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1   **The Strawberry Bank Lagerstätte reveals insights into Early Jurassic life**

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8

9   **Abstract:** The Strawberry Bank Lagerstätte provides a rich insight into Early Jurassic marine

10   vertebrate life, revealing exquisite anatomical detail of marine reptiles and large pachycormid

11   fishes thanks to exceptional preservation, and especially the uncrushed, three-dimensional

12   nature of the fossils. The site documents a fauna of Early Jurassic nektonic marine animals

13   (five species of fishes, one species of marine crocodilian, two species of ichthyosaurs,

14   cephalopods, and crustaceans), but also over 20 species of insects. Unlike other fossil sites of

15   similar age, the three-dimensional preservation at Strawberry Bank provides unique evidence

16   on palatal and braincase structures in the fishes and reptiles. The age of the site is important,

17   documenting a marine ecosystem during recovery from the end-Triassic mass extinction, but

18   also exactly coincident with the height of the Toarcian Oceanic Anoxic Event, a further time

19   of turmoil in evolution.

20

A long-forgotten site in Somerset, UK

The early Toarcian Strawberry Bank Lagerstätte from Ilminster, Somerset, UK, has produced a substantial assemblage of fossils of marine nektonic animals, including ichthyosaurs, crocodiles, fishes, cephalopods, and crustaceans, together with abundant remains of insects from the nearby land. These fossils preserve soft parts in certain cases, but they are remarkable for the fact that many are preserved in three dimensions, allowing unique access to anatomical details otherwise unknown from other Early Jurassic faunas, including such coeval Lagerstätten as Holzmaden in Germany. What is especially extraordinary is that the site was found in the 1840s and yielded thousands of exquisite specimens, and yet has remained largely unknown since then.

In the late 1840s, Charles Moore (1815-1881), a locally born geologist, discovered a diverse and spectacularly preserved marine fauna within limestone nodules from a small quarry on Strawberry Bank. He recognised its age as Upper Lias, and within the *falciferum* Ammonite Zone of the Toarcian. Moore made an extensive collection from the horizon, and noted the Strawberry Bank fossils in several papers (Moore 1853, 1866), but never described the fauna in any detail. The fishes were reviewed by Woodward (1897), and brief mentions were made in wider reviews by Rayner (1948) and Patterson (1975), with further references to the fishes and reptiles by McGowan (1978) and Duffin (1979). Otherwise, the Moore collection was neglected (Duffin 1978; Copp *et al.* 1999), and it was not afforded the attention it deserved.

The Strawberry Bank site is unusual in that the specimens were collected by one person during a limited span of time. Nearly all of these are held by Bath Royal Literary and Scientific Institution (BRLSI) and the South West Heritage Trust, Taunton (TTNCM), with one or two specimens, presumably exchanged, in the Natural History Museum, London, and the National Museum of Ireland, Dublin. The Bath and Taunton collections have been

46 recurated and concerted studies began after 2005. The first publication was a paper describing

47 the crocodilian *Pelagosaurus* (Pierce and Benton 2006), and one of the three-dimensional

48 skulls was CT-scanned, with excellent results

49 (http://digimorph.org/specimens/Pelagosaurus_typus/whole/). Further work included a

50 revision of the ichthyosaur specimens (Caine and Benton 2011). The aim of this paper is to

51 introduce the geology and stratigraphy of the Strawberry Bank Lagerstätte, to review its

52 remarkable fossils, and to explore their mode of preservation and significance.

53

54 **Location and age**

55 The Strawberry Bank site is located within the town of Ilminster, Somerset, UK, in the

56 middle of the snaking outcrop of Lower Jurassic that runs from Dorset to Yorkshire (Fig. 1a).

57 These Lower Jurassic Lias Group sediments were laid down in the European epicontinental

58 sea at the north-western margin of the Tethys Ocean (Simms *et al.* 2004; Golonka 2007). The

59 stratigraphic sequence (Fig. 1b) is divided into the Marlstone Member and Barrington

60 Member ('Beds') of the Beacon Limestone Formation.

61 Moore (1866) indicated that the quarry was situated on the southern slope of Beacon

62 Hill, and Duffin (1979) located it as north of the High Street in Ilminster, in an area called the

63 Triangle (National Grid Reference ST 361148). This area is filled and built over, so there is

64 no chance to see the successions from which Moore made his collections. However, there

65 may be hope in the future of locating lateral exposures of the fossiliferous horizons.

66 The vertebrate fossils at Strawberry Bank are contained within calcareous concretions

67 that preserve them in three dimensions (see Box 1). These concretions occur within a unit

68 traditionally called the 'Junction Bed', 6 m thick at Ilminster and 0.7–2.0 m thick around

69 Bristol. This unit, understood in the broad sense, was formalised as the Beacon Limestone

70 Formation by Cox *et al*. (1999), overlying the Dyrham Formation, and lying below the

71 Bridport Sand Formation, in the Wessex Basin, including the Dorset coast and South

72 Somerset. In the Ilminster area, the succession is expanded, and the Beacon Limestone

73 Formation comprises the Marlstone Member overlain by the Barrington Member (Bristow

74 and Westhead 1993; Cox *et al*. 1999).

75 Moore (1866) provided a detailed measured section for the Upper Lias at Strawberry

76 Bank, the only such section by an eyewitness before the quarry was closed (Fig. 1c).

77 However, in the 1920s, excavations were made at Barrington Court, 5 km northeast of

78 Ilminster, and Hamlet (1922) matched his beds 3, 4, and 7 with Moore's section. The Moore

79 section spans Hamlet beds Middle Lias 1–2 and Upper Lias 1–12. Cope *et al*. (1980) equate

80 Hamlet's Upper Lias beds 3-11, totalling 1.45 m in thickness and including the *Leptaena* Bed

81 and the Fish Bed, with the *Harpoceras exaratum* Ammonite Subzone of the *Harpoceras*

82 *falciferum* Ammonite Zone. The 'saurian and fish bed' (Hamlet's Upper Lias Bed 4) then lies

83 low in the *exaratum* Ammonite Subzone. When using continental Jurassic zoning schemes,

84 Moore's 'Leptaena Clay' and 'Fish Bed' are assigned to the Lower Toarcian Serpentinum

85 Chronozone and Elegantulum Subchronozone, equivalent to the foraminiferal zone FJ9

86 (Boomer *et al*. 2009).

87 The exact age is determined from a high-resolution U-Pb radio-isotopic age of a sample

88 from the initial reversed polarity phase (Pl-To R) of the Karoo basalts in South Africa, with a

89 corrected age of 182.7 ± 0.7 Ma (Gradstein *et al*. 2012), corresponding to the basal

90 *tenuicostatum* Ammonite Zone (Fig. 1b). Durations of the ammonite zones in the Toarcian

91 are based on cycle-stratigraphy of zones in France and Portugal, so giving an age of c. 183

92 Ma for the *falciferum* Ammonite Zone. This is confirmed by correlation of ash beds in a

93 sedimentary succession with ammonites in Peru, and by matching carbon isotopic excursions

94 between continents (Sell *et al*. 2014). High-precision U-Pb dating of zircons from the

95 Peruvian ash beds place the top of the *tenuicostatum* Zone at 183.22 ± 0.25 Ma, and the

96   middle of the *bifrons* Zone at 181.99 ± 0.13 Ma, so confirming an age for the intervening

97   *falciferum* Zone around 183 Ma.

98

99   **A time of environmental crisis**

100   The *falciferum* Zone corresponds in age precisely to the height of the Toarcian oceanic

101   anoxic event (T-OAE). The T-OAE spanned the upper part of the underlying *semicelatum*

102   Ammonite Subzone, and extended through the *exaratum* Ammonite Subzone, peaking at

103   about one-third of the way through the latter (Schootbrugge *et al.* 2005). The entire T-OAE

104   isotopic excursion has been estimated as lasting 0.3–0.5 Myr (Boulila *et al.* 2014) or 0.6 ± 0.1

105   Myr (Huang and Hesselbo 2014), with the two major anoxic episodes, termed T-OAE1 and

106   T-OAE2 falling on either side of the 183 Ma age estimate (Ikeda and Hori 2014; Sell *et al.*,

107   2014). The substantial carbon isotopic anomaly has been explained by input of large volumes

108   of isotopically light carbon from the Karoo-Ferrar basaltic province (Suan *et al.* 2010;

109   Burgess *et al.* 2015).

110   The T-OAE was a time of environmental turmoil and extinction. Suan *et al.* (2010)

111   identified a cooling episode immediately before the T-OAE, when sea surface temperatures

112   fell by ~5 °C, followed by prolonged warming of ~7–10 °C through the early Toarcian. The

113   greenhouse warming and biocalcification crisis were associated with volcanic eruption,

114   possible methane release and sea level changes associated with icecap development and

115   melting (Kemp *et al.* 2005; Wignall *et al.* 2005; Suan *et al.* 2010; Caruthers *et al.* 2013).

116   The T-OAE extinction extended through five ammonite zones, spanning 4 Myr, and

117   peaking in the *falciferum* Zone, at 183 Ma (Little & Benton 1995; Danise *et al.* 2015). The

118   significance of the Strawberry Bank Lagerstätte is that it dates to immediately after these

119   assembled crises, within the first 1 Myr of recovery time, when oceans were still

120   experiencing the peak of the negative carbon isotopic shift, and following the peak of

121 extinction, but while extinction rates were still high. The extinction among nekton, the bulk

122 of the Strawberry Bank fauna, was controlled by variations in weathering, nutrient runoff,

123 and primary productivity (Danise *et al*. 2015).

124

125 **Faunal Overview**

126

127 *Invertebrates*

128 By far the most impressive invertebrates from Strawberry Bank are the insects, representing

129 many typical orders of the Early Jurassic, confirming that land was nearby (see Box 2). The

130 high number of complete beetles with their elytra closed indicates that they were washed into

131 the area of deposition, which was probably very close to a land mass.

132 Among marine invertebrates are rare crustaceans, some of which belong to the extinct

133 group Thylacocephala, the first such records from the Mesozoic of the UK. Thylacocephalans

134 are of uncertain affinities, usually classed as crustaceans, and allied variously with barnacles,

135 crabs, remipedes, or branchiopods. Other crustacean remains appear to be barnacle plates and

136 at least one species of large decapod crustacean, *Coleia moorei*.

137 Ammonites, brachiopods, bivalves, and other typical marine fossils have been

138 reported from below and above the nodule-bearing bed, but they are relatively rare in and

139 around the nodules. Several specimens of teuthid cephalopods occur, preserving their ink

140 sacs. All these invertebrates await detailed study.

141

142 *Fishes*

143 There are at least five actinopterygian taxa, including two small bony fishes. The

144 leptolepiform *Leptolepis* (Fig. 2b) and the semionotiform *Lepidotus* are 4–8 cm and 40–45

145 cm long, respectively. In both cases, the body is fusiform, the paired fins are small, the dorsal

146 and anal fins are short and deep, and the caudal fin is short and more-or-less symmetrical.

147 The head is heavily ossified, and the strong, short jaws are lined with compressed marginal

148 teeth and stouter inner teeth. The scales are thick and shiny-surfaced, rhombic in shape. The

149 amiiform *Caturus* is known two specimens, including an isolated neurocranium (BRLSI

150 M1288), which Rayner (1948) described in detail from serial sections.

151 Most important is the pachycormiform *Pachycormus* (Fig. 2a, c-e), with total lengths

152 ranging from 23.5cm (BRLSI M1337) to 85 cm (BRLSI M1308). Most parts of the anatomy

153 have been preserved in exquisite detail. Pachycormiforms were nearly all large, and they are

154 characterised by having reduced pelvic fins and a bony rostrum. There are 17 genera in

155 Pachycormidae, ranging in age from Early Jurassic to Late Cretaceous. Their relationships

156 are debated, although they are generally placed close to semionotiforms, aspidorhynchids,

157 and pholidophorids, on the teleost stem (Friedman *et al*. 2010; Friedman 2011; Arratia 2013).

158 The Ilminster pachycormid specimens can nearly all be assigned to the type species,

159 *Pachycormus macropterus* (Blainville 1818), described originally from the Toarcian of

160 Grandmont, Beaune in France, and later also from the Toarcian of southern Germany. One

161 Ilminster specimen, BRLSI M1308, is larger than the others (estimated length, 85 cm), and

162 might belong to the closely related *Saurostomus esocinus* Agassiz, 1833, as suggested by

163 Woodward (1897). The Ilminster *Pachycormus* has a strongly constructed head (Fig. 2a). The

164 eye is large and equipped with an ossified sclerotic ring. The teeth are small, stout, and

165 pointed. The pectoral fins (Fig. 2e) are elongate and scythe-like in shape, with rays that

166 bifurcate posteriorly, giving the back edge of the fin a frayed appearance, typical of the clade.

167 The tail fin is symmetrical, with long, symmetrical lower and upper portions; taken together,

168 the depth of the tail fin is nearly half the length of the body, a remarkably large tail fin, as

169 seen also in other pachycormiforms, and presumably evidence of powerful, fast swimming.

170

171 *Reptiles*

172 *Ichthyosauria.* Strawberry Bank has yielded eight ichthyosaur skeletons preserved in three

173 dimensions, some with soft tissues (Fig. 3a-c). These ichthyosaurs were first noted by Moore

174 (1866), and he named them all *Ichthyosaurus acutirostris*, but they were subsequently

175 reidentified by McGowan (1978) as *Stenopterygius hauffianus*. Caine & Benton (2011)

176 recognised two distinct taxa, *Stenopterygius triscissus* and *Hauffiopteryx typicus*. Further

177 work on 3D scans (Marek *et al.* 2015) shows details of the palate and braincase in *H. typicus*,

178 and suggests that this species might instead belong to the genus *Leptonectes*.

179   Most striking is that the specimens are all juveniles (five specimens) or infants (three

180 specimens), ranging from one-tenth to one-half the normal adult length of the species. The

181 small size of the ichthyosaurs and crocodilians, and their possible juvenility, might indicate

182 that the Strawberry Bank deposit was formed in a shallow-water, protected area that acted as

183 a seasonal nursery for some of the marine reptiles.

184   The diet of the ichthyosaurs consisted of small fishes, belemnites and squid-like

185 cephalopods (Motani 2005). The two Ilminster ichthyosaurs, interestingly, appear to show

186 different dietary adaptations: *Hauffiopteryx typicus* has small, slender, pointed teeth,

187 suggesting the 'pierce guild' of Massare (1987), marine reptiles that snatched fast-moving

188 fish and impaled them on sharp teeth to prevent their wriggling free. On the other hand,

189 *Stenopterygius triscissus* has larger, more curved teeth, indicating the 'smash guild',

190 ichthyosaurs that grasped and punctured hard-shelled prey such as cephalopods.

191

192 *Mesoeucrocodylia.* Moore (1853) reported three well-preserved individuals of *Teleosaurus*,

193 later (Moore 1866, 1870) assigned to the species *Teleosaurus temporalis*. They were then

194 identified as two species, *Pelagosaurus moorei*, and *Pelagosaurus typus* (Moore 1879;

195 Wilson 1893; Woodward 1893). Duffin (1979) presented a description of the skull of the

196 juvenile, and assigned the Ilminster material to *P. typus*, a view followed by Pierce and

197 Benton (2006) in their full description. The material comprises four isolated skulls and

198 associated postcranial skeletal elements, as well as two articulated specimens, one of which

199 (BRLSI M1418) is a small juvenile (Fig. 3d, e).

200 The skull of the Ilminster *Pelagosaurus typus* is narrow, long, and heavily sculptured

201 (Fig. 3d). The snout comprises more than 75% of the total skull length. It is narrow

202 anteriorly, with teeth that are well spaced, needle-like and recurved. The posterior portion of

203 the skull is broad, and the orbits circular and facing upwards. The limbs are reduced,

204 suggesting that *Pelagosaurus* may have had limited mobility on land. The legs and feet are

205 larger, and presumably used in swimming and steering. The torso bears a broad abdominal

206 armour below, and a double series of broad armour plates from the back of the head to the tip

207 of the tail. The tail is long and slightly deepened and laterally flattened, confirming its likely

208 use as a propulsive organ that beat from side to side.

209 The Ilminster *Pelagosaurus* appear to have been active, lightweight swimmers,

210 classified as high-speed pursuit predators (Massare 1988). *Pelagosaurus* preyed on small

211 fishes such as *Leptolepis*, as well as perhaps crustaceans and soft-bodied animals, as well as

212 possibly even insects flying over the surface. The juvenile *Pelagosaurus* (BRLSI M1418)

213 even contains a vertebral column and caudal fin of *Leptolepis* within its rib cage, possible

214 primary evidence of diet (Pierce and Benton 2006).

215

216 **Taphonomy**

217 Overall, the Strawberry Bank fauna presents detailed evidence of life in near-shore, shallow

218 waters (Fig. 4). The taphonomy cannot be studied *in situ*, and details must be gleaned from

219 specimens and historical accounts (Duffin 1978, 1979). The fishes, reptiles, ammonites,

220 belemnites, and teuthoids are generally preserved in carbonate-rich concretions. They are

221   usually completely enclosed, and sometimes the concretion mimics the rough shape of the

222   fossil; this is especially the case for the fishes. With larger specimens, for example some of

223   the ichthyosaurs and crocodiles, parts of the skeleton may be surrounded by a concretion, and

224   other portions may stick out beyond the concretion. The insects, crustaceans, and *Leptolepis*

225   are preserved as isolated specimens in muddy limestone, with no sign of concretions, though

226   it is not clear whether Moore trimmed the blocks down from a larger concretion in some of

227   these specimens, as the matrix is lithologically similar.

228   The fish and reptile skeletons are generally articulated, with varying degrees of

229   disarticulation of the skull and girdles. These probably became detached following microbial

230   scavenging and storm activity, which might also explain the absence of other skeletal

231   elements, particularly the tail, snout tip, and distal paddle elements (cf. Martill 1987, 1993).

232   The bones show a range of preservation quality, from immaculate, with striations and

233   capillary canals, to poorly preserved eroded surfaces. In the fish specimens, the scales,

234   branchiostegal bones (Fig. 5a), and fin rays are in pristine condition, with surface texture and

235   lustre still preserved. Evidence from thin sections suggests that branchial arches, branchial

236   rays, and gill rakers may commonly be preserved internal to the fish skulls. Gut traces are

237   phosphatised in at least three fish specimens (Fig. 5b). Soft tissue is present in the

238   ichthyosaurs (Fig. 5c, d) as both a white layer (probably calcium phosphate) with structure

239   and a greyish amorphous material. Teuthoid cephalopods may show soft tissues such as the

240   ink sac, stomach, gladius, and possibly mantle/fin structures (Fig. 5e).

241   The high degree of articulation of the fish and reptile skeletons suggests that: (1) post-

242   mortem drifting was minimal and individuals died where they lived; (2) carcasses reached the

243   sea floor soon after death, prior to the onset of decay; (3) once on the sea floor, nodule

244   formation began very rapidly and the carcasses were rapidly buried in sediment and / or sank

245   completely into the soupy bottom muds; and (4) after initial burial, the sea bed conditions

246 represented a low-energy setting. These observations suggest that the Strawberry Bank

247 deposit is an *in situ* accumulation (Konservat Lagerstätte) rather than a site of concentration

248 of skeletons from a wider area (Konzentrat Lagerstätte).

249 Burial was probably fast, as suggested by the absence of encrusters and burrowers on

250 the bone surfaces (Martill 1987, 1993). In addition, the pristine condition of the scales and

251 tail spines of the fish specimens also indicates rapid burial. The carbonate concretions

252 provided protection against compression from overburden pressures during diagenesis and

253 thus preserved the fossils in three dimensions. The modes of preservation require further

254 study (Box 1).

255

256 **Comparisons**

257 In assessing the significance of the Strawberry Bank Lagerstätte it is essential to consider

258 coeval deposits offering similar preservation. Closest in these regards are two sites in France.

259 Woodward (1908) reported a three-dimensional *Pachycormus* from the 'Upper Lias of La

260 Caine (Calvados)'. The paper provides no further geological information, but the specimen

261 presumably came from the 'Argiles à Poissons' of La Caîne in Normandy, source also of

262 specimens of the ichthyosaur *Stenopterygius longifrons*, a juvenile ichthyosaur, and the

263 crocodilian *Pelagosaurus* (Dugué *et al*. 1998). The Argiles à Poissons is correlated with the

264 *Harpoceras serpentinus* Zone (= *falciferum* Zone, lower Toarcian), exactly the same age as

265 the Reptile Bed at Strawberry Bank (Dugué *et al*. 1998).

266 The second French unit, the 'Couches de Belmont' in the Lafarge Quarry at Charnay,

267 Beaujolais (Rhône, SE France), is a fossiliferous succession of mudstones, marlstones and

268 limestones of Toarcian to Bajocian age (Suan *et al*. 2013). In horizons dated to the

269 *serpentinum* Zone (= *falciferum* Zone), two ichthyosaurs were preserved in three dimensions,

270 showing uncrushed bones and possible soft tissues, one in bedded limestone and the other in

271   a calcareous nodule. These fossils add to previous discoveries throughout the Toarcian and

272   Aalenian here, of bony fishes, sharks, ichthyosaurs, plesiosaurs, and marine crocodilians, but

273   these were mainly isolated bones, teeth, and scales (Vincent *et al.* 2013), apart from one

274   nearly complete skeleton, *Temnodontosaurus azerguensis*, from a compressed mudstone of

275   the *bifrons* Zone (Martin *et al.* 2012). At present, the coeval French faunas appear similar to

276   that from Strawberry Bank, but remains are much more sparse.

277   More famous, and better documented, comparable early Toarcian sites occur at

278   Whitby in Yorkshire and Holzmaden in southern Germany. The vertebrate faunas show

279   major differences in taxa and proportions (Fig. 6, top). Strawberry Bank is dominated by

280   *Leptolepis* and pachycormid fishes, whereas ichthyosaurs are much more abundant at

281   Holzmaden and Whitby, and the latter two sites also yield plesiosaurs and pterosaurs, not

282   known at Strawberry Bank. The entomofaunas of these locations show similar lists of taxa,

283   but proportions are different (Fig. 6, bottom), with dominance by beetles at Strawberry Bank,

284   and by Odonata and Hemiptera at Holzmaden, and Hemiptera and Diptera at Grimmen in

285   Germany.

286   The Yorkshire sites, focused around Whitby, have yielded numerous specimens of

287   marine reptiles from the lower Toarcian, with 14 specimens from the Jet Rock Formation and

288   144 from the Alum Shales Formation (*falciferum*, *bifrons* zones; Benton and Taylor 1984).

289   Most of the Yorkshire early Toarcian marine reptiles are different taxa from those at

290   Strawberry Bank, except the small thalattosuchian crocodilian *Pelagosaurus*. The Yorkshire

291   specimens are found in organic mudstones, with individual elements preserved in three

292   dimensions, but bones may be crushed and disarticulated by scavenging and sedimentary

293   processes, and soft tissues are not present.

294   The early Toarcian marine faunas of the Posidonienschiefer of SW Germany (e.g.

295   Holzmaden, Ohmden, Boll, Banz, Altdorf) are equally well known. The fishes and marine

296   reptiles come from bituminous laminated shales and grey marlstones, dated to the

297   *tenuicostatum* to *bifrons* Zones of the lower Toarcian. Hauff (1921) records about 350

298   specimens of ichthyosaurs, about 70 specimens of crocodiles, ten specimens of plesiosaurs,

299   as well as rare pterosaurs, and perhaps 300 fishes, including sharks, and the bony fishes

300   *Lepidotes*, *Caturus*, *Dapedium*, *Leptoplepis*, and *Pachycormus*. Other fossils include plants

301   derived from nearby land, bivalves, crinoids, ammonites, belemnites, The fossils may show

302   soft tissues, famously the body outlines of ichthyosaurs, a result of minimal decay and

303   scavenging because of anoxic conditions (Röhl *et al*. 2001). Most of the fossils occur in

304   black, anoxic oil shales and they are substantially compressed. Less common are specimens

305   enclosed within the limestones, and these may be preserved in three dimensions, but they

306   have proved hard to extract. The vertebrate faunas are similar, but Strawberry Bank has

307   yielded much more abundant fish remains, and these and the reptiles are not flattened, as is

308   commonly the case at Holzmaden.

309

310   **Conclusion**

311   The Strawberry Bank Lagerstätte is significant for four reasons, its contribution to our

312   knowledge of marine life in the Early Jurassic, as evidence for unusual amounts of

313   exceptional preservation at a time of substantial environmental perturbation, its exceptional

314   three-dimensional preservation, and its unique insight into life in a near-coastal marine

315   setting.

316   The Early Jurassic was an important time in the evolution of life, with modern-style

317   benthic ecosystems becoming established. Among predators, decapod crustaceans,

318   cephalopods, neopterygian fishes, and reptiles were new forms that emerged in the Triassic,

319   during recovery from the devastating Permo-Triassic mass extinction (Benton *et al*. 2013).

320   Many of these clades received a further setback during the end-Triassic extinction (ETE), and

321 they were just recovering from that crisis when the T-OAE caused further environmental

322 stress (Friedman and Sallan 2012; Danise *et al*. 2015). The ETE had imposed a

323 macroevolutionary bottleneck on various groups of fishes and reptiles, in which some clades,

324 such as ichthyosaurs, bounced back in terms of diversity but not in terms of disparity (Thorne

325 *et al*. 2011).

326   Fossil vertebrates and other taxa are relatively abundant in the Upper Lias of Europe,

327 and they are especially abundant and well preserved exactly at the height of anoxia of the T-

328 OAE (*falciferum* Zone). Likely the anoxic conditions of the time directly preserved more than

329 the usual number of exceptional fossils at different locations in England, France, and

330 Germany. Further, the concentration of similarly preserved entomofaunas in shallow marine

331 sediments across Germany and England at exactly the same time, coincident with the T-OAE,

332 is further evidence for a shared killing model, yet to be determined.

333   In contrast to the more famous coeval deposits of the Jet Rock and Alum Shales

334 formations and the Posidonienschiefer, the Strawberry Bank Lagerstätte offers unusually

335 perfect three-dimensional preservation coupled with the survival of soft tissues. Such three-

336 dimensionality is not known from any other Early Jurassic site, except the less fossiliferous

337 Argiles à Poissons and Couches de Belmont, and the Strawberry Bank fossils are making, and

338 will make, significant contributions to understanding of the anatomy and palaeobiology of

339 individual fish and reptile taxa.

340   Finally, the Strawberry Bank deposits were probably located closer to the coastline

341 than coeval deposits. Evidence is the abundance of beetles (terrestrial insects) and the

342 likelihood that the site was a nursery for marine reptiles, which are largely juveniles (Caine

343 and Benton 2011). Further, unlike Holzmaden and Yorkshire, the succession is not dominated

344 by black shales and it yields far fewer deep-marine fossils (e.g. ammonites, belemnites,

345 echinoderms, brachiopods).

346

355

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544

545   **Box 1. Lithology of the nodules**

546   The Strawberry Bank fossils are preserved in buff-coloured calcareous nodules, which are at

547   least partly depositional and certainly formed before any substantial compaction from

548   overlying sediments or digenesis. Though we cannot describe the exposure in the field, the

549   lithology can be described from microfacies analysis of thin sections. The nodule matrix is a

550   biomicritic mudstone to packstone with concentrations of sparry calcite within the voids

551   created by macrofossils (Fig. a-d). Bioclasts consist mainly of numerous very small, mostly

552   complete, gastropod shells (Fig. c) alongside the infrequent brachiopod, ostracod, bone and

553   fish scale fragments. The gastropods range between 700 and 100 μm, small enough to

554   represent a meroplanktonic larval stage, a common component of brackish-lagoonal

555   ecosystems (Ambrogi *et al.* 1989).

556   There is little sorting of these bioclasts, beyond some occasional weak alignment by

557   size along planes parallel to the nodule surface, indicating their concentric deposition (Fig. d).

558   No definitively terrigenous clasts are evident, though mud grade terrestrial sediments may be

559   present in low concentrations. Given the palaeogeographical, ecological, and taphonomic

560   evidence of a nearby landmass and a warm-wet climate, fine ferruginous grains or crystals

561   within the sediment might have been sourced from a palaeosol, such as a pedogenic laterite,

562   but this requires further investigation.

563   There is some evidence for high organic content in these sediments, probably the

564   result of anoxic conditions at the sea-sediment interface. Moore's (1866) account suggests

565   that some of the nodules where blue-grey in the interior when originally excavated. More

566   compelling evidence come from a contemporary section near Charnay (Rhône-Alps

567   Department, France), a site within the same palaeogeographic marginal sea as Strawberry

568   Bank, which also bears nodules, with a very similar lithology, at exactly the same horizon

569   (see *Significance*). Analysis of the sediment and nodules there shows that recent weathering

570   has led to preferential removal of ^{12}C-enriched organic carbon and dramatic TOC loss over

571   most of the exposure (Suan *et al.* 2013).

572

573   [Box 1 Figure] Photomicrographs of blue-dyed, resin-impregnated thin sections of nodule

574   matrix from Strawberry Bank. (**a**) A nodule bearing the anterior part of a partial

575   *Pachycormus* (BRLSI M3913), the gill arches of the specimen seen in dorsoventral section to

576   the left of the field, and the sediment is a biomicritic packstone with bioclasts including

577   gastropods and fragments of fish bone/ scales. (**b**) Within the skull in the same section the

578   void spaces not filled by micrite have been infilled by sparry calcite, and the main bone here

579   is one of gill arch elements, with smaller, subtriangular structures below being transverse

580   sections through the associated mineralized branchial rays. (**c**) The nodule matrix contains

581   numerous minute gastropods as small as 100μm in diameter and one echinoid spine (centre,

582   star-shaped). (**d**) Transverse section through the pectoral fin of a *Pachycormus* specimen, the

583   matrix prepared off the dorsal surface, but the ventral surface is unprepared, and here

584   bioclasts are less common, roughly sorted, and weakly aligned.

585

586   **Box 2. The Strawberry Bank Insects**

587   The Strawberry Bank site has yielded over 800 insect specimens, which were mentioned by

588   Brodie (1849), but not described then or since. Moore clearly had a very good eye and

589   collected everything, as many of the specimens are very faint, poorly preserved and

590   fragmentary, unusual for 19th century collectors. The limestone containing the insects is

591   slightly coarse, so the insects are often poorly preserved. They consist of wings, wing

592   fragments, complete insects and body parts (Fig. a-e), and parts are separated from

593   counterparts. For the rarer orders, it was straightforward to try to re-unite parts with

594   counterparts. For the more abundant orders this was only possible where one part was

595   examined very soon after the other, so the totals given for the more abundant orders are

596   probably overestimates.

597   Nine orders were identified among the 528 identifiable specimens. Odonata

598   (dragonflies and damselflies) are represented by a small and a large form (19 specimens;

599   3.6% of identifiable specimens; Fig. c). Blattodea (cockroaches) include a small and large

600   species, based on isolated forewings (10; 1.9%). We report here the first record of an earwig

601   (Dermaptera) from the Upper Lias of the UK, based on a single elytron (0.2%). Orthoptera

602   (grasshopper, crickets and locusts) are represented mainly by isolated wings (Fig. d),

603   although some are pairs of overprinted wings, assigned to three families, some showing

604   original striped and spotted pigmentation (35; 6.6%). Hemiptera (bugs) are abundant (47;

605   8.9%), consisting of complete insects and isolated wings that indicate several taxa (Fig. a, e).

606   Most abundant are Coleoptera (beetles), represented mostly by isolated elytra, but also paired

607   elytra and complete beetles (387; 73.7%), representing several species (Fig. b). Flies

608   (Diptera) are very rare in the Jurassic, but we report at least a single wing here (0.2%) with

609   wing venation consistent with *Architipula* (Limoniidae). Some incomplete wings may

610   represent Diptera, or more likely Mecoptera (scorpionflies), close relatives (21; 4.0%).

611   Finally, Neuroptera (lacewings) are identified from poorly preserved, incomplete wings (7;

612   1.3%), with at least two taxa. This compares with the five species in four families of

613   Neuroptera reported by Whalley (1988) from the Upper Lias of Gloucestershire.

614   The Ilminster Upper Lias insect fauna can be compared with the Gloucestershire

615   Alderton-Dumbleton sites (Woodward 1911; Whalley 1988), which yielded much smaller

616   collections, and the rich German Upper Lias entomofauna, represented by over 4800

617   specimens, belonging to 21 orders, primarily from the localities Dobbertin, Schandelah,

618   Grimmen, Kerkhofen, Mistelgau, and Holzmaden (Ansorge 1996, 2003). All these localities

619   from central Europe represent similar offshore settings, and they are restricted to a narrow

620 temporal window coincident with the T-OAE, so providing a rich, but isolated snapshot of

621 insect evolution during an important time before the origin of angiosperms and the evolution

622 of insect groups associated with flowering plants. The most striking difference between the

623 German localities and Strawberry Bank is the very high abundance of beetles in the latter,

624 and it is uncertain whether this reflects genuine higher abundance, or some aspect of collector

625 bias or differential preservation.

626

627 [Box 2 Figure] Insect fossils from Strawberry Bank, all from the Somerset Heritage Centre

628 (TTNCM). (**a**) Spotty planthopper forewing (Hemiptera: *Fulgoridulum* sp.), TTNCM

629 39/2011/0594, length 6.5 mm. (**b**) Beetle (Coleoptera), TTNCM 39/2011/0640, length 12

630 mm. (**c**) Partial dragonfly forewing (Odonata: Liassogomphidae), TTNCM 39/2011/0509,

631 preserved length 26 mm. (**d**) Grasshopper forewing (Orthoptera: Elcanidae), TTNCM

632 39/2011/0523, width 3.5 mm. (**e**) Paired bug forewings (Hemiptera: Archegocimicidae),

633 TTNCM 39/2011/0707, width 2.7 mm.

634 **Figure 1.** (**a**) Geographic location of Ilminster in England. (**b**) Stratigraphy of the Middle and

635 Upper Lias deposits in Somerset, England. (**c**) Reconstructed sedimentary log through the

636 Lias succession at Strawberry Bank, taken from the measured section by Moore (1866, pp.

637 132-133). Bed numbering follows Moore (1866). His major stratigraphic subdivisions, and

638 fossil reports (brachiopods, vertebrates) are also indicated. Abbreviations: LEPTAENA,

639 Leptaena Beds; SFZ, Saurian and fish zone; U. CEPHALO., Upper Cephalopoda Beds. (A,

640 B, from Pierce & Benton 2006.)

641

642 **Figure 2.** Fishes from Strawberry Bank. (**a**) Lateral view of *Pachycormus* (BRLSI M1297);

643 note the degradation of the body to the anterior and the exposed phosphatized gut towards the

644 ventral margin. (**b**) Complete specimen of *Leptolepis* (BRLSI M1259), at 10 cm long, one of

645 the largest specimens of this genus from Strawberry Bank. (**c**) Anterior portion of

646 *Pachycormus macropterus* (BRLSI M1359), prepared in ventral aspect; note the perfectly

647 preserved branchiostegal bones and the lack of compressional distortion. (**d**) Detail of the

648 ventral abdominal scales of *P. macropterus* (BRLSI M1359). (**e**) Detail of the pectoral fin of

649 *P. macropterus* (BRLSI M1395).

650

651 **Figure 3.** Reptiles from Strawberry Bank. (**a, b**) The skull of a juvenile ichthyosaur,

652 *Hauffiopteryx typicus* (BRLSI M1399), in right lateral view (**a**), and in dorsal view, to show

653 the lack of compression. (**c**) Articulated juvenile ichthyosaur, *Stenopterygius triscissus*

654 (BRLSI M1409). (**d**) Skull of a sub-adult thalattosuchian crocodile *Pelagosaurus typus*

655 (BRLSI M1413). (**e**) Articulated infant thalattosuchian *Pelagosaurus typus* (BRLSI M1418).

656

657 **Figure 4.** A reconstruction of the Strawberry Bank scene, by John Sibbick. Situated near to a

658 sub-tropical island on the north-western margin of Tethys, the shallow seas of Strawberry

659 Bank provided a habitat for diverse macrofauna, amongst which early teleost fishes were the

660 most abundant component. Here larger *Pachycormus* hunts shoaling *Leptolepis*, and

661 opportunistically takes a mayfly that has alighted on the sea surface.

662

663 **Figure 5.** Soft tissues, and delicate elements, in fossils from Strawberry Bank. (**a**)

664 Branchiostegal bones in the ventral throat region of a *Pachycormus* skull (BRLSI M1297).

665 (**b**) Gut trace exposed beneath the disrupted scales of an articulated *Pachycormus* (BRLSI

666 M1383). (**c**) Skin and probable muscle fibres from an ichthyosaur (genus and species

667 unknown, as this is separation from the main specimen) (TTNCM 39/2011/0357). (**d**) Grey

668 amorphous matter preserving the outline of the forelimb of *Hauffiopteryx typicus* (BRLSI

669 M1399). (**e**) Soft tissue preservation of a teuthid (*Geotheuthis*?) showing preservation of the

670 ink sac, stomach, gladius, and possibly mantle/fin structures (BRLSI M1226a).

671

672 **Figure 6.** Comparison of key vertebrate (top row) and insect (bottom row) components of the

673 Strawberry Bank, Holzmaden, Whitby, and Grimmen faunas. Faunal data on Holzmaden

674 come from Hauff (1922) and other sources, and on Whitby from Benton and Taylor (1984)

675 and other sources. Insect faunal counts come from Ansorge (2013).

a

Lower Jurassic
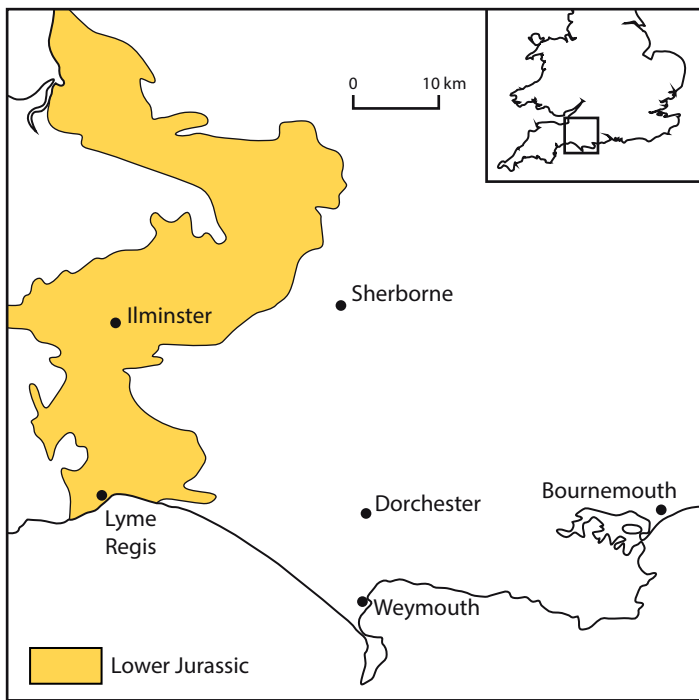
b

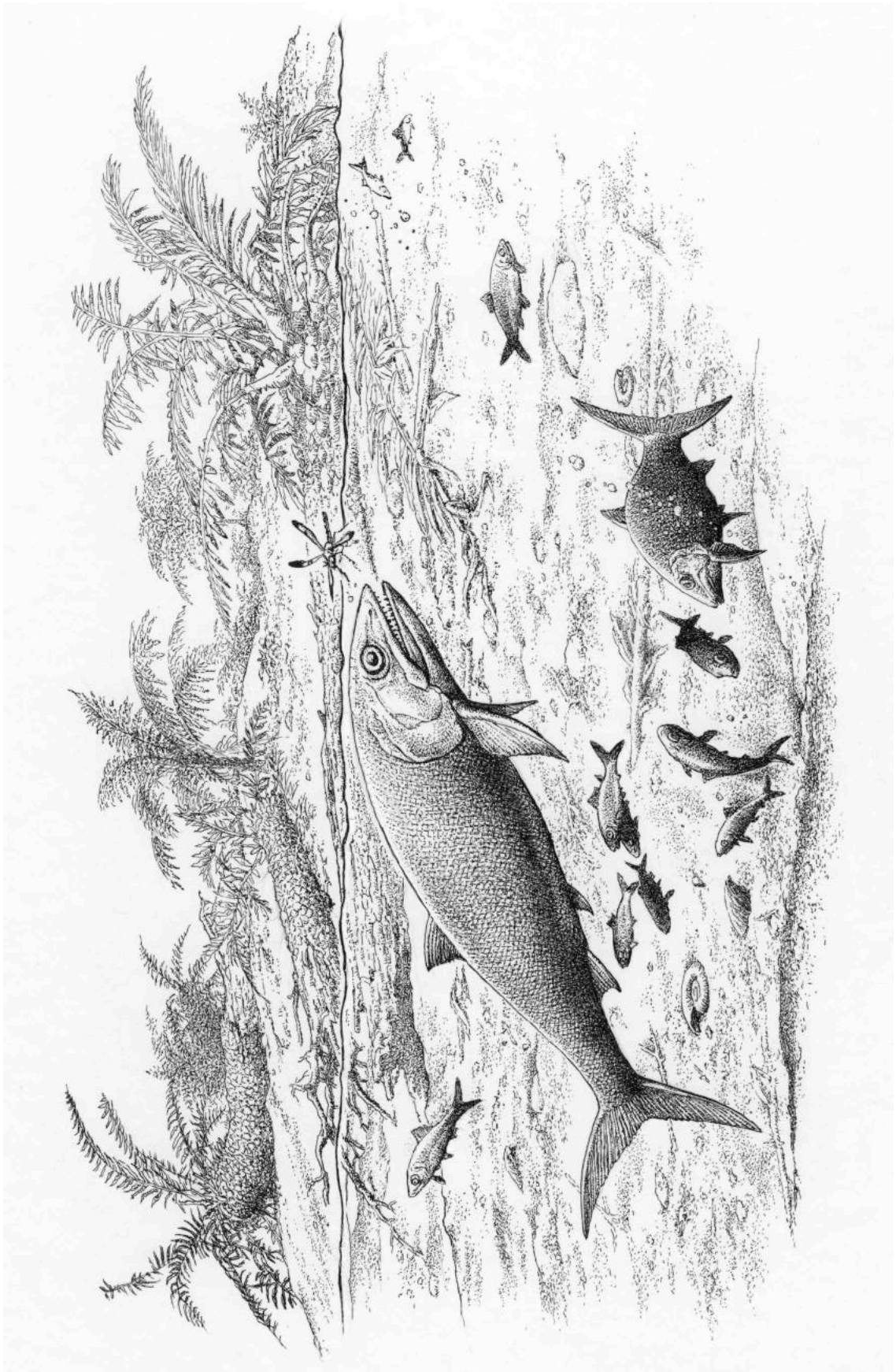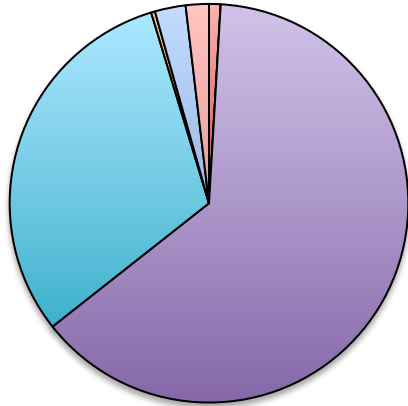| Regional Classification		Ammonite Zones	Local Classification	
Toarcian (Upper Lias)	Upper	*thouarsense*	Yeovil Sands	
		variabilis	Cephalopod Bed	Barrington Beds
	Lower	*bifrons*		
		falciferum	Reptile Bed	
		tenuicostatum	*Leptaena* Shale	Absent (Unconformity)
Pliensbachian (Middle Lias)		*spinatum*	Marlstone	
		margaritatus	Pennard Sands	

c

m	U. CEPHALO.	C.f
		C.e
		C.d
		C.c
4		C.b
	SFZ	C.a
		B.c
		B.b
	LEPTAENA	B.a
		A.e
		A.d
		A.c
		A.b
		A.a
3	MIDDLE LIAS	
2		ML.d
1		
		ML.e
		ML.f

a

30mm

b

20mm

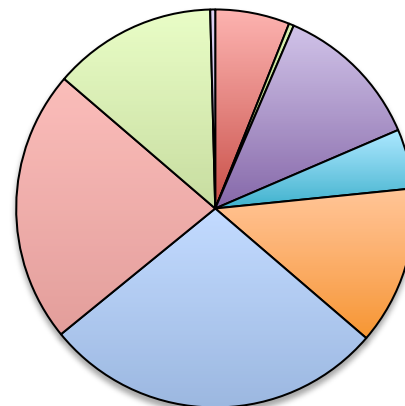M.1259.
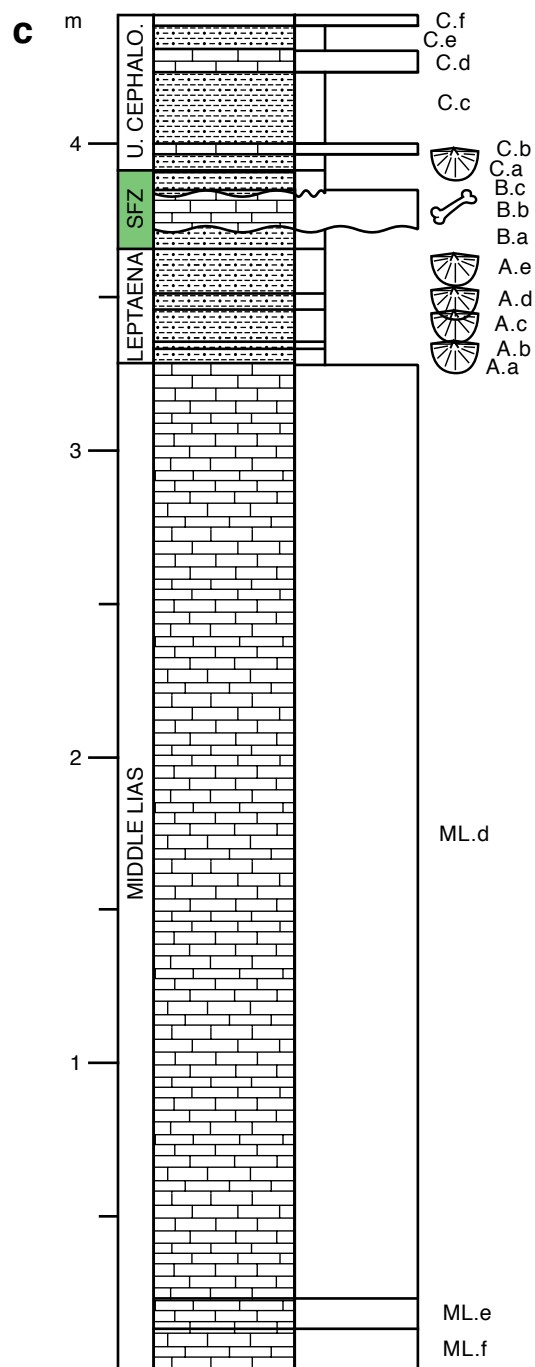
c

30mm

d
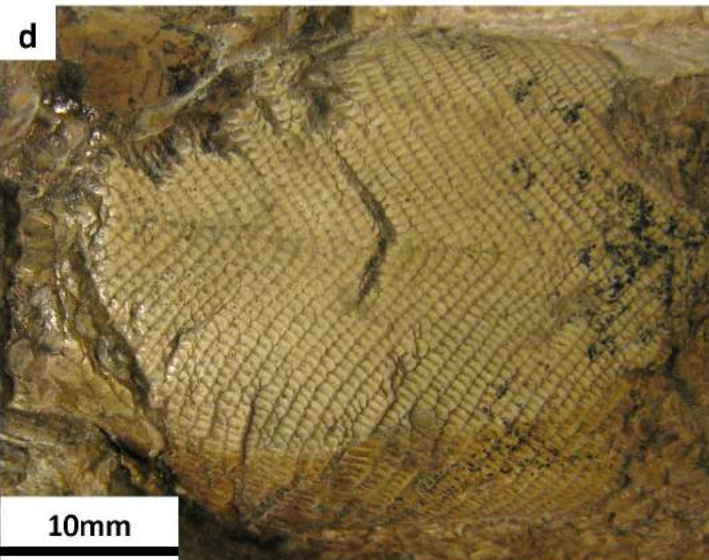
10mm

e

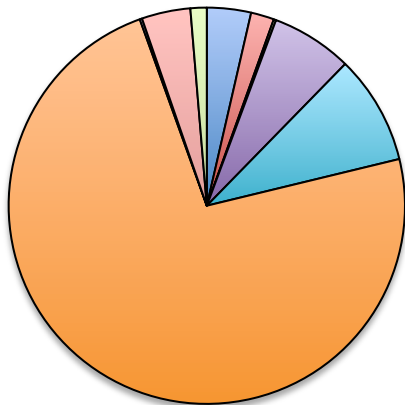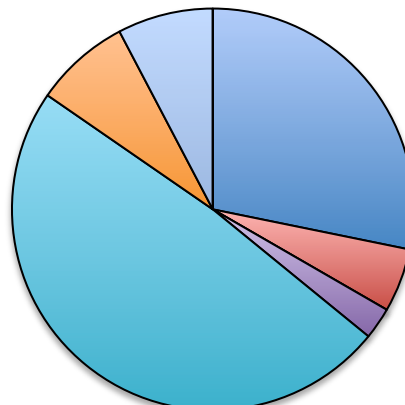5mm
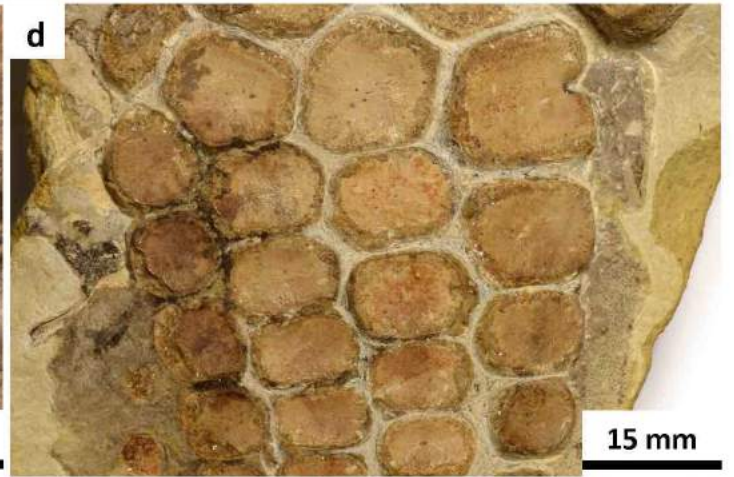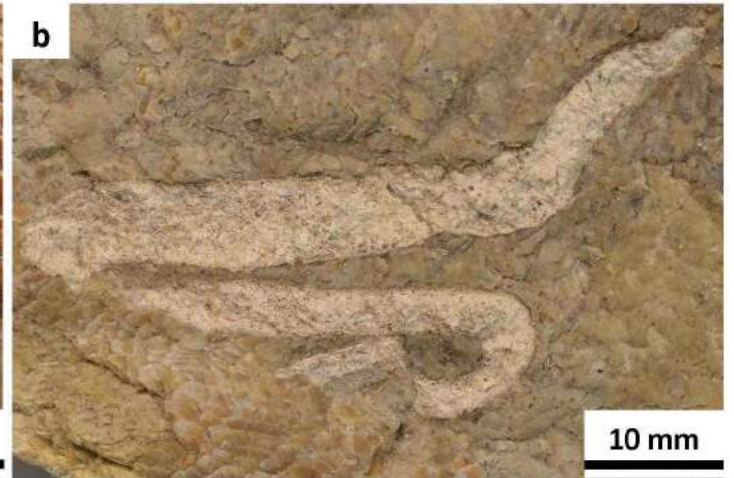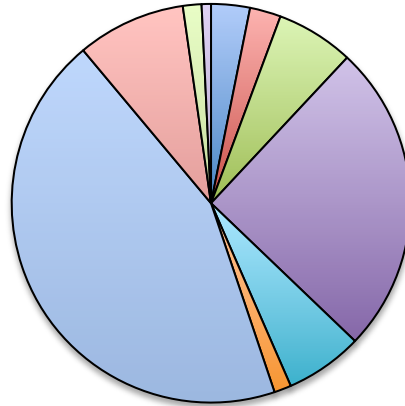
Strawberry Bank   **Holzmaden**   **Whitby**

- Chondrichthyes
- *Lepidotus*
- *Dapedium*
- *Leptolepis*
- *Pachycormidae*
- Other fishes
- Ichthyosaurs
- Pelagosaurus
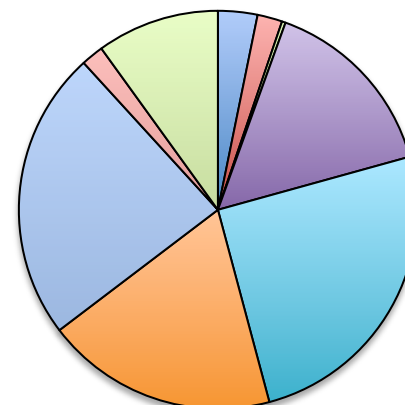- *plesiosaurs*
- pterosaur

Strawberry Bank   **Holzmaden**   **Grimmen**

- Odonata
- Blattodea
- Dermaptera
- Orthoptera
- Hemiptera
- Coleoptera
- Diptera
- Mecoptera
- Neuroptera

a

1mm

b

2mm

c

5mm

d

2mm

e

1mm