## 1. The Origin of the Crumina in Beyrichiid Ostracodes

#### By

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ABSTRACT.—This report presents a part of the studies on ostracode carapace morphology which form the basis for a forthcoming treatise on the beyrichiid faunas of the Silurian of Gotland.

The dimorphism in palaeocope ostracodes always appears suddenly, in the last (or occasionally in an earlier) moult stage, and there are normally no intermediary stages to be found among the fossil carapaces. The examination of a very large material, however, has revealed a few specimens of *Beyrichia* spp. (*sensu latissimo*) in which the formation of the crumina is incomplete and which can be regarded as more or less atavistic. The crumina originates from the double-walled dolon of the eurychilinacean type which, phylogenetically as well as ontogenetically, develops into a closed or almost closed pouch.

In *Beyrichia* (*Mitrobeyrichia*) and related forms the edge of the dolon is extended into a flap which is inserted in the dolonal opening. At this stage a furrow is already formed, beginning to part the two layers of the dolon. In these forms it is doubtful whether the separation of the two layers is completed or whether the inner layer is reduced more or less in juxtaposition to the outer one. In different more advanced beyrichids where the opening of the dolon is not closed by a flap the separation of the dolonal layers and the incorporation of carapace wall elements are of major importance for the formation of the crumina. In all cases the space increases by the expansion of particularly the outer layer of the dolon and adjoining parts of the carapace wall into the more or less spherical crumina which is practically single-walled. Thus the dolonal opening does not migrate over the free edge into the carapace in the primitive beyrichids. Characteristic remains of the dolonal opening with the squeezed dolonal flap and of the velar edge are of great importance for the classification.

**Introduction.** — The present report is extracted from a forthcoming comprehensive treatise on the very differentiated beyrichiid faunas of the Silurian of Gotland which was begun in 1954. This study will comprise an analysis of the features in the carapace morphology, *i.e.* the internal and ornamental structures of the carapace wall, the contact conditions of the valves, and, especially, the adventral structures which are of essential importance for the classification of these ostracodes. The other main object of the study is a taxonomic treatment of the faunas (including also the other palaeocope families, particularly the Primitiopsidae and the Hollinidae). The considerable amount of time required in order to obtain a sufficient and well-preserved material for systematic descriptions, however, has delayed the publication of the morphological results, and as meanwhile papers on the same morphological problems and even on material from the same localities have appeared (most recently the important studies on the palaeocope hinge by POKORNÝ 1959), I feel it necessary to keep up with the development and publish one of the main results around which many of the forthcoming morphological and taxonomical discussions will be grouped.

Two other preparatory studies have already been published (MARTINSSON 1955 and 1956). The terminology used here is largely explained in these 1 - 603286 Bull. Geol. Vol. XXXIX

papers and in JAANUSSON's treatise of 1957. The reader is referred to the latter basic paper for a broad discussion of the implications of dimorphism on palaeocope taxonomy, based on a very differentiated Ordovician material.

**Material.** — The conditions and morphological details described here are strongly differentiated throughout the entire family *Beyrichiidae* and are, as mentioned, of great importance for a natural classification of the family, but for practical reasons this report will concentrate on a group of genera with a tubulous, broad velum. Most of the cases described here belong to undescribed species of the subgenus *Beyrichia* (*Mitrobeyrichia*) HENNINGSMOEN, one specimen belongs to the well-known *Beyrichia* (*Mitrobeyrichia*) clavata (KOLMODIN), and a number of specimens belong to a new species of a new subgenus. Systematic descriptions as well as details of the preparation will be given in the forthcoming paper, and until then the species are called species A and B (*B.* [*Mitrobeyrichia*] spp. from the upper Wenlockian Slite marls at Follingbo and Klinte, respectively), *B.* (*Mitrobeyrichia*) clavata (from the Mulde marl at Fröjel, uppermost Wenlockian), and species C (n. subg., n.sp. from the Ludlovian Hamra group at Grötlingbo).

**Earlier, phylogenetic, approach.** — By comparison of the lobation, velar structures, and ornamentation in a number of genera, KESLING (1957, cf. KESLING & ROGERS 1957) came to the conclusion that the beyrichiids developed from eurychilinid ostracodes (piretellids in the paper quoted, cf. JAANUSSON 1957). The development is supposed to be illustrated by the appearance of the different stages chronologically. The dolonal pouch in the Middle Ordovician genus *Chilobolbina* is regarded as the origin of the crumina. "During very late Ordovician or early Silurian time the beyrichiids developed from the piretellids [=eurichilinids] when the distal edge of the false [=dolonal] pouch fused with the contact margin to form a brood pouch [=crumina]. Probably at the same time, a part of the valve wall enclosed by the brood pouch receded from the brood pouch. The remaining part of the valve wall served as a partition between the pouch and the rest of the valve. The internal structures described in beyrichiid females are relicts of the ancestral valve wall."

KESLING's theory that the beyrichiids developed from the eurychilinids, or, more precisely, from eurychilinacean-like ancestors with a tendency of developing dolon of a somewhat earlier type than that represented by *Chilobolbina*, is strongly corroborated by the present study. The development of the crumina, however, is quite different from this theory.

KESLING (*l.c.*) expected intermediary forms to be found in the future in the Middle and Upper Ordovician. The dating of the development of the crumina is certainly fairly tenable, but it is very doubtful whether we can find that "missing link"—or its close relatives—which is required for the following

up of this phylogenetic line. There is, however, also a possibility of following the development of the crumina by ontogenetic evidence.

**Ontogenetic approach.** — As shown by earlier investigations (cf. MAR-TINSSON 1956) the dimorphic characters in the palaeocope ostracodes appear very suddenly, without any transitional forms, in the last moult stage, or, more seldom, in one of the preceding stages. In the beyrichiid female the last moulting is a veritable metamorphosis. The male carapace is very little affected by this procedure; it usually only comprises a slight broadening of the velum anteroventrally.

Only in some very rare cases the cruminal metamorphosis was not completed before the carapace of the adult ostracode had hardened, as in the specimens treated here. The development has been arrested at somewhat different stages in the different specimens (which will not be described in detail in this report) and therefore even the development which normally only comprises the soft tissues of the animal can be observed and described in terms of the hard carapace. These atavistic specimens are extremely rare. A rough estimate shows that major developmental defects occur in one of 3000-4000 adult specimens of species A and less than one of 10,000 adult specimens of species B and B. (Mitrobeyrichia) clavata. The adult specimens of Beyrichia, furthermore, constitute about one per cent or less of all ostracodes in a normal sample.

Adventral structures. Velum, dolon, and crumina. — The ventral part of the palaeocope carapace has different frill-, flange-, ridge-, or crest-like extensions, the adventral structures, the terminology of which will be briefly summarized and extended here. In the beyrichiids they are represented by the velar and marginal structures. The delicate marginal structures usually consist of two main elements, a covering frill and the paired vertical frills, together with accessory frills or rows of minute tubercles and spines, different in different taxa. In some ostracodes there is another, undescribed element in the subvelar field, viz. a more or less ridge-like, usually striated structure, the torus or toric structure which is of certain importance for the classification and for the homologization of different carapace structures.

In the velum as well as in the marginal structure there is a close interrelation between coherent flange-like structures, apparently formed from a simple epidermal fold, and tubulous, coherent frills or rows of spines, tubes, or tubercles, apparently formed from an epidermis which was morphologically or physiologically differentiated in a corresponding way. Even the *histial structure* distinguished by JAANUSSON (1957) in the hollinaceans shows the same development. The development in the velum and the histium is beautifully illustrated by KESLING (1955) who regards the frills as consisting of fused spines. As far as the beyrichiids are concerned the development of these structures, as well as of the lateral fields of tubercles on the valves, rather seems to lead to an isolation and simplification of the small elements. In the eurichilinacean females the dimorphic pouch is formed by a simple bulge in the velum, the *dolon*, and its wall consists of two layers, as suggested already in THORSLUND'S (1940) drawings of sections of *Chilobolbina*. The beyrichild pouch, without external opening, is called the *crumina*.

The structures enumerated here will be described in detail in connection with the forthcoming taxonomic treatment of the entire material where they are of great importance. Here they are mentioned only as far as they are necessary for the discussion or are seen in the figures. In one of the figures (Pl. IV, fig. 8) the *calcarine tubercle*, another important systematic character, is also shown.

The closing of the dolon. — As the first stage in the development of a beyrichiid crumina a small semi-ovoid dolonal pouch is formed (Fig. 1; Pl. II figs. 1, 2, and 5; Pl. III, figs. 1-7). The relatively smallest dolon observed is in species B where the diameter of the dolon is little more than half the diameter of the normal crumina (and the volume consequently about 1/8 of the normal cruminal volume, cf. Fig. 1). Already at this stage the closing procedure has reached fairly far. The specimen of species B (No. G 205, cf. Fig. 1) shows that a very thin flap-like extension of the velar edge is bent in over the opening of the dolonal pouch towards the vertical frill of the marginal structure which is more separated from the covering frill inside the dolon than in front of and behind this place (Pl. III, figs 1-3). In Beyrichia (Mitrobeyrichia) clavata the same dolonal flap is observed. It is thicker than in species B, and the figure (Pl. I, fig. 2) shows that it is extended from the outer of the two characteristic edges of the velum. In the continuation of the outer of these edges there remains in both species a small arch which persists even in the completely developed specimens.

Species A shows essentially the same development, but it is smaller and shows the conditions in less detail. One of the specimens (Pl. III, figs. 6 and 7) has reached a stage where the dolonal opening is very small but where there is still no internal opening.

One of the specimens of species C (Pl. V, Figs. 1 and 2) has reached a stage where the dolon is completely closed but where there is no internal cruminal opening. This species, however, which has a very voluminous crumina, differs somewhat from *Beyrichia* (*Mitrobeyrichia*) in the development. Constrictions of the subvelar field seem to be of greater importance for the closing of the dolonal opening, and the rôle of the dolonal flap has not been demonstrated.

In all species the edge of the velum continues unrestricted past the dolon at this stage.

**The formation of the internal opening.** — The first sign of an internal opening is in *Beyrichia* (*Mitrobeyrichia*) a more or less perfectly crescent-shaped groove or furrow on the internal side of the valve, coinciding with the upper

4

part of the circumference of the crumina (Fig. 3, Pl. II, fig. 3). In species C, where the entirely closed dolon is observed (*i.e.* where the contact of the dolon with the carapace wall is an almost complete circle), the furrow is c-shaped; the space between the free ends of the furrow, however, is relatively much narrower than in this letter.

After this initial stage the space of the pouch is increased, and by expansion ("inflation") of the dolonal wall a globular pouch, the crumina, is formed.

No specimens of *Beyrichia* (*Mitrobeyrichia*) are known from the expansion stage. In the other subgenus, represented by species C, however, an incomplete expansion is fairly common; three cases have been observed. These specimens have failed in the expansion of the most distal part of the dolon. The crumina has been calcified in a stage when the expansion has resulted in an almost ring-shaped space, fairly wide along the former circumference of the dolon and tapering down in both directions towards the point where the ends of the c-like furrow had met each other. The cruminal wall in these specimens bulges inwards, probably due to the fact that the distal part of the outer dolonal layer still sticks to the inner layer and to the remains of the wall fragment within the c-shaped furrow. The normal crumina is in this species very large (cf. Pl. V, figs. 1-5), which is probably one of the causes of the developmental defect.

The formation of the internal opening, however, can take place in two different ways, *i.e.* (1) by a complete separation of the two layers of the dolon before the expansion of the velum or (2) by a secondary perforation of the carapace wall between the domicilium and the dolonal space.

The cruminal morphology of some of the more advanced beyrichiids suggests that the former procedure has taken place. In *Beyrichia (Mitrobeyrichia)* the former dolon is already closed by the flap, and there is no need for a further separation of the two layers in order to form the cruminal space. The results of a special investigation of this detail are somewhat contradictory.

It is very difficult to observe the finest details of the inside of the crumina in thin sections owing to the calcite recrystallization which has taken place even in marl-filled specimens. For the same reason it is also almost impossible to excavate the crumina completely, as its wall is lined with the calcite. The opening of the crumina, however, can mostly be exposed.

In about 100 specimens prepared in this way the remains of the wall and the inner layer of the velum only consist of two small folds along that part of the opening which is situated immediately above the former dolonal opening (Pl. V, fig. 10). It would seem, therefore, as if the layers in the dolonal wall had been entirely separated by the inflation of the crumina. These folds would, then, constitue the proximal parts of the piece of the carapace wall, coherent with the inner layer of the dolon, which has been folded down into the crumina.

In one specimen, however (Pl. V, fig. 11), there is a thin calcified membrane coherent with these small folds, broadening towards the opposite part of the margin of the opening. It is limited by a furrow which is evidently homologous

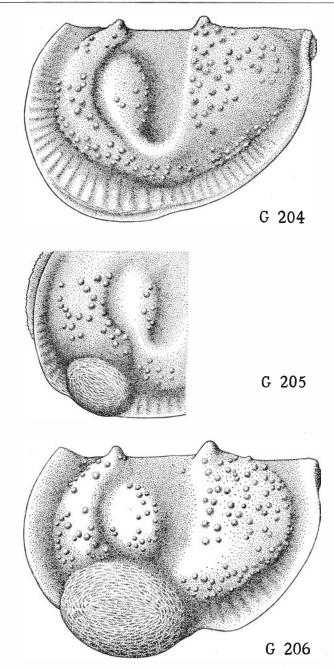
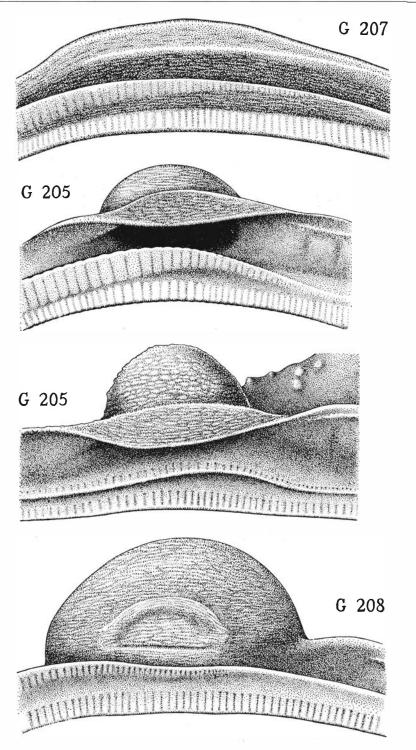


Fig. 1 (above). Beyrichia (Mitrobeyrichia) sp. B. Left valves of a male (Mus. Pal. Inst. Univ. Uppsala No. G 204), an incompletely developed female (No. G 205), and a normal female specimen (No. G 206). 40 ×.

Fig. 2 (right). Beyrichia (Mitrobeyrichia) sp. B. Anteroventral parts of left valves of a male (No. G 207), an incompletely developed female (No. G 205, in ventral and oblique ventral view), and a normal female specimen (No. G 208). 80 × . Drawn by E. Ståhl.



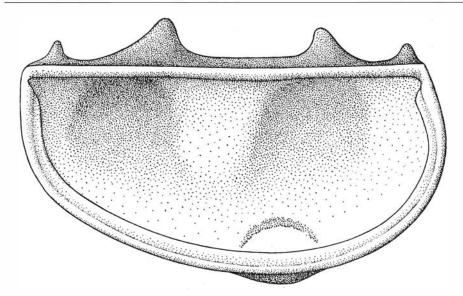


Fig. 3. Beyrichia (Mitrobeyrichia) sp. A. Left valve of an incompletely developed female specimen (internal view) showing the crescent-shaped groove along the base of the dolon. (Mus. Pal. Inst. Univ. Uppsala, No. G 212.) 75 ×.

with the crescent-shaped furrow formed in the initial stage of the formation of the crumina. The membrane has a secondary opening and is finely folded around this opening. It is, at present, impossible to state whether this is an abnormal case where the inner layer of the dolon has not separated from the outer one or whether it was formed by an epidermal layer in normal position but with an extraordinarily far-reaching calcification. In another genus (shown in Pl. IV, figs. 5 and 6, but not treated further here) a membrane of similar type is normal, which corroborates but does not prove the former explanation. On the other hand more advanced forms have a more simplified formation of the crumina, and it is not improbable that *Beyrichia* (*Mitrobeyrichia*) represents a first stage in the development towards a simple splitting up and expansion of the two layers of the velum.

The functional problem in connection with this question, *viz*. how and when the brood was introduced into the crumina, will not be discussed here.

Our present knowledge of this detail, which will be studied further, can be summarized as follows:

In *Beyrichia* (*Mitrobeyrichia*) the first stage of the formation of the cruminal opening is marked by a crescent-shaped furrow on the level of the tubules in the dolonal part of the velum. The calcification of the inner layer of the dolon and of the carapace wall coherent with it is strongly reduced, and the crumina is practically single-walled. It is not entirely clear whether the inner layer separated completely from the outer one during this procedure or whether a secondary opening was normally required to establish the connection of the crumina with the domicilium. There is normally no calcified continuation of the carapace wall separating the crumina from the domicilium.

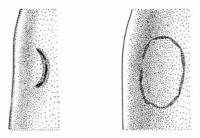


Fig. 4. The crescent-shaped groove in an incompletely developed female of *Beyrichia (Mitrobeyrichia) clavata* (KOLMODIN) and the circular groove in *Beyrichia* (n. subg.) sp. C. Both specimens have reached a stage where the dolon has been closed or almost closed but where no cruminal opening has developed. In later stages the groove of *Beyrichia (Mitrobeyrichia)* assumes a shape similar to the groove in the other species (cf. Pl. V, fig. 11). About 30 and 35 ×, respectively.

**Traces of the dolonal opening and of the velar edge.** — As stated above the dolonal flap in *Beyrichia* (*Mitrobeyrichia*) is inserted so far in the dolonal opening that its edge lies in contact with the proximal part of the edge of the opening. During the expansion the flap is squeezed against this edge. In the normal crumina the edge of the flap lies, as seen in thin sections, in a notch between the former edge of the opening and what seems to be the remains of the carapace wall within the dolon.

These traces of the dolonal stage are indicated by the velar arch on the crumina below an external furrow which marks the former dolonal opening. In some old species (Pl. IV, fig. 4) it is very apparent even in normal specimens how the dolonal flap is inserted in the furrow.

In species C the velar edge is very characteristically developed. It forms a ridge the edge of which is bent in three small bows, the central one being the smallest and most sharply bent. A small tubercle in this bow corresponds to a short internal tubule. There is no furrow marking the old dolonal opening in this species.

Secondary changes in the velum and in the carapace wall. — The expansion of the crumina in the few species selected for this preliminary report chiefly comprises the outer layer of the original dolon. Adjoining parts of the carapace have also been assimilated, and the zygal ridge disappears in the females of *Beyrichia* (*Mitrobeyrichia*).

In the cases of developmental defects discussed here the velar edge continues without interruption past the crumina or atavistic dolon. In all corresponding normal specimens there is a constriction of the velum in front of and behind the crumina, and in species A it even forms a wing-like extension behind the latter constriction.

The ornamentation of the crumina is sometimes very helpful for the identification of the different parts of the dolon and of the normal crumina (cf. Figs. 1

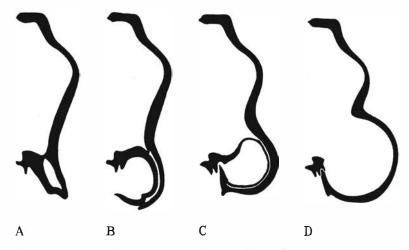


Fig. 5. The development of the crumina in *Beyrichia* (*Mitrobeyrichia*). The valves (left valves, seen in front view) are supposed to have been calcified in different stages of the development which normally involves only soft parts.

In stage A the velum is supposed to be unaltered; the moulting has resulted only in an increase in size, and the specimen cannot be distinguished from a male specimen. In stage B a dolonal pouch has developed, and a flap is extended from the edge of the dolon. In stage C the inner layer of the dolon and the piece of the carapace wall coherent with it have begun to be reduced; it is not known whether the inner layer remains in this position during the continued procedure and is secondarily perforated or whether it is separated from the outer layer before it becomes entirely reduced. Stage D shows a normal female specimen.

Magnified  $30 \times$ .

and 2). In the species treated here there are no tubercles with corresponding pores, nor any other kind of typical carapace wall ornamentation in the crumina. The crumina is only striated or very finely reticulated.

In other species, however, larger parts of the carapace wall are engaged in the formation of the crumina, and the ornamentation of the carapace wall often extends over the larger part of the cruminal wall. In some of these cases even the margin of the valve is affected by the cruminal metamorphosis (cf. MARTINSSON 1956, Pl. II, fig. 5).

KESLING (1957, p. 64) has pointed out the fact that the velum can be either interrupted or not interrupted by the crumina and indicates two possible explanations, *viz*. "(1) that during the phylogeny the frill [=velum] retreated from the brood pouch [=crumina], or (2) that it gradually grew across the brood pouch [=crumina]". The explanation is probably that the splitting up of the velum in the dolonal region has been more or less far-reaching (cf., *e.g.*, the conditions in *Dibolbina*).

The cruminal opening in most beyrichiins comprises the entire contact zone of the valve wall and the crumina, and there is generally no internal wall of the kind described by KESLING in other beyrichiids, *viz*. the treposellins *Phlyctiscapha* and *Hibbardia* (op. cit., fig. 5). A wall as constructed by KESLING in *B.* (*Mitrobeyrichia*) clavata (="jonesii", op. cit., Fig. 4) does not exist; that the

existence of a wall was suggested by the thin section on which the construction was based is due to the fact that the crumina was cut rather distally by the section. But there are occasionally in this subgenus, and more regularly in related forms, membranous partitions between the crumina and the domicilium which do not, however, restrict the opening of the crumina considerably.

Further comparisons with species outside the group described here cannot be made in this short extract. Modern photographs showing examples of the extremely varied subcruminal morphology have been published by MARTINS-SON (1956, Pls. I–III) and KESLING & ROGERS (1957, Pls. 127–131; N.B. the furrow marking the closed dolonal opening in some species).

Institute of Palaeontology, University of Uppsala, March 14th, 1960.

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## Explanations of the plates

The specimens have been coated with ammonium chloride. A slight retouch, chiefly of matrix parts and details in the background, has been undertaken. The numbers are original numbers in the collections of the Institute of Palaeontology, University of Uppsala. Photographs by ANDERS MARTINSSON.

#### Plate I

Figs. 1-3. Beyrichia (Mitrobeyrichia) clavata (KOLMODIN). Mulde marl, Mulde, Fröjel. 45 ×.

- Fig. 1. Male carapace, ventral view (No. G 213). Note the characteristic double edge of the velum (the inner edge is a toric structure) and the covering and vertical marginal frills. The tubes are to be seen in the broken parts of the frills.
- Fig. 2. Female carapace, ventral view (No. G 214).
- Fig. 3. Left valve of the female specimen (No. G 215), internal view, showing the subcruminal morphology.

#### Plate II

Figs. 1-3. Beyrichia (Mitrobeyrichia) clavata (KOLMODIN). Fragment of a right female valve (No. G 216). The development of the crumina has been interrupted in the dolonoid stage. 45 ×.

Fig. 1. Lateral view.

Fig. 2. Oblique ventral view.

Fig. 3. Inner side, oblique dorsal view.

Figs. 4-6. Beyrichia (Mitrobeyrichia) sp. B. Slite marl, Klinte. 30 × (cf. Text-figs. 1 and 2).

Fig. 4. Left valve of male specimen (No. G 204), lateral view.

Fig. 5. Fragment of a left valve of a female specimen (No. G 205) with incompletely developed crumina. Lateral view.

Fig. 6. Left valve of a normal female specimen (No. G 206), lateral view.

#### Plate III

Figs. 1-3. Beyrichia (Mitrobeyrichia) sp. B. Slite marl, Klinte. Female specimen, left valve (No. G 205). The development of the crumina has been interrupted in the dolonoid stage.  $45 \times .$ 

Fig. 1. Ventral view.

Fig. 2. Ventral view, different light.

Fig. 3. Oblique ventral view.

Figs. 4-8. Bevrichia (Mitrobevrichia) sp. A. Slite marl, Follingbo. Left valves of female specimens. 30 × .

Fig. 4. Specimen with incompletely developed crumina (No. G 217), lateral view.

Fig. 5. Same specimen, inner side, oblique dorsal view.

Fig. 6. Specimen with incompletely developed crumina (No. G 218), lateral view.

Fig. 7. Same specimen, oblique ventral view.

Fig. 8. Normal specimen (No. G 219), lateral view.

#### Plate IV

Ventral morphology of the crumina in the groups of beyrichiids treated in this report. Figs. 1-4 are left valves, Fig. 5 an entire carapace, and Figs. 6-8 left valves. 54 ×.

Fig. 1. Beyrichia (Mitrobeyrichia) sp. A. Slite marl, Follingbo (No. G 220).

Fig. 2. Beyrichia (Mitrobeyrichia) sp. B. Slite marl, Klinte (No. G 208).

Fig. 3. Beyrichia (Mitrobeyrichia) sp. B. Slite marl, Klinte (No. G 221).

- Fig. 4. Beyrichia (Mitrobeyrichia) sp. Högklint marl, Visby (No. G 222).
- Fig. 5. Beyrichiid, n.g.?, n. sp. (aff. Apatobolbina?). Lower Visby marl, Lummelunda (No. G 223).

Fig. 6. Same genus, n.sp. Högklint marl, Visby (No. G 224).

Fig. 7. Beyrichiid, n.g., n.sp. Eke marl. Lau (No. G 225).

Fig. 8. Beyrichia (n. subg.) n.sp. Hamra marl, Grötlingbo (No. G 226). Note the calcarine tubercle.

### Plate V

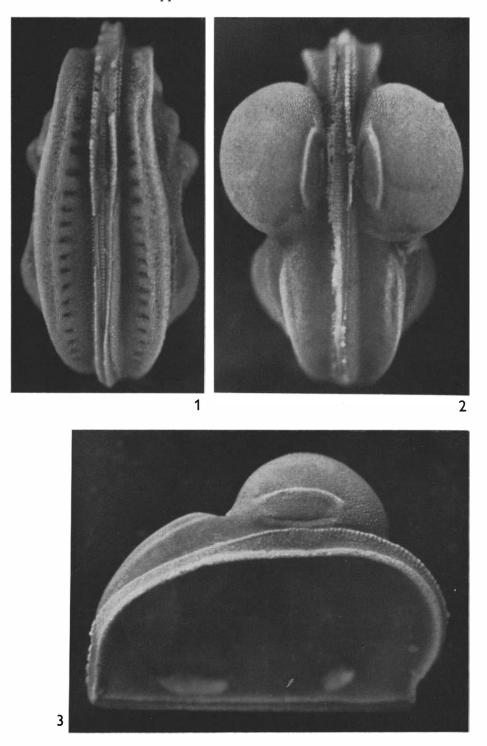
Figs. 1-9. Beyrichia (n. subg.) n.sp. (=species C). Hamra marl, Grötlingbo. 30 ×.

- Fig. 1. Right female valve (No. G 227) with incompletely developed crumina. Lateral view (cf. Pl. V, fig. 7).
- Fig. 2. Same specimen, inner side, oblique ventral view.
- Fig. 3. Left female valve (No. G 228) with incompletely developed crumina. Lateral view.
- Fig. 4. Right female valve (No. G 229) with incompletely developed crumina. Lateral view (cf. Pl. V, fig. 8).
- Fig. 5. Left valve of a normal female specimen (No. G 230).
- Fig. 6. Left valve of a male specimen (No. G 231).
- Fig. 7. Same specimen as in Pl. V, fig. 1, oblique ventral view. Fig. 8. Same specimen as in Pl. V, fig. 3, oblique ventral view.
- Fig. 9. Normal left female valve (No. G 232), oblique ventral view.
- Figs. 10 and 11. Beyrichia (Mitrobeyrichia) clavata (KOLMODIN). Mulde marl, Mulde, Fröjel. Opening of the crumina.  $45 \times$ .

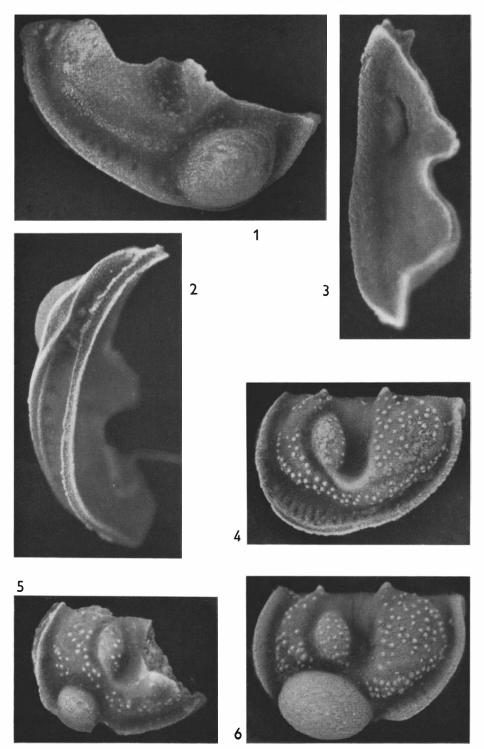
Fig. 10. Normal specimen, left valve (No. G 233).

Fig. 11. Specimen with calcareous membrane in the cruminal opening (No. G 234).

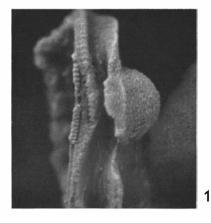
Bull. Geol. Inst. Univ. Uppsala. Vol. XXXIX: 1

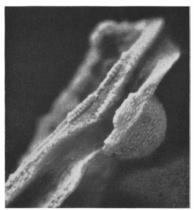


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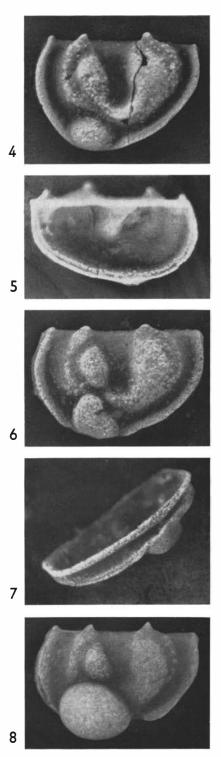
# Bull. Geol. Inst. Univ. Uppsala. Vol. XXXIX: 1

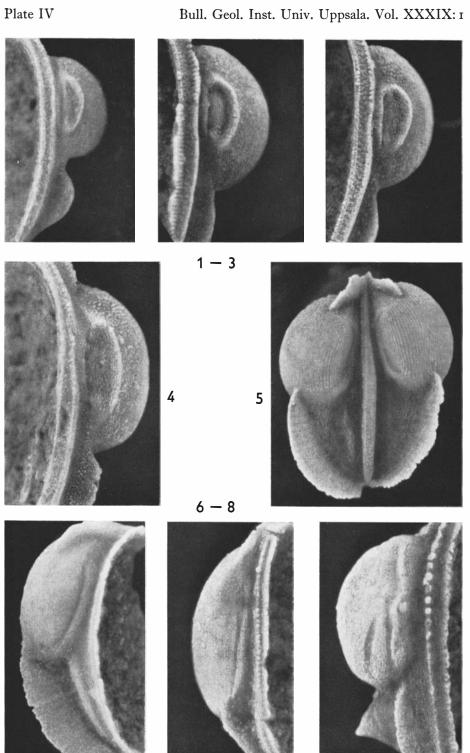


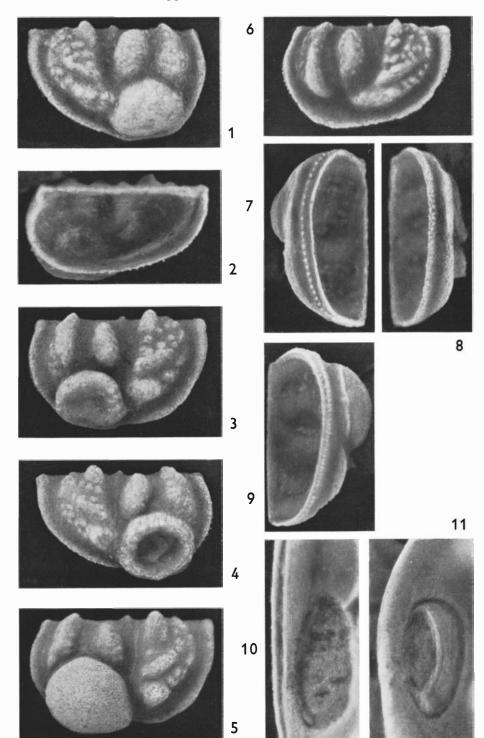












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