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A new genus and species of cornulitid tubeworm from the Hirnantian (Late Ordovician) of Estonia

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Non-technical Summary.—Tubeworms form an important part of the modern marine fauna. They were also common in the geological past. We discovered a new genus and species of tubeworms from the latest Ordovician of Estonia. These tubeworms grew on the lithified sea floor during the time of the end-Ordovician mass extinction. Our discovery helps better understand and reconstruct the marine life during this extraordinary time interval.

Abstract.—A new cornulitid genus and species, *Porkuniconchus fragilis* new genus and species, is here described from the Ärina Formation (Hirnantian, Porkuni Regional Stage) of northern Estonia. This new taxon differs from most cornulitids by having a fusiform ornamentation pattern that is somewhat similar to that of *Kolihaia*. All studied specimens are attached to a carbonate hardground. The hardground fauna is by abundance and encrustation area dominated by cornulitids. Other encrusters are represented only by a single sheet-like cystoporate bryozoan. The cornulitid specimens represent different growth stages, which suggest that the hardground was continuously colonized by cornulitid larvae. The high encrustation density indicates that the studied hardground may have represented a high-productivity site in the Hirnantian of the Baltic Basin.

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Introduction

Cornulitids are a group of problematic tubicolous lophophorates that have a stratigraphic range from the Darriwilian (Middle Ordovician) to the late Carboniferous (Vinn, 2010). The zoological affinities of cornulitids have been long debated, but they most likely belong to the Lophotrochozoa (Vinn and Zatoń, 2012) and could represent stem-group phoronids (Taylor et al., 2010). Their fossils often provide us with important paleoecological information because, as hard substrate encrusters, they generally retain their original position on the substrate through fossilization (Taylor and Wilson, 2003). Most cornulitids are general hard substrate encrusters (Zatoń and Borszcz, 2013; Zatoń et al., 2017), and all were stenohaline, which differs from their close relatives the microconchids, which were euryhaline (Zatoń et al., 2012, 2016). Cornulitids are common fossils in shallow marine sediments of the Paleozoic, especially those associated with carbonate platforms (Richards, 1974; Zatoń et al., 2017; Musabelliu and Zatoń, 2018). The Ordovician cornulitids from Estonia have been systematically studied by Vinn (2013) and Vinn et al. (2023a, b), but further research on the group is needed to fully understand their diversity and ecology, especially on hardgrounds.

Carbonate hardgrounds are synsedimentarily lithified carbonate layers that have been exposed on an ancient seafloor (Wilson and Palmer, 1992). Hardgrounds form excellent substrates for encrusting and bioeroding organisms (Palmer, 1982; Taylor and Wilson, 2003). These organisms otherwise dwell on carbonate cobbles or shells of various invertebrates. Ordovician hardground faunas are globally well documented, but not much is known about hardgrounds from the important Hirnantian mass-extinction interval.

The aims of this paper are to: (1) compare a new genus and species of cornulitid tubeworm with various previously known cornulitids and tubicolous organisms, (2) discuss the zoological affinities of the fossil, and (3) discuss the ecology and evolution of hardground faunas in the Ordovician of Baltica.

Geological background and locality

A shallow warm epicontinental sea covered what would become modern northern Estonia during the Hirnantian. The Hirnantian sequence of northern and middle Estonia is represented by tropical carbonate rocks belonging to the Ärina Formation (Porkuni Regional Stage) (Hints and Meidla, 1997; Hints et al., 2000; Kröger, 2007). There was a significant climatic change in the Katian of Baltica, when the paleocontinent drifted from a temperate climatic zone into the tropical realm (Torsvik et al., 2012). Carbonate sedimentation intensified during the warming of the climate early in the Katian (Nestor and Einasto, 1997). The tropical

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fauna, including tabulate corals and stromatoporoids, that appeared in the early Katian was common in the Hirnantian.

The Reinu quarry is located in northern Estonia (latitude 59.08768°N, longitude 24.74044°E) in Rapla County (Hints et al., 2023) (Fig. 1). Carbonate rocks of latest Katian to Rhuddanian age (Pirgu to Juuru regional stages) are exposed here (Hints et al., 2023) (Fig. 2). The Ärina Formation (~2.5 m thick, Hirnantian) consists of various shallow-marine carbonates and contains the Siuge Member with characteristic kerogenous limestones and a hardground at its upper contact with the Koigi Member (uppermost Hirnantian) (Hints et al., 2023).

Materials and methods

A limestone slab with fossils of *Porkuniconchus* was collected during a visit to the Reinu quarry in 2023. The limestone slab contained a surface with numerous tubeworm fossils. This surface was cleaned and photographed using an apochromatic zoom system Leica Z16 APO.

Repository and institutional abbreviation.—Types, figured, and other specimens examined in this study are deposited in the Department of Geology, Tallinn University of Technology (GIT).

Systematic paleontology

Superphylum Lophophorata Emig, 1984
Phylum uncertain
Class Tentaculitida Bouček, 1964
Order Cornulitida Bouček, 1964
Family ?Cornulitidae Fisher, 1962
Porkuniconchus new genus

Type species.—*Porkuniconchus fragilis* n. gen. n. sp.

Diagnosis.—Almost straight, curved to slightly meandering tubes with thin calcareous walls and smooth lumen. The tube exterior is densely covered by fine fusiform irregular transverse ornamentation.

Occurrence.—Hirnantian of northern Estonia.

Etymology.—After the type horizon, Porkuni Regional Stage, and shell (conch).

Remarks.—The new genus is based on the combination of unique fine fusiform perpendicular ornamentation, which separates it from *Conchicolites* Nicholson, 1872, and lack of processes, which separates it from *Kolihaia* Prantl, 1946. The new genus is tentatively assigned to Cornulitidae because of its broad, thin-walled conical calcareous tube.

Porkuniconchus fragilis new species
Figures 3, 4

Holotype.—Holotype (complete tube GIT 494-49-1), paratypes (complete tubes GIT 494-49-2, GIT 494-49-3 and GIT 494-49-4).

Figure 1. Locality map. The locality is indicated by the red dot. Dev.- = Devonian; EST. = Estonia.

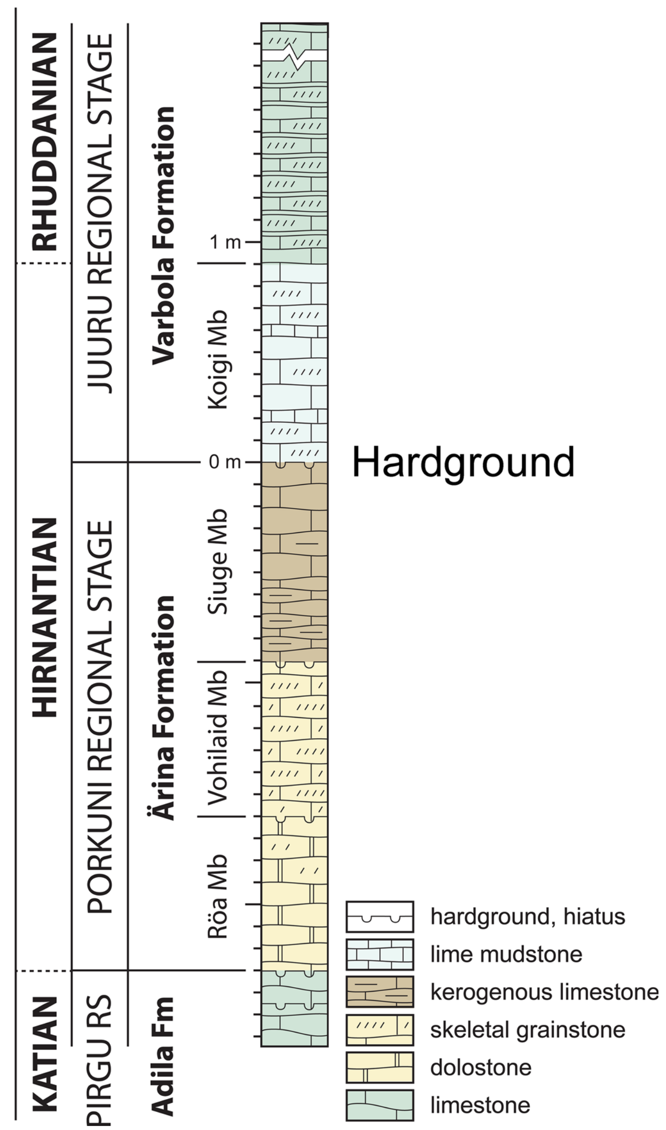

Figure 2. Stratigraphic section of Reinu quarry with location of the hardground (modified after Hints et al., 2023, p. 50, fig. 8.3).

Diagnosis.—Almost straight, curved to slightly meandering, moderately large tubes with thin calcareous walls and smooth lumen. The tube exterior is densely covered by fine fusiform and continuous irregular transverse ornamentation.

Occurrence.—Reinu quarry, northern Estonia; Ärina Formation (Hirnantian), Siuge Member.

Description.—Almost straight, curved to slightly meandering tubes. Tubes are up to 25 mm long and 2.0–3.5 mm wide at the aperture. Shell wall is thin and calcareous. The exterior is covered by fine dense and irregular transverse ridges. The transverse ridges are very low, and the sides of the tube are almost smooth and only slightly zig-zagged in profile (Fig. 3.2, 3.3). The transverse ridges have convex profiles in longitudinal section. The ridges can fuse and appear in the interspaces between two ridges (Fig. 4.1, 4.2). There are 10–11 ridges in 1 mm near the tube aperture. The transverse ridges are variably developed. Some smaller transverse ridges are conjoined to form larger annuli. The tubes are devoid of any longitudinal ornamentation. Tubes are flattened and contain longitudinal fractures resulted from burial compression. The interior of the tube appears to be smooth (Fig. 4.3). The tube wall is extremely thin (about 0.07 mm). The tube grew moderately to rapidly in diameter. The apical angle of the flattened tube is 13–14°, but the actual value may be smaller as all tubes are compressed. The morphology of the tube's apex is not clear on the studied fossils; it seems to be pointed in some specimens and bulbous in one specimen. The original tube structure is not preserved and is replaced with sparry calcite (Fig. 4.3, 4.4).

Etymology.—After *fragilis* (Latin), meaning "fragile, brittle."

Materials.—Fifteen complete compressed tubes cemented to a hardground surface.

Remarks.—*Porkuniconchus fragilis* n. gen. n. sp. is most similar to *Conchicolites rossicus* Vinn and Madison, 2017 from the Kõrgessaare Formation (Katian) (Vinn et al., 2023b, p. 3–5, fig. 5D, E) in its conical shell that is covered by fine perpendicular ridges, but differs by fusiform perpendicular ornamentation, much larger tubes, and lack of attachment structures. *P. fragilis* also resembles *Kolihaia eremita* Prantl, 1946 with its fusiform perpendicular ornamentation and similar size of tubes but differs most remarkably by the lack of radiciform processes. In addition, the perpendicular ornamentation of *K. eremita* is stronger than in *P. fragilis*. The tube structure of this new species is not preserved, but considering the extremely thin tube wall, there would not have been space for vesicles in the sense of *Cornulites*. This new species differs from all other cornulitids by its extremely thin tube wall and its tube size.

Discussion

The interpretation of fossils.—The longitudinal cracks in the walls of most of the compacted tubes indicate that the tubes had rigid mineral walls before sediment compression. Thus, *Porkuniconchus* n. gen. had biomineralized calcareous tubes. The light microscope study suggests that the microstructure of tubes has likely been diagenetically altered. All tubes originally had circular or oval cross sections. The occurrence of tubes on hardground surfaces suggests that they were cemented with their lower side to the hardground. The well-preserved fine ornamentation of the studied specimens indicates that they were buried relatively quickly after their death as there is no sign of abrasion. All specimens are likely in situ as is usually the case with hard-substrate encrusters (Taylor and Wilson, 2003).

Zoological affinities and systematic position.—To find a proper systematic position for *Porkuniconchus* n. gen., one should compare it with the morphologically closest Paleozoic tubicolous organisms. *Porkuniconchus* shares most characters with tentaculitoid tubeworms and somewhat fewer characters with byroniids and *Kolihaia*.

Tentaculitoid affinities.—Encrusting tentaculitoid tubeworms are usually cemented to hard substrates by one side of their tube,

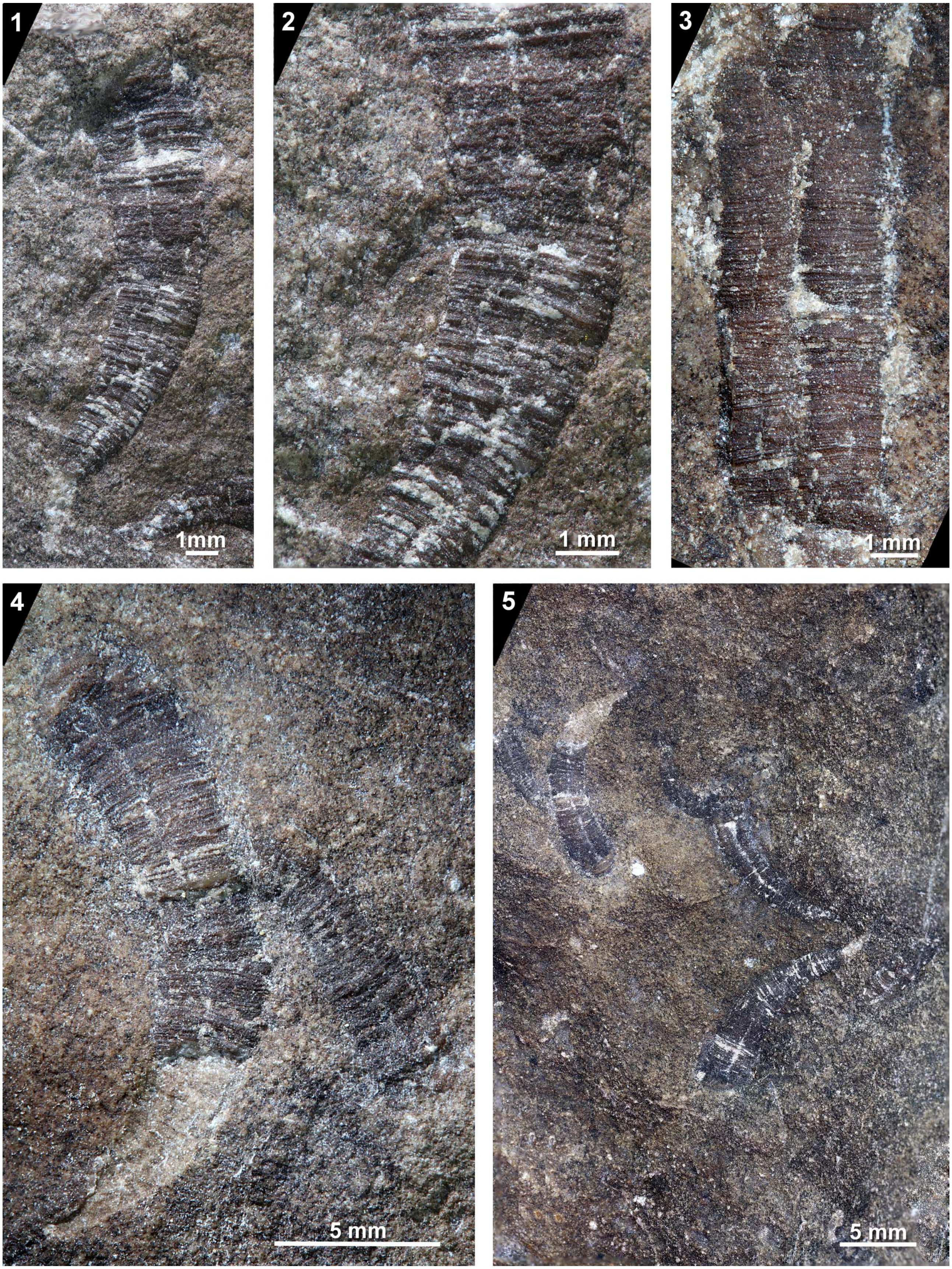

Figure 3. *Porkuniconchus fragilis* n. gen. n. sp. from Ärina Formation (Hirnantian), Reinu quarry, northern Estonia. (**1, 2**) Holotype GIT 494-49-1. (**3**) Paratype GIT 494-49-2 showing fusiform transverse ornamentation. (**4**) Paratypes GIT 494-49-3 and GIT 494-49-4. (**5**) Tubeworms on the surface of hardground.

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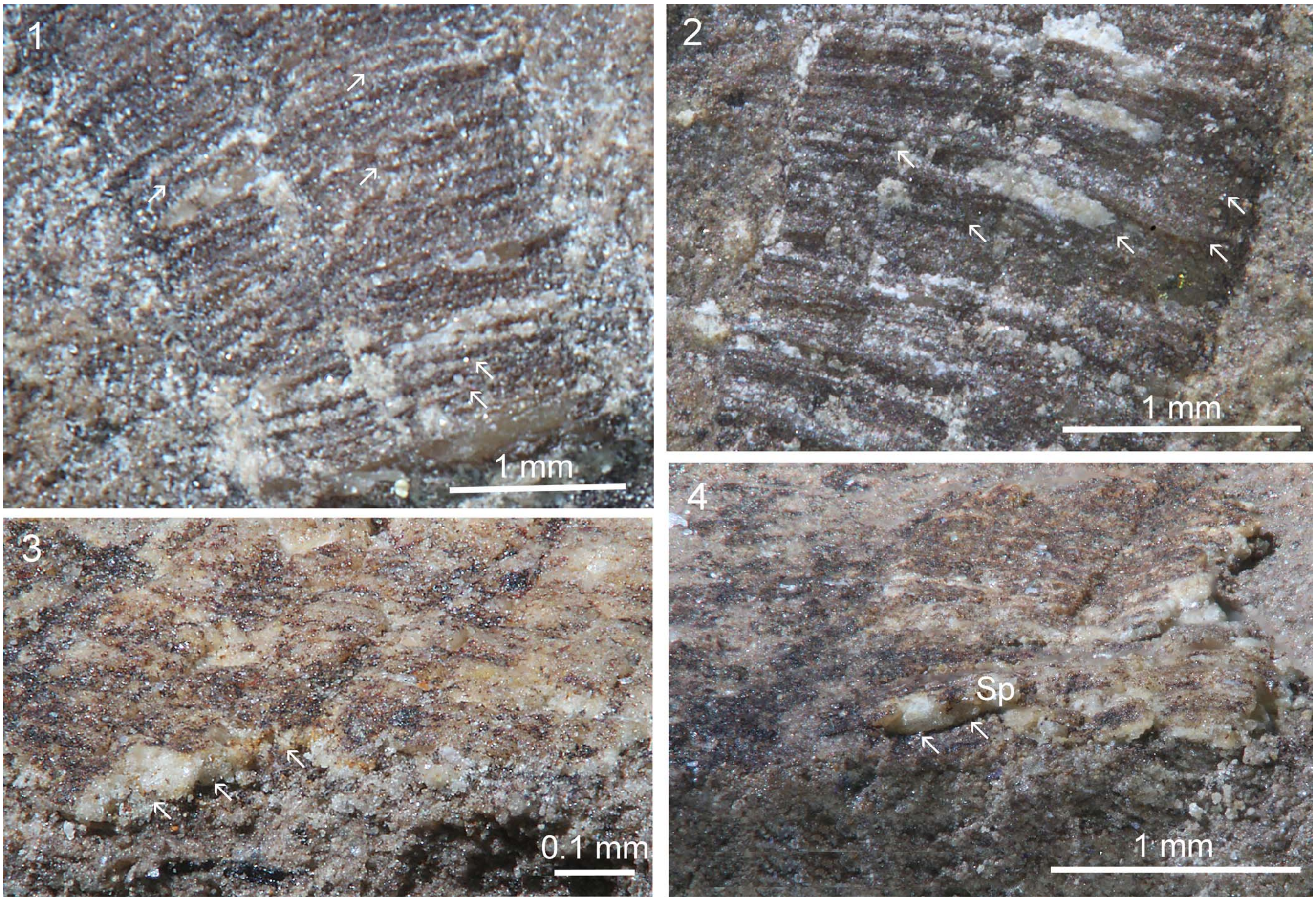

Figure 4. (**1, 2**) Arrows point to discontinuous transverse ridges. (**3**) Longitudinal section of the tube wall (arrows) showing structureless sparry calcite. (**4**) Transverse section of the tube wall (arrows) showing sparry calcite (Sp).

making them similar to *Porkuniconchus*. Encrusting tentaculitoid tubeworms were all suspension feeders and belonged to the lophophorates (Taylor et al., 2010; Vinn and Zatoń, 2012). Among the encrusting tentaculitoid tubeworms, microconchids (Zatoń and Olempska, 2017) and anticalyptraeids (Zatoń et al., 2022, 2023) have spiral tubes that differ from tubes of *Porkuniconchus*. However, cornulitids have conical nonspiral tubes that are almost identical to the tubes of *Porkuniconchus*. Nevertheless, fusiform perpendicular ornamentation of *Porkuniconchus* is unusual for cornulitids. On the one hand, the ornamentation of some species of *Conchicolites* slightly resembles *Porkuniconchus*. On the other hand, the unique ornamentation of *Porkuniconchus* is more similar to the ornamentation of the lining of the trace fossil *Oikobesalon* than to any species of *Conchicolites*. Despite its rather atypical ornamentation for a cornulitid, *Porkuniconchus* is still best placed within the family Cornulitidae Fisher, 1962. The only remaining doubt about this placement is related to the unknown morphology of the tube apex in *Porkuniconchus*. If it turns out to be pointed instead of bulbous, even the placement within tentaculitoid tubeworms could be in jeopardy.

Byroniid affinities.—The Byroniida have a somewhat similar conical conch to *Porkuniconchus* n. gen. They are externally covered by perpendicular ornamentation that somewhat resembles the ornamentation of *Porkuniconchus*. Byroniids are small tube-shaped fossils that have a stratigraphic range from the Cambrian to Permian (Bischoff, 1989). Their composition is variable, with both phosphatic and organic tubes included within the group (Bischoff, 1989). Their tubes were attached to the substrate by a small disk-shaped holdfast (Holmer, 2004). Byroniids have been considered an extinct order of thecate scyphozoans (Bischoff, 1989; Zhu et al., 2000; Van Iten et al., 2014). The attachment to the substrate by only a holdfast and their organo-phosphatic biomineralization rules out byroniid affinities for *Porkuniconchus*.

Kolihaia *affinities.*—*Kolihaia* is a problematic tubicolous organism with a calcareous tube and similar fusiform perpendicular ornamentation to *Porkuniconchus* n. gen. Prantl (1946) originally placed *Kolihaia eremita* in the phylum Annelida Lamarck, 1809 with serpulid polychaetes. Later, Fischer (1966) included the genus within the family Cornulitidae Fischer, 1962. An alternative view on the zoological affinities of *Kolihaia* was published by Kříž et al. (2001). They interpreted *Kolihaia* as an epiplanktic cnidarian and possible rugose or tabulate coral. The *Kolihaia* affinities of *Porkuniconchus* can be ruled out as the former was a free-living organism or was attached to the substrate with radiciform processes (Gnoli, 1992; Kříž et al., 2001), which is

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different from the encrusting life mode of *Porkuniconchus*. Moreover, *Porkuniconchus* lacks radiciform processes, which are one of the defining characters of *Kolihaia*.

First hardground fauna from the Hirnantian of Baltica.—The Hirnantian is an important interval of the end-Ordovician mass extinction. There are few data from Baltica on the hard substrate faunas of the Hirnantian interval, but these faunas are important for understanding the influence of mass extinctions on hard substrate encrustation and the fate of encrusting organisms. The observable hardground area is about 100 cm^2, and about 12% of the area is covered by encrusters. Thus the hardground surface is rather densely encrusted for the Ordovician hardgrounds of Baltica (i.e., usually less than 1.3% of the hardground area is encrusted; Vinn, 2015; Vinn and Toom, 2015) and does not show any adverse effects of mass extinction on the process of encrustation. The encrustation area of studied hardground is similar to the Middle Ordovician Kanosh Shale hardground, where 10.5% of the area is covered by encrusters (Wilson et al., 1992). It has been suggested that low encrustation of the other Estonian hardground could be due to low productivity (Vinn and Toom, 2015). Thus it is possible that the studied hardground represents a high-productivity site (Lescinsky et al., 2002) in the Hirnantian of the Baltic Basin. This is also supported by the high organic content of the host rock (Hints et al., 2023). It is also possible, however, that the amount of encrustation on any marine hard substrate is a function of exposure time on the seafloor (Taylor and Wilson, 2003; Zuschin and Baal, 2007). Substrates exposed longer may accumulate more skeletal encrusters regardless of productivity rates.

The hardground fauna is numerically (N = 15) and by encrustation area dominated by cornulitids. The other groups are represented by only a single specimen of the sheet-like cystoporate bryozoan *Ceramopora*. The cornulitid specimens represent different growth stages (i.e., sizes), which suggests that the hardground was continuously colonized by new cornulitid larvae. The lack of orientation of the cornulitids indicates that there were no unidirectional currents near the seafloor as it would have forced cornulitid tubeworms to orient their apertures toward the current for most efficient suspension feeding. The lack of signs of abrasion indicates quiet conditions or moderate water movements. Encrusting unilaminar growth habits of bryozoans may indicate an environmental setting near the shore (Tolokonnikova and Ernst, 2017).

One specimen of *P. fragilis* n. gen. n. sp. is encrusting a sheet-like bryozoan (Fig. 5). Some cornulitids have been overgrown by the other cornulitids (Figs. 3.4, 4). The sheet-like bryozoans are good competitors for space, but their compactness means that they do not disperse their zooids very widely (Taylor and Ernst, 2008). However, no certain signs of spatial competition occur on the studied hardground surface.

In Baltica, the temporally closest lower Katian hardground is from the Vasalemma Formation, where cornulitids are similarly accompanied by bryozoans but with the occurrence of some *Trypanites* borings (Vinn and Toom, 2015). The most striking characteristic of this hardground fragment is the lack of bioerosion, but the studied area is too small to claim that there was no bioerosion at all. The lack of borings could be caused by some local environmental conditions such as location in a shallow topographical depression, where *Trypanites* borings were less common. Nield (1984) suggested that, in addition to selecting favorable water currents, larvae of the *Trypanites* producers concentrated on topographic highs. With gradual sedimentation, topographic highs would be exposed longest, allowing more time for bioerosion (Nield, 1984; Knaust et al., 2023). There are reefs in the Ärina Formation in Reinu quarry, and bioerosion is not common in the reef facies in the Ordovician Basin of Estonia (Toom, 2019). However, bioerosion is not common in the Porkuni Regional Stage and was long considered absent there (Toom et al. 2019, 2023), which could point to the influence of the end-Ordovician mass extinction event in the Baltic region.

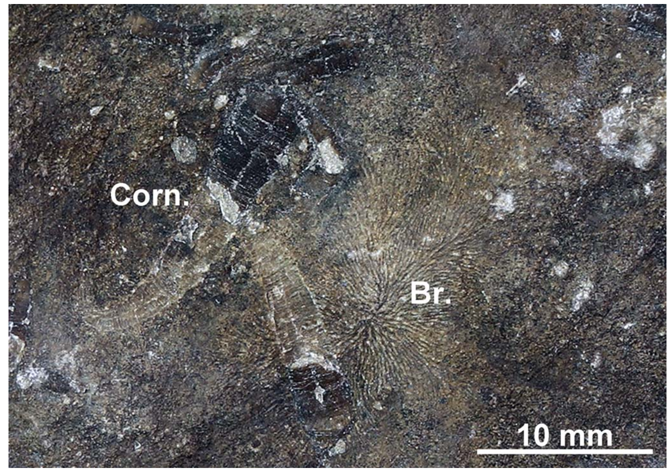

Figure 5. Tubeworm *P. fragilis* n. gen. n. sp. (Corn.) and encrusting sheet-like cystoporate bryozoan *Ceramopora* sp. (Br) on the surface of the hardground (GIT 494-49-5).

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Declaration of competing interests

The authors declare none.

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