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A new microconchid species from the Silurian of Baltica

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Abstract. The diversity of Silurian microconchids is still poorly understood. Here, a new microconchid tubeworm species, *Palaeoconchus wilsoni*, is described from the Silurian (Ludlow) encrusting rugose corals from Estonia (Saaremaa Island) and a brachiopod shell from Sweden (Gotland). In Estonia, the microconchids are a dominant constituent of the encrusting assemblages, associated with cornulitids, *Anticalyptraea*, auloporids, trepostome bryozoans, hederelloids and enigmatic ascodictyids. It is notable that these Silurian encrusting assemblages are clearly dominated by tentaculitoids (microconchids, cornulitids and *Anticalyptraea*) which very often co-exist on the same coral host. Morphologically similar microconchids and *Anticalyptraea* may have exploited a more similar ecological niche than the straight-shelled cornulitids. However, the clear predominance of microconchids over *Anticalyptraea* in the communities may indicate that this genus was a less effective competitor for food than microconchid tubeworms.

Key words: Microconchida, encrustation, epibionts, Estonia, Gotland.

INTRODUCTION

Microconchid tubeworms were very common sedentary tentaculitoids associated with Palaeozoic firm and hard substrate habitats. Appearing during the Late Ordovician, these tiny, spirorbiform encrusters inhabited marine palaeoenvironments until the Middle Jurassic (Late Bathonian) when the group became extinct (Zatoń & Vinn 2011). However, between the Early Devonian and at least the Late Triassic, some species were also able to colonize a variety of non-marine habitats (Taylor & Vinn 2006; Zatoń et al. 2012a). The opportunistic nature of microconchids is evident in their domination during the post-extinction intervals when they were either the most abundant (Zatoń & Krawczyński 2011a; Zatoń et al. 2013, 2014a) or even the sole encrusters of shelly and microbial substrates (Fraiser 2011; He et al. 2012; Yang et al. 2015).

Although microconchids were locally very abundant, the knowledge about their taxonomy and diversity is very patchy both in time and space. In the marine Palaeozoic, the most recognized, albeit still poorly known, are Devonian forms (Zatoń & Krawczyński 2011a, 2011b; Zatoń et al. 2012b). The least recognized are those coming from the Late Ordovician, Silurian and Permian, while those from the marine Carboniferous are completely unknown with respect to their taxonomic identity. In order to draw any conclusions about the diversity dynamics of the group through their evolutionary history, an urgent requirement is to recognize the taxonomic status of as many species as possible from different palaeogeographical regions. This is hampered by the few specialists on the group, the very conservative morphology of microconchids and the poor preservation of many specimens.

In the present paper we describe a new microconchid species from the Silurian of Baltica (Gotland and Estonia). As Silurian microconchids are very poorly recognized, with only two species having been formally named (Vinn 2006), any additional taxonomic data are important to enrich our knowledge about the diversity of this group of encrusters in the Silurian period.

MATERIAL AND METHODS

Material and its provenance

Tens of specimens come from the temporary excavations in the town of Kuressaare and Muratsi locality in Saaremaa Island, Estonia (Fig. 1A). The specimens were found encrusting rugose corals derived from bluish-grey, argillaceous nodular limestones and marls of the Kuressaare Formation (Ludfordian Stage, Ludlow, Fig. 2). The deposits originated in a normal marine, shallow shelf palaeoenvironment corresponding to an open shelf facies zone (Kaljo 1970). One specimen was

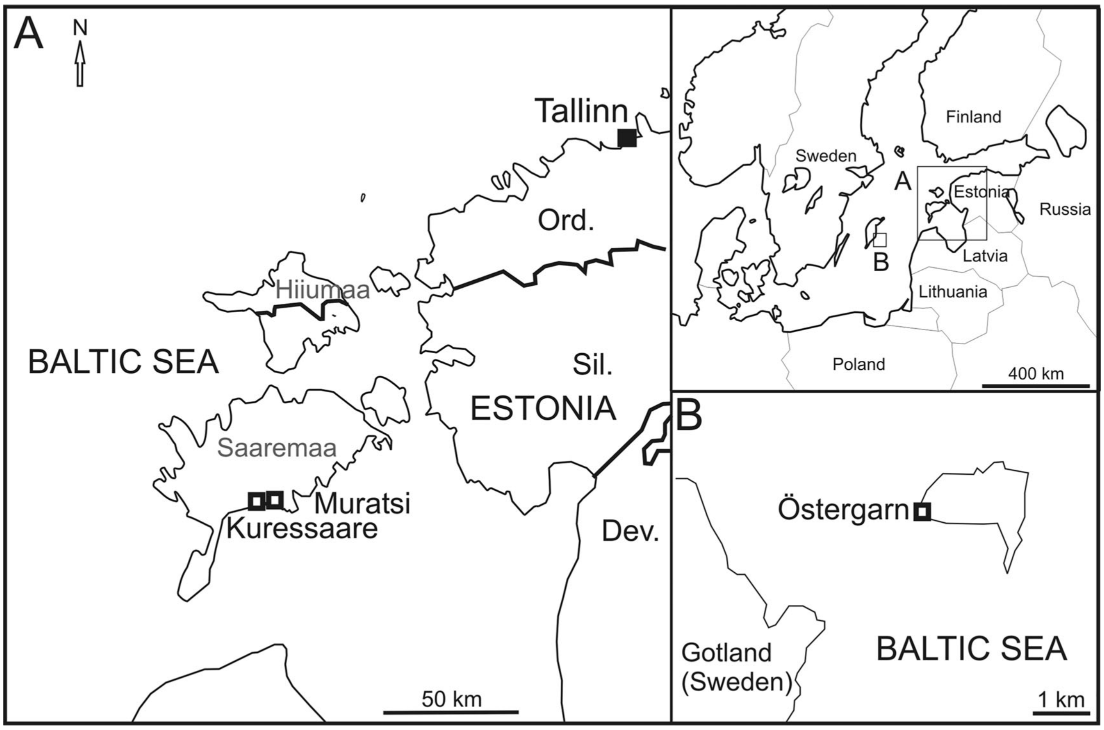

Fig. 1. Sketch map of the Baltic region showing the sampled localities of Saaremaa Island, Estonia (**A**) and Östergarn, Gotland, Sweden (**B**). Ord., Ordovician; Sil., Silurian; Dev., Devonian.

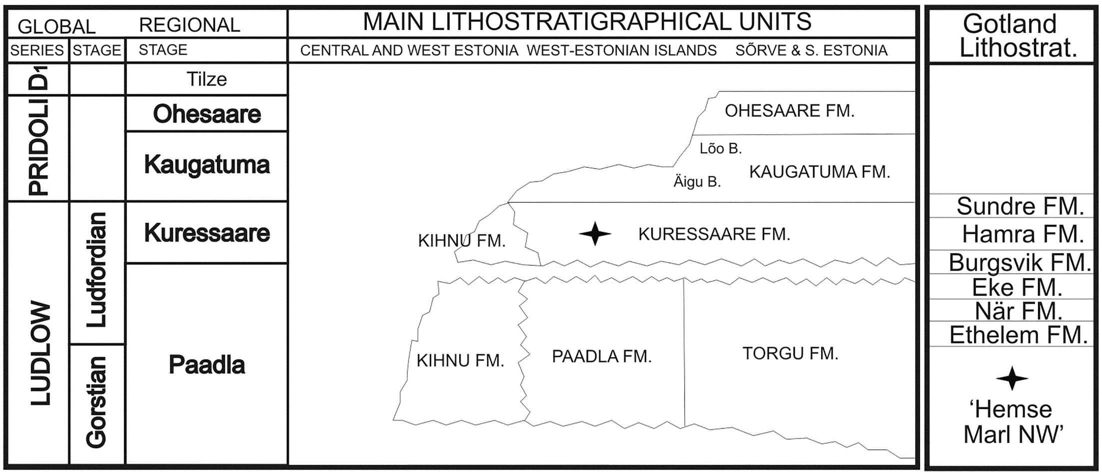

Fig. 2. Lithostratigraphical scheme showing the position of the Kuressaare Formation in Saaremaa Island, Estonia and Hemse Beds in Gotland, Sweden (based on Hints et al. 2008). B., Beds; Fm., Formation.

found encrusting a brachiopod shell which comes from Östergarn in Gotland, Sweden (Fig. 1B). The specimen was derived from a pocket of greenish-grey marl in a dense crinoidal limestone belonging to the Hemse Beds (Gorstian Stage, Fig. 2), which originated in a normal marine, shallow shelf palaeoenvironment (Larsson 1979).

Methods

After cleaning, the fossils were inspected under a binocular microscope and the best-preserved specimens were further analysed using a Philips XL30 environmental scanning electron microscope (ESEM) at the Faculty of Earth Sciences in Sosnowiec, Poland. The specimens were studied in an uncoated state using back-scattered electron (BSE) imaging. Both external features and internal microstructural details on sectioned specimens have been documented.

For palaeoecological data, 21 rugose corals were inspected under the binocular microscope and all epibionts encountered were determined and counted. This procedure provides a general insight into the diversity, abundance and dominance of encrusters, allowing for comparisons with other examples reported in the literature.

The specimens are housed at the Institute of Geology at Tallinn University of Technology in Tallinn, Estonia (abbreviated GIT 687).

SYSTEMATIC PALAEONTOLOGY

Class TENTACULITA Bouček, 1964
Order MICROCONCHIDA Weedon, 1991
Genus *Palaeoconchus* Vinn, 2006

Type species. *Palaeoconchus minor* Vinn, 2006

Palaeoconchus wilsoni sp. nov.

Figures 3A–F, 4A, B

Material. Tens of specimens encrusting rugose corallites and one specimen encrusting a brachiopod shell, including the holotype (GIT 687-117-1) and five paratypes (GIT 687-3-1, GIT 687-3-2, GIT 687-110-1, GIT 687-109-1, GIT 687-117-2).

Locality. Kuressaare, Saaremaa Island, Estonia.

Sratigraphy. Kuressaare Formation (Ludfordian Stage, Ludlow, Silurian).

Etymology. In honour of Mark A. Wilson (The College of Wooster, Ohio), our great friend and scientist working on hard substrate biotas, including microconchids.

Differential diagnosis. From the Silurian *Palaeoconchus minor* Vinn and *Palaeoconchus tenuis* Sowerby, the new species differs in the presence of distinct perpendicular ridges and nodes. From *Annuliconchus siluricus* Eichwald, it differs in the presence of distinct nodes and a complete lack of annuli within the lumen.

Description. Tubes planispirally (dextrally) coiled, up to 2.7 mm in diameter. Umbilicus open, varying in width among specimens, with rounded margin and steep slope. Aperture varies in outline from elliptical to horseshoe-like. Tube exterior ornamented by thick transverse ridges (ribs), running from the base of the umbilical slope to the tube base. On the umbilical margin the ridges are distinctly thickened, forming elevated nodes. On the nodes, the ridge may split into a few finer ridges. The transverse ridges are crossed by fine longitudinal striae running in the direction of tube growth. Albeit irregularly, the striae are developed over the entire surface of the tube. Tube origin barely visible, but may be ornamented with thin, transverse ridges. Although tube microstructure is not well preserved, its microlamellar fabric is still discernible. However, any distinct (pseudo)punctae disturbing the microlaminae are not evident. Probably the original microstructure was punctate, but was later obliterated by diagenesis.

Comparison. Although externally the specimens investigated may be somewhat similar to those of *Annuliconchus siluricus* Eichwald, the tube lumen is smooth, lacking the annulations characteristic of the genus *Annuliconchus* (see Vinn 2006). The new species also has distinct nodes which are absent in *Annuliconchus siluricus*. The absence of any distinct punctae, which are normally clearly visible on the exfoliated, external tube surface, is a difference from species referred to the genus *Microconchus* (e.g., Zatoń et al. 2013, 2014b). Instead, the lamellar microstructure of the tube, which originally was probably pseudopunctate, makes the species very close to the genus *Palaeoconchus*, which dates back to the Late Ordovician (Vinn 2006).

The species *Palaeoconchus minor* Vinn from the Upper Ordovician (Ashgill) of Estonia differs in its smaller size (up to 1.2 mm, see Vinn 2006, table 1) and much smoother external surface that bears only weakly developed growth lines; it may also possess septa (Vinn 2006). From the species *Palaeoconchus tenuis* Sowerby from the Silurian (Wenlock) of England (see Vinn 2006), the new species differs in having stronger ornamentation of the tube exterior in the form of distinct, perpendicular ridges and nodes. With respect to external ornamentation, *Palaeoconchus wilsoni* sp. nov. differs from younger, Devonian marine species. For example, *Palaeoconchus variabilis* from the Upper Devonian of Russia (see Zatoń & Krawczyński 2011a) possesses finer transverse riblets and lacks thickened nodes. *Palaeoconchus sanctacrucensis* from the Lower–Middle Devonian of Poland (see Zatoń & Krawczyński 2011b) has thickened transverse ribs but lacks distinct nodes. *Palaeoconchus angulatus* (Hall) from the Middle Devonian of the USA (see Zatoń et al. 2012b) has finer ornamentation and irregularly distributed smaller tubercles.

Occurrence. Silurian (Ludlow) of Gotland and Estonia.

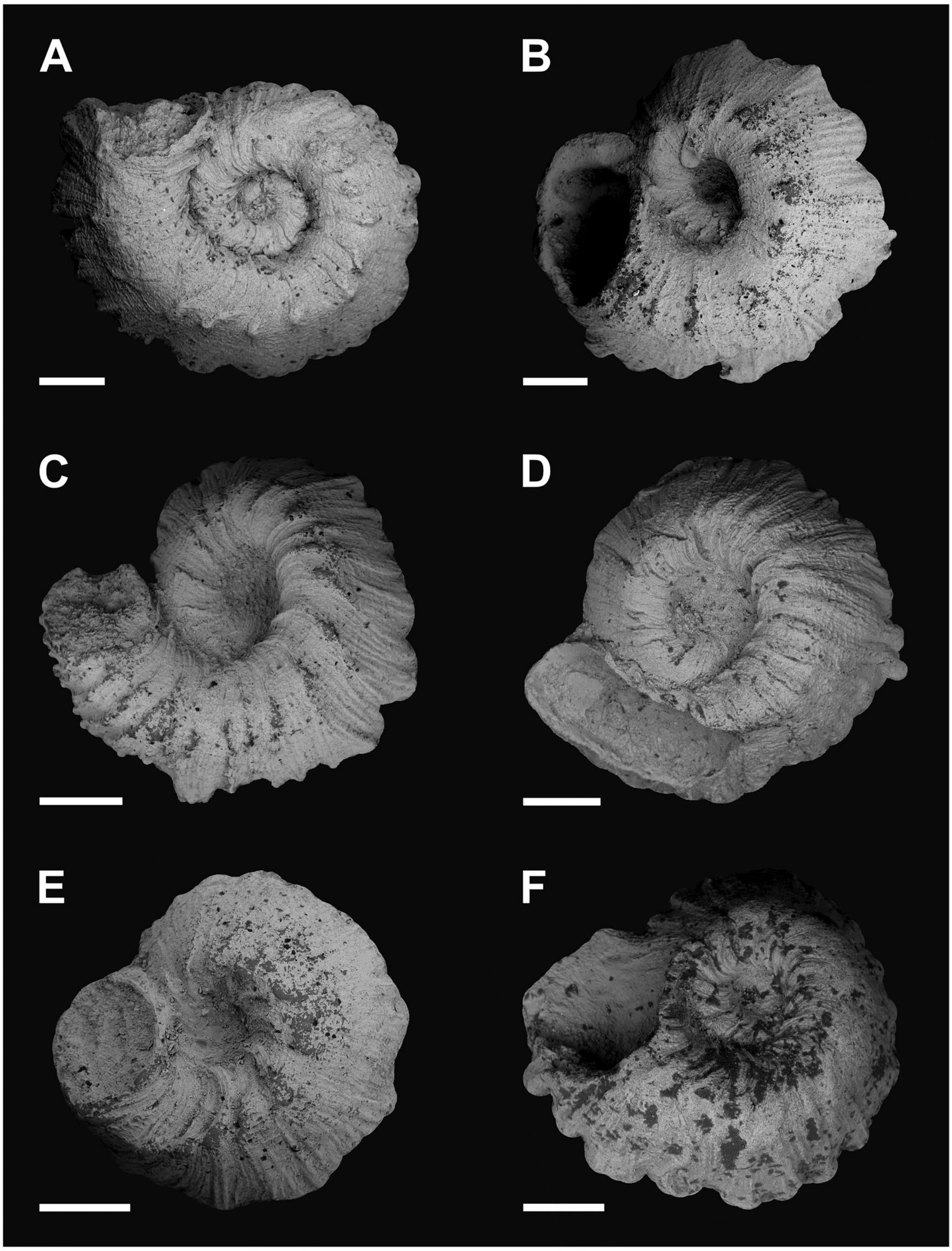

Fig. 3. *Palaeoconchus wilsoni* sp. nov. from Saaremaa Island, Estonia (**A**–**E**) and Gotland, Sweden (**F**). A, holotype, GIT 687-117-1, Kuressaare. B, paratype, GIT 687-3-1, Kuressaare. C, paratype, GIT 687-3-2, Kuressaare. D, paratype, GIT 687-110-1, Kuressaare. E, paratype, GIT 687-109-1, Kuressaare. F, GIT 305-1-1. Scale bars 500 µm.

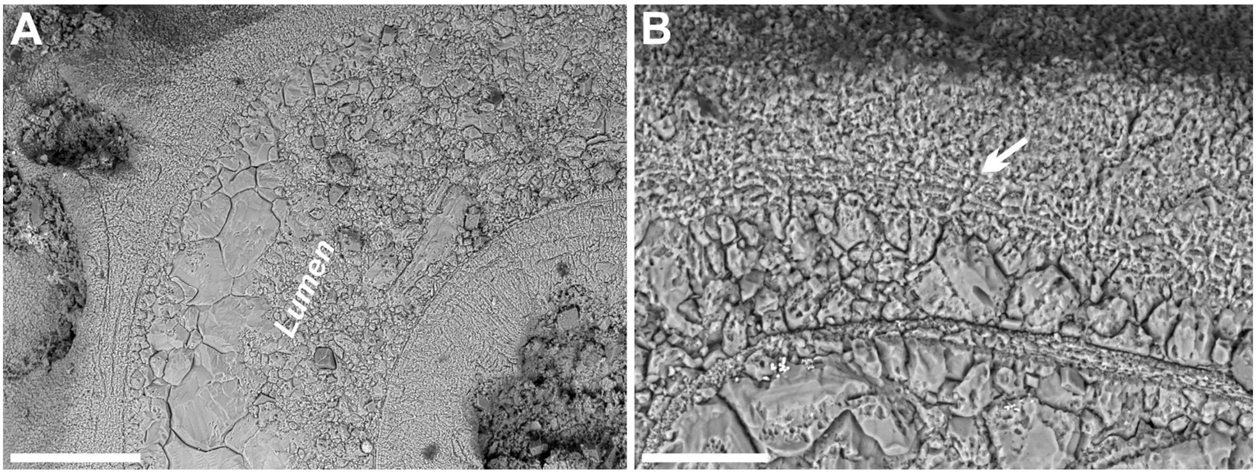

Fig. 4. Sectioned and polished tube of *Palaeoconchus wilsoni* sp. nov. from Kuressaare, Estonia, GIT 687-1-1. **A**, smooth lumen, devoid of any annulations; scale bar 200 µm. **B**, diagenetically altered tube, showing poorly preserved lamellar microstructure (arrowed); scale bar 50 µm.

DISCUSSION

As the Silurian microconchids are very poorly recognized in comparison to their Devonian representatives, the identification of a new species – *Palaeoconchus wilsoni* – clearly suggests that much work is left to be done in order to recognize the full diversity of these encrusters during their early evolutionary history. The abundant specimens of *P. wilsoni* found encrusting rugose corals indicates that encrusting microconchids were very common in shallow, shelfal palaeoenvironments during Silurian times, increasing the chances for finding even more species in the future.

As only one specimen of *P. wilsoni* was found encrusting a brachiopod shell from Gotland, we focus here on the more abundant specimens from Estonia. As evidenced from the rugose corals (mostly *Entelophyllum* and *Trypalasma*) from the Ludlow Kuressaare Formation of Saaremaa Island, microconchids were prolific components of encrusting communities. Rugosans were abundant in the soft-bottom community of the Kuressaare Formation (Kaljo 1970) and were among the most available hard substrates in the community. In addition to numerous rugosans, the tabulate *Favosites forbesi* was common. Larger stromatoporoids were represented only by *Parallelostroma typicum* (Kaljo 1970). Some hard substrates were also provided by numerous rhynchonelliform brachiopods and crinoids (Kaljo 1970). Molluscs are represented by two species of bivalves (*Pteronitella retroflexa* and *Ilionia prisca*) and one nautiloid species (*Michelinoceras bullatum*) (Kaljo 1970). The rugose corals served as a hard substrate for a number of different epibionts (Fig. 5), which apart from rugose spatfall and microconchids, consist of the tabulate *Aulopora*, trepostome bryozoans and such problematic encrusting taxa as the cornulitid *Conchicolites* (e.g., Vinn & Mutvei 2005), tentaculitoid *Antycalyptraea* (e.g., Vinn & Isakar 2007), hederelloids (e.g., Wilson & Taylor 2006) and ascodictyids (e.g., Olempska & Rakowicz 2014; Wilson & Taylor 2014). No borings were recognized. Excluding confamilial rugose spatfalls, the rugose corals are encrusted by a total of seven encrusting taxa. However, on any given rugose corallite, microconchids are either the only encrusters or the dominant ones, distinctly outnumbering the rest of the epibionts (Fig. 6). The large number of microconchids (up to 42 individuals), at different ontogenetic stages, suggests continuous colonization of the same coral substrate by successive spatfalls. The overwhelming presence of epibionts on different sides of the rugose epithecae and their absence in the calyx suggests that colonization probably occurred during the life of the coral hosts. In some instances the calyx is occupied by a few individuals of young rugose corals, suggesting fouling after death of the host.

Very little qualitative and quantitative data are available on epibionts colonizing rugose corals and such data concern epibionts of post-Silurian rugose corals. When compared with other encrusted rugose corals, it seems that epibiont diversity present on the Silurian specimens from Estonia is not small, especially given that these corals are small-sized (up to 4.5 cm in height), suggesting that they did not offer much space for colonization. When we look at the encruster diversity

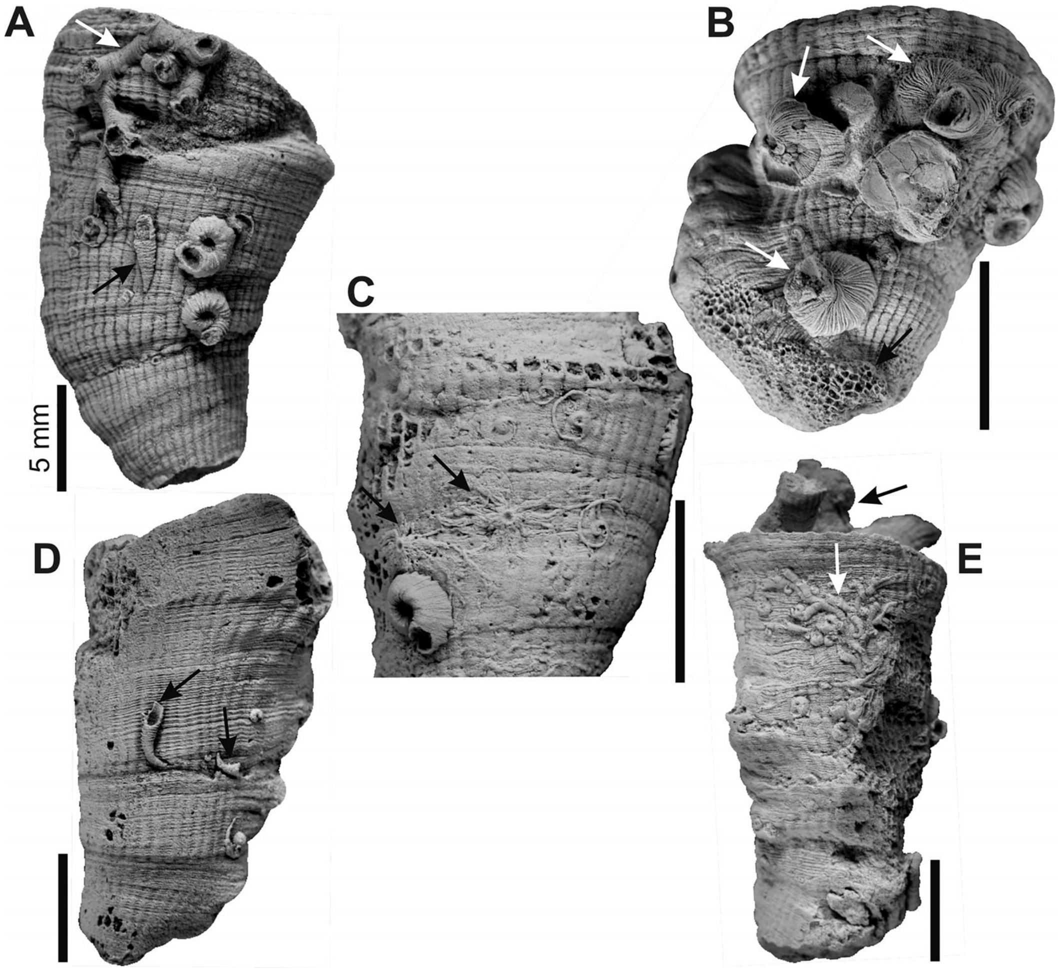

Fig. 5. Encrusted rugose corals from Saaremaa Island, Estonia. **A**, auloporids (white arrow), cornulitid *Conchicolites* (black arrow) and two associated microconchids, GIT 687-3, Kuressaare. **B**, *Anticalyptraea* (white arrows) and trepostome bryozoan colony (black arrow), GIT 687-8, Muratsi. **C**, ascodictyids (black arrows) and associated microconchids, GIT 687-7, Kuressaare. **D**, cornulitid *Conchicolites* (black arrows), GIT 687-11, Kuressaare. **E**, rugose spatfalls within the calyx (black arrow) and a hederelloid colony (white arrow), GIT 687-13, Kuressaare.

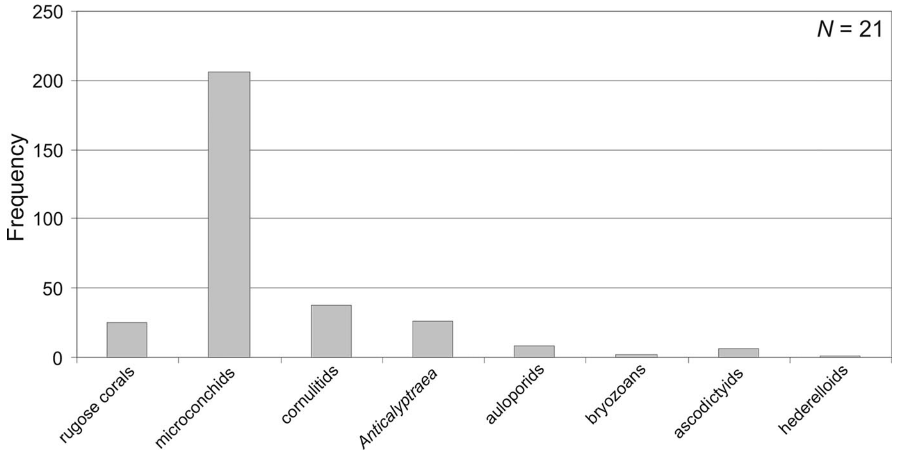

Fig. 6. Frequency of particular encrusters on the rugose corals from Kuressaare, Estonia. *N* = number of rugose corals.

(36 taxa in total) present on the large rugose corals from the Middle Devonian Hamilton Group of the USA (see Baird & Brett 1983), it seems that coral size mattered and controlled the diversity of the encrusters. However, as was recently pointed out by Mistiaen et al. (2012), such features as size and even ornamentation are not the sole factors determining the diversity of the epibionts. Indeed, there are examples where still larger corals than those studied here possessed fewer epibiontic taxa. Sando (1984) found only four encruster taxa (the foraminifer *Tolypammina*?, the bryozoan *Eridopora*, the brachiopod *Petrocrania* and microconchids) colonizing larger (up to 7 cm in height) individuals of the coral *Barytichisma* sp. from the Upper Mississippian of Utah. Recently, Zatoń et al. (2015) found that the Upper Devonian rugose corals from Russia, which are similar in size and ornamentation to the Silurian corals studied here, were encrusted by seven taxa. However, excluding encrusting confamilial rugose corals and auloporid tabulates which formed the main biomass of the coral biostrome, the other epibionts consisted of dominant foraminifera and single specimens of productid brachiopods, stromatoporoids, microconchids and cornulitids. Thus, with respect to both diversity and abundance, the Silurian corals are much richer.

The abundance of microconchids also differs between particular coral-encrusted assemblages. In the case of the Middle Devonian corals from the USA, Baird & Brett (1983, table 5A) recorded that microconchids were the most abundant of all encrusters present. Sando (1984) noted that microconchids were the second dominant group following the foraminifer *Tolypammina* on his Carboniferous corals. Recently, Balon (2015) found that microconchids were the second most abundant group encrusting Middle Devonian rugose corals from the Holy Cross Mountains in Poland. On Upper Devonian rugose corals from Russia, on the other hand, microconchids were a minor component of the encrusting assemblages (Zatoń et al. 2015).

If not depending on the size and external sculpture of the host, such differences in the composition of the encrusting assemblages may have resulted from biological factors. It is known (e.g., Pineda et al. 2002; Paul D. Taylor, pers. comm. 2016) that modern sessile communities are controlled by the availability of larvae (‘larval supply’) that can recruit onto new hard substrates, and that the proximity of source populations is therefore very important. This, however, is difficult to detect in the fossil record.

Other factors responsible for the composition of the encrusting assemblages are those concerning external environment. Zatoń et al. (2015) pointed out that the scarce epibionts on Late Devonian rugose corals, and especially the distinct rarity of microconchids, probably resulted from low-productivity, oligotrophic conditions. Indeed, microconchids are known to have occurred abundantly in shallow-marine palaeoenvironments where nutrient delivery and resultant productivity were probably high (Zatoń et al. 2012a). It is also known from Recent marine environments that sclerobionts are least abundant when sedimentation is high and productivity is low (Lescinsky et al. 2002). Thus, it is possible that the diverse epibiotic community containing numerous microconchids colonizing the Silurian rugose corals resulted from a very suitable palaeoenvironmental setting characterized by a low sedimentation rate and sufficient productivity to support a diverse, suspension-feeding community. The late Ludfordian (Kuressaare Formation) is supposed to be characterized by arid climate, high δ^{13}C and δ^{18}O values and intense evaporation in low palaeolatitudes where Saaremaa was then located (Bickert et al. 1997). Such climatic conditions favoured the formation of reefs and carbonate platforms on shallow shelves (Bickert et al. 1997). Sediments of the Kuressaare Formation are not typical of shallow shelf developing in arid climate. They are characterized by argillaceous limestones and marls which indicate local terrigenous sediment influx from a nearby continent (Jürgenson 1988). Moderate terrigenous sediment influx together with nutrients may have also been responsible for relatively high marine productivity in the late Ludfordian of Saaremaa. Similar palaeoenvironmental conditions may have supported other Silurian encruster communities where microconchids were also abundant, such as those developed on stromatoporoids from the Pridoli of Saaremaa Island (Vinn & Wilson 2012) or the calices of camerate crinoids from the Wenlockian of the USA (Liddell & Brett 1982).

An interesting aspect of the encrusting community of the Kuressaare Formation is the abundance of other tentaculitoid tubeworms in the association, such as *Conchicolites* and *Anticalyptraea* in addition to dominant microconchids. This fact indicates that microconchids did not outcompete their suspension-feeding close relatives. This can be explained by differences in the ecology between various encrusting tentaculitoid tubeworms, so that they did not occupy exactly the same ecological niche in the ecosystem. There is a possibility that ecological niches of similar spirally coiled *Anticalyptraea* and microconchids were more similar than were niches of microconchids and non-spiral *Conchicolites*. If this is true, the lower abundance of *Anticalyptraea* among the tentaculitoids in the community may have resulted from the competition pressure with more effective microconchids.

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Uus mikrokonhiidiliik Baltika Silurist

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Siluri mikrokonhiitide mitmekesisust on vähe uuritud. On kirjeldatud uut mikrokonhiidiliiki *Palaeoconchus wilsoni*, mis leiti Saaremaalt rugooside ja Gotlandilt käsijalgse küljest. Eestis moodustavad mikrokonhiidid peamise osa inkrusteerivast faunast ja esinevad koos kornuliitide, *Anticalyptraea*, auloporiitide, sammalloomade, hederelloidide ning problemaatiliste askodiktüiididega. Tähelepanuväärne on tentakulitoidide (mikrokonhiidid, kornuliidid ja *Anticalyptraea*) domineerimine kirjeldatud Siluri-vanuste inkrusteerivate loomade koosluses. Tentakulitoidid esinesid tihti koos samal peremeeskorallil. Morfoloogiliselt sarnaste mikrokonhiitide ja *Anticalyptraea* ökoloogilised nišid olid sarnased ning erinesid sirgekojaliste kornuliitide nišist. Mikrokonhiitide suurem arvukus *Anticalyptraea*'dega võrreldes viitab nende suuremale efektiivsusele toitumiskonkurentsis.