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Arm hooks of coleoid cephalopods from the Jurassic succession of the Wessex Basin, Southern England

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Jurassic onychites (hooks from squid-like cephalopods) from the Wessex Basin, southern England.

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ABSTRACT

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1. Introduction

Modern squid have few easily preservable components. These include the crystalline lens of the eye (Clarke, 1993), the gladii or chitinous backbone (La Roe, 1971), mandibles or chitinous jaws (Clarke, 1965), onychites (squid arm and tentacle hooks) and statoliths (Clarke, 1966). As statoliths are calcareous (aragonite), and grow in size during ontogeny, they have the potential to record the development and age of the parent animal (Clarke, 1966; Jackson, 1994; Arkhipkin, 2005) but, as demonstrated by Kear et al. (1995, p. 117) in experimental work, they are often destroyed by the decay of the dead animal. Kear et al. (1995, p. 124) also indicated that while statoliths have a fossil record, none had been reported within a body fossil. Wilby et al (2004, ...), however, indicated that some specimens of *Belemnotheutis antiquus* may have statoliths present in the area of the head.

Modern coleoid (squid-like) cephalopods have arms that carry arrays of both suckers and hardened, organic hooks. Fossil arm hooks have been known since their description by Sternberg in 1823, although he identified them as plant remains. During the twentieth century there were a number of brief descriptions of hooks but it was Kulicki & Szaniawski (1972) who described 22 morphotypes from the Jurassic of Poland. These authors gave these ‘forms’ names using a binomial classification though, with many lacking defined (and figured) holotypes and , in some cases, only one recorded specimen, some of their designations should probably be regarded as invalid. Some of their morphotypes have, however, been reported from DSDP sites on the Falkland Plateau (Wind et al., 1977) as well as New Zealand (xxxxxxx), Germany, Poland and the United Kingdom (Hart et al., 2016). Arm hooks are reported from the mid-Carboniferous to the Cretaceous/Paleogene boundary (Young et al., 1998, fig. 2) and these records appear to be different to the arms of modern squids that have suckers that can vary in size, with some containing a chitinous ring (Roper et al., 1984; Hanlon and Messenger, 1996, fig. 4.3). Other squid-like cephalopods are also known to bear hooks on the end of their club-like tentacles (Roper et al., 1984; Hanlon and Messenger, 1996, fig. 4.3c).

In the fossil record it is clear that the hooks belong to widely distributed members of the Belemnitida and Phragmoteuthida, and occur in three different situations:

- Discrete hooks that are found in either samples processed for other microfossils (e.g., Hart et al., 2016) or in acid reductions of limestones (e.g., Kulicki & Szaniawski,1972);
- Assemblages of hooks associated with soft-bodied preservation of the arms of squid-like cephalopods (e.g., the specimen of *Belemnotheutis antiquus* illustrated by Clements et al., 2016, fig. 1D); or
- Occasional hooks that are either present in the preserved stomach contents of vertebrate fossils (e.g.,.......) or in coprolites (e.g.,........)

Using the abundance of material available to us from the Wessex Basin, we are attempting to identify, where possible, the host animals. If this can be established then it should be possible, using micropalaeontological samples, to determine the stratigraphical and palaeoecological ranges of some of the host macro-fossils, many of which are otherwise rarely preserved. There are some important questions to answer before tackling this issue:

- Are all the hooks in any specimen identical or is there a variation along the length of the arms?
- Do the hooks present in any taxon remain the same throughout the total stratigraphical range or do they change through time?

- Is it possible to use the occasional hooks found in preserved stomach contents or corpolites to identify the species that have fallen victim to predation?

In attempting to answer these questions we have studied a range of specimens from a number of key locations in the Wessex Basin of Jurassic age.

2. Christian Malford

Exceptional soft-bodied preservation of species such as *Belemnotheutis antiquus* Pearce 1847 from the Callovian–Oxfordian of the United Kingdom has allowed the identification of the host animal of some hook morphotypes, though the majority remain un-attributable. In the Christian Malford lagerstätte (Upper Callovian) of Wiltshire large numbers of hooks (including forms described as *Acanthuncus*, *Arites*, *Deinuncus*, *Falcuncus*, *Longuncus* and *Paraglycerites*) are found associated with an abundance of statoliths (cephalopod ‘ear bones’) and macrofossil evidence of both belemnites and other squid-like cephalopods, some of which includes exceptional soft-bodied preservation (see Wilby et al., 2004, 2008; Hart et al., 2016).

The Christian Malford ‘squid bed’ (Page and Doyle, 1991) and associated strata have yielded *B. antiquus*, occasional *Mastigophora brevipinnis*, and unique specimens of *Romaniteuthis* sp. and *Trachyteuthis* sp.. The history of *B. antiquus* has been fully documented by Donovan and Crane (1992), who illustrated their account with a number of photographs of specimens housed in the Pearce Collection of the City of Bristol Museums and Art Gallery (BRSMG). All of Pearce’s material came from the Oxford Clay Formation of Christian Malford during construction of the Great Western Railway in 1840. The associated ammonites are characteristic of the Phaeinum Subzone (Athleta Zone) of the Callovian Stage (Donovan, 1983, pp. 486–487; Page *in* Martill and Hudson, 1991, p. 156; Wilby et al., 2008; Hart et al., 2016). Preservation is exceptional (Allison, 1988; Wilby et al., 2004) and includes permineralized soft tissues, ink sacs, aragonitic phragmacones, statoliths (ear bones) and onychites (hooks). In disaggregated samples of the clays, Hart et al.

(2016) record the presence of abundant benthic foraminifera (including aragonitic taxa), ostracods, otoliths (fish ‘ear bones’), statoliths and hooks.

The specimens described by Donovan and Crane (1992, pls. 1–5, text-figs 2, 3) show a range of structures, though no statoliths are mentioned. In particular they illustrate (Donovan and Crane, 1992, pls 2, 4(1), text-figs 2, 3) the characteristic hooks of *B. antiquus*. In all these illustrations the hooks appear to be almost identical and are characterized by a smooth outline, simple curved uncinus and no sign of a spur (Fig. 1). There is evidence of slight variability in the form of the hooks along the arms although, as noted by Donovan and Crane (1992, p. 291) this may be an artefact of preparation. The specimen from Christian Malford (NHMUK 25966) illustrated by Clements et al. (2016, fig. 1D) shows a series of paired hooks in the arms that appear remarkably constant in appearance. Donovan and Crane (1992, p. 282) record the earliest *Belemnotheutis* from the Kellways Rock (Calloviense Zone, Lower Callovian) in Wiltshire, while the youngest appears to be Kimmeridgian in age. Riegraf (1987) reported a crushed phragmacone from the Kimmeridge Clay Formation of Kimmeridge Bay (Dorset), though no precise position is known. Donovan and Crane (1992, p. 282) suggest a position in the Pseudomutabilis Zone or Gigas Zone. The youngest recorded specimen is given as Upper Kimmeridgian (?Pallasiodes Zone).

The ‘Etches Collection’, part of which is now on display in the village of Kimmeridge (Dorset), contains numerous examples of *Belemnotheutis*, including several specimens (www.theetchescollection.com) that show the characteristic layout of the arms and – in places – the paired hooks that are almost identical to those illustrated by Donovan and Crane (1992). These specimens are all from the Kimmeridge Clay Formation of Dorset and confirm the range of the species from Lower Callovian to Upper Kimmeridgian.

Doyle (1991, p. 172) records a (?)*Belemnotheutis* phragmacone from the Nordenskjöld Formation of the Antarctic Peninsula, which is probably late Kimmeridgian in age. In DSDP cores on the Falkland Plateau, Wind et al. (1977) pl. 2(7)) record a smooth *Belemnotheutis*-like hook from the Oxfordian. Wind et al. (1977, pls 1–6) also illustrate a range of hook morphotypes that are mostly characterized by the presence of spurs. These are attributable to the 'taxa' described by Kulicki & Szaniawski (1972), and record them as *Paraglycerites*, *Urbanekuncus* and *Longuncus*. Wind et al. (1977, pl. 4, p. 830) also describe a new morphotype (*Accoluncus*) with a spur much further along the shaft towards the uncinus (Fig. 1C). The variety of morphotypes, though not identical, is reminiscent of the range of forms seen in samples from Christian Malford (Hart et al., 2016, fig. 3).

3. Lower to Middle Jurassic hooks

The range of hook morphotypes present in the samples from Christian Malford (Hart et al., 2016) is suggestive of a much greater range of taxa being present than is currently known from soft-bodied material and phragmacones. Hart et al. (2016) also only reported two types of statolith being present: described as Jurassic sp. A and Jurassic sp. C by Clarke (2003). Most of the non- hooks fall into two main groups:

- Elongate forms included in *Longuncus* by Kulicki & Szaniawski (1972); and
- Forms with a distinctive spur that were mainly included in *Parglycerites* by Kulicki & Szaniawski (1972).

Donovan (2006), in a review of the Phragmoteuthida from the Lower Jurassic of Dorset, has indicated that they are rare in the Charmouth Mudstone Formation (Sinemurian, Jurassic). Two species – *Phragmoteuthis huxleyi* Donovan (1966) and *P. montefiorei* J. Buckman (1880) – are described, each reflecting a different style of preservation. Donovan (2006, text-fig. 1) illustrates the holotype of *P. montefiorei* (specimen BMNH C5026), which shows the presence of slightly curved hooklets and these are also visible in Donovan's (2006, text-fig. 2) illustration of another specimen from Lyme Regis. Donovan (2006, p. 677) goes on to note that the hooks associated with *P. montefiorei* are similar to those of *P. bisinuata* (Bronn, 1859) from the Upper Triassic and *P. conocauda* Quenstedt, 1849 from the Lower Jurassic of southern Germany (Riegraf, 1996, fig. 4c; Riegraf et al., 1984, pl. 10, fig. 11, text-fig. 43c). Donovan (2006, p. 677) also indicates that the specimens of *P. huxleyi* are (mainly) from the Black Ven Marls Member of the Charmouth Mudstone Formation (Obtusum Chronozone), with one specimen labelled as ‘Monmouth Beach’ , west of Lyme Regis. The specimens of *P. huxleyi* and *P. montefiorei* illustrated by Donovan (2006) show no evidence of statoliths but are clearly potential hosts of Jurassic sp. B (Clarke, 2003; Hart *et al.,* 2015). *P. conocauda* (from the Toarcian) could be the host of another statolith, which has been recorded in SW Germany from the uppermost Toarcian (Aalensis Chronozone) and lowermost Aalenian (Opalinum Chronozone): *fide* Dr Wolfgang Riegraf (Münster, Germany).

Hyde (2012) has described two specimens of phragmoteuthid cephalopods that are in the collections of Manchester Museum: specimen numbers L6809 and L.6923). These are recorded as being from ‘Lyme Regis’ and attributed to the Lower Lias “somewhere near the top of the *A. bucklandi* Zone”. Hyde (2012, fig. 1) illustrates specimen L6923, which includes part of the pro-ostracum and phragmacone and hooks. Hyde (2012, p. 443) notes that the hooks appear to be paired with one being long and gently curved with a “bifurcated base” and the other being shorter, more robust and triangular in shape. Hyde (2012, p. 444, fig. 2) also indicates that specimen L6809 has paired hooks which can be used to define the arms. It seems clear, therefore, that these early Jurassic forms have paired hooks, of different appearance, with the larger, curved hooks having a distinctive ‘base’. No spur, *sensu* Kulicki and Szaniawski (1972), is described or illustrated in these individuals.

In the Paleontological Museum of the University of Florence (via Giorgio La Pira 4, Firenze) is Specimen Igf 10966 which is listed as *Geoteuthis bollensis*, and which is attributed to the Upper Lias of Boll, Württenberg, Germany. It is a two-sided specimen, one of which preserves an elongated ink sac. There is no visible sign of any arms and no hooks are visible in the surrounding matrix. It is quite difficult to determine the details of the head area and there is, therefore, no location in which to search for statoliths. There are no details of who described this specimen or the geology of the site from which it was collected.

In Leeds City Museum and Art Gallery is another specimen attributed to *G. bollensis*, and this is labelled as being from Lyme Regis. There are no further details as to the stratigraphical location of the specimen, though many squid-like cephalopods come from bed 88f (in the Lang, 1914, 1917, 1924, 1932, 1936 nomenclature). This specimen was recently described by Robert Chandler.....

Summary

Acknowledgements

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Figure Captions

Figure 1. Terminology applied to the hooks of squid-like cephalopods. A; typical hook of *Belemnotheutis antiquus*: B; typical appearance of a hook identified as *Paraglycerites* by Kulicki and Szaniawski (1972): C; the species identified as *Accoluncus falklandensis* Wind et al. (1977), showing the small spur near the uncinus: D; the elongate form described as *Longuncus* by Kulicki and Szaniawski (1972)

Figure 2.