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Sexual dimorphism and pore systems in Ordovician ostracodes

ROGER E.L. SCHALLREUTER and INGELORE C.U. HINZ-SCHALLREUTER

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Open antra, a special form of external brood pouches in Ordovician ostracodes suitable for both egg and brood care, are enabled by the associated pore system. Special kinds of radial pores connected with the adventral sculptures are described for the first time. Relationships exist between antral development and lifestyle in that open antra occur in nektobenthic taxa, while closed antra (false brood pouches) are connected with a benthic lifestyle. Taxa, particularly those with open antra, which are morphologically very similar in being non-lobate or non-sulcate, can be distinguished by the construction of the respective antra and the associated pore systems, as exemplified by *Levisulculus*, *Swantina*, and *Ampletochitina*.

Key words: Arthropoda, Crustacea, Ostracoda, *Levisulculus*, *Swantina*, *Ampletochilina*, erratic boulders, dimorphism, adventral radial pores, Ordovician, Baltoscandia.

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Introduction

The widespread sexual dimorphism of Palaeozoic ostracodes is so unique that it has attracted much attention since the second half of the 19th century. Dimorphism is typically expressed by the formation of a brood-pouch in the anterior part of the female valve. This contrasts with the situation in Recent ostracodes where brood chambers—if present at all—are located in the posterior part of the valve. This fact has led to controversy over the orientations of Palaeozoic taxa and many discussions about the function of these structures.

While in the stratigraphically younger taxa (Silurian onwards) the function of the chamber as a brood-pouch has been proved by finds of young instars, the interpretation of dimorphic features in Ordovician ostracodes is much more problematic. It has been assumed with a high degree of confidence that these structures were used only for egg-care. Particularly problematical are taxa with long ventral pouches, which are permanently open to the outside, both in the opened as well as the closed carapace condition. Based on the genera presented herein, an attempt is made to substantiate whether the pouches really functioned as brood chambers.

Although representatives of *Levisulculus* and related genera occur abundantly in glacial erratic boulders (German "Geschiebe") of Northern Germany and Sweden, nevertheless they are poorly known from outcrops in Baltoscandia. A main reason for this lack of record is difficulty of identification, particularly of tecnomorphic valves, and their distinction from similar genera such as *Swantina* and *Ampletochilina*. This is even more complicated when the valves are still embedded in rock matrix and impossible to extract out of the rock due to the procedure used in the investigated erratic boulders. It commonly results in descriptions in open nomenclature. Meidla (1996: 28, pl. 2: 11), for example, described in his monograph only one species of *Levisulculus* (*Levisulculus* sp. nov.) from the Rakvere Stage and Sidaravičienė (1992: 140–141) described in her monograph identified only two specimens as *Levisulculus* (*Levisulculus* sp. A and *Levisulculus*? sp. B) and all the others as species of *Swantina*. The taxonomically important dimorphic features of the females can be studied on excellently preserved material resulted from hydrofluoric acid treatment of cherts or cherty limestones.

The ampletochilinine genera *Levisulculus* Jaanusson, 1957, *Ampletochilina* Schallreuter, 1969 and *Swantina* Schallreuter, 1986 are very similar to each other in lacking or having very weakly developed lobal and sulcal sculptures together with similar adventral sculptures. The most important distinctive feature is the type of antrum. However, this feature is often not visible in lateral view, particularly on valves still embedded in rock.

The present paper focuses on the taxonomically significant dimorphic features of excellently preserved material recovered from Upper Ordovician glacial erratic boulders of northern Central Europe (Northern Germany and Poland) and Sweden. The ostracodes were extracted from the rock by application of hydrofluoric acid (HF). Specimens sourced from cherty silicified limestones comprise of originally cal-

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careous carapaces that have been changed into calcium fluoride during the preparation process (Schallreuter 1982). By contrast, rock material from the Isle of Sylt has both matrix and ostracodes silicified. Therefore, the duration of HF application had to be reduced to a minimum in order to preserve the silicified ostracode valves etched out of the rock.

Institutional abbreviations.—GG, Institute of Geography and Geology of the Ernst Moritz Arndt University Greifswald; TUG, Geological Museum of the University of Tartu, Estonia; UM, Museum of the Palaeontological Institute, University of Uppsala, Sweden.

Other abbreviations.—G, glacial erratic boulders; H, height (without sculptures protruding over the straight hinge line); Hm, maximal H; L, length; LD (HD), L (H) of the domicilium; LV, left valve; RV, right valve; S2, median sulcus; tec, tecnomorph. Measurements are in mm. The domicilium has been measured from the inner borders of the contact margin in interior view. Note that the ratios L:H and LD:HD were computed before rounding off the L, H, LD, and HD values.

Sexual dimorphism in palaeocope ostracodes

Palaeocope dimorphism is characterised by modifications of special features, such as adventral sculptures, sculptures at the marginal surface, and the "…. flattened area adjacent to free edge of the valve and set off from lateral surface…" (Moore 1961: Q52). There are three different kinds of adventral sculptures: the main adventral sculpture, the velum, and the marginal sculpture situated below the velum and close to the free margin. Rarely observed is a further ridge-like sculpture, called histium, which may be developed above the velum.

The marginal sculpture is located directly at the free margin (marginal) or near the free margin (admarginal). The terms "marginal" and "admarginal" are defined by their position relative to the free margin (Jaanusson 1957: 188). The free margin (edge) is defined as the "… line, exclusive of the hinge line, formed where the two valves come together when they are tightly closed" (Kesling 1951: 111). Therefore, the free margin has different positions in the two valves of a carapace: in the overlapping valve it is the outermost border of the valve; in the overlapped valve, particularly when seen as an isolated valve, it is located some distance from the outermost border of the valve. Therefore, in the smaller valve the marginal ridge may not be an admarginal ridge.

Palaeocope dimorphism is mainly expressed by the velum, but the histal and marginal sculptures may be incorporated. In general, two types of palaeocope dimorphism can be distinguished based on the position of the brood chamber with regard to the domicilum (Schallreuter and Hinz-Schallreuter 2007: text-fig. 1). Cruminal dimorphism is characterised by the formation of a brood pouch (crumina) which is directly connected with the domicilium, the inner space of a carapace. By contrast, antral dimorphism refers to external brood pouches without direct connection to the domicilium. The antrum may be formed by the flange-like velum which is planar in tecnomorphs but strongly convex in females, constituting a sausage-like pouch on the outside of the domicilium (dolonal antrum; Schallreuter and Hinz-Schallreuter 2007: figs. 2.1–2, 4–5), or at the other extreme consisting exclusively of the concave marginal surface bordered by the marginal sculpture and a rudimentary dolon (admarginal antrum; Schallreuter and Hinz-Schallreuter 2007: figs. 2.3–4). Intermediate antra are formed by both the concave marginal surface and a more or less broad and convex dolon (Schallreuter and Hinz-Schallreuter 2007: fig. 3).

Cruminal dimorphism, which was developed by the end of the Ordovician and became so dominant in the Silurian, had a great advantage concerning brood care because the animal had direct contact to the brood chamber. Some authors have argued against the function of the crumina as a brood pouch because it prevented locomotion of the appendages or might even have endangered the eggs from being eaten when positioned close to the oral appendages (e.g., Hessland 1949: 125). However, evidence from Recent ostracodes does not point against an anterior position of the eggs even close to the mouth, e.g., in *Heterocypris incongruens* (Hartmann 1975: 639) eggs which protrude at the posterior end of the body are transported by the extremities towards the mouth region, where they are frequently touched by the antennae. The use of the crumina as a brood pouch has been confirmed by finds of broods inside this organ. Although Hessland (1949: 125) considered the crumina as a dangerous place for eggs or brood, in the same article he published his observations of larval stages in both the crumina as well as in the dorsal part of a carapace of *Beyrichia kloedeni*. Spjeldnaes (1951: 745, pl. 103: 1–2) discovered the first three instars in the cruminae of closed carapaces of *Beyrichia jonesii* (recte *Craspedobolbina clavata*), with similar findings by later authors (Becker 1968: fig. 10 left middle; Adamczak 1968: pl. 17: 4a).

While the Ordovician was a time of antral dimorphism in palaeocopes, typical Silurian representatives are characterised by cruminal dimorphism. However, Devonian times witnessed a renaissance of antral dimorphism.

The problem of brood care in antra

Very different kinds of antra are found in various ostracodes. Apart from four basic kinds, i.e., the botulate and loculate type observed in both dolonal and admarginal antra (Schallreuter and Hinz-Schallreuter 2007: fig. 2), many variations and transitional developments exist. In a few species with dolonal antra, the dolones are so strongly convex that in the closed carapace condition the antral marginal borders of both

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valves are in contact with each other, thus forming a so-called "false brood pouch". The latter lacks any contact to both the environment and the domicilium (e.g., *Bromidella sarvi*, Schallreuter 1973: pl. 20: 2). In many other species the dolones are only weakly convex and form a pouch open to the environment (Schallreuter 1973: pl. 22: 3; Schallreuter and Hinz-Schallreuter 2007: fig. 3).

The antra are usually "sausage-shaped" (Henningsmoen 1965: 343; "wurstförmiger Hohlraum" Kummerow 1939: 91), "channel-shaped" or "channel-formed" (Henningsmoen 1965: 343, 355), with mostly the anterior rather than the posterior end being bluntly rounded. Such antra are termed botulate (Schallreuter 1977a: 35). More advanced taxa may have their antra partitioned into separate cavities (loculi) by transverse "septa" (Henningsmoen 1965: 343). These are termed loculate antra.

Ordovician palaeocopes with an external brood pouch undoubtedly had more problems with brood care than cruminal dimorphic taxa. Hessland (1949: 124, 126) saw no difficulties in the transference of eggs to an anteroventral brood pouch, because the whole procedure took place within the closed carapace. In antral dimorphic taxa the carapace "… had to be open, since the pouch is separated from the interior of the carapace when the latter is closed" (Hessland 1949: 126). Hessland (1949: 126) stated that "It might not have been impossible to transfer eggs to such pouches but many eggs may have been lost during the transference". Hessland (1949: 126–127) did not believe in open antra as booding spaces as neither eggs nor larvae might have been attached to the walls. Jaanusson (1957: 209) partly concurred in concluding that "… these characters had certainly nothing to do with brood care" but "…. that the velar and histial dolon may have been used as egg care" by sticking eggs "to the walls by means of some secretion".

Henningsmoen (1965: 356) presented a logical argument that antra, in particular loculate antra, served as egg shelters similar to the containers for eggs found in a refrigerator. That also the channel-formed antra might have served as egg shelter is emphasised by a few species, e.g., *Triemilomatella prisca* and *Sylthis syltensis,* showing very faint depressions in their antra comparable to loculi in status nascendi (Jaanusson and Martinsson 1956: pl. 1: 1a, v, 2a, v; Schallreuter 1980b: pl. 24: 2–4). Whether antra beyond their function as egg shelters also served for brood care like the crumina remains questionable. This could be tested only by sectioning antral dimorphic species like *Bromidella sarvi* that have a false brood pouch containing young instars. However, closed carapaces of such species are extremely rare.

Especially in the Upper Ordovician, species with a false brood pouch are rarer than those with open antra. Therefore, the latter kind of antra is suggested to have been the optimal and thus, the more successful brood chamber. *Levisulculus*, *Ampletochilina*, and *Swantina* are genera with well-developed open antra and are therefore of special interest in this respect. They are very similar in general morphology but differ distinctly in their antral construction.

Levisulculus, *Ampletochilina*, and *Swantina* and the construction of their antra

General features.—All morphological features are called sculptures. Structures refer to special constructions of the material of the shell (differently constructed layers, for example prismatic layer, organic rich layer etc.).

Size and shape.—For definition of size see Table 1.

The shape (Gestalt) is defined by the length:height (L:H) ratio (Table 2). According to the definitions given above, adult *Levisulculus*, *Ampletochilina*, and *Swantina* are small- to medium-sized. Their shape varies between rather high and rather long, and the domicilium is rather long to very long. The carapaces are essentially equivalved but the left valve overlaps the right valve at the contact margin.

The outline is amplete or preplete. The cardinal corners are approximately rectangular to distinctly blunt. Often, the cardinal corners of the left valve carry acroidal spines (Figs. 1A, 3C, D_1, H, $4F_2$, 5E, M_1, 6A, F), which are relatively longer in larvae (Fig. 6K, L).

Lobal and sulcal sculptures.—Lobal and sulcal features are very weakly developed in these genera. Most Baltic species are nonsulcate or nearly nonsulcate, having only a faint sulcal depression as in the type species of *Levisulculus* (*L. lineatus*). Often a rounded muscle spot is present (Figs. 5E, 6C), rarely exhibiting muscle scars (Fig. 6E). Anterodorsally of the muscle spot an indistinct small preadductorial node may be present, which is most recognisable from the inner surface view of the respective valves (e.g., Fig. $4A_1$).

Table 1. Conventional definition of size classes.

Size (mm)	Denotation
>20.0	gigantic
5.0–20.0	very large
2.0–5.0	large
1.0–2.0	medium-sized
0.5–1.0	small
<0.5	very small

Table 2. Conventional definition of shape types (Schallreuter et al. 2006: table 4). Abbreviations: H, height (without sculptures protruding over the straight hinge line); L, length.

L:H	Denotation
<1.25	extremely high
1.25–1.45	very high
1.45–1.55	high
1.55–1.65	rather high
1.65–1.75	moderately high
1.75–1.85	moderately long
1.85–1.95	rather long
1.95–2.05	long
>2.05	very long

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Stronger lobes and sulci are developed in some non-Baltic species referred formerly to *Levisulculus*. In *L. michiganensis* the S2 is slightly sigmoidal, consisting of a shallow sulcus that extends down from the dorsal border immediately above the small, distinct, vertically elongate preadductorial node, then curves around L2, and terminates in a distinct pit at midheight on the domicilium (Kesling 1960: 353; pl. 1: 2). The anteroventral portion of the postsulcal area is the highest part of the domicilium, thus indicating a weak indistinct posteroventral lobe, which is very distinct in *L. posteroventrolobatus*. In that species the S2 consists of a sulcal depression with a muscle spot in its centre posteroventrally to a small but distinct preadductorial node (Schallreuter et al. 2001: pl. 2: 1). In contrast, the Bohemian species *L. smolai* is characterised by a long and deep sigmoidal sulcus (Schallreuter and Krůta 1991: figs. 1–2, 2001: text-fig. 1.1–2).

Velar sculptures.—In the genera discussed the velum is a restricted frill, which is developed mainly in the ventral half of the valve at some distance from the free margin (Fig. 1A). The frill terminates posteroventrally in a more or less strong spine (terminal velar spine, Fig. 1A). The characteristic tubules of the frill are mostly recognisable by the radial striation of the latter. They are hollow but this is extremely difficult to observe (Fig. 6I).

The velum displays dimorphic features. It is broader in females and forms an antrum, which also incorporates the marginal surface between velum and marginal sculpture (dolonal-admarginal antrum; see Schallreuter and Hinz-Schallreuter 2007: fig. 2). The dolon is generally only weakly convex (Fig. 5C, D) but may be strongly convex in certain parts. In *Levisulculus* it is strongly convex in the anterior part and weakly convex ventrally (Fig. 4A). In *Swantina crassiconvexa* it is strongly convex ventrally and weakly convex anteriorly (Fig. 4C). In strongly convex dolones the wall of the dolon itself forms the outer antral fence of the antrum, but in weakly convex dolones or parts of the antrum it is bordered by a special antral fence close to the peripheral border of the dolon (Figs. 1B, 5C).

The antrum may be open at either end (Fig. 5C) or closed anteriorly, resulting in a strongly convex dolonal portion (Fig. 4A). Alternatively, it may be closed posteriorly (Fig. 4C), often by a terminal velar spine (Fig. 1B, Table 3).

Surface sculptures.—In the type species of *Levisulculus* and in *L. dactylus* the lateral surface is covered with irregular, more or less vertically directed faint ridges. The adventral sculptures, especially the dolon, may show ornamentation different from that of the lateral surface (Fig. 3A; Schallreuter et al. 2001: pl. 2: 7).

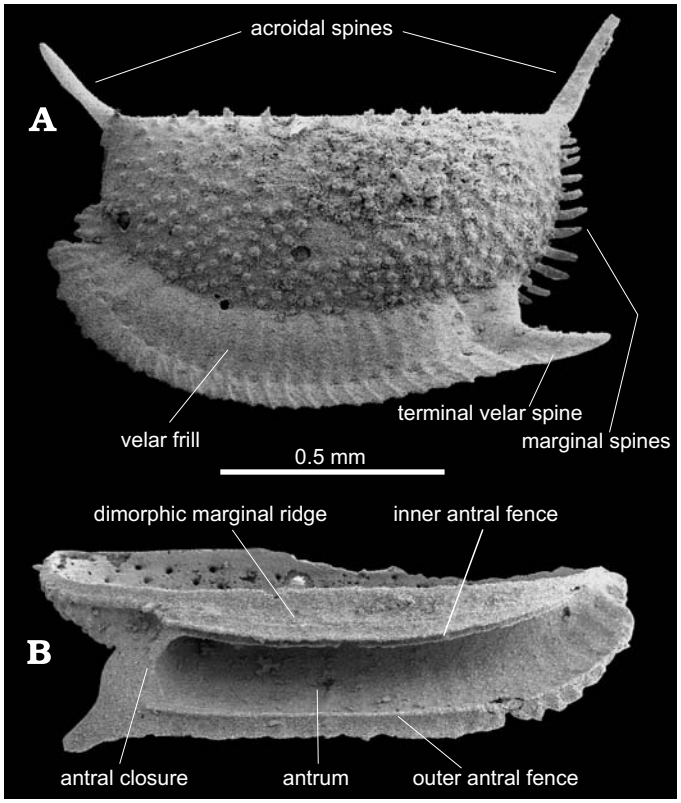

Fig. 1. Morphological terminology explained in *Swantina pseudobliqua*.

Very faint ridges occur at the adventral sculptures, the outer part of the dolon (Fig. 7B, C), and the marginal flange (Fig. $7A_3$). Special vertical pillars are developed at the outermost part of the marginal flange between the borders of the flange and inner antral fence (Fig. $7A_2$).

The tubules of the velar flange may appear as radial ridges on the outer surface. In some cases they form into separate spines (Fig. 4E). The spines are declined posteriorly, and the ridges may show an abrupt bend in the posterior direction (Figs. 5E, 7D).

In a few cases the lateral surface appears completely smooth (Fig. $5A_1$), except for the densely set normal pores (Fig. 5B, D_1). However, in most cases the pores are developed as pustules resulting in a more or less tuberculate outer surface (Figs. 5E, H, J, K_1, 6).

Table 3. Main morphological differences between the genera discussed.

Features	*Levisulculus*	*Swantina*	*Ampletochilina*
outline	preplete	amplete	amplete
cardinal angles	slightly >90°	~ 90°	obtuse
dolon	present antero- to centroventrally, anteriorly strongly convex	present antero- to centroventrally, weakly convex	present antero- to posteroventrally, weakly convex
antrum	anteriorly closed	posteriorly closed, with separate antral fences	open at both ends, with separate antral fences
surface	pustulate	pustulate	smooth, with pores

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The function of open antra

The idea of antra having been used for egg or brood care was heavily criticised by several authors (Jaanusson 1957: 201), mainly because of their external, mostly anteroventral position which, apart from resulting in a difficult egg transfer, was inappropriate to protect eggs or brood from falling out of the pouch.

Countering Triebel's (1941: 357, 359) argument that the pouch was only accessible in the opened carapace condition, resulting in the loss of its content, Kummerow (1948: 19) replied that he did not see a problem for egg transfer since some kind of fixation for the eggs, such as a thin skin or a similar sculpture, may easily have been present.

Of the two discussed ways to fix eggs in an antrum by some secretion or the development of a thin protective skin, the latter possibility seems to have been realised in the species described in the systematic part. They are characterised by weakly convex dolones which accordingly, have largely opened antral spaces. The distal borders of both dolon and marginal ridge display an additional separate ridge each (tori sensu Martinsson 1962: 79, text-fig. 1B). The tori are orientated relatively to each other. With regard to their position along the dolon and marginal ridge, they functioned as outer and inner antral fences. They are assumed to have been used as attachment area for the protective skin mentioned above. Such tori do not occur in species with a strongly convex antrum.

Pore system

Although the ostracode animal generally is completely protected when the carapace is closed, a pore canal system recognisable in both Recent and fossil ostracodes guarantees contact with the outer environment. The pore canals penetrating the shell are termed normal pores and may contain sensory organs such as setae. Special developments are sieve pores. A second pore type is represented by the marginal or radial pores, which are restricted to the marginal zone and run within the concrescence zone. False marginal pores (Kesling 1951: 124; Hinz-Schallreuter and Schallreuter 1998: 35, fig. 38; Olempska 2008: 719, fig. 1) are normal pores close to the concrescence zone.

Even though pores have been observed in a number of Ordovician ostracode species, detailed descriptions are available for a few taxa only. The recorded pore systems comprise also pore types that are unknown from other ostracode groups.

The most common pores observed in Ordovician taxa are simple normal pores or pustules. A pustule (in German "Porenkegel") is defined as "...a protuberance with a pore in the middle" (Kesling 1951: 115). A special development are sickle-shaped pores, which keep the movement of the setae canalised (like in *Bolbina*; Schallreuter 1983a: pl. 13.9, 1990: pl. 1.9).

Another type of pore is developed in *Baltonotella kuckersiana* (Bonnema, 1909). Its outer surface is characterised by elongate puncta, which are not pores. They originate from a reticulation, modified such that the lumina are reduced to small unipolar openings surrounded by comparably broad walls. Very fine pores, which are open at both ends, are distributed on these walls (Schallreuter 1996: pls. 70.1-3, 72.1-2). Close to the free margin a row of marginal pores is developed (Schallreuter 1996: pl. 72.3-4).

A further pore type was recorded from *Brevidorsa fabuliformis* (Hessland, 1949). Spjeldnaes (1951: fig. 3E) figured a bulb-shaped pore redrawn from Hessland's thin-section (Hessland 1949: pl. 12: 5). Within the shell the pore is more or less bulb-like but narrows considerably towards either end. On both outer and inner surface such pores appear as tiny openings with an average diameter of 2–3 μm, while its maximum extent ranges up to about 27 μm (carapace height 0.45 mm).

In *Pinnatulites procerus* (Kummerow, 1924) (= *P. reticulatus* [Steusloff, 1895]) funnel-shaped pores were observed by Hessland (1949: 201) and Schallreuter (1994: 532). It was, however, Olempska (1994: 158, text-fig. 14), who gave a detailed description of this kind of pore. They appear as large openings forming long triangles on the outer shell surface that protrude from the shell and terminate as round openings with a diameter of about 40–70 μm on the inner shell surface. Morphologically, the triangles resemble the elongate punctae of *Baltonotella* but are true pores in the case of *P. procerus*. Despite their special characteristics, Spjeldnaes (1951: fig. 3F) figured such a pore as a "simple pore".

Sieve pores are rare even within Palaeozoic ostracodes and have never been observed in Recent taxa. They occur in two different varieties in the following species:

(i) *Miehlkella cribroporata* Schallreuter, 1977. Here the lateral surface is covered by small, densely set pores with differently developed ends. On the outer surface they appear as simple round openings, which pass into ring-like sieve-pores on the inner shell surface (Schallreuter 1977b: pls. 10–16).

(ii) *Klimphores planus* Schallreuter, 1966. This species has all lumina (Martinsson 1962: 76; = fossa of Olempska 2008: 720) of the reticulated outer surface developed as large sieve pores. In contrast to *Miehlkella* with its pores arranged in rings, they are irregularly distributed in each lumen and visible on both outer and inner shell surfaces (Schallreuter 1980a: pls. 14.4, 16.4; 1983b: fig. 2.1a, b, pl. 1: 5–7).

The diameter of the pores varies considerably between the above mentioned species. In *Baltonotella kuckersiana* the pores are very fine (~ 4 μm) in comparison with the large punctae (35–40 μm, valve length 1.17 mm). The pores of *Miehlkella cribroporata* (length 0.77–1.00 mm) are rather small (~10 μm) compared to the punctae of other species. But in *K. planus* (length 0.64–0.71 mm) the sieve pores are very large (30–40 μm) and occupy the entire lumina of the reticulation.

The relations between antral dimorphism and the pore system

Antral dimorphic ostracodes generally lack both a duplicature and a concresence zone, and their marginal pores are devel-

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oped as false marginal pores (see above). In contrast to the heteromorphs, tecnomorphs have their pores usually developed as pustules that are distributed on the velum. Antrum-bearing specimens, however, show a concentration of pores in two places around the suggested brood pouch: (i) between the marginal border of the dolon and the outer antral fence, and (ii) between the marginal ridge and the free margin.

In general, the setae of these pores are interpreted as tactile receptors to detect contact with the substratum (e.g., Olempska 2008: 719). This may be the case for the irregularly distributed pores between marginal ridge and free margin (Fig. $7A_3$). However, the linearly arranged pores between the marginal border of the dolon and the outer antral fence in heteromorphs (Fig. $7A_1$) suggest that they might have also had some function connected with egg or brood care as they may have produced some sort of curtain for protection.

Lifestyle

It is unequivocally accepted that the beyrichioid cruminae served as brood pouches. The fact that Spjeldnaes (1951: pl. 103: 1) discovered larval stages 1 and 2 together in a brood-pouch of *Craspedobolbina clavata* together suggests continuous brood care. Recent ostracodes may carry eggs that all show the same developmental stage (e.g., Myodocopa and Platycopa), while in other groups such as Darwinulidae and Cytheridae eggs are deposited in irregular intervals (Hartmann 1975: 642).

In Recent ostracodes egg care also includes oxygenation by permanent movements of the maxillulae (Hartmann 1975: 642).

The fact that instars found in the pouches of *Craspedobolbina clavata* are not smaller than the youngest free instar (Martinsson 1962: 81) suggests that they might have used the pouches as a temporary shelters against danger.

In antrum-carrying taxa evidence like that mentioned above is lacking. However, a fundamental question is why antra can be weakly or strongly convex. These differences are interpreted to have been a result of both their function and the lifestyle of the respected animal.

It can be assumed with a high degree of confidence that antra had been used as egg shelters since both the form and diameter of the loculi in loculate antra correspond to the form and size of ostracode eggs. However, their use for brood care was dismissed by Jaanusson (1957: 209).

Although taxa with a false brood pouch are relatively frequent in the Middle and lower Upper Ordovician, they are still outnumbered by species with open antra. The change to loculate antra in more advanced taxa that occur mainly from the Upper Ordovician onward.

In antra with a separate loculus for every egg, the eggs would have been better stored than in a channel-like antrum. The number of loculi varies between two (*Perspicillum*), five (*Foramenella*, *Pleurodella*), and six (*Loculibolbina*). *Sigmobolbina* and *Ceratobolbina* have only one anteriorly situated loculus, but behind the latter a channel-like antrum is developed, presumably for more eggs. The number of eggs in the channel-like antra is unknown. It would certainly have depended on the length of the antrum.

A false brood pouch or deep antrum has often been observed on thick-shelled valves. These ostracodes probably lived as bottom dwellers (crawlers?) and the antra had the function of protecting the eggs from contact with the substrate (Henningsmoen 1965: 355). Triebel (1941: 359) and Hessland (1949: 127) were of the opinion that the eggs would fall out of the carapace when it was opened. We favour an alternative explanation—that the carapace might have been closed until the hatched nauplii had to be released. The duration of embryonal development is unknown and even in Recent ostracodes it is incompletely known. It ranges between 6 and 10 days in *Heterocypris incongruens* (Hartmann 1968: 512) but may take months in other taxa. Contrary to open antra, the false brood pouch was probably used only for egg storage and embryonal development, because access was possible only in the open carapace condition.

Open antra, however, are accessible for young instars in both the closed and opened carapace conditions. The advantage of brood care in protecting young instars probably made the respective taxa more successful and thus, more frequent. In contrast to many benthic species with false brood pouches, those with widely open antra are assumed to have been swimming forms, at least during the time of brood care. This can be deduced from their distribution, as exemplified by *Perspicillum perspicillum* from the lower Upper Ordovician of Baltoscandia. This is one of the few species that occur in both confacies belts (CB) of the Baltoscandian palaeobasin, the North Estonian CB and the Central Baltoscandian CB. *Perspicillum perspicillum* has two admarginal loculi in the anteroventral part of each valve. Originally, this region "… has been suggested to be an unlikely place for an egg shelter. However, in swimming forms this would, from a hydrodynamic point of view, be a suitable place …" (Henningsmoen 1965: 354).

Systematic palaeontology

Ostracoda Latreille, 1802

Order Beyrichiocopa Pokorný, 1954

Suborder Palaeocopa Henningsmoen, 1953

Infraorder Beyrichiomorpha Henningsmoen, 1965

Superfamily Eurychilinoidea Ulrich and Bassler, 1923

Family Oepikellidae Jaanusson, 1957

Subfamily Ampletochilininae Schallreuter, 1975
= Platybolbininae Ivanova, 1979

Genus *Levisulculus* Jaanusson, 1957

Type species: *Levisulculus lineatus* Jaanusson, 1957 (original designation); Tvären area, glacial erratic boulder of lowermost Ludibundus limestone.

Species included.—*Primitia elongata obliqua* Steusloff,

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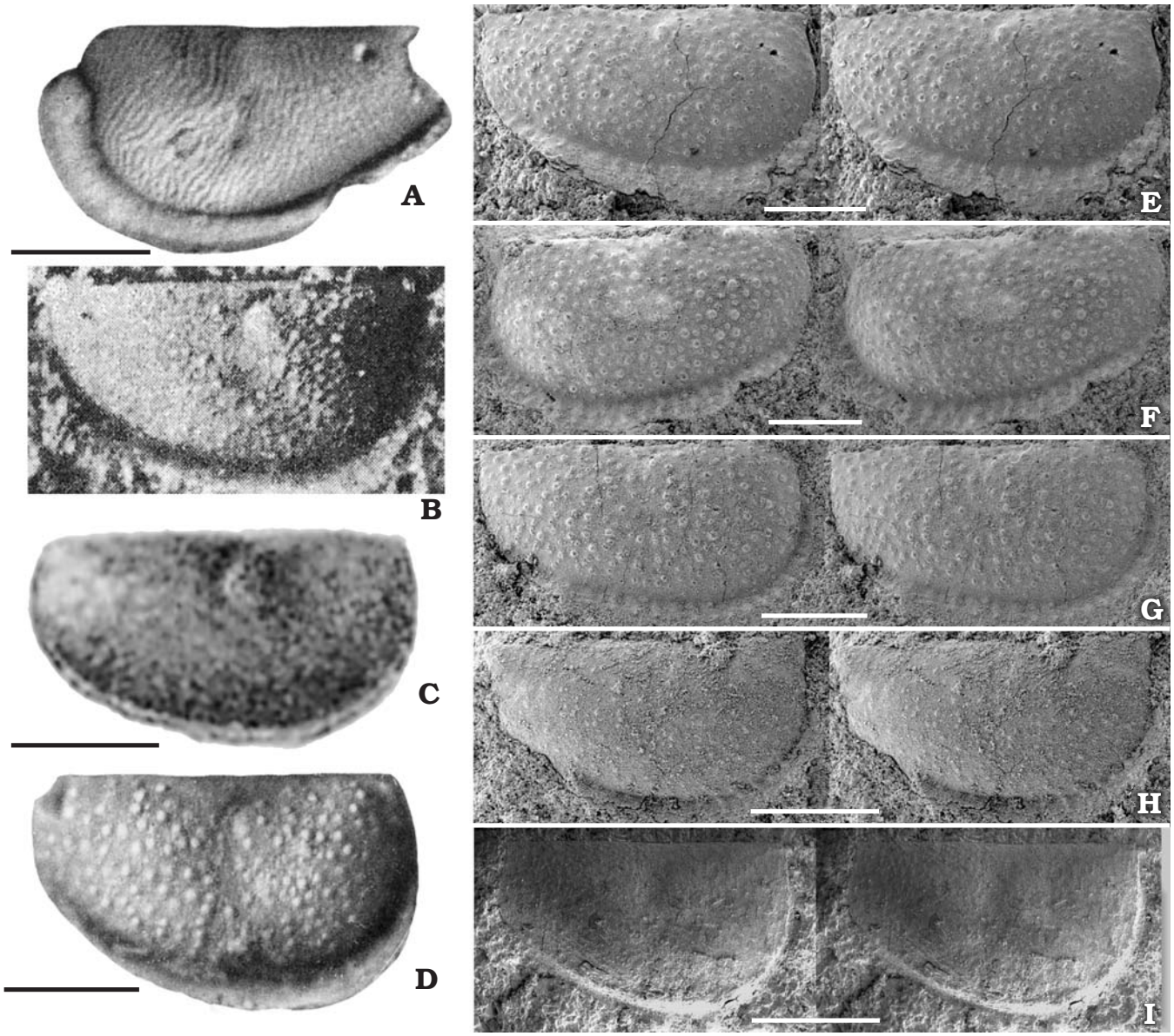

Fig. 2. Oepikellid ostracods from Palaeozoic erratic boulders. **A**. Holotype of the type species of the oepikellid ostracod *Levisulculus*, *Levisulculus lineatus* Jaanusson, 1957 (UM T89), female left valve, length (L) 0.89 mm. **B**. Holotype of *Primitia extraria* Öpik, 1937 (TUG 1120-1; Kukruse Stage, Estonia), tecnomorphic right valve, L 0.88 mm. **C**. Holotype of *Primitia troedssoni* Thorslund, 1940 (UM T10), tecnomorphic right valve, L 0.79 mm. **D**. Holotype of *Primitia granulosa* Thorslund, 1940 (UM T11), tecnomorphic right valve, L 0.86 mm (Jaanusson 1957: pl. 8: 12, Öpik 1937: pl. 10: 19, Thorslund 1940: pl. 1: 16, 13). **E–H**. *Primitia elongata obliqua* Steusloff, 1895: type series, all tecnomorphic valves embedded in rock. Geschiebe (glacial erratic boulder) from Neubrandenburg. **E**. Lectotype GG 114-27, left valve, L 1.16 mm (without velum). **F**. GG 114-26, right valve, L 1.07 mm. **G**. GG 114-28, right valve, L 0.99 mm (without velum). **H**. GG 114-29, right valve, L 0.82 mm. **I**. *Primitia canaliculata* Steusloff, 1895, holotype GG 114-25, steinkern of a juvenile right valve embedded in rock, L 0.70 mm, same erratic boulder.

1895; *Primitia canaliculata* Steusloff, 1895 (= *Levisulculus obliquus*); *Primitia*? *extraria* Öpik, 1937; *Primitia troedssoni* Thorslund, 1940 (= *Levisulculus extrarius*); *Primitia granulosa* Thorslund, 1940 (= *Levisulculus extrarius*); *Levisulculus michiganensis* Kesling, 1960; *Ampletochilina ryghooftensis* Schallreuter, 1987; *Swantina*? *levis* Sidaravičienė, 1992; *Ampletochilina priscina* Olempska, 1994; *Bulbosulculus dactylus* Schallreuter, Kanygin, and Hinz-Schallreuter, 2001, *Levisulculus priscina* seems to be a synonym of *Levisulculus ryghooftensis* (compare Olempska 1994: pl. 33: 1–3 and Schallreuter 1987a: fig. 2.1–2).

Diagnosis (emended).—Small to medium-sized. Outline usually preplete, sometimes amplete. Cardinal angles rectangular to slightly blunt. Left valve may carry acroidal spines in adults, too. Nonsulcate to unisulcate. S2 pit-like or as a weak sulcal depression. If nonsulcate a muscle spot may be present which may be located posterior to mid-length also in adults. A more or less distinct preadductorial node may be present. Convexity of dolon anteriorly very strong, decreasing in posterior direction. Antrum correspondingly closed anteriorly and opened posteriorly, sometimes also closed posteriorly. Marginal sculpture developed as row of spines or ridge, in the

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antral region as narrow flange forming the inner antral fence. Surface striate, rugose, tuberculate or pustulate. Velum undulate or tubulose.

Discussion.—*Levisulculus* resembles *Ectoprimitia* Bouček, 1936 and "may prove to be a junior synonym" because "loculi may be absent by *Ectoprimitia* also" (sic!) (Meidla 1996: 28). In fact, the type-species of both genera resemble each other in their surface ornamentation. Also, the dolon is similar and more distinctly limited anteriorly than posteriorly. However, the loculi in the dolon of the type species of *Ectoprimitia* (Schallreuter 1987a: pl. 1A: 4) are only loculi in status nascendi—comparable to the loculi in *Sylthis syltensis* (Schallreuter, 1980)—and of less taxonomic importance. The main difference between the genera is the presence of dorsal plica in *Ectoprimitia* only. Therefore, the genera are not considered to be synonymous.

For the two Middle Ordovician species from Siberia, *Levisulculus fragilis* Kanygin, 1971 and *Levisulculus ornatus* Kanygin, 1971, Ivanova (1979: 105) established the genus *Bulbosulculus*. As expressed by the name the genus should be characterised by the distinct preadductorial node. But this node is distinct only in *B. ornatus* and weak in the type-species *L. fragilis*. The holotype of *L. fragilis* is considered as a female in which the dolon is rather narrow and the antrum rather short (Kanygin 1971: pl. 4: 7) and therefore, different from those of *Levisulculus*. In terms of outline, shape, lobation and dimorphism the holotype resembles more *Gryphiswaldensia*, but the tecnomorphic paratype figured by Kanygin (1971: pl. 4: 6) agrees with *Levisulculus* in outline and shape. The dolon of *Bulbosulculus dactylus* from Novaya Zemlya is very similar to that of typical species of *Levisulculus* (compare Schallreuter et al. 2001: pl. 2: 7; Jaanusson 1957: pl. 8: 14–15). This species therefore, is better placed in *Levisulculus*, whereas the exact systematic position of Kanygin's (1971) *Levisulculus* species and the genus *Bulbosulculus* remains uncertain.

Eurybolbina Copeland, 1982 is very similar to *Levisulculus* but according to Williams and Miller (1992: 115) it differs from the latter genus by several features. In *Levisulculus* the dolonate antrum is "more distinct anteriorly" and the velum "tends to be less well developed posteriorly". Contrary to *Levisulculus*, *Eurybolbina* has a "fluted overlap frill of the right valve". Furthermore, *Levisulculus* is generally more elongate and more distinctly preplete.

Ivanova (1979: 102) assigned *Ctenobolbina obliqua* Ulrich, 1900 to *Levisulculus*, but did not consider the resulting homonymy with *L. obliquus* (Steusloff, 1895) Schallreuter, 1967. She also disregarded the fact that Thorslund (1940: 174) had already substituted the name *C. obliqua* Ulrich, 1900 with *C. ulrichi* Thorslund, 1940 because of the homonymy with *C. obliqua* (Krause, 1892) Öpik, 1937. *Ctenobolbina ulrichi* was not mentioned by Kraft (1962: 46) or Kempf (1986a, b, 1987, 1995a–c).

ICZN Article 59.3 (Secondary homonyms replaced before 1961 but no longer considered congeneric) states: "A junior secondary homonym replaced before 1961 is permanently invalid unless the substitute name is not in use and the relavant taxa (recte: taxon) no longer considered congeneric, in which case the junior homonym is not to be rejected on grounds of that replacement" (Ride et al. 1999: 62). *Ctenobolbina oblique*, therefore, should not be considered invalid.

For *C. obliqua* Kraft, 1962, Copeland (1982: 10) introduced the new genus and species *Eurybolbina krafti*, which should be distinct from *C. obliqua* by the missing posteroventral "tubercle". Williams and Miller (1992: 115) considered *E. krafti* as a synonym of *E. bispinata* (Harris, 1957) and this nominal species tentatively as a synonym of *C. obliqua* (*E. ulrichi*).

The holotype of *E. bispinata*—a tecnomorphic juvenile carapace (not an adult male)—lacks a velum in the posterior regions and the velar frill terminates spine-like posteroventrally (Copeland 1982: pl. 2: 10; Williams and Miller 1992: pl. 118: 1, 3). Also females of *E. bispinata* (Copeland 1982: pl. 2: 3, 7–9) have their velum developed spine-like posteroventrally. This is in contrast with the situation in *E. krafti* (Copeland 1982: pl. 2: 14–16; Williams and Miller 1992: pl. 116: 1). Therefore, *E. krafti* may be a species distinct from *E. bispinata*.

Levisulculus posteroventrolobatus Schallreuter, Kanygin, and Hinz-Schallreuter, 2001 is referred to *Eurybolbina* here. The species differs from *E. krafti* and *E. bispinata* mainly in having a weaker S2 but a distinct posteroventral lobe (Schallreuter et al. 2001: pl. 2: 1). In *E. bispinata* the S2 is more distinct than in *E. posteroventrolobata* but less developed than in the type species (Williams and Miller 1992: pl. 116: 1, 4 and 118: 1, 3).

Levisulculus smolai Schallreuter and Krůta,1991 is also assigned to the genus *Eurybolbina*. In this species the S2 is much more distinct than in the type species (Schallreuter and Krůta 1991, 2001: fig. 1.1–2) and thus agrees more with the characteristics of *Eurybolbina*.

Levisulculus planus Copeland, 1965 and *Levisulculus undatus* Copeland, 1965 are also placed here in *Eurybolbina*.

Concerning lobal and sulcal sculptures *Levisulculus michiganensis* resembles *Eurybolbina* (compare Kesling 1960: pl. 1: 2 and Williams and Miller 1992: pl. 116) but in the construction of the dolon it is very similar to typical *Levisulculus* species. It is the oldest species of *Levisulculus* known so far.

Fig. 3. Oepikellid ostracods from Palaeozoic erratic boulders. **A**–**D**. *Levisulculus extrarius* (Öpik, 1937). All from lower Upper Ordovician Sandö flint erratic boulder Jas-17 from Jastrzębia Góra, Northern Poland. **A**. GG 347-1a, female right valve, L 0.96 mm; lateral (A_1), ventral (A_2), anterior (A_3) views and detail of A_2 (A_4). **B**. GG 347-1b, tecnomorphic right valve, L 0.60 mm; lateral (B_1) and ventral (B_2) views. **C**. GG 347-2, female left valve, L 0.98 mm; lateral view. **D**. GG 347-1c, Tecnomorphic left valve, L 0.52 mm; lateral (D_1) and ventral (D_2) views. **E**–**I**. *Levisulculus obliquus* (Steusloff, 1895). All from the upper Upper Ordovician Öjlemyr flint erratic boulder G287 from the Isle of Gotland, Baltic Sea. **E**. GG 278-1a; Female right valve, L 1.19 mm; lateral (E_1), ventral (E_2), and anterior (E_3)views. **F**. GG 278-1b, tecnomorphic right valve, L 0.85 mm; lateral view. **G**. GG 347-3a, tecnomorphic right valve, L 1.05 mm; interior view. **H**. GG 278-1c, tecnomorphic left valve, L 1.00 mm; lateral view. **I**. GG 347-3b, a, tecnomorphic left valve, L 1.00 mm; interior view (I_1) and detail of orifices of normal pores (I_2). Stereo-pairs, except of A_4, B_2, D_2, G, I_1, and I_2. Scale bars 0.3 mm. →

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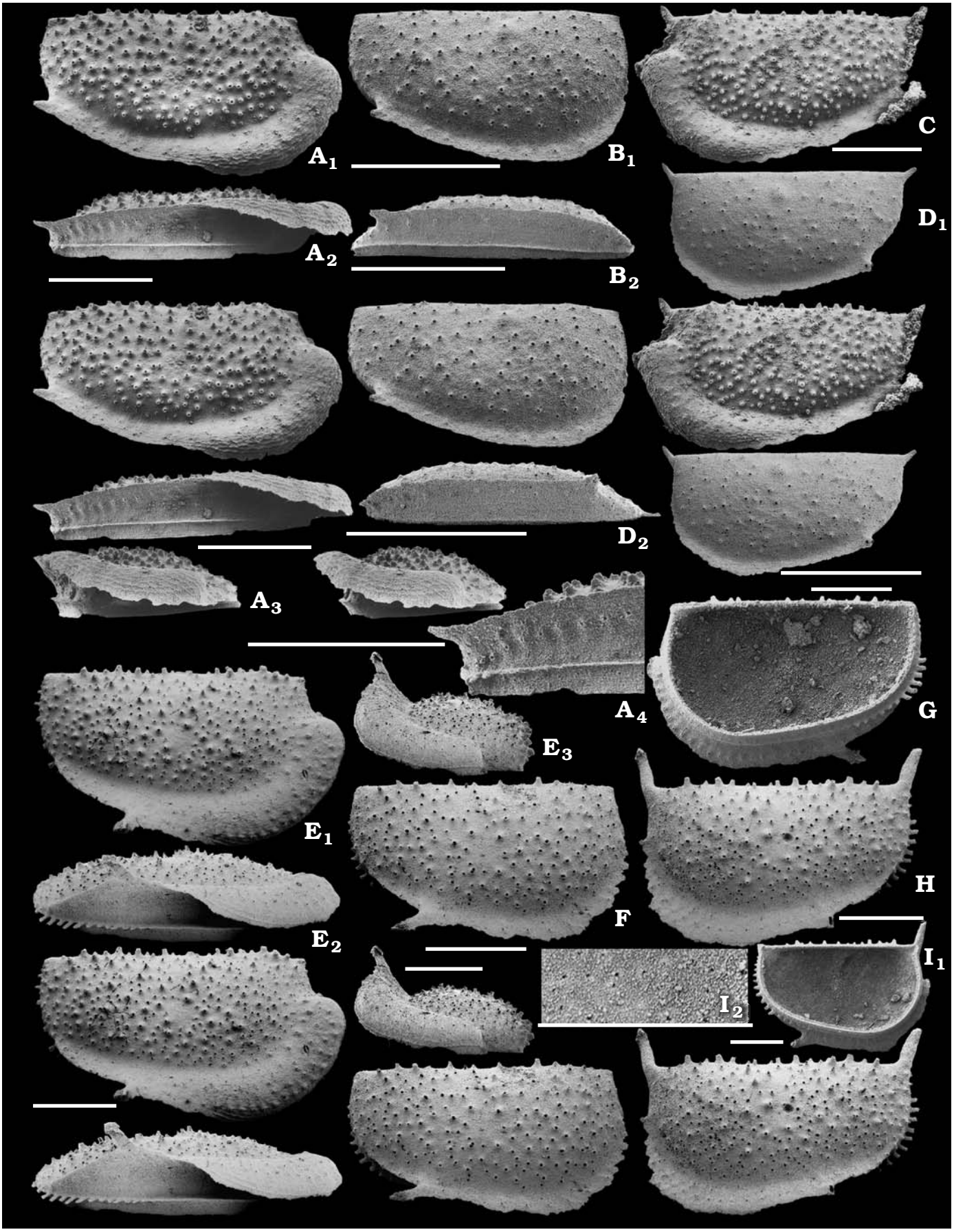

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Table 4. Measurements (in mm) of *Levisulculus extrarius*. Abbreviations: G, glacial erratic boulders; H, height (without sculptures protruding over the straight hinge line); Hm, maximal H; L, length; LD (HD), L (H) of the domicilium; LV, left valve; RV, right valve; tec, tecnomorph.

No. GG	G	Valve	Figs.	L	H	Hm	L:H	LD	HD	LD:HD
347-2	Jas-17	♀LV	3C	0.98	0.52	0.54	1.86	0.83	0.40	2.09
347-1a	Jas-17	♀RV	3A, 7C	0.96	0.50	0.52	1.90	0.78	0.39	2.00
347-1d	Jas-17	tec LV		0.76	0.42	0.42	1.83	0.69	0.34	2.04
347-1b	Jas-17	tec RV	3B	0.60	0.32	0.32	1.88	0.56	0.28	2.04
347-1c	Jas-17	tec LV	3D	0.52	0.27	0.28	1.88	0.49	0.24	2.04

Evolution within the genus appears to be connected with a reduction of the sulcus. With regard to reticulation and the pit-like S2, this species is transitional between *Eurybolbina* and *Levisulculus*.

Stratigraphic and geographic range.—Upper Ordovician of Baltoscandia, Novaya Zemlya, and Michigan.

Levisulculus extrarius (Öpik, 1937)

Figs. 3A–D, 7C.

1937 *Primitia extraria* n. sp., *Primitia*? *extraria* n. sp.; Öpik 1937: 69, 82, 133 (5, 18, 69), pl. 10: 19.

1940 *Primitia troedssoni* n. sp.; Thorslund 1940: 163–164, 186, pl. 1: 13–15.

1940 *Primitia granulosa* n. sp.; Thorslund 1940: 163–164, 186, pl. 1: 16.

1957 *Levisulculus extraria* (Öpik), *L. extraria* Öpik; Jaanusson 1957: 180, 321, 325, 326.

1957 *Levisulculus troedssoni* (Thorslund, 1940); Jaanusson 1957: 321, 323, 324–325, table 24; text-fig. 32A, pl. 8: 16–18.

1957 *Levisulculus granulosus* (Thorslund, 1940), *L. granulosa*; Jaanusson 1957: 321, 326, text-fig. 32B, pl. 8: 19.

1959 *Levisulculus extraria* (Öpik); Sarv 1959: 41–42, table 2 (p. 186), pl. 7: 1.

1975 *Levisulculus extrarius* (Öpik,1937) [after Sarv possibly synonymous witht *L. troedssoni* and *L. granulosa*]; Schallreuter 1975: 157, 158.

1979 *Levisulculus extraria* (Oepik, 1937) = *Primitia troedssoni* Thorslund, 1940 = *Primitia granulosa* Thorslund, 1940, *L. troedssoni*, *L. granulosus*, *L. treedssoni*; Ivanova 1979: 102–103, 188, pl. 7: 5.

1992 *Levisulculus extraria* (Öpik, 1937) = ?*Levisulculus troedssoni* (Thorslund, 1940) + *L. granulosus* (Thorslund, 1940); Sidaravičienė 1992: 140, 143.

Holotype: Tecnomorphic right valve, TUG 1120-1 (Öpik 1937: pl. 10: 19; Sarv 1959: pl. 7: 1).

Type horizon: Kohtla-Järve, Estonia.

Type locality: Kukruse formation (C2α), lower Upper Ordovician.

Diagnosis (emended).—Length at least up to 0.98 mm (holotype 0.88 mm). Shape mostly moderately long to rather long, domicilium mostly long to very long. Very small preadductorial node. Posteriorly directed velar spine at the border between the posteroventral and posterocentral regions. Lateral surface pustulate.

Dimensions and proportions.—See Table 4.

Disscussion.—Sarv (1959: 41), Ivanova (1979: 102–103) and Sidaravičienė (1992: 140) considered *Levisulculus extrarius*, *Levisulculus granulosus*, and *Levisulculus troedssoni* to be possible or definite synonyms. For the present, we agree with their assessment because the holotypes of these nominal species—all right valves—are not only very similar to each other (Fig. 2B–D) but also come from about the same stratigraphical level (C2α or "lowermost *Ludibundus* limestone", respectively).

Levisulculus extrarius is very similar to *L. obliquus*. Distinctly different, however, is the position of the velar spine. *L. extrarius* is slightly smaller and a little more elongate than *L. obliquus*. The younger *Levisulculus levis* is larger (1.22–1.48 mm) and the antrum appers to be a little longer posteriorly (Sidaravičienė 1992: pl. 36: 4, 7; Meidla 1996: pl. 2: 11). A velar spine is unknown in *L. levis* as is the small preadductorial node.

Stratigraphic and geographic range.—Estonia: Kukruse formation (C2α), lower Upper Ordovician. Tvären: erratic boulder of lower *Chasmops* limestone (lowermost *Ludibundus* limestone).

Levisulculus obliquus (Steusloff, 1895)

Figs. 3E–I, 4A, 7B.

1895 *Primitia elongata* Kr. var. *obliqua* n. v.; Steusloff 1895: 783, pl. 58: 12.

1895 *Primitia canaliculata* n. sp.; Steusloff 1895: 782, pl. 58: 9.

non 1897 *Primitia elongata* Krause var. *obliqua* Steusloff.; Krause 1897: 934.

1934 *Primitia* (?*Eurychilina*) *elongata obliqua* Steusloff; Bassler and Kellett 1934: 70, 443.

Fig. 4. Oepikellid ostracods from Palaeozoic erratic boulders. **A**. *Levisulculus obliquus* (Steusloff, 1895), erratic boulder G-287, GG 347-5a, female right valve, L 1.20 mm; interior (A_1) and anterior (A_2) views. **B**, **C**. *Swantina crassiconvexa* sp. nov. from erratic boulder 1B1. **B**. Paratype, GG 33-19, right tecnomorphic valve, L 1.02 mm; lateral (B_1) and ventral (B_2) views. C. Holotype, GG 33-18, female left valve, L 1.17 mm; lateral (C_1), ventral (C_2), and anterior (C_3) views. **D**. *Swantina pseudobliqua* Schallreuter,1986 from erratic boulder Sy-208. GG 347-6, tecnomorphic left valve, L 0.93 mm; lateral view (ventral view: Fig. 6F). **E**, **F**. *Swantina serrata* Schallreuter, 1986 from erratic boulder Sy-208. **E**. GG 347-7, anterodorsally incomplete tecnomorphic right valve, L 0.67 mm (without spines); lateral view. **F**. Neotype, GG 347-8, female left valve, L 1.06 mm; anterior (F_1) and lateral (F_2) views. **G**. *Swantina serrata* Schallreuter, 1986 from erratic boulder G30. GG 347-9a, female right valve with borings parallel to surface, L 0.93 mm; detail of frill with the borings (G_1) and specimen in lateral view (G_2). **H**. *Ampletochilina*? *granulifera* (Sarv, 1962) from erratic boulder Sy-208. GG 347-4, left tecnomorphic valve, L 1.09 mm; lateral view. Stereo-pairs, except of A_2, B_2, and H. Erratic boulder 1B1 of lower Upper Ordovician Backsteinkalk of Swedish origin from the Isle of Hiddensee, Baltic Sea, all other erratic boulders are of upper Upper Ordovician Öjlemyr flint and came from the Isle of Gotland, Baltic Sea (G) and the Isle of Sylt, North Sea (Sy). Scale bars 0.3 mm. →

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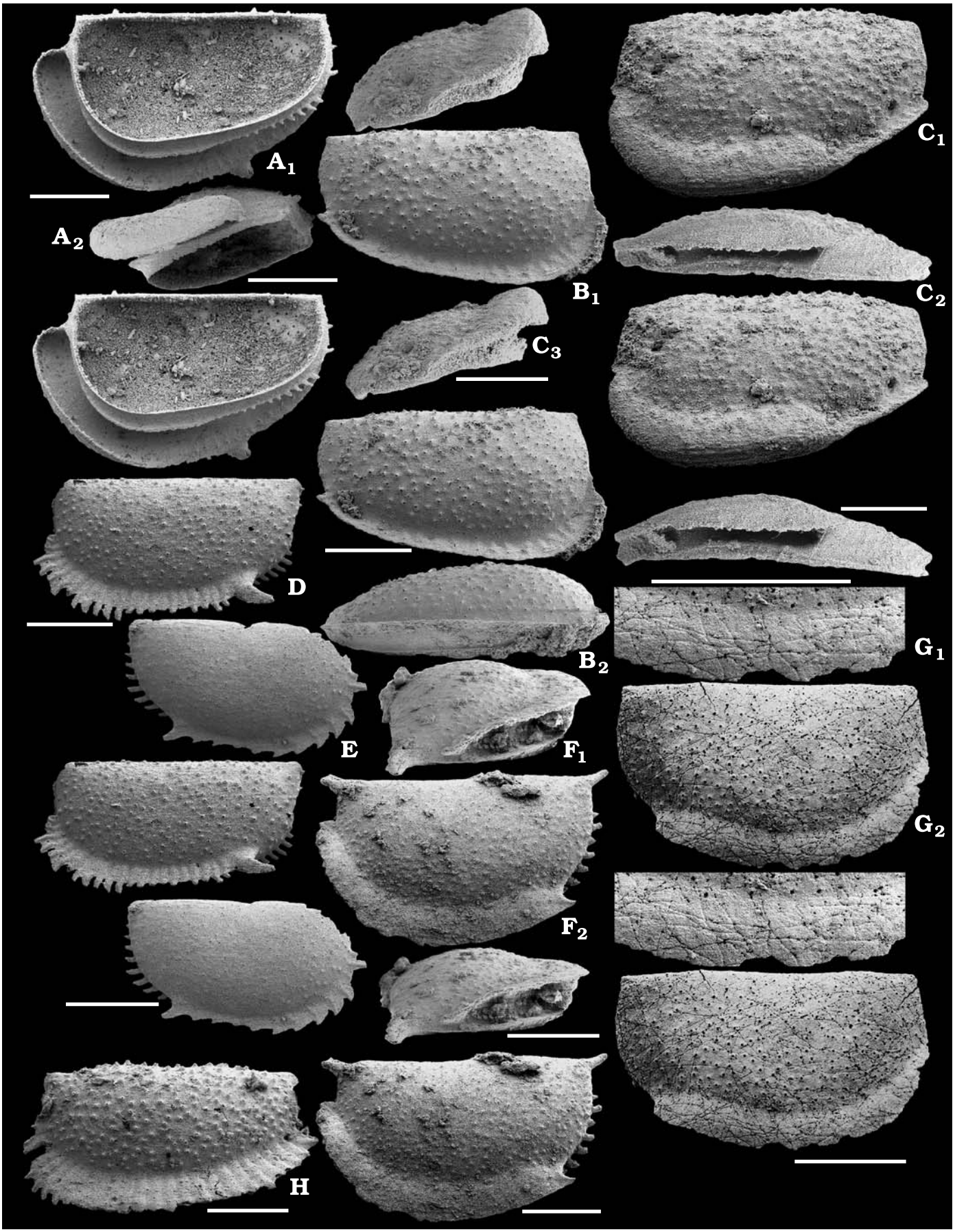

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Table 5. Species from Steusloff's 1895 erratic boulder of Borkholmer Kalk. Occurrences in Estonia after Meidla 1996. Abbreviations: E, Rakvere Stage; F1a, Nabala Stage; F1b, Vormsi Stage; F1c, Pirgu Stage; F2, Porkuni Stage; o.c., opus citatus.

Species mentioned or described by Steusloff (1895) and further species	Revised name	Catalogue of Herrig and Nestler (1989)	GG 114-	fig.	Occurrence Estonia				
					E	F1a	F1b	F1c	F2
Primitia jonesii	*Uhakiella jonesii = U. jonesiana = U. magnifica*				?	X	X	X	X
Primitia distans	*Platybolbina distans*				unknown				
Primitia plana	*Platybolbina plana*				X	X	X	X	X
Leperditia praelonga	*Longiscula praelonga = L. porrecta*	122	22	o.c. 1.2			?	?	X
Primitia cuneata	*Steusloffina cuneata = S. diversa*	176	42–49, 61		X	X	X	X	X
Primitia rugosa	*Piretia rugosa*	183	30					X	
Primitia canaliculata	*Levisulculus canaliculatus*	175	25		unknown				
Primitia elongata obliqua	*Levisulculus obliquus*	178	27		unknown				
Rectella carinaspinata	*Rectella carinaspinata*		62		X	X	X	X	X

Table 6. Measurements (in mm) of *Levisulculus obliquus*. Abbreviations: G, glacial erratic boulders; H, height (without sculptures protruding over the straight hinge line); Hm, maximal H; L, length; LD (HD), L (H) of the domicilium; LV, left valve; RV, right valve; tec, tecnomorph.

No. GG	G	Valve	Figs.	L	H	Hm	L:H	LD	HD	LD:HD
347-5a	G-287	♀RV	4A	1.20	0.70	0.71	1.70	1.00	0.54	1.86
278-1a	G-287	♀RV	3E, 7B	1.19	0.69	0.70	1.73	1.00	0.53	1.91
278-1c	G-287	tec LV	3H	1.00	0.60	0.61	1.66	0.90	0.47	1.94
278-1b	G-287	tec RV	3F	0.85	0.49	0.50	1.74	0.78	0.42	1.86
347-3a	G-287	tec RV	3G	1.05	0.67	= H	1.57	0.93	0.48	1.92
347-3b	G-287	tec LV	3I	1.00	0.63	= H	1.60	0.89	0.48	1.86

1954 *Primitia elongata obliqua* Steusloff, 1894 = ? *Platybolbina plana* (Krause, 1889); Henningsmoen 1954: 87, 89.

1957 *Platybolbina obliqua* (Steusloff, 1894); Jaanusson 1957: 260.

1967 *Levisulculus obliquus* (Steusloff, 1895); Schallreuter 1967: 616.

non 1979 *Levisulculus obliqua* (Ulrich, 1900) (Ctenobolbina); Ivanova 1979: 102 (= *Eurybolbina ulrichi*).

1986 *Levisulculus obliquus* (Steusloff, 1895); Schallreuter 1986: 16, pl. 1: 12.

?1992 *Swantina*? *levis* sp. n.; Sidaravičienė 1992: 243–244 (partim); pl. 36: 6.

1993 *Levisulculus* [*Primitia*] *canaliculatus* (St.); Schallreuter 1993: 17, table 2.

1999 *Levisulculus* cf. *obliquus* (Steusloff, 1895); Schallreuter et al. 1999: pl. 1: 2.

Type material: Lectotype: Left tecnomorphic valve embedded in rock GG 114-27, designated by Herrig and Nestler 1989: 23 (see Fig. 2E), figured by Steusloff 1895: pl. 58: 12. Catalogue of Herrig and Nestler 1989 no. 178 (not mentioned in the catalogue of Keyser and Schöning 1996). Paratypes: GG 114-26, GG 114-28, and GG 114-29, all right tecnomorphic valves (Fig. 2F–H).

Type locality: Neubrandenburg, Mecklenburg, ~53°35' N ~13°15' E, erratic boulder.

Type horizon: Geschiebe of "Borkholmer Kalk". From the yellow-white dense limestone boulder Steusloff (1895: 781–783) described four further species and mentioned three more (Table 5). Another species recovered from this boulder by Schallreuter (1972) is *Rectella carinaspinata* Schallreuter, 1972. Apart from ostracodes, the boulder yielded trilobites, brachiopods, and crinoid columnals.

Diagnosis (emended).—Length at least up to 1.20 mm (holotype without velum 1.16 mm). Shape mostly moderately high, domicilium mostly rather long. Posteriorly directed velar spine at the border between centroventral and posteroventral regions. Lateral surface irregularly pustulate.

Dimensions and proportions.—See Table 6.

Remarks.—Henningsmoen (1954: 87) considered *Primitia elongata obliqua* to be a possible synonym of *Platybolbina plana*. Accordingly, Jaanusson (1957: 260) did not include *P. obliqua* in his new genus *Levisulculus*.

Fig. 5. Oepikellid ostracods from Palaeozoic erratic boulders. **A–C**. *Ampletochilina trapezoidea* Schallreuter, 1969 from erratic boulder G-287. **A**. GG 347-11a, tecnomorphic right valve, L 1.36 mm; lateral (A_1) and ventral (A_2) views. **B**. GG 347-11b, tecnomorphc right valve, L 0.90 mm; lateral view. **C**. GG 347-12, female right valve, L 1.37 mm; oblique interior view. **D**. *Ampletochilina trapezoidea* Schallreuter, 1969 from erratic boulder 794. Holotype, GG 25-10, a, female right valve, L 1.61 mm; lateral (D_1) and ventral (D_2) views. **E–H**. *Swantina pseudobliqua* Schallreuter, 1986. **E**. Holotype, GG 400-3347, female left valve, L 1.14 mm; lateral (E_1) and ventral (E_2) views; erratic boulder Sy-207. **F**. GG 347-6, tecnomorphic left valve, L (domicilium) 0.86 mm; ventral view (lateral view: Fig. 4D); erratic boulder Sy-208. **G**. GG 347-10a, tecnomorphic right valve, L 0.99 mm; ventrolateral view, (lateral view: Fig. 6G); erratic boulder Sy-60. **H**. GG 347-13, female right valve, L 1.07 mm; lateral view; erratic boulder Sy-208. **I–L**. *Swantina swantia* (Schallreuter, 1969). **I**. GG 347-14, female left valve, L 1.23 mm; oblique ventral view; erratic boulder 1B1. **J**. GG 347-15, female right valve, L 1.10 mm; lateral view; erratic boulder 1B2. **K**. GG 347-16a, tecnomorphic right valve, L 1.10 mm; lateral (K_1) and ventral (K_2) views; erratic boulder 1B16. **L**. GG 347-16b, tecnomorphic left valve, L 1.02 mm; ventral view; erratic boulder 1B4. **M**. *Swantina serrata* Schallreuter, 1986 from erratic boulder Sy-208. GG 347-17, tecnomorphic left valve, L 1.04 mm; lateral (M_1) and ventral (M_2) views. Stereo-pairs, except of A_2, D_2, E_2, F, G, K_2, L, and M_2. Erratic boulders 1B1, 1B2, 1B4, and 1B16 of lower Upper Ordovician Backsteinkalk boulders of Swedish origin from the Isle of Hiddensee, Baltic Sea, all other erratic boulders are of upper Upper Ordovician Öjlemyr flint and came from the Isle of Gotland, Baltic Sea (G) and the Isle of Sylt, North Sea (Sy). Scale bars 0.3 mm. →

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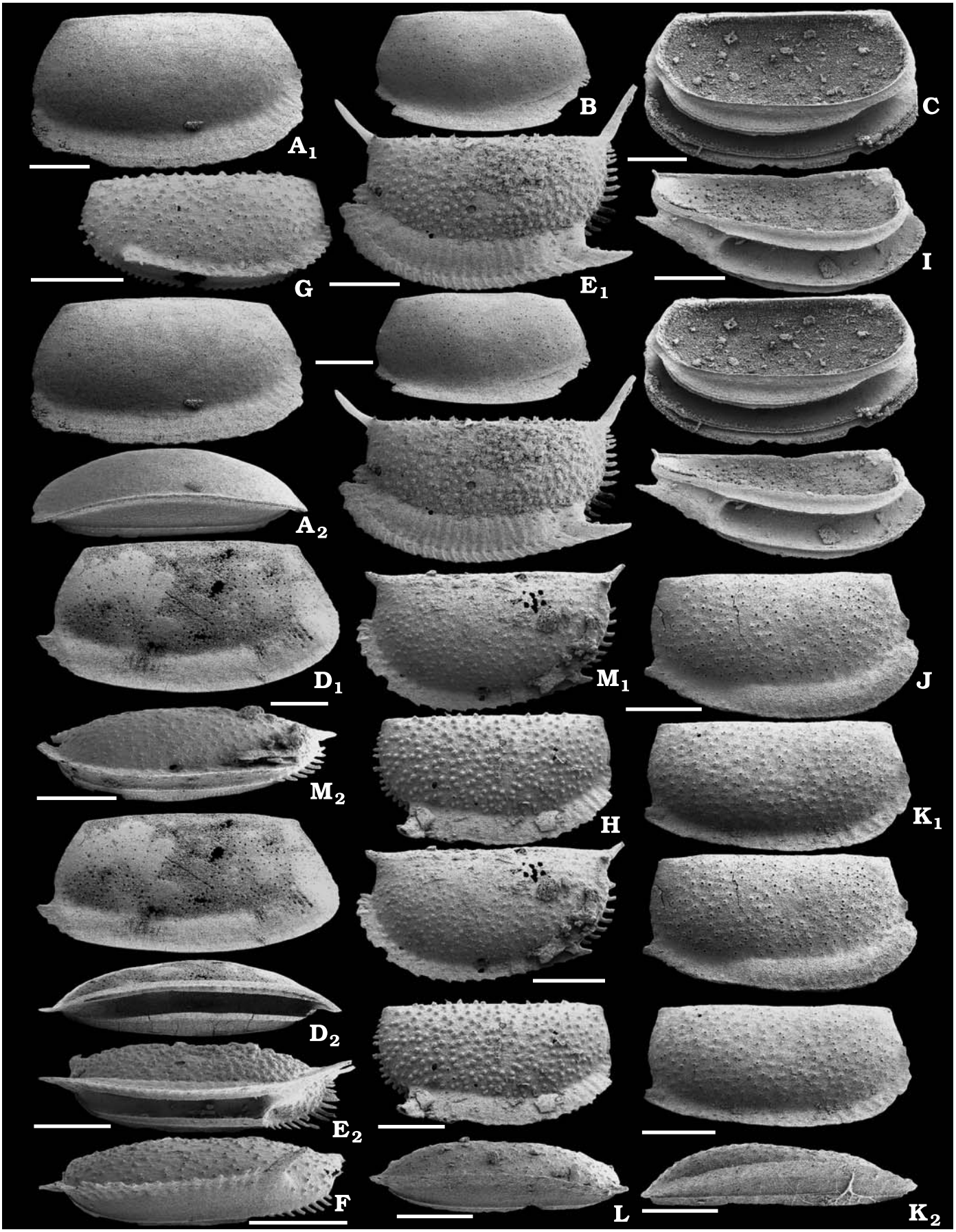

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The female valve from the Pirgu Stage (F1c) of Lithuania figured as *Swantina*? *levis* by Sidaravičienė (1992: pl. 36: 6) may belong to *Levisulculus obliquus*. However, the specimen is larger (1.40 mm) than the largest specimen of *L. obliquus* figured here (1.20 mm).

Primitia canaliculata Steusloff, 1895 (Fig. 2I) is based on an internal mould of a larval right valve. It co-occurs with the lectotype of *Primitia obliqua* and could be considered as a synonym of the latter species or as a nomen dubium.

Stratigraphic and geographic range.—Known only from glacial erratic boulders of Northern Germany and Sweden (Isle of Gotland). Öjlemyr flint erratic boulders of the Isle of Gotland, Baltic Sea (791 [6 specimens], 794 [2], G-287 [12]) and the Isle of Sylt, North Sea (Sy-60 [3], Sy-75 [1], Sy-115; Schallreuter 1986: pl. 1: 12).

Genus *Swantina* Schallreuter, 1986

Type species: *Ampletochilina swantia* Schallreuter, 1969, Isle of Hiddensee (Baltic Sea), erratic boulder of Backsteinkalk of younger Swedish type (age like Keila stage of Estonia, D2).

Species included.—*Swantina serrata* Schallreuter, 1986; *Swantina pseudobliqua* Schallreuter, 1986; *Swantina schallreuteri* Olempska, 1994; *Swantina crassiconvexa* sp. nov.

Diagnosis (emended).—Small to medium-sized. Outline amplete or preplete. Non-sulcate and non-lobate. Velar frill restricted. Dolon slightly convex or strongly convex centroventrally. Antrum open anteriorly, closed posteriorly. Marginal sculpture dimorphic, developed as row of spines and/or ridge. Lateral surface pustulate.

Remarks.—Sidaravičienė (1992: 142) cited Neben and Krueger (1973) as authors of the genus but in that paper the name is a nomen nudum (Schallreuter 1975: 160).

Swantina differs from *Levisulculus* mainly by the generally amplete outline and the antrum, which is weakly convex in all parts.

Ectoprimitia is distinct from *Swantina* mainly by presence of a dorsal plica and the antrum, which is more distinctly bordered anteriorly than posteriorly.

Stratigraphic and geographic range.—Upper Ordovician of Baltoscandia.

Swantina swantia (Schallreuter, 1975)

Fig. 5I–L.

1983 *Ampletochilina swantia* Schallreuter, 1969; Schallreuter 1983a: 169, 191, table 16, pl. 13: 4 (p. 169 further synonymy).

1986 *Swantina swantia* (Schallreuter, 1969); Schallreuter (1986): 9.

Holotype: Female left valve, GG 25-8 (Schallreuter 1969: fig. 1.1–2). Catalogue of Herrig and Nestler no. 37, catalogue of Keyser and Schöning 1996 no. 96.

Type locality: Beach of the Dornbusch, Isle of Hiddensee (Baltic Sea); erratic boulder.

Type horizon: Swedish Backsteinkalk (erratic boulder 1B16), age: like Skagen limestone, lower Upper Ordovician.

Material.—More than 70 valves (including 20 females).

Dimensions and proportions.—See Schallreuter (1969: 347, 1975: table 9).

Diagnosis (emended).—Females mostly between 1.00 and 1.20 mm long. Outline rounded to rectangular, amplete or subamplete. Cardinal angles only slightly exceed 90°. Domicilium weakly convex. Rounded muscle spot clearly in front of centre, mostly not very distinct and not depressed. Velar frill restricted, terminating in the posteroventral region with a short spine in line with the cardinal corner. Frill in tecnomorphs narrow, in females broader and slightly convex. Antrum terminating rather distinctly far in front of terminal velar spine at the border between centroventral and posteroventral regions. Marginal sculpture developed as ridge and dimorphic in being broader at the antrum. Antrum bordered at either side by special antral fences. Lateral surface pustulate.

Stratigraphic and geographic range.—See Schallreuter (1983a: 169).

Swantina crassiconvexa sp. nov.

Fig. 4B, C.

1973 *Levisulculus* sp. n.?; Neben and Krueger 1973: pl. 89: 4.

1975 *Levisulculus* sp. n.?; Schallreuter 1975: 158–159, pl. 4: 9–12, pl. 8: 12, 13.

1983 *Levisulculus* sp. n.? sensu Schallreuter (1975); Schallreuter 1983a: 169.

?1992 *Swantina* aff. *swantia* (Schallreuter, 1969); Sidaravičienė 1992: 142, 243, pl. 36: 3.

Etymology: After the ventrally strongly convex velum.

Holotype: Female left valve, GG 33-18 (Fig. 4C; Neben and Krueger 1973: pl. 89: 4; Schallreuter 1975: pl. 4: 9–11).

Type locality: Beach of the Dornbusch, the high-lands of the Isle of Hiddensee (Baltic Sea); glacial erratic boulder.

Type horizon: Swedish Backsteinkalk (erratic boulder 1B1), age: like Skagen limestone, lower Upper Ordovician.

Material.—See Schallreuter (1975: table 8).

Fig. 6. Oepikellid ostracods from Palaeozoic erratic boulders. **A**–**F**. *Swantina serrata* Schallreuter, 1986. **A**. GG 347-9b, female left valve, L 0.99 mm; lateral view; erratic boulder G-287. **B**. GG 347-9d, tecnomorphic right valve, L 0.85 mm; lateral view; erratic boulder Sy-2. **C**. GG 347-9f, female right valve, L 0.79 mm; lateral view; erratic boulder G-30. **D**. GG 347-9c, female right valve, L 1.00 mm; ventral view, erratic boulder G-30. **E**. GG 347-9e, tecnomorphic right valve, L 0.98 mm; lateral view; erratic boulder G-30. **F**. GG 347-9g, tecnomorphic left valve; lateral view; erratic boulder Sy-2. **G**–**L**. *Swantina pseudobliqua* Schallreuter, 1986. **G**. GG 347-10a, tecnomorphic right valve, L 0.99 mm; lateral view (ventrolateral view: Fig. 5G); erratic boulder Sy-60. **H**. GG-347-10c, female right valve, L 0.98 mm; lateral view; erratic boulder Sy-60. **I**. GG 347-10e, female left valve, L 1.05 mm; lateral view; erratic boulder 791. **J**. GG 347-10b, female left valve, L 1.00 mm; ventral view; erratic boulder Sy-60. **K**. GG 347-10d, tecnomorphic left valve, L 0.72 mm, lateral view; erratic boulder G-287. **L**. GG 347-10f, anteriorly incomplete young tecnomorphic left valve, L 0.66 mm; lateral view; erratic boulder Sy-2. Stereo-pairs. All erratic boulders are of the upper Upper Ordovician Öjlemyr flint and came from the Isle of Gotland, Baltic Sea (G) and the Isle of Sylt, North Sea (Sy). Scale bars 0.3 mm. →

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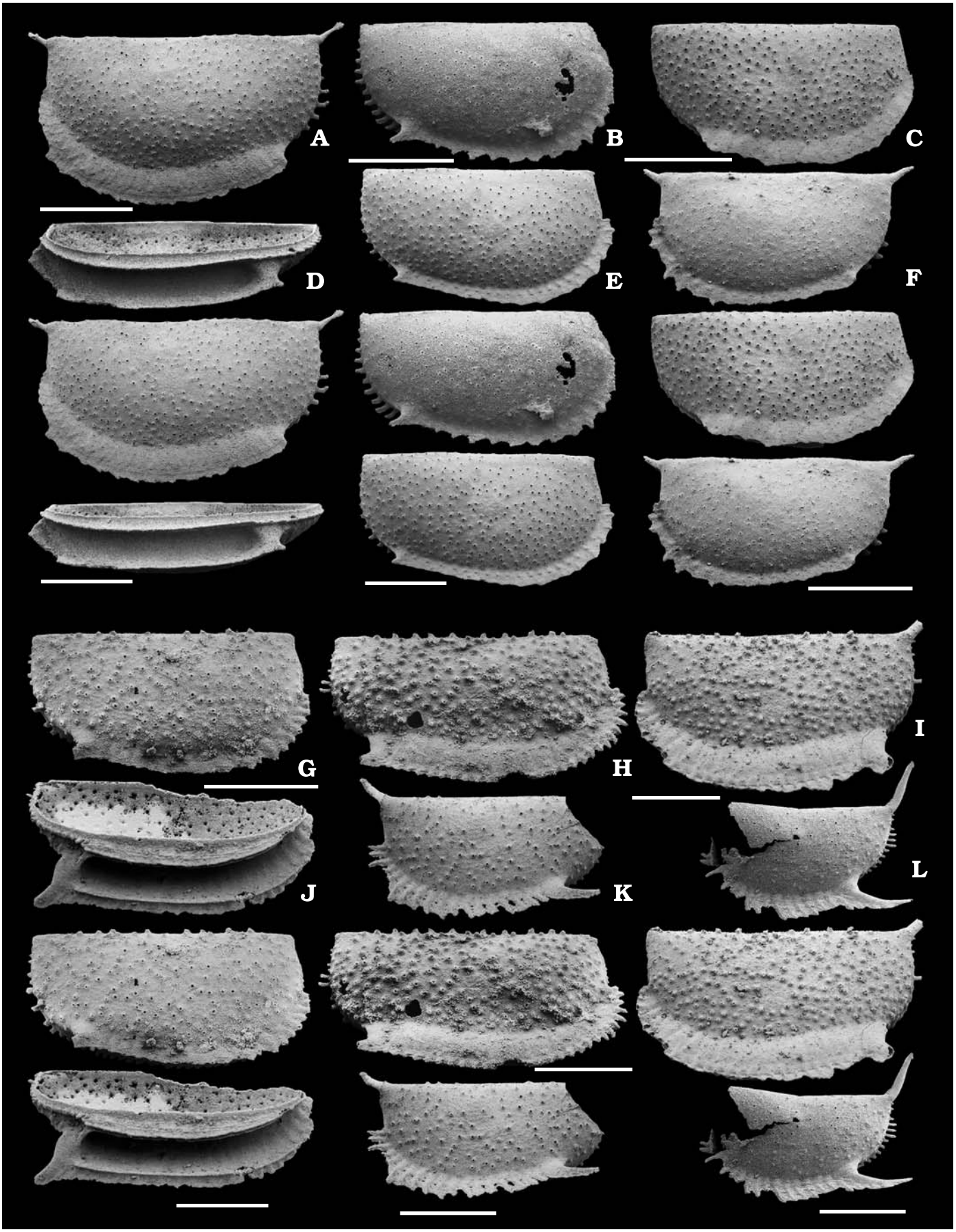

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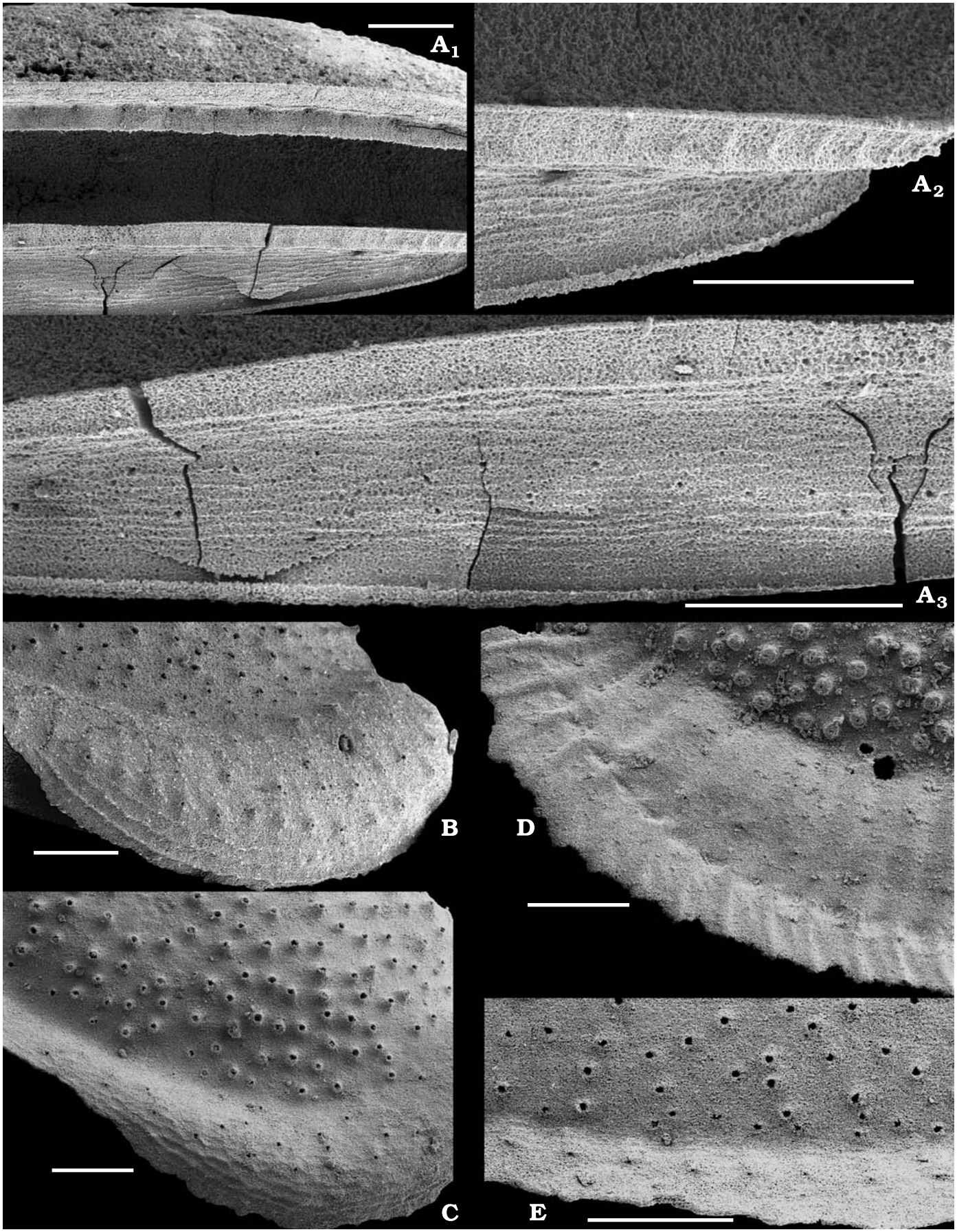

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Table 7. Measurements (in mm) of *Swantina pseudobliqua*. Abbreviations: G, glacial erratic boulders; H, height (without sculptures protruding over the straight hinge line); Hm, maximal H; L, length; LD (HD), L (H) of the domicilium; LV, left valve; RV, right valve; tec, tecnomorph.

No. GG	G	Valve	Figs.	L	H	Hm	L:H	LD	HD	LD:HD
347-10e	791	♀LV	5I	1.05	0.59	0.60	1.79	0.95	0.46	2.05
347-10b	Sy-60	♀LV	5J	1.00	0.55	0.56	1.82	0.93	0.43	2.18
347-10c	Sy-60	♀RV	5H	0.98	0.51	0.52	1.93	0.87	0.42	2.10
347-10a	Sy-60	tec RV	5G, 6G	0.99	0.52	0.52	1.89	0.74	0.37	1.99
347-10d	G-287	tec LV	5K	0.72	0.41	0.41	1.76	0.67	0.33	2.05
347-10f	Sy-2	tec LV	5L	0.66	0.38	0.38	1.75	0.59	0.29	2.00
347-6	Sy-208	tec LV	4D, 6F					(0.86)		
347-13	Sy-208	♀RV	6H	1.07						

Dimensions and proportions.—See Schallreuter (1975: table 8).

Diagnosis (emended).—Adults at least up to 1.17 mm. Outline distinctly preplete. Very short terminal velar spine in line with posterior cardinal corner. Dolon strongly convex centroventrally. Antrum terminating very distinctly in the posterior centroventral region.

Remarks.—This new species, which may co-occur with *S. swantia*, differs from the latter by its distinctly preplete outline and the velum, which is strongly convex centroventrally.

Swantina aff. *swantia* Sidaravičienė (1992: pl. 36: 3; L 1.1 mm) from the Johvi Stage of Lithuania may belong to the new species.

Stratigraphic and geographic range.—Until now, known only from erratic boulders of the younger Swedish Backsteinkalk (1B1 type; Skagen limestone, corresponds to the Keila Stage, D2, of Estonia; Männil 1990: 18), mid-Viru, lower Upper Ordovician (upper Sandbian/lower Katian).

Swantina pseudobliqua Schallreuter, 1986

Figs. 4D, 5E–H, 6G–L, 7D.

1986 *Swantina pseudobliqua* sp. n.; Schallreuter 1986: 9, 16 (1987: 209, 216), pl. 1: 11.

Holotype: Female left valve, GG 400-3347 (Schallreuter 1986: pl. 1: 11). Catalogue of Keyser and Schöning 1996 no. 3467.

Type locality: Former gravel pit near Braderup, Isle of Sylt, Germany; erratic boulder.

Type horizon: Öjlemyrflint (Braderup type), erratic boulder Sy-207. Pirgu (F1c) or Porkuni Stage, upper Upper Ordovician.

Material.—More than 100 valves, mostly larvae.

Dimensions and proportions.—See Table 7.

Diagnosis (emended).—Females 0.79–1.14 mm (holotype) long. Outline amplete or slightly preplete. Cardinal angles slightly exceeding 90°. Rounded muscle spot only a little below centre and not depressed. Velar frill restricted, extending from anterocentral to posteroventral region. Terminal velar spine distinct. Tubules of the velar frill densely set and may terminate as short spines. Tubules of the dolon bending abruptly in posterior direction in outer part of the frill. Marginal sculpture as a row of spines, at the antrum as a ridge which is broader than in the tecnomorphs. On both side of the antrum small toral ridges function as the antral fences. Lateral surface with densely set coarse pustulae.

Comparisons.—Tecnomorphs of *S. pseudobliqua* are very similar to tecnomorphs of the co-occurring *Levisulculus obliquus*. In general, *L. obliquus* is more distinctly preplete. Furthermore, the terminal velar spine is located within the velar flange and thus, slightly more anteriorly. However, in small tecnomorphs of *L. obliquus* the velar frill behind the spine may be developed weakly, or may even be missing, which makes its distintion from *S. pseudobliqua* problematic. Apart from that, the velar frill may sometimes terminate anteriorly in *L. obliquus* in a small spine (Schallreuter 1986: pl. 1: 12).

Stratigraphic and geographic range.—The species has been found in several Öjlemyr flint boulders from the Isle of Gotland, Baltic Sea (erratic boulders G-2 [9], 791 [4], G-287 [3]) and of the Isle of Sylt, North Sea (erratic boulders Sy-2 [18], Sy-56 [9], Sy-60 [68], Sy-75 [12], Sy-207 [33]).

Swantina serrata Schallreuter, 1986

Figs. 4E–G, 5M, 6A–F, 7E.

1986 *Swantina serrata* sp. n.; Schallreuter 1986: 9, 16 (1987: 209, 216), pl. 1: 10.

1992 *Swantina* cf. *serrata* Schallreuter, 1986; Sidaravičienė 1992: 144, 244, table 2, pl. 36: 9.

Type material: Holotype: female right valve, lost (Schallreuter 1986: pl. 1: 10). Catalogue of Keyser and Schöning 1996 no. 3468. Neotype (designated herein): female left valve GG 347-8 (Fig. 4F).

Type locality: Former gravel pit near Braderup, Isle of Sylt, Germany; erratic boulder.

← Fig. 7. Oepikellid ostracods from Palaeozoic erratic boulders. **A**. *Ampletochilina trapezoidea* Schallreuter, 1969. GG 25-10 (Fig. 6D), details of holotype female right valve, row of pores between border of dolon and inner antral fence (A_1), region between border of marginal flange and inner antral fence with short vertical pillars (A_2), and irregularly distributed pores between border of marginal flange and free margin (A_3). **B**. *Levisulculus obliquus* (Steusloff, 1895). GG 278-1a (Fig. 3E), detail of anterior part of the female right valve showing pustules of lateral surface and dolon. **C**. *Levisulculus extrarius* (Öpik, 1937). GG 347-1a (Fig. 3A), detail of anterior part of the female right valve, showing pustules of lateral surface and dolon. **D**. *Swantina pseudobliqua* Schallreuter, 1986. GG 400-3347 (Fig. 6E), detail of anteroventral part of holotype, a female left valve, with tubules of the frill bending abruptly in posterior direction at outermost part and few pores in outer half of frill. **E**. *Swantina serrata* Schallreuter, 1986. GG 347-9e (Fig. 5E), centroventral part of tecnomorphic right valve showing pustulae of lateral surface and row of pustules at velar frill. Scale bars 100 µm.

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Type horizon: Öjlemyrflint (Braderup type), erratic boulder Sy208; Pirgu (F1c) or Porkuni Stage, upper Upper Ordovician.

Material.—More than 100 valves, mostly larvae.

Dimensions and proportions.—See Table 8.

Diagnosis (emended).—Length at least up to 1.06 mm (holotype 1.00 mm, neotype 1.06 mm). Rounded muscle spot in centre, or slightly in front of centre. Velar frill of tecnomorphs distally often developed as a row of short, posteriorly declined spines which may appear serrated. Terminal velar spine short. Outer surface weakly pustulate.

Discussion.—*Swantina serrata* and *Swantina pseudobliqua*, which may co-occur, are very similar. *S. serrata* differs from *S. pseudobliqua* by the arrangement of the velar spines in tecnomorphs. The spines are less dense in *S. serrata* and are declined posteriorly. This is often more distinct in smaller tecnomorphs. The terminal velar spine is only weak in *S. serrata*. The granulation of the lateral surface is generally stronger in *S. pseudobliqua*.

Stratigraphic and geographic range.—Sidaravičienė (1992: pl. 36: 9) figured the species from the Vormsi stage (F1b) of Lithuania and mentioned the occurrence of the species also in the Rakvere (E), Nabala (F1a), and Pirgu Stages (F1c). The species has been found in several Öjlemyr flint boulders from the Isles of Gotland, Baltic Sea (erratic boulders G-2 [3 valves], G-30 [21], G-287 [1]) and of the Isle of Sylt, North Sea (erratic boulders Sy-2 [12], Sy-56 [3], Sy-60 [33], Sy-61 [4], Sy-75 [23], Sy-207 [26], Sy-208 [4]).

Genus *Ampletochilina* Schallreuter, 1969

Type species: *Ampletochilina trapezoidea* Schallreuter, 1969, Öjlemyrflint erratic boulder (upper Ordovician), Isle of Gotland (Baltic Sea).

Species included: ?*Platybolbina* ?*granifera* (Sarv, 1962) Schallreuter, 1969.

Diagnosis.—Medium-sized. Outline amplete. Cardinal angles distinctly >90°. Tubulate velar frill restricted, from anterocentral to posteroventral region, short posterior terminal spine. Weakly convex dolon, open at both ends, i.e., no distinct terminations. Marginal sculpture as ridge, dimorphic: broader in females at the antrum. Antrum bordered on both sides by faint ridge-like antral fences. Surface smooth, punctate.

Remarks.—*Ampletochilina ryghooftensis* Schallreuter, 1987 is assigned here to the genus *Levisulculus*, mainly because of the slightly preplete outline, the dolon being anteriorly more strongly convex than ventrally (but not as strong as in other species of the genus), and the antrum terminating posteriorly already in the centroventral region without abrupt termination (Schallreuter 1967: text-fig. 2.1).

Comparisons.—*Ampletochilina* differs from *Levisulculus* and *Swantina* by its amplete outline, larger cardinal angles, and the long antrum, which gradually terminates at both ends.

Stratigraphic and geographic range.—Late Upper Ordovician (Vormsi-Pirgu, ?Porkuni), Baltic region.

Ampletochilina trapezoidea Schallreuter, 1969

Figs. 5A–D, 7A.

1969 *Ampletochilina trapezoidea* gen. et sp. nov.; Schallreuter 1969: 347–348, fig. 2.

1984 *Ampletochilina trapezoidea* Schallreuter; Sarv and Meidla 1984: 12, table 2 (p. 9), 4 (p. 19).

1986 *Ampletochilina trapezoidea* Schallreuter, 1969; Schallreuter 1986: 16 (1987: 216), pl. 1: 7; 17 (1987: 217).

?1987 *Ampletochilina* cf. *trapezoidea* Schallreuter, 1969; Schallreuter 1987b: 19.

1990 *Ampletochilina trapezoidea* Schallreuter, 1969; Abushik in Abushik et al. 1990: 57, 232, pl. 6: 5 (= Schallreuter 1969: fig. 2.1)

non 1992 *Ampletochilina* aff. *trapezoidea* Schallreuter, 1969; Sidaravičienė 1992: 142, 243, fig. 3 (faunal log), table 2 (p. 214), pl. 36: 2.

?1993 *Ampletochilina* cf. *trapezoidea* Schallreuter, 1985; Schallreuter 1993: 46, 242, 243, pl. 47B: 1.

1996 *Ampletochilina trapezoidea* Schallreuter, 1969; Meidla 1996: 29, 30, table 9 (p. 203), figs. 24, 29 (cf.), 31–32, 34 (logs), pl. 3: 7.

?1996 *Ampletochilina* aff. *trapezoidea* Schallreuter, 1969; Sidaravičienė 1996: fig. 3 (log); table 11 (p. 36).

Holotype: Right female valve GG-25-10. Catalogue of Herrig and Nestler 1989 no. 38, catalogue of Keyser and Schöning 1996 no. 97 (Fig. 5D; Schallreuter 1969: text-fig. 2.1–2; Abushik in Abushik et al. 1990: pl. 6: 5 [= Schallreuter 1969: fig. 2.1]).

Type locality: Beach of Visby, Isle of Gotland.

Type horizon: Erratic boulder 794 (Inv. XII 1302).

Diagnosis.—Females mostly between 1.30 and 1.70 mm

Table 8. Measurements (in mm) of *Swantina serrata*. Abbreviations: G, glacial erratic boulders; H, height (without sculptures protruding over the straight hinge line); Hm, maximal H; L, length; LD (HD), L (H) of the domicilium; LV, left valve; RV, right valve; tec, tecnomorph.

No. GG	G	Valve	Figs.	L	H	Hm	L:H	LD	HD	LD:HD
347-9c	G-30	♀RV	5D	1.00	0.61	0.62	1.64	0.93	0.46	2.00
347-9b	G-287	♀LV	5A	0.99	0.60*	0.61*	1.65	0.91	0.45	1.99
347-9h	G-30	tec RV	–	0.98	0.56	0.57	1.76	0.95	0.46	2.05
347-9e	G-30	tec RV	5E, 7E	0.98	0.54	0.56*	1.81	0.90	0.45	2.00
347-9a	G-30	♀RV	4G	0.93	0.56	0.57	1.65	0.89	0.44	2.00
347-9d	Sy-2	tec RV	5B	0.85	0.47	0.48	1.83	0.80	0.40	2.01
347-9g	Sy-2	tec LV	5F	0.83	0.46	0.47	1.79	0.76	0.39	1.96
347-9f	G-30	♀RV	5C	0.79	0.45	0.45	1.78	0.76	0.38	2.00
347-7	Sy-208	tec RV	4E	0.67						
347-8 neot.	Sy-208	♀LV	4F	1.06						
347-17	Sy-208	tec LV	6M	1.04						

* inclusive of the velar spines

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long. Outline trapezoidal, amplete. Dorsal angles both distinctly exceeding 90°. Domicilium weakly convex. Muscle spot indistinct. Tecnomorphic velar frill rather broad, terminating spine-like posteriorly. Velar dolon open at both ends, terminating in the posteroventral region. Lateral surface with pores, otherwise smooth.

Comparison.—*Ampletochilina*? *granifera* (Sarv, 1962) differs from *A. trapezoidea* in being slightly larger (1.78 mm), and strongly pustulate (Fig. 4H; Sarv 1962: pl. 1: 4–7).

Stratigraphic and geographic range.—Estonia: Vormsi-Pirgu (Meidla 1996), Lithuania: ?Vormsi (Sidaravičienė 1992). Öjlemyr flint boulder of the Isle of Gotland (Baltic Sea) and the Isle of Sylt (North Sea).

Conclusions

Beyrichiocopes are characterised by either cruminal or antral dimorphism. While the development of a crumina has been unequivocally accepted as functioning in both egg and brood care, such direct evidence is missing for antral dimorphic taxa.

Based on loculate dimorphic species that display a special development of the antrum Henningsmoen (1965) drew the conclusion that certain antra played a role as egg shelters. However, this interpretation has not been applied to strongly convex antra, so-called false pouches, and also the question of brood care remained open.

Detailed investigations of special antral dimorphic taxa with regard to location and possible function of the so-called marginal pores suggest that brood care occurred in taxa with open antra but not in taxa with a false brood pouch. The different life styles of the respective taxa deduced from both carapace characters and regional distribution support this interpretation.

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