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1 Major coral extinctions during the early Toarcian global
2 warming event

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18

19 **ABSTRACT**

20

21 The current loss of taxa from our planet is considered by many scientists to be the sixth mass
22 extinction; in particular, coral reefs are experiencing significant damage. Scleractinian coral reefs

23 constitute the framework of some of the most diverse ecosystems on Earth today as well as
24 throughout the last 250 million years. The Pliensbachian-Toarcian (Pl-To) transition in the Early
25 Jurassic is an important geologic analogue for present-day global disruptions as it provides
26 insights about the ability of corals to survive significant changes in climatic and oceanic
27 conditions. Based on a revised and greatly expanded taxonomy of Tethyan coral faunas for both
28 stages, we reveal a catastrophic extinction (49% at genus and 90.9% at species level) and
29 subsequent radiation for the group during the early Toarcian. The devastation during the late
30 Pliensbachian and early Toarcian biotic crisis suggests that this interval is potentially the most
31 important extinction event for scleractinian corals and fundamentally shaped the future of
32 diversity and morphological disparity within the coral clades that flourished during the Jurassic
33 and Cretaceous. Consequently, this interval should be considered a key period in the
34 evolutionary dynamics of the group and reef ecosystems more broadly. These data on coral
35 survival and recovery during the Early Jurassic event are particularly pertinent for questions
36 about present day ecosystem collapse and conservation of coral habitats.

37

38 Keywords: early Toarcian, Ocean anoxic event, corals, crisis, Scleractinia,

39

40 **1. INTRODUCTION**

41

42 The history of life is punctuated by extinction events that drove evolutionary dynamics, and
43 scientists posit that the Earth is currently entering a similar mass extinction (Ceballos et al.,
44 2015). Five major “first-order” biotic crises are reported for the Phanerozoic, followed by
45 “second-order” crises, such as the Pliensbachian-Toarcian crisis at ca. 183 Ma (e.g., Raup and

46 Sepkoski, 1982; Bambach et al., 2004). The distinction between first and second-order crises
47 remains unclear as the ranking of crises varies according to the considered characters, such as
48 taxonomic scale (i.e., families, genera, species), functional niche loss, consideration of associated
49 palaeoenvironmental upheaval, and the different ways to statistically weigh raw data (Benton,
50 1995).

51 The Pliensbachian-Toarcian (PI-To) transition was marked by drastic and repeated
52 palaeoenvironmental disturbances associated with the emplacement of the Karoo-Ferrar igneous
53 province in southern Gondwana (Burgess et al., 2015). These environmental changes included
54 major shifts in the temperature, chemistry, and oxygenation of the oceans, culminating in the
55 Toarcian Oceanic Anoxic Event (T-OAE) (e.g., Suan et al., 2010; Gómez and Goy, 2011;
56 Caruthers et al., 2011; Dera et al., 2011, Reolid et al., 2020). Following the middle Pliensbachian
57 warm period (Gómez et al., 2016), the latest Pliensbachian is marked by a significant cooling
58 event with important sea-level fluctuations (de Graciansky et al., 1998; Aurell et al., 2003; Suan
59 et al., 2010; Pittet et al., 2014; Krencker et al., 2019). The PI-To boundary coincides with a
60 pronounced warming event (Suan et al., 2010), enhanced continental weathering, and a
61 widespread demise of neritic carbonate ecosystem (Bodin et al., 2016; Krencker et al., 2020),
62 which often led to strong condensation of the sedimentary record or even a hiatus in
63 sedimentation (Morard et al., 2003; Léonide et al., 2012; Krencker et al., 2014; Pittet et al.,
64 2014). Climate cooling is observed during the remainder of the earliest Toarcian (Polymorphum
65 zone; Ruebsam et al., 2019; Krencker et al., 2020), allowing renewed neritic carbonate
66 production in several areas across the Tethys Ocean (Léonide et al., 2012; Trecalli et al., 2012;
67 Krencker et al., 2020). At the onset of the T-OAE, a second demise of neritic carbonate
68 ecosystems occurred, likely triggered by a profound carbon cycle perturbation, soaring global

69 temperature (Suan et al., 2010; Korte et al., 2015), and a second pulse of continental weathering
70 (Bodin et al., 2010; Krencker et al., 2020; Ettinger et al., 2021). Neritic carbonate production
71 resumed along the southern Tethyan margin during the recovery of the carbon isotope excursion
72 associated with the T-OAE (Trecalli et al., 2012; Krencker et al., 2014, 2015) but not until at
73 least the middle Toarcian along the northern Tethyan margin (Blomeier and Reijmer, 1999;
74 Aurell et al., 2003; Léonide et al., 2012; Brigaud et al., 2014).

75 The PI-To transition is one of the five most significant reefal crises in the geological record
76 (Flügel and Kiessling, 2002; Kiessling and Simpson, 2011; Kiessling, 2011) and this event is
77 correlated with significant extinctions across a wide number of marine taxa (Little and Benton,
78 1995; Ruban, 2004; Mattioli et al., 2009; Dera et al., 2010; Caruthers et al., 2013; Brame et al.,
79 2019) as well as continental plants (Slater et al., 2019). The existing literature on corals during
80 the PI-To transition was highly dependent on the taxonomic work of Beauvais (1986). Indeed,
81 previous studies (Kiessling et al., 2007; Lathuilière and Marchal, 2009) identified the need for
82 more original field data followed by a revision of the taxonomy based on these new specimens
83 and with consideration of possible intraspecific variability. This study provides a stronger
84 analysis of Pliensbachian and Toarcian coral assemblages based in extensive new collections
85 from Morocco (Middle and High Atlas), Italy (Calabria), France (Calvados and Pyrenees) and a
86 deep revision of taxa from the literature (Vasseur, 2019; Vasseur and Lathuilière, 2020 in press).
87 It also offers the first opportunity to examine coral assemblages in between the
88 Pliensbachian/Toarcian stage boundary and T-OAE.

89

90 **2. MATERIAL:**

91

92 Data have been gathered by the authors from five field missions in Morocco (Dadès Valley,
93 Amellagou, Ziz Valley and Guigou Plateau) and one in Italy (Caloveto, Calabria). In addition to
94 corals, ammonites were also collected to improve the age calibrations for this material using the
95 most recent revisions of ammonite determination and biozones (Dommergues and Meister,
96 2017). New specimens collected by Marc Chesnier from Normandy (France) and Philippe Fauré
97 from the French Pyrenees were also included. In addition, the dataset integrates updated coral
98 descriptions from the literature with revised descriptions of the corresponding samples when
99 available (collections of the Muséum d'Histoire Naturelle in Paris, Muséum d'histoire naturelle
100 de Genève). These taxa are described in Vasseur (2019) and in a monograph for Pliensbachian
101 corals (Vasseur and Lathuilière 2020, in press). The dataset thus compiled includes records from
102 Algeria, France, Italy, Morocco, Slovenia, Belgian, Germany, England, Argentina, Indonesia,
103 Spain, Switzerland, Tajikistan.

104

105 **3. RESULTS AND ANALYSES:**

106

107 **3.1. Pliensbachian coral assemblages**

108

109 In the field, Pliensbachian coral faunas are widely dominated in both diversity and quantity by
110 solitary and phaceloid forms, while highly integrated forms (i.e., plocoid, cerioid,
111 thamnasterioid, and meandroid) are rare and often occur as diminutive colonies (Tab. 1, Fig.1).
112 One exception to this general trend is in the Middle-Atlas and Calabria, where large, high-
113 integration corals occur with higher diversity and skeletal volume in quite distal position.

114

115

116

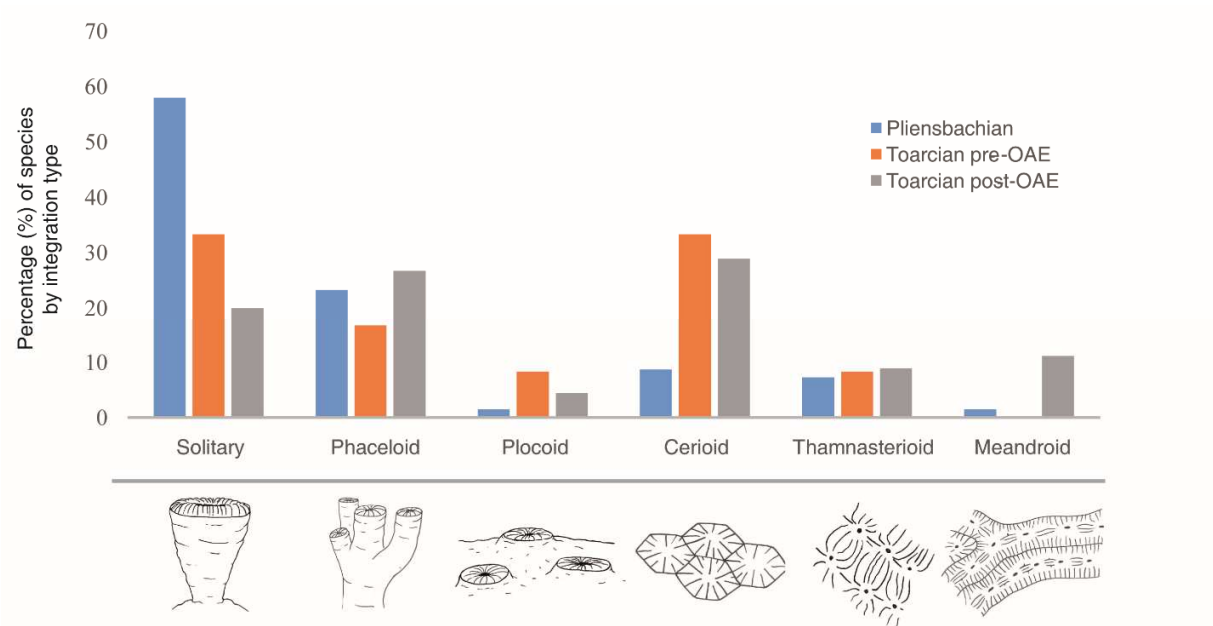
117

	Solitary			Phaceloid			Plocoid			Cerioid			Thamnasterioid			Meandroid		
	Pli	To 1	To 2	Pli	To 1	To 2	Pli	To 1	To 2	Pli	To 1	To 2	Pli	To 1	To 2	Pli	To 1	To 2
Gu	7	-	3	7	-	6	1	-	1	7	-	7	1	-	3	1	-	5
Am	25	-	1	2	-	3	1	-	1	3	-	8	1	-	-	-	-	3
Da	4	1	2	2	2	2	1	1	-	2	3	-	-	1	-	-	-	-
Zi	-	-	-	1	-	3	-	-	-	-	-	-	1	-	-	-	-	1
Ca	6	-	-	5	-	-	2	-	-	5	-	-	2	-	-	-	-	-
Br	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Es	3	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Li	18	-	7	3	-	3	-	-	-	-	-	3	2	-	1	-	-	2

118

119 Table 1. Number of species of each morphological type (solitary, phaceloid, plocoid, cerioid,
120 thamnasterioid, meandroid) in each studied time zone (Pliensbachian [Pli], Toarcian pre-OAE
121 [To1], and Toarcian post-OAE [To2]) for every studied locality with additional information from
122 the published literature (Gu: Guigou Plateau/Aïn Leuh (Morocco); Am: Amellagou (Morocco);
123 Da: Dades Valley (Morocco); Zi: Ziz valley (Morocco); Ca: Calabria (Italy); Br: Brûlon
124 (France); Es: Estivère Pass (France); Li: literature).

125



126

127 Figure 1. Coral integration types as a percentage of total species among Tethyan coral faunas
 128 during the Pliensbachian, pre-T-OAE Toarcian, and post-T-OAE Toarcian.

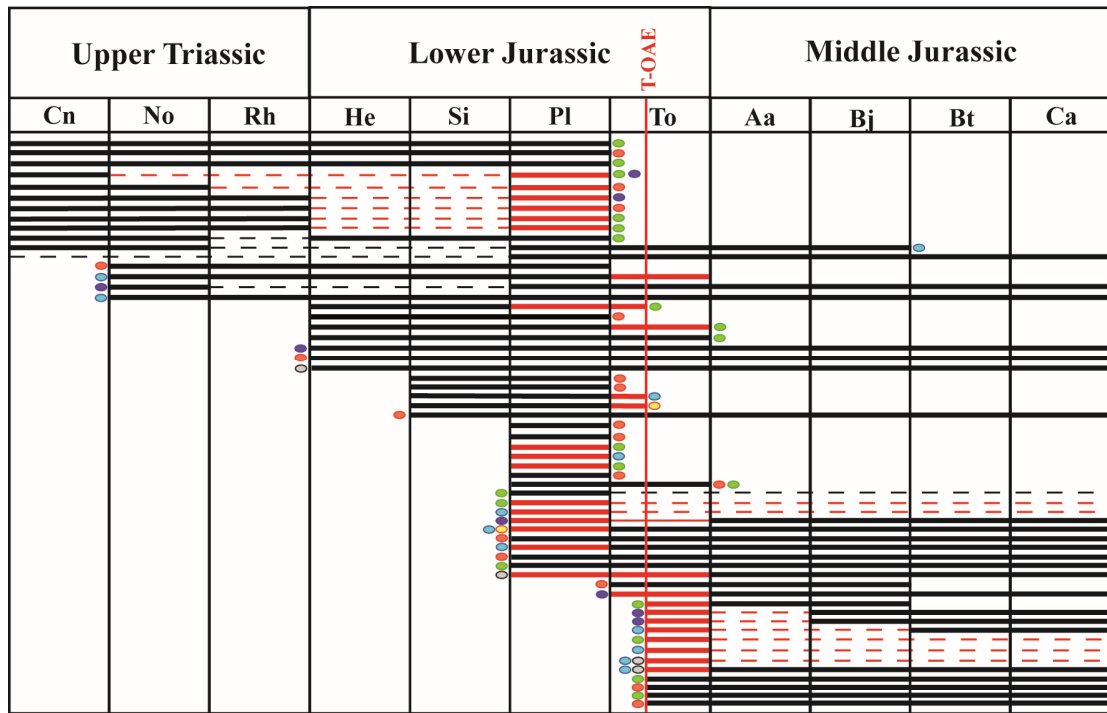
129

130 In proximal environments, corals sometimes lived in close relationship with lithiotid bivalves;
 131 such reefs and biostromes can be found in the Moroccan High-Atlas Mountains, Spain, Oman,
 132 Slovenia, Italy, Switzerland, the Himalayas, and Timor (Brame et al., 2019) but we found no
 133 such association in Calabria and the Middle-Atlas Mountains. In the Middle-Atlas Mountains,
 134 coral populations were established in giant offshore bioherms detached from any inner platform
 135 on a gently sloping tilted block in Guigou Plateau (El Arabi *et al.*, 1987; Vasseur, 2019). In the
 136 Longobucco basin (Calabria), reefs are smaller and occur on steep slopes (Santantonio, 2012;
 137 Santantonio et al., 2016).

138

139 Pliensbachian coral populations are composed predominantly of genera with Triassic or Early
 140 Jurassic roots but very few of these genera persist through the T-OAE (Fig. 2). The

141 Pliensbachian is characterized by a surprising radiation event: 17 genera appeared, including
 142 5 solitary and 5 phaceloid genera. Among these 17 genera, 11 persisted after the T-OAE. All
 143 genera that are exclusively Pliensbachian are solitary or phaceloid with one exception.



144
 145 Figure 2. Range chart of Tethyan Pliensbachian and Toarcian coral genera. New data are in red;
 146 thick line: observed taxon within the stage, dotted line: interpolated occurrence. The colored dots
 147 refer to the integration types presented in Fig. 1: red for solitary; green for phaceloid; yellow for
 148 plocoid; blue for cerioid; purple for thamnasterioid; grey for meandroid. See supplemental data
 149 (Appendix) for taxonomy.

150

151 3.2. Toarcian coral assemblages

152

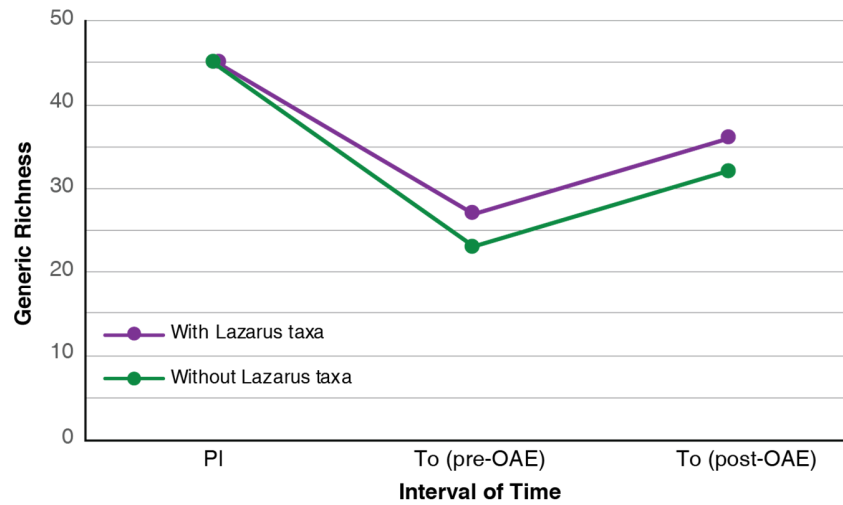
153 No coral reefs have been observed in the earliest Toarcian strata (i.e., before the onset of the T-
 154 OAE) and this paucity of sampling localities complicates the assessment of the dominant forms

155 in terms of volume in the assemblage. Nevertheless, the analyses of reworked corals and corals
156 that occur in lithiotid-coral biostromes reveal faunas composed of taxa that evolved during the
157 Early Jurassic mixed with taxa that are classically observed in Middle/Upper Jurassic strata
158 (Fig.2). These observations suggest a transitional period when coral extinctions occurred in
159 association with radiations. During the pre-T-OAE, highly integrated forms are more common,
160 both in terms of diversity and biomass, than they are in the Pliensbachian. These strata contain
161 the last important associations of lithiotid bivalves before their extinction at the onset of the T-
162 OAE (Brame et al., 2019, Posenato et al., 2018).

163 Large reefs have been observed in post-T-OAE intervals (in Dades Valley and Aïn Leuh,
164 Morocco) and in these reefs the diversity and biomass of highly integrated corals are equal to
165 phaceloid forms. Most of the genera that constitute these assemblages persisted and diversified
166 during the Middle/Late Jurassic (Vasseur, 2019). 14 genera survived through the entire Toarcian,
167 including 4 exclusively phaceloid and 3 solitary ones. The evolution of generic richness through
168 the Pliensbachian, Toarcian pre-OAE, and Toarcian post-OAE is presented in figure 3.

169

170



171

172 Figure 3. Evolution of generic richness through the three time intervals studied: Pliensbachian,
 173 Toarcian pre-OAE, and Toarcian post-OAE with and without Lazarus taxa (Lazarus taxa
 174 correspond to taxa that have not been found in the considered stage but exist in previous and
 175 later stages).

176

177 3.3. Accounting for biases

178

179 Analyses have been performed on normalized data as well as the raw data. The normalized data
 180 have been weighted either by the duration of stages to calculate the diversity or by the total
 181 diversity to calculate the extinction rates, according to the methods used in Lathuilière and
 182 Marchal (2009). Stage durations have been calculated using the 2018 international stratigraphic
 183 chart and the age of the T-OAE from Krencker et al. (2014) and considering a duration of 450
 184 kyr for the T-OAE (Boulila et al., 2019):

185 Pliensbachian: $190.8 - 182.7 = 8.1$ Ma;

186 Toarcian: $182.7 - 174.1 = 8.6$ Ma;

187 Toarcian pre-T-OAE: $182.7 - 181.7 = 1$ Ma;

188 Toarcian post-T-OAE: $8.6 - 1.45 = 7.15$ Ma.

189

190 Pre-T-OAE Toarcian and post-T-OAE Toarcian have been discriminated in the analyses, despite
191 the important difference of sampling quality between these two periods.

192

193 Sampling biases have also been minimized by removing the following singletons from the
194 analyses: *Araiophyllum*, *Archaeosmiliopsis*, *Astraeomorpha*, *Dimorpharaea*, *Gillismilia*,
195 *Microsolena*. In the present generic analysis, singletons correspond to genera including one
196 single species, itself represented by one single specimen (Foote 1994, 2000; Aberhan and
197 Kiessling, 2012). Lazarus taxa correspond to taxa that have not been found in the considered
198 stage but exist in previous and later stages.

199

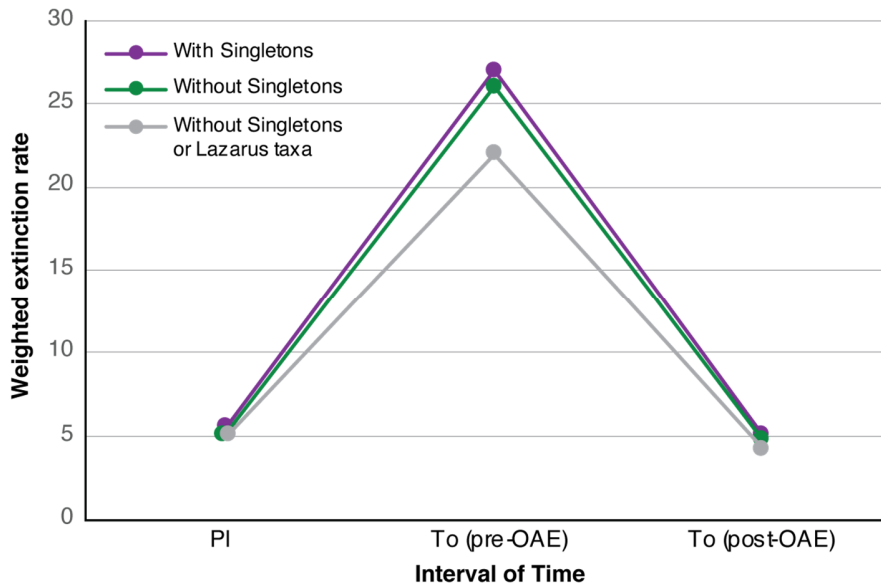
200 Weighted analyses have been produced on the data with (1) and without (2) the singletons and
201 also without both singletons and Lazarus taxa (3):

202

	Weighted analysis of coral diversity as a function of stage duration			
	Pliensbachian stage	Toarcian stage	Pre-OAE Toarcian	Post-OAE Toarcian
Weighted analysis* with singletons	$45 / 8.1 = 5.56$	$39 / 8.6 = 4.53$	$27 / 1 = 27$	$36 / 7.15 = 5.03$
Weighted analysis* without singletons	$41 / 8.1 = 5.06$	$37 / 8.6 = 4.3$	$26 / 1 = 26$	$34 / 7.15 = 4.76$
Weighted analysis* without singletons or Lazarus taxa	$41 / 8.1 = 5.06$	$33 / 8.6 = 3.84$	$22 / 1 = 22$	$30 / 7.15 = 4.2$

*Number of genera in the stage / stage duration

203



204

205 Figure 4. Weighted diversity for the Pliensbachian (PI), pre-OAE Toarcian and post-OAE

206 Toarcian calculated with (1) and without (2) singletons, and without both singletons and Lazarus

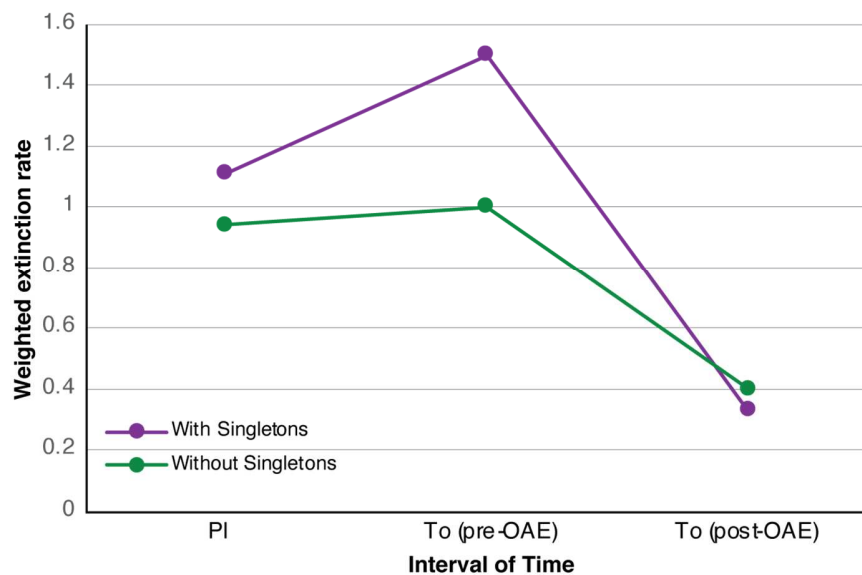
207 taxa (3).

208

	Weighted analysis of extinctions as a function of stage duration			
	Pliensbachian stage	Toarcian stage	Pre-OAE Toarcian	Post-OAE Toarcian
Weighted extinction rate* with singletons	20 / 18 = 1.11	3 / 14 = 0.21	3 / 2 = 1.5	4 / 12 = 0.33
Weighted extinction rate* without singletons	17 / 18 = 0.94	2 / 12 = 0.17	2 / 2 = 1	4 / 10 = 0.4

*Number of extinctions / number of occurrences

209



210

211 Figure 5. Weighted extinction rates for the Pliensbachian (PI), pre-OAE Toarcian and post-OAE

212 Toarcian calculated with (1) and without (2) singletons.

213

214 The results of the raw data and weighted data are comparable (Fig. 4, 5); in fact, Pliensbachian

215 and Toarcian stages show similar durations with taxa and singletons equally distributed between

216 the two stages.

217

218 3.4. Family scale analysis

219

220 Analyses at the family scale provide good appreciation of disparity *sensu* Gould (1991).

221 Moreover, fossil coral families are primarily defined by the microstructures of skeletal septa that

222 are considered as relevant evolutionary novelties. According to our results (Fig.6), 6 families of

223 Triassic affinity disappear at the PI-To boundary and 2 families of Middle/Late Jurassic affinity

224 appear just after the T-OAE. In addition, four coral families that are key builders of Middle and

225 Upper Jurassic coral reefs radiate during the earliest Toarcian (i.e., before the OAE):
 226 Thecosmiliidae (= ex Montlivaltiidae), Comoseridae (=ex Microsolenidae), Stylinidae, and
 227 Thamnasteriidae. Furthermore, this study is the first to document the Deltocyathiidae family in
 228 the Mesozoic fossil record; this family was hypothesized to split at the base of the “robust” coral
 229 clade in the scleractinian phylogeny (Kitahara et al., 2016).

Coral families	PI	To pre-OAE	To post-OAE
Astraeomorphidae Frech 1890			
Coryphylliidae Beauvais 1981			
Margarophylliidae Cuif 1977			
Protoheterastraeidae Cuif 1977			
Reimaniphylliidae Melnikova 1975			
Zardinophyllidae Montanaro Gallitelli 1975			
Hispaniastraeidae Boivin et al. 2019			
Archaeosmiliidae Melnikova 1975			
Actinastreidae Alloiteau 1952			
Axosmiliidae Geyer 1955			
Cladophylliidae Morycowa & Roniewicz 1990			
Dermosmiliidae Koby 1889			
Epismiliidae Alloiteau 1952			
Deltocyathiidae Kitahara, Cairns, Stolarski and Miller 2012			
Latomeandridae Alloiteau 1952			
Comoseriidae Fromentel 1861			
Procycolitidae or Conophylliidae			
Stylinidae d’Orbigny 1851			
Stylophyllidae Frech 1890			
Thamnasteriidae Vaughan and Wells 1943			
Thecosmiliidae Duncan 1884			
Aplosmiliidae Fromentel 1861			
Caryophylliidae Dana 1846			

230
 231 Figure 6. Worldwide known range chart of coral families that occur within the Pliensbachian and
 232 Toarcian stages.

233

234 **4. DISCUSSION:**

235

236 The results presented here illustrate the importance of the PI-To crisis in coral communities; the
 237 Pliensbachian – Toarcian crisis marks the disruption between an early period of high disparity
 238 (represented by the amount of Pliensbachian families) and the later diversification of surviving
 239 taxa during the Toarcian and later. Furthermore, the Pliensbachian and post-T-OAE intervals

240 mark the development of coral pioneers in the colonisation of deeper environments, with many
241 specimens recovered from hemipelagic deposits (Deltocyathiidae and Caryophylliidae), a
242 phenomenon that implies the conquest of new ecological niches. Some of the genera that
243 survived the crisis are assumed to be zooxanthellate corals because of their highly-integrated
244 morphology, high growth rates, living environments and colony shape variations (e.g.,
245 *Dimorphastrea*, *Microphyllia*, *Thamnasteria* – Vasseur, 2019). This is inconsistent with the
246 hypothesis that photosymbiosis is lost during crises periods (Rosen, 2000), unless these genera
247 developed an ability to live without symbionts during crisis time. On the other hand, it is
248 consistent with the high correlation between coloniality and photosymbiosis (Simpson, 2013) as
249 all of these genera are colonial.

250

251 **4.1. Extinction Rates**

252

253 According to the revised and enhanced scleractinian coral dataset, 23 genera among 45 went
254 extinct during the early Toarcian (Fig. 2), including extinctions at the Pl-To boundary and the T-
255 OAE, which corresponds to an extinction rate of 51.1% at the genus scale, 48.7% without
256 singletons (19 genera among 39). Compared to other extinction events, these values are
257 substantial and exceed the revised values of $39 \pm 8\%$ calculated for the Cretaceous/Paleogene
258 (K/Pg) crisis by Kiessling and Baron-Szabo (2004) (evaluated by counting genera that exist just
259 before the extinction but have no record in the Cenozoic). At a finer scale, only 6 of 66 species
260 identified in the Pliensbachian stage survived through the early Toarcian, an extinction rate of
261 90.9%.

262 Another major implication of these results is that Triassic/Jurassic (T/J) coral extinction rates
263 must be recalculated as many Triassic genera thought to go extinct at the T/J were found in the
264 Pliensbachian. Nevertheless, before a T/J extinction rate recalculation can be done, the taxonomy
265 needs revision to minimize taxa overestimation. Kiessling et al. (2007) considered taxa
266 overestimation for the T/J and estimated an extinction rate of 51%–53% at the genus level. All in
267 all, the newly obtained value for Pl-To is still significantly above the mean extinction
268 background signal of $12 \pm 4\%$ for scleractinian coral genera calculated by Kiessling and Baron-
269 Szabo (2004) from Sepkoski (2002) over the total range of Scleractinia. In summary, our new
270 data highlight the significance of the Pl-To coral crisis and elevate it to the level of other mass
271 extinctions as one of the three most severe scleractinian coral crises ever. Moreover, this event
272 was likely the most severe extinction event for Scleractinia throughout their entire evolutionary
273 history.

274

275 Concerning the issue of “dead clade walking” (i.e., clades surviving the extinction but becoming
276 extinct soon after, Kiessling *et al.*, 2004), 16.67% (4 genera among 24) survived the early
277 Toarcian but went extinct after the T-OAE and are absent in Aalenian strata. This value is higher
278 than the 3% calculated in Sepkoski’s compendium (Kiessling et al., 2004) and even higher than
279 the 13% value calculated by Kiessling et al. 2004 for the K/Pg. The subsequent environmental
280 crises in the middle and late Toarcian (Dera et al., 2010; Krencker et al., 2014) might also
281 account for the extinction of these coral genera.

282

283 **4.2. What factors explain evolutionary patterns in the Pl-To interval?**

284

285 During the Pliensbachian, corals in proximal environments lived in association with lithiotids
286 (corals have been found within or near lithiotid-bearing strata in Morocco, Spain, Oman,
287 Slovenia, Italy, Switzerland, the Himalayas, and Timor; see Brame et al. 2019), which probably
288 lived in organic-rich, turbid waters due, at least in part, to their filter-feeder activity and own
289 feces production (Brame et al., 2019). Solitary and phaceloid forms were probably able to
290 accommodate a shared ecological niche and cohabitation with lithiotids because of their
291 biological ability to cope with high sediment loads (Klaus et al., 2011; Brame et al., 2019). This
292 niche likely favoured the origination of many solitary forms in proximal, lagoonal environments
293 during the Pliensbachian, whereas more integrated forms would have been living in offshore
294 environments. Important extinctions occurred in coral and lithiotid faunas at the PI-To boundary
295 and during the T-OAE. The irreversible demise of lithiotid communities at the T-OAE left
296 vacant ecological niches, which encouraged the radiation of many massive coral genera. In
297 Morocco, both the PI/To boundary and T-OAE coral extinctions are associated with neritic
298 carbonate productivity shutdown (Krencker et al. 2020), likely associated with ocean
299 acidification events (Müller et al., 2020). They also correspond to periods of increased delivery
300 of coarse siliciclastic material, highlighting the intimate link between carbonate factory crisis and
301 increased continental weathering correlated with climate changes (Krencker et al. 2020).

302

303 **5. CONCLUSION**

304

305 This study highlights the significance of both the PI/To boundary and the T-OAE crises in coral
306 evolution. These events resulted in extinction rates as high as 51.1% at the generic level and
307 90.9% at the species level, and combined (i.e., the PI-To interval) rank as one of the three most

308 important extinction and recovery periods in the geological history of Scleractinia, on par with
309 (or even more devastating than) the T/J and K/Pg extinctions. Although it is not considered a
310 first order biotic crisis, the second-order Pl-To extinction is as significant for corals as a first-
311 order biotic crisis. The extinction resulted in a loss of coral diversity and disparity, as well as a
312 significant reef collapse. This crisis shaped the future of diversity and morphological disparity
313 within the coral clades that flourished during the Jurassic and Cretaceous. Consequently, it must
314 be considered a key period in the evolutionary dynamics of Scleractinia. Given the significance
315 of the Pl-To crisis to coral and reef communities, their survival and recovery during this event
316 are particularly pertinent for questions about present day ecosystem collapse and conservation of
317 coral habitats. Unique characteristics of this extinction, such as the survival of zooxanthellate
318 coral, may prove important for understanding current coral bleaching and conservation.

319

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570

571 FIGURE CAPTIONS

572

573 Table 1. Number of species of each morphological type (solitary, phaceloid, plocoid, cerioid,
574 thamnasterioid, meandroid) in each studied time zone (Pliensbachian [Pli], Toarcian pre-OAE

575 [To 1], and Toarcian post-OAE [To 2]) for every studied locality with additional information
576 from the published literature (Gu: Guigou Plateau/Aïn Leuh (Morocco); Am: Amellagou
577 (Morocco); Da: Dades Valley (Morocco); Zi: Ziz valley (Morocco); Ca: Calabria (Italy); Br:
578 Brûlon (France); Es: Estivère Pass (France); Li: literature).

579

580 Figure 1. Coral integration types as a percentage of total species among Tethyan coral faunas
581 during the Pliensbachian, pre-T-OAE Toarcian, and post-T-OAE Toarcian.

582

583 Figure 2. Range chart of Tethyan Pliensbachian and Toarcian coral genera. New data are in red;
584 thick line: observed taxon within the stage, dotted line: interpolated occurrence. The colored dots
585 refer to the integration types presented in Fig. 1: red for solitary; green for phaceloid; yellow for
586 plocoid; blue for cerioid; purple for thamnasterioid; grey for meandroid. See supplemental data
587 (Appendix) for taxonomy.

588

589 Figure 3. Evolution of generic richness through the three time intervals studied: Pliensbachian,
590 Toarcian pre-OAE, and Toarcian post-OAE with and without Lazarus taxa (Lazarus taxa
591 correspond to taxa that have not been found in the considered stage but exist in previous and
592 later stages).

593

594 Figure 4. Weighted diversity for the Pliensbachian (PI), pre-OAE Toarcian and post-OAE
595 Toarcian calculated with (1) and without (2) singletons, and without both singletons and Lazarus
596 taxa (3).

597

598 Figure 5. Weighted extinction rates for the Pliensbachian (PI), pre-OAE Toarcian and post-OAE
599 Toarcian calculated with (1) and without (2) singletons.

600

601 Figure 6. Worldwide known range chart of coral families that occur within the Pliensbachian and
602 Toarcian stages.