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Large onychites (cephalopod hooks) from the Upper Jurassic of the Boreal Realm

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We report on the discovery of large cephalopod arm hooks (mega-onychites) from the Kimmeridgian and Volgian of Spitsbergen (Agardhfjellet Formation). This includes a largely uncompressed hook in a seep carbonate, with preservation of surface sculpture. We suggest the use of logarithmic spirals as morphological descriptors for the outer part of cephalopod arm hooks, with implications for systematics and functional morphology. Comparison with Upper Jurassic material from Greenland, northern Norway and the North Sea demonstrates a remarkably consistent morphology, which we assign to the same form species, *Onychites quenstedti*. Considering the relatively small stratigraphic (Kimmeridgian–Volgian) and biogeographic (Boreal) range of this large form, it is likely that it represents a single biological species or genus.

Key words: Onychites, cephalopod hooks, Jurassic, Spitsbergen, Boreal.

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Introduction

Cephalopods are known to develop arm hooks easily distinguishable in the fossil record (Kulicki and Szaniawski 1972). Cephalopod arm hooks from the Mesozoic (onychites) are usually attributed to belemnoids. Rare, articulated belemnoid animal fossils with soft-part preservation show rows of hooks along the arms (Reitner and Engeser 1982; Engeser and Reitner 1992; Donovan and Crane 1992; Doyle and Shakides 2004; Donovan 2006; Klug et al. 2009; reviewed by Stevens 2010).

Very large hooks (5–40 mm long) are referred to as mega-onychites (Engeser 1987; Stevens 2010). These are much rarer than the small hooks, or micro-onychites. Exceptional belemnoid fossils show that some individuals possessed two disproportionately large hooks within the base of the arm crown (Riegraf and Hauff 1983: fig. 1A, 2A; Fuchs 2006: fig. 19D; cf. Stevens 2010). These are generally believed to be an expression of sexual dimorphism and were presumably only present in males (Engeser 1987; Stevens 2010).

In the Boreal Realm, mega-onychites have been reported previously from the Upper Jurassic of northern Norway (Sokolov 1912), Greenland (Donovan 1953) and the north-

ern North Sea (Christensen 1995). We here report on several new specimens from the Upper Jurassic of Spitsbergen that are morphologically similar to the previously known Boreal mega-onychites.

Institutional abbreviation.—PMO, Palaeontological Museum (Natural History Museum), Oslo, Norway; UNIS, The University Centre in Svalbard, Norway.

Material and methods

Most of the material described here was collected by us in the Slottsmøya Member (Volgian to Ryazanian) of the Agardhfjellet Formation in the Sassenfjorden area, Spitsbergen (Fig. 1). The levels in the sections given below are relative to a yellow, silty marker horizon about 50 m below the top of the formation and 27 m below the so-called *Dorsoplanites* bed (Fig. 2). Based on organic carbon isotope curves and foraminiferal biostratigraphy, Hammer et al. (2012) suggested that this level corresponds more or less to the base of the Middle Volgian. The material comprises a total of four large (3.2–4.3 cm) mega-onychites specimens (Fig. 3A–E).

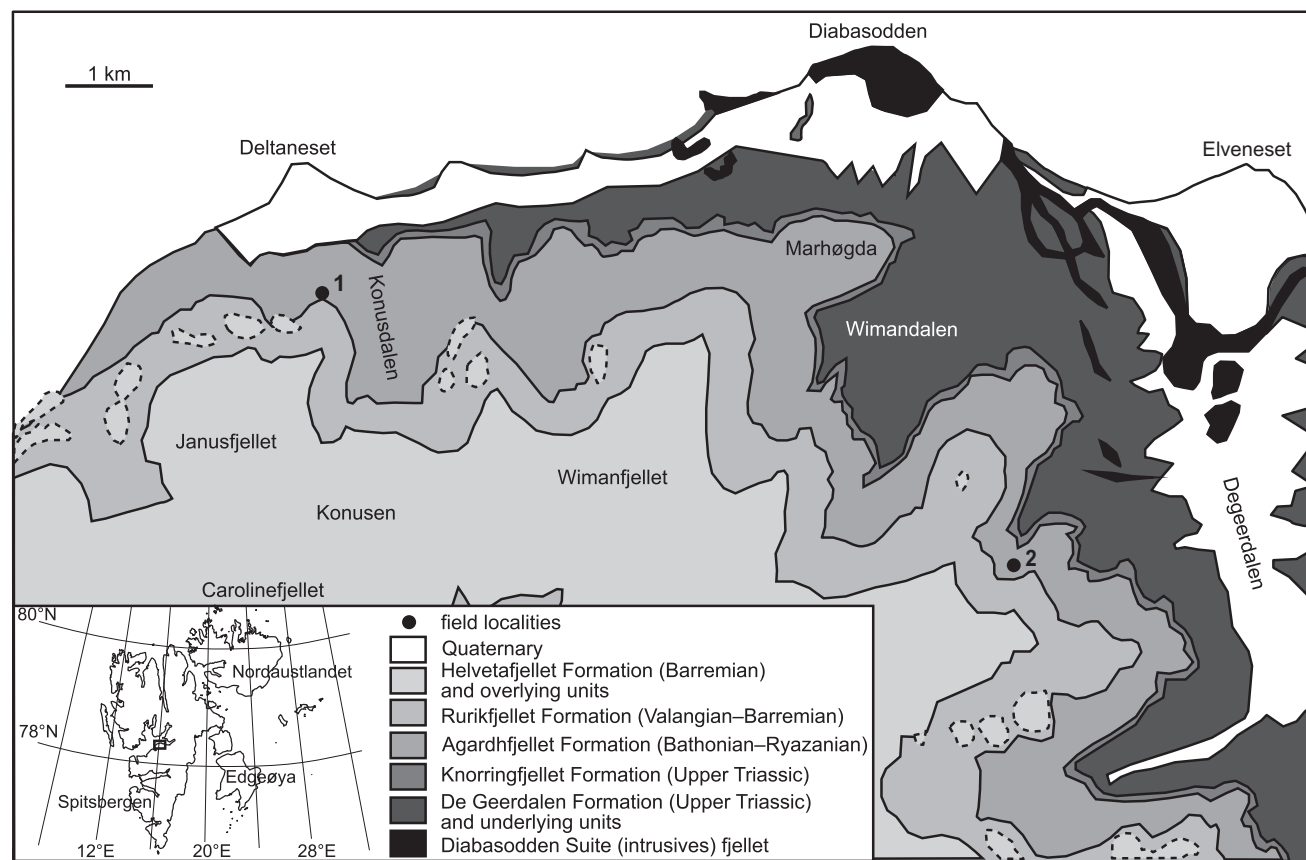


Fig. 1. Geological map of the Sassenfjorden area, central Spitsbergen. Sampling locality: 1, Janusfjellet; 2, Knorringfjellet. Redrawn from Dallmann et al. (2001).

In addition, we had access to a siltstone slab with three smaller (circa 2 cm) mega-onychites (Fig. 4) collected in the same area during a University of Svalbard (UNIS) field excursion. The lithology and fossil preservation are typical of the underlying Oppdalsåta Member (Kimmeridgian to Lower Volgian). The surface also contains numerous small arm hooks and other fossils.

From Boreal localities outside Spitsbergen, we investigated several specimens collected by Ole Bruun Christensen from northern North Sea core samples (Christensen 1995), including two relatively complete, flattened hooks (Fig. 3F, G), 2.8 cm and 3.6 cm long, and also a sample with a partially preserved mega-hook in association with smaller hooks (Fig. 5). We also investigated a specimen figured by Sokolov (1912) from Andøya, northern Norway, 4.0 cm long (Fig. 3H).

Figures 3, 4A, and 5 were photographed using the Polynomial Texture Mapping technique (Hammer et al. 2002). The software Past, version 2.14 (Hammer et al. 2001) was used for least-squares fitting to logarithmic spirals and plotting of kernel density map. Whorl expansion rate is reported as the exponent b in the polar coordinates equation for the logarithmic spiral:

$$r = ae^{b\theta}$$

where r is radius, θ is angle and a is a scaling coefficient, and e , base of the natural logarithm.

Results and discussion

Shape and shape parameters.—All the hooks have a similar morphology. The base is rounded, the internal spur small and the external spur rudimentary or absent (see Fig. 6 for morphological terms). The shaft has a stronger curvature than the slender, lanceolate uncinus, but the transition is completely continuous and a division point between shaft and uncinus can not be defined. The tip nearly reaches or projects slightly beyond a line drawn through the base.

The inner and outer edges of the complete hooks were fitted to logarithmic spirals (Fig. 7), with the whorl expansion rate and the pole (center) of the spiral as fitted parameters. The fits are very good. In all cases the pole is situated near the base. The whorl expansion rate coefficients b for the inner and outer edges are given in Table 1 and Fig. 8. The ratio between inner and outer expansion rates is close to 1.7 for most of the specimens (RMA regression slope 1.7 ± 0.3). Interestingly, all three hooks from the Slotsmøya Member in Spitsbergen have similar coefficients, and these are also similar to PMO 223.383 from the Draupne Formation, northern North Sea. The hooks PMO 210.229 from the North Sea and PMO 74149 from Andøya expand more rapidly. PMO 223.381 (the Oppdalsåta Member specimen) expands more slowly, very similar to a specimen of *Onychites quenstedti* figured by Engeser (1987: pl. 2: 5), which we have included for reference.

Surface sculpture.—PMO 223.380, preserved in limestone, shows traces of ornamentation. The uncinus (Fig. 3A) is partly covered with a chevron-like pattern previously reported by Stevens (2010) in *Onychites macnaughti* from the Kimmeridgian–Tithonian of New Zealand. The shaft shows weak, circular impressions of a type that is rarely reported in any mega-onychites (Fig. 3B; but see also Engeser 1987). Considering that the shaft was possibly embedded in soft tissue (Kulicki and Szaniawski 1972), these impressions may represent muscle attachment points.

The association of hooks on the UNIS specimen.—PMO 223.381 (Fig. 4A) from the Oppdalsåta Member, Kimmeridgian, is of interest as it preserves a number of elements of probable belemnoid origin. Most prominent are three superposed specimens of mega-onychites, slightly smaller (circa 2 cm) than those of the overlying Slotsmøya Member and more comparable in size to Lower Toarcian and Upper Kimmeridgian specimens from Germany figured by Quenstedt (1857). In addition, the surface contains numerous micro-onychites arranged vaguely along two or three curved lines that may represent cephalopod arms (Fig. 4B). We counted 58 obvious micro-onychites, in addition to a large number of fragments that probably derive from hooks. In comparison, well-preserved belemnoid specimens of different species typically have approximately 40 hooks on each arm (Engeser and Reitner 1981; Reitner and Urlichs 1983; Riegraf and Hauff 1983; Schweigert 1999; Klug et al. 2009).

The presence of three, rather than two mega-onychites indicates that the collection of hooks on this slab derives from more than one individual, and probably represents a coprolite or regurgitated mass from a predator such as an ichthyosaur (cf. Pollard 1968), a plesiosaur, or a large fish. Schweigert (1999: pl. 7: 1) figures a similar association of four mega-onychites and numerous micro-onychites from the Upper Kimmeridgian of Germany, which he describes as a regurgitated mass. Some Jurassic groups of coleoids are known to possess hooks of different shapes and sizes occurring along a single arm, sometimes with groups of three or more hooks which are markedly larger than others (Garassino and Donovan 2000), but not approaching the size difference seen on our specimen.

Table 1. Fitted expansion coefficients (b) for the inner and outer edges of hooks. The *Onychites quenstedti* specimen was measured from Engeser (1987: pl. 2: 5) for reference.

Specimen	Inner b	Outer b
PMO 223.380	0.99	0.37
PMO 223.382	1.05	0.42
PMO 223.379	1.04	0.47
PMO 223.383	0.89	0.51
PMO 210.229	1.48	0.74
PMO 223.381	0.56	0.26
PMO 74149	1.24	0.74
<i>Onychites quenstedti</i>	0.54	0.28

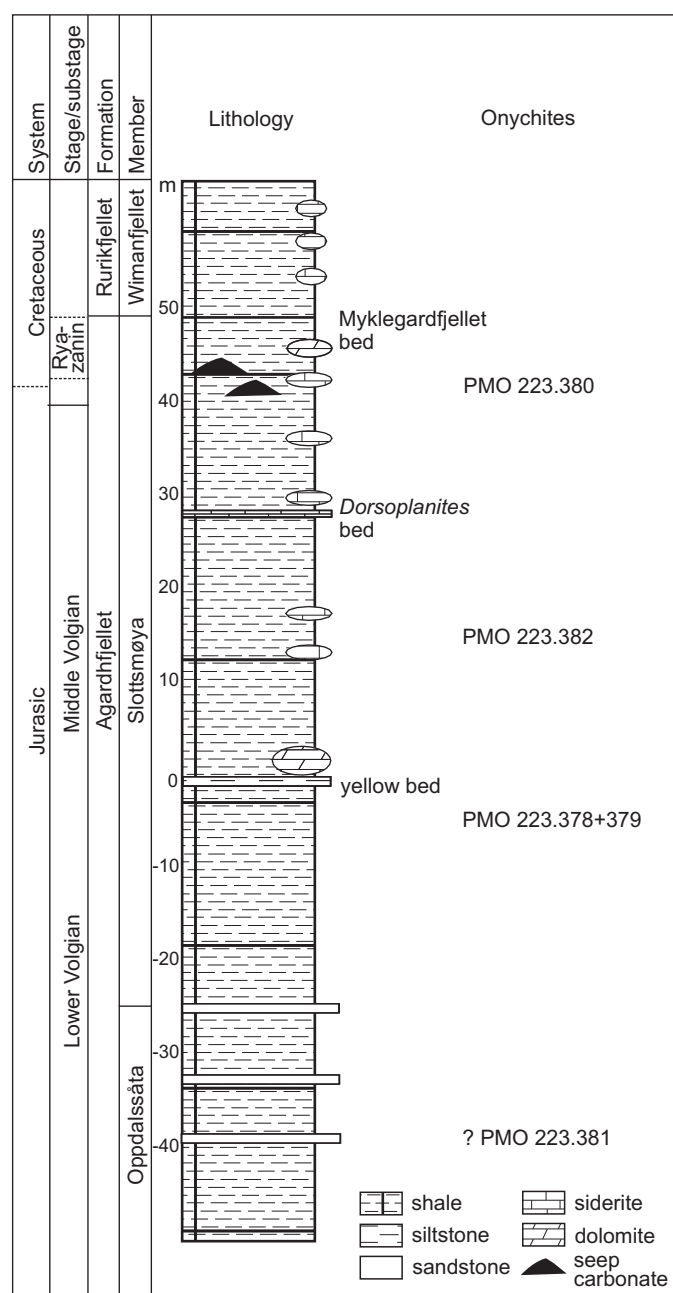


Fig. 2. Simplified stratigraphy of the upper part of the Agardhfjellet Formation in the Sassenfjorden area, Spitsbergen, with positions of mega-onychites. The Upper Volgian is highly condensed. Modified from Hammer et al. (2011).

The association of hooks on a North Sea specimen.—PMO 223.405, from Statoil well 33/9-C27 in the North Sea, depth 3187.7 m (Upper Jurassic) contains a partial mega-hook together with a number of smaller hooks (Fig. 5). Although the mega-hook is only partially preserved, with base and tip missing, we assume from its shape and large size, together with its stratigraphic and geographic position, that it belongs to the same type as the other mega-onychites described herein. The smaller onychites are up to 8 mm long and therefore technically qualify as mega-onychites, but considering their number

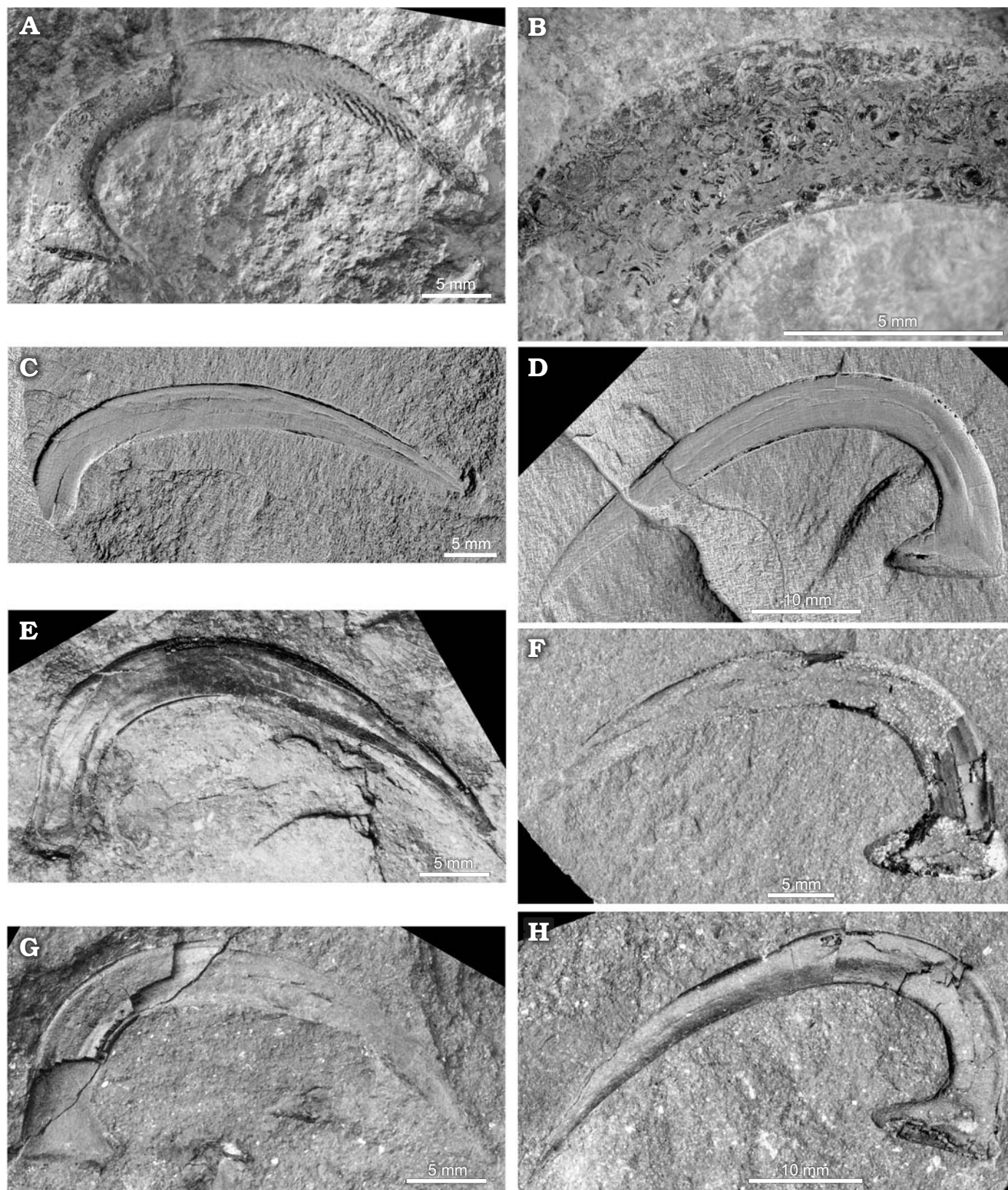


Fig. 3. Belemnoid mega-onychites *Onychites quenstedti* Engeser, 1987 from Boreal localities. **A.** PMO 223.380, seep carbonate, earliest Late Volgian, Knorringfjellet, Spitsbergen; entire specimen. **B.** Close-up of shaft on PMO 223.380, showing rows of circular tubercles. **C.** PMO 223.378, latest Early Volgian, Janusfjellet, Spitsbergen. **D.** PMO 223.379, latest Early Volgian, Janusfjellet, Spitsbergen. **E.** PMO 223.382, Middle Volgian, Janusfjellet, Spitsbergen. **F.** PMO 210.229, latest Early or early Middle Volgian, well 7/4-1, North Sea. **G.** PMO 223.383, Late Jurassic, well 34/7-23A, North Sea. **H.** PMO 74149, Late Jurassic, Andøya, northern Norway.

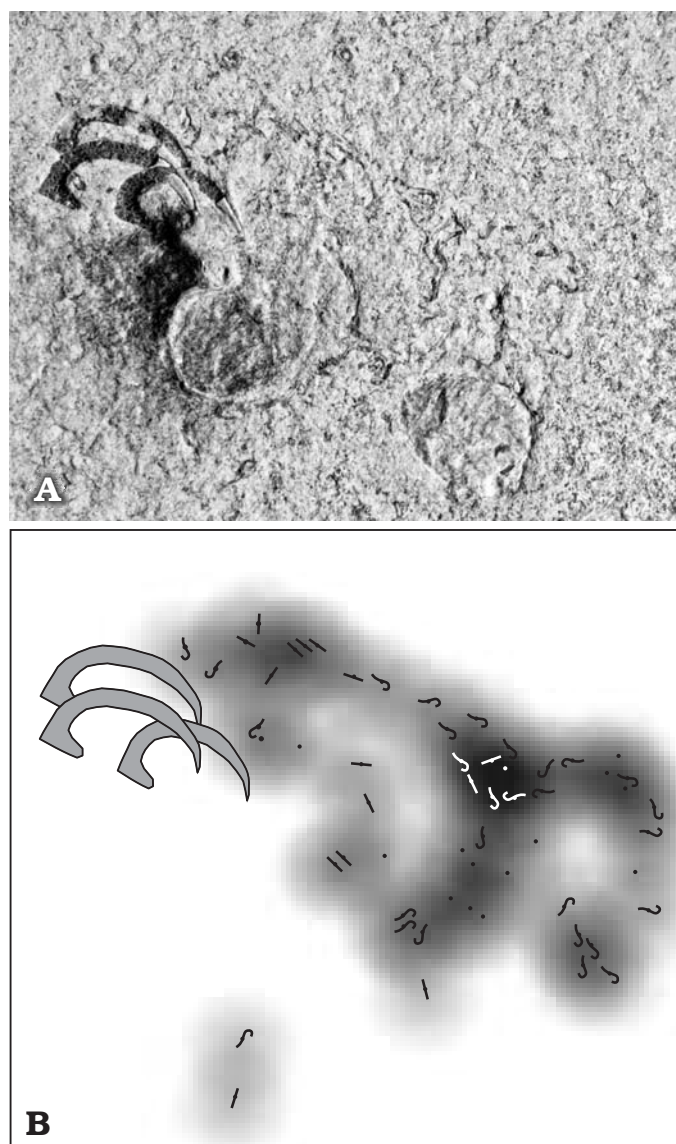


Fig. 4. Belemnoid mega- (*Onychites quenstedti* Engeser, 1987) and micro-onychites from the Agardhfjellet Formation (probably Oppdalsåta Member), Upper Jurassic, Spitsbergen. PMO 223.381. **A.** Photograph. **B.** Explanatory drawing. Micro-onychites marked as hooks (complete specimens), lines and dots (incomplete specimens). Density of micro-onychites in gray scale, computed using the kernel density method.

and the association with the much larger hook we assume they are functionally micro-onychites.

Functional notes on the logarithmic spiral shape.—Most animal hooks and claws are shaped like a section of a logarithmic spiral. Thompson (1917) explained this in developmental terms, as a logarithmic spiral is very easy to form by accretionary growth at the base, with a larger growth rate on one side than the other. This argument only applies when growth proceeds in a direction away from the pole of the spiral, such that the tip end is oldest and has largest curvature (Fig. 9C). This is not the situation for the arm hooks described here, which have a higher curvature proximally (Fig.

9A). Mattheck and Reuss (1991) calculated that the logarithmic spiral shape is optimal for a claw from a mechanical point of view, as stresses are distributed evenly and no point is therefore more susceptible to failure.

Another functional argument stems from the equiangular property of the logarithmic spiral: any line drawn from the pole will meet the spiral at the same, constant angle, decided by the given whorl expansion rate. This means that, as the claw is penetrating the prey, it can meet the surface at a constant angle, avoiding lateral wiggling, while maintaining a constant force direction. The situation is analogous to that of an old-fashioned ship's anchor, with an arm digging into the seafloor while being pulled in a constant (subhorizontal) direction. Chapman (1796) found an optimal angle of attack of 67.5° , and argued that in order to maintain this angle as the fluke was digging in and the shaft of the anchor rotated, the arm should be in the form of a logarithmic spiral. In this case, the fluke is pointing in the general direction of the applied pulling force (but at an angle of 67.5° to it), and the pole of the spiral is distal (Fig. 9C, D). This is similar to most predatory claws, and allows the claw to be pulled straight back towards the predator when operating (conversely, if the prey tries to escape distally, it will only cause the claw to dig in further).

A constant angle of penetration and a constant force direction are also achieved when the pole of the spiral is proximal and the smallest curvature is at the tip, as in our specimens of *Onychites quenstedti*, but in this case, both the tip and the force are directed away from the attacker (Fig. 9A, B). The action is therefore pushing (thrusting) rather than pulling, which suggests that small and enlarged hooks had different functions.

Engeser (1987) and Stevens (2010) suggested that the mega-onychites are probably male organs associated with reproduction and used by the male to gain a hold on the female. Arm hooks with such a function are known from the Recent scaled squid *Lepidoteuthis grimaldii* (Jackson and O'Shea 2003). Adult males of this squid species are usually less than 450 mm in length, which is half the body length of the adult female. However, as compensation, males develop large (> 30 mm) and straight hooks from a modified 8th sucker ring on each dorsolateral arm. During mating, these hooks are used as a compulsive device, either thrust into the female's body or locked onto her scales to enable copulation and insemination. A similar function for the Jurassic mega-onychites is very likely, as suggested by Engeser (1987) and Stevens (2010). Additionally or alternatively, the mega-onychites could be used in male-male agonistic behaviour during spawning (Hannon and Messenger 1998; Jackson and O'Shea 2003).

Systematic palaeontology

Phylum Mollusca Linnaeus, 1758

Class Cephalopoda Cuvier, 1794

Subclass Coleoidea Bather, 1888

Superorder Belemnoidea Steinmann, 1890

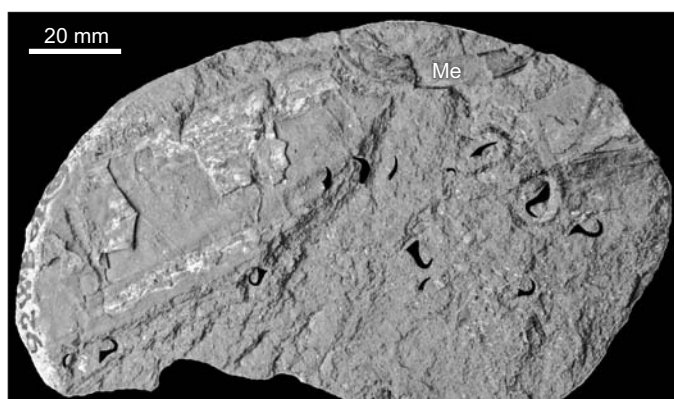


Fig. 5. Mega- (Me) and micro-onychites (retouched). From Statoil well 33/9-C27, depth 3187.7 m (Upper Jurassic). PMO 223.405.

Belemnoid arm hooks = Uncinifera Engeser, 1990

Remarks.—The taxonomical hierarchy is of a hybrid nature, as the Uncinifera (a unit of ordinal level) and lower taxa are parataxa (form taxa) for cephalopod arm hooks not associated with identifiable cephalopods and therefore may not represent biological taxa. The current practice for naming cephalopod arm hooks is liberal and there are several genera erected (Kulicki and Szaniawski 1972; Engeser 1987; Stevens 2010) for better bookkeeping of these forms.

Genus *Onychites* Quenstedt, 1857

Type species: *Onychites ornatus* Quenstedt, 1857, subsequent designation Quenstedt 1866; Upper Callovian (Braunjura zeta), Baden-Württemberg, Germany.

Onychites quenstedti Engeser, 1987

Figs. 3, 4.

1857 *Onychites barbatus* n. sp.; Quenstedt 1857: 804; pl. 99: 15.
cf. 1857 *Onychites runcinatus* n. sp.; Quenstedt 1857: 247; pl. 34: 4.
1912 *Acanthoteuthis* sp.; Sokolov 1912: 10; pl. 1: 55.
1953 “*Onychites*” type I; Donovan 1953: 76–78; fig. 6a; pl. 15: 3–5.
cf. 1953 “*Onychites*” type II; Donovan 1953: 76–78; fig. 6b; pl. 15: 6–7.
1987 *Onychites quenstedti* n. sp.; Engeser 1987: 14; pl. 2: 2, 4, 5.
1995 “Donovan-type” of onychite; Christensen 1995: pl. 1: 4, 5.
1999 *Onychites barbatus* Quenstedt, 1857; Schweigert 1999: pls. 5: 2, 5; 7: 1.

Material.—PMO 223.380 (Fig. 3A, B). This specimen was collected from a hydrocarbon seep carbonate near the top of the Slottsmøya Member at Knorringfjellet, Spitsbergen (Hammer et al. 2011). Based on ammonite biostratigraphy, Wierzbowski et al. (2011) dated this particular carbonate body, seep no. 13, to the earliest Late Volgian. The shaft of the hook is preserved in three dimensions, while the uncinus is broken off, leaving a carbonaceous film. Length 3.2 cm (tip missing). PMO 223.378 (Fig. 3C). Level -4 m, latest Early Volgian, Slottsmøya Member, Agardhfjellet Formation, Janusfjellet, Spitsbergen. Basal part broken off. 4.0 cm long, external, flattened mould with thin carbonaceous film. PMO 223.379 (Fig. 3D), level -4 m, latest Early Volgian, Slottsmøya Member, Agardhfjellet Formation, Janusfjellet, Spits-

bergen. A complete hook, 4.3 cm long, preservation similar to PMO 223.378. PMO 223.382 (Fig. 3E). Level 14.6 m, Middle Volgian, Slottsmøya Member, Agardhfjellet Formation, Janusfjellet, Spitsbergen. A nearly complete hook with only a small part of the inner spur missing, 3.4 cm long, somewhat flattened, carbonaceous preservation. A relatively large number of additional, fragmented specimens were observed at the same stratigraphic level. PMO 210.229 (Fig. 3F). Statoil well 7/4-1, depth 3020.1 m, latest Early–early Middle Volgian, Farsund Formation, North Sea. Complete hook, 3.6 cm long. Preservation mainly as PMO 223.378, but with part of the shaft preserved in prismatic carbonaceous material. PMO 223.383 (Fig. 3G). Saga well 34/7-23A, depth 3284.5 m, Late Jurassic, Draupne Formation, northern North Sea. Nearly complete hook (tip missing), 2.8 cm long, preservation as PMO 210.229. PMO 74149 (Fig. 3H). Unknown level in drill core, Late Jurassic, “middle beds”, Andøya, northern Norway. 4.0 cm long, preservation as PMO 210.229. Illustrated by Sokolov (1912; pl. 1 fig. 5). PMO 223.381 (Fig. 4). Probably from the Oppdalsåta Member (Kimmeridgian) of the Agardhfjellet Formation, Sassenfjorden area, Spitsbergen. Siltstone slab with three overlap-

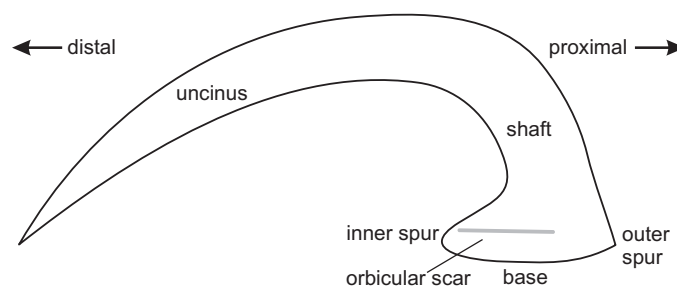


Fig. 6. Morphological terms for mega-onychites, based on Engeser (1987).

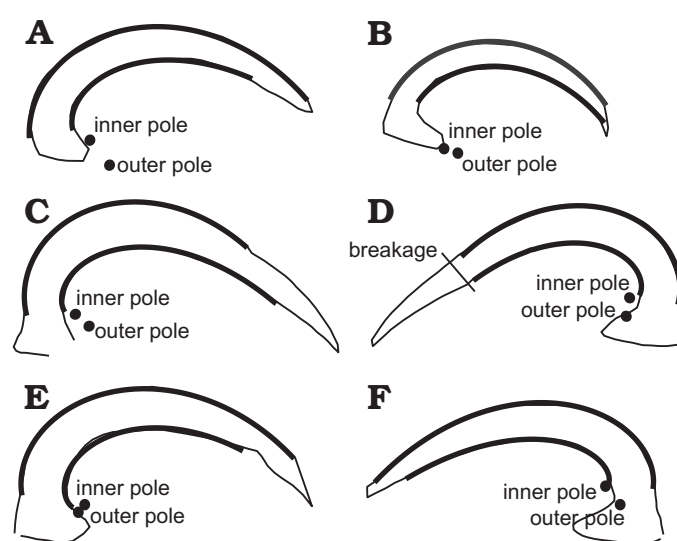


Fig. 7. Fitting of inner and outer edges of hooks to logarithmic spiral segments (thick lines). A. PMO 223.380. B. PMO 223.381. C. PMO 223.382. D. PMO 223.379. E. PMO 223.383. F. PMO 210.229.

ping hooks, each ca. 2 cm long, preserved as carbonaceous films, but two of the hooks retain their tips relatively unflattened.

Description.—Variable size; 0.8–0.95 cm long in Germany (Engeser 1987), circa 2 cm long in the Kimmeridgian of Spitsbergen (PMO 223.381), much larger, up to 4.4 cm, in the remaining Boreal material. Large curvature proximally (shaft), increasing distally (uncinus), approximating to a logarithmic spiral with the centre situated proximally. Whorl expansion rates variable, circa 0.5–1.5 (inner) and 0.3–0.7 (outer). Slender, lanceolate, tip of uncinus very sharp, nearly touching or projecting slightly beyond a line drawn through the base. Cross section lenticular. Inner spur short, robust, rounded, outer spur rudimentary or absent (slightly more extended in Germany; Engeser 1987). Base nearly straight or slightly convex. Orbicular scar (sensu Engeser 1987) broad but quite distinguishable, situated roughly half-way up the basal area. Shaft covered with weak, circular tubercles near the base, uncinus with weak chevron-type ornamentation in a herring-bone (reticulate) pattern.

Remarks.—The mega-onychites *O. runcinatus* as illustrated by Quenstedt (1857) in his pl. 34: 4 is identical with the material described herein. However, Engeser (1987) could not locate this specimen in the collections at Tübingen, and also observed that it does not resemble the *O. runcinatus* shown as fig. 5 on the same plate. He therefore removed this specimen from *O. runcinatus*.

A specimen of *O. barbatus* illustrated in the same volume (Quenstedt 1857: pl. 99: 15) is also a close match. Engeser (1987), however, observed that the specimens included in *O. barbatus* by Quenstedt (1857) belong to more than one form species, and erected *O. quenstedti* for the one resembling our material (but see also Schweigert [1999] for taxonomical comments on *O. barbatus* and the priority of Fraas [1855] for the species name). The three hooks on PMO 223.381 are more than twice the size of Engeser's (1987) illustrated specimens (Schweigert 1999: pl. 6: 5 shows a larger specimen), have slightly more rounded, shorter internal spurs, and external spurs are practically ab-

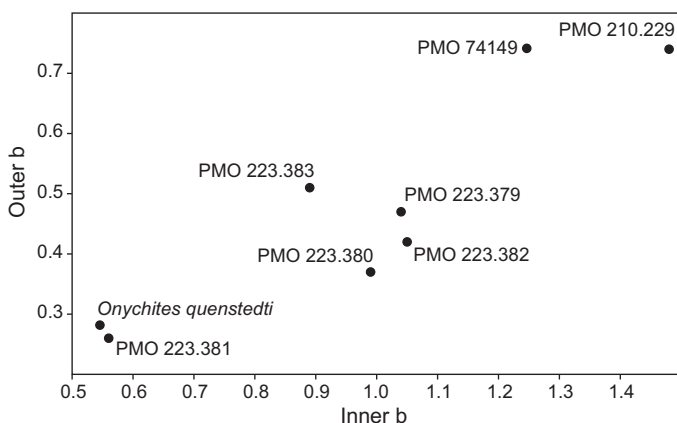


Fig. 8. Whorl expansion coefficients (b) for inner and outer spirals. *Onychites quenstedti* as figured by Engeser (1987: pl. 2: 5).

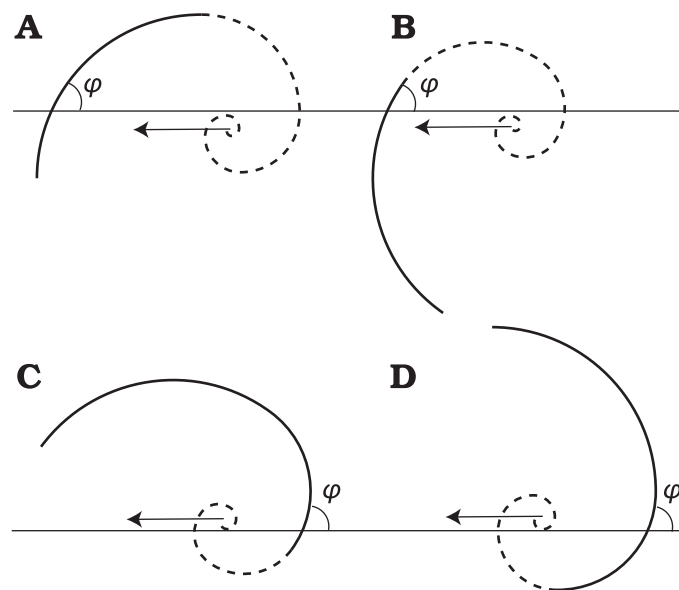


Fig. 9. Functional morphology of a hook or claw in a logarithmic spiral shape, penetrating a surface. **A, B.** Thrusting action, pole proximal. The angle φ at the contact point and the direction of the force vector (arrow) are constant during penetration. **C, D.** Pulling action, pole distal.

sent, but these differences do not appear sufficient to separate the three hooks from *O. quenstedti*. The whorl expansion rates are also very similar (Fig. 8).

Our remaining Boreal mega-onychites have considerably larger whorl expansion rates and are also much larger in size than the type *O. quenstedti*, but we do not find sufficient grounds for erecting a new form species for them. Sokolov (1912) appears to be the first author to describe this larger form, from the Upper Jurassic of Andøya, northern Norway. Sokolov claimed a similarity to *Onychites Fraarsi* (sic!) Quenstedt, 1857, however, *O. fraasi* is of completely different shape with an enormous inner spur, and is only a third the size. He suggested the hook came from the belemnoid *Acanthoteuthis*, but this was probably based only on the general fact that arm hooks had been observed on *Acanthoteuthis* specimens with soft-body preservation. However, these are small and of totally different shape, with long and straight shaft and weakly curved uncinus (Donovan and Crane 1992; Fuchs 2006).

Donovan (1953) described five specimens of mega-onychites from the Kimmeridgian of Greenland. Referring to the hooks figured on plate 24 in Quenstedt's (1857) monograph, he did not find a perfect match, and therefore used open nomenclature. The similar hooks figured by Christensen (1995) were referred to by him as "Donovan-type". However, as mentioned above, we see strong similarity with hooks illustrated on other plates in Quenstedt (1857).

Geographic and stratigraphic range.—Possibly Lower Toarcian of Germany (the lost "*O. runcinatus*" illustrated by Quenstedt 1857); Upper Kimmeridgian to Lower Tithonian of Nusplingen, Germany (Quenstedt 1857; Engeser 1987; Schweigert 1999); ?Lower Kimmeridgian of East Greenland (Dono-

van 1953); Draupne Formation spanning the Kimmeridgian–Ryazanian in the northern North Sea (Christensen 1995); Lower–Middle Volgian Farsund Formation in the North Sea; Volgian at Andøya, northern Norway (Sokolov 1912); Volgian Agardhfjellet Formation in the Sassenfjorden area, Spitsbergen (herein); ?Kimmeridgian of the Agardhfjellet Formation in the Sassenfjorden area, Spitsbergen (herein).

Biological affinity

It is remarkable that all of the large (> 3 cm) mega-onychites known from the Late Jurassic of the Boreal Realm (Greenland, North Sea, Andøya and Spitsbergen) appear to belong to the same form type (also the smaller PMO 223.381 is broadly similar in shape). Conversely, we are not aware of any reports of such large *O. quenstedti* outside this area. Considering the relatively large interspecific variation in mega-onychites morphology (Stevens 2010) it is possible that all the large *O. quenstedti* mentioned here belonged to one or a small number of biological belemnoid species endemic to the Boreal Realm. As with ammonites (see Page 2008 for review and references), Boreal belemnoid faunas were at least partly endemic during the Late Jurassic (Stevens 1963; Doyle 1987), represented by a small number of typical taxa such as *Pachyteuthis* and *Cylindroteuthis* (Stevens 1963; Doyle and Kelly 1988). Since large arm hooks are features connected with sexual maturity and mating, it is also possible that the Boreal Realm was a spawning area for hook-bearing animals.

Although relatively rich in mega-onychites, the Volgian succession in Spitsbergen is almost barren in belemnite rostra. A possible explanation, although based on negative evidence, is that these arm hooks derive from a belemnoid without rostrum. The belemnite (the unconventional spelling is discussed by Donovan and Crane 1992) genera *Acanthoteuthis* and *Volgobelus* are relatively common in the Middle Jurassic to Lower Cretaceous of Russia (Rogov and Bizikov 2006), and Sokolov's (1912) assignment of his Andøya mega-hook to *Acanthoteuthis*, although probably unfounded at the time, is therefore noteworthy. However, in contrast to true belemnites, articulated belemnite fossil shells have never been found with large hooks (e.g., Donovan and Crane 1992; Doyle and Shakides 2004).

Conclusions

All mega-onychites that we are aware of from the Upper Jurassic of Norway, the North Sea, Spitsbergen, and Greenland are very large and belong to the same form species *Onychites quenstedti*. These hooks may belong to a single species or a group of closely related forms endemic to the Boreal Realm. Future work may constrain this form more precisely in space and time, possibly with implications for Late Jurassic biogeography and stratigraphy.

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