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Belemnoteuthis polonica: A Belemnite with an Aragonitic Rostrum

(*Belemnoteuthis polonica:* Ein Belemnit mit Aragonit-Rostrum)

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With 31 Text Figures

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Abstract: *Belemnoteuthis,* on the basis of the composition and shape of the phragmocone, is a "normal" belemnite. Differences in the shape of the first chamber of *Belemnoteuthis* are due to shell damage that was healed during the life time of this Jurassic squid. Therefore, *Belemnoteuthis* represents a separate genus of belemnites but not a separate order. The rostrum of *Belemnoteuthis* is composed of aragonite from embryonic to mature life and contrasts from other belemnites by not changing primordial rostrum mineralogy; its conch is that of a normal belemnite.

Kurzfassung: *Belemnotheutis* ist ein "normaler" Belemnit, was Zusammensetzung und Form des Phragmokons angeht. Unterschiede in der Gestalt der 1. Kammer von *Belemnoteuthis* gehen auf Schalenverletzung zurück und wurden noch zu Lebzeiten dieser Jura-Form ausgeheilt. Das Rostrum besteht aus Aragonit, u.zw. sowohl embryonal als auch adult. Der fehlende Wechsel der primären Rostralmineralogie steht im Gegensatz zu den übrigen Belemniten. Die Schale ist jedoch die eines normalen Belemniten. *Belemnoteuthis* wird als eigene Gattung aber nicht als eigene Ordnung aufgefaßt.

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1. Introduction

Makowski (1952) described a new species of the genus *Belemnoteuthis* Pearce from Callovian concretions that were collected from glacial drift near Lukov in Poland. *Belemnoteuthis polonica* Makowski 1952 consists of a short rostrum, preserved in its original modification of the $CaCO_3$ as aragonite, and a phragmocone with the ultrastructure of the shell unaltered; only the originally organic siphuncular tube is transformed into very fine-grained phosphorite.

Makowski (1952) noted that the rostrum of *Belemnoteuthis,* in contrast to Naef's (1922) observations, shows concentric growth lines in cross section, but he did not notice the aragonitic modification of the guard and, therefore, its difference to most belemnite rostra, which are calcitic. Naef also was not aware of the difference in the mineralogical composition existing between "normal" calcitic belemnite rostra and the aragonitic rostrum of *Belemnoteuthis*.

Belemnoteuthis polonica, according to Makowski (1952), differs from normal belemnites by the presence of a cup-like first chamber (protoconch), whereas the normal case in belemnites is a spherical first chamber. The early shell of *Belemnoteuthis* was interpreted as more primitive than that of the belemnites; Makowski therefore placed belemnoteuthids apart from belemnites and considered them to be a sister group to the belemnites with close affinities to their ancestors. Naef (1922), in contrast, considered the genus *Belemnoteuthis* a close relative of the belemnites and discussed the possibility of a close relationship with *Acanthoteuthis speciosa* from the Upper Jurassic of Solnhofen, an idea that was again taken up by Engeser & Reitner (1981). But the authors placed the genera *Belemnoteuthis* and *Acanthoteuthis* into the order Belemnoteuthida, which was considered different from the order Belemnitina, mainly due to the presence of the cup-like first chamber. This feature, which was discovered by Makowski (1952), was also interpreted by Donovan (1977) to represent an important systematic characteristic. Jeletzky (1966), in contrast, gave minor importance to this feature and classified *Belemnoteuthis* as a member of the family Belemnoteuthididae Zittel 1885 of the order Belemnitinae.

We are grateful to Dr. Henryk Makowski (Warszawa) for providing us with several individuals for use in this for study, therefore allowing them to be fractured and cut; thanks also to Dr. Gerhard Schairer for loaning some specimens of *Belemnoteuthis antiquus* from the collection of the Institute of Paleontology in Munich.

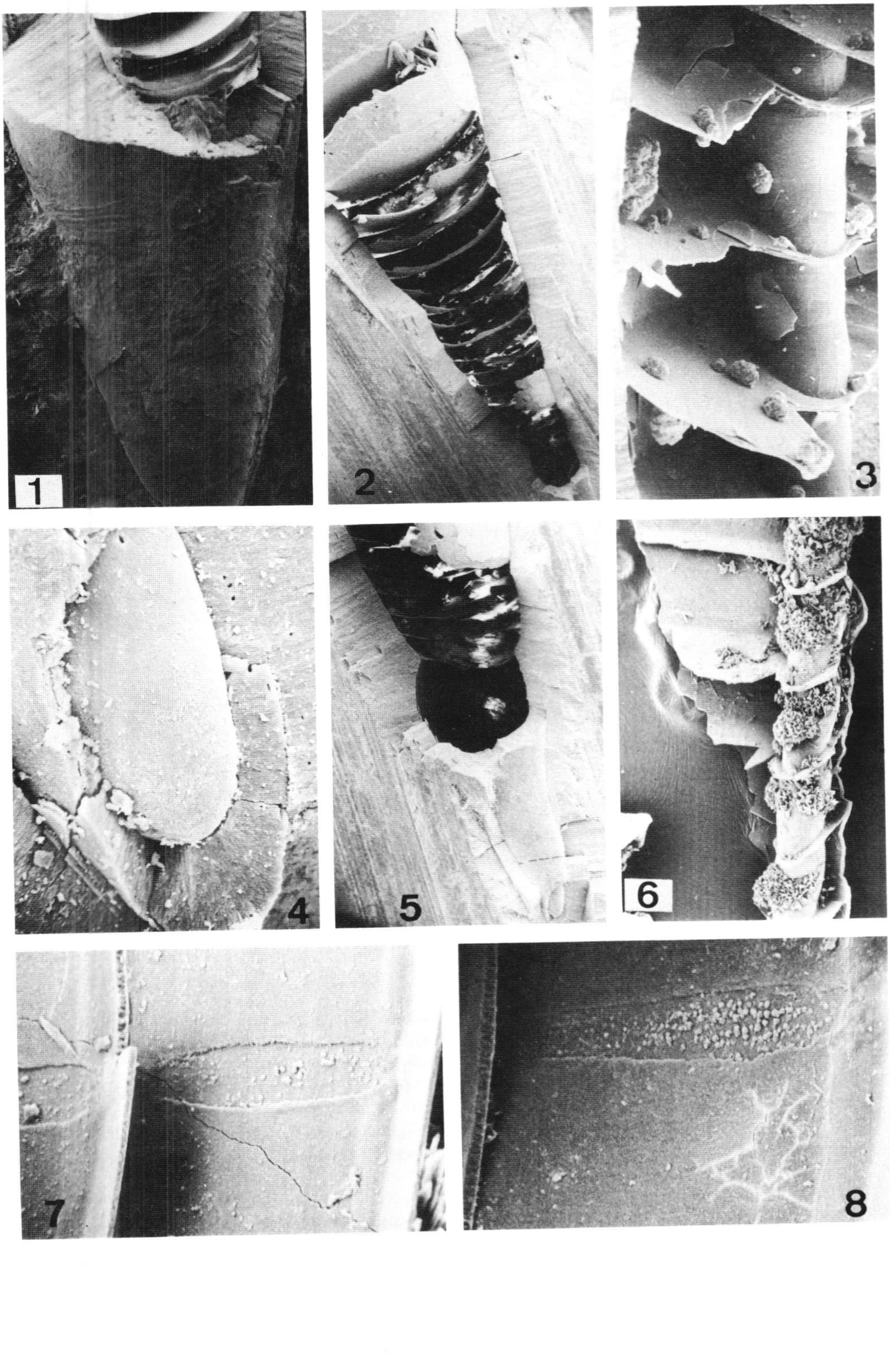
2. Observations

The rostrum of *Belemnoteuthis polonica* consists of concentric prismatic layers composed of aragonitic needles. In fractured rostra, the crystallites appear to continue without interruption from the phragmocone wall to the outer side of the rostrum (Text Fig. 2, 15). Cut, polished, and etched rostrum surfaces show growth lines perpendicular to the prismatic needles (Text Fig. 10), differentiating layers that

Text Figs. 1-5, 7-25, 29-31 *Belemnoteuthis polonica*

Text Figs. 6, 26-28 *Megateuthis* sp.

Text Fig. 1. Photograph of specimen that was later polished and etched. ×50.
Text Fig. 2. Opened rostrum showing the complete phragmocone. ×50.
Text Fig. 3. Siphuncular tube of specimen in Text Fig. 2. × 200.
Text Fig. 4. Primordial and juvenile rostrum of complete specimen in Text Fig. 2. Detail of Text Fig. 5. ×250.
Text Fig. 5. Spherical first chamber with primordial rostrum of individual in Text Fig. 2. Ventral side lies at left and is shown in detail in Text Fig. 31. ×120.
Text Fig. 6. The siphuncular tube extracted from the individual shown in Text Fig. 26. ×90.
Text Figs. 7 and 8. Tissue attachment scar preserved on the inner dorsal wall of individual shown in Text Fig. 2. ×250.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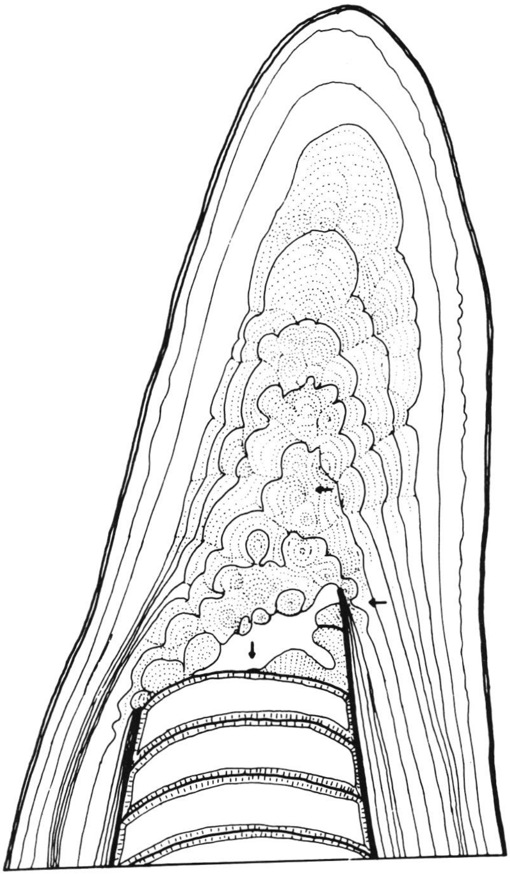

Text Fig. 9. Sketch of individual shown in Text Fig. 1 after being polished and etched. The phragmocone was fractured and the healed portion of the rostrum shows spherulitic structure. Detail of left side shown in Text Fig. 10.

Text Fig. 10. Polished and etched surface of the fractured left side of the phragmocone wall shows cement filling the chambers (right) and repair of rostrum (arrow). Many borings have penetrated the conch after death and before burial now appearing as irregular tubes. ×300.

Text Fig. 11. Etched spherulite of the kind that formed to repair the rostrum of the individual shown in Text Fig. 1 and sketched in Text Fig. 9. ×600.

Text Fig. 12. First aragonitic cements formed on the septum surface after chambers apical to it had been broken off (lower part); they differ from cameral deposits formed within the chamber (upper part). (Polished and etched surface). ×600.

Text Fig. 13. Fracture that shows the last septum preserved when individual shown in Text Figs 14 & 15 was damaged. As in Text Fig. 12, cement crust formed from the repair liquid of muscular mantle (lower part) is of much coarser fabric than cement crust formed within the undamaged chamber (upper part) in the still living animal. ×250.


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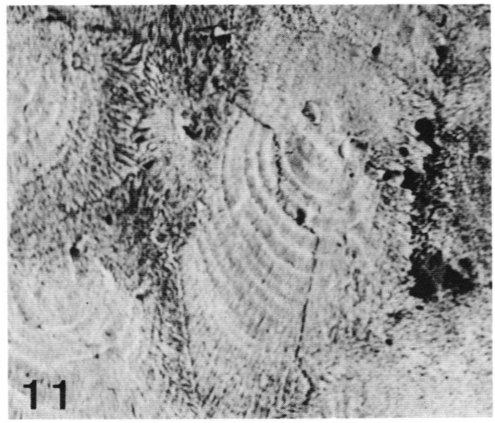
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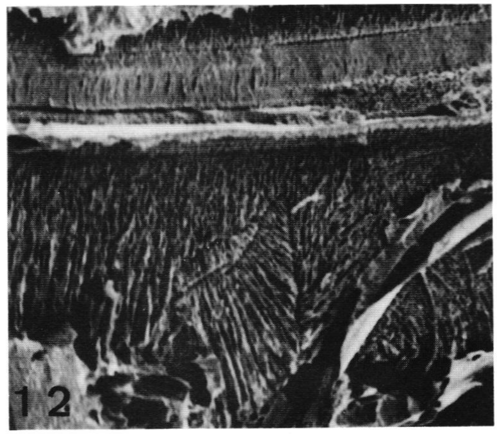
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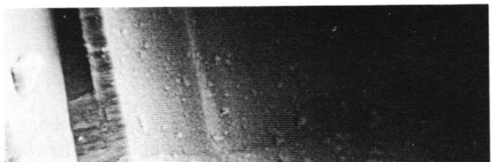
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originally contained organic material in relatively smaller or greater amounts. The layers reflect the original surface of growth of the rostrum. Minute tubes which are filled or open crisscross the etched surface and represent bore holes, etched into the substrate by endolithic organisms, probably algae or fungi (Text Fig. 10). They do not only penetrate rostral layers but also the phragmocone wall and must have been etched into the shell after death of the animal.

All here studied individuals are almost equal in size and have almost the same rostrum thickness (Text Figs. 1, 2, 15). But their apical ends show major differences. While one individual has an almost spherical first chamber and a regular, wellformed juvenile rostrum attached to its apical portion (Text Figs. 2, 4, 5), the second and third ones display a blunt first chamber with an irregular apical base and an irregular mass of spherulitic aragonite below more regular prismatic layers of the rostrum on top of it (Text Figs. 9, 14). The polished, etched individual clearly reveals the second case (Text Figs. 9, 10).

Evidently, the first individual represents an unaltered situation, while individuals two and three show repair of injured phragmocones and juvenile rostra. Comparison with Makowski's description (1952, fig. 11) reveals that he also saw and studied repaired rostra in his *Belemnoteuthis polonica*.

The uninjured individual shows that the first chamber was closed by an organic septum as in the belemnite *Hibolithes* (Bandel et al. 1984, fig. 1). The organic septum itself is not preserved but its attachment ridges are present on the wall of the phragmocone (Text Fig. 31, arrow). The second septum touches the end of the ventral siphuncular tube (Text Fig. 31), just as in the case of *Hibolithes*. But unlike *Hibolithes* and the other two studied individuals of *Belemnoteuthis*, the siphuncular tube is well preserved. Mineral septal necks are short (Text Figs. 24, 25) and the organic substance of the nacre is continuous into the organic tube. The originally organic material of the tube was transformed into a phosphatic substance during diagenesis. One can still that it was once thin, flexible, and (in parts) wrinkled (Text

Text Fig. 14. Opened rostrum and phragmocone of an individual, which had become damaged during life, lost several of the initial chambers of the conch and repaired the whole rostrum in such a way that the adult conch looks just like that of undamaged individual shown in Text Fig. 1. ×10.

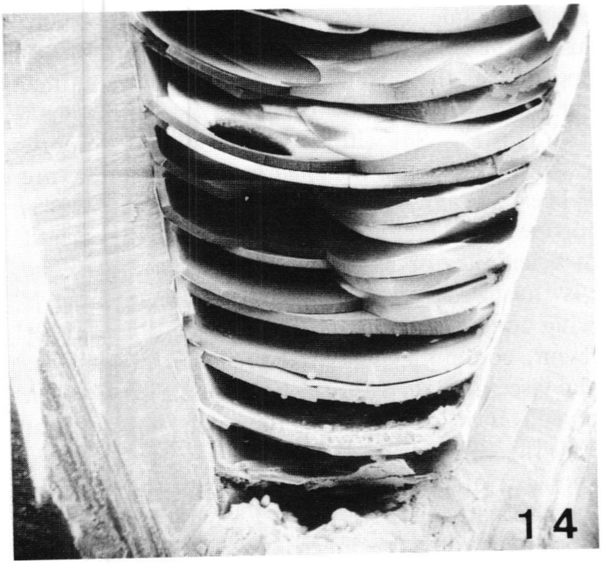
Text Fig. 15. Same individual as that shown in Text Fig. 14 before phragmocone was opened. The position of the siphuncular tube lies where a series of holes is seen. ×5.

Text Fig. 16. Detail of Text Fig. 15 shows the dorsal side of the phragmocone with cameral aragonitic deposits covering cameral surfaces. A bubble of gas may be responsible for the round gap without cameral deposits. ×180.

Text Fig. 17. Detail of Text Fig. 15 shows the ventral side of the phragmocone with septal necks preserved (right). The cameral aragonitic cement formed during life, after repair it became thickest near the siphuncular tube, but did not cover the tube. For similar recrystallized crusts, see Bandel & Spaeth (this volume). ×250.

Text Fig. 18. Fracture through the phragmocone shows aragonitic layers with rostrum at left, and periostracal spherulite sectors following and grading into the nacre (centre), which is underlain by the inner prismatic layer (right). ×550.

Text Fig. 19. Detail of Text Fig. 18 shows transition from prismatic structure into *Nautilus*-type nacre of phragmocone wall. ×2500.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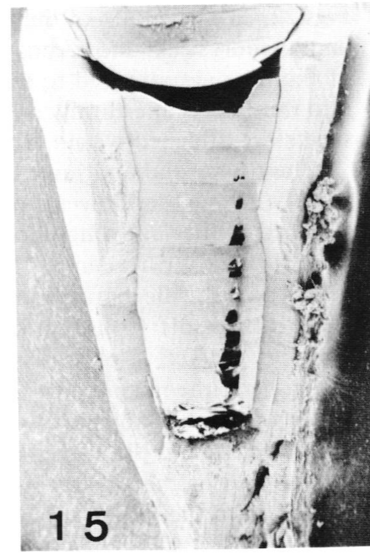
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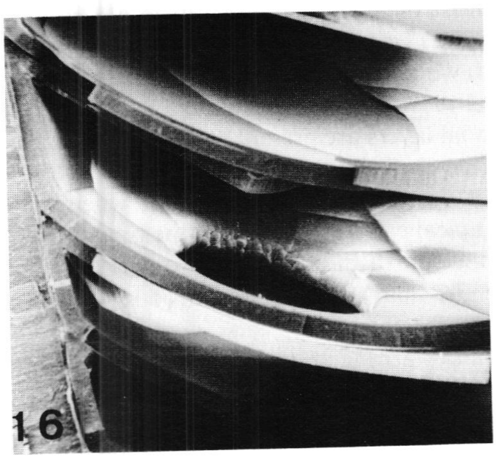
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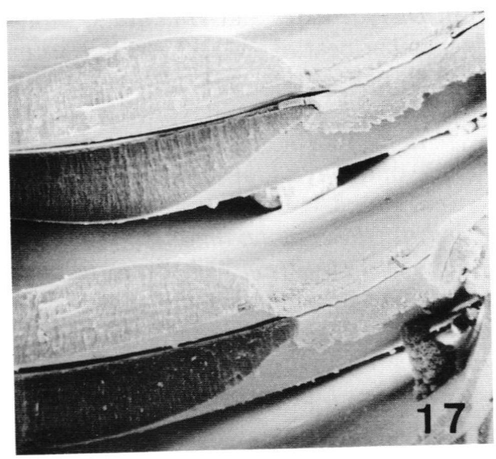
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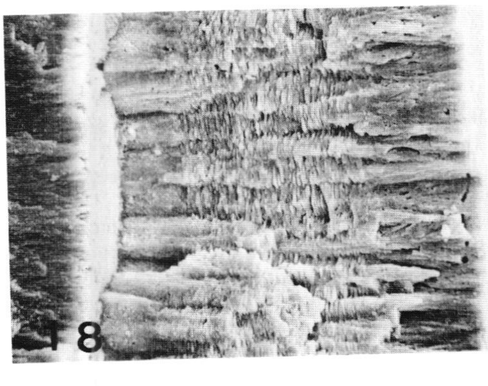
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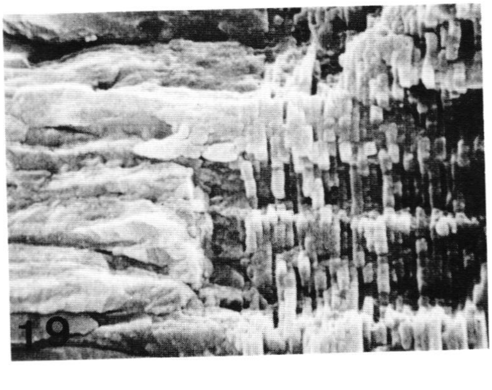
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Figs 22, 23). The bulk of the tube is an organic continuation of the mineral septum and its short neck, and it ends on and in the next, more apical neck. The outer sheets of the tube are attached to the septum near the opening of the neck and continue into thin sheets aperturally covering the chamber (Text Figs. 22, 23), while the inner sheets are attached within the neck (Text Fig. 24) without much mineral support.

The primordial and juvenile rostrum attached to the spherical first chamber are slightly inclined to the ventral side (Text Fig. 5). The sphere of the first chamber is attached to the following phragmocone in an inclined position, so that the earliest shell is weakly cyrtoconic, like in belemnites or bactritids (Text Figs. 2, 5). The apical part of the phragmocone is thus weakly curved and the first chamber is spherical, set off from the following cone by a constriction. On the dorsal inner chamber surface, a groove is present, containing scattered prismatic crystallites. Along here, the mantle covering the visceral mass was attached (Text Figs 7, 8). In the first chamber no scar is preserved, but it probably was the same shape as that seen in *Hibolithes* (Bandel et al. 1984, fig. 18).

The wall of the phragmocone consists of three layers, an outer prismatic layer connected to the periostracum, a central nacreous layer (Text Figs. 18, 19), and an inner prismatic layer. The septa are connected to this inner layer (Text Fig. 20). As in *Dictyoconites* and *Hibolithes,* septa consist of a nacre characteristic of Recent chamber-bearing coleoid shells (*Spirula*-type) (Text Fig. 21) (Bandel & Boletzky 1979, Bandel 1982, 1985, Bandel et al. 1984) while the central layer of the phragmocone shows the normal type of nacre (Bandel 1977).

In the individuals two and three, additional layers are present which were deposited onto layers of the phragmocone after shell injury. Comparison with the undamaged individual one indicates that at least 5 chambers were lost when the juvenile *Belemnoteuthis* was injured at the apical end of its body. At the time of the injury, the rostrum had grown to about one fourth the width and four fifths the length of the adult rostrum; it was more slender than an adult rostrum (Text Figs. 9, 10).

The repaired rostrum consists of spherulites arranged around a central axis in such a way that they take the shape of the rostrum that had been lost due to damage

Text Fig. 20. Phragmocone wall (left) with septum connected to it. ×1100.

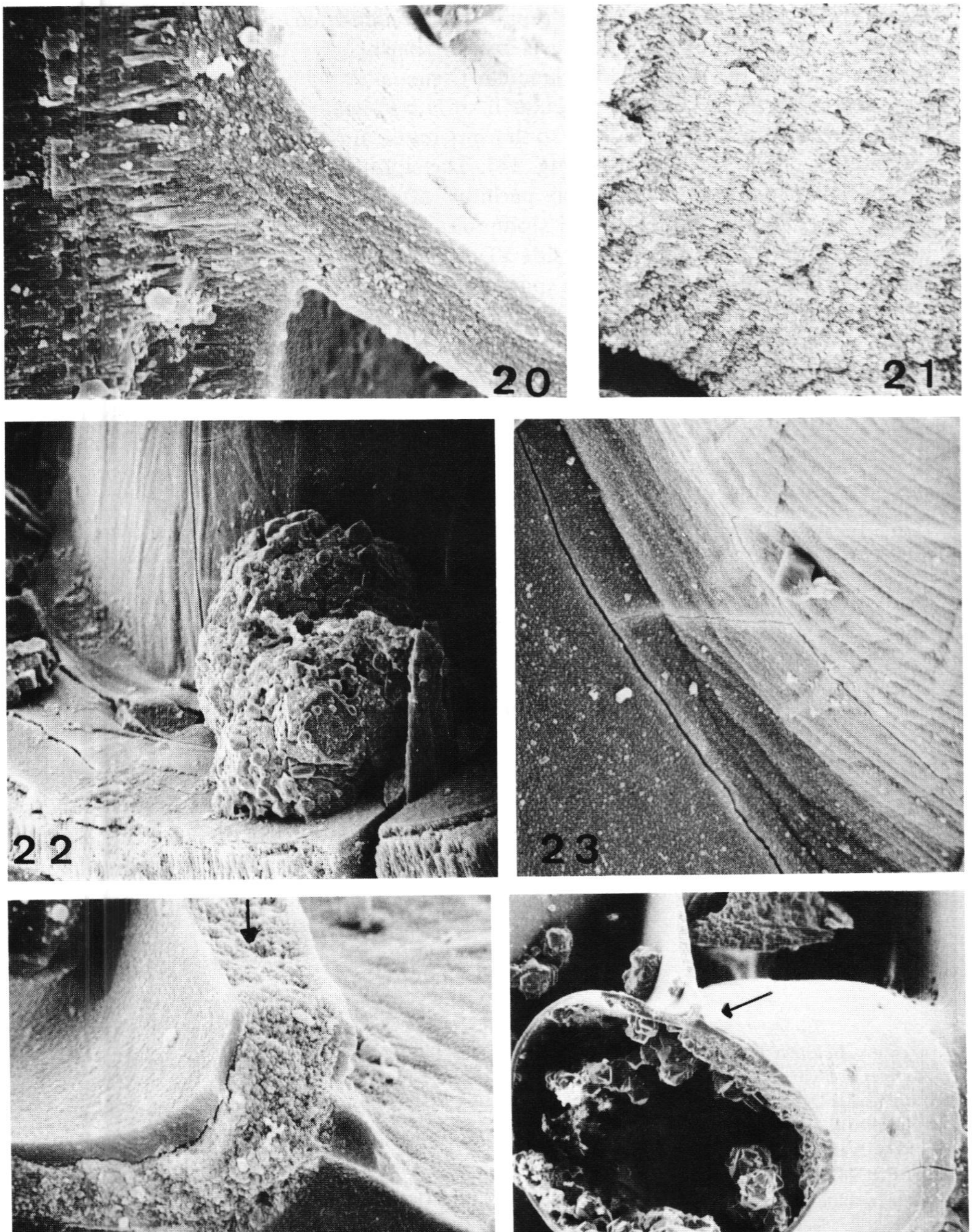
Text Fig. 21. Detail of text Fig. 20 shows that nacre of the septum is *Spirula*-type. ×6500.

Text Fig. 22. The siphuncular tube, before becoming phosphatised, consisted of organic sheets which were folded and stretched and covered the chamber surface near septal necks. ×1000.

Text Fig. 23. Folds of the former organic sheets of the siphuncular tube continue onto the surface of the septum. ×2000.

Text Fig. 24. The detail of Text Fig. 25 shows a septal neck and the siphuncular tube that is connected to it. The mineral septum (arrow) grades into the organic tube (left). The tube is attached in the septal neck only with minute prismatic deposits and is connected to the septum as well as the inner side of the septal neck. ×1100.

Text Fig. 25. The segment of the siphuncular tube is fractured at its attachment to the septum. The upper neck (arrow) is shown in detail in Text Fig. 24. ×50.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(Text Fig. 9). Several steps in the repair can be identified. First, the last fractured chamber was sealed by organic sheets and small aragonite crusts (Text Figs 12, 13). After healing of the damaged siphuncular tissue, situated below the rostrum (which were still complete when the muscular mantle had healed around the wound) were flooded with fluid rich in $CaCO_3$, so that prismatic aragonite cement started coating the interior chamber walls (Text Fig. 14). The siphuncular tube itself remained free of deposits (Text Fig. 17) and may perhaps (after it had healed) have pumped the chambers empty again. Near the siphuncle, deposits are thickest (Text Fig. 17), become thinner near the dorsal side (Text Fig. 16). A remaining bubble of gas prevented prismatic growth in one spot (Text Fig. 16). Cement crusts are observed in all 15 chambers that could be studied below the rostrum in the preserved phragmocone, so that all of these chambers must have been flooded during and after repair, but may have been emptied later.

The rostrum itself was reconstructed after repair and regrowth of the apical tissue of the muscular mantle. Beginning with several spherulitic centres arranged along a median line, aragonitic bodies grew until they touched each other and could again be covered by a continuous layer of prismatic aragonite (Text Fig. 10, 11, 29). While damage occurred when about one fourth of the rostrum was completed, repair of the smooth rostrum was finished in the last one fourth of rostrum growth before death of the outgrown individual. Repair, therefore, should have taken some time and intermediate rostra certainly should have looked less regular (Text Fig. 9).

3. Comparison with Megateuthis

For comparison, a large rostrum of *Megateuthis* from Lukov was fractured and the apical portion of the phragmocone was split open. This revealed the first chamber, succeeding chambers, a well preserved siphuncular tube and dorsal scars of the tissue attachment to the shell (Text Figs. 6, 26, 28). The primordial rostrum is a low structure, much shorter than that of *Hibolithes* (Bandel et al. 1984), but, like the

Text Fig. 26. Opened calcitic rostrum of *Megateuthis* with phragmocone, siphuncular tube (at left), and spherical first chamber. × 30.

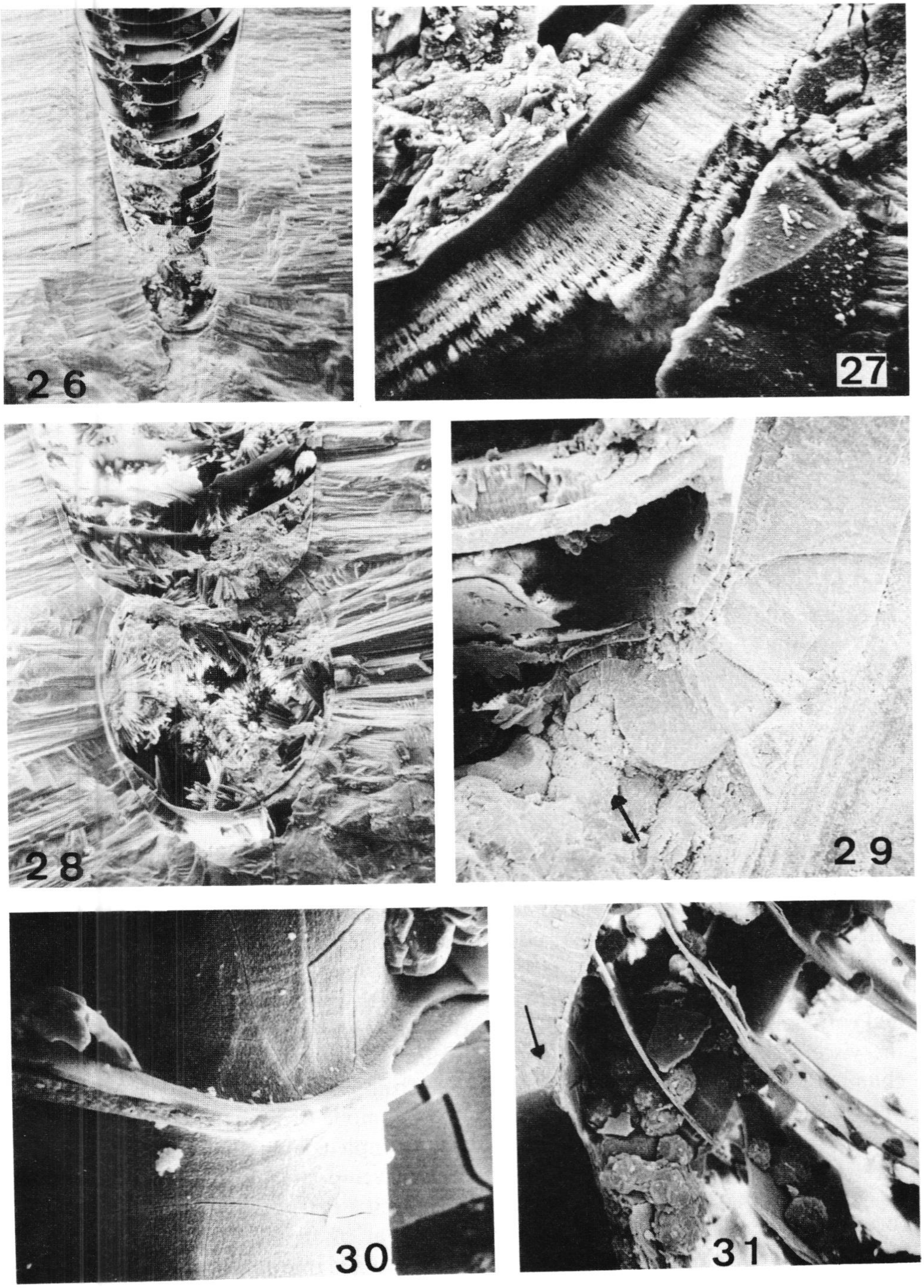
Text Fig. 27. Detail of Text Fig. 28 showing the dorsal portion of the layers of the primordial rostrum. In contrast to the orthorostrum, this shallow structure consists of aragonitic layers which probably graded into an organic layer (now cavity). × 850.

Text Fig. 28. The first chamber of the individual shown in Text Fig. 26 with shallow primordial rostrum visible as shallow bowl at lower (apical) end (detail of Text Fig. 27). × 85.

Text Fig. 29. Detail of Text Fig. 14 (right lower side) showing the end of the fractured phragmocone and juvenile rostrum. First repair deposits (arrow) are spherical aragonite. × 180.

Text Fig. 30. Siphuncular tube in its course through a septum (detail of Text Fig. 3). The organic walls of the tube show wrinkles and folds now preserved as phosphorite. × 1000.

Text Fig. 31. Detail of Text Fig. 14 showing the end of the siphuncular tube in the septal neck of the second septum (first mineral septum). The first, organic septum is not preserved but its attachment ridge is present on the wall (arrow). × 450.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latter, it is composed of aragonite and organic material which disappeared due to diagenesis (Text Figs. 27, 28). The siphuncular tube is preserved and has the same composition and morphology as that of *Belemnoteuthis* (Text Fig. 3).

The conotheca is preserved beyond the embryonic shell, and its walls show a composition like that of *Belemnoteuthis*. While the septa are composed of lamellar *Spirula*-like nacre, the phragmocone walls have nacre platelets like the *Nautilus* nacre. Only the early portion of the belemnite shell (the part which was formed within the shelter of the egg capsule) has no *Nautilus*-like nacre (Bandel et al. 1984); instead, it is composed of prismatic aragonite, like the ammonitella (Bandel 1982) or the early shells of archaeogastropods (Bandel 1979).

The actual rostrum covering the shallow primordial rostrum and the phragmocone consists of prismatic calcite, with crystallites having become quite coarse and thick due to recrystallization during diagenesis (Text Figs 26, 28).

4. Discussion

Belemnoteuthis polonica is a typical representative of the genus *Belemnoteuthis,* and it is difficult to distinguish it from *Belemnoteuthis antiquus,* the type species of the genus *Belemnoteuthis*. Longitudinal ridges on the distal end of the phragmocone and the thin rostrum covering it were utilized by Pearce (see Mantell 1848) to differentiate the genus *Belemnoteuthis* from other genera of the belemnites. Such ridges on the dorsal side are not present in the same way in other belemnites; Pearce, therefore presented a new generic name. If one compares Mantell's (1848, pl. 13, fig. 5; 1850, pl. 29, figs. 7, 9, 10) figures of *Belemnoteuthis antiquus* from the Oxford Clay with figures presented by Makowski (1952, Fig. 8) of *B. polonica,* a separation of the two species is difficult. When material from the collection of the University of Munich of *B. antiquus* is compared with the matrial presented here, the same difficulties are encountered.

The morphology and structure of the phragmocone and the primordial rostrum (first rostrum attached to apical end of first chamber) of *Belemnoteuthis* are like *Hibolithes* (Bandel et al. 1984) and *Megateuthis* in all essential details. A reconstruction of hatching time and type of young leaving the egg thus would not differ from that presented by Bandel et al. (1984) for *Hibolithes*. In their model, it was suggested that a miniature belemnite was hatched with an aragonitic/organic primordial rostrum attached to a gas bubble-bearing first chamber, which was closed from the visceral mass by an organic (first) septum. This gas bubble developed in the chamber when the embryo pumped liquid from it, making the young animal buoyant and allowing it to take up a planktonic mode of life. It would have been about 10 mm long (soft body included). The complete siphuncular system, (as in other belemnites and in aulacoceratids) could develop later during life in the sea.

As in aulacocerids and belemnites, the nacre of the *Belemnoteuthis* phragmocone formed after hatching is *Nautilus*-like, while that of the septum is *Spirula*-like. Nacre of the outer wall thus consists of platelets, while that of the septa consists of fine rods arranged in layers (Mutvei 1964, 1970, Bandel 1977, Bandel & Boletzky 1979). Unlike aulacocerids and like belemnites, the conch is open aperturally of the last chamber. There, only the dorsal side of the mantle covering the visceral mass and the pallial cavity contains an interior shell, the proostracum. In aulacocerids, in contrast, the shell is tubular up to the apertural end; the siphuncular tube of the chambered phragmocone also differs from that of the belemnites. In aulacocerids, the siphuncular tube resembles that of *Spirula* (Mutvei 1971, Bandel 1985), while that of *Belemnoteuthis* and *Megateuthis* is similar to that of the ammonites. The belemnite sipho, at least in members of these two genera, is simple, and cameral water could have passed through it easily. It is not two-layered as assumed by Jeletzky (1966) for siphuncles (connecting rings) of *Belemnitida*.

Only the mineralogy of the postembryonic rostrum of *Belemnoteuthis* differs from that of characteristic belemnites. A difference in structure was already noted by Mantell (1850). We now know that a switch from aragonitic to calcitic shell deposition and *vice versa* during rostrum secretion in belemnites cannot be regarded as high-ranking in systematics (Bandel & Spaeth, this volume). Such a change occurs in the ontogeny of many or all belemnites in the transition from the primordial to the later rostrum; it occurs where epirostra are present, and it may even differentiate male and female rostra of the same species.

To summarize: *Belemnoteuthis,* on the basis of the morphology and structure of its conch, has to return to the belemnites where it was thought to belong by Naef 1922 and Jeletzky 1966. There is no separate order Belemnoteuthida as Engeser & Reitner (1981) assumed, although there may be a family Belemnoteuthidae Zittel 1885; in any case, there is definititely a separate genus *Belemnoteuthis,* well differentiated from other belemnite genera by the structure and shape of the rostrum.

References

Bandel, K. (1977): Übergänge von der Perlmutter-Schicht zu prismatischen Schichttypen bei Mollusken. - *Biomineralisation, 9:* 28-47; Stuttgart.

— (1979): The nacreous layer in the shell of the gastropod-family Seguenziidae and its taxonomic significance. - *Biomineralisation, 10:* 49-61; Stuttgart.

— (1982): Morphologie und Bildung der frühontogenetischen Gehäuse bei conchiferen Mollusken. - *Facies, 7:* 1-198; Erlangen.

— (1985): Composition and ontogeny of *Dictyoconites* (Aulacocerida, Cephalopoda). - *Paläont. Z., 59:* 223-244; Stuttgart.

Bandel, K. & Boletzky, S. v. (1979): A comparative study of the structure, development and morphological relationship in chambered cephalopod shells. - *Veliger, 21:* 313-354; Berkeley.

Bandel, K., Engeser, T. & Reitner, J. (1984): Die Embryonalentwicklung von *Hibolithes* (Belemnitida, Cephalopoda). - *N. Jb. Geol. Paläont. Abh., 167:* 275-303; Stuttgart.

Bandel, K. & Spaeth, Chr. (1988): Structural differences in the ontogeny of some belemnite rostra. - (This volume).

Crick, G.C. (1897): On an example of *Acanthoteuthis speciosa,* Münster, from the Lithographic Stone, Eichstädt, Bavaria. - *Geol. Mag., N. S. 4:* 1-4.

Donovan, D.T. (1977): Evolution of the dibranchiate Cephalopoda. - *Symp. Zool. Soc. London, 38:* 15-48; London.

Engeser, T. & Reitner, J. (1981): Beiträge zur Systematik von phragmokontragenden Coleoiden aus dem Untertithonium (Malm zeta, "Solnhofener Plattenkalk") von Solnhofen und Eichstädt (Bayern). - *N. Jb. Geol. Paläont. Mh., 1981:* 527-545; Stuttgart.

Jeletzky, J.A. (1966): Comparative morphology, phylogeny, and classification of fossil Coleoidea. - *Univ. Kansas Paleont. Contr., Mollusca, Art. 7:* 1-162; Lawrence, Kansas.

Makowski, H. (1952): La faune calovienne de Lukov en Pologne. - *Palaeont. polonica, 4:* 1-64; Warszawa.

Mantell, G.A. (1848): Observations on some Belemnites and other fossil remains of Cephalopoda, discovered by Mr. Reginald Neville Mantell, C.E. in the Oxford Clay near Trowbridge, in Wiltshire. - *Phil. Trans. roy. Soc. London, 1847:* 171-181; London.

— (1850): Supplementary observations on the structure of the Belemnite and *Belemnoteuthis*. - *Phil. Trans. roy. Soc. London, 1850:* 393-398; London.

Mutvei, H. (1970): On the shells of *Nautilus* and *Spirula* with notes on the shell secretion in non-cephalopod molluscs. - *Ark. Zool., 16:* 221-278.

— (1970): Ultrastructure of the mineral and organic components of molluscan nacreous layers. - *Biomineralisation, 2:* 48-72; Stuttgart.

— (1971): The siphonal tube in Jurassic Belemnitida and Aulacocerida (Cephalopoda: Coleoidea). - *Bull. geol. Inst. Univ. Upsala., N. S. 3:* 27-36, Upsala.

Naef, A. (1922): Die fossilen Tintenfische. - P., Jena (Fischer).

Zittel, K.A. (1985): Grundzüge der Paläontologie (Paläozoologie). 111 p., München, Leipzig (Oldenbourg).