Estonian Journal of Earth Sciences, 2016, **65**, 1, 19–26 doi: 10.3176/earth.2016.01

A sparsely encrusted hardground with abundant *Trypanites* borings from the Llandovery of the Velise River, western Estonia (Baltica)

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Received 11 February 2015, accepted 25 June 2015

Abstract. The Päärdu hardground from the Telychian (Rumba Formation) of western Estonia is sparsely encrusted (0.4% of the studied surface) by possible tabulate corals, sheet-like bryozoans and discoidal echinoderm holdfasts. Both the upper and cryptic sides of the hardground are intensely bioeroded by *Trypanites* borings. The taxonomic composition of the Päärdu hardground association is rather different from the characteristic Silurian association in being dominated by tabulate corals, while bryozoans and echinoderms played a minor role in the association. The Päärdu hardground is more sparsely encrusted than common for the Late Ordovician and Silurian hardgrounds, but this may be a characteristic feature of the hardgrounds of Baltica. The Päärdu hardground is important among the Silurian hardgrounds because it has unusually low encrustation combined with high bioerosion.

Key words: bioerosion, *Trypanites*, hardgrounds, tabulates, bryozoans, echinoderms.

INTRODUCTION

Carbonate hardgrounds are surfaces of carbonate layers that have been synsedimentarily cemented and exposed on the seafloor. Such hardgrounds are more common in calcite seas than in aragonite ones because of favourable conditions for early cementation of carbonate sediments in the seafloor (Wilson & Palmer 1992). Hardgrounds form excellent attachment surfaces for encrusting and bioeroding organisms (Palmer 1982). The Silurian Period was characterized by calcite seas (Stanley 2006), and hardgrounds were common, though probably less abundant than in the Ordovician (Taylor & Wilson 2003).

Silurian hardground faunas, especially the early Silurian ones, are similar to those of the Ordovician (Taylor & Wilson 2003; Vinn & Toom 2015). Silurian hardgrounds are dominated by bryozoans and echinoderms, particularly crinoids (Taylor & Wilson 2003), but late Silurian (Pridoli) hardground faunas include also numerous microconchids (Vinn & Wilson 2010) (Table 1). Devonian encrusting communities differ from the Silurian ones in being dominated by microconchids, hederelloids and tabulate corals instead of bryozoans and echinoderms, although the latter two groups are still common (Kesling et al. 1980; Brett & Cottrell 1982; Alvarez & Taylor 1987; Taylor & Wilson 2003). During some time intervals microconchids may be absent or have a low abundance (Zatoń et al. 2015). However, Devonian encrusting communities are better known on shells than other hard substrates (Taylor & Wilson 2003).

Only seven detailed studies are known on Silurian hardground communities. Halleck (1973) described hardground encrusting crinoids, corals and brachiopods from the Wenlock of Indiana. Thomka & Brett (2014, 2015) found various echinoderm encrusters also from the Wenlock of Indiana. Franzén (1977) described hardground encrusting echinoderm holdfasts from the Silurian of Gotland. Cherns (1980) found a bioeroded hardground from the Ludlow of the Welsh Borderland. Sumrall et al. (2009) described edrioasteroids cemented to the hardground from the middle Silurian of Pennsylvania (Table 1).

Two hardground faunas have previously been described from Baltica (Einasto 1964), including crinoids from Gotland, Sweden (Franzén 1977) and a microconchid-dominated association from the Pridoli of Saaremaa, Estonia (Vinn & Wilson 2010). Hardgound faunas of the Llandovery of Baltica have remained undescribed. These early Silurian communities are especially interesting regarding to the question of how and when typical Ordovician sclerobiont communities recovered after Ordovician–Silurian mass extinction.

This paper aims to (1) describe for the first time a hardground association of Llandovery age from Baltica, (2) test whether the Päärdu hardground association is typical for the Silurian, (3) test whether the density of bioerosion is negatively correlated with the encrustation density and (4) compare the hardground fauna from the Llandovery of western Estonia to other Silurian and Late Ordovician analogues.

Table 1. Silurian hard substrate faunas from Estonia and beyond

Location	Lithology (substrate)	Encrusting fauna (in order of importance)	Bioerosion	Age	Reference
Estonia (Baltica)	Dolomitized limestone (hardground)	Tabulates, bryozoans, echinoderms	*Trypanites* (abundant)	Llandovery	Present study
Estonia	Intrabiosparite (hardground)	Microconchids, *Anticalyptraea*, trepostome bryozoans, crinoids, graptolites, cornulitids, tabulates	*Trypanites* (abundant)	Pridoli	Vinn & Wilson (2010)
Estonia (Baltica)	Pelletal limestone (stromatoporoids)	Rugosans, microconchids, auloporids, cornulitids, trepostome bryozoans, favositids, crinoids	*Trypanites* (abundant)	Wenlock	Vinn & Wilson (2012a)
Estonia (Baltica)	Argillaceous limestones (stromatoporoids)	Microconchids, bryozoans, tabulates, rugosans, crinoids	*Trypanites* (rare)	Pridoli	Vinn & Wilson (2012b)
Welsh Borderland (Avalonia)	Conglomeratic limestone (hardground)	Absent	*Trypanites* (abundant)	Ludlow	Cherns (1980)
Indiana (Laurentia)	Limestone (hardground)	Crinoids, blastozoan echinoderms	Absent	Wenlock	Thomka & Brett (2014, 2015)
Indiana (Laurentia)	Limestone (hardground)	Crinoids, auloporid corals, craniid brachiopods	Absent	Wenlock	Halleck (1973)
Pennsylvania (Laurentia)	Ostracode grainstones to brachiopod packstones (hardground)	Edrioasteroids	Absent	Wenlock–Ludlow	Sumrall et al. (2009)

GEOLOGICAL BACKGROUND AND LOCALITY

In the Silurian the Baltica continent was located in equatorial latitudes drifting northwards (Melchin et al. 2004). An epicontinental Baltic palaeobasin was located on the area of modern Estonia (Fig. 1). This basin was characterized by a wide range of tropical environments and diverse biotas (Hints 2008).

Nestor & Einasto (1977) established a general facies model for the basin including the following facies belts: tidal flat/lagoonal, shoal, open shelf, transitional (basin slope), and a basin depression. The first three facies belts formed a carbonate platform (i.e. carbonate shelf), the latter two a deeper pericratonic basin with fine-grained clastic deposits (Raukas & Teedumäe 1997).

The Päärdu outcrop is located on the right bank of the Velise River 200 m west of the Tallinn–Pärnu highway bridge in western Estonia. Marls and nodular dolomitic limestones of the Rumba Formation are exposed at Päärdu (Fig. 2).

MATERIALS AND METHODS

Twelve samples have been collected by scientists of the Institute of Geology at Tallinn University of Technology from the hardground of the Velise River outcrop during the past several decades. The samples were cleaned with water and brushes and then their upper and lower sides were photographed with scale bar using Nikon 7000. The studied total hardground surface area was 580.11 cm^2. Unfortunately the orientation is not marked on the pieces of the hardground in the collection of the Institute of Geology (GIT), so the upper and lower surface features are not distinguished in this study. A maximum number of *Trypanites* borings was counted in 4 cm^2 using a grid drawn on a transparent film and calibrated photos. The 4 cm^2 area was chosen to follow the methodology of Tapanila et al. (2004) for the study of Ordovician and Silurian hard substrates. On calibrated photos a grid was also used to measure the area of the studied hardground surface and a grid drawn on a transparent film was used to measure the area covered by encrusters. The

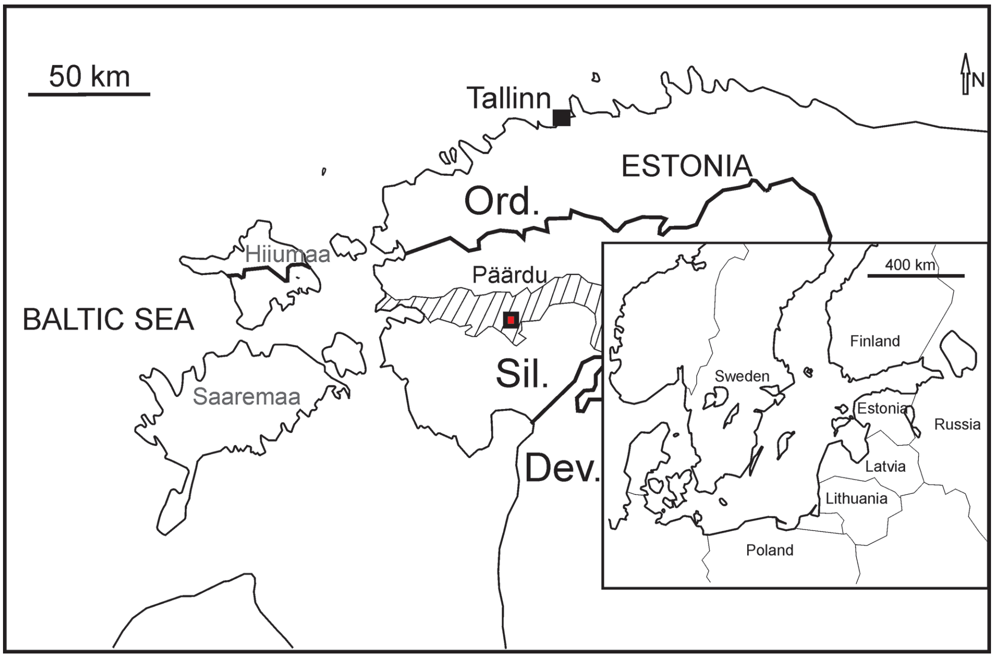

Fig. 1. Location of the Päärdu outcrop at the Velise River, western Estonia. Exposure of the Adavere Regional Stage (incl. Rumba Formation) is marked with slanting lines.

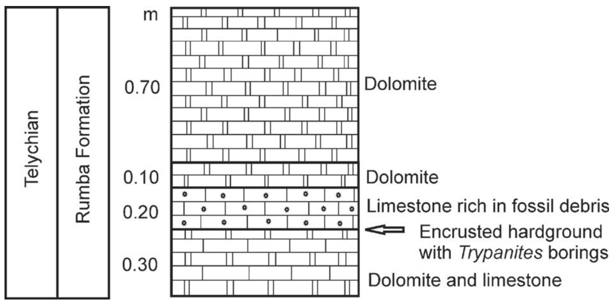

Fig. 2. Section of limestones and dolomites of the Rumba Formation (early Telychian) in the Päärdu outcrop; modified after field notes of Rein Einasto.

encrusting fauna was identified to the lowest possible taxonomic level. Several papers on hard substrate faunas were used as guides to aid the identification (Halleck 1973; Franzén 1977; Brett & Liddell 1978; Tapanila et al. 2004).

RESULTS

The hardground surface is relatively flat, but in some places it can be bumpy with pronounced relief. Its surface is mostly relatively smooth, but it also has regions which have rougher microrelief. Both upper and lower hardground surfaces are strongly mineralized by pyrite and have a dark colour, in contrast to the light grey colour of the matrix. The hardground is strongly abraded and partially broken into cobbles. There are also few somewhat linear fractures that reach through the hardground. Signs of possible microbio-erosion are observed on both surfaces of the hard-ground. Numerous *Trypanites* borings occur in the upper as well as the lower surface of the hardground (Fig. 3A). The intensities of the borings seem to be similar on both surfaces. The *Trypanites* borings have a somewhat patchy distribution, with a maximum of 27 borings found per 4 cm^2. The diameter of the borings is 0.5 to 2.4 mm ($N = 17$, mean 1.2 mm, $sd = 0.5$). Their apertures are mostly circular, in some cases slightly oval or subcircular. The apertures of some borings are merged.

The hardground surface is very sparsely encrusted by possible tabulates (Fig. 3C), sheet-like trepostome

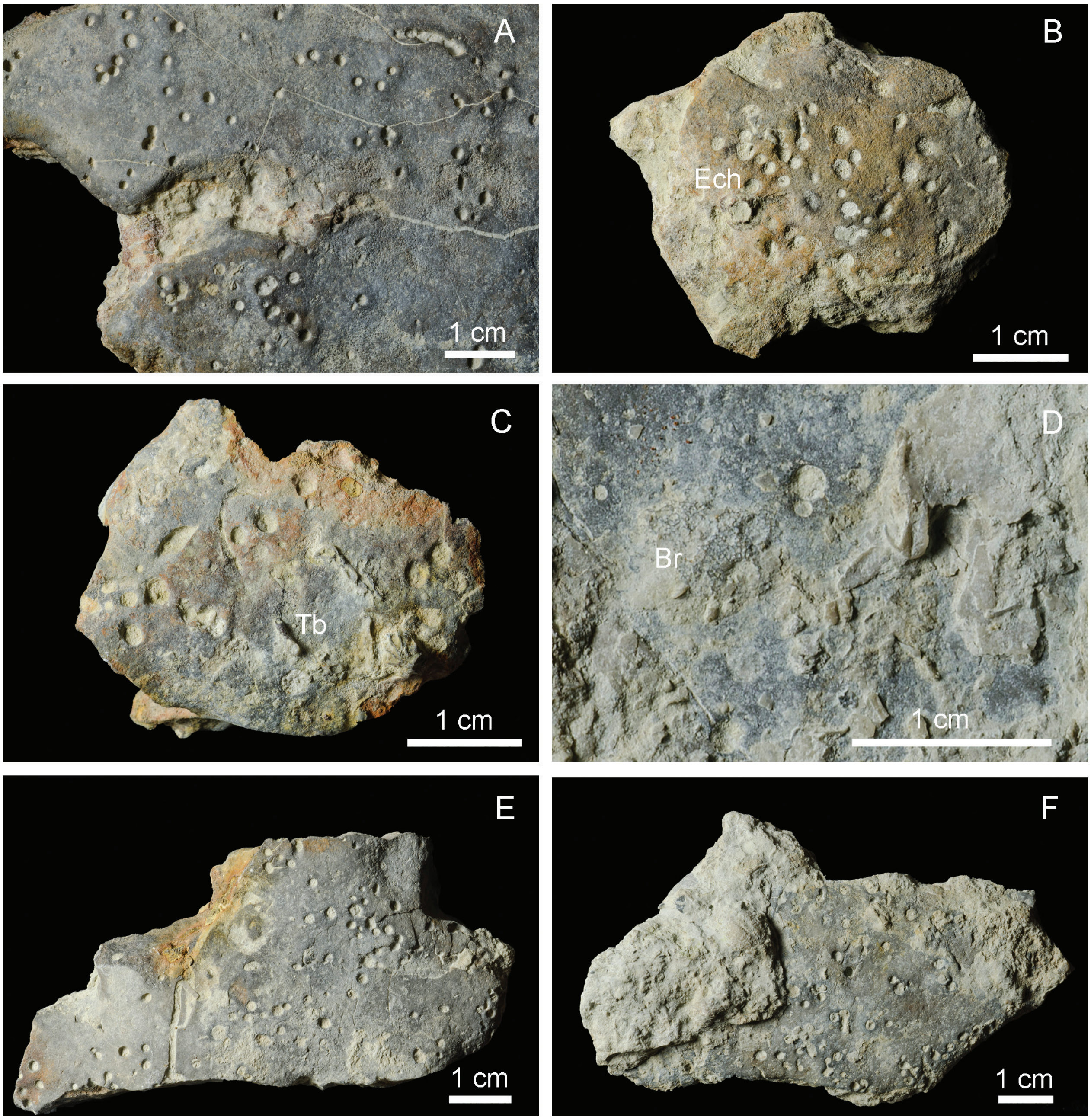

Fig. 3. Päärdu hardground surfaces with encrusters and abundant *Trypanites* borings from the Rumba Formation, early Telychian of the Velise River, western Estonia. **A**, *Trypanites* borings (GIT 362-100); **B**, discoid echinoderm holdfast (GIT 362-101); **C**, possible tabulate corals (auloporids?) (GIT 362-105); **D**, bryozoa (possibly trepostome) (GIT 362-104); **E**, hardground surface with *Trypanites* borings (GIT 362-102); **F**, hardground surface with *Trypanites* borings (GIT 362-104).

bryozoans (Fig. 3D) and echinoderm holdfasts (only 0.4% of the studied 580.11 cm^2; Fig. 3B). Presumed tabulates are the dominant group by number ($N = 3$) and also by the area of encrustation. Tabulates include two possible auloporids with the encrustation area of 0.3 cm^2 and remains of an eroded tabulate with the encrustation area of 1.5 cm^2. Both sheet-like bryozoa with the encrustation area of 0.25 cm^2 and a discoidal echinoderm holdfast with the encrustation area of 0.2 cm^2 are represented by one specimen. The preservation of encrusters is variable; some are well preserved (i.e. not eroded) as a single large discoidal echinoderm holdfast, while remains of a plausible tabulate are strongly eroded. We did not notice any consistent differences between encrustation intensities and the encrusting fauna across the hardground relief, but *Trypanites* borings seem to be more common in elevated regions.

DISCUSSION

Mineralization, fractures and palaeoenvironment

In Laurentia, many hardgrounds are strongly impregnated by minerals, but it is commonly phosphate that has developed (Sullivan et al. 2014). This contrasts with the pyrite mineralization of the Päärdu hardground. It is possible that pyrite mineralization may reflect the differences between palaeocontinents. Alternatively, the absence of phosphate can rule out the hypothesis that excess nutrients triggered anomanously high bioerosion frequencies.

The Päärdu hardground has been fractured into a series of polygonal sections (Fig. 3). Carlton Brett and James Thomka (pers. comm. 2015) have found very similar ‘platter hardgrounds’ in the Llandovery-age Brassfield Formation of the midcontinent USA, as well as within tentatively correlative units in the Medina Group in the Appalachian Foreland Basin. It is possible that hardgrounds of this type are widely traceable marker beds reflecting some underlying stratigraphic or palaeoceanographic process.

The encrusting echinoderm holdfast has a discoidal morphology. It likely indicates a very stable, clean, hard substrate rather than something that was slightly shifting, poorly winnowed or poorly sorted (Thomka & Brett 2015).

Päärdu hardground association

It is interesting that boring intensities of the upper and lower hardground surfaces seem to be similar. According to Nield (1984), *Trypanites* organisms prefer open surfaces and elevations, because they probably were suspension feeders. As the Päärdu hardground includes large cryptic areas densely covered by *Trypanites* borings, it possibly had voluminous cryptic spaces with a good influx of suspended nutrients, necessary for *Trypanites* organisms. James Thomka (pers. comm. 2015) has found that the undersides or edges of raised substrata (i.e. tabulate coral colonies) are often densely encrusted in the Palaeozoic Laurentian hardgrounds. These areas might represent areas where horizontally flowing currents ‘swirl up’ over the encrusted obstructing substratum, making them sites of elevated current velocity or more consistent flow; hence, they might be preferred settlement sites (J. Thomka pers. comm. 2015). Our material was not large enough to study the possible polarity (i.e. upper surface *versus* cryptic fauna) of the hardground association. The Päärdu hardground association is strongly dominated by endobenthic organisms (i.e. *Trypanites*), presumably both by the number of specimens and biomass, while the skeletal epibenthos forms the minor part of the association. However, it is possible that the extremely low skeletal cover of the hardground was due to its being preoccupied by soft-bodied encrusters that did not fossilize. Soft-bodied encrusters such as sponges are common in modern seas. Alternatively, microbial mats might have covered some portion of the hardground and prevented encrustation (J. Thomka pers. obs. 2015). A similar hypothesis for a Devonian edrioasteroid-encrusted hardground was elaborated by Cornell et al. (2003). In the latter case the association may have been less tilted towards the dominance of endobenthos. Among the epibenthic organisms not elevated surface dwellers dominated (sheet-like bryozoans and possible tabulates), while elevated stemmed forms (i.e. echinoderms) formed a minor part.

Taxonomic composition

Typical Ordovician–Silurian hardground associations are in general similar and dominated by bryozoans and echinoderms (Taylor & Wilson 2003). One would expect the early Silurian associations to be very similar to the Ordovician ones. Thus, the taxonomic composition of the Päärdu hardground association is rather different from the characteristic Silurian association in being dominated by tabulate corals, while bryozoans and echinoderms play a minor role. Regarding the position of tabulates in the association, the Päärdu hardground fauna is surprisingly modern, slightly Devonian-like, where tabulates form an important part of the associations. An association of stromatoporoid encrusters from the late Sheinwoodian of Saaremaa, Estonia, is somewhat similar to the Päärdu association (Vinn & Wilson 2012a). Sheinwoodian stromatoporoids of Saaremaa had also an unusually high number of encrusting corals (i.e. rugosans and tabulates). Bryozoans occur also in all other hard substrate associations described from the Silurian of Estonia (Vinn & Wilson 2010, 2012a, 2012b). Similarly, crinoids are usually found in hardground associations (Vinn & Wilson 2010) of Baltica (Franzén 1977; Vinn & Wilson 2010). Several Silurian hardgrounds from North America (Sumrall et al. 2009; Thomka & Brett 2014, 2015) differ from the Päärdu hardground by the lack of boring organisms in the association. In addition, the group diversity (i.e. number of higher taxa) of the Päärdu hardground is higher than in many North American examples (Sumrall et al. 2009;

Thomka & Brett 2014, 2015). Only the hardground fauna described by Halleck (1973) shows a group diversity similar to the Päärdu hardground. However, its taxonomic composition is different (Table 1). The lack of cornulitids in the association is taxonomically interesting. Cornulitids are common on the Late Ordovician hardgrounds of Baltica (Vinn & Toom 2015). Another interesting aspect is related to the lack of microconchids (Zatoń & Vinn 2011; Zatoń et al. 2015). These tiny tentaculitoid tubeworms appeared in the Late Ordovician of Baltica (Vinn 2006) and form an important part of the Pridoli hardground faunas in Estonia (Vinn & Wilson 2010). Thus, it is possible that microconchids were primarily organic substrate dwellers in the Late Ordovician and early Silurian of Baltica, and adapted to life on hardgrounds later in the Silurian.

Encrustation intensity

The Päärdu hardground is relatively sparsely encrusted for the Late Ordovician and Silurian hardgrounds (Halleck 1973; Sumrall et al. 2009; Vinn & Wilson 2010; Thomka & Brett 2015). In general the Ordovician and Silurian hardgrounds of Baltica seem to be more sparsely encrusted (Vinn & Wilson 2010; Vinn & Toom 2015) than the North American analogues (Brett & Liddell 1978; Brett & Brookfield 1984; Wilson et al. 1992). However, due to numerous boring organisms that inhabited the Päärdu hardground, its general population density was not low for the Silurian.

Bioerosion

Bioerosion of the Päärdu hardground was rather intense for the Early Palaeozoic with maximum boring intensities of >20 *Trypanites* per 4 cm^2. Tapanila et al. (2004) considers >20 *Trypanites* per 4 cm^2 to be very high bioerosion intensity for the stromatoporoids of the Late Ordovician–earliest Silurian of Anticosti Island, North America. Relatively high bioerosion intensities seem to be characteristic of the Ordovician (Vinn et al. 2015) and probably also Silurian hardgrounds of Baltica (Vinn & Wilson 2010). Such high bioerosion intensities could either indicate high nutrient contents in seawater (Lescinsky et al. 2002) or long exposure times of the hardgrounds (Wilson & Palmer 2006). The encrusters of the Päärdu hardground are taphonomically variable. This shows that multiple generations are preserved within a single, time-averaged assemblage (Thomka & Brett 2014), indicating fairly convincingly that the hardground was characterized by a long exposure time. The long exposure time might help to explain the origin of high bioerosion rates of the Päärdu hardground. The hardground described by Thomka & Brett (2014, 2015) from the Wenlcok of Indiana is totally devoid of *Trypanites* borings. It is densely encrusted by diverse biota, but bioerosion structures occur entirely within large bioclasts and not in the hardground surface itself.

Bioerosion *versus* encrustation

Bioerosion and encrustation are two fundamentally opposite processes in the oceans that shape the hard substrates. Bioerosion leads to loss of the weight and density of the substrate, while encrustation leads to the accretion of additional mineral and organic layers on top of the hard substrate. It is important to know how these two opposite processes were working together in the Silurian on the same substrate. The Päärdu hardground fauna indicates that high bioerosion densities could correlate with low encrustation densities. This may not be a general rule because bioerosion and encrustation can have a patchy distribution as in the case of the Ohessaare hardground from the Pridoli of Saaremaa (Vinn & Wilson 2010). However, when the hardground surface was first colonized by numerous boring organisms, it could have prevented the formation of dense encrustation. This might be a form of trophic group amensalism, wherein the abundance of bioeroders precluded the settlement of larvae of encrusters and/or prevented the growth of the existing encrusting colonies (J. Thomka pers. comm. 2015).

Acknowledgements. Financial support to O. V. was provided by the Palaeontological Association Research Grant, and 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 G. Baranov, Institute of Geology at Tallinn University of Technology for photographing the specimens, and to J. R. Thomka and an anonymous reviewer for the constructive reviews.

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Hõredalt asustatud *Trypanites*'e käikudega tsementeerunud Llandovery-aegne kihipind Lääne-Eestist Velise jõe äärest

Olev Vinn ja Ursula Toom

Sedimentatsiooniga samaaegselt tsementeerunud kihipinna külge olid hõredalt kinnitunud okasnahksed, korallid ja sammalloomad. Tsementeerunud kihipind sisaldas arvukalt sinna sisse uuristatud *Trypanites*'e käike. Enkrusteerivate loomade hõre asustus ja arvukad *Trypanites*'e käigud tunduvad olevat iseloomulikud Baltika kontinendi Ordoviitsiumi ning Siluri tsementeerunud merepõhjale.