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1 **How quick was marine recovery after the end-Triassic mass extinction and what**
2 **role did anoxia play?**

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6 **Abstract**

7 **Oxygen restricted conditions were widespread in European shelf seas**
8 **after the end-Triassic mass extinction event and they are reported to have**
9 **hindered the recovery of marine benthos. Here we reconstruct the redox history**
10 **of the Early Jurassic Blue Lias Formation of southwest Britain using pyrite**
11 **framboid size analysis and compare this with the recovery of bivalves based on**
12 **field and museum collections. Results suggest widespread dysoxia punctuated**
13 **by periods of anoxia in the region, with the latter developing frequently in deeper**
14 **water settings. Despite these harsh conditions, initial benthic recovery occurred**
15 **rapidly in the British Jurassic, especially in shallowest settings, and shows no**
16 **relationship with the intensity of dysoxia. A stable diversity was reached by the**
17 **first recognised ammonite zone after the end-Triassic mass extinction. This**
18 **contrasts with the deeper-water, more oxygen-poor sections where the diversity**
19 **increase was still continuing in the earliest Sinemurian Stage, considerably**
20 **longer than previously reported. Similar recovery rates are seen amongst other**
21 **groups (brachiopods and ammonites). Oxygen-poor conditions have been**
22 **suggested to delay recovery after the Permo-Triassic mass extinction, but this**
23 **is not the case after the end-Triassic crisis. We suggest that this was because**

24 **the European dysoxia was only a regional phenomenon and there were plenty**
25 **of well-ventilated regions available to allow an untrammelled bounce back.**

26

27 **Keywords: Pyrite framboids, Early Jurassic, Blue Lias Formation, benthic**
28 **recovery, diversification**

29

30 **1. Introduction**

31 Marine anoxia has been implicated as a cause of delayed biotic recovery from the
32 end-Triassic mass extinction event, especially in Western Europe (Clémence et al.,
33 2010; Hallam, 1996; Jost et al., 2017; Luo et al., 2018; Mander et al., 2008; Richoz et
34 al., 2012). The evidence for oxygen-restriction includes widespread black shale
35 deposition in the epicontinental seaway of Europe during the earliest Hettangian and
36 again during the Sinemurian (Richoz et al., 2012; van de Schootbrugge et al., 2013;
37 Wignall and Hallam, 1991). The intensity of oxygen deficiency has been assessed
38 using a range of proxies: redox sensitive trace metals such as Th/U (Hallam, 1995;
39 Wignall, 2001) and molybdenum (Breward et al., 2015), pyrite sulphur isotopes
40 (Jaraula et al., 2013; Luo et al., 2018), uranium isotopes (Jost et al., 2017) and the
41 presence of isorenieratane (Blumenberg et al., 2016; Jaraula et al., 2013; Naeher and
42 Grice, 2015; Richoz et al., 2012).

43 Many studies have only focussed on short stratigraphic intervals in the earliest
44 Hettangian sedimentary record in Western Europe, because this is the immediate
45 post-mass extinction interval. These show that dysoxic conditions, punctuated by
46 episodic anoxia and photic zone euxinia (PZE), were widespread at this time (e.g.
47 Hallam, 1997, 1995; Jaraula et al., 2013; Naeher and Grice, 2015; Paris et al., 2010;

48 Richoz et al., 2012; Wignall, 2001). Studies in Germany, Luxemburg and Switzerland
49 demonstrate that these conditions persisted from the middle Hettangian to the
50 lowermost Sinemurian (Luo et al., 2018; Richoz et al., 2012; Schwab and
51 Spangenberg, 2007). Away from the European epicontinental sea there is some
52 suggestion of PZE from north-eastern Panthalassa (Kasprak et al., 2015) but oxic
53 deposition is suggested in other regions of this ocean recorded in accreted terranes
54 of Japan (Fujisaki et al., 2016; Wignall et al., 2010). In no region is it clear how long
55 the marine recovery took and how it relates to the redox record.

56 This study aims to reconstruct redox conditions of southwestern Britain from
57 the beginning of recovery following the end-Triassic mass extinction through to the
58 Sinemurian Stage, using pyrite framboid size analysis. This will then be compared with
59 the bivalve recovery, based on field and museum collections, to evaluate the notion
60 that anoxia delayed recovery at this time. The size distribution of pyrite framboids is a
61 powerful tool used to assess redox conditions (e.g. Huang et al., 2017; Wignall and
62 Newton, 1998). Framboids are spheres of aggregated pyrite microcrysts that form at
63 the boundary between oxic and sulphidic waters (Wilkin et al., 1996). Under euxinic
64 conditions the redox boundary occurs in the water column where framboids grow, but
65 they do not achieve diameters much beyond 5 μm before sinking to the seabed (Wilkin
66 et al., 1996). In contrast, in dysoxic settings the redox boundary is within the uppermost
67 sediments and framboids grow to a wide range of sizes with a larger mean diameter
68 (Wilkin et al., 1996). This size distribution has been shown for the modern (Wilkin et
69 al., 1996) and also in ancient sediments where framboid analyses have been
70 corroborated by independent palaeontological and geochemical redox indicators
71 (Huang et al., 2017; Wignall and Newton, 1998). Variable degrees of oxygen restriction

72 are thought to be represented by differing size classes of framboid populations (Table
73 1 in Bond and Wignall, 2010).

74 Defining a biotic recovery can be problematic, and several different alternatives
75 have been used. The onset of recovery is often defined as the point when origination
76 rates exceed extinction rates and recovery is assumed complete once pre-extinction
77 diversity is attained (Kauffman and Erwin, 1995). Such a simple measure is not
78 suitable for the British record of the recovery from the end-Triassic mass extinction,
79 because diversity in the pre-extinction interval was low due to unusual salinities that
80 were quite different to the fully marine settings that develop in the aftermath (Hallam
81 and El Shaarawy, 1982). A period of rising diversity followed by stabilisation may
82 provide a better assessment of the recovery interval (Damborenea et al., 2017). An
83 alternative four-phase model for recovery, incorporating ecological parameters, was
84 created based on observations of the recovery following the end-Permian mass
85 extinction (Twitchett, 2006, referred to here as the Twitchett recovery model). Phase
86 one consists of high abundance, low diversity faunas (low evenness) with small body
87 sizes and minimal ecological tiering. The following stages of recovery see an
88 expansion of benthic tiering levels, an increase in evenness, species richness, body
89 size and appearance of key ichnotaxa.

90

91 **2. Geological setting**

92 The Cotham Member of the Lilstock Formation features rippled fine
93 sandstones, deep fissures and severe soft sediment deformation (Simms, 2003). It is
94 within this member that the end-Triassic extinction is located (Wignall and Bond,
95 2008), and is succeeded by the Langport Member of the same formation. Micritic

96 carbonates dominate the Langport Member and were deposited within a shallow
97 epicontinental sea of uncertain salinity (Hallam and El Shaarawy, 1982). An erosion
98 surface and intraformational conglomerate caps the Member in Devon (Wignall, 2001),
99 although in other areas the contact is more gradational and apparently conformable.

100 The Hettangian to lowermost Sinemurian (Early Jurassic) Blue Lias Formation
101 of southwestern Britain was deposited in an epicontinental sea that covered much of
102 north-western Europe during the Lower Jurassic (Hallam, 1960). The Formation
103 consists of rhythms of limestone, marl and shale (Hallam, 1960; Paul et al., 2008) that
104 are thought to record climate-driven cycles in seafloor oxygenation and sedimentation
105 due to Milankovitch periodicities (Bottrell and Raiswell, 1989; Clémence et al., 2010;
106 Moghadam and Paul, 2000; Ruhl et al., 2010; Weedon, 1986; Wignall, 2001). Weedon
107 (1986) defined the five lithotypes of the Blue Lias used here:

108 Bioturbated limestones may occur as semi-continuous beds, or nodular
109 horizons within pale marls. These often bear irregular and uneven bed contacts though
110 they can also be planar. Beds are homogenous and bioturbated with up to seven
111 ichnotaxa recorded and are considered to have formed under a fully aerated water
112 column (Moghadam and Paul, 2000; Weedon, 1986). Bivalves, including *Plagiostoma*,
113 *Gryphaea* and *Pinna*, are typically common. Total organic carbon (TOC) is variable,
114 with values ranging from 0.14-1.64 wt% (Weedon et al., 2018a). These beds become
115 increasingly dominant in shallower water sections (Hallam, 1964).

116 Pale marls are light blue-grey, homogenous beds bearing a diverse trace fossil
117 assemblage, suggesting good seafloor oxygenation. TOC is typically higher than in
118 the limestones at 0.38-4.41 wt% (Weedon et al., 2018a), and silt-grade quartz grains
119 are more common (Hallam, 1960).

120 Dark marls are similar to pale marls, however they have a weak fissility,
121 especially when weathered. These marls show planar contacts with the pale marls
122 and have an increased TOC range of 0.51-6.51 wt% (Weedon et al., 2018a). Dark
123 marls also have less diverse trace fossil assemblages dominated by Chondrites and
124 only one or two additional ichnospecies, suggesting weaker oxygenation than seen in
125 the pale marls (Moghadam and Paul, 2000).

126 Shales appear as dark brown or black beds, these weather to become very
127 fissile, occasionally showing millimetre-scale laminae. Fossils are usually confined to
128 nektonic organisms and small bivalves (Hallam, 1960). Of the five lithologies of the
129 Blue Lias, the shale beds have the highest TOC values, typically between 1.53 -12.8
130 wt%, and record intervals of anoxia (Ebukanson and Kinghorn, 1990; Weedon et al.,
131 2018a; Wignall and Hallam, 1991).

132 Laminated limestones exhibit planar bedding surfaces and are laminated. TOC
133 values can be twice as great as seen in bioturbated limestones with values of 0.9-3
134 wt% and they have a fetid odour when freshly broken (Weedon, 1986; Weedon et al.,
135 2018a). The laminated limestones are considered to have originally been black shales,
136 which have been diagenetically-replaced by carbonate (Arzani, 2004).

137 The relative contribution of each lithology varies between location and
138 stratigraphic interval allowing regional members of the Blue Lias Formation to be
139 defined and correlated using ammonite biozonation schemes (Fig. 1).

140 Limestone beds are most prevalent in the Pre-planorbis Beds and planorbis and
141 angulata zones, whereas the liasicus Zone has lower proportions of limestones and is
142 thought to be due to deepening caused by accelerated sea-level rise at this time
143 (Hesselbo and Jenkyns 1998; Sheppard 2006; Weedon et al. 2018a). The higher

144 proportions of limestones in the succeeding angulata Zone is attributed to a lowering
145 of relative sea-level prior to another deepening episode during the bucklandi Zone
146 (Sheppard, 2006). Limestone-rich sections on the Glamorgan coastline were
147 deposited closer to a palaeo-shoreline than the mud-dominated Somerset sections
148 (Johnson and McKerrow, 1995; Wobber, 1965).

149

150 **3. Materials and methods**

151 Sampling was undertaken in three regions (Fig. 2): Glamorgan (south Wales),
152 Somerset and Devon (southwest England). Stratigraphic height of sampling was
153 determined using published sedimentary logs where available (Bloos and Page, 2002;
154 Hesselbo and Jenkyns, 1995; Simms, 2004) or logged by the authors during sampling
155 and dated by use of ammonites. For Glamorgan two localities were sampled:
156 Lavernock Point (ST 188 682 – ST 183 679) spanning the Langport Member to liasicus
157 Zone and Nash Point (SS 911 692 – SS 921 679) covering the angulata to bucklandi
158 zones. For Somerset, again two localities were sampled: St Audrie's Bay (ST 103 434
159 – ST 099 433) and East Quantoxhead (ST 134 442 – ST 142 444), spanning the upper
160 Langport Member to liasicus Zone and angulata to bucklandi zones respectively. For
161 Devon only Pinhay Bay (SY 317 907 – SY 333 914) was sampled, this spanning
162 topmost Langport Member to bucklandi Zone. The five lithologies of the Blue Lias:
163 bioturbated limestone, pale marl, dark marl, shale and laminated limestone (described
164 above) were recorded and sampled.

165 At each sample horizon bivalve diversity was assessed by species counts and
166 life modes assigned from published sources (Supplementary appendix 1). First
167 occurrence of crinoids was also noted. In mudstones, marls and shales bivalves were

168 identified from freshly split surfaces of approximately equal volume of rock (~0.5 x 0.5
169 x 0.3 m). For limestone beds fossils were identified in situ on weathered bedding
170 surfaces, owing to this different sampling method abundance data are presented
171 separately. In addition, bivalve diversity was also assessed by combining field
172 observations with occurrences based on museum specimens. This was undertaken
173 only for Glamorgan due to the extensive collection of stratigraphically-tied specimens
174 housed within the National Museum of Wales (NMW) and conducted at the resolution
175 of ammonite zone. For the lower interval of the Blue Lias Formation lacking ammonites
176 the Pre-planorbis Beds are used here as a time bin as is the Langport Member.

177 For each section a subset of sampled horizons was used to test for changes in
178 oxygenation regime using pyrite framboids. The method was adapted from that of
179 Wignall and Newton (1998). Pyrite framboid diameters were measured from polished
180 stone chips approximately 2 x 1 cm in size set into resin blocks. These were carbon
181 coated and viewed using a Tescan VEGA3 XM scanning electron microscope (SEM)
182 with a backscatter electron detector. By adjusting the brightness and contrast this
183 allows pyrite to stand out from the matrix. Framboids were then located by scanning
184 across the sample surface and diameters measured using inbuilt measurement
185 applications of the SEM. Each sample was analysed for up to one hour or until 100
186 framboids had been measured. Mean framboid diameter and standard deviation were
187 then calculated per sample and plotted on what are referred to herein as a Wilkin
188 diagram (Wilkin et al., 1996). Results of framboid analysis of bed H1 from Pinhay Bay
189 presented in Wignall (2001) are incorporated into this study. It is important to note that
190 each 1 cm-thick sample area can record up to several thousands of years of deposition
191 (Weedon et al. 2018b). Thus, each sample potentially records a range of oxygenation
192 regimes developed during such intervals and accounts for the fact that euxinic

193 populations can sometimes occur in samples with benthic fossils that record seafloor
194 oxygenation (Bond and Wignall, 2010).

195 Mean framboid diameters and standard deviations are correlated with raw
196 species richness per sample horizon using Spearman's rank correlation, conducted in
197 PAST statistical software (Hammer et al., 2001).

198

199 **4. Results**

200 4.1 Pyrite framboids

201 4.1.1 Lithological variability

202 Pyrite framboids were found in all samples from both the Langport Member and
203 the Blue Lias Formation irrespective of lithology. Photographic representations of
204 pyrite framboids formed under anoxic and dysoxic regimes are shown in figure 3.

205 In the Langport Member, only two samples are examined for framboids, these
206 were collected from Lavernock Point (LP9 and LP21). Framboids are not abundant but
207 both samples still yield at least 100, although euhedral crystals of pyrite are more
208 common. These samples have an average framboid diameter of 10.7 μm , but show
209 wildly different standard deviations placing LP21 in the mid-dysoxic region of a
210 framboid mean-standard deviation plot (Wilkin diagram), whilst LP9 plots in the
211 uppermost dysoxic field (Fig. 4).

212 Fifty-one samples of bioturbated limestone are analysed and, of the five Blue
213 Lias lithotypes, they are found to have the least pyrite, with euhedral crystals, and
214 pyrite-replaced bioclasts being more common than framboids. Despite this
215 observation, only four samples failed to yield 100 framboids within the allotted one-
216 hour analysis time. Framboids are typically concentrated into discrete clusters or loose

217 patches. Average diameter of framboids is 8.7 μm , with the largest being 70.0 μm . The
218 populations typically plot in the mid to upper dysoxic region of the Wilkin diagram (Fig.
219 4). Three samples plot in the anoxic field, these are two from St. Audrie's Bay (SAB52,
220 SAB53) and one from East Quantoxhead (Q76) – these are not laminated limestones
221 although they do exhibit planar contacts in the field (Figs. 5 & 6).

222 Forty-seven samples of bioturbated, pale marl are analysed, and found to
223 typically contain a low to moderate abundance of pyrite with a mixture of framboidal
224 and euhedral forms and void-filling internal spaces of bioclasts. Pyrite framboids are
225 restricted to specific horizons or clusters often bound by a dense carbonate cement.
226 Average framboid diameter is 7.9 μm with largest being 75.3 μm (Fig. 4). The
227 framboids exhibit the largest variability of all Blue Lias lithotypes on the Wilkin diagram,
228 with four samples plotting as anoxic (Fig. 4).

229 Twenty-three samples of dark marl are analysed to reveal a mixture of euhedral
230 and, more commonly, framboidal forms of pyrite. In contrast to the framboids found in
231 pale marls, they occur evenly distributed throughout the samples. Average framboid
232 diameter is 6.9 μm , the largest being 43.2 μm . Most dark marl samples plot within the
233 anoxic—mid dysoxic field (Fig. 4).

234 Thirty-one samples of shale are studied. These contain very high
235 concentrations of pyrite, with the majority being small framboids. Average diameter is
236 5.2 μm although rare, large framboids attain a maximum of 33.9 μm (Fig. 4). Most plot
237 within the euxinic/anoxic field.

238 Only one sample of Laminated Limestone is analysed, collected from between
239 two shale beds at Lavernock Point (Fig. 7). Pyrite is common with small framboids

240 scattered evenly throughout. Average diameter is 6.9 μm placing it in the lower dysoxic
241 field (Fig. 4).

242

243 4.1.2 Regional variability

244 As framboids were only analysed in the Langport Member of Glamorgan
245 regional variability is only assessed for Blue Lias Formation samples. Glamorgan
246 sections were deposited close to a palaeo-shoreline and are the most proximal ones
247 examined in this study (Johnson and McKerrow, 1995; Wobber, 1965). Overall, the
248 framboids from this region have the largest average diameter (8.13 μm), and the
249 greatest variability with an average standard deviation of 4.23 μm indicating the
250 highest oxygenation levels. At Lavernock Point two of the beds plot in the anoxic field
251 (LP10 and LP12) (Fig. 7). The former (LP10) being from the Bull Cliff Member, which
252 is distinct from other levels of the Blue Lias Formation in showing planar beds with a
253 high abundance of fossil oysters. That aside, the remaining four samples from the Bull
254 Cliff Member plot as mid-upper dysoxic populations. Despite shales and laminated
255 limestones featuring in the planorbis Zone of Lavernock Point these beds do not plot
256 as anoxic. The greater part of the Lavernock section plots as variably dysoxic. Very
257 little of the Lavernock Shale Member was sampled as these are poorly exposed in the
258 foreshore, however the succeeding Porthkerry Member is well exposed at Nash Point.
259 This section shows a marked upward increase in both the abundance and thickness
260 of limestone beds and lacks shales (Fig. 8).

261

262 A total of 38 of the 40 samples from this section plot as mid-upper dysoxic, with
263 pale marls and limestones potting within the same region and dark marls nestled within

264 (Fig. 9). Two anoxic beds are recorded, the lower of these occurs within a dark, weakly
265 laminated marl in the lower portion of the section where limestones are thin and
266 nodular. The second occurs directly below a distinct thick, grey limestone. The
267 limestone itself (NP21a) plots within the dysoxic field and makes a good marker bed,
268 being one of the few limestones not of yellow-beige colour.

269 The Somerset sections record the deepest-water settings studied (Fig. 2). SEM
270 analysis shows the sediments contain less silt-grade quartz than seen in Glamorgan
271 and are more coccolith- and clay-rich. Across the span of the study interval the classic
272 lithological rhythms of the Blue Lias are well developed. Somerset, overall has the
273 smallest average framboid diameters of the three regions studied (6.72 μm and
274 standard deviation of 3.07 μm). The framboid size distributions with the shales and
275 most of the dark marls plot within the euxinic-anoxic region whilst pale marls and
276 limestones generally plot in the mid-upper dysoxic field (Figs. 5 & 6). Across Somerset
277 an approximately 2 m-thick, blue-grey weathering shale occurs, that contains large
278 numbers of the ammonite *Psiloceras*, the bivalve *Anningella* and fish debris. The
279 framboids from this level plot in the anoxic field (Fig. 5). Unlike the Nash Point section,
280 East Quantoxhead (which is of equivalent age) features many euxinic, paper shales,
281 that are often thickly developed (Figs. 6 & 8).

282 Pinhay Bay is a limestone-dominated section that is by far the most condensed
283 of all the sections in the three regions studied. All limestones beds contain framboids
284 that plot within the dysoxic field (Figs. 9 & 10). Of the few marls and shales sampled
285 the greater majority plot as anoxic, suggesting the anoxic-dysoxic rhythms seen in
286 Somerset are also present in Devon (Fig. 10). Devon has an overall mean framboid
287 diameter of 8.22 μm (standard deviation of 3.24 μm), this being comparable to the
288 Glamorgan average, albeit with a smaller standard deviation. Both Devon and

289 Glamorgan represent deposition in shallower, better oxygenated waters than those of
290 Somerset and the average framboid diameters reflect this, being smaller in the deeper
291 water.

292

293 4.1.3 Temporal variability

294 Dividing the 155 samples from all localities into ammonite zone time bins
295 (including the Pre-planorbis Beds and the Langport Member) allows for long-term
296 temporal trends to be tested. All zones plot as mostly dysoxic with occasional forays
297 into anoxic or euxinic conditions (Fig. 11). The average of mean framboid diameters
298 and standard deviations varies little between each zone (Fig. 11), with no two
299 subsequent zones showing a significant difference (t-test, $p(a) > 0.05$). There is a
300 distinct lack of directional trend through time, with the only significant size increase in
301 framboid diameters found when populations of the pre-planorbis beds and angulata
302 Zone are compared (t-test, $p(a) = 0.05$), however these zones are indistinct from all
303 other zones. The same result is found when ammonite zones are compared for
304 individual areas.

305

306 4.2 Faunas

307 4.2.1 Field collections

308 Bed-by-bed raw species counts are shown in figures 5-8 and 10 alongside
309 pyrite framboid size distributions whilst range charts for the bivalves are shown in
310 figures 12-14 (for raw sampling data see supplementary appendix 2).

311 These show that bivalve diversity does not correlate strongly with mean
312 framboid diameters or standard deviation ($r = +0.18$, $p(a) = 0.02$, $n = 155$ and $r = +0.22$,

313 $p(a) = 0.01$, $n = 155$ respectively). Although a higher diversity occurs in beds that show
314 a larger mean framboid diameter, the converse is not always true. Similarly beds with
315 an anoxic signal have been found to contain bivalves. LP12 is a pale marl from the
316 base of the planorbis Zone of Lavernock Point and, despite its anoxic framboid
317 population, it also contains a relatively diverse fauna including *Modiolus* and *Chlamys*.
318 Another bivalve associated with framboid populations suggestive of anoxia is
319 *Anningella* (SAB19 and SAB23) (Fig. 5), but they are occasionally found attached to
320 fossil drift wood suggesting a pseudoplanktonic lifestyle unhindered by seafloor
321 conditions. In contrast, the anoxic beds from Devon are associated with low diversity
322 bivalve assemblages (0-1 typically) with diversity showing a stronger positive
323 correlation to framboid diameters and standard deviations ($r = +0.81$, $p(a) = 0.0003$, n
324 $= 15$ and $r = +0.81$, $p(a) = 0.0003$, $n = 15$ respectively).

325 Generally, Glamorgan hosts the greatest bivalve diversity per zone (Fig. 15),
326 and includes deep infaunal bivalve species (*Pleuromya liasina*, and *Gresslya*
327 *galathea*; Fig. 12). The Nash Point section features several beds that contain the
328 solitary coral *Stylophylloopsis* and large, disarticulated and occasionally stacked
329 *Plagiostoma* shells that are heavily encrusted on all surfaces by *Liostrea*, *Atreta* and
330 corals. Two of the coral beds at Nash Point (NP36, NP38), have framboid mean
331 diameters that are indistinct from the rest of the limestone and marl beds (Fig. 8).
332 Overall there is a temporal trend of increasing species richness per zone (Fig. 15).
333 For Glamorgan and Devon the main rise occurs between the Pre-planorbis Beds and
334 planorbis Zone. With bivalve species richness per zone remaining between seven
335 and nine for Devon. The greatest species richness is achieved in the angulata Zone
336 of Glamorgan, before falling slightly in the bucklandi Zone (Fig. 15). For Somerset

337 species richness rises at a lessening rate throughout the Hettangian and into the
338 Sinemurian and fossils are rare throughout (Figs. 5 & 6).

339 At the bed level the Langport Member of Glamorgan can host four times the
340 diversity of species than the Pre-planorbis Beds, however in regards to ecological
341 tiering this is only greater by one – featuring shallow infaunal species. Benthic tiering
342 is reduced to epifauna with subordinate semi-infaunal components in the Pre-planorbis
343 Beds, for Somerset the middle Pre-planorbis Beds also feature rare shallow infaunal
344 bivalves (*Protocardia phillipianum*). This latter tiering level is not seen in Devon until
345 the upper planorbis Zone. Deep infaunal life modes are not encountered in Somerset,
346 however they are recorded in the *angulata* and *bucklandi* zones of Glamorgan and
347 Devon respectively. An increase in epifaunal tiering levels is noted by the presence of
348 ossicles of the crinoid *Isocrinus psilonoti*, these first appear in the Pre-planorbis Beds
349 of Lavernock Point and the planorbis Zone of St Audrie's Bay and Pinhay Bay.

350

351 4.2.2 Museum collections

352 Bivalve diversity by zone for Glamorgan is assessed by incorporating bivalve
353 specimens housed in the NMW alongside field observations. For the Langport Member
354 incorporation of these specimens does not enhance diversity from that encountered in
355 the field (eight species). Between the Langport Member and the Pre-planorbis Beds
356 diversity increases greatly with 21 species present this rising to a stable diversity of
357 around 26 species in the planorbis Zone and persisting into younger levels (Fig. 15).
358 Deep infaunal suspension feeding bivalves are also recognised far sooner than seen
359 during the field study, occurring in the Pre-planorbis Beds, and further members of this
360 guild appear in the planorbis Zone (supplementary appendix 3). Species richness rises

361 to 29 in the semicostatum Zone, however this is represented by a silicified fauna that
362 has been shown to be more diverse than un-silicified time-equivalent sections (Wright
363 et al., 2003).

364

365 **5. Discussion**

366 5.1 Recovery

367 Most studies of recovery from the end-Triassic mass extinction in Britain have
368 concentrated on the initial aftermath (planorbis to the early part of the liasicus zones)
369 (Clémence et al., 2010; Mander et al., 2008). Here we extend the time interval of our
370 analysis to the bucklandi Zone, of the Sinemurian Stage.

371 The majority of the beds from Pinhay Bay (Devon) suggest an environment with
372 moderate oxygen restriction, with occasional intervals of anoxia. In spite of this, biotic
373 recovery occurs rapidly, with a sharp increase in species richness by the planorbis
374 Zone and ecological tiering being also well developed by this time.

375 Our field observations show low diversity with assemblages dominated by
376 *Liostrea* in the lower Pre-planorbis Beds. This is consistent with the findings of Pugh
377 et al. (2014), and conforms to phase one of the Twitchett recovery model. The
378 definition of recovery phase two is the expansion of infaunal tiering levels. This was
379 reported by Pugh et al. (2014) from the upper Pre-planorbis Beds using the trace fossil
380 data of Barras and Twitchett (2007) and Twitchett and Barras (2004). However, the
381 range charts of Pugh et al. (2014) show the infaunal tier was occupied before this time
382 by *Pteromya tatei* in the lower Pre-planorbis Beds (Bed H2). This is earlier than our
383 own field observations which show the appearance of *Cardinia ovalis* in the planorbis
384 Zone being the first infaunal species.

385 Defined as an expansion in the epifaunal tiering levels, phase three occurs in
386 the planorbis Zone in both our data and that of Pugh et al. (2014). The planorbis Zone
387 also contains the key ichnotaxa for phase three with *Rhizocorallium* and
388 *Thalassinoides* that are, at this interval, small in size (Twitchett and Barras, 2004).
389 Defining the final stage of recovery is less clear-cut. Pugh et al. (2014) use the
390 presence of deep infaunal bivalves in the angulata Zone, however their range charts
391 show that this ecology was already present in the planorbis Zone (cf. Paul et al., 2008).
392 Our data shows species richness had broadly stabilised by the planorbis Zone,
393 considerably earlier than reported previously (Pugh et al., 2014). However, a trend of
394 shell-size increase is seen after this time which persisted until the late angulata Zone
395 (Atkinson et al., 2019).

396

397 In Somerset, this deep-water region records a greater number of episodes of
398 anoxia than the shallower regions in Glamorgan. A background of dysoxic condition
399 was punctuated by anoxic intervals, a situation that persists from the Pre-planorbis
400 Beds into the bucklandi Zone. Biotic recovery is still seen, even in these adverse
401 conditions, albeit represented by a gradual rise in species richness; several of the key
402 features of Twitchett's recovery model occur by the planorbis Zone.

403 As with Devon the lower beds of the Pre-planorbis interval are dominated by
404 oysters and is again consistent with phase one of recovery. The appearance of
405 infaunal tiering occurs in the upper Pre-planorbis Beds according to the range charts
406 of Mander et al. (2008) who reported the shallow infaunal bivalve *Rollieria* at this level
407 and is broadly consistent with our data which shows shallow infaunal tiers occupied
408 from the mid Pre-planorbis interval. There is a discordance with the trace fossils,

409 because Barras and Twitchett (2007) do not report any trace fossils from the Pre-
410 planorbis Beds of St Audrie's Bay.

411 Phase three (epifaunal tiering development) was not reported by Mander et al.
412 (2008) from Somerset. However, this is contradicted by our finding of *Isocrinus*
413 *psilonoti* in the mid-planorbis Zone at St Audrie's Bay and in upper Pre-planorbis Beds
414 at Lilstock. Ichnotaxa were slower to recover, although rare *Rhizocorallium* occur in
415 the planorbis Zone, and becomes more frequent from the angulata Zone (Barras and
416 Twitchett, 2007). Our results show that diversity continues to rise steadily in the
417 earliest Jurassic of Somerset up to the bucklandi Zone but at no point is benthos
418 abundant, and deep infaunal bivalves do not appear. Thus, recovery phase four is
419 much later in the offshore Somerset sections than in the nearer, shallower sections of
420 Devon.

421 Glamorgan represents the most near-shore region in this study, and also shows
422 fewer anoxic intervals than the more distal Somerset sections. All the same, no sample
423 lacked pyrite framboids, suggesting that oxygen restriction, to some degree, was still
424 present even in these shallower waters up to the Sinemurian. Nonetheless, biotic
425 recovery occurred promptly as seen in both field and museum collections which show
426 an early rise in species richness into the planorbis Zone.

427 The Langport Member is discordant with the predictions of the Twitchett
428 recovery model for an initial post extinction because several ecological tiers are
429 occupied and no single species dominates the assemblage. At the bed level the
430 Langport Member can attain a greater diversity than the succeeding Pre-planorbis
431 Beds however when considered as a time bin, with the inclusion of NMW specimens
432 this interval is comparably depleted in bivalve diversity, with a great increase occurring

433 with the transition to Blue Lias facies (Fig. 15). This may be driven by a rapid sea-level
434 rise and development of fully marine conditions.

435 The lower Pre-planorbis Beds, with their high numbers of *Liostrea* and *Modiolus*
436 *minimus*, are far more characteristic of supposed phase one recovery than the earlier
437 Langport Member. Two shallow infaunal species are present in the Langport Member
438 but our field collecting did not find further infaunal bivalves until the lower angulata
439 Zone, where deep infauna appear (*Gresslya*, *Pleuromya* and *Pholadomya*). However,
440 Mander et al. (2008) recorded shallow infaunal deposit feeding bivalves in the upper
441 Pre-planorbis Beds and specimens housed in the NMW include *Pteromya*,
442 *Protocardia*, *Pleuromya*, *Rollieria*, *Mactromya* and *Cardina* all in the Pre-planorbis
443 Beds. Thus, this tiering level was not lost with the changing facies. The expansion of
444 epifaunal tiering (recovery phase three) is seen in upper Pre-planorbis Beds with the
445 presence of *Isocrinus psilonoti*. However, as with Somerset, key ichnotaxa of these
446 phases are lacking, with *Thalassinoides* occurring later in the lower planorbis Zone
447 and rare *Rhizocorallium* later still in the bucklandi Zone (Wobber, 1968). The ordered
448 succession of recovery phases does not match the record seen in Glamorgan.

449 Based on field collecting alone, diversity rose rapidly into the planorbis Zone
450 and was highest in the angulata Zone – a time when all the tiering levels were filled.
451 The largest limid bivalves and *Thalassinoides* burrows were recorded from the
452 bucklandi Zone (Atkinson et al., 2019; Hallam, 1960; Wilson et al., 1990). However,
453 using the data from museum collections shows that diversity and tiering had stabilised
454 far earlier (in the planorbis Zone). Diversity from combined field and NMW collections
455 was also far higher than direct field observations alone this likely relates to the ability
456 of museum collections to capture rare faunal elements based on many years of
457 collecting effort and samples from temporary exposures.

458

459 In both Devon and Glamorgan recovery occurs quickly and was complete by
460 the planorbis Zone, as monitored by stable, high diversity and restoration of tiering
461 levels, (Figs. 12, 14 & 15). Diversity is slower to increase in the offshore/deeper water
462 Somerset sections. Based on body and burrow sizes the recovery is more gradual and
463 slower taking up to the angulata and bucklandi zones. The recovery patterns do not fit
464 Twitchett's recovery model with its progressive development of tiers and diversity in
465 the shelly fauna occurring out of synch with trace fossil records. The model only
466 accords with the recovery pattern seen at Pinhay Bay, there trace fossils recover hand-
467 in-hand with the shelly fauna. The timing of the appearance of key ichnotaxa and shelly
468 fauna tiering and diversity is ill fitted in Somerset and Glamorgan. For example, there
469 is a near absence of trace fossils in Somerset until the angulata Zone (Barras and
470 Twitchett, 2007), despite the recovery of the bivalves. Recovery should be deemed
471 complete once a stable diversity is attained, however we acknowledge the necessity
472 for ecological factors to be also considered and retain the ideas of Twitchett (1999)
473 that benthic tiering is an important indicator of recovery also. Body size and presence
474 of particular trace fossils are perhaps controlled by other factors (substrate, sea level
475 and so on) and do not appear relatable across different regions or recovery intervals.

476 Looking further afield recovery also appears to have been rapidly completed
477 within the Hettangian. High diversity shell beds with low dominance and highly
478 specialised forms are reported from early Hettangian of Tibet (Hautmann et al.,
479 2008). In the Neuquén Basin, Argentina, recovery appears slower than Tibet,
480 because there is an interval barren of bivalves roughly equivalent to the planorbis
481 Zone, followed by rising diversity and increased occupation of tiering until the
482 canadensis Zone equivalent to the upper angulata Zone (Damborenea et al., 2017).

483 Ammonites also recovered very quickly, with a rapid diversification in the
484 immediate aftermath of the end-Triassic mass extinction with peak originations
485 occurring in the planorbis Zone (Guex et al., 2012). This diversification was also
486 accompanied by an increase in size disparity over the first four standard ammonite
487 zones of the Jurassic, with some of the largest forms of the Lower Jurassic occurring
488 in the bucklandi Zone (Dommergues et al., 2002). Recovery amongst the
489 brachiopods occurs on broadly the same time span as seen amongst bivalves
490 (Tomašových and Siblík, 2007). In the Northern Calcareous Alps of Germany and
491 Austria, brachiopod recovery occurs in the calliphyllum and megastoma zones
492 (equivalent to planorbis to lower angulata zones of the UK, cf. Page 2003).

493

494 5.2 Duration of recovery

495 A recent reappraisal of the cyclostratigraphy of the Blue Lias has suggested
496 that the Hettangian stage was longer than previously thought, being perhaps >4.1
497 Myr (Weedon et al., 2018b) compared to earlier estimates of 1.7- 2 million years
498 (Guex et al., 2012; Hüsing et al., 2014; Ruhl et al., 2016, 2010; Schaltegger et al.,
499 2008). This has clear implications for the timing of the recovery. Evidence for a short
500 Hettangian comes from U-Pb dating of poorly biostratigraphically constrained ash
501 beds in northern Peru (Schaltegger et al., 2008; Schoene et al., 2010; Wotzlav et al.,
502 2014) and cyclostratigraphic study of the St Audrie's Bay and East Quantoxhead
503 sections (Hüsing et al., 2014; Ruhl et al., 2016, 2010). Weedon et al.'s (2018b) work
504 improves on these earlier cyclostratigraphies by including the tilmanni Zone
505 (encompassing part of the Pre-planorbis Beds), and also constructing chronologies
506 from several Blue Lias sites. This has allowed for the detection of hiatuses and
507 missing sedimentary cycles, and so generated a longer composite chronology for the

508 Hettangian (Weedon et al., 2018a, 2018b). Based on this new >4.1 Myr duration for
509 the Hettangian and accounting for the 0.15 Myr between the End-Triassic extinction
510 and the Triassic-Jurassic boundary (Wotzlaw et al., 2014) the pace of recovery can
511 be assessed.

512 Despite Somerset recording a greater level of oxygen restriction, the duration
513 of early recovery phases between all three regions are broadly similar. The biotic
514 recovery from the end-Triassic mass extinction event appears to have begun
515 extremely rapidly; it was substantially complete within <0.7 Myr in both Somerset and
516 Glamorgan (excluding trace fossils). Devon lagged behind and took > 2 Myr to reach
517 a similar stage. Following the initial rapid recovery later, incremental diversity
518 increases were ongoing for > 4 Myr. Although we favour the most recent Hettangian
519 time scale, as some controversy remains we also present an alternative duration of
520 recovery using the time scales of Ruhl et al. (2016), under this chronology recovery
521 was exceedingly rapid, significant expansion of tiering was restored within 0.22 Myr
522 for Somerset and Glamorgan and with stable diversity and fully restored tiers in both
523 Devon and Glamorgan within 0.53 Myr. Equally the incremental diversity increases
524 seen in Somerset were ongoing for >2.14 Myr.

525

526 5.3 Role of anoxia in recovery

527 There is no suggestion of the involvement of anoxia in the end-Triassic
528 extinction event itself in the region (Wignall and Bond, 2008), but oxygen restriction
529 clearly occurred during the earliest Jurassic and this has been suggested to have
530 impeded the recovery (e.g. Clémence et al., 2010; Hallam, 1996; Luo et al., 2018;
531 Mander et al., 2008). Our redox study fails to shows this link. Anoxic and dysoxic

532 conditions were regularly developed during the Hettangian and lower Sinemurian in
533 Somerset and Devon, whilst less intense dysoxia persisted in the nearer
534 shore/shallower Glamorgan sections with fewer anoxic intervals recorded. Much the
535 same redox history has been demonstrated for other regions of the European Shelf
536 Sea (Quan et al., 2008; Richoz et al., 2012; Schwab and Spangenberg, 2007).

537 Despite the oxygen restriction, rapid recovery in the basal Jurassic occurred
538 unhindered (Fig. 14). Nonetheless, some influence of dysoxia can be seen because
539 the greatest diversity increase occurred in nearshore sections whilst the continued
540 deposition of anoxic, black shales in Somerset into the bucklandi Zone lowered the
541 diversity and abundances at least at the bed level and prolonged the local recovery.

542 The rapid initial recovery of the Early Jurassic is in marked contrast to the muted
543 recovery seen during the Early Triassic when anoxia has also been proposed to have
544 hindered recovery (e.g. Dai et al., 2018; Hallam, 1991). However, the environmental
545 extent of anoxia in the earlier interval was much greater, with anoxia frequently
546 extending into shallow, inner shelf settings (Wignall et al., 2016; Wignall and Twitchett,
547 1996). During the Early Jurassic it is possible that species from the shallower, dysoxic
548 setting of south Wales replenished deeper water populations following periods of
549 anoxia in the Early Jurassic, thereby allowing punctuated recovery even in the deeper
550 waters. It is important to remember that this is a regional story for two basins, each
551 responding in subtly different ways. Although episodic anoxia continued into the
552 Sinemurian, uranium isotope ratios suggest that, on a global scale, a major expansion
553 of sea-floor anoxia lasted for only around 45 kyr after the extinction, before improving
554 gradually in the next 200 kyr (Jost et al., 2017). However, Jost et al.'s (2017) work
555 used the astrochronological timescale of Ruhl et al. (2010). The more recent timescale
556 of Weedon et al. (2018b) doubles the duration of the widespread anoxia episode. The

557 oxygen-poor environmental conditions in NW Europe were unusually harsh compared
558 to elsewhere in the Early Jurassic, ensuring that there were sufficient locations beyond
559 this region where benthic diversity was able to diversify unimpeded.

560

561 **6. Conclusions**

562 The Hettangian and lowermost Sinemurian shelf seas of Britain show pyrite
563 framboid size distributions that suggest conditions were commonly dysoxic
564 especially in more distal, offshore settings. Despite this observation, the poor
565 aeration did not hinder biotic recovery from the end-Triassic mass extinction event as
566 recorded by the dominant bivalve fauna. Even in deeper water where a greater
567 severity of oxygen restriction was recorded a rapid initial recovery can be detected. It
568 may be that diversification took place in the best oxygenated shallowest-water
569 settings and helped stock the benthos in offshore, dysoxic settings during transient
570 times of improved oxygenation. This is supported by the evidence from the
571 nearshore sections of Glamorgan where recovery was potentially faster (achieved
572 within 0.7 Myr). Other facets of the recovery, seen in benthic tiering levels, both
573 epifaunal and infaunal, improved rapidly and synchronously: there is little support for
574 models that view recovery to occur in a set of distinct stages or phases.

575

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584

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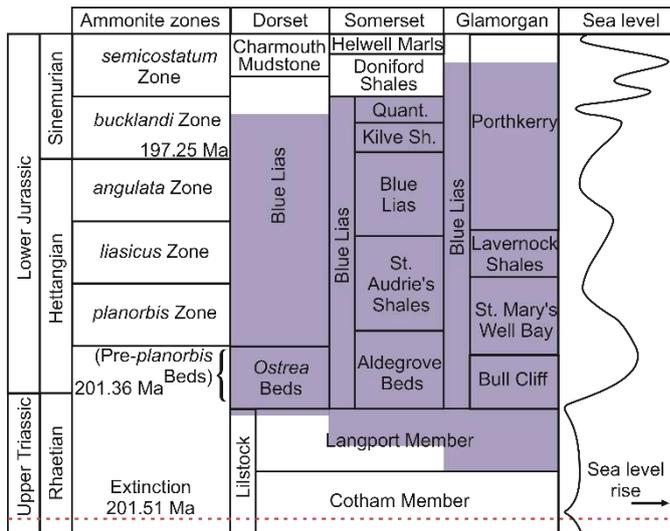
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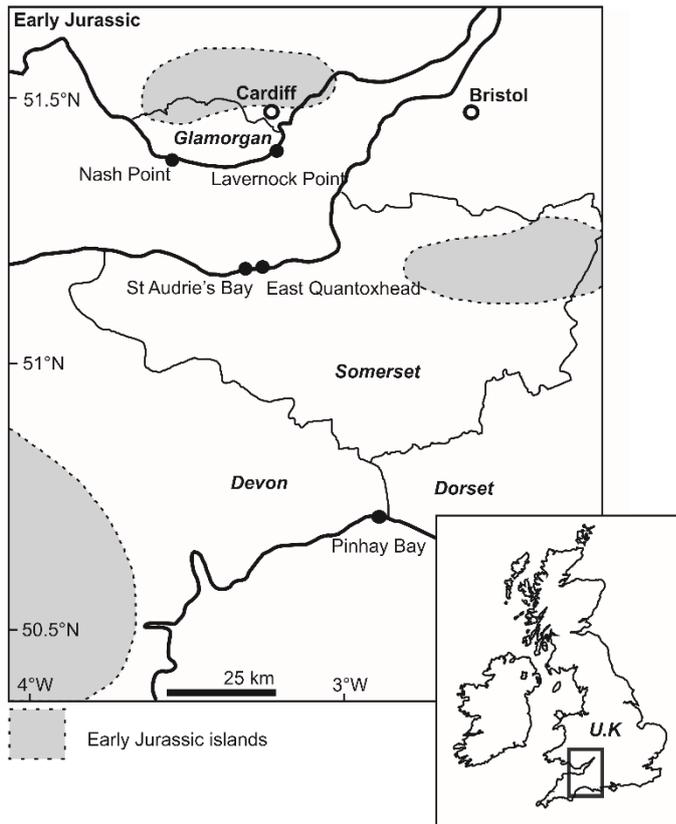
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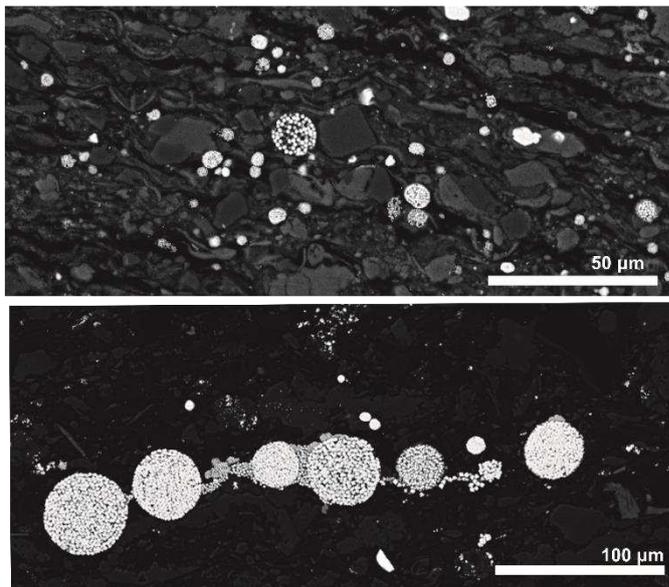
861

862 **Figure 1. Lithological correlation of members of the Blue Lias Formation, after**
 863 **Hodges (2000). Quant. – Quantock Beds, Kilve Sh. – Kilve Shales. Shaded**
 864 **regions depict sampled interval, dashed line position of extinction horizon.**
 865 **Relative sea-level curve based on Hesselbo and Jenkyns (1998); Hesselbo et al.**
 866 **(2004) and Wignall and Bond (2008), extinction and boundary ages from Wotzlaw**
 867 **et al. (2014) and Weedon et al. (2018b).**



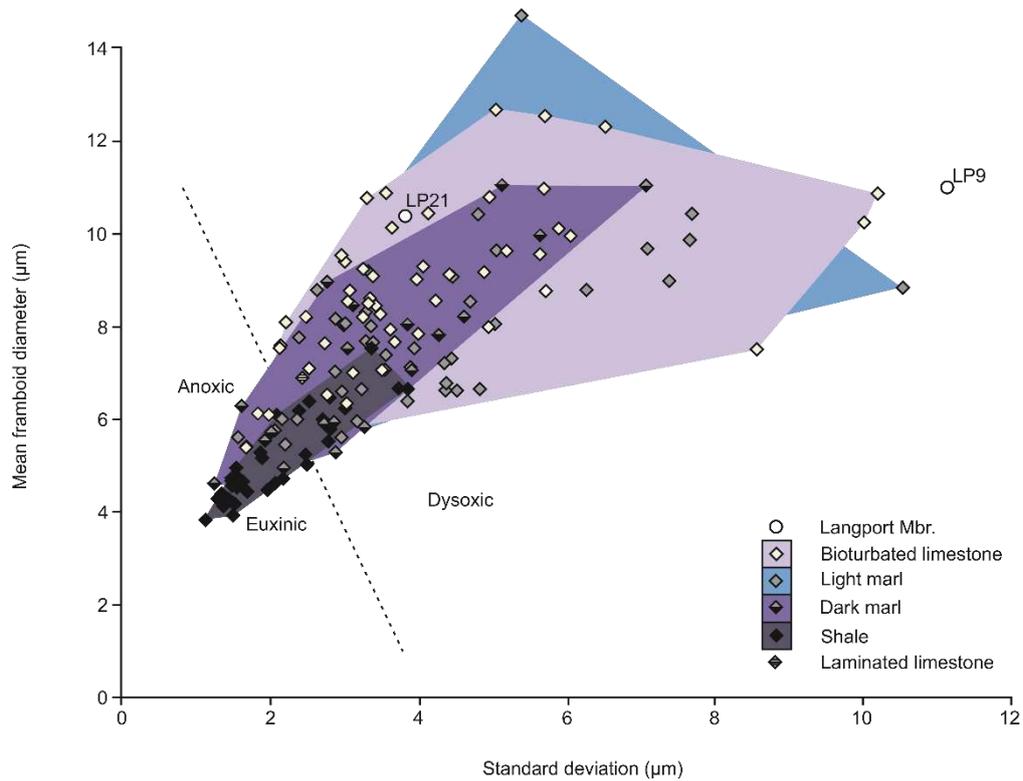
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869 **Figure 2. Location map and palaeogeography of southwestern Britain, Early**
 870 **Jurassic islands indicated by shaded regions, modified from Martill et al. (2016).**



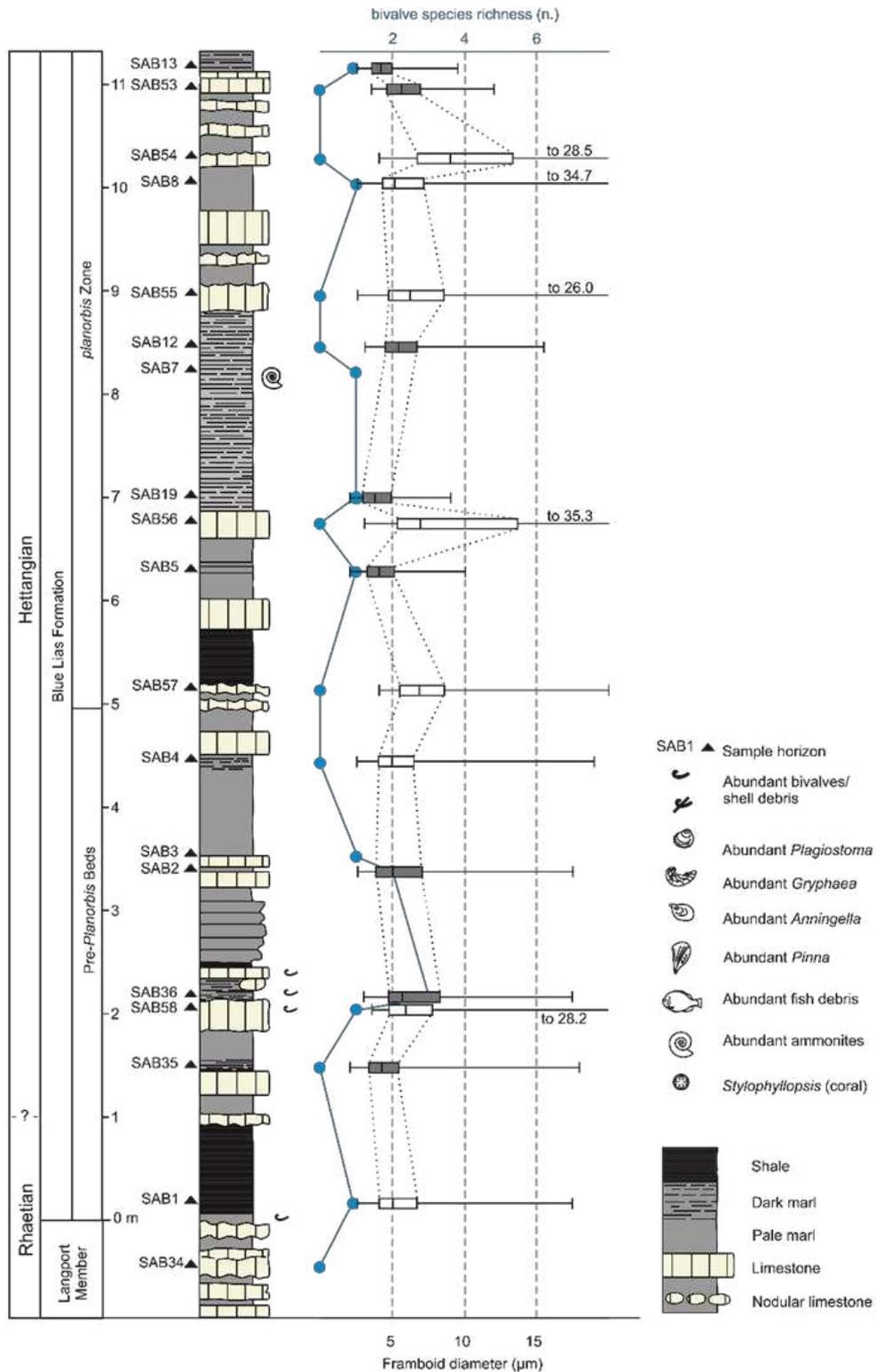
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872 **Figure 3. Example populations of pyrite framboids from an anoxic mudstone**
 873 **(Q39, top) and a dysoxic marl (NP15, bottom).**



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875 **Figure 4. Mean framboid diameter (µm) against standard deviation of framboid**
 876 **diameters (Wilkin diagram), samples plotted according to lithology. Dashed line**
 877 **dictated anoxic-dysoxic threshold. Shaded regions illustrate spread of results.**



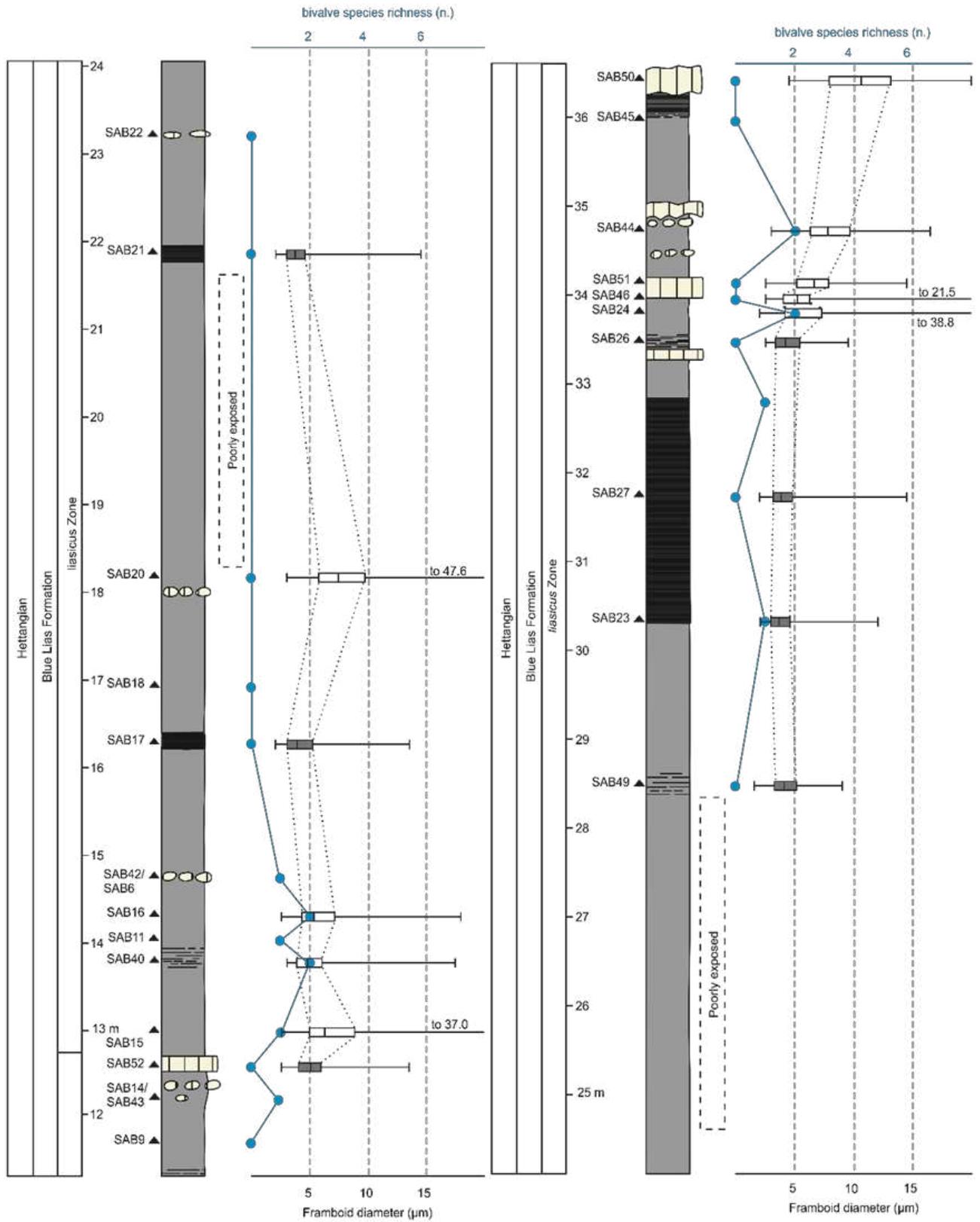
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879 **Figure 5. St. Audrie's Bay, Somerset. Box and whisker plots, box depicts 25th**

880 **and 75th percentiles, central line is median, whiskers illustrating minimum and**

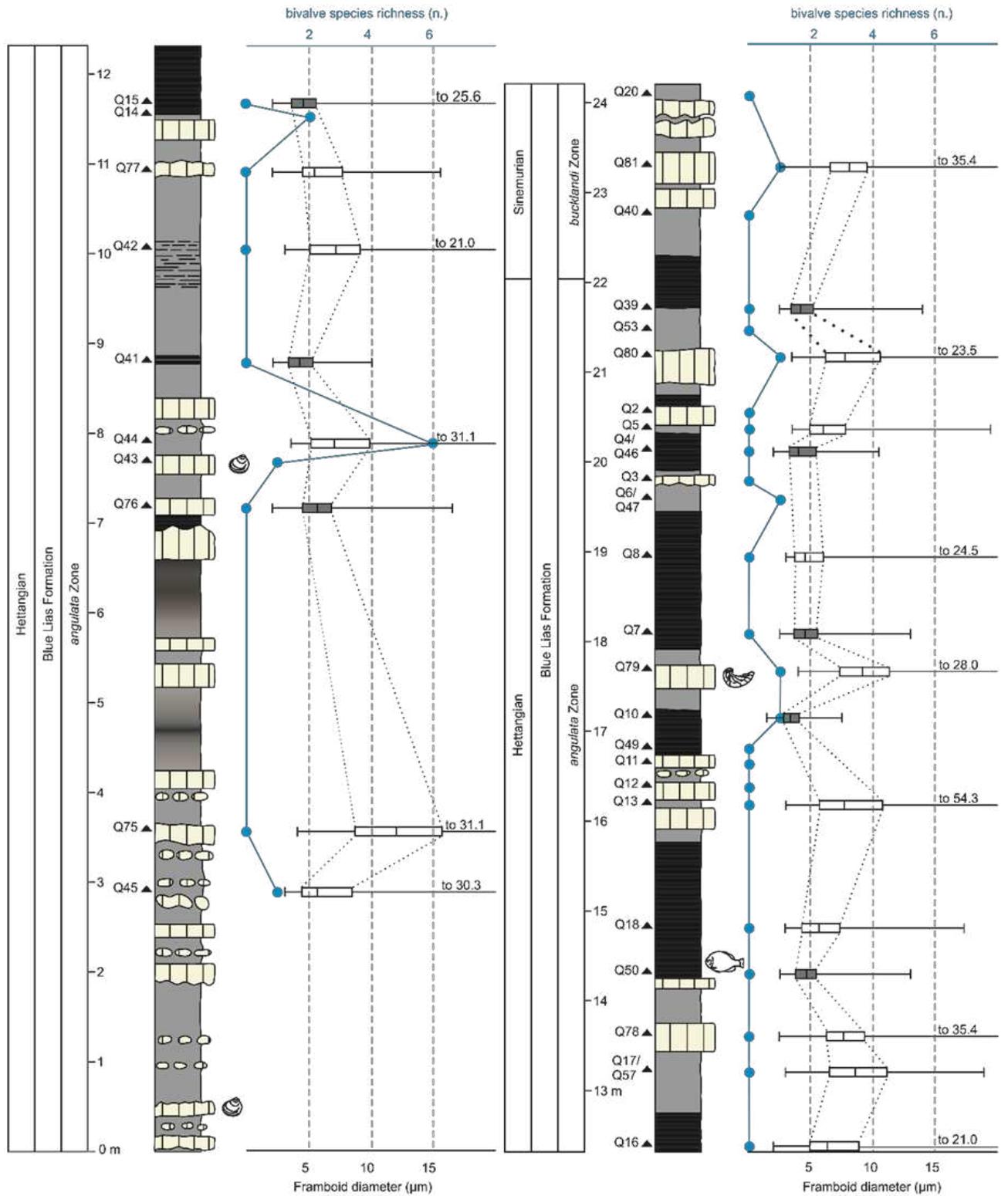
881 **maximum framboid diameters. Shaded boxes indicate samples that plot below**

882 the oxic-anoxic line on a Wilkin diagram. Solid circles record raw species
883 richness per sampled horizon. Approximate position of Triassic-Jurassic
884 boundary from Weedon et al. (2018b).



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886 (Figure 5 continued)

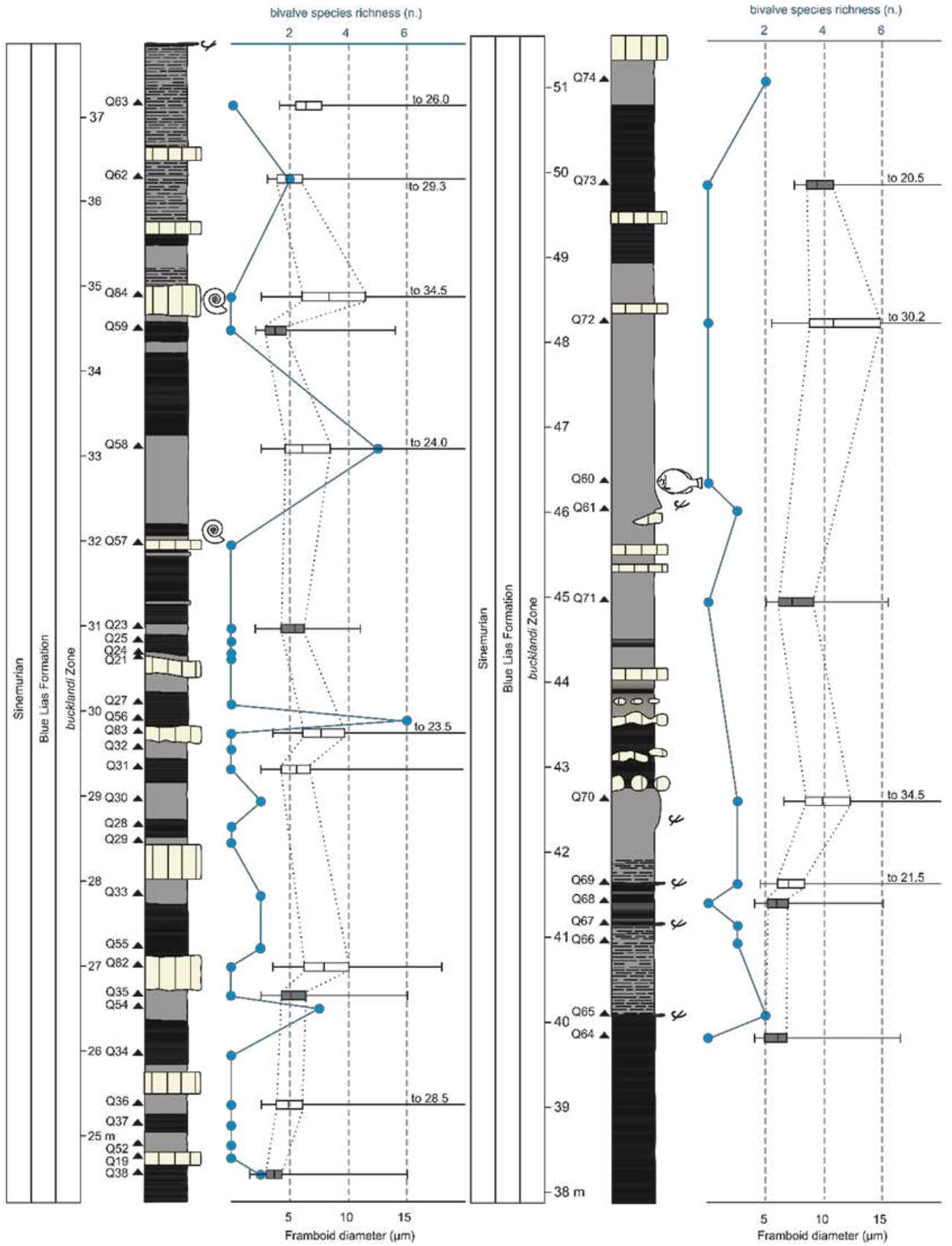


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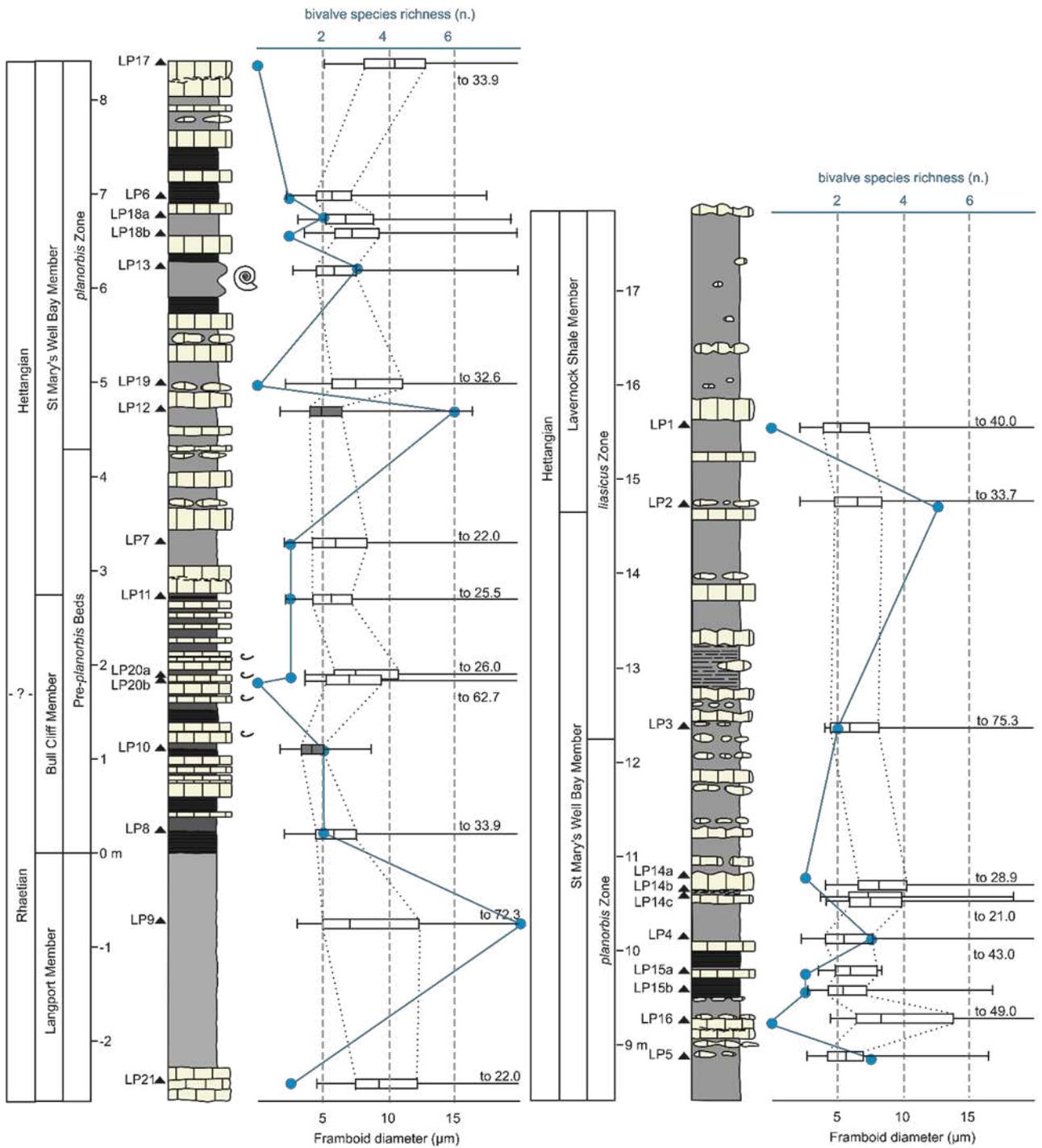
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Figure 6. East Quantoxhead Somerset, sedimentary log modified from Bloos and Page (2002) see figure 5 for details.



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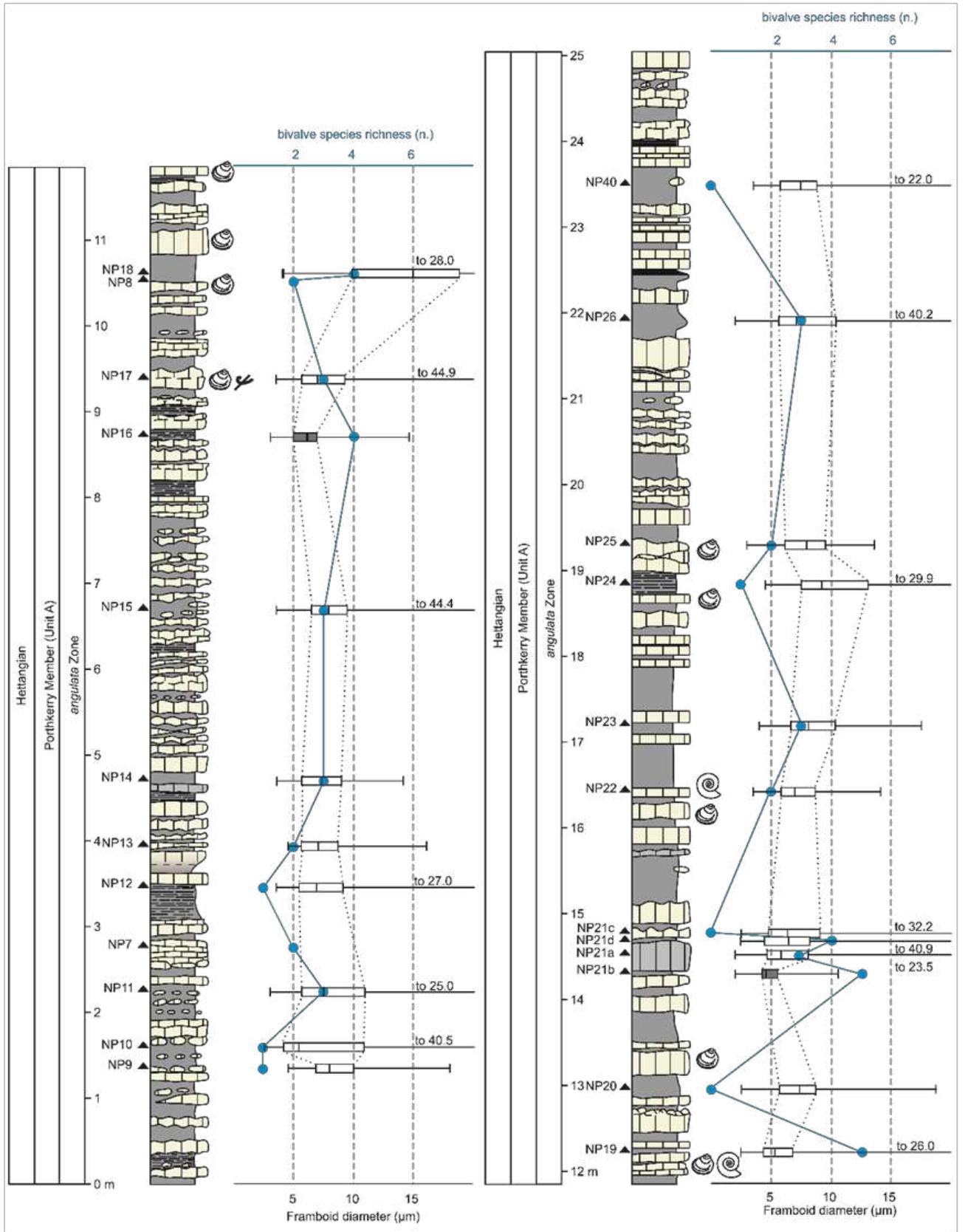
891 (Figure 6 continued)



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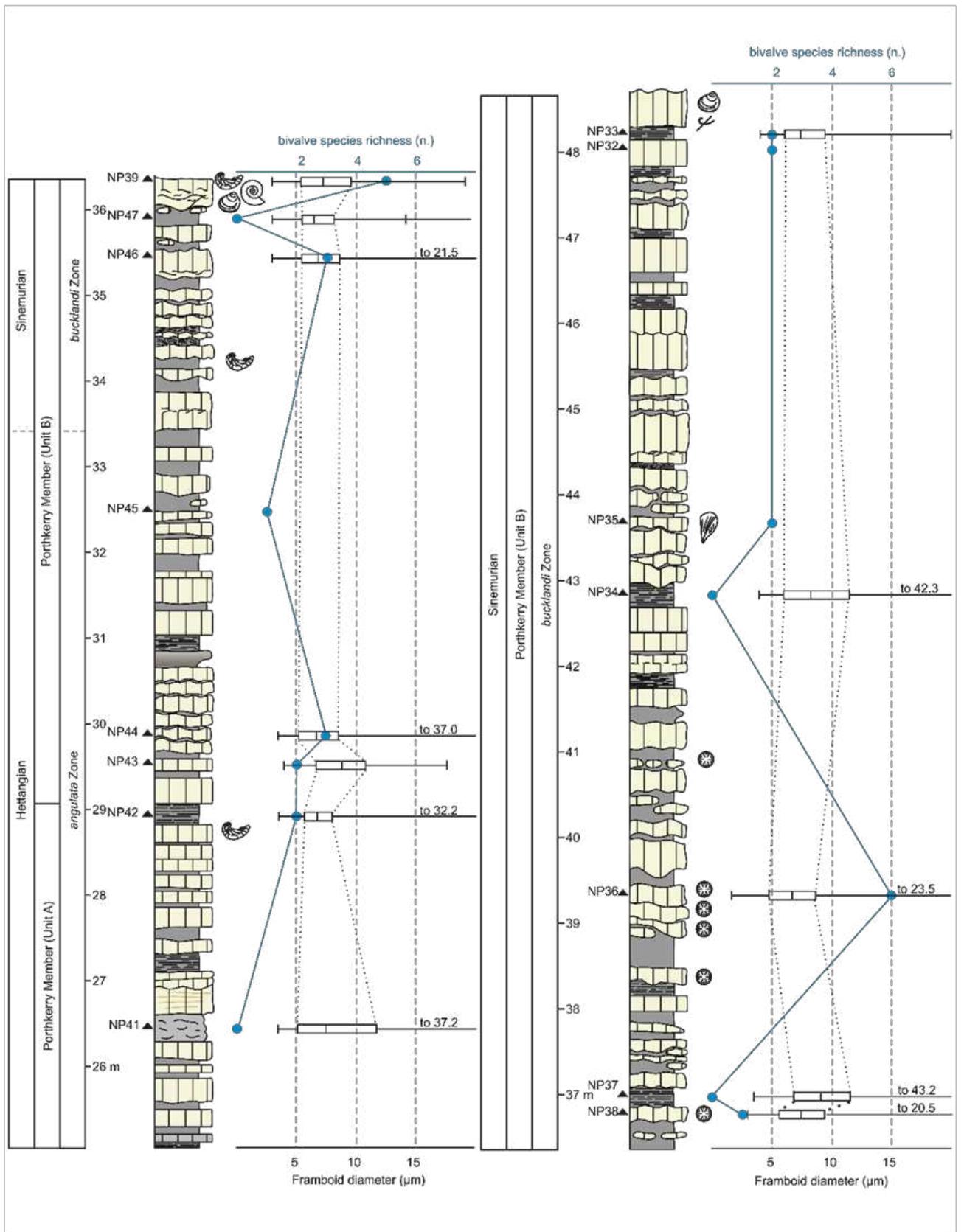
893 **Figure 7. Lavernock Point, Glamorgan. Sedimentary log modified from Simms**

894 **et al. (2004). See figure 5 for details.**



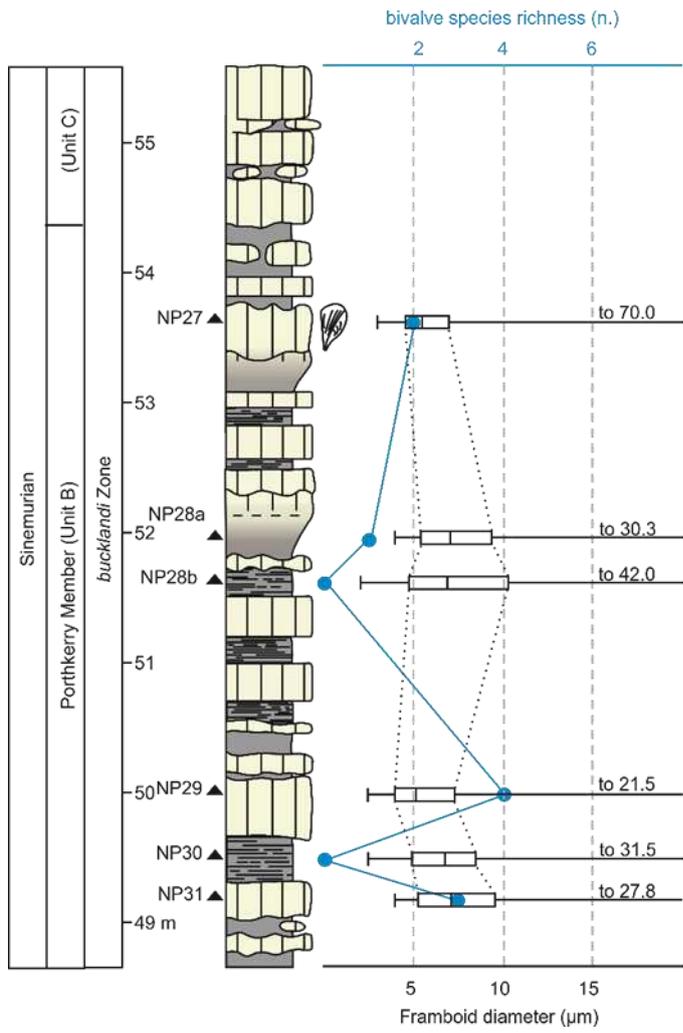
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896 Figure 8. Nash Point, Glamorgan, see figure 5 for details.



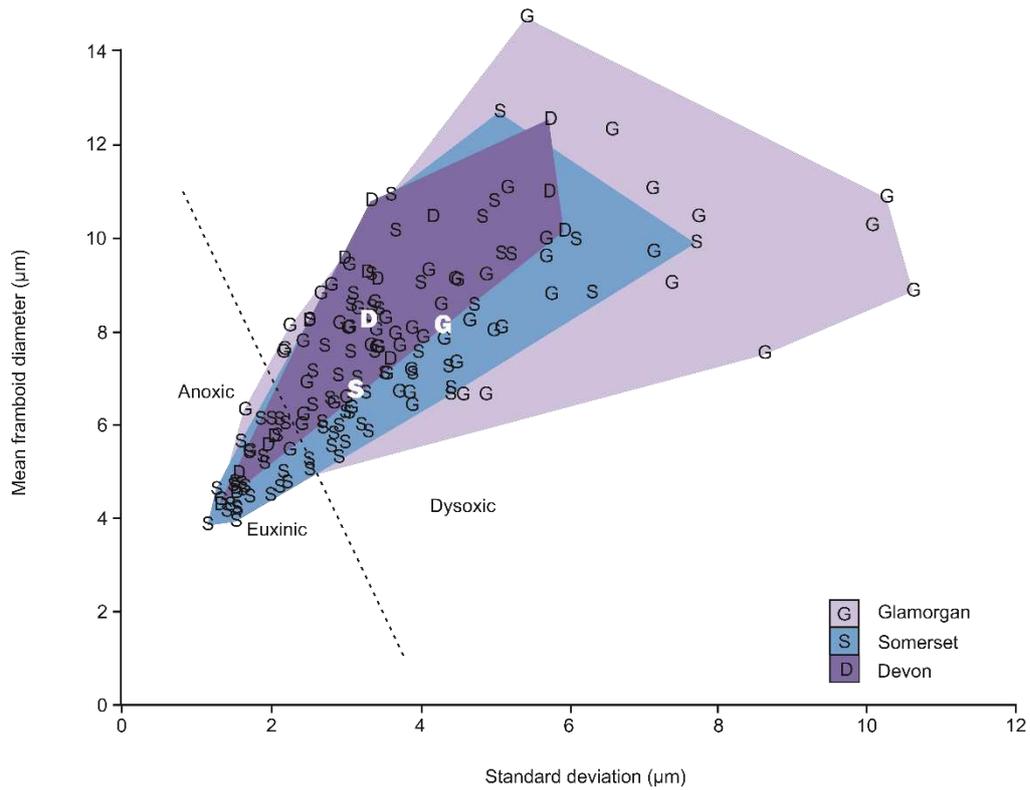
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898 (Figure 8 continued)



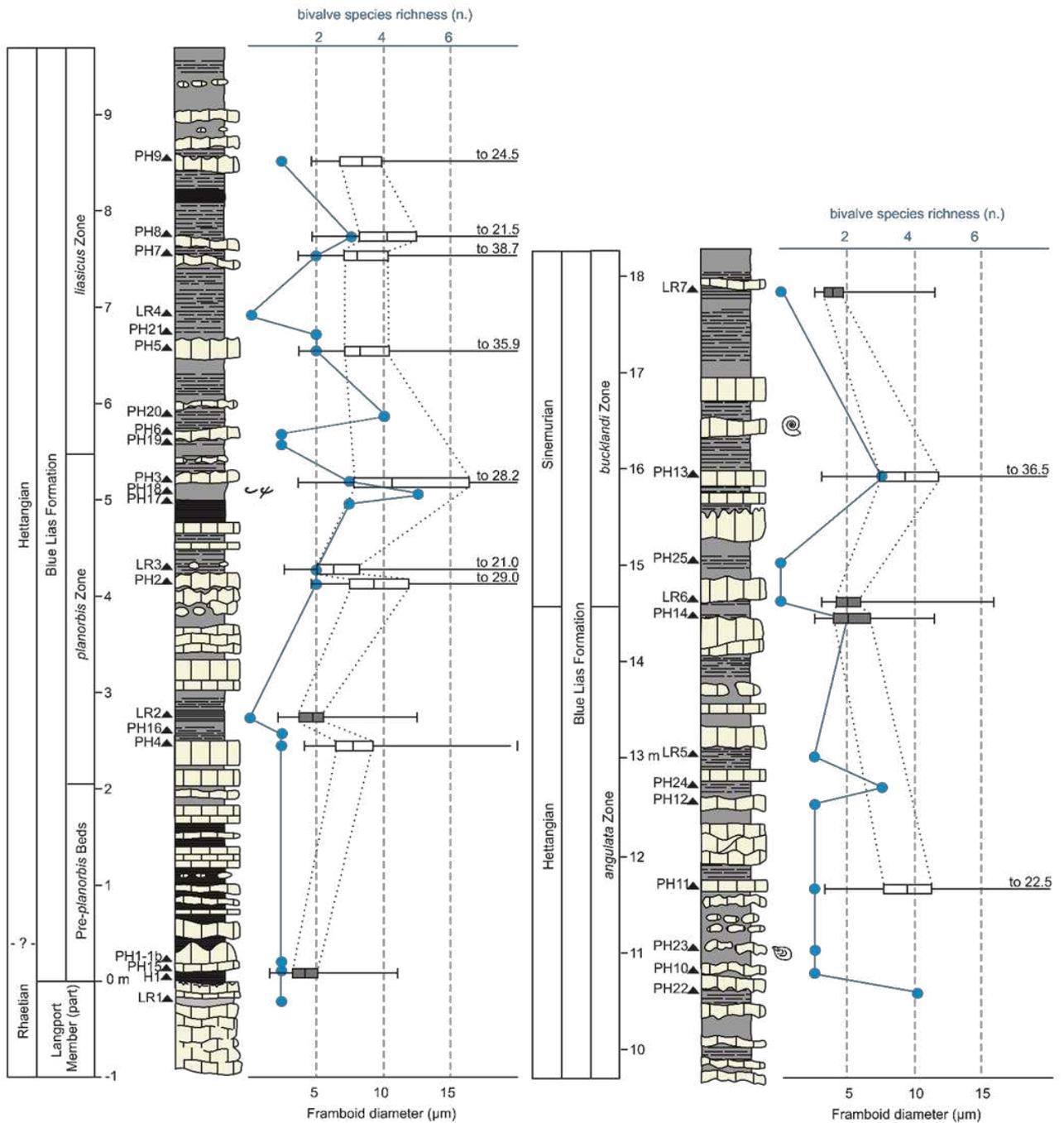
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900 (Figure 8 continued)



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902 **Figure 9. Wilkin diagram, samples plotted according to geographic region. D –**
 903 **Devon, S – Somerset, G – Glamorgan. Means of each location indicated as a**
 904 **bold white letter.**

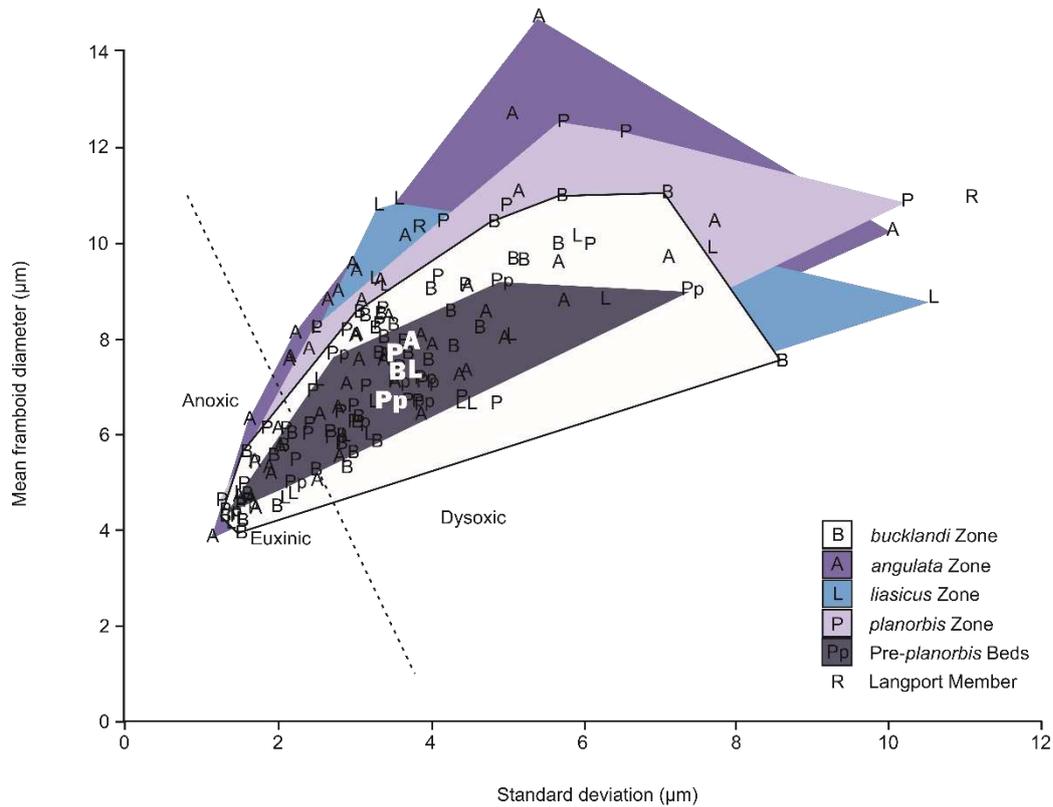


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Figure 10. Pinhay Bay, Devon. Sedimentary log modified from Hesselbo and Jenkyns (1995). See figure 5 for details.



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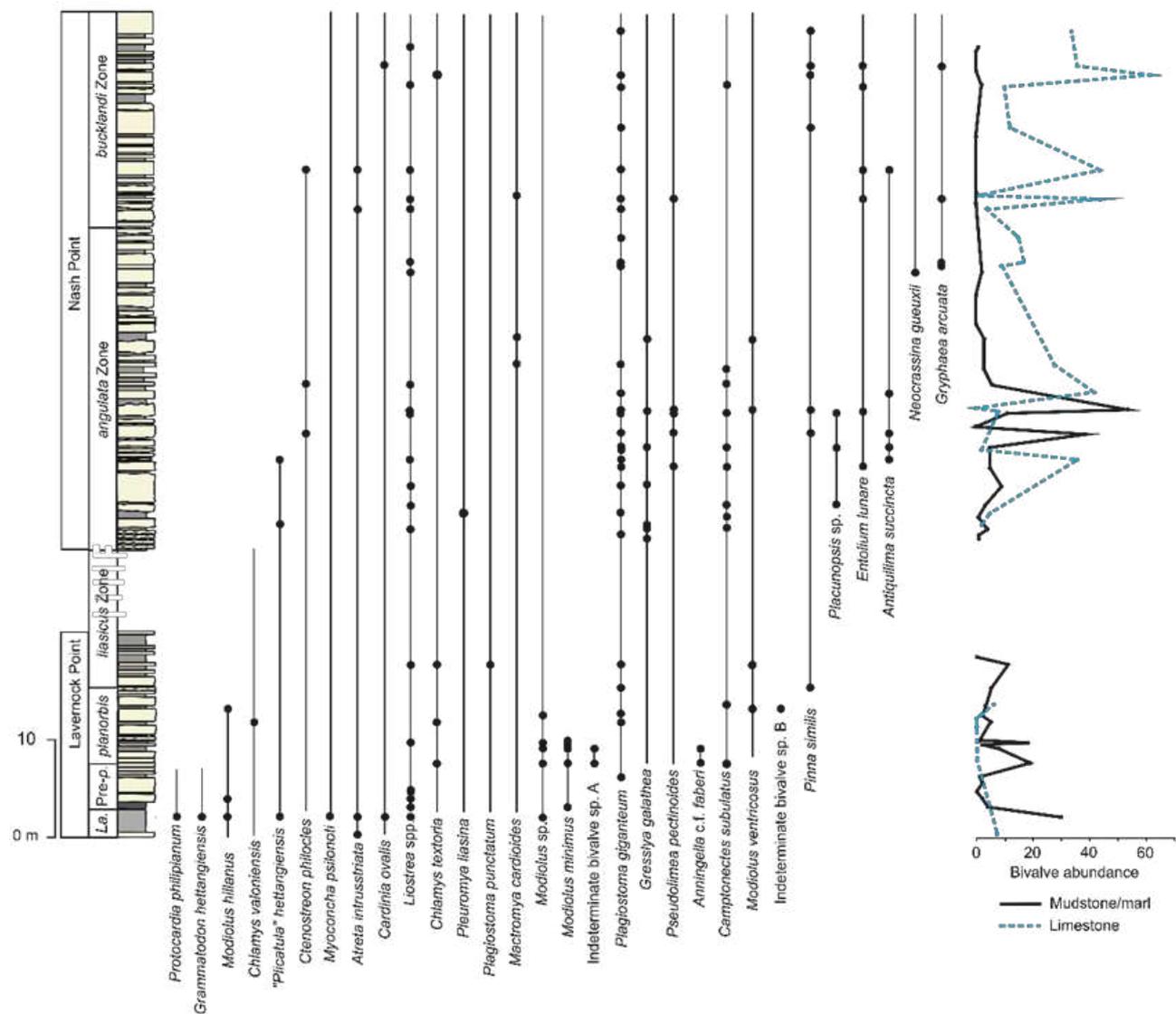
909 **Figure 11. Wilkin diagram, samples plotted according to ammonite zone/time**

910 **bin. R – Langport, Pp – Pre-planorbis Beds, P – planorbis Zone, L – liasicus**

911 **Zone, A – angulata Zone, B – bucklandi Zone. Average for each zone indicated**

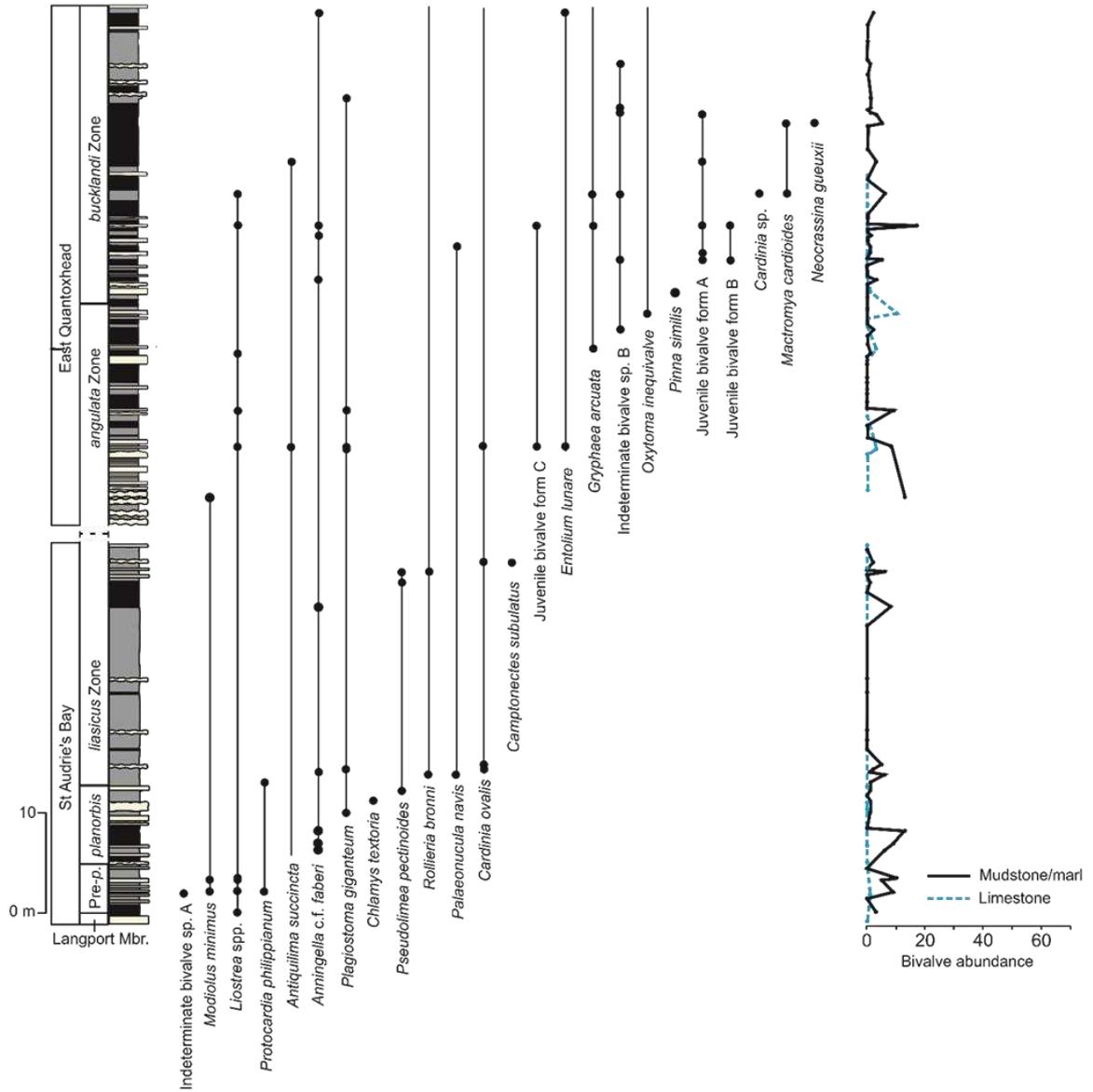
912 **as a bold white symbol, no average is given for the Langport (R) owing to the**

913 **large disparity in standard deviations of the two samples.**



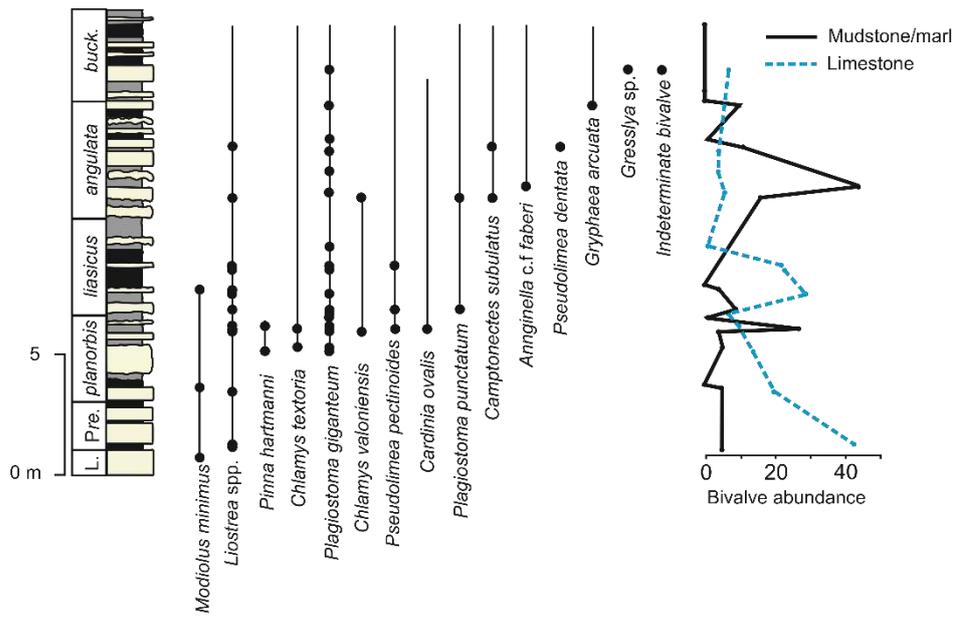
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915 **Figure 12. Species range chart and bivalve abundances for Glamorgan**
 916 **(Lavernock Point and Nash Point). For range chart dark circles show horizons**
 917 **species were encountered during field collections. Connecting line indicates**
 918 **range of species, extensions to ranges based on personal observations,**
 919 **museum collections of NMW, Bath Royal Literary and Scientific Institute, Bristol**
 920 **City Museum and Art Gallery, and published literature (Hodges, 2018, 2000;**
 921 **Ivimey-Cook et al., 1999; Palmer, 2010). For abundance plot solid line depicts**
 922 **bivalve abundances from mudstones and marls, dashed line from limestones.**



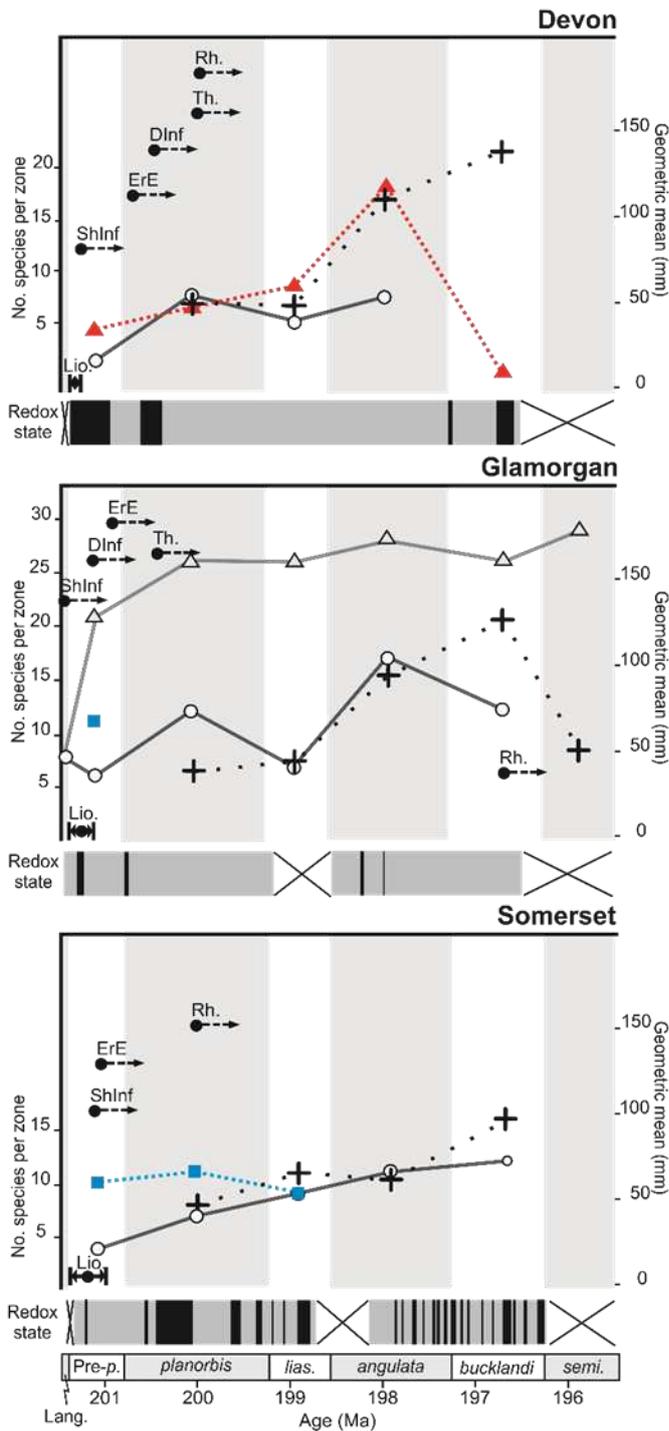
923

924 **Figure 13. Species range chart for Somerset (St Audrie's Bay and East**
 925 **Quantoxhead). See figure 12 for details.**



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927 **Figure 14. Species range chart for Devon (Pinhay Bay). See figure 12 for details.**



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Figure 15. Compiled recovery metrics and oxygenation states for each of the three studied regions. Hollow circles show number of species encountered per zone, from this study. Hollow triangles show number of species per zone from combined field and museum collections of Glamorgan. Squares show species richness per zone from range charts published in Mander et al. (2008) and

934 **solid triangle the same from Pugh et al. (2014). Crosses depict average**
935 **geometric mean shell size of Plagiostoma giganteum per location per zone**
936 **from Atkinson et al. (2019). Filled circles and arrows show first recorded**
937 **position of key recovery features of stages from Twitchett recovery model,**
938 **codes as follows: Lio. – Liostrea shell beds (stage 1), ShInf – shallow infauna**
939 **(stage 2), Rh. – Rhizocorallium burrows (stage 3), Th. – Thalassinoides**
940 **burrows, ErE – erect epifauna (crinoids, stage 3), DInf – Deep infauna. For**
941 **redox starts grey bars indicate periods with dysoxic framboid size**
942 **distributions, black bars anoxic distributions, regions crossed out lack data.**
943 **Time scaled to Weedon et al. (2018b).**

944

945