2. Kloedenia and Related Ostracode Genera in the Silurian and Devonian of the Baltic Area and Britain

By

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ABSTRACT.—Submerged parts of the youngest Silurian sequence in the Gotland area, corresponding beds in Scania, and the lowermost Devonian beds in the Welsh Borderland contain a series of ostracode species more or less closely related to *Kloedenia wilckensiana* (JONES 1855). Species included in this taxion and in *K. kiesowi* (KRAUSE 1891) are referred to the new genera *Frostiella* and *Londinia* with two species each (see Contents).

In the genus *Kloedenia*, as restricted herein, no adult tecnomorphs have been found. The heteromorphic characters are acquired during the last moulting, but intermediate specimens are not uncommon, in contrast to conditions in all other *Beyrichiacea*. The slight cruminal metamorphosis in *Kloedenia* is the extreme, orthogenetic, opposite to the complicated palingenetic metamorphosis in *Craspedobolbina*; in *Kloedenia* only a simple inflation takes place along the strongly reduced velar fold, and the striate swelling along the velar edge is divided into three ridges.

With the publication of the present study, the carapace morphology and the systematically important cruminal ontogeny of all major beyrichiacean groups, except the *Zygobolbinae*, have been treated on the basis of a representative material. The *Beyrichiacea* are subdivided into two families, *Craspedobolbinidae* and *Beyrichiidae*, representing two developmental branches in velar morphology and cruminal metamorphosis. The main features in the beyrichiacean system are discussed.

The study is largely based on new collections of erratic *Beyrichienkalk* ("*Beyrichia* Limestone") from Pomerania and Rügen. The occurrence of these erratics and their geographical and stratigraphical origin are briefly discussed.

Contents

Introduction

In a recent paper (MARTINSSON 1962) it has been shown that the main branches of the beyrichiacean ostracodes are characterized by different stages or trends in the development of the cruminal metamorphosis, i.e. in the transformation of an anteroventral part of the velum, during the last moulting, into a spherical brood pouch, the crumina. In the subfamilies treated hitherto, branches with a very complicated, characteristically palingenetic metamorphosis were represented (e.g. *Craspedobolbininae*) as well as branches where the recapitulation of the phylogenetic development had been reduced to a minimum (e.g. *Beyrichiinae*). However, in all subfamilies treated hitherto the metamorphic changes during the last moulting implied very far-reaching morphological differentiations in the anteroventral region of the heteromorphic carapace, not preceded by any transitional changes in the normal tecnomorphic carapaces of the penultimate moult stage.

During the preparation of the paper quoted, it became evident that the *Kloedeninae* must be considerably different from other beyrichiaceans as to dimorphism. *Kloedenia wilckensiana*, the type species of the genus, had been revised by KESLING (1956), who also described its ontogeny and dimorphism. However, it could be concluded from the results of the beyrichiacean study quoted, in combination with the excellent figures provided by KESLING (op.cit., Pls. VI and VII), that the dimorphism of *Kloedenia* must either imply lobal differentiations (a syllobial cusp appearing in the male and in some moult stages, but absent in other moult stages and in the female) quite unknown in other palaeocopes, or must result in only heteromorphs in the adults. In the latter case, *Kloedenia wilckensiana* var. *plicata*, small tecnomorphs of which had proved to possess a similar syllobial cusp (cf. MARTINSSON 1962, p. 17), must be represented with one kind of dimorphs in the figures referred to. However, the strange ventral morphology of the crumina and of the presumptive velar edge in the tecnomorphs had to be explained if the problem was to be solved. Available collections were not sufficient for this.

In order to obtain the necessary material, collecting was made along the coast of Pomerania where erratics containing *Kloedenia* occur in great number. In connection with this, KRAUSE's old collections of ostracodes from erratics, recently redeposited by the Soviet authorities in the Palaeontological Museum of the Humboldt University in Berlin (cf. DIEBEL 1960), were examined and found to contain a valuable material of kloedeniines.

During the field work in 1961 a number of localities along the Pomeranian coast between Rowy and Rewal (Fig. 3) were visited; Dr. A. URBANEK kindly continued the collecting during his field work farther westwards along the coast. A small material was also collected from localities in Berlin (Kiesgrube Parey in Spandau) and on Rügen.

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Origin and erratic occurrence of the Beyrichia Limestone

Boulders, or rather pebble-sized erratics, of greenish grey, when weathered whitish grey, more or less arenitic limestone, known as *Beyrichienkalk*, occur in the deposits of the Quaternary glaciations in the area south of the Baltic Sea. They occur, in deposits of the penultimate (Saale) glaciation, as far westwards as in the neighbourhood of Groningen. The eastern boundary of the distribution area is not well known, as the records of Silurian erratics with "*Beyrichia*" often lack faunistic specifications. GREWINGK (1861, Pl. E) states a limit of the "Upper Silurian zone 8, with *Beyrichia*" through Kolkasrags (Domesnäs) and Kuldiga (Goldingen). In a later paper (GREWINGK 1879, p. 79), the eastern limit of the fan with *Beyrichienkalk* was moved to a line from Sloka (Schlock) to Kaunas (Kowno). JENTZSCH (1880, p. 627), however, provides more exact information as to the distribution of the "true" *Beyrichienkalk* in East Prussia; the eastern limit of the fan containing these rocks passes E of Tilsit (COBETCK), near Goldap (Gołdap), and W of Lyck (Ełk), and in the eastern zone of the distribution area the frequency of these erratics is very low. REUTER (1885, p. 679) reports an easternmost find of *Beyrichienkalk*, containing some *Kloedenia wilckensiana*, from Pillkallen.

These are probably the most authoritative statements on the easternmost finds of the *Beyrichiengestein*, i.e. the not particularly argillaceous limestones containing *Amygdalella subclusa*, *Sleia kochi*, *Hemsiella maccoyiana*, *Macrypsilon salterianum*, *Berolinella steusloffi*, *Neobeyrichia buchiana*, *N. tuberculata*, *Frostiella plicata*, *Kloedenia wilckensiana*, and *K. leptosoma*. It must be borne in mind, however, that *Beyrichia wilckensiana* in older papers often stands for the entire subfamily *Kloedeniinae*, and *Beyrichia tuberculata* for most *Beyrichiinae*, and that *Beyrichienkalk* in some cases might signify material from lower levels in the Estonian exposures. The faunistic definition of the *Beyrichienkalk* given above restricts the unit in question to some extent. Even then, however, it is not a very homogeneous unit, as may be concluded from the subdivisions given by REUTER (1885, pp. 668–677); some of the faunistic characteristics of the Pomeranian material will be discussed in a forthcoming paper.

As far as the Pomeranian material found in the moraines of the last glaciation is concerned, it can be concluded that rocks referred by REUTER (op. cit.) to the *Baueri*, *Bronni*, *Noetlingi*, *Bigibbosa*, and *Gibbosa* limestones, containing *Neobeyrichia* (*Nodibeyrichia*) spp. with strongly dissected lobes, are absent or extremely rare. They probably have their maximal distribution in East Prussia, and this probably explains why they are practically unrepresented in the Berlin Museum; they offer several taxionomical problems (cf. MARTINSSON 1962, pp. 23 and 323). It also seems obvious, when collecting along the coast, that the frequency of *Beyrichienkalk*, and particularly its softer varieties, decreases towards the west at the same time as the *Graptolithengestein* generally increases, both in relative frequency and in the size of the pieces; in East Prussia the *Graptolithengestein* is known only from a few occurrences (cf., e.g., JENTZSCH 1880, p. 628). It seems, then, as if the erratic *Beyrichienkalk* treated here has its distributional maximum in the great Berlin lobe of the Weichsel ice sheet, between the mouth of the Oder and Königsberg. According to extant information on the ice movements, the ice masses in this lobe must have passed through the Middle Baltic Depression (Fig. 3), and the Pomeranian material can be expected to be derived from the floor of the Baltic not very far east of Gotland.

In the first paper dealing with the geographical and stratigraphical provenance of the *Beyrichienkalk*, based on comparative studies of the Silurian of Gotland as well as corresponding strata on Ösel, SCHMIDT (1861 b, pp. 460–464, cf. SCHMIDT 1861 a, p. 77) suggested that the *Beyrichiengestein* came from the morphological continuation of the Ohesaare Pank, the clint along the west coast of the Sõrve Peninsula on Ösel.

> "Die Beobachtung lehrt, dass dieser Pank früher ungleich weiter nach Westen reichte. Mir sind Steine einige hundert Schritte weit im Meere gezeigt worden, die früher auf dem Hofe von Bauernwohnungen gestanden haben. Jährlich stürzen noch überhängende Theile des Panks, der an seinem Fusse von den Wellen unterwaschen wird, ins Meer. Leicht mag der Ohhesaare-Pank eine Brücke bis zum südlichen Gothland gebildet haben, das so viele Zeichen einer mit Oesel identischen Schichtenbildung zeigt. Die nachherige Zerstörung dieser Brücke durch Treibeis und andre Ursachen war der Grund, dass die erwähnten Geschiebe sich über das norddeutsche Tiefland, das zum Theil noch von Wasser bedeckt war, ausbreiteten" (SCHMIDT 1861 a, p. 77).

With the exception that "*andre Ursachen*", i.e. glacial erosion and transportation during the Quaternary glaciations, the importance of which was first realized just at the time when SCHMIDT's paper was published, have taken the place of the enormous rate of marine abrasion suggested by SCHMIDT, this view is still tenable in its main features. This is the primary source for all later quotations and re-quotations regarding the origin of the *Beyrichiengestein* (cf., e.g., KRAUSE 1877, p. 7, REUTER 1885, pp. 660–679, and KESLING & WAGNER 1956, pp. 36–39). It had been stated earlier that the Silurian erratics have come "von der Insel Gottland selbst oder aus einem ihr nahe liegenden seitdem zerstörten silurischen Gebiete" (ROEMER 1858, p. 272), but SCHMIDT seems to have been the first to verify this by personal investigations in all three areas concerned.

SCHMIDT's (1861 b, pp. 462–463) statements that *Kloedenia wilckensiana* (*s.l.*) occurs in the Ohesaar Beds was confirmed in later investigations by HOPPE (1932) and is correct at least in so far as a kloedeniine, a *Frostiella* species, is represented by young moult stages in the collections of Ohesaar material in Uppsala, Lund, and Stockholm. It is still questionable, however, whether any *Kloedenia wilckensiana* (*s.str.*) has been found on Ösel; furthermore the lithology of the *Beyrichienkalk* does not invite a comparison with any of those rock specimens which have been available. *Neobeyrichia tuberculata* and *Macrypsilon* cf. *salterianum* have been found on one of the slabs investigated (Mus. Pal. Inst. Univ. Uppsala). These species provide the best confirmation hitherto that the Ohesaar Beds may be contemporaneous or penecontemporaneous with the *Beyrichia* Limestone. Additional material from Ösel for ostracode revisions has not been obtainable so far.

Kloedenia wilckensiana has also been recorded from the Kaugatuma Beds at Vanamõisa by HOPPE (1932, p. 52), and LUHA (1930, p. 13, cf. p. 12) mentions *Kloedenia* from the (Rootsiküla-) Kaarma Beds in the section of the Vesiku Brook.

It is noteworthy that the typical *Beyrichienkalk* is not dolomitized at all. This fact has also been found remarkable by vertebrate palaeontologists who have worked both with these erratics and with Upper Ludlovian material from Estonia (*fide* Dr. T. ØRVIG). Large parts of the Lower Palaeozoic of Estonia, including beds from which *Kloedenia* has been reported, are regionally dolomitized; the intensity of the dolomitization of the Silurian increases eastwards from the western part of Ösel. West of the Baltic, on Öland and Gotland, dolomitization is practically absent. This fact strengthens the probability that the *Beyrichienkalk* as defined here might come from submarine occurrences in the Baltic between Gotland and Ösel.

As shown in an earlier study (MARTINSSON 1958), the *clint* morphology of the Baltic provides a possibility of constructing an acceptable map of the distribution of the Palaeozoic systems in the floor of the Baltic. Even if considerable sources of error, owing to the lack of subsurface information, are taken into consideration, the horizontal distribution of the systems cannot be expected to deviate much from the conditions sketched in the map (op. cit., Fig. 10); in sections (op. cit., Figs. 3–9) the boundaries have been drawn as simple projection lines, without further suggestions as to the configuration of the basin or other changes in facies or thickness than those verified or suggested by the results of borings.

An analysis of the depth conditions S and SW of Gotland, as made known on the nautical charts (Fig. 1), shows that the Hoburg Bank forms a longish feature on the sea floor along the strike of the stratigraphical units of the Silurian of Gotland. The evidence of the ostracode faunas of Gotland verifies

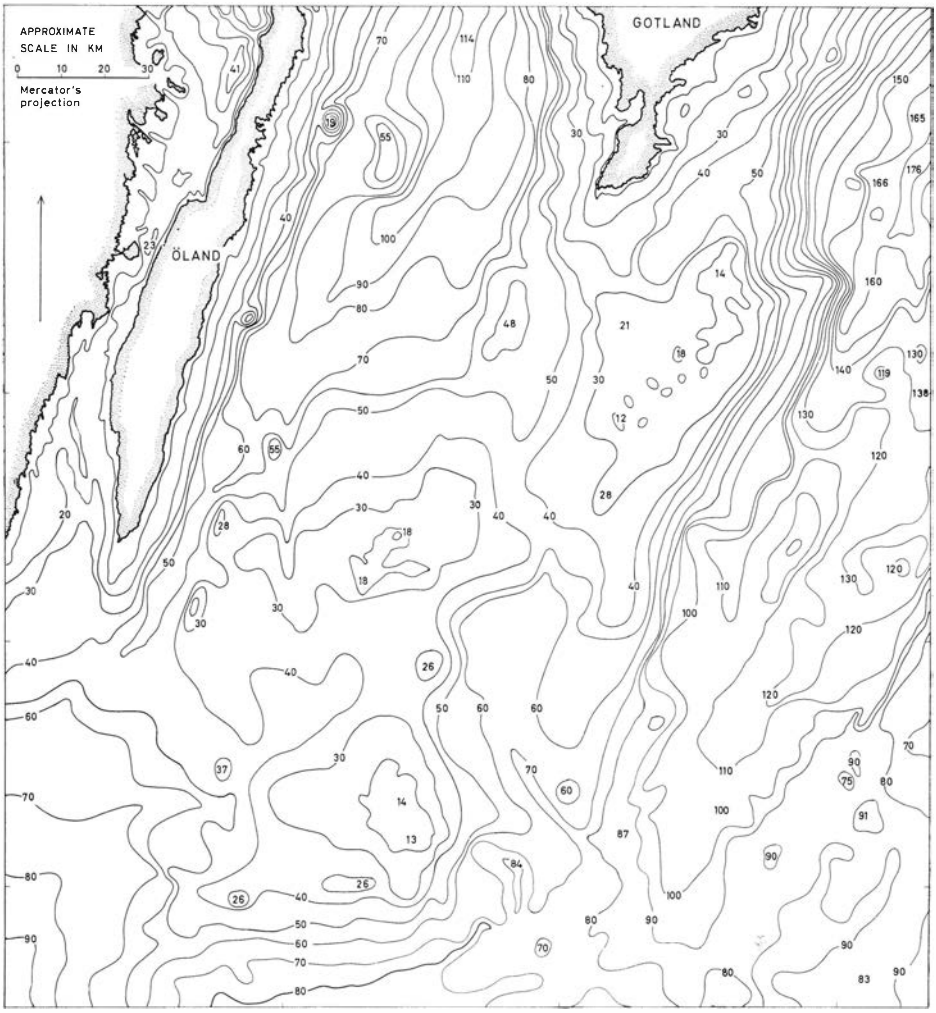


Fig. 1. Topography of the sea-floor of the Baltic south of Gotland, between the Middle Baltic Depression and Öland, compiled from the nautical charts.

that the *Beyrichienkalk* must be younger than any strata represented on Gotland. Facial differences cannot explain the absence of the faunas of the *Beyrichia* Limestone there. However, the fauna has, if the total number of taxia is considered, a more primitive aspect than that of the *Beyrichienkalk*; at the same time *Neobeyrichia* (*Nodibeyrichia*) and *Amphitoxotidinae* show clear affinities to species represented in the Ludlovian of Gotland.

The Hoburg Bank may be regarded as a morphological feature developed in younger beds but otherwise of the same kind as Sudret, the southernmost peninsula of Gotland, probably consisting of predominantly bedded limestones in its basal parts and possibly crowned by smaller reef bodies. A some-

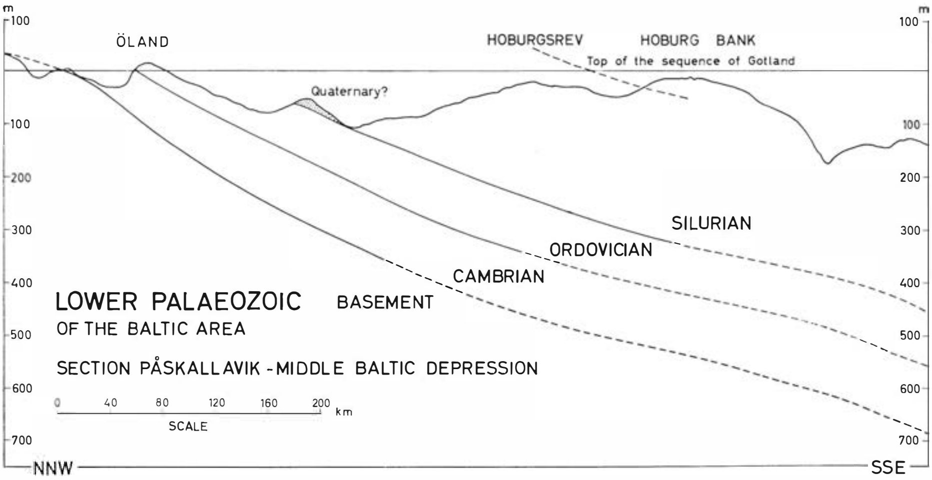


Fig. 2. Section across the western part of the Baltic, across the northern part of Öland and Hoburg Bank south of Gotland, compiled from available data on morphology, structure and thickness of the Palaeozoic in this area. However, this section provides a much thinner sequence than the total 500 m generally stated for the entire Silurian sequence of Gotland; as the lower boundary of the Cambrian is on the whole better established than higher datum levels, a sequence of this thickness would not permit much space for the Cambro-Ordovician. A boring through the Silurian on south-easternmost Gotland is needed to throw light on this complex problem and those facial changes which are indicated by conditions further referred to in the text.

what similar feature on the same morphological level is provided by the South Mid-Sea Bank (cf. Figs. 3 and 1); the North Mid-Sea Bank must lie lower in the sequence than the two other banks.

Fig. 2 is a section drawn on the basis of our present knowledge as to the depth of the Precambrian basement and the borings in the area (Martinsson 1958, Fig. 11; cf. Атлас литолого-палеогеографических карт Русской платформы; unfortunately only a small part of the borings east of the Baltic have been treated in publications) and the estimated thicknesses and dips of the strata exposed on Gotland. In the latter respect, however, a compilation of the thickness data of the beds which are not known to thin out and disappear in SW direction within Gotland, results in a thickness of 477 m (cf. Hede 1960); the submarine Llandoverian sequence of Gotland is about 140 m thick in the Visby area (cf. Thorslund & Westergård 1938 and the log in Hedström 1923). The basement in the Hoburgen area cannot be much deeper than 500 m, and there is, then, no room for the Cambrian and Ordovician in the sequence. This is probably explained by the fact that Hede's estimates include huge limestone units which are probably absent in the SW area (cf. below). Fig. 2 is based on the principles that the lower boundary of the Cambrian is the best datum available in the area and that Cambrian and Ordovician are drawn with minimum thicknesses. This only allows for a depth below sea level of the Silurian-Ordovician boundary in the Hoburgsrev area of ca.

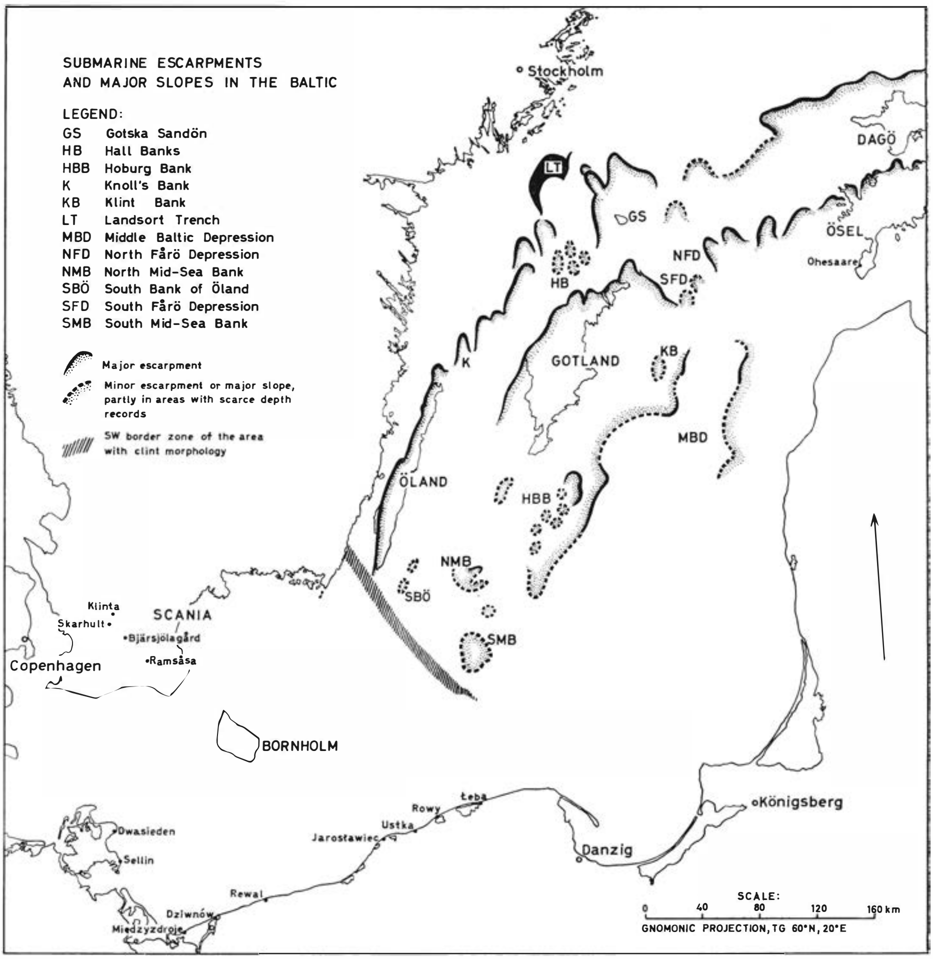


Fig. 3. Morphological map of the Palaeozoic of the Baltic area. A number of ostracode localities of major interest with respect to faunas around the Siluro-Devonian boundary have been indicated. Province and major place names according to international usage; minor place names according to administrative use in 1962. Synonyms: Scania–Skåne, Copenhagen–København, Jershöft–Jarosławiec, Stolpmünde–Ustka, Danzig–Gdańsk, Königsberg–Калининград, Ösel–Saaremaa, Dagö–Hiiumaa.

250 m and of ca. 330 m in the Hoburg Bank area. The youngest beds of Gotland are found at about 37 m above sea level in the Klev and at 20 m in Hoburgen. This area, however, is situated very far from borings reaching the basement, and all surprises as to the thickness and facies are possible.

If the dips are not considerably different from the estimates presented in Fig. 2, the Silurian sequence at Hoburg Bank must continue upwards through 40–60 m, at least, of beds younger than those represented in the Hoburgen-Klev area. As seen in Fig. 2, the slope towards the Middle Baltic Depression cuts right through this sequence again, down to about the level of the Sundre and Hamra Beds. Large parts of the floor of this depression, east of the valley with maximal depths, may also be expected to be covered with rocks of the same age as those in Hoburgs Bank (cf. the projection line "top of the sequence of Gotland" in Fig. 2). These areas are the most probable place of origin of the *Beyrichienkalk*.

The same sequence may be expected to be present in the South Mid-Sea Bank. It is, however, questionable how far to the south-west there existed any limestones of morphological importance in the Silurian.

As seen in the morphological map, Fig. 3, the scarp continuing the clint constituted by soft Llandoverian-Wenlockian marls crowned by a cover of resistant Wenlockian limestone, constituting the NW coast of Gotland, disappears SW of this island. This can be explained by a transition of all the Silurian sequence represented into a more argillaceous—and graptolitiferous—facies, as also suggested by trends in the outcrops on Gotland, resulting in the obsoletion of the complex of marls with a limestone cover which has led to the formation of scarps in the Silurian elsewhere in the Baltic (cf. MARTINSSON 1958). The areas around the North Mid-Sea Bank are probably the place of origin of the *Graptolithengestein* (Uppermost Wenlockian–Lower Ludlovian).

The South Bank of Öland and the South Mid-Sea Bank are the last features in SW direction in the floor of the Baltic which can be claimed as features in the clint landscape. SW of a zone marked in Fig. 3 the very even sea-floor slopes gently down towards the tectonically disturbed Bornholm region. In how far this surfaces is the continuation of the peneplain facet mapped as the Mesozoic (?) peneplain of southern Sweden by RUDBERG (1954, Pl. 1) or is covered by younger sediments, is very difficult to establish. In the SE part of this area we know from the Leba boring that already the Zechstein transgression invaded a land surface in Silurian rocks (cf. DAHLGRÜN & SEITZ 1943).

The conditions discussed stress the importance of a boring on southwesternmost Gotland and of an extensive investigation of the surface of Hoburgs Bank. The latter investigation, at least, seems to be made possible in a near future. It is probable that this work will prove the existence of an uppermost Ludlovian limestone cover over a much more argillaceous Silurian sequence than that exposed on Gotland.

A discussion of the position of the Silurian-Devonian boundary in this area is left outside the scope of this paper. The palaeocope faunas of Scania, the *Beyrichienkalk*, and the Leba core will be discussed before this problem will be taken up.

As occurring along the coast of Pomerania the erratics of *Beyrichienkalk* are flattened pepples, some cm thick and generally about palm-sized or smaller; comparatively seldom do they reach boulder dimensions. In the fresh sections in the moraines they are very difficult to find, but they are concentrated by the abrasion of the cliffs and are easily found along the beaches. The shape of

Fig. 4. The coast of Pomerania east of Ustka (Stolpmünde). Erratics of *Graptolithengestein* and *Beyrichienkalk* occur sparsely in the moraines of this area and are seldom found in fresh sections but are concentrated on the beaches of outwash material. Photo A. MARTINSSON 19.6.1961.

the pieces and an argillaceous cover sometimes found along the surfaces suggest that the thin limestone beds have been interbedded with calcareous shales.

This material is seldom affected by weathering. Most older collections of *Beyrichienkalk* in the museums are heavily weathered and are very much easier to prepare as far as lobal features and entire valves are concerned. Even the ornamental features are easily freed by preparation but may be destroyed by even the most cautious washing or brushing, which should be borne in mind when handling such material. In the unweathered material excellent surfaces with fine striation or reticulation are obtained, but it is very difficult to get fine preparations of entire lobate valves.

Historical review of *Kloedenia*

C. F. WILCKENS (1769, Pl. VII, Fig. 38) first figured a specimen of a *Kloedenia* under the name of *Agnostus pisiformis*; this is apparently the first record of a palaeocope ostracode in literature. It is evident, too, that four of the specimens included by K. F. KLÖDEN (1834, Pl. I, Figs. 16–19) in *Battus tuberculatus* belong to the genus *Kloedenia*. Both authors regarded these fossils as trilobites, in contrast to VON BUCH (1831) who believed them to be young brachiopods; attention is drawn, however, to KLÖDEN's statement (op. cit., p. 113) that those forms of *Battus* which have "the shape of a bean, but only the size of a poppy seed up to that of a millet grain" are similar to the ostracode *Cypris Faba.* The definite recognition of the beyrichiaceans in the rocks later termed *Beyrichienkalk* by KADE (1855) was achieved by BEYRICH (1845).

On a journey to Germany Sir CHARLES LYELL was given a material of drift material from Germany by BEYRICH at the request of T. R. JONES. The investigation of this material resulted in the first number in JONES's long series of *Notes on the Palaeozoic Bivalved Entomostraca* (1855 a). With reference to KLÖDEN's figures JONES described *Beyrichia Wilckensiana* and *B. Wilckensiana* var. *plicata,* referred to the group of *Beyrichiae corrugatae* introduced by him; his later (1855 b, p. 175) attribution of these two forms to the *Beyrichiae simplices* was due to an erratum (JONES 1855 c, p. 83, foot-note). Figures in the first of these papers (1855 a, Pl. V, Figs. 18 b and 20 b) show that *B. Wilckensiana* has a crumina with three ventral ridges and that var. *plicata* has a narrower, simple velar ridge or bend. Later BOLL (1862, Pl. I, Fig. 14 b) published a figure where the three ventral ridges on the crumina of *B. Wilckensiana* (*s.l.*) are seen in anterior view, drawn in a fully correct manner. KRAUSE (1877, p. 36) recognized var. *plicata* and regarded it as a further developed form of *B. Wilckensiana.*

JONES & HOLL (1886 a, pp. 347 and 362) introduced the genus *Kloedenia* for species referred to the former group of *Beyrichiae corrugatae,* covering very different ostracodes named *K. Wilckensiana, K. Wilckensiana* var. *plicata,* and *K. intermedia* var. *marginata*; three other species were at the same time removed from the *Corrugatae.* In 1892 MILLER (p. 708) designated "*K. wilkensana*" as the generotype of *Kloedenia.*

A large number of species, most of them doubtless not belonging to the subfamily *Kloedeniinae* in the present sense, have later been referred to *Kloedenia* (cf. e.g. BASSLER & KELLETT 1934, pp. 360–367). Not until KESLING's studies of a collection of weathered erratics from Berlin—brought together by C. L. ROMINGER during those years when *Beyrichia* and the beyrichiids received their place in the scientific discussion and later deposited in the Museum of Paleontology, Ann Arbor, Michigan—any essential information was published as to the genus *Kloedenia sensu stricto* (KESLING 1956). This paper has already been discussed in the Introduction.

At present kloedeniine ostracodes are known, on the evidence of material treated in this revision or sufficiently well illustrated in other papers, from Ösel (SCHMIDT 1861 a and b, etc.), the floor of the Baltic, i.e. in drift material in the area south of this sea (WILCKENS 1769, cf. JONES 1855 a, etc.), Scania (GRÖNVALL 1897, MOBERG & GRÖNWALL 1909, etc.), the Welsh Borderland (ELLES & SLATER 1906, STRAW 1929), and in Arisaig, Nova Scotia, (JONES 1870, COPELAND 1960). These forms occur in a restricted sequence below and above the Siluro-Devonian boundary as defined and accepted by British geologists in the Welsh Borderland. Only these forms will be treated in more detail here.

Carapace morphology in the *Kloedeniinae*

LOBATION.—The only prominent lobal feature in the carapace of *Kloedenia* is the preadductorial lobe which protrudes further over the hingeline than in any other beyrichiaceans.

In the present paper the new genus *Londinia* is included in the *Kloedeniinae*. This genus has a lower but essentially similar preadductorial lobe, an anterior lobe and a syllobium which, during the ontogenetic development, is divided into a narrow lobe immediately behind the adductorial sulcus, protruding over the hingeline with its cusp, and a narrow, low posterior lobal feature along the posterior margin. All lobes are characteristically flattened or faceted laterally.

The sulci of *Londinia* are more marked than in other beyrichiaceans; in *L. reticulifera* they completely dissect the lateral side of the carapace, and no traces of the zygal arch, which is probably a primitive feature in the beyrichiaceans, is found in the species treated here. In *Kloedenia* the prenodal and preadductorial sulci largely consist of the angles between the preadductorial lobe and the even carapace sides; the adductorial sulcus is, however, somewhat set off even from the syllobial part of the carapace, and a muscle

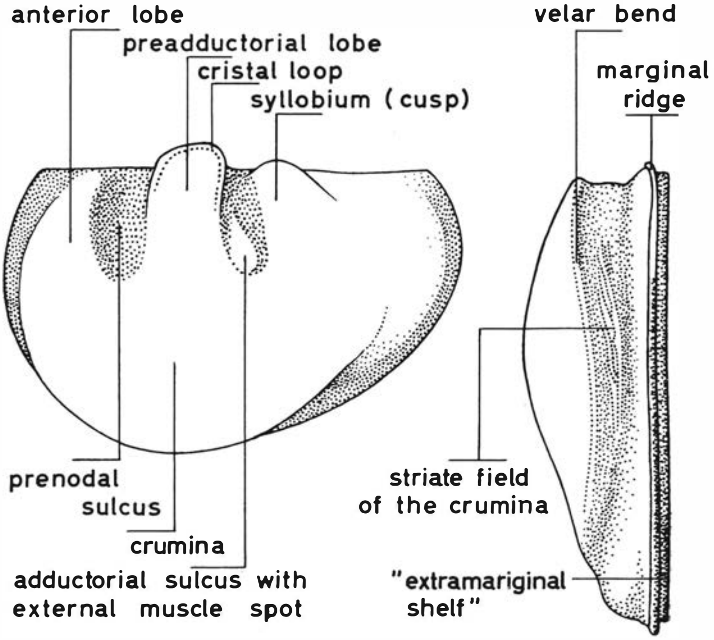


Fig. 5. Terminology of the kloedeniine carapace.

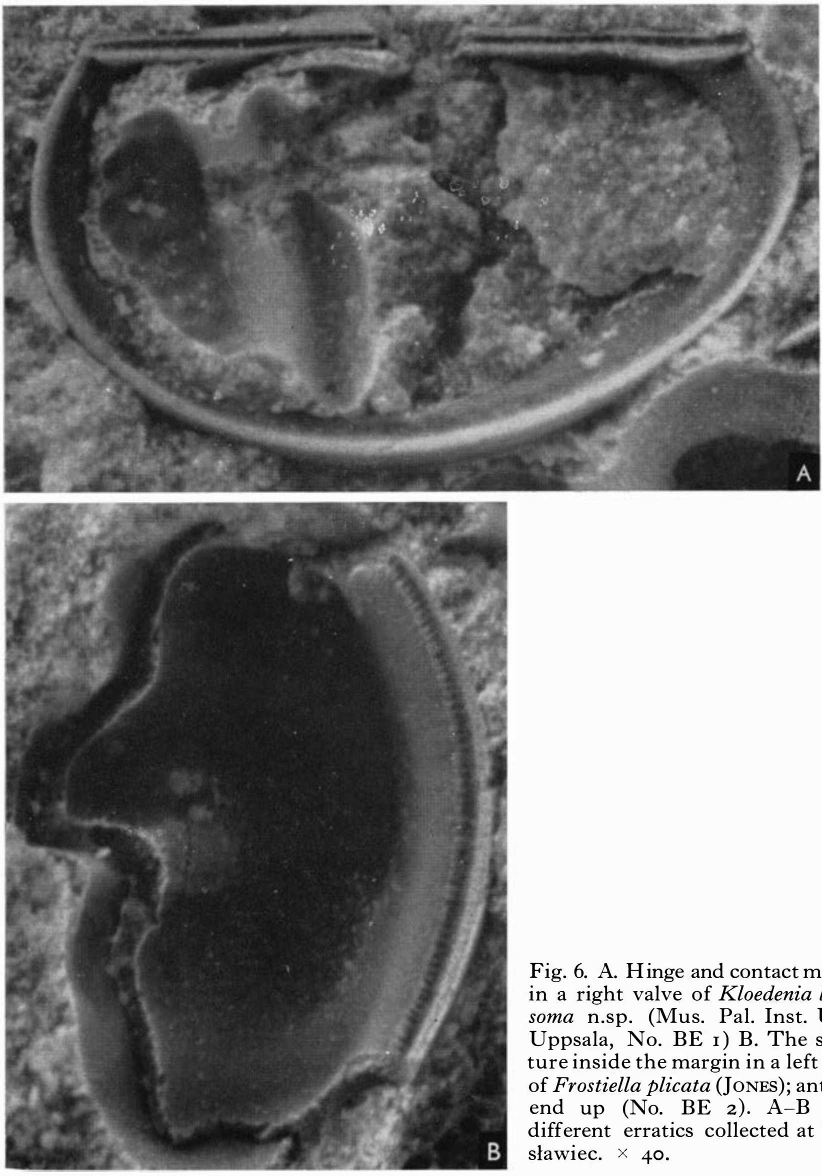


Fig. 6. A. Hinge and contact margin in a right valve of *Kloedenia leptosoma* n.sp. (Mus. Pal. Inst. Univ. Uppsala, No. BE 1) B. The structure inside the margin in a left valve of *Frostiella plicata* (JONES); anterior end up (No. BE 2). A–B from different erratics collected at Jarosławiec. × 40.

spot of the type earlier demonstrated in other beyrichiaceans, characteristically tapering in dorsal direction, may sometimes be observed in the lower part of this sulcus.

I would be very difficult to recognize any certain relationships between the extremely specialized *Kloedenia* and the very different *Londinia* or with any other beyrichiaceans if there had not been any intermediate forms.

Such forms are found in the genus *Frostiella*. In *F. groenvalliana* the lobation invites comparisons with the genus *Londinia*. It is evident, however, that

Frostiella is much nearer to the *Kloedenia* lineage than *Londinia* which has specialized in another direction. In *F. biplicata* the lateral sides of the carapace have reached the development of *Kloedenia*; only a cusp or short cuspidal plica remains of the syllobium. In *F. groenvalliana*, however, there is a wide lateroventral lobe connecting the other lobal parts of the carapace in the tecnomorphs, corresponding to the larger part of the crumina in the females. The third sulcus or sulcule is in this species developed in a manner similar to that of *Londinia*; in the *Kloedenia* carapace the lobe or lobule separated by it has become almost obsolete.

ADVENTRAL STRUCTURES.—The velum in the *Kloedeniinae* is much reduced. The sharp bend or ridge along the lateroventral lobe is regarded as homologous with, or as derived from, the velar structure.

The marginal structures are, too, flange- or ridgelike. The left valve slightly overlaps the right one along the ventral contact of the valves. The margin of the left valve is folded over a shelf along the right one; along this shelf there is a rounded ridge. With experience with other beyrichiaceans in mind, one would expect a similar ridge also in the left valve and some kind of covering flange or frill between them. However, a structure which might well be a reduced frill of the normal beyrichiaceans, dissolved into a row of minute denticles, has been found squeezed in the angle between the normally thick carapace wall and the covering flange of the left valve, both in *Kloedenia* and in *Frostiella* (Fig. 6 B).

HINGE.—The hinge mechanism of the *Beyrichiacea* is formed by a ridge in one of the valves—usually the left one—articulating in a groove in the other. It is probably a primitive feature that the groove, and even the ridge, may be split into two subequal units, the dorsal of which has a tendency to be suppressed (MARTINSSON 1962). In the advanced *Kloedeniinae* (Fig. 6 A) there is one main groove in the right valve entirely dominating the hinge mechanism; sufficiently good preparations of the corresponding ridge have not been obtained. There are, however, very fine accessory furrows along this groove, one below its posterior end and one above the anterior. The arrangement leaves us without any definite conclusion as to which of the branches in the primitive beyrichiaceans might be homologous with the groove in the *Kloedeniinae*.

ORNAMENTATION.—The normal ground pattern in the *Kloedeniinae* is a more or less sparse punctation; only in *Londinia groenvalliana* is there a reticulate area within the lateral facet of the preadductorial lobe (Fig. 7 B).

This lobe or node is of special interest as to the ornamentation in the different

Fig. 7 (opposite page). Ornamentation of the preadductorial lobe in different *Kloedeniinae*. Adult females. Oblique dorsal view, anterior end up. × 60. A. *Londinia kiesowi* (KRAUSE), right valve (Pal. Mus. Humboldt Univ. Berlin; KRAUSE's sample No. 549). B. *Londinia reticulifera* n.sp., right valve (Mus. Pal. Inst. Univ. Lund No. LO 4080 T, holotype, Klinta). C. *Frostiella groenvalliana* n.sp., left valve (Pal. Mus. Humboldt Univ. Berlin; KRAUSE's sample *Ringshö 1*, Klinta). D. *Frostiella plicata* (JONES), right valve (Mus. Pal. Inst. Univ. Uppsala, No. BE 3, Ustka). E. *Kloedenia leptosoma* n.sp., left valve (No. BE 4, Jarosławiec). F. *Kloedenia wilckensiana* (JONES), left valve (No. BE 5, Jarosławiec).

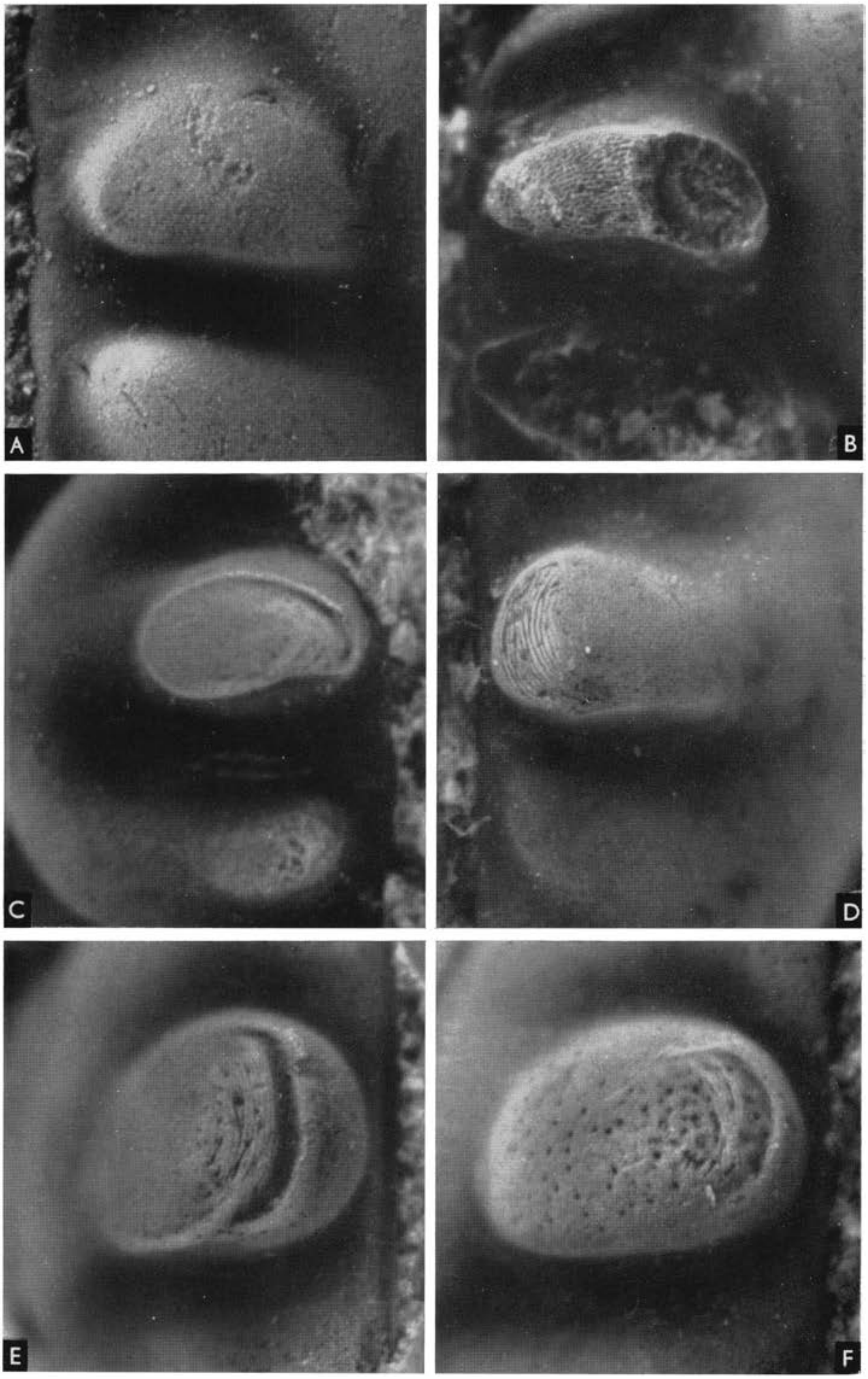

A
B
C
D
E
F

Fig. 8. Ornamentation of the preadductorial lobe in *Frostiella groenvalliana* n.sp. Same specimen as in Fig. 7 C, but in more strictly dorsal view than in the series in Fig. 7; anterior end up. × 60.

Kloedeniinae. In *Frosiella* and *Kloedenia* there is a ridge-like structure occupying the same position as the edge fo the lateral facet in *Londinia.* Without further claims as to homology (cf. p. 58) the term cristal loop is taken up for this structure. Inside this loop there is, then, a reticulation tending to striation, a more or less perfect striation, and a punctation associated with and sparsely breaking through these kinds of ornamentation. Figs. 7 and 8 show different types of ornamentation in the three genera *Londinia*, *Frostiella*, and *Kloedenia.* They are further described and discussed in the following chapters.

The marginal structures in *Kloedenia* show the same longitudinal striation as the ventral ridges on the crumina described below.

Lobal, Velar, and Ornamental Features of the Crumina.—Though leaving no doubt of an origin in common with that of the beyrichiaceans, the advanced kloedeniine crumina is very specialized. The changes occurring in *Kloedenia* can hardly be termed a metamorphosis, and the velum is involved only in so far as the ornamentation along it is affected. The crumina is essentially an inflation of the lateroventral lobal part of the valve.

Except for the large size, the crumina in the genus *Londinia* is essentially of the beyrichiine or zygobolbine type, but it differs from them in not affecting the contact margin or the marginal structures at all. These advanced conditions have been achieved even in advanced *Beyrichiinae*, and it is possible that the *Zygobolbinae* reached a similar stage, too.

The striation of the ventral side of the crumina in *Londinia* is of the beyrichiine type, and the inflation of the large crumina has made every trace of a velar structure obsolete (Fig. 13). In *Frostiella* there is a striate field inside the velar edge (Figs. 17 and 23). In *Kloedenia*, however, the striation is distributed as three separate, more or less rounded ridges, and the outer, less striate, of these ridges may be claimed to be homologous with the velar edge with more right than the others. *Frostiella biplicata* shows some features (cf. p. 40) supporting this homology.

TERMINOLOGY.—The terminology as discussed in this chapter is synthesized in Fig. 5 (cf. MARTINSSON 1962, Fig. 15).

Ontogeny of *Kloedenia*

Moult stages of *Kloedenia* and *Frostiella*, some of them from very early parts of the ontogeny, have been described by KESLING (1956).

The present material contains comparatively few tecnomorphs of *Londinia*. *Frostiella* is better represented. These genera had an ontogeny which was in all essential respects similar to that of other beyrichiaceans. All preadult moult stages were typical tecnomorphs, and the crumina appeared suddenly after the last moulting, without any intermediate stages. There are, too, adult tecnomorphs—males.

In *Kloedenia* the ontogeny was very different. Figs. 25 and 26 present different moult stages of *Kloedenia leptosoma* in lateral view, in reversed order. The youngest specimen figured corresponds in size to stage No. 6, counted from the adult one, No. 1; possibly there were three still younger stages as in the best ontogenetic series of beyrichiaceans investigated hitherto, in *Craspedobolbina* and *Kozlowskiella* (SPJELDNAES 1951, MARTINSSON 1956, ADAMCZAK 1958). All lobal and rudimentary velar structures are only inconsiderably and gradually modified during the part of the ontogeny represented, and the appearance of the crumina implies no obvious break in the gradual series.

If the critical parts of the carapaces are seen in ventral view, the gradual development is confirmed and illustrated by essential details.

In young moult stages, about No. 5 or 4, a somewhat thickened, striate part of the velar edge begins to separate from an outer, thinner ridge. This separation becomes gradually more pronounced in later stages. The sharp admarginal limitation of the striate ridge tends to become separated from the ridge as a torus-like structure (Fig. 28 B–D).

In the adult stage, finally, there appears a third, broader and more flattened, striate ridge between the others and the margin. This seems to take place through a division of the first striate ridge. The division is not always complete; both the ridges and the inflation of the crumina appear gradually. Fig. 28 E shows one of the fairly common intermediate stages; F and G of the same figure show a less complete division than H and I. The separation of the torus-like structure in the subadult stages certainly represents a transitional stage towards a third striate ridge which has not, however, proved to be developed, even occasionally, in subadult stages in the material studied.

All adult specimens are heteromorphs characterized by a stronger inflation of the cruminal part of the valve, more pronounced anteriorly, and with the changes in the ventral ornamentation last described.

Origin and development of the kloedeniine dimorphism

It is evident that *Frostiella* is very nearby related to the lineage leading to *Kloedenia.* In *Frostiella groenvalliana* there is still a fairly limited crumina, appearing as a marked anteroventral swelling of the lateroventral lobe after the last moulting. The conditions in *F. biplicata* are nearer to those of *Kloedenia*, but the typical beyrichiacean dimorphism in the adult stage is still retained.

The crumina in *Frostiella* and *Kloedenia* is longish and has extended from the restricted space known to be the primordial site of the crumina into the syllobium and even into the anterior lobe. The crumina consists almost exclusively of carapace elements.

It is very probable that this crumina originated from a longish crumina, more markedly set off from the valve than in the genera hitherto mentioned. One would expect, too, that this crumina might, in forms developing towards more advanced kloedeniines, have less influence on the marginal structures and the contact margin itself than the similar beyrichiine and zygobolbine cruminae.

These conditions are found in the genus *Londinia.* They are perfectly correlated with a considerable number of fairly specialized features occurring in the *Kloedeniinae.* The preadductorial lobe is protuberant, protruding considerably over the hingeline in *L. reticulifera*, *Frostiella*, and *Kloedenia.* The syllobial morphology is essentially the same, and the preadductorial lobe and the narrow main body of the syllobium are very near to each other, so that a very narrow and deep sulcus is formed. The ornamentation is a not very dense punctation, except on the lateral surface of the preadductorial lobe which shows reticulation and striation in the different genera; it has already been pointed out that there is ample reason for regarding the edge of the facet of the preadductorial lobe in *Londinia* as homologous with the cristal loop in the other genera.

In all genera concerned the velum is ridge- or bend-like, and the marginal structures of *Londinia* might well be regarded as a more primitive type of the same structures in *Frostiella* and *Kloedenia.*

Several of these features also invite comparison with the *Zygobolbinae*, as briefly discussed below (p. 57).

The far-reaching correlation of several very characteristic morphological trends indicate that *Londinia* is closer related with *Frostiella* and *Kloedenia* than any other forms known, being derived from a lineage separated from the *Frostiella-Kloedenia* lineage at a very early stage.

In a previous paper (MARTINSSON 1962) the subfamily *Craspedobolbininae* was characterized as the beyrichiacean group exhibiting the most far-reaching palingenesis in the cruminal metamorphosis. The *Kloedeniinae* represent its orthogenetic opposite among the forms described hitherto. They developed through forms with a large crumina, set off in about the same way as the globular crumina of the *Beyrichiinae*. The velum was gradually strongly reduced, and the obsoletion of the lobation reached its maximum in *Kloedenia*. Parallel to this development, the crumina was entirely incorporated with the carapace well, and the cruminal metamorphosis became almost obsolete. All surviving specimens of *Kloedenia* passed, without any real metamorphic changes, into heteromorphs with a more pronounced anteroventral swelling and an extra striate swelling or ridge along a lone indicating the position of the obsolete or rudimentary velar edge.

The apparent absence of adult tecnomorphs makes the genus *Kloedenia* one of those palaeocope taxia which might be taken into consideration as exhibiting parthenogenesis.

Subfamily *Kloedeniinae* Ulrich & Bassler 1923

Type Genus.—*Kloedenia* Jones & Holl 1886.

Genera.—*Londinia* n.g.
Frostiella n.g.
Kloedenia Jones & Holl 1886.

Diagnosis.—*Beyrichiidae* with a longish, more or less distinctly anteroventral crumina, extending from the anterior lobe to the mid-length of the syllobium, set off from the domiciliar part of the carapace—without any marked proximal constriction—as an ellipsoidal structure, or strongly assimilated with the domicilium. The formation of the crumina does not influence the free margin or marginal structures. The lobes tend to protrude considerably over the hingeline and to develop lateral facets or cristal loops.

Remarks.—There is a group of beyrichiids, consisting of "*Kloedenia*" *normalis* Ulrich & Bassler and associated species, *Lophokloedenia* Swartz & Whitmore, *Bingeria* Martinsson, *Welleria* Ulrich & Bassler, *Welleriopsis* Swartz *Pseudobeyrichia* Swartz & Whitmore, and, possibly, *Zygobeyrichia* Ulrich, from which most North American "*Kloedenia*" species have been recruited or which have been associated with *Kloedenia* in earlier systems (Ulrich & Bassler 1908 and 1923, Henningsmoen 1953 and 1955). These forms have in common with the *Kloedeniinae* a longish crumina which is more or less assimilated with the domicilium. In most other respects, however, as the lobal pattern and the ventral morphology of the crumina (known in detail only in *Bingeria*) they exhibit beyrichiine characteristics. They differ from the typical *Beyrichiinae* mainly by their characteristic, mostly more or less irregular reticulation. With our present knowledge it is necessary to include this group of genera in the *Beyrichiinae* (cf. p. 56).

Occurrence.—Known from marine Upper Silurian and Lower Devonian deposists in Baltoscandia, Britain, and Nova Scotia (cf. p. 41).

Genus *Londinia* n.g.

Cf. Figs. 9–13.

Derivation of the Name.— An adjective *Londinius*, inhabitant of [the vicinity of] Lund (*Londinum Gothorum*, *Londinium Scanorum*).

Type Species.— *Londinia reticulifera* n.sp.

Species.—*Kloedenia kiesowi* Krause 1891.
Londinia reticulifera n.sp.

Diagnosis.—*Kloedeniinae* with ellipsoidal crumina well set off from the domicilium. Preadductorial lobe and anterior lobule of the syllobium subequal in size and shape, more or less narrow, subtriangular, merging with the lateroventral part of the tecnomorphic valve on both sides of a narrow adductorial sulcus. Anterior lobe and posterior lobule of the syllobium narrow, low, subequal in size and shape and merging with the lateroventral part of the tecnomorphic valve. A considerable field on the admarginal part of the crumina with undifferentiated finger-print striation.

Remarks.—The characteristics first and last mentioned in the diagnosis are sufficient to distinguish *Londinia* from all other *Kloedeniinae*, but the subsymmetrical arrangement of the lobal features on both sides of the adductorial sulcus (in lateral view) is very conspicuous and applies to the tecnomorphs which are found incomparably more frequently than the females.

The two species are very different as to the relative prominence of the lobal features, and the cuspidal parts of the lobes do not protrude over the hingeline in the same characteristic way as in all other kloedeniines. Though there is some tendency to a development of lateral facets on the lobes of *L. kiesowi*, this development is incomparably more pronounced in *L. reticulifera*.

Not only the general arrangement of the lobation but even what is known about its ontogeny stress, however, the similarity of the two species. The adductorial sulcus is in young tecnomorphs relatively short, and only the corresponding cuspidal parts of the lobes are developed. In older tecnomorphs the sulcus becomes longer. However, in *L. kiesowi* it does not reach far below mid-height of the valve, in contrast to *L. reticulifera* where it almost dissects the side of the valve into two halves. In this species the anterior sulcus and the syllobial sulcule, too, become longer and cut in the adult male right through the lateroventral lobal part of the valve.

Possibly there exists one more *Londinia* species among ostracodes hitherto described. This species is *Kyammodes tricornis* Ulrich & Bassler, from the McKenzie Formation of Maryland. It differs from the species described here by its broad and undissected syllobium and by the apparent absence of lateral facets on the lobes (Ulrich & Bassler 1923, Pl. LV, Figs. 1–5). The young tecnomorphs described as *Kyammodes swartzi* (op. cit.; cf. Pl. LV, Figs. 14–16) also exhibit lobal characteristics of *Londinia* type.

Londinia kiesowi (KRAUSE 1891)

Figs. 7A, 9, 10, and 13B.

1891 *Kloedenia kiesowi* n. sp.—KRAUSE, p. 506; Pl. XXXII, figs. 12–13.
1908 *Kyammodes kiesowi* (KRAUSE)—ULRICH & BASSLER, p. 304; Figs. 57–58.
1909 *Kloedenia Kiesowii* A. KRAUSE—MOBERG & GRÖNWALL, Pl. IV, figs. 16 and 17; pp. 64–66 (*partim*!).
1923 *Kyammodes* (*Kloedenia*) *kiesoui* (KRAUSE)—ULRICH & BASSLER, Fig. 18:11.
1948 *Kyammodes kiesowi* (KR.)—KUMMEROW, p. 22; Fig. 7.

LECTOTYPE (selected herein).—A left female valve, figured by KRAUSE 1891, Pl. XXXII, fig. 13, refigured in this paper, Fig. 10 A (cf. Fig. 9), KRAUSE's boulder No. 459, Palaeontological Museum, Humboldt University, Berlin.

TYPE STRATUM AND TYPE LOCALITY.—Erratic. Upper Silurian (– Devonian) Beds in the Central Baltic area occuring as drift in the area S of the Baltic.

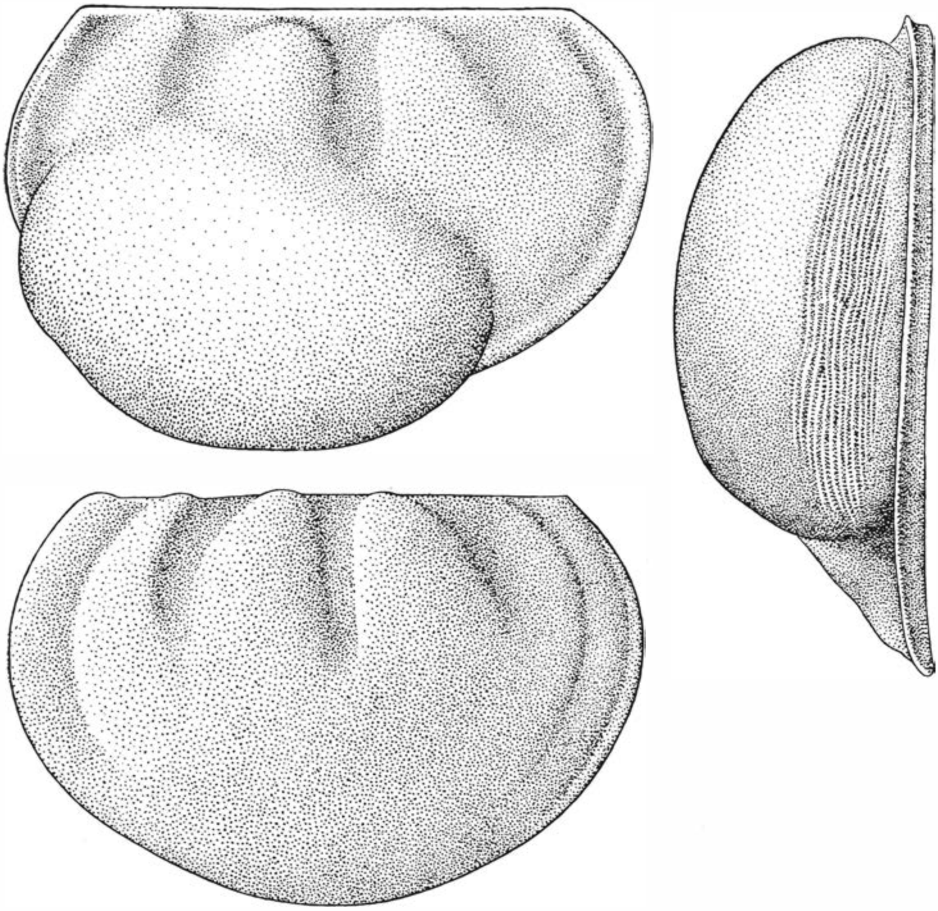


Fig. 9. *Londinia kiesowi* (KRAUSE 1891). Female and male in lateral view and female in ventral view. ×30.

Diagnosis.—*Londinia* species with low lobes which do not protrude over the hingeline. Adductorial sulcus not reaching far below mid-height of the valve. No distinct lateral lobal facets.

Description.—Outline subamplete to amplete; adductorial sulcus narrow and relatively deep. Preadductorial lobe and anterior lobule of the syllobium low, rounded, symmetrically arranged on both sides of the adductorial sulcus. The lobal cusps do not reach above the hingeline. A very slight tendency to a development of lateral lobal facets may be observed on the preadductorial lobe (Fig. 7 A). The anterior lobe and the posterior lobule of the syllobium very low, subsymmetrically arranged on both sides of the main lobal features mentioned; their cuspidal parts gently merge with the lateral side of the valve in the hinge region and do not, consequently, reach over the hingeline with their cuspidal parts. These lobal features are, too, set off from the anterior and posterior borders of the lateral surface of the valve by shallow sulcal features.

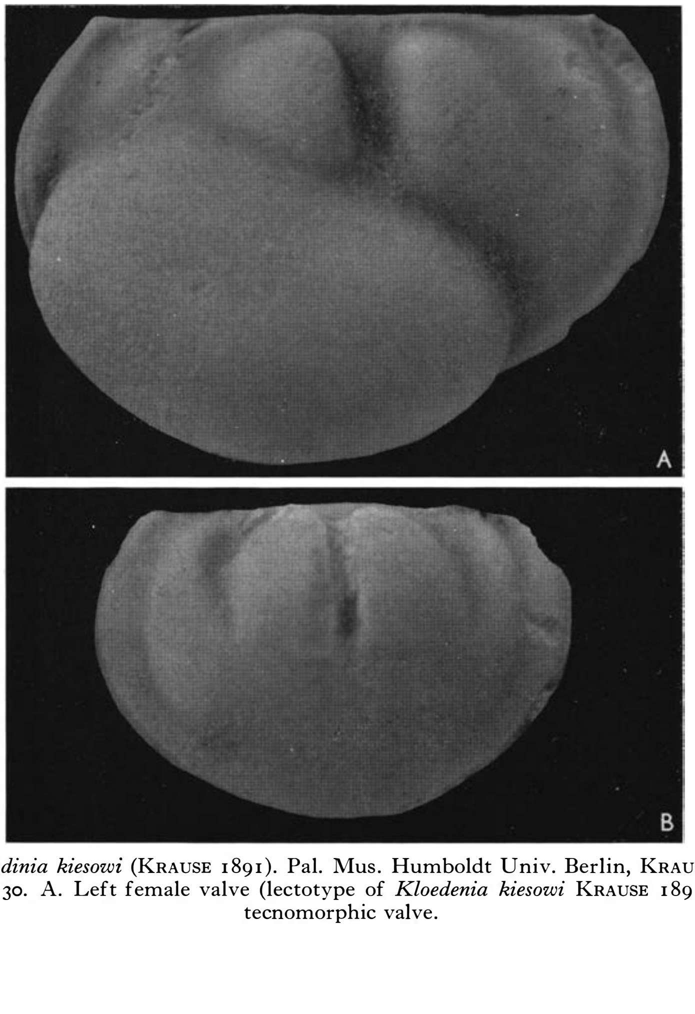


Fig. 10. *Londinia kiesowi* (Krause 1891). Pal. Mus. Humboldt Univ. Berlin, Krause's sample No. 549. × 30. A. Left female valve (lectotype of *Kloedenia kiesowi* Krause 1891). B. Left tecnomorphic valve.

Velum strongly reduced. In the tecnomorph it may be observed as a somewhat thickened bend close to the free margin, forming the ventral part of the lateral outline; subvelar field, thus, very narrow, almost obsolete. Marginal structure thin, flange-like.

Carapace almost smooth. A faint punctation may be observed on its most protruding lobal parts, particularly on the preadductorial lobe and the anterior lobule of the syllobium.

Crumina extremely large, extending from a point almost vertically below the anterior end of the valve to the anterior part of the syllobial sulcule, very distinctly set off from the domicilial part of the valve but not considerably constricted proximally. The crumina engages considerable parts of the anteroventral region of each valve, causing the obsoletion of the lower ends of the sulci. More than a third of the ventral surface of the crumina, as seen in strictly ventral view, occupied by a suggestively fingerprint-like striation. The crumina does not disturb the development of the marginal region of the valve and does not even deflect the marginal structure.

DIMENSIONS.—Hinge length of the two female specimens figured here, both from KRAUSE's boulder No. 549, 2295 μ (lectotype) and 2630 μ; height over the adductorial sulcus, including the crumina, 2075 μ and 2385 μ, respectively.

REMARKS.—The material from KRAUSE's boulder No. 549 comprises 2 female and 3 tecnomorphic specimens, less weathered than most other specimens in the collection. The species has not been found in any of the numerous boulders of *Beyrichienkalk* collected for this investigation. It is fairly frequent, however, in the part of the Leba core dated as the Öved-Ramsåsa Stage by DAHLGRÜN & SEITZ (1942, p. 89). The material last mentioned will, for technical reasons, be treated in detail in a separate paper. The material from Ramsåsa examined comprises one entire and one fragmentary female and 16 tecnomorphs.

Londinia kiesowi differs from *Londinia reticulifera* mainly by its lower lobes without prominent, cusps, and by the lack of the reticular elements in the ornamentation. It is, furthermore, considerably larger than the generotype.

There is, as briefly mentioned above, some tendency in the adductorial sulcus to extend further in ventral direction of the valve during ontogeny. The Leba material contains specimens representing the latter portion of the ontogeny which ascertain that the sulci never dissect the valves as completely as in *Londinia reticulifera*.

The short synonymy list above illustrates the taxionomic status and the different figures published of the species since it was described. ULRICH & BASSLER (1908) regrouped it from *Kloedenia* to *Kyamodes* (*errore*: *Kyammodes*) and provided a new figure (1923), obviously redrawn from KRAUSE. KUMMEROW (1948) provided a new, schematic figure.

The originals figured by MOBERG & GRÖNWALL (1909) require some special remarks. The tecnomorph in Pl. IV, Fig. 16 is No. LO 2181 (Mus. Pal. Inst. Univ. Lund) and the female in Pl. IV, Fig. 17 is No. LO 2182. Like several of the originals in this series, these specimens are covered with a crust of a finely crystalline, water-soluble, non-sublimating salt. The calcite of the carapaces has been more or less severely attacked chemically in connection with the presence of this salt, and some small specimens of other ostracodes have been entirely decomposed. No. LO 2181 is severely damaged, but No. LO 2182 has been attacked only locally.

The crumina of the female, from Bed 4 at Ramsåsa, is shorter than in other specimens observed, and the adductorial sulcus is somewhat wider. This is confirmed, too, by the damaged tecnomorph which, furthermore, shows greater asymmetry in the lobal elements on both sides of the sulcus. There is no additional material available to disprove or sustain possible doubts as to the specific identity of these specimens.

MOBERG & GRÖNWALL (1909, p. 64) point out that N. P. ANGELIN figured this species in his undistributed *Tabula A* of 1854. Like several other beyrichiids, *Londinia kiesowi* is represented (*Tab. A* Figs. 16 and 17) with both dimorphs figured in pairs, proving that ANGELIN recognized the beyrichiid dimorphism.

MOBERG & GRÖNWALL (op. cit., p. 65) mention that a specimen of this species has been found on Gotland. The specimen referred to has probably been identified. The label, stating only "Gotland" as collecting locality, and all other circumstances lead to the conclusion that this specimen cannot be accepted as documentation for the occurence of *Londinia* in the well known sequence of Gotland. Specimens from erratics found S of the Baltic are commonly referred to as coming from Gotland.

OCCURRENCE.—Submarine exposures in the Baltic and in the Leba core, associated with a fauna very similar to that of the Öved-Ramsåsa Beds in Scania. It occurs, furthermore, in these beds at Ramsåsa ("Bed 4"), but the material referred to as *Kloedenia Kiesowii* by GRÖNWALL (1897) and MOBERG & GRÖNWALL (1909) from Klinta is, as far as still identifiable in their collection, identical with the following species.

Londinia reticulifera n. sp.

Figs. 7B, 11, and 12.

1897 *Kloedenia Kiesowii* KR.—GRÖNVALL (later GRÖNWALL), p. 18; *non* 39.
1909 *Kloedenia Kiesowii* A. KRAUSE—MOBERG & GRÖNWALL, p. 65 (*partim*; *non* Pl. IV, figs. 16 and 17).

DERIVATION OF THE NAME.—Latin *reticulifer*, carrying or bringing a small net, referring to the preadductorial lobe facet.

HOLOTYPE.—A right female valve, Figs. 12 B, 13 A, and 7 B, with damages on the preadductorial lobe, the faceted lobule of the syllobium, and the anterior

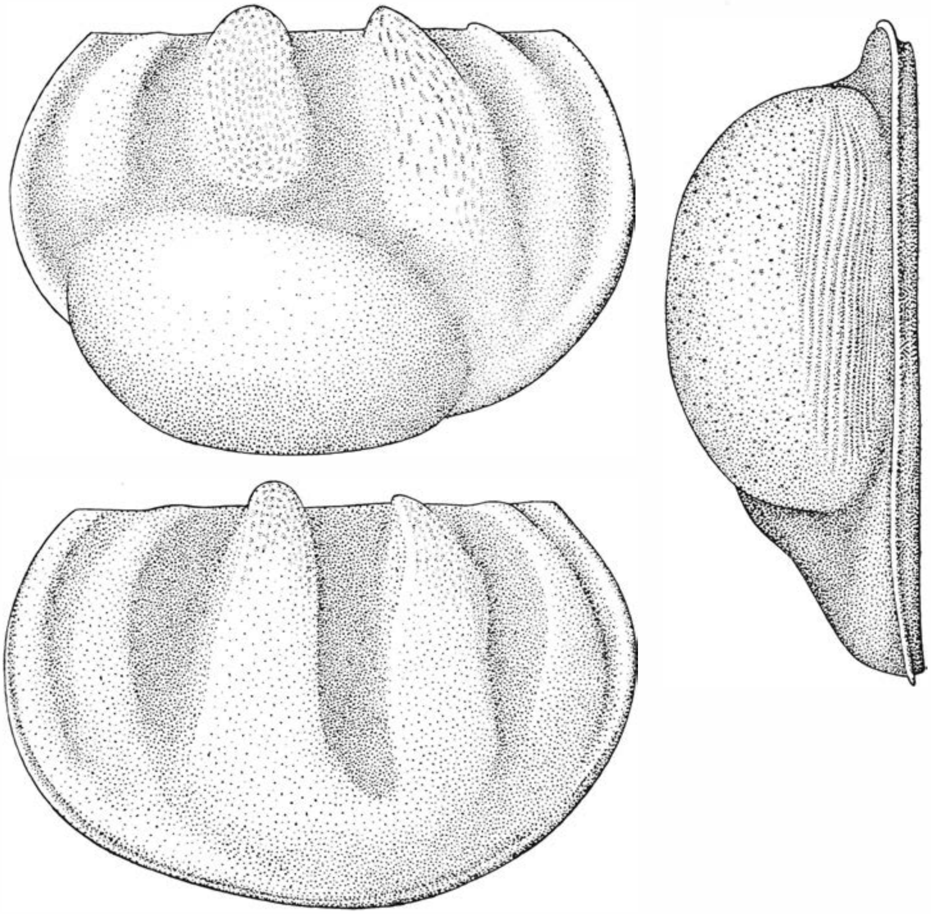


Fig. 11. *Londinia reticulifera* n.sp. Female and male in lateral view and female in ventral view. ×40.

part of the crumina; Pal. Inst. Univ. Lund, No. LO 4080 T (coll. K. A. Grönwall).

Type Stratum and Type Locality.—Shore of the lake Östra Ringsjön near Klinta, parish of Bosjökloster, Scania, "Bed 1" according to Moberg & Grönwall (l.c.; "Zone 1" *fide* label).

Diagnosis.—*Londinia* species with high, faceted, and more or less reticulate lobes which protrude ofer the hingeline. The sulci and the syllobial sulcule almost completely separate the lobes in adult males.

Description.—Outline subamplete to amplete. Adductorial sulcus long, narrow, and deep; in the adult male almost completely dissecting the lobal complex surrounding it. This complex consists of the preadductorial lobe and the anterior lobule of the syllobium which are in the adult male very acutely triangular, protruding with their cuspidal parts over the hingeline. The cusp of the preadductorial lobe is more rounded, that of the syllobial lobule more acute. These lobes have well developed lateral facets but lack the loop-like cristal swelling around the edge of the facets characteristic of other kloedeniines. The anterior lobe and the posterior lobule of the syllobium are subsymmetrically arranged around this lobal complex; the lateral surfaces of these elements form comparatively sharp edges along the prenodal sulcus and syllobial sulcule, respectively; both elements are bent according to the anterior and posterior outline of the valve, and their cuspidal parts merge with the bottoms of the sulcal parts of the valve after a gentle bow and protrude slightly over the hingeline.

The velum may be traced as a bend-like swelling along the margin, and the subvelar field is reduced to a minimum. The marginal structure is thin and flangelike and tends to form the larger part of the lateral outline in normally preserved specimens.

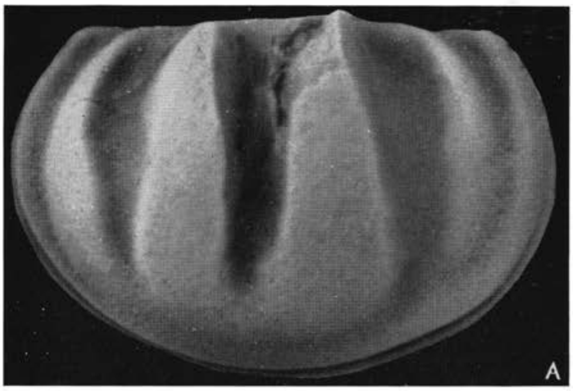
The crumina is very large, but its anterior end does not protrude further than vertically below the anterior limit of the anterior lobe, extending backwards to a point right below the anterior limit of the syllobial sulcule. It is not constricted proximally and occupies large ventral parts of the triangular lobal elements on both sides of the adductorial sulcus. The preadductorial lobe, however, does not merge with the crumina; its remaining portion is constricted ventrally so that it is separated by a deep and rather narrow sulcule. Similar conditions are also found between the faceted lobule of the syllobium. The most ventral part of this lobule has been displaced in a slight bow round the posterior end of the crumina.

The ventral side of the crumina is ornamented with a finger-print striation; there is no irregularity in the free margin or the marginal structure in this region.

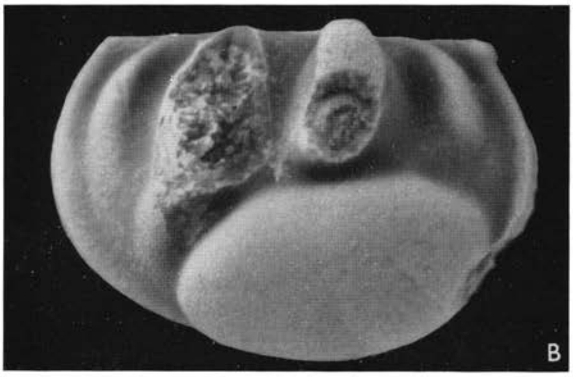
More distal parts of the crumina are punctate like large parts of the lobes. The punctation is denser along the outer base of the velar swelling which is entirely smooth. The densest ornamentation is found on the cuspidal parts of the lobes. In the female the entire facet of the preadductorial lobe is finely reticulate (Fig. 7 B), and on the corresponding part of the syllobium, as well as on the preadductorial lobe of the tecnomorph, the coarse reticulation or dense punctation has been extended into a pattern of short, dash-like pits (shown very schematically in Fig. 11).

Younger tecnomorphs differ from the description given above in some essential respects. The few young tecnomorphs known suggest that in younger stages the preadductorial node is more rounded, and the facetted surfaces are less pronounced than in the adult specimens. Moult stages from "Bed 1" show a shorter adductorial sulcus than the adult males known, becoming deeper and longer during ontogeny. The largest tecnomorph found here almost reaches the length dimensions of the female but hardly the volume expected for the adult male. The tecnomorphs from this bed suggest, more-

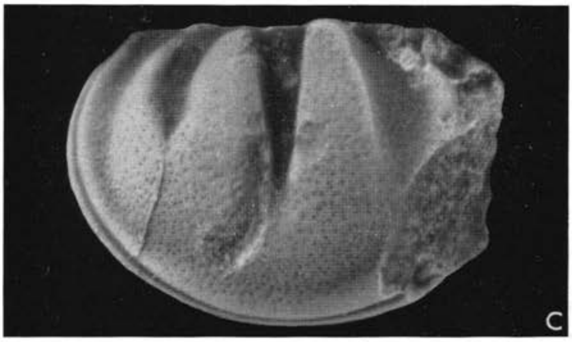
Fig. 12. *Londinia reticulifera* n.sp. Material from Klinta; GRÖNWALL's "Lag 1" (stratigraphical position of Fig. 12 A somewhat doubtful, cf. p. 29). × 30. Mus. Pal. Inst. Univ. Lund.



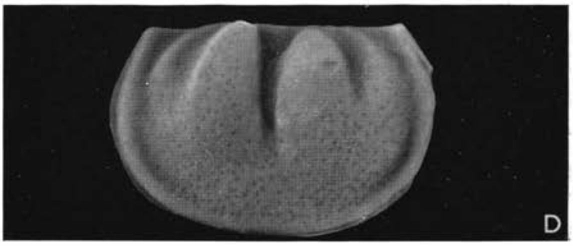
A. Left male valve, No. LO 4081 t.



B. Right female valve (holotype), No. LO 4080 T.



C. Large left tecnomorphic valve, No. LO 4082 t.



D. Small right tecnomorphic valve, No. LO 4083 t.

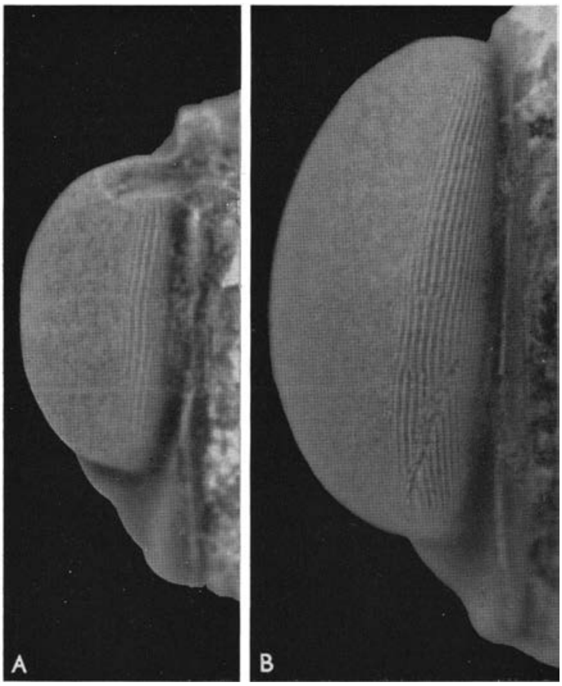


Fig. 13. Ventral side of the crumina in the genus *Londinia.* × 30. A. *Londinia reticulifera* n.sp., holotype, Mus. Pal. Inst. Univ. Lund, No. B. *Londinia kiesowi* (KRAUSE), Pal. Mus. Humboldt Univ., Berlin; KRAUSE's sample No. 549.

over, that during ontogeny the preadductorial lobe becomes longer, more strictly triangular, and somewhat protruding over the hingeline.

The adult male from "Bed 3" corresponds to the shape of the male of *Londinia reticulifera* as suggested by the ontogenetic development sketched and the shape of the female, and three further tecnomorphs from the same sample corroborate this. It seems natural, with the present evidence, that the definite isolation of the lobes and their extension, resulting in a somewhat stretched ornamentation, took place during the last moulting. As the material available is scarce, it is necessary to be cautious as to MOBERG's & GRÖNWALL's recording of this species in "Bed 3" at Klinta, particularly with respect to doubts as to the correct labelling of the sample discussed (see below).

In addition to the specimens figured the material consists of 1 female and some 20 tecnomorphs, largely buried in the matrix, from "Bed 1" and 3 tecnomorphs from "Bed 3" (?).

DIMENSIONS.—Hinge length of the lectotype 1775 μ; height over the adductorial sulcus, including the crumina, 1530 μ.

REMARKS.—*Londinia reticulifera* differs from *L. kiesowi* mainly by its high, long faceted lobes, with reticulation or a somewhat distorted reticulation on the cuspidal parts of the facets; the cusps protrude over the hingeline. This species does not attain anything like the size of *L. kiesowi.*

OCCURRENCE.—Scania; known only from Klinta and occurring there in "Bed 1"—the type stratum—and "Bed 3", according to the label of one sample ("Kloedenia wilckensiana/Silur: Öved–Ramsåsa-serien. Zon 3. Grw/Kalksten i gråblå skiffer. Sk.: Klinta/Grw). No other samples from this level contain the species, and it is not recorded by GRÖNVALL (1897) from "Bed 3". The label is fairly recent and type-written, and the original label is not preserved. Furthermore, GRÖNWALL's "Bed 1" corresponds to EICHSTÄDT's "Zone 3" (cf. MOBERG & GRÖNWALL 1909, p. 4). The circumstances indicate that the "zone" designations might have been confused.

Genus *Frostiella* n.g.

Cf. Figs. 14–23.

DERIVATION OF THE NAME.—Feminine diminutive of *Frostius*, inhabitant of Frosta Härad in Scania.

TYPE SPECIES.—*Frostiella groenvalliana* n.sp.

SPECIES.—*Frostiella groenvalliana* n.sp.
Beyrichia Wilckensiana var. *plicata* JONES 1855.

DIAGNOSIS.—*Kloedeniinae* with crumina strongly assimilated with the domicilum; crumina with a narrow, striate, and somewhat swollen field between the distinct velar bend and the marginal structure. Syllobium with protruding cusp.

REMARKS.—The relationship of this genus with *Kloedenia* is evident, as may be concluded from the morphological chapter. *Frostiella* shows, furthermore, a division of the syllobium into lobules which is very similar to the conditions in both *Londinia* and *Kloedenia*, as far as any syllobial features can be traced at all in the latter genus. The lateral lobal facets known from *Londinia* are present in the preadductorial lobe of *Frostiella*, too, and the punctation or reticulation here show a stretching of the pattern which is to some extent shown in *Londinia* and is conspicuous in *Kloedenia*. The ventral morphology of the crumina is, too, more or less intermediate between *Londinia* and *Kloedenia*.

OCCURRENCE.—The genus is represented in marine Siluro-Devonian deposits in the Baltic area and Scania and in the Downtonian sandstones of Great Britain.

Frostiella groenvalliana n.sp.

Fig. 7C, 8, and 14–17.

1897 *Kloedenia Wilckensiana* JONES—GRÖNVALL, *passim*.
1909 *Kloedenia Wilckensiana* JONES et var. *plicata* JONES—MOBERG & GRÖNWALL 1909, pp. 66–67; Pl. VI, figs. 6 and 7.

DERIVATION OF THE NAME.—Adjective derived from *Groenvallius*, latinized for *Grönwall*, named in honour of Dr. KARL A. GRÖNWALL (1869–1944), geologist in the Geological Surveys of Denmark and Sweden and professor in Lund.

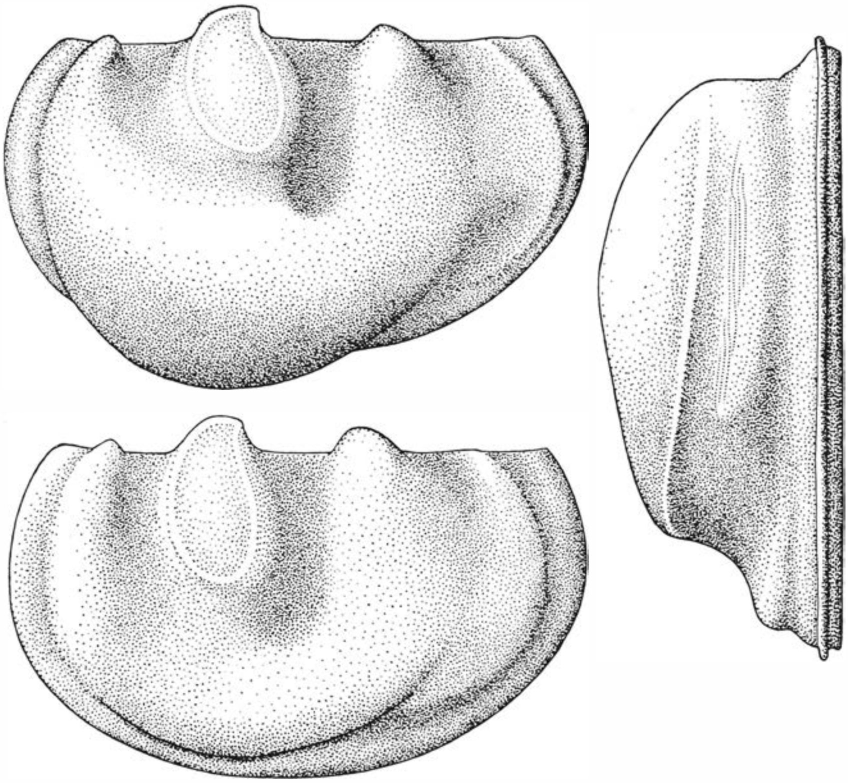


Fig. 14. *Frostiella groenvalliana* n.sp. Female and male in lateral view and female in ventral view. ×30.

Holotype.—A left female valve, Mus. Pal. Inst. Univ. Lund, No. LO 4084 T, Fig. 15 B herein.

Type Stratum and Type Locality.—"Beds 3–4", *sensu* Grönwall, at Ramsåsa, Scania.

Diagnosis.—*Frostiella* species with well developed lobation, with a cusp even on the anterior lobe. Complete cristal loop on the preadductorial lobe.

Description.—Outline subpreplete in the tecnomorphs, distinctly preplete in the female. Adductorial sulcus deep, not very narrow; lobes rounded except for the facet on the preadductorial lobe. This lobe protrudes considerably over the hingeline and is drawn up in the cuspidal part so that the facet becomes more or less pointed dorsally. The anterior lobe has a pointed cusp but is not very high. The syllobium is divided into a main body—a cuspidate lobule—and a posterior, curved lobule along the posterior margin. The midlength of the valve goes through the adductorial sulcus, but the difference in shape between the lobal elements causes a marked asymmetry of the anterior and the posterior portions of the valve. In the tecnomorphs all lobes are united lateroventrally into a connecting lobe of about the same height as the main lobes. There is no zygal arch.

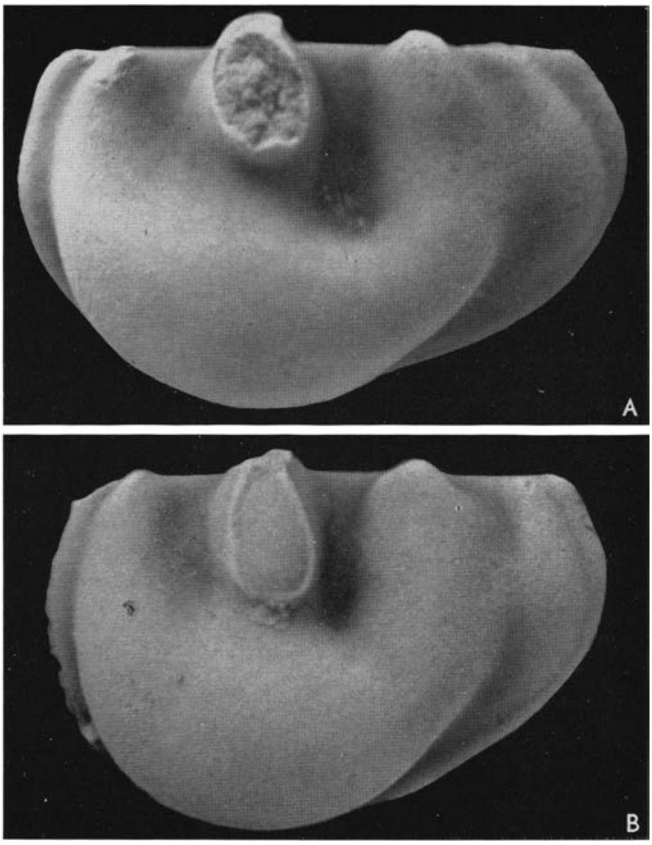


Fig. 15. *Frostiella groenvalliana* n.sp. Left female valves, × 30. A. From Klinta; KRAUSE's sample *Ringshö 1* (Pal. Mus. Humboldt Univ., Berlin). B. From Ramsåsa (Mus. Pal. Inst. Univ. Lund. No. LO 4084 T. Holotype).

A sharp bend or fold along this lobe or along the crumina occupying it in the female is identified as the velum. The subvelar field is very broad. There is a thick, flange-like marginal structure in the right valve and an "extra-marginal" shelf outside it, but the left valve covers this shelf without any corresponding structure; a low, ridge-like thickening may be observed, however, along the ventral edge of this valve.

The crumina occupies and inflates the ventral parts of the anterior and preadductorial lobes, also slightly incorporating the syllobium, and the latero-ventral connection between these lobes. It is ornamented ventrally with a narrow, striate, somewhat thickened zone between the velar edge and the marginal structure. The crumina does not deform the marginal structure or any other part of the margin by its inflation.

The carapace is entirely smooth except for this ornament and the ornamentation of the facet on the preadductorial lobe. The edge of this facet is marked

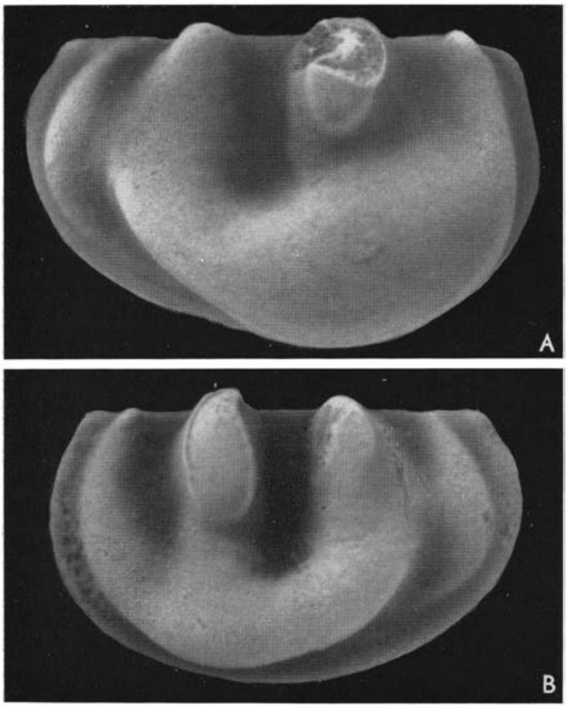


Fig. 16. *Frostiella groenvalliana* n.sp. from Klinta. × 30. Pal. Mus. Humboldt Univ., Berlin. A. Right female valve. KRAUSE's sample *Ringshö 1*. B. Left male valve. KRAUSE's sample *Ringshö 2*.

by a cristal loop, rounded ventrally and slightly pointed and bent backwards dorsally. In the rounded, ventral end it tends to be lower than elsewhere, and in the pointed, dorsal end it encloses a small area with a reticulation which is stretched and distorted by the extension of the cuspidal part of this lobe.

DIMENSIONS.—Hinge length of the holotype ca. 2265 μ, height from the cusp of the preadductorial lobe to the ventral outline of the crumina ca. 1690 μ. Corresponding measurements of three female valves in KRAUSE's samples *Ringshö 1* and *2*: 2195 μ–1490 μ, 1995 μ–1550 μ, 1965 μ–1545 μ.

REMARKS.—At least a hundred specimens of this species, in different collections from different localities and in different ontogenetic stages have been examined. The main material comes from "Bed 3" at Klinta in Scania.

This species differs from the following mainly by its comparatively well developed lobes and by the shape and ornamentation of the preadductorial lobe facet.

OCCURRENCE.—GRÖNWALL's "Bed 3" and "Beds 3–4" at Klinta and Ramsåsa in Scania, in glacial drift from the floor of the Baltic, and from the beds in the Leba core correlated with the Öved-Ramsåsa Beds. The Leba material, however, shows some differences from the Scanian material. The cristal loop is not pointed, and the only crumina observed is slightly more restricted.

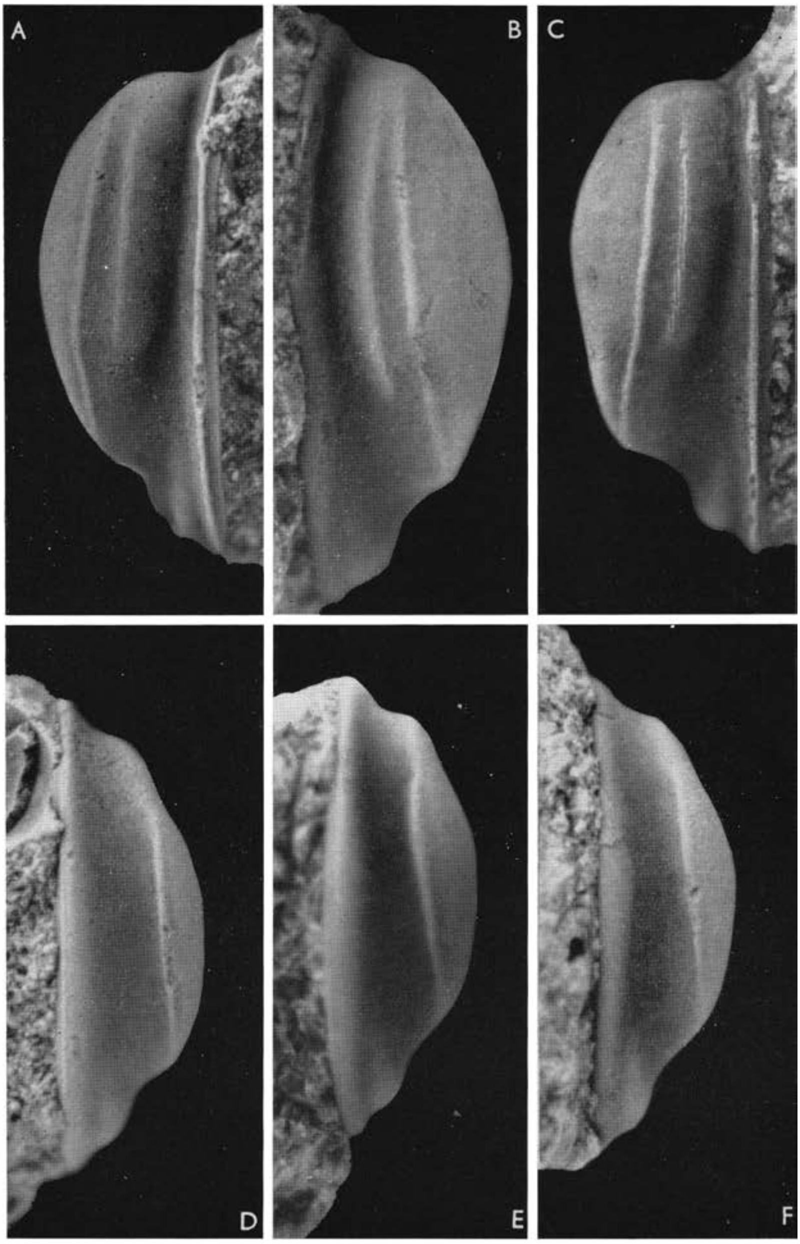


Fig. 17. *Frostiella groenvalliana* n.sp. from Klinta. KRAUSE's samples *Ringshö 1* (A, B, E, F) and *2* (C, D), Pal. Mus. Humboldt Univ., Berlin. Ventral view, anterior end up. × 30. A–C. Females. D–F. Males.

Frostiella cf. *groenvalliana*

Fig. 18.

REMARKS.—This species is known only from internal and less well preserved external moulds. Only the kind of preservation prevents a fully objective conviction that the species in Fig. 18 is identical with *Frostiella groenvalliana* from Northern Europe. If any difference at all is suggested by the material examined, it is that the lateroventral lobal connection may be slightly broader than in the North European tecnomorphs examined.

ELLES & SLATER (1906, Fig. 1, etc.) described a series of "*Beyrichia*-Bands" in the Downton Castle Sandstones at the exposure of the Ludlow Bonebed at Ludford Lane. STRAW (1929, pp. 101–102) discusses the occurrence of these beyrichiids in more detail:

> "The Downton Castle Sandstone group is characterised by *Kloedenia* (*Beyrichia*) *wilckensiana* (JONES). This fossil occurs in enormous numbers in certain bands in this formation, as for example in the "*Beyrichia* bands" above the Ludlow Bone-Bed in the Ludford Lane section at Ludlow, described by G. L. Elles and I. L. Slater. In Central Wales it has been found only in the Tilestones and nowhere I have seen it below the base of the Downtonian. It passes up into the Temeside Shales in Shropshire . . ."

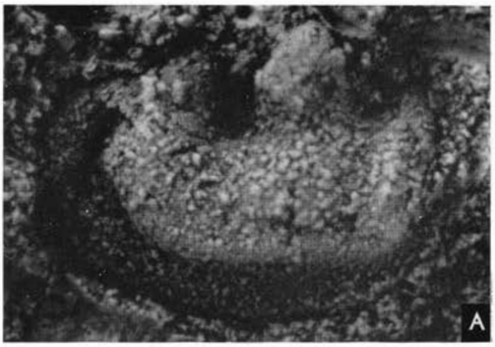
Fig. 18 shows four specimens from a sample collected about 120 cm above the Ludlow Bonebed at Ludford Corner (referred to as *Kloedenia* (*s.str.*) by MARTINSSON 1962, p. 359). The occurrence of these ostracodes provide a strong indication that the Downtonian sandstones and GRÖNWALL's "Beds 3–4" are of the same age. This is in close accordance with the classical correlation of these beds as a result of GRÖNWALL's studies (GRÖNVALL 1897, p. 58; MOBERG & GRÖNWALL 1909, p. 83, cf. EICHSTÄDT 1888, p. 156).

There exists at least one more species of this genus, in the drift material from the Baltic area, *F.* aff. *groenvalliana.* It is more tumid than *F. groenvalliana*, has less pronounced lobation, a more rounded preadductorial lobe, and a wide striate field ventrally on the crumina. A material from KRAUSE's erratic sample No. 600 in the Palaeontological Museum of the Humboldt University in Berlin contains both dimorphs but is too heavily weathered to be used for a description. It is more or less intermediate between *F. groenvalliana* and *F. plicata.*

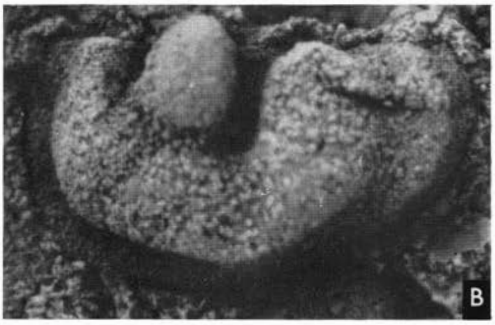
Frostiella plicata (JONES 1855)

Figs. 6B, 7D and 19–23.

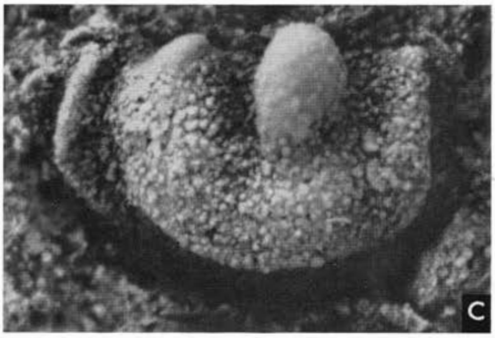
1855 *Beyrichia Wilckensiana*, var. *plicata*—JONES, p. 90; Pl. V, figs. 20 and 21.
1892 *Beyrichia* (*Kloedenia*) *Wilckensiana* var. *plicata* JONES—KIESOW, p. 102; Pl. XXIV, figs. 15 and 16.
1956 *Kloedenia wilckensiana* (JONES)—KESLING, pp. 64–66, *partim*; Pl. VII, figs. 1 and 9–13.



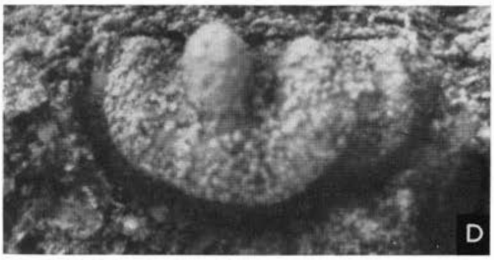
Internal mould of right tecnomorphic valve. No. EW 14.



Internal mould of left tecnomorphic valve. No. EW 15.



Internal mould of right tecnomorphic valve. No. EW 16.



Internal mould of left small tecnomorphic valve. No. EW 17.

Fig. 18. *Frostiella* cf. *groenvalliana.* Ludford Corner, Ludlow, Shropshire. Thin bone-bed in the Downton Castle Sandstone about 120 cm above the Ludlow Bonebed. × 30. (Mus. Pal. Inst. Univ. Uppsala.)

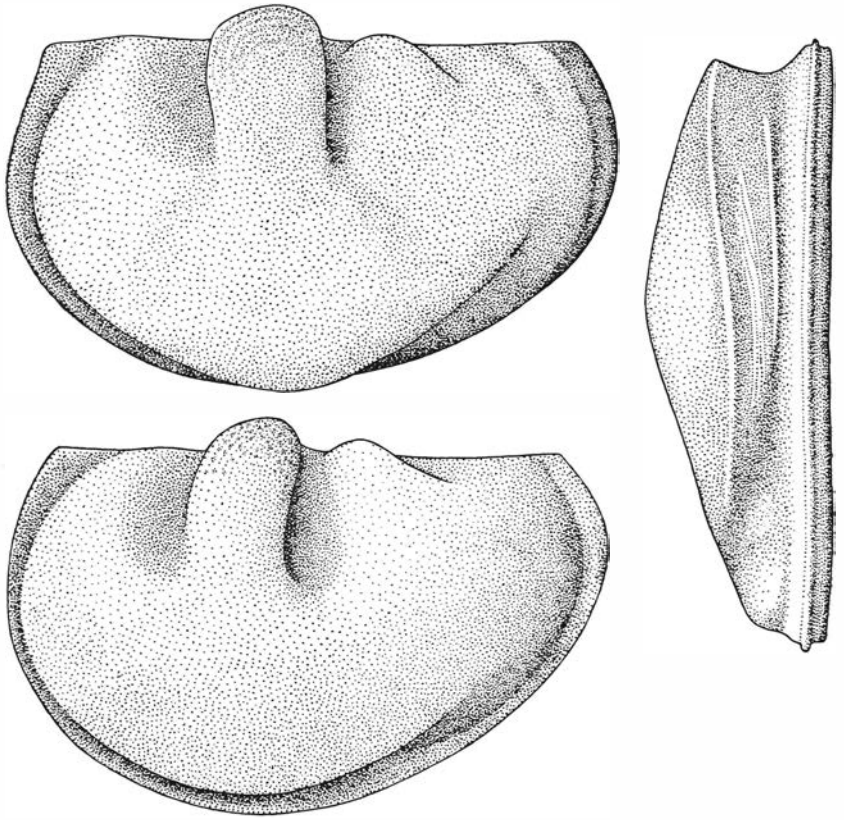


Fig. 19. *Frostiella plicata* (Jones 1855). Female and male in lateral view and female in ventral view. × 30.

Lectotype (designated herein).—A right tecnomorphic valve, British Museum (Natural History) No. I 6919, from Jones's *Scandinavian limestone No. 1*. According to Martinsson (1962, p. 17) the material of this species from erratic No. 1 consists of Nos. I 6918–6921. During a personal survey of Jones's collection (cf. p. 61) in 1962 one more specimen of this species, No. I 6917, stated to be the original of Jones's Pl. V, fig. 15 (sic!) was identified.

Diagnosis.—*Frostiella* species without other prominent lobal elements than a well-developed preadductorial lobe and a small hump corresponding to the cuspidal part of the syllobium. Ornamented facet on the preadductorial lobe but no distinct cristal loop.

Description.—Outline strongly preplete, even in the tecnomorph. In the tecnomorph the lateroventral connecting lobe occupies the larger part of the volume of the valve and forms an almost even surface which is interrupted only by a distinct adductorial sulcus and a shallower prenodal sulcus between which the preadductorial lobe projects, with a somewhat rounded subrec-

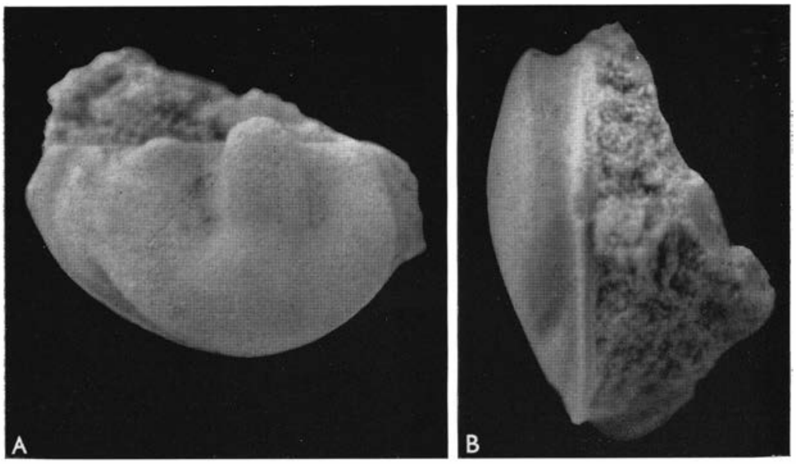


Fig. 20. *Frostiella plicata* (JONES 1855). Lectotype of *Beyrichia Wilckensiana* var. *plicata* JONES 1855. Young right tecnomorphic valve in lateral (A) and ventral view (B; anterior end up). × 30. From *Limestone Specimen 1* ("near Berlin") in the collection granted to T. R. JONES by E. BEYRICH and brought to England by Sir CHARLES LYELL. Brit. Mus. (Nat. Hist.) No. I 1619.

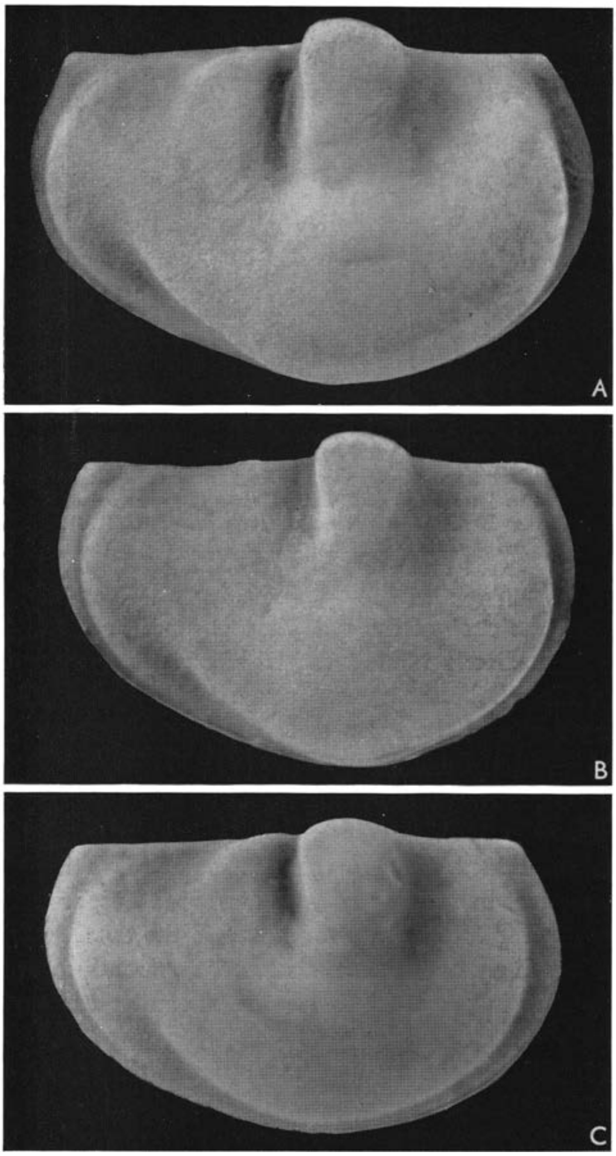
tangular outline. Furthermore, the cusp of the syllobium is more or less well marked near the hingeline immediately behind the adductorial sulcus. The posterior, lunular lobule of the syllobium, known from all kloedeniines, lies very close to the posterior margin of the valve and bends down below the level of the structure identified as the velum.

This velum is a simple fold, fairly sharp-edged in the tecnomorphs and well-developed in the female also. Posteriorly, it tends to bend towards the level of the lunular lobule mentioned. The marginal structure is a broad, rounded flange on the right valve, but the apparently corresponding area on the left valve lacks a corresponding feature. However, inside the overlapping border of this valve there is a finely denticulate structure, apparently corresponding to a tubulous structure in other beyrichiaceans. A similar structure is known from *Kloedenia.*

The crumina is a simple inflation of the antero-ventral part of the carapace, occupying chiefly the anterior part of the lateroventral connecting lobe. It is associated with a narrow, somewhat swollen field of fingerprint striation in the subvelar field and with a very low ridge between the striate field and the marginal structure. The crumina does not influence the margin or marginal structure in any way.

Except for the subcruminal striation there is an ornamentation of very fine striae on and along the marginal structure and the flattened border of the opposite valve. The facet of the preadductorial lobe is contoured dorsally by a series of dense striae, probably an extremely stretched reticulation or punctation (Fig. 7 D); the main puncta, however, break the pattern.

In this species the muscle spot, longish, rounded ventrally but slowly



A. Right female valve (Mus. Pal. Inst. Univ. Uppsala, No. BE 3).

B. Right female valve (No. BE 6).

C. Right male valve (No. BE 7).

Fig. 21. *Frostiella plicata* (Jones 1855). Three specimens from the same erratic (*Ust 1*) from Ustka, Pomerania. Right valves. × 30. N.B. the muscle spot, particularly conspicuous in B.

tapering dorsally, is clearly marked in the lower part of the adductorial sulcus (Fig. 21).

Dimensions.—Hinge length of the lectotype, a young tecnomorph, 1545 μ; height from the top of the preadductorial lobe to the ventral outline, formed by the velar edge, 1110 μ.

Corresponding measurements on two females from Krause's erratic sample

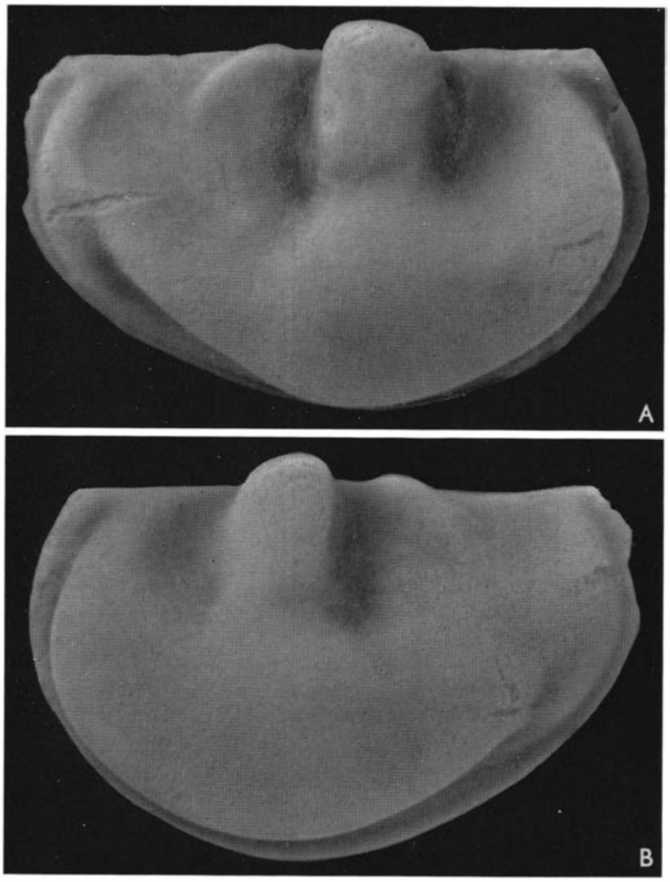


Fig. 22. *Frostiella plicata* (JONES 1855). Two female specimens from the same piece of rock (Pal. Mus. Humboldt Univ., Berlin; KRAUSE's sample No. 552). × 30. N.B. the difference in size and development of the syllobial cusp as compared with the specimens in Fig. 21. A. Right valve. B. Left valve.

No. 552: 2445 μ–1695 μ, 2365 μ–1795 μ. Same dimensions in female specimens from sample *Ust 1*: 2116 μ–1675 μ, 2050 μ–1595 μ.

REMARKS.—The species as defined here shows some intraspecific variability between different populations, as illustrated in Figs. 21 and 22. Sometimes the cusp of the syllobium is very prominent, sometimes it is lower; this feature is very constant within the population contained in each erratic unit. All transitions seem to exist in the total material examined. Sometimes the preadductorial lobe, the sides of which are normally subparallel in lateral view, is somewhat bent backwards. It is typical that occasionally very large male specimens, with an unusually long postadductorial portion of the carapace, occur in populations where the females do not reach anything like the same length (cf. KESLING 1956, Pl. VII, Figs. 9–11). This phenomenon remains unexplained and is insufficiently analysed; though the number of more or

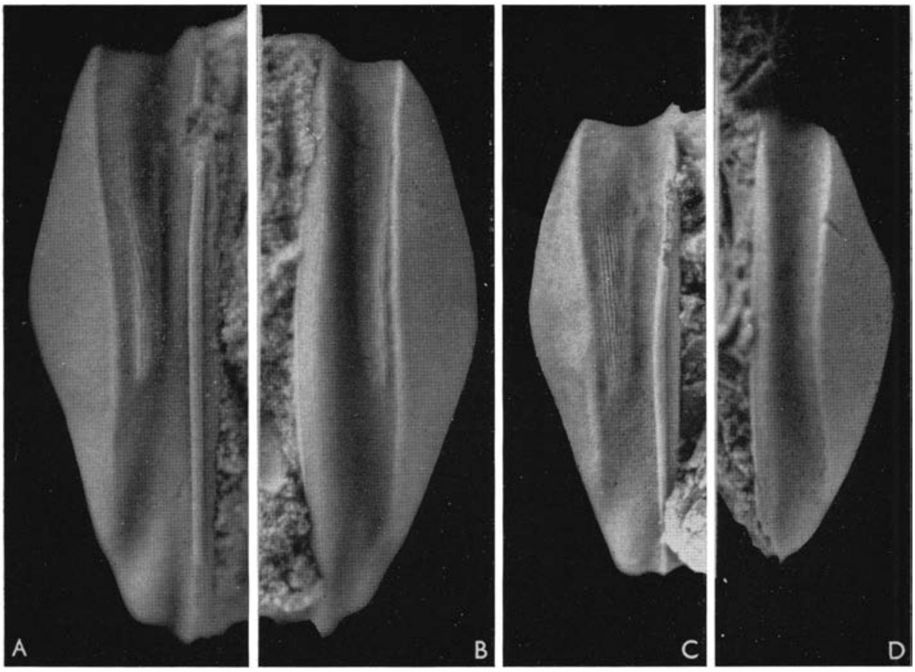


Fig. 23. *Frostiella plicata* (JONES 1855). Ventral view, anterior end up. × 30. A and B. The female specimens in Fig. 22. C. Right female valve from sample *Ust 1* (Mus. Pal. Inst. Univ. Uppsala, No. BE 8). D. Left tecnomorphic (male ?) valve from the same sample (No. BE 9).

less fragmentary specimens of *Frostiella plicata* available for this study may be said to be unlimited, no male of this size has come out of the matrix in a figurable state.

This species differs from *F. groenvalliana* mainly by its far-reaching reduction in lobation and by the ornamentation of the less marked facet of the preadductorial lobe. Further, it has a very low ridge between the striate field of the crumina and the marginal structure. This ridge may indicate that *F. plicata* is very close to the *Kloedenia* lineage where distinct subcruminal ridges appear and adult males are missing.

OCCURRENCE.—*Frostiella plicata* is known with certainty only from erratic *Beyrichia* Limestone from the Baltic area. The *Frostiella* material from the Ohesaar Beds (*Ohesaare lade*; the place name appears in the genitive in Estonian) of Ösel must be referred to as *F.* cf. *plicata* until a revision of better material can be made; for the present study only some badly preserved or young tecnomorphs have been available.

Genus *Kloedenia* JONES & HOLL 1886

Cf. Figs. 24–33.

TYPE SPECIES.—*Beyrichia wilckensiana* JONES 1855, designated by MILLER (cf. MILLER 1889) in his First Appendix of 1892 (p. 708; *Kloedenia wilkensana*; cf. p. 11 herein).

SPECIES.—*Kloedenia leptosoma* n. sp.
Beyrichia wilckensiana (JONES 1855).

DIAGNOSIS.—*Kloedeniinae* without a syllobial cusp and with very reduced lobation. Preadductorial lobe very prominent, with an open cristal loop. Ventral ornamentation of the crumina consisting of three striate ridges the lateral of which may be reduced.

REMARKS.—As mentioned above, all specimens of the last moult stage examined are more or less tumid in the cruminal region and have acquired the typical ventral ornamentation mentioned in the diagnoses. The genus *Kloedenia* differs from *Frostiella* by this ontogenetic development—which may indicate the occurrence of parthenogenesis—by the absence of other prominent lobal elements than the preadductorial lobe, by the morphology of the cristal loops, and by the complete differentiation of the cruminal striation into ridges.

This differentiation, however, may have been anticipated even within the genus *Frostiella*. In *F. groenvalliana* there are no indications of this, but in *F. plicata* there is a very faint ridge between the striate field and the marginal structure (Figs. 23 A and C). The following homologies are obvious: The outer, lateral, ridge is the velar edge of *Frostiella*, as also confirmed by the ontogeny of *K. leptosoma*. This ridge is mostly very reduced in *K. wilckensiana*. The middle ridge is the striate field of *Frostiella*. The inner, admarginal, ridge of *Kloedenia* is the low, torus-like ridge of *Frostiella plicata* referred to above.

It is dangerous to identify tecnomorphs of *Kloedenia* on the basis of figures in literature illustrating valves in lateral view. Some of KESLING's (1956) figures and the tecnomorphs figured by COPELAND (1960, Pl. 23, Fig. 18) are neither referred to in the present synonymy lists of *F. plicata* nor in those of *Kloedenia*.

OCCURRENCE.—In the "*Beyrichia* Limestone" of the Baltic Area and the Stonehouse Formation in Nova Scotia. Material from Ösel, Scania, and Britain referred to *Kloedenia wilckensiana* in literature has not, as far as available for this study, hitherto proved to belong to *Kloedenia*.

Kloedenia leptosoma n.sp.

Figs. 7E and 24–29.

1956 *Kloedenia wilckensiana* (JONES 1855)—KESLING, pp. 61–66 (*partim*); Pl. VI, figs. 1–5 and 6–8; Pl. VII, figs. 3–4 and 5–8.

1962 *Kloedenia wilckensiana* (JONES 1855)—MARTINSSON, Fig. 201.

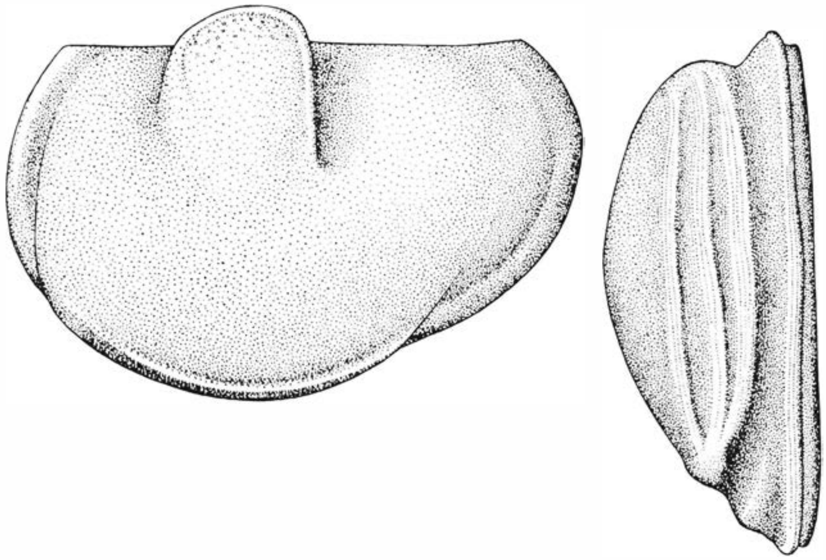


Fig. 24. *Kloedenia leptosoma* n.sp. Adult valve in lateral and ventral view. × 30.

DERIVATION OF THE NAME.—From Greek λεπτος, slender, and σῶμα, body, referring to the less tumid appearance of this species in comparison with *K. wilckensiana.*

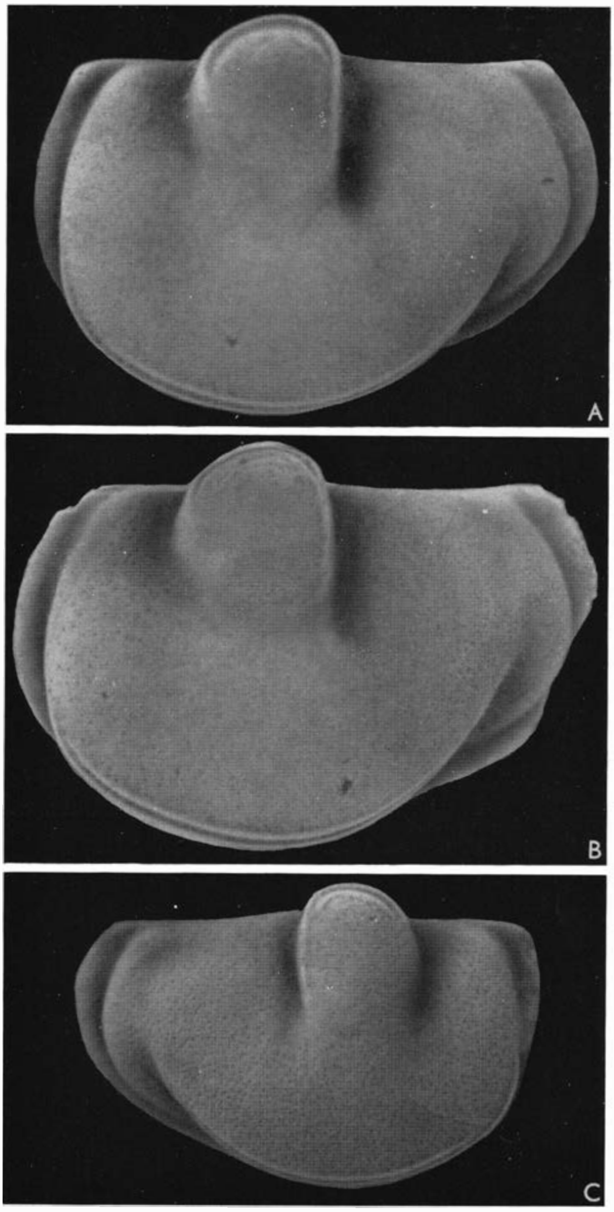
HOLOTYPE.—A left female valve, Pal. Inst. Univ. Uppsala, No. BE 1.

TYPE STRATUM AND TYPE LOCALITY.—*Beyrichia* Limestone, occurring as drift from the Baltic area. The type material comes from a boulder (*Jar 3*) from Jarosławiec in Pomerania, Fig. 25 A.

DIAGNOSIS.—*Kloedenia* species with three well developed striate ridges ventrally on the crumina which is not conspicuously tumid. Preadductorial lobe long, vertical, not inclined backwards, with a well-developed but open cristal loop.

DESCRIPTION.—Lateral outline distinctly preplete. The preadductorial lobe is large, projecting considerably over the hingeline. There are no further lobal cusps. The lobal part of the carapace corresponding to the anterior lobe and the syllobium gently merge with the large lateral surface of the connecting lateroventral lobe; both the anterior lobe and the lunular posterior lobule are, however, well set off from the subvelar field; the lobule mentioned bends down below the level of the velar bend on the lateroventral connecting lobe. The adductorial sulcus is well marked along the preadductorial lobe but not along the syllobium; the prenodal sulcus is hardly set off at all from the anterior lobe and consists mainly of the angle between this lobe and the preadductorial lobe.

Velar edge almost incorporated with a simple but striate ridge in very young tecnomorphs; the edge region soon divides, however, into a narrower



A. Mus. Pal. Inst. Univ. Uppsala, No. BE 10.

B. No. BE 4.

C. No. BE 12.

Fig. 25. *Kloedenia leptosoma* n.sp. Two right adult valves (A, B) and one right tecnomorphic valve (C) from Jarosławiec (sample *Jar 3*). × 30.

velar ridge or bend, and a broader, striate ridge (Figs. 28 B–D). In some older tecnomorphs a third ridge may be visible, but a complete division of the striate ridge into two ridges, the inner of which is always broader and flatter, does not occur until the last moulting (Figs. 28 E–I). Occasionally this division

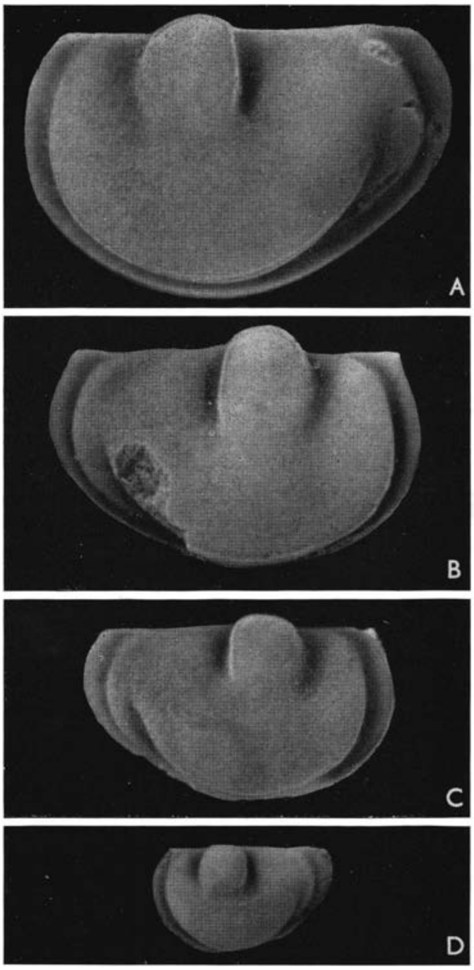


Fig. 26. *Kloedenia leptosoma* n.sp. Tecnomorphs from the same sample (*Jar 3*) as in Fig. 25. ×30. A. Left valve, No. BE 13. B. Right valve, No. BE 14. C. Right valve. No. BE 15. D. Left valve, No. BE 16.

of the ridge is incomplete (Figs. 28 E). In the adult stage the outer, lateral, ridge becomes distinctly striate.

The marginal structure is a thick ridge along the medioventral part of the margin of the right valve, tapering from this region in both directions, ornamented with the same kind of striation as the ventral part of the crumina. The margin of the left valve is a covering flange with the same striation. Inside it there is a row of tubercular elements of the same kind as figured in *Frostiella plicata* (Fig. 6 B).

Except for the striation described, the ornamentation consists of a dense and fine punctation covering large parts of the valves. It is present even between the striate ridges on the crumina.

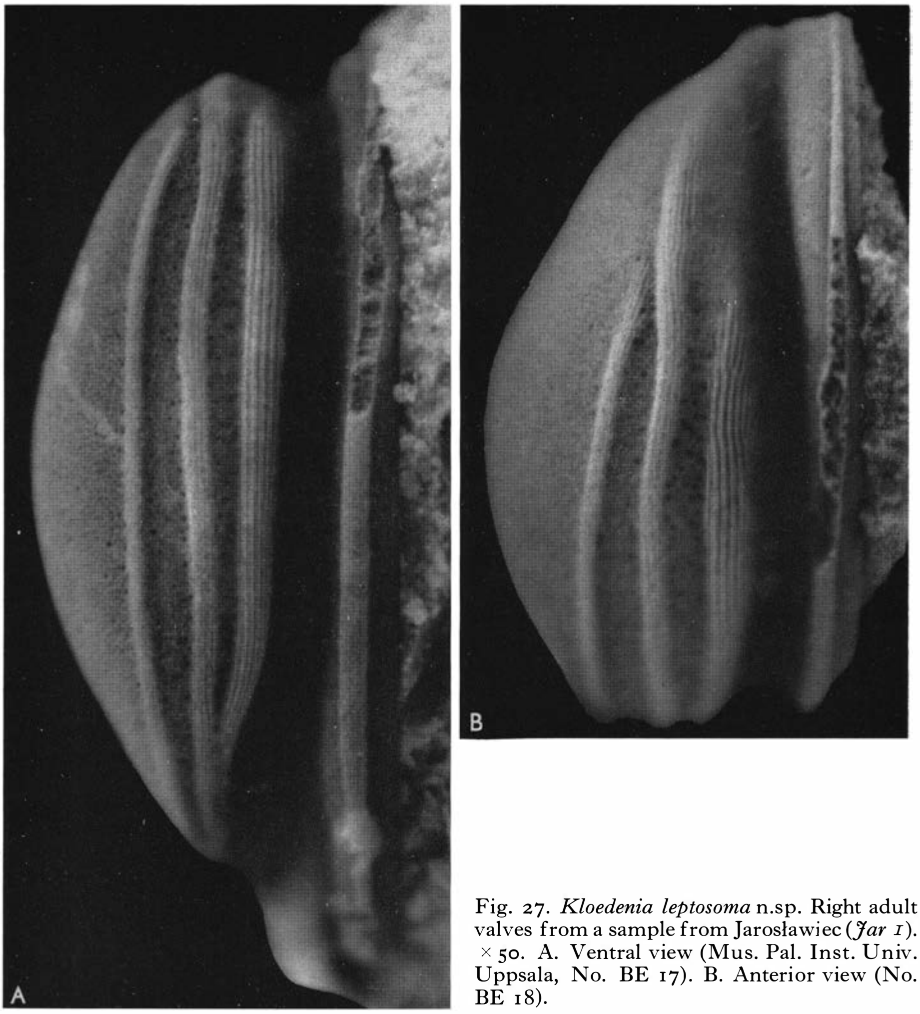


Fig. 27. *Kloedenia leptosoma* n.sp. Right adult valves from a sample from Jarosławiec (*Jar 1*). × 50. A. Ventral view (Mus. Pal. Inst. Univ. Uppsala, No. BE 17). B. Anterior view (No. BE 18).

A feature of special interest is the cristal loop. I surrounds almost all the contour of the preadductorial lobe but is open towards the connecting lateroventral lobe. The portion running along the adductorial sulcus is at right angles to the hingeline. There is a pronounced, long groove along its bend over the cuspidal part of the lobe, separating it from an area of striation with more pronounced puncta.

Dimensions.—Hinge length–distance from the cusp of the preadductorial lobe to the ventral outline of the crumina, measured on 5 adult specimens in a sample from Jarosławiec (*Jar 3*), in microns: 2215–1855, 2170–1865, 2165–1765, 2150–1850, 2095–1430. Cf. also Fig. 29.

Remarks.—Thousands of more or less fragmentary specimens of this species have been available. It differs from *K. wilckensiana* mainly by its less

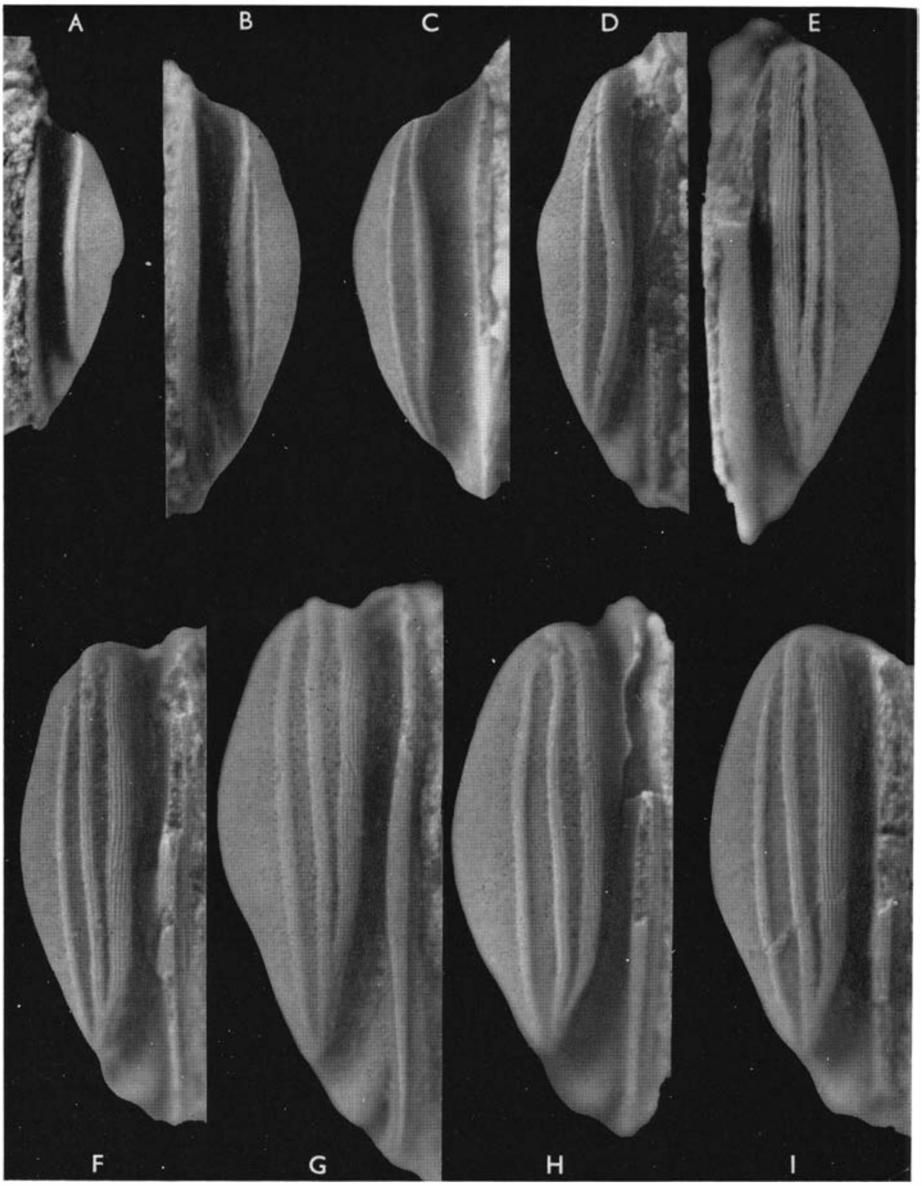


Fig. 28. *Kloedenia leptosoma* n.sp. Ventral view, anterior end up. × 30. (C from sample *Jar 5*, others from *Jar 3*.) A–D. Tecnomorphs. E. Adult valve with imperfect division of the striate ridges. F–I. Normal adult valves. A. Left valve, Mus. Pal. Inst. Univ. Uppsala, No. BE 19. B. Left valve, No. BE 13. C. Right valve, No. BE 20. D. Right valve, No. BE 12. E. Left valve, No. BE 22. F. Right valve, No. BE 23. G. Right valve, No. BE 24. H. Right valve, No. BE 25. I. Right valve, No. BE 26.

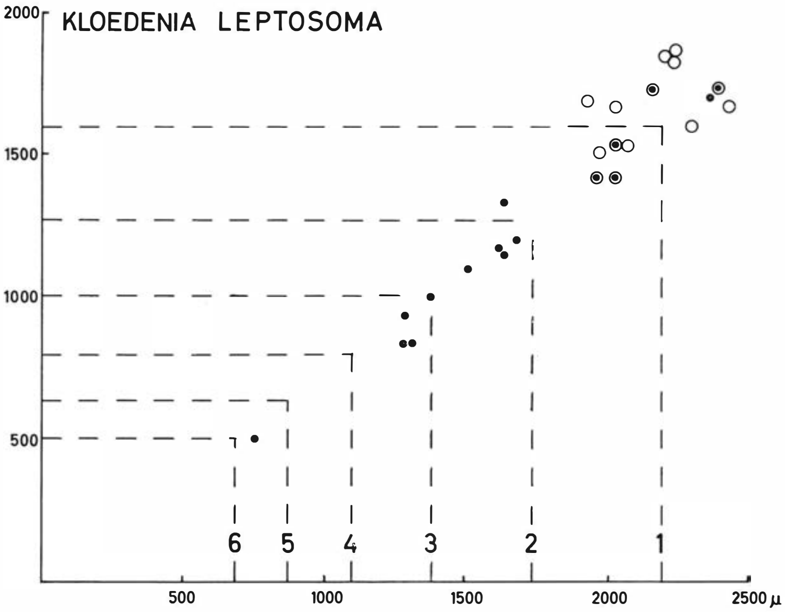


Fig. 29. Parts of the ontogeny of *Kloedenia leptosoma* n.sp. in sample *Jar 3*. Dots: Specimens without separation of a third striate ridge or with apparently imperfect separation. Ringed dots: Slightly imperfect separation of the third striate ridge. Rings: Typical adult specimens with distinctly separated cruminal rigdes. The slight differentiation achieved in this diagram does not reveal anything about a possible sexual dimorphism in the adult stage, as there is no distinct morphological discontinuity between the groups.

tumid appearance—resulting in a longer, more strictly vertical preadductorial lobe—and by its ornamentation on the crumina and on the preadductorial lobe. A consequence of its more slender appearance is, furthermore, the fact that the ventral ornamentation is quite conspicuous in strictly lateral view.

OCCURRENCE.—This species occurs in very great number in the drift material of *Beyrichia* Limestone from the central part of the Baltic area.

Kloedenia wilckensiana (JONES 1855)

Figs. 7 F and 30–33.

1855 *Beyrichia Wilckensiana* nov. sp.—JONES, p. 89; Pl. V, figs. 17 and 18.

LECTOTYPE.—A right female valve (Fig. 30), Brit. Mus. (Nat. Hist.) No. I 7039, from JONES's *Scandinavian Limestone 4*, not figured by JONES (1855). The original of JONES's (op. cit.) Pl. V, fig. 18, is No. I 7030 in the same Museum and comes from the same erratic limestone piece (cf. p. 61).

TYPE STRATUM AND TYPE LOCALITY.—*Beyrichia* Limestone, occurring as drift from the Baltic area. The additional type material consists of at least 13 specimens, Nos. I 7035, 7030–7038, from *Scandinavian Limestone 4* as mentioned above.

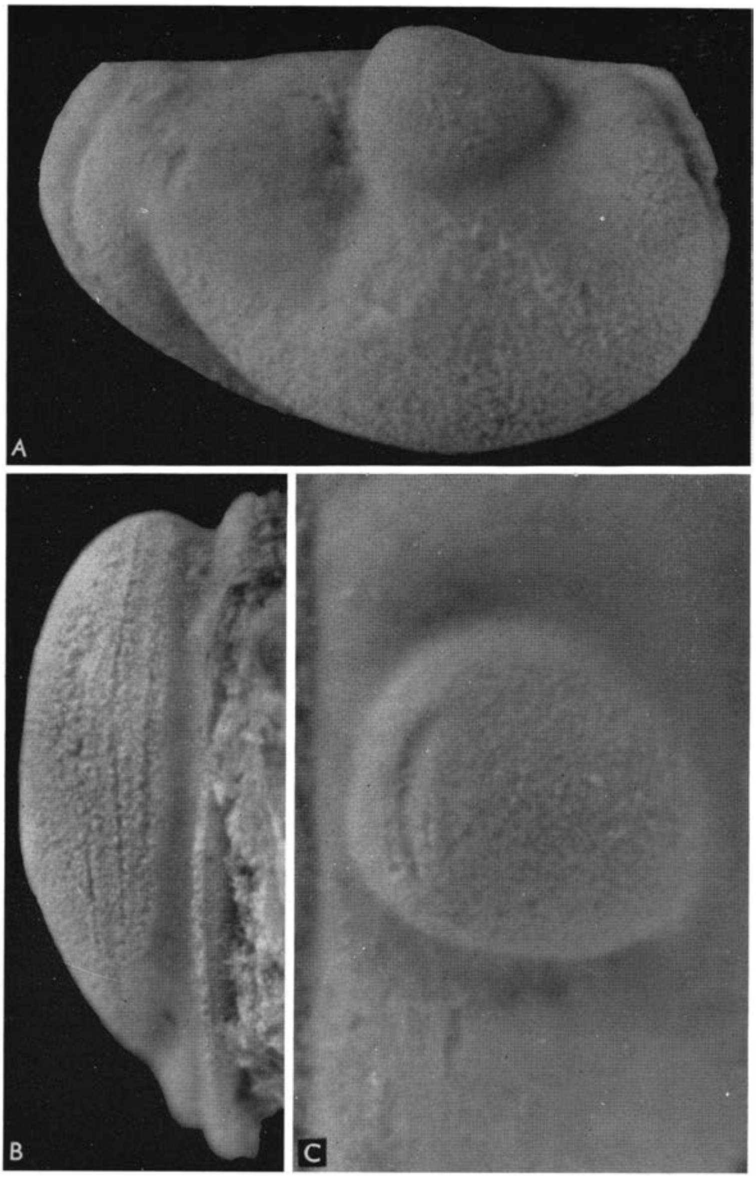


Fig. 30. *Kloedenia wilckensiana* (JONES 1855), lectotype of *Beyrichia Wilckensiana* JONES 1855, Brit. Mus. (Nat. Hist). No. I 7039, *Limestone Specimen 4* ("near Breslau") in the BEYRICH-LYELL-JONES collection (cf. Fig. 20). Right valve. A. Lateral view, × 35. B. Ventral view, × 35. C. Preadductorial lobe in dorsal view, × 60.

DIAGNOSIS.—Tumid *Kloedenia* species with two well developed ridges ventrally on the crumina; the lateral ridge is more or less reduced. Preadductorial lobe short, somewhat inclined backwards, and, owing to the tumid shape of the crumina, set off from the crumina by a distinct depression. Cristal loop present but indistinct.

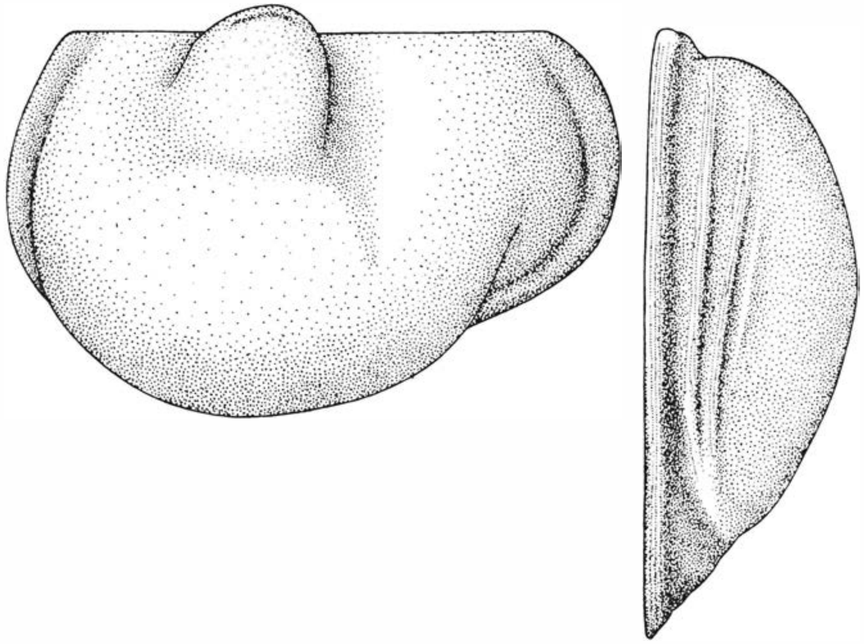


Fig. 31. *Kloedenia wilckensiana* (JONES 1855). Adult valve in lateral and ventral views. × 30.

DESCRIPTION.—Lateral outline distinctly preplete. The preadductorial lobe projects considerably over the hingeline but is short and seems, owing to the oblique depression at its base, to be inclined backwards. There are no further lobal cusps. The syllobium is also set off from the crumina by a shallow depression, less conspicuous than the depression earlier mentioned. The anterior lobe gently merges with the crumina. The posterior lobule is slightly set off from the main body of the syllobium and bends down below the level of the velar bend on the lateroventral connecting lobe or on the crumina, respectively. The sulci mainly consist of the angles between the preadductorial lobe and the lateral surface of the valve in the region of the syllobium and of the anterior lobe; the adductorial sulcus is, though, somewhat better set off in its lower part.

The ridge corresponding to the velar edge on the crumina is more or less reduced. Fig. 33 illustrates a common case. Often, however, this ridge is considerably more distinct, though it never converges with the other ridges anteriorly on the crumina. Weathering affects these structures as shown in Fig. 30 B; a furrow marks the lateral ridge posteriorly on the crumina of the lectotype.

The marginal structure is a ridge along the right valve, thicker in its medioventral portion and tapering in both directions. The left valve overlaps the shelf of the right valve by a flattened flange; these structures, on both valves, are striate.

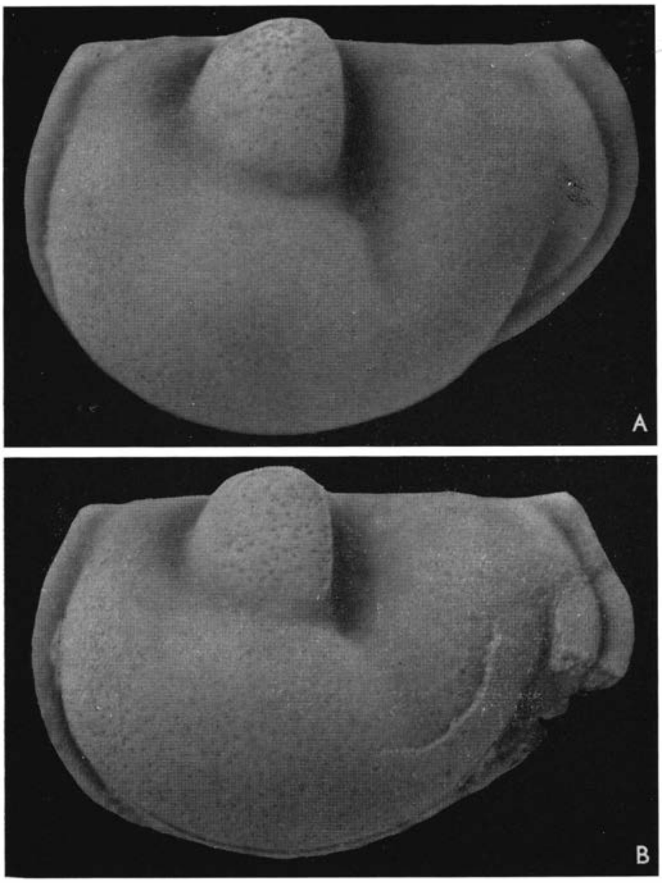


Fig. 32. *Kloedenia wilckensiana* (Jones 1855). Two left adult valves from Jarosławiec (sample *Jar 4*). × 30. A. Mus. Pal. Inst. Univ. Uppsala, No. BE 5. B. No. BE 28.

Except for the striation mentioned, the ornamentation consists of a fine and dense punctation all over the carapace, combined with a very fine reticulation (Fig. 27), thinning out in the sulcal regions. On the cuspidal part of the preadductorial lobe the puncta are particularly distinct, and there is a tendency to formation of a small striate field inside the groove bending over the cuspidal part of the lobe, along the cristal loop. This groove is in this species very short and lunular (Fig. 7 E), and the ridgelike portion of the cristal loop is not much longer. Along the adductorial sulcus, however, the loop may be continued as a bend limiting the lateral facet of the lobe.

Dimensions.—Hinge length of the lectotype 2165 μ, height from the cuspidal contour of the preadductorial lobe to the ventral contour of the crumina 1650 μ. Same dimensions for three females from a sample from Jarosławiec (*Jar 4*), in microns: 2345–1945, 2290–1815, and ca. 2260–1795.

Remarks.—This species differs from *K. leptosoma* mainly by its tumid

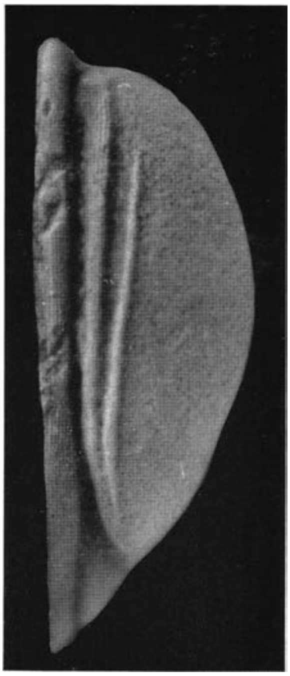


Fig. 33. *Kloedenia wilckensiana* (JONES 1855). Left female valve in ventral view; anterior end up. × 30. Jarosławiec (sample *Jar 4*). Mus. Pal. Inst. Univ. Uppsala, No. BE 5.
In this particular specimen the velar ridge is almost obsolete, as is often the case. In most populations, however, a more distinctly developed velar bend or ridge is more common.

appearance, by the short and inclined preadductorial lobe, and by the depression separating this lobe from the crumina or from the lateroventral connecting lobe in the older tecnomorphs. Furthermore, the complex of ornamentation ventrally on the crumina or on the cuspidal part of the preadductorial lobe is less developed. Nothing or very little of the cruminal ridges is seen in strictly lateral view.

Those specimens and populations which are nearest to *K. leptosoma* in variation have a comparatively well developed velar ridge on the crumina but always retain their tumid appearance and the deflection of the preadductorial lobe. On the other hand, more tumid females of *K. leptosoma* are met with in some samples. These do not, however, show any considerable deflection of the preadductorial lobe or the development of an oblique depression across its base.

The material examined consists of some thousands of specimens, mostly fragmentary or buried in a hard matrix.

In the drift material from the Baltic area two kloedeniine species have never been found together hitherto. About 100 samples of *Beyrichia* Limestone have been examined in this respect. However, it is not known whether *K. wilckensiana* and *K. leptosoma* have different stratigraphical ranges.

The ontogeny of *Kloedenia wilckensiana* has been followed in some detail. The inclination of the preadductorial lobe and the depression across its base is present in younger tecnomorphs, too, and in most populations there is no

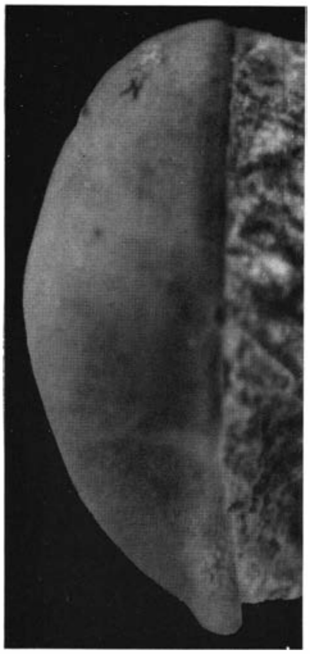


Fig. 34. *Saccarchites saccularis* SWARTZ & WHITMORE 1956. Right female valve in ventral view: anterior end up. × 30. Manlius Limestone, Nearpass quarries W of Port Jarvis, New York. Coll. JEAN M. BERDAN 1953. Mus. Pal. Inst. Univ. Uppsala, No. NA 77.

This apparently cruminate genus does not show any adventral structures or any ornamentation of the crumina which makes it possible to refer it to any of the beyrichiacean groups revised hitherto. Several lineages in the superfamily develop towards a very generalized carapace of this type. Hitherto, the anteroventral position of the inflation in the female is the only indication that the genus may be of beyrichiacean origin.

trace at all of the separation of the velar edge from the first striate ridge. Though more pronounced in the adults, the tumid characteristics are not, then, the results of a general inflation of the carapace in the last moulting when the crumina assumes its final size.

Kloedenia, particularly *K. wilckensiana*, represents the extreme of a development towards simplification of the kloedeniine carapace. If all of the adventral structures, the ventral ornamentation of the crumina, and the very persistent preadductorial lobe had been reduced, we would have obtained ostracodes without lobation and with only a general inflation of the anteroventral part of the carapace in the cruminate specimens, as in *Saccarchites*. The ventral morphology of *Saccarchites* females does not reveal anything as to the suggested and probable beyrichiacean character of the genus (Fig. 34). *Saccarchites* has retained a clear dimorphism. A simplification of the beyrichiacean carapace in the same or a very similar direction is known, too, in the subfamilies *Zygobolbinae* (*Noviportia*), *Beyrichiinae*, and *Treposellinae* and, less advanced, in the *Craspedobolbininae* and *Amphitoxotidinae*.

OCCURRENCE.—Found only in erratic boulders from the central part of the Baltic area.

Present views on beyrichiacean systematics and morphology

With the present study of this subfamily of the *Beyrichiidae*, the *Kloedeniinae*, all major beyrichiacean groups have undergone a first survey as to those characteristics which have proved to be of greatest importance where systematics are concerned. Much detailed work remains to be done with respect to the adventral structures and the ridges in the subvelar field, also in the neglected tecnomorphs, to the contact and symmetry conditions of the valves, and to the "last" phase in the origin of the primitive beyrichiacean crumina, the further development of which is so essential for the subdivision of the *Beyrichiacea.* Some groups, such as the lobate *Zygobolbinae*, the American representatives of the *Bingeria* group of the *Beyrichiinae*, and the American Devonian *Treposellinae*, are relatively insufficiently known from the points of view important in this connection. Nevertheless, it seems desirable and justifiable to draw the main systematical conclusions of the studies presented hitherto and to comment the state of our present knowledge in a brief summary.

THE IMPORTANCE OF THE TUBULOUS VELUM.—There is one group of beyrichiaceans having a mostly broad velum with a radial tubulosity or striation and another group of beyrichiaceans in which this structure consists of a flange or bend without visible internal differentiations. Those members of the superfamily which must be regarded as the most primitive represent the tubulous type of velum, as do those forms with dolonal dimorphism which must be regarded as closest related to the eurychilinacean-like ancestors of the *Beyrichiacea* (cf. MARTINSSON 1962). The group of beyrichiaceans having a tubulous velum also contains advanced or specialized forms, even such as have lost the tubulosity of the velum, but these are linked with the normally tubulous beyrichiaceans by other homologies. The group with the tubulous velum comprises the subfamilies *Craspedobolbininae*, *Treposellinae*, and *Amphitoxotidinae.* The other group comprises the subfamilies *Beyrichinae*, *Zygobolbinae*, *Kloedeninae*, and *Hexophthalmoidinae.*

The former group develops a crumina by closing the opening of a dolonoid pouch by a flap (cf. MARTINSSON 1962). In the latter group even very early forms directly occupied a portion of the velar fold and parts of the domicilial wall for the cruminal space. In the former group the *Amphitoxotidinae* achieved this direct occupation of the velar fold after the dolonoid closing apparatus had been abandoned. In the latter group irregularities in the marginal region—or a plication breaking through the margin in *Zygobolbinae*—often show that these regions have been engaged in the cruminal metamorphosis.

These two groups of subfamilies must be regarded as branches from two major lineages which divided very early in the phylogeny of the *Beyrichiacea.* Even the subfamilies as presented above must have a long independent history and branched off before they became considerably specialized in features other than the velum and the crumina. This may explain why two subfamilies, such as the *Ampitoxotidinae* and *Beyrichiinae*, which are so comparatively remote in velar-cruminal characteristics, have both retained features which are absent or almost absent in the other subfamilies or, possibly, developed them along similar lines.

The separation of the two main branches of the *Beyrichiacea* probably took place already in connection with the great changes in the reproductive system which the transition from the dolonal to the cruminal dimorphism implied. It is not even entirely improbable that two closely related lineages reached the formation of the crumina independently on similar trends.

OUTLINE OF A BEYRICHIACEAN CLASSIFICATION.—The conditions treated above are expressed in the following system which will be further discussed below:

- Superfamily *Beyrichiacea* MATTHEW 1886
  - Family *Craspedobolbinidae* MARTINSSON 1962
    - Subfamily *Craspedobolbininae* MARTINSSON 1962
    - Subfamily *Treposellinae* HENNINGSMOEN 1954
    - Subfamily *Amphitoxotidinae* MARTINSSON 1962
  - Family *Beyrichiidae* MATTHEW 1886
    - Subfamily *Beyrichiinae* MATTHEW 1886
    - Subfamily *Zygobolbinae* ULRICH & BASSLER 1923
    - Subfamily *Kloedeniinae* ULRICH & BASSLER 1923
    - Subfamily *Hexophthalmoidinae* MARTINSSON 1962

DIAGNOSES.—All taxia dealt with here are already established as family-group names, and diagnoses for the subfamilies and designations or indications of type genera are given in connection with the recent revision of the *Beyrichiidae* (MARTINSSON 1962). The only point of difference lies in the translation of the subfamily name *Craspedobolbininae* into a family name. Hence the following diagnoses are given:

FAMILY CRASPEDOBOLBINIDAE: *Beyrichiacea* primarily with tubular structures in the velum which may occasionally be reduced. Crumina originating by invasion of the velar fold along tubules in the anteroventral region; an earlier phylogenetic stage with a dolonoid pouch, tending to be closed by a flap, may be traced in all subfamilies by a dolonoid scar or a deflection of the velar edge on the crumina.

FAMILY BEYRICHIIDAE: *Beyrichiacea* lacking radial tubulosity in the flange- or ridge-like velum but sometimes with radial spines along the velar edge. Crumina originating by invasion of the region around the anteroventral portion of the velar fold. There are traces of the cruminal metamorphosis in the obsoletion of the marginal structure or in a plication breaking through this structure and the free margin of the valve, or these traces may be entirely absent.

The different subfamilies will be surveyed below from the points of view stated in the heading of this section, with special regard to main problems which remain to be solved (for descriptions and references, cf. MARTINSSON 1962).

SUBFAMILY CRASPEDOBOLBININAE.—The ostracodes in this group are distributed on three different morphological groups, characterized by the genera *Craspedobolbina* (lobate and with a sphaeroidal crumina), *Apatobolbina* (non-lobate or almost non-lobate and with a sphaeroidal crumina), and *Aitilia* (sulcate and with a low lobation; the crumina is ellipsoidal and sometimes provided with a spine). Somewhat isolated genera in the *Apatobolbina* group are *Moierina* and the slightly lobate *Bolbibollia*, the crumina of which is not as well set off from the domiciliar wall as in other craspedobolbinines, and *Bolbineossia* which is the only reticulate genus in the group; the surface in all other genera is granulose or smooth. This morphological grouping of the genera does not, however, conceal the apparent homogeneity of the subfamily, manifest in the primitive cruminal metamorphosis (in *Moierina* the dolonoid scars have not been verified).

Clintiella and *Mesomphalus* show possible affinities to the *Treposellinae*. It has not been shown in detail whether the dolonoid scar is due to an "inserted flap" arrangement or to a simpler plication along the velar edge as is possibly the case in *Treposellinae*.

A main morphological problem concerns the detailed reconstruction of the origin of the cruminal opening and the partition or perforation of the velar fold. This is still being studied on ontogenetic material of *Craspedobolbina*, and it is possible that sections through a specimen in a convenient intermediary stage of the cruminal metamorphosis will at length provide additional information.

In connection with the definition of *Clintiella* by MARTINSSON (1962), *Mesomphalus* became once more a monotypical genus. A new species, *M. magnificus*, with the characteristic stout shape and cuspidal plicae of the generotype but with a broader velum and less assimilated crumina, was recently described by COPELAND (1962).

SUBFAMILY TREPOSELLINAE.—Though the American Devonian genera *Treposella* and *Hibbardia* show much clearer the primordial site of the crumina and traces of its origin from a velar structure, the subfamily forms a fairly homogeneous unit. *Phlyctiscapha*, in which the lobation has become entirely obsolete, has retained the marginal structures, and available figures show a plication which possibly marks the velar edge. All European forms belong to a group of genera which may be characterized by *Garniella* (*Strepula*, *Garniella*, *Bolbiprimitia*, and *Retisacculus*) showing different stages in the reduction of the lobal features and in the incorporation of the crumina but no clear traces of earlier stages in the cruminal metamorphosis. A plication along the velar edge may be a structure of this kind.

The generotype of *Bolbiprimitia*, *B. fissurella*, needs a revision of the cruminal morphology. The similarity in lobation between the American and European species, however, seems to guarantee their affinities.

SUBFAMILY AMPHITOXOTIDINAE.—This subfamily shows greater variation in the velar-cruminal morphology as compared with others, and this has resulted in a considerable number of genera with only a few species or of monotypic genera. However, it is evident that the genera *Sleia*, *Hemsiella*, *Macrypsilon* (?), *Lophoctenella*, *Vinculoveliger* (?), and *Berolinella* are represented with more species in the North European faunas. Since unweathered material has now been available, it has been found that *Macrypsilon* is to be placed after *Sleia* and *Hemsiella* in the system (cf. MARTINSSON 1962, p. 257). A forthcoming study will deal with this.

In this subfamily, particularly, the subvelar and velar ridge morphology will provide more information than hitherto, and this notably concerns the tecnomorphs which are largely unanalysed and undescribed in this respect.

SUBFAMILY BEYRICHIINAE.—This subfamily comprises two groups, the mostly spinose and often lobulate *Beyrichia* group with a granulose ground pattern, and the fairly different *Bingeria* group with a complicated, often distorted reticulation and often a thin, smooth velar flange of a type not present in the *Beyrichia* group. The *Bingeria* group is frequently represented in North America and has often, probably with little justification (cf. p. 19) been associated with the *Kloedeniinae* described here. It is represented, too, in Norway and on Gotland.

RELATIONSHIPS AMPHITOXOTIDINAE–BEYRICHIINAE.—The lobation in both these families shows some parallelism in the development. The isolation of the anterior lobe and the obsoletion of the zygal connection occurs in both of them, and this has long been taken as an indication that they might be closely related to each other. Since there is another, even more striking similarity, i.e. the well-developed anteroventral depression common to both subfamilies, and since the establishment of a family boundary between them deviates more than anything else from earlier concepts of the beyrichiaceans, some further comments are necessary.

Primitive beyrichiines occur together with velate ostracodes of craspedobolbinine type in the oldest Llandoverian beyrichiacean faunas described in such detail that any conslusions as to their relationships can be drawn (HARPER 1940). Amphitoxotidines do not occur in the Baltic area lower than in Ludlovian rocks, but in Britain amphitoxotidine tecnomorphs have been observed as far down as in the Buildwas Beds in the lowermost Wenlockian. Due to the incompleteness of the fossil record it is not possible to draw any definite conclusions as to the time of origin of the different beyrichiacean groups, but it may have some significance that the three critical groups may be traced down to about the same time. Tendencies towards isolation of the anterior lobe and towards obsoletion of the zygal arch may be traced down to the uppermost Wenlockian of Gotland. It may further be noted that some Ludlovian genera (*Calcaribeyrichia*, *Gannibeyrichia*, etc.) along the main beyrichiine lineage have better developed velar structures than forms found in older strata.

The beyrichiacean ancestors had a tubulous velum like that of the amphitoxotidines. If the amphitoxotidines branched off from the beyrichiine lineage at the time when the lobal reduction began in genera as *Beyrichia* (*Altibeyrichia*) and *Neobeyrichia* we must assume that the reduced tubulous velum could redevelop in one or more places in the system. If so, there would be no basis for a classification in which the units are characterized by different stages or modes of reduction of the ancestral dolonoid closing mechanism, or, as expressed in a qualified discussion, "traces of the closing mechanism are present because a broad velum is present".

This must imply that an unusually successful reverse mutation has taken place, in conflict with the "law" of irreversibility, and that the amphitoxotidines at the same time adopted and rigidly stabilized a surface reticulation entirely foreign to that beyrichiine lineage from which they were suspected to have branched off. This is not quite in agreement with the accumulated empirical experience of evolution.

It seems, therefore, firmly established that the subfamilies *Beyrichiinae* and *Ampitoxotidinae* separated already when the two main beyrichiacean groups designated as families here, with a strictly tubulous and a non-tubulous but often radially spinose velum, respectively, separated. The evidence provided within each of the beyrichiacean subfamilies suggests that they all branched off very early in the existence of the very specialized superfamily *Beyrichiacea* and that they independantly followed similar trends towards a simplification of the lobation and an assimilation of the egg-or-brood space with the domicilium.

In the present case we must assume that the *Amphitoxotidinae* is that craspedobolbinid subfamily which has retained an anteroventral depression most conservatively, and that the *Beyrichiinae* contain a similar lineage among the beyrichiids in the present sense.

SUBFAMILY ZYGOBOLBINAE.—As now defined, this subfamily consists of two groups, characterized by *Slependia* and *Zygobolba*, respectively, united by their similar development of the admarginal parts of the crumina. Both have a zygal connection, but the *Zygobolba* group develops very high, faceted lobes and a complicated zygal arch, in contrast to the *Slependia* group where the lobation tends to become obsolete. These forms are reticulate or reticulo-striate, except for *Noviportia* which is granulose laterally.

The ventral plication along the crumina needs further investigation, particularly in American representatives of the subfamily.

GENUS DREPANELLINA.—In lateral view the genus *Drepanellina*, which has very protruding lobal cusps and separates a posterior lobule of the syllobium, shows some kloedeniine features. Dr. JEAN M. BERDAN (*in litt.* May 24th, 1962) has studied the cruminal morphology of *Drepanellina* and found structures similar to the transmarginal plication or furrow in the *Zygobolbinae.* This seems quite sufficient for the attribution of *Drepanellina* to this subfamily.

It is not improbable, of course, that primitive kloedeniines with exuberant cruminae had a similar structure, but the conditions in *Londinia* do not support this suspicion.

SUBFAMILY KLOEDENIINAE.—To the treatment of this subfamily in this paper may only be added the remark that some features of unknown systematic value are somewhat similar in the subfamilies *Zygobolbinae* and *Kloedeniinae.*

Both develop lateral facets on the reticulate lobes, and the crumina fills out the velar fold in a very similar manner in both subfamilies. The typical rough beyrichiid finger-print striation forms a very long field on the cruminae. The differences in lobation, however, are more conspicuous. No zygal arch has been observed in the *Kloedeniinae.* and the characteristic cristal loop around the lobal facet is unknown in the *Zygobolbinae.*

SUBFAMILY HEXOPHTHALMOIDIDINAE.—The only genus known in this subfamily is not sufficient to allow conclusions as to its systematic position. The protruding lobal cusps, the cristal loops (if homologous ?), and the lobulation in the syllobium present some kloedenioid features. In any case, *Hexophthalmoides* presents a very isolated branch of development.

One more female specimen of *Hexophthalmoides* has now been encountered, from Sigvalde in the Hemse Beds of Gotland (cf. MARTINSSON 1962, Fig. 203 B). It differs from the holotype of *H. craterilobatus* in having the anterior lobe split into two cristate lobules.

Institute of Palaeontology, University of Uppsala, September 15th, 1962.

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Corrections and additions to "Ostracodes of the family Beyrichiidae from the Silurian of Gotland"

This first paper in a series dealing with a revision of the *Beyrichiacea* (MARTINSSON 1962) contains some errata and needs some addenda. Evidence from current further investigations into beyrichiid morphology and cruminal metamorphosis are not added, except for one important case.

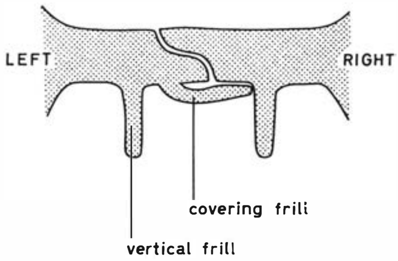

Fig. 35. Schematic section through the ventral contact margin and the marginal structures in a primitive beyrichiacean tecnomorph (cf. p. 62 and Fig. 36).

HISTORICAL NOTES.—In the search for a specimen of *Neobeyrichia lauensis* (KIESOW 1888) for the designation of a type, attention was drawn to the fact that specimens of this and other ostracodes in the KRAUSE collection were collected along KIESOW's route on Gotland (op. cit., Fig. 10; pp. 29 and 319). In connection with the present study it has become evident that KRAUSE collected Silurian fossils on Gotland in 1876 (cf. KRAUSE 1877, p. 4) and that his ostracode collections from Sweden date from this year.

The designation of *Strepula concentrica* as the type species of *Strepula* (op. cit., p. 197) was not made by BASSLER & KELLETT 1934. The correct reference is the "First Appendix, 1892" (cf. p. 711) added to MILLER's "North American Geology and Palaeontology" (1889).

An examination of the ostracode collection in the British Museum (Natural History) in 1962 revealed that earlier information as to the original specimens of beyrichiids is incomplete. Though no complete revision of possible originals has been made, it may be added that JONES's original of *Beyrichia Dalmaniana* (op. cit., p. 17, with reference to JONES 1855) in his Pl. V, fig. 13, is No. I 7018 (*fide* label). A specimen stated to be the original of *Beyrichia Wilckensiana* var. *plicata* in the same Pl. V, Fig. 15, is No. I 6917 (cf. op. cit., p. 17, and p. 36 herein). The material of *B. Wilckensiana*, earlier regarded as not present in the BEYRICH–LYELL–JONES collection, is treated in detail above (p. 47). These complements do not affect any lectotype designations in the paper quoted or herein.

In a statement about ULRICH's erection of the genus *Treposella* in 1891, his "first ostracode paper" is mentioned (op. cit., p. 29). The word "first" should be omitted.

To the statements about the origin of the term *carina* in the palaeocopes (op. cit., p. 77) may, finally, be added that the term was applied to kirkbyids by COOPER 1941 (Illinois State Geol. Survey, Rep. on Investigations No. 77, p. 48 sqq.)

PREOCCUPIED GENERIC NAME.—The generic name *Lauella* MARTINSSON 1962 is, according to NEAVE's Nomenclator Zoologicus, preoccupied by the beetle genus *Lauella* MANN 1921. It is being replaced by the name *Loella* (*in* Geologiska Föreningens Förhandlingar, Vol. 84, in the press).

SILICIFICATION.—A specimen of *Craspedobolbina clavata*, exhibiting dissolution and distortion of the carapace (op. cit., Fig. 40C), is silicified. This fairly conspicuous fact had been overlooked because silicification is otherwise quite unknown among the hundreds of thousands of ostracode specimens collected at this locality. Silicified ostracodes occur very rarely in the Gotland sequence (particularly in the Hemse Beds), but do not, then, exhibit this distorted type of silicification. Brachiopods from the Hemse and Eke Beds, however, are sometimes silicified in this way, though their structure and colour readily reveal the process which has taken place.

COVERING MARGINAL FRILL.—In the text to Fig. 20 (op. cit., p. 75), read "primitive *Beyrichiidae*" for "primitive *Beyrichiinae*". It may be added that current studies

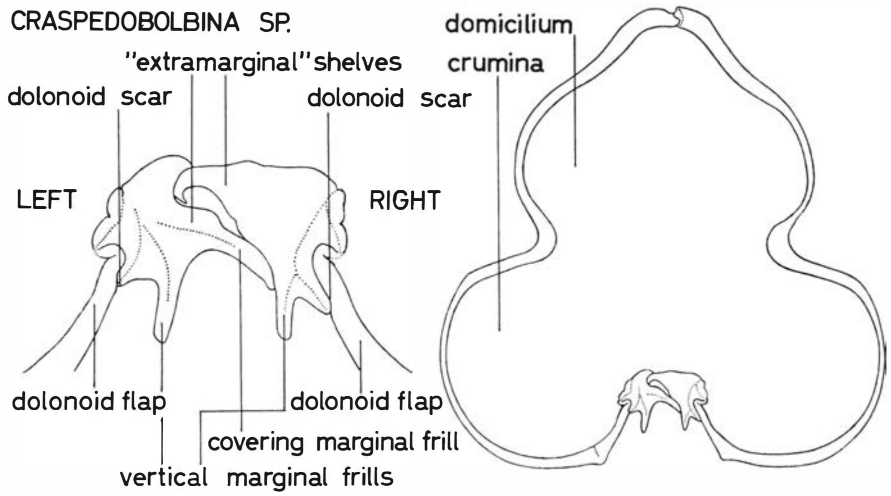

Fig. 36. *Craspedobolbina* cf. *percurrens* Martinsson, female carapace in transversal section through the cruminae, × 40; detail × 120. Mus. Pal. Inst. Univ. Uppsala, No. G 550. Gotland, Fröjelstrand (shore in the parish of Fröjel), probably Slite Beds. Coll. H. Munthe 1884. The figure shows that the edges of the "extramarginal" shelves were bent around each other. A few other sections are through specimens well enough preserved to indicate the same conditions, though this one seems to be an extreme case. The cruminal wall is simple, and the inner, non-calcified layer of the original dolonoid part of the velar fold was reduced, or possibly screened off the cruminal space from the domicilium. All fold structures, including the marginal structures and the folds forming the notch around the edge of the dolonoid flap show a kind of "bisecting lines", developed in a regular way in all specimens. They have the nature of simple cracks, and there are no objective traces of retracted or resorbed epithelium in this position.

suggest that the overlap and symmetry conditions along the contact zone of the valves are of much greater importance than was realized when the schematic figure was drawn. A very schematic illustration of the craspedobolbinine marginal frills is shown in Fig. 35 in this paper. It is the overlapping valve that has the covering structure, in spite of the fact that surface preparations and figures based on them (Martinsson 1962, Figs. 19 A, 18, 25: 1, etc.) often seem to verify the opposite conditions most illustratively. Though many sections have been prepared through well-preserved specimens of *Craspedobolbina clavata* from Mulde, the contact conditions of the valves have always been affected by recrystallization or displacement of the valves, and it has been impossible to give a reliable naturalistic illustration of the conditions concerned. However, a recent re-examination of a *Craspedobolbina* specimen from Fröjelstrand, figured by Hessland (in *Bull. Geol. Inst. Univ. Upsala*, Vol. XXXIII, 1949; Pl. XLV, fig. 9), has proved that the section in question is ideal in this respect. A drawing based on it is shown in Fig. 36.

Misprints.—The following misprints may be of formal importance:
p. 4, line 7 from bottom: *WE*; read: *EW*,
p. 72, line 16 from bottom: (*dolonal*, *dolonat*,; read: (*dolonal*, *dolonat*),
p. 94, top line: dolonid, read: dolonoid,
p. 103, line 19 from bottom: family *Treposellinae*; read: subfamily *Treposellinae*,
p. 109, line 12 from top: this family; read: this subfamily,
p. 112, line 6 from top: No. G 256; read: No. G 680,

p. 178, text to Fig. 75: *Craspedobolbinae*; read: *Craspedobolbininae*,
p. 277, text to Fig. 147: (KIESOW 1888); read: KIESOW 1888,
p. 282, text to Fig. 151 A: Hellvi; read: Längars (parish of Hellvi).

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