Sexual dimorphism and pore systems in Ordovician ostracodes

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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 Ampletochilina.

K e y w o r d s : Arthropoda, Crustacea, Ostracoda, Levisulculus, Swantina, Ampletochilina, erratic boulders, dimorphism, adventral radial pores, Ordovician, Baltoscandia.

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Received 13 May 2009, accepted 10 June 2010, available online 14 June 2010.

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 Šidaračiščė (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 silificed limestones comprise of originally cal
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 domicilium (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 palaeoceans, 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
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.

Orдовикіані палеокопи з іншою броуд пуцю безперечно мали більші проблеми з броуд каре ніж звичайний диморфізм таксі. Hessland (1949: 124, 126) не знайшов жодних труднощів в перетисненні яєць до антра всередині броуд пачу, оскільки вся процедура відбувалася в закритому карапасі. У диморфічних таксах карапас “… був від'єднаний, зокрема, від внутрішньої точки, коли другий закритий” (Hessland 1949: 126). Hessland (1949: 126) зазначив, що “Вона не має бути неможливо перекинута на яйця таких пачей завдяки яйцям, які мали б бути перенесені в трансфері”. Hessland (1949: 126–127) не відбував увагу в автентичному антра антра з броуд просторі, які несуть яйця в домікіліум. У диморфічних таксах яйця, які мали бути прилягати до стінок, Jaanusson (1957: 209) фактично включив у висновки, що “… ці риси не були всерез, що не можна зробити з броуд” але “… що верхній і нижній долони можуть бути перекриті яйцями” за допомогою стикання яйця “до стінка” з метою розчарування в місці зокрема, зокрема, від'єднаний.


Еспейсіаллі в Вордівічіані, види з фальшевим броуд-пуцем є рідкіші, ніж ті з відкритим антра. Тому, останній вид антра є рекомендується як оптимальний і, таким чином, більш успішний броуд камер. Levisulculus, Ampletochilina, і Swantina є генераторами з високо розвиненими відкритими антра і тому особливо цікаві в цьому відношенні. Вони дуже схожі в загальній морфології, але відрізняються в своїх антральних будівлях.

**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 of the 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 equivalent but the left valve overlaps the right valve at the contact margin.

The outline is amplete or preplete. The cardinal horns are approximately rectangular to distinctly blunt. Often, the cardinal horns of the left valve carry acroidal spines (Figs. 1A, 3C, D1, H4, F2, 5E, M1, 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 recognizable from the inner surface view of the respective valves (e.g., Fig. 4A).

**Table 1. Conventional definition of size classes.**

<table>
<thead>
<tr>
<th>Size (mm)</th>
<th>Denotation</th>
</tr>
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<tbody>
<tr>
<td>&gt;20,0</td>
<td>gigantic</td>
</tr>
<tr>
<td>5,0–20,0</td>
<td>very large</td>
</tr>
<tr>
<td>2,0–5,0</td>
<td>large</td>
</tr>
<tr>
<td>1,0–2,0</td>
<td>medium-sized</td>
</tr>
<tr>
<td>0,5–1,0</td>
<td>small</td>
</tr>
<tr>
<td>&lt;0,5</td>
<td>very small</td>
</tr>
</tbody>
</table>

**Table 2. Conventional definition of shape types**

<table>
<thead>
<tr>
<th>L:H</th>
<th>Denotation</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;1,25</td>
<td>extremely high</td>
</tr>
<tr>
<td>1,25–1,45</td>
<td>very high</td>
</tr>
<tr>
<td>1,45–1,55</td>
<td>high</td>
</tr>
<tr>
<td>1,55–1,65</td>
<td>rather high</td>
</tr>
<tr>
<td>1,65–1,75</td>
<td>moderately high</td>
</tr>
<tr>
<td>1,75–1,85</td>
<td>moderately long</td>
</tr>
<tr>
<td>1,85–1,95</td>
<td>rather long</td>
</tr>
<tr>
<td>1,95–2,05</td>
<td>long</td>
</tr>
<tr>
<td>&gt;2,05</td>
<td>very long</td>
</tr>
</tbody>
</table>

*doi:10.4202/app.2009.0056*
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. posteroventrobilobatus*. 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. 4C). In *Swantina crassicosta* 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).

Very faint ridges occur at the adventral sculptures, the outer part of the dolon (Fig. 7B, C), and the marginal flange (Fig. 7A). 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).

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), except for the densely set normal pores (Fig. 5B, D). However, in most cases the pores are developed as pustules resulting in a more or less tuberculate outer surface (Figs. 5E, H, J, K, 6).

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**Table 3.** Main morphological differences between the genera discussed.

<table>
<thead>
<tr>
<th>Features</th>
<th><em>Levisulculus</em></th>
<th><em>Swantina</em></th>
<th><em>Ampletochilina</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>outline</td>
<td>preplete</td>
<td>amplete</td>
<td>amplete</td>
</tr>
<tr>
<td>cardinal angles</td>
<td>slightly $&gt;90^\circ$</td>
<td>$~90^\circ$</td>
<td>obtuse</td>
</tr>
<tr>
<td>dolon</td>
<td>present antero- to centroventrally, anteriorly strongly convex</td>
<td>present antero- to centroventrally, weakly convex</td>
<td>present antero- to posteroventrally, weakly convex</td>
</tr>
<tr>
<td>antrum</td>
<td>anteriorly closed</td>
<td>posteriorly closed, with separate antral fences</td>
<td>open at both ends, with separate antral fences</td>
</tr>
<tr>
<td>surface</td>
<td>pustulate</td>
<td>pustulate</td>
<td>smooth, with pores</td>
</tr>
</tbody>
</table>

[Fig. 1. Morphological terminology explained in *Swantina pseudobilobucha.*]
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: 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 Bobbina; 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) Miehkkella 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 Miehkkella 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 Miehkkella 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 concrescence zone, and their marginal pores are devel-
opposed 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., Olenska 2008: 719). This may be the case for the irregularly distributed pores between marginal ridge and free margin (Fig. 7A₂). However, the linearly arranged pores between the marginal border of the dolon and the outer antral fence in heteromorphs (Fig. 7A₁) 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 crumae in 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 (*Foramellina, 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 antrum 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 anterioventral 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
= Platybolbiniinae 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,
1895; Primitia canaliculata Steusloff, 1895 (= Levisulculus obliquus); Primitia? extraria Öpik, 1937; Primitia troedssoni Thorslund, 1940 (= Levisulculus extrarius); Levisulculus michiganensis Kesling, 1960; Ampletochilina ryghofoftensis 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 ryghohofoftensis (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 preadductor 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

Fig. 2. Oepikellid ostracods from Palaeozoic erratic boulders. A. Holotype of the type species of the eopikellid ostracod Levisulculus, Levisulculus lineatus Jaanusson, 1957 (UM T89), female left valve, length (L) 0.89 mm. B. Holotype of Primitia extraria Opik, 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, Opik 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.
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 Syltis 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 preaductorial 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 L. fragilis characterised by the distinct preadductorial node. But this agrees with tecnomorphic paratype figured by Kanygin (1971: pl. 4: 6) Kanygin, 1971, Ivanova (1979: 105) established the genus Bulbosulculus. As expressed by the name the genus should be characterised by the distinct preaductorial 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 L. fragilis characterised by the distinct preadductorial node. But this agrees with tecnomorphic paratype figured by Kanygin (1971: pl. 4: 6) Kanygin, 1971, Ivanova (1979: 105) established the genus Bulbosulculus. As expressed by the name the genus should be characterised by the distinct preaductorial 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 L. fragilis characterised by the distinct preadductorial node. But this agrees with tecnomorphic paratype figured by Kanygin (1971: pl. 4: 6)

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) Őpik, 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 relevant 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 obliqua, 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 posterovertrorbobatus 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. posterovertrorbobata 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.
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.

<table>
<thead>
<tr>
<th>No. GG</th>
<th>G</th>
<th>Valve</th>
<th>Figs.</th>
<th>L</th>
<th>H</th>
<th>Hm</th>
<th>L:H</th>
<th>LD</th>
<th>HD</th>
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<td>0.49</td>
<td>0.24</td>
<td>2.04</td>
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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 *Eurybolina* 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.


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.


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


**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 (C2č), Leader 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 posterointerial and posterocentral regions. Lateral surface pustulate.

**Dimensions and proportions.**—See Table 4.

**Discussion.**—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 appears 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. Tvärmen: Erratic boulder of lower Chasmosa 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.
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, Parnawa Stage; o.c., opus citatus.

<table>
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<tr>
<th>Species mentioned or described by Steusloff (1895) and further species</th>
<th>Revised name</th>
<th>Catalogue of Herrig and Nestler (1989)</th>
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<th>fig.</th>
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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.

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<th>H ( tec )</th>
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1954 _Primitia elongata obliqua_ Steusloff, 1894 = ? _Platybolbina plana_ (Krause, 1889); Henningse 1954: 87, 89.
1957 _Platybolbina obliqua_ (Steusloff, 1894); Jaanusson 1957: 260.
1967 _Levisulculus obliquus_ (Steusloff, 1895); Schallreuter 1967: 616. non 1979 _Levisulculus obliquus_ (Ullrich, 1900) (Ctenobolbina); Ivanova 1979: 102 (Eurybolbina alirchi).
1986 _Levisulculus obliquus_ (Steusloff, 1895); Schallreuter 1986: 16, pl. 1: 12.
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).

1954 _Primitia elongata obliqua_ Steusloff, 1894 = _Platybolbina plana_ (Krause, 1889); Henningse 1954: 87, 89.
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1986 _Levisulculus obliquus_ (Steusloff, 1895); Schallreuter 1986: 16, pl. 1: 12.

_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).

Fig. 5. Oepikellid ostracods from Palaeozoic erratic boulders. A–C. _Amplectophilina trapezoidea_ Schallreuter, 1969 from erratic boulder G-287. A. GG 347-11a, tecnomorphic right valve, L 1.36 mm; lateral (A1) and ventral (A2) views. B. GG 347-11b, tecnomorphic right valve, L 0.90 mm; lateral view. C. GG 347-12, female right valve, L 1.37 mm; oblique interior view. D. _Amplectophilina trapezoidea_ Schallreuter, 1969 from erratic boulder 794. Holotype, GG 25-10, a. female right valve, L 1.61 mm; lateral (D1) and ventral (D2) views. E–H. _Swantina pseudobliqua_ Schallreuter, 1969. E. Holotype, GG 400-3347, female left valve, L 1.14 mm; lateral (E1) and ventral (E2) 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 swantina_ (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 (K1) and ventral (K2) 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 (M1) and ventral (M2) views. Stereo-pairs, except of A2, D2, E2, F, G, K, L and M2. 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 Öljemyr flint and came from the Isle of Gotland, Baltic Sea (G) and the Isle of Sylt, North Sea (Sy). Scale bars 0.3 mm.
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* Steußloff, 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 glacitectonic boulders of Northern Germany and Sweden and the Isle of Sylt, North Sea (Sy; 60 [3], Sy-75 [1], Sy-115; Gotland, Baltic Sea (791 [6 specimens], 794 [2], G−287 [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.


**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 or subamplete 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.


*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).


**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°. Domi-cilium weakly convex. Rounded muscle spot clearly in front of centre, mostly not very distinct and not depressed. Velar frill restricted, terminating in the posteroverentral 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 posteroverentral 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 pubescent.

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

*Swantina crassiconvexa* sp. nov.

Fig. 4B, C.


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.


*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).
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. S. swantia aff. S. swantia Sídaravičienė (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 (IB1 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.


Type horizon: Koševan flint (Braderup type), erratic boulder Sy−208 (Fig. 3E), detail of anterior part of the female left valve showing pustules of lateral surface and dolon.

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 posteroverentral 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 pustules.

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 distinction 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.


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

Fig. 7. Oepikellid ostracods from Palaeozoic erratic boulders. A. Amplectochilina trapezoida Schallreuter, 1969. GG 25-10 (Fig. 6D), details of holotype female right valve, row of pores between border of dolon and inner antral fence (A1), region between border of marginal flange and inner antral fence with short vertical pillars (A2), and irregularly distributed pores between border of marginal flange and free margin (A3). 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 (Opik, 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 anteroverentral 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.
**Type horizon:** Öjlemyr flint (Braderup type), erratic boulder Sy-208; 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 Estonia and mentioned the occurrence of the species also in the Rakvere (E), Nabala (F1a), and Pirgu Stages (F1c).

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

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**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.

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* inclusive of the velar spines

Comparison.—Ampletochilina? granifera (Sarv, 1962) differs from A. trapezoidea in being slightly larger (1.78 mm), and strongly pubescent (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

Beyrichiopes are characterised by either crinial 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.

Acknowledgements

We are greatly indebted to Mark Williams (University of Leicester, Leicester, UK), Ewa Olempska (Instytut Paleobiologii PAN, Warsaw, Poland), and an anonymous reviewer for their constructive comments which helped to improve the manuscript as well as for language corrections by Mark Williams and Paul D. Taylor (Natural History Museum, London, UK).

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