Asterozoan Pedicellariae and Ossicles Revealed from the Middle Ordovician of Baltica

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Source: Acta Palaeontologica Polonica, 59(2) : 353-358

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2012.0034

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Tinn, O. and Ainsaar, L. 2014. Asterozoan pedicellariae and ossicles revealed from the Middle Ordovician of Baltica. *Acta Palaeontologica Polonica* 59 (2): 353–358.

Isolated asterozoan ossicles and pedicellariae occur in micropalaeontological samples from the Darriwilian (Middle Ordovician) of the Mishina Gora section, north-western Russia. The well-preserved *Bursulella unicornis* type fossils represent the oldest hitherto record of asterozoan pedicellariae. The accompanying ossicles are not diagnostic but allow their tentative placement within the asteroid stem group. The abundance of disarticulated ossicles in the samples proves that asterozoans were not as rare as they have been considered and were important members of Ordovician ecosystems in the Baltic Palaeobasin.

Key words: Echinodermata, Asteroidea, *Bursulella*, pedicellariae, Ordovician, Baltica.

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Received 12 March 2012, accepted 8 March 2013, available online 13 March 2013.

Introduction

Asterozoans are an abundant and diverse group of Echinodermata, which, however, have left behind a rather poor fossil record. The main reason for that is their peculiar skeleton, which consists of thousands of mesodermally produced discrete ossicles (Blake 2000). These ossicles, although tightly bound in the dermal layer during animal's lifetime, separate and fall apart soon after disintegration of soft tissues.

In the Baltoscandian area asterozoans fossils are rare throughout the Lower Palaeozoic, but their record in the Ordovician strata is especially meager. The oldest asterozoan fossils from the Baltica palaeocontinent have been reported from the Volkhov Stage (Dapingian) at the Volkhov River section near St. Petersburg, Russia (Blake and Rozhnov 2007). This find is represented by two arm fragments of *Cnemidactis* sp. However, the authors note, that a number of disarticulated ossicles have also been found in the studied strata, suggesting that there is potential for further finds.

The second oldest find is *Estoniaster maennili* Blake and Rozhnov 2007 from the Keila Stage at Vasalemma (Caradoc), North-Estonia, represented by one relatively complete specimen and two incomplete arm fragments (Blake and Rozhnov 2007).

Two asterozoan species have been described from the Ordovician of Norway (Hansen et al. 2005). These are asteroid *Cnemidactis osloensis* (Hansen et al. 2005) from the Elnes Formation (Llanvirn) in the Oslo-Asker area and cosmopolitan ophiuroid *Stenaster obtusus* (Forbes 1848) from the Furuberg Formation (Caradoc) of the Hamar district. The latter is also by far the richest asteroid find, as it consists of decalcified molds of more than 100 specimens lying on a single bedding plane.

Thus the asterozoan fossils record from the Ordovician of Baltica, consisting of four species only, is particularly poor, and all available data contribute to our understanding of this rarely fossilized group.

However, we should also mention that such poor asterozoan fossil record is not the case elsewhere. For example, the British fauna of Ordovician asterozoans is diverse and well documented (Shackleton 2005).

Institutional abbreviations.—TUG, Natural History Museum of the University of Tartu, Estonia.

Pedicellarian fossil record

The first fossil pedicellariae from starfish were reported by a Bristish palaeontologist Thomas Rupert Jones from the fossil-rich rocks of Silurian age in Gotland in 1887 (Jones 1887), although their biological affinities were at first mistaken. Jones' collection of some twenty specimens included pedicellariae with one and two "spikes" and various out-

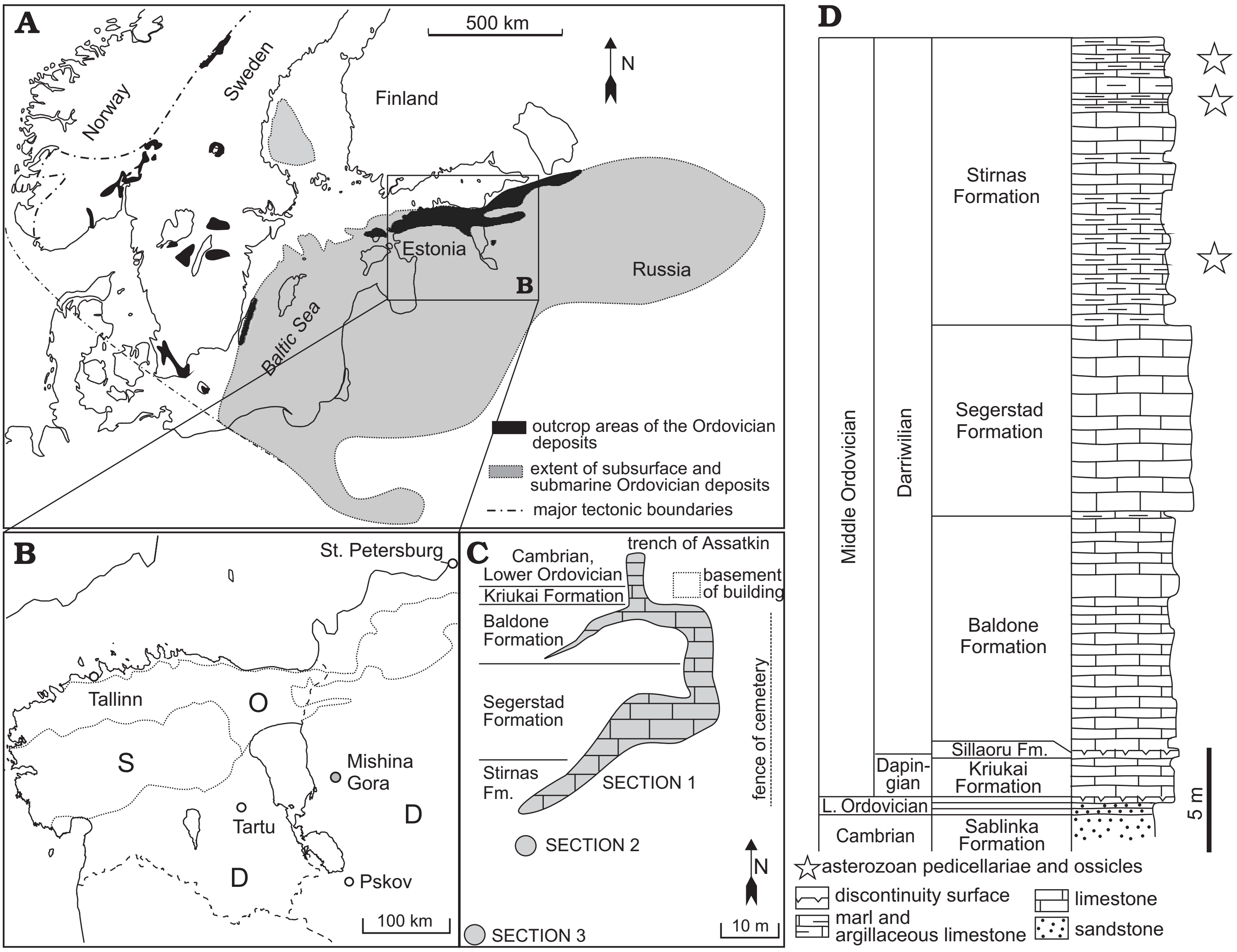

Fig. 1. Location map (**A**), excerpt of the simplified geological map of the area (**B**), plan of the quarry (**C**), and stratigraphy of the Mishina Gora section 1 (**D**). Abbreviations: O, Ordovician; S, Silurian; D, Devonian outcrop area.

lines. However, although he had some doubts giving a determination: "This is a small, bivalved, probably Ostracodal form, with more or less triangular valves, which have one or two horn-like projections on the ventral edge of each valve" (Jones 1887: 409), based on general outline and the number of "spikes" he described three species under a generic name *Bursulella*—*B. triangularis*, *B. semiluna*, and *B. unicornis*—as ostracodes.

The taxonomic placement of *Bursulella* within Ostracoda, has, however been problematic. Bassler and Kellett (1934) classified it within Primitiidae, McKim Schwartz (1936) referred to the genus as *Bursulellela* and classified it in the Leperditellidae, Schmidt (1941) regarded it with reservations in Aparchitiidae, Howe (1955) referred to it under name *Bursullela* in Ostracoda. Kesling and Chilman, with reservations, in Palaeocopida ("... It is our opinion that *Bursulella* is definitely a crustacean and most likely an ostracod") (1978: 116).

Until recently only a few researchers questioned the ostracodal nature of *Bursulella*. It was placed into *Incertae sedis* by Zanina and Polenova (1960) and classified as nomina dubia by Benson et al. (1961: Q412) who stated that it is (...probably not an ostracode...).

Although Jones (1887) published his finds more than 100 years ago, records of similar fossils are still rare. Only a few finds have been reported from the Silurian to the Carboniferous rocks of Europe and North America (Boczarowski 2001). Boczarowski (2001) described similar structures from the limestone and shale beds of the Eifelian–Frasnian and Early Carboniferous of Poland as ophicephalous pedicellariae of *Bursulella*-type and globiferous pedicellariae of ladle type (morphotype III) and identified them as echinoid pedicellariae, based on their stereom microstructure and co-occurrence with echinoid remains.

The true taxonomic affinities of *Bursulella* were conclusively resolved when (almost) complete asterozoan fossils exhibiting *Bursulella*-type paired spines pedicellariae were described by Sutton et al. (2005) from the Silurian (Ludlow) Herefordshire Lagerstätte in England and Hotchkiss and Glass (2010) from the Devonian Hunsrück Slate in Germany. In both cases the starfish bearing these pedicellariae belonged to the family Bdellacomidae.

The Herefordshire specimens with preserved soft tissues indicate clearly that they were articulated structures, presumably capable of closure.

The record of oldest *Bursulella*-type pedicellariae so far recorded come from the Upper Ordovician erratics of Germany, where Schallreuter and Hinz-Schallreuter (2008) described similar fossils from "Backsteinkalk" of Haljala Stage (Caradoc) and Öjlemyrflint of Pirgu or Porkuni age (Ashgill).

Geological setting and stratigraphy

The Mishina Gora structure is situated in the Pskov District, north-western Russia, some 15 km east of Lake Peipsi (Fig. 1A, B). The ring structure in the Devonian outcropping area is deeply eroded and exposes strongly disturbed Lower Palaeozoic sedimentary cover over an area of about 3 km in diameter. The origin of the structure is still under discussion. It has been considered as a Late Palaeozoic impact structure (Shadenkov 1980; Masaitis 1999) or volcanic explosion pipe (Shmaenok and Tikhomirov 1974; Buslovich et al. 2004).

Blocks of disturbed and uplifted bedrock, first studied by Assatkin (1938), have presented a unique opportunity to investigate Ordovician rocks in the area otherwise covered with Devonian sediments. The best outcrop section is situated in an old limestone quarry in the former Mishina Gora village. More than 37 m of 70° southward tilted sedimentary succession have been excavated in the old limestone quarry during the last decades.

Stratigraphically, the section ranges from Middle Cambrian up to the Middle Ordovician (Darriwilian) (Dronov 2004). The age of the section and stage boundaries are based on trilobites and detailed sedimentological studies (Dronov 2004), conodonts, determined by Tolmacheva (2004), and were later confirmed with ostracods (Tinn et al. 2011)

The exposed section (Fig. 1C, D) starts with the sandstone of the Middle Cambrian Sablinka Formation, followed by Lower Ordovician quartzose and glauconitic sandstone (Tosna and Leetse formations) and reddish dolomite (Zebre Formation). Middle Ordovician strata are represented in the main quarry section (Fig. 1D) by reddish dolomitic limestone of the Kriukai Formation, ferriferous ooid-rich limestone of the Sillaoru Formation, grey argillaceous limestone of the Baldone Formation, greenish to reddish limestone of the Segerstad Formation and grey argillaceous limestone and marl of the Stirnas Formation (Dronov 2004). Nearby sections 2 and 3 (Fig. 1C) are dislocated blocks, where the ostracod fauna proves that they "repeat" the Stirnas Formation of the main section (Tinn et al. 2011).

The Ordovician succession of the Mishina Gora section shows transitional lithological characteristics between the Estonian middle ramp facies and Central Baltoscandian outer ramp facies of the cool-water Baltoscandian carbonate basin (Nestor and Einasto 1997).

The asteroid bearing samples come from the upper Darriwilian Stirnas Formation (Fig. 1D) and are clearly older than the pedicellariae from the erratics from Germany, determined as of Caradoc age.

Material and methods

The rock samples were taken primarily for ostracod studies and treated with standard (Tinn et al. 2006) disintegration method with sodium hyposulphite ($Na_2S_2O_3*5H_2O$). About 1 kg of limestone was crushed into pieces of about 3–5 cm diameter. 200 to 300 grams of sodium hyposulphite was added and the mixture was heated on an electric stove and subsequently cooled at the room temperature. The procedure was repeated 30 to 50 times. After most of the rock material was disintegrated and turned into more or less homogeneous mixture, the material was washed and wet sieved into three fractions (>2 mm, 0.5–0.25 mm, <2.5 mm).

Calcitic and phosphatic fossils were picked from all fractions, but the asterozoan ossicles were recovered from only the median fraction, which contained also the largest number and most diverse fauna. Palaeocope ostracodes comprise the most abundant faunal group in the samples; minor groups include linguliformean and (juvenile) rhynchonelliformean brachiopods and gastropods. The samples yielded also a number of asterospongian spicules, machaeridian sclerites, and fragments of graptoloid graptolites, tabulate corals, trilobites, agnostid crustaceans and bryozoans. Besides asterozoan ossicles the samples revealed also a number of fragments of other echinoderm groups, like crinoids and cystoids, but also a number of fragments of undetermined taxa. The largest fraction revealed mostly juvenile brachiopods and the finest fraction contained small-sized or juvenile ostracode species.

Altogether 15 disarticulated asterozoan pedicellariae were found from four samples of the Stirnas Formation of the main section (Fig. 1D). Besides pedicellaria, the samples yielded also several dozens asterozoan ossicles (Fig. 2E–H). Asterozoan ossicles were also found in section 3 (Fig. 1C). The studied and figured material is curated under collection number TUG 1611.

Systematic paleontology

Phylum Echinodermata Klein 1734

Class Asteroidea de Blainville, 1830

Order incertae sedis

Family ?Bdellacomidae Spencer and Wright, 1966

Pedicellariae

1887 *Bursulella unicornis*; Jones 1887: 1–8.
1888 *Bursulella unicornis* Jones 1887; Jones 1888: 410, pl. 22: 7.

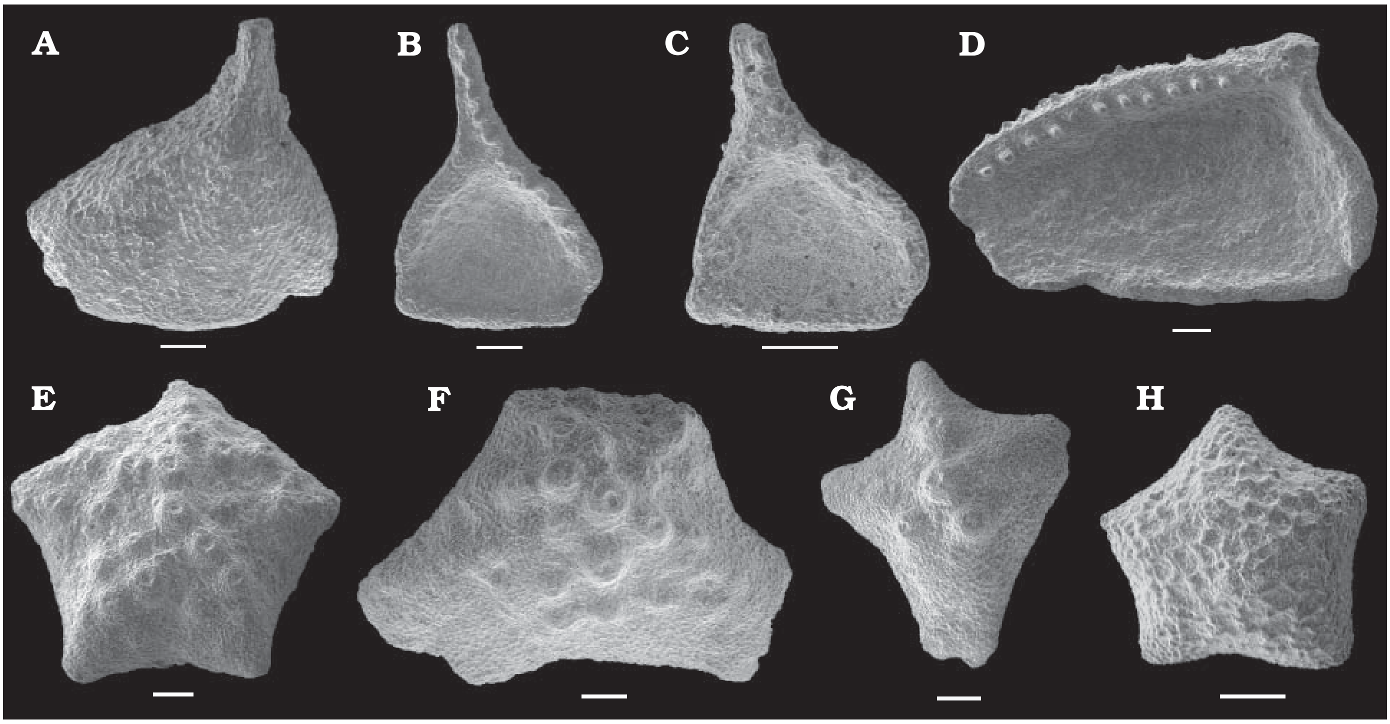

Fig. 2. Asterozoan pedicellariae (**A**–**D**) and ossicles from (**E**–**H**) from the Mishina Gora section, Middle Ordovician. **A**. TUG 1611-1, external view. **B**. TUG 1611-2, internal view. **C**. TUG 1611-3, internal view. **D**. TUG 1611-4, external view. **E**. TUG 1611-5 asterozoan disk (?) ossicle. **F**. TUG 1611-6 asterozoan interradial (?) ossicle. **G**. TUG 1611-7 asterozoan interradial (?) ossicle. **H**. TUG 1611-8 asterozoan disk (?) ossicle. Scale bars 200 μm.

2008 *Bursulella* aff. *unicornis* Jones 1887; Schallreuter and Hinz-Schallreuter 2008: 70–77, pl. 1: 3–4.

Description.—The width of the isolated valves of *Bursulella*-type pedicellariae found in the Mishina Gora section falls between 0.6 and 2 mm (Fig. 2A–D). Although with differences in shape and outline, all specimens are of *B. unicornis* type according to the classification by Jones (1887), and consist of triangular base and a single spine. On the inside the spine shows a fine shallow groove running along its median part. The maximum height of the spines of the studied specimens is 0.6 mm, but on some specimens clear breakage scar can be seen (Fig. 2A, D), indicating that the maximum length might be longer.

Internally, one side of the valve is lined with robust serration that extends from the lowest part of the base up to the end of the spine.

Most pedicellarial valves are asymmetric. Some, mostly smaller specimens show slightly (about 10°) inclined spine (Fig. 2B, C), while the degree of asymmetry of the others depends of the outline shape of the base (Fig. 2A, D). The wide base of the valve is slightly concave.

The specimens described by Schallreuter and Hinz-Schallreuter (2008) from the erratics of Caradoc, Late Ordovician, belong to both, *B. unicornis* and *B. triangularis* types, showing single- and double-spine specimens, accordingly. All specimens revealed from the different samples of the Mishina Gora section are of *Bursulella unicornis* type, featuring a single spine at the tip of the subtriangular basement of the pedicellaria. Among the *B. unicornis*-type pedicellariae described by Schallreuter and Hinz-Schallreuter (2008) were specimens with a different degree of symmetry. The specimen GG 348-4 (Schallreuter and Hinz-Schallreuter 2008: pl. 1: 3) features narrow triangular base and and high, strongly inclined spine. The other specimen GG 348-5 (Schallreuter and Hinz-Schallreuter 2008: pl. 1: 4a) shows slightly wider and more symmetrical triangular base with a shallow groove on its basal edge. Although the spine of the specimen is broken, its lower end reveals a slight inclination only.

However, as the shape of the pedicellariae has been described as variable within and also between the complete specimens (Hotchkiss and Glass 2010), it is difficult to make further decisions about the systematic position of the disarticulated asterozoan specimens from Mishina Gora.

Discussion

Pedicellariae of Lower Palaeozoic asterozoans have been described on body fossils of two species only—*Bdellacoma* sp. from the Silurian Herefordshire Lagerstätte in England (Sutton et al. 2005) and *Urasterella verruculosa* from the Devonian Hunsrück Slate in Germany (Spencer 1914–1940; Hotchkiss and Glass 2010). Both described species belong to Family Bdellacomidae Spencer and Wright, 1966, Order incertae sedis, which has been described as a stem group asteroid. The group features five-rayed or multiradiate body with small disk and arms long for size of disk. According to the description (Hotchkiss and Glass 2010) the only plates of substantial thickness and solidity of the specimens are the *Bursulella*-type pedicellariae on the arms, the robust plates on the mouth frame in the disk, and the aboral interradial madreporite. The *Bursulella*-type pedicellariae are positioned both aborally and as a fringe to the arm. Both described species (*Bdellacoma* sp. and *U. verruculosa*) feature pedicellariae with two spines, of type that was described as *Bursulella triangularis* by Jones 1887.

At present, before further finds of complete specimens with attached pedicellariae, it is not possible to decide with any degree of confidence, whether the described specimens from Mishina Gora represent the same asterozoan family or not.

Besides pedicellariae the samples yielded also a number of disarticulated asterozoan ossicles with complicated morphology and with spine-bases (Fig. 2E–H), are also indeterminate to lower taxonomic level. Spencer (1914–1940) discussed *Bdellacoma* in the last section of his monograph; he also illustrated one of the pedicellariae along with the other illustrations of *Bdellacoma*. However, the comparison of his illustrations with the pedicellariae and also the ossicles derived from our material (Fig. 2E–H) does not help to identify them either, supporting our suggestion that the asterozoan material from Mishina Gora might represent wholly unknown taxa.

Pisera (1994) has discussed similar problem with comparable disarticulated material from the Ordovician of Poland, and noted, that authors have often neglected the details of particular ossicles on complete specimens, thus complicating work with disarticulated material. Although the accompanying ossicles from Mishina Gora are are not diagnostic on lower taxonomic level, they do allow their tentative placement within the stelleroid stem group.

As Hotchkiss and Glass (2010) discussed, almost certainly these pedicellariae were not confined to *Bdellacoma* alone, presumably they existed also in other taxa of the clade. The fossil record of *Bdellacoma* show this taxon as a long lived and widespread clade being reported from the lower Silurian (Llandovery) to Lower Devonian, the *Bursulella*-type pedicellarian fossil record expands it up the Early Carboniferous and shows it to be widespread—the finds refer to the palaeobasins of Baltica, Laurentia, Avalonia (or Laurussia from the Early Devonian onwards [Cocks and Torsvik 2002]).

The finding of asterozoan pedicellariae in the Ordovician sediments has one more aspect besides the taxonomic importance. Sutton et al. (2005), discussing the anatomy of *Bdellacoma* sp., said that some crown group asteroids use articulating pedicellariae in prey-capture and inferred that a similar function could be inferred in *Bdellacoma*. In some asterozoans the pedicellariae are also a site for digestion. This possibility, however, was ruled out in the case of *Bdellacoma*, as there was no substantial soft-part connection to the arm (Sutton et al. 2005).

Coppard et al. (2012), discussing form and function of pedicellariae in echinoids, regarded them also as a response to the growing army of parasites. The pedicellariae offer some defence against ectoparasites and other small pests that would like to colonise the spine canopy on the echinoderms. Although parasites have not left an extensive body fossil record, the trace fossils left by inferred parasites together with the directly observable pests, is sufficient to be traced back to the Cambrian (Conway Morris 1981). Thus the finds of pedicellariae could also be regarded as an indication of much higher faunal diversity than it is evident from the fossilizable faunal record, and perhaps also the presence of parasitic interactions in the ecosystem (Conway Morris 1981; Coppard et al. 2012).

Concluding remarks

Micropalaeontological samples often contain diverse fauna of microscopic groups like ostracodes, microscopic gastropods and brachiopods. The study of disintegrated parts of some macroscopic faunal groups, like the scales of fossil fishes and conodont elements, has become a common practice in palaeontology.

However, the presences of those faunal groups that fall outside the narrow research target of a particular project are routinely ignored and are rarely reported. The fact is especially true about microscopic fragments of groups like echinoderms, where determinations are prone to parataxonomic errors. The asterozoan ossicles and pedicellariae revealed from the Mid-Ordovician micropalaeontological samples suggest that asterozoans were not as rare as it could be inferred by the reports on their macrofossils.

Acknowledgements

The authors thank Frederick H.C. Hotchkiss (Marine and Paleobiological Research Institute, Vineyard Haven, USA) for spotting our single mentioning of *Bursulella* in a short conference abstract, reminding us of the importance of reporting about rare and occasional finds to the wider audience. We are greatful to Chris Schneider (University of California, Davis, USA), Dan Blake (University of Illinois, Urbana, USA), and Andrew Smith (Natural History Museum, London, UK) for their very helpful and constructive comments that have improved the paper. We are particularly grateful to Andrey Dronov (Institute of Geology, Russian Academy of Sciences, Moscow, Russia) for introducing us the intriguing Mishina Gora section. This paper is a contribution to IGCP project 591 *The Early to Middle Palaeozoic Revolution*. The paper was funded by Estonian Science Foundation project SF0180051s08.

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