The development of reefs across the end-Permian extinction

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Abstract

Late Permian stratigraphic reefs, constructed by calcisponges and algae, survived into the latest Permian in a few tropical refuges, indicating the continuation of favourable conditions for reef formation. However, all kinds of reefs collapsed prior to the large-scale biotic crisis of reef-dwelling and level-bottom communities at the Permian-Triassic boundary. This affected even the tropical refuges. Different elements of the reef-forming biota showed distinct patterns of extinction. Whatever the main causes of biotic decline, the reefs did not disappear at the very end of the Permian catastrophically, but had already been strongly affected by the extinction in the Midian (late Guadalupian).

Reefs were not developed until Anisian (Middle Triassic), and at that time radiolarian bedded chert also began to be formed commonly in pelagic environments, indicating global removal of the protracted inhibiting conditions in the ocean. The main reef-builders and their role in reef communities are similar in both Late Permian and Middle Triassic reefs. However, the community structure was later modified by a change in domination among components, such as Scleractinia which acquired algal symbiosis and more efficient skeletal growth.

Long-lasting unfavourable marine environment on a global scale, rather than the severity of the end-Permian extinction itself, hindered biotic recovery everywhere during Early Triassic time despite the presence of Permian holdover groups as potential organisms for reef-building. Both external environmental and biological factors acted together in delaying Triassic reef development. The end-Permian extinction resulted in the restructuring of reef-forming biota in the Middle Triassic from Permian survivors rather than the introduction of a new community.

Key words : reefs, Permian, Triassic, extinction, recovery, corals

Introduction

Carbonates are formed primarily by carbonate-producing organisms which are restricted in range by such factors as water temperature, salinity and depth. Biogenic carbonates, therefore, record environmental fluctuations, and long-term variations in carbonate abundance dependent on biotic constituents have been discussed (e.g., James, 1983 ; Tucker and Wright, 1990). Reefs are especially abundant in the Silurian-Devonian, Jurassic-Cretaceous and post-Eocene times, and each period is distinguished by different associations of main reef-builders : stromatoporoids-Tabulata, Scleractinia-stromatoporoids-rudists, Scleractinia-calcareous algae, respectively.

Repeated extinction events with varying magnitudes are known throughout Phanerozoic time ; some of these extinctions played decisive roles in evolutionary and community patterns in subsequent periods in various ways (Sheehan, 1985 ; Copper, 1988 ; Talent, 1988). The end-Permian extinction produced the largest of all biotic crises, and it is characterised by the extinctions of Rugosa, Tabulata and fusulinids, and great taxonomic declines in brachiopods, ammonoids and bryozoans. Apparent patterns of disappearance have been shown for different taxa, and their possible causes have been argued in terms of environmental fluctuations on various scales (e.g., Teichert, 1990 ; Yang, et al., 1991 ; Erwin, 1993). A marked change occurred also in the community struc-

Perm.	Standard	South China	North America
Late	Changxingian	Changxingian	Ochoan
	Dzhulfian	Wujiapingian	
Mid.	Midian	Maokouan	Guadalupian

Fig. 1. Correlation of late Middle and Late Permian stages based on Klein and Beauchamp (1994).

ture of the marine ecosystem near the Permian–Triassic boundary. The “Palaeozoic Evolutionary Fauna”, dominated by epifaunal suspension feeders, was impoverished at the end of the Permian, whereas the “Modern Evolutionary Fauna”, characterised by infaunal suspension and deposit feeders, was less affected (see Sepkoski, 1984). Holser et al. (1991), Sweet et al. (1992) and Erwin (1993, 1994, 1995) discuss the causes of the end-Permian extinction.

This paper outlines the characteristics of Late Permian and Middle Triassic reefs, and then considers the role of the end-Permian extinction in subsequent reef development, with clues provided by the surviving groups and the spatio-temporal distribution patterns of biogenic sediments. It is beyond the scope of this paper to specify the causes of reef collapse and recovery. A threefold Permian subdivision is adopted in which the Late Permian begins with the Dzhulfian (Fig. 1). The age of the Zechstein is difficult to evaluate, but the integrated time analysis indicates that it ranges from 258 to 251 Ma and is correlative to latest Tatarian (Menning, 1995). The reefs in the Zechstein (e.g., EZ 1 in north-east England) are referable to Late

Permian reefs in this paper. The term reef is used broadly, encompassing ecological reefs (wave-resistant organic frameworks) and stratigraphic reefs (reef mounds). The author uses the term Lazarus taxa for taxa which disappeared from the fossil record during mass extinction events, but reappeared later (Jablonski, 1986).

Late Permian and Middle Triassic reefs

Distribution and composition

Various types of reefs were distributed widely across climatic zones in the Early and Middle Permian. In contrast, the Late Permian (Dzhulfian and Changxingian) reefs are geographically restricted to South China, Greece, the Caucasus and the Zechstein Basin (e.g., see Smith, 1981; Flügel and Reinhardt, 1989; Fan et al., 1990; Fig. 2). The Changxingian (*Palaeofusulina* Zone) reefs occur commonly in South China. The South China Block was situated in the tropics, judging from the presence of chlorozoan and chloralgal skeletal associations of bioclastic carbonates and palaeomagnetic evidence (e.g., Scotese and Langford, 1995). The latest Permian refuges for reef-

Fig. 2. Distribution of Late Permian reefs. Reef types are based on Flügel (1994). Palaeogeographic map modified after Golonka et al. (1994) and Scotese and Langford (1995).

Table 1. Comparison of various aspects of Late Permian and Middle Triassic reefs.

	Late Permian	Middle Triassic
main builders	calcisponges, algae, bryozoans	calcisponges, algae, bryozoans
other components	<i>Archaeolithoporella</i> , Rugosa, <i>Tubiphytes</i> , foraminifera	" <i>Tubiphytes</i> ", bivalves, sclerosponges, Scleractinia
role	binders, bafflers	binders, bafflers
succession	"pioneering-arrested"	pioneering-arrested
distribution	South China, Greece, Caucasus, Zechstein	South China, Europe, North America, Peru

forming organisms were present in the tropics. It is of interest that Early Permian (pre-Maokouan) reefs were absent in South China, implying strong provincialism in sedimentary environments and palaeoceanographic conditions.

Most, if not all, of the Late Permian reefs are constructed by calcisponges and calcareous algae as bafflers, and *Archaeolithoporella* and *Tubiphytes* as binders, forming small-scale stratigraphic reef mounds (Flügel and Reinhardt, 1989; Table 1). Late Permian reefs lack large constructional framebuilders and rarely formed wave-resistant frameworks, although Changxingian barrier reefs, showing lateral zonations of rock types and biotic assemblages, have been recently reported in a carbonate platform of South China (Fan et al., 1990).

Middle Permian reefal limestones, having diverse algae and *Tubiphytes*, were also formed on shallow-water topographic highs with a basaltic basement (Sano et al., 1990) in the open-ocean tropics of the Panthalassa Ocean. However, no Late Permian reefs have been found. Marked environmental changes in the ocean are suggested by the cessation of reef growth during Middle Permian time in the open Panthalassa Ocean.

Marine Permian successions, up to the Upper Permian, are also well represented in northern Pangaea (e.g., the Canadian Arctic, Spitsbergen, Greenland). Tropical-type carbonates, having diverse chlorozoan organisms, of Late Carboniferous to Sakmarian age were succeeded by temperate, shallow-water carbonates with bryozoan buildups in the Artinskian, and finally by cool-water carbonates with limited faunas including brachiopods, bryozoans and echinoderms by the Kazanian, nearly equivalent to the Murgabian in the Tethys region (Worsley et al., 1986; Stemmerik and Worsley, 1989; Beauchamp, 1992, 1994; Ezaki et al., 1994). Cool-water Permian organisms in northern Pangaea became greatly impoverished everywhere in the Middle and Late Permian. In Spitsbergen, they form patterns of disappearance in cool climatic conditions and a tectonic framework established in the mid-Permian (Ezaki et al., 1994). Collapse of the reef ecosystem occurred earlier at these high latitude regions

than in the tropical latitude regions which provided the latest Permian refuges for reef-forming biota. Marked decrease in the spatio-temporal distribution of Late Permian reefs are considered to relate to the extinctions on Pangaea and the South China Block which had already begun in the late Guadalupian (Midian) (Erwin, 1993, 1995; Jin et al., 1994).

The end-Permian extinction decimated benthic organisms, culminating in the Early Triassic reef gap of Flügel (1994). Early Triassic reefs were formed only in limited areas such as the Caucasus, North America and South China, whereas Middle Triassic reefs are distributed more widely in Europe, South China, western North America and Peru (Flügel, 1981, 1982, 1994; Senowbari-Daryan et al., 1993 and references therein). Early Triassic reefs, though rare, are marked by microbial stromatolites in environments with relaxed ecological constraints after the end-Permian extinction (Schubert and Bottjer, 1992).

Small buildups constructed by baffling sponges and binding algae, "*Tubiphytes*" and sponges were apparent again in the Anisian (Middle Triassic) (Table 1). The biotic composition, communities and distribution of the Anisian reefs were well documented in relation to a reef recovery (Fois and Gaetani, 1984; Senowbari-Daryan et al., 1993). The Middle Triassic and early Carnian reefs are characterised by calcisponges, algal crusts, "*Tubiphytes*", Solenoporaceae and scleractinian corals; several reef communities reflecting the different stages in reef formation and different localities, were recognised (Flügel, 1982). Those reef biota were later reorganised in composition, communities and diversity (see Flügel, 1982; Stanley, 1988). Scleractinia and calcisponges acted as binders and bafflers at first, and were dominant later in post-Carnian time as the main reef constructors in abundance, size, and diversity (Flügel, 1981; Fagerstrom, 1987; Stanley, 1988).

Ecological succession

With reference to long-term ecological successions (erathemic successions) of the reef ecosystem in terms of areal extent, architectural complexity and diversity, the Permian constitutes a "climax phase" (Copper, 1988). Reef-forming stromatoporoids and Tabulata

Fig. 3. Schematic diagram showing changes in Upper Permian lithology and reef-dwelling organisms on a carbonate platform in the South China Block. Note the marked unconformities between the Maokouan and the Wujiapingian as well as just below the Permian-Triassic boundary. Corals survived into the uppermost Permian. Biotic data are based on Reinhardt (1988), Fan et al. (1990), Zhang and Zhang (1992), Ezaki (1994), and other references therein.

declined greatly in the Late Devonian extinction, and few large-scale framebuilding reefs were developed. Calcareous sphinctozoan sponges became dominant in the Middle to Late Permian, but they were impoverished by the end-Permian extinction (see Rigby and Senowbari-Daryan, 1995 for recent summary). The Permian reefs were severely affected by the mid-Permian extinction. The present author, therefore, considers at least the Late Permian as "pioneering-arrested phase" (Table 1). The Triassic is divided into an Early Triassic "extinction phase", Middle Triassic and early Carnian "pioneering-arrested phase" and late Carnian to Rhaetian "climax phase" (Copper, 1988). Full-scale reefs were thus developed during the Late Triassic.

In the short term, some Changxingian reefs in southeast Sichuan, South China are characterised by stratigraphic reef mounds, and in places they show an ecological succession from the stabilisation stage marked by shoal facies and submarine lithification to the colonisation stage indicated by sponge boundstone patches (Reinhardt, 1988, 1991). It is remarkable that favourable conditions for reef formation persisted up to the latest Permian (Changxingian), until the lagoonal gymnocodiacean limestone was deposited, without showing the diversification or the domination stages of reefal, ecological successions. The Late Permian reefs were not

eliminated in a pattern indicative of catastrophic episodes.

Their disappearance was followed by extinctions of carbonate-producing organisms just before and/or after the latest Permian regression which led to a widespread deposition of evaporitic carbonates and a sequence boundary (Fig. 3). Level-bottom communities other than reef-dwellers were also greatly impoverished just prior to the Permian-Triassic biostratigraphic boundary. At that time the following events occurred: 1) widespread transgression already initiated in the latest Permian (Yang et al., 1991; Wignall and Hallam, 1993); 2) a major drop in $\delta^{13}\text{C}$ with varying magnitudes and patterns (Yang et al., 1991); 3) deposition of a boundary clay of acidic to intermediate volcanic origin in South China (Li et al., 1991; Yang et al., 1991). In the Southern Alps, the Anisian reef (mound) communities were recovered in a deep environment, showing a succession from the pioneer stage to the colonisation stage marked by highly diverse communities of bryozoans, calcisponges, algae and scleractinian corals (Fois and Gaetani, 1984).

Rugosan extinction and differences with Scleractinia

Both rugose and tabulate corals were typical carbonate-producing organisms in the Palaeozoic, but

they became extinct at the end of the Permian. The faunal composition and the timing of disappearance of Late Permian corals differ from place to place. The Late Permian rugosan fauna is represented by surviving groups from the Middle Permian (Ezaki, 1994).

On the South China Block, Late Permian (Wujiapingian and Changxingian) skeletal limestones, containing abundant calcisponges, calcareous algae, fusulinids and rugose corals, were formed successively from the Middle Permian (Maokouan) with or without major depositional breaks. Fasciculate waagenophyllids (*Waagenophyllum* and *Liangshanophyllum*) occur abundantly on the carbonate platform up to the uppermost Permian (Figs. 3, 4), locally acting as reef-forming organisms, whereas latest Changxingian corals in the slope and lagoonal environments consist of non-dissepimented solitary corals (plerophyllids) having simple morphologies for life-strategic reasons (see Ezaki, 1993, 1994). Coral thickets of colonial *Waagenophyllum*, several tens of centimetres thick, are traced over several kilometres just below the uppermost Permian dolomicrites at Liangshan of Hanzhong, Shaanxi Province. The abundance of individuals indicates that the biomass was not necessarily small. Among the waagenophyllids the complex massive Wentzelellinae disappeared first by the end of the Maokouan, whereas the simpler fasciculate and solitary genera of the Waagenophyllinae survived later in the Permian (Fig. 3). Different patterns of disappearance among these corals reflect phylogenetic trends as well as regional, deteriorating habitat conditions (Ezaki, 1994, in press).

The Scleractinia, which appeared first in the Middle Triassic, occasionally have contributed greatly to reef construction, whereas the Rugosa, their Palaeozoic counterpart, did not. Although the Scleractinia and Rugosa commonly have calcareous skeletons and presumably some similarity in their range of habitat, they differ in their functional role in reef communities and were not closely related to each other phylogenetically (e.g., Oliver, 1980; Ezaki, 1989; Scrutton and Clarkson, 1991). The differences include: biomineralogy (calcite in Rugosa vs. aragonite in Scleractinia); skeletal segregation patterns (solid vs. porous, leading to increased mechanical efficiency and high growth rates); levels of integration within colonies (low vs. high, producing a wide range of forms of coralla and enhanced metabolic activities) (Coates and Oliver, 1973). Framebuilders may have been unable to diversify until the establishment of a symbiotic relationship with algae (zooxanthellae) in Late Triassic time, because algal symbiosis enhances metabolic and skeletal growth activities (see Cowen, 1988; Stanley, 1988). An isotopic analysis of Late Triassic scleractinian corals indicates that those corals possessed zooxanthellae (Stanley and Swart, 1995).

Fig. 4. Thin section photograph of Late Permian Rugosa in South China. Scale bar=0.5 cm. *Waagenophyllum asperum* Zhao, OCU 6531; uppermost Permian just below the dolomicrite beds at Liangshan, Hanzhong, Shaanxi.

Permian-Triassic transition and Permian survivors

In latest Permian time, most organisms, whether reef-building or not, were on the decline. However, in relation to long-term evolutionary cycles of reef development associated with the composition of reef-building taxa and their relative importance, a more fundamental change occurred in the Late Devonian, characterised by a great decline in stromatoporoids and Tabulata, rather than at the end-Permian (James, 1983). The present author considers that the Permian-Triassic boundary falls within the late early period of the second evolutionary cycle initiated in the Carboniferous, because scleractinian corals and stromatoporoids, which were important reef-builders, became dominant in the Late Triassic in spite of the prominence of calcisponges in the Permian. The Permian-Triassic boundary was not accompanied by a major qualitative break.

As emphasised by Stanley (1988), it was during the Anisian when reefs similar to the Late Permian reefs in the composition of the main reef-builders and their functional role in reef communities were formed again by Lazarus taxa such as inozoan and sphinctozoan sponges, bryozoans and calcareous algae. The Permian carbonate buildups were precursors for the Triassic reefs. Scleractinian-like corals, having the same basic body plan as the Scleractinia, evolved early in the Palaeozoic (Scrutton and Clarkson, 1991), and it is highly probable that its skeletonless relatives survived as Lazarus taxa across the Permian-Triassic boundary into the Early Triassic, giving rise to the scleractinians in the Middle Triassic (Ezaki, 1995). The precise locations of the refuges, where Permian holdovers survived across the Permian-Triassic boundary, are uncertain.

During the earliest Triassic, the shallow-marine

Fig. 5. Comparison of the siliceous and calcareous facies across the Permian-Triassic boundary. Deterioration and recovery occurred commonly in both oceanic environments. For further explanation see text. Dzh.: Dzhulian; Cha.: Changxingian; Gri.: Griesbachian; Spa.: Spathian.

faunas were poorly diversified, level-bottom communities and formed mixed-fauna beds with Permian relics and typical Triassic components (Sheng et al., 1984; Yin, 1985). However, the Lazarus taxa of concern are separated from those ecological generalists and opportunists which survived only temporarily.

Very recently, a doubt has been cast on "*Tubiphytes*" as a Permian holdover based on differences in microstructure between Permian and Triassic forms (Senowbari-Daryan and Flügel, 1993; Flügel, 1994), and a new term Elvis taxa was proposed for such convergent forms (Erwin and Droser, 1993). The origin of Triassic "*Tubiphytes*" as well as the differences between Permian and Triassic calcareous algae and sponges remain open questions. Further palaeontological studies are needed. Early Triassic biota during the reef gap period were very impoverished, but may contribute to the resolution of that problem.

Discussion and summary

Permian reefs were formed widely until Midian (pre-Dzhulian) time, and survived into the latest Permian (*Palaeofusulina* Zone) only in a few refuges in the tropics. In the tropical pelagic realm in the Panthalassa Ocean, radiolarian-bearing bedded chert continued to be deposited into the uppermost Permian (see Sashida and Tonishi, 1985; Ishiga, 1986; Kuwahara and Sakamoto, 1992; Ezaki and Kuwahara, in press). Thus, favourable habitats for reef building and bedded chert deposition commonly persisted up to the Late Permian, especially in tropical latitudes. However, the Late Permian reef ecosystems collapsed later in the tropical refuges as shown in the ecological

successions of reefs in South China. The Rugosa and the Tabulata became extinct, and calcisponges and calcareous algae were impoverished greatly at the Permian-Triassic boundary, resulting in the demise of reefs. The disappearance patterns of reef-forming organisms, such as the Rugosa, indicate gradual environmental deterioration with a sudden pulse of more rapid change within the last biostratigraphical zone of the Permian.

Whatever the main causes of end-Permian extinction, the aftereffects prevailed for many millions of years, and the Permian holdovers survived as Lazarus taxa in restricted environments such as deeper offshore areas and isolated islands (Stanley, 1988). Potentially reef-building organisms of the Early Triassic were considered to have been unable to flourish owing to the protracted environmental perturbations rather than to the severity of the end-Permian extinction itself and/or the time interval necessary for reef community reorganisation. It may be suggestive that it was an open-ocean seamount where the Carboniferous organic frameworks (e.g., Akiyoshi organic reef complex), constructed by chaetetids, calcareous algae, tabulate and rugose corals, were re-established after the Late Devonian reef collapse (Ota, 1968; Sugiyama and Nagai, 1994 and references therein).

Small-scale stratigraphic reefs began to be rebuilt in the Anisian. The Permian and Triassic reefs differ in styles of reef construction following the Late Triassic dominance of Scleractinia. Those differences are connected to some biological factors which were introduced and/or became obvious in the Middle to Late Triassic time as already noted. Extrinsic environments, including sea-water chemistry and temper-

ature, may have been different between Palaeozoic and Mesozoic times (Railsback and Anderson, 1987). Other factors, including the development of shallow shelf areas, were also important for the evolution of Triassic reefs (Flügel, 1982; Flügel and Stanley, 1984).

In the pelagic realm, the Permian-Triassic transition beds consist of intergrading siliceous claystone, black mudstone, grey to black chert and dolostone (e.g., Ishida et al., 1992; Ezaki and Kuwahara, in press). Radiolarians radiated again in the Middle Triassic and radiolarian-bearing bedded chert (*Hozmadia gifuensis* to *Triassocampe deweveri* Assemblage Zones) was widely formed (e.g., Imoto, 1984; Matsuda and Isozaki, 1991; Sugiyama, 1992). After the Permian-Triassic boundary, the "lag phase" of Erwin (1993) lasted up to the Spathian, and taxonomic radiation was extremely restricted not only in nearshore, shallow-marine environments but also in pelagic environments.

A deteriorating environment on a global scale decimated the Permian biota in the last refuges in the tropics and hindered biotic recovery everywhere during Early Triassic time despite the presence of potential organisms for reef-building. Improvement in shallow-water and pelagic habitats was nearly coeval near the Early-Middle Triassic boundary, indicating global removal of the protracted inhibiting conditions in the ocean (Fig. 5). After the end-Permian extinction events, the Permian survivors formed small-scale stratigraphic reefs in the Middle Triassic. Both external environmental and biological factors acted together in delaying Triassic reef development. The end-Permian extinction resulted in the restructuring of reef-forming biota in the Middle Triassic rather than the introduction of a new community.

Further research is needed on the magnitude and causes of the end-Permian extinction and on the recovery pattern of the Triassic reef ecosystem. In addition, the patterns of imposition and amelioration of limiting factors, as well as the ecological mechanisms and geographic patterns of the Lazarus taxa based on detailed taxonomic work, need more study. Lower Triassic strata will provide a crucial key to decipher the timing and patterns of "phase transition" between Permian and Triassic reef ecosystems.

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(要 旨)

Ezaki, Y., 1995, The development of reefs across the end-Permian extinction. *Jour. Geol. Soc. Japan*, **101**, 857-865. (江崎洋一, 1995, ペルム紀末の生物絶滅前後での生物礁の発達. 地質雑, **101**, 857-865.)

ペルム紀中期に生じた絶滅事変に強く影響を受けた生物礁の一部は、その後熱帯域に残された避難場所でペルム紀最後期まで形成された。しかし、生物礁はペルム-トリアス紀境界での生物危機よりも早期に、構成群ごとに異なる消滅様式を示しながら崩壊する。生物礁はAnisianになって再び発達し、遠洋域では放散虫層状チャートの形成が普通に認められるようになる。このことは生息阻害要因が海洋域で広域的に除去されたことを示している。ペルム紀後期とトリアス紀中期の礁は、構成要素や構成上の役割の点で類似しているが、群集構造は、その後六射サンゴなどが卓越するにつれて変化する。礁形成のための生き残り群が存在したにもかかわらずトリアス紀生物礁の発達が遅れた原因は、海洋環境の持続的な悪化などの環境要因並びに生物要因に求められる。ペルム紀末の絶滅事変は、新たな礁群集の出現ではなく、トリアス紀中期における再構築に大きな役割を果たしている。