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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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12   RRH – *JURASSIC STATOLITHS FROM CHRISTIAN MALFORD*

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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 *Belemnotheutis* 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 $32m^2$ 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 preceeding 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 belemnoteuthid 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 *Meleagrinella*

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 stellicostata* 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 (40ºC) 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   MICROPALEONTOLOGY

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; Arkhipin,

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; Arkhipin, 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   Arkhipin, 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   (Pseuomutabilis 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. stellicostata* 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 *Bullopora* spp. (especially *B. rostrata* Quenstedt). These individuals are often

296 attached to the semi-infaunal bivalve *Mesosacella morrisi* (Deshayes) but are seen on other

297 taxa, otoliths, statoliths and – rarely – other foraminifera. Broken *Bullopora* 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 *Belemnotheutis 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 *Belemnotheutis antiquus*; occasional *Mastigophora*

359   *brevipinnis*; and unique specimens of *Romaniteuthis* sp. and *Trachyteuthis* sp.. Crucially, the

360   specimens of *Belemnotheutis* (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 *Belemnotheutis 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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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   *Bullopora 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 100µm): 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.