

Staloliths from the Jurassic succession of south-west England, United Kingdom

Malcolm B. Hart¹ · Malcolm R. Clarke² · Alex De Jonghe^{1,3} · Gregory D. Price¹ · Kevin N. Page¹ · Christopher W. Smart¹

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Abstract The occurrence of staloliths within the Jurassic succession of south-west England and other parts of Europe is reviewed. Five ‘morphospecies’ have been identified, ranging in age from Hettangian to Kimmeridgian. With so little published information on staloliths, the presently known geological record is incomplete, although new occurrences are continually being discovered. The occurrence of staloliths, in the absence of soft-bodied fossils, may ultimately provide a more complete indication of the distribution of the soft-bodied host animals. At the present time, however, only one of the stalolith ‘morphospecies’ can be, tentatively, linked to a known species of teuthid.

Keywords Staloliths · Jurassic · Teuthids · Otoliths · United Kingdom

Introduction

Staloliths are the small aragonitic ‘stones’ which lie in the fluid-filled cavities or statocysts within the cartilaginous heads of all living and (probably) all fossil members of the Coleoidea (Clarke and Fitch 1975, 1979; Clarke 1978,

2003; Clarke and Maddock 1988a, b; Clarke et al. 1980a, b; Lipinski 1980, 1986, 2001; Jackson 1993, 1994; Arkhipkin and Bizikov 1997, 2000; Arkhipkin 2003, 2005; Hart et al. 2013). In the Jurassic sediments of the Wessex Basin, southern England, staloliths are found co-occurring with otoliths and, being of similar appearance, size, mineralogy (aragonite) and colour, there are a number of instances where staloliths have been confused with otoliths (e.g. Frost 1926, figs. 13, 14; Martin and Weiler 1954, pl. 3, fig. 116; Rundle 1967, text-fig. 4). Whilst Clarke (1996) noted the occurrence of staloliths in Jurassic sediments, it was his later paper (Clarke 2003) that described three ‘species’ of Jurassic staloliths from southern England as Jurassic sp. A, Jurassic sp. B and Jurassic sp. C (Clarke 2003, figs. 14, 15). The material figured by MRC is, apparently, ‘lost’ and is presently being sought by both his family and the curators in the Palaeontology Department, Natural History Museum (London).

Materials and methods

Clarke’s material came from amateur fossil collectors who prepared their large samples using rather unorthodox methods and which generated a significant amount of breakage (see Hart et al., in review). Having broken the clay into fragments, they dried it in the open air, soaked it in water and ‘forced’ it through an 850- μ m sieve (thereby failing to collect smaller specimens). The residue was then sieved in a ‘nylon stocking’ with the fine material being decanted. In some of his unpublished data, MRC records a significant number of damaged staloliths with what he termed ‘broken ends’, which are rarely found in our residues. The breakage recorded by MRC is, therefore, an artefact of processing and not taphonomy. All of our

Malcolm R. Clarke—Deceased.

✉ Malcolm B. Hart
mhart@plymouth.ac.uk

¹ School of Geography, Earth and Environmental Sciences, Plymouth University, Drake Circus, Plymouth PL4 8AA, UK

² Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK

³ Present Address: Roberston International Oil and Gas Consultants, Tyn-y-Coed, Llandudno, Gwynedd LL30 1SA, UK

material was prepared using normal micropalaeontological techniques, as the residues have also been used for an investigation of foraminifera, ostracods, ichthyoliths, otoliths and holothurian sclerites. This involved slow drying (at <40 °C in an oven) of the fragmented samples, soaking in White Spirit (see Brasier 1980), removal of the White Spirit and soaking in deionised water until breakdown occurred and then washing on a 63-µm sieve. Residues were then oven-dried (<40 °C) and studied in a number of size fractions (>500, 500–250, 250–125 and 125–63 µm). These fractions were all weighed and the data tabulated. Whilst foraminifera were picked to a statistically valid number (usually 250–300 as a minimum from each size fraction), all the statoliths and otoliths were picked as there is no proven methodology for dealing with these microfossils.

All of the processed samples from our research, including Christian Malford, yielded statoliths, otoliths (fish ‘ear’ bones), oncytes (squid arm and tentacle hooklets), foraminifera and ostracods. Whilst the foraminifera and ostracods are typical of Callovian strata elsewhere in the UK and northern France (Cordey 1963a, b; Coleman 1974, 1982; Gordon 1965; Barnard et al. 1981; Shipp 1989; Morris and Coleman 1989; Henderson 1997; Page et al. 2003; Oxford 2004), the numbers of statoliths recovered are exceptional. They, and the squid hooklets, confirm the presence of large numbers of squid throughout the succession and, coupled with the famous soft-bodied fossils from Christian Malford and Ashton Keynes, make this an exceptionally interesting paleoenvironment.

Christian Malford

During construction of the Great Western Railway, over 170 years ago, excavations near Christian Malford (Fig. 1) yielded a number of exceptionally preserved specimens of *Belemniteuthis* and *Mastigophora*, as well as a number of fish and other macrofossils (Pearce 1841; Owen 1844; Mantell 1848). This assemblage has been redescribed by, for example, Donovan (1983), Allison (1988), Martill and Hudson (1991), Page and Doyle (1991), Donovan and Crane (1992), Tang (2002) and Wilby et al. (2004). This locality has become known as the “Christian Malford Squid Bed” (Wilby et al. 2008) and—quite rightly—identified as a lagerstätte because of the exceptional soft-bodied preservation of the teuthids (including muscle fibres, ink sacs, tentacles, etc.). As part of a reinvestigation of the area in 2006/2007 a number of boreholes were drilled and a trial pit dug within the upper part of the Peterborough Member, Oxford Clay Formation (Phaeinum Subchronozone, Athleta Chronozone, Upper Callovian).

Samples from core 10 of this investigation have been processed using standard micropalaeontological techniques (see above), all of which yielded an abundant microfauna of foraminifera, ostracods, ichthyoliths, oncytes (squid hooklets), statoliths and otoliths (Price et al. in press; Hart et al. in review). The statoliths are well-preserved, rarely broken, and—apparently—still showing the original aragonite that preserves the internal (daily?) growth lines (see, for example, Clarke 1966; Jackson 1993, 1994; Lipinski 1980, 1986, 2001; Arkhipkin 2005, and references therein). Many of the specimens show the presence of tiny pyrite framboids but are otherwise pristine. In the samples prepared by the fossil collectors for MRC, they recovered an average of 0.1 statoliths per kg of initial dry sediment, with otoliths invariably outnumbering statoliths. In the samples from the Christian Malford core, the average yield of statoliths is <400 per kg, with otoliths always being present in lower numbers; a complete reversal of all the other locations studied by MRC.

In the Christian Malford samples there are two, quite distinct, ‘morphospecies’ of statolith (Fig. 2), described initially by Clarke (2003, pp. 42–44, figs. 14, 15). Jurassic sp. A (~95 % of the assemblage) and Jurassic sp. C (~5 % of the assemblage) have been recorded in exceptional numbers, making this a unique occurrence of these enigmatic microfossils. The numbers of statoliths should, it is suggested, reflect the relative abundance of the two species of host animals. Page and Doyle (1991) reported four taxa of coleoid from the Oxford Clay Formation of Christian Malford: common *Belemniteuthis antiquus*; occasional *Mastigophora brevipinnis*; and single specimens of *Romaniteuthis* sp. and *Trachyteuthis* sp. Crucially, the specimens of *Belemniteuthis* (LEIUG 121817(2)) from Rixon Gate (Ashton Keynes) figured by Wilby et al. (2004, pl. 1, figs. 1, 2 and pl. 2, fig. 3) appear to show a pair of statoliths within the head area. The statoliths are reported as being oval on cross section and about 1.5 × 0.5 mm² in size. They are described as having a brown core and a thin, white, outer layer. Kear et al. (1995) claim that the aragonitic statoliths would have been subjected to recrystallization in the post-mortem rotting of the dead squid, although much of our material appears to be aragonite and, when sectioned, still showed (daily?) growth increments. As most of the material described by the early collectors (Pearce 1841) and Wilby et al. (2004, 2008) is placed in *Belemniteuthis antiquus*, it is likely that the most abundant statolith (Jurassic sp. A) belongs to this species. The evidence from the squid hooklets supports this interpretation (Donovan and Crane 1992), but this can only be confirmed if a soft-bodied specimen is found, or located in a museum collection, with an example of Jurassic sp. A, unequivocally located within the soft tissue of the head. The animal that hosted Jurassic sp. C is presently unknown, other than

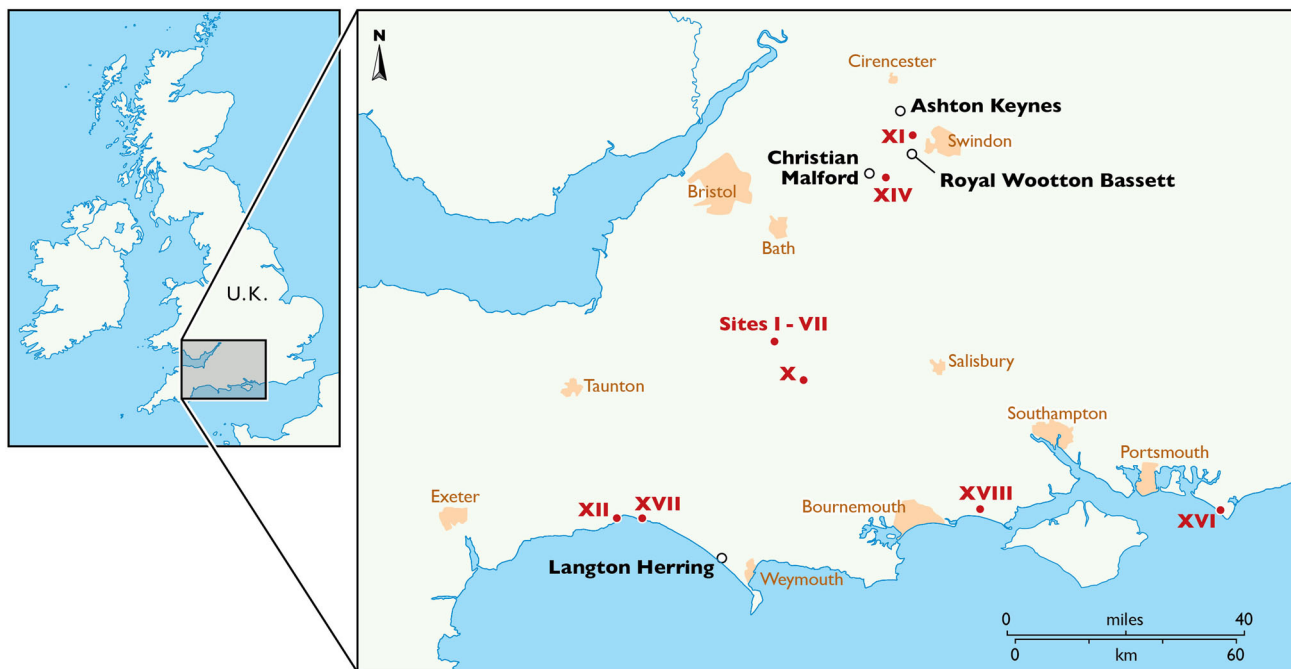


Fig. 1 Locality map showing the locations in southern England from which staloliths have been recovered by the authors. The site of the Christian Malford excavations and the site at Ashton Keynes are also indicated

which it would be expected to have been much rarer than *B. antiquus* in the Phaeinum Subchronozone sediments of Wiltshire.

The large numbers of staloliths recorded in many of the micropalaeontological samples from Christian Malford are exceptional, and well above the levels normally recorded in comparable Jurassic mudstone samples. Clarke (2003, p. 43) indicated that "...living cephalopods on the continental shelves often form large aggregations during spawning followed by death and, unless a deposit encompassed such an area, most of the mature sized cephalopods might well seem sparse compared to fish. If spawning areas come to light in fossil deposits, far more staloliths than otoliths should be found". Christian Malford may well record such a setting (see Hart et al. in review).

Distribution of other stalolith 'morphospecies' in the Jurassic

The five known 'morphospecies' recorded from the Jurassic display what are, almost certainly, incomplete ranges (Fig. 3) as records of staloliths are relatively limited. Aside from the two 'morphospecies' recorded from Christian Malford and other locations in Wiltshire and Somerset, the other three 'morphospecies' are isolated occurrences with little evidence of the soft-bodied preservation of potential host animals. The ranges of these

potential host animals are also unknown, with records of teuthids often limited to single, or intermittent occurrences.

An example of such an isolated occurrence is that recorded by Hart et al. (2009) from the Wattonensis Beds (Bathonian) of Rodden Hive Point near Langton Herring (Dorset). Material from this succession has yielded otoliths in the past (Stinton and Torrens 1968) and our material also contained a number of otoliths (Hart et al. 2009, fig. 3) and very rare staloliths ('morphospecies' Jurassic sp. D). This form (Fig. 2) has a distinctly hooked rostrum, and appears (morphologically) between Jurassic sp. B and Jurassic sp. A (though lacking any sign of marginal crenulations).

The morphospecies described here as Jurassic sp. B (see Clarke 2003, fig. 15) was collected from the Lower Jurassic (Obtusum Chronozone) of Somerset (locality 1 on Fig. 1). The precise horizon is not known as the sample was collected by amateur fossil collectors Mr. and Mrs. Hiscock, and given to MRC as a washed residue. It is also recorded as having been found on the Dorset Coast at Site XII near Lyme Regis (from either the Blue Lias or the Charmouth Mudstone Formation) and at Site XVII between Charmouth and Golden Cap. If the age determination of the mudstones is correct then this morphospecies probably comes from Bed 88f of the Obtusum Chronozone (Lang and Spath 1926; Lang 1932) of the Sinemurian (Lias Group, Charmouth Mudstone Formation).

Donovan (2006), in a review of the Phragmoteuthida from the Lower Jurassic of Dorset, has indicated that they

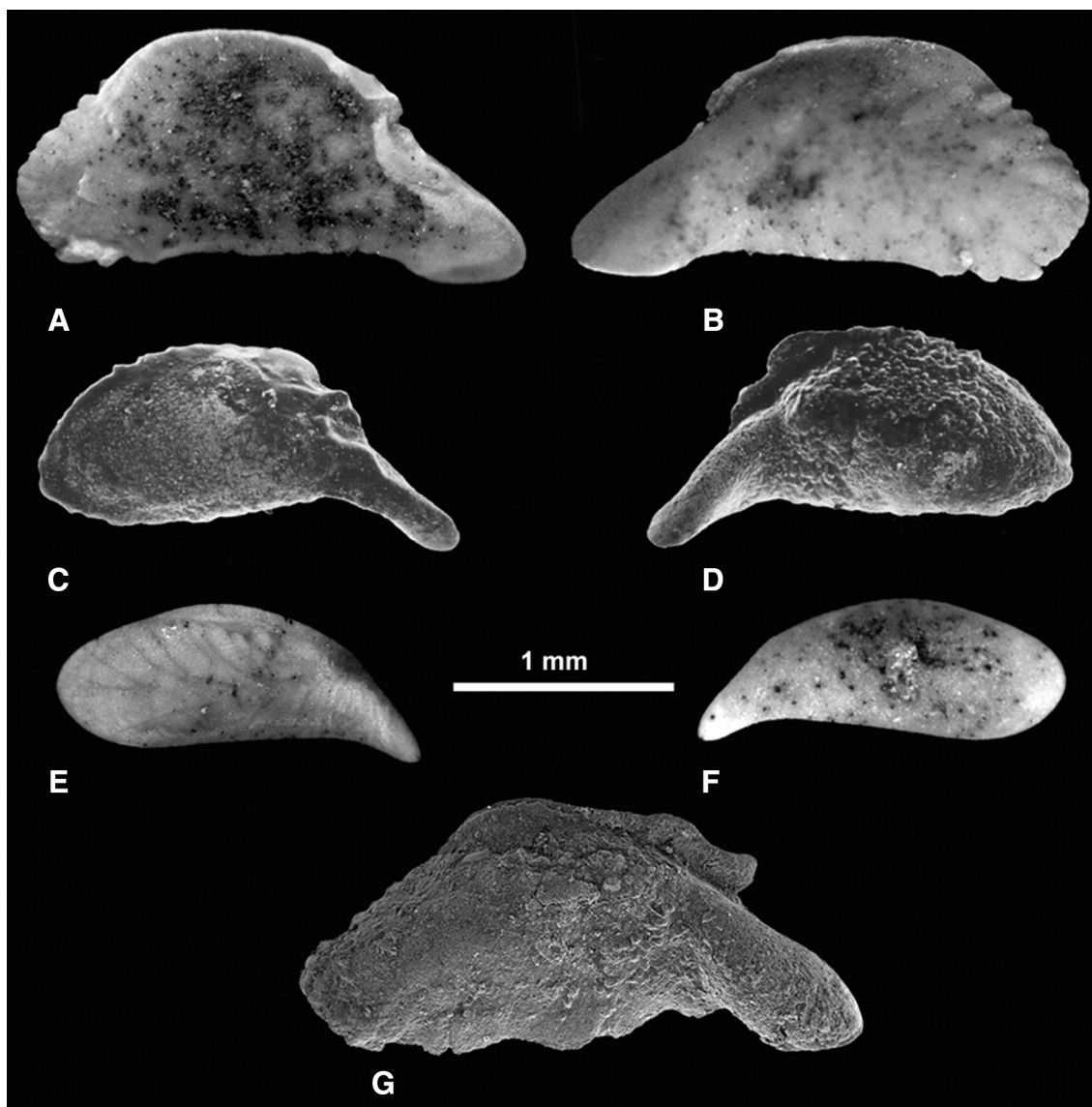


Fig. 2 A, B Jurassic sp. A from the Oxford Clay Formation of locality II (Somerset). The main characteristics of this ‘morphospecies’ are the large size, curved rostrum and crenulated margin: C, D Jurassic sp. B from the Lias Group mudstones of the Dorset Coast east of Charmouth. The main characteristics of this ‘morphospecies’ are the distinctly hooked rostrum and wide, rounded, margin with no signs of any crenulations: E, F Jurassic sp. C from the Oxford Clay Formation of locality VII (Somerset). The main characteristics of this

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 hooklets associated with *P.*

‘morphospecies’ are the smoothed outline, with no crenulations on the margin and markings that look like the veins of a leaf. The structure of these features, and their purpose, is completely unknown as they have not been seen in any of the other ‘morphospecies’: G Jurassic sp. D from the Wattonensis Bed, Frome Clay Formation, Upper Bathonian (Jurassic) of the Rodden Hive Point section (see Hart et al. 2009 for location details). Scale bar is 1 mm

montefiorei (now *Clarkeiteuthis montefiorei* following Fuchs et al. 2013) are similar to those of *P. bisinuata* (Bronn, 1859) from the Upper Triassic and *P. conocauda* Quenstedt, 1849 (now *Clarkeiteuthis conocauda* following Fuchs et al. 2013) 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

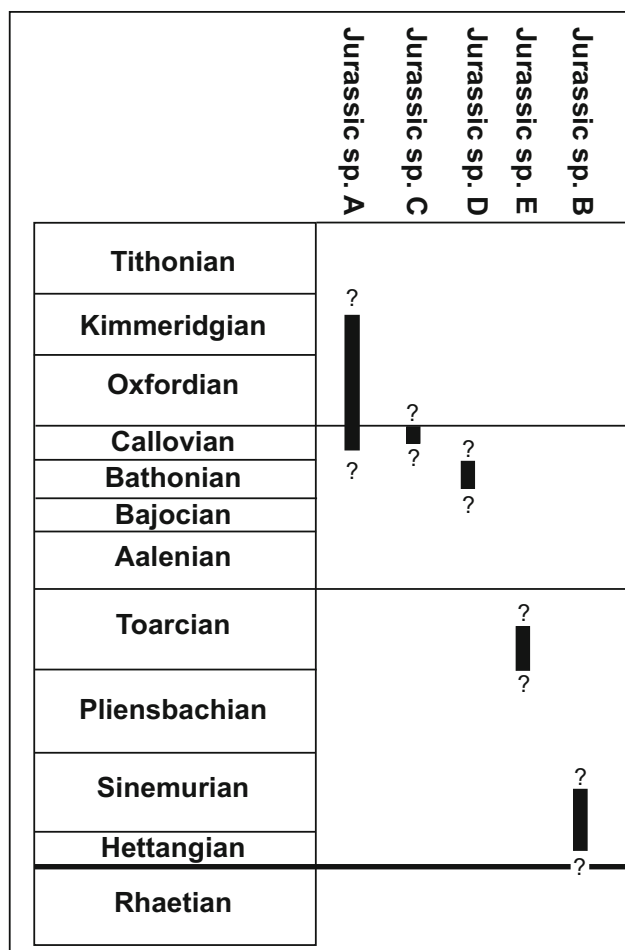


Fig. 3 Known ranges of statolith ‘morphospecies’ in the Jurassic of Europe

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. *Clarkeiteuthis conocauda* (from the Toarcian) could be the host of Jurassic sp. E (Fig. 3), which has been recorded in SW Germany from the uppermost Toarcian (Aalensis Chronozone) and lowermost Aalenian (Opalinum Chronozone) *vide* Dr. Wolfgang Riegraf (Münster, Germany).

Clearly it is necessary to: (1) collect micropalaeontological samples from the horizons from which phragmoteuthids have been collected; and (2) search the well-preserved specimens in the various museum collections for the presence of statoliths. At the present time, there are no records of any teuthids from the Wattonensis Beds (Bathonian) of the Dorset area and the host of Jurassic sp. D, therefore, remains undetermined.

Engeser (1990), in a cladistic analysis of the Coleoidea, included the Phragmoteuthida in the Belemnnoidea, whilst Doyle et al. (1994) excluded the phragmoteuthids from the

Belemnnoidea. Whilst none of these relationships can be determined by the statoliths, these small aragonitic fossils may be able to document the ranges of some of these taxa once the host animals have been determined.

Summary

The five ‘morphospecies’ of Jurassic statoliths described herein are known from the Hettangian to the Kimmeridgian. It is clear that more information on the distribution of the ‘morphospecies’ is required, but it is only by being aware of their potential presence that will ensure that micropalaeontologists routinely begin to record the presence of these microfossils. The challenge, at present, is to link the statoliths with the parent animals in order to test Clarke’s (2003, p. 46) suggestion that the evolution of the Jurassic coleoids may be better understood once the distribution of the statoliths is better known. At the present time, only Jurassic sp. A has been tentatively linked to a known taxon (*Belemnnotheutis antiquus*); see Hart et al. (in review).

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