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ORIGIN OF BEYRICHIID OSTRACODS

BY

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# CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

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INTRODUCTION

FROM a survey of existing knowledge of ostracods in the family Beyrichiidae, it is now possible to postulate the origin of the family with some confidence. As with other extinct groups of animals, the investigation of phylogeny is beset with many problems, such as the incompleteness of the paleontological record and the fragmentary nature of the fossils. During the last decade, however, many new species of beyrichiids have been described, new specimens of species established many years ago have been found and studied, and noteworthy contributions have been made to the taxonomy of the family.

Beyrichiid ostracods have been known for more than a century. The earliest note appears to be that by von Buch in 1828 (p. 71), who for some unexplained reason thought them to be the young of a brachiopod with which they were associated in Silurian rocks. Klöden (1834, pp. 115-17), Burmeister (1843, pp. 72-73), Geinitz (1845, p. 237), and Quenstedt (1852, p. 302) studied certain species and decided they were cephalons of small trilobites. It was Goldfuss (1843, p. 542) who first suggested that they were ostracods. Beyrich (1845, p. 47), for whom the genus *Beyrichia* was named, also reached this conclusion. During the last half of the nineteenth century numerous species were described in Europe, many of them from boulders in glacial drift, by such competent paleontologists as Jones, Schmidt, Grewingk, Roemer, Krause, Kiesow, Reuter, and Verwor. By the end

of the century, enough was known about the beyrichiid ostracods from the Silurian strata of northern Europe to show some of the important variations in the group and to prove their stratigraphic value.

The first significant taxonomic work on the family was done by Ulrich and Bassler in 1908. They stated (pp. 279-80), "As the investigations are far from complete, the attempt must, to a considerable extent, be preliminary to the final effort to be made in the proposed monograph. While confessing its preliminary nature, it should not be supposed that the results here presented are founded on studies of only a part of the species immediately concerned. On the contrary, the authors have taken into account not only every recognizable described or figured Beyrichian, but also a host of unpublished species." The family Beyrichiidae as treated by Ulrich and Bassler contained straight-hinged Paleozoic ostracods, many of which were not dimorphic. Of their genera, only *Beyrichia* and *Trepostella* remain in the Beyrichiidae and the rest have been removed to the families Eurychilinidae, Kloedeniidae, Kloedenellidae, Hollinidae, Tetradellidae, and Drepanellidae.

In 1923 (pp. 310-12) Ulrich and Bassler created the superfamily Beyrichiacea and sharply restricted the family Beyrichiidae. They described the family as: "Valves trilobate or quadrilobate, deeply sulcated; brood pouch when present, very prominent, subglobular or egg-shaped, on the ventral slope." They retained *Tetradella* and *Hollina* in the Beyrichiidae and placed *Apatobolbina* and *Bolbibollia* in the family Primitiidae.

Bassler and Kellett (1934, pp. 26-29) expanded the family to include *Ctenobolbina*, *Ceratopsis*, *Kiesowia*, *Aechminella*, *Hippa*, *Eoconchoecia*, *Tetrasulcata*, *Hollinella*, and several other genera which lack brood pouches. They repeated the description of the family given by Ulrich and Bassler in 1923 and quoted above. In 1936 (pp. 547-49) Swartz emended the family and put many genera into new families, but retained some Ordovician genera without brood pouches, including *Coelochilina*, *Apatochilina*, *Eurychilina*, and *Chilobolbina*. He stated (p. 545), however: "In the writer's opinion, these pouches represent an anatomical structure more fundamental than the degree of lobation, and more indicative of genetic relationship; especially when the pouches occur in combination with the peculiar margin frill."

Henningsmoen (1953, p. 264), in his revision of Paleozoic straight-hinged ostracods, gave the following diagnosis of the family:

"Family Beyrichiidae:—Vellate structure entire. Dimorphism as (carinal ?) swellings of the carapace wall, either as a not very well defined swelling, or as a more or less well defined pouch. 1-3 sulci, S1 more persistent than S2. L2 usually node-like.

"Subfamily Beyrichiinae:—As family. Sulci short. Often well defined pouch. Velate structure developed as ridge or frill.

"Subfamily Zygobolbinae:—As family. L2 and L3, or ridge on top of L3, joined ventrally to form a U-shaped ridge. Velate structure developed as ridge or narrow frill."

Later (1954, p. 20), Henningsmoen changed his diagnosis to: "Dimorphic Beyrichiacea, where one of the dimorphs of each species has a pouch. Non- to trisulcate. S1 more persistent than S3. Velate structure usually present as a ridge or frill." He divided the Beyrichiidae into four subfamilies, the Beyrichiinae, Kloedeniinae, Zygobolbinae, and Treposellinae.

As used in this paper, the Beyrichiidae includes those genera which Henningsmoen placed in the subfamilies Beyrichiinae and Treposellinae. These are *Beyrichia* McCoy, *Craspedobolbina* Kummerow, *Apatobolbina* Ulrich and Bassler, *Dibolbina* Ulrich and Bassler, *Bolbibollia* Ulrich and Bassler, *Bolbiprimitia* Kay, *Hibbardia* Kesling, *Phlyctiscapha* Kesling, and, very questionably, *Mesomphalus* Ulrich and Bassler. To these should be added an unnamed Silurian genus, the species of which are presently assigned to *Chilobolbina*. Specimens of the type species of *Craspedobolbina*, *C. dietrichi* Kummerow, are no longer available, and it is not possible to prove whether this uppermost Ordovician ostracod has a brood pouch (and belongs in the Beyrichiidae) or a false pouch (and belongs in the Pireteliidae). With the possible exception of *Craspedobolbina*, the beyrichiid ostracods are found only in Silurian and Devonian rocks.

The character which is unique to the beyrichiids is a well-defined brood pouch. Most genera have pouches with distinct boundaries on all sides, but two Devonian genera, *Hibbardia* and *Phlyctiscapha*, have pouches that are posteriorly confluent with the rest of the valve. It seems advisable to regard the Kloedeniidae and Zygobolbidae as families, because ostracods of these taxa have pouches formed by so-called "swellings," which gradually slope into the rest of the valves and lack clear boundaries on all sides. These ostracods quite likely evolved independently and developed pouches in a manner different from that in the Beyrichiidae.

There has been much speculation about the use of the brood pouch. Richter (1869, p. 774) designated as females the specimens with "überquellender Randwulst." This description undoubtedly refers to the brood pouch. Ulrich and Bassler (1923, p. 310) called the structure a "brood pouch" without offering any proof that it was utilized for brood care. German authors called it "Brutkammern," "Brutraum," "Bruttasche," and "Bruthöcker." Kummerow (1933, p. 48) reported eggs in the false pouch of *Piretella reticulata* (Krause): ". . . der nach aussen konvexe gefälte Randsaum der weiblichen Klappen innen eine Anzahl hohler, nach dem

Schalenraum hin offener und durch Scheidenwände getrennter Querfächer von 0,30 mm Länge und 0,07 mm Breite, in denen die Eier aufbewahrt wurden. Bei einem Exemplar hatten sich je 1-3 Eier in die Wand ihres Faches eingedrückt und haben so besondere Hohlräume als deutliche Spuren ihrer Anwesenheit hinterlassen." Triebel later (1943, p. 203) studied this species and concluded that the structures called eggs by Kummerow were actually nodes on the outer surface of the false pouch of the female and on the frill of the male, "Es ergibt sich also, dass die Vertiefungen, die nach K. 'nur von Eiern herrühren' können, *beiden* Geschlechtern zukommen, sich *nur* auf dem Abdruck der Velum-Aussenfläche finden, in Wirklichkeit also Knötchen der *Oberfläche* darstellen."

Schmidt (1941, pp. 11-12) thought that the beyrichiid pouches might have been gas-filled chambers: "... halten wir es aber für wahrscheinlicher, dass die 'Bruthöcker' der Beyrichiacea und andere ähnliche Formen von 'Brutlagern' nicht zur Aufnahme von Eiern, sondern von geschlüpfter Brut dienen. Ihre Lage im vorderen Abschnitt des Gehäuses erscheint dann durchaus möglich. Die Beobachtung, dass diese Form der 'Brutlager' bald wieder verschwand, könnte man dann so deuten, dass die rostrade Lage derselben die Bewegung der Tiere wirklich sehr gehemmt habe, oder dass diese Art Brutpflege eine Sackgasse der Organisation war, bzw. beide Ursachen zusammengewirkt haben." He further suggested (p. 12) that the pouched dimorph was the male, and that the pouches were used for storage of spermatozoa. Triebel (1941, p. 365) also believed that the pouches belonged to the male, which utilized them for sperm vesicles.

In 1949 (Pl. 14, Fig. 9) Hessland illustrated a cross section of a pouch-bearing specimen of *Beyrichia kloedeni* in which carapaces of young instars were enclosed within those of the adults. He also (pp. 123-28) commented in detail on the brood pouch problem. Spjeldnaes (1951, Pl. 103, Fig. 1) showed immature specimens within the brood pouches of *Beyrichia jonesii* Boll. There seems little room for doubt that the brood pouches were used to house the young during part of their ontogeny.

As already pointed out by Hessland (1949, p. 126), for taxonomic work it is necessary to differentiate the brood pouch, which occurs in beyrichiids, from the false pouch, which is formed in certain other ostracods by the convexity of the frill. *Laccochilina* and *Eurychilina*, genera of the Eurychilinae, have strongly curved frills, which have been described by several authors as "sausage-shaped." No ostracods in this family are known to be dimorphic. The female dimorphs of *Piretella*, *Rakverella*, *Öpikium*, and *Chilobolbina*, genera of the Piretellidae, have the anteroventral parts of the left and right frills so strongly incurved that they meet to form a false pouch when the carapace is closed. Female ostracods of *Hollina*,

type genus of Hollinidae, have similar false pouches. There is no evidence that false pouches were used for brood care. In nearly all species in which the female has a false pouch, the male has a very broad frill. The dimorphism of the frills, as suggested by Hessland (1949, p. 127), may have been a necessary adaptation for copulation.

In this paper many species of beyrichiid genera have been restudied. Type specimens of several have been examined, new specimens of others have been found, and the descriptions have been appraised with reference to current terminology. It was learned that many of the type specimens have critical structures still buried in the rock and that others are very fragmentary. For some species it was possible to obtain new specimens that were better preserved and more complete than the type specimens. Many of the old descriptions are seriously lacking in detail and are written in ambiguous terms. For the species which are described only briefly and illustrated poorly it was judged essential to study specimens. All known beyrichiid species could not be included in this paper, for their numbers would require a monograph. Insofar as possible, however, the genera were investigated in type species, in well-known species, or in species for which excellent specimens are available.

Many workers contributed to this study. Dr. Gunnar Henningsmoen of the Paleontologisk Museum, Oslo, Norway, sent specimens of *Craspedobolbina armata* Henningsmoen and *Beyrichia jonesii* Boll and loaned type specimens of *Beyrichia kiaeri* Henningsmoen. Dr. Remington Kellogg, Dr. A. R. Loeblich, Jr., and Dr. I. G. Sohn loaned type specimens from the United States National Museum. Dr. G. M. Ehlers, Dr. C. A. Arnold, and Dr. L. B. Kellum critically read the manuscript and offered helpful revisions. To all who generously aided in making this paper possible I am deeply indebted.

Some of the specimens on which the illustrations are based are catalogued and deposited in the Museum of Paleontology of the University of Michigan; they are identified by the initials UMMP. Others are the property of the United States National Museum (USNM) and the Paleontologisk Museum at Oslo (PMO).

#### CHARACTERISTICS OF THE BEYRICHIIDAE

The search for the ancestors of beyrichiid ostracods can logically begin with a critical appraisal of the characteristics of the family. Certain unusual characteristics, which are absent or rare in other ostracods of the superfamily Beyrichiacea, appear to be phylogenetically significant. The following lines of evidence are discussed below: (1) extreme variations

in size, lobation, and velate structure, (2) the existence of a well-developed brood pouch in the oldest known beyrichiids, (3) internal structures found within female valves, (4) relationships of velate structures and brood pouches, and (5) ornamentation of the pouch.

*Extreme variations in size, lobation, and velate structure.*—The adult female of *Bolbibollia labrosa* on one of two pieces of rock labeled "Cotype 82406" at the U. S. National Museum is only 0.67 mm. long. An adult female of an undescribed beyrichiid species from the Middle Silurian of Michigan is 0.73 mm. long. The female of *Bolbiprimitia fissurella*, USNM Cotype 63607, is 1.14 mm. in length. In sharp contrast to these small ostracods, an adult male of *Beyrichia tuberculata*, UMMP No. 32101, is 3.35 mm. and a female, UMMP No. 32082, 3.10 mm. long. Most adult beyrichiids are between 1.5 and 2.5 mm. in length. Great variations in size occur within one genus. For example, adult males of *Dibolbina steusloffii* are about 1.30 mm. long, whereas those of *Dibolbina cristata* are 2.10 mm. *Beyrichia salteriana* and *B. buchiana*, both placed in the subgenus *Neobeyrichia* by Henningsmoen (1954, p. 25), have adult females which measure 1.40 and 2.30 mm., respectively.

The lobation in beyrichiid genera is also extremely variable; some are distinctly trilobate, others are bilobate, and two genera are unilobate. In the trilobate ostracods the lobes are of several kinds. *Beyrichia buchiana* (Pl. III, Fig. 1) has long narrow lobes of about the same size; *B. tuberculata* (Pl. III, Fig. 4) has two nodes for L1, an elongate small lobe for L2, and a large L3 crossed by two sloping furrows; *B. salteriana* (Pl. III, Fig. 7) has a long full lobe for L1, an elongate lobe for L2, and a very large L3; *B. maccoyiana sulcata* (Pl. IV, Fig. 7) has about the same lobation as *B. salteriana* but with a conspicuous curved furrow across the upper half of L3; and *B. kochii* (Pl. VI, Fig. 7) and *B. kiaeri* (Pl. V, Fig. 1) resemble *B. tuberculata* except that L1 is a long full lobe. *Dibolbina steusloffii* (Pl. IV, Fig. 1) has lobes much like those of *Beyrichia salteriana* but with a more elongate L2. *Treposella stellata* (Pl. VI, Fig. 4), *Treposella lyoni* (Pl. VII, Fig. 7), and *Craspedobolbina armata* (Pl. VI, Fig. 1) differ from most trilobate beyrichiids in having L1 and L3 confluent with a large ventral lobe. The sulci in those species also vary: *Beyrichia buchiana* (Pl. III, Fig. 1) has very broad and long sulci; *Dibolbina steusloffii* (Pl. IV, Fig. 1) and *Beyrichia salteriana* (Pl. III, Fig. 7) have long narrow sulci; and *Treposella stellata* (Pl. VI, Fig. 4) and *T. lyoni* (Pl. VII, Fig. 7) have short sulci, of which S1 is shallow and S3 is deep and, in *T. lyoni*, contains a pit.

Of the bilobate species, *Bolbiprimitia fissurella* (Pl. II, Fig. 4) has a very long narrow sulcus, "*Chilobolbina*" sp. (Pl. IV, Fig. 4) has only a central circular pit for S2, and *Hibbardia lacrimosa* (Pl. VII, Fig. 1) has a



shallow sulcus in the dorsal part of the valve and a conspicuous central pit. *Bolbibollia labrosa* (Pl. V, Fig. 4) has the lobation confined to a relatively small U-shaped ridge around the sulcus.

Two genera, one from the Middle Silurian and the other from the Middle Devonian strata, have no sulcus whatever. *Apatobolbina* sp. (Pl. II, Fig. 7) and *Phlyctiscapha apleta* (Pl. VII, Fig. 4) are representative species of these genera.

There is, in addition, very little correlation between lobation and ornamentation. Of the ostracods that are distinctly reticulate, *Treposella lyoni* (Pl. VII, Fig. 7) is trilobate and *Hibbardia lacrimosa* (Pl. VII, Fig. 1) is bilobate. Of those that are smooth, or nearly so, *Apatobolbina* sp. (Pl. II, Fig. 7) and *Phlyctiscapha apleta* (Pl. VII, Fig. 4) are unilobate, but *Dibolbina steusloffii* (Pl. IV, Fig. 1) and *Beyrichia salteriana* (Pl. III, Fig. 7) are trilobate.

Velate structures range from low, inconspicuous ridges that cannot be seen in lateral view, as in *Beyrichia tuberculata* (Pl. III, Fig. 6) and *B. buchiana* (Pl. III, Fig. 3), to unusually wide frills, as in "*Chilobolbina*" sp. (Pl. IV, Figs. 4-6) and *Dibolbina steusloffii* (Pl. IV, Figs. 1-3). *Beyrichia kiaeri* (Pl. V, Fig. 1) has velate spines. In some species, such as *Treposella stellata* (Pl. VI, Figs. 4-5), the frills of male and female are essentially alike, whereas in others, such as *Beyrichia maccoyiana sulcata* (Pl. IV, Figs. 7-8), they are conspicuously different.

Since there is no obvious trend of evolution in the size and lobation in beyrichiid ostracods, it is impossible to infer a particular size or lobation for their ancestors.

*Well-developed brood pouch in oldest known beyrichiids.*—Unfortunately, *Craspedobolbina dietrichi* Kummerow, the type species of its genus, is now known only from literature. All known specimens of this uppermost Ordovician ostracod have been lost, and one cannot determine if it is really a beyrichiid. Illustrations and descriptions indicate that it has a well-developed pouch, but do not indicate whether the pouch is a brood pouch or a false pouch. All of the Silurian beyrichiids have brood pouches with distinct boundaries. There is no morphological or chronological series of ostracods known in which the brood pouch developed first as a slight convexity on the valve and became progressively larger and more bulbous. It would seem, therefore, that the brood pouch evolved from a strongly convex homologous structure in the beyrichiids' ancestors.

*Internal structures within female valves.*—In the thin sections of *Beyrichia jonesii* illustrated by Spjeldnaes (1951, Pl. 103, Figs. 1-2) there is shown a wall separating the pouch from the rest of the interior of the valve. Kesling (1953, p. 225, Fig. 1, Pl. II, Figs. 8-14) described and

figured a partition inside female valves of *Phlyctiscapha rockportensis*. Within each female valve of *Hibbardia lacrimosa* there is a rodlike strut joined at its ends to the top of the brood pouch at the junction with the lateral part of the valve and to the contact margin. Figures 4 and 5 show sections of *Beyrichia jonesii* and *Hibbardia lacrimosa* containing these structures.

At first I thought that such structures developed in beyrichiid ostracods after the brood pouch had become functional, and served as partitions to screen off the pouch space from the oral region of the adult female, thereby affording the young protection both from external enemies and from the indiscriminate feeding of the mother animal. It is just as reasonable, however, to assume that these structures are not secondary adaptations but relicts of structures that existed in the ancestors. The position of the structures strongly suggests that they are homologous with the ventral part of the valve wall in the progenitors.

*Relationships of velate structures and brood pouches.*—It is a curious circumstance that in some beyrichiid females the velate structure is completely interrupted by the pouch, in others it encroaches onto the ends of the pouch, and in a few it continues across the entire pouch. These relationships indicate two possible explanations: (1) that during phylogeny the frill retreated from the brood pouch, or (2) that it gradually grew across the brood pouch. I endorse the second explanation, because the frill does not extend onto the pouch in Lower Silurian ostracods, such as *Beyrichia paucituberculata* Henningsmoen, *B. zygophora* Henningsmoen, *B. osloensis* H., *B. skienensis* H., and *Craspedobolbina armata* H. It likewise seems significant that the oldest known ostracods to have a frill across the brood pouch are from Upper Silurian rocks.

In *Craspedobolbina armata* (Pl. VI, Figs. 2-3) the velate ridge is divided into two parts, a posterior which joins with the rear end of the pouch (but does not extend onto it) and an anterior part which lies ahead of the pouch. The velate ridge is completely interrupted by the pouch in many species of *Beyrichia*, including *B. buchiana* (Pl. III, Figs. 2-3), *B. tuberculata* (Pl. III, Figs. 5-6), *B. salteriana* (Pl. III, Figs. 8-9), and *B. kiaeri* (Plate V, Figs. 2-3).

The frill is confluent with the ends of the pouch in *Apatobolbina* sp. (Pl. II, Figs. 8-9) and *Beyrichia kochii* (Pl. VI, Figs. 8-9); in "*Chilobolbina*" sp. (Pl. IV, Figs. 5-6), *Treposella stellata* (Pl. VI, Figs. 5-6), and *T. lyoni* (Pl. VII, Figs. 8-9) it extends onto the brood pouch but not completely across it. The encroachment of the frill onto the brood pouch culminated in the Upper Silurian species *Dibolbina steusloffii* (Pl. IV, Figs. 2-3) and

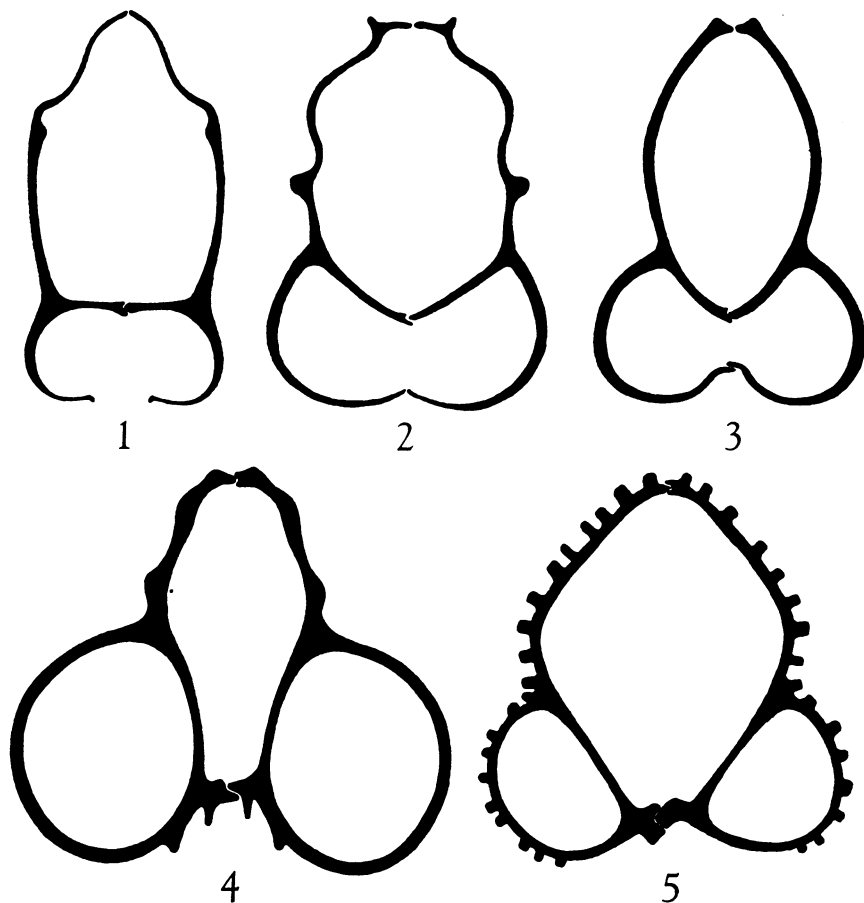


FIG. 1. *Eurychilina dorsotuberculata* Hessland. Lower Ordovician, strata *G* and *R II*, Sweden. Cross section taken from Hessland, 1949, Pl. 15, Fig. 20. Height of section, 0.92 mm.

FIG. 2. *Piretella acmaea* Öpik. Middle Ordovician, Lyckholm formation, Estonia. Hypothetical cross section based on Öpik, 1937, Pl. 4, Figs. 6a-b and Pl. 7, Figs. 6-9. Height of section, 1.55 mm.

FIG. 3. *Chilobolbina dentifera* (Bonnema). Middle Ordovician, Kukruse formation, Estonia. Hypothetical cross section based on Öpik, 1937, Pl. 7, Figs. 1-3; Hessland, 1949, Pl. 15, Fig. 21; and on USNM topotype specimens No. 58376. Height of section, 0.69 mm.

FIG. 4. *Beyrichia jonesii* Boll. Middle Silurian, Wenlockian series, Gotland. Hypothetical cross section based on Spjeldnaes, 1951, Pl. 103, Figs. 1-2. Height of section, 1.47 mm.

FIG. 5. *Hibbardia lacrimosa* (Swartz and Oriol). Middle Devonian, Ludlowville formation, New York. Cross section of female. Height of section, 1.05 mm.

the Lower Devonian species *Beyrichia fittsi* (Pl. V, Figs. 8-9), in which the frill continues across the pouch without interruption.

An unusual relationship of velate structures and brood pouch exists in *Beyrichia maccoyiana sulcata* (Pl. IV, Figs. 8-9). A frill extends from the posterior region of the valve onto the pouch and reaches the anterior end of the pouch; a velate ridge, separate from the frill, extends along the anterior border parallel to the free edge, with its ventral end situated proximal to the front end of the frill. It is interesting to note that the velate structure of the male also changes form in the anteroventral region; along the ventral border it is a thick flaring frill, on the anteroventral border it projects sharply outward and then abruptly inward, and along the anterior border it continues as a narrow velate ridge parallel to the free edge.

In another group of the beyrichiids the velate structure extended along the proximoventral side of the brood pouch instead of on it. This group is also characterized by elongate ventral brood pouches more or less confluent with the lateral surface of the valve at their posterior ends. The Upper Silurian species *Bolbiprimitia fissurella* (Pl. II, Figs. 5-6) has the velate ridge extending below and inside the pouch but separated into two parts. The Middle Devonian species *Phlyctiscapha apleta* (Pl. VII, Figs. 5-6) and *Hibbardia lacrimosa* (Pl. VII, Figs. 2-3) have velate structures complete below the pouch. The frill in *Hibbardia lacrimosa* has a unique development in the anteroventral region; the proximal part continues across this region but the distal part is divided into two short, curved ridges that extend onto the ventral surface of the pouch.

The sequence of relationships of velate structure and brood pouch indicates that the immediate ancestors of the Beyrichiidae did not have a velate structure across or on any part of the feature which later developed into the brood pouch.

*Ornamentation of brood pouches.*—Anteroventral brood pouches of beyrichiid females possess a kind of ornamentation on the ventral surface that differs from that on the rest of the pouch. For example, the pouches in *Apatobolbina* sp. (Pl. II, Figs. 8-9) and *Treposella lyoni* (Pl. VII, Figs. 8-9) have fine striae on the ventral part and much coarser striae on the rest of the surface. The pouch in *Craspedobolbina armata* (Pl. VI, Figs. 2-3), however, exhibits exactly the opposite arrangement, with coarse striae below and fine striae elsewhere. "*Chilobolbina*" sp. (Pl. IV, Figs. 5-6) and *Beyrichia maccoyiana sulcata* (Pl. IV, Figs. 8-9) have coarse reticulation on the venter and fine reticulation on the sides of their pouches. In *Beyrichia tuberculata* (Pl. III, Figs. 5-6) the ventral part of the pouch is ornamented with small tubercles, whereas the rest of the

pouch has large pustules. In *Beyrichia kiaeri* (Pl. V, Figs. 2-3) the ventral part of the pouch is striate, but the rest is ornamented with low tubercles.

It should also be noted that among ostracods with ornamented ventral brood pouches, the ornamentation on the anterior and anteroventral parts is different from that on the rest of the pouch. *Bolbiprimitia fissurella* (Pl. II, Figs. 5-6) has smooth anterior and anteroventral areas and reticulation elsewhere on the pouch; *Hibbardia lacrimosa* has small pits in the anterior and anteroventral areas and reticulation elsewhere on its pouch. It is impossible to judge whether the shell material in smooth or nearly smooth pouches has similar variations in structure in different parts of the pouch.

Insofar as the variations in brood pouch ornamentation may be interpreted, they indicate that the ancestors of the beyrichiids probably had similar variations in ornamentation on the homologue of the brood pouch.

#### PROBABLE ANCESTORS OF THE BEYRICHIIDAE

In seeking the origin of the Beyrichiidae, one can limit investigation to the ostracods that lived during a certain interval of time and that possess certain features. Obviously, the ancestors of the beyrichiids must be sought among Ordovician ostracods, inasmuch as the oldest known ostracods of the superfamily Beyrichiacea are Lower Ordovician and the oldest known Beyrichiidae are latest Ordovician or earliest Silurian. Since lobation in beyrichiids is extremely variable, it is likely that their forebears were similarly variable; lobation, therefore, is not a critical consideration. The brood pouch, the distinguishing feature of the Beyrichiidae, is of prime importance. Because the brood pouch is fully developed in the oldest known beyrichiids, there is good reason to believe that a homologous structure existed in the ancestors. Furthermore, if the assumption is correct that the internal structure in beyrichiid females is a relict of the valve wall, then the brood pouch was derived from a structure which was outside of, and not a part of, the valve wall. One can also presume, since numerous Ordovician ostracods have been investigated, that the homologous structure is a feature already discovered. The only structure that fully satisfies all these expectations is a specialized part of the frill.

*The family Piretellidae.*—Although there is no general agreement on the content of the Piretellidae, this family should include at least the ostracods with a well-developed frill in the male and an anteroventral false pouch in the female, such as are found in the type genus. In addition to *Piretella* Öpik, the family includes *Rakverella* Öpik, *Öpikium* Agnew,

and *Chilobolbina* Ulrich and Bassler. The false pouches in female dimorphs of these ostracods are formed by strong convexity of the frills. Lobation in piretelliids is varied. *Piretella acmaea* Öpik (Pl. I, Figs. 7-8) appears to be trilobate, with a deep sulcus for S2 and a shallow groove for S1, which is partly obscured by an ornamental crest. *Rakverella bonnemai* (Pl. I, Figs. 1-2) has the lobation restricted to the central and dorsal areas, but seems to be trilobate, with S1 and S2 confluent as a deep, depressed area and the lobes formed by three spines projecting from a common ridge. *Öpikium tenerum* (Pl. I, Figs. 4-5) is bilobate with a long sulcus for S2, and *Chilobolbina dentifera* (Pl. II, Figs. 1-2) is bilobate with only a central pit for S2.

The function of the dimorphic frills is not known. Certainly, such frills were poorly suited for brood care in the female, since the false pouches that they form were open whenever the valves were apart. Hessland (1949, p. 127) proposed that the frills of the male may have acted as runners wherewith the animal skidded the carapace along the muddy sea floor and that the narrower, strongly convex frills may have developed in the female so that it could copulate with the wide-frilled male.

Of the piretelliid ostracods *Chilobolbina dentifera* is worthy of particular attention, because in lateral view it so closely resembles beyrichiids that Ulrich and Bassler (1923, p. 304) assumed that it had a brood pouch, made it the type species of their genus *Chilobolbina*, and assigned to *Chilobolbina* several true beyrichiids from the Silurian of North America. As first discovered by Öpik (1937, p. 22), this species has a bulbous false pouch formed as an enlargement of part of the frill, and not a brood pouch. There is a disagreement on whether the distal edges of the two frills meet when the valves are together. Thorslund (1940, Fig. 57) showed that the edges of the frills would not be in contact when the carapace was closed, but Hessland (1949, Pl. 15, Fig. 21) presented a cross section in which the two edges touched. From an examination of one of two female valves catalogued in the U. S. National Museum under the number 58376, I conclude that the distal edge of the frill in the region of the false pouch has a delicate lip (Pl. II, Fig. 3), which, when the carapace was complete, not only met that of the opposite frill but overlapped it to form a kind of closure (as presumed in Fig. 3). The false pouch of *C. dentifera* has faint radial markings on the proximal part, low convexities on the central part, and striae on the distal part. Thus, it seems to presage the two kinds of ornamentation on beyrichiid pouches. The false pouch is bulbous, and, as already shown by Öpik (1937, Pl. 7, Fig. 3), the distal part is curved inward so that its edge lies very near the contact margin of the valve. Only by cross sections or by interior views of isolated valves can the false

pouch in *Chilobolbina* be distinguished from a brood pouch. *Chilobolbina* admirably fulfills the requirements for an immediate ancestor of the Beyrichiidae.

Other piretellig ostracods have the distal part of the frill turned inward only slightly, if at all, and have less bulbous false pouches. *Rakverella bonnemai* (Pl. I, Figs. 2-3) has a false pouch that extends from the posteroventral region nearly to the anterior corner. The velate spines, which in the male (Pl. I, Fig. 1) are discrete, are fused in the female (Pl. I, Figs. 2-3) to make a solid frill, which is bent sharply near its junction with the lateral surface of the valve. The male of *Öpikium tenerum* (Pl. I, Fig. 4) has a very wide flaring frill, which is radially striate with small concentric elements on the striae, but the female (Pl. I, Figs. 5-6) has an incurved frill, which is ornamented distally with concentric striae having small radial markings. *Piretella acmaea*, the type species of *Piretella*, has a thick frill of closely spaced spines in the male (Pl. I, Fig. 7) and a thick frill with shallow radial grooves in the female (Pl. I, Figs. 8-9) forming a subovate false pouch. A hypothetical cross section of *P. acmaea*, based on several views published by Öpik (1937, Pl. 4, Figs. 6a-b and Pl. 5, Figs. 6-9), is shown in Figure 2. The distal edges of the frills meet in this species but are not curved inward as far as those in *Chilobolbina dentifera* (Fig. 3).

*The family Eurychilinidae.*—Certain ostracods in this family developed so-called "sausage-shaped" convex frills during Lower Ordovician time. The convexity in eurychilinids extends from the anterior end nearly to the posterior, and is not, as in piretelligs, confined to the anteroventral and ventral parts of the frill. Insofar as is known, the eurychilinids were not dimorphic and did not have the frills incurved so far as to form false pouches. As demonstrated by Hessland (1949, Pl. 15, Fig. 20) and shown in Figure 1, the convex frills in *Eurychilina dorsotuberculata* do not meet.

Ostracods of the family Eurychilinidae have already been suggested as ancestors of the Beyrichiidae. Hessland (1949, p. 127) hinted at such a relationship when he said, "It may be of interest that the type of pouch which was practically impossible as a brood pouch (the *Eurychilina* type) is that which first appears geologically (Lower Ordovician). The one which most certainly served as breeding space (*Beyrichia kloedeni*) is the youngest one (Gotlandian). The intermediate type (*Chilobolbina*) is of intermediate age (Middle Ordovician)." Henningsmoen stated (1954, p. 34), "It is generally assumed that the beyrichiids developed from the eurychilinids," and added later (1955, p. 241), "*Craspedobolbina dietrichi* Kummerow, 1924, from a glacial drift boulder of probably late Ordovician limestone in northern Germany, is possibly the earliest known beyrichiid.

It reminds one of primitiids and eurychilinids, from which the Beyrichiidae may have developed . . . .”

The strong resemblance of the eurychilinid convex frill to the piretelliid false pouch supports the theory that the Piretelliidae descended from the Eurychilinidae. Similarly, the resemblance of the bulbous false pouch in *Chilobolbina* to the beyrichiid brood pouch advances the theory that the Beyrichiidae in turn evolved from the Piretelliidae. The chronological and morphological sequence indicates that the brood pouch developed as the acme of frill convexity wherein the distal edge of the frill fused with the contact margin of the valve.

#### CONCLUSIONS

From a study of representative species of beyrichiid genera, it becomes apparent that the family Beyrichiidae is typified by certain characteristics, which are discussed in detail above. These may be summarized as follows. Lobation of beyrichiids is extremely variable. The brood pouch is fully developed in the earliest known beyrichiids. No Lower Silurian ostracods have any part of the frill extending onto the brood pouch, but certain Upper Silurian and Lower Devonian species have a frill continuous across the brood pouch. Female valves that have been investigated by sectioning or polishing have been found to possess internal structures which are confluent with the dorsal part of the valve wall, extend to the contact margin, and separate part of the brood pouch from the interior of the valve. Ornamented brood pouches have ornamentation in the ventral or anteroventral areas that differs from that on the rest of their surfaces.

From a consideration of these characteristics, the following may be inferred. (1) The ancestors of the Beyrichiidae were probably variable in lobation. (2) The brood pouch developed from a homologous structure in the ancestors, very likely from a structure with more than one kind of ornamentation. (3) Because the frill did not extend onto the brood pouch in the earliest beyrichiids, it probably did not extend onto the homologue in the ancestors. The ancestral structure from which the brood pouch developed may, therefore, have been part of the frill itself. (4) Progenitors of the Beyrichiidae probably had some morphological feature homologous to the internal structure present in each valve of beyrichiid females.

Characteristics of certain Ordovician ostracods appear to be related to those in the Beyrichiidae. Piretelliid ostracods are dimorphic, with a well-developed frill in the male and a false pouch in the female. The false pouch in *Chilobolbina* is bulbous, and in lateral view cannot be distinguished



from the brood pouch of beyrichiids; it is so strongly convex that its distal edge is near the contact margin of the valve. The false pouch in *Chilobolbina* and certain other piretellids has ornamentation on the distal part that differs from that on the proximal part. In addition, the piretellids have variable lobation. Some Lower Ordovician eurychilid ostracods have broad convex frills, which differ from the false pouches in piretellids in being longer and in failing to meet on their edges.

The following evolutionary sequence in the origin of beyrichiid ostracods is postulated:

1. During Lower Ordovician time certain eurychilid ostracods developed strongly convex frills.

2. During Middle Ordovician time dimorphism in the form of the frill appeared in the descendants of the eurychilids, the piretellids. This dimorphism, as Hessland suggested, may have evolved as a necessary adaptation in the female for copulation with the wide-frilled male. The frills of female piretellids became so strongly convex that their edges met to form false pouches.

3. One genus of the piretellids, *Chilobolbina*, developed a bulbous false pouch that was curved inward at its distal margin.

4. During very late Ordovician or early Silurian time the beyrichiids developed from the piretellids when the distal edge of the false pouch fused with the contact margin to form a brood pouch. Probably at the same time, a part of the valve wall enclosed by the brood pouch receded from the contact margin to produce an opening from the interior of the valve to 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.

5. The use of the beyrichiid pouch for brood care may have started quite fortuitously when the young instars took advantage of the protection it afforded. Beyrichiids show no progressive enlargement of the brood pouch, such as one might expect if these structures were developed for the purpose of accommodating the immature offspring.

Subsequent investigations of Middle and Upper Ordovician ostracods may reveal species with structures which tend to substantiate or disprove this hypothesis. A species in which the edge of the false pouch almost, but not quite, touches the contact margin of the valve would be the "missing link" between *Chilobolbina* and the beyrichiids, and would offer additional evidence that the beyrichiid brood pouch evolved from the piretellid false pouch.

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## PLATES

All figures are restorations. Some are based on specimens and others on published figures. For each species a male and a female right valve are illustrated to show the dimorphism and the nature of the brood pouch. All male valves are enlarged to approximately the same length. The actual size of each specimen is indicated in the plate explanation.

## EXPLANATION OF PLATE I

*Rakverella bonnemai* Öpik

Middle Ordovician, Kukruse formation, Estonia.

FIG. 1. Lateral view of male right valve, based on Öpik, 1937, Pl. 9, Fig. 4 and Pl. 15, Figs. 10-11. Length, 1.50 mm.

FIGS. 2-3. Lateral and ventral views of female right valve, based on UMMP specimen No. 32076. Length, 1.68 mm.

*Öpikum tenerum* (Öpik)

Middle Ordovician, Kukruse formation, Estonia.

FIG. 4. Lateral view of male right valve, based on UMMP specimen No. 32078 and on Öpik, 1937, Pl. 5, Figs. 1-2. Length, including frill, 3.40 mm.

FIGS. 5-6. Lateral and ventral views of female right valve, based on UMMP specimen No. 32077. Length, 1.80 mm.

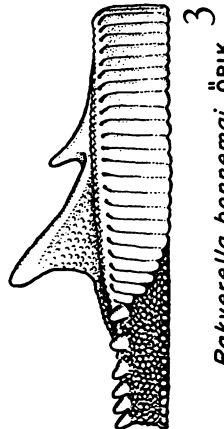
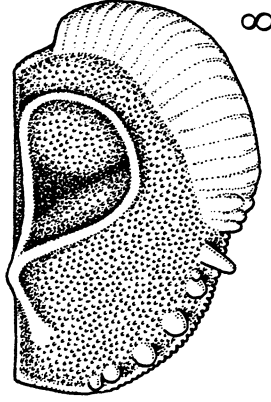
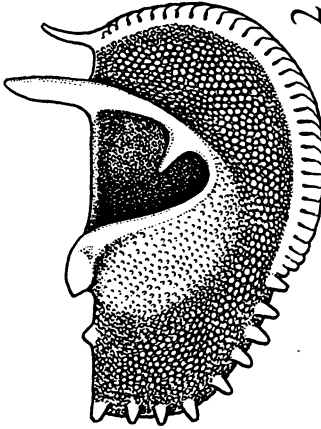
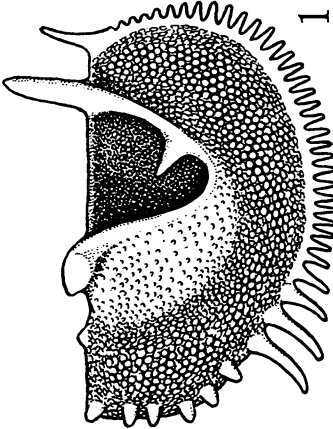
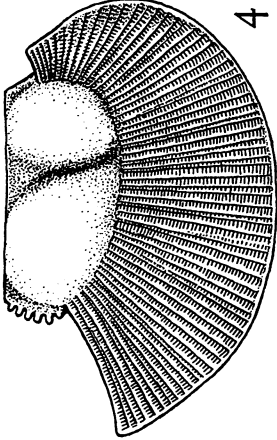
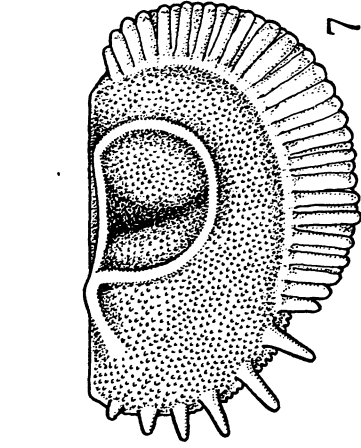
*Piretella acmaea* Öpik

Middle Ordovician, Lyckholm formation, Estonia.

FIG. 7. Lateral view of male right valve, based on Öpik, 1937, Pl. 4, Fig. 7. Length, 2.35 mm.

FIGS. 8-9. Lateral and ventral views of female right valve, based on Öpik, 1937, Pl. 4, Figs. 6a-b and Pl. 7, Figs. 6-9. A hypothetical cross section of a female carapace is shown in Figure 2 in the text. Length, 2.50 mm.

PLATE I

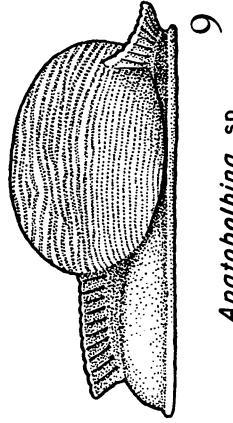
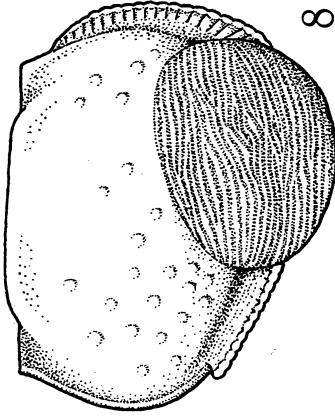
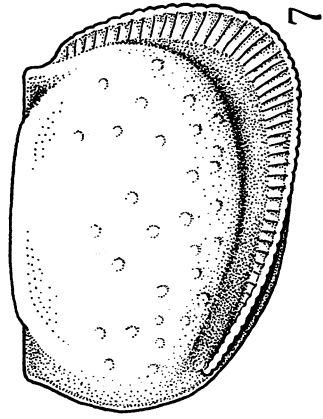


*Piretella acmaea* ÖPIK

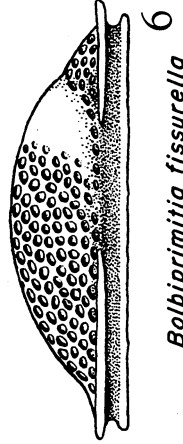
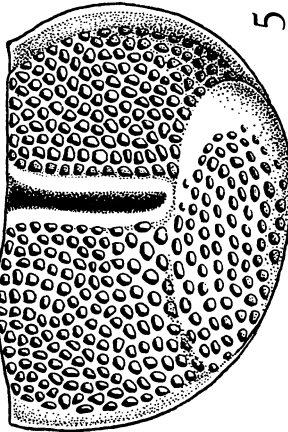
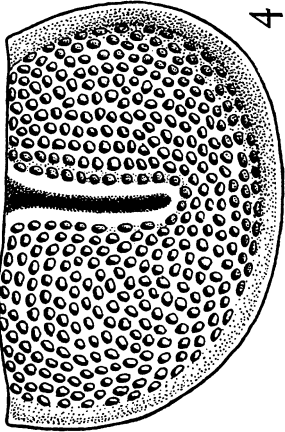
*Öpikium tenerum* (ÖPIK)

*Rakverella bonnemai* ÖPIK

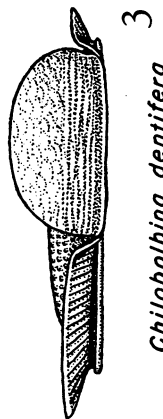
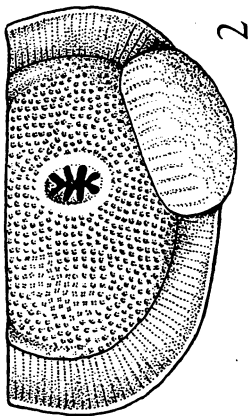
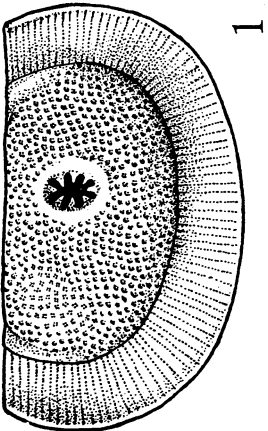
PLATE II



*Apatobolbina* sp.



*Balpiprimitia fissurella*  
(ULRICH AND BASSLER)



*Chilobolbina dentifera*  
(BONNEMA)

## EXPLANATION OF PLATE II

*Chilobolbina dentifera* (Bonnema)

Middle Ordovician, Kukruse formation, Estonia.

FIG. 1. Lateral view of male right valve, based on USNM specimens No. 58376 and on Bassler and Kellett, 1934, Figure 7-1. Length, 1.75 mm.

FIGS. 2-3. Lateral and ventral views of female right valve, based on USNM specimens No. 58376 and on Öpik, 1937, Pl. 7, Figs. 1-3. A hypothetical cross section of a female carapace is shown in Figure 3 in the text. Length, 2.03 mm.

*Bolbiprimitia fissurella* (Ulrich and Bassler)

Upper Silurian, Tonoloway limestone, West Virginia.

FIG. 4. Lateral view of male right valve, based on UMMP specimen No. 33747a and on Ulrich and Bassler, 1923, Pl. 37, Fig. 22. Length, 0.92 mm.

FIGS. 5-6. Lateral and ventral views of female right valve, based on UMMP specimen No. 33747b and on Ulrich and Bassler, 1923, Pl. 37, Fig. 23. Length, 1.12 mm.

*Apatobolbina* sp.

Middle Silurian, Manistique formation, Michigan.

FIG. 7. Lateral view of male right valve, based on UMMP specimens Nos. 30494 and 30496. Length, 1.65 mm.

FIGS. 8-9. Lateral and ventral views of female right valve, based on UMMP specimens Nos. 30492 and 30495. Length, 1.65 mm.

## EXPLANATION OF PLATE III

*Beyrichia buchiana* Jones

Upper Silurian, Ludlovian series, Gotland. Blank areas in lateral views are positions of muscle scars.

FIG. 1. Lateral view of male right valve, based on UMMP specimens Nos. 33741, 33742, and 33743, from drift near Berlin. Length, 2.28 mm.

FIGS. 2-3. Lateral and ventral views of female right valve, based on UMMP specimen No. 30516, from drift near Berlin. Length, 2.40 mm.

*Beyrichia tuberculata* (Klößen)

Upper Silurian, Ludlovian series, Gotland. Blank areas in lateral views are positions of muscle scars.

FIG. 4. Lateral view of male right valve, based on UMMP specimens Nos. 32079, 32090, and 32095, from drift near Berlin. Length, 2.70 mm.

FIGS. 5-6. Lateral and ventral views of female right valve, based on UMMP specimens Nos. 32100 and 32103, from drift near Berlin. Length, 2.73 mm.

*Beyrichia salteriana* Jones

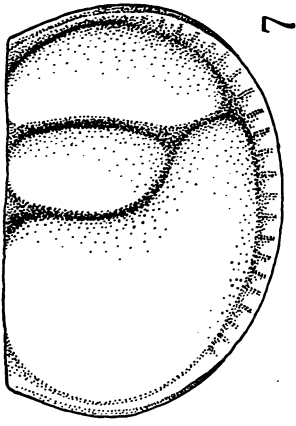
Upper Silurian, Ludlovian series, Gotland.

FIG. 7. Lateral view of male right valve, based on UMMP specimens Nos. 30517, 33744, 33745, and 33746, from drift near Berlin. Length, 1.16 mm.

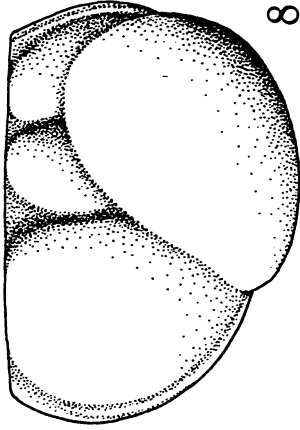
FIGS. 8-9. Lateral and ventral views of female right valve, based on UMMP specimen No. 30510, from drift near Berlin. Length, 1.40 mm.



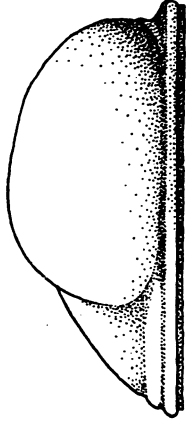
PLATE III



7

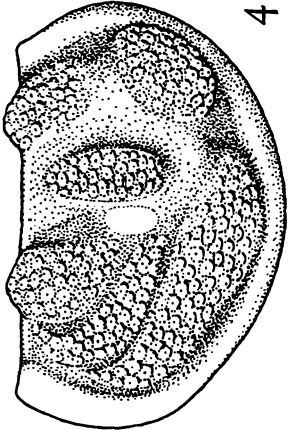


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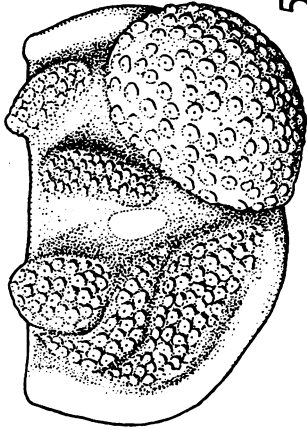


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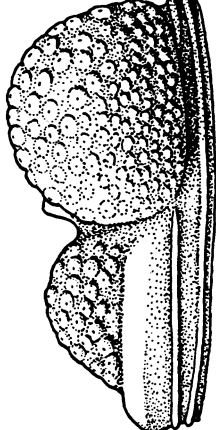
*Beyrichia salteriana* JONES



4

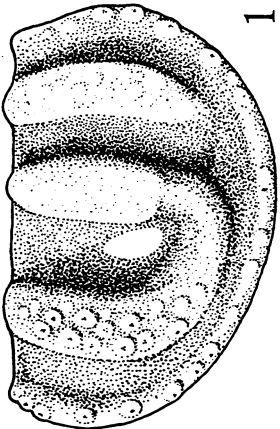


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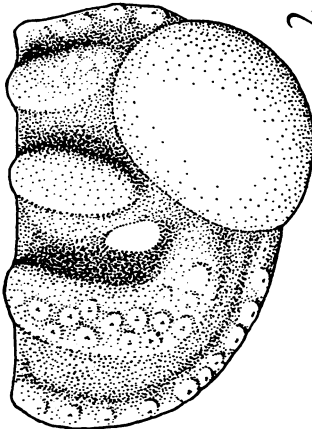


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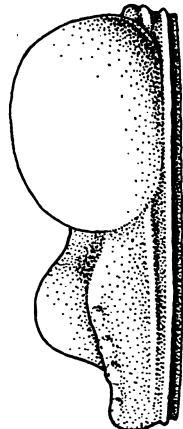
*Beyrichia tuberculata* (KLÖZEN)



1



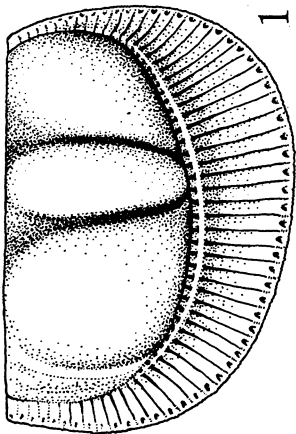
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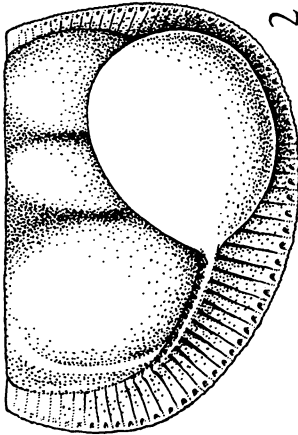
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*Beyrichia buchiana* JONES

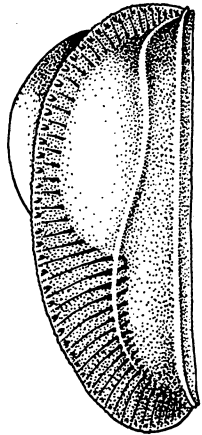
PLATE IV



1

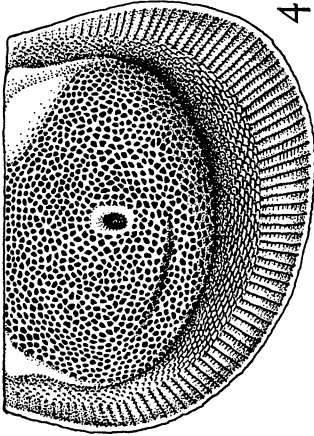


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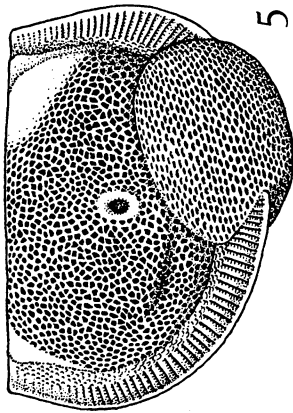


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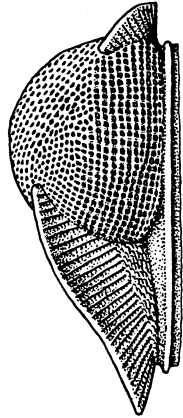
*Dibolbina steustoffi* (KRAUSE)



4

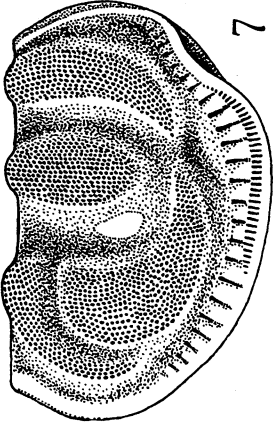


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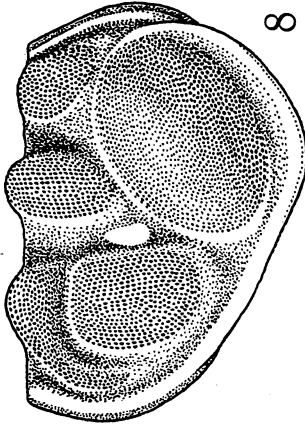


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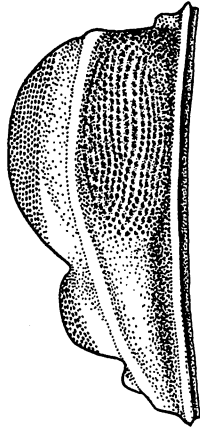
"*Chilobolbina*" sp.



7



8



9

*Beyrichia maccoyiana* JONES  
var. *sulcata* REUTER

## EXPLANATION OF PLATE IV

*Dibolbina steusloffii* (Krause)

Upper Silurian, Ludlovian series, Gotland.

FIG. 1. Lateral view of male right valve, based on UMMP specimens Nos. 32688a and 32688b. Length, 1.25 mm.

FIGS. 2-3. Lateral and ventral views of female right valve, based on UMMP specimen No. 32690 and on Krause, 1891, Pl. 4, Figs. 1-6. Length, 1.24 mm.

*Chilobolbina* sp.

Middle Silurian, Manistique formation, Michigan. This species is congeneric with other Silurian species which are presently assigned to *Chilobolbina* but which are not in the same genus, or even in the same family, as *Chilobolbina dentifera* (Bonnema), the type species. A new genus will be proposed for the Silurian species at a later time.

FIG. 4. Lateral view of male right valve, based on UMMP specimens Nos. 33748, 33749, and 33750. Length, 1.55 mm.

FIGS. 5-6. Lateral and ventral views of female right valve, based on UMMP specimens Nos. 33751 and 33752. Length, 1.55 mm.

*Beyrichia maccoyiana* Jones var. *sulcata* Reuter

Upper Silurian, Ludlovian series, Gotland.

FIG. 7. Lateral view of male right valve, based on UMMP specimen No. 33759. Length, 2.47 mm.

FIGS. 8-9. Lateral and ventral views of female right valve, based on UMMP specimens Nos. 33762 and 33763. Length, 2.15 mm.

## EXPLANATION OF PLATE V

*Beyrichia kiaeri* Henningsmoen

Middle and Upper Silurian, Wenlockian and Ludlovian series, Norway.

FIG. 1. Lateral view of male right valve, based on PMO specimen No. 66449a. Length, 2.50 mm.

FIGS. 2-3. Lateral and ventral views of female right valve, based on PMO specimen No. 46559b. Length, 2.50 mm.

*Bolbibollia labrosa* Ulrich and Bassler

Middle Silurian, Jupiter River formation, Anticosti Island.

FIG. 4. Lateral view of male right valve, based on USNM specimens on piece of limestone catalogued No. 82406. Length, 0.75 mm.

FIGS. 5-6. Lateral and ventral views of female right valve, based on USNM specimens on piece of limestone catalogued No. 82406. Length, 0.90 mm.

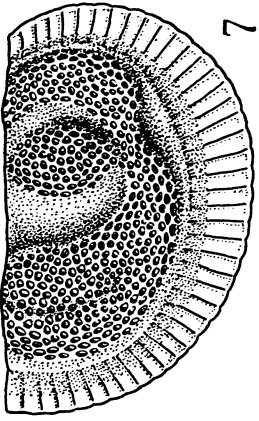
*Beyrichia fittsi* Roth

Lower Devonian, Haragan shale, Oklahoma. There are some doubts about the specimens and the content of the species. Roth (1929, pp. 340-41, Pl. 35, Figs. 6a-d) described and illustrated a male and a female valve. Warthin (1937, Card 18) restudied the specimens, questioned whether the two belonged to one species, and published an emended description based on the male valve. In September, 1956, I studied the USNM specimens No. 80655, which are on one slide labeled Holotype. The female now on this slide is not the one illustrated by Roth and later by Warthin. It is more complete than the female type specimen, but is crushed and distorted in the posterior region. The differences in size and lobation in the male and female are minor, and those in ornamentation can be attributed to preservation. I am inclined to regard the two specimens now on the slide as conspecific. The ventral part of the brood pouch is not well preserved in the female valve and my restoration may not be quite correct. Ornamentation in the figures is based on the reticulate pattern seen very clearly on the female valve. The frill definitely passes around the pouch.

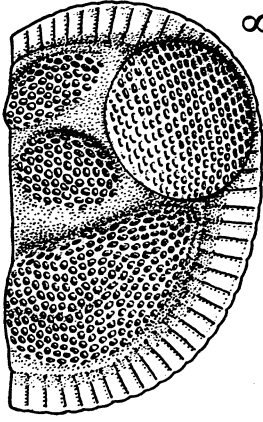
FIG. 7. Lateral view of male right valve. Length, 1.48 mm.

FIGS. 8-9. Lateral and ventral views of female right valve. Length, 1.50 mm.

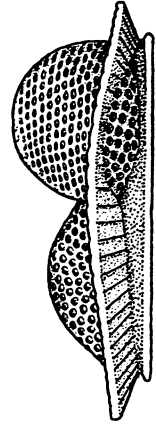
PLATE V



7

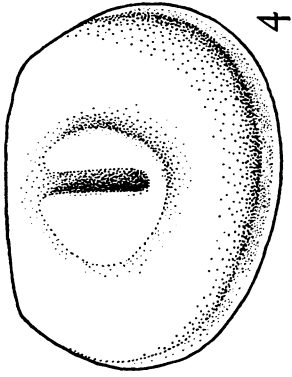


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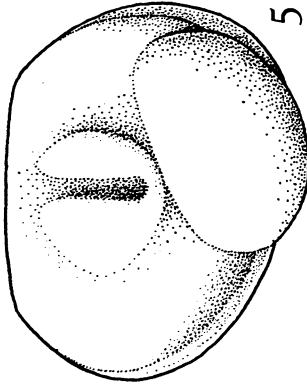


9

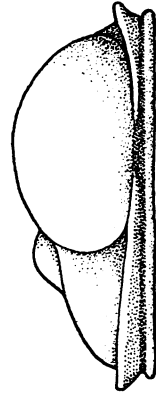
*Beyrichia fittsi* ROTH



4

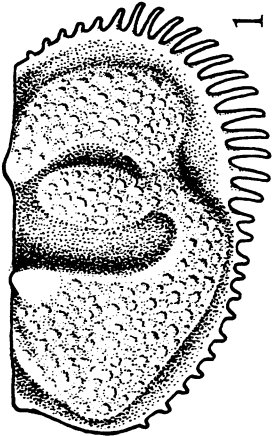


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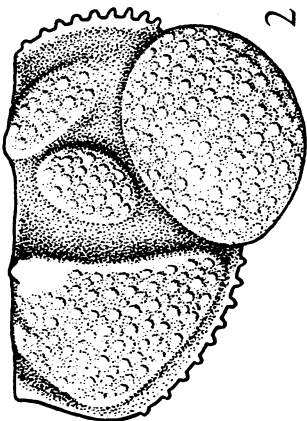


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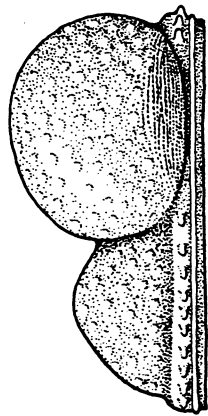
*Balbipollia labrosa*  
ULRICH AND BASSLER



1



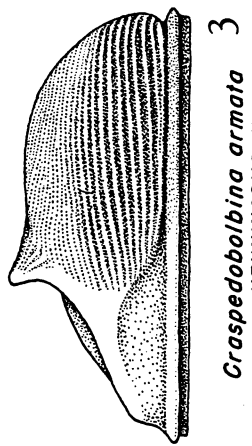
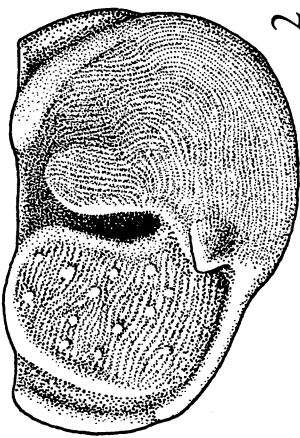
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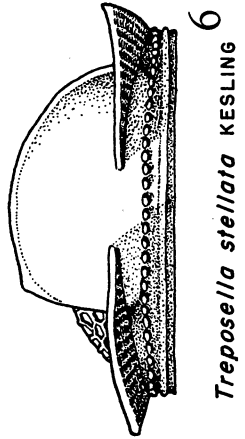
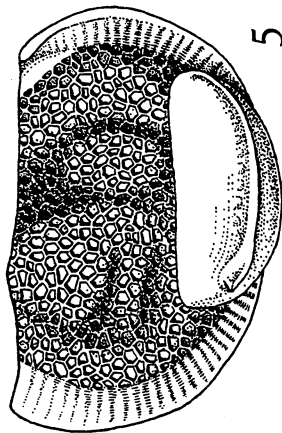
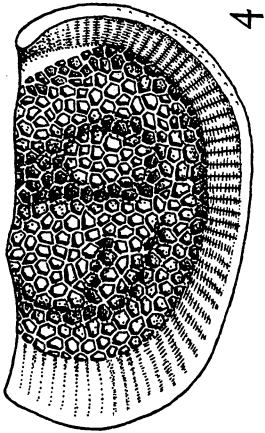
3

*Beyrichia kjaeri*  
HENNINGSMOEN

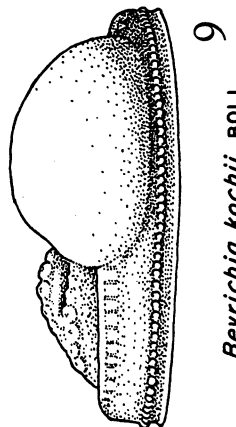
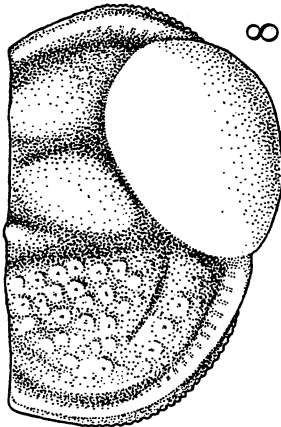
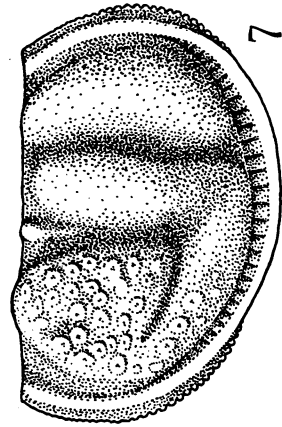
PLATE VI



*Craspedobolina armata*  
HENNINGSMOEN



*Treposella stellata* KESLING



*Beyrichia kochii* BOLL

## EXPLANATION OF PLATE VI

*Craspedobolbina armata* Henningsmoen

Lower Silurian, Llandoveryian series, Norway.

FIG. 1. Lateral view of male right valve, based on UMMP specimens Nos. 33753, 33754, and 33755. Length, 1.55 mm.

FIGS. 2-3. Lateral and ventral views of female right valve, based on UMMP specimens Nos. 33756, 33757, and 33758. Length, 1.70 mm.

*Trepostella stellata* Kesling

Middle Devonian, Centerfield limestone, New York.

FIG. 4. Lateral view of male right valve, based on UMMP specimens Nos. 30502 and 30503. Length, 1.97 mm.

FIGS. 5-6. Lateral and ventral views of female right valve, based on UMMP specimen No. 30501. Length, 1.98 mm.

*Beyrichia kochii* Boll

Upper Silurian, Ludlovian series, Gotland.

FIG. 7. Lateral view of male right valve, based on UMMP specimens Nos. 33764, 33765, and 33766. Length, 1.40 mm.

FIGS. 8-9. Lateral and ventral views of female right valve, based on UMMP specimen No. 33767. Length, 1.54 mm.

## EXPLANATION OF PLATE VII

*Hibbardia lacrimosa* (Swartz and Oriol)

Middle Devonian, Ludlowville formation, New York.

FIG. 1. Lateral view of male right valve, based on fragmentary uncatalogued specimens at UMMP. Length, 1.75 mm.

FIGS. 2-3. Lateral and ventral views of female right valve, based on UMMP specimen No. 28455 and on nine carapaces destroyed in making polished surfaces. Length, 1.80 mm.

*Phlyctiscapha apleta* Kesling

Middle Devonian, Ferron Point formation, Michigan.

FIG. 4. Lateral view of male right valve, based on UMMP specimen No. 30490. Length, 1.72 mm.

FIGS. 5-6. Lateral and ventral views of female right valve, based on UMMP specimens Nos. 30482 and 30483. Length, 1.74 mm.

*Treposella lyoni* (Ulrich)

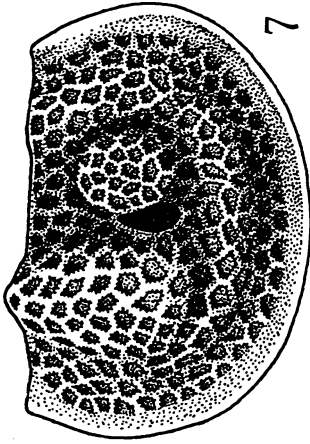
Middle Devonian, Jeffersonville limestone, Falls of the Ohio.

FIG. 7. Lateral view of male right valve, based on UMMP specimens Nos. 30513 and 30515. Length, 1.40 mm.

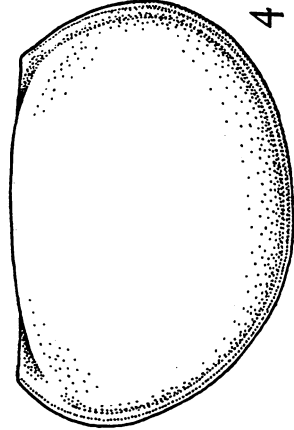
FIGS. 8-9. Lateral and ventral views of female right valve, based on UMMP specimen No. 30511. Length, 1.65 mm.



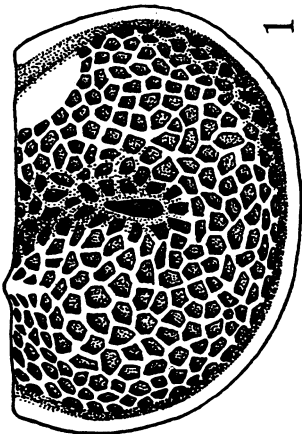
PLATE VII



1



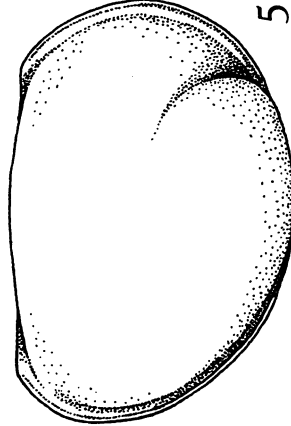
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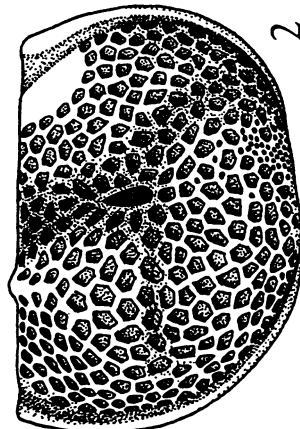
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8



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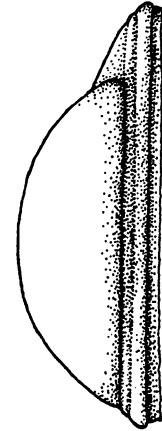


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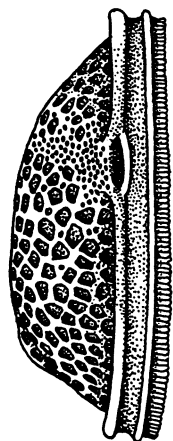
9

*Treposella lyoni* (ULRICH)



6

*Phlyctiscapha apteta* KESLING



3

*Hibbardia lacrimosa*  
(SWARTZ AND ORIEL)

