

# ULTRASTRUCTURE OF *BELEMNOTHEUTIS* FROM THE OXFORD CLAY (CALLOVIAN), ENGLAND, AS A KEY FOR ELUCIDATING THE ORIGIN OF THE PRO-OSTRACUM

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**Abstract:** The postulate that the pro-ostracum of extinct coleoids is a dorsal extension of the phragmocone wall (conotheca), and is therefore a homologue of the shell wall of ectococheate precursors (Naef, 1922; Jeletzky, 1966) is analysed in the light of the shell ultrastructure in *Belemnotheutis antiquus* Pearce.

Three shells of *B. antiquus* from the Oxford Clay (Middle Jurassic, Callovian) of Christian Malford, Wiltshire, England, were examined with the SEM. For comparison, additionally five gladii of the living squids *Loligo* and *Berryteuthis* were studied with the SEM. It is shown that in *B. antiquus* (1) the apical part of the rostrum is composed of a dense, outer prismatic portion and a porous, inner prismatic portion; towards the aperture the rostrum decreases in thickness, losing first the porous inner portion and finally the outer dense portion; (2) the conotheca from the apical to the middle part consists on the dorso-lateral sides of the outer prismatic, nacreous and inner prismatic layers; towards the aperture it loses, first, the outer prismatic layer and then the nacreous layer; (3) the pro-ostracum differs remarkably from the conotheca – it exhibits irregular mineralization while the nacreous and prismatic layers of the conotheca and the prismatic rostrum are standard in their ultrastructure; the pro-ostracum is a micro-laminated, possibly mainly organic, structure, made up of vertical, horizontally micro-laminated, columns; (4) fine micro-lamination of the pro-ostracum is similar to the micro-lamination of the chitinous gladius in modern squids.

The ultrastructural data on *Belemnotheutis* favours the concept of the pro-ostracum as a separate, innovative part of the skeleton in coleoids (Doguzhaeva, 2002; Doguzhaeva et al., 2002a, 2003, 2005a, b; 2006 in press) rather than a dorsal projection of the conotheca.

**Key words:** Middle Jurassic coleoid, shell morphology and ultrastructure, pro-ostracum, evolutionary morphology, England

## INTRODUCTION

The pro-ostracum is a key skeletal element from which it was inferred that in belemnite-like cephalopods the body was not wholly surrounded by the body chamber of the shell but had “open” ventral and ventro-lateral sides covered by an elastic muscular wall, or mantle (Voltz, 1830; Mantell, 1848). The fossilized muscular mantle from the outside of the pro-ostracum was reported in the Middle Jurassic *Belemnotheutis* Pearce (Owen, 1844; Pearce, 1847) and more recently was studied in detail with the scanning electron microscope (Kear et al., 1995). Imprints of the mantle tunic on the side of the shell, marking the attachment of the mantle to the lateral margins (hyperbolar zones) of the pro-ostracum were described in the Middle Jurassic *Mega-teuthis* (Doguzhaeva et al., 2002a).

The pro-ostracum is a fragile structure, seldom preserved, that has been observed in the Late Triassic *Phragmoteuthis* (Bronn, 1859; Suess, 1865; Mojsisovics, 1882) and Jurassic *Cylindroteuthis* (Mantell, 1848), *Chondroteuthis* (Crick, 1896) and *Acanthoteuthis* (Crick, 1897;

Rogov & Bizikov, 2005). More often the pro-ostracum is preserved as imprints on the dorsal side of the phragmocone and/or on the internal surface of the rostrum (see Phillips, 1865–70; Naef, 1922). This was possible because of the relief on its external and internal surfaces. On the external (dorsal) surface the crescent-shaped growth increments along a median line form a central field bordered laterally in phragmoteuthids by the lateral lobes and in belemniteuthids, belemnitids and diploconitids by the hyperbolar zones, marked by thin, longitudinal, forwardly converging ribs and grooves. The internal (ventral) side of the pro-ostracum is even more rarely exposed. It is known in belemnitids in which it has a fine feather-like pattern formed by slightly curved or straight discrete lines diverging from both sides of the median line (Crick, 1896; Doguzhaeva et al., 2002a). In Early Jurassic belemnitids and probably in younger taxa as well, the pro-ostracum was present from early growth stages. This is shown by the impression of the pro-ostracum on the surface of the first camerae of the phragmocone (immediately after the protoconch) in the Early Jurassic *Passaloteuthis* (Doguzhaeva et al., 2003a). This indicates

that the pro-ostracum was already present in belemnite hatchlings.

Morphological investigations are here combined with analysis of shell ultrastructure to provide new data to help elucidate the evolutionary morphology of the pro-ostracum. This double method was applied for the first time to the Middle Jurassic belemnite *Megateuthis* (Doguzhaeva et al., 2002a) and then to the Early Jurassic *Passaloteuthis* (Doguzhaeva et al., 2003a). The ultrastructural observations revealed the significant difference between the pro-ostracum and the conotheca in these two genera (Belemnitida Zittel, 1895) and thereby threw doubt on the concept of the pro-ostracum as a dorsal continuation of the phragmocone wall. If that concept was correct one would expect the conotheca and pro-ostracum to be ultrastructurally similar.

In the present paper the double method, combining morphological and ultrastructural investigations, is applied to the study of the pro-ostracum in *Belemnotheutis* (Belemnitida Stolley). In this genus the presence of the pro-ostracum has been known since the genus was erected (Pearce, 1842). This "atypical belemnite" with a short rostrum forming a thin sheath-like covering of a breviconic phragmocone has been a focus of many investigations (Huxley, 1864; Naef, 1922; Makowski, 1952; Jeletzky, 1966; Bandel & Kulicky, 1988; Donovan & Crane, 1992; Funchs et al., 2004; Doguzhaeva et al., 2005a). Makowski (1952: Fig. 8) illustrated the pro-ostracum in *B. polonica* Makowski as a comparatively narrow, long tongue-like structure covering about one half of the circumference of the phragmocone.

#### MATERIAL STUDIED, STATE OF PRESERVATION AND METHODS

Three specimens of *B. antiquus* from the Oxford Clay (Jurassic; Callovian) of Christian Malford, Wiltshire, England were studied. They were collected in the nineteenth century and purchased by the British Museum (Natural History) (two specimens) and the Swedish Museums of Natural History (one specimen). The specimens are slabs of dark grey clay each with a flattened shell, coated with shellac in an attempt to preserve the shell.

All three shells have been strongly compressed approximately in a dorso-ventral direction so that their dorsal and ventral sides are almost in contact (Pl. 1). The shells are ca. 80 mm, 60 mm and 50 mm in length. They expose dorso-lateral and lateral sides. In the apical part of the shell the rostrum is comparatively thicker than at later ontogenetic stages and solid, and therefore the shell is less deformed there than anteriorly where the shell wall is fractured into a mosaic. The fragments retain their original positions. Horizontal fractures run along the mural parts of the septa.

In two specimens the shellac was removed, firstly by solution in acetone and then by cautious scraping. In places the sheath was removed together with the shellac because they were strongly bound together. Due to this removal, mainly near the aperture where the sheath is thin, the pro-ostracum became partly exposed. The lateral surface of the pro-ostracum is exposed in the anterior parts of two specimens. It is characterised by fine longitudinal striation at some distance from the median line. In places these hyperbolar zones have

a thin coating of black material. In *B. antiquus* the position of the hyperbolar zones corresponds to that in *B. polonica* (Makowski, 1952: Fig. 8) so that the proportion of the central field to the hyperbolar zones in these two species is similar. The curved growth lines of the central field between two hyperbolar zones were not observed in the material examined. During the "cleaning" of the shell the pro-ostracum must have been partly removed together with the shellac and the rostrum.

The samples of the shell wall selected for scanning electron microscope (SEM) examination were taken from the dorsal and dorso-lateral sides including places where the hyperbolar zones were exposed. To observe the ontogeny of the shell ultrastructure small pieces of the shell were taken at different distances from the apex. The samples were not etched. Fractured surfaces of the fragments of shell wall were examined with the SEM.

The gladii of the modern squids *Loligo* and *Berryteuthis* were dried before they lost water and became brittle and than studied with the SEM. Fractured surfaces of the gladii were investigated.

The samples were studied with a scanning electron microscope Hitachi 4300 at the Swedish Museum of Natural History, Stockholm, Sweden.

#### OBSERVATIONS: SHELL ULTRASTRUCTURE IN *BELEMNOTHEUTIS*

##### Rostrum (Pl. 1; 2, A; 3, A; 4, C)

The apical portion of the rostrum consists of an outer and an inner layer. The outer layer has a solid, simple prismatic structure with needle-shaped crystallites. The inner layer is composed of similar prismatic units but they are loosely packed. The two portions of the rostrum differ in colour – the external one is shiny yellowish and the internal is chalky white. Towards the aperture the rostrum loses its inner layer and the outer layer becomes spherulitic-prismatic in structure. The crystalline units form sectors in which they radiate towards the shell surface and become loosely packed. Small interspaces between some of the crystalline units indicate higher organic content. The outer surface of the rostrum is covered by a thin, possibly originally organic, layer.

##### Conotheca (Pl. 2, E; 3, C; 4, A, C)

The apical part of the conotheca (up to approximately 50 mm from the apex) consists of a thin outer prismatic, a thick nacreous and a thin inner prismatic layer. Samples taken a somewhat greater distance from the apex show that the conotheca is composed only of the nacreous and the inner prismatic layers, both having the same thickness of ca 0.6 mm. In our largest specimen samples taken at a distance of 65 mm from the shell apex show that the conotheca is here composed only of the inner prismatic layer that is about 0.1 mm thick. Thus, at earlier growth stages the conotheca has three layers but at older stages first the outer prismatic layer and finally the nacreous layer wedge out.

##### Pro-ostracum (Pl. 1; 2, A–F; 3, A–E; 4, A–F)

In higher magnification a criss-cross pattern of the pro-ostracum is observed below the rostrum (Pl. 2A). The surface

of the pro-ostracum is penetrated, both vertically and horizontally, by a great number of canals of boring organisms, with a diameter somewhat less than 1  $\mu\text{m}$ . The presence of these canals indicates that the pro-ostracum consisted mainly of organic matter that was only partially calcified. The striae of the hyperbolar zones of the pro-ostracum have a somewhat compact, plate like structure, and the interspaces between them have a porous net- or lace-like structure (Pl. 2, C–D). Immediately beneath the pro-ostracal surface there follows a thin layer, ca 15  $\mu\text{m}$  thick, that is clearly visible on vertical fracture surfaces of all three shells. Because it is rich in organic matter this layer shows a great difference in mode of preservation from the calcified, uniformly well preserved prismatic and nacreous layers of the same shell. This layer of the pro-ostracum is in places composed of columnar units about 5  $\mu\text{m}$  in diameter (Pl. 4, D). These columns seem to be composed of predominantly organic, very thin laminae (Pl. 4, E–F), ca 0.5  $\mu\text{m}$  thick. In surface view (Pl. 2, F) the distal end of each column forms a polygonal field; its periphery composed of numerous, irregularly shaped, radially arranged plates in contact with each other; its central portion consists of several smaller, angular, elements separated by interspaces of various widths. In other places the pro-ostracum consists of vertical elements of highly variable diameter separated by interspaces of irregular shapes and sizes (Pl. 4, D–E). Some of these elements seem to be plate-like and show series of deep, horizontal, narrow incisions (Pl. 3, C–E; 4, A–B). Thus, the pro-ostracum has a unique structure that has no resemblance either to the adjacent, outer prismatic layer of the conotheca, or to the prismatic layers of the rostrum.

#### DISCUSSION: THE EVOLUTIONARY MORPHOLOGY OF THE PRO-OSTRACUM

The evolutionary morphology of the skeleton in coleoid cephalopods, including the pro-ostracum, is at present inadequately known. For a long time the evolutionary morphology of the skeleton in coleoids was based mainly on the shell morphology in Jurassic–Cretaceous, and a smaller number of Triassic representatives. However, a coleoid archetype was evidently developing in the Carboniferous when the coleoids (although relatively few of this age are known) displayed the high morphological diversity and plasticity (Doguzhaeva, 2002a) that is a typical feature of the early evolutionary stages of any group of animals or plants (Mamkaev, 1968). Therefore elucidating the evolutionary transformation of the skeleton on the basis of Mesozoic members only can hardly be effective any longer.

The Early Carboniferous coleoid *Hematites* Flower & Gordon yielded important information for the question under consideration. This form has a short body chamber (less than two camerae in length) in combination with the absence of a pro-ostracum (Doguzhaeva et al., 2002b: Pl. 1, Figs. 1–3). According to the classic concept (Naef, 1922; Jeletzky, 1966) a gradual elimination of the ventral and ventro-lateral sides of the body chamber resulted in the formation of a pro-ostracum on the dorsal side. In other words, the pro-ostracum is the dorsal part of the body chamber remaining after the reduction of the long body chamber

in the supposed bactritoid ancestors. Hence a morphological combination such as a short body chamber and absence of the pro-ostracum, according to this concept, would be impossible. On the other hand, a long body chamber is combined with an ink sac and a short pro-ostracum in the Late Carboniferous coleoid *Donovaniconus oklahomensis* Doguzhaeva, Mapes & Mutvei (2002d, 2003b: Figs. 1, 2, 4). This observation also conflicts with the classic concept, because coleoids were believed to have no body chamber. Moreover, the Late Carboniferous coleoids preserved with a phragmocone and an ink sac seemed to be diverse in a respect of the pro-ostracum/terminal chamber development (Doguzhaeva et al., 2002c; 2004: Figs. 1A, B; Mapes et al., in prep.). These data on Palaeozoic phragmocone-bearing coleoids require, for their explanation, re-evaluation of the classic concept of the formation of the main characters of the skeleton in coleoids (Doguzhaeva, 2002a).

The ultrastructural approach has also revealed new data that conflict with the classic concept. For the classic concept to be true, (1) the pro-ostracum should have the same or comparable ultrastructure to that of the conotheca, and (2) in the section of the shell there should be no layers between the rostrum and the conotheca. To be a homologue of the shell wall in coleoid ancestors (bactritoids), the pro-ostracum in belemnite-like coleoids and the shell wall in bactritoids should have a similar or a comparable ultrastructure. In bactritoids the shell wall consists of a thin outer prismatic and a thick nacreous layer. The inner prismatic layer was absent or secreted only at late ontogenetic stages (Doguzhaeva, 2002b: Pl. 3, Fig. 5). It is now clear that the structure of the conotheca in belemnite-like coleoids is remarkably variable. It is practically impossible to identify the shell layers without tracing them forwards from the protoconch stage. This opinion is close to the views of Grandjean (1910), Christensen (1925) and Müller-Stoll (1936) who thought that the conotheca differs essentially from the shell wall of ectocochlians. However, the contrary idea on the conotheca or phragmocone wall retaining the structure of the ectocochleate shell wall has been dominant (Voltz, 1830; d'Orbigny, 1842; Flower, 1945; Flower & Gordon, 1959; Mutvei, 1964; Barskov, 1973; Dauphin, 1985; Bandel, 1989; Bandel et al., 1984; Bandel & Kulicky, 1988). Nevertheless, SEM study of well preserved shells of the Valanginian *Conobelus* (Duvallidae) revealed that in the first 20 or so camerae the conotheca proper is missing, and the wall of the phragmocone consists of the long mural parts of the septa and/or a thin prismatic sheath-like continuation of the primordial rostrum (Doguzhaeva et al., 1996). This continuation of the primordial rostrum in *Conobelus* seems to correspond to the outer prismatic layer of the conotheca of Christensen (1925) and Müller-Stoll (1936). Christensen (1925) observed that in belemnites the outer layer of the two calcified layers forming the conotheca is a continuation of the prismatic wall of the protoconch. Müller-Stoll (1936) described presumably aragonitic outer and inner layers in the conotheca, with a thin, apparently mainly conchiolin layer between the first two. Mutvei (1964) emphasized that the outer calcified layer in the conotheca is formed by alternation of thin aragonitic lamellae and conchiolin membranes. He assumed that this layer was correlated with the nacreous layer of the shell wall in Recent *Nautilus*. Barskov (1973) observed that in the Late

Jurassic *Pachyteuthis* and the Lower Cretaceous *Conobelus* and *Neohibolites* the inner prismatic layer of the conotheca corresponds to the long part of the first septum that runs along the whole phragmocone. Similarly in juvenile *Hibolites* the inner layer of the conotheca is formed by a continuation of the mural part of the first septum (Bandel et al., 1984). Druschits et al. (1984) found that in the Lower Cretaceous *Tauriconites* (Diplobelida) the conotheca is formed by a prismatic layer that was a continuation of the prismatic wall of the protoconch. In the conotheca of *Belemnotheutis* and *Megateuthis*, Bandel & Kulicky (1988) described the periostracum, outer prismatic, nacreous and inner prismatic layers. According to Doguzhaeva et al. (2002a) in *Megateuthis* the conotheca consists of two layers: inner prismatic and nacreous. In juvenile Lower Jurassic *Passaloteuthis* the conotheca proper is missing and the phragmocone wall is formed by a continuation of the mural part of the first septum (Doguzhaeva et al., 2003a).

To be certain of observing the true ultrastructure of the pro-ostracum one must restrict observations to the thickness of the shell between the outer and inner surfaces of the pro-ostracum, recognisable by their characteristic patterns. In *Megateuthis* this revealed that the pro-ostracum was formed of organic fibres with 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 are covered by thin, compact pellicles (Doguzhaeva et al., 2002a). A similar case was found in *Passaloteuthis* in which the description of the ultrastructure of the pro-ostracum was based on the SEM examination of the wall thickness between the outer and inner surfaces exposing the relief of both sides of the pro-ostracum (Doguzhaeva et al., 2003a). In this belemnite the pro-ostracum is described as consisting of two compact prismatic layers with a fine lamellar, loosely calcified, originally organic-rich layer between them. The original high content of organic material was indirectly confirmed by the presence of numerous borings on exposed broken surfaces of the pro-ostracum (Doguzhaeva et al., 2003a: Pl. 4).

As described above, the pro-ostracum in *Belemnotheutis* consists of vertical columns made up of predominantly organic lamellae, ca 0.05 µm thick. Their thickness is similar to that of the lamellae forming the gladii, formed of chitin-protein complexes (Hunt & Nixon, 1981), in living squids (Pl. 5). On the basis of our SEM observations on the pro-ostracum in *Belemnotheutis* we propose the name “organic lamello-columnar ultrastructure” (Pl. 4, D–F) as a new type of shell ultrastructure in cephalopods.

The pro-ostracum would have had an ultrastructure close to that of the conotheca if it arose from the latter. The concept of the pro-ostracum as an innovation in coleoid cephalopods was originally based on SEM studies of “ordinary” belemnites (Doguzhaeva et al., 2002a, 2003). Our present results on the “abnormal” belemnite *Belemnotheutis* support this idea.

Huxley (1864, p. 18) observed a specimen of *Belemnotheutis* in which “from one lip of the phragmocone there obviously proceeds the horny-looking plate (*a*, *a*), the two lateral contours of which, obscurely defined from the matrix, pass into one another at an acute angle at *b*. A narrow band of horny-looking matter, marked by oblique striae, is dis-

cernible at *c*, and is quite distinct from the remains of the mantle (*f*), under which it seems to pass.” The ultrastructural features of the pro-ostracum, presented herein, agree with Huxley’s interpretation of the pro-ostracum as a “horny” structure.

To summarize, the SEM study shows that in *Belemnotheutis*: (1) the apical part of the rostrum is composed of a dense, outer prismatic portion and a porous, inner prismatic portion; towards the aperture the rostrum decreases in thickness, losing first the porous inner portion and finally the outer dense portion; (2) in the middle part of the shell the conotheca consists of outer prismatic, nacreous and inner prismatic layers; towards the aperture it gradually decreases in thickness: first, the outer prismatic layer disappears and then the nacreous layer; the most anterior portion of the conotheca is solely formed by the thin, inner prismatic layer; (3) the pro-ostracum consists of horizontally laminated vertical columns; the distal end of each column represents a polygonal field that at its periphery is composed of numerous, irregularly shaped, radially arranged plates, and in its central portion of several angular, smaller elements separated by interspaces of various widths. Delicate lamination of the pro-ostracum in *Belemnotheutis* is similar to the lamination of the chitin-protein material in the gladius of the living squids *Loligo* and *Berryteuthis* as examined with the SEM. The pro-ostracum in *Belemnotheutis*, is thus a shell element with unique structure without any similarity to that of the conotheca or rostrum.

The ultrastructural data on *Belemnotheutis* favour the concept of the pro-ostracum as a separate, innovative part of the shell rather than a dorsal projection of the conotheca.

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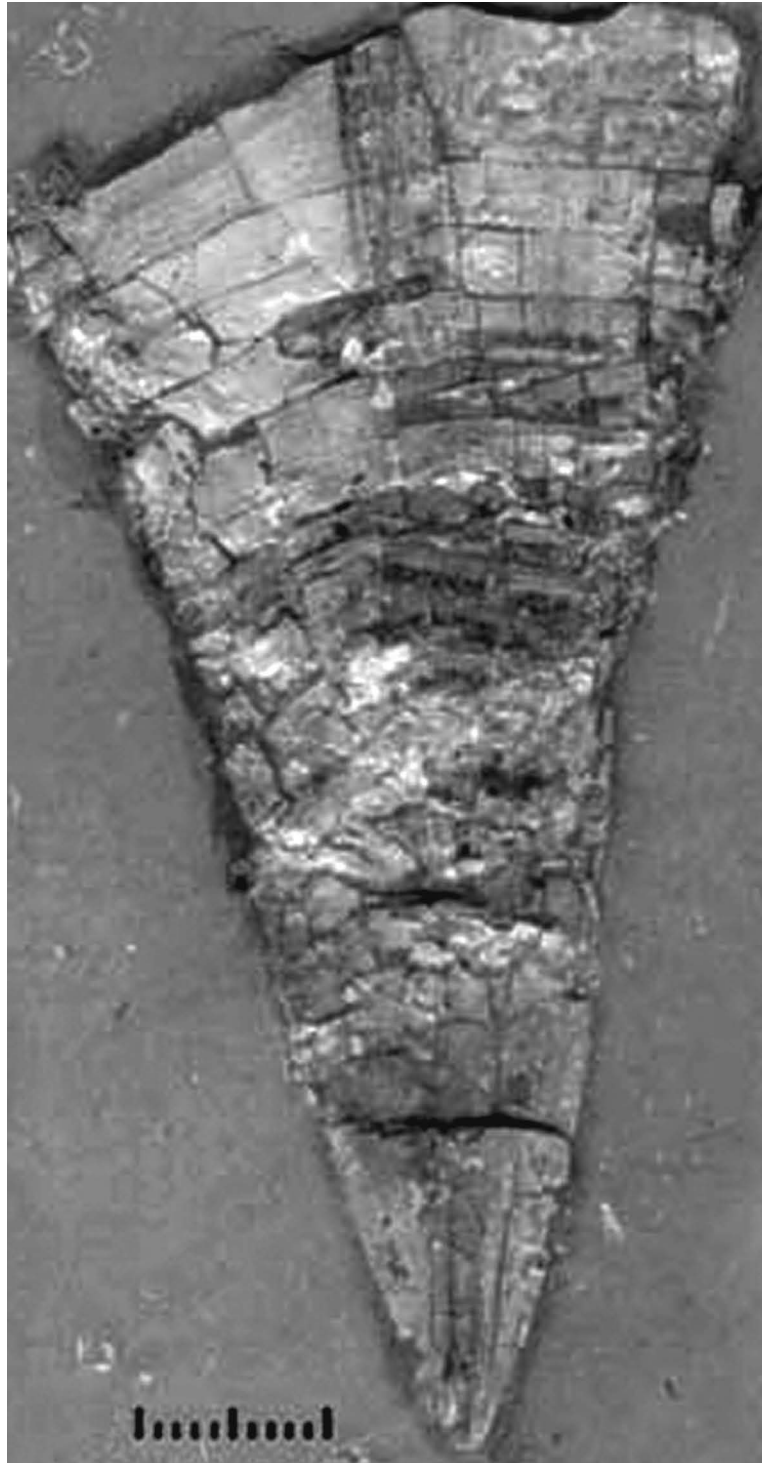


Plate 1. *Belemnnotheutis antiquus*, specimen no. BMNH 37412; Oxford Clay, Jurassic; Callovian, Christian Malford, Wiltshire, England: 1 – General view of the shell deformed by compaction. The smooth apical portion, about 1/3 of the total length shows a rostrum; two short ridges separated by a short groove mark the dorsal side; anteriorly the rostrum becomes thinner and the phragmocone is less protected against compaction, being more strongly crushed and slightly shifted to the right; the shifting results in an artifact that gives an erroneous view as if the hyperbolar zone is situated along the median line that in the apical part is between the two ridges. The transverse lines of the phragmocone are fractures along the mural parts of septa; scale bar is 10 mm.

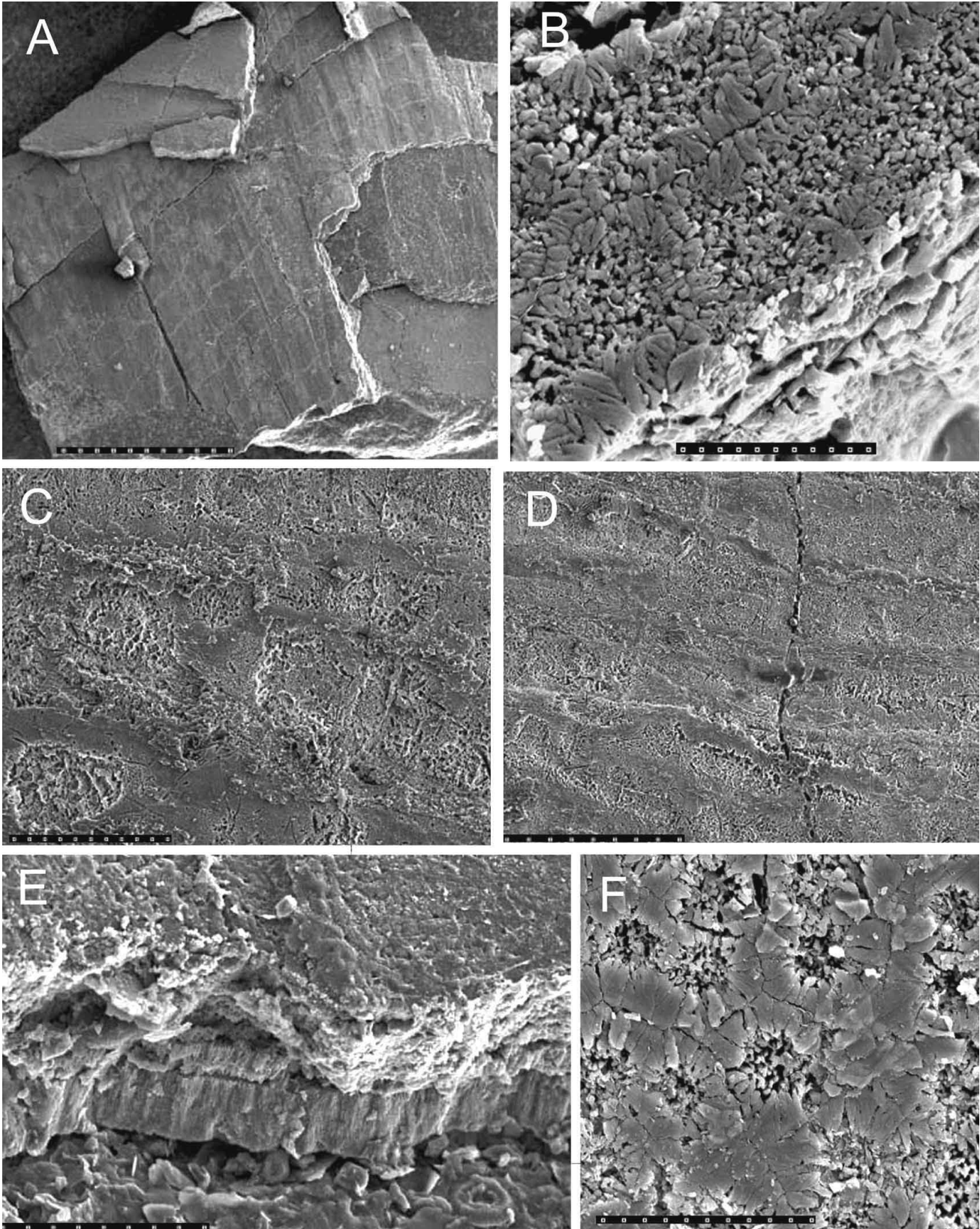


Plate 2. A–F. Surface view of a fragment of the anterior portion of the shell: a criss-cross pattern of the surface of the pro-ostracum, above is a fragment of the rostrum; scale bar is 0.6 mm. B. Close up of A: two views of the pro-ostracum: from the surface and from the longitudinal fracture plane to show its high porosity in combination with a lamination; scale bar is 6  $\mu$ m. C, D. Surface view of the hyperbolar zone to show the porosity of the material within the grooves and more compact material of the ridges; scale bar: C is 60  $\mu$ m; D is 150  $\mu$ m; E. Close up of A (centre) to show the laminated pro-ostracum (upper part) and inner prismatic layer of the conotheca; the outer prismatic and nacreous layers are missing at the apertural part of the shell but present at early and middle ontogenetic stages; scale bar is 30  $\mu$ m; F. The porous outer surface of the pro-ostracum shows a “rosette” -like pattern formed by a combination of porous centres and elongated plates around them; scale bar is 12  $\mu$ m.



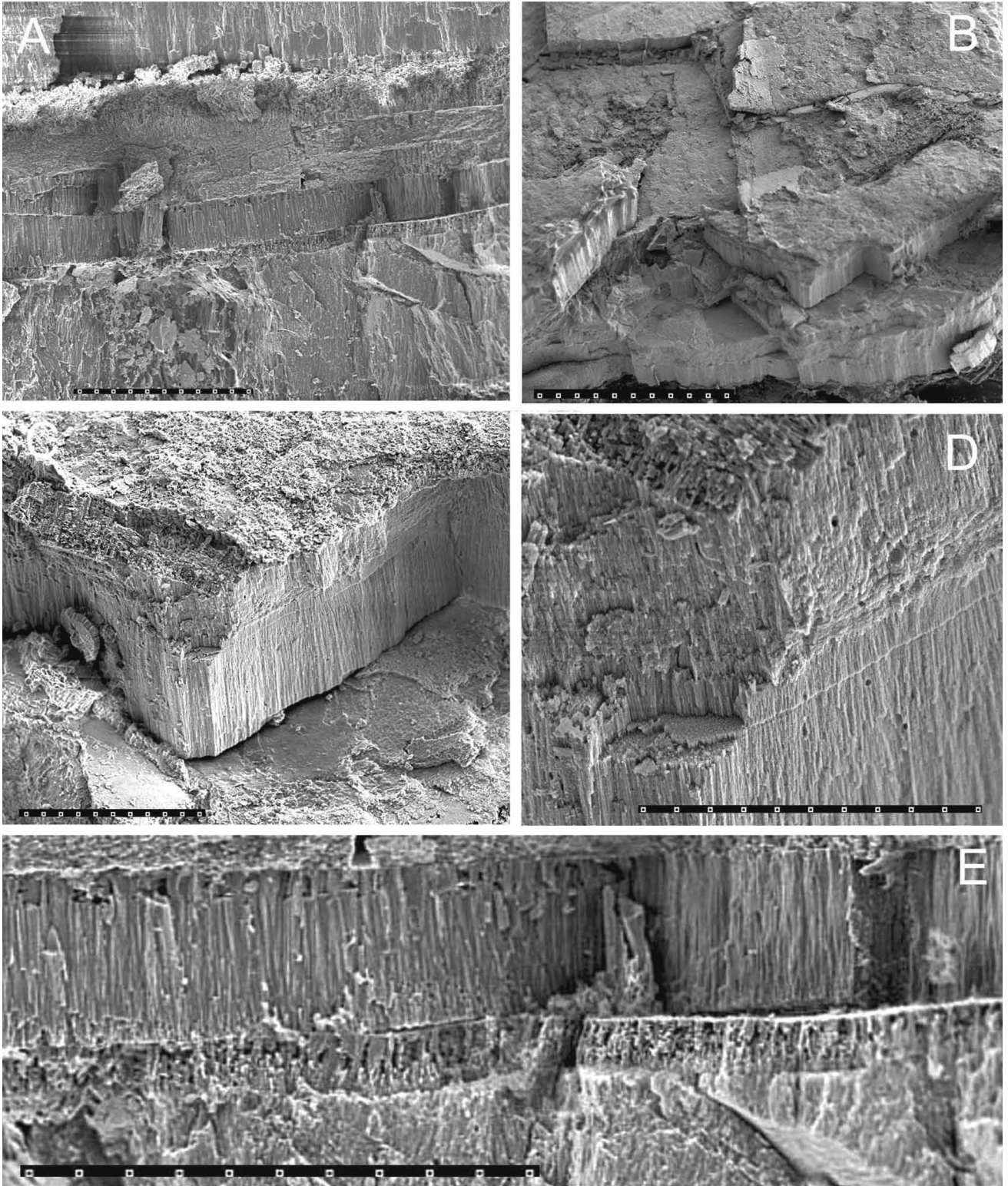


Plate 3. A–E. Fracture of a compressed shell with a rostrum running through the middle part of the photo, below a thin pro-ostracum and a thick nacreous layer of the conotheca; scale bar is 150  $\mu\text{m}$ . B. General view of the compressed and fractured shell exposing different structural elements; the hyperbolar zone of the pro-ostracum is at the top; scale bar is 0.6 mm. C. Detail of B (central part) to show a fragment of the shell with a thin pro-ostracum that is distinguished by its porous ultrastructure; scale bar is 120  $\mu\text{m}$ . D. Closeup of C with a fragment of the pro-ostracum exposed at top left corner; scale bar is 60  $\mu\text{m}$ . E. Middle part of the shell with a thin porous pro-ostracum situated between a rostrum (top) and a nacreous layer of the conotheca (bottom); scale bar is 120  $\mu\text{m}$ .

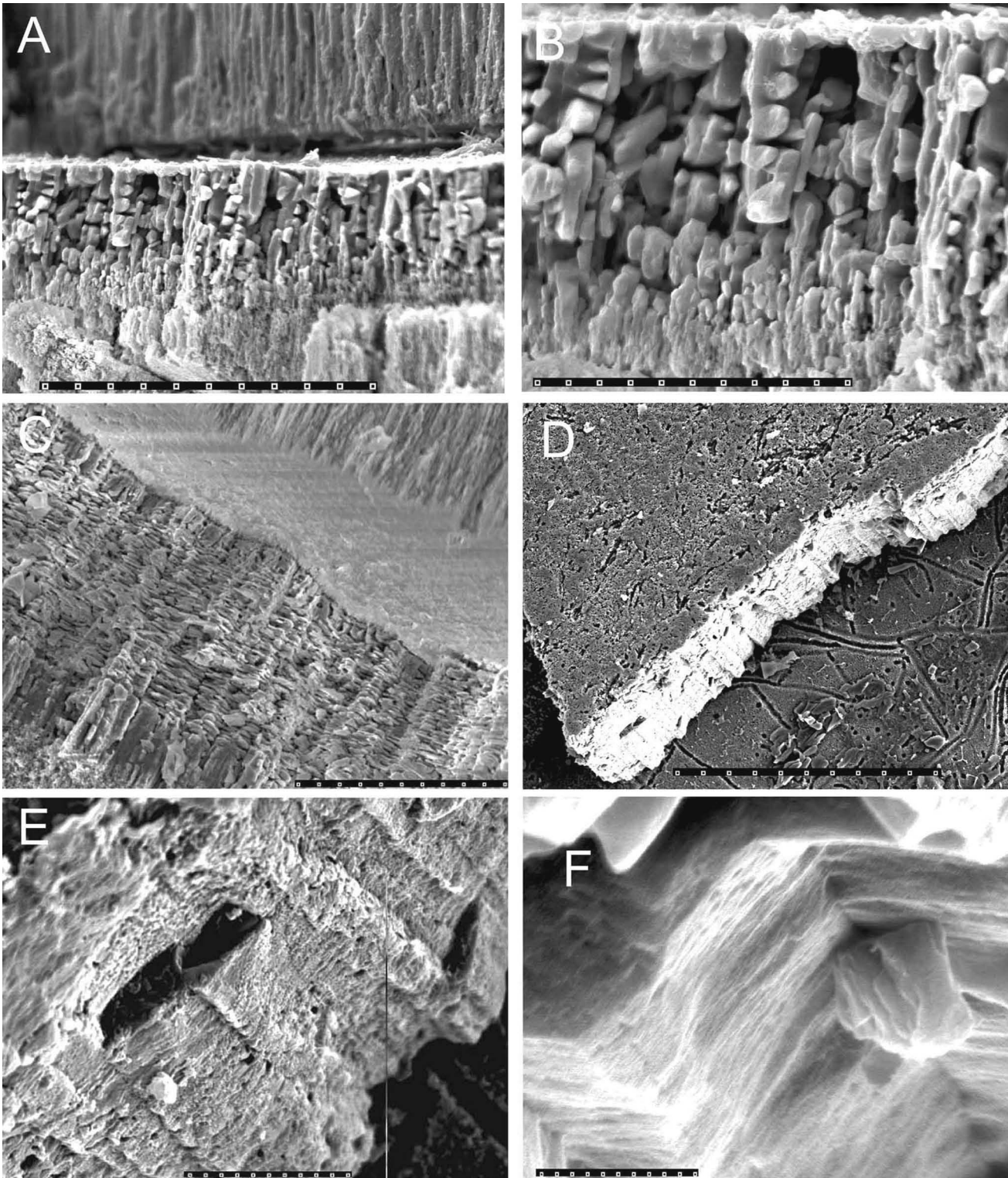


Plate 4. A–F. Close up of 3E to show a distinct contact between the pro-ostracum and the rostrum (top); scale bar is 30  $\mu\text{m}$ . B. Enlarged detail of A: the pro-ostracum is formed by vertical elements of varying shape with regular horizontal incisions, the inner portion of the pro-ostracum is comparatively more compact; scale bar is 12  $\mu\text{m}$ . C. Middle part of the shell showing (from the top right corner to the bottom left corner): a prismatic rostrum with an exposed whitish plane of the basal part, a pro-ostracum (a thin layer below the whitish layer) and two layers of the conotheca: a nacreous and an inner prismatic one; the outer prismatic layer is missing; the inner prismatic layer is about twice as thick as the pro-ostracum; scale bar is 30  $\mu\text{m}$ . D. A fragment of the pro-ostracum at a late ontogenetic stage; scale bar is 60  $\mu\text{m}$ . E. Enlarged detail of D to show columnar units of the pro-ostracum; scale bar is 6  $\mu\text{m}$ . F. Enlarged detail of E to show the micro-laminae of the columnar units probably indicating its initially organic composition; scale bar is 1.2  $\mu\text{m}$ .

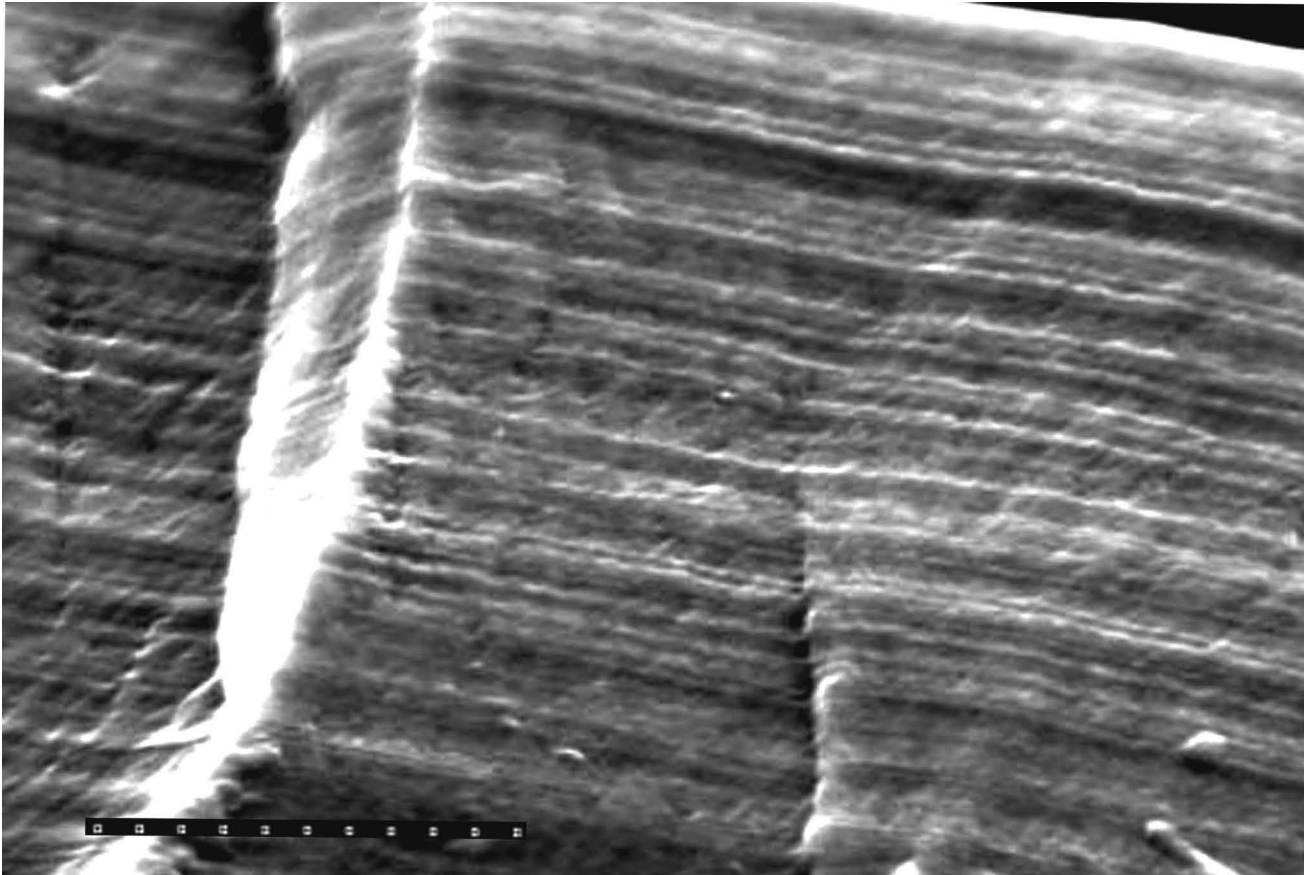


Plate 5. Micro-lamination of a chitinous gladius in a living squid *Berryteuthis magister*; scale bar is 12  $\mu\text{m}$ .