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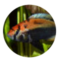

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The palaeobiology of belemnites – foundation for the interpretation of rostrum geochemistry

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ABSTRACT

Belemnites are an extinct group of Mesozoic coleoid cephalopods with a fossil record ranging from the early Late Triassic [about 240 million years ago (Mya)] to the Cretaceous/Palaeogene boundary (65 Mya). Belemnites were widely distributed, highly abundant and diverse, and an important component of Mesozoic marine food webs. Their internal shells, specifically their low-Mg calcite rostra, have been used as palaeoenvironmental carbonate archives for the last 70 years. This is primarily due to the assumption that the rostrum calcite formed in equilibrium with the oxygen isotope composition of ambient sea water. Of prime importance for the reliable interpretation of isotope data derived from these biogenic carbonates is a robust reconstruction of the palaeobiology of their producers. Here we provide a critical assessment of published reconstructions of belemnite soft-body organization and their lifestyle and habitats. Different lines of evidence, including sedimentological, geochemical, morphological, and biomechanical data, point towards an outer shelf habitat of belemnites, for some taxa also including the littoral area. Belemnite habitat temperatures, oxygen content, salinities, and life span are constrained based on observations of the ecology and life history of modern coleoids. Belemnite habitat depth might have been largely controlled by food and temperature, with a temperature optimum between 10°C and 30°C. The distribution of modern coleoids is for most species restricted to well-oxygenated water masses and a salinity between 27 and 37 psu. The trophic position of belemnites as both predators and prey is documented by unique fossil finds of stomach contents and soft tissue preservation, such as jaws, hooks, and ink sacs. Belemnites were medium-sized predators in the epipelagic zone (not deeper than ∼200 m) hunting for crustaceans, other cephalopods, and fishes. Taxa with elongated rostra probably were fast and highly manoeuvrable swimmers. Forms with conical rostra represent slow but highly manoeuvrable swimmers, and forms with depressed rostra likely had a bottom-related life habit. Predators of adult belemnites were sharks, bony fishes, and marine reptiles. Belemnites, like most of the modern coleoids, were relatively short lived, most likely living only for 1–2 years. Understanding the biomineralization of belemnite rostra is highly relevant for an improved interpretation of their geochemistry. Here we confirm that belemnite rostra are composed of low Mg-calcite fibres, but they do not contain distinct types of laminae. These fibres are composed of two distinct calcite phases. One phase is a filigree network of tetrahedral organic-rich calcite and the second phase is represented by organic-poor calcite.

Key words: palaeobiology, belemnites, palaeoenvironment, biomineralization, carbonate archives, palaeobiogeography, cephalopods, geochemistry, Coleoidea.

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I. INTRODUCTION

Belemnites were a group of coleoid cephalopods whose fossil remains are common in Jurassic and Cretaceous marine sediments. They originated during the Late Triassic and went extinct at the Cretaceous/Palaeogene boundary (Iba *et al.*, 2011, 2012). Belemnite rostra are iconic fossils and were among the first carbonates used for palaeotemperature estimates based on the oxygen isotope method (Urey, 1948; Urey *et al.*, 1951; Lowenstam & Epstein, 1954). Belemnites have become the predominant marine geochemical archive for palaeo-environmental studies of the Jurassic to Early Cretaceous.

Formerly, belemnites were regarded as a part of the ‘Belemnoidea’, a group which united basal, rostrum-bearing coleoids (e.g. Jeletzky, 1966; Doyle, Donovan & Nixon, 1994; Fig. 1A). Belemnoidea, however, is paraphyletic and belemnites are now again, after Naef (1922), placed at the base of the decabrachian coleoids (Fuchs *et al.*, 2013; Klug *et al.*, 2016; Fig. 1B). The belemnotheutids and diplobelids are coleoid groups that are potentially closely related to the belemnites *sensu stricto*, i.e. all species with a calcitic rostrum. Herein, we restrict the terms belemnite and Belemnitida to these calcite-rostrum-bearing forms (Reitner & Engeser, 1982; Engeser, 1990; Fuchs *et al.*, 2013). We refer to the paraphyletic assemblage of the Belemnitida, Belemnotheutida, and Diplobelida as ‘belemnoids’. The interrelationships of these ‘belemnoids’ with crown-Decabrachia are largely unresolved. It is, for example, unclear if characters like the fins and suckers of belemnotheutids were present in belemnites (Fuchs, Boletzky & Tischlinger, 2010; Klug *et al.*, 2015, 2016).

Herein we collect and review data available for the reconstruction of belemnite palaeobiology and the structure of their internal skeletons. Based on this, we critically evaluate belemnite palaeobiology, which can in turn be used for the interpretation of geochemical data derived from the mineralized internal belemnite skeleton.

II. PALAEOBIOLOGY OF BELEMNITES

(1) Introduction

Most of the scientific and popular reconstructions of belemnite animals are based on sparse evidence from rare soft-part preservation of few konservatlagerstätten (e.g. Seilacher, 1970; Reitner & Urlichs, 1983; Schweigert, 1999, 2018; Klug *et al.*, 2010, 2015, 2016). Even in such deposits, belemnite fossils tend to be less well preserved than co-occurring gladius-bearing octobrachians, probably due to the original presence of ammonia in the soft tissues of decabrachians (Clements *et al.*, 2017) or perhaps because neutral buoyancy resulted in longer *post mortem* drift periods (see Donovan, 1989 and Yacobucci, 2018 for *post mortem* drift in cephalopods).

Some of the uncertainties related to the palaeoenvironmental interpretation of geochemical data from belemnites are due to the poorly constrained palaeobiology of the belemnite animals. Belemnite habitat depth during rostrum formation presumably had the largest impact on the oxygen isotope composition of the carbonate *via* the ambient temperature. Attempts to reconstruct belemnite habitat depths include sedimentological evidence, oxygen isotope data, rostrum morphology, comparisons with modern coleoids, and mechanical analysis. Belemnites may have migrated (diurnally or seasonally) or changed their depth habitat during ontogeny. Further, different species with different ecology, potentially reflected by different rostrum

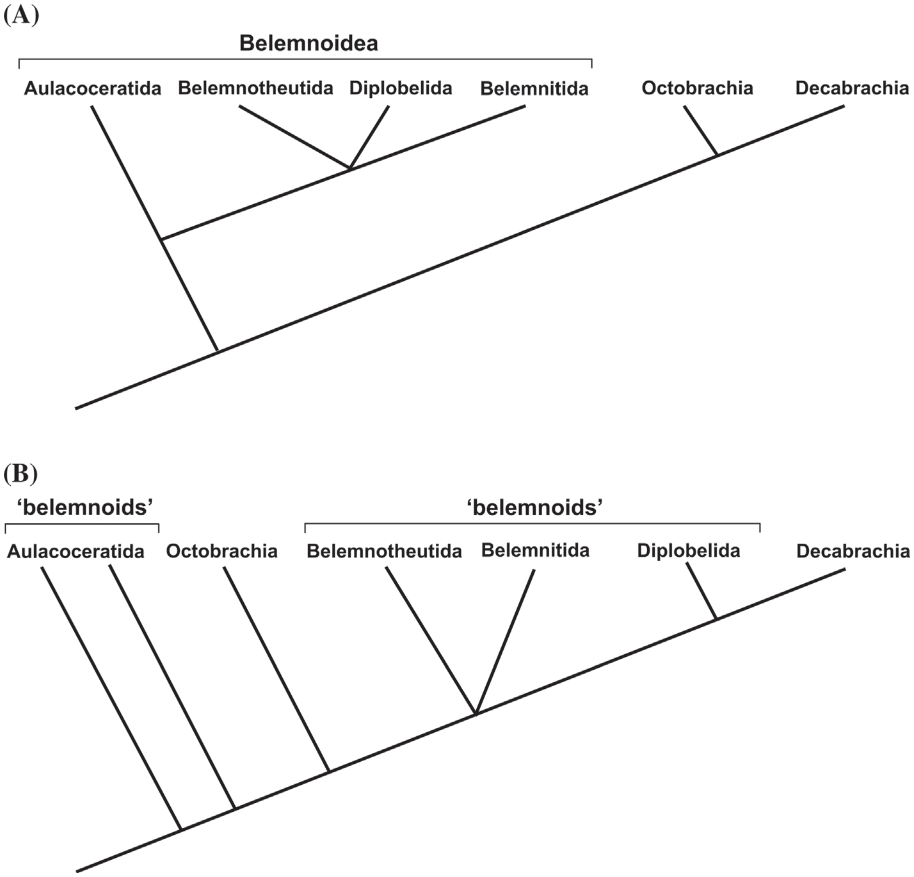

Fig. 1. (A) The obsolete hypothesis of coleoid phylogeny placed belemnites (Belemnitida) together with similar taxa, the belemnotheutids and diplobelids, and the basal coleoids (Aulacoceratida) in a group called Belemnoidea (e.g. Jeletzky, 1966; Doyle *et al.*, 1994). (B) Belemnites, belemnotheutids, and diplobelids are now regarded as stem-decabrachians (after Fuchs *et al.*, 2013).

morphology (Dera, Toumoulin & De Baets, 2016), as well as behavioural differences between the sexes could have affected their geochemistry.

Other environmental parameters constraining belemnite ecology, such as water temperature, oxygen, and salinity are largely derived from observations of modern coleoids. Salinity tolerance of belemnites might be a crucial factor because changes in salinity might have affected the oxygen isotope composition of the belemnite calcite and which could result in unrealistic reconstructed palaeotemperatures.

Another important aspect of belemnite palaeobiology deals with their palaeobiogeographic distribution. Temporal changes in belemnite distribution can be used to detect regional or global climate changes (e.g. Mutterlose, 1998).

The reconstruction of belemnite buoyancy is of interest to clarify if these animals were active continuous swimmers or not. Except for error-prone mathematical models (e.g. Hewitt, 2000) no calculation of buoyancy based on high-resolution tomographic data or precise computer-based models exists. This significant lack of data is due to the usually incomplete preservation of belemnite phragmocones, but detailed three-dimensional (3D)-models might help to overcome this limitation (see Peterman, Barton & Yacobucci, 2019). Results of such investigations could clarify whether belemnites record bottom or sea-surface water temperatures and might further elucidate their lifestyle and swimming mode (e.g. for ammonites, see Lemanis *et al.*, 2015).

Similar to the reconstruction of potential belemnite habitats, the reconstruction of belemnite life span is also based largely on information from modern coleoids, which almost all share the 'live fast and die young' life-history strategy (O'Dor & Webber, 1986). Increment counts of belemnite rostra might seem a good indicator for age estimates but comparison with 'recording structures' of modern coleoids casts doubt on this method (Arkhipkin *et al.*, 2018).

Based on their wide global distribution and high abundance in the fossil record of Jurassic and Cretaceous deposits, belemnites clearly represent a key component of their ecosystems. Information about the position of belemnites in the Mesozoic food chain can be derived from belemnite stomach contents, stomach contents of belemnite predators, or palaeopathologies. Further, the presence or absence of armaments such as jaws and hooks, or defence strategies, such as an ink sac or camouflage using skin colour patterns comparable to modern coleoids, might be informative.

Other factors that affect the interpretation of oxygen isotope ratios derived from belemnite rostra are the unknown timing of formation, the unknown biomineralization pathways, and the presence or absence of vital effects (e.g. McConnaughey, 1989*a*,*b*, 2003; Hoffmann *et al.*, 2016; Stevens *et al.*, 2017). No reliable data are available regarding where and when (in terms of water depth and temperature) belemnites formed their internal skeleton. It also remains unclear whether belemnites had uroliths (calcium phosphate granules formed by the renal organs) and if they used them as a Ca depot comparable to modern *Nautilus* (Ward *et al.*, 2014; see Section II.11).

Problems may arise from the improper description of the sample site within the examined rostra. Due to potential differences in the mineral composition and distribution of distinct microstructures, which are characterized by different crystal fabrics, varying amounts of organic matter, and differences in elemental composition within the rostrum, it is important to use a uniform terminology to distinguish between the sampled rostrum regions (see Section III). In addition, this necessitates correct taxonomic identification of the studied rostra.

(2) Soft-body reconstruction and locomotion

Belemnites have often been reconstructed as torpedo-shaped, squid-like cephalopods with large lateral eyes, fins, an ink sac, and ten arms of equal length (no tentacles, i.e. long, ejectable, specialized arms) equipped with paired chitinous hooks. The presence of about 40 micro-hooks per arm (10 arms ≈400 hooks in total), a streamlined body, and a sharp beak (Klug *et al.*, 2010 for *Hibolithes semisulcatus*), indicates that belemnites were active predators (Rexfort & Mutterlose, 2006, 2009; Fuchs *et al.*, 2010; Hoffmann, Weinkauf & Fuchs, 2017).

While many of these characters have been found in body fossils of, e.g. the Lower Jurassic genera *Passaloteuthis* and *Acrocoelites* (Reitner & Urlichs, 1983; Donovan & Fuchs, 2016; Fuchs & Hoffmann, 2017), we still lack evidence for large eyes and fins. Similarly, a radula, present in most cephalopods, has not been reported for true belemnites. A radula was, however, described for the 'belemnoid' belemnotheutid *Acanthoteuthis* by Klug *et al.* (2016).

The internal skeleton of belemnites might have served as a muscle attachment site for fins, specifically the longitudinal grooves on the surface of belemnite rostra have been interpreted as fin attachment sites (Stevens, 1965; Schlegelmilch, 1998; Klug *et al.*, 2010). Fins have recently been reported for the closely related belemnotheutid *Acanthoteuthis* by Klug *et al.* (2016). It is, however, unclear if this suggests the presence of fins in belemnites proper, as direct evidence is still lacking. Further, the rostrum is regarded as a counterweight mechanism ensuring horizontal orientation of the longest body axis. Belemnites share the presence of a phragmocone as a buoyancy device with modern sepiids and *Spirula spirula*. The presence of a fully developed phragmocone suggests that belemnites were neutrally buoyant and could swim freely in the water column (Naef, 1922; Stevens, 1965; Bandel & Spaeth, 1988; Monks, Hardwick & Gale, 1996). Due to the reduction of the calcareous body chamber to an organic dorsal pro-ostracum, the mantle cavity was enlarged and the muscular mantle more powerful compared to cephalopods bearing a closed living chamber, like externally shelled cephalopods and basal coleoids. The increased volume of the mantle cavity improved jet-propulsion-based locomotion, which in turn allowed fast swimming.

Fuchs *et al.* (2016) reviewed the locomotion system of Mesozoic Coleoidea. They found that the marginal attachment of the muscular mantle in belemnites had a ventro- or dorsomarginal position (see also Doguzhaeva, Mutvei & Donovan, 2002; Doguzhaeva *et al.*, 2014). The putative nuchal-locking cartilage tentatively identified in two belemnoids together with a funnel-locking cartilage was proposed as a synapomorphy for a group comprising 'belemnoid' stem-decabrachians and crown-Decabrachia (Fuchs *et al.*, 2016). The presence of such a nuchal- and funnel-locking apparatus, together with a ventrally open body chamber and the muscular mantle producing the main locomotory force instead of a chamber-pump mechanism, renders rostrum-bearing belemnites as fast, highly manoeuvrable medium-sized predators [e.g. Klug *et al.*, 2010 and herein].

Belemnites might have resembled extant shelf-dwelling loliginid squids morphologically (e.g. *Loligo*, *Sepioteuthis*; Naef, 1922; Stevens, 1965; Jarvis, 1980), but shared a similar construction of the mantle musculature with the nektobenthic sepiids (Monks *et al.*, 1996; Bizikov, 2008). Compared to sepiids, *Loligo vulgaris* has a higher mantle cavity pressure resulting in a much higher jet velocity for propulsion. Froude efficiency is highest for *L. vulgaris* at 0.3 (*Sepia officinalis* is 0.16) and lowest for *Nautilus pompilius* and *N. belauensis* (0.09–0.15), providing squids of the genus *Loligo* with a very effective propulsion mechanism (Chamberlain jr., 1987).

One discussion about the swimming direction of belemnites was based on borings produced by cirripeds (ichnogenus *Rogerella*) on belemnite rostra (Seilacher, 1968; Petriconi, 1971; Seilacher & Gischlick, 2015). It was suggested that cirripeds infested belemnites during their lifetime, that the mantle tissue was very thin or did not cover the rostrum at all in adult specimens, and that the orientation of the cirriped borings indicates a dominant swimming orientation of belemnites in frontal direction. This is rejected here due to a lack of a reaction of the host to the infestation during its lifetime (see Section II.12 and Fig. 5I, J; see also Keupp, 2012; Hoffmann *et al.*, 2018*a*). Belemnites could most likely modulate their swimming direction *via* the siphon, but probably travelled fast or for longer distances in a posterior direction like modern coleoids.

(3) Habitat depth and migration patterns

(*a*) *Sedimentological evidence*

Shelf habitats were reported for the Jurassic and Cretaceous belemnites of New Zealand (Stevens, 1965), for *Hibolithes jaculoides* from NW Germany and NE England by Mutterlose (1978), and *Belemnitella* and *Gonioteuthis* are also likely to have occupied shelf habitats (Hoffmann & Stevens, personal observations; see Fig. 5K,L). According to Jarvis (1980) and Christensen (1997*b*), Late Cretaceous belemnitellids lived for the most part on the continental shelf, but probably spawned and, at least in females, died in littoral settings. Jarvis (1980) based this on the presence of belemnite rostra of all ontogenetic stages in nearshore, shallow-marine sediments like biocalcarenites, greensands, marls, and shallow water chalks, and on the lack of rostra in deeper water chalks. A littoral to inner shelf environment was reported by Christensen (1976) as the most likely habitat for belemnites. Belemnite rostra are also commonly found in lagoonal carbonates of the Late Jurassic Nusplingen Plattenkalk as well as in conglomeratic and sandy littoral facies of the Aalenian of Western Europe and the Upper Cretaceous of southern Sweden (Schweigert, 1999, 2018; Weis & Mariotti, 2007; Stevens, Mutterlose & Schweigert, 2014).

Doyle & Bennett (1995) reported belemnite rostra from a series of facies ranging from littoral to offshore depositional environments. This interpretation is much closer to modern neritic, shelf-dwelling squids like loliginids (Doyle & Pirrie, 1999). Following the work of Anderson *et al.* (1994, see Section II.3.*b*), many researchers proposed a nektobenthic lifestyle for belemnites to explain cooler-than-expected temperatures reconstructed from the stable oxygen isotope composition of rostrum calcite. A bottom-dwelling lifestyle, however, seems unlikely due to the presence of belemnite rostra in sediments deposited under anoxic conditions, e.g. black shales (Rexfort & Mutterlose, 2009; Malkoč, Mutterlose & Pauly, 2010). Black shales that mostly lack any benthic or nektobenthic organisms due to anoxic bottom waters, e.g. the Early Jurassic Posidonienschiefer (Posidonia Shale) of Holzmaden, yielded well-preserved belemnite rostra including *Acrocoelites*, *Parapassaloteuthis* and *Passaloteuthis* (Hauff & Hauff, 1981; Seilacher, Reif & Westphal, 1985; Oschmann *et al.*, 1999). Transportation of these rostra seems unlikely due to the fine and undisturbed lamination of those shales and the occurrence of some of the most complete belemnite fossils from these strata. Sediments rich in organic matter of Barremian age (Hauptblätterton of NW Germany) lack any benthic organisms but contain a rich nektic fauna including fishes, reptiles, and belemnites of the genus *Aulacoteuthis* (Mutterlose, 1983; Rexfort & Mutterlose, 2009; Malkoč & Mutterlose, 2010). Actively swimming cephalopods do not tolerate low oxygen concentrations, which also seems likely to have been the case for belemnites (O'Dor & Webber, 1986; Seibel *et al.*, 1997; Guerra, 2006). These findings support the notion that belemnites in general had a pelagic, nektic mode of life.

Martill *et al.* (1994) reported that fossil coleoids (*Belemnopsis*, *Belemnotheutis*, *Cylindroteuthis*, *Mastigophora*, *Romaniteuthis* and *Trachyteuthis*) only appear late in transgressive sequences, which they interpreted as evidence for an offshore habitat of these taxa. Reports like these may have led some authors to consider belemnites as inhabitants of deeper hemipelagic environments. Interestingly, Jarvis (1980) and Schweigert (2018) reported the presence of nearly all ontogenetic stages in the same depositional setting which contrasts with the assumption of long lateral or vertical migrations (see Fig. 5K,L for *Belemnitella* and *Gonioteuthis*).

(*b*) *Interpretation based on stable oxygen isotope data*

Based on stable oxygen isotope analyses, Stevens & Clayton (1971), Doyle & Bennett (1995) and Schmid (2011), assumed a neritic or neritic-pelagic and vertical migrating lifestyle for belemnites. By contrast, Anderson *et al.* (1994) and subsequent workers (e.g. Martill *et al.*, 1994; Wierzbowski, 2002; Dera *et al.*, 2009; Wierzbowski & Joachimski, 2009; Price & Teece, 2010; Wierzbowski & Rogov, 2011; Wierzbowski *et al.*, 2013, 2017; Wilmsen & Niebuhr, 2017) assumed a general nektobenthic lifestyle for belemnites. According to these authors, palaeotemperatures from belemnite calcite therefore provide a bottom-water signal. Ullmann *et al.* (2014) postulated that belemnites (*Passaloteuthis*, *Acrocoelites*, *Parapassaloteuthis*, *Youngibelus*, *Pseudohastites*) changed their habitat from cold bottom waters to warmer surface waters due to seafloor anoxia during the Toarcian Oceanic Anoxic Event and afterwards inhabited a wide range of depths. Some authors (Wierzbowski, 2013; Wierzbowski *et al.*, 2017) found different palaeotemperatures in contemporaneous species from the same locality suggesting species-specific habitats. Armendáriz *et al.* (2012) refer to species-specific biological fractionation effects in belemnites in order to develop a δ^{18}O-independent palaeotemperature proxy (Mg/Ca ratio). Only a few authors discuss vital effects for oxygen isotopes (McArthur *et al.*, 2002; Lécuyer, Reynard & Martineau, 2004; Li, McArthur & Atkinson, 2012; Stevens *et al.*, 2017). Price *et al.* (2011) called for species-specific temperature equations related to lifestyle, habitat depth, and constructional differences of the belemnite rostrum. However, such species-specific temperature equations are probably not feasible, because belemnites are extinct and even calcitic biominerals are lacking in nearly all coleoids.

(*c*) *Implications based on rostrum morphology*

Based on functional–morphological constraints, belemnite rostrum morphology is governed by trade-offs between different factors such as hydrodynamics, economy of the formation of skeletal material and growth, as explained by Tendler, Mayo & Alon (2015) for ammonites as Pareto optimality (Dera *et al.*, 2016). For Jurassic belemnites from the Swabian Alb, Dera *et al.* (2016) distinguished three morphotypes analogous to the Westermann Morphospace approach in ammonoids (Ritterbush *et al.*, 2014). They suggested that hastate, club-shaped rostra were present in fast swimmers of deeper water masses and that this morphotype became dominant during the Late Jurassic. At the same time conical rostra, with poor hydrodynamic properties and long apical grooves suggesting higher manoeuvrability vanished. The dominance of hastate streamlined rostra during the Late Jurassic was regarded as a progressive optimization for swimming velocity and energy efficiency and could be linked to the Mesozoic Marine Revolution. Hydrodynamic properties of a third morphotype, with stocky to robust cylindrical and cylindroconical rostra, remain enigmatic with species probably inhabiting various environments. Their intermediate properties in terms of manoeuvrability and velocity suggest spatial or vertical migrations over long distances (Dera *et al.*, 2016).

Teis, Naidin & Saks (1968), based on isotopic temperature data, argued that belemnites with slender, elongate rostra were good swimmers capable of migrating towards deeper, cooler waters, whereas belemnites with short, massive rostra were poor swimmers restricted to the warmer littoral waters. However, Teis *et al.* (1968) did not apply any diagenesis screening, so their findings should be viewed critically. Mutterlose & Wiedenroth (2008) and Mutterlose *et al.* (2010) speculated that specimens with short, thick rostra (e.g. *Acroteuthis*) had a nektobenthic mode of life, while slender and elongated forms (e.g. *Hibolithes*) were fast swimmers, and taxa with laterally flattened (compressed) rostra (e.g. *Duvalia*) had a benthic mode of life. However, it is unclear why compressed rostra of duvaliids should indicate a benthic or rather nektobenthic lifestyle as such would be more likely to be present in dorsoventrally flattened (depressed) species, comparable in morphology to modern nektobenthic sepiids or loliginids of the genus *Sepioteuthis*. The compressed morphology of duvaliids actually argues against a bottom-dwelling lifestyle unless one imagines them similar to modern flatfishes, which is highly unlikely.

(*d*) *Perspectives from modern coleoids*

Besides generalizations regarding the belemnite lifestyle it seems plausible to assume that each species had its own ecological niche with specific temperature, salinity, pH, and food requirements. Modern cephalopods are all carnivores and occupy epibenthic, pelagic and epipelagic habitats (Nixon, 1988; Jereb & Roper, 2005; see Table 1). The evolution of ammonia-rich tissues for buoyancy (and not a rigid shell) clearly played a major role in allowing cephalopods to colonize the deep oceans. The general ecology of modern coleoids was summarized by Clarke (1996): the inshore coastal region is inhabited by octopods on rocky or coral shores and sepiolids on sand or mud. On the continental shelf, outside the wave zone, Loliginidae and Sepiidae predominate, but deep-water oceanic squids may appear seasonally although they return into deep water to spawn and live there for most of their lives.

Belemnites are likely morphologically best compared with loliginid squids and sepiids. *Loligo* generally inhabit water depths between 120 and 330 m, while sepiids predominantly inhabit depths of 0–200 m (Bettencourt & Guerra, 1999; Guerra, 2006), with an observed maximum depth of 470 m (Roeleveld, 1972). Sepiids enter shallower water for mating and at night for feeding (Naef, 1922). Squids populate shallow and deep waters, with some being eurybathic and others stenobathic. Specifically, the Ommastrephidae and Loliginidae are typically surface dwellers and are rare below 200 m (Boycott, 1965). The depth distribution of many squids is controlled by food and temperature. Different factors such as sea-surface temperature, salinity, oxygenation, and thermocline depth also affect the vertical distribution patterns of modern coleoid hatchlings (Ruvalcaba-Aroche *et al.*, 2018). It might be reasonable to conclude that the depth distribution of belemnites depended on similar factors.

Maximum observed habitat depths of modern cephalopods with a mineralized shell are 706 m for *Nautilus pompilius* (Dunstan, Ward & Marshall, 2011), and about 600–700 m during the day and 100–300 m during the night for the phragmocone-bearing extant deep-sea squid *Spirula spirula* (Clarke, 1969; Hoffmann & Warnke, 2014). Price *et al.* (2009) reported water temperatures calculated from stable oxygen isotope data ranging from 10°C to 22°C for *S. spirula*. These temperatures are comparable to water depths between 200 and 500 m. Lukeneder *et al.* (2008) calculated temperatures between 6°C and 12°C and considered *S. spirula* to hatch at a depth of more than 1000 m. This also agrees with stable oxygen isotope data from live-caught *S. spirula* from the Canary Islands indicating a variation of habitat depth during ontogeny between 350 and 800 m (Warnke, Oppelt & Hoffmann, 2010).

(*e*) *Mechanical limitations*

According to Birchall & Thomas (1983) the porosity of the cuttlebone of *Sepia officinalis* is high (93%) but it can withstand pressures of up to 20 atm (Denton & Gilpin-Brown, 1961*a*,*b*,*c*). This corresponds to about 200 m water depth and encompasses the 0–150 m depth distribution of adult *S. officinalis* (Ward & Boletzky, 1984; Neige & Boletzky, 1997). Ward & Boletzky (1984) reported that large cuttlebones implode at 150–200 m depth, while newly hatched animals implode between 50 and 100 m. Sepiids show different adaptations of their endoskeletons to deeper waters, e.g. greater curvature of the cuttlebone and its septa, more complex pillars, and denser septal spacing resulting in changes in the cuttlebone density (Ward, 2000). According to Naidin (1969), Westermann (1973), Hewitt, Westermann & Judd (1999) and Hewitt (2000) the depth limit of belemnites based on mechanical calculations of septal strength was about 100–200 m (Table 2; see also Hoving *et al.*, 2014; Wierzbowski, 2004; B. Westermann, personal communication), making migration into water depths below 200 m unlikely (Fig. 2).

Based on the presence of very thin aragonitic phragmocone walls and septa, the distribution of belemnites must have been confined to the epipelagic zone (Jeletzky, 1966; Donovan, 1977; Hewitt, Yoshike & Westermann, 1991; Arkhipkin, Bizikov & Fuchs, 2012; Doguzhaeva & Meléndez, 2017). Vertical migration of belemnites down to 1000 m depth as proposed by Zakharov *et al.* (2006, 2011) thus is rejected here. Based on observations of early ontogenetic skeleton development in belemnites such as *Hibolithes* and *Passaloteuthis*, Doguzhaeva, Mutvei & Weitschat (2003) and Doguzhaeva *et al.* (2014) described the embryonic skeletal structure of all belemnites to be designed for a nektopelagic lifestyle of the hatchlings. The embryonic skeleton comprises the protoconch, one

Table 1. Ecomorphological life modes following Aleyev (1977), from Whalen & Briggs (2018)

Ecomorphological category	Explanation	Example
Planktic – euplankton	Unstreamlined or parachute morphologies; true passive drifters	Graptoloids, *Vampyroteuthis infernalis*?
Planktic – nektoplankton	Unstreamlined or parachute morphologies, planktic animals with some swimming capability	Euphausiids, *Spirula spirula*
Demersal – eudermersus	Dorsoventrally depressed, obligate swimmers restricted to near-benthic settings	Holocephalans, *Nautilus* (although its shell morphology is not dorsoventrally depressed), sepiids
Demersal – nektobenthos	Dorsoventrally depressed, suprabenthic organisms capable of temporary swimming	Xiphosurans, octopuses
Nektic – planktonekton	Laterally compressed and tapering morphologies, weak–poor swimmers with nektic as opposed to planktic morphologies	Conodonts
Nektic – eunekton	Well-streamlined strong swimmers not confined to the near-benthos; cephalopod-specific: good jet propulsion	'Palaeonisciform' actinopterygians; loliginids

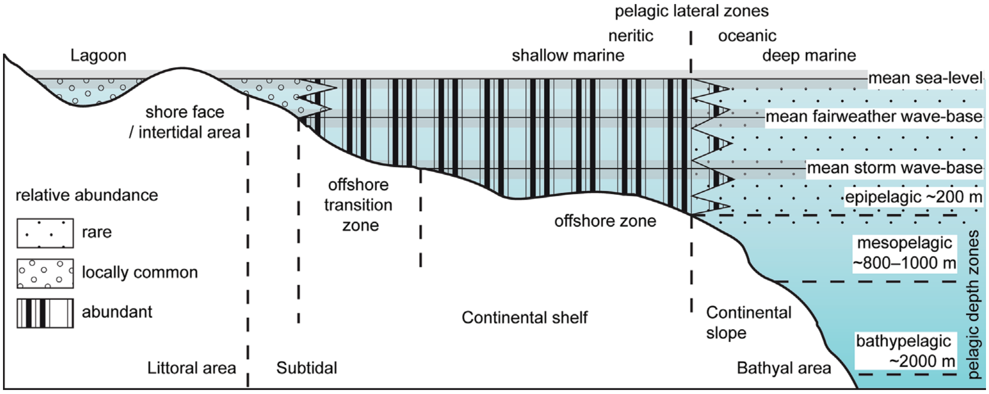

Fig. 2. Depth and lateral distribution and relative abundance of belemnites. Schematic structure of passive continental shelf modified after Flügel (1978) and Immenhauser (2009).

Table 2. Minimum and maximum habitat depth limits calculated for six belemnite taxa (data from Hewitt, 2000)

Taxon	Minimum habitat depth limit (m)	Maximum habitat depth limit (m)
Acrocoelites	82	178
Cylindroteuthis	95	189
Hastites	61	
Hibolithes		215
Pachybelemnopsis	123	157
Passaloteuthis	94	

or two phragmocone chambers, a light-weight organic-rich and probably aragonitic primordial rostrum, and the proostracum, and is about 1.5–2.0 mm long. Different scenarios for the embryonic development of shell elements have been summarized by Bandel, Engeser & Reitner (1984) and Wani *et al.* (2018) suggesting that belemnite hatchlings possessed only a protoconch with no or a few chambers. The assumed active nektopelagic lifestyle of the belemnite hatchlings could have contributed significantly to their wide geographic distribution and evolutionary success (see e.g. Villanueva *et al.*, 2016 for modern cephalopods).

(4) Habitat temperature, oxygen content and salinity

Modern cephalopods are exclusively marine animals. They have a near-cosmopolitan distribution and inhabit surface and deep waters of all oceans and seas except for the Black Sea. As summarized by Jereb & Roper (2005), modern cephalopods occur in all marine habitats with just a few caveats. One of these limiting factors is salinity. Modern cephalopods are generally restricted to salinity concentrations between 27 and 37 psu with rare exceptions [17–40 psu; see Guerra, 2006 for *Sepia officinalis*]. While modern cephalopods without a mineralized internal skeleton can be found as deep as 5000 m, most cephalopods live at depths around 200–700 m (see Section II.3 for modern coleoids with mineralized shells).

Nautilus can survive short-term exposure to temperatures of 28°C (Ward, 1987; Vandepas *et al.*, 2016), but a temperature maintained above 25°C may be lethal. Due to seasonal temperature changes some coleoids, e.g. sepiids, migrate seasonally. Sepiids live at water temperatures between 10°C and 30°C with species-specific ranges (Jereb & Roper, 2005; Guerra, 2006). Christensen (1976) assumed the Late Cretaceous belemnitellids to be stenothermal and adapted to life in warm-temperate waters. Dimitobelids were also regarded as stenothermal shallow-water dwellers (Doyle & Howlett, 1989), but, in contrast to belemnitellids, it seems that they were restricted to cooler waters (Christensen, 1997*b*).

Most modern cephalopods need well-oxygenated water for their survival. This is largely due to their relatively inefficient jet-propulsion-based locomotion (O'Dor & Webber, 1986) and to some extent also to their use of a copper-containing protein in their blood cells (haemocyanin), which is a less-efficient oxygen transporter than the iron-containing protein haemoglobin. Data on oxygen concentrations in coleoid habitats are scarce, but for *Sepia*, concentrations between 1.5 and 3.5 ml/l have been reported (Jereb & Roper, 2005). In contrast to coleoids, *Nautilus pompilius* makes use of anaerobic respiration during periods of high activity and can survive for significant periods in a hypoxic (6.666 kPa or 30% of air-equilibrated surface water) environment (Jereb & Roper, 2005; Neil & Askew, 2018). This is achieved by lower minimum metabolic costs of locomotion in nautilids compared to coleoids achieved by a high whole-cycle propulsive efficiency and by their ability to use oxygen stored in the shell chambers (Boutilier *et al.*, 1996). Similar oxygen-depleted habitat use has been reported for the vampire squid *Vampyroteuthis infernalis*, which lives in the oxygen minimum zone (Seibel *et al.*, 1997; Seibel, Thuesen & Childress, 1998). Oxygen minimum zones occur in modern oceans at depths >500 m and were presumably also present in Mesozoic oceans (Takashima *et al.*, 2006). We predict, without any direct evidence but based on data from recent shelf-dwelling, active swimming coleoids, that most belemnites inhabited well-oxygenated water masses at depths between 1 and 200 m, with a salinity between 27 and 37 psu, and temperatures that ranged between 10°C and 30°C.

(5) Belemnite palaeobiogeography and evolution

Belemnites first occurred during the Late Triassic in the north-eastern Tethys (Iba *et al.*, 2012) and have been recorded from Hettangian deposits from Europe where they experienced a rapid radiation in the neritic domains (Weis & Delsate, 2006; Iba *et al.*, 2015). Since at least the Early Jurassic (Toarcian; see Doyle & Pirrie, 1999) belemnites were globally distributed with higher diversity towards higher palaeolatitudes during the Jurassic (Dera *et al.*, 2016). While it is beyond the scope of this review to document migration patterns for specific belemnite taxa (e.g. Christensen, 1997*b* for Late Cretaceous belemnitellids, and Pirrie *et al.*, 2004 for dimitobelids), it is worth pointing out that despite their global distribution, the development of a Boreal and Tethyan belemnite realm took place in the Middle Jurassic that persisted until the Early Cretaceous (Doyle, 1987; Fig. 3). Iba, Sano & Mutterlose (2014) reported a completely different belemnite fauna from the Sinemurian of Japan, which attests to provincialism in the NW Pacific during this period. Cooling during the Valanginian to Aptian seems to correlate with the development of a fourth, the Austral Realm during the Early Cretaceous (Stevens, 1963, 1965; Doyle & Pirrie, 1999). It is largely accepted that the distribution and/or endemism of belemnite groups, e.g. the Belemnitellidae and Dimitobelidae of the Cretaceous were largely controlled by temperature. Temperature changes or other palaeoenvironmental factors (e.g. oxygenation, salinity concentration, pH, water quality, increasing predation, food availability) may have been the underlying causes of several faunal turnovers and palaeobiogeographic changes during the Jurassic and Cretaceous (Doyle, 1987; Doyle & Bennett, 1995; Christensen, 1997*a*; Mutterlose, 1998; Dera *et al.*, 2016). The causes of regional extinctions of belemnites in the North Pacific (Iba *et al.*, 2011) and during the Cenomanian (Combémorel *et al.*, 1981), as well as their final extinction during the Cretaceous/Paleogene (K/Pg) boundary event are poorly understood.

Belemnites are mostly absent from deep-sea deposits, except for very rare findings (Christensen, 1997*b*; Mitchell, 2005; Zakharov *et al.*, 2006, 2011). For example, adult belemnitellids have been collected on rare occasions from offshore, deeper water chalks (Christensen, 1976; Surlyk & Birkelund, 1977). Belemnite migration patterns include pathways along coastlines on the shelf but not directly over open ocean waters. Similar observations have been made for modern sepiids and nautilids (Jereb & Roper, 2005; Guerra, 2006; Vandepas *et al.*, 2016). *Sepia officinalis* populations in the Mediterranean Sea are known to make seasonal migrations between shallower and deeper waters (inshore during spring and summer for reproduction; and offshore in autumn). Not all animals migrate at the same time, size, age, or over the same distances (from dozens to several hundred nautical miles). Active migration of nektic cephalopods is influenced by water temperature, photoperiod, and light intensity (Mangold, 1966; Boucaud-Camou & Boismery, 1991; Guerra, 2006). An important phase of dispersal is the planktic paralarval stage in modern coleoids. Three common planktic dispersal patterns were reported by Roura *et al.* (2019): coastal, coastal–oceanic, and oceanic. In general dispersal patterns are governed by the ability of cephalopod paralarvae to undergo diel vertical migration (Zeidberg & Hamner, 2002; Vidal, Zeidberg & Buskey, 2018). Coastal dispersal patterns followed by loliginids, ommastrephids, and sepiolids are explained by an active control of the vertical position of the paralarvae: moving downward effectively limits offshore dispersal while favouring alongshore retention. Similar behaviour has been observed in crustacean larvae (Queiroga *et al.*, 2007). A coastal–oceanic dispersal pattern is

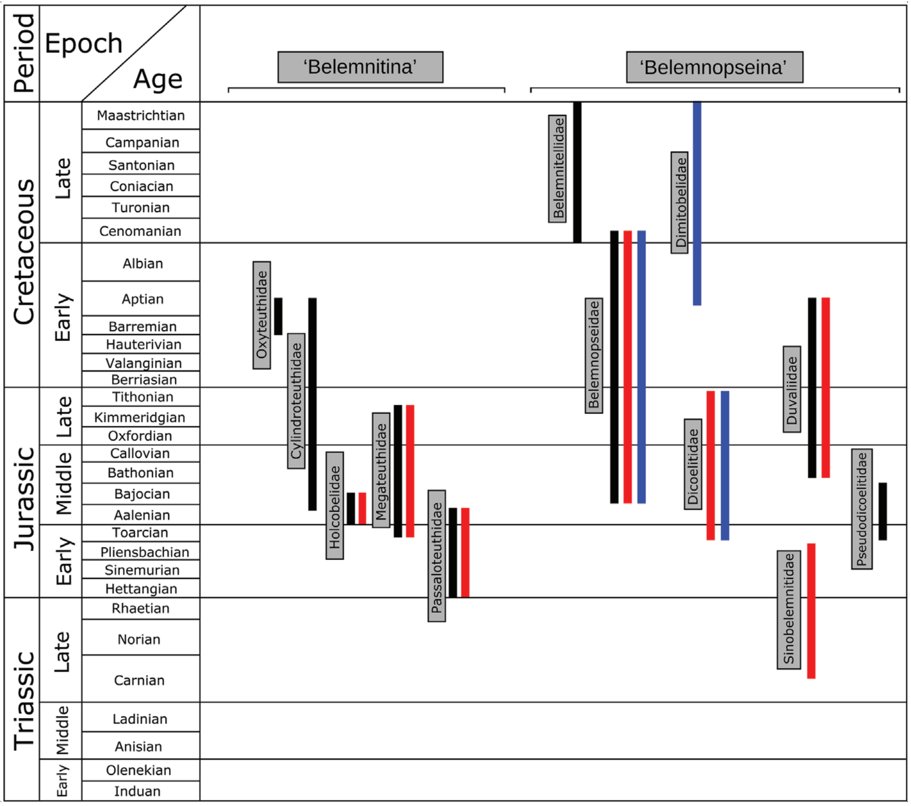

Fig. 3. Stratigraphic and palaeogeographic distribution of the most important belemnite families, red = Tethyan Realm, blue = Austral Realm, black = Euro-boreal Realm, based on data from Mutterlose (1988), Christensen (1997*b*), Schlegelmilch (1998), Iba *et al.* (2012), Weis, Mariotti & Riegraf (2012) and Ippolitov *et al.* (2017).

exclusively followed by *Octopus vulgaris*, where paralarvae are found beyond the continental shelf. This also requires a tight coupling of vertical migration behaviour and ocean currents, e.g. with oceanward upwelling filaments. Ommastrephid and sepiolid taxa followed an oceanic dispersal pattern with an increase in abundance with distance from the coast.

In conclusion, belemnites were largely restricted to epicontinental seas, which is in line with their calculated maximal depths (see Section II.3, Table 2). It seems reasonable to assume that taxa that produced fully developed hatchlings exclusively migrated along the shelves or that planktic paralarvae coupled their vertical migration behaviour with ocean current patterns to minimize dispersal, e.g. *via* upwelling currents, to stay in close proximity to the hatching area (Christensen, 1997*a*; Zakharov *et al.*, 2006; Alsen & Mutterlose, 2009; Sorensen *et al.*, 2015; Roura *et al.*, 2019). On the other hand, taxa with a near-global distribution, e.g. *Neohibolites*, probably had planktic paralarvae that dispersed *via* surface currents. Long-distance migrations have been reported for the modern squid *Illex argentinus*, which traverses large latitudinal ranges in the shelf seas off South America (Arkhipkin *et al.*, 2012). Dera *et al.* (2016) stated that belemnites inhabited surface to deep waters of epicontinental seas [see Remin, 2017 for the distribution of *Belemnella* during the Maastrichtian]. Based on the observation that Late Cretaceous belemnites were shelf dwellers, Christensen (1997*b*) speculated that oceans with deep water may have acted as physical barriers for belemnites and precluded, as is the case in *Nautilus* populations (Dunstan, Bradshaw & Marshall, 2011), the spread of these belemnite taxa. In a similar fashion, water temperature, sea-level changes, palaeocurrents, ecological tolerance, and competition could have affected the palaeobiogeographic distribution of belemnites (Christensen, 1997*b*).

(6) Buoyancy calculations

The first buoyancy calculations for belemnites were made by Hafferl (1916), cited in Abel, 1916). More recently, detailed buoyancy calculations have been conducted by Spaeth (1975), Ebel (1987), Monks *et al.* (1996) and specifically for a cylindroteuthid belemnite by Hewitt *et al.* (1999). These attempts used simplified geometries like cylinders to reconstruct the shape of the belemnite animal and may have been biased by the general acceptance of belemnites as nektic organisms. Hoffmann *et al.* (2014) and Lemanis *et al.* (2015), who used high-resolution computed-tomography data, showed relatively large errors in geometry-based buoyancy calculations for ammonoids. These errors cast doubt on the accuracy of prior belemnite buoyancy calculations due to their lack of detail.

The belemnite rostrum would have had the largest effect in such calculations because of its carbonate composition.

The precise estimation of its volume and original density (see Section III.5) will significantly affect the estimated buoyancy and position of the centre of gravity of the belemnite animal. For a precise determination of the centre of gravity and buoyancy, and thereby on swimming position, accurate estimates of the rostrum, phragmocone and soft-body volumes are important factors for the clarification of the rostrum function (counterweight model). If the centre of gravity is below the centre of buoyancy but in close proximity to it, the belemnite would have been able to swim in a horizontal orientation (Jenny *et al.*, 2019; Peterman *et al.*, 2019). If the buoyancy was equal to the gravitational force, the belemnite could have achieved stability within the water column. Obtaining accurate values of these variables is of course limited by fossil preservation. The best specimens that would allow such an attempt would be soft-body preserving specimens such as those from the Holzmaden black shales (Fig. 4B, D; Riegraf & Hauff, 1983; Jenny *et al.*, 2019), however, the aragonitic phragmocone is not preserved in these specimens. Note also that negative buoyancy of belemnites would not necessarily mean that they were unable to stay in the water column. Active swimming might have counteracted sinking of the animal, or the presence of ammonia in their soft tissue might have supplied additional buoyancy (Lemanis *et al.*, 2015; Clements *et al.*, 2017).

(7) Lifespan

All modern, active and nektic coleoids grow rapidly and reach a maximum age of about 5 years, although 1 to 2 years is more common (Jereb & Roper, 2005). They share a 'live fast and die young' lifestyle (O'Dor & Webber, 1986; Nesis, 1987; Rexfort & Mutterlose, 2006). Estimates of belemnite lifespan based on 'seasonal' variations in oxygen isotopes, e.g. Urey *et al.* (1951), Spaeth, Hoefs & Vetter (1971), or Zakharov *et al.* (2011), range from two to five years but require reinterpretation (Longnelli, 1969; Podlaha, Mutterlose & Veizer, 1998). Given the lifespans of most of their extant relatives, it is likely that belemnites lived for 1–2 years (Guerra, 2006; Rexfort & Mutterlose, 2006; Wierzbowski & Joachimski, 2009; Zakharov *et al.*, 2011). Antarctic incirrate octopods may reach ages in excess of three years, which follows the general trend that cold-water molluscs live longer than their warm-water relatives (Schwarz *et al.*, 2019). Cold-water belemnites accordingly might have had longer lifespans than warm-water species.

Belemnite growth increments and the stripe lines found in the venter of sepiid cuttlebones, which are caused by the septa of the cuttlebone and form the striated zone, might share a daily formation cycle (Choe, 1963; Wierzbowski & Joachimski, 2009). Under insufficient feeding, however, cuttlebone stripe lines do not appear or are unrecognizable. Based on the assumption of daily increment formation, the lifespan of a specimen of *Hibolithes beyrichi* was estimated to have been 1.5–2 years (Wierzbowski, 2013). Godwin (1998) counted 250 increments in Upper Cretaceous *Belemnitella* and consequently suggested that the rostrum was formed in less than 1 year. For the giant *Megateuthis gigantea* Dunca *et al.* (2006) postulated a 1.5-year lifespan based on growth increment counts. Arkhipkin *et al.* (2015) counted for the same genus 871–1084 growth increments and assumed that growth of the orthorostrum took about 2 years while formation of the epirostrum could have taken 4 months.

Rostrum formation with alternating organic-rich and calcite-rich layers also resembles the formation of coleoid statoliths. Lifespan estimates based on statolith increment counts, however, are not necessarily straightforward in all cephalopod species. Bettencourt & Guerra (2001) counted one increment per day for the first 240 days in *Sepia officinalis*. Afterwards, growth increments become weaker in their expression, resulting in poor resolution and age underestimates of about 80%. Growth lamellae on cephalopod jaws may also provide reliable structures for age determination (Arkhipkin *et al.*, 2018) but the fossil record of belemnite jaws is very limited (e.g. Klug *et al.*, 2010).

(8) Predator and prey relationships

Belemnites were likely a key component of the Jurassic and Cretaceous food chain and important as medium-sized predators in marine ecosystems. Belemnite remains such as rostra or onychite mega-hooks have been reported from stomach contents of vertebrates like sharks, elasmosaurid plesiosaurs (Urlichs, Wild & Ziegler, 1994; McHenry, Cook & Wroe, 2005), pliosaurids (Janensch, 1928), ichthyosaurs (Dick, Schweigert & Maxwell, 2016), and the metriorhynchid crocodiles *Metriorhynchus* (Martill, 1986) and *Cricosaurus* (Schweigert, 2018). The major part of the preserved stomach contents is the chitinous coleoid hooks, while the calcitic rostra seem to have been bitten off or otherwise discarded by predators (Hölder, 1955; Schweigert, 1999; Keupp, 2012). Given that the relationship between micro-hook parataxa and coleoid biotaxa remains enigmatic, these reports must be considered with caution for the reconstruction of the predator–prey relationships of belemnites (Fuchs & Hoffmann, 2017). Calcitic rostra are extremely rare as stomach contents but are known from a famous specimen of a hybodont shark from the Posidonia Shale of southern Germany, which contains approximately 200 *Acrocoelites* rostra (Fig. 4A). Some belemnite 'battlefields', such as the Yorkshire battlefield, which are characterized by many hooks, may have accumulated due to vertebrate predation and subsequent regurgitation (Doyle & Macdonald, 1993). Based on tooth morphology, wear patterns, and occasionally preserved stomach contents, Massare (1987) established different guilds (crush, crunch, smash, pierce, and general) for large Mesozoic marine predators of the Jurassic and Cretaceous, e.g. ichthyosaurs, plesiosaurs and pliosaurs, metriorhynchids, teleosaurs, and mosasaurs. These marine reptiles predominantly caught pelagic prey, as do most modern marine toothed whales, seals and large predatory fishes like billfishes and sharks. These species today fill the niche of large, mobile, pelagic predators of macroscopic prey. Functional morphological analyses revealed that reptiles belonging to the 'smash' guild, e.g. ichthyosaurs, with straight, robust cone-shaped teeth with a blunt tip and a

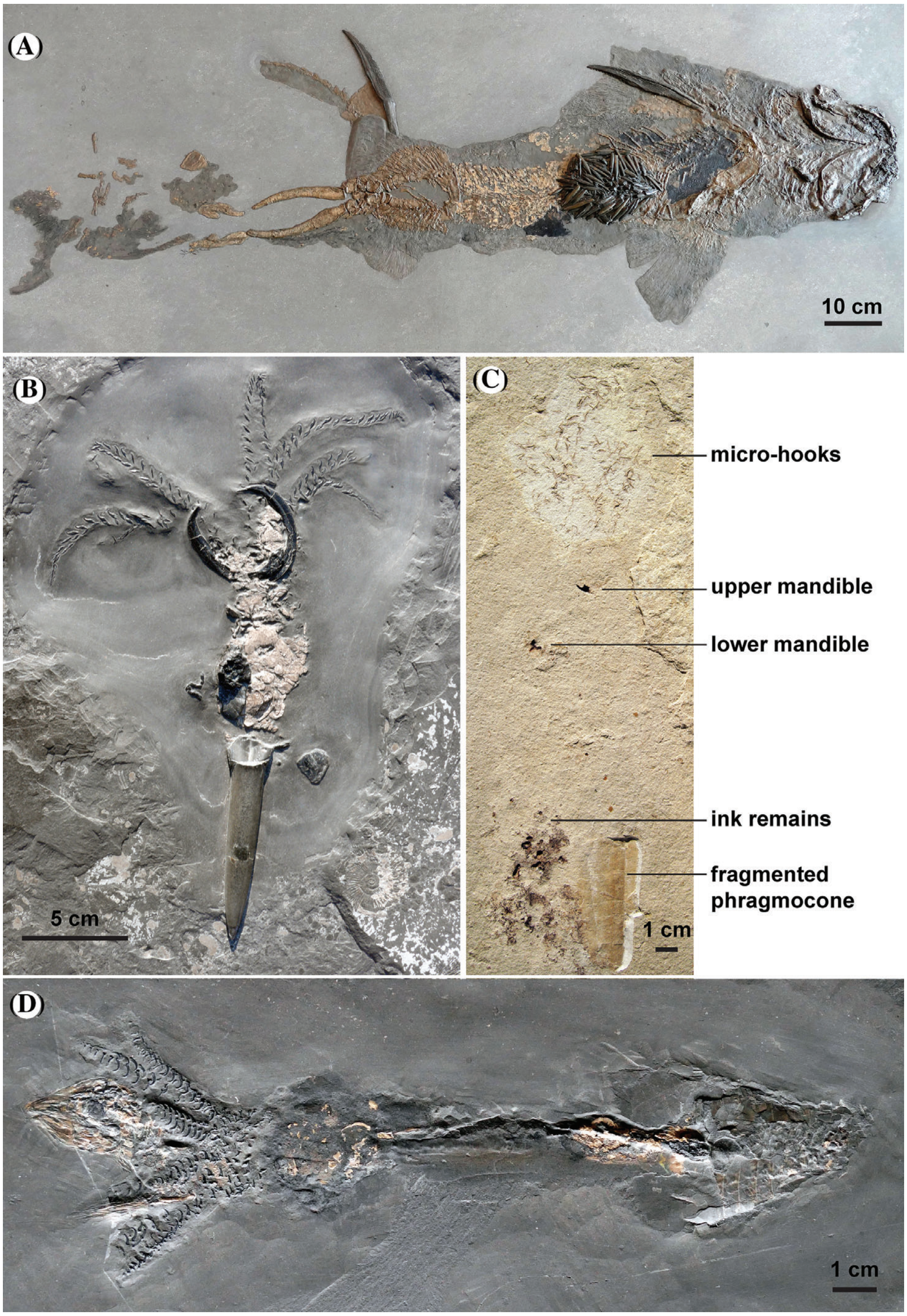

Fig. 4. Palaeoecology of belemnites. (A) The iconic shark *Hybodus* from the Early Jurassic Posidonia Shale with about 200 belemnite rostra in its stomach. (B) Early Jurassic *Passaloteuthis* from the Posidonia Shale with preserved arm armature including micro-hooks and a pair of mega-hooks tentatively regarded as characteristic feature of male belemnites. (C) Rare preserved jaw elements in the Late Jurassic *Hibolithes* from Nusplingen, SW Germany (modified after Klug *et al.*, 2010). (D) Early Jurassic *Clarkeiteuthis* from the Posidonia Shale preserved with micro-hooks and its last meal – a leptolepid fish.

circular cross section, most likely used their teeth for grasping belemnites and other soft cephalopods or fishes (Massare, 1997). Using similar arguments, chimaeras are proposed as potential belemnite predators based on their dentition (Hölder, 1955; Keller, 1977; Keupp, 2012). The very small (1–2 mm) but highly abundant belemnite hatchlings may have played a large role in Mesozoic food webs as zooplankton (primary consumer) and may have been consumed by large filter feeding invertebrates or vertebrates, e.g. pachycormid fishes (Tajika, Nützel & Klug, 2018).

In agreement with the escalation theory of Vermeij (2008, 2013) it was suggested by Dera *et al.* (2016) that the increasing number of belemnite taxa with streamlined rostra was the result of an adaptive response to the rise of new predators during the Mesozoic Marine Revolution. Belemnites themselves probably had a diet like modern squids and sepiids, e.g. of fishes, crustaceans, and other cephalopods (Bandel & Spaeth, 1988; Keupp, 2012). For example, Boucot (1990) depicted a *Belemnotheutis* with a fish in its arm crown. Recently, Klaschka (2018) and Jenny *et al.* (2019) described unique fossils from Holzmaden showing the 'belemnoid' *Clarkeiteuthis* preserved with its prey, a small teleost fish (?*Leptolepis*) in its arm crown (Fig. 4D). This finding supports the notion that belemnites, which are similarly equipped with numerous hooks, might have also hunted small vertebrates. Schweigert (2018) reported on a bitten belemnite rostrum (*Hibolithes semisulcatus*) associated with fossil ink and accumulations of bitten lamellaptychi. This find tentatively suggests that these belemnites hunted small oppeliid ammonites and could explain the abundant presence of regurgitates full of lamellaptychi in the Nusplingen Plattenkalk. Further, given the wide distribution of cannibalism in modern coleoid cephalopods (Nixon, 1987; Villanueva, Perricone & Fiorito, 2017), it seems likely that belemnites also ate their conspecifics.

(9) Jaws and hooks

In contrast to other fossil coleoids, ammonoids, or nautiloids, belemnite jaws are extremely rare. So far, an incomplete upper and lower jaw have been reported by Klug *et al.* (2010) for *Hibolithes semisulcatus* from the Late Jurassic Nusplingen Plattenkalk (southern Germany). Both jaw elements resemble types known from other coleoids (Fig. 4C), supporting interpretations of a predatory lifestyle for belemnites. Poorly preserved jaw remains have been found for *Passaloteuthis* [Riegraf & Hauff, 1983; see also Donovan & Fuchs, 2016 for a review]. An upper jaw from the Lower Aptian of NW Germany, potentially belonging to *Neohibolites* or the 'belemnoid' *Conoteuthis*, was recently reported by Lehmann *et al.* (2016).

The oldest arm-hooks are Carboniferous in age (Fuchs & Hoffmann, 2017). 'Belemnoid' hooks range in length from 0.3 to 70 mm and are divided into two categories: mega- and micro-hooks. While micro-hooks are thought to have been used to catch prey, mega-hooks are assumed to have been sexual traits of males, perhaps used to hold onto the female during reproduction. *Passaloteuthis* is the only belemnite genus in which specimens directly associated with mega-hooks are known (Fig. 4B; Riegraf & Hauff, 1983). Isolated mega-hooks were reported by Stevens (2010) from the Upper Jurassic of New Zealand and by Fraas (1855) and Schweigert (2018) from the Upper Jurassic of southern Germany.

In belemnites each of the ten arms is equipped with about 40 micro-hooks, resulting in about 400 hooks in total per specimen forming the arm crown. By contrast, only one pair of mega-hooks have been found per specimen. The absence of true tentacles, long extendable arms with sucker-bearing clubs, does not exclude the possibility of arm differentiation. Micro-hooks generally do not show significant variation in shape suggesting that each arm had a similar function. The 'belemnoids' *Chondroteuthis wunnenbergi* (Hoffmann *et al.*, 2017) and *Ostenoteuthis siroi* (Garassino & Donovan, 2000), however, show differentiated arms, although no true tentacles. So far, complete arm crowns are known for only two true belemnite genera, *Passaloteuthis* (Fig. 4B) and *Acrocoelites* (Fuchs & Hoffmann, 2017; Hoffmann *et al.*, 2017). Engeser (1987) assumed that each 'belemnoid' species might have had its own micro-hook type, suggesting that micro-hooks might be valuable index microfossils. Micro-hooks of true belemnites were assumed to be characterized by the presence of a small spur (e.g. in *Paraglycerites*). This spur has so far been reported only for rostrum-bearing belemnites, however, none have been directly associated with a calcitic rostrum (see Hart *et al.*, 2018). Furthermore, the micro-hooks of *Passaloteuthis* do not show this presumed characteristic spur (Fuchs & Hoffmann, 2017; Hoffmann *et al.*, 2017). This calls the strict assignment of micro-hooks bearing a spur to true belemnites into question.

(10) Ink sac

In their recent review of the systematics of octopod cephalopods, Strugnell *et al.* (2014) found the presence of an ink sac to be a volatile character that was lost in numerous lineages. Loss of certain characters can be associated with habitat changes and may occur rapidly (Pfenninger *et al.*, 2005; Skinner, Lee & Hutchinson, 2008), e.g. during colonization of the deep sea (D'Acoz & Vader, 2009). A lost character is also usually not regained upon return to the original habitat (D'Acoz & Vader, 2009). Allcock & Piertney (2002) concluded that ink sac loss in octopods was associated with habitat depth. Ink is used for camouflage during a predator attack or to produce a confusing 'pseudomorph' (Hanlon & Messenger, 1996; Bush & Robison, 2007). Below the photic zone ink would lose this function and retaining the ink sac thus would provide no advantage. Therefore, loss of the ink sac can represent adaptation to the deep sea (Voss, 1988). It is widely accepted that belemnites had an ink sac (Naef, 1922). The first records of fossilized ink sacs date back to Buckland (1830) for the 'belemnoid' *Belemnotheutis*, indicating a shallow marine habitat for this genus. Ink sacs for true belemnites have been reported by Donovan & Fuchs (2016) for *Passaloteuthis* and by Klug *et al.* (2010) for *Hibolithes semisulcatus*. Nautilids and the extinct externally shelled ammonoids do not possess an ink sac; this character first evolved within the coleoids. *Spirula spirula*, a representative of ten-armed deep-sea decabrachian coleoids, has a relatively small ink sac (Chun, 1915; Hoffmann & Warnke, 2014). A few deep-sea squids have retained their ink sac too, possibly because ink can provide not only optical but also chemical camouflage (Gilly & Lucero, 1992). In summary, ink sacs can be expected to have been present in most or all belemnites and may provide further evidence for a shallow-water habitat of these coleoids.

(11) Uroliths and statoliths

The role of uroliths (nephroliths, spherites) in cephalopod shell precipitation is not fully understood. According to Schipp & Martin (1987) and Westermann *et al.* (2002) uroliths are present in both major cephalopod clades the pal-cephalopods (nautiloids) and neo-cephalopods (ammonites, coleoids including belemnites). These hydroxyapatite concrements rich in Ca, Mg, and P were reported for extinct ammonites [e.g. *Aspidoceras* (Keupp, Röper & Seilacher, 1999; Keupp, 2000, 2012; Keupp *et al.*, 2016)] but are unknown for cephalopods without a mineralized shell. It is known that *Nautilus* feeds on corals and other biogenic carbonates and stores up to 5 mg as uroliths, with a time correlation between cyclic septa secretion and resorption of uroliths (Ward, 1987; Ward *et al.*, 2014). Uroliths therefore potentially serve as a Ca^{2+} depot for septal formation and for regulation of the blood Mg/Ca ratio during shell secretion (Crick *et al.*, 1985). It is highly speculative, since we lack any fossil evidence, but it seems possible that belemnites, as carbonate-forming cephalopods, also possessed uroliths and used them as sources of carbonates during shell formation. Uroliths potentially impact the signal of non-traditional isotope systems (Ca, Mg) although this is so far unexplored in recent cephalopods.

Statoliths of modern coleoids are composed of alternating organic-rich and carbonate-rich layers with a radiating prismatic structure – somewhat similar to the structure of the belemnite rostrum. Statoliths of fossil and modern coleoids are, however, composed of aragonite (Clarke & Maddock, 1988*a*,*b*; Clarke & Hart, 2018) and the single layers are referred to as growth increments. Statoliths are the balance organs of coleoids and with their structure and mineral composition represent a remarkable convergence with teleost fish otoliths, which function in balance as well as hearing (e.g. Schulz-Mirbach *et al.*, 2018).

Statolith growth increments have been used for age determination by assuming a daily formation analogous to the growth increments of belemnite rostra, which have also been regarded as daily formations (Jereb, Ragonese & Boletzky, 1991). Similarly, Bettencourt & Guerra (2000) showed that dark rings (rich in organic matter) were formed during the day and light rings (rich in calcium carbonate) were formed during the night. Together, one dark and one light ring form one growth increment. The first fossil cephalopod statoliths were reported by Clarke & Fitch (1975). Statolith shape can be used to distinguish between higher taxonomic groups of modern coleoids, e.g. between Decabrachia and Octopoda, but also to distinguish between genera. Further, statolith shape, like rostrum shape, can be used to infer potential habits. Their form and function are discussed in Clarke (1978). Correlation of some characteristic features with body form, life habits, or behaviour of the animals is discussed by Clarke & Hart (2018). Other features of statolith shape are said to be unrelated to function but may indicate common ancestry. The size of statoliths in modern coleoids is often correlated with mantle length and body mass but varies markedly among genera and families (Clarke & Hart, 2018). So far, statoliths have been described for ‘belemnoids’ from the Tithonian plattenkalks of Solnhofen by Klug *et al.* (2016) and from the Callovian Christian Malford Lagerstätten by Clarke & Hart (2018) but have not been recorded for true belemnites (Fig. 5H).

(12) Palaeopathology

The oldest reports on pathological belemnite rostra date back to de Blainville (1827), Raspail (1829), and Duval-Jouve (1841), and Hoffmann *et al.* (2018*a*) recently provided a comprehensive overview. For a long time, these pathological forms were reported as natural curiosities without recognizing their palaeobiological implications. While the field of palaeopathology seems to be largely restricted to the study of human remains, a few reports exist for other fossils (Buikstra, Cook & Bolhofner, 2017). Pathologies in fossil cephalopods, mostly abnormalities of ammonites, have been the focus of reconstructions of predator–prey relationships (e.g. Hölder, 1955; Keupp, 2002, 2012).

Where a belemnite survived a predatory attack in which its mantle tissue (mantle sac) and/or the rostrum were involved, healed injuries can be identified. Keupp (2012) differentiated between three main causes of pathological belemnite rostra: (*i*) injuries from a predator; (*ii*) endogenic causes, e.g. parasites; (*iii*) impact injuries resulting in rostrum fractures. Rostra that form after a predatory attack can be blunt, knee-like (Fig. 5C–G), form irregular areas with granular growth of the calcite (Fig. 5A,B), or display missing parts of the juvenile phragmocone. Endogenic reasons such as parasites that could also cause the formation of granules or blister pearls are difficult to distinguish. Irregular patterns of minerals that contain a drainage-like channel may indicate underlying inflammation of the mantle tissue. Pathological rostra are often asymmetrical, hook-shaped, or very short, can have more than one tip or form blisters. Specimens showing such pathologies can contribute to the understanding of predator–prey relationships, to the palaeobiology of belemnites, and to the functional morphology of their rostrum.

One case of parasitism has been recently described for *Goniocamax* from Santonian (Late Cretaceous) deposits in Denmark. The rostrum shows a 2 mm high and 4 mm long blister-pearl suggesting the presence of an endogenous parasite. Hoffmann *et al.* (2018*a*), based on the internal structure of this blister, tentatively suggested infection by a polychaete flatworm as the underlying cause. Recently, Hoffmann *et al.* (2018*b*) extended the application of computed tomography to pathological shells of the deep-sea decabrachian coleoid *Spirula spirula* and found evidence for predator attacks, parasitism, and inflammation. For modern cephalopods Gestal *et al.* (2019) recently summarized all available data.

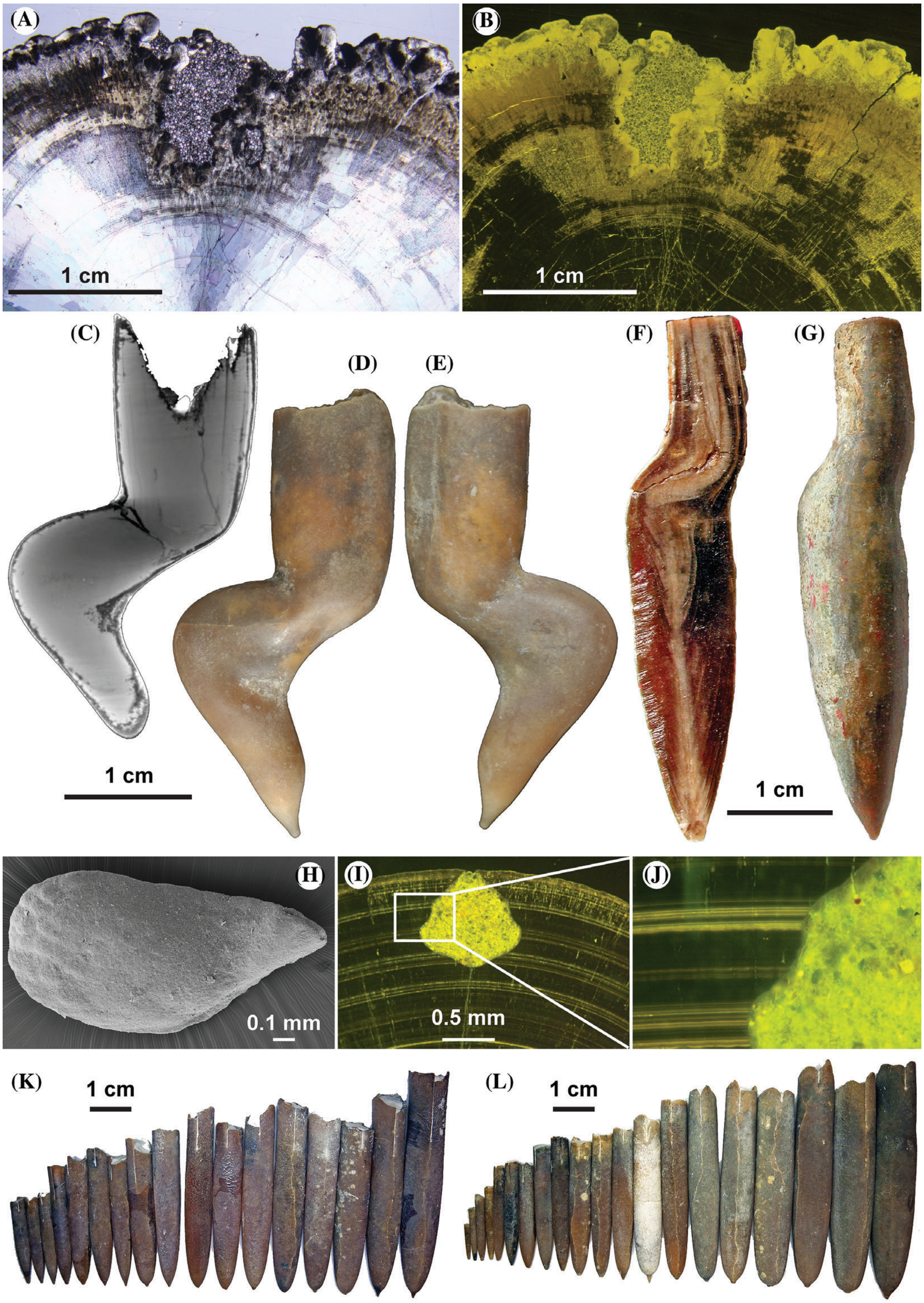

Fig. 5. Palaeopathology and ontogeny of belemnites. (A,B) Thin section of a pathological *Passaloteuthis* rostrum with a granular surface due to a dysfunctional mantle epithelium: transmitted light (A) and fluorescence (B) images with organic-rich areas appearing as lighter green colours. (C–E) *Gonioteuthis quadrata* forma aegra *angulata*. Median section shown in C was reconstructed from computed-tomography data (Late Cretaceous from Höver, NW Germany; see Keupp, 2012, Fig. 396). (F, G) Late Bajocian *Hibolithes* with forma aegra *angulata* (see Keupp, 2012, Fig. 381). Broken juvenile rostrum visible in F. From Sengenthal (S Germany). (H) Statolith from an unidentified coleoid from the Early Jurassic clay pit Buttenheim in S Germany; (I, J) *Gonioteuthis* containing boring produced by *Rogerella* isp., largest diameter of boring trace about 1 mm. (K) Different ontogenetic stages of *Belemnitella mucronata* all from one locality (Höver, NW Germany). (L) Different ontogenetic stages of *Gonioteuthis quadrata* all from one locality (Höver, NW Germany).

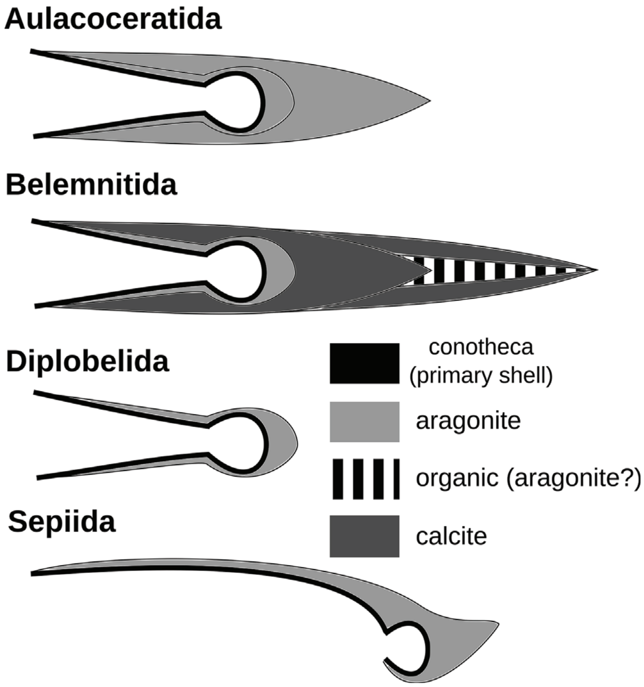

Fig. 6. Homology of coleoid internal hardparts. After Fuchs (2012) and Stevens (2017).

III. BELEMNITE INTERNAL SHELL: MORPHOLOGY, FUNCTION, FORMATION AND COMPOSITION

(1) Introduction

The mineralized hardparts of the belemnite internal shell, such as the rostrum, phragmocone and statoliths, are composed of either low-Mg calcite or aragonite. In addition, non-mineralized hardparts, such as hooks, jaws, or radula teeth, which were originally composed of a chitin–protein complex, can occasionally be found in the fossil record (Figs 6 and 7). Below we provide a short description of the internal shell and its major growth stages, before focussing in more detail on the belemnite rostrum. Herein, we prefer the term 'rostrum' over the term 'guard', due to the incorrect functional connotation of a defensive function of the latter, following Doyle & Kelly (1988).

(2) General construction and growth stages

The belemnite internal shell consists of four parts: the proostracum, phragmocone, the primordial rostrum, and the rostrum proper. The phragmocone is divided into a series of chambers by the septa. All chambers, except for the initial chamber (= protoconch) are connected by the siphuncle. The siphuncle is an organic strand that removes chamber liquid after septum formation (e.g. Denton, 1974). The septa form septal necks around the ventrally positioned siphuncle. The septa, septal necks, and the phragmocone wall together form the aragonitic conotheca. In some coleoid groups, e.g. the aulacoceratids, the conotheca forms a tubular body chamber. The proostracum of the belemnites, however, is poorly mineralized and represents the dorsal remnant of this cone-shaped 'body chamber', i.e., the lateral and ventral parts of the former body chamber are reduced (Fig. 7). The primordial rostrum is initially aragonitic and covers the protoconch and subsequently formed chambers of the phragmocone. The rostrum of adults might have accounted for one-fifth to one-third of the total length, including the arms, of the belemnite animal (Reitner & Urlichs, 1983) and probably represented a considerable investment of energy and materials (Monks *et al.*, 1996). The anterior extension of both the primordial rostrum and the orthorostrum during ontogeny is difficult to reconstruct but its extent is potentially important for buoyancy calculations. The rostrum is thought to have been composed of low-Mg calcite (Hoffmann *et al.*, 2016). The orthorostrum is divided into two parts (Fig. 7) – the posterior rostrum solidum, and the phragmocone-bearing rostrum cavum (Müller-Stoll, 1936). Some belemnite taxa, mainly Jurassic forms, developed an epirostrum during late ontogeny. This epirostrum is composed of low-Mg calcite and according to some authors additionally of aragonite (Bandel & Spaeth, 1988) or organic material (Stevens *et al.*, 2017).

Homology between the belemnite skeleton and modern coleoid skeletons like the sepiid cuttlebone (sepion) remains largely unresolved. Some authors consider the structure called the 'rostrum' or 'spine' located posteriorly in sepiid cuttlebones to be homologous to the belemnite rostrum (Rexfort & Mutterlose, 2006). Fuchs (2012) considered the rostrum proper to have no homologous structure in modern coleoids but considered the sepiid 'sheath' as corresponding to the primordial rostrum of belemnites.

The orientation of belemnites is defined as follows: the rostrum and epirostrum are posterior while the main part of soft body including the head and arm crown are anterior to the phragmocone (Fig. 7). The position of the siphuncle defines the ventral side. For sections and thin sections of the rostrum the terms longitudinal section for the median plane of the longest axis, and cross section (perpendicular to the longitudinal section), are preferred.

Fuchs (2012) distinguished four shell formations appearing during ontogeny for the belemnite skeleton. The rostrum is divided into the primordial rostrum, orthorostrum and epirostrum, with the ortho- and epirostrum together forming the 'rostrum proper' (Spaeth, 1975; Bandel & Spaeth, 1988; Dauphin, Williams & Barskov, 2007; Fuchs, 2012; Fig. 7). (*i*) During the first ontogenetic stage of skeleton formation the aragonitic conotheca including the initial chamber, phragmocone, and septa was secreted; (*ii*) The aragonitic/organic primordial rostrum is present, covering the entire primary shell (protoconch wall, conotheca and later parts grown anteriorly) and is enveloped by the calcitic orthorostrum; (*iii*) The orthorostrum is divided into the posterior orthorostrum solidum beginning at the initial chamber (protoconch) and the anterior orthorostrum cavum, which surrounds the phragmocone, forming the alveolus. For some belemnites a primarily aragonitic composition of

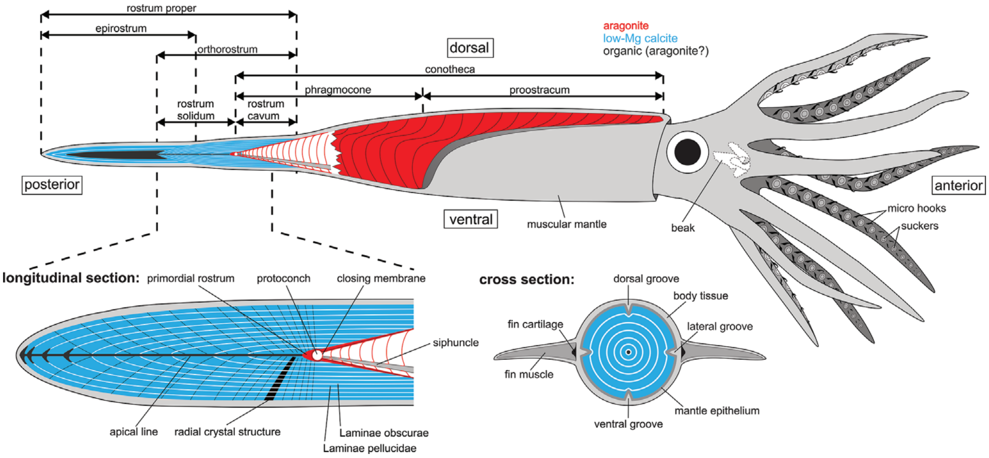

Fig. 7. Descriptive terminology for the belemnite animal and its hardparts (compiled after Spaeth, 1975; Bandel *et al.*, 1984; Bandel & Spaeth, 1988; Sælen, 1989; Fuchs *et al.*, 2010; Fuchs, 2012; Iba *et al.*, 2012; Stevens *et al.*, 2017; Ippolitov *et al.*, 2018).

the rostrum cavum was suggested (Košťák & Wiese, 2008); and (*iv*) The presence of a calcitic/organic (aragonitic?) epirostrum represents the latest ontogenetic development and envelops the posterior orthorostrum. The epirostrum is interpreted as a sexually selected character that was probably sexually dimorphic (Doyle, 1985; Schlegelmilch, 1998; Stevens *et al.*, 2017). For a detailed description of mineralized hardparts other than the rostrum, e.g. the initial chamber, phragmocone with conotheca, septa, and siphuncle, or the proostracum, and the primordial rostrum, see Doguzhaeva *et al.* (2002); Doguzhaeva *et al.* (2003); Doguzhaeva *et al.* (2014).

Three basic longitudinal outline morphologies of belemnite rostra can be distinguished: (*i*) hastate, i.e. lancet shaped (e.g. *Hibolithes*); (*ii*) cylindrical (e.g. *Cylindroteuthis*); and (*iii*) conical (e.g. *Acroteuthis*) (Fig. 8). Note that these basic shapes form a continuous and overlapping spectrum. In addition, three morphologies of the apex region can be distinguished: mucronate (e.g. *Belemnitella*), acute (e.g. *Neoclavibelus*), and rounded (e.g. *Dactyloteuthis irregularis*). Belemnite rostra are further distinguished by diverse alveolar and apical furrows and so-called doppellinien, which might have been fin-attachment sites, and by cyrtolineate, goniolineate and ortholineate apical lines (Stevens, 1965) (Fig. 8). Alveolar furrows might be additionally developed as so-called slits, connected with slit fields, i.e. flat surfaces that extend inside the rostrum (Fig. 8). The following cross-section morphologies of belemnite rostra can be distinguished: quadrate (e.g. *Gonioteuthis*), circular (e.g. *Belemnitella*), compressed (dorsoventral diameter exceeds the lateral diameter; e.g. *Duvalia*) and depressed (lateral diameter exceeds the dorsoventral diameter; e.g. *Suebibelus*).

(3) Colour patterns

Shell colour patterns in molluscs are the result of pigments or features of the surface structure (structural colours). Many different types of colour patterns can result, such as: transparency, achromatism, monochromatism, iridescent colour patterns, irregular and regular spot patterns, transverse zigzags, chevrons, and radial or longitudinal stripes or bands. Reports of preserved colour patterns are rare in the fossil record.

There are only two reports on colour patterns of belemnite rostra (Jordan, Scheuermann & Spaeth, 1975; Spaeth, 1983). Assumed colour preservation found on Middle Jurassic *Megateuthis* rostra by Jordan *et al.* (1975) led to speculations regarding their soft-body organization. These colour markings only appear in larger specimens (first on the dorsal side, later extending to the ventral and finally the lateral sides) and were suggested to aid camouflage. Jordan *et al.* (1975) proposed that only a very thin layer of mantle tissue covered the rostrum or even that adult specimens had no mantle covering their rostra. Spaeth (1983) provided evidence for colour patterns for the Barremian (Lower Cretaceous) genus *Oxyteuthis* largely following the interpretations of Jordan *et al.* (1975). By contrast, Keupp (2012) argued that these patterns simply reflect a heterogeneous distribution of organic matter within the rostrum without providing further functional interpretations. In some *Megateuthis gigantea* specimens these ‘colour patterns’ grade into small knobs at the alveolar region giving the surface a somewhat tuberculate appearance (Fig. 9). An alternative interpretation of this surface could be a muscle attachment site (Stevens, 1965).

Identification of biological colour patterns is complicated by the existence of false colour patterns produced by shell thickening or diagenetic processes. For ammonoids, Klug, Riegraf & Lehmann (2012) reported false colour patterns related to regions where growth slowed down or stopped and was accompanied by the production of faint ribs. In some cases, muscle attachment structures can be preserved as dark to brownish patterns mimicking true colour patterns.

In mollusc shells polyenes produce most shell pigments (Hedegaard, Bardeau & Chateigner, 2006) using *in situ* Raman spectroscopy. Barnard & de Waal (2006) investigated

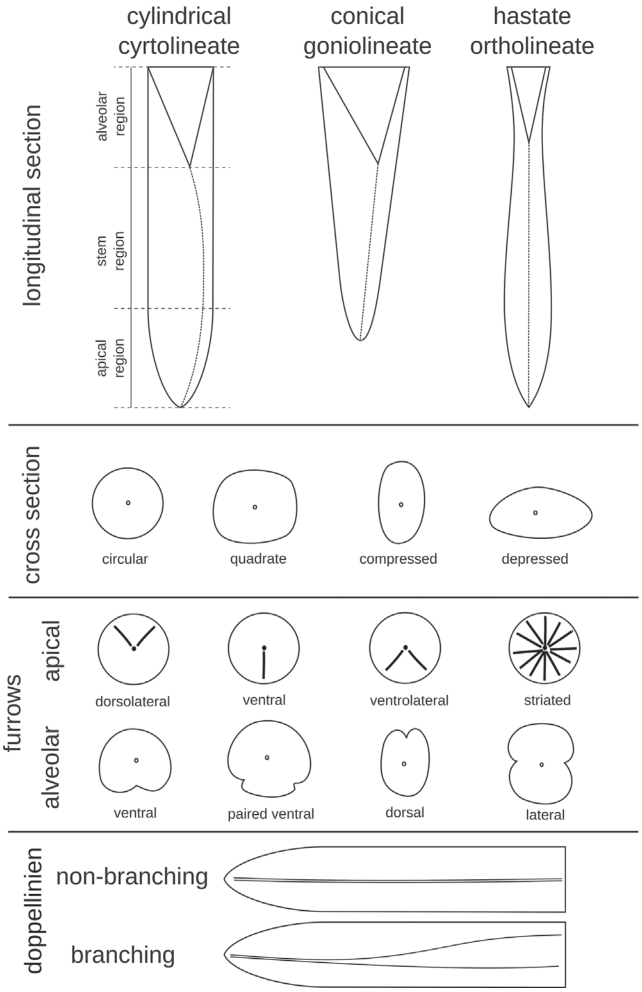

Fig. 8. Descriptive terminology of belemnite rostrum morphology based on Mutterlose (1983), Doyle (1990), and Schlegelmilch (1998). Note that the outline types shown in longitudinal section are not necessarily associated with any particular apical shape, and that all three apical shapes can occur for each longitudinal outline shown.

pigments in modern mollusc shells and found that carotenoids, a subgroup of polyenes, are the dominant shell pigment. Raman spectroscopy offers promise as a non-invasive tool for the detection of fossilized pigments, not only melanin in ink sacs but also polyene pigments in cephalopod shells, but has not yet been applied to belemnites, ammonites, or fossil nautiloids.

(4) Petrography

Thin sections of belemnite rostra reveal numerous, concentric rings apparently representing discontinuities in crystallite formation (Bøggild, 1930). These rings have been traditionally regarded as growth increments and assumed to represent primary growth texture (Veizer, 1974; Sælen, 1989). Müller-Stoll (1936) regarded these growth rings as reflecting a primary organic/carbonate layering of the rostra. Sælen (1989) proposed that the calcitic but organic-rich layers were originally porous and contained organic matter, which was replaced with diagenetic calcite *post mortem* (see also Veizer, 1974; Rosales, Robles & Quesada, 2004). Sælen (1989) did not find a bipartite morphology of growth increments using scanning electron microscopy (SEM) and blue fluorescence and accordingly rejected the interpretations of Müller-Stoll (1936). Following Sælen (1989) it is likely that the rostrum does not consist of alternating distinct types of laminae, but small changes in organic matter content, a finding that received support from Hoffmann *et al.* (2016).

Central longitudinal sections of belemnite rostra reveal all growth stages of a rostrum. The so-called apical line (Fig. 7) is formed by the sequential positions of the apex of the rostrum during ontogeny (ontogenetic trajectory of the apex, ranging from the apex of the alveolus to the apex of the preserved rostrum). The curvature of the apical line in dorso-ventral median sections has some taxonomic implications (Fig. 8). Normally the apical line is in a central or subcentral position within the ortho- and epirostrum.

The radially arranged calcite fibres forming the rostrum maintain their continuity (syntaxial) as they cross the growth rings as seen in thin section and SEM (O'Neill, Manger & Hays, 2003). The apical line is characterized by a spherulitic arrangement of smaller calcite fibres (Fig. 10). Electron backscattered diffraction (EBSD) analyses showed that single calcite fibres are arranged in bundles with similar to identical orientation of their a-axes (Hoffmann *et al.*, 2016; Stevens *et al.*, 2017). In contrast to most publications that assume that the observed fabric of belemnite rostra is primary, authorities such as Müller-Stoll (1936) and Jeletzky (in Voigt, 1965) regarded the large radial calcite crystals as a secondary feature. The carbonate-rich layers of the rostrum were assumed to be composed of smaller crystals orientated perpendicular to the rostrum surface and covered by an organic membrane. During diagenesis, the organic layer was destroyed and accordingly did not form a distinct layer in fossil rostra. Further, single crystals merged together to form larger crystals reaching from the rostrum surface to its apical line. This view was supported by the presence of curved crystals in the apical line area (Müller-Stoll, 1936, p. 189). Based on observed boring traces, Voigt (1965) concluded that recrystallisation must have taken place very early during diagenesis.

Recent mollusc shells, however, frequently show similar bundles of radiating and indented crystals 'transected' by growth lines (Wilbur, 1972, p. 125; Grégoire, 1972, pp. 47–51). Thus these structures can be argued to represent original features of belemnite rostra (Sælen, 1989; Richter *et al.*, 2011). Etching experiments resulted in relief differences between the organic-rich and calcite-rich layers (Spaeth, 1973; Podlaha *et al.*, 1998). A higher proportion of organic matter with higher acid resistivity can be assumed for organic-rich or 'diagenetic' (e.g. Fe and/or Mn rich, laminae obscurae) areas that are less affected (dissolved) by weak acids (Sælen, 1989).

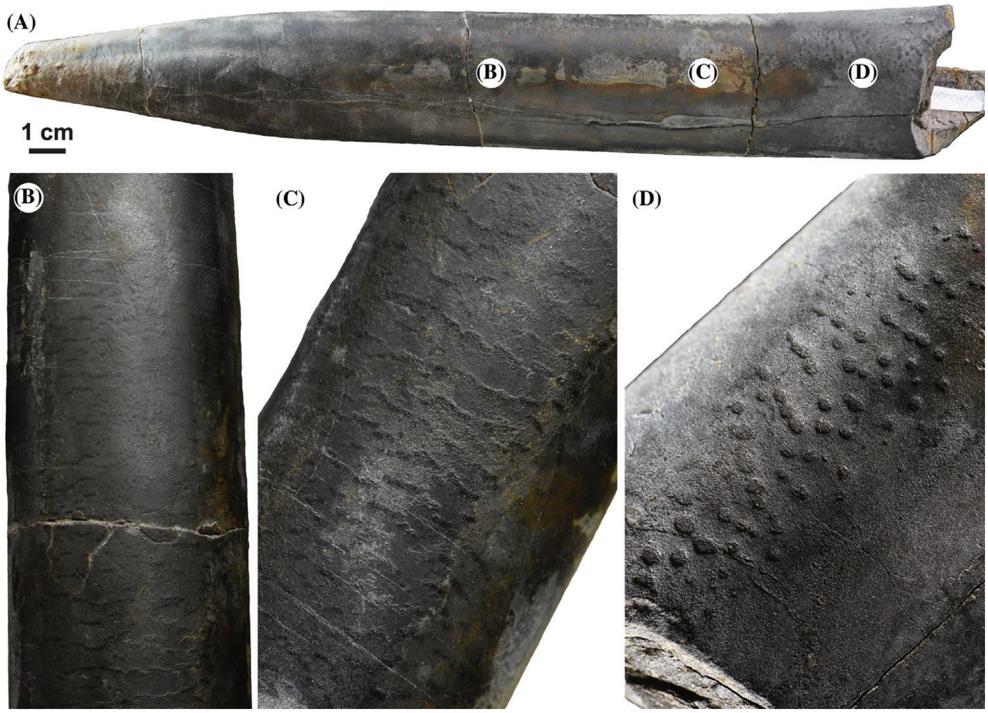

Fig. 9. Rostrum of Middle Jurassic *Megateuthis gigantea* showing features interpreted previously as colour patterns but could also be regarded as muscle attachment structures.

Further, Dunca *et al.* (2006) argued that the alternating light/dark growth increments are the result of different crystal sizes and density and that organic matter (inter- and intracrystalline) is homogeneously distributed within the rostrum except for an enrichment of carbon at the outer margin. Because these two types of layers are sometimes difficult to distinguish, we suggest the simple use of 'increment' for all distinct rostrum layers.

A sponge-like ultrastructure for belemnite rostra was postulated by Kabanov (1959, 1967) and Vetter (1968). Spaeth (1971, 1973, 1975) and Westbroek *et al.* (1979) assumed that a sponge-like ultrastructure for the rostra of *Neohibolites minimus*, comparable to the extant cuttlebone of sepiids, would give it a primary porosity of 20%, while Veizer (1974), Veizer & Fritz (1976), and Bandel & Spaeth (1988) suggested a maximum porosity of 10%, and Podlaha *et al.* (1998) calculated 6%. Podlaha *et al.* (1998) estimated a mean ± 2 S.D.value of 2 ± 1.3% of secondary calcite abundance (range 0–6.8%). In addition to this sponge-like porosity, a triangular pore structure in the apical region was documented by Spaeth (1971, 1975) and Richter *et al.* (2003). Further suggestions of high levels of primary porosity (50–90% by volume) within belemnite rostra were based on observations of the composite nature of belemnite calcite fibres. Hoffmann *et al.* (2016) and Benito, Reolid & Viedma (2016) documented two calcite generations composing these fibres (Figs. 11 and 12). These two calcite generations differ in their petrography, elemental composition, and the amount of organic matter (Hoffmann *et al.*, 2016). Hoffmann *et al.* (2016) proposed that these two calcite generations are due either to a high primary porosity of the rostra or to a two-phase formation of calcite in the belemnite rostrum during biomineralization. Stevens *et al.* (2017) rejected the proposal of high primary porosity of the belemnite *N. minimus*, in part due to the presence of 'restart points', i.e. growth cessations, which document new nucleation of calcite fibres only in the ontogenetic growth direction. For *Sepia* spp. Sherrard (2000) recorded differences in the density of the cuttlebone related to habitat depth. Therefore, it seems reasonable to assume that the primary microstructure in belemnite rostra might also have varied with habitat depth. A similar relationship between pressure and dimensions of biogenic hardparts was reported by Hoffmann *et al.* (2019) for the thickness distribution of ammonite nacre tablets.

In stark contrast to the above data, most authors interested in the reconstruction of Mesozoic seawater properties assume that the rostrum was a primary dense structure, not easily permitting the passage of diagenetic fluids (e.g. Sælen, 1989; van de Schootbrugge *et al.*, 2000; Niebuhr & Joachimski, 2002; Wilmsen & Niebuhr, 2017). From data on the decomposition of organic matter and microfractures, Florek *et al.* (2004) reconstructed a secondary porosity of belemnite rostra of 5–10%.

(5) Function

Several hypotheses have been advanced for the function of the belemnite rostrum: it could have acted (*i*) as a counterweight to the soft body (Stevens, 1965; Denton, 1974; Seilacher & Wiesenauer, 1978; Doyle, 1985);

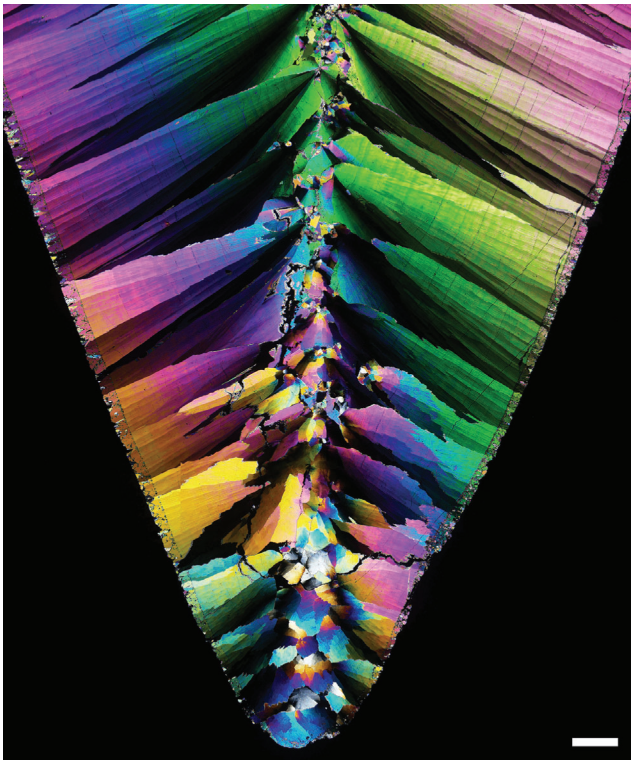

Fig. 10. Ultra-thin section of a *Gonioteuthis* rostrum under cross polarized light showing the spherulitic arrangement of calcite fibres along the apical line (centre), and fibre bundles crossing the growth lines. Scale bar, 500 μm.

(*ii*) as a supporting element or muscle attachment site for the posterior fins (Stevens, 1965; Spaeth, 1975; Bandel & Boletzky, 1988; Bandel & Spaeth, 1988); (*iii*) as a hydrostatic device, analogous to the sepiid cuttlebone (Spaeth, 1971, 1975); (*iv*) in protection of the phragmocone (Müller, 1994); or (*v*) to compensate for positive buoyancy (Müller, 1994).

It is generally accepted that the massive orthorostrum acted as a counterweight to the soft body (Spaeth, 1975; Monks *et al.*, 1996). The orthorostrum and soft body can be modelled as centres of gravity while the phragmocone represents the centre of buoyancy. With this construction the belemnite animal was able to swim oriented horizontally, which is important for an active, torpedo-shaped predator. However, given the relative densities of aragonite (2.94 g/cm^3) and calcite (about 2.6 g/cm^3), the latter would appear to be less efficient for its proposed counterweight function. Further the likely high primary porosity of belemnite rostra, and the presence of organic matter in the calcitic rostrum, suggest that we should reconsider this function using detailed 3D models.

Rostra are commonly considered to have the same density as inorganic calcite (2.5–2.7 g/cm^3). Shells of extant cephalopods, e.g. *Nautilus pompilius*, comprise a volume fraction of about 5–15% intercrystalline and 1–5% intracrystalline organic material (F. Nudelman, personal communication), i.e. approximately 20% (estimates for *Sepia officinalis* are 10–40%), which will reduce the overall carbonate density. Taking this total organic matter into account, the aragonitic *Nautilus* shell has a density of 2.5–2.7 g/cm^3, i.e. lower than that of abiogenic aragonite.

Accordingly, a reduced density can be predicted for biogenic belemnite calcite of between 2.0 and 2.4 g/cm^3 for an organic matter content of 10–40%. If liquid or extracrystalline organic matter (1.03 g/cm^3) – with a density comparable to that of sea water (1.026 g/cm^3) – filled the pore space of living belemnites, an overall density of the rostrum ranging between 1.1. and 1.7 g/cm^3 (mean 1.4 g/cm^3) can be tentatively assumed as a working hypothesis. If these assumptions hold true, then the belemnite rostrum had a cumulative density significantly lower than that of stoichiometric calcite. This should be taken into consideration when comparisons with soft body volumes are made in buoyancy calculations for horizontally swimming belemnites.

A function of the rostrum as a supporting element or muscle attachment site for the anterior fins was discussed by Stevens (1965) and many subsequent workers. We still lack direct evidence of fins for true belemnites and the interpretation of doppellinien as fin-cartilage attachment sites is not unequivocal. A possible analogue may be a structure reported from the modern ommastrephid squids *Onykia robsoni* and *O. robusta* that bears remarkable morphological similarity to the belemnite rostrum. *Onykia robsoni* and *O. robusta* have a purely organic 'rostrum' that due to its very low density does not act as a counterweight for the soft body. It is thought to support the posterior part of the mantle and fins [providing axial stability according to Bizikov & Arkhipkin (1997) and Arkhipkin *et al.* (2015)]. Rare cases of fossil 'belemnoid' coleoids (e.g. *Chitinoteuthis decidua*) with a non-calcified rostrum have been reported by Müller-Stoll (1936).

A hydrostatic function, analogous to the sepiid cuttlebone as suggested by Spaeth (1971, 1975) is rejected herein based on the lack of supporting structures that could remove fluids and refill the pore space, i.e. a siphuncle-like structure, and the fact that the pore space is filled *syn vivo* with calcite. This would restrict the functional area to the outermost 100 μm thick rostrum layer. Further, adhesive forces are likely to be extraordinarily large given the small dimensions of the pores (rarely larger than 100 μm), and the limited amount of pore space compared to the hydrostatic apparatus of modern nautilids, for example.

(6) Growth patterns and biomineralization

A general overview of the rapidly growing field of biomineralization and the huge variety of analytical techniques applied was recently published by Pérez-Huerta, Coronado & Hegna (2018) with a focus on fossil biominerals. Useful summaries of the formation and biomineralization of mollusc shells are provided by Cuif, Dauphin & Sorauf (2011), Marin, Le Roy & Marie (2012), and Checa (2018). Westermann, Schmidtberg & Beuerlein (2005) described the biomineralization of *Nautilus pompilius*, Checa *et al.* (2015)

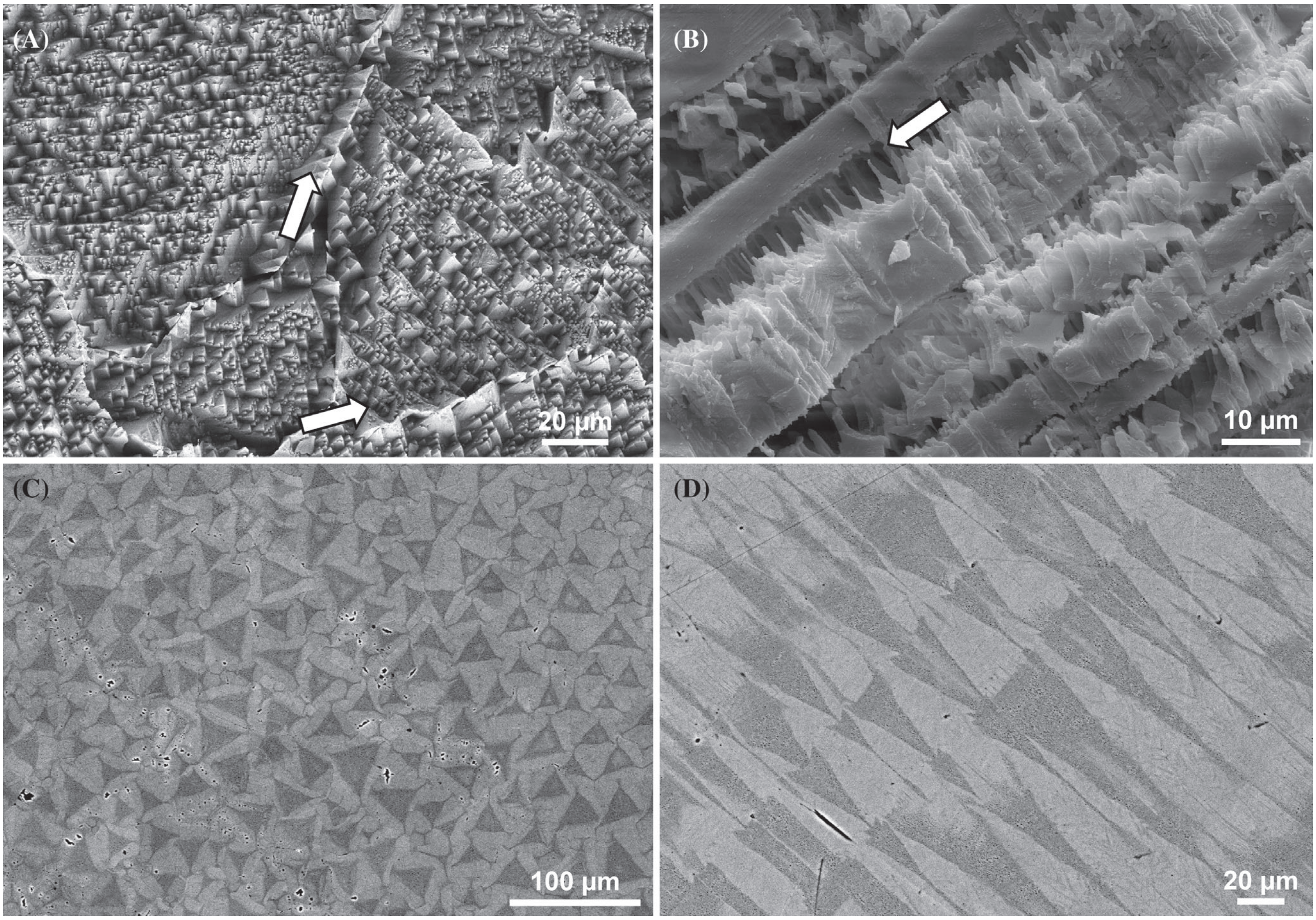

Fig. 11. Scanning electron micrograph (SEM) images providing details of the architecture of belemnite rostra. (A, B) Lower Cretaceous *Neohibolites ewaldi* from Alstätte (Germany). (A) Naturally etched surface perpendicular to the calcite fibre c-axis. Arrows indicate fibre bundle boundaries marked by larger crystals and changing orientation of the fibre a-axis. (B) Naturally etched surface showing side view of tetrahedral elements (arrow), representing the primary biogenic skeleton. Tips of tetrahedral elements point outwards, i.e. in the growth direction. (C, D) SEM-BSE (backscattered electrons) images of a Middle Jurassic *Megateuthis gigantea*. (C) Thin section perpendicular to the c-axis of calcite fibres showing the darker triradial organization of the organic-rich filigree skeletal framework, surrounded by lighter organic-poor calcite cements. (D) Thin section parallel to the c-axis of the calcite fibres showing the darker triangular, organic-rich skeletal elements and the lighter calcite cement generation. Each calcite fibre is a composite of two calcite generations.

of *Sepia officinalis*, and Immenhauser *et al.* (2016) provides a comprehensive review of cephalopod biomineralization.

Observations of the shell-forming soft tissue of *Nautilus pompilius* were reported by Westermann *et al.* (2005). These authors showed structural similarities between the *N. pompilius* mantle and bivalve mantles with active transport epithelia. Ion- or water-transporting epithelia are characterized by large concentrations of mitochondria, a well-developed apical microvillar border, a paucity of rough endoplasmatic reticulum, and Golgi complexes. The presence of Ca^{2+}-ATPase (an enzyme that transports Ca^{2+} out of the cell into the intercellular space) and the occurrence of microvilli indicate that in this region of the mantle epithelium the main route of calcium transfer through the outer epithelium takes place *via* intercellular spaces. The formation of the external shell of *N. pompilius* takes place in the extrapallial space (EPS, only a few nanometres thick) that is filled with extrapallial fluid (EPF), which is isolated from ambient seawater by the periostracum, the shell itself, and the mantle epithelium (Wilbur & Saleudin, 1983). The EPF is supplied with carbonate derived from the seawater bicarbonate pool (90%) but metabolic CO_2 also contributes (0–10%) to shell carbonate (Wheeler, Blackwelder & Wilbur, 1975; Dillaman & Ford, 1982). This shell-formation process is widely distributed among molluscan taxa including bivalves, gastropods and cephalopods, and the same is likely to be true for extinct cephalopods.

Belemnites presumably formed their internal skeleton in the shell sac, which was closed by fusion of the muscular mantle above the shell mantle (Bandel & Boletzky, 1979; Bandel, 1982). In extant cephalopods, different parts of the mantle are responsible for the secretion of different parts of the shell. The aragonitic phragmocone of belemnites, including the conotheca, proostracum, septa and the

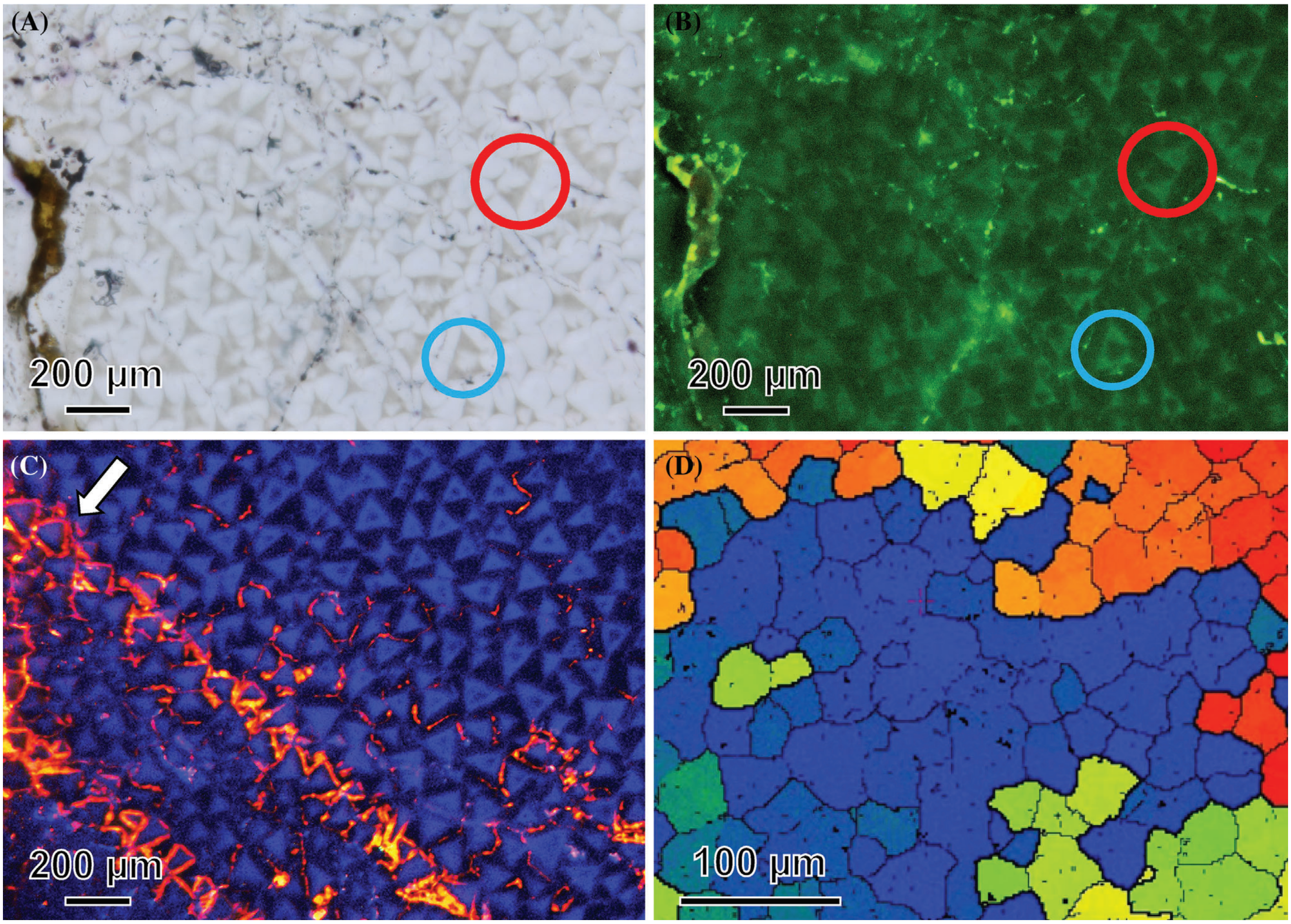

Fig. 12. Complex spatial geochemistry of belemnite rostra. Middle Jurassic rostrum of *Megateuthis*. (A) Transmitted light image with brownish triradial skeletal elements (circled). (B) Fluorescence image of the section shown in A with the triradial elements showing a brighter fluorescence compared to the surrounding cement. Note the different orientation of the a-axis of the triradial elements in the red and blue circles. (C) Cathodoluminescence image with triradial elements showing a slightly lighter bluish intrinsic luminescence compared to the surrounding cement. Orange luminescence is restricted to late diagenetic cements filling cracks, sometimes retracing the triradial biogenic skeletal elements (arrow). (D) Electron backscattered map with colour-coded orientation of crystallographic a-axes. Similar or identical colours refer to similar or identical orientation.

protoconch, would be formed by the periostracum gland zone and the shell mantle behind it. The belemnite rostrum would be secreted by the posterior mantle tissue, which originally lay anterior to the periostracum zone, but in endocochleate cephalopods (cephalopods with an internal shell) is fused above the shell mantle thereby covering it (Bandel & Spaeth, 1988).

Growth of the primordial rostrum is initiated at the top of the protoconch (initial chamber of the phragmocone) and consists of aragonite and organic material (Spaeth *et al.*, 1971; Spaeth, 1975; Bandel & Spaeth, 1988). It was first proposed that the primordial rostrum was subsequently completely covered by calcitic rostrum material, however, Fuchs (2012) demonstrated that the primordial rostrum is deposited throughout ontogeny. Rostral carbonate is added periodically by simultaneous accretion over the outer surface of the rostrum (Mutvei, 1964; Doyle, 1985; Sælen & Karstang, 1989). Each period of carbonate addition covers the entire surface of the rostrum (O'Neill *et al.*, 2003), and changes in the growth rate of rostrum calcite across the surface result in changes in rostrum shape during ontogeny. Accordingly, each layer represents an isochronous phase of carbonate. Stevens *et al.* (2017) suggested that the apical line was primarily of organic composition, analogous to the central organic layer of the shell of modern octopuses of the genus *Argonauta*.

The mode of deposition of belemnite rostra can be compared with deposits of the *Sepia* cuttlebone sheath (Bandel & Spaeth, 1988; Fuchs, 2012), as modern sepiids and extinct belemnites share an internal shell (Naef, 1922).

Hoffmann *et al.* (2016) provided a detailed petrographic description of different calcite phases [calcite phases 1 and 2 (CP1, CP2) and late diagenetic calcite (LDC)] composing the rostra of *Megateuthis*, *Belemnitella*, and *Gonioteuthis*. A multi-calcite-phase composition was documented by Benito *et al.* (2016) for *Hibolithes* and *Belemnopsis*. Given this taxonomic and stratigraphic distribution it seems reasonable to assume that all calcitic rostra share a similar construction. In contrast to their importance for the reconstruction of Jurassic and Cretaceous marine palaeoenvironments, no detailed biomineralization model for belemnite rostra is available.

(7) Primary mineral composition

Belemnite rostra are thought to have been composed of low-Mg calcite (Chave, 1952; Veizer & Fritz, 1976; Sælen, 1989; Dunca *et al.*, 2006; see also Hoffmann *et al.*, 2016) One argument for a primary low-Mg calcite composition of the rostra is the lack of microdolomites (Richter & Füchtbauer, 1978, p. 844): if the rostra were originally composed of high-Mg calcite, recrystallization to low-Mg calcite during diagenesis should have resulted in the formation of microdolomites (Sælen, 1989). Furthermore, low-Mg calcite belemnites are often found in the same sections/layers as abundant well-preserved aragonitic fossils, which suggests good preservation of the primary minerals in these rostra. High-Mg calcite is not found in recent cephalopods (Sælen, 1989) except for the shells of *Argonauta* females (Mitchell, Phakey & Rachinger, 1994; Stevens *et al.*, 2015). These shells are, however, produced by the membranous arms of those cephalopods and are not homologous to the molluscan shell.

By contrast, Kabanov (1967), Spaeth (1971, 1973), and Dauphin *et al.* (2007) considered the rostrum to be a product of complete or partial recrystallization of metastable carbonate minerals such as aragonite (Veizer, 1974). Košťák & Wiese (2008) argued for the primary coexistence of aragonite and calcite in *Praeactinocamax* aff. *Plenus* rostra without providing unequivocal evidence, e.g. X-ray diffraction (XRD) or Raman data. Belemnite rostra from the Middle Jurassic of Spain have been reported by Doguzhaeva & Meléndez (2017) with white central rod-like structures but without any difference in mineralogical composition compared to other parts of the rostra. Accordingly, Doguzhaeva & Meléndez (2017) rejected interpretation of white parts of belemnite rostra as indicators of a primary aragonitic composition (e.g. Košťák & Wiese, 2008). XRD data indicating the presence of aragonite in the rostrum solidum were published for a Turonian *Goniocamax* (=*Praeactinocamax*) (Naidin, Barskov & Kiyachko, 1987), and recently by Ippolitov *et al.* (2018) for the Bathonian belemnite genus *Barskoviella*, a megateuthid belemnite formerly described as *Nannobelus* or *Paramegateuthis*. Belemnotheutids possessed aragonitic rostra (Bandel & Kulicki, 1988) like stem-group coleoids ('aulacoceratids'; e.g. Jeletzky, 1966; Reitner & Engeser, 1982). Pérez-Huerta *et al.* (2018) regarded the presence of aragonite in belemnite rostra as secondary. Aragonite precipitation could have resulted from early diagenetic processes promoted by high Mg/Ca ratios – perhaps due to the decomposition of organic matter (relatively high concentrations of Mg in the biogenic skeleton of belemnite rostra were shown by several authors (e.g. Hoffmann *et al.*, 2016). Although the formation of aragonite during diagenesis is a rare phenomenon, the presence of organic compounds has been recognized in belemnites by Drozdova (1969) and others (see Section III.8), while high amounts of Mg in the soft tissue of modern molluscs have been documented by Segar, Collins & Riley (1971) and Szefer & Szefer (1990). The amount of Mg within the soft tissues of several bivalves and gastropods varied between 860 and 25,000 ppm (the latter value for the gastropod *Crepidula formicata*). Table 3 provides Mg concentrations in the muscle tissue, blood plasma, and surrounding sea water for three extant cephalopods. These data demonstrate that Mg contents of the blood plasma are similar to sea water, but reduced in muscle tissues, which might hold true for biomineralizing mantle tissue. A primary aragonitic composition was discussed for the inner part of the epirostrum by Bandel & Spaeth (1988) but rejected by Stevens *et al.* (2017).

Table 3. Mean magnesium concentrations in tissues of three coleoid cephalopods (three specimens per species; data from Robertson, 1965)

Taxon	Muscle (mg Mg/kg water)	Blood plasma (mg Mg/kg water)	Sea water (mg Mg/kg water)
Sepia officinalis	22.3	57.7	56.1
Loligo forbesi	15.2	51.6	49.4
Eledone cirrhosa	22.8	54.2	50.0

(8) Organic matter

The presence of organic matter in belemnite rostra has been described by many workers, however, the amount and type of organic matter has rarely been explored (e.g. Müller-Stoll, 1936; Veizer, 1974; Sælen, 1989; Dunca *et al.*, 2006). It is generally accepted that the apical line is characterized by the highest amounts of organic matter within the rostrum (Drozdova, 1969; Spaeth, 1975; Bandel & Spaeth, 1988; Stevens *et al.*, 2017). After death, organic matter is subject to microbial decomposition and diagenetic alteration, which can degrade proteins to individual amino acids and eventually to simple hydrocarbons (Collins & Gernaey-Child, 2001). Westbroek *et al.* (1979) reported on the soluble macromolecular fractions of well-preserved *Gonioteuthis* rostra and identified components with peptidic and saccharidic properties. Also, components with an amino acid composition, very similar to that of modern *Nautilus*, i.e., dominated by glycine and alanine, have been identified. Some components had their original antigenic properties preserved suggesting that the biochemical materials derived from this rostrum were original belemnite compounds. Primary porosity was believed to be filled with gas, liquid, or organic matter (Hoffmann *et al.*, 2016). An organic-filled pore space agrees with Sælen (1989) and the presence of phosphate within the rostra (Longinelli, Iacumin & Ramigni, 2002; Gröcke *et al.*, 2003; Longinelli, Wierzbowski & Di Matteo, 2003). Longinelli *et al.* (2003) found that the phosphate content of belemnite rostra results from diagenetically altered organic matter and is variable but low (less than 0.3%), comparable to values found in extant cephalopods (e.g. *Sepia officinalis*). Such organic matter presumably decomposed during early diagenesis (Hückel & Hemleben, 1976) or was originally incorporated into the calcite crystal lattice. *Post mortem* reducing conditions inside the rostrum and resulting anaerobic degradation of organic matter could have led to H_2S production associated with pyrite formation analogous to processes observed in ammonite chambers (Bayer, 1975). An excess of carbon in belemnite calcite was observed by Florek *et al.* (2004) and in other mollusc shells by Weiner *et al.* (1979), who regarded it as potential remnants of original biogenic matter. Their findings suggest the presence of organic scaffolds forming the triradial mineralized elements of the biogenic skeleton. The shell matrix of modern molluscs is both inter- and intracrystalline and consists mainly of proteins (Wilbur, 1972; Lutz & Rhoads, 1980). Intercrystalline organic matter is likely to be affected first by decomposition (see Tan & Hudson, 1974, p. 108; Bayer, 1975, p. 22) and thus might have increased the original porosity or created porous zones (Sælen, 1989). Based on observation of *Sepia officinalis* cuttlebone Florek *et al.* (2009) considered that Na and Mg were most likely located in the organic matrix. These findings fit well with observations that Na and Mg had opposite trends in concentration compared to Ca in belemnite rostra, suggesting that Ca-deficient areas were rich in organic matter (Florek *et al.*, 2004). Data presented by Hoffmann *et al.* (2016) support at least the Mg/Ca relationship.

Mietchen *et al.* (2008) used magnetic resonance imaging (MRI) on belemnite rostra and speculated that water or organic matter could explain the distribution of the observed mobile ^1H nuclei. To test their hypothesis, belemnite rostra were frozen to $-20^\circ C$ and then heated first to $70^\circ C$ and then for 8 h at $200^\circ C$; all procedures did not alter the magnetic resonance (MR) spectra or images. Belemnite material was powdered and subjected to ^1H and ^{13}C nuclear MR magic-angle-spinning (NMR MAS) spectroscopy revealing the presence of water or hydroxyl-group and C—O or C—S double bonds, respectively. These results are consistent with those obtained from organo-chemical analyses, which did not reveal any traces of lipids (Mietchen *et al.*, 2008). Water or hydroxyl-groups, potentially bound to the mineral matrix, seem to have been the major signal contributor to the MRI results.

Birchall & Thomas (1983) report 30–40% organic matrix for the dorsal sheath of the sepiid cuttlebone, which has been seen as a homologous structure to belemnite rostra (Bandel & Spaeth, 1988) or more specifically to the primordial rostrum (Fuchs, 2012), and about 10% organic matrix was reported for the phragmocone (Birchall & Thomas, 1983; Florek *et al.*, 2009). The cuttlebone contains more organic material than other mollusc shells (Hare & Abelson, 1965). Kabanov's (1959, 1967) proposal of an elastic belemnite rostrum, likely based on observations on *Moroteuthis* or on pathological specimens, was rejected by Pugaczewska (1961).

Further analyses of belemnite organic matter are required using additional analytical tools such as Fourier-Transform-Infrared spectroscopy (FTIR) (allows for the detection of, e.g. β-chitin), Raman spectroscopy, or time-of-flight secondary ion mass spectroscopy (ToF-SIMS) analyses for more detailed specification of any organic molecules, e.g. differentiation between microbial and metazoan organic remnants.

IV. CONCLUSIONS

(1) Our observations in combination with published data on belemnite soft body structures, skeletal organization, habitat, and rostrum ultrastructure have resulted in a more detailed and robust reconstruction of belemnite palaeobiology. This reconstruction is supplemented by considerations of the ecological requirements of closely related modern coleoids. Our review provides a useful background for those concerned with the interpretation of geochemical data derived from belemnite rostra.

(2) Belemnites were streamlined, torpedo-shaped, squid-like predators with sharp, triangular jaws, possessing an ink sac and ten arms of equal length each equipped with about 40 micro-hooks. We lack direct and conclusive evidence in belemnites for large lateral eyes, fins, colour patterns, the radula, uroliths, statoliths, and suckers.

(3) The presence of an internal shell with a rostrum and complete phragmocone with an open body chamber suggests that belemnites were neutrally buoyant, fast and highly manoeuvrable swimmers. Precise 3D-models will be required to test the postulated counterweight function of the rostrum, and implied horizontal swimming behaviour together with the assumed neutral buoyancy of belemnites.

(4) The presence of a chambered phragmocone and an ink sac, among other morphological traits, and shell mechanics indicates that belemnites inhabited the upper 200 m of the water column. Several lines of evidence point to a shallow marine habitat, and that belemnites were predominantly hemipelagic shelf dwellers also including littoral zones.

(5) Belemnites were a key group in the Jurassic and Cretaceous seas as both predators and prey. Belemnites predominantly fed on crustaceans, other cephalopods, and fishes. Predators of adult belemnites were sharks, bony fishes, ichthyosaurs, and other marine reptiles as inferred from stomach contents and pathologies. Belemnite hatchlings, as part of the plankton, were likely consumed by large filter feeding invertebrates or vertebrates, e.g. pachycormid fishes.

(6) Belemnites, like most modern coleoids, were probably relatively short lived, most likely for only 1 or 2 years.

(7) A bottom-dwelling lifestyle of belemnites seems unlikely due to records from sediments deposited under anoxic bottom-water conditions. Different lifestyles of

belemnites might be suggested by variations in rostrum morphology including: (*i*) club-shaped/slender-elongated rostra = fast swimming, open water; (*ii*) conical rostra = slow swimming, highly manoeuvrable, shallow marine; and (*iii*) depressed = nektobenthic. Similar to recent cephalopods, belemnite habitat depth might have been largely controlled by food and temperature.

(8) Some modern coleoids, e.g. sepiids, perform temperature-related seasonal migrations with temperature optima between 10°C and 30°C and salinities between 27 and 37 psu. Active predatory cephalopods require a well-oxyenated environment due to their use of relatively inefficient jet propulsion and haemocyanin for blood oxygen transport. Changes in environmental parameters would have resulted in changes in belemnite distribution, which thus can be used to reconstruct changes in palaeoenvironments. Belemnite taxa that preferentially lived in cold and warm water masses can be distinguished. Changes in their palaeogeographic distribution and faunal turnovers have been used to track global changes in seawater temperatures. Such migrations probably occurred parallel to the coastline on the shelf with deeper water masses acting as physical barriers.

(9) Belemnite rostra are not composed of alternating distinct types of laminae and are primarily composed of low-Mg calcite. A detailed description of rostrum growth and potential biomineralization pathways suggests rostrum formation in two steps. During the first step, a belemnite rostrum layer is composed of a filigree network of tetrahedral organic-rich calcite with high amounts of pore space between the tetrahedrals (CP1). This layer formed under strict biological control. During a second mineralization stage the pore space is occluded by isopachous organic lean calcite crystals (CP2). The presence of two phases of geochemically distinct calcite deposited in at least some belemnites (*Megateuthis*, *Gonioteuthis*, *Belemnitella*, *Hibolithes* and *Belemnopsis*) suggests that belemnite calcite fibres record a mixed signal of different environmental conditions and fluid geochemistry.

(10) Finally, we encourage the application of a proper taxonomic identification of sampled rostra, at least at the generic level. While the position of belemnites within the Coleoidea as stem-decabrachians has been demonstrated, detailed systematics of belemnites remain unclear. Well-resolved belemnite systematics will benefit investigations of belemnite evolution and ecology and consequently the interpretation of their geochemical data.

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