

A CRUSTOID GRAPTOLITE LITHOIMMURED INSIDE A MIDDLE ORDOVICIAN NAUTILOID CONCH FROM NORTHERN ESTONIA

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Abstract: A light grey nautiloid conch has a dark brown colony attached to its internal surface. This colonial fossil resembles hederellids and bryozoans, but is in fact a crustoid graptolite (*Hormograptus?* sp.). The colony has been lithoimmured inside this nautiloid conch by early cementation. Crustoid graptolites were a part of the encrusting communities in the Middle Ordovician of Baltica, but their abundance among encrusters of biogenic substrates reached a peak in the middle Sandbian. The cryptic mode of life appeared very early in the evolution of the crustoids. The discovery of this crustoid graptolite in a nautiloid conch indicates that the Baltic Middle Ordovician cryptic communities were taxonomically more diverse than was known previously. The nautiloid conch studied is sparsely encrusted with an encrustation density that is similar to those of other Middle Ordovician cryptic surfaces described from Estonia.

Key words: Encrustation, graptolites, nautiloids, cryptic fauna, Darriwilian, Baltica.

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INTRODUCTION

Middle Ordovician hard substrates, both biogenic and inorganic, are commonly encrusted by various sclerobionts. There was a dramatic increase in encrustation and bioerosion on hard substrates at the time of the Great Ordovician Biodiversification Event (Taylor and Wilson, 2003; Buatois *et al.*, 2016). Ordovician hard-substrate communities usually were dominated by bryozoans and echinoderms (Taylor and Wilson, 2003). The encrusting faunas of Estonian Ordovician hardgrounds recently have been studied in detail (Vinn, 2015; Vinn and Toom, 2015), but less is known about encrusters on biogenic substrates (Vinn *et al.*, 2017). Empty nautiloid shells often were colonized by cryptic encrusters in the Ordovician of Estonia (Vinn *et al.*, 2018). Typical Ordovician cryptic biotas were dominated by bryozoans (Brett and Liddell, 1978; Taylor and Wilson, 2003) and this is also true for the Ordovician of Estonia (Vinn *et al.*, 2018). The cryptic biotas of the Palaeozoic are relatively well known (Spjeldnaes, 1975; Kobluk, 1980, 1981, 1988; Segars and Liddell, 1988; Taylor and Wilson, 2003; Jakubowicz *et al.*, 2014; Buttler and Wilson, 2018; Zatoń *et al.*, 2018; Berkowski *et al.*, 2019), but only two previous studies exist for the Ordovician of Baltica (Vinn *et al.*, 2017, 2018). This topic needs further study.

The aims of this paper are (1) to report, for the first time, a cryptic crustoid graptolite from the Ordovician of Baltica,

and (2) to assess the cryptic communities of the Ordovician of Baltica

GEOLOGICAL BACKGROUND

In northern Estonia, Ordovician limestones are exposed as a wide belt from the Narva River in the northeast to Hiiumaa Island in the west (Mõtus and Hints, 2007). The total thickness of the Ordovician sedimentary rocks in Estonia ranges from 70 to 180 m (Mõtus and Hints, 2007). In the Middle Ordovician and the Sandbian, the western part of the East European Platform was covered by a shallow, epicontinental sea. This sea had little bathymetric differentiation. The Middle Ordovician basin of Estonia was characterized by an extremely low sedimentation rate (Jaanusson, 1972; Mõtus and Hints, 2007). The Kunda Regional Stage (lower Darriwilian) in the Harku Quarry trench (Fig. 1) is characterized by limestones and sandy limestones with iron ooids and layers of marly limestones (Nestor and Einasto, 1997). The total thickness of the Kunda Regional Stage in the Harku Quarry trench (latitude: 59.400139, longitude: 24.609767) is approximately 30 cm. Its upper boundary is marked by a discontinuity surface with goethite impregnation. Its lower boundary is marked by a complex of pyritized and phosphatized

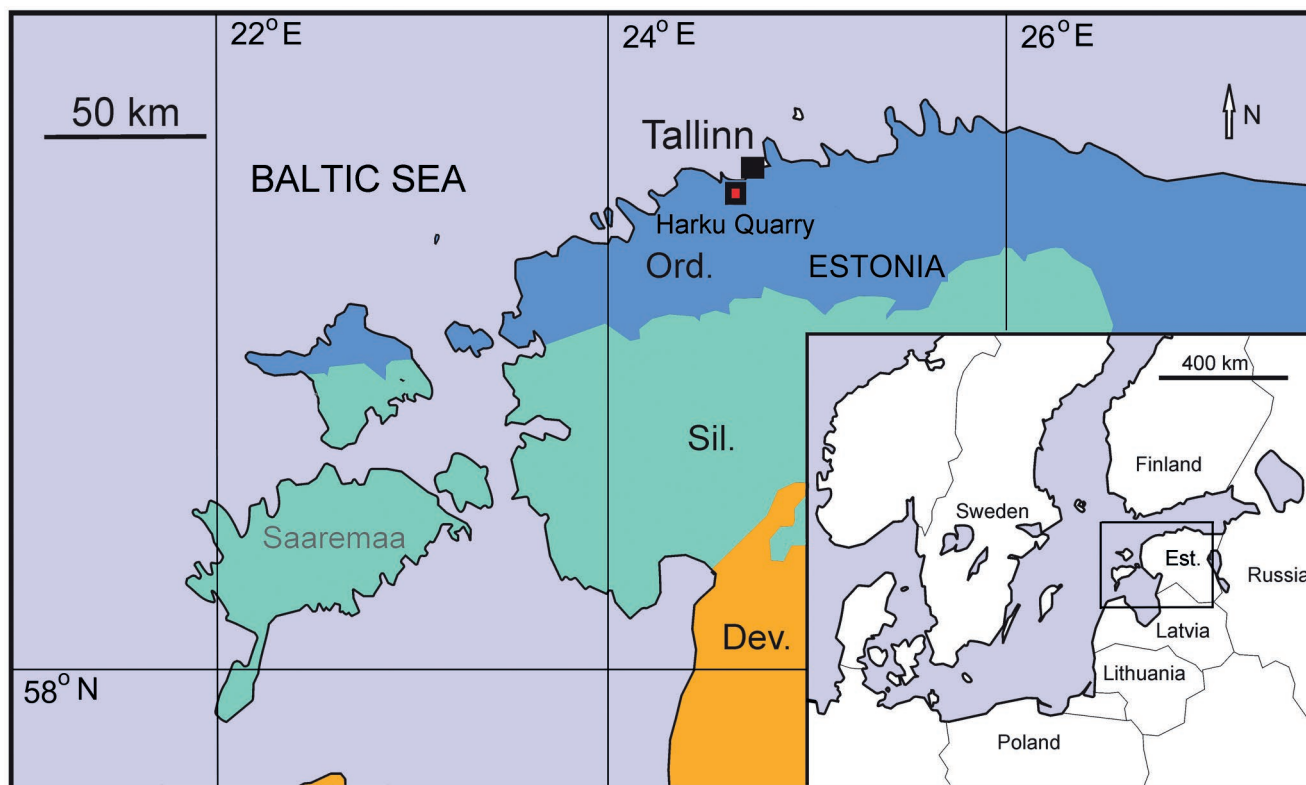


Fig. 1. Locality map showing the location of the Harku Quarry (Kunda Regional Stage, lowermost Darriwilian). Ord. – Ordovician, Sil. – Silurian, Dev.– Devonian.

tic discontinuity surfaces (Põlma, 1985). On the carbonate platform, a series of grey, calcareous-argillaceous sediments accumulated, represented now by argillaceous limestones and marls (Nestor and Einasto, 1997). There was a trend in sedimentation of decreasing bioclasts and increasing clay in an offshore direction (Nestor and Einasto, 1997). During the Ordovician, the Baltica palaeocontinent drifted from the temperate climatic zone to the subtropical realm (Torsvik *et al.*, 1992, 2013; Nestor and Einasto, 1997).

MATERIAL AND METHODS

The steinkern of the nautiloid was studied under a binocular microscope. The specimen was photographed digitally using a Canon EOS 5Dsr camera digital camera and apochromatic zoom system Leica Z16 APO. Measurements of the encrusting colony were taken from calibrated photos. Several acetate peels were made from the fossil. The specimens studied are deposited at the Department of Geology, Tallinn University of Technology (GIT) and Natural History Museum (Geological Museum), University of Tartu (TUG).

RESULTS

The light grey mould of the nautiloid conch preserved in 3D (the phosphatized shell was broken off mechanically) has a dark brown colony attached to its internal surface (Fig. 2A–C). The diameter of the colony is approximately 1.5 cm. There are no remnants of a carbonaceous covering and the material of the colony is most likely organic.

The colony is divided into four branches that bifurcate at irregular intervals. The branches are composed of conical zooids of moderate length (1.30 to 2.10 mm long). The lengths of the zooids are 2.5 times their width. The zooids have some asymmetry. The apertures of consecutive zooids are always turned to the opposite side, compared to those of the preceding zooids. The budding of the zooids is at one side of the parent zooid, near its aperture. Budding for bifurcation takes place at both sides of the parent zooid, near its aperture. There are traces of a thin cord running through the colony (Fig. 2C). The peels show no morphological details but plucked out lines of tiny phosphatic fragments parallel to the growth directions. This colony is the only encruster on the internal surface of the nautiloid and the total encrustation area is relatively very small.

DISCUSSION

Nature of the colony

Small branching colonies of possible Hydrozoa have been described from the Visean of Scotland (Zapalski and Clarkson, 2015). The colony of the present account differs from hydrozoan colonies in both its branching pattern and the presence of a stolon. One of the earlier interpretations by the present authors of the colonial fossil studied was that it might be a hederelloid. Its Middle Ordovician age would make it the earliest representative of the group. Colonies of hederelloids generally are uniserial, but biserial or narrowly multiserial colonies can also occur (Taylor and Wilson,

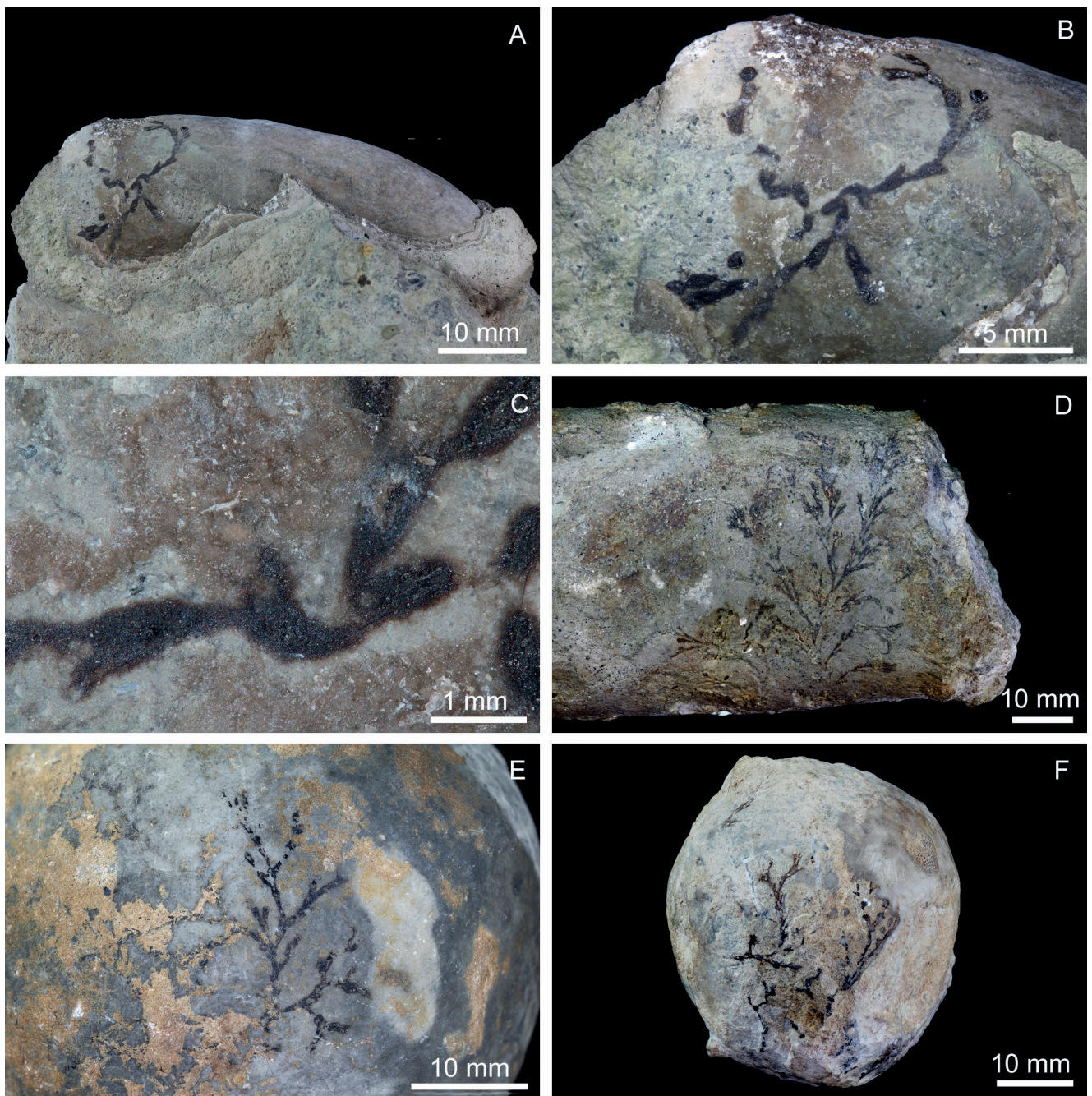


Fig. 2. Hormograptid graptolites from the Ordovician of Estonia. **A–C.** *Hormograptus?* sp., attached to the internal surface of a nautiloid conch; Harku Quarry, Kunda Regional Stage (lowermost Darrwilian) (GIT 494-41-1). **D.** *Hormograptus ramulus* (Öpik, 1928), attached to the internal surface of a nautiloid conch; Lilli, northern Estonia, Keila Regional Stage (upper Sandbian to lowermost Katian), TUG 1317-3, holotype. **E.** *Hormograptus defensor* (Öpik, 1928), attached to the cystoid *Echinospaerites*, Kohtla, NE Estonia, Kukruse Regional Stage (lowermost Sandbian), TUG 1317-6, holotype. **F.** *Hormograptus sphaericola* (Öpik, 1928), attached to the cystoid *Echinospaerites*; Vanamõisa, northern Estonia, Kukruse Regional Stage (lowermost Sandbian), TUG 1317-4, holotype.

2008). Hederelloid zooids commonly lap onto the sides of other zooids (Taylor and Wilson, 2008), which is very different from the pattern in the colony under consideration, in which zooids do not lap onto the sides of other zooids. All hederelloids are calcareous, but there is no evidence of a calcitic skeleton under the microscope or in peels of the fossil studied, and the budding would be highly unusual for a hederelloid. The authors interpret the remnants of the thin cord running through the colony as most likely being

a stolon. The new hypothesis of the present authors is that this specimen represents a crustoid graptolite that has been lithoimmured inside the nautiloid conch by early cementation. This kind of lithoimmuration by early cementation is rarely seen in the Ordovician and beyond. *In situ* Ordovician crustoid graptolite colonies have been described previously from an Upper Ordovician hardground in south-western Ohio (Mitchell *et al.*, 1993). These graptolites somewhat resemble the colony studied in this nautiloid conch. The col-

ony of the present authors resembles a species of crustoid graptolites of the genus *Hormograptus*, described from the Late Ordovician of Estonia (Õpik, 1928, 1930; Fig. 2D–F).

Encrusting graptolites in the Ordovician of Estonia

The earliest remains of sessile, encrusting graptolites appear in the Tremadocian of Estonia (O.V. personal observations), but they were found detached from their substrate in micropalaeontological samples. Fossils of various sessile encrusting graptolites have been described from erratic boulders of Baltic origin (Mierzejewski, 1978, 1985). Sessile encrusting camaroid graptolites were described previously from the Middle Ordovician (Kunda Regional Stage; Mierzejewski, 2000). Similarly, crustoid graptolites are common in the Upper Ordovician of Estonia (Obut and Rytzk, 1958; Obut, 1960), but they have not been described previously from the Kunda Regional Stage. Crustoid graptolites encrust cystoid echinoderms (e.g., *Echinospaerites*) in large numbers in the Sandbian of eastern Estonia. This is unusual, since echinoderms have an epidermis on the outside of the skeleton. The present authors have not found any evidence of a reaction on the part of the host cystoid and it is unknown whether live echinoderms or reworked thecae were encrusted after pre-fossilization. They are usually associated with cystoids found in the middle Sandbian oil shale (kukersite) (Õpik, 1928, 1930). The oil shale environment was peculiar in many ways, compared to the normal carbonate platform sediments of the Middle Ordovician (Raukas and Teedumäe, 1997). The carbonate mud in the oil shale basin was very rich in organics, derived from vast, nearshore, cyanobacterial mats (Raukas and Teedumäe, 1997). It is possible that productivity in the oil shale basin may have been higher than in the surrounding areas of the Baltic Basin. The organic-rich waters of the oil shale basin could have created favourable conditions for suspension-feeding, crustoid graptolites. Settling on dead cystoids also may have been somehow beneficial for crustoid graptolites. This discovery of a crustoid graptolite on the interior of an empty shell of a nautiloid from the Kunda Regional Stage indicates that crustoid graptolites were a part of encrusting communities in the Middle Ordovician of Baltica. However, their abundance among encrusters of biogenic substrates reached a peak in the middle Sandbian. Fossils of the earliest crustoid graptolites are known from the lower Darriwilian (Kozłowski, 1962). The occurrence of cryptic crustoids in the earliest Darriwilian of Baltica indicates that a cryptic mode of life must have appeared very early in crustoid evolution. One might explain the early appearance of cryptic life in terms of its great usefulness. The relatively weak, nonmineralized skeletons of crustoids were most likely easy targets for Middle Ordovician predators and grazers. Thus, cryptic surfaces might have offered crustoids some protection against these organisms.

Cryptic invertebrates in the Ordovician

In the Middle Ordovician of Baltica, only bryozoans, cornulitids and echinoderms previously have been found encrusting hard substrates (Vinn *et al.*, 2018; Rozhnov,

2019). Echinoderms encrusted the upper surfaces of hardgrounds during the entire Middle Ordovician (Rozhnov and Palmer, 1996; Rozhnov, 2017, 2019; Paton *et al.*, 2019). Cornulitids settled both on open and cryptic surfaces of biogenic, hard substrates in the Lasnamägi and Uhaku Regional Stages (Vinn *et al.*, 2018). Bryozoans also encrusted both open and cryptic surfaces of biogenic substrates and the upper surfaces of hardgrounds during the Middle Ordovician of Estonia (Vinn *et al.*, 2018). In addition to bryozoans and cornulitids, *Arachnostega* trace makers were also common inhabitants of cryptic spaces in the Middle Ordovician of Estonia (Vinn *et al.*, 2014). The cryptic cornulitids and especially bryozoans are small, compared to the cornulitids and bryozoans on open surfaces in the Ordovician of Estonia (Vinn *et al.*, 2018). This can be explained by the more restricted space available for growth on cryptic surfaces and possibly restricted access to the nutrient-rich waters of the outer environment. A crustoid graptolite *Hormograptus ramulus* (Õpik, 1928) has been described from the interior of a nautiloid conch from the Keila Regional Stage (latest Sandbian to earliest Katian; Fig. 2D). The discovery by the present authors of a crustoid graptolite in a nautiloid conch from Kunda Regional Stage indicates that the Middle Ordovician cryptic communities in Baltica were taxonomically more diverse than was known previously. Cryptic, biogenic surfaces were sparsely encrusted in the Middle Ordovician of Estonia (Vinn *et al.*, 2018). The nautiloid conch studied is not exceptional and in encrustation density resembles the other Middle Ordovician cryptic surfaces, described from Estonia (Vinn *et al.*, 2018). Only bryozoans and echinoderms (holdfasts) encrusted cryptic surfaces on a Late Ordovician hardground from Ontario, North America (Brett and Liddell, 1978). Other Late Ordovician hardgrounds from North America also contain rich, cryptic faunas (Paton *et al.*, 2019), but no cryptic hormograptids have been reported from these hardgrounds.

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