



# First record of a belemnite preserved with beaks, arms and ink sac from the Nusplingen Lithographic Limestone (Kimmeridgian, SW Germany)

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## LETHAIA



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A recent discovery of an unusually preserved belemnite from Nusplingen comprises the extraordinarily rare remains of beaks and nearly *in situ* arm hooks, as well as the ink sac and an incomplete phragmocone. So far, *Hibolites semisulcatus* (Münster, 1830) is the only belemnite known from the Nusplingen Lithographic Limestone (Upper Jurassic, Late Kimmeridgian, Beckeri Zone, Ulmense Subzone; SW Germany) that has the same phragmocone shape and size, and thus we assign the new specimen to this taxon. The rostrum was probably lost due to a lethal predation attempt in which the prey was killed but not entirely eaten. For the first time a specimen reveals details of the belemnite beak morphology, which we compare with the beaks of other Jurassic coleoids. This specimen presently represents the only known rostrum-bearing belemnite of post-Toarcian age with preserved non-mineralized body parts. With the new discovery, Nusplingen now represents the only locality which has yielded complete beak apparatuses from all major Jurassic cephalopod groups. □ Beaks, Belemnitida, Coleoidea, Germany, Late Jurassic, morphology, taphonomy.

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In the past two decades Nusplingen has become famous for exceptionally preserved fossils, including various cephalopods that show details of otherwise rarely preserved non-calcified tissues (e.g. Dietl & Schweigert 1999a; Schweigert 1999; Schweigert & Dietl 1999, 2001, 2008a,b; Klug *et al.* 2005). During an excavation within thin-bedded limestones of Late Jurassic age (Kimmeridgian, Beckeri Zone, Ulmense Subzone, *hoelderi* biohorizon; Schweigert *et al.* 1996; Schweigert 1998, 2007) at the protected Nusplingen Quarry (south of Balingen in SW Germany; Fig. 1) in 2008, an unusually preserved belemnite specimen was discovered. This preserves the arm-crown, remains of the ink sac, phragmocone and, additionally, the beaks. This is remarkable because, as far as we know, belemnite beaks have never been found in such a complete state, and thus new morphological information is revealed (compare Kaiser & Lehmann 1971). Additionally, this discovery represents the first post-Toarcian belemnite which preserves more than phragmocone, rostrum or the usually isolated arm hooks.

The aim of this article was to describe this specimen and to compare the belemnite beak with beaks of other Jurassic cephalopods. When considering the history of research on coleoid beaks, on Nusplingen coleoids, and the palaeontology of Nusplingen in general, we refer to Westphal (1992), Schweigert (1999), Dietl & Schweigert (1999b,c, 2001, 2004) and Klug *et al.* (2005) for details and references.

In contrast to the lithographic limestones of Solnhofen and vicinity, the slightly older limestones of Nusplingen preserve carbonaceous remains of originally chitinous (and other) structures such as cephalopod beaks (Dietl & Schweigert 1999a; Schweigert 1999; Schweigert & Dietl 1999, 2001, 2008a,b; Klug *et al.* 2005). While belemnoid remains with arm crown and/or other preserved soft-tissues are known from the Early Jurassic (Naef 1922; Hölder 1973; Reitner & Urlichs 1983; Riegraf & Hauff 1983; Riegraf *et al.* 1984, 1998; Etter & Tang 2002; Klug & Fuchs in press) and lowermost Middle Jurassic (Riegraf & Hauff 1983), the Late Jurassic has so far only yielded remains of the belemnite rostrum.

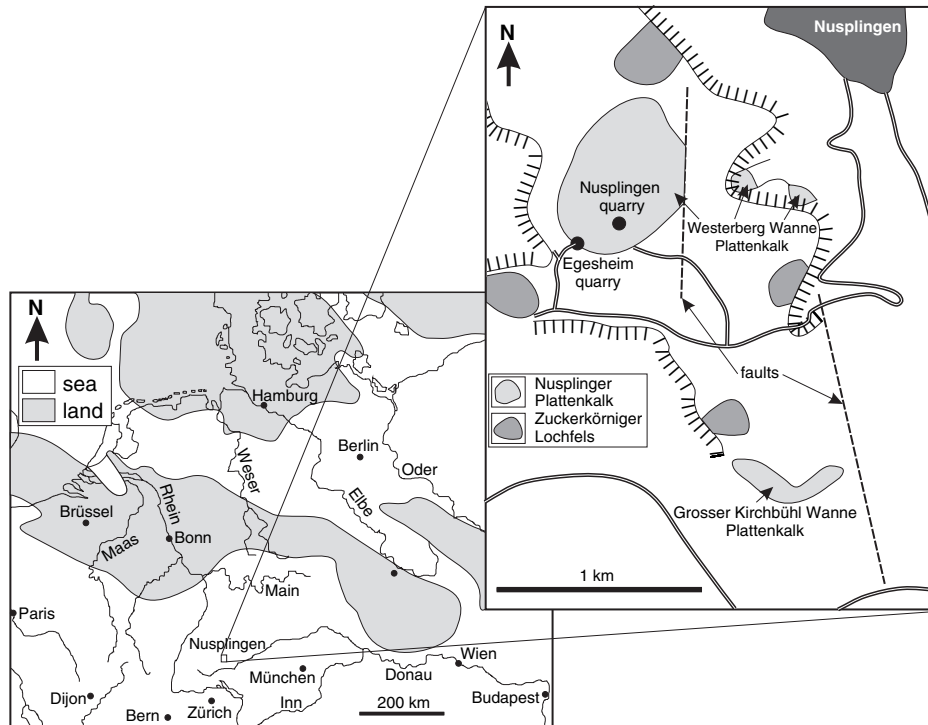


Fig. 1. Map with the location of the Nusplingen and Egesheim quarries, SW Germany, showing the distribution of land and sea during the Late Kimmeridgian (from Klug *et al.* 2005).

*Acanthoteuthis* and *Belemniteuthis* (Angermann 1902; Engeser & Reitner 1981, 1992; Donovan & Crane 1992; Frickhinger 1994, 1999; Riegraf *et al.* 1998), isolated arms, hooks (the smaller hooks which occur in large number in the arms of belemnites; we here largely follow Jeletzky 1966; Fuchs 2006) or mega-onychites (only one pair, much larger than the other hooks, is present per individual) of true belemnites (Engeser 1987a,b; Schweigert 1999). We do not know of any Cretaceous belemnite that is preserved with more than phragmocone, rostrum or arm hooks.

## Material and methods

The new belemnite was collected by the Stuttgart excavation team and is deposited in the Staatliches Museum für Naturkunde in Stuttgart (SMNS 67335). Terminology of the beaks and arm hooks is explained in Figure 2 and largely follows Clarke (1962, 1986), Clarke & Maddock (1988), Schlegelmilch (1998) and Tanabe *et al.* (2006, 2008). As none of the preserved parts are phosphatised, the otherwise useful method to examine fossil specimens from Fossil-lagerstätten with UV light (e.g. Larson *et al.* 2007, in press) did not yield any further information.

## Taxonomic remarks

The new specimen (Figs 3, 4) lacks the rostrum, which slightly hampered the taxonomic assignment. We interpret the specimen as belonging to *Hibolites semi-sulcatus* (Münster, 1830) for four reasons:

1. After over a century of excavations by various groups (Dietl & Schweigert 2001), only the remains of this belemnite species and one single specimen of the minute species *Rhaphibelus acicula* (Münster, 1830) have been found (Schweigert & Dietl 2008b). The exceptional preservation at this increasingly famous Fossil-lagerstätte would certainly have yielded any additional belemnite species if they ever lived in this region, especially as the excavation has lasted already several decades and has produced thousands of fossil cephalopod remains. The depositional area of this laminated limestone was a ca. 80-m-deep and 1500-m-wide basin surrounded by small islands. This situation hampered the circulation of the sea water and caused oxygen depletion in the deeper parts of the basin (e.g. Bantel *et al.* 1999). Therefore, organic material accumulated and is still preserved as kerosene in some of the beds, like the find-level bearing the belemnite specimen described here.



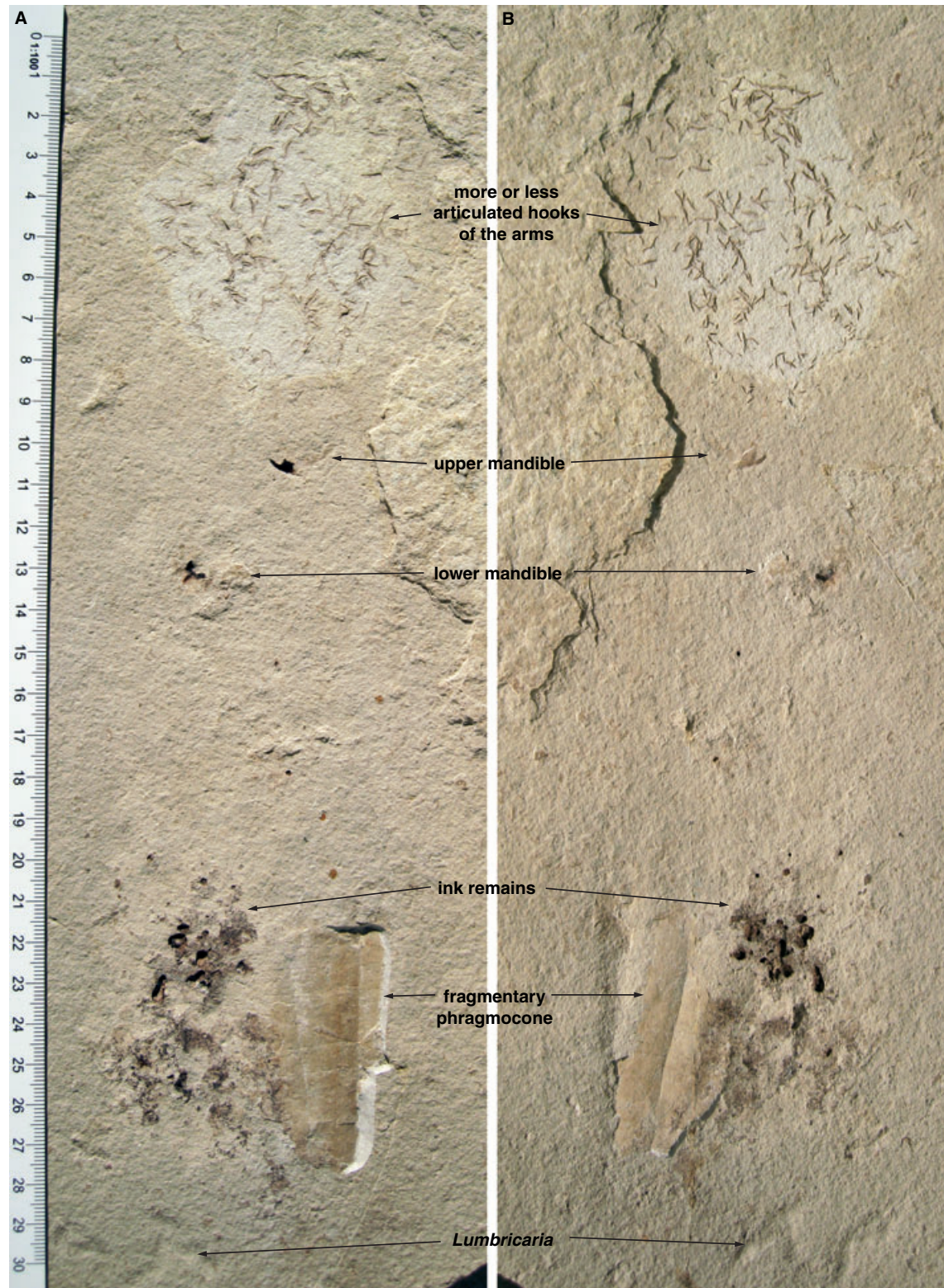


Fig. 2. *Hibolites semisulcatus* (Münster, 1830) preserved with phragmocone, ink sac remains, beaks and arms from the Nusplingen Lithographic Limestone (Upper Jurassic, Late Kimmeridgian, Beckeri Zone, Ulmense Subzone), SMNS 67335. A, slab; B, counterslab.

2. The shape and the size of the phragmocone of the new specimen and specimens of *H. semisulcatus*, which are preserved with rostrum and

phragmocone *in situ* from the same locality, show no differences. The size, the apical angle, the septal spacing and the preservation are similar (Fig. 5).

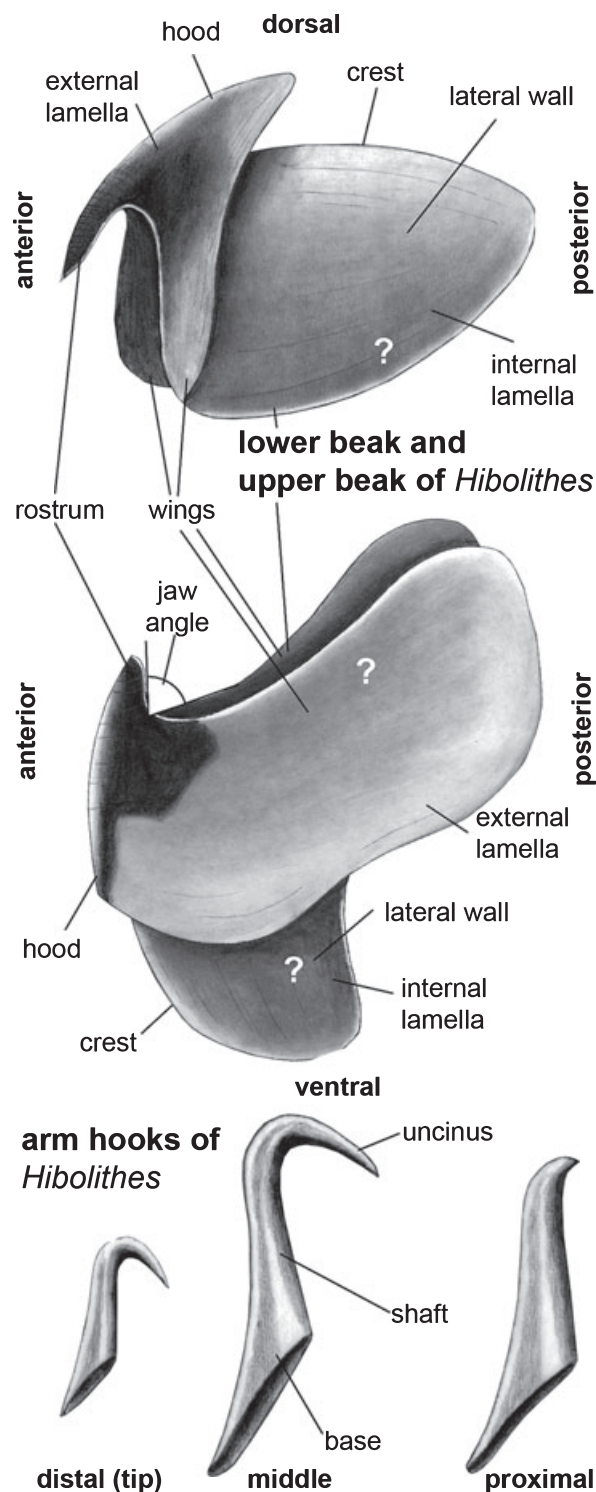


Fig. 3. Terminology of the beaks and arm hooks according to Clarke (1962, 1986), Clarke & Maddock (1988), Schlegelmilch (1998) and Tanabe *et al.* (2008), shown on the upper and lower beak as well as three different arm hooks of *Hibolites semisulcatus* (Münster, 1830).

3. The morphology of the hooks (onychites) is identical to hooks that Schweigert (1999: p. 11, pl. 2, 6) related to *H. semisulcatus*. The only other coleoid

group carrying hooks superficially similar to those of the new specimen is the belemnoteuthids, such as the Tithonian *Acanthoteuthis* or the Toarcian *Chondroteuthis* (compare Engeser 1987a). Belemnoteuthids have only been recorded in Nusplingen as poorly preserved phragmocones and dissolved rostra assignable to *Pavloviteuthis kapitzei* Engeser, 1995. *Acanthoteuthis* hooks differ from *Hibolites* in the smaller uncini and the larger angle between uncinus and shaft. *Chondroteuthis* has larger uncini on shorter shafts.

4. Several regurgitates from Nusplingen (compare Schweigert 1999) contain rostrum fragments of *Hibolites* associated with hooks identical to those found in the new specimen.

For a discussion of the type species of *Hibolites*, see Schlegelmilch (1998), Riegraf *et al.* (1998) and Schweigert (1999). These publications also provide synonymy lists of the genus and *H. semisulcatus*.

## Description

### Phragmocone

The entire specimen SMNS 67335 measures approximately 270 mm in length. The rostrum is not preserved, but a similar phragmocone from Nusplingen (compare Figs 3–5) is preserved with rostrum and we thus suggest that these two are conspecific, as noted above. The phragmocone is 61 mm long and maximally 39 mm wide; it is flattened, incomplete and the aragonite is dissolved. Its irregular outline clearly shows that it is incomplete (see the taphonomy chapter). The few longitudinal fractures were probably formed during the compaction of the sediment. As aragonite is only rarely preserved in the Nusplingen limestones, the phragmocone displays the straight sutures of ten, roughly equidistant, septa.

### Ink sac

Adjacent to the phragmocone, remains of ink, perhaps the ink sac, and the ink duct are preserved (Figs 3, 4). In some spots these remains are more massive and occur in thicker masses, which we interpret as remains of perhaps ink sac or duct. These thicker remains are maximally 6 mm long and a few millimetres wide and 1–2 mm thick.

### Proostracum

A gap of 80 mm width separates the ink and the phragmocone from the lower beak. In this gap, the





Fig. 4. Drawing of the parts preserved in the new specimen of *Hibolites semisulcatus* (Münster, 1830) from Nusplingen (compare with Fig. 2), SMNS 67335.

bedding plain shows no remains belonging unequivocally to the belemnite; only some fish scales are present. The width of the gap roughly corresponds to the length of the proostracum, which is not preserved (compare Engeser & Reitner 1981).

#### The lower beak

The upper and lower mandibles of the beak are separated by a gap of 30 mm. Although the beaks are incompletely preserved, they still display some interesting morphological features. The beak, situated closest to the phragmocone, is interpreted as the lower beak, flattened dorso-ventrally (Fig. 6C). The anterior edge and anterior mid-ventral ridge of the rostrum are preserved as darker areas. These are 5 mm long and accidentally have the outline of a flying squirrel (*Glaucomys volans*), with the 'wings' extending on the wings of the external lamella. On both sides, the sediment surface is covered with irregular brownish patches we interpret as remains of the more delicate wings of the external lamella. Like many lower beaks of other fossil coleoids (e.g. Dzik 1986; Klug *et al.* 2005; Tanabe *et al.* 2006) and nautilids (e.g. Mundlos 1973; Schweigert 1999; Klug 2001), the internal lamella did speculatively not extend far beyond the external lamella; its absence indicates that it is either not concealed or not preserved. It is unclear whether the external lamella covered the entire internal lamella (as in *Nautilus*) or not (as in *Octopus*).

#### The upper beak

As far as it is visible, the upper beak resembles the upper beaks of other coleoids in overall morphology (Fig. 6D–F). Like most other coleoid beaks from Nusplingen, it was embedded lying on its side (Klug *et al.* 2005) and is thus flattened laterally. Again, a darker portion and a lighter portion can be differentiated; but in this case, the lighter portion

vaguely shows the outline of the internal lamella. The darker portion consists again of the rostrum and the anterior portion of the external lamella. It is 7 mm long. The rostrum forms a long, pointed hook with strongly arched ventral edges at the transition to the wings. In order to reconstruct the overall outline of the upper beak, we superimposed images of the slab and counterslab (Fig. 6F). The resulting image shows that the dorsal crest of the internal lamella is slightly vaulted longitudinally. Additionally, some brownish patches are here interpreted as remains of the mandible marking the ventral ends of the wings. The precise shape of the wings is, however, not visible. We give a partially speculative reconstruction of the outlines of both beaks in Figure 4 and a tentative reconstruction of the entire beaks in Figures 2 and 7D.

#### Arms

The onychites (i.e. small hooks) of the arms lie in a light, irregularly sub-oval area covering a surface of approximately  $80 \times 70 \text{ mm}^2$  (Figs 3, 4, 6A, B). This whitish area is separated from the upper beak by a gap 10 mm wide. Not all hooks lie within it. We counted approximately 400 hooks; about 50 of these were outside. The hooks are partially still arranged in irregular rows which we consider as some kind of incomplete articulation, following the orientation of some of the arms (Figs 3, 4).

Presuming that most hooks are preserved and visible, each of the ten arms had carried approximately 40 hooks, i.e. 20 per longitudinal row. This roughly corresponds to the situation in *Passaloteuthis bisulcata* from the Toarcian of Holzmaden (Reitner & Ulrichs 1983; Riegraf & Hauff 1983; Riegraf *et al.* 1984; Hauff 1985; Schlegelmilch 1998). The biserial arrangement of the arm hooks as known from *Passaloteuthis* and *Acanthoteuthis* is, however, not evident, although in some cases, pairs of hooks of similar size and shape lie very close to each other.

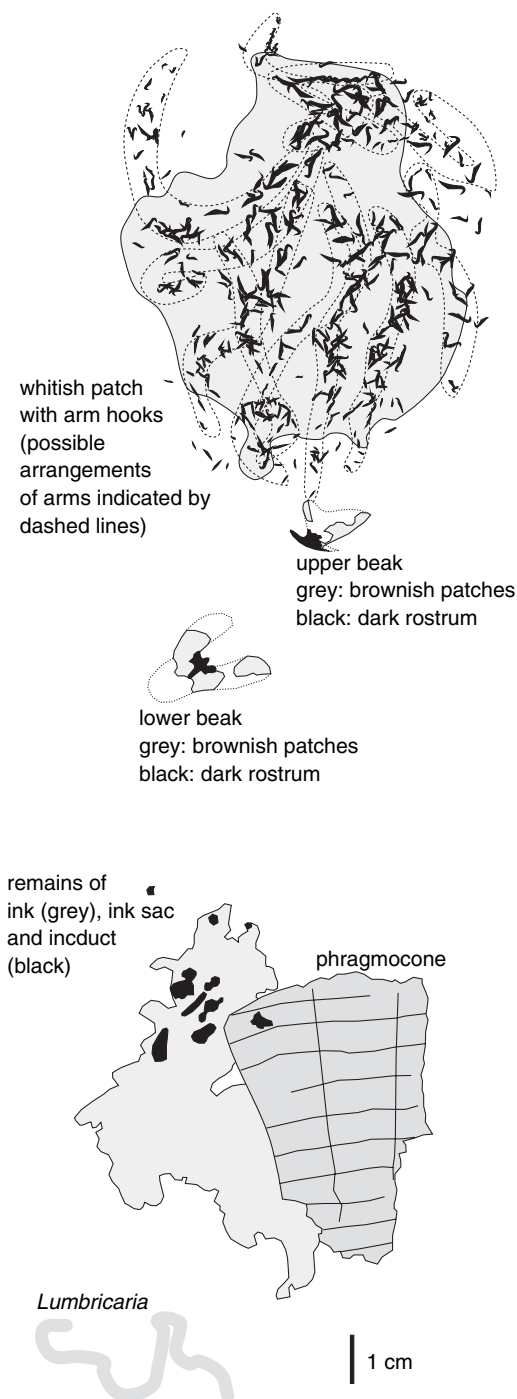


Fig. 5. *Hibolites semisulcatus* (Münster, 1830) from the Nusplingen Lithographic Limestone, SMNS 64878, preserved with rostrum, phragmocone and posterior end of the proostracum (lateral field bases). Total length 195 mm.

As far as is visible, arm length amounted to 60–80 mm. According to the spatial arrangement of the hooks, it appears that eight of the ten arms were aligned sub-parallel to the animal's longitudinal axis with the tips turned slightly towards the longitudinal axis. The remaining two arms are apparently curled

up in front of the tips of the other arms (on the top of the images in Fig. 3). This arrangement of the arms is unusual because in many belemnite and belemnoteuthitid arm crowns the arms are bent outward (e.g. Schlegelmilch 1998: pl. A, fig. 1, B, figs 1, 5). Additionally, these two differently arranged arms might, speculatively, represent a pair of longer arms.

### Arm hooks

In contrast to hooks known from the Early Jurassic times (e.g. Reitner & Urlichs 1983; Riegraf & Hauff 1983; Schlegelmilch 1998), those of the new Kimmeridgian specimen are not preserved as carbonaceous remains of the originally chitinous hook material. This is surprising as originally chitinous structures usually tend to be well preserved in Nusplingen (e.g. Klug *et al.* 2005). Instead, the hooks left imprints that precisely redraw their outer shapes. The relation between the original material and this kind of preservation requires, however, some further investigation.

Proximal hooks have rather slender bases, which form an acute angle between the posterior edge and the anterior edge (Figs 2, 6A, B). The uncinus is very weakly developed or nearly absent and the term hook seems almost inappropriate for these forms. Their size ranges from between 1 to almost 4 mm.

Hooks in more central positions are the largest and have the strongest uncini. The widest part of their bases can be twice as wide as the narrowest part of the shaft. They reach up to 6 mm in length with an uncinus of 2 mm length. At the transition from shaft to uncinus, the uncinus has a slightly flattened, broader base. Towards the tip of such hooks, the uncinus becomes more circular in cross section. Many distal hooks resemble the middle hooks except for their smaller size and the uncinus may also be reduced.

### Comparison of belemnoid hooks

While the hooks of *Rhaphibelus* are still unknown, Schweigert (1999) presented the first specimen of *H. semisulcatus* with associated hooks and rostrum. In the light of the present specimen, the specimen of Schweigert (1999: pl. 2, fig. 3) exhibits only a handful of proximal hooks as documented by the weakly incurved uncini.

Compared with other belemnoids, the hooks of *H. semisulcatus* appear to be intermediate between those of *Passaloteuthis* and *Acantoteuthis* on one side and *Chondroteuthis* on the other side. The proximal hooks of *H. semisulcatus* exhibit strongly inclined shafts with poorly developed uncini similar to *Passaloteuthis* and



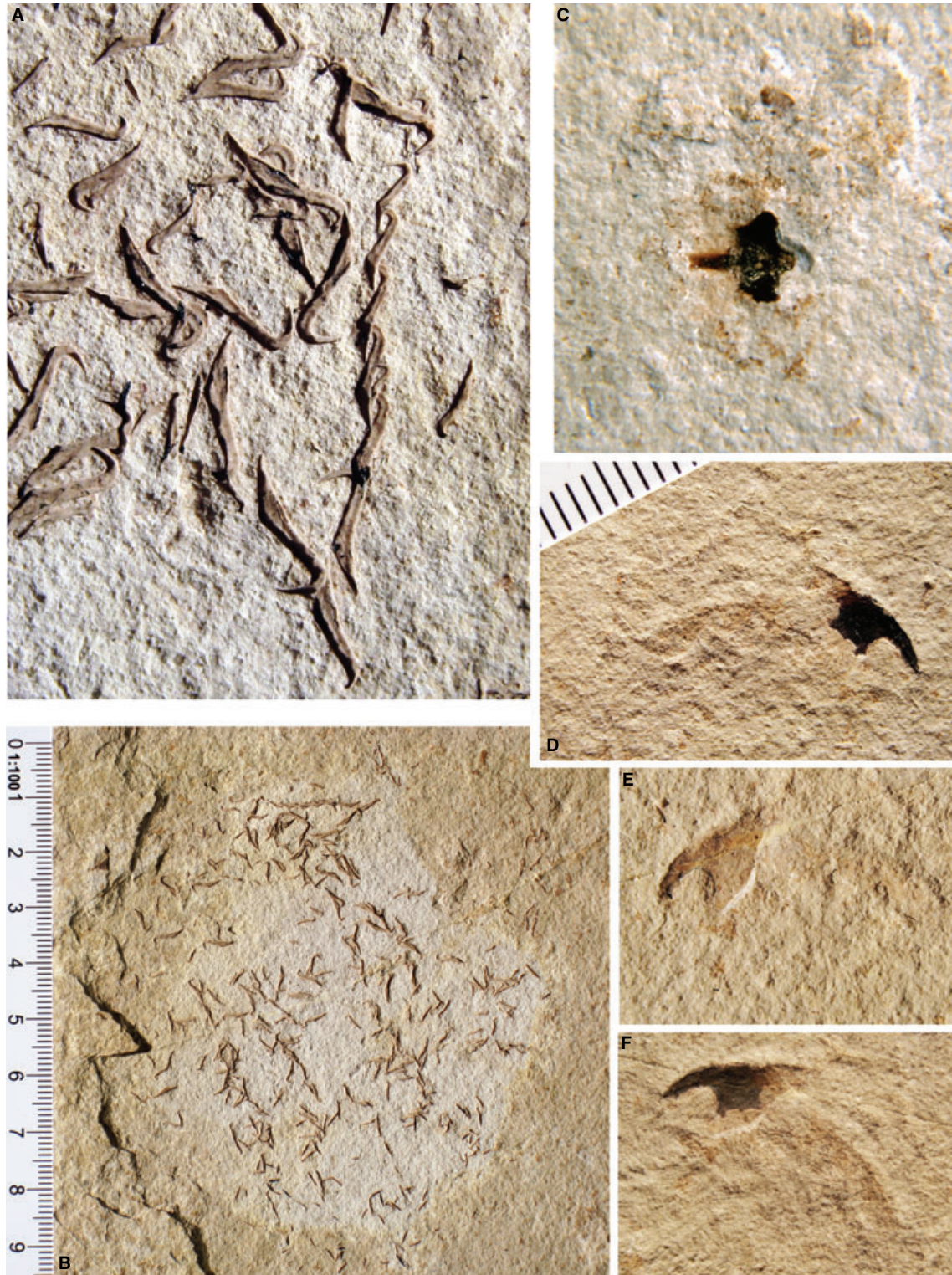


Fig. 6. *Hibolites semisulcatus* (Münster, 1830), SMNS 67335, details of Figure 3. A, detail of (B) to show the morphology of the hooks and its partial 'para-articulation'. The large hooks with strong uncini are from the middle portion of the arms while smaller ones in this case from the tips. B, whitish area with the ca. 400 arm hooks. Proximal hooks lie predominantly closer to the base of the image. C, lower beak with the slightly pointed tip and very vaguely preserved wings (light brownish patches). D–F, upper beak. D, slab; most of the carbonaceous matter sticks to this specimen; note the hook-shaped tip of the beak and the dorsal edge of the internal lamella. E, counterslab. F, superimposed images of D and E to show the remains of slab and counterslab combined.



*Acantoteuthis*. Central and distal hooks, by contrast, are more similar to *Chondroteuthis* in having sharply incurved uncini.

Schweigert (1999: p. 11, pl. 2, fig. 3; pl. 6, figs 1, 6) clearly demonstrated that *H. semisulcatus* possessed mega-onychites. He also showed that mega-onychites are sometimes absent (1999: p. 12, pl. 8, fig. 2). The present specimen confirms this observation. The absence of mega-onychites in the specimens from Nusplingen is here interpreted as being primary. The smaller hooks are more likely to be dislocated by currents than the much larger mega-onychites. Additionally, the preservation potential of mega-onychites is likely to be much higher than that of the beaks. Thus, we conclude, some belemnite specimens preserved with arm-crowns but without mega-onychites do not lack them because of a post-mortem loss but rather because they did not possess these parts. A sexual dimorphism appears likely.

## Comparison of cephalopod beaks

The Fossil-lagerstätten between the villages of Nusplingen and Egesheim have yielded the remains of more than 20 beak elements, which have been assigned to the Coleoidea (*Trachyteuthis*?, *Leptoteuthis*?, *Plesiotheuthis*) based on their general morphology and, in the case of *Trachyteuthis*, because of the repeated association of articulated (or at least spatially close) beak

pairs and the characteristic gladius (Klug *et al.* 2005). Additionally, the complete beak apparatus of the nautilid *Pseudaganides* sp. has been described from the same locality (Dietl & Schweigert 1999a). Nusplingen also represents one of the rare localities from which complete beaks of ammonoids have been described (for example of *Lithacoceras*, *Neochetoceras*, *Physodoceras*; see Schweigert & Dietl 1999, 2001, 2008a,b; Dietl & Schweigert 2001). For the completion of this list, we can now add the complete beak of the belemnite *H. semisulcatus* (Münster, 1830).

All well-known beak apparatuses from Late Jurassic ammonites clearly differ from the beaks of *Hibolites* (Fig. 7). Many Late Jurassic ammonites have calcitic aptychi as lower beaks and the upper beaks usually consist of mainly two long wings and a small outer lamella. The upper beak of *Hibolites*, however, has a strongly developed internal lamella that merges into the moderately long wings. The beak of the nautilid is a typical nautilid beak with massive calcitic portions, the rhyncholite and the conchorhynch. Such calcifications are clearly missing in the *Hibolites* beak. This statement can probably be generalized because beak remains have been found with the Early Jurassic genus *Passaloteuthis*, which also clearly lack calcitic parts. This is evident in spite of poor preservation that prevents a reliable reconstruction of outline (compare Riegraf & Hauff 1983). Generally speaking, the beak apparatus of *Hibolites* is a typical coleoid beak.

## Cephalopod beaks from the Kimmeridgian of Nusplingen

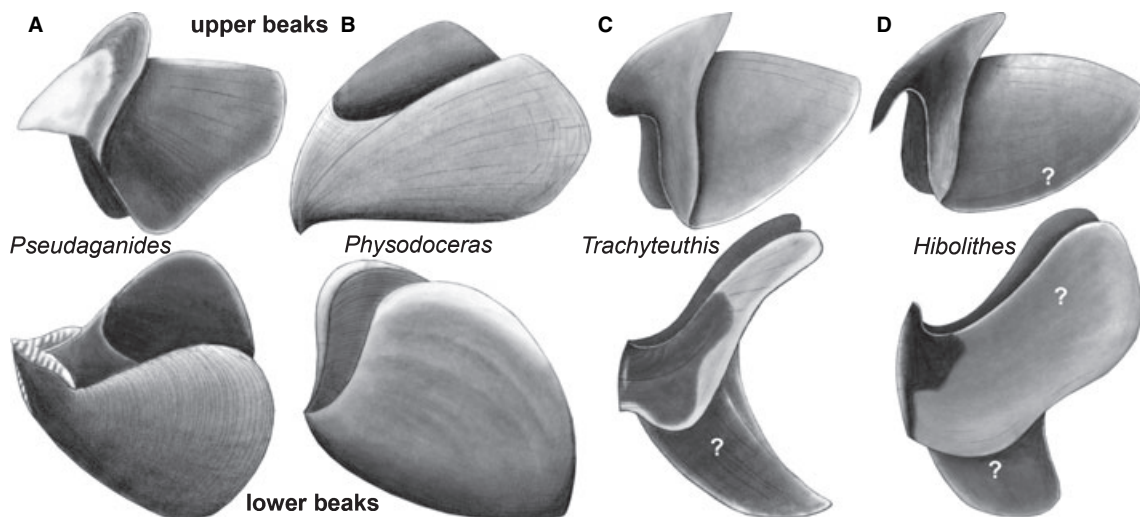


Fig. 7. Reconstructions of the beaks of all important cephalopod groups from Nusplingen. A, *Pseudaganides* sp.; after Dietl and Schweigert (1999a,b,c); the upper beak was ca. 30 mm long at a shell diameter of ca. 130 mm. B, *Physodoceras nattheimense* Schweigert 1998; after Dietl & Schweigert (2001); at a conch diameter of 35 mm, the lower beak (*Laevaptychus*) measured ca. 13 mm in length. C, *Trachyteuthis nusplingensis* Fuchs *et al.* 2007; after Klug *et al.* (2005), at a gladius length of ca. 210 mm, the wings of the lower beak are ca. 20 mm long. D, *Hibolites semisulcatus* (Münster, 1830); at an estimated rostral length of 160 mm, an estimated length of the hard parts of 340 mm (rostrum, phragmocone and proostracum included), and a total length of the animal of perhaps 500 mm, the beaks measured ca. 15–20 mm in length.



Consequently, we compare the beak of *Hibolithes* with those of other coleoids known from Nusplingen. Klug *et al.* (2005) differentiated between seven morphological forms. Four of these are lower beaks and three upper beaks. Two of these forms can be assigned to *Trachyteuthis* as they were associated with, and roughly in the correct position relative to, the gladii. Both the upper beak and the lower beak of *Hibolithes* have much more pointed and curved rostra, while the lower beak of *Trachyteuthis* has a rounded rostrum and that of the upper beak has a rather small tip. The same is true for all other coleoid beaks from Nusplingen. Even in those forms with the most pointed and curved rostra (upper beaks forms 5 and 7 of Klug *et al.* 2005), these are not as slender and pointed as in *Hibolithes*. Nevertheless, with only one available specimen no conclusion can be drawn on intraspecific variability, and potentially these upper beaks might also be belemnite beaks. 'Form 7', however, appears to be clearly larger than the upper beak of *Hibolithes*. Logically, it is not possible yet to define a characteristic belemnite beak.

A comparison with Recent coleoid beaks is somewhat limited by the imperfect preservation. The lower beak of *Hibolithes* clearly differs from that of *Vampyroreuthis* in the shorter rostrum, and, as far as visible in the fossil specimen, in the narrower outer lamella. Most octopod lower beaks have pronounced elongate inner lamellas. Interestingly some specimens of *Sepioteuthis* and some other decapods (compare Clarke 1986: fig. 114b) also show the two lateral lobes on each side of the dark part of the rostrum. The shape of the lower beak thus corroborates a closer relationship of belemnites to decapods, which is not surprising as both taxa have ten arms.

## Taphonomy

The lack of the rostrum, the incompleteness of the phragmocone, and its irregularly fractured posterior end, all suggest that this specimen was the victim of a successful predation attempt. This is in accordance with earlier discoveries of belemnite rostra in Nusplingen, which were apparently bitten off by a predator (Schweigert 1999). It is suggested that some predators bit off the rostra; probably in order to avoid potentially lethal digestive disorders (as documented from a Toarcian hybodontid shark: Urlichs *et al.* 1994). Bite marks and fragmented rostra cava represent evidence for such behaviour (Hölder 1955; Urlichs *et al.* 1994; Schweigert 1999). Thus, the new specimen probably represents the remains of the victim of a predator. This is indicated by the absence of the rostrum (cf. Schweigert 1999) and the fragmentary preservation

of the phragmocone. Additionally, the wide gap between the beaks and the arms on one side and the phragmocone and the ink on the other side might also be caused by the predator. Speculatively, the predator may have avoided all hard parts in order to eat the mantle with its contents only, hence the gap. In the Nusplingen Fossil-lagerstätte, the preservation potential of the entire specimen would have been quite high if the undamaged specimen had been embedded (cf. Kear *et al.* 1995).

An interesting feature is the position of the arm with the tips bent inward instead of outward as in many other specimens from, for example, the Solnhofen Plattenkalk (Frickhinger 1994, 1999), the Toarcian of Holzmaden and Dotternhausen (Riegraf & Hauff 1983; Hauff 1985) or the Callovian of Christian Malford (Tang 2002; Wilby *et al.* 2004). Apparently, the arms tend to bend outwards post-mortem caused perhaps by rigour mortis or relaxation (P. Wilby, personal communication). In the new specimen, however, the arm crown was only partially intact at the time of burial. Many of the hooks still lie in rows while some others are chaotically arranged. It remains unclear whether this arrangement is simply a phenomenon of necrosis or predation. It is remarkable, however, that the arm crown, the beaks and the phragmocone more or less reflect the proportions of the belemnite animal (as known from *Passaloteuthis*) and the positions of these body parts correspond well to those when the animal was alive (cf. Kear *et al.* 1995). It thus appears unlikely that scavengers disturbed the carcass once it had reached the sediment surface. Speculatively, a predator bit off the rostrum, fed on the mantle and the soft parts below the periostracum (which explains the missing proostracum; this can be explained, however, alternatively by its delicate nature) and left the body parts, with more massive or spiny hard parts, behind (i.e. phragmocone, arms, head and rostrum). The spatial proximity of the belemnite remains could be explained by a predator that rested on the ground after catching the prey and while feeding; alternatively, the situation of the remains may be interpreted by minor disorganization during decay.

According to an EDAX analysis performed on a mandible fragment of *Plesioteuthis* from Nusplingen, we know that the dark coatings of the cephalopod beaks consist of carbon with oxygen and small amounts of other elements (Klug *et al.* 2005). As far as the white area is concerned, it is well conceivable that this area represents a 'reduction halo, where disseminated [trivalent] Fe has been reduced in the vicinity of the fossil, either during decay, or perhaps more likely during modern weathering' (P. Wilby,

personal communication). The latter assumption appears more likely because the dissolved space of the arm hooks might have provided an improved hydraulic conductivity to let reducing water circulate around the hook moulds. As the ink is preserved as a dark patch, the whitish area certainly does not represent ink remains.

## Reconstruction

A specimen of *H. semisulcatus* (Münster, 1830) preserving phragmocone and proostracum with the complete rostrum, was described by Quenstedt (1867, 1885) and again by Engeser & Reitner (1981). In this specimen, the rostrum is ca. 155 mm long, the phragmocone extends 76 mm out of the rostrum and the proostracum measures 90 mm in length and 48 mm in width (in its flattened state). Most probably, the mantle margin coincided with the anterior end of the proostracum. The gap between phragmocone and the beaks roughly reflects the extension of the mantle and the proostracum respectively. Assuming a maximum length of the complete rostrum of 155 mm combined with additional 76 mm extending out of the rostrum cavum and 90 mm of proostracum, estimated 50 mm for the length of the head plus an arm length of 100 mm, a maximum body length of the *Hibolithes* animal of roughly 500 mm appears to be a reasonable estimate. Based on the above, the new specimen of *Hibolithes* would have had a body length of about 400 mm (when applying a phragmocone/rostrum length ratio of 0.5 and a proostracum/rostrum length ratio of 0.6).

Although the arrangement of hooks does not allow an unequivocal designation of ten arms, the total number of hooks (about 400) divided by the number

of hooks per arm known from *Passaloteuthis* (about 20 per row at two rows per arm) is consistent with there having been ten arms. Additionally, many of the hooks are grouped in such a way that they can be assigned to one arm.

Usually the lateral furrows on belemnite rostra are interpreted as attachment sites of fins. The shape of these fins has been reconstructed in various ways (Naef 1922: fig. 80C; Riegraf *et al.* 1984: fig. 9A; Monks *et al.* 1996; Schlegelmilch 1998: fig. 2). We assumed that the width of the fins decreases both posteriorly, towards the tip of the rostrum, and anteriorly towards the rostrum cavum because the lateral cartilage furrows fade out posteriorly and anteriorly in *Hibolithes* rostra. It thus appears unlikely that the fins in the new specimen extended along the entire mantle of the belemnite animal (Fig. 8). Remains of belemnite fins have, however, never been found and thus a definitive decision on this matter has to await such discoveries.

The beaks of *H. semisulcatus* do not show all details needed for a confident reconstruction. Nevertheless, some information can be extracted from the new specimen. In both beaks, most of the outer lamella is preserved, especially the rostra, much of the hoods and the bases of the wings. The jaw angle is also preserved and reveals the relative position of rostrum and wings. In the upper beak, the crest of the inner lamella is preserved, thus yielding some information about the total upper beak length. The length of the internal lamella in the lower beak is speculative. It might have been short as no unequivocal traces can be seen on slab or counterslab. It appears likely, however, that the wings of the lower beaks were rather wide and oriented dorsally to maximally slightly anteriorly, as indicated by the jaw angle which is nearly 90°. The hood probably had a narrowly pointed posterior indentation.



Fig. 8. Life reconstruction of *Hibolithes semisulcatus* (Münster, 1830) from the Kimmeridgian. For a discussion of the reconstruction see the text. The entire adult animal attained a length of approximately 500 mm.



## Conclusions

For the first time, a belemnite fossil is available which displays morphological details of the beaks. Previous discoveries of soft-tissue belemnites are extremely rare and restricted to the European Toarcian. The new specimen thus represents the only non-Toarcian belemnite preserved with non-mineralized parts. The taxonomic assignment of the new specimen is hampered by the missing rostrum but the shapes of the hooks and of the phragmocone allow an unequivocal assignment of this specimen to *H. semisulcatus* (Münster, 1830).

The present specimen represents the second with both hooks and hard parts. As *H. semisulcatus* is known to possess one pair of mega-onychites, the absence of those in the present specimen provides evidence of sexual dimorphism in *H. semisulcatus*. This phenomenon was previously presumed for all belemnites, but it is known only from *Passaloteuthis* with certainty as the rostrum of the latter is unambiguously associated with an arm crown that occasionally includes one pair of mega-onychites (Schlegelmilch 1998).

Like all coleoid beaks, those of *Hibolithes* lack calcitic portions. In this respect, they differ from the beaks of the ectocochleate cephalopods represented in Nusplingen by various ammonites and nautilids. The imperfect preservation of the belemnite beaks hampers a detailed comparison with other Recent and fossil coleoid beaks. Some morphological characters (low width of the outer lamella, double lateral lobes of the dark parts of rostrum and hood, possibly short internal lamella) of the lower beak of *Hibolithes* more closely resemble Recent decapods than Recent octopods. The upper beak of *Hibolithes* differs in the long, narrow and curved rostrum from those coleoid beaks previously known from Nusplingen. The dark part of the lower beak also shows a unique outline with a short and pointed rostrum, an elongate postero-ventral extension and two small rounded sinuses, which pointed towards the wings (sometimes similarly developed in Recent *Sepioteuthis*). It appears likely that this beak form is quite characteristic and it might reflect a special diet of the belemnites. Taking their probably high swimming velocity (fins, stream-lined body and horizontal orientation of the longest body axis) with the arm hooks and the sharp beaks into account, it appears quite likely that belemnites were fast-swimming, effective, medium-sized predators.

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