

## Composition and ontogeny of *Dictyoconites* (Aulacocerida, Cephalopoda)

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With 25 figures

**Kurzfassung:** *Dictyoconites* aus der mitteltriassischen Cassian Formation von Cortina d'Ampezzo stellt einen typischen Vertreter der aulacoceraten Coleoiden dar. Hinsichtlich der Embryonalentwicklung und des Aufbaues des Phragmokons bestehen Übereinstimmungen mit jurassischen Belemniten. Das Siphonalrohr weist aber eine doppelte Wand auf. Im Gegensatz zum Doppelrohr von *Spirula* ist es jedoch in der Fortsetzung des perlmutterigen Septenkragens organisch und besitzt einen prismatischen Rohreinsatz. Die röhrenförmige »Wohnkammer« und das zweischichtige Rostrum sind kennzeichnende Merkmale triassischer Aulacoceraten. Das Tier kann als schlanker Tintenfisch rekonstruiert werden, dessen Schale vom Weichkörper umhüllt war.

**Abstract:** *Dictyoconites* from the middle Triassic Cassian Formation is a characteristic representative of the Aulacocerida. Embryonic development and construction of the phragmocone is like that of Jurassic belemnites. The siphuncular tube is double-walled with a long retrochoanitic mineralized septal neck continuing into an organic tube. The extended decoupling zone resembles that of *Spirula*. Characteristic of *Dictyoconites* are the tubular »living chamber« and two layered deposits of the muscular mantle on the phragmocone. The Triassic coleoid was a slender squid with visceral mass and mantle cavity encapsuled in shell and the whole conch covered by muscular mantle extending in two lateral apical fins attached to the aragonitic rostrum.

### Introduction

Aulacoceratids and belemnites are common fossils and are of such similar shape that it is difficult to distinguish one from the other. The bulk of the aulacoceratids lived during Permian and Triassic times in the Tethys ocean, most of the belemnites preferred the boreal seas during Jurassic and Cretaceous times. Before the Permian, belemnite-like fossils are rare and are difficult to place in either group (FLOWER 1945, FLOWER & GORDEN 1959). Ancestors to the aulacoceratids may have lived as long ago as the Lower Devonian (BANDEL et al. 1983).

Morphological differences between these two cephalopod groups appear at first sight to be small. Only the apical portion of the shell, where the chambered conch (phragmocone) was covered by additional mineral deposits (rostrum) from the outside, is commonly preserved. These deposits may be organic and/or calcareous in composition. The calcareous deposits may be either aragonite or calcite. The phragmocone is usually only preserved where covered by layers of the rostrum, and has been destroyed by erosion or diagenesis in all parts that lie anterior to the rostrum.

Information is available regarding the most anterior portion of the belemnite conch but such complete shells of aulacoceratids have not yet been definitely described. NAEF's (1922)

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statement that actual growth lines of the wall of the phragmocone (conotheca) have not been observed in undisputed aulacoceratids is still valid.

The main differences between belemnites on the one hand and aulacoceratids on the other hand were supposed in the apical angle of the chambered portion of the shell (phragmocone) and in the distance between individual septa, before JELETZKY (1966) published his large monograph on fossil coleoids. Previously, aulacoceratids were considered to be characterized by a small apical angle and thus by a small increase in chamber width during growth of the phragmocone, and by high chambers. JELETZKY (1966), however, showed that these differences were not valid, but that on the basis of other features, the two groups of rostrum-bearing cephalopods should be placed in separate orders, in contrast to the proposal of NAEF (1922), who placed them in separate families of the same order. JELETZKY based his opinion on the morphology of the septum and siphuncular tube. Whereas the septa of true belemnites were considered to be continuing into the siphuncular tube and, thus, turned backwards (retrochoanitic), JELETZKY believed that the septa continued into forward bent septal necks (prochoanitic), and are not continuous with the siphuncular tube. These observations were in contrast to NAEF's (1922) descriptions, according to which septal necks bend backwards in representatives of both groups.

Both authors also reconstructed differently the soft body that once had been connected with the conch and had secreted the shell. JELETZKY (1966) considered that aulacoceratids had been essentially ectocochlear. He thought that they did not have a muscular mantle. However, in that case they could not have functioned as recent dibranchiates do, which have a muscular mantle. In his reconstruction, the rostrum was secreted by mantle flaps that could be folded over the chambered shell, but were not fused around it. Soft parts could be withdrawn into the shelter of the long living chamber.

NAEF (1922), in contrast, reconstructed the aulacoceratids as slender squids that looked similar to Recent ones. He thought that their morphology was similar to that of belemnites on one hand and orthoceratids on the other, but that the aulacoceratid mantle covered all the shell and was fused around it.

The early ontogeny of *Aulacoceras* has recently been reconstructed by DAUPHIN (1982, 1983), following a model proposed by BARSKOV (1972) to explain belemnite ontogeny. BARSKOV's reconstruction however, could, in the case of the Jurassic belemnite *Hibolithes* (BANDEL et al. 1984), not be verified. The embryonic conch of possible Lower Devonian coleoids (BANDEL et al. 1983) also supports NAEF's suggestion that belemnites and aulacoceratids alike hatched as miniature adults, much in the same way as Recent coleoids (BOLETZKY 1974). The interpretation of NAEF (1922) that an endocochleate shell is present from the embryonic stage onward is incompatible with that of JELETZKY (1966) that ectocochleate organisation is found during the whole life in aulacoceratids or during part of the ontogeny of belemnites.

The construction of the rostrum and its mineralogy composition was considered to be a further difference separating aulacoceratids from the belemnites by JELETZKY (1966). DAUPHIN (1982), in contrast, believed that both were originally composed of aragonite and that the aragonite in the belemnite rostra was altered diagenetically into calcite. She referred to SPAETH (1971, 1975) but these publications do not support such conclusions (personal communication, CHR. SPAETH). The belemnite *Hibolithes*, and most other Jurassic and Cretaceous belemnites as well, change the mineralogy and composition of their rostrum during their ontogeny. The adult rostrum was originally calcite. The initial chambers of aulacoceratids and belemnites, as far as they have been studied up to date, are basically alike (lit. see DAUPHIN 1982 and BANDEL et al. 1984), as are the mineral structure and type of nacre composing the septa in the phragmocone of representatives of both groups. The nacre resembles that of recent *Spirula* and *Sepia* (MUTVEI 1964a, b, 1970, BANDEL & BOLETZKY 1979) and is different from that of recent *Nautilus* and fossil *Pseudorthoceras* (ERBEN et al. 1969).

Because of the difference in their first stratigraphic occurrences, it was hypothesized that aulacoceratids may have developed from a Silurian branch of the michelinoceratids, whereas the belemnites may have evolved from Carboniferous bactritids (BANDEL et al. 1983, 1984). These proposals followed earlier suggestions by ERBEN (1964).

Epithelia secreting the rostrum have been reconstructed in a number of ways. BARSKOV (1972) and DAUPHIN (1983) have revived a theory presented originally by NAEF (1922) that the mineral deposits of the rostrum are homologues to the shell layers of ectocochleate cephalopods. *Aulacoceras*, according to DAUPHIN, produced periostracal layers after the rostrum had been secreted. In the belemnite *Hibolithes*, however, BANDEL et al. (1984) have found a periostracum layer below the embryonic as well as the adult rostrum. For recent phragmacone-bearing cephalopods like *Spirula* and *Sepia*, BANDEL & BOLETZKY (1979) have shown that the periostracum is formed at the shell edge just as in other conchiferan molluscs, and mineral layers are deposited onto it from below and above. The organogenesis of the molluscan mantle in all conchiferan molluscs is essentially similar, regardless of external (ectocochlear) or internal (endocochlear) position of the shell (BANDEL 1982).

Some of the above mentioned problems and questions concerning the aulacoceratids have been tackled utilizing some well preserved rostra of *Dictyoconites* from the Cassian beds (Ladinian) of Cortina d'Ampezzo, Italian Alps, that could be fractured to reveal their chambered interior. This material had been collected and made available for study by R. ZARDINI. Thin sections were prepared and fractures of sections were studied with the scanning electronic microscope after being coated with gold.

We thank Dr. CHR. DULLO for his patience on the scan, GERARDA VAN SPAENDONK-BANDEL for the drawings and RENATE NEUFERT for photowork. The English text was checked by R. STANTON (Texas). The study was supported by the Deutsche Forschungsgemeinschaft.

## 1. Phragmocone

### a) Initial chamber

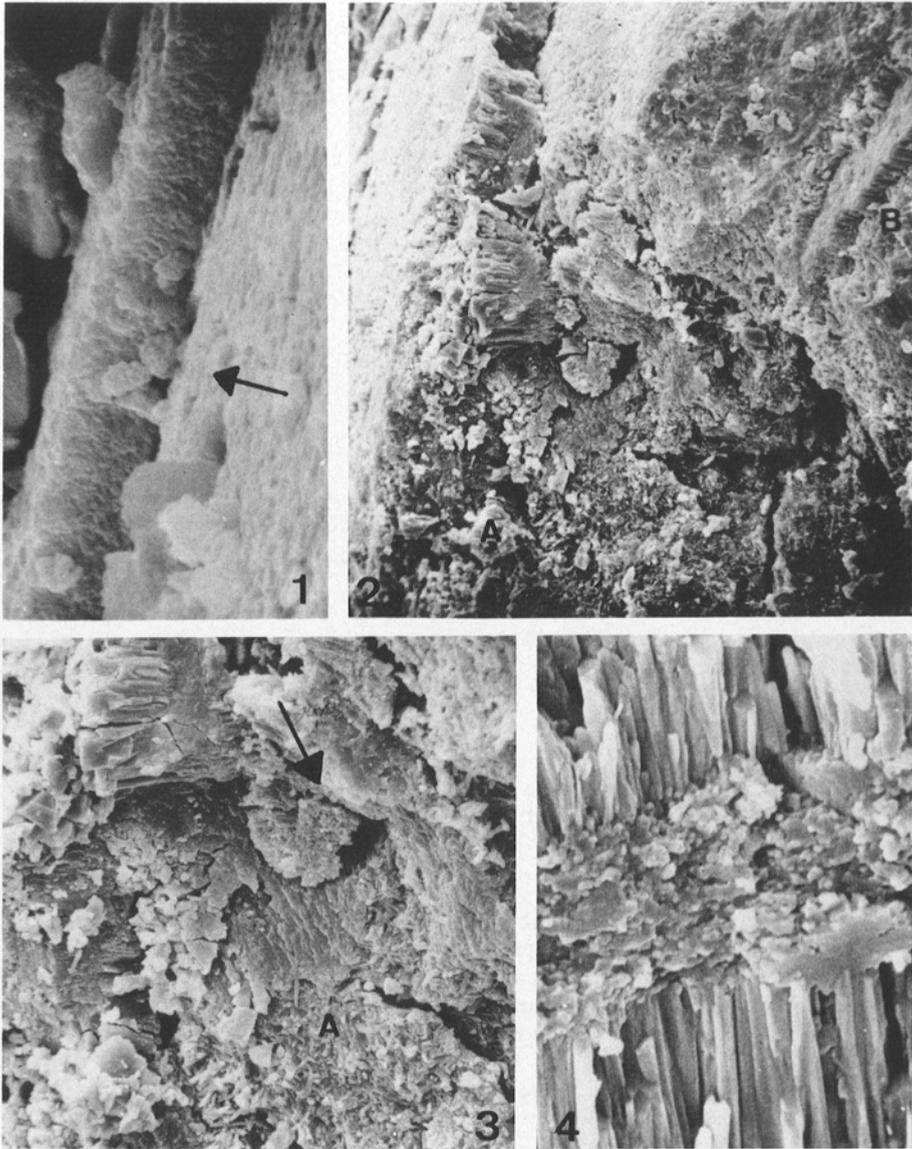
**Description:** The first (initial) chamber of the phragmocone in the conch of *Dictyoconites* is well rounded, of almost spherical shape, about 0.5 mm wide and 0.3 mm high. It is separated from the following conch by a constriction that is deeper on the ventral than on the dorsal side. The central axis of the initial chamber deviates slightly from the long axis of the following conch and, therefore, appears to be ventrally inclined on the apical end of the tubular phragmocone.

The aperture of the first chamber is closed by a septum consisting of two sheets that unite before they reach the inner wall. The sheets of this first septum are phosphatic but, most probably, were originally organic (Fig. 1).

The 3  $\mu\text{m}$  thick mineral outer wall of the initial chamber consists primarily of aragonitic crystallites arranged normal to the shell surface.

In thin sections of *Metabelemnites* (JELETZKY 1966) and of *Atractites* (BANDEL et al. 1984) the organic first septum can be seen. The first septum of *Dictyoconites* and related aulacoceratids resembles that of *Hibolithes* and other belemnites in its organic composition and in not being pierced by the siphuncular tube (GRANDJEAN 1910).

DAUPHIN (1983) described the structure of the first septum of an *Aulacoceras* from Turkey as semiprismatic, but this is a result of diagenetic changes that occurred in the originally organic sheets.



Figs. 1-4

1: Fractured first organic septum (arrow); SEM  $\times$  5000.

2: Fractured mineralized second (A) and third septum (B); SEM  $\times$  500.

3: Detail of Fig. 2 with prochoanitic septal neck of second septum  $\times$  1000.

4: Seventh septum with central layer of nacre (*Spirula*-type). The prismatic layers have in part been secreted during septum formation and have continued in growth during diagenesis; SEM  $\times$  5000.

Abb. 1-4

1: Erstes Septum (Pfeil) im Bruch; SEM  $\times$  5000.

2: Mineralisiertes zweites (A) und drittes (B) Septum im Bruch; SEM  $\times$  500.

3: Vergrößerter Ausschnitt von Abb. 2, zeigt den prochoanitischen Kragen des zweiten Septums;  $\times$  1000.

4: Siebentes Septum mit der zentralen Perlmutterlage vom *Spirula* Typus, über- und unterlagert von Prismenschichten, die teils während des Lebens, teils danach, während der Diagenese aufwuchsen; SEM  $\times$  5000.

Fig. 5. Sketch of the embryonic conch of *Dictyoconites*. The initial chamber (a) is closed by sheets of the organic first septum (b). The second septum (c) show prochoanitic septal necks in which the siphuncular tube ends. Second chamber is narrow, while third chamber (d) and following ones are regularly spaced. All septa from the third (e) onward are nacreous and the apertural opening (f) has a low ventral lip and a regularly rounded dorsal lip.

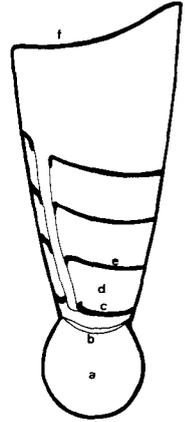


Abb. 5. Skizze der Embryonalschale von *Dictyoconites*. Die erste Kammer (a) wird durch organische Schichten des ersten Septums (b) geschlossen. Das zweite prismatische Septum (c) zeigt den nach vorne gebogenen Septenkragen, in welchem das Siphonalrohr endet. Während die zweite Kammer sehr eng ist, sind von der dritten Kammer (d) an folgende Kammern von regelmäßigem Abstand zueinander. Die Septen sind vom dritten Septum an perlmutterig (e), und die Schalenöffnung besitzt eine schwach zurückgezogene ventrale Lippe und eine regelmäßig vorgewölbte dorsale Lippe (f).

The outer wall of the initial chamber of *Dictyoconites* closely resembles in composition and construction the inner mineral layer of the initial chamber of the belemnite *Hibolithes* (BANDEL et al. 1984), and the recent sepiid *Spirula* (BANDEL & BOLETZKY 1979). In *Dictyoconites*, the following organic wall is not preserved and was not observed in *Aulacoceras* by DAUPHIN (1982: figs. 8, 9, 10), but the prismatic layer is thicker; the following aragonitic outer prismatic layer is preserved. It represents the innermost layer of the rostrum. A similar layer is seen in *Hibolithes*, but is not continuing into the calcitic adult rostrum.

### b) Second septum

**Description:** The second septum is very close to the first septum. It is attached to the constriction of the outer wall of the phragmocone just apertural of the first septum, almost on top of its anchorage to the wall. The second septum is composed of aragonitic crystallites arranged in a subprismatic structure. The septum is pierced with a 0.1 mm wide foramen in subventral position. It is evenly concave, the margins of the foramen are bent forward forming a prochoanitic septal neck (Fig. 2).

The septum is covered on both sides with a cement crust consisting of prismatic aragonitic crystallites that grew in optical continuity of the primary crystal-faces. The cement layer on the apertural side follows the septal neck-outline closely (Fig. 3). The cement layer on the apical side deviates from the surface of the septum at the foramen and continues across the aperture to the other side of the neck, providing evidence for an organic layer that closed the foramen of the second septum when aragonitic cement crusts formed during early diagenesis (Fig. 3).

**Discussion:** On the basis of the embryonic shell of *Hibolithes*, the poorly preserved and understood structure of *Dictyoconites* can be established. The chambers of *Hibolithes*, in contrast to those of *Dictyoconites*, remained unfilled and were not covered by aragonitic cement crusts. The second septum in both genera is composed of subprismatic, aragonite crystallites. The septal neck bends aperturally, providing the holdfast for the blind end of the siphuncle (Fig. 5).

### c) Third and following septa and chambers

**Description:** While the structure of the first mineralized septum (the second septum) is subprismatic, that of all following septa and septal necks is nacreous, as in *Spirula* (Fig. 4).

The second chamber is very low (Fig. 5); the following 6 or 7 chambers are about 0.2 mm in height. Septa are attached within the tube of the conotheca in slightly inclined position (Fig. 11). The suture, therefore, has a more apertural position on the ventral side and extends in the apical direction on the dorsal side. The course of the suture in this early portion of the conotheca is exactly opposite to that of the sculpture of the conothecal walls.

Beyond the eighth or ninth septum, the following 5 chambers are about 0.5 mm in height and the septa are not inclined (Fig. 11). The height of subsequent chambers slowly increases relative to chamber width. In the first 10 chambers the height is less than one third of the width. From 10<sup>th</sup> to 15<sup>th</sup> it is less than half of the width. Beyond the 20<sup>th</sup> chamber height is greater than half of the width, but later it again becomes less than half of the width and in a 33 mm wide conch the height of the final chamber is 10 mm, which is less than one third of its width.

From the third septum onwards, all the septa are basically alike. Septum thickness gradually increases from about 5 µm in the third septum to 10 µm in the sixth and 80–100 µm in the last septa preserved in the phragmocone. Septa are composed of an inner nacreous layer, which is attached to the inner walls of the conch by a ring-like prismatic ridge and by thicker prismatic layers on both sides (Fig. 4). These represent a continuation of the crystal growth of thin primary prismatic layers at the base and the top of the nacre during early diagenesis.

**Discussion:** The presence of nacre from the third septum onwards is also found in belemnites (BANDEL et al. 1984, MUTVEI 1964). The construction of the septa of *Dictyoconites* is also very similar to that of the recent *Spirula* (BANDEL & BOLETZKY 1979). The thin prismatic layers developed on the nacreous septa of *Spirula* show quite well developed crystal heads. A similar situation must have been present in the phragmocone of *Dictyoconites*. When diagenesis began, aragonite crystals grew on the chamber surfaces as continuations of the biocrystals of the prismatic layers. On surfaces such as the organic siphuncular wall, where the crystals were less well ordered, the orientation of crystals in the diagenetic crusts is more erratic.

The aragonitic crusts do not represent cameral fillings that had formed during the life of *Dictyoconites*, because they can be found in all chambers, not only the most apical ones. It is usually a little thicker on larger septa.

The change of orientation and spacing of the septa may reflect a change in the living mode of the animal. The septum orientation in early portions of the conch is opposite in inclination to the conch sculpture. This is also the case in some bacitritids, as for example *Annulobacitrites* (MAPES 1979).

#### d) Siphuncular tube

**Description:** Traces of the blind end of the siphuncular tube are preserved in the septal collar of the aperture of the second septum as described above (Figs. 2, 3). From the first nacreous septum (3rd septum) onwards the siphuncular tube represents a continuation of the retrochoantic septal neck (Fig. 6). The nacreous layer of the septum twists sharply into the septal neck and nacre forms the siphuncular tube that continues into the chamber lumen for about half of its height (Fig. 8). From there onward the tube consists of organic material (Fig. 9) and extends into the mineral portion of the segment of siphuncular tube belonging to the next septum in the apical direction (Figs. 6, 7). Here the tube consists of prismatic crystallites

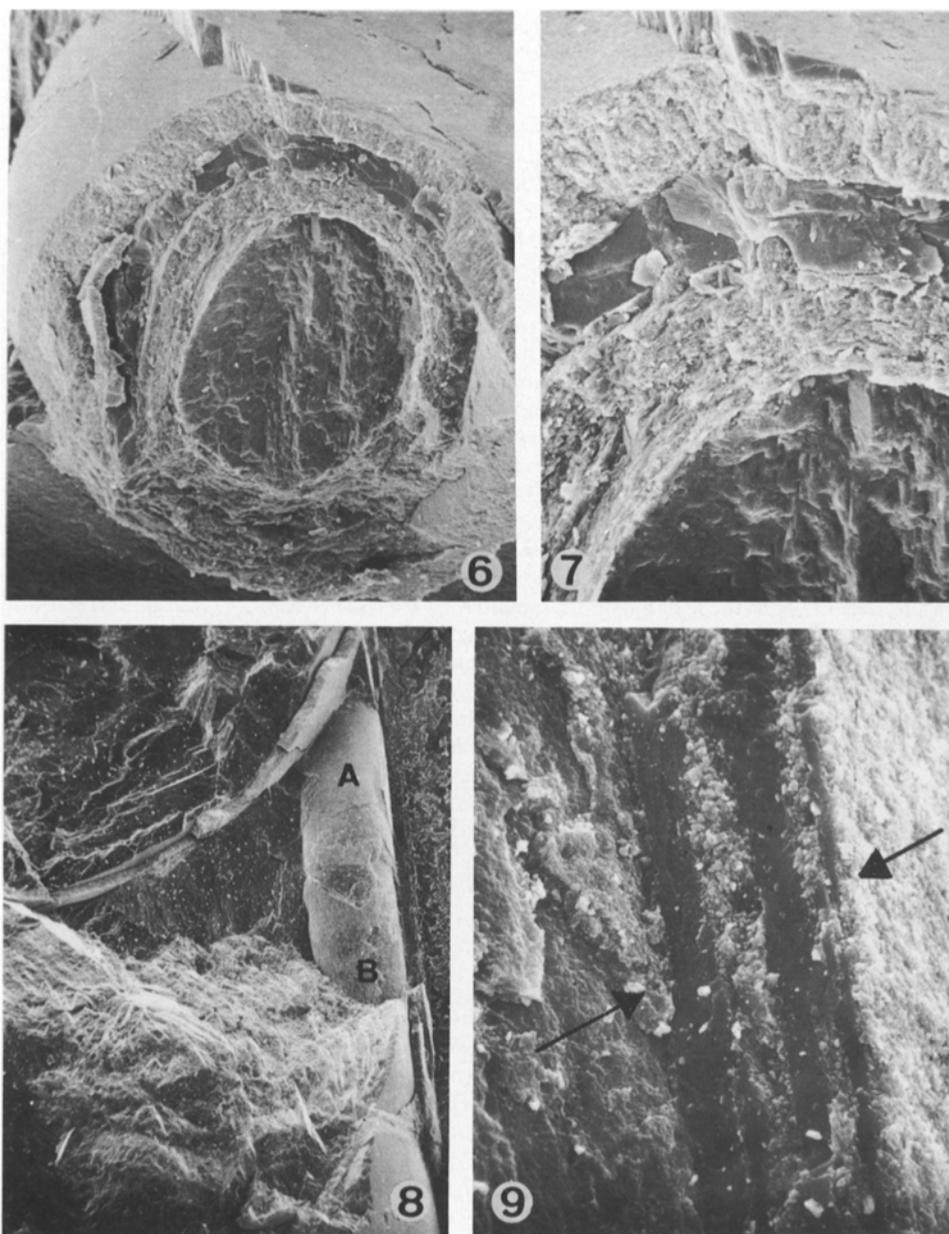
Abb. 6–9

6: Das nahe dem Septenkragen aufgebrochene Siphonalrohr zeigt zwei mineralisierte Wände; SEM × 200.

7: Der vergrößerte Ausschnitt von Abb. 6 zeigt, daß das äußere Rohr aus Perlmutter besteht, während das innere prismatisch aufgebaut ist; SEM × 500.

8: Siphonalrohr mit mineralisiertem Teil (A) und organischem Teil (B); SEM × 50.

9: Im mittleren Teil des Siphonalrohres sind beide Wände (Pfeil) organisch; SEM × 2000.



Figs. 6-9

- 6: Siphuncular tube fractured near septal neck. Both layers of the double tube are mineralized; SEM  $\times$  200.
- 7: Detail of Fig. 6 with nacreous outer tube section (septal neck) and prismatic inner tube section; SEM  $\times$  500.
- 8: Siphuncular tube with its mineral portion (A) and the organic section (B); SEM  $\times$  50.
- 9: In the central portion of the siphuncular tube both walls are organic. Arrows point at double walls; SEM  $\times$  2000.

(Fig. 7). The space between both tubes is usually filled with secondary prismatic, somewhat spherulitic aragonitic cement or with calcite (Fig. 6). The siphuncular tube is thus double walled, with a mineral apertural section and an organic apical section (Figs. 8, 10).

**Discussion:** The structures seen in *Dictyoconites* can again be interpreted with the aid of recent *Spirula*. In the latter the siphuncular tube is double walled, as had been reported also from Jurassic belemnites and aulacoceratids by MUTVEI (1971) and a Triassic belemnoid by FISCHER (1951). In *Dictyoconites* the mineral septal necks forming the apertural portion of each segment of the siphuncular tube are only half as long as those of *Spirula* (Fig. 10). It is of the same length as *Choanoteuthis* (FISCHER 1971), but quite a bit larger than of *Nautilus* (BANDEL & BOLETZKY 1979). The free space between both tubes was supported by aragonitic pillars which, during early diagenesis, were surrounded by the crystals of the aragonitic cement. The former pillar zone, thus, is now filled with a prismatic layer that continues in the crystal layer covering the septum proper or with secondary calcite. The chamber could have been emptied along the porous zone and through the apical organic double walled tube.

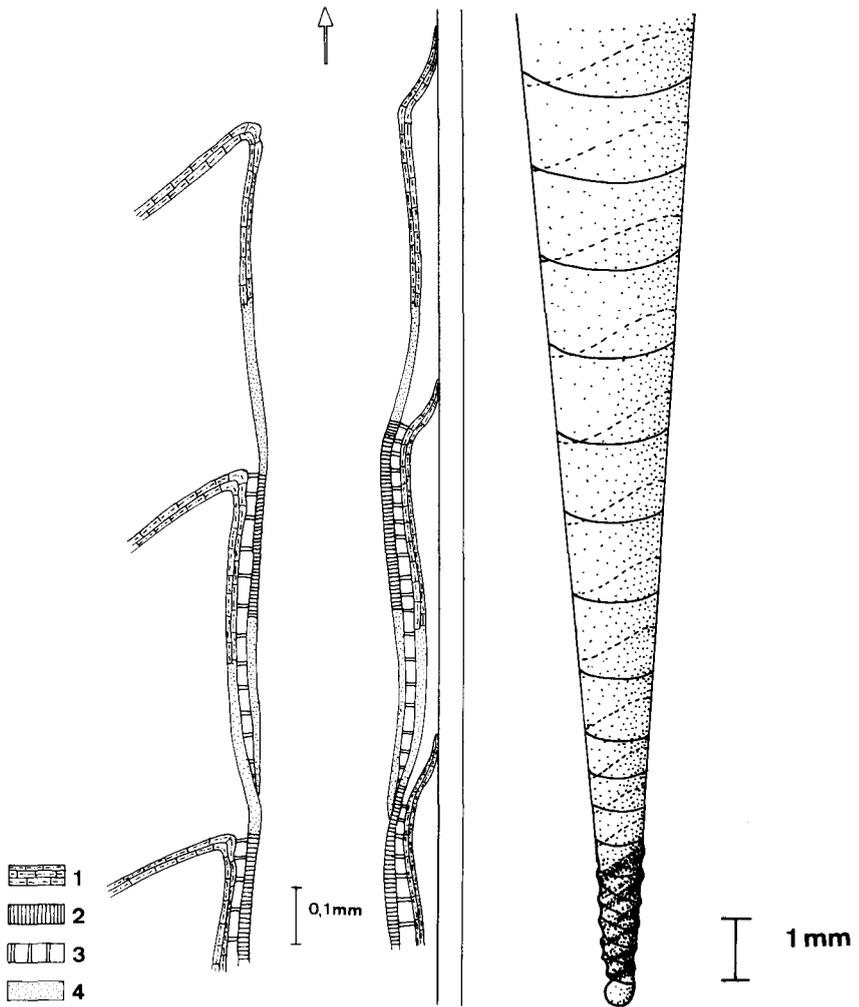
In his diagnosis of the genus *Aulacoceras*, which also encompassed *Dictyoconites*, HAUER (1866) noted that the siphuncular tube is covered with calcareous shell. Backward recurved septal necks were expected to exist in representatives of the aulacoceratids by HAUER (1866), BÜLOW (1915), NAEF (1922), FLOWER (1945), FISCHER (1951), FLOWER & GORDEN (1959) and ERBEN (1964). JELETZKY (1966) postulated that these observations were wrong, and thus, following MOJSISOVIC (1872) and STEINMANN (1910), reconstructed the septal necks of aulacoceratids, in contrast to those of belemnites, bend forwards (prochoanitic). The siphuncular tube of *Dictyoconites*, which is preserved in its original shell composition, indicates that JELETZKY's proposal is not valid for this genus, which is so close to the original types of the aulacoceratids in general. Diagenesis is probably responsible for these incorrect interpretations. In aulacoceratids with recrystallized shell, original aragonitic layers can no longer be differentiated from each other and from aragonitic crystal covers formed during early diagenesis. Commonly, structures of minute aragonite crystallites (about 0.2 µm wide) found in real biomineralisates of molluscs (BANDEL & HEMLEBEN 1975), will disappear during diagenetic transformation of aragonite into calcite, and are replaced by new structures which do not reveal the original composition and structure (BANDEL 1981).

#### e) Walls of the conch (conothecal walls)

**Description:** The apical end of the conch consists of the subspherical initial chamber. It is displaced from the remainder of the conch towards the ventral side and set off from it by a constriction of the outer shell wall (Fig. 5). The subsequent cylindrical conch is slightly cyrtconical (up to 1.7 mm in length) and is regularly orthoconical afterwards. It is circular in cross-section. The wall of the conch (conotheca of the phragmocone) is thin. In the early conch, low annulations mark the former outline of the aperture; in a 1.5 mm wide conch about 8 annulations are present in 1 mm of conch-length (Fig. 11). The aperture of the juvenile conch consists of a straight ventral lip and a projecting dorsal, saddle-like lip.

In later shells, as for example in the conotheca of a 33 mm wide phragmocone, annulations are absent, and only faint growth lines occur. On the dorsal side rounded crests represent the former outline of the projecting outer lip of the aperture. The lateral continuation of these lines run into the straight ventral lip. The growth lines resemble those of *Dictyoconites* as illustrated and described by ZITTEL (1891–1895), NAEF (1922) and JELETZKY (1966; pl. 6, fig. 4) and appear similar to those of *Austroteuthis* JELETZKY & ZAPFE (1967) and *Aulacoceras* (BÜLOW 1915).

The wall of the conch of *Dictyoconites* consists of three layers (Fig. 14). The central layer is nacreous; it is overlain by a thin sheet of subprismatic to spherulitic crystallites (Fig. 15) and



Figs. 10-11

10: Reconstruction of the siphuncular tube of *Dictyoconites* shown in longitudinal section. The nacreous structure (1) continues into the organic tube (4) which is attached to the inner side of the septal neck by a prismatic tube section (2). Both walls of the tube are held apart by prismatic pillars (3).

11: Sketch of the conothec of the juvenile *Dictyoconites*. In the early section septa are inclined and annulations follow the lines of growth. Later septa are straight and outer walls smooth.

Abb. 10-11

10: Die Rekonstruktionszeichnung zeigt das Siphonalrohr von *Dictyoconites* im Längsschnitt. Das Perlmuttseptum (1) setzt sich in das organische Rohr hin fort (4), welches seinerseits mit einem prismatischen Rohranteil dem Septenkragen innen eingefügt ist (2). Beide Wände der Röhre werden von prismatischen Pfeilern auseinandergehalten (3).

11: Die Zeichnung des Gehäuses eines jugendlichen *Dictyoconites* zeigt geneigte Septen und Außenwülste der Schale, die der Septenneigung entgegenlaufen und Anwachszonen widerspiegeln. Spätere Septen sind gerade und die Außenwand glatt.

underlain by a prismatic layer. A wall structure composed of 0.2  $\mu\text{m}$  thick basal elements of aragonitic fabric as present on the outer layer is the characteristic biomineralisate of conchiferan molluscs, usually present right below the organic periostracum (BANDEL 1978).

The central nacreous layer which is similar to the *Nautilus*-like nacre is composed of tablets of aragonite (Fig. 15). The inner layer has become thickened secondarily during early diagenesis by the growth of aragonite cement. The cement-crystallites grew in the same orientation as the biomineralisate below it. The layer of the former periostracum is in turn overlain by the deposits of the rostrum (Figs. 14, 15). This microstructure is similar to that of *Spirula* in the early parts of its internal shell (BANDEL & BOLETZKY 1979).

**Discussion:** The earliest portion of the phragmocone of *Dictyoconites* closely resembles in shape and sculpture members of the Parabacritidae as described by MAPES (1979). Here members of the genera *Annulobacrites*, *Sinuobacrites*, *Eobacrites* and *Gymnobacrites* show growth lines with a dorsal saddle. The juvenile conch of *Atractites* and *Hibolithes* are very similar to *Dictyoconites*, but in these we do not know the pattern of growth lines yet.

A long tubular living chamber is considered characteristic for aulacoceratids in general. Evidence for this however in aulacoceratids like *Aulacoceras*, *Dictyoconites*, *Atractites* is only indirect, because no living chamber is preserved. Where it is preserved, conchs carry no rostrum such as *Mojisovisctenthis* (JELETZKY 1966). Such conchs could have been formed by aulacoceratids, but as well by bacritids with an extended dorsal apertural margin (HORNY 1957, MAPES 1979). *Protoaulacoceras* from the Lower Devonian possessed a long tubular living chamber (BANDEL et al. 1983) but its relation to Permian-Triassic genera like *Dictyoconites* is not yet known.

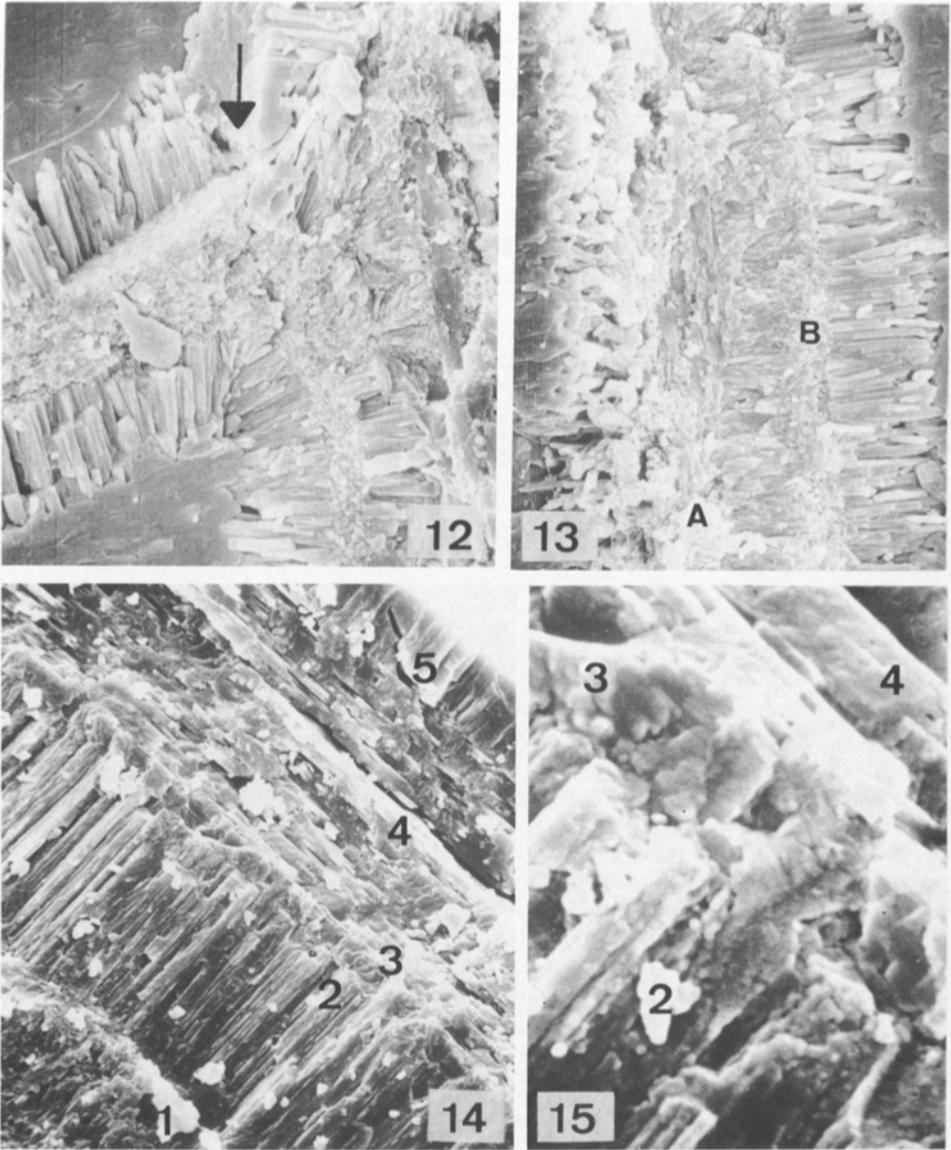
The structure of the phragmocone wall of *Dictyoconites* from Cortina d'Ampezzo differs from that described by DAUPHIN (1982) for *Aulacoceras* from Turkey in one vital detail. DAUPHIN described only two layers which represent the middle and the lower layers. She did not note the outer layer (Fig. 15) representing the periostracum along with the thin mineral layer below it and above the nacre. She considered that the periostracum was absent, in contrast to ectocochlean cephalopods, and had been transformed into the rostrum. This is a variation of BARSHKOV's (1972, 1973) ideas that the rostrum (of belemnites) is formed by the same type of epithelium that forms the nacreous layers (endostracum) of *Nautilus* and that the periostracum was lost.

The periostracum layer was neither lost nor was it transformed into rostrum layers. The conothecal wall structure of *Dictyoconites* is like that of Recent *Spirula* and *Sepia* (BANDEL & BOLETZKY 1979) and like Jurassic *Hibolithes* (BANDEL et al. 1984) composed of a periostracal layer with different mineral layers below it. All shell layers characteristic of ectocochleate conchiferan molluscs are present in addition to typical layers found in endocochleate cephalopods on top of them (rostrum).

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Abb. 12-15

- 12: Der Bruch durch den dorsalen Septenkragen zeigt eine scharfe Knickkante hier (Pfeil); SEM  $\times$  2000.  
 13: Bruch durch den Septenkragen zeigt den Übergang von Perlmutterstruktur zum organischen Siphorohr (B) und, eingefügt, den prismatischen Endteil (A) des Innenrohres; SEM  $\times$  2000.  
 14: Der Bruch durch die Wand der Konothek zeigt die Schichten vom Rostrum (links) bis zur inneren Prismenschicht (rechts). 1. äußere Rostrumlage; 2. innere Rostrumlage; 3. Periostracum; 4. Perlmutter; 5. innere Prismenschicht; SEM  $\times$  1700.  
 15: Vergrößerter Ausschnitt von Abb. 14 mit dem Periostracum zwischen Perlmutter (*Nautilus*-Typ) und innerer Rostrum-Schicht; SEM  $\times$  8500.



Figs. 12-15

- 12: Dorsal septal neck fractured shows the sharp edge of the nacre septum here (arrow); SEM  $\times$  2000.  
 13: Detail of inner septal neck with the prismatic portion of the inner part of the siphuncular tube. Prismatic layer (A), nacreous septal neck in transition to organic tube (B); SEM  $\times$  2000.  
 14: Fracture through conothecal wall. From the rostrum (left) to the inner prismatic layer (right). 1. outer layer of rostrum; 2. inner layer of rostrum; 3. periostracum-layer; 4. nacreous layer; 5. inner prismatic layer; SEM  $\times$  1700.  
 15: Detail of Fig. 14 with periostracal layer between the nacreous layer (*Nautilus* type) and the inner rostral layer; SEM  $\times$  8500.

### f) Attachment scars

**Description:** The dorsal interior side of each chamber, opposite to the ventral siphuncular tube, bears a longitudinal scar (Fig. 16) consisting of a low depression that is indistinctly striated longitudinally (Fig. 17). The scar is continuous from one chamber to the next and each septum covers it with its attachment ring. The scar, therefore, was formed independent of and before the septum.

**Discussion:** A similar scar had already been noted in specimens of the *Aulacoceras* by BÜLOW (1915). He correlated this feature with the so called »Normallinie« that had been noted in both some orthoceratids and belemnites. BÜLOW could think of no purpose this scar could have served.

The mode of formation and the function of the scar became evident when a similar feature was found in Recent *Spirula*. Dissection of the animal showed that the apical muscular mantle was attached to the shell along this scar (BANDEL 1982). In contrast to those cephalopods that use their shell as »house« the coleoids use it as an internal skeleton. Consequently, they do not need muscles to retract the body into the shell. These muscles in ammonites (BANDEL 1982) and in Recent *Nautilus* and its fossil relatives (MUTVEI 1964) are attached to the shell in round to oval scars on the posterior wall of the living chamber. The shell of aulacoceratids and belemnites (BANDEL et al. 1984) was attached to the visceral mass along a central dorsal line as in Recent *Spirula*.

## 2. Rostrum

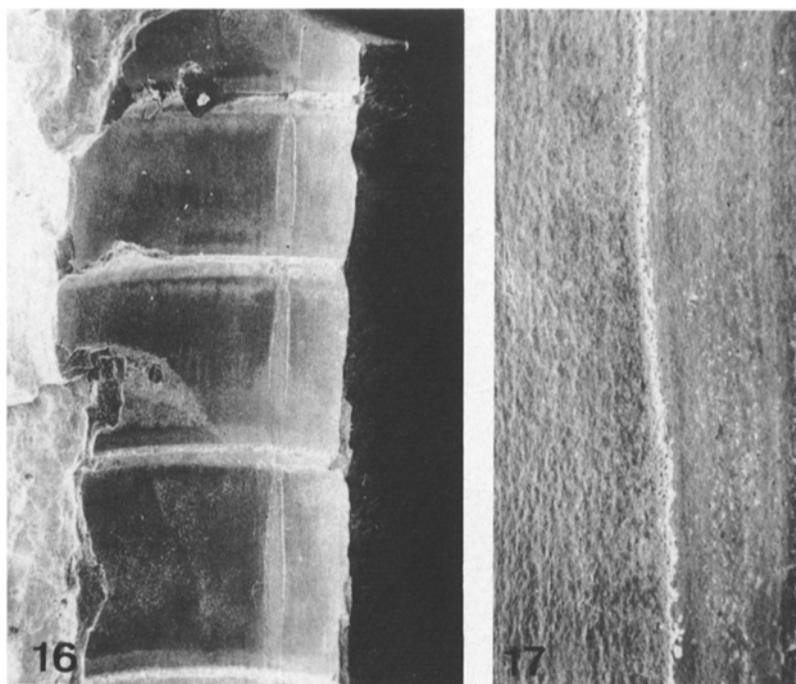
### a) Basal layer

**Description:** The basal layer of the rostrum is different in morphology and construction from later layers of the rostrum. Although the rostrum is limited to the apical portion of the conch, the basal layers cover most or all of the conch, probably almost to the apertural lips (Fig. 18).

Thin and sharp longitudinal rib material is present on the basal layer. The ribs are separated by flat interspaces and are connected by minute transverse lirae that follow the growth line pattern of the conch. A conch 5 mm wide has 76 ribs and a conch 35 mm wide has only 90 ribs. Thus, distance between the ribs increases, along with conch diameter. The transverse lirae become covered and less distinct towards the actual rostrum as the thickness of the basal layers increases slowly. Several dorsolateral longitudinal ribs become thickened and higher than other ribs. These lie in a position below the furrows of the actual rostrum, when it covers the basal layer.

**Discussion:** BÜLOW (1915) thought that the sculptural pattern of the basal layer represented the outer side of the actual conch and could be compared to similar sculptures found on ectocochleates (orthoceratids). NAEF (1922) corrected that opinion and showed that the rib pattern was produced by the roof of the shell sac surrounding the whole conch, as is the case in the Recent *Sepia* and *Spirula*. The basal layer of *Dictyoconites* is well illustrated by MOJSISOVICS (1871) and JELETZKY (1966: pl. 6).

MAPES (1979) described a number of bactritids, of the genera *Ctenobactrites*, *Orbobactrites* and *Rugobactrites*, possessing similar sculpture patterns of longitudinal and transverse lirae and/or costae. Because many of the conchs studied by MAPES from Upper Carboniferous and Permian strata were from juvenile individuals, and because we do not know the early ontogenetic stages of true aulacoceratids, some of these bactritids may well represent shells of juvenile aulacoceratids.



Figs. 16–17

16: Dorsal scar (Normallinie); SEM  $\times 43$ .17: Dorsal scar enlarged; SEM  $\times 440$ .

Abb. 16–17

16: Dorsale Normallinie; SEM  $\times 43$ .17: Vergrößerte dorsale Normallinie; SEM  $\times 440$ .

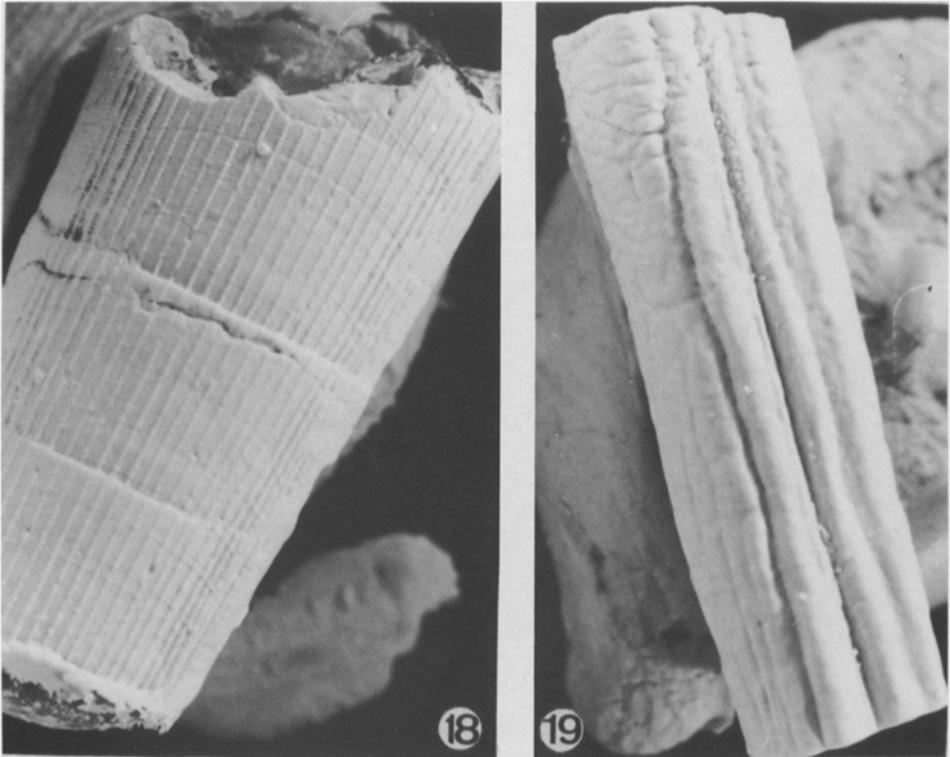
### b) Early rostrum

**Description:** The conch of the hatching young may have had a short simple cone-like primordial rostrum. After hatching, however, a characteristic slender juvenile rostrum formed consisting of stacked slender cones. In this way a 4 mm long angular rostrum is secreted that is attached to the initial chamber and is 0.4 mm wide at its base and 0.2 mm near its apex (Fig. 24).

With further growth, the rostral layers encroach onto the phragmocone and the rostrum acquires a slender, long quadrangular shape. The early, needle-like rostrum contained much organic material, but following layers were mainly aragonitic. In many specimens, the central portion of the rostrum collapsed as a result of sediment compaction after the organic shell had decomposed (Fig. 22).

The rostrum is slender to a length of about 5 cm, when the width is about 5 mm. The adult rostrum forms around this slender juvenile rostrum mainly by lateral shell deposits and little further growth occurs in the apical direction until the rostrum is fully formed with a length of about 6 cm (Fig. 23).

The adult rostrum of *Dictyoconites* from Cortina d'Ampezzo is bullet-shaped or club-like with somewhat flattened dorsal and ventral surfaces. On either side of the rostrum, two deep furrows separate a central ridge from two lower crests (Fig. 19). These lateral furrows extend the full length of the rostrum but the adapical portion is usually fractured and not preserved.



Figs. 18–19

18: The inner, basal layer of the rostrum consists of sharp ribs on the conothecal surface that shows the dorsal saddle in its lines of growth;  $\times 8$ .

19: Deep lateral furrows on the rostrum of a half-grown individual. Here fins were attached to the rostrum and blood vessels serving fin musculature left impressions;  $\times 10$ .

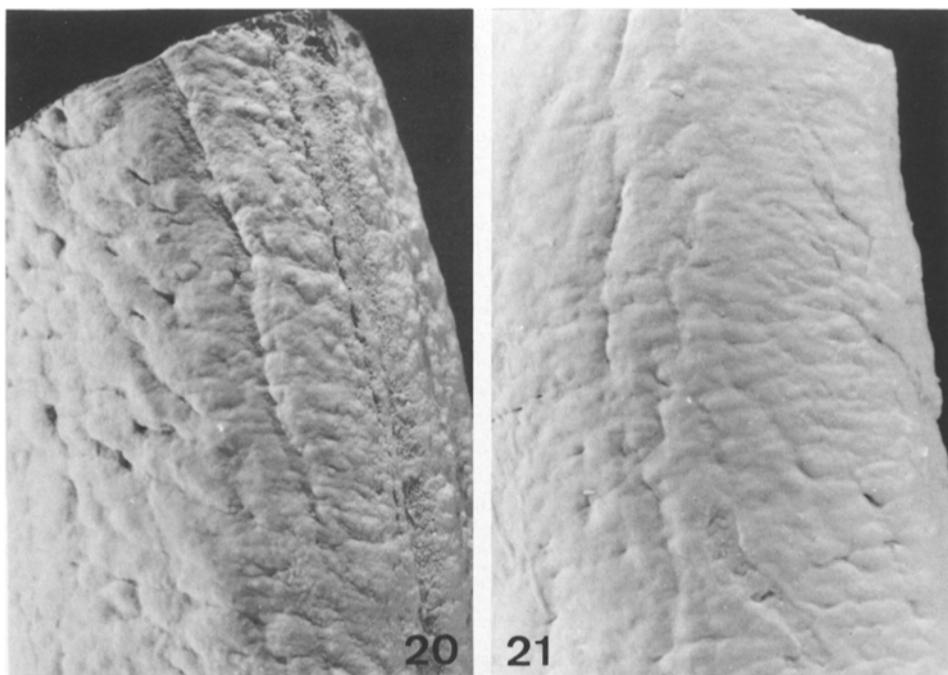
Abb. 18–19

18: Die Oberfläche der Konothek ist überlagert von den Rippen der inneren Rostrumlagen, deren Schichten die Anwachsstreifung nachzeichnen;  $\times 8$ .

19: Tiefe Seitenfurchen auf dem Rostrum eines halberwachsenen Individuums zeichnen den Anheftungs-ort der Flossen ab. Die Blutgefäße, die die Muskulatur versorgten, haben Eindrücke hinterlassen;  $\times 10$ .

The ventral and dorsal orientation is determined by the position of the siphuncular tube within the phragmocone. The siphuncle is marginal within the chambered part of the conch, lying close to the ventral side. Deposits on the ventral side of the rostrum are thicker than those on the dorsal side. Thus, the lower part of the animal in living portions was heavier. In an 8 mm high rostrum, for example, with a phragmocone 1.5 mm wide (alveolar diameter), the rostrum is 3.5 mm thick on the ventral side and 3 mm thick on the dorsal side.

The dorsal and ventral surfaces of the adult rostrum are wrinkled by three sets of ornamentation with different orientation that results in a network of crests and pits. One set consists of low longitudinal ribs, most visible in the internal layers and near the apical end of the rostrum. These reflect the underlying longitudinal ribs of the basal layer that covers the conch. The second set consists of closely spaced fine transversal grooves that cross the rostrum surface form



Figs. 20–21

20: One of the two furrows of the dorsal side of the adult rostrum reflect the position of major blood vessels here;  $\times 6$ .

21: Blood vessels imprinted on the ventral side of the adult rostrum;  $\times 6$ .

Abb. 20–21

20: Auf der Dorsalseite des ausgewachsenen Rostrums zeichnen sich die Positionen der Hauptblutgefäße ab;  $\times 6$ .

21: Eindrücke der Blutgefäße auf der ventralen Seite des Adultrostrums;  $\times 6$ .

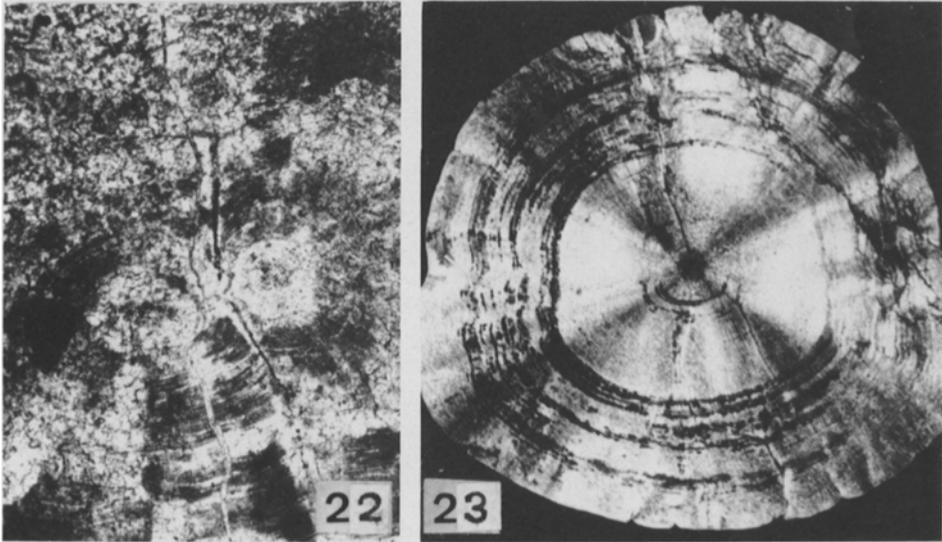
lateral ridge to lateral ridge. The third set consists of coarser, more or less longitudinal, somewhat sinuous furrows (Figs. 20, 21).

On the dorsal side only two of these coarse furrows are present and, in marginal position, close to the apertural end (Fig. 20). On the ventral side, two to four branching grooves are strongly imprinted on the rostrum surface aperturally, but are less distinct apically (Fig. 21). Grooves of the second set connect with these furrows.

**Discussion:** The rostrum of *Dictyoconites* was originally composed of aragonitic and organic shell material. In the close relative, *Austroteuthis* from the Rhaetian Zlambach marls, JELTZKY & ZAPPE (1967) found unaltered aragonite. In *Dictyoconites* from Cortina d'Ampezzo, the aragonite of the rostrum has recrystallized to calcite, whereas the aragonite of the chambered conch has remained unaltered. This difference in preservation results from differences in the primary structure of the aragonite crystallites, as confirmed by *Pseudorthoceras* from the same deposits. In this genus, crystallites like those of the *Dictyoconites* rostrum formed within the camerae. During diagenesis they have partly remained unchanged and aragonitic and partly have been transformed into calcite crystals with a similar morphology. Where the ac-

tual conch of *Pseudorthoceras* was affected by recrystallization, in contrast, the primary structure of the nacre has been totally destroyed. The different types of organic mineral deposits of the aragonitic molluscan shell react differently to recrystallization. Those grouped among true biomineralisates by BANDEL & HEMLEBEN (1975) and composed of basal elements do not preserve their shape in recrystallization into calcite (BANDEL 1978; DULLO 1983). Those shell deposits with more inorganic fabric in the sense of BANDEL & HEMLEBEN (1975) may be transformed into similar looking calcite crystals. The differential diagenesis of aragonitic shell has caused quite a bit of confusion and has given rise to many misinterpretations.

HANAI (1982) for example believed that the belemnite rostrum had been composed primarily of alternating layers of compact nacre and less compact, mainly organic-lined cavities that were secondarily filled with prismatic crystallites. Then, with diagenesis, a porous rostrum, constructed like the cuttlebone of Recent *Sepia*, was altered into the radially fibrous belemnite rostrum. HANAI reached this interpretation from data presented by SPAETH (1971, 1975), who showed that the rostrum of belemnites is not always solid, but may have a lattice-like structure. SPAETH's data, however, can not be used to support this theory, nor the opinion of DAUPHIN (1982), DAUPHIN & CUIF (1980), CUIF & DAUPHIN (1979) that the belemnite rostrum was aragonitic. The study by BANDEL et al. (1984) on unaltered material of the Jurassic belemnite *Hibolithes* proved that the rostrum is fully calcitic with some organic interlayers. When these decompose, the rostrum may become porous and even lattice-like in structure, as was observed by SPAETH (1971).



Figs. 22-23

22: The central rostrum portion was rich in organic matter and collapsed during diagenesis;  $\times 30$ .

23: Section through adult rostrum shows different shapes of rostra at different growth stages;  $\times 12$ , thin section.

Abb. 22-23

22: Im zentralen Bereich war das Rostrum vornehmlich aus organischer Substanz aufgebaut, die sich auflöste, so daß der Hohlraum bei der Diagenese zusammenbrach;  $\times 30$ .

23: Der Querschliff durch das adulte Rostrum zeigt die verschiedenen Formen, die das Rostrum während seiner Bildung besessen hat;  $\times 12$ .

Figs. 24–25

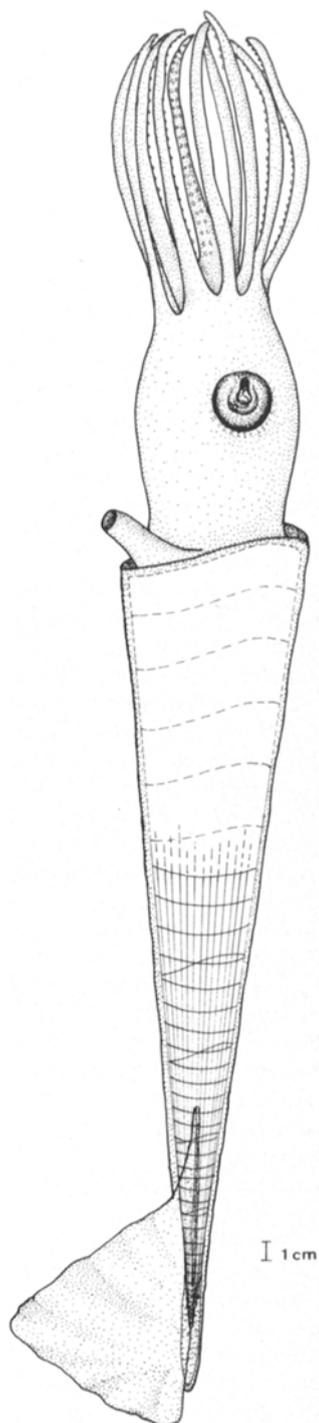
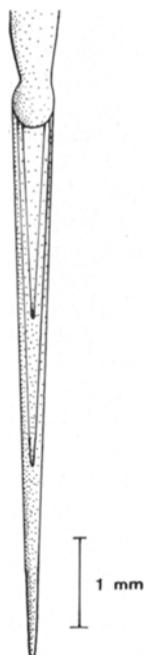
24: Sketch of the early ontogenetic rostrum, which is very slender and attached only to the first chamber.

25: Possible reconstruction of *Dictyoconites*.

Abb. 24–25

24: Zeichnung des frühontogenetischen Rostrums mit seiner schlanken Gestalt und Anheftung an der ersten Kammer.

25: Rekonstruktionsversuch eines *Dictyoconites*.



Aulacoceratids of the genera *Aulacoceras*, *Dictyoconites*, *Austroteuthis* had an aragonitic rostrum, whereas most belemnites had a calcitic adult rostrum. These differences may be of limited value for greater systematic arguments, however, because a belemnite can produce an aragonitic rostrum. The primordial rostrum of many species is aragonitic – as in *Hibolithes* (BANDEL et al. 1984), and it may remain so as in *Belemnoteuthis*. Where epirostra are formed as in Lower Jurassic representatives of the genera *Dactyloteuthis* and *Salpingoteuthis*, calcite and aragonite deposition occurs at different growth stages. Such recrystallised aragonitic epirostra may show a microstructure that is just like that of *Dictyoconites* from the Permian (FISCHER 1947).

HAUER (1866), MOJSISIVICS (1872), ZITTEL (1881–85), STEINMANN (1910), and NAEF (1922) had interpreted the wrinkles on the surface of the rostrum of *Dictyoconites* as imprints of blood vessels on the conch surface, and compared them to similar marks on Cretaceous belemnites such as *Belemnitella lanceolata* and *Goniotentis quadrata*. STEINMANN (1910) suggested that because of these imprints, *Dictyoconites* might be considered the ancestor to the Cretaceous *Belemnitella* stock. MOJSISOVICS (1872), BÜLOW (1915) and JELETZKY (1966) noted imprints of blood vessels on the rostrum, and NAEF (1922) had interpreted them as sound evidence for the endocochlear nature of the rostrum and of the total conch of the aulacoceratids and the belemnites.

The blood system in the muscular mantle of the common squid *Loligo* provides a good model for the interpretation of the imprints on the rostrum of *Dictyoconites*. In recent *Loligo vulgaris*, the main heart pumps blood through a ventral artery (Aorta posterior) into the muscular mantle. This artery splits, with its main branches occupying a central position to the end of the muscular mantle. Its lateral branches split into smaller veins until numerous more or less transverse veinlets continue to the dorsal side, where they reunite into two sublateral veins (Vena pallialis) through which the blood returns through the gill to the heart.

The posterior artery in *Loligo* crosses from the heart into the mantle without going forwards. In the case of the belemnites, at least in the adult animal, the squid case is present. However, in an animal with a long »living chamber« as the aulacoceratid, the posterior artery had to go forward and around the inner margin of the aperture of the conch before it could reach the muscular mantle that covered the shell. Blood had to be pumped forwards before it could go backwards to the mantle throughout life.

The wrinkles on the rostrum surface of *Dictyoconites* reflect the more apical course of the blood system, as it occurs in *Loligo*. The muscular-mantle system in both is separated from the visceral mass-head loop and thus the skin and fins are well supplied with fresh blood. Fins are a part of the muscular mantle and thus derived from the rudiment of all mantle epithelia, the shell gland. The fins in *Dictyoconites* were probably attached to the rostrum along the lateral furrows. NAEF (1922) observed that there is a close connection between shell and fin during embryonic development in modern squid, however, the cartilaginous finbase becomes separated from the shell during ontogeny. In *Dictyoconites* and some Cretaceous belemnites the close attachment between finbase and shell must have remained during life, and fins and internal skeleton remained in close contact. The mantle may have been attached along palisade-like specialized cells, similar to those described by BANDEL & SPAETH (1983) from the *Nautilus* mantle-shell attachment.

Main blood vessels extend into the fin base in recent cephalopods, and this was probably also the case in Triassic to Cretaceous belemnoid squids. SPAETH (1975) and HANAI (1982) suggested that the lateral furrows of the belemnite rostrum represent attachment scars of the finbase to the rostrum. NAEF (1922) had suggested this earlier, but did not incorporate this idea into his reconstruction of belemnite soft parts, but instead showed the fins attached not at the end of the conch where the rostrum lies, but more forwards (NAEF, 1922: fig. 67).

The rostrum served not only as a counterweight to the light gas-filled chambers of the phragmocone but also as base for the fins. NAEF's interpretation of the rostrum functioning as counterweight only, was perhaps based on the erroneous observation by previous cephalopod workers that a new chamber was built around a bubble of gas. However, DENTON & GILPIN-BROWN (1961, 1966) have shown that it is actually liquid-filled.

### 3. Results and conclusions

JELETZKY (1966) commented very sharply on NAEF's (1922, 1928) interpretation of the belemnoid cephalopods and wrote: »It has thus been demonstrated that NAEF's approach to the restoration of the phylogeny of the belemnite-like coleoids and teuthids by postulating ideal and utterly hypothetical ancestral forms largely on the basis of embryonical and morphological investigation of the best known Recent and fossil coleoids leads to completely erroneous results and therefore is inadmissible in principle.«

But let us look at the main characters presented by JELETZKY (1966) to describe Aulacoceratida and to differentiate it from true *Belemnites* and compare these characters with those of *Dictyoconites* from Cortina d'Ampezzo. *Dictyoconites* represents a genus which was originally described as *Aulacoceras* by HAUER (1866) and belongs to the core of these Triassic rostrum-bearing cephalopods.

I. According to JELETZKY the rostrum of a typical aulacoceratid should have been composed mainly of organic shell whereas that of belemnites should have been predominantly calcareous. The *Dictyoconites* rostrum, in contrast, was predominantly calcareous. This is also true for rostra of *Aulacoceras* and *Atractites*, which were aragonite prior to diagenesis. Belemnite rostra are predominantly calcareous, but some were largely or even predominantly organic and or aragonitic within the Jurassic relatives of *Salpingoteuthis* and *Dactyloteuthis*.

II. The proostracum and the hyperbolar zone should be absent in aulacoceratids but present in belemnites. This part of JELETZKY'S diagnosis is supported by the data extracted from *Dictyoconites*.

III. Aulacoceratids, according to JELETZKY, are characterized by a siphuncle with forward-recurved septal necks, in contrast to belemnites which have backward-recurved septal necks. The septal necks of both *Dictyoconites* and belemnites are bent backwards. The siphuncle of *Dictyoconites* resembles that of Recent *Spirula*.

IV. The »living chamber« of aulacoceratids is like that of a nautiloid, whereas belemnites had no living chamber. This part of JELETZKY'S diagnosis is only correct if we disregard the dorsal attachment scars of the *Dictyoconites* »living chamber«. These scars are a feature common to the tubular »living chamber« of *Dictyoconites*, probably all other true aulacoceratids, and the open »living chamber« of belemnites and the short closed »living chamber« of *Spirula*.

V. An opinion based on non-preserved soft tissue, such as JELETZKY'S that aulacoceratids had no muscular mantle while belemnites had one is not appropriate in a diagnosis of a fossil group. In any case though, it is probably not correct. *Dictyoconites* must have had a muscular mantle that was attached to the rostrum. Otherwise the vascular system could not have become imprinted on the rostrum.

Of the five characters JELETZKY considered important for differentiating aulacoceratids from true belemnites, only one remains fully valid: The »living chamber« of Aulacoceratids is tubular and shows only a small dorsal lip projection, whereas in belemnites it is open at the ventral side. This typical feature of the aulacoceratids however, is also common to the bactritids, thus raising the problem of how to differentiate these two groups.

The differences between bactritoids and aulacoceratoids as listed by MAPES (1979) are: Bactritoids lack a rostrum and internal deposits of the chambers; they possess a wrinkle layer

in their conch walls, and variable septal orientation. Based on *Dictyoconites*, the aulacoceratids possess internal deposits on chamber walls consisting of cement crusts and not chamber deposits formed during life. The septa in the juvenile conch in both *Dictyoconites* and atracitids from South America are variable both in orientation and in spacing.

Some of the sculptures noted by MAPES to be present on bactritoids indicate that rostrum deposition may begin early. The wrinkle layer may represent a feature that is related to the diagenetic alteration of the nacreous conch walls as is shown in the case of Devonian lamellorhoceratids BANDEL & STANLEY (1986).

There are still three features which separate true belemnites from aulacoceratids like *Dictyoconites*. Belemnites have no ribbed or other basal layers that covers the phragmocone in front of the rostrum. Belemnites seem to have always a ventrally open »living chamber«. The fins in belemnites are not attached to the lateral rostrum, but to the dorsal portion of it. NAEF's (1922) characters for aulacoceratids are: Siphuncular tube thin, constricted at septa and widened in chambers; septal necks recurved backwards; phragmocone wall smooth, longitudinal ribs added secondarily; growth lines not conclusive. Aulacoceratids represent slender squids with endocochlear conch from embryonic stage onwards. They are relatives and perhaps precursors to the belemnites.

The study of *Dictyoconites* confirms NAEF's views to a large extent and conflicts with JELETZKY's diagnosis in many ways. This indicates that models based on the ontogeny of recent coleoids lead to better interpretations of extinct cephalopods than do models that are formulated without observations on recent animals, but are based instead largely on the researcher's imagination.

## Ergebnisse

JELETZKY (1966) attackierte NAEF's (1922, 1928) Vorstellungen über die systematische Zugehörigkeit der Aulacoceraten zu den Belemniten. Er führte in der Diagnose 5 Punkte auf, die Aulacoceraten von Belemniten scheiden sollen. Die untersuchte Art der Gattung *Dictyoconites* gehört einer Form an, die dem Kernbereich der Aulacoceraten zugehört und der Typusgattung *Aulacoceras* nahesteht. *Dictyoconites* kann daher gut zum Testfall der Diagnose-Bedingungen JELETZKY's dienen:

I. Das Rostrum von Aulacoceraten soll vornehmlich organisch aufgebaut sein, jenes von *Dictyoconites* war aber kalkig, und zwar aragonitisch.

II. Der Schalenrand der Aulacoceraten zeigt keinen dorsalen Vorsprung des Proostracums, wie er für Belemniten typisch ist. Dieser Teil der Diagnose JELETZKY's wird bestätigt.

III. Der Siphon im Aulacoceratenphragmocon soll einem nach vorne umgebogenen Septenkragen aufsitzen und damit im Gegensatz zu Belemniten stehen, deren Septenkragen nach hinten weisen. Die Septenkragen von *Dictyoconites* sind aber nach hinten umgebogen und setzen sich im organischen Siphonalrohr fort, wie dies auch bei Belemniten der Fall ist. Ansonsten ähnelt der Siphon von *Dictyoconites* mehr dem Doppelrohrsiphon von *Spirula* als dem einfachen Siphon jurassischer Belemniten.

IV. Die »Wohnkammer« der Aulacoceraten soll der der Nautiloideen entsprechen, während Belemniten keine Wohnkammer mehr besitzen. Wie die Belemniten besaßen aber auch Aulacoceraten – wie *Dictyoconites* – keine Wohnkammer, und der Weichkörper war dorsal der Schale von innen angeheftet. Dies ist auch noch bei der rezenten *Spirula* zu beobachten.

JELETZKY meinte, daß die Aulacoceraten keinen Muskelmantel besessen hätten, während ein solcher bei Belemniten vorhanden gewesen sei. *Dictyoconites* erweist, daß die zylindrische Schale der Aulacoceraten genauso von einem Muskelmantel umhüllt war, der sich in apikal gelegenen Flossen fortsetzte, wie die Belemniten.

Es zeigt sich also, daß von den 5 Punkten der Aulacoceraten-Diagnose JELETZKYS sich nur ein Punkt bestätigt, der zudem nicht strittig war. Allerdings gibt es ganz ähnlich gestaltete Phragmocone auch bei den Bacriten, so daß eine Trennung letzterer von Aulacoceraten ohne Rostrum problematisch bleibt. Die Unterscheidungen, die MAPES (1979) aufführte, können nicht weiterhelfen, weil mit ihrer Hilfe beide Gruppen nicht getrennt werden können. Dies wird deutlich, wenn einige der von MAPES abgebildeten Bacriten einen Anflug von Rostrumbildungen zeigen.

Von Aulacoceraten trennt die Belemniten:

I. Sie besitzen keine Zwischenschichten, die zwischen Phragmocon und Rostrum gelegen sind.

II. Die »Wohnkammer« der Belemniten ist ventral offen, bei Aulacoceraten geschlossen.

III. Flossen der Belemniten saßen dem Rostrum dorsal auf, während sie bei Aulacoceraten lateral verankert waren.

NAEF (1922) nennt als Charakteristika der Aulacoceraten: Dünnes Siphonalrohr; Rohr dünner im Durchgang der Septen, weiter im Bereich der Kammer; Septenkrägen nach hinten gekrümmt; Phragmocon glatt; berippte Lage sekundär aufgelagert; Anwachsstreifen von unsicherer Bedeutung. Seiner Meinung nach stellen Aulacoceraten die Reste schlanker Tintenfische dar, deren Schale schon beim Embryo innen lag, und die Verwandte oder gar die Vorläufer der Belemniten bilden.

NAEFS Vorstellungen können weitgehend bestätigt werden, während JELETZKYS Diagnose in vielen Punkten der Analyse der *Dictyoconites*-Schale widerspricht. Dieser Gegensatz spiegelt wider, daß eine Interpretation, die von lebenden Tieren ausgeht, oft realistischere Rekonstruktionen ausgestorbener Tiere ermöglicht, als die Bewertung von diagenetisch oft stark veränderten Fossilien allein es vermag.

### Literature

- BANDEL, K. (1978): Übergänge von einfacheren Strukturtypen zur Kreuzlamellenstruktur bei Gastropodenschalen. – *Biominalisation*, 10: 9–37; Stuttgart.
- (1981): Struktur der Molluskenschale im Hinblick auf ihre Funktion. – *Paläont. Kursbücher*, 1: 25–48; München.
- (1982): Morphologie und Bildung der frühontogenetischen Gehäuse bei conchiferen Mollusken. – *Facies*, 7: 1–198; Erlangen.
- BANDEL, K. & BOLETZKY, S. V. (1979): A comparative study of the structure, development and morphological relationship in chambered cephalopod shells. – *The Veliger*, 21: 313–354; Berkely.
- BANDEL, K.; ENGESER, T. & REITNER, J. (1984): Die Embryonalentwicklung von *Hibolithes* (Belemnitida, Cephalopoda). – *N. Jb. Geol. Paläont. Abh.*, 167: 275–303; Stuttgart.
- BANDEL, K.; REITNER, J. & STÜRMER, W. (1983): Coleoids from the Lower Devonian Black Slate (Hunsrück-Schiefer) of the Hunsrück (West Germany). – *N. Jb. Geol. Paläont. Abh.*, 165: 397–417; Stuttgart.
- BANDEL, K. & HEMLEBEN, C. (1975): Anorganisches Kristallwachstum bei lebenden Mollusken. – *Paläont. Z.*, 49: 298–320; Stuttgart.
- BANDEL, K. & SPAETH, C. (1983): Beobachtungen am rezenten *Nautilus*. – *Mitt. Geol.-paläont. Inst. Univ. Hamburg*, 54: 9–26; Hamburg.
- BANDEL, K. & STANLEY, G. (1986): Reconstruction of a Devonian cephalopod family (Lamellorthoceratidae) with unique cameral deposits. – [In press].
- BARSKOV, I. S. (1972): Microstructure of the skeletal layers of belemnites compared with external shell layers of other mollusks. – *Palaeont. J.*, 4: 492–500; Tel Aviv.
- BOLETZKY, S. V. (1974): The »larvae« of Cephalopoda: A review. – *Thalassia Jugosl.* – 10: 45–76; Zagreb.
- BÜLOW, E. (1915): *Orthoceras* und Belemniten der Trias von Timor. – *Paläontologie von Timor, Lief. 4 (7)*: 1–72; Stuttgart.

- CUIF, J. P. & DAUPHIN, Y. (1979): Minéralogie et microstructures d'Aulacocerida (Mollusca-Coleoidea) du Trias de Turquie. – *Biomínéralisation*, 10: 70–79; Stuttgart.
- DAUPHIN, Y. (1982): Analyse microstructurale d'un *Aulacoceras* (Mollusca – Coleoidea) juvenile du Trias de Turquie. – *Paläont. Z.*, 56: 53–75; Stuttgart.
- (1983): Les subdivisions majeures de la classe Céphalopodes: bases de la systématique actuelle – apport de l'analyse microstructurale. – Thèse Univ. Paris-Sud: 1–284; Paris.
- DAUPHIN, Y. & CUIF, J. P. (1980): Implications systématiques de l'analyse microstructurale des rostrés de trois genres d'Aulacoceratidés triasiques (Cephalopoda-Coleoidea). – *Palaeontographica*, A, 169: 28–50; Stuttgart.
- DENTON, E. J. & GILPIN-BROWN, J. B. (1961): The buoyancy of the cuttlefish *Sepia officinalis* (L.). – *J. Mar. biol. Ass. U. K.*, 41: 319–342; Plymouth.
- (1966): On the buoyancy of the pearly *Nautilus*. – *J. Mar. biol. Ass. U. K.*, 46: 723–739; Plymouth.
- DULLO, W. C. (1983): Fossildiagenese in miocänen Leitha-Kalk der Paratethys von Österreich: Ein Beispiel für Faunenverschiebungen durch Diageneseunterschiede. – *Facies*, 8: 1–112; Erlangen.
- ERBEN, H. K. (1964): Bactritoidea. – [In:] MOORE, R. C. (ed.): Treatise on invertebrate paleontology, Part K, Mollusca 3, Geol. Soc. America & Univ. Kansas Press: K491–K505; New York.
- ERBEN, H. K.; FLAJS, G. & SIEHL, A. (1969): Die frühontogenetische Entwicklung der Schalenstruktur ectocochleater Cephalopoden. – *Palaeontographica*, A, 132: 1–154; Stuttgart.
- FISCHER, A. G. (1947): A belemnoid from the Late Permian of Greenland. – *Medd. o. Gronl.*, 133: 1–24; Kopenhagen.
- (1951): A new belemnoid from the Triassic of Nevada. – *Am. J. Sci.*, 249: 285–293;
- FLOWER, R. H. (1945): A belemnite from a Mississippian boulder of the Caney Shale. – *J. Paleontology*, 19: 490–503; Tulsa.
- FLOWER, R. H. & GORDON, M. (1959): More Mississippian belemnites. – *J. Paleontology*, 33: 809–842; Tulsa.
- GRANDJEAN, F. (1910): Le siphon des ammonites et des bélemnites. – *Bull. Soc. géol. France*, sér., 4, 10: 496–519; Paris.
- HANAI, T. (1982): A story of the belemnite-developmental approach to fossil morphology. – *Trans. Proc. Palaeont. Soc. Japan*, n. S., 128: 421–432.
- HORNÝ, R. (1957): *Bojobactrites ammonitans* n. g., n. sp. (Bactritoidea) from the Devonian of Central Bohemia. – *Ustred. ustav geol. Sb.*, CSR, 23: 285–305; Prag.
- HAUER, F. v. (1888): Die Cephalopoden des Bosnischen Muschelkalkes von Han Bulog bei Sarajevo. – *Denkschr. Akad. Wiss. Wien.*, 54: 1–56; Wien.
- JELETZKY, J. A. (1966): Comparative morphology, phylogeny, and classification of fossil Coleoidea. – *Paleont. Contr.*, Mollusca Art. 71–162; Lawrence.
- 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; Wien.
- MAPES, R. H. (1979): Carboniferous and Permian Bactroidea (Cephalopoda) in North America. – *Univ. Kansas Paleont. Contr.*, 64: 1–751; Lawrence.
- MOJSISOVICS, D. v. (1872): Über das Belemnitidengeschlecht *Aulacoceras* FR. v. HAUER. – *Jb. geol. Reichsanst.*, 21: 41–57; Wien.
- MUTVEI, H. (1964): Remarks on the anatomy of recent and fossil Cephalopoda. – *Stockholm Contrib. Geol.*, 11: 79–102; Stockholm.
- (1964): On the shells of *Nautilus* and *Spirula* with notes on the shell secretion in non-cephalopod molluscs. – *Ark. Zool.*, 16: 221–278;
- (1970): Ultrastructure of the mineral and organic components of molluscan nacreous layers. – *Biomínéralisation*, 2: 48–72; Stuttgart.
- (1971): The siphonal tube in Jurassic Belemnitida and Aulacocerida (Cephalopoda: Coleoidea). – *Bull. geol. Inst. Univ. Upsala*, n. S., 3: 27–36; Upsala.
- NAEF, A. (1922): Die fossilen Tintenfische. – 322 S.; Jena (Fischer).
- (1928): Die Cephalopoden – In: *Fauna und Flora des Golfes von Neapel*, Monogr. 35,2: 148–864; Neapel.
- SPAETH, C. (1971): Aragonitische und calcitische Primärstrukturen im Schalenbau eines Belemniten aus der englischen Unterkreide. – *Paläont. Z.*, 45: 33–40; Stuttgart.
- (1975): Zur Frage der Schwimmverhältnisse bei Belemniten in Abhängigkeit vom Primärgefüge der Hartteile. – *Paläont. Z.*, 49: 321–331; Stuttgart.
- STEINMANN, G. (1910): Zur Phylogenie der Belemnioidea. – *Z. induktive Abstammungs- und Vererbungslehre*, 4: 103–122;
- ZITTEL, K. A. (1881–1885): *Palaeozoologie* II. Bd. – 893 S.; München (R. Oldenbourg).