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Hart, Malcolm

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EXCEPTIONAL ACCUMULATIONS OF STATOLITHS IN ASSOCIATION WITH THE
CHRISTIAN MALFORD LAGERSTÄTTE (CALLOVIAN, JURASSIC) IN WILTSHIRE,
UNITED KINGDOM

MALCOLM B. HART*, ALEX DE JONGHE**, KEVIN N. PAGE,
GREGORY D. PRICE & CHRISTOPHER W. SMART

*School of Geography, Earth & Environmental Sciences, Plymouth University,
Drake Circus, Plymouth PL4 8AA, United Kingdom*

** corresponding author, mhart@plymouth.ac.uk*

*** currently at Robertson International Oil and Gas Consultants, Pentywyn Road,
Tyn-y-Coed, Llandudno LL30 1SA, United Kingdom*

RRH – *JURASSIC STATOLITHS FROM CHRISTIAN MALFORD*

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ABSTRACT

In the shell-rich, laminated clays of the Phaeinum Subchronozone (Athleta Chronozone, Upper Callovian, Middle Jurassic) of the Peterborough Member of the Oxford Clay Formation large numbers of statoliths and otoliths have been recorded. This apparent mass mortality is associated with the Christian Malford Lagerstätte in which there is exceptional, soft-bodied preservation of coleoid fossils. Statoliths are the aragonitic ‘stones’ that are found in the fluid-filled cavities (or statocysts) within the cartilaginous head of all modern and probably many fossil coleoids. Jurassic statoliths are largely undescribed and there are no known genera or species available to aid their classification. Otoliths, which may be of somewhat similar appearance, are the aragonitic stato-acoustic organs of bony (teleost) fish. These are more familiar to

micropalaeontologists and have a better known, though limited, fossil record. The abundance of statoliths in the Phaeinum Subchronozone at Christian Malford may indicate a mass mortality of squid that extends over some 3 m of strata and, therefore, a considerable interval of time. This has been tentatively interpreted as a record of a breeding area (and subsequent death) of squid-like cephalopods over an extended period of time rather than a small number of catastrophic events.

INTRODUCTION

In the 1840s, during the construction of the Great Western Railway west of Swindon (Wiltshire, U.K.) a significant number of exceptionally preserved coleoids (belemnites and squid-like cephalopods) were found (Pearce, 1841; Owen, 1844; Mantell, 1848). These famous specimens of *Belemnotheritis* and *Mastigophora* have been re-described by Donovan (1983), Page and Doyle (1991) and Donovan and Crane (1992). The other macrofossils from the assemblage, including a number of fish, have also been described (e.g., Allison, 1988; Martill and Hudson, 1991; Tang, 2002; Wilby et al., 2004) in the context of a fossil lagerstätte under the name of the ‘Christian Malford Squid Bed’. Most of these specimens, appear to come from the Phaeinum Subchronozone (Athleta Chronozone, Upper Callovian, Middle Jurassic) of the Oxford Clay Formation, and many contain soft tissue, muscle fibres and the content of their ink sacs (Wilby et al., 2004).

The historical finds of exceptionally preserved fossils at Christian Malford (near Swindon, Wiltshire, U.K.) and the nearby location of Ashton Keynes (Wilby et al., 2004, 2008), led to the development of this project, which was designed to collect more specimens of the coleoids and promote a multi-disciplinary analysis of the depositional environment. In

2006 a programme of exploratory drilling was undertaken along a 4 km transect adjacent to the railway line immediately south of Christian Malford (Fig. 1) in order to provide some stratigraphical control. In October 2007, an area of 32m² was excavated to a depth of ~ 5 m, yielding ~240 tonnes of fossil bearing mudstones belonging to the upper part of the Peterborough Member of the Oxford Clay Formation. Ammonites were common throughout the material excavated and were dominated by abundant *Kosmoceras* (*Lobokosmoceras*) ex grp *phaeinum* (S. Buckman) which places the bulk of the material within the Phaeinum Subchronozone (Athleta Chronozone, Upper Callovian). Only a few *Kosmoceras* (*Zugokosmoceras*) ex grp *grossouvrei* Douvillé were recovered, indicating the top of the preceeding Grossouvri Subchronozone of the Coronatum Chronozone (Middle Callovian). A brief report on the macrofossils recorded from the excavation is provided by Wilby et al. (2008) and representative figures of *Kosmoceras phaeinum* from Christian Malford are provided by Page (1991).

MATERIALS AND METHODS

Following the exploratory drilling in 2006, the British Geological Survey organised an excavation (in October 2007) of a site ~100 m from the original, nineteenth century, excavations in the area that were associated with the construction of the railway line (Fig.1). The 2007 excavation provided some new examples of belemnite phragmocones as well as many ammonites, bivalves and gastropods, most of which are well preserved, except for some diagenetic crushing (Wilby et al., 2008). Many excavated bedding surfaces were covered with almost monospecific assemblages of bivalves, including *Meleagrinella braamburiensis* (Phillips) and *Bositra buchii* (Roemer), and gastropods (including *Procerithium damonis* (Lycett) and *Dicroloma* spp.). A small number of bedding surfaces

were also covered in foraminifera, mainly *Epistomina stellicostata* Bielecka & Pozaryski. The molluscan assemblage is typical of a number of the Peterborough Member biofacies recognised by Duff (1975).

As this excavation became water-filled very quickly, it was impossible to collect a suite of *in-situ* samples appropriate for a micropaleontological investigation. From the suite of cores drilled in 2006, Core 10 was selected for analysis as it was both one of the longest and had already been studied for its macrofossil content (Fig. 2). This core was ~5 m in length and split into 6 sections, each of which are 62–108 cm in length. Forty-one samples were collected from the measured core at regular intervals. Particular note was taken of shell debris, macrofossils, sedimentary structures and the presence of any dark, potentially organic-rich, sediments. The uppermost 10 cm of soil/clay within Core 10 was omitted from the processing as the sediments were probably contaminated by surface processes. Following removal of the ‘smeared’ outer surface of the core, samples were carefully disaggregated to gravel-sized pieces and weighted in a dry condition. These dried samples were processed using the white spirit method of Brasier (1980). After being soaked in white spirit for ~ 4 hours, decanted, and then immersed in deionised water for 24 hours, samples were washed on a 63µm sieve. The processed residues were then dried in a cool oven (40°C) for ~12 hours before dry sieving into the >500µm, 500–250µm, 250–125µm and 125–63µm size fractions. These fractions were all weighed and the data tabulated for subsequent analysis. While 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 accepted methodology for dealing with these microfossils. While all the foraminifera, statoliths and otoliths were recorded, those in the >500 µm size fraction were studied and identified but were omitted from the absolute and/or relative abundance counts. This is because that size

fraction contains pyritized molluscs that would have distorted any calculations (based on weight of dry sediment). One significant problem is the counting of adherent foraminifera as many of the marine clays in the Middle and Upper Jurassic of the United Kingdom contain shell fragments, otoliths, etc., that are host to specimens of adherent foraminifera (e.g., *Bullopore*, *Vinelloidea* and *Nubeculinella*). In some cases these have become detached and could be counted alongside other species/genera of foraminifera in processed residues. Many, however, remain attached to shell fragments (e.g., Hart et al., 2009, fig. 3) and are not, therefore, available for counting in their appropriate size fraction. Their presence is, as a result, often un-recorded. Even where specimens have become detached, they often break apart and, in the case of *Bullopore*, could easily form 2, 3, or more, separated chambers, potentially distorting any statistical approach.

All of the processed samples from Core10 yielded statoliths, otoliths, onychites (cephalopod arm and tentacle hooks), foraminifera and ostracods. While 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 et al., 2000, 2004; Wilkinson and Whatley, 2009), the numbers of statoliths recovered are exceptional. They, and the hooks, confirm the presence of large numbers of squid-like cephalopods throughout the succession and, coupled with the famous, soft-bodied fossils from Christian Malford and Ashton Keynes, make this an exceptionally interesting paleoenvironment.

MICROPALEONTOLOGY

Statoliths

Statoliths are the small, paired, aragonitic stones found in the fluid-filled cavities (or statocysts) within the cartilaginous heads of all modern and probably all fossil coleoids (Clarke and Fitch, 1975, 1979; Clarke, 1978, 1996; Clarke and Maddock, 1988a; Arkhipkin, 2003, 2005; Hart et al., 2013). Jurassic statoliths (Fig. 3) have yet to be described in any detail as there are only a few references to them in the literature (Clarke et al., 1980a, b; Clarke and Maddock, 1988b; Clarke, 2003; Hart et al., 2015). Otoliths, which are of similar appearance, are the aragonitic, stato-acoustic organs of bony (teleost) fish and have a better-known, though still limited, fossil record (e.g., Frost, 1924, 1926; Neth and Weiler, 1953; Rundle, 1967; Stinton and Torrens, 1968; Hart et al., 2009, Nolf, 2013). Some of these publications include illustrations of what are probably statoliths, though they were not identified as such at the time of publication (e.g., Frost, 1926, figs. 13, 14; Rundle, 1967, text-fig. 4).

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), onycites (squid arm and tentacle hooklets) 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). Using squid maintained in aquaria, it has been recognised that the growth increments in many modern statoliths are daily (Lipinski, 1993, 2001; Arkhipkin, 1988, 2004, 2005; Jackson, 1994, 2004). It was, however, Clarke (1978) who extended a biological approach to the study of fossil material (Clarke and Fitch, 1979; Clarke and Maddock, 1988a, b; Clarke et al., 1980a, b; Clarke, 2003).

Clarke (2003) suggested that statoliths could be used to interpret coleoid evolution and, in a seminal paper, described three ‘species’ of Jurassic statoliths (Jurassic sp. A, B, C; Clarke, 2003, p. 42, 43, figs. 14, 15). Two of these statolith ‘taxa’ (Jurassic sp. A and Jurassic sp. C) have been recorded in the material from Christian Malford (Fig. 3), while Clarke’s Jurassic sp. B is a Lower Jurassic taxon from the Lias Group sediments of Dorset (UK). Jurassic sp. A represents ~95% of the Christian Malford assemblage, being characterised by an elongate spur with a distinct rostrum at an angle to an often large crenulated lateral dome. Larger statoliths, which almost certainly come from older squid (or perhaps males), possess lateral domes with more pronounced crenulations and a rostrum at a greater angle to the lateral dome than their smaller counterparts. This change in statolith shape with growth was also illustrated by Clarke (2003, fig. 14). Statoliths were identified in the >500 µm, 500–250 µm and 250–125 µm size fractions and abundance was calculated by scaling-up the 500–250 µm and 250–125 µm size fraction abundance to per gram of bulk rock sediment.

The highest numbers of statoliths occur over a 3 m thickness of strata with the greatest abundance ~1 m below the Christian Malford Squid Bed (Fig. 4). The numbers recorded in this part of the Phaeinum Subchronozone are well above background levels in the rest of the Jurassic in the UK (Malcolm Clarke, personal communication, 2010) where several kg of sediment must be washed to recover <200 statoliths. Indeed, the average figure quoted by Clarke (2003, p. 43) is 0.1 statoliths per kg of sediment while the average in this core is 0.4 statoliths per gram (= 400 per kg). Clarke, in his work on Jurassic assemblages, received ready-processed material from two amateur fossil collectors, who prepared the samples in their kitchen, using rather ‘crude’ methods. Having broken the clay into fragments they dried it in the open, soaked it in water and ‘forced’ it through an 850 µm 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, Clarke records a significant number of statoliths with what he termed broken ends; which are rarely found in our residues. The breakage recorded by Clarke is, therefore, an artefact of processing and cannot be used in any paleoecological assessment of the environment of deposition.

In Core 10, the elevated levels of statolith abundance extend from 0.25 m down-core to 4.25 m down-core, with the highest levels of abundance at 2.70 m down-core. Otoliths show a similar pattern (Fig. 6), although their numbers are always below that of the statoliths: a reversal of the normal situation where otoliths invariably dominate (see Clarke, 2003, p. 43, 44; Hart et al., 2009).

When fractured and observed under the light microscope, statoliths are seen to be constructed of aragonite with a distinct fibrous appearance (Fig. 3 (F, G)). When sectioned, specimens show growth rings throughout, comparable to those observed in modern squid (Hurley et al., 1985; Arkhipkin, 2005; Miyahara et al., 2006).

Jurassic statoliths are distinct from those of modern squid, there being only three ‘morphospecies’ currently recognised (Clarke, 2003, Jurassic sp. A, B and C), identified only by their external morphology. Modern work (e.g., Arkhipkin and Bizikov, 1998, 2000; Arkhipkin, 2003, 2005) has shown that statoliths are helpful in the detection of movement within the water column (e.g., rolling, pitching, yawing, acceleration) and the recognition of gravity (e.g., way-up). Using their work as a guide, Clarke (2003) suggested that his Jurassic sp. A, with a distinct rostrum, may have been a bottom-dwelling species of squid while his Jurassic sp. C may be more indicative of a squid living in the middle of the water column: see, however, Price et al. (2015). Malcolm Clarke (pers. comm., 2010) has indicated that the Jurassic statoliths in his collection came from 12 sites across southern England and many of

these are being re-collected, with additional sites at Rodden Hive Point (see Hart et al., 2009) and Charmouth (Dorset).

Statoliths from a number of Core 10 samples have been measured and compared in a simple bivariate analysis (Fig. 5). While there is a clear scatter along a presumed growth curve, there is a concentration towards smaller individuals. If this was a reproductive assemblage, it might be expected that almost all the specimens would be of similar maturity and, therefore, size. The very large statoliths, which can sometimes be attributed to male individuals in modern assemblages, do not appear to be present in our data. It is known, however, from studies of modern faunas that reproductive behaviour within cephalopods, which involves courtship, copulation, fertilization and spawning, is incredibly variable (Hanlon and Messenger, 1996, p. 114–118, fig. 6.22; Arkhipkin, 2005), and that spawning ‘events’ can be marked by a change in the growth lines (Arkhipkin, 2005).

Hooks

The arms and tentacles of modern squid carry suckers that can vary in size, with some containing a chitinous ring (Roper et al., 1984; Hanlon and Messenger, 1996, fig. 4.3). Other teuthids 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). The species of *Belemnotheutis* illustrated by Wilby et al. (2008, fig. 1) from Christian Malford shows a number of hooks associated with the arms. They are closely comparable to the arm hooks illustrated by Donovan and Crane (1992, pl. 2, text-figs 2, 3), who described the type material of *Belemnotheutis antiquus* Pearce, 1847. The type specimen, BRSMG Cd21 (from City of Bristol Museum and Art Gallery) shows hooks from a number of arms, the phragmocone and ink sac. There is no mention of statoliths being recorded. Donovan and Crane (1992, text-fig. 3) show details of

the hooks and, in another illustration (Donovan and Crane, *op. cit.*, text-fig. 2) show a specimen with 100+ hooks visible. The hooks are distributed along the arms and show only a slight variation in morphology. While all of Pearce's specimens were from the 19th Century excavations in the Upper Callovian of Christian Malford, *B. antiquus* is also known from the Kellaways Rock of Wiltshire (Lower Callovian) and the Kimmeridge Clay Formation (Pseudomutabilis Zone or Gigas Zone) of Kimmeridge Bay, Dorset (Riegraf, 1987).

Fossil coleoid arm hooks have been known for over 150 years (Quenstedt, 1857) and described intermittently since that time (Naef, 1923; Kulicki and Szaniawski, 1972; Wind et al., 1977; Engeser, 1987; Engeser and Clarke, 1988). Engeser and Clarke (1988, fig. 2) illustrated hooks from a number of Jurassic taxa, including *Belemnotheutis antiquus*, "*Phragmoteuthis montefiorei*", etc., several of which were recorded from Southern England. They illustrated eight basic forms of hook and demonstrated their stratigraphical distribution. In the Christian Malford samples there are a large number of hooks, including a number illustrated by Engeser and Clarke (1988). Many of the hooks recovered have also been described by Kulicki and Szaniawski (1972), including long and thin forms described as '*Longuncus*' and forms with a distinct spur (described as '*Falcuncus*' or '*Paraglycerites*'): see Figure 3(H–O). There are forms that appear to be close to those illustrated by Engeser and Clarke (1988) and Donovan and Crane (1992) as attributable to *Belemnotheutis antiquus*, and others that we do not find in the literature available to us.

The abundance of hooks has not been calculated, as there is no indication of what such a 'count' would demonstrate. The number of hooks in a fossil coleoids is probably 100+ (Engeser and Clarke, 1988; Donovan and Crane, 1992) but, as each of our compacted mudstone samples probably represents <1kyr, it is uncertain as to what any meaningful

calculations would indicate in terms of paleobiology or paleoecology. It is clear, however, that the samples from Christian Malford contain large numbers of new ‘form taxa’ (*sensu* Stevens, 2010 and references therein) and require further, detailed investigation.

Otoliths

Otoliths (Lowenstein, 1971; Nolf, 2013) are the stato-acoustic organs of bony (teleost) fish and are better known than the statoliths, especially in Cenozoic sediments. Jurassic records are relatively sparse and there are few well-known taxa with which to compare new records (Frost, 1924, 1926; Neth and Weiler, 1953; Rundle 1967; Stinton and Torrens, 1968; Patterson et al., 1993; Patterson, 1998, 1999; Hart et al., 2009; Price et al., 2009; Nolf, 2013). In the samples from Core 10 a number of taxa have tentatively been identified (Fig. 3A–C) and the distribution of the otoliths in the core shown in Figure 6.

Ichthyoliths

The remains of Chondrichthyes, a class which includes the pelagic cartilaginous fish, sharks, rays and chimaeras that shed teeth throughout their lifetime, are identified in most samples of Core 10. *Sphenodus longidens* Agassiz, *Heterodontus* sp., *Orectoloboides pattersoni* Thies and *Hybodus obtusus* Agassiz have been identified as teeth shed from small species’ of shark (Martill and Hudson, 1991). Other, unidentified, taxa are also recorded.

Foraminifera

The benthic foraminifera recovered from Core 10 are dominated by calcareous taxa of the Suborder Rotaliina (Fig. 7) and a taxonomic list is provided as an Appendix. Calculation of the absolute abundance of benthic foraminifera (Fig. 8) identifies a sharp rise to peak values

of 43 benthic foraminifera/gram of bulk sample at 50–70 cm, followed by a return to more average values (<4 benthic foraminifera/gram) down-hole. There are minor variations in abundance, mostly the result of changes in the smaller size fractions. Abrupt peaks and more gradual rises in total absolute abundance of benthic foraminifera coincide with low values of species richness (measured by the Shannon-Weiner Function $H(S)$ based on information theory: see Shannon and Weaver (1963) and Smart (2002)), and high species dominance (Fig. 9). These patterns are most clearly seen in the minor ‘peak’ total absolute abundances at 160–180 cm, 270–280 cm and 420–430 cm, with the major total absolute abundance peak (50–70 cm) coincident with raised heterogeneity and lowered dominance. In contrast, sediments of low total absolute foraminiferal abundance at a depth of 300–390 cm coincide with high species richness and low species dominance, with peak heterogeneity and lowest dominance values identified at 340–350 cm.

Plotting the numbers of foraminifera by means of wall type (Fig. 10) shows that agglutinated taxa are, generally, very rare, being limited to only a few occurrences. This is quite typical of assemblages within the Oxford Clay Formation of the UK and northern France (Cordey, 1963a, b; Coleman, 1974, 1982; Gordon, 1965, 1967; Barnard et al., 1981; Shipp, 1989; Morris and Coleman, 1989; Henderson, 1997; Page et al., 2003; Oxford et al., 2000, 2004; Hart et al., 2007). Aragonite-walled taxa, dominated by floods of *Epistomina*, are found throughout Core 10 (Figs. 10, 11). *E. regularis* Terquem is the most common species, with *Reinholdella lutzei* Barnard, Cordey and Shipp only recorded in occasional samples. There is a flood occurrence of *E. stellcostata* Bielecka and Pozaryski near the top of the core and this species was found covering whole bedding surfaces (Fig. 12) in the trial pit. As this flood occurrence is 50–60 cm from the top of the core this would appear to place this level accurately within that excavation. Wilby et al. (2004, text-fig. 2) record the presence of

epistominids with their organic lining still preserved: another example of the special preservation of the site at Ashton Keynes within the Phaeinum Subchronozone. Epistominids, within Upper Jurassic and Lower Cretaceous strata (Oxford et al., 2000, 2004; Hart et al., 2009), often typify maximum flooding surfaces, partly due to the enhanced preservation of aragonite in the clay-rich sediments. In the Oxfordian succession of south Dorset, Oxford et al. (2000) showed how variations in epistominid numbers appear to indicate a within-sequence cyclicity which was tentatively interpreted as parasequences. A similar cyclicity is possibly seen in Core 10 (Fig. 11).

The overall assemblage is dominated by calcareous taxa of the Suborder Lagenina, especially the species *Lenticulina muensteri* Lamarck. This species is thought to include a wide range of morphology (degree of uncoiling, level of depression of sutures and the prominence of the umbilical boss), though much of this recorded variation probably represents a number of distinct taxa that have been included within this species for ‘convenience’ over the last 200 years.

There are quite significant numbers of adherent foraminifera in many of the samples, including *Bullopore* spp. (especially *B. rostrata* Quenstedt). These individuals are often attached to the semi-infaunal bivalve *Mesosacella morrisi* (Deshayes) but are seen on other taxa, otoliths, statoliths and – rarely – other foraminifera. Broken *Bullopore* were found to have an almost granular wall (often incorporating the coccolith *Ellipsagelosphaera keftalrempti*) rather than the perforate, calcareous wall described by Adams (1962). It is almost impossible to make a meaningful count of these adherent foraminifera as the shell fragments are often found in the larger size fractions and, if detached, one species can easily break across the inter-chamber stolons, creating 5+ ‘individuals’.

Pyrite steinkerns are found throughout the core, making counts of foraminifera by weight of sediment rather spurious. Some foraminifera, including epistominids, often contain a pyrite infilling of their chambers, even where the aragonitic test is still preserved. There were rare specimens that are thought to be *Conoglobigerina* sp., preserved as is often the case in the Oxford Clay Formation (Hart et al., 2007) as pyrite steinkerns. In the Callovian/Oxfordian boundary succession exposed at Redcliff, on the South Dorset coast east of Weymouth, specimens of *Conoglobigerina* sp., with the same mode of preservation, are known from the uppermost Callovian and lowermost Oxfordian. The presence of near-surface dwelling planktic foraminifera is suggestive of a water depth ~75–100 m as a minimum (Hart et al., 2012). This would support the interpretation of Hesselbo (2008) that the Upper Callovian was marked by a sea level highstand.

The assemblages of foraminifera are typical of the Oxford Clay Formation, with aragonitic taxa preserved in the dense, pyrite-rich, claystones. As a result, there is little evidence to suggest that this is not an *in-situ* assemblage. More important is the evidence that foraminifera occur in every residue (see Figs. 8–11), often in significant numbers. There is also no evidence to suggest that fine fraction material has been preferentially winnowed from any of the samples. There could not, therefore, have been lengthy periods of sea floor anoxia represented by the Core 10 sediments.

Deformed foraminifera (Fig. 9(P, Q)) are recorded in some samples forming <5% of the assemblage. This is quite unusual in geological samples and clearly represents some form of environmental stress. In modern estuarine and near-shore marine environments (Olugbode et al., 2005; Hart et al., 2015) metal pollution (often associated with Cu, Cd, Zn; Stubbles, 1999; Hart et al., 2015) is often thought to be responsible for growth restrictions, double

chambers and multiple apertures. In this geological setting it is almost impossible to speculate on a cause, other than point to a disturbance of the environment, though this was not severe enough to cause a wholesale change in, or loss of, the assemblage. Alve (1995), in a review of test deformities, indicates that high organic content in an environment is often the cause of malformation. The death of the squid represented by the abundance of statoliths could, perhaps, account for the high organic content of the sediments and this presence of deformed individuals.

DISCUSSION

The Phaeinum Subchronozone (Athleta Chronozone) of the Peterborough Member (Oxford Clay Formation) at Christian Malford represents an organic-rich, fine-grained mudstone succession that appears to have been deposited in relatively deep water within a marine area with restricted circulation (Hesselbo, 2008). The palaeogeography of the time (Hart et al., 2007, fig. 5) suggests a connection between the UK, France, Germany, Poland and parts of Western Russia (e.g., the Pechora Basin). Records of Oxfordian planktic foraminifera in Dorset (and rare specimens in the Christian Malford material) include the occurrence of *Compactogerina stellapolaris* (Grigelis) – an homeomorph of the modern, cool/cold water, *Neogloboquadrina pachyderma* (Ehrenberg) – which was first described from the Pechora Basin of northern Russia. The water depths postulated by Wilby et al. (2004) are, possibly, too shallow for the community represented by the benthic foraminifera and the presence of planktic foraminifera. There is little evidence of wave or current activity through much of the succession and the majority of the sediments were, therefore, deposited below storm wave base – which would place the water depth at about 75–100 m.

The numbers of statoliths encountered in the processed samples are exceptional, and well in excess of ‘normal’ mid-Upper Jurassic samples from southern England and northern France (Hart et al., 2009). In almost all of the samples previously studied the numbers of otoliths (which are never overly abundant) always exceed the number of statoliths. The presence of so many statoliths, together with squid hooklets, confirms the presence of squid throughout the studied succession at Christian Malford, as opposed to only at the level (or levels) that provided the famous occurrences of soft-bodied *Belemnnotheutis antiquus* Pearce and *Mastigophora brevipinnis* Owen.

The 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 *Belemnnotheutis antiquus*; occasional *Mastigophora brevipinnis*; and unique specimens of *Romaniteuthis* sp. and *Trachyteuthis* sp.. Crucially, the specimens of *Belemnnotheutis* (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, though broken, are reported as being oval in cross-section and about 1.5 x 0.5 mm 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 subject to recrystallization in the post-mortem rotting of the dead squid, although much of our material appears to be aragonite and, when sectioned, still showing (daily?) growth increments. As most of the material described by the early collectors (e.g., Pearce, 1841) and Wilby et al. (2004, 2008) is placed in *Belemnnotheutis antiquus*, it is probable that the most abundant statolith (Jurassic sp. A of Clarke, 2003) belongs to this species. Unfortunately, the broken statoliths in the specimen illustrated by Wilby et al. (2004) do not show sufficient detail to make a positive identification, despite Jurassic sp. A of Clarke (2003) having a

characteristic rostrum. The evidence from the hooklets in our samples supports this interpretation, but can only be confirmed if a soft-bodied specimen is found, or located in a museum collection, with an example of the statolith, Jurassic sp. A, unequivocally located within the soft tissue of the head. The animal that hosted Jurassic sp. C is presently unknown, other than it would be expected to be much rarer than *B. antiquus*.

The relative rarity of guard-carrying belemnites in the same stratigraphical interval at Christian Malford suggests that this group did not produce the recovered numbers of statoliths, as the extremely resistant calcified guards would also have been preserved. Concentrations of belemnites (especially elsewhere in the Jurassic) may, however, had similar taphonomic origins to the concentration of coleoids at Christian Malford. The former have frequently been described as belemnite battlefields (Doyle and MacDonald, 1993) and ascribed to a number of formative mechanisms, including:

- (1) predation;
- (2) condensation;
- (3) re-sedimentation;
- (4) post-spawning mass mortality; or
- (5) catastrophic mass mortality.

For a variety of reasons, Wilby et al. (2004) rejected causal mechanisms (1) – (3) and the micropaleontological evidence would agree with that conclusion. Wilby et al. (2004) suggested that (4) should be a monospecific, high density, accumulation of similar-aged adults. A catastrophic mass mortality (5), on the other hand, might be expected to affect a large size range of individuals, representing different levels of maturity.

Brongersma-Sanders (1957) indicated that likely causes of catastrophic mass mortalities could be (in a changed order):

(1) changes in temperature;

(2) changes in salinity;

(3) algal blooms;

(4) volcanism; or

(5) anoxia.

These various mechanisms were discussed thoroughly by Wilby et al. (2004), with anoxia selected as the favoured mechanism. The micropaleontological data would certainly suggest that temperature and/or salinity change were unlikely as all the samples contained a similar assemblage of benthic foraminifera, ostracods, statoliths, otoliths and ichthyoliths. Algal blooms or the repeated occurrence of 'red tides' (the toxic blooms of dinoflagellates cysts) are known to have a quite devastating impact on organisms unfortunate enough to be affected. Such events can last from a few hours to days or weeks and it would be difficult to suggest a continued, or repeated, red tide event lasting many kyrs. There is no confirmed evidence of 'red tides' as samples processed from the interval in question contained a normal, diverse, Callovian assemblage of dinocysts (Jim Riding, *pers. comm.*, 2011). Red tides are normally caused by the over-abundance of a single taxon and the presence of a diverse flora suggests that this may not have been the cause of the mass mortalities. Volcanism can be ruled out as a cause as there are no records of volcanic ashes in the succession, nor the clay minerals derived from the decomposition of volcanic minerals. Work in the Caribbean Sea on the impacts of volcanism on both planktic and benthic communities have been shown to

generate distinct changes in the assemblage (Wall-Palmer et al., 2011), including complete loss of the benthic foraminifera. Nothing comparable is recorded in the Core 10 succession.

The occurrence of abundant, though low diversity, benthic assemblages, including bivalves, gastropods and foraminifera, points to a generally oxic, though occasionally stressed, environment. The preservation of the foraminifera is exceptionally good, with no sign of pitting or post-mortem dissolution. Some of the epistominids still retain their original organic linings (Wilby et al., 2004, text-fig. 2). The significant (though low) proportion of deformed foraminifera in the assemblages appears to confirm that the environment was, at times, less than optimal but still able to support a relatively species-rich and abundant population. In low-oxygen environments, agglutinated foraminifera may often become more abundant, as compared to calcareous taxa, but this is not the case in this succession. The abundance of *Epistomina* spp. in the succession is, however, reliant on the favourable preservation of aragonite (Oxford et al., 2000) in the clays of the Phaeinum Subchronozone and may also be indicative of a sea level highstand at this time (Hesselbo, 2008). A sea level highstand would provide a suitable environment for the deposition of fine-grained mudstones and the quiet-water conditions in which to deposit the intact soft-bodied fossils. While the presence of benthic foraminifera indicates a generally oxygenated environment, the preservation of tissue, ink sacs, etc., suggests the occasional presence of short-lived sea floor dysoxic or anoxic conditions. The presence of so many statoliths is indicative of mass mortality, which could explain the intermittent lack of oxygen. The conditions that created these mass mortalities extended over the time represented by ~3.0 m of fine-grained strata that would have been compacted by up to 80% (Oxford et al., 2000) from the original sediment thickness. As indicated above, this level of compaction and the slow rate of mudstone sedimentation means that each micropaleontological sample may represent < 1 kyr

and could, therefore, record a number of subtle environmental changes. Issues relating to the temporal resolution of samples has been discussed by Berger and Heath (1968) and Ruddiman (2014, p. 63–64).

It must also be assumed that squid, in such numbers, would tend to avoid anoxic waters and not become trapped in such an environment (assuming that they were still alive at the time), although Clarke (2003) indicates that the morphology of Jurassic sp. A may be indicative of a bottom-dwelling species. Current transport of dead squid is also unlikely as there is little sedimentological evidence for currents, excepting some possible, limited winnowing leading to a concentration of shelly material on some bedding surfaces. Crucially, however, the exceptional preservation of the coleoid fauna seen in the Christian Malford succession indicates minimal, if any, post-mortem disturbance. Significant winnowing of the statoliths on the sea floor is, however, is unlikely as the range of sizes seen in the statoliths, otoliths and foraminifera does not suggest preferential removal of the smaller size fractions.

The annual spawning of female squids massively enlarges their ovaries and this breaks down the body wall leaving spent individuals to die (Hanlon and Messenger, 1996). Such a concentration of squids depositing their ‘egg mops’ (Hanlon and Messenger, 1996, chapter 6) could have created the numbers of statoliths and hooklets and, while decomposing on the sea floor, create the anoxic water conditions that facilitated the soft-bodied preservation of a few of the individuals. Masses of dead squid (or the eggs) may have attracted the numbers of fish recorded by the relative abundance of otoliths and shark’s teeth in the same sediments. Squid returning to the same general area year-on-year could also explain the stratigraphical range of the unusual concentrations. Nevertheless, any anoxia must have been the exception, rather than the norm, as this would have had a negative effect on

breeding squid populations by killing the eggs released into the environment. This may explain why most of the succession appears to yield only statoliths and hooklets and only one level in the newly sampled sequence appears to yield soft-body preservation, due to a short-lived – perhaps one season only – anoxic event.

The recorded presence of ‘paired’ squid (Wilby et al., 2004, pl. 2(4)) was interpreted as cannibalism, rather than a reproductive position (which only lasts for seconds). Copulation would be unlikely in an anoxic environment, while squid feasting on the dead squid that resulted from egg-laying might be regarded as normal. It could also account for the variety of sizes present in the environment and the range of statolith sizes recorded. The numbers of statoliths recorded far out-number the soft-bodied squid that are preserved and indicate that the squid macrofossils represent only a snap-shot of the total population.

Clarke (2003, p. 43, 44), who was an acclaimed authority on squid biology, indicated that – in his work – he may have underestimated the numbers of statoliths present in his samples. In most of the Jurassic samples studied by MBH, this is probably not the case, except for the samples from Christian Malford. In this location the excessive numbers of statoliths far exceed the numbers of otoliths and this was the main criteria that Clarke would have used to identify a spawning area.

SUMMARY

The abundance of fossil statoliths in the clays of the Phaeinum Subchronozone of the Peterborough Member (Oxford Clay Formation) may record the existence of a squid breeding area which existed for many 10s of thousands of years during the Late Callovian (Middle Jurassic). This may be the first record of such a phenomenon in the fossil record and is especially significant as it is based on one of the first comprehensive records of the existence

of Callovian statoliths in association with the potential host animals. While other possible scenarios have, and are being considered, the spawning model seems to conform to a known squid life-style. This, together with the occurrence of the soft-bodied fossils and exceptional preservation (aragonite) seen in the macrofossil assemblage, confirms the importance of the Christian Malford Lagerstätte.

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During the work for this paper the authors were saddened to learn of the death (in 2013) of Malcolm Clarke. It had been hoped that it may have been possible to discuss our paleobiological interpretations with him when he visited family near Plymouth. Mrs Dorothy Clarke has kindly provided MBH with all his computer files relating to fossil statoliths, including further unpublished information on Jurassic statoliths that has guided some of our interpretations.

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753

754 **Appendix: Taxonomic notes on Foraminifera**

755 The species mentioned in the text are well known from Jurassic strata in the UK and a full
 756 taxonomy is not presented. The species are listed in alphabetical (not taxonomic) order.

757 *Bullopore rostrata* Quenstedt, 1857, p. 580, pl. 73, fig. 28.

- 758 *Citharina flabellata* (Gümbel, 1862) = *Marginulina flabellata* Gümbel, 1862, p. 223, pl. 3,
759 fig. 24.
- 760 *Compactogerina stellapolaris* (Grigelis, 1977) = *Globuligerina stellapolaris* Grigelis, 1977,
761 p.
- 762 *Dentalina pseudocommunis* Franke, 1936, p. 30, pl. 2, fig. 20.
- 763 *Eoguttulina liassica* (Strickland, 1846) = *Polymorphina liassica* Strickland, 1846, p. 31, text-
764 fig. b.
- 765 *Epistomina regularis* Terquem, 1883, p. 379, pl. 44, figs 1-3.
- 766 *Epistomina stellicostata* Bielecka and Pozaryski, 1954, p. 71, pl. 12, fig. 60a-c.
- 767 *Frondicularia franconica* Gümbel, 1862, p. 219, pl. 3, fig. 13a-c.
- 768 *Frondicularia irregularis* Terquem, 1870, p. 125, pl. 4, fig. 12a, b.
- 769 *Lenticulina muensteri* (Roemer, 1839) = *Robulina muensteri* Roemer, 1839, p. 48, pl. 20,
770 fig. 29.
- 771 *Neogloboquadrina pachyderma* (Ehrenberg, 1861) = *Globigerina pachyderma* (Ehrenberg) =
772 *Aristerospina pachyderma* Ehrenberg, 1861, p. 276–277, 303, but figured by
773 Ehrenberg, 1873 (for 1872), pl. 1, fig. 4.
- 774 *Nodosaria hortensis* Terquem, 1866, p. 476, pl. 19, fig. 13.
- 775 *Reinholdella lutzei* Barnard, Shipp, and Cordey, 1981, p. 432, pl. 4, figs 3, 7.
- 776 *Verneuilinoides tryphera* Loeblich and Tappan, 1950, p. 42, pl. 11, fig. 16a, b.

777

778 FIGURE CAPTIONS

779 **FIGURE 1** – Locality map for Christian Malford, Wiltshire, UK. The excavation site
780 and coring locations are immediately to the south of the railway line, adjacent to
781 which were the 19th century excavations that discovered the original fossil
782 material.

783 **FIGURE 2** – Core 10: sediment log, lithostratigraphy and biostratigraphy.

784 **FIGURE 3** – Illustration of otoliths (A–C), statoliths (D–G) and hooks (H–O) from
785 Core 10: A) *Cleidogonia antiqua* Stinton & Torrens (1968), inner face of left
786 sacculith (scale bar 100 µm); B) *C. antiqua*, inner face of right sacculith (scale
787 bar 100 µm); C) *Pholidophorus prae-elops* Stinton and Torrens (1968), right
788 sacculith (scale bar 200 µm); D) Jurassic sp. C (Clarke, 2003) showing the
789 characteristic ‘vein-like’ structures and the smooth outline that characterize this
790 taxon (scale bar 500 µm); E) Jurassic sp. A (Clarke, 2003), anterior view of
791 large left statolith showing distinct crenulations of margin of the dome (scale bar
792 200 µm); F) Abraded and broken statolith (missing rostrum) showing aragonite
793 crystals (scale bar 100 µm); G) Broken statolith showing radiating crystal
794 structure (scale bar 100 µm); all the following hooks are from Core 10, Section
795 7, 60–80 cm, H) hook, *Paraglycerites*-type (scale bar 200 µm); I) hook, *Arites*-
796 type (scale bar 200 µm); J) hook, *Paraglycerites*-type (scale bar 200 µm); K)
797 hook, *Paraglycerites*-type (scale bar 200 µm); L) hook, *Longuncus*-type (scale
798 bar 200 µm); M) hook, *Paraglycerites*-type (scale bar 200 µm); N) hook,

799 *Deinuncus*-type (scale bar 200 μm); O) hook, *Deinuncus*-type (scale bar 500
800 μm).

801 **FIGURE 4** – Abundance of statoliths (500–250 μm and 250–125 μm size fractions)
802 and abundance within the 500–250 μm and 250–125 μm size fractions, relative
803 to background sediment in Core 10. Numbers (1 – 4) denote samples selected
804 for measuring statolith diameter (shown in Fig. 5) and letters (A, B) denote
805 samples from which statoliths were thin-sectioned to confirm presence of
806 internal (daily?) growth lines.

807 **FIGURE 5** – Bivariate analysis of the statoliths (maximum length plotted against
808 maximum width) from the four samples indicated in Figure 4. There is a strong
809 positive correlation between statolith length and height.

810 **FIGURE 6** – Total abundance of otoliths (500–250 μm and 250–125 μm size
811 fractions) and abundance within the 500–250 μm and 250–125 μm size
812 fractions, relative to background sediment in Core 10.

813 **FIGURE 7** – Illustration of some of the foraminifera recovered in the samples from
814 Core 10: A) *Verneuilinoides tryphera* (scale bar 50 μm); B) *Verneuilinoides* sp.
815 2 Morris and Coleman, 1989 (scale bar 50 μm); C) *Trochammina* sp. (scale bar
816 100 μm); D) *Oolina* sp. (scale bar 20 μm); E) *Oolina* sp. (scale bar 100 μm); F)
817 *Eoguttulina liassica* (scale bar 100 μm); G) *Frondicularia irregularis* (scale bar
818 100 μm); H) *Dentalina pseudocommunis* (scale bar 100 μm); I) *Citharina*
819 *flabellata* (scale bar 100 μm); J) *Nodosaria hortensis* (scale bar 100 μm); K)
820 *Frondicularia franconica* (scale bar 100 μm); L) *Lenticulina muensteri* (scale bar
821 100 μm); M) *L. muensteri* with no umbilical boss (scale bar 100 μm); N) *L.*

822 *muensteri* showing uncoiling (scale bar 100 µm); O) *Lenticulina* sp., showing
 823 distinct uncoiling and thickened sutures (scale bar 100 µm); P) *L. muensteri*,
 824 showing test deformation (scale bar 100 µm); Q) *Lenticulina* sp., showing
 825 chamber deformation and, what appears to be an additional chamber (scale bar
 826 100 µm); R, S) *Epistomina regularis* (scale bar 100 µm); T) *Epistomina*
 827 *stellicostata* Bielecka and Pozaryski (scale bar 100 µm); U) *Reinholdella lutzei*
 828 (scale bar 100 µm); V?, W) *Conoglobigerina* sp., an example of a pyritic
 829 steinkern of a planktic foraminiferid (scale bar 50 µm); X) *Bullopora* sp.
 830 adherent on shell fragment (scale bar 200 µm).

831 **FIGURE 8** – Absolute abundance of foraminifera recorded in samples from core 10.

832 **FIGURE 9** – Heterogeneity of benthic foraminifera, H(S), and percentage frequency
 833 of dominant species (Dominance%).

834 **FIGURE 10** – Distribution of foraminifera showing relative abundance of the
 835 agglutinated, aragonitic and calcitic wall types.

836 **FIGURE 11** – Distribution of aragonitic foraminifera showing the ‘flood’ of *Epistomina*
 837 *stellicostata* at 60 cm downhole and the potential cyclicity in the distribution of
 838 *Epistomina regularis*.

839 **FIGURE 12** – Bedding surface from the excavation covered in *Epistomina*
 840 *stellicostata*. Field of view 2.5 cm. Note that the range of sizes from large
 841 (adults) to small (juveniles) indicates that this was probably a living assemblage
 842 rather than one that has been transported.