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

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11

12 RRH – *JURASSIC STATOLITHS FROM CHRISTIAN MALFORD*

13 LLH – *HART ET AL.*

14 Keywords: Statoliths, otoliths, foraminifera, Callovian, lagerstätte

15

16 **ABSTRACT**

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

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

33

34

INTRODUCTION

35 In the 1840s, during the construction of the Great Western Railway west of Swindon
36 (Wiltshire, U.K.) a significant number of exceptionally preserved coleoids (belemnites and
37 squid-like cephalopods) were found (Pearce, 1841; Owen, 1844; Mantell, 1848). These
38 famous specimens of *Belemnotherutis* and *Mastigophora* have been re-described by Donovan
39 (1983), Page and Doyle (1991) and Donovan and Crane (1992). The other macrofossils from
40 the assemblage, including a number of fish, have also been described (e.g., Allison, 1988;
41 Martill and Hudson, 1991; Tang, 2002; Wilby et al., 2004) in the context of a fossil
42 lagerstätte under the name of the ‘Christian Malford Squid Bed’. Most of these specimens,
43 appear to come from the Phaeinum Subchronozone (Athleta Chronozone, Upper Callovian,
44 Middle Jurassic) of the Oxford Clay Formation, and many contain soft tissue, muscle fibres
45 and the content of their ink sacs (Wilby et al., 2004).

46 The historical finds of exceptionally preserved fossils at Christian Malford (near
47 Swindon, Wiltshire, U.K.) and the nearby location of Ashton Keynes (Wilby et al., 2004,
48 2008), led to the development of this project, which was designed to collect more specimens
49 of the coleoids and promote a multi-disciplinary analysis of the depositional environment. In

50 2006 a programme of exploratory drilling was undertaken along a 4 km transect adjacent to
51 the railway line immediately south of Christian Malford (Fig. 1) in order to provide some
52 stratigraphical control. In October 2007, an area of 32m² was excavated to a depth of ~ 5 m,
53 yielding ~240 tonnes of fossil bearing mudstones belonging to the upper part of the
54 Peterborough Member of the Oxford Clay Formation. Ammonites were common throughout
55 the material excavated and were dominated by abundant *Kosmoceras* (*Lobokosmoceras*) ex
56 grp *phaeinum* (S. Buckman) which places the bulk of the material within the Phaeinum
57 Subchronozone (Athleta Chronozone, Upper Callovian). Only a few *Kosmoceras*
58 (*Zugokosmoceras*) ex grp *grossouvrei* Douvillé were recovered, indicating the top of the
59 preceding Grossouvri Subchronozone of the Coronatum Chronozone (Middle Callovian). A
60 brief report on the macrofossils recorded from the excavation is provided by Wilby et al.
61 (2008) and representative figures of *Kosmoceras phaeinum* from Christian Malford are
62 provided by Page (1991).

63

MATERIALS AND METHODS

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

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

76 As this excavation became water-filled very quickly, it was impossible to collect a
77 suite of *in-situ* samples appropriate for a micropaleontological investigation. From the suite
78 of cores drilled in 2006, Core 10 was selected for analysis as it was both one of the longest
79 and had already been studied for its macrofossil content (Fig. 2). This core was ~5 m in
80 length and split into 6 sections, each of which are 62–108 cm in length. Forty-one samples
81 were collected from the measured core at regular intervals. Particular note was taken of shell
82 debris, macrofossils, sedimentary structures and the presence of any dark, potentially organic-
83 rich, sediments. The uppermost 10 cm of soil/clay within Core 10 was omitted from the
84 processing as the sediments were probably contaminated by surface processes. Following
85 removal of the ‘smeared’ outer surface of the core, samples were carefully disaggregated to
86 gravel-sized pieces and weighted in a dry condition. These dried samples were processed
87 using the white spirit method of Brasier (1980). After being soaked in white spirit for ~ 4
88 hours, decanted, and then immersed in deionised water for 24 hours, samples were washed on
89 a 63µm sieve. The processed residues were then dried in a cool oven (40°C) for ~12 hours
90 before dry sieving into the >500µm, 500–250µm, 250–125µm and 125–63µm size fractions.
91 These fractions were all weighed and the data tabulated for subsequent analysis. While
92 foraminifera were picked to a statistically valid number (usually 250–300 as a minimum from
93 each size fraction), all the statoliths and otoliths were picked as there is no accepted
94 methodology for dealing with these microfossils. While all the foraminifera, statoliths and
95 otoliths were recorded, those in the >500 µm size fraction were studied and identified but
96 were omitted from the absolute and/or relative abundance counts. This is because that size

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

108 All of the processed samples from Core10 yielded statoliths, otoliths, onychites
109 (cephalopod arm and tentacle hooks), foraminifera and ostracods. While the foraminifera and
110 ostracods are typical of Callovian strata elsewhere in the UK and northern France (Cordey,
111 1963a, b; Coleman, 1974, 1982; Gordon, 1965; Barnard et al., 1981; Shipp, 1989; Morris and
112 Coleman, 1989; Henderson, 1997; Page et al., 2003; Oxford et al., 2000, 2004; Wilkinson
113 and Whatley, 2009), the numbers of statoliths recovered are exceptional. They, and the
114 hooks, confirm the presence of large numbers of squid-like cephalopods throughout the
115 succession and, coupled with the famous, soft-bodied fossils from Christian Malford and
116 Ashton Keynes, make this an exceptionally interesting paleoenvironment.

117 MICROPALAEONTOLOGY

118 Statoliths

119 Statoliths are the small, paired, aragonitic stones found in the fluid-filled cavities (or
120 statocysts) within the cartilaginous heads of all modern and probably all fossil coleoids
121 (Clarke and Fitch, 1975, 1979; Clarke, 1978, 1996; Clarke and Maddock, 1988a; Arkhipkin,
122 2003, 2005; Hart et al., 2013). Jurassic statoliths (Fig. 3) have yet to be described in any
123 detail as there are only a few references to them in the literature (Clarke et al., 1980a, b;
124 Clarke and Maddock, 1988b; Clarke, 2003; Hart et al., 2015). Otoliths, which are of similar
125 appearance, are the aragonitic, stato-acoustic organs of bony (teleost) fish and have a better-
126 known, though still limited, fossil record (e.g., Frost, 1924, 1926; Neth and Weiler, 1953;
127 Rundle, 1967; Stinton and Torrens, 1968; Hart et al., 2009, Nolf, 2013). Some of these
128 publications include illustrations of what are probably statoliths, though they were not
129 identified as such at the time of publication (e.g., Frost, 1926, figs. 13, 14; Rundle, 1967,
130 text-fig. 4).

131 Modern squid have few easily preservable components. These include the crystalline
132 lens of the eye (Clarke, 1993), the gladii or chitinous backbone (La Roe, 1971), mandibles or
133 chitinous jaws (Clarke, 1965), onycites (squid arm and tentacle hooklets) and statoliths
134 (Clarke, 1966). As statoliths are calcareous (aragonite), and grow in size during ontogeny,
135 they have the potential to record the development and age of the parent animal (Clarke, 1966;
136 Jackson, 1994; Arkhipkin, 2005). Using squid maintained in aquaria, it has been recognised
137 that the growth increments in many modern statoliths are daily (Lipinski, 1993, 2001;
138 Arkhipkin, 1988, 2004, 2005; Jackson, 1994, 2004). It was, however, Clarke (1978) who
139 extended a biological approach to the study of fossil material (Clarke and Fitch, 1979; Clarke
140 and Maddock, 1988a, b; Clarke et al., 1980a, b; Clarke, 2003).

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

154 The highest numbers of statoliths occur over a 3 m thickness of strata with the
155 greatest abundance ~1 m below the Christian Malford Squid Bed (Fig. 4). The numbers
156 recorded in this part of the Phaeinum Subchronozone are well above background levels in the
157 rest of the Jurassic in the UK (Malcolm Clarke, personal communication, 2010) where
158 several kg of sediment must be washed to recover <200 statoliths. Indeed, the average figure
159 quoted by Clarke (2003, p. 43) is 0.1 statoliths per kg of sediment while the average in this
160 core is 0.4 statoliths per gram (= 400 per kg). Clarke, in his work on Jurassic assemblages,
161 received ready-processed material from two amateur fossil collectors, who prepared the
162 samples in their kitchen, using rather ‘crude’ methods. Having broken the clay into fragments
163 they dried it in the open, soaked it in water and ‘forced’ it through an 850 µm sieve (thereby
164 failing to collect smaller specimens). The residue was then sieved in a ‘nylon stocking’ with

165 the fine material being decanted. In some of his unpublished data, Clarke records a significant
166 number of statoliths with what he termed broken ends; which are rarely found in our residues.
167 The breakage recorded by Clarke is, therefore, an artefact of processing and cannot be used in
168 any paleoecological assessment of the environment of deposition.

169 In Core 10, the elevated levels of statolith abundance extend from 0.25 m down-core
170 to 4.25 m down-core, with the highest levels of abundance at 2.70 m down-core. Otoliths
171 show a similar pattern (Fig. 6), although their numbers are always below that of the statoliths:
172 a reversal of the normal situation where otoliths invariably dominate (see Clarke, 2003, p. 43,
173 44; Hart et al., 2009).

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

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

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

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

200 Hooks

201 The arms and tentacles of modern squid carry suckers that can vary in size, with some
202 containing a chitinous ring (Roper et al., 1984; Hanlon and Messenger, 1996, fig. 4.3). Other
203 teuthids are also known to bear hooks on the end of their club-like tentacles (Roper et al.,
204 1984; Hanlon and Messenger, 1996, fig. 4.3c). The species of *Belemnotheutis* illustrated by
205 Wilby et al. (2008, fig. 1) from Christian Malford shows a number of hooks associated with
206 the arms. They are closely comparable to the arm hooks illustrated by Donovan and Crane
207 (1992, pl. 2, text-figs 2, 3), who described the type material of *Belemnotheutis antiquus*
208 Pearce, 1847. The type specimen, BRSMG Cd21 (from City of Bristol Museum and Art
209 Gallery) shows hooks from a number of arms, the phragmocone and ink sac. There is no
210 mention of statoliths being recorded. Donovan and Crane (1992, text-fig. 3) show details of

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

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

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

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

237 Otoliths

238 Otoliths (Lowenstein, 1971; Nolf, 2013) are the stato-acoustic organs of bony
239 (teleost) fish and are better known than the statoliths, especially in Cenozoic sediments.
240 Jurassic records are relatively sparse and there are few well-known taxa with which to
241 compare new records (Frost, 1924, 1926; Neth and Weiler, 1953; Rundle 1967; Stinton and
242 Torrens, 1968; Patterson et al., 1993; Patterson, 1998, 1999; Hart et al., 2009; Price et al.,
243 2009; Nolf, 2013). In the samples from Core 10 a number of taxa have tentatively been
244 identified (Fig. 3A–C) and the distribution of the otoliths in the core shown in Figure 6.

245 Ichthyoliths

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

251

252 Foraminifera

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

256 of 43 benthic foraminifera/gram of bulk sample at 50–70 cm, followed by a return to more
257 average values (<4 benthic foraminifera/gram) down-hole. There are minor variations in
258 abundance, mostly the result of changes in the smaller size fractions. Abrupt peaks and more
259 gradual rises in total absolute abundance of benthic foraminifera coincide with low values of
260 species richness (measured by the Shannon-Weiner Function $H(S)$ based on information
261 theory: see Shannon and Weaver (1963) and Smart (2002)), and high species dominance (Fig.
262 9). These patterns are most clearly seen in the minor ‘peak’ total absolute abundances at 160–
263 180 cm, 270–280 cm and 420–430 cm, with the major total absolute abundance peak (50–70
264 cm) coincident with raised heterogeneity and lowered dominance. In contrast, sediments of
265 low total absolute foraminiferal abundance at a depth of 300–390 cm coincide with high
266 species richness and low species dominance, with peak heterogeneity and lowest dominance
267 values identified at 340–350 cm.

268 Plotting the numbers of foraminifera by means of wall type (Fig. 10) shows that
269 agglutinated taxa are, generally, very rare, being limited to only a few occurrences. This is
270 quite typical of assemblages within the Oxford Clay Formation of the UK and northern
271 France (Cordey, 1963a, b; Coleman, 1974, 1982; Gordon, 1965, 1967; Barnard et al., 1981;
272 Shipp, 1989; Morris and Coleman, 1989; Henderson, 1997; Page et al., 2003; Oxford et al.,
273 2000, 2004; Hart et al., 2007). Aragonite-walled taxa, dominated by floods of *Epistomina*, are
274 found throughout Core 10 (Figs. 10, 11). *E. regularis* Terquem is the most common species,
275 with *Reinholdella lutzei* Barnard, Cordey and Shipp only recorded in occasional samples.
276 There is a flood occurrence of *E. stellcostata* Bielecka and Pozaryski near the top of the core
277 and this species was found covering whole bedding surfaces (Fig. 12) in the trial pit. As this
278 flood occurrence is 50–60 cm from the top of the core this would appear to place this level
279 accurately within that excavation. Wilby et al. (2004, text-fig. 2) record the presence of

280 epistominids with their organic lining still preserved: another example of the special
281 preservation of the site at Ashton Keynes within the Phaeinum Subchronozone. Epistominids,
282 within Upper Jurassic and Lower Cretaceous strata (Oxford et al., 2000, 2004; Hart et al.,
283 2009), often typify maximum flooding surfaces, partly due to the enhanced preservation of
284 aragonite in the clay-rich sediments. In the Oxfordian succession of south Dorset, Oxford et
285 al. (2000) showed how variations in epistominid numbers appear to indicate a within-
286 sequence cyclicity which was tentatively interpreted as parasequences. A similar cyclicity is
287 possibly seen in Core 10 (Fig. 11).

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

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

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

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

321 Deformed foraminifera (Fig. 9(P, Q)) are recorded in some samples forming <5% of
322 the assemblage. This is quite unusual in geological samples and clearly represents some form
323 of environmental stress. In modern estuarine and near-shore marine environments (Olugbode
324 et al., 2005; Hart et al., 2015) metal pollution (often associated with Cu, Cd, Zn; Stubbles,
325 1999; Hart et al., 2015) is often thought to be responsible for growth restrictions, double

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

333 DISCUSSION

334 The Phaeinum Subchronozone (Athleta Chronozone) of the Peterborough Member (Oxford
335 Clay Formation) at Christian Malford represents an organic-rich, fine-grained mudstone
336 succession that appears to have been deposited in relatively deep water within a marine area
337 with restricted circulation (Hesselbo, 2008). The palaeogeography of the time (Hart et al.,
338 2007, fig. 5) suggests a connection between the UK, France, Germany, Poland and parts of
339 Western Russia (e.g., the Pechora Basin). Records of Oxfordian planktic foraminifera in
340 Dorset (and rare specimens in the Christian Malford material) include the occurrence of
341 *Compactogerina stellapolaris* (Grigelis) – an homeomorph of the modern, cool/cold water,
342 *Neogloboquadrina pachyderma* (Ehrenberg) – which was first described from the Pechora
343 Basin of northern Russia. The water depths postulated by Wilby et al. (2004) are, possibly,
344 too shallow for the community represented by the benthic foraminifera and the presence of
345 planktic foraminifera. There is little evidence of wave or current activity through much of the
346 succession and the majority of the sediments were, therefore, deposited below storm wave
347 base – which would place the water depth at about 75–100 m.

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

356 The statoliths should, it is suggested, reflect the relative abundance of the two species
357 of host animals. Page and Doyle (1991) reported four taxa of coleoid from the Oxford Clay
358 Formation of Christian Malford: common *Belemnnotheutis antiquus*; occasional *Mastigophora*
359 *brevipinnis*; and unique specimens of *Romaniteuthis* sp. and *Trachyteuthis* sp.. Crucially, the
360 specimens of *Belemnnotheutis* (LEIUG 121817(2)) from Rixon Gate (Ashton Keynes) figured
361 by Wilby et al. (2004, pl. 1, figs. 1, 2 and pl. 2, fig. 3) appear to show a pair of statoliths
362 within the head area. The statoliths, though broken, are reported as being oval in cross-
363 section and about 1.5 x 0.5 mm in size. They are described as having a brown core and a thin,
364 white, outer layer. Kear et al. (1995) claim that the aragonitic statoliths would have been
365 subject to recrystallization in the post-mortem rotting of the dead squid, although much of our
366 material appears to be aragonite and, when sectioned, still showing (daily?) growth
367 increments. As most of the material described by the early collectors (e.g., Pearce, 1841) and
368 Wilby et al. (2004, 2008) is placed in *Belemnnotheutis antiquus*, it is probable that the most
369 abundant statolith (Jurassic sp. A of Clarke, 2003) belongs to this species. Unfortunately, the
370 broken statoliths in the specimen illustrated by Wilby et al. (2004) do not show sufficient
371 detail to make a positive identification, despite Jurassic sp. A of Clarke (2003) having a

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

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

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

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

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

396 (1) changes in temperature;

397 (2) changes in salinity;

398 (3) algal blooms;

399 (4) volcanism; or

400 (5) anoxia.

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

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

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

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

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

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

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

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

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

480

SUMMARY

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

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

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505 paleobiological interpretations with him when he visited family near Plymouth. Mrs Dorothy
506 Clarke has kindly provided MBH with all his computer files relating to fossil statoliths,
507 including further unpublished information on Jurassic statoliths that has guided some of our
508 interpretations.

509

510

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

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- 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) *Bullopore* 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.