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Syn vivo encrustation of *Porambonites* Pander, 1830 (Brachiopoda) by craniid brachiopods in the Late Ordovician of Estonia

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ABSTRACT:

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Two new brachiopod–brachiopod symbiotic overgrowths have been discovered from the Kukruse Regional Stage (Sandbian, Ordovician) of Estonia. Both the *Philhedra rivulosa*–*Porambonites* sp. and the *Petrocrania* sp.–*Porambonites* sp. overgrowths were beneficial to the encrusting craniid and might have been slightly harmful to the host brachiopod. The craniids could have been facultative kleptoparasites. Our data show that craniids significantly preferred the smooth shells of *Porambonites* sp. over the coarsely ribbed shells of *Platystrophia* sp. and the moderately ribbed shells of *Cyrtonotella* sp. and *Glossorthis* sp. This suggests that, at least against craniids, having strong ribs could have been a successful antifouling strategy.

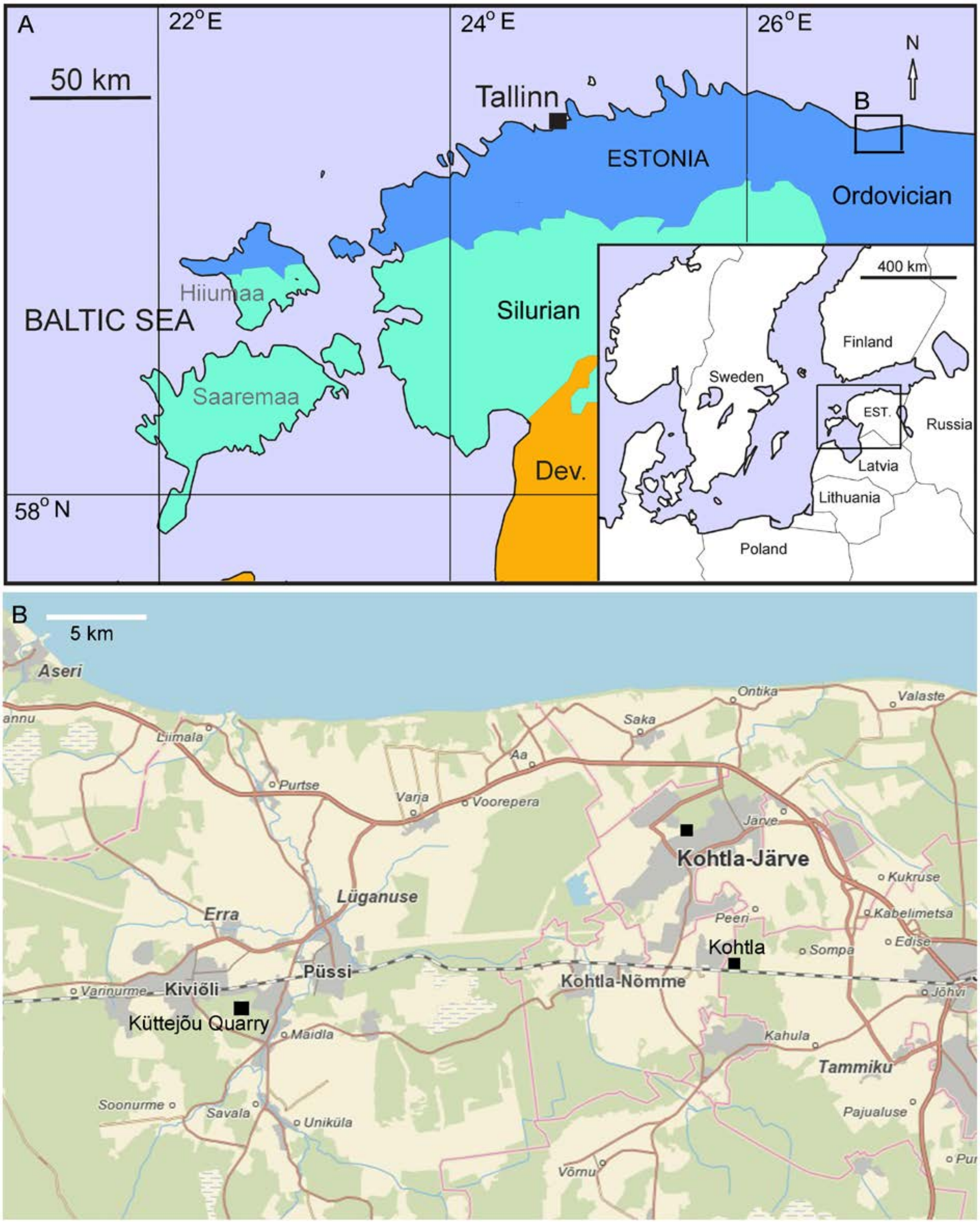
Key words: Symbiosis; Brachiopods; Epibionts; Encrustation; Sandbian; Baltica.

INTRODUCTION

Hard substrates are often associated with various sclerobionts, i.e., organisms that live on, bore into, or otherwise form close associations with hard substrates, often using other organisms as these substrates (Taylor and Wilson 2002). The most commonly studied hosts for sclerobionts are typically stationary suspension feeders like brachiopods, pteriomorph bivalves, and hyolithids (Galle and Parsley 2005; Barclay *et al.* 2013; Freeman Peters *et al.* 2024). However, mobile organisms, including echinoids, trilobites, and cephalopods, could also serve as hosts for sclerobionts (Baird *et al.* 1989; Brandt 1996; Taylor and Brett 1996; Schneider 2003).

Sclerobionts offer a unique opportunity for conducting ecological studies using the fossil record, as the communities they form are often preserved *in situ* and can reflect a complete ecological snapshot (Freeman Peters *et al.* 2024). Each host, from the perspective of encrusting organisms, acts as a patch or 'island', allowing individual sclerobiont assemblages on a single host to be analysed as a community (Brett 1988). Many sclerobiont taxa are thought to have originated during the Ordovician (Lescinsky 1996; Ma *et al.* 2021), so understanding their evolutionary patterns and ecological distribution during this period is critical (Freeman Peters *et al.* 2024).

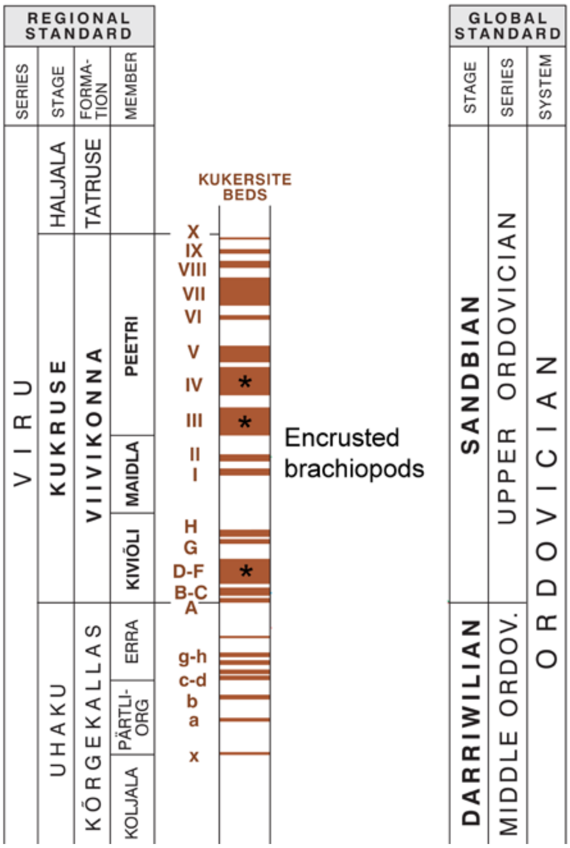
Sclerobionts often colonize other organisms during their life. Such *syn vivo* interactions are especially important for understanding the evolution of symbiotic interactions between organisms. Symbiosis refers to any close and long-term biological interaction between two different species, encompassing mutualistic, commensalistic, or parasitic relationships. Modern ecology and biology textbooks generally adhere to the 'De Bary' definition (De Bary 1879) or even broader interpretations, where all long-term interspecific bio-



Text-fig. 1. Position of the fossil localities on a general geological map of Estonia (A) and a high-resolution map (B, black squares).

logical interactions fall under the term symbiosis. The narrower definition, in which symbiosis only indicates mutualism, has largely fallen out of favour (Martin and Schwab 2013). Symbiotic interactions have likely played an important role in the evolution of organisms since the Cambrian period (Vinn 2017). Recently, De Baets *et al.* (2021) have analysed the evolution of parasitic associations, whereas the symbiotic associations of early Palaeozoic brachiopods were recently summarized by Vinn *et al.* (2023). Nevertheless, numerous symbiotic associations have still to be discovered. The preserved symbiotic associations offer a snapshot of past marine life, allowing scientists to reconstruct the ecological frameworks of ancient seas. By analysing these fossilized relationships, researchers can infer the living conditions, behaviours, and interactions of organisms that thrived hundreds of millions of years ago. Such reconstructions are vital for understanding the historical biodiversity and the factors that influenced the distribution and abundance of marine species during the Ordovician Period. Studying these ancient symbiotic relationships can inform modern biological and ecological theories. The concept of symbiosis, encompassing mutualism, commensalism, and parasitism, is fundamental in contemporary ecology. Observing how these interactions played out in the distant past provides a long-term perspective on the stability and evolution of symbiotic relationships.

The aim of the current paper is to: (1) describe two new brachiopod–brachiopod associations, and (2) analyse the palaeoecology of these associations.



Text-fig. 2. Stratigraphy of the Kukruse Regional Stage (after Bauert and Nõlvak 2014, fig. 2, modified). The asterisks denote the stratigraphic position of the encrusted brachiopods.

GEOLOGICAL BACKGROUND

The Ordovician limestone exposures in Estonia form a wide belt that stretches from Narva River in the northeast to Hiiumaa Island in the west (Mõtus and Hints 2007; Text-fig. 1). The total thickness of the Ordovician varies, from about 70 m in northern Estonia up to 180 m in southern Estonia (Mõtus and Hints 2007). During the Sandbian, the western part of the East-European Platform was covered by a shallow epicontinental sea with little variation in bathymetry. The Ordovician basin in Estonia had an extremely low sedimentation rate (Mõtus and Hints 2007). Across the entire carbonate platform, a series of grey calcareous-argillaceous sediments accumulated, now forming argillaceous limestones and marls. There was a tendency for increasing clay content as the sediments were deposited further offshore (Nestor and Einasto 1997). During the Ordovician, the Baltica palaeocontinent moved from a temperate climatic zone to a subtropical realm (Nestor and Einasto 1997; Torsvik and Cocks 2013). The Sandbian in Estonia is characterized by temperate carbonates (Toom *et al.* 2019). The Kukruse Regional Stage (Text-fig. 2) is notable for its alternating layers of limestone and oil shale (kukersite) deposited on a carbonate platform in normal marine conditions. The thickness and distribution of these layers varied, reflecting the geological and environmental conditions at the time of deposition.

MATERIAL AND METHODS

A collection of brachiopods from the Kukruse Regional Stage at the Natural History Museum, University of Tartu, was searched for *syn vivo* encrusters (see Table 1 for full list of analysed specimens). A single specimen of *Porambonites* sp. from Kohtla (TUG 1766-453) and a single specimen of *Porambonites* sp. from Kohtla-Järve (TUG 72-593)

Specimen number	Substrate	Encruster (number)	Locality
TUG 72-593-4	*Porambonites* sp.	*Philhedra rivulosa* (Kutorga, 1846) (3) dorsal/**symbiotic** (1)	Kohtla-Järve
TUG 72-589-3	*Porambonites baueri* Noetling, 1883	*Philhedra rivulosa* (Kutorga, 1846) (1) ventral	Kohtla-Järve
TUG 1766-453	*Porambonites* sp.	*Petrocrania* sp. (1) dorsal/**symbiotic**	Kohtla
TUG 72-590-1	*Porambonites* sp.	*Petrocrania* sp. (1) ventral	Kohtla-Järve
TUG 1766-464	*Porambonites* sp.	*Petrocrania* sp. (1) ventral	Kohtla-Järve
TUG 1766-396	*Porambonites* sp.	*Petrocrania* sp. (3) ventral	Kohtla-Järve
TUG 58-60-2	*Porambonites* sp.	*Petrocrania* sp. (1) ventral	Küttejõu Quarry
TUG 1766-461	*Porambonites* sp.	*Petrocrania* sp. (1) ventral	Kohtla-Järve
TUG 1766-465	*Porambonites* sp.	*Petrocrania* sp. (1) ventral	Kohtla-Järve

Table 1. List of specimens of *Porambonites* spp. encrusted with craniids from the Kukruse Regional Stage of Estonia.

showed possible *syn vivo* encrusters. The encrusted brachiopods were cleaned with the help of brushes or a needle. The specimens were digitally photographed in an uncoated state with a CANON EOS R6 camera. The measures were digitally obtained from calibrated photographs. An online Z Score Calculator for 2 Population Proportions was used to estimate the encrustation preferences of craniids. The encrusted brachiopods are deposited at the Natural History Museum, University of Tartu (TUG).

RESULTS

Philhedra rivulosa (Kutorga, 1846) encrusts both ventral (two valves) and dorsal (single valve with three specimens) valves in *Porambonites* sp. They do not show any preference for attaching to any particular part of the dorsal or ventral valves. A maximum of three specimens of *P. rivulosa* are attached to a single valve of *Porambonites* sp. A single specimen of *P. rivulosa* (TUG 2-593-2) is attached to the lateral part of the dorsal valve near the anterior commissure so that its one side is aligned with the anterior commissure of *Porambonites* sp. (Text-fig. 3A). The growth lines of *P. rivulosa* are not curved but straight at the side of the anterior commissure of *Porambonites* sp., whereas on the opposite side, they are concentrically curved. A single *P. rivulosa* is located within the ventral sulcus of *Porambonites baueri* Noetling, 1883 (TUG 72-589-3) and has a slightly deformed shape that corresponds to the shape of the sulcus (Text-fig. 3B).

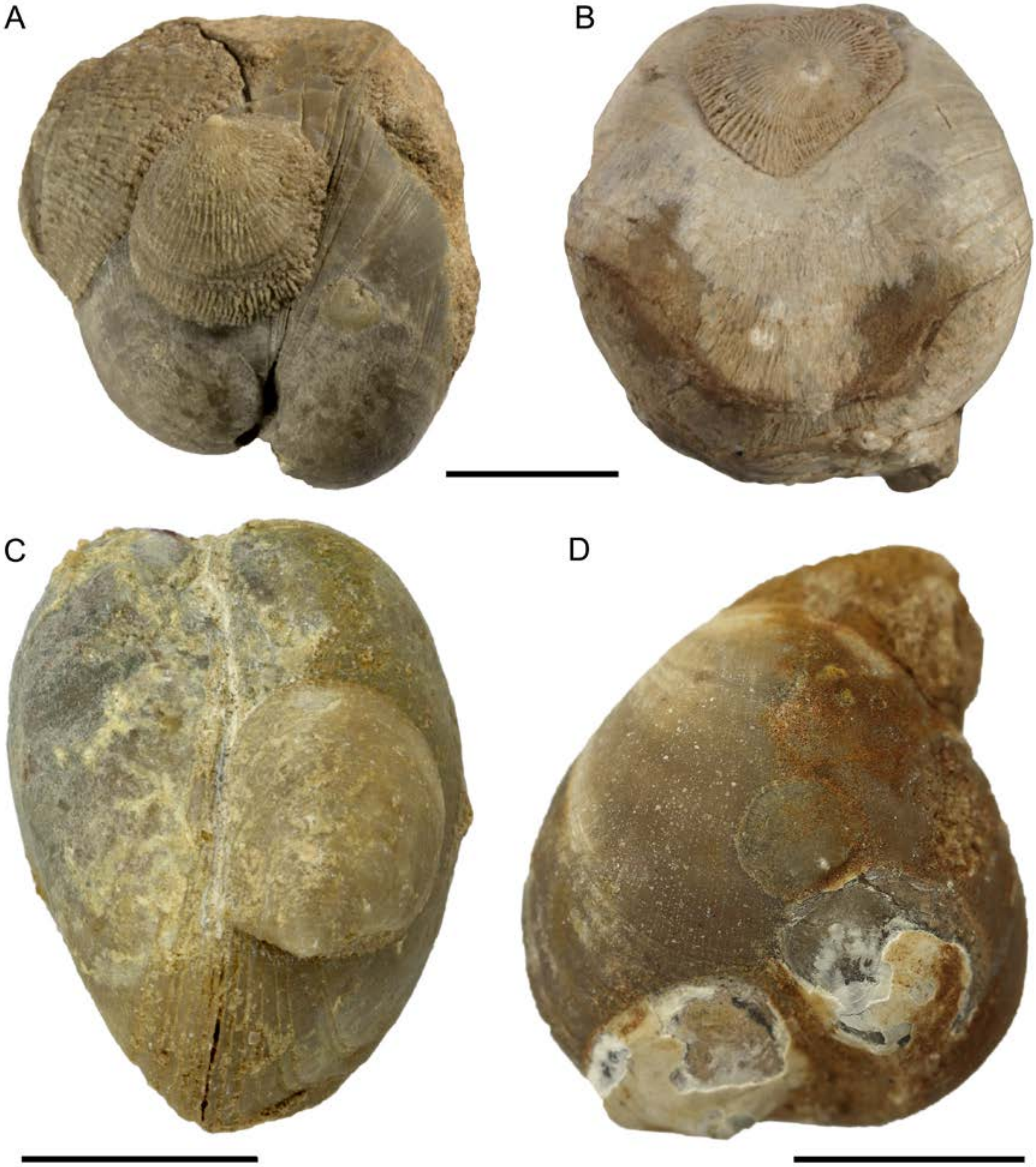
Petrocrania sp. specimens occur on both dorsal (N = 1) and ventral valves (N = 5) of *Porambonites* sp. They do not show any preference for attaching to any particular part of the dorsal and ventral valves (Text-fig. 3C, D). There are a maximum of three specimens of *Petrocrania* sp. attached to a single valve of *Porambonites* sp. (TUG 1766-396; Text-fig. 3D). A single specimen of *Petrocrania* sp. (TUG 1766-453) is attached to the lateral part of the dorsal valve near the anterior commissure so that its one side is aligned with the anterior commissure of *Porambonites* sp. (Text-fig. 3C). The growth lines of *Petrocrania* Raymond, 1911 are not curved but straight on the side of the anterior commissure of *Porambonites* sp., whereas they are more curved on the opposite side.

Specimens representing four brachiopod genera were studied. Craniids occur only on the smooth shells of *Porambonites* Pander, 1830 (36 shells/9 encrusted shells). Coarsely ribbed *Platystrophia* King, 1850 (21/0), moderately ribbed *Cyrtonotella* Schuchert and Cooper, 1932 (39/0) and *Glossorthis* Öpik, 1930 (19/0) were not encrusted by craniids. Z Score Calculator for 2 Population Proportions found that craniids significantly preferred smooth shelled *Porambonites* (36/9) over ribbed brachiopods (79/0). The value of z is 4.6289. The value of p is < .00001. The result is significant at p < .05.

DISCUSSION

Relief of the substrate

Richards (1972) found that the Richmondian craniids, *Philhedra* Koken, 1889 and *Petrocrania*, seem to have had similar habits to *Crania* Retzius, 1781. Both of these taxa preferably encrusted the smooth shells typical of many brachiopods in the Late Ordovician of Indiana and Ohio (Richards 1972). However, sometimes, they were also found on shells with pronounced ribs (Richards 1972). Out of several hundred craniids examined by Richards (1972), only two were found on shells with coarse ribs [*Philhedra* on *Platystrophia clarksvillensis* Foerste, 1910, and *Petrocrania* on *Rhynchotrema dentatum* (Hall, 1847)], and just six were found on shells with fine ribs (*Petrocrania* on *Hebertella* sp.). Similarly, Alexander and Scharpf (1990) found that *Petrocrania scabiosa* (Hall, 1866) might have preferred attaching to smoother surfaces in the Late Ordovician of



Text-fig. 3. Encrusting craniids on *Porambonites* sp. from the Kukruse Regional Stage (Sandbian, Ordovician) of northern Estonia. A – *Philhedra rivulosa* (Kutorga, 1846) attached to dorsal valve near the commissure of *Porambonites* sp. inferring a symbiotic relationship (TUG 72-593-2). B – *Philhedra rivulosa* (Kutorga, 1846) attached to the ventral sulcus of *Porambonites baueri* Noetling, 1883 (TUG 72-589-3). C – *Petrocrania* sp. attached to the lateral part of the dorsal valve near the anterior commissure of *Porambonites* sp. inferring a symbiotic relationship (TUG 1766-453). D – Three specimens of *Petrocrania* sp. attached to the ventral valve of *Porambonites* sp. (TUG 1766-396). Scale bars equal 1 cm.

Laurentia, as these would make their characteristic concentric growth easier. Our data confirm these findings and show that indeed craniids (*Philhedra* and *Petrocrania*) significantly preferred the smooth shells of *Porambonites* over the coarsely ribbed shells of *Platystrophia* and the moderately ribbed shells of *Cyrtonotella* and *Glossorthis*. This suggests that, at least for craniids, having strong ribs was a successful antifouling strategy. Our data also show that with regard to the surface of the substrate, the craniids in the Late Ordovician of Laurentia and Baltica had a similar encrustation strategy.

Philhedra rivulosa–Porambonites sp. overgrowth

Philhedra rivulosa likely encrusted *Porambonites* during its life, as indicated by the position of the sclerobiont at the edge of the anterior commissure of the host (Text-fig. 3A). The deformation of growth lines also suggests that the encrusting *P. rivulosa* tried to inhibit its growth in order to avoid growing over the host's anterior commissure. Growing over the anterior commissure would have prevented the host shell from opening for filter feeding and so would have killed its host. It is not sure whether the aberrant growth was the result of the movement of host shell valves or whether *P. rivulosa* avoided creating problems for its host. The position of *P. rivulosa* at the host's inhalant currents suggests (LaBarbera 1984) that the craniid could have taken advantage of the host's feeding currents. Thus, it is possible that this *P. rivulosa* specimen presumably acted as a kleptoparasite (Zhang *et al.* 2020). Kleptoparasitism is broadly known from the Palaeozoic brachiopod associations (Zatoń and Borszcz 2012; Musabelliu and Zatoń 2018; Zatoń *et al.* 2022). Situations where the encruster appears to depend on the food-rich water currents generated by a brachiopod's lophophore, as in this case, are referred to as 'scramble' competition (Zapalski 2005). Instances of encrusters growing towards the brachiopod's commissure are common and well-documented, such as in auloporid tabulates (Alvarez and Taylor 1987; Zapalski 2005). In case of *Philhedra rivulosa–Porambonites* sp., both the encruster and its host are filter-feeding brachiopods, making the feeding competition between them extremely likely. However, the other *P. rivulosa* specimens had different positions on the host, even within the ventral sulcus (i.e., location of exhalant currents), and if they were all encrusting living hosts it is likely that they did it not for exploiting the feeding currents but simply for the need for the suitable hard substrate. In addition to possible stealing of food, the encrusting *P. rivulosa* specimens would have negatively influenced their host by putting extra weight on its shell. Only a small fraction of *Porambonites* sp. shells were encrusted by *P. rivulosa*, which indicates that this association was clearly facultative for the *Porambonites* individuals.

Petrocrania sp.*–Porambonites* sp. overgrowth

A specimen of *Petrocrania* sp. encrusted the shell of *Porambonites* sp. during the latter's lifetime, based on the sclerobiont's location near the commissure of the host (Text-fig. 3C). The deformation in the host's shell side close to the host commissure suggests that the encrusting *Petrocrania* altered its growth pattern to avoid extending over the host's commissure, which could have prevented the shell from opening for filter feeding and, ultimately, killed the host. It remains unclear whether this atypical growth was due to the host's shell valves moving or if *Petrocrania* deliberately avoided causing harm to its host. The placement of *Petrocrania* near the host's inhalant currents (LaBarbera 1984) suggests that the craniid might have benefited from the host's feeding currents, raising the possibility that it acted as a kleptoparasite (Zhang *et al.* 2020). Given that both the encruster and its host are filter-feeding brachiopods, there is a strong likelihood of feeding competition between them. On the other hand, other *Petrocrania* sp. specimens were found in different positions on the host shell. If these sclerobionts also encrusted living hosts, they might have been attracted simply by the need for a suitable hard substrate rather than exploiting the feeding currents. Besides potential food theft, encrusting *P. rivulosa* specimens could have added extra weight to the host's shell, further affecting it. Only a fraction of *Porambonites* sp. shells were encrusted by *Petrocrania* sp., indicating that this association was clearly facultative for *Porambonites* sp. and not a necessary relationship.

Early brachiopod–brachiopod associations

Brachiopod–brachiopod associations are uncommon in the early Palaeozoic (Vinn *et al.* 2023). The earliest example of such an association dates back to the early Cambrian, where the brachiopod *Diandongia pista* Rong, 1974 served as a host for another brachiopod, *Longtancunella chengjiangensis* Hou, Bergström, Wang, Feng and Chen, 1999, providing a hard substrate for attachment (Vinn 2017). This interaction, discovered in a Cambrian Lagerstätte in South China (Hou *et al.* 1999; Zhang *et al.* 2010), has limited preservation potential, and its exact nature – whether mutualistic, commensalistic, or parasitic – remains unknown (Vinn *et al.* 2023). Another association involving brachiopods is the *Nisusia–Nisusia* interaction from the Miaolingian in Utah (Holmer *et al.* 2018). Late Ordovician specimens of *Petrocrania scabiosa* were found encrusting the shells of *Rafinesquina alternata* Conrad, 1838 (Alexander and Scharpf 1990). This symbiont likely benefited from the hard substrate provided by its host and might have also taken advantage of the feeding currents of *Rafinesquina* (Vinn *et al.* 2023). Similarly, in the Wenlock of Gotland, craniids have been observed encrusting the strophomenid *Leptaenoidea rugata* (Lindström, 1861) (Hoel 2007), again benefiting from the solid attachment surface

(Vinn *et al.* 2023). The craniid-strophomenid and craniid-rhynchonellate associations have a better preservation potential compared to earlier examples, providing valuable insights into these interactions and their ecological implications (Vinn *et al.* 2023). The brachiopod–brachiopod associations typically involve one species providing a hard substrate while the other might benefit from the host's feeding currents or other ecological factors (Vinn *et al.* 2023). Our data identify the first brachiopod–brachiopod symbiosis from the Ordovician of Baltica. The finding of a symbiotic overgrowth involving craniids from Baltica suggests that the brachiopod symbiosis was similar to that of Laurentia. This is not surprising considering these regions palaeogeographic proximity and similarity in latitude. By preferentially encrusting the smooth shells of *Porambonites* sp. over the ribbed shells of other brachiopods, these craniids may have influenced the evolutionary paths of their hosts. Such interactions likely exerted selective pressures, driving the evolution of shell morphology as a defensive adaptation against encrustation.

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