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

Christian B. Skovsted1,2,* , Glenn A. Brock1, Anna Lindström3, John S. Peel4, John R. Paterson4 and Margaret K. Fuller5

1Centre for Ecosatigraphy and Palaeobiology, Department of Earth and Planetary Sciences, Macquarie University, New South Wales 2109, Australia
2Department of Earth Sciences, Uppsala University, Norbyvägen 22, 752 36 Uppsala, Sweden
3Department of Palaeozoology, Swedish Museum of Natural History, PO Box 50007, 104 05 Stockholm, Sweden
4Division of Earth Sciences, School of Environmental Sciences and Natural Resources Management, University of New England, Armidale, New South Wales 2351, Australia
5South Australian Museum, North Terrace, Adelaide 5000, Australia

*Author for correspondence (christian.skovsted@geo.uu.se)

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 Orarpanina 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). 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 1992). 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 (Babcock 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 subquadrat compartments. Marocella and the similarly shaped Scenella Billings have been interpreted as the floats of chondrophorine hydrozoans (Yochelson & Gil Cid 1984), but their calcareous...
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 1a–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 line of breakage and along its entire length. The new shell material was added parallel to the line of breakage but also 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 unbroken shell (figure 1c).

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
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 injuries 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.

We thank three anonymous reviewers for their insightful comments and helpful suggestions. Dave Mathieson (Macquarie University) provided photographic assistance; Ian and Di Fargher at ‘Angorichina Station’ and Glen Gabe at ‘Mt Little Station’ provided access to the field localities. This work was supported by grants from the National Geographic Society Committee for Exploration and Research and Macquarie University (to G.A.B., C.B.S. and J.R.P.) and from the Swedish Research Council (to C.B.S.).


