CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

UNIVERSITY OF MICHIGAN

Vol. XIII, No. 2, pp. 33–79 (8 pls., 4 figs.) March 30, 1956

SILURIAN OSTRACODS COLLECTED BY DR. CARL LUDWIG ROMINGER FROM GLACIAL DEPOSITS IN GERMANY

BY

ROBERT V. KESLING and PHILIP L. WAGNER

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By Robert V. Kesling and Philip L. Wagner

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From the
Ermine Cowles Case Memorial Volume

MUSEUM OF PALEONTOLOGY
UNIVERSITY OF MICHIGAN
ANN ARBOR

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Director: Lewis B. Kellum

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PART I. INTRODUCTION AND REVIEW OF *BEYRICHIA TUBERCULATA* (KLÖDEN)

By Robert V. Kesling and Philip L. Wagner

INTRODUCTION

MORE than a century ago Dr. Carl Ludwig Rominger collected fossils from the glacial drift of northern Germany. His European collections were deposited in the Museum of Paleontology of the University of Michigan. Among them were the Silurian ostracods which are the subject of this report. The first part of the paper contains the story of how the ostracods came from their original burial place somewhere at the bottom of the Baltic Sea to the Museum of Paleontology. Studies of three of the species of ostracods represented follow.

The authors wish to thank Dr. Chester A. Arnold, Dr. George M. Ehlers, and Dr. Lewis B. Kellum for their helpful criticism and to express their appreciation to the Horace H. Rackham School of Graduate Studies of the University of Michigan for providing the photographic equipment used in preparation of the plates. Dr. David Nicol and Dr. Remington Kellogg of the United States National Museum kindly made possible the loan of the types of *Dibolbina cristata* Ulrich and Bassler. With this exception, all specimens used or figured are catalogued and deposited in the Museum of Paleontology of the University of Michigan.

Discovery of Ostracods

The ostracods first came to our attention in 1954, when the senior author examined two pieces of limestone accompanied by a small label. The label, written in German script in brown ink on stained and faded, coarse, blue paper, was the key to the history of the two rocks and the ostracods. One rock was unweathered and it was impossible to separate its fossils from the matrix. The other was weathered all the way through and, although the piece weighed a little less than 4 ounces, several hundred ostracod valves were separated from it, all well preserved and most of them complete or nearly so. A few brachiopods were also uncovered. Many of the ostracod valves were partly exposed as the rock was finely chipped with a small chisel. The rest of each specimen so exposed was cleaned by scraping, gouging, and digging with small needles.

Collection by Dr. Rominger

With the piece of limestone from which the ostracods were taken was the label written in German script referred to above. It is reproduced in Figure 1. The handwriting matches other writing known to be by Dr.

Rominger and he is presumed to have been the collector. The history of the fossils, however, would be incomplete without some details in the life of Dr. Rominger. They were compiled from an account by Merrill (1908, pp. 79–82) and one in the *Ann Arbor Daily Times* (April 23, 1907).

Carl Ludwig Rominger was born at Schnaitheim, in Würtemberg, on December 31, 1820. In 1839 he entered the University of Tübingen and in 1842 received his doctorate in medicine. From 1842 to 1845 he remained at Tübingen as an assistant in chemistry and devoted his spare time to the study of geology and paleontology under the eminent Professor Friedrich August von Quenstedt. From 1845 to 1848, under a grant from the government of Würtemberg, young Dr. Rominger studied geologic structures of northern and central Europe. In the course of this research he traveled on foot over much of Germany, Hungary, Austria, Switzerland, France,

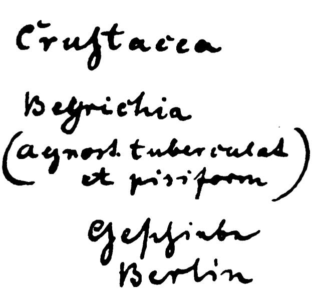

FIG. 1. Label accompanying rocks from which Silurian ostracods were obtained. The writing is believed to be that of Dr. Carl Ludwig Rominger.

and Belgium. It was probably during these travels that the fossiliferous rocks were picked up near Berlin. There is no evidence that Dr. Rominger ever again collected in that region.

The label on the specimens gives the name *Beyrichia,* which had been established by McCoy in 1846. It is interesting to note that Rominger wrote "Agnostus tuberculatus" in parenthesis. This name had been applied by Goldfuss in 1843 (p. 542). Quenstedt, with whom Rominger studied, also used the name *Agnostus tuberculatus* in 1852 (p. 302). Inasmuch as the manuscript was in preparation for several years, Rominger was no doubt familiar with Quenstedt's classification before it appeared in print. From this, it would seem that Rominger obtained the specimens and wrote the label between 1846, the date of *Beyrichia,* and 1848, when he left Germany for America.

In 1848 a revolution broke out in central Europe, the government lost control in Vienna, barricades were thrown up in the streets of Berlin, and the little German states were in chaos. Dr. Rominger joined many of his countrymen in an exodus to America and somewhere in his possessions, we believe, were the ostracod-bearing Silurian rocks he had gathered from the drift at Berlin a short time before. Dr. Rominger had only a meager knowledge of English and arrived in New York unable to understand the natives or make himself understood. He migrated to Cincinnati, where many other German people had settled. There he established himself in the practice of medicine, a profession in which he was to continue for the following 24 years. After he had been in Cincinnati for a few months, he moved to Chillicothe, Ohio. His collections show that he was an ardent collector of fossils in America during his spare time for many years. In 1860 he moved to Ann Arbor, Michigan, where he lived the rest of his life.

In 1864, when Dr. Rominger was Assistant Curator in the Museum of Geology, Zoology, and Botany of the University of Michigan, he deposited most of his large collection of fossils from Europe in the Museum. After a long period of negotiation the University purchased them in 1891 for $5000. After his death in 1907, the rest of Dr. Rominger's extensive paleontological collection was divided between the University of Michigan and the United States National Museum. As Merrill observed (1908, p. 82), "Unlike many of the earlier paleontologists, Rominger was most careful to accurately label his material, giving the exact horizon and locality. This, of course, added enormously to the value of his collections."

Age of Fossils

The ostracods and brachiopods in the piece of limestone belong to species identified many years ago by European workers and are known to occur in outcrops of Downtonian (Upper Silurian) strata. The ostracods comprise *Beyrichia tuberculata* (Klöden), *B. salteriana* Jones, *B. buchiana* Jones, *B. maccoyiana* Jones, *Dibolbina steusloffi* (Krause), and *Kloedenia wilckensiana* (Jones). The brachiopods are *Pholidops antiqua* (von Schlotheim) and *Chonetes striatellus* (Dalman). The ostracods are preserved only as single valves. Absence of complete carapaces indicates that the dead animals were moved by currents of sufficient agitation to dissociate the valves before burial. The specimens are very little abraded, however, and probably were not transported very far. The limestone is the same age as the fossils and was deposited during the Downtonian epoch.

Site of Original Deposition

The Silurian limestone containing the ostracods was carried from somewhere in the Baltic region to the vicinity of Berlin by Pleistocene glaciers. Determination of the exact source of a glacial deposit is always difficult and sometimes impossible. Source regions for many north European glacial deposits, however, have been established by comparing the fossils in transported boulders and pebbles with those in outcrops. Many Paleozoic invertebrates were known from glacial deposits long before they could be traced to outcrops of the formations from which they were derived. Indeed, some species have never been found in outcrops.

Reuter (1885) studied the ostracod faunas of different types of Silurian limestones from the drift of northern Europe and compared them with the faunas of Silurian formations cropping out in southern Sweden (then called Schonen), the island of Gotland, and the island of Ostrov Sarema (then called Oesel). He (pp. 668–78) distinguished eleven faunas and described the lithology of the rocks in which each occurred. The Rominger ostracods are in a limestone which appears to be that Reuter (p. 672) called, "Tuberculatakalk mit Buchiana, Salteriana und Wilkensiana." The source region for this limestone he gave (p. 673), as "Muthmaasslich das Gebiet zwischen Gotland und Oesel." He stated (p. 666): "Ein bemerkenswerther Unterschied zwischen den Beyrichienformen beider Inseln besteht also darin, dass auf Gotland *B. Wilkensiana* noch von keinem Forscher beobachtet worden ist, während auf Oesel *B. Maccoyana* ganz fehlt und *B. Buchiana lata* nebst *Salteriana* nur vereinzelt vorkommen."

Faunal lists for Gotland and Ostrov Sarema have not been changed since Reuter's publication. Our fauna includes *Beyrichia maccoyiana,* which is known from Gotland but not from Ostrov Sarema, and *Kloedenia wilckensiana,* which is known from Ostrov Sarema but not from Gotland. Hence, it is logical to assume, as did Reuter, that the rocks containing this association of ostracods crop out at the bottom of the Baltic Sea, somewhere beween Gotland and Ostrov Sarema.

Transportation by Glaciers

The drift around Berlin, in which the ostracods were found, was laid down by continental glaciers during the Pleistocene epoch. Figure 2 locates Gotland, Ostrov Sarema, and Berlin, the end moraines of some of the stages of glaciation, and the flow lines of the glaciers. Data for the end moraines are taken from Antevs (1929, Figs. 14–15). The line for Weichsel moraine is the farthest advance of glaciation during the Weichsel stage and agrees at most points, with the moraines of the Brandenburg and Frankfurt–Posen divisions of the Weichsel stage as given by Zeuner (1945, Fig. 15).

DeGeer (1895, Pl. 13) illustrated flow lines of Pleistocene glaciers based on the distribution of distinctive kinds of rocks from the Baltic region. These lines are shown in Figure 2. Evidently, DeGeer confused

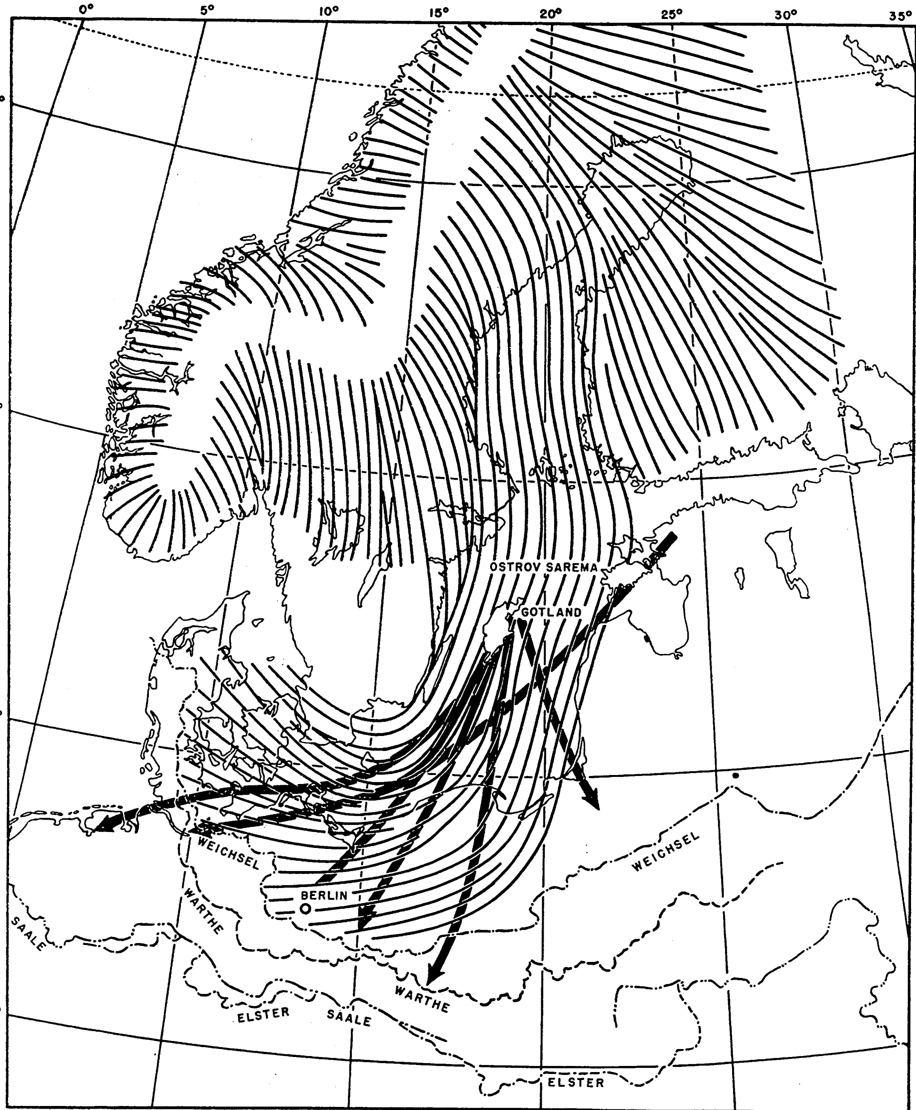

FIG. 2. Moraines and flow lines of continental glaciers in northern Europe. Position of the moraines is taken from Antevs (1929, Figs. 14–15). Light lines (from De Geer, 1895, Pl. 13) are flow lines extending into northern Germany and Denmark that probably belong to the Weichsel glaciation. Heavy lines with arrows (from Geikie, 1881, Pl. D) represent movement of continental glaciers, based on the discovery of pieces of rock from Gotland and Estonia in glacial deposits at several places in northern Europe.

some of the moraines formed during the Brandenburg and Frankfurt-Posen divisions with those formed during the Finiglacial division of the Weichsel stage, for he terminated the flow-line pattern in southern Sweden and in southern Finland at approximately the positions where Zeuner (1945, Fig. 15) shows terminal moraines of the Finiglacial division. DeGeer and later authors agree, however, in the pattern of the flow lines that extend into the region of Berlin and in the position of the moraine in northern Germany and Denmark. It is interesting to note, in this connection, that the flow line to Berlin (Fig. 2) passes between Gotland and Ostrov Sarema through the supposed site of the original deposition of the ostracods.

Geikie (1881, Pl. D) illustrated some flow lines based on glacial transportation of rocks from Gotland and Estonia. His lines are also given in Figure 2. They emphasize that rocks from the Baltic region were picked up by the ice during several stages of glaciation. The continental glaciers followed somewhat different routes in each stage of glaciation and some deposits of earlier glaciations were moved again by later advances of the ice sheet. It is impossible, therefore, to determine the exact path that the fossils traveled, or the time or times when they were transported. The most logical conjecture, in accord with present knowledge of Pleistocene glaciation in northern Europe, is that they were carried close to or along the flow line suggested by DeGeer and that all of their transportation took place during the early part of the Weichsel stage.

REVIEW OF *Beyrichia tuberculata* (KLÖDEN)

Examination of the material from the Rominger collection led to our re-evaluation of the arguments for considering *Beyrichia tuberculata* (Klöden) the type species of the genus. The results are presented here and some of the variations in the valves described. The specimens are also grouped into instars.

Systematic Position

Order OSTRACODA

Superfamily Beyrichiacea

Family Beyrichiidae

Genus *Beyrichia* McCoy

Type species.—By original designation, *Beyrichia klödeni* McCoy, 1846, p. 58, = *Battus tuberculatus* Klöden.

The wording of the original description of the type species raises a question as to what species is the type. McCoy wrote (1846, p. 58), in the last two lines of his description of *Beyrichia,* "The species I propose naming after its original discoverer," and as the following two lines indicate (1846, p. 58), McCoy at that time regarded *B. klödeni* and *B. tuberculata* as one species:

"BEYRICHIA KLÖDENI, M'Coy

"*Syn.* Battus tuberculatus. *Klöden. Ref.*—Agnostus tuberculatus. Sow. Sil. Syst. Pl. 3, fig. 17."

It also is significant of McCoy's indecision that in his description of the genus *Beyrichia* he (1846, pp. 57–58) alluded to "*Agnostus (Battus) tuberculatus,* Klöd." and to "*Agnostus tuberculatus,*" but not to the name *Beyrichia klödeni.* Later McCoy (1851, p. 135) decided that the two were distinct species. In the synonymy of *Beyrichia klödeni* he wrote, "(not *B. tuberculatus* of Klöden)." He further stated:

This species does not exactly accord with any of those figured by Klöden, as varieties of his *Battus tuberculatus* . . . I therefore think that Mr. Salter, in the Survey Reports, and the editors of the Ray edition of Burmeister's work on Trilobites, are not justified in replacing my name as above, by that of '*tuberculata* (Klöd. Sp.).' Anyone attentively reading the elaborate description, or looking at the figures given by that author in his rare work, the *Versteinerungen der Mark Brandenburg,* will readily perceive, as I have above mentioned, that his *Battus tuberculatus* includes many species —the peculiarities of which he recognized as varieties.

In 1847, the year after McCoy's paper describing *Beyrichia,* Ernst Boll wrote (p. 127):

Den fälschlich so genannten, und schon so verschieden gedeuteten Battus tuberculatus Klöden schliesse ich mit Beyrich von den Trilobiten aus, nach dessen Urtheil er eine besondere Gattung neben Cytherina bilden muss. Ich schlage für dieselbe, da Beyrich diesem Körper zuerst seine richtige Stellung im System angewiesen hat, den Namen Beyrichia vor (Char: 'zweiklappige Schale mit unsymetrisch geordneten Lappen und Tuberkeln'), und nenne diese Art, welche in unseren Silurischen (Ludlow) Kalksteingeschieben in unermesslicher Anzahl vorkommt, und sich auch hin und wieder in Geschieben des old red zeigt, Beyrichia tuberculata.

We cannot find out whether Boll independently arrived at the name *Beyrichia* or knew of McCoy's publication of the name in the preceding year. Boll made no reference to McCoy in his brief paper. No matter how it was conceived, the *Beyrichia* of Boll is a junior synonymous homonym of the *Beyrichia* of McCoy. Incidentally, Boll was in error or was misleading when he claimed, in the last sentence of the paragraph quoted above, the authorship of the species *Beyrichia tuberculata.* Ulrich and Bassler (1908, p. 283) discussed the problem of the type species of Beyrichia at some length. They stated:

His 'rough sketch' of the valves of the Irish species that first convinced McCoy that these fossils were bivalved crustacea and not trilobites gives a crude idea of the common Silurian form subsequently identified by Jones and others with *B. kloedeni* McCoy. As McCoy ranks '*Battus tuberculatus*' of Kloeden as a synonym of his *Beyrichia kloedeni,* and as the two forms are distinguishable species, it is difficult to decide which of the two should rank as the genotype. However, as they are unquestionably congeneric, the point is of little consequence.

Later, Straw (1928, pp. 197–203, Pl. I) restudied and figured the specimens from the National Museum of Ireland that were used by McCoy in his original investigation. The specimens are internal molds in sandstone. Straw retained the name *Beyrichia kloedeni* McCoy and applied it to the species from the Upper Llandovery beds of Great Britain and Ireland. Bassler and Kellett (1934, p. 26) in their Bibliographic Index of Paleozoic Ostracoda listed "*Beyrichia kloedeni* McCoy" as the type species of *Beyrichia*. They treated *B. kloedeni* (p. 196) and *B. tuberculata* (pp. 208–9) as separate species.

Although Swartz (1936, p. 548) wrote, "*Beyrichia* McCoy; Silurian, Devonian; genotype *Beyrichia kloedeni* McCoy," he, too, raised the question of the type species (pp. 548–49):

> Unfortunately, however, the use of the name Beyrichiidae is complicated by questions concerning *Beyrichia* and its genotype . . . . If further studies support the view that the relationships of *B. Kloedeni* lie with *Kloedenia,* as now understood, rather than with *B. tuberculata* and *B. moodeyi,* it will be necessary either (1) to place the two latter species in one or two new genera, and rename the family here described; or else (2) to consider *B. tuberculata* the genotype of *Beyrichia*—if McCoy's discussion is such as to permit this under the rules of nomenclature—and to refer *B. kloedeni to Kloedenia.*

In a reference (p. 586) Swartz quoted McCoy's unusual statement about naming the species after its original discoverer, and added, "It seems clear, especially from the latter remark, that *Beyrichia tuberculatus* (Kloeden) not only can, but must be regarded as the genotype of *Beyrichia.*"

Henningsmoen (1954, p. 23) examined McCoy's specimens. He chose to consider "*Beyrichia kloedeni* McCoy 1846" as the type species of the genus (p. 21), to make *Beyrichia kloedeni* the type species of his subgenus *Beyrichia* (p. 22), and to place *Beyrichia tuberculata* (Klöden) in the subgenus *Nodibeyrichia* (p. 26). Henningsmoen seems to base his opinion of the type species on the fact that in 1851 McCoy emphasized that *B. tuberculata* and *B. klödeni* were not one species.

After careful consideration of the evidence, which we summarize above, we conclude (1) that *Beyrichia* is a valid genus and its author is McCoy; (2) that the type species of *Beyrichia* is *Battus tuberculatus* Klöden; (3) that, because the name *Beyrichia Klödeni* McCoy was invalid at the time of its publication, it has never been the name of a species and its only standing is that of a junior synonym of *Beyrichia tuberculata* (Klöden); (4) that the ostracods studied by McCoy (1846) and later redescribed by Straw (1928) and Henningsmoen (1954) are not *Beyrichia* *tuberculata* (Klöden); and (5) that *Beyrichia tuberculata* (Klöden) is a valid species and is now restricted to ostracods of the types illustrated by the original author (Klöden, 1834) in his Plate 1, Figures 20–23.

Our first three conclusions are based on the belief that the type species of a genus is determined by the published statements and form of the original designation and that it cannot be changed in a subsequent publication, by the original designator or by anyone else. Any question about what species is the type must be settled by the original designation. Because McCoy wrote that he was naming his species "after its original discoverer," it seems obvious that, at the time of McCoy's writing, Klöden had already discovered the species that McCoy was designating as the type of *Beyrichia* and that the species Klöden had discovered was *Battus tuberculatus*. McCoy's listing of *Battus tuberculatus* as a synonym of his *Beyrichia klödeni* strengthens our belief that he thought, at the time of the original designation (1846), the two names were for one species. Inasmuch as Klöden's name *Battus tuberculatus* was established in 1834, McCoy's name for the same species, *Beyrichia klödeni,* was a junior synonym and stillborn at the time of publication. If our interpretation is correct, McCoy invalidated for all time the trivial name *klödeni* for any species of *Beyrichia*.

Although the Irish ostracods studied by McCoy are not, according to published descriptions, conspecific with *B. tuberculata,* they cannot have the name *klödeni,* and, insofar as we know, they have never been named. Contrary to McCoy's claim in 1846, Klöden did not "discover" the Irish species which McCoy studied. There is no evidence that Klöden ever saw a specimen from the Silurian of Ireland. Because McCoy said his species was that which Klöden discovered and listed *Battus tuberculatus* in the synonymy of *B. klödeni,* however, we are forced to assume that he spoke of *Beyrichia tuberculata* (Klöden).

It is true that, in his description and illustrations of *Battus tuberculatus,* Klöden included ostracods which were later made into other species. We wish to point out, however, that the validity of the species and its authorship by Klöden are in no way affected by the fact that Klöden interpreted the boundaries of his species broadly—far too broadly in the opinion of later workers who split off other species from his *B. tuberculata*.

Subgenus *Beyrichia*

The following type species, diagnoses, and geologic and geographic occurrences for subgenera of *Beyrichia* are given by Henningsmoen (1954, pp. 22–27) and abridged by us:[1]

[1]For a comparison of Henningsmoen's terms with ours, see Terminology, below.

Eobeyrichia: Beyrichia (Eobeyrichia) zygophora Henningsmoen. "*Beyrichia* species with zygal ridge uniting L2 and Lp, with extra-lobate groove, and with tuberculate (spinose ?) velate ridge." Llandoverian of Europe.

Beyrichia: Beyrichia kloedeni McCoy. "*Beyrichia* species with the three lobes joined ventrally, although an antero-ventral depression may be present. A fissus is usually seen. Velate structure developed as a smooth, nodular, or spinose ridge. Surface finely granulose with scattered coarser granules (or spines), but the surface ornamentation may be more or less effaced." Upper Llandoverian, Wenlockian, and Ludlovian of Europe.

Velibeyrichia: Beyrichia moodeyi Ulrich and Bassler. "*Beyrichia* species with the three lobes more or less well united ventrally. Velate structure developed as a frill, usually rather wide. No fissus is present. Surface reticulate or pitted, but the ornamentation may be effaced." Upper Clinton, Niagaran, McKenzie, and ?Devonian of North America.

Neobeyrichia: Beyrichia buchiana Jones. "*Beyrichia* species with L1 isolated from L2 and Lp. L2 and Lp may be united or not. Velate structure developed as a ridge or a narrow ridge-like frill. Surface granulose or smooth." Upper Ludlovian, Downtonian, and Devonian of Europe.

Nodibeyrichia: Beyrichia bronni Reuter. "*Beyrichia* species with L1 split into two nodes. Lp may also be split into two or more nodes. A secondary fissus may be present. Velate structure developed as a ridge. Surface granulose or smooth." Uppermost Ludlovian and Downtonian of Europe; Arisaig of Nova Scotia.

Mitrobeyrichia: Beyrichia jonesii Boll. "*Beyrichia* species with L2 and Lp united by a zygal ridge. A groove is developed below this ridge. Velate structure developed as a narrow frill with a thickened margin." Upper Valentian to Downtonian of Europe; Upper Clinton of North America.

Henningsmoen (1954, p. 26) placed *Beyrichia tuberculata* (Klöden) in the subgenus *Nodibeyrichia*. If *B. tuberculata* is, as we maintain, the type species of the genus *Beyrichia*, it should also be the type species of the subgenus *Beyrichia*. As the subgenera of *Beyrichia* are defined by Henningsmoen, *B. tuberculata* has the characteristics of *Nodibeyrichia* and not those of the subgenus *Beyrichia*. We believe, therefore, that Henningsmoen's subgenus *Nodibeyrichia* should rightly be called the subgenus *Beyrichia*, and that Henningsmoen's subgenus *Beyrichia* should be renamed. Inasmuch as we have not studied in detail all European species of *Beyrichia*, we decline renaming and redefining the subgenus called "*Beyrichia*" by Henningsmoen.

Beyrichia tuberculata (Klöden)

(Fig. 3; Pls. I–III)

?*Leptaena lata* von Buch (*partim*), von Buch, 1828, p. 71, Pl. 3, Fig. 1 (15); 1831, Pl. 8, Fig. 1 (15).

Battus tuberculatus Klöden, 1834, pp. 115–17, Pl. 1, Figs. 21–23 (not Figs. 16–20); Beyrich, 1845, p. 47; McCoy, 1846, p. 58; Bell and Forbes, 1846, pp. 124–25.

Odontopleura ovata Emmrich (*partim*), Burmeister, 1843, pp. 72–73; Geinitz, 1845, p. 237.

Agnostus tuberculatus Goldfuss, 1843, p. 542; Bronn, 1848, p. 20; Quenstedt, 1852, p. 302, Pl. 23, Figs. 25–28.

Agnostus (Battus) tuberculatus, McCoy, 1846, p. 57; Bell and Forbes, 1846, p. 124.

Beyrichia tuberculata Boll, 1847, p. 127; McCoy, 1851, p. 135; Murchison, 1854, pp. 234, 236, 486, Fig. 45, No. 4, Pl. 34, Fig. 21; Kade, 1855, p. 88; Jones, 1855*a,* pp. 86–87, Pl. 5, Figs. 4–9*b*; Jones, 1855*b*, p. 175; Boll, 1856, pp. 321–24; Schmidt, 1858, p. 193; Roemer, 1858, p. 270; Schmidt, 1859, pp. 448, 455, 461–63; Eichwald, 1860, p. 1346; Grewingk, 1861, pp. 571, 665–66; Roemer, 1862, p. 601; Boll, 1862, pp. 119–21, Pl. 1, Figs. 1*a–b*; Bigsby, 1868, p. 73; Feistmantel, 1874, pp. 224–25; Krause, 1877, pp. 30–32, Pl. 1, Figs. 12*a–b*; Martin, 1878, p. 45; Kolmodin, 1879, p. 136; Kiesow, 1884, pp. 226–27, 229, 276–77; Reuter, 1885, pp. 632–634, Pl. 25, Figs. 1*a–b*; Roemer, 1885, pp. 339 (92), 355 (108), Pl. 30 (7), Figs. 10*a, d*; Zittel, 1885, pp. 553–54, Fig. 739; Jones and Holl, 1886, pp. 347–49; Verworn, 1887, p. 31, Pl. 3, Fig. 12; Kiesow, 1888, p. 3; Krause, 1889*a*, p. 25; Krause, 1889*b*, pp. 11, 14, 16; Dames, 1890, p. 1129; Kayser, 1891, p. 56 (not Pl. 7, Fig. 6); Krause, 1891, pp. 514, 516, 518–20; Kiesow, 1892, p. 97 (not pp. 98–99); Lake, 1893, p. 70 (not Pl. 7, Fig. 6); Schmidt, 1894, p. 136; Koken, 1896, p. 432; Gürich, 1896, pp. 31, 386–87; Ulrich and Bassler, 1908, pp. 283, 289–91; Figs. 4, 16, 20, Pl. 37, Figs. 1–2; Bonnema, 1913*a*, pp. 117–23, Figs. 3, 5–6; Bonnema, 1913*b,* pp. 67–73, Figs. 3, 5–6; (*partim*) Bassler, 1915, p. 123; Bonnema, 1916, p. 16, Pl. 1, Figs. 3–4; Botke, 1916, p. 26; Straw, 1928, pp. 201–2; Bonnema, 1930, pp. 115–16, Figs. 9, 14; Bonnema, 1933, Fig. 10 (p. 30), Fig. 11, (p. 31), p. 36; Bonnema, 1934, p. 84; Lamcke, 1934, p. 189; Swartz, 1936, pp. 548–49, Pl. 78, Figs. 8*c–e*, Pl. 84, Fig. 3*g*, p. 586; Schmidt, 1941, p. 45; Shimer and Schrock, 1944, p. 675, Pl. 283, Fig. 32; Wright, 1948, p. 27; Henningsmoen, 1954, pp. 21–22, 26.

?*Beyrichia tuberculata* Jones, 1888, p. 402, Pl. 21, Fig. 12; Heidenhain, 1869, pp. 172, 175–77, Pl. 1, Fig. 14.

Beyrichia tuberculata var. *nuda* Jones, 1855*a,* p. 87, Pl. 5, Fig. 10; Krause, 1877, p. 31; Reuter, 1885, p. 634; Krause, 1891, p. 516.

Beyrichia klödeni McCoy, 1846, p. 58; *et al.*

Beyrichia nuda Bassler and Kellett, 1934, p. 202.

non Battus tuberculatus Klöden, 1834, Pl. 1, Figs. 16–20 [Probably = *Kloedenia wilckensiana* (Jones 1855*a*), *Beyrichia salteriana* Jones 1855, and *Beyrichia bolliana* Reuter 1885].

non Agnostus tuberculatus Sowerby 1839, p. 604, Pl. 3, Figs. 17–17*a* [Probably = *Kloedenia* sp.].

non Beyrichia tuberculata Jones, 1870, p. 492; Roemer, 1876, Pl. 19, Figs. 9*a–d* [= *B. bronni* Reuter]; Jones, 1881*a*, p. 344, Pl. 10, Figs. 8–10; Jones, 1881*b*, pp. 313–14; Hoernes, 1884, p. 378, Figs. 525*c–d* [= *B. bronni*]; Haas, 1887, p. 201, Figs. 404*c–d* [= *B. bronni*]; Kiesow, 1888, pp. 12–13; Jones, 1890*b*, pp. 551–52; Jones, 1891, pp. 74–75, Pl. 11, Fig. 3; Ami, 1892, p. 191.

non Beyrichia tuberculata var. *antiquata* Jones, 1855*a,* pp. 87–88, Pl. 5, Fig. 12.

non Beyrichia tuberculata var. *bigibbosa* Reuter, 1885, p. 635, Pl. 25, Fig. 3.

non Beyrichia tuberculata var. *gedanensis* Kiesow, 1884, p. 277, Pl. 4, Fig. 5.

non Beyrichia tuberculata var. *foliosa* Jones, 1888, p. 403, Pl. 21, Figs. 15–17.

non Beyrichia tuberculata var. *gibbosa* Reuter, 1885, p. 634, Pl. 25, Figs. *2a–b*.
non Beyrichia tuberculata var. *gotlandica* Kiesow, 1888, pp. 4–5, Pl. 1, Fig. 1.
non Beyrichia tuberculata var. *lineato-tuberculata* Chapman, 1901, pp. 151–52, Pl. 3, Fig. 11.
non Beyrichia tuberculata var. *noetlingi* Jones, 1891, p. 78, Pl. 11, Figs. 4–5.
non Beyrichia tuberculata var. *pustulosa* Jones, 1890*a*, pp. 18–19, Pl. 2, Figs. 1*a–c* [= *B. pustulosa* Hall 1860].
non Beyrichia tuberculata var. *spicata* Jones, 1888, pp. 402–3, Pl. 21, Figs. 13–14.
non Beyrichia tuberculata var. *strictispiralis* Jones, 1891, pp. 77–78, Pl. 11, Fig. 1.
non Beyrichia tuberculato-buchiana Reuter, 1885, p. 640, Pl. 25, Figs. 8*a–b*.
non Beyrichia tuberculato-kochiana Reuter, 1885, p. 643, Pl. 26, Fig. 14.
non Beyrichia kloedeni McCoy var. *tuberculata* Salter, Chapman, 1920, pp. 101–2, Pl. 17, Fig. 7.

The synonymy may be incomplete, but we believe it contains most of the references to *Beyrichia tuberculata* (Klöden) and it expresses our concept of the ostracods to be included in, or excluded from, the species. Insofar as we know, ostracods of this species were first observed in 1828 by von Buch, who thought they were immature specimens of the brachiopod *Leptaena lata* and called them (p. 71) "Junge Brut von Leptaena." We cannot understand why he reached this conclusion, for the ostracod and the brachiopod species have little in common except their occurrence in Upper Silurian rocks. The original author of the species, Klöden (1834), considered each valve to be the complete cephalon of a small trilobite. Quenstedt (1852), who was of the same opinion, assigned the species to the genus *Agnostus*.

Burmeister (1843) and Geinitz (1845), after noting the asymmetry of the valves, concluded that each valve was a broken fragment of the cephalon of the trilobite *Odontopleura ovata* Emmrich. Burmeister wrote (1843, p. 73), "*Battus tuberculatus* Klöden's beruht enschieden auf Kopfbruchstücken dieser Art . . . ." Apparently, he believed that the dorsal node of L1 and the brood pouch were the glabella of the trilobite and that the hinge line was the posterior edge of the cephalon.

Although McCoy (1846) and Boll (1847) each claimed to have named *Beyrichia* in honor of the paleontologist who first assigned the genus to its correct taxonomic position, it appears that Goldfuss, not Beyrich, was the first worker to suggest that the *Battus tuberculatus* of Klöden was an ostracod. In 1843, two years before Beyrich's publication appeared, Goldfuss wrote (p. 542):

Die beiden letzten [*Agnostus tuberculatus* (Klöden) and *A. gigas* (Klöden)] scheinen nicht zu dieser Gattung zu gehören, da sie keinen symmetrischen Bau haben. Auf den Schalen jener ersten [*tuberculatus*] findet sich der grössere Höcker bald auf der rechten, bald auf der linken Seite; eine Symmetrie stellt sich jedoch her, wenn man sie als zusammengehörige rechte und linke Klappen betrachtet. Sollten sie daher wirklich zu den Krustazeen gehören, so würden sie der Gattung Cypris nahe stehen.

Beyrich (1845) thought the species was an ostracod belonging to a new genus, which he declined to name, close to the genus *Cytherina*. He suggested that each specimen was a left or right valve. He stated (p. 47):

> *Battus tuberculatus* Klöden, welchen Burmeister als synonym zu *Odontopleura ovata* citirt, ist weder ein Battus noch überhaupt ein Trilobit. Er hat eine zweiklappige Schale, deren Oberfläche mit ganz unsymmetrisch geordneten Lappen und Tuberkeln bedeckt ist, und muss eine besondere Gattung neben Cytherina bilden.

McCoy (1846) and Boll (1847) also arrived at the idea of a bivalved ostracod to explain the asymmetry of valves of *Beyrichia tuberculata*.

Jones was one of the first workers to notice immature instars of the species; he wrote (1855*a*, p. 87), "The surface of the valves is coarsely granulated, except in the very young state." Nevertheless, he created a variety (1855*a*, p. 87), *Beyrichia tuberculata* var. *nuda,* for small unornamented specimens which we believe to be immature instars of *Beyrichia tuberculata*.

Richter (1869, p. 774) seems to have been the first to designate males and females in *Beyrichia*. He said:

> Ebenfalls findet sich für die Randwulst der Beyrichien ein, wenn auch nicht vollkommenes, Analogen in der seitlichen Auftreibung des Panzers bei den weiblichen Individuen von *Cythere gibba* Müll., so dass hiernach die fossilen Individuen mit überquellender Randwulst als solche weiblichen Geschlechts betrachtet werden könnten.

Krause (1877, p. 32) noted that adults were dimorphic and that the brood pouches did not seem to be characteristic of old age:

> Gegen die Annahme aber, dass diese Ventralhöcker nur Altersmerkmale sind, spricht der Umstand, dass, wenn sie auch nur bei erwachsenen Individuen beobachtet wurden, doch die meisten vollständig entwickelten Formen keine Spur derselben zeigen.

Most of the publications after 1877 that mentioned *Beyrichia tuberculata* were reports of new occurrences of the species and not morphological studies. The descriptions and figures of specimens from Ireland and Nova Scotia lead us to conclude that they are not conspecific with *Beyrichia tuberculata*.

Descriptions

Terminology.—The terms used by Henningsmoen (1954), in the descriptions of subgenera of *Beyrichia* above, differ somewhat from those employed by us. Hence, a sketch of a female left valve labeled with some of our designations is given (Figure 3). The Lp of Henningsmoen (p. 18) is our L3. His "fissus" and "secondary fissus" (p. 19), which divide L3 into three unequal parts, we call grooves. His "anterior horn," "inner posterior horn," and "outer posterior horn" (p. 18) all refer to projections of L1 and L3 above the hinge line. Henningsmoen introduced (p. 23) the term "extra-lobate area," which we retain but limit the application in

Beyrichia tuberculata to the part of the lateral area not included in lobation and sulcation. We apply "extralobate area" to the part of the valve which Henningsmoen called the "submarginal ridge" (p. 19) and "velate ridge" (p. 44). We use "velate ridge" for a low ridge on the ventral part of the marginal surface, which does not, in any of our specimens, extend to the anterior or posterior corner.

Adult female.—Each valve subovate to subelliptical in lateral view. Hinge line straight, about five-sixths as long as the entire valve. Anterodorsal border nearly straight; anterior border subround with a radius of

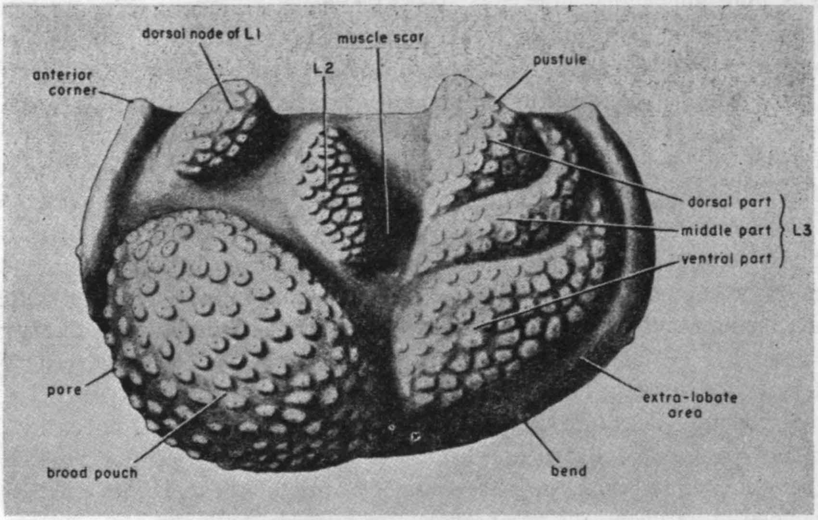

FIG. 3. Female left valve. Some features labeled with terms used in this paper.

curvature about equal to one-third the height of the valve. Anteroventral part of the free edge hidden by the large brood pouch, which forms the anteroventral part of the free border. Ventral border nearly straight, short, sharply curved at its junction with the posteroventral border; posteroventral border gently curved; posterior and posterodorsal borders subround with radius of curvature about equal to two-thirds the height of the valve.

Lateral surface separated from the dorsum by a low ridge (Pl. II, Fig. 12) and from the marginal surface by a bend. Dorsum an elongate, flat area about 0.15 mm. wide extending from the anterior corner to the posterior corner. Lateral surface may be divided into a lobate area and an extralobate area. Extralobate area separated into two parts by the brood pouch. Lobate area separated from each part of the extralobate area by a smooth, shallow groove. Anterior part of the extralobate area a curved band with nearly parallel sides, its width equal to one-eighth the height of the valve, extending from the anterior corner to the anterior edge of the brood pouch; posterior part of the extralobate area about the same width as the anterior, extending from the posteroventral edge of the brood pouch to the posterior corner. Marginal surface broad, extending from the anterior to the posterior corner, widest in the ventral part where its width is more than one-third that of the valve; a part of the marginal surface is interrupted by the brood pouch, so that the marginal surface is very narrow in its anteroventral part (Pl. II, Figs. 4, 6, 8, 17).

Dorsal node of L1 and dorsal part of L3 projecting approximately 0.15 mm. above the hinge line. Dorsal node of L1 egg-shaped, its long axis inclined anteroventrally at an angle of 60 degrees with the hinge line, separated from L2 by S1 and from the brood pouch by a narrow sulcus. L2 elongate, subelliptical in outline, its long axis inclined posteroventrally at an angle of 75 degrees with the hinge line. L3 semicircular to subtriangular, divided into three unequal parts by two narrow grooves. Dorsal part of L3 subtriangular, strongly arched and almost knoblike, its anterior edge nearly vertical; middle part of L3 narrow, C- or S-shaped, its posterodorsal end extending nearly to the hinge line, sharply curved around the posterior corner of the dorsal part of L3, its central part nearly straight but inclined anteroventrally, and its anterior end tapering and directed downward; ventral part of L3 large, elongate, subtriangular, its posterodorsal tip extending to a point about 0.5 mm. from the dorsal border, its anteroventral end blunt and broad, separated from the brood pouch by a narrow part of S2. Brood pouch bulbous, egg-shaped, projecting laterally approximately 1.5 mm. from the contact margin of the valve, its long axis inclined posteroventrally at an angle of 60 degrees with the hinge line.

All sulci with flat or gently concave bottoms. S1 geniculate; its dorsal part separating the dorsal node of L1 and L2, and its ventral part separating the brood pouch and L2. The dorsal end of S1 confluent with S2 above L2, the geniculation confluent with the narrow sulcus between the dorsal node of L1 and the brood pouch, and the ventral end confluent with S2 below L2. S2 slightly sinuous; its dorsal part broad, separating L2 and L3, and its ventral part narrow, separating the brood pouch and L3; the dorsal end confluent with S1 above L2 and the ventral part confluent with S1 below L2.

A low marginal or submarginal ridge at or near the ventral part of the free edge, anteriorly and posteriorly decreasing in height, indistinct or absent in the anterodorsal and posterodorsal parts of the marginal surface. A low velate ridge subparallel to the marginal or submarginal ridge, separated from it by a smooth, flat-bottomed channel, extending from the posterior edge of the brood pouch to the posterior part of the marginal surface. The velate ridge lies between the marginal ridge and the bend, closer to the former than to the latter.

Ornamentation on the dorsal node of L1, L2, the three parts of L3, and the brood pouch consists of large pustules and a few tubercles. Each pustule is subcircular to subrectangular and has a small pore near or at its distal end. Broken pustules on the brood pouch (Pl. III, Figs. 1*a–b*) reveal that the pore canal has a larger diameter in the middle of the pustule than at the pore. The tubercles, slightly smaller than the pustules, are irregularly spaced near the edges of the lobes, but form the only ornamentation on the ventral surface of the brood pouch (Pl. II, Figs. 4, 6, 17). Each valve bears a few tubercles (Pl. I, Figs. 2*a–b*; Pl. III, Figs. 1*a–b*) or pustules (Pl. II, Fig. 3) on or near the bend.

An oval, vertically elongate adductor muscle scar near the middle of S2, immediately behind the ventral part of L2.

Measurements of length and height of female valves are listed in Table I. Length and height were measured from the free border and do not include the brood pouch.

TABLE I

MEASUREMENTS OF FEMALE VALVES OF *Beyrichia tuberculata* (KLÖDEN)

Left Valve				Right Valve			
Cat. No.	Length (mm.)	Height (mm.)	Ratio (H/L)	Cat. No.	Length (mm.)	Height (mm.)	Ratio (H/L)
32082*	3.10	1.70	.55	32100*	3.15	1.85	.59
32083*	3.00	1.80	.60	32081*	3.15	1.90	.60
32080*	2.95	1.75	.59	32167	2.95	1.85	.63
32103*	2.75	1.60	.58	32085*	2.65	1.60	.60
32157	2.60	1.50	.58	.....	...	...	..
32084*	2.50	1.60	.64	.....	...	...	..
Mean	2.82	1.66	.59	.....	2.98	1.80	.61

* Specimen illustrated.

Adult male.—The dorsal part of each valve has lobation and ornamentation like that of the female. In the ventral part of each valve, however, each male valve has a ventral node of L1 in the position corresponding to that of the brood pouch in the female. The ventral part of L3 extends farther forward than does that in the female. Furthermore, the L2 is more nearly vertical than that of the female.

Ventral node of L1 subround (Pl. I, Figs. 5*a–b*) or suboval (Pl. I, Figs. 1*a–b*), slightly larger and projecting farther laterally than the dorsal node of L1. The extralobate area is continuous around the ventral node of L1. The sulcus between the dorsal and ventral nodes of L1 is wider and shallower than the sulcus between the dorsal node of L1 and the brood pouch in the female. The ventral part of L3 extends as far forward as the front edge of L2. The ventral node of L1 and the ventral part of L3 are ornamented with pustules and tubercles like those of the other parts of the lobation.

The marginal or submarginal ridge and the velate ridge extend from the anterior part of the marginal surface to the posterior part; they are

TABLE II
MEASUREMENTS OF MALE VALVES OF
Beyrichia tuberculata (KLÖDEN)

Left Valve				Right Valve			
Cat. No.	Length (mm.)	Height (mm.)	Ratio (H/L)	Cat. No.	Length (mm.)	Height (mm.)	Ratio (H/L)
32101*	3.35	1.85	.55	32139*	3.00	1.65	.55
32090*	2.90	1.60	.55	32095*	2.95	1.65	.56
32153	2.80	1.75	.62	32089*	2.80	1.65	.59
32169	2.80	1.70	.61	32178	2.80	1.65	.59
32182	2.70	1.65	.61	32163	2.70	1.65	.61
32110	2.65	1.75	.66	32132	2.70	1.65	.61
32144	2.65	1.60	.60	32105	2.70	1.60	.59
32141	2.60	1.60	.62	32165	2.65	1.75	.66
32162	2.60	1.55	.60	32091	2.60	1.65	.63
32188	2.60	1.70	.65	32094	2.60	1.60	.62
32151	2.55	1.60	.63	32087	2.50	1.55	.62
32164	2.55	1.60	.63	32093*	2.45	1.60	.65
32175	2.55	1.60	.63	32108	2.45	1.50	.61
32170	2.50	1.55	.62	32152*	2.40	1.55	.65
32079*	2.45	1.60	.65	32171	2.40	1.60	.67
32106	2.45	1.70	.69	32146	2.40	1.50	.63
32123	2.45	1.55	.63	.....	...	...	..
32150	2.45	1.55	.63	.....	...	...	..
32176	2.40	1.50	.63	.....	...	...	..
32180	2.40	1.50	.63	.....	...	...	..
Mean	2.62	1.63	.62	.....	2.63	1.61	.61

* Specimen illustrated.

subparallel in the ventral part of the valve but close together in the anteroventral part (Pl. II, Fig. 15).

Measurements of length and height of male valves are listed in Table II.

The immature instars of *Beyrichia tuberculata* (Klöden) are numbered in the sequence which results when the adult is called the ninth instar. The work of Spjeldnaes (1951, pp. 747–49) on *Beyrichia jonesi* Boll indicates that at least some species of *Beyrichia* have more than eight immature instars. Our system of numbering instars, therefore, may be wrong, but even if so is useful.

Eighth instar.—Valves have the same shape as those of the adult male. Ornamentation is absent in some and varies in others from distinct to barely discernible. Measurements of length and height are listed in Table III.

TABLE III

MEASUREMENTS OF VALVES OF *Beyrichia tuberculata* (KLÖDEN) IN EIGHTH INSTAR

Left Valve				Right Valve			
Cat. No.	Length (mm.)	Height (mm.)	Ratio (H/L)	Cat. No.	Length (mm.)	Height (mm.)	Ratio (H/L)
32097	2.25	1.50	.67	32092	2.30	1.40	.61
32104	2.25	1.50	.67	32102	2.25	1.40	.62
32096	2.20	1.40	.64	32140	2.25	1.40	.62
32128	2.20	1.45	.66	32099	2.20	1.45	.66
32115	2.15	1.50	.70	32116	2.20	1.40	.64
32137	2.10	1.30	.62	32086	2.15	1.45	.67
32156	2.10	1.30	.62	32166	2.10	1.25	.60
32183	2.10	1.40	.67	32177	2.05	1.25	.61
32112	2.05	1.35	.66	32184	2.05	1.35	.66
32179	2.00	1.40	.70	32088	2.00	1.35	.67
32145	1.95	1.20	.62	32107	2.00	1.25	.63
32181	1.95	1.20	.62	32148	2.00	1.20	.60
32121	1.90	1.20	.63	32126	1.95	1.25	.64
32124	1.85	1.20	.65	32149	1.95	1.30	.67
32098*	1.80	1.25	.69	32172	1.95	1.20	.62
.....	...	...	..	32174	1.95	1.20	.62
.....	...	...	..	32118	1.90	1.20	.63
.....	...	...	..	32154	1.90	1.20	.63
.....	...	...	..	32160*	1.85	1.20	.65
Mean	2.06	1.34	.66	.....	2.05	1.30	.63

* Specimen illustrated.

Seventh instar.—Valves differ from those in the eighth instar in having a greater percentage of specimens without ornamentation. Each valve has a shallower and less distinct dorsal groove in L3 and less prominent lobes than those of the eighth instar. Measurements of length and height are listed in Table IV.

TABLE IV

MEASUREMENTS OF VALVES OF *Beyrichia tuberculata* (KLÖDEN) IN SEVENTH INSTAR

Left Valve				Right Valve			
Cat. No.	Length (mm.)	Height (mm.)	Ratio (H/L)	Cat. No.	Length (mm.)	Height (mm.)	Ratio (H/L)
32109	1.80	1.20	.67	32185	1.85	1.10	.59
32120	1.75	1.10	.63	32168	1.80	1.10	.61
32161	1.70	1.10	.65	32143	1.70	1.10	.65
32114	1.55	1.00	.65	32119	1.55	1.05	.68
32117	1.55	1.05	.68	32155	1.55	1.00	.65
32187	1.45	0.95	.66	32127	1.45	0.95	.66
32186	1.40	0.95	.68	.....	...	...	..
Mean	1.60	1.05	.66	.....	1.65	1.05	.64

Sixth instar.—None of the valves has ornamentation on the lobes. Lobes are less prominent than those in valves of the seventh instar. The dorsal tips of L1 and L3 do not extend above the hinge line. Dorsal groove in L3 is very indistinct or absent. Measurements of length and height are listed in Table V.

TABLE V

MEASUREMENTS OF VALVES OF *Beyrichia tuberculata* (KLÖDEN) IN SIXTH INSTAR

Left Valve				Right Valve			
Cat. No.	Length (mm.)	Height (mm.)	Ratio (H/L)	Cat. No.	Length (mm.)	Height (mm.)	Ratio (H/L)
32158	1.50	0.85	.57	32113	1.35	0.90	.67
32129	1.45	.90	.62	32136	1.35	.85	.63
32122	1.40	.90	.64	32131	1.20	.75	.63
32142	1.25	.80	.64	.....	...	..	..
32159	1.20	.75	.63	.....	...	..	..
32173	1.15	.80	.70	.....	...	..	..
Mean	1.33	.83	.63	.....	1.30	.83	.64

Fifth instar.—Nodes of L1 are less prominent and closer together than those in valves of the sixth instar. A dorsal groove across L3 is absent in all valves; the ventral groove of L3 is indistinct in some and absent in others. The sulci are shallow, particularly the one between the dorsal and ventral nodes of L1. Measurements of length and height are listed in Table VI.

TABLE VI

MEASUREMENTS OF VALVES OF *Beyrichia tuberculata* (KLÖDEN) IN FIFTH INSTAR

Right Valve			
Cat. No.	Length (mm.)	Height (mm.)	Ratio (H/L)
32125	1.15	0.70	.61
32111*	1.10	.70	.64
32147	0.95	.60	.63
Mean	1.07	.67	.63

* Specimen illustrated.

Fourth instar.—The dorsal and ventral nodes of L1 are separated in some valves by a very shallow sulcus, and in others are fused to form an elongate lobe. The ventral end of L2 is not clearly divided from the front end of the ventral part of L3. L3 in most valves is undivided, and in others has a faint ventral groove. L2 is the most prominent lobe. Measurements of length and height are listed in Table VII.

TABLE VII

MEASUREMENTS OF VALVES OF *Beyrichia tuberculata* (KLÖDEN) IN FOURTH INSTAR

Left Valve				Right Valve			
Cat. No.	Length (mm.)	Height (mm.)	Ratio (H/L)	Cat. No.	Length (mm.)	Height (mm.)	Ratio (H/L)
32130	0.80	0.50	.63	32133	0.90	0.60	.67
.....	...	...	..	32134	.80	.50	.63
.....	...	...	..	32138	.75	.45	.60
.....	...	...	..	32135	.70	.45	.64
Mean	.80	.50	.63	.....	.79	.50	.64

Variation within Instars

The great extent of variation among specimens of *Beyrichia tuberculata* was recognized by Jones and Holl, who wrote (1886, p. 349), "We must remember that by themselves neither the splitting-up of the lobes nor the granulation of the surface can be taken as specific characters, so many instances of the capricious adoption of these features being known." Although our specimens were all obtained from a rock about 1 inch thick, they may not represent a single population. We do not know how much time was required to deposit this thickness of limestone. The ostracods at the top may not have been contemporaries of those at the bottom. Indeed, it is unlikely that more than a few of the specimens ever lived at one time. Furthermore, the ostracods that were deposited side-by-side may not have lived in the waters immediately above their burial place; currents may have carried them after death for several miles before they came to rest on the sea floor. Some variations may have been caused by evolution of the species during the span of time from the date of the oldest specimen

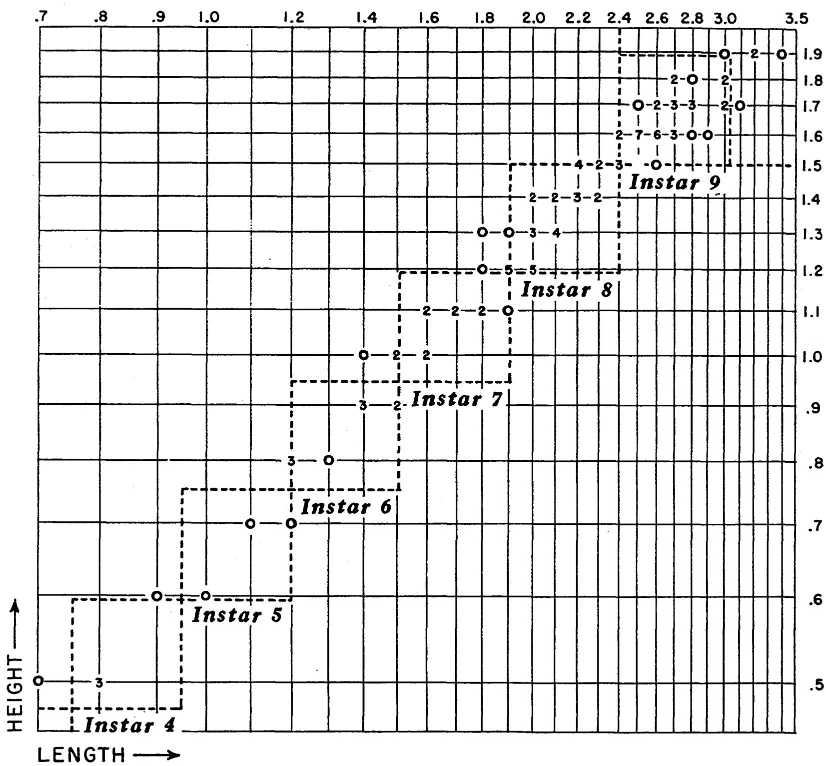

FIG. 4. Distribution according to instars of specimens of *Beyrichia tuberculata* (Klöden). Figures indicate the number of specimens having the particular measurements of length and height specified; small circles represent single specimens. Dashed lines are boundaries of ideal instars, which increase each dimension by a factor of 1.26 from one instar to the next.

to that of the most recent; others may have been due to differences in the environments of the living animals.

Variations in adults.—Adults vary in size (Fig. 4), shape, lobation, and ornamentation. Four female valves (Table I) and one male valve (Table II) are longer or higher than the specimens within the limits of the ideal adult instar (Fig. 4, Instar 9), which has lower and upper limits of length and height separated by a factor of 1.26. These five valves do not have lobation or ornamentation different from those of most other adult valves. There are many variations in shape. The height/length ratio varies from .55 to .69 (Tables I and II); the mean ratio for all adult valves is .61. Although valves of the same length vary slightly in height, there seems to be a relation between size and shape: the lowest value of the height/length ratio, 0.55, occurs only in valves having a length of 2.90 mm. or more. In other words, all extremely elongate valves are large, and most of the large valves are more elongate than the small valves.

Lobes vary in size and in shape. In some male valves the lobes are narrow and steep-sided (Pl. III, Figs. *3a–b*; Pl. II, Fig. 9), whereas in others the lobes are broad and gently arched (Pl. III, Figs. *4a–b*). The long valves (Plate I, Figs. *5a–b*; Pl. III, Figs. *4a–b*) have proportionally larger L3's than the short valves (Pl. I, Figs. *1a–b*; Pl. II, Fig. 20). In some specimens the front half of the ventral groove of L3 is about midway between the dorsal and ventral borders (Pl. II, Fig. 14), but in others it is in the ventral half of the valve (Pl. I, Figs. *5a–b*). In some male valves L2 is small and separated from the anteroventral end of L3 by a broad area of S2 (Pl. II, Fig. 14); in others L2 is elongate and separated from L3 by a short saddle in S2 (Pl. I, Figs. *5a–b*). A series can be selected to show a progressive development in size, shape, and positions of lobes. The pustules and tubercles on the lobes are small in some specimens (Pl. II, Fig. 14), intermediate in size in others (Pl. II, Fig. 19), and large in a few (Pl. III, Figs. *3a–b;* Pl. II, Fig. 3).

Variation in immature instars.—Valves in each of the immature instars vary in size (Fig. 4), in development of the ornamentation, and in lobation. The immature instars have smaller variations in shape and lobation than the adult instar. In the ontogenetic series of instars (Tables I to VII) the height/length ratio reaches a maximum in the seventh instar and a minimum in the adult instar. In *Beyrichia tuberculata* the valves did not, therefore, become progressively elongate with growth.

PART II. REVISION OF *DIBOLBINA STEUSLOFFI* (KRAUSE)

By Robert V. Kesling

THE Rominger specimens of this ostracod, originally named *Beyrichia steusloffi* by Krause (1891, p. 505), have features that are also present in the type of *Dibolbina*. In consequence, they are assigned to that genus. Both the genus and species are redescribed and their characters discussed in this section. The type species of *Dibolbina, D. cristata* Ulrich and Bassler, is figured and compared with the reassigned *D. steusloffi* (Krause). Although previous workers have retained *D. steusloffi* (Krause) in *Beyrichia,* it should be noted that Henningsmoen stated (1954, p. 29), "It is possible that *Beyrichia steusloffi* Krause 1891 from the Downtonian of Europe should also be included in this genus [*Dibolbina*], in spite of its being bisulcate."

Systematic Position

Genus *Dibolbina* Ulrich and Bassler

Type species.—By original designation, *Dibolbina cristata* Ulrich and Bassler, 1923, pp. 312, 659.

Original description.—Ulrich and Bassler describe *Dibolbina* twice in the Maryland Geological Survey Silurian Volume (1923). On page 312 they state briefly that the genus consisted of "Widely frilled Beyrichiidae with trilobation of surface much obscured, only the middle lobe being definitely developed. Brood pouch nearly hemispheric, mainly posterior in position." On page 658 they give a more detailed description:

> Widely frilled Beyrichiidae in which the median lobe is almost completely merged with the posterior lobe by great shallowing and practical elimination of the posterior sulcus. However, the median lobe is still indicated by a small prominence located nearly in the middle of the valves excluding the frill. Just in front of it is a fairly deep curved sulcus or depression that fails to reach the dorsal edge and on the opposite side passes into a much shallower post-ventral depression. In the females the latter is covered by the inner half of a semiglobose brood pouch, the outer half lying on the frill.

Remarks.—Only three species of this genus are known: *Dibolbina cristata* Ulrich and Bassler (1923, p. 659, Pl. 63, Figs. 13–15), *D. producta* Ulrich and Bassler (1923, p. 660, Pl. 63, Fig. 16), and *D. steusloffi* (Krause), here assigned to the genus. The first two species are from North America and the last from Europe. Each of the three occurs only in Upper Silurian rocks. The female valve in each has a true pouch, so the assignment of *Dibolbina* to the family Beyrichiidae is correct. The orientation used by Ulrich and Bassler is the reverse of that used here.

An examination of specimens of the type species, *D. cristata,* reveals that a few characters were incorrectly interpreted or not emphasized in the generic description of *Dibolbina* or the specific description of its type species. The three cotypes of the type species are deposited in the United States National Museum under the number 63705. One of the two male valves (Pl. IV, Fig. 12) is not crushed, but the other (Pl. IV, Fig. 11) is much flattened and abraded. The third, a female valve (Pl. IV, Fig. 13), is crushed in its anterior half and has an irregular fracture extending from the hinge line to the ventral border through S2 and the rear part of the brood pouch. The better male valve has a narrow crest near the proximal edge of the frill; it extends from the anteroventral to the posteroventral part. Striae on the outer part of the frill are interrupted by this crest, but continue from the proximal side of the crest to a juncture with the lateral surface. The frill in this male specimen also has closely spaced faint grooves concentric to the edge of the frill. Although the striae are deeper and more conspicuous than the concentric grooves, the frill should be called reticulate. Ulrich and Bassler do not mention that the frill continues beyond the brood pouch in the female valve. The greatest height of the lateral surface in all three specimens is through L3 and immediately behind S2.

In the original description of *D. producta* by Ulrich and Bassler (1923, p. 660) the nature of the frill is not discussed and it is not clear from the figure (1923, Pl. 63, Fig. 16) whether there is a crest on the proximal part of the frill. The greatest height of the valve is shown to be through L3. The "low crescentically curved ridge behind the acuminate anterior extremity" spoken of by Ulrich and Bassler (1923, p. 660) may correspond to the low ridge along the rear edge of L3 in *D. steusloffi* and to the crest on the posteroventral slope of L3 in *D. cristata.*

Dibolbina steusloffi (Krause)

(Pl. IV, Figs. 1–10; Pl. V, Figs. 1–6)

Beyrichia Steusloffi Krause, 1891, pp. 505–6, 518–19, Pl. 32, Figs. 6, *7a–b*, 8, 9.
Beyrichia steusloffi Bassler and Kellett, 1934, pp. 67, 70, 206–7.
Beyrichia steusloffi Henningsmoen, 1954, p. 29.

Remarks.—Other references to this species are in Bassler and Kellett, 1934, pp. 206–7. The characters that *D. steusloffi* (Krause) has in common with *D. cristata* Ulrich and Bassler, the type species, are: (1) Valves trilobate; (2) S2 elongate, ventral half narrow and extending to the frill and dorsal half becoming broad and very shallow toward the hinge line; (3) L3 consisting of one complete lobe, not divided into segments as in many species of *Beyrichia;* (4) narrow crest near the proximal edge of the frill; (5) L2 vertically elongate; (6) frill of the female extending around the ventral edge of the pouch; and (7) greatest height of the lateral surface posterior to S2. It is these characters that justify, in my opinion, the assignment of *D. steusloffi* to the genus *Dibolbina.*

Descriptions

Original description (Krause, 1891, p. 505).—

> Die Schale ist halbkreisförmig, mit fast geradem, dem Dorsalrand parallel laufenden Bauchrande. Die Oberfläche ist wenig gewölbt. Vom Dorsalrande aus durchziehen zwei Querfurchen die ganze Schale bis zum Ventralrande.
>
> Die vordere ist stärker und erscheint in ihrer ganzen Ausdehnung als eine gleich breite und tiefe, zum Dorsalrande senkrecht stehende Furche; die hintere, schwächere, ziegt in der Mitte eine leichte Einbiegung nach innen. Durch diese Furchen ist die Schale in 3 Theile getheilt; der mittlere ist der schmälste und an seinem Dorsalende ein wenig angeschwollen. An den Ventralrand setzt sich ein breiter, regelmässig gestrichelter Saum, der auch nach beiden Seiten zu sich fortsetzt.
>
> Die weiblichen Individuen zeigen einen angeschwollenen Ventralhöcker, an welchen der unter einem stumpfen Winkel von der Schalenfläche abstehende Saum sich anlegt.

Krause's description is essentially correct. His "vordere Querfurchen" is S1; "hintere Querfurchen," S2; "mittlere Theile," L2; and "angeschwollenen Ventralhöcker," the brood pouch. The orientation used by Krause in his figures, in which the brood pouch of the female is anteroventral, agrees with mine. The following additions are made to his descriptions of male and female valves.

Male.—S2 broad and shallow at its dorsal end. L3 separated from the posterior part of the valve by a shallow curved groove, extending from the rear part of the dorsal border to the posteroventral edge of the lateral surface, nearly parallel to the posterior border. A low, inconspicuous ridge along the rear edge of L3, next to the groove (Pl. IV, Figs. 7–8). Posterior part of the valve with the shape of half a crescent.

Frill broad and flaring (Pl. IV, Fig. 8), extending from corner to corner, broadest in its anteroventral part. A narrow high crest on the proximal part of the frill, near the junction of the frill and the lateral surface, extending from the anteroventral to the posteroventral part of the frill (Pl. IV, Figs. 7, 9–10). Frill composed of numerous small tubules perpendicular to its proximal edge. Tubules fused at their lateral contacts, with a strongly impressed stria along each contact. Distinct small pits between the narrow crest and the lateral surface, aligned with the striae and undoubtedly representing their proximal continuations. Inner surface of frill not seen.

Female.—Sulci and structure of the frill like that of the male. The narrow high crest on the proximal part of the frill joined to the posterior edge of the brood pouch and extending to the posteroventral part of the frill (Pl. IV, Figs. 1, 6). Frill seemingly with about the same outline as that of the male, narrow in that part joined to the distal edge of the pouch. On the outer face of the frill, the junction of the frill and pouch marked by a semisulcus. On the inner face (Pl. IV, Figs. 4–5), the tubules nearly confluent with the surface of the pouch, their junction inferred from the proximal limits of the striae.

The inner face of the pouch elongate, elliptical, and slightly but evenly convex. A narrow crest along the proximal edge of the pouch, extending toward the front and toward the rear on the proximal margin of the frill (Pl. IV, Fig. 5). The part of this crest behind the pouch lies opposite the crest on the outer face of the frill.

Submarginal ridge low, narrow, separated from the crest on proximal edge of the inner faces of the brood pouch and frill by a smooth, slightly convex area (Pl. IV, Fig. 3). This area is much wider in its posterior than its anterior part.

Remarks.—The distal edge of the inner and outer faces of the frill are abraded in the female specimen, an incomplete right valve. It is difficult to determine the exact nature of the details of this part of the frill. In the region immediately below the rear end of the pouch, the edge is less abraded than elsewhere. Here, the striae do not appear to extend to the distal edge. There is a short shallow groove in the middle of each tubule near its distal end and faint radial lines along the edge of the thin, delicate margin. These features may be primary, but it is also possible that the shallow groove was formed when abrasion broke the shell material from the outer surface of the tubule; the radial lines may only be the marks left by such abrasion.

The reconstructions in Plate V are based on the specimens illustrated in Plate IV and on figures given by Krause (1891, Pl. 32, Figs. 6, *7a–b*, 8, 9). Nearly all parts of both the male and the female carapace are represented in one or both of these sources, so that the reconstructions are the most accurate possible at this time. Even so, the structure of the distal part of the frill may be questioned.

The remarkable feature of *Dibolbina steusloffi* (Krause) is the great elevation of the free edges of the valves above the distal edges of the frill (see Pl. IV, Fig. *2*; Pl. V, Fig. 4). It is difficult to conceive how the ostracod lived. If the animal was benthonic at any stage, the appendages used for locomotion and feeding must have been extremely long to enable it to reach the surface on which the carapace rested. The margins of the frill are very fragile; it is questionable whether they could have supported the weight of the carapace. If the animal was nektonic, however, the swimming appendages must have been very strong and the wide frill must have been a cumbersome, hindering structure.

Although specimens of other species of beyrichiid ostracods are abundant in Silurian rocks, those of *D. steusloffi* are rare. The scarcity may in part be attributed to the thinness of the valves, but it may also be related to the ecology of the animal. If ostracods of this species were adapted to live only under special and rare ecological conditions, their population was probably very restricted.

Hypotypes.—Two male left valves embedded in a piece of limestone, Nos. 32688*a* and 32688*b;* one male right valve, No. 32689; part of a female right valve, No. 32690.

PART III. *KLOEDENIA WILCKENSIANA* (JONES) AND ITS RELATIONSHIPS

By Robert V. Kesling

STUDY of the new examples of *Kloedenia wilckensiana* (Jones), the type species, reveals that the original description of *Kloedenia* is incomplete and that subsequent ones are, in part, erroneous. The pouch of the female of *K. wilckensiana* is very different from that of many species which have been assigned to the genus. I have here rewritten the generic description to agree with the characters of the type and discussed the dimorphism and ontogeny of the type species. *Kloedenia* is closely related to, but distinct from, *Welleria,* a genus to which some of its species have been referred. Because the differences between them have not been analyzed, a revision of *Welleria* is included, together with a discussion and figure of its type species, *W. obliqua* Ulrich.

Revision of Kloedenia and Welleria

Family Kloedeniidae Ulrich and Bassler

Ulrich and Bassler (1923, p. 306) created the Kloedeniinae as a subfamily of the Zygobolbidae. Bassler and Kellett (1934, p. 22) also used that classification. In 1953 (p. 238), Henningsmoen stated, "*Kloedenia* is so close to *Beyrichia* that the Kloedeninae are regarded here as a synonym of the Beyrichiinae." The following year (1954, p. 29), however, Henningsmoen revived the subfamily Kloedeniinae and placed it in the family Beyrichiidae. I regard the Kloedeniidae as of family rank, although it is much more closely related to the Beyrichiidae than to other families.

Genus *Kloedenia* Jones and Holl

Type species.—By designation of Jones and Holl, 1886, p. 347, *Beyrichia wilckensiana* Jones, 1855, p. 89.

Original description.—Jones and Holl (1886, p. 347) follow their discussion of *Beyrichia wilckensiana* with the statement: "*B. Wilckensiana* differs so much in general features from typical *Beyrichiae* that we think this purse-like form ought to be raised to generic distinction as *Kloedenia* . . . ." On pages 362 to 363 of the same article they add: ". . . and the smooth convexity of the main portion of the valve, the very short sulci, and the small but prominent midlobe, reaching to the dorsal edge, strongly distinguishing these species, we propose to separate them from their Beyrichian allies, under the generic title of *Kloedenia*."

The first appearance of the name "*Kloedenia*" is on p. 347 of the original article. Since the only species mentioned at that place is *Beyrichia* *wilckensiana,* I consider that Jones and Holl thereby designated *B. wilckensiana* Jones as the type of *Kloedenia*. Henningsmoen (1954, p. 30), however, believes the type species to have been designated by Ulrich and Bassler (1908).

Remarks.—Kloedenia has been very broadly interpreted by American workers. Their concept of the genus is based more on the discussion given by Ulrich and Bassler (1908, pp. 300–305) and the brief description by Bassler and Kellett (1934, p. 23) than on the original description by Jones and Holl or the characters present in the type species. Ulrich and Bassler (1908, p. 305) wrote:

> The type of the genus *Kloedenia, K. wilckensiana,* occupies an intermediate position between two sections into which the genus is divisible. One of these sections, the smaller, includes, with the genotype, most of the European species, while all the known American forms fall into the second. The first section is characterized by a tendency to produce and attenuate the anterior extremity and to develop on this part one or two accessory furrows. In consequence, the outline of the valves is more or less triangular and comparatively elongate. In the American section of the genus the valves are usually shorter, the ends approximately equal and the anterior one without distinct furrows.

Bassler and Kellett (1934, p. 23) described the genus as follows:

> Obese carapaces like *Plethobolbina* and approaching the simpler forms of *Mastigobolbina* in having median and posterior sulci and the median lobe partly separated as a rounded or subovate node; sulci short, confined to the dorsal half. Brood pouch well developed, large and rather distinctly outlined, projecting beyond the ventral edge and most of it behind the midlength of valves.

Ulrich and Bassler and Bassler and Kellett in the passages quoted use an orientation that is the reverse of mine. The description by Bassler and Kellett fits most of the American species, but not the type species. The brood pouch of *Kloedenia wilckensiana* is not "rather distinctly outlined," and much of it lies posterior to mid-length.

Henningsmoen (1954, p. 30) also divides the species of *Kloedenia* into two taxa, the group of *K. wilckensiana* and the group of *K. normalis,* but he states, "Perhaps it may be better later on to restrict *Kloedenia* to the species agreeing with *K. wilckensiana* . . ., and assign *K. normalis* and allied species to a new subgenus or genus, or possibly to *Welleria.*" It is obvious from the descriptions, figures, and specimens that *K. wilckensiana* differs more in lobation and dimorphism from *K. normalis* than it does from the type species of *Welleria* (*W. obliqua* Ulrich and Bassler), *Kyamodes* (*K. whidbornei* Jones), or *Zygobeyrichia* (*Z. apicalis* Ulrich). In *Kloedenia normalis* the brood pouch has a distinct semisulcus at its junction with the rest of the lateral surface, and the L2 of each dimorph is located well below the hinge line and bounded ventrally by a sulcus; the form of the brood pouch and the position and form of L2 are very similar to those in species of *Beyrichia*. In *Kloedenia wilckensiana,* and also in *Welleria obliqua, Kyamodes whidbornei,* and *Zygobeyrichia apicalis,* the brood pouch has no distinct boundary with the lateral surface, and the L2 in each dimorph is located near or a little above the hinge line and is not ventrally separated from the rest of the lateral surface by a distinct sulcus.

I agree with Henningsmoen that the species in the *Kloedenia normalis* group should be separated from the genus *Kloedenia,* but I do not believe they can be assigned to *Welleria*. They are more closely related to *Beyrichia*. If a new genus is erected for them, it will differ from *Beyrichia* in having a relatively short S1 and S2 and the ventral half of each valve smooth, unbroken, and confluent with L1 and L3; it will differ from *Kloedenia* and *Welleria* in having the brood pouch separated from the rest of the lateral surface by a distinct semisulcus or groove.

Revised description.—Dimorphic beyrichiacean ostracods. Outline oval or elongate oval. Hinge line straight, free border smoothly curved. Two short sulci (S1 and S2) reaching the dorsal border. L2 ventrally nearly confluent with the rest of the lateral surface, not bounded by a prominent sulcus. The posterior approximately one-fifth of each valve, arched outward much less strongly than the rest of the valve, particularly in the ventral half. The anteroventral and ventral regions forming a smoothly arched, strongly convex lobe, separated from the posterior region by a concave semisulcus and from the marginal ridge by a distinct channel. Strongly convex lobe in the female forming the pouch and projecting distally in its ventral part much farther than that in the male. Pouch in each female valve not sharply defined along its dorsal border, merging with the dorsal part of the valve without a semisulcus or distinct line of contact. No frill in either dimorph.

Genus *Welleria* Ulrich and Bassler

Type species.—By original designation, *Welleria obliqua* Ulrich and Bassler, 1923, p. 641.

Original description.—Ulrich and Bassler (1923, p. 641) defined the genus as follows:

> Form and lobation of valves of males essentially as in *Kloedenia* from which it differs in the character of the ventral swelling in the female. This instead of forming a definitely outlined large subovate and prominent pouch covering the posterior two-thirds of the ventral slope, forms a low undefined swelling taking in nearly or quite the whole of the ventral two-thirds of the valves. At the base it is compressed and slightly overhangs the ventral edge.

Again, the orientation is the reverse of that I use.

Remarks.—Contrary to the original description quoted above, the lobation of male valves in *Welleria* is not essentially as in *Kloedenia.* In both genera the ventral part of each valve forms a ventral lobe, but in *Welleria* the ventral lobe includes all of the ventral area, whereas in *Kloedenia* it is limited to the anterior four-fifths of the ventral area (Pl. VII, Figs. 1–2). In regard to the pouch in each female valve the description of *Welleria* is correct, although the inference that *Kloedenia* has a "definitely outlined large subovate and prominent pouch covering the posterior two-thirds of the ventral slope" is false.

Dimorphic differences in convexity of the ventral part of the valve in *Welleria* can be distinguished better in ventral view than in lateral. In lateral view, the ventral part of the female valve overhangs the free edge, whereas that of the male valve meets the free edge.

The differences between *Welleria* and *Kloedenia,* as exemplified in their type species, are in the prominence of L2, the convexity of the posterior part of the valve, and the channel between the ventral lobe and the marginal ridge. *Welleria* has a low L2, the posterior part of the valve confluent with the rest of the ventral lobe, and a very shallow channel if any. *Kloedenia,* on the contrary, has a very prominent L2, the posterior part of the valve much less convex than the ventral lobe, and a broad, distinct channel. In *Welleria obliqua* (Pl. VIII, Figs. 1, 4) L2 is difficult to distinguish because S1 is a very shallow groove.

Revised description.—Dimorphic beyrichiacean ostracods having all of the free border smoothly curved, two short sulci (S1 and S2) limited to the dorsal part of each valve, and a smoothly arched ventral lobe including all the ventral part of the valve and dorsally confluent with at least L1 and L3. Ventral lobe in the female forming the pouch, more convex in its ventral part than that of the male, extending ventrally a little beyond the free edge, and dorsally confluent with the rest of the lateral surface.

Dimorphism in Kloedenia wilckensiana (Jones)

Valves show dimorphism in the convexity of the ventral lobe, the number and spacing of crests on the ventral lobe, the prominence of L2, and the presence of a low, humplike ridge behind S2. In ventral view, the ventral lobe of male valves (Pl. VII, Figs. 11) is gently convex, evenly curved, and nearly confluent with the posterior region of the valve, but that of female valves (Pl. VI, Figs. 3, 8; Pl. VII, Fig. 7) is strongly convex and separated from the posterior region by a shallow but distinct concave semisulcus. In lateral view, the posterior edge of the ventral lobe is rather indistinct in the male (Pl. VII, Fig. 1), but much more sharply defined in the female (Pl. VI, Fig. 1; Pl. VII, Fig. 3).

The ventral lobe or pouch of the female (Pl. VI, Fig. 8; Pl. VII, Fig. 4) invariably has three distinct and separate crests along its ventral edge. The inner crest is the shortest; posteriorly (Pl. VI, Figs. 3–4; Pl. VII, Figs. 7–8) it is very low and joined to the middle crest, but anteriorly (Pl. VI, Fig. 5) it ends rather abruptly and is not joined to the middle crest. The two outer crests are parallel throughout most of their length; their posterior ends (Pl. VI, Fig. 4) are joined at an acute angle near the middle of the valve as seen in end view; anteriorly (Pl. VI, Fig. 5), the two crests converge below mid-height and continue for a short way as one. Most male valves, on the other hand, have a sharp edge on the ventral lobe and no crests (as in Pl. VII, Fig. 11); a few have two or three closely set and very faint crests (as in Pl. VII, Fig. 2).

All female valves have a shallow groove between L2 and the pouch, and most (see, for example, Pl. VI, Fig. 1; Pl. VII, Fig. 3) have a low crest along the rear and ventral edges of L2. Male valves have L2 nearly or completely confluent with the ventral lobe and lack a crest on L2. Male valves have one characteristic not found in female valves. It is a low, curved humplike ridge behind L2 (Pl. VII, Figs. 1, 9–10), which projects slightly above the hinge line.

Ontogeny of Kloedenia wilckensiana (Jones)

If the smallest specimen recovered is designated as the first instar, the adults are to be considered in the eighth. Only five immature specimens were found and not all instars are represented. Even though the ontogenetic series is incomplete, however, certain progressive trends are evident.

L2 is the dominant feature of lobation in the adult valves, both male (Pl. VII, Fig. 1) and female (Pl. VII, Fig. 3). Even the first instar (Pl. VII, Fig. 15) has a prominent L2. In fact, the L2 in this instar is proportionately larger than that of the adult. In the third (Pl. VII, Fig. 14), fifth (Pl. VII, Figs. 12–13), and seventh (Pl. VI, Fig. 10) instars, the L2 is also large and prominent.

During ontogeny the bottom edge of the ventral lobe approaches the free edge. Unfortunately, the only valve in the first instar (Pl. VII, Fig. 15) has the anterodorsal and ventral parts of the marginal area broken off; nevertheless, in the anteroventral region it can be seen that there is a broad marginal or extralobate area between the ventral lobe and the free border. A well-preserved valve in the fifth instar (Pl. VII, Fig. 13) has a rather wide marginal area, although proportionately somewhat narrower than that in the first instar. In the seventh instar (Pl. VI, Fig. 10) the marginal area is narrower yet. In the adult male (Pl. VII, Figs. 1, 9) the bottom edge of the ventral lobe is very close to the free border, and in the female (Pl. VI, Figs. 1, 6; Pl. VII, Figs. 3, 5) the ventral edge of the pouch is tangent to the free edge or slightly overhangs it.

Although the height/length ratio in adult valves is variable and very few immature valves have been found, the ratio seems to decrease during ontogeny. Several valves from each instar are needed to determine the ratios more exactly. The valve in the first instar has the height only a little less than the length, whereas those in later instars have heights much less than the lengths. In addition, the position of S2 shifts forward during growth. In the first instar it is behind the anterior border by a distance equal to almost two-thirds the length, but in the adult it is nearly at the mid-point of the length.

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Received for publication August 1, 1955

EXPLANATION OF PLATE I

(All figures × 20)

PAGE

Beyrichia tuberculata (Klöden) 43

FIGS. 1*a–b*. Stereoscopic lateral views of male left valve. Hypotype No. 32079. Ventral view, Plate II, Figure 10.

FIGS. 2*a–b*. Stereoscopic lateral views of female left valve. Hypotype No. 32103.

FIGS. 3*a–b*. Stereoscopic inclined lateral views of female left valve. Hypotype No. 32080. Lateral, dorsal, and anterior views, Plate II, Figures 11–13.

FIGS. 4*a–b*. Stereoscopic inclined ventral views of female left valve. Hypotype No. 32084. Lateral view, Plate II, Figure 18.

FIGS. 5*a–b*. Stereoscopic lateral views of male right valve. Hypotype No. 32139.

PLATE I

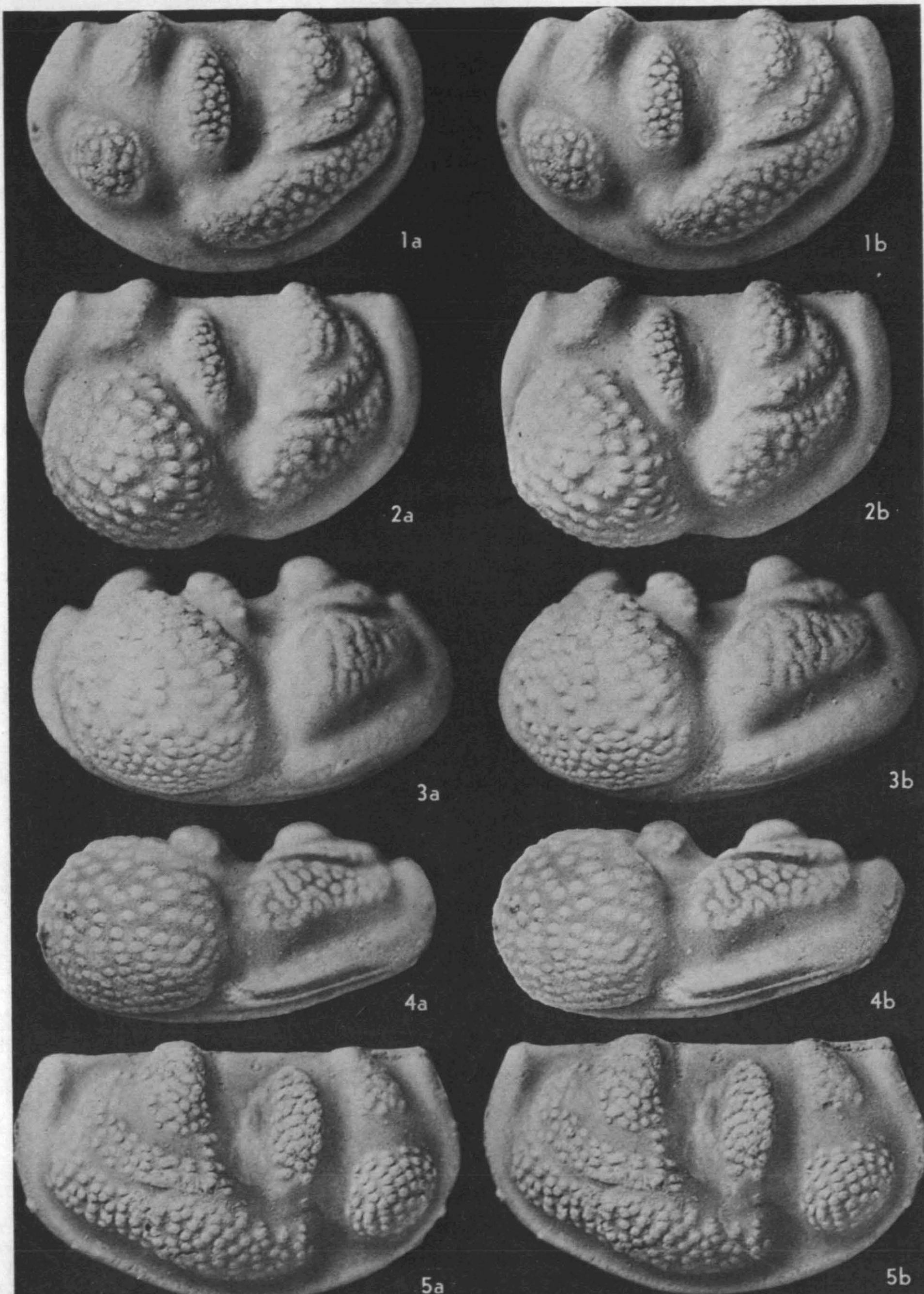
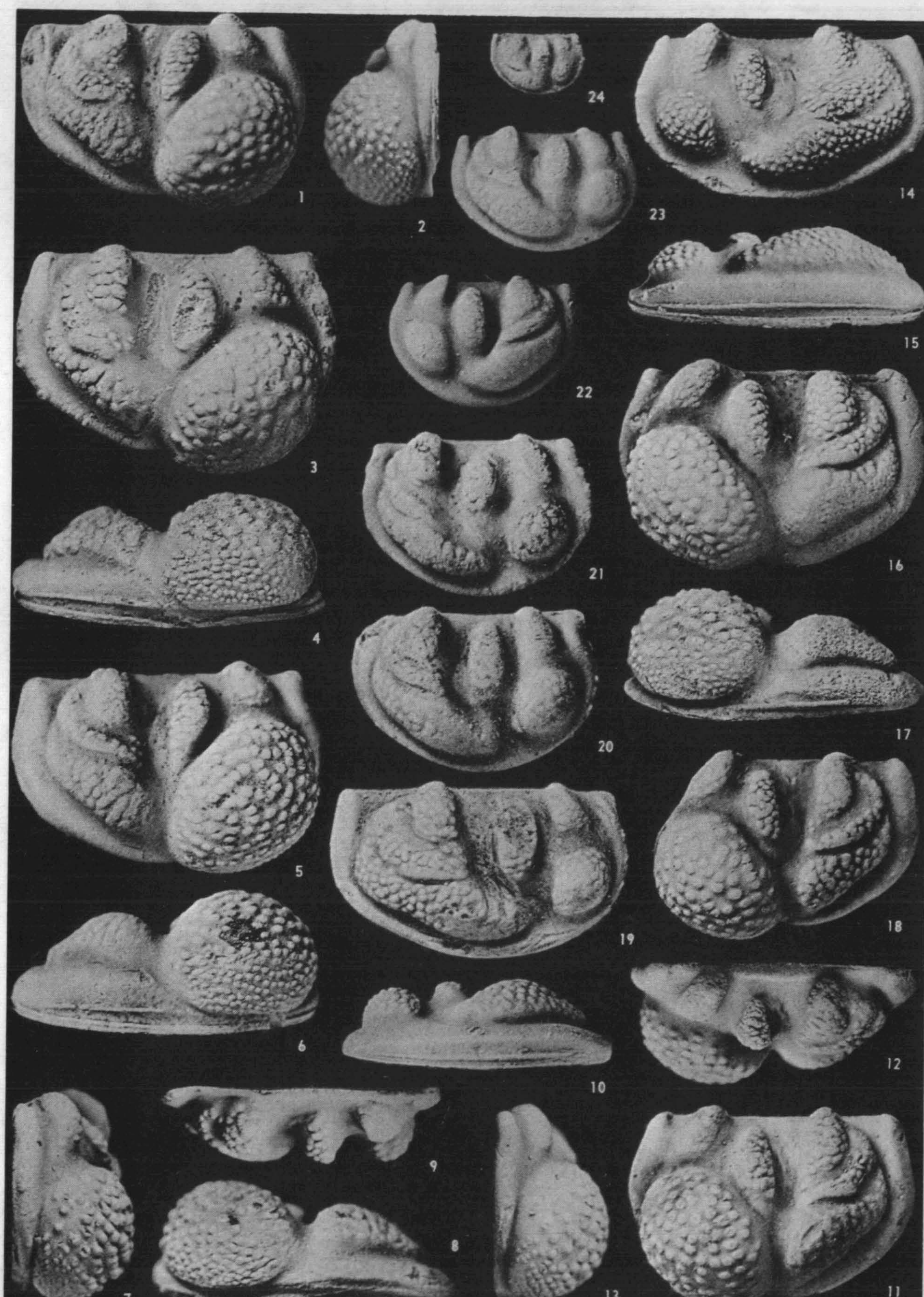


PLATE II



EXPLANATION OF PLATE II

(All figures × 13.3)

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Beyrichia tuberculata (Klöden) 43

FIGS. 1–2. Lateral and anterior views of female right valve. Hypotype No. 32085. Stereoscopic inclined lateral views, Plate III, Figures 2*a–b*.

FIGS. 3–6. Lateral and ventral views of two female right valves. Hypotypes Nos. 32081 and 32100.

FIGS. 7–8. Anterior and ventral views of female left valve. Hypotype No. 32083. Stereoscopic lateral views, Plate III, Figures 1*a–b*.

FIG. 9. Dorsal view of male right valve. Hypotype No. 32089. Stereoscopic lateral views, Plate III, Figures 3*a–b*.

FIG. 10. Ventral view of male left valve. Hypotype No. 32079. Stereoscopic lateral views, Plate I, Figures 1*a–b*.

FIGS. 11–13. Lateral, dorsal, and anterior views of female left valve. Hypotype No. 32080. Stereoscopic inclined lateral views, Plate I, Figures 3*a–b*.

FIGS. 14–15. Lateral and ventral views of male left valve. Hypotype No. 32090.

FIGS. 16–17. Lateral and ventral views of female left valve. Hypotype No. 32082.

FIG. 18. Lateral view of incomplete female left valve. Hypotype No. 32084. Stereoscopic inclined ventral views, Plate I, Figures 4*a–b*.

FIG. 19. Lateral view of male right valve. Hypotype No. 32095.

FIGS. 20–21. Lateral views of two male right valves. Hypotypes Nos. 32093 and 32152.

FIGS. 22–23. Lateral views of a left and a right valve of specimens in the eighth instar. Hypotypes Nos. 32098 and 32160.

FIG. 24. Lateral view of a right valve of specimen in the fifth instar. Hypotype No. 32111.

EXPLANATION OF PLATE III

(All figures × 20)

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Beyrichia tuberculata (Klöden) 43

FIGS. 1*a–b*. Stereoscopic lateral views of female left valve. Hypotype No. 32083. Anterior and ventral views, Plate II, Figures 7–8.

FIGS. 2*a–b*. Stereoscopic inclined lateral views of female right valve. Hypotype No. 32085. Lateral and anterior views, Plate II, Figures 1–2.

FIGS. 3*a–b*. Stereoscopic lateral views of male right valve. Hypotype No. 32089. Dorsal view, Plate II, Figure 9.

FIGS. 4*a–b*. Stereoscopic lateral views of male left valve. Hypotype No. 32101.

PLATE III

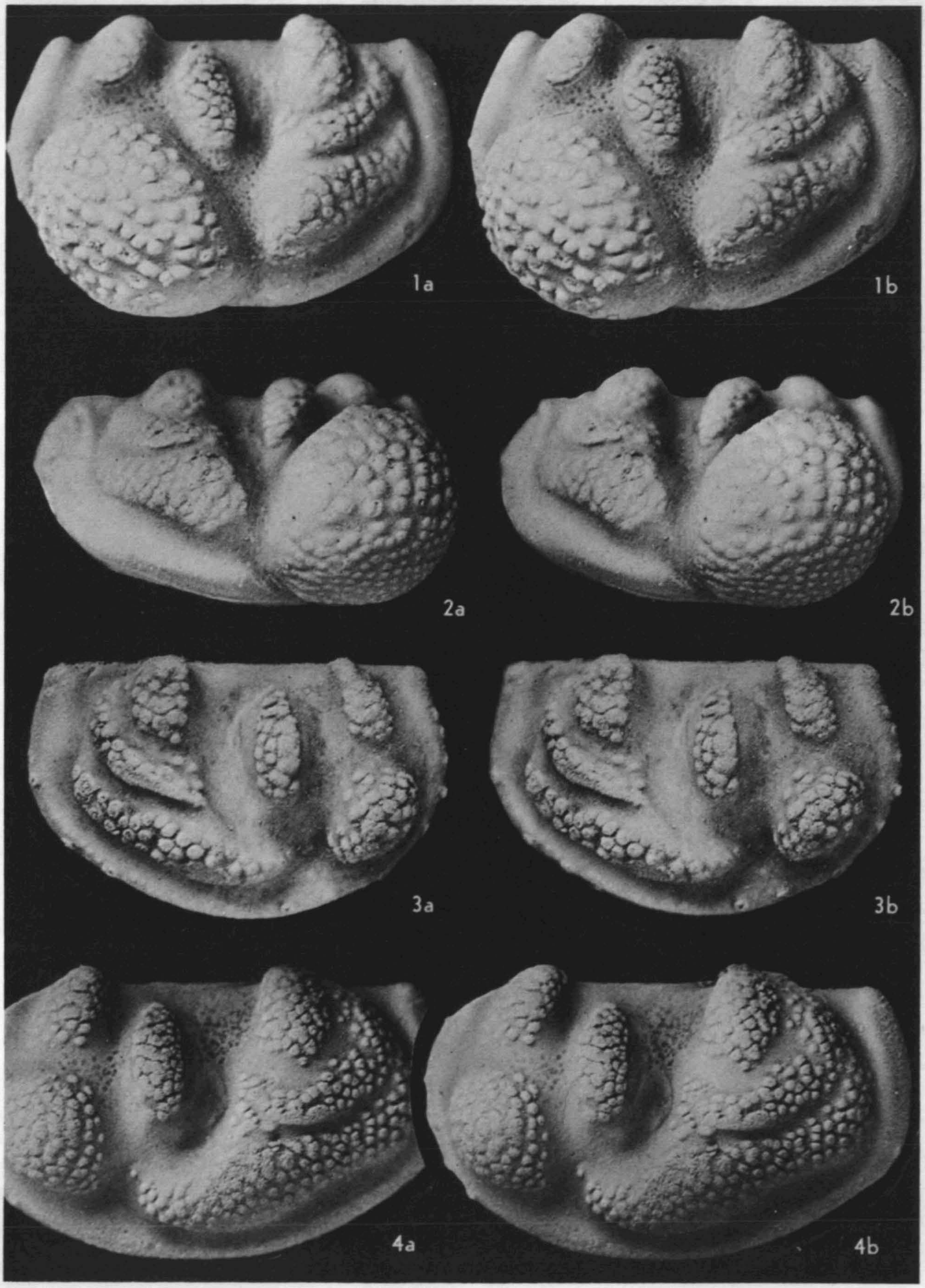
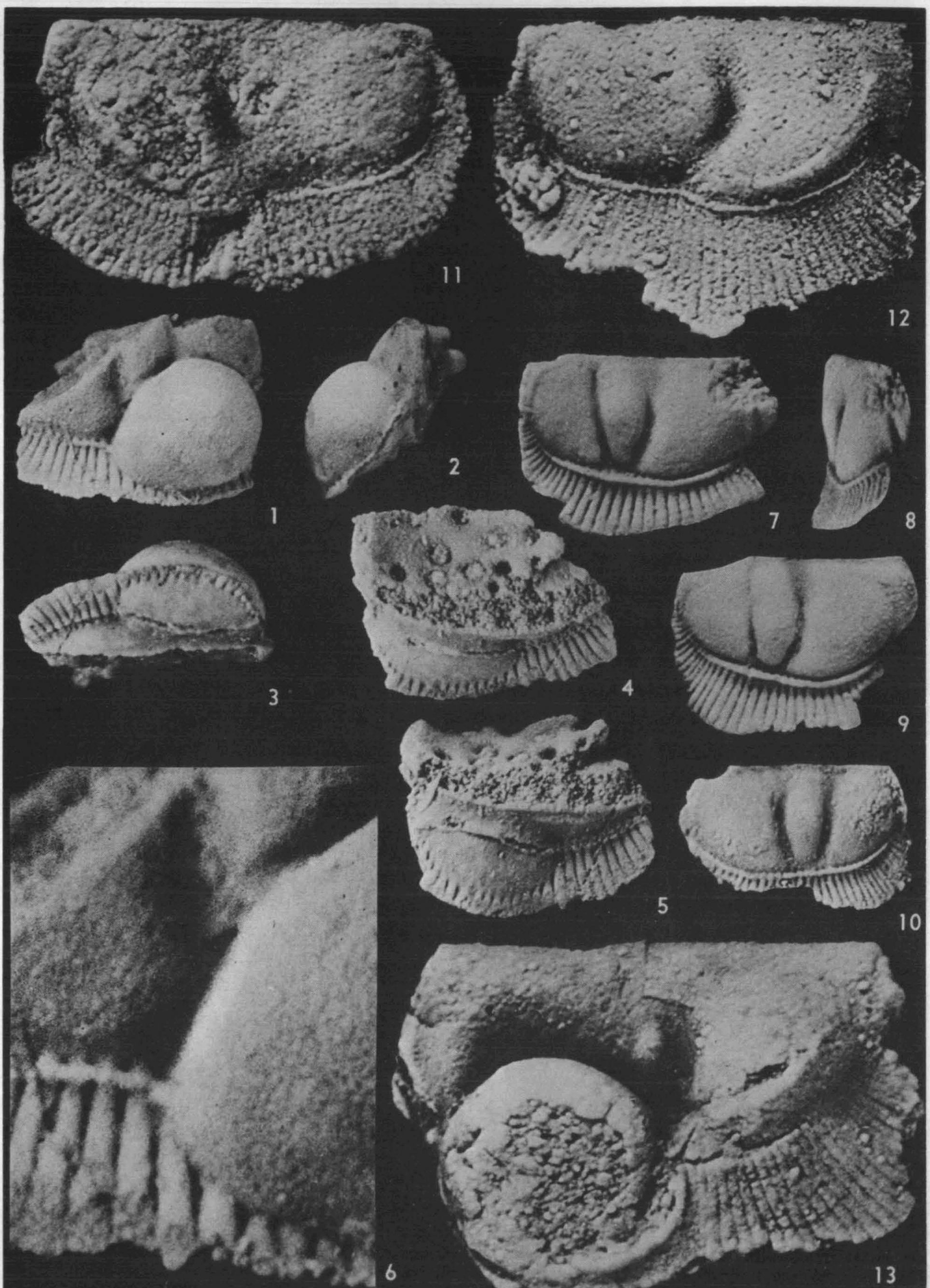


PLATE IV



EXPLANATION OF PLATE IV

(All figures × 30, except as noted)

PAGE

Dibolbina steusloffi (Krause) 57

FIGS. 1–5. Lateral, anterior, ventral, interior, and inclined interior views of part of a female right valve, Hypotype No. 32690. Specimen not coated with ammonium chloride in Figures 2 and 3.

FIG. 6. Enlargement of part of Figure 1, showing structure of the frill. × 100.

FIGS. 7–8. Lateral and inclined posterior views of a male left valve. Hypotype No. 32688*a*.

FIGS. 9–10. Lateral views of a male left and a male right valve. Hypotypes Nos. 32688*b* and 32689.

Dibolbina cristata Ulrich and Bassler 56

FIGS. 11–13. Lateral views of a male right, a male left, and a female left valve, U. S. National Museum Cotypes No. 63705. The figures of these specimens given in Ulrich and Bassler, 1923, Pl. 63, Figs. 13–15, are greatly retouched and more nearly represent restorations than photographs.

EXPLANATION OF PLATE V

(All figures × 46)

PAGE

Dibolbina steusloffi (Krause) 57

FIGS. 1–4. Reconstruction of a female carapace as seen in right lateral, dorsal, ventral, and anterior views, based on specimen in Plate IV, Figures 1–6, and on illustrations in Krause (1891, Pl. 32, Figs. *7a–b,* 9).

FIGS. 5–6. Reconstruction of a male carapace as seen in left lateral and dorsal views, based on specimens in Plate IV, Figures 7–10, and on illustrations in Krause (1891, Pl. 32, Figs. 6, 8).

PLATE V

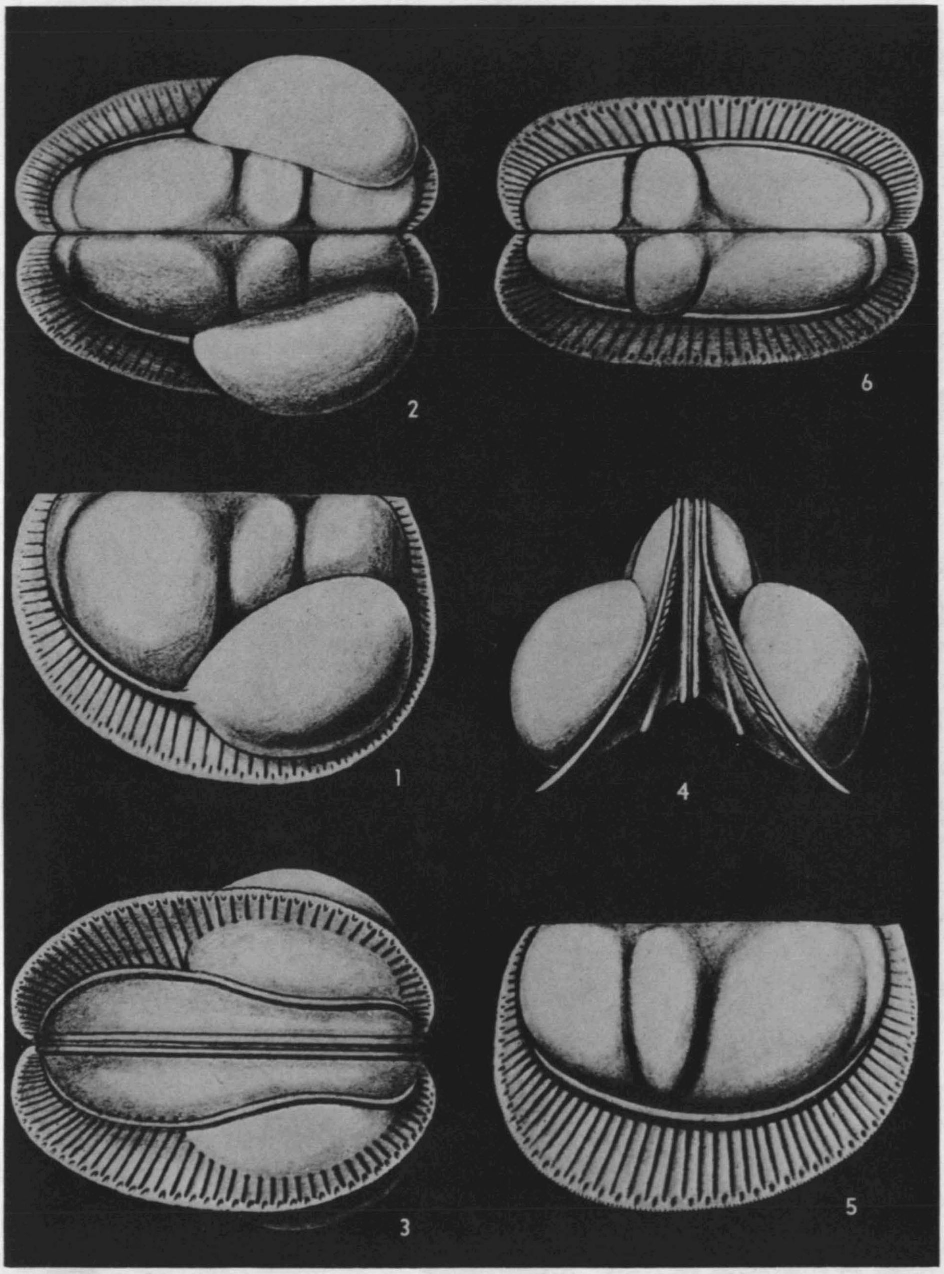
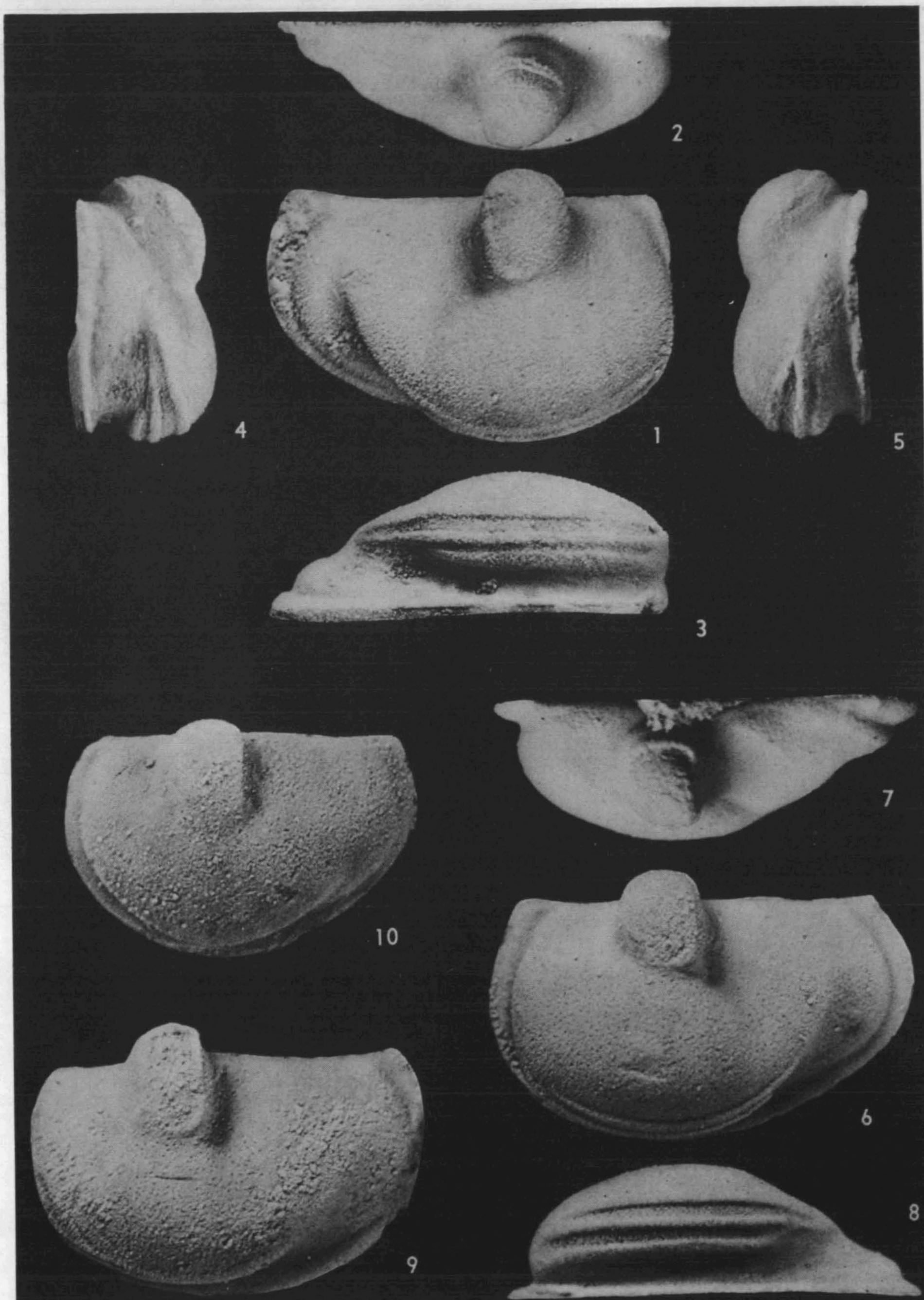


PLATE VI



EXPLANATION OF PLATE VI

(All figures × 20)

PAGE

Kloedenia wilckensiana (Jones) 64

FIGS. 1–5. Lateral, dorsal, ventral, posterior, and anterior views of a female right valve. Hypotype No. 32758.

FIGS. 6–8. Lateral, dorsal, and ventral views of a female left valve. Hypotype No. 32759. Part of the adhering matrix seen in dorsal view.

FIGS. 9–10. Lateral views of a female and an ultimate immature left valve. Hypotypes Nos. 32760 and 32761.

EXPLANATION OF PLATE VII

(All figures × 20)

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FIGS. 1–2. Lateral and slightly inclined ventral views of a male left valve. Hypotype No. 32762.

FIGS. 3–4. Lateral and slightly inclined ventral views of a female left valve. Hypotype No. 32763.

FIGS. 5–8. Lateral, dorsal, ventral, and posterior views of a female right valve. Hypotype No. 32764.

FIGS. 9–11. Lateral, dorsal, and ventral views of a very large male left valve. Hypotype No. 32765.

FIGS. 12–13. Lateral, views of two left valves in the fifth instar. Hypotypes Nos. 32766 and 32767.

FIG. 14. Lateral view of a left valve in the third instar. Hypotype No. 32768.

FIG. 15. Lateral view of a right valve in the first instar. Hypotype No. 32769.

PLATE VII

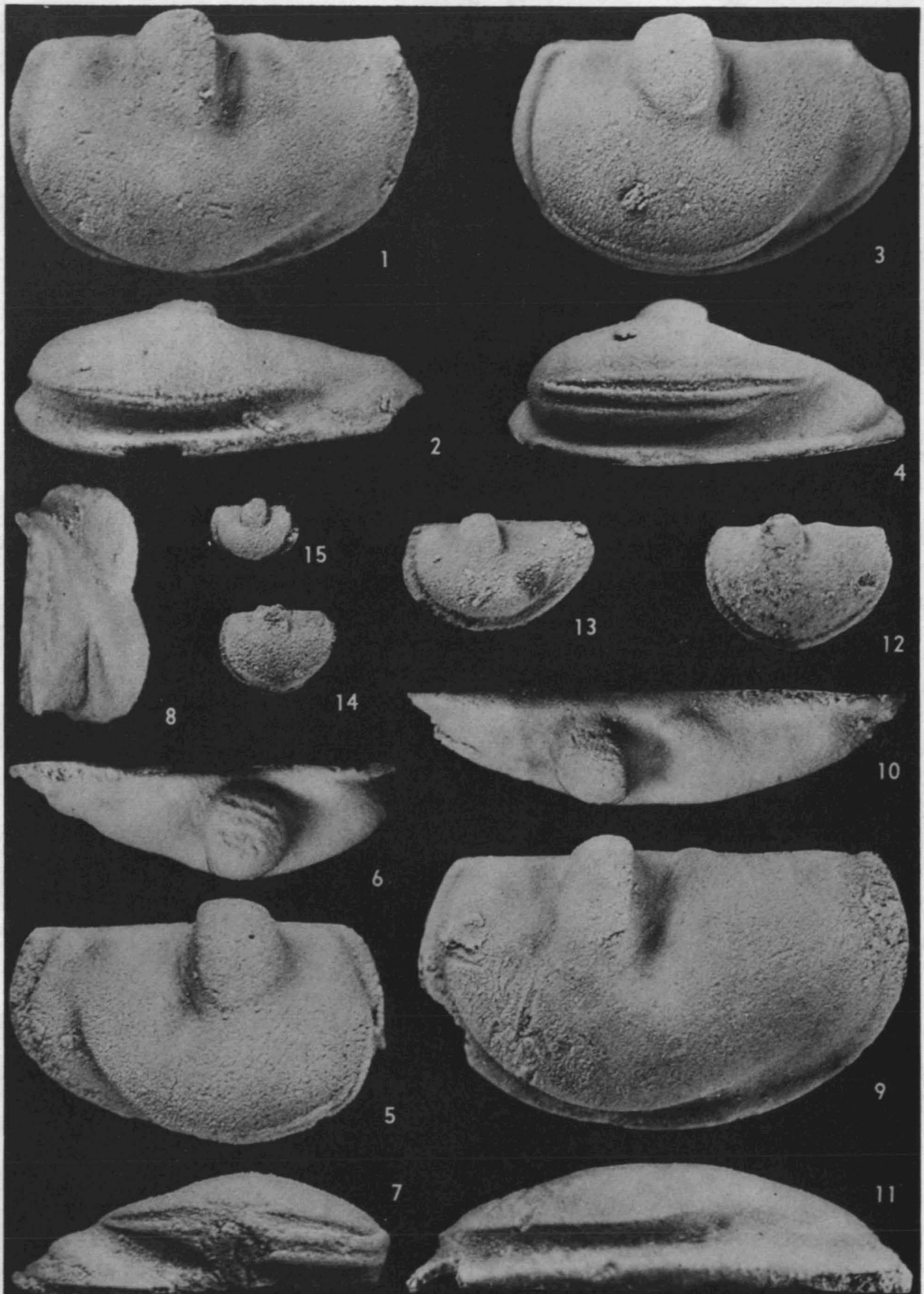

PLATE VIII

EXPLANATION OF PLATE VIII

(All figures × 20)

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FIGS. 1–3. Lateral, dorsal, and ventral views of a female left valve. Hypotype No. 32770.

FIGS. 4–5. Lateral and ventral views of a female right valve. Hypotype No. 32771.

FIG. 6. Lateral view of a right immature valve. Hypotype No. 32772.