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Lower Cambrian helcionelloid macromolluscs from South Australia

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ABSTRACT

Early Cambrian univalve molluscs are predominantly represented by microscopic forms (body length of 1–3 mm), preserved mainly as phosphatised internal moulds with limited definable features. Macromolluscs (≥5 mm) are generally rare, occur in low abundance and are poorly preserved, often lacking apical features and ornament which hinders taxonomic assessment. New and previously undescribed material from lower Cambrian Hawker Group carbonates of the Flinders Ranges in South Australia includes four new taxa, *Minastirithella silivreni* gen. et sp. nov., *Galeacalvus coronarius* gen. et sp. nov., *Helcionella histosia* sp. nov., and *Ilsanella enallaxa* sp. nov. Three-dimensional silicified shell material preserved with intact apices offers new insight into protoconch morphology, growth habit (isometric vs. allometric) and developmental mode. This material supports previous suggestions that some micromollusc taxa may in fact be early ontogenetic stages (juveniles) of larger macroscopic taxa; such that the millimetric size range of helcionelloids conforms to the dimensions of earliest apical portion in some macromolluscs documented herein. However, taphonomic limitations associated with phosphatisation show that the morphology (especially height vs. width) of the apex can greatly influence the probability of steinkern formation and preservation potential for both micro- and macro-scale helcionelloids. Artificial inflation in the appearance of millimetric helcionelloids with an optimal morphology for phosphatisation is thus directly linked to taphonomic biases in the fossil record.

1. Introduction

Helcionelloids are univalve conchiferan molluscs with low cap-shaped to high orthoconic shells that are an important component of the Cambrian radiation (Peel, 1991a,b; Parkhaev, 2008; Vendrasco, 2012). Most described taxa rarely reach more than a few millimetres in size (Runnegar and Jell, 1976; Runnegar, 1983; Peel, 1991b; Haszprunar, 1992), and are diverse, locally abundant and geographically widespread during the Cambrian. Larger macroscopic univalves with shell lengths in excess of 5 mm but reaching up to 30 mm are well known with over 70 nominal species documented from the Lower to Middle Cambrian (see Appendix A).

The existence of larger univalve molluscs assumes the presence of a smaller juvenile or larval stage in early development (Mus et al., 2008). Investigation of the apical (first formed) portion of original or replaced macromolluscan shells is thus crucial in identifying morphological transitions between the early ontogenetic stages (Parkhaev, 2008; Vendrasco et al., 2010; Nützel, 2014; Parkhaev, 2014). Discovery of a large (centimetre scale), limpet-like mollusc from the lower Cambrian Rio Huso Group, Montes de Toledo, central Spain with an apical shell morphologically 'indistinguishable' from some millimetre-scale helcionelloids provided a clear potential ontogenetic link between millimetric and macroscopic helcionelloids (Mus et al., 2008). Furthermore, the apparent isometric (proportional) growth of the shell from a 2 mm-long helcionellid-like apical portion to a 2 cm-long adult suggested that some (but not all) micromolluscan helcionelloids may represent juvenile or larval (planktotrophic) shells of larger macroscopic, limpet-like univalve molluscs. Investigation of early ontogeny in large helcionellid taxa has been hindered by a paucity of material and poor preservation or breakage of the apical portion (Mus et al., 2008). Whilst the Spanish material provides crucial insight into the early developmental phases of the organism, the material is severely compressed and does not preserved the three-dimensionality of the adult shell, accretionary features, ultrastructure or measurable allometric changes throughout shell growth.

Until recently, previous studies which focused on the morphology of helcionelloid 'protoconchs' were almost entirely restricted to steinkern material (Nützel et al., 2006; Parkhaev, 2006, 2008). New discoveries of shell material preserved in micro-scale helcionelloids from the lower Cambrian of the Siberian Platform and China provide crucial information regarding the developmental strategies of ancestral molluscs (Parkhaev, 2014). In extant gastropods, planktotrophic developers possess a protoconch consisting of an embryonic shell (protoconch I) and a larval shell (protoconch II). In direct and lecithotrophic developers the larval shell is absent and the teleoconch forms directly from the embryonic shell (Jablonski, 1985; Haszprunar et al., 1995; Nützel, 2014). Modern monoplacophorans are lecithotrophic and possess a bulbous protoconch ranging between 123 and 150 μm in length, which will often break off during development of the adult shell (Wingstrand, 1985; Lindberg, 2009; Wilson et al., 2009; Haszprunar

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and Ruthensteiner, 2013). The ability to delineate the separate ontogenetic stages in not only micromolluscs but also macromolluscs can aid in the current debate on the advent of lecithotrophy vs. planktotrophy in stem molluscan lineages (Nützel et al., 2006; Freeman and Lundelius, 2007; Nützel et al., 2007; Runnegar, 2007; Nielsen, 2013; Nützel, 2014).

An association between large helcionelloid species and small helcionellids would have profound taxonomic, nomenclatorial, and ultimately phylogenetic implications for deciphering early molluscan evolution. The current taxonomic compendium of helcionelloid taxa likely contains a mixture of named ontogenetic growth stages, some of which may be conspecific. The implications for taxonomic resolution of morphospecies have previously been flagged by Brock and Paterson (2004) in revising the macromollusc *Tannuella* Missarzhevsky in Rozanov et al., 1969, indicating that millimetric-sized univalves (especially steinkerns) previously attributed to the genus did not exhibit septation and should be removed from the genus sensu stricto.

Understanding early ontogeny is fundamental to understanding the taxonomy and palaeoecology of fossil groups, though in the case of the helcionelloids (both large and small) the taphonomic pathway(s) involved in preserving shell material is a major limiting factor. In this paper we describe a number of new macromolluscan taxa (taken to be adult forms) from carbonate successions through Cambrian Series 2 (Stages 3–4) Hawker Group rocks in the Flinders Ranges of South Australia. These new specimens provide important new data on size distribution, growth habit and developmental mode in helcionelloids from early Cambrian East Gondwana. The material described herein mainly consists of replaced (silicified) shells supplemented by both phosphatised and non-phosphatised internal and external moulds from previously unpublished collections housed in the South Australian Museum, as well as material derived from collections made by GAB over the last decade. A compendium of known macromollusc species (>5 mm) from the Lower to Middle Cambrian is also provided herein, detailing systematics, size, age range and geographic occurrence (Appendix A).

2. Geological setting

2.1. Hawker Group, Arrowie Basin

The Hawker Group comprises a wide spectrum of depositional regimes across a broad intracratonic (epeiric) shelf with carbonate shoals and bioherm complexes, slope deposits and basinal facies (Clarke, 1990a,b; James and Gravestock, 1990; Gravestock and Cowley, 1995; Jago et al., 2012). Extensive folding during the Ross–Delamerian and Petermann Orogenies (Zang et al., 2001; Zang, 2002; Foden et al., 2006) produced a wide expanse of often tightly folded anticlinal and synclinal outcrop of Cambrian units especially manifest in the Bunkers Range, Bunkers Graben (= the “Wirrelapa Hinge Zone” sensu Gravestock and Cowley, 1995), as well as the Chace and Druid Ranges, Elder Range, Mount Scott Range and Mount Chambers Region.

Geology of the regions and depositional environments has previously been discussed in some detail by Brock and Paterson (2004), Topper et al. (2009), and Skovsted et al. (2011) and summarised in Topper et al. (2013). A summary of the localities is provided in Fig. 1A–E.

2.2. Mount Scott Range — Ajax Limestone

Macromolluscan material is derived from two stratigraphic sections; AJX-M (base of section coordinates: 30°35′49″S, 138°19′59.3″E — WGS84) and AJX-N (base of section coordinates: 30°35′07.3″S, 138°19′56.5″E — WGS84) in the Mt Scott Range, Flinders Ranges (Fig. 1B–C). These sections measured through the Ajax Limestone are located approximately 2 km apart, and whilst there are differences in the thickness and outcrop the lithologies are very similar. The lower ~120 m of each section consists of shallow-water microbial, stromatolitic and finely laminated limestones displaying pervasive secondary dolomitisation and is generally unfossiliferous. In AJX-M, the upper 120 m of section is dominated by bioclastic to mottled nodular limestones (commonly silicified), succeeded by grey to buff nodular limestone beds and red massive bioclastic limestones. This richly fossiliferous interval incorporates the *Abadiella huoi* and *Pararaia tatei* trilobite Zones and ranges up to a disconformable boundary at approximately 239 m true thickness above the base of the section.

Most of the macromolluscan material is derived from the upper ~130 m of AJX-N section in distinctive pink to red archaeocyathan-dominated and richly bioclastic carbonates, occasionally interbedded with grey bioclastic limestone with iron-replaced (?haematite) crusts which preserve macromolluscs, as well as archaeocyaths and calciate brachiopods. Specimens of *Ilsanella enallaxa* sp. nov. were recovered from the following samples: AJX-N/318.5 (182.7 m true thickness) and AJX-N/334 (191.6 m true thickness) (Fig. 2). Additional specimens of *I. enallaxa* sp. nov. were collected from loose haematised replaced material adjacent to the AJAX-N section at a spot locality with coordinates 30°34′58″S, 138°19′01.7″E. Rarer macromolluscan specimens include silicified shell material of *Helcionella* sp. nov. from AJX-M/266 (148.7 m true thickness), and AJX-M/267.5 (149.6 m true thickness), and internal moulds of Helcionellid gen. et sp. indet. 1 are from AJX-N/244 (139.95 m true thickness) (Fig. 2).

2.3. Chace Range — Wirrapowie Limestone

Specimens were recovered from two stratigraphic sections measured through the Wirrapowie Limestone and overlying Mernmerna Formation in the Chace Range, southern Flinders Ranges (Fig. 1B, D). Macromolluscs derived from the first section, CR-1 (base of section coordinates: 31°44′38.8″S; 138°36′19.7″E) appear within the upper 55 m (between 865 and 920 m above the base of the section) in poorly outcropping ferruginous shale. This unit is interpreted to represent the upper part of the Wirrapowie Limestone. The boundary between the top of the Wirrapowie Limestone and the overlying lower Mernmerna Formation is not well exposed, but is within metres of a distinctive white siltstone marker horizon that defines the top of the CR-1 section at coordinates 31°44′50.6″S; 138°36′28.5″E (Fig. 1B, D). The Wirrapowie Limestone is estimated to reach a total thickness of approximately 904 m that incorporates predominantly nodular limestone and ferruginous shale outcropping from 465 m above the base of the section (Topper et al., 2013). The unit outcrops discontinuously to the north-east and can be traced for approximately 6 km along strike to the base of the second measured stratigraphic section, CR-2 (base of section coordinates: 31°41′41.7″S; 138°42′23.7″E) (Fig. 1D). Importantly, the first appearance datum (FAD) of the trilobite *A. huoi*, which is the eponym of the *A. huoi* trilobite Zone, occurs at 885 m above the base of the CR-1 section within the white horizon. *Minastirithella silivreni* gen. et sp. nov. co-occurs with *A. huoi*, but also ranges slightly higher at 893 m above the base of the CR-1 section and ranges from 0.0 to 10.6 m above the base of the CR-2 section (Fig. 2). Additional specimens were collected in July 2014 from outcrops of the white horizon close to the base of the CR-2 section on the northern (coordinates: 31°41′41.8″S; 138°42′24.6″E) and southern banks (coordinates: 31°41′42.1″S; 138°42′23.9″E) of an unnamed tributary 1.7 km south-west of Borgas Dam.

Fig. 1. Locality, regional landmarks and geology maps showing the position of sampled stratigraphic sections and spot localities in the Arrowie Basin, Flinders Ranges, South Australia. A, General locality map with the position of the study area in South Australia. B, Enlarged map of regional landmarks, broader study sites and spot locality at Erengunda Creek. C, Generalised geological map of the Mount Scott Range showing the location of the AJX-M and AJX-N sections. D, Generalised geological map of the Chace and Druid Ranges with location of the CR-1 and CR-2 sections. E, Geological map of the Bunkers Range showing the location of the MMF and OS sections, as well as spot locality MMF North. F, Generalised geological map of the Bunkers Graben with the 10MS and 10MS–W sections on the eastern limb.