

Lower Permian brachiopods from Wasp Head Formation, Sydney Basin, southeastern Australia

Author(s): Gabriela A. Cisterna and G. R. Shi

Source: *Journal of Paleontology*, 88(3):531-544. 2014.

Published By: The Paleontological Society

DOI: <http://dx.doi.org/10.1666/13-004>

URL: <http://www.bioone.org/doi/full/10.1666/13-004>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.



LOWER PERMIAN BRACHIOPODS FROM WASP HEAD FORMATION, SYDNEY BASIN, SOUTHEASTERN AUSTRALIA

GABRIELA A. CISTERNA¹ AND G. R. SHI²

¹Consejo Nacional de Investigaciones Científicas y Técnicas-Museo de Ciencias Naturales, Universidad Nacional de La Rioja, Avda. Dr. Luis M. de La Fuente s/n, La Rioja 5300, Argentina, <gabriela.cisterna@conicet.gov.ar>; and ²School of Life and Environmental Sciences, Deakin University, Melbourne Campus at Burwood, 221 Burwood Highway, Burwood, Victoria 3125, Australia, <grshi@deakin.edu.au>

ABSTRACT—Although there is a generally accepted framework for the Permian marine biogeography of Australia, significant uncertainties remain concerning the temporal biogeographical changes closely related to the timing of Permian glacial–interglacial events. Several recent studies along these research lines demonstrate the importance of a reliable high-resolution biostratigraphical timescale for paleobiogeographical and paleoclimatic reconstructions. This paper provides, for the first time, a full taxonomic and biostratigraphical study of the brachiopod fauna from the Wasp Head Formation, southern Sydney Basin, southeastern Australia. The fauna is associated with deposits of the first Permian glacial interval suggested for eastern Australia. Three brachiopod assemblages are recognized. The lower and middle assemblages contain scarce brachiopods although associated bivalves are comparatively more common. Despite very low diversity and low abundance, these two brachiopod assemblages contain characteristic species of the *Strophalosia concentrica* and *Strophalosia subcircularis* brachiopod zones, both considered of late Asselian age. The third assemblage, occurring in the uppermost part of the formation, contains more brachiopods than bivalves and is referred to early Sakmarian in age. The species diversity and stratigraphic occurrences of the brachiopod assemblages in relation to sedimentary facies suggest that the lower two assemblages may represent an intra-glacial interval while the younger third assemblage, characterized by abundant occurrences of *Trigonotreta* and *Tomioptis* species, accompanied by the bivalve *Eurydesma*, is more indicative of a post-glacial benthic marine fauna comparable to coeval brachiopod faunas found elsewhere in Gondwana.

INTRODUCTION

THE PERMIAN marine fossil record of Australia has long been known to exhibit marked provincial patterns (Archbold, 2000, and references therein). With the exception of the earliest Permian (Asselian–early Sakmarian), when a distinctive unified single marine province developed across Australia and the Himalayan region (the Indoralian Province; Shi and Archbold, 1993), two shallow marine biotic provinces appear to have persisted throughout most of the Permian (Fig. 1): the Austrazean and Westralian provinces (Archbold, 1983). The notion of a united Asselian–early Sakmarian Indoralian province for India and Australia has been confirmed by a recent study of stage-by-stage Cisuralian (early Permian) global brachiopod biogeography, using a statistical approach by Shen et al. (2013). On the other hand, the same study also revealed that the Westralian province has statically much stronger faunal affinities than previously thought with those of peri-Gondwanan terranes in south and southeast Asia from Sakmarian onwards. This raises the possibility that a single, large, transitional biogeographic zone (province) may have existed throughout the middle to late early Permian, straddling across much of the northern margin of Gondwana and co-existing with the Austrazean province that was at that time confined to the eastern margin of Gondwana (Shen et al., 2013, fig. 6).

Despite the generally accepted framework for the Permian marine biogeography of Australia, significant uncertainties remain concerning the fine details of each of the recognized biotic provinces. This is particularly significant with regard to their faunal composition, their contraction and expansion in space and through time, and whether these temporal biogeographical changes closely paced and tracked contemporaneous climate change tempos as identified by Fielding et al. (2008a) for eastern Australia. Several recent studies have produced

research along these lines (Clapham and James, 2008, 2012; Waterhouse and Shi, 2010, 2013; Waterhouse, 2011), but they have each reached either inconclusive results or markedly different conclusions for many of the same aspects investigated. For example, contrary to their expectations, Clapham and James (2012) did not detect any consistent and persistent latitudinal migration patterns among eastern Australian Permian brachiopod genera despite the well-recognized significant glacial–interglacial cycles identified by Fielding et al. (2008a) and Waterhouse and Shi (2013). Clapham and James (2012) cautiously attributed their findings to possible sampling noises in their data and/or the coarse temporal scale used for their analysis. Similarly, substantial difference also exists between Waterhouse (2011) and Clapham and James (2012) in regards to the temporal projections of extinction rates of Permian brachiopod genera in eastern Australia (e.g., Clapham and James, 2012, fig. 5B vs. Waterhouse, 2011, fig. 10). In part, their discrepancy may be explained by the use of two different Permian biostratigraphical timescales: Clapham and James based their study on the Permian timescale of Briggs (1998), in contrast to Waterhouse’s study which is largely based on his own biozonation scheme (Waterhouse, 2008). Both of above cases demonstrate the importance of a reliable high-resolution biostratigraphical timescale for paleobiogeographical and paleoclimatic reconstructions.

Despite its potential biostratigraphical significance representing possibly the oldest Permian marine fauna in mainland eastern Australia, the species composition and stratigraphic distribution of the Wasp Head Formation fauna remains poorly known. This fauna is fully described for the first time in the current study, and its age and correlation discussed and established. The significance of this study should not be understated for at least two reasons. Firstly, as will be detailed

below, the brachiopod fauna of the Wasp Head Formation is characterized by a group of diagnostic species whose individual occurrence appears to have particular importance in defining the marine Carboniferous–Permian boundary in eastern Australia. Secondly, the Wasp Head Formation is one of the basal Permian units in eastern Australia that records the Asselian–Sakmian glacial to deglacial transition. Not only is the transition well expressed through the sedimentary record (Gostin and Herbert, 1973; Rygel et al., 2008), it also manifests itself clearly in the stratigraphic distribution of the brachiopod and associated molluscan species throughout the formation. This biostratigraphical aspect of the Wasp Head fauna, especially with respect to its possible implication for timing the onset of the earliest Permian glacial event in eastern Australia, is also discussed in this paper.

PREVIOUS WORKS

Extensive revisions of the eastern Australian marine faunas were realized by Waterhouse (2008, 2011, and references therein). The new biostratigraphical scheme of Waterhouse (2008) for eastern Australia is based on the recognition of robust biozones of both brachiopod and bivalve faunas, each defined on the basis of the first appearance datum (FAD) of a number of species at a type section that is known to be underlain and overlain by rocks with critical key fossil or fossil assemblages of the preceding and succeeding biozones.

Although a considerable advance was achieved by Waterhouse leading to his establishment of a unified eastern Australia–New Zealand Permian macro-faunal biostratigraphical scale, some of the faunas in his scheme still await detailed systematic studies. This is the case, for example, for the *Strophalosia concentrica* and *Strophalosia subcircularis* zones, recognized by Waterhouse (2008) as representing the two oldest Permian brachiopod zones in eastern Australia. A third, possibly older, brachiopod zone, the *Nambuccalinus bourkei* fauna, has recently also been added to the succession of eastern Australian macro-invertebrate biozones by Waterhouse (2011), but the age of this fauna and its stratigraphical relationships with the two supposedly succeeding *Strophalosia* biozones and, further up, the *Bandoproductus macrospina* Zone, remains an open question that requires further study.

Both *Strophalosia concentrica* and *Strophalosia subcircularis* zones in Waterhouse (2008) scheme were established based on low-diversity faunal assemblages in Tasmania, where they have been partly described (Clarke, 1969, 1990, 1992). In mainland eastern Australia, correlative faunas of these two zones have been noted from Victoria (Archbold, 1991), Sydney–Bowen basins (Armstrong, 1969; Briggs, 1998; McClung, 1978; McClung and Armstrong, 1975, 1978; Waterhouse et al., 1983), New England Orogen (Briggs, 1998) and the Cranky Corner basin (Archbold, 2003). Among these faunas, that of Tasmania is the best known in terms of systematics and stratigraphy, and many of the other correlative faunas from mainland eastern Australia are yet to be fully described. Included is the brachiopod fauna from the Wasp Head Formation in the southern Sydney Basin, southeastern Australia.

The first particular study of the Wasp Head Formation brachiopod assemblage was realized by Dickins et al. (1969), who made a list of species by localities and provided illustrations of some key species, but gave no systematic descriptions. Later, the fauna was studied by Nilsen (1982) as a yet unpublished M.Sc. thesis. The brachiopod species from the Wasp Head Formation, as reported by Dickins et al. (1969) and Nilsen (1982), included the following: *Pseudosyrinx* n. sp., *Neospirifer* n. sp., *Ambikella konincki* (Etheridge Jr.),

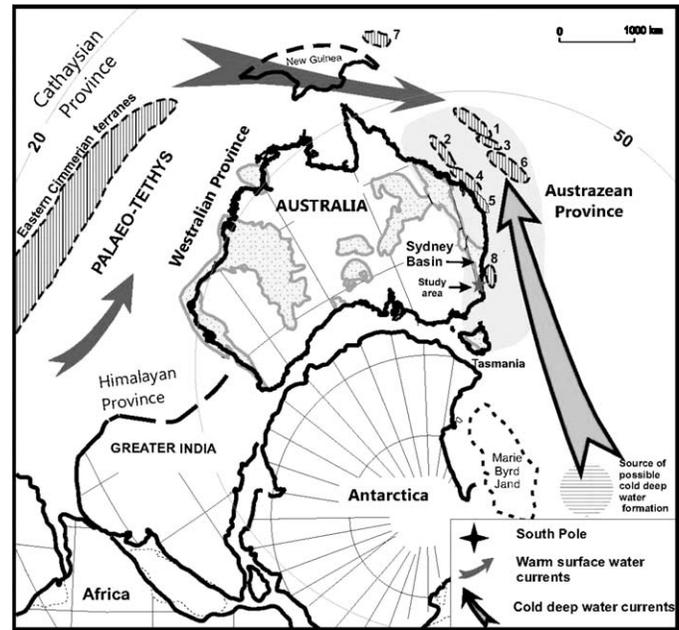


FIGURE 1—Schematic Permian paleogeographical reconstruction of southeastern Gondwana, showing major ocean currents, shallow marine biotic provinces, and key tectonic blocks including terranes off eastern Australia. The numbered terranes are: 1, Rakaia; 2, Western New Caledonia; 3, Aspiring; 4, Brook Street; 5, Gympie; 6, Caples; 7, Bay of Islands; 8, Parapara. Map modified from Shi et al. (2010).

Fletcherithyris sp., *Streptorhynchus curvilamellatus* n. sp., *Strophalosia subcircularis* King, *Tomiopsis konincki* (Etheridge), *T. ovata* (Campbell), *Trigonotreta stokesi* Koenig, *Pseudosyrinx* sp., *Fletcherithyris* cf. *farleyensis* Campbell, and *Gilledia* sp. A relatively diversified molluscan (bivalves and gastropods) assemblage had also been reported from the same formation, many of which co-occur with the brachiopods (Runnegar, 1969). According to Runnegar (1969), the molluscan assemblage includes the following bivalve species: *Eurydesma cordatum* Morris, *Neoschizodus australis* Runnegar, *Megadesmus globosus* Sowerby, *Pyramus laevis* (Sowerby), *Australomya hilliae* Runnegar; and three gastropod species: *Warthia* sp., *Keeneia ocula* (Sowerby), and *Mourlonia (Mourlonia)* sp.

STRATIGRAPHICAL DISTRIBUTION OF THE BRACHIPOD FAUNAL ASSEMBLAGES

The Wasp Head Formation is a shallow marine sandstone dominated unit well exposed along the coast between Myrtle Beach and Depot Beach on the South coast of New South Wales, southeastern Australia (Fig. 2). The stratigraphic and sedimentological aspects of this formation have been well studied by a number of authors (e.g., Gostin and Herbert, 1973; Tye et al., 1996; Rygel et al., 2008). These authors suggested that the Wasp Head Formation was deposited during a transition to a nonglacial period following the late Asselian to early Sakmian glaciation in eastern Australia. In addition, Rygel et al. (2008) proposed a detailed depositional model for this formation and suggested that the basal part records a gradual deepening upward trend from upper to middle shoreface water depths, and that the upper part consists of alternations between shoreface to offshore deposits that reflect the response to relatively rapid (glacioeustatic) sea level rises. Although ice-rafted debris is present throughout the formation, the amount and size of the clasts generally decrease upwards through this unit.

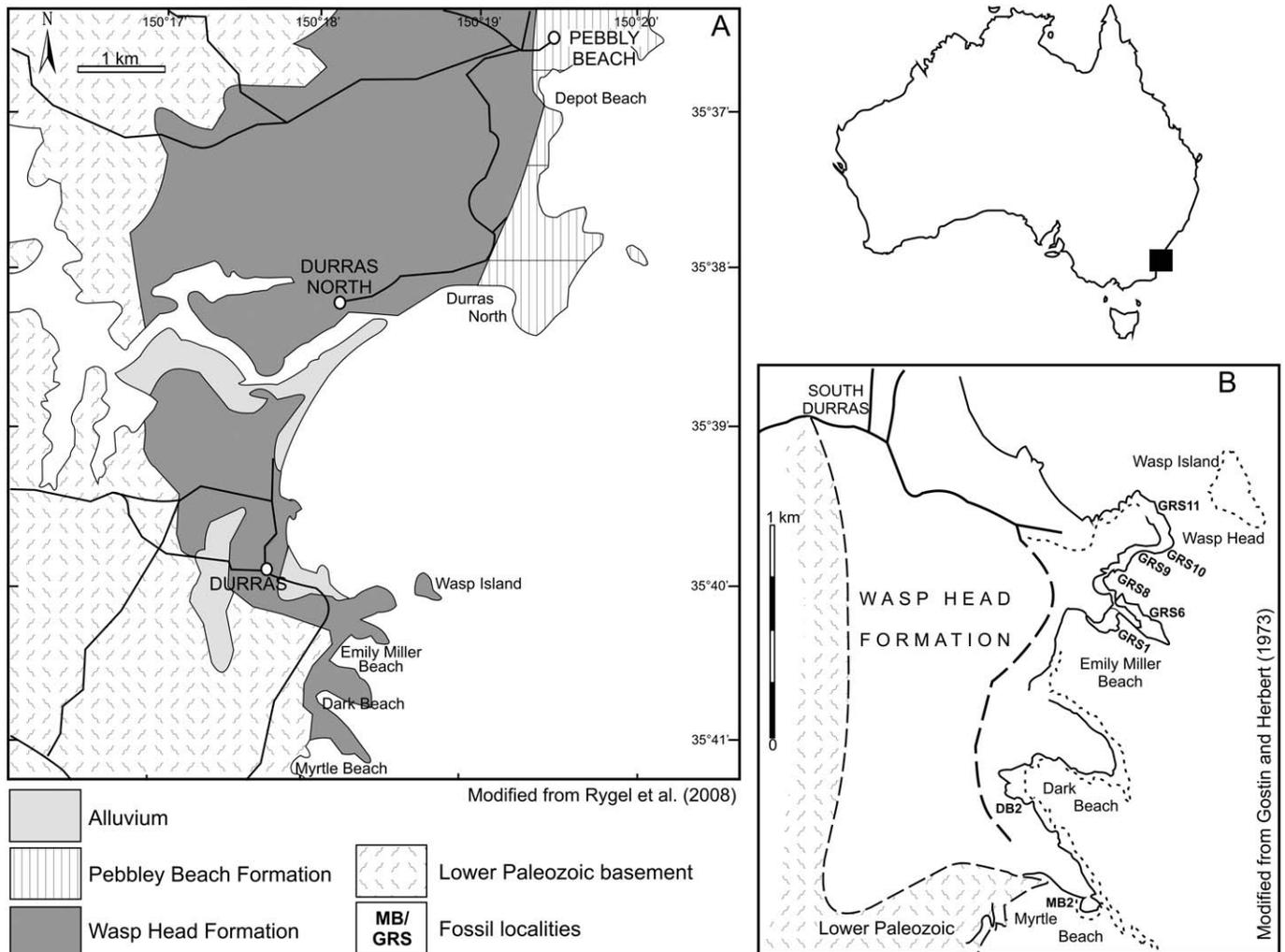


FIGURE 2—A, location map showing the distribution of the Wasp Head Formation and the localities studied (modified from Rygel et al., 2008); B, detailed map with the fossiliferous sites sampled (modified from Gostin and Herbert, 1973).

The depositional environment and especially the succession of facies changes as documented by Rygel et al. (2008) is evidently reflected in the compositional, taphonomic, and paleocological features of the faunal assemblages recognized throughout the formation. In particular, the stratigraphic pattern of the species occurrences and diversity (Fig. 3) also suggests a transition from a cold glacial period to a non-glacial condition. Overall, marine invertebrate fossils are rare in the lower part of the formation, becoming common upwards and, where they occur locally in abundance, tending to form coquina beds. There is a pronounced stratigraphic pattern in the composition of the stratigraphic assemblages: lower assemblages are dominated by bivalves, whereas those in the upper part of the formation are brachiopod-dominated.

Three brachiopod assemblages have been recognized based on their different species compositions (Fig. 3). The lower assemblage, located in a fossiliferous interval about 2 meters thick, appears associated with the breccia horizons in the basal part of the section at the Myrtle Beach and Dark Beach localities (Fig. 2B). This assemblage is bivalve-dominated, with rare occurrences of gastropods and brachiopods. The brachiopod species identified in the assemblage are *Arctitreta* sp., *Strophalosia concentrica* Clarke, *Tomiopsis konincki* (Etheridge),

and *Pseudosyrinx?* sp. Among these brachiopods, the spiriferid *Tomiopsis konincki* is relatively the most common species.

In the middle part of the Wasp Head Formation (Fig. 3), at Turrise Point and Emily Miller Beach localities, the diagnostic brachiopods *Strophalosia subcircularis* and *Tomiopsis konincki* of the *Strophalosia subcircularis* Zone have been recognized. These species are associated with a bivalve-dominated assemblage in which the brachiopods are very rare and fragmentary. This assemblage appears in an interval of fine-grained to coarse-grained sandstone with conglomeratic beds that characterize the middle shoreface facies association (Rygel et al., 2008). The fauna identified is usually associated with some of these conglomeratic horizons.

The third of the brachiopod assemblages appears in a 3-m thick interval in the uppermost part of the formation, exposed onshore from Emily Miller Beach to Wasp Head (Figs. 2B, 3). At Wasp Head, this assemblage is commonly associated with admixed pebbly sandstone and mudstone rocks, abundant dropstones, and conglomerate layers. The stratigraphical interval that contains the faunal assemblage has been interpreted as the product of alternating shoreface and offshore environments with frequent sea surface rafting ice (Rygel et al., 2008). Two brachiopod-dominated subassemblages have been recognized in this assemblage: the lower, in a conglomerate layer

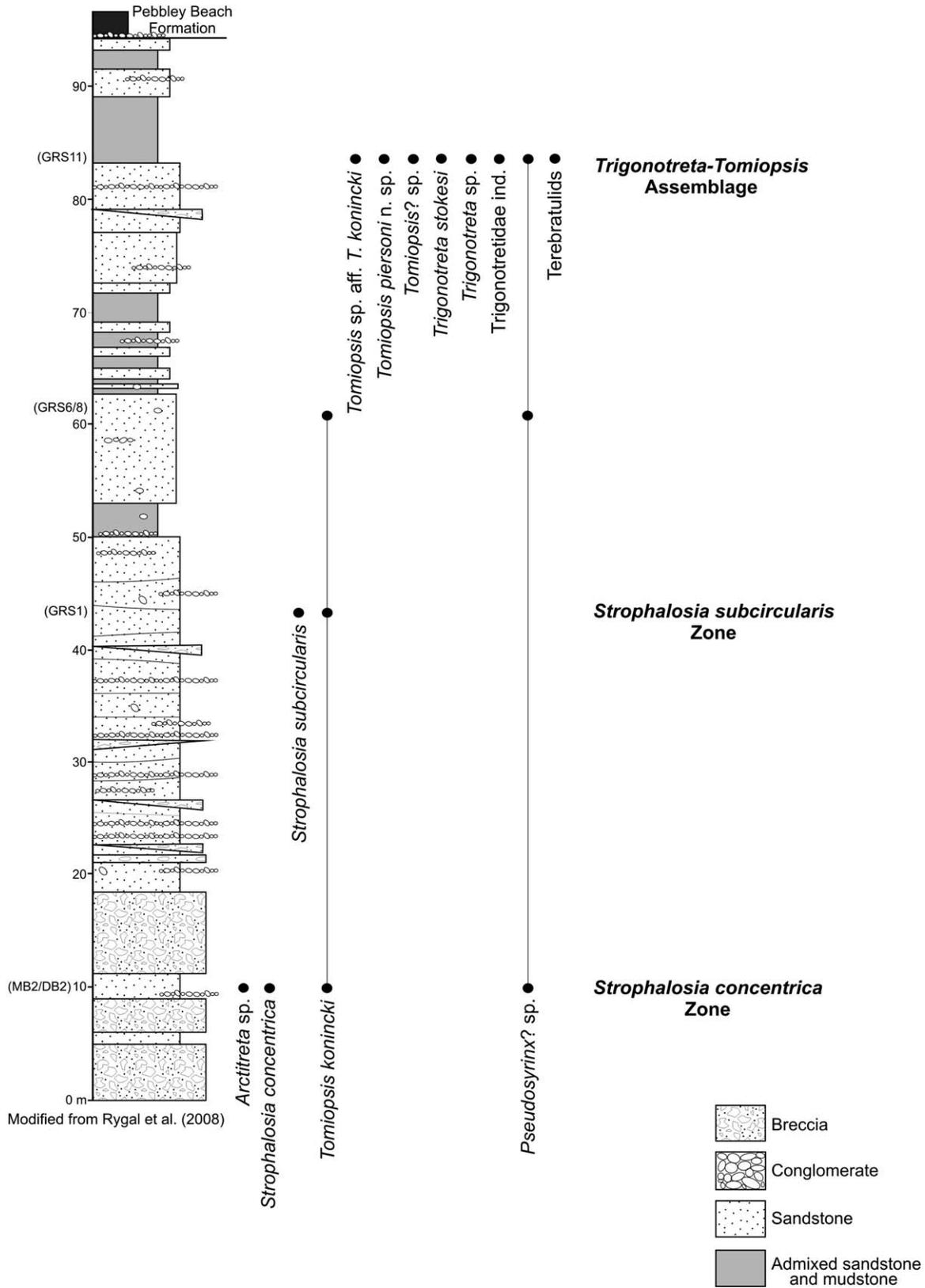


FIGURE 3—Stratigraphical section of the Wasp Head Formation (modified from Rygal et al., 2008) and vertical distribution of the brachiopod faunas.

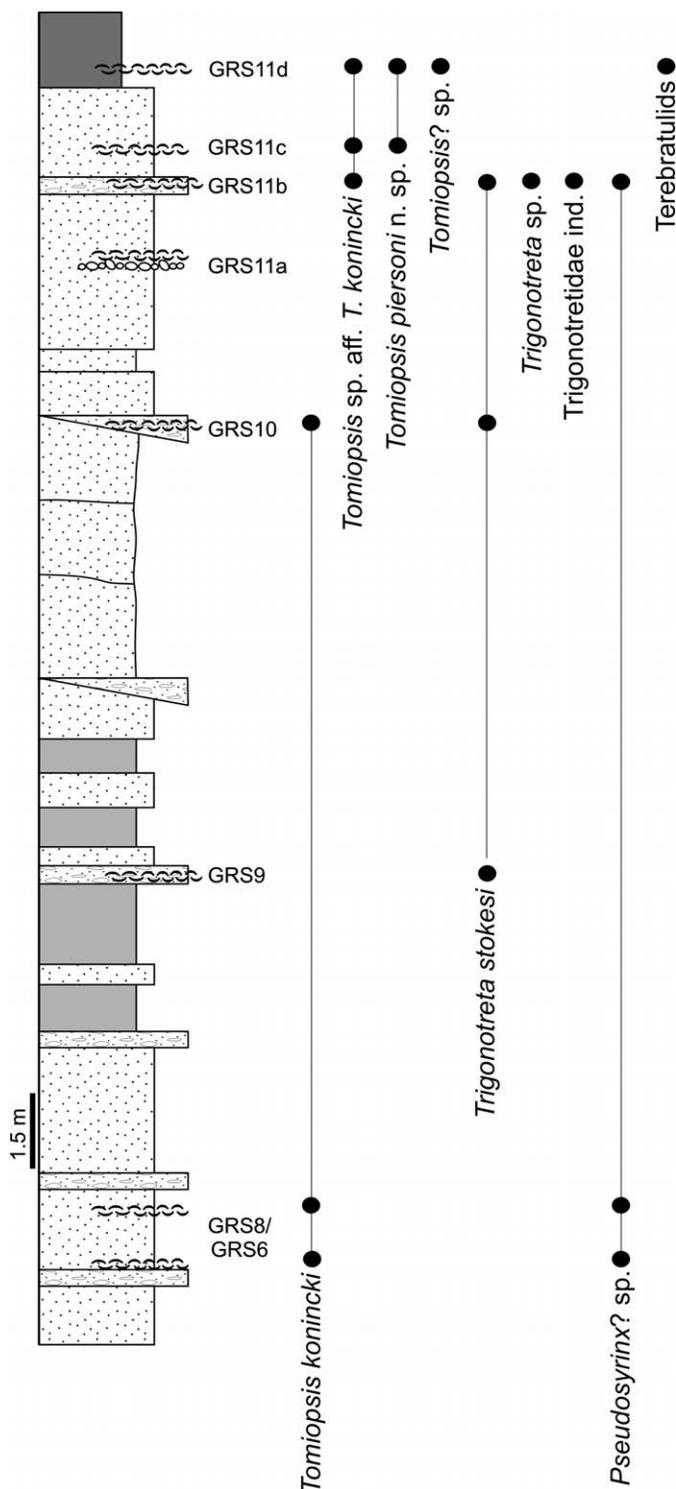


FIGURE 4—Detailed section of the upper part of Wasp Head Formation and vertical distribution of the brachiopod faunas.

(Fig. 4), is dominated by *Trigonotreta stokesi* Koenig, accompanied by very scarce *Trigonotreta* sp., *Trigonotretidae* ind., *Tomiopsis* sp. aff. *Tomiopsis konincki*, and *Pseudosyrinx?* sp. The associated fauna is mainly represented by the bivalve *Eurydesma cordatum* (Morris). Immediately above the conglomerate layer, the second subassemblage occurs. This youngest Wasp Head Formation brachiopod subassemblage is

represented by a relatively high-diversity fauna dominated by *Tomiopsis* spp. At least three *Tomiopsis* species are present here: *Tomiopsis* sp. aff. *Tomiopsis konincki* (Etheridge), *Tomiopsis piersoni* n. sp., and *Tomiopsis?* sp. Other brachiopods are rare (e.g., *Pseudosyrinx?* sp. and the terebratulids *Fletcherithyris?* sp. and *Gilledia?* sp.). Associated non-brachiopod species are represented by bivalves and very rare gastropods. The following distinctive taphonomic and paleoecologic features of this subassemblage have been noted: fossil concentrations occur as shell beds; *Tomiopsis* shells usually appear in nests; bioclasts show poor sorting and a random distribution; shells show low degree of abrasion and fragmentation; shells show very high percentage (>80%) of articulate specimens; and a high degree of shell size mixing involving shells of different ontogenetic stages. All these features indicate a fossil assemblage of para-autochthon to autochthon origin.

AGE AND CORRELATION

The age of the Wasp Head Formation is usually based on brachiopod and bivalve faunas and referred to the Sakmarian (Dickins et al., 1969; Runnegar, 1980; Briggs, 1998) and, most recently, to the Asselian by Waterhouse (2008, 2011). The fauna herein studied belongs to the group of the brachiopods typical of the early Permian of eastern Australia, previously described by Runnegar (1969), Clarke (1990, 1992), and Archbold (2003). Among the three main brachiopod assemblages recognized in this study (Fig. 3), the oldest is found from the Myrtle Beach and Dark Beach localities in the lower part of the formation. This assemblage contains the diagnostic species *Strophalosia concentrica* Clarke that also characterizes the Faunizone 2 of Tasmania (Clarke, 1992), a biozone that was later formally established as the *Strophalosia concentrica* Zone by Briggs (1998) and extended to mainland eastern Australia. At Turrise Point and Emily Miller Beach, the two localities located in the middle part of the Wasp Head Formation, two key brachiopod species occur together: *Strophalosia subcircularis* Clarke and *Tomiopsis konincki* (Etheridge). The co-occurrence of these two species strongly suggests a correlation with the Faunizone 2–3 of Tasmania (Clarke, 1992), equated to the *Strophalosia subcircularis* Zone of Briggs (1998).

Strophalosia concentrica and *Strophalosia subcircularis* Zones are well developed in both the Sydney and Tasmanian basins where they are characterized by faunal assemblages usually dominated by mollusks and spiriferid brachiopods. In proposing these biozones, Briggs (1998) cautioned that these two biozones were only sparsely distributed in southeast Australia, and hence they would be of only limited biostratigraphical utility compared to younger productoid-based brachiopod zones. The age, composition, regional geographic distribution, and biostratigraphical correlations of both biozones have been discussed by Briggs (1998) and Waterhouse (2008). According to Waterhouse (2008), the *Strophalosia concentrica* Zone in eastern Australia is typically comprised of the following brachiopod species: *Strophalosia concentrica* Clarke, *Arctitreta costellata* (Clarke), *Trigonotreta stokesi* Koenig, and *Tomiopsis elongata* (McClung and Armstrong). No stratotype has been selected for this zone but the Anderson Creek and West Arm sections of the Massey Creek Group in Tasmania have been proposed as significant reference sections (Clarke and Farmer, 1976; Clarke, 1992; Waterhouse, 2008). There, the *Strophalosia concentrica* Zone occurs immediately above glacial deposits that also contain palynomorphs assignable to the Asselian *Potoniesporites* spp. and *Microbaculispora tentula* zones. The *Strophalosia subcircularis* Zone is defined by the key species *Strophalosia subcircularis* Clarke, usually associated with

Tomioopsis konincki (Etheridge). Although there was no type section originally designated by Briggs (1998) when proposing this biozone, this is well developed in Tasmania, above the fauna that characterizes the *Strophalosia concentrica* Zone in the reference sections (Clarke, 1992; Waterhouse, 2008). *Strophalosia concentrica* and *Strophalosia subcircularis* Zones have been assigned to the Sakmarian, by correlation with sequences containing microflora (Briggs, 1998; Archbold, 2001; Foster and Archbold, 2001; Archbold, 2003). Waterhouse (1987), however cautioned about the use of the palynological data for the correlation of Late Carboniferous–Early Permian macrofaunas and sequences in Australia because of the suspected diachroneity of the palynomorph-based biozones between eastern and western Australia. This author consequently preferred an Asselian age for the two basal Permian eastern Australian brachiopod zones (Waterhouse, 2008, 2011).

The younger two brachiopod subassemblages identified in the uppermost part of the Wasp Head Formation are represented by a particular association of brachiopod species, dominated in the lower subassemblage by *Trigonotreta stokesi* Koenig associated with the bivalve *Eurydesma* and, immediately above, by a diverse fauna of *Tomioopsis* species. Outside the study area, the closest faunas to these two subassemblages are known from the Beckers Formation in the Cranky Corner Basin in New South Wales in which Archbold (2003) reported a succession of three brachiopod assemblages. His assemblage 1 is characterized by *Eurydesma cordatum* and *Keeneia* species, with no brachiopods found. Archbold's assemblage 2 is dominated by brachiopods with these species: *Tomioopsis elongata*, *Sulciplica crassa*, and *Trigonotreta tangorini* Archbold. This author correlated his assemblages 1 and 2 with the *Strophalosia subcircularis* and *Strophalosia concentrica* zones, respectively. In some sections in eastern Australia, as noted by Briggs (1998), *Tomioopsis elongata* and *Tomioopsis konincki* appear to overlap in their local stratigraphic ranges.

The Wasp Head Formation encloses records of the first Permian glacial interval suggested for eastern Australia (P1 in Fielding et al., 2008b). The occurrence of brachiopods characteristic of the *Strophalosia concentrica* and *Strophalosia subcircularis* zones in the lower and middle parts of the unit, where ice-rafted debris are common, could be used to constrain the age of the onset of this first Permian glacial episode. Significantly, the lower two brachiopod assemblages could be considered as representing an intra-glacial interval in view of their stratigraphic relationship with tillite horizons. The youngest brachiopod assemblage, identified in the uppermost part of the Wasp Head Formation, is characterized by the abundant occurrences of *Trigonotreta*, *Eurydesma*, and *Tomioopsis* species. The relative high species diversity compared to the lower two assemblages, together with substantially reduced tillite and dropstone occurrences in the associated sedimentary facies, is consistent with the characteristics of post-glacial benthic marine faunas of Late Carboniferous–Early Permian age found elsewhere in Gondwana (Cisterna and Sterren, 2008, 2010) and Perigondwana (Shen et al., 2000). *Tomioopsis piersoni* n. sp., a dominant species identified in the uppermost *Tomioopsis* subassemblage, is close to *Tomioopsis branxtonensis* (Etheridge) from the Farley Formation in the northern Sydney Basin. This species has been considered the youngest in the *Tomioopsis* group that characterizes Early Permian sequences of eastern Australia (McClung, 1978; Clarke, 1990). Although rare, the presence of brachiopod terebratulids, assigned to the genera *Fletcherithyris* and *Gilledia* (Campbell, 1965; Nillsen, 1982), could also indicate an early Permian age for this assemblage as

Fletcherithyris and *Gilledia* species also occur in the Farley Formation (Campbell, 1965).

Direct biostratigraphical correlation of the Wasp Head Formation faunas with those from Western Australia is not possible at present. Eastern Australian marine faunas seem to be strongly provincial with few if any species shared with Western Australia (Archbold, 1996, 2001; Briggs, 1998). The brachiopod biozones of earliest Permian (Asselian and Sakmarian) age between eastern and western Australia have been correlated with one another with some success through the use of shared palynological elements (Mory and Backhouse, 1997; Briggs, 1998; Apak and Backhouse, 1999; Foster and Archbold, 2001).

Remote to Australia, the Wasp Head Formation brachiopod fauna as a whole appears to bear some significant similarities in species composition to an early Permian marine fauna from the Sauce Grande Basin, in central eastern Argentina. The Argentinean fauna is found in the lower part of the Bonete Formation (Buenos Aires Southern Hill), and characterized by the typical "*Eurydesma* fauna" that appears associated with the *Glossopteris* flora (Pagani, 2000; Di Pascuo et al., 2008). The fauna contains two *Eurydesma* species originally described from eastern Australia: *E. cordatum* Morris and *E. hobartense* (Johnston), as well as two rare brachiopod species: *Tivertonia pillahuincensis* (Harrington) Archbold and *Tomioopsis harringtoni* Archbold and Thomas (Harrington, 1955; Archbold and Thomas, 1986; Pagani, 1998, 2000). As in the Wasp Head Formation, the *Eurydesma*–*Tomioopsis* fauna of the Bonete Formation has also been interpreted as representing a post-glacial interval following the main Carboniferous–Permian glacial event in South America (López Gamundi et al., 1995).

In conclusion, the age of the Wasp Head Formation fauna herein studied can be considered late Asselian–early Sakmarian: brachiopod assemblages located in the lower and middle parts of the section, containing elements of the *Strophalosia concentrica* and *Strophalosia subcircularis* zones, are assigned to the late Asselian, while the uppermost assemblage dominated by *Trigonotreta* and *Tomioopsis* species is referred to early Sakmarian.

SYSTEMATIC PALEONTOLOGY

The materials described are registered by the prefix NMVP, housed in the paleontological collections of Museum Victoria, Melbourne, Australia, as well as UQF, housed the Queensland Museum, Brisbane, Australia. The classification of Brachiopoda adopted herein follows Brunton et al. (2000) for Productida, Williams et al. (2000) for Orthotetida and Carter et al. (2006) for Spiriferida.

- Phylum BRACHIOPODA Duméril, 1806
- Subphylum RHYNCHONELLIFORMEA Williams et al., 1996
- Class STROPHOMENATA Williams et al., 1996
- Order PRODUCTIDA Sarytcheva and Sokolskaya, 1959
- Suborder STROPHALOSIIDINA Schuchert, 1913
- Superfamily STROPHALOSIOIDEA Schuchert, 1913
- Family STROPHALOSIIDAE Schuchert, 1913
- Subfamily STROPHALOSIINAE Schuchert, 1913
- Genus STROPHALOSIA King, 1844
- STROPHALOSIA CONCENTRICA Clarke, 1990
- Figure 5.1, 5.2

- 1990 *Strophalosia concentrica* CLARKE, p. 60, fig. 5H–5R.
- 1992 *Strophalosia concentrica* CLARKE, p. 16, fig. 5H–5R.
- 1998 *Strophalosia concentrica*, BRIGGS, p. 67, fig. 36A–36C.

Material.—Two ventral internal molds (UQF 73018, 73020);

one ventral external mold (UQF 73078); one dorsal internal mold (UQF 73045).

Occurrence.—Lower part of Wasp Head Formation, Dark Beach and Myrtle Beach localities; late Asselian.

Remarks.—Although rather fragmentary, the material studied show a number of features characteristic to the genus *Strophalosia* (i.e., slightly transverse subrounded outline with ill-defined small ears; hinge less than maximum width; concentric ornament weak ventrally, spines cover ventral valve, suberect, semi-recumbent; medium septum connected to cardinal process reaching two-thirds disk length). These strophalosiid specimens with small, globose, and almost circular outline are herein assigned to *Strophalosia concentrica* Clarke. Nillsen (1982) included this material in *Strophalosia subcircularis* Clarke; however the dense, fine ventral spines (about 0.7 mm in diameter on the posterior margin) and a relatively small size (maximum width 18 mm, length 13 mm) are characteristic of *Strophalosia concentrica*, not *S. subcircularis*. In a study of the strophalosiid from the Sydney Basin, Briggs (1998) also assigned the specimens herein figured to *Strophalosia concentrica*.

STROPHALOSIA SUBCIRCULARIS Clarke, 1990

Figure 5.3–5.5

- 1969 *Strophalosia subcircularis* CLARKE, p. 22, pl.1, figs. 1–8; pl. 2, figs. 1–8; pl. 3, figs. 1–8; pl. 4, figs. 1–9.
 1992 *Strophalosia subcircularis*, CLARKE, p. 16, fig. 5A–5G.
 1998 *Strophalosia subcircularis*, BRIGGS, 1998, p. 69, fig. 36D–36L.

Material.—Two ventral internal molds (UQF 73133, 73017); one ventral external mold (NMV P309890).

Occurrence.—Middle part of the Wasp Head Formation, Turrise Point, and Emily Miller Beach localities; late Asselian.

Remarks.—These three medium-sized specimens (maximum width 24 mm, length 32 mm), all show a conspicuous and high ventral adductor platform and a diagnostic pear-shaped and subdivided adductor scar (Fig. 5.3). These features suggest *Strophalosia subcircularis* Clarke. Additionally, the ventral spines are strong, numerous and subquincuncially arranged, as was described and diagnosed by Clarke (1990) for *Strophalosia subcircularis*. This species is larger and more coarsely spinose when compared to *Strophalosia concentrica* and can therefore be easily differentiated from the latter. Two specimens here studied (UQF 73133, 73017) were included in *Strophalosia subcircularis* by Briggs (1998, p. 70); these specimens appear to be close to those from the Warwick, Alum Rock, Texas Block (Alum Roks beds), also figured by Briggs (1998, p. 68, fig. 36I, 36J) as *Strophalosia subcircularis*.

Order ORTHOTETIDA Waagen, 1884
 Suborder ORTHOTETIDINA Waagen, 1884
 Superfamilia ORTHOTETOIDEA Waagen, 1884
 Family SCHUCHERTELLIDAE Williams, 1953
 Subfamily STREPTORHYNCHINAE Stehli, 1954
 Genus ARCTITRETA Whitfield, 1908

ARCTITRETA sp.
 Figure 5.6–5.9

Material.—One internal mold of ventral valve and its external counter mold (UQF 73011-73009); one internal mold of dorsal valve (UQF 73179).

Occurrence.—Lower part of Wasp Head Formation, Dark Beach locality; late Asselian.

Remarks.—Two fragmentary medium-sized specimens (ventral valve, maximum width 30 mm; dorsal valve, maximum width 18 mm, length 5 mm), are tentatively referred to *Arctitreta*. Because the ventral valve is deformed, it is not possible to determine whether it is subpentagonal as in *Arctitreta* or conical as

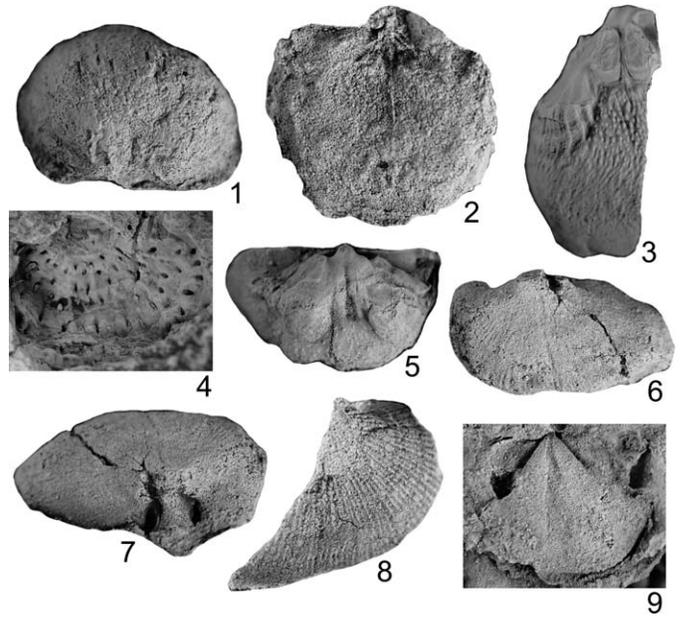


FIGURE 5.—1, 2, *Strophalosia concentrica* Clarke: 1, UQF 73018, ventral internal mold, $\times 2.2$; 2, UQF 73045, internal dorsal mold, $\times 2.2$; 3–5, *Strophalosia subcircularis* Clarke: 3, UQF 73133, ventral internal mold, $\times 1$; 4, NMV P309890, ventral external mold, $\times 1.5$; 5, UQF 73017, ventral internal mold, $\times 1.2$; 6–9, *Arctitreta* sp.: 6, 7, UQF 73011, internal mold of ventral valve, ventral ($\times 1$) and posterior ($\times 1.1$) views; 8, UQF 73009, fragmentary ventral external mold of ventral valve, $\times 1.1$; 9, UQF 73179, internal mold of dorsal valve, $\times 1.2$.

Streptorhynchus. However, the concentric ornamentation that usually appears in *Streptorhynchus*, is absent. The ornament is composed of rounded and regular costae that appear to increase anteriorly by intercalation, and number about 9 to 10 per 5 mm at the anterior margin. A conspicuous dental ridge in the ventral valve and short diverging dorsal socket plates have been observed from the Wasp Head specimens. Material herein described was included in the unpublished Nillsen's thesis (1982) as *Streptorhynchus curvilamellatus* sp. nov., but the specimens figured by Nillsen are scarce and fragmentary, lacking the diagnostic features of *Streptorhynchus* and are insufficient to propose a new species.

Order SPIRIFERIDA Waagen, 1883
 Suborder SPIRIFERIDINA Waagen, 1883
 Superfamily MARTINIOIDEA Waagen, 1883
 Family INGELARELLIDAE Campbell, 1959
 Subfamily INGELARELLINAE Campbell, 1959
 Genus TOMIOPSIS Benediktova, 1956

Diagnosis.—Small to medium sized Ingelarellinae. Fold and sulcus usually distinct, flanks normally plicate. Well-developed ventral adminicula and dorsal tabellae. Microornament of long, shallow, radially linear grooves arranged in quincunx (Archbold and Thomas, 1986).

Remarks.—The diagnosis and morphological limits of *Tomiopsis* and its comparison with other Late Paleozoic ingelarellid genera have been widely discussed in several studies (Waterhouse, 1971, 1986, 1998; McClung, 1978; Archbold and Thomas, 1986; Clarke 1992). Particularly, the validity of using microornament (the presence or absence of microspines) as a taxonomic criterion to discriminate the various ingelarellid genera (Campbell, 1959; Armstrong, 1970; Brunton, 1976; Waterhouse, 1998), has been questioned because the microspines are a character of doubtful value rarely preserved due to the possibilities of alteration by weathering or diagenesis (Balinski,

1975; McClung, 1978; Clarke, 1992). Nevertheless, micro-ornament has been regarded by some authors as of considerable taxonomic significance for discriminating species, genera, and even some higher taxa because it is considered to reflect a fundamental character of the mantle edge (Brunton, 1976; Archbold and Thomas, 1986; Weldon and Shi, 2001). Waterhouse (1988) attempted to segregate the Carboniferous *Tomiopsis* species from the Permian *Tomiopsis* species based mainly on the characteristics of the ventral sinus, plicae on the flanks, thickening of shell, ventral plates, dorsal adminicula, and the presence of a ventral internal ridge in front of the muscle field. Emphasizing the taxonomic significance of these diagnostic features, Waterhouse erected several subgenera within *Tomiopsis*: *Tomiopsis* (*Tomiopsis*) Benediktova, 1956; *Tomiopsis* (*Ambikella*) Sahni and Srivastava, 1956; *Tomiopsis* (*Ingelarella*) Campbell, 1959; *Tomiopsis* (*Johndearia*) Waterhouse, 1998; and *Tomiopsis* (*Geothomasia*) Waterhouse, 1998. In the revised Treatise on Brachiopoda, these subgenera have been given full genus status (Carter and Gourvenec, 2006; Gourvenec and Carter, 2007), which is also followed here.

TOMIOPSIS KONINCKI (Etheridge, 1892)

Figure 6.1–6.11

- 1892 *Martiniopsis subradiata* var. *konincki*, ETHERIDGE, p. 239.
 1969 *Ambikella konincki* (Etheridge), RUNNEGAR, p. 294, pl. 20, figs. 1–5.
 1975 *Martiniopsis konincki* (Etheridge), RUNNEGAR AND MCCLUNG, pl. 31, fig. 3.
 1978 *Ingelarella konincki* (Etheridge), MCCLUNG, p. 44, pl. 3, figs. 1–6.
 1990 *Tomiopsis konincki* (Etheridge), CLARKE, p. 66, fig. 11A–11J.
 1992 *Tomiopsis konincki* (Etheridge), CLARKE, p. 22, fig. 11A–11J.

Diagnosis.—Shell weakly transverse, fold and sulcus moderate, rounded or rarely grooved; lateral slopes with three or four very low rounded plications; commissure uniplicate; posterolateral regions in ventral valve moderately thickened; dorsal adminicula short, sometimes slightly flexed (Clarke, 1990).

Description.—Small sized (maximum width 14–24 mm; length 20–11 mm), slightly transverse with maximum width located at about mid-length of the shell. Sinus wide and flat and fold low, rounded or subrectangular. Flanks with three low, rounded plicae. Ventral interior with conspicuous long sub-parallel dental plates that enclose a relative wide muscle field, whose width is widely variable in the specimens examined (Fig. 6.4, 6.8), regardless their ontogenetic stages. Dorsal interior with short, straight and divergent dorsal adminicula (tabellae). A delicate dorsal median septum extending about one third of valve length.

Material.—Six ventral internal molds (UQF 73032, 73033, 73035, 73039, 73047, NMV P309893); ten dorsal internal molds (UQF 73031, 73034, 73036, 73037, 73038, 73041, 73046, 73048, NMV P309891, 309892).

Occurrence.—Lower-middle part of the Wasp Heap Formation, Dark Beach, Myrtle Beach and Emily Miller Point (GRS 6–8) localities; late Asselian.

Remarks.—The diagnostic features of the studied material suggest *Tomiopsis konincki* (Etheridge). This species has been considered as an intermediate member in the lineage *Tomiopsis elongata*–*konincki*–*branxtonensis*, in which the main trends would be towards stronger lateral plicae, increased height of the fold and sulcus, shorter and more flexed dorsal adminicula, and a less elongate ventral muscle field (McClung, 1978). McClung (1978) has also suggested that intermediate forms could occur but

identification is usually possible only if sufficiently large collections are available.

The comparison of some specimens assigned to *Tomiopsis konincki* by McClung (1978), indicates that the ventral muscle field is a character widely variable to intra specific level (McClung, 1978, pl. 3, figs. 1, 6), a feature also observed in some Western Australian *Tomiopsis* species, such as *Tomiopsis woodwardi* Archbold and Thomas (Archbold and Thomas, 1986, fig. 3.15, 3.22). On the other hand, different species of *Tomiopsis* may show a similar pattern of ventral muscle field; for example, *Tomiopsis konincki* and *Tomiopsis branxtonensis* (McClung, 1978, pl. 3, fig. 1, pl. 4, fig. 1). Also, the variations of the ventral muscle field in the specimens herein studied, suggest that this variability appears to be independent of the ontogenetic stages.

Tomiopsis konincki was recently assigned to the genus *Monklandia* Waterhouse (Waterhouse, 2008), whose type species is characterized by the micro-ornament of slender shallow grooves, each one arising in front of a slender C-shaped spine (Waterhouse, 1998, p. 38). Although the micro-ornament of *Tomiopsis konincki* is poorly known from the type material (Konincki, 1877), surface ornamentation of elongate pits of the type described by Campbell (1959), has been indicated for specimens referred to *Tomiopsis konincki* by Runnegar (1969). Waterhouse et al. (1983) mentioned that the fine grooves making up the micro-ornament are up 0.7 mm long and rather crowded in the anterior sinus. However in no case has this micro-ornament been figured in existing literature for *Tomiopsis konincki*.

Specimens herein studied are smaller in comparison with the neotype of *Tomiopsis konincki* proposed by Waterhouse et al. (1983, pl. 3, fig. 14) from the Allandale Formation, but a number of diagnostic features suggested by McClung (1978) and Clarke (1990) have been recognized. Although the material described here is only composed of internal molds, Nilsen (1982) mentioned the presence of micro-ornament characterized by thin grooves arranged subquicunxially, in specimens from the same stratigraphical horizons as the material here described.

TOMIOPSIS sp. aff. TOMIOPSIS KONINCKI (Etheridge, 1892)

Figure 6.12–6.30

Description.—Medium sized (maximum width 35–27 mm; length 32–23 mm), weak to moderately biconvex, slightly to moderately transverse in mature stages. Ventral valve with conspicuous umbo strongly recurved; sinus wide, flat, broadly concave in cross section, beginning at umbo. Umbonal angle about 95–110°. Flanks with three to four inconspicuous low, broad and rounded plicae that arise close to umbo. Dorsal valve no more convex than ventral valve, with a conspicuous fold rounded to slightly sub-rectangular in section. Lateral flanks with three plicae markedly more conspicuous than the ventral. Commissure uniplicate. Micro-ornament is poorly preserved and has only been observed in one specimen (NMV P309913), featured by typical grooves, without spines, that characterize *Tomiopsis*. Growth lamellae conspicuous, well preserved on anterior part of shell. Ventral interior with conspicuous long, subparallel dental plates, enclosing a long and strongly impressed muscle field. Dorsal tabellae distinct, characteristically short, divergent and slightly flexed.

Material.—GRS 11c–d. One ventral valve (NMV P309894); six articulate specimens (NMV P309895, 309896, 309899, 309905, 309906, 309912); ten internal molds of articulate specimens (NMV P309897, 309898, 309900, 309903, 309904, 309907, 309908, 309909, 309910, 309911); two ventral internal molds (NMV P309901, NMV P309902). GRS11b. Five ventral valves (NMV P309913, 309915, 309918, 309919, 309921); two

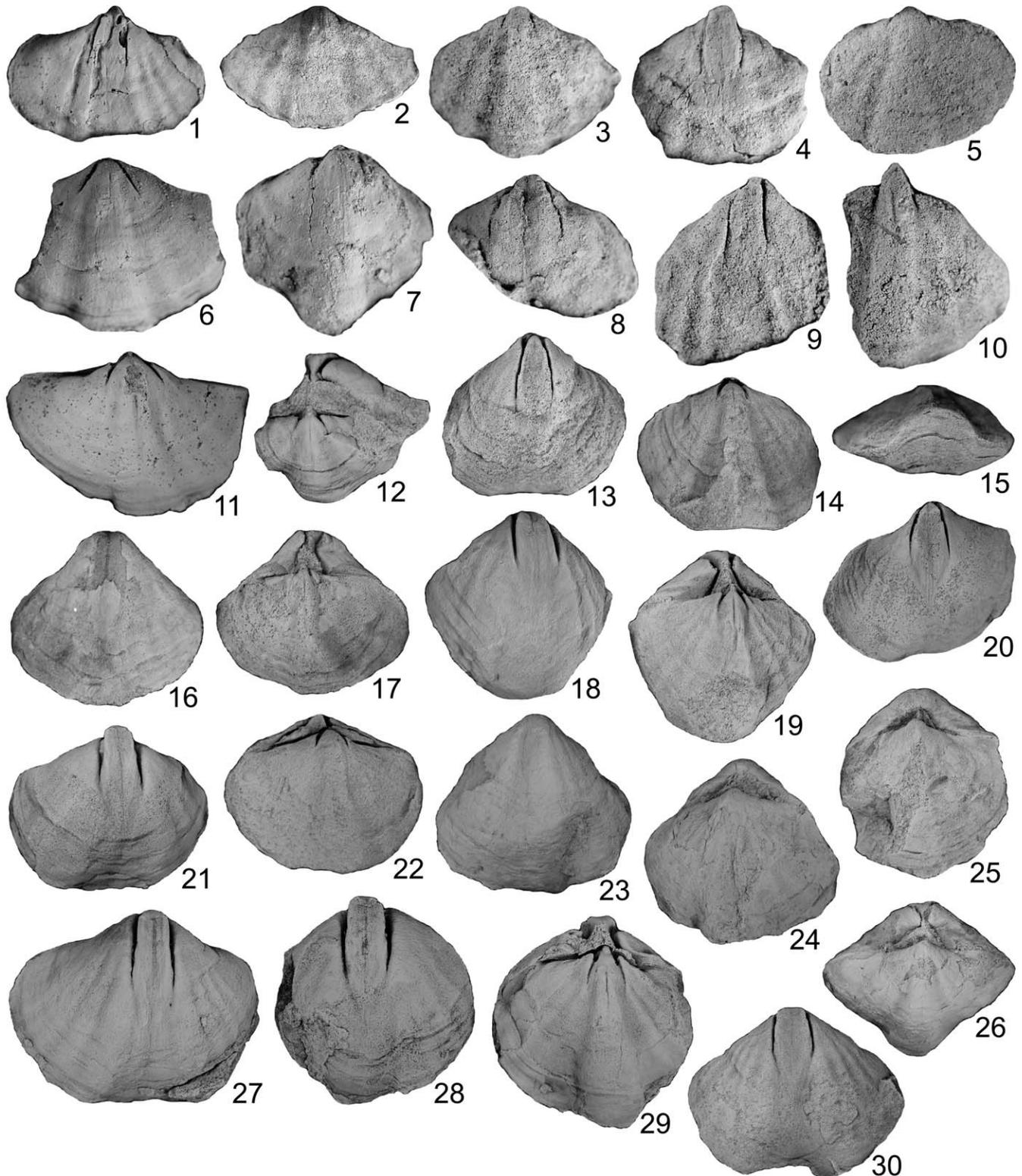


FIGURE 6—1–11, *Tomiopsis konincki* (Etheridge): 1, UQF 73035, ventral internal mold, $\times 1.8$; 2, UQF 73048, dorsal internal mold, $\times 1.8$; 3, UQF 73041, dorsal internal mold, $\times 2.3$; 4, UQF 73032, ventral internal mold, $\times 2.4$; 5, UQF 73034, dorsal internal mold, $\times 1.5$; 6, UQF 73036, ventral internal mold, $\times 2.3$; 7, UQF 73038, dorsal internal mold, $\times 1.7$; 8, UQF 73047, ventral internal mold, $\times 2.3$; 9, UQF 73039, ventral internal mold, $\times 2.4$; 10, UQF 73046, ventral internal mold, $\times 2.3$; 11, NMV P309891, dorsal internal mold, $\times 1.1$; 12–30, *Tomiopsis* sp. aff. *T. konincki* (Etheridge): 12, NMV P309907, internal mold of articulate specimen, $\times 1.2$; 13–15, NMV P309911, internal mold of articulate specimen, ventral, dorsal, and anterior views, $\times 1.2$; 16, 17, NMV P309912, articulate specimen, ventral and dorsal views, $\times 1.2$; 18, 19, NMV P309900, internal mold of articulate specimen, ventral and dorsal views, $\times 1.2$; 20, ventral internal mold, NMV P309902, $\times 1.2$; 21, 22, NMV P309910, articulate specimen, ventral and dorsal views, $\times 1.2$; 23, 24, NMV P309895, articulate specimen, ventral and dorsal views, $\times 1.2$; 25, NMV P309899, articulate specimen, dorsal view, $\times 1.2$; 26, articulate specimen, NMV P30905, dorsal view, $\times 1.2$; 27, NMV P309898, internal mold of articulate specimen, ventral view, $\times 1.1$; 28, 29, NMV P309897, internal mold of articulate specimen, ventral and dorsal views, $\times 1.2$; 30, NMV P309901, ventral internal mold, $\times 1.1$.

dorsal valves (NMV P309914, 309920); one ventral internal mold (NMV P309916).

Occurrence.—Upper part of the Wasp Head Formation (GRS11b–d), Emily Miller–Wasp Head localities; early Sakmarian.

Remarks.—The specimens described as *Tomioopsis* sp. aff. *T. konincki* can be differentiated from *Tomioopsis konincki* of the lower part of the section by their larger size and notably less conspicuous plicae, more prominent sinus and fold, and possessing an important ventral secondary shell thickening. The dorsal adminicula are, generally, shorter and notably more flexed when compared to *Tomioopsis konincki*. Runnegar (1969, p. 291, fig. 2) described a specimen from the same horizon as that of *Tomioopsis* sp. aff. *T. konincki* herein studied; both are considered conspecific.

TOMIOOPSIS PIERSONI new species
Figure 7.1–7.28

Diagnosis.—Medium to large (maximum width 44–30 mm; length approximately 35–28 mm), transverse shell. Sinus and fold conspicuous. Lateral flanks generally smooth. Commissure uniplicate to weakly parasulcate. Umbonal cavities moderately to distinctly thickened. Dorsal tabellae normally short, straight, and divergent.

Description.—Shell medium to large, moderately biconvex, and markedly transverse. Ventral valve with umbo weakly recurved, sinus conspicuous and begins at umbo, distinctly widening to the anterior margin. Lateral flanks generally smooth. Dorsal valve with a prominent sub-rectangular fold well differentiated from flanks. In some specimens inconspicuous plicae could be observed on flanks, but otherwise smooth. Commissure uniplicate to weakly parasulcate. Micro-ornament generally poorly preserved, but evidence of it observed in one specimen, which shows the typical grooves characteristic of *Tomioopsis*. The ventral valve interior with dental plates conspicuous, sub-parallel, flexed and extended about one third to middle of the valve length. The muscle field is widely variable but in mature specimens it is markedly elongate and strongly impressed. Umbonal cavities are moderately to distinctly thickened in mature specimens. The dorsal valve interior with tabellae normally short, straight, and divergent. In some juvenile specimens they can be flexed and sub-parallel.

Etymology.—For Roger Pierson in recognition of his significant assistance in the field work.

Types.—Holotype, an internal mold of articulate specimen NMV P309931.

Other material.—Three ventral valves (NMV P309922, 309925, 309930; three ventral internal molds (UQF 73042, 73040; NMV P309923); one dorsal internal mold (UQF 73043); fourteen internal molds of articulate specimens (NMV P309924, 309926, 309927, 309928, 309929, 309932, 309933, 309934, 309935, 309936, 309937, 309938, 309939, 309940).

Occurrence.—Upper part of Wasp Head Formation (GRS11c–d), Wasp Head locality; early Sakmarian.

Remarks.—Specimens of the new species described here can be compared with those from the Tiverton Formation, assigned to *Tomioopsis elongata* by Waterhouse et al. (1983, pl. 3, figs. 5, 10, 13). However, Clarke (1992) claimed that the Waterhouse specimens were misidentified because he thought they were

closer to *Tomioopsis branxtonensis* (Etheridge). McClung (1978) noted some morphological variability in *Tomioopsis branxtonensis* and suggested that the older specimens of this species show less variation in height and number of lateral plicae than those from younger beds. Weakly plicate specimens of *Tomioopsis branxtonensis* from younger beds resemble *Tomioopsis ovata* Campbell, 1959, whereas those with stronger plicae are more similar to *Tomioopsis profunda* Campbell, 1961. Specimens of the new species from Wasp Head Formation here proposed are weakly plicate to smooth, thus suggesting a strong affinity with the younger specimens of *Tomioopsis branxtonensis*.

TOMIOOPSIS? sp.
Figure 7.29

Material.—One internal mold of articulate specimen (NMV P309941).

Occurrence.—Upper part of the Wasp Head Formation (GRS11c–d), Wasp Head locality; early Sakmarian.

Remarks.—This specimen has a maximum width of 32 mm and length of 24 mm. It is possibly a species of *Tomioopsis*, but different to those described above because of its conspicuous and wide sinus, a parasulcate commissure, and three strong angular plicae on each flanks. Its ventral interior has short subparallel ventral plates which enclose a barely impressed long muscle field. Some internal molds described by McClung (1978, pl. 9, figs. 22–24) as *Ingelarella davidi* from Elderslie Formation, northern Sydney Basin, then reassigned to *gen.? davidi* by Waterhouse (1998), appears to be close with the specimen here described.

Superfamily SPIRIFEROIDEA King, 1846
Family TRIGONOTRETIDAE Schuchert, 1893
Subfamily TRIGONOTRETINAE Schuchert, 1893
Genus TRIGONOTRETA Koenig, 1825

Diagnosis.—Medium to large, impunctate and uniplicate shells of typical spiriferid form with lateral fasciculate costae; delthyrial plate absent, but apex of delthyrium usually blocked by bulbous callist; ventral interior with dental plates; dorsal valve without crural plates; ventral postero-cardinal regions heavily thickened with callus (Clarke, 1979).

TRIGONOTRETA STOKESI Koenig, 1825
Figure 8.1–8.16

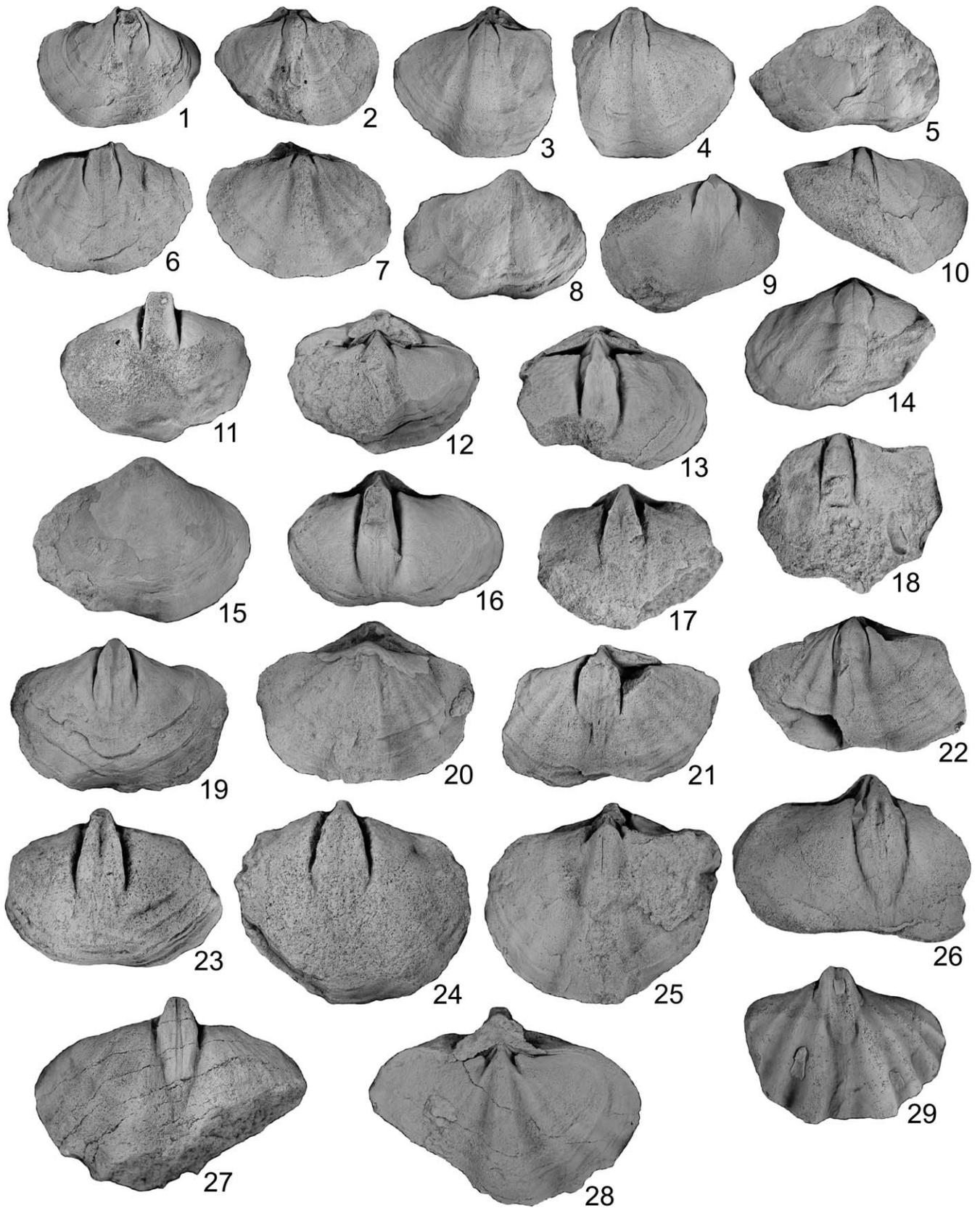
- 1979 *Trigonotreta stokesi* Koenig, CLARKE, 1979, p. 199, pl. 1, figs. 1–9, pl. 2, figs. 1–9.
1990 *Trigonotreta stokesi*, CLARKE, p. 62, fig. 7A–7H.
1992 *Trigonotreta stokesi*, CLARKE, p. 18, fig. 7A–7H.

Diagnosis.—Ventral muscle platform long, narrow, almost parallel-sided, and frequently notched posteriorly (Clarke, 1979).

Material.—One ventral internal mold (UQF 73023); two dorsal internal molds (UQF 73022; NMV P309958); seventeen ventral valves (UQF 73021, NMV P309942, 309943, 309945, 309946, 309947, 309948, 309949, 309950, 309951, 309952, 309953, 309954, 309955, 309956, 309959, 309961); two fragmentary articulate specimens (NMV P309944, 309960); one fragmentary dorsal valve (NMV P309957).

Occurrence.—Upper part of the Wasp Head Formation (GRS9, GRS10, GRS11b), Emily Miller Beach, and Wasp Head localities; early Sakmarian.

FIGURE 7—1–28, *Tomioopsis piersoni* n. sp.: 1, 2, NMV P309927, internal mold of articulate specimen, ventral and dorsal views, $\times 1.2$; 3, 4, NMV P309928, internal mold of articulate specimen, dorsal and ventral views, $\times 1.2$; 5, NMV P309925, ventral valve, $\times 1.2$; 6, 7, NMV P309929, internal mold of articulate specimen, ventral and dorsal views, $\times 1.1$; 8, NMV P309930 ventral valve, $\times 1.1$; 9, 10, internal mold of articulate specimen, ventral and dorsal views, NMV P309924, $\times 1.1$; 11, 12, NMV P309936, internal mold of articulate specimen, ventral and dorsal views, $\times 1.2$; 13, 14, NMV P309926, internal mold of articulate specimen, ventral and dorsal views, $\times 1.2$; 15, NMV P309922, ventral valve, $\times 1.2$; 16, NMV P309923, ventral internal mold, $\times 1.2$; 17, 18, NMV P309938, internal mold of articulate specimen, ventral and dorsal views, $\times 1.2$; 19, 20, holotype, NMV P309931, internal mold of articulate specimen, ventral and dorsal



views, $\times 1.2$; 21, 22, NMV P309937, internal mold of articulate specimen, ventral and dorsal views, $\times 1.2$; 23, NMV P309935, internal mold of articulate specimen, ventral view, $\times 1.1$; 24, 25, NMV P309932, internal mold of articulate specimen, ventral and dorsal views, $\times 1.1$; 26, NMV P309940, internal mold of articulate specimen, ventral views, $\times 1.1$; 27, 28, NMV P309933, internal mold of articulate specimen, ventral and dorsal views, $\times 1.1$; 29, *Tomiopsis?* sp., NMV P309941, ventral internal mold, $\times 1.1$.

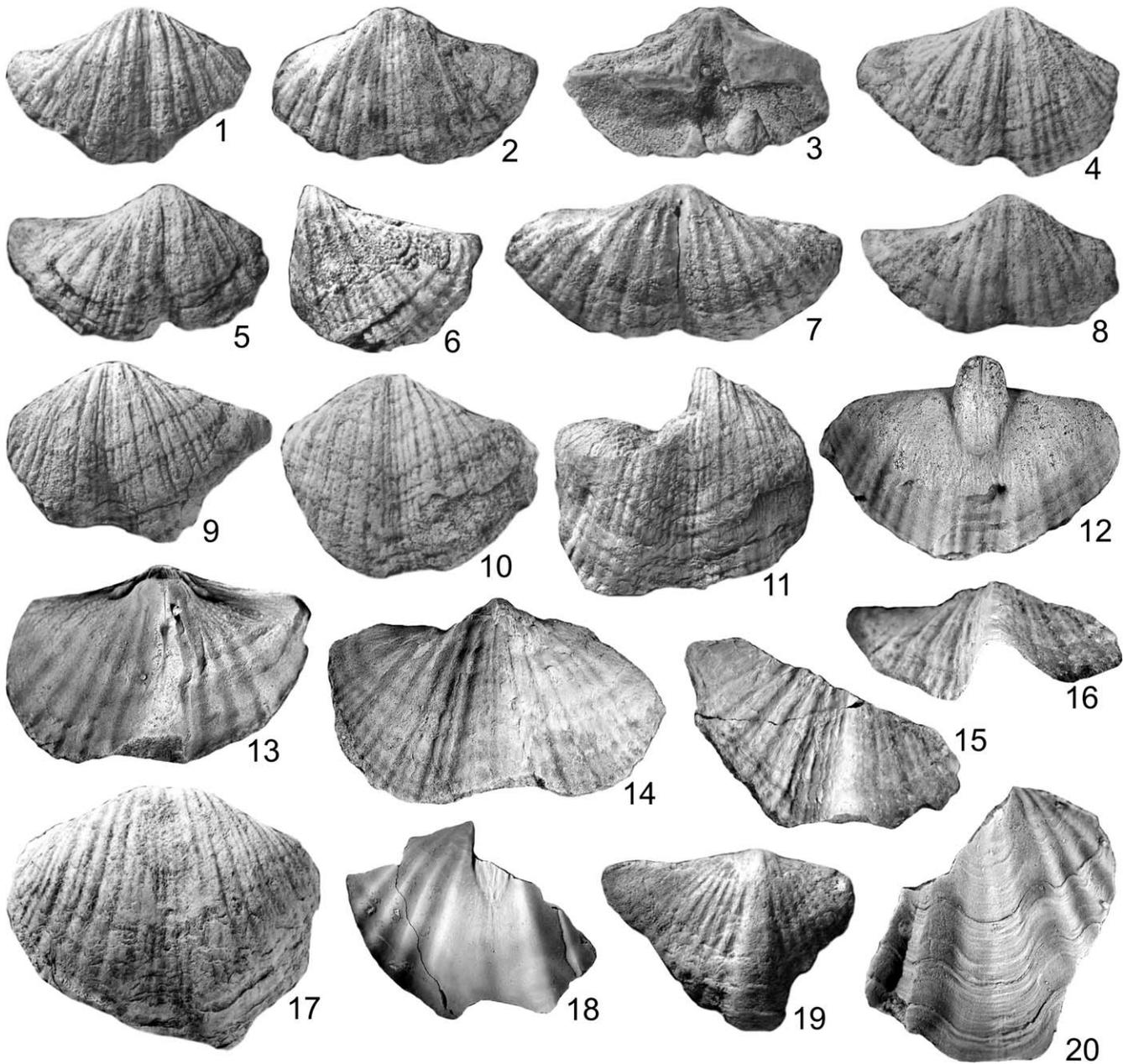


FIGURE 8—16, *Trigonotreta stokesi* Koenig: 1, NMV P309942, ventral valve, $\times 1.1$; 2, 3, NMV P 309943, ventral valve, frontal view interarea views, $\times 1.1$; 4, NMV P309945 ventral valve, $\times 1.1$; 5, NMV P309946, ventral valve, $\times 1.1$; 6, NMV P309947, fragmentary ventral valve showing the fasciculation pattern, $\times 1.1$; 7, NMV P309950, ventral valve, $\times 1.1$; 8, NMV P309952 ventral valve, $\times 1.1$; 9, NMV P309954, ventral valve, $\times 1$; 10, NMV P309956, ventral valve, $\times 1$; 11, NMV P309955, ventral valve, $\times 1$; 12, UQF 73023, ventral internal mold, $\times 1$; 13, UQF 73022, dorsal internal mold, $\times 1.1$; 14, NMV P309958, dorsal internal mold, $\times 1.1$; 15, 16, NMV P309957, fragmentary dorsal valve, dorsal and anterior views, $\times 1.1$; 17, Trigonotretidae ind., NMV P309962, ventral view, $\times 1$; 18–20, *Pseudosyrinx?* sp.: 18, 20, NMV P309964a–b, fragmentary ventral internal and external mold, $\times 1$; 19, NMV P309963, dorsal internal mold, $\times 1$.

Remarks.—In addition to the diagnosis suggested by Clarke (1990), *Trigonotreta stokesi*, usually characterized by costae in bundle of three, can also exhibit a costae pattern widely variable from more coarsely to more finely fasciculate. The wide range of variation of the costae pattern is usually only observable in large populations (Clarke, 1992). More equidimensional forms tend to be coarsely fasciculate (Clarke, 1992, fig. 7F) whereas more transverse forms are more finely fasciculate with more equidimensional costae (Clarke, 1992, fig. 7E). Also, although a long and narrow ventral muscle platform has been proposed as a specific diagnosis for this species Clarke (1979), the studies of large populations of other Trigonotretinae species indicate that this character can also be variable and susceptible to ontogenetic

changes, even within the same species (Cisterna and Archbold, 2007).

Two small eastern Australian species of *Trigonotreta*, *T. victoriae* from Bacchus Marsh of Victoria (Archbold, 1991) and *T. tangorini* from the Cranky Corner Basin of New South Wales (Archbold, 2003), are both characterized by possessing relatively uniform coarse costae, somewhat similar to *Trigonotreta stokesi*. Consequently, they were treated by Archbold (2003) as two separate subspecies of *Trigonotreta stokesi*. However, in view of the above explained, these species could be considered as synonymy. Recently, *Trigonotreta tangorini* has been included by Waterhouse (2008) in his new genus *Neilotreta*. But *Neilotreta*

was defined to include trigonotretids with four or five pairs of simple plicae on each valve and costae limited mainly to sulcus and fold, as well as that the crest of the plicae rarely split into two costae. In *Trigonotreta tangorini*, the costae (Archbold, 2003, fig. 4.7) appear to be very close to those in *Trigonotreta stokesi* (Clarke 1990, fig. 7G; Clarke, 1992, fig. 7F). Also of note is that fasciculation in this species is more regularly developed on ventral flanks than on dorsal flanks, and therefore the comparison with other species should be based on the ventral fasciculate pattern.

ACKNOWLEDGMENTS

The authors wish to thank to R. Pierson for his valuable help in the field and laboratory work, and also for his assistance in editing parts of this paper; to Deakin University and CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina) that provided the financial support for the stay in Australia of GAC. The study was in part supported by an Australian Research Council Discovery grant (DP0772161, to GRS). Thanks are extended to A. Pérez Huerta and S. Shen for reviewing the manuscript, providing constructive suggestions.

REFERENCES

- APAK, S. N. AND J. BACKHOUSE. 1999. Stratigraphy and petroleum exploration objectives of Permo–Carboniferous succession on the Barbwire Terrace and adjacent areas, northwest Canning Basin Western Australia. *Geological Survey of Western Australia*, 29:267–276.
- ARCHBOLD, N. W. 1983. Permian marine invertebrate provinces of Gondwana Realm. *Alcheringa*, 7:59–73.
- ARCHBOLD, N. W. 1991. *Trigonotreta* (Spiriferida, Brachiopoda) from the Early Permian of Victoria. *Alcheringa*, 15:321–326.
- ARCHBOLD, N. W. 1996. Paleobiogeography of Australian Permian brachiopod faunas, p. 19–23. *In* P. Copper and J. Jisuo (eds.), *Proceeding of the Third International Brachiopod Congress*. A. A. Balkema, Rotterdam.
- ARCHBOLD, N. W. 2000. Palaeobiogeography of the Australasian Permian. *Memoir of Association of Australasian Palaeontologists*, 23:287–310.
- ARCHBOLD, N. W. 2001. Pan-Gondwanan, Early Permian (Asselian–Sakmarian–Aktastinian) correlations, p. 29–39. *In* R. H. Weiss (ed.), *Contributions to Geology and Palaeontology of Gondwana in honour of Helmut Wopfner*. Geological Institute, University Cologne, Cologne.
- ARCHBOLD, N. W. 2003. Marine Early Permian (Asselian–Sakmarian) invertebrates Palaeontology of DM Tangorin DDH1Cranky Corner Basin, New South Wales. New South Wales department of Mineral Resources, Coal and Petroleum Bulletin, 4:155–166.
- ARCHBOLD, N. W. AND G. A. THOMAS. 1986. Permian Ingelarellidae (brachiopoda) from Western Australia and Argentina. *Journal of Paleontology*, 60:581–605.
- ARMSTRONG, E. C. 1969. The Martiniacean species occurring at Glendon, New South Wales, the type locality of *Notospirifer darwini* (Morris). *Journal of the Royal Society of New South Wales*, 101:197–204.
- ARMSTRONG, E. C. 1970. Micro-ornaments of the spiriferid brachiopods *Notospirifer*, *Ingelarella* and *Subansiria*. *Lethaia*, 3:287–300.
- BALINSKI, A. 1975. Secondary changes in microornamentation of some Devonian ambocoelid brachiopods. *Palaeontology*, 18:179–189.
- BENEDIKTOVA, R. N. 1956. Spiriferidy Ostrogskoj svity Kuzbassa. *Voprosy Geologii Kuzbassa, Materialy vtorogo soveshcheniya po stratigrafii ugljenosnykh otlozhenii*, 1:169–182. (In Russian)
- BRIIGGS, D. J. C. 1998. Permian Productidina and Strophalosiidina from the Sydney-Bowen Basin and New England Orogen: Systematics and biostratigraphic significance. *Memoir of the Association of Australasian Palaeontologists*, 19:1–258.
- BRUNTON, H. C. 1976. Micro-ornamentation of some spiriferide brachiopods. *Palaeontology*, 19:767–771.
- BRUNTON, H. C., S. S. LAZAREV, AND R. E. GRANT. 2000. Productida, p. 350–643. *In* A. Williams et al. (eds.), *Treatise on Invertebrate Paleontology*, Pt. H, Brachiopoda (revised) 2–3. Geological Society of America and University of Kansas Press, Lawrence.
- CAMPBELL, K. S. W. 1959. The *Martiniopsis*-like spiriferids of the Queensland Permian. *Palaeontology*, 1:333–350.
- CAMPBELL, K. S. W. 1961. New species of the Permian spiriferoids *Ingelarella* and *Notospirifer* from Queensland and their stratigraphic implications. *Palaeontographica*, Abteilung A, 117:159–192.
- CAMPBELL, K. S. W. 1965. Australian Permian Terebratuloids. *Bulletin of the Department of National Development Bureau of Mineral Resources, Geology and Geophysics*, 68:1–146.
- CARTER, J. L. AND R. GOURVENNEC. 2006. Martinioida, p. 1747–1768. *In* R. L. Kaesler (ed.), *Treatise on Invertebrate Paleontology*, Pt. H, Brachiopoda (revised) 5. Geological Society of America and University of Kansas Press, Lawrence.
- CARTER, J. L., J. G. JOHNSON, R. GOURVENNEC, AND H.-F. HOU. 2006. Spiriferida, p. 1689–1870. *In* A. Williams et al. (eds.), *Treatise on Invertebrate Paleontology*, Pt. H, Brachiopoda (revised) 5. Geological Society of America and University of Kansas, Lawrence.
- CISTERNA, G. A. AND N. W. ARCHBOLD. 2007. Spiriferoida (brachiopoda) from the early Permian del Salto Formation of Argentina. *Alcheringa*, 31:3–16.
- CISTERNA, G. A. AND A. F. STERREN. 2008. Late Carboniferous *Levipustula* fauna in the Leoncito Formation, San Juan province, Argentine Precordillera: Biostratigraphical and palaeoclimatological implications. *Proceedings of the Royal Society of Victoria*, 120:137–147.
- CISTERNA, G. A. AND A. F. STERREN. 2010. “*Levipustula* Fauna” in central-western Argentina and its relationships with the Carboniferous glacial event in the southwestern Gondwanan margin. *Geological Society of America Special Paper*, 468:133–147.
- CLAPHAM, M. E. AND N. P. JAMES. 2008. Paleocology of early-middle Permian marine communities in eastern Australia: Response to global climate change in the aftermath of the late Palaeozoic ice age. *Palaios*, 23:738–750.
- CLAPHAM, M. E. AND N. P. JAMES. 2012. Regional-scale marine faunal change in eastern Australia during Permian climate fluctuations and its relationship to local community restructuring. *Palaios*, 27:627–635.
- CLARKE, M. J. 1969. Tasmanian Strophalosiidae. *Record of Geological Survey of Tasmania*, 10:1–51.
- CLARKE, M. J. 1979. The Tasmanian Permian spiriferid brachiopods *Trigonotreta rachi* Koenig, 1825, *Grantonia hobartensis* Brown, 1953 and *Spirifer tasmaniensis* Morris, 1845. *Journal of Paleontology*, 53:197–207.
- CLARKE, M. J. 1990. Late Palaeozoic (Tamarian; Late Carboniferous–Early Permian) cold-water brachiopods from Tasmania. *Alcheringa*, 14:53–76.
- CLARKE, M. J. 1992. Hellyerian and Tamarian (Late Carboniferous–Lower Permian) invertebrate faunas from Tasmania. *Geological Survey of Tasmania Bulletin*, 69:1–52.
- CLARKE, M. J. AND N. FARMER. 1976. Biostratigraphic nomenclature for late Palaeozoic rocks in Tasmania. *Papers and Proceedings of the Royal Society of Tasmania*, 110:91–109.
- DICKINS, J. M., V. A. GOSTIN, AND B. N. RUNNEGAR. 1969. The age of the Permian sequence in the southern part of the Sydney Basin, p. 211–255. *In* K. S. W. Campbell (ed.), *Stratigraphy and Palaeontology, Essays in Honour of Dorothy Hill*. Australian National University Press, Canberra.
- DI PASCUO, M., M. MARTÍNEZ, AND H. FREJE. 2008. The first palynological record of the Sauce Grande Formation (Pennsylvanian–Cisuralian) at the Australes range, Buenos Aires province, Argentina. *Ameghiniana*, 45:69–81.
- DUMÉRIL, A. M. C. 1806. *Zoologie analytique ou rachi naturelle de classification de animaux*. Allais, Paris, 344 p.
- ETHERIDGE, R. 1892. The organic remains of the Permo–Carboniferous System. Class Brachiopoda, p. 225–264. *In* R. L. Jack and R. Etheridge (eds.), *The Geology and Palaeontology of Queensland and New Guinea*. Government Printer, Brisbane and Dulau and Company, London.
- FIELDING, C. R., T. D. FRANK, L. P. BIRGENHEIER, M. C. RYSEL, A. T. JONES, AND J. ROBERTS. 2008a. Stratigraphic imprint of the late Palaeozoic Ice Age in eastern Australia: A record of alternating glacial and nonglacial climate regime. *Journal of the Geological Society*, 165:129–140.
- FIELDING, C. R., T. D. FRANK, L. P. BIRGENHEIER, M. C. RYSEL, A. T. JONES, AND J. ROBERTS. 2008b. Stratigraphic record and facies associations of the late Palaeozoic age in Eastern Australia (New South Wales and Queensland). *Geological Society of America Special Paper*, 441:41–57.
- FOSTER, C. B. AND N. W. ARCHBOLD. 2001. Chronologic anchor points for the Permian and early Triassic of the eastern Australian basins, p. 175–197. *In* R. H. Weiss (ed.), *Contributions to Geology and Palaeontology of Gondwana, in Honour of Helmut Wopfner*. Geological Institute, University of Cologne.
- GOSTIN, V. A. AND C. HERBERT. 1973. Stratigraphy of the Upper Carboniferous and Lower Permian sequence, southern Sydney Basin. *Journal of the Geological Society of Australia*, 20:49–70.
- GOURVENNEC, R. AND J. L. CARTER. 2007. Spiriferida and Spiriferinida, p. 2772–2796. *In* P. A. Selden (ed.), *Treatise on Invertebrate Paleontology*, Part H, Brachiopoda (revised) 6 supplement. Geological Society of America and University of Kansas, Lawrence.
- HARRINGTON, H. J. 1955. The Permian *Eurydesma* fauna of eastern Argentina. *Journal of Paleontology*, 29:112–128.
- KING, W. 1844. On a new genus of Palaeozoic shells. *Annals and Magazine of Natural History*, 14:313–317.
- KING, W. 1846. Remarks on certain genera belonging to the class Palliobranchiata. *Annals and Magazine of Natural History*, London 18: 26–42, 83–94.
- KOENIG, C. 1825. *Icones Fossilium Sectiles*. British Museum, London, 4 p.

- KONINCKI, L. G. 1877. Recherches sur les rachio Palaeozoïques de la Nouvelle-Galles du Sud (Australie). Mémoires de la Société des Sciences de Liège, 2(7):1–235.
- LÓPEZ GAMUNDÍ, O. R., P. J. CONAGHAN, AND E. A. ROSSELLO. 1995. The Tunas Formation (Permian) in the Sierras Australes fold belt, east central Argentina: Evidence for syntectonic sedimentation in a foreland basin. *Journal of South American Earth Sciences*, 8(2):129–142.
- MCCLUNG, G. 1978. Morphology, palaeoecology and biostratigraphy of *Ingelarella* (Brachiopoda: Spiriferida) in the Bowen and Sydney Basins of Eastern Australia. Geological Survey of Queensland, Publication 365, Palaeontological Paper, 40:17–60.
- MCCLUNG, G. AND J. D. ARMSTRONG. 1975. New species of *Martiniopsis* (Brachiopoda: Spiriferida) from the Permian of eastern Australia. *Queensland Government Mining Journal*, 76:231–234.
- MCCLUNG, G. AND J. D. ARMSTRONG. 1978. Species of *Glendonina* gen. nov. (Ingelarellinae: Spiriferida) in the Permian of eastern Australia. Geological Survey of Queensland Publication 365, Palaeontological Paper, 39:1–9.
- MORY, A. J. AND J. BACKHOUSE. 1997. Permian stratigraphy and palynology of the Carnarvon Basin, Western Australia. Geological Survey of Western Australia Report, 51:1–41.
- NILSEN, S. A. A. 1982. A paleontological study of the Permian Wasp Head Formation and the lowermost Pebbly Beach Formations of the southern Sydney Basin, New South Wales. Unpublished M.Sc. Thesis, Department of Geology and Mineralogy, University of Queensland, 188 p.
- PAGANI, M. A. 1998. Braquiópodos y gastrópodos pérmicos de las Formaciones Piedra Azul Bonete (Provincia de Buenos Aires). *Ameghiniana*, 35:265–270.
- PAGANI, M. A. 2000. Bivalvos del Pérmico Inferior de la Formación Bonete, Sierras Australes (provincia de Buenos Aires, Argentina). *Ameghiniana*, 37:301–329.
- RUNNEGAR, B. N. 1969. Permian fossils from the southern extremity of the Sydney Basin, p. 276–298. In K. S. W. Campbell (ed.), *Stratigraphy and Palaeontology*. Australian National University Press, Canberra.
- RUNNEGAR, B. N. 1980. Biostratigraphy of the Shoalhaven Group. *Bulletin of Geological Survey NSW*, 26:376–382.
- RUNNEGAR, B. N. AND G. MCCLUNG. 1975. A Permian time scale for Gondwanaland, p. 425–441. In K. S. W. Campbell (ed.), *Gondwana Geology Papers presented at the Third Gondwana Symposium*. Australia National University, Canberra.
- RYGEL, M. C., C. R. FIELDING, K. R. BANN, T. D. FRANK, L. P. BIRGENHEIER, AND S. C. TYE. 2008. The Lower Permian Wasp Head Formation, Sydney Basin: High-latitude, shallow marine sedimentation following the late Asselian to early Sakmarian glacial event in eastern Australia. *Sedimentology*, 55:1517–1540.
- SAHNI, M. R. AND J. P. SRIVASTAVA. 1956. Discovery of *Eurydesma* and *Conularia* in the eastern Himalaya and description of associated faunas. *Journal of the Palaeontological Society of India*, 1:202–214.
- SARYTCHEVA, T. G. AND A. N. SOKOLSKAYA. 1959. O klassifikatsin lozhnoporistykh brachiopod. *Akademiia Nauk SSSR, Doklady (Moscow)*, 125:181–184. (In Russian)
- SCHUCHERT, C. 1913. Class Brachiopoda. The Lower Devonian deposits of Maryland. Maryland Geological Survey, Baltimore, p. 290–2449.
- SCHUCHERT, C. 1893. A classification of the Brachiopoda. *American Geologist*, 11(3):141–167.
- SHEN, S. Z., G. R. SHI, AND K. Y. ZHU. 2000. Early Permian brachiopods of Gondwana affinity from the Dingjiazhai Formation, Baoshan Block, western Yunnan, China. *Rivista Italiana di Paleontologia e Stratigrafia*, 106:263–282.
- SHEN S. Z., H. ZHANG, G. R. SHI, W. Z. LI, J. F. XIE, L. MU, AND J. X. FAN. 2013. Early Permian (Cisuralian) global brachiopod palaeobiogeography. *Gondwana Research*, 24:104–124.
- SHI, G. R. AND N. W. ARCHBOLD. 1993. Distribution of Asselian to Tastubian (early Permian) Circum Pacific brachiopod faunas. *Memoir of Association of Australasian Palaeontologists*, 15:343–351.
- SHI, G. R., J. B. WATERHOUSE, AND S. MCLOUGHLIN. 2010. The Lopingian of Australasia: A review of biostratigraphy, correlations, palaeogeography, and palaeobiogeography. *Geological Journal*, 45:230–263.
- STEHLI, F. G. 1954. Lower Leonardian Brachiopoda of the Sierra del Diablo. *Bulletin of American Museum of Natural History*, 105:257–358.
- TYE, S. C., C. R. FIELDING, AND B. G. JONES. 1996. Stratigraphy and sedimentology of the Permian Talaterang and Shoalhaven Groups in the southernmost Sydney Basin, New South Wales. *Australian Journal of Earth Sciences*, 43:57–69.
- WAAGEN, W. 1883. Salt Range Fossils. I. Productus-Limestone Fossils. *Memoirs of the Geological Survey of India, Palaeontologia Indica, Series 13*, 4:391–546.
- WAAGEN, W. 1884. Salt Range Fossils. I. Productus-Limestone Fossils. *Memoirs of the Geological Survey of India, Palaeontologia Indica, Series 13*, 4:547–610.
- WATERHOUSE, J. B. 1971. The brachiopod genus *Tomioopsis* Benedictova from the Permian of Canada. *Journal of Paleontology*, 45:68–80.
- WATERHOUSE, J. B. 1986. A new Permian brachiopod genus related to *Ambikella* Sahni and Srivastava. *Bulletin Indian Geological Association*, 19(2):109–112.
- WATERHOUSE, J. B. 1987. Late Palaeozoic Mollusca and correlations from the Southeast Bowen Basin, east Australia. *Palaeontographica, Abteulung A*, 198:1–233.
- WATERHOUSE, J. B. 1998. Ingelarelloidea (Spiriferida: Brachiopoda) from Australia and New Zealand, and reclassification of Ingelarellidae and Notospiriferidae. *Earthwise*, 1:1–48.
- WATERHOUSE, J. B. 2008. Golden Spikes and black flags: Macro-invertebrate faunal zones for the Permian of east Australia. *Proceedings of the Royal Society of Victoria*, 120(1):345–372.
- WATERHOUSE, J. B. 2011. Origen and evolution of Permian brachiopods of Australia. *Memoirs of the Association of Australasian Palaeontologist*, 41:205–228.
- WATERHOUSE, J. B. AND G. R. SHI. 2010. Evolution in a cold climate. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 298:17–30.
- WATERHOUSE, J. B. AND G. R. SHI. 2013. Climatic implications from the sequential changes in diversity and biogeographic affinities for brachiopods and bivalves in the Permian of eastern Australia and New Zealand. *Gondwana Research*, 24:139–147.
- WATERHOUSE, J. B., D. J. C. BRIGGS, AND S. M. PARFREY. 1983. The major faunal assemblages in the Early Permian Tiverton Formation near Homevale Homestead, Northern Bowen basin, Queensland, p. 121–138. In C. B. Foster (ed.), *Permian Geology of Queensland*, Brisbane. Geological Society of Australia, Queensland Division.
- WELDON, E. A. AND G. R. SHI. 2001. The Late Palaeozoic Brachiopod Genus *Tomioopsis* Benediktova, 1956 from Eastern Australia: Palaeobiogeographic implications. *Gondwana Research*, 4:822–823.
- WHITFIELD, R. P. 1908. Notes and observations on Carboniferous fossils and semifossil shells brought home by members of the Peary expedition of 1905–1906. *Bulletin of the American Museum of Natural History*, 24(2):51–58.
- WILLIAMS, A. 1953. The classification of the strophomenoid brachiopods. *Washington Academy of Sciences Journal*, 43:1–13.
- WILLIAMS, A., S. J. CARLSON, C. H. C. BRUNTON, L. E. HOMER, AND L. E. POPOV. 1996. A supra-ordinal classification of the Brachiopoda. *Philosophical Transactions of the Royal Society of London, Series B*, 351:1171–1193.
- WILLIAMS, A., C. H. C. BRUNTON, AND A. D. WRIGHT. 2000. Orthotetida, p. 644–689. In A. Williams et al. (eds.), *Treatise on Invertebrate Paleontology*. Pt. H. Brachiopoda (revised) 3. Geological Society of America and University of Kansas, Lawrence.