



**HAL**  
open science

## Major coral extinctions during the early Toarcian global warming event.

Raphaël Vasseur, Bernard Lathuilière, Iuliana Lazăr, R.C. Martindale,  
Stéphane Bodin, Christophe Durllet

### ► To cite this version:

Raphaël Vasseur, Bernard Lathuilière, Iuliana Lazăr, R.C. Martindale, Stéphane Bodin, et al.. Major coral extinctions during the early Toarcian global warming event.. *Global and Planetary Change*, 2021, 207, pp.103647. 10.1016/j.gloplacha.2021.103647 . hal-03430189

**HAL Id: hal-03430189**

**<https://hal.science/hal-03430189>**

Submitted on 16 Oct 2023

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

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

3 Vasseur, R.<sup>1</sup>(corresponding author), Lathuilière, B.<sup>1</sup>, Lazăr, I.<sup>2</sup>, Martindale, R.C.<sup>3</sup>, Bodin,  
4 S.<sup>4</sup>, Durllet, C.<sup>5</sup>

5  
6 <sup>1</sup> *Université de Lorraine, CNRS, lab. GeoRessources, UMR 7359, BP 70239, 54506,*  
7 *Vandoeuvre-lès-Nancy Cedex, France, e-mails: raphaelvasseur@wanadoo.fr,*  
8 *bernard.lathuiliere@univ-lorraine.fr*

9 <sup>2</sup> *University of Bucharest, Faculty of Geology and Geophysics, Department of Geology and*  
10 *Paleontology, 1, N. Bălcescu Ave., RO – 010041, Bucharest, e-mail: iuliana.lazar@g.unibuc.ro*

11 <sup>3</sup> *Department of Geological Sciences, Jackson School of Geosciences, University of Texas at*  
12 *Austin, 2275 Speedway Stop C9000, Austin, TX, United States, 78712, e-mail:*  
13 *martindale@jsg.utexas.edu*

14 <sup>4</sup> *Aarhus University, Department of Geoscience, Høegh-Guldbergs Gade 2, 8000 Aarhus C,*  
15 *Denmark, e-mail: stephane.bodin@geo.au.dk*

16 <sup>4</sup> *UMR CNRS 6282 Biogéosciences, Université Bourgogne Franche-Comté, 21000 DIJON*  
17 *(France), e-mail: christophe.durllet@u-bourgogne.fr*

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
<b>Gu</b>	7	-	3	7	-	6	1	-	1	7	-	7	1	-	3	1	-	5
<b>Am</b>	25	-	1	2	-	3	1	-	1	3	-	8	1	-	-	-	-	3
<b>Da</b>	4	1	2	2	2	2	1	1	-	2	3	-	-	1	-	-	-	-
<b>Zi</b>	-	-	-	1	-	3	-	-	-	-	-	-	1	-	-	-	-	1
<b>Ca</b>	6	-	-	5	-	-	2	-	-	5	-	-	2	-	-	-	-	-
<b>Br</b>	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Es</b>	3	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Li</b>	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

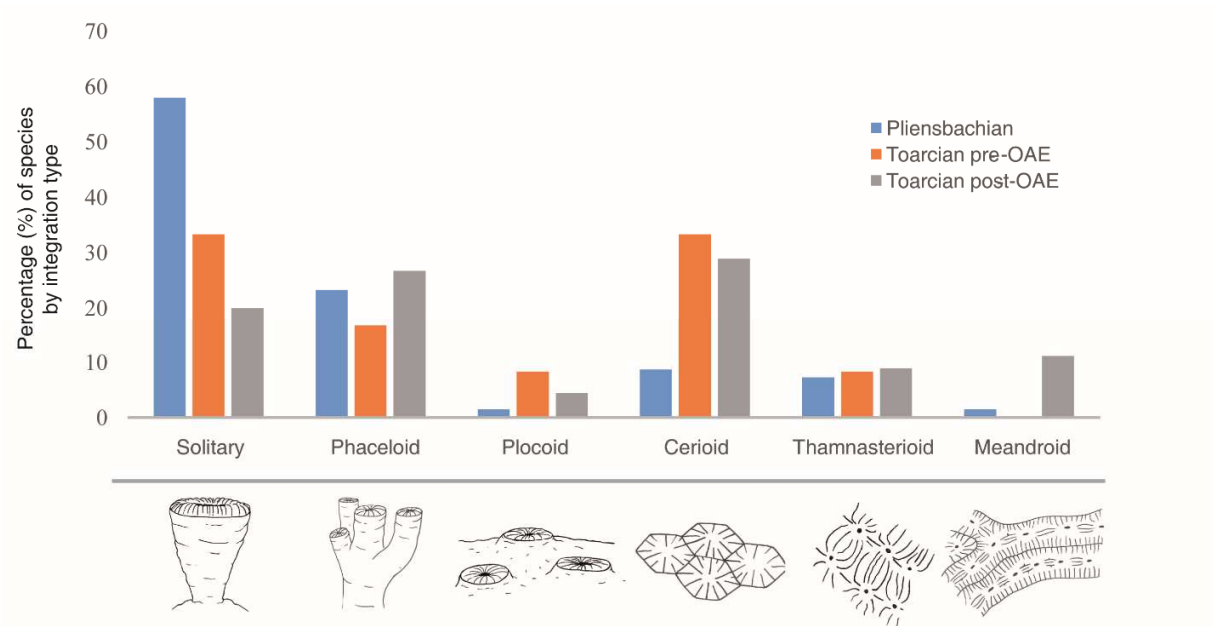
121 [To1], and Toarcian post-OAE [To2]) for every studied locality with additional information from

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

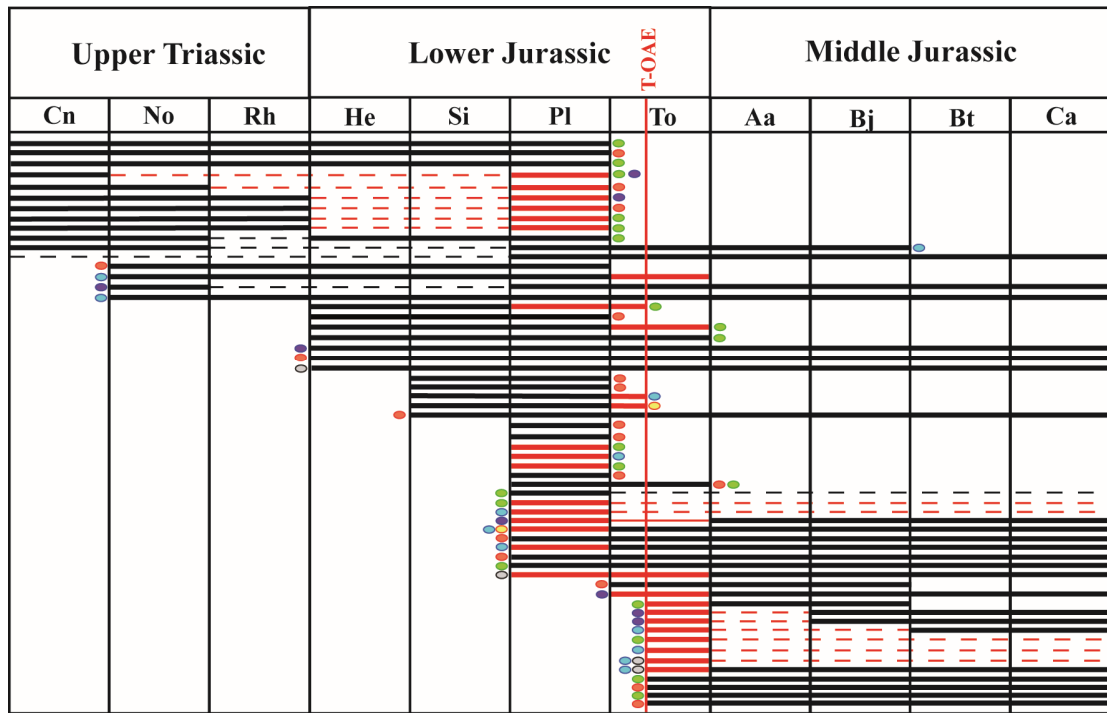
130 In proximal environments, corals sometimes lived in close relationship with lithiotid bivalves;  
 131 such reefs and biostromes can be found in the Moroccan High-Atlas Mountains, Spain, Oman,  
 132 Slovenia, Italy, Switzerland, the Himalayas, and Timor (Brame et al., 2019) but we found no  
 133 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

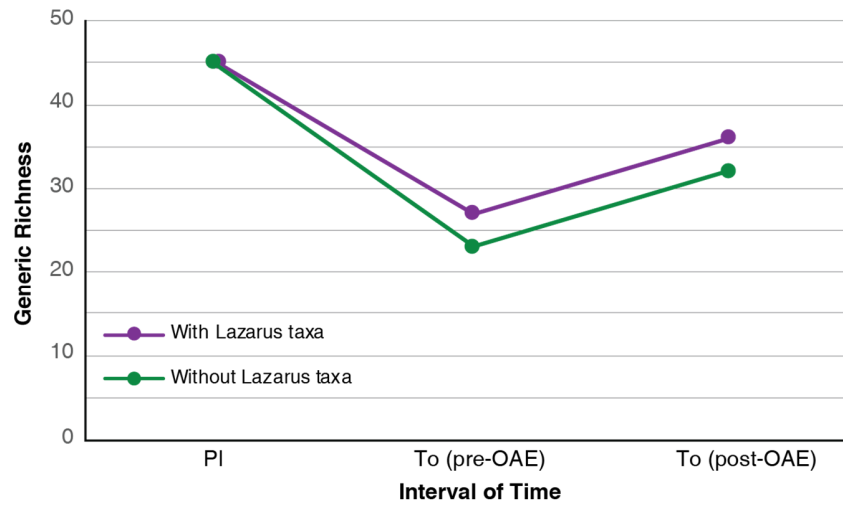
153 No coral reefs have been observed in the earliest Toarcian strata (i.e., before the onset of the T-  
 154 OAE) and this paucity of sampling localities complicates the assessment of the dominant forms

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

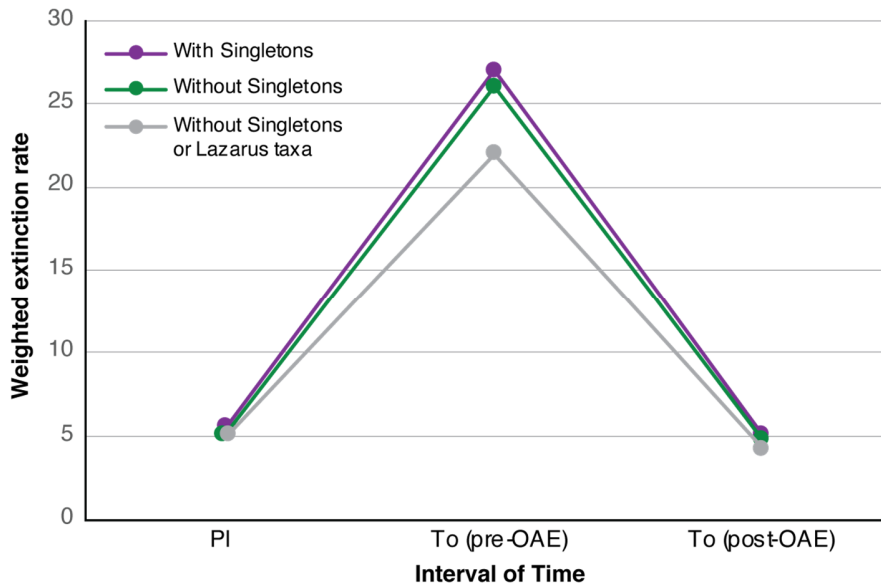
200 Weighted analyses have been produced on the data with (1) and without (2) the singletons and  
201 also without both singletons and Lazarus taxa (3):

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

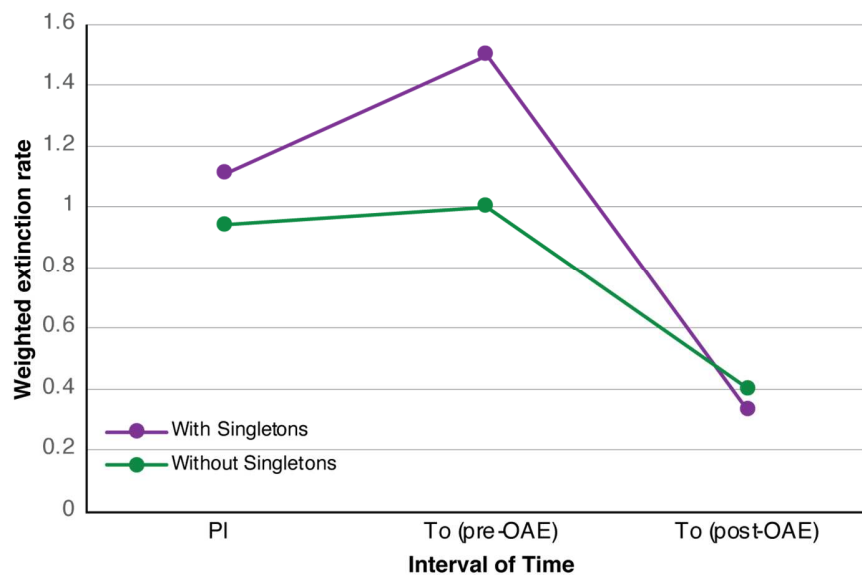
207 taxa (3).

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

## 320 **ACKNOWLEDGEMENTS**

321

322 We are indebted to a number of people who took part in the field work, collection of specimens  
323 and work in museums. For our five field missions in Morocco we thank Hamid Haddoumi,  
324 Khalid Elhmidi, Mohamed Ousri, Rossana Martini, Simon Boivin, Hassan El Arabi, André  
325 Charrière, Thomas Saucède, Pierre Pellenard, Nicholas Ettinger, and Hannah Brame. We are  
326 especially thankful to Philippe Fauré who collected corals from the Pyrenees and who waited so  
327 long for the results. We thank Massimo Santantonio for organizing the unforgettable field work  
328 in Calabria with Giulia Innamorati and Simone Fabbi. We also thank Marc Chesnier for access to  
329 his private collection from western France and are indebted to the team at the Muséum d'Histoire  
330 Naturelle in Paris, especially Sylvain Charbonnier and Jean-Michel Pacaud who welcomed us to

331 work on samples from Morocco and Normandy on various occasions. We would like to express  
332 our gratitude to Cyrille Delangle and the Terrae Genesis association as well as to John Moine  
333 and Alexandre Flammang from Georessources litholamellage platform for the precious help with  
334 thin sections. The authors are grateful to the reviewers that provided detailed comments that  
335 helped us substantially improve this manuscript and refine its focus. Rowan Martindale would  
336 like to acknowledge the NationalScience Foundation as this research was supported by an NSF  
337 CAREERaward #1848393.

338

339

#### 340 **REFERENCES CITED**

341

342 Aberhan, M.,Kiessling, W., 2012. Phanerozoic marine biodiversity: a fresh look at data,  
343 methods, patterns and processes.Earth and life (pp. 3-22). Springer, Dordrecht.  
344 [https://doi.org/10.1007/978-90-481-3428-1\\_1](https://doi.org/10.1007/978-90-481-3428-1_1)

345

346 Aurell, M., Robles, S., Bádenas, B., Rosales, I., Quesada, S., Meléndez, G., Garcia-Ramos, J. C.,  
347 2003. Transgressive – regressive cycles and Jurassic palaeogeography of northeast Iberia.  
348 *Sediment. Geol.*, 162(3-4), 239-271.

349

350 Bambach, R. K., Knoll, A. H., Wang, S. C., 2004. Origination, extinction, and mass depletions of  
351 marine diversity. *Paleobiology*, 30(4), 522-542.

352

353 Beauvais, L., 1986. Monographie des madréporaires du Jurassique inférieur du Maroc.  
354 Palaeontogr. Abt., A 194(1/3):1-68.  
355

356 Benton, M. J., 1995. Diversification and extinction in the history of life. *Science*, 268(5207), 52-  
357 58.  
358

359 Blomeier, D.G., Reijmer, J.G., 1999. Drowning of a Lower Jurassic carbonate platform: Jbel  
360 Bou Dahar, High Atlas, Morocco. *Facies*, 41, 81–110.  
361

362 Bodin, S., Mattioli, E., Fröhlich, S., Marshall, J. D., Boutib, L., Lahsini, S., Redfern, J., 2010.  
363 Toarcian carbon isotope shifts and nutrient changes from the Northern margin of Gondwana  
364 (High Atlas, Morocco, Jurassic): palaeoenvironmental implications. *Palaeogeogr.*  
365 *Palaeoclimatol. Palaeoecol.*, 297(2), 377-390.  
366

367 Bodin, S., Krencker, F.-N., Kothe, T., Hoffmann, R., Mattioli, E., Heimhofer, U., Kabiri, L.,  
368 2016. Perturbation of the carbon cycle during the late Pliensbachian – Early Toarcian: New  
369 insight from high-resolution carbon isotope records in Morocco. *J. African Earth Sci.*, vol. 116:  
370 89-104. <https://doi.org/10.1016/j.jafrearsci.2015.12.018>  
371

372 Boulila, S., Galbrun, B., Sadki, D., Gardin, S., Bartolini, A., 2019. Constraints on the duration of  
373 the early Toarcian T-OAE and evidence for carbon-reservoir change from the High Atlas  
374 (Morocco). *Glob. Planet. Chang.*, 175, 113-128.  
375

376 Brame, H. M. R., Martindale, R. C., Ettinger, N. P., Debeljak, I., Vasseur, R., Lathuilière, B.,  
377 Kabiri, L., Bodin, S., 2019. Stratigraphic distribution and paleoecological significance of Early  
378 Jurassic (Pliensbachian-Toarcian) lithiotid-coral reefal deposits from the Central High Atlas of  
379 Morocco. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 514, 813-837.  
380 <https://doi.org/10.1016/j.palaeo.2018.09.001>

381  
382 Brigaud, B., Vincent, B., Carpentier, C., Robin, C., Guillocheau, F., Yven, B., Huret, E., 2014.  
383 Growth and demise of the Jurassic carbonate platform in the intracratonic Paris Basin (France):  
384 interplay of climate change, eustasy and tectonics. *Mar. Pet. Geol.*, 53, 3-29.

385  
386 Burgess, S.D., Bowring, S.A., Fleming, T.H., Elliot, D.H., 2015. High-precision geochronology  
387 links the Ferrar large igneous province with Early-Jurassic ocean anoxia and biotic crisis. *Earth*  
388 *Planet. Sci. Lett.*, v. 415, p. 90–99. <https://doi.org/10.1016/j.epsl.2015.01.037>.

389  
390 Caruthers, A.H., Gröcke, D.R., Smith, P.L., 2011. The significance of an Early Jurassic  
391 (Toarcian) carbon-isotope excursion in Haida Gwaii (Queen Charlotte Islands), British  
392 Columbia, Canada. *Earth Planet. Sci. Lett.*, v. 307, p. 19–26.  
393 <https://doi.org/10.1016/j.epsl.2011.04.013>.

394  
395 Caruthers, A. H., Smith, P. L., Gröcke, D. R., 2013. The Pliensbachian–Toarcian (Early Jurassic)  
396 extinction, a global multi-phased event. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 386:104-118.  
397 <https://doi.org/10.1016/j.palaeo.2013.05.010>

398

399 Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015.  
400 Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Sci.*  
401 *Adv.*, 1(5), e1400253.  
402

403 Dera, G., Neige, P., Dommergues, J.-L., Fara, E., Laffont, R., Pellenard, P., 2010. High-  
404 resolution dynamics of Early Jurassic marine extinctions: the case of Pliensbachian–Toarcian  
405 ammonites (Cephalopoda). *J. Geol. Soc. London*, vol. 167:21–33. [https://doi.org/10.1144/0016-](https://doi.org/10.1144/0016-76492009-068)  
406 [76492009-068](https://doi.org/10.1144/0016-76492009-068)  
407

408 Dera, G., Brigaud, B., Monna, F., Laffont, R., Pucéat, E., Deconinck, J.-F., Pellenard, P.,  
409 Joachimski, M.M., Durllet, C., 2011. Climatic ups and downs in a disturbed Jurassic world.  
410 *Geology*, 39, 215 – 218.  
411

412 Dommergues, J.-L., Meister, C., 2017. Ammonites du Jurassique inférieur (Hettangien,  
413 Sinémurien, Pliensbachien) d’Afrique du Nord (Algérie, Maroc et Tunisie). *Atlas*  
414 *d’identification des espèces. Rev. de Paléobiologie*, 36(2):189-367.  
415

416 El Arabi, H., Canerot, J., Charrière, A., 1987, Dynamique récifale et tectonique distensive en  
417 blocs basculés: l’exemple des récifs liasiques du bloc du Guigou (Causse moyen atlasique-  
418 Maroc). *Mem. Soc. Phys. Hist. nat. Geneve*, 259- 271.  
419

420 Ettinger, N. P., Larson, T. E., Kerans, C., Thibodeau, A. M., Hattori, K. E., Kacur, S. M.,  
421 Martindale, R. C., 2021. Ocean acidification and photic-zone anoxia at the Toarcian Oceanic  
422 Anoxic Event: Insights from the Adriatic Carbonate Platform. *Sedimentology*, 68(1), 63-107.

423

424 Flügel, E., Kiessling, W., 2002, Patterns of Phanerozoic reef crises. *SEPM Special Publication*,  
425 72, 691-734.

426

427 Foote, M., 1994. Temporal variation in extinction risk and temporal scaling of extinction metrics.  
428 *Paleobiology*, 20, 424-444.

429

430 Foote M., 2000, Origination and extinction components of taxonomic diversity: general  
431 problems. *Paleobiology* 26:74–102.

432

433 Gómez, J.J., Goy, A., 2011. Warming-driven mass extinction in the Early Toarcian (Early  
434 Jurassic) of northern and central Spain. Correlation with other time-equivalent European  
435 sections. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, v. 306, p. 176–195.  
436 <https://doi.org/10.1016/j.palaeo.2011.04.018>.

437

438 Gómez, J.J., Comas-Rengifo, M.J., Goy, A., 2016. Palaeoclimatic oscillations in the  
439 Pliensbachian (Early Jurassic) of the Asturian Basin (Northern Spain). *Clim. Past.*, 12, 1199–  
440 1214. <https://doi.org/10.5194/cp-12-1199-2016>.

441



442 Gould, S. J., 1991. The disparity of the Burgess Shale arthropod fauna and the limits of cladistic  
443 analysis: why we must strive to quantify morphospace. *Paleobiology*, 17(4), 411-423.

444

445 Graciansky, P. C., Jacquin, T., Hesselbo, S. P., 1998. The Ligurian cycle: an overview of Lower  
446 Jurassic 2nd-order transgressive/regressive facies cycles in Western Europe. *Society for*  
447 *Sediment. Geol.*, 60.

448

449 Kiessling, W., Baron-Szabo, R. C., 2004. Extinction and recovery patterns of scleractinian corals  
450 at the Cretaceous-Tertiary boundary. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 214(3), 195-223.

451

452 Kiessling, W., Aberhan, M., Brenneis, B., Wagner, P.J., 2007. Extinction trajectories of benthic  
453 organisms across the Triassic-Jurassic boundary. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 244,  
454 201.

455

456 Kiessling, W., 2011. Patterns and Processes of Ancient Reef Crises. *The Paleontological Society*  
457 *Papers*, 17, 1-14. <https://doi.org/10.1017/S1089332600002412>

458

459 Kiessling, W., Simpson, C., 2011. On the potential for ocean acidification to be a general cause  
460 of ancient reef crises: Ancient Reef Crises. *Glob. Change Biol.*, 17, 56–67,  
461 <https://doi.org/10.1111/j.1365-2486.2010.02204.x>.

462

463 Kitahara, M. V., Fukami, H., Benzoni, F., Huang, D., 2016. The new systematics of Scleractinia:  
464 integrating molecular and morphological evidence. *The Cnidaria, past, present and future*, pp.  
465 41-59. Springer, Cham.

466

467 Klaus, J. S., Lutz, B. P., McNeill, D. F., Budd, A. F., Johnson, K. G., Ishman, S. E., 2011. Rise  
468 and fall of Pliocene free-living corals in the Caribbean. *Geology*, 39(4), 375-378.

469

470 Korte, C., Hesselbo, S. P., Ullmann, C. V., Dietl, G., Ruhl, M., Schweigert, G., Thibault, N.,  
471 2015. Jurassic climate mode governed by ocean gateway. *Nat. Commun.*, 6, 10015.

472

473 Krencker, F.-N., Bodin, S., Hoffmann, R., Suan, G., Mattioli, E., Kabiri, L., Föllmi, K.B.,  
474 Immenhauser, A., 2014. The middle Toarcian cold snap: trigger of mass extinction and carbonate  
475 factory demise. *Glob. Planet. Chang.*, 117, 64-78.

476

477 Krencker, F. N., Bodin, S., Suan, G., Heimhofer, U., Kabiri, L., Immenhauser, A., 2015.  
478 Toarcian extreme warmth led to tropical cyclone intensification. *Earth Planet. Sci. Lett.*, 425,  
479 120-130. <https://doi.org/10.1016/j.epsl.2015.06.003>

480

481 Krencker, F. N., Lindström, S., Bodin, S., 2019. A major sea-level drop briefly precedes the  
482 Toarcian oceanic anoxic event: implication for Early Jurassic climate and carbon cycle. *Sci.*  
483 *Rep.*, 9(1), 1-12.

484

485 Krencker, F. N., Fantasia, A., Danisch, J., Martindale, R., Kabiri, L., El Ouali, M., Bodin, S.,  
486 2020. Two-phased collapse of the shallow-water carbonate factory during the late Pliensbachian–  
487 Toarcian driven by changing climate and enhanced continental weathering in the Northwestern  
488 Gondwana Margin. *Earth-Sci. Rev.*, 103254.

489

490 Lathuilière, B., Marchal, D., 2009. Extinction, survival and recovery of corals from the Triassic  
491 to Middle Jurassic Time. *Terra Nova*, 2, 57-66. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-3121.2008.00856.x)  
492 [3121.2008.00856.x](https://doi.org/10.1111/j.1365-3121.2008.00856.x)

493

494 Léonide, P., Floquet, M., Durlet, C., Baudin, F., Pittet, B., Lécuyer, C., 2012. Drowning of a  
495 carbonate platform as a precursor stage of the Early Toarcian global anoxic event (Southern  
496 Provence sub-Basin, South-east France). *Sedimentology*, 59, 156-184.

497

498 Little, C. T., Benton, M. J., 1995. Early Jurassic mass extinction: a global long-term event.  
499 *Geology*, 23(6), 495-498.

500

501 Mattioli, E., Pittet, B., Petitpierre, L., Mailliot, S., 2009. Dramatic decrease of pelagic carbonate  
502 production by nanoplankton across the Early Toarcian anoxic event (T-OAE). *Glob. Planet.*  
503 *Chang.*, 65(3-4), 134-145.

504

505 Morard, A., Guex, J., Bartolini, A., Morettini, E., De Wever, P., 2003. A new scenario for the  
506 Domerian – Toarcian transition. *Bull. Soc. Géol. Fr.*, 174, 4, 351-356.  
507 <https://doi.org/10.2113/174.4.351>

508

509 Müller, T., Jurikova, H., Gutjahr, M., Tomašových, A., Schlögl, J., Liebetrau, V., Duarte, L.V.,  
510 Milovský, R., Suan, G., Mattioli, E., Pittet, B., Eisenhauer, A., 2020. Ocean acidification during  
511 the early Toarcian extinction event: Evidence from boron isotopes in brachiopods. *Geology*, 48,  
512 1184–1188.

513

514 Pittet, B., Suan, G., Lenoir, F., Duarte, L. V., Mattioli, E., 2014. Carbon isotope evidence for  
515 sedimentary discontinuities in the lower Toarcian of the Lusitanian Basin (Portugal): Sea level  
516 change at the onset of the Oceanic Anoxic Event. *Sediment. Geol.*, 303, 1-14.

517

518 Posenato, R., Bassi, D., Trecalli, A., Parente, M., 2018. Taphonomy and evolution of Lower  
519 Jurassic lithiotid bivalve accumulations in the Apennine Carbonate Platform (southern Italy).  
520 *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 489, 261-271.  
521 <https://doi.org/10.1016/j.palaeo.2017.10.017>

522

523 Raup, D. M., Sepkoski, J. J., 1982. Mass extinctions in the marine fossil record. *Science*,  
524 215(4539), 1501-1503.

525

526 Reolid, M., Mattioli, E., Duarte, L. V., Marok, A., 2020. The Toarcian Oceanic Anoxic Event  
527 and the Jenkyns Event (IGCP-655 final report). *Episodes* 43(2), 833-844.

528

529 Rosen, B. R., 2000. Algal symbiosis, and the collapse and recovery of reef communities: Lazarus  
530 corals across the KT boundary. *Biotic response to global change*, 164-180.

531

532 Ruban, D. A., 2004. Diversity dynamics of Early-Middle Jurassic brachiopods of Caucasus, and  
533 the Pliensbachian-Toarcian mass extinction. *Acta Palaeontol. Pol.*, 49(2).

534

535 Ruebsam, W., Mayer, B., Schwark, L., 2019. Cryosphere carbon dynamics control early Toarcian  
536 global warming and sea level evolution. *Glob. Planet. Chang.*, 172, 440-453.

537

538 Santantonio, M., 2012. Mesozoic evolution of the Caloveto Group, NE Calabria. *Rendiconti*  
539 *Online Soc. Geol. Ital.*, 21, 295-297.

540

541 Santantonio, M., Fabbi, S., Aldega, L., 2016. Mesozoic architecture of a tract of the European–  
542 Iberian continental margin: Insights from preserved submarine palaeotopography in the  
543 Longobucco Basin (Calabria, Southern Italy). *Sediment. Geol.*, 331, 94-113.  
544 <https://doi.org/10.1016/j.sedgeo.2015.10.010>

545

546 Sepkoski, J. J., 2002. A compendium of fossil marine animal genera. *Bull. Am. Paleontol.*, 363,  
547 1-563.

548

549 Simpson, C., 2013. Species selection and the macroevolution of coral coloniality and  
550 photosymbiosis. *Evolution*, 67(6), 1607-1621.

551

552 Slater, S.M., Twitchett, R.J., Danise, S., Vajda, V., 2019. Substantial vegetation response to  
553 Early Jurassic global warming with impacts on oceanic anoxia. *Nat. Geosci.*, v. 12, p. 462–467.  
554 <https://doi.org/10.1038/s41561-019-0349-z>.

555

556 Suan, G., Mattioli, E., Pittet, B., Lécuyer, C., Suchéras-Marx, B., Duarte, L. V., Philippe, M.,  
557 Reggiani, L., Martineau, F., 2010. Secular environmental precursors to Early Toarcian (Jurassic)  
558 extreme climate changes. *Earth Planet. Sci. Lett.*, vol. 290, n° 3-4: 448-458.  
559 <https://doi.org/10.1016/j.epsl.2009.12.047>

560

561 Trecalli, A., Spangenberg, J., Adatte, T., Föllmi, K. B., Parente, M., 2012. Carbonate platform  
562 evidence of ocean acidification at the onset of the early Toarcian oceanic anoxic event. *Earth  
563 Planet. Sci. Lett.*, vol. 357-358: 214-225. <https://doi.org/10.1016/j.epsl.2012.09.043>

564

565 Vasseur, R., 2019. Extinctions et recouvrements de coraux au cours de la crise Pliensbachien –  
566 Toarcien. Nancy, Université de Lorraine, 542 pp.

567

568 Vasseur, R., Lathuilière, B., 2020. Pliensbachian corals from the Western Tethys. *Geodiversitas*,  
569 in press.

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.