

CRYPTIC ENCRUSTING FAUNA INSIDE INVERTEBRATE FOSSILS FROM THE ORDOVICIAN OF ESTONIA

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Abstract: This is the first report of encrusted cryptic surfaces in the Ordovician of Estonia. Only bryozoans and cornulitids occurred in nautiloids and trilobites. Bryozoans were the dominant encrusters, in terms of both the number of specimens and the encrustation area. Stalked echinoderms are common on the hardgrounds in the Middle and Upper Ordovician of Baltica, but the restricted space in nautiloid living chambers and trilobites probably prevented colonization by stalked echinoderms. Cryptic surfaces in nautiloids and trilobites usually are somewhat more encrusted than the open surfaces of hardgrounds in the Ordovician of Estonia. Encrusters presumably favoured cryptic surfaces, as these were less accessible for predators and grazers. Low encrustation densities, compared to North American hard substrates, seem to be characteristic for the Ordovician Baltic Basin.

Key words: Encrustation, bryozoans, trilobites, cornulitids, cryptic fauna, Ordovician, Baltica.

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INTRODUCTION

Nautiloids and trilobites are among the major groups in the middle- and low-latitude, shallow-marine environments in the Ordovician. Their cryptic surfaces provided a unique niche, where environmental conditions differed from those of the exposed surfaces. These partially or totally dark habitats enabled only reduced photosynthesis and were less exposed to water dynamics and sedimentation than open surfaces (Kobluk, 1988). In the Early Palaeozoic, cryptic biotas diversified considerably at the species and higher taxonomic levels (Segars and Liddell, 1988). In general, Ordovician hard-substrate communities are primarily dominated by bryozoans and echinoderms. Accordingly, typical Ordovician cryptic biotas are dominated by bryozoans (Taylor and Wilson, 2003). There are some similarities at the phylum level between modern and Ordovician cryptic biotas, mostly restricted to the important role of bryozoans and to the presence of zonation, with diversity and percent coverage decreasing significantly from the outer edge to the interior of the cryptic surface (Segars and Liddell, 1988; Wilson, 1998). Cryptic biotas of the Phanerozoic are relatively well known (Spjeldnaes, 1975; Kobluk, 1980, 1981, 1988; Wil-

son, 1986, 1998; Segars and Liddell, 1988; Taylor and Wilson, 2003; Zatoń *et al.*, 2018), but no previous studies exist for the Ordovician of Baltica.

The aims of this paper are (1) to report, for the first time, a cryptic hard-substrate community from the Ordovician of Baltica and (2) to determine whether this community is typical for the Ordovician of Baltica and beyond.

MATERIAL AND METHODS

A large collection of nautiloids (933 specimens, approximately 80% of specimens exposing cryptic surfaces) and trilobites (1600 specimens, approximately 13% of specimens exposing cryptic surfaces) from the Ordovician of Estonia was examined for the presence of cryptic encrusters and borings. The area of each cryptic surface was overlain with a fine grid. The approximate percentage of the area covered by encrustation was found by counting the squares of the grid. The cryptic surfaces were digitally photographed, using a Canon EOS 5DsR camera and the apochromatic zoom system Leica Z16 APO. The specimens studied are depos-

ited at the Natural History Museum, University of Tartu (TUG), and the Department of Geology, Tallinn University of Technology (GIT).

GEOLOGICAL BACKGROUND

The Ordovician limestones of Estonia are exposed in a wide belt from the Narva River in the northeast to Hiiu Island in the northwest (Nestor and Einasto, 1997). The total thickness of the Ordovician strata in Estonia varies from 70 to 180 m (Nestor and Einasto, 1997). In the Middle and Late Ordovician, the western part of the East European Platform was covered by a shallow, epicontinental sea. The Middle and Late Ordovician basin had weak bathymetric differentiation in Estonia, with a trend in sedimentation of decreasing proportions of bioclasts and increasing clay content in an offshore direction (Nestor and Einasto, 1997). Drifting Baltica reached the subtropical realm by the Late Ordovician (Nestor and Einasto, 1997; Torsvik and Cocks, 2013). The Late Ordovician climatic change resulted in an increase in carbonate production and sedimentation rate in the Baltic Basin. During the Late Ordovician, the first reefs associated with a warm climate appeared (Nestor and Einasto, 1997).

RESULTS

A large collection of nautiloids and trilobites revealed only a few specimens with a cryptic fauna (Tables 1, 2). Only two groups, bryozoans and cornulitids, encrusted cryptic surfaces in the Ordovician of Estonia (Figs 1, 2). Seventeen sheet-like bryozoan colonies and four cornulitids were found on the internal surfaces of trilobite pygidia and cranidia (Fig. 1B). The present authors expected these surfaces to be cryptic, because they were surrounded both dorsally and ventrally by cuticle. Twenty sheet-like bryozoans and a single cornulitid were found attached to internal surfaces of nautiloid living chambers (Fig. 1A, C–E). Bryozoans were the dominant encrusters, in terms of both the number of specimens and encrustation area. The cryptic surfaces in trilobites (0.2–2.9% of the area) seem to be usually less encrusted than those of nautiloids (2.3–5.5% of the area) in the Ordovician of Estonia. The maximal encrustation density of cryptic surfaces in trilobites (57%) and nautiloids (48.8%) is high to similar extents. There is no clear stratigraphic trend in the encrustation density or the number of encrusting specimens in the Ordovician of Estonia.

In nautiloids, bryozoan colonies are smaller than the ceramoporids known from Baltica, being 3–5 mm in diameter, compared with expansions of several centimetres in colonies from exposed biotopes. All of the bryozoans in nautiloid shells are sheet-like (Fig. 1). The most common form has a circular base. Some larger colonies have lateral outgrowths with semicircular bases.

In trilobites, small cryptic bryozoans encrust the internal surfaces of pygidia and cranidia in the Ordovician of Estonia. They are smaller than the ceramoporids, known from Baltica. All bryozoans in trilobites are sheet-like colonies (Fig. 2). The most common form has a circular base. The earliest bryozoans encrusting trilobites occur in the Kunda Regional Stage.

DISCUSSION

Cryptic community

Ordovician cryptic encrusting and boring communities have been well studied. They are often associated with cavities in bryozoan reefs (Cuffey, 1974; Kobluk, 1980, 1981) and underneath hardground ledges (Brett and Liddell, 1978). Taylor and Wilson (2003) found that these cavities are considerably larger than their Cambrian counterparts and in many cases they appear to have remained open for relatively long periods. A cryptic fauna is relatively rare in the trilobites and nautiloids of the Ordovician of Estonia. In the Ordovician of Estonia, cryptic surfaces were inhabited by two groups of encrusters (bryozoans and cornulitids) and *Arachnostega* trace makers (possible polychaetes; Vinn *et al.*, 2014). The Ordovician of Estonia is characterized by a rich and diverse fauna of invertebrates (Raukas and Teedumäe, 1997). It seems that the cryptic life mode was suitable for only a few invertebrate groups in the Ordovician of Baltica and that bryozoans were better suited to cryptic life than were cornulitids. The cryptic habitats studied had relatively restricted space, which probably prevented colonization by larger invertebrates, such as many brachiopods. In the Ordovician, cryptic encrusters include numerous bryozoans, stalked echinoderms and calcareous algae (Taylor and Wilson, 2003). The latter could grow only near the openings of cryptic spaces, where some light was still available. Many cavities also housed *Trypanites* trace makers (worm-like boring organisms; Taylor and Wilson, 2003). Taylor and Wilson (*op. cit.*) found that the Ordovician cryptic communities are remarkably similar to those found on the adjacent, exposed hard substrates and there was only a weak polarity between these environments. Calcareous algae have not been described from the hard substrates of the Ordovician of Estonia. However, stalked echinoderms are common on hardgrounds in the Middle and Upper Ordovician of Baltica (Vinn and Toom, 2015; Rozhnov, 2017). The boring *Trypanites* occurs in hardgrounds, brachiopod shells (Vinn, 2005), bryozoans (Wyse Jackson and Key, 2007), rugose corals and stromatoporoids in the Ordovician of Estonia. Interestingly, the two latter groups are lacking in the nautiloids and trilobites studied. Possibly, restricted space did not allow normal development for stalked echinoderms. *Trypanites* is missing, presumably owing to the very small substrate thickness, which did not provide enough space for making a boring.

Detailed study of bryozoans in cryptic habitats has proved difficult, because they are mainly visible from the base, where they were attached to the substrate. These species share common features, apparently linked to the specific environment. Firstly, all these bryozoans produce colonies in the form of unilaminar sheets, mainly with a rounded shape. Secondly, these bryozoans (mainly cystoporates, but a few trepostomes) have uniformly small autozoecia. The measured aperture width show ranges of 0.11–0.15 mm, 0.12–0.18 mm, 0.17–0.21 mm, and 0.18–0.23 mm in the samples studied. Comparable ceramoporid species (the genus *Crepipora* with unilaminar, encrusting colonies) from the Ordovician of Baltic region have much larger aper-

tures: 0.39–0.59 mm (*Crepipora lunatifera* Bassler, 1911), 0.17–0.37 mm (*C. schmidti* Bassler, 1911), 0.35–0.51 mm (*C. schmidti* Bassler, 1911), or even 0.58–0.88 mm (*C. magna* Pushkin, 1990).

This clear division in the aperture size shows that bryozoans from cryptic habitats were apparently adapted to narrow spaces, in which long and large lophophores were useless or even hindering. On exposed sites, bryozoans could benefit from larger lophophores and subsequently grew faster than species with smaller lophophores. Differences in the lophophore size could be crucial for ecological success (compare Lidgard *et al.*, 1993). The clear absence of species with

small apertures from the published literature on the Baltic bryozoans can be explained by the fact that such habitats were neglected by researchers.

Encrustation densit

Cryptic surfaces in nautiloids (2.3–5.5% of the area) and trilobites (0.2–2.9% of the area) are usually somewhat more encrusted than the open surfaces of hardgrounds in the Ordovician of Estonia (0.02–1.3% of total hardground area; Vinn, 2015; Vinn and Toom, 2015). This may indicate the presence of some polarity in the encrustation den-

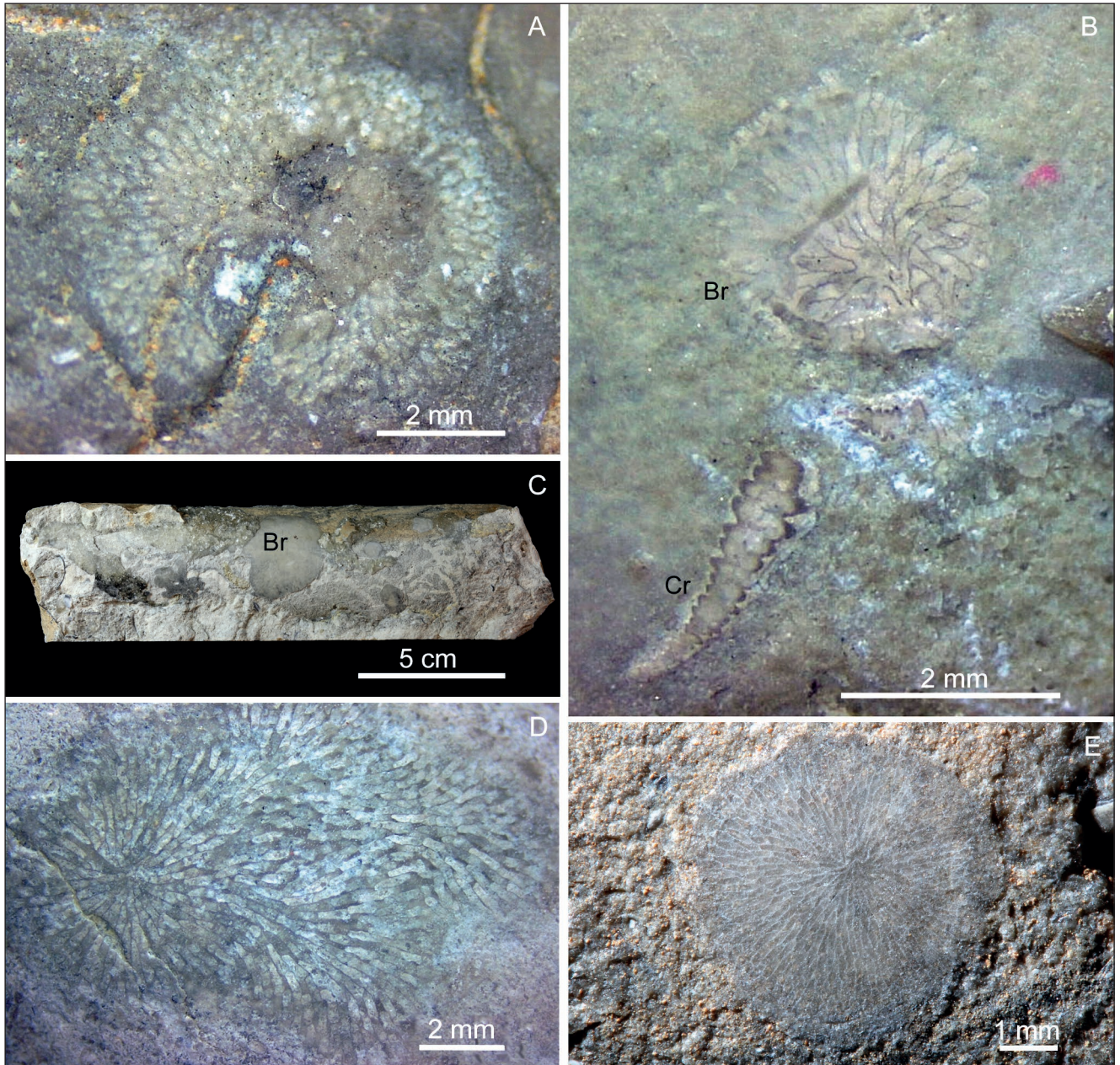


Fig. 1. Encrusters occupying the cryptic habitats. **A.** Bryozoan in nautiloid living chamber from Anija, northern Estonia; Haljala Regional Stage (Sandbian), TUG 46-244. **B.** Cornulitid (Cr) and bryozoan (Br) on inner surface of illeanid cranidium from Lasnamägi, northern Estonia; Lasnamägi Regional Stage (Darriwilian), TUG 2-690. **C.** Bryozoans (Br) in nautiloid living chamber from Kohta-Nõmme, northern Estonia; Kukruse Regional Stage (Sandbian), GIT 343-298. **D.** Bryozoans in nautiloid living chamber from Kohta-Nõmme, northern Estonia; Kukruse Regional Stage (Sandbian), GIT 343-298. **E.** Bryozoan in nautiloid living chamber from Ilumäe, northern Estonia; Lasnamägi Regional Stage (Darriwilian), TUG 94-1.

Table 1

Cryptic fauna in nautiloids from the Ordovician of Estonia

Specimen number	Locality/rock	Regional Stage (international stage)	Bryozoans number (encrustation area %)	Cornulitids number (encrustation area %)	Total encrustation area %
TUG 1355-248	Saxby, NW Estonia/Limestone	Vormsi (Katian)	2 (1.0)	–	1.0
TUG 665-57	Paope Quarry/Limestone	Vormsi (Katian)	2 (0.2)	–	0.2
TUG 1355-149	Paluküla, Hiiumaa Island/Limestone	Vormsi (Katian)	1 (57.0)	–	57.0
GIT 343-301	Vanaküla Quarry, NE Estonia/Oil shale	Kukuruse (Sandbian)	4 (2.9)	–	2.9
GIT 360-135	NE Estonia/Oil shale	Kukuruse (Sandbian)	1 (0.7)	–	0.7
TUG 1355-247	Ontika Quarry, NE Estonia/Limestone	Lasnamäe (Darriwilian)	1 (1.7)	1 (0.6)	2.3
TUG 2-690	Lasnamägi/Limestone	Lasnamäe (Darriwilian)	2 (0.6)	3 (0.6)	1.2
TUG 1355-252	Kadaka/Limestone	Kunda (Darriwilian)	4 (1.6)	–	1.6

Table 2

Cryptic fauna in trilobites from the Ordovician of Estonia

Specimen number	Locality/rock	Regional stage (International stage)	Bryozoans number (encrustation area %)	Cornulitids number (encrustation area %)	Total encrustation area %
TUG 939-59	Hosholm, Vormsi Island/Limestone	Pirgu (Katian)	2 (4.2)	–	4.2
TUG 663-8	Männiku, northern Estonia/Limestone	Haljala (Sandbian)	5 (48.7)	1 (0.1)	48.8
TUG 46-244	Anija/Limestone	Haljala (Sandbian)	1 (2.3)	–	2.3
GIT 343-298	Kohtla-Nõmme, NE Estonia/Oil shale	Kukuruse (Sandbian)	5 (5.4)	–	5.4
TUG 1693-34	Kunda-Aru Quarry/Limestone	Lasnamäe (Darriwilian)	3 (4.6)	–	4.6
TUG 94-1	Ilumäe Quarry/Limestone	Lasnamäe (Darriwilian)	4 (5.5)	–	5.5

sity between open and cryptic surfaces in the Ordovician of Estonia. Encrusters may have favoured cryptic surfaces, as these were less accessible for predators and grazers. Cryptic surfaces in trilobites were usually less encrusted than the living chambers of nautiloids. This can be explained by the larger cavity volume in nautiloids, which enabled a greater influx of food.

Unfortunately, the cryptic faunas of North American nautiloids and trilobites have not been described. However, Brett and Liddell (1978) described a densely encrusted (31%) cryptic surface in a hardground from the Ordovician of North America. Trilobites and nautiloids from the Ordovician of Estonia usually show relatively low encrustation densities, compared to the latter hardground. However, exceptional specimens show even higher encrustation densities than those described for the cryptic hardground surfaces from the Ordovician of North America. Generally low encrustation densities seem to be character-

istic for the Ordovician Baltic Basin (Vinn, 2015; Vinn and Toom, 2015). This could represent a palaeobiogeographic difference, caused by a slightly colder climate in Baltica during the Darriwilian and Sandbian and possibly by differences in faunal composition and sedimentation (Dronov and Rozhnov, 2008; Vinn and Toom, 2015). It can also be explained by low nutrient levels in the local sea water of Baltic Basin (low productivity, e.g., Lescinsky *et al.*, 2002; Wilson *et al.*, 2015; Zatoń *et al.*, 2015) or by a large area of cryptic surfaces being occupied by soft-bodied organisms in the community, which did not preserve as fossils. However, most likely, there were high nutrient levels in the Baltic Basin, as indicated by intense bioerosion and great diversity of the boring ichnotaxa. Low skeletal coverage may also indicate a short exposure time of the cryptic surfaces (Lescinsky *et al.*, 2002), although this seems unlikely, considering the relatively low sedimentation rates in the Baltic Basin (Jaanusson, 1973; Raukas and Teedumäe, 1997).

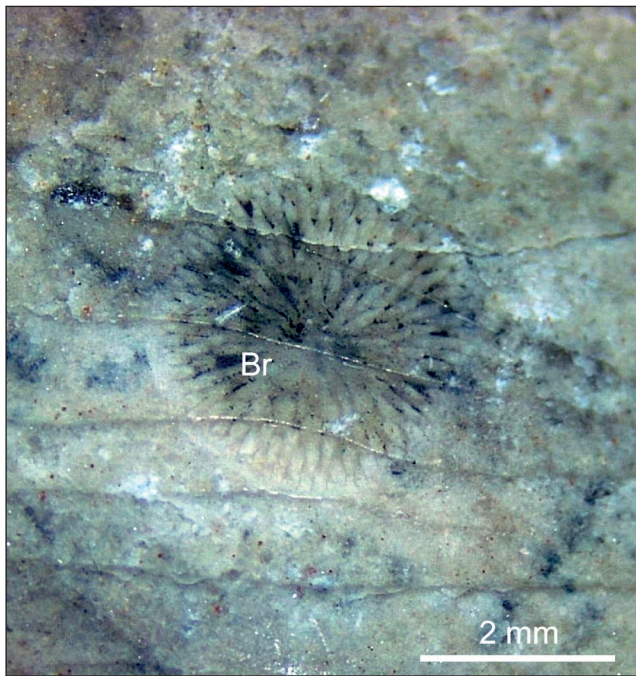


Fig. 2. Bryozoan on the internal surface of illaenid pygidium from Paope, NW Estonia, Vormsi Regional Stage (Katian), TUG 665-57.

A bryozoan-dominated fauna that inhabited small caves underneath a carbonate hardground has been described from the Corryville Formation (Upper Ordovician, Katian) in the USA (Buttler and Wilson, 2018). This fauna supports the hypothesis that early cave-dwelling organisms were little differentiated from their exposed counterparts (Buttler and Wilson, 2018). The results of the present study do not refute the hypothesis mentioned above.

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