The earliest cornulitid on the internal surface of the illaenid pygidium from the Middle Ordovician of Estonia

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Abstract. The earliest cornulitid *Cornulites* sp. appears in the Darriwilian (Lasnamägi Regional Stage) of Estonia. Internal annulation is present in all Middle Ordovician cornulitids and could be a plesiomorphic character for the group. The encrusted trilobites are rare in the Ordovician of Estonia. Illaenid pygidia and cranidia were encrusted by cornulitids and trepostome bryozoans. The encrustation of both Middle Ordovician and Late Ordovician trilobites took place post mortem. The studied hard substrate communities of Middle Ordovician and Late Ordovician trilobite pygidia and cranidia are typical of the Ordovician.

Key words: trilobites, encrustation, tentaculitoids, cornulitids, Ordovician, Baltica.

INTRODUCTION

Ordovician hard substrate faunas are relatively well documented. They are among the best studied hard substrate faunas in general, especially the North American examples, while much less information is available from Baltica and the eastern Baltic. Encrusters are preserved in situ, retaining their spatial relationships to one another and to the substrate (Taylor & Wilson 2003). Spatial competition, ecological succession and oriented growth can all be observed or inferred (Taylor & Wilson 2003). Bryozoans and echinoderms commonly encrusted hard substrates in the Ordovician (Taylor & Wilson 2003). Additional encrusting organisms on Ordovician hard substrates are sphenothallid worms, cornulitids, corals, articulate and inarticulate brachiopods, crustoid graptolites and problematica (Wilson 1985; Taylor & Wilson 2003). Trilobite remains form excellent attachment surfaces for encrusting organisms.

Cornulitids belong to encrusting tentaculitoid tubeworms. They are evolutionarily closely related to free-living tentaculitids (Vinn & Mutvei 2009). Their zoological affinities have long been debated, but they likely belong to the Lophothrochozoa (Vinn & Zatoń 2012) and could represent stem group phoronids (Taylor et al. 2010).

The faunas of cornulitids and bryozoans in the Ordovician of Estonia are relatively well studied (Bassler 1911; Öpik 1930; Modzalevskaya 1953; Männil 1959, 1961; Lavrenteva 1990; Goryunova 1992, 1996; Pushkin & Gataulina 1992; Goryunova & Lavrenteva 1993; Vinn 2013).

The aim of this paper is (1) to report the occurrence of the earliest cornulitid from the Middle Ordovician of Estonia and (2) to discuss the palaeoecology of encrusting cornulitids.

GEOLOGICAL BACKGROUND

During the Ordovician Baltica drifted from the temperate climatic zone into the subtropical realm (Cocks & Torsvik 2005; Torsvik et al. 2013). In the Darriwilian the area of modern Estonia was covered by a shallow epicontinental sea with little bathymetric variation and an extremely low sedimentation rate (Nestor & Einasto 1997). A series of grey argillaceous and calcareous sediments accumulated along the ramp. The content of bioclasts decreased and that of clay increased in the offshore direction (Nestor & Einasto 1997). The climatic change in the Katian caused an increase in the carbonate production and sedimentation rate on the carbonate shelf (Nestor & Einasto 1997).

The Dapingian to Hirnantian succession in Estonia is characterized by various carbonate rocks that formed in

normal marine conditions (Nestor & Einasto 1997). Mostly limestones are exposed in northern Estonia. They accumulated in the shallow part of the basin. In addition to limestones, carbonate oil shales and marls are found in somewhat lesser amounts. The purest limestones occur mostly in the Katian of northern Estonia, while the Sandbian is characterized by a higher content of clay in carbonate rocks. The Sandbian of northern Estonia is also rich in kerogenous carbonates (oil shales) (Nestor & Einasto 1997). Carbonate buildups became common in the early Katian of northern Estonia beginning with the Keila Regional Stage (Nestor & Einasto 1997).

MATERIAL AND METHODS

The geological collections of Natural History Museum, University of Tartu (TUG), contain more than 2000 Ordovician trilobites. The collections of the Department of Geology, Tallinn University of Technology (GIT), contain more than 650 Ordovician illaenid trilobites. The trilobites of both collections were searched for the encrustation. Three encrusted illaenid pygidia and two encrusted illaenid cranidia were found (Figs 1, 2). Trilobite remains are preserved on the rock surface. Thus, the remain always hides one of its side (ventral or dorsal) and it is possible that some hidden surfaces may contain uncounted encrusters. The encrusted pygidia and cranidia were photographed using a Nikon D7000 digital camera and Canon 760D. The dimensions of encrusters were obtained from calibrated photographs.

RESULTS

The internal surface of the pygidium of *Illaenus* sp. from the Lasnamägi Regional Stage (Darriwilian) is encrusted by a cornulitid (Fig. 2A) and two trepostome bryozoan colonies with circular cross section. The attachment surfaces of the cornulitid and bryozoans are exposed on the surface of the internal mould of the sparsely encrusted trilobite pygidium. The cornulitid specimen from the Lasnamägi Regional Stage has a small tube and exhibits internal annulation of the tube wall. The internal annuli are characteristic of the genus *Cornulites*, supporting preliminary assignment of the specimen to the genus as *Cornulites* sp. The vesicular

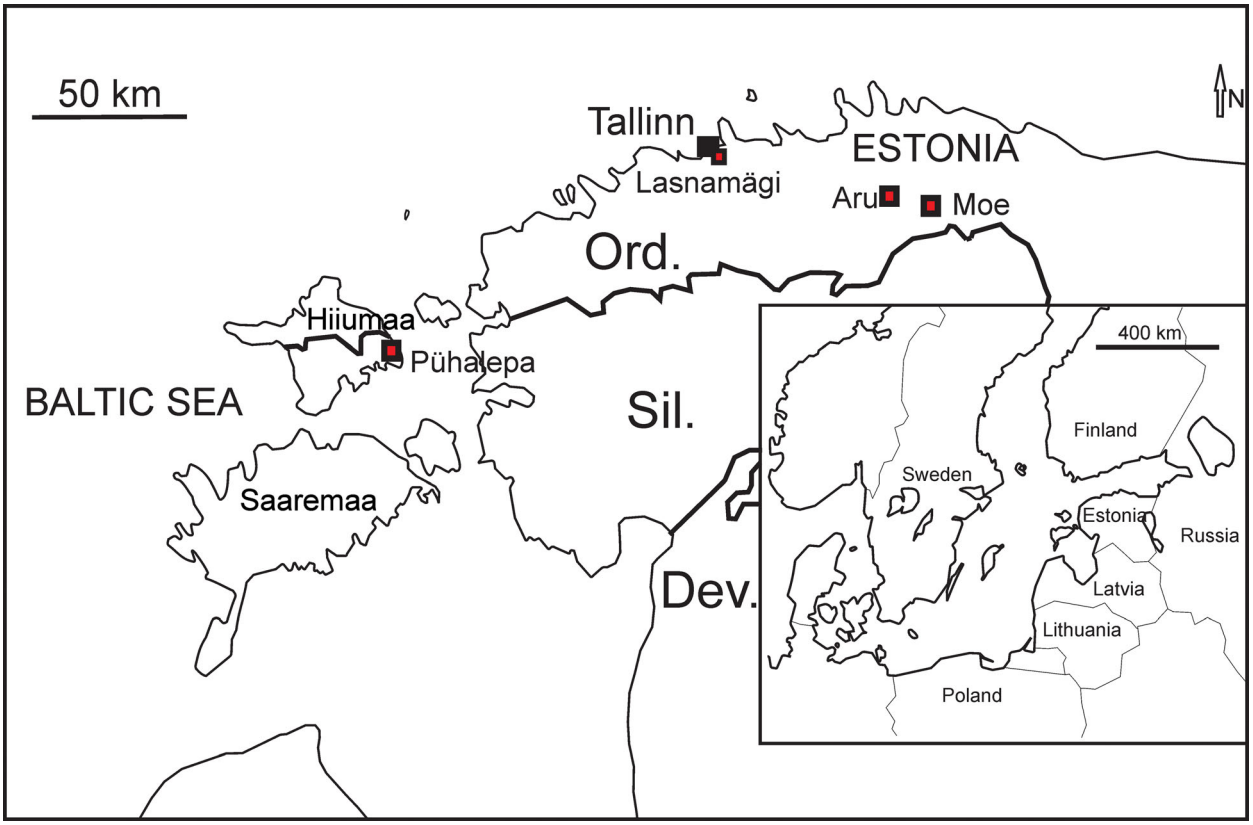

Fig. 1. Locality map.

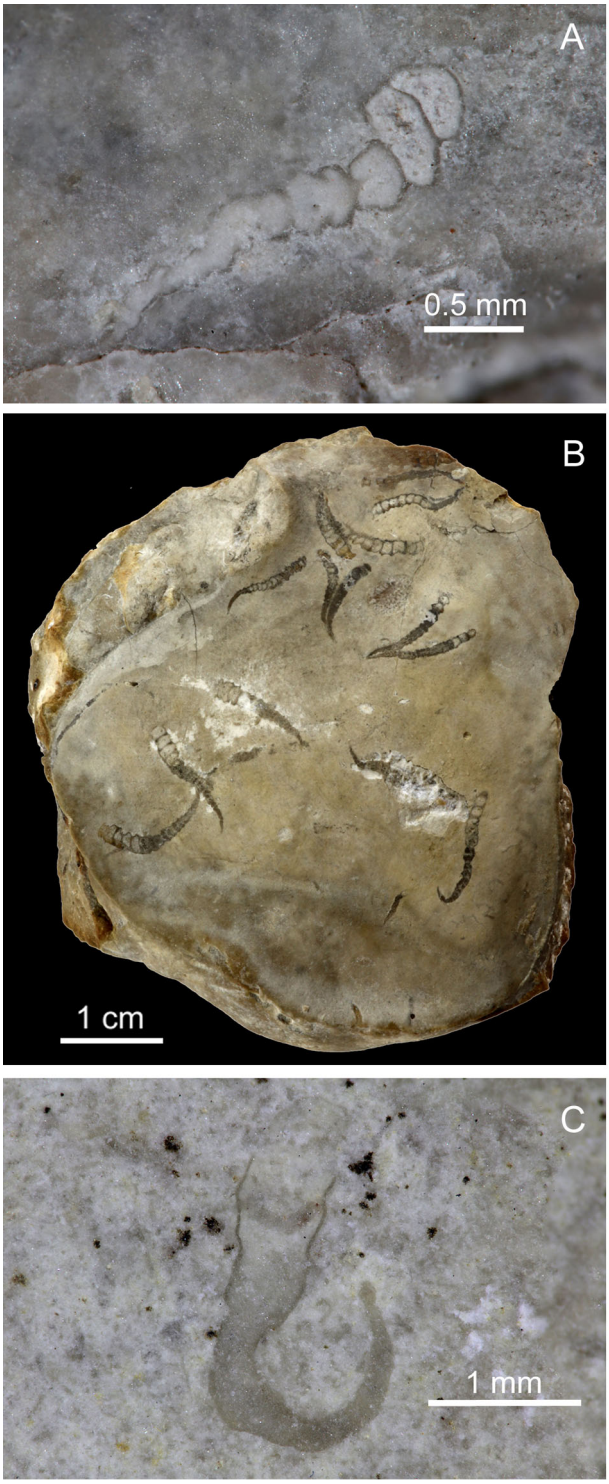

Fig. 2. A, *Cornulites* sp. on the internal mould of the *Illaenus* sp. pygidium from Aru, northern Estonia, Lasnamägi Regional Stage (Darriwilian) (TUG 35-55); **B**, *Cornulites* sp. tubes on the internal mould of the illaenid pygidium from Pühalepa, Hiiumaa Island, Nabala Regional Stage (Katian) (TUG 2-650); **C**, *Conchicolites*? sp. on the internal mould of the illaenid pygidium from Moe ditch, northern Estonia, Vormsi Regional Stage (Katian) (GIT 437-509).

structure of the tube wall is either lacking or is not exposed on the attachment surface of the tube.

The internal surfaces of two *Illaenus* sp. cranidia from Lasnamäe quarry, Uhaku Regional Stage (Darriwilian), are encrusted by a single trepostome bryozoan colony. The attachment surfaces of bryozoans are exposed on the surfaces of internal moulds of the trilobite cranidia. The attachment surfaces of trepostome colonies have subcircular to circular outline. One trepostome colony is large and has a maximal diameter of 1.5 cm.

The internal surface of the pygidium of the illaenid trilobite from the Nabala Regional Stage (middle Katian) is encrusted by multiple cornulitids ($N = 15$) and a single trepostome bryozoan colony with circular cross section (Fig. 2B). The attachment surfaces of the cornulitids and bryozoan are exposed on the surface of the internal mould of the trilobite pygidium. The encrustation is somewhat patchy but does not show clear preference for any particular region of the pygidium. Some parts of the pygidium are densely encrusted by cornulitids, with up to four specimens occurring in 1 cm^2. The cornulitids are mostly solitary and may grow close to each other. The cornulitids lack the orientation and never cross each other. The apertures of some very closely spaced specimens are directed towards each other. The tubes of cornulitids are of similar size; only one juvenile is found. The cornulitid specimens from the Nabala Regional Stage show internal annuli supporting their assignment to the genus *Cornulites*. The tubes are of moderate size and resemble that of *Cornulites* sp. C described from the Katian of Estonia (Vinn 2013). The vesicular structure of the tube wall is not exposed on the attachment surface of the tube.

The internal surface of an illaenid pygidium from the Vormsi Regional Stage (late Katian) is encrusted by a single small cornulitid (Fig. 2C). The attachment surface of the cornulitid is exposed on the surface of the internal mould of the illaenid pygidium. The cornulitid tube lacks clear internal annulation and resembles tubes of *Conchicolites*.

DISCUSSION

Encrustation

The encrustation of both Middle Ordovician and Late Ordovician trilobites took place post mortem, because during the life the inner surface of the pygidium and cranidium was not exposed to encrustation and was in contact with soft tissues of the trilobite. The taxonomic composition of the described encrusting communities is typical for the Ordovician. Both cornulitids and trepostome bryozoans were common encrusters in the Ordovician seas (Taylor & Wilson 2003).

Illaenus sp. from the Nabala Regional Stage shows that the inner surface of the pygidium was not exposed to encrusters long enough to allow several generations of cornulitids to colonize it. The numerical dominance of large *Cornulites* sp. specimens is indicative of a single colonization event where most of the specimens reached adult size after settling on the pygidium of *Illaenus*. High juvenile mortality occurs in many modern invertebrates, but only a single juvenile tube was found on the pygidium. The situation with the cornulitids on the pygidium of *Illaenus* sp. can either be explained by low juvenile mortality or weaker preservation potential of juvenile specimens. However, low juvenile mortality seems more feasible because it is hard to imagine how empty juvenile tubes could have been selectively destroyed by the hydrodynamic activity of waters inside the concave inner surface of the pygidium. The random orientation of the tubes may indicate the lack of unidirectional water currents (Vinn & Toom 2015). Alternatively it may indicate random settlement of larvae or lack of larvae reorientation after settlement (Vinn & Toom 2015). In the case of unidirectional water current, the cornulitids would have oriented their apertures up-current to achieve a better position for suspension-feeding. Cornulitids behaved similarly on brachiopods (Schumann 1967) where they presumably took advantage of the feeding currents of the host. Closely located cornulitid tubes that face each other's apertures may have not been all alive at the same time or they did not interfere with each other's feeding. In the latter case their possible lophophores must have been rather small.

Cornulitids in the Middle Ordovician

As compared to the Late Ordovician, cornulitids are relatively rare in the Middle Ordovician, whereas their occurrences are restricted to Baltica (Vinn 2013). They all represent substrate cemented solitary life mode. The hitherto earliest record of *Cornulites* and all cornulitids originates from the Uhaku Regional Stage of northern Estonia (Vinn 2013). Thus, the occurrence of *Cornulites* sp. in the Lasnamägi Regional Stage indicates that the first appearance of the group took place earlier than previously known. The cornulitids in the Uhaku Regional Stage are rather large, contrasting with the minute size of *Cornulites* sp. from the Lasnamägi Regional Stage. One could speculate that the earliest representatives of the genus *Cornulites* and cornulitids in general may have been small in size. It is also likely that the internal annulation present in all Middle Ordovician cornulitids could be a plesiomorphic character for the group.

Cornulitids on trilobites

Cornulitids have been relatively rarely reported to be attached to trilobites. They have been found attached to the cephalon of *Flexicalymene* from the Late Ordovician of North America, whereas the trilobite may have been alive during the encrustation (Brandt 1996). Morris & Rollins (1971) described a single trilobite specimen with encrusting *Cornulites* from the Late Ordovician of North America. They found that a cluster of four cornulitid tubes was attached to a crushed fragment of an *Isotelus* cephalon and genal spine. Presumably cornulitids encrusted the *Isotelus* cephalon post mortem (Morris & Rollins 1971). In contrast, Tetreault (1992) found that *Cornulites* tubes were *syn vivo* attached to a Silurian lichid trilobite *Arctinurus*. He concluded that the presence of suspension-feeding *Cornulites* on the ventral doublure of *Arctinurus* precluded even a shallow-burrowing habit for this genus. Numerous epibionts (e.g., the brachiopod *Stegerhynchus*) have also been reported from dorsal surfaces of large specimens of *Arctinurus* (Whittington 1992, pl 111).

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Kõige varajasem kornuliit illaeniidi sabakilbi sisepinnalt Eesti Kesk-Ordoviitsiumist

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Esimesed kornuliidid Eestis ilmusid Lasnamäe lademes. Kojasisene rõngastest struktuur esines juba kõige esimestel kornuliitidel. Inkrusteeritud trilobiidid on Eesti Ordoviitsiumis haruldased. Illaeniidide saba- ja peakilpide külge kinnitusid pärast surma kornuliidid ning sammalloomad. Uuritud trilobiitide saba- ja peakilpidel esinevad kõva substraadi kooslused olid Ordoviitsiumile tüüpilised.