A new early Cambrian bradorioid (Arthropoda) assemblage from the northern Flinders Ranges, South Australia

Marissa J. Betts\textsuperscript{a*}, Timothy P. Topper\textsuperscript{b}, James L. Valentine\textsuperscript{a}, Christian B. Skovsted\textsuperscript{c}, John R. Paterson\textsuperscript{d}, Glenn A. Brock\textsuperscript{a}

\textsuperscript{a} Department of Biological Sciences, Macquarie University, Sydney, New South Wales, 2109, Australia
\textsuperscript{b} Geological Museum, Natural History Museum of Denmark, University of Copenhagen, Øster Voldgade 5-7, DK-1350 Copenhagen K, Denmark
\textsuperscript{c} Department of Palaeozoology, Swedish Museum of Natural History, P.O. Box 50007, SE-104 05 Stockholm, Sweden
\textsuperscript{d} School of Environmental and Rural Science, University of New England, Armidale, New South Wales, 2351, Australia

*Corresponding author. Tel.: +61 2 9850 7719; fax: +61 2 9850 8245. Email address: marissa.betts@students.mq.edu.au
Abstract

A new assemblage of early Cambrian bivalved arthropods (Bradoriida) is described from the Arrowie Syncline in the northern Flinders Ranges, South Australia. The well preserved, largely endemic fauna comprises a total of six taxa (including five new species): *Jiucunella phaseloa* sp. nov., *Jixinlingella daimonikoa* sp. nov., *Mongolitubulus anthelios* sp. nov., *Neokunmingella moroensis* sp. nov., *Phasoia cf. spicata* (Öpik, 1968), and *Sinskolutella cuspidata* sp. nov. This assemblage is derived from a carbonate sedimentary package representing a high energy, shallow water archaeocyath-*Renalcis* biohermal facies of Terreneuvian, Stage 2 age which transitions up-section to a more restricted, low energy, intra-shelf lagoonal environment that correlates with a Cambrian Series 2, Stage 3 age. The new taxon *Jiucunella phaseloa* sp. nov., has a first appearance datum (FAD) in shallow water biohermal facies of the Hideaway Well Member of the Wilkawillina Limestone at a level 47 m below the FAD of *Pelagiella subangulata* which is taken to approximate the base of Series 2, Stage 3 in South Australia. Along with *Liangshanella circumbolina*, this makes *J. phaseloa* sp. nov. amongst the oldest bivalved arthropods in South Australia and potentially greater Gondwana. The presence of 25 bradoriid taxa from the early Cambrian of South Australia suggests East Gondwana represents a major centre of origin for the Bradoriida.

Keywords: Early Cambrian; Bradoriida; *Abadiella huoi* Biozone; bivalved arthropod; *Pelagiella subangulata*

1. Introduction
Bradoriid arthropods achieved global distribution during the early Cambrian (Williams et al. 2007; 2011) and were significant benthic faunal elements in terms of abundance and diversity during the Cambrian radiation (Siveter and Williams, 1997; Hou et al., 2002; Vannier et al., 2005; Zhang, 2007; Dies Álvarez et al., 2008). Much of the known species diversity is based on specimens derived from both “crack out” material and acid processed carbonates (Shu, 1990; Siveter and Williams, 1997; Williams and Siveter, 1998; Hou et al., 2002; Zhang, 2007; Williams et al., 2007; Topper et al., 2011) and appears to be closely tied to fluctuating oxygen levels on marine shelves throughout the Cambrian (Williams et al., 2011). Recent investigations documenting early Cambrian (Series 2, Stages 3-4) phosphatic skeletal faunas from carbonate shelf facies in the Flinders Ranges, South Australia have revealed an unexpectedly high diversity of bradoriid species (Skovsted et al., 2006; Topper et al., 2007, 2011). Topper et al. (2011) recently described a bradoriid assemblage from the Ajax Limestone in the Mt Scott Range that included *Liangshanella circumbolina*, a taxon that has a first appearance before the incoming of trilobites and the FAD of the widely distributed micromollusc *Pelagiella subangulata* which has been suggested as a potential tool to define the base of Cambrian Series 2, Stage 3. *Liangshanella circumbolina* was recognised as the earliest known bradoriid taxon from East Gondwana. Topper et al. (2011) also revealed a strong provincial signal for bradoriids from East Gondwana, though a clear biogeographic link with South China was also documented. This study documents a new assemblage of six bradoriid taxa, including five new species from the Arrowie Syncline in the northern Flinders Ranges of South Australia. Many of the genera have Chinese affinities that have not previously been reported from East Gondwana. The new fauna brings the total number of bradoriid genera known from the early Cambrian of Australia to 25, suggesting East Gondwana was a major centre for the origin and early diversification of the group. Of particular significance is the new taxon, *Jiucunella*...
phaseloa sp. nov., which has a first appearance datum in the upper part of the Hideaway Well Member of the Wilkawillina Limestone. Regionally, this stratigraphic level is at least equivalent (possibly older) than the FAD level of L. circumbolina (Topper et al., 2011) in the Mt Scott Range, and thus indicates Jiucunella phaseloa is one of the oldest known bivalved arthropods from East Gondwana. The new assemblage re-enforces generic-level biogeographic links to South China (Topper et al., 2011) and high species endemicity of bradoriid faunas in East Gondwana during the early Cambrian.

2. Locality and Lithostratigraphy

Bradoriids described in this study are derived from samples collected along a stratigraphic section (Moro) measured through the lower Cambrian Hawker Group succession in the Arrowie Syncline, northern Flinders Ranges, Arrowie Basin, South Australia (Fig. 1). The Moro section (Fig. 2) is located approximately 5 km south of Moro Gorge on the north-eastern limb of the Arrowie Syncline, a ~25 km long south-west plunging syncline located immediately north of the Stirrup Iron Range. The lower part of the section includes lowstand to transgressive Parachilna Formation and highstand Woodendinna Dolomite of sequence系统 tract Е1.1А of Zang et al. (2004). The base of the Moro section is located at the top of the Parachilna Formation (co-ordinates: 30° 43.616’ S; 139° 12.528’ E), a well sorted, iron-rich quartz sandstone. The lower 72.5 m of section is obscured by alluvium that covers the contact between the Parachilna Formation and the overlying Woodendinna Dolostone. The Woodendinna Dolostone consists of laminated microbialites, often with muddy interlaminations and centimetre scale digitate stromatolites, though pervasive dolomitisation has destroyed much of the original carbonate fabrics.
The Woodendinna Dolostone is disconformably overlain (Jago et al., 2012) by 171 m of the Mt. Mantell Member of the Wilkawillina Limestone. This package is dominated by stromatolites, peloidal carbonates, transported archaeocyath fragments and well-rounded quartz grains reflecting a high energy, shallow water platform environment well above wave base, located relatively close to the palaeocraton. Dolomitisation is present in the upper 40 m of the Mt. Mantell Member in the Moro section (Fig. 2).

The contact between the laminated microbialites and stromatolites of the Mt. Mantell Member and the overlying biohermal Hideaway Well Member occurs at 430 m above the base of the section (Fig. 2). The Hideaway Well Member in the Moro section consists of 59 m of an archaeocyath-\textit{Renalcis} biohermal facies. These build-ups formed large mound-like structures that measure up to 100 m in lateral extent (an example is transected by the Moro section) and occur for more than 2 km along strike to the north of the section line. Biohermal architecture in the Hideaway Well Member consists of a build-up of closely spaced regular and irregular archaeocyaths bound together by envelopes of encrusting calcimicrobes such as \textit{Girvenella}, \textit{Renalcis} and \textit{Epiphyton}, in addition to irregular archaeocyaths that facilitated sequential biohermal accretion and topographic relief above the surrounding shelf sediments. The flanks of the bioherms are dissected by deep, narrow channels filled with intraclastic carbonate, fragmented shelly debris and micrite that were shed into deeper lagoonal or outer shelf-slope environments. Localised archaeocyath bioherms such as the one transected by the Moro section line are a common feature on the extensive shallow water platform represented by the Wilkawillina Limestone in the Wirrealpa Hinge Zone \textit{sensu} Gravestock and Cowley (1995).

Immediately above the biohermal slope facies of the Hideaway Well Member at 564.5 m above the base of the Moro section the lithology changes dramatically to a succession of massive carbonate, bioclastic grainstones alternating with micritic and microbial laminated
carbonates representing the Winnitinny Creek Member. This distinctive unit is over 135 m thick and suggests a rapid change in depositional environment from a moderate to high energy, shallow water biothermal platform to a more restricted, low energy, intrashelf, and possibly slightly deeper lagoonal environment. Archaeocyaths are relatively rare and sporadically developed throughout this part of the succession (see Fig. 2). The contact between the Hideaway Well Member and the overlying Winnitinny Creek Member is described as disconformable by Clarke (1986) in the type area in the Bunkers Range, but is not immediately apparent in the Moro section.

At approximately 701.8 m true thickness above the base of the Moro section (Fig. 2), the upper part of the Winnitinny Creek Member interfingers with, and is partially overlain by the Wirrapowie Limestone. The Wirrapowie Limestone is at least 139 m thick in the Moro section and is characterised by fine-grained ribbon limestones, interpreted to have been deposited in a sheltered lagoonal environment. The lack of cross-beds, desiccation mudcracks or detrital material suggests that this environment remained mostly submerged and stable (Haslett, 1975). The interfingering of units in this part of the Moro section is interpreted to represent partially coeval carbonate deposition, representing different, though likely adjacent, facies in an intracratonic shelf-type setting. A similar interfingering relationship between the upper Wilkawillina Limestone and the Wirrapowie Limestone has been mapped in the Eregunda Creek area in the Wirrealpa Hinge Zone (Haslett, 1975; Gravestock and Cowley, 1995; Zang et al., 2004). The distinctive reddened, karstic microstromatolitic horizon at the top of the Winnitinny Creek Member which marks the regionally significant Flinders Unconformity in other parts of the Arrowie and Stansbury Basins (Gravestock and Cowley, 1995; Brock and Paterson, 2004; Paterson and Brock, 2007) is absent in the Moro section, possibly reflecting the transitional (and continuous) deposition of laterally interfingering carbonate shelf facies.
3. Age and Biostratigraphy

Paterson and Brock (2007) demonstrated that the FAD of trilobites in the Arrowie Basin, including the eponym of the oldest trilobite zone, *Abadiella huoi* Zhang, 1966, occurs in the upper half of the Winnitinny Creek Member of the Wilkawillina Limestone and equivalent strata in the Ajax Limestone (cf. Topper et al., 2011). The *A. huoi* Zone is equivalent to the *Parabadiella* Zone in China (Jago et al. 2002; Paterson and Brock, 2007) based on the co-occurrence of *A. huoi* in both regions. Traditionally, the *A. huoi* Biozone is considered to be younger than the *Profallotaspis* and *Fallotaspis* zones in Siberia (see Peng et al., 2012, fig. 19.3), though Yuan et al. (2011) have indicated that the *Parabadiella* Zone in China can be interpreted as time-equivalent to the *Eofallotaspis* Zone in Morocco and *Profallotaspis jakutensis* Zone in Siberia. Given the difficulties in defining and correlating the base of Series 2, Stage 3 using trilobites, Peng et al. (2012) have indicated that the FAD of the micromollusc *Pelagiella subangulata* and/or the lobopodian *Microdictyon effusum* could be a useful supplementary proxy for defining this boundary over intercontinental scales. In this regard, it is important to note that the FAD of *P. subangulata* always precedes the base of the *A. huoi* Zone in the Ajax Limestone, Mt. Scott Range (Brock, unpubl. data) and the approximated base in the Moro section (Fig. 2).

The FAD of *P. subangulata* in the Moro section is at 581.7 m above the base of the section in the lower Winnitinny Creek Member of the Wilkawillina Limestone (Fig. 2). This level is taken to approximate the base of Cambrian Series 2, Stage 3 in South Australia (Fig. 2). This horizon is 87 m below the estimated base of the *A. huoi* Zone using small shelly fossil proxy data suggesting that trilobites occur later in Australia than elsewhere (see below). The lack of trilobites in the upper part of the Winnitinny Creek Member of the Wilkawillina
Limestone and interfingering Wirrapowie Limestone in the Moro section is presumably facies controlled, but may be a result of sampling bias despite extensive collecting efforts; trilobites are known to be poorly represented in facies associated with the Wirrapowie Limestone (Topper et al., 2011, p. 314). Whilst the lack of trilobites in the Moro section clearly hinders precise correlation, it is possible to at least approximate the position of the base of the *A. huo i* Biozone using the known biostratigraphic ranges of tommotiids and bradoriids as a proxy for age assessment and correlation.

Shelly fossils are absent from the Woodendinna Dolostone and Mt. Mantell Member of the Wilkawillina Limestone in the Moro section. Shelly fossils first appear in the Moro section in the lowermost horizons of the biohermal facies in the Hideaway Well Member at sample horizon 570.8, equivalent to 433.48 m true thickness above the base of the section. The fauna includes the oldest known brachiopod from South Australia, *Askepasma* *saproconcha* Topper, Holmer, Skovsted, Brock, Balthasar, Larsson, Petterson Stolk and Harper, (2013a), along with the tommotiids *Dailyatia macroptera* (Tate, 1892) and *Kulparina rostrata* Conway Morris and Bengtson, 1990, all of which have FADs considerably below the FAD of trilobites in South Australia (Fig. 2; Jago et al., 2006; Paterson and Brock, 2007; Skovsted et al., 2009; 2011). Topper et al. (2013a) report that *A. saproconcha* occurs in the lower half of the Wilkawillina and Wirrapowie limestones across the Arrowie Basin; these stratigraphic levels can be confidently correlated with pre-trilobitic strata of Terreneuvian, Cambrian Stage 2 age. The FAD of *Askepasma toddense* Laurie, 1986 occurs ~4.5 m above the LAD of *A. saproconcha* in the Moro section. *Askepasma toddense* subsequently ranges through the upper half of the Hideaway Well Member, the entire Winnitinny Creek Member of the Wilkawillina Limestone and into the Wirrapowie Limestone (Fig. 2) which broadly equates with *Abadiella huo i* trilobite Zone.
The stratigraphic ranges of the tommotiids *Kulparina rostrata* and *Eccentrotheca helenia* in the Moro section are perhaps the most instructive and reliable proxies to help constrain the approximate base of the *A. huoi* Zone in South Australia. Based on detailed investigation of the biostratigraphic ranges of these taxa from six separate stratigraphic sections measured through Hawker Group rocks in the Bunkers Graben and Mt. Scott Range, Skovsted et al. (2011, fig. 2, p. 256) demonstrated that *K. rostrata* and *E. helenia* have mutually exclusive stratigraphic ranges. The LAD of *K. rostrata* is invariably located at a level stratigraphically below (sometimes significantly below) the base of the *A. huoi* Zone in all measured sections (Skovsted et al., 2011, fig. 2). The FAD of *E. helenia* occurs within the Winnitinny Creek Member above the LAD of *K. rostrata*. The total stratigraphic range of *E. helenia* is broadly equivalent with the *A. huoi* Zone in the Bunkers Graben and Mt. Scott Range, and the FAD of *E. helenia* is broadly coincident with the FAD of *A. huoi* Zone trilobites in all measured sections (see Skovsted et al., 2011).

In the Moro section, the FAD of *Kulparina rostrata* is at 433.8 m true thickness above the base of the section within the Hideaway Well Member, and its stratigraphic range extends into the lowermost Winnitinny Creek Member (LAD 568.3 m true thickness above the base of the section). The FAD of *Eccentrotheca helenia* in the Moro Section is ~100 m above the LAD of *K. rostrata* at 668.7 m true thickness above the base of the section in the Winnitinny Creek Member. In the absence of trilobites in the section, this level is taken as an approximation of the base of the *A. huoi* Zone in the section (Fig. 2).

The first appearance of bradoriids in the fossil record is generally thought to be coincident with, or slightly postdate, that of trilobites around the globe (Williams et al., 2007, 2011; Kouchinsky et al., 2012). A recent global compilation of the stratigraphic ranges of Cambrian bivalved arthropod genera presented by Williams et al. (2011, fig. 4) indicates this interval also corresponds to peak diversification of Bradoriida associated with the Cambrian
Arthropod Radiation Event (CARE; Zhu et al., 2006). It thus seems reasonable to surmise that the actual origin of the Bradoriida precedes this radiation event. The fact that bradoriids appear prior to the defined base of Series 2, Stage 3 based on *P. subangulata* in Australia and trilobite faunas in China (Hou et al., 2002) reinforces a pre-trilobitic origin for the group. Five of the six bradoriids from the Moro section have FADs at stratigraphic levels above the defined base of Series 2, Stage 3 and below the approximated base of the *A. huoi* Biozone (Fig. 2). Importantly, *Jiucunella phaseloa* sp. nov. has a FAD in the uppermost Hideaway Well Member of the Wilkawillina Limestone (534.1 m above the base) which is 47.6 m below the Series 2, Stage 3 boundary based on the FAD of *P. subangulata* (Fig. 2). This taxon ranges into the upper Winnitinny Creek Member. The presence of *J. phaseloa* in the uppermost Hideaway Well and lower Winnitinny Creek Members of the Wilkawillina Limestone would appear to equate with stratigraphic levels that are at least equivalent or possibly slightly older than the strata yielding *L. circumbolina* in the Ajax Limestone, which has a FAD 11.52 m below the defined Series 2, Stage 3 boundary based on the FAD of *P. subangulata* (Topper, unpubl. data). In summary, this would mean that *J. phaseloa*, along with *L. circumbolina*, first appear during Terreneuvian, Stage 2 and therefore represent the oldest known bivalved arthropods from Cambrian East Gondwana.

4. Methods & Terminology

Bradoriid soft parts are rarely preserved and therefore their taxonomy is necessarily based on features of the shield (Hou et al., 2002). Bradoriids may be acid leached from the surrounding matrix or examined as ‘crack-out’ specimens on bedding planes. Acid leached specimens have a tendency to preserve microstructures in finer detail than crack-out specimens and are therefore well suited for taxonomic investigation (Zhang, 2007; Topper et
Material for this study was leached in weak acetic acid (10%), the residues washed, dried and examined using a stereo binocular microscope. Selected specimens were mounted on stubs, gold sputter coated and imaged using a JEOL JSM-6480LA Analytical Scanning Electron Microscope. Descriptive terms used herein follow Siveter and Williams (1997), Williams and Siveter (1998), Hou et al. (2002) and Topper et al. (2011).

5. Systematic Palaeontology

Figured material has been allocated SAM P numbers and is lodged in the South Australian Museum (palaeontological collections).

Phylum Arthropoda Siebold and Stannius, 1845

Order Bradoriida Raymond, 1935

Family Comptalutidae Öpik, 1968

**Jiucunella** Hou and Bergstrom, 1991

*Type species.* **Jiucunella paulula** Hou and Bergström, 1991 from the lower Cambrian Qiongzhusi Formation, Chengjiang County, Yunnan Province (Maotianshan section).

**Jiucunella phaseloa** sp. nov. (Fig. 3A-M)

*Type material.* The Moro Section (and spot localities) yielded 242 individual valves of **Jiucunella phaseloa** (Table 1), including six with conjoined shields. Most specimens from the Moro Section are from the Wilkawillina Limestone (Winnitinny Creek Member), the richest horizons within the section are 866.0 (668.71 m true thickness) and 881.6 (681.0 m true
thickness). Two valves also occur within the Hideaway Well Member at 534.1 m and 564.5 m true thickness. A spot locality to the north of the section, also in the Wilkawillina Limestone (Spot Locality D; 30° 43.316’S; 139° 11.990’E) is also very rich. The holotype (SAM P48652; Fig. 3E, H, J) with conjoined valves is derived from horizon 881.6 (681.0 m true thickness). Paratypes: Fig 3A, L (SAM P48648), B (SAM P48649), C (SAM P48650), D (SAM P48651), F, M (SAM P48653), G, K (SAM P48654) and I (SAM P48655) are from horizon 881.6 (Winnitinny Member of the Wilkawillina Limestone). Figure 3G is derived from horizon 844.0 (Winnitinny Creek Member, Wilkawillina Limestone). Unfigured paratypes include an additional 233 individual valves and two conjoined specimens.

Etymology. From the Greek ‘phaselos’ meaning kidney-bean, in reference to the bean-shaped lobe in the anterodorsal region of the shield.

Diagnosis. Strongly postplete, straight hinge line. Anterior cardinal corner spicate. Posterior cardinal corner less acute. Weak rim present with continuous shallow groove between cardinal corners. Single, prominent bean-shaped lobe at the anterior with weak or no sulcus to the posterior. Remainder of carapace smooth. Coarse punctae visible internally.

Occurrence. Hideaway Well and Winnitinny Creek Members of the Wilkawillina Limestone, Arrowie Syncline, Flinders Ranges, South Australia; Terreneuvian, Stage 2.

Description. Strongly postplete, hinge line straight or with very weak anterodorsal cusp. Anterior cardinal spine tapers more sharply than posterior spine. Anterior cardinal spine joins rounded anteroventral margin. Posterior cardinal corner joins concave posterodorsal margin. Spine variably present on posterodorsal curve (Fig. 3A, G, L). Ventral margin straight.
Posterodorsal margin strongly curved. Single, elongated, bean-shaped lobe occurs at anterior, curve mirroring shape of anteroventral margin. Sulcus behind lobe very weak or absent.

Shield smooth. Narrow, lip-like rim continuous between cardinal corners, thickening toward the posterior. Groove separates rim from main part of shield. Shield smooth externally, punctae visible internally (Fig. 3M). Shields close snugly with no ventral gape (Fig. 3G and K).

**Remarks.** Shield outline is characteristic of the comptalutids with a straight hinge line, and acute angles at both cardinal corners and the posterodorsal and anterodorsal curves.

*Jiucunella phaseloa* sp. nov. is strongly postplete with a ridge that is entire between the cardinal corners. Lobation is concentrated at the anterior, and external ornament is smooth with coarse punctae visible internally. Comptalutids often bear pronounced sulci behind the anterior lobation, but *J. phaseloa* shows none or only a very weak sulcus behind the anterodorsal lobe, and very occasionally shows evidence for a weak dorsal cusp (Fig. 3B).

*Jiucunella phaseloa* is similar to the comptalutids *Comptaluta* Lee, 1975, and *Alutella* Kobayashi and Kato, 1951. However, while these bradoriid taxa have prominent anterodorsal lobation, they also feature strong sulci separating lobes from the inflated shields. *Jiucunella phaseloa* most strongly resembles the type species, *Jiucunella paulula* Hou and Bergström, 1991, from the lower Cambrian Qiongzhusi Formation, Chengjiang County, Yunnan Province, South China in that it is non-sulcate, with a smooth shield and a single lobe (Hou et al., 2002, p. 388, fig. 21). They differ in that the lobation in *J. phaseloa* is concentrated in the anterior, rather than toward the ventral part of the shield. In addition, the lobe is bean-shaped with rounded ends and does not taper as in *J. paulula*. *Jiucunella paulula* also features a wide lateroadmarginal ridge, whereas *J. phaseloa* has a more lip-like rim.
Jiucunella phaseola shields are well preserved and feature a suite of finely preserved details. The texture of the carapace is noteworthy and demonstrates the level of detail that can be revealed by acid-leaching techniques. The texture of the shields shows that they were made of recalcitrant organic material or only very lightly mineralised. The outer layer of the carapace is often dented and folded in many places, and appears to have been relatively flexible. In the holotype, soft circular features occur around the anterior node (Fig. 3J). These are not present in other specimens and thus are likely to be preservational artefacts.

The Moro specimens exhibit a distinct layering of the carapace, particularly in areas that have been damaged (Fig. 3G, K). In some cases much of the outer layer has been effaced, with the remaining outer layer showing evidence of abrasion. This indicates that accurate description of carapace texture can often be problematic, with descriptions of degraded specimens possibly erroneous (see also Siveter and Williams 1997). Nevertheless, in this case comparison between highly abundant specimens has permitted the establishment of the standard suite of features present in this taxon.

Phasoia Hinz-Schallreuter, 1993

Type species. Ophiosema spicatum Öpik, 1968. Middle Cambrian Yelvertoft Beds, Queensland, Australia.

Remarks. This genus was originally named Ophiosema by Öpik (1968) which was a homonym of a lepidopteran genus. Phasoia was proposed by Hinz-Schallreuter (1993) as a replacement.

Phasoia cf. spicata (Öpik, 1968) (Fig. 4A-I)
Material. Ten damaged individual shields and several fragments with a similar microornament. All specimens were retrieved from a single stratigraphic horizon, Moro 1043.0, located 809.76 m true thickness above the base of the section, in the Wirrapowie Limestone (Table 1), Fig. 4A, G (SAM P48656), B (SAM P48657), C, H, I (SAM P48658), D (SAM P48659), E, F (SAM P48660). Unfigured specimens include a further five poorly preserved shield fragments.

Occurrence. Wirrapowie Limestone, Arrowie Syncline, Flinders Ranges, South Australia; Cambrian Series 2, Stage 3.

Description. Most complete specimen displays a straight hinge line (Fig. 4A). Most parts of the rim generally broken away. Distinctive open, looping ridge remains intact. Loop subcircular, running from anterodorsal region around free margin, toward centrodorsal region and terminating posterior of the anterodorsal sulcus (Fig. 4C). Internally, loop presents as a continuous trough in carapace with angular corners near hinge zone (Fig. 4A, B).

Microornament consists of fine, nested pustules (approximately 5 µm in diameter; Fig. 4H and I). Pustulation reduced over loop ridge.

Remarks. The only other bradoriid family to feature prominent, curved continuous ridges that join the anterior and posterior nodes is the Hipponicharionidae. Phasoiids are unique however, in having a ridge that connects the nodes and loops in an almost complete circle.

Phasoiids from the Moro section are poorly preserved with margins rarely intact. A single specimen (Fig. 4A) shows an oblique posterior cardinal corner, as seen in the material of Phasoia described by Ö pik (1968) and Hinz-Schallreuter (1999). This specimen also
shows evidence for a spine at the posterior margin, a feature that has not been previously
described (all previous examples of the taxon are crack-out specimens). The looped
continuous ridge is particularly distinctive and allows confident assignment of these
specimens to *Phasoia*. Of the two species within the genus, the Moro specimens most closely
resemble *P. spicata* originally described from the middle Cambrian of the Mt. Isa region in
Queensland, which features a similar sub-circular, continuous, open loop (Hinz-Schallreuter
et al., 1999, pl. 2, figs 1, 3). This is in contrast to the loop on the shield of *P. rogerensis*,
which is interrupted at the ventral area, then continues toward the posterior, terminating at the
dorsoposterior corner of the shield (Hinz-Schallreuter et al., 1999, pl. 2, fig. 2).

There is a notable stratigraphic disjunction between the phasoiids recovered from the
Moro section (Cambrian Series 2, Stage 3) and previously described material (Middle
Cambrian). This implies either that this taxon has a very long stratigraphic range or that the
Moro material represents a new taxon. Lack of adequately preserved early Cambrian material
precludes erection of a new species and as such this material is compared with reservation to
*Phasoia spicata*.

Family *Hipponicharionidae* Sylvester-Bradley, 1961

*Neokunmingella* Zhang, 1974

*Type species. Neokunmingella minuta* Zhang, 1974. Lower Cambrian (Canglangpu
Formation). Shijiangjung section, Wuding, Yunnan, south China.

*Neokunmingella moroensis* sp. nov. (Fig. 5A-O)
Type material. Twelve specimens, mostly derived from a spot locality in the Winnitinny Creek Member (Wilkawillina Limestone) ~370 m along strike (north) of the Moro Section (Spot Locality D; 30° 43.316'E/139° 11.990'S). Additional specimens were collected from the Moro section line at horizon 836.7 (643.0 m above the base of the section; Winnitinny Creek Member, Wilkawillina Limestone), and 1043.0 (809.7 m above the base of the section; Wirrapowie Limestone) (Table 1). Holotype Fig. 5G, M (SAM P48667) and paratypes Fig. 5A (SAM P48661), B (SAM P48662), C (SAM P48663), D (SAM P48664), E (SAM P48665), F (SAM P48666), and K (SAM P48670) are derived from Spot Locality D in the Winnitinny Creek Member of the Wilkawillina Limestone. Paratypes Fig. 5H, J, N (SAM P48668) and I, O (SAM P48669) come from horizon 836.7 in the Winnitinny Creek Member, Wilkawillina Limestone. Unfigured paratypes include a further two fragmentary shields from Spot Locality D in the Winnitinny Creek Member of the Wilkawillina Limestone.

Etymology. Named after Moro Gorge, a site of cultural significance to the Adnyamathana People of Nepabunna, located 6 km north of the Moro section (Fig. 1).

Diagnosis. Outline postplete with confluent U-shaped lobation. Lobation variably emphasised at anterior and posterior. Straight hinge line. Weakly defined central node is irregularly shaped, tilts from hinge line toward anterior. Short spine projects from posterodorsal curve. Microornament present as scales or micro-scale polygons with centrally located raised lumps.

Occurrence. Wilkawillina Limestone and Wirrapowie Limestone, Arrowie Syncline, Flinders Ranges, South Australia; Cambrian Series 2, Stage 3.
Description. Postplete shield with smooth, rounded rim around posteroventral margin. Dorsal margin straight. Anterior cardinal corner tapering at acute angle. Posterior cardinal corner oblique. Posterodorsal margin concave. Short spine on posterodorsal curve (Fig. 5B, G and M). Complete shields range from approximately 1100 to 1400 µm in length. Confluent anterior and posterior lobation forms a U-shape ridge that follows shape of free margin; centre of shield depressed. Lateroadmarginal rim narrow and smooth, with a broad flat area between rim and posterior lobe at posterior curve. Small, irregularly shaped central node present close to hinge, inclined at an angle to dorsal margin. Microornament variable; may be present as a fine, polygonal network with small raised lumps in centre of each polygon. Each discrete polygon is approximately 5 µm in diameter (Fig. 5O). Microornament may also consist of scale like lumps (approximately 5 µm in diameter) (Fig. 5M). Development of microornament varies over shield.

Remarks. Neokunmingellids exhibit all the classic features of the Hipponicharionidae including a postplete shield, subtriangular outline; confluent lobation and granulose microornament. The Moro specimens exhibit distinctive neokunminellid features such as confluent anterior and posterior lobes, amplete to postplete shield and a sub-ovate node sub-parallel with the dorsal margin (Hou et al., 2002, p. 398, fig. 24 a-l).

The Moro specimens display a distinctive polygonal and scaly microornament that was not noted in Chinese specimens of Neokunmingella minuta by Zhang (1974) or Neokunmingella cf. minuta by Hou et al. (2002), probably because fine details of ornament are rarely preserved in crack-out specimens. Microornament on the shield of Neokunmingella shuensis Zhang 2007 consists of a combination of pitting and low pustules (Zhang, 2007, pl. 19, figs 1-15), unlike that on Neokunmingella moroensis. Development of the ornament is variable and occasionally appears distinctly more pustulose than reticulate (Fig. 5M).
Variability in microornament was also documented in *Albrunnicola bengtsoni* from lower Cambrian glacial erratics from King George Island, Antarctica by Wrona (2009). These specimens display great variation in preservation and demonstrate that the true external microornament is often exfoliated, leaving behind a ‘false’ microornament on underlying layers consisting of a series of lumps or scales (Wrona 2009, p. 359, fig. 7a-d). These are similar to the pustules present in some of the Moro specimens (Fig. 5K, M). Such differences between individuals are likely the result of differential preservation and abrasion.

A single (fragmentary) shield from the Moro Section (Fig. 5H) has a U-shaped ridge giving the impression that this specimen is more amplete than other specimens. However, this specimen also displays the polygonal microornament (Fig. 5O) that links it to the postplete individuals. Shield breakage at the anterior margin makes it difficult to clearly establish an amplete outline for this specimen. The anterior and posterior lobes of the specimens derived from the Moro section also vary in development. Most are clearly confluent, creating the U-shaped ridge (Fig. 5A, E, F), while in others the lobes are more isolated and ‘pinch-out’ toward the ventral margin (Fig. 5C, G, H). The U-shaped ridge is still visible in these individuals, though it is weakly developed. Similar lobe and ridge variation is also documented in *Neokunmingella shuensis* Zhang, 2007 (pl. 19, figs 1-11) from the lower Cambrian Yu’anshan Formation in South China. However, *N. moroensis* has a uniformly curved, semi-circular outline (Fig. 5A-H) which differs from the postplete, sub-triangular outline in *N. shuensis*. Additionally, none of the specimens derived from acid processing figured by Zhang (2007) from the lower Cambrian of China display the characteristic polygonal microornament of *N. moroensis*. Furthermore, neither *N. minuta* nor *N. shuensis* display a short spine at the posterodorsal curve as in *N. moroensis*.

Hou et al. (2002) described the central node in specimens of *N. cf. minuta* as having variable size and shape. All Moro specimens display a similar node that also varies in shape.
and prominence. The node is inclined to the hinge line, consistently tilted toward the anterior.

The variability in the shape and size of these nodes may also represent intraspecific variation attributed to ontogenetic changes or sexual dimorphism.

Family ?Bradoriidae Matthew, 1902

Remarks. *Sinskolutella* was originally assigned to the *Alutidae* (Melnikova, 1998), a family which grouped together bradoriids with a border around the free margin of the shield (Shu and Chen, 1994). Grouping bradoriids in this way is now considered taxonomically insignificant and the taxonomic name ‘*Aluta*’ is now regarded as a *nomen dubium* (Shu and Chen, 1994).

Family level attribution of the genus is difficult due to the presence of a combination of characters that occur in a wide range of family groups, and uncertainty regarding the taxonomic significance of valve size, shape, lobation and ornament. *Sinskolutella cuspidata* sp. nov. is non-lobate and features a distinctive dactiloscopic, fingerprint-like microornament which allies it with the Bradoriidae Matthew, 1902. However, the Bradoriidae are generally larger, reaching lengths of 6 – 7 mm (Siveter and Williams 1997). Additionally, the type species of *Sinskolutella* Melnikova, *S. ordinata* has a maximum length of up to 8.0 mm while the length of the new species does not exceed 2.0 mm. The Bradoriidae generally have a straight hinge (Siveter and Williams 1997), whereas *Sinskolutella* often has a prominent dorsal cusp (Fig. 6A-C, E, I, J, L; Melnikova 1998, pl. 2, figs 1, 2).

The presence of the dorsal cusp, in addition to the postplete outline, valve dimensions and finely textured microornament in *Sinskolutella cuspidata* sp. nov. could also point to a relationship with the Kunmingellidae. However, kunmingellids feature prominent anterior and posterior lobation which is not present in *S. cuspidata*. Cambriids are also similar to *S.*
cuspidata in that they feature a similar dorsal cusp. However, cambriids may also be lobate and are much larger than the Moro specimens, with a diagnostic size range between 6.0 and 17.5 mm in length (Hinz-Schallreuter et al. 2007). In addition, cambriids while occasionally bearing granulose microornament, do not feature dactiloscopic microornament. Assignment to the Bradoriidae is tentative due to the combination of character states in the new taxon.

Sinskolutella Melnikova, 1998

Type species. Bradoria ordinata Melnikova, 1983. Cambrian Series 2, Stages 3-4 (Botoman) of the Siberian Platform (Sinskoe Formation).

Emended diagnosis (after Melnikova, 1998, p. 359). Shield postplete, strongly convex with strong hinge line and dorsal cusp. Sharp anterodorsal curve; posterodorsal curve of margin at right angles to obtuse. Shield with pronounced posterior curve projecting past posterodorsal curve. Free margin bears smooth, flattened rim. Microornament on main part of shield pulvinate or dactiloscopic.

Remarks. Previously published work describes Sinskolutella as having a straight hinge line (Melnikova, 1998), but the emended diagnosis recognises the fact that a distinct dorsal cusp is apparent in the crack-out specimens illustrated by Melnikova (1998, pl. 2, figs 1, 2). The microornament consists of a fingerprint-like, dactiloscopic pattern (Fig. 6D, G, N), and the shields are non-lobate and strongly convex, indicating that the Moro specimens belong to Sinskolutella.

Sinskolutella cuspidata sp. nov. (Fig. 6A-O)
Type material. The Moro section yielded 223 specimens. These most often occur as individual shields, though some are conjoined. *Sinskolutella cuspidata* is most abundant at horizon 1081.0 where the end of the section has been offset by 90 m towards the north-northeast (839.7 m true thickness above the base of the section – see Table 1). *Sinskolutella cuspidata* outnumbers all other taxa (100+ specimens) at this horizon in the Wirrapowie Limestone. *Sinskolutella cuspidata* is also Limestone Formation), and 893.0 (690.0 m above the base of the section; Winnitinny Creek Member of the Wilkawillina Limestone) (Table 1).

Holotype Fig. 6C (SAM P48673) from horizon 933.2 (Wirrapowie Limestone). Paratypes Fig. 6A, M (SAM P48671), B (SAM P48672), I (SAM P48679), J (SAM P48680) and L (SAM P48682) from horizon 1081.0 where the section has been offset, Wirrapowie Limestone. Paratypes Fig. 6D (SAM P48674) E, O (SAM P48675) F (SAM P48676), G, N (SAM P48677) and H (SAM P48678) from horizon 933.2, also in the Wirrapowie Limestone. Additional unfigured paratypes include 210 separated valves and a seven conjoined specimens.

Occurrence. Wilkawillina Limestone and Wirrapowie Limestone, Flinders Ranges, Arrowie Syncline, South Australia; Cambrian Series 2, Stage 3.

Etymology. From the Latin 'cuspidatus' meaning pointed, for the sharp dorsal cusp and spine at the posterodorsal curve.

Diagnosis. Shield postplete, rounded, with pronounced convexity at posterior margin which extends past posterior cardinal corner. Sharp dorsal cusp located immediately anterior of central part of hinge line. Non-lobate. Rim flattened, smooth, continuous between cardinal
corners, somewhat thicker around curved ventral-posterior part of shield. Small spine at posterior curve. Microornament dactiloscopic formed by series of micron scale pulvinate mounds. Total length of shield does not exceed 2 mm.

Description. Outline postplete, valves inflated, free margin strongly curved. Dorsal margin bearing pronounced anterodorsal cusp. Lateroadmarginal rim well developed; smooth, flat, entire between cardinal corners, thickest and most strongly curved at posteroventral margin. Posterior cardinal corner oblique, with anterior cardinal corner tapering to a short spine. Short spine also on posterodorsal curve of each shield. Shield non-lobate with very weak anterodorsal sulcus. Microornament over shield micro-pulvinate (Fig. 6D, G) consisting of pillow-like mounds ~20-30 µm across, surrounded by smaller mounds ~5 µm across (Fig. 6N). Internally, coarse punctae visible (Fig. 6O). Shields do not exceed 2 mm in length.

Remarks. The Moro specimens strongly resemble S. concentrisulcata as described and illustrated by Melnikova (1998, pl. 2, figs 9-11) from the lower Cambrian of Siberia. However, the short spine on the posterodorsal curve in S. cuspidata is not present in S. concentrisulcata, nor the similar taxon Bradoria scrutator Matthew, 1899. Bradoria scrutator has a similar dactiloscopic ornament to S. cuspidata (Siveter and Williams, 1997, pl. 1, figs 1-14), but this species features a smooth, circular node at the anterodorsal margin and lacks a dorsal cusp. Other genera featuring similar fingerprint-like microornament include Walcottella Ulrich and Bassler, 1931 and Indiana Matthew, 1902. However, Walcottella features an anterocentral and weak dorsal node, and Indiana does not have an admarginal rim (Siveter and Williams 1997).

A crack-out specimen of Matthoria? sp. described by Vannier et al. (2005) from the lower Cambrian Pardailhan Formation, southern France is considerably larger than S.
**Sinskolutella cuspidata** (4 mm), though closely resembles the Moro specimens since it also has a strong dorsal cusp and weak lobation. This taxon is described as lacking surface ornament, though comparing ornament between crack out and acid etched specimens is complicated by the fact that even the well preserved external microornament in some Moro specimens is prone to peel away and leave a smooth surface (Fig. 6A, B, M).

_Sinskolutella cuspidata_ is generally well preserved, often with shields strongly conjoined (Fig. 6F, H, K). The shape of the lateral outline and width of the marginal rim displays intraspecific variation; some specimens show little evidence of a wide rim (e.g. Fig. 6D, F). The external ornament also appears to be prone to exfoliation, often revealing a smooth layer underneath. In this regard there are a few specimens (Fig. 6A) with a well developed marginal rim but which lack strong dactilosopic ornament. Differential damage to the margin and the shedding of the distinctive ornament has implications for accurate identification and taxonomic comparisons, especially between crack-out and acid derived material. The Moro material emphasises that significant taxonomic details may be missing even in specimens that appear relatively well preserved.

**Family Haoiidae** Shu, 1990

**Jixinlingella** Lee, 1975


**Emended diagnosis** (after Zhang, 2007, p. 136). Postplete shield, less than 2 mm in length.

Prominent reticulate (hexagonal) ornament of raised coarse ridges over shield. Inflated
anterior lobe connected via curved submedian ridge to submedian node. Well developed anterior sulcus. Subdorsal swelling variably developed. Marginal groove separating marginal spinose frill from main valve. Duplicature well developed.

Remarks. The Haoiidae consists of two genera characterised by a prominent network of coarse interconnected raised ridges forming a distinctive reticulation over the surface of the valves. These ridges form hexagonal, honeycomb-like patterns (Fig. 7) or long dorso-ventral ridges traversing the shield (Shu, 1990, pl. 1, figs 1-6, 9; Zhang, 2007, pl. 14m, figs 9-14). Zhang (2007, p. 136) noted the close similarity between Haoia and Jixinlingella but suggested these taxa can be discriminated based on a more complex reticulation, a broad anterior lobe and a well-developed marginal rim with frill. Haoia is characterised by having fewer, larger and more elongate polygonal fossae in the central region of the shield and lacks a marginal frill (Shu, 1990, pl. 1, figs 1-6, 9). Jixinlingella, in contrast, has a well-developed marginal frill and smaller, more uniformly spaced polygonal reticulation (Fig. 7A-N; Zhang 2007, pl. 14, figs 9-14). The carapace of Jixinlingella daimonikoa sp. nov. is postplete, with a well-developed anterior sulcus, marginal groove and frilled rim (Fig. 7A). These features in combination with the coarse, reticulate network of ridges suggest that the new taxon is congeneric with Jixinlingella.

Shu (1990) also erected the new taxon, Eotuzoia minima Shu, 1990, based on fragmentary material, but did not assign it to a family. The specimens feature coarse, honeycomb reticulation that suggests Eotuzoia belongs to the Haoiidae. Skovsted et al. (2006, p. 32, fig. 13A) described a poorly preserved conjoined specimen from the Third Plain Creek Member of the Mernmerna Formation (Pararaia bunyeroensis Zone) as Haoia cf. shaanxiensis. This specimen has centrally located elongate geometric fossae characteristic of
Haoia shaanxiensis. This broken specimen also appears to lack a marginal frill seen in both *J. clithrocosta* and *J. daimonikoa*.

*Jixinlingella daimonikoa* sp. nov. (Fig. 7A-N)

**Type material.** Holotype (SAM P 48683) has conjoined valves (Fig. 7A, C, L) from horizon 1043.0, Wirrapowie Limestone, lower Cambrian of the Flinders Ranges, South Australia. This is supplemented by nine unfigured and nine figured paratypes (Fig. 7B, J, K [SAM P48684], D [SAM P48685], E [SAM P48686], F [SAM P48687], G [SAM P48688], H [SAM P48689], I [SAM P48690], M [SAM P48691], N [SAM P48692]) in the form of isolated shields and one conjoined specimen from horizons 893.0 (690.0 m true thickness above the base of the section), 881.6 (681.0 m true thickness above the base of the section), 866.0 (668.7 m true thickness above the base of the section) in the Winnitinny Creek Member of the Wilkawillina Limestone and 1081.0 (839.7 m true thickness above the base of the section) in the Wirrapowie Limestone (Table 1).

**Etymology.** From the Greek ‘*Daimonikos*’ meaning of demons, for the paired, horn-like spines on the posterodorsal margin of the carapace.

**Diagnosis.** Postplete with coarse hexagonal to pentagonal network of polygonal ridges forming uniform reticulation over shield. Anterior and posterior cardinal spines present. Anterior sulcus broad and smooth. Subdorsal swelling absent. Marginal furrow present with frilled rim. Spine pair on posterodorsal margins of carapace.
Occurrence. Winnitniny Creek Member of the Wilkawillina Limestone and Wirrapowie Limestone, Arrowie Syncline, Flinders Ranges, South Australia; Cambrian Series 2, Stage 3.

Description. Shield postplete, with anterodorsal cusp. Anterior and posterior cardinal corners tapering to spines. Prominent anterior cardinal spine joins straight anteroventral margin. Weaker posterior cardinal spine joins concave posterodorsal margin. Ventral margin straight. Posteroventral margin strongly curved. Coarse, geometric, reticulate network of ridges defining hexagonal and pentagonal fossae approximately 200-250 µm across, strongly developed over central part of shield. Smaller pentagonal fossae developed closer to margins. Anterior sulcus broad and smooth. Subdorsal swelling absent. Anterodorsal node elongate. Some specimens display a small swelling with a distinctive dorso-ventral cleft situated behind the anterodorsal node (Fig. 7J). Reticulate network interconnects nodes and ridges. Marginal furrow separates valve from frilled rim with short, stubby regularly spaced (mean 40 µm) spines along free margin; absent from posterodorsal margin. Frill particularly well-developed around posteroventral margin, where shield lobation is most prevalent (Fig. 7C, L). Posterodorsal shield margin features small tapering, hollow horn-like spine (Fig. 7A, L). Weakly pustulose microornament in fossae, absent from ridge crests (Fig. 7K). Duplicature well developed (Fig. 7E, F). Internally, reticulate ornament presents as deep furrows (Fig. 7E).

Remarks. Jixinlingella daimonikoa differs from the type species J. clithrocosta from the lower Cambrian Shuijiangtuo Formation of South China (Lee, 1975) as it has more regular geometric reticulation defining hexagonal and pentagonal fossae. Additional features that distinguish J. daimonikoa from the type species are the presence of an anterodorsal cusp,
anterior and posterior cardinal spines and a distinctive pair of posterodorsal spines at the free margin (Fig. 7A, C, L). The subdorsal swelling in J. clithrocosta is absent in J. daimonikoa. 

*Eotuzoia minima* has a similar geometric reticulate ornament to *J. daimonikoa*, but it is continuous over the majority of the carapace, including the area occupied by the sulcus in *J. daimonikoa* (Shu, 1990, fig. 43). The hand drawn illustration of *E. minima* indicates a more complete outline and shows no evidence of an anterodorsal cusp. Additionally, there is no evidence for a frilled margin or a posterodorsal spine in *E. minima*.

Family Mongolitubulidae Topper, Skovsted, Harper and Ahlberg, 2013b

*Mongolitubulus* Missarzhevsky, 1977


**Remarks.** Within this genus, six species are currently recognised: *Mongolitubulus squamifer* Missarzhevsky, 1977, *M. henrikseni* Skovsted and Peel, 2001, *M. unispinosa* Topper, Skovsted, Brock and Paterson, 2007, *M. unialata* (Zhang, 2007), *M. reticulatus* Kouchinsky, Bengtson, Clausen, Gubanov, Malinky and Peel, 2011 and *M. aspermachaera* Topper, Skovsted, Harper and Ahlberg, 2013b. Spines of *Mongolitubulus* are often found in isolation, and in the past the affinities of these fossils have been problematic with suggestions of their affinities ranging from protoconodonts (Missarzhevsky, 1977) to hyolithelminths (Rozanov, 1986) and lobopodians (Dzik, 2003). Similarly ornamented spines may also be convergent among diverse taxa, for example trilobite spines have been shown to have similar ornament to *Mongolitubulus* (Li et al., 2012).
Skovsted and Peel (2001) suggested that *Mongolitubulus* spines projected from the shields of bradoriid arthropods and this has been demonstrated with the discovery of *M. henrikseni*, *M. unispinosa* and *M. unialata* with intact spines (Skovsted, 2005; Topper et al., 2007; Zhang, 2007). Similar spine and shield relationships have not yet been confirmed for the type species, *M. squamifer*. *Mongolitubulus unispinosa* from the Mernmerna Formation in the Donkey Bore Syncline has a single spine, at least as long as the hinge line, attached to the central portion of the shield (Topper et al., 2007, fig. 6A, B). In *M. unialata* from the lower Cambrian of China, a similarly long spine is attached to the anterior part of the valve (Zhang, 2007, pl. 17, figs 1-7). The Cambrian Series 3 Stage 5 species *M. reticulatis* also hosted a single, elongate spine, but the position of the spine on the shield has not been confirmed (Kouchinsky et al., 2011). The strong microstructural similarities between the spines of *M. squamifer* and bradoriid shields provides convincing evidence for a bradoriid arthropod affinity for the type species (Topper et al., 2013b). Specimens of the new species *M. anthelios* from the Moro section also include conjoined spines and shields, confirming their bradoriid origin (Fig. 8B, H).

The function of the spine in *Mongolitubulus* remains enigmatic. During life, the spines would have protruded at a acute angle from the shields, and doubtless had an effect on locomotion. The presence of such extravagant spines would not appear to be conducive for burrowing or free swimming. The spines may have been a defensive mechanism to deter predators, particularly in taxa such as *M. henrikseni* which had shields encrusted with a number of spines of variable shapes and sizes (Skovsted, 2005).

*Mongolitubulus anthelios* sp. nov. (Fig. 8A-Q)
Type material. Twenty-three *Mongolitubulus anthelios* specimens have been extracted from
the Moro section. Eleven of these are individual spines, four are shields with the spine
broken, five are shields with the spine intact and three are crushed, mostly complete
individuals. Majority of *M. anthelios* specimens were recovered from horizons 866.0, 881.6
and 889.0, corresponding to 668.71 m, 681.0 m and 687.62 m true thickness above the base
of the section, respectively (Winnitinny Creek Member, Wilkawillina Limestone). Additional
localities include 918.5 (711.6 m true thickness above the base of the section, Wirrapowie
Limestone), horizon 855.3 (660.3 m true thickness from the base, Winnitinny Creek Member,
Wilkawillina Limestone) and a spot locality along strike to the north of the section, (Spot
Locality Ab; 30˚ 43.474°E/139˚ 12.094°S) (Table 1). Holotype Fig. 8H, L (SAM P48700),
and paratypes Fig. 8A, N, O (SAM P48693), B (SAM P48694), C (SAM P48695), D (SAM
P48696), E, J (SAM P48697), F (SAM P48698), G, K (SAM P48699), I (SAM P48701), M
(SAM P48702), P (SAM P48703), Q (SAM P48704) Additional unfigured paratypes include
four individual spines, three damaged shields with intact spines, three damaged shields with
the spine broken and one crushed individual.

Etymology. From the Greek ‘*anthelion*’ meaning a tuft or plume of a reed, in reference to the
tufted arrangement of the scales on the tip of the spines.

Occurrence. Winnitinny Creek Member of the Wilkawillina Limestone and Wirrapowie
Limestone, Arrowie Syncline, Flinders Ranges, South Australia; Cambrian Series 2, Stage 3.

Diagnosis. Single spine emerging from centre of convex shield. Spines hollow, gently arched,
tapering to a sharp point. Two sizes of scales on spines - dispersed, larger rhomboid scales
(~25 um long) surrounded by more numerous smaller (~5 um), stubby scales or bumps. All
scales form a loosely imbricating pattern. Shield displays toothed ornament around free margin. Shield texture smooth.

**Description.** Shield strongly convex, single spine occurring at centre of shield. Spine hollow, approximately 100 µm diameter at base, gently arched and apically tapering to a sharp point. Longest spines over 1 mm in length. Scale ornament well developed on spine. Two sizes of scales; larger rhomboid, occasionally spinose scales (max. length ~50 µm) surrounded by smaller low tubercles or bumps (Fig. 8E, F, G, J, K). Larger scales occasionally with twinned tips (Fig. 8K). Distribution of ornament along spines is variable. Some spines remain smooth close to carapace with ornament developing about a third to a quarter along the spine (Fig. 8E-G). Other spines display ornament over nearly entire surface. Free margin of valve ornamented by small teeth spaced at regular (~50 µm) intervals (Fig. 8A, C, L). External microtexture of valve smooth.

**Remarks.** *Mongolitubulus anhelios* spines feature a unique pattern of two different sized scales – larger rhomb-shaped, occasionally tapering scales interspersed with many low, bump-like scales. Ornament becomes more established toward the distal end with the tips having slightly more elongate scales that make the spine appear ‘feathery’. Isolated spines share identical microornament and can be confidently assigned to *M. anhelios*.

The central location of spine attachment to the shield in *M. anhelios* is similar to that in *M. unispinosa* from the Mernmerna Formation in South Australia. However, *M. unispinosa* is characterised by spines with a uniformly distributed pustulose microornament (Topper et al., 2007, fig. 6C-J). The spines of *M. henrikseri* exhibit an ornament of similarly sized, imbricate, well-spaced, blunt scales. The heavily ornamented shields of *M. henrikseri* also
have shorter spines concentrated around the rim and larger spines extending from the central part of the shield (Skovsted and Peel 2001., fig. 4A, B, D-F).

The scales on *M. anthelios* spines are also unlike the scales of *M. squamifer* which usually exhibit regularly spaced, uniformly sized, diamond-shaped scales over the length of the spine. *Mongolitubulus anthelios* spines also do not exhibit the same hooked tip as seen in many specimens of *M. squamifer* (Topper et al., 2007, fig. 5A-K, M, N) or *M. unispinosa* which are thorn-like and often recurved (Topper et al., 2007, fig. 6A, J). The shield of *M. unispinosa* is smooth to pustulose with no ornament around the rim unlike the frilled rim in *M. anthelios*.

*Mongolitubulus anthelios* can also be distinguished from other taxa by the finely toothed frill on the rim of the shield. The toothed, frilled rim distinguishes *M. anthelios* from *M. aspermachaera* described from the Furongian of Sweden (Topper et al., 2013b). The shields and spines of the Swedish taxon are also covered in minute, raised subcircular structures and the shield displays a distinct, broad latero-admarginal ridge (see Topper et al., 2013b, figs 4, 5), morphological features not seen in *M. anthelios*. The shield of *M. reticulatus* is smooth like that of *M. anthelios*, though it shows no evidence of an ornamented rim, and the spine in this taxon is not centrally placed.

6. Conclusions

Bradoriid faunas from the early Cambrian of South Australia have proven to be highly diverse and abundant (Skovsted et al., 2006; Topper et al., 2007, 2011). The new assemblage described herein consists of six taxa, including five new species, from a variety of bradoriid families including Comptalutidae, Hipponicharionidae, Mongolitubulidae and Haoiidae. The assemblage, like others described from Australia is highly endemic at species level, but shows close biogeographic ties to South China at genus level. This study has demonstrated
that the origin of bradoriids pre-date the incoming of trilobites in the lower Cambrian succession of South Australia, suggesting East Gondwana is a likely centre of origin for the Bradoriida. Along with coeval shelly taxa (such as tommotiids), the documented diversity, abundance and high fidelity preservation of bradoriids from East Gondwana (and South China) have great potential for establishing regional chronostratigraphic stages and series for the lower Cambrian of East Gondwana that should facilitate intercontinental correlation.

Acknowledgements

Financial support for this project was provided by ARC Discovery Project 120104251 to GAB and JRP and the Carlsberg Foundation Grant to TPT. We would also like to thank Julie and Bill Reschke for accommodating the field team at Mulga View and Dave Mathieson and Brett Pyemont for their assistance in the field. Thanks to Dean Oliver at Dean Oliver Graphics for drafting figures 1 and 2. Thanks also to Nicole Vella and Debra Birch from the Microscopy Unit at Macquarie University for their assistance with SEM imaging. We are also grateful to the Adnyamathanha People of Nepabunna for allowing the team to conduct field-work on their land. The manuscript benefited from the constructive reviews of Jean Vannier (Lyon) and one anonymous reviewer.

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Figure captions

Fig. 1. Regional locality and detailed geological map showing the study area in the Arrowie Syncline, Flinders Ranges, South Australia. The Moro section was measured through the Wilkawillina Limestone and Wirrapowie Limestone on the eastern limb of the syncline.

Fig. 2. Stratigraphic ranges of bradoriids and key tommotiid, brachiopod and molluscan taxa through the Wilkawillina Limestone and Wirrapowie Limestone in the Moro section. The approximate base of the Abadiella huoi biozone is shown at horizon 866.0 (= 668.7 m true thickness above the base of the section). The stratigraphic range of the micromollusc P. subangulata is shown, the FAD of this taxon (dashed line) is used to approximate the base of Cambrian Series 2, Stage 3 (sensu Peng et al., 2012). Note the FAD of Jiucunella phaseloa occurs 134.6 m below the base of A. huoi zone and 47.6 m below the FAD of P. subangulata within the biothermal slope facies of the Hideaway Well Member (Wilkawillina Limestone).
Fig. 3. *Jiucunella phaseloa* sp. nov. All figured specimens are from the Winnitinny Creek Member of the Wilkawillina Limestone, except for D, which is from the Hideaway Well Member. A, L, lateral view of right shield with spine preserved at posterior curve, SAM P48648, sample 881.6. B, lateral view of right shield with elongate anterior cardinal spine, SAM P48649, sample 738.0. C, right lateral view of specimen with conjoined shields, anterior node compressed, SAM P48650, sample 881.6. D, lateral view of left shield with damage at margins, SAM P48651, sample 699.5 (Hideaway Well Member). E, H, J, holotype, oblique view, shields conjoined, SAM P48652, sample 881.6. F, M, internal view of right shield showing coarse punctae, SAM P48653, sample 881.6. G, K, oblique view of specimen with tightly closed shields, spine pair visible at posterior curve, SAM P48654, sample 844.0. I, lateral view of right shield, SAM P48655, sample 881.6.

Fig. 4. *Phasoa* cf. *spicata* (Öpik, 1968), all specimens from the Wirrapowie Limestone in the Moro section, sample 1043.0. A, G, lateral view of left shield with looping ridge, straight hinge and base of hollow spine at posterior, SAM P48656. B, internal view of right shield, margins damaged, loop present internally as a continuous furrow, SAM P48657. C, H, I, lateral view of right shield, ornament consists of nested pustulations, SAM P48658. D, fragmentary shield, looped ridge visible, SAM P48659. E, F, fragmentary shield showing abraded ornament, SAM P48660.

Fig. 5. *Neokunmingella moroensis* sp. nov. A-G, L, M all from Spot Locality D (Wilkawillina Limestone; Winnitinny Creek Member), H, J, N and K from horizon 836.7 (Winnitinny Creek Member, Wilkawillina Limestone), I, O from horizon 1043.0 (Wirrapowie Limestone). A, L, lateral view of left shield, abraded polygonal microornament visible, SAM P48661. B, internal view of right shield showing confluent lobation, SAM P48662. C, anterior fragment...
1012 of left shield, with prominent anterior lobation and central node, SAM P48663. D, internal
1013 view of posterior fragment of left shield, spine at posterior curve, SAM P48664. E, lateral
1014 view of right shield, SAM P48665. F, lateral view of right shield, SAM P48666. G, M,
1015 holotype, lateral view of right shield with strong lobation, microornament appears pustulose,
1016 spine preserved on dorsal-posterior curve, SAM P48667. H, J, N, lateral view of left shield
1017 with breakage at anterior, shows faint polygonal ornament, sample 836.7 (Wilka willina
1018 Limestone; Winnitiny Creek Member), SAM P48668. I, O, fragmentary specimen, posterior
1019 lobation visible, polygonal ornament well preserved, sample 1043.0 (Wirrapowie Limestone),
1020 SAM P48669. K, severely abraded right shield, SAM P48670.

Fig. 6. Sinskolutella cuspidata sp. nov. A, B, I, J, K, L from sample 1081.0 EOS (end of
section), where the Moro section has been offset ~90 m to the NNE; Wirrapowie Limestone.
C, D, E, F, G, H from sample 933.2 (Wirrapowie Limestone). A, M, lateral view of left shield
with rim well preserved, micro-pulvinate ornament has been abraded from central part of
shield, SAM P48671. B, left lateral view of two shields, separated at hinge, dorsal cusp
visible, SAM P48672. C, holotype, left shield with spine at posterior curve, SAM P48673. D,
right shield, rim abraded, showing well-preserved ornament, SAM P48674. E, O, lateral,
internal view of left shield with coarse punctae visible, SAM P48675. F, right lateral view of
conjoined shields, SAM P48676. G, N, lateral view of left shield, micro-pulvinate ornament
well preserved, SAM P48677. H, lateral view of left shield, SAM P48678. I, overlapping,
separated shields, SAM P48679. J, separated shields, SAM P48680. K, conjoined shields,
broken through posterior, SAM P48681. L, internal view of right shield with remains of
broken left valve adhered to hinge, SAM P48682.
Fig. 7. *Jixinlingella daimonikoa* sp. nov. A, C, L, holotype, conjoined shields gape slightly at anterior, frill present around margin, spine pair at posterior curve, SAM P48683, sample 1043.0 (Wirrapowie Limestone). B, J, K, lateral view of left shield with a spine at posterior curve, broad anterior sulcus and eleft in node at anterior, low pustules in depressions between reticulations, SAM P48684, sample 738.0 (Wilkawillina Limestone; Winnitinny Creek Member). D, right lateral view of abraded articulated valves, SAM P48685, sample 1043.0 (Wirrapowie Limestone). E, internal view of right shield showing reticulate ornament, SAM P48686, sample 1043.0 (Wirrapowie Limestone). F, internal view of duplicature at spine, SAM P48687, sample 1043.0 (Wirrapowie Limestone). G, abraded left shield, SAM P48688, sample 1043.0, (Wirrapowie Limestone). H, abraded left valve, SAM P48689, sample 1081.0, Wirrapowie Limestone) M, abraded left shield with broad anterior sulcus, SAM P48691, sample 1043.0, (Wirrapowie Limestone). N, lateral view of right shield, SAM P48692, sample 1043.0 (Wirrapowie Limestone).

Fig. 8. *Mongolitubulus anthelios* sp. nov. All specimens from the Winnitinny Creek Member of the Wilkawillina Limestone. A, N, O, abraded shield, marginal frill, hole where spine has broken away, SAM P48693, sample 881.6. B, spine intact, compressed into dented carapace, SAM P48694, sample 881.6. C, compressed shields with base of spine preserved, SAM P48695, sample 889.0. D, proximal end of hollow spine, SAM P48696, sample 866.0. E, J (SAM P48697), F (SAM P48698), G, K (SAM P48699) individual spines, ornament of rhomboid scales and bumps develop toward tip, all from sample 889.0. H, L, holotype, ornamented spine emerging from convex shield, remains of frill present at margin, SAM P48700, sample 881.6. I, proximal part of spine with flared base, SAM P48701, sample 889.0. M, compressed specimen, spines have been folded together, remaining carapace...
crushed around base of spines, SAM P48702, sample 889.0. P, spine with flared base, SAM P48703, sample 855.3. Q, abraded spine, SAM P48704, sample 899.0.

Table 1. Moro Section Bradoriid Counts. NB: ‘+’ = additional fragments, ‘Comp’ = Comptalutidae, ‘Hippon’ = Hipponicharionidae, ‘?Brad’ = ?Bradoriidae, ‘Hao’ = Haoiidae, ‘Mongo’ = Mongolitubulidae. See Figure 2 for Spot Locality information.
Other Pre-Cambrian Wilpena Group

Pre-Cambrian Alluvium, silcrete, sediments, etc

Diapiric breccia

Grindstone Range Sandstone

Pantapinna Sandstone

Moodlatana Formation

Wirrealpa Limestone

Narina Greywacke

Bunkers Sandstone

Nepabunna Siltstone

Midwerta Shale

Mernmerna Formation

Wirrapowie Formation

Wilkawillina Limestone

Parachilna Formation

Uratanna Formation

Pre-Cambrian Wilpena Group

Other Pre-Cambrian

Fig 1

Fig 2
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