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Dirk Fuchs and René Hoffmann

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PART M, CHAPTER 10: ARM ARMATURE IN BELEMNOID COLEOIDS

DIRK FUCHS¹ and RENÉ HOFFMANN²

¹Earth and Planetary System Science, Department of Natural History Sciences, Sapporo, Japan, drig.fuchs@gmail.com; ²Ruhr-Universität Bochum, Institute for Geology, Mineralogy, and Geophysics, Branch Paleontology, Universitätsstrasse 150, 44801 Bochum, Germany, rene.hoffmann@rub.de]

INTRODUCTION

Among other key innovations, such as the development of a powerful jet propulsion, the arm armature is jointly responsible for the successful evolution of coleoid cephalopods (Fig. 1). Their multiple appendages armed with suckers and sharp hooks are well known since they inspired classical mythology. It is reasonable to assume that the extraordinary cognitive capabilities of coleoids have been triggered by this defense and predation apparatus. In any case, the first appearance of cephalopod arm hooks in Carboniferous deposits indicates that arming started very early in coleoid evolutionary history (e.g., JOHNSON & RICHARDSON, 1968; ENGESER & CLARKE, 1988; MAPES, WELLER, & DOGUZHAEVA, 2010).

Since hooks of extant oegopsid squids differ from fossil hooks, most strikingly through their ontogenetic formation, both structures have commonly been accepted as convergent developments (e.g., ENGESER, 1987a; ENGESER & CLARKE, 1988; YOUNG, VECCHIONE, & DONOVAN, 1998; FUCHS, BOLETZKY, & TISCHLINGER, 2010; FUCHS, HEYNG, & KEUPP, 2013). Instead, the normally biserial arrangement along the oral surfaces of each arm has led the same authors to assume a homology between fossil hooks, octobranchian cirri, and decabranchian trabeculae. The assumption of HAAS (1989) that fossil hooks and suckers represent homologues has been rejected by FUCHS, BOLETZKY, and TISCHLINGER (2010), who confirmed the co-occurrence of hooks and suckers in belemnite belemnites (DONOVAN & CRANE, 1992).

Fossil arm hooks are sometimes called “onychites,” although QUENSTEDT (1858, p. 201) originally differentiated between smaller hooks (his “kleinere Krallen,” meaning small claws) and distinctly larger Onychiten. Today, cephalopod experts mostly distinguish between micro-hooks (micro-onychites) and mega-hooks (also, mega-onychites or macro-hooks) (Fig. 2). Both are presently considered as diagnostic only for Paleozoic and Mesozoic belemnoid coleoids. The only Cenozoic example of an arm hook, reported by HARZHAUSER (1999) from the middle Miocene (Langhian) of Austria, has been attributed to the oegopsid family Onychoteuthidae. Sucker rings, typical for extant squids and cuttlefishes, were assumed by MANTELL (1852) in a belemnoid and by FISCHER and RIOU (1982) in a nonbelemnoid coleoid, but their interpretations have not yet been confirmed.

Paleontologists distinguish between 1) articulated (*in situ*) hooks (mostly arranged in biserial longitudinal rows, ideally reflecting an arm crown); 2) disarticulated (scattered) hooks; and 3) isolated hooks (mostly obtained from micropaleontological assemblages). Articulated or disarticulated hooks are often associated with shell and other body remains (Table 1). Isolated hooks co-occurring with belemnoid body fossils in the same strata can sometimes be referred to orthotaxa, whereas isolated hooks from localities without any evidence of belemnoid body fossils can only be classified in a parataxonomic system introduced by KULICKI and SZANIAWSKI (1972). The hook-based parataxonomy, which has mainly been

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Fuchs, Dirk, & René Hoffmann. 2017. Part M, Chapter 10: Arm armature in belemnoid coleoids. *Treatise Online* 91:1–20, 9 fig., 1 table.



FIG. 1. Recent arm hooks of *Ancistrocheirus lesueurii* ORBIGNY, 1842 in FERUSSAC and ORBIGNY, 1835-1848, scale bar, 10 mm (Tree of Life Web Project; tolweb.org).



FIG. 2. *Passaloteuthis* sp., Posidonia Shale, lower Toarcian, Schierbach (southern Germany) (Staatliches Museum für Naturkunde, Stuttgart, Germany, SMNS 70313), articulated micro-hooks and one pair of mega-hooks constituting an (incomplete) arm crown; scale bar, 10 mm (new).

applied by micropaleontologists, is reviewed in HOFFMANN in *Treatise Online*, Part M, Coleoidea, Chapter 22H.

HISTORIC REVIEW AND EARLY IDEAS

Though misinterpreted as plant remains, STERNBERG (1833, pl. 8, *l*) figured the first cephalopod arm crown (Fig. 3.1). MÜNSTER (1834, p. 42) is credited with being the first to correctly recognize a cephalopod arm crown. Biserial rows of S-shaped imprints on a slab from the Upper Jurassic (lower Tithonian) Solnhofen Plattenkalks led him to interpret them as unusual suckers. Five years later, after fruitful discussions with his contemporaries and on the basis of new specimens, MÜNSTER corrected his earlier view and reinterpreted these structures as arm hooks (MÜNSTER, 1839, p. 91, pl. 9; Fig. 3.2). He followed a proposal by Rudolf WAGNER, who suggested the name *Acanthoteuthis* WAGNER in MÜNSTER, 1839 for the arm crowns. The similarity with modern hook-bearing oegopsid squids, such as *Enoploteuthis* ORBIGNY, 1844 in Rüppell, 1844, and *Onychoteuthis* LICHTENSTEIN, 1818, led both researchers to assume teuthid relationships (Fig. 3.2–3.5). MÜNSTER (1839) therefore hypothesized that co-occurring, arrow-shaped gladii belong to the arms of *Acanthoteuthis*. At the same time, British workers discovered the first hook-bearing coleoids from the Callovian Oxford Clay of Christian Malford (PEARCE, 1842; OWEN, 1843). OWEN (1844) is credited with being the first to illustrate these hooks, which were found along with muscular tissues and phragmocone remains of *Belemnoteuthis antiqua* PEARCE, 1847 (see DONOVAN & CRANE, 1992; Fig. 4.1–4.2). Although OWEN (1844, p. 81) denoted similarities between the hooks of *Belemnoteuthis* PEARCE, 1842 and Recent *Onychoteuthis*, he placed *Belemnoteuthis* with rostrum-bearing belemnitids rather than with gladius-bearing squids. QUENSTEDT (1849), who emphasized his conviction about teuthid affinities of both *Acanthoteuthis* and *Belemnoteuthis*, presented the first hooks from

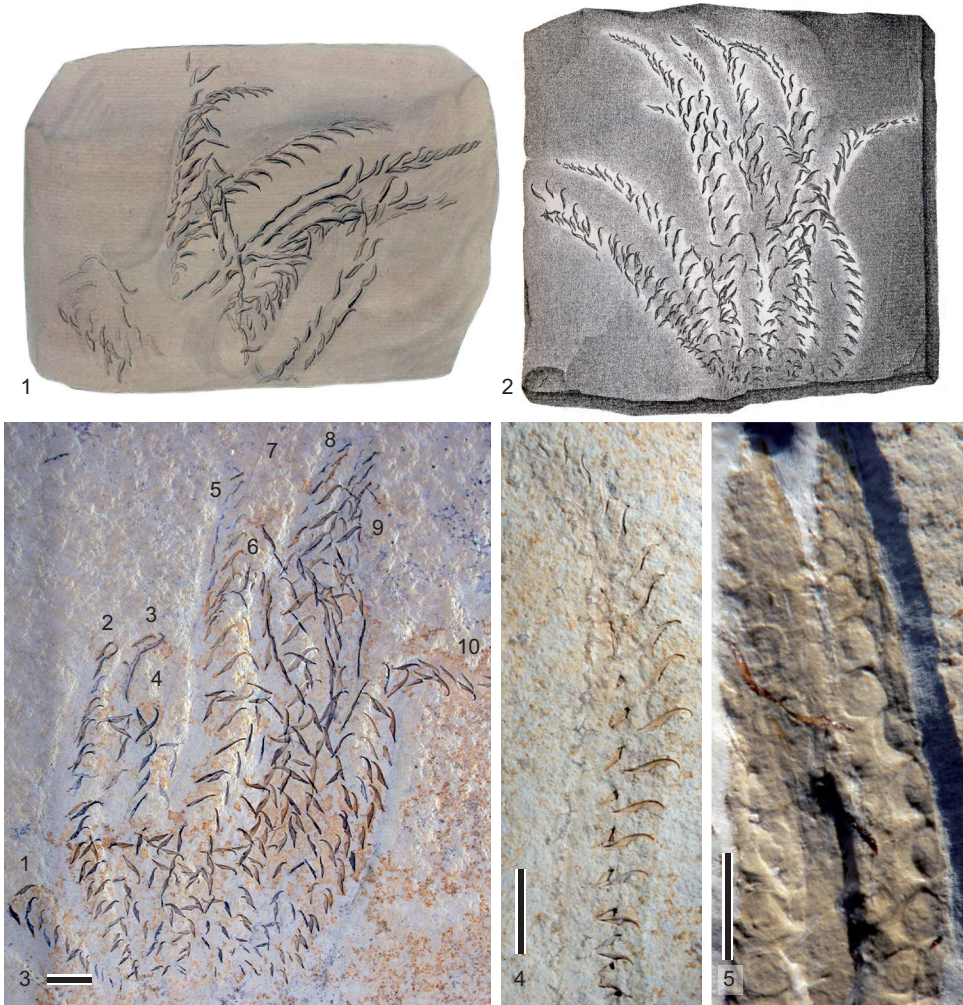


FIG. 3. Arm armature of *Acanthoteuthis speciosa* MÜNSTER, 1839, Solnhofen Plattenkalks, Eichstätt (southern Germany). 1, Earliest illustration of a fossil cephalopod arm crown by Sternberg (1833, pl. 8, I); 2, illustration by MÜNSTER (1839, pl. 9); 3, articulated (*in situ*) micro-hooks forming a complete arm crown, with arms 1–10 noted (Bürgermeister Müller Museum, Solnhofen, Germany), scale bar, 10 mm (new); 4, individual arm with biserial micro-hooks (Musé National d'Histoire Naturelle, Paris, France, MNHN F13426), scale bar, 10 mm (new); 5, close-up of two arms showing the co-occurrence of hooks and suckers (H. Tischlinger collection), scale bars, 10 mm (new).

the Toarcian Posidonia Shale of southern Germany belonging to *Clarkeiteuthis* (formerly *Onychoteuthis* or *Phragmoteuthis*) *conocauda* (QUENSTEDT, 1849; Fig. 4.3). Later, QUENSTEDT added mega-hooks from lower Jurassic deposits from southern Germany (QUENSTEDT, 1858) to the mega-hooks first discovered by FRAAS (1855) in coproliths (or regurgitates) from the Kimmeridgian Nusplingen Plattenkalks. Since WOODWARD

(1851), paleontologists increasingly accepted *Acanthoteuthis* as a belemnoid rather than a teuthid. Shortly after HUXLEY (1864) introduced the first Sinemurian hooks from the Charmouth Mudstone Formation of Lyme Regis belonging to *Clarkeiteuthis* (formerly *Phragmoteuthis* or *Belemnoteuthis*) *montefiorei* (BUCKMAN, 1880), SUSS (1865) presented the first Triassic hooks. The hooks and their associated hard and soft parts

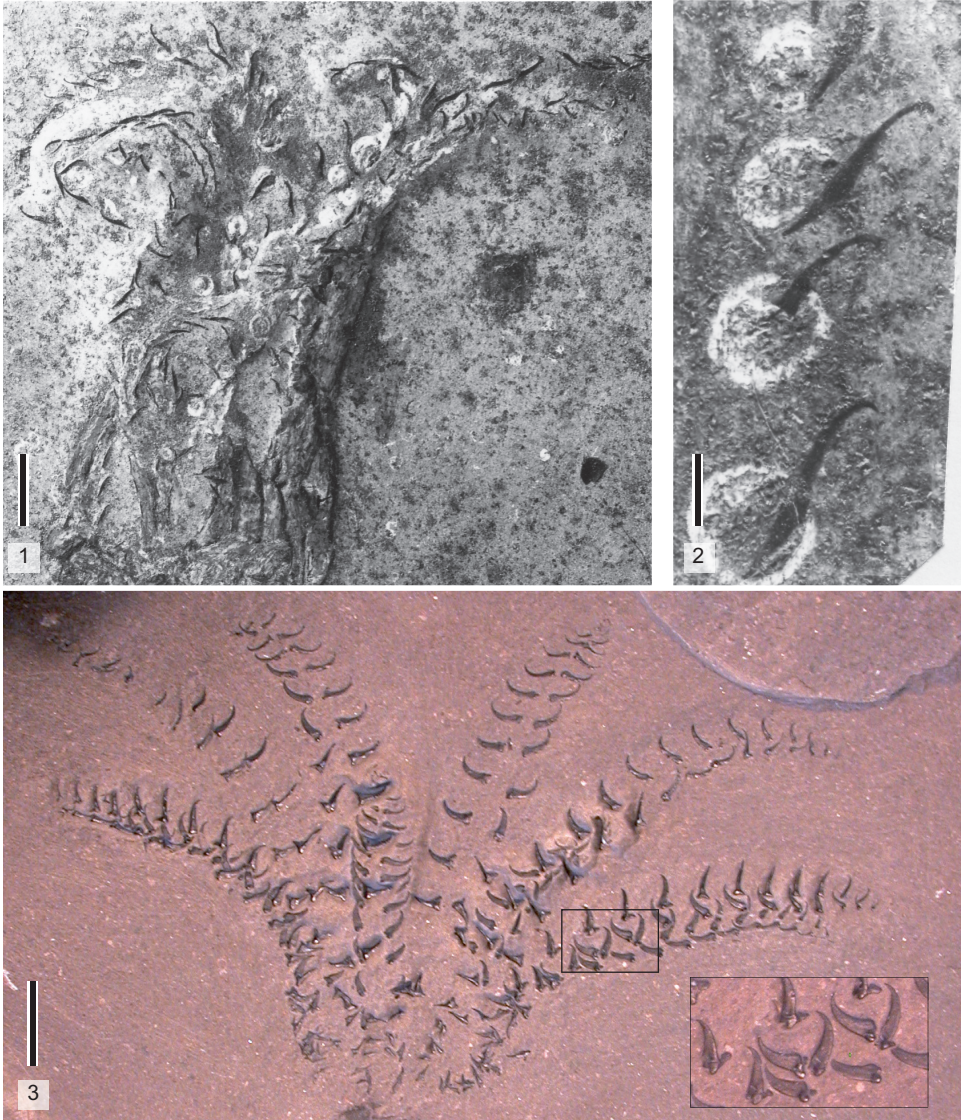


FIG. 4. Micro-hook-bearing arm crowns. 1–2, *Belemnotheutis antiquus* PEARCE, 1847 (Belemnotheutidina, Belemnitida); 1, specimen from Oxford Clay, Christian Malford (UK), upper Callovian (Bristol Museum and Art Gallery, Ca5240), scale bar, 10 mm (Donovan & Crane, 1992, pl. 2, 1); 2, close-up of same specimen showing hooks (black) and suckers (white, circular), scale bar, 1 mm; 3, *Clarkeiteuthis conocauda* (QUENSTEDT, 1849), putative Diplobelida, lower Toarcian, specimen from Posidonia Shale, Holzmaden (southern Germany), with close-up in lower right (Urweltmuseum Hauff, Holzmaden, Germany), scale bar, 10 mm (new).

came from the Rhaetian of Raibl (Austria) and were ascribed to *Acanthoteuthis*. Today, we know that the latter forms belong to *Phragmoteuthis* MOJSISOVICS, 1882, the type genus of the Phragmoteuthidae (Fig. 5.1).

Cretaceous hook-bearing arm crowns are limited to a very few specimens from the Plattenkalks of Häkel (ROGER, 1946; ENGESER & REITNER, 1986). The bulk of isolated Cretaceous hooks have been found

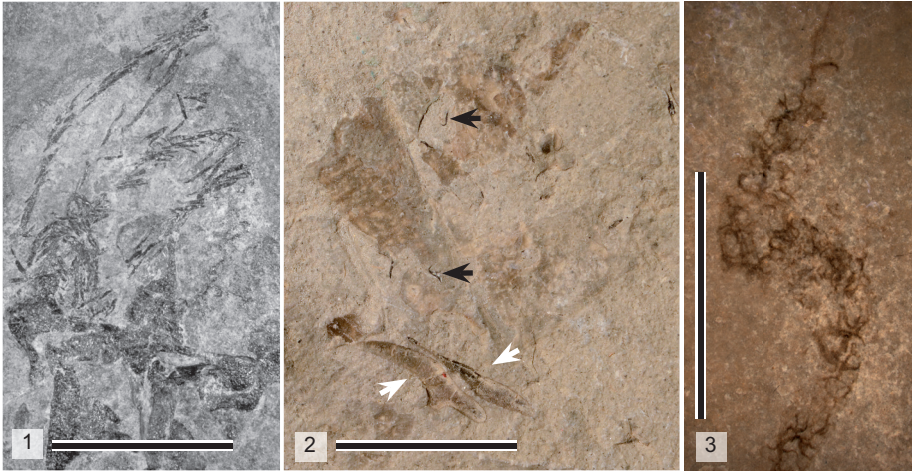


FIG. 5. Articulated (1, 3) and disarticulated micro-hooks. 1, *Phragmoteuthis bisinuata* (BRONN, 1859), Carnian, Fish Shales, Cave del Predil, northern Italy (formerly Raibl, Austria) (Geologische Bundesanstalt, Austria, GBA 2006 011 00001), scale bar, 10 mm (Rieber, 1970, pl. 2,1); 2, specimen indet. (?Aulacoceratida, ?Phragmoteuthida), upper Permian, East Greenland (Natural History Museum of Denmark, MMK 9643), note the presence of micro-hooks (black arrowheads) and unusual mega-hooks (white arrowheads) (new); 3, *Gordoniconus beargulchensis* MAPES, WELLER, & DOGUZHAeva, 2010, lower Carboniferous (upper Serpukhovian), Bear Gulch Limestone, Montana, USA, holotype (American Museum of Natural History, New York, USA, AMNH 43263), scale bar, 10 mm (new, photo courtesy of Royal Mapes).

in micropaleontological assemblages (e.g., KULICKI & SZANIAWSKI, 1972; ENGESER, 1987a; ENGESER & SUTHHOF, 1992; LEHMANN, SOLARCZYK, & FRIEDRICH, 2011). The honor to have first recovered Cretaceous hooks (upper Hauterivian, northern Germany) belongs to Leonard RIEDEL (RIEDEL, 1936, 1938).

The first Paleozoic hooks (and simultaneously the first hooks outside Europe) have been described by ROSENKRANTZ (1946). His hook assemblage originated from the upper Permian (Changhsingian) of East Greenland and included mega- and micro-hooks (Fig. 5.2). Additional records of rostra and phragmocones from the same deposits led him to assign all structures to *Permotoothis*. The first Carboniferous hook-bearing coleoid, *Jeletzkyia* JOHNSON & RICHARDSON, 1968 was discovered by JOHNSON and RICHARDSON (1968) among the famous Mazon Creek fauna (Illinois, USA). The oldest records of hooks found so far were recently introduced by MAPES, WELLER, and DOGUZHAeva (2010), who described *Gordoniconus* MAPES,

WELLER, & DOGUZHAeva, 2010 from the lower Carboniferous of the United States (Fig. 5.3).

Geographically, hooks are presently known from many other parts of the world: Russia (HECKER & HECKER, 1955); South America (WIND, DINKELMAN, & WISE, 1976, 1977); China (KEUPP & STEINER, 2010); New Zealand (STEVENS, 2010); Japan, (personal observations).

GENERAL MORPHOLOGY AND MORPHOMETRY OF BELEMNOID HOOKS

According to STEVENS (2010) and RIEGRAF, WERNER, and LÖRCHER (1984), belemnoid arm hooks range in length from 0.32 to 70.00 mm. Mega-hooks and micro-hooks represent two informal categories with 5.0 mm as an informal boundary (KULICKI & SZANIAWSKI, 1972). Former studies described micro-hooks as structures divided into three parts: base, shaft, and uncinus (KULICKI & SZANIAWSKI, 1972; ENGESER, 1987a; ENGESER & CLARKE, 1988) (Fig. 6). Later, this three-

fold division was also applied to mega-hooks (ENGESER, 1987b).

MICRO-HOOKS

The base of each hook was probably embedded in soft tissue. Some hooks show an orbicular scar, which is believed to represent the line to which the hook was embedded into soft tissue (ENGESER, 1987a). In some taxa, that scar was located at the lower base, dividing off the base from the shaft (KULICKI & SZANIAWSKI, 1972), while others possessed an orbicular scar distant from the base, usually dividing off the shaft from the uncinus (ENGESER & CLARKE, 1988). The lowermost part of the base can develop a thickened margin or an inner/outer or lateral extension, referred to as the process. In some hooks, the base is flat; in others concave. Besides the orbicular scar, the base shows no additional ornamentation. In some cases, a narrow basal opening of variable shape and dimensions has been reported. This opening is nearly symmetrical and is connected to an internal cavity (pseudo-pulp cavity of KULICKI & SZANIAWSKI, 1972; HAAS, 1989) already present in the Early Permian *Glochynomorpha* GORDON, 1971 as reported by DOGUZHAeva and MAPES (2014). The internal cavity, most probably present in all belemnoid hooks, was hollow during the animal's lifetime, and was of varying sizes and shapes in different taxa (ENGESER & CLARKE, 1988).

The base is followed by the shaft, which may or may not be separated from the base by a small constriction, and occasionally possesses a spur. That spur—"sporn" in REITNER and ENGESER (1982) or "Nebenspitze" in RIEGRAF (1996)—can be located closer to the base, directly at the boundary between base and shaft, to the uncinus, or almost exactly equidistant between the base and the uncinus (ENGESER & CLARKE, 1988). So far, the spur has only been reported in rostrum-bearing belemnitids. Hooks tentatively assigned to phragmoteuthids or belemnoteuthids do not develop a spur (ENGESER, 1987a). Some hooks develop another small morphological

detail, a fine hump on their outer margin, which is also of discriminant value. The shaft can be gently curved or distinctly bent, while it remains perpendicular and straight in other forms. The shaft can be of similar thickness throughout, or widening, or thinning towards the base of the uncinus. Ornamentation of the shaft may be comprised of pits or knobs, wrinkles, ridges, grooves, and furrows. Often associated with the spur, two distinct longitudinal ridges occur mostly along the inner margin of the shaft.

The most distal part is called the uncinus, which can follow the curvature of the shaft or show a distinct bending. Sometimes the distinction between shaft and uncinus is difficult to ascertain. Bending and/or ornamentation changes may indicate the boundary between these two parts. The uncinus is strongly or slightly curved internally and can end above the baseline, at base level, or below the base (Fig. 6). It is rarely curved externally. Like the shaft, the uncinus can show a distinct pattern of ornamentation.

Micro-hooks can reach up to several millimeters in length. Those recorded in micropalaeontological samples suggest a high degree of variability, although within an arm crown micro-hooks generally do not show a significant variation in shape. Exceptions are *Chondroteuthis wunnenbergi* BODE, 1933 from the Early Toarcian Posidonia Shale and *Ostenoteuthis siroi* GARASSINO & DONOVAN, 2000, both of which show a broad range of variation in the hooks along an arm (see below). It is presumed that the large majority of Mesozoic micro-hooks belong to rostrum-bearing belemnitids. These show the largest morphological variability of all belemnoid micro-hooks. However, so far we know of only two complete arm crowns of true belemnitids, namely *Parapassaloteuthis* RIEGRAF, 1980 and *Acrocoelites* LISSAJOUS, 1915. ENGESER (1987b) assumed that it may turn out that each species had its own micro-hook type, suggesting micro-hooks as a potential microfossil group of biostratigraphic interest.

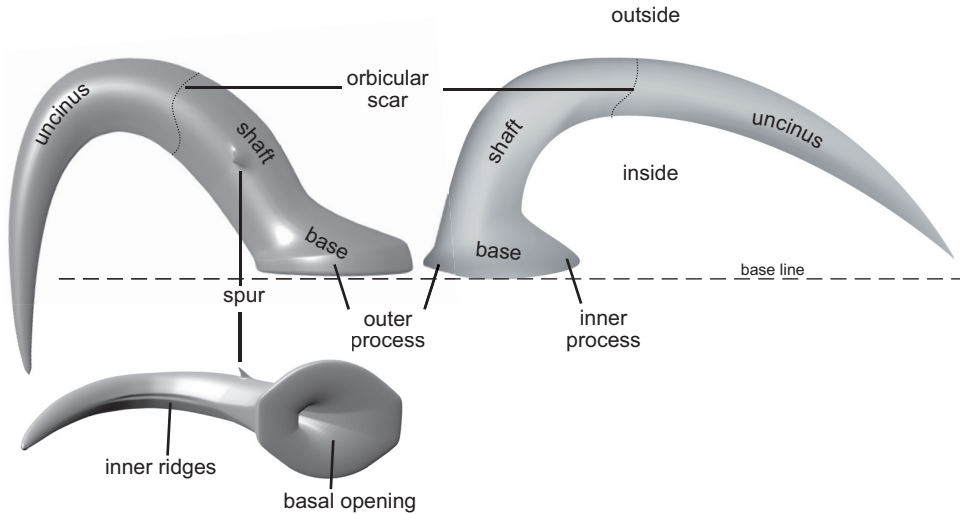


FIG. 6. Morphology and terminology of belemnoid hooks. Left, micro-hook in lateral view; right, mega-hook in lateral view; below, micro-hook in basal view (adapted from Hoffmann, Weinkauf, & Fuchs, 2017).

MEGA-HOOKS

Arm crowns of *Acanthoteuthis speciosa* demonstrate that not all belemnoids were equipped with a pair of mega-hooks. In fact, *Passaloteuthis paxillosa* (SCHLOTHEIM, 1820) from the lower Toarcian Posidonia Shale, thanks to an *in situ* record, is the only identified mega-hook-bearing belemnite found so far (RIEGRAF & HAUFF, 1983). Moreover, *Hibolites semisulcatus* from the Nusplingen Plattenkalks has also been suggested to carry mega-hooks (SCHWEIGERT, 1999). However, the morphological variety as well as the geographical and stratigraphical occurrences of isolated mega-hooks implies a wide taxonomic appearance.

Based on outlines of a selection of published mega-hooks, STEVENS (2010) has recently demonstrated the relatively consistent morphology in mega-hooks. His research may show that their morphology is similar regionally, even if they are of different stratigraphic ages. For instance, forms of mega-hooks from the Swabian Alb have a concave base with elongated inner and outer processes, while those from East Greenland have a flattened base and a short, rounded outer process. Accordingly, Polish forms are

more similar to the Swabian forms, while new reports of mega-hooks from the Upper Jurassic of Spitsbergen, are morphologically similar to the contemporaneous, previously known Boreal (Greenland, North Sea, Andøya) mega-hooks, i.e., belonging to the same form group (HAMMER & others, 2013). In a single case, HAMMER and others (2013) reported on the presence of weak, circular impressions potentially representing muscle attachment points. The uncinus, like the shaft, can show a distinct pattern of ornamentation, e.g., a chevron-like pattern (STEVENS, 2010; HAMMER & others, 2013). Its tip can be acute or blunt.

The oldest known mega-hooks were found in the upper Permian of East Greenland by ROSENKRANTZ (1946) and FISCHER (1947). The general shape of these mega-hooks, unlike the clasp-shaped morphology described above, were more similar to micro-hook types (Fig. 5.2). The first characteristic mega-hooks assignable to the parataxon *Onychites* QUENSTEDT, 1858 appear in the Lower Jurassic (Pliensbachian).

Where present, it is evident that only one pair of mega-hooks occurred per arm crown. Whether both mega-hooks were

located on one arm or were separated on complementary arms—and most importantly, which arm pair—is still unknown. Also, their position along an individual arm is still unclear. ENGESER and CLARKE (1988) assumed a proximal position (Fig. 2), while other authors have postulated a distal position (e.g., RIEGRAF & HAUFF, 1983; STEVENS, 2010).

MORPHOMETRY

Besides narrative descriptions of shapes, a few studies have supplied standard linear and angular measurements (e.g., ENGESER, 1987a; FUCHS, 2006; LEHMANN, SOLARCYK, & FRIEDRICH, 2011) (Fig. 7). These measurements include: a) the maximum hook length, defined as the distance on a horizontal line between the tip of the uncinus and the outer process of the base; and b) the length of the base from the inner to the outer process. In order to calculate the hook curvature, ENGESER (1987a) introduced the baseline, which is a horizontal prolongation of the base. Oriented in that way, the tip of the uncinus can lie above, exactly at, or below the baseline. Differences in the orientation of the connecting line between the tip of the uncinus and the baseline intersecting at the outer process are given as angular values. Maximal height (= width in ENGESER, 1987a) is given as the maximal distance between the baseline and outer margin of a hook. This point plotted perpendicular to the baseline gives information about the location of the highest point and the inflexion of curvature. Further important measurements are the breadth and the bending of the shaft. Bending of the shaft is measured as the angle between the baseline and a line at the middle of the shaft pointing towards the highest point of the hook. From these primary parameters, some ratios, such as total length/length of the base or total length/total height of the hook, can be inferred.

For well-preserved, complete hooks, the landmark approach can be applied. The inner and outer margin of the base and the tip of the uncinus represent geographical

landmarks, while the highest point of the hook at its outer and inner margin represent mathematical landmarks. For hooks with a concave base, a mathematical landmark can also be created. These landmarks provide distinct coordinates (morphospace) that can be compared with other hooks.

Most animal hooks and claws are shaped like a section of a logarithmic spiral. That shape is optimal, from a mechanical point of view, because stresses are distributed evenly and no point is therefore more susceptible to failure than any other (MATTHECK & REUSS, 1991). HAMMER and others (2013) used the inner and outer edges of complete mega-hooks and fitted them to logarithmic spirals, with the whorl expansion rate and the pole (center) of the spiral as fitted parameters. Their study showed that mega-hooks from the same locality shared similar values for the expansion rate.

Based on STEVENS (2010), we suggest several additional measurements that can be used to describe the hook morphology. The maximal length can be divided into base length and uncinus length. In addition to the maximal height measured as the distance between the horizontal baseline and the highest point at the outer margin of the hook, the height can also be measured for the inner margin of the hook. The difference between these heights gives the thickness of the hook at its highest point. The inflexion point of the hook curvature can be used as a mathematical landmark. A line connecting the tip of the uncinus with that landmark can be used to describe the curvature of the uncinus, while a point at the middle of the base connected with that landmark provides information about the bending of the shaft.

The elliptic Fourier analysis (EFA) offers a promising opportunity to distinguish between slightly different hook morphologies (KUHLE & GIARDINA, 1982; HOFFMANN, WEINKAUF, & FUCHS, 2017). This method requires the use of images of sufficient contrast to clearly distinguish between the object and the surrounding material. The analysis is much improved if a distinct starting point for the

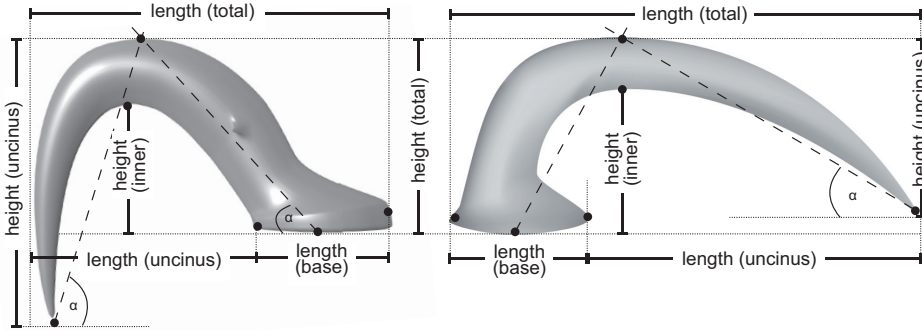


FIG. 7. Standard linear and angular measurements as well as landmarks (*black dots*) useful to characterize micro-hooks (left) and mega-hooks (right) (new).

outline extraction, i.e., a morphologically homologous feature of the object, can be chosen. During the outline extraction procedure, a sufficient number of points along the outline of each hook are extracted. The raw outlines (described as a Fourier function), are then normalized for size, and superimposed upon each other, enabling an objective comparison of hook shapes. This method allows the creation of a distinct morphospace for the analyzed hooks, including the application of quantitative methods to differentiate between hook morphotypes.

CHEMICAL COMPOSITION AND PRESERVATION OF BELEMNOID HOOKS

CHEMICAL COMPOSITION

The original composition of fossil hooks is difficult to determine and for a long time remained uncertain because of the pervasive carbonization as well as the effects of recrystallization and mineralization. First, KULICKI and SZANIAWSKI (1972) speculated about a chitin or conchiolin composition. ENGESER (1987b) and BERTHOLD and ENGESER (1987) stated that hooks were most likely composed of chitin but of a different composition compared to the hooks and sucker rings of extant coleoids, a conclusion indicated by different fossilization potential and occurrence (ENGESER & CLARKE, 1988). Based on the observation that Recent coleoid

hooks are made of beta-chitin (HUNT & NIXON, 1981; KEAR, BRIGGS, & DONOVAN, 1995), a similar composition for fossil coleoid hooks was assumed by RIEGRAF (1996). Similar findings have been reported by DOGUZHAIEVA and MAPES (2014) for an Early Permian coleoid made of a chitinous substance comparable to the composition of arm hooks of extant squids. These fossil hooks were composed of 46% iron, 7% nitrogen, and 5% calcium but with a high content (30%) of silica. A detailed comparative study of protein composition in the chitin-protein complexes for *Octopus CUVIER*, 1797 suckers was provided by HUNT and NIXON (1981). They found that *Octopus* suckers contain 51.2% chitin and 48.8% protein and they further provided a detailed list of the amino acid composition. According to HAAS (1989), the hook's microtexture, including canaliculi and supposed vesicular structures, is similar to that of decabrachian sucker rings. HAAS (1989) also assumed that there are no chemical differences between decabrachian sucker rings and belemnoid hooks. In addition to chitin, STEVENS (2010) discussed cartilage as a possible material for belemnoid hooks because modern squids have a number of cartilaginous structures, e.g., mantle- and funnel-locking cartilages (see BIZIKOV & TOLL, 2016).

GENERAL PRESERVATION

Despite a comparatively low preservational potential, belemnoid hooks arranged

in complete arm crowns are frequent in Konservat-Lagerstätten such as the Posidonia Shale (e.g., RIEGRAF & HAUFF, 1983; REITNER & URLICHS, 1983; FUCHS, DONOVAN, & KEUPP, 2013); in fine claystones like the Ornatenton Formation (QUENSTEDT, 1858); the Oxford Clay (e.g., DONOVAN & CRANE, 1992); or lithographic limestones (e.g., SCHWEIGERT, 1999; KLUG & others, 2010; FUCHS, BOLETZKY, & TISCHLINGER, 2010; FUCHS, HEYNG, & KEUPP, 2013). In other deposits, fossil arm hooks are normally found isolated in the sediment. Rather unusual finds of well-preserved hooks come from coprolites (GARASSINO & DONOVAN, 2000), regurgitates (SCHWEIGERT, 1999; McARTHUR & others, 2007), and gut and/or stomach content of various large vertebrates, such as long-necked plesiosaurs (ANDREWS, 1910–1913); ichthyosaurs (POLLARD, 1968; KELLER, 1976; BÖTTCHER, 1989; BRINKMANN, 1997); crocodylians (MARTILL, 1986), pliosaurs (MARTILL, 1992); and in large sharks (URLICHS, WILD, & ZIEGLER, 1994). REICH (2002) described the rare occurrence of micro-onychites (*Striatuncus* ENGESER 1988, and *Paraglycerites* EISENACK, 1939) of Maastrichtian hooks from acid sieve residues of the trace fossil *Lepidenteron* FRIČ, 1878. Also, anoxic or oxygen-depleted benthic conditions favored the preservation of belemnite hooks (DURSKA & DEMBICZ, 2015).

Often, particularly in limestones, hooks are preserved as well-defined negatives (imprints) in the rock (FUCHS, BOLETZKY, & TISCHLINGER 2010; KLUG & others 2010; FUCHS, HEYNG, & KEUPP, 2013; DURSKA & DEMBICZ, 2015), sometimes with some remains of organic matter preserved. DOGUZHAeva and MAPES (2014) report on iron-oxidized hooks from the Early Permian *Glochynomorpha*. Hooks that are substantially preserved are black (see Fig. 2, Fig. 4–5, Fig. 8), usually dull, often broken or strongly fractured due to the collapse of its central cavity, but can be removed from the surrounding rocks by the use of acid. During diagenesis (e.g. carbonization) most

of the minute surface ornamentation will be destroyed and smaller features like the spurs will not survive these processes.

HIGHER-LEVEL SYSTEMATIC OCCURRENCES OF HOOKS

A closer look at all known coleoid species with *in situ* hooks shows that the orders Donovaniconida, Phragmoteuthida, and Belemnitida (including Belemnotheutidina, Belemnitina, and Belemnopseina), with certainty, possessed arm hooks (Table 1). Although belemnoids are often generalized as hook-bearing coleoids, their occurrence in the Diplobelida, Aulacoceratida, and Hematitida is still unclear. However, in Diplobelida and Aulacoceratida, there exists some evidence that the lack of *in situ* records is a systematical and/or taphonomical issue.

DIPLOBELIDA

The question of whether or not this rostrumless group was equipped with arm hooks is currently dependent on the systematic assignment of some problematic hook-bearing taxa. JELETZKY (1966, 1981) and ENGESER (1990, 1995) indirectly assumed the existence of diplobelid hooks when they included *?Acanthoteuthis syriaca* ROGER, 1944 and *Chondroteuthis wunnenbergi* in the Diplobelida. However, other authors, such as ENGESER and CLARKE (1988); RIEGRAF, JANSSEN, and SCHMIDT-RIEGRAF (1998); and DOYLE and SHAKIDES (2004) excluded the same taxa from the Diplobelida, leaving the Diplobelida without evidence of hooks. FUCHS, DONOVAN, and KEUPP (2013) recently provided new evidence of their existence when they classified hook-bearing *Clarkeiteuthis conocauda* (Fig. 4.3) and *Clarkeiteuthis montefiorei* as diplobelids.

With the exception of *?Acanthoteuthis syriaca*, all of the above-mentioned problematica have been reassigned to the Diplobelida, owing to the shared possession of a narrow pro-ostracum. If the relative width of the pro-ostracum is a reliable character to delineate belemnitids from diplobelids, the

TABLE 1. List of belemnoid coleoids with associated arm hooks: X, present; /, unknown; 0, absent; ?, uncertain or ambiguous; *, associated shell remains doubtful; **, unpaired (new).

stratigraphic occurrence	species	order	suckers	disarticulated micro-hooks	articulated micro-hooks	ten uncinated arms	no. hook pairs/arm	associated mega-hooks	co-occurring mega-hooks	hook diff./arm	arm diff.	one arm pair modified as tentacles		
Cretaceous	<i>?Acanthoteuthis syriaca</i>	?	/	X	X	/	?	/	/	0	/	/		
	<i>Chondroteuthis wuennenbergi</i>	?Diplobelida	/	X	X	/	13–20**	/	X	X	X	0		
	<i>Clarkeiteuthis concauda</i>		/	X	X	X	0	X	0	0	0	0		
	<i>Clarkeiteuthis monteforei</i>		/	X	X	/	17	0	/	0	0	0		
Jurassic	<i>Acanthoteuthis speciosa</i>	Belemnitida	X	X	X	X	20–22	0	/	0	0	0		
	<i>Belemnoteuthis antiquus</i>		X	X	X	?	0	/	0	0	0	0		
	<i>Sueviteuthis zellensis</i>		/	X	X	X	>12–13	0	X	0	0	0	0	
	<i>Sueviteuthis schlierbachensis</i>		/	X	X	X	?	0	X	0	0	0	0	
	<i>Ostenoteuthis stroi</i>		/	X	X	X	31	0	/	/	X	X	0	
	<i>Uncinoteuthis cuvieri</i>		/	X	X	/	?	0	/	/	0	0	0	
	<i>Hibolites semisulcatus</i>		/	X	X	/	?	/	X	0	0	/	?	
	<i>Acrocoelites raii</i>		/	X	X	X	?	/	/	X	0	0	?	
	<i>Acrocoelites quenstedti</i>		/	X	/	/	?	/	/	/	0	/	?	
	<i>Passaloteuthis paxillosa</i>		/	X	X	/	?	X	X	0	0	/	?X	
	Triassic		<i>Winkleriteuthis problematica</i>	?Phragmoteuthida	/	X	X	/	?	0	/	0	0	0
			<i>?Phragmoteuthis ricinensis</i>	?Phragmoteuthida	/	X	X	X	28–34	0	/	0	0	?
<i>Phragmoteuthis bisinuata</i>		Phragmoteuthida	/	X	X	/	?	0	/	0	0	?		
Permian	<i>Permotoothis groenlandica</i>	?Phragmoteuthida	/	?X*	/	/	/	X	X	0	0	?		
	<i>Glochimonorpha stiftli</i>	?	/	?X*	/	/	/	/	/	/	/	?		
	<i>Jelzkyia douglassae</i>	?	/	X	X	?X	?	/	/	0	0	0		
Carboniferous	<i>Saundersites illinoisensis</i>	Donovanconida	/	X	/	/	/	/	/	/	/	?		
	<i>Gordoniconus beargulchensis</i>		/	X	X	/	/	/	/	/	/	?X		

assumption of hook-bearing diplobelids is reasonable, at least in their earliest forms.

Apart from systematic arguable taxa, FUCHS, REICH, and WIESE (2004) put forward taphonomical arguments for the presence of hooks in diplobelids. These authors suggested that isolated hooks from the Turonian of northwest Germany might have belonged to diplobelids. This conclusion is mainly based on the total absence of belemnite rostra in the same strata (although calcified rostra can frequently be found in Upper Cretaceous deposits in northwest Germany).

AULACOCERATIDA

Aulacoceratid remains, in fact, still lack any evidence of *in situ* arm hooks (see ENGESER & CLARKE, 1988). This led some authors to speculate about a primary lack of hooks (e.g., NAEF, 1922, p. 188; JELETZKY, 1966, p. 23; DOYLE, DONOVAN, & NIXON, 1994). ENGESER (1990) went even further and distinguished between hookless Aulacoceratida and the “Uncinifera,” uniting hook-bearing Phragmoteuthida, Belemnitida, and Diplobelida. DOYLE and SHAKIDES (2004, table 1) mentioned justifiable doubts about the presumed absence of hooks when they referred to FISCHER (1947), who described upper Permian hooks with co-occurring aulacoceratid rostra (*Prographularia groenlandica* FISCHER, 1947). ROSENKRANTZ (1946) linked the same hooks with phragmoteuthid-like remains (*Permoteuthis*), but, as JELETZKY (1966, p. 38) correctly stated, the hooks cannot properly be assigned. Taking into consideration the high number of recorded hooks and aulacoceratid rostra compared to a single phragmoteuthid-like fragment, it appears more plausible to link the hooks with abundant aulacoceratids than with obviously rare phragmoteuthids. In the latter context, it is important to refer the reader to Triassic localities such as the Zlambach Formation (Rhaetian, Austria) or the Luoping biota (Anisian, southern China) where hooks are known to co-occur with aulacoceratid rostra (MOJSISOVIC, 1902, p. 199, pl. 23,5–6; HU & others, 2011).

PRIMARY ABSENCE OF HOOKS IN MESOZOIC GLADIUS-BEARING OCTOBRACHIANS

This nonbelemnoid group of coleoids have long been considered as “fossil teuthids.” It is therefore not surprising that hooks have occasionally been assumed, particularly in plesiotheuthids, whose arrow-shaped gladius resembles those of hook-bearing oegopsids (e.g., MÜNSTER, 1839, 1846; ORBIGNY, 1845 in 1845–1847; WAGNER, 1860). As already outlined above, the views of MÜNSTER (1839, 1846) and ORBIGNY (1845 in 1845–1847) were based on the erroneous idea that the arm crowns of *Acanthoteuthis* belonged to plesiotheuthid gladii. WAGNER (1860, p. 779) correctly described hooks along with “*Celaenonica*,” but did not recognize the presence of a calcified phragmocone. NAEF (1922, p. 183) exposed this form as an enigmatic belemnoid (FUCHS, HEYNG, & KEUPP, 2013). In this context, JELETZKY (1966, p. 138) noted: “...NAEF (1922) carefully investigated all material available and insisted that arm hooks are invariably present in all well-preserved, identifiable belemnite remains and consistently absent in all similarly preserved, identifiable teuthid remains. The writer’s own study of the original material fully confirms these conclusions of NAEF (1922).” According to ENGESER and CLARKE (1988, p. 135), “...despite thousands of finds of fossil “teuthids” with preserved soft part remains, none of them showed arm hooks or even impressions of hooks (as might be expected if they had been of different chemical composition and not preserved).” Thousands of new specimens excavated in the last two decades from the Solnhofen and the Lebanon Plattenkalks ascertain the primary absence of hooks (and sucker rings) in Mesozoic gladius-bearing octobrachiids.

NUMBER OF ARMS INFERRED FROM THE ARRANGEMENT OF HOOKS

Records of articulated micro-hooks arranged in longitudinal rows are indispensable for

determining the number of arms. Today, cephalopod researchers generally accept that hooks exclusively belonged to belemnoids and that each of their ten subequal arms was equipped with hooks (e.g. NAEF, 1922, p. 187; JELETZKY, 1966, p. 138; ENGESER & CLARKE, 1988; DOYLE, DONOVAN, & NIXON, 1994; YOUNG, VECCHIONE, & DONOVAN, 1998; FUCHS, 2006). Before NAEF (1922), this view was heavily debated. Inconsistent observations and interpretations were largely influenced by incomplete (or in some cases even faked) specimens and/or by different morphological-systematical attitudes. Ideas about the arm crown morphology of belemnoids therefore varied between six hook-bearing arms (CRICK, 1902, 1907; ABEL, 1916), six hook-bearing plus four hookless arms (PRELL, 1922), eight hook-bearing arms (OWEN, 1843, p. 338, fig. 133, eight hook-bearing arms plus two hookless arms (OWEN, 1844; QUENSTEDT, 1845–1849, p. 524; RIEGRAF & HAUFF, 1983; and ten hook-bearing arms (MÜNSTER, 1839; ORBIGNY, 1845 in 1845–1847; ENGESER, 1987a). Since MÜNSTER (1939, pl. 9), and later MANTELL (1852, fig. 3), figured arm crowns of *Acanthoteuthis* and *Belemnotheutis* consisting of at least nine hook-bearing arms, it was plausible to assume ten hook-bearing arms, at least for rostrumless belemnitids. HUXLEY (1864) is believed to have studied the first arm crowns of rostrum-bearing belemnitids from the Sinemurian. However, as DONOVAN (1977) discovered, two of HUXLEY's specimens were artificial combinations of rostra from *Passaloteuthis bruguieriana* ORBIGNY, 1842 in ORBIGNY, 1842–1851 and *Passaloteuthis elongata* MILLER, 1826, and the arm crown of rostrumless *Clarkeiteuthis montefiorei* (see also *Treatise Online*, Part M, Chapter 22). The latter misinterpretation also fundamentally influenced the argumentation of CRICK (1902, 1907). Although a complete arm crown of *C. montefiorei* is still unknown, numerous arm crowns of *C. conocauda* characterized by identical hook shapes, clearly imply the existence of ten subequal and hook-

bearing arms (DONOVAN, 2006; FUCHS, DONOVAN, & KEUPP, 2013). Fortunately, RIEGRAF and REITNER (1979) prevented new confusion when they again exposed faked “soft-part belemnites” (see *Treatise Online*, Part M, Chapter 22). RIEGRAF and HAUFF (1983) and REITNER and URLICHS (1983) finally recovered the first pristine rostrum-bearing belemnitids with *in situ* hooks, *Passaloteuthis paxillosa* and *Acrocoelites rauii* (WERNER, 1912). The specimen of REITNER and URLICHS (1983) distinctly shows that rostrum-bearing belemnitids likewise possessed ten arms, each of which was armed with a biserial row of hooks.

In summary, ten hook-bearing and subequal arms have been documented in Belemnitida (Belemnotheutidina, Belemnitina, Belemnopseina) and putative Diplobelida. Whether the remaining belemnoid orders Hematitida, Donovaniconida, Aulacoceratida, and Phragmoteuthida had the same arm configuration still needs confirmation. Assumptions of ten arms in the Phragmoteuthida were based on *Clarkeiteuthis conocauda* and on *?Phragmoteuthis ticinensis* RIEBER, 1970. However, the former taxon has been recently reassigned from Phragmoteuthida to Diplobelida (FUCHS, DONOVAN, & KEUPP, 2013). Similarly, current phragmoteuthid affiliations of the latter taxon are still uncertain since diagnostic shell characters are unknown.

DIFFERENTIATIONS, SPECIALIZATIONS, AND SEXUAL DIMORPHISM

ARRANGEMENT AND DIFFERENTIATION OF MICRO- HOOKS ALONG INDIVIDUAL ARMS

In general, hook pairs are equally scattered along each arm and complementary hooks are usually of the same size and shape (Fig. 3–5, Fig. 8). The number of pairs, which varies only slightly between the subequal arms, range from 13 to 34 in the taxa we know (Table 1). For instance, numbers provided by ENGESER and CLARKE (1988)

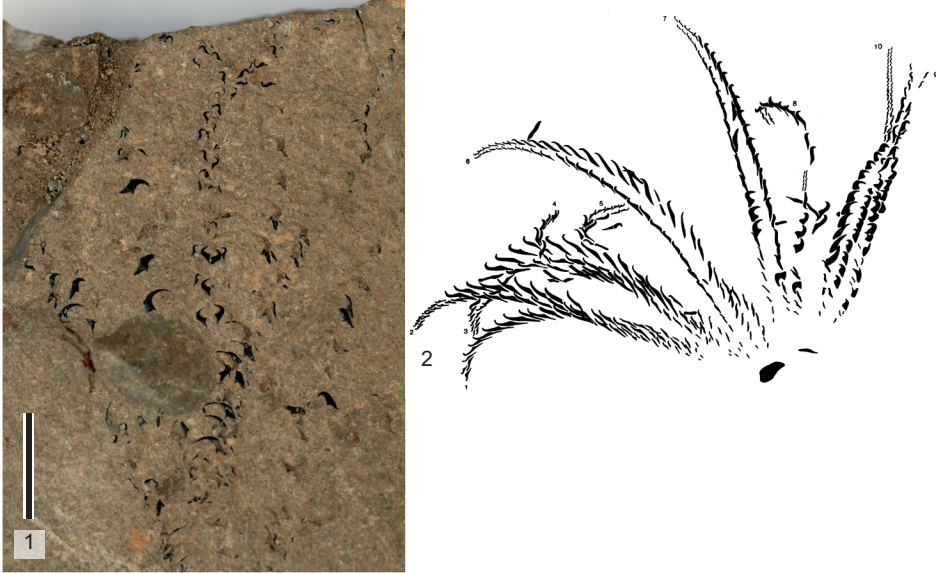


FIG. 8. Belemnoid arm crowns equipped with heterogeneous set of micro-hook types. 1, *Chondroteuthis wunnenbergi* (putative Diplobelida), Posidonia Shale, lower Toarcian, northern Germany, (Bundesanstalt für Geowissenschaften und Rohstoffe, Hannover, Germany, BGR/NLFB 574), scale bar, 10 mm (new); 2, *Ostenoteuthis siroi* (putative Belemnitheutidina), lower Sinemurian, Moltrasio Limestone Formation, Osteno (Italy), holotype, Museo Civico di Storia Naturale Milano, Italy, MSNM i24730 (Garassino & Donovan, 2000, fig. 3).

of up to 100 hook pairs per arm need to be confirmed. Hook sizes gradually increase from proximal until two-thirds of each arm and then decrease towards distal tips. The latter size modifications can be accompanied by a gradual alteration of shape. REITNER and URLICHS (1983) described two different hook types in *Acrocoelites raui*, but the differences are gradual rather than sudden. The only taxa with a pronounced hook differentiation along individual arms are *Chondroteuthis wunnenbergi* (Fig. 8.1) and *Ostenoteuthis siroi* (Fig. 8.2). The former taxon is most unusual as it is the only known belemnoid with uniserial (unpaired) hooks (HOFFMANN, WEINKAUF, & FUCHS, 2017). Ontogenetical alterations of hook types are so far unknown.

DIFFERENTIATION OF ARMS

While five arm pairs are currently accepted, the question of whether or not belemnoid arms were differentiated is still subject to controversy. Nineteenth-century scientists generally assumed a belemnoid arm crown including an elongated arm pair (often

called “tentacles”). Early reconstructions of belemnites accordingly show a tentacle-like arm pair either with (e.g., WOODWARD, 1851) or without hooks (e.g., OWEN, 1844; MANTELL, 1848; see DONOVAN & CRANE, 1992, fig. 1). In addition, records of paired mega-hooks gave reason to assume arm differentiation, at least in rostrum-bearing belemnitids (FRAAS, 1855; QUENSTEDT, 1858; SCHWEIGERT, 1999; STEVENS, 2010). NAEF (1922, p. 182–183) was however undecided in this context: “...clear differentiation of the tentacular arms did not exist.... We may ask ourselves whether an inconspicuous differentiation of the fourth arm pair (counted from above) is nevertheless likely.”

JELETZKY (1966, p. 138) similarly remarked: “So far as known, the Belemnitida were characterized by the absence, or very rudimentary development of tentacles.” After the confirmation of ten hook-bearing arms in rostrum-bearing belemnitids in the early 1980s, experts have still been divided. Authors such as RIEGRAF and HAUFF (1983), ENGESER and SUTHHOF (1992), or STEVENS

(2010) have assumed a tentacle-like arm differentiation, while others such as REITNER and URLICH (1983), ENGESER and CLARKE (1988), GARASSINO and DONOVAN (2000), or DONOVAN (2006) have considered all belemnites as tentacleless decabrachians. The poorly supported tentacle hypothesis rests on the fact that a complete arm crown consisting of ten subequal arms is still unknown in rostrum- and mega-hook-bearing belemnites (e.g., in *Passaloteuthis*; note that mega-hooks are still unknown in *Acrocoelites*).

The absence of true tentacles does not exclude the possibility of moderate arm differentiations in at least some belemnoid taxa. For instance, *Chondroteuthis wunnenbergi* (Fig. 8.1) and *Ostenoteuthis siroi* (Fig. 8.2) are known to exhibit different hook types on different arms (ENGESER, 1987a; (GARASSINO & DONOVAN, 2000; HOFFMANN, WEINKAUF, & FUCHS, 2017). Although the more or less uniform micro-hooks in rostrum-bearing *Passaloteuthis* and *Hibolithes* point to undifferentiated arms, the paired co-occurrence of mega-hooks suggests a specialization of at least one arm or arm pair (Fig. 2).

The function of the mega-hooks has been interpreted in two different ways. The idea of a sexual dimorphism is widespread (e.g., BRUUN CHRISTENSEN, 1995; KLUG & others, 2010; STEVENS, 2010; HAMMER & others, 2013). Owing to a relative rarity of mega-hooks compared to micro-hooks, ENGESER (1987b) and ENGESER and CLARKE (1988, p. 138) suggested that only males developed mega-hooks as a copulation organ in order to clasp females during mating. A pair of mega-hooks interpreted as copulation organs would induce the presence of a hectocotylied arm pair, which is unusual in extant coleoid males where hectocotyliation involves only an individual arm (either the left or the right arm of the third lateral arm pair). Conspicuously small mega-hooks (only a few millimeters) reported by ENGESER (1987b) and SCHWEIGERT (1999) might have belonged to either females or to adolescent males indicating that mega-hooks represent

early ontogenetic developments rather than an adult feature. By contrast, RIEGRAF and HAUFF (1983) and RIEGRAF (1996, p. 20) rejected the copulation approach and considered the mega-hooks as a hunting device.

COMPARISON WITH RECENT ARM HOOKS

As mentioned above, the appearance of likewise chitinous hooks along the arms of Recent decabrachians is widely accepted as a homoplasy. Within extant decabrachians, only a few families (Onychoteuthidae, Octopoteuthidae, Enoploteuthidae, Ancistrocheiridae, Pyroteuthidae, Gonatidae, Cranchidae) of the order Oegopsida are hook-bearing (Fig. 1, Fig. 9). Their hooks can occur on both regular arms and tentacles (Enoploteuthidae, Ancistrocheiridae, Gonatidae, *Mesonychoteuthis*), only on tentacles (Onychoteuthidae, *Galiteuthis*, *Taonius*) or only on arms (Octopoteuthidae) (see, for example, JEREB & ROPER, 2010). Where present on regular arms, not every arm must be equipped with hooks (e.g. Pyroteuthidae). Also, the number of hook rows is variable. Gonatid hooks are arranged in four rows, while remaining families display only one to two series. In contrast to belemnoids, oegopsid hooks are often restricted only to a short arm portion. As also assumed for belemnoids, oegopsid hooks are enveloped by a fleshy sheath.

The main difference between belemnoid and oegopsid hooks concerns the morphology of the hook base, which is solid, wide, and posteriorly extended in belemnoids and very delicate and with a central aperture in oegopsids. The aperture mainly accounts for the ontogenetical derivation of hooks from sucker rings (NAEF, 1922; ENGESER & CLARKE, 1988). Oegopsid squids may exhibit all intermediate stages between a sucker ring and a fully developed arm hook on one arm (compare NAEF 1922; KULICKI & SZANIAWSKI, 1972). There is currently no evidence in the fossil record of unambiguous sucker rings that might point to a similar morphogenesis of belemnoid hooks.

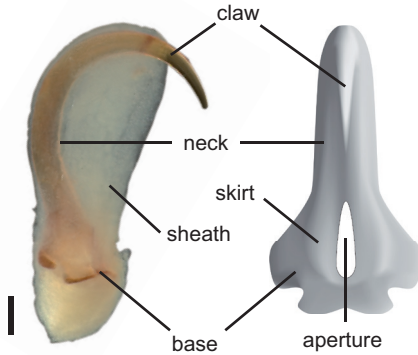


FIG. 9. Terminology and morphology of Recent oegopid hooks; left: arm hook of *Watasenia scintillans* (BERRY, 1911) in lateral view (Enoploteuthidae); scale bar, 0.2 mm; right: schematic drawing in oral view (new).

MISIDENTIFICATIONS WITH OTHER HOOK-LIKE MICROFOSSILS

Besides belemnoid arm hooks, there are many other hook-shaped microfossils from different stratigraphic levels. Scolecodonts (annelid jaws) are a prime example because these microfossils co-occur with belemnoid hooks and the two are often mistaken for each other (KULICKI & SZANIAWSKI, 1972; SZANIAWSKI, 1974). A second group of microfossils that share similar shapes with belemnoid hooks are the conodonts, particularly coniform conodonts (MURDOCK, SANSOM, & DONOGHUE, 2013). Belemnoid hooks and conodonts co-occur in Triassic deposits and can be misidentified. Conodonts went extinct at the Triassic-Jurassic boundary. To distinguish between scolecodonts and conodonts, MARSHALL, NOWACZEWSKI, and MARSHALL (2013) successfully developed a microchemical method. Due to their significantly different chemical composition, it is believed that this method can be successfully applied to distinguish between conodonts and belemnoid hooks. Unfortunately, an analysis to distinguish between the chitin of scolecodonts and the chitin of belemnoid hooks has not yet been tested.

Another group of hook-shaped microfossils comes from the molluscs themselves, namely their radula teeth. Radula teeth are highly variable, from unicuspidate to

multicuspidate and sometimes also hook-shaped (BERTSCH & others, 1973). When found isolated, these radular teeth are within the size variation of coleoid arm hooks. CRUZ, LINS, and FARINA (1998) showed that at least major mollusc groups (Aculifera and Conchifera) can be distinguished on the basis of the biogenic minerals in their radula teeth. It seems likely, but has not yet been tested, that chemical analyses accompanied by ultrastructural analysis could help to distinguish between radular teeth and belemnoid arm hooks. Lesser-known groups, such as the trematodes, polychaetes, chaetognaths, echiurans, lamprey, and fish, can also produce hook-like microstructures. LEATHAM (1985) interpreted the haptors of trematodes as attachment organs that anchor the animal to the gills of fish. Haptors are arranged pairwise with their hooked ends radiating outwards, which is the opposite for belemnoid hooks. But when found isolated, it might be difficult to distinguish them from belemnoid hooks except for their very small size (0.05 mm).

Besides scolecodonts, polychaetes possess tiny structures called chaetae that are also hook-shaped and predominantly occur in taxa that live in tubes. They range in size between 0.1–0.01 mm. The distally curved tip of the chaetae functions as an anchor for tube-dwelling polychaetes, with the tip of the hook facing the direction in which the worm could be extracted from the tube (MERZ & WOODIN, 2000, 2006). Belemnoid hooks, trematode haptors, and polychaete chaetae are all made of chitin and it might be difficult to distinguish between them based on nothing other than their chemical composition. Chaetognaths possess some spines and teeth in their mouth region that were probably functional analogues to coniform conodonts (see KASATKINA, 1982; BIERI, 1983). Echiurans, a group of marine worms, now assigned to the annelids, possess a pair of hook-shaped chaetae on the anterior ventral side and several straight to hook-shaped anal chaetae arranged in posterior rings (LEHRKE, 2011).

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