

AN UNIQUE UPPER TRIASSIC COLEOID FROM THE AUSTRIAN ALPS REVEALS PRO-OSTRACUM AND MANDIBULE ULTRASTRUCTURE

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Abstract: A recently discovered Late Triassic (Lower Carnian) coleoid (Doguzhaeva & al., 2005a) from the Austrian Alps (locality Schindelberg, Lunz, Niederösterreich) is described as *Lunzoteuthis schindelbergensis* n. gen. et sp. The remnants of the small-sized coleoid comprise (1) a fragmentarily preserved, breviconic phragmocone compressed by compaction (about 10 mm broad and 5 mm long; estimated apical angle ca. 15–20°), (2) a proostracum that is discernible by the growth lines on the dorsal side of the phragmocone, and (3) a lower mandible that is relatively large, broad (about 4 mm long), black and glassy. The rostrum is absent.

The proostracum in *L. schindelbergensis* is similar to that in Early Jurassic *Belemnotheutis* but differs by its narrow central field, bordered by hyperbolar zones, from the tripartite proostracum of the contemporaneous *Phragmoteuthis*, Middle Triassic *Breviconoteuthis* and Upper Permian *Permoteuthis*. Contrary to *Belemnotheutis*, it has no rostrum. The lower mandible in *L. schindelbergensis* is similar to that in recent squids and bears no resemblance to the structure described as mandibles in *Phragmoteuthis* (Mojsisovics, 1882).

SEM examination shows that the proostracum material in *L. schindelbergensis* is finely laminated, making it similar to (1) the chitinous gladii in modern squids *Loligo* and *Beryteuthis* here studied, (2) the fossil gladii of several squid-like coleoids (Doguzhaeva & Mutvei, 2003; 2005, 2006 herein) and (3) the proostracum of *Belemnotheutis* (Doguzhaeva et al., 2005b; 2006b herein). The proostracum in *L. schindelbergensis* has neither prismatic nor nacreous layers and therefore is not considered to be a projection of the phragmocone wall (conotheca). It is built up of two layers: (1) the inner layer of vertical columnar units formed by micro-lamellae (“organic lamello-columnar” ultrastructure), (2) the outer layer of micro-plates that have a wedge-like shape and are arranged more or less parallel to the surface. The new data supports the concept that the proostracum is an innovative morphological element in coleoid evolution (Doguzhaeva, 2002; Doguzhaeva et al., 2002a, b, 2003a, b, 2005a, b; 2006b herein).

The presumable lower mandible of *L. schindelbergensis* is characterized by broad wings and a distinct beak (= rostrum) that has a thickened anterior edge. The wings are formed by inner and outer laminae fused near the rostrum. The length ratio of the two laminae is unclear because the posterior portion of the mandible was destroyed during preparation. The mandible has a micro-laminated ultrastructure similar to that of chitinous mandibles in *Loligo* and in the contemporaneous ceratitid *Austrotrachyceras* from the same locality (Doguzhaeva et al., 2007a in press). In: *L. schindelbergensis* the mandible must therefore have been originally chitinous.

The initial shell ontogeny in *Lunzoteuthis* n. gen. remains unknown, and the systematic position of the new genus is uncertain. In the gross morphology of the phragmocone and proostracum it is comparable with *Belemnotheutis* but is distinguished by having no rostrum. It is temporarily referred to the Suborder Belemnoteuthidina Stolley.

Key words: Late Triassic coleoid, shell morphology and ultrastructure, pro-ostracum, mandibles evolutionary morphology, Austria

INTRODUCTION

Starting from the Early Jurassic, ca. 135 MY ago, belemnites were widespread all over the world. All were characterized by a proostracum, an important component of the soft body/skeleton architecture. However, the record of the pre-Jurassic proostracum-bearing coleoids is restricted to a few taxa; since most of these were represented by only one or two available specimens, the pre-Jurassic “history” of the proostracum remains obscure. Among Triassic coleoid cephalopods, the

proostracum has been observed in *Phragmoteuthis* (Bronn, 1859; Suess, 1865; Mojsisovics, 1882) and *Breviconoteuthis* (Rieber, 1974). The Upper Triassic *Phragmoteuthis bisinuata* BRONN from the black fish shales of Raibl in Carinthia (formerly in the Austro-Hungarian Empire, now: Cave del Predil in Italy) is well illustrated and represented by about 100 specimens stored at the Museum of Natural History and Austrian Geological Survey in Vienna. The broad (ca. 3/4 of the circumference of the phragmocone) tripartite proostracum of the above two genera differs essentially from that of Jurassic-

Cretaceous Belemnoida, which is tongue-like and flanked by hyperbolic zones. The proostracum of the “*Phragmotheuthis*” type has been considered as a “morphological bridge” between the bactritoids, which have a long body chamber with a deep ventral sinus in some taxa (*Pseudobactrites bicarinatus* Ferrière), and the belemnoids, which lack a body chamber but have a proostracum. The proostracum is generally interpreted as a dorsal remnant of the body chamber wall in the precursors (see Naef, 1922; Jeletzky, 1966; Donovan, 1977). This interpretation remains convincing and valid, although it has not been reevaluated taking into account new data obtained since its introduction. Recently, the conotheca and proostracum were found to differ essentially at the ultrastructural level (Doguzhaeva, 2002; Doguzhaeva et al., 2002a, b; 2003a, b; 2005a, b; 2006b herein). If, however, the proostracum is a remnant of the body chamber wall, then the proostracum and conotheca should be similar ultrastructurally. This inconsistency calls for additional data to help elucidate the evolutionary transformation of an external skeleton into an internal one in cephalopod evolution.

The present paper deals with a recently reported, unique Upper Triassic coleoid from the Austrian Alps (Doguzhaeva et al., 2005a). It shows a rarely observed combination of a shell and a mandible preserved in one and the same fossil (Pl. 1 A–C; Pl. 2). Moreover, the shell surface is well preserved and bears growth lines indicating the presence of a proostracum. This study provides new morphological data that helps to elucidate the evolutionary morphology of the coleoid skeleton. Apart from the shell, the mandible in extinct coleoids is itself a rare and important fossil. In the present case, the mandible material, which was originally organic, is of special interest for ultrastructural comparison with the material of the proostracum in the same specimen.

The paper contains (1) a systematic description of the Upper Triassic coleoid, and (2) comparisons between the ultrastructure of the proostracum and mandible in this coleoid and the gladii and mandibles of the living squids *Berryteuthis* Berry and *Loligo* Lamarck, and (3) a discussion on the evolutionary morphology of the proostracum.

MATERIAL, LOCALITY, STATUS OF PRESERVATION AND METHOD

The studied material comprises: (1) a single shell and a mandible of the Late Triassic coleoid from the Lower Carnian – *Austriacum* Zone at Lunz (locality Schindelberg), Lower Austria and (2) five gladii and mandibles of the Recent squids *Berryteuthis* and *Loligo*.

The fossil specimen (Pl. 1–7) was found in the old collections of the ceratitid *Austrotrachyceras*. More than 100 years ago, the material was excavated with the permission of Mr. Habermayer, the director of the coal mine at Lunz, in 1885 for the Geological Survey of Austria and in 1902 for the Museum of Natural History in Vienna. The sites are now inaccessible for collecting. The remains of this coleoid, comprising a tiny shell and a mandible, were buried near a comparatively large (ca. 50 mm diameter) shell of *Austrotrachyceras*. The larger ammonoid shell possibly hindered the post-mortem disintegration of the shell and mandible of this small-sized coleoid. The exceptional preservation of

the shell material in *Austrotrachyceras* from this locality has already been elucidated (Doguzhaeva et al., 2004). All the ammonoid shells here are crushed by compaction, with the left and right body chamber walls more or less in contact with each other. Nevertheless, the pieces of the shells remain together in a fractured mosaic pattern. At the Schindelberg locality the mandibles are known to be associated with the ammonoid specimens and located in front of or partly within the body chamber (Trauth, 1935; Krystyn, 1991; Doguzhaeva et al., 2004, 2007a in press). Shiny, black, asphalt-like material is located between the body chamber shell walls in places. The ultrastructural and energy dispersive analyses of this black material revealed that it represented bituminous soft body tissues (Doguzhaeva et al., 2004). The low-oxygen, near-bottom depositional environment of the shales helped preserve the originally non-mineralised organic material (Griffin, 1977).

The studied Carnian coleoid is crushed by dorso-ventral compaction. The shell deformation is similar to that of the recently studied Jurassic specimens of *Belemnotheuthis* (Doguzhaeva et al., 2005b). In both, the longitudinal and transverse (along the mural rings) fractures exhibit a mosaic pattern formed by rectangular fragments. The proostracum is discernible by the typical growth lines of its central field and by the longitudinal ribs on its hyperbolic zones. The mode of preservation and dislocation of the shell and mandible (dorso-ventral compression of the shell, mandible positioned immediately in front of the anterior edge of the phragmocone) indicates that the mandible must have been buried and protected by the proostracum before it was partially destroyed, and that these two structures apparently belonged to the same individual. The shell/mandible size ratio points to a relatively large jaw apparatus. In modern squids the ratio between the length of the body and buccal apparatus is approximately 1/10 (Morton & Nixon, 1987; Tanabe et al., 2006).

The ultrastructure of gladii and mandibles of the modern squids *Berryteuthis* and *Loligo* was studied after one-year drying.

The specimens were examined without etching with a scanning electron microscope Hitachi 4300 at the Swedish Museum of Natural History, Stockholm, Sweden.

The fossil specimen is deposited in the Museum of Natural History, Vienna, Austria, under the inventory number NHMW 2005z0005/1.

PRO-OSTRACUM MORPHOLOGY AND ULTRASTRUCTURE (FIGS. 1; 3–7)

The proostracum is about 3 mm wide, which is approximately 1/6–1/7 of the estimated shell circumference (Pl. 1, A). It has a narrow central field with narrowly rounded growth lines, and hyperbolic zones with longitudinally converging ribs but no asymptotes (Pl. 1, A–C). In the adoral part of the central field, the growth lines form an acute angle of ca. 60–80°. The narrow growth lines are of two orders: about 5 broad and 30 narrow lines. The proostracum covers five or six camerae of the phragmocone; the camerae are about 0.8 mm long.

The proostracum is ca. 50 µm thick. It consists of the two layers of about the same thickness (Pl. 3, A, B). The inner

layer is composed of vertical columnar units about 4–5 μm in diameter (Pl. 4, A–B; Pl. 5, A–B). The columns are separated by interspaces and composed of ca. 0.05 μm -thick micro-laminae (Pl. 5, A–B). In surface view the distal end of each column has an irregular polygonal shape. The outer layer consists of horizontally arranged micro-plates that are ca. 0.2–0.3 μm thick (Pl. 4, A; Pl. 5, A). They were probably originally organic, as were the lamellae in the chitinous mandible of living coleoids (Pl. 8, A–B). Thus, the proostracum ultrastructure is unique and bears no resemblance to either the prismatic or nacreous layers of the phragmocone wall.

MORPHOLOGY AND ULTRASTRUCTURE OF THE LOWER MANDIBLE (FIGS. 2, 7)

Judging from its broad, spoon-like shape, the preserved mandible is the lower mandible (Pl. 2; Pl. 7, A). In modern coleoids the lower mandible is usually broader than the upper one (Clarke, 1962; Hernández-García, 2003). The mandible consists of broad wings, a flattened crest (the bottom of the mandible) and a beak (= rostrum), the latter having a thickened anterior edge (Pl. 7, A–B). The wings are formed by inner and outer laminae fused near the beak. The length ratio of the two laminae is unclear because the posterior portion of the mandible was destroyed during preparation. The mandible has a micro-laminated ultrastructure (Pl. 7, C), being in this respect similar to the chitinous mandibles in *Loligo* (Pl. 8, A–B) and in the contemporaneous ceratitid *Austrotrachyceras* from the same locality (Doguzhaeva et al., 2007a in press).

The beak (= rostrum) is fractured in a “step-like” pattern (Fig. 7, C), similar to the fractioned chitinous mandibles and gladii in the living squids *Berryteuthis* and *Loligo* (Pl. 8, A–B). Similar fracture patterns have also been observed in broken gladii of fossil squid-like coleoids (Doguzhaeva & Mutvei, 2003; Pl. II, Fig. 1a; Pl. III, Fig. 1a). In modern squids this pattern is determined by a “glassy” ultrastructure of the chitin material both in the mandibles and gladii (Pl. 8, A–B). Based on this ultrastructural similarity, the fossil mandibles are considered to have been originally composed of chitin.

SYSTEMATIC PALAEOLOGY

Class Cephalopoda CUVIER, 1794

Subclass Coleoidea BATHER, 1888

Ordinal status uncertain

? Suborder Belemnoteuthididina STOLLEY, 1919

? Family

Genus *Lunzoteuthis* n. gen.

Type-species: *Lunzoteuthis schindelberensis* n. sp.

Derivation of name: From the town of Lunz (Lower Austria), close to where the specimen was found.

Diagnosis: Small-sized breviconic phragmocone with apical angle ca. 15°–20°, short camerae with broad (ca. 1/3 of camera length) mural parts of septa. Proostracum shorter than phragmocone; with narrow central field (ca. 1/6 of phragmocone circumference) and hyperbolar zones; no asymptotes;

curvature of growth lines in central field ca. 70–80°; hyperbolar zones with thin longitudinal converging ribs; angle between them and median line of proostracum about 40°. No rostrum. Lower mandible with broad wings and a distinct beak (= rostrum).

Notes: The genus is erected based on a tiny fragment of a single, small-sized shell and mandibles positioned in front of the anterior edge of the shell (Pl. 1, A–B; Pl. 2; Pl. 7, A). The apical portion of the shell is unknown. Based upon the solid mandible the specimen might have belonged to a small-sized mature individual. In living squids the juveniles have a solid beak (= rostrum) but the hood is softer (Hernández-García, 2003).

Discussion. The systematic position of the new genus is unclear. The gross morphology of the phragmocone and proostracum may allow a placement of the genus within the Suborder Belemnoteuthididina. However, the apical portion of the shell is unknown and whether it had a rostrum, like in *Belemnoteuthis*, is uncertain. Should this coleoid have no rostrum at early ontogenetic stages, it should be placed in a new suborder.

Geographical range: locality Schindelberg, Lunz, Lower Austria.

Stratigraphical range: Lower Carnian, *Austriacum* Zone, Upper Triassic.

Lunzoteuthis schindelbergensis n. sp.

(Figs. 1A–C; 2)

Holotype: NHMW 2005z0005/1 is an incompletely preserved, small-sized (about 10 mm broad and 5 mm long), breviconic phragmocone, compressed by compaction, with exposed dorso-lateral surface and a black, organic, lower mandible located near an anterior edge of the shell.

Derivation of name: From the name of the locality Schindelberg.

Type locality: Schindelberg, Lunz, Lower Austria, Northern Calcareous Alps.

Stratum typicum: Lower Carnian, *Austriacum* Zone, Upper Triassic

Diagnosis: As for the genus.

Description: The remnants of the small-sized coleoid comprise (1) a fragmentarily preserved, breviconic phragmocone (about 10 mm wide and 5 mm long; estimated apical angle ca. 15–20°), compressed by compaction, (2) a proostracum that is discernible by the growth lines on the dorsal side of the phragmocone, and (3) a lower mandible that is relatively large, broad (about 4 mm long), black and glossy.

The shell wall is thin and, by compression, crushed into small rectangular pieces forming a mosaic pattern. The camerae are short and the mural parts of septa are broad; camerae with a length ratio ca. 3:1. The dorsal and lateral shell surfaces and a small piece of the inner surface on the ventral side are exposed (Pl. 1, A). The estimated shell diameter near the aperture is 5 mm. The total length of the phragmocone is estimated to be ca. 20 mm. The proostracum has a central field, typically ornamented by curved growth lines, and hyperbolar zones, ornamented by longitudinal, converging ribs. The asymptotes are not developed. The proostracum length is estimated approximately to be one half of the phragmocone length. The lower mandible is partly exposed and has a broad, flattened crest (bottom),

broad wings and a non-calcified beak (= rostrum). It consists of a black, anthracite-like, glossy material. The wings are formed by the inner and outer laminae. Because of imperfect preservation, the size and three-dimensional shape of the mandible are unknown. The maximum size of the preserved mandible fragment is equal to the maximum diameter of the phragmocone.

Geographical and stratigraphical range: as for the genus.

DISCUSSION

In Paleozoic coleoids the proostracum is known in the Late Permian *Permoteuthis groenlandica* Rosenkrantz and in the Late Carboniferous *Donovaniconus oklahomensis* Doguzhaeva, Mapes & Mutvei. In *P. groenlandica* the proostracum has only been observed in a single shell fragment (Rosenkrantz, 1946: p. 161, Fig. 6); according to Jeletzky (1966: p. 38), all other phragmocones referred to this taxon show no traces of proostraca and belong to the parabactritid genus *Tabantaloceras* Shimansky. The proostracum in *P. groenlandica* represents the long and broad, tripartite “*Phragmoteuthis*” type (see Jeletzky, 1966: p. 38). In *D. oklahomensis* the proostracum covers the entire shell but has a short, dorsal, lobe-like, broadly rounded anterior projection beyond the aperture with a length of approximately 1.5–2 camerae length. Its thickness is approximately 1/2–2/5 of the conotheca thickness. The proostracum is composed of a thin outer prismatic sublayer and a thick inner sublayer with an irregularly granular ultrastructure containing numerous empty spaces, probably originally filled by organic material. Transverse and longitudinal smooth ridges ornament the external and internal surfaces of the proostracum. On the dorsal external surface the transverse ridges are strongly curved adorally. They show no indications of the tripartite pattern (Doguzhaeva et al., 2002b: Fig. 2; 2003a: Fig. 2) and therefore the proostracum in *D. oklahomensis* cannot be referred to the “*Phragmoteuthis*” type.

In the Middle Triassic *Breviconoteuthis* (Rieber, 1974) and Late Triassic *Phragmoteuthis* (Bronn, 1858; Suess, 1865; Mojsisovics, 1882) the proostracum is long (exceeding the phragmocone length) and broad (3/4 of the phragmocone circumference), tripartite, without hyperbolar zones, and differs from the proostraca in all other coleoids with the exception of *Permoteuthis*.

Huxley (1864) and subsequent authors (Suess, 1865; Mojsisovics, 1882; Naef, 1922; Jeletzky, 1966; Donovan, 1977) emphasized the phylogenetic significance of the peculiar proostracum in *Phragmoteuthis*. Based on this characteristic, Mojsisovics 1882 erected the family Phragmoteuthidae that Jeletzky later ranked as an order Phragmoteuthida Jeletzky (in SWEET, 1964). The “*Phragmoteuthis*” type of a proostracum has been considered as a feature indicating the bactritoid/coleoid affinity (Jeletzky, 1966). This concept assumes that a gradual reduction of the ventral side of the body chamber in ancestral bactritoids resulted in the formation of the initially broad proostracum in early coleoids. The broad proostracum was believed to gradually narrow and create a “*Belemnite*” type of the proostracum. Naef (1922), however, believed that the earliest

coleoids had a narrow proostracum, although at that time the earliest known proostracum-bearing coleoid was *Phragmoteuthis* with broad proostracum.

In the Late Triassic *L. schindelbergensis* n. gen. et sp. the external dorsal surface of the phragmocone bears two kinds of ornament. The median part exhibits anteriorly curved growth lines and is therefore probably the central field of the proostracum. On each side of the central field there is a longitudinal zone with straight, longitudinal, anteriorly converged lines. The latter zones are considered to be the hyperbolar zones of the proostracum. The genus lacks asymptotes that, in the “*Belemnite*” proostracum type, lie between the central field and the hyperbolar zones. Judging of the Early Jurassic juvenile belemnites in which the proostracum was observed in the first camera of the phragmocone (Doguzhaeva et al., 2002c: p. 42, Figs. 1, 4; 2003b: p. 81, Figs. 1–3), the asymptotes are present throughout the ontogeny in the “*Belemnite*” type. This leads to a conclusion that the proostracum of *L. schindelbergensis* cannot be referred to the “*Belemnite*” type. Nevertheless, it shows certain elements of differentiation (central field and hyperbolar zones) of the “*Belemnite*” type. The proostracum morphology clearly demonstrates that *L. schindelbergensis* is not a juvenile or adolescent individual of the contemporaneous *Phragmoteuthis*.

The proostracum of *L. schindelbergensis* yields new ultrastructural data for the discussion on the origin and transformation of the shell in coleoid cephalopods. The proostracum lacks the nacreous and prismatic layers that are typical for the aragonitic conotheca but possesses a fine lamination that characterizes organic substances such as chitin. The micro-lamellae are arranged in vertical columns in the inner layer and in micro-plates in the outer layer. The thickness of the micro-lamellae corresponds to that of the micro-lamellae forming the chitinous gladii in living squids. Similar micro-lamellae are observed in the proostracum of the Early Jurassic *Belemnotheutis* (Doguzhaeva et al., 2005b, 200Xb, herein). Thus, the proostracum in the specimen studied was originally mainly composed of an organic material. This provides additional proof for the concept (Doguzhaeva, 2002; Doguzhaeva et al., 2002a, 2003a, b; 2005a, b, 2006b herein) that the proostracum originated as an innovative morphological structure in coleoid evolution rather than as a derivate of the conotheca in the precursors.

Mandibles of extinct coleoids are rare, especially in association with a shell or gladius. Mojsisovics (1882) described the mandibles in the contemporaneous *Phragmoteuthis bisinuata*. Accordingly, the mandibles commonly lie in front of the proostracum at a distance of about 1/2 – 3/4 the proostracum length (Mojsisovics, 1882: Taf. XCIV, Figs. 1, 4a, 5, 6). They are glossy, black and small, and consist of two symmetrical branches with two upwards pointed, tubercular processes. The tentacles with double rows of hooks are linked up to the mandibles. According to the illustrations the mandibles are partly exposed from the shale and their real shape can hardly be reconstructed based on the illustrations. They appear to differ essentially from the mandibles in living coleoids.

In Late Jurassic *Trachyteuthis hastiformis* Rüppell the lower and upper mandibles were found in association with a gladius, being still articulated in one of the two specimens

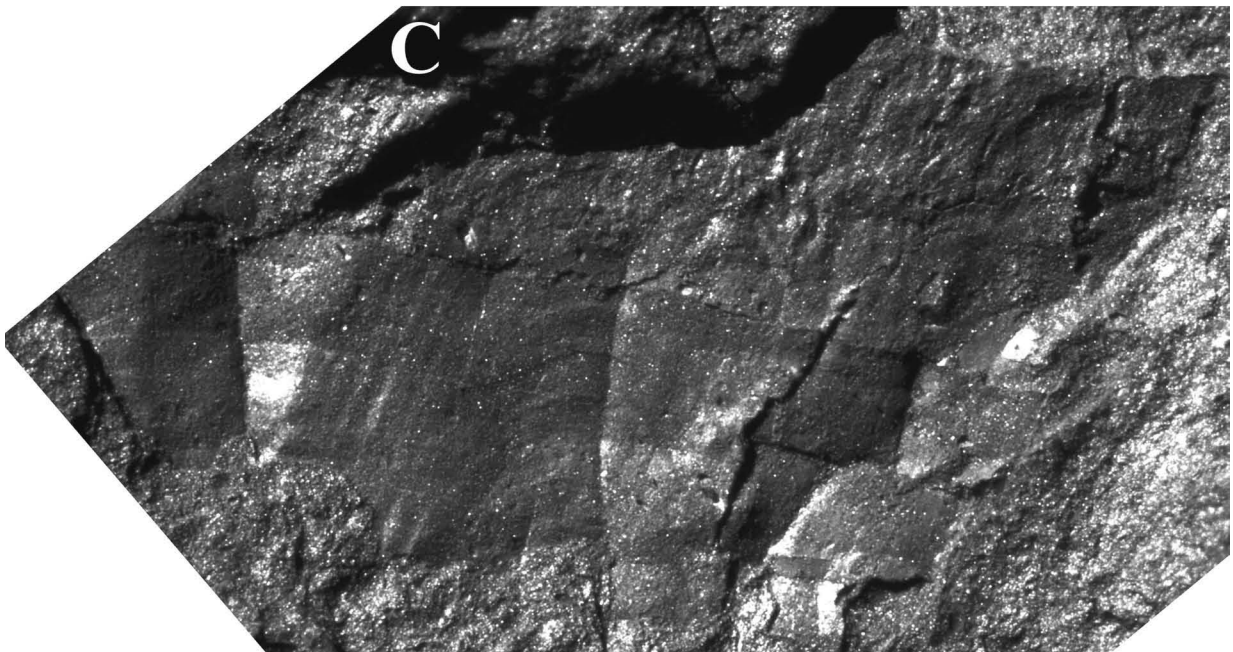
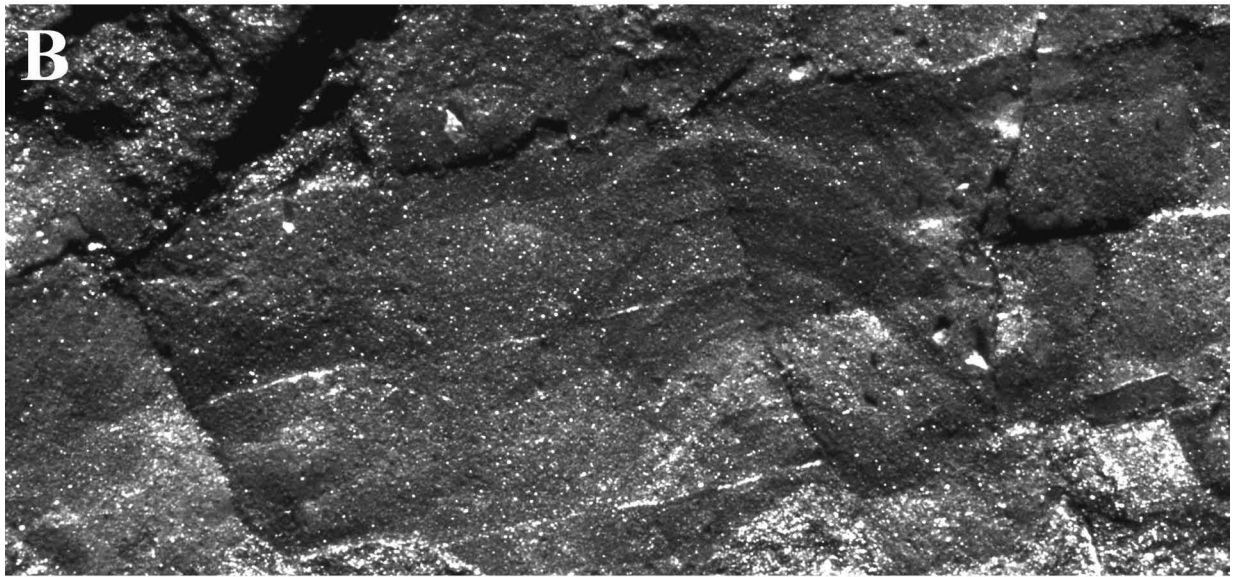
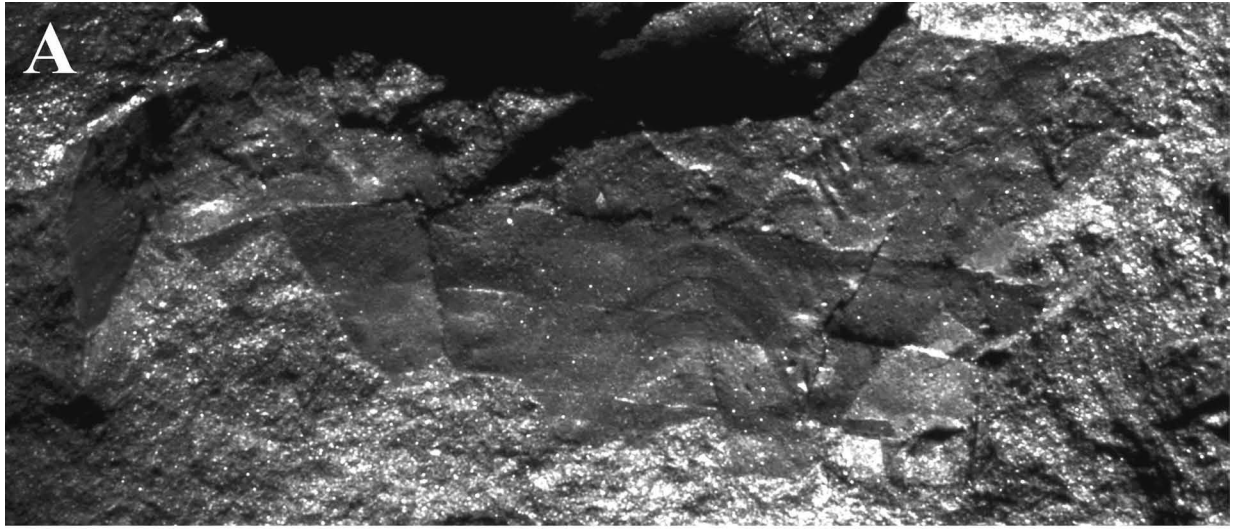
(Klug et al., 2004). The mandibles lie a short distance in front of the anterior edge of the gladius. In having a short hood (the outer lamina) and a long crest (the inner lamina), the reconstructed lower mandible of *T. hastiformis* is similar to that of modern *Octopus* but different from that in *Vampyrotheuthis infernalis* Chun (Klug et al., 2004: Fig. 1A, B, C, E).

The lower mandible of *L. schindelbergensis* n. gen. et sp. consists of black shiny “glassy” material. The mandible is characterized by the broad wings and distinct beak (= rostrum). The wings are formed by the inner and outer lamellae fused near the rostrum. The length ratio of the two laminae is unknown because the posterior portion of the mandible is damaged. The mandible has a micro-laminated ultrastructure similar to that of the chitinous mandibles of *Loligo* (Pl. 8, A–B) and of the contemporaneous ceratitid *Austrotrachyceras* from the same locality (Doguzhaeva et al., 2007a in press). In *L. schindelbergensis* the mandible must have been originally chitinous.

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Plates 1–7 – *Lunzoteuthis schindelbergensis* n. gen. et sp.; NHMW 2005z0005/0001; Lower Carnian, U. Triassic; Lower Austria

Plate 1. A–C. A. General view of the breviconic shell, strongly fractured by compression; $\times 15$. B. Closeup of A to show forwardly curved growth lines of the central field of the proostracum and three fracture lines along the septum/shell wall attachment; distances between the lines correspond to the camera length, $\times 40$. C. Closeup of A to show longitudinal ridges of the hyperbolar zone of the proostracum on the left side of the central field; two camerae of the phragmocone are visible, $\times 20$.

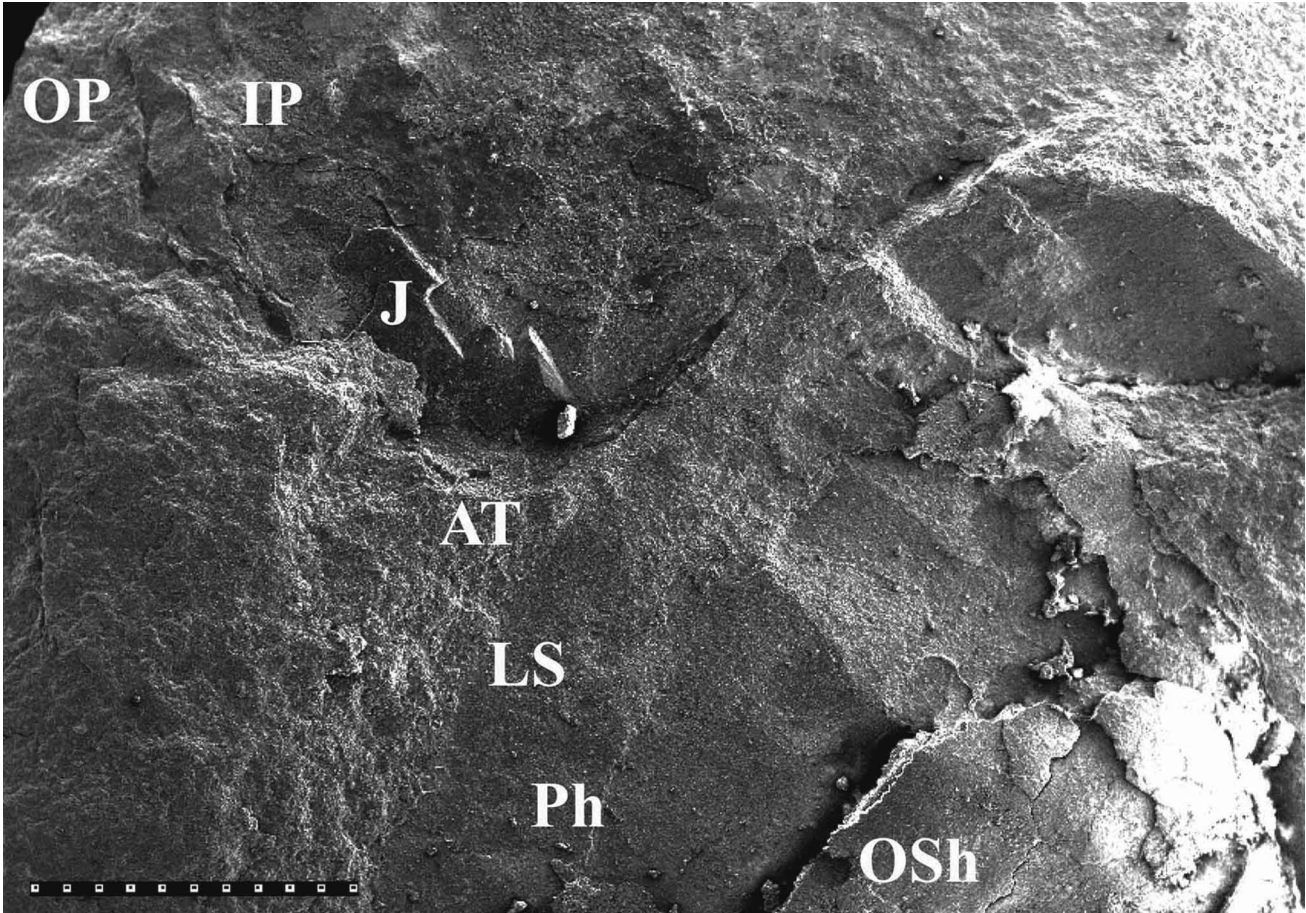


Plate 2. Lower mandible (anterior part) positioned in front of the anterior edge of the phragmocone: M – mandible; IP – inner plate; LS – last septum, OP – outer plate, OSh – outer shell surface, Ph – phragmocone; scale bar is 12 mm.

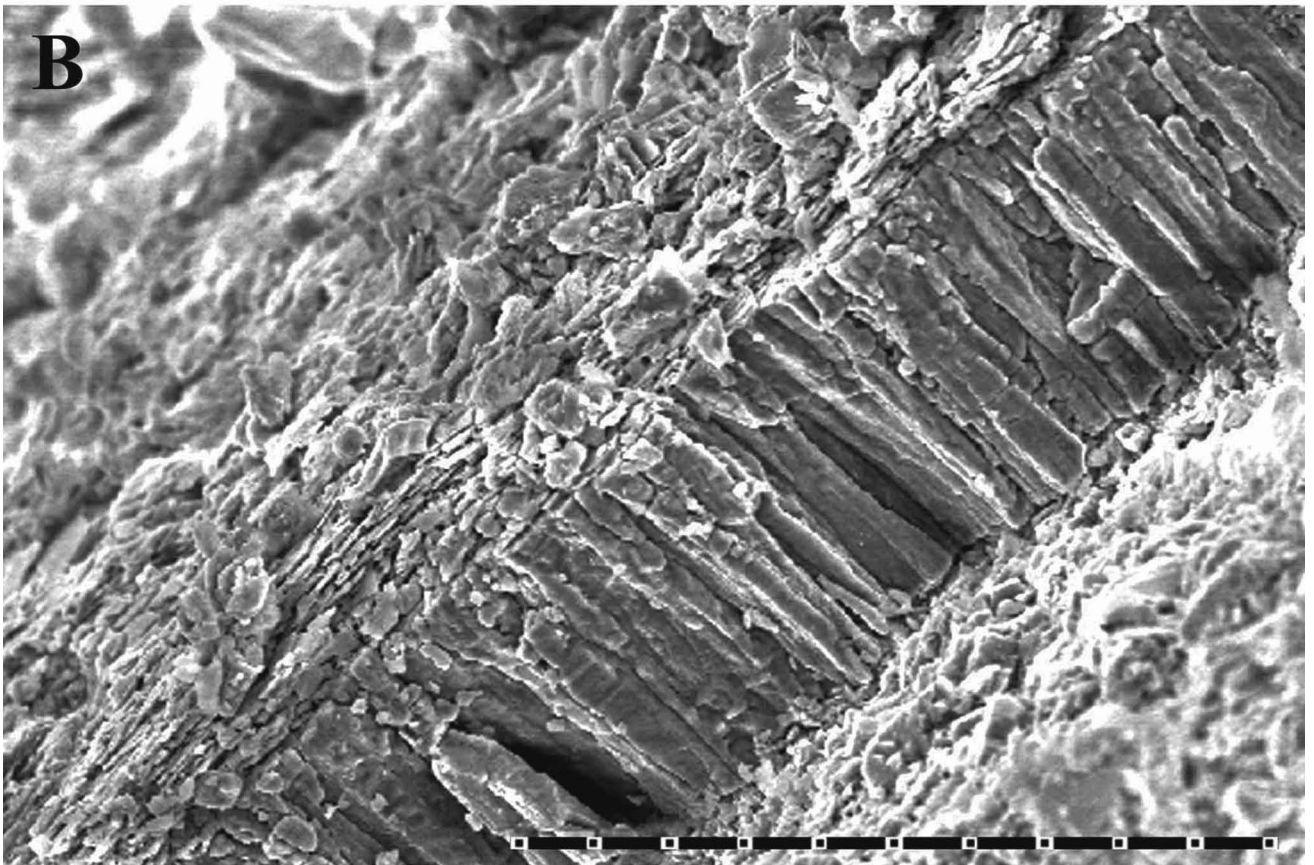
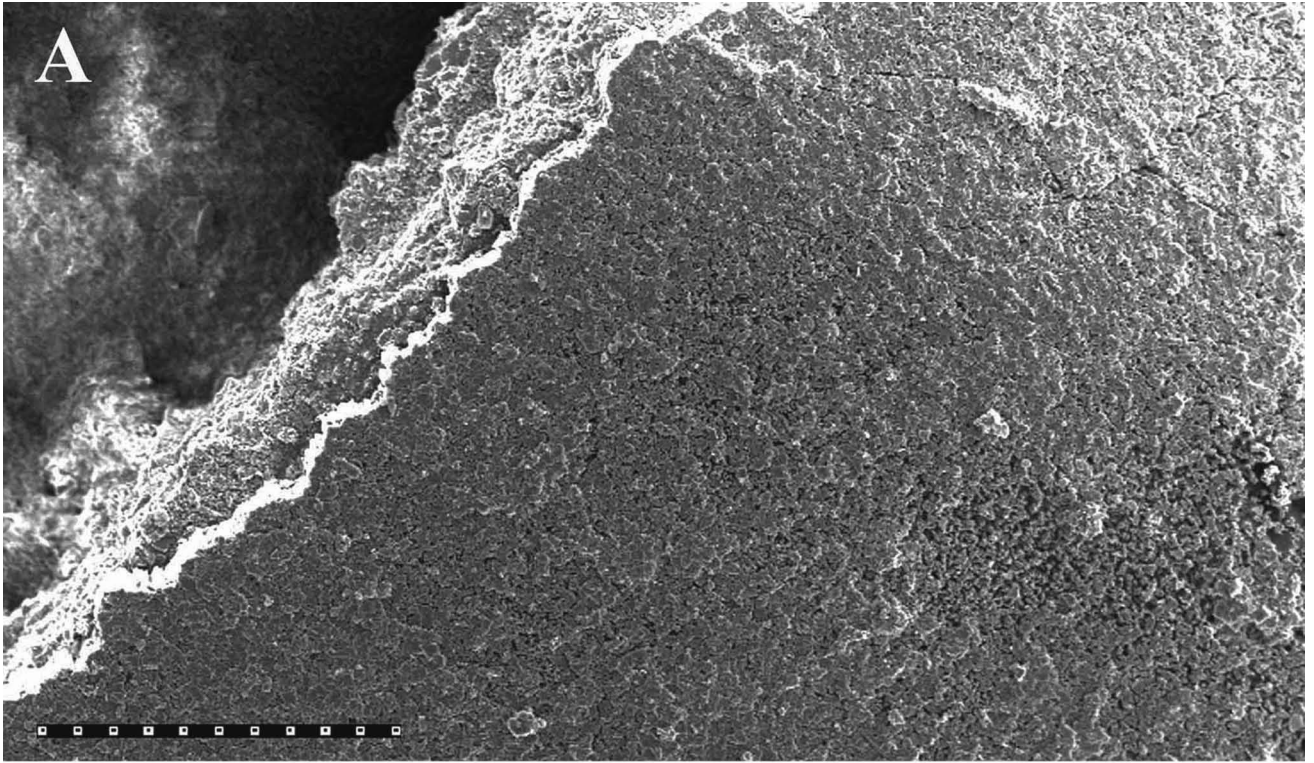


Plate 3. A–B. A. Porous outer surface of the proostracum (external surface, dorso-lateral side), scale bar is 150 μm ; B. Longitudinal fracture of the proostracum showing the two layers, scale bar is 6 μm .

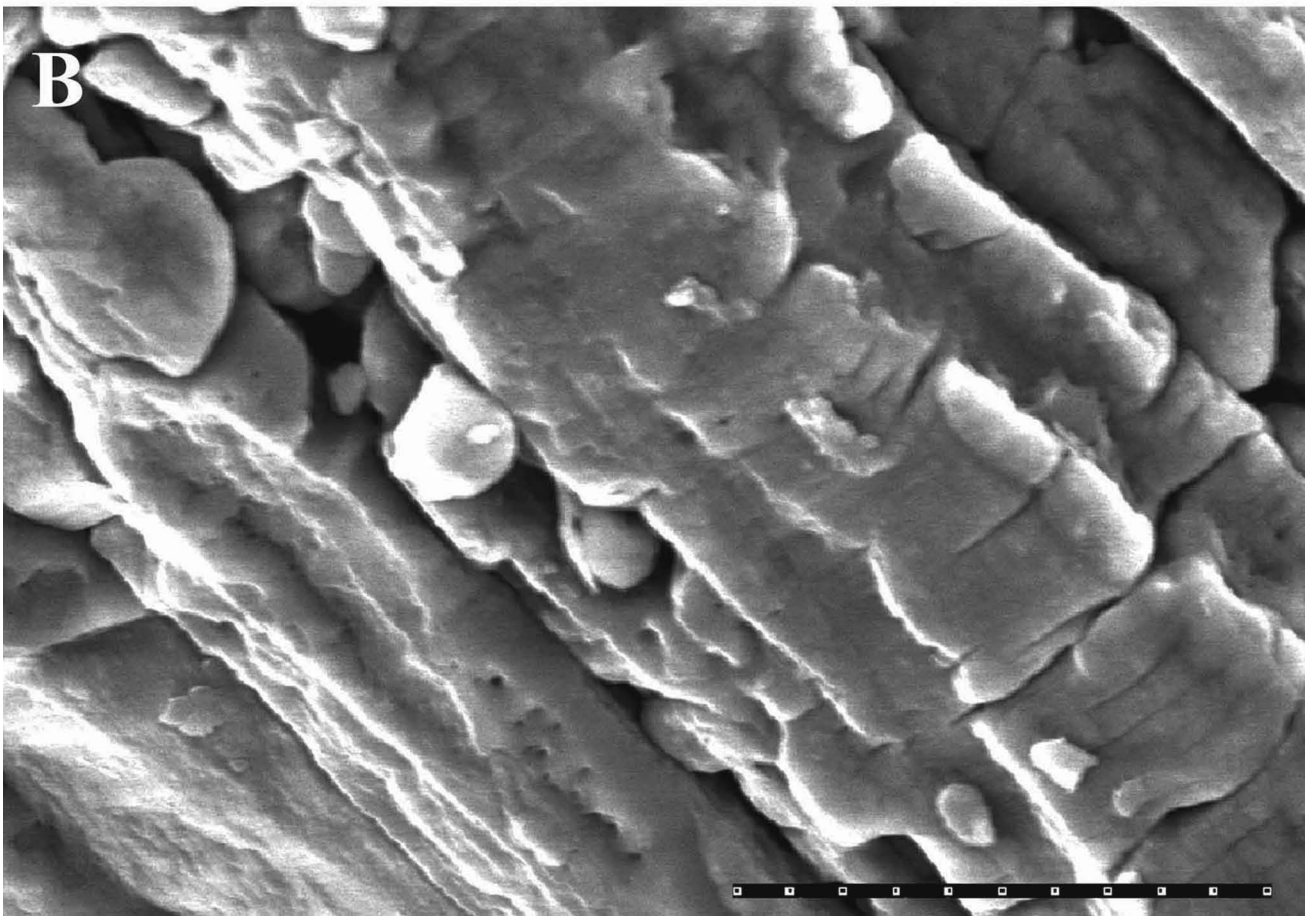
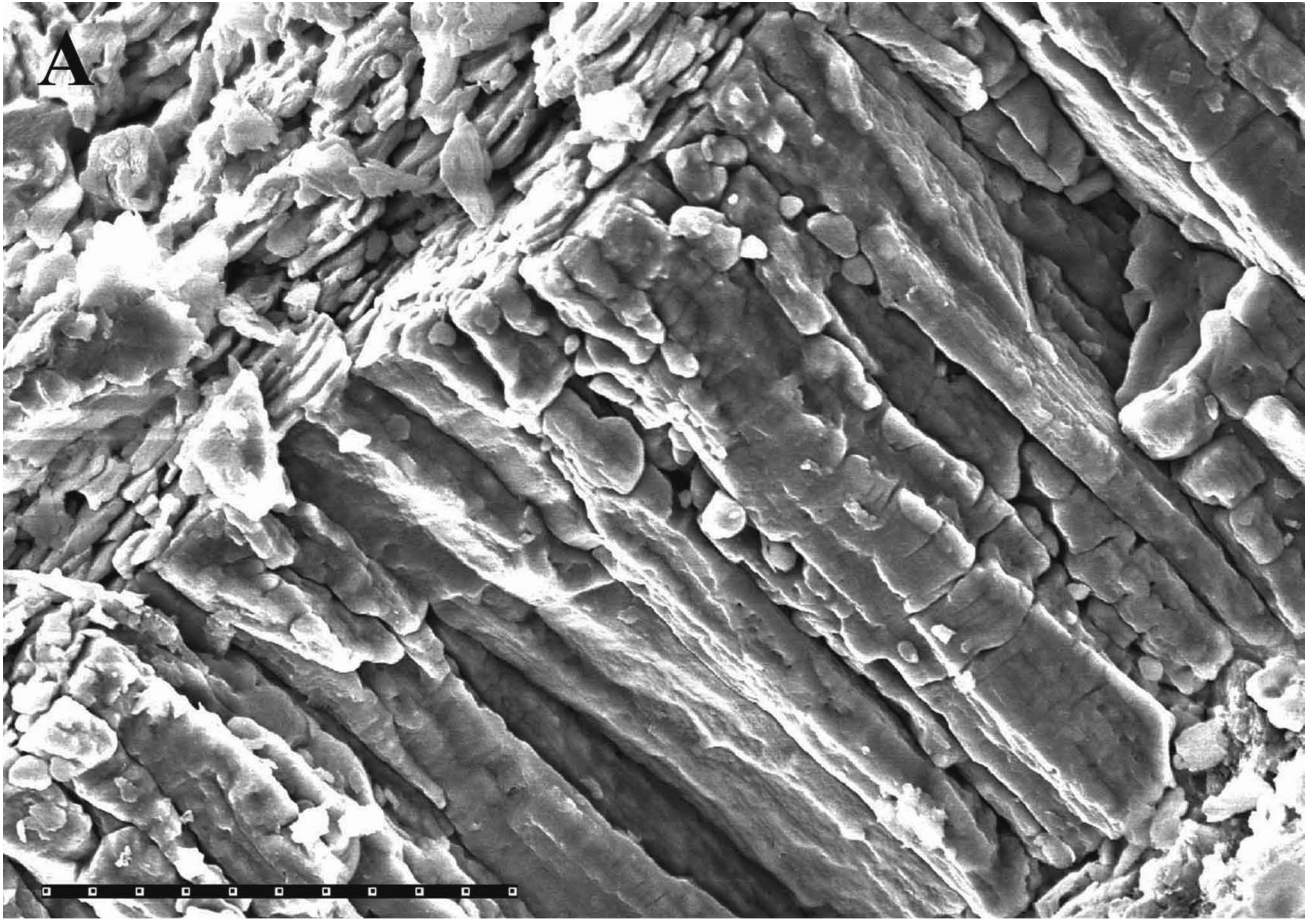


Plate 4. A–B. Closeup of 3B to show the micro-plate structure of the outer layer and the lamello-columnar structure of the inner layer of the proostracum, scale bar is 15 μm . B. Closeup of the columnar units of the inner layer showing horizontal micro-lamellation, scale bar is 6 μm .

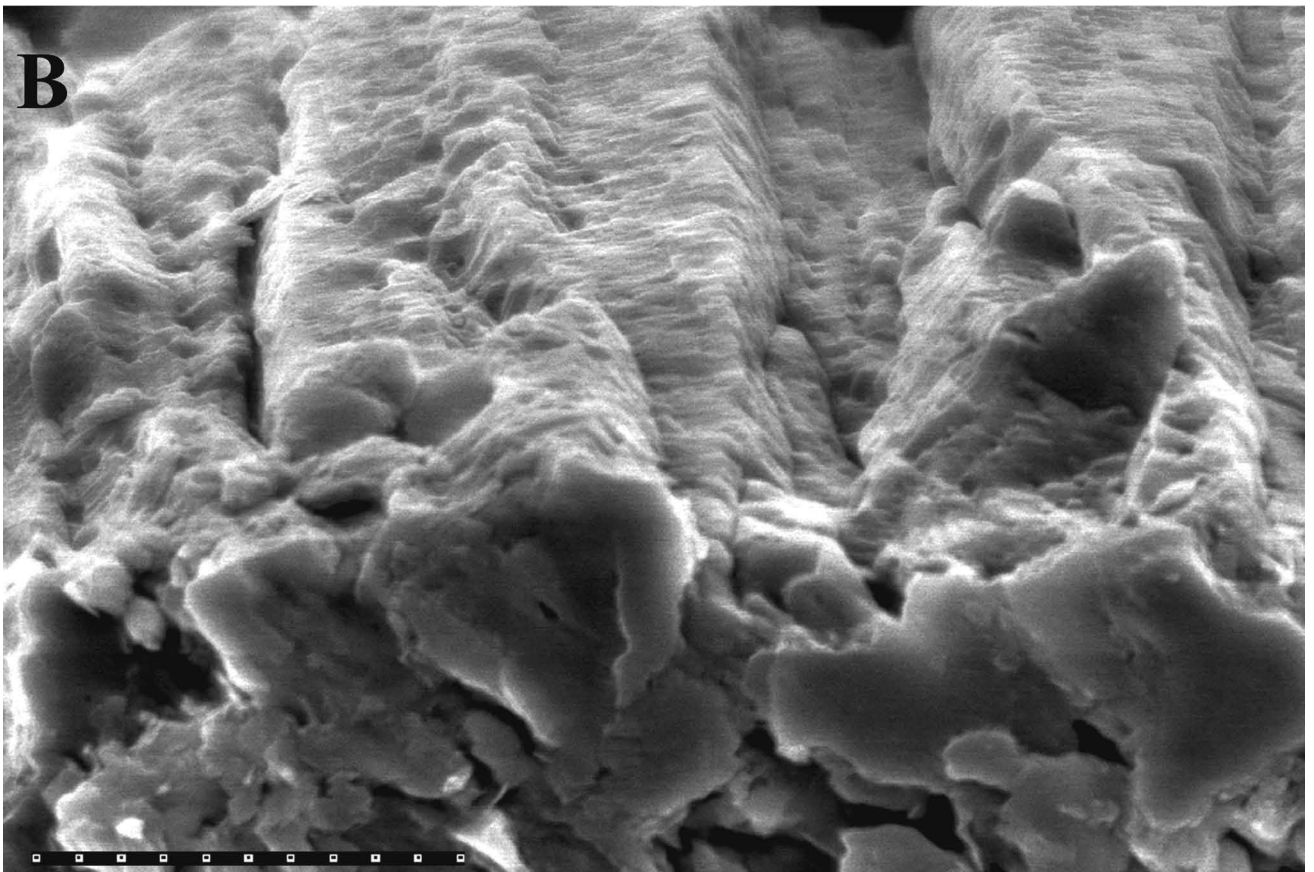
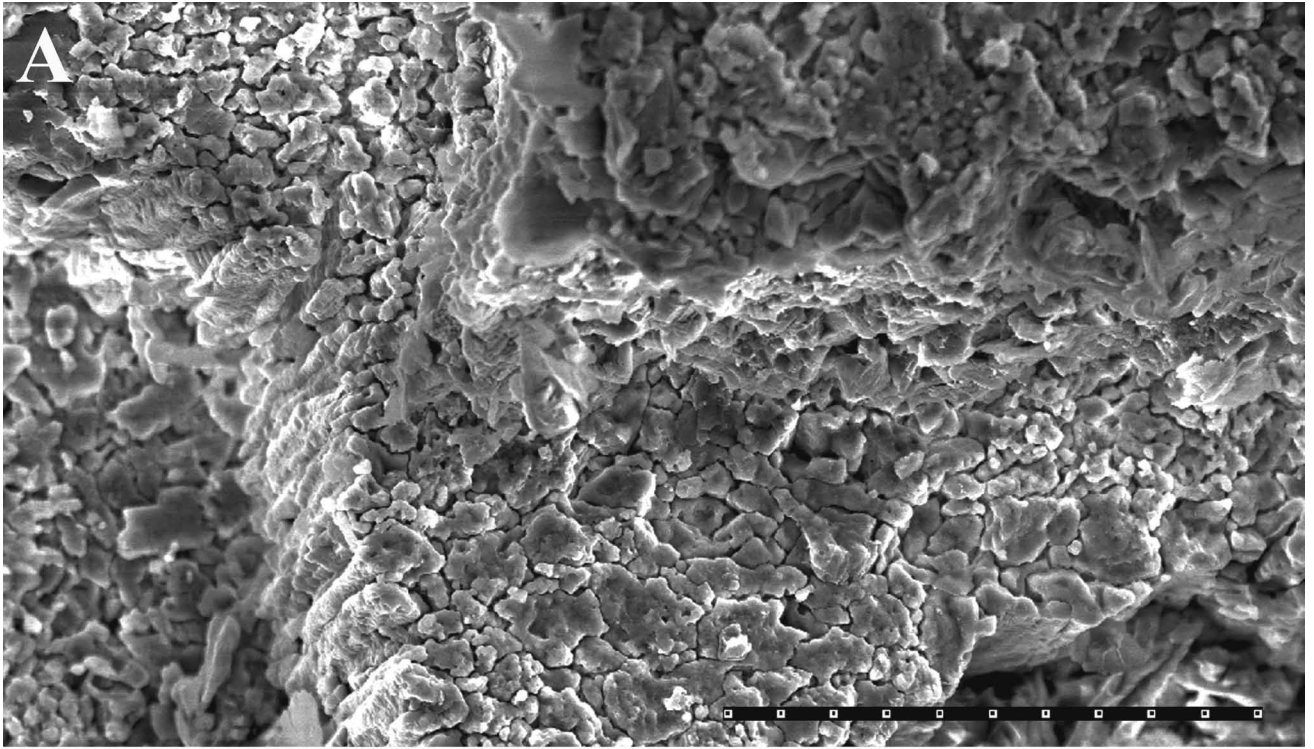


Plate 5. A–B. Surface view on the proostracum to show irregularly shaped end surfaces of the columnar units of the inner layer, scale bar is 30 μm ; B. Micro-lamination of the columnar units of the inner layer of the proostracum, scale bar is 6 μm .

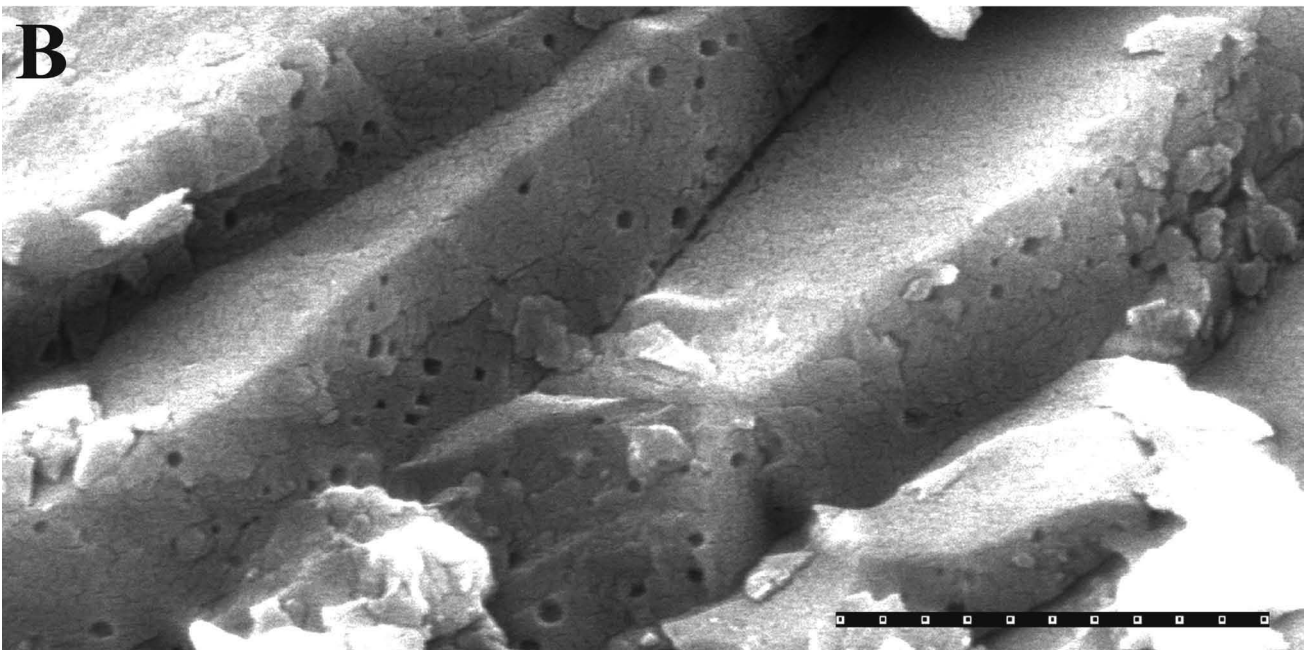
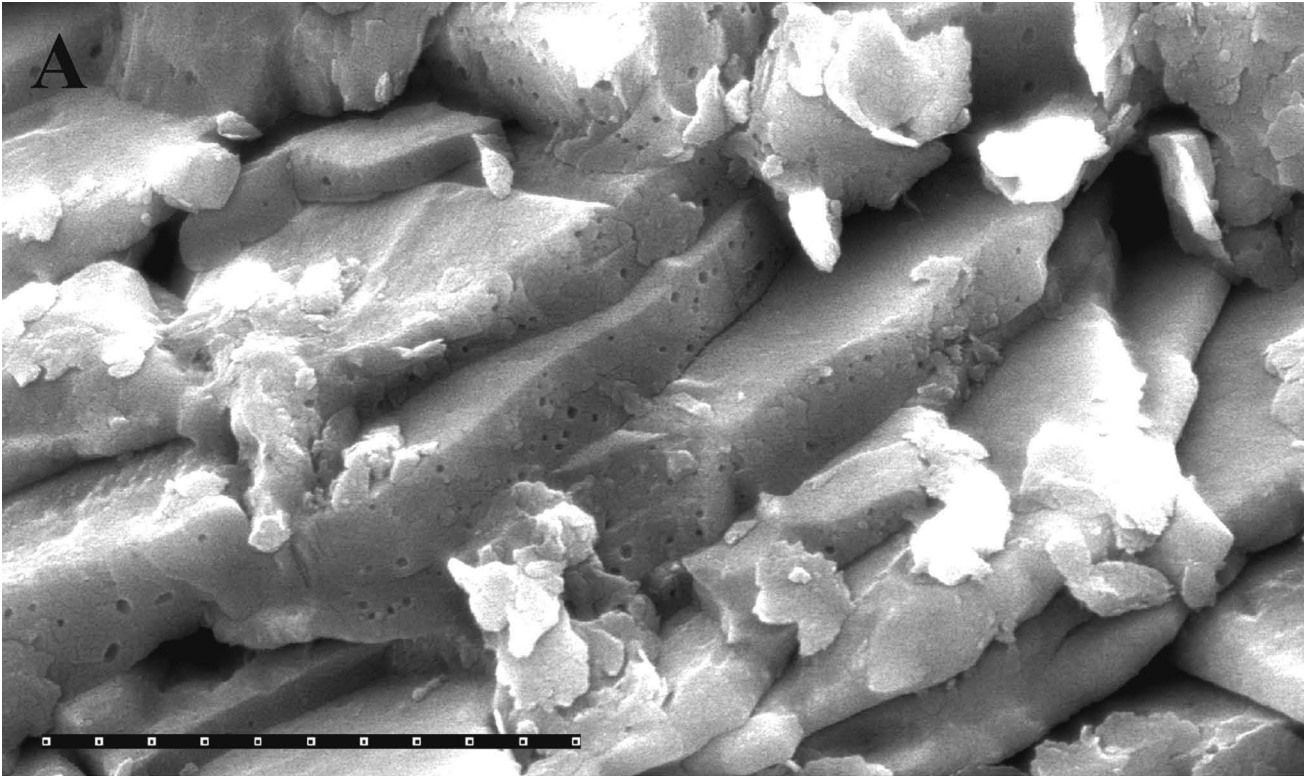


Plate 6. A–B. Vertical oblique fracture plane of the outer layer of the proostracum to show the micro-plates, scale bar is 3 μm; B. Closeup of A to show the wedge-like shape of the plates, scale bar is 1.2 μm.

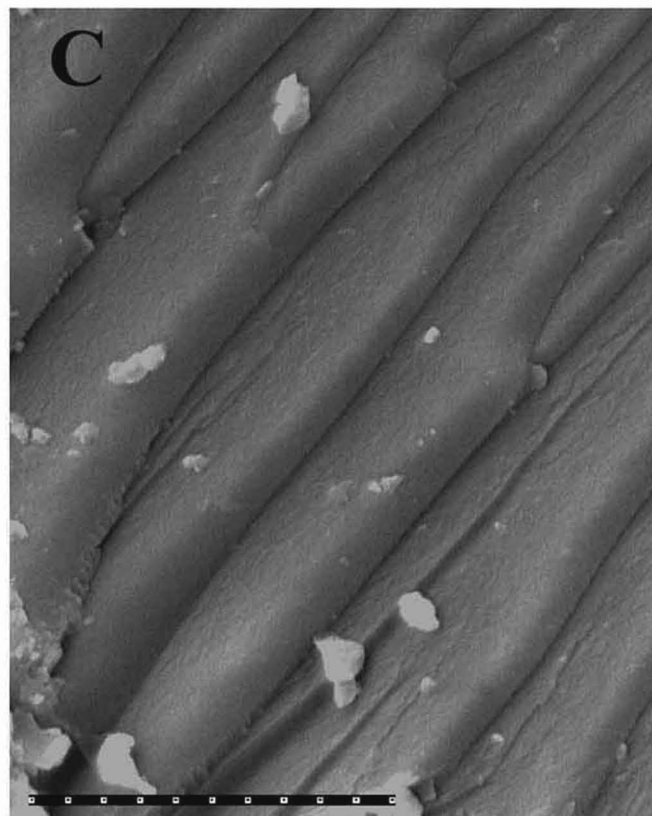
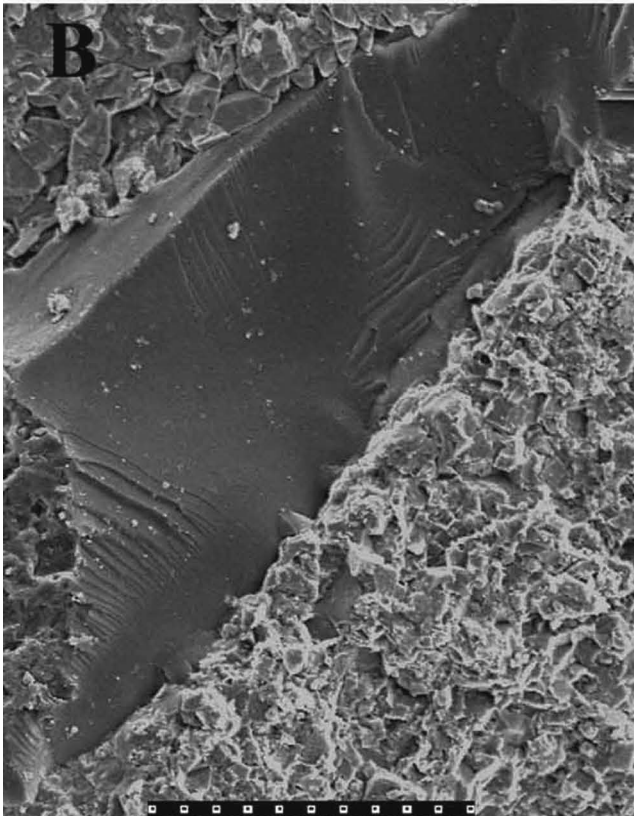
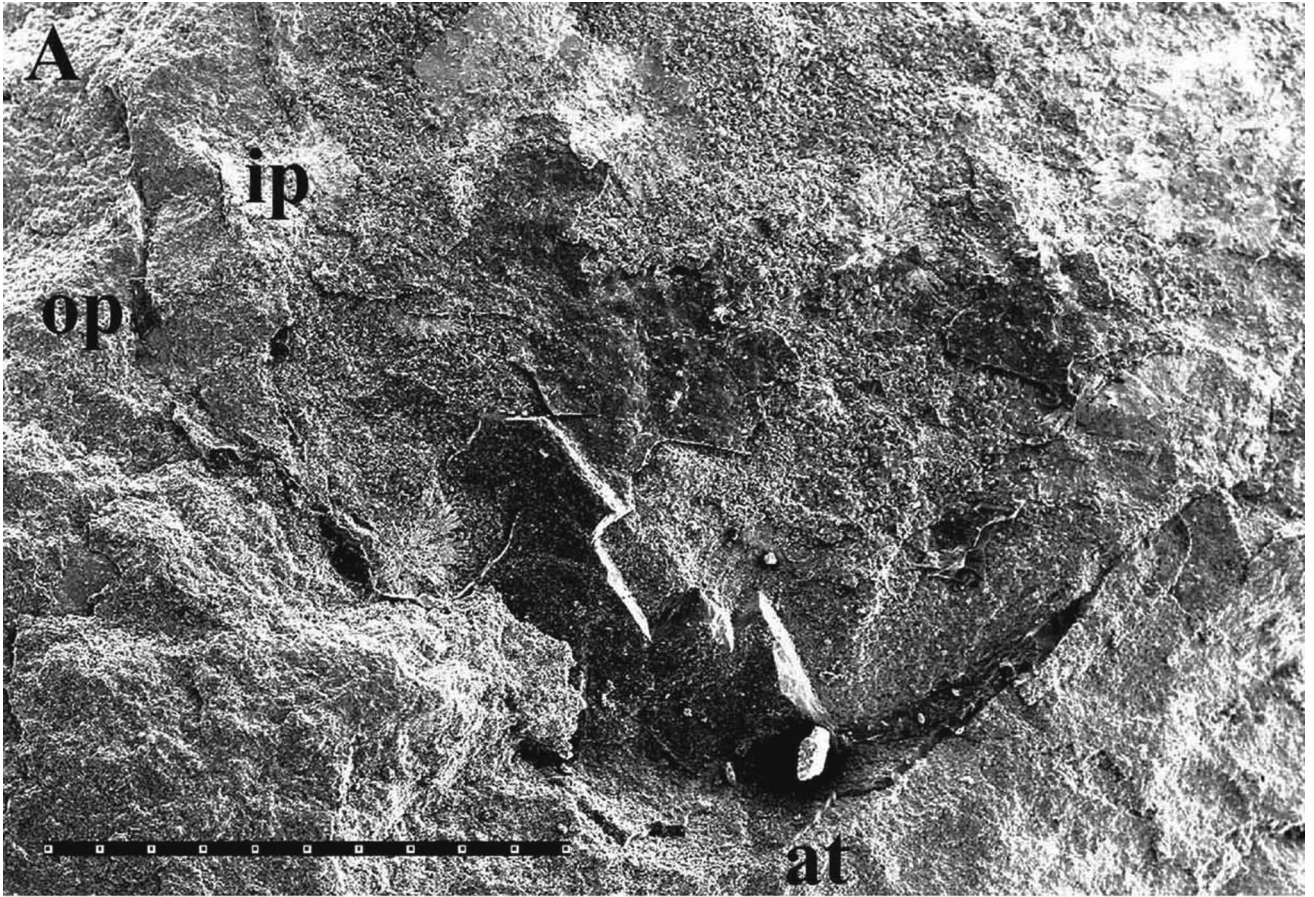


Plate 7. A–C. General view of the mandible located in front of the anterior edge of the shell, scale bar is 1.2 mm. B. Fracture of the beak (= rostrum) showing “glassy” material of the mandible, scale bar is 60 μ m. C. Step-like pattern of the fracture plane in the mandible, indicating a laminar structure, scale bar is 6 μ m.

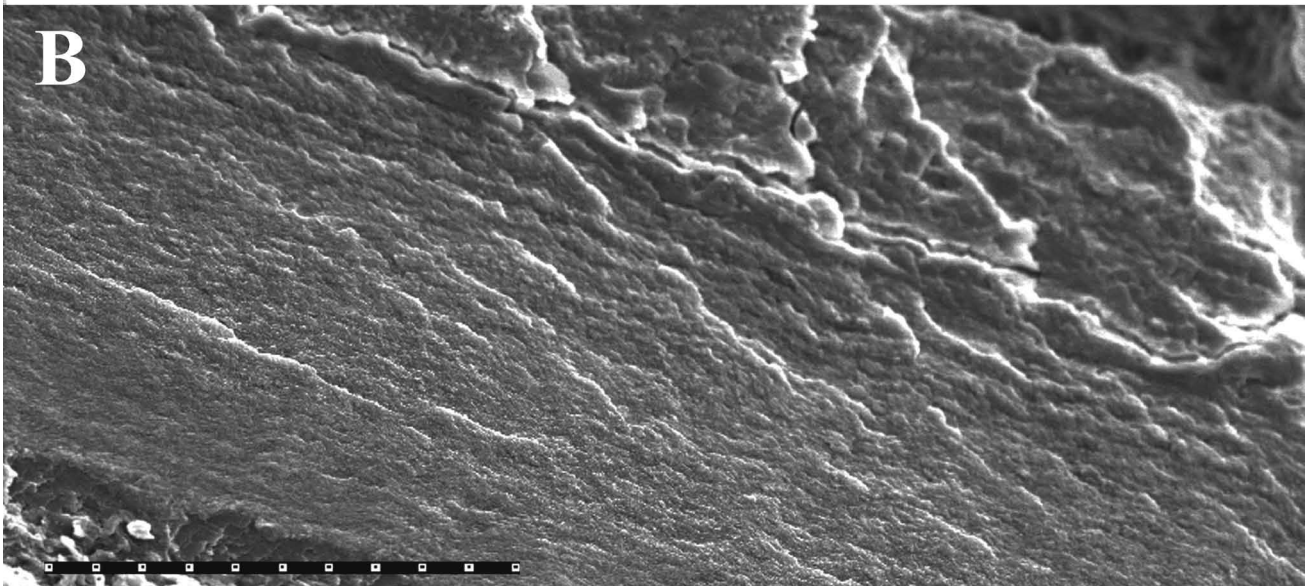
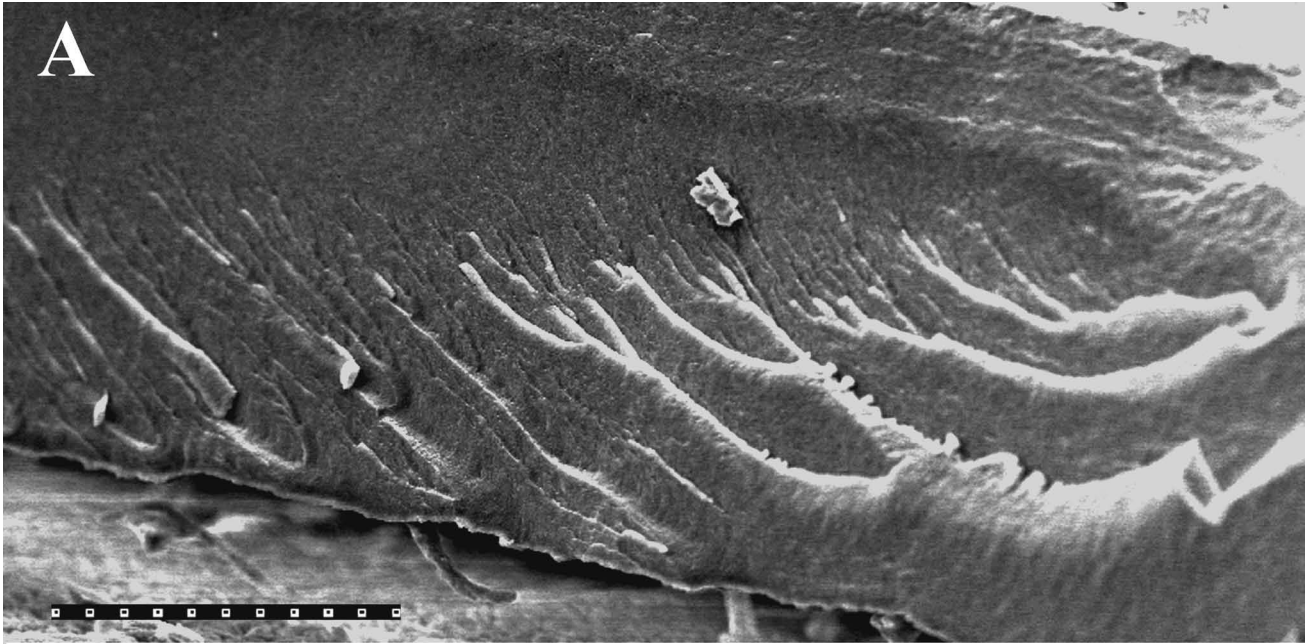


Plate 8. A–B. Vertical fracture plane of the mandible in living *Loligo* to show a step-like pattern formed by fractured chitinous material, scale bar is 60 μm ; B – Micro-lamination of two layers forming the mandible in *Loligo*, scale bar is 60 μm .