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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

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## 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.

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