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

Olev VINN [1]

Mark A. WILSON [2]

Ursula TOOM [3]

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* tracemakers preferred 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.

Citation: VINN O., WILSON M.A. & TOOM U. (2015).- Distribution of *Conichnus* and *Amphorichnus* in the Lower Paleozoic of Estonia (Baltica).- *Carnets Geol.*, Madrid, vol. 15, nº 19, p. 269-278.

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; MIKULÁŠ & DRONOV, 2005; ERSHOVA *et al.*, 2006; KNAUST *et al.*, 2012; KNAUST & DRONOV, 2013; VINN *et al.*, 2014b). The Ordovician ichnofossils of Estonia that have been described are mostly hard substrate borings (VINN, 2005; VINN & WILSON, 2010; VINN *et al.*, 2014a).

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; PICKERILL *et al.*, 1992; KNAUST, 2007; PACZEŚNA, 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

[1] Department of Geology, University of Tartu, Ravila 14A, EE-50411 Tartu (Estonia)
Olev.Vinn@ut.ee

[2] Department of Geology, College of Wooster, Wooster, Ohio 44691 (USA)
mwilson@wooster.edu

[3] Institute of Geology, Tallinn University of Technology, Ehitajate tee 5, EE-19086 Tallinn (Estonia)
Ursula.Toom@ttu.ee

Published online in final form (pdf) on December 2, 2015
[Editor: Brian PRATT; technical editor: Christian EMIG]

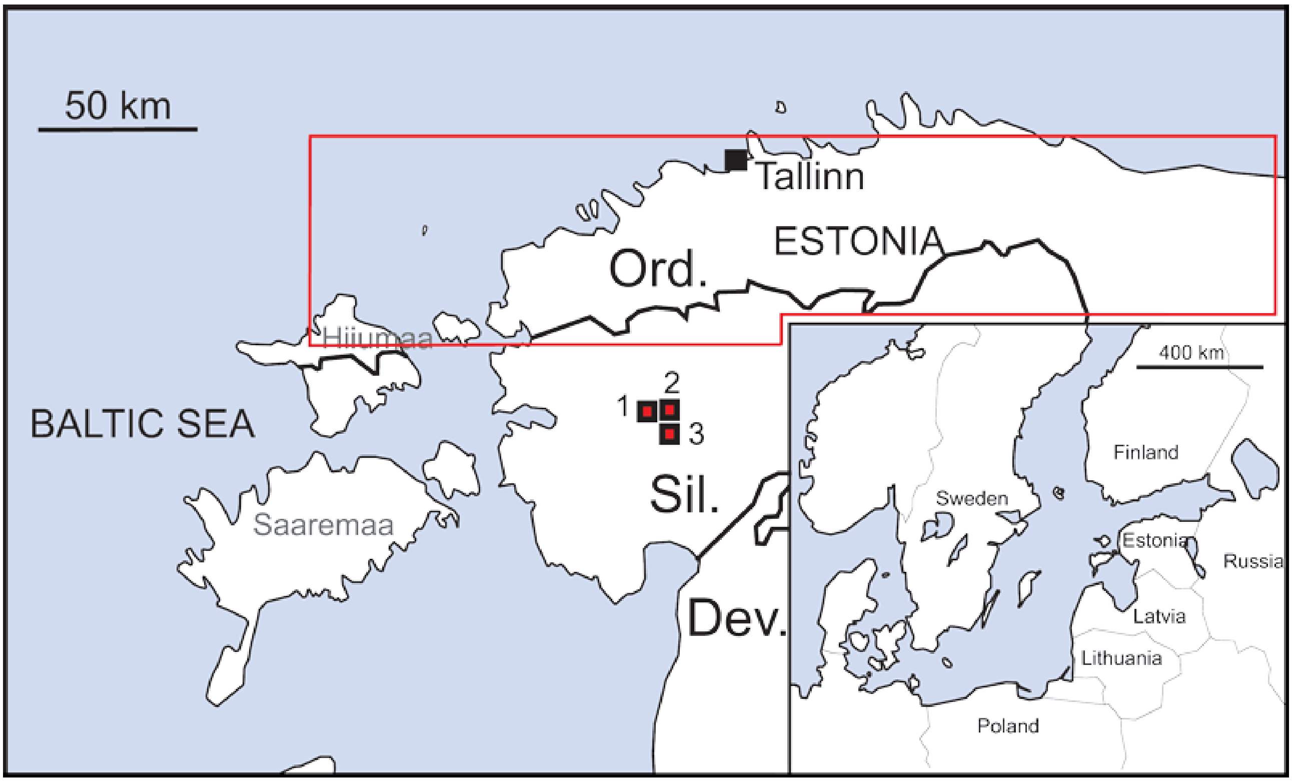


Figure 1: Schematic line drawing showing the Estonia and localities (red-area covered with samples from Ordovician). 1 - Valgu River, 2 - Valgu ditch, 3 - Velise-Kõrgekalda.

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, 1997). 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.

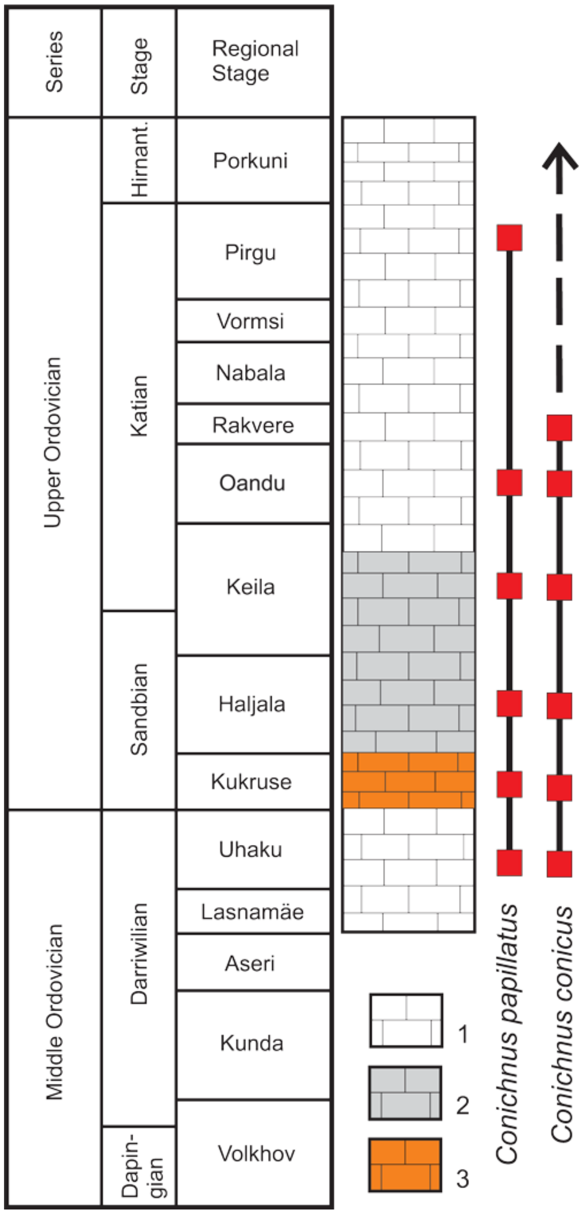


Figure 2: Stratigraphic distribution of *Conichnus conicus* and *Amphorichnus papillatus* in the Ordovician of Estonia. 1 - limestones, 2 - clay rich limestones, 3 - oil shale (kukersite) with limestone.

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-bedded 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) (KIIPLI *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 Piilse and Tudu members of the Rägavere Formation. The stage is at its thickest (28 m) in western Estonia and it thickness decreases notably in the southeastern direction (HINTS & MEIDLA, 1997). The lower Piilse 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 & Teedumäe, 1997).

The Adavere Regional Stage (Fig. 2) is distributed in the southernmost part of Hiiumaa Island, on Saaremaa and Muhu islands and in the southwestern part of mainland (Nestor, 1997). The Stage is represented by thin-bedded to nodular wackestones and packstones with marl- to mudstones above (Velise Formation). The clay content increases westwards. The Velise 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 & Teedumäe, 1997). Metabentonite layers are very common (Hints *et al.*, 2006; Kiipli *et al.*, 2008, 2014).

Table 1: Distribution of *Conichnus* and *Amphorichnus* in the Ordovician and Silurian of Estonia.

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 onshore 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 Telychian (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*, Häntzschel, 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 diameter/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

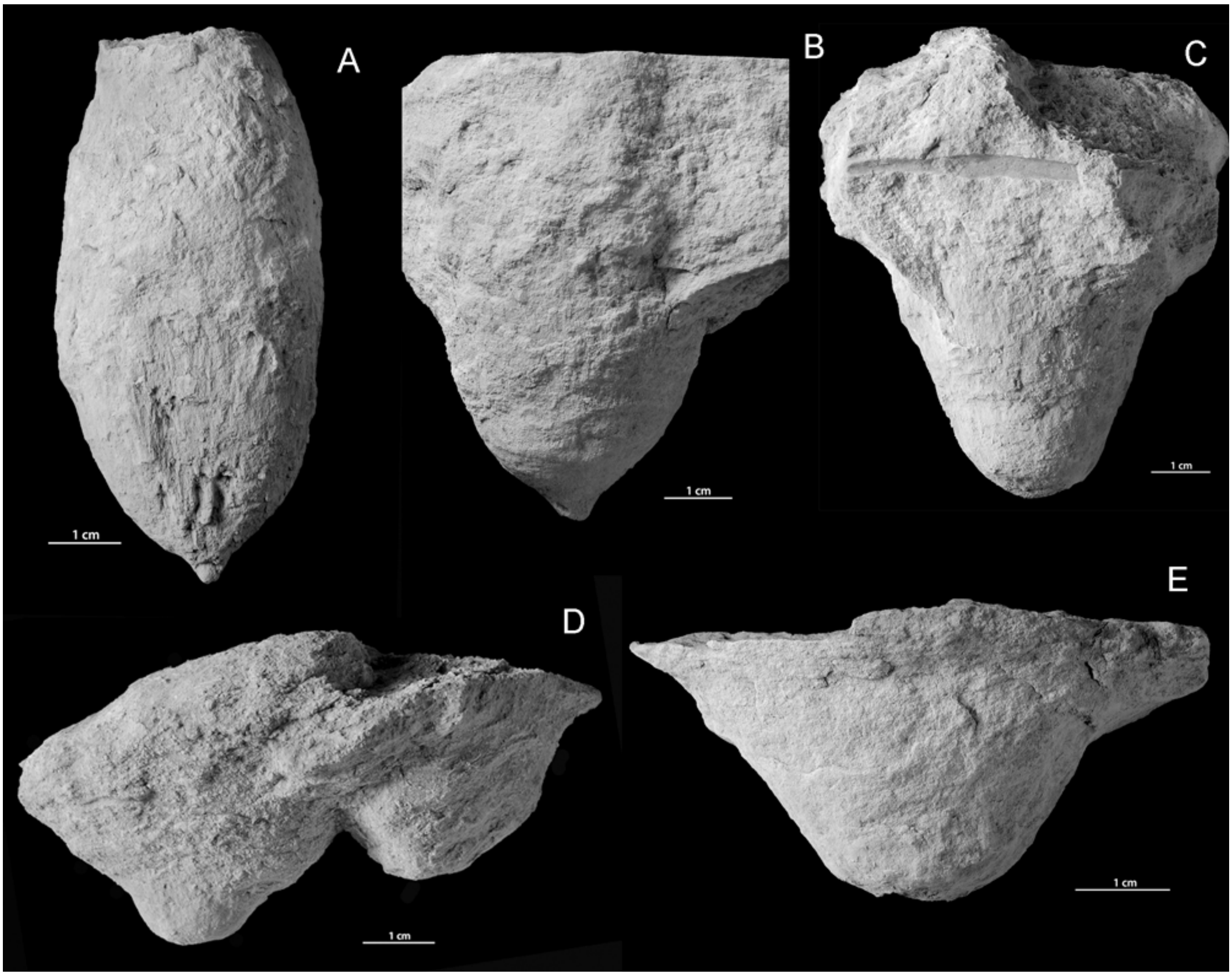


Figure 3: **A**. *Amphorichnus papillatus* MÄNNIL, 1966 (Holotype GIT 107-1) from Anija, northern Estonia, Jõhvi Formation (Sandbian). **B**. *A. papillatus* (GIT 107-2) from Kämbemäe, northern Estonia, Jõhvi Formation (Sandbian). **C**. *Conichnus conicus* MÄNNIL, 1966 (GIT 107-5) from Rae, northern Estonia, Jõhvi Formation (Sandbian). **D**. *C. conicus* (GIT 107-6) from Aluvere quarry, northern Estonia, Vasavere Formation (Sandbian). **E**. *C. conicus* (GIT 362-483) from Valgu, Velise Formation (Llandovery).

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* HÄNTZSCHEL, 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-I.

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, sd=1.60). 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.

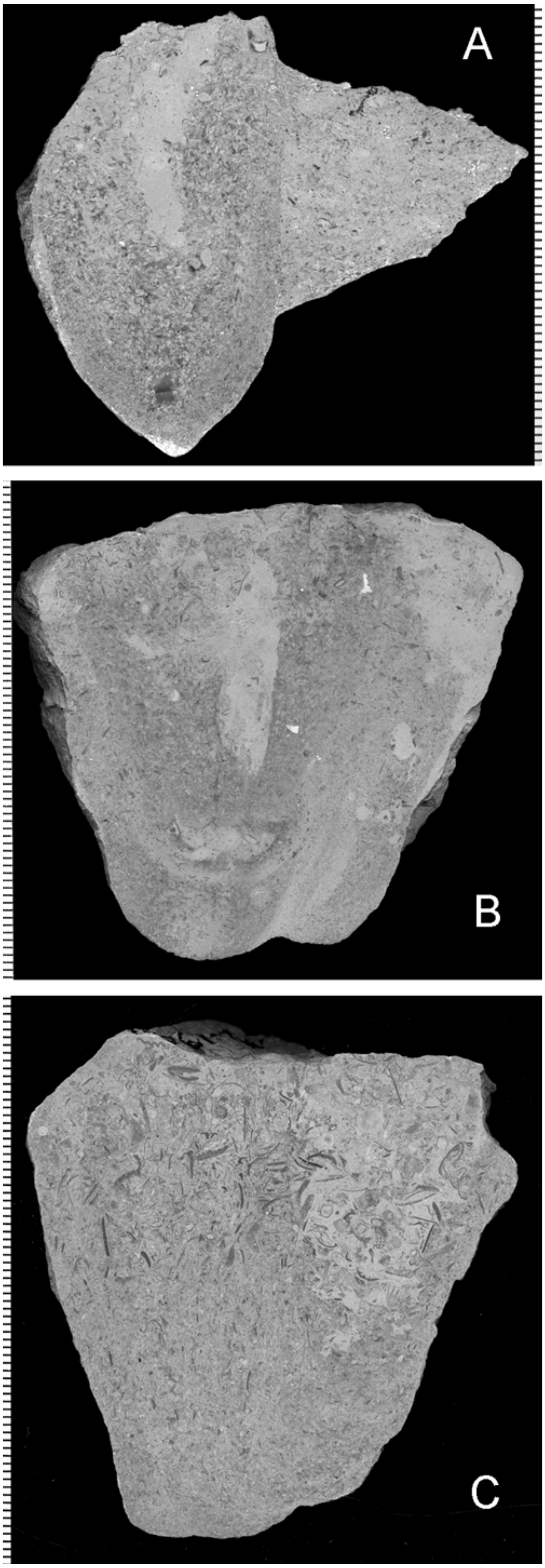
Sedimentation environment

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; KIIPLI *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). PACZEŚNA (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, tracemakers 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.

Acknowledgements

Financial support to O.V. was provided by the Palaeontological Association Research Grant, Paleontological Society SEPKOSKI Grant, Estonian Research Council projects ETF9064 and IUT20-34. This paper is a contribution to IGCP 591 "The Early to Middle Palaeozoic Revolution". We are grateful to Brian PRATT and Dirk KNAUST for their reviews. We are grateful to G. BARANOV, Institute of Geology, Tallinn University of Technology for photographing the specimens.

Bibliographic references

COCKS L.R.M. & TORSVIK T.H. (2005).- Baltica from the late Precambrian to mid Palaeozoic: the gain and loss of a terrane's identity.- *Earth-Science Reviews*, vol. 72, p. 39-66.

DRONOV A.V., MIKULÁŠ R. & LOGVINOVA M. (2002).- Trace fossils and ichnofabrics across the Volkhov depositional sequence (Ordovician, Arenigian of St. Petersburg Region, Russia).- *Journal of the Czech Geological Society*, Prague, vol. 47, nº 3-4, p. 133-146

ERSHOVA V.B., FEDOROV P.V. & MIKULÁŠ R. (2006).- Trace fossils on and above the transgressive surface: substrate consistency and phosphogenesis (Lower Ordovician, St. Petersburg region, Russia).- *Geologica Carpatica*, Bratislava, vol. 57, p. 415-422.

FREY R.W. & HOWARD J.D. (1981).- *Conichnus* and *Schaubcylindrichnus*: redefined trace fossils from the Upper Cretaceous of the Western Interior.- *Journal of Paleontology*, Lawrence, vol. 56, p. 800-804.

FREY R.W. & HOWARD J.D. (1982).- Trace fossils from the Upper Cretaceous of the Western Interior: potential criteria for facies models.- *Mountain Geologist*, Denver, vol. 19, p. 1-10.

HÄNTZSCHEL W. (1975).- Trace fossils and problematica. *In*: TEICHERT C. (ed.), Treatise on Invertebrate Paleontology. Part W, Miscellanea, supplement 1.- Geological Society of America, Boulder; University of Kansas Press, Lawrence, p. W1-W269.

HOWARD J.D. & FREY R.W. (1984).- Characteristic trace fossils in nearshore to offshore sequences, Upper Cretaceous of east-central Utah.- *Canadian Journal of Earth Sciences*, Ottawa, vol. 21, p. 200-219.

HURST V.J. (1979).- Field conference on kaolin, bauxite, and Fuller's earth.- Clay Minerals Society, Annual Meeting, Georgia Institute of Technology, Atlanta, 107 p.

JONES B. & PEMBERTON G.S. (1989).- Sedimentology and ichnology of a Pleistocene unconformity-bounded, shallowing-upward carbonate sequence: The Ironshore Formation, Salt Creek, Grand Cayman.- *Palaios*, Lawrence, vol. 4, p. 343-355.

JÜRGENSON E. (1988).- Osadkokonakoplenie v silure pribatiki [Sedimentation in the Silurian of Baltic].- Akademiya Nauk ESSR, Institut geologiy, Valgus, 175 p. [in Russian].

KIIPLI T., SOESOO A. & KALLASTE, T. (2014).- Geochemical evolution of Caledonian volcanism recorded in the sedimentary rocks of the eastern Baltic region. *In*: CORFU F., GASSER D. & CHEW D.M. (eds.), New perspectives on the Caledonides of Scandinavia and related areas.- *Geological Society, London, Special Publications*, vol. 390, p. 177-192.

KIIPLI T., ORLOVA K., KIIPLI E. & KALLASTE T. (2008).- Use of immobile trace elements for the correlation of Telychian bentonites on Saaremaa island, Estonia, and mapping of volcanic ash clouds.- *Estonian Journal of Earth Sciences*, Tallinn, vol. 57, p. 39-52.

HINTS L. (1997).- Uhaku Stage. *In*: RAUKAS A. & TEEDUMÄE A. (eds.), Geology and mineral resources of Estonia.- Estonian Academy Publishers, Tallinn, p. 68-70.
URL: http://geoloogia.info/

HINTS L. & MEIDLA T. (1997).- Keila Stage. *In*: RAUKAS A. & TEEDUMÄE A. (eds.), Geology and mineral resources of Estonia.- Estonian Academy Publishers, Tallinn, p. 74-76.
URL: http://geoloogia.info/

HINTS O., AINSAAR L., MÄNNIK P. & MEIDLA T. (2008).- The Seventh Baltic Stratigraphical Conference. Abstracts and Field Guide.- Geological Society of Estonia, Tallinn, 46 p.

HINTS R., KIRSIMÄE K., SOMELAR P., KALLASTE T. & KIIPLI T. (2006).- Chloritization of Late Ordovician K-bentonites from the northern Baltic Palaeobasin - influence from source material or diagenetic environment?.- *Sedimentary Geology*, vol. 191, p. 55-66.

KALJO D. (ed., 1970).- The Silurian of Estonia.- Valgus, Tallinn, 343 p. [in Russian].

KNAUST D. (2007).- Invertebrate trace fossils and ichnodiversity in shallow-marine carbonates of the German middle Triassic (Muschelkalk).- *SPEM Special Publications*, vol. 88, p. 233-240.

KNAUST D., CURRAN H.A. & DRONOV A. (2012).- Shallow-marine carbonates. *In*: KNAUST D., BROMLEY R.G. (eds.) Trace Fossils as Indicators of Sedimentary Environment.- *Developments in Sedimentology*, vol. 64, p. 703-750.

KNAUST D. & DRONOV A. (2013).- *Balanoglossites* ichnofabrics from the Middle Ordovician Volkhov formation (St. Petersburg Region, Russia).- *Stratigraphy and geological Correlation*, New York, vol. 21, p. 265-279.

MÄNNIL R.M. (1966).- O vertikalnykh norkakh zaryvanija v ordovikskikh izvestijakakh Pribaltiki [On vertical burrows in the Ordovician limestones of Baltic]. *In*: Organizm i sreda v geologischeskom proshlom.- Akademiya Nauk SSSR, Paleontologicheskiy Institut, Nauka, Moskva, p. 200-207 [in Russian].

METZ R. (2011).- Pleistocene trace fossils in the Ironshore Formation, Little Cayman, British West Indies.- *Central European Journal of Geosciences*, Warszawa, vol. 3, p. 71-76.

MIKULÁŠ R. & DRONOV A.V. (2005).- Trace fossils.- *In*: DRONOV A.V., TOLMACHEVA T., RAYEVSKAYA E. & NESTELL M. (ed.), Cambrian and Ordovician of St Petersburg Region.- St Petersburg State University & A.P. KARPINSKY All-Russian Research Geological Institute, St Petersburg, p. 33-38.

MÕTUS M.A. & HINTS O. (2007).- Excursion guidebook. *In*: 10th International Symposium on Fossil Cnidaria and Porifera. Excursion B2: Lower Paleozoic geology and corals of Estonia (August 18-22, 2007).- Institute of Geology, Tallinn University of Technology, 66 p.

NESTOR H. (1997).- Adavere Stage. *In*: RAUKAS A. & TEEDUMÄE A. (eds.), Geology and mineral resources of Estonia.- Estonian Academy Publishers, Tallinn, p. 95-96.
URL: http://geoloogia.info/

NESTOR H. & EINASTO R. (1977).- Model of facies and sedimentology for Paleobaltic epicontinental basin.- *In*: KALJO D.L. (ed.), Facies and Fauna of the Baltic Silurian.- Institute of Geology AN ESSR, Tallinn, p. 89-121 [in Russian, with English summary].

NESTOR H. & EINASTO R. (1997).- Ordovician and Silurian carbonate sedimentation basin. *In*: RAUKAS A. & TEEDUMÄE A. (eds.), Geology and mineral resources of Estonia.- Estonian Academy Publishers, Tallinn, p. 192-204.
URL: http://geoloogia.info/

PACZEŚNA J. (2010).- Ichnological record of the activity of Anthozoa in the early Cambrian succession of the Upper Silesian Block (southern Poland).- *Acta Geologica Polonica*, Warszawa, vol. 60, p. 93-103.

PEMBERTON S.G. & FREY R.W. (1983).- Biogenic structures in Upper Cretaceous outcrops and cores.- Canadian Society of Petroleum Geologists, Mesozoic Conference, Fieldguide nº 8, 161 p.

PEMBERTON S.G., FREY R.W. & BROMLEY R.G. (1988).- The ichnotaxonomy of *Conostichus* and other plug-shaped ichnofossils.- *Canadian Journal of Earth Sciences*, Ottawa, vol. 25, p. 866-892.

PICKERILL R.K., DONOVAN S.K. & DIXON H.L. (1992).- The Richmond Formation of eastern Jamaica revisited - further ichnological observations.- *Caribbean Journal of Science*, Mayaguez, vol. 28, p. 89-92.

RAUKAS A. & TEEDUMÄE A. (eds., 1997).- Geology and mineral resources of Estonia.- Estonian Academy Publishers, Tallinn, 436 p.
URL: http://geoloogia.info/

SEILACHER A. (2007).- Trace Fossil Analysis.- Springer, 226 p.

TORSVIK T.H., SMETHURST M.A., VOO R. van der, TRENCH A., ABRAHAMSEN N. & HALVORSEN E. (1992).- Baltica. A synopsis of Vendian-Permian palaeomagnetic data and their palaeotectonic implications.- *Earth Science Reviews*, vol. 33, p. 133-152.

TORSVIK T.H. & COCKS L.R.M. (2013).- New global palaeogeographical reconstructions for the Early Palaeozoic and their generation. *In*: HARPER D.A.T & SERVAIS T. (eds.), Early Palaeozoic biogeography and palaeogeography.- Geological Society Memoirs, London, vol. 38 p. 5-24.

VINN O. (2005).- The distribution of worm borings in brachiopod shells from the Caradoc Oil Shale of Estonia.- *Carnets Geol.*, Madrid, vol. 5, nº A03 (CG2005_A03), 11 p.

VINN O. & WILSON M.A. (2010).- Early large borings from a hardground of Floian-Dapingian age (Early and Middle Ordovician) in northeastern Estonia (Baltica).- *Carnets Geol.*, Madrid, vol. 10, nº L04 (CG2010_L04), 4 p.

VINN O., WILSON M.A. & MÕTUS M.-A. (2014a).- The earliest giant *Osprioneides* borings from the Sandbian (Late Ordovician) of Estonia.- *PLoS ONE*, San Francisco, vol. 9, nº 6, e99455, 6 p.

VINN O., WILSON M.A., ZATOŃ M. & TOOM U. (2014b).- The trace fossil *Arachnostega* in the Ordovician of Estonia (Baltica).- *Palaeontologia Electronica*, Amherst, 17.3.41A, 9 p.