



Estonian Journal of
Earth Sciences
2023, 72, 1, 110–113

<https://doi.org/10.3176/earth.2023.23>

www.eap.ee/earthsciences
Estonian Academy Publishers

SHORT COMMUNICATION

Received 22 March 2023
Accepted 5 April 2023
Available online 14 June 2023

Keywords:

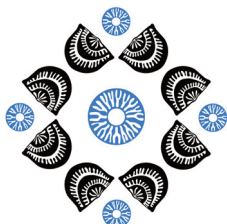
brachiopods, Ordovician, Baltica,
symbiosis, parasitism, shell damage

Corresponding author:

Olev Vinn
olev.vinn@ut.ee

Citation:

Vinn, O., De Baets, K., Isakar, M. and Toom, U. 2023. Parasite-induced shell damage in brachiopod *Porambonites (Porambonites) laticaudata* from the Late Ordovician (Sandbian) of Estonia. *Estonian Journal of Earth Sciences*, 72(1), 110–113. <https://doi.org/10.3176/earth.2023.23>



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ESTONIA 2023

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Parasite-induced shell damage in brachiopod *Porambonites (Porambonites) laticaudata* from the Late Ordovician (Sandbian) of Estonia

Olev Vinn^a, Kenneth De Baets^b, Mare Isakar^c and Ursula Toom^c

^a Department of Geology, Institute of Ecology and Earth Sciences, University of Tartu, Ravila 14a, 50411 Tartu, Estonia

^b Institute of Evolutionary Biology, University of Warsaw, Żwirki i Wigury 101, PL-02089 Warsaw, Poland

^c Natural History Museum, University of Tartu, Vanemuise 46, 51003 Tartu, Estonia

^d Department of Geology, Tallinn University of Technology, Ehitajate 5, 19086 Tallinn, Estonia

ABSTRACT

A new type of shell damage has been described in Ordovician brachiopods in *Porambonites (Porambonites) laticaudata*. There is a pair of small pits with somewhat different outline in the shell surface at the anterior commissure of the brachiopod. These pits are oriented in lateral direction, about 40° from the direction of the sulcus on the anterior commissure. Previously known shell damage has resulted from failed predatory attacks by durophagous predators and differ from the shell damage in *P. (P.) laticaudata*. The pits in the shell margin are most likely the result of shell malformation caused by the presence of symbionts. It is plausible that the symbionts of the *P. (P.) laticaudata* benefitted from inhalant currents and were cleptoparasites. The symbionts caused damage to the host brachiopod, which also suggests a parasitic relationship.

Introduction

Shell damage is common in Palaeozoic brachiopods, whereas most of the shell damage has been interpreted as the result of failed predatory attacks. Damaged shells have been described in lower Cambrian lingulates (Walcott 1912; Zhang et al. 2011; Peel 2014) and Upper Ordovician rhynchonelliform brachiopods (Alexander 1986). Four distinct types of shell repair occur in Late Ordovician brachiopods (Alexander 1986). In addition to predators, parasites also caused malformations in brachiopod shell. The earliest parasite-induced structures have been described from lower Cambrian brachiopods (Bassett et al. 2004; Peel 2014). Macroscopic invertebrate symbionts in brachiopods are sometimes preserved as bioclastrations, which are among the best examples of symbiotic interactions in the fossil record (Bassett et al. 2004; Vinn et al. 2014). The fossil record of all parasitic associations has been analysed most recently by De Baets et al. (2021a, 2021b). Nevertheless, in contrast to predation, parasitic associations involving brachiopods remain poorly known and most evidence so far has been reported from the Palaeozoic (e.g., De Baets et al. 2021a, 2021b). The majority of research has focused on parasitic interactions in bivalve molluscs, with the earliest evidence dating from the Silurian to the Devonian (De Baets et al. 2011). These interactions became more diverse in the Mesozoic and Cenozoic (Huntley et al. 2021).

The aims of this paper are to: 1) describe a new type of shell damage in Ordovician brachiopods; 2) discuss the nature of shell damage; and 3) discuss the ecology of the possible parasitic association.

Geological background

During the Sandbian, Baltica was located in the temperate climatic zone (Nestor and Einasto 1997; Torsvik and Cocks 2013). The lower Sandbian of Estonia is characterized by temperate carbonates (Dronov and Rozhnov 2007). The Kukruse

Regional Stage (RS; lower Sandbian) contains intercalation of limestone and carbonaceous oil shale (kukersite) layers of various thicknesses deposited on a carbonate platform in normal marine conditions. The Kukruse Age is characterized by a high diversity of both macro- and microfauna in Baltoscandia (Kaljo et al. 2011). Kiipli et al. (2010) suggested that the rise in bioproduction during the Kukruse Age was associated with regional seawater circulation and coastal upwelling. *Porambonites* (*Porambonites*) *laticaudata* was first described from the Kukruse RS (Bekker 1921). The specimen with shell malformation was collected from the Kukruse RS of the Estonian Oil Shale Basin, but its accurate locality is unknown.

Materials and methods

Collections 408 (TUG) and 188 (GIT) of *Porambonites* brachiopods from the Kukruse RS, NE Estonia, were searched for signs of bioerosion and shell damage. Only one brachiopod (0.17 %) from the Kukruse RS showed shell damage and no signs of bioerosion were detected. The brachiopod with shell damage was cleaned and photographed with a digital camera (Canon EOS 5DSR). The shell damage was photographed using an apochromatic zoom system Leica Z16 APO. The measurements of the shell damage were obtained from calibrated high-resolution photographs. The studied collections are housed at the Natural History Museum, University of Tartu (TUG), Department of Geology at Tallinn University of Technology (GIT), Estonia, except for the specimen of a figure with shell malformation (Fig. 1), which is deposited at Paleontological Museum of

St. Petersburg State University (Russia), with collection number PMSPU 110-1.

Results

There is a pair of pits (2.4 and 2.5 mm in diameter) in the shell surface at the anterior commissure of the brachiopod *Porambonites* (*Porambonites*) *laticaudata* Bekker (Fig. 1), but they do not form a mirror image. The pit in the ventral valve has an elliptical outline and its walls are equally steep around its perimeter. There is another less developed and shallower pit slightly posterior to the elliptical one in the ventral valve. The pit in the dorsal valve has a slightly crescent-shaped or semicircular outline with a steep and sharp edge near the commissure, and its bottom on the other side is almost flush with the shell surface. The brachiopod is 36.3 mm high and 37.1 mm wide, corresponding to the size of adult specimens of this species. The dimensions of *P. (P.) laticaudata* in the GIT collection range from 26.3 × 28.4 mm to 42.5 × 45.4 mm. The pits are oriented in lateral direction, about 40° from the direction of sulcus on the anterior commissure. The pits are located almost exactly opposite each other in the ventral and dorsal valves. Both larger pits are about 2 mm deep. The shell surface inside the pits is covered with costae and has a normal appearance besides forming a depression. There is no sign of shell breakage associated with the pits. The frontal edges of the pits are 1.0 mm and 0.5 mm away from the anterior commissure. The anterior commissure is laterally invaginated at the pits. The invagination of the commissure is about 5 mm long and 2 mm deep. The invagination is broad, V-shaped, with a rounded terminus.

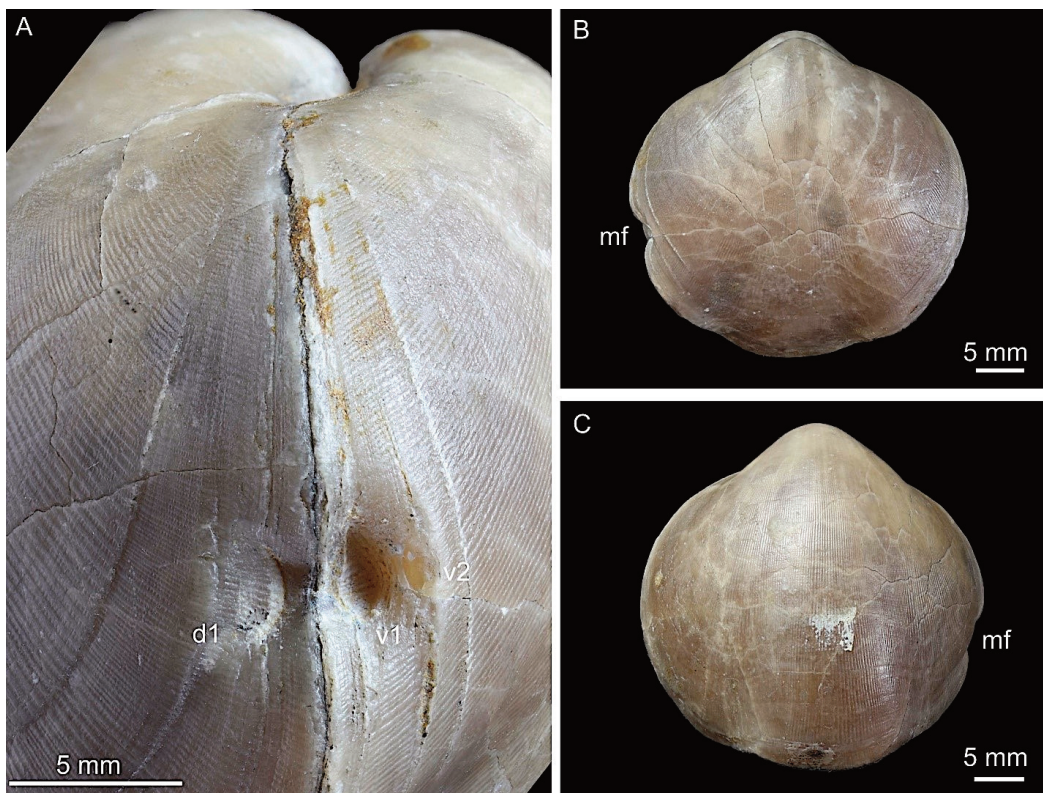


Fig. 1. Shell malformation (mf) in the brachiopod *Porambonites* (*Porambonites*) *laticaudata* from the Sandbian (Kukruse Regional Stage) of the Estonian Oil Shale Basin. **A** – detailed view of two malformations on both sides of the commissure: v1 – large elliptical pit, v2 – small shell deformation, d1 – large pit; **B** – ventral valve; **C** – dorsal valve.

Discussion

Comparison with predatory shell damage in Palaeozoic brachiopods

Scalloped valve damage in brachiopods displays a ‘micro-escarpment’ that is anteriorly or laterally concave to straight but concentrically discontinuous (Alexander 1986). Scalloped valves sometimes have arched fractures positioned contiguously around the former commissure (Alexander 1986). The shell damage in *Porambonites* (*Porambonites*) *laticaudata* has an outline somewhat similar to some scalloped shell damage (Alexander 1986, 275, fig. 3.1–3) but differs in the lack of shell fracture and in the opposite morphology of the pits, where the steepest slope is the anteriormost one. The cleft type of valve damage in brachiopods has a common direction, which is usually approximately parallel to the costae (Alexander 1986, 276, fig. 5). The matching slits in both valves narrow posteriorly and resemble somewhat the lateral invagination in both valves of *P. (P.) laticaudata*, but the latter lacks a slit. Divoted valve damage in brachiopods displays parabolic to chevron-shaped fractures which outline a roughly triangular area of resecreted shell surface that is depressed below the surface posterior and lateral to the fracture (Alexander 1986, 276, fig. 4). The divoted valve damage is least similar to the morphology of the shell damage in *P. (P.) laticaudata*. There is also an embayed type of valve damage in Ordovician brachiopods, which display a meandering or zigzag fracture that outlines a jagged piece of the valve surface that was removed and resecreted (Alexander 1986, 277, fig. 6). The latter damage has no resemblance to the shell damage in *P. (P.) laticaudata*. All shell damage listed above has resulted from failed predatory attacks by durophagous predators and differ from the shell damage in *P. (P.) laticaudata* in the presence of a fracture. Thus, it is unlikely that the shell damage in *P. (P.) laticaudata* was induced by durophagous predators. One should also explore the possibility that such shell damage could result from drilling predation. However, the studied shell damage shows no sharp boundaries characteristic of the drill holes and their elliptical to crescent-shaped outline is also alien to typical drill holes. We can also exclude spontaneous tissue damage, as the resulting shape of shell damage would have had less depth and most likely a more slit-like morphology as well. Mechanical tissue damage (e.g., temporary detachment of mantle) is also unlikely, as it would result in re-attachment of the mantle and the start of a new shell layer, which would leave sharper boundaries, different patterns in ornamentation and cross-sectional profile, and is often associated with a slit-like opening in bivalves.

Comarginal parasites

The described structures are most likely the result of interference of shell secretion and associated shell malformation caused by the presence of symbionts (compare Kinne (1983) and Mironenko (2016) for cases of modern and fossil shell-secreting molluscs), as there is no indication of shell breakage that would point to predators. Similar shell damage without shell breakage is known from Cambrian brachiopods, where

parasitic epibionts attached to the inside of the commissure produced globose callosities and V-shaped invaginations in the growing margin (Peel 2014). Deep, V-shaped invaginations occur commonly in the comarginal growth ornamentation of larger lingulate brachiopod (*Botsfordia*) specimens from the lower Cambrian of Greenland, but the overall lack of fractures transgressing growth lines indicates that these were not caused by breakage (Peel 2014, 153, fig. 3D, K, N). Similar structures are also present in *Diandongia* Rong from the Cambrian of Southwest China (Zhang et al. 2011, fig. 2C, D) and in *Botsfordia pulcher* Matthew from the middle Cambrian of New Brunswick (Walcott 1912, pl. LXII, fig. 5i). In addition to brachiopods, similar marginal invaginations occur in the operculum-like *Mobergella holsti* (Moberg) from the lower Cambrian of Sweden (Bengtson 1968, fig. 16B). The lack of shell breakage makes these structures similar to the ones in *P. (P.) laticaudata*, but the elliptical shape of the pits in the latter does not resemble the shape of the shell damage in lower Cambrian *Botsfordia* from Greenland or in other Cambrian brachiopods. Thus, the shell damage in *P. (P.) laticaudata* was likely made by a different organism than the damage in Cambrian lingulates and *Mobergella*. It is also more discrete and rarer than other malformations reported in brachiopods and attributed to disease (Zong and Gong 2022). Zhang et al. (2020a) described a drilling in a rhynchonelliform brachiopod from the Katian of Central China. Even if we cannot see inside the shell damage in *Porambonites*, it differs from drillings (e.g., Deline et al. 2003) in not being smooth (ornamentation present), in the larger size, the clear inward deflection of the shell material and the presence of the deformations on both valves.

Encrusting worm-like organisms on brachiopods have been interpreted as cleptoparasites as early as stage 4 of the Cambrian (Zhang et al. 2020b), but these interactions were much more numerous (47.79% of the 429 sampled brachiopods were encrusted). Worm-like organisms have also been implicated in various other brachiopod shell deformations or internal structures in the Palaeozoic (Chatterton 1975; Basset et al. 2004; Baliński and Sun 2010; Vinn et al. 2014), as well as in the Mesozoic (Kiel 2008) or modern brachiopods (Rodrigues 2007).

The shape and depth of the pits in *P. (P.) laticaudata* indicates that the trace maker was likely not a worm-like animal which would have needed a deeper hole, but something similar to a small sea anemone in the body plan. If the trace maker fed on small food particles in sea water, it could have benefitted from the feeding currents of the host brachiopod. Based on the ecological studies of modern brachiopods, it is now commonly accepted that brachiopods have separate inhalant and exhalant feeding currents (LaBarbera 1984). The inhalant water currents are located on both sides of the shell, and the exhalant water current is located in the central part of the shell. Thus, it is possible that the symbionts of the *P. (P.) laticaudata* benefitted from inhalant currents and were cleptoparasites, as suggested for Cambrian worm-like encrusters (Zhang et al. 2020b). The symbiont-caused damage to the host brachiopod suggests also

parasitic relationship. As the culprit remains unknown, but all points to a parasitic interaction, with support for negative effects on the afflicted individual, we assign it to category 3 (i.e., the symbiont caused definite harm to the host, but it may have also been beneficial to the host in other ways) in the sense of the De Baets et al. (2021a).

Acknowledgements

Financial support to O. Vinn was provided by a research grant from the Institute of Ecology and Earth Sciences, University of Tartu, and a Sepkoski Grant from the Paleontological Society. K. De Baets was supported by the I.3.4 Action of the Excellence Initiative – Research University Programme at the University of Warsaw, funded by the Ministry of Education and Science of Poland. U. Toom was funded by the Estonian Research Council, grant no. PUTJD1106. We are grateful to G. Baranov, Department of Geology, Tallinn University of Technology, for digital photographing of the specimen. This paper is a contribution to the IGCP Project 735 ‘Rocks and the Rise of Ordovician Life’. We are grateful to journal reviewers Zhongyang Chen and Oive Tinn for constructive comments on the manuscript. The publication costs of this article were partially covered by the Estonian Academy of Sciences.

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