Distribution of Conichnus and Amphorichnus in the Lower Paleozoic of Estonia (Baltica)

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Abstract: Conichnus conicus and Amphorichnus papillatus occur in clay-rich carbonate rocks in the Ordovician of Estonia. Conichnus conicus also occurs in clay-rich carbonates of the early Silurian of Estonia. Lateral adjustment traces are more common in C. conicus than previously recorded. The lack of adjustment traces in Amphorichnus, together with its morphology, does not support synonymy of Conichnus and Amphorichnus. The Conichnus conicus and Amphorichnus papillatus traces referred to shallow water carbonate environments with high clay content. They were rare or did not occur in deeper water muddy environments or where shallow water carbonates accumulated. A high content of volcanic ash in the depositional environment is characteristic of both the Ordovician and Silurian maxima of Conichnus conicus occurrence. C. conicus may have been more common in the temperate seas of Baltica than in the tropics.

Key Words: Ichnofossils; burrows; endichnia; Ordovician; Silurian; Baltica.

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Résumé : Répartition de Conichnus et d'Amphorichnus dans le Paléozoïque inférieur d'Estonie (bouclier balte).- Conichnus conicus et Amphorichnus papillatus sont présents dans des roches carbonatées riches en argiles de l'Ordovicien d'Estonie. Conichnus conicus est également présent dans des roches carbonatées riches en argiles du Silurien inférieur d'Estonie. Les signes d'ajustements latéraux sont plus fréquents chez C. conicus que ce que nous connaissions auparavant. L'absence de signes d'ajustements chez Amphorichnus, conjointement à sa morphologie, ne vient donc pas corroborer la synonymie de Conichnus et d'Amphorichnus. Les organismes à l'origine des traces de type Conichnus conicus et Amphorichnus papillatus préféraient des environnements peu profonds, carbonatés mais présentant une teneur élevée en argile. Ils sont, par contre, rares ou absents dans des environnements peu profonds mais où les carbonates s'accumulent ou dans des environnements plus profonds et boueux. Une forte teneur en cendres volcaniques dans l'environnement de dépôt représente un trait caractéristique des pics d'abondance ordoviciens et siluriens de Conichnus conicus. C. conicus semble avoir été plus fréquent dans les mers tempérées du bouclier balte que dans celles sous les tropiques.

Mots-clefs : Ichnofossiles ; terriers ; endichnia ; Ordovicien ; Silurien ; bouclier balte.

1. Introduction

Ichnofossils are important environmental indicators, and they provide us with valuable information on animal behavior in the geological past (Seilacher, 2007). Ichnofossil assemblages of the Ordovician and Silurian in many areas are relatively well known (Seilacher, 2007), but the number of studies devoted to the Ordovician and Silurian ichnofaunas of Estonia and the eastern Baltic is limited (Männil, 1966; Dronov et al., 2002; Mikulaš & Dronov, 2005; Ershova et al., 2006; Knaust et al., 2012; Knaust & Dronov, 2013; Vinn et al., 2014). The Ordovician ichnofossils of Estonia that have been described are mostly hard substrate borings (Vinn, 2005; Vinn & Wilson, 2010; Vinn et al., 2014).

Conichnus Männil, 1966 and Amphorichnus Männil, 1966 are common ichnogenera of plug-shaped burrows (Männil, 1966; Frey & Howard, 1981; Pemberton et al., 1988). They are found in various sedimentary rocks of marine origin from the Cambrian onwards (Männil, 1966; Frey & Howard, 1981; Jones & Pemberton, 1989; Pickering et al., 1992; Knaust, 2007; Paczšena, 2010; Metz, 2011). Conichnus has been interpreted as the resting trace or dwelling structure of anemone-like animals (Frey & Howard, 1981). Ordovician Conichnus traces were described in detail by Männil (1966), but their Silurian occurrences have remained problematic (Männil, 1966).

This paper addresses the following questions:
1) To which ichnospecies does the Conichnus in
the Silurian of Estonia belong? 2) How are Conichnus and Amphorichnus traces distributed in the Lower Paleozoic of Estonia? 3) How does the abundance of Conichnus change in the Ordovician and Silurian of Estonia? Are such abundance changes correlated with climatic change (temperate versus tropical climate) and changes in sedimentation? 4) How do the dimensions and morphology of Conichnus differ in the Ordovician and Silurian of Estonia?

2. Paleoenvironments

Paleogeography and sedimentation in Baltic basin

During the Ordovician, the paleocontinent Baltica moved from the temperate climatic zone into the subtropical realm (TORSVIK et al., 1992; NESTOR & EINASTO, 1997; TORSVIK et al., 2013). In the Middle Ordovician and Sandbian, the area of modern Estonia (Fig. 1) was covered by a shallow, epicontinental sea with little bathymetric variability and an extremely low sedimentation rate (MÕTUS & HINTS, 2007). Along the entire extent of the ramp a series of grey calcareous and argillaceous sediments accumulated with a trend of increasing clay and decreasing bioclasts in the offshore direction (NESTOR & EINASTO, 1977). In the Late Ordovician the climatic change resulted in an increase in carbonate production and sedimentation rate on the carbonate shelf and the occurrence of the first carbonate buildups in the basin.

During the Silurian, Baltica was located in equatorial latitudes and drifting northwards (COCKS & TORSVIK, 2005; TORSVIK et al., 2013). An epicontinental basin covered middle and western Estonia (Fig. 1) with wide range of tropical environments and diverse biotas (HINTS et al., 2008). Five main facies belts have been recognized in the Estonian part of Baltic basin: tidal flat/lagoonal, shoal, open shelf, basin slope and a basin depression (NESTOR & EINASTO, 1977). The first three facies belts formed a carbonate platform (RAUKAS & TEEDUMÄE, 1997).

Sedimentation in study area

The Tremadoc to Floian section of the Ordovician of Estonia is characterized by a terrigenous sedimentation in relatively shallow normal marine basin. Various sandstones dominate the succession (Pakerort, Hunneberg and Billingen regional stages), along with kerogenous argillites (Varangu Regional stage) and phosphatic brachiopod coquinas (Pakerort Regional Stage) (RAUKAS & TEEDUMÄE, 1997).

The Dapingian to Hirnantian succession is characterized by various normal marine carbonate rocks, mostly limestones, in northern Estonia, which accumulated in the shallow part of the basin. In addition to limestones, marls occur in lesser amounts. The purest limestones are in the Dapingian-Darriwilian and most of the Katian of northern Estonia. The Sandbian is characterized by a higher content of clay in carbonate rocks. In addition to limestones, oil shales (i.e.,
kerogenous carbonates) accumulated in the Sandbian (Kukruse Regional Stage) of northern Estonia. The carbonate sediments of the Haljala Regional Stage are especially rich in clay. Carbonate buildups are common in the northern Estonia starting in the early Katian (Oandu Regional Stage). The Dapingian to Hirnantian succession of southern Estonia is characterized by terrigenous sediments, mostly marls and argillites, which accumulated in the deeper part of the basin (RAUKAS & TEEDUMÄE, 1997).

The Silurian succession in middle and western Estonia is characterized by various normal marine carbonate rocks, mostly limestones and secondary dolomites, which accumulated on a carbonate platform. Bioherms are common throughout the Silurian in the middle and western Estonia (KALJO, 1970; RAUKAS & TEEDUMÄE, 1997). Marginal marine lagoon dolomites also occur in the Silurian of western Estonia; they may have formed in elevated salinities (KALJO, 1970; RAUKAS & TEEDUMÄE, 1997). In some parts of the section argillaceous limestones and marls are common (i.e., Adavere Regional Stage and Jaani Regional Stage) (KALJO, 1970). The Silurian succession in southern Estonia is characterized by an alternation of marls and argillaceous rocks that accumulated in the deeper part of the basin (KALJO, 1970; RAUKAS & TEEDUMÄE, 1997).

3. Material and methods

A collection of 461 Conichnus conicus from the Ordovician and Silurian of Estonia was studied, along with a collection of 611 Amphorichnus papillatus traces from the Ordovician of Estonia. These collections are deposited at the Institute of Geology, Tallinn University of Technology. The best preserved Conichnus conicus (n=69) and Amphorichnus papillatus (n=63) specimens were measured with calipers to an accuracy of 0.1 mm. Selected traces were photographed using a Nikon D7000 camera. Some traces were cut longitudinally and transversely in order to study their internal structure.

4. Geological background

Northern Estonia has abundant well-studied Ordovician outcrops. Similarly, the Silurian is well exposed and studied in middle and western Estonia. The deeper water Ordovician and Silurian sections of southern Estonia are well covered by hundreds of drill cores and thoroughly studied by numerous palaeontologists from the Institute of Geology (TUT) during the past fifty years (RAUKAS & TEEDUMÄE, 1997). Thus the samples in the collections of the Institute of Geology, Tallinn University of Technology, are not biased towards certain stratigraphic intervals or depositional environments.

The thickness of the Uhaku Stage (Fig. 2) in northern Estonia varies from 5-10 m in the west to about 20-25 m in the east. In northern Estonia the lower part of the Uhaku Stage is composed of hard bioclastic limestones belonging to the Väo Formation. The formation has a rather consistent thickness (4-5 m). The upper part of the Uhaku Stage is made up of relatively thin-beded argillaceous limestones of the Kõrgekallas Formation that contain Conichnus conicus. The formation is subdivided into the Koljala, Pärtlioru and Erra members (HINTS, 1997). In the upper part of the section there are also thin layers of oil shale. The argillaceous limestones of the Uhaku Stage were deposited in a relatively shallow epicontinental sea with normal salinity (RAUKAS & TEEDUMÄE, 1997).
The thickness of the Kukruse Regional Stage (Fig. 2) in northern Estonia ranges from about 3 m in the west to more than 20 m in the east (HINTS, 1997). The stage consists of three formations. The argillaceous bioclastic limestones with intercalations of oil shale (kukersite) and marls of the Viivikonna Formation occur northeast of the line Osmussaar Island - south coast of Lake Peipsi. Oil shale contains 15-46% kerogen, 26-5% carbonates and 18-42% terrigenous material (HINTS, 1997). Based on the abundance of kukersite seams, the Viivikonna Formation is subdivided into the Kiviõli, Peetri and Maidla members. Viivikonna Formation yields numerous C. conicus. The boundaries of the Viivikonna Formation are diachronous due to the facies shift of the kukersite beds. The upper part of the Viivikonna Formation (Peetri Member) is absent in northeastern Estonia (HINTS, 1997). The Viivikonna Formation was deposited in a shallow epicontinental sea with normal salinity.

The Haljala Regional Stage (Fig. 2) is divided into the Idavere and Jõhvi substages. The lower part of the Idavere Substage (Tatruse Formation) comprises the regularly bedded hard bioclastic limestones. The upper part of the Idavere substage (Vasavere Formation) yields abundant Conichnus conicus and Amphorichnus papillatus. The Vasavere Formation contains argillaceous limestones with intercalations of marls and some thin K-bentonites (HINTS, 1997). The Idavere substage has the most reduced sequence in northern Estonia, and in some places in the vicinity of Tallinn it is entirely absent (HINTS, 1997). The Vasavere Formation contains usually two, but in the west up to 18 K-bentonite beds, which belong to the Grefsen complex of bentonites (Vasavere Formation) (KUPLI et al., 2014). Argillaceous limestones and marls of Vasavere Formation were deposited in a relatively shallow epicontinental sea with normal salinity (RAUKAS & TEEDUMÄE, 1997).

In most of northern Estonia, the Keila Regional Stage (Fig. 2) comprises the argillaceous bioclastic limestones of the Kahula Formation (HINTS & MEIDLA, 1997). Argillaceous limestones of the Kahula Formation contain intercalations and occasionally thicker (up to 4 m) intervals of relatively pure limestones. The argillaceous layers yield Conichnus conicus and Amphorichnus papillatus. The total thickness of the Kahula Formation is about 30 m, and in northwestern Estonia its main part corresponds to the Keila Stage (HINTS & MEIDLA, 1997). The thickness of the Keila Stage part of the formation (usually 10-15 m) decreases in the southeast direction. In the same direction, the formation becomes lithologically more homogeneous and argillaceous. In a restricted area in northwestern Estonia, the upper part of the Kahula Formation is replaced by the Vasalemma Formation where the greatest thickness of the Keila Stage (more than 30 m) has been recorded (HINTS & MEIDLA, 1997). The argillaceous limestones of the Kahula Formation were deposited in a relatively shallow epicontinental sea with normal salinity (RAUKAS & TEEDUMÄE, 1997).

In northern Estonia, the Oandu Regional Stage (Fig. 2) comprises rocks of two different lithofacies forming the Vasalemma and Hirmuse formations. The Vasalemma Formation is distributed in northwestern Estonia. It consists of fine- to coarse-grained bioclastic limestones with irregular bodies of carbonate buildups (HINTS & MEIDLA, 1997). The argillaceous limestones and marls of the Hirmuse Formation are exposed on the banks of the Oandu River in northeastern Estonia (HINTS & MEIDLA, 1997). The Hirmuse Formation thins out within a rather short distance in the southern direction. Hirmuse Formation contains Conichnus conicus and Amphorichnus papillatus. The argillaceous limestones and marls of the Hirmuse Formation were deposited in onshore shallow epicontinental sea with normal salinity (RAUKAS & TEEDUMÄE, 1997).

In northern Estonia, the Rakvere Regional Stage (Fig. 2) is characterized by pure micritic (fine-grained) limestones that intercalate with more or less argillaceous varieties. The clayey parts of the cycles are characterized by the appearance of abundant new taxa (HINTS & MEIDLA, 1997). The Rakvere Stage consists of the Piilsė and Tudu members of the Rägavere Formation. The stage is at its thickest (28 m) in western Estonia and its thickness decreases notably in the southeastern direction (HINTS & MEIDLA, 1997). The lower Piilsė Member with a thickness of up to 27 m consists of pure limestones with a low content of terrigenous material (3 - 9 %) and skeletal sand (< 5%). The member is characterised by abundant pyritized burrows (HINTS & MEIDLA, 1997). The upper Tudu Member is up to 10 m thick and contains more skeletal sand (about 15 %) and thin, up to 3 cm thick kukersite layers. Tudu Member yields rare Conichnus conicus. It was deposited in a relatively shallow epicontinental sea with normal salinity (RAUKAS & TEEDUMÄE, 1997).

In northern Estonia, the Pirgu Regional Stage (Fig. 2) contains two successive rock units of grey-colored limestones: the - lower - Moe and the - upper - Adila formations (HINTS & MEIDLA, 1997). The Moe Formation is up to 40 m in thickness, it consists of micritic and bioclastic nodular or bedded limestones with argillaceous intercalations (HINTS & MEIDLA, 1997). The calcareous alga Palaeoporella is abundant in the lower part of the formation. In some places carbonate mounds are developed, quite similar to the Boda mounds in the Siljan district of Sweden (HINTS & MEIDLA, 1997). The Adila Formation contains predominantly bioclastic limestones with a thickness of 10-15 m. Cyclically alternating pure and argillaceous limestones and numerous discontinuity surfaces characterize the
upper part of the formation. The Adila Formation yields *A. papillatus*. The sediments of the Adila Formation were deposited in a relatively shallow epicontinental sea with normal salinity (RAUKAS & TEEUMÄE, 1997).

The Adavere Regional Stage (Fig. 2) is distributed in the southwestern part of Hiiumaa Island, on Saaremäe and Muhu islands and in the southwestern part of mainland (NESTOR, 1997). The Stage is represented by thin-bedded nodular wackestones and packstones with marl- to mudstones above (Velise Formation). The clay content increases westwards. The Veli-se Formation contains rather rich shelly fauna of *Clorinda* communities (NESTOR, 1997). Velise Formation yields *C. conicus*. The argillaceous limestones and marls of Velise Formation were deposited in a relatively shallow epicontinental sea with normal salinity (RAUKAS & TEEUMÄE, 1997). Metabentonite layers are very common (HINTS et al., 2006; KIPLI et al., 2008, 2014).

| Regional Stage | Number of localities | *Conichnus conicus* | *Conichnus papillatus* |
|----------------|----------------------|---------------------|------------------------|
| Adavere (upper Llandovery) | 2 | 15 | - |
| Pirgu (upper Katian) | 1 | - | 1 |
| Rakvere (middle Katian) | 1 | 1 | - |
| Oandu (lower Katian) | 1 | 2 | 1 |
| Keila (upper Sandbian-lower Katian) | 21 | 55 | 31 |
| Haljala (middle Sandbian) | 18 | 356 | 571 |
| Kukruse (lower Sandbian) | 9 | 29 | 6 |
| Uhaku (upper Darriwilian) | 3 | 3 | 1 |

5. Distribution of plug-shaped burrows in the Lower Paleozoic of Estonia

There are two species of plug-shaped burrows, *Conichnus conicus* and *Amphorichnus papillatus*, in the Ordovician and one species, *Conichnus conicus*, in the Silurian of Estonia. *Conichnus* occurs in shallow water epicontinental carbonate rocks in the Ordovician of northern Estonia. Similarly, it is found in argillaceous limestones of shallow water epicontinental on-shore settings in the Silurian. *Conichnus* is abundant only in the most clay-rich shallow-water carbonates in the Ordovician and Silurian of Estonia. *Conichnus* is most abundant in the interval of numerous metabentonite layers in the Ordovician. Similarly, active volcanic ash deposition also characterizes the Silurian environments in which *Conichnus* formed. *Conichnus* seems to be more common in the temperate climate part of the Ordovician (Sandbian) than in the tropics of the Silurian (Telychian) as there are 385 Sandbian records versus 15 in the Tely-chian (Table 1).

6. Systematic ichnology

**Ichnogenus Conichnus Männil, 1966**

Type ichnospecies: *Conichnus conicus* Männil, 1966.

*Conichnus conicus* Männil, 1966

Fig. 3C-E, Fig. 4B-C

1966 *Conichnus conicus* Männil, p. 201, Figs. 1B, IC, Pl. 1, figs. 4-6, Pl. 2, figs. 1, 4.
1975 *Conichnus conicus*, Hänitzschel, p. W52, Fig. 31.3.
1981 *Conichnus conicus*, Frey & Howard, p. 800-801, Figs. IA, 2A-2E.
1982 *Conichnus conicus*, Frey & Howard, Fig. 20.
1983 *Conichnus conicus*, Pemberton & Frey, p. 61, Pl. 1, figs. 1-2.
1984 *Conichnus conicus*, Howard & Frey, p. 203, Fig. 7.?

? 2006 *Conichnus* isp. Ershova et al., p. 420, Fig. 5A-B.

Holotype: GIT 107-4 from Pääsküla, northern Estonia, Keila Regional Stage.

Material: 15 Silurian specimens, 10 well preserved; 488 Ordovician specimens.

Occurrence: Silurian (Telychian): Valgu River, Valgu ditch, Velise-Kõrgekalda and Võiva, western Estonia; Ordovician (Darriwilian to Katian): all of northern Estonia.

Description: Short conical, limestone filled burrows with unornamented shafts, circular to elliptical in a transverse section. Limestone filling is often rich in fossil debris. No linings occur. The morphology of the Ordovician and Silurian specimens is slightly different. Silurian specimens are somewhat wider relative to their height than the Ordovician specimens. The Ordovician specimens are in average slightly higher than wide. Their diameter/height ratio is 0.59 to 1.59 (n=59, mean 0.98). Ordovician forms are 1.52 cm to 8.91 cm high (n=59, mean 5.31 cm, sd=1.77) and 1.82 cm to 9.53 cm wide (n=59, mean 5.22 cm, sd=1.68). Silurian forms are remarkably wider than high. Their diame-ter/height ratio is 0.80 to 2.20 (n=10, mean 1.70). They are 1.02 to 5.81 cm high (n=10, mean 2.54 cm, sd=1.47) and 1.72 to 6.51 cm wide (n=10, mean 3.91 cm, sd=1.63). Some Ordovician forms often show adjustment traces, usually two or three but in some cases up to five stages in lateral directions and up to two stages in vertical directions. The Silurian specimens do not show any lateral adjustment structures. Both Ordovician and Silurian burrows are often filled.
with coarse fossil debris. Basal part smooth and rounded, without apical protuberance. The burrows are preserved in full relief as endichnia.

Remarks: The oval transverse section of some Telychian burrows links them to forms described from the Upper Cretaceous of Utah, USA (Frey & Howard, 1981; Howard & Frey, 1984). The described Silurian forms differ from typical Conichnus (Pemberton et al., 1988) by being in average significantly wider than high. According to Männil (1966), the maximum length of C. conicus from the Ordovician of Estonia is 12 cm, which is slightly more than that measured in new material (8.91 cm). New material shows that lateral adjustment traces are more common in the Ordovician C. conicus than previously known.

Ichnogenus Amphorichnus
Männil, 1966

Type ichnospecies: Amphorichnus papillatus Männil, 1966.

Amphorichnus papillatus Männil, 1966

Fig. 3 A-B, Fig. 4A

1966 Amphorichnus papillatus Männil, p. 202, Figs. IA, ID; Pl. 1, figs. 1-3; Pl. 2, figs. 2-3, 5.
1975 Amphorichnus papillatus Hántzschel, p. W36, Fig. 24.3.
1979 Amphorichnus sp., Hurst (partim), Figs. 12B, C.
? 2006 Amphorichnus isp., Ershova et al., p. 419, Figs. 3B-L, 4A-1.

Holotype: GIT 107-1 from Anija, northern Estonia, Haljala Regional Stage (Sandbian).

Material: 637 Ordovician specimens.

Occurrence: Uhaku to Pirgu Regional Stages (Darriwilian to upper Katian), northern Estonia.

Description: Short to elongate nearly cylindrical to amphora-shaped, limestone filled burrows with unornamented shafts and slightly constricted apertures, circular to slightly elliptical in a transverse section. Maximal diameter is between 1/3 to 2/3 of the burrow height. Burrows are 1.10 to 7.71 cm height (n=63, mean 4.73 cm,
Aperture of the burrows is 0.60 to 3.31 cm wide (n=63, mean 1.91 cm, sd=0.53). Maximal diameter of the burrows is 0.91 to 3.62 cm (n=63, mean 2.50 cm, sd=0.65). Limestone filling is often rich in fossil debris. In most of specimens burrow filling is homogeneous, but in some specimens it contains indistinct laminae. These laminae indicate successive stages in filling of the burrow with sediments. No linings occur. Burrows are often filled with coarse fossil debris. Basal part smooth rounded to conical, with an apical protuberance. The development of apical protuberance is variable. The burrows are preserved in full relief as endichnia.

Remarks: Frey & Howard (1981) transferred Amphorichnus papillatus to the ichnogenus Conichnus Männil, 1966 based on similar plug-shaped morphology of C. conicus. However, the morphology of Amphorichnus papillatus considerably differs from Conichnus by its amphora-like shape and the papillate termination and is better accommodated under its original name, Amphorichnus. Amphorichnus also differs from Conichnus by presence of lateral adjustment traces. In addition, its shape resembles Gastrochaenolites oelandicus. However, G. oelandicus is a hard substrate boring, not a soft-sediment burrow, implying completely different behavior.

7. Discussion

Comparison of Ordovician and Silurian forms of Conichnus conicus in Estonia

Männil (1966) found that C. conicus traces in the oil shale of the Kukruse Regional Stage are larger than the other Ordovician C. conicus traces. This is confirmed by our study. It seems that C. conicus traces were larger in the Ordovician than in the Silurian of Estonia. The smaller size of the Silurian traces probably correlates with the smaller size of the trace makers, as Conichnus has been interpreted as the living burrow of a cnidarian (Frey & Howard, 1981; Jones & Pemberton, 1989). The Silurian specimens are somewhat wider relative to their height than the Ordovician specimens, probably because of taxonomic differences between the Ordovician and Silurian C. conicus trace makers. Alternatively, Ordovician C. conicus specimens differ because of vertical adjustment in response to higher sedimentation rates. The lack of lateral adjustment traces in the Silurian forms of C. conicus may be a result of differences in the mud substrate dynamics. The muddy bottom of the Telychian (Adavere Regional Stage) may have been more stable than the bottoms in the Sandbian of Estonia. Alternatively, it could be an artefact of sampling bias (i.e., there are many more specimens known from the Ordovician than from the Silurian) and future C. conicus finds from the Silurian Estonia could reveal also the lateral adjustment traces.

Sedimentation environment

It appears that the sedimentary environment controlled the distribution of Conichnus in the Ordovician and Silurian of Estonia. Most likely the Conichnus traces were made by shallow-water animals in the Ordovician and Silurian of Estonia. One should also consider that preservation bias may have influenced the distribution of Conichnus traces. However, it seems reasonable to assume that the preservation potential in deeper and calm water marls and argillites was not lower than in shallow-water clayey limestones. Thus, the Conichnus trace makers were likely present only in the shallow water parts of the Ordovician and Silurian basin in Estonia. The lack or rarity of Conichnus in shallow water pure limestones possibly reflects the trace maker's preferences for the substrate, but alternatively it may represent a preservation bias. Either the Conichnus trace maker's substrate preference or preservation bias is responsible for the lack of Conichnus in the Lower Ordovician sandstones and argillites. However, Conichnus is not known from the Cambrian of Estonia and it is possible that Conichnus trace makers may have arrived in the Estonian part of the Baltic Basin during the Middle Ordovician.

The maximum abundance of Conichnus traces coincides with the highest amount of volcanic ash in the sedimentation environment both in the Sandbian and Telychian (Hints et al., 2006; Kiipi et al., 2008, 2014). This may be a coincidence, but it is possible that numerous volcanic ash sedimentation episodes created ecologically favorable conditions for the Conichnus trace makers, such as better sediment cohesion with elevated clay content. Reduced bioturbation intensities may have also been favorable for Conichnus trace makers.

Climate change

During the Katian, Baltica moved into the tropics (Cocks & Torsvik 2005; Torsvik et al., 2013). Conichnus conicus occurred both in temperate climate (Darriwilian) and tropics (Llandovery). The clayey limestones containing C. conicus in the Sandbian are very similar to those found in the Telychian of Estonia (Kaljo, 1970, Jürgenson, 1988; Raukas & Teedumäe, 1997). Thus, it is unlikely that the differences in the substrate or preservation caused the differences in the abundance of C. conicus between the Sandbian and Telychian. Instead, it is possible that C. conicus trace makers may have preferred muddy bottoms of the temperate seas more than their tropical equivalents. Tropical seas have different and more abundant benthos, which may have caused the decrease of C. conicus abundance. It is also possible that the increased water temperature could affect C. conicus abundance.
Comparison to other occurrences of Conichnus and Amphorichnus

Conichnus isp. and Amphorichnus isp. are known from the Lower Ordovician of St Petersburg region, Russia (Baltica) (Ershova et al., 2006). Paczešna (2010) described Conichnus conicus and C. papillatus from Lower Cambrian sandstones of southern Poland, which formed a part of Brunovistulian terrane. Conichnus has also been described from the Upper Cretaceous of North America (Frey & Howard, 1981; Howard & Frey, 1984). Jones and Pemberton (1989) described C. conicus traces from shallow carbonate sediments of the Pleistocene of Grand Cayman. It is interesting that C. conicus occurs only in certain parts of the Ordovician and Silurian of Estonia (Baltica), while globally it occurs in various sedimentary rocks from Cambrian onwards. This could be explained by the different ecological requirements of Conichnus trace makers. These traces were presumably made by various animals with different environmental preferences.

8. Conclusions

1. Conichnus conicus and Amphorichnus papillatus are common in the Ordovician of Estonia. They are more common in the clay-rich carbonate rocks of the Sandbian than in the pure carbonates of the Katian. Only Conichnus conicus occurs in argillaceous carbonates of the Lower Silurian (Llandovery). The peaks in the abundance of Conichnus traces coincide with the highest amount of volcanic ash in the sedimentation environment in the Sandbian and Telychian. Thus, trace makers of both C. conicus and Amphorichnus papillatus preferred clay-rich carbonate sediments over the pure carbonate muds.

2. Conichnus conicus is more abundant in the temperate Sandbian and than in the tropical Telychian. It is possible that C. conicus trace makers may have preferred muddy bottoms of the temperate seas more than their tropical equivalents.

3. The morphology of the studied traces does not support synonymy of Conichnus and Amphorichnus. Amphorichnus differs significantly from Conichnus by its amphorous shape, papillate terminations, and the presence of lateral adjustment traces.

Figure 4: A. Longitudinal section of Amphorichnus papillatus Männil, 1966 (GIT 107-17) from Aluvere, northern Estonia, Vasavere Formation (Sandbian). B. Longitudinal section of Conichnus conicus Männil, 1966 (GIT 156-1736) showing lateral adjustment traces from Aluvere quarry, northern Estonia, Vasavere Formation (Sandbian). C. C. conicus (GIT 156-1910) showing lateral adjustment traces from Küttejõu, northern Estonia, Kiviõli Formation (Sandbian). Scale bar in mm.
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