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A Darriwilian (Middle Ordovician) bivalve-dominated molluscan fauna from the Stairway Sandstone, Amadeus Basin, central Australia

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A bivalve-dominated molluscan fauna is described from the Darriwilian (Middle Ordovician) Stairway Sandstone, Amadeus Basin, central Australia. The fauna comprises 16 species of bivalves and rostroconchs plus six gastropod species which are treated under open nomenclature. Two new bivalves, *Sthenodonta paenesymmetrica* sp. nov. and *Modiolopsis pojetai* sp. nov., are described. The relatively low-diverse molluscan fauna constitutes around 62% of the total benthic macrofauna. Approximately 75% of the molluscs comprise bivalves, especially nuculoids, which were biogeographically restricted to low latitudes during the Ordovician. The molluscan assemblage displays a very high degree of endemism at species level, though the bivalve *Sthenodonta eastii* also occurs in the Georgina Basin farther to the northeast. This indicates a possible marine connective seaway between the Georgina and Amadeus basins during the Darriwilian. *Nuculites*, *Cyrtodonta*, and *Modiolopsis* are cosmopolitan and previously reported from North China, Avalonia, and Southern Gondwana.

Key words: Mollusca, Bivalvia, endemism, biodiversity, Ordovician, Darriwilian, Central Australia.

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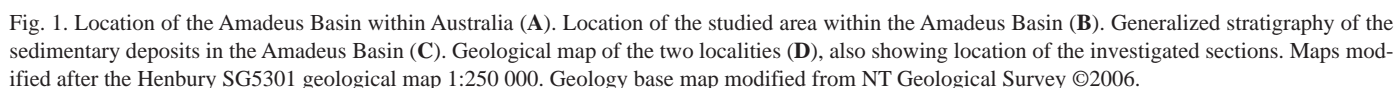
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Introduction

During the Great Ordovician Biodiversification Event (GOBE), recognized as the longest interval of sustained biodiversification during the Phanerozoic (Sepkoski 1995; Webby 2004; Harper 2006; Servais et al. 2010), three diversity maxima occurred. The first major biodiversity surge took place during the Middle Ordovician with an extensive expansion of the benthos (Babin 1993, 1995, 2001; Cope and Babin 1999; Cope 2002, 2004; Fang 2006; Fang and Sánchez 2012). The event was diachronous not only across different regions but also across different fossil groups with bivalves initially favouring siliciclastic environments in deeper wa-

ter at high latitudes (Novack-Gottshall and Miller 2003). The Stairway Sandstone, a thick (up to 600 m) package of siliciclastics in the Amadeus Basin, central Australia, was deposited during the peak of this biodiversity expansion in the early Darriwilian (Middle Ordovician). The depositional environment was a shallow-marine epeiric shelf, part of the so-called Larapintine Sea, covering large parts of central Australia during the Early and Middle Ordovician (see also Webby 1978; Haines and Wingate 2007). The fauna of the Stairway Sandstone is dominated by molluscs in preference to brachiopods that are common at this stratigraphic level in other regions (Harper 2006).

The main goal of this study is to document the benthic diversity among the molluscs from the Stairway Sandstone.



Areyonga Gorge (232 m thick) were logged and systematically sampled for microfossils (Fig. 1). Most beds suspected to contain carbonate were sampled for conodonts in order to provide age control and broader scale correlation. The present study represents the first palaeontological analy-

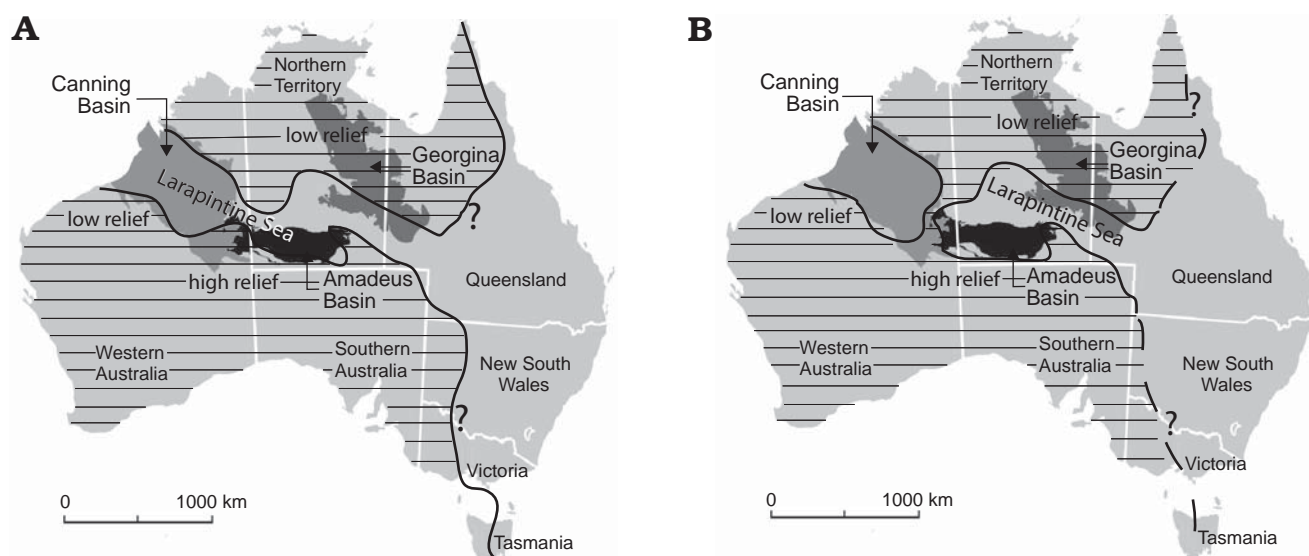


Fig. 2. Distribution of the Larapintine Sea in the Middle Ordovician. The extent of the Canning, Amadeus, and Georgina basins, all containing Middle Ordovician deposits, have been inferred together with the extent of continental landmass (marked with horizontal lines). Base map modified from Webby 1978. **A.** Webby's interpretation (1978). **B.** New interpretation based on faunal correlation. Note the broken connection between the Amadeus–Georgina basins and the Canning Basin.

sis of systematically collected samples through the entire Stairway Sandstone package and provides new data on biodiversity, biofacies and correlation of faunas.

Institutional abbreviations.—CPC, Commonwealth Palaeontological Collections, Geoscience Australia, Canberra, Australia; SAM T, South Australian Museum, Adelaide, Australia, collection of the type material investigated by Pojeta and Gilbert-Tomlinson (1977).

Geological setting

Australia straddled the Equator during the Middle Ordovician, forming part of the northeastern margin of Gondwana (Scotese 2002; Blakey 2011; Torsvik et al. 2014). Australia hosts a number of Late Proterozoic to Mesozoic sedimentary basins including the Georgina Basin, Canning Basin, Ngalia Basin, Officer Basin, Warburton Basin, Eromanga Basin, and Amadeus Basin (e.g., Edgoose 2012). Ordovician deposits are only present in some of these basins and exposures of Middle Ordovician strata occur mainly in the Georgina and Amadeus basins (Fig. 2). The Canning Basin in Western Australia, stretching towards central Australia, contains Middle Ordovician strata in the subsurface.

An extensive and long-lived Ordovician transgression resulted in development of the epicontinental Larapintine Sea, originally interpreted to have stretched across the central sector of the continent (Webby 1978). The shallow marine siliciclastics that comprise the Darriwilian Stairway Sandstone were deposited in the central part of the proposed Larapintine Sea in the Amadeus Basin (Fig. 2A) according to Webby (1978). The palaeoclimate at this time was probably semi-arid to arid (Cook 1970; Wells et al. 1970) and

the palaeolatitude is inferred to have been around 15° N (cf. Scotese 2002; Blakey 2011; Torsvik et al. 2014).

The Larapintine Sea is interpreted by some workers to have developed from the late Tremadocian (Early Ordovician) onwards, when the western margin was connected to a narrow shelf and the open ocean (Webby 1978; Walley et al. 1991). To the east, the outer shelf and deeper water environments of the Larapintine Sea is interpreted to have extended into the palaeo-Pacific Ocean. The main axis of the Larapintine Sea was originally interpreted to straddle the Canning–Amadeus and Warburton basins with the Georgina Basin representing the northern margin of the seaway (Webby 1978; see Fig. 2). However, connection between the Canning and Amadeus basins during the Middle Ordovician is not supported by a number of authors (e.g., Veevers 1976; Haines and Wingate 2007; Jakobsen et al. 2014b), as little evidence corroborates the presence of a “Larapintine Seaway” across central Australia. A generalized outline of the Middle Ordovician Larapintine Sea based on the mollusc fauna is shown in Fig. 2B.

The early to middle Darriwilian was an interval of a maximal transgression and the Canning, Georgina, and Amadeus basins were at their maximum geographic extent in the Ordovician, demonstrated by the distribution of the lower Nita and Goldwyer formations in the Canning Basin (subsurface), the upper Stairway Sandstone and basal Stokes Siltstone formations in the Amadeus Basin and the middle part of the Nora Formation in the Georgina Basin (Webby 1978).

The Stairway Sandstone.—The Stairway Sandstone forms part of the siliciclastic dominated Larapinta Group (Fig. 3), which has a total maximum thickness of 2230 m (Laurie et al. 1991). The group comprises five formations, from the bottom to the top (maximum thickness indicated

in brackets): the Pacoota Sandstone (710 m), Horn Valley Siltstone (120 m), Stairway Sandstone (600 m), Stokes Siltstone (650 m), and Carmichael Sandstone (150 m). The Stairway Sandstone is ca. 250 m thick in each of the sections investigated but thickens northward through the Amadeus Basin. It disconformably overlies the Horn Valley Siltstone in the northern part of the basin, whereas it overlaps progressively older units to the south with a marked angular unconformity (Webby 1978; Laurie et al. 1991). The clastic facies of the Stairway Sandstone are a common trait for many lower Palaeozoic shallow water epeiric marine successions globally, being dominated by comparatively clean quartz sandstone (Lindsey and Gaylord 1992; Johnson and Baldwin 1996; Davies and Sansom 2009).

The Stairway Sandstone comprises a lower and an upper fine to medium grained quartzite unit of varying thickness separated by finer clastics in the middle part. The lower sandstone unit (average thickness 67 m in the investigated sections) alternates between planar cross-bedding, parallel lamination and wavy lamination with abundant ichnofossils at certain levels. Soft-sediment deformation such as contorted laminations and load structures are locally common and probably signal rapid sedimentation (Cook 1972). The middle unit is on average 110 m thick in the investigated sections and consists mostly of poorly exposed siltstone interbedded with fine grained thin sandstone beds and subordinate dolomitized calc-sandstone beds. This fine grained middle unit was deposited in a deeper-water, mid-shelf setting located farther offshore than the high energy, shallow marine setting characterized by deposition of the quartzite-dominated lower and upper units of the Stairway Sandstone. The upper sandstone is on average 60 m thick in the investigated sections and the base is defined by a thin conglomerate present in both sections (see also Shergold 1986).

The Stairway Sandstone hosts a diverse ichnofauna, which has been described and discussed by Gibb et al. (2009) and Davies et al. (2011). The ichnofauna represents *Skolithos* and *Cruziana* facies (e.g., Seilacher 1967; Ritchie and Gilbert-Tomlinson 1977). *Skolithos* ichnofacies and mixed *Skolithos*–*Cruziana* ichnofacies (e.g., Davies et al. 2007) dominated the high energy environment that prevailed during deposition of the lower and upper units of the Stairway Sandstone, whereas *Cruziana* ichnofacies dominate the middle fine grained unit (cf. Seilacher 1967: fig. 2). The sedimentary facies of the lower and upper sandstone units are similar with frequent cross-stratification although bioturbation in the lower unit generally is more frequent than in the upper unit.

Shergold (1986) provided a faunal list for the Stairway Sandstone. Some bivalves and rostroconchs were described by Pojeta and Gilbert-Tomlinson (1977) and Pojeta et al. (1977), but in most cases the stratigraphic level within the

Stairway Sandstone of the described fossils is unknown. All fossils were in this study collected systematically along measured stratigraphic sections through the Stairway Sandstone to provide new information on stratigraphy, biostratigraphy, local biodiversity and biofacies.

Apart from the molluscs (documented herein), trilobites and brachiopods make up about one third of the invertebrate fauna (Jakobsen et al. 2014a, b). Less common fossils include acritarchs, sponges, bryozoans, and conodonts, as well as arandaspid fishes (see Ritchie and Gilbert-Tomlinson 1977; Shergold 1986; Young 1997). The cephalopods (mostly endoceratids) are fairly rare and are not dealt with in this paper.

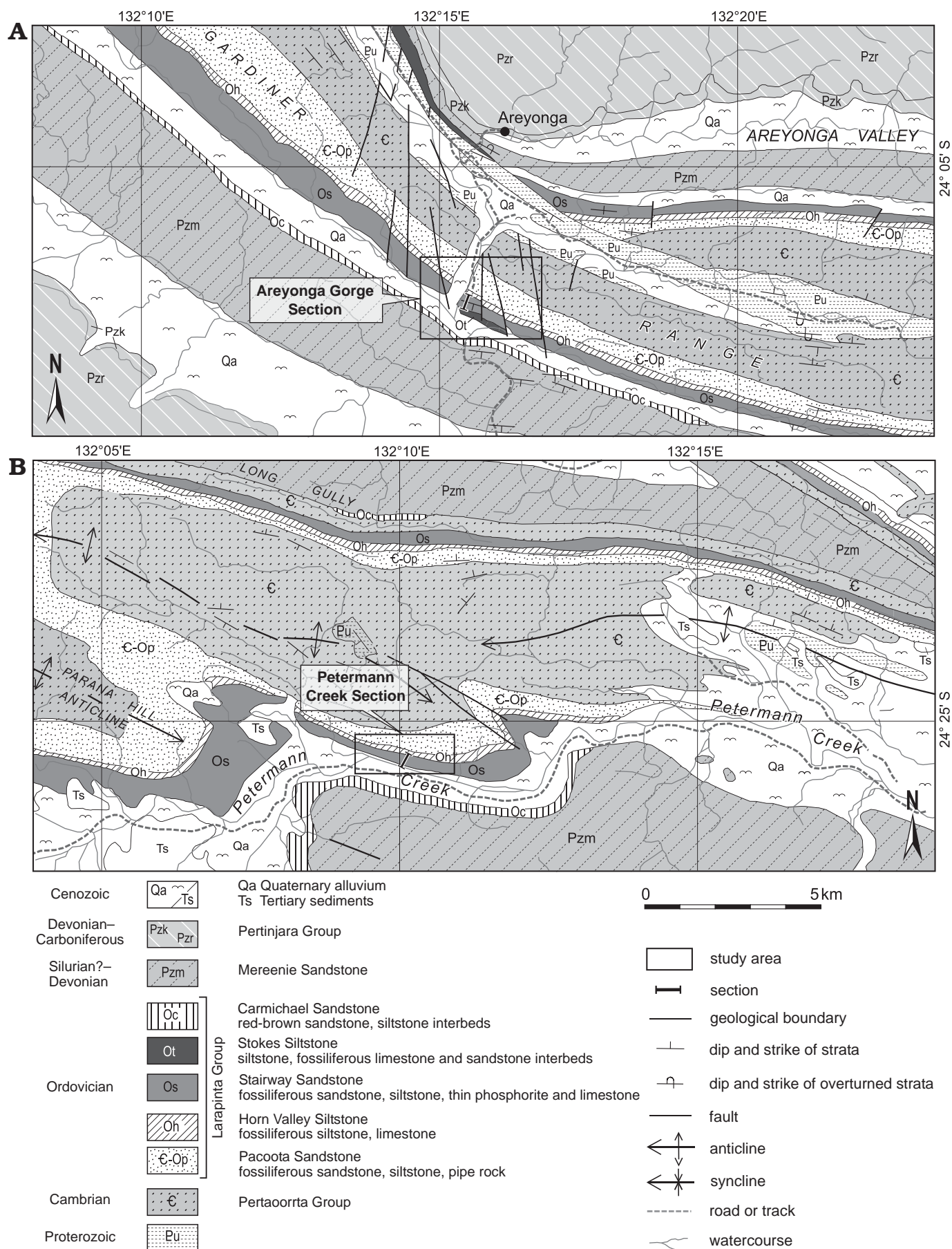
Conodonts from the Stairway Sandstone have previously been assigned to *Erraticodon*, possibly *E. balticus* Dzik, 1978, and *Aphelognathus* (Nicoll 1991). New conodont samples collected from the middle unit during this study have yielded a few hundred specimens, including *Erismodus* (Branson and Mehl 1933), *Paraprioniodus*? (Ethington and Clark 1982), *Drepanoistodus* (Lindström 1971) and *Oistodus* (Pander 1856) that accord with a broad Darriwilian age.

Cope (2004: fig. 20.2) correlated the Stairway Sandstone with Darriwilian time slice 4b (for definition see Webby et al. 2004: 47). The boundary between time slices 4a–b coincides with the base of the British Llanvirn Series, or the Dw2 stage slice (see Cooper and Sadler 2012).

Localities and lithostratigraphy.—Stratigraphic sections were measured through the Stairway Sandstone at Areyonga Gorge and Petermann Creek in the central Amadeus Basin, some 180 km southwest of Alice Springs (Fig. 3). As far as possible, the two sections were sampled bed by bed, but the more fine-grained units were generally poorly exposed. Each bed yielding fossils was numbered, using the prefix A for beds in the Areyonga Gorge section and PC for the beds in the Petermann Creek section. A conglomeratic bed present in both sections (called A 0 and PC 0, respectively) provided a well-defined stratigraphic marker. Beds below the marker bed are numbered with a sequential negative series (e.g., A -1, A -2 or PC -1, PC -2) whereas beds above the marker bed are numbered with positive series (e.g., A +1, A +2 or PC +1, PC +2).

Areyonga Gorge section.—The Stairway Sandstone is about 232 m thick in this section (Fig. 4). The base of the Areyonga Gorge section is located at 132°15'37.58"E and 24°06'46.4"S, whereas the top of the section is located at 132°15'31.20"E and 24°07'00.75"S. Quartzite is exposed as prominent ridges, especially in the lower and upper part of the formation, whereas siltstone beds and other fine clastics in the middle part of the unit tend to be less resistant to erosion and therefore more difficult to locate in outcrop in the valleys between the quartzite ridges. The strata have an average strike of 130° and dip 45° to the southwest.

Fig. 3. Location of the investigated Areyonga Gorge (A) and Petermann Creek (B) sections including the stratigraphy of the sedimentary formations in the area including the Ordovician Larapinta Group. Geology base map modified from Henbury SG5301 © Copyright Commonwealth of Australia (Geoscience Australia) 1996. →



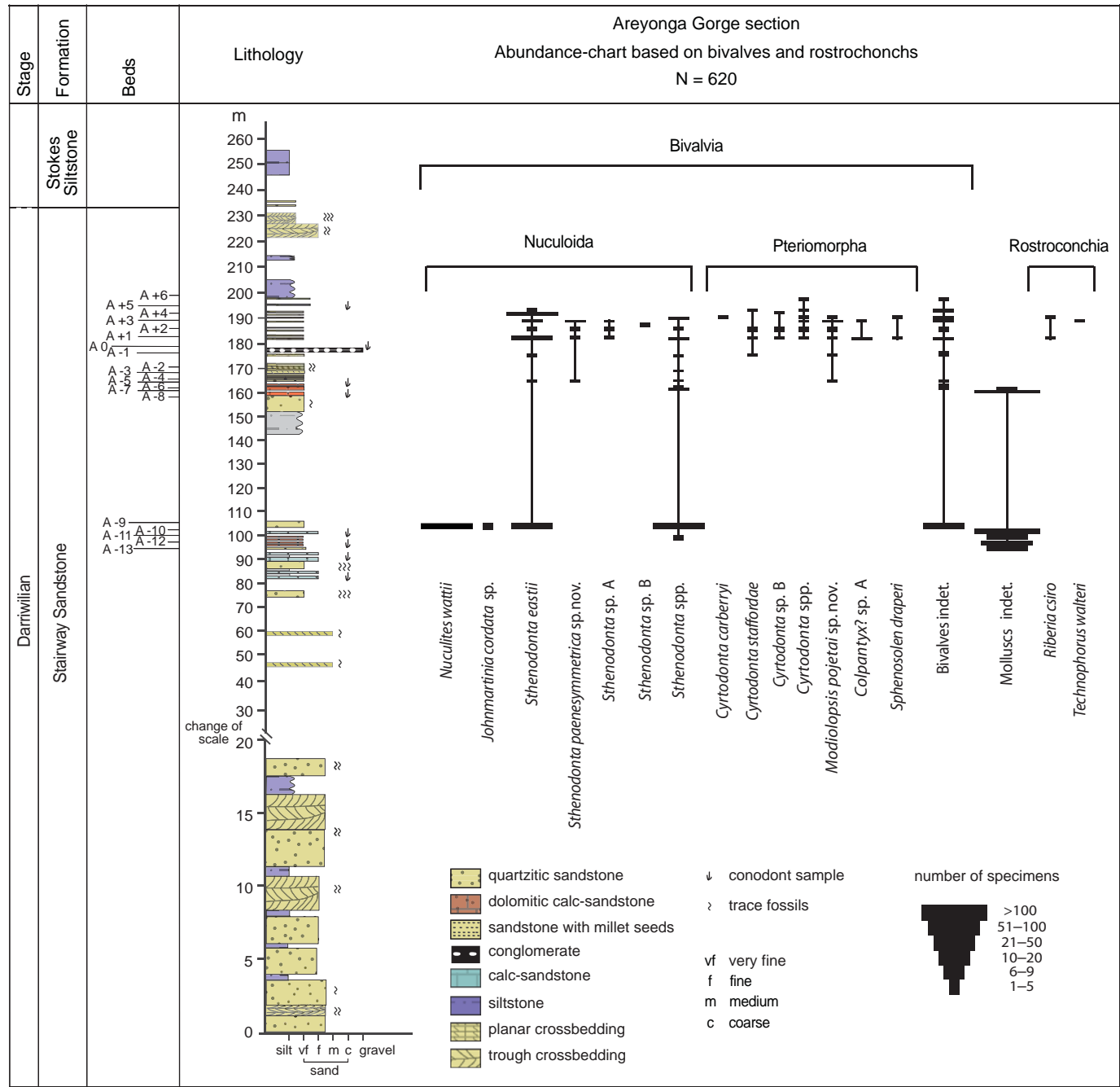


Fig. 4. Composite log of the Stairway Sandstone and abundance-charts showing distribution of bivalves and rostroconchs in the Areyonga Gorge section.

The lower unit is around 60 m thick and consists of fine to medium grained quartzite dominated by planar cross-bedding and parallel lamination with minor thin silty beds. Many ichnofossils (notably *Skolithos*, *Cruziana*, and *Diplocraterion*) are present (Gibb et al. 2009; Davies et al. 2011) whereas no body fossils were found. Above the lower unit, poor exposure and alluvial cover obscure the next 15 m of section. The middle unit, 75 m thick, is dominated by siltstone and fine sandstone with numerous well-cemented thin sandstone stringers. The first body fossils (poorly preserved casts of molluscs), were recovered from bed A -13 (a heavily dolomitized calc-sandstone) at about 96 m above the

base of the section (Fig. 4). Alluvial cover obscures the next 22 m of section. The conglomerate marker bed (A0) at 177 m defines the base of the upper unit of the Stairway Sandstone and the succeeding 20 m of very fine sandstone comprises the most fossiliferous interval in the Areyonga Gorge section (Fig. 4). The incoming of very fine sand followed by reddish carbonate rich siltstone at 232 m signals the base of the conformably overlying Stokes Siltstone Formation. The lithology, sedimentary structures and ichnofossils of the lower quartzite unit and the top part of the upper quartzite unit suggest a high energy, shallow marine depositional

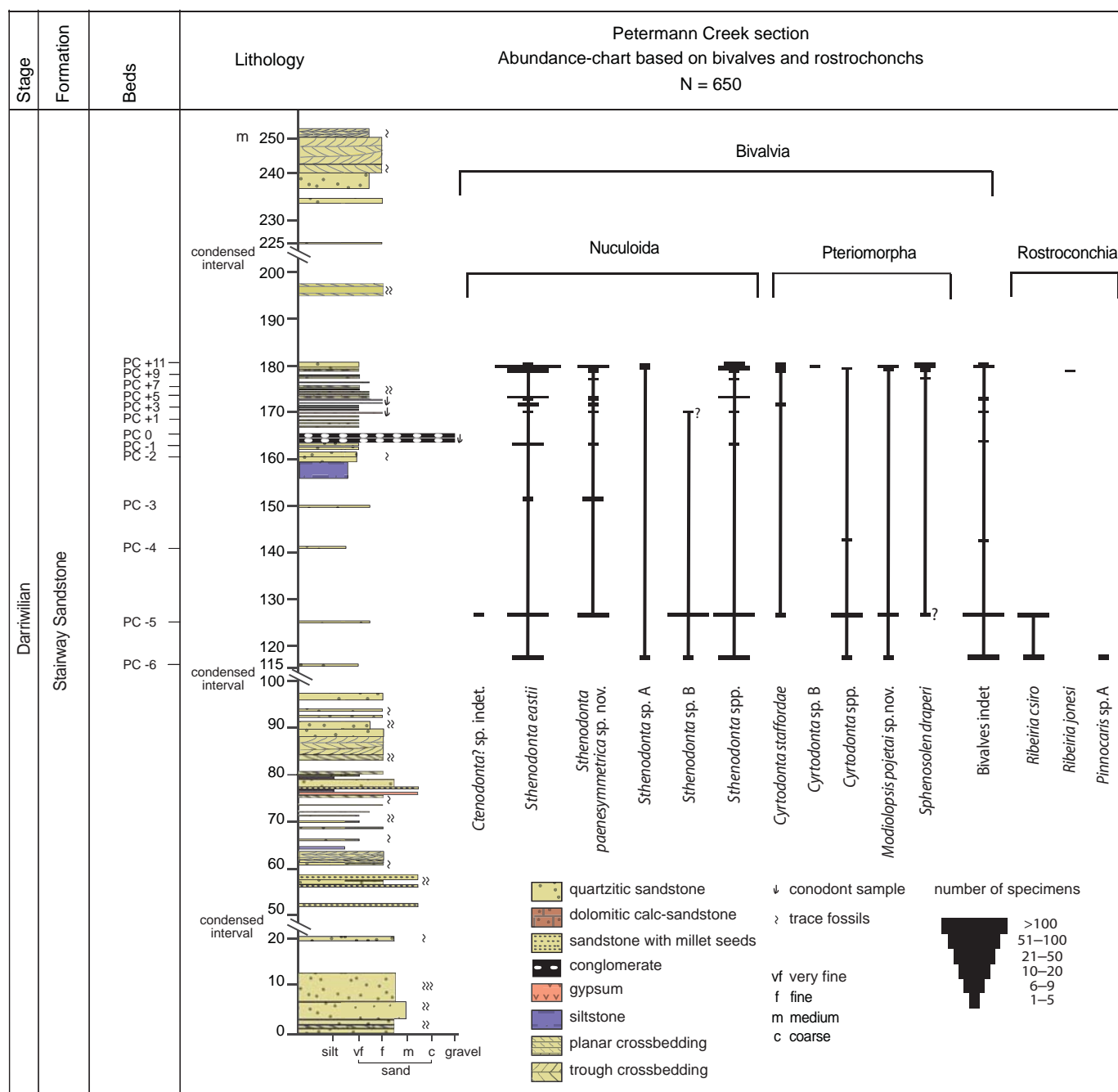


Fig. 5. Composite log of the Stairway Sandstone and abundance-charts showing distribution of bivalves and rostroconchs in the Petermann Creek section.

environment with the thin siltstone beds possibly indicating short-lived higher order sea level rises (4th or 5th order). The increase in fine clastics and predominance of thin sheeted sandstone (likely storm beds) in the middle part of the section (75–205 m) is taken to signal deposition in deeper water at some distance from the shore.

Petermann Creek section.—The Stairway Sandstone is about 249 m thick in the Petermann Creek section and can, like in the Areyonga Gorge section, be divided into a lower and an upper quartzitic unit, sandwiching a middle fine-grained unit (Fig. 5). The base of the Petermann

Creek section is located at 132°10'04.1"E and 24°25'22.4"S, whereas the top of the section is located at 132°10'02.7"E and 24°25'34.1"S. The strata have an average strike of 100° and dip 45° to the southwest.

The lower quartzitic unit strongly resembles the corresponding strata in the Areyonga Gorge section, the only difference is a few medium to coarse grained "millet seed" sandstone beds, presumed wind-blown, occurring in the upper part. No body fossils were recovered from the lower unit. The upper boundary is tentatively defined at about 60 m above the base of the section where the lithology becomes finer. The succeeding interval from 60 to 100 m consists of fine grained

sand and siltstone beds in the lower part and fine to medium sandstone in the upper part. Following an unexposed, and therefore likely fine-grained interval, the section is succeeded by a quartzitic bed (PC -6) at 115 m which yielded the first body fossils in the section, including abundant molluscs (see Fig. 5). Only a few beds are exposed above bed PC -6 in the upper part of the middle unit, of which bed PC -5 yielded the highest number of fossils in the section. The conglomeratic marker bed (PC 0) is equivalent to bed A0 in the Areyonga Gorge section, and defines the base of the upper unit at 165 m (Fig. 5). Several fine sand and silt-dominated beds in the lower part of the upper unit contained body fossils. They are overlain by the upper quartzitic unit representing the same suite of facies as recognized in the lower quartzitic unit, and sandstone dominates the remaining upper part of the section.

The lithology and ichnofossil content indicate that the lower unit was deposited in a nearshore shallow marine environment, apparently with regular supply of aeolian sand. Overall the Stairway Sandstone was deposited during a transgressive-regressive cycle with the deepest depositional environment, probably a mid-shelf setting, being represented by the generally finer grained and poorly exposed middle part of the formation.

Material and methods

Around 2300 mollusc specimens in total were collected bed-by-bed from the two investigated sections. The specimens were subsequently prepared using a pneumatic tool to remove matrix and the best preserved specimens were coated with ammonium-chloride and photographed. Pojeta and Gilbert-Tomlinson (1977) pioneered work on the bivalve and rostroconch fauna of the Stairway Sandstone.

Species that already have been treated by these authors are not re-described, but the diagnostic characters are re-emphasised and representative material is illustrated. The systematic terminology and taxonomic hierarchy for Bivalvia follows that of Cope (2000). The collected material consists primarily of internal moulds, but a few supplementary latex casts made from external moulds are also available.

Correlation and biostratigraphy

Local correlation.—Within greater central Australia, Middle Ordovician strata are also present in the Georgina and Canning basins (Fig. 2). In the latter, the Goldwyer Formation developed in the southwestern part of the basin (Haines and Wingate 2007) consists of mudstone and limestone and is considered approximately equivalent in age to the Stairway Sandstone (Jones et al. 1998; Haines and Wingate 2007). Correlation between the Canning and Amadeus basins is largely based on conodonts (Jones et al. 1998, see also Haines and Wingate 2007: fig. 3). In the southern Georgina Basin, the upper part of the Nora Formation and most of the Carlo Sandstone are considered approximately coeval with the Stairway Sandstone, based on studies of nautiloids (Wade 1977), facies relationships (Webby 1978) and conodonts (Kuhn and Barnes 2005). The chart illustrated in Fig. 6 shows the regional stratigraphic relationships based on the information from the authors referred to above.

Bivalves.—The bivalve fauna of the Stairway Sandstone represents a fairly low-diversity assemblage comprising seven species previously described by Pojeta and Gilbert-Tomlinson (1977), as well as four new species treated under open nomenclature and two new species described herein. The bivalve fauna is similar across the two investigated

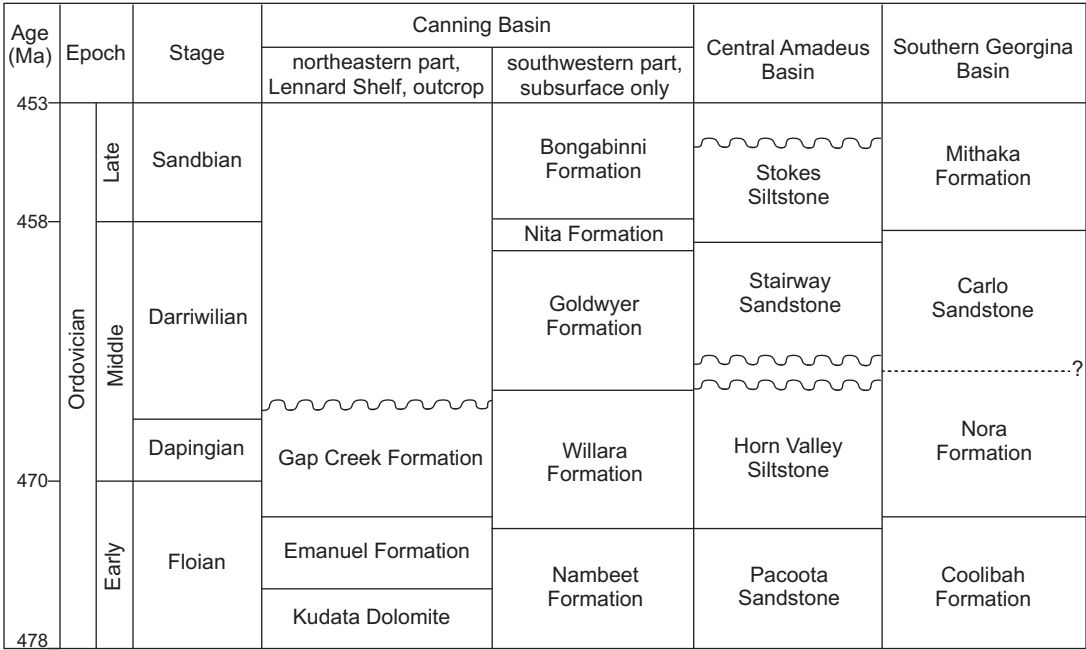


Fig. 6. Generalized chart showing stratigraphic relationships between selected formations in the Canning, Amadeus, and Georgina basins. The entire extent of the lowermost formations is not shown on the figure. Ages adopted from Cooper and Sadler (2012).

sections, but *Colpantyx*? sp. A, *Johnmartinia cordata* Pojeta and Gilbert-Tomlinson, 1977, *Nuculites wattii* Tate, 1896, and *Cyrtodonta carberryi* Pojeta and Gilbert-Tomlinson, 1977 are only found in the Areyonga Gorge section. Except for a few very poorly preserved internal moulds, possibly representing *Ctenodonta*?, no bivalve species are restricted to the Petermann Creek section. Outside Australia, single specimens of *Cyrtodonta* cf. *wattii* and *Cyrtodonta* cf. *stafordae* have been reported by from the lower Floian of South Wales (Cope 1996).

Except for *Sthenodonta eastii*, the bivalves present in the Areyonga Gorge section occur only in 35 m (true thickness) of the section from bed A -4 to A +5 (Fig. 4). The bivalves present in the Petermann Creek occur in more than 65 m (true thickness) from bed PC-6 to PC+10 (Fig. 5). *Sthenodonta eastii* is the most long-ranging species, and by far the most abundant. Pojeta and Gilbert-Tomlinson (1977: 17) reported this species from the lower Nora Formation of the Georgina Basin and from the Stokes Siltstone in the Amadeus Basin. Additionally, *Palaeoneilo smithi* was also reported by Pojeta and Gilbert-Tomlinson (1977: 7) from the Nora Formation and the Stairway Sandstone. *Sthenodonta eastii* and *Palaeoneilo smithi* are important for regional correlation between the Amadeus and Georgina basins. All other bivalve species of the Stairway Sandstone are endemic to the Amadeus Basin and no bivalve species are shared with the Canning Basin.

Due to the high level of endemism amongst Ordovician bivalves (almost 80% of the 144 known genera are endemic) they are of limited value for palaeobiogeographic analysis (Sánchez and Babin 2003). Despite this, some basic trends are apparent. At the genus level *Sthenodonta* represents 75% of all bivalves in the Stairway Sandstone. *Sthenodonta*, *Johnmartinia*, *Colpantyx*, and *Sphenosolen* are endemic to Australia, whereas *Nuculites*, *Cyrtodonta*, and *Modiolopsis* are cosmopolitan. Darriwilian occurrences of *Nuculites* have been reported from South Korea (Kobayashi 1934) and France (Babin 1966). *Cyrtodonta* is found in the Middle Ordovician strata at some localities in the United Kingdom and at several localities in the Sandbian (Upper Ordovician) of North America (e.g., Wilcox and Lockley 1981; Sepkoski 1998) but is also known from North China (Stratigraphic Group of Qinghai Province 1980). *Modiolopsis* is known from Darriwilian strata in Argentina (Sánchez 1990) and South Korea (Kobayashi 1934). *Modiolopsis* was also reported from Sandbian strata in Canada (Sepkoski 1998). Polechová (2013: 28) additionally listed Middle Ordovician occurrences of *Modiolopsis* from Bohemia, Spain, North China, and Wales.

In the Early Ordovician most bivalves were confined to the margins of Gondwana (cf. Cope and Babin 1999; Cope 2002). The genera recovered from central Australia suggest some exchange of bivalves between Northern Gondwana, Southern Gondwana, North China, Laurentia, and Avalonia in the Middle Ordovician. Ordovician bivalves may have possessed lecithotrophic larvae (Sánchez and Babin 2003), which could explain the restricted distribution of many Ordovician bivalve genera. Larval type is important for the

dispersal of bivalves and between 65–70% of Recent bivalve species possess planktotrophic larvae (Jablonski and Lutz 1980), permitting dispersal across large distances. This study indicates that a few Ordovician bivalve genera possibly had planktotrophic or teleplanktic larvae, rather than lecithotrophic larvae, due to the wider dispersal mentioned above.

Modiolopsis is widespread during the Middle Ordovician and its dispersion is probably the result of having long-lived teleplanktic larvae. The palaeogeographic dispersal of *Nuculites*, *Cyrtodonta*, and *Modiolopsis* during the Middle Ordovician is illustrated in Fig. 7. It should be noted that the earliest *Cyrtodonta* in North America is Sandbian in age. All bivalves listed in the past as from the Middle Ordovician of North America are in fact from the Upper Ordovician as now understood (John C.W. Cope personal communication 2013).

Rostroconchs.—The rostroconch fauna consists of 27 specimens, of which 22 belong to *Ribeiria* Sharpe, 1853. Four species are present with *Ribeiria csiro* Pojeta Pojeta, Gilbert-Tomlinson, and Shergold, 1977 as the most abundant. It is the only species present in both sections (Figs. 4, 5). *Ribeiria csiro* was originally described from the Stairway Sandstone by Pojeta et al. (1977). *Ribeiria jonesi*? is represented by a single specimen from bed PC +8 in the upper Petermannn Creek section (Fig. 5). The species has also been documented from the Furongian part of the Pacoota Sandstone (Amadeus Basin) and the coeval Tomahawk Beds in the Georgina Basin (Pojeta et al. 1977). It thus provides some evidence of a marine connection between the Georgina and Amadeus basins already during the Early Ordovician.

Pinnocaris sp. A occurs in bed PC -6 in the lower part of the Petermann Creek section; Pojeta et al. (1977) described a single specimen from the Stairway Sandstone. A single specimen of *Technophorus walteri* was recovered from horizon A +3 in the upper part of the Areyonga Gorge section (Fig. 4). *Technophorus walteri* has been documented from Furongian and Lower Ordovician beds in the Pacoota Sandstone (Amadeus Basin) (Pojeta et al. 1977), so the range of the species can now be extended into the Middle Ordovician.

All rostroconch species are endemic to central Australia, but some genera are known from elsewhere. *Ribeiria* was widespread during the Ordovician, and Darriwilian occurrences have been reported from the Czech Republic (Havlíček and Vanek 1966), Argentina (Aceñolaza 1968), and Spain (Gutiérrez-Marco et al. 1984). *Technophorus* is also known from the Darriwilian of Spain (Gutiérrez-Marco et al. 1984). In Australia *Pinnocaris* is exclusively known from the Northern Territory, whereas *Ribeiria* and *Technophorus* have been reported from several localities in the Georgina Basin as well as the Amadeus Basin (Pojeta et al. 1977: 10–11).

Gastropods.—The material is referred to *Raphistomina*? sp., *Scalites*? sp., *Teiichispira*? sp., and Archinacelloid spp. A–C. In the Petermann Creek section, more than 80% of the gastropods were recovered from a single quartzitic bed (PC -5) in the lower part of the section, whereas 70% of the

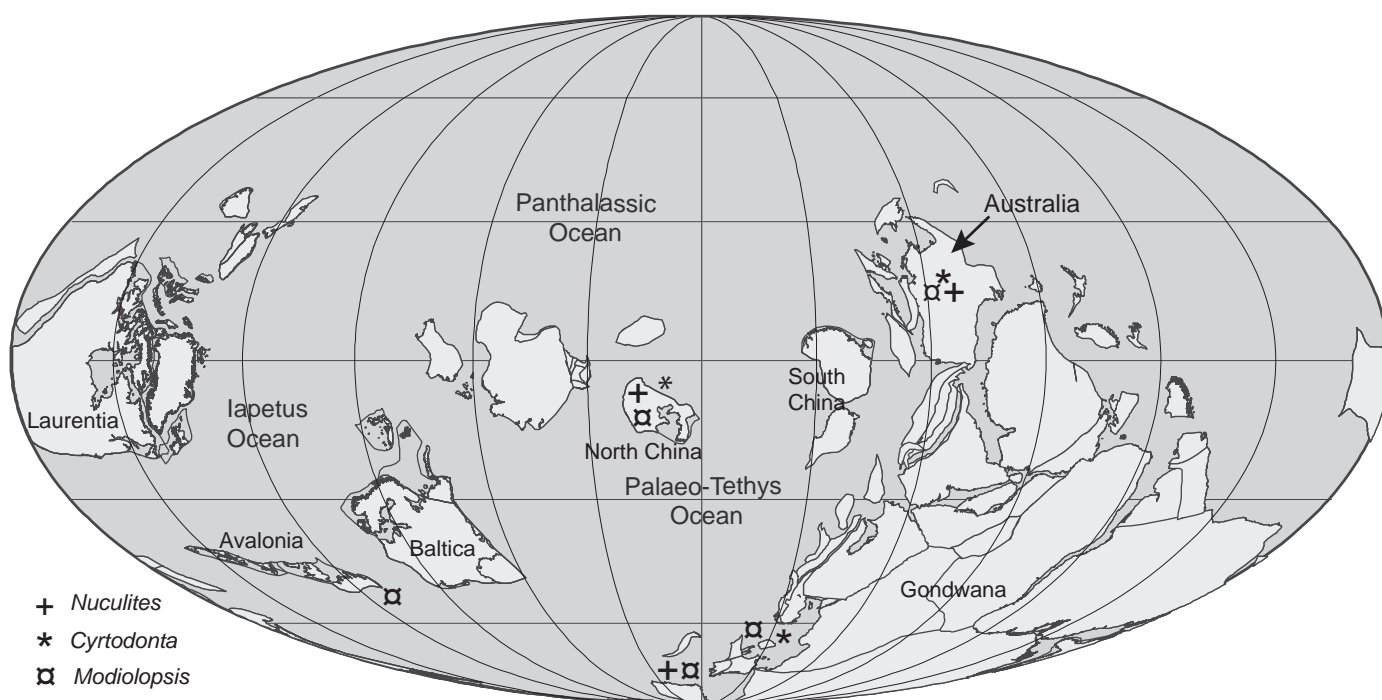


Fig. 7. Distribution of the cosmopolitan genera *Modiolopsis*, *Cyrtodonta*, and *Nuculites* found in the Stairway Sandstone and coeval strata elsewhere during the Middle Ordovician. Map modified from Torsvik et al. (2014).

specimens in the Areyonga Gorge section are from a few beds (A+1–A+4) in the upper part of the section.

Raphistomina? sp. is the most abundant gastropod with specimens occurring in the upper part of each section, though the taxon is much more abundant in the Areyonga Gorge section. *Raphistomina?* was also reported by Pojeta and Gilbert-Tomlinson (1977: 41) from the Nora Formation of the Georgina Basin.

Scalites? sp. occurs in the lower part of both sections, but is about three times more abundant in the Petermann Creek section. Overall the genus is the second most abundant and it has also been reported from the Darriwilian of North America and North China (Raymond 1906; Kobayashi 1934).

Teiichispira? sp. is only known from a few float samples of the Stairway Sandstone found at Petermann Creek. *Teiichispira* is also reported from the Lower Ordovician of the Georgina Basin (Pojeta et al. 1977: 43) and the Canning Basin (Yu 1993: 437). Outside Australia the genus is common in the Lower Ordovician of North America (e.g., Yochelson and Wise 1972).

Most archinacelloids were recovered from the lower part of the Petermann Creek section (bed PC-5), whereas they are restricted to the upper part of the Areyonga Gorge section (A+1–A+5). About four times as many archinacelloids were recovered from the Petermann Creek section. Archinacelloid sp. A is the dominant archinacelloid in the Petermann Creek section; it is absent from the Areyonga Gorge section. Archinacelloideans have also been reported from the Darriwilian of North America (Raymond 1906), Czech Republic (Horný 1997) and Norway (Yochelson 1963).

Palaeoecology

Early Ordovician bivalves were restricted to peri-Gondwanan shelves and favoured inshore clastic sedimentary environments, but during the Middle Ordovician some lineages of bivalves migrated to other continents (cf. Cope and Babin 1999). The majority of the bivalves in the Stairway Sandstone belongs to the order Nuculoida, but representatives of the Pteriomorpha and Heteroconchia are also present (Fig. 8). The bivalves comprise 45% of the entire macrofauna in the studied sections (Fig. 9).

Seventeen molluscan species (excluding cephalopods) were recovered from the Petermann Creek section; eight belong to Bivalvia, six to Gastropoda, and three to Rostroconchia. Nineteen benthic molluscan species were recovered from the Areyonga Gorge section; twelve belong to Bivalvia, five to

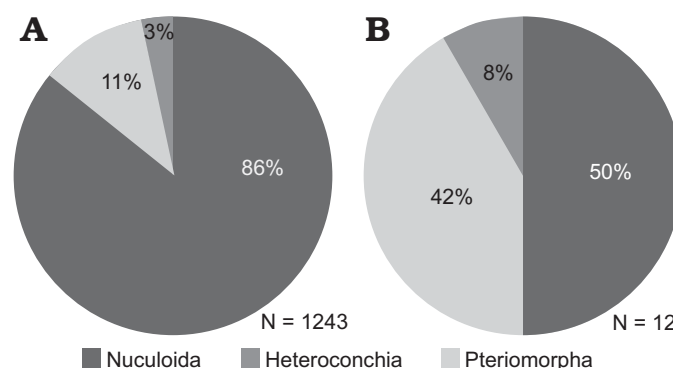


Fig. 8. Number of individual bivalves (A) and bivalve species (B) distributed within orders/infraclasses in the Areyonga Gorge and Petermann Creek sections.

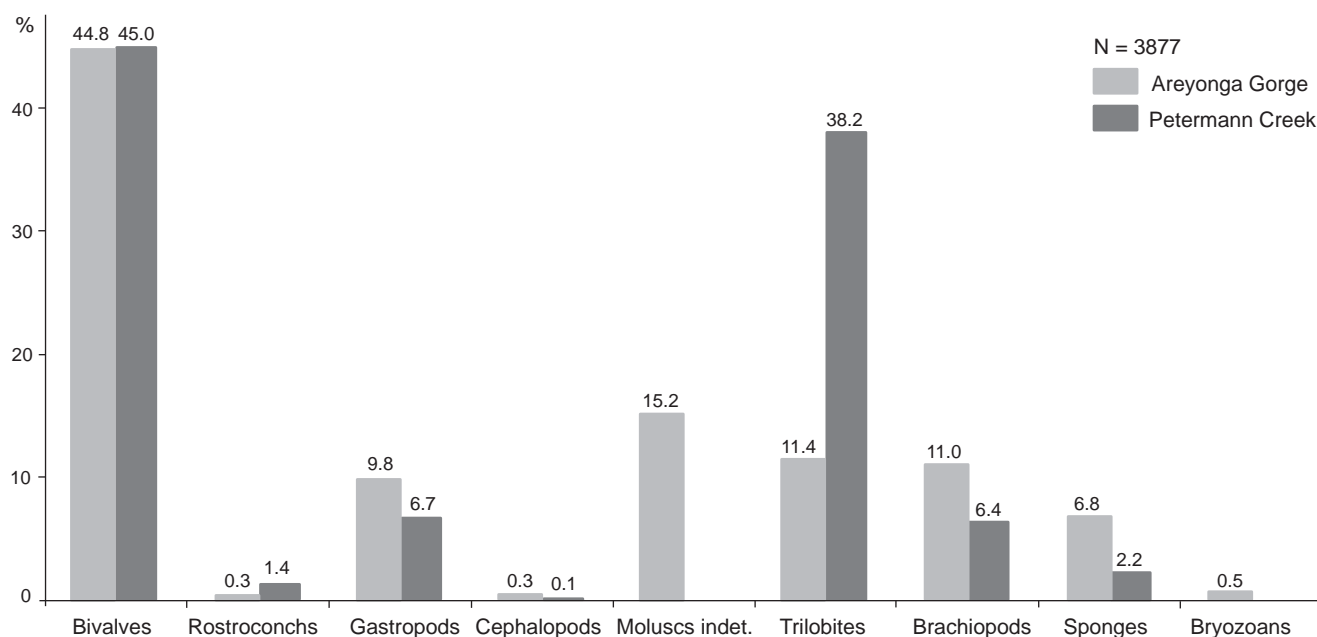


Fig. 9. Diversity of entire shelly fauna in the Areyonga Gorge and Petermann Creek sections.

Gastropoda, and two to Rostroconchia. Many of the species occur in both sections. The local biodiversity does not follow the global trend where the number of bivalve species at equatorial latitudes was twice that of the highest latitude assemblages (cf. Cope 2002), though this may be the result of information loss due to taphonomy and time averaging. In comparison, Darriwilian (Middle Ordovician) high-latitude bivalve faunas from Spain and the Czech Republic contained 15 and 12 species, respectively (Cope 2002; Polechová 2013). Pojeta and Gilbert-Tomlinson (1977) recorded 22 bivalve and rostroconch species from the Stairway Sandstone based on 65 localities, but unfortunately, the exact stratigraphic levels for most localities are impossible to pinpoint.

Most species in the Stairway Sandstone have a very restricted distribution, but a few like *Sthenodonta eastii*, which is very abundant, is also known from the Nora Formation in the Georgina Basin (Pojeta and Gilbert-Tomlinson 1977: 7).

Pojeta (1971) reconstructed the life habits of Middle Ordovician bivalves and, accordingly, the majority of the bivalve fauna from the Stairway Sandstone was probably infaunal (for details see Pojeta 1971: 30–34). The Stairway Sandstone high-energy environment was probably too hostile to support epifaunal benthos though rare *Modiolopsis*, constituting 2.5% of the bivalve fauna, might be an exception.

Except for the latitudinal differences in occurrence, there are also possible local palaeoenvironmental differences controlling species diversity and specimen density. Overall, the number of bivalves is almost the same in the two sections (when including all the indeterminate specimens), but the diversity is highest at the Areyonga Gorge. The lithology in the Petermann Creek section is generally more silty than in the Areyonga Gorge section and the relative abundance and species diversity of trilobites is about three times higher than in the latter section (see Fig. 9 and Jakobsen et al.

2014b). These faunal and lithological differences probably reflect a more proximal, shallow marine environment at Areyonga Gorge and a more distal and slightly deeper shelf environment at Petermann Creek. If so, the bivalve diversity was higher in a shoreward direction within the basin.

Even though the Stairway Sandstone was deposited during a global increase in marine biodiversity (e.g., Harper 2006; Trotter et al. 2008), the high energy shallow-marine environment clearly favoured opportunistic species. It might be, however, expected that generally benthic mollusc fauna at that time inhabited the nearshore belt of the epicontinental Larapintine Sea, far from the open ocean.

Discussion

The scarcity and restricted distribution of the bivalves do not allow reconstruction of a more detailed biofacies model for the Stairway Sandstone depositional environment. *Sthenodonta eastii* is the dominant and long-ranging species among all the macrofossils and it may serve as a guide fossil for the Stairway Sandstone. It is the only species occurring outside the Amadeus Basin, having been also recorded from the Nora Formation, Georgina Basin (Pojeta and Gilbert-Tomlinson 1977: 7). Representatives of Ambonychiidae, *Cyrtodonta*, and *Palaeoneilo* also occur in the Nora Formation and/or Carlo Sandstone of the Georgina Basin (Pojeta and Gilbert-Tomlinson 1977: 7). The gastropod *Teiichispira* is also reported by Pojeta et al. (1977) from the Lower Ordovician Coolibah Formation of the Georgina Basin (see Fig. 6). *Teiichispira* has only been documented from the slightly older Lower to Middle Ordovician Gap Creek Formation of the Canning Basin (Yu

1993), and its absence in younger strata (coeval with the Stairway Sandstone) does not support a connection with the Amadeus Basin in the Middle Ordovician.

The molluscan fauna of the Stairway Sandstone suggests that the Amadeus and the southern Georgina basins were somehow connected during the Darriwilian, whereas a connection between the Amadeus and Canning basins is unlikely, as suggested by the lack of similarity between their mollusc faunas. This corroborates recent views that the Larapintine Seaway did not extend across central Australia (Fig. 2B; cf. Haines and Wingate 2007).

Further support for the connection between the Amadeus and the Georgina basins during Darriwilian comes from similar species of the trilobite *Prosopiscus* found in the Nora Formation (Fortey and Shergold 1984), the Rowena Formation of the Gnalta Shelf, New South Wales (Paterson 2006) and the Stairway Sandstone (Laurie 2006; Jakobsen et al. 2014b).

Cope (2002: 46) documented occurrences of bivalve species from several Ordovician localities worldwide, which he assigned to particular orders and/or infraclasses. For the Middle Ordovician he compared faunal compositions from high-latitude Spain (Babin and Gutiérrez-Marco 1991), mid-latitude Wales (Cope 1999) and low-latitude Australia (Pojeta and Gilbert-Tomlinson 1977). Cope and Kříž (2013) recently updated this Ordovician bivalve database, and included data from an intermediate latitude of West Yunnan, China. A comparison of the Stairway Sandstone bivalve fauna with the results of Cope and Kříž (2013) is discussed below. Since Fang and Cope (2008) have shown that glyptarchoids are pteriomorphians, and not heteroconchs, the results of Cope (2002) had to be revised to include the new reassignments of Cope and Kříž (2013).

According to Cope and Kříž (2013), the Middle Ordovician low-latitude fauna from central Australia (based on studies of the Stairway Sandstone fauna by Pojeta and Gilbert-Tomlinson 1977) contains 75% nuculoids ($n = 255$) and 25% pteriomorphians ($n = 84$). The high-latitude fauna from Spain contains 25% nuculoids ($n = 609$), 14% pteriomorphians ($n = 351$), and 61% heteroconchs ($n = 1522$). The mid-latitude fauna from Wales contains 25% nuculoids ($n = 122$), 67% pteriomorphians ($n = 324$), and 8% heteroconchs ($n = 38$). The mid to high intermediate-latitude fauna from West Yunnan contains 4% nuculoids ($n = 11$), 53% pteriomorphians ($n = 143$), and 43% heteroconchs ($n = 115$). Cope and Kříž (2013) did not list any heteroconchs from central Australia but actually the heteroconch species *Sphenosolen draperi* is present in the current material.

In the studied bivalve material ($n = 1243$) nuculoids, pteriomorphs, and heteroconchs account for 86%, 11%, and 3%, respectively, of the bivalve fauna (Fig. 8A showing species abundance). Although nuculoids are the most abundant, the species diversity is not much higher than among the pteriomorphs. The material at hand includes 12 species, and records the species diversity within orders/infraclasses in the two sections, with pteriomorph species comprising

42%, nuculoids 50% and heteroconchs 8% (Fig. 8B showing species diversity).

Sthenodonta eastii dominates the benthic macrofauna of the Stairway Sandstone, suggesting that nuculoids were even more dominant at low latitudes along northern Gondwana during the Middle Ordovician than previously thought. Compared to Cope and Kříž (2013), the results for central Australia are fairly similar, with the presence of 86% (this study) vs. 75% nuculoids; and 11% (this study) vs. 25% pteriomorphians. The sparse presence of heteroconchs in this study is different to Cope and Kříž (2013), as they did not allocate any species to heteroconchs from the Stairway Sandstone material (based on Pojeta and Gilbert-Tomlinson 1977).

The central Australian Stairway Sandstone bivalve fauna, being dominated by nuculoids (86%), is markedly different in composition in comparison with faunas from the Middle Ordovician of Spain, Wales, and West Yunnan and suggests that nuculoids are the dominant faunal constituent of Middle Ordovician low-latitude bivalve faunas.

Even though all these bivalve faunas occurred in shallow water environments (Cope and Kříž 2013), the nuculoids in the Stairway Sandstone may be indicative of a very shallow-water setting, which is supported by ichnofossil studies of the Stairway Sandstone by Gibb et al. (2009) suggesting a water depth of about 15 m.

Conclusions

More than 90% of the molluscan species of the Stairway Sandstone fauna are endemic. However, a few species are shared between the Amadeus and Georgina basins, which demonstrate some connection during the Darriwilian. Most of the genera in common between the Amadeus, Georgina, and Canning basins are cosmopolitan. At generic level the fauna shows affinity in particular to North China, Southern Gondwana, Laurentia, and Korea.

The bivalves are by far the most common molluscan group in the Stairway Sandstone, whereas rostroconchs are rather scarce and the gastropods are too fragmentary and poorly preserved to be identified with any confidence. Two new bivalve species, *Sthenodonta paenesymmetrica* sp. nov. and *Modiolopsis pojetai* sp. nov., are described together with four possible new species treated under open nomenclature. The bivalve fauna of the Stairway Sandstone is dominated by specimens of nuculoids comprising 86% of the individuals. This dominance is higher than previously recorded by Cope (2002) for low-latitude bivalve faunas from Northern Gondwana.

The Stairway molluscan fauna appears to have been adapted to a nearshore, shallow-water, high energy marine setting with a high influx of terrigenous material. This environment does not seem to have generated high diversity among the molluscs but rather suited a few, relatively common, probably opportunistic species.

The Middle Ordovician global marine diversity hike (e.g., Sepkoski 1995; Harper 2006; Trotter et al. 2008) is

not obvious in the Stairway Sandstone, indicating that here the diversity signal is masked by the local environmental conditions.

Systematic palaeontology

Phylum Mollusca Cuvier, 1797

Class Bivalvia Linnaeus, 1758

Subclass Protobranchia Pelseneer, 1889

Order Nuculoida Dall, 1889

Family Nucularcidae Pojeta and Stott, 2007

Genus *Sthenodonta* Pojeta and Gilbert-Tomlinson, 1977

Type species: *Isoarca eastii* Tate, 1896 by original designation; type locality uncertain but judging from descriptions by Tate (1896: 106) it is within the Stairway Sandstone, Ordovician, Australia.

Sthenodonta eastii (Tate, 1896)

Fig. 10A–J.

1896 *Isoarca eastii* sp. nov.; Tate 1896: 106, pl. 2: 12a.

1896 *Isoarca eastii* var. *modiolaeformis*; Tate 1896: 106, pl. 2: 12b.

1977 *Sthenodonta eastii*; Pojeta and Gilbert-Tomlinson 1977 [partim]: 17, pl. 12: 1–10; pl. 13: 1–6, 8; non pl. 13: 7 [= *Sthenodonta* sp. A].

Type material: Syntypes (SAM T 1274a, b) investigated by Pojeta and Gilbert-Tomlinson (1977: 17), of which they designated lectotype (SAM T 1274a; original of Tate 1896: pl. 2: 12a). It was refigured by Pojeta and Gilbert-Tomlinson (1977: pl. 12: 3, 4).

Type locality: Middle Valley (Tempe Downs), which is in the Amadeus Basin, southern Northern Territory, Australia.

Type horizon: In sandstone and quartzite underlying the fossiliferous limestone, Ordovician.

Material.—550 specimens recovered from the Stairway Sandstone at Areyonga Gorge (n = 130) and Petermann Creek (n = 420), Middle Ordovician of Australia. The nine illustrated specimens, including latex casts, are numbered CPC 41455–41463.

Description.—Highly inequilateral and tumid nucularcid with prominent umbo; shell elongated ovate and extends only slightly anteriorly beyond umbo; dorsal and ventral margins arcuate with anterior and posterior margin rounded; strongly developed anterior myophoric buttress; uninterrupted anterior and posterior taxodont tooth rows that meet at an obtuse angle (>100°), with anterior tooth row much shorter than posterior tooth row; peg-like teeth below umbo with chevron or half-chevron shaped teeth in posterior direction; apex of teeth points toward umbo (see Fig. 10A–G). A distinct border following the ventral margin is particularly pronounced on adult specimens (Fig. 10F). Growth lines are faintly discernible on external moulds (Fig. 10I₂, J₂).

Remarks.—The Nucularcidae include two genera: *Nucularca* Pojeta and Stott, 2007 and *Sthenodonta* Pojeta and Gilbert-Tomlinson, 1977. The former is found in North America and the latter is endemic to central Australia (Pojeta and Gilbert-

Tomlinson 1977; Pojeta and Stott 2007). Nucularcids differ from other Ordovician palaeotaxodonts by having a hinge plate that is broad and arcuate.

Sthenodonta eastii comprises 43% of the determinable bivalves in the two investigated sections. It is readily identifiable if the strongly developed anterior myophoric buttress is preserved (Fig. 10H). Within the investigated sections four times as many specimens were recovered from Petermann Creek as the Areyonga Gorge section (see Figs. 4 and 5). The Petermann Creek section contains more very fine sand to silt-dominated beds, which appears to have been the preferred substrate of *S. eastii* although the species is also found in most facies types in the sections (albeit in lower numbers).

Pojeta and Gilbert-Tomlinson (1977: 17–19) described five species assigned to *Sthenodonta*, of which two were reported from the Nora Formation of the Georgina Basin, one or possibly two from the Stairway Sandstone and two to possibly four from the Stokes Siltstone in the Amadeus Basin (see Fig. 6). *Sthenodonta eastii* is the only species recorded with certainty from the Stairway Sandstone. Tate (1896: 106) reported *Isoarca etheridgei* from “limestone, Middle Valley at Tempe Downs, Petermann Creek by Camp at Laurie’s Creek, north of Tempe Vale, and Chandler Range”. Thus, the type suite of *I. etheridgei* was probably obtained from several localities, but the lithology of most syntypes suggests that they originated from the Stairway Sandstone (Pojeta and Gilbert-Tomlinson 1977: 17).

In the material at hand, *Sthenodonta* is represented by four species, of which three are new. *Sthenodonta eastii* can be separated from *Sthenodonta* sp. A in having a more asymmetric shape and a higher shell profile. *Sthenodonta eastii* is separated from *Sthenodonta* sp. B by its higher shell profile and from *S. paenesymmetrica* sp. nov. by a much more asymmetric shape; whereas the height in shell profiles of these species are very similar.

An example of a well-preserved juvenile internal mould with associated external mould is illustrated on Fig. 10I, J. The external latex cast displays faint growth lines, which separate the species from *Sthenodonta* sp. B having well marked growth lines.

Stratigraphic and geographic range.—*Sthenodonta eastii* has a stratigraphic range from bed PC -6 to PC +11 in the Petermann Creek section encompassing 65 m true thickness and from bed A -9 to A +5 in the Areyonga Gorge section (85 m true thickness). The species is present in almost every fossiliferous bed in these sections (Figs. 4, 5).

S. eastii is a widespread species in the Amadeus Basin, where it is documented from 27 localities by Pojeta and Gilbert-Tomlinson (1977). In 25 of these localities the species was recorded from unknown levels within the Stairway Sandstone. The two additional localities represent occurrences in the overlying Stokes Siltstone. The species is also reported from an uncertain stratigraphic level (probably the Nora Formation) in the Georgina Basin (Pojeta and Gilbert-Tomlinson 1977: 17; see Fig. 6). The range of the Nora Formation is Early to Middle Ordovician (the major

part of the formation is Middle Ordovician). The region is the south-eastern Northern Territory, and the locality is located east of Mt Ultim. This location corresponds to the south-western limit of the Georgina Basin.

Sthendonta paenesymmetrica sp. nov.

Fig. 10K, L.

Etymology: The new name alludes to the almost symmetrical shell shape, which is unusual among sthenodontids in the material.

Holotype: CPC 41464, an internal mould (Fig. 10K).

Type locality: Areyonga Gorge, Amadeus Basin, central Australia.

Type horizon: Bed A -5 in the Areyonga Gorge section (Fig. 4). Darriwilian (Middle Ordovician), Stairway Sandstone (Figs. 1, 3).

Material.—68 specimens, of which two are figured (CPC 41464 and CPC 41465); all specimens are internal moulds recovered from the Petermann Creek section, Middle Ordovician of Australia.

Diagnosis.—Small, nearly equidimensional, sub-circular sthenodontid. Indistinct palaeotaxodont teeth; umbo wide, well-defined, rounded and posteriorly projecting.

Description.—Dorsal margin rounded, sloping rapidly into anterior margin; posterior margin rounded towards dorsum, not projecting. Sub-circular shell shape carrying a wide, rounded and dorsally pointing umbo; shell profile relatively flat. Weakly developed external ornament of growth lines on some specimens (Fig. 10K), otherwise a smooth surface. The holotype is 12 mm high and 13.5 mm long, making the species nearly equidimensional (about 90% as high as long).

Remarks.—The outline of the species is similar to *Sthenodonta etheridgei* (Tate, 1896) figured by Pojeta and Gilbert-Tomlinson (1977: pl. 7: 8, 9). These specimens are latex replicas of external moulds showing strongly developed commarginal striae on the surface. It is difficult to compare the external characters of *S. etheridgei* with *S. paenesymmetrica* sp. nov., as the latter almost entirely consists of internal moulds. The distinct commarginal striae presented on the former is not even indicated on *S. paenesymmetrica* sp. nov., and for this reason the two species are separated.

The two species have the most circular shell outline of the bivalves recovered from the Stairway Sandstone and are as such atypical nucularcids, which usually possess an inequilateral shell shape. Pojeta and Gilbert-Tomlinson (1977: 18) assigned the species *S. etheridgei* to *Sthenodonta* due to the arrangement of teeth (long posterior tooth row and short anterior tooth row). The teeth of *Sthendonta paenesymmetrica* sp. nov. are poorly preserved but the presence of few indistinct teeth indicates a very similar arrangement.

Stratigraphic and geographic range.—*Sthendonta paenesymmetrica* sp. nov. was recovered from bed PC -5 to PC +10 in the Petermann Creek section and bed A -5 to A +3 in the Areyonga Gorge section (Figs. 4, 5). Almost 85% of the species were found in from the Petermann Creek section. The same distributional pattern between the sections is observed for the other sthenodontids. The range of the species

is within the Stairway Sandstone Formation, Darriwilian (Middle Ordovician). The region is in the southern Northern Territory, corresponding to the central part of the Amadeus Basin (Fig. 1).

Sthenodonta sp. A

Fig. 10M, N.

1977 *Sthenodonta eastii*; Pojeta and Gilbert-Tomlinson 1977 [partim]: pl. 13: 7.

Material.—12 specimens (3 from the Areyonga Gorge section and 9 from the Petermann Creek section), Middle Ordovician of Australia. Illustrated specimens: CPC 41466 and CPC 41467. The material was recovered from bed interval PC -6–PC +11 in the Petermann Creek and beds A +1–A +4 in the Areyonga Gorge section (Figs. 4, 5). The species is endemic to the Amadeus Basin and is currently known only from the two studied sections (Fig. 3) as well as from a single specimen from a locality close to Lake Amadeus (Pojeta and Gilbert-Tomlinson 1977: 51, fig. 1). The latter specimen was collected by Peter. J. Cook (Australian Bureau of Mineral Resources) in 1962 and assigned to *Sthenodonta eastii* by Pojeta and Gilbert-Tomlinson 1977.

Description.—Inequilateral *Sthenodonta* species carrying an anteriorly pointing umbo; shell relatively flat and elongate ovate to sub-circular; dorsal margin arcuate, ventral margin straight to rounded anteriorly and posteriorly, anterior margin slightly rounded, posterior margin strongly rounded; taxodont tooth rows meet at an obtuse angle (>100°), with anterior tooth row much shorter than the posterior tooth row; peg-like teeth below beak anteriorly. Admittedly the dentition is difficult to see but CPC 41467 shows dentition and it is more obvious on the actual specimen. Ornament of growth lines weakly developed; circular anterior adductor muscle scar placed about mid-way on valve (ex. sagittal) close to anterior margin (Fig. 10M, N).

Remarks.—*Sthenodonta* sp. A has a less ovate and more sub-circular shell shape than *S. eastii*. The anterior myophoric buttress is not observed in *Sthenodonta* sp. A, and this key difference also separates it from *S. eastii*. *Sthenodonta* sp. A likely represents a new, as yet unnamed species. Due to the generally poor state of preservation among the specimens and lack of preserved characteristic taxonomic features, *Sthenodonta* sp. A has not been described formally as a new species.

Sthenodonta sp. B

Fig. 11A.

Material.—46 specimens, of which we only figure CPC 41468 as most of the specimens are poorly preserved. The bulk of the material was recovered from beds PC -6–PC 2 in the Petermann Creek section and only two specimens from bed A +3 in the Areyonga Gorge section (Figs. 4, 5). Most specimens (39 out of 46) were found in bed PC -5. All Middle Ordovician of Australia.

Description.—Inequilateral sub-ovate *Sthenodonta* species carrying a rounded and anteriorly pointing umbo;

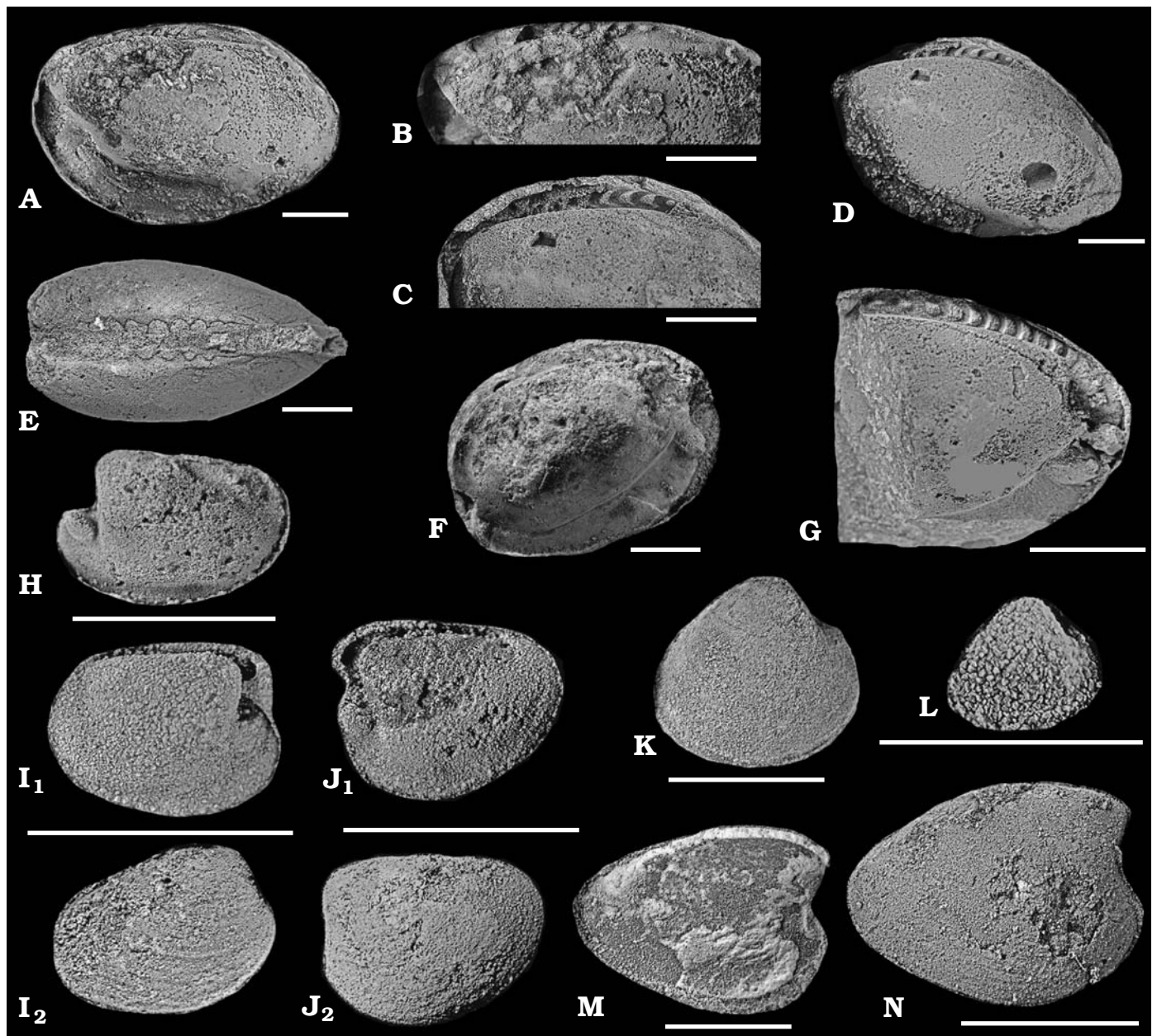


Fig. 10. Nucularcid bivalves from the Stairway Sandstone, Middle Ordovician, Australia. Internal (A–H, I₁, J₁, K–N) and external (I₂, J₂) moulds. A–J. *Sthenodonta eastii* Pojeta and Gilbert-Tomlinson, 1977 from the Petermann Creek. A–D. Specimens in left-lateral views with chevron-shaped palaeotaxodont teeth (A, CPC 41455; B, CPC 41456; C, CPC 41456; D, CPC 41457). E. Specimen in dorsal view with teeth (CPC 41458). F, G. Specimens in right-lateral view with teeth and ventral border (F, CPC 41459; G, CPC 41460). H. Specimen in left-lateral view with anterior myophoric buttress preserved (CPC 41461). I. Specimen in right-lateral view showing indistinct growth lines (CPC 41462). J. Specimen in left-lateral view (CPC 41463). K, L. *Sthenodonta paenesymmetrica* sp. nov. from the Areyonga Gorge (K) and Petermann Creek (L), right-valves in dorsomedial views. K. Holotype (CPC 41464). L. Juvenile specimen (CPC 41465). M, N. *Sthenodonta* sp. A. M. Specimen (CPC 41467) from the Petermann Creek in right-lateral view with anterior muscle scars indicated and part of original shell material preserved. N. Specimen (CPC 41466) from Areyonga Gorge in right-lateral view with curved anterodorsal margin. Scale bars 10 mm.

shell profile relatively flat; dorsal margin straight, ventral margin straight to sub-rounded, anterior margin straight to rounded ventrally and posterior margin rounded. Ornament of growth lines distinct. Outline of teeth uncertain due to poor preservation.

Remarks.—*Sthenodonta* sp. B is quite similar to *Sthenodonta* sp. A and *S. eastii*. As most of the specimens are preserved as external moulds it complicates comparison of internal char-

acters with the other species. *Sthenodonta* sp. B is separated from *Sthenodonta* sp. A due to a more extended posterior part of the valve, making the overall shell shape sub-ovate rather than sub-circular (compare Fig. 11A vs. Fig. 10N).

The species is separated from *S. eastii* due to the much better defined growth lines (compare Fig. 11A vs. Fig. 10J₂) as well as the overall lower shell profile and the less demarcated umbo. The discussed *Sthenodonta* species have

an umbo pointing in an anterior direction and generally the umbo on *Sthenodonta* sp. B is slightly more dorsally directed as compared to the two other *Sthenodonta* species. *Sthenodonta* sp. B likely represents a new, as yet unnamed species. However, due to the generally poor state of preservation among the specimens and lack of preserved characteristic taxonomic features, *Sthenodonta* sp. B has not been described formally as a new species.

Family Malletiidae Adams and Adams, 1858

Genus *Johnmartinia* Pojeta and Gilbert-Tomlinson, 1977

Type species: Johnmartinia cordata Pojeta and Gilbert-Tomlinson, 1977 from the Stairway Sandstone (original designation), Middle Ordovician in the James Range, about 90 km east of Areyonga Gorge, Australia.

Johnmartinia cordata Pojeta and Gilbert-Tomlinson, 1977

Fig. 11B.

1977 *Johnmartinia cordata* sp. nov. Pojeta and Gilbert-Tomlinson 1977: 14, pl. 8: 1–14.

Holotype: Incomplete specimen CPC 15514, figured by Pojeta and Gilbert-Tomlinson (1977: pl. 8, 4–7).

Type locality: James Range, Amadeus Basin, southern Northern Territory, Australia.

Type horizon: Sandstone moulds from the Stairway Sandstone, Middle Ordovician (no specific horizon mentioned).

Material.—Only one specimen (CPC 41469) has been identified with certainty from the Areyonga Gorge section, Middle Ordovician of Australia. Fragmentary internal moulds from the same bed may also belong to this species but they are too poorly preserved to be confidently identified.

Description.—Shell markedly inequilateral. Dorsal margin arcuate, anterior and posterior margins rounded and projecting, ventral margin rounded and projecting. Umbones highly prominent and strongly divergent (Fig. 11B₂), not projecting above dorsal commissure. Teeth anterior to umbo very short or absent (Pojeta and Gilbert-Tomlinson 1977).

Remarks.—*Johnmartinia cordata* shares a number of characters with *Sthenodonta eastii*, including the course of the posterior tooth row, development of umbo and inequilateral shell form. However, the row of teeth anterior to umbo is virtually absent in *Johnmartinia* and there is significant interumbonal growth, which place the umbo far from the midline, precluding assignment to the Nuculariidae.

Johnmartinia cordata has the most acutely tapered and prominent umbo among the bivalves investigated. The figured specimen (Fig. 11B₁) also exhibits an elongate border area following the dorsal delineation. This distinct character is also evident on the internal mould illustrated by Pojeta and Gilbert-Tomlinson (1977: pl. 8: 1–3).

Stratigraphic and geographic range.—In addition to the occurrence in bed A-9 in the Areyonga Gorge section Pojeta and Gilbert-Tomlinson (1977: 15) reported the spe-

cies from the Stairway Sandstone at four localities within the Amadeus Basin. *Johnmartinia* is endemic to Australia. The range of the species is within the Stairway Sandstone Formation, Darriwilian (Middle Ordovician). The region is in the southern Northern Territory, corresponding to the central part of the Amadeus Basin (Fig. 1).

Genus *Nuculites* Conrad, 1841

Type species: Nuculites oblongatus Conrad, 1841 from the Hamilton Group, Devonian, New York State; subsequent designation by Miller (1889).

Stratigraphic and geographic range.—Other palaeotaxodont species assigned to *Nuculites* have been reported from the Lower Ordovician of France (Babin 1966), Tasmania (Corbett and Banks 1974), and South Korea (Kobayashi 1934), whereas Upper Ordovician species have been reported from Wales, Canada (Sepkoski 1998) and USA (Dalve 1948). Depending on taxonomic revisions *Nuculites* may have the widest cosmopolitan distribution of all taxa studied.

Nuculites wattii (Tate, 1896)

Fig. 11C–F.

1896 *Isoarca wattii* sp. nov.; Tate 1896: 108, pl. 2: 17a, b.

1977 *Nuculites wattii* (Tate, 1896); Pojeta and Gilbert-Tomlinson 1977: 16, pl. 6: 6, 7.

Type material: Lectotype (SAM T 1220a) designated by Pojeta and Gilbert-Tomlinson (1977: pl. 6: 6, 7). Syntype figured by Tate (1896: pl. 2: 17a).

Type locality: Locality between Tempe Downs and Petermann Creek (about 5 km apart) in the Amadeus Basin (Tate 1896).

Type horizon: Judging from the quartzitic lithology of the type suite of *Nuculites wattii*, the taxon is probably from the Stairway Sandstone, probably Darriwilian (Middle Ordovician).

Material.—90 specimens, all from the Areyonga Gorge section, Middle Ordovician of Australia. The material is rather fragmentary and some of the non-illustrated specimens are tentatively assigned. The four (CPC 41470–41473) best preserved internal moulds are illustrated (Fig. 11C–F).

Description.—Shell tumid and shape ovate with prominent anterior myophoric buttress and highly prosogyral umbo. Posterior tooth row consists of about 20 chevron or half-chevron shaped teeth with apex pointing towards umbo (Fig. 11F) and constitute about 75% of the total length (transverse) of the valve.

Remarks.—*Nuculites* is a designation typically used for early Palaeozoic palaeotaxodonts with a prominent anterior myophoric buttress, and the group is in need of taxonomic revision. Tate (1896: 108) discussed the dentition and noted that there are a few large anterior teeth but numerous smaller teeth located posteriorly. There may be space for a few teeth anteriorly in the specimens but they appear very indistinct (see Fig. 11F). Tate (1896) counted about 20 teeth posteriorly, which is the same number observed on specimens collected for this study.

When a cast of the species is viewed from above the um-

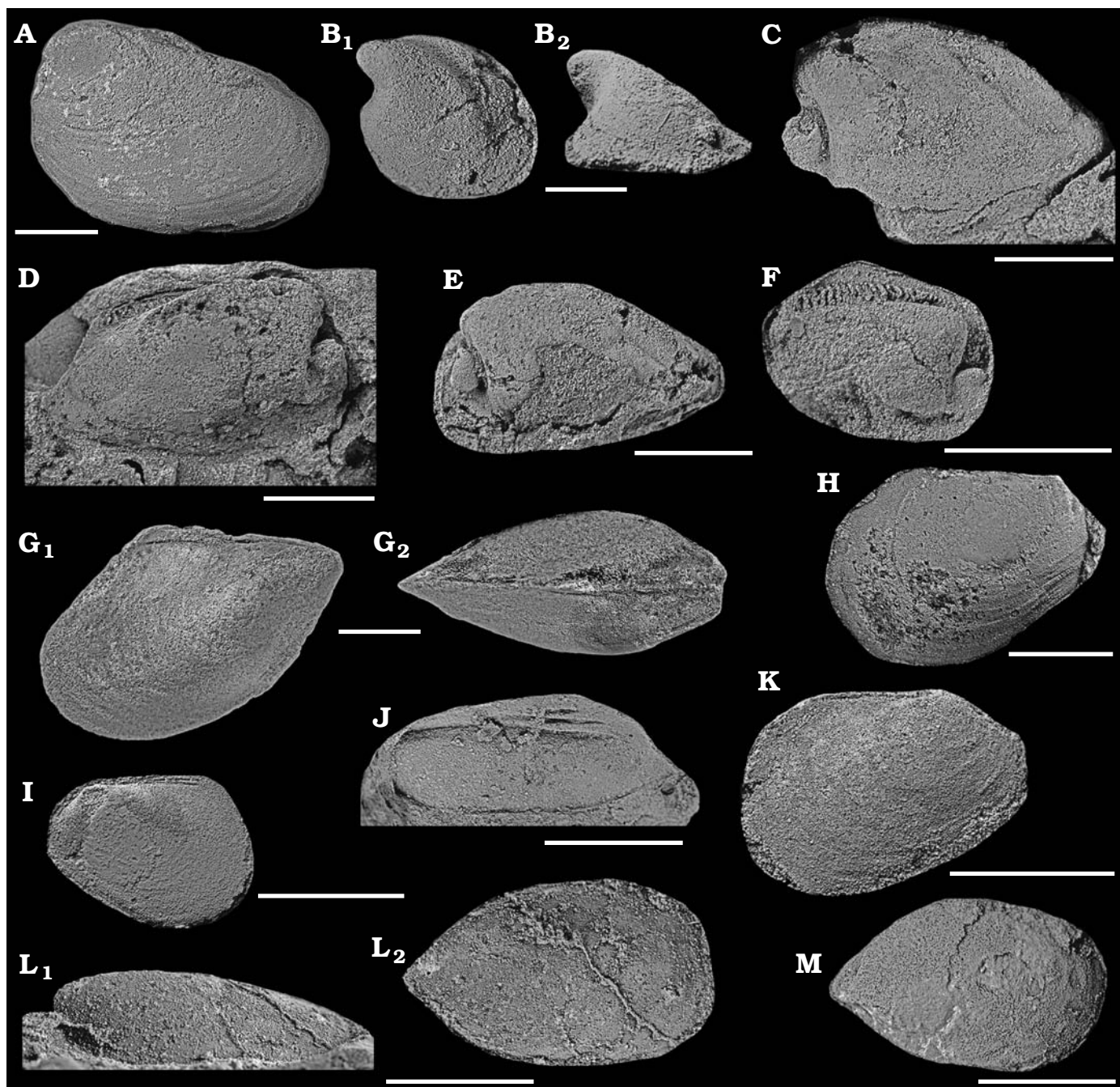


Fig. 11. Nucularcid and pteriomorphian bivalves from the Stairway Sandstone, Middle Ordovician, Australia. Internal moulds (B–K) and latex casts of external moulds (A, L, M). **A.** *Sthenodonta* sp. B (CPC 41468) from Petermann Creek, left-lateral view showing well marked growth lines. **B.** *Johnmartinia cordata* Pojeta and Gilbert-Tomlinson, 1977 (CPC 41469) from Areyonga Gorge; left-lateral view with dorsal border (B₁), anterior view showing the pointy beak (B₂). **C–F.** *Nuculites wattii* Tate, 1896 from Areyonga Gorge. **C–E.** Specimens in left (C, E) and right-lateral (D) dorsal views, showing well-defined anterior myophoric buttress, D additionally shows dorsal teeth (C, CPC 41470; D, CPC 41472; E, CPC 41472). **F.** Right-lateral view of fragmentary specimen with chevron shaped posterior teeth pointing anteriorly (CPC 41473). **G.** *Cyrtodonta carberryi* Pojeta and Gilbert-Tomlinson, 1977 (CPC 41474) from Areyonga Gorge; in right-lateral view with growth lines and at least one dorsal lateral tooth (G₁), dorsal view illustrating the height of shell profile (G₂). **H–K.** *Cyrtodonta staffordae* Pojeta and Gilbert-Tomlinson, 1977 from Petermann Creek (H–I, K) and Areyonga Gorge (J). **H.** Specimen in right-lateral view showing distinct growth lines (CPC 41475). **I.** Specimen in left-lateral view with three posterior lateral teeth (CPC 41476). **J.** Fragmentary posterior margin with duplivincular ligament and indications of three posterior lateral teeth (CPC 41478). **K.** Specimen in right-lateral view with a posterior lateral tooth (CPC 41477). **L, M.** *Cyrtodonta* sp. B. **L.** Anterior (L₁) and left-lateral (L₂) views of sub-ovate shell-profile (CPC 41479) from Petermann Creek. **M.** Sub-ovate shell-profile with growth lines (CPC 41480) from Areyonga Gorge. Scale bars 10 mm.

bonal ventricosity hides the hinge-line posteriorly and this is a way of separating *Nuculites wattii* from rather similar *Sthenodonta eastii* if the myophoric buttress is not preserved.

Stratigraphic and geographic range.—*Nuculites wattii* is endemic to central Australia. The exact type locality is unknown but seems to be close to the Petermann Creek sec-

tion studied here (see type material). However, not a single specimen assigned to *Nuculites wattii* was recovered from this section and all specimens derive from bed A -9 (Fig. 4) in the Areyonga Gorge section located some 40 km further north (Fig. 3). The range of the species is within the Stairway Sandstone Formation, Darriwilian (Middle Ordovician). The region is in the southern Northern Territory, corresponding to the central part of the Amadeus Basin (Fig. 1).

Subclass Autobranchia Grobben, 1894

Infraclass Pteriomorphia Beurlen, 1944

Order Arcoida Stoliczka, 1871

Family Cyrtodontidae Ulrich, 1894

Genus *Cyrtodonta* Billings, 1858

Type species: *Cyrtodonta rugosa* Billings, 1858 from the Black River Fauna of south eastern Canada; subsequent designation by Williams and Breger (1916).

Stratigraphic and geographic range.—The genus ranges through most of the Ordovician from the Floian to the end of the Hirnantian (e.g., Cope 2004) and represents one of the long-ranging Ordovician bivalves. Except for the Amadeus Basin material, Pojeta and Gilbert-Tomlinson (1977: 21) listed a single specimen assigned to *Cyrtodonta* sp. A from the Middle Ordovician Toko Group of the Georgina Basin. As the Australian specimens of the genus represent some rare Southern Hemisphere appearances they may prove useful for Middle Ordovician palaeobiogeographic reconstructions, as the genus is abundant particularly in Laurentia (Pojeta 1987) but also is present in Avalonia (Cope 1996).

Cyrtodonta carberryi Pojeta and Gilbert-Tomlinson, 1977

Fig. 11G.

1977 *Cyrtodonta carberryi* sp. nov.; Pojeta and Gilbert-Tomlinson 1977: 20, pl. 16: 3–5.

Type material: Holotype (CPC 15549) figured by Pojeta and Gilbert-Tomlinson (1977: pl. 16: 5). Paratypes (CPC 15547 and CPC 15548) figured by Pojeta and Gilbert-Tomlinson (1977: pl. 16: 3, 4). All specimens are composite moulds.

Type locality: Gardiner Range, Amadeus Basin, southern Northern Territory, Australia.

Type horizon: Stairway Sandstone, Darriwilian (Middle Ordovician).

Material.—Five fragmentary specimens from the Areyonga Gorge section, Middle Ordovician of Australia. The best preserved composite mould (CPC 41474) is figured (Fig. 11G₁, G₂). The material was recovered from bed A +4 in the Areyonga Gorge section. Pojeta and Gilbert-Tomlinson (1977: 20 and 53) reported additional eight specimens from a single locality in the Gardiner Range, about 30 km north west of the Areyonga Gorge section. All known material of *C. carberryi* is from the Stairway Sandstone (Pojeta and Gilbert-Tomlinson 1977; this study).

Description.—*Cyrtodonta* with bulbous profile, oblique quadrate shape and prosogyral umbo. Dorsal margin straight

and anterior margin straight to slightly oblique. Ventral margin rounded and posterior margin straight. Ornament of commarginal growth lines present. The illustrated adult specimen is 42 mm long and 25 mm high.

Remarks.—Many species have been assigned to *Cyrtodonta*. It is especially abundant in the Upper Ordovician of eastern North America, and the central Australian occurrences reported by Pojeta and Gilbert-Tomlinson (1977) were the first record of the genus from the Southern Hemisphere. *Cyrtodonta carberryi* differs from other Australian species of *Cyrtodonta* by its oblique quadrate shape and straight anterior margin. *Cyrtodonta carberryi* can be differentiated from *C. staffordae* by possessing a less symmetric shape as well as a slightly wider shell.

According to Pojeta and Gilbert-Tomlinson (1977: 20) the only known internal feature is two posterior lateral teeth in the left valve. However, the figured specimen (Fig. 11G₁) is a right valve and at least one and possibly two impressions of posterior lateral teeth are indicated.

Stratigraphic and geographic range.—*Cyrtodonta carberryi* is endemic to central Australia. All known material of *C. carberryi* is from the Stairway Sandstone (Pojeta and Gilbert-Tomlinson 1977; this study) at localities in the Gardiner Range, Areyonga Gorge, and Petermann Creek, southern Northern Territory.

Cyrtodonta staffordae Pojeta and Gilbert-Tomlinson, 1977

Fig. 11H–K.

1977 *Cyrtodonta staffordae* sp. nov.; Pojeta and Gilbert-Tomlinson 1977: 20, pl. 14: 1–3.

Type material: Holotype (CPC 15541) is illustrated by Pojeta and Gilbert-Tomlinson (1977: pl. 14: 1, 2). Paratype (CPC 15540) figures by Pojeta and Gilbert-Tomlinson (1977: pl. 14: 3). Both specimens are sandstone moulds.

Type locality: Deering Creek, Amadeus Basin, southern Northern Territory, Australia.

Type horizon: Stairway Sandstone, Darriwilian (Middle Ordovician).

Material.—17 specimens from the Petermann Creek section and 13 specimens from the Areyonga Gorge section, Middle Ordovician of Australia. We illustrate three internal moulds (CPC 41475–41478).

Description.—Shell subquadrate with straight dorsal margin; anterior margin rounded and projecting dorsally, ventral and posterior margins broadly rounded. Umbo subdued and projecting only slightly above dorsal commissure. A single posterior lateral tooth is present in the right valve (Fig. 11K).

Remarks.—*Cyrtodonta staffordae* strongly resembles *C. wattii*. The shape of *C. wattii*, however, appears slightly more elongate as compared to *C. staffordae* which broadens in a posterior direction (compare Pojeta and Gilbert-Tomlinson 1977: pl. 14: 3 vs. pl. 15: 3). The left valve has three elongate posterior lateral teeth and at least three anterior teeth according to Pojeta and Gilbert-Tomlinson (1977: 21). Anterior teeth are not observed in the material at hand and most specimens

only preserve one lateral posterior tooth. A single fragmentary specimen, however, shows three posterior lateral teeth (Fig. 11J) as well as a duplivincular ligament very similar to that of *C. wattii* (see Pojeta and Gilbert-Tomlinson 1977: pl. 15: 3, 5). Due to the fragmentary state of the specimen it is uncertain whether it belongs to *C. wattii*, as other cyrtodontids also possess three posterior lateral teeth (e.g., *Cyrtodonta hazeli* Pojeta and Gilbert-Tomlinson 1977: pl. 16).

Pojeta and Gilbert-Tomlinson (1977) noted that *C. staffordae* has a subdued umbo whereas *C. wattii* possesses a prominent umbo. This is not always clear from their illustrations (compare Pojeta and Gilbert-Tomlinson 1977: pl. 14: 3 vs. pl. 15: 2), further complicating discrimination of the two species. Separation can be based on the posterior lateral tooth or teeth. *Cyrtodonta staffordae* is further distinguished from the equally subquadrate *C. carberryi* by having broadly rounded anterior and posterior margins rather than straight oblique margins.

Cyrtodonta staffordae can be separated from the *C. carberryi* and *Cyrtodonta* sp. B by a less elongated profile or more symmetric shape as well as a slightly lower shell profile. *Cyrtodonta staffordae* is separated from *Modiolopsis pojetai* sp. nov. by possessing a less elongated profile (or a more symmetric shape).

Stratigraphic and geographic range.—*Cyrtodonta staffordae* ranges over 55 m through most fossiliferous beds in the Petermann Creek section (PC -5–PC +11; Fig. 5), whereas it has a shorter range over 18 m in the Areyonga Gorge section (bed A -1–A +5; Fig. 4). Pojeta and Gilbert-Tomlinson (1977: 20 and 53) reported *C. staffordae* from the Stairway Sandstone at two localities (based on two specimens) in the Gardiner Range.

Cope (1996) reported *C. cf. staffordae* from the lower Floian of South Wales based on one specimen. The specimen is thus somewhat older, smaller, and there are indications of a left lateral tooth, which is not present in typical *C. staffordae*. It seems unlikely the two species are conspecific. Cope (1996) also reported two specimens of *C. cf. wattii* from the lower Floian of South Wales. *Cyrtodonta wattii* was reported by Pojeta and Gilbert-Tomlinson (1977: 21) from the Stairway Sandstone at 12 localities in the Amadeus Basin, not including the Petermann Creek or Areyonga Gorge. The range of the species is within the Stairway Sandstone Formation, Darriwilian (Middle Ordovician). The region is in the southern Northern Territory, corresponding to the central part of the Amadeus Basin (Fig. 1).

Cyrtodonta sp. B

Fig. 11L, M.

Material.—Three specimens from the Petermann Creek section and four specimens from the Areyonga Gorge section, Middle Ordovician of Australia. The material is found in bed PC+10 in the Petermann Creek section and beds A +1 to A +4 in the Areyonga Gorge section (Figs. 4, 5). The two

illustrated specimens (CPC 41479 and CPC 41480) are latex casts made from external moulds.

Description.—Near equilateral sub-ovate cyrtodontid with slightly curved dorsal and ventral margins; slightly pointy anterior margin and broadly rounded posterior margin. Umbo subdued, pointy and anterodorsally projecting. No teeth preserved in the specimens, possibly due to a preservational artefact. Shell profile low and ornament of commarginal growth lines.

Remarks.—*Cyrtodonta* sp. B is the most flat-profiled and symmetrically shaped cyrtodontid in the collections (Fig. 11L₁). It is differentiated from *Cyrtodonta carberryi* by the lower shell profile, more rounded dorsal and ventral margins as well as a less pronounced umbo. Furthermore, *Cyrtodonta* sp. B exhibits a rounded and gradually declining shell from the midline towards anterior margin, whereas the course of the shell in *C. carberryi* declines abruptly about halfway from the midline towards the anterior margin.

The overall equilateral shape of *Cyrtodonta* sp. B separates it from the inequilateral *C. staffordae*, whereas the latter exhibits a more symmetrical rounded overall shape. *Cyrtodonta* sp. B likely represents a new, as yet unnamed species. Due to the generally poor state of preservation among the specimens and lack of preserved characteristic taxonomic features, *Cyrtodonta* sp. B has not been described formally as a new species.

Order Mytiloida Ferussac in Ferussac and d'Audebard, 1822

Family Modiolopsidae Fischer, 1885

Genus *Modiolopsis* Hall, 1847

Type species: *Pterinea modiolaris* Conrad, 1838; original designation. The exact type locality is uncertain, as the museum label (Smithsonian Institution, National Museum of Natural History) accompanying the holotype gives the locality as “from Pulanski beds [Late Ordovician], Rome, N.Y. State”. This deviates from the description given by Conrad (1838).

Modiolopsis pojetai sp. nov.

Fig. 12A, B.

Etymology: In honour of John Pojeta Jr. (Smithsonian Institution, National Museum of Natural History, Washington D.C., USA), who did much pioneering work on Ordovician molluscs from central Australia.

Type material: Holotype CPC 41481 (Fig. 12A). Paratype CPC 41482 (Fig. 12B), derived from the type locality.

Type locality: Petermann Creek section, close to Tempe Downs, Amadeus Basin, southern Northern Territory.

Type horizon: Bed PC +9 of the Stairway Sandstone in the Petermann Creek section (Figs. 3, 5).

Material.—17 specimens from the Petermann Creek section and 16 specimens from the Areyonga Gorge section, Middle Ordovician of Australia. The material consists exclusively of internal moulds.

Diagnosis.—Inequilateral *Modiolopsis* species with sub-rounded and well-defined umbo. Shell expands in posterior

direction and is delineated by rounded posterior margin; umbo prominent and steeply descending anteriorly. A discrete longitudinal slit-like mark reaching far posterior on internal moulds. No teeth present in the material.

Description.—Shell ovate-elongate with rounded posterior margin and straight to oblique dorsal and ventral margins. Shell profile high at umbonal area but fades out in posterior direction and becomes relatively flat. Internal moulds show a longitudinal slit-like mark, probably due to a longitudinal rib that has been present (Fig. 12A).

Remarks.—*Modiolopsis* Hall, 1847 is regarded as being edentulous by Ulrich (1924), and the absence of this important character supports the generic assignment of the Stairway Sandstone specimens. Ulrich (1924) described the ligament of *Modiolopsis* (*Modiodesma*) as having both inner and outer parts, the inner part being supported by a longitudinal rib which left a slit-like mark on moulds (see e.g., Pojeta 1971: pl. 12: 4). This slit-like mark appears present in *Modiolopsis pojetai* sp. nov. (see Fig. 12A). Usually, however, silicified specimens of Ordovician modiolopsids show no sign of an internal longitudinal rib (Pojeta 1971: 21) and it is possible that the “longitudinal slit” was made by the dorsal margin of the shell. Admittedly the slit has been difficult to photograph and may not be perfectly clear on the figures. However, it is clearly present when looking at the actual specimens. The slit may also be referred to as a preduplivincular ligament (see Carter et al. 2012).

Pojeta and Gilbert-Tomlinson (1977: 26) discussed *Modiolopsis?* sp. A based on three specimens found in the Stairway Sandstone in the James Range about 150 km east of Areyonga Gorge. One poorly preserved internal mould was illustrated (Pojeta and Gilbert-Tomlinson 1977: pl. 23: 10) and the ovate and elongate shape somewhat resembles that of *M. pojetai* sp. nov., but the dorsal and ventral margins are straight without being oblique. More importantly, the shell of *Modiolopsis?* sp. A is not nearly as expanding posteriorly as in *M. pojetai* sp. nov.

Modiolopsis gordonensis was reported from the Ordovician Gordon Limestone (Gordon Group) of Tasmania by Johnston (1888). This species is truncate so that the umbo is terminal and this feature differentiates it from *M. pojetai* sp. nov. In this species the umbo descends steeply towards the anterior margin, but is not terminal positioned. For further discussion on *M. gordonensis*, see Pojeta and Gilbert-Tomlinson (1977: 26).

The North American species *Modiolopsis modiolaris* (Conrad, 1838) is somewhat similar to *Modiolopsis pojetai* sp. nov., except that the projection of the anterior margin descends more steeply, resulting in a somewhat shorter (transverse) anterior margin in *M. pojetai* sp. nov. (compare Fig. 12A vs. Pojeta 1971: pl. 15: 1 and pl. 16: 2). However, *M. pojetai* sp. nov. somewhat resembles *Modiolopsis cuyana* Sánchez, 1990, as reported from the Upper Ordovician in the Precordillera, Argentina by Sánchez (compare Fig. 12A vs. Sánchez 1990: pl. 1: 8). No obvious differences can be distin-

guished and *Modiolopsis cuyana* Sánchez, 1990 is probably more closely related to *M. pojetai* sp. nov. compared to the North American species of *Modiolopsis modiolaris*.

Stratigraphic and geographic range.—*Modiolopsis pojetai* sp. nov. ranges from bed PC -6 to PC +10 in the Petermann Creek section and from bed A -4 to A +4 in the Areyonga Gorge section (see Figs. 4, 5). The new species is endemic to the Amadeus Basin and it is one of very few modiolopsids recovered from Middle Ordovician successions in the Southern Hemisphere. The genus ranges through most of the Ordovician from the Floian to the end Hirnantian (e.g., Cope 2004) and may eventually prove useful for palaeobiogeographic correlation. The range of *Modiolopsis pojetai* sp. nov. is in the middle part of the Stairway Sandstone Formation, Darriwilian (Middle Ordovician). The region is in the southern Northern Territory, corresponding to the central part of the Amadeus Basin (Fig. 1).

Family Colpomyidae Pojeta and Gilbert-Tomlinson, 1977

Genus *Colpantyx* Pojeta and Gilbert-Tomlinson, 1977

Type species: *Colpantyx woolleyi* Pojeta and Gilbert-Tomlinson, 1977 from the late Cambrian to Early Ordovician Pacoota Sandstone, Amadeus Basin, Australia; original designation.

Colpantyx? sp. A

Fig. 12C, D.

Material.—10 fragmentary internal and external moulds found in beds A +1 to A +3 in the Areyonga Gorge section only (Fig. 4), Middle Ordovician of Australia. The two figured specimens (CPC 41483 and CPC 41484) are latex casts made from external moulds.

Description.—Small slightly rounded triangular colpomyid with well-defined umbonal radial ribs, of which two are present anteriorly and one posteriorly (Fig. 12D). Except for radial ribs the surface appears smooth. Anterior ribs short and almost straight, radiating until they reach anterior-most part of ventral margin. Posterior rib long and curving towards posterior margin. Anterior and ventral margins straight to broadly rounded; posterior margin straight, oblique towards dorsum. Umbo subdued (Fig. 12C) and shell profile low.

Remarks.—*Colpantyx* is endemic to Australia. The only other species assigned is *Colpantyx woolleyi* Pojeta and Gilbert-Tomlinson, 1977 from the upper Tremadocian part of the Pacoota Sandstone of the Amadeus Basin (e.g., Shergold 1991; Cope 2004).

The slightly rounded triangular overall shape, the radial well-defined umbonal ribs and the delineation of the margins are quite similar among the two *Colpantyx* species. However, *C. woolleyi* has pronounced commarginal ornament and only one or two posterior umbonal radial ribs. Furthermore the posteroventral margin is sinuous between the ribs. In comparison *Colpantyx?* sp. A possesses a smooth surface completely lacking commarginal ornament. It is unknown whether these differences are due to preserva-

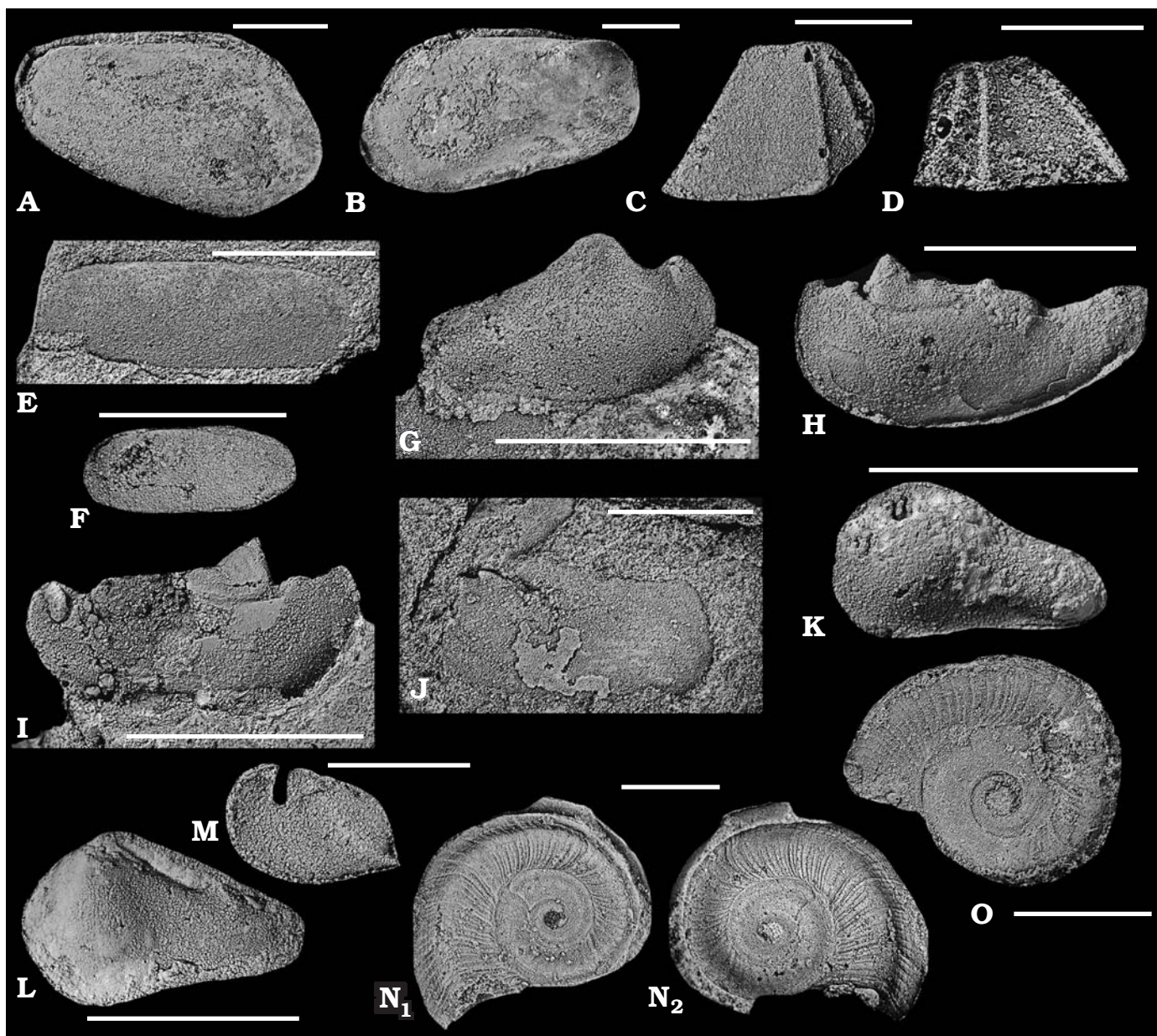


Fig. 12. Pteriomorphian and heteroconchian bivalves, rostroconchs and gastropods from the Stairway Sandstone, Middle Ordovician, Australia. Internal moulds (A, B, E–M, N₁) and latex casts of internal (N₂, O) and external (C, D) moulds. **A, B.** *Modiolopsis pojetai* sp. nov. from Petermann Creek. **A.** Holotype (CPC 41481) in left-lateral view showing discrete longitudinal dorsal slit-like mark. **B.** Paratype (CPC 41482) in right-lateral view with umbo steeply descending anteriorly. **C, D.** *Colpantyx?* sp. A from Areyonga Gorge; in right (C, CPC 41483) and left-lateral (D, CPC 41484) views with two umbonal radial ribs anteriorly and one posteriorly. **E, F.** *Sphenosolen draperi* Pojeta and Gilbert-Tomlinson, 1977 from Petermann Creek (**E**, CPC 41485; **F**, CPC 41486), specimens with flat shell and narrow elongated sub-rectangular shape. **G–M.** Rostroconchia. **G–I.** *Ribeiria csiro* Pojeta, Gilbert-Tomlinson, and Shergold, 1977 from Areyonga Gorge (**G**) and Petermann Creek (**H–I**); note the prominent triangular beak and curved ventral margin (**G**, CPC 41487; **H**, CPC 41488; **I**, CPC 41489). **J.** *Ribeiria jonesi?* from Petermann Creek, sub-rectangular profile and strong dorsally projecting umbo (CPC 41490). **K, L.** *Pinnocaris* sp. A from Petermann Creek with inflated pear-shaped profile (**K**, CPC 41491; **L**, CPC 41492). **M.** *Technophorus walteri* Pojeta, Gilbert-Tomlinson, and Shergold, 1977 from Areyonga Gorge (CPC 41493) with a single lateral radial rib and prominent nearly erect pegma indicated. **N, O.** Gastropoda, *Scalites?* sp. from Petermann Creek. **N.** CPC 41494 (N₁), latex cast with clear growth lines (N₂). **O.** CPC 41495, specimen with 3.5 to 4 whorls. Scale bars 10 mm, except C, D, M, 5 mm.

tional artefacts, as the material from the Stairway Sandstone is dolomitized. The posteroventral margin is somewhat sinuous between the ribs but not nearly as pronounced as observed on *C. woolleyi*. The three umbonal ribs present on *Colpantyx?* sp. A are very consistent and differ from the condition in *C. woolleyi* where only one or two ribs are de-

veloped (compare Fig. 12D vs. Pojeta and Gilbert-Tomlinson 1977: pl. 24).

The related species *Colpantyx woolleyi* occurs in the Pacoota Sandstone at 11 different localities in the Amadeus Basin (Pojeta and Gilbert-Tomlinson 1977: 28). When more material from the Stairway Sandstone becomes available the

generic assignment should be investigated, and if identified with confidence as *Colpantyx*, the range of this genus should be extended from the Tremadocian into the Darriwilian.

Infraclass Heteroconchia Hertwig, 1895

Order Veneroida Adams and Adams, 1858

Family Orthonotidae Miller, 1877

Genus *Sphenosolen* Pojeta and Gilbert-Tomlinson, 1977

Type species: *Sphenosolen draperi* Pojeta and Gilbert-Tomlinson, 1977 from the Stairway Sandstone, Middle Ordovician of Australia; original designation.

Sphenosolen draperi Pojeta and Gilbert-Tomlinson, 1977

Fig. 12E, F.

1977 *Sphenosolen draperi* sp. nov.; Pojeta and Gilbert-Tomlinson 1977: 31, pl. 25: 1, 2.

Type material: Holotype (CPC 15582) is figured by Pojeta and Gilbert-Tomlinson (1977: pl. 25: 1). Paratype (CPC 15583) figured by Pojeta and Gilbert-Tomlinson (1977: pl. 25: 2) from the type locality.

Type locality: Stairway Sandstone, East of Maryvale Homestead, Amadeus Basin, southern Northern Territory, Australia.

Type horizon: Decalcified friable buff/white fine-grained silty sandstone horizon within the Stairway Sandstone.

Material.—40 specimens, mostly fragmentary internal and external moulds; 4 specimens from the Areyonga Gorge section and 36 specimens from Petermann Creek section, Middle Ordovician of Australia. The two figured specimens are numbered CPC 41485 and CPC 41486.

Description.—Narrow elongated sub-rectangular orthoconid with flat shell. Dorsal margin straight; anterior margin rounded; posterior margin rounded to straight and oblique toward the dorsum; ventral margin broadly rounded anteriorly, straight posteriorly. Umbo hardly discernible.

Remarks.—*Sphenosolen draperi* is the only heteroconch recovered from the investigated sections. The shell shape is distinctly different from all other species due to the reduced height and increased length. Cope (2004) placed the genus *Sphenosolen* within the anomalodesmatans but we follow Pojeta and Gilbert-Tomlinson (1977), who assigned the genus to the heteroconchs; for further discussion see Cope (2002, 2004). *Sphenosolen* is a middle Darriwilian taxon (Cope 2004: fig. 20.3), like the nuculoids *Sthenodonta* and *Johnmartinia*.

Stratigraphic and geographic range.—A single specimen from bed PC -5 in the Petermann Creek section is tentatively assigned to *S. draperi*, whereas the remaining 35 specimens derive from bed PC +7 to PC +11 in the upper part of the section (Fig. 5). The species also ranges through the upper part of the Areyonga Gorge section from bed A +1 to A +4 (Fig. 4).

Pojeta and Gilbert-Tomlinson (1977: 31) described and illustrated *Sphenosolen draperi* based on nine specimens, all from the same locality about 150 km east of the Areyonga

Gorge in the Amadeus Basin. All known specimens found are from the Stairway Sandstone. Heteroconchs are uncommon in low-latitude faunas, and seemingly preferred high-latitude environments (Cope 2002). The range of *Sphenosolen draperi* is within the Stairway Sandstone Formation, Darriwilian (Middle Ordovician). The region is in the southern Northern Territory, corresponding to the central part of the Amadeus Basin (Fig. 1).

Class Rostroconchia Pojeta, Runnegar, Morris, and Newell, 1972

Order Ribeirioidea Kobayashi, 1933

Family Ribeiriidae Kobayashi, 1933

Genus *Ribeiria* Sharpe, 1853

Type species: *Ribeiria pholadiformis* Sharpe, 1853 by monotypy, from the Ordovician near Bussaco, Portugal.

Ribeiria csiro Pojeta, Gilbert-Tomlinson, and Shergold, 1977

Fig. 12G–I.

1977 *Ribeiria csiro* sp. nov.; Pojeta et al. 1977: 13, 14, pl. 3: 3, 4.

1977 *Ribeiria csiro*; Pojeta and Gilbert-Tomlinson 1977: 31, pl. 29: 17.

Type material: Holotype (CPC 14715), internal mould. Paratype (CPC 14716), largely imbedded in sandstone with partly preserved shell from the type locality. Both figured by Pojeta et al. (1977: pl. 3: 3, 4).

Type locality: Stairway Sandstone, South of Maryvale Homestead, Amadeus Basin, southern Northern Territory, Australia.

Type horizon: Silicified sandstone horizon within the Stairway Sandstone.

Material.—21 specimens, all internal moulds, of which 18 are from the Petermann Creek section and 3 from the Areyonga Gorge section, Middle Ordovician of Australia. Three specimens (CPC 41487–41489) are figured (Fig. 12G–I).

Description.—Medium sized *Ribeiria* with slightly concave and narrow dorsum. Beak projecting above rest of dorsal margin; anterior margin projecting forward of beak; ventral margin arcuate and shell markedly attenuated posteriorly. Internally a prominent oblique pegma and a shell thickening along the posterodorsal margin produce a notch on internal moulds (Fig. 12H). The most distinct character for the species is the prominent triangular beak that projects high above the remaining dorsal margin. In front of the steeply forward descending beak the anterodorsal margin flattens out before ascending slightly towards anterior margin, from where the anterior delineation begins to curve ventrally.

Remarks.—The well-defined prominent beak makes species identification easy if preserved (see Fig. 12G–I). *Ribeiria csiro* is the most abundant rostroconch in the collection. *Ribeiria* is a widespread genus reported from Europe, Morocco, China, Australia and North America (Pojeta and Runnegar 1976). Pojeta et al. (1977) erected five new Cambro-Ordovician species, all endemic to Australia, of which *Ribeiria csiro* is the only species reported from the Stairway Sandstone.

Stratigraphic and geographic range.—The specimens from the Petermann Creek section were found in the two lowermost fossiliferous beds (PC -6–PC -5), whereas the species is occurring at higher stratigraphic levels in the Areyonga Gorge section (bed A +1–A +4), see Figs. 4 and 5. Additional to the type material Pojeta and Gilbert-Tomlinson (1977: pl. 29: 17) illustrated an internal mould (CPC 15601) from a different Stairway Sandstone locality very close to the Petermann Creek section. Together there is a total of four occurrences of the species. The range of *Ribeiria csiro* is within the Stairway Sandstone Formation, Darriwilian (Middle Ordovician). The region is in the southern Northern Territory, corresponding to the central part of the Amadeus Basin (Fig. 1).

Ribeiria jonesi? Pojeta, Gilbert-Tomlinson, and Shergold, 1977

Fig. 12J.

?1977 *Ribeiria jonesi* sp. nov.; Pojeta et al. 1977: 15, pl. 4: 1, 2, 6–9; pl. 11: 8–15.

Type material: Holotype (CPC 14787) figured by Pojeta et al. (1977: pl. 11: 14). Eight paratypes (CPC 14709, 14711, 14782, 14783, 14784, 14785, 14786, 14788) figured by Pojeta et al. (1977: pl. 4: 1, 2, 6–9; pl. 11: 8–13, 15) from type locality.

Type locality: Pacoota Sandstone in the Amadeus Basin, Australia.

Type horizon: Saukiid trilobites found in the same beds indicate a late Cambrian (Furongian) age.

Material.—A single internal mould (CPC 41490) recovered from bed PC +8. It is the only rostroconch from the upper part of the Petermann Creek section (Fig. 5), Middle Ordovician of Australia. The facies in this upper part is more silty than the quartzite in which *Ribeiria csiro* occurs in the lower part of the section.

Description.—Small *Ribeiria* with sub-rectangular profile. Strong dorsally projecting umbo, the dorsal margin is convex but flattens out in posterior direction. Anterior margin projecting forward of beak; ventral margin straight or nearly straight; posterior margin nearly straight to slightly rounded. Pegma strong and oblique.

Remarks.—Due to the fragmentary umbo on the specimen it cannot be assigned to *Ribeiria jonesi* with certainty. However, part of the umbo may be partly preserved above the specimen (Fig. 12J) and indicates a strong and prominent umbo. The strong pegma also resembles that of *Ribeiria jonesi* figured by Pojeta et al. (1977: pl. 11: 8–15) and the straight ventral margin is also characteristic. In comparison with *Ribeiria csiro* the beak of specimen CPC 41490 appears more posteriorly directed versus straight dorsally directed in *R. csiro* (compare Fig. 12H vs. Fig. 12J). The overall shape also differs with *R. jonesi* being more rectangular and sharply demarcated versus more rounded ventral, anterior and posterior margins in *R. csiro*.

Comparison of *R. jonesi* with one of the paratypes figured by Pojeta et al. (1977, pl. 11: 11) shows no obvious differences. The specimen certainly belongs to *Ribeiria* and

if not representing *Ribeiria jonesi*, it probably belongs to a new closely related species.

Stratigraphic and geographic range.—All of the type material was found in the late Cambrian (Furongian) to Early Ordovician Pacoota Sandstone, Australia. However, additional material from the coeval Tomahawk sandstone beds in the Georgina Basin was mentioned but not illustrated by Pojeta et al. (1977: 15). *Ribeiria jonesi* ranges from the late Cambrian (Furongian) to the Middle Ordovician (Darriwilian), if the specimen found in the Stairway Sandstone is correctly assigned.

Genus *Pinnocaris* Etheridge, 1878

Type species: *Pinnocaris lapworthi* Etheridge, 1878, by monotypy, from the Ordovician of Girvan, Scotland.

Pinnocaris sp. A sensu Pojeta et al. 1977

Fig. 12K, L.

1977 *Pinnocaris* sp. A; Pojeta et al. 1977: 18, pl. 8: 11.

Material.—Four specimens from the Petermann Creek section, Middle Ordovician of Australia. Additional specimens probably belonging to this species are too badly preserved to be safely identified. The two illustrated specimens are numbered CPC 41491 and CPC 41492.

Description.—*Pinnocaris* sp. A is pear-shaped in outline being widest anteriorly and tapering rearwards. Shell profile relatively inflated. Ventral margin is arcuate throughout, with dorsal margin tapering from the distinct beak towards posterior margin. Anterior and posterior margins rounded.

Remarks.—According to Pojeta et al. (1977: 18) the species has a highly placed nearly erect pegma. This character cannot be observed in the available specimens due to the state of preservation, but may be indicated by a near vertical trace anterodorsal in one of the illustrated specimens (compare Pojeta et al. 1977: pl. 8: 11 vs. Fig. 12K).

The specimens at hand somewhat resemble one of the paratypes of *Pinnocaris wellsi* Pojeta, Gilbert-Tomlinson, and Shergold, 1977: pl. 9: 9 from the Pacoota Sandstone. However, *P. wellsi*, as well as other Australian species assigned to *Pinnocaris* possesses a more narrow-elongated pear-shape.

Pojeta and Gilbert-Tomlinson (1977: pl. 29: 18) illustrated a specimen of Conocardioid sp. A from Tempe Downs (near Petermann Creek). The specimen was originally figured by Tate (1896: pl. 2: 13) and probably derives from the Stokes Siltstone. It resembles specimen CPC 41492 (Fig. 12L) regarding overall shape, but the beak is much more prominent in Conocardioid sp. A, which distinguishes it from *Pinnocaris* sp. A (compare Pojeta and Gilbert-Tomlinson 1977: pl. 29: 18 vs. Fig. 12L).

Due to the generally poor state of preservation among the specimens and lack of preserved characteristic taxonomic features, *Pinnocaris* sp. A has not been described formally as a new species.

The species was originally described by Pojeta et al.

(1977) based on a single specimen from the Stairway Sandstone. In the present study four specimens were recovered from bed PC -6 in the Petermann Creek section. Pojeta et al. (1977: 17, 18) described two other species and two other species of *Pinnocaris* from central Australia of late Cambrian (Furongian) age, making *Pinnocaris* sp. A the youngest Australian species. *Pinnocaris* is also known from North America and Scotland (Pojeta and Runnegar 1976) and these occurrences are not older than Middle Ordovician.

Family Technophoridae Miller, 1889

Genus *Technophorus* Miller, 1889

Type species: Technophorus faberi Miller, 1889, by monotypy; Upper Ordovician of North America.

Stratigraphic and geographic range.—*Technophorus* ranges from the Early Ordovician, or possible Furongian (late Cambrian), to Late Ordovician and occurs except for in the Amadeus and Georgina basins (Pojeta et al. 1977: 20) also in Spain (Gutiérrez-Marco et al. 1984), North America (Frey 1987) and South America (Přibyl and Vanek 1980). Four endemic Australian species are described from the Amadeus and Georgina basins. The current finding extends the range of *Technophorus walteri* into the Middle Ordovician.

Technophorus walteri Pojeta, Gilbert-Tomlinson, and Shergold, 1977

Fig. 12M.

1977 *Technophorus walteri*; Pojeta et al. 1977: 21, pl. 10: 14–16.

1977 *Technophorus walteri*; Pojeta and Gilbert-Tomlinson 1977: 32, pl. 29: 13–16.

Type material: Holotype (CPC 14775), internal mould figured by Pojeta et al. (1977: pl. 10: 16). They also described two additional internal moulds found at the same locality.

Type locality: Pacoota Sandstone, Waterhouse Range, Amadeus Basin, southern Northern Territory, Australia.

Type horizon: Probably of Early Ordovician age (see Pojeta et al. 1977: 22).

Material.—One internal mould (CPC 41493) of a left valve from the Areyonga Gorge section, Middle Ordovician of Australia.

Description.—Small *Technophorus*, the specimen is 5.8 mm long and 3.3 mm high, with a single lateral radial rib intersecting the posteroventral angle of the shell. Anterior and ventral margins arcuate; posterior margin erect and strongly tapered. Umbo projecting slightly above the otherwise more or less straight dorsal margin. A prominent nearly erect pegma is clearly indicated.

Remarks.—The single lateral rib intersects the dorsal margin at an angle of about 45°, which is also in accordance with the description by Pojeta et al. (1977: 22), reporting that this angle is >40°. Pojeta and Gilbert-Tomlinson (1977: pl. 29: 13–16) also figured an articulated internal mould and a left valve exterior from the Pacoota Sandstone but from different localities than the type material. The left valve

illustrated on their pl. 29: 13 is very similar to the specimen at hand (compare to Fig. 12M).

Stratigraphic and geographic range.—The discussed specimen was found in the silt dominated bed A +3 at Areyonga Gorge (Fig. 4). All four rostroconchs found in this section were recovered from a few closely spaced beds in the upper part of the section. The range of *Technophorus walteri* is within the Stairway Sandstone Formation, Darriwilian (Middle Ordovician). The region is in the southern Northern Territory, corresponding to the central part of the Amadeus Basin (Fig. 1).

Class Gastropoda Cuvier, 1797

Remarks.—Almost 300 fragmentary gastropod specimens (internal and external moulds) have been recovered from the two investigated sections and are about equally distributed between them. As most taxonomically important characters usually revolve around the shell morphology, generic discrimination of the gastropod species is very difficult and we have taken a cautious approach to leave all gastropod taxa in open nomenclature. Six different species are distinguished, tentatively referred to as *Scalites?* sp., *Raphistomina?* sp., *Teiichispira?* sp., and Archinacelloid spp. A–C (the latter three are limpet-shaped archinacelloids).

Shergold (1986: 10) listed the gastropods *Clathrospira?* sp. and *Helicotoma?* sp. as well as a Monoplacophora indet. from the Stairway Sandstone. These two gastropod species do not seem to be present in the studied material (Jan O. Ebbestad, personal communication 2013). The specimens initially identified as “monoplacophorans” consist of limpet-shaped patelliform gastropods, here placed tentatively within the superfamily Archinacelloidea, which is allied with Gastropoda according to Peel and Horný (1999). The Gastropoda are here treated as a monophyletic group, whereas Monoplacophora is split into Class Tergomya and Class Helcionellida (see Peel 1991; Wagner 2002). Distinction between tergomyans and gastropods is based on muscle scars which appear in pairs in the former and in a band in the latter. This character, however, is not preserved in any of the specimens in the current collection, precluding confident taxonomic determination.

Scalites? sp. (CPC 41494, internal mould and latex cast of internal mould and CPC 41495, internal mould) is exclusively preserved as bases of large gastropods (Fig. 12N, O). The species occurs in the lower fossiliferous part of both investigated sections, but it is most abundant in the Petermann Creek section. The base contains 3.5 to 4 whorls. The aperture seems radial with the basal keel and reticulate ornamentation corresponding to what Wagner (2002) named *Scalites*. Tate (1896) listed *Scalites? eremos* from the Stokes Siltstone. The genus is also described from the Ordovician of North America (Raymond 1906), Korea (Kobayashi 1934), and China (Endo 1935).

Raphistomina? sp. (CPC 41496) is a small gastropod and the most abundant in the material (36% of the gastropods). It has 4 whorls but no other characters are preserved (Fig. 13A).

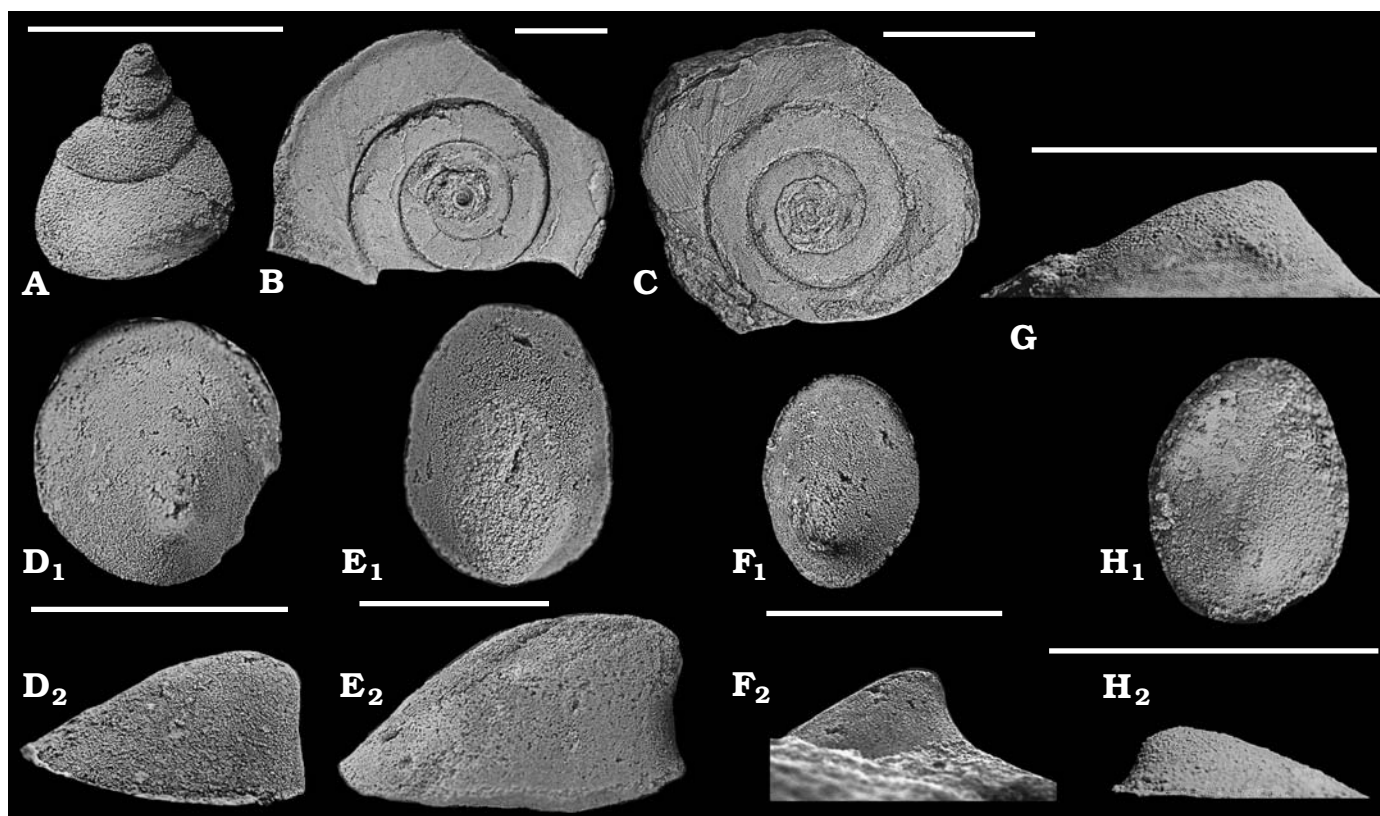


Fig. 13. Gastropods from the Stairway Sandstone, Middle Ordovician, Australia. All internal moulds. **A.** *Raphistomina*? sp. from Areyonga Gorge with 4 whorls (CPC 41496). **B.** **C.** *Teiichispira*? sp. from loose samples from Petermann Creek; with a very flat base, perhaps 5 whorls present (**B.** CPC 41497; **C.** CPC 41498). **D.** **E.** Archinacelloid sp. A (**D.** CPC 41499; **E.** CPC 41500) from Petermann Creek; with slightly concave subapical surface and steeply inclined slightly curved apex, in anterior (**D**₁, **E**₁) and left-lateral (**D**₂, **E**₂) views. **F.** **G.** Archinacelloid sp. B from Areyonga Gorge (**F.**) and Petermann Creek (**G.**). **F.** Specimen with subcentral and sharply pointed apex (CPC 41501), in anterior (**F**₁) and left-lateral (**F**₂) views. **G.** Specimen with subcentral and pointy apex (CPC 41502), in left-lateral view. **H.** Archinacelloid sp. C from Petermann Creek with low shell profile and inclined slightly curved apex (CPC 41503), in anterior (**H**₁) and left-lateral (**H**₂) views. Scale bar 10 mm.

The species occurs in both investigated sections mainly in the upper fossiliferous part, but is most abundant in the Areyonga Gorge section.

Etheridge (1891) described the gastropod *Raphistoma brownii* from an unknown unit at Tempe Downs (close to the Petermann Creek section). Shergold (1986) listed this species from the Horn Valley Siltstone. The species *Raphistoma tasmanica* is reported from the Middle Ordovician of Tasmania by Pojeta and Gilbert-Tomlinson (1977: 55). Pojeta and Gilbert-Tomlinson (1977: 41) listed *Raphistomina*? from the Nora Formation of the Georgina Basin. Additionally *Raphistoma* is also reported from the Darriwilian of North America (Rohr et al. 1992) and North China (Kobayashi 1934). *Raphistomina* and *Raphistoma* are distinct but closely related genera. The material at hand does not justify a closer affiliation due to the lack of diagnostic characters.

Teiichispira? sp. (CPC 41497 and CPC 41498) is a large gastropod with a very flat base, perhaps five whorls and probably with an anisostrophic planispiral shape of the shell (Fig. 13B, C). The aperture is tangential. Growth lines sweep back from the aperture, curving more strongly abaperturally near the periphery. The species is only known from a few loose samples of the Stairway Sandstone found at Petermann Creek.

Teiichispira is also reported from the Lower Ordovician of the Georgina Basin (Pojeta et al. 1977: 43) and the Canning Basin (Yu 1993: 437). Outside Australia it is a common Ordovician genus in North America (Yochelson and Wise 1972) but it is also reported from Malaysia (Kobayashi 1959).

Archinacelloid sp. A (CPC 41499 and CPC 41500) is the largest among the limpet-shaped patelliform gastropods in the Stairway Sandstone with ovate aperture shape, twice as long as high, with slightly curved apex towards the posterior margin. Subapical surface slightly concave and steeply inclined (Fig. 13D, E). The species is the dominant archinacelloid in the Petermann Creek section; it has not been found in the Areyonga Gorge section. In the former section almost all archinacelloids were recovered from the lower part of the section, whereas archinacelloids are restricted to the upper part of the Areyonga Gorge section. About four times as many archinacelloids were found in the Petermann Creek section as compared to the Areyonga Gorge section. Archinacelloideans have also been reported from the Darriwilian of North America (Raymond 1906), Czech Republic (Horný 1997), and Norway (Yochelson 1963) but the taxon has not previously been described from the Ordovician of Australia.

Archinacelloid sp. B (CPC 41501 and CPC 41502) is a relatively small species with ovate aperture, apex subcentral or slightly towards the posterior, apex sharply pointed. Anterior surface slightly convex, subapical surface nearly straight or slightly convex (Fig. 13F, G). The species occurs in both investigated sections in about equal numbers. Archinacelloid sp. C (CPC 41503) resembles Archinacelloid sp. A, but the shell is lower, with a height corresponding to about one third of its length (Fig. 13H). It may represent a variant of Archinacelloid sp. A, but is tentatively separated due to the lower shell profile (compare Fig. 13D₂ vs. Fig. 13H₂). The species occurs in both investigated sections with a few more representatives in the Petermann Creek section. In the Areyonga Gorge section specimens are only found in the upper part of the section, whereas the specimens found in the Petermann Creek section are ranging through most of the fossiliferous beds.

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