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# The reorganization of reef communities following the end-Permian mass extinction

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## Abstract

The transition from Permian to Triassic time, amidst the largest extinction in the history of life, is characterized by the loss of metazoan reefs followed by a protracted and total reorganization of reef ecosystems. This restructuring of reefs was permanent, and involved a succession from the Permian reef optimum to their total demise, followed by a long-term absence of metazoan reefs in the Early Triassic and then ultimately a delayed recovery in the Middle Triassic. During the end-Permian mass extinction, reef building metazoans suffered a major extinction that resulted in a severe drop in reef skeletal carbonate production by > 99%. Following the extinction, microbial reefs that formed without metazoans took over for 5–6 Myr during the entire Early Triassic. This microbial reef resurgence has been widely studied and is thought to represent long-term environmental stress related to the end-Permian mass extinction that suppressed the recovery of metazoans while simultaneously fostering microbialite development. In the Middle Triassic, metazoan reefs became re-established, although pre-extinction biodiversity values were not attained until the Late Triassic. *To cite this article: S.B. Pruss, D.J. Bottjer, C. R. Palevol 4 (2005).*  
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## Résumé

**La réorganisation des communautés récifales après la crise biologique de la fin du Permien.** La transition du Permien au Trias, contemporaine de la plus importante phase d'extinction de l'histoire de la vie, est caractérisée par la disparition des récifs édifiés par les métazoaires. Il lui succède une longue période d'une réorganisation complète des écosystèmes récifaux. La restructuration des récifs était continue, impliquant une succession d'étapes, depuis l'optimum récifal du Permien jusqu'à l'entière disparition des récifs à métazoaires, leur absence prolongée pendant le début du Trias et, finalement, leur reconquête progressive au cours du Trias moyen. Lors des extinctions massives de la fin du Permien, les métazoaires constructeurs de récifs subirent une

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crise majeure par suite d'une diminution dramatique, plus de 99%, de la production de carbonates provenant d'organismes récifaux à squelettes calcaires. Après les extinctions, la relève fut assurée durant un intervalle de 5 à 6 Ma, c'est-à-dire durant toute la durée du début du Trias, par des récifs microbiens édifiés sans la participation de métazoaires. Cette résurgence des récifs microbiens a été largement étudiée et a été interprétée comme significative d'un stress environnemental de longue durée, en relation avec les extinctions massives de la fin du Permien, qui ont empêché la reconquête des métazoaires, tout en stimulant conjointement le développement des microbialites. Au cours du Trias moyen, les récifs à métazoaires réapparaissent, mais leur biodiversité n'atteindra un niveau comparable à celui d'avant la crise, qu'à la fin du Trias. **Pour citer cet article : S.B. Pruss, D.J. Bottjer, C. R. Palevol 4 (2005).**

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**Keywords:** Early Triassic; Microbial reefs; Biotic recovery; End-Permian mass extinction

**Mots clés :** Début du Trias ; Récifs microbiens ; Reconquête biologique ; Crise biologique de la fin du Permien

## 1. Introduction

The end-Permian mass extinction brought about an annihilation of reef-building organisms at the close of the Paleozoic. There is an abrupt extinction of many groups of reef-builders at the end of the Permian followed by an absence of platform margin reefs for the entire Early Triassic, 5–6 Myr [50,52]. The re-establishment of platform margin reefs, constructed by problematic organisms such as *Tubiphytes* (e.g., [21]), began early in the Anisian; however, the recovery of metazoan reef ecosystems may have taken as long as 7–8 Myr [31,32]. Tabulate and rugose corals disappeared forever from reef ecosystems (e.g., [32]) and sponges did not recover until the Anisian (e.g., [15,22,75]). Because of the paucity of reef-building metazoans during the 5–6 Myr following the end-Permian mass extinction, the Early Triassic has been dubbed a reef gap [15]. This view has been subsequently modified because of the discovery of microbial patch reefs in Lower Triassic strata [3,4,43,56,86] (Fig. 1). In the Middle Triassic, sponge-algal patch reefs formed by *Tubiphytes*, *Girtycoelia*, and various trepostome bryozoans became re-established, and scleractinians radiated rapidly [22,25].

The absence of metazoan reef builders from the Early Triassic has been well-documented (e.g., [15]); however, the proliferation of microbial reefs in their absence has only recently been noted (e.g., [43]). Early Triassic microbial reefs have been described from a variety of locations globally including South China [43,46], southern Turkey, Armenia, Iran, and Oman [3,4], as well as Greenland [86] and western North America [56]. Because the true biotic recovery did not begin until the

Middle Triassic, the Early Triassic has been called a 'survival phase' [32] (Fig. 2). Microbial reefs formed during this survival phase in the absence of metazoans acting as framework builders, bafflers, or binders. The widespread occurrence of microbial reefs from earliest to latest Early Triassic time suggests that the suppression of reef-building metazoans may be linked to environmental conditions that favored microbial growth (e.g., [38,43,56]). The gradual demise of reef-building metazoans has been linked to a drop in oxygen levels from Permian to Triassic time [81], and these low oxygen conditions may have acted as a source of environmental stress that favored microbialite development.

Many of the reef-building organisms that appear in the Middle Triassic differ from their Permian predecessors. There are some Lazarus taxa that reappear in the Norian, and this has been attributed to the survival of organisms in unknown refugia [76]. Middle Triassic sponge genera are new despite morphologic similarities to their ancestors [20,71]. *Tubiphytes* specimens are different from Permian examples, and *Girtycoelia* is likely a homeomorph of earlier forms (e.g., [32]). Interestingly, scleractinian corals appear as a diverse fauna when first documented in the Middle Triassic [22,25].

This paper presents a synthesis of the current understanding of changes in reef ecosystems from Permian to Triassic time. The research summarized here emphasizes the devastation of metazoan reef communities and the ensuing long-term effects of the end-Permian mass extinction. Understanding the reasons for the metazoan reef gap of the Early Triassic may ultimately illuminate the environmental parameters that affect the growth and diversification of skeletal reef organisms.

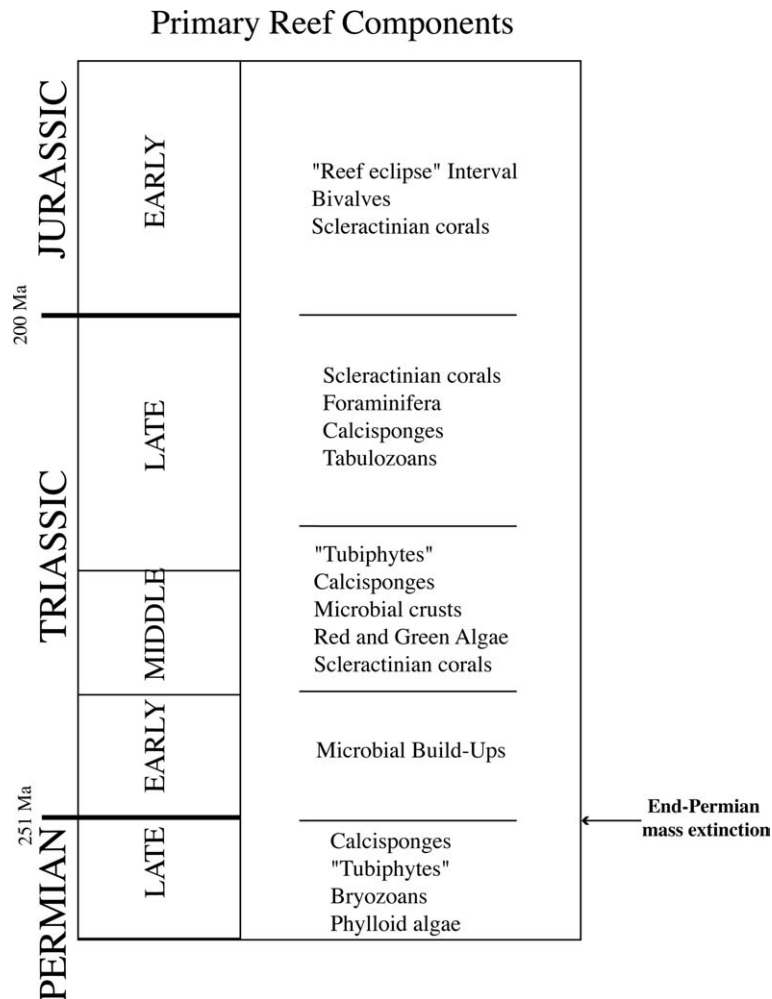


Fig. 1. Diagram of dominant reef components from Late Permian through Early Jurassic time (modified from Pruss and Bottjer [56]).  
Diagramme des constituants biologiques dominants des récifs depuis la fin du Permien supérieur jusqu'au début du Jurassique (modifié d'après Pruss et Bottjer [56]).

## 2. Permian reef occurrences

### 2.1. Example from Delaware Basin, southwestern United States

Permian reef ecosystems suffered a protracted demise from the Lake Maokouan crisis through the end-Permian extinction (e.g., [32]). Reefs from Middle and Late Permian time are known primarily from the margin of Tethys, Tethyan and Panthalassic terranes, and epeiric basins. These reefs vary in composition geographically. Reefs that formed in the Tethyan realm were dominated by carbonate mud and contained algae, corals, brachiopods, and sponges [80]. The Panthalas-

sic marginal basin reefs consisted of microbial-rich reefs and cold-water bryozoan, phylloid algae and stromatolitic reefs at higher latitudes [80]. The epeiric basins were truly unique and contained diverse sponge assemblages with abundant marine cements, microbialites, and problematic fossils [80] (Fig. 3A). The Capitan Reef of the Delaware Basin is one such reef that formed on the margin of an epeiric basin (e.g., [1,51,67]). The Capitan reef is exposed primarily in West Texas and New Mexico and has been widely studied (e.g., [1,40,51,67]). This reef system is characterized by abundant early marine cements as well as a distinct, diverse biota (e.g. [15,30]). The reef ecosystem does not necessarily typify Permian reefs in that it

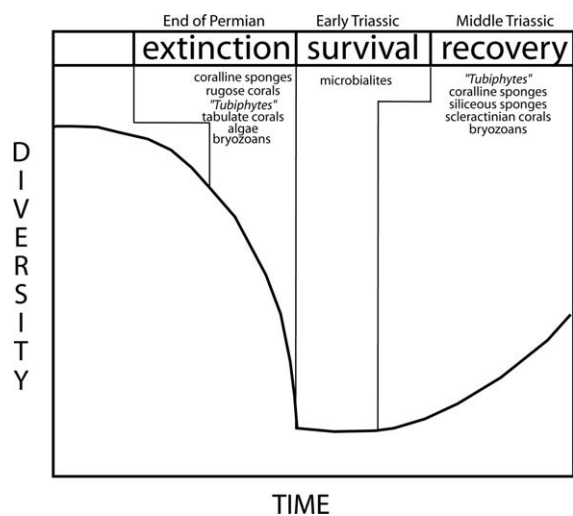


Fig. 2. Diagram showing effects of the end-Permian mass extinction on reef organisms. Dominant metazoan reef builders become extinct during the extinction phase. The survivor phase encompasses disaster forms that build reefs in the aftermath of the extinction. The subsequent radiation of reef organisms begins the recovery phase. This phase also encompasses the re-appearance of taxa that had been absent from the geologic record since the extinction event (modified from [32]; after [37]).

Diagramme illustrant les répercussions de la crise biologique de la fin du Permien sur les organismes récifaux. Les groupes dominants de métazoaires constructeurs de récifs disparaissent durant la phase d'extinction. La phase de survie inclut des formes « désastre », qui édifient des récifs au lendemain de la phase d'extinction. Ultérieurement, lors de la phase de reconquête, débute la radiation des organismes récifaux. Au cours de cette phase s'effectue également la réapparition de taxons qui étaient absents des archives géologiques depuis l'avènement de la crise (modifié d'après [32] ; d'après [37]).

formed in an intracratonic basin; however, the Capitan reef ecosystem is an example of a Late Paleozoic complex that contained abundant metazoans millions of years before their demise at the Permian–Triassic boundary.

Calcified sponges play a prominent role in the formation of the Capitan reef complex, as do unusual organisms such as *Archaeolithoporella* and *Tubiphytes* (*Shamovella*) that have putative origins including algae (e.g., [1,40,51]) and calcimicrobes (e.g., [21]). Sphinctozoan sponges are volumetrically dominant in the reef and can also act as framework builders [39]. There are 34 species of sponges known from the top of the Capitan succession [63], but sponges are more dominant in the lower and middle sections. The occurrence of the large platy sponge *Gigantospongia* represents the optimum growth for this reef community [80] (Fig. 3B)

and is common below the reef–outer shelf break [62]. Other organisms that are locally important, although volumetrically less significant, include fenestrate bryozoans, phylloid algae, microbes, brachiopods, mollusks, and foraminifera (e.g., [1,39,55,70,80]). Because of the diverse biota that helped form a framework for the Capitan reef, dwelled within its cavities, and lived on its surface, this reef system stands in stark contrast to the microbial build-ups that dominated throughout the Early Triassic.

## 2.2. Examples of Upper Permian reef complexes: South China and Skyros, Greece

The Upper Permian reef complexes of South China and Skyros, Greece provide an ecological snapshot of reef systems that existed until the end-Permian extinction event. In Upper Permian deposits of Hubei and Sichuan Provinces of South China, large reef complexes have been described [16,17,59]. This Late Permian reef complex formed a barrier reef belt around the Sichuan-Hubei Platform [17]. On Skyros Island of Greece, Uppermost Permian build-ups crop out in the central part of the island [23]. Both reef complexes show a high diversity of reef faunas that were decimated by the end-Permian mass extinction [23,82].

At Laolongdong in the Sichuan province, intra-platform patch reefs are well-exposed and can be as large as 140 m wide and 70 m thick [82]. The reef faunas are diverse and are comprised of sphinctozoan and inozoan sponges, tabulozoans, hydrozoans, bryozoans and green and red algae [82]. There is also high diversity gleaned from the inter-reef limestones, suggesting that foraminifera, brachiopods, and some echinoderms were diverse and abundant up to ~60 cm below the boundary [82]. The Upper Permian Tudiya build-up in Sichuan, China exhibits similar diversity, with sphinctozoan sponges being important reef builders (Fig. 3C). In addition to sphinctozoan sponges, inozoans, calcareous sponges and algae, *Tubiphytes*, and *Archaeolithoporella* dominate these reefs with other reef-dwellers such as crinoids and brachiopods playing a more minor role [23]. Metazoan reef development terminated in all areas of South China following the end-Permian mass extinction and did not become re-established until Early Anisian time (e.g., [44]).

On Skyros Island of Greece, patch reefs have been described and form a less extensive system than the

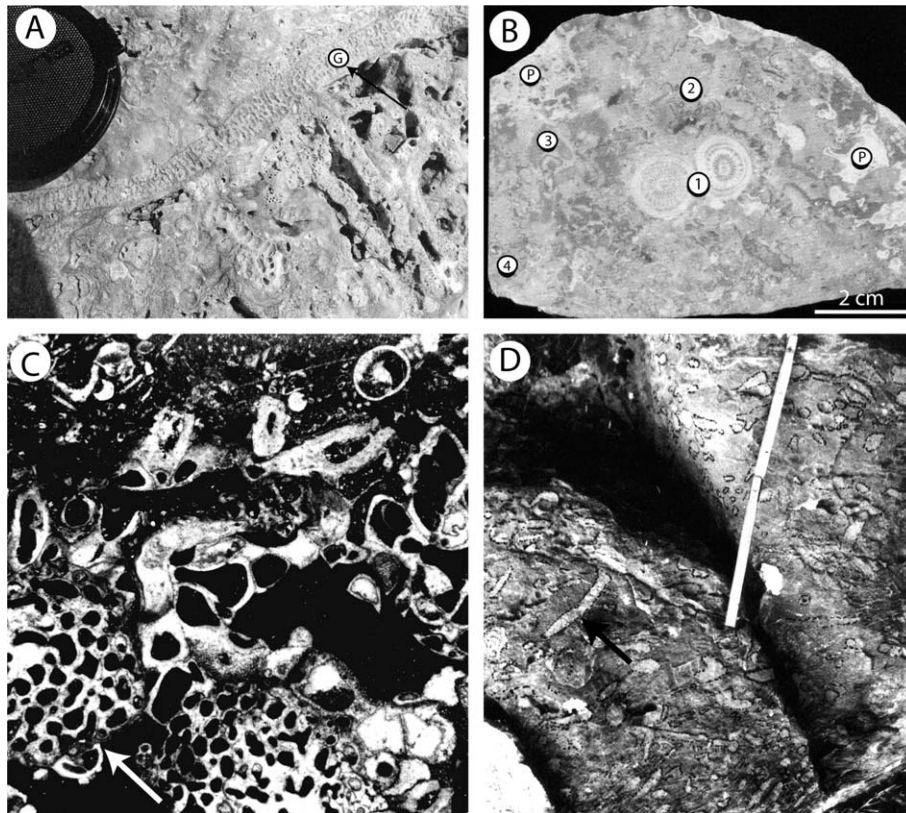


Fig. 3. Photographs showing important reef builders during the Permian. (A) Photograph of *Gigantospongia*, a calcareous platy sponge from the Permian Capitan Reef, Delaware Basin (modified from [41]). (B) Photograph of Permian Tethyan mud-dominated reef. P represents vugs with cement, 1 indicates the coral *Praewentzelella regulare*, 2 and 3 indicate algae, and 4 indicates a sponge (modified from [80]). (C) Outcrop photo of calcareous sponges from the first reef horizon of Skyros, Greece (modified from [23]). Scale bar is 40 cm. (D) Thin-section photograph showing sphinctozoan sponges of the Tudiya build-up, Sichuan China (modified from [23]) ( $\times 6$ ).

Photos des constructeurs de récifs les plus marquants durant le Permien. (A) Photographie de *Gigantospongia*, une éponge calcaire tabulaire du Capitan Reef, d'âge Permien, bassin de Delaware (modifié d'après [41]). (B) Photographie d'un récif à dominante dôme de boue du Permien de la Téthys. P représente des cavités avec ciment, 1 correspond au polypier *Praewentzelella regulare*, 2 et 3 désignent des algues, 4 indique une éponge (modifié d'après [80]). (C) Photo d'un affleurement avec des éponges calcaires du premier niveau récifal de Skyros, Grèce (modifié d'après Flügel et Reinhardt [23]). Échelle = 40 cm. (D) Photo d'une lame mince montrant des éponges sphinctozoaires de la bioconstruction Tudiya, Sichuan, Chine (modifié d'après Flügel et Reinhardt [23]) ( $\times 6$ ).

reefs of South China. The reefs of Skyros are exposed at two stratigraphic horizons and are 15-m and 12-m thick, respectively [23]. The first reef horizon, exposed about ~75 m below the Permian–Triassic boundary, consists of sphinctozoan, inozoan and other calcareous sponges as well as small solitary corals (Fig. 3D) [23]. Approximately 30 m below the Permian–Triassic boundary, the second reef horizon is dominated by various calcareous sponges as well as *Tubiphytes* and *Archaeolithoporella* [23]. Although the patch reefs of Skyros, Greece are less extensive than the barrier and patch reefs of South China, both systems are com-

posed of relatively diverse reef communities that differ greatly from the microbial build-ups of the Early Triassic.

### 2.3. The end-Permian mass extinction

The largest extinction in the history of life occurred ~250 Myr ago and brought about a reorganization of almost every marine ecosystem; the reefs were no exception to this. A variety of mechanisms have been put forth as a possible cause of this extinction including, but not limited to, widespread volcanism and sub-

sequent global warming which caused a catastrophic methane release (e.g., [65]), global anoxia [35,36,83], a runaway greenhouse effect [11], and a bolide impact [2,5]. None of these have been universally accepted as the mechanism for the end-Permian mass extinction.

Many reef building-metazoans became extinct during the end-Permian mass extinction and caused a reduction in carbonate skeletal production in reefs by >99% [81]. Rugose and tabulate corals were so devastated that it marks their total extinction (e.g., [18]). The disappearance of rugose corals was initially thought to be a gradual decrease throughout the Late Permian [18], but later work showed that rugose corals thrived until the end of the Permian [14]. Tabulates underwent a decline during the Late Permian, and only a few survived until the end of the Changxingian [18]. Corals did not recover until the Middle Triassic when scleractinians emerged. Bryozoans suffered major extinctions at the generic level, but only one order, the fenestrates, disappeared entirely [79]. Diversity is low for bryozoans throughout the Early Triassic; a radiation follows in the Middle and Late Triassic [66]. In addition to the dominant reef-building organisms discussed above, many ancillary members of reef ecosystems were also devastated by the end-Permian mass extinction. These include crinoids, brachiopods, and foraminifers, which contributed significantly to Permian reef diversity [16,17], and in some cases were the dominant reef builders. The pattern of the extinction of reef builders has caused some researchers to attribute the demise of metazoan reefs to a drop in oxygen levels, and this may have not only caused the extinction but acted as a long-term source of stress [81].

Another area of growing interest is the delayed recovery from the end-Permian extinction event (e.g., [10]). It has long been recognized that marine ecosystems did not attain pre-extinction diversity levels until the Middle Triassic (e.g., [10,31,32]); however, this too has to date been unsatisfactorily explained. Reef-building metazoans exhibit the same trend as many other metazoans; reef metazoans begin to increase in diversity at a variety of locations globally, after an absence from the world's oceans for 5–6 Myr [50,52]. The Early Triassic experiences a brief resurgence of microbial reefs that have been documented from many locations, and the replacement of microbial reefs by metazoan reefs in the Middle Triassic has been attributed to the dissipation of environmental stress (e.g., [56,69]).

### 3. The Early Triassic: A delay from the biotic recovery

The Early Triassic follows the end-Permian mass extinction and is characterized by low diversity marine faunas and a dearth of marine organisms common during most of the Phanerozoic such as sponges and corals. Opportunists such as microgastropods and lingulid brachiopods were prominent members of marine communities [26,64]; these organisms were able to thrive in the aftermath of the end-Permian mass extinction when other organisms were absent. The depauperate Early Triassic biota is considered highly unusual when compared to diverse benthic communities of the Permian or Middle Triassic (e.g., [32]).

The marine communities are far from the only unusual features of the Early Triassic. Recent work on the carbon isotope record suggests that the carbon cycle of the Early Triassic experienced long-term instability [54]. The sedimentary rock record has garnered much attention because it also reflects unusual environmental conditions following the end-Permian mass extinction. A notable increase in anachronistic facies (*sensu* [72]), including flat-pebble conglomerates [85] and ribbon rock [45] has been well-documented and is thought to represent a return to Early Paleozoic-style carbonate deposition [57]. The Early Triassic has been deemed a chert gap because few siliceous deposits are known from this time [60]. Coal deposits are also absent from the Early Triassic rock record, creating a 'coal gap' from the Permian to the Middle Triassic (e.g., [61]). As previously discussed, the global absence of metazoan reef builders from the Early Triassic has garnered the title 'reef gap' [15]; subsequent work on the proliferation of microbial reefs from this time has modified this concept [43,56] (See Fig. 1).

The occurrences of Early Triassic microbial reefs from a variety of locations have signified that this time period is not a true reef gap. The Early Triassic instead shows a resurgence of a facies not commonly seen since the Cambrian: microbial reefs forming without metazoans. During most other times in the post-Cambrian Phanerozoic, microbial fabrics co-occur with reef-building metazoans. The famous Waulsortian mounds of Carboniferous time are no exception; the baffling activity of fenestrate bryozoans commonly played a significant role in their formation (e.g., [42,57,87]). Deep-water Jurassic reefs commonly contain abundant micro-

bial fabrics, but siliceous sponges act as framework builders in these examples (e.g., [47]). Because the Early Triassic microbial reefs resemble those from much earlier in the Phanerozoic with metazoans notably absent, these represent another type of anachronistic facies.

Despite the resurgence of microbial reefs in Early Triassic time, microbial fabrics have been significant components of reef systems since the Archean. In the Archean and Proterozoic, platforms show environmental zonation that is linked to the diversity of microbial reef systems (e.g., [28]). Microbial reefs dominated carbonate systems during this time, and may have reached their peak in diversity and abundance during the Paleoproterozoic [29,34]. Microbial communities continued to play key roles in reef systems throughout the Phanerozoic, but generally occurred with reef-building metazoans (e.g., [6,8,48,73,88]).

#### 4. Microbial reefs

In recent research conducted in Lower Triassic strata of South China [43,46], southern Turkey, Armenia, Iran, and Oman [3,4], Greenland [86], and the western United States [56], normal marine microbial build-ups have been documented. In addition to the proliferation of build-ups, other microbialites also occur in boundary sections from Japan [68], Iran [33], South China [38,39] and South Tibet [27]. One of the most fascinating aspects of these microbial reef occurrences is that some occurred millions years after the end-Permian mass extinction [43,45,46]. This means that microbial reefs, although also present in the Earliest Triassic, were not isolated to the interval immediately following the mass extinction. For this and other reasons, the occurrence of Early Triassic microbial reefs has been linked to long-term stressful environmental conditions related to the end-Permian mass extinction event [31,43,56].

#### 5. Reef occurrences

##### 5.1. Examples from South China, Southern Turkey, Greenland and the western United States

Early Triassic microbial reefs have now been described from many regions including eastern Pan-

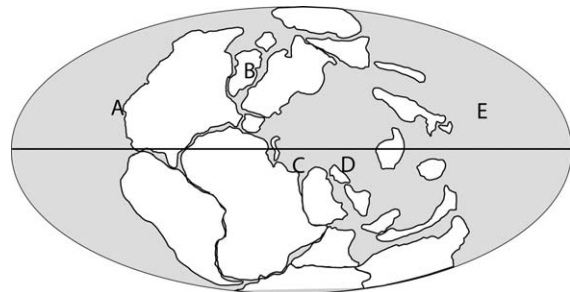


Fig. 4. Early Triassic paleogeographic map showing the approximate locations of microbial reefs. (A) Western United States, deposited on the eastern margin of Panthalassa. (B) Jamesonland, Greenland, deposited in the Boreal Ocean. (C) Southern Turkey, deposited in western Tethys. (D) Iran, deposited in central Tethys. (E) South China, deposited in eastern Tethys (modified from [56], after [10]; with data from [3,4,43,86]).

Carte paléogéographique du début du Trias montrant la localisation approximative des récifs microbiens. (A) Ouest des États-Unis, sur la marge orientale de la Panthalassa. (B) Jamesonland, Groenland, dans l'océan boréal. (C) Sud de la Turquie, dans la Téthys occidentale. (D) Iran, au centre de la Téthys. (E) Sud de la Chine, dans la Téthys orientale (modifié d'après [56], d'après [10] ; avec des données de [3,4,43,86]).

thalassa, eastern, central, and western Tethys, and the Boreal ocean (Fig. 4). These reefs occur primarily as reef mounds that attained a relief of about 2 m above the seafloor. These are generally described as patch reef systems and are not as thick as Permian reefs though individual microbial reef-bearing deposits, like those in South China, are extensive over 10 000 km<sup>2</sup> [46]. The microbial reefs tend to crop out as individual mounds, and exhibit both stromatolitic and thrombolitic features. Some microbial build-ups contain the preserved remains of microbes such as *Renalcis* [43], and others contain only preserved microbial laminations [56].

In Lower Triassic strata of South China, microbial build-ups occur as calcimicrobial mounds and biostromes [43]. The Smithian-Spathian calcimicrobial mounds attained the most significant relief of all the microbialites described from the Great Bank of Guizhou. These formed as domal or inverted conical mounds, and range in size from 0.1 to 1.5 m [43]. Because of their topographic relief, rigid organic framework, and presence of microorganisms such as *Renalcis*, these have been interpreted to represent microbial patch reefs [43].

Other examples of microbial reefs have been described from Lower Triassic strata of southern Turkey

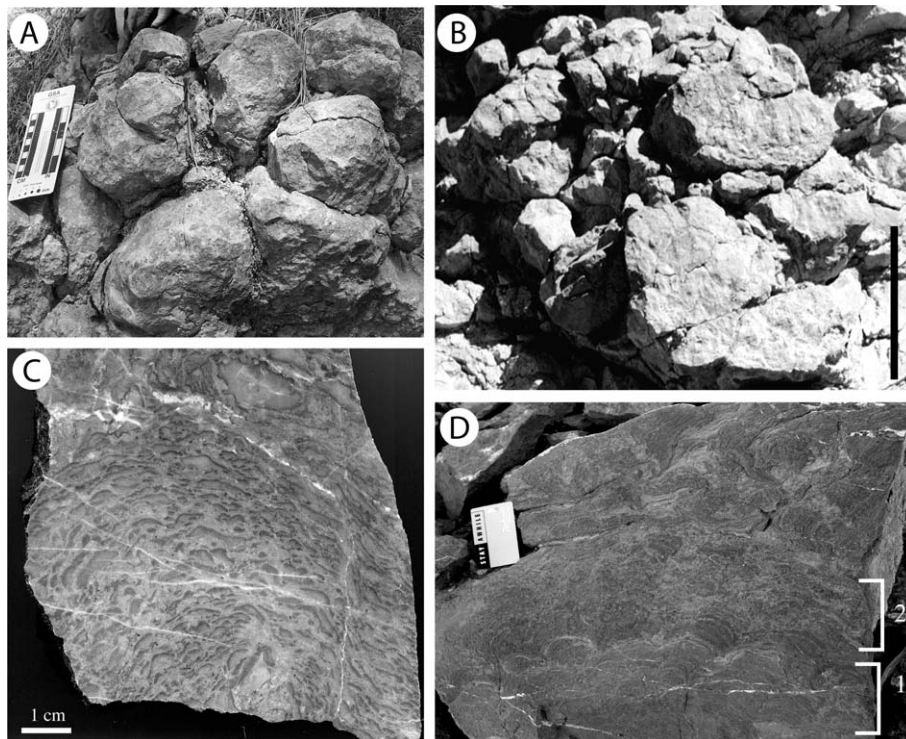


Fig. 5. Examples of Early Triassic microbial build-ups. (A) Thrombolite mound from Lower Triassic Kokarkuyu Formation, Antalya Nappes, southern Turkey. Mound is ~1 m in height. (B) Microbial mound from Lower Triassic Virgin Limestone Member of the Moenkopi Formation, Spring Mountains, southern Nevada, USA (modified from [56]). (C) Slab photograph of one of the microbial fabrics from Lower Triassic Virgin Limestone Member of the Moenkopi Formation, Spring Mountains, southern Nevada, USA (modified from [57]). (D) Photograph showing microbial fabrics in outcrop (modified from [57]); (1) indicates stromatolitic fabric and (2) indicates thrombolitic fabric. Card is ~8 cm for scale. Exemples de constructions microbiennes du début du Trias. (A) Dôme à thrombolites de la formation Kokarkuyu du Trias inférieur, nappes d'Antalya, Sud de la Turquie. Les dômes mesurent environ 1 m de hauteur. (B) Dôme microbien du Trias inférieur du Virgin Limestone Member de la formation Moenkopi, Spring Mountains, Sud du Nevada, USA (modifié d'après [56]). (C) Photo d'une dalle exhibant l'une des textures microbiennes du Trias inférieur du Virgin Limestone Member de la formation Moenkopi, Spring Mountains, Sud du Nevada, États-Unis (modifié d'après [57]). (D) Photo illustrant des textures microbiennes à l'affleurement (modifié d'après [57]) ; (1) indique des textures stromatolitiques et (2) des textures thrombolitiques. Échelle : carte = 8 cm.

[3,4] (Fig. 5A). A variety of microbialites have been described including, but not limited to, columnar, domal, and conical stromatolites, and thrombolites [4]. The giant domal stromatolites attained a relief of ~2 m above the seafloor. Some examples of these giant stromatolites extend laterally for 10 m. Thrombolites consisting of massive mounds of clotted micrite measure up to 2 m in height and 10–20 m laterally [4].

Stromatolitic bioherms have been documented from Lower Triassic strata of Greenland [86]. These occur in Lower Griesbachian strata and consist of small, laterally extensive build-ups (< 1 m) that formed within laminated silty shales [86]. These build-ups formed on a thin bed of broken stromatolite and thick-shelled bivalve debris (*Promyalina*). In thin-section, the bio-

herms consist of alternating dark and light laminae of micrite. These carbonate build-ups are noticeable features surrounded by siliciclastics (P.B. Wignall, pers. commun., 2004).

Early Triassic microbial build-ups have been described from the western United States. Schubert and Bottjer [69] first noted that these stromatolites represent disaster forms that were able to flourish in the aftermath of the end-Permian mass extinction. Subsequent work on these microbial build-ups has suggested that they attained significant relief above the seafloor and therefore formed patch reefs [56] (Fig. 5B). The build-ups occur in one bed in which they are laterally extensive. Thin limestone beds lap out against the sides of the individual mounds suggesting a topographic relief



of 1 m or more. In outcrop and on cut slabs, stromatolitic and thrombolitic fabrics are obvious features (Fig. 5C and D). In thin-section, microbial laminations, clotted fabrics, open framework crypts with bladed cements, and disarticulated metazoan debris are common features [56].

In addition to the various reports of microbial build-ups, other microbialites and possible microbial crusts have been noted from various sections around the world. Microbialites from Japan [68], Iran [33], and South China [38,39] have been described from Lowermost Triassic sections. These occurrences reflect an expansion of microbial fabrics immediately following the end-Permian mass extinction, and the distribution of microbialites throughout the Early Triassic indicates that microbialite formation was sustained for millions of years.

### 5.2. Middle Triassic: Recovery of metazoan reefs

The diversification of metazoan reef-dwelling organisms took place in the Anisian (e.g., [22]). In addition to the diversification of reef-building metazoans (Fig. 6A and B), reef abundance also increased during this time. The oldest Tethyan reefs have been reported from the Pelsonian Dont Formation in the Dolomites of Italy (e.g., [25]). These reefs exhibit abundant *Tubiphytes*, although the *Tubiphytes* are considered to represent different forms than those of the Permian [25]. The Peri-Tethyan region of Silesia contains a reef system of a similar age to the Dont Formation. An increase in *Tubiphytes*-bearing reefs occurs in Middle Triassic strata of the Nanpanjiang Basin of South China (J.-L. Payne, pers. commun., 2003). Middle Triassic reef occurrences represent the recovery of metazoan reefs, a facies that had been absent from the rock record for ~7 Myr [15,21].

The metazoan reefs that re-appeared during the Anisian are composed of microbes and possible calcimicrobes (*Tubiphytes*), calcareous and siliceous sponges, bryozoans, and corals, with other organisms being locally important [21,25]. Low-diversity communities dominate many reefs of this time; however, a few examples of high diversity sponge-coral reefs have been described from southern Spain, the Dolomites of Italy, and Austria (e.g., [21] and references therein). The initial radiation of scleractinian corals occurred during the Middle Triassic, with the earliest ancestors reported

from allochthonous deposits of platform carbonate blocks transported into offshore settings [58,77]. Scleractinians do not take over as dominant reef builders until later in the Triassic (e.g., [77]). Reef proliferation that began in the Anisian continued into the Ladinian and Early Carnian, and many of those reefs share characteristics with their Anisian predecessors.

Examples of Ladinian and Early Carnian reefs include bivalve build-ups in Germany, algal and microbial mounds in Spain, and microbial-calcareous sponge mounds in the Alps [21]. Ladinian and Early Carnian reefs are comprised of the same constructional reef types as Anisian reefs; however, the late Middle Triassic reefs are more widely distributed and abundant than those of the Anisian [21]. Additionally, the taxonomic composition of the Ladinian–Early Carnian reefs differs markedly from Anisian reefs; many Anisian sponges and corals became extinct prior to the Ladinian. The establishment of large reef complexes occurred later in the Triassic during the Norian–Rhaetian reef bloom, and at this time, scleractinian corals replaced calcareous sponges in many reef successions, illustrating the initial rise to dominance of scleractinian reefs (e.g., [74]). The Norian also marks the appearance of Lazarus taxa that had been absent since the Permian, suggesting a long-term existence in refugia [21].

## 6. Reef occurrences

### 6.1. Examples from South China and northern calcareous Alps

During Anisian to Carnian time, reefs dominated the Tethyan realm, most especially western Tethys. Anisian reefs fall into a few broad categories based on their dominant faunas and these include thrombolite reefs, *Tubiphytes* reefs, calcareous sponge reefs, coral reefs, algal reefs and bivalve build-ups [21]. During Early Anisian time, reefs formed in the Yangtze Platform of South China, the Dont Formation of the Dolomites, and the Camorelli Platform of northern Italy [21]. Other small Anisian biostromes are known from deposits in British Columbia [89]. The descriptions of South China and the Northern Calcareous Alps provide two examples of regions that were dominated by reef systems for much of the Middle and Late Triassic, but by no means encompass all of the diversity of reef types and faunas captured in Middle and Upper Triassic strata.

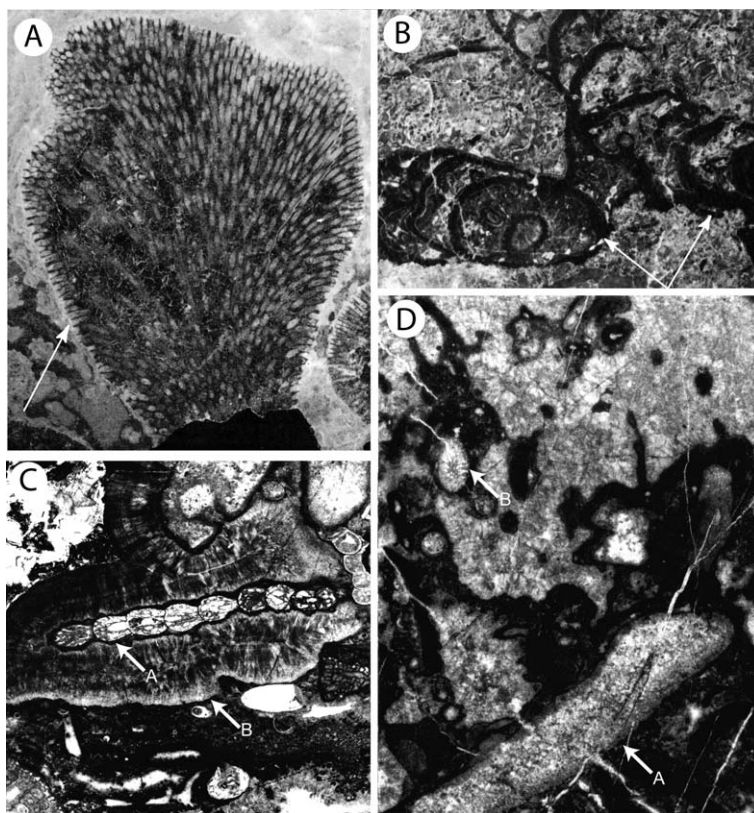


Fig. 6. Photographs showing examples of Middle–Late Triassic reef builders (A–B) and fabrics (C–D). (A) An example of a tabulozoan from Upper Triassic reefs in the northern Calcareous Alps. Arrow shows edge of tabulozoan (modified from [19]) ( $\times 20$ ). (B) A calcareous sponge from the Upper Triassic of British Columbia. Arrows indicate two sponges (modified from [78]). (C) Thin-section photograph showing typical fabric of the Ladinian–Carnian Hafelekar Reef complex, Wetterstein Limestone, Northern Calcareous Alps. Thin-section contains sphinctozoan sponge encrusted by *Tubiphytes* (A). Note fibrous spar that infilled cavity space (B) (modified from [7]) ( $\times 3.9$ ). (D) Thin-section showing a common reef fabric of the Goetheweg Reef, which represents the initial phase of reef development of the Ladinian–Carnian Hafelekar Reef Complex. Note plate-like hydrozoan. (A) and bryozoans (B) encrusted by *Tubiphytes* (modified from [7]) ( $\times 3.2$ ).

Photos montrant des exemples de constructeurs récifaux (A–B) et des textures associées (C–D) du Trias moyen et supérieur. (A) Exemple de tabulozoaire des récifs du Trias supérieur des Alpes calcaires septentrionales. La flèche indique le bord du tabulozoaire (modifié d'après [19]) ( $\times 20$ ). (B) Éponge calcaire du Trias supérieur de la Colombie britannique. Les flèches montrent deux éponges (modifié d'après [78]). (C) Photo d'une lame mince montrant des textures caractéristiques du complexe récifal de Hafelekar, d'âge Ladinien–Carnien, calcaire du Wetterstein, Alpes calcaires septentrionales. La lame mince renferme des éponges sphinctozoaires encroûtées par des *Tubiphytes* (A). Remarquer les cavités garnies de sparite fibreuse (B) (modifié d'après [7]) ( $\times 3,9$ ). (D) Lame mince montrant une texture récifale commune dans le récif de Goetheweg, correspondant à la phase initiale du développement récifal du complexe récifal de Hafelekar, d'âge Ladinien–Carnien. Remarquer les hydrozoaires lamellaires (A) et les bryozoaires (B) encroûtés par des *Tubiphytes* (modifié d'après [7]) ( $\times 3,2$ ).

Middle Triassic reefs initially occur without scleractinian corals acting as framework builders. Anisian reefs from South China formed along an east-west trending warm seaway in the Tethyan realm (e.g., [77]). In the Guizhou province of South China, initial build-ups lacked scleractinians acting as framework builders [58]. Instead, scleractinian corals made their first appearances in transported carbonate platform blocks that were deposited in offshore environments [9,58].

With the onset of major reef development during the Middle and Upper Anisian, major carbonate contributors included calcareous algae, sponges, mollusks, bryozoans, problematic organisms such as *Tubiphytes*, and microbialites [24]. During this time, there was a change in carbonate shelves to systems that were dominated by skeletal organisms after an absence of significant skeletal deposits for much of the Early Triassic. Although initially the main components of reefs in South

China did not include scleractinians, they became extremely important in reef ecosystems later in the Triassic [77].

In the northern Calcareous Alps, major reef development began in the Late Anisian to Early Ladinian and persisted through the Late Triassic. Early Middle Triassic reefs of this region consist of small 10–100-m thick build-ups within the Steinalm Limestone [19]. Large-scale reefs, like the Wetterstein reefs, became established during the Ladinian and formed vast reef complexes in the Northern Calcareous Alps that were several tens to hundreds of square kilometers in size [19,21]. Calcareous sponges and problematic organisms such as *Tubiphytes* dominated these reefs [53] with lesser components being scleractinian corals, calcareous algae, and bivalves [21]. Although the reef facies is continuous through hundreds of meters, at any given time, individual reefs likely attained a relief of tens of meters [21].

Reefs of the northern Calcareous Alps that formed during Norian–Rhaetian time show a distinct change in reef faunas from those of the Ladinian–Carnian. These reefs, called the ‘Dachstein reefs’, developed along platform edges of Tethyan basins [21]. The Dachstein reefs contain calcareous sponges and corals as important framework builders, which differentiate them from Ladinian–Carnian reefs (see above) [19]. The Dachstein reefs of the Northern Calcareous Alps are composed of randomly situated patch reefs that persist through tens to hundreds of meters of strata.

## 7. Discussion

The decimation of reef ecosystems at the end of the Permian brought about a long-term absence of metazoan reefs in the Early Triassic. For millions of years after the end-Permian mass extinction, microbial reefs proliferated in their absence. As discussed above, the re-appearance of metazoan reefs took place in the Anisian in regions such as Peri-Tethys (central Europe), western Tethys (southern Alps and Greece), and the South China plate [21]. The long-term replacement of metazoan reefs by microbial reefs has been interpreted to represent prolonged environmental stress [3,4,43,56]. The demise of reef-dwelling metazoans has recently been linked to low oxygen conditions, which may have acted as an environmental stress [81].

A variety of criteria must be assessed when discussing the causal mechanisms of the absence of metazoan reefs from Lower Triassic strata. The first consideration is ecospace availability because without environments conducive to reef development, reefs could not form. During the Early Triassic, however, a widespread transgression facilitated the development of shelves on continental margins of northern and western Tethys, South China, and eastern Panthalassa (e.g., [32]). Therefore, reef ecospace was available during the Early Triassic. Another consideration is the time it took for metazoans to recover from the devastating end-Permian extinction. Biotic recovery is sometimes difficult to elucidate because groups of organisms recover at different rates; however, an example of a relatively short biotic recovery is that from the Cretaceous–Tertiary event. Biotic recovery of certain clades occurred between 10 000 and 100 000 years after the K–T extinction (e.g., [32]). In comparison, assuming the biotic recovery from the end-Permian mass extinction was delayed for 5–6 Myr after the extinction [50,52], the start of the recovery took ~50–60 times longer than the recovery from the K–T extinction. Additionally, the re-appearance of Lazarus taxa in Late Triassic time suggests that some organisms survived the end-Permian event but either existed in low numbers [12] or in refugia [21] for most of the Triassic. All of these findings suggest that environmental parameters were the dominant control on the biotic recovery from the end-Permian mass extinction because ecospace was available, biotic recovery from mass extinction can occur in a much shorter time frame than ~6 Myr, and some Permian reef-dwellers had passed through the end-Permian extinction event but likely persisted in refugia for millions of years. A more detailed study of Middle Triassic reef faunas is necessary to determine whether or not the perceived Lazarus taxa are true survivors or if they are Elvis taxa, organisms whose morphologies are convergent on earlier forms [13,84].

## 8. Depositional model for Early Triassic microbial reefs

The following interpretation for microbial reef development during the Early Triassic is proposed (Fig. 7): (1) the end-Permian extinction event devastated colonial reef ecosystems so an ensuing metazoan reef gap

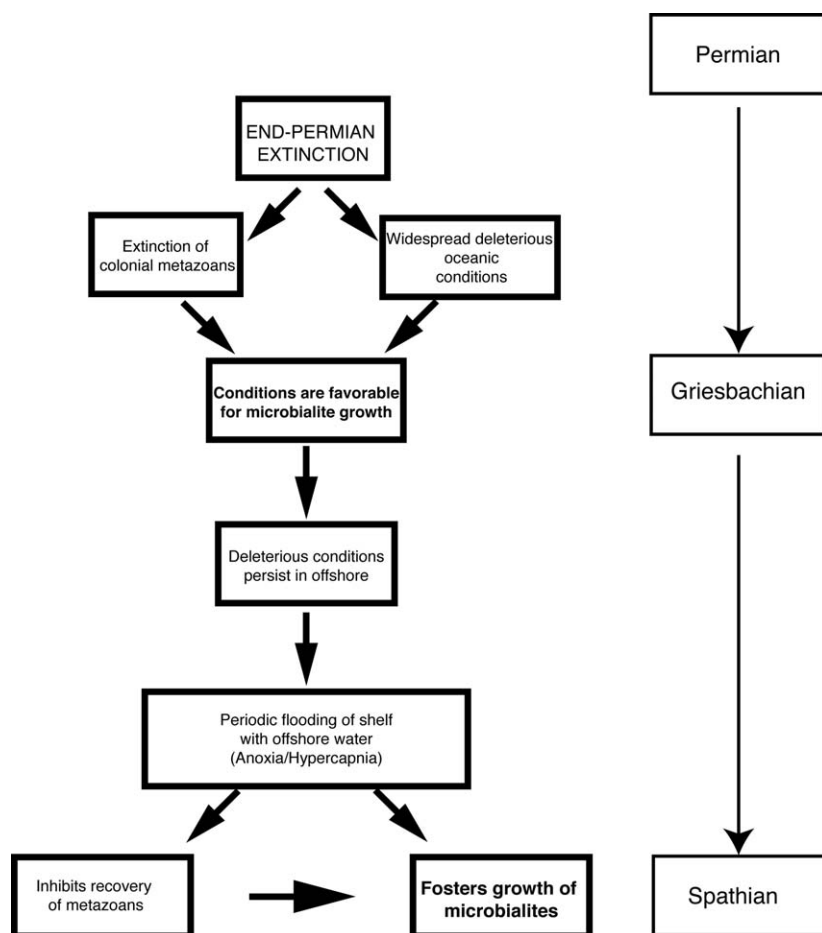


Fig. 7. Diagram showing the effects of the end-Permian mass extinction on microbial reef development during the Early Triassic. Note two intervals of microbial reef development during the Early Triassic.

Diagramme illustrant les répercussions de la crise biologique de la fin du Permien sur le développement des récifs microbiens au cours du début du Trias. Remarquer l'existence de deux intervalles de prolifération des récifs microbiens durant cette période.

followed throughout the Early Triassic [20]; (2) immediately following the mass extinction, microbialites flourished in Earliest Triassic time in a variety of regions globally including southern Turkey, Greenland, and south China [3,4,38,39,43,86]; (3) the Spathian Virgin Limestone microbial mounds formed several million years later in an inner–middle shelf paleoenvironment coevally with more offshore carbonate seafloor precipitates documented by Woods et al. [88] that have been interpreted to represent deleterious deep-water conditions [49] – Spathian microbial reef mounds have also been reported from south China [43] –; and (4) the occurrence of microbial reef mounds during at least two intervals of the Early Triassic suggests that shelf environments may be influenced by stressful deep-water

conditions (perhaps anoxic or CO<sub>2</sub>-rich waters) that could have inhibited metazoans while simultaneously fostering the growth of microbialites. The global occurrence of microbial build-ups and the absence of metazoan reefs throughout the Early Triassic (5–6 Myr) [50,52] imply that the conditions favoring microbialite development may be linked to those that delayed the recovery of colonial and other metazoans [46,56].

## 9. Conclusions

The end-Permian mass extinction brought about one of the greatest reorganizations of metazoan reef ecosystems since their advent in the Cambrian. After a near

annihilation of reef building organisms such as sponges and corals at the close of the Permian, a metazoan reef gap ensued [15]. This reef gap encompassed the entirety of the Early Triassic; however, in the absence of metazoan reefs, microbial reefs proliferated. Microbial build-ups have now been reported from Griesbachian (earliest Triassic) [3,4,43,86] and Spathian strata (late Early Triassic) [43,56], and these occurrences have been linked to the presence of stressful environmental conditions such as low levels of oxygen in the aftermath of the end-Permian mass extinction [81]. Following a gap of ~7 Myr, metazoan reefs re-appear at a variety of locations globally in the Anisian. These reefs were initially dominated by microbes, calcimicrobes, calcareous and siliceous sponges, bryozoans, and corals; however, in Late Triassic time, corals and sponges took over as the dominant reef builders, establishing in some aspects the ‘modern-reef’ ecosystem [21].

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