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THE PRO-OSTRACUM AND PRIMORDIAL ROSTRUM AT EARLY ONTOGENY OF LOWER JURASSIC BELEMNITES FROM NORTH-WESTERN GERMANY

L. A. Doguzhaeva[1], H. Mutvei[2] & W. Weitschat[3]

[1]Palaeontological Institute of the Russian Academy of Sciences 117867 Moscow, Profsoyuznaya St., 123, Russia, planetbond@mail.ru

[2] Swedish Museum of Natural History, Department of Palaeozoology, S-10405 Stockholm, Sweden, Harry.Mutvei@nrm.se

[3] Geological-Palaeontological Institute and Museum University of Hamburg, Bundesstrasse 55, D-20146 Hamburg, Germany, weitschat@geowiss.uni-hamburg.de

ABSTRACT

The structure of pro-ostracum and primordial rostrum is presented at early ontogenic stages in Lower Jurassic belemnites temporarily assigned to ?*Passaloteuthis* from north-western Germany. For the first time the pro-ostracum was observed in the first camerae of the phragmocone. The presence of a pro-ostracum in early shell ontogeny supports Naef's opinion (1922) that belemnites had an internal skeleton during their entire ontogeny, starting from the earliest post-hatching stages. This interpretation has been previously questioned by several writers. The outer and inner surfaces of the juvenile pro-ostracum were studied. The gross morphology of these surfaces is similar to that at adult ontogenetic stages. Median sections reveal that the pro-ostracum consists of three thin layers: an inner and an outer prismatic layer separated by a fine lamellar, predominantly organic layer. These layers extend from the dorsal side of the conotheca to the ventral side. The information obtained herein confirms the idea that the pro-ostracum represents a structure not present in the shell of ectocochleate cephalopods (Doguzhaeva, 1999, Doguzhaeva *et al.* 1999b, 2002a).

The primordial rostrum surrounds the protoconch and continues as a distinct prismatic layer along the phragmocone, at least along the first 25-30 camerae. The conotheca proper is absent. The phragmocone wall (= conotheca) is composed of an inner prismatic layer that continues from the mural part of the first septum, and three thin layers, which belong to the pro-ostracum. The latter layers are externally covered by the prismatic layer of the primordial rostrum. This shows significant differences in the shell wall structure betwen ectocochleates and belemnites.

INTRODUCTION

Lower Jurassic erratic glacial boulders of north-west Germany contain belemnoid shells with the initial portion of the phragmocone well preserved. The shells are only slightly recrystallised and the camerae are still empty, without post-mortem fillings (Weitschat & Bandel 1999). This well-preserved material has allowed us to examine with SEM seldom preserved shell structures at early otogenetic stages, such as pro-ostracum, primordial rostrum, phragmocone wall, and body/shell attachment scars.

The precise taxonomic determination of the belemnites is uncertain, although they can be temporarily assigned to ?*Passaloteuthi*s. We place the two species that have been recorded previously from these boulders: "*Belemnites*" *elongatus* and/or "*B*." *milleri* (Ernst & Schulz 1987) in this genus. However, our observations on the phragmocone morphology, mainly the large range of the angle of expansion, seem to indicate the presence of more than one genus in the examined material. The Domerian age of the material is proved by the associated ammonites *Amauroceras ferrugineum* and *Pleuroceras hawskerense* (Weitschat & Bandel 1999). The pro-ostracum is known in several genera, but only at adult ontogenetic stages (e.g. Voltz

1830, Mantell 1848, Huxley 1864, Phillips 1865, Crick 1896, Naef 1922, Jeletzky 1966, Doguzhaeva *et al.* 1999b, 2002a). It has been widely interpreted as a dorsal extension of the phragmocone wall (=conotheca), and thus, as a remnant of the wall of the living chamber in ancestral ectocochleate cephalopods (Phillips 1865, Naef 1922, Jeletzky 1966). However, in light of recently obtained information on *Conobelus*, *Mesohibolites* and *Megateuthis*, the pro-ostracum seems to represent a structure not present in the shell of ectocochleate cephalopods (Doguzhaeva, 1999, Doguzhaeva *et al.* 1999b, 2002a).

MATERIAL AND METHODS

The available material includes 15 fragments of juvenile belemnoid shells, from which four specimens are presented here, extracted from carbonate concretions within glacial erratic boulders of north-western Germany, close to the town of Ahrensburg. The ammonites *Amauroceras ferrugineum* and *Pleuroceras hawskerense* found in these boulders are assigned to the Lower Jurassic Domerian stage, spinatum Zone, hawskerense Subzone. The rest of the fauna from the boulders includes the "*Belemnites" elongatus, "B." milleri* and also scaphopods, gastropods, bivalves and an annelid worm tube (Weitschat & Bandel 1999, Weitschat & Gründel 2002). The mature belemnites are referred to *Passaloteuthi*s, and it is possible that the juvenile belemnites dealt with herein also belong to that genus.

The specimens preserve the protoconch and initial portions of the phragmocone consisting of approximately the first 15-25 camerae without sediment or crystalline precipitations. The internal shell structure was exposed by splitting the rostra. Five specimens of the total material exhibit imprints of the outer surface of the pro-ostracum. These specimens show also the layers belonging to the pro-ostracum. Altogether 10 specimens were studied with a Philips 35 C scanning electron microscope (SEM) at the Swedish Museum of Natural History, Stockholm. The internal and external surfaces of the shells were examined also in section. The exposed surfaces of the shells were studied without etching, while the sectioned specimens were embedded in plastic, cut, polished and etched with 2-5 per cent hydrochloric acid for 2-7 sec. The fractured sections were etched in the same manner.

The studied material is stored in the Geological-Palaeontological Institute and Museum, University of Hamburg.

OBSERVATIONS AND COMPARISONS

Protoconch (Figs 9, 10, 13-15, 17, 19)

The shape of the protoconch was observed in four specimens. It is spherical (Fig. 19) or egg-shaped (Figs 9, 13, 17). Its longitudinal axis either coincides with that of the phragmocone, but in two specimens it is inclined ventrally at an angle of about fifteen degrees. The protoconch wall is thin and prismatic (Figs 10, 14, 15). It wedges out near the aperture of the protoconch (Fig. 15). The enclosing membrane is not preserved.

Pro-ostracum (Figs 1-4, 7, 8)

As described by numerous authors (e.g. Voltz 1830, Huxley 1864, Crick 1896, 1897, Naef 1922, Jeletzky 1966, Doguzhaeva *et al.* 1999b, 2002a), three principal regions can be distinguished on the dorsal surface of the pro-ostracum in adult belemnites. A *median field* (Mittelplatte of Naef 1922) possesses curved growth lines. It is delimited on both sides by a pair of longitudinal ridges with closely spaced growth lines, termed by Naef the *medial asymptotes.* This area changes abruptly into a zone where the growth lines curve from a longitudinal to a transverse direction; this is the *hyperbolar zone* (Voltz 1930, Seitenplatte of Naef).

The inner surface of the pro-ostracum is less frequently preserved. It shows a pattern of narrow and shallow grooves diverging from both sides of the median line (Mantell 1848, Crick 1896, Doguzhaeva *et al.* 1999, 2002a).

The pro-ostracum in juvenile belemnites was hitherto unknown. It is described in the following four juvenile specimens:

Specimen no. 1 (Figs 1-6) - This specimen is about 7 mm both in length and width, and comprises the initial portion of the phragmocone surrounded by the rostrum (Fig. 1). In the initial portion of the

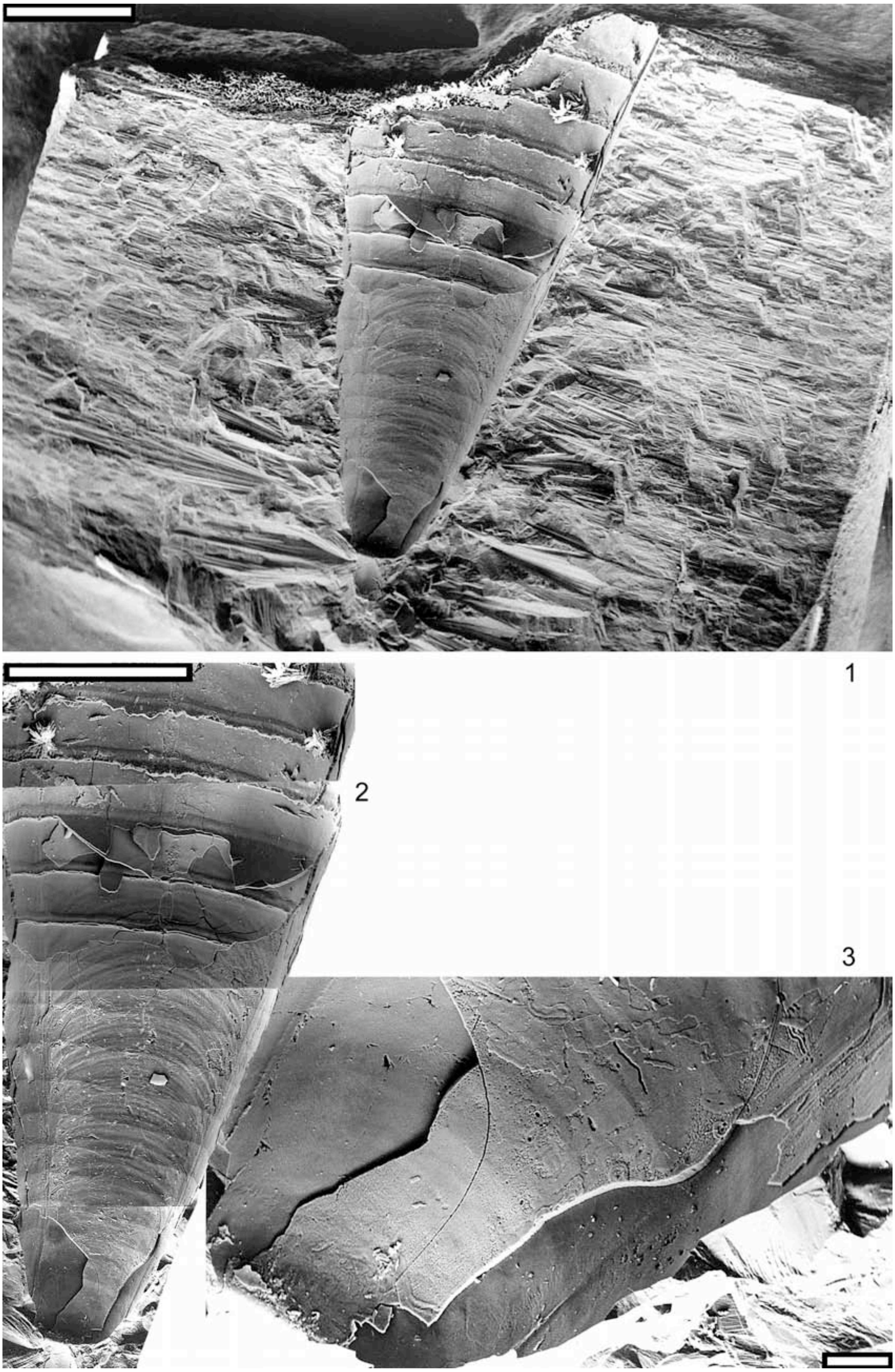
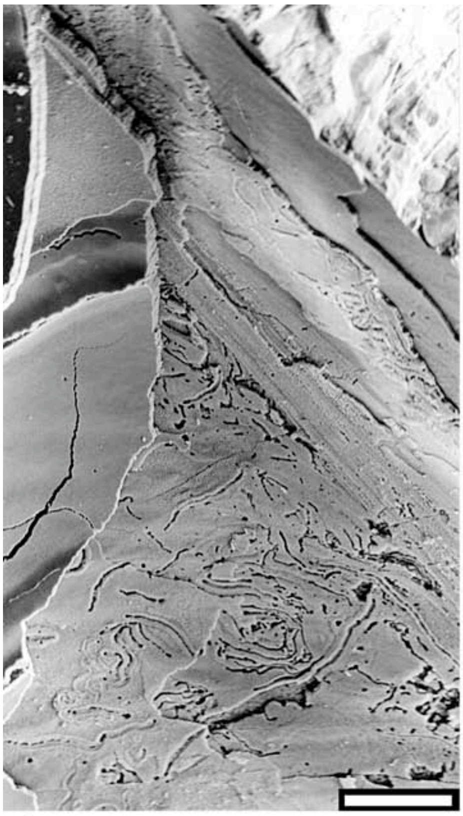


Figure captions. Fig. 1 Specimen no. 1. Longitudinal fracture of the rostrum revealing the initial part of the phragmocone, showing an imprint of the pro-ostracum and the inner surface of the shell wall with septa. Scale bar - 1 mm. **Fig. 2** Enlarged detail of Fig. 1, showing the concentric growth lines of the median field of the pro-ostracum, the hyperbolar zones with longitudinal lines, with the asymptotes between them, and dorsal mid-central unpaired attachment scars. Scale bar - 1 mm. **Fig. 3** Further enlarged detail of posterior portion, also shown in Fig. 2. Note that the median field, the hyperbolar zones and the asymptotes of the pro-ostracum appear at the aperture of the protoconch. Scale bar - 0.1 mm



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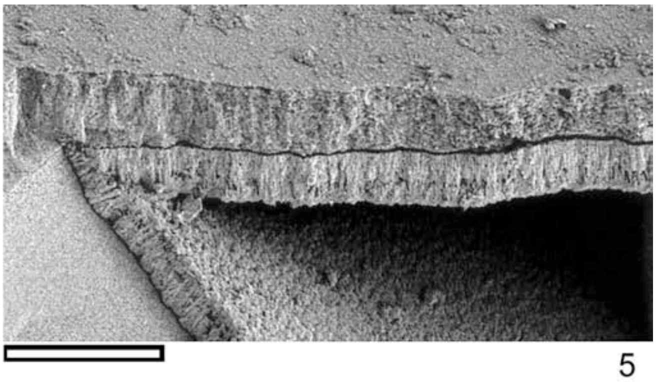

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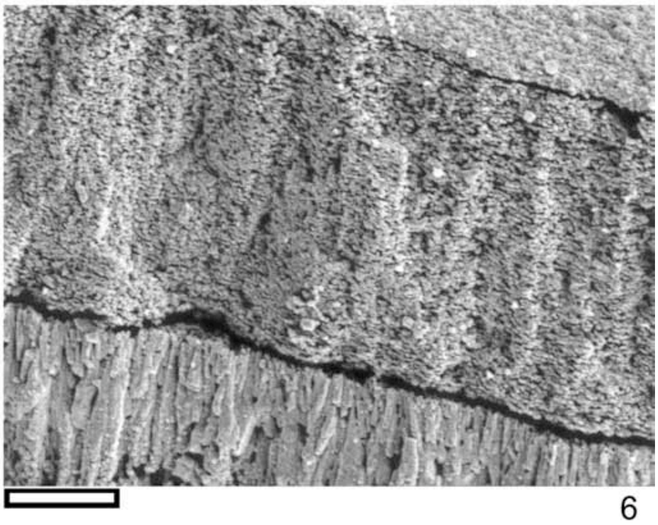

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Figure captions. Fig. 4 Specimen no.1, inner surface of the pro-ostracum at approxemately 15th-17th camerae shows furrows parallel to the pro-ostracal layers. Note thin layers of the pro-ostracum. Scale bar - 0.1 mm. **Figs 5, 6** Enlarged detail, showing the lamella-fibrilla nacre of the septum of specimen no. 1. **5** The septum does not show tabular nacre x 500. **6** Close up of Fig. 5 to show the lamello-fibrillar nacre x 3500. **Fig. 7** Specimen no. 3. The outer surface of the phragmocone with the well preserved imprint of the pro-ostracum: the median field shows concentric growth lines of two orders and the hyperbolar zones - longitudinal ribs diverge anteriorly. Two distinct groove-shaped asymptotes are visible between them. Scale bar - 1 mm. **Fig. 8** Specimen no. 3. Lateral view to show the asymptote which runs along the median line of the lateral side; the median field is above it and the hyperbolar zone is below it. Scale bar - 1 mm phragmocone, comprising about 10 camerae, the shell wall is broken off. The alveolus shows a distinct imprint of the inner surface of the pro-ostracum (Figs 1, 2). The median field, hyperbolar zones and asymptotes are observed immediately in front of the protoconch (Fig. 3), which demonstrates that the pro-ostracum was developed at the earliest ontogenetic stage. The concentric growth line pattern of the median field and asymptotes are reflected even on the inner surface of the camerae where the conotheca wall is preserved (Fig. 2). The median field is broad with broadly rounded growth lines (Figs 1, 2). The growth lines extend to the asymptotes and run in a short distance parallel to them. The hyperbolar zones show converging oblique lines (Fig. 3). The pro-ostracum is formed by three thin layers, the middle of which seems to have been rich in organic matrix. The organic nature of this layer is indicated by numerous borings that extend parallel to the inner surface of the layer (Fig. 4).

Specimen no. 3 (Figs 7, 8) - The specimen comprises a fragment of the phragmocone, 8.5 mm in length and approximately 4 mm in maximum diameter, without the rostrum. The pro-ostracum is exposed on the outer surface of the phragmocone. It has the median field, hyperbolar zones and two asymptotes. The medan field is broad, with concentric growth lines which are slightly acute medially. These lines are of two orders: numerous weak lines alternating with a few stronger lines (Fig. 7). The growth lines are crossed by longitudinal striations (Fig. 8). At higher magnification, the median field shows numerous small pits. Similarly in adult *Megateuthis* (Doguzhaeva *et al.* 1999b, 2002b), the median field is pitted and shows delicate longitudinal striae. In contrast, the median field in the juvenile pro-ostracum of our material does not show a dorsal axis as found in adult *Megateuthis*. The asymptote is a groove-like structure between the median field and the hyperbolar zone (Fig. 8). The hyperbolar zones show obliquely arched lines, meeting the asymptotes at an angle of about 15-20 degrees. The lateral sides of the hyperbolar zone are coated by a thin layer which probably belongs to the rostrum (Fig. 8).

Specimen no. 4 (Figs 9-12) - In a median section, three thin pro-ostracal layers can be distinguished (Figs 11, 12). The outer and inner layers show a prismatic structure. They are separated by a layer that is dark and has a lamellar structure. The latter layer is predominantly organic, being only slightly calcified.

Specimen no. 5 (Fig. 16) - In this specimen the inner, ventral surface of the pro-ostracum is partially exposed (Fig. 13). This surface shows narrow grooves that have a feather-like pattern. It is probable that this pattern represents the similar feather-like pattern seen on the inner surface of the pro-ostracum in adult *Megateuthis* (Doguzhaeva *et al.* 2002a).

Primordial rostrum (Figs 9, 10, 14, 15)

Bandel and co-workers (1984) distinguished two portions in the apical end of the primordial rostrum of *Hibolithes*: an inner portion that covers the protoconch wall with thin layers of prismatic aragonite, and an outer portion that is organic matter. A single aragonitic layer of the primordial rostrum continues toward the apertural direction and covers the phragmocone wall on all sides. Also in *Conobelus,* the prismatic primordial rostrum covers the protoconch and the early portion of the phragmocone (Doguzhaeva *et al.* 1999a, b).

The specimen no. 4 is a median section of a juvenile phragmocone. The primordial rostrum is composed of a prismatic layer that shows numerous, more or less distinct, sublayers. It surrounds the protoconch and covers the entire preserved phragmocone (Figs 9-12) in a way similar to the corresponding layer in *Hibolihtes* and *Conobelus*. It is thickened at the apex of the protoconch, but thinner on its lateral sides. It is also thickened at the corner between the protoconch and the phragmocone (Fig. 10), and along the ventral side of the phragmocone (Fig. 11). Several spherulites of different sizes, separated by wider or narrower interspaces, occur behind the apex of the protoconch (Fig. 9). They have a lamellar structure, and each lamella consists of acicular crystallines. The spherulites are either completely calcified or have an empty center. They seem to have grown in an organic matrix that probably corresponds to the outer organic portion of the primordial rostrum in *Hibolithes* (Bandel *et al.* 1984). The boundary between the protoconch wall and the primordial rostrum is indistinct because they both have a similar prismatic structure (Fig. 14).

Conotheca (Figs 4, 10-12, 14, 16)

The conotheca proper is missing. The first septum is prismatic and its mural part continues in the apertural

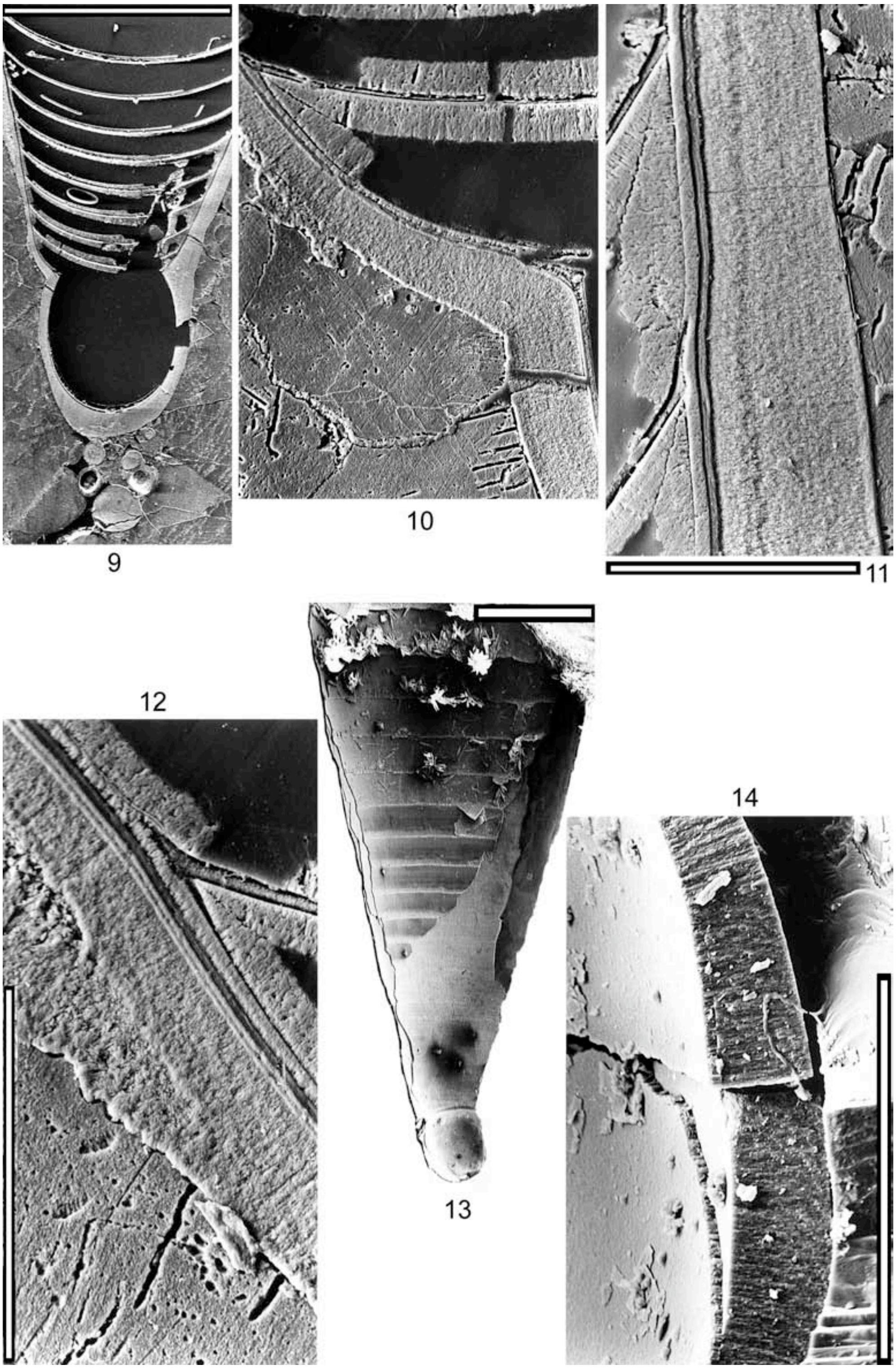
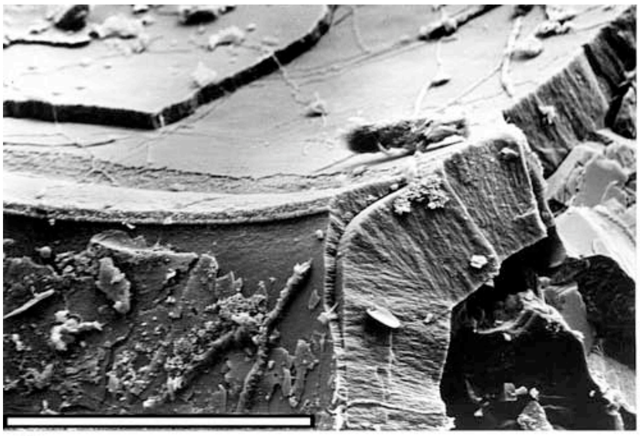


Figure captions. Fig. 9 Specimen no. 4. Longitudinal median section showing the submarginal siphuncle, and the primordial rostrum which continues along the phragmocone as a uni-layered structure; near to the top of the protoconch several aragonitic spheres are present. Scale bar - 1 mm. **Fig. 10** Enlarged detail of Fig. 9 showing the left corner between protoconch and phragmocone. Note the different ultra-structure of the premordial and the true septum. The mural part of the first septum continues to the whole length of the first camera. Both surfaces of the 2^{nd} septum are covered by thick ?cameral deposits. Scale bar - 0.1 mm. **Figs 11, 12** Close up of the shell wall of specimen no. 4: **11** Ventral side, scale bar - 0.1 mm. **12** Dorsal side, scale bar - 0.1 mm. **Fig. 13** Specimen no. 5. General view on the protoconch and the first approximately 20 camerae. The inner concave surface of the protoconch and the phragmocone are exposed. Scale bar - 1 mm. **Fig. 14** Enlarged detail, showing the inner surface of the protoconch, the thin prismatic shell wall of the protoconch and the thick prismatic primordial rostrum; the latter gets thinner from the apex towards the mouth of the protoconch. Scale bar - 0. 1 mm



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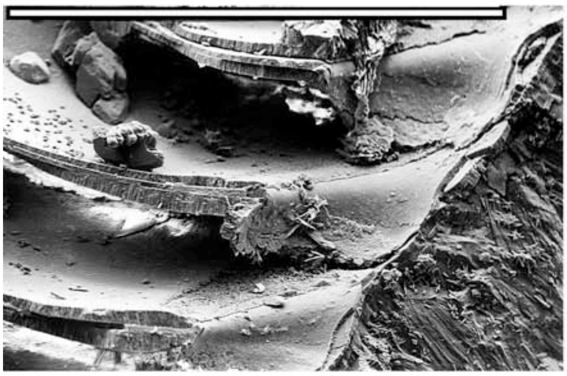

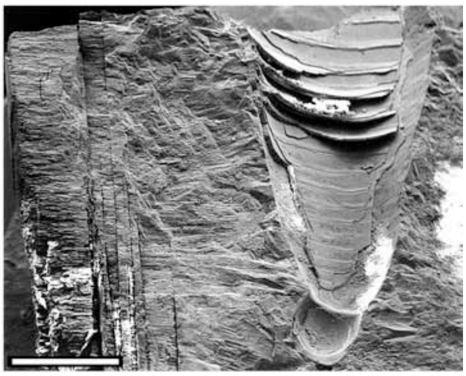

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Figure captions. Fig. 15 Specimen no. 5. The area near to the mouth of the protoconch. The thick primordial rostrum (to the right) does not wedge out near the first septum, but continues along the phragmocone. The thin prismatic wall of the protoconch wedges out here. The first septum is attached to the protoconch wall just before it wedges out. Scale bar - 0. 1 mm. **Fig. 16** Specimen no. 5. The fracture of the shell wall in different places of the phragmocone. Five layers [from inside (left) to outside (right)] between the inner surface of the phragmocone (marked by mural ring) and the rostrum: 1) a comparatively thick prismatic layer ; 2) a thin loosely calcified layer; 3) a more compact one as thin as previous layer; 4) another thin, probably prismatic layer; 5) a slightly thicker, probably prismatic layer. Scale bar - 0.1 mm. **Fig. 17** Specimen no. 6. General view of the protoconch and the initial part of the phragmocone, with the sipuncle to the right. Scale bar 1 mm. **Fig. 18** Enlarged detail of three septa with the septal necks. Scale bar - 1 mm. **Fig. 19** Specimen no. 7. Longitudinal fracture of the rostrum with the protoconch and initial part of the phragmocone. The inner surface of the protoconch is exposed. Scale bar - 1 mm direction forming the prismatic inner layer of the conotheca. External to this layer follow three, thin pro-ostracal layers, covered by the prismatic layer of the primordial rostrum.

Similarly in juvenile *Mesohibolites* and *Pachyteuthis* (Barskov 1973), *Hibolithes* (Bandel *et al.* 1984) and *Conobelus* (Doguzhaeva *et al.* 1999) the inner layer of the phragmocone wall is formed by a continuation of the mural part of the first septum. However, the pro-ostracal layers have not been identified previously at early ontogenetic stages in those genera.

Septa (Figs 5, 6, 17-19)

In about the 15th septum, a lamello-fibrillar, nacreous ultrastructure (nacre type 2) was observed in section and on the septal surface (Figs 5, 6). The fibers have globular sections with the diameter ca. 1 µm on the adoral septal surface. In cross section, the fibers are arranged in horizontal nacreous lamellae. Each lamella is composed of one layer of fibers, and the thickness of the lamellae is approximately the same as the diameter of the fibers.

Attachment scars (Figs 1, 2)

Dorsal, unpaired attachment scars are preserved on the inner surface of the phragmocone (Figs 1, 2). In the earliest stages, approximately 14 camerae, the shell wall is broken off and therefore the scars are not preserved. Approximately at the15th camera, the scar has an oval, elongated shape and it is slightly shorter than the camera. In the following camerae, the scars become longer and have approximately the same length as the camerae. Unpaired attachment scars have been observed in several other belemnoid taxa (Bandel *et al.* 1984), in aulacocerids (Bülow 1915, Bandel 1985), in Recent *Spirula* (Bandel 1982) and in the spirulid *Naefia* (Doyle 1986, Doguzhaeva 1996) as well as in bactritoids (Doguzhaeva 1996, 1999, 2002) and orthoceroids.

DISCUSSION

The dorsal surface of adult pro-ostracum is known in the following taxa: "*Belemnites*" *elongatus* Miller (Huxley 1864), "*B.*" *paxillosus*, "*B.*" *apicicurvatus*, "*B*". *voltzi*, "*B*". *inorvatus*, "*B*". *ellipticus*, "*B*". *quinquesulcatus*, "*B.*" *parallelus*, "*B.*" *sulcatus* (Phillips 1865-70: Pl. 6, Figs 15, 16; Pl. 17, Fig. 43; Pl. 18, Fig. 46; Pl. 21, Fig. 53; Pl. 24, Fig. 57; Pl. 27, Fig. 66; Pl. 29, Fig. 71), "*Belemnites*" *paxillosus* (Crick 1896), "*Acanthoteuthis speciosa*" (Crick 1897), *Hibolites* (Quenstedt 1849, Zittel 1881-1885), *Megateuthis* (Naef 1922, Doguzhaeva *et al.* 1999, 2002a). The ventral surface of adult pro-ostracum is so far only known in three taxa: *Cylindroteuthis puzosi* (Mantell 1848), "*Belemnites*" *paxillosus* (Crick 1896) and *Megateuthis* (Doguzhaeva *et al.* 1999b, 2002a). It is characterized by a feather-like pattern composed of numerous thin lines that diverge from a median line. These lines were interpreted as attachment marks of the inner tunic to the pro-ostracum (Doguzhaeva *et al.* 2002a). As shown in the present paper, the pro-ostracum is formed already at the earliest ontogenetic stage and shows all characteristics of adult pro-ostracum. This shows that the pro-ostracum has a similar morphology during the ontogeny. Phillips (1865: p. 17) wrote that "whatever be the form of this pro-ostracum it is properly a dorsal extension of the conotheca of the Belemnites." This opinion was generally shared by Naef (1922) who did not, however, completely exclude the possibility that pro-ostracum might have been absent in belemnitid ancestors. The interpretation of the pro-ostracum as a dorsal remnant of the body chamber is widespread (e.g. Jeletzky 1966). However, ultrastructural studies of the shell wall, combined with observations on the morphology of the pro-ostracum in the Lower Cretaceous *Mesohibolites* from North-West Caucasus, and in the Middle Jurassic *Megateuthis* from Novaya Zemlya and north Germany lead to the conclusion that the pro-ostracum cannot be considered as a continuation of the conotheca (Doguzhaeva *et al.* 1999b, 2002a). In *Mesohibolites* and *Megateuthis,* the adult pro-ostracum is a distinct, but thin, irregularly mineralized layer, with a high organic content, situated between the conotheca and the rostrum. As shown herein, the juvenile pro-ostracum is irregularly mineralized, with a high organic content middle layer as well. There is no similar layer in the shell wall of cephalopods with external shells. This leads to the conclusion that the pro-ostracum is a new morphological feature of the coleoids which has no comparable layer in the shell wall of their ectocochleate precursors.

In the juvenile belemnites examined here, the phragmocone wall is mainly prismatic. It consists of (1) an inner prismatic layer that is a continuation of the mural part of the first septum, (2) loosely calcified thin pro-ostracal layers, and (3) a prismatic primordial rostrum layer. In adult *Belemnoteuthis* (Bandel & Kulicki 1988) and *Megateuthis* (Mutvei 1964, Doguzhaeva *et al.* 2002b), a nacreous layer also occurs in the phragmocone wall. The latter layer is missing at the early ontogenetic stage in belemnites dealt with herein. Information of conotheca structure in belemnites of different taxa and ages is still incomplete. Nevertheless, it has become obvious that the conotheca structure is remarkably variable.

The septa of the Recent *Spirula* and Upper Jurassic belemnite *Pachyteuthis* (Mutvei 1970, Pls. 6d, 7, text-fig. 3), Lower Cretaceous spirulid *Naefia* (Doguzhaeva 1996), Lower Cretaceous belemnite *Conobelus* (Doguzhaeva *et al.* 1999) and Upper Pennsylvanian phragmoteuthid? *Donovaniconus* (Doguzhaeva *et al.* 2002c) are known to consist of lamello-fibrillar nacre originally described as nacre type 2 (Mutvei 1970). This type of septal nacre (with a fiber diameter about the same as in *Spirula*) is secreted at early ontogenetic stages in the belemnites from northwestern Germany.

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