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Major coral extinctions during the early Toarcian global warming event

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ABSTRACT

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

1. Introduction

The history of life is punctuated by extinction events that drove evolutionary dynamics, and scientists posit that the Earth is currently entering a similar mass extinction (Ceballos et al., 2015). Five major “first-order” biotic crises are reported for the Phanerozoic, followed by “second-order” crises, such as the Pliensbachian-Toarcian crisis at ca. 183 Ma (e.g., Raup and Sepkoski, 1982; Bambach et al., 2004). The distinction between first and second-order crises remains unclear as the ranking of crises varies according to the considered characters, such as taxonomic scale (i.e., families, genera, species), functional niche loss, consideration of associated palaeoenvironmental upheaval, and the different ways to statistically weigh raw data (Benton, 1995).

The Pliensbachian-Toarcian (Pl-To) transition was marked by drastic and repeated palaeoenvironmental disturbances associated with the emplacement of the Karoo-Ferrar igneous province in southern Gondwana (Burgess et al., 2015). These environmental changes included major shifts in the temperature, chemistry, and oxygenation of the oceans, culminating in the Toarcian Oceanic Anoxic Event (T-OAE) (e.g.,Suan et al., 2010; Gómez and Goy, 2011; Caruthers et al., 2011; Dera et al., 2011; Reolid et al., 2020). Following the middle Pliensbachian warm period (Gómez et al., 2016), the latest Pliensbachian is marked by a significant cooling event with important sea-level fluctuations (De Graciansky et al., 1998; Aurell et al., 2003; Suan et al., 2010; Pittet et al., 2014; Krencker et al., 2019). The Pl-To boundary coincides with a pronounced warming event (Suan et al., 2010), enhanced continental weathering, and a widespread demise of neritic carbonate ecosystem (Bodin et al., 2016; Krencker et al., 2020), which often led to strong condensation of the sedimentary record or even a hiatus in sedimentation (Morard et al., 2003; Léonide et al., 2012; Krencker et al., 2014; Pittet et al., 2014). Climate cooling is observed during the remainder of the earliest Toarcian (Polymorphum zone; Ruebsam et al., 2019; Krencker et al., 2020), allowing renewed neritic carbonate production in several areas across the Tethys Ocean (Léonide et al., 2012; Trecalli

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et al., 2012; Krencker et al., 2020). At the onset of the T-OAE, a second demise of neritic carbonate ecosystems occurred, likely triggered by a profound carbon cycle perturbation, soaring global temperature (Suan et al., 2010; Korte et al., 2015), and a second pulse of continental weathering (Bodin et al., 2010; Krencker et al., 2020; Ettinger et al., 2021). Neritic carbonate production resumed along the southern Tethyan margin during the recovery of the carbon isotope excursion associated with the T-OAE (Trecalli et al., 2012; Krencker et al., 2014, 2015) but not until at least the middle Toarcian along the northern Tethyan margin (Blomeier and Reijmer, 1999; Aurell et al., 2003; Léonide et al., 2012; Brigaud et al., 2014).

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

2. Material

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

3. Results and analyses

3.1. Pliensbachian coral assemblages

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

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

Pliensbachian coral populations are composed predominantly of genera with Triassic or Early Jurassic roots but very few of these genera persist through the T-OAE (Fig. 2). The Pliensbachian is characterized by a surprising radiation event: 17 genera appeared, including 5 solitary and 5 phaceloidgenera. Among these 17 genera, 11 persisted after the T-OAE. All genera that are exclusively Pliensbachian are solitary or phaceloid with one exception.

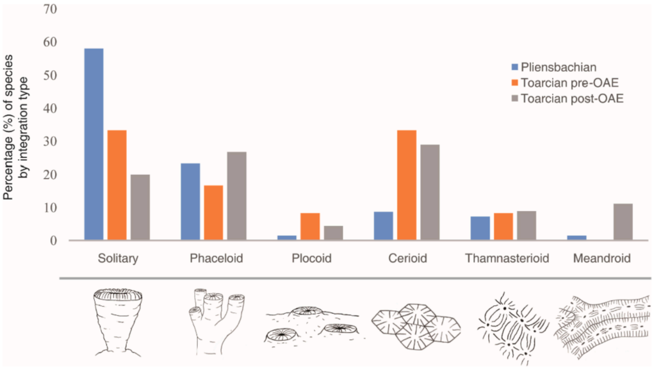

Fig. 1. Coral integration types as a percentage of total species among Tethyan coral faunas during the Pliensbachian, pre-T-OAE Toarcian, and post-T-OAE Toarcian.

Table 1

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

	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

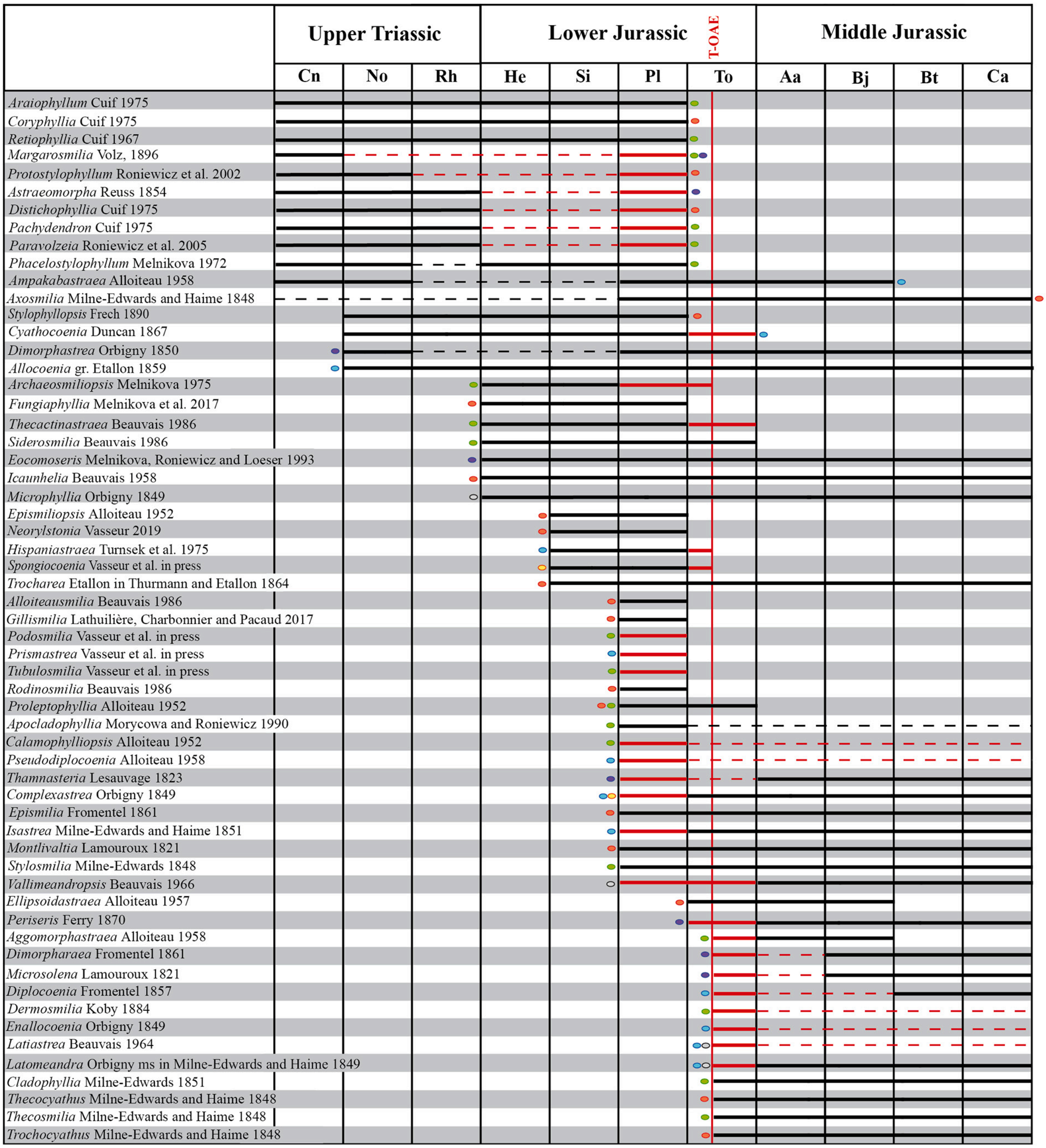

Fig. 2. Range chart of Tethyan Pliensbachian and Toarcian coral genera. New data are in red; thick line: observed taxon within the stage, dotted line: interpolated occurrence. The colored dots refer to the integration types presented in Fig. 1: red for solitary; green for phaceloid; yellow for plocoid; blue for cerioid; purple for thamnasterioid; grey for meandroid. See supplemental data (Appendix) for taxonomy. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. *Toarcian coral assemblages*

No coral reefs have been observed in the earliest Toarcian strata (i.e., before the onset of the T-OAE) and this paucity of sampling localities complicates the assessment of the dominant forms in terms of volume in the assemblage. Nevertheless, the analyses of reworked corals and corals that occur in lithiotid-coral biostromes reveal faunas composed of taxa that evolved during the Early Jurassic mixed with taxa that are classically observed in Middle/Upper Jurassic strata (Fig. 2). These observations suggest a transitional period when coral extinctions occurred in association with radiations. During the pre-T-OAE, highly integrated forms are more common, both in terms of diversity and biomass, than they are in the Pliensbachian. These strata contain the last important associations of lithiotid bivalves before their extinction at the onset of the T-OAE (Brame et al., 2019; Posenato et al., 2018).

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

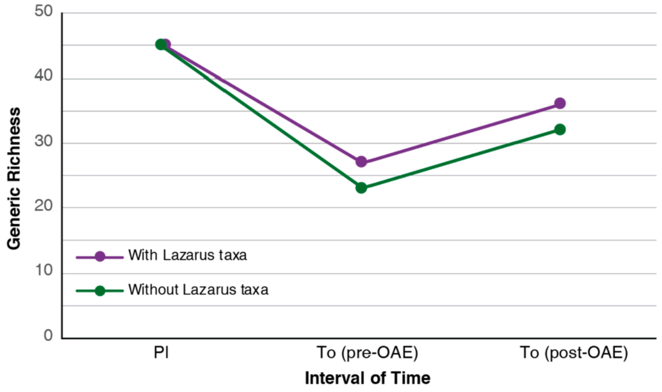

Fig. 3. Evolution of generic richness through the three time intervals studied: Pliensbachian, Toarcian pre-OAE, and Toarcian post-OAE with and without Lazarus taxa (Lazarus taxa correspond to taxa that have not been found in the considered stage but exist in previous and later stages).

3.3. *Accounting for biases*

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

Pliensbachian: 190.8–182.7 = 8.1 Ma;
Toarcian: 182.7–174.1 = 8.6 Ma;
Toarcian pre-T-OAE: 182.7–181.7 = 1 Ma;
Toarcian post-T-OAE: 8.6–1.45 = 7.15 Ma.

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

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

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

	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.

	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

(*continued on next column*)

(*continued*)

*Number of extinctions/number of occurrences

The results of the raw data and weighted data are comparable (Figs. 4, 5); in fact, Pliensbachian and Toarcian stages show similar durations with taxa and singletons equally distributed between the two stages.

3.4. *Family scale analysis*

Analyses at the family scale provide good appreciation of disparity sensu Gould (1991). Moreover, fossil coral families are primarily defined by the microstructures of skeletal septa that are considered as relevant evolutionary novelties. According to our results (Fig. 6), 6 families of Triassic affinity disappear at the Pl-To boundary and 2 families of Middle/Late Jurassic affinity appear just after the T-OAE. In addition, four coral families that are key builders of Middle and Upper Jurassic coral reefs radiate during the earliest Toarcian (i.e., before the OAE): Thecosmiliidae (= ex Montlivaltiidae), Comoseridae (=ex Microsolenidae), Stylinidae, and Thamnasteriidae. Furthermore, this study is the first to document the Deltocyathiidae family in the Mesozoic fossil record; this family was hypothesized to split at the base of the “robust” coral clade in the scleractinian phylogeny (Kitahara et al., 2016).

4. Discussion

The results presented here illustrate the importance of the Pl-To crisis in coral communities; the Pliensbachian – Toarcian crisis marks the disruption between an early period of high disparity (represented by the amount of Pliensbachian families) and the later diversification of surviving taxa during the Toarcian and later. Furthermore, the Pliensbachian and post-T-OAE intervals mark the development of coral pioneers in the colonisation of deeper environments, with many specimens recovered from hemipelagic deposits (Deltocyathiidae and Caryophylliidae), a phenomenon that implies the conquest of new ecological niches. Some of the genera that survived the crisis are assumed to be

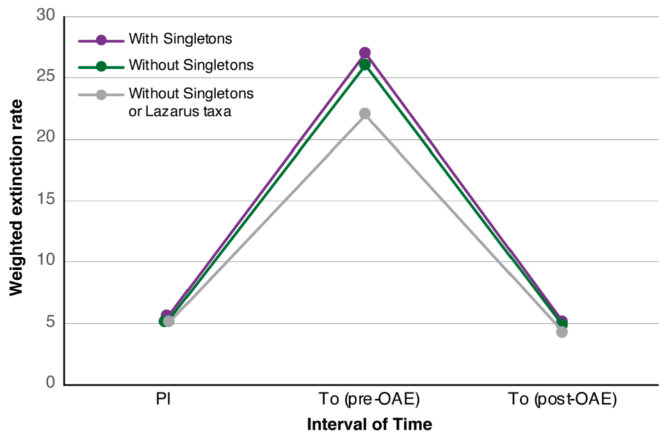

Fig. 4. Weighted diversity for the Pliensbachian (Pl), pre-OAE Toarcian and post-OAE Toarcian calculated with (1) and without (2) singletons, and without both singletons and Lazarus taxa (3).

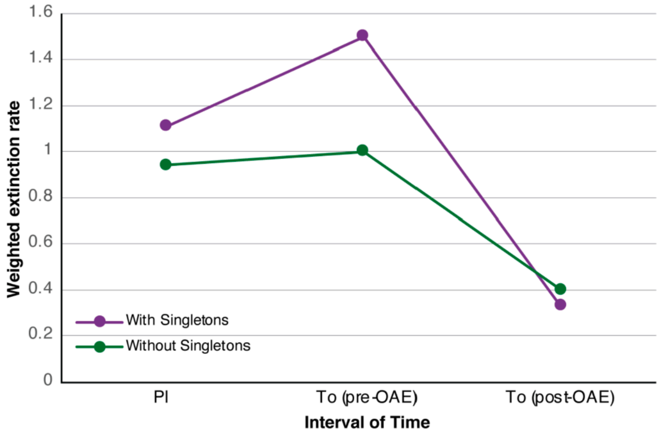

Fig. 5. Weighted extinction rates for the Pliensbachian (Pl), pre-OAE Toarcian and post-OAE Toarcian calculated with (1) and without (2) singletons.

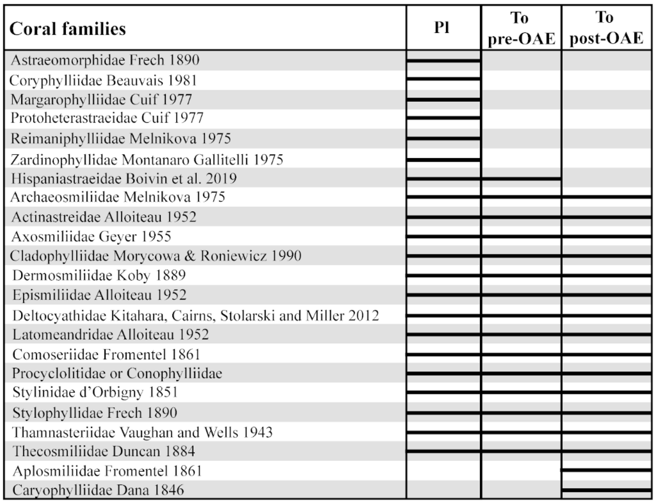

Fig. 6. Worldwide known range chart of coral families that occur within the Pliensbachian and Toarcian stages.

zooxanthellate corals because of their highly-integrated morphology, high growth rates, living environments and colony shape variations (e.g., *Dimorphastrea*, *Microphyllia*, *Thamnasteria* – Vasseur, 2019). This is inconsistent with the hypothesis that photosymbiosis is lost during crises periods (Rosen, 2000), unless these genera developed an ability to live without symbionts during crisis time. On the other hand, it is consistent with the high correlation between coloniality and photosymbiosis (Simpson, 2013) as all of these genera are colonial.

4.1. Extinction rates

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

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

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

4.2. What factors explain evolutionary patterns in the Pl-to interval?

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

5. Conclusion

This study highlights the significance of both the Pl/To boundary and the T-OAE crises in coral evolution. These events resulted in extinction rates as high as 51.1% at the generic level and 90.9% at the species level, and combined (i.e., the Pl-To interval) rank as one of the three most important extinction and recovery periods in the geological history of Scleractinia, on par with (or even more devastating than) the T/J and K/Pg extinctions. Although it is not considered a first order biotic crisis, the second-order Pl-To extinction is as significant for corals as a first-order biotic crisis. The extinction resulted in a loss of coral diversity and disparity, as well as a significant reef collapse. This crisis shaped the future of diversity and morphological disparity within the coral clades that flourished during the Jurassic and Cretaceous. Consequently, it must be considered a key period in the evolutionary dynamics of

Scleractinia. Given the significance of the Pl-To crisis to coral and reef communities, their survival and recovery during this event are particularly pertinent for questions about present day ecosystem collapse and conservation of coral habitats. Unique characteristics of this extinction, such as the survival of zooxanthellate coral, may prove important for understanding current coral bleaching and conservation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gloplacha.2021.103647.

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