

Chapter 14

Ultrastructural Analyses on the Conotheca of the Genus *Belemnotheutis* (Belemnitida: Coleoidea)

Dirk Fuchs,¹ Helmut Keupp,¹ Vasilij Mitta,² and Theo Engeser¹

¹Institute of Geological Sciences, Paleontology, Freie Universität Berlin, Malteserstrasse 74–100. D-12249 Berlin, Germany, drig@zedat.fu-berlin.de;

²Russian Academy of Sciences, Palaeontological Institute, Profsojuznaja 123, Moscow 117997, Russia, vmitta@mail.ru

| | | |
|-----|--|-----|
| 1 | Introduction | 299 |
| 2 | Previous Studies | 300 |
| 3 | Material and Methods | 301 |
| 4 | Ultrastructural Observations on the Conotheca of <i>Belemnotheutis</i> | 305 |
| 4.1 | Ventral Conotheca (Phragmocone Diameter = 10mm) | 305 |
| 4.2 | Lateral Conotheca (Phragmocone Diameter = 10mm) | 305 |
| 4.3 | Dorsolateral Conotheca (Phragmocone Diameter = 10mm) | 305 |
| 4.4 | Dorsal Conotheca (Phragmocone Diameter = 10mm) | 309 |
| 5 | Discussion | 309 |
| 6 | Conclusions | 310 |
| | References | 313 |

Keywords: *Belemnotheutis*, ultrastructure, conotheca, proostracum, periostracum

1 Introduction

The internal skeleton of extinct belemnoids consists of the phragmocone (Fig. 14.1) and the rostrum. The rostrum covers the posterior part of the phragmocone and acts as a counterweight that brings the animal into a horizontal swimming position. Structural elements of the phragmocone are the septal-siphonal complex and the conotheca (phragmocone wall). If the proostracum (Fig. 14.1), the anterior dorsal projection of the phragmocone, is also part of the phragmocone or an independent development, is currently under discussion. The proostracum is usually considered to be the dorsal remnant of the body chamber inherited from ectocochlean ancestors (Crick, 1896; Naef, 1922; Jeletzky, 1966; Doyle and Shakides, 2004). Rostral layers (primordial rostrum + rostrum) and the mural parts of the septa do not belong to the conotheca proper.

Although the conothecal ultrastructure of belemnoids has been studied for a long time (Jeletzky, 1966; Barskov, 1972; Bandel et al., 1984; Doguzhaeva et al., 1999; Doguzhaeva et al., 2002; Doguzhaeva et al., 2003a, b), morphological knowledge of this very important feature is still incomplete.

This is partly due to the bad preservational potential of these fragile aragonitic structures. In most cases, only empty alveola without remains of the phragmocone are available. Only in a few cases phragmocones are preserved, but usually their ultrastructure has been recrystallized. Especially Bandel et al. (1984) and Bandel (1989) warned of diagenetic alterations and mentioned that ultrastructural analyses on the conotheca require unaltered material.

Additionally, data about the conothecal wall ultrastructure is problematic to compare as important methodological details such as preparation, magnification, ontogenetic stage, or morphological orientation (ventral, lateral, dorsal) given in previous publications are often insufficient. This resulted in an inconsistent terminology in the literature. Today, it is difficult to correlate conothecal layers observed in previous investigations. In order to overcome these obstacles, a consistent method and terminology are necessary.

New material of *Belemnotheutis* provided by one of us (Dr. V. Mitta, Moscow, Russia) exhibits the ultrastructure of well-preserved unaltered conothecal layers. Comparisons and correlations with previous studies on belemnoid ultrastructure were possible and could give additional information about the poorly understood belemnoid morphology.

It is the purpose of the present study to reinvestigate the conotheca of *Belemnotheutis* and to correlate the conothecal layers with those of other belemnoid taxa described in previous studies.

2 Previous Studies

In Table 1, we have summarized important ultrastructural analyses on the belemnoid conotheca. It seems that the sequence of layers within the conotheca is highly variable.

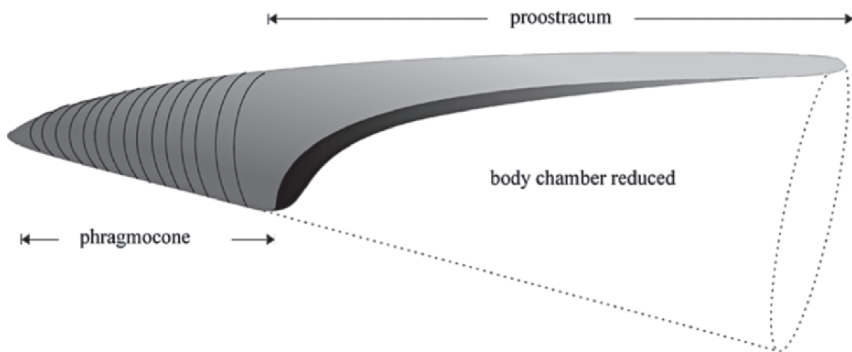


Fig. 14.1 General morphology of the internal skeleton of belemnoids (rostrum not drawn).

Interests in the ultrastructure of the belemnoid conotheca started with Christensen (1925) and Müller-Stoll (1936). Jeletzky (1966) revised older literature and postulated a belemnoid conotheca consisting of a thin inner prismatic layer, a thin central mineralized layer, and a thick outer prismatic layer. Jeletzky (1966: 110) also added: "Our ideas about microscopic structure of phragmocone and conotheca of the Belemnitida are now in a state of confusion." Since microscopic magnifications have proved to be insufficient for ultrastructural analyses, these older investigations are negligible. Modern SEM analyses with adequate magnifications started with Barskov (1972). In *Conobelus*, *Pachyteuthis*, and *Mesohibolites*, Barskov observed an inner prismatic and an outer nacreous layer in the conotheca. Observations are in agreement with those of Jeletzky (1966), at least concerning the presence of an innermost prismatic conothecal layer.

Especially concerning the presence of an outer prismatic layer, observations are inconsistent. As is well documented by Bandel et al. (1984) and Doguzhaeva et al. (1999, 2003b), the layer forming the primordial rostrum continues in a layer along the outside of the conotheca. It is possible that this layer was sometimes interpreted as the outer prismatic layer of the conotheca (Table 14.1), because Bandel and Kulicki (1988) identified a comparably thin outer prismatic layer within the conotheca of *Belemnotheutis* not belonging to the primordial rostrum.

Likewise it is difficult to correlate intermediate layers. Interpretations vary between a thick nacreous layer (Mutvei, 1964; Barskov, 1972; Hewitt and Pinkney, 1982; Bandel and Kulicki, 1988; Doguzhaeva et al., 1999, 2002) and thin organic sheets (Doguzhaeva et al., 2003b).

3 Material and Methods

Several well-preserved phragmocones from the Upper Callovian (– *lamberti* – zone) of Dubki near Saratov, Russia (provided by Dr. V. Mitta) were investigated (for the stratigraphy of Dubki, see Keupp and Mitta, 2004).

Our phragmocones might be easily assigned to *Belemnotheutis polonica* Makowski, 1952, which occurs in the – *lamberti* – zone of Lukow (Poland). But as there are no distinctive characters for a morphological differentiation between our specimens and the type material of *B. antiquus* Pearce, 1847 (Donovan and Crane, 1992; Doyle and Shakides, 2004) from the Callovian (– *athleta* – zone) of Christian Malford, England, we consider these taxa in synonymy.

Six uncrushed specimens (MC-1–MC-6) are between 22–31mm in maximum length and 12–22 mm in maximum diameter (Fig. 14.2). The cross section is almost circular. The apical angle is always 20°. The earliest chambers including the protoconch are not preserved. Another dorsoventrally flattened specimen (MC-7), which is 100mm in maximum length, might be considered as fully grown. In the same specimen the most apical part of the rostrum is preserved but the earliest camerae including the conotheca are replaced by pyrite. None of the studied specimens retains a proostracum in situ.

Table 1. Comparison of previous ultrastructural observations on *belemnoid conotheca*.

| Order | Authors | Sequence of layers | | | | Investigated stage | Ontogenetic taxa | plane |
|-------|-----------------------------------|--|-------------------------|-----------------|---|-------------------------|---|-------|
| | | External | Intermediate | Investigated | Ontogenetic taxa | | | |
| | Christensen, 1925 | Prismatic (= primordially rostrum?) | – | Prismatic | <i>Megateuthis</i> | embryonic | ? | |
| | Müller-Stoll, 1936 | Thick Prismatic (=primordially rostrum?) | Thin organic | Thin prismatic | <i>Chitinoteuthis</i> | embryonic | ? | |
| | Mutvei 1964 (p. 97) | Periostracum? | Nacreous | Thin prismatic | <i>Megateuthis</i> | ? | longitudinal? | |
| | Jelitzky 1966 (p. 124) | Thick Prismatic (Primordially rostrum?) | Very thin, mineralized | Thick prismatic | <i>Megateuthis</i> | Embryonic | Medial (ventral) | |
| | Barskov, 1972 | – | Nacreous | Prismatic | <i>Conobelus</i> , <i>Pachyteuthis</i> , <i>Mesohibolites</i> | Embryonic | ? | |
| | Hewitt and Pinkney, 1982 (p. 144) | ? | Thick nacreous | Thin prismatic | <i>Acroteuthis</i> | Juvenile-adult | Transversal (dorsal?) | |
| | Bandel et al., 1984 (p. 276, 285) | Primordially rostrum | Organic | Thin prismatic | <i>Hibolites</i> | Embryonic-postembryonic | Medial | |
| | Bandel and Kulicki, 1988 (p. 310) | Thin Prismatic | Nacreous | Thin prismatic | <i>Belemnotheutis</i> <i>Megateuthis</i> | Adult? | ? | |
| | Doguzhaeva et al., 1999 (p. 255) | Primordially rostrum | Nacreous | – | <i>Conobelus</i> | Embryonic-postembryonic | Medial | |
| | Doguzhaeva et al. 2002 (p. 324) | Thin proostracal layers | Nacreous | Prismatic | <i>Megateuthis</i> | Adult | Longitudinal (dorsal) | |
| | Doguzhaeva et al. 2003b (p. 83) | Primordially rostrum | Thin proostracal layers | Prismatic | <i>Passaloteuthis?</i> | Embryonic-postembryonic | Medial + Transversal (dorsal + ventral) | |

| | | | | | | | | |
|----------------------|--|----------------------------------|--|--|--|--|-------------------------------|------------------|
| Aulaco- cerida | Dauphin, 1983 Bandel, 1985 (p. 233) Cuif and Dauphin, 1979 Doguzhaeva et al., 2002 | - Periostracum - - - | - Thin prismatic Organic - | Lamellar Nacreous Nacreous Nacreous | Prismatic Prismatic Prismatic Prismatic | <i>Aulacoceras</i> <i>Dictyoconites</i> <i>Atracites</i> <i>Murveiconites</i> | ?? Adult ?? Juvenile | ? |
| Hematitida | Doguzhaeva et al., 2002, 2003a | - | 5-6 prismatic layers without nacre? | | | <i>Hematites</i> | Postembryonic | ? |
| Phragmo- teuthida | Doguzhaeva et al., 2003a (p. 67) | Irregularly mineralised | Proostracal layers | Lamello- fibrillar | Prismatic | <i>Donovaniconus</i> | Juvenile-adult | Medial (dorsal?) |

The thin sheath-like rostrum surrounding the phragmocone has a brownish color. X-ray diffraction analyses revealed that it is typically composed of aragonite. On the mid-dorsal line of the rostrum, characteristic rounded ridges (Fig. 14.2) are present. As demonstrated by Makowski (1952), they run parallel in the earliest ontogenetic stages but diverge at later stages until they disappear at a phragmocone diameter of approximately 18 mm. Specimen MC-7 demonstrates that the dorsal ridges are already developed at the earliest ontogenetic stages.

Conotheca and septal sutures are visible where the thin rostrum has flaked off. When this is the case in the dorsolateral region, a sharp and colored separation is evident on the outer conothecal surface (Fig. 14.2). Toward the dorsum, the surface is black. Weak imprints of proostracal growth lines are visible. They are similar to those described by Doguzhaeva et al. (2002) in *Megateuthis*. Toward the venter, the surface exhibits an iridescence that takes up two-thirds of the ventral phragmocone circumference.

Two specimens selected for ultrastructural studies (MC-8, MC-9) were fractured. Cross and longitudinal fractures were produced between a phragmocone diameter of 4 mm and 10 mm. This region corresponds presumably to the 10th–36th camera, i.e., juvenile, adolescent, and presumably adult stages.

Opened camerae were completely filled with sediment. Due to diagenetic dissolution, the septal and siphonal morphology of *Belemnnotheutis* could not be investigated.

Shell fractures were only cleaned, coated with gold, and studied with SEM. All specimens (MC-1–MC-9) are stored in the Institute of Geological Sciences, Paleontology, Freie Universität Berlin.

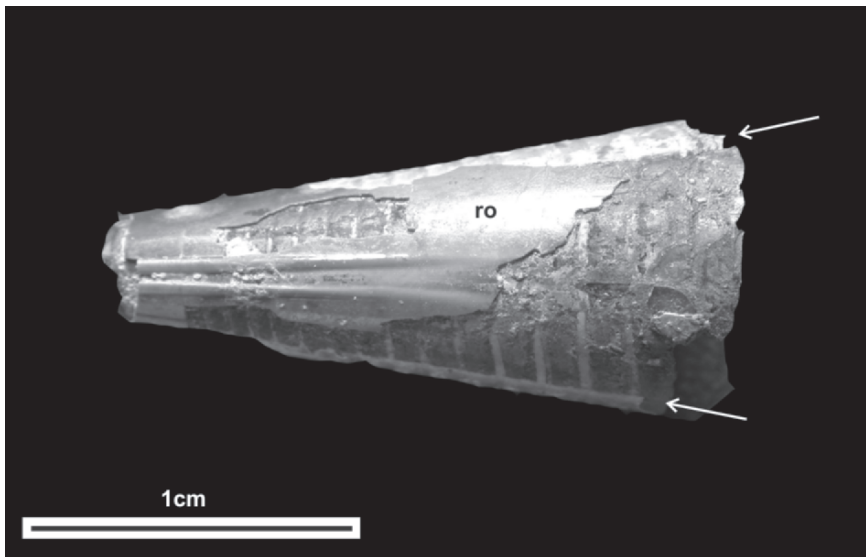


Fig. 14.2 *Belemnnotheutis antiquus* (=polonica). Dorsal view of specimen MC-5. The paired ridges are visible. Where the rostrum (ro) is flaked off on the dorsolateral part, an abrupt change in color is visible (arrows).

4 Ultrastructural Observations on the Conotheca of *Belemnotheutis*

4.1 Ventral Conotheca (Phragmocone Diameter = 10 mm)

Ventrally to ventrolaterally, the conotheca consists of (from inside out) an inner prismatic, a nacreous, a thin outer prismatic, and a lamellar layer (Fig. 14.3). The rostrum overlies the outermost lamellar layer. The inner prismatic layer is between 17 μm and 25 μm thick. Thickness increases lateralward. The outer prismatic layer is constantly 3–4 μm thick (Fig. 14.3B). A well-developed 20–40 μm thick nacreous layer (platelets-nacre, *Nautilus*-Type, Type 1) separates the inner and outer prismatic layer. Longitudinal fractures between a phragmocone diameter of 4 mm and 10 mm show that the thickness of nacre is correlated with the ontogenetic stage, i.e., the thickness of nacre increases with the phragmocone diameter. Prisms of the inner and outer layer are clearly delimited from the intermediate nacreous layer. There are absolutely no interspaces between them.

The outside of the outer prismatic layer is covered by a 4–5 μm thick lamellar layer (Figs. 14.3B, 14.4A). Only the rostrum occurs outside this lamellar layer.

4.2 Lateral Conotheca (Phragmocone Diameter = 10 mm)

Laterally, the conotheca is composed of (from inside out) an inner prismatic, a nacreous, a thin outer prismatic, and a lamellar layer. The only difference between the ventral and the lateral conotheca is the comparatively thin nacreous layer (10 μm). Figure 14.4B shows that sometimes there might be a hollow gap between the outer prismatic layer and the rostrum. The lamellar layer must have disintegrated.

4.3 Dorsolateral Conotheca (Phragmocone Diameter = 10 mm)

Dorsolaterally (between 10 o'clock and 2 o'clock respectively on both sides of the conotheca), the most remarkable observation is the wedging out of the nacreous layer (Fig. 14.5A, B). At a distance of 200 μm , the nacreous layer thins out and disappears completely (Fig. 14.5B). Consequently, both inner and outer prisms merge together (25 μm) and are no longer distinguishable. The laminar layer

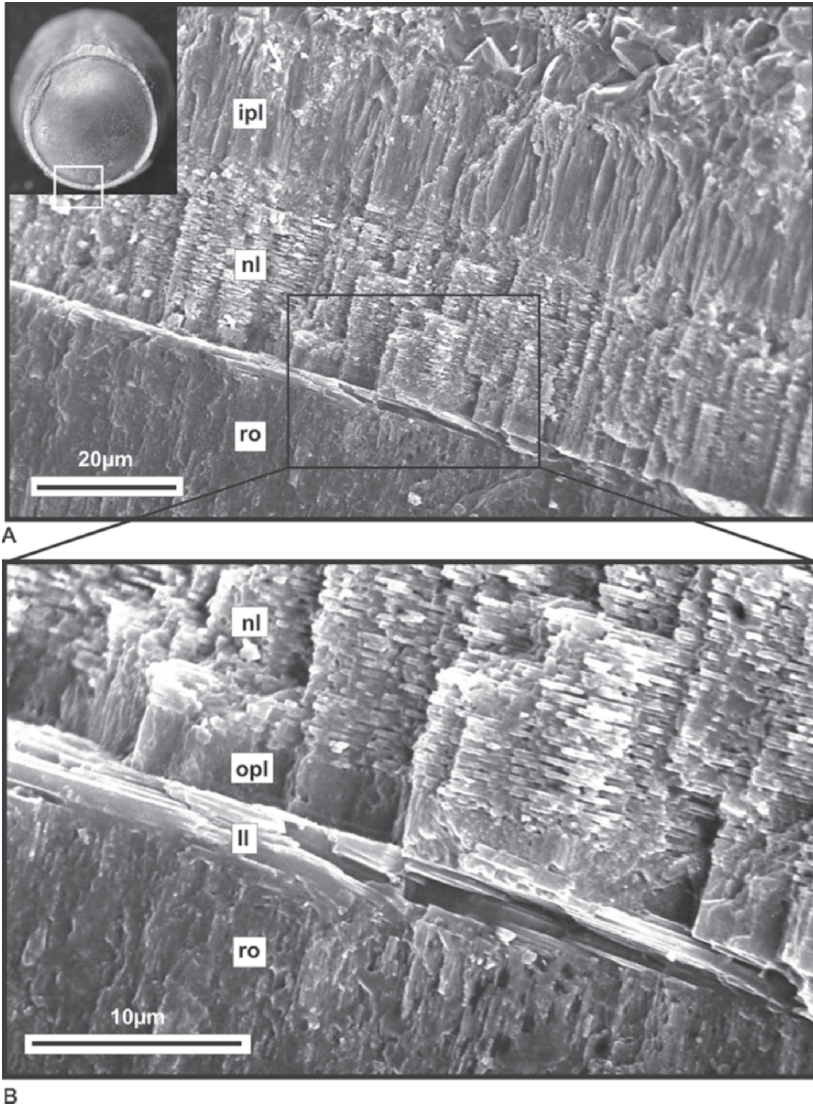
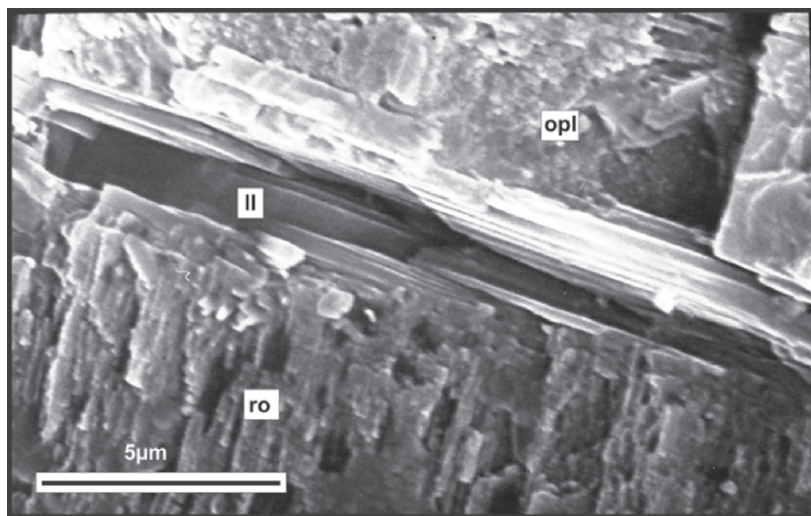
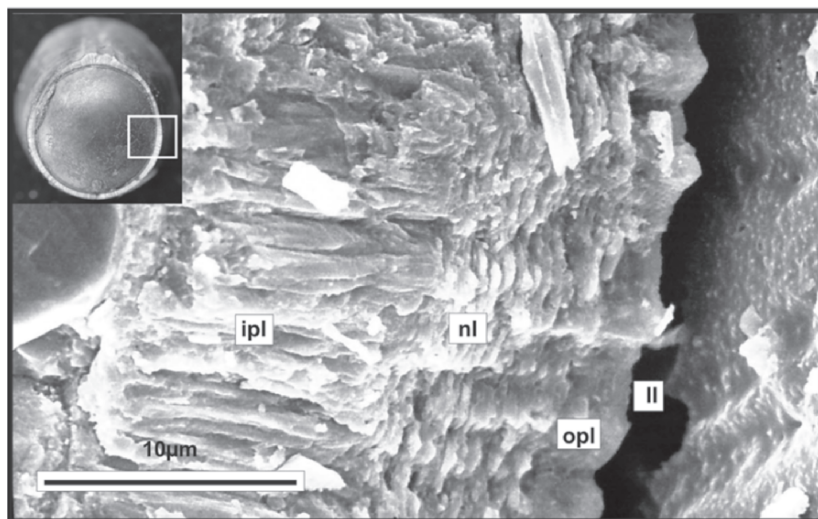


Fig. 14.3 (A) Ventral cross-fracture of specimen MC-8 (phragmocone diameter = 10mm) to show inner prismatic layer (ipl), nacreous layer (nl), and rostrum (ro); 1,000× enlarged. (B) Detail of (A) to show nacreous layer (nl), outer prismatic layer (opl), lamellar layer (ll), and rostrum (ro); 3,000× enlarged.

between the rostrum and the now single inner prismatic layer is still present (2–3µm). In some places (Fig. 14.5A), the inner surface of the rostrum displays similar borings as described in Doguzhaeva et al. (2003b), which indicate a high organic content. In other places, gaps are filled with secondary calcite (Fig. 14.5B).

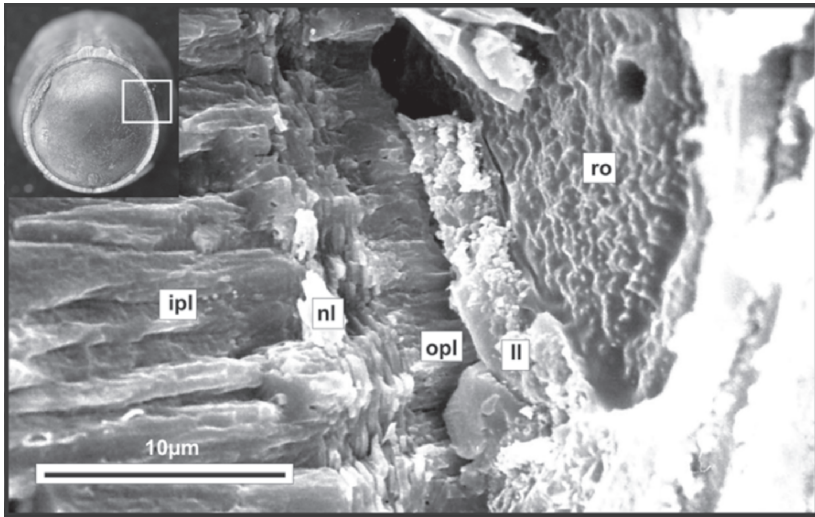


A

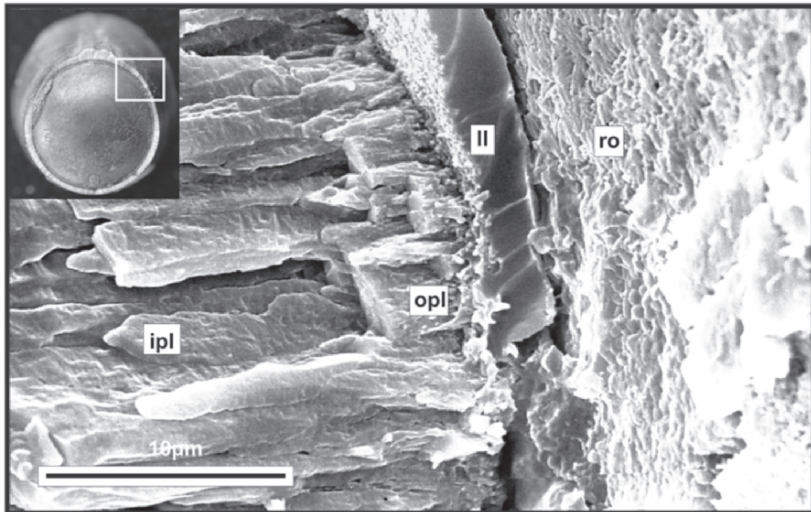


B

Fig. 14.4 (A) Detail of Fig. 14.3B to show outer prismatic layer (opl), lamellar layer (ll), and rostrum (ro); 7,000 \times enlarged. (B) Lateral cross-fracture of specimen MC-8 (phragmocone diameter = 10 mm) to show inner prismatic layer (ipl), nacreous layer (nl), and outer prismatic layer (opl). The lamellar layer (ll) is disintegrated; 3000 \times enlarged.



A



B

Fig. 14.5 (A) Dorsolateral cross-fracture of specimen MC-8 (phragmocone diameter = 10 mm) to show inner prismatic layer (ipl), thin nacreous layer (nl), outer prismatic layer; lamellar layer (ll), and inner surface of rostrum (ro). The lamellar layer is bored; 3,000 \times enlarged. (B) Dorsolateral cross-fracture (only 50 μ m dorsal from A). The nacreous layer wedged out. The lamellar layer is replaced by secondary calcite; 3,000 \times enlarged.

4.4 Dorsal Conotheca (Phragmocone Diameter = 10 mm)

Dorsally, the conotheca is composed of an inner prismatic layer and a layer that corresponds to the lamellar layer. No nacreous layer is observable either in cross fractures or in longitudinal fractures.

Sideward from the paired ridges on the outer surface of the rostrum, the lamellar layer is 4–5 μm thick. Laminae were sometimes replaced by presumably phosphorus granules similar to those described by Doguzhaeva and Mutvei (2003). They are nearly 1 μm in diameter.

Mid-dorsally below the paired ridges the layer under discussion swells up to a spindle-like bulge of 40 μm in thickness (Fig. 14.6A). The spindle has a length of 500 μm . Here the lamellar layer is preserved as secondary calcite (Fig. 14.6B).

5 Discussion

Our results partly confirm earlier observations by Bandel and Kulicki (1988) in which the conotheca of *Belemnotheutis* consists of an inner and an outer prismatic layer separated by a nacreous layer (Fig. 14.7). In contrast to Bandel and Kulicki (1988), we found a fourth lamellar layer, which is external to the outer prismatic layer. It occurs all around the phragmocone. Most probably, the laminae of this layer were primarily organic because in some places they are penetrated by borings (fungi? algae?), disintegrated or replaced by secondary calcite.

However, a four-layered construction of the conotheca does not occur all around the whole phragmocone circumference (Fig. 14.7). Whereas Bandel and Kulicki (1988) assumed a persistent conotheca, we conclude from our observations that in the genus *Belemnotheutis* only two-thirds of the phragmocone circumference consist of four layers. The remaining dorsal one-third of the circumference is built of only two layers. Ventrolaterally to dorsolaterally the thickness of the nacreous layer decreases continuously until it wedges out. As a result, inner and outer prismatic layers merge together. Consequently, only a single inner prismatic layer and an outer lamello-organic layer constitute the dorsal conotheca.

Because of its outermost position, it seems reasonable to interpret the lamello-organic layer as the periostracum. As characteristic for most shelled molluscs the periostracum covers the inner mineralized layers. Dorsally, where the nacreous layer is absent, the rather thin periostracum is modified into a comparably thick layer. Where the sheath-like rostrum has been removed, this sudden shift from a nacre-dominated conotheca to a periostracum-dominated conotheca is even visible macroscopically (Fig. 14.2). Weak, forwardly curved growth lines on the dorsal black surface of the periostracal layer are typical for a belemnoid proostracum. This led us to assume that the periostracum forms the proostracum.

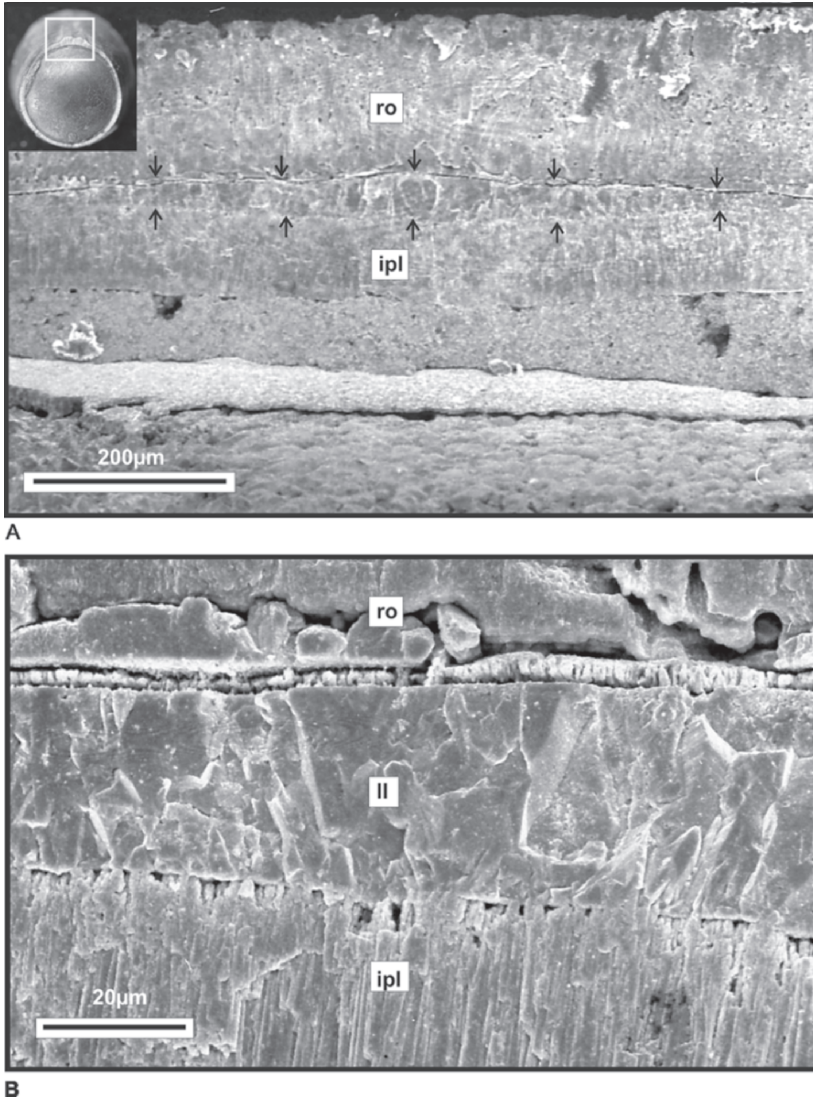


Fig. 14.6 (A) Dorsal cross-fracture of specimen MC-8 (phragmocone diameter = 1 cm) to show inner prismatic layer (ipl), spindle-like swelling of the lamellar layer (arrows), and rostrum (ro); 100× enlarged. (B) Detail of (A). The lamellar layer (ll) between the inner prismatic layer (ipl) and the rostrum (ro) is comparatively thick and replaced by secondary calcite; 1,000× enlarged.

6 Conclusions

It was previously unknown that nacre does not occur along the entire phragmocone circumference in belemnoid shells. Certainly, the presence of nacre depends on the ontogenetic stage. According to our material, nacre is already present after completion of the tenth camera (phragmocone diameter = 4 mm). The absence of nacre in

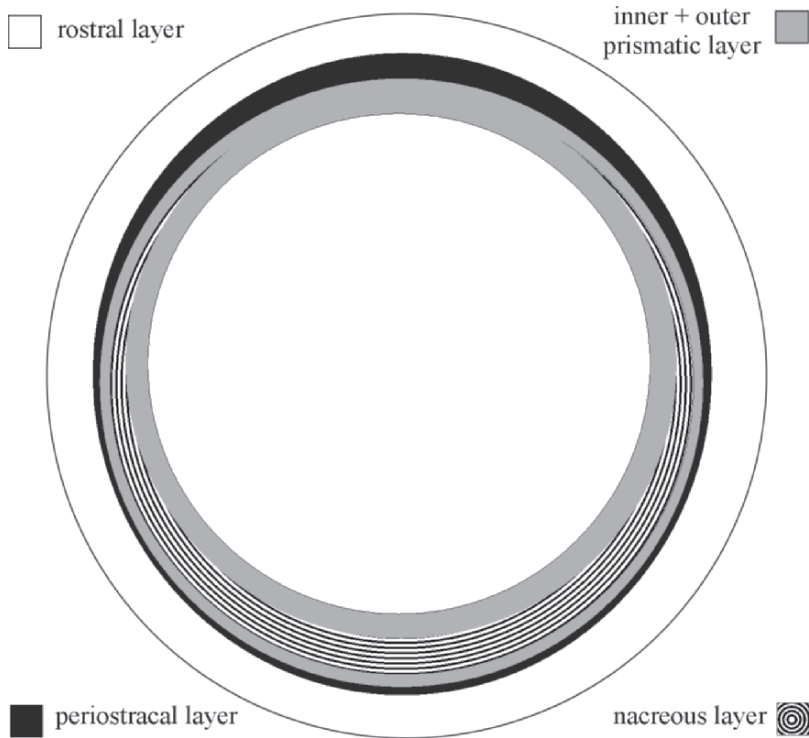


Figure 14.7. Schematic cross section through the conotheca and the rostrum of *Belemnotheutis*. Ventrally the conotheca is four-layered. Dorsolaterally the nacreous layer wedges out. As a result, the inner and the outer prismatic layer merge together. Dorsally the periostracal layer increases in thickness.

the dorsal part can be observed in these presumably juvenile and in later stages. MC-8, a specimen with approximately 36 chambers and a phragmocone diameter of 10 mm, is probably still an adolescent. Nevertheless, our conclusions can also be applied to adult forms, because specimen MC-7 (phragmocone length = 100 mm) shows the distinct color difference between the dorsum and the remaining ventral side. We are aware that *Belemnotheutis* is an unusual representative of the Belemnitida and that dorsal reduction of nacre is not necessarily a feature of all Belemnoidea. Nevertheless, previously analyzed specimens should be reinvestigated in the light of this new ultrastructural pattern. Our observations might explain why nacre sometimes was not observed in earlier studies on belemnoid shells (Table 14.1). It is likely that if just dorsal fragments of individuals are investigated, no nacre is detectable. Older statements that the nacreous layer forms the bulk of the belemnoid conotheca must be revised, if future observations on other taxa support our observations.

So far only Bandel (1985) and Bandel and Kulicki (1988) observed a thin outer prismatic layer in the belemnoid conotheca. In the present study, it was difficult to confirm this thin outer prismatic layer. We suppose that most workers who did not

find this outer prismatic layer either overlooked it or investigated dorsal parts of the conotheca where only a single prismatic layer occurs (Fig. 14.7). Consequently, we conclude that a thin outer prismatic layer is present at least in the ventral to dorso-lateral parts of the belemnoid conotheca.

An irregularly mineralized or predominantly organic layer external to a nacreous layer was reported by Mutvei (1964) from presumably adult *Megateuthis*, by Doguzhaeva et al. (2002) from adult *Megateuthis*, by Doguzhaeva et al. (2003b) from adult *Passaloteuthis*, and by Doguzhaeva et al. (2003a) from adult *Donovaniconus*. Bandel et al. (1984) described an organic layer (“innere organische Zwischenschicht”) between the inner prismatic protoconch wall and the primordial rostrum, which continues without interruption into the postembryonic stages. Judging by the difficulty of detecting the thin outer prismatic layer, these predominantly organic layers most probably correspond to our outermost lamello-organic layer. Doguzhaeva et al. (2003b) called their irregularly mineralized layer with a high organic content “proostracal layer.” They believed that the layer under discussion forms the proostracum, but cannot be considered as a continuation of the conotheca, because it is situated between the conotheca and the rostrum. However, Doguzhaeva et al. (2003a, b) did not refer to the possibility that their organic layer might correspond to the periostracum, which is a typical feature of all mollusc shells. Already Bandel (1985) stated that belemnoids display exactly the same sequence of conothecal layers (including a periostracal layer) as nautilus and ammonoids (Fig. 14.8). In the conotheca of spirulid and sepiids, in contrast, a nacreous layer is completely absent (Doguzhaeva, 1996; Fuchs, 2006).

Independently if the lamello-organic layer corresponds to the periostracum or not, we follow Doguzhaeva et al. (2003a, b) in considering this layer as the layer that forms the proostracum. (1) The lamello-organic layer in the belemnoid conotheca seems to possess the ability to accomplish remarkable swellings in the dorsal region. (2) Strongly forwardly curved growth lines on the dorsolateral surface of the layer

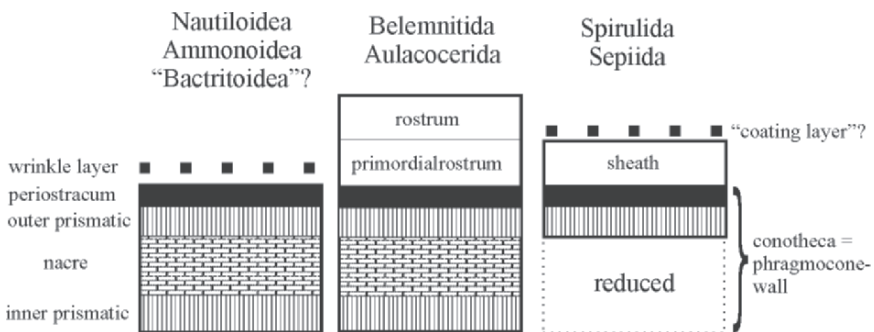


Fig. 14.8 Homologous conothecal layers of Cephalopoda. Structures such as the wrinkle layer, rostrum, primordial rostrum, and sheath do not belong to the conotheca. Belemnoids exhibit the same sequence of conothecal layers as ectocochleates, whereas in spirulids and sepiids the nacreous layer is reduced. The periostracum and an inner prismatic layer are present in each taxon.

under discussion (i.e., the phragmocone surface) are characteristic for a belemnite proostracum (Fig. 14.1). (3) The comparatively abrupt change from a nacre-dominated conotheca into a more organic conotheca accomplished by a colored separation on the dorsolateral phragmocone surface appears where the proostracal growth lines bend forward. It remains unclear whether the inner prismatic layer also helps to form the projecting part of the proostracum. So far reliable data on cross sections through a proostracum are poor (Hewitt and Pinckney, 1982).

According to our interpretation regarding the proostracum as a derivation of the periostracum, the proostracum is part of the conotheca. This idea contradicts Doguzhaeva et al. (2002, 2003a, b) in that the belemnoid proostracum is independent and not involved in the composition of the conotheca. Doguzhaeva et al. (2002, 2003) argued that the possession of a proostracum is unique and therefore apomorphic within the Coleoidea, because ectocochleate cephalopods lack a comparable layer. They further concluded that their idea does not support the widely accepted hypothesis by which the proostracum is a dorsal remnant of the body chamber (Naef, 1922; Jeletzky, 1966). The development of the coleoid proostracum through the progressive reduction of the ventral part of a formerly closed body chamber, hence, affords the involvement of the periostracum. Our conclusions therefore strongly support the ideas of Naef (1922) and Jeletzky (1966). The apomorphic status of the proostracum as a dorsal extension of the phragmocone within the Coleoidea is beyond any doubt, but the layer that builds up the proostracum, namely the periostracum, is plesiomorphic within the Coleoidea.

References

- Bandel, K. 1985. Composition and ontogeny of *Dictyoconites* (Aulacocerida, Cephalopoda). *Paläontologische Zeitschrift* **59**: 223–244.
- Bandel, K. 1989. Cephalopod shell structure and general mechanisms of shell formation. In Carter, J. G. (editor), *Skeleton Biomineralization: Patterns, Processes and Evolutionary Trends*, pp. 97–115. New York: Van Nostrand Reinhold.
- Bandel, K., T. Engeser, and J. Reitner. 1984. Die Embryonalentwicklung von *Hibolithes* (Belemnitida, Cephalopoda). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **167**: 275–303.
- Bandel, K., and C. Kulicki. 1988. *Belemniteuthis polonica*: a belemnite with an aragonitic rostrum. In J. Wiedmann, and J. Kullmann (editors), *Cephalopods – Present and Past*, pp. 303–316. Stuttgart: Schweitzerbart'sche Verlagsbuchhandlung.
- Barskov, I. S. 1972. Microstructure of the skeletal layers of belemnites compared with the shell layers of other molluscs. *Paleontological Journal* (Translation of the Paleontologicheskii Zhurnal) **4**: 492–500.
- Christensen, E. 1925. Neue Beiträge zum Bau der Belemniten. *Neues Jahrbuch für Geologie und Paläontologie* **51**: 118–158.
- Crick, G. C. 1896. On the Proostracum of a belemnite from the upper Lias of Alderton, Gloucestershire. *Proceedings of the Malacological Society* **2**: 117–119.
- Cuif, J.-P., and Y. Dauphin. 1979. Mineralogie et microstructures d'Aulacocerida (Mollusca-Coleoidea) du Trias de Turquie. *Biomineralisation* **10**: 70–79.

- Dauphin, Y. 1983. Microstructure du phragmocone du genre triassique *Aulacoceras* (Cephalopoda-Coleoidea) – remarques sur les homologies des tissus coquilliers chez les Cephalopodes. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **165**: 418–437.
- Doguzhaeva, L. A. 1996. Two early Cretaceous spirulid coleoids of the northwestern Caucasus: their shell ultrastructure and evolutionary implications. *Paleontology* **39**(3): 681–707.
- Doguzhaeva, L. A., R. H. Mapes, and H. Mutvei. 2003a. The shell and inc sac morphology and ultrastructure of the Late Pennsylvanian cephalopod *Donovaniconus* and its phylogenetic significance. *Berliner Paläobiologische Abhandlungen* **3**: 61–78.
- Doguzhaeva, L. A., and H. Mutvei. 2003. Gladius composition and ultrastructure in extinct squid-like coleoids *Loligosepia*, *Trachyteuthis* and *Teudopsis*. *Revue de Paleobiologie* **22**: 877–894.
- Doguzhaeva, L. A., H. Mutvei, and D. T. Donovan. 2002. Pro-ostracum, muscular mantle and conotheca in the Middle Jurassic belemnite *Megateuthis*. *Abhandlungen der geologischen Bundesanstalt* **57**: 321–339.
- Doguzhaeva, L. A., H. Mutvei, G. K. Kabanov, and D. T. Donovan. 1999. Conch ultrastructure and septal neck ontogeny of the belemnite *Conobelus* (Duvallidae) from the Valangian of the Crimea (Black Sea). In F. Oloriz, and F. J. Rodriguez-Tovar (editors), *Advancing Research on Living and Fossil Cephalopods*, pp. 47–57. New York: Kluwer Academic/Plenum.
- Doguzhaeva, L. A., H. Mutvei, and W. Weitschat. 2003b. The pro-ostracum and primordial rostrum at early ontogeny of Jurassic belemnites from north-western Germany. *Berliner Paläobiologische Abhandlungen* **3**: 79–89.
- Donovan, D. T., and M. D. Crane. 1992. The type material of the Jurassic cephalopod *Belemniteuthis*. *Palaeontology* **35**(2): 273–296.
- Doyle, P. 1986. *Naefia* (Coleoidea) from late Cretaceous of southern India. *Bulletin of the British Museum of Natural History* **40**(4): 133–139.
- Doyle, P., and E. V. Shakides. 2004. The jurassic belemnite suborder Belemnotheutina. *Palaeontology* **47**: 983–998.
- Fuchs, D. 2006. Fossil erhaltungsfähige Merkmalskomplexe der Coleoidea (Cephalopoda) und ihre phylogenetische Bedeutung. *Berliner Paläobiologische Abhandlungen* **8**: 1–121.
- Hewitt, R. A., and G. Pinckney. 1982. On the occurrence and the microstructure of the phragmocone and pro-ostracum of the belemnite Genus *Acroteuthis* Stolley. *Palaeontographica, Abteilung A* **179**: 142–147.
- Jeletzky, J. A. 1966. Comparative morphology, phylogeny and classification of fossil Coleoidea. *Paleontological Contributions, University of Kansas, Mollusca* **7**: 1–162.
- Keupp, H., and V. V. Mitta. 2004. Septenbildung bei *Quenstedtoceras* (Ammonoidea) von Saratov (Russland) unter anomalen Kammerdruckbedingungen. *Mitteilungen des Geologisch-Paläontologischen Instituts, Universität Hamburg* **88**: 51–62.
- Makowski, H. 1952. La faune callovienne de Lukow en Pologne. *Palaeontologia Polonica* **4**: 1–64.
- Müller-Stoll, H. 1936. Beitrage zur Anatomie der Belemnoidea, *Nova Acta Leopoldina*. New Series **4**: 159–226.
- Mutvei, H. 1964. Remarks on the anatomy of recent and fossil Cephalopoda – with description of the minute shell structure of belemnoids. *Stockholm Contributions to Geology* **11**: 79–102.
- Naef, A. 1922. *Die fossilen Tintenfische – Eine paläozoologische Monographie*. Jena: Fischer Verlag.
- Pearce, J. C. 1847. On the fossil Cephalopoda from the Oxford Clay constituting the genus *Belemniteuthis*, Pearce. *Proceedings of the Geological Society of London* **3**: 592–594.