, and Buchiidae Cox, 1953 (Waterhouse 2008a). Many other bivalves continued to expand and flourish, and many brachiopods persisted, though with less evolutionary innovation than during Sakmarian times, especially amongst Spiriferida and Terebratulida, whereas Strophalosoidea and to lesser degree Productidina continued to diversify, especially at a specific rather than generic level.

The Kungurian Stage saw the renewal of very cold conditions, as represented by the *Glendella dickinsi* Zone of the Gebbie Formation, with only a low diversity fauna dominated by the eurydesmid bivalve *Glendella* in Queensland. There are only four brachiopod genera, each typical of the Permian in east Australia (*Terrakea*, *Ingelarella*, *Notospirifer* and *Marinurnula*), making up 4 EAD, surely indicative of very unfavourable and cold conditions. The fauna may be matched with the upper Pebbley Beach faunas of the south Bowen Basin,

with *Echinalosia*, *Acanthalosia*?, *Ingelarella*?, *Notospirifer*, *Tabellina* and *Paragilledia*, a handful of genera in 4 EAD and all characteristic of low-diversity cold water faunas, again in a ratio like that the Queensland value. They were dominated in biomass by *Eurydesma*, which persisted into the lower Snapper Point Formation. At Wairaki Downs of New Zealand, the Caravan Formation, with a band 25m thick of boulders up to 0.5m in diameter (see Waterhouse 1982, Fig. 6) is either a till, or laharc deposit, indicative of very cold climate (Waterhouse & Flood 1981). Fossils are rare in the formation, with only two brachiopod EAD, and a few molluscs.

The overlying *Wyndhamia typica* Zone has a few more fossils, but was still cold-water. Still requiring updated systematic coverage for the Sydney Basin, some ten genera have been provisionally recognized, belonging to six EAD, with no exceptional genera, and four EAD in the Freitag Formation of the southwest Bowen Basin, though Freitag correlation is possibly slightly younger, equivalent to the *Echinalosia discinia* Zone. Faunas were clearly cold-water, consonant with the cold-water attributes of the sediments (Fielding et al. 2007). In New Zealand, in a limited number of samples from sediments fringing the volcanic arc, nine of the dominant east Australian groups are present, together with *Lethamia*, and a punctate spiriferinid, of modest diversity. This fauna also includes *Spiriferella*, a genus well developed in temperate paleolatitudes, including Western Australia but completely absent from east Australia, so that the diversity ratio at 0.5 is somewhat higher, consistent with its position in an offshore volcanic arc.

Macrofaunal zone	Number of non EAD genera	Number of EAD groups	Ratio
	A	B	A/B
<i>discinia</i>	6	5	1.1
<i>typica</i> (NSW)	0	8	0
<i>dickinsi</i>	0	4	0

Table 3. Changes in brachiopod diversity for the Kungurian Stage Prime values from southeast Bowen Basin with *typica* from New South Wales.

Marked climatic amelioration ensued during the development of the *Echinalosia discinia* Zone. In the Brae Formation of southeast Queensland, a mere five EAD genera are overwhelmed in number by exceptional forms such as *Lethamia*, *Stenoscisma*, *Cleiothyridina*, *Martiniopsis*, *Spinomartinia* and *Pustuloplica*, as well as bivalves such as *Echinorbis* and *Elimata*. Several of these genera are more typical of warmer water faunas, as in southeast Asia. There is some differentiation in faunas (Waterhouse 1987a, p. 214), with *Gondaconularia* at the base, *Echinalosia denisoni* and *Paucispinauria paucispinosa* in higher beds, and *Stenoscisma* and *Lethamia* in the upper beds, indicative of increasing diversity and warmth. The zone was also well diversified in New Zealand, and subdivided into a lower *Echinalosia discinia* Zone, a brief subzonal interval characterized by *E. denisoni*, and an upper *Lethamia ligurritus* Subzone, much as in the Brae Formation, and with a high number of less than usual genera, *Neochonetes*, *Lethamia*, *Costatumulus*, *Cleiothyridina* and *Pustuloplica*, as well as more east Australian dominants (eight) than in Queensland. The *Echinalosia discinia* Zone is well represented in the Wandrawandian Formation of the south Sydney Basin (Shi & McLoughlin 1997), and full monographic treatment is pending (Prof. G. R. Shi, pers. comm). Tasmania remains an open question, through lack of adequate systematic publication.

COEVAL INTERNATIONAL CHANGES TO CLIMATE

At the time of peak glaciation in the Permian Period of east Australia, large swathes of Gondwana suffered similar glaciation, and faunas were meagre and involved such east Australian genera such as *Eurydesma*. These levels are overlain widely by a distinctive and more diversified fauna typified by *Bandoproductus* in Thailand, Tibet, India, Pakistan, Afghanistan and Oman as summarized on p. 221, and assigned by all authors to late Asselian, with strong support provided by fusulines in Tibet (Jin & Sun 1981). Overlying species and genera found in Tiverton Formation and Buffel Subgroup of east Australia are shared especially with the *Coronalsia irwinensis* Zone of the Carnarvon Basin and coeval faunas of Western Australia and the faunas of Ko Yao Noi Formation, Thailand (Waterhouse et al. 1981) and extensive faunas of south Asia. These faunas have ammon-

oids and occasionally conodonts and fusulines pointing to correlation with the Sakmarian faunas of the world stratotypes. There are even faunal ties with Arctic Canadian faunas through such west Australian genera as *Cimmeriella* Archbold, and ammonoids, and links to eastern Australia through the brachiopod family Ingelarellidae.

The warm-temperature implications of the Greta Coal Measures in the north Sydney Basin and Byro Group of Western Australia are strongly endorsed in the stratigraphic and faunal successions of northern Canada, as far as Axel Heiberg Island, above faunas mirroring the east and west Australian successions in their diversity changes with occasional generic links. Fusulines become abundant, having spread northwards from subtropical and tropical waters, and these are of Baigendzinian age, as reinforced by conodonts (Waterhouse 2020).

Worldwide, a sharp change in macrofaunas followed in the Filippovian level of the lower Kungurian Stage, as shown by Stepanov (1973). In east Australia, this matched the faunally depauperate levels such as the *Glendella dickinsi* Zone of the Bowen Basin, and the upper Pebbley Beach Formation of the south Sydney Basin, with radiometric support provided by A. Nutman (Shi et al. 2020), as well as the ammonoid *Aricoceras* from overlying beds (Leonova 1998). The cool to cold water implications in a series of cyclothems of cool to cold water faunas followed by equally brief warm-water faunas persisted throughout the overlying Guadalupian Series of Middle Permian age.

During early Permian times, when glaciation prevailed over much of Gondwana, faunas flourished in the paleotropics, as if life had been squeezed into the warmest of climatic belts, and there was little input from Gondwana. But through time, cold-water marine life had adapted to cold conditions, flourished in the ensuing Sakmarian warmer time, and penetrated paleotropical faunas during the Guadalupian Series, notably in the Glass Mountains of Texas, as will be discussed in a subsequent Earthwise volume on Middle and Upper Permian faunas in east Australasia.

SUMMARY

To summarize, the imprint of climate on fossil brachiopods and molluscs distributed throughout the marine Permian of eastern Australia, including the volcanic arc now preserved

in the Gympie Province of Queensland and New Zealand, provides a record of temperature changes, both through diversity changes, and the affinities of individual species and genera with allied taxa from other parts of the globe. The faunas demonstrate a series of glacial advances and retreats, simplistically reducible to two major cold intervals, Asselian and Kungurian to Capitanian, each interspersed with interglacial episode, superimposed on overall but far from steady increase in warming throughout the period. In east Australia, the Early Permian Asselian Stage, represented by two macrofaunal zones and a subzone, witnessed a time of great cold and widespread glaciation that continued from earliest Permian or late Carboniferous, followed by a much warmer interval during the late Asselian *Bandoproductus macrospina* Zone. The overlying Sakmarian Stage saw a time of increased temperatures as compared with basal Asselian, and a time of overall stability in climate, nowhere as constrained by the sort of extensive glaciation and cold temperatures that occurred during Asselian time, so that faunas largely peculiar to east Australia flourished and diversified, with a brief slightly cooler interval at the start of the Sakmarian (*Echinalosia curtosa* Zone) and a comparatively warm interval during the *Azygidium mitis* Subzone. Faunal diversities and links with south Asian faunas increased to culminate in the *Taeniothaerus subquadratus* Zone at the top of the Sakmarian Stage. The oldest Artinskian fauna is known only for the volcanic arc in New Zealand, as the *Notostrophia zealandicus* Zone, as a time of high faunal diversification, and presumably moderately warm temperatures, conceivably due to local rather than world-wide factors. The overlying *N. homeri* Zone equivalent to the *Echinalosia preovalidis* - *Ingelarella plica* Zone in the Bowen Basin of Queensland saw a sharp reduction in the number of taxa, with a depauperate fauna pointing to severely cold conditions, closing off the major Aktastinian Substage of the Artinskian Stage. In the overlying Baigendzinian Substage, coal measures accumulated in east Australia, reflecting isostatic rebound of the earth's crust, now free from the weight of ice. Loughnan (1973, 1975) declared that conditions were subtropical, pointing to the nature of the soil, which would also explain the luxuriant growth of forests, leading to coal. In Western Australia and in New Zealand, marine conditions persisted, and faunas were comparatively warm-water in their affinities. The west Australian faunas showed many links with faunas of south Asia. Marine conditions persisted in New Zealand, although strongly

under the same climate regime as east Australia, and saw the entry of genera from Western Australia.

Colder times and less diversified faunas prevailed during the Kunguran Stage and severely depauperate faunas characterized the early middle Kungurian (Filippovian) as the *Glendella dickinsi* Zone, followed by the *Wyndhamia typica* Zone in the Snapper Point, early Wandrawandrian Formation, Grange Mudstone of Tasmania and middle Letham Formation of New Zealand, followed by more benign conditions assigned to the late Kungurian, although this requires further assessment.

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