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Palaeontology

Early Cambrian record of failed durophagy and shell repair in an epibenthic mollusc

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Predation is arguably one of the main driving forces of early metazoan evolution, yet the fossil record of predation during the Ediacaran–Early Cambrian transition is relatively poor. Here, we present direct evidence of failed durophagous (shell-breaking) predation and subsequent shell repair in the Early Cambrian (Botoman) epibenthic mollusc *Marocella* from the Mernmerna Formation and Oraparinna Shale in the Flinders Ranges, South Australia. This record pushes back the first appearance of durophagy on molluscs by approximately 40 Myr.

Keywords: predation; durophagy; Early Cambrian; Mollusca; South Australia

1. INTRODUCTION

The importance of predation as a selective influence on the evolution, diversification, biomineralization and ecology of metazoans has been the focus of intensive research interest over the last 20 years (e.g. Vermeij 1987; Conway Morris & Bengtson 1994; Kowalewski & Kelley 2002). The earliest evidence of predation in the fossil record comes from drill holes in the oldest known skeletal fossil, *Cloudina* from Ediacaran strata in China (Bengtson & Yue 1992; Hua *et al.* 2003).

Durophagy, the macropredatory consumption of prey protected by a mineralized skeleton (Aronson 2001), is, by its very definition, detectable only in the fossil record after the 'biomineralization event' associated with the Cambrian radiation (Bengtson 1994; Conway Morris 1998; Marshall 2006) and substrate revolution (Bottjer *et al.* 2000). Direct evidence of predation is generally lacking in Ediacaran faunas (Narbonne 2005) and thus macropredatory lifestyles probably evolved around the time of the Ediacaran–Early Cambrian transition. Direct evidence for predation in the Cambrian fossil record includes drill holes in lingulate brachiopods (Conway Morris & Bengtson 1994) and healed injuries in Cambrian arthropods and problematic fossils (Ebbestad & Peel 1997, figure 1; Nedin 1999; Babcock 2003). Further definitive examples of predation have also been recorded in Cambrian lagerstätte (Bruton 1981; Nedin 1999; Babcock 2003; Zhu *et al.* 2004).

Univalved molluscs were among the first metazoans to produce a mineralized shell (Gubanov & Peel 1999). Diverse assemblages of molluscs are known from richly fossiliferous Lower Cambrian successions in the Flinders Ranges, South Australia (Bengtson *et al.* 1990; Parkhaev 2001; Brock & Paterson 2004). This region is thus ideal for seeking evidence of repaired shell injuries in order to more accurately constrain the advent of durophagous predation in the Early Cambrian.

Direct evidence of predation can be found in the skeletons of prey organisms (Vermeij 1987). Mollusc shells are formed continuously by marginal accretion and thus record non-lethal damage that the organism endured. Extant mollusc faunas show a high incidence of repaired shell injuries (Alexander & Dietl 2003). The main cause of damage in almost all modern environments is predation by durophagous animals, although wave-propelled rocks or ice boulders may cause damage in the littoral zone (Cadee 1999). However, not all predators of molluscs break the shells of their prey. Predation by drilling may leave characteristic holes in the shell, but some predators, such as sea stars, target soft tissue and rarely damage the shell (Mauzey *et al.* 1968).

The low frequency of repaired injuries in Palaeozoic faunas reflects the supposed inefficiency of Palaeozoic predators in breaking calcified shells (Vermeij 1987). Few Palaeozoic animals possessed specialized hard parts capable of breaking mollusc shells, especially before the appearance of jawed vertebrates in the Devonian (Signor & Brett 1984). Rare, healed injuries in trilobite exoskeletons have been found worldwide, although some of these may have occurred during moulting (Babcock 2003). Trilobite fragments also occur in Early Cambrian coprolites (Vannier & Chen 2005) and in the guts of Middle Cambrian arthropods (Bruton 1981; Conway Morris & Robison 1988; Zhu *et al.* 2004). Healed injuries have also been reported in Lower Cambrian problematic cap-shaped fossils *Estoniadiscus* (Peel 2003) and *Mobergella* (Bengtson 1968).

2. DESCRIPTION OF REPAIR SCARS IN *MAROCELLA*

The Early Cambrian calcareous, limpet-like, shell of *Marocella* Geyer has an oval to sub-rectangular outline and an eccentric apex. Mature portions of the shell ornament consist of rounded concentric or spiralling folds that frequently bifurcate (figures 1 and 2). Fine concentric striae represent growth increments (Evans 1992). *Marocella* is unique among molluscs in that the internal surface of the shell is divided into a network of intersecting concentric ridges and radiating septa that serve to strengthen the shell and form distinct subquadrate compartments. *Marocella* and the similarly shaped *Scenella* Billings have been interpreted as the floats of chondrophorine hydrozoans (Yochelson & Gil Cid 1984), but their calcareous

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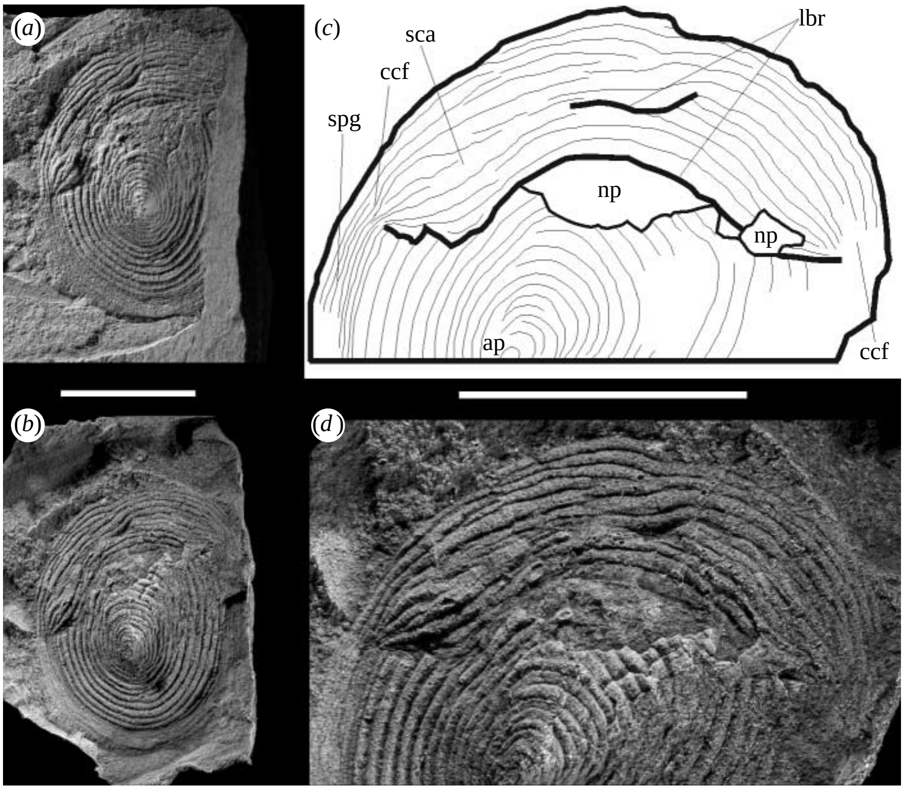

Figure 1. *Marocella* sp. from the Oraparinna Shale in the vicinity of Eregunda Creek, South Australia at 31° 05′ 34.4″ S, 138° 51′ 15.2″ E. (*a*) SAMP41943a: internal mould with repaired injury on the supra-apical and left-lateral shell. (*b*) SAMP41943b: latex mould of counterpart specimen in (*a*). (*c*) Schematic drawing of damaged portion of SAMP41943b, based on (*d*). (*d*) Detail of damaged portion of SAMP41943b, latex mould of counterpart. Scale bar, 10 mm. ap, apex; ccf, converging concentric folds of injured and uninjured shell; np, portions of specimen without preserved shell; lbr, line of breakage; sca, differential shell growth on scar; spg, slowed post-traumatic growth of undamaged shell.

composition, the presence of fine growth striae (Evans 1992) and, at least in *Marocella*, evidence of shell repair do not support this interpretation.

Here, *Marocella* is regarded as a mobile epibenthic mollusc. It is widely distributed in the upper Lower Cambrian of Gondwana and has been recorded from Spain, Morocco, Antarctica, Australia and China (Parkhaev 2001). Three specimens (SAMP41943a, SAMP14600a and SAMP14606) out of a total of 38 specimens from the Lower Cambrian (Botoman) Mernmerna Formation and Oraparinna Shale in the Flinders Ranges, South Australia show repaired shell injuries (figures 1 and 2). Specimen SAMP41943 (figure 1*a*–*d*) displays a second minor damage to the repaired shell. The estimated length of the specimens at the time of initial injury varied between 10 and 18 mm. Damage is concentrated around the supra-apical and adjacent lateral margins of the shell (figures 1 and 2). Each fracture cuts across 4–6 concentric folds of the shell but then continues parallel to the folds throughout most of its length. New shell material was added parallel to the line of breakage and along its entire length. The new shell material displays well-developed folds, although less regularly developed than before the break occurred (figure 1*c*,*d*). Undamaged portions of the shell continued to grow normally, but seemingly at a slower rate, based on the width of the concentric folds. At the endpoints of the breaks, the folds of the newly formed shell were laid down at an angle to the original folds but converge with the narrow post-traumatic folds of the uninjured shell (figure 1*c*).

3. DISCUSSION

By analogy with repaired shell injuries in modern molluscs, the scars in *Marocella* are interpreted as repaired injuries following failed predation. The host sediments (calc-siltstones and mudstones) of the upper Mernmerna Formation contain well-preserved, often articulated, specimens of trilobites, articulated bradoriids, complete sponges and hyolithids with attached opercula. The presence of articulated specimens, some with intact fragile spines, suggests minimal transportation of the assemblage and effectively rules out a mechanical (non-biological) origin as the cause of the damage to *Marocella* shells. The occurrence of blind trilobites (*Atops* and *Serrodiscus*) also suggests that the entire assemblage inhabited outer shelf to slope facies, possibly below the photic zone, far removed from the littoral zone where it is sometimes difficult to discriminate between physical and biological agents of shell fragmentation (Zuschin *et al.* 2003).

The injuries in *Marocella* are consistently located at the supra-apical margin of the shell. This may be a weaker area of the shell since the concentric folds are wider in this region. This location corresponds to the head region if *Marocella* is interpreted as a

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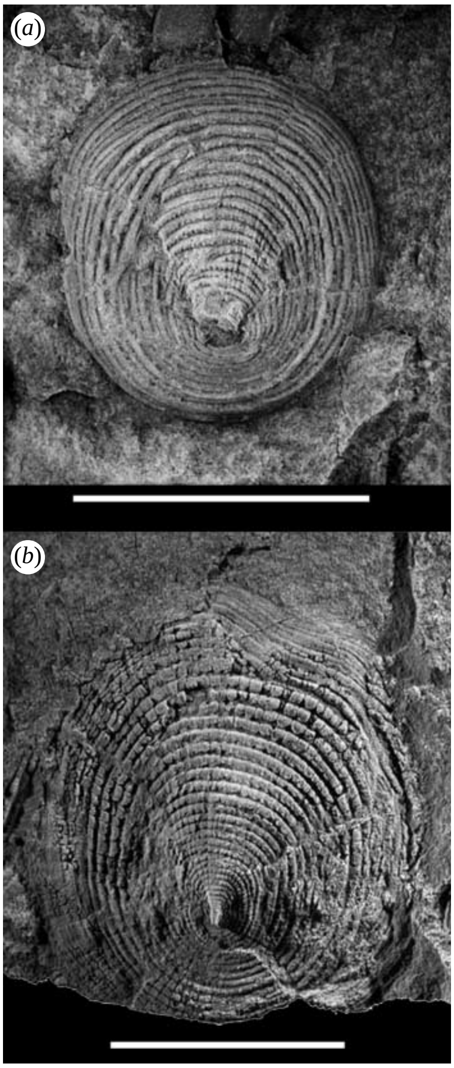

Figure 2. *Marocella* sp. from South Australia. (*a*) SAMP14600a from upper Mernmerna Formation section ER-6, Elder Range 31° 24′ 21″ S, 138° 25′ 46″ E; shell with repaired injury to left-lateral part. (*b*) SAMP14606 from upper Mernmerna Formation, locality B11c at the western end of Bunyeroo Gorge on Edeowie Station at 31° 24′ 49″ S, 138° 33′ 29″ E; partial shell/internal mould with damage to supra-apical and right-lateral shell. Scale bar, 10 mm.

helcionelloid or to the posterior if interpreted as a tryblidiidan monoplacophoran (Peel 1991). However, *Marocella* is unlike known Tryblidiida which also lack an Early Cambrian record (Peel 1991).

The predator responsible for the attack on *Marocella* is unknown. One possible candidate includes the arthropod *Anomalocaris* Whiteaves, which is known from coeval Lower Cambrian strata on Kangaroo Island, South Australia (Nedin 1999). *Anomalocaris* and arachnomorph arthropods did not possess specialized hard parts for handling or breaking prey, but may have used their appendages to manipulate prey. Thus, *Anomalocaris* presumably used its two great anterior appendages to capture and hold prey while ingesting it (Nedin 1999). Trilobites and other Cambrian arthropods (e.g. *Sidneya* Bruton 1981 and *Utahcaris* Conway Morris & Robison 1988) macerated food using the gnathobases on the basal endites of the walking legs, in a similar way to extant *Limulus*. Although its gnathobases are not mineralized, *Limulus* is capable of breaking the shells of bivalves (Fortey & Owens 1999). *Marocella* may also have been the prey of contemporaneous redlichiid trilobites whose gnathobasic limbs suggest a predatory lifestyle (Fortey & Owens 1999; Babcock 2003).

The repaired shell injures in *Marocella* from Botoman strata in the Flinders Ranges represent the oldest record of non-lethal predatory attack on a mollusc. The oldest previously recorded examples of shell repair following failed predation come from Early Ordovician gastropods (summary in Ebbestad & Peel 1997; Lindström 2005) and are thus approximately 40 Myr younger than the specimens of *Marocella* described here.

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