Structural Differences in the Ontogeny
of Some Belemnite Rostra

(Struktur-Unterschiede in der Ontogenese einiger Belemniten-Rostren)

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With 1 Text Figure and 5 Plates

Abstract: Belemnite rostra were secreted by the muscular mantle of squid-like cephalopods to serve as support for the apical fins. Three different substances, calcite, aragonite, and organic material, composed this most apical portion of the internal conch; all three with different reactions to diagenesis. Some Jurassic and Cretaceous belemnites changed the morphology of the rostrum during late ontogeny, adding epirostra to orthorostra. Some Upper Cretaceous genera built orthorostra composed adorally of aragonite and apically of calcite. Damage during life and repair also result in special deposits within the phragmocone and on the rostrum. Together with ontogenetic, mineralogical and morphological changes, all these factors have to be considered for a satisfactory belemnite classification.

Kurzfassung: Das Rostrum eines Belemniten wurde vom Muskelmantel des Tintenfisches als Stütz-element der rückwärtigen Flossen ausgeschieden. Dieser am weitesten hinten gelegene Teil des Innen-skeletts besteht aus Calcit, Aragonit und organischem Material. Bei der Diagenese reagiert jedes dieser drei Bauelemente verschieden. Einige jurassische und kretazische Belemniten veränderten die Gestalt des Rostrums im Verlauf der späten Ontogenese, indem an das Orthorostrum ein Epirostrum angefügt wurde. Einige kretazische Gattungen schieden Orthorostra aus, welche vorn aragonitisch und hinten kalzitisch aufgebaut waren. Verwundungen des Rostrums konnten am lebenden Tier durch die An-lagerung von spezieller Schalensubstanz von außen und im Inneren des Phragmokons ausheilen. Minera-logische Zusammensetzung, morphologischer Umbau während verschiedener Ontogenesestadien und bei Reparatur sowie Diageneseabläufe müssen berücksichtigt werden, wenn eine befriedigende Klassifikation der Belemniten angestrebt wird.

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1. Introduction

Belemnites represent the characteristic decapod squids of Jurassic and Cretaceous times. In contrast to Recent teuthid squids which usually have a flexible unminer-alized internal shell (gladius), belemnites had a calcified internal shell connected with a chambered phragmocone, which in most species was covered in its apical portion by additional shell layers forming the characteristic rostrum (guard). The muscular mantle anterior to the chambered shell portion could contract and expand

laterally and ventrally because only the dorsal portion of the shell (proostracum) continued to the mantle edge. The rostrum was the base and solid anchor of the fin musculature (see Text Figs. 4, 5, 6 in Bandel & Boletzky, this volume). The resulting squids looked quite similar to Recent pelagic squids like *Loligo*, and they were probably also good swimmers. They swam in the water in a horizontal position and, when at rest, hovered with head lower than fins, again like Recent *Loligo*. Like these Recent counterparts in the teuthid squid, belemnites were pelagic swimmers as well as nectic bottom dwellers.

Bony fish, sharks, and marine reptiles preyed upon belemnites, as is documented by some exceptionally well preserved sharks and ichthyosaurs (in the Holzmaden and Solnhofen fossil collections) where rostra are found in the stomachs. Hölder (1973) described belemnite rostra with tooth imprints scratched into them, and Abel (1916) showed many repaired rostra. Naef (1922) noted that, since totally fractured rostra commonly did not fall off but became healed, the internal shell of the belemnites must have been contained in a solid sheath of muscular mantle. In the case of Recent *Sepia*, S. v. Boletzky collected a fair number of cuttlebones at Banyuls-sur-Mer which had been partly to totally ruptured by hunters with spears and had subsequently been repaired. Repair even in badly hurt animals is thus very common in the Recent *Sepia*, as it was possible in the Jurassic and Cretaceous belemnites.

Belemnites, like Recent squid, hunted smaller prey — mostly crustaceans and small fish — and they would expell a cloud of ink when they wanted to escape attack.

The belemnite shell formed an internal skeleton. As assumed by Naef (1922) and shown by Bandel et al. (1984), the young belemnite hatched from its egg as a miniature adult with an internal shell. Most probably, belemnites formed the shell from first shell secretion onward in the shell sac, which had already closed by fusion of the muscular mantle above the shell mantle (Bandel & Boletzky 1979, Bandel 1982). Young belemnites hatched with or without an embryonic, primordial rostrum and with at least one organic, functional septum.

Different parts of the mantle are responsible for the secretion of different parts of the shell. The phragmocone is formed by the periostracum gland zone and the shell mantle behind it. The rostrum, in contrast, is produced by secretions of the muscular mantle, which originally lies anterior of the periostracum zone, but in the endocochleate cephalopods is fused above the shell mantle covering it. The rostrum serves as a muscular base for the fins and consists of deposits which are of more simple fabric than those of the phragmocone (see Dullo & Bandel, this volume). In the mode of deposition, rostra of belemnites can be compared to deposits on the dorsal side of the cuttlebone of *Sepia*, including its spine, also to rostra of the aulacoceratids and many fossil spirulisepiids.

2. Embryonic and early juvenile rostrum
(Pl. 1, Figs. 3, 4; Pl. 5, Figs. 1, 2)

The rostrum deposited on top of the first spherical chamber of the belemnite phragmocone consists of aragonite and organic material. Müller-Stoll (1936) called this first rostrum, which is easily distinguished from later rostrum by its shape and mostly by its mineralogy, the "Calcar primordialis". In different belemnite species, the primordial rostrum has a characteristic and probably species-specific shape. The short, stubby primordial rostrum of *Hibolithes* (Bandel et al. 1984, figs. 1a, b) and the even flatter one of *Megateuthis* (Bandel & Kulicki, this volume) may have been present when the young hatched from its egg. The long, slender, pointed primordial rostrum of the *Neohibolites minimus* species group (Pl. 5, Fig. 1) was certainly secreted after the animal hatched from the egg and was still a small planktonic squid.

The cup-like apical additions as well as the thread-like central portions in longer primordial guards have been variously interpreted. This has been discussed extensively by Bandel et al. (1984). A common characteristic of primordial belemnite guards seems to be their organic and aragonitic composition and their shape, deviating from that of the rostrum of juvenile and adult squid described below.

3. Orthorostrum

Most belemnites of Jurassic and Cretaceous times covered the primordial rostrum with a solid, smooth, calcitic rostrum which, in some cases, like in *Megateuthis,* grew to sizes of more than 60 cm in length and 6 cm in width, extending far backwards from the end of the phragmocone. In other cases, as the *Nannobelus,* only a small, thin cover remained on the apical phragmocone. Thin, slender forms are present as well as thick, rounded guards. During ontogeny, the shape of this guard may have remained about the same or it may have changed greatly, a feature observed by Abel (1916). He stressed its importance in the description of belemnite species and genera, an advice which has only rarely been followed by authors concerned with belemnite systematics.

The orthorostrum is composed of calcite and has always been calcitic. This original structure is preserved in the case of *Hibolithes* (Bandel et al. 1984), and recrystallisation changes it very little (Dullo & Bandel, this volume). Spaeth (1971, 1975) showed that much of the internal lamellar orthorostrum may have been unmineralized, and assumption shown to be correct. Veizer (1974) studied the geochemical data on belemnite rostra and interpreted their original mineralogy as low Mg-calcite, with at least 10% of the shell organic or porous.

The prismatic calcite grew in smooth layers exactly reflecting the original, smooth growth surface, as can be seen in transversal thin section, showing concentric layering, interrupted only by furrows that may characterize the later dorsal side, the apical end, or the ventral side. Organic layers are concentrations in growth surfaces with few or no calcitic prisms. There is no indication that Kabanov's (1967)

idea, confirmed by Dauphin (1984), is correct, that the orthorostra of all belemnites are composed of primary aragonite and that calcite is only a diagenetic product.

4. Epirostrum

The terms orthorostrum and epirostrum were introduced by Müller-Stoll (1936) in his study on the composition of the belemnite guard. In many belemnites, a complete calcitic rostrum (orthorostrum) is covered by an additional rostrum, commonly of quite different morphology and also different in structure. Usually, the structure of this additional epirostrum consists of an inner part, called the "corpus pulposum" and an outer layer called the "tubus lamellosus" by Müller-Stoll.

The epirostrum was built only after the belemnite had reached an adult stage, thus marking late ontogenetic growth that increased the length of the rostrum. The most apical part of the shell of a belemnite was called the "rostrum solidum" by Müller-Stoll (1936) in contrast to that part of the guard that was deposited on the chambered shell (alveolus), the "rostrum cavum".

The difference in construction of epirostra in comparison to the orthorostra was noticed by early workers, like Quenstedt (1858) and Branco (1879). Quenstedt found in a group of belemnites that the solid orthorostrum was covered by an epirostrum that, in transverse section, showed a more angular nucleus and somewhat irregular lines of growth (Pl. 1, Fig. 6). He noted the appearance of (1) this group in the Upper Pliensbachian marls (Lias Delta); (2) in the Lower Toarcian (Lias Epsilon), a variety of forms with short as well as long orthorostra, with well distinguished epirostrum and others with more indistinct transition from the orthorostrum to epirostrum; (3) in the Upper Toarcian (Lias Zeta) of southern Germany, a group with short orthorostra or finger-like orthorostra.

The earliest representative of this group, according to Quenstedt (1848), has a thumb-like orthorostrum. The early parts of the orthorostrum of thumb-like forms often consist of a juvenile rostrum of conical, more or less slender shape, as noted by Abel (1916) and as can be seen in all thin sections of such forms. Quenstedt (1848) grouped all belemnites with slender, outgrown rostra containing an orthorostrum portion and an epirostrum added to it into the genus *Belemnites acuarius*. His subspecies *Belemnites acuarius amalthei* as first representative of this group in the Upper Pliensbachian "Schwarzjuraton" owns a long orthorostrum followed by an epirostrum of about the same length while the subspecies *Belemnites acuarius macer* from the Upper Toarcian for example has a very short, conical orthorostrum and a very long, slender epirostrum.

Quenstedt (1848) also noted differences in the outer morphology of the calcitic orthorostrum, which is smooth, and that of the epirostrum, which shows longitudinal crests and furrows. This morphology is preserved when epirostra are covered with a thin, massive layer (Quenstedt 1848, pl. 25, figs. 1a, 12, 21, 22) or where the epirostrum was attached to the orthorostrum (pl. 25, figs. 27-30).

Branco (1879) noted that in *Belemnites acuarius ventricosus* a short solid ortho-rostrum was followed by a long, tubular, "spongeous" rostrum covered with a thin solid layer. Abel (1916) studied specimens of this species and suggested three steps of rostrum formation: 1) construction of orthorostrum; 2) rapid growth of a flexible pike-shaped, spongeous guard; and 3) a rigid covering.

Doyle (1985) elaborated his own theory of epirostrum formation based on the structural differences in guards of *Belemnites acuarius tubularis (Youngibelus tubularis)*. According to him, the calcitic outer tube of the epirostrum is secondarily filled with a structureless, porous, granular mass, while the orthorostrum protruded into the epirostral cavity. Similarly, Riegraf (1980) described hollow, long epirostra in the *Belemnites acuarius ventricosus* of Quenstedt (*Dactyloteuthis (Cuspiteuthis) ventricosus*).

The studied material from different localities in the Fränkische Alb (southeastern Germany) from Toarcian beds shows that orthorostra vary in width from 5-20 mm, in length from 1-52 mm, in shape from conical to well-rounded and finger-like, and with or without 1-3 apical furrows. Epirostra vary from small central areas (evenly surrounded by smooth layers) and caps (Pl. 2, Fig. 6) to long or very long tubular shapes, with thick or thin, even-layered cover (Pl. 2, Fig. 1).

The structure of the rostra provides clear evidence of deposition of the ortho-rostrum substance at the same time and associated with the epirostrum substance (Pl. 2, Figs. 4, 6; Pl. 3, Figs. 1, 4). Growth lines pass from one substance to the next so that neither a hollow tube formed (Riegraf 1980, Doyle 1985) nor a flexible rod stage was present (Abel 1916). The differences in mineral structure found in the orthorostrum and epirostrum clearly indicate that the materials originally compos-


Text Fig. 1

A: Sketch of *Belemnites acuarius longisulcata* from Lias Zeta in Blumenhof (Franconia) with short orthorostrum and transition into the epirostrum. A calcitic cover surrounds the aragonitic core of the epirostrum. Actual length of rostrum about 7 cm.

B: Sketch of *Belemnites acuarius* with a medium-sized (5 cm long) orthorostrum connected to a slightly longer epirostrum. The calcitic cover of the aragonitic core of the epirostrum covers the whole rostrum except for the apical portion. Such ontogenetic stages of rostrum growth resulted in empty tubes when the aragonitic core was dissolved, allowing sediment to enter during early diagenesis or redeposition. Specimen used as model is from Hausheim, Franconia, Lias Zeta.

C: Sketch of *Belemnites acuarius tubularis* from Lias Epsilon of Mistelgau, Franconia, with medium-sized orthorostrum (4 cm) and very slender, long epirostrum. The aragonitic core of the epirostrum is covered by a continuous sheet of calcite so that the epirostrum, during diagenesis, either collapsed and became compacted or the core was recrystallized as blocky calcite.

D: Sketch of *Dactyloteuthis irregularis* from Lias Zeta of Hausheim, Franconia, showing the thumb-like orthorostrum, an even broader transitional rostrum, and the short epirostrum.

E: Sketch of *Megateuthis* cf. *gigantea* from Bajocian of Osnabrück region, Westfalia, with transitionally secreted calcitic epirostrum. Only the small inner part originally was mostly aragonitic. Actual length of whole rostrum 36 cm.

F: Sketch of *Neohibolites minimus* from middle Albian of Hildesheim, Lower Saxony, with short but complete epirostrum. Actual length of whole rostrum 4 cm.
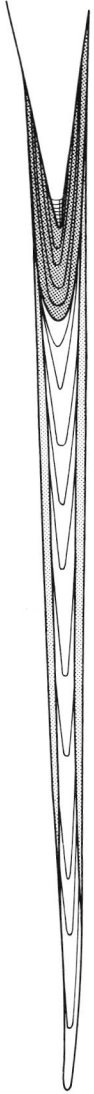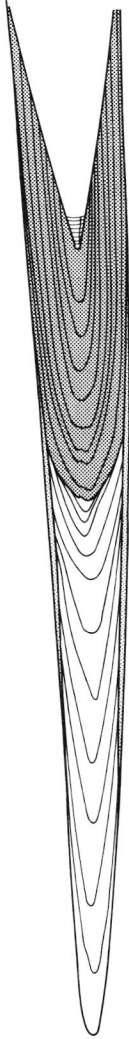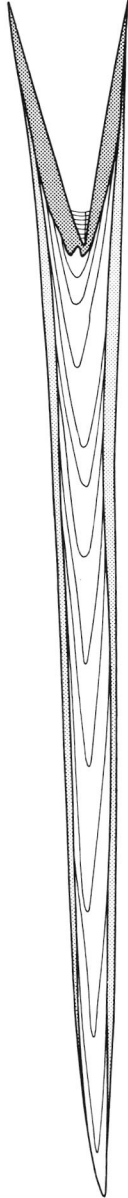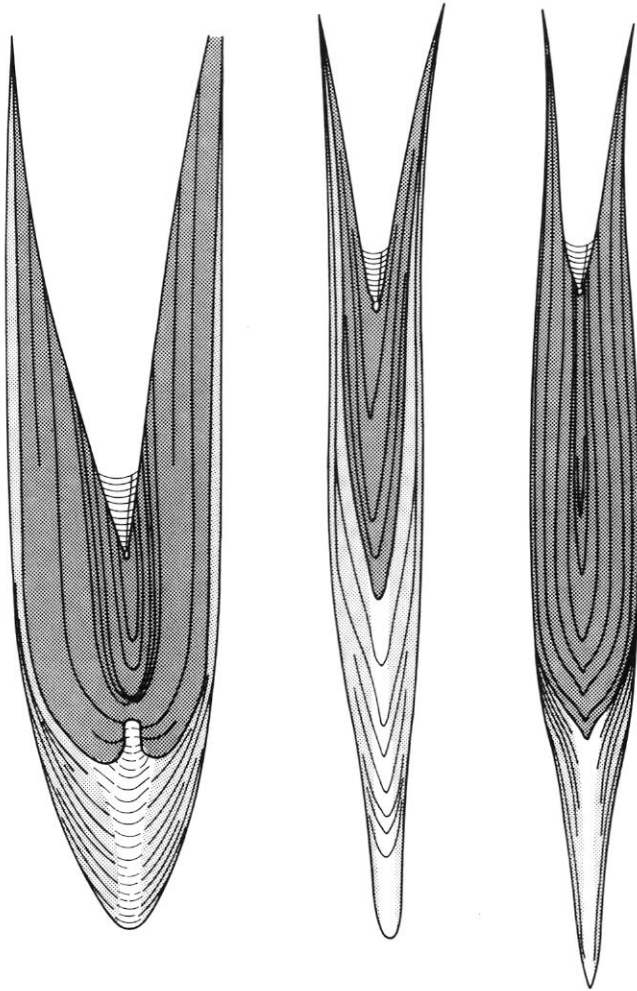
Orthorostrum

Epirostrum

Calcite

Aragonite

ing them were different. The orthorostrum was and is composed of calcite, while the epirostrum mainly consisted of aragonite which during diagenesis either was transformed into calcite (see Dullo & Bandel, this volume) or was dissolved, leaving a cavity which was filled either with sediment (Pl. 2, Fig.1) or cement. (Pl. 2, Fig. 2).

The modifications of the $CaCO_3$, calcite and aragonite, not only differ in their crystal structure and their stability during diagenesis, but also in the preferred arrangement of their crystals. Calcite grows in fine prismatic layers with crystal needles parallel to each other, while aragonite is commonly arranged in spherulite sectors (Bandel 1975, pl. 7, figs. 1-4; 1977, pl. 2, figs. 1-4). In aulacoceratids like *Aulacoceras* and related genera, the rostrum was aragonitic (Jeletzky & Zapfe 1967), commonly with longitudinal ridges and furrows, as seen in Toarcian epirostra (Pl. 1, Figs. 1, 2, 6), Lower Cretaceous *Neohibolites* (Pl. 5, Fig. 4), and in the "rostra" of Eocene *Vasseuria* (Steinmann 1910). When such originally aragonitic rostra were transformed into calcitic fossils, they commonly retained part of their structure by preserving undulating lines of growth as well as areas richer in organic material, which filled the small space between neighbouring spherulite sectors (Fischer 1947, Gordon 1966). Characteristic radial structures like those shown in Pl. 1, Figs. 1, 2 result in branching rays and undulating surfaces.

From observations of the morphology, diagenetic history, and remains of the original structure, it can be safely assumed that the primary mineral composition of epirostra was aragonitic. However, parts of the epirostra could also be composed of organic sheets with crystal spherulites scattered on and between them (Pl. 3, Fig. 1; Pl. 2, Figs. 5, 6) and cavities between sheets and mineral layers filled with liquid or gelatinous mucus substance, as seen in modern oyster shells.

Naef (1922) stated that "the rostrum of a belemnite is a relatively small terminal end of the skeleton and its shape and surface structure should not be overemphasized in their value for systematics". But even with this as a warning, systematic classification of Jurassic belemnites commonly disregards features which can be observed on rostra in favour of one or few other characteristics. In the most recent taxonomic evaluation of these belemnites, one of the major criteria in the diagnosis of the superfamily Belemnitidae Riegraf (1980) is that the rostrum is massive and composed of primary calcite. In many cases, neither primordial nor late adult rostra of members of this superfamily are totally calcitic but contain aragonitic as well as organic shell layers. All Jurassic epirostrum-bearing forms discussed in this paper belong to the family Polyteuthidae which, as this name indicates, includes species with rostra of many shapes, except that none have a dorsal and/or ventral furrow. Riegraf (1980, 1981) suggested several genera to compose the subfamily Acrocoelitinae of which *Acrocoelites, Youngibelus,* and *Dactyloteuthis* have species with and without epirostra. All species of *Salpingoteuthis* have epirostra, while species of *Brachybelus* and *Rhabdobelus* are small and bear only orthorostra. Authors like Schwegler and Riegraf have placed major importance on the shape of the outgrown orthorostrum, but since the internal structure of rostra was not considered, no clear criterion can be given that allows a distinction between juvenile and early adult or later adult rostra.

To put it bluntly, the classification of southern German Toarcian belemnites of the *Belemnites acuarius* group of Quenstedt has, in the course of later studies of

members of this group, not been improved. The reason for the confusion is that neither rostrum structure nor the change in rostrum shape during the course of ontogeny has ever been considered.

Belemnites with long epirostra thus have been placed into four different genera and several more subgenera according to 1) the shape of the orthorostrum (*Acrocoelites* and *Dactyloteuthis*); 2) the size of the orthorostrum (*Youngibelus* and *Salpingoteuthis*); and 3) the presence of furrows on the orthorostrum (*Acrocoelites* and *Youngibelus*).

Matters have become even more complicated after Doyle's (1985) revival of an idea first expressed by d'Orbigny (1842) and cited by Quenstedt (1848) that we also have to consider sexual dimorphism. On the basis of similar morphologies found among Recent squid d'Orbigny thought that females may have had short rostra while males produced long epirostra after becoming mature. Doyle suggested that *Youngibelus tubularis,* which has an extremely long epirostrum, had a partner which is known as *Y. levis,* which had no epirostrum. Other pairs could easily be matched, in many cases crossing generic or at least subgeneric boundaries.

There is also no clear indication of whether certain orthorostra shapes gave rise to others. Possibly the oldest representative of the whole group is *Belemnites dens* (= *Coeloteuthis dens*), which according to Werner (1912, pl. 10, fig. 7) shows the characteristic evolutionary step of epirostrum formation on a solid triangular conical orthorostrum. It is found in the Upper Sinemurian. The Pliensbachian form, observed by Quenstedt (1848), has a thumb-like orthorostrum. Species with very thin orthorostra and very long, slender epirostra are known from the Upper Toarcian (Lias Zeta) with *B. acuarius macer,* but *Chitinobelus acifer* from the Lower Toarcian (Fischer 1981) may be practically the same rostrum, only with a totally decalcified epirostrum (due to diagenesis). It is quite unlikely that *Chitinobelus* is an epirostrum-bearing belemnoteuthid as assumed by Engeser & Reitner (1983).

Epirostra were originally described only from Jurassic belemnite species of the above-mentioned genera. The first description of a well definable epirostrum in a Cretaceous belemnite was published by Delattre (1953) who illustrated a specimen of *?Hibolites escragnollensis* from the southern Alpine Neocomian. Spaeth (1971) found a high percentage (over 50% on the average) of epirostrum-bearing specimens preserved in several Middle and Upper Albian species and subspecies of the *Neohibolites minimus* (Miller) group in northwestern Germany, Britain, and France.

In Upper Cretaceous belemnites, no epirostra seem to have been preserved (or were not built in general).

Especially in the Albian *Neohibolites minimus* group, epirostra often obscure the characteristic shape of the adult orthorostrum (Text Fig. 1 F). This has already had consequences on taxonomy, such as when J. de Sowerby (1829) regarded the elongation by an epirostrum in *Neohibolites minimus* (Miller) as species-specific character and named those forms "*Belemnites attenuatus*". Using a series of longitudinal thin sections Spaeth (1971) proved that only a varying percentage of individuals of the *Neohibolites minimus* species group have a preserved epirostrum.

Adult *Neohibolites* specimens with a developed, preserved epirostrum can generally only be identified in a longitudinal section of the whole guard. Spaeth (1971) rejected the assumption of Müller-Stoll (1936) that epirostra might have grown and been resorbed at least two or more times during the life span of a (Liassic) belemnite individual. It is also quite impossible to assume continued growth of the orthorostrum after one or more resorption phases of the epirostrum, as suggested by Müller-Stoll (1936).

In many cases, epirostra of the *Neohibolites minimus* group show the same characteristic mode of building as in the Liassic belemnites, although the Albian species never reached the epirostral length (relative to the orthorostrum) of the Jurassic specimens.

An apparently different way of epirostral elongation in late ontogenic growth can be observed in longitudinal sections of some megateuthids of mainly Bajocian age. Although the longest belemnites which ever existed lived during this epoch, these forms do not always distinctly show typical epirostrum secretion. The mode of growth is frequently transitional and mostly adds to the width of the whole rostrum (Pl. 4, Fig. 1). There may be a remarkable elongation by epirostra of about 60%, but their growth is generally much more like the solid secretion of the orthorostrum in most megateuthis. In many specimens, however, the apical innermost region of the epirostrum shows a rather irregular secretion of the growth lamellae, thus resembling the epirostral type of the Liassic forms (Pl. 4, Fig. 1); these growth lamellae were originally partly aragonite.

These observations suggest that the epirostra in megateuthids were secreted primarily as calcite, with the exception of a narrow central zone that consisted of aragonite.

5. Pseudalveola

In Upper Cretaceous belemnites, the species of the genera *Actinocamax, Gonio-teuthis,* and *Belemnellocamax* have an angular adapical cavity, the pseudalveola. This cavity is the result of post-mortem dissolution of the aragonitic phragmocone and the aragonitic adapical portion of the rostrum. Here we have no differentiation of epi- and orthorostrum, so that the adapical portion of the orthorostrum is an integral part of the rostrum.

The shape and depth of the pseudalveola is species-specific and can help to characterize genera. The cavity of the rostrum is wider than the actual alveolus, containing the chambered portion of the shell that was covered by the rostrum. Usually, only the area of the first chamber is still visible in the pseudalveolus, so that in the most apical portion the alveolus and pseudalveolus meet. In an interesting case (Pl. 5, Fig. 6), the steinkern of the alveolus formed before the pseudalveolus was etched from the orthorostrum. The time of dissolution of the aragonitic adapical portion of the rostrum can be fixed prior to final sediment compaction, so that the sediment-filled adveolus became deformed. This shell of *Gonioteuthis* landed on the bottom after death. Here the chambered portion of the shell that had been destroyed became infilled with sediment. After burial in the sediment, the

aragonitic portion of the rostrum dissolved, leaving the pseudalveolus. Afterwards, the surrounding sediment became further compacted, flowing around the solid calcitic rostrum, while the sedimentary fill of the alveolus remained in place and was not further compacted.

Further evidence for an originally aragonitic adapical rostrum is obtained from features seen on the surface of the pseudalveola. There, conellae are common (Pl. 5, Fig. 7). Such "barnacle-like" calcite cones have been described from the steinkerns of several ammonites by Hölder (1973). They form when aragonite layers are replaced by calcite crystals during early diagenesis (see Dullo & Bandel, this volume). Conellae-like structures formed when recrystallization of the calcite rostrum continued into the aragonitic portion of the rostrum, before the aragonitic portion dissolved. Conellae provide evidence for early diagenetic alteration of simple aragonitic shell structures, as suggested by Bandel & Hemleben (1975). In *Gonioteuthis,* conellae formed still within the aragonitic rostrum portion and before it had dissolved and the pseudalveolus developed.

In the Upper Cretaceous belemnites, an orthorostrum was deposited on the phragmocone, which consisted of regular aragonitic layers in the most anterior portions and calcitic layers in the posterior portions. The area of transition during ontogeny regularly moved in an anterior direction and from the surface of the first chamber.

6. Repair and cameral deposits

As in *Belemnoteuthis* (Bandel & Kulicki this volume), damage of the first chambers which occurred in juvenile individuals was repaired (Pl. 1, Fig. 5). An individual belonging to rostra of the *Acrocoelites* type was later damaged and healed. In another case, a late juvenile rostrum ("*Acrocoelites* stage") of a *Dactyloteuthis* type with thumb-like adult rostrum was damaged; the apical rostrum fragments remained below the muscular mantle and were cemented to the rostrum (Pl. 3, Fig. 2). Repair of the muscular mantle was accompanied by irregular deposition of rostrum layers (Pl. 3, Fig. 3). Such deposits are well known and have been illustrated by Riegraf (1981, pl. 9) who did not understand their origin. Similar spherulitic calcite deposits can also be present in the transition from the calcitic orthorostrum to the aragonitic epirostrum (Pl. 2, Fig. 4).

Jeletzky (1966) stated that all representatives of the Belemnitidae have cameral deposits in the apical chambers of the phragmocone. In some individuals of the material here studied, such deposits were also noted, but definitely not in all of them. Commonly, chambers were filled completely or partially by pyrite during early diagenesis so that cameral deposits would have become preserved. But only about one out of three specimens with chambers preserved well enough for safe judgement had cameral deposits of the type shown in Pl. 3, Fig. 6. The others had none (Pl. 3, Fig. 5).

7. Results

While mineral shell layers of the phragmocone of Jurassic and Cretaceous belemnites are aragonitic, those of the rostrum can be calcitic and aragonitic. The mineralogy of the rostrum changes during ontogeny. The primordial rostrum and that of very young, hatched belemnites is aragontic in all well-studied cases. The subsequent orthorostrum, in most cases (with the exception of the Upper Cretaceous one) is calcitic. In a late ontogenetic stage, the adult animal may secrete an epirostrum, probably connected with mating migrations and habits, which commonly contains aragonitic portions.

During ontogeny, the morphology as well as the structure of the belemnite rostrum changes. A systematic classification of belemnites that does not take these changes into account is incomplete and most likely incorrect. Fossils with different modifications of the $CaCO_3$ in the construction of their shell (like all belemnites) have to be studied in a way that accounts for diagenetic changes.

Belemnites were a major source of food for many larger cephalopods, fish, and a few reptiles, and were hunted throughout their life. Non-fatal damage of the shell, especially at the rostrum, is common, thus repair is also frequent. This calls for caution when single individuals are described and features seen only once or rarely are interpreted.

Calcite exists as well as aragonite in the form of different biominerals and biostructures. Prismatic calcite layers, as present in the belemnite rostrum, show regular crystallite arrangement; spherulitic arrangement is rare or present only when mineralisation was spotty. Aragonite, in contrast, tends to grow in a spherulitic manner, especially when biological control is not very tight. Calcitic growth surfaces thus tend to be smooth while aragonitic surfaces may show ridges and furrows. This is certainly no rule, but only a common observation, since aragonitic prismatic layers can also have smooth growth surfaces and parallel needle arrangement.

8. Discussion

According to Naef, belemnite rostra have been known for thousands of years, but the name *Belemnites* was introduced by Agricola (1546). That the rostrum is connected to a chambered part (phragmocone, alveolus) was discovered by Luidius (1699) and Scheuchzer (1702). Ehrhardt (1727) demonstrated that belemnites were marine animals related to modern *Spirula.* Quenstedt (1848, 1858) and Branco (1879) found belemnite rostra which had changed morphology and composition during the animal's lifetime. Steinmann (1910) tried to differentiate belemnites, including aulacoceratids and *Vasseuria,* according to the longitudinal ribs and furrows and the impressions of the vascular system on the rostrum surface. This method could not be continued when it was discovered that aulacoceratids and belemnites are different groups of coleoids and that *Vasseuria* belongs to a group totally separate from that (Naef 1922, Jeletzky 1966). Imprints of the vascular system on the rostrum is a convergence between some aulacocerids and some belemnites (Bandel 1985); the structure and surface sculpture of the rostrum is a

matter that is related to shell structure, as demonstrated here. But an aragonite rostrum does not have to have longitudinal ridges and a structure of spherulite sectors, as seen in *Belemnoteuthis* (Bandel & Kulicki, this volume).

Dauphin's (1984) opinion that the belemnitid rostrum in general was primarily aragonitic and was transformed into calcite during ontogeny is proved wrong. This opinion cannot be based on data published by Spaeth (1971: 38-40) who discussed the existence of preserved aragonite in the adoral rostral part of a *Neohibolites minimus* specimen. It was pointed out (op. cit., p. 40) that the preservation of the studied specimen from the Gault clay of Folkestone (Brit. Mus. Nat. Hist., No. C 45848) did not allow a distinct separation of the deformed, thin, adoral part of the rostrum cavum into a calcitic rostral substance and possibly deformed proostracum material, which is primarily aragonitic. Several subsequent authors seem to have misunderstood or overemphasized the presence of aragonite (e.g. Dauphin 1984). The question of aragonite and/or calcite discussed by Spaeth (1971) did not refer to the embryonic and primordial rostrum and the epirostrum complex.

Unfortunately, in an article on the isotopic composition of belemnites by Spaeth, Hoefs & Vetter (1971), in table 2 on page 3144 "aragonite" was erroneously printed instead of "calcite" in the second column. This error has doubtlessly caused some confusion concerning aragonite/calcite preservation in belemnites.

9. Conclusions

The belemnite rostrum is the product of secretions by the muscular mantle on the actual shell produced by the periostracum gland zone and the shell mantle. Mineral deposits of the epithelium have a simpler structure than those of the shell mantle. Four deposits can be formed in the rostrum. The first is calcite, either in spherulites or (more commonly) in regular, fine prisms with crystal axes parallel to each other and arranged in well ordered prismatic layers; the second is aragonite, with needle-like crystallites arranged in spherulites, commonly into spherulitic sectors and less commonly into prismatic layers with needles parallel to each other.

The third shell deposit consists of organic sheets which may be fused to form layers which may connect crystal aggregates and layers, perhaps forming compartments and blisters which hold the fourth and last component of the rostrum, liquid, either water or mucus. Such blisters and liquid inclusions may well have been present in some parts of the epirostra.

The belemnite rostrum is a support structure of the muscular mantle and is related to the muscular base of the fins. Rapid growth of rostra indicates a change in the biology of a belemnite, as in some Recent squid, where males enlarge their apical end (Naef 1922) before mating occurs. Perhaps some belemnites, like many Recent squid, lived for only one year, with mating in many species being preceded by rostrum-fin reconstruction and rearrangement, as suggested by Doyle (1985).

Acknowledgments

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Plate 1

1 Thin section through the epirostrum of *Belemnites acuarius subtubularis* from Lias Zeta of Wallen-
  bach, Franconia. Originally aragonitic arrangement of spherulite sectors is preserved in the calcite.
  × 8.

2 Thin section through the epirostrum of *Belemnites acuarius* from the Lias Zeta of Hausheim, Fran-
  conia, with a thin calcitic cover that protected the aragonitic spherulite sectors, which subsequently
  recrystallized as calcite. Lines of growth have been preserved and reflect longitudinal ribbing of the
  aragonitic epirostrum, while its calcitic portion was smooth. × 5.

3 Thin section through apical end of the phragmocone of *Belemnites acuarius longisulcata* from Lias
  Zeta south of Hausen, Franconia. The shape of the primordial rostrum is easily visible (arrow) as well
  as traces of the cameral deposits (double arrow). Both were originally aragonitic. × 18.

4 The primordial and early juvenile rostrum of *Belemnites acuarius subtubularis* from the Lias Zeta of
  Wallerbach, Franconia, was aragonitic and longitudinally ribbed. Calcitic orthorostrum layers reflect
  this ribbing at first, but subsequent calcitic covers are smooth. × 16.

5 This section through the apical end of the phragmocone of *Belemnites acuarius* from Lias Epsilon of
  Mistelgau, Franconia, shows fractured and repaired early shell with at least 10 chambers broken off.
  Repair followed paths similar to those observed in *Belemnoteuthis* (Bandel & Kulicki 1987). × 38.

6 Thin section of an *Acrocoelites* from the Lias Epsilon of Mistelgau, Franconia, showing a recrystal-
  lized epirostrum of angular shape surrounded by a recrystallized ribbed portion and finally a thick,
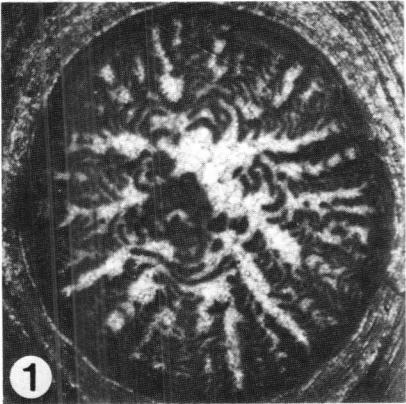 evenly laminated originally calcitic cover. × 4.
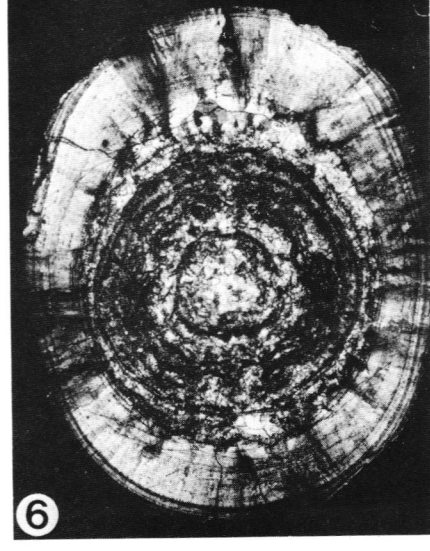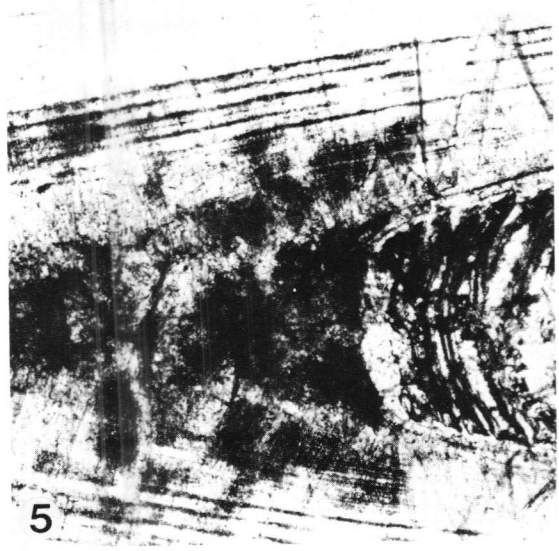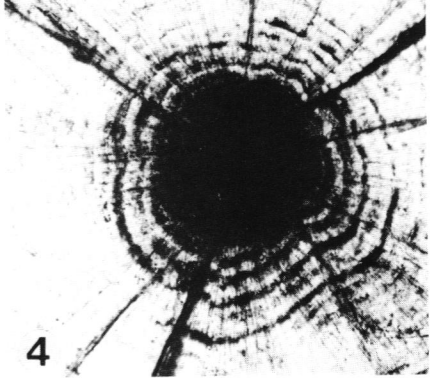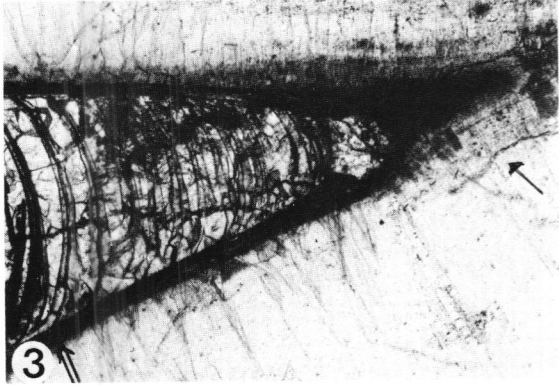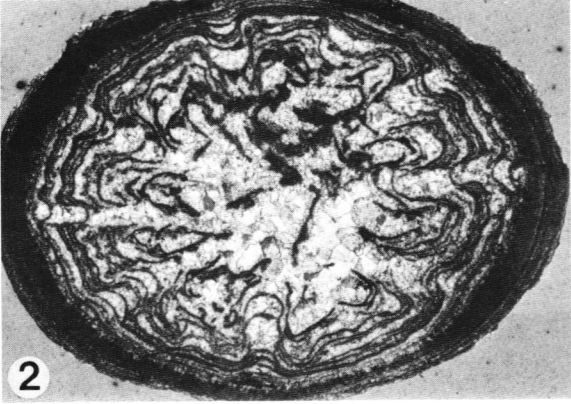
Plate 2

1 *Belemnites acuarius tubularis,* thin-sectioned with aragonitic portion dissolved during early diagenesis so that the tube thus formed became filled with sediment. From Lias Zeta of Teufelsgraben, Franconia. ×9.

2 Transition from orthorostrum to epirostrum in *Belemnites acuarius inaequistriata* from the Lias Zeta of Hausheim, Franconia. The orthorostrum is preserved in its original composition, while the aragonitic epirostrum is recrystallized and may, in part, have been totally dissolved, the cavity then filling with calcitic cement. Growth increments that were rich in organic material were preserved as pyritic crusts. ×6.5.

3 The epirostrum of *Belemnites acuarius longisulcata* from Lias Zeta south of Hausen, Franconia, was not totally covered by calcitic sheets, so that it dissolved in its apical portion which was then filled with sediment, while aragonitic structures were transformed into calcite during later diagenesis. ×6.

4 Thin section of the transition between the original, calcitic layers of the orthorostrum and the recrystallized layers of the epirostrum in *Belemnites acuarius longisulcata,* a form with a very short orthorostrum; from Lias Zeta south of Hausen, Franconia. ×5.

5 Thin section with orthorostrum covered rather abruptly by the epirostrum, which recrystallized and in its more apical portion was dissolved and filled by pyrite. *Belemnites acuarius* from Lias Zeta of Hausheim, Franconia. ×5.

6 Transition of orthorostrum into the epirostrum in specimen of *Dactyloteuthis digitalis* from Lias Zeta of Hausheim, Franconia. Aragonitic layers in the center of the epirostrum grade laterally into calcitic layers. ×5.
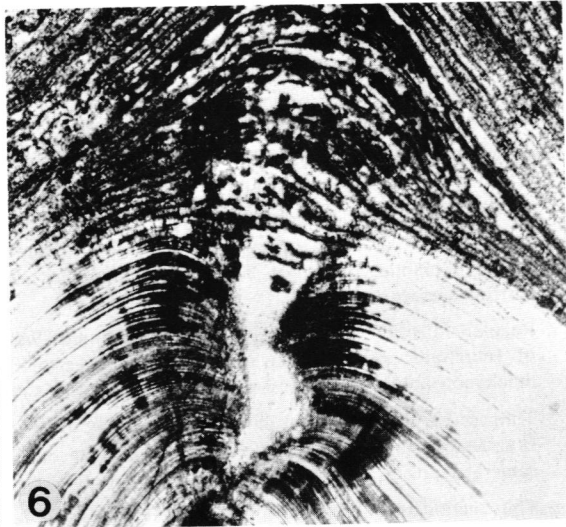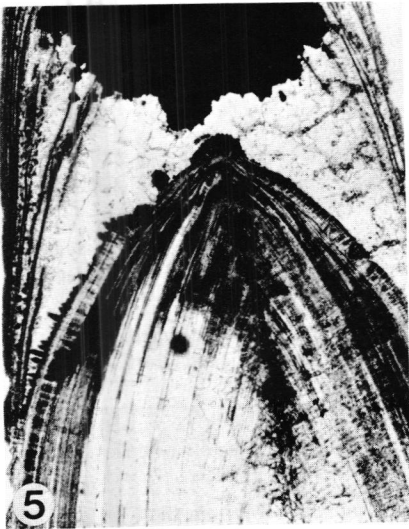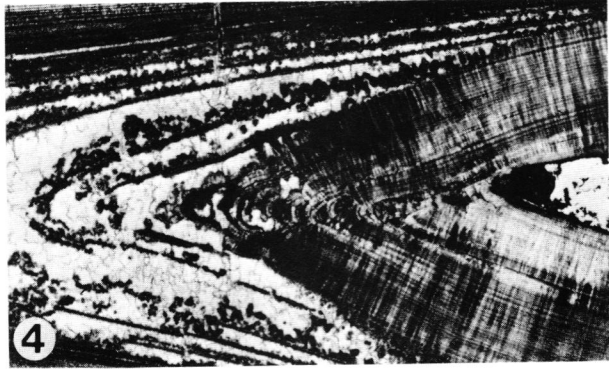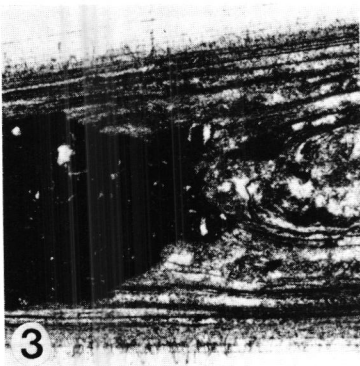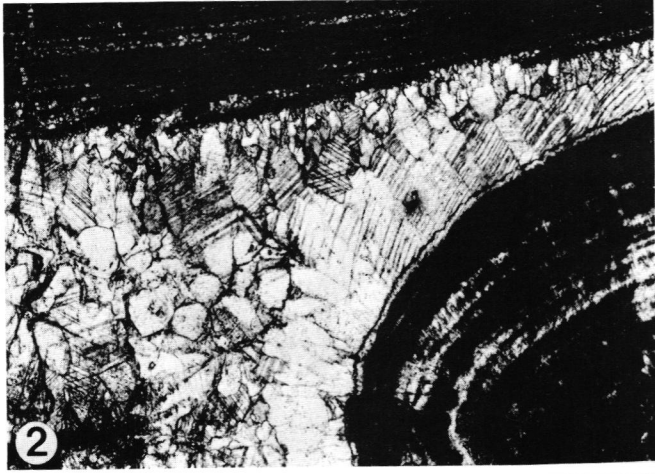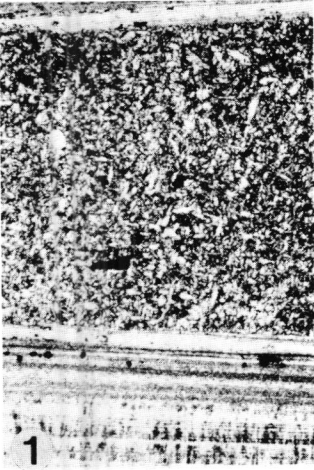
Plate 3

1 Transition of orthorostrum and epirostrum of *Dactyloteuthis irregularis* of the Lias Zeta from Haus-
   heim, Franconia. While former aragonitic layers were dissolved and cavities later filled by cement,
   organic layers were preserved and covered with pyrite. The rapid transition from calcite to aragonite
   along a growth line is evident. × 8.

2 A repaired rostrum of *Dactyloteuthis* from Lias Zeta from Hausheim, Franconia, in thin section. The
   fragments of the damaged rostrum remained in place, but repair of the muscular mantle resulted in a
   change in deposition from regular to irregular (see Fig. 3). × 5.

3 Detail of the type of rostrum growth that followed damage of the apical end of the rostrum and the
   muscular mantle covering it. Spherulitic columns of calcite grew, resulting in a tubular, irregular
   rostrum surface. × 15.

4 Regular transition of calcitic layers of the rostrum of *Belemnites acuarius longisulcata* from Lias Zeta
   of Teufelsgraben, Franconia, into aragonitic layers of the epirostrum. A regular transition without
   much morphological change is present from the ortho- to epirostrum. × 4.

5 Thin section through apical phragmocone of *Dactyloteuthis irregularis* from Lias Zeta of Hausheim,
   Franconia, showing a well-preserved siphuncular tube (left side) and septa totally uncovered by
   cameral deposits. This is the more common case. × 42.

6 Thin section through apical phragmocone of *Belemnites acuarius tubularis* from the Lias Zeta of
   Teufelsgraben, Franconia, showing septa with cameral deposits (arrows) and the siphuncular tube
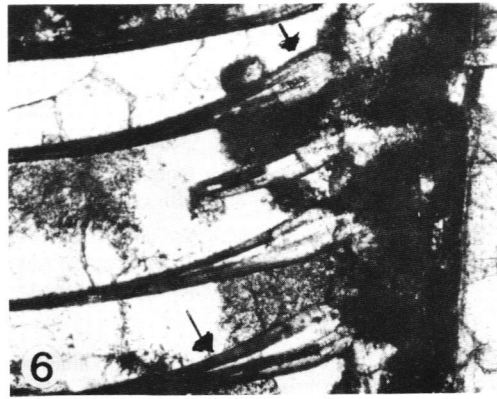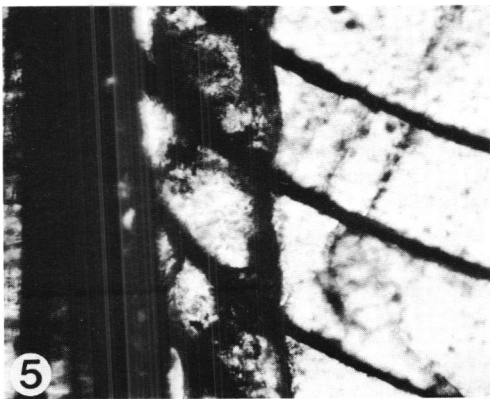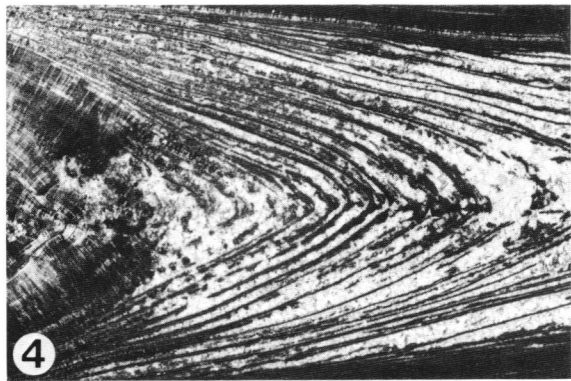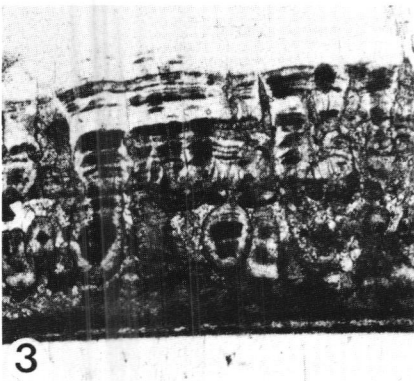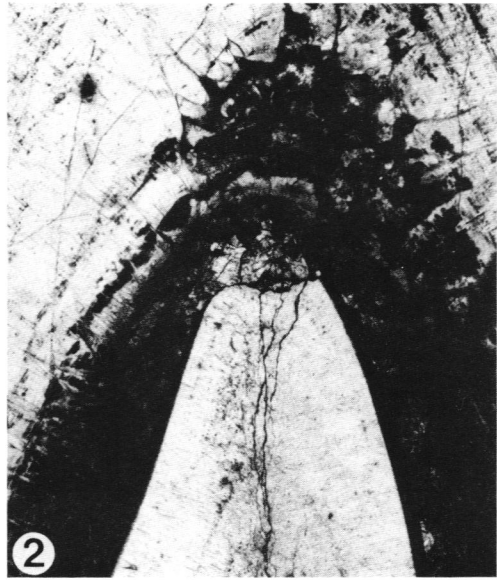   (right side). × 27.

Plate 4

1 Dorsoventral section through orthorostrum and epirostrum of young specimen of *Megateuthis* cf. *gigantea* (v. Schloth.) from Bajocian of Osnabrück region, Westfalia, showing massive calcitic epirostrum with originally aragonitic central part. Ventral side left. × 1.

2 Longitudinal thin section of *Neohibolites oxycaudatus* Spaeth from Upper Albian of Lüneburg, Lower Saxony, with complete epirostrum on apical end of orthorostrum. Inner (white) portion of epirostrum was originally aragonitic. Thin section was used as photo negative. × 3.

3 Same as 2. × 10.

4 Thin section of complete epirostrum on apical end of orthorostrum of *Neohibolites minimus* (Miller) from Middle Albian of Salzgitter, Lower Saxony. Outer calcitic and inner, originally aragonitic part clearly visible.
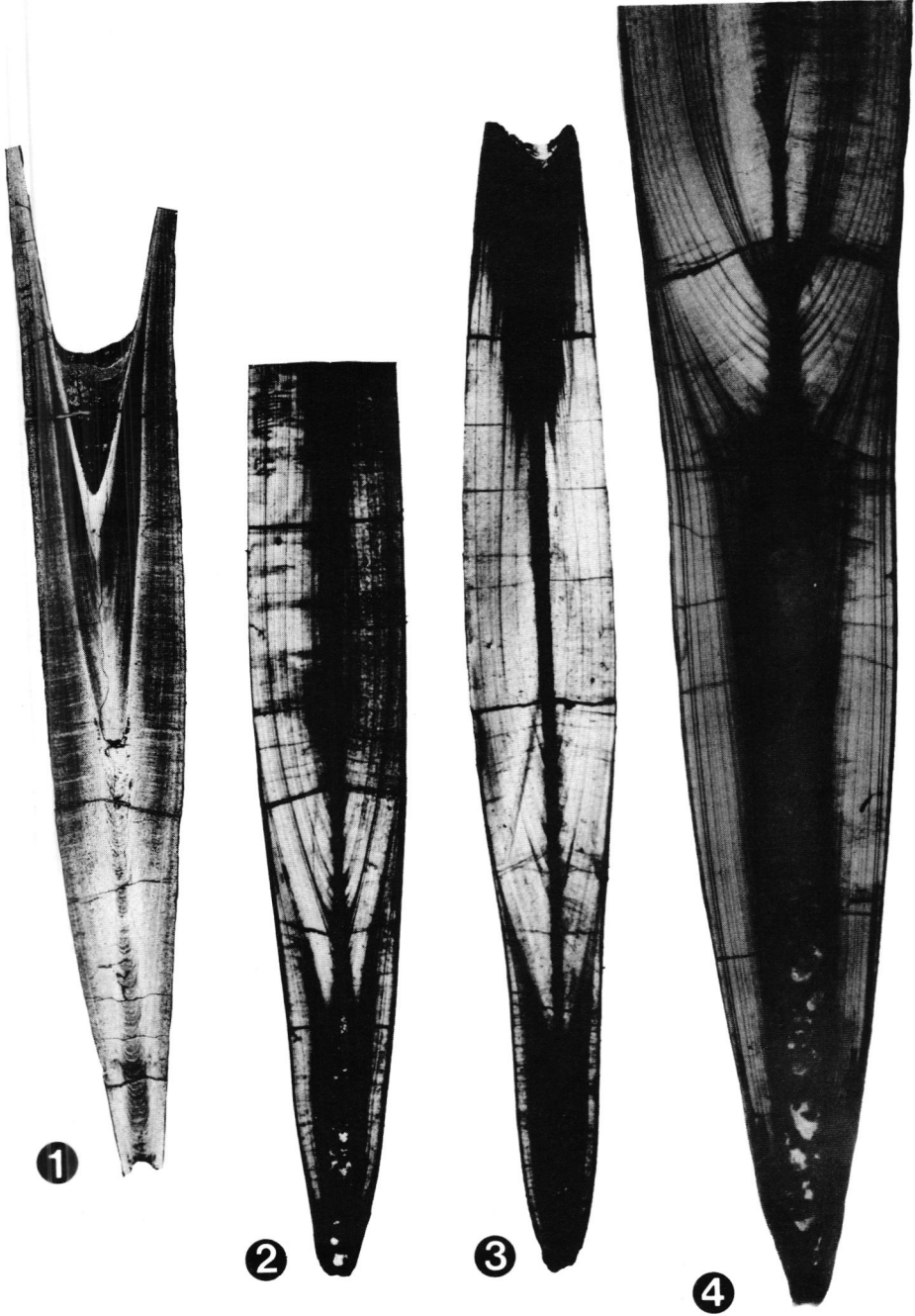Thin section was used as photo negative. × 10.

Plate 5

1 Thin section of primordial cone and primordial rostrum of *Neohibolites minimus* (Miller) from middle Albian of Hildesheim, Lower Saxony. Primordial cone and rostrum consisted originally of aragonite and organic layers; in later growth stages they were covered by calcitic rostral lamellae. ×35. (from Spaeth 1971).

2 Thin section through primordial rostrum of *Neohibolites minimus* (Miller), originally consisting of aragonite (center) and discordantly covered by calcitic rostral layers of the juvenile to adult rostrum. Middle Albian of Hildesheim, Lower Saxony. ×100. (from Spaeth 1971).

3 *Neohibolites ernsti* Spaeth, upper Albian from Winzenburg, Lower Saxony. Longitudinal thin section through adult rostrum with epirostrum, showing inner part with diagenetic, coarse, clear calcite crystals (not hollow!). Ventral side left.
Thin section used as photo negative. ×2. (from Spaeth 1971).

4 Early growth stage of epirostrum on apical end of *Neohibolites minimus* (Miller) from middle Albian of Salzgitter, Lower Saxony, showing longitudinal furrows and ridges on outer surface. Apical tip broken off. ×9.5. (from Spaeth 1971).

5 Transverse section through complete epirostrum of *Neohibolites minimus* (Miller) from middle Albian of Hildesheim, Lower Saxony, showing furrows and ridges in the inner to middle part and circular lamellar preservation of the outer layers originally consisting of calcite. ×18. (from Spaeth 1971).

6 *Gonioteuthis granulata* (Blainville) from upper Santonian of Braunschweig, NW Germany, with partly preserved (though slightly deformed) phragmocone cast in the pseudalveolus. ×1. (Coll. Geol. Pal. Inst. Mus. Univ. Hamburg).

7 Pseudalveolus of *Gonioteuthis quadrata* (Blainville) from Lower Campanian of NW Germany, with conellae seen from oral end of rostrum. ×9. (Coll. Geol.-Pal. Inst. Mus. Univ. Hamburg).