The Ordovician ostracodes established by Aurel Krause, Part I

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Abstract
The lack of a revision of the ostracodes described by Aurel Krause at the end of the 19th century from glacial erratic boulders from Berlin and the Mark Brandenburg (Northern Germany) has led to taxonomic confusion in the corresponding literature of the 20th century. To attain stability in names, some of Krause's ostracode species have been revised based on the types stored in the Museum für Naturkunde Berlin, namely Primitia plana, P. plana tuberculata, P. intermedia, P. globifera, Entomis sigma antiquata, Bollia v-scripta, B. granulosa, B. duplex, Strepula lineata, Isochilina canaliculata, Beyrichia dissecta, B. mamillosa, B. signata, and B. bidens. Most species have up to four younger synonyms among species described later from outcrops or borings in Baltoscandia or glacial erratic boulders of Northern Germany and Sweden. Three of Krause's species, which have been considered as nomina dubia by Jaanusson are in fact valid species. Some of Krause's species or of their synonyms are type species.

Introduction
Systematic descriptions of Ordovician ostracodes from Baltoscandia have been started by the end of the 19th century with Aurel Krause. Between 1889 and 1897 he described in several papers new ostracodes from glacial erratic boulders from Berlin and the Mark Brandenburg. Before him, only few ostracode species were sporadically established by Eichwald (1854, 1860), F. Schmidt (1858), Bock (1867), Linnarsson (1869), and Brögger (1882). Apart from Bonnema's (1909) and Öpik's (1937) monographs on the ostracodes of the Uhaku and Kukruse stages of Estonia and few other but small papers, the main investigations on Ordovician ostracodes from Baltoscandia took place not before the end of the war (Henningsmoen 1948, 1953a, 1954a, 1954b; Neckaja 1952, 1953, 1958, 1966, 1973; Stumbur 1956; Jaanusson 1957, 1966; Sarv 1959, 1962, 1963; Thorslund 1940, 1948). However, these papers clearly document the utmost necessity of a modern revision of the ostracodes described by Krause at the end of the 19th century.

It has been generally assumed that the types of the species described by Krause formerly belonging to the Geologisch-Paläontologisches Museum of the Friedrich Wilhelm-Universität Berlin were lost during the war (Jaanusson 1962, 412). However, in 1958 the material was returned from the former Soviet Union to Berlin and has been housed in the Paläontologisches Museum der Humboldt Universität (Diebel 1960), now Museum für Naturkunde Berlin.

Enabled by a loan of Krause’s types to Uppsala, Valdaar Jaanusson started a revision of Krause’s Ordovician ostracodes at the beginning of the sixties. In 1962 Jaanusson published a short note on these ostracodes in which he cited nine species with their younger synonyms described later from outcrops or borings in Baltoscandia or glacial erratic boulders of Northern Germany and Sweden. Three of Krause’s species, which have been considered as nomina dubia by Jaanusson are in fact valid species. Some of Krause’s species or of their synonyms are type species.

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<table>
<thead>
<tr>
<th>Krause’s species</th>
<th>year</th>
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<th>actual combination</th>
<th>synonyms (*no more, see Table 2)</th>
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<td>Hesperidella g.</td>
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Material

Krause’s material came from glacial erratic boulders of both Berlin region and Mark Brandenburg. Most of the samples were collected in the former sand and gravel pits near Müggelheim at the Müggel Isle (Berlin) (Krause 1889: 22). They came from different glacial erratic boulders which Krause (1889: 24) called “Untersilurischer Beyrichienkalk” (Ordovician Limestone) – an unsuitable name because the term refers to many types of Middle and Upper Ordovician limestone glacial erratic boulders of Baltoscandia (Kummerow 1924: 409; Schallreuter 1993: 13–14). A second group of ostracode-bearing glacial erratic boulders Krause (1892: 399) called “Geschiebe mit Beyrichia rostrata” (glacial erratic boulders with Sigmoopsis rostrata). From this group he described a complete ostracode fauna so that this type is better characterized faunistically. This fauna was found several years ago in a boulder from Münsterland which allowed its revision (Schallreuter 1985). However, for political reasons the types had not been available for the author at that time.

Most of the species revised here came from different boulders (Tab. 2). Only three of these species originate from one boulder (no. 670) of the so-called “rostrata” type group. Stratigraphically, the boulder was referred to as the Keila Stage (D2) (Schallreuter 1976: 164). Later, the group to which this boulder belongs was called “Harpakalk” (Schallreuter 1985: 101). It is assumed to originate from the northern Middle Baltic Sea (Schallreuter 1985: 102). The age of the other glacial erratic boulders could be gained from the stratigraphical occurrences of the synonyms of the respective species.

Many of the figured specimens of Krause’s ostracodes were stored in small glass tubes together with a small label inside the tube. The tubes were kept together with some labels in open boxes.

Some of the ostracodes were glued on the cork of the tube. This fact combined with the coating with MgO for previous photography badly affected the respective specimens.

The oldest labels seem to be those inside the glass tubes. However, they could not be from Krause himself, because such tubes and labels are used also for few of Kummerow’s (1924) species in the museum’s collection. The label without an institutional assignment (only: Inv. Geol. S.) were probably labels of the former Märitsches Museum or Geologisches Landesmuseum Berlin. The 3rd labels are from the “Geol.-Pal/C229ont. Mus. Berlin”. Many types have a 4th label from Jaanusson (1962); [2] p. 29 [3] p. 329 [4] p. 89 [5] p. 104. If not stated otherwise the glacial erratic boulders with the types of Krause’s species came from the type locality, the former gravel/sand pits near Müggelheim on Müggel Isle (Berlin), 52°25’ N, 31°19’ E.

Paleontological dating of glacial erratic boulders is generally only possible if their fossil content is also known from Baltoscandian out-

<table>
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<tr>
<th>Krause’s species</th>
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<th>synonyms (*valid as subspecies)</th>
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<td><em>Oepikium antiquatum</em></td>
<td><em>Streplula lineata Steusloff, 1895</em>&lt;br&gt;<em>Uthakiella granulosa Ulrich &amp; Bassler, 1908</em>&lt;br&gt;<em>Uthakiella coelodesma O.</em>&lt;br&gt;<em>Bilobatia serralobata Schallreuter, 1976</em>&lt;br&gt;<em>Bilobatia bidens</em></td>
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**Oepikella canaliculata** (Krause, 1892)

Figure 1A

1892 Isochilina canaliculata Krause: 385, 399, pl. 21, figs 1a–b. non 1897 Isochilina cf. canaliculata. – Krause: 932, 938, pl. 25, fig. 15 (= Tvaerenella ? sp.).

1934 Aparichites canaliculatus. – Bassler & Kellett: 55, 157, 338.

1937 Macronotellina bonnemai Öpik: 5, 23, 60, 69, 87, 124, pl. 1, figs 7–8.


1940 Öpikella canaliculata. – Thorslund: 181, 182.

1940 Öpikella bonnemai. – Thorslund: 181.

1940 Öpikella asklundi Thorslund: 182, pl. 1, figs 3–5.

1957 Oepikella tvaerensis. – Jaanusson: 270, 271–275, tabs 11, 40, figs 8, 19–20, pl. 4, figs 9–19, pl. 13, figs 1–13 (syn.).

1959 Oepikella bonnemai. – Serv: 15–16, tab. 2, pl. 2, figs 12–13 (= Öpik 1937, pl. 1, figs 7a–b).

1979 Öpikella bonnemai. – Ivanova: 73, 187, pl. 5, fig. 3.

1985 Oepikella canaliculata. – Schallreuter: 102, 134, tab. 1, pl. 3, fig. 5, pl. 8, fig. 1.


1990 Oepikella tvaerensis. – Ivanova in Abushik et al.: 56, 232, pl. 6, fig. 2.

1990 Oepikella? canaliculata. – Hints et al. in Ari et al.: 138, fig. 30 (cf.: faunal log).

Lectotype (designated here). Juvenile left tecnomorphic valve, MB. HS 2010-9, Figure 1A, Krause 1892, pl. 21, fig. 1.

**Type locality and horizon**. Müggehaim; Krause’s glacial erratic boulder no. 670, age Keila (D2).

**Dimensions**. Lectotype L 1.98 mm, H 1.32 mm. The largest specimen measured by Jaanusson (1957, tab. 11) reaches 3.61 mm, i.e. the lectotype is not adult.

**Definition**. At least up to 3.61 mm length. Posterior cardinal angle distinctly > 90°. Cardinal corners separated from lateral surface by short bulge-like swellings in prolongation of the more indistinct tecnomorphic bulge-like velum. Dolon extending from antero-central region to centro-ventral region. Outer shell surface finely punctate.

**Comparisons**. According to Jaanusson (1957: 275) Oepikella bonnemai Öpik, 1937 differs from the type species only by the ornamentation (“widely punctate”, Öpik 1937: 87 or 23). Also for O. tvaerensis Jaanusson (1957: 272, fig. 20a) mentioned “scattered pits”, and Öpik 1940, pl. 3, figs 4a–b and Jaanusson 1957, pl. 13, figs 11–13). Tvaerenella stossmeisteri is therefore considered here also as a synonym of the associated O. canaliculata (Schallreuter 1985, pl. 3, figs 4–5).

**Oepikella luminosa** Sarv, 1959 (Oandu to Porkuni stages, holotype from Pirgu stage; Meidla 1996: 21) is smaller (< 1.62–2.00 mm; Sarv 1959: 17; Sidaraviciene 1992: 244) but has a longer dolon and may be distinctly reticulate (compare Jaanusson 1957, pl. 13, figs 1, 9 and Sarv 1959, pl. 2, fig. 14; see also Sidara-
vičienė 1992, pl. 36, fig. 10). According to Sarv (1959: 17), only the anterior of the bulge-like swellings (“diagonal lobes”) of the cardinal corners is developed. The posterior end of the valve is less convex.

Oepikella ? alta Schallreuter, 1984 reaches only 1.25 mm and has a long dolon extending from the anteroventral region to the posterocentral region (Schallreuter 1984a, fig. 1.1). Tectomorphic valves of that species are unknown (designation therefore only with “?”).

Remarks. Since O. canaliculata is the most common ostracode species in the glacial erratic boulder (age: D2) described by Krause (1892: 385), Andersson (1893: 125) called this association “Isochilina canaliculata-Fauna” and considered it (Andersson 1893: 219) as an equivalent of the Chasmops macrourus zone (Keila stage, ? Oandu stage) of Öland. In the boulders of the Tvären area (age: Kuukruse to J/C192hvi stages, C2), Ludibundus, Rixdorf, Mark Brandenburg (now part of Germany), museum-fossilrecord.wiley-vch.de

Family Oepikiidae Jaanusson, 1957

Oepikium Agnew, 1942


Type species. Bisflabellum tenerum Öipik, 1935; by original designa-

tion.

Definition. Schallreuter 1975: 175.

Oepikium antiquatum (Krause, 1889)

Figure 1B

1889 Entomis sigma var. – Krause: 13, 23, pl. 1, fig. 13.
1891 Entomis sigma v. antiquata Krause: 309, 518.
? 1992 Oepikium sp. – Sidaravičienė: 151, 244, tab. 2, pl. 38, fig. 2.
? 1993 Vittella ? aff. antiquata. – Schallreuter: 36, 244, pl. 48b, fig. 1.

Holotype (monotypy). Right valve, frill posteroventrally incomplete, MB. HS 2010-10, Figure 1B, Krause 1889, pl. 1, fig. 13.

Type locality and horizon. Rixdorf, Mark Brandenburg (now part of Germany), Ordovician.

Dimensions. Holotype: L with frill anteriorly but without posterior spines 2.32 mm, H with frill 1.45 mm.

Definition. At least up to 2.32 mm. Long sigmoidal S2, being deep also in its ventral part, lobes strongest in ventral part, top of posteroventral lobe node- or spine-like, ventral ends of lobes connected by an indistinct ridge.

Remarks. The top of the posteroventral lobe is broken away so that it is unclear whether it terminates in a node or spine (Stachel = lobal spine). Velar flange broad and plane, radially striated and with very fine ridges parallel to the border.

Comparisons. O. antiquatum differs from all other Baltoscandian species of the genus O [flabelliferum (Krause, 1892) = Bisflabellum reticulatum Öipik, 1937 = B. crista Öipik, 1937; O. tenerum (Öipik, 1935), O. porkuniensis Henningsmoen, 1954, O. novum Sarv, 1959] mainly by the more distinct S2 and the ventrally stronger developed lobes (Öipik 1937, pl. 5, figs 1–8; Schallreuter 1975, pl. 8, figs 2–3; Schallreuter 1993, pl. 61b, fig. 4; Schallreuter & Hinz-Schallreuter 2007, fig. 4).

Oepikium sp. A Jaanusson, 1957 from the South Bothnian glacial erratic boulder Erken no. 10 (Crassicu-dâu limestone = Uhaku stage, C1c) has a similar S2 but differs also by the ventrally weaker lobes (Jaanusson 1957, pl. 14, fig. 5). The specimen figured by Jaanusson is smaller (L 1.79 mm) and probably a female. The sausage-shaped elevation of the frill (Jaanusson 1957: 408) seems to be an antrum restricted to the inner part of the frill because it has the width of the presumed diameter of the eggs stored in similar constructions of other species and genera (O. tenerum, Öipik 1937, pl. 5, fig. 2; Tallinmellina divelata, Sarv 1963, pl. 2, figs 4–5; Snaitlād radians, Schallreuter 1976, pl. 8, figs 4–5; Femerensia gealbertii, Schallreuter 1983c, pl. 94, fig. 2).

Occurrence. Despite its large size (L 2.32 mm) the species has not been found in Baltoscandian outcrops. Sidaravičienė (1992, pl. 38, fig. 2) figured an incomplete and compressed specimen of Oepikium from the Lasnamägi stage (C1b) of Lithuania (L 1.65 mm without velar frill), which may be conspecific to O. antiquatum.

The incomplete left valve figured by Schallreuter (1993, pl. 48b, fig. 1; L 2.34 mm) may also belong to that species. Unfortunately the portion ventral to the center of S2 is broken away. The boulder has been referred to the middle and upper Kunda stage (B3[δ–γ]).
Despite the differences between Bromidella and Uhakiella some Baltoscandian authors have not agreed with the assignment of B. sarvi and related species to Bromidella and still consider them as species of Uhakiella (Gailit 1973; Jaanusson 1976; Sidaravičienė 1992). Nevertheless, Sidaravičienė (1996: 55, fig. 13) noted that these species represent at least a separate branch within Uhakiella. Therefore, we consider it as a possible new genus or subgenus of Uhakiella.

**Uhakiella granulosa** (Krause, 1889)

Figure 1F


1908 *Beyrichia granulifera* Ulrich & Bassler: 285, 294, 328, fig. 32, pl. 38, fig. 7 (after Krause 1889, pl. 2, fig. 2).

19909 *Bollia granulosa*. – Bonnema: 63–65, 78, 84, pl. 4, figs 12–18 (= *Uhakiella kohtlensis* Ōpik, 1937: 108 or 44).


1941 *Bromidella granulosa*. – Schmidt: 33, 80.


1988b *Uhakiella granulosa*. – Schallreuter: 41, fig. 2.2.


**Lectotype** (designated by Ōpik 1937: 106 or 42). Right δ valve, MB. HS 2010–12 – Figure 1F: Krause 1889, pl. 2, fig. 2; Ulrich & Bassler 1908, fig. 32, pl. 38, fig. 7; Schallreuter 1988b, fig. 2.2.

**Type locality and horizon.** Müggehelm (Berlin), Krause’s glacial erratic boulder no. 339, age Viruan.

**Dimensions** (L – H in mm – L : H). Lectotype 2.08 – 1.30 – 1.60. Sidaravičienė 1992, pl. 22, fig. 10 (left δ valve, C3) 2.65 – 1.75 – 1.51, pl. 23, fig. 1 (left δ valve, C2) 2.55 – 1.65 – 1.55, pl. 23, fig. 2 (left δ valve, C3) 2.45 – 1.60 – 1.53.

**Definition.** Adults 2.08–2.65 mm. S2 as a distinct relatively broad pit, PAN weak, ± distinct zygal crista, dorsal plica and ventral bulge, tecnomorphic velum as an indistinct narrow bulge, in δ centroventrally reduced, with closed false brood pouch in the anteroventral region. Surface of domicilium and antrum with closely set spines.

**Comparisons.** *U. granulosa* resembles very much *U. coelodesma* which differs mainly by the weaker plica (compare Figure 1F and Ōpik 1937, pl. 3, figs 1, 3; Sarv 1959, pl. 4, figs 6–7; Sztejn 1985, pl. 1, fig. 5; and Sidaravičienė 1992, pl. 22, fig. 10, pl. 23 figs 1–2).

In *U. jaanussoni* (especially in the nominate subspecies) the ornamental features are even weaker than in *U. granulosa*, so that there is no furrow between the lateral surfaces of domicilium and brood pouch (Schallreuter 1973, pl. 19, fig. 3; Sidaravičienė 1992, pl. 23, fig. 3). In the younger (Skagen, Keila stage) *U. jaanussoni skageni* ornamentation is more distinct.

A common feature of *U. granulosa*, *U. coelodesma*, and *U. jaanussoni* is the centroventral incisure of the δ ventum (Ōpik 1937, pl. 3, fig. 1; Sarv 1959, pl. 4, fig. 7; Sidaravičienė 1992, pl. 23, fig. 2; Schallreuter 1973, pl. 19, figs 1, 8). This feature has been observed in these three species only. Therefore, they may represent only one species with several subspecies (cf. Schallreuter 1973: 79) because transitions exist in other features. However, Jaanusson (1963: 25, 28) who studied the type of *U. granulosa* (Jaanusson 1962: 412; 1963: 5), considered *U. granulosa* and *U. coelodesma* as different species, and also Sidaravičienė 1992 cited *U. coelodesma*, *U. granulosa* and *U. jaanussoni* as different species of a phylogenetic lineage within *Uhakiella* (Sidaravičienė 1996: 55, fig. 13).

With up to 2.75 mm *Uhakiella jonesiana* (Schmidt, 1941) (= *Primitia jonesii* Krause, 1889 = *U. magnifica* Sarv,1959; Schallreuter 1973: 78) becomes larger (Sidaravičienė 1992: 238) and differs also by the narrower S2, the stronger plica, and the weaker ventral bulge, which is documented only by an accumulation of tuber-
cles. Furthermore, the pouch exhibits a finer granulation than the lateral surface of the domicilium (Sarv 1959, pl. 3, fig. 10, pl. 4, fig. 16; Sidaravičienė 1992, pl. 24, fig. 3; Meidla 1996, pl. 4, figs 10–11). Whether or not the male velum has a ventral incisure is unknown.

Uhakiella labrosa (Krause, 1889) (= U. aequigranosa Jaanusson, 1957, uppermost Crassicauda limestone) is of about the same size (holotype of U. aequigranosa 2.10 mm) and differs from U. granulosa and other species of the genus by its ornamentation and the indistinct ornamental ridges (Jaanusson 1957: 291, pl. 5, fig. 10). Males seem to be unknown so that it is also not known whether a ventral incisure exists or not.

In Uhakiella oanduenensis Sarv, 1963 the ventral incisure is apparently lacking. The plica is more distinct and the surface ornamentation consists of granules and few tubercles instead of spines (Meidla 1996, pl. 4, figs 12–13).

Remarks. For Bollia granulosa Ulrich & Bassler (1908: 294, 328) introduced the replacement name Beyrichia granulifera after assigning this species to the genus Beyrichia (secondary homonymy). Already Bonnema (1909: 84) considered the shifting of Bollia granulosa into Beyrichia only weakly founded, but it became irrelevant (Schmidt 1941: 33 footnote) when Öpik, on one hand and Schmidt, on the other hand, assigned this species to Uhakiella (Öpik 1937: 42–43, 106–107) or Bromidella, respectively (Schmidt 1941: 33).

In unawareness of this remark, the name granulifera has been further used, but mostly only in lists in the sense of ICZN art. 23.9.6. In the few papers contributing to the knowledge of the taxon the name granulosa has been preferred. This also applies to the present paper (in the sense of ICZN art. 59.29) despite the existence of a replacement name since its irrelevancy has been recognized already in 1941.

Kummerow (1933: 48–49, fig. 8) mentioned the external sausage-like brood pouch (“false” brood pouch) in Eurychilina kuckersiana and Ctenobolbina (= Bollia) granulosa from weathered Backsteinkalk glacial erratics, and figured a steinkern of Eurychilina kuckersiana, which Öpik (1937: 43) considered as Uhakiella sp.

Kummerow (1939: 89) disagreed and stated that both species occur together in the Backsteinkalk. For comparative reasons he reproduced his figure 8 (1939 as fig. 9) and figured copies of both species from Bonnema (1909, pl. 7, figs 13–14).

However, the copy of Bollia granulosa in fact represents Bromidella kohtlensis Öpik, 1937 (= Bollia granulosa: Bonnema, 1909) with a distinct false brood pouch like U. granulosa.

The refigured E. kuckersiana on the other hand represents in reality Severobolbina kuckersiana, which lacks a false brood pouch contrary to U. granulosa but displays quite another kind of dimorphism. However, it seems that Kummerow erroneously figured (same species name!) the wrong figure of Bonnema. He probably meant Laccochilina kuckersiana which has a false brood pouch like U. granulosa. In accordance with this assumption Sarv (1959: 9) cited Eurychilina kuckersiana Kummerow, 1933 under Laccochilina kuckersiana.

Later investigations of Backsteinkalk ostracodes by the senior author evidenced, that Kummerow’s Ctenobolbina granulosa is identical with Bromidella sarvi (Schallreuter 1973: 86). The latter is very similar to Bromidella kohtlensis according to the figure of that species reproduced by Kummerow. According to his short description (Kummerow 1939: 89) his Eurychilina kuckersiana seems to be identical with Uhakiella jaanussoni Sarv, 1964. Posthumously, one must agree Öpik (1937: 68) in placing Eurychilina kuckersiana sensu Kummerow (1933, 1939) in Uhakiella.

Occurrence. Lithuania: Sidaravičienė 1996 mentioned U. granulosa and U. coelodesma both from the Lasnamägi stage and Uhaku stage, U. granulosa also up to undivided Idavere/Johvi (= Haljala stage) but not from Johvi stage. In her figure 13 (stratigraphical and phylogenetical ranges) U. coelodesma is restricted to Lasnamägi stage and Uhaku stage, U. granulosa to the Kukruse stage and lower Idavere substage. Western Latvia: Kukruse and Haljala stages, eastern Latvia: Kukruse stage.

Signakiella Schallreuter, 1988

Type species: Streupola signata Steusloff, 1895 (= Signakiella steusloffi Schallreuter, 1988b); by original designation. = Beyrichia signata Krause, 1892 (= Steuslofia wandae Széjsz, 1989 = Piretella paese rensis Sidaravičienė, 1992.

Definition. Large, ample or slightly preplete, unisulcate, S2 as a distinct pit behind of a small but distinct PAN. Strong zygal ridge starting from PAN and continuing around S2 and as C3 until the dorsal plica. In front of the PAN the latter is followed by an anterior ridge (C1), which terminates ventrally at the zygal ridge. Posteroventrally of S2 at the zygal ridge C4 starts as a short ridge.

Comparisons. Signakiella is closely related to Uhakiella and very probably a descendent of the latter. Most important common features are the pit-like S2, PAN, dorsal plica, zygal ridge, and ventral bulge (“ventral lobe” of Öpik 1937, fig. 5). Signakiella differs from Uhakiella mainly by the much stronger rich-like ornamental sculptures, particularly by the much stronger ventral bulge and the development of a parable-like ridge around PAN and S2, which incorporates the zygal ridge.

There are several homeomorphic genera with a para ble-like ridge (C1 + C3) around both PAN and S2 such as Piretella, Vauscripta (= Mojczella), Pectidolon, Asteuslofia, and Steuslofia, in which the species partly had been placed. From these genera Signakiella differs mainly by the ventral bulge.

Signakiella also resembles Lennukella Jaanusson, 1957 mainly in the dorsal plica, the PAN and the ventral bulge, but differs by the development of a short ridge, a node below and above the middle of the post-
sulcal area as well as of a narrow velar flange (Öpik 1937, pl. 3, figs 11–12; Jaanusson 1957, fig. 34, pl. 10, fig. 1).

**Signakiella signata** (Krause, 1892)

Figure 1D–E

1989, *Steusloffia (Tetradella) signata* Steusloff; 784–785, pl. 58, fig. 25.


1994, *Strepula signata* Kellett (1934: 476) considered and thus, dimorphism with a strongly convex *Uhakiella*.

1992, *Beyrichia signata* Krause as synonyms. Already Bassler & Paczer 1937, pl. 3, figs 11–12; Jaanusson 1957, fig. 34, pl. 17, figs 6–8; 1989b: 162) mentioned and figured few females with a slightly convex undulate dolon but mentioned also a fragmentary heteromorph with a strongly convex dolon. The female figured by Sidaravičienė (1992, pl. 36, fig. 12) seems to have such a strongly convex dolon forming a long false brood pouch. This specimen is rather large with 2.15 mm, and tecnomorphs may even reach 2.40 mm. This shows that the majority of the material described is juvenile.

**Vauscripta Schallreuter, 1988**

**Synonym.** Mojczella Olempska, 1989

**Type species.** *Bolita v-scripta* Krause, 1889; by original designation.

**Definition.** Medium-sized – large, S2 pit-like, distinct oval PAN, zygal ridge and C3 forming a V-shaped ridge, C1 isolated or connected anteroventrally with C3. C1 and C3 passing dorsally into the two branches of the plica. Velum anteriorly and ventrally as a ridge or more or less broad flange which may be undulate, in females weakly or strongly convex. Outer surface reticulate and tuberculate or smooth.

**Dimorphism.** The knowledge about mode and formation of the dolon/antrum in *Vauscripta* is rather limited since females are extremely rare. Olempska (1989a, pl. 17, figs 5–6; 1989b: 162) mentioned and figured few females with a slightly convex undulate dolon but mentioned also a fragmentary heteromorph with a strongly convex dolon. The female figured by Sidaravičienė (1992, pl. 36, fig. 12) seems to have such a strongly convex dolon forming a long false brood pouch. This specimen is rather large with 2.15 mm, and tecnomorphs may even reach 2.40 mm. This shows that the majority of the material described is juvenile.

**Comparisons.** There are several genera characterized by a parable-like crista formed by C1 and C3 and enclosing both PAN and S2. This feature is, therefore, homeomorphic and complicates the systematic differentiation between *Vauscripta* and *Mojczella* as well as between *Uhakiella* and *Signakiella* (Tvaerenellidae), *Piretella* and *Lembitsarrella* (Piretellidae), *Asteusloffia* (Ctenotominae, Ctenonotellidae), and *Pectidolon* (Wehrliinae, Ctenonotellidae).

Before becoming the type-species of *Vauscripta*, *Bolita v-scripta* was assigned to *Uhakiella*, Tvaerenellidae (Öpik 1937; Schallreuter 1973). Olempska also referred *Mojczella* to the Tvaerenellidae, while Sidaravičienė (1992: 145, 147) assigned it to the Piretellidae. The taxonomic problems are also exemplified by species originally erected within the genus *Piretella: Vauscripta tridactyla* (Jaanusson, 1957).

Features such as the pit-like S2, the PAN, the zygal ridge, and the plica indicate close relationships between

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Vauscripta, Uhakiella and Signakiella. Main differences between the three genera refer to the ventral bulge present in Uhakiella and Signakiella and the C3 and velar flange developed in Vauscripta. In lobation and cristation transitions exist between Uhakiella and Vauscripta as shown, e.g., by the two valves figured by Thorslund (1940, pl. 1, figs 6–7) as Uhakiella coelodesma.

Differences seem to exist in the construction of the tecnomorphic velum and perhaps the dimorphism. In Uhakiella the tecnomorphic velum is reduced to a narrow broad bulge and in typical species with a centroventral incisure in the males. By contrast, Vauscripta has a relatively broad velar flange which forms a weakly convex undulate dolon or strongly convex pouch in females.

More than typical Uhakiella species does Vauscripta very much resemble the Baltic species assigned to Bromidella in their ridge- or flange-like tecnomorphic (part of) velum. It is very likely that Vauscripta (Schallreuter 1988b: 42; 1993, pl. 50a, figs 2–3, pl. 52b, figs 1–3) originated from this Bromidella branch.

Vauscripta also resembles the two ctenentominine genera Asteusloffia and Clemenatoma. Vauscripta and Asteusloffia are very similar in the construction of the plica (compare Fig. 3C and Olempska 1989a, pl. 18, fig. 6) but in Asteusloffia the distance between PAN and C1/3 is larger and a connection between them is lacking. Furthermore, Asteusloffia exhibits a C4.

In the formation of an undulate velar flange as well as in the kind of dimorphism (weakly convex dolon) Vauscripta resembles very much Clemenatoma (Schallreuter 1994, pl. 17, fig. 3). Similarity exists also concerning S2, PAN and postcristal ridge. Vauscripta has only more ridges on the lateral surface.

Comparable features to Steusloffia refer to S2, PAN, cristae and sometimes an undulate velar flange (Schallreuter 1993, pl. 39b, figs 3–4).

In the development of C1/3 Mojczella very much resemble Signakiella also showing the slight bending at the connection point beneath the PAN (Olempska 1989b: 164) (compare Fig. 1G and Olempska 1989a, pl. 19, figs 3–4, 8 – for the first time already at least in the samples MA-58 and MA-59, not MA-65 and MA-66).

Signakiella differs mainly by the ventral bulge, the short C4, and the missing velar flange. This fact clearly demonstrates the striking homeomorphic nature of the C1/3 character.

Piretella to which one synonym of the type-species was originally assigned has an uninterrupted C1/3 like adults of the type-species and M. sanctacrucensis (Olempska 1989a, pl. 19, figs 7–8; Sidaravičienė 1992, pl. 37, figs 1–2). The velum of Piretella consists of a frill with hollow tubules and long spines in both centroventral and posterior region of the valve. Spines may occur also in the posterior region of Vauscripta, but they are only short and restricted to that area because of the longer velar flange. The distance between C1/3 and the velum is shorter in Piretella (e.g. Sidaravičienė 1992, pl. 36, fig. 11, and pl. 37, figs 1–2). Piretella has a reticulate shell, while Vauscripta may have only a reticulogranulate outer surface (Olempska 1989a, pl. 18, figs 3–6). It is, however, mostly more or less granulate to smooth. Young Piretella instars may have C1 and C3 separated anteroventrally (Schallreuter 1975, pl. 5, fig. 2) like in the oldest species assigned to Mojczella and in larvae of M. jaanussoni (Olempska 1989a, pl. 17, figs 1–7, pl. 18, figs 1, 4–5).

**Phylogeny.** Olempska reconstructed an evolutionary lineage of Mojczella from the Ordovician Mójca Limestone of the Holy Cross Mountains. The lineage consists of the three chronospecies (M. polonica, M. jaanussoni, M. sanctacrucensis) distinguished on the basis of morphologic differences and stratigraphical occurrence. They have been “... defined in such way that the two most significant gaps in the record separate them ... and it is clear that this way of discrimination of species is actually quite arbitral” (Olempska 1989b: 167).

*M. jaanussoni* has been defined by C1 “... ending below PAN”, and *M. sanctacrucensis* by “... C1 and C3 united beneath PAN”. The largest figured valve of *M. jaanussoni*, a female valve (Olempska 1989a, pl. 19, fig. 4; L 2.03 mm), which is older than the smaller holotype of that species, shows already a connected C1/3 like in the younger but smaller tecnomorphic holotype of *M. sanctacrucensis* (Olempska 1989a, pl. 19, fig. 8; L 1.80 mm) which is not adult. Sidaravičienė (1992, pl. 37, fig. 1) figured a female (?) valve of 2.40 mm length. The unification of C1 and C3 is therefore apparently a matter of palingenesis.


**Vauscripta v-scripta** (Krause, 1889)

Figure 1G

1889 *Bollia v-scripta* Krause: 13–14, 23, 24, pl. 1, fig. 18 (non fig. 17).

1890 *Bollia v-scripta*. – Koken: 39, 383, fig. 26d (after Krause 1889, pl. 1, fig. 18).

1908 *Byrichia v-scripta*. – Ulrich & Bassler: 299, fig. 48 (= Krause 1889, pl. 1, fig. 18), pl. 38, fig. 8.


1985 *Piretella tridactyla*. – Sztejn: 61 (partim); non 61 (partim), 86, tab. 1, pl. 1, figs 2a–b = Mojczella sanctacrucensis, Sidaravičienė 1992: 147.
Remarks. The second specimen (MB. HS 2010–6) figured by Krause (1889, pl. 1, fig. 17) which came from another boulder (glacial erratic boulder no. 311) represents another species (*Bromidella cf. kohlensis*) because the zygal crista is not connected with the posterior plical bow.


### Euprimites Hasseld, 1949

**Type species.** *Euprimites reticulogranulatus* Hasseld, 1949, by original designation.

### Euprimites intermedius* (Krause, 1889)

**Figure 2F**

1889 *Primitia intermedius* Krause: 11, 23, pl. 1, fig. 16.
1934 *Eurychilina intermedius*. – Bassler & Kellett: 55, 315, 446.
1962 *Primitia intermedius* = *Euprimites* sp. indet. – Jaanusson: 413.
1983a *Euprimites locknensis*. – Schallreuter: 174 (syn.).
1993 *Euprimites (Euprimites) locknensis*. – Schallreuter: 44, 116–117, 172, pl. 12b, fig. 3 (syn.).

**Lectotype** (designated by Jaanusson 1962: 413). Left female valve, MB. HS 2010–7, Figure 2F; Krause 1889, pl. 1, fig. 16.

**Type locality and horizon.** Mühlgemheim; Krause's glacial erratic boulder no. 339, a grey, marly limestone, age presumably like *Ludibundus* limestone of Sweden.

**Dimensions.** L of lectotype 1.46 mm, holotype of *E. locknensis* 1.46 mm.

**Definition.** Females between 1.30 and 1.70 mm and mostly moderately high. Outline more or less amplete. Domiciliary rather weakly convex. Sulcus very broad and relatively long, in its central part somewhat constricted, anterovelar depression present. Velum in tegmiforms as flange-like keel, in females as a flange. Anterovelar part of flange extending perpendicular, centrovelar part parallel to straight dorsal margin. End of dolon anteriorly indistinct, antrum not very deep, anteriorly open and posteriorly indistinctly closed. Lateral surface reticulate.

**Remarks.** After investigation and designation of the lectotype Jaanusson (1962: 413) considered *P. intermedius* as a *nomen dubium*. However, new SEM stereopairs clearly evidence that it is a senior synonym of *E. locknensis*. The broad S2 is a very characteristic feature.
Occurrence. *E. locknensis* is reported from outcrops and borings of the Central Baltoscandian confacies belt (Sweden, SE Estonia, Latvia, Lithuania, Belorussia, former East Prussia) from the Aseri stage (C1a) up to the Kulm stage (D1) (Schallreuter 1993: 117). From Swedish outcrops, the probable origin of the respective glacial erratic boulder, the species is recorded exclusively from the *Ludibundus* Limestone (= Kukruse – Haljala stages) where it is one of the commonest species (Jaanusson 1957: 310).

**Tvaerenella Jaanusson, 1957**

Type species. *Primitia carinata* Thorslund, 1940 (OD); by original designation. = *Primitia tuberculata* Krause, 1892 = *Primitiella indistincta* Öpik, 1937 = *Primitiella granosa* Öpik, 1937.


**Tvaerenella tuberculata** (Krause, 1892)

Figure 2E

1892 *Primitia plana* Krause var. *tuberculata* Krause: 385, 399, pl. 21, fig. 8.

1934 *Apatochilina plana tuberculata*. – Bassler & Kellett: 55, 163, 452.

1937 *Primitiella indistincta* Öpik: 5, 13, 60, 69, 77, 124, pl. 1, fig. 4.

1937 *Primitiella granosa* Öpik: 5, 14, 72, 69, 78, 136, pl. 13, figs 6–9.

1940 *Primitiella (?) carinata* Thorslund: 163, 186, pl. 4, fig. 8.

1959 *Tvaerenella granosa*. – Serv: 30–31, pl. 5, figs 4–7 (= Öpik 1937, pl. 13, figs 6–9) non figs 8–9 (= Öpik 1937, pl. 15, figs 7–8), tab. 2.


1983a *Tvaerenella granosa*. – Schallreuter: 165, 175–176, 191, tab. 16 (12/7), pl. 12, fig. 7 (syn.).

1985 *Tvaerenella tuberculata*. – Schallreuter: 107–108, 130, tab. 1, pl. 6, fig. 7 (syn.).


Lectotype (designated by Schallreuter 1985: 107). Right ♀ valve, MB. HS 2010-8 – Figure 2E; Krause 1892, pl. 21, fig. 8. Type locality and horizon. Müggeheim, Krause’s glacial erratic boulder no. 670.

Dimensions (L, H in mm, L : H. Lectotype 1.23 – 0.75 – 1.64. Holotype of *P. granosa* (tecmomorphic carapace) 1.30 – 0.80 – 1.63 (Öpik 1937), 1.20 – 0.88 – 1.36 (Serv 1959). Holotype of *P. carinata* (left ♀ valve) 1.16 – 0.68 – 1.71, of *P. indistincta* 0.80 – 0.45 – 1.77.

Definition. Females 1.10 – 1.30 mm long and rather high to moderately high. Domicilium with indistinct sulcal depression. PAN very small and flat, situated anterodorsally of an oval, more or less distinct muscle spot with a weak interior sulcation. Tecnomorphic velum developed as keel, rounded bend or completely lacking. Dolon posteriorly extending up to the posterozonal region. Surface smooth or reticulate and more or less covered with tubercles.

Remarks. *Apatochilina uibaënsis* Öpik, 1937 has been tentatively considered as a synonym of *T. granosa* (Serv 1959: 30–31; Schallreuter 1973: 103–104) but the presence of a dorsal plica (Öpik 1937, pl. 1, fig. 10, pl. 15, figs 7–78) clearly distinguishes this species from typical *Tvaerenella* species. Together with *Tvaerenella caesura* Schallreuter, 1993 this species possibly represents a new genus.

Occurrence. Sweden (Brunflo-Lockne area, Jämtland; Fjäck, Siljan District); *Ludibundus* beds. Estonia: Ulu-ku and Kukruse. Glacial erratic boulders: Ringsö, Tvären; Backsteinkalk types IB2 (Dalby), IB3 (Skagen), 14B2 and 1B13 (Haljala Stage); Harpa Limestone (D2).

**Tvaerenella plana** (Krause, 1889)

Figure 2A

1889 *Primitia plana* Krause: 5–7, 22, 24, pl. 1, fig. 1a–b. 1896 *Primitia plana*. – Koken: 381, fig. 26c (after Krause).


1934 *Apatochilina plana*. – Bassler & Kellett: 55, 162, 452.


1945b *Öpikella cf. umbilicata*. – Henningsmoen: 94–95, 101, pl. 5, figs 1–6.


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**Figure 2. A. Tvaerenella plana** (Krause, 1889), holol- or lectotype, left ♀ valve (MB. HS 2010-1), lateral view, L 1.51 mm; Müggeheim (Berlin), Krause’s glacial erratic boulder no. 310, Harjuaan; **B. Kiesowia dissecta** (Krause, 1892), holotype, anterior incomplete right tecnomorphic valve (MB. HS 2010-3), lateral view, L 2.05 mm, Müggeheim (Berlin), Krause’s glacial erratic boulder no. 616, age Pirgu or Porkuni stage (F1c or F2); **C. Kiesowia dissecta leviscomexa** (Schallreuter, 1967), holotype, right female valve (GG 25–3), lateral view, and ventrolateral views, L 1.20 mm, Isle of Gotland, Öljemyr flint, glacial erratic boulder (no. 794), age Pirgu or Porkuni stage (F1c or F2); **D. Kiesowia dissecta** (Krause, 1892), holotype of *K. namilliosa* (Krause, 1892), right tecnomorphic valve (MB. HS 2010-4), lateral, and ventral views, L 2.05 mm, Müggeheim (Berlin), Krause’s geschiebe no. 667, age Pirgu or Porkuni stage (F1c or F2); **E. Tvaerenella tuberculata** (Krause, 1892), lectotype, right female valve (MB. HS 2010-8), lateral view, L 1.23 mm, Müggeheim (Berlin), Krause’s glacial erratic boulder no. 670, age: Keila (D2); **F. Euprimites intermedius** (Krause, 1889), lectotype, left female valve (MB. HS 2010-7), L 1.46 mm, Müggeheim (Berlin), Krause’s geschiebe no. 339, age presumably like *Ludibundus* limestone of Sweden; **G. Balticella globifera** (Krause, 1892), holotype of *Balticella bino- dis* (Krause, 1897), steinkern of a right valve (Rijksmuseum van Geologie en Mineralogie Leiden no. 34116), lateral view in two focus levels, L. 1.28 mm, glacial erratic boulder from Zweib hill near Lochem (Staring no. 11068), age Haljala stage (C/D1); **H. Balticella globifera** (Krause, 1892), dorsally incomplete external mould of lost holotype (steinkern), left valve, (MB. HS 2010–16), internal lateral view, and photographic cast, L 0.85 mm, Müggeheim (Berlin), Krause’s glacial erratic boulder no. 666, age presumably Haljala stage (C/D1). All stereo-pairs except of C (ventrolateral view), and G.
2008 *Tvaerenella umbilicata*. – Schallreuter & Hinz-Schallreuter: 809–812, fig. 1.1–4. (syn.).

*Holo- or lectotype*. Left ∨ valve, MB. HS 2010–1 – Figure 2A, Krause 1889, pl. 1, fig. 1.

Krause wrote that he found the species only once in a bright-grey glacial erratic boulder. It is not clear whether he meant only one specimen or several specimens in one boulder.

**Type locality and horizon.** Müggelheim (Berlin), Krause’s glacial erratic boulder no. 310, together with *Platybolbina distans*. The latter seems to be a junior synonym of *P. orbiculata*, which occurs in Estonia from the Oandu (?) to Porkuni Stages (Meidla 1996: 23). *Tvaerenella expedita* is reported from Vormsi to Porkuni Stages of Estonia (Meidla 1996: 39), the age of the boulder is therefore, Vormsi Pirgu or Porkuni Stage.

**Dimensions** (L – H in mm – L : H). Lectotype 1.51 – 0.98 – 1.54.

**Definition.** At least up to 1.63 mm. Cardinal angles almost equalized. Dolon relatively short, terminating posteriorly already in the centroventral region.

**Comparisons.** *T. plana* differs from *T. tuberculata* mainly by the smaller anterodorsal cardinal angle and the shorter dolon.

**Remarks.** *P. plana* is a senior synonym of *Tvaerenella umbilicata* and *Tvaerenella expedita*.

Twenty years after Bassler & Kellett (1934) had assigned *Primitia plana* to the genus *Apatochilina* Henningsmoen (1953a) established the new genus *Platybolbina* for Krause’s *P. distans*. Henningsmoen (1954b) considered *Primitia plana* as a possible synonym of *P. distans*. Reinvestigation of the type specimen of *P. plana* revealed, however, that it in fact belongs to the genus *Tvaerenella*. Accordingly, most citations in the literature concerning *Platybolbina plana* or *Platybolbina cf. plana* refer to *Platybolbina distans*.

In 1959 Sarv introduced the new species *Platybolbina orbiculata*, but Meidla (1996: 23) stated that “… until the type specimen of *P. plana* is redescribed the relationship between *P. plana* and *P. orbiculata* remains uncertain”. There does not exist any relationship between *Tvaerenella plana* and *Platybolbina orbiculata*.


Superfamily *Tetradelloidea* Swartz, 1936

Family *Ctenonotellidae* Schmidt, 1941

Subfamily *Ctenentominae* Schmidt, 1941

*Asteusloffia* Schallreuter, 1993

**Type species:** *Strepula lineata separata* Steusloff, 1895; by original designation = *Beyrichia erratica* acuta Krause, 1891.

**Definition.** Medium-sized. Unisulcate, with distinct S2 and PAN. Dorsal plica complete or only partially developed. Three generally vertically arranged cristae: C2 missing, C1/C3 parable-like with C4 branching off from its posteroventral part C4 may or may not reach the dorsal margin.

**Comparisons.** From other genera with a parable-like crista around PAN and S2 (e.g., *Steusloffia*, Jaanussorn 1955, fig. 38) *Asteusloffia* is distinguished mainly by the development of a C4. The similar *Steusloffia* in which adults and larger larvae are also characterized by a C4, has a C2 developed. Further, the C3 is centrally interrupted and terminates on the spine-like posteroventral lobe (Schallreuter 1993, pl. 54a, fig. 1). Although being stratigraphically older, *Asteusloffia* cannot be regarded as a possible synonym of *Steusloffia* because of the already lacking C2, which is in that lineage an advanced character.

Already Henningsmoen (1953b: 223) assumed that *Steusloffia* developed from forms with “normal” tetradellid arrangement of the cristae like *Tallinnellina lanceolata* and *Rigidella mitis*.

Also *Steusloffia* displays these four cristae, but has the C2 separated from the other cristae. The C2 is still present in the youngest species of *Steusloffia*, *S. levis* Sarv, 1959 from the Rakvere stage (E) of Estonia (Sarv 1959, pl. 15, fig. 7). By contrast, *Astusloffia acuta* (= *Steusloffia polynodulifera* Hessland, 1949) lacks a C2 and therefore, is regarded as member of another lineage characterized by an early reduction of the C2.

*Asteusloffia lineata* (Krause, 1889)

Figure 3B

1889 *Strepula lineata* Krause: 15, 23, pl. 2, fig. 3.


1962 *Steusloffia lineata* = *Steusloffia sp.* indet. – Jaanussorn: 413.

**Lectotype** (designated by Jaanussorn 1962: 413). Right valve (MB. HS 2010–11), Fig. 3B, Krause 1889, pl. 2, fig. 3.

**Type locality and horizon.** Müggelheim (not mentioned on labels), Krause’s glacial erratic boulder no. 106, exact age unknown.

Figure 3A. *Asteusloffia acuta separata* (Steusloff, 1895), lectotype, left valve (GG 114–51), lateral views in different positions to the SEM detector, L 0.98 mm, Neubrandenburg, glacial erratic boulder, age B3, lower Darriwillian; B. *Asteusloffia lineata* (Krause, 1889), lectotype, right valve (MB. HS 2010–11), lateral, and oblique dorsal views, L 1.05 mm, Müggelheim (Berlin), Krause’s glacial erratic boulder no. 106, age unknown; C. *Asteusloffia acuta* (Krause, 1891), right valve (GG 400–G123–18), lateral view, L 1.23 mm. Black Orthoceras limestone (B3f), local glacial erratic boulder (no. Gis–84) from Gislövsåkrammar, Scania; D. *Asteusloffia acuta* (Krause, 1891), left valve (GG 400–2539), lateral view, L 1.22 mm. Same boulder as fig. 3; E. *Asteusloffia acuta separata* (Steusloff, 1895), paratype, external mould of right valve (GG 114–50A), internal lateral view, and photographic cast, L 1.22 mm, same glacial erratic boulder as fig. 1; F. *Bilobatia bidens* (Krause, 1892), lectotype, female right valve (MB. HS 2010–14), lateral view, L 0.98 mm, Müggelheim (Berlin), Krause’s glacial erratic boulder no. 670, age Keila stage (D2). All stereo-pairs.
Dimensions. Lectotype L 1.05 mm, H 0.61 mm.

Definition. At least up to 1.05 mm. Plica nearly completely missing. C1 and C3 forming a U-shaped cuticle around small PAN and relatively narrow S2. C4 bow-shaped, both ends directed anteriorly; dorsal end may be connected with the dorsal end of C3. Plica nearly completely missing, only represented by the short dorsal portion of C4.

Comparisons. The missing plica distinguishes *A. lineata* from all other species of the genus. Differences exist also in the cristal arrangement: C1 plus C3 are U-shaped in *A. lineata* and V-shaped in *A. acuta*. In *A. lineata* both C3 and C4 reach the dorsal margin, C3 extends perpendicularly to the latter. C4 forms a slight bow with its ends anteriorly directed; its dorsal part represents a short plica. In *A. acuta*, the C3 passes dorsally into the posterior part of the plica, C4 terminates blindly in the dorsal half of the valve (Fig. 3C-D). *A. acuta* has a larger PAN and a broader S2 than *A. lineata*. Consequently, C3 is located directly at the posterior border of S2.

*A. separata* (Steusloff, 1895) has been originally described as a subspecies (var.) of *A. lineata*. Ōpik (1937: 117 or 53) considered this taxon as a species of Rigida, Jaanusson (1957: 359) referred it to Steusloffia, and Schallreuter (1993: 68) regarded it as the type-species of Asteusloffia. However, *A. separata* is more similar to *A. acuta* (Krause, 1891). Both differ only in their plicae which is present in all parts in *A. acuta separata* (Fig. 3A, E; Schallreuter 1993, pl. 33b, fig. 3, pl. 34a, figs 1f, 2, 3, pl. 34b, fig. 4), while the centrnodal part is lacking in *A. acuta acuta* (Figure 3C–D; Schallreuter 1993, pl. 31b, fig. 1r, pl. 36a, fig. 4, pl. 39a, figs 1f, 2). Therefore, *A. acuta separata* is considered here as a subspecies of *A. acuta*, and not as a variety because of the constantness of this feature in all investigated samples.

Although the lectotype of *A. lineata* is smaller (1.05 mm) than the largest known specimens of both *A. acuta separata* (1.25 mm) and *A. acuta acuta* (1.56 mm) the lack of the plica is not an organotactical feature in this case. The plica is present in the species mentioned above already in specimens of about the same size (Schallreuter 1993, pl. 33b, fig. 3) or even smaller ones (Schallreuter 1993, pl. 39a, fig. 3). As demonstrated by species of the related genus Steusloffia the plica appears already in the A-3 stage with the C4 still not developed (Schallreuter 1976: 189, pl. 5, fig. 5; Hinz-Schallreuter & Schallreuter 1998, fig. 81).

Occurrence. Known only from type locality.

Subfamily Wehrliinae Schallreuter, 1965

**Bilobatia Schallreuter, 1976**

Type species: *Bilobatia serralobata* Schallreuter, 1976; by original designation. = *Beyrichia* (*Urichia*) *bidens* Krause, 1892.


**Bilobatia bidens** (Krause, 1892)

**Figure 3F**

1892 *Beyrichia* (*Ulrichia*) *bidens* Krause: 396, 399, pl. 22, fig. 12.
1909 *Urichia bidens*. – Bonnema: 54, 81; non 54, 77, 81–82, pl. 6, fig. 27 = *Ctenonotella elongata* Ōpik, 1937.
1976 *Bilobatia serralobata* Schallreuter: 205–207, 215, tab. 12; fig. 14, pl. 8, figs 1–2 (syn.).
1982 *Bilobatia serralobata*. – Schallreuter: 9–15, pl. 10, figs 1–2, pl. 12, figs 1–3, pl. 14, figs 1–2, pl. 16, figs 1–2.
1985 *Bilobatia bidens*. – Schallreuter: 110–111, 120, tab. 1, pl. 1, figs 5–6 (syn.).
1997 *Bilobatia bidens serralobata* – Schallreuter: figs 18a–e.
1998 *Bilobatia bidens serralobata* – Hinz-Schallreuter & Schallreuter: fig. 96a–e (= Schallreuter 1997: fig. 18).
1999 *Bilobatia bidens serralobata* – Schallreuter et al.: pl. 1, fig. 4.

Lectotype (designated by Sarv 1959: 73, not by monotypy as mentioned by Sarv). Right valve, MB. HS 2010-14, Figure 3F, Krause 1892, pl. 22, fig. 12.

Type locality and horizon. Müggelheim (Berlin); Krause’s glacial erratic boulder no. 670.

Dimensions. Lectotype L 0.98 mm, H 0.66 mm, L : H 1.48.

Definition. As for the genus which is presently monotypic.

Remarks. In the population of the glacial erratic boulder Sy-108 described by Schallreuter (1982) yielded females that are much smaller (0.90–0.96 mm) than the holotype of the nominal type-species *B. serralobata* (1.25 mm). They were therefore considered (Schallreuter 1982: 13) as a possibly smaller subspecies, which the lectotype of *B. bidens* with a size of 0.98 mm is referred to.

Occurrence. Estonia: Haljala Stage (C3/D1) and Keila Stage (D2). Glacial erratic boulders: Harpa Lst. (D2); Krause’s glacial erratic boulder no. 670, Ahl-1001; Baltic Backsteinkalk = Sandöffit (14B2 type, glacial erratic boulder 14B2, 1B341, Ho-2); Rollsteinkalk (glacial erratic boulder Ro-2 (D2); Lavenderblue Cherts (Hornsteine) of Sylt, types Sy-154 (D1), Sy-167 (C3/D1), Sy-108 (*Cyclorinus* Lst., D2).

Family Tetradellidae Swartz, 1936

Subfamily Sigmoopsinae Henningsmoen, 1953

**Kiesowia Ulrich & Bassler, 1908**

Type species. *Beyrichia dissecta* Krause, 1892; by original designation.

Definition. Quadrilobate, lobes disintegrated into single nodes. Each node is composed of two nodes. Females anteriorly and ventrally with an undulate velar flange. A shorter hystial ridge may branch off from the velar flange anterocentrally and may extend to the centroventral region. Marginal sculpture developed as a row of spines. Surface with spines and granules.
Kiesowia dissecta (Krause, 1892)

Figure 2B–D

1892 Beyrichia dissecta Krause: 391–393, 398–399, pl. 21, fig. 3.
1892 Beyrichia mamillosa Krause: 386, 393, 399, pl. 22, fig. 14.
1923 Kiesowia (Beyrichia) dissecta. – Ulrich & Bassler: 311, fig. 20.6 (presumably after Krause 1892: pl. 21, fig. 3).
1934 Kiesowia mamillosa. – Bassler & Kellett: 349–350 (partim), 481.
1951 Kiesowia mamillosa, Kiesowia dissecta. – Kesling: 157–158, pl. 4, fig. 3, pl. 5, fig. 3.
1956 Kiesowia septenaria Stumbur: 188–189, 194, pl. 2, fig. 1.
1965 Kiesowia dissecta. – Pokorny: 145.
1967 Hithis leviconvexus Schallreuter: 619–621, fig. 3.
1977 Kiesowia dissecta. – Helm dash: fig. 18.
1979 Kiesowia (Kiesowia) dissecta. – Schallreuter: 79, 81, 83, 85, pl. 6, 80, figs 1–4, pl. 6, 82, figs 1–4, pl. 6, 84, figs 1–5, pl. 6, 86, figs 1–6.
1986 Kiesowia (Kiesowia) dissecta. – Schallreuter: 7, 22, pl. 4, fig. 4.
1987b Kiesowia (Kiesowia) dissecta. – Schallreuter: 207, 222.
1988a Kiesowia (Kiesowia) dissecta. – Schallreuter: 1042, 1045, pl. 1, fig. 7.
1990 Kiesowia dissecta. – Abushik in Abushik et al.: 61, 233, pl. 7, fig. 10.
1992 Kiesowia mamillosa = K. septenaria. – Sidaravičienė: 52–54, 233, tab. 2, (non pl. 12, fig. 3, see below).
1996 Kiesowia dissecta. – Meidla: 56–57, tabs 5, 9, figs 9–10, 20 (faunal logs), pl. 10, fig. 3.
1998 Kiesowia dissecta. – Hinz-Schallreuter & Schallreuter: fig. 85b.


Locotyple of Beyrichia dissecta: tecnomorphic right valve, MB. HS 2010–3 – Figure 2B; Krause 1892, pl. 21, fig. 3. The part of the valve anteriorly of the fine crack seen at Krause’s figure is broken away later (Meidla 1996: 57). The valve was still complete when Heidrich prepared a drawing of the valve (Helmdach 1977, fig. 18).

Type locality and horizon. Müggehl, Krause’s glacial erratic boulder no. 616, age: upper Upper Ordovician, presumably Porkuni (F2).

Holotype of Beyrichia mamillosa (monotypy), right tecnomorphic valve, MB. HS 2010–4 – Figure 2D; Krause 1892, pl. 22, fig. 14. Müggehl, Berlin; Krause’s glacial erratic boulder no. 667, a yellowish crystalline glacial erratic boulder with Primitia elongata Krause, 1891.

Holotype of Kiesowia septenaria. left tecnomorphic valve, Tartu Os 5005 – Stumbur 1956, pl. 2, fig. 1, Sarv 1962, pl. 4, fig. 9, Porkuni, F2.

Holotype of Hithis leviconvexus. right female valve, GG 25–3 – Schallreuter 1967, fig. 3. Isle of Gotland (Baltic Sea), Öjlemsyrfint (glacial erratic boulder no. 794), Fl/e/F2.

Dimensions. Holotype of K. dissecta L > 2.05 mm, H 1.22 mm; holotype of K. mamillosa L 1.15 mm, H 0.61 mm; holotype of K. septenaria L 2.40 mm (Stumbur 1956: 188) or 1.70 mm (Sarv 1962: 109); holotype of Hithis leviconvexus L 1.20 mm, H 0.79 (incl. velar flange).

Definition. Females 1.20–2.15 mm (Sarv 1962: 109), ? 2.40 mm. Histum short or completely missing.

Comparison. K. prussica Schallreuter, 1987 (1.66–2.35 mm) has a histoidal ridge which extends further posteriorly than in K. dissecta and may reach the ventral end of L3 (Schallreuter 1987b, pl. 1b, fig. 1; Sarv 1959, pl. 21, fig. 17; Sidaravičienė 1992, pl. 12, figs 3–5).

Remarks. Kiesowia dissecta is quadrilobate with the lobes split into single nodes with each being composed of two nodes. L1 is represented by the anterocentral node (L1m) and a less distinct, smaller anterodorsal node or spine (L1d). The anterocentral node has been often considered as the ventral node of L1 (L1v) but represents in fact the ventral node of L2 (L2v). L2 consists of L2m and L2v. Since L1m is usually fused with L2v, the latter has been often misinterpreted as anterocentral node of L1 (L1v) and made Henningsmoen (1954b: 79) state “... L1 tends to split into three nodes. This is especially seen in larval valves”. However, as lobes in their dorsoventral extend are generally forwardly directed, the above interpretation would lead to a posteriorly directed extend of L1.

In palaeocopes, females are usually more important for taxonomic determinations than tecnomorphs. Specimens of K. dissecta with frill (= females) were firstly figured by Henningsmoen (1954b, pl. 2, figs 2–3, L 1.89 – 2.04, according to magnification). Additional and better preserved material was provided by Schallreuter (1979) in the Stereo-Atlas of Ostracod Shells. The figured females are smaller (1.43–1.58 mm) but all with fused L1m/L2v. In these specimens the frill has the same extent (posteriorly up to L4v) like in the valves figured by Henningsmoen. Therefore, they must be considered as adults and accordingly may represent a new, smaller (older ?) subspecies (Schallreuter 1979: 85).

By contrast, in Hithis leviconvexus the frill terminates posteriorly already ventrally of L3v. The smaller size and the development of three anterior nodes with L1m not being fused with L2v could be interpreted as larval feature. Also the shorter velar frill may be a larval character as, e.g, in tecnomorphs of Piretella triebeli and Laccocchila lateris (Schallreuter 1975: 165, 173, pl. 3, fig. 5, pl. 5, fig. 2). However, since the antrum is fully developed with a flange-like inner antral fence (Fig. 2C), which indicates that it is an adult and not a pre-adult female. In typical specimens of K. dissecta the inner antral fence is formed by a row of spines having their distal portion connected by a thin horizontal bar (Schallreuter 1979, pl. 6, 80, figs 2–3, pl. 6, 82, fig. 3). Taxonomically, Hithis leviconvexus is
therefore, considered here as a subspecies of *K. dissecta* because of the differences not only in size. 

Sidaravičienė (1992: 53–54) considered *K. mamillosa* as a separate species characterized by the distinct L1m. Her figured *K. mamillosa* (Sidaravičienė 1992, pl. 12, fig. 3) as well as her K. sp. A (Sidaravičienė 1992, fig. 4) both belong to *K. prussica*. The development or lack of L1m is merely a matter of variation (see above). *K. prussica* is characterized by its distinct histium, while in *K. dissecta* the histium is usually lacking; if present at all, it is only short (Schallreuter 1979, pl. 80, fig. 1). The specimens of *K. prussica* figured as *K. mamillosa*, K. sp. A and K. sp. B by Sidaravičienė (1992, pl. 12, figs 3–5) have differently long developed.histia and represent the variation range of *K. prussica*. Already Sidaravičienė (1992: 55) assumed intraspecific variation concerning the very short histium in *K. sp. B*.


The occurrence in Lithuania is questionable. Meidla (1996: 57) mentioned the occurrence in Vormsi Stage and ? Pirgu Stage but Sidaravičienė (1992: 54) listed only one specimen of *K. cf. dissecta* from the Vormsi Stage. It seems that *K. dissecta* is in the Baltic region restricted to the North Estonian confacies belt. In size the lectotype is conform with the Estonian material. The smaller material considered as a possible subspecies (see above) occurs more westernly in the northern Middle Baltic Sea.

Suborder **Binodicopa** Schallreuter, 1972 
Superfamily **Drepanelloidea** Ulrich & Bassler, 1923 
Family **Drepanellidae** Ulrich & Bassler, 1923

**Duplexibollia Schallreuter, 1987**

**Type species.** *Bollia duplex* Krause, 1892; by original designation.

**Remarks.** The genus is presently monotypic. By contrast, Sidaravičienė (1992: 158) considered *Duplexibollia duplex* sensu Schallreuter (1987a) as a different species, which would be a case of "misidentified type species" according to ICZN art. 70.3. Only for this case *Duplexibollia duplex* sensu Schallreuter (1987a) should be suggested as type species instead of Krause’s species (but see also “comparisons”).

**Definition.** Large, outline amplete or subamplete. Quadriradicate with two broad, lobe-like, u-shaped cristae parallel to free margin and separated from the latter by a u-shaped furrow. Inner crista ventrally of S2 reduced. Marginal border flattened and with short spines.

**Duplexibollia duplex** (Krause, 1892) 
Figure 1C

1892 Bollia duplex Krause: 386, 389, 392, 399, pl. 21, fig. 7. 

1987a *Duplexibollia duplex*. – Schallreuter: 39–40, fig. 3.3. 
1990 *Duplexibollia duplex*. – Meidla et al. in Aru et al.: fig. 28 (faunal log). 

**Holotype** (monotypy, not lectotype as given by Henningsmoen 1954b: 98). Anteriorly incomplete left valve, MB. HS 2010-15, Figure 1C; Krause 1892, pl. 21, fig. 7. 

**Type locality and horizon.** Müggelheim; Krause’s glacial erratic boulder no. 640, a yellow-whitish glacial erratic boulder together with *Platybollina distans* and *Cystomatichilina umbonata*, age Nabala, Vormsi or Pirgu Stage after the occurrences of *Cystomatichilina umbonata* and *Duplexibollia duplex* in Estonia and Lithuania (Meidla 1996: 25; Sidaravičienė 1992: 158; Sidaravičienė 1996, tab. 2).

**Dimensions and proportions** (*L, H in mm, L : H*). 
Holo-type: 2.75 – 1.59 – 1.73. Carapaces Sidaravičienė 1992, 245, pl. 39, figs 7–8) heteromorph 3.00 – 1.85 – 1.62, teconomorph 2.75 – 1.60 – 1.72. Left valve (Schallreuter 1987a, fig. 3.3) 2.37 – 1.45 – 1.63 (domicilium 2.27 – 1.36 – 1.68). Henningsmoen 1954b, left valves pl. 2 figs 6–7: 2.33 – 1.33 – 1.75, 2.40 – 1.52 – 1.58 (according to magnification).

**Definition.** As for the genus.

**Remarks.** Sidaravičienė (1992: 157–158, pl. 39, figs 7–8) mentioned sexual dimorphism in *Duplexibollia duplex* which is expressed by the development of a narrow restricted velum extending from the anterior cardinal corner to the posteroventral region and not covering the free margin. However, what Sidaravičienė considered as velum seems to be merely the result of an ontogenetically increasing development of the adjacent semifurrow. Therefore, *Duplexibollia* is not a dimorphic taxon. Her arguments are not convincing. The “velum” (pseudovelum) which is present in few large valves only seems to be more a function of the strength of development of the neighbouring furrow which seems to be dependant from the ontogeny.

Sidaravičienė (1992: 158) considered *D. duplex* Schallreuter, 1987 from the Ōjelemyr flint boulder no. G287 from the Isle of Gotland as a possible new species, which is distinct from Krause’s species by a small adductorial lobe, an interrupted inner connecting lobe, the occurrence of marginal tubercles, and the more distinct cardinal corners (cf. Schallreuter 1987a, fig. 3.3; Sidaravičienė 1992, pl. 39, figs 7–8). Since the above outlined differences are only a matter of ontogenesis, Sidaravičienė’s respective interpretation is also declined.

**Occurrence.** Oslo region: Oslo–Asker (Hovedøya): 5b, Ringerike (Frogny, Stavnestangen): 5a (Henningsmoen 1954b: 99); Estonia: Saunja Fm., Nabala Stage (Meidla et al. in Aru et al. 1990, fig. 28); Lithuania: Pirgu (F1c), Nadtaucˇionys (~ upper F2 (Sidaravičienė 1992: 158), or uppermost Pirgu or Tommarp (Sidaravičienė 1996, tab. 2)]. Glacial erratic boulders: Ōjelemyr flint of the Isle of Gotland (Schallreuter 1987a), type locality.
Order Podocopa Sars, 1866
Superfamily Bairdiocypridoidea Shaver, 1961
Family Balticellidae Schallreuter, 1968

Balticella Thorslund, 1940

Type species. Balticella oblonga Thorslund, 1940; by original designation.

Definition. Schallreuter 1968: 135

Balticella globifera (Krause, 1892)

Figure 2G–H

1892 Primitia (Ctenobolbina?) globifera Krause: 389–390, 399, pl. 22, fig. 9.

1897 Primitia binodis Krause: 934, 938, pl. 25, fig. 16.

1934 Kloedenia globifera. – Bassler & Kellett: 70, 362, 444.

1940 Hesperidella globifera. – Thorslund: 179 (partim); non 179 (partim), 187, pl. 3, fig. 12, pl. 5, fig. 6 = H. esthomica (Bonnerma, 1909).


1941 Ctenentoma binodis. – Schmidt: 35–37.

1962 Hesperidella sp. indet. – Jaanusson: 413.

1964 Balticella binodis = B. oblonga. – Schallreuter: 95.

1968 Balticella binodis. – Schallreuter: 135–137, fig. 10 (syn.).

1973 Balticella binodis. – Neben & Krueger: pl. 95, fig. 4 (= Schallreuter 1968, fig. 10.4).

1976 Balticella binodis. – Jaanusson: 312–313, fig. 9 (faunal log, no. 42).

1985 Balticella binodis. – Schallreuter & Siveter: pl. 69, fig. 4 (= Schallreuter 1968, fig. 10.4).

1990 Balticella binodis. – Schallreuter: 278, pl. 7, fig. 8.


Holotype (monotypy). Steinkern and external mould of a juvenile right valve, MB. HS 2010-16, Krause 1892, pl. 22, fig. 9 (stein kern), Figure 2.8 (external mould).

Among the material, which came back from Uppsala to Berlin by the end of the 1990s, the respective slide with the holotype (stein kern) of Balticella globifera was empty due to the broken cover glass. However, the glass tube from which the steinkern had been removed in order to store it in a slide still contained the – dorsally incomplete – external mould of the specimen, which is now the holotype.

Type locality and horizon. Müggelheim, Krause’s glacial erratic boulder no. 666, age presumably Haljala Stage (C3/D1) or Keila Stage (D2).

Dimension. Length of holotype 0.85 mm.

Definition. See definition of Balticella binodis, Schallreuter 1968: 135.

Comparisons. With the placement of Primitia globifera in Kloedenia, Bassler & Kellett (1934: 362) were closer to the truth than later Thorslund (1940) and Jaanusson (1957, 1962) with their determination as a species of Hesperidella.

Thorslund (1940: 179) considered Primitia globifera and Primitia esthomica as synonyms, which became, however, never accepted. Despite his assumption that “... these species may be identical. ...”, Jaanusson (1957: 329) regarded H. globifera as a nomen dubium, also after having studied the holotype (not lectotype) (Jaanusson 1962: 413).

Reinvestigation of the holotype clearly shows that it belongs to Balticella binodis (= B. oblonga), which is characterized by both PAN and a posterior tubercle or spine. This species was erected by Krause 1897 who did not realize the synonymy with his previous Primitia globifera (Krause, 1892) (Fig. 2G). By contrast, in the external mould of the holotype of B. globifera a spine is not visible. It is uncertain whether the posterodorsal part including the spine or only the spine itself is primarily lacking. However, the spine proved to be variable in both strength and position (Schallreuter 1968, fig. 10). In the largest valve (L 1.65 mm) it is only tubercle-like and situated posteriorcentrally in height of the central portion of the PAN. In smaller specimens the spine is stronger and located in height of the dorsal part of the PAN. Thorslund (1940: 180, pl. 1, figs 18–20) neither described nor figured a spine in B. oblonga but mentioned “... small tubercles, sometimes with a larger one on the antero-dorsal slope” from his vice versa orientated valves.

The holotype is very weakly reticulogranulated. The surface ornamentation varies in this species between nearly smooth and granulated with some scattered tubercles (Schallreuter 1968, fig. 10; Schallreuter 1990, pl. 7, fig. 8).

Occurrence. B. globifera is known from outcrops in Sweden (Kinnekulle, Fjäckja, Central Locke Area) from the Ludibundus beds and the Skagen Limestone and borings from Lithuania from the Jõhvi stage. The best material came from glacial erratic boulders of Tvären and Backsteinkalk glacial erratic boulders of Northern Central Europe (Swedish, Baltic and intermediate types).

Epilogue

In many cases Krause’s drawings were considered of bad quality or “... somewhat diagrammatic” (Jaanusson 1962: 412). However, reinvestigation of his original material with SEM stereotechnique revealed, that Krause recognized almost all relevant characters of the respective taxa except for fine surface ornamentations. Apart from the latter, his illustrations are still informative and suitable for taxonomic work. Already assumed synonymy of many new taxa later described from outcrops, borings and also glacial erratic boulders based on Krause’s illustrations could be verified by the present study.

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