

RHYNCHOLITES

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INTRODUCTION

Rhyncholites, as etymology of the name indicates, are stone (fossil) beaks. A considerable variety of organic remains fits such a designation, and so it is necessary to specify the particular category of fossil beaks which has been differentiated by usage under this term. The objects are identified as jaw parts of cephalopods, since many of them closely resemble the calcareous parts of the upper and lower jaws of modern *Nautilus pompilius* and allied species of this genus. The certainty that some known kinds of rhyncholites, perhaps a majority of them, are skeletal elements secreted by nautiloids cannot be accepted as indication that only nautiloids are represented by this group of fossils. A number of workers, including JELETZKY, who is a *Treatise* author working on Coleoidea, have held the opinion that some rhyncholites belong to belemnites and that upon more detailed study and comparison of these fossils with the beaks of Recent coleoid cephalopods, their relationships will become apparent. The systematic position of rhyncholites is discussed in a section of the present chapter under "Relationships."

It was BIGUET (1819, p. 58) who first published the name "*Rhyncholite*." Plainly he used it both as a vernacular term (e.g., *le Rhyncholite, les Rhyncholites*) and also as part of binominal designations, both vernacular and with Latin specific names, for five different kinds of fossil beaks which he described briefly (e.g., *Rhyncholite mouette, R. Larus*, p. 58). The Latin specific names given by BIGUET unquestionably are valid as "indications" in zoological nomenclature, and in our view BIGUET's "*Rhyncholite*" qualifies as a generic name because this author consistently applied the principles of binominal nomenclature (Zool. Code, 1961, Art. 11,c) and employed the Latin- or Greek-derived name coined by him as a noun in the nominative singular, as required by zoological rules (Art. 11,f).

It is true that the spelling "*Rhynco-*" is neither correctly transliterated from the Greek "*rhynchos*" (neuter gender), meaning snout or beak, nor accurately transcribed from the Latin "*rhynchus*" (masculine gender, Art. 30,a,1), derived from Greek. Adjectival specific names published by BIGUET uniformly have masculine endings, as is correct for agreement with a generic name terminating in -lite (Greek, *lithos*, masculine).

Rhyncholite, as a generic name, is not emendable to *Rhyncholite*, on the ground of improper transliteration or latinization of *Rhyncholite*, because imperfection of this sort is rejected as an inadvertent error subject to correction (Art. 32,a,ii); also, it cannot be changed to *Rhyncholites, Rhyncholithes, Rhyncholithus*, or other spelling and attributed to BIGUET. The spelling "*Rhyncholyte*," found in one place (p. 58), seems clearly to be inadvertent. Accordingly, we propose to recognize *Rhyncholite* BIGUET, 1819, as a generic name and to employ the spelling rhyncholite (pl., rhyncholites) as the inclusive vernacular designation for all sorts of cephalopod jaw parts (beaks). The fact that the name *Rhyncholite* is open to criticism on etymological grounds is well counterbalanced by the advantage of clear distinction between *Rhyncholite* (nominal genus) and rhyncholite (common noun).

HISTORICAL REVIEW

Rhyncholite fossils had been observed for a number of years before they were given formal names and were either described simply as "beaks of birds" or "duck's beaks," because of their resemblance to these known objects; they were called "histerolites" or "glossopetrae" by some pre-Linnean authors.

In 1819, FAURE BIGUET described five species of what he termed "rhyncholites," but he figured only one. These fossils were included in a work on belemnites because BIGUET considered them to belong to this group. BIGUET's specimens seem to have

come from Triassic rocks of southeastern France.

VON SCHLOTHEIM (1820) published a rhyncholite (conchorhynch) description and figure under the name *Lepadites avirostris*, thinking the form was related to barnacles. Thus he mistakenly extended the use of the generic name *Lepadites* BLUMENBACH, 1803, which was in reality introduced for fossil cirripeds, to include conchorhynchs. However, BLUMENBACH (1803, p. 21, pl. 2) gave only the name "*sepium rostra*" to two kinds of rhyncholites which he described and figured.

GAILLARDOT (1824) described and figured these same two types of rhyncholites (probably M. Trias., France) (Fig. 338), which he did not undertake to name, designating them merely as "first species" (pl. 22, fig. 3-14) (later named *Conchorhynchus* by DE BLAINVILLE, 1827) and "second species" (pl. 22, fig. 15-26), the original *Rhyncholite* of BIGUET. GAILLARDOT believed that these fossils belonged to cephalopods closely related to *Sepia*. His drawings were excellent and seemingly very accurate.

D'ORBIGNY (1825, p. 212, 215) used the generic name *Rhyncholites* which he incorrectly ascribed to BIGUET, referring it to arrowhead-shaped forms, as BIGUET had done. He described four species with Latinized names, two of which were figured (Trias.-Jur., France, Germany). D'ORBIGNY's "Division 1, espèces à capuchon," were the *Rhyncholite*-type which he believed belonged to the genus *Nautilus*. His "Division 2, espèces sans capuchon," were what was later named *Conchorhynchus*.

In 1827, DE BLAINVILLE divided the rhyncholites known to him into two genera based upon a distinct difference in form. That equivalent to BIGUET's *Rhyncholite* he named *Rhyncholithes* (Fig. 339,1) (GAILLARDOT's fig. 15-26, pl. 22), and the other he defined as the new genus *Conchorhynchus* (Fig. 339,2) (GAILLARDOT's fig. 3-14, pl. 22, and D'ORBIGNY's 1825 *Rhyncholites Gaillardoti*). DE BLAINVILLE apparently thought that these were structures belonging to belemnites.

ZIETEN (1830), MÜNSTER (1829), and MERIAN (1835) used the generic name *Rhyncholites* and the latter two named new species, although MERIAN's is a *nomen*

nudum. ROEMER (1836), followed by QUENSTEDT (1852), and OOSTER (1863), published descriptions of additional rhyncholites of Jurassic age. HAGENOW (1842) and MÜLLER (1847) were first to describe rhyncholites of Cretaceous age.

ROEMER (1854) and BÖHM (1912) have described the only nautiloid mandibles known from beds of Paleozoic age in Germany; later BRADY (1955) reported similar occurrences from Lower Permian rocks of the USA (Arizona).

In an important paper published in 1847, D'ORBIGNY named a third new genus belonging to this group of fossils, *Rhyncho-teuthis*, with about a half dozen species (all of Cretaceous age), some new and some reassigned from the old genus *Rhyncholite*. The next new genus included in this group was *Palaeoteuthis* described by D'ORBIGNY in 1850, with but a single species.

Another new genus, *Scaptorhynchus* BELLARDI, 1871 (Miocene, Italy), is strikingly different from all previous ones (Fig. 344,2).

Lengthy papers by TILL (1906, 1907, 1908, 1909, 1910, 1911) contained the new genera *Hadrocheilus*, *Leptocheilus*, *Akidocheilus*, *Gonatocheilus*, and *Mesocheilus* and numerous reassignments of former genera and species. As some authors before him had done, TILL reduced to subgeneric status some of the previously recognized genera of rhyncholites [e.g., *Temnocheilus* (*Rhyncholithes hirundo* BIGUET) and *Nautilus* (*Rhyncholithes giganteus* D'ORBIGNY)], thus linking the names with recognizable nautiloid conchs.

RÜGER (1921), MOOS (1924), and BESSLER (1938) made significant contributions to the knowledge of rhyncholites of Jurassic age in Germany.

SHIMANSKIY (1947, 1949, 1959) further revised genera and species, including those of TILL, naming new genera, subgenera, and species.

RUTTE (1962) recently has reported on some exceptionally well-preserved nautiloid mandibles in the Middle Triassic (Muschelkalk) of Germany. His consideration of the possibility that what he called *Rhyncholithes* (= *Rhyncholite*) is the upper jaw of *Germanonautilus bidorsatus* and *Conchorhynchus* is its lower jaw (Fig. 340) led

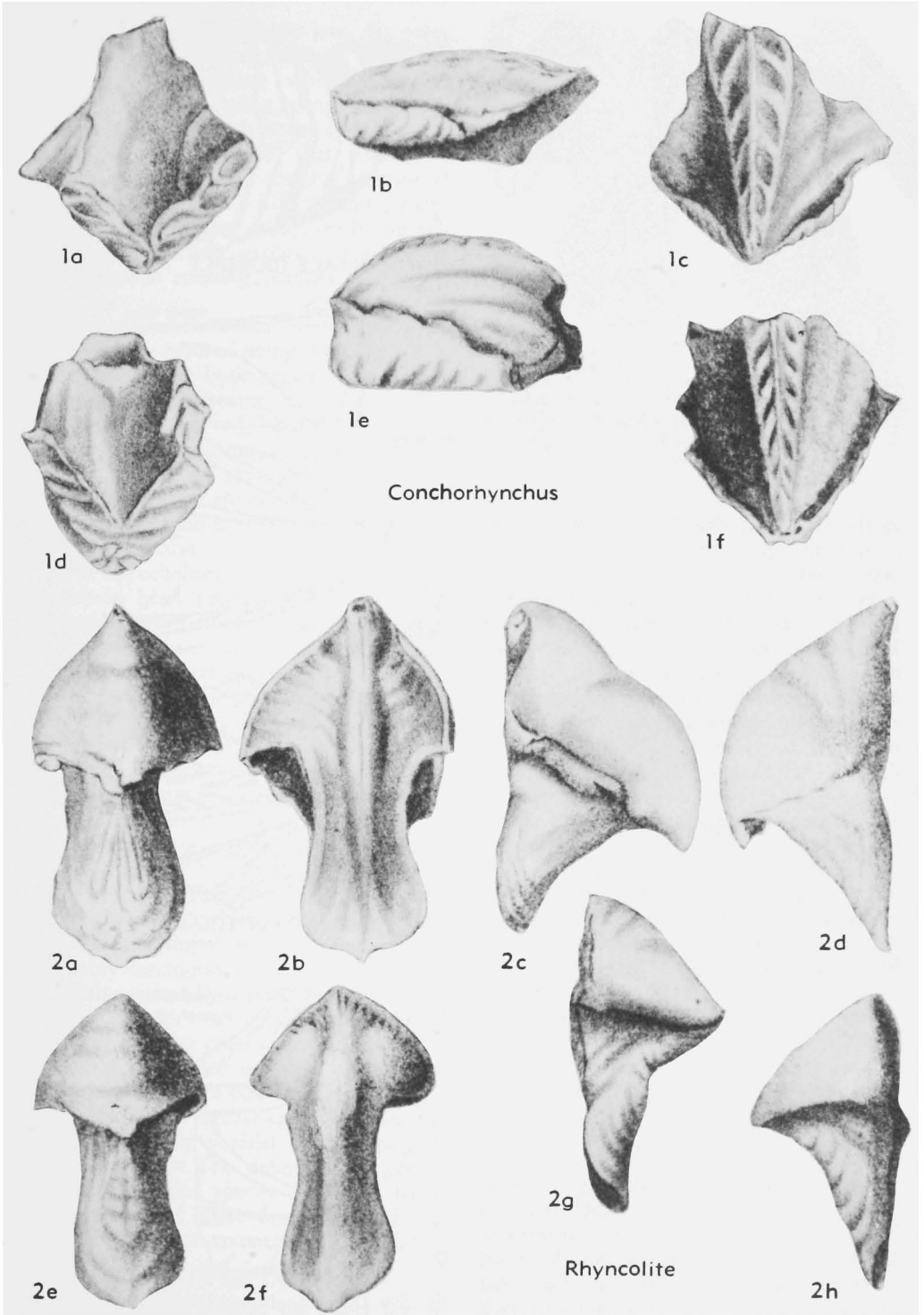


FIG. 338. Rhyncholites figured and described by GAILLARDOT (1824); 1a-f, "première espèce," the new genus **Conchorhynchus* of DE BLAINVILLE, 1827; 2a-h, "seconde espèce," the original **Rhyncholite* of BIGUET, 1819; all $\times 2$ (18) (p. K477-K478).

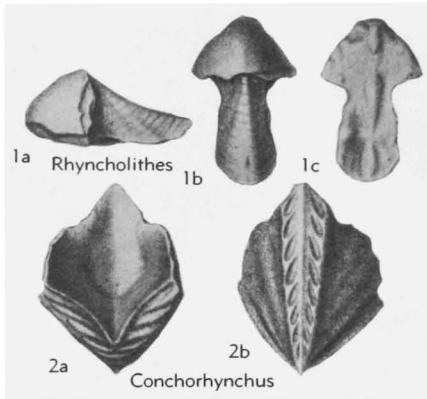


FIG. 339. Rhyncholithes figured and described by DE BLAINVILLE (1827) showing his nomenclature; 1a-c, *Rhyncholithes* (= *Rhyncholite* BIGUET, 1819); 2a, b, *Conchorhynchus*; $\times 0.75$ (7).

to the judgment that this is very probably correct, though complete proof has not yet been produced.

MÜLLER (1851), EUDES-DESLONGCHAMPS (1858), ROLLE (1862), and LAUBE (1868, 1870) described supposed nautiloid mandibles as the genera *Peltarion*, *Cyclidia*, *Scaphanidia*, and *Rhynchidia*; these were subsequently determined to be gastropod opercula by ZITTEL (1884), VINCENT (1900), and TILL (1906-10).

MORPHOLOGY

A description of the main morphological features observed in a study of rhyncholithes is introduced advantageously by observing characters of the upper and lower jaws of living *Nautilus* (Fig. 341, 341A). These have been described by STENZEL in a foregoing chapter on "Living Nautilus" (p. K61, Fig. 44A).

Rhyncholithes vary in size rather widely, since their length or width ranges from 2 or 3 mm. to more than 50 mm.

UPPER JAW

The upper jaw of living *Nautilus* may be compared to a flaring cape which is broadly open toward the front (anteroventral side) and hooded at the top, this hood bearing a turned-back rim or collar that projects above the rounded sides and back (dorsal side) of the cape. The hood is sharply pointed at its peak which forms

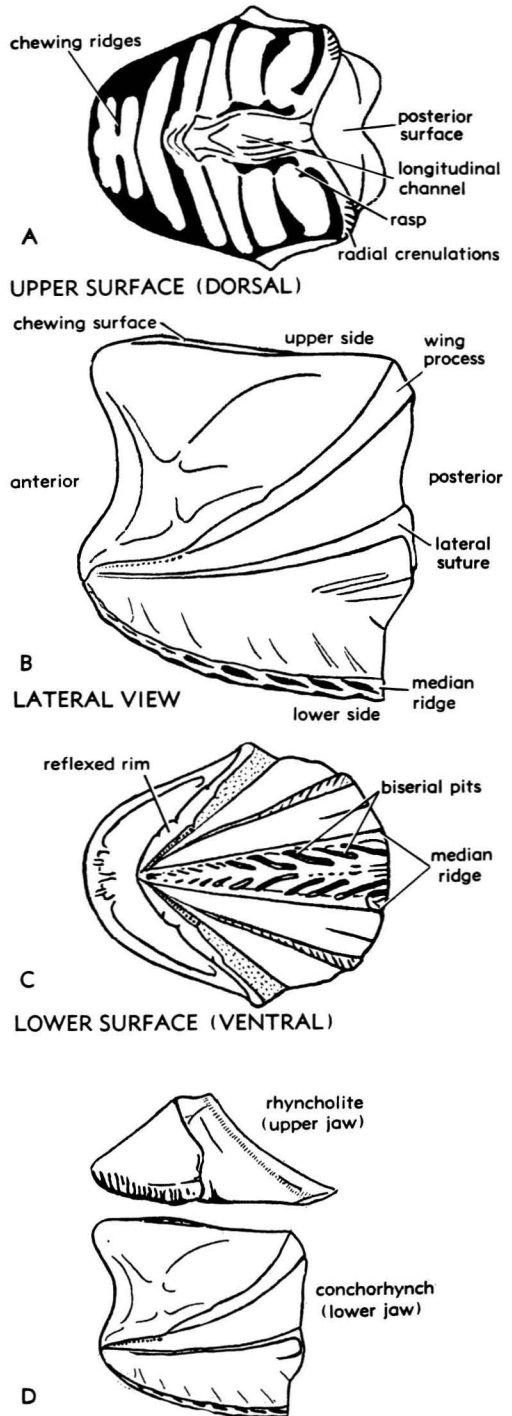


FIG. 340. Diagrams of lower jaw (conchorhynch) in three views (A-C) and of both jaws in side view (D), representing features of cephalopod mandible (41).

the main biting part of the jaw. Its outer portion consists of hard, smooth, shiny calcareous shell substance which covers a relatively soft, somewhat spongy inner calcareous layer. The calcareous structure has a shaftlike prolongation that extends a short distance into the concave interior of the curved upper jaw. All remaining parts, including the reflexed collar, are horny and dark-colored. Their surface is marked by fine striations running parallel to the jaw margins.

Fossil rhyncholites that correspond most closely to jaw parts of living *Nautilus* represent the calcified beak region, but the adjoined horny structures, or "wings," are only rarely preserved. Fossils similar to those described and named by BIGUET (5), now interpreted to represent upper beaks, may be classed as **rhyncholites** in the narrow sense, because it is they which were so named by BIGUET.

Such rhyncholites consist of a rhomboid or deltoid head (termed the **hood**) fixed on a distinctly narrower **shaft** (Fig. 342). The anterior tip of the hood, which constitutes the biting extremity of the jaw, may be irregular or broken in fossil forms. In side view, the shaft appears triangular in outline, with two long sides formed by the dorsal and ventral surfaces and a short side marking the junction of the shaft with the head. The shaft is transversely convex on the dorsal side and gently concave on the ventral side.

According to TILL (48, p. 657), numerous rhyncholites which he considered to represent the upper beaks of cephalopods (probably nautiloids other than *Nautilus*) are distinguished by a hood that is notched on the posterior side opposite the pointed tip, by an angular cross section of the shaft, instead of a rounded one, and by differentiation of the convex side of triple prolongations, one in a median position and the other two nearly parallel or diverging in lateral position. The definition of genera and of numerous species has been based on variations of these features which are presumed to have taxonomic significance.

LOWER JAW

The calcareous part of the lower jaw in living *Nautilus* also bears fine, concentric striae. It is more arcuate and has greater

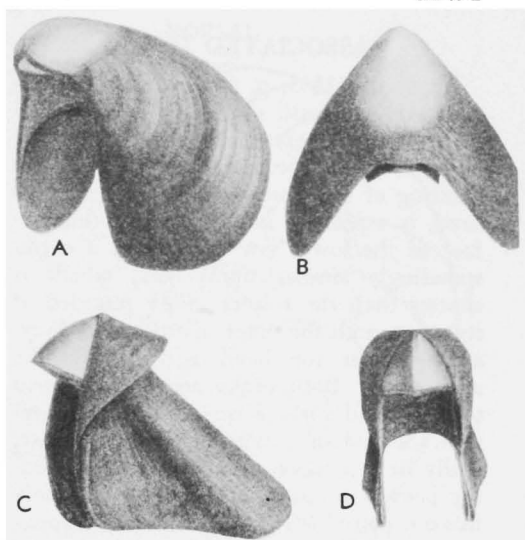


FIG. 341. Mandibles of living *Nautilus*. A,B, lower jaw, lat. and ventral views; C,D, upper jaw, lat. and ventral views, $\times 1$ (47).

breadth and depth than the upper jaw. Its anterior cutting surface is dentated and its posterior extremity opposite the beak is concave. The beak is calcareous, as in the upper jaw, but the calcareous matter is deposited on both sides of a thin layer of horny substance (also concentrically laminated), which would tend to disintegrate in the course of fossilization. Hence, the lower jaws (beaks) occur less commonly as fossils.

A type of rhyncholite that was first described and illustrated by BLUMENBACH (1803) and later named *Conchorhynchus* by DE BLAINVILLE (1827) is inferred to be the preserved part of a lower jaw. Such rhyncholites are termed **conchorhynchs**. They have a broadly scalloped, arcuate outline or a nearly quadrangular shape, without any extension that is interpretable as a shaft (Fig. 339,2). Rhyncholites of this sort, which are extremely rare as compared with those judged to have been structures of upper jaws, resemble a rather thin shell (conch). Some Mesozoic conchorhynchs are distinguished by corrugated margins on the concave side adjacent to the pointed beak and on the convex side by a median keel bordered by acute-angled, short lateral ridges in approximately paired or slightly alternating opposed position.

ASSOCIATED JAWS

MÜNSTER (1843, p. 69) recorded the occurrence of a fossil showing the lower and upper jaws preserved in contact with one another. This specimen, found after the printing of the plate and therefore not figured, is especially interesting. To the surface of the lower jaw is attached a correspondingly similar upper jaw, which is shorter than the former, more rounded at its point, with the outer side not as convex, and without the band with feather-like channeling. Both beaks are firmly joined together and form a quadrangular projection. Should this, as seems to be the case, really be a junction of the two corresponding jaws, it is remarkable that there is only this one paired jaw among at least 150 specimens studied and that no free upper jaw was found among so many lower jaws.

DIMORPHISM

TILL (49, p. 586; 50, p. 424) has suggested the possible occurrence of sexual dimorphism in species of *Hadrocheilus*, because he observed that otherwise very similar forms, found in the same locality, differ only in the length of the shaft.

ONTOGENY

The ontogeny of rhyncholites is little known. TILL (50, p. 413) found that in one species of *Hadrocheilus* the small, presumably younger, specimens are flatter, but are similar in all other proportions to the larger specimens. In another species of the same genus (p. 423) a stronger curvature of the hood seems to occur during ontogeny, accompanied by a broadening of the shaft furrow, and a rounding of the shaft edges.

CLASSIFICATION

Rhyncholites present the same sorts of problems to paleontologists as those which are encountered in studies of conodonts, otoliths, and discrete fragments of several groups of animals found as isolated fossils. That some rhyncholites are remains of genera classifiable in the order Nautilida (although none certainly belonging to *Nautilus*) can hardly be doubted. Several

records of such an association have been reported (see chapter on "Biostratonomy"). Classification and nomenclature of rhyncholites in terms of parataxa would be suited for work on these fossils but cannot be accepted in the *Treatise* because (1) parataxa have not been sanctioned by international Rules and (2) authors have consistently treated rhyncholites as objects appropriate for recognition as natural taxa. Among these, at the generic level, are some rhyncholites which were presumed to belong to *Nautilus*, *Temnocheilus* (*recte Peripetoceras*), *Germanonautilus*, *Somalinautilus*, *Cenoceras*, *Hercoglossa*, *Pseudonautilus*, *Aturia*, and numerous others as questionably identified forms. BÖHM (9) referred a late Permian rhyncholite (*Conchorhynchus*) to the nautiloid species *Temnocheilus Freieslebeni* (GEINITZ) (= *Peripetoceras freieslebeni*), because this was the only nautiloid known in strata containing the rhyncholite. The rhyncholite was then designated as *Temnocheilus* (*Conchorhynchus*) *Freieslebeni* GEINITZ. Another rhyncholite distinguished as *Conchorhynchus avirostris* (SCHLOTHEIM), from the Triassic, was similarly referred to *Nautilus* or *Temnocheilus bidorsatus* VON SCHLOTHEIM (subsequently made the type-species of *Germanonautilus* by MOJŠISOVICS, 1902). It is noteworthy that these identifications rest solely on assumptions that the Permian and Triassic rhyncholites cited must belong to the indicated species previously described on the basis of conchs, because the latter happen to be the only nautiloids known to occur in proximity with the rhyncholite fossils. Obviously, such evidence has value only as support for a guess.

Accordingly, rhyncholites having morphological resemblance to the jaw parts of living *Nautilus* are herein designated by the generic name *Rhyncholite* BIGUET, but this name is not considered to be a synonym of *Nautilus*. The fossils classed as rhyncholites are assigned to no family and are not definitely included in the order Nautilida, even though some seem to belong there. CHENU (1859) established a family, Palaeoteuthidae, to include all rhyncholites known up to that time, as well as the "genre aptychus," in addition. In view of the difficulties experienced in determining the relationships between various groups of

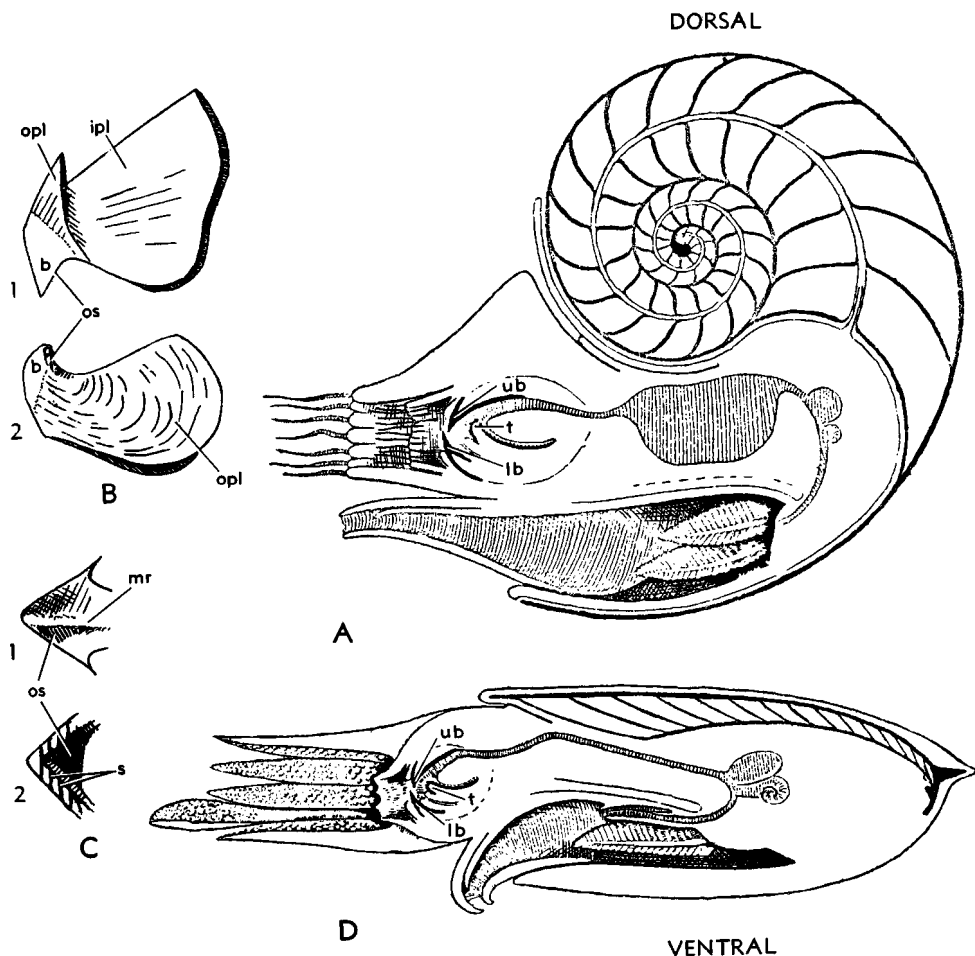


FIG. 341A. A. Schematic median sec. of *Nautilus pompilius* showing placement of upper and lower beaks in relationship to body organs; *ub*, upper beak, *lb*, lower beak, *t*, tongue (Compare Fig. 44A).—B. Jaws of *N. pompilius*, lat. view; 1, upper jaw showing beak (*b*), occludent surface (*os*), outer plate (*opl*) (exposed), and inner plate (*ipl*) (covered by muscle tissue and cartilage); 2, lower jaw showing beak (*b*), occludent surface (*os*), and outer plate (*opl*) (inner plate on lower jaw is completely covered by outer plate).—C. Enlarged diagrammatic representation of occludent surfaces of upper and lower beaks, 1, showing median ridge (*mr*) on upper beak, 2, showing serrations (*s*) on lower beak (occludent surface, *os*).—D. Schematic median sec. of *Sepia* sp. showing position of beaks for comparison with those in *Nautilus* (letter symbols as in A); (adapted from 27a) (p. K470).

rhyncholites and between them and shell-bearing cephalopods, we judge that grouping of rhyncholites into one or more families would be an artificial procedure.

RELATIONSHIPS

The most detailed discussion of systematic relationships of the fossils known as rhyncholites has been published by SHIMANSKIY (45). He noted that some nominal genera considered by their authors

to be rhyncholites almost certainly belong to mollusks other than cephalopods (e.g., Gastropoda, Amphineura) and these may be dismissed from attention. The description of a conchorhynch-type of rhyncholite by VON SCHLOTHEIM (1820) under the name *Lepadites avirostris* can be accepted as validly establishing this species, but the reference of it to BLUMENBACH'S (1803) nominal genus of cirripeds can be regarded as merely an interesting, curious mistake. BIGUET (1819), DE BLAINVILLE (1827), and

ZIETEN (1830) were of the opinion that rhyncholites were hard parts located somewhere in the soft body of supposed dibranchiate cephalopods, for the fossils were found in belemnite-bearing Mesozoic strata and their dark color and apparently fibrous microcrystalline structure resembled characters of belemnoid rostra. GAILLARDOT (1824) interpreted the rhyncholites studied by him as almost surely fossilized jaw parts of *Sepia*-type cephalopods, if not of *Sepia* itself.

D'ORBIGNY (1825) was first to suggest that some rhyncholites may belong to the "genus *Nautilus*," and stated (1847) that some (*Rhynchoteuthis*) had been placed by him in the belemnites ("Céphalopodes Acétabulifères"). Although ammonoids are extremely abundant in many Triassic, Jurassic, and Cretaceous deposits which yield rhyncholites, none of the latter have ever been found in an ammonoid conch.

OWEN (1832, *Memoir on the Pearly Nautilus*, p. 21), after an excellent description of the jaws of modern *Nautilus*, concluded: There are, however, certain fossils called *Rhyncholites*, formerly considered to be the beaks of fossil birds, but recognized by Blumenbach as appertaining rather to the Cephalopods, although evidently differing from all the recent genera then known. M. d'Orbigny having invariably met with a large kind of these *Rhyncholites* in the same stratum with the fossil shell of a large *Nautilus* (*Nautilus gigas*), suspected from the circumstance that they might be the mandibles of that species (see his Memoir in the *Ann. des Sci. Nat.*, v. [5], p. 241, pl. 6). The calcareous extremities of the mandibles of *Nautilus pompilius*, and peculiarities of their form, especially the flattened superior surface of the upper mandible, fully confirm that conjecture, and at the same time show that a small portion only of the beak is represented by the fossil.

In 1849, D'ORBIGNY (*Cours Élémentaire de Paléontologie et Géologie*, p. 281) grouped some genera of rhyncholites (e.g., *Conchorhynchus*, *Rhynchoteuthis*, *Palaeoteuthis*) in a separate category of his classification of cephalopods, placing them neither in the so-called dibranchiates nor in the tetrabranchiates. On the other hand, in 1843, this author (*Paléontologie Française, Description des Mollusques et Rayonnes Fossiles, Terrains Jurassiques*, p. 163, pl. 39, 40) had unqualifiedly assigned *Rhyncholites gigantea* D'ORBIGNY, 1825, to *Nautilus giganteus* D'ORBIGNY, 1825, and

illustrated rhyncholites as "*Bec de Nautilus giganteus*" and "*Bec de Nautilus lineatus* Sow."

FOORD (1891, *Catalogue of fossil Cephalopoda*, p. 364), in agreement with OWEN, wrote:

The resemblance between the calcareous extremity of the upper mandible of *Nautilus pompilius* . . . and the corresponding fossil mandibles . . . will not be disputed. There seems to be, therefore, sufficient evidence upon which to rest the assumption that the fossil mandibles referred to belonged to the genus *Nautilus*. They do, indeed, vary in detail; but such variations may be significant of specific, rather than of generic differences in the animals to which the beaks belonged, or they may be due simply to difference in age.

TILL (1906, and later comprehensive papers) divided the rhyncholite genera and species studied by him into "*Nautilus-Schnäbel*" and "*Nicht-Nautilus-Schnäbel*" or "*Nicht-Nautilus-Rhyncholithen*."

RÜGER (40) expressed doubts about the suggested affinity of rhyncholites with genera of Nautilidae. He pointed out that rhyncholites appear in significant numbers first in Triassic rocks at a time when nautiloid cephalopods were declining, and that a discrepancy generally exists between the number of rhyncholites and the number of nautilid shells in rocks of this age. RÜGER suggested that the so-called "*Nautilus beaks*" of TILL did not belong to nautilids, ammonites, or belemnites, but to an unknown cephalopod group from which no other parts have been found preserved. These hypothetical cephalopods were interpreted to have been comparatively rare in numbers of individuals, though diversified into many genera and species. For the Lower Jurassic rhyncholites studied by him, RÜGER concluded that their bearers had no shells and were adapted to a benthonic life.

Opposed to RÜGER's views, Moos (25) pointed out that TILL's "*Nautilus beaks*" are highly peculiar and specialized organs which admittedly are very similar to the beaks of modern *Nautilus*. He found it difficult to believe that such specialized structures would have developed independently in two entirely different lineages of cephalopods.

BESSLER (4) believed that *Hadrocheilus* beaks did not belong to ammonoids or belemnites, because if they did they could

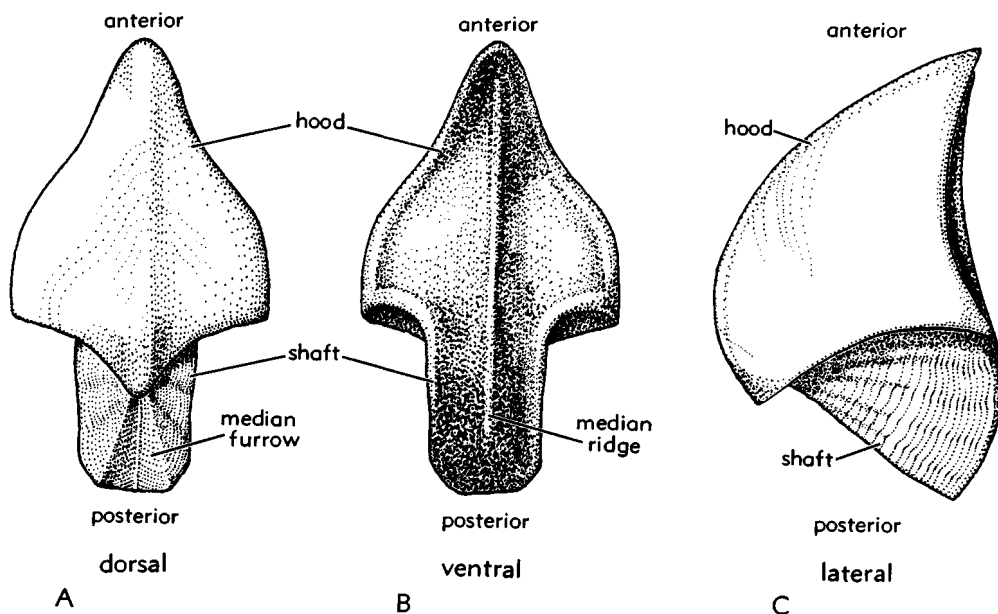


FIG. 342. Rhyncholite terminology. *A*, dorsal view; *B*, ventral view; *C*, lateral view (Teichert, Moore, & Zeller, n).

be expected to be much more common in Jurassic deposits. The first appearance of *Hadrocheilus* coincides approximately with that of the Chitinotheuthidae. However, this group is restricted to the Middle Lias, whereas *Hadrocheilus* persists into the Upper Cretaceous. He also expressed the opinion that the "not-*Nautilus* beaks" belong to cephalopods lacking other hard parts and with soft body parts as yet unknown. He concluded (apparently in agreement with RÜGER, 40, and MOOS, 25) that the present distribution of "not-*Nautilus* beaks" may be assumed to indicate the approximate range of distribution of the animals to which they belonged and that their relative abundance probably indicated population density.

SHIMANSKIY (45) undertook to analyze evidence for and against four hypotheses with respect to the relationships of rhyncholites. These were that (1) only nautiloids are represented by these sorts of fossil remains; (2) only external-shelled, supposed tetrabranchiate cephalopods (nautiloids and ammonoids) produced rhyncholites; (3) in addition to nautiloids and possibly ammonoids, some supposed dibranchiates (belemnoids) gave rise to rhyncholites; and

(4) nautiloids and some unknown types of shell-less cephalopods are the animals to which rhyncholites belonged.

Among suggestive observations reviewed by SHIMANSKIY is the reported occurrence of some 250 belemnoid rostra in the stomach contents of a Liassic fish without a single associated rhyncholite. Clearly, these ingested belemnites must have lacked fossilizable jaw parts. Also, it must be significant that in none of the rather numerous ammonoid conchs which have been discovered with aptychi remaining in the apertural region has a rhyncholite been found. The record of a fossil collection from a single Jurassic locality (Verkhni-Rechensk) in the USSR in which some 10,000 belemnoid rostra, 2,000 ammonoids, and miscellaneous other remains are associated with 150 rhyncholites, but in which no specimen of nautiloid is found, lacks significance, especially in view of the much-too-small size of the belemnoid rostra in comparison with the moderately robust rhyncholites. It is sufficient to report SHIMANSKIY's conclusion that only negative evidence can be adduced for support of any of the hypotheses advanced by him, but he was able to exclude probabilities that rhyncholites are hard parts

of cephalopods other than nautiloids and soft-bodied forms without an external or internal skeleton. That is to say, ammonoids and belemnoids were not thought by him to be organisms represented by remains classed as rhyncholites. An effort to correlate the known stratigraphic distribution of different sorts of rhyncholites with nautiloid genera having like range is interesting and suggestive, but not more than that. The known facts are best accommodated by the interpretation that rhyncholites were formed by unknown cephalopods, some of which probably belong to the Nautilida. These unknown cephalopods are classifiable in terms of genera and species based on the characters of their rhyncholite remains.

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION

The great majority of all rhyncholites are known from rocks of Mesozoic age in France, southern Germany, southern Poland, and the southern part of the European USSR. They are generally rare fossils and occurrences of more than a few individuals in any one locality are unusual.

In pre-Mesozoic rocks rhyncholites do exist, but they are even more rare, only three specimens having been made known from the Carboniferous and Permian Systems: *Tillicheilus? sella* (ROEMER), doubtfully recorded from the Lower Carboniferous of Germany, *Rhynchoteuthis kaibabensis* BRADY from the Lower Permian of Arizona (USA), and an unnamed *Conchorhynchus?* from the Upper Permian Kupferschiefer of Germany. The specimens described from the Permian of Arizona are the more remarkable in that they are the only rhyncholites so far recorded from the Western Hemisphere. A suggestion made by TILL (48, p. 148) that *Aptychus? knoxvillensis* STANTON (1895) from the Cretaceous of California may be a rhyncholite is rejected by us.

The only rhyncholites of Mesozoic age known outside of Europe are *Hadrocheilus kossmati* TILL (50) and *Rhynchoteuthis sonii* SAHNI & JAIN (41a) from the Upper Cretaceous of southern India and *Hadrocheilus costatus* TILL from the Lower Cretaceous of Algeria (46a). In addition,

rhyncholite- and conchorhynch-type beaks have been described from the Eocene of Egypt (51).

The reasons for the geographically restricted distribution of rhyncholites are not clear, but perhaps this distribution pattern is more apparent than real. Additional finds in Asia may be expected which would materially affect the present picture.

PALEOECOLOGY

GASIOROWSKI (19) found rhyncholites in the Jurassic-Cretaceous Klippe zone of the Carpathian Mountains to be restricted to rocks thought to have been deposited in deep water; among these rocks are radiolarites and nodular limestones with and without calpionellids. From these observations one might conclude that the cephalopods from which the rhyncholites came were essentially eupelagic. It is interesting to compare this observation with reports of mass occurrences of cephalopod beaks in the deeper parts of the Arabian Sea and the Gulf of Aden, where up to 15,000 beaks per square meter have been dredged up (14).

On the other hand, many jaw-bearing cephalopods undoubtedly lived in shallow water as shown by the occurrence of rhyncholites in the German Muschelkalk.

BRADY (10, p. 102), in discussing a collection of specimens of *Rhynchoteuthis* from the Kaibab Limestone of southern Arizona (USA), wrote:

David Nicol (1944, p. 553) describes the strata from which the material here described was collected as 'thin bedded dolomites, dolomitic sandstone . . .' and believes that they represent deposits in shallow, landlocked and somewhat hypersaline seas, and that the nautiloids were swept into these sediments by waves or currents. He recognized, however, the possibility that they may be true facies fossils, species which had adapted themselves to conditions somewhat abnormal for such cephalopods.

It is significant that all of the specimens in question were collected in the particular horizon near the top of the formation from which almost all the nautiloids of the Kaibab have come.

BIOSTRATONOMY

After the death of a jaw-bearing cephalopod, the jaws and soft parts would sink to

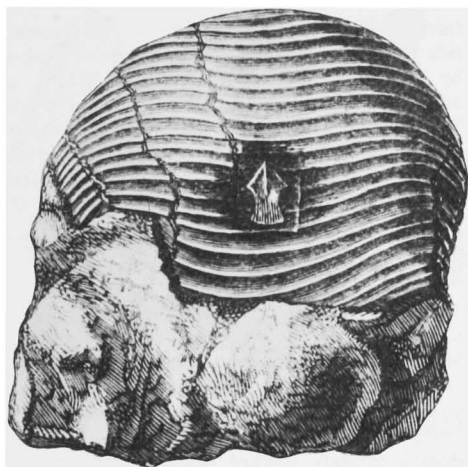


FIG. 343. *Somalinautilus libanoticus* (FOORD & CRICK), U.Cret., Lebanon, with rhyncholite preserved in ventral side of body chamber, $\times 1$ (17) (p. K477).

the bottom and, if the cephalopod possessed a shell, this very likely would become separated from the jaws. Several nautilid shells with rhyncholites embedded in the matrix filling their body chambers are on record, but few of these specimens have ever been described adequately. Thus, BUCKLAND (12) mentioned "a specimen of a fossil *Nautilus* from the Lias of Lyme Regis [England] in which the external open chamber contains a rhyncholite." FOORD (17) reported that the British Museum possessed five specimens of *Nautilus* (recte *Somalinautilus*) *libanoticus* from the Upper Cretaceous of Lebanon (of which he figured one¹), "exhibiting the mandibles associated with the shell, and in each example there is a brownish stain surrounding the mandible caused, no doubt, by the decay of animal matter." All beaks are exposed on the surface of the internal mold on the ventral side of the body chamber (Fig. 343). Additional information is lacking. As far as one can judge, all five "mandibles" are upper jaw parts and no lower jaw parts are present. TILL (51) referred to "*Nautilus*" shells with rhyncholites in their body chambers deposited in the Senckenberg Museum, Germany, but he failed to give age(s) and localities.

As a rule it may be expected that the jaws and soft parts attached to them would sink

¹ According to L. R. Cox (personal communication), preserved in the British Museum (Natural History).

slowly through the water. If currents existed in the water body, they would carry the slowly sinking cephalopod remains a variable distance. Lower beaks of the *Conchorhynchus* type, as shown by RUTTE (41), have horny parts that are larger than those of upper beaks; thus, the two jaws might become separated on their downward journey to the sea floor.

TILL (47) has observed that, on drying, the calcareous part of an upper beak of Recent *Nautilus* broke away from the horny parts, whereas the calcareous part of the lower beak disintegrated into small particles. This observation may account for the fact that remains of lower beaks (conchorhynchus) are much rarer as fossils than those of upper beaks (rhyncholites). RUTTE (41) found that specimens of *Conchorhynchus* in marl were embedded either lying on their sides or with the median ridge pointing upward.

TILL (50) reported that in rhyncholites of *Rhynchoteuthis* type (with dorsal furrow) the hood breaks away easily from the shaft. The posterior edges of such hoods are almost always broken. Chipping and breaking during transportation and sedimentation may considerably affect the shape of rhyncholites.

Possible horizontal transportation of cephalopod jaw parts after death of the animal, as previously suggested, must have been relatively small. Therefore, the present distribution of rhyncholites in deposits of any given age may be presumed to coincide approximately with the range of the cephalopods to which they belonged. Furthermore, since rhyncholites are not easily destroyed during sedimentation or diagenesis, abundance of these fossils in sedimentary rocks may reflect the relative population density of their bearers (4, 25, 40).

SYSTEMATIC DESCRIPTIONS

Class CEPHALOPODA Cuvier, 1797

Order and Family UNCERTAIN

[Arrangement of genera is in chronological order of their description]

Rhyncholite BIGUET, 1819, p. 58 [**R. hirundo*; SD TEICHERT, MOORE & ZELLER, herein] [= *Rhyncholites* D'ORBIGNY, 1825, p. 212; *Rhyncholithes* DE

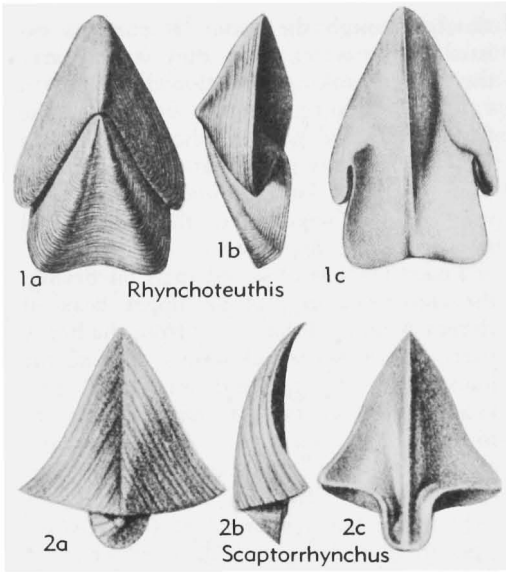


FIG. 344. Rhyncholites. 1, *Rhynchoteuthis astieriana* D'ORBIGNY, $\times 1$ (32). 2. **Saptorrhynchus miocenicus* BELLARDI, $\times 2$ (2) (p. K478-K479).

BLAINVILLE, 1827, p. 114 (obj., type, *R. hirundo*—*lapsus pro R. hirundo*—BIGUET, 1819, p. 59); *Rhyncholites* ZIETEN, 1830, p. 49 (type, *R. hirundo* BIGUET, 1819; SD TEICHERT, MOORE & ZELLER, herein); *Rhyncholites* MÜNSTER, 1829, p. 70 (*nom. null.*) (type, *R. duplicatus*; M); *Rhyncholithus* BRONN, 1853, p. 180 (obj., type, *R. hirundo* BIGUET, 1819; SD TEICHERT, MOORE & ZELLER, herein); *Rhyncholythes* BELLARDI, 1873, pl. 3 (*nom. null.*); *Rhombocheilus* SHIMANSKIY, 1947, p. 1476 (obj.); *Nautilorhynchus* FRIČ, 1910, p. 15 (*nom. null.*); *Longocapuchones* SHIMANSKIY, 1947, p. 1476 (type *Rhyncholites gigantea* D'ORBIGNY, 1825, p. 215)]. Inferred upper beak with relatively broad rhomb-shaped hood, elevated median upper part rounded to keel-like, lower surface gently concave, shaft convexly rounded dorsally, concave ventrally, triangular in side view. *M.Trias.-Mio.*, Eu.-Afr.(Egypt).—FIG. 338,2. **R. hirundo*, *M.Trias.*, Eu.(Fr.); 2a-h, upper (dorsal), lower (ventral), and lateral views of 2 specimens, $\times 2$ (18).

Conchorhynchus DE BLAINVILLE, 1827, p. 115 [**C. ornatus* (= *Lepadites avirostris* VON SCHLOTHEIM, 1820, p. 169; “première espèce” GAILLARDOT, 1824, p. 485; *Rhyncholites Gaillardoti* D'ORBIGNY, 1825, p. 219; *Rhyncholites Gaillardoti* ZIETEN, 1830, p. 49; *Sepia Gaillardoti* KEFERSTEIN, 1834, p. 53; *Conchorhynchus avirostris* BRONN, 1837); OD(M)] [= *Onchorhynchus* OPPENHEIM, 1906, p. 346 (*nom. null.*); *Conchorhynchus* TILL, 1906, p. 91 (*nom. null.*)]. Inferred lower beak, subrhombic in outline, thin, upper (dorsal) side gently concave, surface sloping to shallow median

furrow, edges near tip corrugated; lower (ventral) side transversely slightly convex, mid-line marked by keel with short side ridges that diverge at acute angle from keel. *U.Perm.-M.Trias.*, Eu.; ?*L. Tert.(Eoc.)*, Eu.(Belg.)-Afr.(Egypt).—FIG. 338, 1. **C. avirostris* (VON SCHLOTHEIM), *M.Trias.*, Eu.(Fr.); 1a-f, upper (dorsal), lat., and lower (ventral) views of 2 specimens, $\times 2$ (18).

[The zoological Code (Art. 30,a,i,3) classes generic names with endings in *-us*, based on latinized Greek words of feminine or neuter gender (e.g., *-rhynchus*, *-cheilus*), as having masculine gender.]

Rhynchoteuthis D'ORBIGNY, 1847, p. 593 [**R. astierianus* D'ORBIGNY, 1847, p. 598; SD TEICHERT, MOORE & ZELLER, herein] [= *Rhyncholites* AUCTT. (*non* CHUN, 1903, p. 716); *Rhynchoteuthis* COLLINGE, 1893 (*nom. null.*); *Rhynchoteuthis* TILL, 1906, p. 133 (*nom. van.*)]. Head arrowhead-shaped, strongly notched opposite point and set off from shaft by relatively deep and narrow indentation, upper (dorsal) side with median part narrowly rounded, lower (ventral) side marked by keel that extends onto shaft, which is moderately broad and short, with dorsal side marked by diverging curved ridges having well-rounded summits, median area shallowly depressed, sides steep-sloping, ventral side of shaft divided into 2 gently concave areas. [SHIMANSKIY's (44, p. 1476) designation of *R. astierianus* as the type-species of *Hadrocheilus* TILL, 1907, is invalid because this species was not listed by TILL among forms originally assigned by him to *Hadrocheilus*.] *L.Perm.*, N.Am.(Ariz.); *L.Jur.(Lias.)-U.Cret.(Senon.)*, Eu.; *U.Cret.(Cenoman.)*, Asia(India).—FIG. 344,1. **R. astieriana*, *L.Cret.(Apt.)*, Eu.(Fr.); 1a-c, dorsal, lat., ventral views, $\times 1$ (32).

Palaeoteuthis D'ORBIGNY, 1849, p. 281 [**P. Honoratianus* D'ORBIGNY, 1849 (1850), p. 327; SM] [*non Palaeoteuthis* ROEMER, 1855; *nec* AMEGHINO, 1889] [= *Palaeoteuthis* TILL, 1906, p. 91 (*nom. van.*)]. Hood triangular, somewhat rounded at anterior tip; median furrow on dorsal side extending almost one-half distance from tip to base; shaft broad and short; prominent median ridge extending along entire ventral surface. *M. Jur.(Callov.)*, Eu.(Fr.).—FIG. 344A. **P. honoratianus*; 1a-c, dorsal, lat., and ventral views, $\times 4$ (14a).

[Original description (in D'ORBIGNY's *Cours Élémentaire*, 1849, p. 281): “*Palaeoteuthis*, d'Orb., 1847. Bec voisin des *Rhynchoteuthis* mais bien plus étroit, très-pointu, lancéolé en avant, sans ailes latérales, pourvu seulement d'un talon postérieur, plus large que reste. Une seule espèce connue est de l'étage callovien.” No illustration was given and no species was named. Subsequently, in the *Prodrome de Paléontologie*, bearing date of 1849 but published in 1850, a nearly identical description was given (33, p. 327), accompanied by the notation: “*Honoratianus* d'Orb., 1847. La seule espèce connue. France, Chaudon (Basses-Alpes).” This is thus the type by subsequent monotypy. The type was redescribed and illustrated by COTTREAU (14a, 14b) in the *Annales de Paléontologie* (t. 8, fasc. 4, 1913; t. 14, fasc. 4, 1925). The type-specimen (no. 3154) still exists in the d'Orbigny Collection in the Muséum National d'Histoire Naturelle (personal communication from Mme. S. Freneix, Muséum National d'Histoire Naturelle, Paris, to L. R. Cox.)]

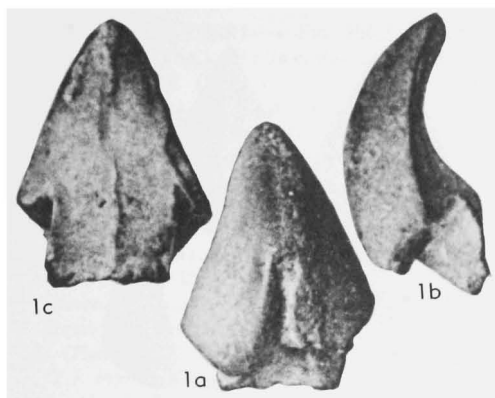


FIG. 344A. **Palaeoteuthis honoratianus* D'ORBIGNY, $\times 4$ (14a).

Scaptorhynchus BELLARDI, 1871, p. 12 [**S. miocenicus*, 1873, p. 42; SM] [= *Scaptorhynchus* ZITTEL, 1885, p. 387 (*nom. null.*)]. Hood thin, narrowly triangular, lateral margins slightly sinuate, posterior edge knife-sharp, slightly sinuate, bowing outward near tip and inward near posterolateral corners, dorsal side convex but with narrow longitudinal furrow, ventral side concave except for straight, prominent median keel; shaft narrow and very short, on dorsal side separated from hood by suture-like depression but on ventral side continuous with hood and its keel. *Mio.*, Eu. (Italy).—FIG. 344,2. **S. miocenicus*;

2a-c, dorsal, lat., ventral sides of upper beak, $\times 2$ (2). [See note under *Conchorhynchus*.]

Hadrocheilus TILL, 1907, p. 568 [**H. Theodosiae*, p. 586; SD TEICHERT, MOORE & ZELLER, herein] [As noted under *Rhynchoteuthis*, SHIMANSKIY'S (44, p. 1476) designation of *R. astierianus* D'ORBIGNY, 1847, as type-species of *Hadrocheilus* is invalid]. Head arrow-like, posterior margin strongly notched, dorsal side with moderately steep slopes from rounded median ridge, ventral side gently concave, with narrow keel that extends onto shaft; shaft large and wide, dorsal side clearly divided into 3 areas by diverging slightly curved ridges that extend from center of notch in hood to posterolateral extremities of shaft, median area gently concave. *Jur.-Cret.*, Eu.-USSR; *L.Cret.*, Afr. (Algeria). [See note under *Conchorhynchus*.]

H. (Hadrocheilus). Longitudinal profile wavy on lower (ventral) side. *Jur.-Cret.*, Eu. (Ger.-USSR). —FIG. 345,1. **H. (H.) theodosiae*, U.Jur. (Tithon.), Crimea; 1a-c, dorsal, lat., ventral views, $\times 2$ (48).

H. (Arcuatobeccus) SHIMANSKIY, 1947, p. 1476 [**Hadrocheilus procerus* TILL, 1907, p. 606; OD]. Ventral side of hood somewhat concave. *Jur.-L.Cret.*, Eu. (Fr.-USSR). —FIG. 345,2. **H. (A.) procerus* TILL, *L.Cret.* (Neocom.), Fr.; 2a-c, dorsal, lat., ventral sides, $\times 2$ (48).

H. (Convexiterbeccus) SHIMANSKIY, 1947, p. 1476 [**Hadrocheilus convexus* TILL, 1907, p. 576; OD]. Longitudinal profile uniformly convex on

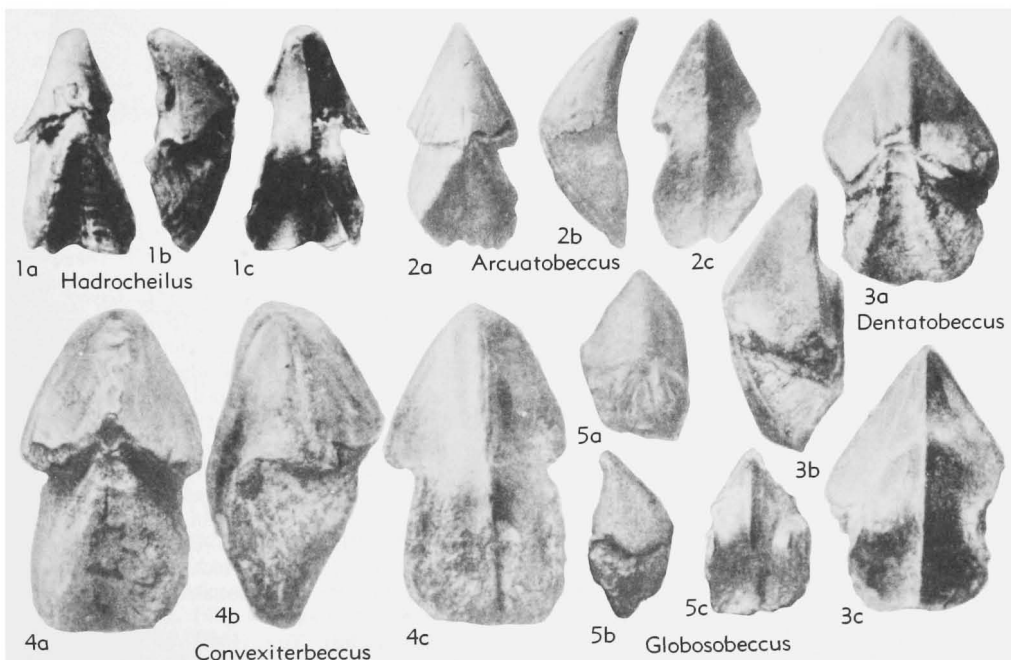


FIG. 345,1-5. Rhyncholites, $\times 1.5$ (48, 49) (p. K479-K480).

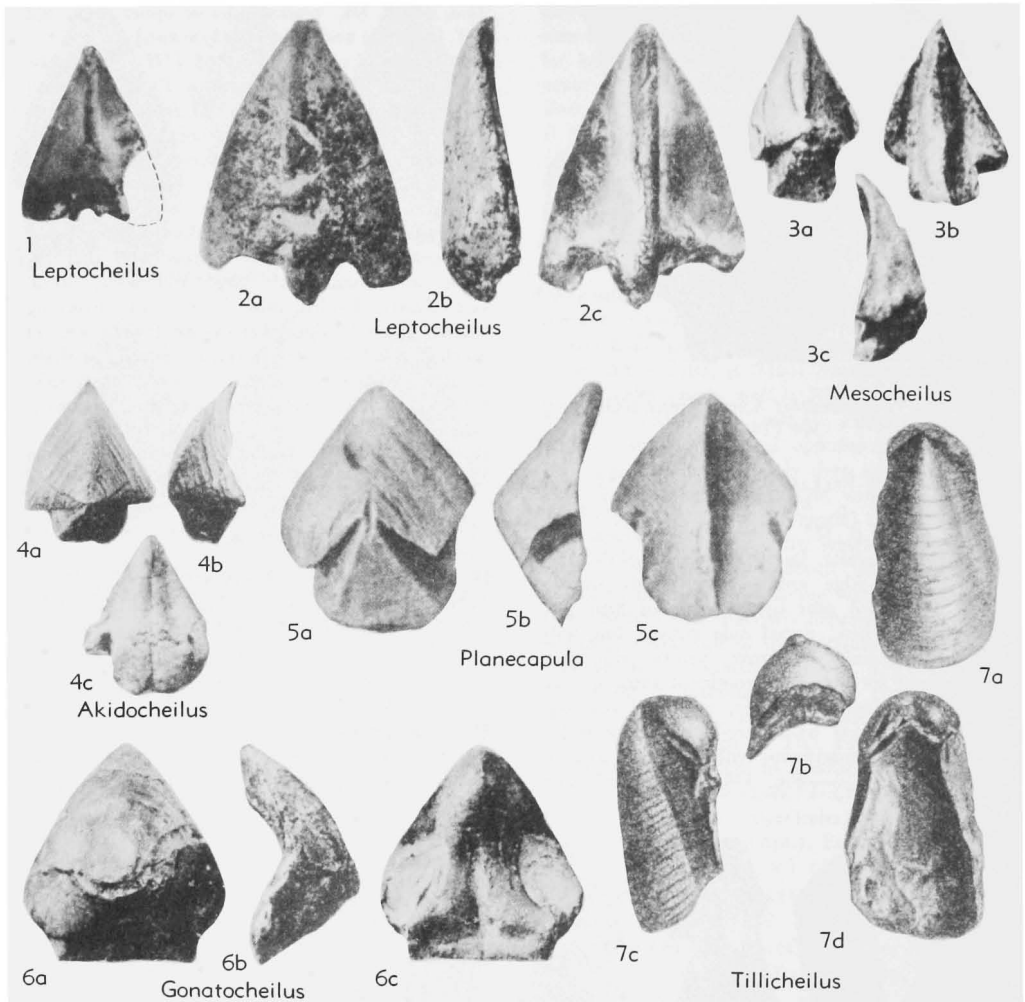


FIG. 346,1-6. Rhyncholites, $\times 1.5$ (44, 48, 49) (p. K480-K481).

ventral side. *L.Cret.(Neocom.)*, Eu.(Fr.-USSR).
 —FIG. 345,4. **H. (C.) convexus* TILL, Fr.;
 4a-c, dorsal, lat., ventral sides, $\times 2$ (48).

H. (Dentatocheilus) SHIMANSKIY, 1947, p. 1476
 [**Hadrocheilus gibber* TILL, 1907, p. 590; OD].
 Ventral side with strong, sharp, generally wide
 toothlike outgrowth beneath middle of hood or
 its apex. *M.Jur.-L.Cret.*, Eu.(Fr.-USSR).—FIG.
 345,3. **H. (D.) gibber* TILL, *L.Cret.(Neocom.)*,
 Fr.; 3a-c, dorsal, lat., ventral sides, $\times 2$ (48).

H. (Globosobeccus) SHIMANSKIY, 1947, p. 1476
 [**Hadrocheilus globosus* TILL, 1909, p. 585;
 OD]. Both dorsal and ventral sides strongly
 convex, whole upper beak subspheroid. *L.Jur.-*
M.Jur., Eu.(Fr.-USSR).—FIG. 345,5. **H. (G.)*
globosus TILL, *L.Jur.*, Fr.; 5a-c, dorsal, lat.,
 ventral sides, $\times 2$ (49).

Leptocheilus TILL, 1907, p. 617 [**L. Geyeri*; SD
 SHIMANSKIY, 1947, p. 1477]. Thin, with arrow-
 head-like hood bearing well-defined longitudinal
 median rib on dorsal side, shallowly concave
 ventral side also with longitudinal keel; shaft small,
 sulcate in transverse section. *M.Jur.-L.Cret.*, Eu.
 (Fr.-Aus.-USSR).

L. (Leptocheilus). Shaft very diminutive, less
 than half length of hood and much narrower.
M.Jur.-L.Cret., Eu.(Fr.-Aus.-USSR).—FIG.
 346,1. **L. (L.) geyeri*, U.Jur., Austria; dorsal
 side, $\times 2$ (48).—FIG. 346,2. *L. (L.) excavatus*
 TILL, U.Jur., Fr.; 2a-c, dorsal, lat., ventral sides,
 $\times 2$ (48).

L. (Mesocheilus) TILL, 1909, p. 601 [**Meso-*
cheilus proceroides; SD SHIMANSKIY, 1947, p.
 1477]. Shaft nearly equal to hood in length.

M. Jur., Eu. (Fr.-USSR).—FIG. 346,3. **L. (M.) proceroides* (TILL), Fr.; 3a-c, dorsal, ventral, and lat. sides, $\times 2$ (49).

Akidocheilus TILL, 1907, p. 629 [**A. ambiguus*; OD]. Like *Leptocheilus* but dorsal side of hood smooth and shaft, though short, notably wider, ventral side concave, with low median keel on hood and with or without narrow furrow on shaft. *M. Jur.-L. Cret.*, Eu. (Fr.-USSR).

A. (Akidocheilus). Shaft with furrow. *M. Jur.-L. Cret.*, Eu. (Fr.-USSR).—FIG. 346,4. *A. (A.) tauricus* TILL, U. Jur., USSR (Crimea); 4a-c, dorsal, lat., ventral sides, $\times 2$ (48).

A. (Planecapula) SHIMANSKIY, 1947, p. 1477 [**A. (P.) infirus*; OD]. Shaft without furrow, its dorsal side flat. *L. Cret.*, Eu.—FIG. 346,5. **A. (P.) infirus*, Apt., USSR (Crimea); 5a-c, dorsal, lat., ventral sides, $\times 1.3$ (44).

Gonatocheilus TILL, 1907, p. 641 [**Rhynchotethis Brunneri* OOSTER, 1857, p. 6; OD]. Hood thin, sharp-pointed, heart- to arrowhead-shaped, dorsal side smooth, ventral side concave, with strong tooth near anterior extremity; shaft thin, moderately broad, nearly concealed by hood in dorsal view, ventral side with narrow fissure-like groove. *M. Jur.-L. Cret. (Apt.)*, Eu. (Ger.-Fr.)-USSR (Crimea).—FIG. 346,6. **G. brunneri* (OOSTER), U. Jur., Fr.; 6a-c, dorsal, lat., ventral sides, $\times 2$ (48).

Tillicheilus SHIMANSKIY, 1947, p. 1477 [**Rhyncholithes obtusus* TILL, 1906, p. 121; OD] [= *T. (Unguibeccus)* SHIMANSKIY, 1949, pl., p. 201 (*nom. nud.*)]. Hood diminutive, subglobular, smooth, prominent in front view but barely visible in dorsal view, marked off from shaft by suture-like furrow; shaft large, width slightly greater than hood but length at least 3 times greater, dorsal side strongly convex, sides flattened or slightly concave, ventral side distinctly concave both transversely and longitudinally, smooth. *Carb.-L. Cret.*, Eu.—FIG. 346,7. **T. obtusus* (TILL), *L. Cret.*, Ger.; 7a-d, dorsal, ant., lat., ventral views, $\times 2$ (47).

Erlangericheilus SHIMANSKIY, 1947, p. 1477 [**E. insignis*; OD (M)]. Hood short, conical, tooth-like, distinct from well-defined shaft which on dorsal side bears longitudinal furrow bordered by ridges, ventral side slightly convex. *L. Cret. (Apt.)*, USSR (Crimea).—FIG. 347,1. **E. insignis*; 1a-c, dorsal, lat., ventral sides, $\times 1.3$ (44).

GENERA ORIGINALLY CLASSED AS NAUFILOID MANDIBLES BUT LATER AS GASTROPOD OPERCULA

Cyclidia ROLLE, 1862, p. 121, 122 [**C. valida*; OD (M)] [*non Cyclidia* GUENÉE, 1857]. Believed by author to be cephalopod beak; according to ZITTEL (54) and TILL (47) is a gastropod operculum. *Tert. (Mio.)*, Eu. (Ger.).

Peltarion EUDES-DESLONGCHAMPS & EUDES-DESLONGCHAMPS, 1858, p. 153 [**P. unilobatum*; SD

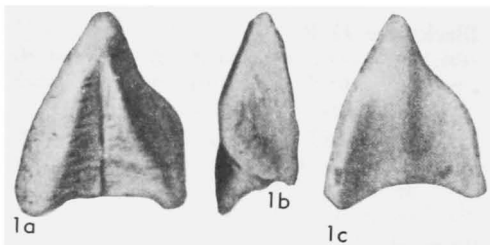


FIG. 347. **Erlangericheilus insignis* SHIMANSKIY, $\times 1.3$ (44) (p. K481).

TEICHERT, MOORE & ZELLER, herein] [*non Peltarion* JACQUINOT & LUCAS, 1853 (1847?). *Lias?* (*L. Jur.*), Eu. (Fr.-Ger.).

Rhynchidia LAUBE, 1870, p. 54, 56 [**R. cassiana*; OD (M)] [= *Rhynchidia* LAUBE, 1868, p. 538 (*nom. nud.*)]. Originally thought to be cephalopod beak, but ZITTEL (54, p. 387) described it as gastropod operculum. *Trias.*, Eu. (Austria).

Scaphanidia ROLLE, 1862, p. 127 [**Rhyncholithus Buchi* MÜLLER, 1851; OD] [= *Peltarion* EUDES-DESLONGCHAMPS & EUDES-DESLONGCHAMPS, 1858, according to ZITTEL (54, p. 387)]? *Jur.*, Eu. (Fr.-Eng.); *Cret.*, Eu. (Ger.).

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DOUBTFUL TAXA

By CURT TEICHERT

[United States Geological Survey]

ORDER UNCERTAIN

Family NEPTUNOCERATIDAE

Shimanskiy, 1956

Weakly cyrtoconic conchs, slightly expanding, with subquadrangular cross section; surface ornamented by fine, transverse ribs. [Assigned to Nautilida, superfamily Rutocerataceae, by SHIMANSKIY, but lack of knowledge of siphuncle structure makes this placement doubtful. May be intermediate between Oncocerida and Nautilida. According to FURNISH, GLENISTER & HANSMAN (1962) the specimens on which the two genera of this family are based may well represent growth stages of *Brachycycloceras*, a genus of deciduous Pennsylvanian orthocerids.] *U.Carb.*

Neptunoceras SHIMANSKIY, 1949 [**N. sakmarensense*; OD]. Cyrtoconic conchs with quadrangular cross section; weakly annulate; sutures slightly wavy; siphuncle unknown. *U.Carb.*, S.USSR.—FIG.

348,2. **N. sakmarensense*; 2a, convex side, 2b, lat., ×3 (11).

Tetrapleuroceras SHIMANSKIY, 1949 [**T. karpinskyyi*; OD]. Weakly cyrtoconic conchs with subquadrangular cross section; surface weakly annulate; sutures almost straight; siphuncle near convex side. *U.Carb.*, S.USSR.—FIG. 348,1. **T. karpinskyyi*; 1a, concave side, 1b, lat., 1c, adapical, ×2 (11).

Order & Family UNCERTAIN

Dartoceras FOERSTE, 1936 [**D. nodosum*; OD]. Weakly cyrtoconic, rapidly expanding conch with weak transverse annulations and single row of widely spaced nodes along each ventrolateral side; siphuncle unknown. [Possibly a barrandocerid.] *M.Sil.*, E.Can.—FIG. 349. **D. nodosum*, Gaspé Penin.; ×1 (4).

Hedstroemoceras FOERSTE, 1930, p. 126 [**H. hael-luddense*; OD (M)]. Conch small, erect, dorsal outline faintly convex, ventral outline more distinctly convex; cross section nearly circular,

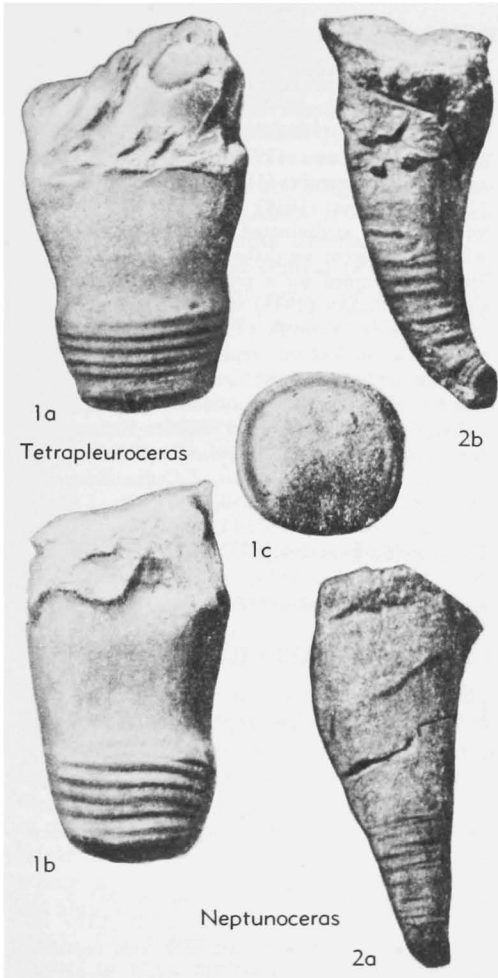


FIG. 348. Order Uncertain, Family Neptunoceratidae (p. K484).

slightly compressed laterally; living chamber enlarging but slightly; siphuncle located near ventral side of conch, but not in contact with it, its segments fusiform in outline. *L.Ord.* (*Vaginatium Ls.*), Eu. (Sweden, Öland Is.).

TAXA DOUBTFULLY CLASSIFIABLE AS NAUTILOIDS

This section is set apart for treatment of some puzzling fossils which have been considered by various authors to be primitive representatives of the class Cephalopoda, and if so, most closely related to one or more of the nautiloid orders. On the other hand, there is ample room for doubt that they are cephalopods at all. [Some notes by



FIG. 349. **Dartoceras nodosum* FOERSTE, Order and Family Uncertain (p. K484).

D. W. Fisher have been incorporated into this section.]

Order VOLBORTHELLIDA Kobayashi, 1937

[*nom. correct* ZHURAVLEVA, 1955, ex *Volborthellidea* KOBAYASHI, 1937] [=Protochoanites GRABAU & SHIMER, 1910 (order); *Volborthellacea* KUHN, 1949 (order)]

Small, orthoconic, or slightly cyrtconic shells of circular cross section, having closely spaced septa with central perforations that may indicate presence of a siphuncle. *L.Cam.-M.Cam.*

Family VOLBORTHELLIDAE Kiaer, 1916

[=Paleonavitili VOLBORTH (1869, MS.) in GEKKER, 1928]

Minute longiconic shells of circular cross section, divided internally by very closely spaced conical partitions having narrow perforations at their tips so as to form central tube interpreted by some authors as analogous to siphuncle of cephalopods, conical partitions about 6 to 8 in 1 mm., spaces between them filled with quartz and dark minerals. [The nature of the central tube is problematical, since no outer wall has been observed with certainty. Also the character of the shell material is doubtful; it may have consisted of some organic substance or possibly it was calcareous with organic admixtures. Originally included in the order was *Volborthella* alone, believed to be a cephalopod. Probably the assemblage should be more widely construed to include representatives of short-lived abortive groups of Early Cambrian animals that competed unsuccessfully with trilobites, gastropods, and hyolithids.] *L.Cam.-M.Cam.*

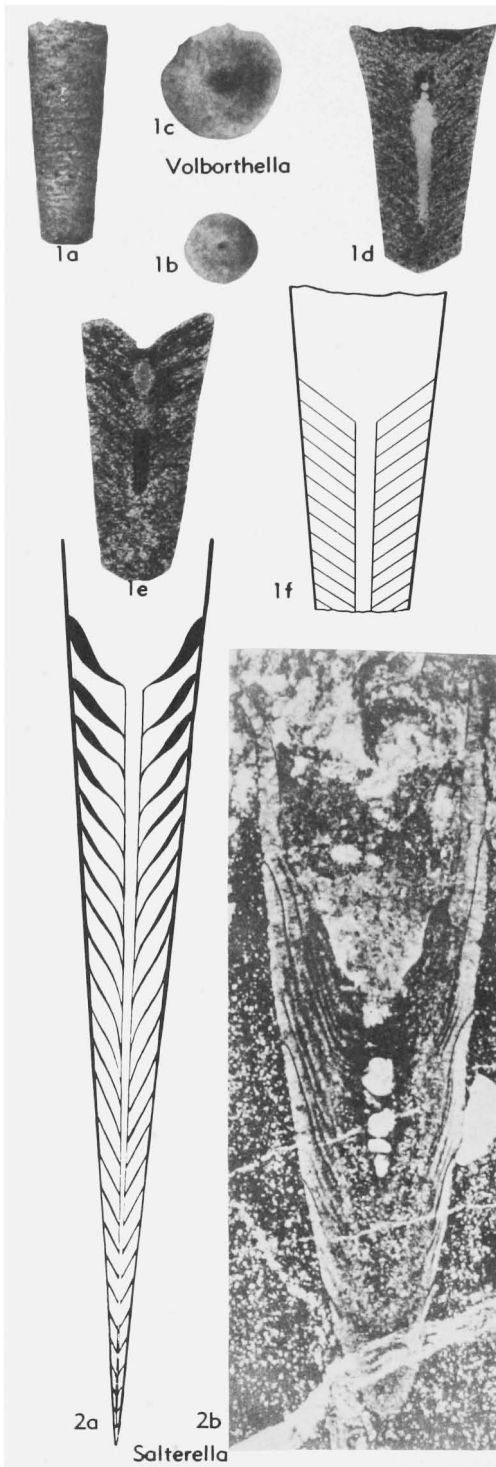


FIG. 350. Volborthellidae (p. K486); Salterellidae (p. K486).

Volborthella SCHMIDT, 1888 [**V. tenuis*; M] [= *Volborthella* DAVITASHVILI, 1958 (*nom. null.*)]. Characters of family. [External characters of this genus have been described by SCHMIDT (1888), KARPINSKY (1903), BRAASTED (1915), and KIAER (1916), and internal characters by KARPINSKY (1903) and SCHINDEWOLF (1928). GÜRICH (1934) compared *Volborthella* with certain agglutinated protozoans and also with some Recent ascidians. SCHINDEWOLF (1928, 1934) has argued for a primitive cephalopod assignment. MILLER (1943) was convinced that they are pteropods. FLOWER (1954) pointed out that the oldest undoubted cephalopods (Cambrian) possessed cyrtoconic, not orthoconic conchs. The affinities of *Volborthella* continue to be controversial.] *L.Cam.*, Eu. (USSR-Est.-Sweden-Norway)-N. Am. (Can.)-Australia; *M.Cam.*, Eu. (Czech.-Pol.). —FIG. 350,1a. **V. tenuis*, *L.Cam.*, Est.; side view, $\times 10$ (9). —FIG. 350,1b,c. *V. sp.*, *L.Cam.*, Est.; apical, oral views, $\times 10$ (9). —FIG. 350,1d,e. *V. conica* SCHINDEWOLF, *L.Cam.*, Est.; long. secs., $\times 13$ (9). —FIG. 350,1f. *V. sp.*, diagram. sec. as interpreted by Schindewolf (9).

Family SALTERELLIDAE Poulsen, 1932

Small, slender, conical calcareous conchs with strongly conical septa; shell long and straight or gently curved, with encircling striae on exterior; thick, slightly sinuate septa resembling invaginated cones; foramen at apex of conch may be surrounded by elongated collar. *L.Cam.*

Salterella BILLINGS, 1861 [**S. rugosa*; SD S. A. MILLER, 1889]. Characters of family. [The internal structures of this fossil have been regarded by some authors as septa and septal necks, respectively. Similarly, a central tube has been considered to be a siphuncle. CLARK (1925) and POULSEN (1932) regarded *Salterella* as a primitive cephalopod. TEICHERT (1935) and FLOWER (1943, 1954) interpreted it as an invertebrate of uncertain affinities. BILLINGS, COBBOLD, and WALCOTT considered *Salterella* to be a pteropod. KOBAYASHI (1937) thought that *Salterella* and *Volborthella* were allied, forming a "solid group of fossils intermediate between the hyolithids and nautiloids, but closer to the latter." A. K. MILLER (1943) regarded these two genera as pteropods, but such an assignment is quite unsubstantiated. It seems probable that *Salterella* is molluscan in nature but having very slight affinities with any modern representative of the Mollusca.] *L.Cam.*, N. Am. (Mex.-USA-Can.-Greenl.)-Eu. (Eng.)-Asia. —FIG. 350,2a. *S. conulata* CLARK, Can.; diagram. sec., $\times 4$ (1). —FIG. 350,2b. **S. rugosa*, Greenl., transv. sec., $\times 10$ (7).

Family VOLOGDINELLIDAE

Balashov, 1962

Very small cylindrical conchs of depressed cross section; weakly concave transverse partitions that are as thick as the spaces between them are long, having central perforation. [BALASHOV interprets transverse partitions as septa covered with cameral deposits and the central perforation as siphuncle. No septal necks or connecting rings have, however, been observed.] *M. Cam.*

Vologdinella BALASHOV, 1962, p. 72 [**Orthoceras? antiquus* VOLOGDIN, 1930] [= *Vologdinella* SHIMANSKIY, 1956 (*nom. nud.*)]. Characters of family. Very poorly known. *M. Cam.*, USSR (Kazakhstan).

NAUTILOID TRACE FOSSILS

The most authentic record of impressions and trails made by nautiloid cephalopods is from the Upper Ordovician of Ohio, USA (3). The following types, all ascribed to action of individuals belonging to the genus *Orthonybyoceras*, have been distinguished: (1) orthoconic cephalopod shells at the end of linear trails, made by forward movement of the animal shortly before death; (2) short linear trails, rounded at both ends, made where a cephalopod came to rest on the sea bottom, moved forward, and then swam away; (3) similar trails clustered around masses of organic debris, indicating a feeding place; and (4) crescentic impressions arranged more or less in a semicircle in groups of ten, believed to be left by distal ends of tentacles seeking a hold on the bottom (Fig. 351). According to FLOWER (1942), "Similar markings are associated with *Petryoceras* in the Sherburne member [Upper Devonian], and with various smooth-shelled Pseudorthoceratidae and with *Bactrites* in higher beds."

Although the evidence is admittedly tenuous, it suggests that the Orthocerida and Actinocerida might have possessed ten arms, rather than a much larger number of tentacles, as in living *Nautilus*. This suggestion is interesting in view of the fact that, from altogether different lines of evidence, it is concluded that the Orthocerida are ancestral to the belemnites and to modern Dibranchiata, including the Decapoda.

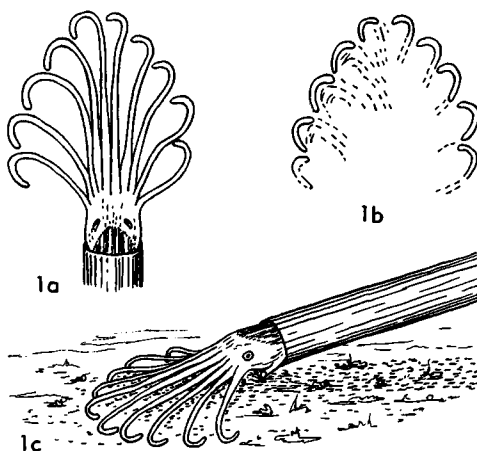


FIG. 351. 1a-c. Possible reconstruction of orthocerid with tentacles in position in which they may have made impressions; 1b. Impressions interpreted as those of an orthocerid (adapted from 3).

The following trace fossils have been formally named and believed by the authors to be due to the action of cephalopods.

Petalichnus S. A. MILLER, 1880 [**P. multipartitus*; M]. *U. Ord.*, N. Am. (Ohio). [See p. W208; interpreted as trilobite track.]

Saerichnites BILLINGS, 1866 [**S. abruptus*; M]. *Ord.*, Can. (Anticosti). [See p. W215.]

Teratichnus S. A. MILLER, 1880 [**T. confertus*; M]. *U. Ord.*, N. Am. (Ohio). [See p. W218; interpreted as probable trilobite track.]

Trachomatichnus S. A. MILLER, 1880 [**T. numerosus*; SD S. A. MILLER, 1889]. *U. Ord.*, N. Am. (Ohio). [See p. W219; interpreted as probable trilobite track.]

These trace fossils (all included by HÄNTZSCHEL in *Treatise Part W*) are in need of restudy and modern analysis before their cephalopodous origin can be accepted.

DOUBTFUL AND REJECTED GENERA

BARRANDE (1867) divided breviconic and short cyrtoconic shells with lobate apertures into groups according to the number of apertural lobes. These conchs now are distributed among the Oncocerida and Discosorida. In tables (p. 203, 265) he attached names to these groups, but did not italicize

the names nor did he introduce or discuss them in the text. Seemingly these names published without description or discussion should be regarded as formulae which have no standing in zoological nomenclature (ICZN, Opinion 2).

Dimeres BARRANDE, 1867. Species group of *Phragmoceras*, characterized by 2 apertural lobes. *M.Sil.*

Dimorion BARRANDE, 1867. Species group of *Gomphoceras*, characterized by 2 apertural lobes. *M.Sil.*

Hexameres BARRANDE, 1867. Species group of *Phragmoceras*, characterized by 6 apertural lobes. *M.Sil.*

Hexamorion BARRANDE, 1867. Species group of *Gomphoceras*, characterized by 6 apertural lobes. *M.Sil.*

Octameres BARRANDE, 1867. Species group of *Phragmoceras*, characterized by 8 apertural lobes. *M.Sil.*

Pentamorion BARRANDE, 1867. Species group of *Gomphoceras*, characterized by 5 apertural lobes. *M.Sil.*

Tetrameres BARRANDE, 1867. Species group of *Phragmoceras*, characterized by 4 apertural lobes. *M.Sil.*

Tetramorion BARRANDE, 1867. Species group of *Gomphoceras*, characterized by 4 apertural lobes. *M.Sil.*

Trimorion BARRANDE, 1867. Species group of *Gomphoceras*, characterized by 3 apertural lobes. *M.Sil.*

UNRECOGNIZABLE SUPPOSED NAUTILOID GENERA

Achelois DEMONTFORT, 1808 [**A. pyramidatum*; M]. Described as straight, chambered, conical shell with central siphuncle, from Altdorf, Switz., hence probably Mesozoic belemnite phragmocone and rostrum. [FOORD (1888, p. 1) listed name in synonymy of *Orthoceras*.]

Amblyceras GLOCKNER, 1842 [**A. rittbergense*; M]. Gyroconic conch. *Paleoz.*, Czech.

Animomus DEMONTFORT, 1808 [**A. elephantinus*; M]. Described as straight-chambered, curved shell with central siphuncle and entire aperture. Boetstein, Altdorf, Switz., hence probably Mesozoic. [Possibly a crinoid stem. FOORD (1888, p. 262) listed name in synonymy of *Cyrtoceras*.]

Bisiphites DEMONTFORT, 1808.

Curvites PETTER, 1959 [cited by SHIMANSKIY, 1962, p. 118].

Deltoceras HYATT, 1894, p. 449 [**D. planum*; OD]. Compressed, inconspicuously ornamented subdiscoidal serpenticones, rapidly expanded dorsoventrally, not impressed dorsally; at maturity,

adapical part of conch not in contact with adjacent volution. Sutures with slight lateral lobes. Siphuncle subventral, interior unknown. *L.Ord.* (?*U.Canad.*), Can., ?Eu. [Type-specimen never illustrated.] [W. C. SWEET.]

Diadiploceras HYATT, 1884.

Gyrocerus KING, 1844 [no assigned species]. "Tendrill-shaped or open-coiled" shells. Horizon and locality unknown.

Hortulus DEMONTFORT, 1808 [**H. convolvans*; M]. Described as being similar to *Lituites*. From dark limestone near Namur, Belg., hence probably *Carb.*

Koleoceras PORTLOCK, 1843 [no type-species] [= *Coleoceras* M'COY, 1846 (*nom. null.*)]. Flattened fossils that may be either orthocerid conchs or endocerid siphuncles. Several species described from "*Sil.*," Ire.

Nautilites PALLAS, 1771 [**N. complanatus*; M]. Hand-sized smooth shell with depressed, evenly convex cross section, sharp keel, and undulating sutures. Age unknown, Volga region, USSR.

Oceanus DEMONTFORT, 1808 [**O. flammeus*; M]. Name given to rather widely varied fossil and Recent involute nautilids. [Possibly includes *Nautilus umbilicatus* LAMARCK (1808) and could thus be a junior synonym of *Nautilus* LINNÉ (1758).]

Parksoceras FOERSTE & SAVAGE, 1927 [**Orthoceras (Thoracoceras) lepidodendroides* PARKS, 1915; OD]. Large orthoconic conch preserved as internal mold with tuberculate elevations arranged in diagonally intersecting rows. Siphuncle unknown. [May be orthocerid or oncocerid.] *U.Ord.*, N.Am.(Can.).

Pteronautilus MEEK in MEEK & HAYDEN, 1865 [**Nautilus seebachianus* GEINITZ, 1861; OD]. Strongly involute conch, outer (?body) chamber very large, its inner (?dorsal) side wide open and its lateral margins expanded to form large wing-like flanges. [Cephalopod affinities uncertain; might be a bellerophonid gastropod.] *U.Perm.*, Ger.

Remeleceras HYATT, 1894 [**R. depressum*; M] [= *Remeleoceras* HYATT in ZITTEL, 1900 (*nom. null.*)]. Based on whorl fragments; whorl section with slightly impressed dorsal zone and sutures with broad dorsal lobes. Age and locality of type material unknown. [See B. KUMMEL, 1963, p. 326.]

Schoulgoceras SHIMANSKIY, 1951 [cited by SHIMANSKIY, 1962, p. 154, as invalid name].

Ungroceras STURGEON & MILLER, 1948 [**U. ungeri*; OD]. Cyrtoceraconic conch with compressed cross section; surface with fine longitudinal and coarse, sinuous, transverse ribs; sutures with broad, shallow lateral lobes and dorsal and ventral saddles; siphuncle unknown. (Could be either a nautilid (?*Rutoceratidae*) or an orthocerid (?*Kionoceratinae*)). *M.Penn.*, USA (Ohio).

NAMES FOR HYPOTHETICAL NAUTILOID GENERA

The following names proposed for nautiloid cephalopods are invalid because not based on actual specimens, living or fossil.

Lituunculus BARRANDE, 1867. Proposed for forms resembling *Lituites*, but with simple apertures; no such specimens known.

Metorthoceras NAEF, 1921. Proposed for hypothetical cephalopods transitional between Tetrabranchiata and Dibranchiata.

Proteropiloceras RUEDEMANN, 1905. Proposed for forms like *Piloceras*, but noncamerate in apical part; no such specimens known.

Protorthoceras NAEF, 1921. Hypothetical ancestor ("Ur-form") of all cephalopods.

Protovaginoceras RUEDEMANN, 1905. Hypothetical ancestor of *Proterovaginoceras* RUEDEMANN, 1905 (endoceratid).

Teilhardoceras GRABAU, 1929. ". . . primitive ancestral form of the Holochoanites which . . . has not yet been discovered with certainty. . . ." [Name was validated by TEILHARD DE CHARDIN, 1931, by being made an objective synonym of *Biconulites* TEILHARD DE CHARDIN, 1931; taxonomic position uncertain; see p. W138.]

NAUTILOID NOMINA NUDA

Arctinoceras FLOWER & KUMMEL, 1950 [*non* DE CASTELNAU, 1843, *nom. null. pro Actinoceras* BRONN, 1832]. Listed with family Brevioceratidae; no species assigned. [See p. K204, *Actinoceras*.]

Bisonoceras KOTTELOWSKI, FLOWER, THOMPSON, & FOSTER, 1956, and FLOWER, 1958 (*nom. nud.*). Undescribed piloceratid, *L.Ord.(up.Mid.Canad.)*, USA(W.Tex.-N.Mex.).

Conorthoceras TROEDSSON, 1931. Intended for *Orthoceratites conicus* HISINGER, but not formally established. *Ord.*, Sweden. (See also JAANUSSON & MUTVEI, 1953, p. 19.)

Cyrtacleistoceras FLOWER, 1943.

Diphragmoceras HYATT in ZITTEL, 1900. [See SCHUCHERT & DUNBAR, 1934, p. 47.] *Ord.*, Can. (Newf.).

Endogomphus FLOWER, 1938. Possibly *nom. null. pro Endoplanoceras*.

Engorthoceras FLOWER, 1962, p. 34 [*"Orthoceras wortheni* MEEK & WORTHEN"; OD]. Cited type-species seemingly nonexistent. Reported to occur in M. Dev. of Ohio. Genus designated as type of Engorthoceratidae FLOWER, 1962. [W. C. SWEET.]

Eosacoceras SHIMIZU & OBATA, 1935 [**E. minimum* (= *Armenoceras nanum* ENDO, 1932; *non* GRABAU, 1922)]. Published without diagnosis or description. *M.Ord.*, Manchuria.

Exosiphonites SALTER, 1865 (*fide* BLAKE, 1882). [See also ETHERIDGE, 1888, p. 122.] *Sil.*,? Eng.

Kolyoceras TEICHERT, 1929. Intended to be established as subgenus of *Spyroceras* HYATT but not done.

Kutorgoceras BALASHOV, 1961. Listed with *Clitendoceras*, *Cotteroceras*; no species assigned.

Mistioceras BALASHOV, 1961. Listed with *Proterocameroceras* and *Penhsioceras*; no species assigned.

Northoceras MEEK & HAYDEN, 1864. Included in a list of genera of Nautilidae (*s.l.*).

Orchadoceras FOERSTE, 1928. A single species (*O. incertum*, *Sil.*, Anticosti Is.) described under this name was only tentatively assigned to the genus, which was never formally described.

Proterokaipingoceras OBATA, 1940. Mentioned in comparison with *Neokaipingoceras* OBATA (*gen. dub.*).

Ptenacleistoceras FLOWER & KUMMEL, 1950. Listed with family Acleistoceratidae; no species assigned.

SUPPOSED NAUTILOIDS, REJECTED FROM NAUTILOID ORDERS

Aganides DEMONTFORT, 1808 [**A. capucinus* SCHLOTHEIM, 1820; SM]. Originally described without assigned nominal species. Frequently cited as possible senior synonym of *Aturia* BRONN, 1838 (see *Treatise*, p. L75), because of action taken by D'ORBIGNY (1826, p. 161) who assigned *Nautilus aturi* BASTEROT (type-species of *Aturia*) and *N. zigzag* SOWERBY to this genus, overlooking the fact that VON SCHLOTHEIM had formally named the species described (but not named) by DEMONTFORT. Since the fossil on which DEMONTFORT based his generic description was reported to come from black, fetid limestone in the vicinity of Namur, Belgium, it is almost certainly a goniatite of Carboniferous age and possibly senior synonym of *Imitoceras* SCHINDEWOLF, 1923, an ammonoid. *L.Carb.*, Belg. (See J. S. TURNER, 1962, p. 183.)

Brittsoceras MILLER, DOWNS & YOUNGQUIST, 1949 [**B. ornattissimum*; OD] [= *Porcellia* LEVEILLE, 1835 (gastropod) (see MILLER, 1950, p. 506)]. *Miss.*, USA(Mo.).

?**Coeloceratoides** DERVILLE, 1931 [**C. fragilis*; M] [= *Koninckopora* LEE, 1912 (calcareous alga) (see JOHNSON & KONISHI, 1956, p. 48-122)]. *Carb.*, Fr.

Coelonautilus FOORD in FOORD & CRICK, 1889 [*nom. subst. pro Trematodiscus* MEEK & WORTHEN, 1861 (*non* HAECKEL, 1860)] [= *Discus* KING, 1844 (obj.); *Trematoceras* HYATT, 1884 (*non* EICHWALD, 1860) (obj.); *Streptodiscus* MILLER, 1889 (obj.); *Collonautilus* TILL, 1907 (*nom. null.*)]. Long regarded as synonym of *Vestinautilus* RYCKHOLT, 1852, but technically synonymous with *Ammonellipsites* PARKINSON, 1822 (ammonoid) (see TURNER, 1954).

Elkoceras LINTZ & LOHR, 1958 [**E. volborthi*; OD]. Originally believed to be member of family Ruto-

ceratidae, subsequently recognized as synonym of gastropod *Straparollus* (*Euomphalus*) (LINTZ, 1962). *Miss.*, Nev.

Gyroceras DEKONINCK, 1844. Originally used for Carboniferous nautiloids as *nom. van. pro Gyroceratites* MEYER, 1831 (ammonoid) (see MILLER, DUNBAR, CONDRA, 1933).

Pichyceras RUSCONI, 1955 [**P. jorusconii*; M]. Probably stem fragment of pelmatozoan echinoderm (?eocrinid, ?paracrinoid). *M.Cam.*, S.Am.(Arg.).

?**Shelbyoceras** ULRICH & FOERSTE, 1930 [**S. robustum* ULRICH & FOERSTE, 1936; SD ULRICH & FOERSTE, 1936]. Small, weakly cyrtoconic conchs with compressed cross section, surface with annulations that slope adapically from concave to convex side of shells. Siphuncles not discovered and no comparable Cambrian cephalopods known. [Originally described as cephalopod, without any named species; the genus cannot be assigned with certainty to any class or phylum until internal structure becomes known (2).] *U.Cam.*, USA (Mo.-Texas).

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BACTRITOIDEA

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INTRODUCTION

The bactritoids are cephalopods that have long been interpreted as the most primitive representatives of the Ammonoidea, but also by some authors as belonging to one of the nautiloid orders, or with about equal justification assignable to either nautiloids or ammonoids. Also, they have been classified noncommittally as external-shelled (ectocochleate) cephalopods of uncertain affinities.

GENERAL SHELL FEATURES

The shell of the Bactritoidea [and of its single contained order, the Bactritida]¹ is relatively uniform in shape. It consists of a small protoconch and a much larger conch which includes the camerate phragmocone and a rather large body chamber. Aptychi or anaptychi and jaw structures are not known.

The protoconch is globular to egg-shaped with circular cross section, generally with a slightly to strongly constricted aperture. The caecum has been observed, but a prosiphon and a cicatrix are still not known in the Bactritida.

The conch is orthoconic or slightly cyrtoconic. The surface generally is smooth, sculptured forms being exceptions. Color markings have not been observed. Apertural constrictions of adult stages are not known. The ontogenetic development and shape of the peristome are considered to be reflected by the development and shape of the growth lines (Fig. 352). These are generally simple. In the Bactritidae they always contain at least a ventral (hyponomic)

sinus, to which, in most forms, a dorsal saddle is added. Other elements (lateral sinus, and even ventrolateral and dorso-lateral saddles, or dorsal sinus) appear only in two exceptional genera. On the flanks, the growth lines typically are rursiradiate, rectiradiate lirae being restricted to a very few forms. The growth lines of the Parabactritidae are known only in *Parabactrites*. Here they are straight and rectiradiate, lacking the hyponomic sinus.

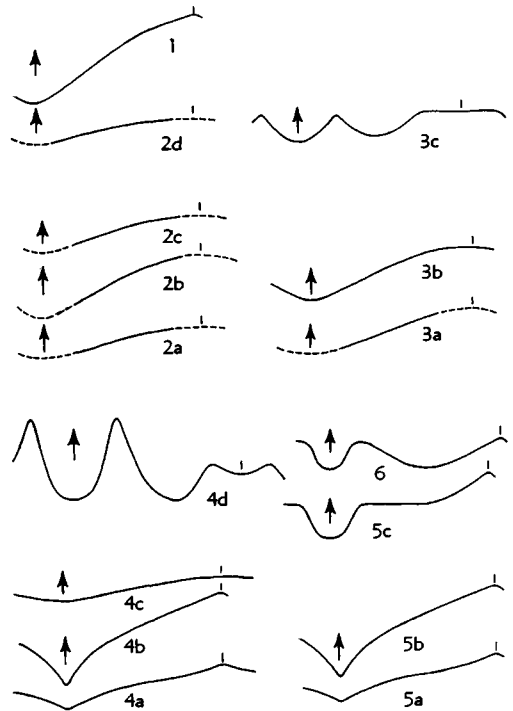


FIG. 352. Diagrams illustrating development of growth lines in some Bactritida (7, 8).—1. *Lobobactrites ellipticus* (FRECH), adult stage.—2. *Bactrites gracilior* CLARKE; 2a, from early, 2b, from middle, 2c, from final part of the second ontogenetic phase; 2d, adult stage.—3. *Pseudobactrites peneau* ERBEN; 3a, from early, 3b, from middle stage of second ontogenetic phase; 3c, from adult stage.—4. *Pseudobactrites bicarinatus* FERRONNIÈRE; 4a, from early, 4b, from middle, 4c, from final part of second ontogenetic phase; 4d, from adult stage.—5. *Cyrtobactrites asinuatus* ERBEN; 5a, from early, 5b, from middle part of second ontogenetic phase; 5c, from adult stage.—6. *Cyrtobactrites sinuatus* ERBEN, adult stage.

¹ The group of fossils included in this section of Part K is considered by Dr. ERBEN to be best classified as a suborder (Bactritina) placed in the order Ammonoidea. Under urging of Dr. TEICHERT, who thinks that these cephalopods should be ranked at least on a level with the several nautiloid orders and considered to belong in intermediate position between Orthocerida and Ammonoidea, use of the ordinal name Bactritida was agreed to by Dr. ERBEN. Subsequently, as outlined in a foregoing discussion of "Main Divisions of Cephalopoda," decision has been made to recognize six subclasses of cephalopods one of which, named Bactritoidea, contains a single order, the Bactritida.—R. C. Moore.

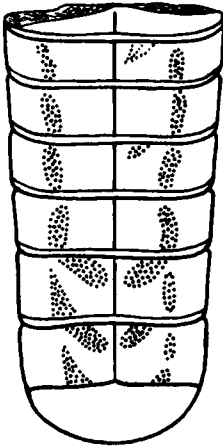


FIG. 353. *Bactrites ausauensis* STEININGER, U.Dev., Ger., $\times 12$. Dorsal view showing septal furrow and lateral to dorsolateral depressed "annular elevations" (7).

On the dorsum of well-preserved internal casts a septal furrow (*Normallinie*, *ligne normale*) appears. Series of horseshoe-shaped annular elevations (Fig. 353), which have been found by ERBEN (7) on the dorsal and dorsolateral zone of exceptionally well-preserved internal casts, represent contact areas of the retractor muscles (in the sense of MURVEI, 1957).

In all Bacritida the septa are concave adorally. Prosepta have not yet been observed. The septal necks are invariably retrosiphonate. They are orthochoanitic in primitive forms and suborthochoanitic to cyrtchoanitic in advanced genera (Fig. 354). Straight connecting rings have been observed in some specimens in connection with orthochoanitic necks. With cyrtchoanitic septal necks they have been reported to be inflated. Siphuncular and cameral deposits are unknown. In adult stages, the siphuncle has a ventral position. In the earliest ontogenetic stages it is subventral and may be subventral in the latest stage also.

The sutures are always simple, the adult stage having at least one small, shallow, V-shaped ventral lobe. In more advanced genera a dorsal saddle and lateral lobes may be added.

The test seems to consist of three main layers, as in other cephalopods. In *Bactrites*

and *Lobobactrites* the "wrinkled layer" (*Runzelschicht*) has been observed by ERBEN (7). *Parabactrites* has been claimed by SHIMANSKIY (24) to have a test consisting of numerous lamellae similar to an initial belemnoid rostrum. The illustration, however, shows no more than what could be expected from an ordinary cephalopod test, the few layers of which were split during diagenesis or weathering, as may be observed not infrequently in similarly preserved tests of nautiloids, ammonoids, and also in conothecas of belemnoid phragmocones.

ONTOGENY

The ontogeny of *Bactrites*, *Lobobactrites*, *Pseudobactrites*, and *Cyrtobactrites* is known, but that of *Ctenobactrites* remains doubtful. In several genera three phases have been observed, and in all genera at least the first one seems to be present. They become evident by shell constrictions and changes of the configuration of growth lines (8). The first phase comprises the formation of the protoconch from its apex to its invariably constricted peristome (first shell constriction). The second phase includes the "nepionic stage" of HYATT and reaches from the first shell constriction to a rather ill-defined second shell constriction (in ammonoids often wrongly called "first constriction") where a sudden change in the configuration of growth lines may occur. The third phase includes the "neanic stage" of HYATT and all later developments. It extends from the change of growth lines and, if present, the second constriction to the latest part of the conch.

FIRST PHASE

Although the protoconch is commonly globular to ovoid, its shape may even show variations within a species. Its axis generally coincides with the axis of the following conch, but in some it may be slightly inclined (Fig. 355, 1d, 1f, 3b, 2, 3a). The growth lines are imperfectly known, but the peristome commonly is straight and rectiradiate, except in the above-mentioned example of an inclined protoconch.

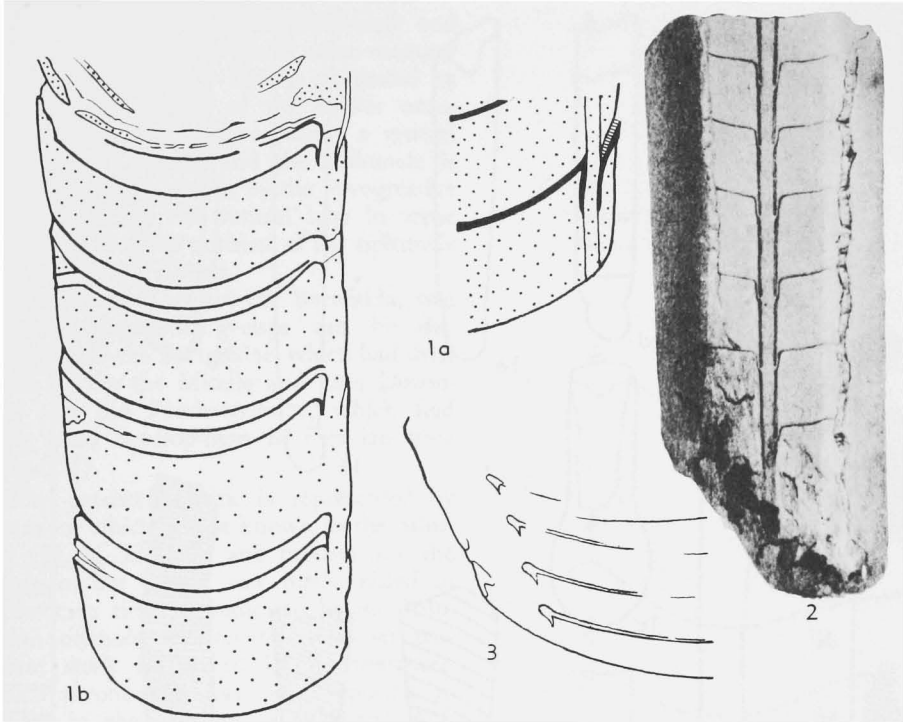


FIG. 354. Diagrams illustrating septal necks in the Bactritida.—1. *Bactrites*; 1a, *B. büdesheimensis* ROEMER, orthochoanitic, with connecting rings, U.Dev., Ger., $\times 8$; 1b, *B. schlotheimi* (QUENSTEDT), orthochoanitic, M.Dev., Ger., $\times 3$ (8).—2. *Lobobactrites timanicus* SCHINDEWOLF, orthochoanitic, with connecting rings, U.Dev., USSR, enlarged (12).—3. *Belemnitomimus palaeozoicus* SHIMANSKIY, cyrtochoanitic, L.Perm., USSR, $\times 8.5$ (24).

SECOND PHASE

In the second ontogenetic phase, after the first shell constriction, the cross section may (Fig. 355, 1a, b, g) or may not (Fig. 355, 1c, i, A) regain the size of the largest cross section of the protoconch, and it may become even larger.

The growth lines always have a ventral sinus; also, in most specimens a dorsal saddle appears and the position of the growth lines is strongly rursiradiate. In *Pseudobactrites* it has been observed that near the end of this phase a secondary, almost rectiradiate, position is suddenly regained, the ventral sinus and dorsal saddle becoming abruptly reduced (Fig. 352, 4a-c; 355, 3b). In *Bactrites* (Fig. 352, 2a-d; 355, 1a), the change to a less rursiradiate position of the growth lines is not so abrupt. The end of this second phase may (Fig. 355, 1b, g, h, 3b) or may not (Fig. 355, 1a, d-f, i, A) be characterized by a minor reduction in cross section, called the second constriction.

THIRD PHASE

In this phase after the weak constriction and the secondary simplification of growth lines, the final development starts. A ventral sinus and dorsal saddle develop again and are retained; additional elements appear (lateral sinus, and others) and the mature cross section develops.

The first ontogenetic phase probably represents the embryonic stage, while the second phase may be correlated with the larval and the third one with the postlarval development.

The different stages of development of the suture cannot be exactly correlated with the above-mentioned phases, for each septum is formed at a later stage than the corresponding part of the conch in which it appears, each part representing the former living chamber before origin of the corresponding septum. It is evident from observation of some exceptional individuals (Fig. 355, 1d, g) and of a specimen that

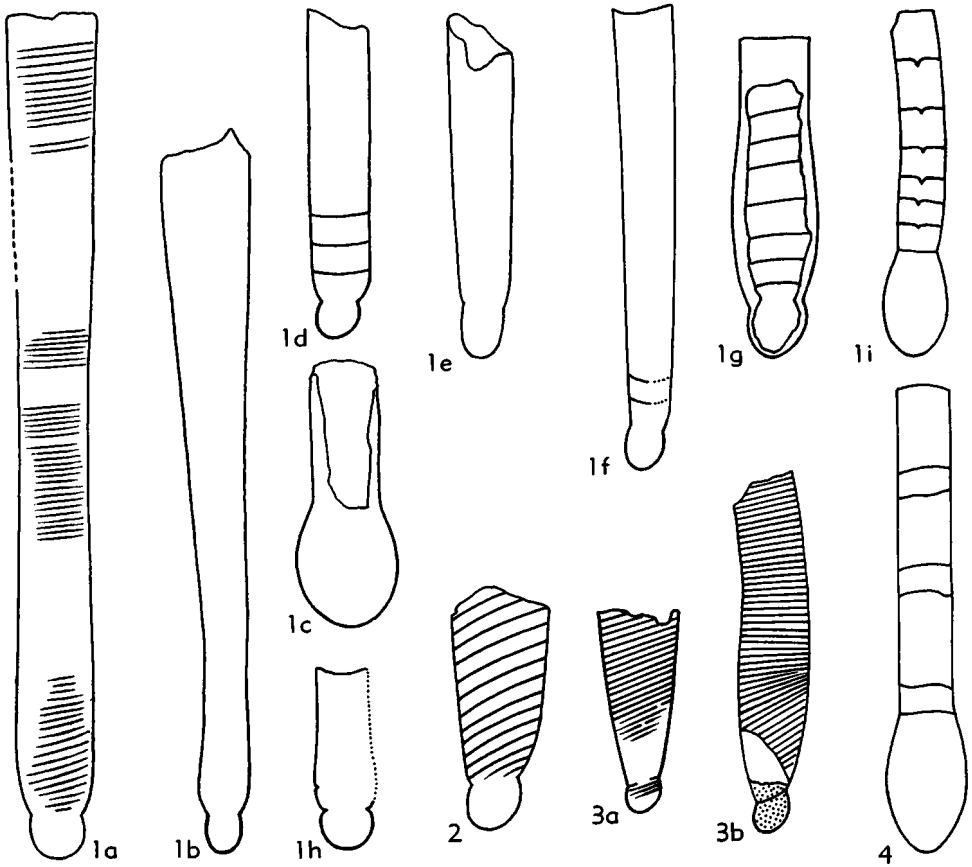


FIG. 355. Diagrams illustrating types of protoconchs of the Bactritida.—1. *Bactrites*; 1a, *B. gracilior* CLARKE, U.Dev., USA, $\times 22.5$ (15); 1b, *B.? aciculum* (HALL), U.Dev., USA, $\times 19$ (15); 1c, *B.? sp.*, L.Dev., Fr., $\times 15$ (7); 1d, *B. gracilior* CLARKE, U.Dev., USA, $\times 13.5$ (7, 15); 1e, *B.? aciculum* (HALL), U.Dev., USA, $\times 11$ (15); 1f, *B.? aciculum* (HALL), U.Dev., USA, $\times 19$ (15); 1g, *B. gracilior* CLARKE, U.Dev., USA, $\times 13.5$ (7, 15); 1h, *B. primus* (SHIMANSKIY), L.Perm., USSR, $\times 11$ (25); 1i, *B. schlotheimi* (QUENSTEDT), M.Dev., Ger., $\times 17$ (21).—2. *Cyrtobactrites asinuatus* ERBEN, L.Dev., Fr., $\times 7.5$ (8).—3. *Pseudobactrites*; 3a, *P. peneau* ERBEN, L.Dev., Fr., $\times 7.5$ (8); 3b, *P. bicarinatus* FERRONNIÈRE, L.Dev., Fr., $\times 7.5$ (8).—4. *Lobobactrites ellipticus* (FRECH), M.Dev., Ger., $\times 11$ (21). (Where orientation was possible, the venter is on the left.)

seems to be the internal cast of a not-yet camerate larva (Fig. 355,1c), that the first septum probably appeared in the late stages or at the end of the second ontogenetic phase.

At least the first septum lacks the ventral lobe (Fig. 356,1a) that develops in the following stages. In this septum, the siphuncle lies on the ventral side of the center (8). It acquires its ventral position in subsequent stages.

During later ontogenetic stages the ventral lobe may become obsolete and the

siphuncle may shift secondarily from a ventral to subventral position (7). Such regressive development occurs, however, only in rare individuals, excepting *Kokenia*, where it is the rule in the late ontogenetic stages (Fig. 356,3b).

PHYLOGENY AND EVOLUTION

The Bactritida are thought to have evolved, probably in Ordovician time, from orthoconic and longiconic orthochoanitic

nautiloids with a globular protoconch and eccentric siphuncle (probably some member of the Orthocerida). This is suggested by the primitive shape of the earlier ontogenetic stages of *Bactrites* where a ventral lobe is still lacking and the siphuncle is still eccentric, as well as by the retrogressive development of the ventral lobe in some specimens and the position of the siphuncle in gerontic individuals.

It seems that within the Bactritida, two main phylogenetic groups can be distinguished—the Bactritidae, which had their acme during the Middle and Late Devonian, and the Parabactritidae, which had their main development in Permian time (Fig. 357).

The persistent stock is represented by *Bactrites*, which is first known in the Silurian (33, pl. 136-137) and persists into the Permian, but which may have existed in Ordovician time, as indicated by its Ordovician offshoot, *Eobactrites*. Another persistent stock is formed by *Lobobactrites*, which erroneously has been reported to appear in the Silurian (Ludlovian) (7), whereas the oldest known true representatives actually come from the Early Devonian (late Siegenian, Emsian). It is known, therefore, from Early to Late Devonian.

Since *Eobactrites* is stratigraphically isolated from other bactritids, some authors have suggested that it should be excluded from the Bactritida. However, the fact that *Bactrites* now is known from the Silurian makes the stratigraphic interval separating *Eobactrites* from later bactritids seem less significant.

It is believed that a trend toward decrease in size of the protoconch can be discerned in the evolution of the Bactritida (25) and that possibly the larval phase became generally prolonged, as has been demonstrated in *Cyrtobactrites* and *Pseudobactrites* (8). The available evidence, however, is as yet incomplete.

Iterative evolution is evident in the formation of a lateral lobe and lateral sinus which were acquired independently in different lines, as indicated by the pattern of sutures (e.g., *Lobobactrites*, *Koķenia*, *Aktastioceras*, *Tabantaloceras*) or growth lines (e.g., *Cyrtobactrites*, *Pseudobactrites*). Homeomorphy occurs in *Pseudobactrites*,

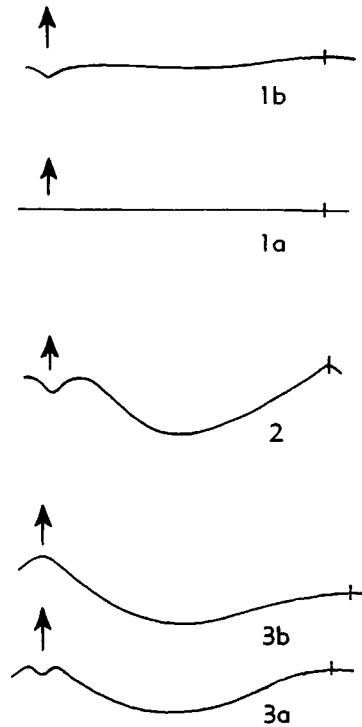


FIG. 356. Diagrams illustrating the development of the suture in some Bactritida.—1. *Bactrites schlotheimi* (QUENSTEDT); 1a, earliest suture; 1b, adult suture (8, 21).—2. *Lobobactrites*; adult suture (21).—3. *Koķenia obliquecostata* HOLZAPFEL; 3a, early suture; 3b, late suture (7).

in which the biconvex, rectiradiate growth lines and peristome resemble those of the Agoniatitidae and Anarcestidae. Furthermore, the ventrolateral ridges of *Pseudobactrites bicarinatus* strikingly resemble analogous ridges of certain representatives of the ammonoid *Gyroceratites*.

The Bactritidae seem to have given rise to the Parabactritidae, as suggested by intermediate features (septal necks, apical angle, length of camerae) of the primitive genus *Parabactrites*.

Some authors, especially SCHINDEWOLF, have regarded the Bactritidae as ancestors of the coiled ammonoids (17, 21), whereas others, especially SPATH (28), believed that the ammonoids were derived from coiled nautiloids of the type of *Barrandeoceras*. The latter postulate is based on the similarity in shape of the conchs of these genera and those of early coiled ammonoids. Fundamental differences, however, are seen

in the shape of the protoconch and in absence of a ventral lobe in the above-mentioned nautiloids. In my opinion (6,8), evolution of early ammonoids probably took place in the very early Devonian (probably Siegenian) via *Bacrites*→*Lobobacrites*→*Cyrtobacrites*→*Anetoceras*→*Teichtoceras*→(?*Convoluticeras*)→*Mimagoniatites*→Anarcestidae. The evidence consists of (1) the combination of a ventral siphuncle and ventral lobe, which is common to both Bacritidae and early coiled Ammonoidea; (2) the morphological identity (primitive species of *Anetoceras*), or at least similarity, of early ontogenetic stages in both; (3) the *Lobobacrites*-like growth lines, peristome, sutures, and whorl section of the most primitive Anarcestaceae; (4) the similarity of annular elevations in both groups; and (5) the gradual increase of coiling and involution, which, among other features, characterizes the above-mentioned sequence of genera.

The Bacritida have been regarded as the ancestors of the Belemnoidea (*sensu lato*), first by HYATT & SMITH (1905, p. 204), later by GRABAU (11), and finally by SHIMANSKIY (24), whereas other authors look for ancestors of the belemnoidea in orthoconic nautiloids. The first-stated opinion, however, is supported by the invariable ventral position of the siphuncle, as well as by the identical shape of the protoconchs (and their inclination in some specimens) in both Bacritida and Belemnoidea. Recently, ERBEN (6) has suggested a diphyletic origin of the Belemnoidea from different groups of the Bacritida. He considered the Bacritidae as ancestors of the Protobelemnoidea and the Parabacritidae as those of the Belemnoidea *s.s.* The first suggestion is supported by the small apical angles and longiconic shapes of the conchs, by the orthochoanitic septal necks with cylindrical connecting rings, and by the relatively high camerae in the phragmocones of both Bacritidae and early Protobelemnoidea. The evidence supporting the second suggestion consists of the large apical angles and breviconic shapes of the conchs, the tendency to develop cyrtchoanitic septal necks with inflated connecting rings, and the invariably short camerae of the phragmocones in the Parabacritidae and the Belemnoidea *s.s.*¹

DISTRIBUTION

The oldest known bacritids have been found in Morocco, Czechoslovakia (Bohemia), and Germany (Hunsrück, Harz and Kellerwald Mountains). Thus, they come from regions which once were part of the Mediterranean Tethyan sea, or at least marginal extensions of it. This accords with the fact that in Early Devonian time bacritids apparently are restricted to the Hercynian-Bohemian magnafacies where they are found to be common in Middle Devonian beds, and that they have never been found in the typical Rhenish magnafacies. The persistent stocks of *Bacrites* and *Lobobacrites* were world-wide in distribution during Middle and Late Devonian, as well as in Carboniferous and Permian times. The short-range offshoots, however, always seem to have a more restricted geological distribution.

The oldest known species ("*Orthoceras*" *pygmaeum* DEKONINCK) tentatively referred to the Parabacritidae comes from the Lower Carboniferous of Belgium, whereas the Mississippian *Bacrites nevadensis* YOUNGQUIST from Nevada (USA) is considered to be close to their direct ancestor (24). On the other hand, the same species was cited by FLOWER & GORDON (10) as possibly related to the Carboniferous belemnites. The main development of this group, however, apparently occurred in the Uralian geosyncline in Permian time.

¹ It should be noted that FLOWER & GORDON (10) deny any difference between Protobelemnoidea ("*aulacoceratids*") and Belemnoidea *s.s.* The same view was expressed by FLOWER (1944) in pointing out that intermediate forms serve to connect the two groups. This view, however, is based on errors of earlier authors (MOJSISOVIC, GEMMELLARO, and others) who wrongly included some Triassic phragmocones (e.g., "*Aracitites*" *convergens* HAUER, 1847; "*A.*" *conicus* and "*A.*" *ellipticus* MOJSISOVIC, 1871; "*A.*" *meneghinii* SALOMON, 1895; "*A.*" *giganteus* GEMMELLARO, 1904; "*A.?*" *breviconus* REIS, 1907 [= "*A.*" sp., MOJSISOVIC, 1886, pl. 16, fig. 4], and *Zugmontites mojsisovici* REIS, 1907) in the Protobelemnoidea (former "*Aulacoceratidae*"), perhaps influenced by the idea, commonly held in earlier times, that true Belemnoidea first occur in the Lower Jurassic and that all earlier dibranchiats must have been aulacoceratids. That the above-mentioned species are not representatives of the Protobelemnoidea, however, is demonstrated by their cyrtchoanitic septal necks with inflated connecting rings and their short camerae, as well as by the breviconic shape and large apical angle of their phragmocones. In these features, they differ strongly from all protobelemnooids and resemble the Belemnoidea *s.s.*; they must, therefore, be included in the latter. Thus, no intermediate forms between Protobelemnoidea and Belemnoidea exist. On the contrary, a strong morphological difference between both groups, as expressed in the above-mentioned characters, is evident.

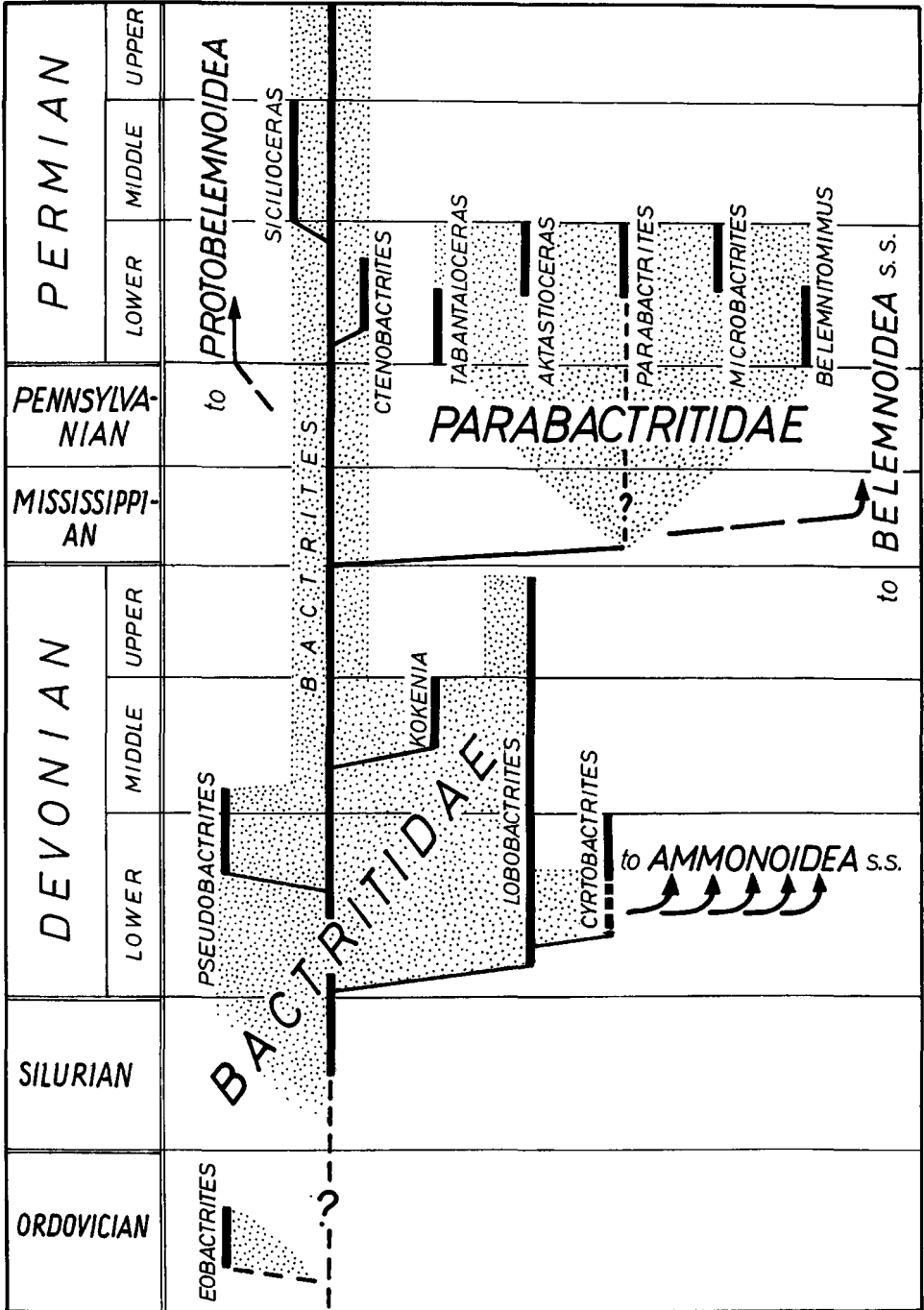


Fig. 357. Suggested phylogeny of the Bactritida (8).

TAXONOMIC POSITION

Differing opinions concerning affinities of the bacritids have been noted in the introduction. The Bacritida are morphologically intermediate between the nautiloid orders and coiled Ammonoidea, showing generally the orthoconic conch of the former and the combination of marginal siphuncle and siphonal lobe of the latter. The cyrtocoenic *Cyrtobacrites* shows that this intermediate position is also expressed in the shape of the shell. This morphologically intermediate position, in the opinion of certain authors, including myself, seems to imply an intermediate position in phylogeny. Under these circumstances, it would seem that the Bacritida, from the point of view of morphology, as well as of phylogeny, could be included with equal justification in either of the two groups, i.e., their ancestors or their descendants, if questions of diagnosis were not involved.

It has been claimed (21) that the basic and only fundamental difference between nautiloids and ammonoids is the simultaneous presence of a marginal siphuncle and a siphonal lobe in the latter. If this is upheld, the Bacritida *per definitionem* would have to be assigned to the Ammonoidea. Although the taxonomic value of siphuncle position and suture shape has been questioned (28,29), the objections have been rejected (2,17,22). In the meantime, however, at least five undoubted nautiloid genera (*Lobendoceras*, *Cyrtendoceras*, *Ventroloboceras*, *Thylacoceras*, *Catoraphiceras*) have been described (31,32) with some species showing a marginal (ventral) siphuncle and at the same time a siphonal (ventral) lobe that in shape and position strongly resembles the corresponding lobe of the Bacritida and primitive coiled ammonoids. However, width of the siphuncle, presence of endocones, or shape of the septal necks suggests that these are examples of homeomorphy. Since in other groups of animals the occurrence of homeomorphic forms neither alters nor affects the basic structure of natural groups, the features mentioned should be regarded as general diagnostic characters of the Ammonoidea. For this reason, I am inclined to include the bacritids in this order.

Recently, some authors (17,24) have regarded the bacritids as an independent order, or even superorder, on the same level with the Nautiloidea and the Ammonoidea. In view of their obvious phylogenetical significance, in a way this may seem to be justified. However, the diagnostic differences between bacritids and ammonoids (i.e., the former never being perfectly coiled and their ventral lobe being less developed) are judged by me to have comparatively low taxonomic value and do not seem to support this suggestion.

CLASSIFICATION

As emphasized by SHIMANSKIY (24), the characters of highest taxonomic value in the Bacritida evidently are the apical angle (i.e., the longiconic or breviconic shape of the conch), and the relative height of camerae. Furthermore, the shape of the septal necks has been shown to be of equal importance (7). It must be noted, however, that the relative height of the camerae is rather variable in longiconic bacritids; only in breviconic forms does it become somewhat stabilized. The cited features have been used to distinguish two phylogenetic groups as families, namely, the Bacritidae and the Parabacritidae.

Shells of the Parabacritidae closely resemble exfoliated phragmocones of the Belemnoida *s.s.*, a feature that has led to the suggestion by FLOWER & GORDON (10) that they may not belong to the Bacritida but to the Coleoidea. These authors have pointed out two features which seem to support this interpretation—(1) the shell surfaces of the Parabacritidae, being smooth or having only a very faint relief, could be interpreted, in the opinion of the authors, as one of the two inner layers of a conotheca, and (2) no living chamber had been found in the Parabacritidae. However, more recently a living chamber of *Parabacrites ruzhencevi* has been figured by SHIMANSKIY (26, pl. 12, fig. 4) (see Fig. 360, I). As far as FLOWER & GORDON's first argument is concerned, I cannot share their view, because smooth or only very faintly sculptured surfaces are by no means restricted to the inner layers of the belemnoid phragmocone. They are, however, very

common in the outer layer of the bactritids, particularly in less advanced forms, and only in some advanced forms does the sculpture become more prominent.

Also the question has been discussed whether the Parabactritidae could be phragmocones of belemnites which had chitinous rostra, not preserved in fossils (10). Such an assumption would support J. ROGER's (1952) opinion that the chitinous rostra of the Lower Jurassic Chitinotheuthidae may represent an archaic condition. This was not accepted by FLOWER & GORDON and both concepts seem very improbable indeed.

The problem of the morphological differences between belemnite phragmocones and the conchs of the Parabactritidae is still under discussion. FLOWER & GORDON (10) quoted SHIMANSKIY (24) as suggesting that the relatively long septal necks of the bactritids differed from the short ones of atracitid belemnites, and they denied this difference. SHIMANSKIY (26), however, pointed out that he had been misunderstood, apparently on account of an incorrect translation of his paper, and that he had stated, on the contrary, that the short septal necks of the Parabactritidae are in contrast to long ones of the belemnite *Atractites*. FLOWER & GORDON (10) also denied that an important difference in size distinguishes genera of the Parabactritidae from fossils classed as belemnites, because some species of *Atractites* are very small.

This discussion seems to afford little help, because *Atractites* (= *Ausseites* of FLOWER) is referred to as an example of the belemnites. However, this genus does not belong to the Belemnnoidea *s.s.* but to the Proto-belemnnoidea (= "aulacoceratids"), which strongly differ in the nature of their phragmocones from both the Parabactritidae and Belemnnoidea. On the other hand, the species "*A.* *convergens*", with which this discussion is concerned, does not belong to *Atractites* but to a new genus of Triassic Belemnnoidea *s.s.* In this species the exact length of the septal necks is not well known and from the figures given by MOJŠIŠOVIĆ distinction between septal necks and connecting rings cannot be made. Generally, septal necks of the Belemnnoidea *s.s.* are relatively short, particularly in Jurassic and Cretaceous genera. Thus, no significant dif-

ference from the bactritids seems to be observable in this respect. In some Proto-belemnnoidea the septal necks are considerably longer (e.g., *Choanoteuthis*). In most genera (e.g., *Aulacoceras*, *Atractites*=*Ausseites*) they are about the same in length or only slightly shorter than in the Bactritida. In general, it seems that the length of the septal necks is no criterion for distinguishing phragmocones of the Coleoidea and conchs of the Parabactritidae.

Solution of these problems depends on whether the Parabactritidae were ectocochleate or endocochleate cephalopods. It is true that the absence of rostra in fossils belonging to the Parabactritidae could be explained by conditions of preservation. Thus, no conclusive evidence seems to favor an assumption that this group was not endocochleate. On the other hand, ectocochleate cephalopod shells generally are characterized by the presence of a living chamber. Furthermore, the ectocochleate position of the shell can be indicated by the presence of a hyponomic sinus. Although the latter has not yet been described from the Parabactritidae and has been found lacking in the one example of figured growth lines (*Parabactrites*; 26, pl. 12, fig. 3a), this group has been found to possess true living chambers, as previously mentioned. Therefore, and in agreement with SHIMANSKIY (24, 26), they are placed here in the Bactritida.

On the basis of presence of ribs, a family named Ctenobactritidae has been established (24), which, however, has been shown not to represent a natural unit (7), because the principal characters of its genera coincide with those of the Bactritidae. Furthermore, because of the striking configuration of growth lines and peristome of the fossils, a separate family (Bojobactritidae) has been proposed for *Bojobactrites* (13), a junior synonym of *Pseudobactrites*. However, the growth lines and peristome of bactritids are generally to be considered as characters of subordinate taxonomic value, and similar trends are indicated among some Bactritidae. For these reasons, the family Bojobactritidae is rejected (7).

In the Bactritida the most important features for differentiation of genera are judged to be (1) general shape of the suture, (2) nature of the growth lines, (3)

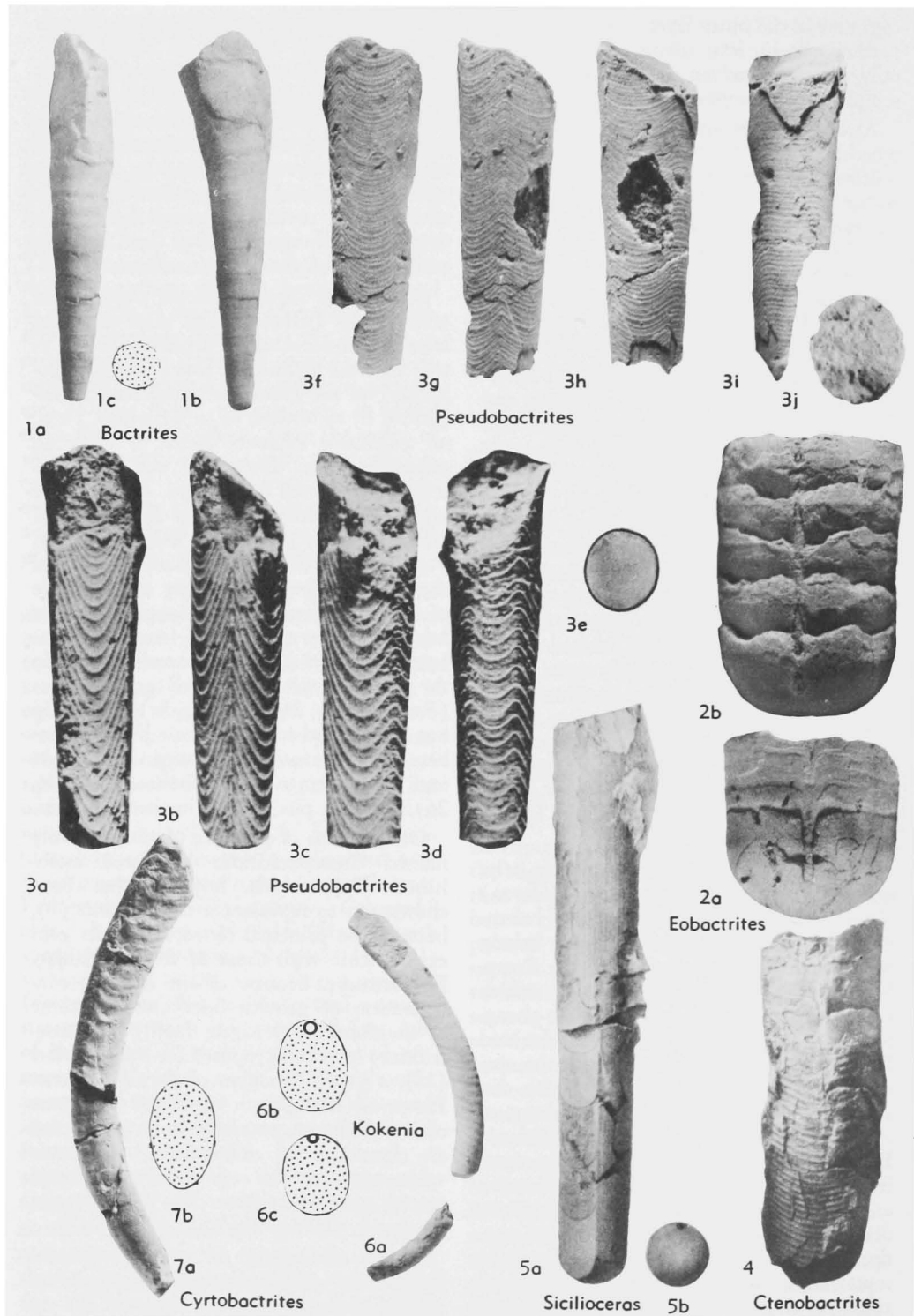


FIG. 358. Bactritidae (p. K501-K502).

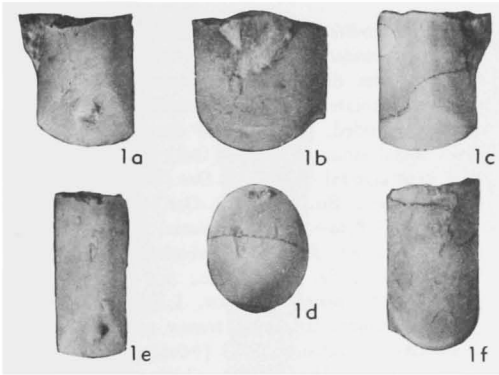


FIG. 359. **Lobobacrites ellipticus* (FRECH)
(Bacritidae) (p. K501-K502).

characters of the peristome, and (4) shape of the conch, including its cross section. Variations of these features are regarded as secondary in importance and are used for distinction of species.

SYSTEMATIC DESCRIPTIONS

Subclass BACTRITOIDEA Shimanskiy, 1951

[*nom. transl.* MOORE, herein (*ex* order Bacritoidea SHIMANSKIY, 1951)] [=Bacritoidea RUZHENTSEV, 1957 (superorder)]

Conch orthoconic to cyrtoconic, longiconic or breviconic, with small or large apical angle. Siphuncle narrow, invariably in contact with ventral wall; septal necks orthochoanitic to cyrtochoanitic. Suture uniformly with V-shaped ventral lobe. Protoconch globular to egg-shaped (7,17,21,24). *Ord.-Perm.*

Order BACTRITIDA Shimanskiy, 1951

[*nom. correct.* SHIMANSKIY, 1954 (*pro* order Bacritoidea SHIMANSKIY, 1951)] [=Bacritina MILLER & FURNISH, 1954 (suborder)]

Characters of the subclass. *Ord.-Perm.*

Family BACTRITIDAE Hyatt, 1884

[=Bacritaceae KINDLE & MILLER, 1939 (superfam.); incl. Ctenobacritidae SHIMANSKIY, 1951; Bojobacritidae HORNÝ, 1957; Lobobacritidae SHIMANSKIY, 1962; Bacritaceae SHIMANSKIY, 1962]

Conch orthoconic to cyrtoconic, longiconic, with small apical angle (less than about 10 degrees). Septal necks orthochoanitic. Height of camerae variable (7,21, 24). *Ord.-Perm.*

Bacrites SANDBERGER, 1843 [**B. subconicus*; OD] [=?*Stenoceras* D'ORBIGNY, 1849; *Hemibacrites* SHIMANSKIY, 1954]. Conch orthoconic, cross section nearly circular to broadly oval. Sutures almost straight, with small ventral lobe only, on flanks rectiradiate or prorsiradiate. Growth lines rursiradiate, with broad shallow ventral sinus and low dorsal saddle (15,18,21,24). ?*Sil., L.Dev. (U. Siegen.)-U. Perm., Eu.(Ger.-Fr.-Urals-Sicily)-N. Afr.(Morocco)-Australia-N. Am.(USA-Mex.)-S. Am.(Peru).*—FIG. 358,1. **B. subconicus*, M. Dev., Ger.; 1a-c, holotype, vent., lat., transv. sec., $\times 3$ (Erben, n).

?**Ctenobacrites** SHIMANSKIY, 1951 [**C. costatus*; OD]. Like *Bacrites* but with rursiradiate ribs forming broadly rounded ventral sinus and broad dorsal saddle (23-25). [If the isolated conical protoconch figured by SHIMANSKIY (25) really belongs to *Ctenobacrites*, this genus should be excluded from the Bacritida.] *L.Perm., USSR.*

C. (Ctenobacrites). Ribs rounded and intercostal space relatively broad (27). *L.Perm., USSR.*—FIG. 358,4. **C. costatus*, Urals; vent., $\times 0.75$ (24).

C. (Mirites) SHIMANSKIY, 1962 [**C. mirus* SHIMANSKIY, 1954; OD]. Ribs flattened and intercostal space narrow (27). *L.Perm., USSR.*

Cyrtobacrites ERBEN, 1960 [**C. sinuatus*; OD]. Conch exogastrically cyrtoconic, with narrow oval cross section. Growth lines with linguiform ventral sinus; ventrolateral saddles, lateral sinuses, and dorsal saddle lacking or slightly developed (7, 8). *L.Dev.(Ems.), Eu.(N.Fr.-Ger.)*.—FIG. 358,7. **C. sinuatus*, Ger.; 7a, lat., $\times 2$; 7b, transv. sec., $\times 5$ (7).

Eobacrites SCHINDEWOLF, 1932 [**Bacrites sandbergeri* BARRANDE, 1867; OD]. Like *Bacrites* but cross section circular, ventral lobe narrower and deeper, and growth lines rectiradiate without dorsal saddle (1,20,22). *L.Ord.(Llandeil.)*, Eu. (Czech.-Norway).—FIG. 358,2. **E. sandbergeri* (BARRANDE), Czech.; 2a,b, vent. views, $\times 1$ (Erben, n).

Kokenia HOLZAPFEL, 1895 [**K. obliquecostata*; OD]. Conch exogastrically cyrtoconic to almost gyroconic, with oval cross section and with fold-like sigmoidal rursiradiate ribs which are faint dorsally and ventrally. Sutures of juvenile stages with small ventral lobe, deeply rounded lateral lobes and prominent dorsal saddle. In late ontogenetic stage place of ventral lobe is taken by secondary ventral saddle and siphuncle shifts from ventral to subventral position (7). *M.Dev. (Givet.)*, Eu.(Ger.-Fr.-Czech.).—FIG. 358,6. **K. obliquecostata*, Ger.; 6a, lat. (venter right), $\times 1.5$; 6b, transv. sec. adult shell, $\times 5$; 6c, transv. sec. juv. shell, $\times 5.4$ (7).

Lobobacrites SCHINDEWOLF, 1932 [**Bacrites ellipticus* FRECH, 1897 (= *Bacrites carinatus* SAND-

BERGER & SANDBERGER, 1852 (*partim*), non *Orthoceras carinatus* MÜNSTER, 1840; OD]. Like *Bactrites* but cross section more narrowly oval, some forms with flattened flanks and rarely with dorsal carina. Sutures with small ventral lobe, well-developed lateral lobes and dorsal saddle. Growth lines as in *Bactrites* but more strongly rursiradiate, dorsal saddle more prominent and commonly pointed (20,21,30). *L.Dev.*(?*U.Siegen.*)-*U.Dev.*, Eu.(N.Fr.-S.Fr.-Ger.-Pol.-Czech.-USSR)-N. Afr.(Morocco)-Asia (China)-Australia-N. Am.—FIG. 359,1. **L. ellipticus* (FRECH), M.Dev., Ger.; 1a-d, lectotype (SANDBERGER & SANDBERGER, 1852, pl. 17, fig. 3, *partim*), vent., dors., lat. (venter at right), adapical, $\times 2$; 1e,f, another of the SANDBERGERS' specimens, vent., lat. (venter at left), $\times 2$ (Erben, n).

Pseudobactrites FERRONNIÈRE, 1921 [**P. bicarinatus*

(=*Bojobactrites ammonitans* HORNÝ, 1957); OD] [= *Bojobactrites* HORNÝ, 1957]. Like *Bactrites* but growth lines differentiated; ventral sinus linguiform, ventrolateral saddle prominent, lateral sinus deeply rounded, and likewise dorsolateral saddle and dorsal sinus (7,9,13). [Only the type-species has ventrolateral ridges.] *L.Dev.*(*U.Ems.*)-*M.Dev.* (*basal Eifel.*), Eu.(Fr.-Czech.-Ger.)-Asia(Turkey). —FIG. 358,3a-e. **P. bicarinatus*, L.Dev., Czech. (3a-d)-Fr.(3e); 3a-d, vent., ventrolat., lat., dors., $\times 2.25$ (13); 3e, transv. sec., $\times 3$ (7). —FIG. 358,3f-j. *P. péneati* ERBEN, L.Dev., Fr.; 3f-j, vent., ventrolat., lat., dors., transv. sec., $\times 1.5$ (7). *Siciloceras* SHIMANSKIY, 1954 [**Orthoceras paternoii* GEMMELLARO, 1887; OD]. Like *Bactrites* but with straight longitudinal ribs (24). *M.Perm.*, Eu. —FIG. 358,5. **S. paternoii* (GEMMELLARO), Sicily; 5a,b, vent., transv. sec., $\times 0.5$ (34).

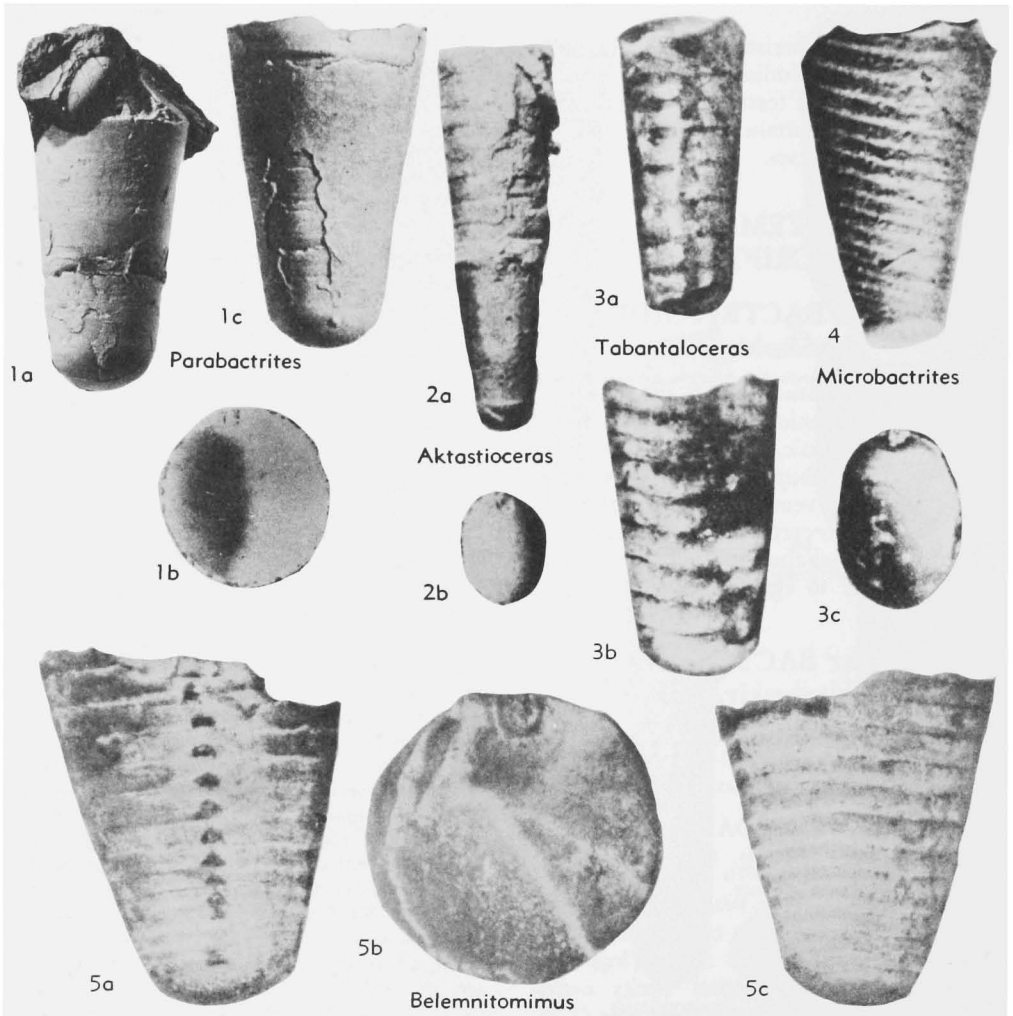


FIG. 360. *Parabactritidae* (p. K503).

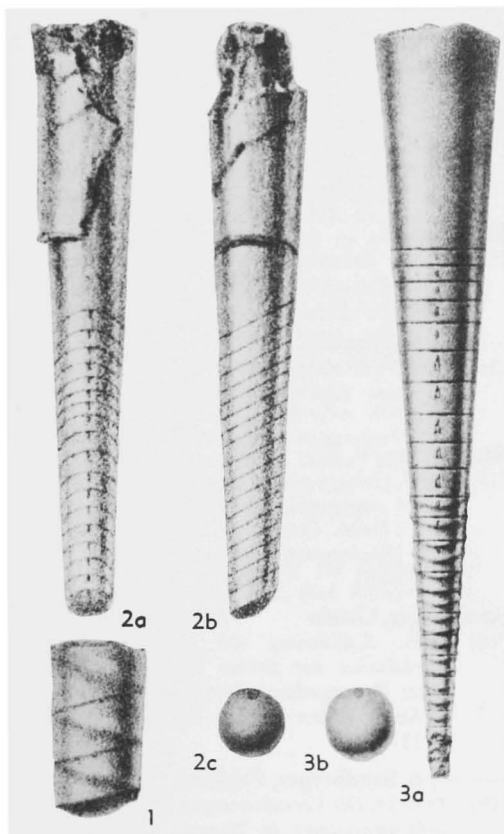


FIG. 361. Doubtful Genera; 1, *Cyclobactrites*; 2, *Devonobactrites*; 3, *Cochleiferoceras* (p. K503).

Family PARABACTRITIDAE Shimanskiy, 1951

[=Parabactritaceae SHIMANSKIY, 1962]

Conch orthoconic and breviconic, with large apical angle (more than about 10 degrees). Septal necks ?orthochoanitic or suborthochoanitic to cyrtchoanitic. Length of camerae equal to, or less than, 0.3 of conch diameter (7,24). ?*Carb.*, *Perm.*

Parabactrites SHIMANSKIY, 1948 [**P. ruzhencevi*; OD]. Conch slightly breviconic (apical angle 12 to 18 degrees); cross section almost circular to broadly oval. Septal necks ?orthochoanitic or ?suborthochoanitic. Sutures rectilinear except for ventral lobe (23,24). ?*Carb.*, *L.Perm.*, USSR.—FIG. 360,1. **P. ruzhencevi*, Urals; 1a, vent., with body chamber, $\times 1.36$ (SHIMANSKIY, 1960); 1b,c, oral, vent., $\times 2$ (24).

Aktstioceras SHIMANSKIY, 1948 [**A. kruglovi*; OD]. Conch slightly breviconic; cross section broadly to narrowly oval. Siphuncle with septal

necks ?suborthochoanitic. Suture with small ventral lobe, rounded lateral lobes and dorsal saddle (23). *L.Perm.*, USSR.—FIG. 360,2. **A. kruglovi*, Urals; 2a,b, vent., transv. sec., $\times 3$ (24).

Belemnitomimus SHIMANSKIY, 1954 [**B. palaeozoicus*; OD]. Like *Microbactrites* but conch much more strongly breviconic (apical angle about 30 degrees), camerae shorter, shell smooth, and sutures with weak dorsal saddle and some specimens without ventral lobe (24). *L.Perm.*, USSR.—FIG. 360,5. **B. palaeozoicus*, Urals; 5a-c, vent., adoral, lat., $\times 2.5$ (24).

Microbactrites SHIMANSKIY, 1954 [**M. scorobogatovae*; OD]. Conch strongly breviconic (apical angle about 20 degrees); camerae very short; cross section almost circular to broadly oval. Siphuncle with cyrtchoanitic septal necks. Sutures with small ventral lobe only. Surface of shell bearing oblique folds (24). *L.Perm.*, USSR.—FIG. 360,4. **M. scorobogatovae*, Urals; lat., $\times 9$ (24).

Tabantaloceras SHIMANSKIY, 1954 [**T. planum*; OD]. Like *Aktstioceras* but cross section more narrowly oval, with flattened flanks and cyrtchoanitic septal necks (24). *L.Perm.*, USSR.—FIG. 360,3. **T. planum*, Urals; 3a-c, vent., lat., transv. sec., $\times 2.5$ (24).

DOUBTFUL GENERA

Cochleiferoceras SHIMANSKIY, 1962 [**Orthoceras cochleiferum* SANDBERGER & SANDBERGER, 1852; OD]. Similar to *Bactrites*, but apical angle larger, camerae less high, ventral lobe and dorsal saddle absent and sculpture consisting of strong oblique foldlike ribs (27). [May not belong to Bactritida.] *M.Dev.*, Eu.(Ger.).—FIG. 361,3. **C. cochleiferum* (SANDBERGER & SANDBERGER); 3a,b, vent., adoral; $\times 2$ (19).

Cyclobactrites SHIMANSKIY, 1955 [**C. erbeni* (= *Bactrites carinatus* SANDBERGER & SANDBERGER, 1852, pl. 17, fig. 3e, non cetera); OD]. Like *Bactrites*. Sculpture consisting of oblique foldlike ribs (27). [Generic independence doubtful because of occurrence of same sculpture in adult stages of *Bactrites* and *Lobobactrites*.] *M.Dev.*, Eu.(Ger.).—FIG. 361,1. **C. erbeni*; venter on right; $\times 4$ (19).

Devonobactrites SHIMANSKIY, 1962 [**Orthoceratites obliquiseptatum* SANDBERGER & SANDBERGER, 1852; OD]. Like *Bactrites*. Sutures dorsally inclined and camerae relatively low (27). [Generic independence doubtful because of highly variable orientation of sutures within single individuals of certain representatives of *Bactrites*. Lowness of camerae in this case appears not to be a diagnostic criterion, being caused here by normal crowding of sutures in late ontogenetic stages, which occurs in all ectocochleate cephalopods. *M.Dev.*, Eu.(Ger.).—FIG. 361,2. **D. obliquiseptatus* (SANDBERGER & SANDBERGER); 2a,b, vent., lat. with venter on right; $\times 2$; 2c, adoral; all $\times 1$ (19).

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SOURCE OF ILLUSTRATIONS

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