Pro-ostracum, Muscular Mantle and Conotheca in the Middle Jurassic Belemnite *Megateuthis*

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Zusammenfassung

Erstmals wird die Untersuchung des Proostracums mit REM-Studien von Ultrastrukturen der Schale und der Mantelhülle von Belemniten verbunden. 19 gut erhaltene Schalen von *Megateuthis* aus dem mittleren Jura von Novaja Semlja (Russland) und Hannover (Deutschland) standen zur Verfügung.

Das Proostracum beginnt etwa in der Hälfte des Phragmokons. Es besteht aus organischen Fasern unterschiedlicher Orientierung, abwechselnd mit unregelmäßig calcifizierten, parallel zur Oberfläche liegenden Zwischenlagen, die aus locker gepackten, ungeregelten Kristalliten aufgebaut sind. Die äußere und die innere Oberfläche des Proostracums ist mit dünnen kompakten Membranen bedeckt. Die äußere Oberfläche zeigt die deutlich ausgeprägten Zuwachsstreifen des mittleren Bereichs und der Längsrippen und die Gruben des mediolateralen Bereichs; die innere Oberfläche zeigt ein federartiges Muster bestehend aus fünf von einer Mittelachse auseinanderstrebenden Linien. Die Rippen der äußeren Oberfläche tragen flache Kämme mit einer Reihe von Gruben, die denen auf den Rippen der äußeren Oberfläche des Rostrums des oberkarbonen Coleoiden *Hematites* bemerkenswert ähnlich sind (DOGUZHAEVA et al., dieser Band). Das scheint zu zeigen, dass bei *Megateuthis* die Befestigung von Schale und Weichteilen auf das Proostracum beschränkt war, während die Weichteile von *Hematites* am gesamten Rostrum befestigt waren. Längsschnitt und Querschnitte der Schale zeigen, dass das Proostracum zwischen der Conothek und

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dem Rostrum liegt, vier oder fünf schwach calcifizierte, an organischer Substanz reiche Lamellen besitzt und nur ¹/₇ oder ¹/₈ der Dicke der Conothek aufweist. Die Conothek umfasst äußere Perlmutter- und innere Prismenschichten mit einer dünnen unregelmäßig calcifizierten Auskleidung, reich an organischer Substanz und im Allgemeinen ähnlich dem Proostracum. Deshalb kann die weitverbreitete Ansicht, dass die Conothek der verbleibende Dorsalteil der Wohnkammer der ectocochleaten Vorfahren sei, schwerlich länger unterstützt werden. Dadurch wird der phylogenetische Abstand zwischen Ectocochleaten und Endocochleaten größer und weniger klar, als früher angenommen.

Das Vorhandensein eines aus Muskulatur bestehenden Mantels wird durch den Abdruck seiner äußeren Hülle spiraliger Kollagenfibrillen gezeigt, die wie bei den rezenten Kalmaren ein kreuz und quer verlaufendes Muster bilden. Die Fibrillen sind gebündelt am Rand des Proostracums befestigt und erzeugen alternierende Schichten an der anderen Seite. Die Abdrücke der Fasern der inneren Mantelhülle sind auf der Innenseite zu sehen.

Abstract

For the first time the investigation of the pro-ostracum was combined with the SEM studies of the shell ultrastructure and mantle tunic of belemnites. This method was used for examination of the 19 available well-preserved shells of *Megateuthis* from the Middle Jurassic of Novaya Zemlya, Russia, and Hannover area, Germany.

The pro-ostracum originates from about half the circumference of the phragmocone. It is formed of organic fibres of different orientations, alternating with irregularly calcified sublayers which are built of loosely packed, criss-crossed crystallites lying parallel to the surface. The outer and inner surfaces of the pro-ostracum are covered by thin, compact pellicles. The outer surface shows the pronounced growth lines of the median area and longitudinal ridges and grooves of medio-lateral areas; the inner surface exhibits a feather-like pattern of fine lines diverging from a median axis. The ridges of the external surface have flat crests bearing a row of pits remarkably similar to those on the ridges of the outer surface of the rostrum in the Lower Carboniferous coleoid *Hematites* (DOGUZHAEVA et al.., herein). This seems to indicate that in *Megateuthis* the shell/soft tissues attachment was restricted to the pro-ostracum, while in *Hematites* the soft tissues were attached to the whole rostrum. The longitudinal and cross shell sections demonstrate that the pro-ostracum lies between the conotheca and the rostrum, comprises four or five weakly calcified, organic-rich lamellae, and is only about ¹/₇ or ¹/₈ the thickness of the conotheca; the conotheca comprises outer nacreous and inner prismatic layers, with a thin inner lining which is irregularly calcified, rich in organic matrix and generally similar to the pro-ostracum. Thus, the widely spread opinion that the conotheca is a remaining dorsal part of the body chamber of the ectocochlean ancestors (NAEF, 922; JELETZKY, 1966) can hardly be supported any longer. This makes the phylogenetic relationship between ectocochleates and endocochleates more distant and more obscure than was previously believed.

The presence of a muscular mantle is shown by the impression of its outer tunic of helical collagen fibres, forming a criss-cross pattern like that in Recent squids. The fibres are attached to the pro-ostracum margin in bundles, alternate layers of the tunic originating on opposite sides of the pro-ostracum. The impressions of fibres of the inner tunic are seen on the internal surface of the pro-ostracum.

1. Introduction

The pro-ostracum is the attribute of the belemnite shell that pre-supposes the presence of the muscular mantle around the soft body. The pro-ostracum is widely believed to be a dorsal remnant of the living chamber of the ectocochleate ancestors, although this idea was not so far proved by direct observations. Well-preserved shells of *Megateuthis* from the Middle Jurassic of Novaya Zemlya, Russia, and Hannover area, Germany, has allowed us to examine the general pro-ostracum morphology, shell ultrastructure, mantle tunic and to trace the position of the pro-ostracum between the conotheca and rostrum. This is the first detailed show of its kind and is of direct relevance to understanding belemnite morphology and origin.

The existence of a dorsal projection to the peristome in belemnites was first inferred by VOLTZ (1830). By the time MANTELL (1848) figured *Cylindroteuthis* with a complete phragmocone it was clear that belemnites did not have a complete living chamber, but only the dorsal projection bounded by the hyperbolar zones of VOLTZ. This structure was subsequently named the pro-ostracum by HUXLEY (1864). NAEF (1922, Figs. 63, 73, 87) later summarised the then available information, and was of the opinion that in belemnites the pro-ostracum represented a dorsal remnant of the living chamber of their ancestors. In most belemnite genera the existence of the pro-ostracum, where it is known at all, has to be inferred from the course of growth lines on the external surface of the phragmocone, preserved by the growth of the rostrum over it (see HEWITT & PINCKNEY, 1982). The extremely fragile delicate actual pro-ostracum, or at least an impression of it, has been found in a few genera:

Chondroteuthis from the Upper Lias (Toarcian) of England (CRICK, 1896), *Cylindroteuthis* from the English Oxford Clay (Callovian) (MANTELL, 1848) and *Acanthoteuthis* from the Solnhofener Plattenkalk (CRICK, 1897).

The pro-ostracum of *Megateuthis* has not been previously described in any detail although the growth lines on the outer (dorsal) surface of the pro-ostracum in *Megateuthis* were illustrated by NAEF (1922, Fig. 73). The inner surface is here reported for the first time. In this genus some details of conotheca and phragmocone were given by CHRISTENSEN (1925), JELETZKY (1966) and BANDEL & KULICKI (1988).

The existence of the pro-ostracum pre-supposes the presence of a muscular mantle. So far this has only been identified in a few taxa. OWEN (1844) showed the presence of fossilised muscular mantle in *Belemnoteuthis*, and later the pro-ostracum in this genus was illustrated by MAKOWSKI (1952, Fig. 8B) and the conotheca structure was observed by BANDEL & KULICKI (1988). KEAR et al. (1996) showed the mantle in *Belemnoteuthis* to have a detailed structure identical with that of modern squids. In this paper we demonstrate the presence of a muscular mantle and its attachment to the pro-ostracum in *Megateuthis*.

2. Material and Methods

Among studied shells three specimens of *Megateuthis* were collected in 1875 in Novaya Zemlya (Bezymyannaya Bay) during the Arctic "Vega" expedition. A fragment of a largest phragmocone, without rostrum is about 60 mm in diameter and 100 mm in length. According to the label it was originally identified as a Palaeozoic nautiloid. Two smaller examples are represented by the fragments of the small-sized rostra; their diameter is about 20 mm.

All remaining 16 examples are from the Middle Jurassic of the Hannover area, Germany. These have well preserved phragmocones and rostra. They are smaller than the large specimen from Novaya Zemlya, the largest is about 30 mm in diameter. Some of the shells preserve the phragmocone, in others it is missing but the imprint of the conotheca can be seen on the inner surface of the rostrum.

The pro-ostracum was observed in the cases when it was possible to expose the phragmocone surface splitting the shells along this surface. Usually the external surface of the pro-ostracum was exposed, and in few cases its internal surface became visible. To make the relief of the pro-ostracum more distinct the specimens were cleaned ultrasonically. To study the ultrastructure and to find the placement of the pro-ostracum in the shell wall the specimens were cut longitudinally and transversally, and those selected for SEM study were polished, weakly etched and coated with gold.

All the specimens are preserved in the collections of the Department of Palaeozoology, Swedish Museum of Natural History, Stockholm.

3. Observations on *Megateuthis*
3.1. Pro-ostracum
3.1.1. Outer Surface
(Pl. 1, Figs. 1, 2; Pl. 2, Figs. 1, 2; Text-Figs. 1, 2)

The surface of the large phragmocone from Novaya Zemlya shows morphological details of the pro-ostracum (Text-Fig. 1a, b). Growth lines show the pro-ostracum to be about twice as long as wide, with a bluntly pointed anterior margin. The lateral margins appear to converge forwards, but one must remember that Text-Fig. 1b is a conical surface reproduced on a flat surface.

A pair of longitudinal ridges limits the median area (Mittelplatte of NAEF, 1922) on each side. They approximate to the "mediale Asymptote" of NAEF. Laterally to this is a medio-
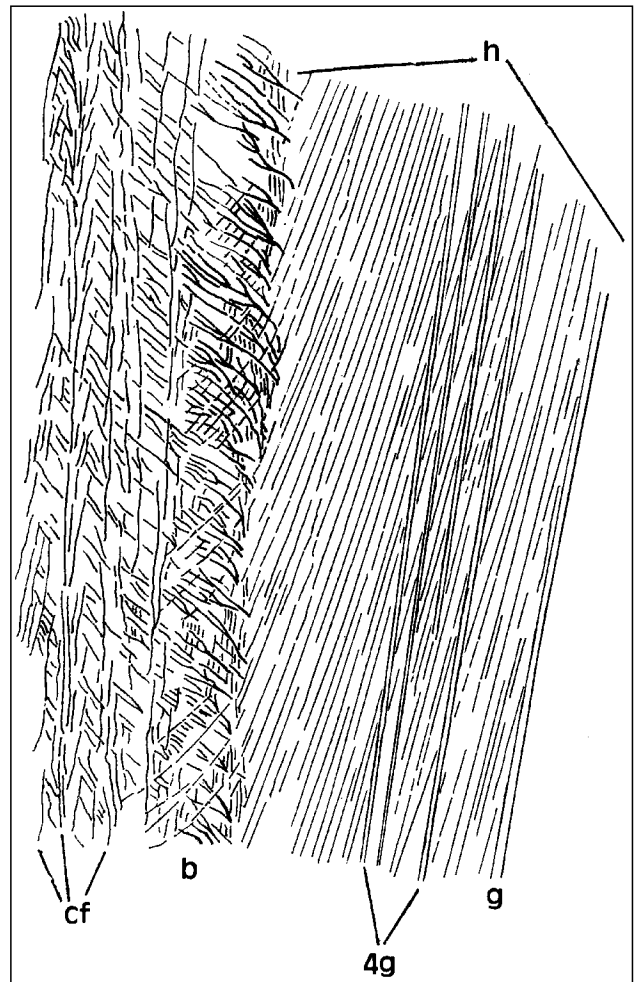
Text-Fig. 2.
Passaloteuthis sp.
The diagram based on Pl. 2, Fig. 1, shows the lateral part of the pro-ostracum and part of the mantle tunic.
h = hyperbolar zone; g = groove; 4g = group of four weak grooves; b = branching collagen fibres, attachment of tunic to pro-ostracum; cf = fibres of an alternate helix.
Approx. × 125.

Text-Fig. 1.   ▼ ▽ ▼
a) Growth lines, grooves and ridges traced from the surface of the phragmocone of *Megateuthis* sp. from Novaya Zemlya.
   Natural size.
b) Restoration of pro-ostracum based on 1a.
g = groove; r = ribs; dr = rib on the mid-dorsal line; v = mid-ventral line.
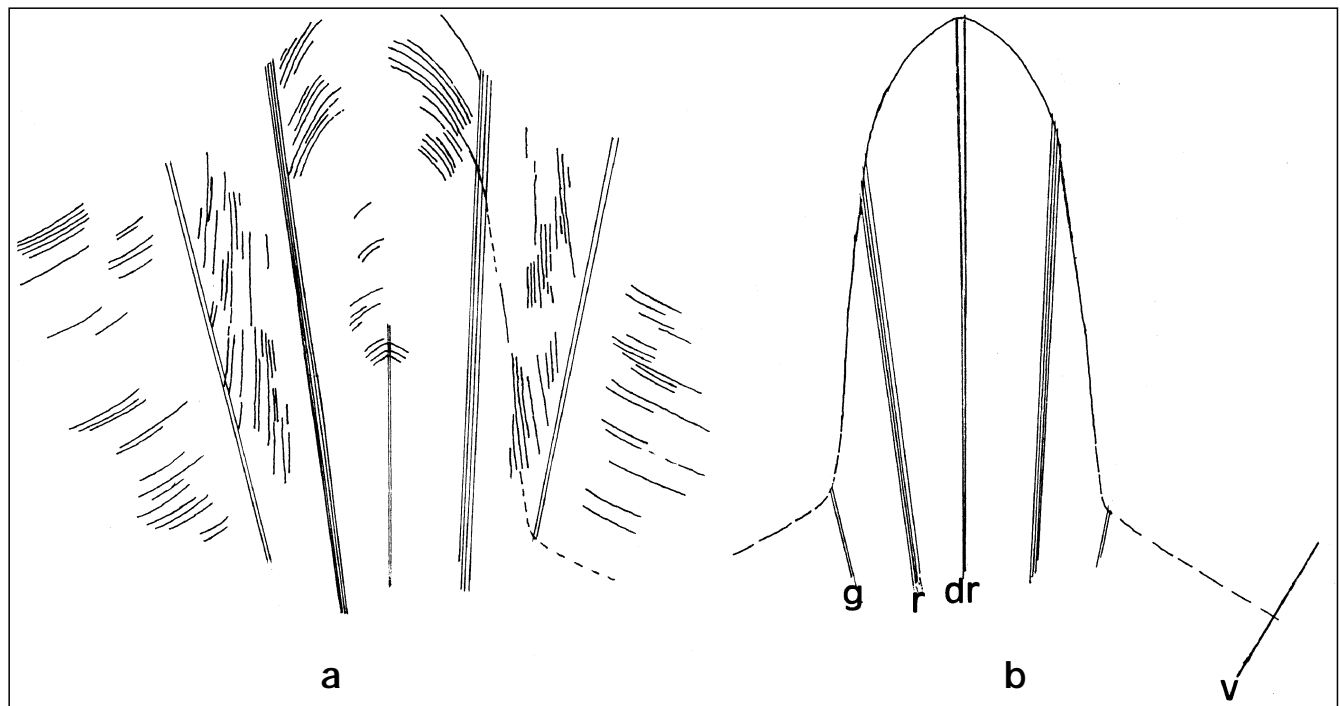
lateral area (Hyperbolar region of VOLTZ [1830]; Seiten-platte of NAEF [1922]) with closely-spaced growth lines. This medio-lateral area changes rather abruptly, along a longitudinal line ("laterale Asymptote" of NAEF), into a zone where the growth lines curve from a longitudinal to a transverse direction ("Seitenbogenzone" of NAEF [1922]). A weak groove lies approximately along the middle of the Seitenbogenzone.

Under high magnification the growth lines are low and broad ridges, separated by narrow grooves.The surface of each ridge is not smooth but shows numerous, small, shallow depressions. In the bottom of each groove there is a narrow elevation.

3.1.2. Inner Surface
(Pl. 3, Figs. 1,2; Pl. 4, Figs. 1–3; Pl. 4, Figs. 1,2)

The inner surface of the pro-ostracum is seldom observed. It shows a pattern of narrow and shallow grooves diverging from both sides of the median line, that forms a slight elevation (Pl. 3, Figs. 1, 2). These are interpreted as the impressions of collagen fibres (see below, section 3.4.). Very fine striations are visible between these lines (Pl. 4, Fig. 2), making an angle of about 60 degrees with them. These may be needle-like prisms or rods which contribute to the formation of the pro-ostracum, in which case they indicate that the pro-ostracum was partly calcified and not wholly organic as generally believed. Where this ventral layer is broken away another layer is seen behind it (Pl. 4, Fig. 1).

3.1.3. Structure, Ultrastructure and Relation to Conotheca Structure
(Pl. 3, Figs. 2,3; Pl. 4, Figs 1,2; Pl. 5, Figs. 1,3)

The main portion of the pro-ostracum consists of several lamellae, originally of organic composition, each of which is formed of organic fibres of different orientations, alternating with irregularly calcified sublayers. This main portion is covered on both sides by thin, compact pellicles. The outer pellicle shows the median field bearing growth lines and the lateral hyperbolar zones with longitudinal ridges and grooves. The inner pellicle shows a feather-like pattern of fine lines.

The pro-ostracum is seen in longitudinal section of the dorsal phragmocone wall (Pl. 5, Fig. 3). Here it appears to consist of lamellae of originally organic composition, alternating with irregularly calcified sublayers. The pro-ostracum is approximately one-sixth of the thickness of the conothecal wall or less. Thus the pro-ostracum is composed of a thin layer situated externally to the conotheca. Laterally it occupies about the dorsal half of the circumference of the phragmocone.

3.2. Conotheca
3.2.1. Ultrastructure
(Pl. 5, Figs. 1–3; Pl. 6, Fig. 4)

The conotheca consists of an inner prismatic layer and a slightly thicker outer nacreous layer. The latter has oblique growth lines in longitudinal section. The prismatic layer has a porous structure. The inner surface has a very thin layer, perhaps originally organic, which extends on to the mural ridges of the septa and terminates in the angle made by the adjacent septum.

On fractured surfaces the nacreous layer of the conotheca shows polygonal tablets with central cavities (Pl. 6, Fig. 4). Each tablet consists of radial elements that radiate from the central cavity.

3.2.2. Mantle Attachment to Conotheca

A dorsal unpaired scar occurs in each chamber as a linear depression on the inner surface of the conotheca on the mid-dorsal line. Mural parts of septa are "diverted" around the ends of the scar. The scars mark sites where soft tissue of the posterior end of the body was attached to the shell prior to secretion of the next septum.

3.3. Rostrum

The general morphology of the rostrum of *Megateuthis* was described in detail by PUGACZEWSKA (1961), and its ultrastructure was observed by BANDEL & KULICKI (1988). Our material shows that three zones can be distinguished in transverse section (Pl. 6, Fig. 1). The central zone (Pl. 6, Fig. 2) can look as if plastically deformed because it is weakly calcified with high organic content. It is mainly developed in the post-alveolar region but forms a thin coating around the phragmocone. The middle portion of the rostrum is weakly calcified and shows spongy structure. The outer portion (Pl. 6, Fig. 3) shows compact structure, but this could be the result of postmortal transformation of an originally porous structure into a solid one.

3.4. Muscular Mantle and Attachment to Pro-ostracum
(Pl. 1, Figs. 1,2; Pl. 2, Figs. 1,2; Pl. 3, Figs. 1–3; Pl. 4, Figs. 1,2)

Although the muscles themselves are not preserved, the former presence of a muscular mantle is indicated by the impression of the mantle tunic on the outer surface of the conotheca. The ventro-lateral side of the hyperbolar zone shows branching narrow grooves more or less perpendicular to the growth lines (Pl. 1, Figs. 1, 2). Further in the ventro-lateral direction is a criss-cross pattern of grooves with an angle of about 30 degrees to one another. These grooves are interpreted as the imprint of collagen fibres of the outer tunic of the muscular mantle, identifiable because it is similar to that in Recent squids, as discussed below.

The grooves along the lateral asymptote of the pro-ostracum represent a series of fibres, spaced at about 0.25 mm intervals, which branch ventralwards (Pl. 1, Fig. 1). Some of the branches curve forwards and form one set of the intersecting fibres mentioned above. These bunches of fibres are taken to be the attachment of the tunic to the pro-ostracum, overgrown in due course by the ventral margin of the phragmocone wall and later again by the rostrum.

On the ventral surface of the pro-ostracum the feather-like pattern of grooves (Pl. 3, Figs. 1, 2; Pl. 4, Figs. 1, 2) is interpreted as the impression of collagen fibres of the inner tunic of the muscular mantle. The grooves leave the median line at a small angle and curve outwards to form an average angle of about 35 degrees with the median line. The grooves on the left-hand side (as seen on the imprint) indicate fibres which continued to form a right-handed helix, and vice versa, the two helices combining to form the tunic. Like the impressions of the outer tunic, a criss-cross pattern is not seen. Presumably the distal ends of each set of fibres terminated at the margin of the pro-ostracum.

4. Discussion
4.1. Ultrastructure of the Conotheca and Origin of the Pro-ostracum in Belemnites

CRICK (1896), in his very careful description of a belemnite later identified as *Chondroteuthis* (Jurassic: Toarcian)

(PHILLIPS, 1982, p. 63) stated (1896, p. 119) that the specimen

> " ... seems to show that the wall of the phragmocone did not enter into the formation of the pro-ostracum ... "

though he could not decide whether the "epicuticula" (i.e. periostracum) of the phragmocone alone formed the pro-ostracum, or whether its dorsal surface

> "was wholly or in part covered by a forward continuation of the guard."

Nevertheless later most other authors believed the pro-ostracum to be composed of continuations of the layers of the conotheca.

MÜLLER-STOLL (1936) distinguished three layers in the conotheca and pro-ostracum of belemnoids:

1) The outer Stratum callosum (the nacreous layer of more recent authors),
2) the thinner, transparent Stratum album (the prismatic layer) and
3) the inner layer, the Stratum profundum, that shows fine lamellae parallel to the surface.

Layer 3 is presumably the "layer x" of our Pl. 5.

JELETZKY (1966, p. 108) also stated that the pro-ostracum is an extension of the conotheca:

> " ... the writer... restricts proostracum to the spatulate or fanlike protuberances of the conotheca ... "

and

> "It is well established that, unlike Aulacocerida, all representatives of the Belemnitida lack the lateral and ventral parts of the closed, tubular body chamber, ... "(JELETZKY, 1966, p. 109).

BARSKOV (1972) and HEWITT & PINCKNEY (1982) distinguished in the conotheca and pro-ostracum a thick outer nacreous layer and thin inner prismatic layer.

BANDEL & KULICKI (1988) described the periostracum, outer prismatic, nacreous and inner prismatic layers in the conotheca of *Belemnoteuthis* and *Megateuthis*.

Thus, the conotheca itself was believed (assumed?) to be homologous with the shell wall of ectocochleates, and the pro-ostracum was assumed to represent the dorsal part of the living chamber wall in ectocochleates. This interpretation, however, had not been proved by direct observation. Our own observations confirm CRICK'S (1896) view that the pro-ostracum is a thin layer external to the conotheca. The pro-ostracum consists of several sublayers (Pl. 5, Fig. 3), and difference between the dorsal and ventral surfaces, plus the extra layer seen in Pl. 4, Fig. 1, shows that these have different ultrastructures.

4.2. Dorsal Surface of Pro-ostracum

NAEF (1922, Fig. 73a) gave a detailed reconstruction of the ornamentation on the outer surface of the pro-ostracum in *Megateuthis*. Little attention has been paid to longitudinal ornament other than the growth lines in the hyperbolar zones. CRICK (1896) in *Chondroteuthis* recorded a median

> " ... narrow, hollow rib, about 0.5 mm wide ... bearing [on its ventral surface] a very narrow median groove."

He observed that it

> " ... is seen gradually to become wider and less distinct towards the anterior end of the pro-ostracum."

We have observed a similar rib in *Megateuthis* (Text-Fig. 1) but we do not know if it was hollow.

Longitudinal ribs and grooves in other situations do not seem to have been previously reported. In *Megateuthis*

(Text-Fig. 1) we find a pair of ribs along the dorsal boundary of the hyperbolar zone and a groove near its outer (lateral) limit, in the region of NAEF's "Seitenbogenzone". In *Passaloteuthis* from the Lower Jurassic of England (Pl. 2, Fig. 1; Text-Fig. 2) we find several weak grooves in the hyperbolar zone.

Thickened or calcified hyperbolar zones have been reported from several Jurassic genera, beginning with *Cylindroteuthis puzosianus* (D'ORBIGNY) figured by MANTELL (1848, Pl. 14, Fig. 2; Pl. 15, Fig. 3) who termed them dorsal processes. There is no other sign of the pro-ostracum in these figures (but see below). Another specimen of the same species figured more recently (PAGE & DOYLE, 1991, Text-Fig. 5.1) shows similar processes. These specimens show that in *Cylindroteuthis*, at least, there were aragonitic lateral supports for the pro-ostracum, but the structure itself was uncalcified. CRICK (1896) in *Chondroteuthis* noted that the outer boundary of each process is further thickened. We have not observed such processes in *Megateuthis*.

The pro-ostracum has mainly been described from Jurassic belemnites and there is inadequate information on any evolutionary modifications which it may have undergone.

4.3. Ventral Surface of Pro-ostracum

As remarked above, MANTELL's first figures (1848) of *Cylindroteuthis puzosianus* showed no remains of the pro-ostracum between the dorsal processes. In 1850, however, MANTELL figured another example (1850, pl. 30), apparently of the same species, in which a faint feather-like pattern was visible between the processes. It was described as

> " ... a thin pellicle of a dark integument marked with very fine diverging parallel striae ... "

and was evidently not calcified. CRICK (1896) illustrated a similar pattern in *Choanoteuthis*.

A similar pattern is present in *Megateuthis* and is seen in more detail than previously in our pictures, with numerous fine, oblique lines between the "barbs" of the feather pattern. We cannot at present explain the origin or significance of this pattern. It is puzzling that the ventral surface does not show any growth lines and we have no idea how it is secreted.

4.4. Muscular Mantle and its Tunics

4.4.1. Muscular Mantle

Fossilised muscular mantle was reported in *Belemnotheutis* (Jurassic: Callovian) by OWEN (1844) and described in detail by KEAR et al. (1995), who showed that the microscopic structure is the same as in Recent squids. *Belemnotheutis* is an atypical belemnite because it possesses a thin, aragonitic rostrum instead of the massive calcitic rostrum usual in Jurassic and Cretaceous belemnites. The present paper shows for the first time that these "normal" belemnites also possessed a muscular mantle, and also shows in part how the mantle was attached to the pro-ostracum.

4.4.2. Mantle Tunics

Muscular mantle in recent squids and cuttlefishes consists of alternating blocks of circular and radial muscles. The inner and outer surfaces are covered by tunics formed of collagen fibres, which serve to prevent distortion of the mantle during contraction. These tunics are

" … robust layers of collagen fibers, with the collagen be-ing arranged in 6–10 layers of crossed-helical fibers. The layers formed alternating right- and left-handed helices, with a very regular fiber angle of 27 degrees relative to the long axis of the mantle." (GOSLINE & SHADWICK, 1983, p. 388).

That is, the angle between alternate sets of fibres is about 54°.

In *Megateuthis* the pattern of alternate sets of fibres can be clearly recognised (Pl. 1, Figs. 1, 2). The angle between alternate sets is about 30°, and the spacing of fibres is about 130 μm. In *Passaloteuthis* from the Lower Jurassic of England (Pl. 2, Fig. 1; Text-Fig. 2) the fibres are more closely spaced and are clearly in layers, fibres of the sur-face layer being continuous and those of the next layer beneath being seen through gaps between them. The an-gle between fibres of these two layers is about 40°.

4.4.3. Attachment of the Tunic

In both *Megateuthis* and *Passaloteuthis* the margin of the outer tunic is clearly defined along the ventro-lateral limit of the hyperbolar zone. Bundles of fibres occur at fairly regular intervals and were presumably attached at or near the edge of the pro-ostracum. Individual fibres branch from these bundles and curve forwards to form one (or more?) of the layers of the tunic. Because the surface of the alveolus pre-serves only the impression of the outer surface of the tunic, we have no information as to the number of alternate layers of helical fibres. We assume, but cannot show, that each branching bundle contributes to all the helices of one type (i.e. left- or right-handed), and further, that all the bundles on one side contribute to helices of the same sense. That is, fibres originating on the left side all become part of left-handed helices, and vice versa (Text-Fig. 3).

In Recent squids such as *Loligo* the muscular mantle forms a complete cylinder and the tunic fibres are pre-sumably continuous around the mantle. In *Sepia*, the man-tle does not form a cylinder but is attached to the lateral
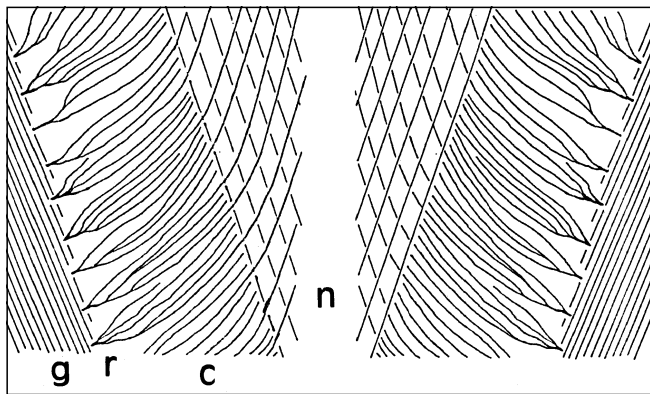
Text-Fig. 3.
Schematic diagram of the outer tunic of the muscular mantle in *Megateu-this.* For further comment see text.
g = growth lines of hyperbolar zone, not shown where they continue beneath the tunic; r = branching fibres attaching tunic to pro-ostracum; c = collagen fibres; n = network formed by alternating helices of fibres. For clarity outer two helices only shown.

margins of the cuttlebone (NAEF, 1923, Fig. 290). The mode of attachment has not been described, so that the structure in belemnites cannot be compared with that in *Sepia.* In some squids also the mantle is not a complete cylinder. However, again the attachment of the mantle has not been described in detail. R.E. YOUNG kindly re-ports that

"Squids rarely show any obvious muscle attachment marks on the gladius. The muscles attach to the shell sac and the attachment is not clearly reflected in the structure of the gladius."

However, in *Abralia* (Recent Family Enoploteuthidae) he finds the posterior part of the mantle attached to the dor-sal surface of the wings of the gladius. On the rachis, but not obviously related to the muscle attachment, he ob-served

" … surface lines … that are quite irregular but still form a loose pattern that runs approximately at right angles to the growth lines … The pattern of these lines is not unlike that which you illustrate …"

(i.e. the fibre bundles of the present paper) (R.E. YOUNG, personal communication).

5. Phylogenetic Implications

The widely accepted idea on the origin of coleoids from ectocochleates is mainly based on observations of the pro-ostracum and short "body chamber" in belemnites. Up to now it has been reasonable to combine these two observations and to assume that the pro-ostracum is a remaining dorsal part of the body chamber which was left after the reducing of the long body chamber in ectococh-lean ancestors (NAEF, 1922; JELETZKY, 1966). However, for a long time this attractive hypothesis has not been tested by direct comparison of the pro-ostracum and conotheca structures. A priori, it has been supposed that they have a similar structure. Now when we know more about the structure and position of the pro-ostracum in the shell wall of *Megateuthis* the idea under consideration can hardly be supported any longer. Besides, it has been recently found that the Lower Carboniferous coleoid *Hematites* exhi-bits "incompatible" features: a short "body chamber" while the pro-ostracum is absent (DOGUZHAEVA et al., herein), although according to JELETZKY (1966, p. 8)

" … absence of the pro-ostracum in living sepiids appears to be a secondary and only recently acquired feature. The highly advanced and specialized Octopida, however, are characterized by complete absence of the proostracum, which must have been lost by their ancestors in pre-Cre-taceous time. Only in the ancient and primitive Aula-cocerida is absence of a proostracum a primary feature inherited from ectocochlian ancestors. This feature, coupled with presence of an ectocochlian body chamber, sets the aulacocerids well apart from all other coleoids."

Thus, the recently obtained ultrastructural data on *Mega-teuthis* and also on *Hematites* (DOGUZHAEVA et al., herein) shows that the phylogenetic relationships between ecto- and endocochleates were more distant and more obscure than it was previously believed.

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Plate 1

Megateuthis sp.

Fig. 1: Surface of the alveolus of the rostrum showing impressions of growth lines and other features on the outer surface of the phragmocone.
In centre of picture, the hyperbolar region with closely-spaced growth lines. To the right, the left hand side of the median field. The steep angle of the growth lines is exaggerated by the curvature of the specimen. To the left, growth lines curve through the "Seitenbogenzone" to a transverse course on the ventro-lateral side of the phragmocone. Superimposed on the growth lines in the left hand part of the picture is an impression of the outer collagen tunic of the muscular mantle, preserved by the phragmocone wall which grew forwards over it. The criss-cross pattern characteristic of the tunic passes dorsally (to the right) into a series of branching fibres marking the attachment of the tunic to the margin of the pro-ostracum.
Scale bar 1 mm.
Fig. 2: Higher magnification of the left-hand part of Fig. 1.
Impressions of collagen fibres intersecting at about 30° are replaced ventrally (to the left) by nearly parallel fibres.
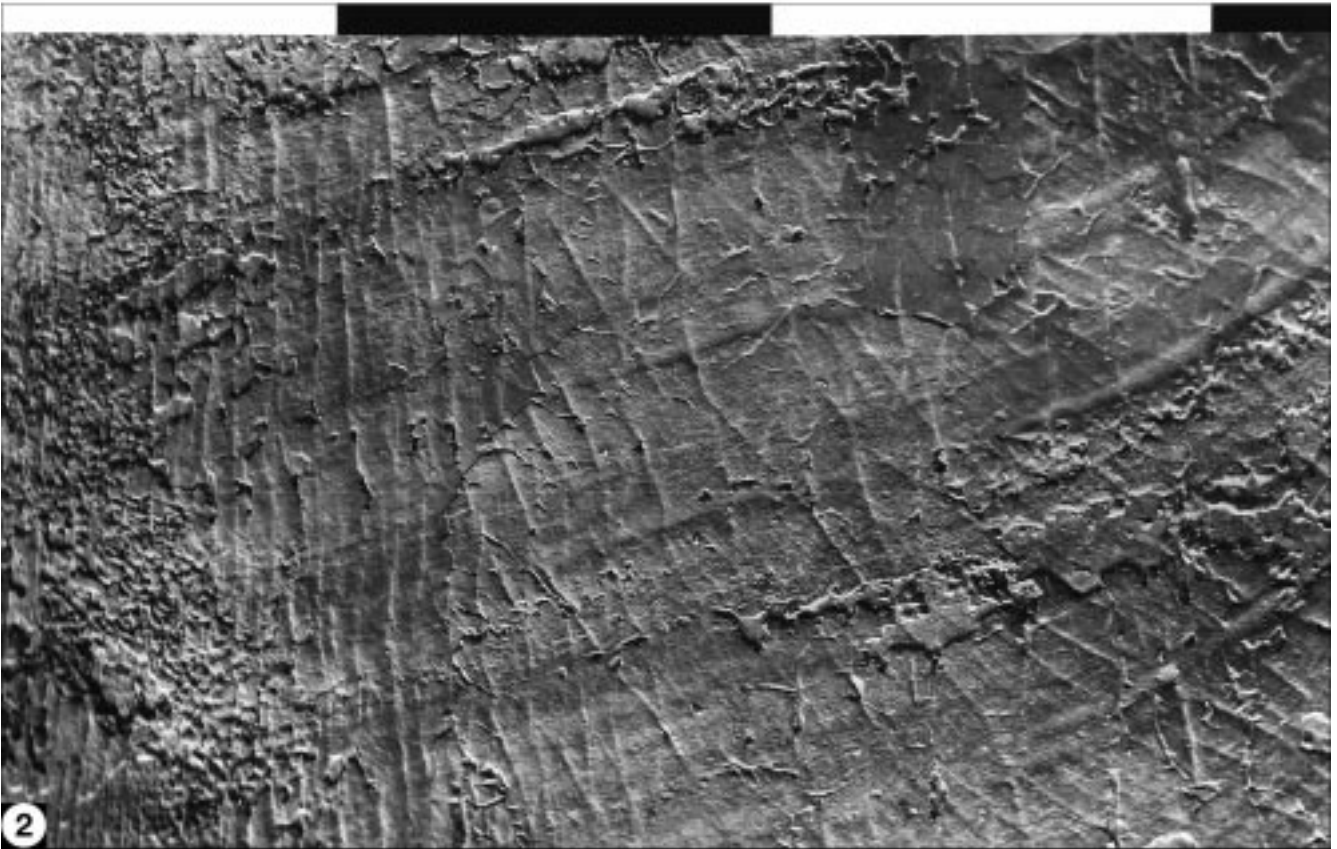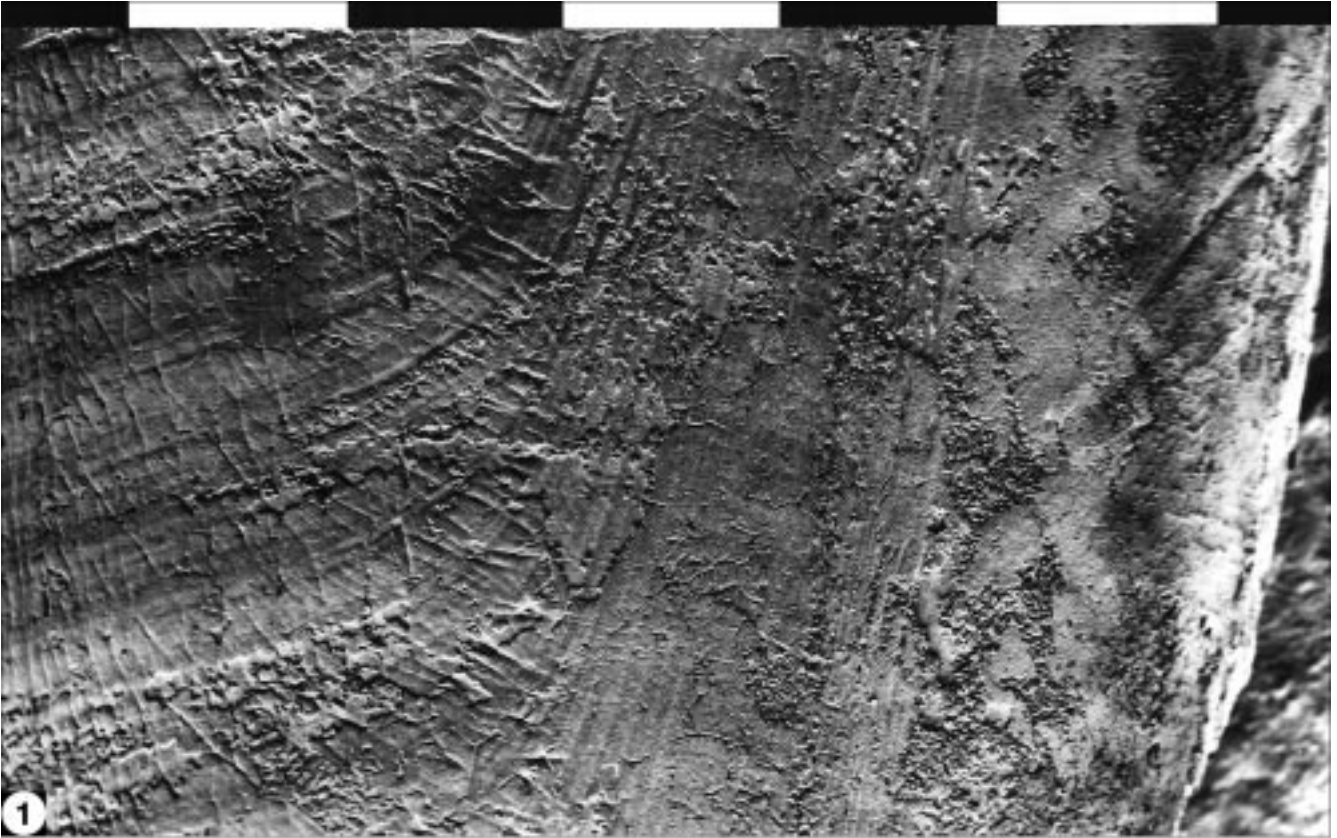
Plate 2

Fig. 1: *Passaloteuthis* sp.
Surface of the alveolus of the rostrum showing impression of outer surface of phragmocone (adoral direction to left).
Upper (dorsal) part is the hyperbolar zone, bounded at top by a groove (ridge on the impression). Below (ventrally) the "Seiten-bogenzone", arcuate growth lines largely obscured by branching collagen fibres which curve anteriorly (to the left). Near the bottom edge of the specimen, collagen fibres of the outer layer of the tunic.
See also Text-Fig. 2.
Scale bar 1 mm.
Fig. 2: *Megateuthis* sp.
Hyperbolar zone to right, with longitudinal, flat-topped ridges.
To left the "Seitenbogenzone" with impressions of branching collagen fibres at their attachment to the pro-ostracum.
Scale bar 1 mm.

330
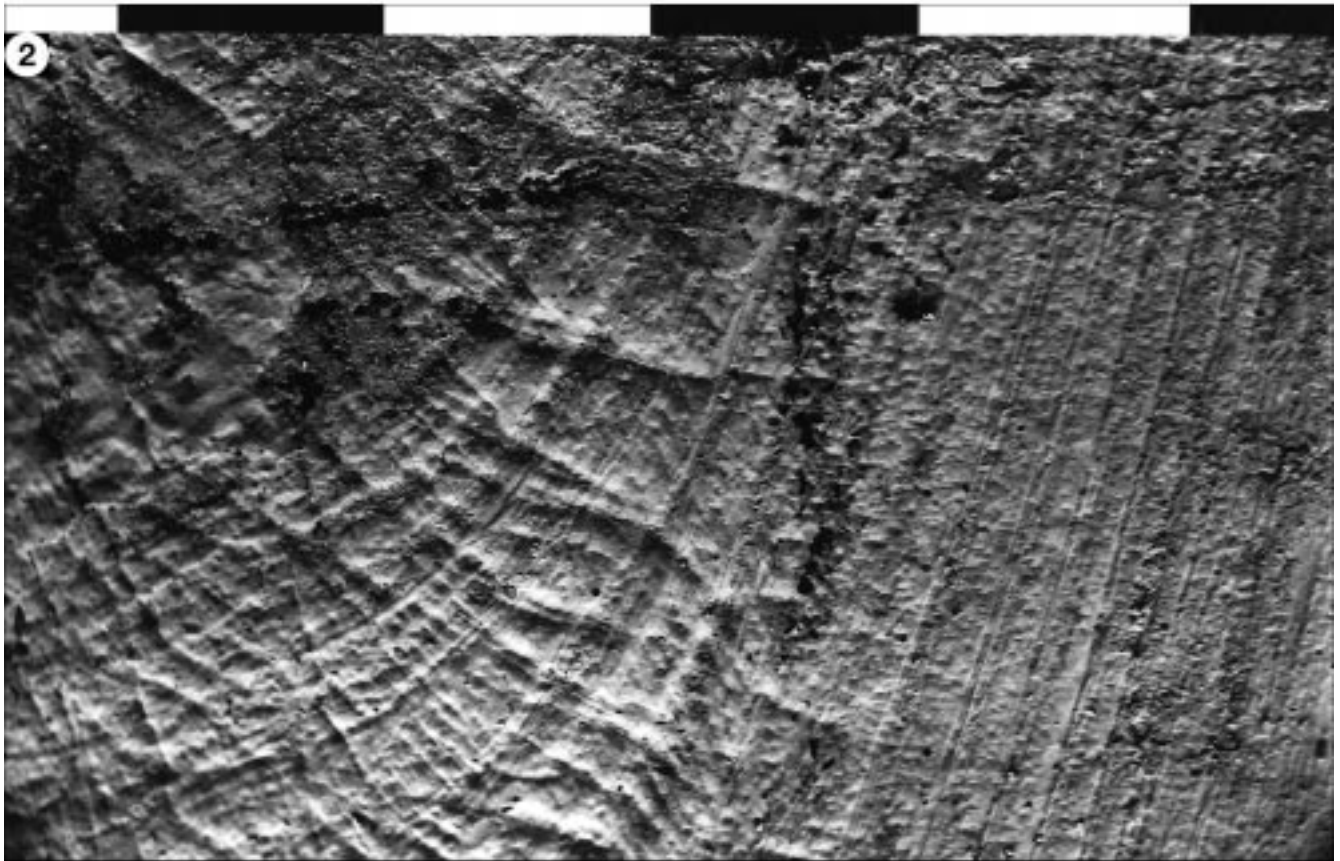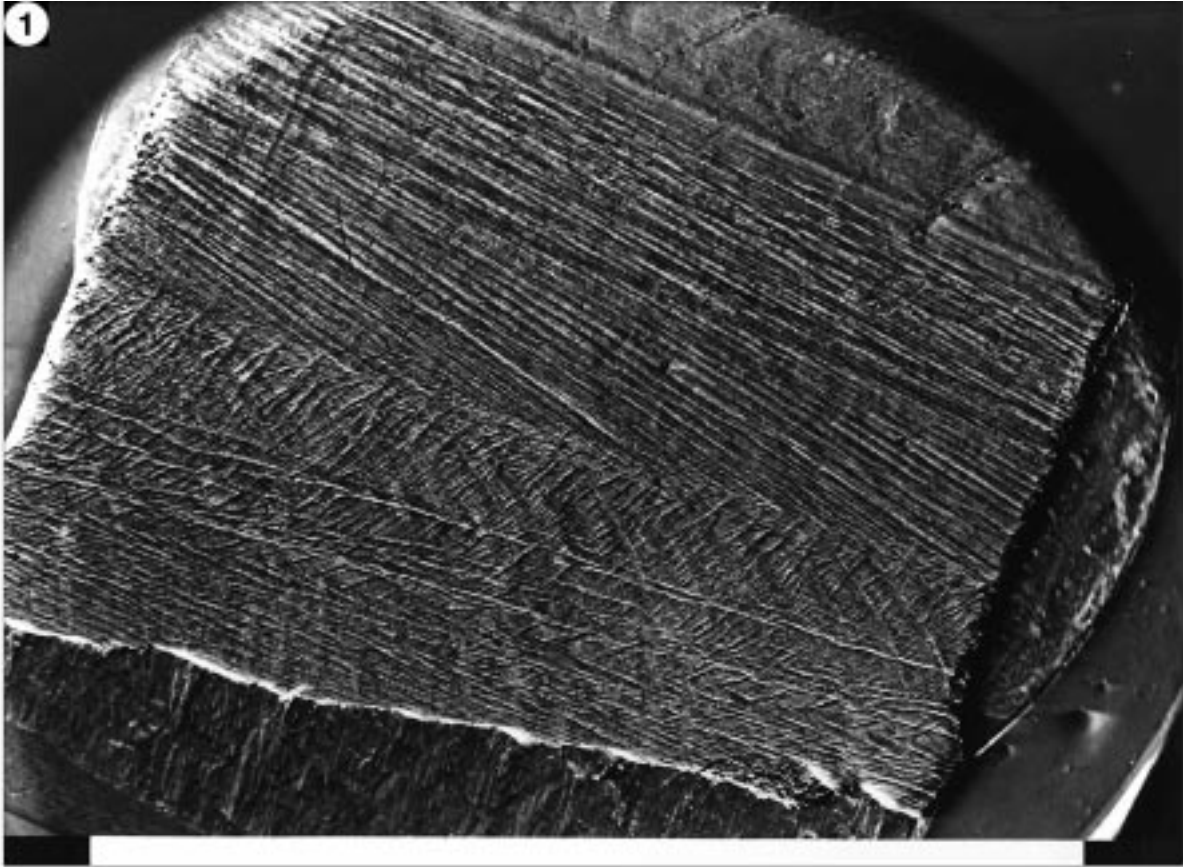
Plate 3

Megateuthis sp.

Fig. 1: Inner surface of the pro-ostracum (adoral direction to top left).
   Narrow, shallow grooves diverging from a median axial line are interpreted as impressions of collagen fibres. Faint longitudinal grooves are seen about 1 mm either side of the axial line.
   Scale bar 1 mm.
Fig. 2: Inner surface of the pro-ostracum (adoral direction to top right).
   Shallow grooves seen about 1 mm each side of the axial line.
   Scale bar 1 mm.
Fig. 3: Inner surface of pro-ostracum showing thin lamellae with a different orientation of parallel crystallites.
   Scale bar 0.1 mm.
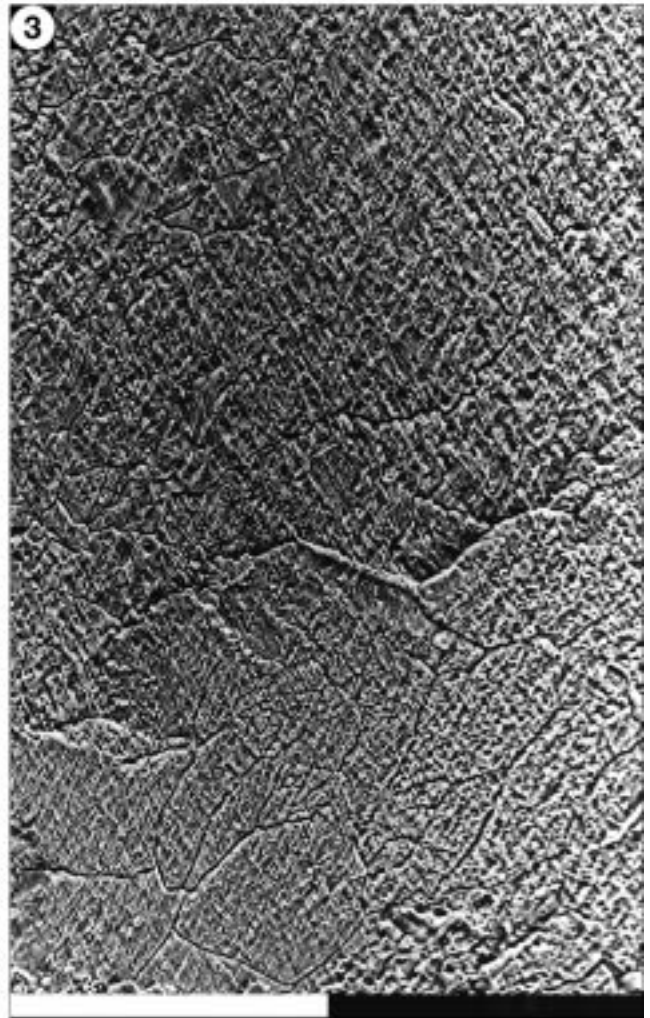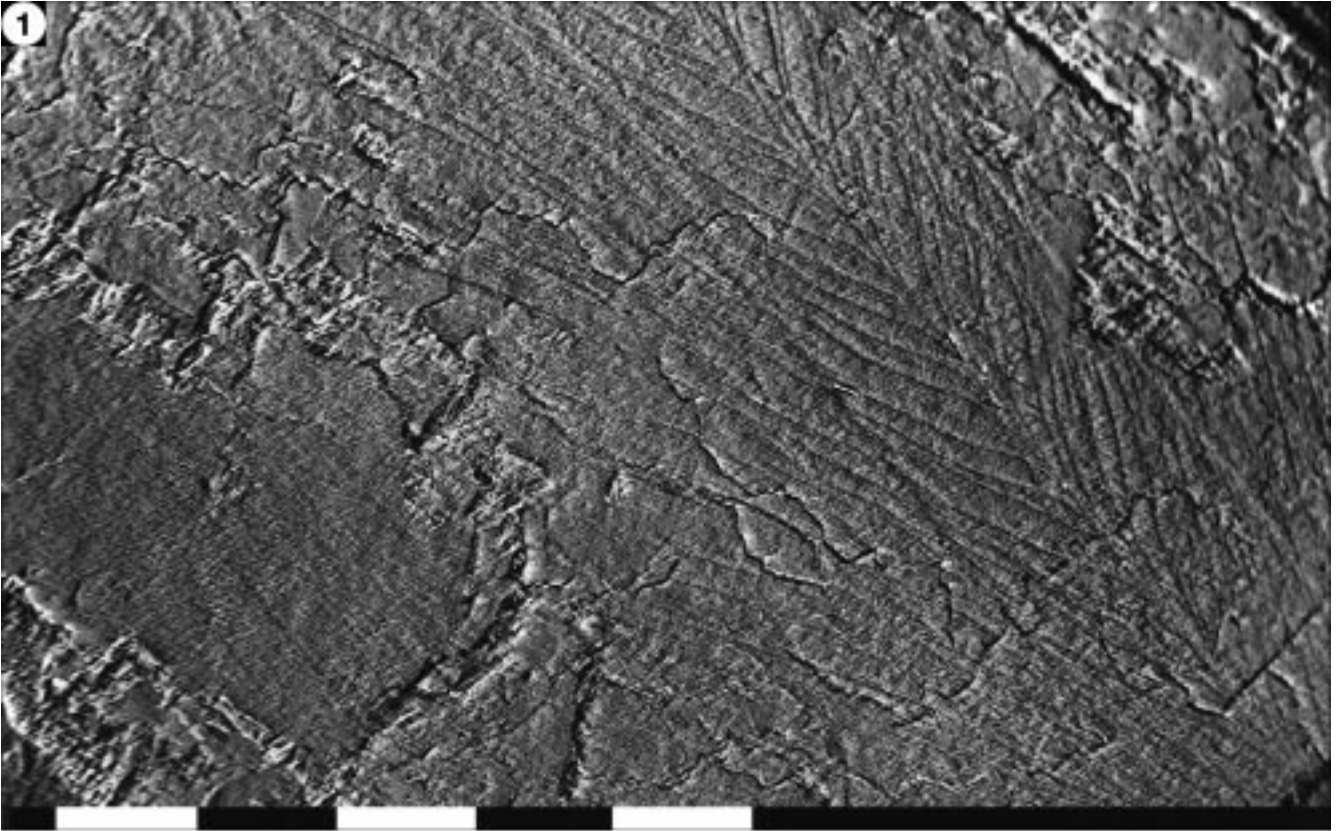
Plate 4

Megateuthis sp.

Fig. 1: Inner surface of pro-ostracum, adoral direction towards top.
Shows different orientation of crystallites in adjacent lamellae, cf. Pl. 3, Fig. 3.
Scale bar 1 mm.
Fig. 2: Same as Fig. 1.
Note minute pits concentrated in the grooves.
Scale bar 1 mm.
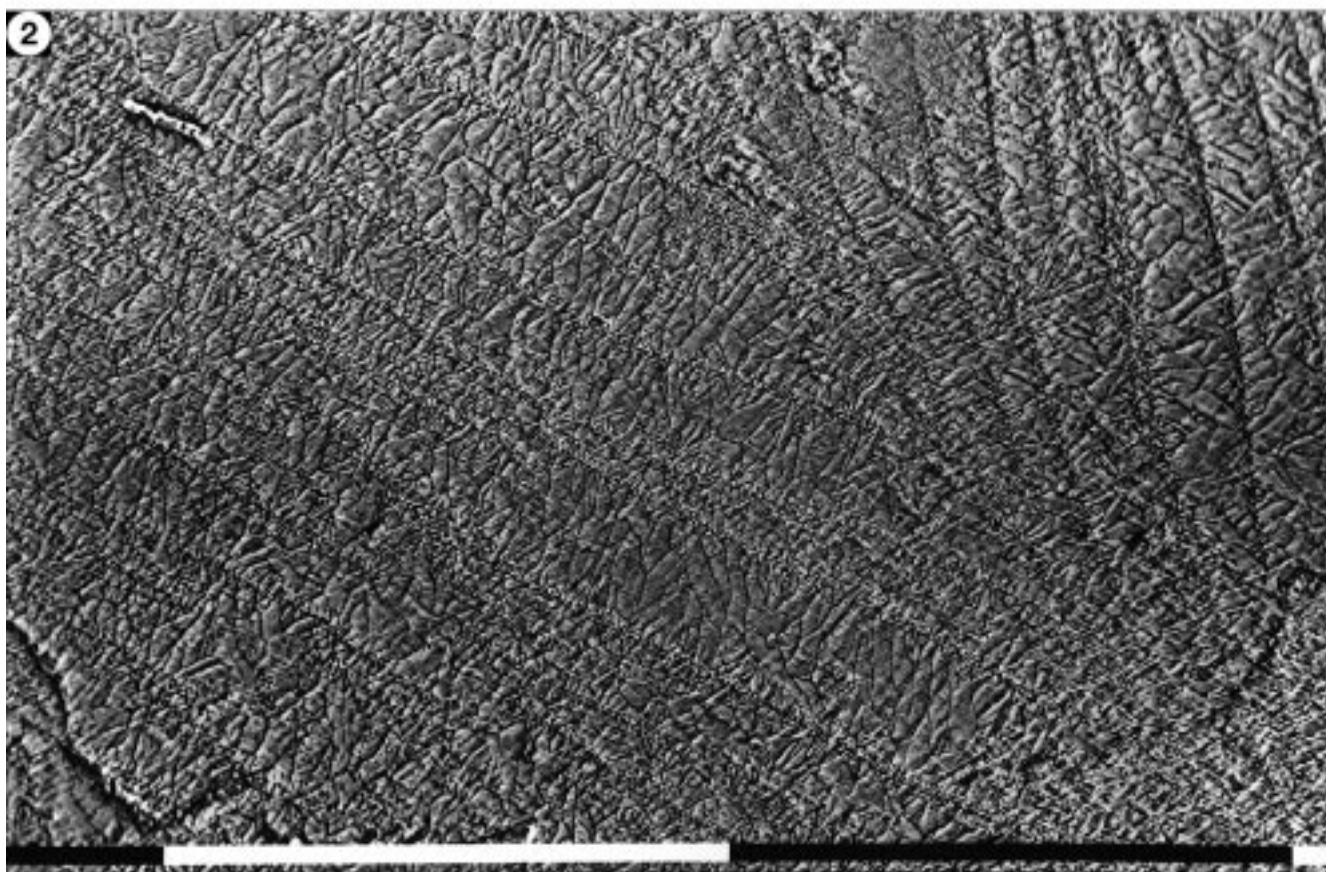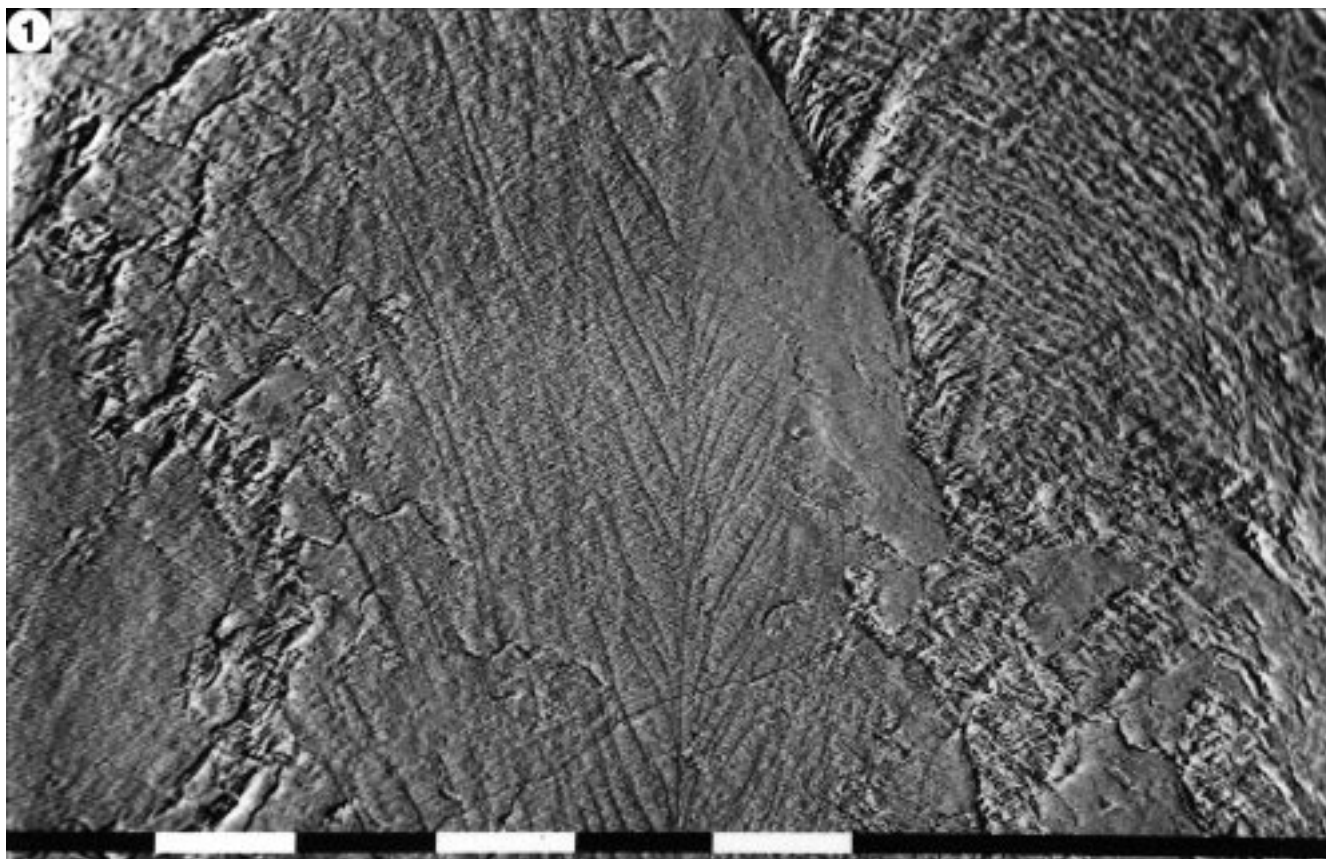
Plate 5

Megateuthis sp. – Longitudinal sections.

Fig. 1: Layers from top down:
Rostrum (r), predominantly organic pro-ostracum (pr), nacreous layer (nac) of conotheca, thinner inner prismatic layer (pr), and thin layer of unknown origin (bottom layer is secondary calcite?).
Scale bar 0.1 mm.
Fig. 2: Enlargement of part of Fig. 1.
(x) is thin layer of unknown origin.
Scale bar 0.1 mm.
Fig. 3: Multi-lamellar pro-ostracum (pro) external to nacreous layer.
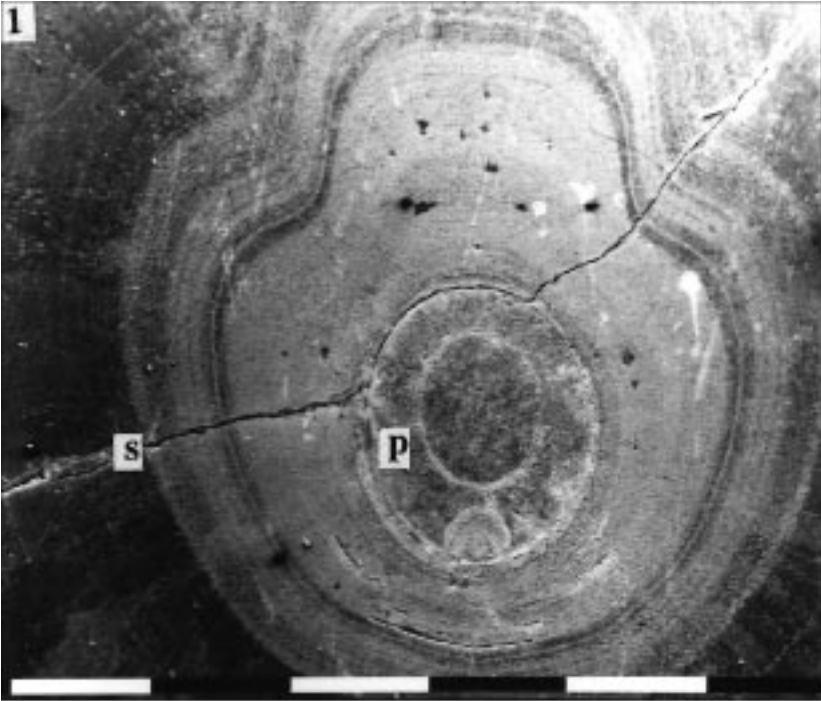Scale bar 0.1 mm.
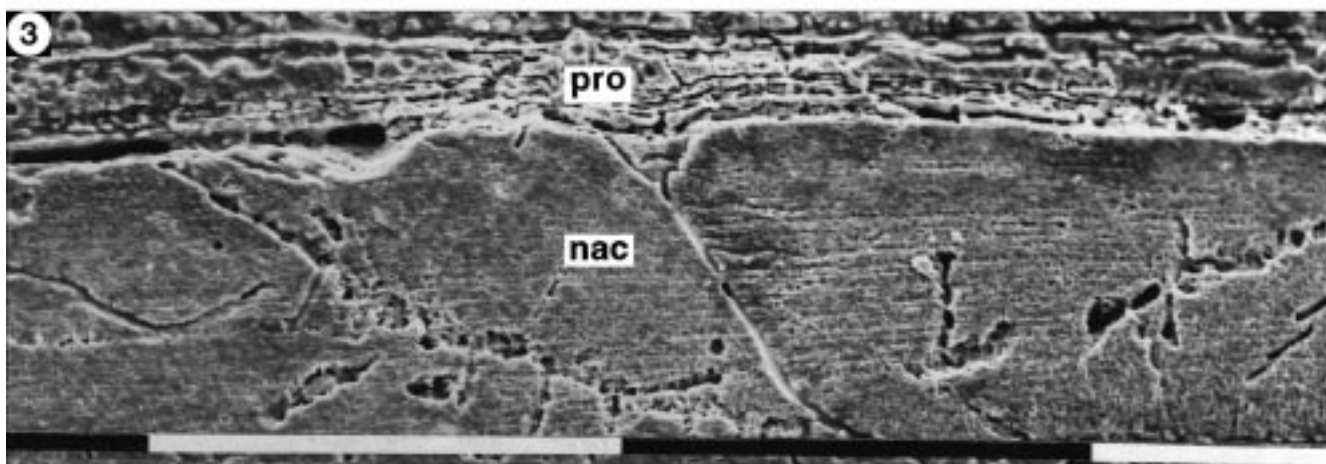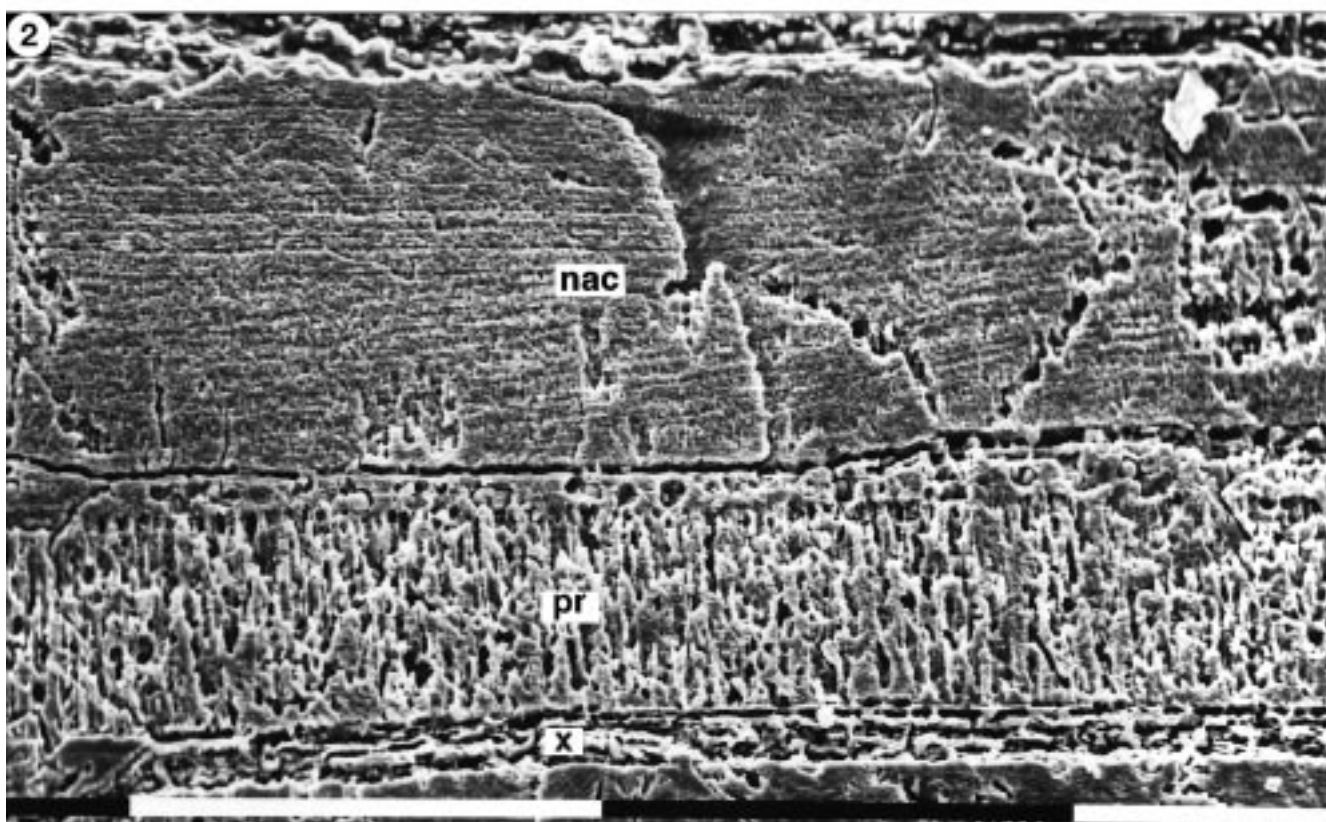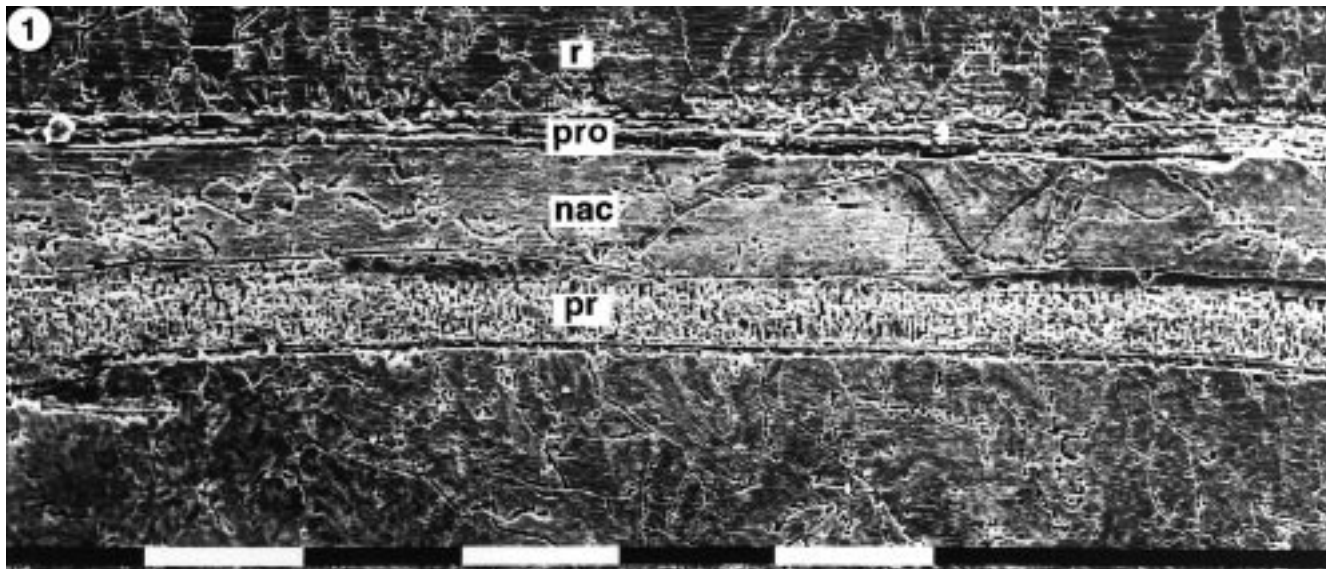
Plate 6

Megateuthis sp.

Fig. 1:   Cross section of the central portion of a rostrum and phragmocone to show a porous inner zone, surrounding the phragmo-
            cone (p), and a solid outer zone (s).
            Scale bar 1 mm.
Figs. 2,3: Details in higher magnification in the structure in the porous zone and solid zone, respectively.
            Scale bars 0.1 mm.
Fig. 4:   Nacreous tablets in the nacreous layer of the conotheca; note their large size and numerous radial sectors that represent
            cyclic twins; each tablet shows a central cavity originally occupied by calcified organic matrix.
            Scale bar 0.1 mm.