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Cornulitid tubeworms and other calcareous tubicolous organisms from the Hirmuse Formation (Katian, Upper Ordovician) of northern Estonia

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Abstract.—Seven species of cornulitids, one unidentified tubicolous shell, and the problematic bryozoan *Lagenosypho* Spandel, 1898 are here described from the Katian of Baltica. Three new species—*Cornulites lindae* new species, *Cornulites meidlai* new species, and *Conchicolites kroegeri* new species—are described. The unidentified tubicolous organism has punctate shell structure and setae-like structures that can best be affiliated with lophophorates. The Hirmuse fauna indicates that the diversity and number of cornulitids in the Ordovician of Baltica has been underestimated and it is likely that the Baltic cornulitid fauna was as diverse and abundant as the fauna of Laurentia. Clay mud-bottom environments supported the highest cornulitid diversity in the Late Ordovician of Baltica. The occurrence of intermediate forms indicates that some tentaculitid characters, e.g., regular annulation and a nearly straight shell, which were thought to be apomorphies of free-living tentaculitids, were actually inherited from ancestral cornulitids. The cornulitid fauna of the Late Ordovician of Laurentia somewhat resembles the cornulitid fauna of the Late Ordovician of Baltica, but there are fewer common faunal elements between Gondwana and Baltica.

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Introduction

Cornulitid tubeworms are an order of encrusting tentaculitoids that are phylogenetically closely related and likely ancestors of free-living tentaculitids (Vinn and Mutvei, 2009; Vinn, 2010a; Vinn and Zatoń, 2012). The cornulitids have a global distribution and stratigraphic range from the Middle Ordovician to the late Carboniferous (Vinn, 2010a, b). The biological affinities of cornulitids have long been debated (Herringshaw et al., 2007), but with some certainty they belong to the Lophothrochozoa (Vinn and Zatoń, 2012). It is possible that cornulitids represent stem group phoronids (Taylor et al., 2010). Cornulitids are a paleoecologically important group of hard-substratum encrusters because they generally retain their original position on the substratum after fossilization (Taylor and Wilson, 2003). Cornulitid tubeworms only inhabited normal marine environments, differing from their close relatives, the microconchids, which lived in waters of various salinities (Zatoń et al., 2012, 2016; Shcherbakov et al., 2021). Fossils of cornulitid tubeworms are most common in shallow marine sediments. Cornulitids had a diverse ecology with several life modes that ranged from simple hard-substratum encrusters (Zatoń and Borszcz, 2013; Zatoń et al., 2017) to endobiotic symbionts of stromatoporoids and corals (Vinn, 2010a).

Cornulitids have rarely been studied from the Ordovician of Estonia, mostly because of their minor stratigraphical importance. The cornulitids from Estonia were first mentioned by Schmidt (1858) and Eichwald (1860). Recently, several species have been described from the Ordovician of Estonia (Vinn and Mõtus, 2012; Vinn, 2013; Vinn and Eyzenga, 2021).

The aims of this paper are to: (1) systematically describe the fauna of small cornulitids and other tubicolous organisms from the Hirmuse Formation; and (2) discuss the phylogeny, diversity, ecology, and biogeography of the Ordovician cornulitids.

Geological background and locality

A shallow, warm, epicontinental sea covered what would become modern northern Estonia during the Late Ordovician. The Ordovician sequence of northern Estonia is relatively complete (i.e., all stages are present) and is represented mostly by carbonate rocks. There was a great climatic change in the Ordovician of Baltica when the paleocontinent drifted from the southern high latitudes to the tropical realm (Torsvik et al., 2012). Carbonate sedimentation intensified during the warming of the climate (Nestor and Einasto, 1997). The first evidence of a tropical climate, e.g., tabulate corals and stromatoporoids, appeared in the early Katian.

The large Vasalemma Quarry operated by Nordkalk is situated in Vasalemma village in northwestern Estonia (Fig. 1). The Katian limestones of the Vasalemma Formation and marls of

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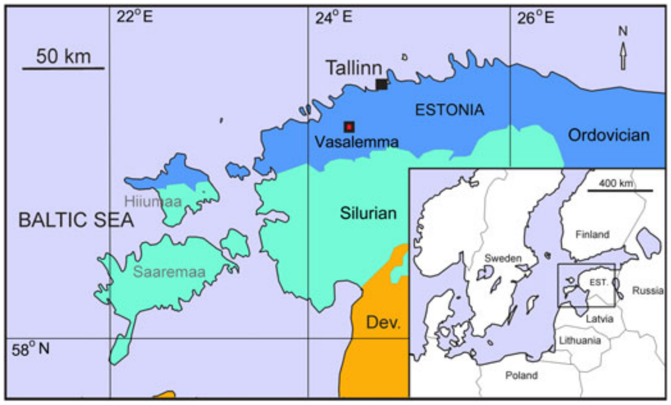

Figure 1. Map of Estonia, with locality at Vasalemma indicated by a red dot. Dev. = Devonian; EST. = Estonia.

the Hirmuse Formation are exposed in the quarry. They are excavated down to the ripple-marked upper surface of the Pääsküla Member of the underlying Kahula Formation (Hints and Miidel, 2008). The rocks of the Vasalemma Formation are represented in the quarry by a succession of bioclastic grainstones to 15 m thick. The grainstone layers contain numerous intercalated reef bodies. These reefs are composed of bryozoan framestone-bindstone, echinoderm bindstone, receptaculitid-bryozoan-microbial framestone, and tabulate bafflestone. The reef bodies can be > 50 m wide (Kröger et al., 2014). The marls and thin-bedded argillaceous limestones of the Hirmuse Formation overlie the Vasalemma Formation in the northeastern corner of the quarry. The Hirmuse Formation is characterized by a rich, normal, marine fauna including brachiopods, bryozoans, echinoderms, trilobites, and rugose corals (Hints and Meidla, 1997). The early Katian Guttenberg isotope carbon excursion (GICE) occurs in the middle and upper part of the Vasalemma Formation (Kröger et al., 2014).

Materials and methods

The single sample AM-01-21 from the Vasalemma Partek Nordkalk Quarry, outcrop 19, containing ~5 kg of marl from the upper part of section, was washed with water, and 40 complete small tubes or fragments of larger tubes of cornulitids were manually picked from the washed residue. Specimens were later coated with platinum and photographed using a scanning electron microscope (SEM) at the Paleontological Institute of the Russian Academy of Sciences. Measurements were obtained from calibrated SEM images.

Repositories and institutional abbreviations.—Types, figured, and other specimens examined during this study are deposited in the following institutions: Department of Geology, Tallinn University of Technology (GIT), and the Geological Collections of the Natural History Museum, University of Tartu (TUG).

Systematic paleontology

Class Tentaculitida Bouček, 1964
Order Cornulitida Bouček, 1964
Family Cornulitidae Fisher, 1962
Genus *Conchicolites* Nicholson, 1872

Type species.—*Conchicolites gregarius* Nicholson, 1872.

Conchicolites kroegeri new species
Figure 2.1–2.4

Type specimens.—Holotype, GIT 421-137, Vasalemma Partek Nordkalk Quarry, northern Estonia, Hirmuse Formation, lower Katian, Upper Ordovician; paratypes, GIT 421-135, 421-136, 421-138, 421-139, 421-140, and 421-134, same locality.

Diagnosis.—Small tube with very rapidly growing diameter and well-developed, densely spaced, regular, perpendicular ridges.

Occurrence.—Only known from Vasalemma Partek Nordkalk Quarry, northern Estonia, Hirmuse Formation, lower Katian, Upper Ordovician.

Description.—Small tubes usually attached to the substrate only in their proximal part. The tubes are 0.6–1.7 mm long and to 0.6 mm wide at the aperture. Tube diameter expands rapidly in the initial growth stage. The angle of divergence is 20–30°. Free distal parts of the tubes sometimes tilt away from the substratum. The tube base is widened in the form of protruding perpendicular ridges making the horizontal contour of the tube base serrated. The perpendicular ridges are much stronger at the tube's contact with the substratum than on the top of the tube. There are 10 perpendicular ridges of 0.5 mm at the distal part of the tube. The perpendicular ridges are regular, densely spaced, well-developed, sharp, but rather low at the top of the tube and not always continuous along the exposed surface of the tube. The tube interior is smooth without any annulation.

Etymology.—Named in honor of Björn Kröger for his detailed studies on the paleontology and sedimentology of the rocks exposed in the Vasalemma quarries.

Remarks.—This new species is assigned to the genus *Conchicolites* because of its smooth tube interior. It closely resembles *Conchicolites rossicus* (Vinn and Madison, 2017) (Vinn and Madison, 2017, p. 238, fig. 2) by its regular, dense, well-developed, perpendicular ridges. This new species differs from *Conchicolites rossicus* in that its broad tubes expand much more rapidly in diameter than the tubes of *Conchicolites rossicus*. It also resembles *Cornulitella minor* Nicholson, 1872 (Hall, 1888, pl. 115, fig. 3) from the Upper Ordovician of North America with its regular, dense, well-developed, perpendicular ridges, but differs by its much broader tube. The broad tubes of *Cornulites devonicus* Pacht in Helmersen and Pacht, 1858 (Vinn et al., 2019, p. 71, figs. 5A, B, 6A–H) resemble tubes of this new species, but they differ in having an annulated tube interior and external longitudinal striation.

Conchicolites sp. indet. A
Figure 2.5

Occurrence.—Vasalemma Partek Nordkalk Quarry, northern Estonia, Hirmuse Formation, lower Katian, Upper Ordovician.

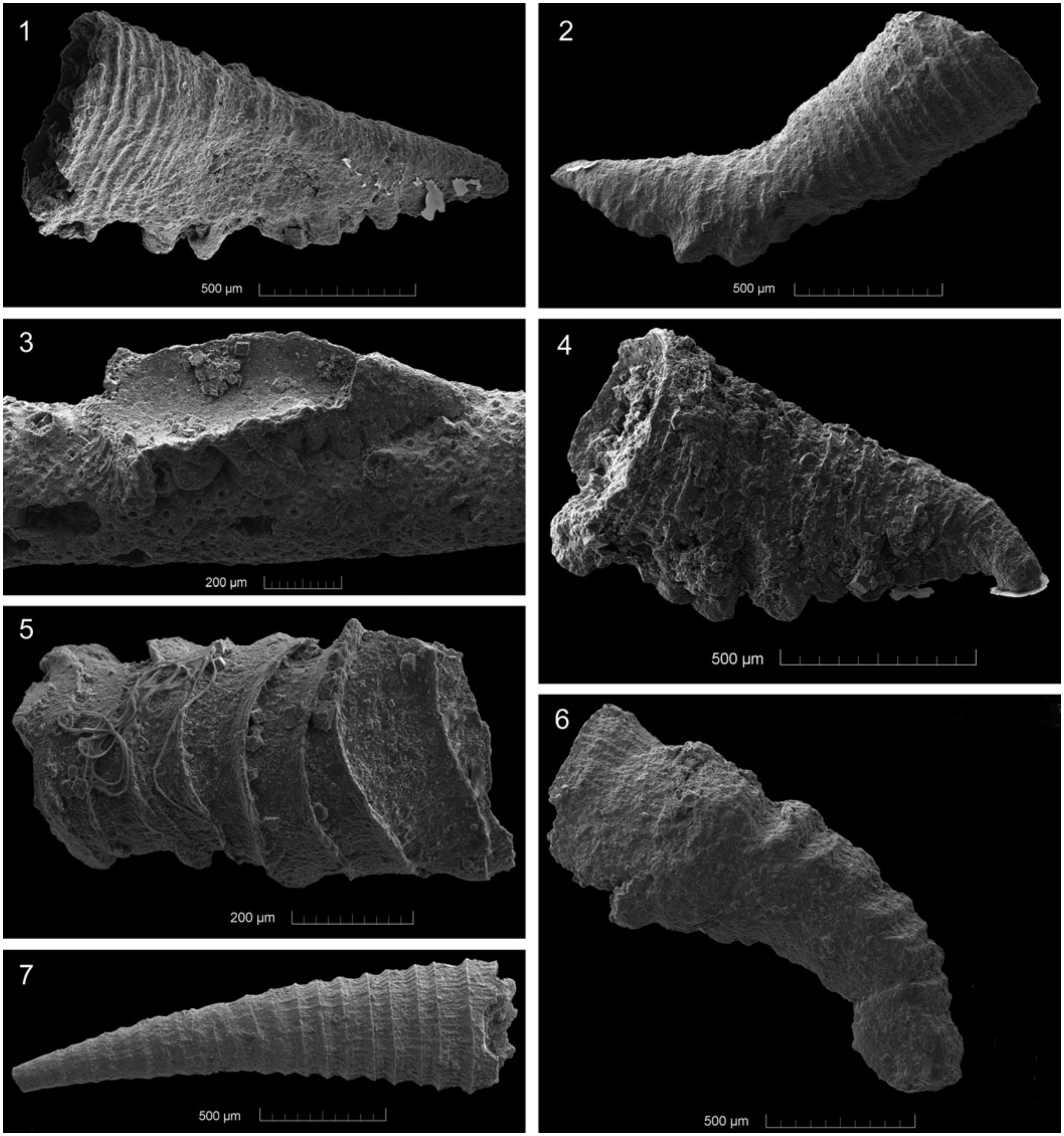

Figure 2. Cornulitid tubeworms from Vasalemma Partek Nordkalk Quarry, northern Estonia, Hirmuse Formation, Upper Ordovician: (**1–4**) *Conchicolites kroegeri* n. sp.: (**1**) holotype, GIT 421-137; (**2**) paratype, GIT 421-135; (**3**) paratype, GIT 421-138, with tube interior exposed; (**4**) paratype, GIT 421-139; (**5**) *Conchicolites* sp. indet. A, GIT 421-133; (**6**) *Cornulites* cf. *C. sterlingensis* Meek and Worthen, 1866, GIT 421-127; (**7**) *Cornulites lindae* n. sp., holotype, GIT 421-144.

Description.—Fragmentarily preserved small tube (diameter to 0.4 mm). The tube slowly expands in diameter and is sparsely covered with prominent but thin, sheet-like, and high-perpendicular to subperpendicular ridges that tilt toward the tube aperture. The interspaces between the ridges are smooth and flat, rarely slightly concave. The ridges are ∼10 um thick; distances between them vary from 50–180 µm.

Materials.—GIT 421-133-2.

Remarks.—*Conchicolites* sp. indet. A does not resemble any other Ordovician cornulitid. It differs from *Conchicolites rossicus* (see Vinn and Madison, 2017, p. 238, fig. 2) from the Katian of northwestern Russia, and *Conchicolites kroegeri* n. sp., by very long interspaces between the perpendicular ridges. *Conchicolites* sp. indet. A resembles *Conchicolites* sp. indet. 1 (Vinn and Wilson, 2013, p. 365, fig. 13) from the Rhuddanian of Estonia in its peristome-like perpendicular ridges that are slightly tilted toward tube aperture, but it differs by its smaller size and unattached tube part. *Conchicolites* sp. indet. A resembles in its peristome-like perpendicular ridges the annulation of *Cornulites*? *semiapertus* Öpik, 1930 (Vinn, 2013, p. 109, figs. 3, 4) from the Darriwilian to Sandbian of Estonia, but it differs by its smaller size and smooth tube interior. We are not erecting a new species because we have studied too few specimens.

Genus *Cornulites* Schlotheim, 1820

Type species.—*Cornulites serpularius* Schlotheim, 1820.

Cornulites cf. *C. sterlingensis* Meek and Worthen, 1866
Figure 2.6

1888 *Cornulites sterlingensis*; Hall, pl. 115, fig. 7.
2017 *Cornulites* cf. *sterlingensis*; Vinn and Madison, p. 238, fig. 3.

Occurrence.—Vasalemma Partek Nordkalk Quarry, northern Estonia, Hirmuse Formation, lower Katian, Upper Ordovician.

Description.—Small tube expanding moderately in diameter. The maximum diameter of the tube is ~0.5 mm. The tube bears a linear, deep attachment scar in its entire length. The tube is covered with strong, regular annulations with sharp crests. The interspaces between the annuli are deep and concave. There are six annuli/mm in the distal part of the tube. The tube is covered with strong longitudinal striae. There are approximately four striae per 0.1 mm.

Materials.—GIT 421-127, 421-128, and 421-129.

Remarks.—The studied specimens resemble *Cornulites sterlingensis* (see Hall, 1888, pl. 115, fig. 7) from the Cincinnatian (Katian) of Ohio, but are much smaller. We consider our specimens juveniles and assign them tentatively to *Cornulites sterlingensis*. Our material also resembles *Cornulites* cf. *C. sterlingensis* from the Katian of northwestern Russia (Vinn and Madison, 2017), but our specimens are also somewhat smaller. Poorly preserved specimens of possible *Cornulites* cf. *C. sterlingensis* have also been described from the Takche Formation, Himalaya (Shabbar et al. 2022), but their state of preservation does not allow proper comparison with our specimens.

Cornulites lindae new species
Figures 2.7, 3.1–3.3

2013 *Cornulites* sp. A; Vinn, p. 110, fig. 6.

Type specimens.—Holotype, GIT 421-144, Vasalemma Partek Nordkalk Quarry, northern Estonia, Hirmuse Formation, lower Katian, Upper Ordovician; paratypes, GIT 421-145, 421-147, 421-151, and 421-152, same locality.

Diagnosis.—Small, moderately expanding, almost straight tubes with delicate longitudinal striae, moderately developed annulation, and sharp, but not strong, annular crests.

Occurrence.—Vasalemma Partek Nordkalk Quarry, northern Estonia, Hirmuse Formation, lower Katian, Upper Ordovician.

Description.—Small (to 1.9 mm long, 0.5 mm wide) nearly straight tube. The tube is circular in cross section and expands moderately in diameter. The angle of tube divergence is ~15°. Tubes are covered with more or less regular, moderately developed annulations. The annuli are stronger near the aperture, with sharp crests. The interspaces of the annuli are concave and V- to U-shaped in longitudinal section. The deepest part of the interspaces is usually located midway between two adjacent annular crests. There are six annuli per 0.5 mm near the tube aperture. The tube is covered with moderately developed regular longitudinal striae. The striae are stronger near the aperture. There are six striae per 0.1 mm at the tube aperture.

Etymology.—Named in honor of Linda Hints for her studies on the paleontology and sedimentology of the rocks exposed in the Vasalemma quarries.

Remarks.—*Cornulites lindae* n. sp. most closely resembles *Cornulites* sp. indet. A from the Sandbian of Estonia in its weak striae and the general shape of the tube, but it differs by its smaller size, slightly broader tube, and sharper annular crests. Despite some differences, we have synonymized *Cornulites lindae* n. sp. and *Cornulites* sp. indet. A (Vinn, 2013) because they likely represent different growth stages of the same species. This new species also somewhat resembles *Cornulites serpularius* (see Vinn and Wilson, 2013, p. 360, figs. 3, 4) from the Wenlock of Estonia in its moderately expanding tube and relatively faint longitudinal striae. This new species differs from *Cornulites serpularius* in having sharper annular crests on the tube exterior and more regular annulation.

Cornulites meidlai new species
Figure 3.4–3.7

2013 *Cornulites* sp. C; Vinn, p. 110, fig. 8.

Type specimens.—Holotype, TUG 1383-5, Rakvere, northern Estonia, Keila Regional Stage, lower Katian, Upper Ordovician; paratypes, GIT 421-125, 421-126, 421-78, 421-155, and 421-156, Vasalemma Partek Nordkalk Quarry, northern Estonia, Hirmuse Formation, lower Katian, Upper Ordovician.

Diagnosis.—Tubes externally covered with strong reticulate ornament, with divergence angle ~12° and vesicular wall structure at the annular crests.

Occurrence.—Vasalemma Partek Nordkalk Quarry, northern Estonia; previously reported by Vinn (2013) from Rakvere (three complete shells), Rägavere (one complete shell), Keila to Rakvere stages, Katian, Upper Ordovician.

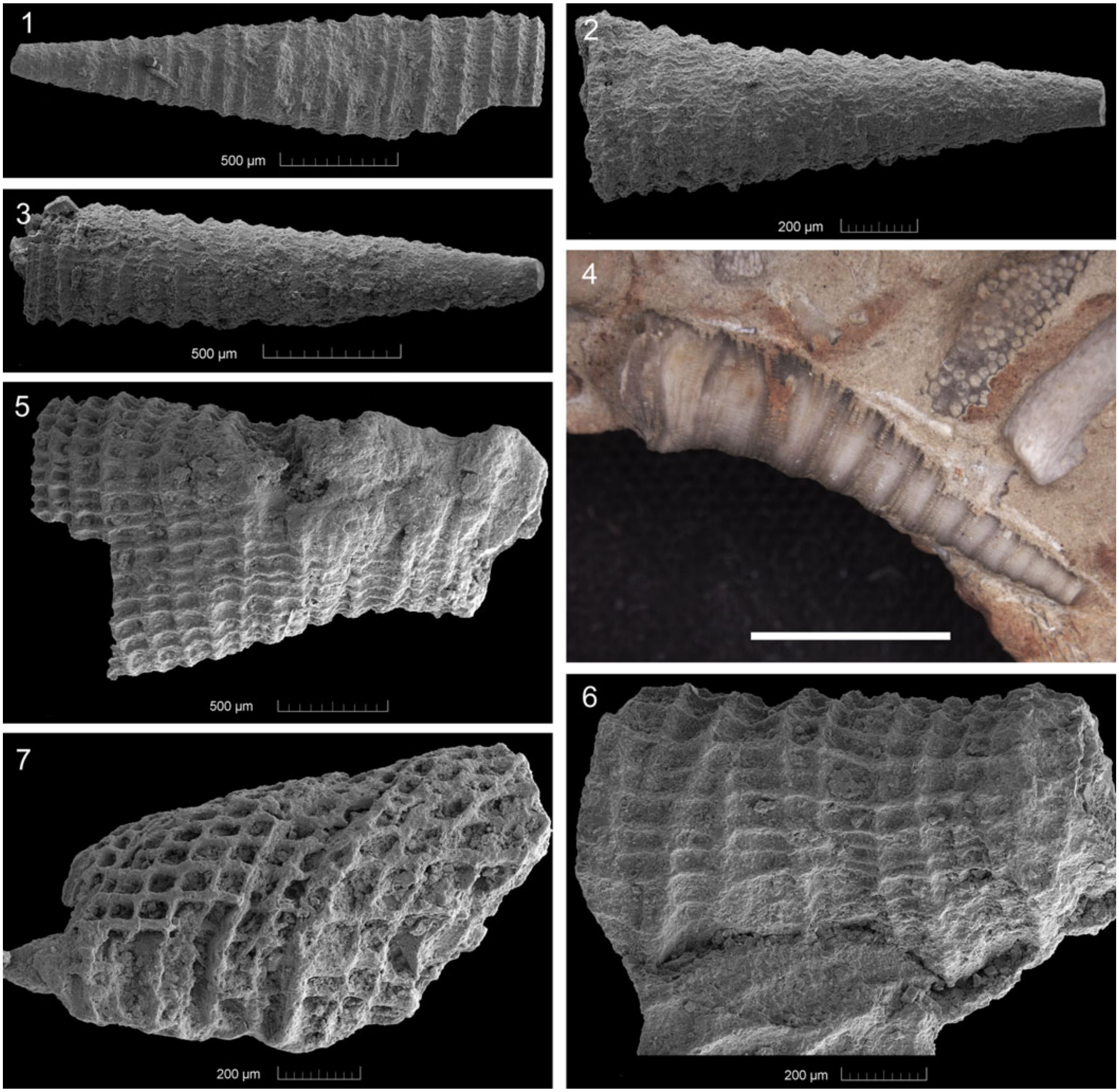

Figure 3. (**1–3**) *Cornulites lindae* n. sp., Vasalemma Partek Nordkalk Quarry, northern Estonia, Hirmuse Formation, Upper Ordovician: (**1**) paratype, GIT 421-145, somewhat flattened; (**2**) paratype, GIT 421-151, somewhat flattened; (**3**) paratype, GIT 421-152; (**4–7**) *Cornulites meidlai* n. sp.: (**4**) holotype, TUG 1383-5, Rakvere, Keila Regional Stage, scale bar = 0.5 mm; (**5–7**) paratypes, Vasalemma Partek Nordkalk Quarry, northern Estonia, Hirmuse Formation, lower Katian, Upper Ordovician: (**5**) GIT 421-126; (**6**) GIT 421-155; (**7**) GIT 421-156.

Description.—Tube of moderate size covered with strong reticulate ornament. The mature tubes are 13–15 mm long and 3.0–4.0 mm wide at the aperture. Long free tube parts can occur. The tube fragments from Vasalemma with reticulate ornament are to 1.2 mm wide. The reticulate ornament is formed by equally strong and well-developed perpendicular growth lines and longitudinal striae. The annulation on the tube exterior is somewhat irregular and not always clearly visible. The tube interior is regularly annulated. The tube expands moderately in diameter. The divergence angle of the tube is ∼12°. The tube wall is vesicular at the annular crests. The distance between annular crests is ∼1.7 mm at the tube diameter of 4 mm. The basal edge is not widened. Emended from Vinn (2013).

Etymology.—Named in honor of Prof. Tõnu Meidla for his great contributions to the study of Estonian Ordovician fossils and facilitating paleontological research at the University of Tartu.

Remarks.—The prominent longitudinal striae of the new species resemble those of *Cornulites sterlingensis* (see Hall, 1888, pl. 115, fig. 7) from the Cincinnatian (Katian) of Ohio, but the

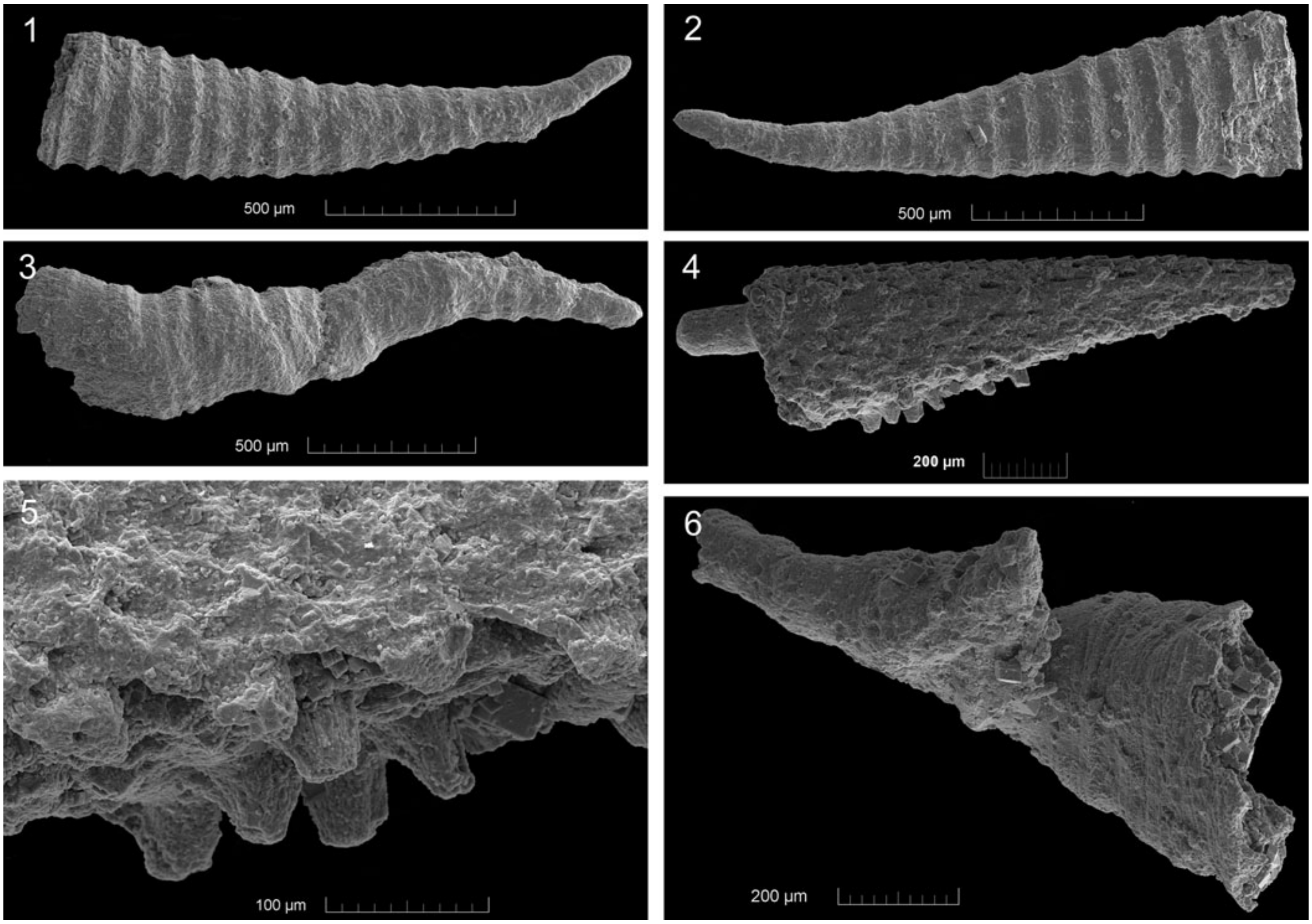

Figure 4. (**1, 2**) *Cornulites* sp. indet. A, Vasalemma Partek Nordkalk Quarry, northern Estonia, Hirmuse Formation, Upper Ordovician: (**1**) GIT 421-142; (**2**) GIT 421-143; (**3**) *Cornulites* sp. indet. B, GIT 421-146, Vasalemma Partek Nordkalk Quarry, northern Estonia, Hirmuse Formation, Upper Ordovician; (**4, 5**) unidentified conical shell, GIT 421-148, Vasalemma Partek Nordkalk Quarry, northern Estonia, Hirmuse Formation, Upper Ordovician: (**4**) entire specimen; (**5**) setae-like structures on (**4**); (**6**) *Lagenosypho* sp. indet., GIT 421-131, Vasalemma Partek Nordkalk Quarry, northern Estonia, Hirmuse Formation, Upper Ordovician.

former differs in the lack of well-developed external annulation and by stronger perpendicular growth lines. This new species also resembles *Reticornulites reticulatus* Lardeux, Jaouen, and Plusquellec, 2003 (Lardeux et al., 2003, p. 652–654, fig. 2) in its reticulate ornamentation with predominant transverse rings and fine longitudinal striae, but it differs by its regularly annulated interior.

Cornulites sp. indet. A
Figure 4.1, 4.2

Occurrence.—Vasalemma Partek Nordkalk Quarry, northern Estonia, Hirmuse Formation, lower Katian, Upper Ordovician.

Description.—Small tubes to 1.6 mm long and 0.35 mm wide. The tube is circular in cross section, slightly curved, with a long free part. There are no signs of attachment structures. The tube expands moderately in diameter. The angle of divergence is ~15°. The tube is covered with regular, well-developed annulation. The crests of the annuli are rather sharp and the interspaces are concave and V- to U-shaped in longitudinal section. There are approximately seven annuli per 0.5 mm in the distal part of the tube. The annuli are stronger near the aperture.

Materials.—GIT 421-142, 421-143, 421-153, and 421-154.

Remarks.—*Cornulites* sp. indet. A closely resembles *Cornulites lindae* n. sp. in its regular and moderately developed sharp annuli, but it differs in the absence of longitudinal striae. *Cornulites* sp. indet. A might belong to *Cornulites lindae* n. sp. if the lack of striae is an artifact of preservation.

Cornulites sp. indet. B
Figure 4.3

Occurrence.—Vasalemma Partek Nordkalk Quarry, northern Estonia, Hirmuse Formation, lower Katian, Upper Ordovician.

Description.—Immature tube small (1.9 mm long, 0.4 mm wide), slightly meandering but generally straight, and externally covered with irregularly developed annuli. Some annuli are prominent on one side of the tube and weakly developed on the opposite side. There are approximately five annulations per 0.5 mm near the tube aperture. The tube expands moderately in diameter. The angle of divergence is ∼15°. No attachment structures are visible. The mature tubes are large (11 mm long, 3.2 mm wide) and covered by faint longitudinal striae. There are approximately eight striae per 0.5 mm near tube aperture. The mature tubes are attached in their entire length and have a prominent widened base.

Materials.—Immature GIT 421-146; mature GIT 421-124.

Remarks.—The described specimens most closely resemble *Cornulites*? sp. indet. D (Vinn, 2013, p. 111, fig. 9) from the Vasalemma Formation in its somewhat irregular annulation and relatively narrow tube.

Unidentified conical shell
Figure 4.4, 4.5

Occurrence.—Vasalemma Partek Nordkalk Quarry, northern Estonia, Hirmuse Formation, lower Katian, Upper Ordovician.

Description.—Small, straight, conical shell (1.2 mm long, 0.4 mm wide) that expands rapidly in diameter. The angle of divergence is ∼19°. Inside the cone, on one side, is a slightly conical tube running throughout. The diameter of the external cone expands faster than the diameter of the internal conical tube. The diameter of the internal tube at the aperture of the external cone is 0.12 mm. The tilted ornamentation of the external tube is posteriorly directed and affiliated with the punctae. The punctae are ∼10–15 µm in diameter (GIT 421-148) and well pronounced at one side of the cone, whereas on the other side, the punctae seem to be penetrated by conical appendages.

Materials.—One almost complete shell (GIT 421-148).

Remarks.—The appendages on its one side strongly resemble the phosphatized setae of lower Paleozoic brachiopods (Jin et al., 2007), but this does not prove a shared origin in terms of structure or secretion process. The structure of setae-like appendages in the conical shell is not known and thus cannot be compared with the structure of phosphatized setae in brachiopods.

Phylum Bryozoa Ehrenberg, 1831
Order Cyclostomata Busk, 1852
Family Corynotrypidae Dzik, 1981
Lagenosypho Spandel, 1898

Type species.—*Lagenosypho permianus* Spandel, 1898.

Lagenosypho sp. indet.
Figure 4.6

Occurrence.—Vasalemma Partek Nordkalk Quarry, northern Estonia, Hirmuse Formation, lower Katian, Upper Ordovician.

Description.—Conical zooecia with oval cross sections. The external walls of the zooecia are covered by fine growth lines to eight per 0.1 mm. The walls of the zooecia are very thin. The zooecia are 0.6 mm long and 0.45 mm wide at the widest side.

Materials.—Single fragment (GIT 421-131).

Remarks.—The described specimen has most in common with corynotrypids (see Dzik, 1981). It is tentatively assigned to *Lagenosypho* (personal communication, P.D. Taylor, 2022).

Discussion

Biological affinities of the unidentified conical shell.—The general shape of this conical shell resembles those of cornulitids and tentaculitids. However, it is devoid of the perpendicular ornamentation characteristic of cornulitids. Moreover, there is a cylindrical structure that reaches through the tube from the proximal to the distal end of the shell. This cylindrical structure is likely not a substratum for the conical body around it, but a part of the organism because its diameter greatly increases from the narrow to the broad end of the shell. The inner tube is not located exactly in the center of conical shell but is closer to one side. The organism could have had differentiated ventral and dorsal sides. Such asymmetry shows that our problematic organism might be affiliated with bilateral animals. Among bilateral animals, nautiloids have conical shells with a siphuncle that is often located closer to one side of the shell wall. However, the inner tube of our organism is rather thick for a typical nautiloid siphuncle and there are no septae connected to the inner tube. Moreover, the punctate shell and setae-like structures are not known in cephalopods. The punctate shell structure and setae-like structures of this organism can be affiliated with lophophorates. The strange appearance of setae-like structures on only one side of the shell is likely an artifact of preservation. In modern brachiopods, setae are located at the anterior commissure of the shell. However, in the early Paleozoic linguliforms, orthides, and even tommotiids, the preserved setae (or punctae preserving the traces of setae) cover the whole shell surface. Therefore, the preserved conical structures are possibly homologues of the setae of lophophorates. One would expect in the case of a lophophorate with a conical shell to also see setae also around its aperture and not everywhere on one side of its exterior. Thus, it is possible that these setae-like structures are not homologues of brachiopod setae, making the possible lophophorate affinities of the organism uncertain.

Diversity and paleoenvironments.—Vinn (2013) concluded that cornulitids seem to be relatively rare in the Late Ordovician of Baltica, which contrasts with the situation in the Late Ordovician of North America where cornulitids seem to be more common (Hall, 1888; Richards, 1974; Morris and Felton, 1993, 2003). The numerous and diverse cornulitids from the Hirmuse Formation indicate that the diversity and abundance of cornulitids in the Ordovician of Baltica has been underestimated and it is likely the Baltic cornulitid fauna was not less diverse and abundant than the fauna of North America. Macroscopic cornulitid fossils of the Ordovician of Estonia were described by Öpik (1930) and Vinn (2013).

However, no previous data exists on the diversity of small to microscopic fossil cornulitids. The large number of tiny cornulitids in the Hirmuse fauna demonstrates that many Ordovician cornulitids were very small and were not always present on large substrata, e.g., brachiopod shells, which were the most common substrata for cornulitids in the Ordovician. Instead, the Hirmuse cornulitids preferred small substrata often less than one millimeter in size. The cornulitids were collected from a clay, which represents a mud-bottom environment in the Hirmuse Formation. The muddy bottom fauna of the Hirmuse Formation might also differ from the encrusting fauna present on brachiopods in the limestones of the Vasalemma Formation. Considering the high diversity of the studied soft-bottom cornulitid fauna, it seems that clay-mud environments supported the highest cornulitid diversity in the Late Ordovician of Baltica. The muddy environment was also inhabited by numerous bryozoans (including erect corynotrypids), tiny brachiopods, and unknown organisms with conical shells. The biodiversity of tubicolous organisms in such muddy environments needs further study; such study could lead to reassessment of biodiversity curves for the Ordovician of Baltica.

Evolutionary notes.—Some cornulitids, e.g., *Cornulites* sp. indet. A and *Cornulites lindae* n. sp. from the Vasalemma fauna, resemble free-living tentaculitids in their general shell shape and very regular, well-developed annulation. The free-living tentaculitids likely appeared sometime in the Ordovician (Vinn, 2010a). However, many supposed Ordovician tentaculitids could actually be tentaculitid-like cornulitids similar to some of our specimens. The free-living tentaculitids presumably evolved from cornulitid ancestors, so the discovery of intermediate forms among the Late Ordovician tentaculitoids is not surprising. These intermediate forms indicate that some tentaculitid characters, e.g., regular annulation and the almost straight shell, which were thought to be apomorphies of free-living tentaculitids, were actually inherited from ancestral cornulitids. The adaptation to encrust microscopic substrata led to the appearance of cornulitid tubes with long free parts that could have played a role in the evolution of typical free-living tentaculitid morphology. Cornulitids have a postlarval shell (Vinn and Mutvei, 2009), whereas in tentaculitids, the shell first appears in the larval stage as a long conical process (Farsan, 2005). The tentaculitids possibly evolved from cornulitids by changes in the life cycle, i.e., by the prolongation of the free-swimming stage with the larva metamorphosing into the juvenile while swimming and forming the shell in the water column as was proposed for other lophotrochozoans (Vinn and Mutvei, 2009).

Paleobiogeography of cornulitid fauna.—The cornulitid fauna of the Late Ordovician of North America (see Hall, 1888) somewhat resembles the cornulitid fauna of the Late Ordovician of Baltica (Vinn, 2013; present paper). *Cornulites sterlingensis* occurs both in the Late Ordovician of Laurentia (Hall, 1888) and Baltica (Vinn and Madison, 2017; present paper). The species of *Conchicolites* described from the Late Ordovician of Baltica (Vinn and Madison, 2017; present paper) are also somewhat similar to *Cornulitella minor* (see Hall, 1888, pl. 115, fig. 3). The cornulitid faunas of Gondwana are relatively well known. The Gondwanan cornulitids have been described from Morocco (Gutiérrez-Marco and Vinn, 2018) and Peru (Vinn and Gutiérrez-Marco, 2016); they also occur in Bohemia (Barrande, 1867), Spain (Verneuil and Barrande, 1855), France (Dreyfuss, 1948), Sardinia (Spano, 1974), and the Himalaya (Shabbar et al., 2022). Nevertheless, there are fewer common cornulitid species (i.e., *Cornulites* cf. *C. sterlingensis*) between Gondwana and Baltica. Moreover, small *Conchicolites*-like forms are unknown from Gondwana but such forms are known both from the Late Ordovician of Baltica (*Conchicolites rossicus* and *Conchicolites kroegeri* n. sp.) and Laurentia (*Cornulitella minor*) (see Hall, 1888).

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Declaration of competing interests

The authors declare none.

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