



MICROCONCHID-DOMINATED HARDGROUND ASSOCIATION FROM THE LATE PRIDOLI (SILURIAN) OF SAAREMAA, ESTONIA

Olev Vinn and Mark A. Wilson

ABSTRACT

A hardground fauna of moderate diversity from normal marine (shoal to open shelf) of the late Pridoli of Saaremaa (Estonia) contains: microconchids (*Palaeoconchus* cf. *tenuis*, and *P.* sp.), *Anticalyptraea calyptrata*, sheet-like trepostome bryozoans, discoid crinoid holdfasts, encrusting graptolites, *Aulopora* sp., *Cornulites* sp. and *Conchicolites* sp. Microconchids are most abundant in the association and form the second most prominent group by encrustation area in the association after trepostome bryozoans. There is a taxonomic polarity between sclerobionts on the upper surface of the hardground and the cryptic fauna beneath. This hardground community shows that the high abundance of microconchids characteristic of Devonian hard substrate communities had been achieved by at least the Pridoli. Microconchids preferred hardground upper surfaces and were able to symbiotically grow within bryozoans when overgrown.

Olev Vinn. Department of Geology, University of Tartu, Ravila 14A, 50411 Tartu, Estonia
olev.vinn@ut.ee

Mark A. Wilson. Department of Geology, The College of Wooster, Wooster, OH 44691, USA.
mwilson@wooster.edu

KEY WORDS: hardground, encrustation, bioerosion, paleoecology, Silurian, Baltica

INTRODUCTION

Carbonate hardgrounds are surfaces of syndimentarily cemented carbonate layers that have been exposed on the seafloor. Carbonate hardgrounds are common in calcite sea conditions because of favorable conditions for early cementation of carbonate sediments in the seafloor (Wilson and Palmer 1992). Hardgrounds form suitable attachment surfaces for encrusting and bioeroding organisms. There was a calcite sea in the Silurian, and hardgrounds were common, though probably

less abundant than in the Ordovician (Taylor and Wilson 2003). There are only four detailed studies of Silurian hardground communities: Halleck (1973), Franzén (1977), Cherns (1980) and Sumrall et al. (2009). However, no hardground fauna has been described from the latest Silurian (Pridoli).

Silurian hardground faunas are in general similar to those of Ordovician. They are dominated by bryozoans and echinoderms, particularly crinoids. Devonian encrusting communities are better

PE Article Number: 13.2.9A

Copyright: Paleontological Society July 2010

Submission: 17 August 2009. Acceptance: 18 April 2010

Vinn, Olev and Wilson, Mark A., 2010. Microconchid-Dominated Hardground Association from the Late Pridoli (Silurian) of Saaremaa, Estonia. *Palaeontologia Electronica* Vol. 13, Issue 2; 9A: 12p;
http://palaeo-electronica.org/2010_2/212/index.html

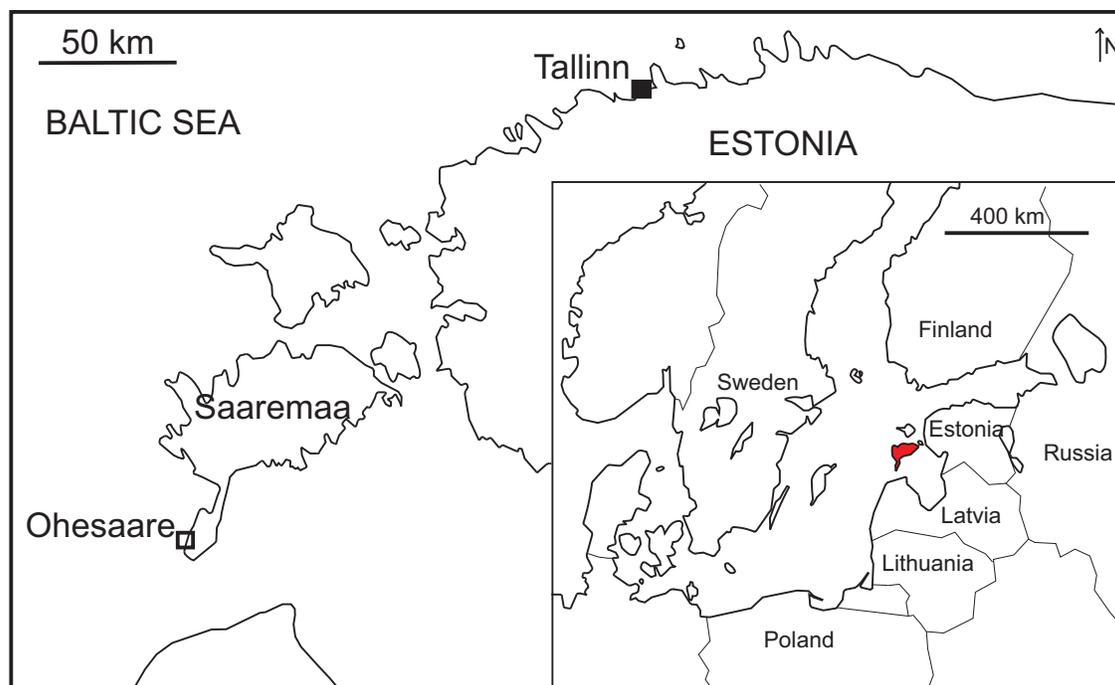


FIGURE 1. Location of the Ohesaare cliff, Saaremaa, Estonia.

known on shells than other hard substrates (Taylor and Wilson 2003). These communities are dominated by microconchids, hederelloids and tabulate corals instead of bryozoans and echinoderms, although the latter two groups are still common (Kesling et al. 1980; Sparks et al. 1980; Bonem 1982; Brett and Cottrell 1982; Alvarez and Taylor 1987; Bordeaux and Brett 1990; Brice and Mistiaen 1992; Grimm 1998, Taylor and Wilson 2003). Especially interesting is the question of how and when typical Ordovician-Silurian sclerobiont communities were replaced by typical Devonian ones.

Hederelloids are extinct colonial animals with calcitic tubular branching exoskeletons, and they appear to be most closely related to phoronids. Tentaculitoid tubeworms could also be phylogenetically closely related to the hederelloids (Taylor and Wilson 2008).

Small, spirally-coiled calcareous worm tubes are common on Paleozoic and Triassic hard substrates (Taylor and Vinn 2006). Such tubeworms have been traditionally assigned to the polychaete genus *Spirorbis*. However, pre-Cretaceous examples have been reinterpreted as microconchids (Class Tentaculita Bouček 1964; Order Microconchida Weedon 1991) on the basis of the early ontogeny and microstructure of their tubes (Weedon 1991, 1994; Dreesen and Jux 1995; Taylor and Vinn 2006; Vinn and Taylor 2007). Two genera of microconchids are known from the Silurian

(Vinn 2006a). Several other groups of problematical calcareous tubeworms referred to the Tentaculita Bouček, 1964, occur in the Paleozoic (Vinn and Mutvei 2005, 2009; Vinn 2010; Taylor et al. in press). They include Tentaculitida Ljaschenko, 1955, Cornulitida Bouček, 1964, and Trypanoporida Weedon, 1991, as well as the genera *Anticalyptraea* (Vinn and Isakar 2007) and *Tymbochoos* (Vinn 2006b). Endosymbiotic *Streptindytes* in the Middle Devonian rugose corals and stromatoporoids may also be a tentaculitoid (Vinn and Mötus 2008).

In this paper, the researchers hope to: 1) describe for the first time a hardground association of Pridoli age; 2) compare the hardground fauna from the Pridoli of Saaremaa to other Silurian and Devonian analogues; 3) contrast upper surface and cryptic communities; 4) discuss the paleoecology of tentaculitid tubeworms; and 5) discern how gradually typical Ordovician-Silurian hardground communities were replaced by typical Devonian communities.

Locality and stratigraphy

The Ohesaare cliff (58°0'2" N, 22°1'10" E) is located on the western coast of the Sõrve Peninsula (Saaremaa, Estonia) near Ohesaare village (Figure 1). The cliff is over 600 m long and up to 4 m high (Figures 2 and 3). The total thickness of the exposed bedrock is 3.5 m, whereas the thick-

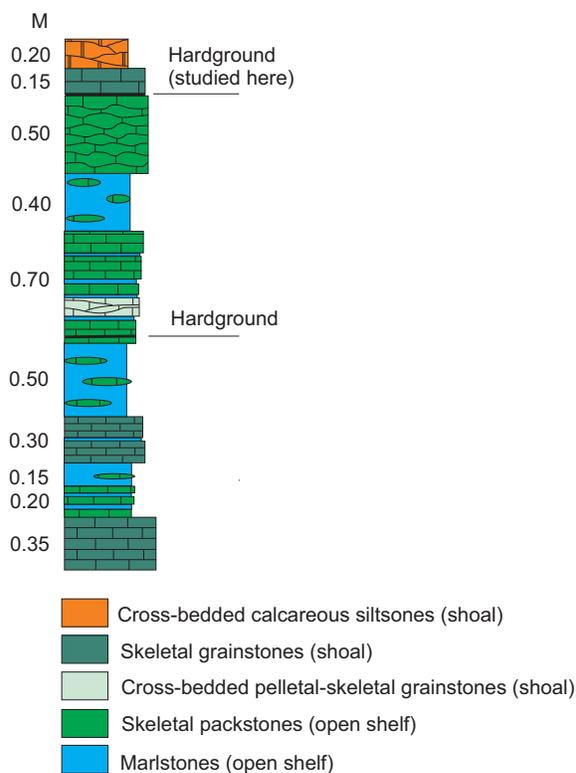


FIGURE 2. Geological section of the Ohesaare cliff (modified after Nestor 1990). Location of the studied hardground in the section.

nesses of individual beds are rather variable throughout the outcrop (Hints 2008). The section is characterized by the intercalation of thin-bedded limestones and marlstones (Figures 2 and 3). There are two hardgrounds in the section, one in the upper part (studied here) and another in the lower middle part of the cliff (Figure 2). The studied hardground is underlain by 0.5 m of skeletal packstone and overlain by 0.15 m silty skeletal grainstone, the upper surface of which bears large ripple marks (Hints 2008). The rocks of Ohesaare section have a high content of terrigenous material. The intense influx of fine siliciclastic material into the basin possibly took place at the final stage of its development (Mõtus and Hints 2007). The rocks of the Ohesaare cliff correspond to the *Monograptus transgrediens* biozone, late Pridoli, Ohesaare Stage (Hints 2008).

During the Silurian the Baltica continent was located in equatorial latitudes drifting northwards (Melchin et al. 2004). The pericontinental Baltic paleobasin in modern Estonia was characterized by a wide range of tropical environments and diverse biotas (Hints 2008). According to the model worked out by Nestor and Einasto (1977), five main



FIGURE 3. The Ohesaare cliff. Hammer at the level of studied hardground.

facies belts can be differentiated in the Baltic Silurian Basin: tidal flat/lagoonal, shoal, open shelf, transitional (basin slope), and a basin depression. The first three facies belts formed a carbonate shelf or carbonate platform and the latter two a deeper pericratonic basin with fine-grained clastic deposits (Raukas and Teedumäe 1997). The rocks of the Ohesaare cliff were formed in shoal and open shelf conditions.

The Ohesaare cliff has a rich and diverse shelly fauna. The most abundant macrofossils are brachiopods, represented by *Delthyris magna* Kozłowski, 1929, *D. elevata* Dalman, 1928, *Homoeospira baylei* (Davidson 1848), *Morinorhynchus orbignyi* (Davidson 1848), *Isorthis ovalis* (Paškevičius 1962). Bryozoans are relatively numerous compared to other eastern Baltic Silurian sections; they include: *Fistulipora tenuilamelata* (Bassler 1911), *F. aculeata* Astrova, 1960 and *Eridotrypa parvulipora* Ulrich and Bassler 1913. Bivalves are represented by *Grammysia obliqua* (McCoy 1852), *Cardiola interrupta* Sowerby, 1839, *Palaeopecten danbyi* (McCoy 1851), and *Modiolopsis complanata* Sowerby, 1839. Trilobites are also common. Corals occur at certain levels in the middle part of section. The middle part of the section has also yielded the tentaculitids *Tentaculites scalaris* (Schlotheim 1820) and *Lowchidium inaequale* Eichwald 1860. The microfossil association is very diverse and rich, especially the ostracodes (Mõtus and Hints 2007).

MATERIAL AND METHODS

All hardground samples were collected from the Ohesaare cliff (Saaremaa, Estonia) (Figure 1). All samples originate from the top 40 cm of the sec-

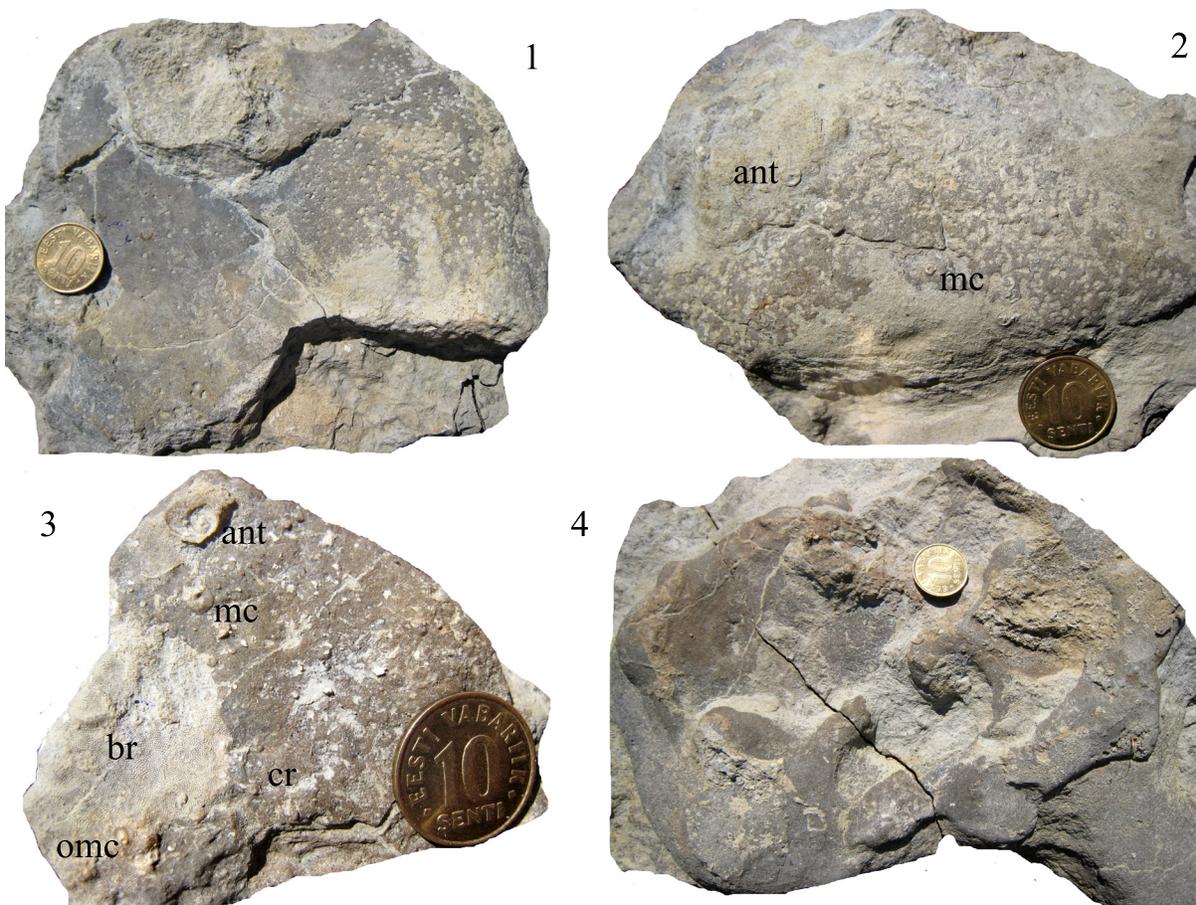


FIGURE 4. Ohesaare hardground samples, late Pridoli, Silurian, 1. Upper surface, showing patchy distribution of *Trypanites* borings and very low encrustation density (TUG 1373-1). 2. Upper surface, showing high microconchid (mc) encrustation density with high *Trypanites* density (TUG 1373-2). 3. Cryptic roof of a hardground ledge showing high encrustation density (TUG 1373-3). 4. Upper surface showing uneven surface relief and very low encrustation and lack of *Trypanites* (TUG 1373-4). Abbreviations: ant- *Anticalyptraea calyptrata*, br – sheet-like trepostome bryozoan, cr – crinoid holdfast, mc – microconchid, omc- overgrown microconchid (with open aperture). Diameter of the coin is 17 mm.

tion, about at the level of the previously reported hardground (Mõtus and Hints 2007) (Figures 2 and 3). Sample orientations were marked during collecting. Thereafter, they were manually cleaned of clay with water and a soft brush. *Trypanites* borings and microconchids were counted in a 5x5 cm grid. All encrusting fossils were drawn on a transparent plastic film, and their surface area was estimated using a millimeter grid. A centimeter grid was used to calculate the total surface area of the hardground samples. We were able to identify microconchid species in the few cases when shells were completely preserved. Most of the spirorbiform shells were partially broken or preserved as spiral attachment scars. They were identified at group level as microconchids if smaller than 3.0 mm in diameter. Juvenile growth stadia of *Anticalyptraea calyptrata* are very similar to those of microcon-

chids, so the actual number of *Anticalyptraea calyptrata* may have been slightly higher and the number of microconchids slightly lower in the association than estimated here. Fragments of encrusting graptolites were very incomplete and too poorly preserved for measuring the surface area of encrustation. *Conchicolites* sp. and *Aulopora* sp. were also too incompletely preserved to measure area of encrustation. Remains of probable cementing brachiopods were too poorly preserved for certain identification. Figured specimens are deposited at the Geological Museum, Museum of Natural History, University of Tartu (TUG).

RESULTS

The Ohesaare hardground is formed from an intrabiosparite containing skeletal debris (brachio-

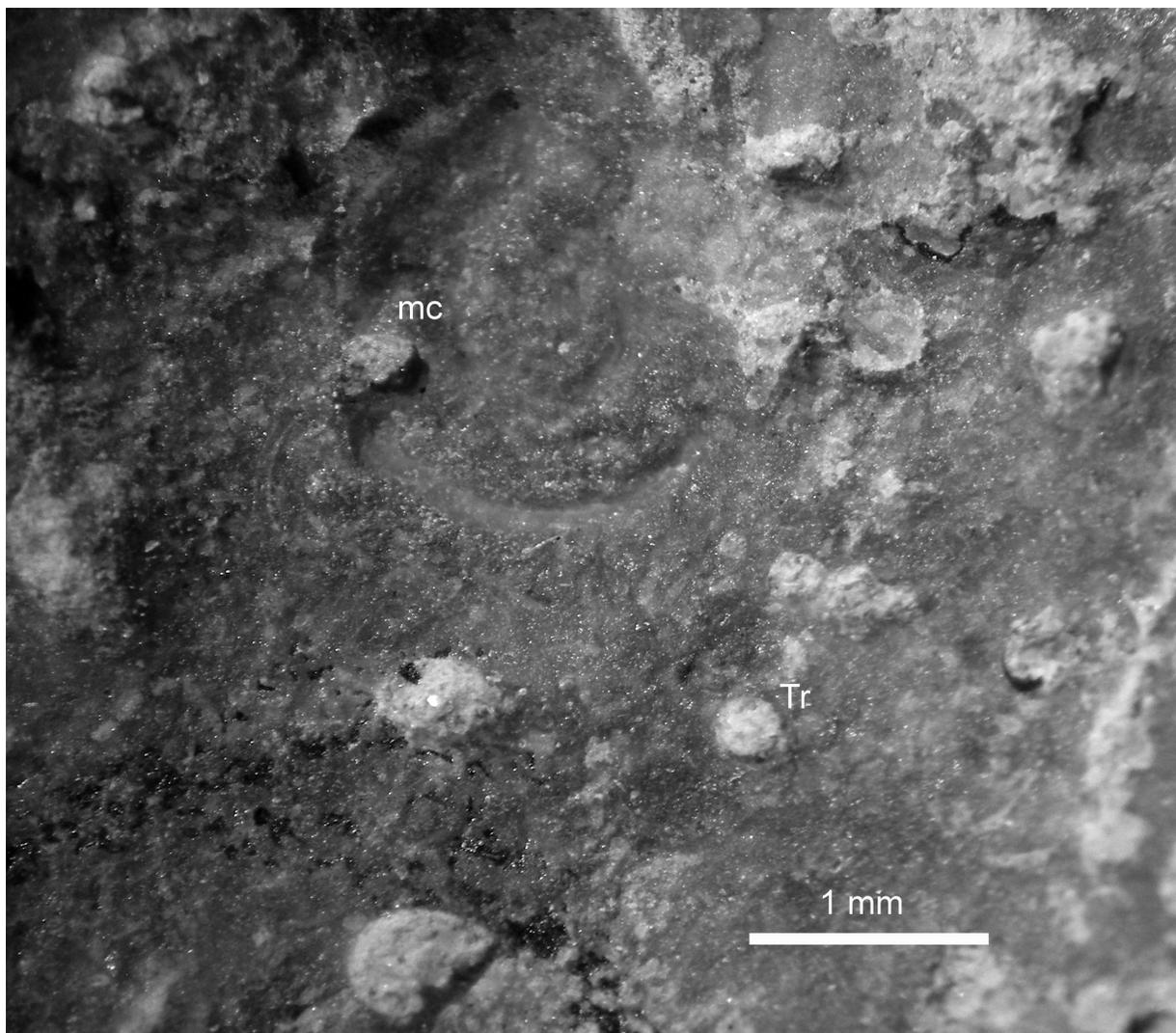


FIGURE 5. *Trypanites* borings (Tr) and an abraded microconchid (mc), upper surface (TUG 1373-3).

pod, bryozoans, echinoderms, mollusks, trilobites, ostracodes, and *Tentaculites*), as well as biomicritic intraclasts. The echinoderm fragments show much syntaxial overgrowth cement. Some parts of the hardground are composed of pure sparitic cement. Bioclasts in the hardground are abraded both on the upper and cryptic sides. The hardground surface is abraded (Figure 4). The crypts are formed under the hardground ledges and are up to 10 cm wide. The hardground ledges are 3 to 30 mm thick. The hardground has a moderate relief (Figure 4). The microrelief is bumpy (Figure 5). There are possible microborings in both surfaces of the hardground. Some parts of the hardground surface are darker than others. There are linear calcite-filled fractures and mud-filled crevices and ledges. The encrusting microconchids (broken tubes) show

marks of slight abrasion (Figure 5). The hardground is covered by light-colored bluish soft marl containing numerous fragments of crinoid columnals, articulate brachiopods, and some fish scales.

The hardground association has a moderate diversity comprising: two species of microconchids (*Palaeoconchus* cf. *tenuis* and *Palaeoconchus* sp.) (Figure 6), *Anticalyptrea calyptrata* (Figure 6), *Cornulites* sp., *Conchicolites* sp., sheet-like trepostome bryozoans (Figures 6 and 7), discoidal crinoid holdfasts, encrusting graptolites, tabulate *Aulopora* sp., *Trypanites* borings (Figure 5), and probably also cementing brachiopods. Microconchid tube-worms dominate in abundance (Table 1). The hardground association shows a moderate taxonomic polarity between the upper surface and cryptic communities (Tables 1 and 2).

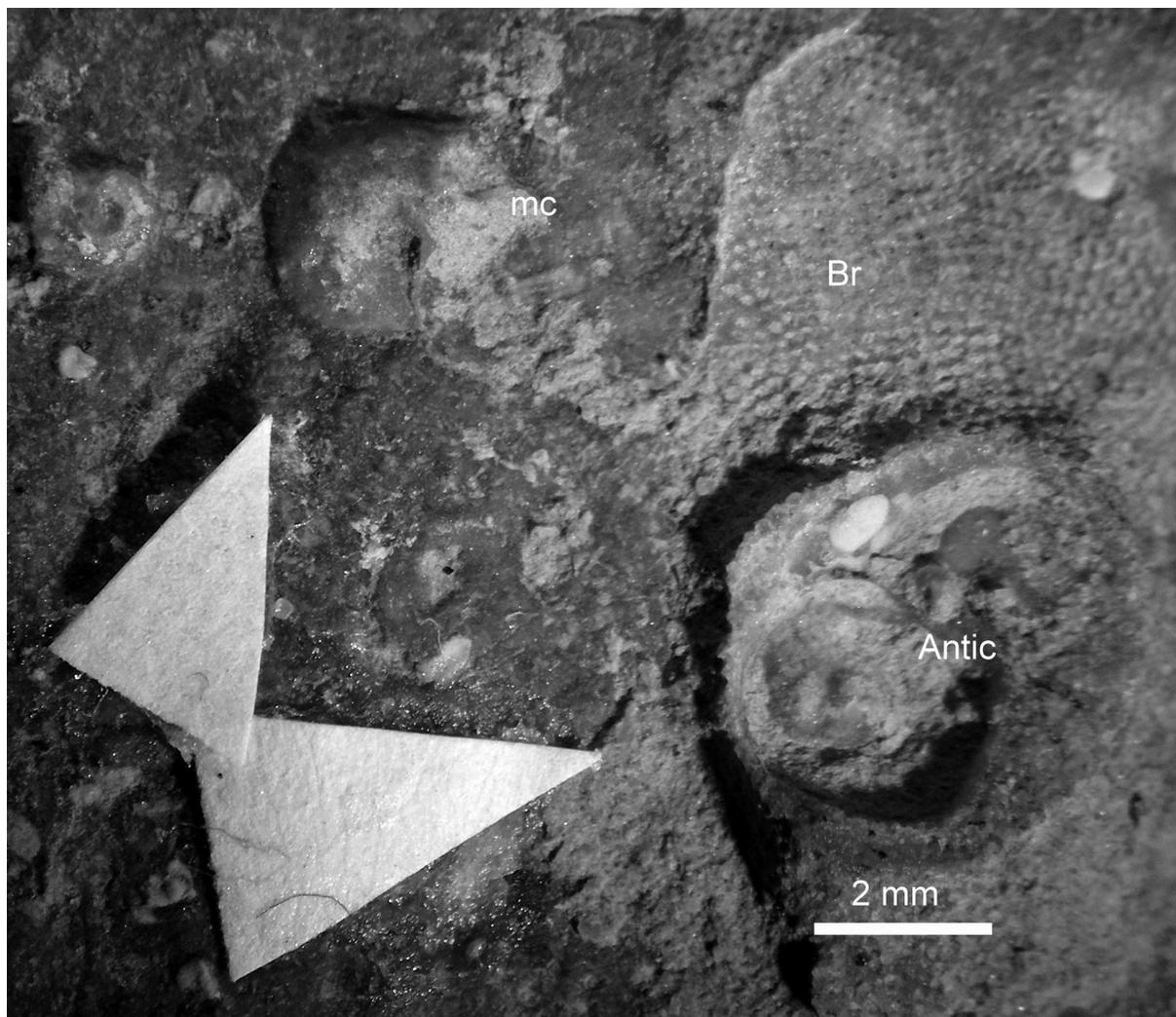


FIGURE 6. Arrows point at microconchid *Palaeoconchus* cf. *tenuis* (mc), and *Anticalyptrea calyptrea* (Antic) partially overgrown by a sheet-like bryozoan (br), cryptic roof of a hardground ledge (TUG 1373-3).

Trypanites range from 0.50 to 2.50 mm in diameter and extend to a maximum depth of 0.5 cm below the substrate surface (Figure 4.4) (Figure 5). There are usually 20 to 180 *Trypanites* borings per 5 cm² of the hardground upper surface, but some areas (up to 5 cm²) have no borings (Figure 4.4). There are a maximum of three *Trypanites* per 5 cm² on the cryptic surfaces of the hardground; most of these surfaces lack *Trypanites* (up to 20 cm²) (Figure 4.3).

The hardground is sparsely covered by encrusting fossils (Figure 4). The hardground cryptic surfaces were more densely populated by skeletal encrusters than the upper surfaces, 6.4 % of total surface area and 1.5 % of total surface area, respectively (Table 2).

Sheet-like trepostome bryozoans showed a strong preference for cryptic roofs of hardground ledges (Table 2) (Figures 6 and 7) as compared to upper surfaces. *A. calyptrea* (3.1 to 6.0 mm in diameter) also had a slight preference for cryptic conditions (Table 2) (Figure 6). In contrast, microconchids (0.8 to 2.9 mm in diameter) had a slight preference for hardground upper surfaces (Table 2) (Figure 4.2) (Figure 5). The percent of microconchids in the total skeletal cover of hardground is several times higher in the upper surface community than it is in the cryptic community (Table 2) (Figure 6) (Figure 7).

The distribution of encrusting fauna on the hardground is patchy, both on upper surfaces and underneath hardground ledges (Figures 4.1-4.2). Distribution of *Trypanites* borings (bioerosion) is

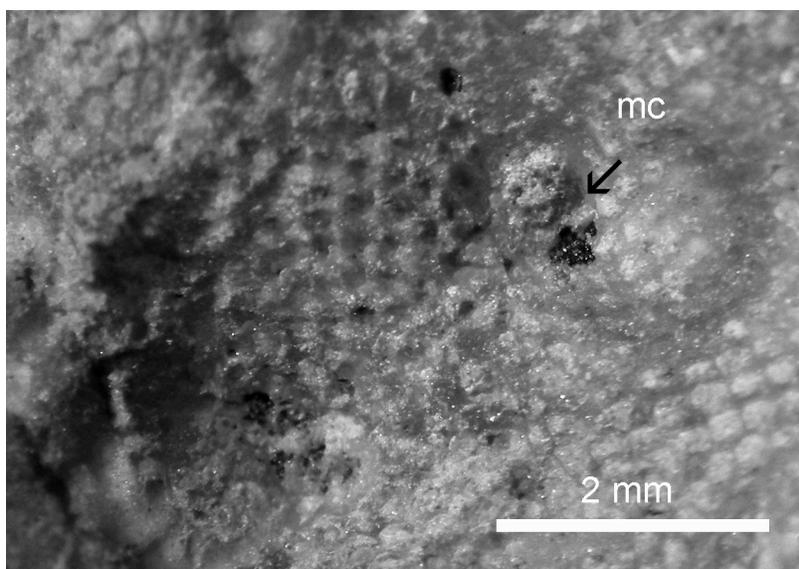


FIGURE 7. Microconchid (mc) is overgrown by a sheet-like bryozoan, arrow points at free aperture of the microconchid, cryptic roof of a hardground ledge (TUG 1373-3).

also patchy on the upper surfaces. *Trypanites* borings are rare underneath hardground ledges. High *Trypanites* densities are found both with very low (Figure 4.1) to high microconchid encrustation frequencies on upper surfaces (Figure 4.2).

Five cases of skeletal overgrowth occur between different encrusting species, four in the cryptic community. All overgrowths occur between the specimens of different taxa. Two cryptic microconchids are overgrown by a sheet-like trepostome bryozoan, but they have elevated apertures, which remained free of the bryozoan skeleton (Figure 7). One sheet-like trepostome bryozoan has overgrown the aperture of one specimen of *A. calyp-*

trata, while the other specimen of *A. calyptrata* which is overgrown by bryozoans has an unencrusted aperture (Figure 6). A specimen of *Aulopora* sp. is almost completely overgrown by a sheet-like trepostome bryozoan. One upper surface microconchid is completely overgrown by a sheet-like trepostome bryozoan.

DISCUSSION

We interpret the environment of the Ohesaare hardground association (Figure 8) as a shallow sea floor of normal salinity below the tidal zone (shelf of moderate depth to shoal). This is supported by the

TABLE 1. Faunal composition of the hardground association.

| Fauna | Upper surface community | Cryptic community |
|---|-------------------------|-------------------|
| Microconchids | 115 (87.8 %) | 15 (62.5 %) |
| <i>Anticalyptrea calyptrata</i> | 4 (3.1 %) | 2 (8.3 %) |
| Sheet-like trepostome bryozoans | 4 (3.1 %) | 3 (12.5 %) |
| Crinoid holdfast (discoïd) | 3 (2.3 %) | 1 (4.2 %) |
| Encrusting graptolite | 3 (2.3 %) | - |
| Unidentified calcareous remains (brachiopod?) | 1 (0.8 %) | 1 (4.2 %) |
| <i>Aulopora</i> sp. | - | 1 |
| <i>Cornulites</i> sp. | 1 (0.8 %) | - |
| <i>Conchicolites</i> sp. | - | 1 (4.2 %) |
| Total | 131 (100 %) | 24 (100 %) |

TABLE 2. Skeletal cover of upper and cryptic surfaces of the hardground.

| Taxa | Upper surface community (708 cm ² mapped) | | | Cryptic community (110 cm ² mapped) | | |
|---|--|-------------------|---------------------|--|-------------------|---------------------|
| | Area covered cm ² | % of area covered | % of skeletal cover | Area covered cm ² | % of area covered | % of skeletal cover |
| Sheet-like trepostome bryozoans | 6.80 | 1.0 | 63.3 | 6.50 | 5.9 | 92.3 |
| Microconchids | 3.02 | 0.4 | 28.1 | 0.25 | 0.2 | 3.6 |
| <i>Anticalyptrea calyptrata</i> | 0.66 | 0.1 | 6.1 | 0.22 | 0.2 | 3.1 |
| Crinoid discoid holdfasts | 0.16 | 0.02 | 1.5 | 0.03 | 0.03 | 0.4 |
| Unidentified calcareous remains (brachiopod?) | 0.06 | 0.008 | 0.6 | 0.04 | 0.04 | 0.6 |
| <i>Cornulites</i> sp. | 0.04 | 0.006 | 0.4 | - | | |
| Total area covered by fossils | 10.74 cm ² (1.5 %) | | | 7.04 cm ² (6.4 %) | | |

shallow water origin of the overlying rocks (Nestor 1990) (Figure 2) and the presence of crinoids. The hardground was probably cemented under the sediment cover and exposed later to do winnowing, which also exposed the cryptic surfaces. The abraded bioclasts in the hardground indicate that the hardground was abraded before the encrustation. The sediment layer below the hardground was probably still soft or less cemented than the hardground during the abrasion.

The high bioerosion density for the Silurian (Tapanila et al. 2004) (Figure 4.1) presumably indicates a relatively long exposure time for the hardground, before it was buried by clayey sediments (overlying marl interlayer).

Tapanila et al. (2004) found that bioerosion of Ordovician-Silurian corals and stromatoporoids was a widespread process, but that high boring density was generally rare. The situation in Ohesaare hardground is slightly different. Usual 20 to 180 borings per 5 cm² of hardground upper surface corresponds roughly to high boring density by Tapanila et al. (2004) (Figure 4.1). However, samples studied by Tapanila et al. (2004) are stratigraphically older (Hirnantian to Telychian), so high boring densities in Ohesaare could reflect an evolutionary trend. They also may reflect simply a longer exposure time of the substrate. The long exposure time is more likely as the major increase in bioerosion intensity took place earlier in the Middle Ordovician (Wilson and Palmer 2006). Alternatively, the high boring densities can be interpreted as reflecting an environmental or biogeographic difference.

The relatively low skeletal coverage of the hardground (Figure 4) as compared to the other Ordovician to Devonian analogues (Brett and Liddell 1978) can be explained by low productivity (low nutrient levels) in the sea water (Lescinsky et al. 2002) or by a large number of soft-bodied organisms in the community, which did not preserve as fossils. Lescinsky et al. (2002) found that modern bioerosion is higher at more productive sites in the ocean. They also found that more productive sites have higher encrustation rates. The Ohesaare hardground has a relatively low encrustation density (Segars and Liddell 1988, Lebold 2000) and a relatively high bioerosion density for the Silurian (Tapanila et al. 2004) (Figure 4). Thus, if these relations were valid in the late Silurian, it is possible that much of the substrate was occupied by biofilms (preventing attachment of several skeletal encrusters) and soft-bodied encrusters (competing with skeletal ones) as compared to typical Silurian hard substrate communities.

The lower skeletal coverage of the upper surfaces as compared to the cryptic surfaces is due to distribution of sheet-like trepostome bryozoans (Table 2), which cover five times more area on cryptic surfaces than they do on upper surfaces (Figures 4, 6, and 7). Such strong preference of sheet-like bryozoans for the cryptic niche could be explained by higher predation pressure of grazers on the upper surface. However, the upper surface may also have been more heavily covered by biofilms or soft-bodied encrusters not tolerated by bryozoans.

The larger number of skeletal overgrowths in the cryptic community as compared to the upper surface community can be explained by the higher

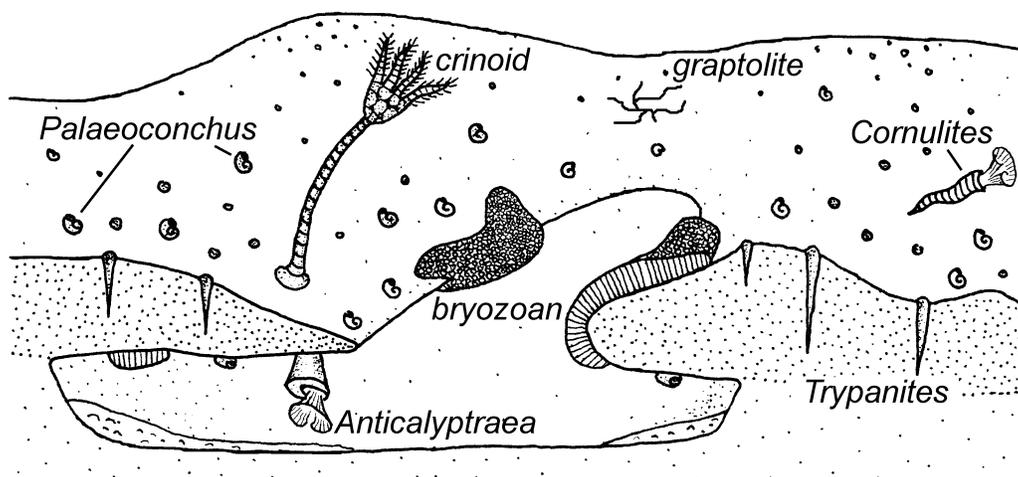


FIGURE 8. Reconstruction of the Ohesaare hardground fauna.

total skeletal coverage of the cryptic surface. This could also reflect the higher spatial competition between the skeletal encrusters in the cryptic community. However, none of the five overgrowths shows signs that overgrowth of one encruster by another led to the death of the first encruster. Cryptic microconchids were able to stay alive when overgrown by bryozoans by keeping their slightly erected apertures free of bryozoans (Figure 7).

The patchy distribution of *Trypanites* borings and microconchids on the hardground can be explained by gregarious larval settling behavior or by space being preoccupied by soft-bodied organisms or by uneven survival of larva because of differences in microenvironmental conditions (Figures 4 and 8 8). The organisms that produced *Trypanites* borings preferentially drilled the high points on hard substrates in the Ordovician, probably for better filter-feeding (Brett and Liddell 1978; Brett and Brookfield 1984; Bodenbender et al. 1989; Wilson and Palmer 1992). This appears to have been the case as well for the Ohesaare hardground.

The Ohesaare hardground fauna is unique for its numerical dominance by *Palaeoconchus* (Figure 6). Their high abundance in the community (Table 1), large total area covered and high percentage of relative skeletal cover (Table 2) are unmatched elsewhere in the Silurian (Segars and Liddell 1988; Lebold 2000). Why did the *Palaeoconchus* dominate this association? They presumably were opportunistic suspension feeding encrusters, successful in conditions of low competition with other suspension feeders. The low total coverage by bryozoans and lack of stromatoporo-

ids and favositids could have enhanced the abundance of *Palaeoconchus* in the community. The unusually high number of *Palaeoconchus* on the Ohesaare hardground compared to other Silurian hard substrate communities (Segars and Liddell 1988; Lebold 2000) presumably also reflects an evolutionary trend. Microconchids are more abundant in Devonian than in Ordovician-Silurian hard substrate communities (Taylor and Wilson 2003). This association is the only hardground fauna known from the Pridoli. Thus, the abundance of microconchids in hard substrate communities may have increased by the Pridoli to the typical Devonian level. Alternatively, the high abundance of *Palaeoconchus* could have been caused by the local environmental factors, such as low abundance of the other sclerobionts. Crinoids are usually a very important component of Silurian hardground communities (Halleck 1973; Franzén 1977). The Ohesaare hardground is not typical for the Silurian because of its low abundance of crinoids (Figure 8). Hederelloids, which are very characteristic of Devonian sclerobiont communities (Taylor and Wilson 2003), are lacking in the Ohesaare hardground fauna. The lack of hederelloids may be due to their later evolutionary diversification in the Devonian (Taylor and Wilson 2008).

It is most intriguing why stromatoporoids and favositids are absent from the Ohesaare hardground (Figure 8). They constitute an important component of other Silurian to Devonian hardground communities (Taylor and Wilson 2003). Stromatoporoids are not known from the Ohesaare cliff, but some favositids such as *Favosites*

forbesi, *F. pseudoforbesi* and *F. vectorius* are common in the section. In addition to tabulates, rugose corals also occur in the Ohessaare cliff (Mõtus and Hints 2007). Possible explanations include the presence of the biofilms preventing settlement of stromatoporoid and favositid larvae, or too much suspended sediment for stromatoporoids and favositids. However, the hardground environment would likely not have had much sedimentation because it is by definition one where deposition rates are very low. Thus, biofilms seem to be the most realistic explanation for the lack of stromatoporoids and favositids. In addition, there may have been a lot of sediment in suspension, creating turbid and/or abrasive conditions.

Palaeoconchus preference for hardground upper surfaces (Figures 4 and 8) could be due to higher concentration of nutrients available in the currents or weaker feeding and spatial competition with the other suspension feeders such as bryozoans (e.g., lower coverage by skeletal encrusters of the upper surface). Our observations are in agreement with the results of previous studies of microconchids on Silurian stromatoporoids. Microconchids are more common on stromatoporoid upper surfaces than on their cryptic surfaces (Segars and Liddell 1988; Lebold 2000). Thus, the preference for upper surfaces of hard substrates may be a general feature of Silurian microconchids. In contrast, the phylogenetically close *Anticalyptraea* (Vinn and Isakar 2007) preferred cryptic surfaces to the upper surfaces of the hardground (Figures 6 and 8). *Anticalyptraea* grew to a much larger size than *Palaeoconchus* and could have been more attractive for the predators, including durophagous predators. This is supported by the occurrence of shell repair presumably resulting from attempted predation in *Anticalyptraea* from the Pridoli of Estonia (Vinn and Isakar 2007). Thus, *Anticalyptraea*'s preference for the cryptic surface of the hardground could be due to predation pressure.

Future work needs to be done on Silurian hardground faunas in order to find whether the high abundance of microconchids in the Ohessaare is a local phenomenon or characteristic of the late Silurian hardground associations. In addition, the palaeoecology of *Anticalyptraea* needs further study, especially regarding the predation and probable preference of cryptic environments.

ACKNOWLEDGMENTS

We are grateful to I. Vinn, W. Ausich, P. Shonk and R. McConnell for assistance during the

field work in Saaremaa. Two anonymous reviewers are thanked for their constructive reviews. This work was partially supported by the Wengerd Fund and the Faculty Development Fund at The College of Wooster. O.V. acknowledges project SF0180051s08 "Ordovician and Silurian climate changes, as documented from the biotic changes and depositional environments in the Baltoscandian Palaeobasin."

REFERENCES

- Astrova, G. G. 1960. *Order Trepostomata. Fundamentals of Paleontology: Bryozoans, Brachiopods*. 57-67pp.; Moscow (Akademy Nauk SSSR) (in Russian).
- Alvarez, F. and Taylor, P.D. 1987. Epizoan ecology and interactions in the Devonian of Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 61:17–31.
- Bassler, R.S. 1911. The Early Paleozoic Bryozoa of the Baltic Provinces. *Bulletin of Smithsonian Institution U.S. National Museum*, 77:1–382.
- Bodenbender, B.E., Wilson, M.A. and Palmer, T.J. 1989. Paleocology of *Sphenothallus* on an Upper Ordovician hardground. *Lethaia*, 22:217–225.
- Bonem, R.M. 1982. Morphology and paleoecology of the Devonian rostroconch genus *Bigalea*. *Journal of Paleontology*, 56:1362–1374.
- Bordeaux, Y.L. and Brett, C.E. 1990. Substrate specific associations of epibionts on Middle Devonian brachiopods: implications for paleoecology. *Historical Biology*, 4: 221–224.
- Bouček, B. 1964. *The Tentaculites of Bohemia*. Publication of the Czechoslovakian Academy of Sciences, Prague, 125 pp.
- Brett, C.E. and Brookfield, M.E. 1984. Morphology, faunas and genesis of Ordovician hardgrounds from southern Ontario, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 46:233–290.
- Brett, C.E. and Cottrell, J.F. 1982. Substrate specificity in the Devonian tabulate coral *Pleurodictyum*. *Lethaia*, 15:247–262.
- Brett, C.E. and Liddell, W.D. 1978. Preservation and paleoecology of a Middle Ordovician hardground community. *Paleobiology*, 4:329–348.
- Brice, D. and Mistiaen, B. 1992. Épizoaires des brachiopodes Frasnien de Ferques (Boulonnais, Nord de la France). *Geobios, Mémoire Spécial*, 14:45–58.
- Cherns, L. 1980. Hardgrounds in the Lower Leintwardine Beds (Silurian) of the Welsh Borderland. *Geological Magazine*, 117:311–408.
- Dalman, J.W. 1828. Uppställning och Beskrifning af de i sverige funne Terebratuliter. *Kungliga Svenska Vetenskapsakademiens Handlingar*, 1827:85–155.
- Davidson, T. 1848. Memoire sur les brachiopodes du système silurien superieur d'Angleterre. *Bulletin de Société géologique de France*, 5:309–338.
- Davidson, T. 1871. Monograph of the British Fossil Brachiopoda, Part VII. The Silurian Brachiopoda. *Palaeontographical Society Monograph*, 4:49–397.

- Dreesen, R. and Jux, U. 1995. Microconchid buildups from the Late Famennian peritidal-lagoonal settings (Eveux Formation, Ourthe Valley, Belgium). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 198:107–121.
- Eichwald, E. 1860. *Lethaea Rossica ou Paléontologie de la Russie*. 1654 pp.; Stuttgart (Schweizerbart).
- Franzén, C. 1977. Crinoid holdfasts from the Silurian of Gotland. *Lethaia*, 10:219–234.
- Grimm, M.C. 1998. Orthocone Cephalopoden als sekundäre Hartgrundssubstrate in Black Shales des Oos-Plattenkalks (Frasniums der Budesheimer Mulde, Eifel, Deutschland). *Mainzer Naturwissenschaftliches Archiv. Beiheft*, 21:39–44.
- Halleck, M.S. 1973. Crinoids, hardgrounds, and community succession: the Silurian Laurel-Waldron contact in southern Indiana. *Lethaia*, 6:239–252.
- Hints, O. 2008. The Silurian System in Estonia. In Hints, O., Ainsaar, L., Männik, P. and Meidla, T. (eds.). The Seventh Baltic Stratigraphical Conference. Abstracts and Field Guide. Geological Society of Estonia, p. 46., Tallinn.
- Kesling, R.V., Hoare, R.D. and Sparks, D.K. 1980. Epizoans of the Middle Devonian brachiopod *Paraspirifer bownockeri*: their relationships to one another and to their host. *Journal of Paleontology*, 54:1141–1154.
- Kozłowski, R. 1929. Les Brachiopodes Gothlandiens de la Podolie. *Palaeontologia Polonica*, 1:1–254.
- Lebold, J.G. 2000. Quantitative analysis of epizoans on Silurian stromatoporoids within the Brassfield Formation. *Journal of Paleontology*, 74: 394–403.
- Lescinsky, H.L., Edinger, E. and Risk, M.J. 2002. Mollusc shell encrustation and bioerosion rates in a modern epeiric sea: taphonomy experiments in the Java Sea, Indonesia. *Palaios*, 17:171–191.
- Ljaschenko, G.P. 1955. Novye dannye o sistematike tentakulitov, novakiyi i stiliolii. Biulleten Moskovskogo Obschestva Ispytatelei Prirody, Otdel Geologichskii, *Novaia Seriya*, 30:94–95 (In Russian).
- McCoy, F. 1851. On some new Silurian Mollusca. *Annals and Magazine of Natural History, Series 2*, 7(37):45–63.
- McCoy, F. 1852. *A synopsis of the classification of the British Palaeozoic rocks, with a systematic description of the British Palaeozoic fossils in the Geological Museum of the University of Cambridge with figures of the new and imperfectly known species*. 661 pp.; London (Parker and Son).
- Melchin, M.J., Cooper, R.A. and Sadler, P.M. 2004. The Silurian Period. In Gradstein, F.M., Ogg, J.G. and Smith, A.G. (eds.). *A Geologic Time Scale 2004*, pp. 188–201; Cambridge University Press.
- Mõtus, M.-A. and Hints, O. 2007. Excursion Guidebook. 10th International Symposium on Fossil Cnidaria and Porifera Excursion B2: Lower Paleozoic geology and corals of Estonia August 18–22, Tallinn, Institute of Geology at Tallinn University of Technology, p. 54–55.
- Nestor, H. 1990. Locality 7:4 Ohesaare cliff. In Kaljo, D. and Nestor, H. (eds.) *Field meeting, Estonia 1990. An Excursion Guidebook*. Institute of Geology, Estonian Academy of Sciences, Tallinn, 175–178.
- Nestor, H. and Einasto, R. 1977. Model of facies and sedimentology for Paleobaltic epicontinental basin. In Kaljo, D.L. (ed.). *Facies and fauna Silurian of Baltica*. Institute of Geology AN ESSR, Tallinn, 89–121 (In Russian).
- Paškevičius, J.U. 1962. *Platyorthis ovalis* sp. nov. in the upper Ludlovian rocks of the southern Baltic Area. *Scientific Reports of Academy of Lithuanian S.S.R. Geology, Geography*, 14:33–44.
- Raukas, A. and Teedumäe, A. 1997. *Geology and Mineral Resources of Estonia*. 436 pp.; Tallinn (Estonian Academy Publishers).
- Schlotheim, E. F. 1820. *Die Petrefaktenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier- und Pflanzenreichs erläutert*. 437 pp.; Gotha (Becker'sche Buchhandlung).
- Segars, M.T. and Liddell, W.D. 1988. Microhabitat analyses of Silurian stromatoporoids as substrata for epibionts. *Palaios*, 3:391–403.
- Sowerby, J. de C. 1839. Shells. In Murchison, R.I., *The Silurian System*. 768 pp.; London (John Murray).
- Sparks, D.K., Hoare, R.D. and Kesling, R.V. 1980. Epizoans on the brachiopod *Paraspirifer bownockeri* (Stewart) from the Middle Devonian of Ohio. *Papers on Paleontology*, 23:1–105.
- Sumrall, C.D., Brett, C.E. and McKinney, M.L. 2009. A new agelacrinid edrioasteroid attached to a large hardground clast from the McKenzie Member of the Mifflintown Member (Silurian) of Pennsylvania. *Journal of Paleontology* 83: 794–803.
- Tapanila, L., Copper, P. and Edinger, E. 2004. Environmental and substrate control on Paleozoic bioerosion in corals and stromatoporoids, Anticosti Island, Eastern Canada. *Palaios*, 19:292–306.
- Taylor, P.D. and Vinn, O. 2006. Convergent morphology in small spiral worm tubes ('*Spirorbis*') and its palaeoenvironmental implications. *Journal of the Geological Society, London*, 163:225–228.
- Taylor, P.D. and Wilson, M.A. 2003. Palaeoecology and evolution of marine hard substrate communities. *Earth Science Reviews*, 62:1–103.
- Taylor, P.D. and Wilson, M.A. 2008. Morphology and affinities of hederelloid "bryozoans", p. 301–309. In Hageman, S.J., Key, M.M., Jr. and Winston, J.E. (eds.), *Bryozoan Studies 2007: Proceedings of the 14th International Bryozoology Conference*, Boone, North Carolina, July 1–8, 2007. Virginia Museum of Natural History Special Publication 15.
- Taylor, P.D., Vinn, O. and Wilson, M.A. (in press). Evolution of biomineralization in 'Lophophorates'. *Special Papers in Palaeontology*.
- Ulrich, E.O. and Bassler, R.S. 1913. Systematic paleontology of the Lower Devonian deposits of Maryland; Bryozoa. *Maryland Geological Survey*, 5:259–290.

- Vinn, O. 2006a. Two new microconchid (Tentaculita Bouek 1964) genera from the Early Palaeozoic of Baltoscandia and England. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 2006 (2):89–100.
- Vinn, O. 2006b. Tentaculitoid affinities of the tubeworm-like fossil *Tymbochoos sinclairi* (Okulitch 1937) from the Ordovician of North America. *Geobios*, 39: 739–742.
- Vinn, O. 2010. Adaptive strategies in the evolution of encrusting tentaculitoid tubeworms. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 292: 211–221.
- Vinn, O. and Isakar, M. 2007. The tentaculitid affinities of *Anticalyptraea* from the Silurian of Baltoscandia. *Palaeontology*, 50:1385–1390.
- Vinn, O. and Môtus, M.-A. 2008. The earliest endosymbiotic mineralized tubeworms from the Silurian of Podolia, Ukraine. *Journal of Paleontology*, 82:409–414.
- Vinn, O. and Mutvei, H. 2005. Observations on the morphology, and affinities of cornulitids from the Ordovician of Anticosti island and the Silurian of Gotland. *Journal of Paleontology*, 79:726–737.
- Vinn, O. and Mutvei, H. 2009. Calcareous tubeworms of the Phanerozoic. *Estonian Journal of Earth Sciences*, 58 (4):286–296.
- Vinn, O. and Taylor, P.D. 2007. Microconchid tubeworms from the Jurassic of England and France. *Acta Palaeontologica Polonica*, 52:391–399.
- Weedon, M.J. 1991. Microstructure and affinity of the enigmatic Devonian tubular fossil *Trypanopora Lethaia*, 24:223–227.
- Weedon, M.J. 1994. Tube microstructure of Recent and Jurassic serpulid polychaetes and the question of the Palaeozoic “spirorbids”. *Acta Palaeontologica Polonica*, 39:1–15.
- Wilson, M.A. and Palmer, T.J. 1992. Hardgrounds and hardground faunas. *University of Wales, Aberystwyth, Institute of Earth Studies Publications*, 9:1–131.
- Wilson, M.A. and Palmer, T.J. 2006. Patterns and processes in the Ordovician Bioerosion Revolution. *Ichnos*, 13:109–112.