



**Shell Morphology and Ultrastructure of the Early Carboniferous Coleoid
Hematites FLOWER & GORDON, 1959 (*Hematitida* ord. nov.)
from Midcontinent (USA)**

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4 Text-Figures and 7 Plates

USA
Carboniferous
Coleoids
Ultrastructure
Phylogeny

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**Schalenmorphologie und Ultrastruktur
des oberkarbonen Coleoiden *Hematites* FLOWER & GORDON, 1959 (*Hematitida* ord. nov.)
aus den USA**

Zusammenfassung

Gut erhaltene Schalen des unterkarbonen Coleoiden *Hematites* aus Arkansas (USA) wurden mit Hilfe des Rasterelektronenmikroskops untersucht. Sie zeigen folgende charakteristische Merkmale:

- 1) Die Conothek ist vielschichtig und unterscheidet sich dadurch von bekannten Coleoiden. Die Hauptschicht und zwei weitere Lagen sind prismatisch. Eine senkrecht lamellierte Lage ist reich an organischer Matrix. Eine eigentliche Perlmutter-schicht und eine waagrecht lamellierte Lage fehlen.
- 2) Das Rostrum ist kurz und gerillt und reich an organischer Matrix mit mehr als zwei Furchen ohne feste Position. Der Kamm zwischen den Längsrillen wird von einer Reihe gefüllter Gruben gebildet, die durch Querwände getrennt sind. Diese "Grübchenkanäle" können durch die gesamte Dicke des Rostrums hindurch verfolgt werden. Die schmalen Zwischenräume zwischen den Kämmen erstrecken sich bis zur Conothek. Die Skulptur des Rostrums von *Hematites* ist vergleichbar mit der der externen Oberfläche des Proostracums bei *Megateuthis* (DOGUZHAeva et al., dieser Band). Die Kämmen und Gruben des Rostrums von *Hematites* scheinen der Befestigung von Weichteilgewebe gedient zu haben, wogegen bei Belemniten die Weichteile an der Oberfläche des Proostracums, nicht aber am Rostrum befestigt gewesen zu sein scheinen.
- 3) Der Protoconch ist kugelig. Gewöhnlich ist er mitsamt den ersten Kammern weggebrochen. Das abgebrochene Ende des Phragmocon ist in der Mitte mit länglichen, calcitischen Stäbchen verfüllt, die am abgebrochenen apikalen Ende des Phragmocon beginnen und sich bis zum adapikalen Ende fortsetzen.

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3) Das Peristom wird von der letzten Kante des Rostrums gebildet, das seinerseits die letzte Kante des Phragmokons umgibt. Das Peristom zeigt bei fehlendem Proostracum eine breite und eher tiefe U-förmige laterale oder ventrolaterale Einbuchtung. Bei zwei Exemplaren mit erhaltenem Peristom ist die "Wohnkammer" 1,5 bis 2 mal so lang wie die letzte Kammer.

Der Hauptunterschied zwischen *Hematites* und anderen, jüngeren rostraten, zu den Aulacocerida gestellten Coleoiden ist, dass *Hematites* ein kurzes Rostrum, eine kurze "Wohnkammer", ein Peristom mit U-förmigem ventralem oder ventrolateralem Sinus und eine vielschichtige Conothek ohne typische Perlmutter-schicht besitzt. Dorsale und ventrale Fortsätze und ein Proostracum fehlen. Im Gegensatz dazu haben Aulacocerida ein langes, schlankes Rostrum mit dorsalen und ventralen Kämme und eine Conothek mit perlmuttriger oder horizontal geschichteter Lage. Auf der Grundlage dieser Unterschiede stellen wir die neue Ordnung Hematitida ord. nov. für die Familie Hematitidae GUSTOMESOV, 1976 auf.

Abstract

Well preserved shells of the Early Carboniferous coleoid *Hematites* from Arkansas (USA) were studied with SEM. They show the following characteristic features:

- 1) The conotheca is multilayered, and structurally different from all known coleoids in this respect. It consists of five to six layers. The principal and two additional layers are prismatic, and a vertically lamellar layer is rich in organic matrix; a typical nacreous layer and horizontally lamellar layer are absent.
- 2) The rostrum is short, ridged, rich in organic matrix, and with more than two furrows without constant position. The crest of each longitudinal ridge is covered by a row of filled pits separated by partitions. The pit-channels can be traced through the entire rostrum thickness. The narrow interspaces between the ridges extend close to the conotheca. The ornamentation of the *Hematites* rostrum is comparable with that on the external pro-ostracal surface in *Megateuthis*, studied with SEM (DOGUZHAeva et al., herein). In the *Hematites* rostrum the ridges and pits seem to have served for attachment of soft tissues, while in belemnites the pro-ostracal surface, but not the rostrum, seems to have been strongly attached to the soft tissues.
- 3) The protoconch is spherical. Together with first chambers it is usually truncated. The broken end of the phragmocone is plugged with central longitudinal, calcareous rods that begin at the broken apical end of the phragmocone and continue to the apical end of the rostrum.
- 4) The peristome is formed by the terminal edge of the rostrum that surrounds the terminal edge of the phragmocone. The peristome is without a pro-ostracum; it shows a broad and rather deep, U-shaped ventral or ventro-lateral sinus. In two specimens with preserved peristome the "living" chamber is equal to about 1.5 to 2 times the length of the last chamber.

The main difference between *Hematites* and other, younger, rostrum-bearing coleoids, assigned to Aulacocerida, is that *Hematites* has a short rostrum, short "living" chamber, a peristome with a broad U-shaped ventral or ventro-lateral sinus, multilayered conotheca without a typical nacreous layer; it has no ventral and dorsal apertural projections and growth lines, and it lacks a pro-ostracum. As a contrast, aulacocerids have a long slender rostrum, a long tubular living chamber with dorsal and ventral crests, and a conotheca with a nacreous or horizontally lamellar layer. On the basis of these differences we erect the order Hematitida ord. nov. for the family Hematitidae GUSTOMESOV, 1976.

1. Introduction

The earliest known rostrum-bearing coleoids were described from the Devonian and Lower Carboniferous (Vise) of Belgium (KONINCK, 1843), and from the Lower Carboniferous (Middle and Upper Mississippian) of the United States (FLOWER, 1945; FLOWER & GORDON, 1959; GORDON, 1965). The existence of Devonian and Carboniferous coleoids was considered at the beginning as incredible, and therefore papers published by KONINCK (1843) and FLOWER (1945) were ignored for a long time. Later numerous specimens from the Upper Mississippian of the USA, described by FLOWER & GORDON (1959), made it unquestionable that the rostrum-bearing coleoids appeared early in cephalopod evolution, and in the Early Carboniferous they were represented by at least four genera. The genus *Hematites* FLOWER & GORDON, 1959 is one of them, and according to GORDON (1966) it shows much similarity to the Visean specimens represented by the apical portion of the rostrum described by KONINCK (1843).

The present paper deals with SEM studies of shell morphology and ultrastructure in *Hematites*. More than 30 specimens of this genus were collected by the second author from the Upper Mississippian in Arkansas. The data obtained confirm the detailed description of the external shell morphology in the genus published by FLOWER & GORDON (1959) and GORDON (1964), and it also includes new information on the conotheca structure, conotheca rostrum/mantle attachment, "living" chamber length, and morphology of the adoral portion of the rostrum.

To clarify the systematic position of the genus and its relationship to aulacocerids and belemnites, special attention was paid for comparison of shell structures in *Hematites* with Triassic aulacocerids and Jurassic belemnites. As a result a new order Hematitida is erected to comprise the family Hematitidae GUSTOMESOV, 1976.

2. Material and Method

The studied specimens assigned to *Hematites* were extracted from small, black, concretions about 5–6 cm in length and little less in width. Usually the length of a concretion is about the same as the length of a rostrum lying inside. Most rostra were strongly pyritized with a few exceptions. The latter were suitable for SEM studies. The exterior of the rostra was cleaned in an ultrasonic apparatus, coated with gold and examined with SEM. The rostrum was split mechanically from the phragmocone in order to study its inner surfaces. To study the ultrastructure, the rostra were cut longitudinally and transversally. The conotheca ultrastructure was studied in fractured or ground specimens in longitudinal and transverse fracture planes. The truncation was studied in longitudinal fractured or cut surfaces.

The material is stored in the Ohio University Zoological Collections (OUZC) in Athens, Ohio.

3. Geological Setting

Hematites is known only in the Lower Eumorphoceras zone of the Unites States – in the Fayetteville shale of northern Arkansas and the Chainman shale of western Utah (GORDON, 1965).

4. Previous Studies on *Hematites*

4.1. Morphology

The rostrum and phragmocone morphology of *Hematites* was described in detail by FLOWER & GORDON (1959) and GORDON (1964).

Erecting *Hematites* FLOWER & GORDON noted (1959, p. 818) that

“At first it seemed that it would not be possible to distinguish this form from the Triassic Aulacoceras, which it resembles in the general aspect of the rostrum, but the absence of good lateral furrows and the concentration of furrows on the venter supplies a difference.”

The authors demonstrated a great variability of many features in the genus, particularly the position and number of furrows, and the apex shape. In *Aulacoceras* the main morphological characters are much less variable.

According to FLOWER & GORDON (1959), the rostrum in *Hematites* is straight and adorally tubular, either with straight, bluntly pointed, or rounded apex. The outer rostral surface shows flat longitudinal ridges, separated by narrow interspaces and furrows. The ridges are crossed by numerous transverse striae. The furrows are traced from the apex to the apertural region, or they end at some distance from the apex. Usually they are situated on the ventral side, and some of them are not clearly distinguishable from the interspaces between ridges. Two species referred to as *Hematites*, *H. barbarae* and *H. burbankensis*, are distinguished primarily by the length of the furrows. In the former species the ventral furrow is present throughout growth, and in the latter the ventral furrow is absent on adult rostra. FLOWER & GORDON (1959) observed that the rostrum is principally fibrous, having no axial elements, nor distinct growth lines. In cross sections the rostra show coarse radial units similar to those in *Aulacoceras* and *Dictyocyonites*. These units are absent in the central zone around the phragmocone where the structure is irregularly vesicular.

The phragmocone structures were characterized by FLOWER & GORDON (1959) as follows. The phragmocones are

“moderately slender, faintly compressed in cross section, and show sutures which slope slightly forward from dorsum to venter but are straight, but sinuated”.

The siphuncle is subventral at early stages but later ventral. The septal necks are short. Segments are weakly swollen close to cylindrical. The authors noted that the initial portion of the phragmocone, including the protoconch, was usually truncated, and explained this as a result of poor calcification or absorption. They noted that the apical portions of the phragmocone had been removed prior to rostrum formation. The conotheca was described as thin and layered. In the material studied by FLOWER & GORDON the length of the “living” chamber, the conotheca surface and pro-ostracum could not be observed.

Among the co-existing Mississippian genera described by FLOWER & GORDON (1959), rostrum morphology in *Bacritimimus* is closely similar to that in *Hematites*, although it is not so well known as in *Hematites*. In this genus, the rostrum also has longitudinal ridges crossed by fine transverse striae and separated by narrow interspaces. The apex of the rostrum is unknown. However, in *Bacritimimus* the phragmocone is more compressed in cross section than in *Hematites*, and the sutures slope more distinctly forward from dorsum to venter, and also show a broad dorsal lobe and a V-shaped ventral lobe, which are missing in *Hematites*. At adult stages in *Bacritimimus* the siphuncle is also marginal and a neck lobe is developed. Septal necks are longer than in *Hematites*.

In *Eobelemnites* FLOWER, 1945 the phragmocone is strongly compressed and expands rapidly; sutures slope strongly forward from venter to dorsum; septal necks are relatively long. The pro-ostracum was illustrated by FLOWER

(1945). It consists of a central field with concentric growth lines and hyperbolar zones showing longitudinal striae.

Another Mississippian genus *Paleoconus* is easily distinguished from *Hematites* by its smooth rostrum with broad, rounded furrows, and by its slightly exogastrically curved apex. Besides, the sutures are straight and transverse, the septal necks are comparatively long, and the rostrum is more calcified than that in *Hematites*.

4.2. Systematics

FLOWER & GORDON (1959) regarded the four genera of the rostrum-bearing coleoids of the Late Mississippian age from the USA as primitive forms that gave rise to Mesozoic belemnites. They placed these genera, including *Hematites*, to the family Belemnitidae. SHIMANSKY (1960) did not accept the idea that all Mississippian coleoids are belemnitids, and assigned *Hematites*, together with *Bacritimimus*, to the family Aulacoceridae.

Also GORDON (1964) assigned *Hematites*, together with *Paleoconus* FLOWER & GORDON, 1959 and *Bacritimimus* FLOWER & GORDON, 1959 to the family Belemnitidae D'ORB., 1845 of the order Coleoidea.

JELETZKY (1966) assigned *Hematites* to the order Aulacocerida, but formally, for unknown reasons, he did not include this taxon in his classification.

GORDON (1966) revised the classification of Mississippian coleoid cephalopods and included three genera: *Hematites*, *Bacritimimus* and *Paleoconus*, to the order Aulacocerida; the two first genera were placed within the family Aulacoceratidae MOJSISOVICS, 1885, and the latter genus to Atractidae JELETZKY, 1965. The genus *Eobelemnites* FLOWER, 1945 was kept within the Order Belemnitida, family Belemnitidae D'ORBIGNY, 1845.

GUSTOMESOV (1976) erected for *Hematites*, *Bacritimimus* and *Paleoconus* a new family Hematitidae.

REITNER & ENGESER (1982) assigned *Hematites* within the order Aulacocerida.

DOYLE (1990) and DOYLE, DONOVAN & NIXON (1994) put *Hematites* together with *Bacritimimus* and *Paleoconus* within the order Aulacocerida.

PIGNATTI & MARIOTTI (1996, 1999) put the family Hematitidae GUSTOMESOV, 1976 within the superfamily Aulacoceratoidea MOJSISOVICS, 1919 in the order Aulacocerida.

5. Description

5.1. Peristome and Length of “Living” Chamber

In two shells the anterior portion of the phragmocone and rostrum is preserved (Pl. 1, Figs. 1–3). The “living” chamber is short, approximately equal to 1.5 to 2 times the length of the last chamber. Thus, in *Hematites* a real living chamber was missing, and the final chamber was as short as that in Recent Spirula.

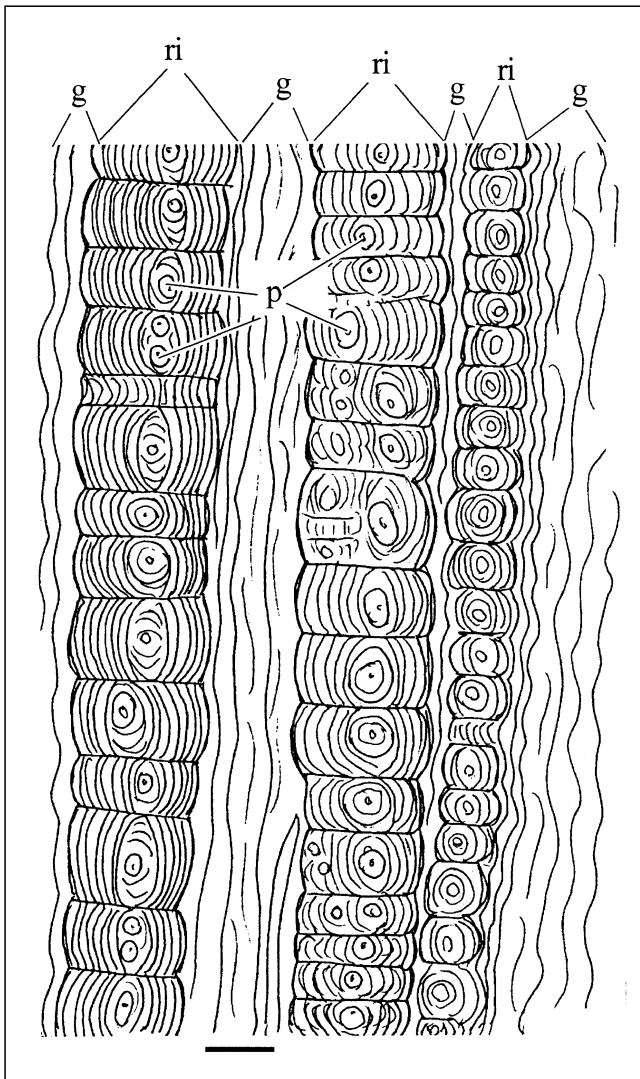
In these two shells the terminal edge of the rostrum surrounds the terminal edge of the phragmocone forming the peristome (indicated by arrows, Pl. 1, Figs. 1–3). In one shell the peristome has a ventral broad and deep U-shaped sinus. This sinus is situated somewhat asymmetrically in relation to the siphuncle (sip, Pl. 1, Fig. 1). On the lateral side the peristome forms a saddle with a mid-lateral, shallow sinus (Pl. 1, Fig. 2). In another specimen the peristome forms a high lateral saddle on the right side and a deep lateral sinus on the opposite side (Pl. 1, Fig. 3). The peristomal edge on the ventral side is therefore very oblique. In the latter shell a longitudinal fracture plane on

the right hand side shows that the rostrum thins out towards the peristomal edge (rst, Pl. 1, Fig. 3). Contrary, on the left hand side the rostrum seems to be thickened at the peristomal edge.

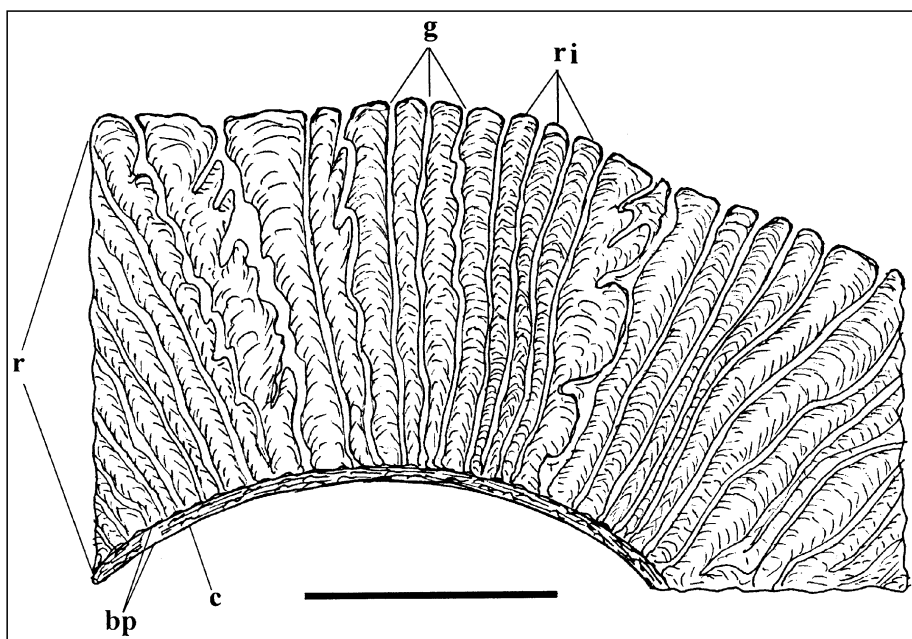
5.2. Rostrum Ultrastructure

The longitudinal ridges, which are a characteristic rostral feature of *Hematites* show a special ornamentation. The flat crest of each ridge shows a row of shallow filled pits, each surrounded by numerous, more or less concentric, growth lines (Pl. 3, Fig. 2; Text-Fig. 1). Adjacent pits are separated by narrow partitions that are transverse to the long axes of the ridges. The pits can be traced through the entire thickness of the rostrum (Pl. 2, Fig. 1–4). In other places, the crests of the ridges are less regularly ornamented. The pits are less distinct and often replaced by shallow grooves between partitions (Pl. 3, Fig. 3). Towards the apical region of the rostrum the crests of the ridges become first less flat and then acute. Here the crests show numerous “cut” marks (Pl. 3, Fig. 1).

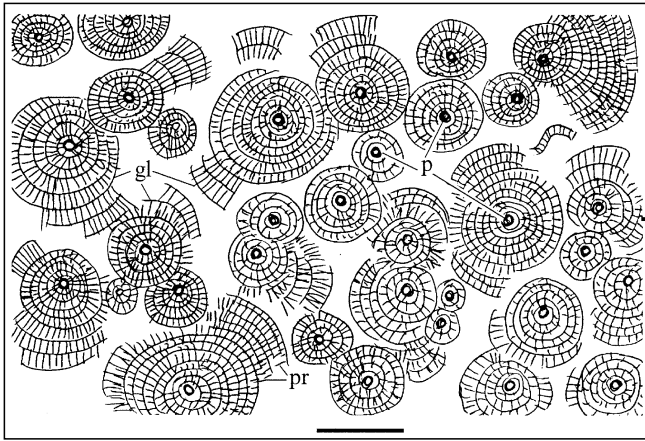
In both longitudinal and transverse sections the ridges show increments distinctly separated by arched growth lines (Pl. 5, Fig. 4; Text-Fig. 2). Each increment is composed of acicular crystallites that in cross section show a feather-like arrangement (Pl. 5, Fig. 3). In the alveolar part the ridges are flat and distinctly separated by regularly placed narrow interspaces (Pl. 5, Fig. 1). In cross section they are radial. The interspaces extend inwards and terminate at a short distance before reaching the conotheca (Pl. 4, Fig. 3; Text-Fig. 2). A thin innermost portion of the rostrum lacks ridges and forms a basal layer (bl). It has a smooth surface and consists of several thin layers parallel to the conotheca (Pl. 4, Fig. 3). The inner surface of this part of the rostrum exhibits numerous irregularly distributed pits of varying sizes (Pl. 4, Figs. 1, 2; Text-Fig. 3). Each pit is surrounded by concentric growth lines and radially oriented acicular crystallites (Pl. 4, Fig. 2; Text-Fig. 3). Some of them have a central pore opening. The layer showing pits is in contact with the conotheca which does not have pores or pits on its surface (Pl. 4, Fig. 1; Text-Fig. 2).



Text-Fig. 1. Schematic diagram of the surface of the rostrum in *Hematites* showing longitudinal ridges bearing rows of pits surrounded by the concentric lines. The ridges are separated by the interspaces, or grooves. Scale bar: 1 mm. g = groove; p = pit; ri = ridge

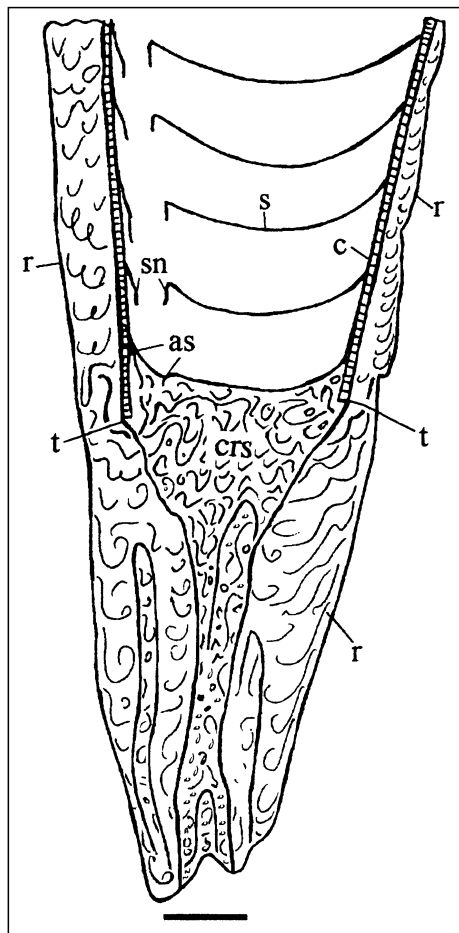


Text-Fig. 2. Schematic diagram of the cross section of the rostrum in *Hematites* showing that it consists of the numerous ridges separated by the deep grooves, with the exception of a thin basal portion which lacks both of these structures. Scale bar: 1 mm. bp = basal portion of rostrum; c = conotheca; g = groove; r = rostrum; ri = ridge.



Text-Fig. 3.
Schematic diagram of the inner surface of the rostrum in *Hematites* showing the numerous pits surrounded by the concentric growth lines, and the radial orientation of the needle-like prisms.
Scale bar: 1 mm.
gl = growth line; p = pits; pr = prism.

The post-alveolar part of the rostrum structurally differs from the alveolar region. Cross sections of this part of the rostrum (Pl. 5, Fig. 2) show that two structural zones are distinguished here: the peripheral and the central ones. The peripheral zone is characterized by an irregular course of the interspaces separating ridges. Thus, the regularly arranged interspaces in the alveolar portion of the rostrum became irregular towards the apex (compare Pl. 5, Fig. 1 and 2). The central zone begins at the broken (truncated) apical end of the phragmocone, and continues to the apical end of the rostrum. This zone closes as a plug the trun-



Text-Fig. 4.
Schematic diagram of the medial shell section in *Hematites* showing the truncation of the initial portion of the phragmocone which is plugged by the central rod structure (crs) and by the additional septum (as).
Scale bar: 1 mm.
as = additional septum; c = conotheca; r = rostrum; s = septum; sn = septal neck; t = place of truncation.

cated apical end of the phragmocone (Pl. 7, Figs. 1, 2; Text-Fig. 4). It is composed of parallel longitudinal calcareous rods which are loosely packed and seem to have been surrounded by an organic matrix (Pl. 5, Fig. 2). The structure of the central zone is called the central rod structure (DOGUZHAeva et al., 1999). It is exposed in the depression at the apical end of larger rostra.

Thus, the idea by FLOWER & GORDON (1959) that in *Hematites* the central part of the postalveolar portion of rostra contained much organic matrix was confirmed by our SEM observations.

The basal part of the rostrum, without ridges, was also observed in *Aulacoceras* (DAUPHIN & CUIF, 1980) and in *Dictyocorites* (BANDEL, 1985).

The feather-like arrangement of acicular crystallites in ridges, as well as the innermost non-ridged portion of the rostrum, occurs in *Aulacoceras* (DAUPHIN & CUIF, 1980, Pl. 9, Fig. 3; Pl. 12, Fig. 4). The feather-like arrangement of acicular crystallites is common in coleoids (BANDEL and BOLETZKY, 1979). It was observed in the Tertiary genera *Belosepia* (DAUPHIN, 1984), *Beloptera* (DAUPHIN, 1985), *Belopterina* (DAUPHIN, 1988), in the Aptian spirulid *Adygeya* (DOGUZHAeva, 1996), in the Lower Cretaceous diplobelid *Tauriconites* and the Eocene coleoid *Belemnosis* (unpublished data by DOGUZHAeva). The only group of coleoid which does not show feather-like arrangement of acicular crystallites are the belemnitids.

5.3. Conotheca

The five to six layers are distinguished in the conotheca (Pl. 6, Fig. 1).

- 1) The innermost layer is ca. 10 μm thick and seems to be composed of vertical lamellae (Pl. 6, Fig. 2).
- 2) It is followed by a 50 μm thick prismatic layer, that is as thick as the remaining four layers in the conotheca wall (Pl. 6, Fig. 2). The vertical prisms show parallel horizontal striations, transverse to the long axes of the prisms. The terminal surface of the prisms shows a plate-like structure. This layer has a certain similarity to the nacreous layer, but it lacks typical nacreous tablets and distinct interlamellar membranes. As pointed out (MUTVEI, 1972), the nacreous layer in *Nautilus* may acquire a spherulitic-prismatic structure when the content of organic matrix increases. However, this seems not to be the case in the prismatic layer under discussion.
- 3) The outermost portion of the conotheca, in contact with the rostrum, is composed of three thin layers: two prismatic layers, 10 and 20 μm in thickness, separated by a porous, vertically lamellar layer, 20–40 μm thick (Pl. 6, Fig. 3). The latter layer seems to have been rich in organic matrix, as indicated by its porosity and by small spherulitic extensions from the adjacent prismatic layers that project into it.

5.4. Truncation of Protoconch and First Chambers

All specimens of *Hematites* at our disposal, as well as all but one specimen studied by FLOWER & GORDON (1959, Pl. 116, Fig. 5), lack the protoconch and several chambers of the phragmocone that are truncated. MAPES (personal communication) found one shell with a spherical protoconch that is not included in the present paper. At the place of the truncation the conotheca has a broken edge (Pl. 7, Figs. 1–4; Text-Fig. 4). The outer surface of

the rostrum shows no signs of damages near the place of truncation. In longitudinal sections can be seen that the broken edge of the phragmocone is closed by several calcareous rods, and the siphuncle is closed by an additional septum (Pl. 7, Figs. 1, 2, Text-Fig. 4). This portion of the rostrum is called here the "central rod structure" and is composed of parallel longitudinal, calcareous rods, probably separated by organic matrix, that begin at the broken apical end of the phragmocone and continue to the apical end of the rostrum. This indicates that the truncation took place before the rostrum was formed.

The length of the rostrum, measured from the broken phragmocone end to the rostral apex, was studied in ten shells. It had a varying length. In one group of shells this length was short, 7–9 mm. In the second group this length was 22–23 mm. The phragmocone diameter at the site of truncation did not show large differences between these two groups. The diameter of the rostrum was 5.5 to 7.5 mm in shells with short rostra, and 9 to 11 mm in those with long rostra.

The truncation in *Hematites* was previously described by FLOWER & GORDON (1959). These writers pointed out (p. 839) that

"... the sections together suggest the possibility that the protoconch and the earliest part of the phragmocone may have been resorbed."

Another well documented case of truncation was described in the ammonite *Ptychoceras* (DOGUZHAEVA and MUTVEI, 1989). In this ammonite the truncation occurred mechanically, probably by muscular contractions, because numerous shell fragments were found at the place of truncation. In *Hematites* the conotheca wall at the broken end of the phragmocone showed no signs of a chemical dissolution (Pl. 7, Figs. 1–4). However, the preservation of the shells did not allow us to observe whether or not shell fragments occur at the truncation site.

6. Discussion and Conclusions

6.1. Comparisons

The most characteristic feature of *Hematites* is the lack of a long tubular "living" chamber and pro-ostracum, which were considered to occur in aulacocerids (MOJISOVICS, 1871, 1902; GEMMELLARO, 1904; WENNER, 1911; BÜLOW, 1915; DUNBAR, 1924). However, as pointed out by BANDEL (1985, p. 232):

"Evidence for this, however, in aulacoceratids like Aulacoceras, Dictyonites, Atractites is only indirect, because no living chamber is preserved. Where it is preserved, conchs carry no rostrum such as Mojsisovicsteuthis (JELETZKY, 1966). Such conchs could have been formed by aulacocerids, but as well by bactritids with an extended dorsal apertural margin (HORNY, 1957; MAPES, 1979)."

A long tubular "living" chamber was described in the shell of the Lower Devonian *Protaulacoceras* (BANDEL et al., 1983). However, later it was shown that a non-cephalopod shell was described under this name (ENGESER, 1990). Nevertheless, a long tubular "living" chamber is widely considered characteristic for aulacocerids in general. NAEF (1922) believed that the slender and long aulacocerid rostrum needed a long pro-ostracum.

In *Hematites* the anterior, peristomal edge of the rostrum and conotheca was directly observed (Pl. 1, Figs. 1–4), so the short "living" chamber in this genus is unquestionable. The anterior edge of the rostrum forms a ventral or ventro-lateral, broad, asymmetrical sinus.

The conotheca in *Hematites* consists of five to six layers. The principal and two additional layers are prismatic, and a vertically lamellar layer is rich in organic matrix; the nacreous layer or a horizontally lamellar layer is absent. In the Triassic aulacocerid genus *Austroteuthis* JELETZKY & ZAPFE (1967, Pl. 3, Fig. 1B) described a four-layered conotheca, which, according to the authors, shows close similarity to the conotheca of Jurassic *Megateuthis* described by MUTVEI (1964). This structure in *Austroteuthis* and *Megateuthis* was observed in thin section. The conotheca of *Megateuthis* is presently being restudied with SEM and revised (DOGUZHAEVA et al., herein). It was found that the conotheca has two principal layers: an inner prismatic and a well developed nacreous layer. In the Triassic aulacocerid genera *Ausseites* and *Aulacoceras* the conotheca consists of two layers: an inner semi-prismatic and an outer, horizontally lamellar (CUIF & DAUPHIN, 1979; DAUPHIN & CUIF, 1982; DAUPHIN, 1983). In the Middle Triassic aulacocerid genus *Dactyconites* the conotheca is formed by three principal layers: the central layer is nacreous similar to the nacreous layer in *Nautilus*, the inner layer is prismatic, and the outer layer is spherulitic-prismatic (BANDEL, 1985). Thus, in Triassic aulacocerids: *Austroteuthis* (JELETZKY and ZAPFE, 1967), *Ausseites* and *Aulacoceras* (CUIF & DAUPHIN, 1979; DAUPHIN & CUIF, 1982; DAUPHIN, 1983) and in *Dactyconites* (BANDEL, 1985) the ultrastructure of the conotheca strongly differs from that in *Hematites*, because a nacreous or horizontally lamellar layer is present in all these four genera but not in *Hematites*. Moreover, the conotheca of Triassic genera does not have a layer rich in organic matrix similar to that in *Hematites*.

JELETZKY (1965) erected the order Aulacocerida because of significant morphological differences between belemnites and aulacocerids. He characterized Aulacocerida by having

- 1) a long tubular "living" chamber
- 2) an aperture with short dorsal and ventral crests
- 3) a conotheca with growth lines
- 4) a rostrum built predominantly of organic substance
- 5) prochoanitic adult septal necks
- 6) a protoconch sealed completely by a closing membrane
- 7) caecum and prosiphon apparently absent
- 8) a rostrum consisting predominantly of organic substance, analogous but not homologous to that in belemnites.

Besides, aulacocerids have longer chambers, and a smaller apical angle than belemnites.

As was shown above, our detailed studies of the shell in *Hematites* revealed several previously unknown morphological features which do not allow us to place this genus to the order Aulacocerida. These features are: short "living" chamber which is approximately 1.5–2 times longer than the last chambers, and a multilayered conotheca which lacks a nacreous or horizontally lamellar layer. Besides, there are no ventral and dorsal apertural projections, and traces of pro-ostracum.

We therefore erect here the order Hematitida ord. nov. for the family Hematitidae GUSTOMESOV, 1976.

6.2. Systematic Position

Subclass: Coleoidea BATHER, 1888

Order: Hematitida DOGUZHAEVA, MAPES & MUTVEI, ord. nov.

Diagnosis: Rostrum-bearing coleoids with short aragonitic-organic rostra with numerous, prominent

ridges. Rostral surface with more than two furrows without constant position. "Living" chamber short, about 1.5 to 2 times the last chamber length. Peristome formed by the terminal edge of the rostrum that surrounds the terminal edge of the phragmocone; peristome characterized by a broad, unsymmetrical, U-shaped ventral or ventro-lateral sinus. Protoconch sphaerical, often truncated together with several first chambers. Phragmocone orthoconic with small apical angle. Conotheca multilayered, mainly prismatic without nacreous or horizontally lamellar layer. Siphuncle narrow, ventral; submarginal at early stages then marginal. Segments weakly inflated between septa. Connecting ring thin, organic. Suture line without ventral sinus.

Genus: *Hematites* FLOWER & GORDON, 1959

Type species: *H. barbarae* FLOWER & GORDON, 1959.

Diagnosis: Rostrum short, slender, ridged, adorally tubular; posteriorly straight uncurved, apex from acute

to blunt. Furrows present, their spacing and number variable, often asymmetrically situated, generally concentrated on ventral side. Phragmocone slender, faintly compressed, generally truncated. Septa straight or slightly inclined from dorsal side posteriorly. Suture nonsinuated.

Acknowledgements

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Plate 1

- Fig. 1: Two ventral views on a "living" chamber with peristome and last but one septum.
Note that a deep, ventral, peristomal sinus is situated somewhat asymmetrically in relation to the siphuncle (sip).
OUZC-3753; $\times 7$.
- Fig. 2: Lateral view of the same shell as in Fig. 1 to show a lateral lobe with a shallow sinus.
OUZC-375; $\times 7$.
- Fig. 3: Ventral view on another "living" chamber with peristome and last septum to show a high lateral lobe on one side and a deep lateral sinus on the opposite side.
Note the longitudinal fracture plane of the anterior portion of rostrum (rs).
Arrows indicate the position of peristomal edge.
OUZC-3754; $\times 7$.



1

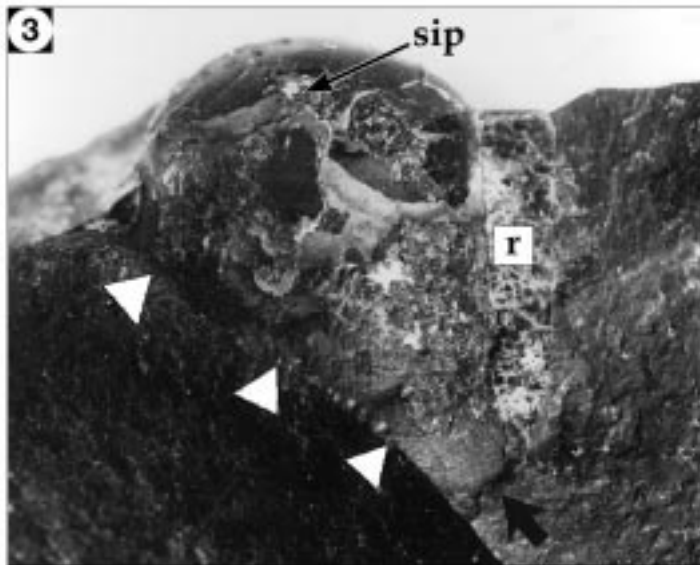
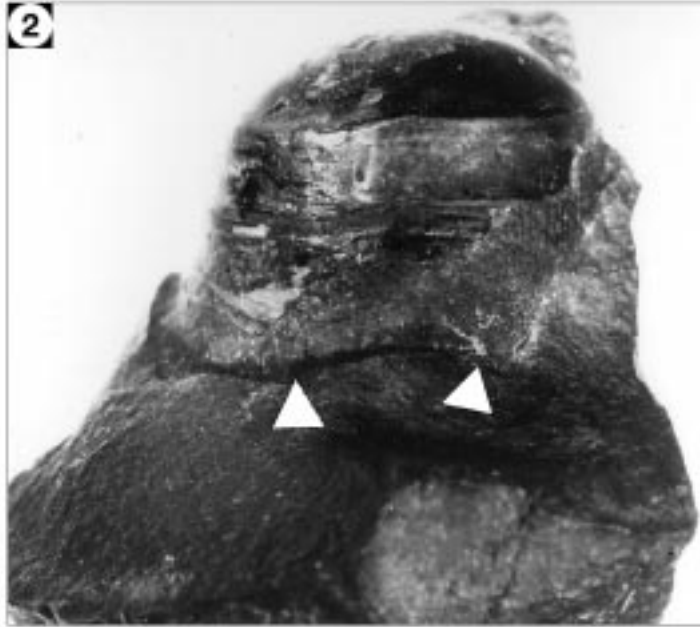


Plate 2

Fig. 1: Apical portion of a rostrum with an oblique cross section.
OUZC-3755.

Fig. 2: Same as in Fig. 1 but in higher magnification.
Note that the crests of the radial ridges are covered by rows of pits that can be traced through the entire rostrum thickness.

Figs. 3,4: Pits in higher magnification on the oblique cross section of the same rostrum as in Fig. 1.

Scale bars: 1 mm for Figs. 1, 2; 0.1 mm for Figs. 3, 4.

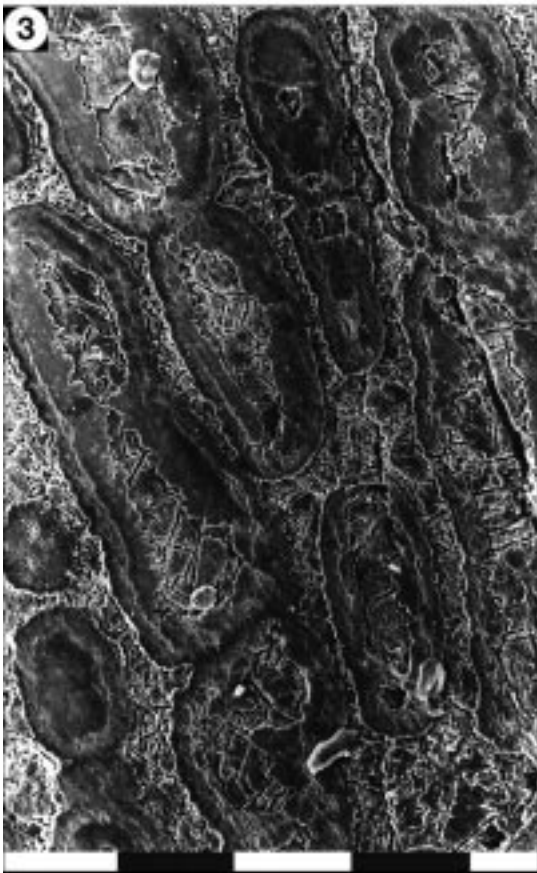


Plate 3

- Fig. 1: Apical end of a rostrum (apex to the right).
The crests of the ridges are acute and show numerous "cut" marks; the outermost ridges end earlier than the underlying ones.
OUZC-3756.
- Figs. 2,3: Flat crests of ridges (closer to the oral part of the rostrum) show rows of filled pits separated by partitions and variations of their shapes.
OUZC-3756

Scale bars: 1 mm.

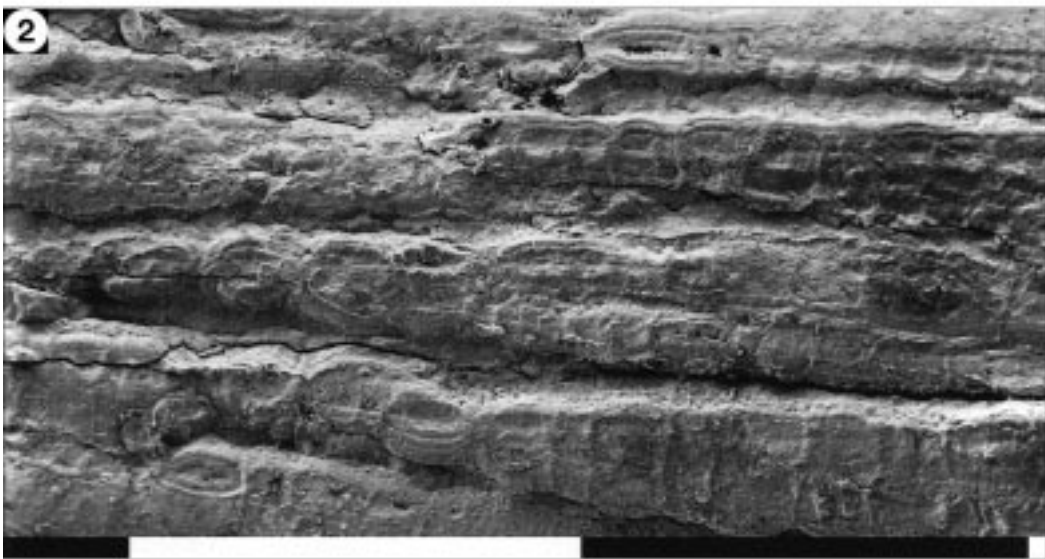
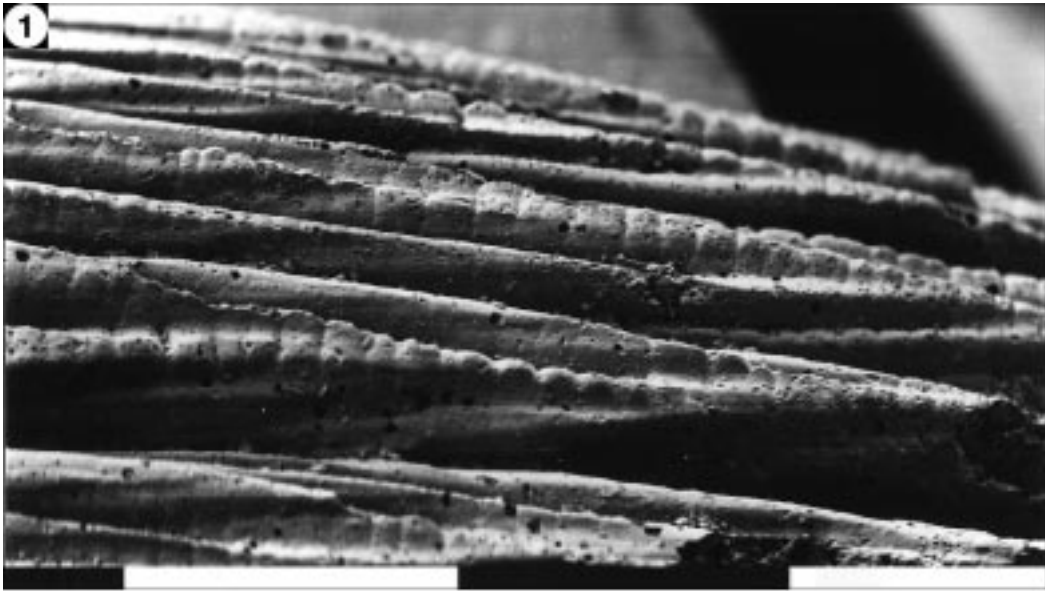


Plate 4

- Fig. 1: Horizontal fracture of the innermost basal layer of the rostrum to show irregularly arranged pits, surrounded by concentric growth lines and fragments of the conotheca (con).
OUZC-3757.
- Fig. 2: Closer view on the pits to show concentric growth lines and radially arranged acicular crystallites.
OUZC-3757.
- Fig. 3: Shell cross section to show the basal layer of the rostrum (bl) with growth lines parallel to the conotheca (con).
Ridges exhibit traces of arched growth lines; where the ridges are strongly pyritized they are black in colour.
OUZC-3758.

Scale bars: 1 mm.

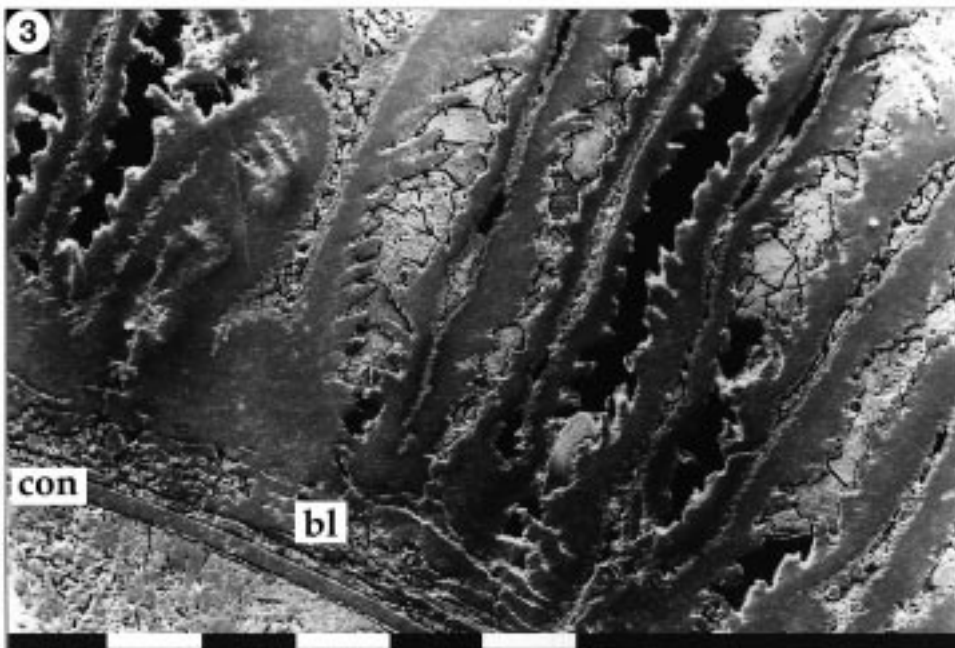


Plate 5

- Fig. 1: General view on a transverse section of the alveolar part of a rostrum to show flat ridges, separated by deep, narrow, interspaces.
OUZC-3759.
- Fig. 2: Transverse section of post-alveolar part of a rostrum to show that in the peripheral zone (pz) the interspaces have an irregular course.
In central rod zone (crz) the calcareous rods are separated by presumably organic matrix.
OUZC-3760.
- Fig. 3: Enlarged detail of Fig. 1 to show that each ridge is formed by feather-like arranged acicular crystallites.
OUZC-3759.
- Fig. 4: Longitudinal section of rostrum showing arched growth lines of the ridges.
OUZC-3761.

Scale bars: 1 mm for Figs. 1, 2; 0.1 mm for Figs. 3, 4.

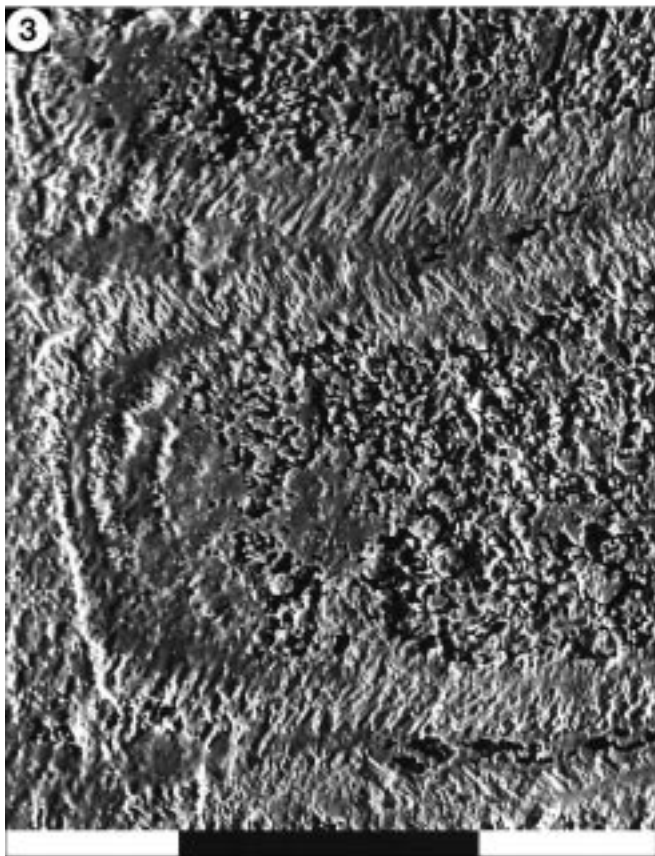
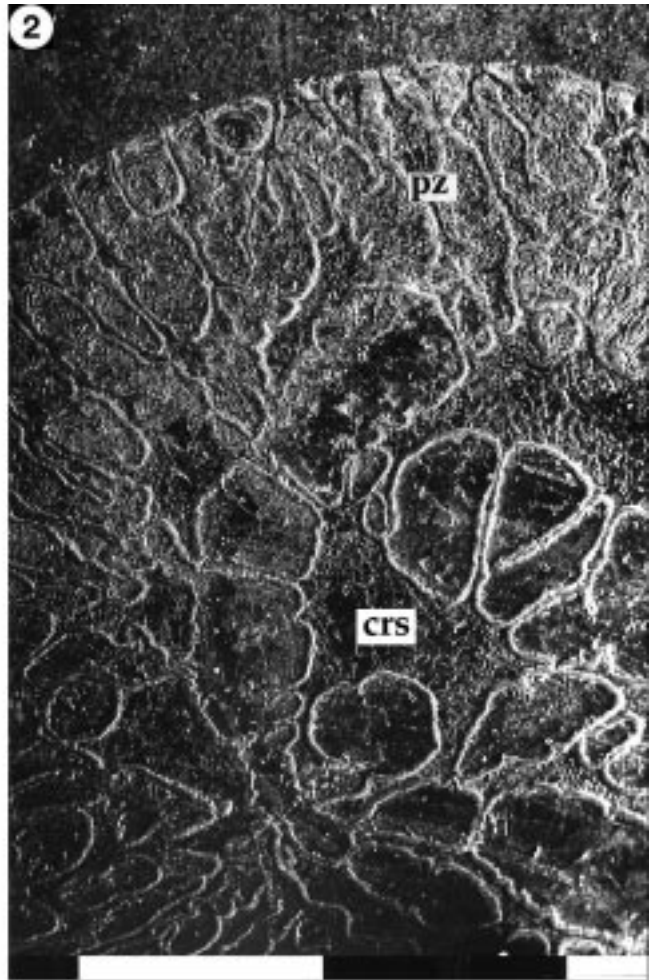
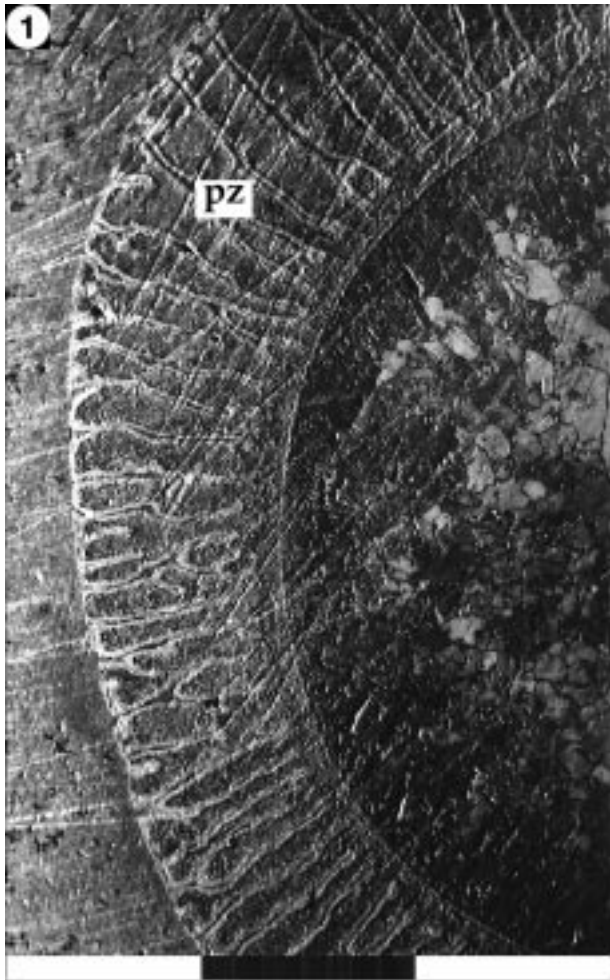


Plate 6

Fig. 1: General view on a fractured section of a rostrum (r) and five layers in conotheca.
OUZC-3762.

Fig. 2: Detail of Fig. 1 in higher magnification to show two innermost conotheca layers: a thin layer built by vertical lamellae (l) and the next thick prismatic layer (pr).
OUZC-3762.

Fig. 3: Fractured sections of three, outermost layers in contact with the rostrum (r): two prismatic layers (pr) with the spherulitic surfaces face the layer between them, which is partly calcified presumably rich in organic matrix (col).
OUZC-3762.

Scale bars: 1 mm for Fig. 1; 0.1 mm for Figs. 2, 3.

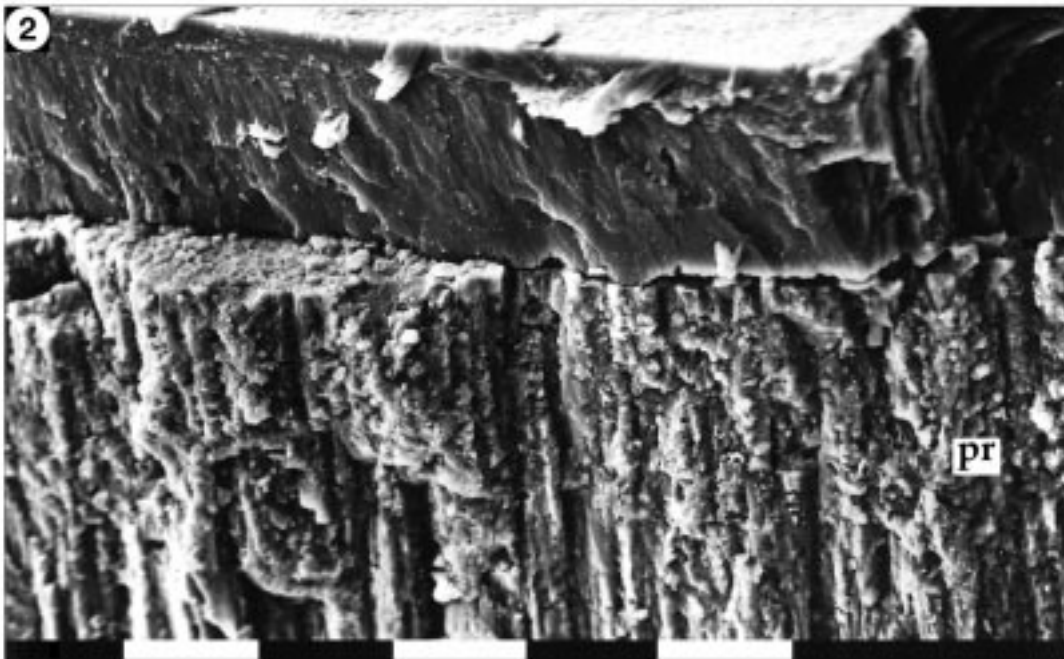
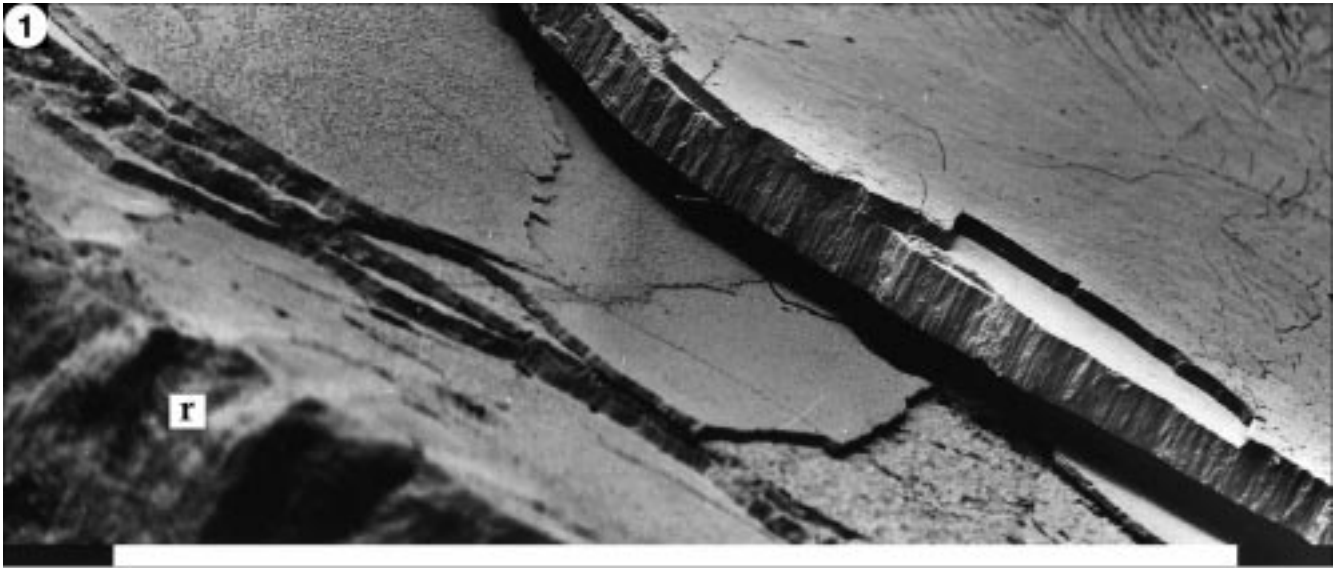
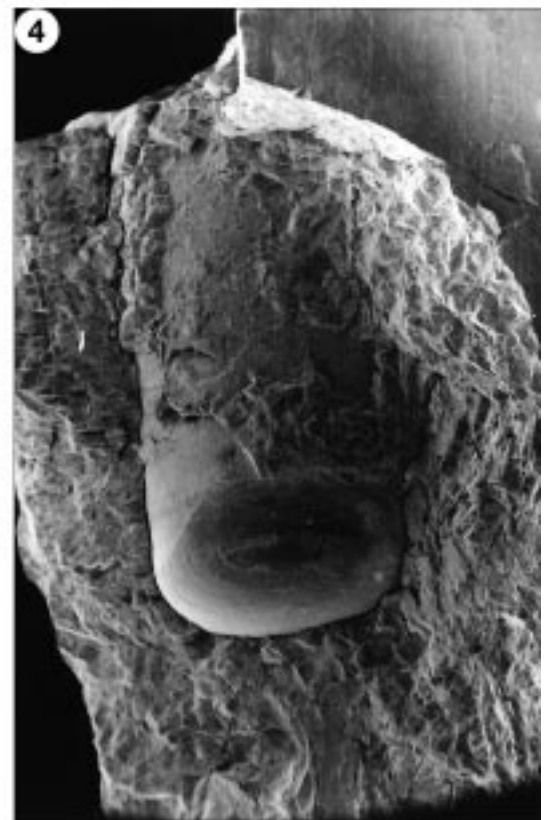
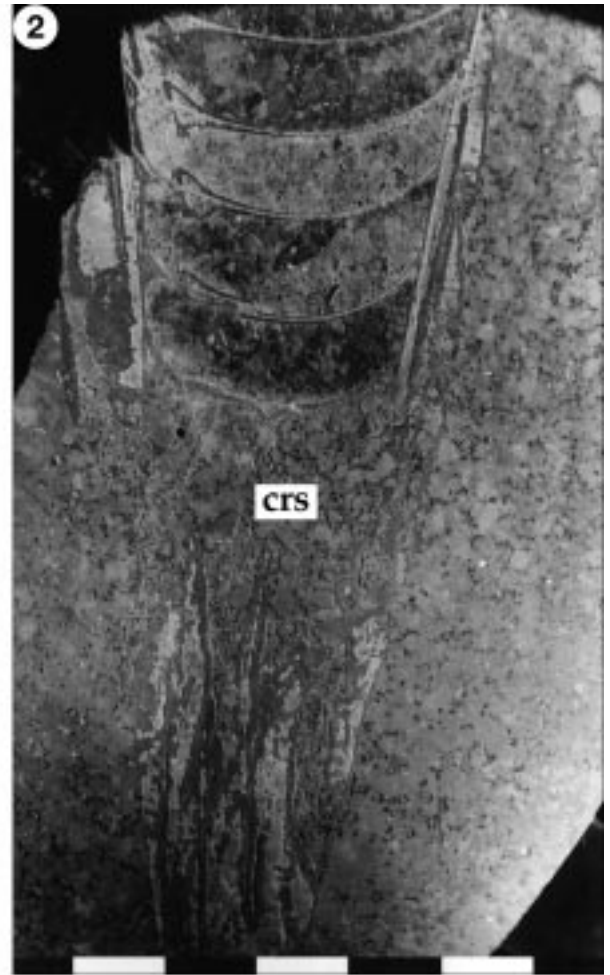


Plate 7

- Figs. 1,2: Longitudinal shell sections to show truncation of the protoconch and initial portion of the phragmocone, surrounded by rostrum; the central rod structure (crs) forms a plug near the broken edge.
On Fig. 1 the ridges of the outer portion of the rostrum do not change their course, but the ridges of its inner portion turns over the broken edge of the conotheca; the central part of the central rod structure (black in colour) presumably originally contained organic matrix.
OUZC-3763, 64.
- Fig. 3: Broken edge of the conotheca (con) at place of truncation and innermost portion of rostrum turning it over.
OUZC-3765.
- Fig. 4: Fractured shell showing the place of truncation with exposed last preserved septum; at right top corner the outer surface of the rostrum is shown.
OUZC-3766.

Scale bar: 1 mm for Figs. 1, 2, 4; 0.1 mm for Fig. 3.



References

- BANDEL, K., 1985: Composition and ontogeny of *Dictyoconites* (Aulacocerida, Cephalopoda). – *Paläont. Z.*, **59**, 3/4, 223–244.
- BANDEL, K. & BOLETZKY, S., 1979: A comparative study of the structure, development and morphological relationships of chambered cephalopod shells. – *Veliger*, **21**, 3, 331–534.
- BÜLOW, E., 1915: Orthoceras und Belemniten der Trias von Timor. – *Paläontologie von Timor*, **4**, 7, 72p.
- CHEN, T.E. & SUN, Z.H., 1982: Discovery of Permian belemnoids in South China with comments on the origin of the Coleoidea. – *Acta Palaeontologica Sinica*, **21**, 181–190.
- DAUPHIN, J., 1982: Analyse microstructurale d'un *Aulacoceras* (Mollusca – Coleoidea) juvenile du Trias de Turquie. – *Paläont. Z.*, **56**, 1/2, 53–75.
- DAUPHIN, J., 1983: Microstructural analysis of the phragmocone in the Triassic genus *Aulacoceras* (Cephalopoda – Coleoidea) with notes on the homology of layers in internal and external shells. – *N. Jb. Paläont. Abh.*, **165**, 3, 418–437.
- DAUPHIN, J., 1984: Microstructure des Cephalopodes. IV Le „rostre“ de *Belosepia* (Dibranchiata). – *Paläont. Z.*, **58**, 1/2, 99–117.
- DAUPHIN, J., 1985: Microstructural studies on cephalopod shells V: the apical part of *Beloptera* (Dibranchiata, Tertiary). – *N. Jb. Geol. Paläont. Abh.*, **170**, 3, 323–341.
- DAUPHIN, J., 1988: Diagenese aragonite-calcite chez les Cephalopodes coleoids: exemples des rostres d'*Aulacoceras* (Trias de Turquie) et de *Beloptera* (Eocene de France). – *Bull. Mus. natn. Hist. nat.*, Paris, 4 ser., **10**, section C, 2, 107–135.
- DAUPHIN, J. & CUIF, J.P., 1980: Implications systematiques de l'analyse microstructurale des rostres de trois genres d'aulacocerides Triasiques (Cephalopoda – Coleoidea). – *Palaeontographica*, Abt., A, **169**, 28–50.
- DOGUZHAEVA, L.A., 1996: Two Early Cretaceous spirulid coleoids of the north-western Caucasus: their shell ultrastructure and evolutionary implications. – *Palaeontology*, **39**, 681–707.
- DOGUZHAEVA, L.A. & MUTVEI, H., 1989: *Ptychoceras* – a heteromorphic lycoceratid with truncated shell and modified ultrastructure (Mollusca: Ammonoidea). – *Palaeontographica*, Abt. A, Bd. **208**, 91–121.
- DOGUZHAEVA, L.A., MAPES, R.H. & MUTVEI, H., 1999: Rostrum and phragmocone structure in the Lower Carboniferous coleoid *Hemalites* and its taxonomic assignment. – In: K. HISTON (Ed.): The fifth Intern. Symp. Cephalopods – Present and Past, Book of abstracts, p. 33.
- DOGUZHAEVA, L.A., MUTVEI, H. & DONOVAN, D.T., 1999: Structure of the pro-ostracum and muscular mantle in belemnites. – In: K. HISTON (Ed.): The fifth Intern. Symp. Cephalopods – Present and Past, Book of abstracts, p. 34.
- DOGUZHAEVA, L.A., MUTVEI, H. & DONOVAN, D.T., 2000: Pro-ostracum, conotheca and muscular tunic in Middle Jurassic belemnite *Megateuthis*. – In: H. SUMMESBERGER, K. HISTON & DAURER, A. (Eds.): Proceedings of the fifth Intern. Symp. „Cephalopods – Present and Past“, *Abh. Geol. B.-A.*, **57**, 321–229.
- DOYLE, P., 1990: The biogeography of the Aulacocerida (Coleoidea). – *Atti II Conv. Int. F.E.A. Pergola*, **87**, 263–271.
- DOYLE, P., DONOVAN, D.T. & NIXON, M., 1994: Phylogeny and systematics of the Coleoidea. – *The Univ. of Kansas Paleontol. Contr.*, **5**, 1–15.
- DUNBAR, C.O., 1924: Phases of cephalopod adaptation. – In: Organic adaptation to environment (New Haven, Conn.), 187–224.
- ENGESER, Th., 1990: Phylogeny of the fossil coleoid Cephalopoda (Mollusca). – *Berliner geowiss. Abh. A*, **124**, 123–191.
- FLOWER, R.H., 1944: *Atractites* and related coleoid cephalopods. – *Am. Midland Naturalist*, **32**, 3, 757–770.
- FLOWER, R.H., 1945: A belemnite from the Mississippian boulder of the Caney shale. – *J. Paleontology*, **19**, 5, 490–503.
- FLOWER, R.H. & GORDON, M.Jr., 1959: More Mississippian belemnites. – *J. Paleontology*, **33**, 5, 809–842.
- GEMMELLARO, G.G., 1904: I cephalopodi del Trias superiore della regione occidentale della Sicilia. – *Giornale Sci. Nat. & Econ. Palermo*, **24**, 322 p.
- GORDON, M.Jr., 1965: Carboniferous Cephalopods of Arkansas. – *Geol. Surv. Prof. Pap.* 460.
- GORDON, M.Jr., 1966a: Classification of Mississippian coleoid cephalopods. – *J. Paleontol.*, **40**, 449–452.
- GORDON, M.Jr., 1965b: Permian coleoid cephalopods from the phosphoria Formation in Idaho and Montana. – *U.S. Geol. Surv. prof. Pap.*, **550-B**, B29–35.
- HORHY, R., 1957: *Bojobactrites ammonitans* n. g., n. sp. (Bactritoidea) from the Devonian of Central Bohemia. – *Ustred. ustav. geol. Sb.*, CSR, **23**, 285–395.
- JELETZKY, J.A., 1965: Taxonomy and phylogeny of fossil Coleoidea (= Dibranchiata). – *Canad. Geol. Survey*, **65**, 2, 72–76.
- JELETZKY, J.A., 1966: Comparative morphology, phylogeny, and classification of fossil coleoidea. – *The Univ. of Kansas Paleontol. Contr.*, **7**, 1–162.
- JELETZKY, J.A. & ZAPFE, H., 1967: Coleoid and orthocerid cephalopods of the Rhaetian Zlambach Marl from the Fischerwiese near Aussee, Styria (Austria). – *Ann. Naturhistor. Mus. Wien*, **71**, 69–106.
- MAPES, R., 1979: Carboniferous and Permian Bactritoidea (Cephalopoda) in North America. – *The Univ. of Kansas Paleontol. Contr.*, **64**, 1–75.
- MOJSISOVICS E., 1871: Über das Belemniten-Geschlecht *Aulacoceras* Fr. v. Hauer. – *Geol. Reichsanst., Jb.*, **21**, 41–57.
- MOJSISOVICS E., 1902: Die Cephalopoden der Hallstätter Kalke. Supplement (1902). – *Geol. Reichsanst., Jb.*, **6**, 175–356.
- MUTVEI, H., 1964: Remarks on anatomy of recent and fossil Cephalopoda; with description of the minute shell structure of belemnoids. – *Acta Univ. Stockholmiensis, Contributions in Geology*, **11**, 4, 79–102.
- MUTVEI, H., 1972: Ultrastructural studies on cephalopod shells. I. The septa and siphonal tube in *Nautilus*. – *Bull. geol. Inst. Univ. Uppsala*, **3**, 237–261.
- NAEF, A., 1922: Die Fossilen Tintenfische: Eine paläozoologische monogr. – Jena, 322 p.
- PIGNATTI, J.S. & MARIOTTI, N., 1996: Systematics and phylogeny of the Coleoidea (Cephalopoda): a comment upon recent works and their bearing on the classification of the Aulacocerida. – *Palaeopelagos*, **5**, [1995], 33–44.
- PIGNATTI, J.S. & MARIOTTI, N., 1999: The Xiphoteuthididae BATHER, 1892 (Aulacocerida, Coleoidea). – In: OLORIZ, F. & RODRIGUEZ-TOVAR, F.J. (Eds.): Advancing research on living and fossil cephalopods, Klumer Academic Plenum Publish., 161–170.
- REITNER, J & ENGESER, T., 1982: Phylogenetic trends in phragmocone-bearing coleoids (Belemnomorpha). – *N. Jb. Geol. Paläont. Abh.*, **164**, 1/2, 156–162.
- SHIMANSKY, V.N., 1960: Review of more Mississippian belemnites by FLOWER and GORDON. – *Paleontologicheskij Zh.*, **2**, 158–162 [in Russian].
- WENNER, E., 1911: Trias cephalopoden von Timor und Rotti. – *N. Jb. Miner., Geol., Paläont.*, **32**, 177–196.
- ZHU, K.Y. & BIAN, Z.X., 1984: Sinobelemitidae, a new family of Belemnitida from the Upper Triassic of Longmenshan, Sichuan. – *Acta Palaeontologica Sinica*, **23**, 300–319.